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A phylogenetic and taxonomic revision of sequestrate *Russulaceae* in Mediterranean and temperate Europe

J.M. Vidal[1*], P. Alvarado[2*], M. Loizides[3], G. Konstantinidis[4], P. Chachuła[5], P. Mleczko[6], G. Moreno[7], A. Vizzini[8], M. Krakhmalnyi[9], A. Paz[10], J. Cabero[11], V. Kaounas[12], M. Slavova[13], B. Moreno-Arroyo[14], J. Llistosella[15]

Key words

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Abstract A comprehensive morphological and genetic study of type material and new collections of sequestrate *Russulales* species formerly belonging to the genera *Arcangeliella*, *Elasmomyces*, *Gymnomyces*, *Hydnangium*, *Hymenogaster*, *Macowanites*, *Martellia*, *Secotium* and *Zelleromyces* is here undertaken, for the purpose of providing a complete taxonomical revision of sequestrate *Russulaceae* species in the Mediterranean and temperate regions of Europe. As a result, seven distinct taxa in the genus *Lactarius* and 18 in the genus *Russula* are identified. Six of them are new species: *L. populicola*, *L. subgiennensis*, *R. bavarica*, *R. candidissima*, *R. hobartiae* and *R. mediterraneensis*, and seven represent new combinations: *L. josserandii* (≡ *Zelleromyces josserandii*), *L. soehneri* (≡ *Hydnangium soehneri*), *R. candida* (≡ *Hydnangium candidum*), *R. cerea* (≡ *Hydnangium cereum*), *R. messapica* var. *messapicoides* (≡ *Macowanites messapicoides*), *R. meridionalis* (≡ *Zelleromyces meridionalis*) and *R. neuhoffii* (≡ *Hydnangium neuhoffii*). Twenty-two of the 25 taxa are illustrated, while descriptions, microscopy images, as well as extensive information on the ecology, chorology and phylogeny for all taxa are provided. A key is further included to facilitate their identification.

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INTRODUCTION

Sequestrate *Russulaceae* produce pseudoangiocarpic ('secotioid') basidiomata, where the stipe is external and more or less reduced, to angiocarpic ('gasteroid') basidiomata, where the stipe is internal, reduced to a columella, or altogether absent. Sequestrate *Russulaceae* seem to be widespread throughout the globe, especially in arid and semi-arid regions of Australia and New Zealand (Bougher 1997, Lebel 1998, 2001, 2002, 2003a, b, Lebel & Trappe 2000, Bougher & Lebel 2001, Lebel & Castellano 2002, Trappe & Claridge 2003, Lebel & Tonkin 2007) and North America (Zeller & Dodge 1919, 1937, Singer & Smith 1960, Smith 1963, Miller & Lebel 1999, Fogel & States 2001, Desjardin 2003, Smith et al. 2006). However, several sequestrate species have also been documented in tropical forests in Africa (Dring & Pegler 1978, Eberhardt & Verbeken 2004, Verbeken & Walleyn 2010, Beenken et al. 2016) and Asia (Corner & Hawker 1953, Heim 1959, Zhang & Yu 1990, Tao et al. 1993, Verbeken et al. 2014a, b), as well as in temperate *Nothofagus* forests in Patagonia (Trierveiler-Pereira et al. 2015).

The generic organization of sequestrate taxa within the *Russulaceae* has long been a subject of debate (Singer & Smith 1960, Pegler & Young 1979, Beaton et al. 1984, Zhang & Yu 1990). The subtle differences between *Gymnomyces*, *Martellia*, *Cystangium*, *Elasmomyces* and *Macowanites*, as well as the latex-bleeding *Arcangeliella* and *Zelleromyces*, led to different taxonomic arrangements to accommodate an increasing number of emerging species (Lebel & Trappe 2000, Trappe et al. 2002, Vidal 2004a). Early authors hypothesized a single evolutionary lineage from the gymnocarpic to the angiocarpic genera in the *Russulales* (Malençon 1931, Heim 1938, Singer & Smith 1960, Oberwinkler 1977), but genetic studies revealed that sequestrate russuloid lineages are polyphyletic and nest within the genera *Russula* and *Lactarius* (Calonge & Martín 2000, Miller et al. 2001, Larsson & Larsson 2003, Eberhardt & Verbeken 2004, Nuytinck et al. 2003, Shimono et al. 2004, Smith et al. 2006, Lebel & Tonkin 2007). The split of *Lactarius* due to genetic evidence (Buyck et al. 2008, 2010) led to the restoration of the old genus *Lactifluus* and the erection of *Multifurca*, although no sequestrate species are yet known to occur in either of these two lineages.

The genus *Gymnomyces*, typified by *G. pallidus* (Massee 1898), a species found in myrtaceous forests whose current name is *R. paneeroides* (Lebel 2017), was characterized by the absence of a stipe-columella and the presence of sphaerocytes in the hymenophoral trama. The European species *G. xanthosporus*

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[1] C/ Massaballs 10, E-17118 Sant Sadurní de l'Heura, Girona, Spain.
[2] ALVALAB, La Rochela 47, E-39012 Santander, Spain;
corresponding author e-mail: pablo.alvarado@gmail.com.
[3] P.O. Box 58499, 3734 Limassol, Cyprus.
[4] Agiou Kosma 25, 51100 Grevena, Greece.
[5] Pieniny National Park, Jagiellońska 107b, PL-34-450 Krościenko nad Dunajcem, Poland.
[6] Institute of Botany, Jagiellonian University in Kraków, Gronostajowa 3, PL-30-387 Kraków, Poland.
[7] Dept. de Ciencias de la Vida (Botánica), Facultad de Biología, Universidad de Alcalá, E-28871 Alcalá de Henares, Spain.
[8] Dipt. de Scienze della Vita e Biologia dei Sistemi, Università di Torino, Viale P.A. Mattioli 25, I-10125 Torino, Italy.
[9] Institute of Evolution and Department of Evolutionary and Environmental Biology, University of Haifa, 199 Abba Khoushy Ave, Haifa, 3498838, Israel.
[10] C/ Vall Ter 791, Urbanització Llac del Cigne, E-17455 Caldes de Malavella, Girona, Spain.
[11] C/ El Sol 6, E-49800 Toro, Zamora, Spain.
[12] Sokratous 40, TK-19016 Artemis Attika, Greece.
[13] Krivolak 4, 1164 Sofia, Bulgaria.
[14] Dept. de Biología Vegetal, Facultad de Biología, Universidad de Córdoba, Colonia San José 4, Campus de Rabanales, E-14014 Córdoba, Spain.
[15] Dept. de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 643, E-08028 Barcelona, Spain.
* These authors contributed equally.

was originally described by Hawker (1952) as a variety of *Hydnangium carneum*, to accommodate some specimens found in the UK, and subsequently re-combined into *Gymnomyces* by Smith (1962), because of its amyloid spores and sphaerocytes. Several species were described later from the Mediterranean basin or re-combined into this genus, such as *G. ilicis* (Llistosella & Vidal 1995), *G. dominguezii* (Moreno-Arroyo et al. 1999, and subsequently validated in Calonge 2000), *G. sublevisporus* (Moreno-Arroyo et al. 2002) and *G. meridionalis* (Vidal 2004a), the latter originally treated in the genus *Zelleromyces* by Moreno-Arroyo et al. (1998b, and subsequently validated in Calonge 2000).

The genus *Martellia*, typified by *M. mistiformis* (Mattirolo 1900), was first described from several collections found in Sardinia (Italy) under *Quercus suber*. It was characterized by the absence of a stipe-columella and lack of sphaerocytes in the hymenophoral trama (Singer & Smith 1960). In the late 20th century, new species and combinations were proposed: *M. mediterranea* (Moreno et al. 1991), *M. pila* (Vidal 1991b), *M. monospora* (Astier & Pacioni 1998), the last two originally described from France in the genus *Hydnangium* by Patouillard (1910) and Boudier & Patouillard (1888) respectively, and *M. aurantiaca* (Astier & Pacioni 1998), originally described from Spain in the genus *Hydnangium* by Heim et al. (1934) and later re-combined into the genus *Stephanospora* by Vidal (2004c). After comparing the types of *Gymnomyces* and *Martellia*, Lebel & Trappe (2000) considered that the presence or absence of sphaerocytes in the hymenophoral trama was of no taxonomic relevance in keeping the two genera separate, and subsumed *Martellia* into *Gymnomyces* (Trappe et al. 2002).

The genus *Elasmomyces*, typified by *E. mattiroloanus* (Cavara 1897), was proposed to accommodate some stipitate collections obtained under *Abies alba* in Italy, that lacked sphaerocytes in the hymenophoral trama. Saccardo & Saccardo (1905) proposed the combinations *E. krjukowensis* and *E. michailowskianus* for two species of the genus *Secotium*, originally found in Russia by Bucholtz (1901, 1903).

The genus *Macowanites*, typified by *M. agaricinus* (Kalchbrenner 1882), which was originally placed in the genus *Macowania* (Kalchbrenner 1876), was first proposed for a stipitate fungus found in Eastern Cape (South Africa), exhibiting sphaerocytes in the hymenophoral trama. Much later, some Mediterranean species were added or re-combined into this genus, namely *M. galileensis* from Mount Carmel, Israel (Moser et al. 1977) and *M. messapicoides* (Llistosella & Vidal 1995), *M. ammophlilus* (Vidal et al. 2002), originally described as *Gymnomyces* by Calonge & Vidal (1999), and *M. vinaceodorus* (Calonge & Vidal 2001), all from Spain. Recently, *M. candidus* (Vidal 2004b), a species originally described from Northern France in the genus *Hydnangium* (Tulasne & Tulasne 1843), was also placed into this genus. Same as for the angiocarpic genera *Gymnomyces* and *Martellia*, the pseudoangiocarpic taxa *Elasmomyces* and *Macowanites* were also considered synonyms by Lebel & Trappe (2000), following comparison of their type collections.

The genus *Cystangium*, typified by *C. sessile* (Singer & Smith 1960), is another russuloid sequestrate genus, but appears to be confined to Australia and South America, with no known representatives in Europe. It is characterized by an epithelial pileipellis, in contrast to *Gymnomyces*, *Martellia*, *Elasmomyces* and *Macowanites*, all of which have a trichodermal or undifferentiated pileipellis. The stipe in this genus can be external, reduced to a columella, or completely absent (Lebel & Trappe 2000).

The latex-bleeding genus *Arcangeliella* was typified by *A. borziana* (Cavara 1900), and proposed for collections found under *Abies alba* in central Italy. *Arcangeliella borziana* is a sessile species that sometimes presents a poorly developed or residual stipe and a percurrent columella, especially in young basidiomata. Despite these features, *Arcangeliella* was chosen by Singer & Smith (1960) to describe several non-European sequestrate species with a well-developed stipe-columella, whereas Vidal (2004a) maintained this genus only for angiocarpic, sessile species, keeping *Gastrolactarius* for pseudoangiocarpic, stipitate species. American mycologists (Dodge 1931, Zeller & Dodge 1935) combined several European taxa into *Arcangeliella*, e.g., *A. asterosperma* var. *asterosperma*, *A. asterosperma* var. *depauperata*, *A. asterosperma* var. *hololeuca*, *A. laevis* or *A. stephensii*; the first four, however, belonging to the order *Boletales*, have since been transferred to the genus *Octaviania* (Paz et al. 2016). Finally, Mader & Mader (1992) proposed *A. volemoides* for a collection made under *Picea abies* in the Austrian Alps, but this species was considered a synonym of *A. borziana* by Nuytinck et al. (2003) and Vidal (2004a).

The latex-bleeding genus *Zelleromyces*, typified by *Z. cinnabarinus* (Singer & Smith 1960), was proposed for angiocarpic species devoid of a stipe-columella. Several Mediterranean and Central European species were later described or re-combined into this genus: *Z. josserandii* from Morocco and France (Malençon 1975), *Z. hispanicus* (Calonge & Pegler 1998) and *Z. giennensis* (Moreno-Arroyo et al. 1998a) from Spain, and *Z. soehneri* (Trappe et al. 2002), originally described from Germany in the genus *Hydnangium* by Zeller & Dodge (1935).

Recently, several taxa previously placed in the sequestrate genera *Cystangium*, *Elasmomyces*, *Gymnomyces*, *Macowanites*, and *Martellia*, were re-combined into *Russula* by Lebel (2017) and Elliott & Trappe (2018). About 30 sequestrate species of *Russulaceae* have been described from Mediterranean and temperate regions of Europe, but the generic placement for many of these still remains unclear. In the present work, all of them are reviewed and revised in the light of extensive genetic data. New sequences were produced from herbarium specimens and new collections of pan-European origins, in order to evaluate the phylogenetic basis of characters traditionally employed to discriminate among sequestrate taxa, and propose the most appropriate supraspecific affiliation of these species within *Lactarius* and *Russula*.

MATERIAL AND METHODS

Fungal collections

Morphological studies include type material and old representative collections of selected species placed in the genera *Arcangeliella*, *Elasmomyces*, *Gymnomyces*, *Hydnangium*, *Hymenogaster*, *Macowanites*, *Martellia*, *Octaviania*, *Secotium* and *Zelleromyces* kept in the public herbaria of BPI (Beltsville, USA), FH (Cambridge, USA), IB (Innsbruck, Austria), K (Kew, UK), M (Munich, Germany), MA (Madrid, Spain), MPU (Montpellier, France), NICE (Nice, France), NY (New York, USA), PC (Paris, France), PRM (Praha, Czech Republic), UPS (Uppsala, Sweden) and WU (Wien, Austria), as well as recent collections from different localities in Europe and the Middle East (Bulgaria, Cyprus, France, Germany, Greece, Hungary, Israel, Italy, Poland, Portugal and Spain) kept in the public herbaria of AH (Alcalá de Henares, Spain), BCN (Barcelona, Spain), HAI (Haifa, Israel), KRA (Kraków, Poland), MCVE (Venezia, Italy), or in private herbaria of the Asociación Vallisoletana de Micología (AVM), B. Moreno Arroyo (BM), G. Konstantinidis (GK), A. Paz Conde (IC), J. Cabero (JC), J.M. Vidal (JMV), M. Loizides (ML), M. Slavova (MSL), V. Kaounas (VK) and other contributors to this paper (see acknowledgements). Newly collected specimens have been deposited in the Herbarium of the Universidad de Alcalá (AH), in the Herbarium of the CeDocBiV of the Universitat de Barcelona (BCN-myc), in the Herbarium of the Jagiellonian University in Kraków (KRA), and in the Mycological Collection of the Bulgarian Academy of Sciences (SOMF).

Morphological study

Most species are fully described, with the exception of the recently described species, for which only a summary description is provided. Detailed macromorphological notes and images were taken from the majority of collections, and the presence/absence of latex and columella, as well as ecological data (altitude, associated vegetation, putative ectomycorrhizal partner, substrate) were annotated. Colour of basidiomata, hymenophore, and spore mass observed in locules was described according to Kornerup & Wanscher (1978). Methuen code colour of fresh specimens was obtained from digital images. For microscopical features, a Carl Zeiss Jena Jenaval microscope with a DIC device, a Leica BM E binocular, and a Leica DMRB with condenser P 1.40 OIL S1, provided with planapochromatic optics 25×, 40×, 50×, 63× and 100×, were employed, coupled with Reflex Pentax K-20 (14.6 Mpx) cameras with remote control. Amyloid reaction was checked from mounts in Melzer's reagent, while ammoniacal (10 %) or potassium hydroxide (2–5 %) Congo red was employed to enhance contrast in microscopical observations.

The terminology of Heilmann-Clausen et al. (1998) is adopted for naming the pileipellis structure. For the different types of secretory hyphae, the terminology of Clémençon (2004) is adopted, using the terms: 1) 'laticifera' for non-septate, latex-containing hyphae of granular content (crystalloid in exsiccata), staining violet in contact with sulfovainillin, typical of *Lactarius* (Fig. 12c, f); 2) 'gloeoplera' for the septate hyphae not bleeding latex, also of granular or crystalloid content, not staining violet with sulfovainillin, which are found in the trama and context of *Russula* and generate both fertile (basidia) and sterile elements (macrocystidia and dermatocystidia) (Fig. 15f); and 3) 'thromboplera' for the tortuose hyphae of homogeneous, non-granular, yellow to brownish content, found in both *Lactarius* and *Russula* (Fig. 10b–c, 12c). We use the term 'cystidiole' (Romagnesi 1944, Josserand 1983) for sterile hymenial elements similar to dermatocystidia first developing in external locules at the same level as basidioles, and sometimes remaining in the mature hymenium as in *Russula mistiformis* (Fig. 25j–l). We apply the term 'paraphysoid cells' (Hawksworth et al. 1995) to cylindrical or slightly clavate and sometimes septate sterile elements without granular content, present in the hymenium of many of the sequestrate species studied, e.g., sterile cells similar to septate basidioles found in the hymenium of *Lactarius josserandii* (Fig. 8g–h), called 'paracystidia' by Malençon (1975), or those in the hymenium of *L. borzianus* and *L. stephensii* (Fig. 11b–c), called 'hymenial hairs' or 'paracystidia' in Vidal (2004a).

The measurements of spores and other elements were obtained with the aid of 'Mycometre VA' software (G. Fannechère). Spores were measured in side view, always excluding ornamentation and hilar appendix, and at least 20 spores from each specimen were studied, indicating the minimum and maximum average and the Q-value. Scanning electron microscopes (SEM) Hitachi S-4100 and Zeiss DSM-960A (Unitat de Microscòpia dels Serveis Tècnics de Recerca de la Universitat de Girona, UdG), Hitachi S-4700 (Laboratory of Scanning Microscopy, Institute of Geological Sciences, Jagiellonian University in Kraków, UJ) and Zeiss DSM-950 (Servicio de Microscopía Electrónica de la Universidad de Alcalá de Henares, AH), were also employed for imaging spores. Light microscopy images of spores were stacked digitally with the aid of 'Helicon Focus' (Helicon Soft Ltd.).

Molecular analysis

DNA extraction, amplification and sequencing

DNA extraction and PCR amplification were performed as described by Alvarado et al. (2012). Primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993) were used for the ITS region; primers LR0R and LR5 (Vilgalys & Hester 1990) were used for the 28S rDNA ribosomal region (28S rDNA); bRPB2-6F2 (reverse from bRPB2-6R2) and bRPB2-7.1R2 (modified from bRPB2-7.1R) for the DNA-directed second largest subunit two of RNA polymerase II (*rpb2*) gene (Matheny 2005, Matheny et al. 2007, Gelardi et al. 2015); and in some samples, EF1-983F and EF1-1567R (Rehner & Buckley 2005) for the translation elongation factor 1α (*tef1*) gene for both, PCR and sequencing. Sequences were edited for errors in MEGA v. 5 (Tamura et al. 2011). New sequences are listed in Table 1 highlighted in **bold** characters, and newly sequenced specimens are marked with an asterisk symbol (*) in the paragraph of material studied. Attempts to obtain genetic data from some old specimens were conducted without success.

Phylogenetic analyses

Newly generated sequences were aligned with the most similar sequences in the International Nucleotide Sequence Database Collaboration (INSDC) identified through BLASTn searches (Altschul et al. 1997). A multigenic ITS – 28S rDNA – *rpb2* alignment of *Russulaceae* was built including all lineages identified in the most recent phylogenetic works (Kong et al. 2015, Looney et al. 2016), as well as all sequences available originated from sequestrate species. Reference publications for the sequences employed are provided in Table 1. *Stereum hirsutum*, *Auriscalpium vulgare*, *Amylostereum laevigatum* and *Echinodontium tinctorium* were employed as outgroups for the general alignment because these are known to be the closest lineages outside the *Russulaceae* clade (Buyck et al. 2008). Sequences were first aligned in MEGA v. 5 (Tamura et al. 2011) with Clustal W (Higgins et al. 1994) and the resulting alignments edited manually. First, a full query for the best-scoring maximum likelihood tree was performed on the general alignment in RAxML (Stamatakis 2006) using the standard search algorithm (ITS, 28S rDNA, *rpb2* data partitioned, 2000 bootstrap replications). Four independent alignments were taken from the general one: 1) *Lactarius*; 2) *Russula* sect. *Ingratae*; 3) *Russula* sect. *Rigidae*; and 4) *Russula* s.str., using *Lactifluus piperatus* as outgroup for all of them. GBlocks v. 0.91b (Castresana 2000) was employed with the most permissive conditions to remove ambiguously aligned positions from ITS rDNA data. Bayesian analyses were performed in MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) employing optimal models determined for ITS, 28S rDNA and *rpb2* partitions in MrModeltest v. 2.3 (Nylander 2004) package loaded in PAUP v. 4.0b10, two simultaneous runs, six chains, temperature set to 0.2, and sampling every 100th generation until convergence parameters (< 0.01) were met after 9.35 M generations in *Lactarius*, 10.4 M in *Russula* sect. *Ingratae*, 0.74 M in *Russula* sect. *Rigidae* and 8.64 M generation in *Russula* s.str. The first 25 % trees were discarded as burn-in. Fig. 1 represents the phylogenetic tree resulting from the ML analysis of all sequences produced in the present work and retrieved from public databases with the major clades condensed. Fig. 2–5 were obtained from the previous one, collapsing all nodes except a single major clade: *Lactarius* (Fig. 2), *Russula* sect. *Ingratae* (Fig. 3), *Russula* sect. *Rigidae* (Fig. 4) and *Russula* s.str. (Fig. 5). Nodes were annotated with support values from Maximum Likelihood and Bayesian analyses if at least one of these was considered significant, or annotated in brackets when at least one of these was considered subsignificant. Support values were considered significant when ML bootstrap (BP) values were above 70 % or posterior probability (PP) values

Table 1 Specimens used in molecular phylogenetic studies and their GenBank accession numbers.

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Eurussuloid clade							
/amylostereaceae							
Amylostereum laevigatum	*Amylostereum laevigatum*	France	olrim409, 623.84 (CBS)	Wang et al. (2004)	AY781246	AF287843	AY218469
/auriscalpiaceae							
Auriscalpium vulgare	*Auriscalpium vulgare*	USA	PBM944 (WTU)	Lutzoni et al. (2004)	DQ911613	DQ911614	–
Echinodontium tinctorium	*Echinodontium tinctorium*	USA	16666 (DAOM)	Binder & Hibbett (2002)	AY854088	AF393056	AY218482
/russulaceae/lactarius							
Lactarius sp.	uncultured			Kohout (unpubl.)	UDB027052	–	–
Lactarius sp.*	*Arcangeliella* sp.	Tasmania	BH2148F, T991 (HO)	Horton (2011)	JF960610	–	–
	Zelleromyces sp.	Tasmania	BH1714P (HO)	Horton (2011)	JF960854	–	–
	Zelleromyces sp.	Tasmania	BH3528R (HO)	Horton (2011)	JF960852	–	–
	Zelleromyces sp.	Tasmania	BH2174F (HO)	Horton (2011)	JF960853	–	–
Lactarius acris	*Lactarius acris*	Germany	EU014 (UPS)	Buyck et al. (2008)	DQ421988	DQ421988	DQ421922
Lactarius akahatsu	*Lactarius akahatsu*	Thailand	AV2004-141 (GENT)	Verbeken et al. (2014b)	KF133269	KF133301	KF133333
*Lactarius angiocarpus**	*Lactarius angiocarpus**	Zambia	DA00-448 (GENT)	Eberhardt & Verbeken (2004), Stubbe et al. (2010)	AY606942	DQ421981	GU258310
Lactarius atroviridis	*Lactarius atroviridis*	USA	AV05-306 (GENT)	Verbeken et al. (2014b)	KF133270	KF133302	KF133334
Lactarius auriolla	*Lactarius auriolla*	Sweden	RW1601 (GENT)	Verbeken et al. (2014b)	KF133257	KF133288	KF133321
Lactarius azonites	*Lactarius azonites*	Belgium	DS08-520 (GENT)	Stubbe & Verbeken (2012)	JQ446096	JQ446168	JQ446231
Lactarius baliophaeus	*Lactarius baliophaeus*	Malawi	AV05-155 (GENT)	Verbeken et al. (2014b)	GU258277	GU265576	GU258312
*Lactarius bisporus**	*Lactarius bisporus**	Thailand	FH12-160 (GENT)	Verbeken et al. (2014a)	KF856293	–	–
*Lactarius borzianus**	*Arcangeliella borziana*	France	JMV800279b (BCN)	**This work**	**MK105610**	**MK105696**	**MK102740**
	Arcangeliella borziana	Italy	16944 (MCVE)	Osmundson et al. (2013)	JF908775	–	–
	Arcangeliella borziana	Switzerland	FA96-05-3344 (WSL)	Peter et al. (2001)	AF286204	AF286203	–
Lactarius camphoratus	*Lactarius camphoratus*	Sweden	UE04.09.2004 (UPS)	Verbeken et al. (2014b)	DQ422009	DQ422009	DQ421933
Lactarius chrysorrheus	*Lactarius chrysorrheus*	Italy	UE04.10.2002-8 (UPS)	Verbeken et al. (2014b)	KF133261	KF133293	KF133325
Lactarius citriolens	*Lactarius citriolens*	Sweden	UE20.09.2004-03 (UPS)	Buyck et al. (2008)	DQ422003	DQ422003	DQ421931
Lactarius crassiusculus	*Lactarius crassiusculus*	Thailand	HTL369 (GENT)	Verbeken et al. (2014b)	EF560684	KF133303	KF133335
*Lactarius crassus**	*Arcangeliella crassa*	USA	T17996	Gordon et al. (unpubl.)	KT968581	KT968636	–
	Arcangeliella crassa	USA	41826 (OSC)	Gordon et al. (unpubl.)	KT968563	KT968615	–
Lactarius cyanescens	*Lactarius cyanescens*	Malaysia	DS06-058 (GENT)	Stubbe et al. (2010)	GU258278	JN388999	JN375602
Lactarius cyathuliformis	*Lactarius cyathuliformis*	Sweden	UE04.09.2004-2 (UPS)	Verbeken et al. (2014b)	KF133266	KF133298	KF133330
Lactarius deliciosus	*Lactarius deliciosus*	Slovakia	JN2001-046 (GENT)	Verbeken et al. (2014b)	KF133272	KF133305	KF133337
*Lactarius echinellus**	*Lactarius echinellus*	Sri Lanka	AV07-169 (GENT)	Verbeken et al. (2014b)	KF133287	KF133320	KF133352
*Lactarius echinus**	*Lactarius echinus**	Sri Lanka	AV07-168 (GENT)	Verbeken et al. (2014b)	KF133273	KF133306	KF133338
Lactarius evosmus	*Lactarius evosmus*	Sweden	536 (UP)	Nygren et al. (2007)	DQ658882	–	–
*Lactarius falcatus**	*Lactarius falcatus**	Thailand	KVP08-038 (GENT)	Verbeken et al. (2014b)	KF133274	KF133307	KF133339
Lactarius flavopalustris	*Lactarius flavopalustris*	Finland	JV23334 (TURA)	Barge et al. (2016)	KR090904	–	KR090982
Lactarius flexuosus	*Lactarius flexuosus*	Sweden	UE06.09.2002-1 (UPS)	Buyck et al. (2008)	DQ421992	DQ421992	DQ421925
Lactarius fuliginosus	*Lactarius fuliginosus*	Sweden	MTB97-24 (GENT)	De Crop et al. (2017)	JQ446111	JQ446180	JQ446240
Lactarius fulvissimus	*Lactarius fulvissimus*	Germany	JKLAC10082002 (GENT)	Wisitrassameewong et al. (2014)	KF432970	–	KR025662
	Lactarius fulvissimus	Germany	JN2012-025 (GENT)	Wisitrassameewong et al. (2014)	KR025576	–	KR025661
Lactarius fumosibrunneus	*Lactarius fumosibrunneus*	Mexico	EG10 (XAL)	Garay-Serrano et al. (2012)	JN797633	–	–
Lactarius fumosus	*Lactarius fumosus*	Canada	HRL0894	Bérubé et al. (unpubl.)	KJ705224	–	–
*Lactarius gardneri**	*Zelleromyces gardneri*	USA	1537 (SOC)	Southworth (2016)	JN022500	–	–
	Zelleromyces gardneri	USA	513 (SOC)	Frank et al. (2006)	DQ453696	–	–
*Lactarius giennensis**	*Zelleromyces giennensis**	Spain	Fungi 38674 (MA)	Calonge & Martín (2000)	AF230900	–	–
	Zelleromyces giennensis	Spain	AVM 1615, JMV800629 (BCN)	**This work**	**MK105611**	**MK105697**	–
	Zelleromyces giennensis	Spain	JC20061020 (pers. herb.)	**This work**	**MK105612**	**MK105698**	**MK102741**
Lactarius glyciosmus	*Lactarius glyciosmus*	USA	20923 (DGB)	Barge et al. (2016)	KR090908	–	KR090985
Lactarius haugiae	*Lactarius haugiae*	Mexico	LM4994 (XAL)	Bandala et al. 2016	KT583642	KT583649	KT736507
Lactarius helvus	*Lactarius helvus*	Sweden	UE08.09.2004-1 (UPS)	Verbeken et al. (2014b)	KF133263	KF133295	KF133327
Lactarius hispidulus	*Lactarius hispidulus*	Guinea	AB152 (GENT)	Verbeken et al. (2014b)	KF133258	KF133289	KF133322

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Lactarius horakii	*Lactarius horakii**	Indonesia	EH8336 (ZT)	Nuytinck et al. (2007)	EF685069	–	–
Lactarius josserandii*	*Lactarius josserandii*	Spain	JMV800621 (BCN)	**This work**	**MK105613**	**MK105699**	**MK102742**
	Zelleromyces hispanicus	Spain	Fungi 37497 (MA)	Calonge & Martín (2003)	AF231911	–	–
	*Zelleromyces hispanicus**	Spain	Fungi 37498 (MA)	Calonge & Martín (2003)	AF231912	–	–
	Zelleromyces hispanicus	Spain	Fungi 53339 (MA)	Calonge & Martín (2003)	AJ555567	–	–
Lactarius kabansus	*Lactarius kabansus*	Zimbabwe	AV99-205 (GENT)	Verbeken et al. (2014b)	KF133259	KF133291	KF133323
Lactarius lanceolatus	*Lactarius lanceolatus**	USA	F 4239 (VPI)	Barge et al. (2016)	KR090915	–	KR090989
Lactarius lignyotus	*Lactarius lignyotus*	USA	PBM2424 (CUW)	Matheny et al. (2007)	DQ221107	AY631898	DQ408128
	Lactarius lignyotus	Sweden	UE06.09.2003-5 (UPS)	Buyck et al. (2008)	DQ421993	DQ421993	DQ421926
Lactarius lilacinus	*Lactarius lilacinus*	Belgium	RW3774 (GENT)	Verbeken et al. (2014b)	KF133275	KF133308	KF133340
Lactarius luculentus var. *laetus*	*Lactarius luculentus* var. *laetus*	USA	F 024643 (DBG)	Barge et al. (2016)	KR090922	–	KR090994
Lactarius luridus	*Lactarius luridus*	Belgium	OB11-011 (GENT)	Verbeken et al. (2014b)	KF241547	–	–
Lactarius mammosus	*Lactarius mammosus*	Sweden	UE09.09.2004-5 (UPS)	Verbeken et al. (2014b)	KF133265	KF133297	KF133329
Lactarius montoyae	*Lactarius montoyae**	India	KD1065 (BSD)	Stubbe et al. (2010)	EF560673	GU265641	GU258380
Lactarius nanus	*Lactarius nanus*	USA	EB106-13 (MONT)	Barge et al. (2016)	KR090928	–	KR091000
Lactarius necator	*Lactarius necator*	France	AV04-231 (GENT)	Verbeken et al. (2014b)	KF133276	KF133309	KF133341
Lactarius olympianus	*Lactarius olympianus*	USA	ED08-018 (GENT)	De Crop et al. (2017)	KR364089	KR364220	KR364320
Lactarius pallidomarginatus	*Lactarius pallidomarginatus*	USA	CLC1470 (MONT)	Barge et al. (2016)	KR090939	KR090939	KR091009
Lactarius peckii	*Lactarius peckii*	USA	JN2004-020 (GENT)	Verbeken et al. (2014b)	KF133277	KF133310	KF133342
Lactarius pomiolens	*Lactarius pomiolens**	Sri Lanka	AV07-159 (GENT)	Verbeken et al. (2014b)	KF133282	KF133315	KF133347
Lactarius populicola*	*Lactarius stephensii*	Belgium	RW2930 (GENT)	Nuytinck et al. (2003)	AY331012	–	–
	*Lactarius populicola**	Greece	GK4831, JMV800648 (BCN)	**This work**	**MK105614**	**MK105700**	**MK102743**
Lactarius psammicola	*Lactarius psammicola*	USA	BPL869 (TENN)	Looney et al. (2016)	KY848507	–	–
Lactarius pterosporus	*Lactarius pterosporus*	France	PAM06100705 (GENT)	Stubbe & Verbeken (2012)	JQ446153	–	JQ446275
Lactarius quieticolor	*Lactarius quieticolor*	Sweden	UE10.09.2004-1 (UPS)	Buyck et al. (2008)	DQ422002	DQ422002	DQ421930
Lactarius quietus	*Lactarius quietus*	Sweden	UE16.09.2004 (UPS)	Verbeken et al. (2014b)	KF133264	KF133296	KF133328
Lactarius repraesentaneus	*Lactarius repraesentaneus*	USA	CLC2318 (MONT)	Barge et al. (2016)	KR090948	–	KR091020
Lactarius romagnesii	*Lactarius romagnesii*	France	UE29.09.2002-6 (UPS)	Buyck et al. (2008)	DQ421989	DQ421989	DQ421923
Lactarius ruginosus	*Lactarius ruginosus*	Italy	DS09-613 (GENT)	Stubbe & Verbeken (2012)	JQ446150	JQ446216	JQ446272
Lactarius salicis-reticulatae	*Lactarius salicis-reticulatae*	Finland	CLC2885 (MONT)	Barge et al. (2016)	KR090959	–	KR091030
Lactarius salmonicolor	*Lactarius salmonicolor*	Germany	UE158/FO46879 (TUB)	Eberhardt et al. (2000)	AF140265	AF325284	–
*Lactarius saturnisporus**	*Lactarius saturnisporus**	Sri Lanka	AV07-170 (GENT)	Verbeken et al. (2014b)	KF133283	KF133316	KF133348
Lactarius scrobiculatus	*Lactarius scrobiculatus*	Italy	732 (MCVE)	Osmundson et al. (2013)	JF908281	–	–
*Lactarius shoreae**	*Lactarius shoreae**	Sri Lanka	AV07-164 (GENT)	Verbeken et al. (2014b)	KF133278	KF133311	KF133343
*Lactarius silviae**	*Arcangeliella camphorata*	USA	64481 (OSC)	Gordon (unpubl.)	EU834192	–	–
	Arcangeliella camphorata	USA	74231 (OSC)	Gordon (unpubl.)	EU644700	EU652366	–
Lactarius soehneri*	*Lactarius soehneri*	Spain	39272 (AH)	**This work**	**MK105615**	**MK105701**	–
	Lactarius soehneri	Spain	46013 (AH)	**This work**	**MK105616**	**MK105702**	**MK102744**
Lactarius sphagneti	*Lactarius sphagneti*	UK	PL2805 (pers. herb.)	Verbeken et al. (2014b)	KF133268	KF133300	KF133332
*Lactarius spinosporus**	*Lactarius spinosporus**	China	FAN445 (BJTC)	Sang et al. (2016)	KY270490	KY270494	–
Lactarius spinulosus	*Lactarius spinulosus*	Sweden	AT2003068 (UPS)	Verbeken et al. (2014b)	KF133262	KF133294	KF133326
*Lactarius stephensii**	*Lactarius stephensii*	Poland	F-2014-147 (KRA)	**This work**	**MK105617**	–	–
	Arcangeliella stephensii	Spain	JMV20010609-1 (BCN)	**This work**	**MK105618**	**MK105703**	**MK102745**
	Zelleromyces stephensii	UK	Kew(M)64067 (K)	Brock et al. (2009)	EU784439	–	–
Lactarius subdulcis	*Lactarius subdulcis*	Belgium	JV2006-024 (GENT)	Verbeken et al. (2014b)	KF133279	KF133312	KF133344
Lactarius subgiennensis*	*Lactarius subgiennensis**	Cyprus	ML211152E, JMV800627 (BCN)	**This work**	**MK105619**	**MK105704**	**MK102746**
	Lactarius subgiennensis	Cyprus	ML61132Z (pers. herb.)	**This work**	**MK105620**	–	–
	Lactarius subgiennensis	Cyprus	ML411172Z (pers. herb.)	**This work**	**MK105621**	**MK105705**	**MK102747**
Lactarius subsericatus	*Lactarius subsericatus*	Sweden	UE11.10.2004-8 (UPS)	Buyck et al. (2008)	DQ422011	DQ422011	DQ421934
Lactarius tenellus	*Lactarius tenellus*	Benin	ADK3598 (BR)	Verbeken et al. (2014b)	KF133280	KF133313	KF133345
Lactarius thyinos	*Lactarius thyinos*	Canada	AVoitk23-08-2004 (GENT)	Verbeken et al. (2014b)	KF133271	KF133304	KF133336
Lactarius torminosus	*Lactarius torminosus*	Czech Republic	RW3183 (GENT)	Verbeken et al. (2014b)	KF133281	KF133314	KF133346

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Lactarius trivialis	*Lactarius trivialis*	Sweden	UE27.08.2002-17a (UPS)	Buyck et al. (2008)	DQ421991	DQ421991	DQ421924
Lactarius uvidus	*Lactarius uvidus*	Estonia	185041 (TAA)	Tedersoo et al. (2003)	AJ534936	AJ534936	–
Lactarius vietus	*Lactarius vietus*	Sweden	UE11.19.2004-1 (UPS)	Verbeken et al. (2014b)	KF133267	KF133299	KF133331
Lactarius zonarius	*Lactarius zonarius*	France	UE27.09.2002-4 (UPS)	Buyck et al. (2008)	EU278678	EU278678	EU278679
Lactarius zonarius var. *riparius*	*Lactarius zonarius* var. *riparius*	USA	CLC2933 (MONT)	Barge et al. (2016)	KX394302	–	–
*Zelleromyces daucinus**	*Zelleromyces daucinus*	Australia	T18311 (OSC)	Miller et al. (2001)	–	AF265543	–
*Zelleromyces striatus**	*Zelleromyces striatus*	Australia	T18858 (OSC)	Miller et al. (2001)	–	AF265544	–
/lactifluus							
Lactifluus edulis	*Lactarius edulis*	Zimbabwe	AV99-041 (GENT)	Buyck et al. (2007)	AY606973	DQ421977	DQ421916
Lactifluus emergens	*Lactifluus emergens*	Zimbabwe	AV99-012 (GENT)	De Crop et al. (2017)	KR364021	KR364148	KR364276
Lactifluus longisporus	*Lactarius longisporus**	Zimbabwe	AV94-557 (GENT), BB00.1519 (PC)	Buyck et al. (2007), De Crop et al. (2017)	KR364118	KR364244	DQ421910
Lactifluus nodosicystidiosus	*Lactarius nodosicystidiosus**	Madagascar	BB97-072 (PC)	Buyck et al. (2007)	AY606975	DQ421976	DQ421915
Lactifluus phlebophyllus	*Lactarius phlebophyllus*	Madagascar	BB00-1388 (PC)	Buyck et al. (2007)	AY606974	DQ421979	DQ421918
Lactifluus piperatus	*Lactarius piperatus*	Sweden	UE09.08.2004-6 (UPS)	Buyck et al. (2008)	DQ422035	DQ422035	DQ421937
Lactifluus vellereus	*Lactarius vellereus*	Sweden	UE20.09.2004-22 (UPS)	Buyck et al. (2007)	DQ422034	DQ422034	DQ421936
Lactifluus velutissimus	*Lactarius velutissimus*	Zimbabwe	AV99-185 (GENT)	Buyck et al. (2007)	AY606982	DQ421973	DQ421912
Lactifluus volemus	*Lactarius volemus*	Sweden	UE09.08.2004-5 (UPS)	Buyck et al. (2008)	DQ422008	DQ422008	DQ421932
/multifurca							
Multifurca furcata	*Lactarius furcatus*	Costa Rica	RH7804 (NY)	Buyck et al. (2008)	DQ421994	DQ421994	DQ421927
Multifurca ochricompacta	*Russula ochricompacta*	USA	BB02.107 (PC)	Buyck et al. (2008)	DQ421984	DQ421984	DQ421940
Multifurca stenophylla	*Multifurca stenophylla*	Australia	CWD584 (MEL)	Lebel et al. (2013)	JX266628	JX266633	–
Multifurca zonaria	*Russula zonaria**	Thailand	DED7442 (PC)	Buyck et al. (2008)	DQ421990	DQ421990	DQ421942
/russula/basal clades							
Russula acrifolia	*Russula acrifolia*	USA	r-05065	Davis (unpubl.)	JF834363	–	JF834460
Russula albonigra	*Russula albonigra*	Sweden	AT2002064 (UPS)	Buyck et al. (2008)	DQ422029	DQ422029	DQ421966
Russula archaea	*Russula* aff. *camarophylla*	USA	BB2004-255 (PC)	Buyck et al. (2017)	EU598165	EU598165	–
Russula cf. *brevipes*	*Russula* cf. *brevipes*	Canada	F30230 (UBC)	Bazzicalupo et al. (2017)	KX812841	KX812863	KX813647
Russula camarophylla	*Russula camarophylla*	France	PAM01081108 (PC)	Buyck et al. (2008)	DQ421982	DQ421982	DQ421938
Russula cascadensis	*Russula cascadensis*	Canada	F23910 (UBC)	Bazzicalupo et al. (2017)	KJ146726	KJ146726	–
Russula aff. *chloroides*	*Russula* aff. *chloroides*	USA	r-01002	Davis (unpubl.)	JF834332	JF834478	JF834427
Russula compacta	*Russula compacta*	USA	BPL242 (TENN)	Looney et al. (2016)	KT933960	KT933819	KT933890
Russula crassotunicata	*Russula crassotunicata*	Canada	F30159 (UBC)	Bazzicalupo et al. (2017)	KX812837	KX812861	KX813645
Russula delica	*Russula delica*	Belgium	FH12-272 (GENT)	Wisitrassameewong et al. (2014), De Crop et al. (2017)	KF432955	KR364224	KR364340
Russula earlei	*Russula earlei*	USA	WCR00-412 (PC)	Buyck et al. (2008)	DQ422025	DQ422025	DQ421963
Russula farinipes	*Russula farinipes*	France	UE28.09.2002-4 (UPS)	Buyck et al. (2008)	DQ421983	DQ421983	DQ421939
Russula littoralis	*Russula littoralis*	Europe	1222IS87, PAM93071601 (pers. herb.)	Miller & Buyck (2002)	AY061702	–	–
Russula metachromatica	*Russula metachromatica*	French Guiana	MCA1856 (pers. herb.)	Smith et al. (2011)	JN168745	JN168745	–
Russula nigricans	*Russula nigricans*	Sweden	UE20.09.2004-07 (UPS)	Buyck et al. (2008)	DQ422010	DQ422010	DQ421952
Russula pallescens	*Russula pallescens*	Norway	146/2002 (TUR)	Buyck et al. (2008)	DQ421987	DQ421987	DQ421941
Russula pallidospora	*Russula pallidospora*	Denmark	JV02-218 (C)	Eberhardt (unpubl.)	DQ422032	DQ422032	–
Russula polyphylla	*Russula polyphylla*	USA	BB07.134 (PC)	Liu et al. (2015)	KP033486	KP033497	KP033508
*Russula pumicoidea**	*Russula pumicoidea**	Australia	T14771 (MEL, OSC)	Lebel & Tonkin (2007)	EU019931	EU019931	–
*Russula sinuata**	*Russula sinuata**	Australia	H4755 (HO)	Lebel & Tonkin (2007)	EU019943	–	–
/ingratae/rigidae/russula s.str.							
Russula sp.	uncultured *Russula*	Iran		Bahram et al. (2012)	FR852097	–	–
	Russula sp.	Estonia	B181	Bahram et al. (2011)	FN669244	FN669244	–
	Russula sp.	China	EMF33	Ding et al. (unpubl.)	JF273535	–	–
	Russula sp.	China	ZWG2011	Ge et al. (2012)	JN129407	–	–
	Russula sp.	China	CFXY10066	Tian (unpubl.), Li et al. (2018)	KR082870	–	–
	Russula sp.	Pakistan	MAM0077 (LAH)	Adamčik et al. (2016)	KU886598	–	–
	Russula sp.	USA	r-03045	Davis (unpubl.)	JF834346	JF834493	JF834442

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Russula sp. *	*Gymnomyces* sp.	USA	T13003 (OSC)	Whitbeck (2003)	AY239337	–	–
	Gymnomyces sp.	USA	T13006 (OSC)	Whitbeck (2003)	AY239340	–	–
	Gymnomyces sp.	USA	1059 (SOC)	Gladish et al. (2010)	FJ789600	–	–
	Gymnomyces sp.	USA	T35827 (OSC)	Frank (unpubl.)	KF386763	–	–
	Gymnomyces alveolatus	USA	TK1719, SNF35	Izzo et al. (2005)	AY558757	–	–
	Martellia sp.	USA	TK165	Izzo et al. (2005)	AY558788	–	–
*Russula absphaerocellaris**	*Russula absphaerocellaris**	China	FAN492 (BJTC)	Sang et al. (2016)	KY270486	KY270493	–
	Russula absphaerocellaris	China	FAN448 (BJTC)	Sang et al. (2016)	KY270489	–	–
Russula aeruginea	*Russula aeruginea*	Sweden	AT2003017 (UPS)	Buyck et al. (2008)	DQ421999	DQ421999	DQ421946
Russula albobrunnea	*Russula albobrunnea*	Australia	TL2136 (MEL)	Lebel & Tonkin (2007)	EU019933	EU019933	–
Russula alutacea	*Russula alutacea*	Italy	6472 (MCVE)	Osmundson et al. (2013)	JF908676	–	–
Russula amethystina	*Russula amethystina*	Germany	hue215 (TUB)	Eberhardt (2002)	AF418640	AY606971	–
*Russula ammophila**	*Macowanites ammophilus*	Portugal	42956 (AH)	**This work**	**MK105622**	–	–
	Gymnomyces ammophilus	Portugal	Fungi 40132 (MA)	Calonge & Martín (2000)	AF230890	–	–
	Gymnomyces ammophilus	Portugal	Fungi 40137 (MA)	Calonge & Martín (2000)	AF230891	–	–
	Macowanites ammophilus	Portugal	Fungi 51167 (MA)	Vidal et al. (2002)	AJ438036	–	–
	Macowanites ammophilus	Spain	Fungi 51165 (MA)	Vidal et al. (2002)	AJ438038	–	–
	Macowanites ammophilus	Spain	Fungi 51166 (MA)	Vidal et al. (2002)	AJ438037	–	–
	Macowanites ammophilus	Spain	43950 (AH)	**This work**	**MK105623**	–	–
	Macowanites ammophilus	Spain	46370 (AH)	**This work**	**MK105624**	**MK105706**	**MK102748**
	Russula ammophila	Spain	IC09010703 (BCN)	**This work**	**MK112566**	**MK108033**	–
Russula amoenicolor	*Russula amoenicolor*	Europe	311IX76, BB99.823 (PC)	Miller & Buyck (2002)	AY061655	–	–
Russula cf. *amoenolens*	*Russula* cf. *amoenolens*	USA	CDW122	Avis (2012)	JQ622327	–	–
	Russula cf. *amoenolens*	USA	PRL4149	Avis (2012)	JQ622333	–	–
	Russula cf. *amoenolens*	USA	12794 (MICH)	Bazzicalupo et al. (2017)	KF245512	–	–
	Russula cf. *amoenolens*	USA	BPL232 (TENN)	Looney et al. (2016)	KT933954	KT933813	KT933884
Russula amoenolens	*Russula amoenolens*	France	12838 (MICH)	Bazzicalupo & Berbee (unpubl.)	KF245510	–	–
	Russula amoenolens	Spain	46371 (AH)	**This work**	**MK105625**	–	**MK102749**
	Russula amoenolens	Spain	46372 (AH)	**This work**	**MK105626**	**MK105707**	**MK102750**
	Russula amoenolens	New Zealand	77763 (PDD)	Johnston & Park (unpubl.)	GU222264	–	–
*Russula andaluciana**	*Gymnomyces sublevisporus**	Spain	BM360 (pers. herb.)	**This work**	**MK105627**	**MK105708**	**MK102751**
	Gymnomyces sublevisporus	Spain	39198 (AH)	**This work**	**MK105628**	–	–
	Gymnomyces sublevisporus	Spain	39239 (AH)	**This work**	**MK105629**	**MK105709**	–
Russula aquosa	*Russula aquosa*	Estonia	101708 (TU)	Bazzicalupo et al. (2017)	UDB011290	KX812873	KX813654
*Russula aromatica**	*Gymnomyces fragrans*	USA	PNW 5607 (OSC)	Whitbeck (2003)	AY239331	–	–
Russula atrorubens	*Russula atrorubens*	Estonia	101718 (TU)	Bazzicalupo et al. (2017)	KX579812	–	–
Russula atroglauca	*Russula atroglauca*	Poland	ID PAN 248	Trocha & Rudy (unpubl.)	KM085418	–	–
Russula atrovirens	*Russula atrovirens*	New Zealand	77744 (PDD)	Johnston & Park (unpubl.)	GU222260	–	–
Russula aurantioflammans	*Russula aurantioflammans*	Europe	r3245	Adamčik et al. (2016)	KU928167	–	–
Russula aurea	*Russula aurea*	Estonia	101733 (TU)	Bazzicalupo et al. (2017)	UDB011363	KX812878	KX813659
Russula azurea	*Russula azurea*	Italy	BB537/08.668 (PC)	Schoch et al. (2012)	JN944002	JN940591	JN993614
Russula aff. *betularum*	*Russula* aff. *betularum*	USA	r-09003	Davis (unpubl.)	JF834375	JF834520	JF834469
*Russula brevipileocystidiata**	*Russula brevipileocystidiata**	China	FAN455 (BJTC)	Sang et al. (2016)	KY270487	KY270492	–
Russula brunneola	*Russula brunneola*	USA	r-03034	Davis (unpubl.)	JF834341	JF834489	JF834438
*Russula brunneonigra**	*Russula brunneonigra**	Australia	H5813 (DAR)	Lebel & Tonkin (2007)	EU019945	–	–
Russula caerulea	*Russula caerulea*	Germany	hue146, 504IS77 (TUB)	Eberhardt (2002)	AF418633	AF325297	–
*Russula californica**	*Martellia californica*	USA	T16027 (OSC)	Whitbeck (2003)	AY239308	–	–
Russula candida*	*Elasmomyces mattiroloanus*	Germany	GG171 (M), JMV799894 (BCN)	**This work**	**MK105630**	–	–
	Russula candida	Spain	JC171001N (pers. herb.)	**This work**	**MK105631**	**MK105710**	**MK102752**
	Russula candida	Spain	JMV20100724b (BCN)	**This work**	**MK105632**	**MK105711**	–
Russula candidissima*	*Macowanites candidus*	Italy	ELG930704-1, JMV800185 (BCN)	**This work**	**MK105633**	**MK105712**	–
	Russula candidissima	Poland	F-2009-57 (KRA)	**This work**	**MK105634**	–	–

