

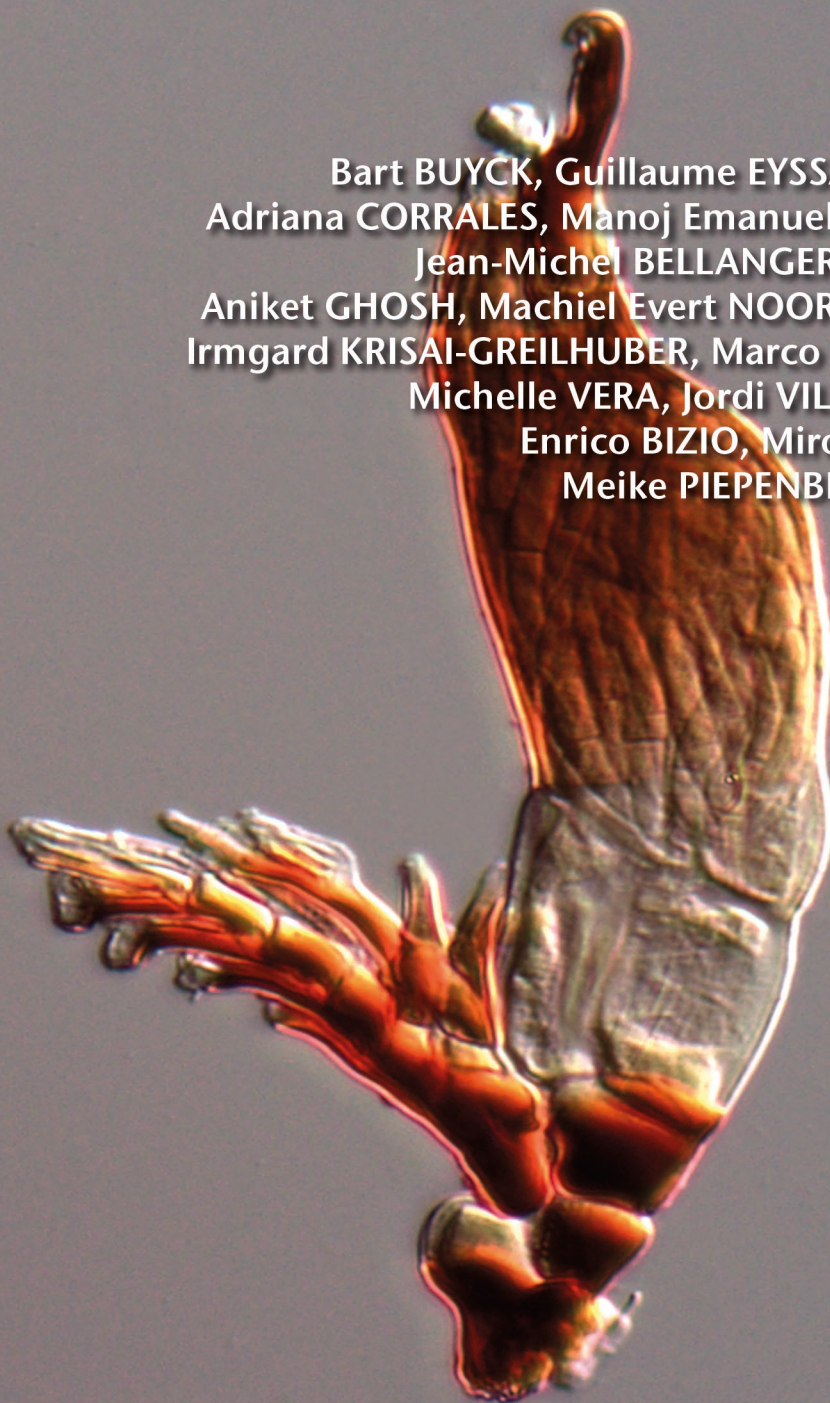
# cryptogamie

## *Mycologie*

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### Fungal biodiversity profiles 111-120

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## ABSTRACT

In this new series of Fungal Biodiversity Profiles, the authors provide descriptions for ten new taxa: *Ilytheomyces uncinatus* W. Rossi & M. Leonardi, sp. nov. (Ascomycota, Laboulbeniales) and several Basidiomycota: in family Entolomataceae for *Entoloma aurantioalpinum* Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov. and *E. nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov., both from France; in family Inocybaceae for *Inocybe hebes* Eyssart. & Buyck, sp. nov., *I. media* Eyssart. & Buyck, sp. nov. and *I. leucophaea* Eyssart. & Buyck, sp. nov., all three gathered from miombo woodland in Zambia (Africa); in family Russulaceae, *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, sp. nov. and subsp. *panamanensis* Corrales & Manz, subsp. nov. from Central America; in Laetiporaceae Jülich for the Indian *Phaeolus sharmae* Hembrom, A. Parihar, K. Das & A. Ghosh, sp. nov.; in family Vuilleminiaceae Maire for *Vuilleminia tropica* Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov., equally from India. All new species of Basidiomycota are supported by newly provided sequence data or already published phylogenetic analyses of sequence data.

