

## Fungal Biodiversity Profiles 41-50

Kanad DAS<sup>a</sup>, Aniket GHOSH<sup>b</sup>, Rajendra Prasad BHATT<sup>b</sup>,  
Dyutiparna CHAKRABORTY<sup>a</sup>, Valerie HOFSTETTER<sup>c</sup> & Bart BUYCK<sup>d\*</sup>

<sup>a</sup>Cryptogamic Unit, Botanical Survey of India, P.O. Botanic Garden,  
Howrah 711103, India,  
email: daskanadbsi@gmail.com, dyuti.parna.mail@gmail.com

<sup>b</sup>Department of Botany & Microbiology, H.N.B. Garhwal University  
(A Central University), Srinagar, Garhwal, 246174, Uttarakhand, India,  
email: bhatt.rajendra123@gmail.com, ghosh.aniket87@gmail.com

<sup>c</sup>Agroscope Changins-Wädenswil Research Station, ACW,  
Department of plant protection, Rte de Duiller, 1260 Nyon, Switzerland;  
valerie.hofstetter@agroscope.admin.ch

<sup>d</sup>Museum National d'Histoire Naturelle, Sorbonne Universities,  
Institut de Systématique, Évolution,  
Biodiversité – UMR 7205 CNRS MNHN UPMC EPHE,  
CP 39, 12 rue Buffon, F-75005 Paris, France,  
email: bart.buyck@mnhn.fr

**Abstract** – This new series of Fungal Biodiversity Profiles presents ten new taxa in the genus *Russula*, including subgenus *Crassotunicata* subg. nov. In subg. *Malodora*, sect. *Edules* sect. nov. is described for a number of African species and a first detailed description is given for the type species, while *R. pseudocompacta* sp. nov. and *R. compactoides* sp. nov. are described in the new section *Pseudocompactae* sect. nov. of the same subgenus; in subg. *Compactae* the new sect. *Polyphyllae* is described, in subg. *Russula*, *R. kewzingensis* sp. nov. is described in subsect. *Roseinae*, as well as the new section *Flaviscicantes*, and the new subsect. *Tricholomopsidae*.

**phylogeny / *Russula* / Russulales / sect. nov. / subg. nov. / subsect. nov. / systematics**

**41. *Russula kewzingensis* K. Das, D. Chakr., & Buyck sp. nov.**

**Figs 1-3**

*Mycobank*: MB 823801

*GenBank*: MG674302 (ITS)

*Systematic position*: Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology*: Referring to Kewzing of South district in Sikkim (India), the type locality.

\* Correspondence: bart.buyck@mnhn.fr

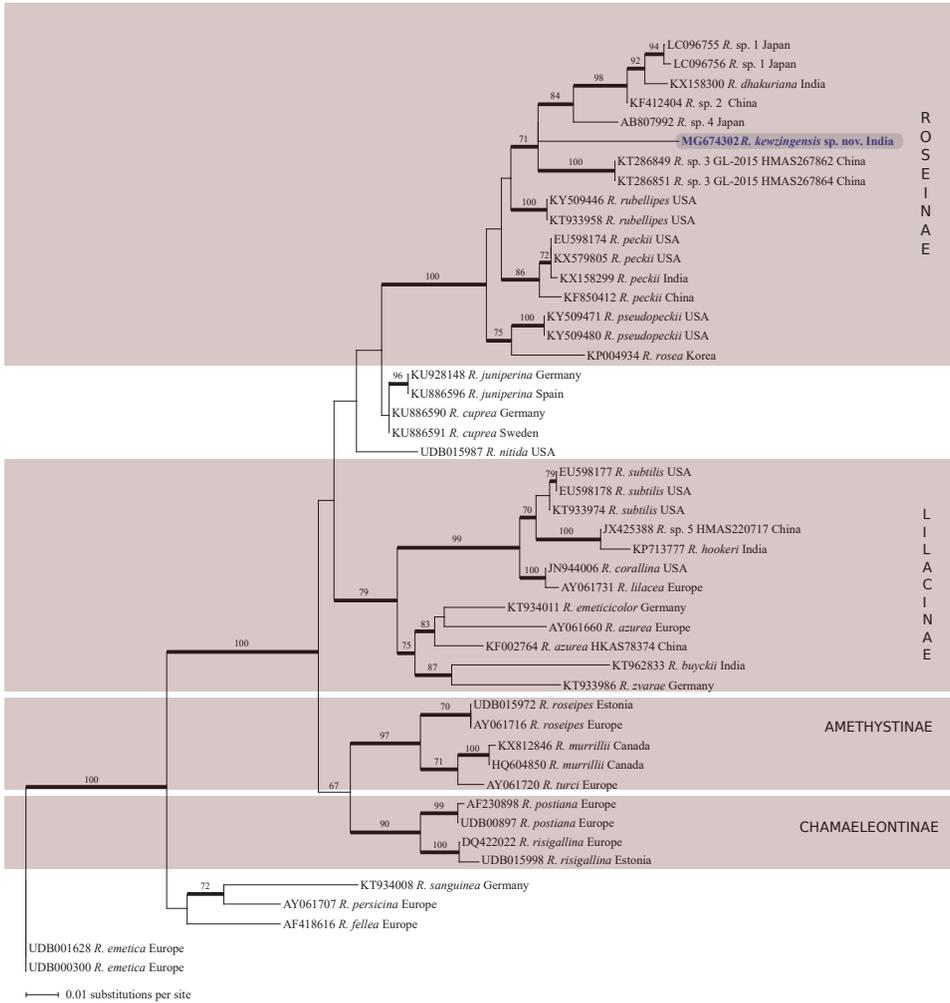
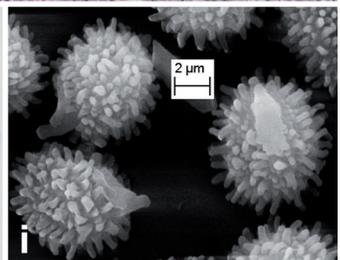
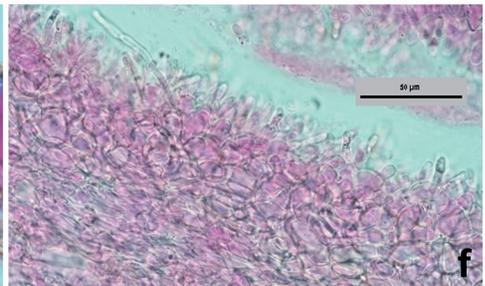
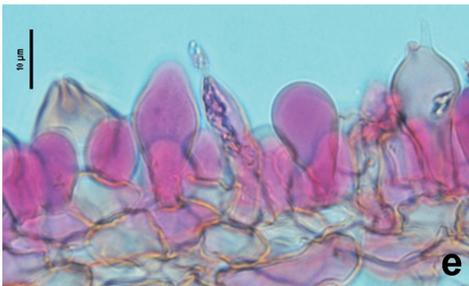
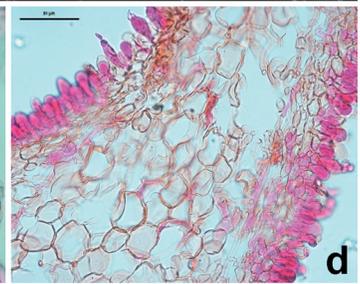
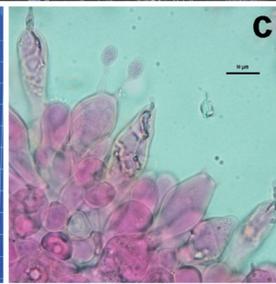


Fig. 1. Most likely tree (-ln = 2759.31024) obtained by phylogenetic analysis of 49 ITS *Russula* sequences conducted in the program PhyML v. 3.0 (Guindon & Gascuel 2003), under a GTR model of nucleotide substitution and with other model parameters estimated during the search. The sequence newly generated for this study is highlighted; species placed in subg. *Incrustatula* are on colored background. Branches that received significant bootstrap support values (BS ≥ 70%; Alfaro *et al.* 2001), based on 500 BS replicates effected in PhyML with the same settings as for the best tree search, are indicated in bold, with corresponding BS values reported along the branches.

Fig 2. *Russula kewzingensis* (KD 17-002, holotype). **a-b.** Fresh basidiomata in the field and basecamp. **c, e.** Hymenium layer showing basidia and pleurocystidia. **d.** Hymenium layer, subhymenium layer and hymenophoral trama. **f-g.** Radial section through pileipellis. **h.** Basidiospores. **i.** Basidiospores under SEM. Scale bars: c, e, g & h = 10 µm, d & f = 50 µm, i = 2 µm.