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Russula candidissima* (cont.)	*Russula candidissima*	Poland	F-2017-2 (KRA)	**This work**	**MK105635**	–	–
	*Russula candidissima**	Spain	JMV20110906-6a (BCN)	**This work**	**MK105636**	**MK105713**	**MK102753**
Russula* aff. *cerea*	*Russula cerea*	Spain	JMV20000817-1 (BCN)	**This work**	**MK105637**	**MK105714**	–
Russula cerea*	*Russula cerea*	Germany	JMV800660 (BCN)	**This work**	**MK105638**	**MK105715**	–
	Russula cerea	Poland	F-2012-28 (KRA)	**This work**	**MK105639**	–	**MK102754**
	Gymnomyces xanthosporus	Spain	JMV961003-8 (BCN)	**This work**	**MK105640**	–	–
	Russula cerea	Spain	JMV20160705 (BCN)	**This work**	**MK105641**	–	–
	Russula cerea	Spain	JMV800656 (BCN)	**This work**	**MK105642**	–	–
	Gymnomyces sp.	U.K.	LM1492	Suz et al. (2014)	KM576488	–	–
Russula cerolens	*Russula cerolens*	China	HE2720	Sun et al. (unpubl.)	KC505578	–	–
	Russula cerolens	China	C3	Chai (unpubl.)	JX434671	–	–
Russula cessans	*Russula cessans*	Slovakia	BB525/07.219 (PC)	Schoch et al. (2012)	JN944011	JN940595	JN993601
Russula cheelii	*Russula cheelii*	Australia	JET1002 (MEL)	Lebel et al. (2013)	JX266623	JX266638	–
Russula chiui	*Russula chiui**	China	250410 (HMAS)	Li et al. (2015)	KF225491	–	–
*Russula chlorineolens**	*Macowanites chlorinosmus*	USA	36339 (OSC)	Gordon (unpubl.)	KT968579	KT968633	–
	Macowanites chlorinosmus	USA	51028 (OSC)	Gordon (unpubl.)	KT968578	KT968632	–
Russula clariana	*Russula clariana*	Europe	492RUS26, BB2733 (PC)	Miller & Buyck (2002)	AY061664	–	–
Russula claroflava	*Russula claroflava*	Germany	FH12-212 (GENT)	Looney et al. (2016)	KT933997	KT933858	KT933929
Russula consobrina	*Russula consobrina*	Estonia	101714 (TU)	Bazzicalupo et al. (2017)	UDB011295	KX812874	KX813655
Russula corallina	*Russula corallina*	USA	BB229/06.324 (PC)	Schoch et al. (2012)	JN944006	JN940605	JN993609
Russula cremeolilacina	*Russula cremeolilacina*	Guadeloupe (FR)	BA02.11.04	Sene et al. (2015)	FR682087	–	–
Russula crustosa	*Russula crustosa*	USA	BPL251 (TENN)	Looney et al. (2016)	KT933963	KT933822	KT933894
Russula cuprea	*Russula cuprea*	Germany	FH12-250 (GENT)	Looney et al. (2016)	KT934010	KT933871	KT933942
Russula curtipes	*Russula curtipes*	Germany	FH12-206 (GENT)	Looney et al. (2016)	KT933995	KT933856	KT933927
Russula cf. *cyanoxantha*	*Russula* cf. *cyanoxantha*	USA	BPL280 (TENN)	Looney et al. (2016)	KT933976	KT933837	KT933908
Russula cyanoxantha	*Russula cyanoxantha*	Germany	FH12-201 (GENT)	De Crop et al. (2017)	KR364093	KR364225	KR364341
Russula decolorans	*Russula decolorans*	Germany	FH12-196 (GENT)	Looney et al. (2016)	KT933992	KT933853	KT933924
Russula dryadicola	*Russula dryadicola*	France	16243 (MCVE)	Osmundson et al. (2013)	JF908710	–	–
	Russula dryadicola	Finland	151632 (TURA)	Adamčik et al. (2016)	KU928146	–	KY616724
*Russula ellipsospora**	*Gymnomyces ellipsosporus*	USA	T61608 (OSC)	Whitbeck (2003)	AY239304	–	–
	Gymnomyces ellipsosporus	USA	58973 (OSC)	Whitbeck (2003)	AY239306	–	–
Russula emetica	*Russula emetica*	Sweden	UE05.10.2003-11 (UPS)	Buyck et al. (2008)	DQ421997	DQ421997	DQ421943
Russula exalbicans	*Russula exalbicans*	Germany	n179/93 (TUB)	Eberhardt (2002)	AF418622	AF325306	–
Russula faustiana	*Russula faustiana*	China	XJ2013100408	Qiao et al. (unpubl.)	KX655858	–	–
Russula fellea	*Russula fellea*	Germany	FH12-185 (GENT)	Looney et al. (2016)	KT933989	KT933850	KT933921
Russula firmula	*Russula firmula*	Sweden	AT2004142 (UPS)	Buyck et al. (2008)	DQ422017	DQ422017	DQ421958
Russula cf. *flavisiccans*	*Russula* cf. *flavisiccans*	USA	BB2004-254 (PC)	Kong et al. (2015)	EU598162	EU598162	–
Russula foetens	*Russula foetens*	Germany	hue124 (TUB)	Eberhardt (2002)	AF418613	AF325299	–
Russula fontqueri	*Russula fontqueri*	Germany	FH12-223 (GENT)	Looney et al. (2016)	KT934003	KT933864	KT933935
*Russula galbana**	*Russula galbana*	Australia	H4667 (MEL)	Lebel & Tonkin (2007)	EU019936	EU019936	–
*Russula galileensis**	*Macowanites galileensis*	Israel	G-83 (HAI)	**This work**	**MK105643**	**MK105716**	–
	Macowanites galileensis	Israel	G-166 (HAI)	**This work**	**MK105644**	**MK105717**	**MK102755**
	Macowanites galileensis	Israel	G-201 (HAI)	**This work**	**MK105645**	–	–
	Macowanites galileensis	Israel	G-202 (HAI)	**This work**	**MK105646**	–	–
	Macowanites galileensis	Israel	G-209 (HAI)	**This work**	**MK105647**	–	–
*Russula gamundiae**	*Cystangium* sp.	Chile	T26316 (OSC)	Trierveiler-Pereira et al. (2015)	KF819810	–	–
*Russula gilkeyae**	*Gymnomyces monosporus*	USA	117360 (OSC)	Gordon & Zych (unpubl.), Trendel et al. (2017)	EU669222	EU669273	–
	Gymnomyces gilkeyae	USA	T2572 (OSC)	Whitbeck (2003)	AY239346	–	–
Russula globispora	*Russula globispora*	Germany	FH2007-BT111 (GENT)	Adamčik et al. (2016)	KU928144	–	KY616671
	Russula globispora	Germany	FH2007-BT121 (GENT)	Adamčik et al. (2016)	KU886594	–	–
Russula gracillima	*Russula gracillima*	Sweden	UE23.08.2004-14 (PC)	Buyck et al. (2008)	DQ422004	DQ422004	DQ421949
Russula granulata	*Russula granulata*	USA	BPL272 (TENN)	Looney et al. (2016)	KT933971	KT933832	KT933903

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Russula grisea	*Russula grisea*	Sweden	UE2005.08.16-01 (UPS)	Buyck et al. (2008)	DQ422030	DQ422030	DQ421968
Russula heterophylla	*Russula heterophylla*	Sweden	UE20.08.2004-2 (UPS)	Buyck et al. (2008)	DQ422006	DQ422006	DQ421951
Russula hiemisilvae	*Russula hiemisilvae*	Cameroon	1203IS83, SLM (pers. herb.)	Kleine et al. (2013)	JQ902080	–	–
Russula hobartiae***	*Russula hobartiae*	Cyprus	ML4193GY (pers. herb.)	**This work**	**MK105648**	**MK105718**	**MK102756**
	Russula hobartiae	Cyprus	ML411161GY (pers. herb.)	**This work**	**MK105649**	–	–
	Russula hobartiae *	Cyprus	ML110131GY, JMV800628 (BCN)	**This work**	**MK105650**	**MK105719**	–
	Russula hobartiae	Cyprus	GK5889, JMV800647 (BCN)	**This work**	**MK105651**	**MK105720**	**MK102757**
Russula ilicis	*Russula ilicis*	Europe	563IC52, MS10/18/99 (pers. herb.)	Miller & Buyck (2002)	AY061682	–	–
Russula illota	*Russula illota*	Sweden	UE26.07.2002-3 (UPS)	Buyck et al. (2008)	DQ422024	DQ422024	DQ421967
Russula inamoena	*Russula inamoena*	Italy	107	Melera et al. (2017)	KJ834597	–	–
Russula inflata	*Russula inflata*	Madagascar	SLM00/344	Kleine et al. (2013)	JQ902062	–	–
Russula insignis	*Russula insignis*	Europe	1223IS85, BB00.2149 (PC)	Miller & Buyck (2002)	AY061700	–	–
Russula integra	*Russula integra*	Germany	FH12-172 (GENT)	Looney et al. (2016)	KT933984	KT933845	KT933916
Russula intervenosa	*Russula intervenosa**	India	AM273 (CUH), 1272 (CAL)	Crous et al. (2016)	KT824241	KU928135	–
Russula kanadii	*Russula kanadii*	India	AM086 (CUH)	Dutta et al. (2015)	KJ866936	–	–
*Russula kermesina**	*Macowanites carmineus*	New Zealand	92049 (PDD)	Johnston & Park (unpubl.)	GU222323	–	–
Russula laricina	*Russula laricina*	Italy	BB575/08.681 (PC)	Schoch et al. (2012)	JN944008	JN940593	KU237846
Russula laricinoaffinis	*Russula laricinoaffinis*	Italy	662 (MCVE)	Osmundson et al. (2013)	JF908646	–	–
*Russula laurae**	*Cystangium* sp.	Chile	T26311 (OSC)	Trierveiler-Pereira et al. (2015)	KF819811	–	–
Russula laurocerasi	*Russula laurocerasi*	Germany	FH12-178 (GENT)	Looney et al. (2016)	KT933988	KT933849	KT933920
Russula lepida	*Russula lepida*	Belgium	HJB9990 (UPS)	Buyck et al. (2008)	DQ422013	DQ422013	DQ421954
Russula lilacea	*Russula lilacea*	Slovakia	BB435/07.213 (PC)	Schoch et al. (2012)	JN944005	JN940592	JN993610
Russula livescens	*Russula livescens*	China	F0177	Xie et al. (2010)	GU371295	–	–
*Russula longisterigmata**	*Cystangium* sp.	Chile	T26265 (OSC)	Trierveiler-Pereira et al. (2015)	KF819808	–	–
Russula maculata	*Russula maculata*	Germany	FH2010-BT184 (GENT)	Adamčik et al. (2016)	KU928154	–	–
Russula mairei	*Russula mairei*	Germany	FH12-262 (GENT)	Looney et al. (2016)	KT934013	KT933874	KT933945
Russula mariae	*Russula mariae*	Korea	19111 (HCCN)	Park et al. (2013)	KF361762	KF361812	KF361712
	Russula mariae	Korea	20120922-08 (SFC)	Park et al. (2013)	KF361778	KF361828	KF361728
*Russula mattiroloana**	*Russula mattiroloana*	Greece	GK3901, JMV800638 (BCN)	**This work**	**MK105652**	**MK105721**	–
	Russula mattiroloana	Greece	GK8136, JMV800644 (BCN)	**This work**	**MK105653**	**MK105722**	**MK102758**
	Russula mattiroloana	Poland	F-2012-153 (KRA)	**This work**	**MK105654**	–	–
	Russula mattiroloana	Poland	F-2017-1 (KRA)	**This work**	**MK105655**	–	–
	Russula mattiroloana	Poland	F-2018-1 (KRA)	**This work**	**MK105656**	**MK105723**	–
	Russula mattiroloana	Poland	F-2018-2 (KRA)	**This work**	**MK105657**	**MK105724**	**MK102759**
*Russula mattsmithii**	*Gymnomyces compactus*	USA	T13171 (OSC)	Whitbeck (2003)	AY239303	–	–
	Gymnomyces compactus	USA	T13565 (OSC)	Whitbeck (2003)	AY239342	–	–
Russula mediterraneensis*	*Russula mediterraneensis*	Greece	GK3930, JMV800639 (BCN)	**This work**	**MK105658**	**MK105725**	–
	Russula mediterraneensis	Greece	GK7286, JMV800642 (BCN)	**This work**	**MK105659**	–	–
	*Russula mediterraneensis**	Greece	GK6710, JMV800641 (BCN)	**This work**	**MK105660**	**MK105726**	–
	Russula mediterraneensis	Italy	MG630, 29085 (MCVE)	**This work**	**MK105661**	–	**MK102760**
	Russula mediterraneensis	Italy	MG636, 29086 (MCVE)	**This work**	**MK105662**	–	**MK102761**
Russula megapseudocystidiata	*Russula megapseudocystidiata**	China	FAN454 (BJTC)	Sang et al. (2016)	KY270488	KY270491	–
*Russula megaspora**	*Gymnomyces megasporus*	Australia	T18717 (OSC)	Miller et al. (2001)	–	AF265535	–
Russula meridionalis*	*Zelleromyces meridionalis**	Spain	BM410 (pers. herb.)	**This work**	**MK105663**	–	–
	Russula meridionalis	Spain	IC20051417 (BCN)	**This work**	**MK105664**	**MK105727**	–
	Russula meridionalis	Spain	IC24051506 (BCN)	**This work**	**MK105665**	**MK105728**	**MK102762**
	Russula meridionalis	Spain	JC180617NR (pers. herb.)	**This work**	**MK105667**	**MK105729**	–
Russula messapica var. *messapica*	*Russula messapica*	Italy	562IC52, MS6/11/89 (pers. herb.)	Miller & Buyck (2002)	AY061692	–	–
	Russula messapica	Italy	46373 (AH)	**This work**	**MK105668**	–	**MK102763**
	Russula messapica	Spain	JL201111182 (BCN)	**This work**	**MK105669**	**MK105730**	**MK102764**
Russula messapica **aff. var. *messapicoides****	*Macowanites messapicoides*	Spain	IC28110613 (BCN)	**This work**	**MK105666**	–	–

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Russula messapica* var. *messapicoides***	*Russula messapica* var. *messapicoides*	Greece	VK2998 (pers. herb.)	**This work**	**MK105670**	**MK105731**	**MK102765**
	Russula messapica var. *messapicoides*	Greece	VK3368 (pers. herb.)	**This work**	**MK105671**	**MK105732**	**MK102766**
	Russula messapica var. *messapicoides*	Greece	VK3411, JMV800682 (BCN)	**This work**	**MK105672**	–	–
	Russula messapica var. *messapicoides*	Greece	GK9341, JMV800645 (BCN)	**This work**	**MK105673**	–	–
	*Macowanites messapicoides**	Spain	JL1493 (BCN)	**This work**	**MK105674**	–	–
*Russula mistiformis**	*Russula mistiformis*	Greece	JMV800652 (BCN)	**This work**	**MK105675**	–	–
	Gymnomyces mistiformis	Italy	AM1653 (pers. herb.)	Whitbeck (2003)	AY472079	–	–
					AY472080	–	–
	Russula mistiformis	Italy	JMV800125 (BCN)	**This work**	**MK105676**	–	–
	Russula mistiformis	Spain	JC170305NR, JMV800661 (BCN)	**This work**	**MK105677**	–	–
	Russula mistiformis	Spain	JC131117NR, JMV800662 (BCN)	**This work**	**MK105678**	**MK105733**	**MK102767**
	Russula mistiformis	Spain	JC101206BT, JMV800663 (BCN)	**This work**	**MK105679**	–	–
	Russula mistiformis	Spain	AMC H-69, JMV971127 (BCN)	**This work**	**MK105680**	–	–
	Russula mistiformis	Spain	JC110102NR (pers. herb.)	**This work**	**MK105681**	–	–
	Martellia pila	Spain	JMV920626-1 (BCN)	**This work**	**MK105682**	–	–
	Russula mistiformis	Spain	JMV20140607-3 (BCN)	**This work**	**MK105683**	–	–
	Russula mistiformis	Spain	JMV20160524-1 (BCN)	**This work**	**MK105684**	–	–
	*Martellia mediterranea**	Spain	GM-RG11057 (AH)	**This work**	**MK105685**	**MK105734**	–
*Russula monospora**	*Russula monospora*	Spain	46459 (AH)	**This work**	**MK105686**	**MK105735**	–
	Russula monospora	Spain	JMV800671 (BCN)	**This work**	**MK105687**	–	–
	Russula monospora	Spain	JMV800672 (BCN)	**This work**	**MK105688**	–	–
	Russula monospora	Spain	JMV800673 (BCN)	**This work**	**MK105689**	–	–
*Russula monticola**	*Gymnomyces monticola*	USA	56167 (OSC)	Whitbeck (2003)	AY239313	–	–
Russula murrillii	*Russula murrillii*	USA	r-04075	Davis (unpubl.)	JF834352	JF834500	JF834449
Russula mustelina	*Russula mustelina*	Germany	FH-12-226 (GENT)	Looney et al. (2016)	KT934005	KT933866	KT933937
Russula nana	*Russula nana*		101701 (TU)	Wood et al. (unpubl.)	KX579809	–	–
Russula nauseosa	*Russula nauseosa*	Germany	FH12-173 (GENT)	Looney et al. (2016)	KT933985	KT933846	KT933917
Russula neerimea	*Russula neerimea*	Australia	2101871 (MEL)	Lebel & Tonkin (2007)	EU019915	EU019915	–
Russula nitida	*Russula nitida*	USA	BB2004-272 (PC)	Hughes & Buyck (unpubl.)	EU598164	EU598164	–
	Russula nitida	Germany	FH12-218 (GENT)	Looney et al. (2016)	KT934001	KT933862	KT933933
*Russula nondistincta**	*Gymnomyces nondistincta*	USA	62139 (OSC)	Gordon (unpubl.)	KP859276	KP859294	–
*Russula nothofagi**	*Cystangium* sp.	Chile	T26350 (OSC)	Trierveiler-Pereira et al. (2015)	KF819809	–	–
Russula nympharum	*Russula nympharum*	France	HM-R-9702 (M)	Adamčik et al. (2016)	KU928159	–	–
Russula ochroleuca	*Russula ochroleuca*	Germany	FH12-211 (GENT)	Looney et al. (2016)	KT933996	KT933857	KT933928
Russula cf. *ochrophylla*	*Russula* cf. *ochrophylla*	USA	BPL231 (TENN)	Looney et al. (2016)	KT933953	KT933812	KT933883
Russula ochrospora	*Russula ochrospora*	Italy	GD20.07.2004 (UPS)	Buyck et al. (2008)	DQ422012	DQ422012	DQ421953
Russula odorata	*Russula odorata*	Slovakia	BB526/07.186 (PC)	Schoch et al. (2012)	JN944010	JN940607	JN993603
*Russula osphranticarpa**	*Gymnomyces redolens*	New Zealand	SLM41I62 (pers. herb.)	Smith et al. (2006)	DQ403803	AF265536	–
Russula paludosa	*Russula paludosa*	Germany	FH12-216 (GENT)	Looney et al. (2016)	KT934000	KT933861	KT933932
Russula parazurea	*Russula parazurea*	Sweden	BW06.09.2002-16/MF01.10.2003 (UPS)	Buyck et al. (2008)	DQ422007	DQ422007	DQ421945
*Russula parksii**	*Gymnomyces parksii*	USA	T14997 (OSC)	Whitbeck (2003)	AY239335	–	–
Russula pauriensis	*Russula pauriensis*	India	1395 (CAL)	Das et al. (2017)	MF535185	–	–
Russula peckii	*Russula peckii*	USA	BPL270 (TENN)	Looney et al. (2016)	KT933970	KT933830	KT933901
Russula pectinatoides	*Russula pectinatoides*	USA	BPL276 (TENN)	Looney et al. (2016)	KT933975	KT933836	KT933907
Russula persicina	*Russula persicina*	Sweden	UE21.09.2003-01 (UPS)	Buyck et al. (2008)	DQ422019	DQ422019	DQ421960
*Russula pila**	*Russula pila*	Spain	JMV970816-8 (BCN)	**This work**	**MK105690**	–	–
	Russula pila	Spain	JMV800654 (BCN)	**This work**	**MK105691**	**MK105736**	**MK102768**
Russula aff. *pilosella**	*Russula* aff. *pilosella*	Australia	H4784 (MEL)	Lebel & Tonkin (2007)	EU019932	EU019932	–
*Russula pilosella**	*Russula pilosella*	Australia	H5974 (BRI)	Lebel & Tonkin (2007)	EU019941	–	–

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
Russula praetervisa	*Russula praetervisa**	Italy	1997/0812 (IB)	Sarnari & Eberhardt (unpubl.)	UDB019331	–	–
Russula pseudocarmesina	*Russula pseudocarmesina*	Burundi	BB5401 (PC)	Kleine et al. (2013)	JQ902068	–	–
Russula pseudopectinatoides	*Russula pseudopectinatoides**	China	251523 (HMAS)	Li et al. (2015)	KM269077	–	–
Russula puellaris	*Russula puellaris*	Estonia	101839 (TU)	Bazzicalupo et al. (2017)	UDB015995	KX812887	KX813668
Russula puellula	*Russula puellula*	Europe	2-1130IS76, RW27065 (E)	Miller & Buyck (2002)	AY061710	–	–
	Russula puellula	Slovakia	F-3107 (SAV)	Cabon et al. (unpubl.)	KY582704	–	KY616697
Russula puiggarii	*Russula puiggarii*	French Guiana	G3130	Roy et al. (2016)	KJ786689	KJ786592	–
Russula pulverulenta	*Russula pulverulenta*	USA	4-1144IS79, RF566 (pers. herb.)	Miller & Buyck (2002)	AY061736	–	–
Russula punicea	*Russula punicea*	USA	r-03043	Davis (unpubl.)	JF834344	JF834492	JF834441
Russula purpureoflava	*Russula purpureoflava*	Australia	JET1128 (MEL)	Lebel et al. (2013)	JX266626	JX266641	–
Russula putida	*Russula putida**	Italy	1997/0791 (IB)	Borovicka (unpubl.)	HG798527	HG798526	–
Russula risigallina	*Russula risigallina*	Sweden	UE03.07.2003-08 (UPS)	Buyck et al. (2008)	DQ422022	DQ422022	DQ421961
Russula romellii	*Russula romellii*	Germany	FH12-177 (GENT)	Looney et al. (2016)	KT933987	KT933848	KT933919
Russula rosea	*Russula rosea*	France	BB430/07.780 (PC)	Schoch et al. (2012)	JN944003	JN940602	JN993613
Russula roseipes	*Russula roseipes*	Estonia	101806 (TU)	Bazzicalupo et al. (2017)	UDB015972	KX812884	KX813665
*Russula rostraticystidia**	*Russula rostraticystidia**	Australia	H6165 (BRI)	Lebel & Tonkin (2007)	EU019938	–	–
Russula rubellipes	*Russula rubellipes*	USA	BPL240 (TENN)	Looney et al. (2016)	KT933958	KT933817	KT933888
*Russula rubrolutea**	*Macowanites rubroluteus**	Australia	T12610 (PDD, OSC)	Lebel & Tonkin (2007)	EU019940	EU019940	–
Russula rubropunctatissima	*Russula rubropunctatissima*	Brazil	JDuque55	Duque et al. (unpubl.)	KY087554	KY087583	–
Russula rugulosa	*Russula rugulosa*	USA	BPL654 (TENN)	Looney et al. (2016)	KY848516	–	KY701373
Russula sanguinea	*Russula sanguinea*	Germany	FH12-240 (GENT)	Looney et al. (2016)	KT934008	KT933869	KT933940
Russula sarnarii	*Russula sarnarii**	India	1395 (CAL)	Ghosh et al. (2017)	KY284154	–	–
*Russula seminuda**	*Cystangium seminudum*	Australia	H5346 (MEL, OSC)	Lebel & Tonkin (2007)	EU019947	–	–
*Russula sessilis**	*Cystangium sessile*	Australia	H5038 (OSC, MEL)	Miller et al. (2001), Lebel & Tonkin (2007)	EU019948	AF265533	–
*Russula setigera**	*Gymnomyces setigerus*	USA	29622 (OSC)	Whitbeck (2003)	AY239317	–	–
*Russula shafferi**	*Gymnomyces brunnescens*	USA	51046 (OSC)	Whitbeck (2003)	AY239327	–	–
Russula shingbaensis	*Russula shingbaensis**	India	KD11-094 (BSHC)	Das et al. (2014)	KM386692	–	–
*Russula sichuanensis**	*Russula sichuanensis*	Pakistan	MSM0025 (LAH)	Saba & Khalid (2015)	KM596865	–	–
*Russula similaris**	*Gymnomyces fallax*	Mexico	GO2009-239 (MEXU)	Kong et al. (2015)	KC152107	–	–
Russula cf. *sororia*	*Russula* sp.	Korea	ASIS22640 (HCCN)	Lee et al. (2017)	KX574703	–	–
	Russula sororia	Korea	2208ASI (HCCN)	Lee et al. (2017)	KX574701	–	–
*Russula stewartii**	*Gymnomyces monosporus*	USA	61382 (OSC)	Gordon (unpubl.)	KP859259	KP859279	–
	Gymnomyces monosporus	USA	61637 (OSC)	Gordon (unpubl.)	KP859261	KT968617	–
Russula cf. *subfoetens*	*Russula* cf. *subfoetens*	Spain	JMV941022-7 (BCN)	**This work**	**MK105692**	**MK105737**	–
*Russula subfulva**	*Gymnomyces subfulvus*	USA	T14998 (OSC)	Whitbeck (2003)	AY239321	–	–
*Russula subloculata**	*Macowanites americanus*	USA	SLM480MC (pers. herb.)	Miller et al. (2001)	AF265540	–	–
*Russula subochracea**	*Gymnomyces subochraceus*	USA	T13386 (OSC)	Whitbeck (2003)	AY239325	–	–
Russula suecica	*Russula suecica*	Norway	JR7994 (KUO)	Vauras et al. (2016)	KX988014	–	–
*Russula tapawera**	*Macowanites tapawera**	New Zealand	T12607 (OSC), 83696 (PDD)	Lebel & Tonkin (2007)	EU019935	EU019935	–
Russula tawai	*Russula tawai*	New Zealand	77760 (PDD)	Johnston & Park (unpubl.)	GU222263	–	–
*Russula theodoroui**	*Cystangium theodoroui*	Australia	SLM43I84 (pers. herb.)	Smith et al. (2006)	DQ403804	–	–
Russula tricholomopsis	*Russula tricholomopsis*	New Zealand	77749 (PDD)	Johnston & Park (unpubl.)	GU222261	–	–
Russula turci	*Russula turci*	Finland	101874 (TU)	Bazzicalupo et al. (2017)	UDB016082	KX812891	KX813672
*Russula unicalifornica**	*Gymnomyces cinnamomeus*	USA	T19930 (OSC)	Whitbeck (2003)	AY239338	–	–
*Russula variispora**	*Russula variispora**	Australia	H5855 (DAR)	Lebel & Tonkin (2007)	EU019934	EU019934	–
Russula velenovskyi	*Russula velenovskyi*	Slovakia	F-2921 (SAV)	Cabon et al. (unpubl.)	KY582701	–	KY616695
Russula venezueliana	*Russula venezueliana*	French Guiana	TH7874 (pers. herb.)	Smith et al. (2017)	KT339269	–	–
Russula versicolor	*Russula versicolor*	USA	r-04039	Davis (unpubl.)	JF834350	JF834498	JF834447
	Russula versicolor	Slovakia	BB589/07.288 (PC)	Schoch et al. (2012)	JN944009	JN940594	KU237859
Russula vesca	*Russula vesca*	Sweden	AT2002091 (UPS)	Buyck et al. (2008)	DQ422018	DQ422018	DQ421959
*Russula vidalii**	*Gymnomyces ilicis*	Spain	JC100508BT01, JMV800688 (BCN)	**This work**	**MK105693**	**MK105738**	–
	Russula vidalii	Spain	JMV20160517-1 (BCN)	**This work**	**MK105694**	**MK105739**	**MK102769**
*Russula vinaceodora**	*Macowanites vinaceodorus*	Spain	Fungi 46524 (MA)	Vidal et al. (2002)	AJ438035	–	–

Table 1 (cont.)

Species (*) sequestrate[1]	Original identification (*) type	Origin	Voucher Id (Herbarium)[2]	Reference	GenBank accession codes		
					ITS rDNA	28S rDNA	RPB2
*Russula vinaceodora** (cont.)	*Macowanites vinaceodorus**	Spain	Fungi 47416 (MA)	Vidal et al. (2002)	AJ438034	–	–
	Macowanites vinaceodorus	Spain	46374 (AH)	**This work**	**MK105695**	**MK105740**	**MK102770**
Russula vinosa	*Russula vinosa*	Sweden	F124791 (UPS)	Looney et al. (2016)	KX812857	KX812900	KX813680
Russula violeipes	*Russula violeipes*	Korea	20121010-06 (SFC)	Park et al. (2013)	KF361808	KF361858	KF361758
	Russula violeipes	Korea	16735 (HCCN)	Park et al. (2013)	KF361783	KF361833	KF361733
Russula virescens	*Russula virescens*	Belgium	HJB9989 (UPS)	Buyck et al. (2008)	DQ422014	DQ422014	DQ421955
Russula viscida	*Russula viscida*	Canada	F 16576 (UBC)	Berbee et al. (unpubl.)	FJ627039	–	–
Russula werneri	*Russula werneri**	Italy	1997/0786 (IB)	Eberhardt (unpubl.)	DQ422021	DQ422021	–
Russula wollumbina	*Russula wollumbina*	Australia	2238232 (MEL)	Lebel & Tonkin (2007)	EU019921	EU019921	–
Russula xerampelina	*Russula xerampelina*	Canada	OUC97303 (DAVFP)	Durrall et al. (2006)	DQ367916	DQ367916	–
*Russula xerophila**	*Gymnomyces xerophilus**	USA	82218, SRC672 (OSC)	Smith et al. (2006)	DQ028473	–	–
	Gymnomyces xerophilus	USA	82219, SRC648 (OSC)	Smith et al. (2006)	DQ028476	–	–
uncultured					UDB027052	–	–
/stereaceae/stereum							
Stereum hirsutum	*Stereum hirsutum*		FPL 8805	Binder & Hibbett (2002)	AY854063	AF393078	AY218520

[1] New species, new combinations and sequences produced from this study are in **bold**. Sequestrate taxa are marked with an asterisk (*) symbol.

[2] Collection sources: AB = Amadou Bâ (GENT); ADK = André De Kesel (BR); AM = Amer Montecchi (pers. herb.); AT = Andrew Taylor (UPS); AV = Annemieke Verbeken (GENT); AVoitk = Andrus Voitk (GENT); BB = Bart Buyck (PC); BH = Bryony M. Horton (HO); BM = Baldomero Moreno-Arroyo (pers. herb.); BPL = Brian P. Looney (TENN); BW = Birgitta Wasstorp (UPS); CLC = Cathy L. Cripps (MONT); CWD = Christopher W. Dunk (MEL); DA = David Arora (GENT); DED = Dennis E. Desjardin (PC, SFSU); DS = Dirk Stubbe (GENT); EB = Edward G. Barge (MONT); EG = Edith Garay-Serrano (XAL); EH = Egon Horak (ZT); EU = Elisabeth Uhlmann (UPS); FA = François Ayer (WSL); FAN = Li Fan (BJTC); FH = Felix Hampe (GENT); FO = Franz Oberwinkler (TUB); GD = Giuseppe Donelli (UPS); GG = Gerhardt Gross (M); GK = Georges Konstantinidis (pers. herb.); GM-RG = Gabriel Moreno and Ricardo Galán (AH); GO = Roberto Garibay Orijel (MEXU); HJB = Henri J. Beker (UPS); HM-R = Hermann Marxmüller (M); HRL = Renée Lebeuf (pers.herb.); HTL = Huyen Than Le (CMU, GENT); IC = Aurelia Paz Conde (BCN); JC = Julio Cabero (pers. herb.); JET = Jennifer E. Tonkin (MEL); JL = Jaume Llistosella (BCN); JMV = Josep M. Vidal (BCN); JN = Jorinde Nuytinck (GENT); JR = Juhani Ruotsalainen (KUO); JV (TURA) = Jukka Vauras (TURA); JV (C, GENT) = Jan Verterholt (C, GENT); KD = Kanad Das (BSD); KVP = Kobeke Van de Putte (GENT); LM = Leticia Montoya (XAL); MAM = Malka Saba (LAH); MCA = M. Catherine Aime (pers. herb.); MF = Marco Floriani (UPS); ML = Michael Loizides (pers. herb.); MS = Mauro Sarnari (pers. herb.); MTB = Maria Teresa Basso (GENT); PAM = Pierre-Arthur Moreau (GENT, PC); PBM = P. Brandon Matheny (CUW, WTU); PL = Patrick Leonard (pers. herb.); RF = Raymond M. Fatto (pers. herb.); RH = Roy E. Halling (NY); RW (GENT) = Ruben Walleyn (GENT); RW (E) = Roy Watling (E); SLM = Steven L. Miller (pers. herb.); T = James M. Trappe (MEL, OSC, PDD); TH = Terry W. Henkel (pers. herb.); TL = Teresa Lebel (MEL); UE = Ursula Eberhardt (TUB, UPS); VK = Vasileios Kaounas (pers. herb.); WCR = William C. Roody (PC); ZWG = Zai-Wei Ge.

were above 0.95, and subsignificant if BP values were above 60 % or PP values were above 0.90.

RESULTS

Maximum-likelihood analysis of the general ITS – 28S rDNA – *rpb2* dataset including all new sequences and those recovered from public databases (Fig. 1) produced a phylogenetic tree consisting of four significantly supported clades, those of genera *Lactarius*, *Lactifluus*, *Multifurca* and *Russula*, in accordance with previous reconstructions of the *Russulaceae* lineage (Buyck et al. 2008, Lebel et al. 2013, Verbeken et al. 2014b, Kong et al. 2015, Looney et al. 2016, Song et al. 2016, De Crop et al. 2017).

Lactarius (Fig. 2) was composed of five main clades, namely *Lactarius* subg. *Plinthogalus*, /*L. hispidulus*, /*L. bisporus*, /*L. kabansus*, and a lineage including *Lactarius* subg. *Lactarius* (= *Lactarius* subg. *Piperites*) and *Lactarius* subg. *Russularia*, all of them receiving significant or subsignificant support, in agreement with previous analyses of *Lactarius* (Eberhardt & Verbeken 2004, Buyck et al. 2008, Verbeken et al. 2014a, b, Barge et al. 2016), except for subg. *Lactarius* (PP 0.88, BP 58). All European taxa of sequestrate *Lactarius* nested within the monophyletic clade formed by *L.* subg. *Lactarius* and *L.* subg. *Russularia*. Seven significantly supported sequestrate species were identified, two of which belong to *L.* subg. *Russularia* and five fall outside and are therefore considered part of *L.* subg. *Lactarius*. *Lactarius* subg. *Russularia* received subsignificant support (PP 0.94, BP 47),

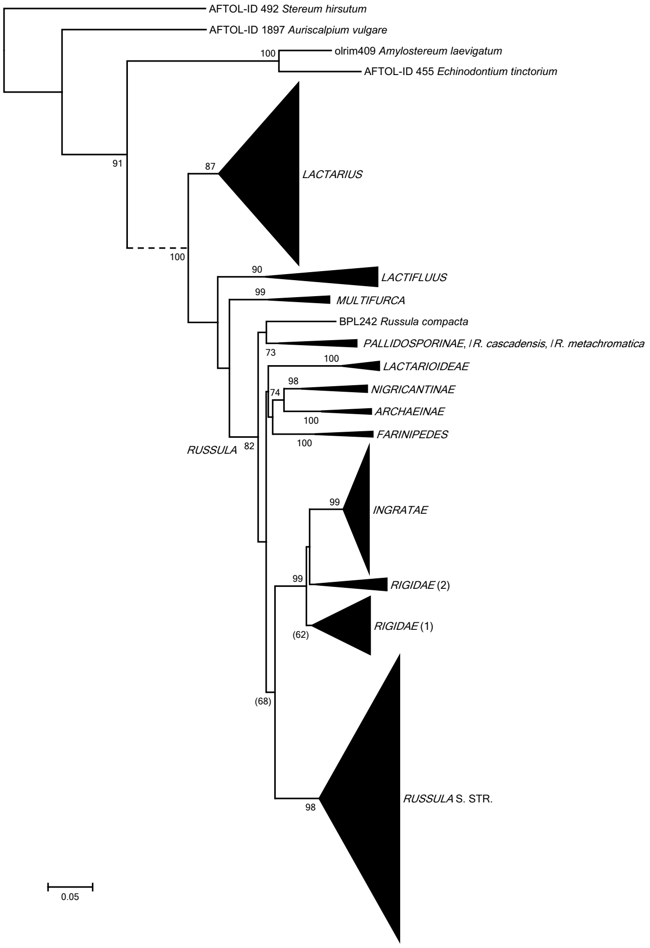

Fig. 1 Consensus phylogram of the family *Russulaceae* obtained in RAxML after 2000 bootstrap iterations of a combined alignment of ITS rDNA, 28S rDNA and rpb2. Major clades were collapsed and rooting branch shortened for publication. Nodes were annotated if supported by > 70 % ML BP, but non-significant support values are exceptionally represented inside parentheses.

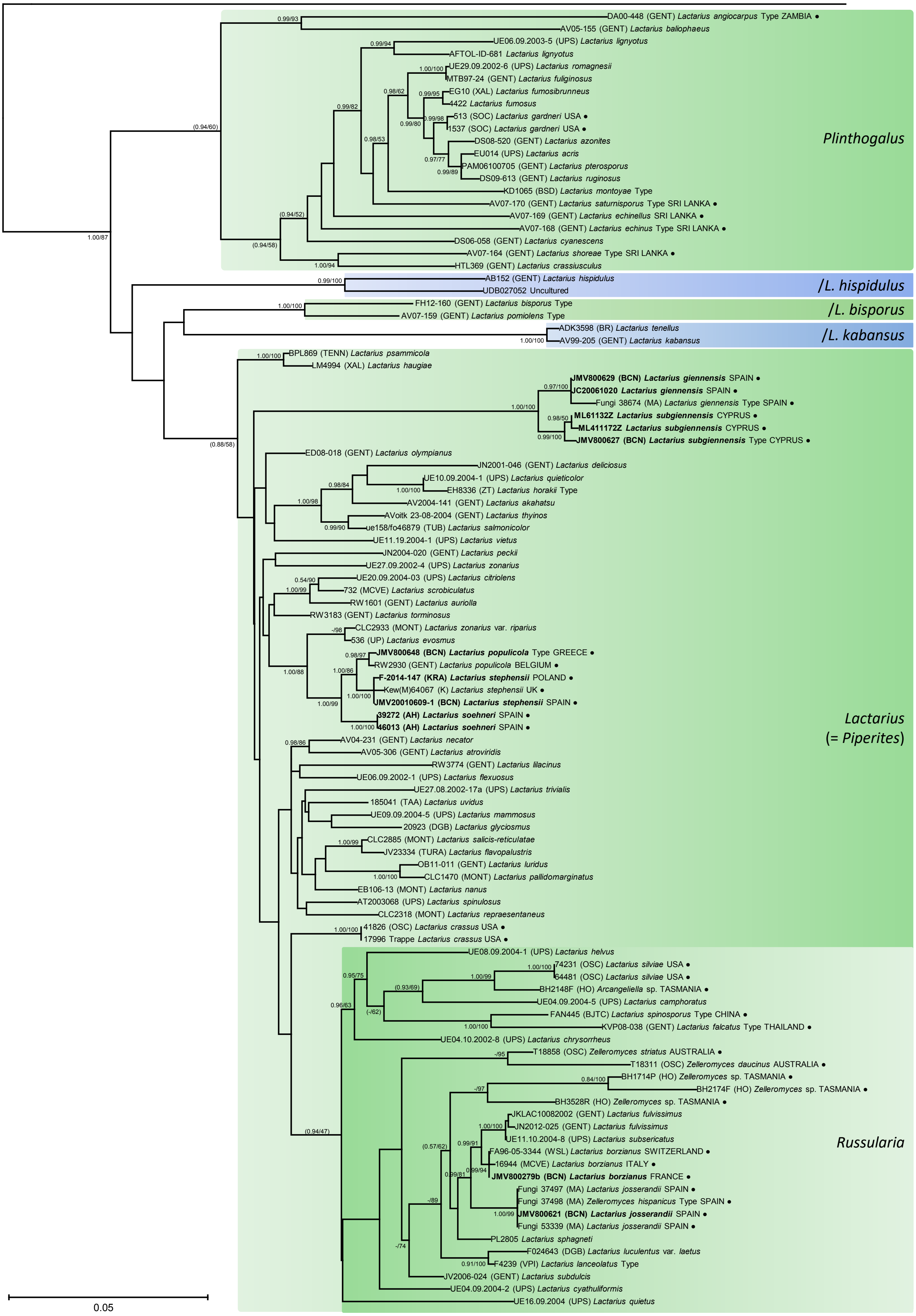

Fig. 2 Extended phylogram of genus *Lactarius* obtained from Fig. 1. Rooting branch was shortened for publication. Nodes were annotated if supported by > 0.95 bayesian PP or > 70 % ML BP, but non-significant support values are exceptionally represented inside parentheses. Major lineages are highlighted with coloured boxes. Sequestrate species are marked with black circle (●) symbols. Specimens sequenced in the present work are highlighted in **bold**.

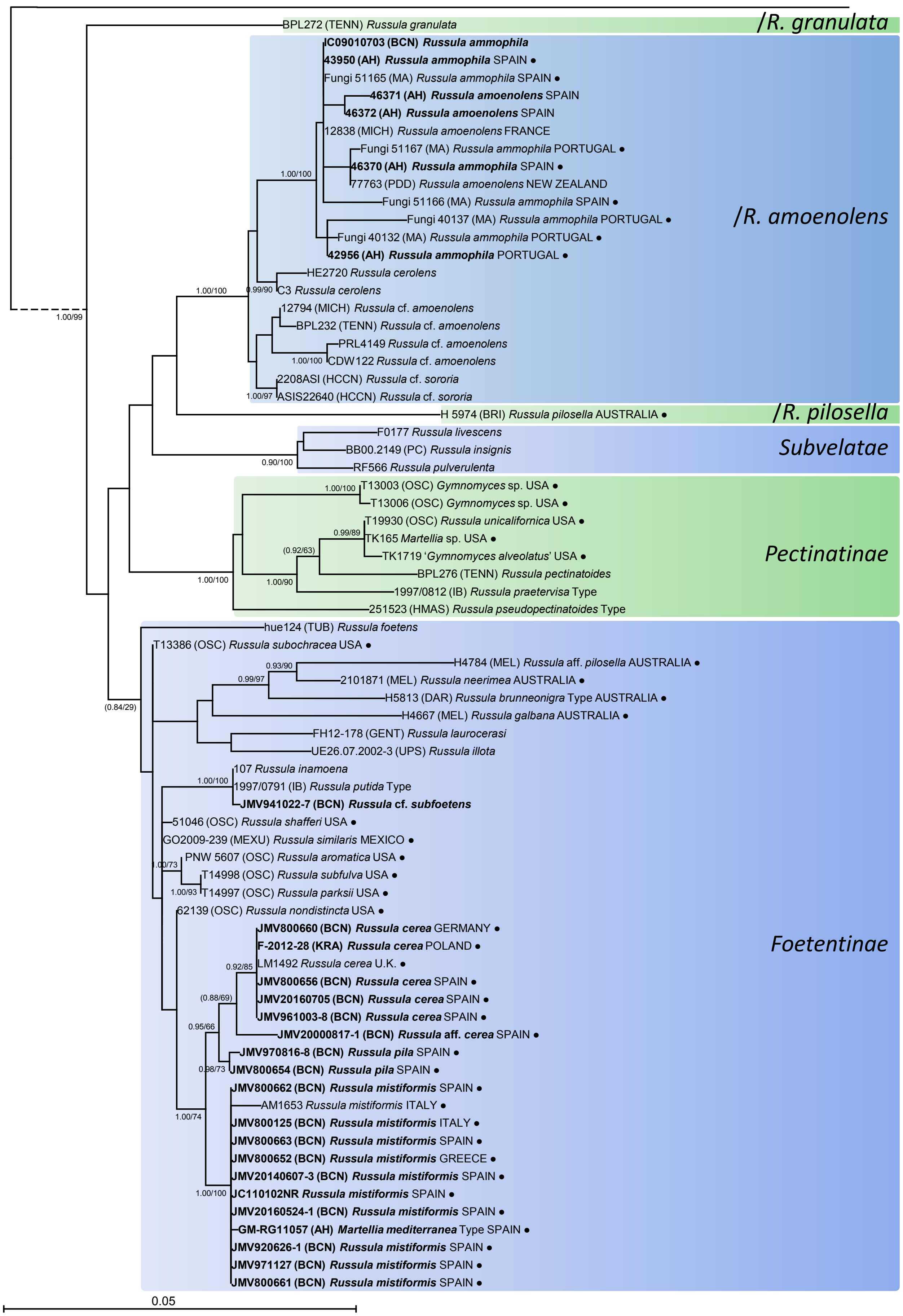

Fig. 3 Extended phylogram of *Russula* sect. *Ingratae* obtained from Fig. 1. Rooting branch was shortened for publication. Nodes were annotated if supported by > 0.95 bayesian PP or > 70 % ML BP, but non-significant support values are exceptionally represented inside parentheses. Major lineages are highlighted with coloured boxes. Sequestrate species are marked with black circle (●) symbols. Specimens sequenced in the present work are highlighted in **bold**.

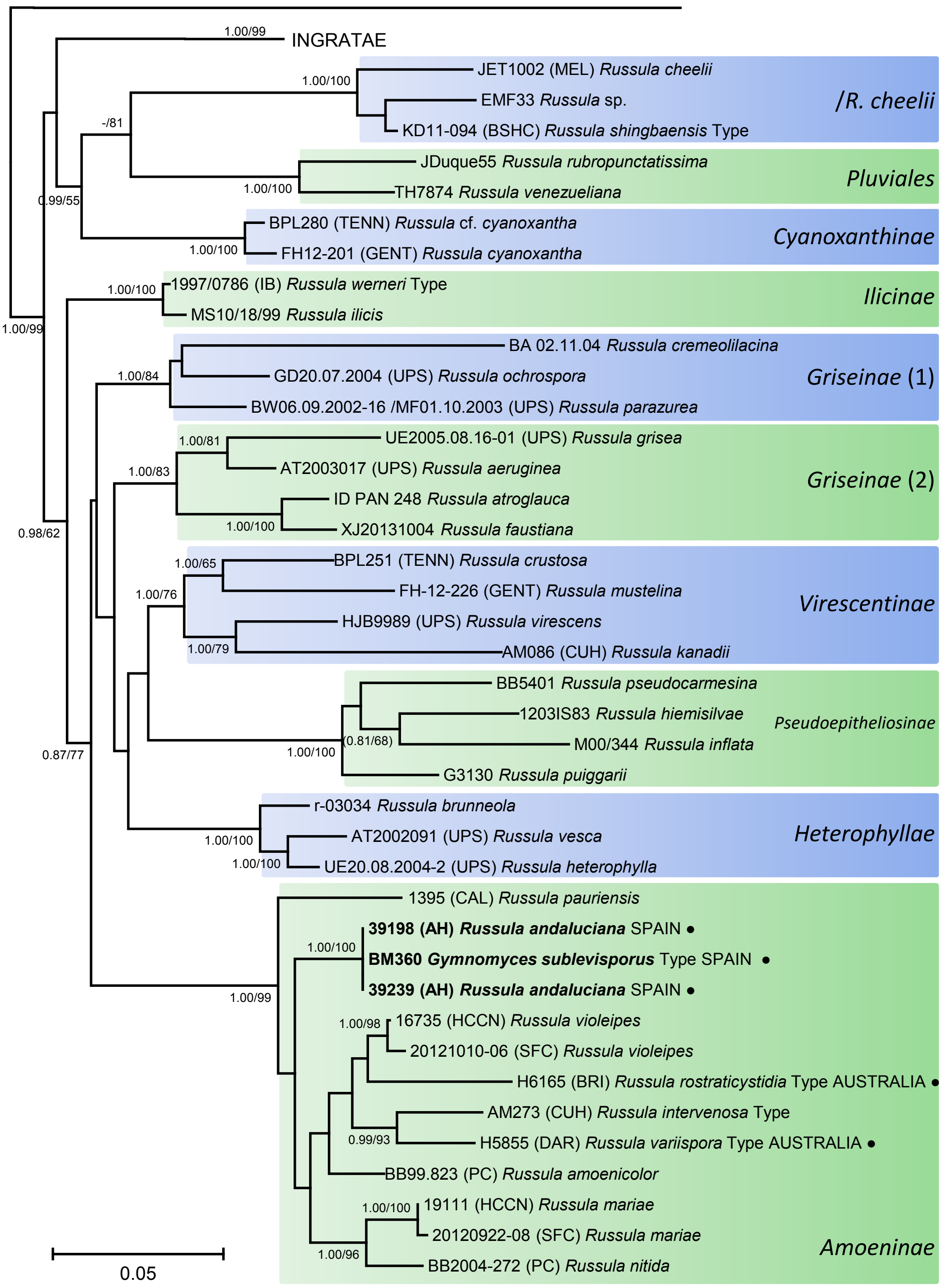

Fig. 4 Extended phylogram of *Russula* sect. *Rigidae* obtained from Fig. 1. Rooting branch was shortened for publication. Nodes were annotated if supported by > 0.95 bayesian PP or > 70 % ML BP, but non-significant support values are exceptionally represented inside parentheses. Major lineages are highlighted with coloured boxes. Sequestrate species are marked with black circle (●) symbols. Specimens sequenced in the present work are highlighted in **bold**.

a result similar to that of Verbeken et al. (2014b), probably due to the insufficient phylogenetic signal in the species analyzed, gaps in the phylogenetic diversity because of an incomplete sampling, or too much phylogenetic noise in the dataset employed. However, a significantly supported clade formed by *L. borzianus*, *L. josserandii* (= *Z. hispanicus*) and some gymnocarpic species, such as *L. fulvissimus* and *L. subsericatus*, in accordance with results of Verbeken et al. (2014b), Liu et al. (2015), or Barge et al. (2016). The remaining European sequestrate *Russulaceae* species included in *L.* subg. *Lactarius* were identified as the existing species *L. giennensis*, *L. stephensii* and *Z. soehneri*, or otherwise accommodated into the new taxa *L. populicola* and *L. subgiennensis*.

Russula was divided in eight significantly supported monophyletic clades (Fig. 1, 3–5):

1) an isolated branch for /*R. compacta*;
2) a clade formed by *Russula* subsect. *Pallidosporinae* (Bon 1988), as well as the lineages of /*R. cascadensis* and /*R. metachromatica*;
3) *Russula* subsect. *Lactarioideae* (including *R. delica*);
4) *Russula* sect. *Nigricantinae*;
5) *Russula* sect. *Archaeinae*;
6) *Russula* subsect. *Farinipedes* (including *R. crassotunicata* and *R. pallescens*);
7) a monophyletic lineage formed by *Russula* sect. *Ingratae* (≡ subg. *Ingratula*) and *Russula* sect. *Rigidae* (≡ subg. *Heterophyllidia*); and
8) a large *Russula* s.str. clade including the remaining species.