## KEY WORDS

Laboulbeniales,  
Basidiomycetes,  
phylogeny,  
new species.

## RÉSUMÉ

*Profils de la biodiversité fongique 111-120.*

Dans cette nouvelle série de dix taxons nouveaux, les auteurs présentent des descriptions pour *Ilytheomyces uncinatus* W. Rossi & M. Leonardi, sp. nov. (Ascomycota, Laboulbeniales) et pour plusieurs Basidiomycota: dans la famille des Entolomataceae pour *Entoloma aurantioalpinum* Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov. et *E. nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov., les deux de la métropole française; dans la famille des Inocybaceae pour *Inocybe hebes* Eyssart. & Buyck, sp. nov., *I. media* Eyssart. & Buyck, sp. nov. et *I. leucophaea* Eyssart. & Buyck, sp. nov., toutes récoltées dans la forêt claire en Zambie (Afrique); dans la famille des Russulaceae, pour *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, sp. nov. et subsp. *panamanensis* Corrales & Manz, subsp. nov. d'Amérique centrale; dans la famille des Laetiporaceae Jülich pour *Phaeolus sharmae* Hembrom, A. Parihar, K. Das & A. Ghosh, sp. nov. d'Inde; et enfin dans la famille des Vuilleminiaceae Maire pour *Vuilleminia tropica* Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov., également d'Inde. Toutes les nouvelles espèces de basidiomycètes sont appuyées par des analyses phylogénétiques de séquences ITS ou multigènes, certaines déjà publiées ailleurs.

## MOTS CLÉS

Laboulbeniales,  
Basidiomycètes,  
phylogénie,  
espèces nouvelles.

## INTRODUCTION

In this new series of Fungal Biodiversity Profiles, the authors provide a description for *Ilytheomyces uncinatus* W. Rossi & M. Leonardi, sp. nov. (Ascomycota, Laboulbeniales) and nine Basidiomycota: in family Entolomataceae for *Entoloma aurantioalpinum* Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov. and *E. nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov., both from France; in family Inocybaceae for *Inocybe hebes* Eyssart. & Buyck, sp. nov., *I. media* Eyssart. & Buyck, sp. nov. and *I. leucophaea* Eyssart. & Buyck, sp. nov., all gathered from miombo woodland in Zambia (Africa); in family Russulaceae, *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, sp. nov. and subsp. *panamanensis* Corrales & Manz, subsp. nov. from Central America; in Laetiporaceae Jülich for the Indian *Phaeolus sharmae* Hembrom, A. Parihar, K. Das & A. Ghosh, sp. nov.; in family Vuilleminiaceae Maire for *Vuilleminia tropica* Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov., equally from India. All new species of Basidiomycota are supported by newly provided sequence data or already published phylogenetic analyses of sequence data.

## MATERIAL AND METHODS

References to a colour code in descriptions follow Kornerup & Wanscher (1981). Short explanations on molecular methods that were used for building phylogenies are given in the legends of the individual phylogenetic trees.

Phylum ASCOMYCOTA R. H. Whittaker  
Class LABOULBENIOMYCETES Engl.  
Order LABOULBENIALES Lindau  
Family LABOULBENIACEAE G. Winter  
Genus *Ilytheomyces* Thaxt

111. *Ilytheomyces uncinatus*  
W. Rossi & M. Leonardi, sp. nov.  
(Fig. 1)

DIAGNOSIS. — Differs from all fifteen previously described species in the same genus for the shape of the hooked pre-apical outgrowth.

HOLOTYPE. — **Nigeria**. Ibadan, 13-24.VI.1977, leg. J. C. Deeming, on the sternites of *Zeros fractivirgatus* (Lamb) (Diptera, Ephydriidae), holo-, FI(WR2357).

INDEX FUNGORUM. — IF559552.

ETYMOLOGY. — From Latin: hooked, because of the shape of the perithecial outgrowth.

## DESCRIPTION

### Receptacle

Basal cell small, hyaline, irregularly shaped, prominent below the base of the appendage, lying side by side with the suprabasal cell, which is somewhat longer and almost wholly opaque.

### Appendage

Relatively short, consisting of a linear series of 7-8 small, blackened cells, the second of which gives rise from its upper, inner angle to a very small, almost hyaline cell bearing distally two large, paired, elongate, brownish antheridia; the third cell bears a short, ramified branch with a few branchlets variably curved and opaque on the inner side; the other cells of the axis producing externally single short branches with recurved and hyaline extremities, which are disorganized in older specimens.

### Perithecium

Stalk cell almost wholly opaque, slightly broader than long, narrower below. The basal cell region distinctly longer than the stalk cell, hyaline, except for a small, dark patch at the base of the secondary stalk cell. Perithecium grayish brown, asymmetrical, with the ventral margin distinctly convex and the dorsal almost straight; the tip very broad, rather abruptly distinguished on the ventral side, which is straight or concave, while the dorsal is slightly convex; the apex rounded and hyaline, subtended by a short, dark, suberect outgrowth ending in a small, paler hook.

