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RESEARCH ARTICLE

# Diversity of *Russula* subg. *Compactae* (*Russulales*, *Basidiomycota*) in Ukraine

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**Abstract.** The article provides the first general overview of the species diversity of *Russula* subgenus *Compactae* in Ukraine in the last 50 years. We used both molecular methods (barcoding and metabarcoding) and results of classical field observations. In addition, literature data and herbarium materials were analyzed. As a result, six species of the subgenus are reported for Ukraine, including two new records for the country, *R. acrifolia* and *R. anthracina*. For the newly reported ones, full descriptions and drawings of their microstructures are given. For all species, data on their distribution in Ukraine and worldwide is provided.

**Keywords:** biodiversity, DNA extraction, fungi, new records, subgenus *Compactae*

## Introduction

*Russula* Pers. ex Fr. is one of the largest genera of ectomycorrhizal fungi with agaricoid or sequestrate basidiocarps consisting of approximately 2000 species worldwide (Das et al., 2020; Xie et al., 2023). Most species of the genus are considered to have a wide range of hosts among conifers and hardwoods, usually species of *Pinaceae* Lindley and *Fagales* Engl. in a temperate zone (Oberwinkler, 2012), although some of them have specific hosts (Looney et al., 2018). For classification purposes, scientists starting from E.M. Fries (Fries, 1836–1838) have worked to develop an infrageneric structure of the genus based on fruit body morphology (Sarnari, 1998). Since the introduction of molecular methods, this classification has become considerably more

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complex (Buyck et al., 2018). To date, numerous infrageneric units (subgenera, sections, subsections, etc.) have been established for the genus *Russula*.

The subgenus *Russula* subg. *Compactae* (Fr.) Bon is one of those infrageneric units characterized by thick-fleshed basidiocarps with dull-colored cap (white, brown, grey to black) and regularly unequal gills. When cut or bruised, the flesh of fruit bodies starts rather quickly blackening, greying, reddening or browning. Mostly disagreeable smell is characteristic. The spores are finely reticulate-verruculose with inamyloid suprahilar spot. Sequestrate species are unknown within the subgenus (Knudsen, Vesterholt, 2008; Buyck et al., 2018; De Lange et al., 2023). There are reportedly 194 species worldwide in the subgenus, according to ITS data (De Lange et al., 2023).

The last comprehensive report on the genus *Russula* in Ukraine was published about 50 years ago, with 57 *Russula* species mentioned, including four from the subgenus *Compactae* (Zerova et al., 1979). Since that time, mycological research in systematics and ecology has substantially transformed, especially in their molecular and computational aspects, resulting in continuous revisions of taxonomy and description of numerous new species. This was particularly important for *Russula* due to its diverse and overlapping macro- and micro-characteristics (Buyck et al., 2018; Adamčík et al., 2019; De Lange et al., 2023).

The first records of species of *Russula* subg. *Compactae* (notably, *R. nigricans* Fr. and *R. densifolia* Gillet) in Ukraine were reported at the beginning of the 20$^{th}$ century by H. Bobyak, Z. Girzhytska, and A. Pilát from the Right-Bank part of Ukraine: Ternopil, Kyiv, and Zakarpattia/Transcarpathian administrative regions (*oblasts*), respectively (Bobyak, 1907; Girzhytska, 1929; Pilát, 1940). In the 1950s to 1980s, the genus *Russula* was studied for the most part by M. Zerova and G. Rozhenko, mainly in the Right-Bank Ukraine and Crimea (Zerova, 1962), also by R. Ganzha in Poltava Region (Ganzha, 1960a, 1960b, 1970), S. Wasser in the Steppe zone (Wasser, 1974; Wasser, Soldatova, 1977), and T. Horova in the Carpathians (Horova, 1979); these records were combined into the first (and, to date, the only one) comprehensive report on the genus *Russula* in Ukraine (Zerova et al., 1979).

Over the last decade, the research on the diversity of the genus *Russula* was conducted primarily by M. Prydiuk, V. Heluta, O. Prylutskyi, and V. Malanyuk (Dudka et al., 2004, 2009a, 2009b, 2019; Dzhagan et al., 2008; Heluta et al., 2011; Malanyuk, 2014; Kozlowska et al., 2015; Prylutskyi et al., 2017), as well as the staff members of several protected areas (Fokshei, Derzhipilskiy, 2018, 2021; Hleb et al., 2023). In general, the representatives of the genus *Russula* appear only in various general species lists, among other basidial macrofungi, and up to now, no study dedicated specifically to this genus has been published in Ukraine.

To assess the diversity of the genus *Russula* in Ukraine, we performed the first molecular analysis for the genus in the country, alongside morphological examination, and a critical analysis of the available literature data about the subgenus *Compactae* in Ukraine.

## Materials and Methods

**Specimens examined.** The study is based on herbarium specimens deposited at the Fungarium of the National Herbarium of Ukraine at the M.G. Kholodny Institute of Botany, NAS of Ukraine (KW-M), and recent collections. The recent material was collected in 2025 by Dr. Mykola Prydiuk, Dr. Olexandr Akulov and members of the Facebook citizen science community *Fungi of Ukraine* ("Гриби України", https://www.facebook.com/groups/1054204501266549/) Serhii Orinenko and Yevhen Rudenko. To determine the species, we started by performing ITS-based screening of the specimens, preidentified as subg. *Compactae* by macromorphology and not heavily damaged by insects, and then examined micromorphology for the species new for Ukraine.

Newly collected specimens were deposited either in the Fungarium of the Herbarium of V.N. Karazin Kharkiv National University (CWU(-MYC)) or Fungarium of the National Herbarium of Ukraine at the M.G. Kholodny Institute of Botany (KW-M) and uploaded to PlutoF database (Abarenkov et al., 2010).

**Morphological studies.** Macroscopic characteristics were observed *in oculo nudo* from basidiocarps. Light microscopy for two newly recorded for the country species was performed on dried material; all structures were observed in distilled $H_2O$. Their taxonomy and identification follow two publications (Sarnari, 1998; De Lange et al., 2023).

**DNA extraction, amplification, and sequencing.** DNA extraction, PCR, and electrophoresis

were done in the M.G. Kholodny Institute of Botany, NAS of Ukraine, and at the Continental Farmers Group. DNA extraction was performed from 50–100 mg of basidiocarp lamellae using the Biocore Spin-Food DNA-50 extraction kit (Biocore Technology, Ukraine). During lysis step 4 μL of Proteinase K (Qiagen, Germany) and 0.5% (v/v) β-mercaptoethanol (UOSlab, Ukraine) were added to each sample immediately before use; samples were incubated for 3 hours at 55 °C. All other steps were taken following manufacturer's instructions. The resulting eluted DNA contained a residual black pigmentation during the work with all specimens, so we additionally filtered the solution using Zymo-Spin III-HRC Filter (Zymo Research, US) following manufacturer's instructions.

The nrITS region was amplified with ITS1-F (Gardes, Bruns, 1993) and ITS4 (White et al., 1990) primers using Pfu-X Polymerase (Larova, Germany) and DreamTaq Green PCR Master Mix 2X (Thermo Fisher Scientific Baltics, Lithuania). Protocol for PCR: (1) initial denaturation: 95 °C, 3 min; (2) 35 cycles: denaturation (95 °C, 30 s), annealing (55 °C, 30 s), elongation (72 °C, 1 min); 3) final elongation: (72 °C, 10 min) (modified protocol from White et al., 1990). PCR products were Sanger sequenced at Macrogen Europe (Amsterdam, the Netherlands). Chromatograms were processed in MEGA 12 (Kumar et al., 2024).

**Environmental DNA analysis.** As an additional source of data, we incorporated identified sequences of ITS2 fragments of total environmental DNA, obtained from 224 soil samples within the project "Tracking Trade Across Symbiotic Networks" (Human Frontiers Science Program, Grant No. R/010525, Project Leader – Dr. Oleh Prylutskyi). Methods are briefly described in Leshchenko et al. (2025). Operational Taxonomic Units (OTU), clustered with 0.97 threshold and identified as representatives of genus *Russula* with greater than 97% similarity against the standard UNITE database (Abarenkov et al., 2024) in LotuS2 (Özkurt et al., 2022), were subsequently used in phylogenetic analysis (Table 1).

**Phylogenetic analysis.** An ITS-only dataset was constructed for phylogenetic analysis. We used European sequences of *Russula* subg. *Compactae* and outgroup from dataset in De Lange et al. (2023) and included newly obtained Ukrainian sequences from specimens (Table 2). All sequence data has been deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

Table 1. **Operational Taxonomic Units (OTUs) identified as representatives of *Russula* subg. *Compactae* from soils (Prylutskyi et al., unpublished)**

| Taxon | OTU | Country | Cumulative number of Illumina reads across all environmental samples |
|---|---|---|---|
| *Russula* aff. *acrifolia* | OTU1053 | Ukraine | 4360 |
| *R. adusta* | OTU124 | Ukraine | 61289 |
| *R. densifolia* | OTU1480 | Ukraine | 2579 |
| *R. nigricans* | OTU45 | Ukraine | 160414 |
| | OTU8086 | Ukraine | 68 |

To match the length of other sequences, we added multiple N on both ends for OTUs. Sequences were aligned using the online version of MAFFT v.7 (Katoh et al., 2019) with E-INS-i strategy (De Lange et al., 2023); leading and trailing ends of alignments were trimmed. ModelTest-NG in RAxML-GUI 2.0.16 (Edler et al., 2021) was used to determine substitution model using corrected Akaike information criterion (AICc). TIM2ef+G4 model was determined to be the most appropriate. Maximum likelihood (ML) analysis was performed in RAxML-GUI 2.0.17 (Edler et al., 2021) (Linux version with RAxML-NG (Kozlov et al., 2019) support) using TIM2ef+G4 model and bootstrapping analysis with 10000 replicates. Subsequent bootstopping test showed convergence after 8250 trees with average weighted Robinson-Foulds distance 1.495%. Bayesian Inference (BI) was executed in MrBayes 3.2.7 (Ronquist et al., 2012) with GTR+G4 model (as MrBayes does not support TIM-models (Lecocq et al., 2013)), 10 million replicates, 3 heated, and 1 cold chains and 20% burn-in. Average standard deviation of split frequencies was 0.0015, potential scale reduction factor (PSRF) was 1.0 for all parameters, and minimal and average Effective Sample Size (ESS) were greater than 100 for all parameters. Phylogenetic tree was visualized using online tool iTOL v.7 (Letunic, Bork, 2024). ML tree was post-processed using Inkscape (https://inkscape.org); branches, which had been absent in BI tree, were marked with an asterisk (*).