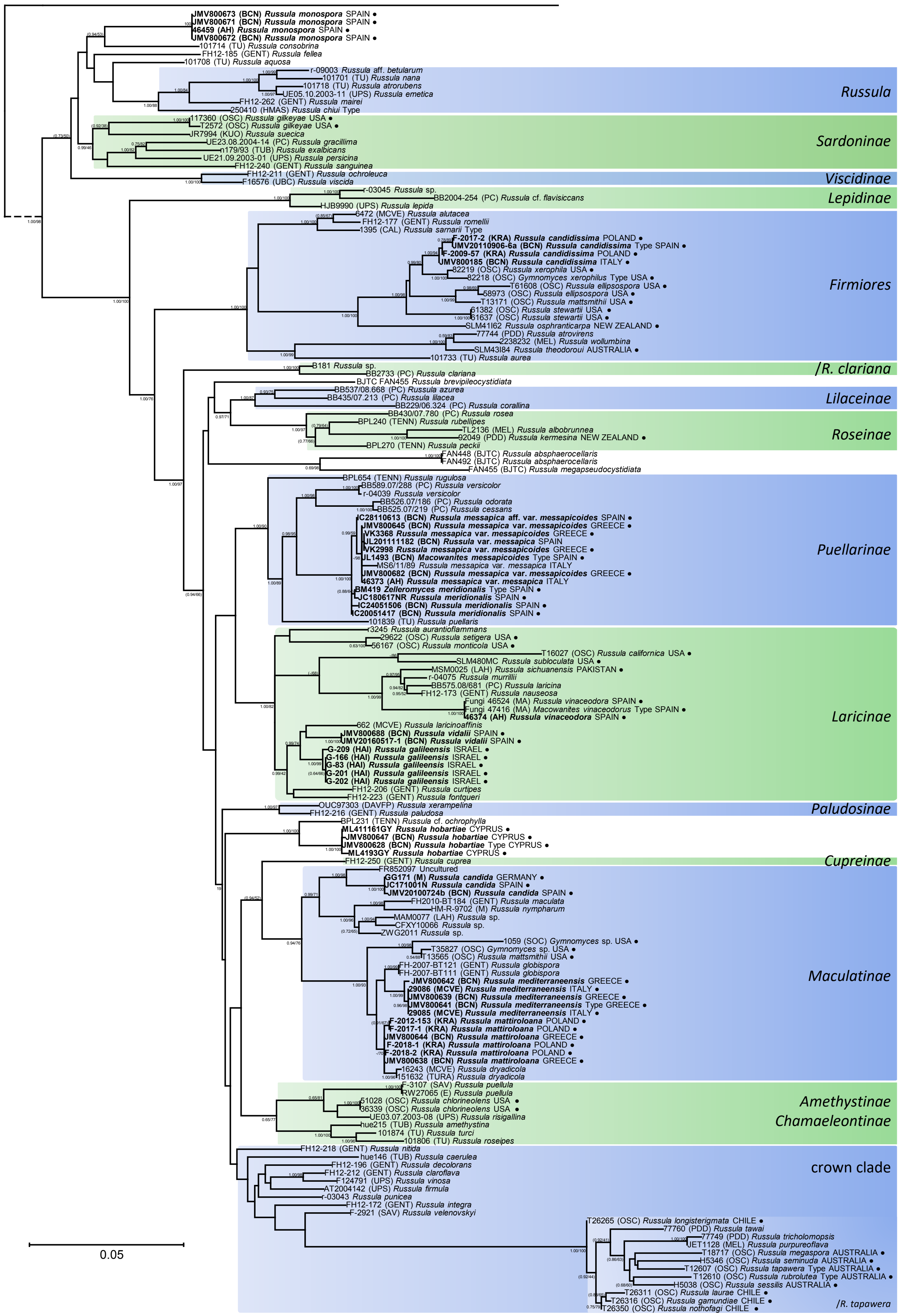

Fig. 5 Extended phylogram of *Russula* s.str. obtained from Fig. 1. Rooting branch was shortened for publication. Nodes were annotated if supported by > 0.95 bayesian PP or > 70 % ML BP, but non-significant support values are exceptionally represented inside parentheses. Major lineages are highlighted with coloured boxes. Sequestrate species are marked with black circle (●) symbols. Specimens sequenced in the present work are highlighted in **bold**.

These clades were also significantly supported by Kong et al. (2015), Looney et al. (2016) and Bazzicalupo et al. (2017). All European sequestrate *Russulaceae* taxa nested within the *Ingratae-Rigidae* clade or *Russula* s.str.

Russula sect. *Ingratae* (Fig. 3) received significant support (PP 1.00, BP 99). It was composed of *R.* subsect. *Subvelatae*, *Pectinatinae*, and *Foetentinae*, as well as the lineages of /*R. granulata*, /*R. amoenolens* and /*R. pilosella*, all of them significantly supported except *Foetentinae* (PP 0.84, BP 29), probably because of incomplete data from many American sequestrate taxa. These results agree with those obtained by other researchers (Kong et al. 2015, Li et al. 2015, Lee et al. 2017, Melera et al. 2017). Sequestrate *Russulaceae* taxa are present in most of these lineages, but all currently known European sequestrate species were related to subsect. *Foetentinae* or the /*R. amoenolens* lineage. *Russula ammophila* was not significantly different from *R. amoenolens* employing ITS, 28S rDNA and *rpb2* data, but significant differences were found in *tef1* gene-data (data not shown).

Russula sect. *Rigidae* (Fig. 4) was split into two clades. The first one was composed of *R.* subsect. *Cyanoxanthinae* and *Pluviales* (Singer 1986, Buyck & Ovrebo 2002, Cheype & Campo 2012), as well as the /*R. cheelii* lineage (PP 0.99, BP 55). The second clade was formed by the remaining species of *Rigidae* (PP 0.98, BP 62). This clade was composed of subsect. *Ilicinae* (BP 100, PP 1.00) on the one side, and the remaining subsections of *Rigidae* (PP 0.87, BP 77) on the other, including subsections *Griseinae* (divided in two clades, those of /*R. ochrospora* and /*R. grisea*), *Virescentinae*, *Pseudoepitheliosinae*, *Heterophyllae* and *Amoeninae*. Most of these clades were also significantly supported by the phylogenetic reconstructions of *Rigidae* conducted by Dutta et al. (2015) and Zhao et al. (2015). The only European sequestrate species related to sect. *Rigidae* was *R. andaluciana*, a replacement name for *Gymnomyces sublevisporus*, whose isotype was significantly related with subsect. *Amoeninae*.

Russula s.str. (Fig. 5) was composed of a basal clade which did not receive significant support (PP 0.73, BP 50), including *Russula* subsect. *Russula*, as well as subsect. *Sardoninae*, subsect. *Viscidinae*, and the lineages of *R. consobrina* (subsect. *Consobrinae*) and *R. fellea* (subsect. *Felleinae*). A second large clade with significant support clustered all other species of *Russula*, and had itself two basal clades: subsections *Lepidinae* and *Firmiores*, the latter including gymnocarpic, pseudoangiocarpic and angiocarpic species. The remaining species of *Russula* grouped into several distinct clades with significant support: subsections *Cupreinae*, *Laricinae*, *Lilaceinae*, *Maculatinae*, *Paludosinae*, *Puellarinae*, *Roseinae*, a monophyletic clade containing subsections *Amethystinae* and *Chamaeleontinae*, and finally the so-called 'crown' clade (Looney et al. 2016), containing species from subsections *Decolorantinae*, *Insidiosinae*, *Integrae*, *Olivaceinae*, *Vinosinae* and *Xerampelinae*, as well as a lineage including the type species of genus *Cystangium* (*C. sessile* ≡ *Russula sessilis*), and many sequestrate and gymnocarpic species from Australia (Lebel & Tonkin 2007) and South America (Trierveiler-Pereira et al. 2015). Most European sequestrate taxa were related to subsections *Firmiores*, *Laricinae*, *Maculatinae* and *Puellarinae*, but there were also two independent lineages: one of them, *R. monospora*, was subsignificantly related with *R. consobrina*, the type species of subsect. *Consobrinae* (PP 0.94, BP 53), while the other, *R. hobartiae*, represented a new species from Cyprus significantly related with a putative specimen of *Russula ochrophylla*.

Lineages matching known species of sequestrate *Russulaceae* are listed below or re-described, and new names are proposed with complete descriptions for those representing new taxa.

TAXONOMY

Lactarius borzianus (Cavara) Verbeken & Nuytinck, Belg. J. Bot. 136, 2: 151. 2003 — Fig. 6

Basionym. *Arcangeliella borziana* Cavara, Nuovo Giorn. Bot. Ital., Nuov. Ser. 7, 2: 126. 1900.

Synonyms. *Octaviania borziana* (Cavara) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 740. 1958.

Arcangeliella stephensii var. *borziana* (Cavara) Krieglst., Z. Mykol. 57, 1: 19. 1991.

Arcangeliella volemoides K. Mader & A. Mader, Österr. Z. Pilzk. 1: 5. 1992.

Basidiomata 1–4 cm wide, angiocarpic, subglobose to tuberiform, often bilobed, sessile or subsessile, with a residual stipe; radially alveolate in the base. *Pileus* dry, first smooth, then areo-

Fig. 6 *Lactarius borzianus*. a. Reproduction of Cavara's plate of *Arcangeliella borziana* (Cavara 1900, tav. VII). — b. MSL1962F0412. Basidiomata. — c–e. AM1973. c. Spores in Melzer; d–e. SEM images of spores. — Scale bars: b = 1 cm, c = 10 μm; d–e = 5 μm. — Photos: b. M. Slavova; c. J.M. Vidal; d–e. UdG.

late, basally closed, or open exposing the hymenophore; initially yellowish white (2A2) to pale yellow (3A3–4A5), then brownish orange (7C7) with reddish brown to dark brown (8E8–F8) maculae. *Hymenophore* loculate, labyrinthoid, yellowish white (2A2), pale yellow (4A4) to pale brown (7D7); locules irregularly arranged, 0.6–1.8 × 0.15–3 mm (1–2 per mm), elongated, sinuous, empty; fresh spore mass in locules yellowish white (4A1–A2). *Columella* percurrent or branched, apparent only in young specimens. *Latex* scant, more abundant in columella and pileal context, colourless to white, changing to yellow. *Odour* of wild bug (*Nazara viridula*) or musky; taste unpleasant, bitterish after a while.

Spores 9.5–13(–15) × 8–10(–11) µm, Q = 1.16–1.28, heterotropic, subglobose to broadly ellipsoid, echinate; warts 1–1.5 µm high, isolated, amyloid; suprahilar plage absent; hilar appendix 1–1.5 µm long, sometimes with a short sterigmal fragment 1–3 µm long. *Basidia* 3–4-spored, 30–65 × 10–15 µm, cylindrical to subclavate; sterigmata conical, curved, 5–8 µm long. *Macrocystidia* absent. *Cystidioles* infrequent, 20–50 × 4–6 µm, septate, cylindrico-rostrate to ventricose-rostrate, acuminate, more abundant in sterile locules. *Paraphysoid cells* abundant, 15–40 × 5–12 µm, cylindrical to slightly clavate, sometimes subglobose, often 1–2-septate. *Pseudocystidia* not observed. *Subhymenium* cellular, formed by prismatic cells 8–25 µm diam. *Hymenophoral trama* homiomerous, formed by septate hyphae 2–6.5 µm diam, with subglobose thickenings up to 12 µm wide in tramal anastomoses. *Pileipellis* and *context* 100–250 µm thick; suprapellis trichodermal to oedotrichodermal, formed by cylindrical, sinuous, septate hairs 10–40 × 3–6 µm, and lanceolate dermatocystidia similar to those of the sterile locules, that soon collapses in a brown mass; subpellis made of prismatic hyphae up to 15 µm diam. *Pileal context* a cutis with the same composition of the hymenophoral trama, plenty of laticifera. *Laticifera* 2.5–10 µm diam, scarce in the hymenophoral trama and more abundant in the pileal context. Thromboplera 2–8 µm diam, abundant in young specimens. Some specimens present isolated sphaerocytes in the hymenophoral trama and pileal context, 15–30 µm diam, being more abundant and grouped in rosettes or chains in the columella.

Habitat, Distribution & Season — Gregarious, hypogeous or semi-hypogeous under needles, in subalpine conifer forests of *Abies* and *Picea*, on siliceous soil. Summer and autumn. So far known from the Alps, Apennine (Italy), and Rhodope mountains (Greece), at 1000–1800 m altitude.

Material studied. Austria, Lower Austria, Gföhl, near Dorf Brunn, under *Picea abies*, 12 Sept. 1970, *A.* & *K. Mader* (WU 10875, holotype of *A. volemoides*). – Bulgaria, Smolyan, Pamporovo, Southern Rhodope mountains, 1650–1750 m, under *Picea abies*, on siliceous soil, 15 Aug. 2017, *M. Slavova* (MSL1962F0412, duplicate BCN JMV800685). – France, Rhône-Alpes, Savoie, Héry-sur-Ugine, Réserve Naturelle du Nant Pareu-Merdassier, 1450 m, under *Picea abies* in the vicinity of *Lactarius aurantiofulvus*, on siliceous soil, 13 Aug. 2002, *P.-A. Moreau* as *A. borziana* (PAM02081306, duplicate BCN JMV800279b)*. – Italy, Emilia-Romagna, Reggio Emilia, Civago, Abetina Reale forest, Tuscan-Emilian Apennines, under *Abies alba*, on siliceous soil, 5 Aug. 1999, *A. Montecchi* as *A. borziana* (AM1973, duplicate BCN JMV800239); Tuscany, Firenze, Reggello, Vallombrosa Forest, Tuscan-Emilian Apennines, 'In silvis abiegnis Vallisumbrosae (Etruria), aestate, *F. Cavara*' (NY, herb. S.M. Zeller, labelled '*Elasmomyces mattiroloanus*, Italy, Vallombrosa, coll. F. Cavara, semiepigeous in fallen needles under *Abies pectinata*, autumn 1896, sent to Zeller by Cavara, type'; isotype of *A. borziana*).

Notes — *Arcangeliella borziana* was collected in the summer of 1898 in Tuscany (Italy) by Cavara (1900), growing hypogeously under *Abies alba*. According to Zeller & Dodge (1937), collections of *A. borziana* preserved in their personal herbaria are duplicates of type material preserved at the Herbarium of the Università degli Studi di Napoli (Naples, Italy), but these were apparently not studied in detail by Zeller & Dodge, who just included in their works a brief description of *A. borziana* taken from Cavara (Zeller & Dodge 1919). Later descriptions by Singer & Smith (1960), Pegler & Young (1979), Lebel & Trappe (2000), probably based on the isotypes of Zeller & Dodge (C.W. Dodge 2087 at FH, and S.M. Zeller 1671 at NY), highlighted the same group of features: presence of a percurrent stipe-columella, hymenophoral trama and pileal context containing nests of sphaerocytes and laticifera, hymenium with abundant macrocystidia, and large ochraceous globose spores measuring 9–15 × 10–13 µm. Vidal (2004a), conducted a detailed study of these specimens, and observed that these microscopical features do not match the protologue of this species, but are more compatible with that of *Elasmomyces mattiroloanus*, suggesting that they do not represent the original concept of *A. borziana* sensu Cavara, and probably both species were erroneously labelled. This is all the more likely if laticifera had been mistaken for gloeoplera. The original concept of *Lactarius borzianus* is of a sessile or subsessile species that may have a rudimentary stipe-columella, a hymenophoral trama and pileal context rarely containing sphaerocytes (sometimes just represented by scattered globose elements, but never forming nests), a fertile hymenium deprived of macrocystidia (with only cystidioles present in the sterile hymenium), and whose spores are hyaline and broadly ellipsoid. It is a silicicolous species growing in wet, subalpine conifer forests of *Abies* and *Picea*, receiving large amounts of precipitation (about 2000 mm).

Genetic studies by Peter et al. (2001) conducted on specimens collected in the Swiss Alps (F. Ayer 96-05-3344 WSL) show that this species is significantly related to members of *L.* subg. *Russularia*. Nuytinck et al. (2003) compared sequences of *Z. stephensii* with those of *A. borziana* obtained by Peter et al. (2001), and found both species to be genetically distinct, recombining them into *Lactarius*. Neither Nuytinck et al. (2003) nor Vidal (2004a) were able to observe any significant macro- or microscopical differences between the type collection of *A. volemoides* and *A. borziana*, and both taxa were therefore considered to be synonyms by these authors. Another specimen (MCVE 16944) collected at Abetina Reale (Reggio Emilia, Italy) by Amer Montecchi was sequenced by Osmundson et al. (2013) and found to be genetically identical with the Swiss collection already mentioned. Species of *Lactarius* subg. *Russularia* are characterized by reddish brown or orange pilei sometimes producing remarkable smells, bleeding white or transparent latex not changing in colour upon exposure or slowly changing to yellow, globose to ellipsoid spores ornamented with a more or less complete reticulum and an inamyloid or distally amyloid plage, as well as dermatocystidia (Hesler & Smith 1979, Wisitrassameewong et al. 2014). Other sequestrate species in *Lactarius* subg. *Russularia* include the European *L. josserandii* (= *Z. hispanicus*), the North American *L. silviae* (≡ *Elasmomyces camphoratus*) and the Australian *Zelleromyces striatus* and *Z. daucinus*, all of them matching the characteristic features of *Lactarius* subg. *Russularia* (Singer & Smith 1960, Beaton et al. 1984, Miller et al. 2001, Verbeken et al. 2014b). The North American species *L. paulus* (≡ *Arcangeliella parva*) and *L. variegatus* (≡ *A. variegata*) could also be related to subgenus *Russularia*, but their phylogenetic affiliation is still dubious because of the scarce genetic data available (Miller et al. 2001).

Lactarius giennensis (Mor.-Arr. et al.) Pierotti, Index Fungorum 254: 1. 2015 — Fig. 7

Basionym. Zelleromyces giennensis Mor.-Arr. et al., Cryptog. Mycol. 19, 1–2: 108. 1998.

Synonym. Arcangeliella giennensis (Mor.-Arr. et al.) J.M. Vidal, Rev. Catalana Micol. 26: 74. 2004.

Basidiomata 1–2.5 cm wide, angiocarpic, subglobose to tuberiform, somewhat lobate, sessile. *Pileus* whitish to pale yellowish,

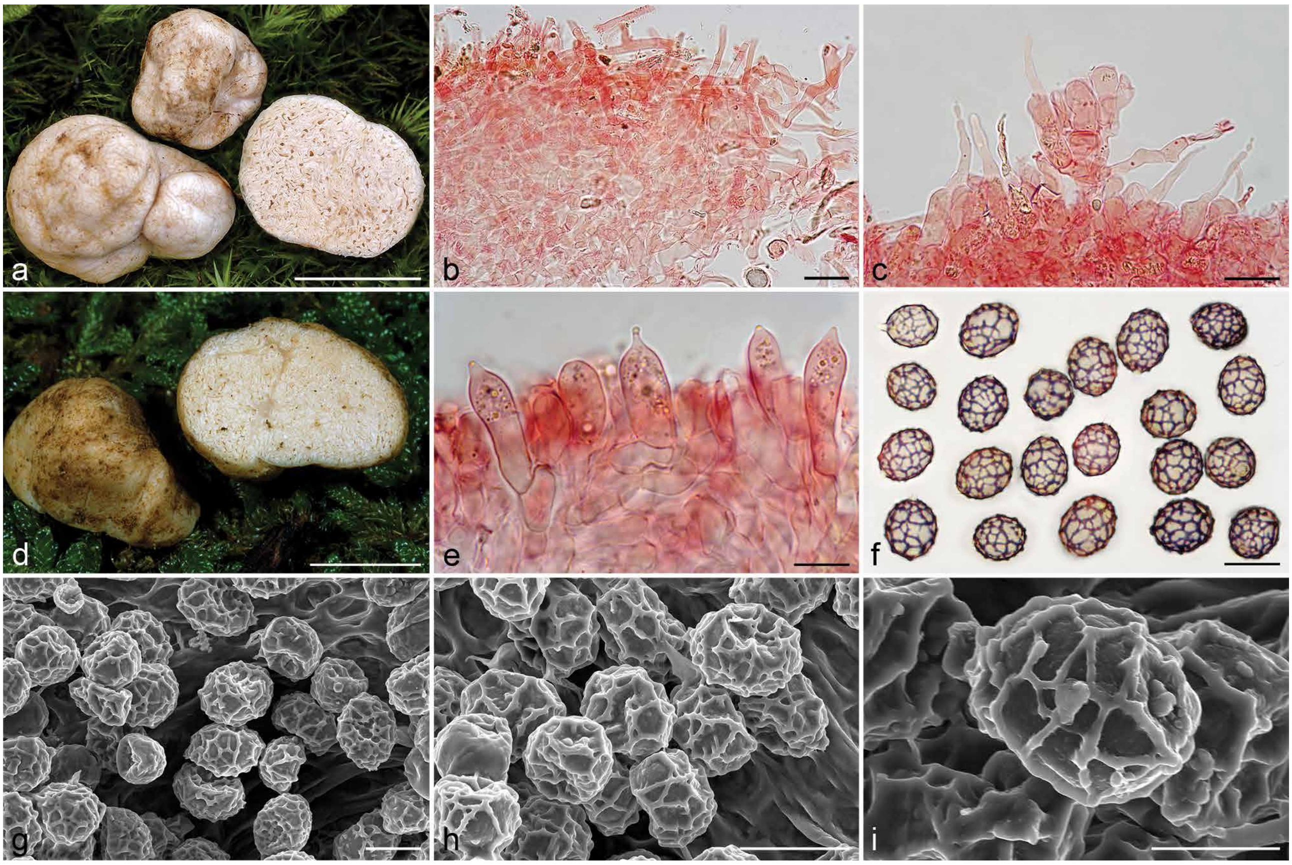

Fig. 7 *Lactarius giennensis*. a. JC20061020. Basidiomata. — b–c. JMV20010204-1. b. Pileipellis and context; c. cystidioles of external immature locule. — d–f. JMV931123-1. d. Basidiomata; e. basidia; f. spores in Melzer. — g–i. JMV20010204-1. SEM images of spores. — Scale bars: a, d = 1 cm; b = 20 µm; c, e–h = 10 µm; i = 5 µm. — Photos: a. J. Cabero; b–f. J.M. Vidal; g–i. UdG.

membranous, smooth, partially evanescent, indistinctly scrobiculate or with some scattered minute openings. *Hymenophore* loculate, whitish to pale cream or pinkish. *Columella* branched, inconspicuous. *Latex* not observed. *Odour* mild.

Spores 10–13 × 7–9 µm, Q = 1.15–1.35, ovoid to ellipsoid, orthotropic; reticulum 1–2 µm high, complete, amyloid. *Basidia* 1-spored, 30–45 × 6–10 µm, cylindrical, clavate or sublageniform. *Macrocystidia* absent. *Cystidioles* 30–42 × 4–8 µm, lageniform-urticiform. *Subhymenium* ramose to cellular. *Hymenophoral trama* homoiomerous, made of septate hyphae 3–6 µm diam. *Pileipellis* and *context* 150–200 µm thick; suprapellis a trichoderm of septate hyphae. *Pileal context* a prosenchyma of intricate hyphae 3–6 µm diam. *Laticifera* 5–8 µm diam, present in the hymenophoral trama and pileal context.

Habitat, Distribution & Season — Gregarious, hypogeous, associated with *Cistus* and *Halimium*, often accompanied by *Pinus*, on siliceous soil. Autumn to spring. Xerophytic. So far restricted to the western Mediterranean region, in Central Spain, between 600–1000 m altitude.

Material studied. Spain, Andalusia, Jaén, La Aliseda, under *Pinus halepensis*, 28 Feb. 1994, *J. Gómez* & *B. Moreno-Arroyo* (MA-Fungi 38674, holotype of *Z. giennensis*); Castilla and Leon, León, Lugan, under *Cistus* sp. and *Eucalyptus* sp., 25 Sept. 1993, *T. Pérez-Jarauta* (BCN JMV930925); Salamanca, Casarito, under *Halimium alyssoides*, on siliceous soil, 6 Dec. 1992, *T. Pérez-Jarauta* (BCN JMV921206); Salamanca, Miranda del Castañar, under *Cistus ladanifer*, 18 Apr. 2003, *A. García-Blanco*, *M. Sanz-Carazo* & *J.B. Del Val* as *Z. giennensis* (AVM 1615, duplicate BCN JMV800629)*; Zamora, Tábara, 825 m, under *Cistus ladanifer* and *Pinus pinaster*, on siliceous soil, 4 Feb. 2001, *P. Juste* & *F. García* (BCN JMV20010204-1); ibid., 20 Oct. 2006, *J. Cabero* as *Z. giennensis* (JC20061020)*; Castilla-La Mancha, Ciudad Real, El Viso del Marqués, under *Halimium ocymoides*, on siliceous soil, 23 Nov. 1993, *T. Pérez-Jarauta* (BCN JMV931123-1).

Notes — *Lactarius giennensis* is morphologically characterized by its whitish to pinkish basidiomata, with a rather thin, membranous pileus with perforations opening to the hymenophoral locules, not bleeding latex when cut. Spores are ovoid or ellipsoid, ornamented with a closed reticulum composed of ridges up to 2 µm high. Abundant laticifera and thromboplera were observed in the hymenophoral trama, as well as lageniform-urticiform cystidioles in the hymenium of immature external locules.

Genetic data from the holotype specimen of *L. giennensis* (MA-Fungi 38674, GenBank AF230900, incorrectly published as AF230800 by Calonge & Martín 2000), evidenced that this species is related with other lactarioid taxa. In the present work this species is subsignificantly related with the lineages of subg. *Lactarius* and *Russularia*, so a hypothetical affiliation with subg. *Lactarius* is suggested. The clade containing *L. giennensis* has an unusually long branch, suggesting it could represent a highly evolved or ancestral lineage, or else evidence an incomplete sampling. The holotype of *L. giennensis* was found at Jaén (Andalusia, Spain) growing subhypogeously under *Pinus halepensis*, but the collections analyzed in the present work suggest a broader distribution, being present in central Spain, associated with *Cistaceae* hosts in acidic soils.

Lactarius josserandii (Malençon) J.M. Vidal & P. Alvarado, *comb. nov*. — MycoBank MB828496; Fig. 8

Basionym. *Zelleromyces josserandii* Malençon, Rev. Mycol. (Paris) 39: 303. 1975.

Synonyms. *Arcangeliella josserandii* (Malençon) J.M. Vidal, Rev. Catalana Micol. 26: 75. 2004.

Zelleromyces hispanicus Calonge & Pegler, Cryptog. Mycol. 19, 1–2: 100. 1998.

Basidiomata 2–5 cm wide, angiocarpic, irregular, obpyriform to subglobose, tuberiform to lobulate, sessile, with a depressed or conical base immersed into the soil. *Pileus* dry, smooth, continuous, with minute circular depressions in the surface, but not exposing the locules; initially pale orange (5A5), then orange-red (8B8), brownish red (8C8) or reddish brown (9D8), like in *Lactarius fulvissimus*, remaining pale orange in unexposed areas. *Hymenophore* loculate, labyrinthoid, pale, initially yellowish white (4A2), then orange-white (5A2); locules 0.5–1.5 × 0.15–0.3 mm (1–2 per mm), elongated, sinuous, empty; fresh spore mass in locules whitish; yellowish white (4A2) in exsiccata. *Columella* absent or rudimentary, with thin whitish veins. *Latex* scant, white, unchanging, more abundant in the pileal context. *Odour* fruity, taste sweetish, later astringent.

Spores 8.5–12.5(–13.5) × 7–9.5(–10.5) µm, Q = 1.1–1.3, subglobose to ellipsoid, heterotropic, initially hyaline then yellow, reticulated; reticulum amyloid, complete or with some interruptions, formed by 0.5–1 µm high ridges and warts; hilar appendix 0.7–1.4 × 0.7–1.1 µm, short, cylindrical to conical; suprahilar plage not seen. *Basidia* typically 4-spored, but also 1–3-spored, 40–50 × 7.5–10 µm, cylindrical, sinuous, with granular content; sterigmata 5–8 µm long, conical. *Basidioles* 20–30 × 7–10 µm, cylindrical. *Macrocystidia* absent. *Cystidioles* 42–44 × 7–8 µm, lageniform, scarce, present only in external immature locules. *Paraphysoid cells* abundant, 10–30 × 4–11 µm, entire or 1–2-septate. *Pseudocystidia* not observed. *Subhymenium* ramose to cellular, formed by chains of prismatic cells 8–10 µm diam. *Hymenophoral trama* 80–125 µm wide,

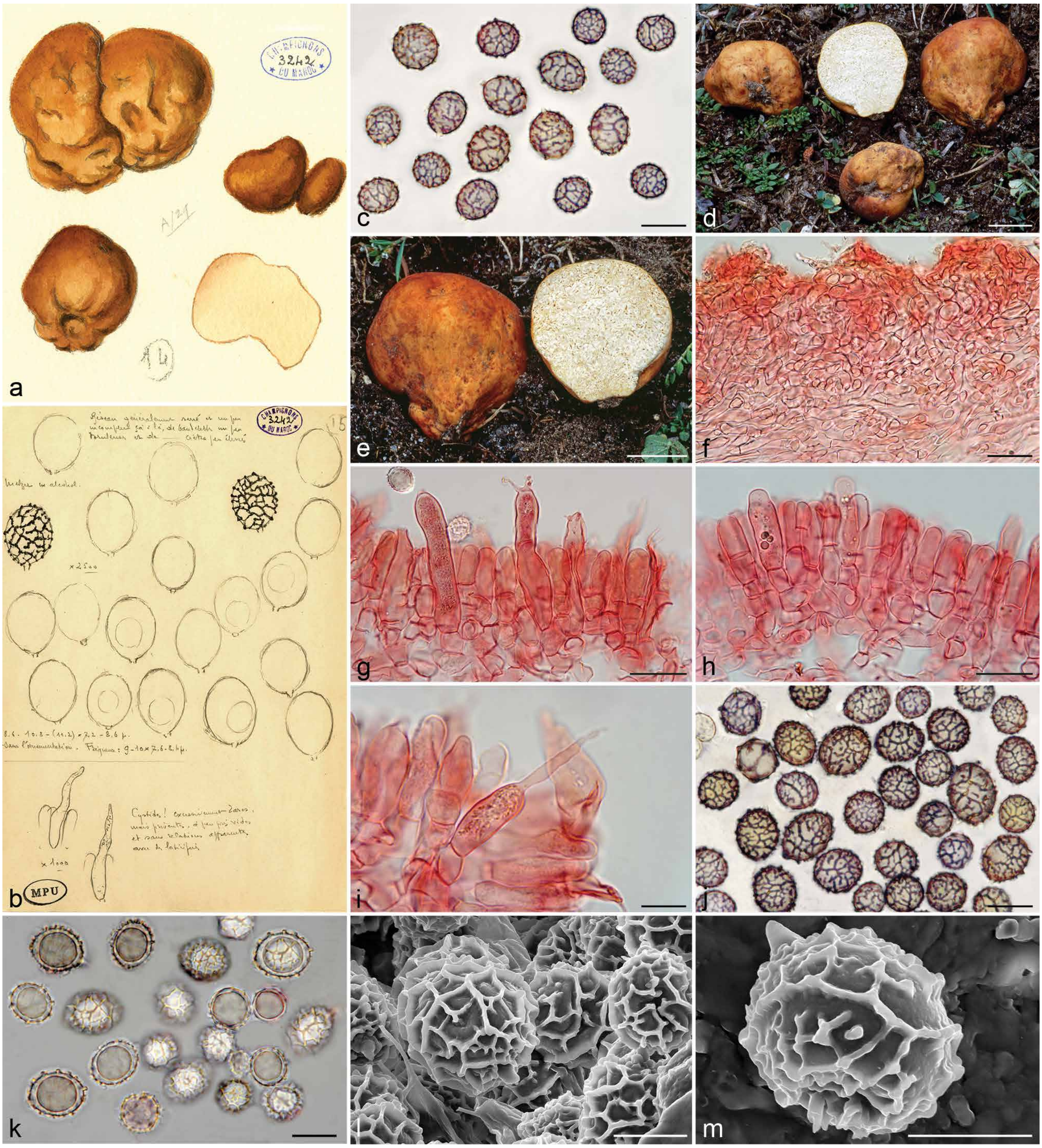

Fig. 8 *Lactarius josserandii*. a–b. Reproduction of Malençon's plates of *Zelleromyces josserandii* corresponding to the sample n° 3242 conserved in the herbarium of Montpellier (MPU C03565, ©Université de Montpellier-Herbier). — c. MPU 0310529 (holotype of *Z. josserandii*). Spores in Melzer. — d–m. JMV800621. d–e. Basidiomata; f. pileipellis and context; g–h. basidia, basidioles, paraphysoid cells and subhymenium; i. cystidiole of an external immature locule; j. spores in Melzer; k. spores in ammonia; l–m. SEM images of spores. — Scale bars: c, i–k = 10 µm; d–e = 1 cm; f–h = 20 µm; l–m = 5 µm. — Photos: c, f–k. J.M. Vidal; d–e. F. García; l–m. UdG.

homoiomerous, formed by septate, tortuous hyphae 2–7 µm diam, some of them inflated, but lacking sphaerocytes, with abundant laticifera 2–8 µm diam, and some thromboplera 2–6 µm diam. *Pileipellis* and *context* 175–300 µm thick; pileipellis 55–65 µm thick, arranged in an oedotrichoderm resembling that of *L. fulvissimus*, formed by: 1) a suprapellis of cylindrical and sinuous septate hairs, soon collapsing in a brown mass; and 2) a subpellis composed of prismatic hyphae 8–10 µm diam. *Pileal context* a prosenchyma, with the same composition of the hymenophoral trama, with plenty of laticifera and some thromboplera.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous, growing under needles in montane conifer forests of *Pinus* and *Cedrus*, on siliceous soil, frequently in the vicinity of *Lactarius aurantiacus*. Autumn. Occurring in submediterranean regions, in Morocco, France and Spain, between 1250–1900 m altitude.

Material studied. Morocco, Taza-Al Hoceima-Taounate, Ketama, Llano Amarillo, 'Rif cristallin, 1600 m, parmi les jeunes cèdres mêlés de *Cistus laurifolius*', 16 Nov. 1957, *G. Malençon* (MPU 0310528, herb. G. Malençon 3242, paratype of *Z. josserandii*); ibid., 'a peu de distance de la 1er (env. 300 m)', 18 Nov. 1957, *G. Malençon* (MPU 0310529, herb. G. Malençon 3242 Bis, holotype of *Z. josserandii*); ibid., 'sous les cèdres', 29-X-1972, *R. Bertault* (MPU 0310527, herb. G. Malençon 7252, paratype of *Z. josserandii*). – Spain, Castilla and Leon, Segovia, Navafría, Puerto de Navafría, El Nevero, Sierra de Guadarrama, 1800–1900 m, under *Pinus sylvestris*, on siliceous soil, 6 Oct. 2006, *F. García* (BCN JMV800621)*; Community of Madrid, Cercedilla, Dehesas, under *Pinus sylvestris*, on siliceous soil, 27 Nov. 1996, *F.D. Calonge* & *C. García-Ruz* (MA-Fungi 37498, holotype of *Z. hispanicus*); ibid., 23 Nov. 1996, *J. Daniel* & *J.M. Santos* (MA-Fungi 37497, paratype of *Z. hispanicus*); ibid., 16 Nov. 1997, *R. Cifuentes* (MA-Fungi 38311, paratype of *Z. hispanicus*).

Notes — Malençon (1975) proposed the name *Zelleromyces josserandii* for an orange hypogeous fungus, bleeding white latex when cut, and displaying reticulate spores, found in 1957 and 1972 in Morocco and France (five collections made by G. Malençon in the Rif mountains, one found in the same area by R. Bertault, and two more collections found by R. Ruffier-Lanche and J. Mornand in the Aitone forest in Corsica under *Pinus nigra* subsp. *laricio* at 1250 m altitude). Later on, Calonge & Pegler (1998) studied several collections found under *Pinus sylvestris* at Sierra de Guadarrama (Madrid, Spain), with morphological features closely resembling those of *Z. josserandii*, which they named *Z. hispanicus*.

Vidal (2004a) proposed a synonymy between *Z. josserandii* and *Z. hispanicus* after observing identical macro- and microscopical features in the type specimens, but all attempts to sequence the type material of *Z. josserandii* have been unsuccessful. Calonge & Pegler (1998) first suggested a close relationship between *Z. hispanicus* and *Lactarius aurantiacus*, and later Calonge & Martín (2000, 2003) highlighted the slight genetic differences (37/634 bp) between ITS sequences of these species, both belonging to *Lactarius* subg. *Russularia*. However, phylogenetic analyses conducted by Verbeken et al. (2014b), as well as present results, suggest a closer affinity to *L. borzianus* and *L. fulvissimus*, which share a similar oedotrichodermal pileipellis.

Lactarius populicola J.M. Vidal, Konstantin., Setkos & Slavova, *sp. nov.* — MycoBank MB828497; Fig. 9

Basidiomata similar to *L. stephensii*, 1–4 cm wide, angiocarpic, sessile, subglobose or tuberiform, lactescent, smooth, at first pale orange, then reddish brown to violet brown. *Hymenophore* loculate, deeply coloured, reddish yellow to orange red. *Columella* absent or inconspicuous. *Latex* watery-white to white, of mild taste. *Odour* fruity, of pears. Microscopy as in *L. stephensii*, except the spores which are subglobose to broadly ellipsoid, measuring 13–15 × 11–13 µm in size, covered by strongly amyloid, conical or tooth-like warts, 1–2 µm long. Hypogeous or semi-hypogeous under *Populus alba*.

Etymology. From Latin, *populus* = poplar, and *-cola* = inhabitant of, who lives in, in reference to its association to poplars (*Populus*).

Holotype. Greece, Central Macedonia, Serres, Sidirokastro, 50 m, under *Populus alba*, 13 Mar. 2010, *G. Setkos* (BCN JMV800648)*; isotype in herb. pers. G. Konstantinidis (GK4831).

Basidiomata 1–4 cm wide, angiocarpic, subglobose or irregular, lobate, reniform, tuberiform, sessile or with a minute sterile base, attached to soil by thin mycelial threads. *Pileus* smooth, viscid, persistent, open basally and exposing the locules in old specimens; at first pale orange (6A3), brownish orange (7C6) or orange-red (8A6) and finally reddish brown (8D6–9E5) to violet-brown (10E6). *Hymenophore* loculate, labyrinthoid, deeply coloured, reddish yellow (4A7), orange (5A6–6B7) to reddish orange (7A6), or orange-red (8A6–B6); locules very small, 0.2–0.5 × 0.02–0.1 mm (3–4 per mm), irregularly arranged, elongated, sinuous; septa 250–500 µm thick; fresh spore mass in locules pale yellow (4A4–A5); pale orange (5A3) to brownish orange (6C5) in exsiccata. *Columella* absent or inconspicuous. *Latex* watery-white in immature basidiomata and white in mature basidiomata, of mild taste. *Odour* strong, aromatic and fruity, reminiscent of pears.

Spores 13–15 × 11–13 µm, Q = 1.07–1.2, subglobose to broadly ellipsoid, orthotropic, echinated, unigutulate, deep orange; warts deeply amyloid, robust, 1–2 µm long, conical or tooth-like, usually curved, with some verrucae among them; suprahilar plage absent; hilar appendix minute, usually united to a fragment of sterigma up to 4 × 2.5 µm. *Basidia* 1-spored, 35–50 × 8–10 µm, cylindrical, straight or sinuous, soon collapsed; initially hyaline and filled with oleiferous guttules, then of dark orange colour; sterigmata central or eccentric, 2–4 µm long. *Basidioles* similar to basidia. *Macrocystidia* and *cystidioles* absent. *Paraphysoid cells* 20–30 × 6–8 µm, usually with 1–2 septa, cylindrical or with a clavate apex. *Pseudocystidia* not observed. *Subhymenium* ramose, formed by septate, cylindrical hyphae, 10–30 × 3–9 µm, perpendicular to the tramal hyphae. *Hymenophoral trama* 60–90 µm thick, homoiomerous, formed by hyaline, thin-walled, subgelatinized hyphae, 3–6 µm diam, finally dark yellow, completely gelatinized, with a prosenchymatous aspect; laticifera abundant, 8–10 µm diam, with thinner branches 3–5 µm diam; sometimes penetrating into the hymenium and terminating as pseudocystidia; thromboplera yellow, 3–5 µm diam. *Pileipellis* and *context* 300–500 µm thick; pileipellis 50–90 µm thick composed of: 1) a trichodermal suprapellis of septate hairs and dermatocystidia, 20–40 × 2.5–4 µm, straight to sinuous, rounded to acute at the apex, with yellow granular content, that soon collapses in a brown granular mass; and 2) a prosenchymatous subpellis 20–50 µm thick, of densely entangled hyphae 1.5–3 µm diam. *Pileal context* an ixocutis 250–400 µm thick, made by subgelatinized, entangled hyphae 2–4 µm diam, crossed by some thromboplera and abundant laticifera.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous in riparian forests under *Populus*, on alluvial soils. Spring to autumn. Distributed in temperate and Mediterranean regions, from Western to Southeastern Europe, from sea level up to 1000 m altitude.

Additional material studied. Bulgaria, Stara Zagora, Parvomai, Mirovo, 130 m, in a riparian forest under *Populus alba* and *Fraxinus ornus*, 12 Dec. 2015, *T. Chokova* MSL1629F6516 (SOMF 29973, duplicate BCN JMV800687). – France, Franche-Comté, Jura, Hérimoncourt, Aug. 1892, *L. Quélet* as '*Hydnangium galatheium*' (UPS F013405). – Greece, Central Macedonia, Serres, Sidirokastro, 50 m, under *Populus alba*, 24 Apr. 2010, *G. Setkos* (GK4969, duplicate BCN JMV800649); West Macedonia, Kastoria, Maniakoi, 650 m, under *Populus alba*, *Corylus avellana* and *Alnus glutinosa*, 7 Oct. 2010, *G. Setkos* (GK5223, duplicate BCN JMV800650); ibid., 25 Nov. 2011, *G. Setkos* (GK5904, duplicate BCN JMV800651). – Italy, Emilia-Romagna, Reggio Emilia, Febbio, 1050 m, under *Populus alba*, 30 Oct. 1991, *A. Montecchi* as '*A. borziana*' (AM1042, duplicate BCN JMV800036); Tuscany, Lucca, Montuolo, 15 m, under *Populus alba*, 1 Nov. 1993, *G. Bernardini* & *L. Gori* as '*A. stephensii*' (ELG931101-2, duplicate BCN JMV800171); ibid., 28 Nov. 1993, *G. Bernardini* & *L. Gori* as '*A. stephensii*' (ELG931128-2, duplicate BCN JMV800169); Lucca, Nozzano Castello, 20 m, under *Populus alba*,

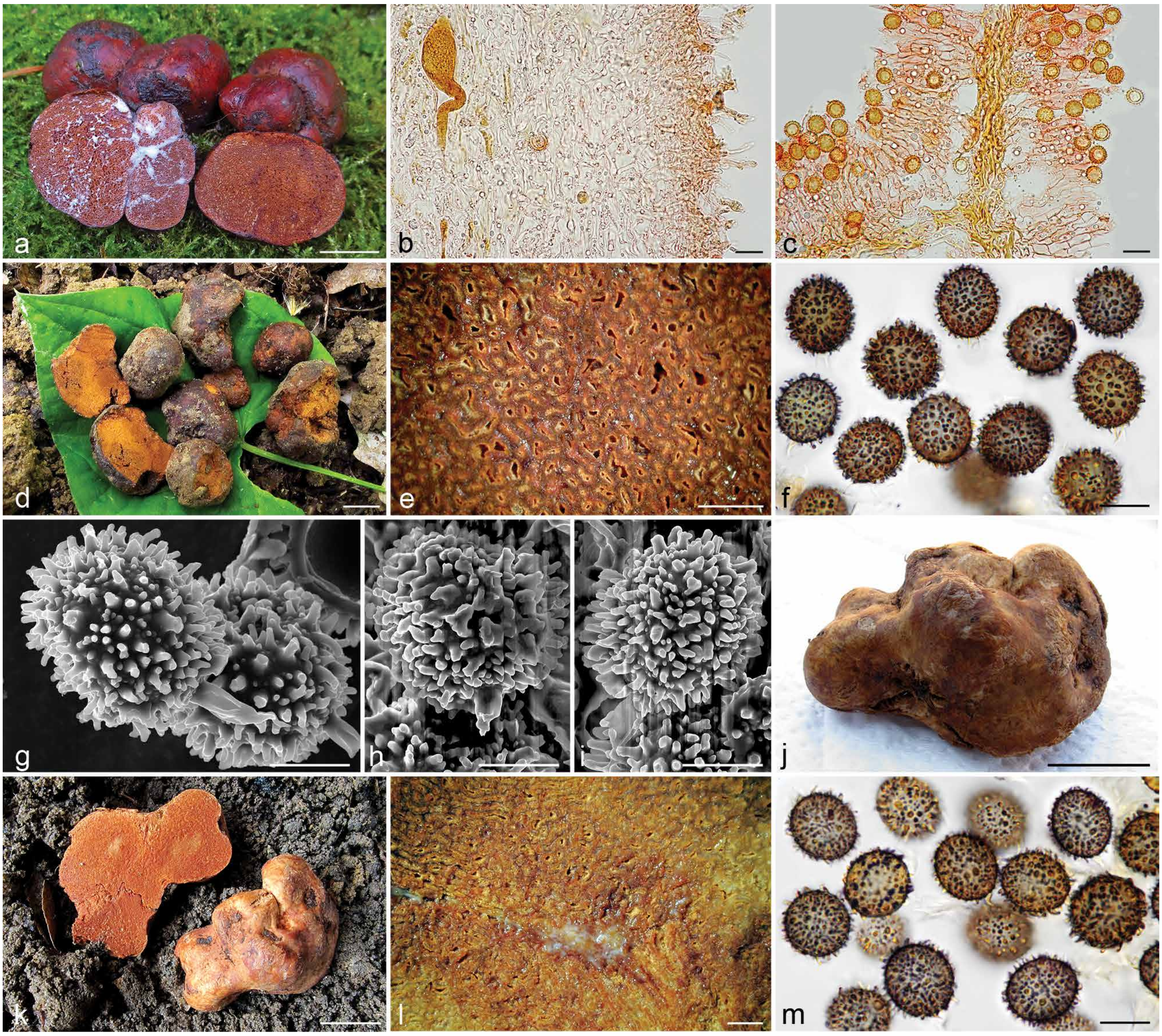

Fig. 9 *Lactarius populicola*. a–c. MSL1629F6516. a. Mature basidiomata and cut of hymenophore bleeding white latex; b. pileipellis and context; c. section of a septum with gelatinized hymenophoral trama. — d. GK4969. Old basidiomata. — e–i. GK4831 (BCN JMV800648, holotype). e. Locules of hymenophore; f. spores in Melzer; g–i. SEM images of spores. — j–l. GK5904. j–k. Young basidiomata; l. cut of hymenophore bleeding watery-white latex. — m. UPS F013405, herb. L. Quélet (as '*Hydnangium galatheium*'). Spores in Melzer. — Scale bars: a, d, j–k = 1 cm; b–c = 20 µm; e, l = 1 mm; f, m = 10 µm; g–i = 5 µm. — Photos: a. M. Slavova; b–c, f, m. J.M. Vidal; d–e, j–l. G. Konstantinidis; g–i. UdG.

31 July 1993, *G. Bernardini* & *L. Gori* as '*A. stephensii*' (ELG930731-1, duplicate BCN JMV800170).

Notes — *Lactarius populicola* has been confused with *L. stephensii* (Nuytinck et al. 2003, Gori 2005) because of their multiple similarities. Microscopically, *L. populicola* has the same pileal and hymenial structure, and identical spore shape with *L. stephensii*, but spores are intensely amyloid and ornamented with robust conical or tooth-like warts, while *L. stephensii* has weakly amyloid spiny spores. Macroscopically, *L. populicola* is distinguished by the violaceous coloration of basidiomata in mature specimens and smaller locules in the hymenophore. While *L. stephensii* is probably associated with *Fagaceae* and *Betulaceae* hosts, *L. populicola* is linked to *Salicaceae* plants.

Genetically, *L. populicola* is a monophyletic taxon significantly related with *L. stephensii*, both forming a significantly monophyletic clade with a third species, *L. soehneri*. These angiocarpic species were also related (PP 1.00, BP 88) with a clade formed by samples identified as *L. evosmus* and *L. zonarius*. The only sequenced specimens of *L. populicola* are by now the type proposed here, and a sample from Belgium (RW2930 GENT) treated as *L. stephensii* by Nuytinck et al. (2003).

Lactarius soehneri (Zeller & C.W. Dodge) J.M. Vidal & G. Moreno, *comb. nov.* — MycoBank MB828498; Fig. 10

Basionym. *Hydnangium soehneri* Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 22: 372. 1935.

Synonyms. *Octaviania soehneri* (Zeller & C.W. Dodge) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 200. 1958.

Martellia soehneri (Zeller & C.W. Dodge) Singer & A.H. Sm., Mem. Torrey Bot. Club 21, 3: 31. 1960.

Zelleromyces soehneri (Zeller & C.W. Dodge) Trappe et al., Mycotaxon 81: 205. 2002.

Hydnangium soehneri var. *ettenbergii* Soehner, Z. Pilzk., N.F. 20, 3–4: 110. 1941 (nom. inval., Art. 39.1).