### Measurements

Length from foot to perithecial apex 110-125 µm; length from foot to tip of perithecial outgrowth 120-140 µm; appendage 50-60 µm; perithecium 55-65 × 23-30 µm.

## NOTES

The genus *Ilytheomyces* includes to date 15 species, 11 of which were described from central and south America, 2 from Cameroon, and 2 from Malaysia (Thaxter 1917, 1918, 1931). All the host insects were reported as unidentified species of *Ilythea* (Diptera, Ephydriidae). It must be pointed out that the latter genus has been split and some species have been transferred to the genus *Zeros* Cresson. The only finding of *Ilytheomyces* published in the 90 years following Thaxter's work consists in 4 species reported from Bolivia on *Zeros fenestralis* (Cresson) (synonym of *Ilythea fenestralis* Cresson) (Rossi 1998).

The new species is easily distinguishable from the other 15 species for the presence and shape of the hooked preapical outgrowth. The only two species previously reported from Africa are *I. kamerunensis* Thaxt. and *I. falcatus* Thaxt., both

described from Cameroon. The first is further distinguished for the "monstrously developed basal cell region" and the very long outgrowth, the latter for its "strongly incurved" thallus and the absence of the preapical outgrowth (words in quotes are the same utilized by Thaxter 1931).

Phylum BASIDIOMYCOTA R. T. Moore

Class AGARICOMYCETES Doweld

Order AGARICALES Underw.

Family ENTOLOMATACEAE Kotl. & Pouzar

Genus *Entoloma* (Fr.) P. Kummer

## 112. *Entoloma aurantioalpinum*

Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov.  
(Figs 2-4)

DIAGNOSIS. — Macromorphologically similar to *Entoloma formosum* and *E. xanthochroum*, two widespread, not strictly alpine species in Europe that occur in lowlands and montane regions, and differ from this *E. aurantioalpinum* sp. nov. by their more distinctly translucently striate pileus, and furthermore, *E. xanthochroum* has a coloured lamella edge.

HOLOTYPE. — **France**. Savoie, Peisey-Nancroix, GR5 route du lac de la Plagne, 2050 m. alt., leg. F. Armada, 25.VIII.2018, holo-, LY(FA 4336).

MYCOBANK. — MB 840117.

GENBANK. — [MZ198885](#) (ITS holotype).

ETYMOLOGY. — From *aureus* (golden) referring to the color of the pileus, and *alpinus* for growing in an alpine environment.

ADDITIONAL MATERIAL STUDIED. — **France**. Savoie, Peisey-Nancroix, GR5 route du lac de la Plagne, 2050 m alt, leg. F. Armada, 23.VIII.2018, LY(FA 4334), ITS[[MZ198882](#)].

**Italy**. Busa de Tasca (Dolomiti), leg. E. Bizio, 23.VIII.2009, *Bizio-23082009i2* L[L-0607578], ITS[[MZ468144](#)]; Trentino-Alto Adige, Passo dello Stelvio/Stilfser Joch, near Berghotel Franzenshöhe, alpine grassland with *Dryas* and *Salix* spp., 2200 m alt., leg. B. Dima, 30.VII.2018, ELTE(DB 2018-07-30-4), ITS[[MZ468145](#)].

**Austria**. Kärnten, Völkermarkt, Eisenkappel: Vellacher Kotschna, 46°22'30"N, 14°32'30"E, mapping grid square 9653/1, alpine grassland, Caricetum firmæ, *Salix reticulata*, calcareous soil, 1500 m s.m., leg. A. Hausknecht, M. E. Noordeloos, M. Meusers, I. Krisai-Greilhuber, and members of the Austrian Mycological Society, 9.IX.1998, WU-Mykol 18644, ITS[[MZ467302](#)] — Niederösterreich, Lilienfeld, St. Aegydt am Neuwalde: Krumbach, Krumbachsattel, 47°48'33.66"N, 15°25'54.85"E, mapping grid square, 8158/4d, altitude 1200 m s.m., alpine grassland, calcareous soil, leg. A. Hausknecht, 6.IX.2006, WU-Mykol 0026678, ITS[[MZ467303](#)].

## DESCRIPTION

### Pileus

15-25 mm, conico-convex, often truncate or with slight umbilicus, with involute then more or less straight margin, at first uniformly orange-yellow to yellow orange towards margin, not or only weakly translucently striate, finely granulose to subsquamulose all over, particularly at center, glabrescent with age.



FIG. 1. — *Ilytheomyces uncinatus* W. Rossi & M. Leonardi, sp. nov. from the type slide. Scale bar: 50  $\mu$ m.

*Lamellae*

Rather crowded, adnate, thin, ventricose, up to 4 mm broad, sometimes a few forked, white then pink, with entire, concolorous edge.

*Stipe*

29-43  $\times$  2.5-4 mm, slender, cylindrical or with longitudinal groove, very brittle, with subbulbous base, pale orange, contrasting with pileus, polished or with a few longitudinal innate fibrils, with white basal mycelium.