**Distribution analysis.** To define distribution patterns for *Russula* subg. *Compactae* in Ukraine,

Table 2. **Sequences with GenBank accession numbers used for phylogenetic analysis in this study**

| Taxon | Voucher collection (herbarium) | Country | ITS |
|---|---|---|---|
| | Reference sequences (De Lange et al., 2023) | | |
| *Russula acrifolia* | **PC0728045 (PC)** | France | OM833109 |
| | RDL 18-037 (GENT) | Sweden | OM833113 |
| | RDL 18-040 (GENT) | Sweden | OM833116 |
| *R.* aff. *acrifolia* | r-05065 | United States | JF834363 |
| *R. adusta* | RDL 18-020 (GENT) | Sweden | MW172317 |
| | RDL 18-024 (GENT) | Sweden | OM833069 |
| | **Rom. 58-431 (PC)** | France | OM833076 |
| *R. albonigra* | **SAV-F 20197 (SAV)** | Slovakia | MW172299 |
| | SAV F-3220 (SAV) | Belgium | OM833121 |
| | SAV-F 3465 (SAV) | Slovakia | MW172293 |
| *R. ambusta* | **SAV-F 3358 (SAV)** | Slovakia | MW172301 |
| *R. anthracina* | FH RUS 14091001 (GENT) | Slovakia | MW172330 |
| | **Rom. 56-62 (PC)** | France | OM833169 |
| *R. atramentosa* | FH 2011-002R (GENT, FH*) | Belgium | MW172322 |
| | **IB91/58 (IB)** | Italy | OM833146 |
| *R. densifolia* | FH 2006 ST03 (GENT, FH*) | Germany | OM833155 |
| | RDL 17-020 (GENT) | Belgium | OM833159 |
| | RDL 17-023 (GENT) | Belgium | OM833158 |
| *R. densissima* | **Rom. 73-131 (PC)** | France | OM833150 |
| *R. marxmuelleriana* | **RDL 17-009 (GENT)** | Belgium | OM833120 |
| *R. nigricans* | RDL 16-007 (GENT) | Belgium | OM833129 |
| | RDL 16-069 (GENT) | Italy | OM833125 |
| | RDL 17-005 (GENT) | Belgium | MW172333 |
| | RDL 17-007 (GENT) | Belgium | MW172334 |
| | RDL 18-051 (GENT) | Belgium | OM833135 |
| *R. nigrifacta* | **RDL 16-044 (GENT)** | Italy | MW172308 |
| *R. picrophylla* | **RDL 16-049 (GENT)** | Italy | OM833095 |
| *R. roseonigra* | **WU36644 (WU)** | Austria | OM833107 |
| *R. thuringiaca* | **FH 2014 ST02 (GENT)** | Germany | OM833081 |
| *R. ustulata* | **AV 16-019 (GENT)** | Norway | MW172312 |
| | Sequences from Ukrainian specimens (this study) | | |
| *R. acrifolia* | CWU(MYC)8876 (CWU) | Ukraine | PZ619217 |
| *R. adusta* | CWU(MYC)8805 (CWU) | Ukraine | PZ619218 |
| *R. albonigra* | CWU(MYC)8872 (CWU) | Ukraine | PZ619215 |
| | KW-M70501 (KW) | Ukraine | PZ619212 |
| *R. anthracina* | KW-M72187 (KW) | Ukraine | PZ619214 |
| *R. nigricans* | CWU(MYC)8874 (CWU) | Ukraine | PZ619216 |
| | KW-M72208 (KW) | Ukraine | PZ619213 |
| | Outgroup (De Lange et al., 2023) | | |
| *R. archaeosuberis* | BB 12.085 (PC) | Italy | KY800355 |
| *R. camarophylla* | MPG11-7-09 (PC) | Spain | KY800353 |
| *R. gossypina* | BB 06.002 (PC) | Madagascar | KY800350 |

Note: Sequences from type material are indicated in bold.

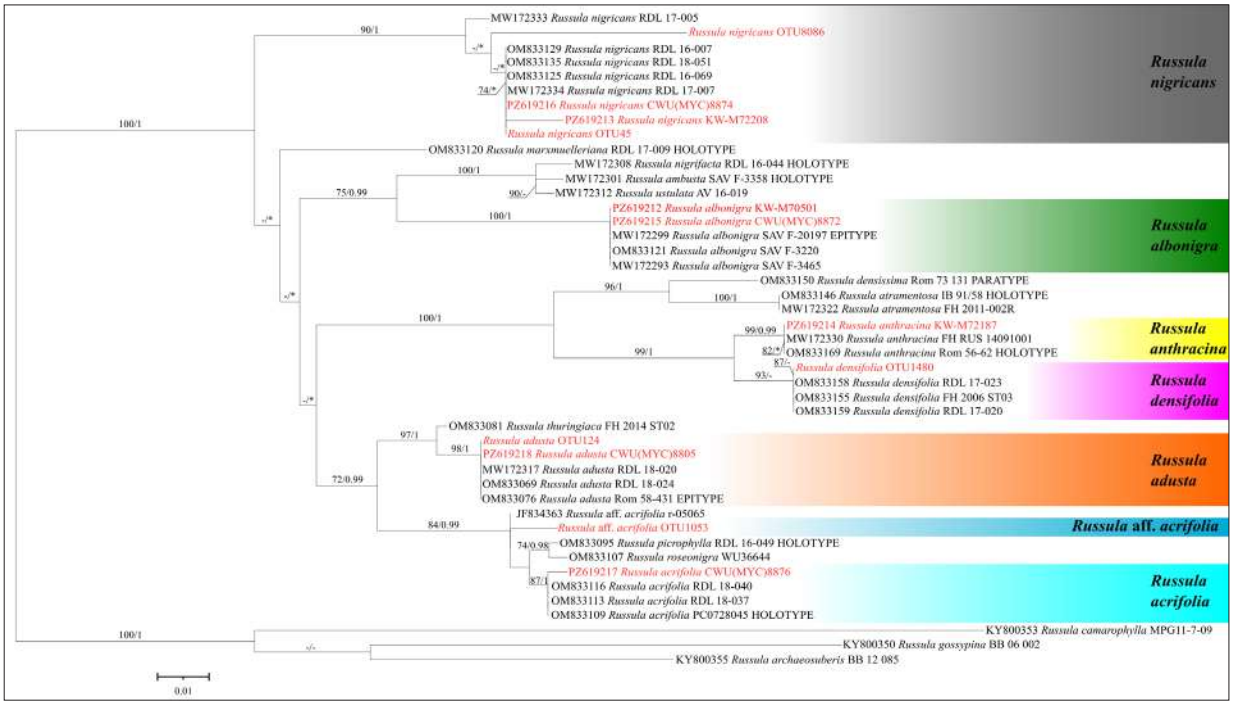



**Fig. 1.** Maximum Likelihood (ML) tree of the European species of *Russula* subg. *Compactae*, based on ITS sequences. ML bootstrap values ≥ 70 and Bayesian Inference (BI) posterior probabilities ≥ 0.95 are shown; the asterisk (*) indicates a missing branch from BI tree. Sequences from Ukrainian specimens or environmental Operational Taxonomic Units (OTU) are highlighted in red font

we analyzed published references for this taxon from open biodiversity databases GBIF (GBIF.org, 2026–onward), PlutoF (Abarenkov et al., 2010), UkrBIN (UkrBIN, 2026–onward), and *Fungi of Ukraine* (Andrianova et al., 2006), as well as relevant publications. All references are added to the distribution list in the Results section. A full dataset, which contains information about six OTUs, seven specimens sequenced and analyzed in this study, and 32 historical specimens is available in Table S1 in Supplementary Material (column names follow Darwin Core, https://dwc.tdwg.org/terms/).

A GBIF dataset (GBIF.org, 2026–onward) was created by selecting the species names and their synonyms in the Scientific Name column following only De Lange et al. (2023) and Sarnari (1998) (without including dubious synonyms marked with "?") worldwide. We decided to ignore GBIF Backbone due to some incorrect taxonomic interpretations, such as synonymizing *Russula adusta* (Pers.) Fr. and *R. nigricans* Fr., or not synonymizing *R. fuliginosa* Sarnari with *R. anthracina* Romagn. Thus, after downloading the dataset, species and their synonyms were selected in the ScientificName column, while a country was determined by level-0Name column.

Terminology for regions of the *Flora of fungi of Ukraine* follows Heluta (2023) and for ecoregions follows OneEarth.org (2026–onward). We used a dataset with the polygons of regions in Geopackage format created by Dr. Oleh Prylutskyi (Prylutskyi, 2024) and post-processed it using Inkscape (https://inkscape.org) to visualize the currently known distribution of *Russula* subg. *Compactae* in Ukraine.

The following abbreviations are used for protected areas: NNP – National Nature Park, NR – Nature Reserve, RLP – Regional Landscape Park.