Basidiomata 1–2 cm wide, angiocarpic, subglobose or irregular, reniform, tuberiform, sessile; sterile base not observed. *Pileus* smooth, viscid, at first pale orange (5A3), then greyish red (9B4) and finally reddish brown (9D4) to violet-brown (10E7), basally open and alveolate in old specimens. *Hymenophore* loculate, labyrinthoid, initially pinkish white (7A2), then deeply coloured, pale red (9A3), dull red (9B4) and finally dull violet (15D4); locules large, 0.4–1.5 × 0.1–0.2 mm (1–2 per mm), irregularly arranged, elongated, sinuous, empty; septa 250–500 µm thick; fresh spore mass in locules greyish ruby (12D6);

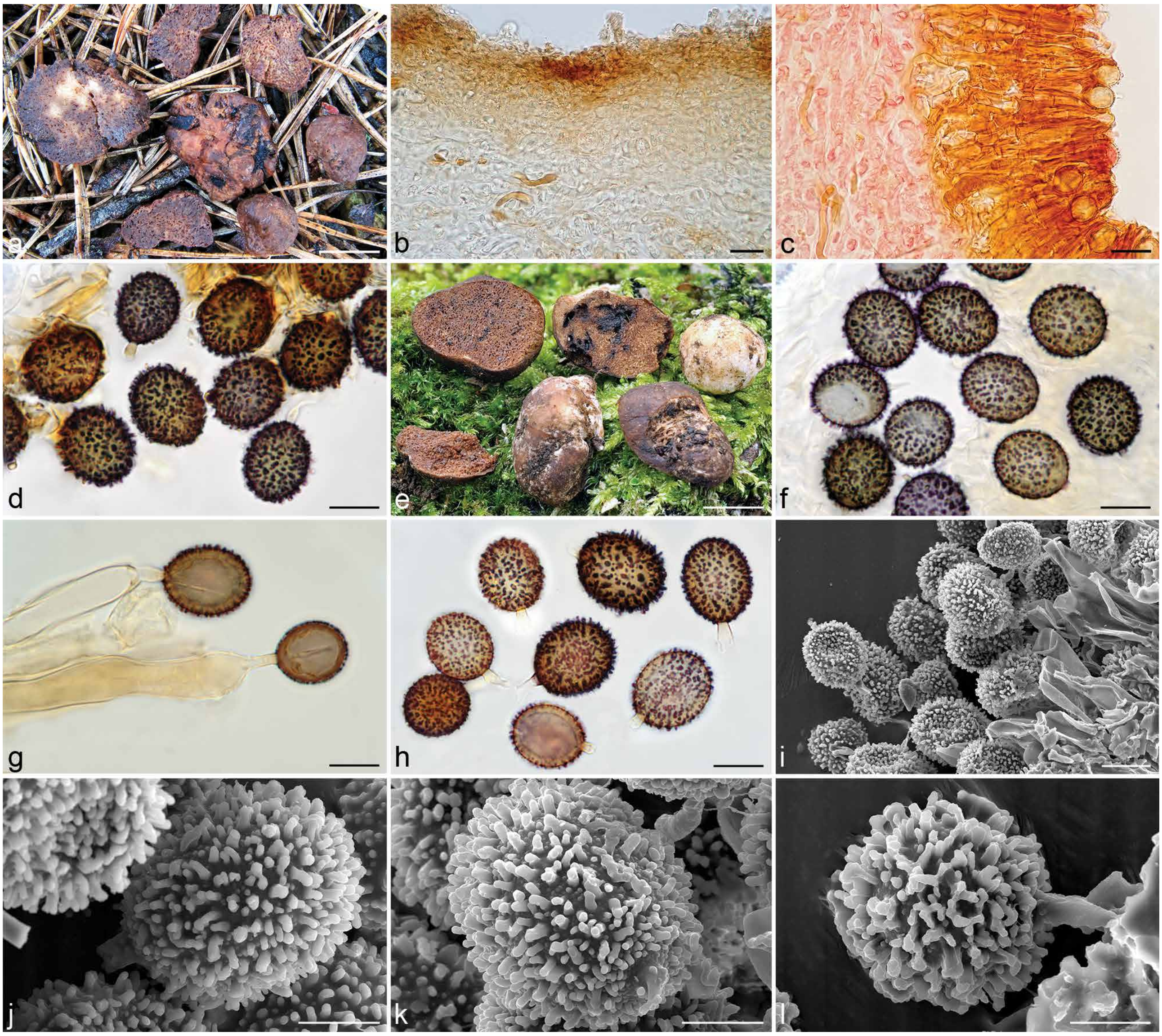

Fig. 10 *Lactarius soehneri*. a. AH 39272. Basidiomata. — b–d. AH 46013. b. Pileipellis and context; c. hymenium and trama; d. spores in Melzer. — e. IC21091207. Basidiomata. — f. M, herb. E. Soehner 1041 (holotype of *Hydnangium soehneri* var. *ettenbergii*). Spores in Melzer. — g–k. M, herb. E. Soehner 1081 (holotype of *Hydnangium soehneri*). g. Basidia; h. spores in Melzer; i–k. SEM images of spores. — l. JMV800677. SEM image of a spore. — Scale bars: a, e = 1 cm; b–c = 20 µm; d, f–i = 10 µm; j–l = 5 µm. — Photos: a. G. Moreno; b–d, f–h. J.M. Vidal; e. C. Lavoise; i–l. UdG.

brownish orange (6C5) to brown (6D7) in exsiccata. *Columella* absent. *Latex* watery, scant or absent. *Odour* fruity. *Taste* earthy. *Spores* 14–18.5 × 12–15 µm, Q = 1.1–1.3, broadly ellipsoid to ellipsoid, orthotropic, echinate, unigutulate, pale orange; warts deeply amyloid, dense, 1–2 µm long, cylindrical, usually curved, sometimes fused forming short ridges, with numerous verrucae among them; suprahilar plage absent; hilar appendix 1.5–3 × 2 µm, usually attached to a fragment of sterigma. *Basidia* 1-spored, 50–70 × 6–10 µm, cylindrical, straight or sinuous, soon collapsed, initially hyaline, with a good number of oil drops inside, later filled with a dark orange substance that finally saturates all the hymenium; sterigmata 3–6 µm long. *Basidioles* similar to basidia. *Macrocystidia* and *cystidioles* absent. *Paraphysoid cells* 30–60 × 2.5–7 µm, 1–3-septate, difficult to observe. *Pseudocystidia* not observed. *Subhymenium* ramose. *Hymenophoral trama* 60–90 µm thick, homoiomerous, devoid of sphaerocytes, formed by hyaline, thin-walled, subgelatinized hyphae, 2–5 µm diam, displaying several yellow-brown thromboplera, 2–5 µm diam, and some laticifera, 3–10 µm diam, which sometimes penetrate into the hymenium terminating as pseudocystidia. *Pileipellis* and *context* 125–250 µm thick; pileipellis 70–150 µm composed of: 1) a trichodermal suprapellis of similar structure to that in *L. stephensii*, constituted by fragile, septate hairs and dermatocystidia, 20–30 × 3–6 µm, rounded to acute at the apex, sometimes mucronate, with dark yellow granular contents and walls up to 0.5 µm, soon collapsing into a brown granular mass formed by remnants of dermatocystidia and yellow granules; and 2) a subpellis 50–80 µm thick of prosenchymatous aspect, composed of subgelatinized hyphae 2–5 µm diam. *Pileal context* an ixocutis 60–120 µm thick, composed of subgelatinized, entangled hyphae, 3–6 µm diam, intersepted by abundant thromboplera and some laticifera.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous in montane forests of conifers (*Abies*, *Pinus*) or under broadleaved trees (*Corylus*, *Quercus*), on calcareous soil. Spring to autumn. Distributed in temperate regions of Germany, Italy and Spain, between 300–1400 m altitude.

Material studied. Germany, Bavaria, 'Ettenberg bei Berchtesgaden', 1100 m, under *Abies alba*, Aug. 1925, *E. Soehner* (M, herb. E. Soehner 1041, holotype of *H. soehneri* var. *ettenbergii*); 'Pupplinger Heide bei Wolfratshausen', 19 Aug. 1919, *E. Soehner* as '*Hydnangium monosporum*' (M, herb. E. Soehner 1374); 'Pupplinger Heide bei Wolfratshausen, Führenwald', 21 Oct. 1928, *E. Soehner* as '*Hydnangium carneum*' (M, herb. E. Soehner 1081, holotype of *H. soehneri*; FH, herb. C.W. Dodge, isotype; NY, herb. S.M. Zeller, isotype). – Italy, Lombardy, Bergamo, San Pellegrino Terme, 350 m, under *Corylus avellana*, on calcareous soil, Sept. 2016, *M. Berbenni*, comm. M. Morara

(BCN JMV800677); Umbria, Perugia, Gubbio, 340 m, under *Quercus* sp. and *Corylus avellana*, in a truffle plantation of *Tuber melanosporum*, on calcareous soil, 21 Sept. 2012, *A. Paz* & *C. Lavoise* (BCN IC21091207). – Spain, Castilla-La Mancha, Guadalajara, Cantalojas, 1300–1400 m, in humus of *Pinus sylvestris*, on calcareous soil, 3 Apr. 2011, *M.A. Sanz* (AH 39272)*; ibid., 9 Apr. 2011, *M.A. Sanz* (AH 46013, duplicate BCN JMV800633)*.

Notes — *Lactarius soehneri* was considered a macrosporic form of *L. stephensii* by several authors (Mader & Mader 1992, Vidal 2004a), because of the very similar microscopic features, especially the presence of laticiferous hyphae and monosporic basidia documented in the type collection by Vidal (2004a). However, *L. soehneri* differs from *L. stephensii* and *L. populicola* by its scarce, watery latex, by the larger hymenophoral locules and by the ellipsoid spores up to 18.5 × 15 μm. The dark orange substance of hymenium that impregnates basidia and spores is another differentiating feature. While *L. stephensii* and *L. populicola* occur exclusively under broadleaved trees, *L. soehneri* also occurs under conifers.

Genetically, *L. soehneri* is significantly related with *L. populicola* and *L. stephensii*, and to a lesser extent to the gymnocarpic species *L. evosmus* and *L. zonarius*, and probably belongs to *Lactarius* subg. *Lactarius*. Unfortunately, no samples from the region where the type was found (Bavaria, Germany) or the same habitat (*Abies* or *Picea* forests) could be analyzed, and therefore the identification made here relies entirely on morphological similarities between the newly collected samples and the type specimen.

Lactarius stephensii (Berk.) Verbeken & Walleyn, Belg. J. Bot. 136, 2: 151. 2003 — Fig. 11

Basionym. *Hydnangium stephensii* Berk., Ann. Mag. Nat. Hist., Ser. I, 13: 352. 1844.

Synonyms. *Octaviania stephensii* (Berk.) Tul. & C. Tul., Fung. Hypog.: 78. 1851.

Arcangeliella stephensii (Berk.) Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 18: 463. 1931.

Zelleromyces stephensii (Berk.) A.H. Sm., Mycologia 54: 635. 1962.

Martellia stephensii (Berk.) K. Mader & A. Mader, Österr. Z. Pilzk. 1: 4. 1992.

Hydnangium galatheium Quél., Enchir. Fung.: 247. 1886 ('*galathejum*').

Octaviania galatheia (Quél.) De Toni in P. A. Saccardo, Syll. Fung. 7, 1: 491. 1888 ('*galatheja*').

Basidiomata 1–3.5 cm wide, angiocarpic, subglobose to tuberiform, lobate, sessile, sometimes with a minute sterile base; basally closed, or open and radially alveolate in old specimens. *Pileus* smooth, viscid, at fist white, then maize yellow (4A6), oxide yellow (5C7) to carrod red (6B7), finally reddish brown (7D8–E8), with the same colour as *L. rufus*. *Hymenophore* loculate, labyrinthoid, initially white or ochraceous, acquiring a reddish brown colour like the pileus; locules small, 0.3–1.5 × 0.1–0.5 mm (2–3 per mm), irregularly arranged, elongated, sinuous; septa 150–300 μm thick; fresh spore mass in locules greyish orange (5B5). *Columella* absent or inconspicuous. *Latex* scant and hyaline, changing to citrine yellow in young specimens, white, abundant, and almost immutable in old basidiomata (orange in contact with KOH), with a bitter and more or less hot taste as in *L. chrysorrheus*. *Odour* mild in young basidiomata, but intensely fruity when mature.

Spores (11.5–)12–14.5(–15) × (10–)11–13 μm, Q = 1.1–1.2, subglobose to broadly ellipsoid, orthotropic, echinate; warts 0.5–2 μm high, isolated, inamyloid or weakly amyloid; suprahilar plage

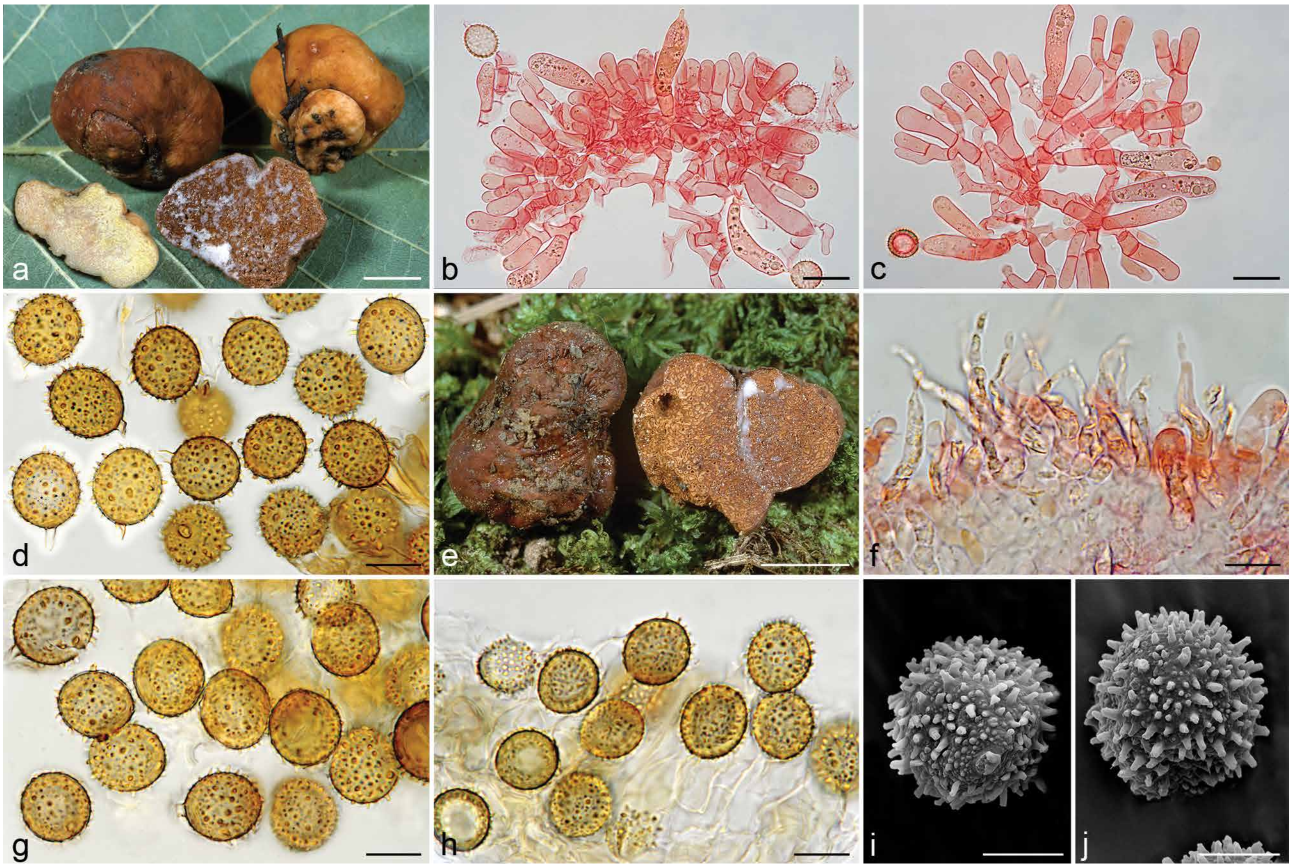

Fig. 11 *Lactarius stephensii*. a–d. JMV970830-1. a. Basidiomata and hymenophore of immature and mature specimens; b–c. hymenium and ramose subhymenium; d. weakly amyloid spores. — e. JMV951012-1. Basidiomata. — f. JMV20010609-1. Pileipellis. — g. K(M)69330 (lectotype of *Hydnangium stephensii*). Spores in Melzer. — h–j. KRA F-2014-147. h. Spores in Melzer; i–j. SEM images of spores. — Scale bars: a, e = 1 cm; b–c, f = 20 μm; d, g–h = 10 μm; i–j = 5 μm. — Photos: a–h. J.M. Vidal; i–j. P. Mleczko, UJ.

absent; hilar appendix inconspicuous, usually united to a fragment of sterigma up to 4 µm long. *Basidia* 1-spored, 35–70 × 6–10 µm, cylindrical, straight to sinuose, soon collapsed; initially hyaline, with a good number of oil drops inside, that become filled with a dark orange substance; sterigmata central or lateral, 4–6 µm long. *Macrocystidia* absent. *Cystidioles* only present in sterile locules, of the same shape and size of dermatocystidia. *Paraphysoid cells* plenty, 20–60 × 6–8 µm, cylindrical or clavate, usually with 1–3 septa. *Pseudocystidia* occasionally observed. *Subhymenium* ramose, formed by cylindrical hyphae 10–30 × 3–9 µm, perpendicular to the tramal hyphae. *Hymenophoral trama* homoiomerous, formed by subgelatinized hyphae 2–5 µm diam, with abundant laticifera. *Pileipellis* and *context* 250–500 µm thick; suprapellis a trichoderm formed by yellow, straight to sinuous, septate dermatocystidia 20–60 × 3–6 µm, with rounded to acute, sometimes mucronate apex, that soon collapses in a brown granular mass. *Pileal context* formed by intricate gelatinized hyphae 2–6 µm diam, crossed by some thromboplera and abundant laticifera 3–10(–12.5) µm diam.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous among plant debris, in montane woods of *Corylus*, *Carpinus*, *Fagus*, *Quercus* accompanied by *Acer*, *Buxus*, *Cornus*, *Fraxinus*, *Sambucus*, *Tilia*, *Ulmus*, on calcareous soil. Summer to autumn. Widely distributed in temperate and submediterranean regions, from almost sea level in the British Isles to 1400 m altitude in Southern Europe.

Material studied. Czech Republic, Central Bohemia, Karlštejn, in a leafy forest, under *Fagus sylvatica* and *Carpinus*, 10 July 1949, *V. Vacek* as '*Hydnangium monosporum*' (PRM 685987); ibid., in a leafy forest, under *Quercus*, *Carpinus*, *Acer campester* and *Tilia*, 17 July 1949, *V. Vacek* as '*Hydnangium monosporum*' (PRM 619116); South Moravia, Dolní Věstonice, Děvičky, in *Acereto-Carpineto*, 28 Aug. 1955, *K. Kříž*, det. M. Svrček as *O. stephensii* (PRM 719216); Veverská Bítýška, Krnovec, under *Carpinus betulus* and *Cornus mas*, 10 Aug. 1955, *K. Kříž*, det. M. Svrček as *O. stephensii* (PRM 719217); Žarošice, Aug. 1937, *V. Vacek* as '*Hydnangium carneum*' (PRM 154169, coll. J. Velenovský); ibid., in a leafy forest, 31 Aug. 1948, *Vl. Vacek* & *V. Vacek* as *H. stephensii* (PRM 685988); ibid., in a leafy forest, under *Tilia*, *Quercus* and *Larix*, 25 Aug. 1949, *V. Vacek* as *H. galatheium* (PRM 619118); ibid., in a leafy forest, under *Tilia*, *Quercus* and *Larix*, 25 Aug. 1949, *V. Vacek* as *H. galatheium* (PRM 685993); Ždánský les, near Žarošice, in a leafy forest, 31 Aug. 1950, *V. Vacek* as *H. galatheium* (PRM 685990); ibid., in a leafy forest, under *Tilia*, *Quercus* and *Fraxinus*, 9 Sept. 1950, *V. Vacek* as *H. galatheium* (PRM 685992); Zdravá Voda, near Žarošice, in a leafy forest, under *Tilia*, *Carpinus*, *Fagus* and *Cornus mas*, 24 Aug. 1949, *V. Vacek* as *H. galatheium* (PRM 685996); ibid., in a leafy forest, under *Carpinus*, *Quercus* and *Tilia*, 29 Aug. 1949, *V. Vacek* as *H. galatheium* (PRM 685994). – Hungary, Central Hungary, Budapest, Normafa, under *Tilia* sp., 25 Aug. 1995, *I. Király* (BCN JMV800071). – Italy, Lombardy, Bergamo, San Pellegrino Terme, 350 m, under *Corylus avellana*, on calcareous soil, 30 Nov. 2016, *M. Berbenni*, comm. M. Morara (BCN IC30111603). – Poland, Silesia, Pogórze Śląskie region, Machowa mountain, Western Carpathians, 15 June 2014, *R. Rutkowski* (KRA F-2014-147, duplicate BCN JMV800668)*. – Spain, Asturias, Somiedo, Parque Natural de Somiedo, under *Corylus avellana*, 8 Apr. 2009, *A. Paz* (BCN IC08040913); Catalonia, Girona, Albanyà, Serra de Corsavell, Can Padern, 800 m, under *Corylus avellana*, on calcareous soil, 9 June 2001, *J.M. Vidal* as *A. stephensii* (BCN JMV20010609-1)*; Girona, La Vall de Bianya, Vall del Bac, Bac de Mariner, 900 m, under *Corylus avellana*, *Fagus sylvatica*, *Quercus humilis* and *Buxus sempervirens*, on calcareous soil, 30 Aug. 1997, *J.M. Vidal* as *A. stephensii* (BCN JMV970830-1); Girona, Montagut, Sant Miquel de Pera, 700 m, under *Corylus avellana*, *Quercus humilis*, *Populus tremula* and *Buxus sempervirens*, on calcareous soil, 15 Oct. 1995, *J.M. Vidal* as *A. stephensii* (BCN JMV951012-1). – United Kingdom, England, Somerset, Clifton, near Bristol, Leigh Woods, 6 Aug. 1843, *C.E. Broome* (K(M)69330, lectotype of *H. stephensii*); ibid., Bristol, 1844, *H.O. Stephens* (K(M)69331, original material of *H. stephensii*); ibid., Bristol, sine dat., ex M.J. Berkeley (PRM 719218, herb. A.C.J. Corda, original material of *H. stephensii*).

Notes — *Hydnangium stephensii* is a lactescent angiocarpic fungus described by Berkeley (1844) from Leigh Woods, North Somerset (UK), which was recombined in the genus *Zelleromyces* by Smith (1962) based on the presence of amyloid spores and laticifera. It is macroscopically characterized by maize yellow to reddish brown basidiomata bleeding white latex (scant and hyaline when young) that turns yellow in contact with air, and microscopically, by its monosporic basidia and warty subglobose to broadly ellipsoid spores, which are inamyloid to weakly amyloid (Vidal 2004a, Fraiture & Derboven 2009, all as *A. stephensii*).

Nuytinck et al. (2003) suggested *L. stephensii* belongs to *Lactarius* subg. *Lactarius*, and considered it a prioritary synonym of *Hydnangium monosporum*, while Vidal (2004a) considered *L. stephensii* (treated as *Arcangeliella stephensii*) to be a prioritary synonym of *Hydnangium soehneri*. Following careful studying of the types and other collections in the present study, *L. stephensii*, *H. soehneri* and *H. monosporum* are here considered to be three distinct species. *Hydnangium monosporum* differs by its perfectly rounded and pink-coloured spores when mature, and *H. soehneri* by its bigger, strongly amyloid and ellipsoid spores. It was not possible to locate original material of *H. galatheium* (Quélet 1875 as '*stephensii*', 1886 as '*galathejum*'), but only a collection made later by Quélet in August 1892 at Hérimoncourt (UPS F013405), which we have identified as *L. populicola*, and another collection without date from Abbévillers (UPS F013936), which we have identified as *Russula monospora*. However, based on descriptions and illustrations provided by Quélet (1875: 446, pl. I, f. 9, as *H. stephensii*) and (1886: 247, as *H. galatheium*), we consider, like Patouillard (1910, 1914) and Zeller & Dodge (1937), *H. galatheium* to be a synonym of *L. stephensii*. The only genetic sequence available in GenBank before the present work from *L. stephensii*, was an ITS rDNA sequence of K(M)64067 specimen (Brock et al. 2009), collected by Brian Spooner in 1999 at North Somerset (UK), probably close to the locality where the type was found. This sequence clearly differs from that produced from specimen RW2930 (GENT) by Nuytinck et al. (2003), which is here considered to represent *L. populicola*.

Lactarius subgiennensis Loizides, J.M. Vidal & P. Alvarado, *sp. nov.* — MycoBank MB828499; Fig. 12

Basidiomata 0.5–2.5 cm wide, angiocarpic, sessile, globose to subglobose or lobate, lactescent, scrobiculate-porate, ivory white. *Hymenophore* loculate, whitish to faintly pinkish. *Latex* white. *Spores* 8.5–11 × 6.5–8 µm, ovoid, reticulated; reticulum 0.5–1 µm high, partially interrupted. *Basidia* 1-spored, 30–42 × 5–9 µm, lageniform-urticiform. *Cystidioles* 32–40 × 5–8 µm, lageniform-urticiform, present only in external locules. *Macrocystidia* absent. *Hymenophoral trama* homoiomerous, prosenchymatous, gelatinized, with laticifera 3–9 µm diam. *Suprapellis* formed by repent to semi-erect, septate hyphae 4–6 µm wide. *Pileal context* prosenchymatous, gelatinized, with abundant laticifera and some thromboplera 4–14 µm diam. Semi-hypogeous in *Cistus* maquis on the island of Cyprus.

Etymology. From Latin, *sub* = nearly, close to, and *-giennensis*, referring to its close phylogenetic and morphological affinity to *Lactarius giennensis.*

Holotype. Cyprus, Larnaca District, Kalavasos, 170 m, under *Cistus salviifolius* and *Cistus creticus*, 25 Nov. 2012, *M. Loizides* (BCN JMV800627)*; isotype in herb. pers. M. Loizides (ML211152E).

Basidiomata 0.5–2.5 cm wide, angiocarpic, irregularly globose, subglobose or tuberiform to weakly lobulate, occasionally more distinctly lobulate to almost irregularly-shaped, sessile, lactescent, loosely attached to the substrate by rhizoids. *Pileus* smooth, silky, subtomentose in parts, moderately to distinctly scrobiculate and porate, ivory white (5A2–6A2), often with ochraceous stains at maturity (5A4–A5), overripe basidiomata sometimes brownish buff (6C6); greyish orange (5B5) in exsiccata. *Hymenophore* loculate, labyrinthoid, white when young, at maturity becoming cream (6A2–A3) or pale ochraceous salmon (7A2); locules 0.5–1 mm long (1–3 per mm), polygonal to somewhat elongated, irregular, mostly empty. *Columella* absent or rudimentary, but thin, sterile veins frequently intersecting the hymenophore. *Latex* abundant in humid conditions, white, unchanging. *Odour* acidic, slightly fruity.

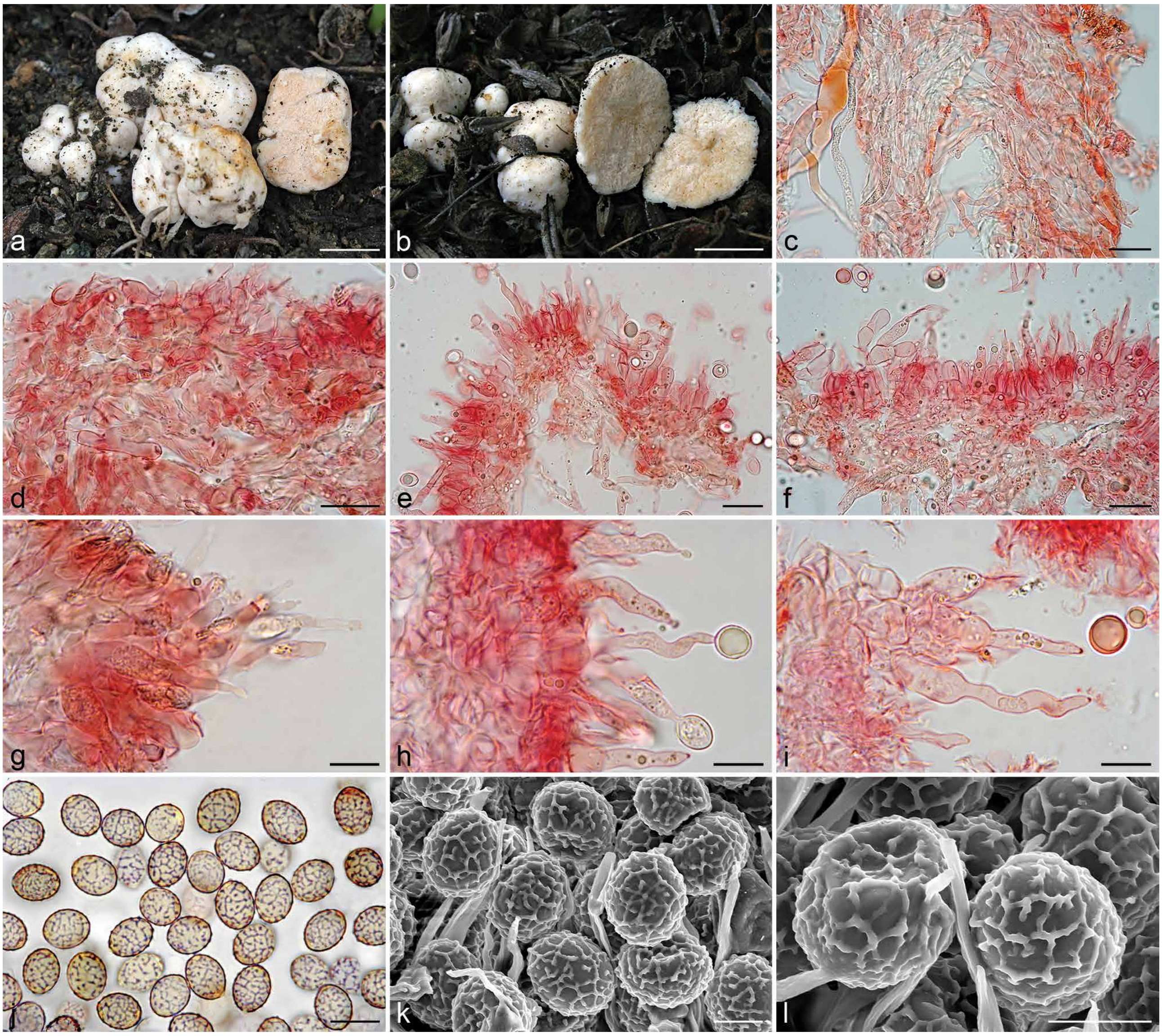

Fig. 12 *Lactarius subgiennensis*. a. ML61132Z. Basidiomata. — b. ML211192Z. Basidiomata. — c–l. ML211152E (BCN JMV800627, holotype). c. Pileipellis and context with one thromboplera and some laticifera; d. detail of the pileipellis; e–f. hymenium (basidia, basidioles and paraphysoid cells), subhymenium and hymenophoral trama with some laticifera; g. cystidioles of external immature locule; h. emerging necks of basidia; i. basidia; j. spores in Melzer; k–l. SEM images of spores. — Scale bars: a–b = 1 cm; c–f = 20 µm; g–j = 10 µm; k–l = 5 µm. — Photos: a–b. M. Loizides; c–j. J.M. Vidal; k–l. UdG.

Spores 8.5–11 × 6.5–8 µm, Q = 1.2–1.4, ovoid, orthotropic, reticulated; reticulum strongly amyloid, formed by well-developed crests projecting 0.5–1 µm in side view, partially interrupted to nearly complete at full maturity; hilar appendix indistinct or rudimentary. *Basidia* 1-spored (rarely 2-spored), 30–42 × 5–9 µm (neck included), lageniform-urticiform, promptly collapsed, with a long and sinuous neck measuring 20–25 × 2.5–4 µm, protruding the hymenium; sterigmata ± 1 µm long, inconspicuous. *Basidioles* 22–24 × 4.5–6 µm, ventricose-rostrate. *Macrocystidia* absent. *Cystidioles* 32–40 × 5–8 µm, lageniform-urticiform, observed only in immature external locules. *Paraphysoid cells* 9–25 × 5–8.5 µm, cylindrical to subclavate, entire or 1-septate. *Subhymenium* ramose to cellular, composed of chains of rounded, polygonal or irregularly elongated cells 5–10 µm diam. *Hymenophoral trama* 90–120 µm wide, homoiomerous, prosenchymatous, formed by intricate, tortuous, thin-walled hyphae 3–6 µm diam, with plenty of lipidic guttules, finally of pseudoparenchymatous aspect, moderately to strongly gelatinized, but without the presence of sphaerocytes; laticifera 3–9 µm diam, thick-walled, tortuous, often branching, sometimes forming projecting pseudocystidia. *Pileipellis* and *context* thin, 50–100 µm thick; pileipellis composed of: 1) an easily collapsable trichodermal suprapellis, comprised of terminal, septate hyphae 4–6 µm diam; and 2) a prosenchymatous subpellis of gelatinized, tightly packed, tortuous, septate hyphae 3–6 µm diam. *Pileal context* undifferentiated from the subpellis with abundant laticifera and some thromboplera 4–11 µm diam, locally enlarged up to 14 µm.

Habitat, Distribution & Season — Gregarious to caespitose, growing semi-hypogeously in thick litter, exclusively associated with *Cistus*, on siliceous soil. Autumn and winter. Xerophytic. So far restricted in the eastern Mediterranean region on the island of Cyprus, at altitudes below 400 m.

Additional material studied. Cyprus, Larnaca District, Kalavasos, 170 m, under *Cistus salviifolius* and *Cistus creticus*, 29 Nov. 2012, *M. Loizides* (ML211192Z); ibid., 200 m, 23 Jan. 2016, *M. Loizides* (ML61132Z)*; Nicosia District, Lythrodontas, 400 m, under *Cistus salviifolius* and *Cistus creticus*, 27 Nov. 2014, *M. Loizides* (ML411172Z)*.

Notes — *Lactarius subgiennensis* differs from the closely related *L. giennensis* in its markedly scrobiculate basidiomata, lageniform-urticiform basidia, and smaller, subreticulated spores with a partially incomplete or discontinuous reticulum, not exceeding 1 µm height in side view. Both species are found in xerophytic environments of Southern Europe in association with *Cistaceae* plants, but seem to be geographically isolated. Additional collections from intermediate localities (Greece, Italy) would be needed to confirm the distribution boundaries between both taxa. Genetically, *L. subgiennensis* seems to be the sister-species of *L. giennensis*. Both taxa seem to have some intraspecific variability, but are significantly different.

Russula ammophila (J.M. Vidal & Calonge) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 231. 2018 — Fig. 13

Basionym. *Gymnomyces ammophilus* J.M. Vidal & Calonge, Bol. Soc. Micol. Madrid 24: 66. 1999.

Synonym. *Macowanites ammophilus* (J.M. Vidal & Calonge) J.M. Vidal & Calonge, Rev. Catalana Micol. 24: 70. 2002.

Basidiomata russuloid, angiocarpic to pseudoangiocarpic, stipitate. *Pileus* 2–7 cm wide, globose to hemisphaerical, orange white to pale orange, with brownish orange and dark brown maculae; margin open, alveolate to sublamellate. *Hymenophore* loculate, orange-white to pale orange. *Stipe-columella* 1–4 × 0.7–2.5 cm, with brownish orange dots; context white. *Odour* fruity; taste sweetish to acrid.
Spores 7–9 × 5.5–7.5 µm, Q = 1.16–1.4, subglobose to ovoid, heterotropic; warts 0.25–0.75 µm high, amyloid, some forming short ridges or connected by short lines. *Basidia* 2–4-spored, 35–45 × 8–11 µm, clavate. *Macrocystidia* 45–60 × 6–10 µm. *Hymenophoral trama* with sphaerocytes 6–35 µm diam. *Pileipellis* 125–200 µm thick; suprapellis an intricate trichoderm made of sinuous, clavate, lanceolate or mucronate tips of hyphae and some poorly differentiated dermatocystidia 15–40 × 2–5 µm; subpellis an intricate cutis of gelatinized hyphae 2.5–7.5 µm diam. *Pileal* and *stipe-columella context* heteromerous.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous in sandy soils, associated with *Pinus*. Spring and autumn. Common in sandy pine forests of the Atlantic coast of Southern Spain and Portugal, more rarely in Northern and Central Spain.

Material studied. Portugal, Setubal, road from Grândola to Santa Margarita do Sado, stabilized dunes, under *Pinus pinea* and *Pinus pinaster* with *Halimium halimifolium* and *Corema*, 26 Mar. 1998, *P.P. Daniëls*, *J.M. Vidal* & *F.D. Calonge* as *G. ammophilus* (MA-Fungi 40132; duplicate BCN JMV980326-11b); Castelo Ventoso, road to Alcácer do Sal, stabilized dunes, under *Pinus pinea* with *Corema*, 26 Nov. 1999, *J.M. Vidal* & *F.D. Calonge* as *M. ammophilus* (MA-Fungi 51167; duplicate BCN JMV991126-1); without loc., without date, as *M. ammophilus* (AH 42956)*. – Spain, Andalusia, Cádiz, Barbate, Loma del Teniente, 120 m, stabilized dunes, under *Pinus pinea* with *Halimium*, 15 Dec. 2012, *M. Becerra* & *E. Robles* (AH 43950, as *M. ammophilus*)*; Cádiz, Sanlúcar de Barrameda, Pinar de Algaida, stabilized dunes, under *Pinus pinea*, 30 Oct. 2014, *M. Becerra* as *M. ammophilus* (AH 46370)*; Huelva, Matalascañas, stabilized dunes, under *Pinus pinea* with *Halimium*, *Corema* and *Juniperus phoenicea*, 27 Nov. 1999, *J.M. Vidal* & *F.D. Calonge* as *M. ammophilus* (MA-Fungi 51165; duplicate BCN JMV991127-8); Mazagón, stabilized dunes, under *Pinus pinea* with *Halimium* and *Corema*, 27 Nov. 1999, *J.M. Vidal* & *F.D. Calonge* as *M. ammophilus* (MA-Fungi 51166; duplicate BCN JMV991127-2); Castilla and Leon, Palencia, Dehesa de Montejo, Tosande, under *Pinus nigra* subsp. *salzmannii* and *Quercus rotundifolia*, in sandy basic soil, 9 Jan. 2007, *A. Paz* (BCN IC09010703)*.

Notes — *Gymnomyces ammophilus* was proposed to accommodate specimens of a fully angiocarpic basidiomycete without any trace of a stipe-columella, found in South-Western Spain and Portugal (Calonge & Vidal 1999). However, new specimens with an evident stipe-columella were later collected by the same authors (Vidal et al. 2002) and DNA data suggested they all represent a single species, so it was concluded that the holotype material was not fully mature and the taxon was re-combined as *Macowanites ammophilus*. Since its formal description, this species has been regularly collected in coastal sand dunes of the South-Western Iberian Peninsula and a high morphological variability has been observed. Recently, this species was re-combined into genus *Russula* by Elliott & Trappe (2018).

A high genetic variability (5.8 %) among ITS sequences from these specimens can be observed (Fig. 3). This could be due in part to sequencing errors in older GenBank accessions (M.P. Martín, pers. comm.), although some variability was found also among newly produced sequences. Most interestingly, ITS sequences did not support significant differences between *R. ammophila* and sequences of the gymnocarpic species *R. amoenolens* produced in the present work and those present in public databases, including one obtained from a specimen identified by Romagnesi (MICH12838, KF245510, Bazzicalupo & Berbee, unpubl. data). These European sequences probably represent the original concept of *R. amoenolens*, and are significantly different from other lineages identified with the same name (Fig. 3). In addition, 28S rDNA and *rpb2* data failed to support any significant difference between *R. ammophila* and *R. amoenolens*, but translation elongation factor 1-alpha (*tef1*) data contains diagnostic differences that can be employed to discriminate them (GenBank MK102724–MK102727). Owing to

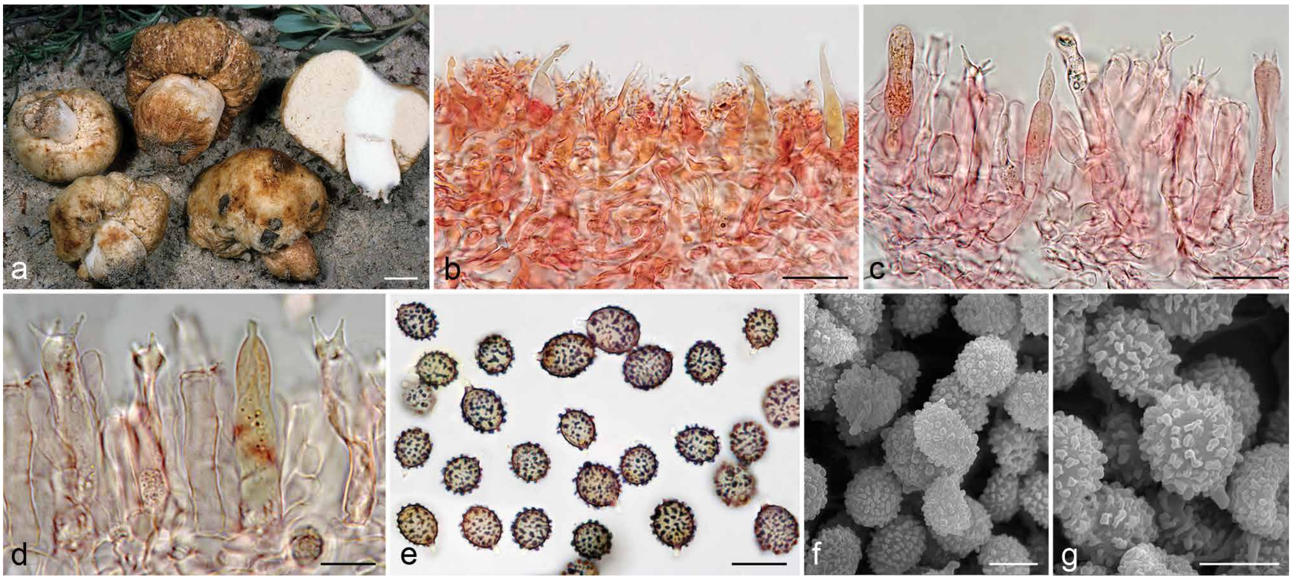

Fig. 13 *Russula ammophila*. a. MA-Fungi 51167 (as *Macowanites ammophilus*). Basidiomata. — b–d. IC09010703. b. Pileipellis; c–d. hymenium. — e. JMV991127-2. Spores in Melzer. — f–g. JMV991126-1. SEM images of spores. — Scale bars: a = 1 cm; b–c = 20 µm; d–e = 10 µm; f–g = 5 µm. — Photos: a–e. J.M. Vidal; f–g. UdG.

genetic differences in *tef1* gene and the lack of a stabilized concept of *R. amoenolens*, we here still accept that *R. ammophila* represents an independent species. Both taxa belong to *R.* sect. *Ingratae*, and are nested within the clade of /*R. amoenolens*, closely related with *R. cerolens*, *R. sororia*, and several other linages identified as *R. amoenolens* not matching Romagnesi's concept of this species. In *R. amoenolens* spores are ellipsoid, measuring 7–8.5(–9) × 5–6.7 µm and ornamented with warts up to 0.75 µm high (Romagnesi 1985), or 6.5–8.4 × 5.2–6.4 µm and with warts up to 0.8 µm high (Sarnari 1998), some warts interconnected with short ridges. Spores of *R. ammophila* are subglobose to ovoid, measuring 7–9 × 5.5–7.5 µm and ornamented with warts up to 0.75 µm high, some of them fused and connected by short ridges.

Russula amoenolens Romagn., Bull. Mens. Soc. Linn. Lyon 21: 111. 1952.

Material studied. SPAIN, Cantabria, Castro Urdiales, Prado Maya, under *Quercus* sp., 23 July 2015, *J.A. Cadiñanos* (AH 46371)*; Castro Urdiales, under *Quercus* sp., 23 July 2015, *J.A. Cadiñanos* (AH 46372)*.

Russula andaluciana T.F. Elliott & Trappe, Fungal Systematics and Evolution 1: 239. 2018 — Fig. 14

Replaced synonym. *Gymnomyces sublevisporus* Mor.-Arr., Llistos. & L. Romero, Rev. Catalana Micol. 24: 179. 2002.

Basidiomata 0.5–2 cm wide, angiocarpic, globose to subglobose, somewhat lobate, sessile. *Pileus* smooth, pruinose, whitish, with brownish red maculae. *Hymenophore* loculate, whitish at first, finally brownish red. *Columella* percurrent, sometimes branched, inconspicuous. *Odour* of bitter almonds; taste mild, slightly bitter. *Spores* (6.5–)7.5–9.5(–11.5) × (6–)7–9(–11) µm, Q = 1.0–1.1, globose to subglobose, orthotropic; warts up to 0.3 µm high, amyloid, some connected with low ridges. *Basidia* 4-spored, 36–50 × 7.5–11 µm, clavate. *Macrocystidia* and cystidioles absent. *Hymenophoral trama* prosenchymatous, of dense interwoven, tortuous hyphae about 2–6 µm diam, with some inflated ampullaceous cells up to 10 µm diam. *Pileipellis* and *context* 125–200 µm thick; suprapellis a trichoderm formed by short, cylindrical to clavate hairs 9–18 × 5–7 µm, and long, subulate, sometimes 1–2-septate hairs 30–49 × 2–7 µm; dermatocystidia absent; subpellis made by ampullaceous cells 8–10 µm diam. *Pileal context* with the same structure as the hymenophoral trama.

Habitat, Distribution & Season — Gregarious, hypogeous, associated with *Cistus ladanifer*, often accompanied by *Quercus rotundifolia* or *Q. suber*, on siliceous soil. Spring. Located in the Western Mediterranean region, in Central Spain, between 400–800 m altitude.

Material studied. SPAIN, Andalusia, Huelva, Cortelazor, finca Galindo, 540 m, under *Cistus ladanifer* with *Cistus crispus*, *Cistus salviifolius* and *Quercus rotundifolia*, 11 Mar. 1995, *L. Romero de la Osa* (BCN JL5101, holotype of *G. sublevisporus*; BM360, isotype)*; Extremadura, Badajoz, Mirandilla, Sierra Bermeja, 400 m, under *Cistus ladanifer* with *Quercus suber*, on siliceous soil, 25 Mar. 2017, *J.L. Becerra* (BCN IC25031720); Cáceres, Cuesta de Jaraiz, under *Cistus ladanifer*, on siliceous soil, 2 Apr. 2011, *C. Gelpi* as *G. sublevisporus* (AH 39239)*; Cáceres, Cuesta de las Veguillas, under *Cistus ladanifer* with *Eucalyptus camaldulensis*, on siliceous soil, 2 Mar. 2011, *C. Gelpi* & *J. Muñoz* as *G. sublevisporus* (AH 39198)*.

Notes — As already mentioned above, *R. andaluciana* is a replacement name proposed by Elliott & Trappe (2018) to re-combine *G. sublevisporus* into *Russula*. This species is distinguished by its whitish to yellowish basidiomata, and by its globose spores, ornamented with very small verrucae not

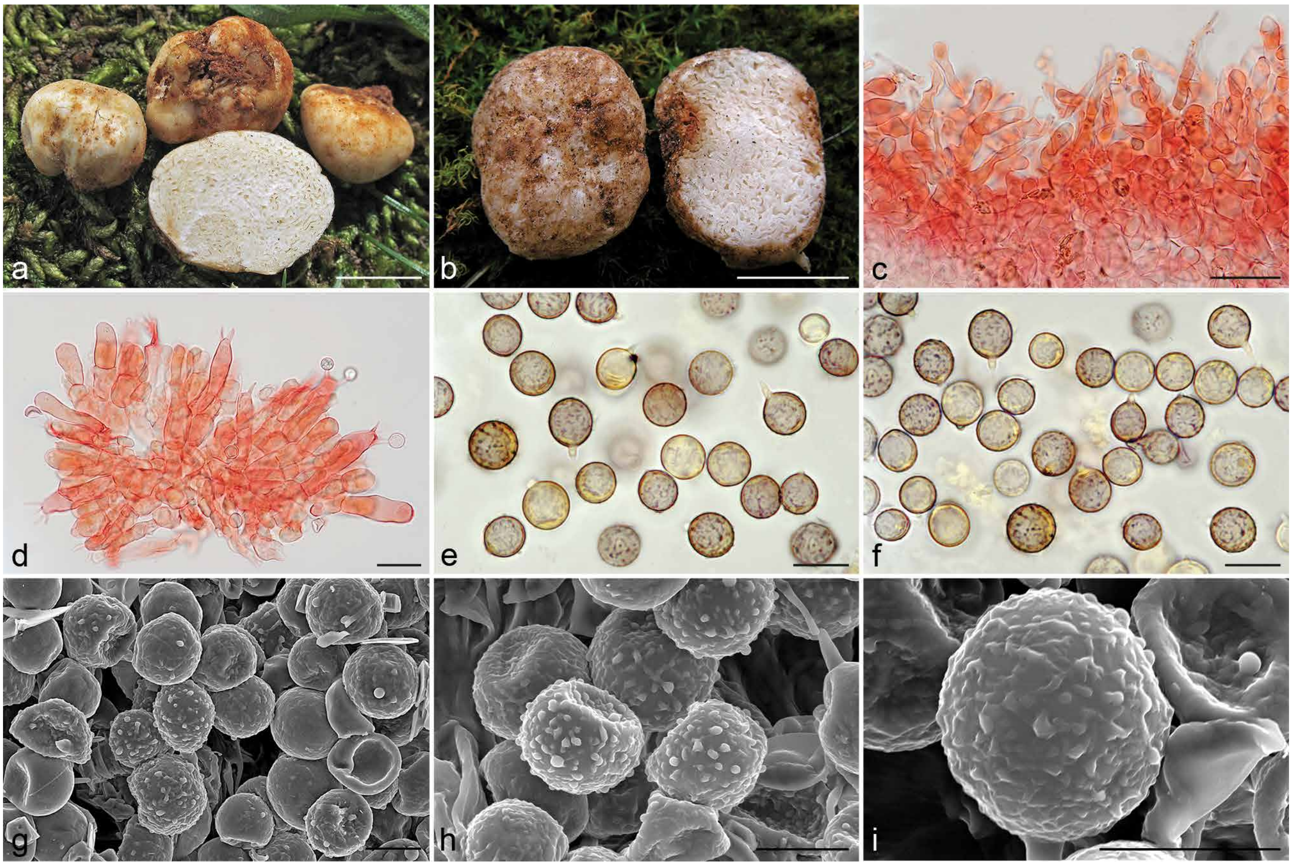

Fig. 14 *Russula andaluciana*. a. AH 39239. Basidiomata. — b. AH 39198. Basidiomata — c–i. BM360 (isotype of *Gymnomyces sublevisporus*). c. Pileipellis; d. hymenium (basidia and paraphysoid cells); e–f. spores in Melzer; g–i. SEM images of spores. — Scale bars: a–b = 1 cm; c–d = 20 µm; e–f = 10 µm; g–i = 5 µm. — Photos: a–b. C. Gelpi; c–f. J.M. Vidal; g–i. UdG.

exceeding 0.3 µm high. Sphaerocytes were not found in our observations, neither in the hymenophoral trama nor in the pileal context. Genetically, *R. andaluciana* is the only known European sequestrate species in *Russula* sect. *Rigidae*. It is nested within *R.* subsect. *Amoeninae*, but shows no clear relationship with any other taxon (Fig. 4).

Russula bavarica J.M. Vidal, *sp. nov.* — MycoBank MB828500; Fig. 15

Basidiomata 1–2 cm wide, angiocarpic, sessile, subglobose to tuberiform, subtomentose, pale orange with brown maculae. *Hymenophore* pale orange, forming small cells or locules. *Spores* 13–15(–15.5) × 12.5–14.5(–15) µm, globose to subglobose, orthotropic, intensely yellow, weakly amyloid, ornamented with dense, curved warts, 1.5–3 µm long. *Basidia* 1-spored, 24–36 × 8–12 µm, clavate. *Macrocystidia* 30–70 × 8–16 µm, clavate, abundant, containing refringent crystals (in exsiccata). *Subhymenium* ramose. *Hymenophoral trama* homoiomerous. *Suprapellis* a trichoderm of repent to semi-erect hyphae and dermatocystidia 50–100 × 2–4 µm; pileal context a subgelatinized cutis.

Etymology. From Latin, *bavaricus* = refers to the German state of Bavaria, where mycologist Ert Soehner collected this sequestrate fungus.

Holotype. GERMANY, Bavaria, 'Wolfratshausen bei München, Pupplinger Heide in der Nähe der Aumühle', 8 July 1923, *E. Soehner* #724 as '*Hydnangium carneum*' (M); isotype in FH (herb. C.W. Dodge).

Basidiomata 1–2 cm wide, angiocarpic, subglobose to tuberiform, sessile. *Pileus* finely tomentose, white to pale orange (5A4) in young specimens, partially covered with brownish maculae (7E6) in mature basidiomata. *Hymenophore* loculate, labyrinthoid, pale orange in colour (5A4–A5); locules 0.4–1 × 0.1–0.4 mm, elongated, sinuous; spore mass in locules pale orange (5A3). *Columella* absent. *Odour* and taste unknown. (Description based on herbarium material). *Spores* 13–15(–15.5) × 12.5–14.5(–15) µm, Q = 1.0–1.1, globose to subglobose, orthotropic, echinate, hyaline when young, yellowish when mature; warts inamyloid or weakly amyloid, 1.5–3 µm long, dense, curved, sharp, with some verrucae among them; hilar appendix short, 0.5–1 µm long, often with remnants of the sterigmata attached. *Basidia* 1-spored, 24–36 × 8–12 µm, clavate, hollow; sterigmata 3–5 µm long, conical. *Basidioles* 15–28 × 6–10 µm, clavate. *Macrocystidia* 30–70 × 8–16 µm, clavate, abundant, filled with highly refringent hyaline needles. *Pseudocystidia* not observed. *Subhymenium* very reduced, ramose, formed by short chains of 1–3 cylindrical elements, measuring 3–10 × 3–7 µm. *Hymenophoral trama* 20–40 µm wide, homoiomerous, formed by an entanglement of branched, tortuous, septate, subgelatinized hyphae about 2–6 µm diam, including scattered endomacrocystidia; sphaerocytes absent. *Pileipellis* and *context* thin, 100–150 µm thick; pileipellis 25–50 µm thick, arranged as a trichoderm formed by hyphae and septate, repent or semi-erect dermatocystidia 50–100 × 2–4 µm, finally collapsing into a brownish mass. *Pileal context* 75–100 µm thick, formed by a cutis of intricate, subgelatinized hyphae 2–5 µm diam, connecting with the hymenophoral trama. Laticifera not observed. Gloeoplera abundant, 2–5 µm diam, present in trama and context.