*Context*

Very thin and brittle, concolorous with surface.

*Odour*

Indistinct.

*Taste*

Mild.

*Basidiospores*

9.5-12  $\times$  (6.5)7.3-8.0(8.5)  $\mu$ m, average 10.3-10.8  $\times$  8.0-8.3  $\mu$ m, Q = 1.2-1.7, Q<sub>av</sub> = 1.45, 6-7 angled in side view.

*Lamella edge*

Heterogeneous to almost sterile, made up of dense clusters of cheilocystidia.





FIG. 2. — Phylogenetic tree depicting the relationship of *Entoloma aurantioalpinum* Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov. and *Entoloma nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov. within subgen. *Cyanula*, clades /Sarcitulum and /Atrcoeruleum, respectively. The new species are highlighted in color rectangles. Newly generated sequences are in **boldface**. The analysis was inferred from nrDNA ITS sequences using PhyML 3.1 with the following settings: GTR+I+G model of evolution, gamma distribution of 10 rate categories, and tree topology search as SPR. Branch support was tested using the non-parametric, Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT). PhyML SH-aLRT support values (>50) are indicated at the branches. Main clades within the subgenus are compressed. *Clitopilus* was chosen as outgroup. Bar indicates 0.05 expected change per site per branch.



FIG. 3. — *Entoloma aurantioalpinum*, Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov., habit in situ (from holotype). Photo: F. Armada.

#### *Cheilocystidia*

40-65 × 10-14 µm, subcylindrical to clavate or broadly clavate.

#### *Pileipellis*

A cutis with transitions to a trichoderm at centre, made up of clavate terminal elements, 10-25 µm wide, with brownish yellow, intracellular pigment.

#### *Clamp-connections*

Absent.

#### *Habitat*

Terrestrial in alpine heaths amongst either *Dryas octopetala* or *Salix* species (*S. retusa*, *S. hastata*, *S. reticulata*), and herbs like *Polygonum viviparum*, and *Alchemilla pentaphyllea*, on calcareous bedrock.

#### *Distribution*

Rare, but probably widespread in the Alps in Austria, France, and Italy.

#### NOTES

*Entoloma aurantioalpinum* sp. nov. belongs to the diversified *E. sarcitulum* clade (Fig. 2), and clusters with two other so far unnamed alpine species. The macromorphologi-

cally similar *Entoloma formosum* and *E. xanthochroum* are widespread species in Europe, occurring in lowlands and montane regions, but not strictly alpine. Both differ from *E. aurantioalpinum* sp. nov. by the more distinctly transversely striate pileus, and furthermore, *E. xanthochroum* has a coloured lamella edge.

The holotype of *E. aurantioalpinum* sp. nov. has, in addition to the intracellular pigment, also some slightly incrusting hyphae, but this has not been observed in the other collections of this species. Incrusting pigments are exceptional in *Cyanula*.

#### 113. *Entoloma nigroflavescens*

Armada, Bellanger, Noordel. & Dima, sp. nov.

(Figs 2; 5; 6)

DIAGNOSIS. — *Entoloma nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov. can be distinguished from *E. turci*, which frequently occurs in similar habitats, by the finely roughened, innately fibrillose stipe, the absence of red staining at stipe base, and the absence of cheilocystidia.

HOLOTYPE. — **France**. Savoie, Bourg-Saint-Maurice, Arc 2000, secteur du lac Marlou, 2500 m alt., leg. F. Armada, 21.VIII.2018, holo-, LY(FA 4277).