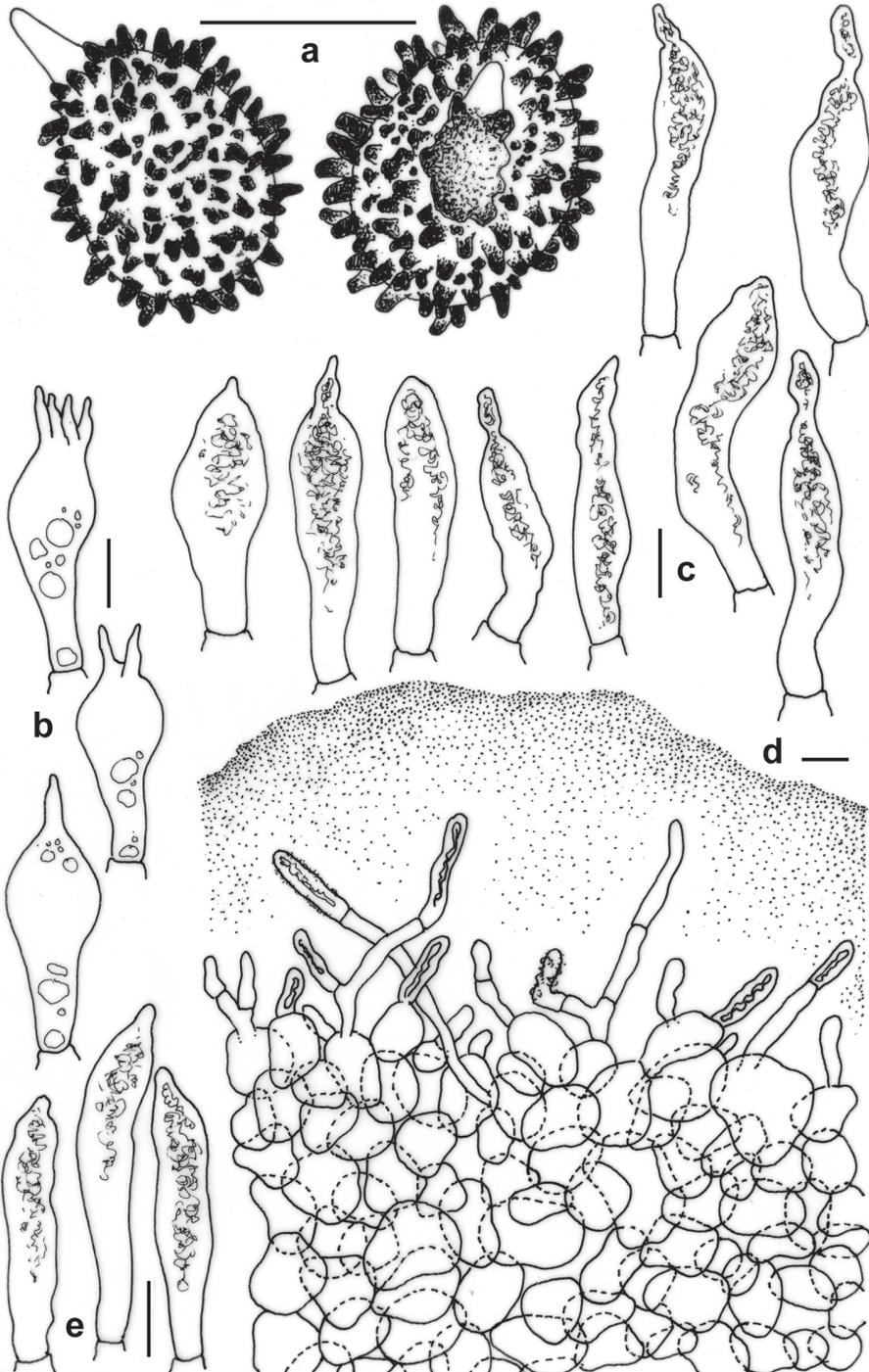


Fig. 3. *Russula kewzingensis* (from KD 17-002, holotype). a. Basidiospores. b. Basidia. c. Pleurocystidia. d. Pileipellis. e. Cheilocystidia. Scale bars: a = 5  $\mu$ m, b-e = 10  $\mu$ m.

*Diagnosis:* Distinct from other *Russula* species in subsect. *Roseinae* mainly by nrITS sequence data, its occurrence under *Castanopsis* sp. in Asia, the intensity of the cap color, basidiospores  $6.5\text{-}7.64\text{-}8.4 \times 6.0\text{-}6.70\text{-}7.5 \mu\text{m}$ , ornamented with  $1\text{-}1.5 \mu\text{m}$  high, conic to cylindrical warts.

*Holotype:* INDIA, Sikkim, South district, Kewzing, N  $27^{\circ} 17'46.5''$  E  $088^{\circ}21'26.6''$ , 1888 m asl., under *Castanopsis* in temperate broadleaf forest, 22 August, 2017, Kanad Das 17-002 (CAL 1636, **holotype!**).

*Pileus* 50-95 mm diam., at first hemispherical to convex, becoming plano-convex with a depressed centre, sometimes uplifted (towards margin) with more maturity; sometimes with an obscured or a rather prominent blunt umbo in the centre, glutinous to sticky when moist, peeling up to  $\frac{1}{4}$  of radius in mature sample mostly red (10A-B7) to deep or dark red or “cock’s comb (red)” (10B-C8), uniform from centre to periphery, not discoloring in rain or at maturity; margin incurved when young, becoming decurved when mature, sometimes slightly uplifted at maturity, faintly to strongly sulcate. *Lamellae* adnexed to almost free, subdistant to rather close (7-8/cm at pileus margin) at maturity, forked near stipe, yellowish white (2A2), unchanging on bruising; edge entire, concolorous to the face of lamellae except  $\frac{1}{6}$  part from the periphery that concolorous to pileus. *Stipe* 60-90  $\times$  15-20 mm, mostly cylindric with abruptly tapering base, surface dry, finely longitudinally venose, white at apex and base and flushed with pink, red (10A7), pastel pink to rose (11-12A3-5) or slightly darker at mid to mid-base region, unchanging when bruised but turning 6C4 with guaiacol and 2A3 with KOH, instantly turning deep red with the application of red with sulfovanillin. *Context* pithy to hollow in stipe, white (1A1) to yellowish white (1A2), unchanging after bruising, turning salmon with  $\text{FeSO}_4$ , red-haired (6C4) with guaiacol, dry context instantly turning deep red (then becoming brownish) with the application of sulfovanillin. *Taste* mild. *Odor* indistinctive. *Spore print* white (1A1).

*Basidiospores*  $6.5\text{-}7.64\text{-}8.4 \times 6.0\text{-}6.70\text{-}7.5 \mu\text{m}$ , ( $n = 30$ ,  $Q = 1.05\text{-}1.20\text{-}1.36$ ), usually subglobose to broadly ellipsoid or rarely ellipsoid; ornamentation amyloid,  $0.3\text{-}1.4 \mu\text{m}$  high, composed of somewhat spinoid to cylindric (mostly with rounded apices) high warts and few conic to pyramidal low warts between high warts, mostly isolated, some laterally fused or rarely connected through connector; suprahilar plage amyloid. *Basidia* 32-40  $\times$  10-12  $\mu\text{m}$ , subclavate to ventricose, 1-4-spored; sterigmata 4-7  $\times$  1.5-2  $\mu\text{m}$ . *Subhymenium* 20-35  $\mu\text{m}$  thick, pseudoparenchymatous. *Pleurocystidia* uncommon, 33-46  $\times$  7-13  $\mu\text{m}$ , emergent 5-18  $\mu\text{m}$ ; content dense, fibrous. *Cheilocystidia* 33-45  $\times$  7-9  $\mu\text{m}$ , emergent 7-12  $\mu\text{m}$ , cylindric to lanceolate, with fusoid, subfusoid or appendiculated apices, thin-walled, content dense, fibrous. *Hymenophoral trama* composed of numerous sphaerocytes and connecting hyphae; sphaerocytes globose to elliptical, 13-47  $\times$  10-24  $\mu\text{m}$ . *Pileipellis* two-layered; upper suprapellis up to 55  $\mu\text{m}$  thick, submerged under moderately thick to thick (35-60  $\mu\text{m}$ ) layer of gluten, composed of erect primordial hyphae and erect septate branched hyphae (3-7  $\mu\text{m}$  broad) consisting of one to few cells, terminal cells cylindric to subcylindric with tapering apex or somewhat clavate with broader apex, few with incrustations; lower subpellis mostly pseudoparenchymatous (10-28  $\times$  6-8  $\mu\text{m}$ ); pileocystidia absent. *Clamp connections* absent in all tissues.

*Specimens examined:* INDIA, Sikkim, South district, Kewzing, N  $27^{\circ} 17'46.5''$  E  $088^{\circ}21'26.6''$ , 1888 m asl., under *Castanopsis* in temperate broadleaf forest, 22 August 2017, Kanad Das 17-002 (CAL 1636); *ibid.*, 23 August 2017, Kanad Das 17-024 (CAL 1637); *ibid.*, N  $27^{\circ}16.781'$  E  $088^{\circ}20.300'$ , 1888 m asl., under *Castanopsis* in temperate broadleaf forest, 25 August 2017, Kanad Das 17-032 (CAL 1638).

*Notes:* The deep and intense red pileus, red-flushed stipe, white spore print, instantaneous red color change when applying sulfovanillin to its context, lack of pileocystidia, but presence of primordial hyphae and a pseudoparenchymatous subpellis place this Asian species unmistakably in *R.* subg. *Incrustatula* sect. *Lilaceinae* subsect. *Roseinae*. (Sarnari 1998, 2005). This is here indeed confirmed by our nrITS-based phylogenetic analysis (Fig. 1) where our new species is placed in a highly supported clade (BS = 100%) composed of species that are known to represent typical *Roseinae*. Our analysis did not resolve sect. *Lilaceinae* or subg. *Incrustatula* as monophyletic. Our new species is here placed in a significantly supported subclade composed of at least four undescribed Asian species, mostly represented by environmental sequences and one sequence for *R. dhakuriana* K. Das, J.R. Sharma & S.L. Mill. The latter species differs morphologically from the present species by its more robust basidiomata (pileus 80-120 mm diam., stipe 50-125 × 20-28 mm), longer basidiospores (6.5-10.2 × 6-7.7 μm) and pleurocystidia (60-115 × 7-12 μm) and occurrence in *Quercus-Rhododendron* forest. (Das *et al.* 2006).

**42. *Russula* subsect. *Tricholomopsidae* Buyck & V. Hofst. subsect. nov.**

*Mycobank:* MB 823805

*Systematic position:* Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology:* named after the type species

Fruiting bodies small to medium-sized. Pileus variously coloured, dull, subglabrous to strongly tomentose or hairy, often coming in shades of purple, violet, red, locally tinted with yellow or green. Stipe mostly flushed with a similar coloration as the pileus. Lamellae pale-colored, equal or nearly so. Spore print pale.