Notes — Collection Soehner num. 724 was cited by Dodge & Zeller (1937) and Soehner (1941), under the name *Hydnangium carneum*. It was found by Soehner in July 1923 near Munich (Bavaria, Germany). After studying the specimens preserved nowadays in M and FH herbaria, amyloid spores, hymenial macrocystidia, dermatocystidia and gloeoplera were observed, suggesting this species does not belong to genus *Hydnangium*. These specimens resemble *R. monospora*, because of the presence of monosporic basidia, echinate and

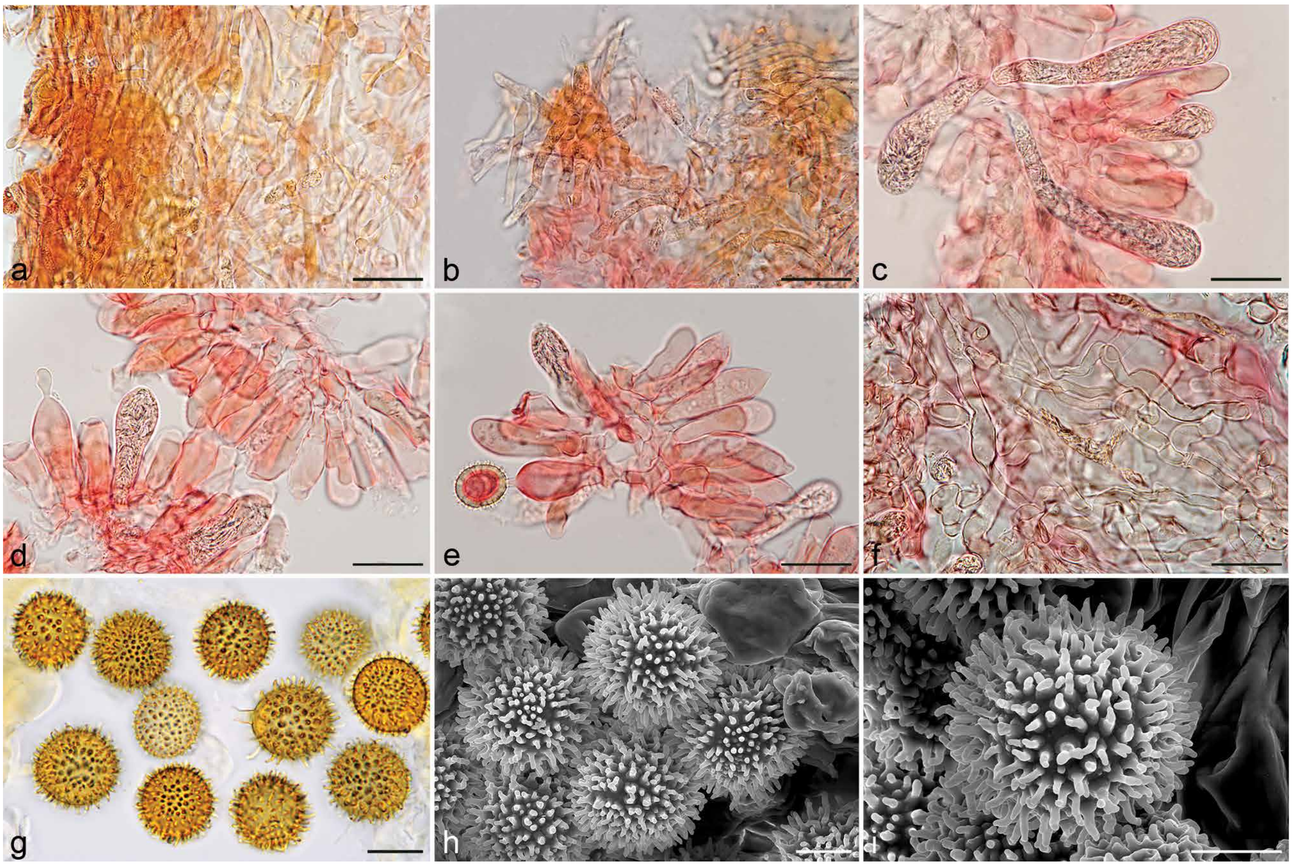

Fig. 15 *Russula bavarica*. a–i. M, herb. E. Soehner 724 as '*Hydnangium carneum*' (holotype). a. Pileipellis and context; b. suprapellis; c. macrocystidia; d–e. basidia, macrocystidia and ramose subhymenium; f. hymenophoral trama with some gloeoplera; g. spores in Melzer; h–i. SEM images of spores. — Scale bars: a–f = 20 µm; g = 10 µm; h–i = 5 µm. — Photos: a–g. J.M. Vidal; h–i. UdG.

weakly amyloid spores, ramose subhymenium, homoiomerous hymenophoral trama, and trichodermal pileipellis. Although it has not been possible to obtain recent collections matching these specimens, we believe it necessary to accommodate the collection Soehner 724 in a new species of *Russula* because of its unique combination of microscopical features, very similar to those of *R. monospora*, but differing and being characterized by the presence of clavate macrocystidia and larger spores ornamented with longer and more acute and dense spines. Further collections are needed to confirm the ecology of this species, which is probably the same as *Lactarius soehneri*, whose holotype was also collected by Soehner in Pupplinger Heide (south of Munich), and also determined as *H. carneum*.

Russula candida (Tul. & C. Tul.) J.M. Vidal, *comb. nov.* — MycoBank MB828501; Fig. 16

Basionym. *Hydnangium candidum* Tul. & C. Tul., Ann. Sci. Nat., Bot., Sér. 2, 19: 376. 1843.

Synonyms. *Octaviania candida* (Tul. & C. Tul.) Lloyd, Mycol. Writings 7, Letter 67: 1142. 1922.

Sclerogaster candidus (Tul. & C. Tul.) Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 23: 570. 1937.

Macowanites candidus (Tul. & C. Tul.) J.M. Vidal, Rev. Catalana Micol. 26: 84. 2004.

Secotium krjukowense Bucholtz, Hedwigia 40: 314. 1901.

Elasmomyces krjukowensis (Bucholtz) Sacc. & D. Sacc. in P.A. Saccardo, Syll. Fung. 17: 218. 1905.

Bucholtzia krjukowensis (Bucholtz) Lohwag, Oesterr. Bot. Z. 73, 7–9: 173. 1924.

Arcangeliella krjukowensis var. *krjukowensis* (Bucholtz) Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 22: 368. 1935.

Hydnangium krjukowense var. *krjukowense* (Bucholtz) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 206. 1958.

Macowanites krjukowensis (Bucholtz) Singer & A.H. Sm., Mem. Torrey Bot. Club 21, 3: 77. 1960.

Russula krjukowensis (Bucholtz) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 235. 2018.

Secotium michailowskianum Bucholtz, Hedwigia 40: 315. 1901.

Elasmomyces michailowskianus (Bucholtz) Sacc. & D. Sacc. in P.A. Saccardo, Syll. Fung. 17: 218. 1905 ('*michailowskjanus*').

Arcangeliella krjukowensis var. *michailowskiana* (Bucholtz) Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 22: 368. 1935.

Secotium krjukowense forma *pleurotopsis* Bucholtz, Bull. Soc. Imp. Naturalistes Moscou 4: 463. 1908 (1907).

Octaviania moravica Velen., Opera Bot. Cech. 4: 95. 1947.

Hydnangium krjukowense var. *moravicum* (Velen.) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 208. 1958.

Basidiomata russuloid, angiocarpic, stipitate. *Pileus* 0.5–3.5 cm wide, globose to subglobose, sometimes lobate, smooth, pruinose, white to yellowish white (4A2), with yellowish orange (4A6) to dark orange (5A8) maculae; margin closed or laterally open, alveolate. *Hymenophore* loculate, labyrinthoid, pale orange (5A3–A4); locules 0.7–3 × 0.1–0.4 mm (1–2 per mm), elongated, irregular, sinuous; fresh spore mass in locules pale yellow (3A3–A4). *Stipe-columella* 0.6–1.5 × 0.15–0.4 cm, usually half stipe, half columella, cylindrical to clavate, central or lateral, sometimes deeply lateral and thus barely visible, pure white, pruinose; context white, not changing on exposure to air. *Odour* fruity; taste mild.

Spores 8.5–11(–12.5) × 7–9(–11) µm, Q = 1.08–1.25(–1.3), subglobose to broadly ellipsoid, heterotropic to subheterotropic, echinate; warts amyloid, 0.5–1.5 µm high, isolated, cylindrical and sometimes curved, with a rounded apex; hilar appendix 1–2.5 × 1.2 µm, straight, cylindrical to conical, occasionally retaining a sterigmal appendage; suprahilar plage amyloid; immature spores sometimes with a non-functional apicular drop. *Basidia* 1–3(–4)-spored, 28–42 × 14–18 µm, clavate. Basidioles clavate, 20–24 × 10–16 µm. *Macrocystidia* 45–70 × 8–12 µm, lanceolate or fusiform, rostrate, narrowly acute or mucronate, easily collapsing. *Paraphysoid cells* absent. *Subhymenium* cellular, formed by subglobose cells of 8–16 µm diam. *Hymenophoral trama* 40–50 µm wide, formed by septate hyphae 1.5–10 µm diam, with frequent enlargements up to 16 µm and abundant sphaerocytes 15–40 µm diam. *Pileipellis* and *context* 80–250 µm thick, thinning in the perimarginal zone; suprapellis a trichoderm of cylindrical dermatocystidia 15–70 × 3–8 µm, with tips of gelatinized hyphae soon collapsing into a brown, granular slimy mass; mediopellis 60–100 µm thick, that consists of an ixocutis of intricate hyphae 2–6 µm diam, with numerous gloeoplera 4–5 µm diam terminating in dermatocystidia; subpellis 50–120 µm thick, formed by an intricate cutis of subgelatinized hyphae 2–6 µm diam, connecting with the pileus and hymenophoral trama. Context of pileus and stipe-columella heteromerous. *Stipitipellis* a turf of repent to erect hyphal tips mixed with dermatocystidia. Thromboplera 3–5 µm diam, present in the trama and context.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous to semi-hypogeous among plant debris, in montane broadleaved woods of *Carpinus* and *Corylus* mixed with *Fagus*, *Populus*, *Quercus*, *Tilia*, *Betula*, *Acer*, *Fraxinus*, *Sambucus*, *Ulmus*, on calcareous soil. Summer and autumn. Widely dis-

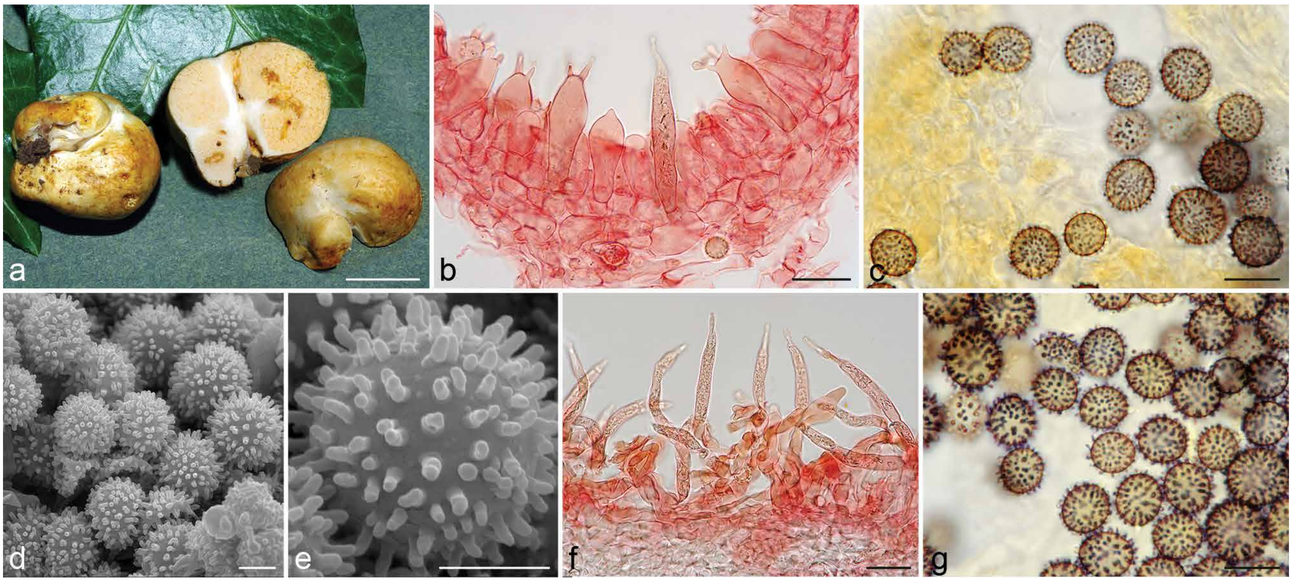

Fig. 16 *Russula candida*. a–e. JMV20100724b. a. Basidiomata; b. hymenium and subhymenium; c. spores in Melzer; d–e. SEM images of spores. — f–g. M, herb. G. Gross 171 (as '*Elasmomyces mattiroloanus*'). f. Pileipellis; g. spores in Melzer. — Scale bars: a = 1 cm; b, f = 20 µm; c–d, g = 10 µm; e = 5 µm. — Photos: a–c, f–g. J.M. Vidal; d–e. UdG.

tributed in temperate regions of Europe, from 100 m altitude in Northern Europe to 1100 m around the Mediterranean basin.

Material studied. Bulgaria, Vraca, Chiren, under *Tilia* sp., 23 June 2018, *M. Slavova* & *O. Ligabue* (MSL2177F3265, duplicate BCN JMV800751). – Czech Republic, Central Bohemia, Černošice, under *Carpinus*, *Tilia* and *Acer*, 9 July 1950, *V. Vacek* as *E. krjukowensis* (PRM 619106); South Moravia, Ždanice, near Bučovice, in forest, July 1941, *F. Neuwirth* (PRM 151648, holotype of *O. moravica*); Ždanice, near Zdravá Voda, in a leafy forest, July 1960, *K. Kříž*, det. M. Svrček as *E. krjukowensis* (PRM 620134). – France, Poitou-Charentes, Vienne, Couhé-Vérac, solitary under *Carpinus*, Oct. 1841, *Tulasne* (PC, herb. Tulasne, holotype of *H. candidum*). – Germany, Saarland, Gerlfangen, under *Fagus*, *Carpinus*, *Quercus* and *Acer*, 26 July 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 171; duplicate BCN JMV799894)*; Honzrath, under *Fagus*, *Carpinus* and *Corylus*, on calcareous soil, 27 June 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 176). – Hungary, Nógrád, Litke, under *Carpinus*, on calcareous soil, 20 Aug. 1996, *Z. Lukács* (BCN JMV800073); Tötökmezö, 250 m, under *Carpinus*, on calcareous soil, 1 Aug. 1996, *Z. Lukács* (BCN JMV800074). – Italy, Lombardy, Monza e Brianza, Monza, Viale Reale, under *Carpinus*, 15 Oct. 1989, *M. Sarasini* as '*E. mattiroloanus*' (MS394, duplicate BCN JMV800003); Monza e Brianza, Monza, Viale Romano, under *Carpinus*, 15 Oct. 1992, *M. Sarasini* as '*E. mattiroloanus*' (MS467, duplicate BCN JMV800004); ibid., 19 Sept. 1994, *M. Sarasini* & *G. Imperatori* as '*E. mattiroloanus*' (MS619, duplicate BCN JMV800005). – Russia, Moscow, Kryukovo, Kryukovo station, 18 July 1899, *F. Bucholtz* (FH, herb. F. Bucholtz, original material of *S. krjukowense*); Podolsk, Michailowskoje station, 20 July 1899, *F. Bucholtz* (FH, herb. F. Bucholtz 290, holotype of *S. michailowskianum*). – Spain, Cantabria, Saja, Reserva Natural del Saja, 658 m, under *Fagus sylvatica*, 1 Oct. 2017, *J. Cabero* (JC171001N)*; Catalonia, Girona, Molló, Coll de la Boixeda, El Querol, 1100 m, under *Corylus avellana*, *Quercus pubescens*, *Tilia platyphyllos* and *Populus tremula*, on calcareous soil, 24 July 2010, *M.A. Pérez-De-Gregorio* (BCN JMV20100724b)*; ibid., 6 Sept. 2011, *J.M. Vidal* & *F. Rodríguez* (BCN JMV20110906-6b).

Notes — Tulasne & Tulasne (1843) collected in the French region of Vienne a fungus of angiocarpic appearance devoid of a stipe-columella, which they named *Hydnangium candidum*. Vidal (2004b) studied the holotype of *H. candidum* preserved in Tulasne's herbarium at PC, as well as the holotype of *Octaviania moravica* preserved in Velenovský's herbarium at PRM and part of the original material of *Secotium krjukowense* and *S. michailowskianum* preserved in Bucholtz's herbarium at FH, and concluded that all these taxa represent a single species, which he re-described as *Macowanites candidus*. *Russula candida* is characterized by its whitish angiocarpic basidiomata, which are maculated with yellowish orange, sometimes developing a minute stipe and a conspicuous columella. Spores are warty, subglobose to broadly elliptical, measuring 8.5–11(–12.5) × 7–9(–11) µm, many of them with a minute suprahilar plage in the base of hilar appendix and conserving a non-functional apicular drop, a character that is also present in other pseudoangiocarpic species of the same clade (*R. mattiroloana* and *R. mediterraneensis*).

This species is genetically nested within *Russula* sect. *Russula*, subsect. *Maculatinae*, and shows a significant relationship with *R. maculata* and *R. nympharum*, although it seems to represent an independent lineage not identified in previous studies of this clade (Adamčík et al. 2016). The complex around *R. maculata* was found by Adamčík et al. (2016) to be characterized by spores which are ornamented with low or medium-sized warts frequently connected and forming small ridges. However, *R. candida* has spiny spores not forming a reticulum or ridges, suggesting that this feature could be variable, or else restricted to the lineage formed by *R. maculata* and *R. nympharum*.

Russula candidissima J.M. Vidal, Pasabán & Chachuła, *sp. nov.* — MycoBank MB828502; Fig. 17

Basidiomata russuloid, angiocarpic to partially pseudoangiocarpic, stipitate. *Pileus* 1.4–2.8 cm wide, globose to lobate, subtomentose, pure white, later featuring pale yellow maculae; margin closed or laterally open, sublamellate. *Hymenophore* loculate, pale yellow to yellow. *Stipe-columella* 1–2 × 0.2–0.4 cm, percurrent, white. *Odour* fruity. *Spores* 9.5–12.5 × 8.5–10.5 µm, subglobose to broadly ellipsoid, heterotropic, amyloid; warts 1.2–2 µm high, isolated or in groups of 2–4, commonly interconnected by low ridges. *Basidia* 2–4-spored, 37–55 × 14–18 µm, broadly clavate. *Macrocystidia* 45–65 × 6–14 µm. *Hymenophoral trama* with sphaerocytes measuring 20–36 µm diam. *Suprapellis* a cutis of repent hyphae 3–8 µm diam, and some dermatocystidia measuring 20–40 × 3–7 µm; pileal context a cutis with some sphaerocytes up to 15 µm diam. Hypogeous or semi-hypogeous between plant debris, in fir and broadleaved montane woods.

Etymology. From Latin, *candidissima* = superlative for *candidus* (white), meaning very white because of its white colour more persistent than that of *Russula candida*.

Holotype. Spain, Catalonia, Girona, Molló, Coll de la Boixeda, El Querol, 1100 m, gregarious under *Corylus avellana*, *Quercus pubescens*, *Tilia platyphyllos* and *Populus tremula*, occurring in the same habitat as *Russula candida*, on calcareous soil, 6 Sept. 2011, *J.M. Vidal* & *F. Rodríguez* (BCN JMV20110906-6a)*.

Basidiomata similar to *Russula candida*, russuloid, angiocarpic to partially hemiangiocarpic, stipitate. *Pileus* 1.4–2.8 cm wide, initially globose or subglobose, finally lobate, with a flattened to depressed apex, laterally open and sublamellate at the base, exposing the hymenophore; initially finely tomentose, then smooth, pure white for a long time, staining pale yellow with manipulation (4A4); greyish orange (5B5) to pale brown in exsiccata (6D7). *Hymenophore* loculate, labyrinthoid, pale yellow to yellow (4A3–A6); pale brown (6D6) to brown in exsiccata (6E7); locules 0.7–1.8 × 0.15–0.3 mm (1–3 per mm), irregular, elongated, sinuous; fresh spore mass in locules pale yellow to yellow (4A3–A5); pale orange (5A4) to greyish orange (5B6) in exsiccata. *Stipe-columella* 1–2 × 0.2–0.4 cm, well developed, cylindrical, attenuate, central or eccentric, straight or curved, percurrent, not branched, pure white; context white, unchanging upon exposure to air. *Odour* fruity, taste mild.
Spores 9.5–12.5(–15) × (8–)8.5–10.5(–13) µm, Q = 1.1–1.2 (–1.3), subglobose to broadly ellipsoid, heterotropic, echinate, yellow; warts amyloid, 1.2–2 µm high, cylindrical and straight, with a truncate apex, in groups of 2–4, interconnected with low inamyloid ridges forming a basal reticulum; hilar appendix 1–1.8 × 1.2 µm, conical or cylindrical, straight; suprahilar plage amyloid; immature spores with a non-functional apicular drop. *Basidia* (1–)2–4-spored, 37–55 × 14–18 µm, broadly clavate; sterigmata 4–5 µm long. *Basidioles* 30–35 × 10–15 µm, clavate. *Macrocystidia* scarce, 45–65(–100) × 6–14 µm, cylindrical, lanceolate or fusiform, rostrate. *Paraphysoid cells* 20–30 × 5–10 µm, 1-septate. *Subhymenium* composed of isodiametric cells 10–20 µm diam. *Hymenophoral trama* 30–50 µm wide, composed of hyaline hyphae 3–8 µm diam, with nests and columns of sphaerocytes 20–36 µm diam. *Pileipellis* and *context* 150–250 µm thick; pileipellis composed of: 1) a suprapellis soon collapsing into a yellow slimy mass, consisting of a cutis of upright to repent hyphae 2–4 µm diam, and some hyaline, cylindrical or clavate dermatocystidia 20–40 × 3–7 µm; and 2) a subpellis 100–130 µm thick, consisting of a subixocutis of densely intricate, hyaline hyphae 2–3 µm diam. *Pileal context* 100–110 µm thick, forming a cutis of intricate hyaline hyphae 2–4 µm diam, with some inflated hyphae and sphaerocytes up to 15 µm diam. *Stipitipellis* a turf of repent to erect hyphal tips mixed with dermatocystidia; context of stipe-columella heteromerous, composed of densely interwoven narrow hyphae mixed with nests of sphaerocytes. Gloeoplera 2–5 µm diam, present in trama and context.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous to semi-hypogeous among plant debris, in broadleaved montane woods of *Carpinus*, *Corylus*, *Fagus*, *Quercus*, accompanied by *Acer*, *Betula*, *Castanea*, *Fraxinus*, *Populus*, *Tilia*, but also under *Abies*, on calcareous soil, frequently found together with *Russula candida*. Summer and autumn. Widely distributed in temperate regions of Europe, from 100 m altitude in Northern countries to 1100 m in Southern countries.

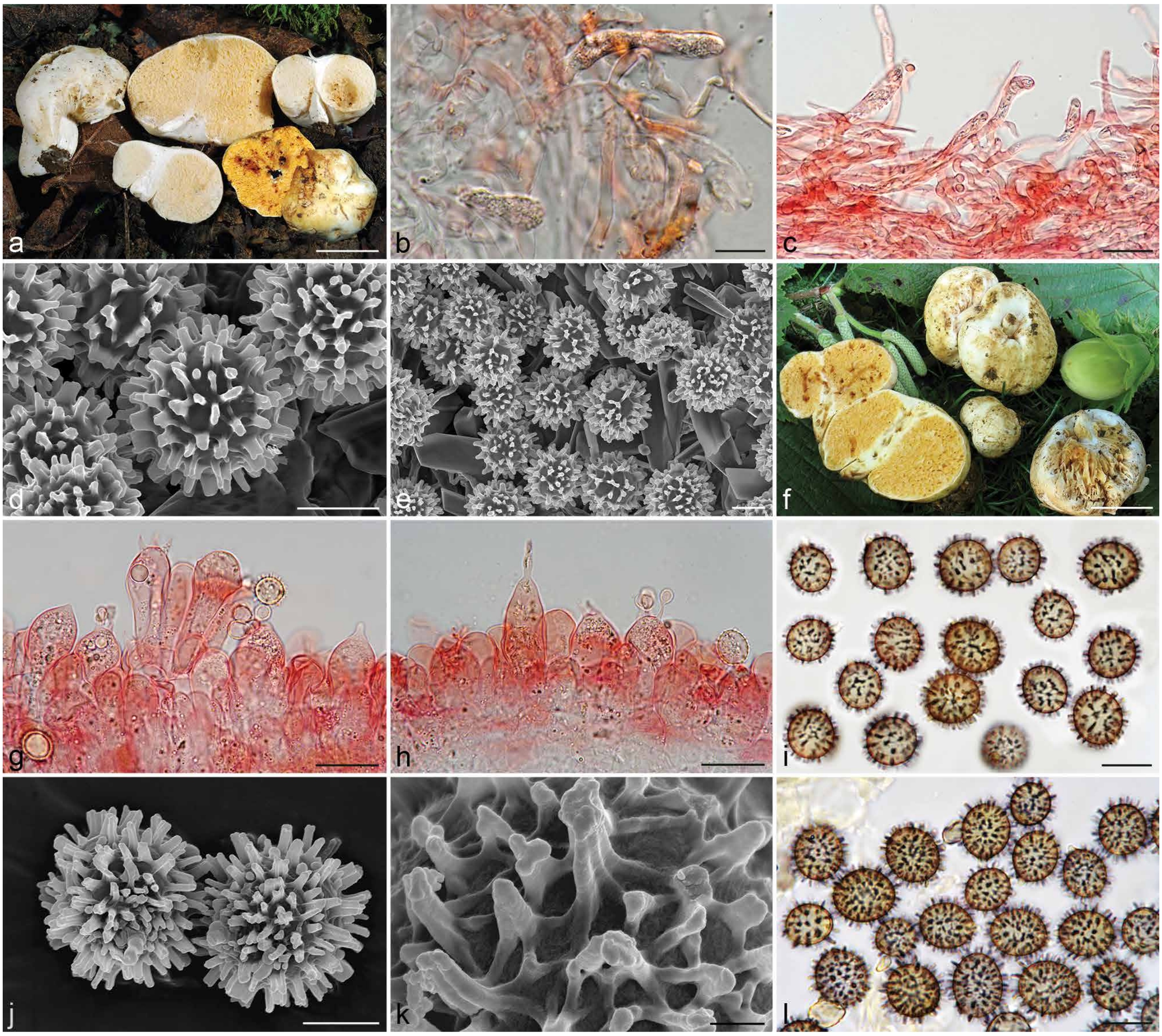

Fig. 17 *Russula candidissima*. a–e. JMV20110906-6a (BCN, holotype). a. Basidiomata; b. pileipellis; c. stipitipellis; d–e. SEM images of spores. — f. JMV800675. Basidiomata. — g–i. JMV20100724a. g–h. Basidia, basidioles and macrocystidium; i. spores in Melzer. — j. KRA F-2013-94. SEM image of spores. — k. KRA F-2009-57. SEM image of sporal ornamentation. — l. PRM 619108. Spores in Melzer. — Scale bars: a, f = 1 cm; b, i, l = 10 µm; c, g–h = 20 µm; d–e, j = 5 µm; k = 1 µm — Photos: a–c, g–i, l. J.M. Vidal; d–e. UdG; f. P.M. Pasabán; j–k. P. Mleczko, UJ.

Additional material studied. Austria, Lower Austria, Wien-Neustadt, Näudorfl, 10 June 1937, *M. Jacob*, det. E. Soehner as '*Hydnangium cereum*' (M, herb. E. Soehner 1894). – Czech Republic, Central Bohemia, Černošice, in a leafy forest, under *Carpinus*, *Crataegus* and *Cornus*, 4 July 1950, *V. Vacek*, det. M. Svrček as '*Elasmomyces krjukowensis*' (PRM 619107); South Moravia, Súchov, under *Carpinus*, *Quercus* and *Fagus*, 8 July 1953, *K. Kříž*, det. M. Svrček as '*Hydnangium krjukowense* var. *moravicum*' (PRM 619108, herb. F. Šmarda). – Germany, Baden-Württemberg, Altbach/Neckar, in a *Carpinetum*, 23 Oct. 1961, *H. Steinnmann* as '*Hydnangium krjukowense*' (PRM 616208); Saarland, Ballweiler, under *Fagus*, *Carpinus* and *Quercus*, on calcareous soil, 19 July 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 161); Bebelsheim, under *Fagus*, *Carpinus* and *Quercus*, on calcareous soil, 27 Aug. 1967, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 82); ibid., 12 July 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 157); ibid., 26 Aug. 1969, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 323); Eimersdorf, under *Carpinus*, *Fagus* and *Quercus*, on calcareous soil, 15 Aug 1968, *Derbsch* & *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 188); ibid., 6 Sept. 1969, *J. Schmitt*, det. G. Gross as '*E. mattiroloanus*' (M, herb. G. Gross 335); Eschringen, under *Fagus*, *Quercus* and *Fraxinus*, 3 Sept. 1967, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 85); Gerlfangen, under *Fagus*, on calcareous soil, 20 July 1968, *J. Schmitt*, det. G. Gross as '*E. mattiroloanus*' (M, herb. G. Gross 164); ibid., under *Fagus*, *Carpinus* and *Quercus*, 20 July 1968, *G. Korn*, det. G. Gross as '*E. mattiroloanus*' (M, herb. G. Gross 164a); ibid., under *Betula* and *Fagus*, 10 Aug. 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 179); Sitterswald, under *Fagus sylvatica*, on calcareous soil, 4 July 1967, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 79'); ibid., 31 Aug. 1967, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 84); ibid., 18 July 1968, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 159); ibid., 10 July 1969, *G. Gross* as '*E. mattiroloanus*' (M, herb. G. Gross 303). – Italy, Tuscany, Lucca, Vagli di Sotto, Monte Roggio, 900 m, under *Corylus avellana*, gregarious, 4 July 1993, *G. Bernardini* & *L. Gori* as '*M. candidus*' (ELG930704-1, duplicate BCN JMV800185)*. – Poland, Lesser Poland, Krościenko nad Dunajcem, Pieniny Nat. Park, near Gródek, Western Carpathians, 480 m, under *Abies alba*, on calcareous soil, 19 Sept. 2009, *P. Chachuła* (KRA F-2009-57, duplicate BCN JMV800664)*; ibid., yellow route from Sromowce Niżne to Szopka pass, 640 m, under *Abies alba*, on calcareous soil, 13 July 2011, *P. Chachuła* (KRA F-2013-94, duplicate BCN JMV800665); Silesia, Cieszyn, Pogórze Śląskie region, Western Carpathians, 296 m, under *Carpinus betulus* and *Quercus* sp., on calcareous soil, 22 Aug. 2017, *P. Chachuła* (KRA F-2017-2, duplicate BCN JMV800669)*. – Spain, Basque Country, Guipúzcoa, Villabona, under *Corylus avellana*, *Castanea sativa* and *Acer* sp., on calcareous soil, 19 Sept. 2004, *P.M. Pasabán* as '*M. candidus*' (BCN JMV800674); Catalonia, Girona, Molló, Coll de la Boixeda, El Querol, 1100 m, under *Corylus avellana*, *Quercus pubescens*, *Tilia platyphyllos* and *Populus tremula*, on calcareous soil, occurring in the same habitat as *Russula candida*, 17/24 July 2010, *M.A. Pérez-De-Gregorio* (BCN JMV20100724a); Navarre, Aizarotz, under *Corylus avellana*, on calcareous soil, 26 Sept. 2006, *P.M. Pasabán* as '*M. candidus*' (BCN JMV800675).

Notes — After carefully studying all basidiomata present in collection JMV20100724 (*Russula candida* from Catalonia, Spain), some of them were found to have spores with interconnected warts forming low ridges, different from the spores with isolated warts found in the remaining specimens of *R. candida*. These basidiomata also had a well-developed stipe-columella. After revisiting all collections of *Macowanites candidus* studied by Vidal (2004b), similar spore ornamentation was found also in Czech, German and Italian collections. The same German collections had been previously described by Gross (1969), under the name of *Elasmomyces mattiroloanus*. Similar spore ornamentation was also depicted in SEM images obtained from Swiss specimens by Pegler & Young (1979). More recently, Calonge & Pasabán (2005), and Gori (2005), described and illustrated new collections (identified by them as *M. candidus*) found in Spain and Italy, respectively, with the same spore morphology.

Russula candidissima can be discriminated macroscopically from *R. candida* because of its more persistently white external colour, its pileus that turns slightly yellowish with handling, and its mature basidiomata, which are opened in the base exposing the sublamellate hymenium, while in *R. candida* pileus becomes intensely yellow or yellowish orange with handling and its hymenium is rarely exposed. Microscopically, *R. candidissima* has a suprapellis composed of more or less parallel hyphae with scattered dermatocystidia and spore warts are interconnected by low ridges, while *R. candida* has a trichodermal suprapellis and spore warts are isolated. *Russula mattiroloana* differs microscopically from *R. candida* and *R. candidissima* by its bigger macrocystidia up to 130 µm long, and by its subglobose to globose spores up to 15.5(–18) × 15(–17) µm, ornamented with isolated warts up to 2.5–3 µm long.

Genetically, *R. candidissima* is significantly related to several sequestrate species from North America such as *R. xerophila*, *R. ellipsospora*, *R. mattsmithii* (a replacement name for *Gymnomyces compactus*), *R. stewartii* (a replacement name for *G. monosporus*), and one from New Zealand, *R. osphranticarpa* (a replacement name for *Gymnomyces redolens*). All these sequestrate species constitute a significantly supported clade related to subsect. *Firmiores*, in concordance with previous results (Smith et al. 2006). Several species of this subsection are characterized by the yellow or yellowish orange colour of their lamellae and spores, a cuticular structure with short emergent hyphal tips, and spores ornamented with a spiny reticulum (Lebel 2002, 2003b, Smith et al. 2006).

Russula cerea (Soehner) J.M. Vidal, *comb. nov.* — MycoBank MB828503; Fig. 18

Basionym. *Hydnangium cereum* Soehner, Kryptog. Forsch. 1, 6: 394. 1924.

Synonyms. *Octaviania cerea* (Soehner) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 197. 1958.

Hydnangium carneum var. *xanthosporum* Hawker, Trans. Brit. Mycol. Soc. 35, 4: 281. 1952. (syn. nov.)

Gymnomyces xanthosporus (Hawker) A.H. Sm., Mycologia 54: 635. 1962.

Russula xanthospora (Hawker) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 240. 2018.

Lectotype of *Hydnangium cereum* (here designated MBT384232): Germany, Bavaria, 'Erharting bei Mühldorf', under oaks, 16 Aug. 1921, *E. Soehner* (M, herb. E. Soehner 527); isolectotype in FH (herb. C.W. Dodge).

Basidiomata 1–3 cm wide, angiocarpic, subglobose, slightly lobate, sessile, sometimes presenting an inconspicuous sterile base and attached to the substrate by a mycelial strand. *Pileus* dry, smooth, membranous, translucent, displaying hymenophoral locules, basally open and alveolate in old specimens; initially white, then greyish orange (5B6) to pale brown (6D6) when handled or upon exposure to the air, finally reddish brown (8E8). *Hymenophore* loculate, labyrinthoid, brown (7D7) to reddish brown (8D8); locules minute, 0.4–1.4 × 0.1–0.3 mm (2–3 per mm), elongated, sinuous; external locules always fertile; fresh spore mass in locules reddish brown (9D6); brown (6E7) in exsiccata. *Columella* absent or rudimentary, but thin sterile veins can be observed in some specimens. *Odour* fruity, taste mild.

Spores (8–)9.5–12.5(–14) µm, Q = 1, variable in size, globose, orthotropic, echinate, orange to reddish in KOH; warts of irregular length, 1–3 µm high, intense yellow, deeply amyloid, dense, robust, conical or cylindrical, obtuse, longitudinally striate, isolated or fused in groups, often interconnected by low ridges; hilar appendix short, inconspicuous. *Basidia* typically 2-spored, 40–50 × 18–24 µm, pyriform to clavate, filled with minute, hyaline to dark reddish droplets, soon collapsing; sterigmata 8–10(–12) µm long, cylindrical to conical. *Basidioles* 22–36 × 10–13 µm, clavate. *Macrocystidia* abundant, (25–)30–50 × (5–)7–12(–16) µm, cylindrical to cylindro-clavate, wall up to 1 µm, with a dark yellow refractive content, rarely exceeding the basidia in length, resembling pseudocystidia because many of them originate at the deep subhymenium or hymenophoral trama. *Paraphysoid cells* abundant, 20–42 × 10–15 µm, vesiculose, 1-septate. *Subhymenium* very thick, pseudoparenchymatous, formed by 2–3 layers of prismatic to globose cells 8–20(–25) µm diam. *Hymenophoral trama* reduced, 10 µm thick, formed by hyphae 3–6 µm diam, and some sphaerocytes 10–20 µm diam, only present in tramal anastomoses. *Pileipellis* and *context* 70–125 µm thick; pileipellis thin, 50–100 µm, consisting of: 1) a trichodermal suprapellis of subulate to lageniform, capitulate dermatocystidia, measuring 15–30 × 3–5 µm, that soon collapses into a yellowish mass; and 2) a prosenchymatous subpellis 20–30 µm thick, formed by a dense mesh of interwoven, subgelatinized yellowish hyphae, measuring only 2–2.5 µm diam. *Peridial context* formed of interwoven hyaline hyphae 2–5 µm diam, lacking sphaerocytes. Gloeoplera and thromboplera present in the trama and context.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous, in montane conifer (*Abies*, *Picea*, *Pinus*) or broadleaved (*Carpinus*, *Castanea*, *Corylus*, *Fagus*, *Quercus*) forests, commonly on siliceous soil. Summer and autumn. Widely distributed in temperate and submediterranean regions of Europe, from almost sea level in Northern countries to 1100 m altitude in Southern countries.

Additional material studied. Germany, Saxony, Chemnitz, Park der OdF, 300 m, under *Castanea sativa*, 20 June 2009, *B. Mühler* & *G. Hensel* (GH20090620, duplicate BCN JMV800660)*. – Hungary, Veszprém, Zirc, under *Fagus* and *Carpinus*, 15 Sept. 2000, *Z. Lukács* (BCN JMV800164). – Italy, Emilia-Romagna, Forli-Cesena, Santa Sofia, Foresta di Campigna, under *Abies alba*, 11 Oct. 1991, *M. Sarasini* as *G. xanthosporus* (MS419, duplicate BCN JMV800006); Tuscany, Lucca, Vagli di Sotto, Monte Roggio, 800 m, under *Corylus avellana*, 4 Dec. 1994, *G. Bernardini* & *L. Gori* as *G. xanthosporus* (ELG941204-3, duplicate BCN JMV800172). – Poland, Lower Silesia, Góry Złote region, Sudety mountains, under *Quercus* sp., *Fagus sylvatica*, *Picea abies*, *Abies alba* and *Acer* sp., 9 Aug. 2012, *M. Kozak* & *P. Mleczko* (KRA F-2012-28, duplicate BCN JMV800667)*. – Portugal, Aveiro, Luso, bosque de Buçaco, 547 m, under *Castanea sativa*, on siliceous soil, 11 Nov. 2015, *A. Paz* (BCN IC11111504). – Spain, Asturias, Perán, under *Castanea sativa*, 17 Aug. 2000, *F. García* (BCN JMV20000817-1)*; Catalonia, Girona, Campelles, Torrent de Prat de Jou, 1100 m, under *Corylus avellana*, *Fraxinus*, *Acer* and *Buxus*, on siliceous soil, 3 Oct. 1996, *J.M. Vidal* as *G. xanthosporus* (BCN JMV961003-8)*; Girona, Espinelves, crossroad to Viladrau, 740 m, in a *Picea abies* plantation, on siliceous soil, 5 July 2016, *F. Rodríguez* (BCN JMV20160705)*; ibid., 4 Sept. 2018, *F. Rodríguez* & *J.M. Vidal* (BCN JMV20180904-3); Navarre, Eratsun, under *Pinus pinaster*, 10 June 2015, *P.M. Pasabán* & *F. Sáinz* (BCN JMV800656)*. – United Kingdom, Wales, Caernarvon, 'Bettws-y-Coed, North Wales, inter acubus emortius Piceae', 13 Sept. 1951, *L.E. Hawker* (K(M)69329, herb. L. Hawker H251, holotype of *H. carneum* var. *xanthosporum*).

Notes — Soehner (1924) described an angiocarpic fungus found under oaks in the German region of Bavaria, which he called *Hydnangium cereum*, but did not select a type collection. In a later paper, Soehner (1941) provided new data and reference

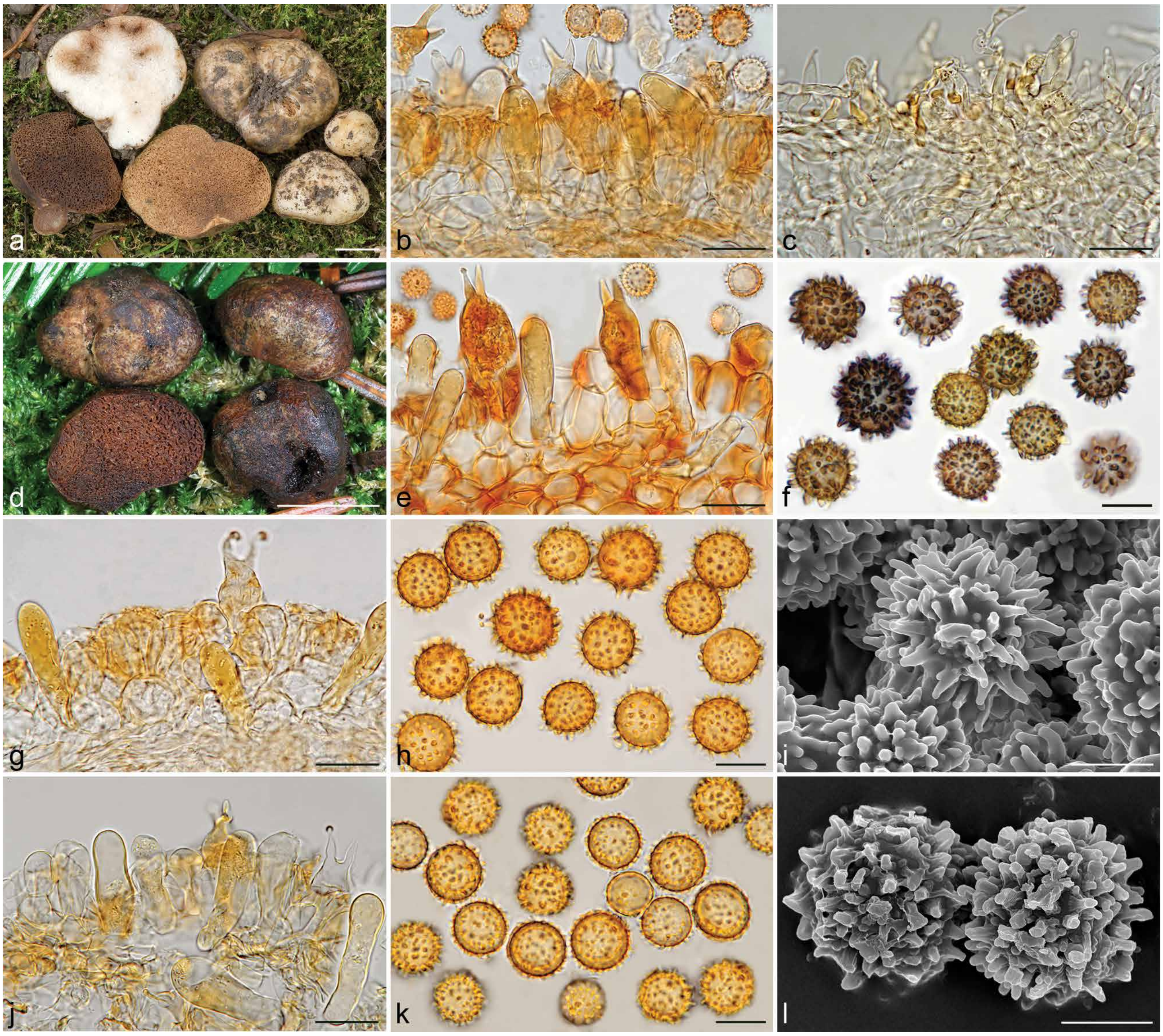

Fig. 18 *Russula cerea*. a–b. GH20090620. a. Basidiomata; b. basidia and macrocystidia. — c. MS419. Pileipellis. — d. JMV20180904-3. Basidiomata. — e. JMV20160705. Basidia and macrocystidia. — f. ELG941204-3. Spores in Melzer. — g–h. M, herb. E. Soehner 527 (original material of *Hydnangium cereum*). g. Basidium and macrocystidia; h. spores in KOH 5 %. — i. JMV20160705. SEM image of spores. — j–k. K(M)69329 (holotype of *Hydnangium carneum* var. *xanthosporum*). j. Basidia and macrocystidia; k. spores in KOH 5 %. — l. KRA F-2012-28. SEM image of spores. — Scale bars: a, d = 1 cm; b–c, e, g, j = 20 µm; f, h, k = 10 µm; i, l = 5 µm. — Photos: a. G. Hensel; b–h, j–k. J.M. Vidal; i. UdG; l. P. Mleczko, UJ.

codes for several collections of this species, indicating that duplicates of a collection labelled ‘Summer 1921’ were sent to several mycologists such as E. Fischer, O. Mattirolo and C.W Dodge. Dodge & Zeller (1937) considered this collection, which they labelled ‘E. Soehner 527’, as the type of *H. cereum*. After studying several original collections of *H. cereum* from E. Soehner’s herbarium at Münich, we found that ‘Soehner no. 527’ is the only collection consisting of mature basidiomata, so it is here designated as lectotype.

Later on, Hawker (1952) described from Wales, UK, an angiocarpic fungus of similar characteristics that she called *Hydnangium carneum* var. *xanthosporum*. Type collections of *H. cereum* and *H. carneum* var. *xanthosporum* were compared in the present work, and found to be probably conspecific because of their bisporic basidia, cylindrical thick-walled macrocystidia, and conspicuously ornamented globose spores, with *H. cereum* being the prioritary name. Interestingly, the presence of hymenial macrocystidia was not observed by Soehner (1924, 1941) in *H. cereum*, neither by Hawker (1952, 1954), Smith (1962), nor by Pegler et al. (1993) in *H. carneum* var. *xanthosporum*, despite them being very conspicuous. Morphological traits as well as genetic data from specimens originating from Central and Southern Europe suggest that this taxon is another sequestrate species of *Russula*, and therefore the combination *R. cerea* is here proposed.

Phylogenetic inferences suggested that *R. cerea* belongs to sect. *Ingratae*, and probably subsect. *Foetentinae*. *Russula cerea* is significantly related to other European sequestrate taxa such as *R. pila* and *R. mistiformis*, being macroscopically very similar to both species, but differing because of its thinner membranous pileus, bisporic basidia and presence of thick walled, clavate macrocystidia. All samples of *R. cerea* seemed genetically similar to each-other, except for JMV20000817-1 from Asturias (Spain), which showed significant differences in ITS (15/564 bp = 2.65 %, including a 7 bp insertion) and 28S rDNA (4/851 bp = 0.5 %). After microscopically studying this specimen, we have been unable to find any distinct features, so it could represent a cryptic species or maybe a hybrid specimen with either *R. pila* or *R. mistiformis*.

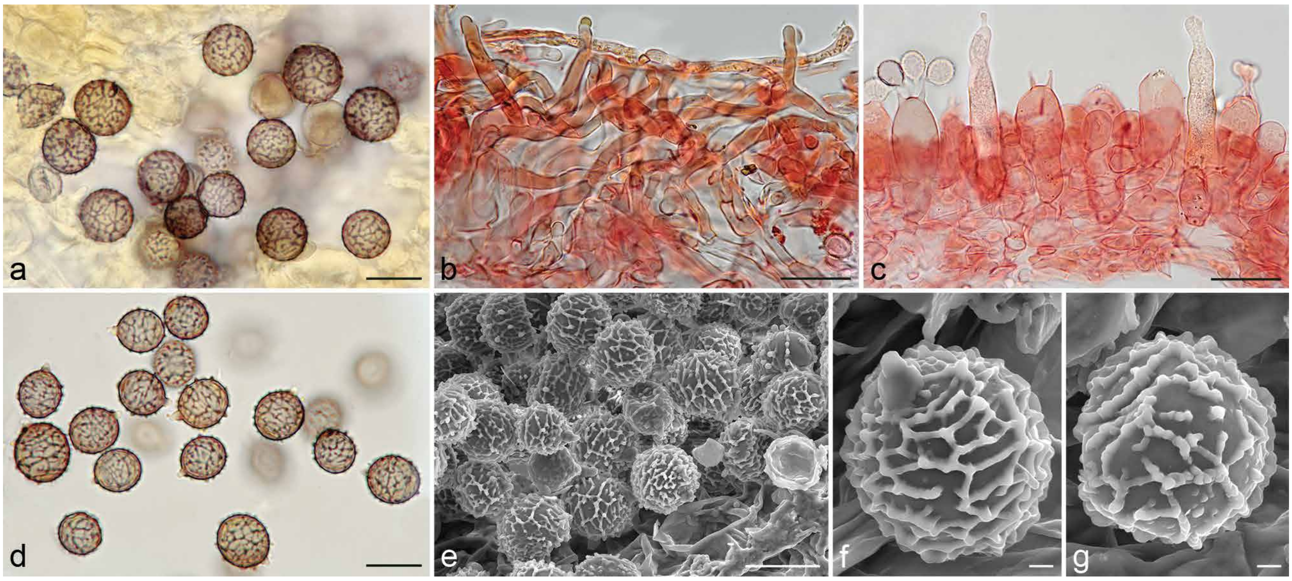

Fig. 19 *Russula galileensis*. a. IB M72.340 (isotype of *Macowanites galileensis*). Spores in Melzer. — b. HAI-G-83. Suprapellis. — c–d. HAI-G-201. c. Hymenium and subhymenium; d. spores in Melzer. — e–g. HAI-G-83. SEM images of spores. — Scale bars: a, d–e = 10 µm; b–c = 20 µm; f–g = 1 µm. — Photos: a–d. J.M. Vidal; e–g. UdG.

Russula galileensis (M.M. Moser et al.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 234. 2018 — Fig. 19

Basionym. *Macowanites galileensis* M.M. Moser et al., Trans. Brit. Mycol. Soc. 68, 3: 371. 1977.

Basidiomata russuloid, angiocarpic, stipitate. *Pileus* 2–6 cm wide, irregular and tuberous, sometimes depressed at the apex, white with cream to pale umber maculae; margin radially alveolate when mature, but not open. *Hymenophore* loculate, cream-ochre. *Stipe-columella* 0.5–3.5 × 0.5–1.7(–3) cm, white. *Odour* and taste mild.