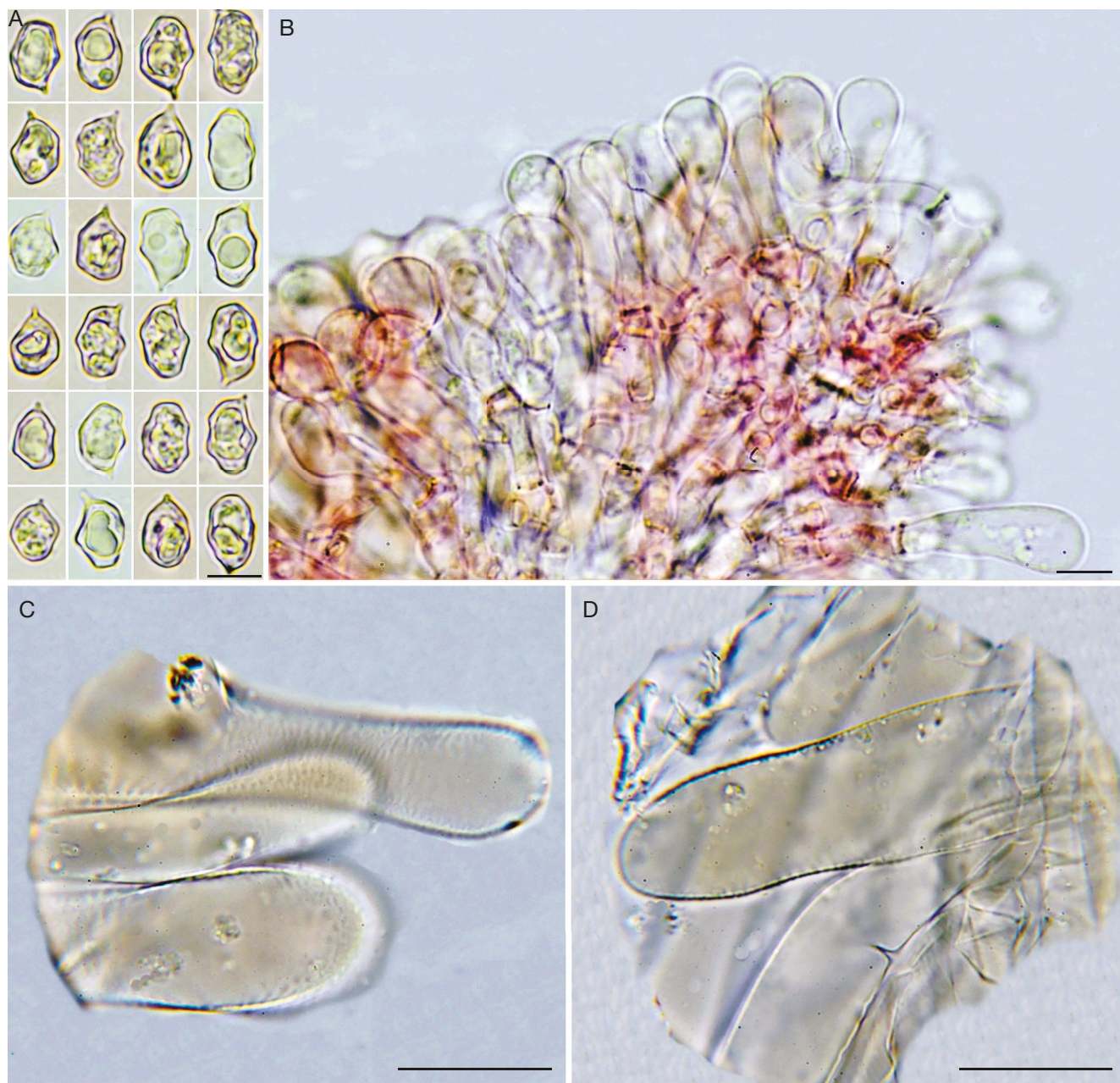


FIG. 4. — Microstructures of *Entoloma aurantioalpinum* Armada, Vila, Bellanger, Noordel., Krisai & Dima, sp. nov.: **A**, spores; **B**, lamella edge with cheilocystidia; **C**, **D**, elements of pileipellis. Photos: F. Armada. Scale bars: A, B, 10 µm; C, D, 20 µm.

MYCOBANK. — MB 840118.

GENBANK. — [MZ198884](#) (ITS holotype).

ETYMOLOGY. — *Nigrus* for black and *flavescens* for yellowing, referring to the colour and colour change of the pileus.

ADDITIONAL MATERIAL STUDIED. — **France**. Savoie, Peisey-Nancroix, secteur du col de la Chal, 2500 m alt., leg. F. & E. Armada, 17.VIII.2010, LY(FA 1726), ITS[[MZ198883](#)].

#### DESCRIPTION

##### *Pileus*

9–22 mm, convex to plano-convex, with slightly inflexed margin, very variably shaped, sometimes umbilicate, with a small central

umbo, or with irregular, undulating margin, not hygrophanous, not translucently striate, entirely very dark blackish brown to sepia brown at first, later on more yellow brown at margin, finally most of the pileus yellow brown with dark brownish-black centre; entirely rugose-tomentose to rimulose-fibrillose at first, breaking up in appressed squamules all over with age.

##### *Lamellae*

Rather distant, adnate-emarginate, thin or somewhat thick, ventricose, up to 3.5 mm broad, frequently intervenose, sordid white to greyish white, then sordid pinkish brown with an entire, thickened, concolorous edge.





FIG. 5. — *Entoloma nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov., habit in situ (from holotype). Photo: F. Armada.

#### Stipe

16–38 × 1.5–3.5 mm, equal, cylindrical, straight or curved, early fistulose, almost white when young, then beige-yellowish to pale yellow brown, minutely pruinose/punctate when young, glabrescent, never strictly polished but with fine, innate fibrils, base attenuate or slightly enlarged, slightly white tomentose, no reddening observed.

#### Context

Very thin, fragile, concolorous with surface, white inside, not reddening.

#### Odour

Weak or vaguely farinaceous.

#### Taste

None.

#### Basidiospores

(9)10.5–12.5 × (6.7)7.0–8.5(9) µm, heterodiametrical, irregularly 7–8(9) angled, sometimes almost nodulose.

#### Basidia

36–45 × 11.5–13 µm, 4-spored.

#### Cheilocystidia

Absent, lamella edge fertile.

#### Pileipellis

A cutis with transitions to a trichoderm, with clavate terminal elements, 30–90 × 13–24 µm. Pigment brown, intracellular.