Spores mostly subreticulate with distinct, interconnected warts and amyloid suprahilar spot, the latter however not always well-differentiated. Gloeoplerous elements distinct on gills. Pileipellis covered by sometimes long, encrusted hyphal extremities, generally partly pseudoparenchymatic; well-differentiated pileocystidia lacking.

*Type species:* *R. tricholomopsis* McNabb, New Zealand J. Bot. 11: 704. 1973

*Notes:* This subsection almost certainly corresponds to Beenken's Sect. "Nothofagineae" nom. nud., based amongst others on the distinctive ectomycorrhizal anatomy of *R. nothofaginea* compared to other *Russula* species, and which can shortly be summarized as follows: a pseudoparenchymatic outer mantle layer composed of puzzle-like cells and dispersed gloeoplerous cells submerged in the outer surface layer, with an overlying hyphal network on top of it; the network embedded in a gelatinous matrix and composed of thin-walled cells forking at straight angles (Beenken 2004).

Unfortunately, clearly identified sequence data are not available for *R. nothofaginea* Singer but environmental sequence data attest the presence of *Tricholomopsidae* in the *Nothofagus* forests of Argentina, and thus indirectly place Singer's species in our new subsection. Beenken had suggested to adopt a sectional level for this species group, but our forthcoming phylogeny (Buyck *et al.*, submitted) places our new subsection with significant support close to subsections *Chamaeleontinae* and *Amethystinae*. Most of the species in our new subsection are specific associates with Nothofagaceae. *Russula nothofaginea* was placed by its author in subsect. *Lepidinae* (Mlz. & Zv.) Singer, a species group which is upgraded to sectional rank below.

**43. *Russula* section *Flaviscantes* Buyck & V. Hofst. sect. nov.**

*Mycobank:* MB 823804

*Systematic position:* Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology*: named after the type species

Fruiting bodies red, firm and hard, often discoloring, slightly yellowing to browning, with smooth margin, dull, mild or often bitter tasting, producing pale cream spore prints.

Spores subreticulate, with an amyoid suprahilar spot. Pileipellis a dense, thick pseudoparenchymatic layer, gloeoplerous elements widely dispersed throughout, SV-.

Ectomycorrhizal mantle with a pseudoparenchymatic outer layer composed of puzzle-like cells and immersed gloeoplerous cells; with an overlaying hyphal network and gelatinous matrix. Rhizomorphs absent.

*Type species*: *R. flavisiccans* Bills, *Mycologia* 81: 57. 1989.

*Notes*: This new section still essentially corresponds to the present concept of subsect. *Lepidinae* (Mlz & Zv.) Singer at this moment. However, due to the very particular phylogenetic position of these species, i.e. basal to a majority of northern hemisphere *Russula* and clearly related to several tropical species groups (Buyck *et al.*, submitted), it requires upgrading to sectional rank. It is likely that several tropical species will join this section.

#### 44. *Russula* subg. *Crassotunicata* Buyck & V. Hofst. **subg. nov.**

*Mycobank*: MB 823806

*Systematic position*: Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology*: named after the type species

Medium-sized to rather small, robust to slender species, moderately fleshy. Pileus pale coloured and white, cream to yellowish, becoming sometimes rapidly brownish in age or where injured, strongly gelatinous to almost dry. Annulus never present. Gills irregularly unequal, with lamellulae fairly frequent but mostly (but not always) distinctly less abundant than normal gills. Context faintly yellowing to strongly browning, medium to strongly acrid. Spore print white. Secotioid and gasteroid representatives unknown.

Spores small to quite large, never completely reticulate, with inamyloid suprahilar spot. Primordial hyphae absent. Gloeoplerous elements abundant and very conspicuous in all parts of the fruiting body, near the surface mostly mucronate with a single, terminal knob. Hyphal extremities of cap surface variably inflated or not.

Ectomycorrhizal mantle with a plectenchymatic outer layer and short emanating hyphal ends. Gloeocystidia conspicuous, emergent, one-celled, near the apex minutely capitate with one terminal knob or sometimes repeatedly constricted and moniliformous. Rhizomorphs common.

*Type species*: *R. crassotunicata* Singer, *Bull. Soc. Mycol. France* 54(2): 132. 1938.

*Notes*: recent phylogenetic studies (Bazzicallupo *et al.* 2017; Looney *et al.* 2016) all point to the isolated position of this small species group. For further details see a forthcoming phylogeny (Buyck *et al.* submitted)

#### 45. *Russula* section *Polyphyllae* Buyck & V. Hofst. **sect. nov.**

*Mycobank*: MB 823807

*Systematic position*: Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology*: named after the type species

*Diagnosis*: Medium-sized to large species, thin- to thick-fleshed. Pileus coming in shades of white to brown, dry to sometimes tomentose, often areolate, dull. Lamellae unequal, variously spaced, becoming often distinctly pinkish when old. Spore print white or very pale.

Spores with low ornamentation; suprahilar spot not amyloid. Gloeoplerous elements in all tissues, pleurocystidia sometimes inflated in the part that is submerged in the subhymenium.

*Type species:* *R. polyphylla* Peck, *Bull. Torrey Bot. Club* 25: 370. 1898.

Notes: this new section finds its place in subgenus *Compactae* (Fr.) Bon as indicated already in Hongsanan *et al.* (2015)

**46. *Russula pseudocompacta*** A. Ghosh, K. Das, R.P. Bhatt & Buyck *sp. nov.*

**Figs 4-6**

*Mycobank:* MB 823803

*GenBank:* MG662160; MG662171 (ITS)

*Systematic position:* Basidiomycota, Agaricomycetes, Russulales, Russulaceae

*Etymology:* referring to it being a look-alike of *R. compacta*, a North American species in *R.* subg. *Malodora*

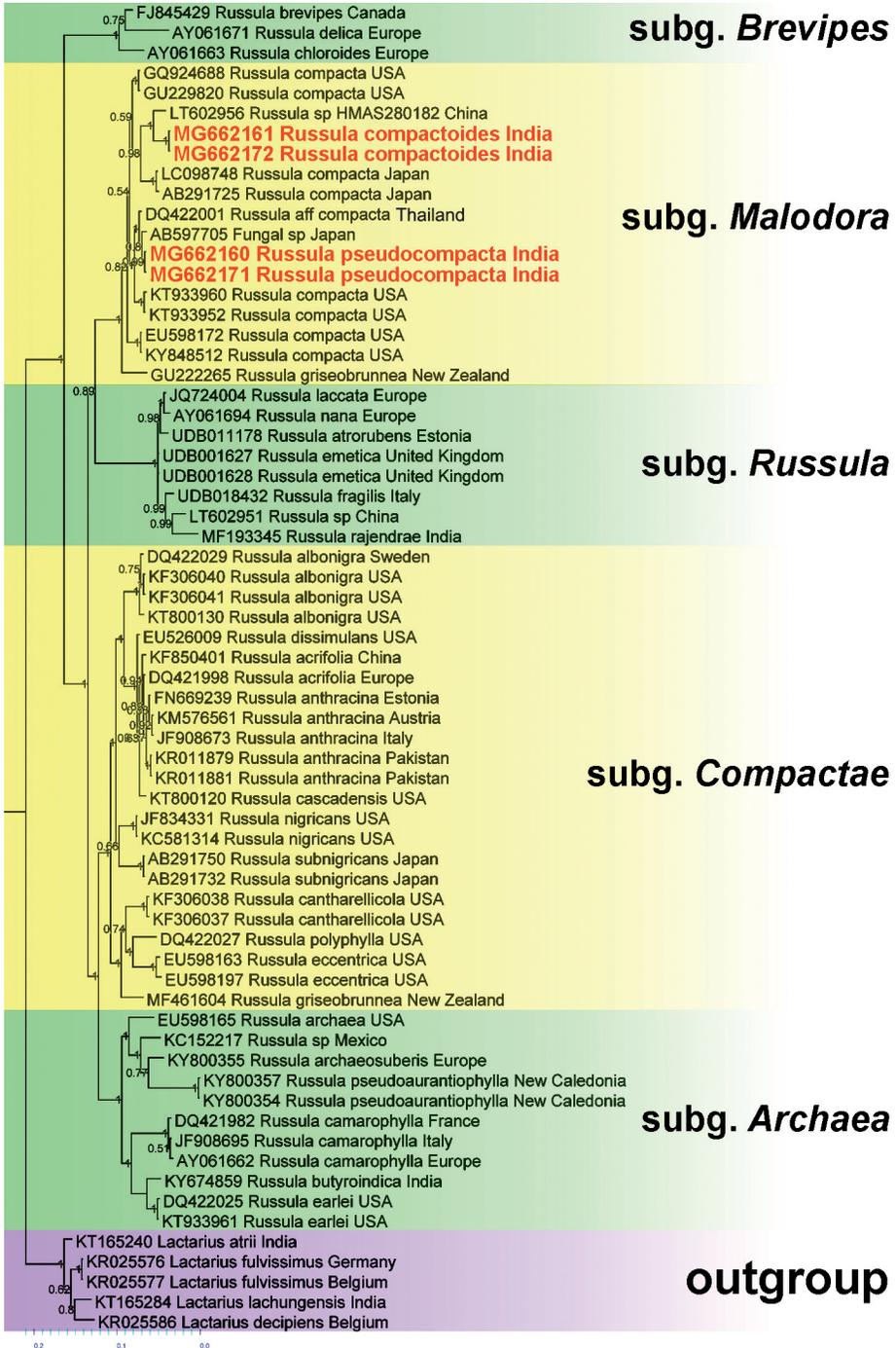
*Diagnosis:* differs from similarly looking taxa in the frequently forked lamellae without hardly any lamellulae, 2- to 4-spored basidia, smaller hymenial cystidia without appendiculate or lageniform apex, and nrITS sequence data. It is likely associated with host trees in Fagaceae.