## Results

According to our study, six species of *Russula* subg. *Compactae* are known in Ukraine to date, including two newly recorded species for the country, *R. acrifolia* and *R. anthracina* (Fig. 1). For Europe in general, at least 15 species are reported (De Lange et al., 2021, 2023). Some of them were recorded in neighboring countries, such as *R. ambusta* De Lange, Adamčík & F. Hampe (Slovakia, from *Quercus*, *Pinus*,

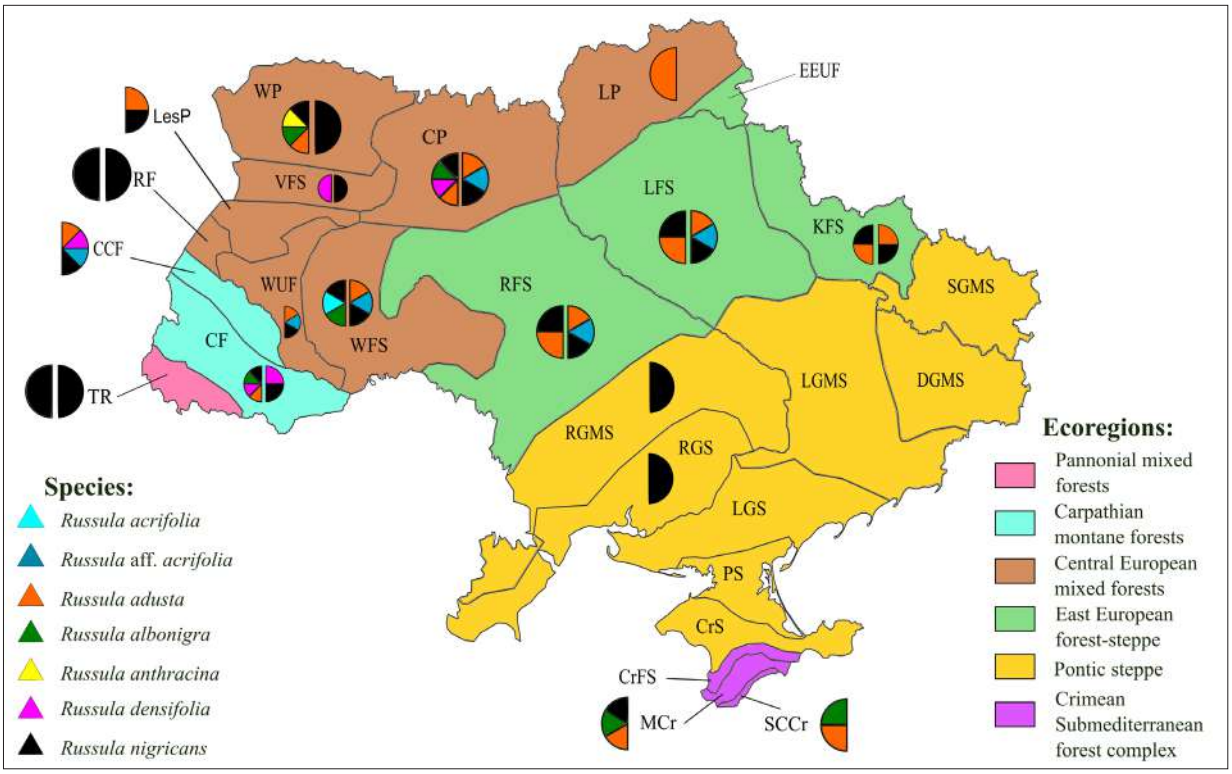



**Fig. 2.** Distribution of *Russula* subg. *Compactae* in Ukraine. Left-oriented circular segments show fruit body-based data (collections, literature references); right-oriented – environmental data (metabarcoding). Terminology for ecoregions follows OneEarth.org (2026–onward). Regions of the *Flora of fungi of Ukraine* (Heluta, 2023): CF – Carpathian Forests, CP – Central (Right-Bank) Polissia, CCF – Cis-Carpathian Forests, CrFS – Crimean Forest-Steppe, CrS – Crimean Steppe, DGMS – Donetsk Grass-Meadow Steppe, EEUF – East European (Central Russian) Upland Forests, KhFS – Kharkiv Forest-Steppe, LBGMS – Left-Bank Grass-Meadow Steppe, LBGS – Left-Bank Grass Steppe, LBFS – Left-Bank Forest-Steppe, LBP – Left-Bank Polissia, LesP – Lesser Polissia, MCr – Mountain Crimea, PS – Polynovyi (*Artemisia*) Steppe, RBGMS – Right-Bank Grass-Meadow Steppe, RBGS – Right-Bank Grass Steppe, RBFS – Right-Bank Forest-Steppe, RF – Roztochchya Forests, SCCr – South Coast of Crimea, SGMS – Starobilsk Grass-Meadow Steppe, TR – Transcarpathia, VFS – Volyn Forest-Steppe, WFS – Western Forest-Steppe, WP – Western Polissia, WUF – Western Ukrainian Forests

and *Betula* forests), *R. atramentosa* Sarnari (Slovakia, from both deciduous and coniferous forests), *R. densissima* Romagn. (Hungary, associated with *Fagus* and *Quercus*), *R. nigrifacta* De Lange & Adamčík (Slovakia, from *Quercus* and *Carpinus* forests), *R. thuringiaca* De Lange, F. Hampe & Girwert (Slovakia, associated with *Castanea* and *Picea*), but so far they are not recorded in Ukraine.

As seen in Fig. 1, the position of OTU1053 on the phylogenetic tree cannot be reliably resolved. It is grouped with enigmatic *Russula* aff. *acrifolia* from the United States, *R. picrophylla*, *R. roseonigra*, and *R. acrifolia*. Due to the lack of a physical voucher, it remains unclear whether it represents one of these or yet another species in a complex due to insufficient DNA data. Nevertheless, this OTU might represent a currently undescribed species in *Russula* subg. *Compactae*.

Moreover, two OTUs were identified as *Russula nigricans* – OTU8086 and OTU45 (Fig. 1). As OTU8086 contains only 68 Illumina reads (compared to 160414 of OTU45) and was observed only in the samples with OTU45, it is yet to be determined if a sequencing error occurred or the current concept of *R. nigricans* should be dealt with as a complex.

According to the distribution map (Fig. 2), the representatives of *Russula* subg. *Compactae* were found in Ukraine primarily in the Carphathian montane forests, Central European mixed forests, East European forest-steppe, and Crimean Submediterranean forest complex, i.e. those regions of

the country where the genus *Russula* was studied in the past. The Pannonial mixed forests ecoregion (or Transcarpathia) is represented in Ukraine by a small area which was insufficiently studied, only reported by Horova (1979). However, it is likely to harbor more *Russula* species to be recorded in future, which have been already reported from Austria, Hungary, and Slovakia (De Lange et al., 2023) within the same ecoregion.

Due to the Russian occupation of some Ukrainian territories, the Crimean Submediterranean forest complex and a large part of the Pontic steppe (CEOBS.org, 2023–onward), unfortunately, cannot be studied. While the South Coast of Crimea and Mountain Crimea (Crimean Submediterranean forest complex ecoregion) are comparatively well-studied (Zerova, 1962; Sarkina, 2001; Dudka et al., 2004), the amount of biodiversity information from the Pontic steppe is scarce. After M. Zerova (Zerova, 1959) and S. Wasser (who reported *R. nigricans* from the steppe: see Wasser, 1974; Wasser, Soldatova, 1977), there is a single report about the entire genus *Russula* from the Pontic steppe (Dudka et al., 2009a). Although tree coverage in steppe is lower than in other natural zones (Lesiv et al., 2019), some species of *Russula* subg. *Compactae* ought to be there, as shown by soil metabarcoding data.

Two of the soil collection points are located in saline grasslands (Odesa Region). Rather unexpectedly, *R. nigricans* DNA was identified in metabarcoding analysis, which remains difficult to explain. Danube Biosphere Reserve is one of the nearest protected areas where mainly *Salix* spp. forests occur, but some areas are covered with *Populus alba* L. and *Pinus nigra* J.F. Arnold, as well as there are afforestations of *P. nigra* subsp. *pallasiana* (Lamb.) Holmboe (https://www.dbr.org.ua/search/label/home_en). As *R. nigricans* was reported to form ectomycorrhiza with *Pinus* spp. (De Lange et al., 2023), the fungal spores might have been dispersed to the salt grassland by the wind.

Below we provide characteristics of the species of the subgenus *Compactae* of *Russula* found in Ukraine; for two species new for the country, descriptions of macro- and microscopic features are added, as well as drawings of their microscopic features.

***Russula acrifolia*** Romagn., Les Russules d'Europe et d'Afrique du Nord: 203. 1967. – Fig. 3.

= *Russula densifolia* var. *caucasica* Singer, Beih. Bot. Centralbl. 46: 90. 1929 = *Russula adusta* f. *rubens* Romagn., Bull. Trimestriel Soc. Mycol. France 59: 71. 1943 = *Russula acrifolia* Romagn. (nom. inval.), Bull. Mens. Soc. Linn. Lyon 31 (6): 173. 1962 = *Russula acrifolia* Romagn. (nom. illeg.), Doc. Mycol. 26 (104): 32. 1997.

**Description** (De Lange et al., 2023; Romagnesi, 1967). Pileus 40–140 mm diam, when mature plano-convex with shallow depression to infundibuliform, smooth surface; yellowish white, yellowish brown to umber, dark brown. Stipe 20–60 × 15–40 mm, cylindrical, firm, surface smooth, white, browning when older. Lamellae segmentiform to subventricose, up to 5 mm deep, narrowly adnate, white to pale cream when older, with pinkish tinge; lamellulae numerous, of different lengths in a regular pattern. Surface of pileus, stipe, and lamellae strongly reddening when touched, then blackening. Context thick, firm, white, slowly turning light to moderately orange red, then slowly greying-blackening; odour fruity, slightly musty when old; taste acrid to strongly acrid. Spore print white (Ia).

Basidiospores (7.0–)7.6–8.1–8.6(–9.6) × (5.4–)6.1–6.6–7.1 (–7.8) µm, broadly ellipsoid; ornamentation of low, very dense amyloid warts; suprahilar spot small, not amyloid. Basidia (45–)50.6–55.2–59.8(–71) × (10–)10.1–11.0–11.9(–13) µm, narrowly clavate, 4-spored. Hymenial cystidia (45–)55.6–63.0–70.4(–77) × (5–)5.8 6.5–7.2(–8) µm, cylindrical to narrowly fusiform, flexuous, irregularly tapering towards the top, apically with one to multiple constrictions or an eccentric appendage, thin-walled; content heteromorphous, oily. Hyphal terminations near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (25–)37.3–49.3–61.3(–79) × (3–)3.3–4.2–5.1(–6) µm, narrowly cylindrical, on average apically constricted. Hyphal terminations near the pileus centre slightly slenderer and apically hardly attenuated; terminal cells (24–)32.6–44.1–55.6(–80) × (2–)2.9–3.6–4.3(–6) µm. Pileocystidia near the pileus margin widely dispersed, 1-celled, (34–)48.7–69.7–90.7(–125) × (4–) 4.4–5.2–6.0(–8) µm, cylindrical, sometimes slightly subulate or slightly fusiform, sometimes slightly flexuous, apically obtuse or with 1–2 eccentric appendages.