#### Clamp-connections

Absent.

#### Habitat

In alpine zone, on mossy soil amongst *Salix herbacea*, *Polygonum viviparum*, and *Alchemilla pentaphyllea*.

#### Distribution

Known from two different localities in the French Alps.

#### NOTES

*Entoloma nigroflavescens* sp. nov. is a remarkable species with its dark, blackish brown basidiomata, which develop yellow tinges when maturing, and the fertile lamella edge without cystidia. In the ITS phylogeny it is a sister species to *E. persprellum*, a recently described new species from the Alps, with a blue, polished stipe, reminiscent of *E. asprellum* (Dima *et al.*



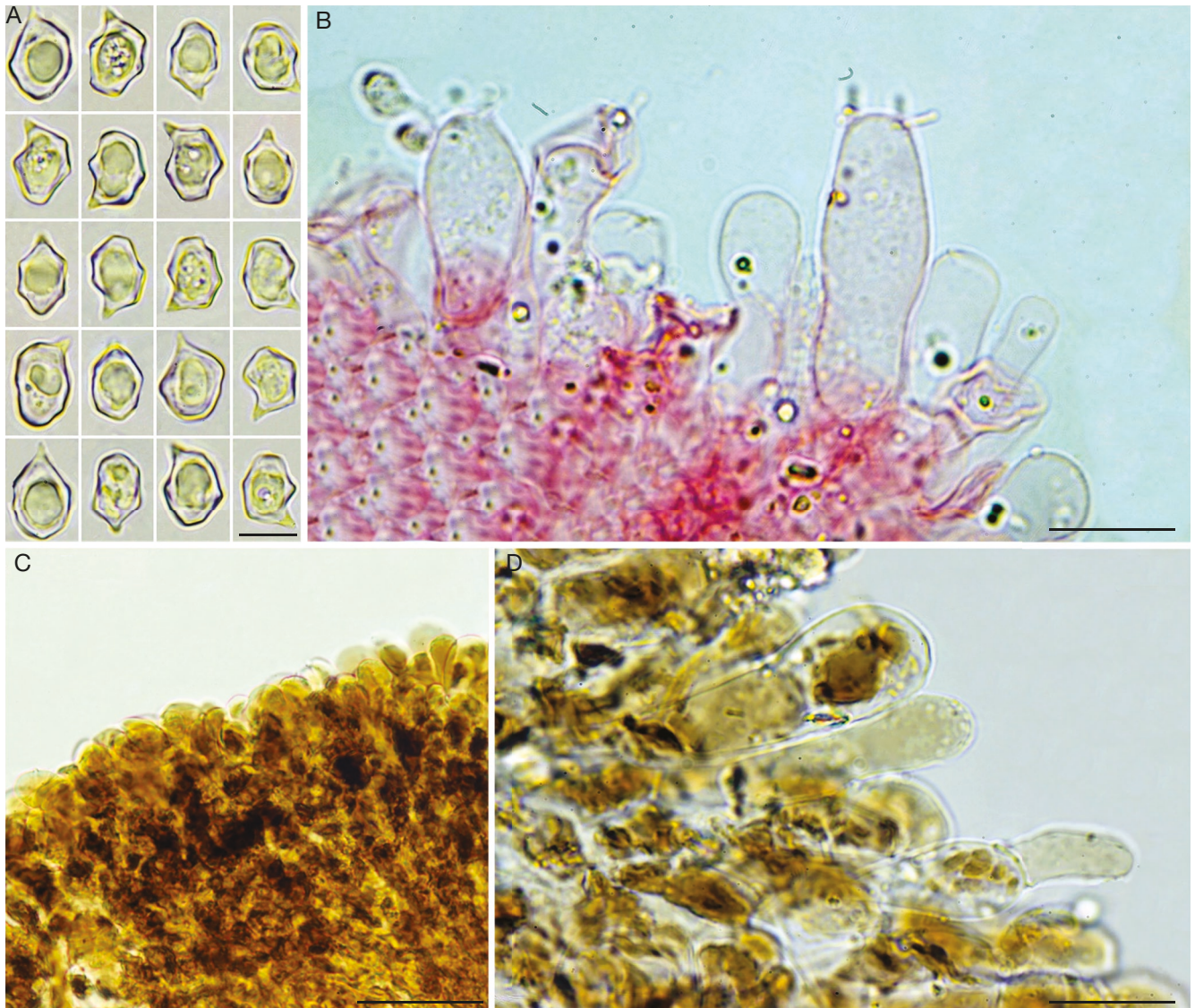


FIG. 6. — Microstructures of *Entoloma nigroflavescens* Armada, Bellanger, Noordel. & Dima, sp. nov.: **A**, spores; **B**, lamella edge with basidia and basidioles; **C**, **D**, elements of pileipellis. Photos: F. Armada. Scale bars: A, 10 µm; B, D, 20 µm; C, 50 µm.