*Holotype:* INDIA, Uttarakhand, Pauri District; Phedkhal, 30°09.688'N, 78°51.110'E, 1923 m asl., under *Quercus* in temperate broadleaf forest, 12 August 2015, *Aniket Ghosh* 905 (CAL 1641, **holotype!**).

*Basidiomata* up to 100 mm in height. *Pileus* 30-110 mm in diam., convex when young, gradually broadly convex, planoconvex to applanate with depressed center at maturity, margin decurved to plane, entire; surface dry, viscid when moist, smooth, cracked to areolate at maturity especially in center, orange (6B8) to brownish orange (6C8) when young, becoming light orange (5A5) to brownish orange (6C8) with age. *Pileus* context 3-12 mm thick, firm, brittle, chalky white (1A1); becoming light orange (5A5) to brownish orange (6C8) when cut or bruised. *Lamellae* moderately close (9-15/cm), frequently and irregularly forked, chalky white (1A1), quickly becoming brownish orange (6C8) to light orange (5A5) on bruising; lamellulae absent. *Stipe* 27-58 × 8-21 mm, cylindrical to subclavate, smooth, chalky white (1A1), becoming brownish orange (6C8) to light orange (5A5) on bruising. *Taste* mild. *Odour* very strong and unpleasant at maturity and on drying. *Spore print* white.

*Basidiospores* globose to subglobose or broadly ellipsoid, (6-)6.04-7.20-7.4-8.94(9.5) × (5-)5.34-6.38-6.80-8.1 μm; **Q** = 1-1.09-1.13-1.2; ornamentation amyloid, up to 1 μm high, with warts and ridges aligned or connected to form a partial to incomplete reticulum; suprahilar plaque inamyloid. *Basidia* 41-56 × 8-11 μm; cylindrical to subclavate, 2-4 spored; sterigmata up to 8 μm long. *Pleurocystidia* 46-72 × 6-9 μm, emergent up to 17 μm, abundant, cylindrical to subclavate with mostly capitate, sometimes blunt or moniliform apex, rarely deeply embedded in the subhymenium; contents with irregular refractive bodies, mostly

Fig. 4. Phylogram generated from Bayesian analysis of ITS-rDNA sequences under a TIMef model. Posterior probabilities were calculated in two simultaneous runs with Markov chain Monte Carlo (MCMC) algorithm (Largent & Simon 1999). Markov chains were run for 1000000 generations, saving a tree every 100th generation. The analysis was terminated when the average standard deviation of split frequencies fell below 0.01. Two novel Indian species *Russula compactoides* (GenBank accession nos. MG662161 & MG662172) and *R. pseudocompacta* (GenBank accession nos. MG662160 & MG662171) are shown in red and bold. ►



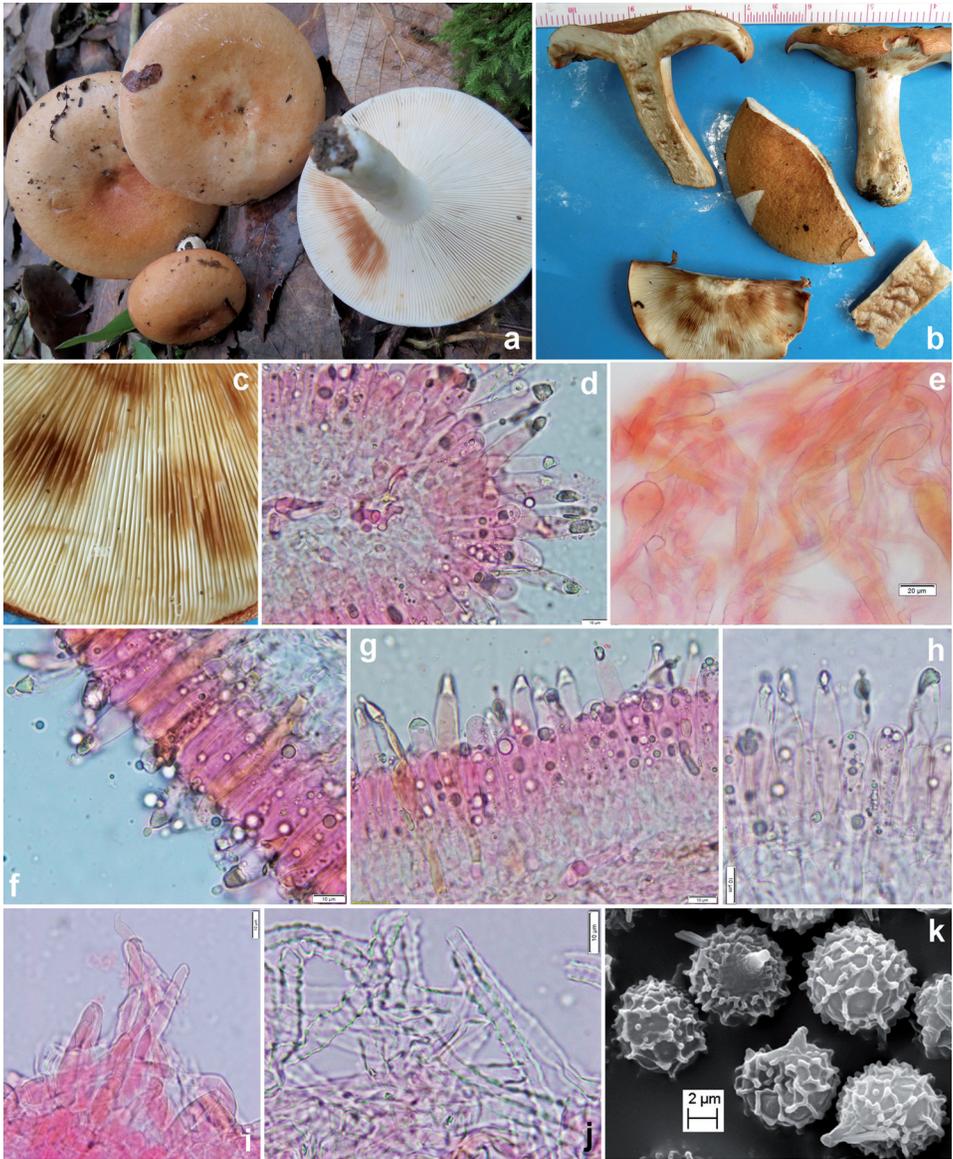
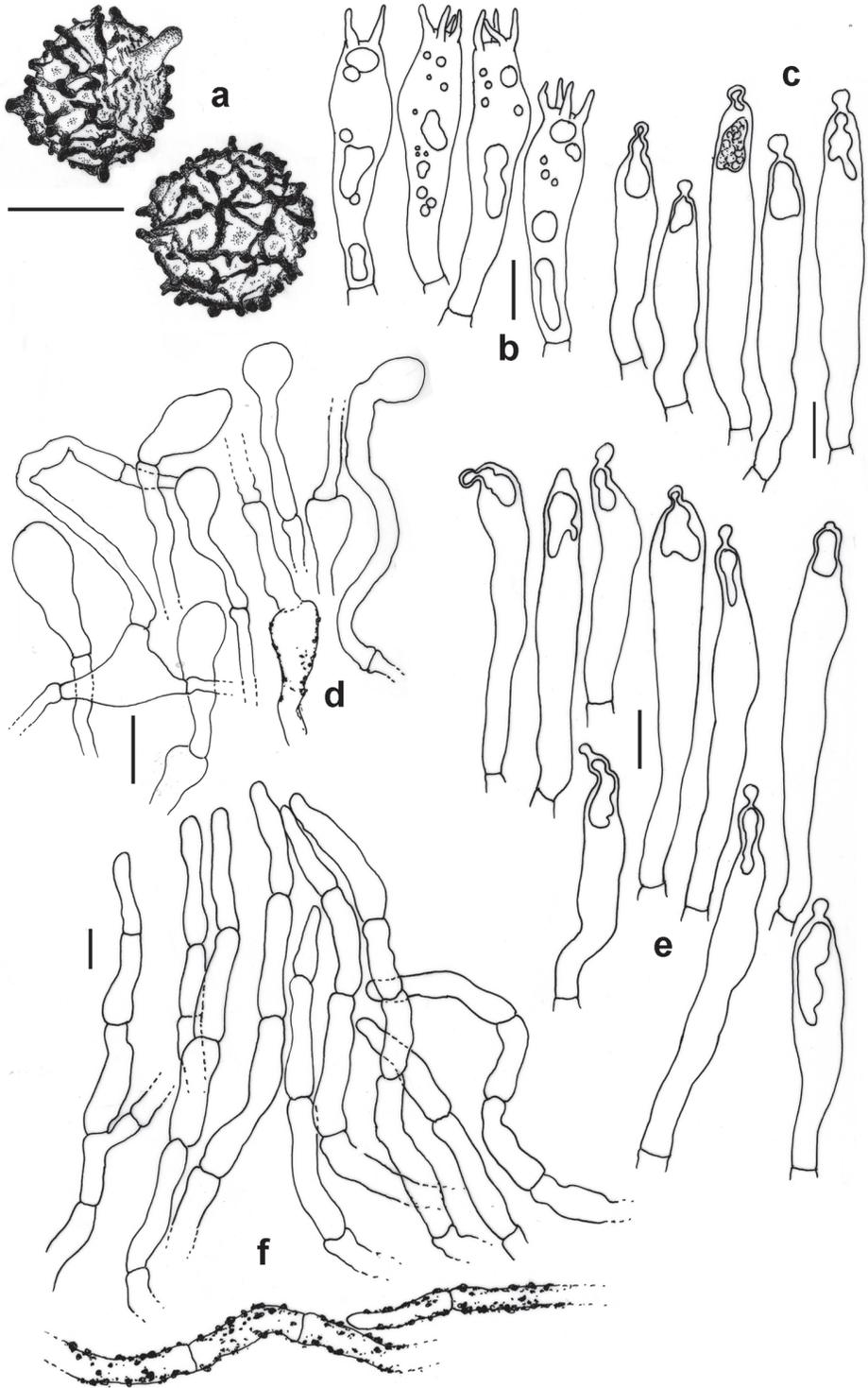


Fig. 5. *Russula pseudocompacta* (KD 17-22, Paratype). **a, b & c.** Fresh/dissected basidiomata in the field or basecamp. **d.** Cheilocystidia. **e.** Transverse section through pileipellis from pileus margin. **f, g & h.** Pleurocystidia. **i.** Transverse section through pileipellis from pileus centre. **j.** Encrusted hyphae in pileipellis. **k.** Basidiospores under SEM. Scale bars: d, f-j = 10  $\mu\text{m}$ , e = 20  $\mu\text{m}$ , k = 2  $\mu\text{m}$ .