Spores (9–)10–11.5(–15) × (7.5–)9.5–10.5(–14) µm, Q = 1.05–1.15, subglobose, heterotropic; reticulum 0.5 µm high, amyloid, composed of crests and warts. *Basidia* 4-spored, 26–37 × 11–13 µm, broadly clavate. *Macrocystidia* 40–60 × 10–15 µm, sometimes 1–2-septate. *Hymenophoral trama* heteromerous. *Pileipellis* and *context* 200–250 µm thick; suprapellis an intricate trichoderm of repent, to semi-erect hyphae and dermatocystidia 2–7 µm diam.

Habitat, Distribution & Season — Subepigeous under fallen leaves, in sclerophyllous woods of *Quercus*, on calcareous soil. From late autumn to spring. So far located only in the eastern Mediterranean region, in Israel, found at low altitudes.

Material studied. Israel, Carmel Mount, Mt Carmel National Park, near Haifa, Shajarat Al Arba'in (Horshat Ha'arbaim), under *Quercus calliprinos*, 12 Dec. 1972, *M. Moser*, *N. Binyamini* & *Z. Avizohar-Hershenzon* 72/401 (IB M72340, isotype of *M. galileensis*); ibid., near *Pinus*, 13 Jan. 2012, *M. Krakhmalnyi* as *M. galileensis* (HAI-G-91); Haifa, Technion, Dec. 2011, *M. Krakhmalnyi* as *M. galileensis* (HAI-G-59); Upper Galilee, Goren Park, Dec. 2011, *Z. Shafranov*, det. M. Krakhmalnyi as *M. galileensis* (HAI-G-83; duplicate BCN JMV800634)*; ibid., Hanita Forest, 22 Dec. 2012, *Z. Shafranov*, det. M. Krakhmalnyi as *M. galileensis* (HAI-G-166)*; Mount Meron National Park, 7 Jan. 2006, *I. Shams*, det. S.P. Wasser as *M. galileensis* (HAI-G-202)*; Nahal Kziv Nature Reserve, 'Evolution Canyon-II', under *Quercus*, 3 Jan. 2001, *S. Reshetnikov*, det. S.P. Wasser as *M. galileensis* (HAI-G-45); ibid., under *Quercus*, 3 Jan. 2001, *T. Pavlichek* & *I. Shams*, det. S.P. Wasser as *M. galileensis* (HAI-G-201; duplicate BCN JMV800635)*; ibid., under *Laurus*, 7 Jan. 2001, *I. Duckman*, det. S.P. Wasser as *M. galileensis* (HAI-G-46); Nahal Zalmon National Park, under *Quercus*, 1 Febr. 2003, *Y. Ur*, det. S.P. Wasser as *M. galileensis* (HAI-G-209)*.

Notes — *Macowanites galileensis* was originally described and illustrated from the specimens collected on Mt Carmel in 1972 (Moser et al. 1977, 1994). Interestingly, the authors initially regarded their collection to be *M. krjukowensis*, due to white colour of basidiomata. Following more careful examination, however, it became evident that new collections possessed a number of distinctive macro- and micromorphological characters, such as a very robust pileus and stipe-columella, as well as warts of spores connected by ridges and crests, features which separated them from the latter. We could not obtain images to illustrate the studied collections. Recently, this species was re-combined into genus *Russula* by Elliott & Trappe (2018).

Current molecular results indicate that *R. galileensis* belongs to *Russula* subsect. *Laricinae*, being significantly related to the *R. laricinoaffinis* clade. Subsection *Laricinae* is characterized by ocher to yellowish spore deposits, short basidia, rare pleurocystidia and multiseptate dermatocystidia (Romagnesi 1985, Li et al. 2013). Other European sequestrate taxa also related to *Laricinae* include *R. vinaceodora* and *R. vidalii* (a replacement name for *Gymnomyces ilicis*), both species apparently endemic to the Mediterranean region (Moser et al. 1977, Llistosella & Vidal 1995, Calonge & Vidal 2001, Cabero 2011). *Russula galileensis* and *R. vinaceodora* produce large basidiomata (up to 5–6 cm across), with a conspicuous stipe-columella that is sublamellate in the lower part, and spores with warts forming small interconnecting ridges, while *R. vidalii* is a smaller fungus (1–2.5 cm diam), with a poorly developed columella, a loculate hymenophore, and spores which are ornamented with more or less isolated warts.

Russula hobartiae Loizides & J.M. Vidal, *sp. nov.* — MycoBank MB828504; Fig. 20

Basidiomata 2–7 cm wide, angiocarpic, turbinate to pyriform, weakly lobate, tomentose, whitish to ochraceous brown, firmly rooted into the substrate. *Hymenophore* loculate, whitish to ochraceous orange, becoming vinaceous in $FeSO_4$; locules minute, rounded to elongate. *Columella* absent or rudimentary, sometimes forming short white veins. *Odour* slightly fruity, with a vague hint of chocolate. *Spores* 7–9.5(–10.5) × 7–9(–10) µm, globose; reticulum complete to incomplete, up to 0.5 µm high. *Basidia* 2–4-spored, 20–35 × 8–12 µm, clavate. *Macrocystidia* 25–40 × 8–10 µm, clavate, scarce. *Hymenophoral trama* prosenchymatous, with scarce sphaerocytes. *Suprapellis* a palisadotrichoderm of clavate dermatocystidia 25–60 × 5–10 µm; pileal context a cutis of hyaline hyphae 1.5–3 µm diam, lacking sphaerocytes. Hypogeous or semi-hypogeous in montane woods of *Pinus nigra* subsp. *pallasiana* on the island of Cyprus.

Etymology. *hobartiae* = in honor of mycologist Caroline Hobart, for her contribution to the study of hypogeous and sequestrate fungi in Cyprus.

Holotype. Cyprus, Nicosia District, Prodromos, 1450 m, under *Pinus nigra* subsp. *pallasiana*, 13 Oct. 2011, *M. Loizides* (BCN JMV800628)*; isotype in herb. pers. M. Loizides (ML110131GY).

Basidiomata 2–7 cm wide, angiocarpic, turbinate, oblate-globose to pyriform and somewhat applanate at the apex, weakly lobate, distinctly tapering at base, longitudinally furrowed and firmly rooted into the substrate. *Pileus* dry, finely tomentose under the lens, often cracked, dirty white, cream-white (5A2–A4) or ochraceous cream (6A2), usually with darker ochraceous or brownish stains (6C5). *Hymenophore* loculate, labyrinthoid, cream at first, at maturity becoming deep ochraceous yellow to ochraceous orange (5A6); instantly turning vinaceous in $FeSO_4$; locules minute, 0.2–1 × 0.1–0.3 mm (3–5 per mm), irregularly rounded to elongated, empty or filled; fresh spore mass in locules pale yellow to yellow (4A3–A4); pale orange (5A4–A5) in exsiccata. *Columella* absent or rudimentary, sometimes forming a sterile base or short white veins, but small sterile patches often scattered throughout the hymenophore. *Odour* slightly fruity, sometimes with a vague hint of chocolate when cut; taste astringent.

Spores 7–9.5(–10.5) × 7–9(–10) µm, Q = 1.0–1.1, globose, orthotropic, reticulated; reticulum complete to incomplete, up to 0.5 µm high, formed by strongly amyloid crests and warts; hilar appendix usually rudimentary, exceptionally up to 2–3 µm long. *Basidia* 2–4-spored, 20–35 × 8–12 µm, clavate, thick-walled; sterigmata 4–6 µm long. *Macrocystidia* 25–40 × 8–10 µm, clavate, scarce, very scattered and immersed in the hymenium. *Paraphysoid cells* 11–34 × 7–12 µm, cylindrical to slightly clavate, 1–2-septate. *Subhymenium* ramose, composed of chains of 1–2 globose to irregularly polygonal or elongated cells 5–15 µm diam. *Hymenophoral trama* 40–70 µm wide, prosenchymatous, formed by septate, tortuous, interwoven hyaline hyphae 3–6(–8) µm diam, with some inflated elements up to 12 µm diam and scattered sphaerocytes or nests of sphaerocytes 6–20 µm diam, especially in tramal anastomoses. *Pileipellis* and *context* 120–250(–400) µm thick; pileipellis consisting of: 1) a palisadotrichodermal suprapellis of yellow, clavate dermatocystidia 25–60 × 5–10 µm; and 2) a prosenchymatous subpellis 30–40 µm thick of branched, densely interwoven, septate hyphae 3–6 µm diam. *Pileal context* 80–200 µm thick, arranged in a cutis of septate, hyaline hyphae 1.5–3 µm diam; sphaerocytes absent. Gloeoplera abundant, up to 8 µm diam.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous to semi-hypogeous, in montane woods of *Pinus nigra* subsp. *pallasiana*, rarely also with *Pinus brutia*, on siliceous, well-drained serpentine soils. Summer and autumn. Xerophytic. Known from the eastern Mediterranean region, where it is probably endemic to the island of Cyprus, between 1100–1800 m altitude.

Additional material studied. Cyprus, Limassol District, Troodos, 1800 m, under *Pinus nigra* subsp. *pallasiana*, 7 Oct. 2008, *M. Loizides* (ML8017GY); ibid., 1700 m, 28 Sept. 2009, *M. Loizides* (ML90982GY); ibid., 1600 m, 4 Nov. 2012, *M. Loizides* (ML21114GY); ibid., 26 Aug. 2014, *M. Loizides* (ML41862GY); ibid., 1650 m, 3 Sept. 2014, *M. Loizides* (ML4193GY)*; ibid., 1700 m, 20 Sept. 2016, *M. Loizides* (ML61902GY); Nicosia District, Prodromos, 1450 m, under *Pinus nigra* subsp. *pallasiana*, 7 Oct. 2011, *M. Loizides* (ML11701GY); Platania, 1100 m, under *Pinus brutia*, 16 Nov. 2011, *M. Tordelli* (ML111161GY); ibid., 1120 m, 20 Nov. 2011, *G. Konstantinidis* & *D. Klisiari* (GK5889, duplicate BCN JMV800647)*; ibid., 16 Nov. 2014, *M. Loizides* (ML411161GY)*.

Notes — *Russula hobartiae* is characterized by the typically turbinate shape of its basidiomata, with a flattened upper side and a conical base that is deeply rooted into the substrate and breaks easily. Hymenial chambers are very small, only visible under a lens, cream at first but turning into an intensely orange colour when mature. Microscopically, it is characterised by its

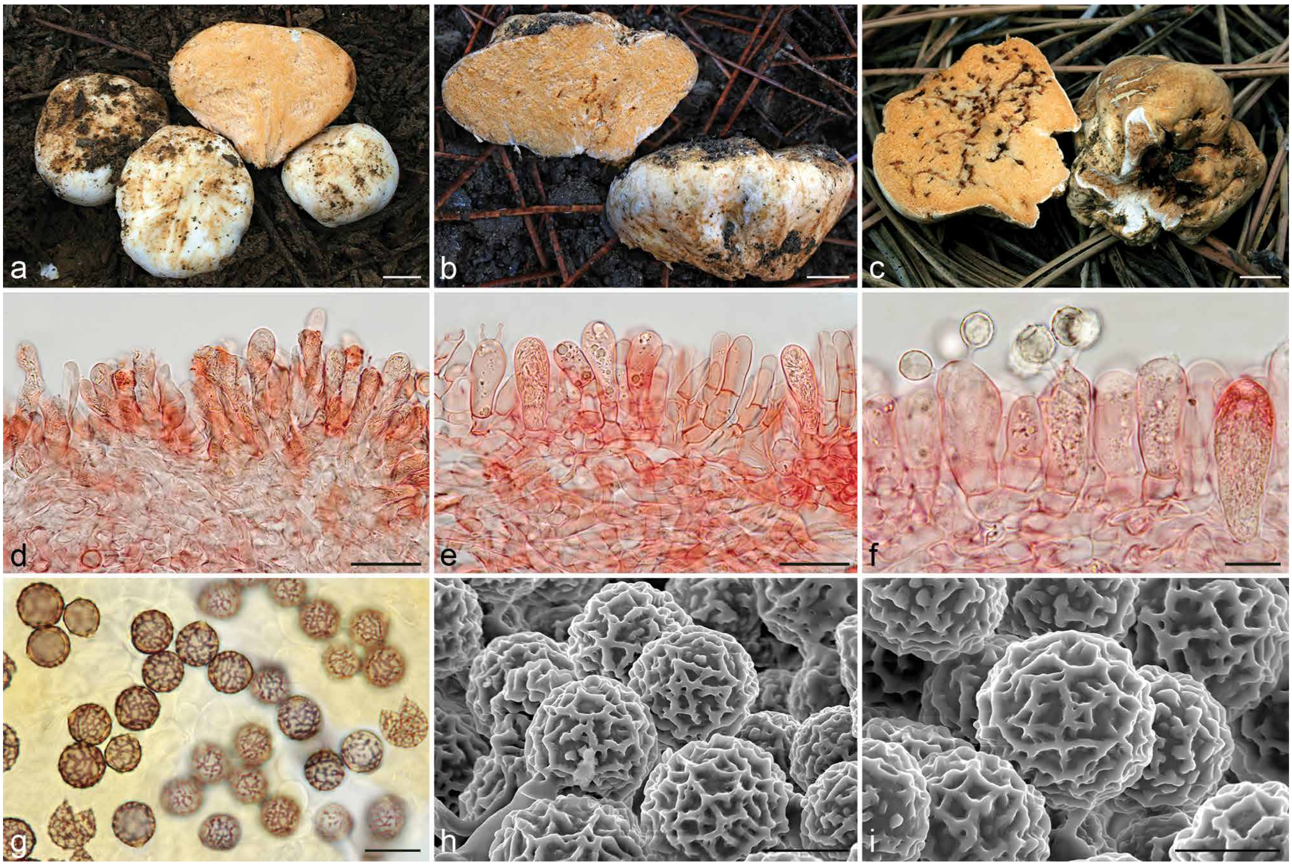

Fig. 20 *Russula hobartiae*. a. ML110131GY (BCN JMV800628, holotype). Basidiomata. — b. ML411161GY. Basidiomata. — c. ML4193GY. Basidiomata. — d–i. ML110131GY (BCN JMV800628, holotype). d. Pileipellis; e. hymenium, subhymenium and hymenophoral trama; f. hymenium and subhymenium; g. spores in Melzer; h–i. SEM images of spores. — Scale bars: a–c = 1 cm; d–f = 20 µm; g = 10 µm; h–i = 5 µm. — Photos: a–c. M. Loizides; d–g. J.M. Vidal; h–i. UdG.

globose or subglobose spores ornamented with a reticulum, its infrequent and very scattered clavate macrocystidia, not exceeding the hymenial layer, and the pileipellis formed by abundant clavate dermatocystidia forming a palisade.

Genetically, *R. hobartiae* is significantly related to a North American specimen identified as *Russula* cf. *ochrophylla* (BPL231, Looney et al. 2016). Currently, there are no other records of *R. ochrophylla* in public databases, so the identity of this sample cannot be confirmed until addtional collections are studied. *Russula ochrophylla* is characterized by a purple pileus, ochraceous yellow lamellae, mild taste, echinulate spores, and preference for broadleaved trees (Peck 1897, Adamčik et al. 2017), features which are remarkably diverse from those of *R. hobartiae*. This morphological disparity could perhaps be explained if: 1) specimen BPL231 does not actually represent *R. ochrophylla*; 2) the features of one of both concerned species are not typical of their lineage; or 3) *R. ochrophylla* and *R. hobartiae* actually belong to different subsections.

Russula mattiroloana (Cavara) T. Lebel, Muelleria 36: 11. 2017 — Fig. 21

Basionym. *Elasmomyces mattiroloanus* Cavara, Malpighia 11, 1–3: 426. 1897 (‘*mattirolianus*’).

Synonym. *Macowanites mattiroloanus* (Cavara) T. Lebel & Trappe, Mycologia 92, 6: 1194. 2000.

Basidiomata russuloid, pseudoangiocarpic, stipitate. *Pileus* 1.2–3.8 cm wide, subglobose to hemisphaerical, open in the base and exposing a marginally sublamellate hymenophore; initially finely tomentose, then smooth, whitish, pale yellow (4A4) to pale orange (5A4), maculated with brownish orange (6C8), finally brownish red (8D7) maculated with dark reddish brown (8E7–F6); greyish orange (5B5) to brown in exsiccata (7E8). *Hymenophore* loculate, labyrinthoid-daedaleoid, initially with an enclosed stipe-columella, soon expanding outwards and exposing the sublamellate hymenium underneath; initially whitish, yellowish white to pale yellow (4A2–A3), then pale yellow (4A5) to pale orange (5A4), finally titian red (7D6); pale orange (5A4) to dark brown in exsiccata (6F7); locules large, 1.5–3 × 0.2–0.8 mm (1–2 per mm), radially arranged,

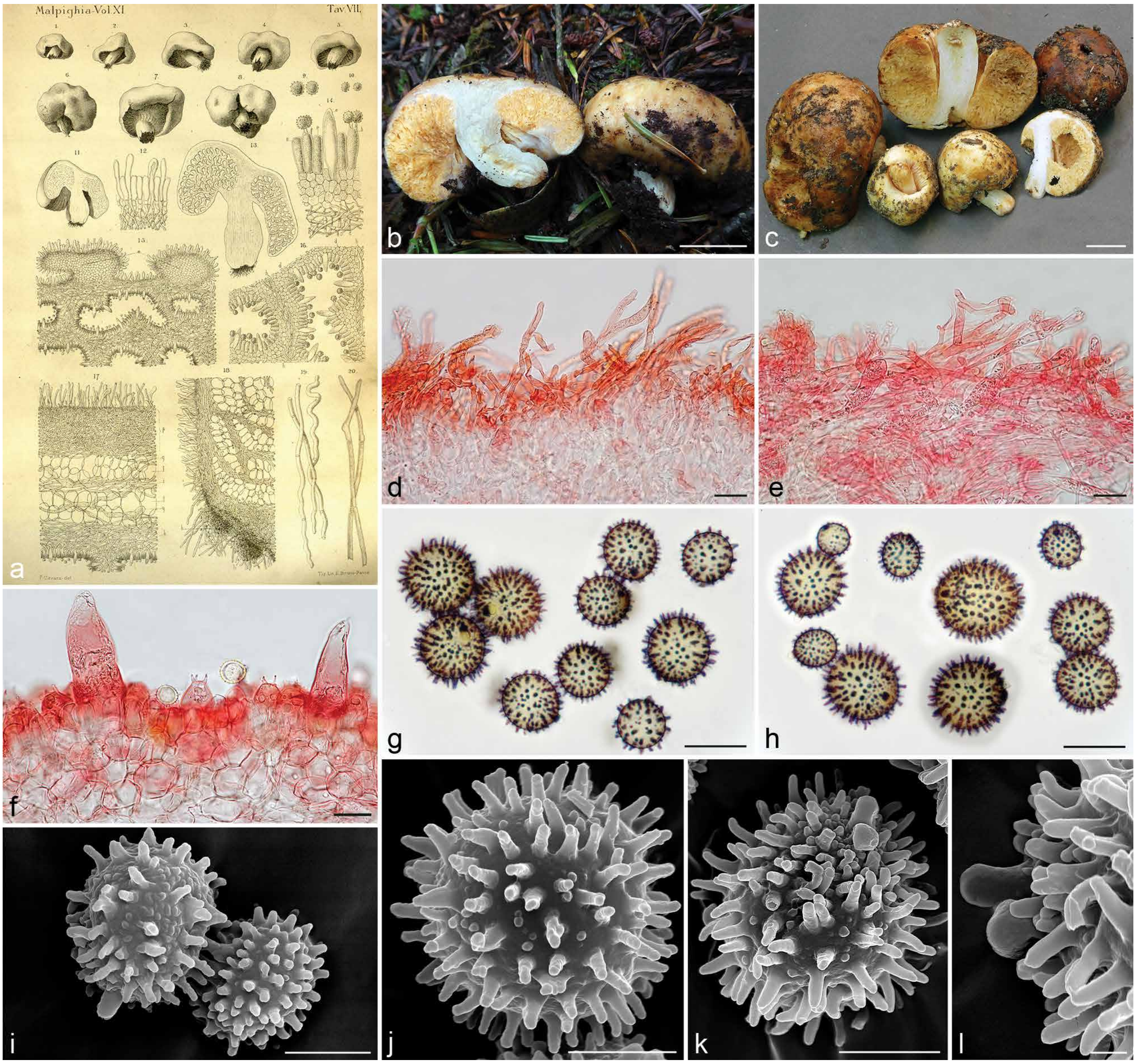

Fig. 21 *Russula mattiroloana*. a. Reproduction of Cavara’s plate of *Elasmomyces mattiroloanus* (Cavara 1897, tav. VII). — b. GK8136. Basidiomata. — c. KRA F-2018-1. Basidiomata. — d–l. KRA F-2012-153. d. Pileipellis; e. stipitipellis; f. hymenium and subhymenium; g–h. spores in Melzer; i–l. SEM images of spores. i. two ellipsoid young spores; j. globose mature spore; k. detached apicular drop over the ornamental warts; l. non-functional apicular drop united to the base of hilar appendix. — Scale bars: b–c = 1 cm; d–f = 20 μm; g–h = 10 μm; i–k = 5 μm; l = 1 μm. — Photos: b. G. Konstantinidis; c. P. Chachuła; d–h. J.M. Vidal; i–l. P. Mleczko, UJ.

elongated, irregular, sinuous; fresh spore mass in locules pale yellow (4A4); pale orange (5A3) to brown (6E6) in exsiccata. *Stipe-columella* 0.8–2.5 × 0.3–1 cm, well developed, percurrent, stipe 2–3 times longer than the columella, cylindrical, generally central, often curved, pruinose, pure white; context white, not changing upon exposure to air, but yellow in the cortical zone. *Odour* and taste mild.

Spores (9–)10.5–15.5(–18) × (8–)10–15(–17) µm, Q = 1.0–1.15, very variable in size, globose to subglobose, some ellipsoid when immature (Q = 1.1–1.2), heterotropic to subheterotropic, echinate; warts (0.7–)1.5–2.5(–3) µm high, isolated, amyloid, conical and straight, with an acute apex; hilar appendix 1.5–2 × 1–1.5 µm, cylindrical, straight, with a minute, inconspicuous, amyloid suprahilar plage in its base and conserving a non-functional apicular drop. *Basidia* 2–4-spored, (25–)45–65 × 17–23 µm, ventricose to broadly clavate; sterigmata 3–5 µm long. *Macrocystidia* abundant, 70–125(–180) × 15–18(–25) µm, cylindrical, lanceolate or fusiform, obtuse or rostrate, with a wall 1 µm thick. *Paraphysoid cells* scarce, 18–28 × 6–8 µm, cylindrical or clavate, aseptate or 1-septate. *Subhymenium* of pseudoparenchymatous aspect, consisting of 3–4 strata of globose to prismatic cells 14–30 µm diam. *Hymenophoral trama* 20–30 µm wide, with scarce sphaerocytes 15–35 µm diam, more abundant in tramal anastomoses. *Pileipellis* and *context* 100–300 µm thick; pileipellis composed of: 1) a trichodermal suprapellis consisting of upright to repent hyphae 2–6.5 µm diam, and abundant, long, cylindrical or clavate, usually 1-septate, yellow dermatocystidia, 60–140 × 3–8 µm; and 2) a subpellis 100–180 µm thick, comprised of a subixocutis of intricate, hyaline hyphae 1.5–5 µm diam, with frequent enlargements 10–20 µm at hyphal ramifications. *Pileal context* heteromerous, 200–1000 µm thick, formed by hyaline hyphae 3–6 µm diam, and abundant nests of sphaerocytes up to 40 µm diam. *Stipitipellis* a turf of repent to erect, septate hyphae, 3–5 µm diam, and clavate dermatocystidia, 50–100 × 5–12 µm, similar in shape and content to those of pileipellis; context of stipe-columella heteromerous, composed of densely interwoven narrow hyphae mixed with nests of sphaerocytes. Gloeoplera 2–5 µm diam, present in trama and context where they terminate as dermatocystidia.

Habitat, Distribution & Season — Solitary to gregarious, subepigeous among needles, in forests of *Abies* and *Picea*, on siliceous or calcareous soils. Summer and autumn. Distributed in temperate and submediterranean regions, from Central to Southern Europe (Carpathian, Pindus and Apennine mountains), between 500–1600 m altitude.

Material studied. Greece, Thessaly, Trikala, Pertouli, Koziakas mountain, Pindus mountains, 1180 m, under *Abies borisii-regis*, 5 July 2009, *G. Konstantinidis* as *M. mattiroloanus* (GK3901, duplicate BCN JMV800638)*; ibid., 1200 m, under *Abies borisii-regis*, 11 July 2015, *G. Konstantinidis* as *M. mattiroloanus* (GK8136, duplicate BCN JMV800644)*. – Italy, Emilia-Romagna, Reggio Emilia, Civago, Abetina Reale Forest, Tuscan-Emilian Apennines, 1500 m, under *Abies alba* and *Fagus sylvatica*, on siliceous soil, 5 Oct. 1983, *A. Montecchi* as '*M. ellipsospora*' (AM1616, duplicate BCN JMV800245); ibid., 1400 m, 10 Aug. 1985, *A. Montecchi* as *E. mattiroloanus* (AM65, duplicate BCN JMV800241); ibid., 16 Aug. 1985, *A. Montecchi* as *E. mattiroloanus* (AM64, duplicate BCN JMV800240); ibid., 1600 m, under *Abies alba* and *Fagus sylvatica*, on siliceous soil, 5 Aug. 1988, *A. Montecchi* as *E. mattiroloanus* (AM825, duplicate BCN JMV800038); Tuscany, Firenze, Reggello, Vallombrosa Forest, Tuscan-Emilian Apennines, 'ad terram sub acubus *Abietis pectinatae* prope S. Giovanni Gualberto Vallisumbrosae (Florentia), *F. Cavara*' (FH, herb. C.W. Dodge 2087; NY, herb. S.M. Zeller 1671; all labelled '*Arcangeliella borziana*, Italy, Etruria, Vallombrosa, forest of firs, autumn 1898, Instituto Botanico di Napoli, coll. F. Cavara, type'; isotypes of *E. mattiroloanus*); Tuscany, 24 Nov. 1899, *O. Mattirolo* as *E. mattiroloanus*, conf. F. Cavara (FH, herb. F. Bucholtz 275). – Poland, Lesser Poland, Pieniny Nat. Park, Western Carpathians, Sokolica massif, close to Hukowa Skała rock, 490 m, under *Abies alba*, on calcareous soil, 13 July 2012, *P. Chachuła* (KRA F-2012-153, duplicate BCN JMV800666)*; ibid., Bajków Groń, 710 m, under *Abies alba*, on calcareous soil, 3 July 2018, *P. Chachuła* (KRA F-2018-1, duplicate BCN JMV800713)*; ibid., Lasek, 660 m, under *Abies alba*, on calcareous soil, 21 July 2018, *P. Chachuła* (KRA F-2018-3, duplicate BCN JMV800715); ibid., Ula mountain, 620 m, under *Abies alba*, on calcareous soil, 8 Nov. 2017, *P. Chachuła* (KRA F-2017-1, duplicate BCN JMV800670)*; ibid., 8 July 2018, *P. Chachuła* (KRA F-2018-2, duplicate BCN-JMV800714)*.

Notes — *Elasmomyces mattiroloanus* was collected under *Abies alba* at the beginning of September 1896 in Tuscany (Italy) by Cavara (1897), who reported it as a russuloid fungus with a pseudoangiocarpic habit, characterized by its globose spores, 14–15 µm diam, and abundant macrocystidia, 70–72 µm long. Singer & Smith (1960) observed microscopical differences between the type material kept at New York Botanical Garden (NY) and the descriptions provided by Cavara: spores were subglobose or ellipsoid, measuring 10–15 × 9.5–13.5 µm, lacked macrocystidia and showed cystidioid 'sterile bodies', measuring 22–27 × 11–12 µm. Lebel & Trappe (2000) studied the same material at NY and confirmed the subglobose to broadly ellipsoid spore shape (although they report different spore measures, 10–12 × 9–11.5 µm), and further discriminated between two different kinds of cystidia: ventricose to clavate, 28–37 × 7–11 µm, and clavate to cylindrical, 8–14 × 3–5 µm. Vidal (2004b) also studied the same type material kept at S.M. Zeller's herbarium in NY (without voucher number) and concluded that microscopical features of these specimens do not match those reported in the protologue of *E. mattiroloanus*, but are compatible with those of *Arcangeliella borziana*, concluding that both species were probably erroneously labelled. The original concept of *E. mattiroloanus* has spores of unequal size and shape, 10.5–15.5(–18) × 10–15(–17) µm, typically globose or subglobose, sometimes ellipsoid when immature, resembling those of *Martellia ellipsospora* sensu Montecchi & Sarasini (2000), and numerous macrocystidia measuring 70–125(–180) × 15–18 µm. In mature spores, it is interesting to observe the intensely amyloid, non-functional apicular drop, which remains located in a basal position in the hilar appendix, immediately above a minute and residual suprahilar plage, which is not always visible, and finally becomes detached on top of ornamental warts, or fused with the suprahilar plage, also observed in spores of *R. mediterraneensis*. Recently, *E. mattiroloanus* was re-combined into genus *Russula* by Lebel (2017).

Genetically, *R. mattiroloana* belongs to the *R. globispora* complex of subsect. *Maculatinae* (Adamčik et al. 2016). Despite ITS rDNA sequences of *R. mattiroloana* sharing a 20 bp deletion not present in any other species of *Maculatinae*, its clade collapsed or received non-significant support (Fig. 5), evidencing the need of additional samples and genetic markers. Subsection *Maculatinae* was originally characterized by species with reddish pilei, acrid taste and a yellow spore print (Romagnesi 1985), but these features are also shared by species not directly related (Adamčik et al. 2016). Interestingly, Sarnari (1998) subsumed *Maculatinae* within subsect. *Urentes*, and highlighted the presence in this group of an amyloid suprahilar spot in spores. The clade formed by *R. globispora* and *R. dryadicola* was reported by Adamčik et al. (2016) to be characterized by spores ornamented with large isolated spines, a feature also observed in *R. mattiroloana*, although also present in species not directly related with this clade, such as *R. candida*. *Russula mattiroloana* seems to be present in *Abies* sp. and *Picea* sp. forests of the alpine Mediterranean regions (Cavara 1897, Montecchi & Lazzari 1986, Montecchi & Sarasini 2000, Konstantinidis 2009) and Central Europe. *Russula globispora* has large, globose spores (Bon 1986, Llistosella 1998, Lejeune 2005) similar to those of *R. mattiroloana*, but spores of *R. dryadicola* and the new species *R. heilongjiangensis* (Li et al. 2018) do not share these features, suggesting that they are not representative of the entire genetic lineage.

Russula mediterraneensis Konstantin., J.M. Vidal, Gelardi, Papadimitriou, Tulli, Angeli & Vizzini, *sp. nov.* — MycoBank MB828505; Fig. 22

Basidiomata russuloid, pseudoangiocarpic, stipitate. *Pileus* 2.3–4.3(–5.2) cm wide, hemispherical to spherical, sometimes lobate, smooth, whitish to yellowish with brown maculae. *Hymenophore* internally daedaleoid and externally lamellate, cream to ochraceous orange. *Stipe-columella* 1.6–4.2 × 0.7–1.8 cm, well developed, percurrent, white. *Odour* of pears or yoghourt and fruit. *Spores* (8–)10–15(–17) × (7–)9–14(–15) µm, subglobose to broadly ellipsoid, heterotropic; warts 0.6–1(–1.5) µm high, isolated or in few groups. *Basidia* 2–3-spored, 30–55 × 11–18 µm, clavate. *Macrocystidia* 70–130 × 12–20 µm. *Hymenophoral trama* heteromerous. *Suprapellis* a trichoderm of erected hyphae 2–6 µm diam, and clavate, septate dermatocystidia 30–160 × 5–10 µm; pileal context heteromerous with nests and columns of sphaerocytes 21–47 µm diam. Found in Greece and Italy, subepigeous under *Quercus* and *Castanea*.

Etymology. From Latin, *Mediterraneum* (*mare*) = Mediterranean Sea, and *-ensis* = from, found in, for its occurrence in Mediterranean localities.

Holotype. GREECE, West Macedonia, Kozani, Vouchorina, 700 m, under *Quercus robur*, 23 July 2013, *G. Konstantinidis* (BCN JMV800641)*; isotype in herb. pers. G. Konstantinidis (GK6710).

Basidiomata russuloid, small to medium sized, pseudoangiocarpic, stipitate. *Pileus* 2.3–4.3(–5.2) cm wide, initially globose to subglobose, sometimes lobate, almost completely closed and covering the whole stipe except its base, later convex to plane, opened basally and exposing a lamellate hymenium, with an involute, dentate margin; rugulose, finely tomentose, white or whitish at first, sometimes with translucent spots, especially at the periphery and margin, later yellowish with ochraceous areas (4A2–A3) and finally mostly bicoloured, yellowish buff (4A4) to ochraceous buff (5A4), with brown maculae (6C8–7D8). *Hymenophore* irregularly loculate inside, daedaleoid, lamellate in the most external parts; locules large, 2–5 × 0.2–1 mm (0.5–1 per mm), labyrinthoid or flexuous in cross-section; lamellae irregular, more or less sinuous, frequently anastomosing and bifurcate, adnate, initially white, later cream, yellowish to ochraceous (4A3–A7), and finally ochre-orange or ochre-buff (6C8), with concolourous, acute or obtuse edges; white remnants of a partial veil can be observed in lamellae edges of some young basidiomata; fresh spore mass in locules yellowish white (4A2). *Stipe-columella* 1.6–4.2 × 0.7–1.8 cm, percurrent, well developed, cylindrical, straight or rarely flexuous, central or eccentric, white, initially solid and later medullary, usually broadening but rarely also tapering at the base; context white, not changing after contact with air. *Odour* pleasantly fruity, of pear or reminiscent of yoghourt and fruit; taste mild to slightly acrid.

Spores (8–)10–15(–17) × (7–)9–14(–15) µm, Q = (1.0–)1.10–1.25(–1.3), very variable in form and size, globose, subglobose, broadly ellipsoid to ovoid, heterotropic, echinate, some with one large, central oil drop; warts 0.6–1(–1.5) µm high, amyloid, irregularly conical or truncated, scattered or packed in few groups, with some verrucae among them; hilar appendix 1.2–1.8 µm long, cylindrical, with a distinct amyloid suprahilar plage in its base and conserving a non-functional apicular drop as in *R. mattiroloana*. *Basidia* (1–)2–3(–4)-spored, 30–55 × 11–18 µm, clavate, some of them with one or more oil droplets and amorphous yellowish content; sterigmata (4–)6.5–7.5 µm long. *Basidioles* 30–35 × 10–15 µm, clavate. *Macrocystidia* abundant (40–)70–130(–180) × 12–20 µm, subcylindrical, lanceolate to fusiform, thin-walled or slightly thick-walled in the central portion, 1–1.6 µm thick, with abundant amorphous yellowish content, and an obtuse to acute or subulate apex, sometimes rostrate. *Paraphysoid cells* scarce, 12–26 × 6–9 µm, cylindrical, entire or 1-septate. *Subhymenium* cellular,

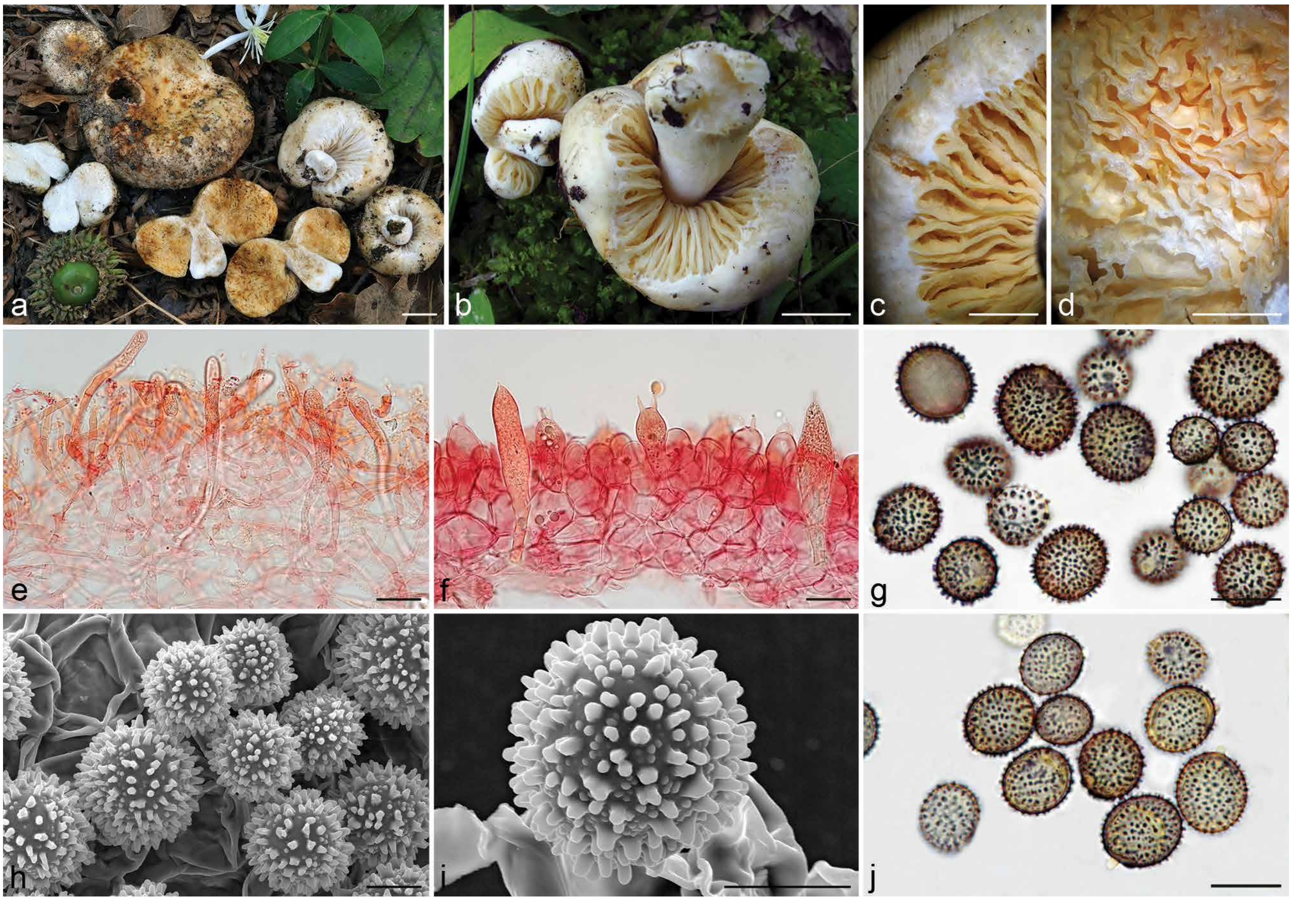

Fig. 22 *Russula mediterraneensis*. a. MG630. Basidiomata. — b–i. GK6710 (BCN JMV800641, holotype). b. Basidiomata; c. external lamellar hymenium; d. daedaleoid hymenophore; e. pileipellis; f. hymenium and subhymenium; g. spores in Melzer; h–i. SEM images of spores. — j. GK7286. Spores in Melzer. — Scale bars: a–b = 1 cm; c–d = 5 mm; e–f = 20 µm; g, j = 10 µm; h–i = 5 µm. — Photos: a. M. Gelardi; b–d. G. Konstantinidis; e–g, j. J.M. Vidal; h–i. UdG.

consisting of 3–4 strata of globose to prismatic cells 9–28 µm diam. *Hymenophoral trama* heteromerous, made of hyaline, loosely interwoven septate hyphae 3–9 µm wide, with abundant sphaerocytes 21–47 µm diam, and some gloeoplera 2–7 µm diam. *Pileipellis* and *context* 100–300 µm thick; pileipellis composed of: 1) a trichodermal suprapellis made of erect to semi-erect, septate hyphae 2–6 µm diam, and abundant clavate, septate dermatocystidia 30–160 × 5–10 µm; and 2) a prosenchymatous subpellis of intricate hyphae 2–6 µm diam. *Pileal context* heteromerous, composed of septate hyphae 2–6 µm diam, mixed with several inflated hyphae and abundant nests and columns of sphaerocytes 21–47 µm diam. *Stipitipellis* a texture of interwoven, branched hyphae similar in shape and content to pileipellis dermatocystidia.

Habitat, Distribution & Season — Gregarious, subepigeous among plant debris, in broadleaved woods of *Quercus* and *Castanea*, on siliceous soil. Summer. Occurring in the central and east-Mediterranean regions, in Greece and Italy, from sea level up to 1000 m altitude.

Additional material studied. Greece, Central Macedonia, Kilkis, Koupa, 590 m, under *Quercus* sp., 8 July 2009, *G. Konstantinidis* (GK3930, duplicate BCN JMV800639)*; North Aegean, Lesbos Island, Agiasos, under *Castanea sativa*, 8 June 2014, sine leg. (GK7286, duplicate BCN JMV800642)*; Thessaly, Trikala, Logga, 1040 m, under *Quercus petraea*, 16 June 2012, *G. Konstantinidis* (GK6072, duplicate BCN JMV800640). – Italy, Lazio, Roma, Nettuno, Torre Astura, 5 m, under *Quercus robur*, *Quercus frainetto* and *Quercus cerris* with presence of *Pinus pinea*, 2 Aug. 2014, *M. Gelardi*, *M. Tulli* & *R. Polverini* (MG630, duplicate MCVE 29085)*; ibid., 9 Aug. 2014, *M. Gelardi*, *M. Tulli* & *R. Polverini* (MG636, duplicate MCVE 29086)*.

Notes — *Russula mediterraneensis* belongs to the *R. globispora* complex of subsect. *Maculatinae*, and is therefore related with *R. mattiroloana*, but differs because of its larger basidiomata, its hymenophore comprised of a daedaleoid, loculate inner part and a clearly lamellate external part, its subglobose to ellipsoid spores with lower warts and a distinct amyloid suprahilar plage, its trama and context featuring abundant sphaerocytes, and its ecological association with broadleaved trees. The large spore size (up to 17 µm) is similar to that observed in *R. globispora* and *R. mattiroloana*, but different from those found in *R. dryadicola* and *R. heilongjiangensis*.

Russula meridionalis (Calonge et al.) J.M. Vidal, Mor.-Arr. & A. Paz, *comb. nov.* — MycoBank MB828506; Fig. 23

Basionym. *Zelleromyces meridionalis* Calonge et al., Bol. Soc. Micol. Madrid 25: 302. 2000.

Synonyms. *Gymnomyces meridionalis* (Calonge et al.) J.M. Vidal, Rev. Catalana Micol. 26: 78. 2004.

Gymnomyces dominguezii Mor.-Arr. et al., Bol. Soc. Micol. Madrid 25: 301. 2000. (syn. nov.)

Russula dominguezii (Mor.-Arr. et al.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 2: 361. 2018.

Basidiomata 1–2 cm wide, angiocarpic, sessile, subglobose to lobate or irregular. *Pileus* smooth, pale cream to ochraceous, drying dark reddish brown, intense red in contact with KOH. *Hymenophore* loculate, pale cream to ochraceous. *Columella* and sterile base present or absent. *Odour* fruity.
Spores 8–11 × 7–10 µm, Q = 1.03–1.12, globose to subglobose, orthotropic; reticulum 0.4–0.6 µm high, composed of isolate warts and ridges, amyloid. *Basidia* 4-spored, 25–40 × 10–16 µm, clavate. *Macrocystidia* absent. *Cystidioles* like in var. *messapicoides*. *Hymenophoral trama* heteromerous. *Suprapellis* a trichoderm of septate hairs less developed than in var. *messapicoides*.

Habitat, Distribution & Season — Gregarious, hypogeous in continental sclerophyllous woods of *Quercus rotundifolia*, commonly on siliceous soil. Autumn and spring. Located in the western Mediterranean region, in Central Spain, between 400–1100 m altitude.

Material studied. Spain, Andalusia, Córdoba, Cabra, under *Quercus rotundifolia*, 21 June 1997, *B. Moreno-Arroyo* & *J. Gómez* (MA-Fungi 38502, holotype of *Z. meridionalis*; BM410, isotype)*; Córdoba, Cabra, La Nava, 1070 m, under *Quercus rotundifolia*, 24 May 2015, *C. Lavoise*, *A. Paz* & *R. Molina* (BCN IC24051506)*; Córdoba, Priego de Córdoba, Dehesilla Carcabuey, 700 m, under *Quercus rotundifolia*, 18 May 1993, *J. Gómez* (MA-Fungi 32069, paratype of *Z. meridionalis*); ibid., 20 May 2014, *J. Gómez* & *A. Paz* (BCN IC20051417)*; Córdoba, carretera de Los Villares, under *Quercus rotundifolia* with *Cistus crispus* and *Pistacia lentiscus*, Feb. 1996, *B. Moreno-Arroyo* & *J. Gómez* BM412 (MA-Fungi 38572, holotype of *G. dominguezii*); Castilla and Leon, Valladolid, Urueña, montes Torozos, 830 m, under *Quercus rotundifolia*, on sandy soil, 17 June 2018, *J. Cabero* (JC-180617NR)*; Extremadura, Cáceres, Torrejón el Rubio, Parque Nacional de Monfragüe, 370 m, under *Quercus rotundifolia*, on siliceous soil, 15 Apr. 2007, *A. Paz* (BCN IC15040721).

Notes — The holotype of *Z. meridionalis* is genetically very similar to the sequences of *R. messapica* and *M. messapicoides* analyzed in the present work. The three taxa seem to represent a monophyletic lineage, where no significant differences in ITS, 28S rDNA or *rpb2* data were found between *R. messapica* and *M. messapicoides*. Both taxa were in turn significantly different from the holotype of *Z. meridionalis* and other samples of this species, although no significant relationship was found between other collections identified as *Z. meridionalis*. Therefore, *M. messapicoides* is subsumed under the prioritary name *R. messapica*, while *Z. meridionalis* is re-combined into *Russula* but retained as an independent species due to the small differences found in ITS rDNA (2/715 bp different from *R. messapica* in sequences MK105663–MK105665 and MK105667) and *rpb2* (6/639 bp different in MK102762). These differences did not produce a significant phylogenetic support for a monophyletic *R. meridionalis*, but this was probably caused by the lack of data, especially *rpb2*, from all specimens tested. *Russula meridionalis* has a restricted geographic distribution (under *Quercus rotundifolia* in Southern and Central Spain), and constitutes at least a partially supported distinct genetic lineage, while *R. messapica* var. *messapicoides* occurs in the same areas as *R. messapica* var. *messapica* (under *Quercus ilex* in the Mediterranean basin, from Eastern Spain to Greece), but did not receive any significant support as a distinct genetic lineage employing ITS, 28S rDNA, *rpb2* and *tef1* data.

Basidiomata of *R. meridionalis* are angiocarpic and sessile or subsessile, with a completely loculate hymenophore, generally with traces of a columella and a small stipe or sterile base. The trichodermis (which is part of the universal veil) is reduced or partially lost in the substrate due to the hypogeous mode of growth, so the pileus does not always react intensely in contact with KOH 10 % as it does in *R. messapica*. Microscopical features of *R. meridionalis* are very similar to those of *R. messapica*, viz. tetrasporic basidia, subreticulate spores ornamented with an incomplete reticulum, and a more or less developed trichodermal suprapellis made of septate hairs with golden yellow encrusted pigment, which turns red in contact with KOH. Microscopical characters of *Gymnomyces dominguezii* (Moreno-Arroyo et al. 1999) also match those of *R. meridionalis*, viz. suprapellis a trichoderm, basidia tetrasporic and globose to subglobose spores 8–10 µm diam, ornamented with an incomplete reticulum 0.4–0.6 µm high. Despite the fact that attempts to produce genetic data from *G. dominguezii* yielded no useful results, this species is here considered a synonym of *R. meridionalis* because of their morphological similarities and identical geographical distribution.

Russula messapica Sarnari var. *messapica* in Sarnari, Boll. Assoc. Micol. Ecol. Romana 5, 18: 12. 1989 — Fig. 24a left

Material studied. Italy, Apulia, Taranto, Avetrana, Bosco Modunato, under *Quercus ilex*, on calcareous soil, 15 Dec. 2013, *C. Agnello* (AH 46373)*. – Spain, Balearic Islands, Menorca, Alaior, Binixems, on calcareous soil, 120 m, under *Quercus ilex*, 18 Nov. 2011, *J. Llistosella* (BCN JL201111182)*; Catalonia, Girona, Rupià, Bosc Geltrú, 120 m, under *Quercus ilex*, close to *R. messapica* var. *messapicoides*, 22 May 1993, *J.M. Vidal* (BCN JMV930522-12a).

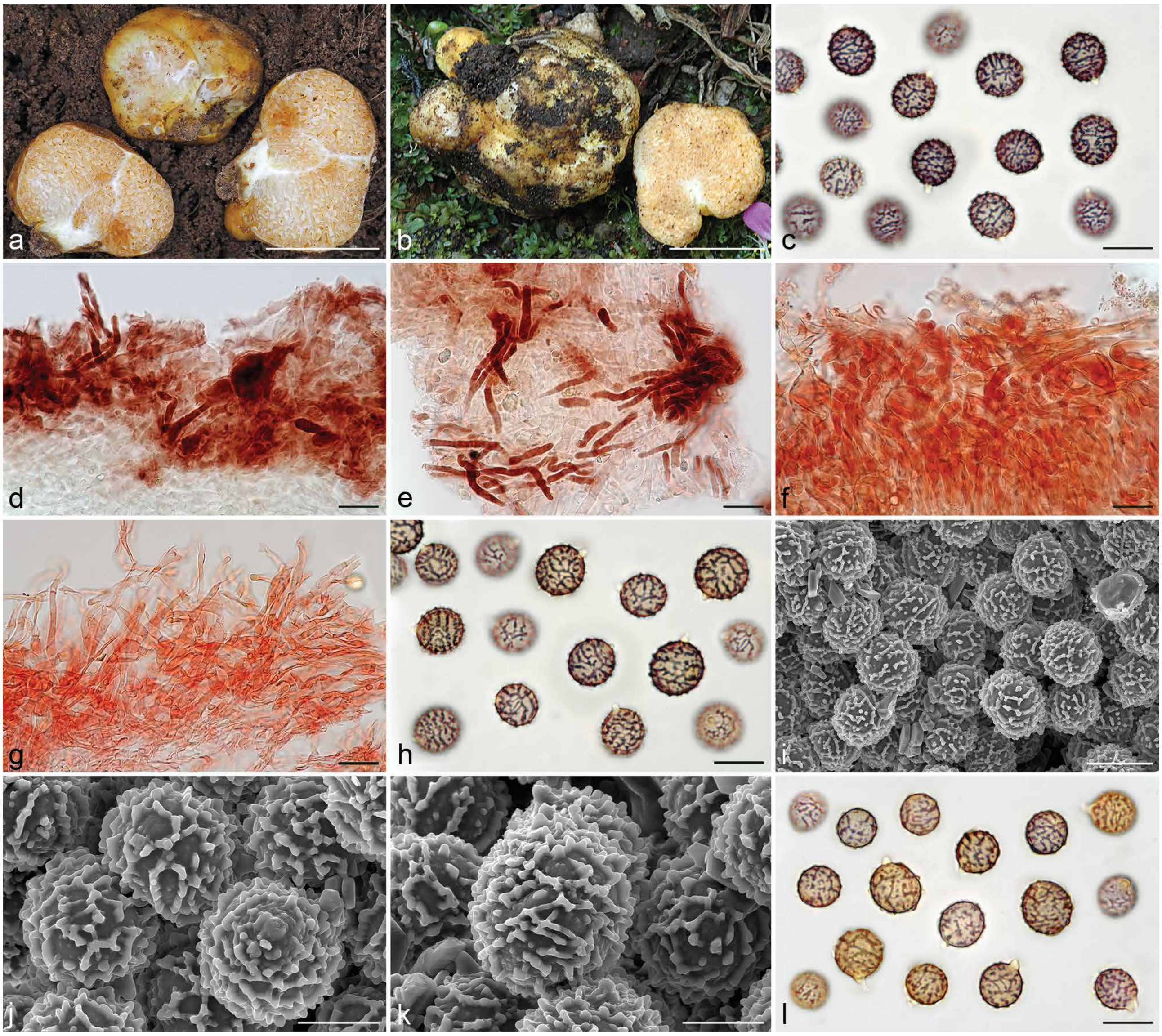

Fig. 23 *Russula meridionalis*. a. JC180617NR. Basidiomata. — b–c. IC15040721. b. Basidiomata; c. spores in Melzer. — d–e. IC20051417. Red reaction of the hairs of the suprapellis in contact with KOH 5 %. — f. IC24051506. Red reaction of the suprapellis in contact with KOH 5 %. — g–k. MA-Fungi 38502 (holotype of *Zelleromyces meridionalis*). g. Suprapellis in KOH 5 % and red Congo; h. spores in Melzer; i–k. SEM images of spores. — l. MA-Fungi 38572 (holotype of *Gymnomyces dominguezii*). Spores in Melzer. — Scale bars: a–b = 1 cm; c, h–i, l = 10 µm; d–g = 20 µm; j–k = 5 µm. — Photos: a. J. Cabero; b. A. Paz; c–h, l. J.M. Vidal; i–k. UdG.