2021). *Entoloma nigroflavescens* sp. nov. can be distinguished from *E. turci* which frequently occurs in similar habitats, by the finely roughened, innately fibrillose stipe, the absence of red staining at stipe base, and the absence of cheilocystidia.

Phylum BASIDIOMYCOTA R. T. Moore  
Class AGARICOMYCETES Doweld  
Order AGARICALES Underw  
Family INOCYBACEAE Jülich  
Genus *Inocybe* (Fr.) Fr.

114. *Inocybe hebes* Eyssart. & Buyck, sp. nov.  
(Figs 7; 8)

DIAGNOSIS. — Resembles *Inosperma curvipes*, but differs from it in its association with trees from the African miombo woodland,

its more vivid brown colours, non spermatic smell, and lageniform often subcapitate cystidia.

HOLOTYPE. — **Zambia**. Near Lusaka, gregarious in miombo woodland, 10.II.1996, *Eyssartier 96110*, (holo-, P[PC0088772]).

INDEX FUNGORUM. — IF558792.

GENBANK. — JN974997 (LSU).

ETYMOLOGY. — Named after the general form of the cap, from the latin adjective *hebes*, “blunt, obtuse”.

#### DESCRIPTION

##### *Pileus*

Measuring 12-20(25) mm in diam., obtuse conico-campanulate then plano-convex to plane, ochraceous-blond, ochraceous beige to dull brown, sometimes darker at the top, fibrillose to coarsely fibrillose, sometimes with erected squamules around the centre.



FIG. 7. — *Inocybe hebes* Eyssart. & Buyck, sp. nov. Photo: B. Buyck.

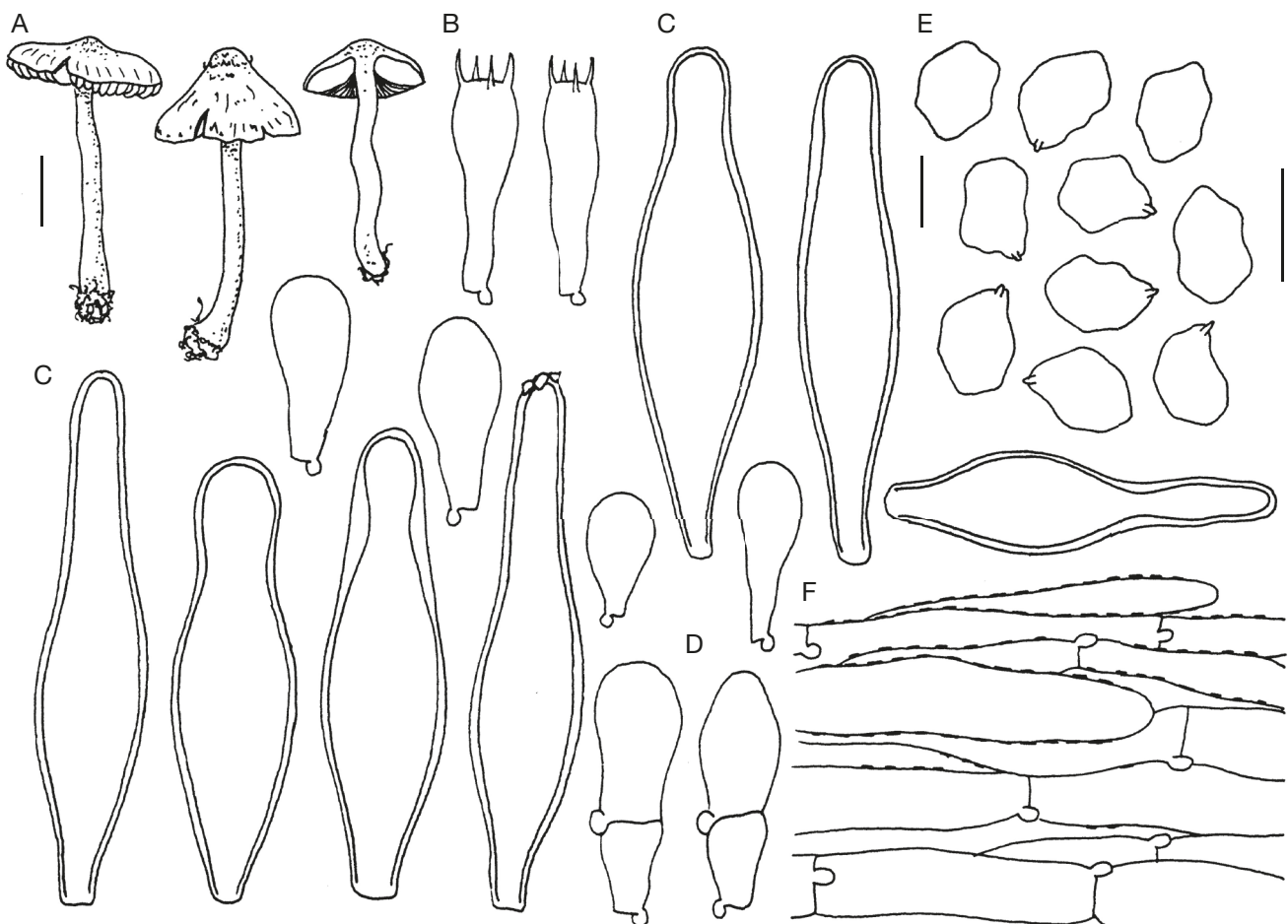


FIG. 8. — *Inocybe hebes* Eyssart. & Buyck, sp. nov. (holotype): **A**, fruiting bodies; **B**, basidia; **C**, cystidia; **D**, marginal cells of the gill edge; **E**, spores; **F**, pileipellis in section (detail). Scale bars: **A**, 1 cm; **B-E**, 10  $\mu$ m. Drawings by G. Eyssartier.