Fig. 6. The Line drawings of *Russula pseudocompacta* (from KD 17-22, Paratype). **a.** Basidiospores. **b.** Basidia. **c.** Cheilocystidia. **d.** Clavate to capitates hyphal extremities in pileipellis (at pileus margin). **e.** Pleurocystidia. **f.** Hyphal elements in pileipellis (at pileus centre). Scale bars: a = 5  $\mu\text{m}$ , b, c, e & f = 10  $\mu\text{m}$ , d = 25  $\mu\text{m}$ .



with yellow ochre pigmentation. *Cheilocystidia* 35-54 × 7-9 µm, emergent up to 27 µm, cylindrical to subclavate, mostly with capitate apex, filled with irregular refractive bodies, sometimes with yellow ochre pigmentation. *Marginal cells* absent or rare. *Subhymenium* up to 16 µm thick, pseudoparenchymatous. *Pileipellis* 200-250 µm thick, two-layered; suprapellis composed of non-encrusted, erect, cylindrical, multiseptate, branched hyphae with cylindrical terminal cells tapering toward an obtuse-rounded apex, toward pileus margin mixed with abundant, clavate to capitate or subcapitate (18-27 µm wide) terminal cells and inflated intercalary cells; subpellis composed of repent subparallel hyphae with distinct incrustations, 4-10 µm diam.; pileocystidia not observed.

*Other specimens examined:* INDIA, Sikkim, South district, Kewzing, 27°17'46.5"N, 88°21'26.6"E, 1888 m asl., under *Castanopsis* in temperate broadleaf forest, 24 August 2017, *Kanad Das* 17-22 (CAL 1643); Uttarakhand, Nainital District, Mukteshwar, 29°28.560'N 79°38.725'E, 2299 m asl., under *Quercus* in temperate broadleaf forest, 17 July 2017, *Aniket Ghosh* 1460 (CAL 1644); Uttarakhand, Champawat District, Mayavai Ashram, 29°22.339'N 80°03.799'E, 1945 m asl., under *Quercus* in temperate broadleaf forest, 17 August 2016, *Aniket Ghosh* 1324 (CAL 1645); Uttarakhand, Pauri District, Phedkhal, 30°09.698'N 78°51.151'E, 1925 m asl., under *Quercus* in temperate broadleaf forest, 24 July 2017, *Aniket Ghosh* 1469 (CAL 1642); Uttarakhand, Pauri District, Chaurikhal, 30°02.389'N 79°03.406'E, 1981 m asl., under *Quercus* in temperate broadleaf forest, 1 August 2017, *Aniket Ghosh* 1509 (CAL 1646).

*Notes:* see under the next entry (*R. compactoides*)

**47. *Russula compactoides* K. Das, A. Ghosh & Buyck sp. nov.**

**Figs 7-8**

*Mycobank:* MB 823802

*GenBank:* MG662161; MG662172 (ITS)

*Systematic position:* Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology:* referring to it being a look-alike of *R. compacta*, a North American species in *R. subg. Malodora*.

*Diagnosis:* differs from similar looking taxa by nrITS sequence data and a combination of unequal, frequently forked lamellae with up to 3 series of lamellulae, relatively long hymenial cystidia with appendiculate or lageniform to capitate, moniliform, subobtusate or mucronate apex, abundant marginal cells and its putative ectomycorrhizal association with conifers (*Abies*).

*Holotype:* INDIA, Sikkim, East district, Between Kyangnosla and Changu, 27°22'21.0"N, 88°44'25.3"E, 3352 m asl., under *Abies densa* in subalpine mixed (coniferous & broadleaf) forest, 25 August 2016, *Kanad Das* 16-55 (CAL 1639, **holotype!**).

*Pileus* 63-173 mm in diam., convex when young, gradually broadly convex, planoconvex to applanate with depressed center at maturity; margin decurved to plane, entire; surface dry, viscid when moist, smooth, cracked to areolate at maturity, light orange (5A4) to orange (5A7), centrally soot brown (5F5) colored; context up to 12 mm thick, firm, brittle, chalky white (1A1), turning light orange (5D7) to brownish orange or brown (6D7) when bruised or cut. *Lamellae* moderately close (10-16/cm), irregularly forked at different distances, chalky white (1A1), becoming light orange (5D7) to brown (6D7) soon after bruising; intercalated with lamellulae of different lengths. *Stipe* 45-110 × 15-38 mm, chalky white (1A1), subclavate to clavate, smooth, turns light orange (5D7) to brown (6D7) after bruising; interior solid, chalky white (1A1), soon light orange (5D7) to brown (6D7) when cut or bruised, turns pale red (9A3) to reddish grey (9B2) to dull red

(9B3) after few minutes with guaiacol; turns light green (27F5) after application of  $\text{FeSO}_4$ . Taste Mild. Odour very strong and unpleasant at maturity or on drying. Spore print white.

*Basidiospores* globose to subglobose or broadly ellipsoid, 6.48-7.72-8.23-10 × 5.86-7.08-7.33-8.89(-9)  $\mu\text{m}$ ,  $Q = 1.0$ -1.09-1.12-1.31; ornamentation amyloid, up to 1  $\mu\text{m}$  high, with warts and ridges aligned or connected to form partial to incomplete reticulum; suprahilar plage inamyloid. *Basidia* 45-64 × 7-9  $\mu\text{m}$ , cylindrical to subclavate, 4 spored; sterigmata up to 10  $\mu\text{m}$  long. *Pleurocystidia* 56-107 × 7-14  $\mu\text{m}$ , emergent up to 25  $\mu\text{m}$ , sometimes deeply embedded, cylindrical to subclavate, with mucronate, capitate, moniliform, obtuse to subobtuse, lageniform or appendiculate apex; contents with irregular refractive bodies and mostly with yellow ochre pigmentation. *Cheilocystidia* 50-83 × 7-9  $\mu\text{m}$ , cylindrical to subclavate, with capitate, moniliform, subobtuse, lageniform to appendiculate apex, filled with irregular refractive bodies and mostly with yellow ochre pigmentation. *Marginal cells* abundant, 7-27 × 5-7  $\mu\text{m}$ , 1-2 septate, with cylindrical to clavate terminal cell. *Subhymenium* up to 30  $\mu\text{m}$  thick, pseudoparenchymatous. *Lamellar trama* composed of nests of sphaerocytes and septate hyphae (2.5-6  $\mu\text{m}$  thick). *Pileipellis* 200-300  $\mu\text{m}$  thick, two-layered; suprapellis composed of encrusted, erect, cylindrical, multiseptate, branched hyphae, with cylindrical terminal cells having a tapering, rounded apex, toward the pileus margin also with a few dispersed clavate to capitate terminal cells (10-25  $\mu\text{m}$  wide); subpellis composed of repent subparallel hyphae with few incrustations; pileocystidia not observed.

*Other specimens examined*: INDIA, Sikkim, East district, Between Kyangnosla and Changu, 27°22'21.0"N, 88°44'25.3"E, 3352 m asl., under *Abies densa* in subalpine mixed (coniferous & broadleaf) forest, 7 August, 2014, Kanaad Das 14E-040 (CAL 1640, Paratype).

*Notes*: Both this species, as well as *R. pseudocompacta* described above, are look-alikes of the North American *R. compacta* Frost (in Peck 1879). Peck's species has known quite a complex history as it has been classified in at least four different subgenera (*Compactae*, *Russula*, *Brevipes*, *Ingratula*) before it was finally assigned as the type species of a new subgenus: subg. *Malodora* Buyck & V. Hofst. (see Hongsanan *et al.* 2015). Both new Indian species share with *R. compacta* the orange-brown overall color of the often fissuring and dull pileus surface with smooth margin, the firm and fleshy habit, the strong brownish discoloration of the context upon bruising, white spore print, the gradual development of a strong and disagreeable smell and predominantly mild taste, and even very similar microscopical features.

*Russula compacta* has repeatedly been described in detail (e.g. Burlingham 1915, Beardslee 1918, Shaffer 1970, Singer 1938) and is generally regarded as an "easy" species to identify due to its unique characters, although confusion with the rare *R. crassotunicata* is possible. Our phylogeny (Fig. 1) now clearly suggests that this name covers a species complex that extends all over the northern hemisphere with the exception of Europe. The difference in habitat noted for the Indian species suggests that some of this cryptic diversity might be related to host preferences as *R. pseudocompacta* is found under broadleaf trees of Fagaceae in temperate Himalaya, while *R. compactoides* is always found in the presence of conifers (*Abies*) in subalpine Himalaya. In the field, *R. pseudocompacta* differs additionally in the frequent forking of the gills and lack of lamellulae, whereas both *R. compacta* and *R. compactoides* share the unequal gills with fewer forkings. The frequently forked gills (without lamellulae) are also typical of most tropical African members of this subgenus.