**Note on our specimen.** Basidiospores 7.5–8.5 × 6–7.5 µm. Basidia 43–48 × 11–14 µm. Hymenial cystidia 55.0–60.0 × 6.5–7.5 µm. Hyphal

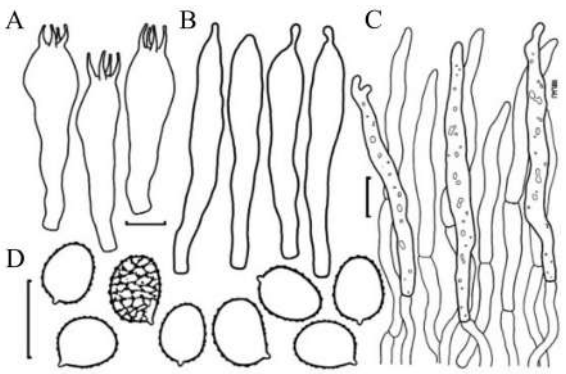



**Fig. 3**. Micromorphological characters of *Russula acrifolia*. A: basidia; B: macrocystidia; C: pileocystidia and elements of pileipellis: D: spores. Bars: 10 μm

terminations 3.0–5.5 μm broad and pileocystidia 45.0–70.0 × 4.5–6.5 μm.

**Ecology** (De Lange et al., 2023)**.** On soil. Associated with *Fagus*, *Picea*, *Pinus*, and *Quercus*.

**Distribution in Ukraine.** Western Forest-Steppe. *Ternopil Region*. Chortkiv District, vicinities of Krutyliv village, Medobory NR (Krasnianske forestry), *Carpinus* forest, 08 Aug. 2025, O. Akulov, CWU-(MYC)8876 (PlutoF, 2026–onward).

**Worldwide distribution** (De Lange et al., 2021, 2023; GBIF.org, 2026–onward; PlutoF, 2026–onward). Africa: Morocco. Asia: China, Japan, Türkiye. Europe: Austria, Belgium, Denmark, Estonia, Finland, France, Germany, Iceland, Ireland, Italy, Latvia, Liechtenstein, Luxembourg, Norway, Poland, Portugal, RF, Slovenia, Spain, Sweden, Switzerland, the Netherlands, Ukraine, United Kingdom. North America: Canada, Mexico, Panama, USA.

***Russula anthracina*** Romagn., Les Russules d'Europe et d'Afrique du Nord: 209–212, 930. 1967. – Fig. 4.

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

**Description** (Romagnesi, 1967; De Lange et al., 2023). Pileus 50–110 mm diam, when mature plano-convex, irregularly expanded, depressed, smooth surface, yellowish white to sand-colored, becoming sooty, greyish brown when older. Stipe 30–60 × 15–28 mm, cylindrical, firm, surface white, greying/blackening when older. Lamellae narrow, segmentiform to subventricose, up to 7 mm deep, narrowly adnate, white, occasionally with a slight pinkish tinge, blackening when bruised; with numerous lamellulae of different lengths in a regular pattern. Context thick, firm, white, then greyish-black, without intermediate reddening; odour slightly fruity/acidic, not very distinctive; taste slightly acrid in pileus/stipe and acrid/peppery in lamellae. Spore print white (Ia).

Basidiospores (6.7–)7.0–7.3–7.6(–7.9) × (4.6–)5.3–5.7–6.1(–6.6) μm, broadly ellipsoid to ellipsoid; ornamentation of low, very dense amyloid warts; suprahilar spot medium-sized, not amyloid. Basidia (38–)45.1–50.0–54.9(–64) × 8.9–9.6–10.3(–11) μm, narrowly clavate, 4-spored. Hymenial cystidia (59–)62.1–68.5–74.9(–85) × (6–) 6.8 7.7–8.6(–9) μm, cylindrical to narrowly fusiform to narrowly clavate, flexuous, apically with central appendage or sometimes double appendage or double constriction, thin-walled; content hyaline. Hyphal terminations near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (37–)43.9–57.3–70.7(–92) × (5–)5.4–6.5–7.6(–9) μm, narrowly cylindrical to subulate. Hyphal terminations near the pileus centre slightly slenderer, less flexuous; terminal cells (22–)45.0–62.8–80.6(–91) × 3.9–4.9–5.9(–7) μm, less attenuated. Pileocystidia near the pileus margin dispersed, hard to find, 1–2-celled, (38–)45.7–74.0–102.3(–148) × (4–)4.8–5.8–6.8(–7) μm, subulate to narrowly fusiform, slightly flexuous, apically with 1–2 eccentric appendages or tapering towards the top.

**Note on our specimen.** Basidiospores 6.5–8.0 × 5.5–6.5 μm. Basidia 43–48 × 11–11.5 μm. Hymenial cystidia 60.0–75.0 × 6.5–8.5 μm. Hyphal terminations 5.0–7.5 μm broad and pileocystidia 43.0–79.0 × 4.5–7.0 μm.

**Ecology** (De Lange et al., 2023)**.** On soil. Associated with *Quercus*. One of the specimens examined by De Lange et al. was reported to be found in a deciduous forest with *Quercus cerris* L. and *Carpinus betulus* L. Our specimen was found in a *Carpinus* forest, which might represent a new host for *R. anthracina*.

**Distribution in Ukraine.** Western Polissia. *Volyn Region*. Kamin-Kashyrskyi District, Prypiat-Stokhid NNP (Svalovytska dacha, 24 quarter), *Carpinus* forest, 19 Jul. 2010, M. Prydiuk, KW-M72187 (PlutoF, 2026–onward).

**Worldwide distribution** (De Lange et al., 2023; GBIF.org, 2026–onward; PlutoF, 2026–onward)**.** Africa: Cameroon, Morocco. Asia: China, India,

Indonesia, RF. Europe: Austria, Belgium, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Norway, Slovakia, Slovenia, Spain, Switzerland, Sweden, the Netherlands, Ukraine, United Kingdom. North America: Canada, Costa Rica, Cuba, USA. Oceania: Australia.

***Russula* aff. *acrifolia***

**Distribution in Ukraine (soil metabarcoding).** Central Polissia. *Zhytomyr Region*. Zhytomyr District, *Pinus sylvestris* L. forest with *Betula* and *Sorbus aucuparia* L., 50.4558 N 29.2114 E. Cis-Carpathian Forests and Western Ukrainian Forests. *Ivano-Frankivsk Region*. Ivano-Frankivsk District, Halych NNP, *Carpinus betulus* forest with *Quercus robur* L., *Tilia cordata* Mill., and *Corylus avellana* L., 49.0981 N 24.7180 E; same NNP, *Fagus sylvatica* L. forest with *Caprinus betulus*, *Tilia cordata*, *Prunus avium* L., and *Euonymus verrucosus* Scop., 49.0958 N 24.7068 E; same NNP (Korolivka tract), mesic grassland with *Malus*, 49.1044 N 24.7482 E. Left-Bank Forest-Steppe. *Poltava Region*. Lubny District, old *Fraxinus excelsior* L. forest with *Carpinus betulus*, *Acer platanoides* L., *Acer campestre* L., and *Corylus avellana*; 50.0517 N 32.9821 E; *Pinus sylvestris* forest with *Quercus robur*, *Sorbus aucuparia*, *Betula*, and *Corylus avellana*, 50.2127 N 32.6059 E; *Acer* forest, *Ulmus minor* Mill., *Pinus sylvestris*, *Tilia cordata*, *Quercus robur*, and *Sambucus*, 50.3285 N 32.2496 E. *Kharkiv Region*. Berestyn District, grass-wormwood steppe with *Prunus spinosa* L., *Rosa*, *Sambucus*, and *Caragana*, in the surrounding area sparsely distributed *Ulmus minor*, *Acer tataricum* L., *Tilia*, *Quercus*, and *Pinus*, 49.4408 N 35.5860 E; *Pinus sylvestris* forest with *Quercus robur*, *Fraxinus excelsior*, *Ulmus*, *Acer tataricum*, *Betula*, *Malus*, and *Sorbus aucuparia*, 49.4392 N 35.5662 E. Right-Bank Forest-Steppe. *Cherkasy Region*. Cherkasy District, Kaniv NR, *Carpinus betulus* forest with *Acer platanoides*, *A. campestre*, *Fraxinus excelsior*, *Ulmus glabra* Huds., and *Tilia cordata*, 49.7247 N 31.5116 E. Western Forest-Steppe. *Khmelnytskyi Region*. Kamianets-Podilskyi District, *Carpinus betulus* forest with *Quercus robur*, *Fraxinus excelsior*, and *Acer platanoides*, 48.7989 N 26.6395 E. *Ternopil Region*. Chortkiv District, vicinities of Nahoriany village, *Carpinus* forest with *Corylus*, 48.7878 N 25.6202 E; Medobory NR, *Carpinus* forest with *Betula*, *Picea*, and *Prunus* subg. *Cerasus*, 49.3256 N 26.1370 E.

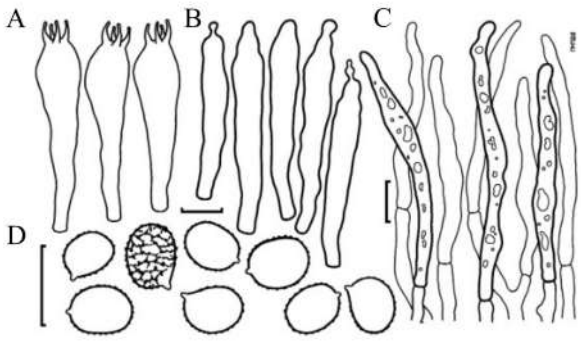



**Fig. 4**. Micromorphological characters of *Russula anthracina*. A: basidia; B: macrocystidia; C: pileocystidia and elements of pileipellis: D: spores. Bars: 10 μm

***Russula adusta*** (Pers.) Fr., Epicr. Syst. Mycol.: 350. 1838. – Fig. 5A, B.

≡ *Agaricus adustus* Pers., Syn. Meth. Fung. 2: 459. 1801 ≡ *Omphalia adusta* (Pers.) Gray, A natural arrangement of British plants 1: 614. 1821 = *Russula adusta* (Pers.) Fr. (nom. inval.), Stirp. Agri Fems.: 57. 1825 = *Russula nigricans* var. *adusta* (Pers.) Barbier, So. Sci. Nat. Sâon.: 191. 1907 = *Russula adusta* f. *gigantea* Britzelm., Bot. Centralbl. 62 (10): 310. 1895 = *Russula subusta* Burl., N. Amer. Flora 9: 207. 1915.