Russula messapica var. ***messapicoides*** (Llistos. & J.M. Vidal) J.M. Vidal, Llistos., Kaounas & P. Alvarado, *comb. & stat. nov*. — MycoBank MB828507; Fig. 24

Basionym. *Macowanites messapicoides* Llistos. & J.M. Vidal, Rivista Micol. AMB 38, 2: 155. 1995.

Synonym. *Russula messapicoides* (Llistos. & J.M. Vidal) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 236. 2018.

Basidiomata russuloid, pseudoangiocarpic, stipitate. *Pileus* 0.5–2 cm wide, rounded or occasionally bi- or trilobate, areolate, papillose, pale yellow to orange-yellow, intensely red in contact with KOH 10 %; margin laterally open, alveolate to sublamellate. *Hymenophore* loculate to sublamellate, pale yellow to pale orange. *Stipe-columella* 0.3–0.7 × 0.15–0.2 cm, concolourous with pileus; context white. *Odour* fruity, similar to fermented fruits of *Sorbus domestica*.

Spores 8–10 × 7.5–9.5 µm, Q = 1.0–1.1, globose to subglobose, subheterotropic to orthotropic; reticulum 0.6–1.2 µm high, amyloid, made by isolate warts forming ridges. *Basidia* 4-spored, 40–56 × 12–15 µm, clavate. *Macrocystidia* absent. *Cystidioles* 44–67 × 7–14 µm, scarce. *Hymenophoral trama* heteromerous. *Suprapellis* a trichoderm arranged in tufts of septate hairs 40–125 × 3–6 µm, with golden yellow encrusted pigment (soon dissolved in KOH) and sometimes also intracellular pigment (reddish brown in KOH); basal elements ampullaceous, 8–30 µm diam; dermatocystidia absent.

Habitat, Distribution & Season — Gregarious, semi-hypogeous under fallen leaves, in sclerophyllous woods of *Quercus ilex* and *Q. coccifera*, commonly on calcareous soil, occasionally coexisting with *R. messapica* var. *messapica*. Spring to autumn. Widely distributed along the Mediterranean littoral, from Greece to Northern Spain, between 100–650 m altitude.

Material studied. Greece, Central Greece, Attica, Katsimidi, 650 m, under *Quercus ilex* with *Pinus halepensis* and *Quercus coccifera*, on calcareous soil, 5 June 2013, *V. Kaounas* (VK2998)*; ibid., 8 May 2014, *V. Kaounas* (VK3368)*; ibid., 28 May 2014, *V. Kaounas* (VK3411, duplicate BCN JMV800682)*; Crete, Retymnon, Arkadi, 520 m, under *Quercus ilex*, on calcareous soil, 27 Mar. 2016, *V. Ramoutsakis* (GK9341, duplicate BCN JMV800645)*. – Spain, Castilla and Leon, León, Santibáñez de la Isla, under *Quercus rotundifolia*, *Quercus faginea* and *Fraxinus angustifolia*, on siliceous soil, 28 Nov. 2006, *A. Paz* as *M. messapicoides* (BCN IC28110613)*; Catalonia, Girona, Rupià, Bosc Geltrú, 120 m, under *Quercus ilex*, in the same habitat as *Tuber aestivum*, 28 Apr. 1992, *J.M. Vidal* (BCN JMV920428-1, paratype of *M. messapicoides*); ibid., 22 May 1993, *J.M. Vidal* (BCN JMV930522-12b, paratype of *M. messapicoides*); ibid., 26 May 1993, *J.M. Vidal* & *J. Llistosella* (BCN JL1493, holotype of *M. messapicoides*)*; ibid., 17 Oct. 2001, *J.M. Vidal* (BCN JMV20011017-1).

Fig. 24 *Russula messapica* var. *messapicoides*. a. JMV930522-12a/b. Basidiomata of *R. messapica* var. *messapica* (left) and var. *messapicoides* (right). — b. VK2998b/3368b. Red reaction of the pileus in contact with KOH 10 %. — c. VK3411. Basidiomata. — d–e. JMV920428-1 (paratype of *M. messapicoides*). d. Basidiomata; e. spores in Melzer. — f. GK9341. Spores in Melzer. — g–m. JMV20011017-1. g. Basidiomata; h. red reaction of the hairs of the suprapellis in contact with KOH 5 %; i. detail of suprapellis and subpellis; j. hymenium with one cystidiole and subhymenium; k–m. SEM images of spores. — Scale bars: a–d, g = 1 cm; e–f = 10 µm; h–j = 20 µm; k–m = 5 µm. — Photos: a, d–j. J.M. Vidal; b–c. V. Kaounas; k–m. UdG.

Notes — *Macowanites messapicoides* was first proposed as a new species more or less identical with *Russula messapica*, except for its sequestrate habit (Llistosella & Vidal 1995). Martín et al. (1999) found that RFLP profiles of mt-LrDNA, mt-SrDNA and ITS nrDNA regions were identical in *R. messapica* and *M. messapicoides*, and only the highly variable IGS region could be used to discriminate between them. However, Martín et al. (1999) only analyzed a single specimen from each species, and these were found growing at the same time only a few meters apart from one-another (Llistosella & Vidal 1995). Martín et al. (1999) suggested that *M. messapicoides* was recently derived from *R. messapica*, but noted that the status of both taxa as independent species could not be confirmed by their results. Later, Miller et al. (2006) referred to this case as an example of an angiocarpic taxon being conspecific with a gymnocarpic species of *Russula*, even though they did not formally propose the synonymy. In the present work, four DNA markers (ITS, 28S rDNA, *rpb2*, *tef1*) were sequenced from several specimens of *M. messapicoides* and *R. messapica*, originating from different countries of the Mediterranean basin. Results show that no significant differences exist between the two taxa (*tef1* GenBank accessions MK102731–MK102735), but both taxa are here kept as distinct varieties because of their different habit. The rank of variety is the first infraspecific category recommended by Art. 4 of the International Code of Nomenclature (Turland et al. 2018), and there is currently no consensus about the application of other ranks, such as subspecies or forma (Turner & Nesom 2000). *Russula messapica* var. *messapica*, *R. messapica* var. *messapicoides*, and *R. meridionalis* were significantly related to subsect. *Puellarinae* (PP 1.00, BP 90), in concordance with previous phylogenetic reconstructions of *Russula* (Miller & Buyck 2002, Bazzicalupo et al. 2017). The species most closely related are *R. cessans*, *R. odorata*, *R. puellaris* and *R. versicolor*.

Morphologically, *R. messapica* var. *messapicoides* is a sequestrate miniature of *R. messapica* var. *messapica*, where lamellae and stipe are progressively transformed into alveoli and columella. In the specimens from Attica (Greece) studied in the present work, the pileus is barely closed, the hymenophore is daedaleoid-sublamellate, and the stipe is well developed. On the other hand, the specimens from Catalonia (Spain) present an almost closed pileus, loculate hymenophore, and a reduced stipe. In all specimens, the suprapellis is a yellowish trichoderm that turns red in contact with KOH, the hymenium is formed by tetrasporic basidia and scattered macrocystidia, and spores are subreticulated. The spores are ellipsoid and heterotropic in *R. messapica* var. *messapica*, showing a suprahilar plage, and subglobose to globose, orthotropic, without a suprahilar plage in *R. messapica* var. *messapicoides*, which produces statismospores, except in Greek collections from Attica where the spores are subheterotropic and the suprahilar plage is still present. Both taxa seem to occur under *Quercus ilex* across the entire Mediterranean region.

Russula mistiformis (Mattir.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 236. 2018 — Fig. 25

Basionym. *Martellia mistiformis* Mattir., Malpighia 14: 81. 1900.

Synonyms. *Hydnangium mistiforme* (Mattir.) Zeller & C.W. Dodge, Ann. Missouri Bot. Gard. 22: 372. 1935.

Octaviania mistiformis (Mattir.) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 743. 1958.

Gymnomyces mistiformis (Mattir.) T. Lebel & Trappe, Mycologia 92, 6: 1199. 2000.

Martellia mediterranea G. Moreno et al., Mycotaxon 42: 227. 1991. (syn. nov.)

Russula mediterranea (G. Moreno et al.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 236. 2018.

Basidiomata 0.6–2.2 cm wide, angiocarpic, subglobose to obovoid or tuberiform, sessile, lacking a sterile base, but occasionally attached to the soil by a fragile mycelial strand the same colour as the pileus. *Pileus* at first finely tomentose, white, then smooth, with olivaceus, pastel yellow (3A4) or cream, pale orange (5A3) tones, finally displaying brown (7E8) maculae because of contact with air and handling; basally open and alveolate in old specimens. *Hymenophore* loculate, labyrinthoid, at first pale yellow (4A3) or pale orange (6A3), finally brown (6C6–7D7–7E8); locules 0.4–1.2 × 0.1–0.4 mm (2–4 per mm), radially arranged, elongated, sinuous; fresh spore mass in locules pale yellow (4A5) to brownish red (8C7); dark brown (6F8) in exsiccata. *Columella* absent. *Odour* in young specimens resembling that of an apple, very intense in mature specimens, similar to *Tuber melanosporum*.

Spores (8.5–)9.5–11(–12.5) × (8–)8.5–10(–10.5) µm, Q = 1.1–1.2, subglobose to ovoid, orthotropic, uniguttulate, echinate, orange to reddish in KOH; warts of regular length, 0.8–1.6(–3) µm high, yellow, deeply amyloid, cylindrical with an obtuse tip, sometimes interconnected with low ridges and with some isolated verrucae among them; hilar appendix about 2 µm long. *Basidia* scarce, typically 4-spored, but sometimes also 1–3-spored, 30–50 × 12–18 µm, clavate to broadly clavate, filled with small dark yellowish or dark reddish oil droplets, soon collapsing, originating in the deep subhymenium; sterigmata 3–7(–10) µm long, conical. *Basidioles* scarce, 21–35 × 7.5–12.5 µm, clavate. *Macrocystidia* absent. *Cystidioles* 27–40 × 6.5–9 µm; abundant in immature external locules, similar to dermatocystidia, cylindrical to fusoid, septate, sinuous, acute, capitulate, moniliform, filled with granular hyaline or yellowish content; rare in mature locules, cylindrical to fusoid or lageniform, typically capitate, not exceeding basidia in length. *Paraphysoid cells* abundant, 20–40 × 8–16 µm, commonly 1-septate. *Subhymenium* pseudoparenchymatous, formed of 2–3 layers of polygonal cells, 7–20(–25) µm diam. *Hymenophoral trama* 10–20 µm wide, formed of hyphae about 3–8.5 µm, connecting with those of pileal context; inflated elements up to 12 µm can be found sometimes in tramal anastomoses as well as sphaerocytes 10–20 µm diam. *Pileipellis* and *context* 80–240 µm thick, separable from the hymenophore; pileipellis thin, consisting of: 1) a trichodermal suprapellis, soon collapsing into a brownish mass, formed of very fragile, tapered dermatocystidia 20–40 × 3–6 µm, frequently with a mucronate apex; and 2) a prosenchymatous subpellis 20–30 µm thick, formed of interwoven subgelatinized hyphae 2–5.5 µm diam, slightly differing from those of the pileal context. *Pileal context* 70–220 µm thick, prosenchymatous, formed by interwoven subgelatinized hyphae about 2–5.5 µm thick, lacking sphaerocytes. Thromboplera abundant in trama and context.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous, associated with *Quercus*, *Castanea* and *Pinus*, on siliceous soil. From spring to late autumn. Found throughout the Mediterranean region, from Greece to Spain, from sea level up to 1200 m altitude.

Material studied. Greece, North Aegean, Lesbos Island, 500 m, under *Castanea sativa* with *Crataegus monogyna* and *Quercus coccifera*, on siliceous soil, 29 Jan. 2017, *G. Fransouas* (BCN JMV800652)*. – Italy, Sardinia, Nuoro, Orune, under *Quercus suber*, May 1900, *U. Martelli* (FH, herb. N. Patouillard, original material of *M. mistiformis*); Oristano, Pau, Is Lottus, 550 m, under *Quercus ilex*, on siliceous soil, 1 May 1989, *P. Fantini* (BCN JMV800124); Oristano, Santu Lussurgiu, Rio e Messi, 650 m, under *Quercus pubescens* and *Alnus glutinosa*, on siliceous soil, 28 Oct. 1999, *P. Fantini* (BCN JMV800125)*. – Spain, Castilla and Leon, Segovia, La Granja de San Ildefonso, 1200 m, under *Quercus pyrenaica*, on siliceous soil, 27 Nov. 1997, *F. García* (AMC H-69, duplicate BCN JMV971127)*; Zamora, Tábara, under *Pinus sylvestris* with *Quercus rotundifolia* and *Erica arborea*, on siliceous soil, 6 Dec. 2010, *J. Cabero* (JC101206BT, duplicate BCN JMV800663)*; ibid., 2 Jan. 2011, *J. Cabero* (JC110102NR)*; ibid., 17 Nov. 2013, *J. Cabero* (JC131117NR, duplicate BCN JMV800662)*; Zamora, Villar del Buey, under *Quercus pyrenaica*, on siliceous soil, 5 Mar. 2017, *J. Cabero* (JC170305NR, duplicate BCN JMV800661)*; Catalonia, Girona, Quart, Sant Mateu de Montnegre, Les Gavarres, 350 m, under *Quercus ilex*, *Quercus suber* and *Pinus pinaster*, 7 June 2014, *F. Rodríguez* (BCN JMV20140607-3)*; Girona, Sant Sadurní de l'Heura, Can Torrent, Les Gavarres, 150 m, under *Pinus radiata*, 23 May 1991, *J.M. Vidal* as '*M. pila*' (BCN JMV910523-3); ibid., 11 May 1992, *J.M. Vidal* as '*M. pila*' (BCN JMV920511-3); ibid., 26 June 1992, *J.M. Vidal* as '*M. pila*' (BCN JMV920626-1)*; ibid., Pla de Banyeres, Les Gavarres, 80 m, under *Pinus pinea*, on siliceous soil, 24 May 2016, *F. Rodríguez* & *J.M. Vidal* (BCN JMV20160524-1)*; Girona, Santa Cristina d'Aro, Romanyà, Can Pons, Les Gavarres, 365 m, under *Pinus pinaster*, 26 Dec. 1990, *J.M. Vidal* as '*M. pila*' (BCN JMV901226-6); ibid., 20 Nov. 1993, *J.M. Vidal*, *A. Montecchi* & *M.P. Martín* (BCN JMV931120-9); ibid., 26 Dec. 1996, *J.M. Vidal* (BCN JMV961226-1); Extremadura, Cáceres, Parque Nacional de Monfragüe, under *Quercus suber* with *Cistus ladanifer*, 9 Nov. 1987, *A. Montecchi et al.* (AH GM-RG11057, holotype of *M. mediterranea*; BCN JMV800632, isotype)*; Cáceres, Jarandilla de la Vera, under *Quercus pyrenaica* and *Pinus* sp., 15 Dec. 2012, *A. Paz* (BCN IC15121207/IC15121208/IC15121209).

Notes — *Martellia mistiformis* was described and illustrated by Mattirolo (1900) to accommodate several collections found by U. Martelli under *Quercus ilex* and *Q. suber* in the island of Sardinia (Italy), as well as additional collections from the island of Sicily. Mattirolo highlighted the hyphal hymenophoral trama, the predominantly tetrasporic basidia and the umber-coloured, globose to subglobose or slightly ellipsoid, echinate spores of 10 µm diam. This species was redescribed by Lebel & Trappe (2000) in a paper dedicated to the study of the generic types of sequestrate *Russulales*, and recombined into the genus *Gymnomyces* after observing sphaerocytes in the hymenophoral trama of the isotypic material at FH and NY herbaria. Recently, this species was re-combined into genus *Russula* by Elliott & Trappe (2018).

The first genetic data of *R. mistiformis* obtained by Calonge & Martín (2000) from specimens collected and illustrated by Vidal (1991a) as *Octaviania pila*, and subsequently described by Vidal (1991b) as *Martellia pila*, were found to have a close relationship with *R. foetens*. These early sequences (AF230893 and AF230894) contained some sequencing errors and so new data from the same collections, GM-RG11057 (AH) and JMV920626-1 (BCN), were produced in this study (Table 1). Whitbeck (2003) obtained additional sequences from a specimen collected by A. Montecchi in Italy (AM1653). In the present work, new collections from Italy and Spain were tested and shown to be genetically identical to one-another. ITS and 28S rDNA obtained from the holotype of *Martellia mediterranea* (AH GM-RG11057), were identical to those of *R. mistiformis*, and both species have also very similar morphology, ecological preferences and geographi-

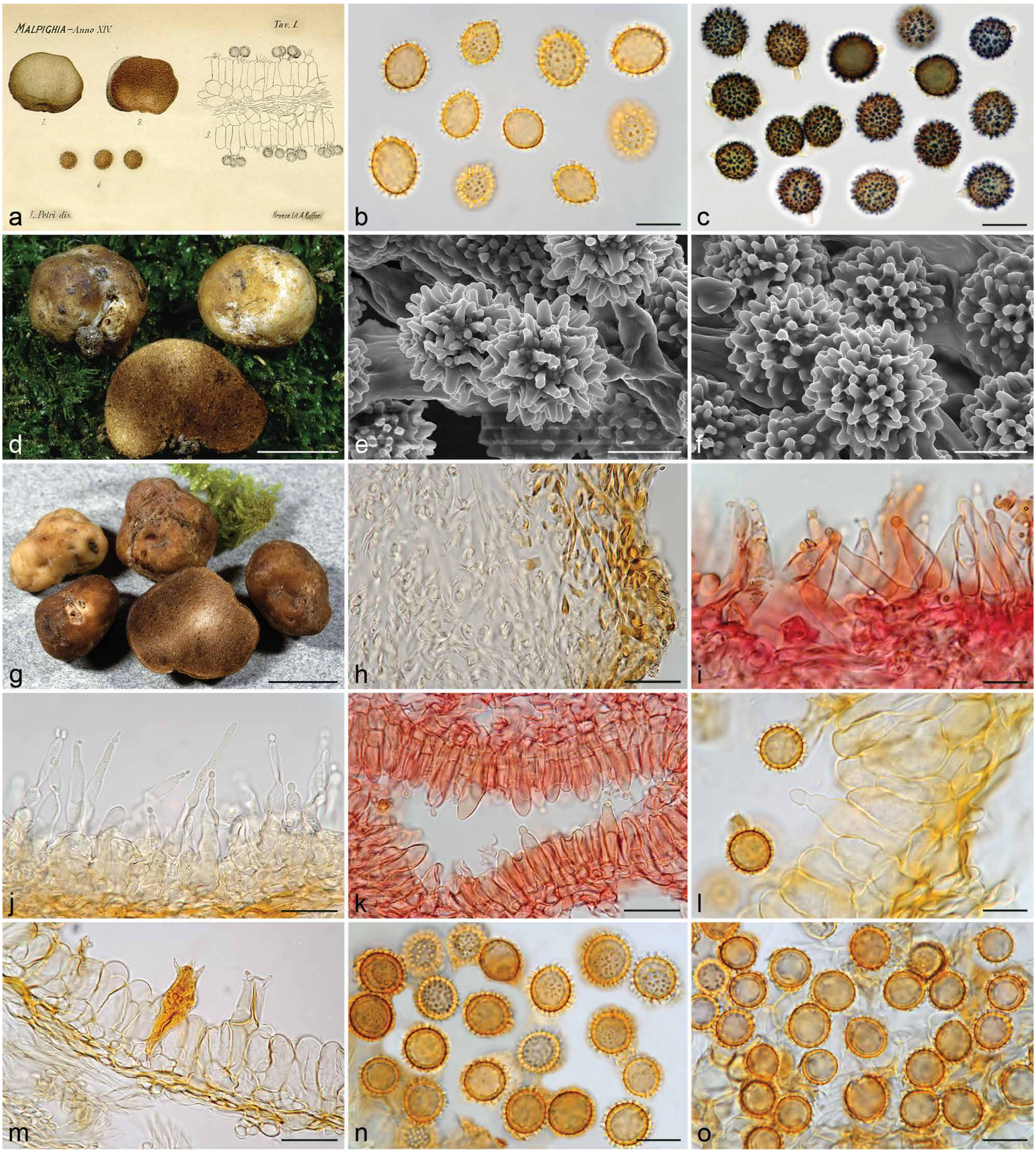

Fig. 25 *Russula mistiformis*. a. Reproduction of Mattirolo's plate of *Martellia mistiformis* (Mattirolo 1900, tav. 1). — b. FH, herb. N. Patouillard (original material of *M. mistiformis*). Spores in KOH 5 %. — c–f. JMV920626-1. c. Spores in Melzer; d. basidiomata; e–f. SEM images of spores. — g–k. JMV961226-1. g. Basidiomata; h. pileipellis and context; i. suprapellis; j–k. cystidioles of external immature locules. — l–n. JMV20160524-1. l. Cystidiole of mature hymenium; m. basidia, basidioles, paraphysoid cells and trama; n. spores in KOH 5 %. — o. AH GM-RG11057 (holotype of *Martellia mediterranea*). Spores in KOH 5 %. — Scale bars: b–c, i, l, n–o = 10 µm; d, g = 1 cm; e–f = 5 µm; h, j–k, m = 20 µm. — Photos: b–d, g–o. J.M. Vidal; e–f. UdG.

cal distribution, so they are here considered synonyms. Trappe (in Moreno et al. 1991), studied the holotype of *M. mistiformis* at TO and the isotype at FH, concluding that the spores of *M. mediterranea* are smaller than those of *M. mistiformis*, and the spore ornamentation thinner. These differences in spore size and ornamentation are here considered merely as part of the intraspecific variability of *R. mistiformis*.

Russula mistiformis belongs to sect. *Ingratae* subsect. *Foetentinae*, and is closely related to other European sequestrate russuloid taxa, such as *R. cerea* and *R. pila*. It differs from these species due to the thickness of pileipellis and context (80–240 µm in *R. mistiformis*, 70–125 µm in *R. cerea*, 150–500 µm in *R. pila*), bisporic or tetrasporic basidia (typically bisporic in *R. cerea*, tetrasporic in *R. pila*), hymenium with capitate cystidioles and abundant paraphysoid cells, but lacking macrocystidia (macrocystidia thick walled and clavate in *R. cerea*, macrocystidia and cystidioles absent in *R. pila*) and subglobose to ovoid spores (globose in *R. cerea* and *R. pila*). In addition, the three species seem to be ecologically isolated, with *R. mistiformis* being apparently endemic to the Mediterranean region under *Quercus* and *Pinus*, while *R. cerea* is associated with lowland and montane trees (conifers and broadleaved trees) in Mediterranean and Central Europe, and *R. pila* shows preference for *Fagus sylvatica* stands of the Mediterranean subalpine range.

Russula monospora (Boud. & Pat.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 236. 2018 — Fig. 26

Basionym. *Hydnangium monosporum* Boud. & Pat., J. Bot., Paris 2, 24: 445. 1888.

Synonyms. *Octaviania monospora* (Boud. & Pat.) Lloyd, Mycol. Writings 7, Letter 67: 1141. 1922.

Martellia monospora (Boud. & Pat.) Astier & Pacioni, Doc. Mycol. 28, 109–110: 9. 1998.

Basidiomata 1.5–5.5 cm wide, angiocarpic, subglobose to ovate-pyriform or tuberiform, often caespitose and deformed, irregularly depressed at the top, sometimes longitudinally plicate and basally alveolate, attached to the soil by a minute sterile base that often remains in the substrate when the basidiomata are extracted. *Pileus* dry, finely tomentose to minutely papillate-squamulose under the lens, evanescent (old specimens nude), pale orange (5A2) to melon (5A6) or greyish orange (5B6), covered by fulvous yellowish to ferruginous brown hairs, with wine-red (11D7) and olivaceous (3C3) maculae when handled; pale orange (5A2) to dark brown (7F7) in exsiccata. *Hymenophore* firm, minutely loculate, labyrinthoid, unevenly ripening, at first pure white to ochraceous, becoming pink (13A3) to purplish red (13A6) at maturity; greyish orange (5B4) to brown (7E5) in exsiccata; locules minute, 0.4–1 × 0.1–0.3 mm (2–4 per mm), elongated, compressed, flexuose, empty or filled of spores; fresh spore mass in locules initially white to yellowish, finally pink (12A3–A6) when mature; yellowish white (4A2) in immature exsiccata, and greyish red (10D5–11D5) to brownish red (10D6–11D6) in mature exsiccata. *Columella* absent. *Odour* pleasant, fruity, strongly of pineapple according to Boudier & Patouillard (1888).

Spores (9–)10–13 µm, Q = 1, perfectly spherical, orthotropic, uniguttulate, echinate, hyaline, colourless for a long time, then yellowish with purplish pink hues, and finally dark pink; in contact with Melzer's reagent the immature hyaline spores stain dark yellow and the mature pink spores stain orange; warts 0.4–1.4(–1.6) µm high, isolated, inamyloid or weakly amyloid, conical, with some verrucae among them; hilar appendix 1.5–3 × 1.5–2 µm long, sometimes retaining a sterigmal appendix. *Basidia* 1-spored (rarely 2-spored), 30–60 × 7–12 µm, cylindrical to oblong-clavate when young, then sinuous, constricted, lageniform-urticiform with a long neck, filled of yellow oleiferous guttules, soon collapsed; sterigmata 4–10 µm long, tapering above. *Basidioles* clavate, 17–38 × 7–17 µm, with numerous oleiferous guttules inside. *Macrocystidia* and *cystidioles* absent. *Paraphysoid cells* abundant, aseptate or 1-septate, similar to basidioles, but internally empty. *Subhymenium* ramose, composed of chains of 1–3 elongated cells measuring 7–15 × 4–9 µm. *Hymenophoral trama* 30–50 µm wide, homoiomerous, composed of loosely interwoven, hyaline, subgelatinized hyphae, 2–6 µm diam, filled of oleiferous guttules; sphaerocytes absent. *Pileipellis* and *context* 150–350 µm thick, lacking in old specimens; pileipellis consisting of: 1) an intricate trichodermal suprapellis of dark yellow, septate hairs and dermatocystidia, 40–100 × 2–4 µm, with a thick wall up to 1 µm, finally collapsing into a brownish mass; and 2) an undifferentiated prosenchymatous subpellis. *Pileal context* 125–250 µm thick, densely prosenchymatous, composed of subgelatinized hyaline hyphae 2–5 µm diam; sphaerocytes absent. Gloeoplera up to 5 µm diam, abundant in the trama and context. Thromboplera also present.

Habitat, Distribution & Season — Hypogeous to semi-hypogeous, solitary to gregarious, sometimes in compact, caespitose groups, under conifers (*Pinus nigra*) or deciduous trees (*Quercus*), on calcareous soil. Summer to winter. Found in Mediterranean and submediterranean regions of Southern Europe (Bulgaria, France and Spain), between 300–1150 m altitude.

Material studied. Bulgaria, Blagoevgrad, Ilindentsi, Struma Valley, 550 m, under *Pinus nigra* subsp. *nigra* with *Corylus avellana*, *Fraxinus ornus* and *Ulmus* sp., on calcareous soil, 16 Jan. 2014, *M. Slavova* (MSL0932F1017); ibid., 31 Jan. 2016, *M. Slavova* (MSL1689F7395); ibid., 11 Dec. 2017, *M. Slavova* MSL2032F2679 (SOMF 29974, duplicate BCN JMV800686). – France, Franche-Comté, Jura, Abbévillers, sine dat., *L. Quélet* as '*H. galatheium*' (UPS F013936, herb. L. Quélet); Provence-Alpes-Côte d'Azur, Nice, July 1885, 'dedit D. Barla' (PC, herb. E. Boudier, lectotype of *H. monosporum*); ibid., sine dat., ex E. Boudier as *H. monosporum* (BPI 712228, coll. C.G. Lloyd 7201); ibid., sine dat., 'fragmentum spec. orig.', ex E. Boudier as *H. monosporum* (UPS F016541, ex herb. G. Bresadola); Nice, Drap, Grand Bois, 12 July 1886, *J.-B. Barla* as '*H. candidum*' (NICE 2012-0-06711/06712); ibid., 23 June 1887, *J.-B. Barla* as '*H. candidum*' (NICE 2012-0-06714); 'environs de Nice', July 1887, as *H. monosporum* (FH, herb. N. Patouillard); Nice, Drap, La Bauma, 8 Aug. 1887, *J.-B. Barla* as '*H. candidum*' (NICE 2012-0-06713); Nice, Drap, Oct. 1890, *J.-B. Barla* as '*H. candidum*' (NICE 2012-0-06715-1); Nice, Drap, Grand Bois, 30 June 1891, *J.-B. Barla* as *H. monosporum* (NICE 2012-0-06715-2/6716/6717/6718). – Spain, Castilla and Leon, Soria, San Leonardo de Yagüe, Sistema Ibérico, under *Quercus rotundifolia*, on calcareous soil, 15 June 2001, *A. Sanz-Becerra* & *N. Redondo* (AH 46459)*; Castilla-La Mancha, Cuenca, Área Recreativa de Los Lagunillos, Serranía de Cuenca, Sistema Ibérico, 1150 m, in *Pinus nigra* subsp. *salzmannii* forest with *Buxus sempervirens* and *Crataegus monogyna*, on calcareous soil, 10 Nov. 2017, *J.A. Martínez* (BCN JMV800671)*; ibid., 1120 m, in *Pinus nigra* subsp. *salzmannii* forest with *Quercus faginea* and *Juniperus communis*, on calcareous soil, 16 Dec. 2017, *A. Carreres* & *J.A. Martínez* (BCN JMV800672)*; ibid., 16 Dec. 2017, *A. Carreres* & *J.A. Martínez* (BCN JMV800673, duplicate AH 50141)*.

Notes — This rare species was collected by J.-B. Barla between 1885 and 1891 in Nice (Southern France), in the vicinity of Drap, in the places called Grand Bois and La Bauma (Trimbach 1996), and initially identified as *Hydnangium candidum*. Parts of these collections were sent to Boudier and also to Patouillard who, after studying them and observing the presence of monosporic basidia in all the specimens, published this species as *Hydnangium monosporum* (Boudier & Patouillard 1888), which was later illustrated by Boudier (1906: pl. 193) in his Icones Mycologicae. The lectotype of *H. monosporum* (PC) designated by Nuytinck et al. (2003), as well as original and authentic collections deposited in various public herbaria (BPI, FH, NICE, UPS), were checked for the purpose of this study. Despite being completely or partially immature, or in some cases parasitized by moulds, several microscopic features were noted, such as a trichodermal pileipellis, monosporic basidia, and globose, echinate spores measuring 9–13 µm diam, still hyaline or yellowish, but showing an intense yellow reaction in contact with Melzer's reagent. Therefore, the specimens collected by Barla were probably too immature and led Boudier (1906) to depict them as yellowish. The sample collected by Quélet (1886) in the Jura region of France displays slightly more mature spores, with purplish pink tones in the spore wall under ammonium 10 %. Modern Spanish and Bulgarian collections studied in the present work show an intense pink colour in mature spores and hymenophore, a unique character discriminating this species from all other European sequestrate *Russulaceae* taxa. Recently, this species was re-combined into genus *Russula* by Elliott & Trappe (2018). *Russula monospora* can be confused with *Lactarius stephensii*, which also has monosporic basidia, a ramose subhymenium, a homoiomerous hyphal trama, and echinate spores. However, in *L. stephensii*, spores are distinctly subglobose instead of spherical, while numerous laticifera are present in the trama and context, which are completely absent in *R. monospora*.

Genetically, *R. monospora* shows no significant relationships, but is probably close to *R. consobrina* (PP 0.94, BP 53) and other lineages such as subsections *Russula*, *Viscidinae* and *Sardoninae* (PP 0.73, BP 50). The only other sequestrate species in these clades is *R. gilkeyae* (Trappe 2572, listed as '*Gymnomyces gilkeyae*', and OSC 117360, as '*G. monosporus*'), which probably belongs to subsect. *Sardoninae* (Trendel et al. 2017).

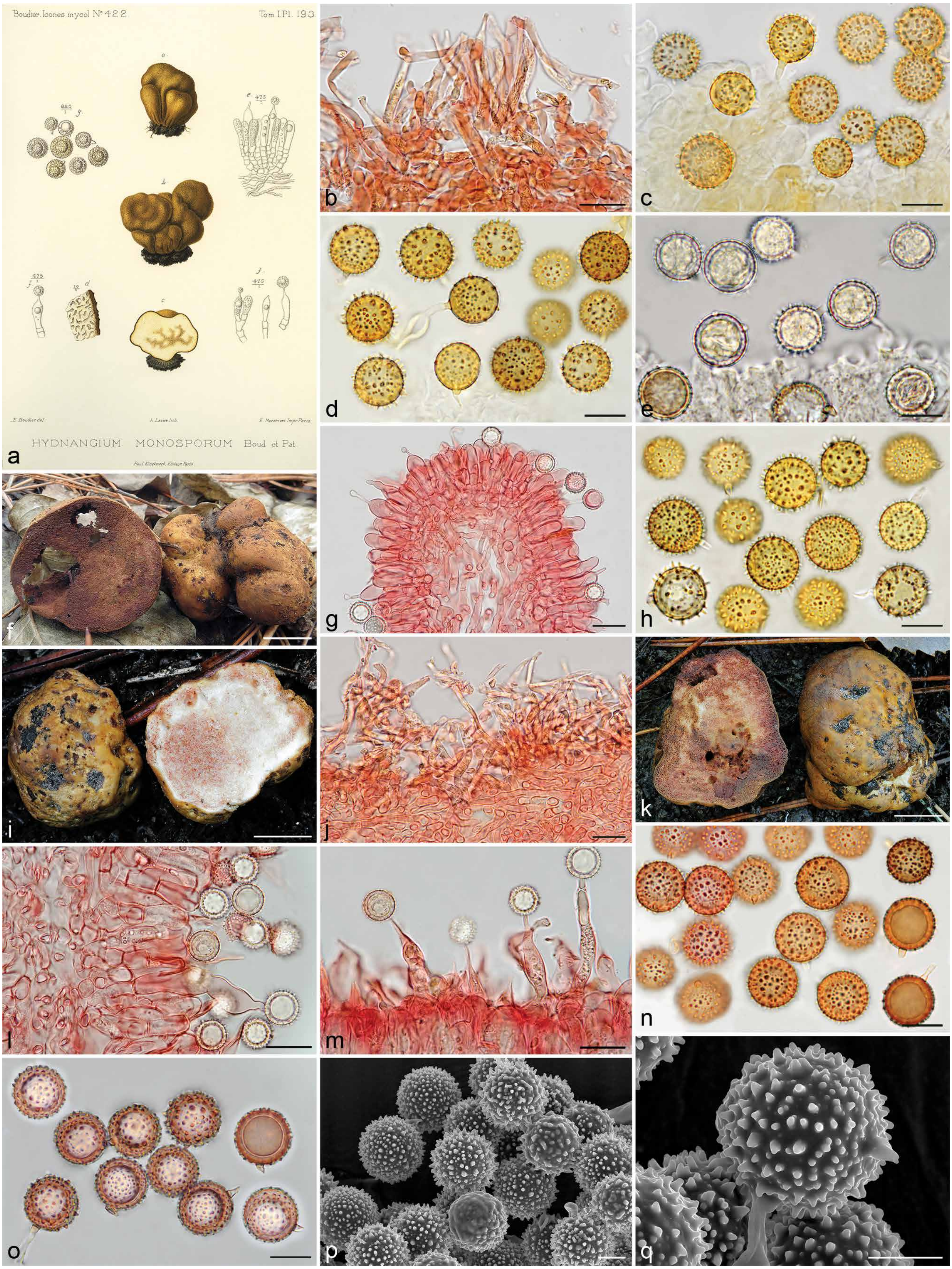

Fig. 26 *Russula monospora*. a. Reproduction of Boudier's plate of *Hydnangium monosporum* (Boudier 1906: pl. 193). — b–c. PC, herb. E. Boudier (lectotype of *H. monosporum*). b. Pileipellis; c. immature spores in Melzer. — d–e. UPS F013936, herb. L. Quélet (as '*Hydnangium galatheium*'). d. Immature spores in Melzer; e. immature spores in ammonia showing the purplish pink hues of the spore wall. — f–h. MSL2032F2679. f. Basidiomata; g. hymenium and trama; h. immature spores in Melzer. — i–j. JMV800672. i. Basidiomata initiating maturation; j. pileipellis and context. — k–q. JMV800673. k. Basidiomata showing the non-uniform ripening of hymenophore; l. detail of monosporic basidium; m. emerging necks of basidia; n. mature spores in Melzer; o. mature spores in ammonia; p–q. SEM images of spores. — Scale bars: b, g, j, l–m = 20 µm; c–e, h, n–o = 10 µm; f, i, k = 1 cm; p–q = 5 µm. — Photos: b–e, g–h, j, l–o. J.M. Vidal; f. M. Slavova; i, k. A. Carreres & J.A. Martínez; p–q. UdG.

Russula neuhoffii (Soehner) J.M. Vidal, *comb. nov*. — MycoBank MB828508; Fig. 27

Basionym. *Hydnangium neuhoffii* Soehner, Z. Pilzk., N.F. 20, 3–4: 111. 1941.

Synonyms. *Octaviania neuhoffii* (Soehner) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 202. 1958.

Hymenogaster pisiformis Velen., Opera Bot. Cech. 4: 96. 1947. (syn. nov.)

Lectotype of *Hydnangium neuhoffii* (here designated MBT384233): Germany, Brandenburg, 'Liebenthaler Wäldchen bei Marienwerder', July 1926, *W. Neuhoff* (M, herb. E. Soehner 1060).

Basidiomata 1–3 cm wide, angiocarpic, globose, ovoid to irregular, slightly sulcate and tuberous, sessile, with a minute sterile base. *Pileus* pruinose, initially pure white, later orange-white to pale orange (5A2–A4), with brown maculae (7D7). *Hymenophore* loculate, labyrinthoid, initially yellow to orange-yellow, then ochre; pale orange in exsiccata (5A4); spore mass in locules pale orange (5A4). *Stipe-columella* not observed. *Odour* mild. (Description based on Soehner 1941, Velenovský 1947 and herbarium material).

Spores 9.5–12.5 × 8.5–11 µm, Q = 1.0–1.1, globose to subglobose, orthotropic to subheterotropic, statismosporic, echinate, intensely yellow; warts 0.5–1 µm high, amyloid, densely packed and short, cylindrical to dentiform, or rounded at the apices, with numerous verrucae among them; hilar appendix 1–2 × 1.5 µm, straight, cylindrical to conical, sometimes retaining a sterigmal appendix; suprahilar plage present, inamyloid. *Basidia* 2–3-spored, 27–40 × 9–15 µm, clavate to broadly clavate; sterigmata 3.5–6.5 µm long. *Macrocystidia* scarce, 55–70 × 7–9 µm, cylindrical, lanceolate, fusiform, or rostrate, with amorphous content, soon collapsed. *Paraphysoid cells* absent. *Subhymenium* made of a layer of globose to prismatic cells about 5–15 µm diam. *Hymenophoral trama* 40–50 µm wide, homoiomerous, made of septate, branched, tortuous hyaline hyphae 1.5–7 µm diam; inflated elements and sphaerocytes rare or absent. *Pileipellis* and *context* 100–150 µm thick; pileipellis a trichoepithelium formed by: 1) a trichodermal suprapellis made of septate hairs and dermatocystidia 15–30 × 2–5 µm, that soon collapses in a yellow granular mass; and 2) a pseudoparenchymatous subpellis 50–80 µm thick, made of ampullaceous cells up to 17 µm wide and globose cells 6–30(–40) µm diam. *Pileal context* 30–100 µm thick, formed by tortuous and intricate hyaline hyphae 2–5 µm diam, with numerous ampullaceous inflated elements up to 14 µm diam and some sphaerocytes up to 16 µm diam. Gloeoplera 3–5 µm diam, present in trama and context.

Habitat, Distribution & Season — Solitary to gregarious, hypogeous under broadleaved trees (*Quercus*, *Carpinus*, *Betula*), on siliceous soil. Summer and autumn. Found in temperate regions of Central Europe.

Additional material studied. Czech Republic, Central Bohemia, Jidášky, near Mnichovice, 'in humo nigro ca 10 cm profundo, supra foliis quercinis et carpineis tecto in duobus speciminibus in betuleto, statio quarcitica', 12 July 1945, *J. Velenovský* (PRM 153797, coll. J. Velenovský, holotype of *H. pisiformis*). – Germany, Bavaria, Planegg, near Munich, in oak forest, 28 Sept. 1941, *E. Soehner* as *H. neuhoffii* (M, herb. E. Soehner 1626).

Notes — Soehner (1941) described an angiocarpic fungus found by W. Neuhoff near Berlin, naming it *Hydnangium neuhoffii*, characterized by whitish basidiomata, yellow to fulvous loculated hymenophore, 1–3-spored basidia and echinate spores. Some years later, Velenovský (1947) described a similar hypogeous species collected in the south of Prague, which he named *Hymenogaster pisiformis*. Type collections of *H. neuhoffii* and *H. pisiformis* were compared in the present work and found to represent a single species of *Russula* characterized by the lack of laticifera, a pileipellis arranged in trichoepithelium, and globose to subglobose amyloid spores provided with an inamyloid plage and ornamented with densely packed short

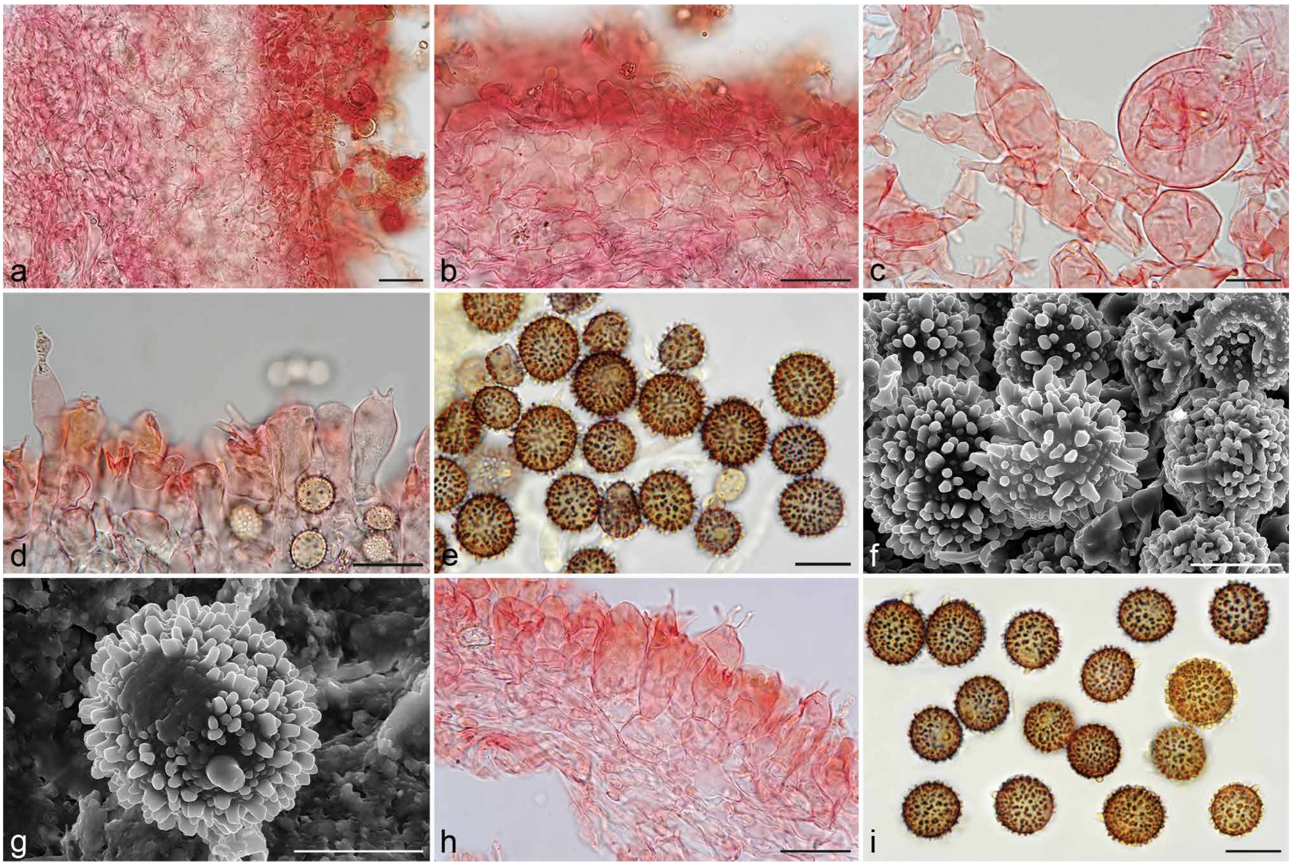

Fig. 27 *Russula neuhoffii*. a–g. M, herb. E. Soehner 1060 (lectotype of *Hydnangium neuhoffii*). a. Pileipellis and context; b. suprapellis and subpellis; c. cells of the subpellis; d. hymenium; e. spores in Melzer; f–g. SEM images of spores. — h–i. PRM 153797 (holotype of *Hymenogaster pisiformis*). h. Hymenium and subhymenium; i. spores in Melzer. — Scale bars: a–b, d, h = 20 µm; c, e, i = 10 µm; f–g = 5 µm. — Photos: a–e, h–i. J.M. Vidal; f–g. UdG.

spines (< 1 µm), with rounded apices. The type material of *H. neuhoffii* and *H. pisiformis* are parasitized by moulds and, unfortunately, we were unable to obtain recent collections of these species to sequence.

Russula pila (Pat.) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 237. 2018 — Fig. 28

Basionym. Hydnangium pila Pat., Bull. Soc. Mycol. France 26: 201. 1910.

Synonyms. Octaviania pila (Pat.) Svrček in Pilát, Flora ČSR B1, Gasteromycetes: 199. 1958.

Martellia pila (Pat.) J.M. Vidal, Butll. Soc. Catalana Micol. 14–15: 172. 1991.

Gymnomyces pila (Pat.) Trappe et al., Mycotaxon 81: 200. 2002.

Basidiomata 1–3 cm wide, angiocarpic, subglobose to tuberiform, frequently caespitose, sessile, with an inconspicuous sterile base, occasionally attached to the soil by a basal mycelial strand. *Pileus* initially densely tomentose, greyish, then smooth, pale orange (5A4) to orange (6B6), finally dark brown (8F8) after handling or in contact with air, with aromatic viscid exudations in mature basidiomata; basally open and alveolate in old specimens. *Hymenophore* loculate, labyrinthoid, at first orange-white (6A2) or greyish orange (6B4), finally brownish orange (6C6); locules 0.3–1 × 0.1–0.3 mm (2–4 per mm), elongated, sinuous, minute; fresh spore mass in locules pale orange (5A4) to reddish brown (5A4–8D8); brown (6E7) in exsiccata. *Columella* absent. *Odour* fruity or similar to tuber, taste mild. *Spores* (9–)10–12(–13) µm, Q = 1, globose, orthotropic, echinate, reddish in KOH; warts of irregular length, 1–2.5 µm high, hyaline to yellow, deeply amyloid, cylindrical with obtuse tips, with some verrucae among them; hilar appendix short, inconspicuous. *Basidia* abundant, typically 4-spored, but also 2–3-spored, 35–45 × 11–17 µm, broadly clavate, filled with granulose or homogeneous dark reddish content, originating deep in the subhymenium, persistent; sterigmata conical, 3–5 µm long in tetrasporic basidia, up to 10 µm in bisporic basidia. *Basidioles* abundant, 25–40 × 10–14 µm, with tiny, hyaline to yellowish oily droplets. *Macrocystidia* absent. *Cystidioles* 30–60 × 3–6 µm, similar to dermatocystidia, 1–3-septate, hyaline, cylindrical to fusoid, sinuous, acute, capitulate, moniliform, present only in immature external hymenial locules. *Paraphysoid cells* scarce, 20–30 × (5–)8–14 µm, commonly 1-septate. *Subhymenium* formed by 2–3 layers of prismatic cells about (6–)10–20 µm diam. *Hymenophoral trama* 10–20 µm wide, formed by branched hyphae (2–)4–6 µm diam, with occasional inflated elements up to 12 µm and chains of sphaerocytes in tramal anastomoses 6–20 µm diam. *Pileipellis* and *context* 150–500 µm thick, homogeneous, separable from the hymenophore; pileipellis consisting of: 1) a trichodermal suprapellis formed

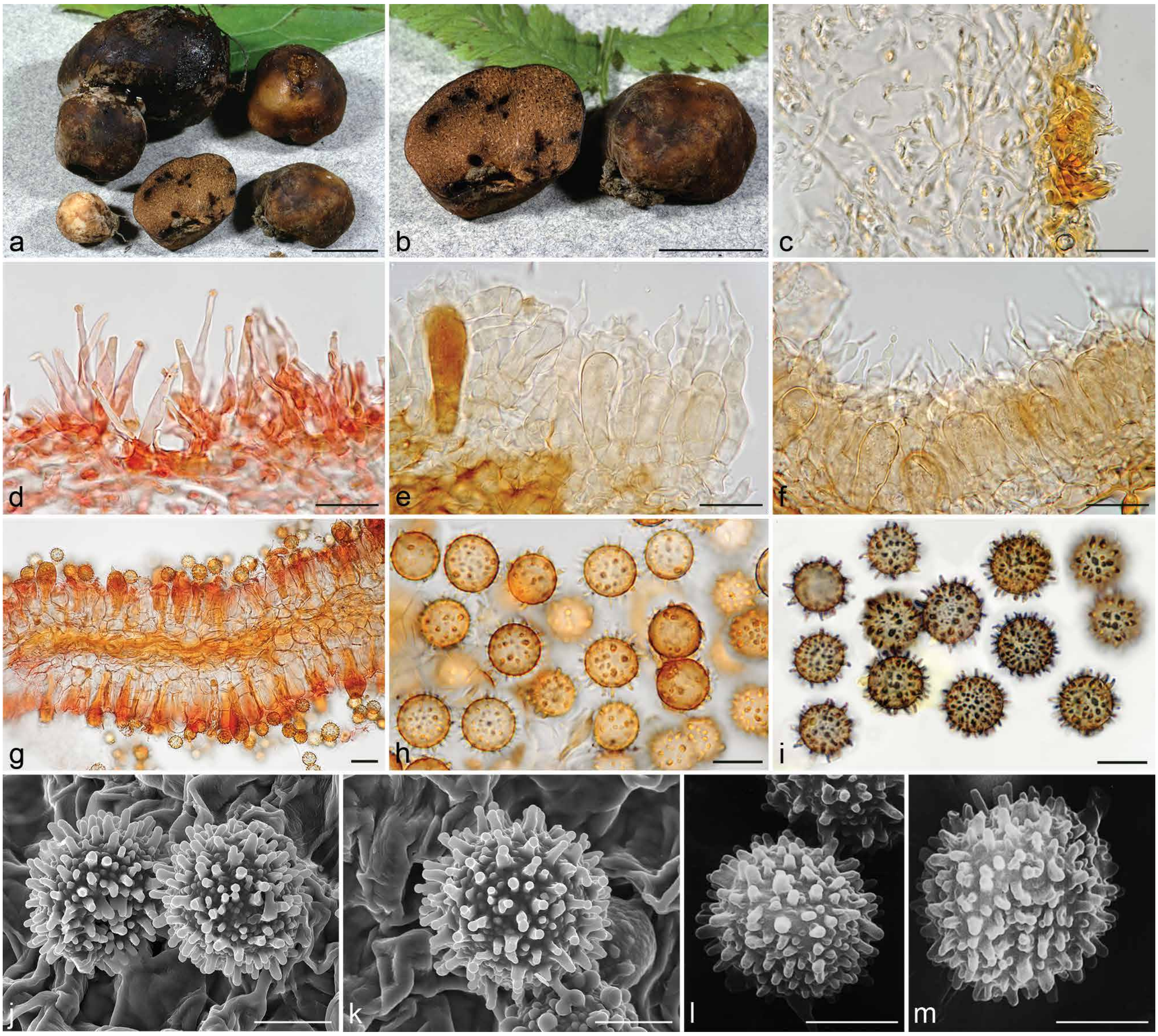

Fig. 28 *Russula pila*. a–k. JMV970816-8. a–b. Basidiomata; c. pileipellis and context; d. suprapellis; e–f. septate cystidioles of external immature locule; g. section of a septum; h. spores in KOH 5 %; i. spores in Melzer; j–k. SEM images of spores. — l–m. FH, herb. N. Patouillard (original material of *Hydnangium pila*). SEM images of spores. — Scale bars: a–b = 1 cm; c–g = 20 µm; h–i = 10 µm; j–m = 5 µm. — Photos: a–i. J.M. Vidal; j–k. UdG; l–m. AH.

of subulate to lageniform, capitulate dermatocystidia 20–40 × 3–6 µm, that soon collapses into a yellowish mass; and 2) a prosenchymatous subpellis 50–250 µm thick, formed by a dense mesh of interwoven, subgelatinized, yellowish hyphae 2–4 µm diam. *Pileal context* 100–300 µm thick, formed by interwoven, subgelatinized, hyaline hyphae 2–4 µm diam, lacking sphaerocytes. Thromboplera present in trama and context.