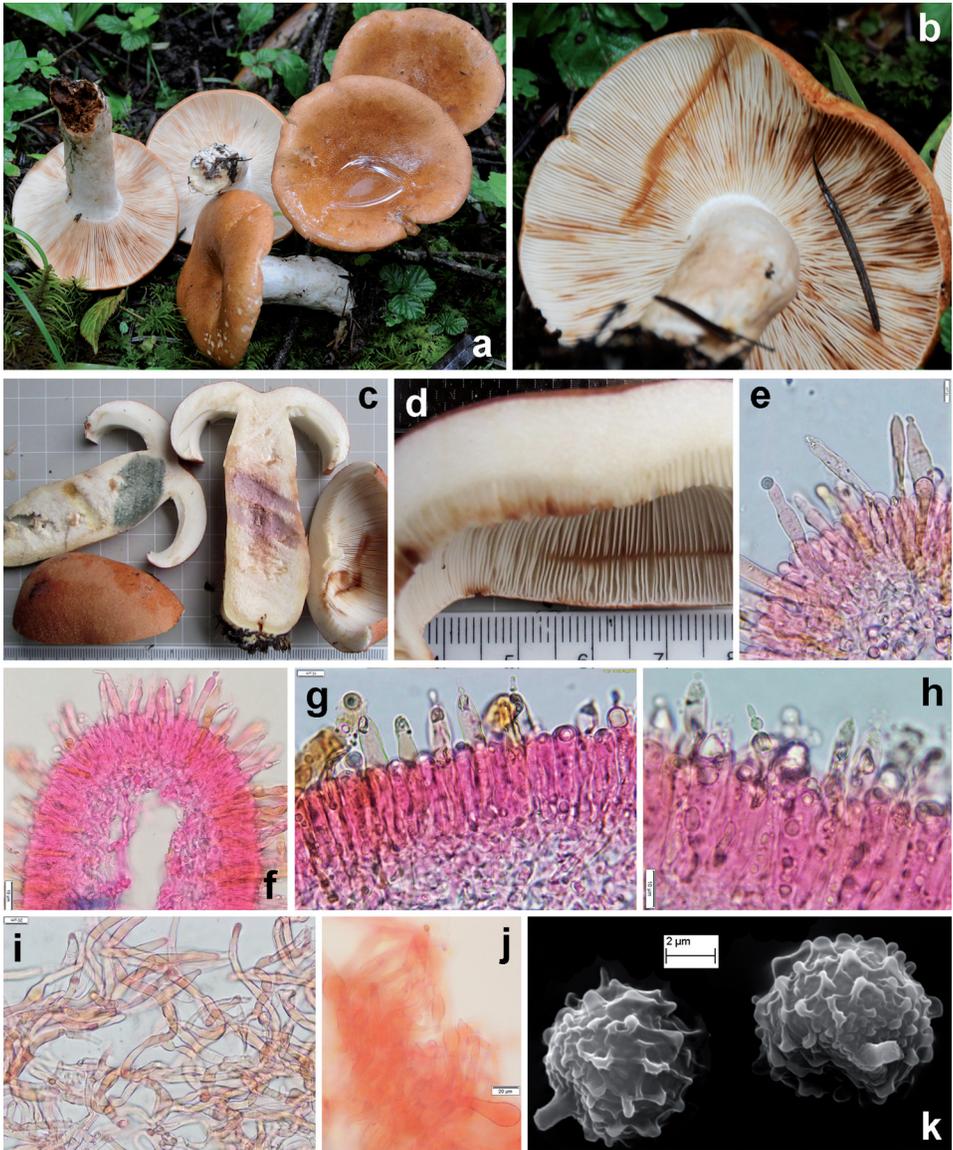
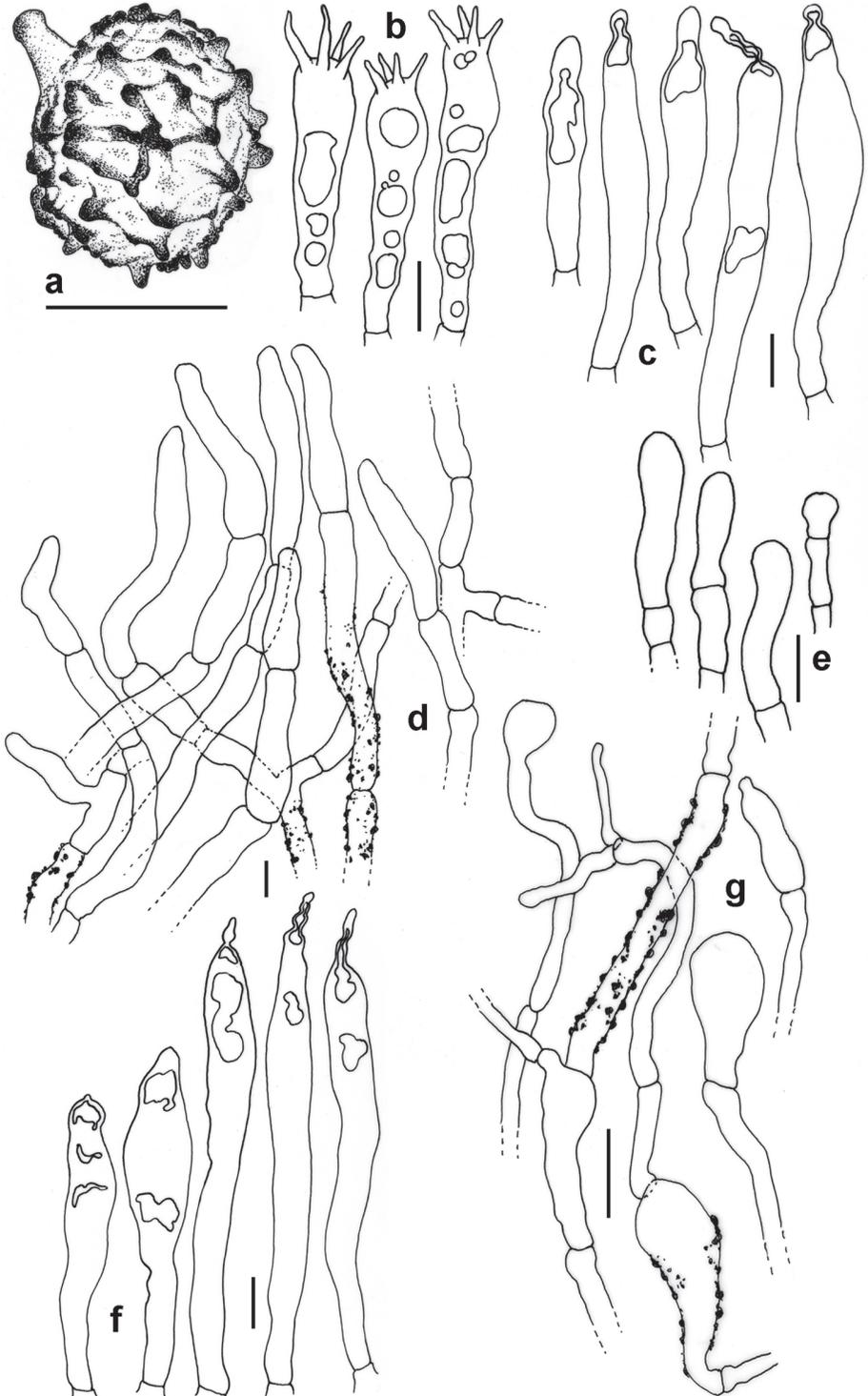


Fig. 7. *Russula compactoides* (KD 16-55, Holotype). **a**, **b** & **c**. Fresh/dissected basidiomata in the field or basecamp. **d**. Lamellae. **e** & **f**. Cheilocystidia. **g** & **h**. Pleurocystidia. **f**, **g** & **h**. Pleurocystidia. **i**. Transverse section through pileipellis from pileus centre. **j**. Transverse section through pileipellis from pileus margin. **k**. Basidiospores under SEM. Scale bars: e-h = 10  $\mu$ m, i-j = 20  $\mu$ m, k = 2  $\mu$ m.

Fig. 8. *Russula compactoides* (from KD 16-55, Paratype). **a**. Basidiospores. **b**. Basidia. **c**. Cheilocystidia. **d**. Hyphal elements in pileipellis (at pileus centre) **e**. Marginal cells at lamellae edge. **f**. Pleurocystidia. **g**. Clavate to capitate hyphal extremities in pileipellis (at pileus margin). Scale bars: a = 5  $\mu$ m, b-f = 10  $\mu$ m, d = 25  $\mu$ m.



Under the microscope, *R. compactoides* has longer hymenial cystidia with appendiculate, lageniform, moniliform or capitate apex and much more abundant marginal cells at the lamella edges, but distinctly fewer inflated, capitate terminal cells in the pileipellis toward the pileus margin. Typical pileocystidia could not be observed in the suprapellis of the Indian specimens and cystidioid hyphae are also absent from deeper tissues. In older taxonomic studies, pileocystidia have typically been described as absent in many members of this subgenus, including *R. compacta*. Nevertheless, a recent type study illustrates their presence in the American *R. compacta* (see Adamcik *et al.* 2018), but they are very rare and inconspicuous, very comparable to what was observed for *R. virescens* (Buyck 2004).

The northern hemisphere taxa within subg. *Malodora* are genetically distinct from the African species and compose separate clades. We, therefore, describe below two new sections corresponding to these clades.

**48. *Russula* section *Pseudocompactae* Buyck & V. Hofst. **sect. nov.****

*Mycobank*: MB 823809

*Systematic position*: Russulales, Russulaceae, *Russula* subg. *Malodora* Buyck & V. Hofst. in Hongsanan *et al.* (2015)

*Etymology*: referring to the name of the type species

*Diagnosis*: Medium-sized to large, firm and fleshy species with sometimes an initially white, but then quickly orange-brown pileus with an often fissuring, dull surface and smooth margin, a strong brownish discoloring context upon injury, gradual development of a strong and disagreeable smell and predominantly mild taste; lamellae forked or unequal; spore print white.