**Ecology** (De Lange et al., 2023). On soil. Associated with *Larix*, *Picea*, and *Pinus*. For some Ukrainian specimens, coniferous hosts have not been reported.

**Distribution in Ukraine.** Carpathian Forests. *Ivano-Frankivsk Region*. Kosiv District, Hutsulshchyna NNP (Prorochuk et al., 2013); Dudka et al., 2019); in the same NNP (Kamenystyi tract, 12 quarter), *Acer pseudoplatanus* L.-*Fagus-Abies* forest with *Picea* (Fokshei, Heluta, 2024; GBIF.org, 2026–onward); same NNP, *Fagus sylvatica* forest (Fokshei, Pohribnyi, 2025). *Zakarpattia Region*. Khust District, Synevyr NNP (Kvasovetske forestry), *Fagus sylvatica* forest with *Carpinus* (Niroda, 2017); same NNP (Ostritske forestry), *Picea-Fagus sylvatica-Abies alba* Mill.-*Acer negundo* L.-*Ulmus* forest (Niroda, 2017). Central Polissia. *Kyiv City*. Mixed forest, 14 Oct. 2025, S. Orinenko, CWU(MYC)8805 (PlutoF, 2026–onward); vicinities of Pushcha-Vodytsia, *Pinus-Quercus* forest, 09 Jul. 1958, G. Rozhenko, KW-M28698 (det. M. Zerova); ibid., *Pinus-Quercus* forest with *Corylus*, 05 Sep. 1958, G. Rozhenko, KW-M28699 (det. M. Zerova); ibid.,

*Quercus-Pinus* forest, 19 Aug. 1956, M. Zerova, KW-M28700 (det. M. Zerova); ibid., *Pinus-Quercus* forest with *Corylus*, 01 Aug. 1958, M. Zerova, KW-M28701 (det. M. Zerova); ibid., *Pinus-Quercus* forest, 09 Jul. 1958, M. Zerova, KW-M28702 (det. M. Zerova) (Zerova et al., 1979; Andrianova et al., 2006; PlutoF, 2026–onward). *Kyiv Region*. Bucha District, near Klavdievo railway station, mixed forest, 18 Aug. 1964, M. Zerova, KW-M28697 (det. M. Zerova) (Zerova et al., 1979; Andrianova et al., 2006; PlutoF, 2026–onward). Vyshhorod District, vicinities of Poliske village (Gabriel et al., 2023); vicinities of Katyuzhanka village (Grodzynska et al., 2025). *Zhytomyr Region*. Korosten' District, Korchevska dacha, under *Quercus* in wet *Pinus-Quercus* forest, 03 Aug. 1945, P. Sosin, KW-M72232 (det. P. Sosin) (Zerova et al., 1979; PlutoF, 2026–onward). Kharkiv Forest-Steppe. *Kharkiv Region*. Chuhuiv District, Homilsha Forests NNP (Prylutskyi et al., 2017). Left-Bank Forest-Steppe. *Poltava Region*. *Quercus* and *Betula* forest strips (Ganzha, 1970; Zerova et al., 1979). Poltava District, vicinities of Poltava, *Pinus sylvestris-Quercus robur* forest (Ganzha, 1960b; Zerova et al., 1979). Left-Bank Polissia. *Kyiv Region*. Vyshhorod District, vicinities of Suvyd village (Grodzynska et al., 2025). *Sumy Region*. Shostka District, Desna-Stara Huta NNP (Starohutsk part, Starohutska dacha tract), *Pinus* forest (Dudka et al., 2009a, 2009b). Mountain Crimea. *Autonomous Republic of Crimea*. *Quercus pubescens* Willd.-*Carpinus orientalis* Mill. forest (Sarkina, 2001). *Pinus* forest with *Juniperus oxycedrus* L., *Q. pubescens*, and *C. orientalis* (Sarkina, 2001). In *Quercus-Pinus* forest (Sarkina, 2001). In *Pinus* afforestation (Sarkina, 2001). Yalta District, the slope of Chatyr-Dah mountain, *Quercus-Carpinus-Fagus* forest (Sarkina, 2020); the slopes of Northern Demerdzhi mountain, *Carpinus-Fagus* forest (Sarkina, 2020); Crimean NR, the northern slopes of Babugan mountain range, *Carpinus-Fagus* forest (Sarkina, 2020); the southern and south-eastern slopes of Hora Parahilmen natural monument, Chamny-Burun mountain and Babugan mountain range, *Quercus-Carpinus-Fagus* forest (Sarkina, 2020); Yalta Mountain-Forest NR (Livadiiske forestry), near Mohabi mountain, *Pinus-Fagus* forest (Sarkina, 2020). Right-Bank Forest-Steppe. *Cherkasy Region*. Cherkasy District, Kaniv NR, *Carpinus* forest, 05 Aug. 1973, M. Yatsenko, KW-M26244 (det. M. Zerova) (Dzhagan et al., 2008). *Kyiv City*. Vicinities of Feofaniia, *Quercus* forest with *Corylus*, 12 Jul. 1960, G. Rozhenko, KW-M28703 (det. M. Zerova) (Zerova et al., 1979; Andrianova et al., 2006; PlutoF, 2026–onward). South Coast of Crimea. *Autonomous Republic of Crimea* (Dudka et al., 2004). Western Polissia (Zerova et al., 1979). *Volyn Region*: Lutsk District, Tsumanska Pushcha NNP (Hleb et al., 2023). Unknown. Zerova et al. (1979) mentioned presence of the species in Grass-Meadow Steppe (according to the old/previously accepted Ukrainian phytogeographic region classification).

**Distribution in Ukraine (soil metabarcoding).** Central Polissia. *Zhytomyr Region*. Zhytomyr District, *Pinus sylvestris* forest with *Populus tremula* L. and *Salix* sp., 50.4679 N 29.2213 E; *Pinus sylvestris* forest with *Betula* and *Sorbus aucuparia*, 50.4558 N 29.2114 E; *Pinus sylvestris* with *Betula* and *Quercus*, 50.4788 N 29.2599 E. Cis-Carpathian Forests and Western Ukrainian Forests. *Ivano-Frankivsk Region*. Ivano-Frankivsk District, Halych NNP (Korolivka tract), mesic grassland with *Malus*, 49.1044 N 24.7482 E. Kharkiv Forest-Steppe. *Kharkiv Region*. Chuhuiv District, Homilsha Forests NNP, *Pinus sylvestris* forest with *Quercus robur*, *Sorbus aucuparia*, and *Frangula alnus* Mill., 49.6638 N 36.4271 E. Left-Bank Forest-Steppe. *Cherkasy Region*. Cherkasy District, Bile Ozero NNP, dry *Pinus sylvestris* forest with *Betula pendula* Roth, *Quercus robur*, *Sorbus aucuparia*, and *Aronia melanocarpa* (Michx.) Elliott, 49.8195 N 31.6018 E. *Poltava Region*. Lubny District, old *Fraxinus excelsior* forest with *Carpinus betulus*, *Acer platanoides*, *A. campestre*, and *Corylus avellana*, 50.0517 N 32.9821 E; *Acer* forest with *Tilia cordata*, *Quercus robur*, *Fraxinus excelsior*, and *Corylus avellana*, 50.3120 N 32.3448 E. *Sumy Region*. Konotop District, Seymskyi RLP, *Tilia cordata* forest with *Acer platanoides*, *A. campestre*, *Fraxinus excelsior*, *Quercus robur*, *Corylus avellana*, and *Euonymus europaeus* L., 51.2908 N 33.1187 E; same RLP, *Quercus robur* forest with *Tilia cordata*, *Acer platanoides*, *A. campestre*, and *Corylus avellana*, 51.3193 N 33.8906 E. Lesser Polissia. *Lviv Region*. Zolochiv District, vicinities of Yasenivtsi village, old *Fagus* forest, 49.8037 N 24.8014 E. Right-Bank Forest-Steppe. *Cherkasy Region*. Cherkasy District, Kaniv NR, *Carpinus betulus* forest with *Acer platanoides*, *A. campestre*, *Fraxinus excelsior*, *Ulmus glabra*, and *Tilia cordata*, 49.7247 N 31.5116 E. Western Forest-Steppe. *Khmelnytskyi Region*. Kamianets-Podilskyi District, *Carpinus betulus* forest with *Quercus robur*, *Fraxinus excelsior*, and *Acer platanoides*, 48.7989 N 26.6395 E; *Carpinus*




**Fig 5.** Basidiomata. A, B: *Russula adusta* (CWU(MYC)8805); C, D: *R. albonigra* (C: KW-M70501; D: CWU(MYC)8872); E, F: *R. nigricans* (E: KW-M72208; F: CWU(MYC)8874). Photos by: A, B – S. Orinenko; C, E – M. Prydiuk; D, F – Ye. Rudenko

*betulus* forest with *Quercus*, *Acer platanoides*, and *A. pseudoplatanus*, 48.7880 N 26.6466 E. *Ternopil Region*. Chortkiv District, Medobory NR, *Carpinus* forest with *Betula*, *Picea*, and *Prunus* subg. *Cerasus*, 49.3255 N 26.1370 E.

**Worldwide distribution** (De Lange et al., 2023; Fokshei, Heluta, 2024; GBIF.org, 2026–onward; PlutoF, 2026–onward). Asia: Armenia, Bhutan, China, Japan, Kazakhstan, Nepal. Europe: Andorra, Austria, Belarus, Belgium, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Norway, Poland, Portugal, RF, Slovenia, Spain, Sweden, the Netherlands, Ukraine, United Kingdom. North America: Canada, USA. Oceania: Australia.