Habitat, Distribution & Season — Commonly gregarious, caespitose, hypogeous to semi-hypogeous, in montane broadleaved woods of *Quercus* and *Fagus*, in different types of substrates. Summer to winter. Found in temperate regions of Southern Europe, between 200–900 m altitude.

Material studied. France, Rhône-Alpes, Ain, Lepinay (Cras-sur-Reyssouze), Jura mountains, under *Quercus* sp., Aug. 1909, *N. Patouillard* (FH, herb. N. Patouillard, original material of *H. pila*). – Spain, Catalonia, Girona, Vall de Bianya, Capsacosta, Coll Pregon, 900 m, under *Fagus sylvatica*, on sandstone soil, 16 Aug. 1997, *J.M. Vidal* (BCN JMV970816-8)*; ibid., 18 Aug. 1997, *J.M. Vidal* (BCN JMV970818-2); Navarre, Lekunberri, road to Aralar, km. 6.5, under *Fagus sylvatica* and *Corylus avellana*, on calcareous soil, 23 Nov. 2011, *P.M. Pasabán* & *F. Sáinz* (BCN JMV800654)*.

Notes — *Hydnangium pila* was proposed by Patouillard (1910), to name some collections of a semi-hypogeous fungus found in oak forests of the calcareous mountain range of French Jura. He reported it as sessile, at first white becoming reddish with age, with a dense and pubescent pileipellis easily separable from the hymenophore, tetrasporic clavate basidia and echinate globose spores measuring 10–12 µm diam, suggesting a close relationship of this species with *Martellia*. *Hydnangium pila* was therefore re-combined into *Martellia* by Vidal (1991b), because of these features, as well as its amyloid spores and the hyphal structure of the hymenophoral trama, and later re-combined into *Gymnomyces* by Trappe et al. (2002), following the synonymy of the genera *Martellia* and *Gymnomyces* proposed by Lebel & Trappe (2000). Recently, this species was placed in genus *Russula* by Elliott & Trappe (2018).

Russula pila exhibits features reminiscent of both *R. mistiformis* and *R. cerea*. *Russula mistiformis* also has tetrasporic basidia, but differs in its subglobose to ovoid spores, thinner pileipellis and context and presence of cystidioles in the mature hymenium. *Russula cerea* also has globose spores, but differs in its abundant hymenial macrocystidia, bisporic basidia, and a thinner membranous pileipellis and context. Finally, *R. pila* and *R. cerea* are commonly found in montane woods, while *R. mistiformis* is found in Mediterranean woods. The three species are genetically related, but *R. cerea* and *R. pila* seem to be significantly closer to one-another. All of them probably belong to *Russula* sect. *Ingratae* subsect. *Foetentinae*.

Russula vidalii Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 234. 2018 — Fig. 29

Replaced synonym. *Gymnomyces ilicis* J.M. Vidal & Llistos., Rivista Micol. AMB 38, 2: 160. 1995.

Basidiomata 0.5–3.5 cm wide, angiocarpic, subglobose to turbinate, bi-lobate, sessile or subsessile, with a residual stipe. *Pileus* pruinose, pure white, with pale orange to reddish brown maculae; old specimens nude, completely alveolate. *Hymenophore* loculate, yellowish white, then yellowish orange, pale orange, and finally deep orange. *Columella* white, branched. *Odour* fruity.

Spores 9–11(–13) µm, Q = 1.0–1.1, globose to subglobose, orthotropic; warts 0.5–1 µm high, isolated, amyloid, some forming short ridges or even an incomplete reticulum. *Basidia* 2-spored, 30–50 × 10–15 µm, clavate. *Macrocystidia* 43–85 × 6–10 µm. *Hymenophoral trama* developing nests of sphaerocytes. *Pileipellis* and *context* 175–300 µm thick, evanescent; supra-

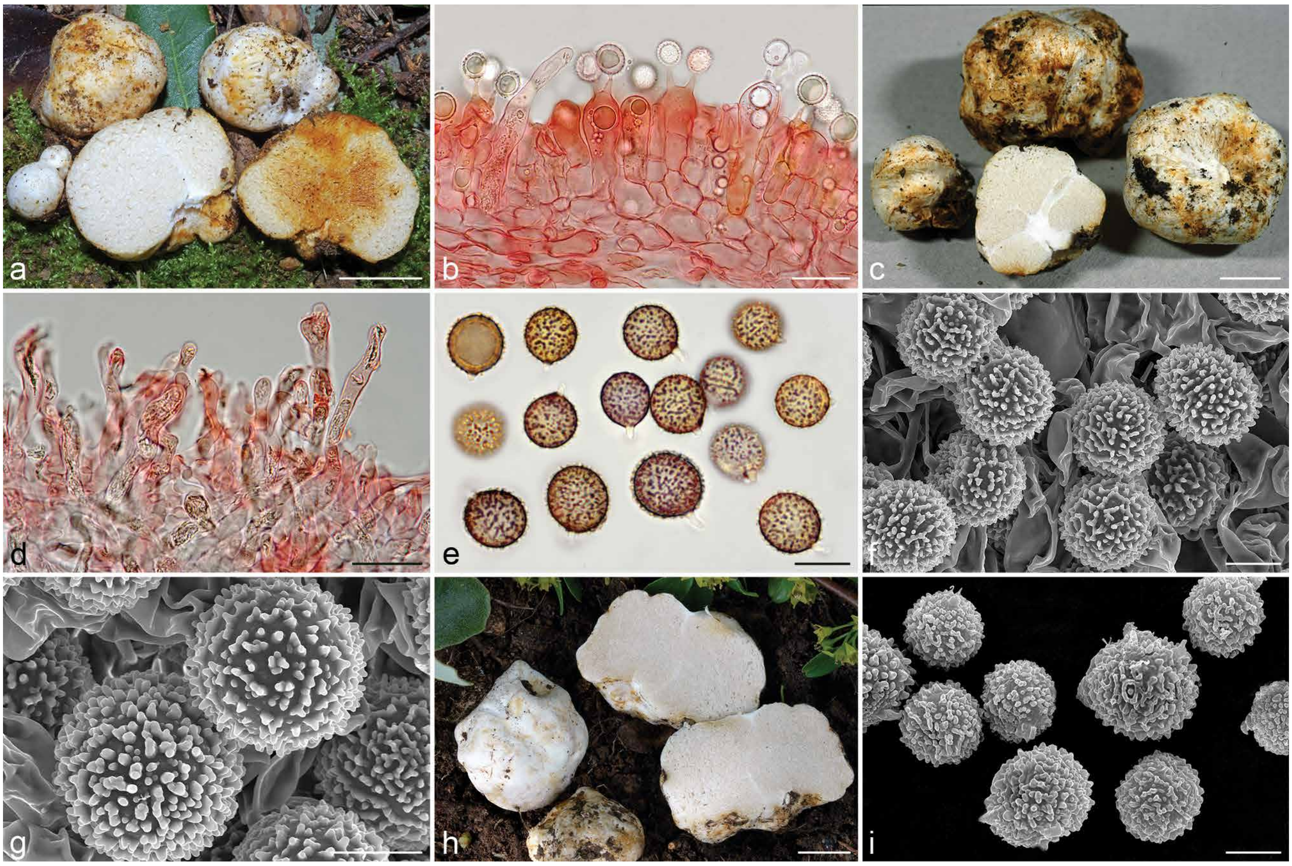

Fig. 29 *Russula vidalii*. a–b. JMV20160517-1. a. Basidiomata; b. hymenium and subhymenium. — c–g. JMV920401-1 (paratype of *Gymnomyces ilicis*). c. Basidiomata; d. suprapellis; e. spores in Melzer; f–g. SEM images of spores. — h–i. JC100508BT01. h. Basidiomata; i. SEM image of spores. — Scale bars: a, c, h = 1 cm; b, d = 20 µm; e = 10 µm; f–g, i = 5 µm. — Photos: a–e. J.M. Vidal; f–g. UdG; h–i. J. Cabero.

pellis a palisadotrichoderm of cylindrical to fusiform, erect dermatocystidia 5–12 µm thick; subpellis a cutis.

Habitat, Distribution & Season — Gregarious, semi-hypogeous under leaf litter of *Quercus ilex* and *Quercus rotundifolia*, sometimes mixed with *Pinus*, on calcareous soil. Spring and autumn. So far known from the western Mediterranean region, in France and Spain, from sea level up to 800 m altitude.

Material studied. France, Provence-Alpes-Côte D'azur, Bouches du Rhône, Saint Rémy de Provence, under *Quercus ilex* and *Pinus halepensis*, 17 Nov. 1993, *L. Riousset* (BCN JL1501, paratype of *G. ilicis*). – Spain, Castilla and Leon, Zamora, Toro, 800 m, under *Quercus rotundifolia*, on calcareous soil, 9 May 2010, *J. Cabero* as *G. ilicis* (JC100508BT01, duplicate BCN JMV800688)*; Catalonia, Barcelona, Sant Just Desvern, Can Fetjó, 220 m, under *Quercus ilex*, 13 Apr. 1992, *J. Llistosella*, *A. Rocabruna* & *J. Vila* (BCN JL1497, holotype of *G. ilicis*); Girona, Rupià, Can Candell, under *Quercus ilex*, 3 Apr. 2005, *F. Rodríguez* (BCN JMV20050403-2); Girona, Sant Sadurní de l'Heura, Can Barris, 90 m, under *Quercus ilex*, on sandy basic soil, 1 Apr. 1992, *J.M. Vidal* (BCN JMV920401-1, paratype of *G. ilicis*); ibid., 17 May 2016, *J.M. Vidal* & *F. Rodríguez* (BCN JMV20160517-1)*; Girona, Viladamat, Gorners, 40 m, under *Quercus ilex*, 10 Apr. 1991, *J.M. Vidal* (BCN JMV910410-3, paratype of *G. ilicis*); Girona, Viladamat, Palau Borrell, under *Quercus ilex*, 11 May 1996, *J.M. Vidal* (BCN JMV960511-2).

Notes — *Russula vidalii* is a replacement name for *Gymnomyces ilicis* (Elliott & Trappe 2018), an epithet originating from the apparent association of this taxon with *Quercus ilex* in the Mediterranean region. However, collections BCN JL1501 (Llistosella & Vidal 1995) and JC100508BT01 (Cabero 2011) were found in mixed stands of *Quercus* and *Pinus*, so it is possible that *R. vidalii* has a wider host range than originally thought. It is characterized by an evanescent pileipellis and context that gives mature basidiomata an alveolate look. Genetically, *R. vidalii* belongs to subsect. *Laricinae*, displaying close affinities with *R. laricinoaffinis* and *R. galileensis*. Basidiomata of *R. vidalii* are relatively small (1–2.5 cm), have a poorly developed columella, a residual stipe, and a loculate hymenophore, while *R. galileensis* produces larger basidiomata (up to 5–6 cm), with a conspicuous stipe-columella and a sublamellate hymenium. Spore warts of *R. vidalii* are isolated or forming short ridges, while basidia are bisporic, and the suprapellis is a palisadotrichoderm. By contrast, spore warts of *R. galileensis* are interconnected by small ridges, basidia are tetrasporic, and the suprapellis is an intricate trichoderm.

Russula vinaceodora (Calonge & J.M. Vidal) Trappe & T.F. Elliott, Fungal Systematics and Evolution 1: 240. 2018 — Fig. 30

Basionym. *Macowanites vinaceodorus* Calonge & J.M. Vidal, Mycotaxon 79: 2. 2001.

Basidiomata russuloid, pseudoangiocarpic, stipitate. *Pileus* 3–8.5 cm wide, convex to plano-convex and depressed, smooth, viscid, initially pale yellow, then pinkish white to purplish brown, darker at the center, with pale orange maculae; margin open, lamellate. *Hymenophore* loculate in the upper zone and sublamellate in the lower, pale orange. *Stipe-columella* 1.5–4 × 0.8–2.5 cm, white; context white. *Odour* vinaceous, intense; taste sweetish to slightly acrid.

Spores 7–11 × 6–9.5 µm, Q = 1.05–1.17, globose to broadly ellipsoid, heterotropic; reticulum 0.7–1.5 µm high, amyloid, made of crests and isolate warts. *Basidia* 2–4-spored, 30–45 × 11–16 µm, broadly clavate. *Macrocystidia* 50–75 × 10–16 µm, fusiform. *Hymenophoral trama* with large sphaerocytes up to 50 µm diam. *Subhymenium* cellular. *Pileipellis* and *context* 150–250 µm thick; suprapellis arranged as an intricate ixotrichoderm of erect hyphae and cylindrical to clavate dermatocystidia 30–75 × 2.5–11 µm; subpellis an intricate ixocutis. *Pileal* and *stipe-columella context* heteromerous.

Habitat, Distribution & Season — Gregarious, hypogeous to semi-hypogeous in sandy substrates, associated with *Pinus*, in fixed coastal dunes. Autumn. Located in the Atlantic coast of Southern Spain.

Material studied. Spain, Andalusia, Cádiz, Sanlúcar de Barrameda, Pinar de Algaida, littoral stabilized sand dunes, under *Pinus pinea*, 30 Oct. 2014, *M. Becerra* as *M. vinaceodorus* (AH 46374)*; Huelva, Mazagón, littoral stabilized sand dunes, under *Pinus pinea* with *Corema*, *Halimium* and *Helichrysum*, 27 Nov. 1999, *J.M. Vidal* & *F.D. Calonge* (MA-Fungi 47416, holotype of *M. vinaceodorus*; BCN JMV991127-4, isotype); ibid., three young specimens growing fasciculate among *Macowanites ammophilus*, 27 Nov. 1999, *J.M. Vidal* & *F.D. Calonge* as *M. vinaceodorus* (MA-Fungi 46524; duplicate BCN JMV991127-5).

Notes — Recently, this species was re-combined into genus *Russula* by Elliott & Trappe (2018). *Russula vinaceodora* is characterized by its russuloid, pseudoangiocarpic basidiomata, with a pinkish white to purplish brown pileal colour, especially in the centre. Mature basidiomata have a very characteristic odour of fermented wine.

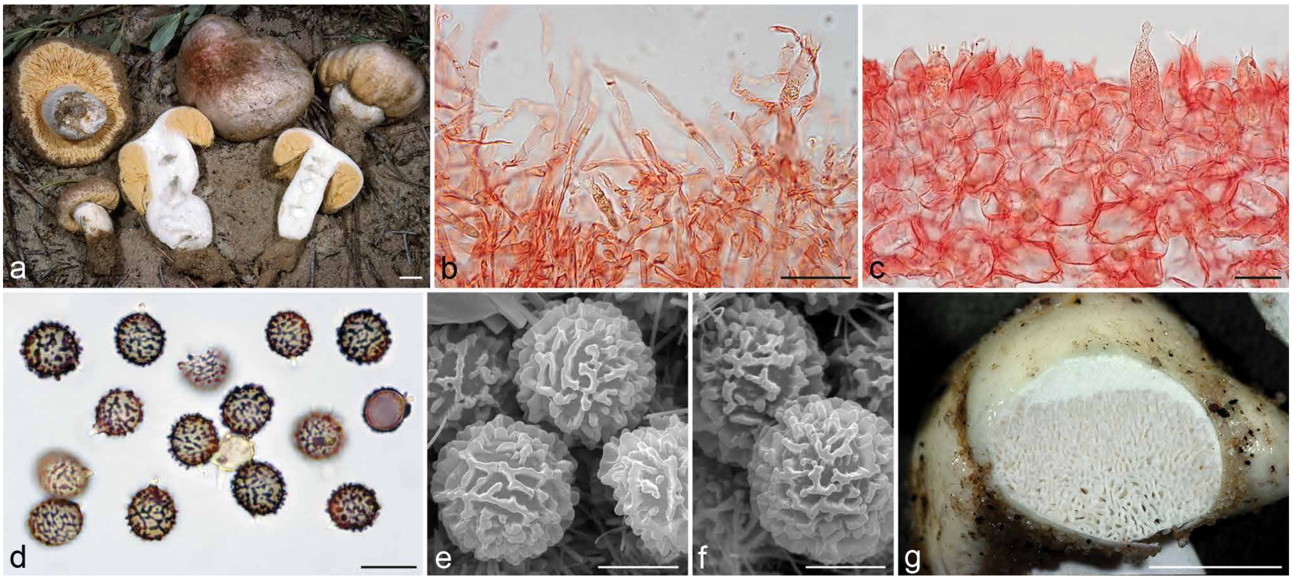

Fig. 30 *Russula vinaceodora*. a. MA-Fungi 47416 (holotype of *Macowanites vinaceodorus*). Basidiomata. — b–f. JMV991127-4 (isotype of *M. vinaceodorus*). b. Suprapellis; c. hymenium and subhymenium; d. spores in Melzer; e–f. SEM images of spores. — g. MA-Fungi 46524 (as *M. vinaceodorus*). Loculated hymenophore of young basidioma. — Scale bars: a, g = 1 cm; b–c = 20 µm; d = 10 µm; e–f = 5 µm. — Photos: a–d, g. J.M. Vidal; e–f. UdG.

Genetically, *R. vinaceodora* belongs to subsect. *Laricinae*, and is closely related to *R. laricina*, *R. murrilli* and *R. nauseosa*. The most closely related sequestrate taxon is *R. sichuanensis* (Li et al. 2013), another pseudoangiocarpic species found in *Picea* forests of Xizang and Sichuan provinces of China, which has similar cream to yellowish lamellae, globose or subglobose spores ornamented with an incomplete reticulum, and short basidia. However, *R. vinaceodora* has a pinkish to violet pileus, different from the cream-coloured one of *R. sichuanensis*, a distinctive odour of wine, and a different habitat under *Pinus pinea*, in Mediterranean coastal sandy soils.

IDENTIFICATION KEY TO EUROPEAN SPECIES OF SEQUESTRATE RUSSULACEAE

1. Hymenophore lactescent or with laticifera. Hymenophoral trama homoiomerous, lacking nests of sphaerocytes . . . . *Lactarius* 2

1. Hymenophore not lactescent, lacking laticifera. Hymenophoral trama heteromerous, with nests of sphaerocytes, especially in tramal anastomoses . . . . *Russula* 8

2. Spores echinate 3

2. Spores reticulate 6

3. Basidia 3–4-spored. — Spores 9.5–13(–15) × 8–10(–11) µm, subglobose to broadly ellipsoid; warts 1–1.5 µm high, isolated. Basidiomata 1–4 cm, subglobose to tuberiform, with a residual stipe, pale yellow with reddish brown maculae. Hymenophore loculate, pale yellow to pale brown. Latex scant, colourless to white, changing to yellow. In subalpine conifer woods (*Abies*, *Picea*). Temperate (Alps to Rhodopes) . . . . *L. borzianus*

3. Basidia 1-spored 4

4. Spores weakly amyloid. — Spores (11.5–)12–14.5(–15) × (10–)11–13 µm, subglobose to broadly ellipsoid; warts 0.5–2 µm high, isolated. Basidiomata 1–3.5 cm, subglobose to tuberiform, maize yellow to reddish brown. Hymenophore loculate, ochraceous to reddish brown. Latex scant and hyaline, changing to citrine yellow in young specimens, white, abundant, and almost immutable in old basidiomata. In montane woods of *Carpinus*, *Corylus*, *Fagus*, *Quercus*, *Tilia*. Temperate to submediterranean (British Isles to Southern Europe) . . . . *L. stephensii*

4. Spores strongly amyloid 5

5. Spores subglobose to broadly ellipsoid. — Spores 13–15 × 11–13 µm; warts 1–2 µm high, isolated or tooth-like fused. Basidiomata 1–4 cm, subglobose to tuberiform, at first pale orange then reddish brown to violet brown. Hymenophore loculate, deeply coloured, reddish yellow to orange red. Latex white. Under *Populus*. Temperate to Mediterranean (Belgium to Bulgaria) . . . . *L. populicola*

5. Spores broadly ellipsoid to ellipsoid. — Spores 14–18.5 × 12–15 µm; warts 1–2 µm high, cylindrical, isolated or forming short ridges. Hymenium completely embebbed in a dark orange substance. Basidiomata 1–2 cm, subglobose to tuberiform, orange to reddish brown or violet brown. Hymenophore loculate, deeply coloured, dull red to dull violet. Latex watery, scant. In montane conifer woods (*Abies*, *Pinus*) or under broadleaved trees (*Corylus, Quercus*). Temperate (Germany, Italy, Spain) .. . . *L. soehneri*

6. Basidia 2–4-spored. — Spores 8.5–12.5(–13.5) × 7–9.5 (–10.5) µm, subglobose to ellipsoid; reticulum 0.5–1 µm high, incomplete. Basidiomata 2–5 cm, obpyriform to tuberiform, pale orange to reddish brown, with minute depressions. Hymenophore loculate, yellowish white to orange-white. Latex scant, white, immutable. Taste sweetish, later astringent. In montane conifer woods (*Cedrus*, *Pinus*). Submediterranean (France, Morocco, Spain) . . . . *L. josserandii*

6. Basidia 1-spored 7

7. Reticulum 1–2 µm high, complete. — Spores 10–13 × 7–9 µm, ovoid to ellipsoid. Basidiomata 1–2.5 cm, subglobose to tuberiform, whitish to pale yellowish, pileus membranous, partially evanescent, indistinctly scrobiculate or with some scattered minute openings. Hymenophore loculate, whitish to pale cream or pinkish. Latex not observed. Under *Cistus* and *Halimium*. Mediterranean (Central Spain) . . . . *L. giennensis*

7. Reticulum 0.5–1 µm high, incomplete. — Spores 8.5–11 × 6.5–8 µm, ovoid. Basidiomata 0.5–2.5 cm, globose to tuberiform, whitish to brownish buff, pileus membranous, partially evanescent, distinctly scrobiculate, with abundant large openings. Hymenophore loculate, whitish to cream or faintly ochraceous pink. Latex white. Under *Cistus*. Mediterranean (Cyprus) . . . . *L. subgiennensis*

8. Basidiomata stipitate, pseudoangiocarpic. Spores heterotropic. Amyloid suprahilar plage present 9

8. Basidiomata sessile, angiocarpic. Spores orthotropic. Amyloid suprahilar plage absent 16

9. Spores verrucose to echinate. Warts isolated or connected by low ridges 10

9. Spores subreticulated 14

10. Macrocystidia 45–70 µm long 11

10. Macrocystidia 70–130 µm long 13

11. Spores subglobose to ovoid. — Spores 7–9 × 5.5–7.5 µm; warts 0.25–0.75 µm high, some forming short ridges or connected by short lines. Pileus 2–7 cm, orange white to pale orange, with brownish orange and dark brown maculae; margin open, alveolate to sublamellate. Hymenophore loculate, orange-white to pale orange. Stipe-columella 1–4 × 0.7–2.5 cm, with brownish orange dots. Common in coastal sand dunes, under *Pinus*. Mediterranean (Southern Portugal and Spain). . . . . *R. ammophila*

11. Spores globose to broadly ellipsoid 12

12. Warts interconnected with low ridges. — Spores 9.5–12.5 × 8.5–10.5 µm; warts 1.2–2 µm high, in groups of 2–4. Pileus 1.4–2.8 cm, pure white, belatedly maculated of pale yellow; margin closed or laterally open, sublamellate. Hymenophore loculate, pale yellow to yellow. Stipe-columella 1–2 × 0.2–0.4 cm. In montane broadleaved woods (*Carpinus*, *Corylus*, *Fagus*, *Quercus*) or conifer woods (*Abies*). Temperate (Eastern to Southern Europe) . . . . *R. candidissima*

12. Warts isolated. — Spores 8.5–11(–12.5) × 7–9(–11) µm; warts 0.5–1.5 µm high. Pileus 0.5–3.5 cm, white to yellowish white, with yellowish orange maculae; margin closed or laterally open, alveolate. Hymenophore loculate, pale orange. Stipe-columella 0.6–1.5 × 0.15–0.4 cm. In montane broadleaved woods (*Carpinus*, *Corylus*). Temperate (Eastern to Southern Europe) . . . . *R. candida*

13. Warts 0.6–1(–1.5) µm high. — Spores (8–)10–15(–17) × (7–)9–14(–15) µm, subglobose to broadly ellipsoid. Pileus 2.3–5 cm, yellowish to yellowish buff, with dark brown maculae; margin open, lamellate. Hymenophore sublamellate-daedaleoid, cream to ochre-orange. Stipe-columella 1.6–4.2 x 0.7–1.8 cm. Under broadleaved trees (*Castanea*, *Quercus*). Mediterranean (Greece and Italy). . . . . *R. mediterraneensis*

13. Warts (0.7–)1.5–2.5(–3) µm high. — Spores (9–)10.5–15.5(–18) × (8–)10–15(–17) µm, globose to subglobose, some ellipsoid when immature. Pileus 1.2–3.8 cm, pale yellow to pale orange with dark brown maculae; margin open, sublamellate. Hymenophore loculate, pale yellow

to titian red. Stipe-columella 0.8–2.5 × 0.3–1 cm. In montane conifer woods (*Abies*, *Picea*). Temperate to submediterranean (Southern Poland, Greece and Italy) . . . . *R. mattiroloana*

14. Reticulum 0.5 µm high. — Spores (9–)10–11.5(–15) × (7.5–)9.5–10.5(–14) µm, subglobose; reticulum made of crests and warts. Pileus 2–6 cm, white with cream to pale umber maculae; margin radially alveolate when mature, but not open. Hymenophore loculate, cream-ochre. Stipe-columella 0.5–3.5 × 0.5–1.7(–3) cm. In sclerophyllous woods of *Quercus*. Mediterranean (Israel) . . . . *R. galileensis*
14. Reticulum 0.7–1.5 µm high 15

15. Macrocystidia present. — Spores 7–11 × 6–9.5 µm, globose to broadly ellipsoid; reticulum made of crests and isolate warts. Pileus 3–8.5 cm, pinkish white to purplish brown; margin open, lamellate. Hymenophore loculate to sublamellate, pale orange. Stipe-columella 1.5–4 × 0.8–2.5 cm. Odour intense, vinaceous. In littoral sand dunes, under *Pinus*. Mediterranean (Atlantic coast of Southern Spain) . . . . *R. vinaceodora*
15. Macrocystidia absent. — Spores 8–10 × 7.5–9.5 µm, globose to subglobose; reticulum made of isolate warts and ridges. Pileus 0.5–2 cm, rounded or bi-trilobate, areolate, papillose, pale yellow to orange-yellow, intense red in contact with KOH; margin laterally open, alveolate to sublamellate. Hymenophore loculate to sublamellate, pale yellow to pale orange. Stipe-columella 0.3–0.7 × 0.15–0.2 cm, concolourous with pileus. In littoral sclerophyllous woods of *Quercus ilex*. Mediterranean (Greece to Spain) . . . . *R. messapica* var. *messapicoides*

16. Spores reticulated 17
16. Spores echinate or verrucose 18

17. Macrocystidia absent. — Spores 8–11 × 7–10 µm, globose to subglobose; reticulum 0.4–0.6 µm high, made of isolate warts and ridges. Basidiomata 1–2 cm, subglobose to lobate or irregular, smooth, pale cream to ochraceous, drying dark reddish brown, intense red in contact with KOH. Hymenophore loculate, pale cream to ochraceous. In continental sclerophyllous woods of *Quercus rotundifolia*. Mediterranean (Central Spain) . . . . *R. meridionalis*
17. Macrocystidia present but scarce. — Spores 7–9.5(–10.5) × 7–9(–10), globose; reticulum 0.5 µm high, complete to incomplete, made of low ridges and warts. Basidiomata 2–7 cm, turbinate, firmly rooted into the substrate, often cracked, cream-white to ochraceous cream, with ochraceous to brownish stains. Hymenophore loculate, ochraceous yellow to ochraceous orange, vinaceous in $FeSO_4$. In montane woods of *Pinus*. Mediterranean (Cyprus) . . . . *R. hobartiae*

18. Pileipellis a trichoepithelium or an oedotrichoderm . . . 19
18. Pileipellis a trichoderm. 20

19. Pileipellis a trichoepithelium. — Spores 9.5–12.5 × 8.5–11 µm, globose to subglobose; warts dense 0.5–1 µm high, isolated. Basidiomata 1–3 cm, globose to irregular, whitish. Hymenophore loculate, yellow, orange yellow to ochre. Under broadleaved trees (*Carpinus*, *Betula*, *Quercus*). Temperate (Central Europe) . . . . *R. neuhoffii*
19. Pileipellis an oedotrichoderm. — Spores (6.5–)7.5–9.5(–11.5) × (6–)7–9(–11) µm, globose to subglobose; warts up to 0.3 µm high, some connected with low ridges. Basidiomata 0.5–2 cm, globose to subglobose, pruinose, whitish, with brownish red maculae. Hymenophore loculate, whitish at first, finally brownish red. Under *Cistus.* Mediterranean (Central Spain) . . . . *R. andaluciana*

20. Basidia 1-spored 21
20. Basidia 2–4-spored 22

21. Macrocystidia present. — Spores 13–15(–15.5) × 12.5–14.5(–15) µm, globose to subglobose, weakly amyloid, yellow; warts dense, 1.5–3 µm high, isolated. Macrocystidia numerous, 30–70 × 8–16 µm, clavate. Basidiomata 1–2 cm, subglobose to tuberiform, finely tomentose, pale orange with brown maculae. Hymenophore loculate, pale orange. Temperate (Germany) . . . . *R. bavarica*
21. Macrocystidia absent. — Spores (9–)10–13 µm, spherical, weakly amyloid, intense pink at maturity; warts 0.4–1.4(–1.6) µm high, isolated. Basidia clavate to lageniform-urticiform, sometimes 2-spored. Basidiomata 1.5–5.5 cm, subglobose to tuberiform, finely tomentose to papillate-squamulose, pale orange to greyish orange with wine red and olivaceous maculae when rubbing. Old specimens nude. Hymenophore loculate, pink to purplish red at maturity. Under *Pinus* and *Quercus*. Mediterranean to submediterranean (Bulgaria, France and Spain). . . . . *R. monospora*

22. Warts 0.5–1 µm high. — Spores 9–11(–13) µm, globose to subglobose; warts isolated, some forming short ridges or even an incomplete reticulum. Basidiomata 0.5–3.5 cm, subglobose to turbinate, with a residual stipe, pruinose, pure white, with pale orange to reddish brown maculae. Old specimens nude, completely alveolate. Hymenophore loculate, yellowish white to yellowish orange or deep orange. In sclerophyllous woods of *Quercus*. Mediterranean (France and Spain). . . . . *R. vidalii*
22. Warts 0.8–3 µm high 23

23. Basidia 2-spored. Macrocystidia present. — Spores (8–)9.5–12.5(–14) µm, globose; warts variable in length, 1–3 µm high, isolated. Macrocystidia (25–)30–50 × (5–)7–12(–16) µm, cylindrical to cylindro-clavate, thick walled. Basidiomata 1–3 cm, subglobose, smooth, greyish orange to pale brown, maculated of reddish brown. Hymenophore loculate, brown to reddish brown. In montane conifer woods (*Abies*, *Picea*, *Pinus*) or broadleaved woods (*Carpinus*, *Castanea*, *Corylus*, *Fagus*, *Quercus*). Temperate to submediterranean (British Isles to Southern Europe) . . . . *R. cerea*
23. Basidia 1–4-spored. Macrocystidia absent 24

24. Spores globose. — Spores (9–)10–12(–13) µm; warts variable in length, 1–2.5 µm high, isolated. Basidiomata 1–3 cm, subglobose to tuberiform, caespitose, pubescent, greyish to pale orange or orange, maculated of dark brown and producing aromatic exudations. Hymenophore loculate, orange-white to greyish orange or brownish orange. In montane broadleaved woods (*Fagus, Quercus*). Temperate (Southern Europe). . . . . *R. pila*
24. Spores subglobose to ovoid. — Spores (8.5–)9.5–11(–12.5) × (8–)8.5–10(–10.5) µm; warts of regular length, 0.8–1.6(–3) µm high, isolated. Basidiomata 0.6–2.2 cm, subglobose to tuberiform, finely tomentose, pastel yellow to pale orange, maculated of brown. Hymenophore loculate, pale yellow, pale orange to brown. In woods of *Castanea*, *Pinus* and *Quercus*. Mediterranean (Greece to Spain) . . . . *R. mistiformis*

DISCUSSION

The multigene phylogenetic analysis and morphological revision of European sequestrate *Russulaceae* taxa carried out in this work, allowed us to clarify several taxonomic issues at specific and supraspecific levels. The overall topology of the multigenic analyses was not different from those obtained by other studies focused on gymnocarpic species (Shimono et al. 2004, Verbeken et al. 2014b, Kong et al. 2015, Looney et al. 2016, Buyck et al. 2017), except for lower support values for some supraspecific lineages of *Lactarius*. These differences could be due to phylogenetic noise introduced by some sequences analyzed in the present work, or differences in the alignment of the highly variable ITS rDNA region. In contrast to *Lactarius*, multiple significant supraspecific clades were found within *Russula*, in concordance with previous phylogenetic reconstructions of this genus (Kong et al. 2015, Looney et al. 2016). Most of these clades include type species of subgenera, sections and/or subsections proposed by different classical authors on the basis of morphological evidence (Romagnesi 1985, Singer 1986, Bon 1988, Sarnari 1998, 2005), but until now, no formal re-arrangement had been proposed to incorporate the current genetic knowledge into the often overlapping nomenclature available. Kong et al. (2015) informally named the genetic lineages of *Russula* with a representative species or a supraspecific name without rank, and discussed the different supraspecific taxa in classical literature putatively matching these lineages. In the present work, eight major clades were found in *Russula* (Fig. 1). The largest ones (*Ingratae*, *Rigidae*, *Russula* s.str.) have often been treated as subgenera or sections, while the remaining were usually considered as sections or subsections. Treating all of them as sections could be a natural solution requiring few nomenclatural changes, with the major phylogenetic clades within these sections deserving the status of subsection.

Most European sequestrate *Russulaceae* species tested in the present work nested within previously known supraspecific clades, except two: *Russula monospora* and *R. hobartiae*. *Russula monospora* nested within a poorly supported clade formed by subsections *Russula* s.str. (= *Emeticinae*), *Sardoninae* (= *Firmae*) and *Viscidinae*. This clade was recovered also in the analyses of Kong et al. (2015), but received no significant support (PP 0.87). *Russula monospora* represents a distinct lineage within this clade, and so it could deserve its own subsection. However, a deeper study of the whole group and the other isolated lineages (e.g., those of *R. consobrina* and *R. fellea*), would be necessary to propose a stable nomenclature at the supraspecific level. The other taxon studied in the present work not matching any known supraspecific clade, is the new species *R. hobartiae*, which is significantly related with a putative specimen of *R. ochrophylla*. The identity of this specimen needs to be compared with the type collection (Adamčik et al. 2017), in order to support the introduction of a supraspecific name for the monophyletic lineage shared with *R. hobartiae*. All other European sequestrate *Russulaceae* taxa belong to existing supraspecific taxa, except for *R. ammophila*, which belongs to a significantly supported clade lacking a formal name, related to subsections *Foetentinae*, *Pectinatinae* and *Subvelatae*, within sect. *Ingratae*. This clade is often referred to as the /*R. amoenolens* clade, but genetic data support a formal name at the same rank of the other clades.

European sequestrate *Russulaceae* taxa have unequal intraspecific variability in the DNA markers analyzed. Some species were found to be genetically homogeneous (e.g., *R. mistiformis*), while others presented conspicuous random differences between most individuals (e.g., *R. candidissima*), or had a genetically homogeneous core and one or few individuals showing some differences (e.g., *R. mediterraneensis*). In addition, there was one species recently evolved from a gymnocarpic taxon, which could only be discriminated from the former using *tef1* marker (*R. ammophila*). The diverse phylogenetic status of these species suggests differences in their evolutive past and present, but these can be due to very different factors, such as their life-cycles, mating systems, metapopulation structure, hybridization and introgression events, or selection pressure, to name a few. The future of these lineages remains, of course, an open question, and so predictions based on their eventual status are risky based on current evidence. Partially or recently isolated lineages may thus:

1) genetically diverge from each other and lead to fully isolated species;
2) merge again if reproductive barriers disappear; or
3) become extinct after the conditions that favored diversification change.

Two varieties of *Russula messapica* are here recognized: the original gymnocarpic phenotype (var. *messapica*) and a pseudoangiocarpic phenotype (var. *messapicoides*) that cannot be phylogenetically discriminated even using up to four DNA markers. This is a very rare case, but a few other examples can be found: for instance, a broad morphological variation from gymnocarpic to angiocarpic habit can be observed in *Hydnangium sublamellatum* (Bougher et al. 1993), or *Setchelliogaster tenuipes* var. *rheophyllus* (Martín & Rocabruna 1999, Lago et al. 2000, Martín & Moreno 2001). Hibbett et al. (1994) demonstrated that a pseudoangiocarpic forma can be triggered by a recessive allele at a single locus in *Lentinus tigrinus*, and so it is possible that specific matings or even environmental factors can be responsible for the apparition of sequestrate phenotypes. However, despite the evidence provided here by multigenic data, we cannot exclude the possibility that none of the markers selected reflect a hypothetical reproductive isolation between *R. messapica* var. *messapica* and *R. messapica* var. *messapicoides*. In addition, a closely related species with an exclusively angiocarpic habit (*R. meridionalis*) was found to have at least a partial genetic isolation, probably linked to its restricted geographic distribution. Despite the fact that ITS and 28S rDNA cannot be employed to significantly discriminate between *R. messapica* and *R. meridionalis*, the latter taxon is retained as an independent species because: 1) this is the most conservative decision in nomenclatural terms; and 2) the only *rpb2* sequence successfully obtained from samples of *R. meridionalis* (MK102762) seems different enough from those of *R. messapica* (MK102763–MK102766), with 6/634 bp varying between both species, vs only 1/634 variable sites among *rpb2* sequences of *R. messapica*. Therefore, a more complete *rpb2* dataset would likely support the separation between *R. meridionalis* and *R. messapica*.

Angiocarpic species are present in most lineages of *Lactarius* and *Russula*, confirming that transitions from gymnocarpic ancestors occurred multiple times. Such transitions were often explained as an evolutive adaption to adverse and arid environmental conditions (Thiers 1984, Buyck 1995, Bougher & Lebel 2001, Trappe & Claridge 2005, Smith et al. 2006), although angiocarpic species could be far more frequent in tropical climates than previously assumed (Verbeken et al. 2014b). Wilson et al. (2011) showed that angiocarpic species in *Agaricomycetes* appeared rather recently, but evolve at similar or even faster rates than the gymnocarpic lineages they have derived from, eventually predominating over them. In the present phylogenetic reconstructions, most angiocarpic species seem to be isolated in gymnocarpic lineages, but small groups of angiocarpic species can be found too (e.g., *R. candidissima* and related species within subsect. *Firmiores*). Interestingly, the clade named /*R. tapawera* is composed mainly of Australian and South American angiocarpic species with scattered gymnocarpic taxa, such as *R. purpureoflava*, *R. tawai* or *R. tricholomopsis* (Lebel & Tonkin 2007, Trierveiler-Pereira et al. 2015). Such an abundance of sequestrate species in the Southern Hemisphere could be due to: 1) very frequent transitions from gymnocarpic to angiocarpic states and/or a faster divergence rate of angiocarpic lineages; 2) an angiocarpic ancestor of the entire lineage with scattered reversions to a gymnocarpic state; or 3) a fragmented picture of the biogeographical distribution of gymnocarpic russuloid taxa in the Southern Hemisphere. Additional information is critically needed to evaluate these hypotheses.

Table 2 Comparison of the different European sequestrate species of *Lactarius* and *Russula* ordered by systematic sections.

	Basidiomata type	Columella	Suprapellis	Hymenophoral trama	Cystidia	Basidia	Spores (µm)	Ornamentation	Host
Lactarius subgen. *Lactarius*									
L. giennensis	angiocarpic, sessile	branched, inconspicuous	trichoderm	homoiomerous	cystidioles	1-spored	10–13 × 7–9	reticulum	*Cistaceae*
L. populicola	angiocarpic, sessile	absent or inconspicuous	trichoderm	homoiomerous	absent	1-spored	13–15 × 11–13	isolated and tooth-like fused warts	*Salicaceae*
L. soehneri	angiocarpic, sessile	absent	trichoderm	homoiomerous	absent	1-spored	14–18.5 × 12–15	isolated warts and short ridges	*Fagaceae* and *Pinaceae*
L. stephensii	angiocarpic, sessile	absent or inconspicuous	trichoderm	homoiomerous	absent	1-spored	12–14.5 × 11–13 (weakly amyloid)	isolated warts	*Fagaceae*
L. subgiennensis	angiocarpic, sessile	branched, inconspicuous	trichoderm	homoiomerous	cystidioles	1-spored	8.5–11 × 6.5–7.8	incomplete reticulum	*Cistaceae*
Lactarius subgen. *Russularia*									
L. borzianus	angiocarpic, sessile	percurrent, branched	trichoderm to oedotrichoderm	homoiomerous	cystidioles	3–4-spored	9.5–13 × 8–10	isolated warts	*Pinaceae*
L. josserandii	angiocarpic, sessile	absent or inconspicuous	oedotrichoderm	homoiomerous	cystidioles	2–4-spored	8.5–12.5 × 7–9.5	incomplete reticulum	*Pinaceae*
Russula sect. *Ingratae*									
R. ammophila	angiocarpic to pseudoangiocarpic, stipitate	stipe-columella	intricate trichoderm	heteromerous	macrocystidia	2–4-spored	7–9 × 5.5–7.5	isolated warts and short ridges	*Pinaceae*
R. cerea	angiocarpic, sessile	absent or inconspicuous	trichoderm	sphaerocysts only in tramal anastomoses	macrocystidia	2-spored	9.5–12.5	isolated warts	*Fagaceae* and *Pinaceae*
R. mistiformis	angiocarpic, sessile	absent	trichoderm	sphaerocysts only in tramal anastomoses	cystidioles	1–4-spored	9.5–11 × 8.5–10	isolated warts	*Fagaceae* and *Pinaceae*
R. pila	angiocarpic, sessile	absent	trichoderm	sphaerocysts only in tramal anastomoses	cystidioles	3–4-spored	10–12	isolated warts	*Fagaceae*
Russula sect. *Rigidae*									
R. andaluciana	angiocarpic, sessile	inconspicuous	oedotrichoderm	prosenchymatous	absent	4-spored	7.5–9.5 × 7–9	isolated warts and low ridges	*Cistaceae*
Russula sect. *Russula*									
R. candida	angiocarpic, stipitate	stipe-columella	trichoderm	heteromerous	macrocystidia	1–3-spored	8.5–11 × 7–9	isolated warts	*Fagaceae*
R. candidissima	angiocarpic to pseudoangiocarpic, stipitate	stipe-columella	cutis of repent hyphae	heteromerous	macrocystidia	2–4-spored	9.5–12.5 × 8.5–10.5	groups of 2–4 warts interconnected by low ridges	*Fagaceae* and *Pinaceae*
R. galileensis	angiocarpic, stipitate	stipe-columella	intricate trichoderm	heteromerous	macrocystidia	4-spored	10–11.5 × 9.5–10.5	reticulum of crests and warts	*Fagaceae*
R. hobartiae	angiocarpic, sessile	absent or inconspicuous	palisadotrichoderm	prosenchymatous	macrocystidia	2–4-spored	7–9.5 × 7–9	reticulum of low ridges and warts	*Pinaceae*
R. mattiroloana	pseudoangiocarpic, stipitate	stipe-columella	trichoderm	heteromerous	macrocystidia	2–4-spored	10.5–15.5 × 10–15	isolated warts	*Pinaceae*
R. mediterraneensis	pseudoangiocarpic, stipitate	stipe-columella	trichoderm	heteromerous	macrocystidia	2–3-spored	10–15 × 9–14	isolated warts	*Fagaceae*
R. meridionalis	angiocarpic, sessile	absent or present	trichoderm	heteromerous	cystidioles	4-spored	8–11 × 7–10	reticulum of ridges and isolated warts	*Fagaceae*
R. messapica var. *messapicoides*	pseudoangiocarpic, stipitate	stipe-columella	trichoderm	heteromerous	cystidioles	4-spored	8–10 × 7.5–9.5	reticulum of ridges and isolated warts	*Fagaceae*
R. monospora	angiocarpic, sessile	absent	intricate trichoderm	homoiomerous	absent	1-spored	10–13 (weakly amyloid)	isolated warts	*Fagaceae* and *Pinaceae*
R. vidalii	angiocarpic, sessile	percurrent, branched	palisadotrichoderm	heteromerous	macrocystidia	2-spored	9–11	isolated warts and short ridges	*Fagaceae*
R. vinaceodora	pseudoangiocarpic, stipitate	stipe-columella	intricate ixotrichoderm	heteromerous	macrocystidia	2–4-spored	7–11 × 6–9.5	reticulum of crests and isolated warts	*Pinaceae*
Russula not classified									
R. bavarica	angiocarpic, sessile	absent	trichoderm	homoiomerous with endomacrocystidia	macrocystidia	1-spored	13–15 × 12.5–14.5 (weakly amyloid)	isolated warts	
R. neuhoffii	angiocarpic, sessile	absent	trichoepithelium	homoiomerous	macrocystidia	2–3-spored	9.5–12.5 × 8.5–11	isolated warts	*Fagaceae*

Speciation processes seem to be quite diverse among European sequestrate russuloid taxa. For example, *L. giennensis* and *L. subgiennensis* seem to represent independent genetic lineages maybe diverging as a result of allopatric speciation. Both species can be found associated with *Cistaceae* hosts in acidic soils in the Mediterranean basin, with *L. giennensis* apparently restricted to Western and Southern Spain, while *L. subgiennensis* is so far known only from the island of Cyprus at the opposite end of the Mediterranean basin. This clade apparently represents one of the few lineages within *Russulaceae* associated with *Cistaceae* hosts, although comprehensive phylogenetic assessments of fungal diversity within *Cistaceae* ecosystems are generally lacking (Fellner & Biber 1990, Lavorato 1991, Vila & Llimona 1999, 2002, 2006, 2009, Comandini et al. 2006, Torrejón 2007, 2009, Campos et al. 2010, Loizides & Kyriakou 2011, Malloch & Thorn 2011, Zambonelli et al. 2014, Leonardi et al. 2016, Loizides 2016). *Russulaceae* species associated with *Cistaceae* are not monophyletic, suggesting that multiple events of host specialization took place in the evolutionary history of this family. Moreover, speciation processes through biogeographic isolation (*L. josserandii* vs *L. borzianus*), host specialization (*L. populicola* vs *L. stephensii*), or climatic regions (*R. mistiformis* vs *R. cerea*), seem to be unstable in time, as no apomorphic features based solely on these factors could be identified in any section or subsection. Despite the loss of aerial spore dispersal, however, the majority of lineages do not appear to be endemic to specific continents, such as the widespread European species *R. candidissima*, which nests within a clade otherwise composed exclusively of American species. These observations are consistent with the 'generalized diversification rate' pattern found in *Russula* by Looney et al. (2016).

Morphological features traditionally employed to discriminate between sequestrate *Russulaceae* species seem to have a phylogenetic basis, although some of them were in need of re-interpretation. In Table 2, all European species studied are compared according to:

1) basidiomata development (pseudoangiocarpic, angiocarpic) and presence or absence of a stipe (stipitate, sessile);
2) presence or absence of a columella (percurrent, branched, stipe-columella);
3) suprapellis structure (trichoderm, intricate trichoderm, palisadotrichoderm, oedotrichoderm, trichoepithelium);
4) hymenophoral trama composition (heteromerous or homoiomerous);
5) presence or absence of cystidia (cystidioles, macrocystidia);
6) number of spores in basidia;
7) size of spores;
8) spore ornamentation (warts, reticulum, ridges, crests); and finally
9) family of putative symbiont plants (*Cistaceae*, *Fagaceae*, *Pinaceae*, *Salicaceae*).

The degree of development of the sequestrate syndrome (gasteromycetation) is indeed not only poorly correlated with classical taxonomical concepts, as already evident in other groups (Hibbett et al. 1997, Peintner et al. 2001, Hosaka et al. 2006), but probably variable within some species, and maybe even between basidiomes from the same mycelium. Hymenophoral trama, suprapellis structure, and number of spores per basidia seem to be features characteristic of supraspecific clades, in concordance with observations by Calonge & Martín (2000) and Lebel & Trappe (2000), and so is ectomycorrhizal morphology (Beenken 2004), while spore size, shape, and ornamentations, ecological traits, as well as classical macroscopic features (size, colour, odor, spore print), are still useful at the species level.

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