Spores with (sub)reticulate ornamentation and inamyloid suprahilar spot. Pileipellis composed of densely septate, rather wide, branching hyphal extremities; mucronate pileocystidia very rare to absent near the surface, without gloeoplerous elements in deeper layers.

*Type species*: *R. pseudocompacta* sp. nov.

**49. *Russula* section *Edules* Buyck & V. Hofst. **sect. nov.****

*Mycobank*: MB 823808

*Systematic position*: Russulales, Russulaceae, *Russula* subg. *Malodora* Buyck & V. Hofst.

*Etymology*: referring to the reputed edibility of most of its species

*Diagnosis*: Differs principally from sect. *Pseudocompactae* in the more variable color of the cap, coming in shades of whitish, cream, yellow, brown, grey and black, sometimes even with some greenish tints, the always frequently forked gills and the more variable discoloration of the context taking often distinct greyish or even pinkish or bluish tints.

*Type species*: *R. edulis* Buyck, *Econ. Bot.* 62: 519. 2008

*Note*: As a complete description was never published for the type species, a description and illustrations are provided below.

**50. *Russula edulis* Buyck, *Econ. Bot.* 62: 519. 2008**

**Figs 9-10**

*Mycobank*: MB 587847

*GenBank*: MG662161; MG662172 (ITS)

*Systematic position*: Basidiomycota, Agaricomycetes, Russulales, Russulaceae.

*Etymology*: named after its local reputation of being a good edible mushroom

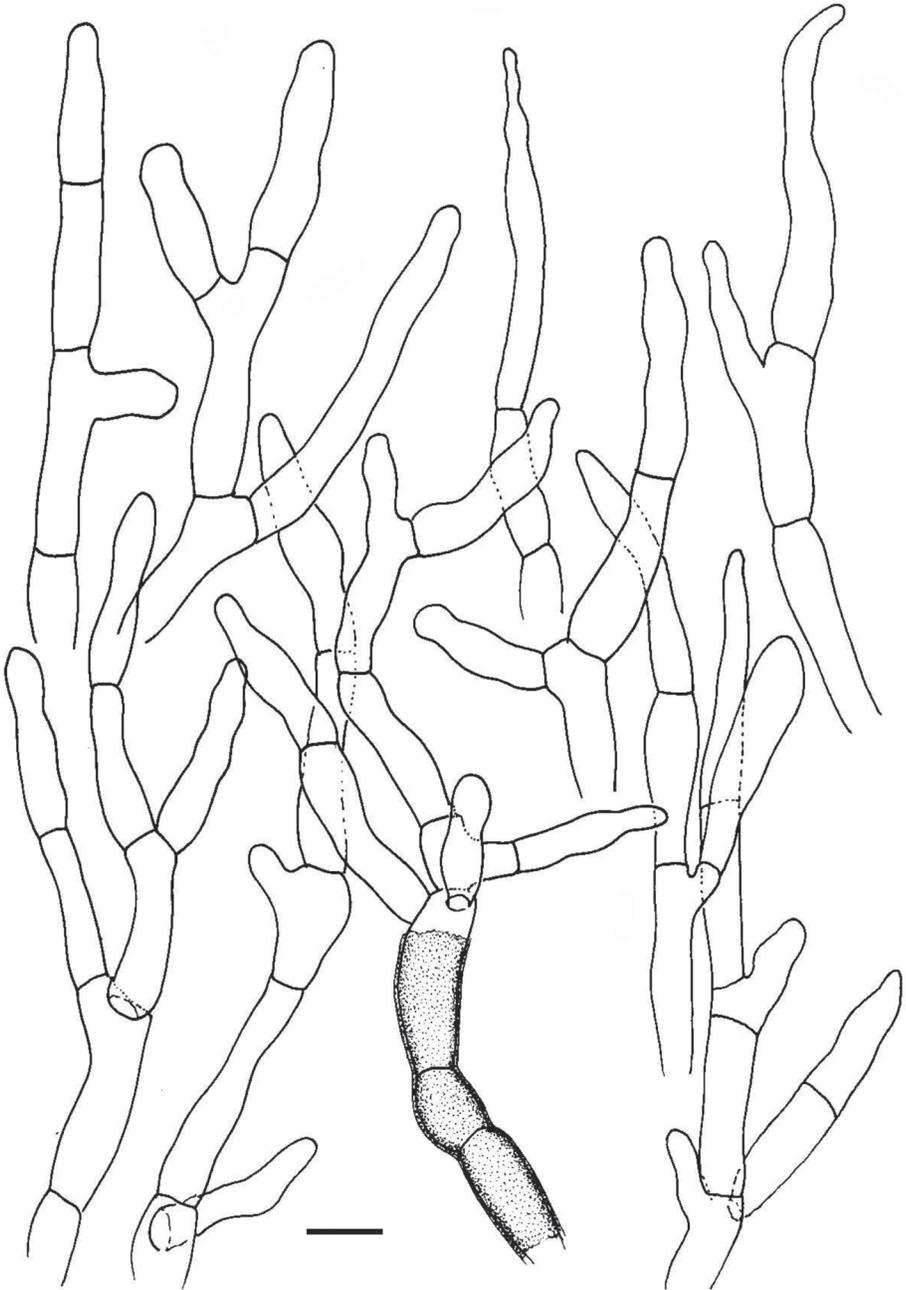


Fig. 9. *Russula edulis* (holotype). Fungal extremities of the pileipellis; note the glutinous mantle sheathing the lower portion of the hyphal extremities as indicated in one element. Scale bar = 10  $\mu$ m.

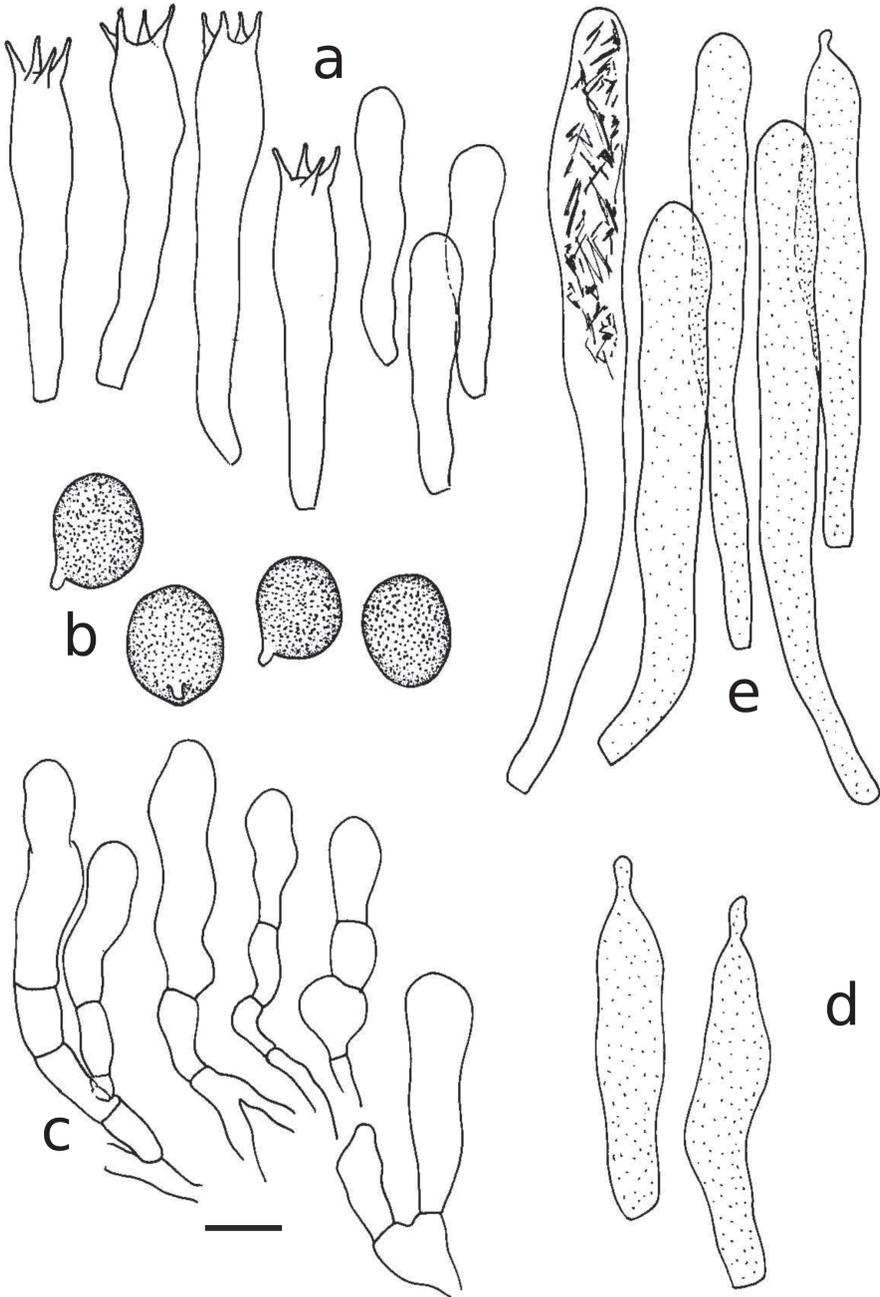


Fig. 10. *Russula edulis* (holotype). Elements of the hymenium: **a.** Basidia and basidiola; **b.** spores in Melzer's reagent (note the absence of a distinct suprahilar spot); **c.** marginal cells of the gill edge; **d.** cheilocystidia; **e.** pleurocystidia with indication of contents in one element. Scale bar = 10  $\mu\text{m}$ , but only 5  $\mu\text{m}$  for spores.