**Note.** Specimen KW-M28696 mentioned as "*Russula adusta* (Pers.) Fr." (Andrianova et al., 2006; Kozlowska et al., 2015) has been reidentified as *Russula decolorans* (Fr.) Fr. using light microscopy. Thus, as of now, there are no records of *R. adusta* from Roztochchya Forests.

***Russula albonigra*** (Krombh.) Fr., Hymenomyc. eur.: 440. 1874. – Fig. 5C, D.

≡ *Agaricus alboniger* Krombh., Naturgetr. Abbild. Beschr. Schwämme 9: 27. 1845 = *Russula nigricans* var. *albonigra* (Krombh.) Cooke & Quél.,

Clav. Syn. Hymen. Eur.: 143. 1878 = *Russula adusta* var. *albonigra* (Krombh.) Massee, Brit. Fung. Fl. 3: 52. 1893 = *Russula albonigra* f. *pseudonigricans* Romagn. (nom. inval.), Bull. Mens. Soc. Linn. Lyon 31(6): 173. 1962 = *Russula albonigra* f. *pseudonigricans* Romagn., Les Russules d'Europe et d'Afrique du Nord: 199–200. 1967.

**Ecology** (De Lange et al., 2021). On soil. Associated with *Fagus*, *Abies*, *Picea* and *Carpinus*.

**Distribution in Ukraine.** Carpathian Forests. *Ivano-Frankivsk Region*. Kosiv District, Hutsulshchyna NNP (Dudka et al., 2019). Nadvirna District, approximately 2 km from Vorokhta village, Carpathians NNP (Vorokhtianske forestry), near *Picea* and *Fagus*, 14 Sep. 2015, M. Prydiuk, KW-M70501 (PlutoF, 2026–onward); Carpathians NNP, *Fagus* forest with *Abies* and *Picea*, 31 Jul. 2025, Y. Rudenko, CWU(MYC)8872 (PlutoF, 2026–onward). *Lviv Region*. Stryi District, Skolivski Beskydy NNP (Dudka et al., 2019). *Zakarpattia Region*. Uzhhorod District, Uzhanskyi NNP (Dudka et al., 2019). Central Polissia. *Kyiv City*. Vicinities of Pushcha-Vodytsia, *Quercus-Pinus* forest, 02 Aug. 1964, M. Konovalenko, KW-M18993 (det. M. Zerova); ibid., *Quercus-Pinus* forest, 01 Oct. 1961, M. Zerova, KW-M18994 (det. M. Zerova); ibid., mixed forest, 20 Sep. 1964, M. Zerova, KW-M18996 (det. M. Zerova); ibid., *Pinus-Quercus* forest, 08 Sep. 1959, G. Rozhenko, KW-M18999 (det. M. Zerova) (Zerova et al., 1979; PlutoF, 2026–onward). Mountain Crimea. *Autonomous Republic of Crimea*: Yalta District, Crimean NR, in *Quercus-Fagus* forest (Sarkina, 2020). Crimean NR, *Quercus-Fagus-Carpinus* forest, 12 Jul. 1956, M. Zerova, KW-M18952 (det. M. Zerova) (Zerova, 1962; Zerova et al., 1979; PlutoF, 2026–onward). Yalta Mountain-Forest NR (Livadiiske forestry), near Mohabi mountain, in *Pinus-Fagus* forest (Sarkina, 2020). In *Fagus* and *Carpinus* forests (Dudka et al., 2004; Sarkina, 2001). South Coast of Crimea. *Autonomous Republic of Crimea*. Yalta District, Yalta Mountain-Forest NR (Livadiiske forestry, near Karahol lake), *Pinus nigra ssp. pallasiana-Fagus* forest, 10 Oct. 2001, M. Prydiuk, KW-M72037 (det. M. Prydiuk) (PlutoF, 2026–onward). Western Forest-Steppe. *Ternopil Region*. Chortkiv District, Medobory NR (Viknianske forestry, Luchianskyi forest, 50 quarter), *Carpinus-Acer-Tilia* forest, near *Hepatica*, 22 Jun. 2007, *M. Prydiuk*, KW-M38408 (det. *M. Prydiuk*) (PlutoF, 2026–onward). Western Polissia. *Rivne Region*. Sarny District, vicinities of Krupove village (88 quarter), *Pinus* forest with *Carpinus*, *Quercus* and *Frangula*, near *Vaccinium*, 08 Aug. 1999, M. Prydiuk, KW-M71995 (det. M. Prydiuk) (PlutoF, 2026–onward); ibid., *Pinus-Quercus* forest with *Betula*, near *Vaccinium* and *Pteridium*, 07 Jul. 1999, M. Prydiuk, KW-M72005 (PlutoF, 2026–onward).

**Worldwide distribution** (De Lange et al., 2021, 2023; Ramshaj, Karadelev, 2025; GBIF.org, 2026–onward; PlutoF, 2026–onward). Africa: Algeria. Asia: Bhutan, China, Georgia, Iran, Japan, Laos, Malaysia, Nepal, RF, South Korea, Thailand, Türkiye, Vietnam. Europe: Andorra, Austria, Belgium, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Ireland, Italy, Kosovo, Latvia, Liechtenstein, Luxembourg, Montenegro, North Macedonia, Norway, Poland, Portugal, Romania, RF, Serbia, Slovakia, Slovenia, Spain, Switzerland, Sweden, the Netherlands, Ukraine, United Kingdom. North America: Belize, Canada, Mexico, USA. Oceania: Australia.

***Russula densifolia*** Gillet, Hyménomycètes: 231. 1874.

= *Agaricus adustus densifolius* Secr. (nom. inval.), Mycogr. Suisse: 476. 1833 = *Russula adusto-densifolia* (Secr.) Singer (nom. inval.), Agaricales: 813. 1986 = *Russula densifolia* f. *hygrophoroides* Reumaux (nom. inval.), Russ. Rar.: 19. 1996.

**Ecology** (De Lange et al., 2023; Ramshaj, Karadelev, 2025). On soil. Associated with *Abies*, *Fagus*, *Halimium*, *Picea*, *Pinus* and *Quercus*.

**Distribution in Ukraine.** Carpathian Forests (Zerova et al., 1979). *Ivano-Frankivsk Region*. Kosiv District, Hutsulshchyna NNP (Holytsia tract), *Abies-Fagus* forest with *Carpinus*, *Pinus*, *Picea*, *Larix* and *Betula* (Fokshei, Derzhipilskiy, 2018); in the same NNP (Prorochuk et al., 2013; Dudka et al., 2019). Nadvirna District, Gorgany NR (13 quarter), *Fagus-Picea* forest (Malanyuk, 2012; Dudka et al., 2019). *Zakarpattia Region*. Rakhiv District, vicinities of Kostylivka village (reported as Berlebáš), near Pip Ivan (reported as Pop Ivan) mountain peak (Pilát, 1940). Carpathians NR (Dudka et al., 2019). Central Polissia. *Kyiv City*. Vicinities of Pushcha-Vodytsia, *Quercus-Pinus* forest, 19 Jul. 1960, M. Zerova, KW-M18596 (det. M. Zerova); ibid., *Quercus-Pinus* forest, 16 Jun. 1957, M. Zerova, KW-M18597 (det. M. Zerova); ibid., *Pinus-Quercus* forest, 16 Jun. 1957, M. Zerova, KW-M18599 (det. M. Zerova) (Zerova et al., 1979; PlutoF, 2026–onward). Volyn Forest-Steppe. *Rivne Region*. Zdolbuniv District, Derman-Ostroh NNP (Mostivske

forestry), *Carpinus* forest, 26 Jun. 2015, M. Prydiuk, KW-M60693 (det. M. Prydiuk) (PlutoF, 2026–onward). Unknown (GBIF.org, 2026–onward).

**Distribution in Ukraine (soil metabarcoding).** Carpathian Forests. *Ivano-Frankivsk Region*: Ivano-Frankivsk District, Syniohora NNP, old *Abies* forest with *Fagus*, 48.6142 N 24.1598 E; same NNP, artificial *Picea* plantation replacing *Abies* forest, 48.6141 N 24.1888 E. Cis-Carpathian Forests. *Ivano-Frankivsk Region*. Ivano-Frankivsk District, *Picea abies* forest with *Carpinus betulus*, *Quercus robur*, *Acer pseudoplatanus*, *Tilia cordata*, *Fagus sylvatica*, and *Rubus hirtus* Waldst. & Kit., 49.0033 N 24.5918 E; *Abies* forest with *Picea abies* (L.) H. Karst., *Quercus robur*, *Tilia cordata*, *Sorbus aucuparia*, and *Corylus avellana*, 49.0237 N 24.5648 E.

**Worldwide distribution** (De Lange et al., 2021, 2023; Ramshaj, Karadelev, 2025; GBIF.org, 2026–onward; PlutoF, 2026–onward). Africa: Benin, Zimbabwe. Asia: Bhutan, China, India, Japan, Laos, Malaysia, Nepal, South Korea. Europe: Austria, Belgium, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Iceland, Ireland, Italy, Liechtenstein, Luxembourg, Kosovo, North Macedonia, Norway, Poland, Portugal, RF, Slovakia, Slovenia, Spain, Sweden, Switzerland, the Netherlands, Ukraine, United Kingdom. North America: Canada, Mexico, USA.

***Russula nigricans*** Fr., Epicr. Syst. Mycol.: 350. 1838. – Fig. 5E, F.

= *Agaricus nigricans* Bull. non O.F. Müller, Herb. France (5): pl. 212. 1785 = *Agaricus nigrescens* Bull. & Vent. (nom. illeg.), Hist. Champ. France (2): 587. 1812 = *Agaricus nigrescens* Krombh., Naturget. Abbild. Schwämme 9: 27, tab. 70, figs 14–15. 1845 = *Agaricus adusta* γγ, *crassa* Alb. & Schwein., Conspectus Fungorum in Lusatiae superioris: 220. 1805.

**Ecology** (De Lange et al., 2023). On soil. Associated with *Abies*, *Fagus*, *Halimium*, *Picea*, *Pinus*, and *Quercus*.