*Holotype*: Madagascar. Central plateau, at Arivonimamo, in *Uapaca bojeri* woodland, 5 Feb. 1997, Buyck 97.264 (PC).

*Pileus* up to 15 cm diam., fleshy and firm, mostly gently depressed in the center, with smooth margin, usually becoming rapidly and sometimes profoundly cracked and fissured, thereby exposing the whitish underlying flesh, glabrous, dull, never viscid, homogeneously dark brown to grayish brown, sometimes with very faint greenish tinges toward the margin, locally discoloring or off – white from the early stages; pileipellis easily separable up to mid-radius. *Stipe* sometimes slightly eccentric, very firm and solid, cylindrical or almost so, whitish in upper part but grayish-brown and tomentose downward because of a dense, minute, fibrillose covering. *Lamellae* adnate to subfree, 4-6 mm high, ivory, sometimes with faint pinkish tint when viewing at an angle, turning somewhat brownish where bruised, close, equal but with many bifurcations at various distances between stipe and pileus margin, not fragile; edges entire and concolorous. *Context* whitish, rapidly but never very intensely graying when exposed, also with faint pinkish tints when cut; very hard and thick (approx. 10-15 mm in pileus center). Reaction to  $\text{FeSO}_4$  slowly orange-brown, then fading progressively to greenish gray. *Taste* mild or refreshing, not acrid. *Odor* strong, agreeable. *Spore print* whitish.

*Spores* globose to shortly ellipsoid,  $(6.7)6.9\text{--}7.25\text{--}7.52\text{--}7.8(8.1) \times (5.6)6.1\text{--}6.47\text{--}6.79\text{--}7.2(7.7) \mu\text{m}$ ,  $Q = 1.0\text{--}1.12\text{--}1.2$ , densely and minutely verruculose; suprahilar spot not differentiated and simply covered by the same low ornamentation. *Basidia* 43-50(58)  $\times$  8-9.5  $\mu\text{m}$ , clavate and usually tortuous-sinuous, clearly yellowish in potassium, 4-spored; sterigmata 4-6  $\times$  2  $\mu\text{m}$ . *Pleurocystidia* very abundant (approx. 3500-4000/mm<sup>2</sup>), 50-80(120)  $\times$  8-10(12)  $\mu\text{m}$ , clavate-pedicellate to fusiformous or slightly inflated apically, minutely appendiculate or capitulate, often optically empty or with poor developed granular contents, although with crystalline contents in upper half when originating deep in the lamellar trama, distinctly greying in SV. *Marginal cells* tortuous, resembling the basidiola but strongly septate, rendering the entire gill edge sterile, mixed with dispersed, clavate, short cheilocystidia; all cells originating from very narrow hyphae, not more than 2  $\mu\text{m}$  diam., often more or less refractive and having distinct zebroid incrustations. *Subhymenium* very dense, composed of poorly inflated cells, and the remarkably narrower hyphae near the gill edge. *Lamellar trama* containing some refractive hyphae, forming a dens tissue with very few large sphaerocytes. *Pileipellis* not gelified, entirely orthochromatic in cresyl blue; suprapellis formed of highly branched, septate, entangled extremities up to 200  $\mu\text{m}$  long, clearly yellowish in potassium, composed of subcylindrical cells of variable length (generally longer towards the pileus margin), 5-7(10)  $\mu\text{m}$  diam., optically empty to slightly refractive, not exactly thin-walled and entirely packed in a sheath of rugulose-punctate incrustations; the terminal cell mostly 20-35  $\mu\text{m}$  long, usually tapering and sometimes apically more or less constricted and subcapitate. Pileocystidia not observed. *Stipitipellis* composed of equally broad, but much more sparsely septate extremities, arising from context hyphae with distinct zebroid incrustations; the terminal element 50-100  $\mu\text{m}$  long; dermatocystidia rare, subcylindrical and appendiculate – capitulate, arising between the other extremities and of similar diam., with crystalline contents. *Clamp connections* absent.

*Notes*: Several other widely consumed *Russula* in Africa and Madagascar have forked gills and may occur side by side with *R. edulis*: e.g. the closely related *R. cellulata* Buyck or *R. liberiensis* Singer, both also belonging to the same section in subg. *Malodora*.

*R. liberiensis* differs microscopically by the more ornamented and more elongate although smaller spores and by the different structure of the extremities in

the suprapellis, which are more tortuous and irregular in outline and originate often from larger, inflated to almost subglobose basal cells. *R. cellulata* has a characteristic rusty stipe base and a dense mat of clavate terminal cells at the pileus surface.

*R. schizoderma* Pat. – still only known from the type – differs from *R. edulis* by the very different structure of the pileipellis with twisted, very irregularly inflated extremities that have usually inflated apices.

*R. ochraceorivulosa* Buyck, otherwise unrelated, also strongly reminds of *R. edulis*, although only when dried. In the field, however, its white color with concolorous small squamae will clearly distinguish it.

Several other, still undescribed species with forked gills, strongly branched long hyphae in the pileipellis and poorly ornamented spores are present in Africa and Madagascar.

**Acknowledgements.** K. Das and coauthors are grateful to the Director, Botanical Survey of India, Kolkata and Head, Department of Botany & Microbiology, HNB Garhwal University, Srinagar Garhwal, for providing the necessary laboratory facilities used for this study. Miss Priyanka Uniyal, Mr. Tahir Mehmood and Mr. Upendra Singh (HNBGU) are duly acknowledged for their assistance in field rendered to Aniket Ghosh.

## REFERENCES

- ADAMČIK S., JANČOVIČOVÁ S. & BUYCK B., 2018 — The Russulas described by Charles Horton Peck. *Cryptogamie, Mycologie* 39(1): 1-110.
- ALFARO M. E., ZÖLLER S. & LUTZONI F.M., 2003 — Bayes or Bootstrap? A simulation study comparing the performance of Bayesian Markov Chain Monte Carlo sampling and Bootstrapping in assessing phylogenetic confidence. *Molecular Biology and Evolution* 20: 255-266.
- BAZZICALLUPO A.L., BUYCK B., SAAR I., VAURAS J., CARMEAN D. & BERBEE M.L., 2017 — Troubles with mycorrhizal mushroom identification where morphological identification lags behind barcode sequence divergence. *Taxon* 66(4): 791-810.
- BEARDSLEE H.C., 1918 — The Russulas of North Carolina. *Journal of the Elisha Mitchell Scientific Society* 33(4): 147-197.
- BEENKEN L., 2004 — Die Gattung Russula. Untersuchungen zu ihrer Systematik anhand von Ektomykorrhizen. Dissertation. Ludwig-Maximilians Universität München; [https://edoc.ub.uni-muenchen.de/3175/1/Beenken\\_Ludwig.pdf](https://edoc.ub.uni-muenchen.de/3175/1/Beenken_Ludwig.pdf)
- BURLINGHAM G.S., 1915 — Russula. North American Flora 9: 201-236.
- BUYCK B., 2004 — Précisions sur *Russula virescens* et sur quelques *Griseinae* leucosporées. *Bulletin de la Société mycologique de France* 120: 385-401.
- BUYCK B., DUHEM B., DAS K., JAYAWARDENA R.S., NIVEIRO N., PEREIRA O.L., PRASHER I.B., ADHIKARI S., ALBERTÓ E.O., BULGAKOV T.S., CASTAÑEDA-RUIZ R.F., HEMBROM M.E., HYDE K.D., LEWIS D.P., MICHLIG A., NUYTINCK J., PARIHAR A., POPOFF O.F., RAMIREZ N.A., da SILVA M., VERMA R.K. & HOFSTETTER V., 2017 — Fungal Biodiversity Profiles 21-30. *Cryptogamie, Mycologie* 38(1): 101-146.
- DAS K., MILLER S.L. & SHARMA J.R., 2006 — *Russula* in Himalaya 2: four new taxa. *Mycotaxon* 95: 205-215.
- GUINDON S. & GASCUEL O., 2003 — A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52(5): 696-704.
- HALL T.A., 1999 — BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- HONGSANAN S., HYDE K.D., BAHKALIA.H., CAMPORESI E., CHOMNUNTIP, EKANAYAKA H., GOMES A.M., HOFSTETTER V., JONES E.B.G., PINHO D.B., PEREIRA O.L., TIAN Q., WANASINGHE D.N., XU J-C. & B. BUYCK, 2015 — Fungal Biodiversity Profiles 11-20. *Cryptogamie, Mycologie* 36(3): 355-380.

- LARGENT B. & SIMON D.L., 1999 — Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution* 16: 750-759.
- LOONEY B.P., RYBERG M., HAMPE F., SÁNCHEZ-GARCÍA M. & MATHENY P.B., 2016 — Into and out of the tropics: global diversification patterns in a hyper-diverse clade of ectomycorrhizal fungi. *Molecular Ecology* 25: 630-647.
- PECK C.H., 1879 — Report of the Botanist. *Annual Report on the New York State Museum of Natural History* 31: 19-60.
- SARNARI M., 1998 — *Monografia Illustrata Del Genere Russula in Europa*. Tomo Primo, Associazione Micologica Bresadola, Trento. Italy, 799 pp.
- SARNARI M., 2005 — *Monografia Illustrata Del Genere Russula in Europa*. Tomo Secondo, Italy, 762 pp.
- SHAFFER R.L., 1970 — Notes on the Subsection *Crassotunicatinae* and other Species of *Russula*. *Lloydia* 33(1): 49-96.
- SINGER R., 1938 — Contribution a l'étude des Russules. 3. Quelques Russules américaines et asiatique (suite). *Bulletin de la Société Mycologique de France* 54: 132-177.