**Distribution in Ukraine.** Carpathian Forests. *Chernivtsi Region*: Chernivtsi District (UkrBIN, 2026–onward). *Ivano-Frankivsk Region*. Ivano-Frankivsk District, Halych NNP, *Carpinus-Quercus* forest (Malanyuk, 2014). Kosiv District, vicinities of Sheshory village, Hutsulshchyna NNP (Sheshorske forestry, near Mertve Ozero), *Fagus* forest, 17 Aug. 2016, M. Prydiuk, KW-M70250 (det. M. Prydiuk) (PlutoF, 2026–onward); same NNP, forests with *Fagus*, *Carpinus*, *Abies*, *Picea*, *Pinus*, and *Quercus* (Fokshei, Derzhipilskiy, 2021). Nadvirna District, Gorgany NR (10 and 11 quarters), *Picea abies* forests (Heluta et al., 2011; Prorochuk et al., 2013; Dudka et al., 2019); vicinities of Yaremche village (GBIF.org, 2026–onward). *Lviv Region*. Stryi District, *Carpinus* forest, 19 Sep. 1972, T. Horova, KW-M18736 (det. T. Horova) (Zerova et al., 1979; PlutoF, 2026–onward); vicinities of Hrebeniv village, Skolivski Beskydy NNP, *Picea* forest, 09 Sep. 1976, T. Horova, KW-M1992 (det. T. Horova) (PlutoF, 2026–onward); vicinities of Smozhe village, *Fagus* forests, KW-M45348 (Horova, 1979; Andrianova et al., 2006); vicinities of Klymets village, *Fagus* forests, KW-M45347 (Horova, 1979; Andrianova et al., 2006). *Zakarpattia Region*. Khust District, Synevyr NNP (Dudka et al., 2019). Rakhiv District, vicinities of Kostylivka village (reported as Berlebáš), near Pip Ivan (reported as Pop Ivan) mountain peak (Pilát, 1940). Tiachiv District, Carpathians NR (Dudka et al., 2019). Uzhhorod District, approximately 1.5 km to the north-west from Stuzhytsia village, Uzhanskyi NNP (Stuzhnytske forestry), *Abies* forest, near green moss, 22 Sep. 2011, M. Prydiuk, KW-M40342 (det. M. Prydiuk) (Dudka et al., 2019; PlutoF, 2026–onward). Central Polissia. *Kyiv Region*. Bucha District, *Quercus-Carpinus* forest with *Pinus*, 17 Aug. 2025, Y. Rudenko, CWU(MYC)8874 (PlutoF, 2026–onward); vicinities of Irpin city (reported as Irpen), *Quercus* forest (Girzhytska, 1929). *Zhytomyr Region*. Zhytomyr District, *Quercus* forest (GBIF.org, 2026–onward). Kharkiv Forest-Steppe. *Kharkiv Region*. Chuhuiv District, Homilsha Forests NNP (Prylutskyi et al., 2017); vicinities of Kamplytsya village, *Pinus* forest (GBIF.org, 2026–onward). Left-Bank Forest-Steppe (Makarenko, 2019). *Chernihiv Region*. Pryluky District, vicinities of Khayenky village, Ichnia NNP, 14 Oct. 2017, M. Shevchenko, KW-M72056 and KW-M72057 (det. M. Shevchenko) (PlutoF, 2026–onward). *Poltava Region*. Poltava District, vicinities of Poltava, *Pinus sylvestris-Quercus robur* forest (Ganzha, 1960b); riparian *Quercus* forest (Ganzha, 1960a). Mountain Crimea. *Autonomous Republic of Crimea*. *Fagus* and *Carpinus* forests (Sarkina, 2001; Dudka et al., 2004). Yalta District, slope of Chatyr-Dah mountain, *Fagus* and *Carpinus-Fagus*, and *Quercus-Carpinus-Fagus* forests (Sarkina, 2020); slopes of Northern Demerdzhi mountain, *Fagus* and *Carpinus-Fagus* and *Quercus-Carpinus-Fagus* forests (Sarkina, 2020); Crimean NR, *Fagus* and *Quercus-Carpinus-Fagus* forests (Sarkina, 2020); south-western slopes of

Uraha mountain, *Quercus-Carpinus-Fagus* forest (Sarkina, 2020); Yalta Mountain-Forest NR (Livadiiske forestry), near Mohabi mountain, *Pinus-Fagus* forest (Sarkina, 2020). Right-Bank Forest-Steppe. *Kyiv City*. Vicinities of Koncha-Zaspa, on the slope near the swamp, 26 Sep. 1964, M. Zerova, KW-M18841 (det. M. Zerova) (Zerova et al., 1979; PlutoF, 2026–onward). Holosiiv NNP (Holosiiv forest, 17 quarter), *Carpinus-Tilia-Corylus* forest, near *Carex*, 29 Aug. 2025, M. Prydiuk, KW-M72208 (PlutoF, 2026–onward). *Cherkasy Region*. Cherkasy District, vicinities of Kaniv city, Kaniv NR, *Carpinus* forest, 05 Aug. 1973, M. Yatsenko, KW-M18840 (det. M. Zerova) (Zerova et al., 1979; PlutoF, 2026–onward); same NR, *Carpinus-Quercus* forest (Dzhagan et al., 2008). Roztochchya Forests (Zerova et al., 1979; Kozlowska et al., 2015). *Lviv Region*. Yavoriv District, in *Fagus* forests (Bazyuk-Dubey, 2010; Kozlowska et al., 2015). Transcarpathia. *Zakarpattia Region*. Khust District (GBIF.org, 2026–onward; UkrBIN, 2026–onward). Tiachiv District, vicinities of Velyka Uholka village, in *Fagus* forests, KW-M45349 (Horova, 1979; Andrianova et al., 2006; Dudka et al., 2019). Western Forest-Steppe: *Ternopil Region*. Ternopil District, vicinities of Berezhany village (Bobyak, 1907). Western Polissia. *Volyn Region*. Lutsk District, Tsumanska Pushcha NNP (Hleb et al., 2023). *Rivne Region*. Rivne District, *Quercus-Carpinus* forest (GBIF.org, 2026–onward; UkrBIN, 2026–onward); mixed forest (UkrBIN, 2026–onward). Sarny District, Dubrovytske forestry (93 quarter), *Quercus* forest with *Pinus*, *Betula*, and *Frangula*, near *Vaccinium*, 21 Jul. 2000, M. Prydiuk, KW-M71975 (det. M. Prydiuk) (PlutoF, 2026–onward); vicinities of Krupove village (88 quarter), *Pinus* forest with *Carpinus*, *Quercus*, and *Frangula*, near *Vaccinium*, 13 Aug. 1999, M. Prydiuk, KW-M71940 (det. M. Prydiuk) (PlutoF, 2026–onward). Unknown (Wasser, 1974). Mixed forest (Wasser, Soldatova, 1977; GBIF.org, 2026–onward).

**Distribution in Ukraine (soil metabarcoding).** Carpathian Forests. *Ivano-Frankivsk Region*: Ivano-Frankivsk District, Syniohora NNP, old *Abies* forest with *Fagus*, 48.6142 N 24.1599 E; same NNP, artificial *Picea* plantation replacing *Abies* forest, 48.6141 N 24.1888 E; same NNP, *Fagus* forest with *Abies*, *Picea*, and *Acer pseudoplatanus*, 48.6715 N 24.2432 E; same NNP, *Picea-Abies* forest with *Fagus*, 48.6219 N 24.1682 E; same NNP, *Fagus-Abies* forest with *Acer pseudoplatanus* and *Populus tremula*, 48.6180 N 24.1751 E; same NNP, old *Abies* forest with *Picea* and *Fagus*, 48.6171 N 24.2043 E. Kosiv District, *Quercus robur* forest with *Abies alba*, *Carpinus betulus*, *Tilia cordata*, and *Corylus avellana*, 48.3085 N 25.1829 E. Nadvirna District, Carpathians NNP (Nadvirnianske forestry), *Fagus sylvatica* forest with *Acer platanoides*, 48.6533 N 24.5720 E; same NNP, *Betula pendula* forest with *Populus tremula*, *Fagus sylvatica*, and *Pinus sylvestris*, 48.5918 N 24.4514 E. *Zakarpattia Region*. Uzhhorod District, Uzhanskyi NNP, *Fagus sylvatica* forest with *Acer pseudoplatanus* and *Abies alba*, 49.0874 N 22.5743 E. Central Polissia. *Zhytomyr Region*. Zhytomyr District, *Pinus sylvestris* with *Betula* and *Quercus*, 50.4788 N 29.2599 E; *Carpinus betulus-Pinus sylvestris-Quercus* forest, 50.4694 N 29.2695 E; *Carpinus betulus-Pinus sylvestris* forest with *Acer*, 50.4503 N 29.2805 E. Cis-Carpathian Forests. *Ivano-Frankivsk Region*. Ivano-Frankivsk District, *Picea abies* forest with *Carpinus betulus*, *Quercus robur*, *Acer pseudoplatanus*, *Tilia cordata*, *Fagus sylvatica*, and *Rubus hirtus*, 49.0033 N 24.5918 E; *Fagus sylvatica* forest with *Picea abies*, *Sorbus aucuparia*, *Frangula alnus*, and *Corylus avellana*, 49.0137 N 24.5874 E; *Abies* forest with *Picea abies*, *Quercus robur*, *Tilia cordata*, *Sorbus aucuparia*, and *Corylus avellana*, 49.0237 N 24.5648 E. Cis-Carpathian Forests and Western Ukrainian Forests. *Ivano-Frankivsk Region*. Ivano-Frankivsk District, Halych NNP, *Carpinus betulus* forest with *Quercus robur*, *Tilia cordata*, and *Corylus avellana*, 49.0981 N 24.7180 E; same NNP, *Fagus sylvatica* forest with *Caprinus betulus*, *Tilia cordata*, *Prunus avium*, and *Euonymus verrucosus*, 49.0958 N 24.7068 E; same NNP, *Carpinus betulus* forest with *Tilia cordata*, *Quercus robur*, and *Acer pseudoplatanus*, 49.1608 N 24.8482 E. Kharkiv Forest-Steppe. *Kharkiv Region*. Bohodukhiv District, Sloboda NNP, old *Quercus robur* forest with *Acer platanoides*, *Ulmus*, *Pinus sylvestris*, and *Prunus padus*, 50.0689 N 35.2894 E; same NNP, *Quercus robur* forest with *Ulmus*, *Acer campestre*, and *A. platanoides*, 50.0970 N 35.2545 E; same NNP, *Pinus sylvestris* forest with *Sorbus aucuparia*, *Quercus robur*, and *Tilia cordata*, 50.0546 N 35.2221 E. Chuhuiv District, Homilsha Forests NNP, *Populus tremula* forest with *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior*, *Ulmus*, *Corylus avellana*, and *Acer campestre*, 49.6267 N 36.3190 E. Kharkiv District, dry grassland with *Quercus robur* and *Caragana arborescens* Lam., 49.7314 N 35.9897 E. Left-Bank Forest-Steppe. *Poltava Region*. Lubny District, *Pinus sylvestris* forest with *Quercus robur*, *Sorbus*

*aucuparia*, *Betula*, and *Corylus avellana,* 50.2127 N 32.6059 E. Lesser Polissia. *Lviv Region*. Zolochiv District, Pivnichne Podillia NNP, old *Fagus* forest, 49.9245 N 24.9805 E. Right-Bank Forest-Steppe. *Cherkasy Region*. Cherkasy District, vicinities of Lubentsi village, Kholodnyi Yar NNP, meadow steppe, 49.1819 N 32.2291 E; Kaniv NR, meadow steppe with *Pyrus communis*, *Betula pendula*, and *Pinus sylvestris*, 49.7198 N 31.5235 E; same NR, *Carpinus betulus* forest with *Acer platanoides*, *A. campestre*, *Fraxinus excelsior*, *Ulmus glabra*, and *Tilia cordata*, 49.7247 N 31.5116 E. Right-Bank Grass-Meadow Steppe. *Kirovohrad Region*. Kropyvnytskyi District, *Acer platanoides-Fraxinus excelsior-Quercus robur* forest, 48.7423 N 32.5780 E. Right-Bank Grass Steppe. *Odesa Region*. Izmail District, salt grassland, 45.6736 N 29.8770 E; salt grassland, 45.6699 N 29.8629 E. Roztochchya Forests. *Lviv Region*. Yavoriv District, Yavoriv NNP, *Fagus sylvatica* forest, 49.9945 N 23.6458 E. Transcarpathia. *Zakarpattia Region*. Mukachevo District, Zacharovanyi Krai NNP, *Fagus sylvatica* forest with *Acer pseudoplatanus*, 48.4505 N 23.0853 E. Volyn Forest-Steppe. *Volyn Region*. Lutsk District, *Carpinus betulus* forest with *Quercus*, 50.7398 N 25.5755 E; Vorotniv Zakaznyk, *Carpinus betulus* forest with *Quercus*, 50.7176 N 25.5605 E; same Zakaznyk, *Carpinus betulus* forest with *Quercus*, *Pinus sylvestris*, and *Betula*, 50.7282 N 25.5480 E. Western Forest-Steppe. *Khmelnytskyi Region*. Kamianets-Podilskyi District, *Carpinus betulus* forest with *Quercus robur*, *Fraxinus excelsior*, and *Acer platanoides*, 48.7989 N 26.6395 E; *Carpinus betulus* forest with *Quercus*, *Acer platanoides*, and *A. pseudoplatanus*, 48.7880 N 26.6466 E. *Ternopil Region*. Chortkiv District, vicinities of Ustechko village, *Carpinus* forest with *Quercus*, 48.7861 N 25.5809 E; to the south from Shutromyntsi village, *Quercus petraea* forest with *Carpinus*, 48.8263 N 25.5060 E; Medobory NR, *Carpinus* forest with *Betula*, *Picea* and *Prunus* subg. *Cerasus*, 49.3255 N 26.1370 E. *Vinnytsia Region*. Khmilnyk District, *Carpinus betulus* and *Quercus robur* forest with *Fraxinus excelsior* and *Acer platanoides*, 49.4720 N 28.0239 E. Western Polissia. *Rivne Region*. Sarny District, *Quercus robur-Carpinus betulus* forest with *Picea abies*, *Pinus sylvestris*, *Frangula alnus*, *Sorbus aucuparia*, and *Corylus avellana*, 51.5708 N 26.4653 E; *Pinus sylvestris* forest with *Quercus robur*, *Betula pendula*, *Sorbus aucuparia*, and *Frangula alnus*, 51.5773 N 26.4627 E; *Quercus robur* forest with *Pinus sylvestris*, *Frangula alnus*, *Betula pendula*, and *Sorbus aucuparia*, 51.5688 N 26.4383 E. *Volyn Region*. Lutsk District, Tsumanska Pushcha NNP, *Alnus glutinosa* forest with *Betula*, *Carpinus betulus*, and *Populus tremula*, 50.9106 N 25.8818 E; same NNP, *Picea abies* forest with *Corylus avellana*, 50.9097 N 25.8778 E; same NNP, *Betula* forest with *Alnus glutinosa*, *Carpinus betulus*, and *Sorbus aucuparia*, 50.9109 N 25.8862 E; same NNP, *Pinus sylvestris* and *Carpinus betulus*, 50.9119 N 25.8924 E.

**Worldwide distribution** (Park et al., 2014; De Lange et al., 2021, 2023; GBIF.org, 2026–onward; PlutoF, 2026). Africa: Democratic Republic of Congo. Asia: Bhutan, China, India, Japan, Laos, South Korea, Thailand, Vietnam. Europe: Austria, Belarus, Belgium, Bosnia and Herzegovina, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Norway, Poland, Portugal, Romania, RF, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, the Netherlands, Ukraine, United Kingdom. North America: Canada, Costa Rica, Mexico, USA. Oceania: Australia.

## Discussion

Our screening of the studied herbarium specimens using routine DNA barcoding, followed by their morphological examination under the light microscope, yielded two new for Ukraine species of *Russula* subg. *Compactae*. In contrast, soil metabarcoding, while providing useful information on the regional biodiversity, did not add new data on the taxonomic richness of the studied fungi (except for the enigmatic *R.* aff. *acrifolia* – OTU1053). However, the latter approach allowed us to update the distribution of taxa of the subgenus within Ukraine – a significant portion of the Central European mixed forests ecoregion (Cis-Carpathian Forests, Lesser Polissia, Western Ukrainian Forests regions) – and to confirm some historical data (records of *R. densifolia* in Ukraine or *R. nigricans* in the Pontic Steppe ecoregion). A major limitation of metabarcoding, as shown in this study, is the lack of physical specimens, precluding future independent verification of interesting findings, such as OTU1053 (*R.* aff. *acrifolia*) and OTU8086 (the second OTU for *R. nigricans*), to exclude potential sequencing errors.

All historical data (including *Russula adusta* and *R. nigricans*), which cannot be confirmed by DNA barcodes and/or morphological data, should

be interpreted with caution as old keys can lead to misidentification (De Lange et al., 2023). This applies *inter alia* to the specimens collected by M. Zerova and G. Rozhenko, since these were treated with naphthalene, which is likely the reason for the failure to retrieve DNA from these specimens in our research. Nevertheless, to preserve historical records, we decided to include all available species diversity data in our evaluation, despite the lack of DNA sequences for some representatives of *Russula* subg. *Compactae*.

Ecological information for the Ukrainian records of taxa of *Russula* subg. *Compactae* mostly aligns with the available literature data (De Lange et al., 2021, 2023). However, *Russula acrifolia* and *R. anthracina* were recorded from *Carpinus* forests, while *Carpinus* has not yet been reported as a host for either of these species. This could be due to insufficient locality data, or else the fungus-host interactions require further studies. Some specimens of *R. nigricans* were also reported from *Carpinus* forests (including the sequenced specimen KW-M72208), but it is currently unknown whether they can form ectomycorrhiza. Moreover, the reports of *R. adusta* from the Mountain Crimea and Right-Bank Forest-Steppe regions, as well as the collection points for half of the soil samples with OTU124 (Table S1), did not mention any coniferous trees. To interpret and analyze these results, sequencing data of some additional root tips is needed. Among the studied areas, the Mountain Crimea region, which is a part of the Crimean Submediterranean forest complex ecoregion, features a highly specific biota (the ecoregion includes only a part of the Crimean Peninsula and the Greater Caucasus) and may harbor new information about hosts for this species. However, this region currently cannot be studied due to the Russian occupation. Some historical specimens of *R. albonigra* were reportedly collected in forests with *Quercus* and *Pinus* (Table S1) which also does not fully correspond to the present data (De Lange et al., 2021).

According to the recent and historical data, *Russula adusta* and *R. nigricans* are widespread in Ukraine and are likely to be found in all or almost all regions of the *Flora of fungi of Ukraine*. On the contrary, *R. albonigra* and *R. densifolia* seem to have narrower distribution patterns, and their ranges are presumably limited to the western part of Ukraine; however, *R. albonigra* was also reported from the Crimean Peninsula. Further molecular and field-based studies on the distribution of *R. acrifolia*, *R.* aff. *acrifolia*, and *R. anthracina* are required before proposing any hypotheses about their distribution in Ukraine.

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SUPPLEMENTARY MATERIAL

This article includes Supplementary Material (Table S1) available as: ukrbotj83-04-304-S1.xlsx (44 KB).

ETHICS DECLARATION

The authors declare that there is no conflict of interest.

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**Різноманітність підроду *Compactae* роду *Russula* (*Russulales*, *Basidiomycota*) в Україні**

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**Реферат.** Стаття містить перший за 50 останніх років загальний огляд видової різноманітності підроду *Compactae* роду *Russula* України. У дослідженні застосовані як молекулярні методи (баркодінг та метабаркодінг), так і результати класичних польових зборів. Крім того, узагальнено проаналізовані дані літератури та матеріали гербаріїв. Як наслідок, в Україні виявлено шість видів вказаного підроду, включно з двома новими для країни видами (*R. acrifolia* та *R. anthracina*), для яких наведені повні діагнози та оригінальні рисунки мікроструктур. Для всіх шести видів узагальнено дані щодо їхнього розповсюдження в Україні та світі.

**Ключові слова:** біорізноманіття, виділення ДНК, гриби, нові знахідки, підрід *Compactae*