### *Lamellae*

Subhorizontal, not very close to quite distant, (1.5)2-3(4) mm broad, emarginate, pale beige then ochraceous brown, with very slightly pruinose edges.

### *Stipe*

20-35(40) × 2-3 mm, slightly broadened at the base up to 5-7 mm, seldom cylindrical but never bulbous, pale beige sometimes with pinkish tinges at the tip, then brownish to dirty brown in the older stages, not pruinose or very finely just under the lamellae.

### *Flesh*

Pale, sometimes with pinkish tinges in the upper part of the stipe.

### *Odor*

Particular, of fresh bread or brioche, sometimes honey-like.

### *Taste*

Mild.

### *Spores*

Nodulose, with 5-6(7) obtuse swellings, (7)8-9(10) × (5.5)6-7(7.5) µm.

### *Paracystidia*

Clavate, small, 15-25 × 8-10 µm.

### *Cheilocystidia*

Lageniform often subcapitate, without or with few crystals, (40)45-55(60) × (10)13-15(18) µm, with thickened walls up to 2-3 µm, hyaline in 10 % ammonia.

### *Pleurocystidia*

Cheilocystidia-like, but slightly bigger, up to 75(90) µm long.

### *Pileipellis*

A cutis of relatively broad hyphae, (5)8-12(15) µm. Pigment incrusting.

### *Clamp-connections*

Present in all parts.

### NOTES

The LSU sequence of our species was part of phylogenetic analyses presented in Ryberg & Matheny (2012) but its systematic position was not discussed. As far as we are aware, it is not mentioned in any other publication so far. nBLAST of this sequence does not suggest high similarities with other African species, although the most similar sequence (96.7 % for 99 % coverage) is obtained from another *Inocybe* from African miombo woodlands: our still unpublished *I. subfuscetipes* nom. prov. *Inocybe curvipes* P. Karst., a species described from Finland but now widely distributed throughout the world (Bougher & Matheny 2011), resembles it in a number of ways, notably in its browning stipe and spore shape, but has more vivid brown

colours, spermatic smell, cylindrical or slightly swollen stipe and larger cystidia, broadly fusiform and noticeably tapered towards the apex; in addition, *Inocybe curvipes* associates with introduced *Quercus* or *Pinus radiata*, and also possibly *Salix*.

### 115. *Inocybe media*

Eyssart. & Buyck, sp. nov.

(Figs 9; 10)

DIAGNOSIS. — Differs from other species of the *asterospora-pileosulcata* clade in its smooth or irregularly angled spores, and its habitat corresponding to the African miombo woodlands.

HOLOTYPE. — **Zambia**. Along Luanshya-Ibenga road, gregarious in very young miombo woodland with *Uapaca pilosa* and *U. kirkiana*, 3.II.1996, Eyssartier 96083, BB 96.285 (holo-, P[PC0088770]).

INDEX FUNGORUM. — IF578795.

GENBANK. — EU600884 (LSU).

ETYMOLOGY. — Name formed by reference to the shape of the spores, intermediate between the smooth and the gibbous type, form the latin *media*, “intermediate, which is between two”.

### DESCRIPTION

#### *Pileus*

Measuring 15-20 mm in diam., conico-campanulate with a large obtuse umbo that is pruinose from a white veil, clear ochraceous beige, pale beige brown with a reddish brown tinge or honey, even at the centre, towards the margin fibrillose, sometimes a little bit rimose.

#### *Lamellae*

Ascendant, 2-3 mm broad, emarginate, quite close, a pale beige ochraceous with white edges.

#### *Stipe*

30-40 × 2-3 mm, sometimes flexuous, bulbous marginate (up to 4.5-6 mm), pale beige, white beige, pruinose lengthwise.

#### *Context*

White in the pileus and the base of the stipe, subconcolorous in the stipe.

#### *Smell*

Very faint.

#### *Taste*

A little bit herbaceous.

#### *Spores*

Of particular shape, smooth or irregularly angled with few inconspicuous nodules, intermediate between the smooth and the gibbose types, (8)9-12(13) × (5)5.5-6.5(7) µm.

#### *Basidia*

Clavate, 4(2)-spored, 25-30 × 8-10 µm.



FIG. 9. — *Inocybe media* Eyssart. & Buyck, sp. nov. Photo: B. Buyck.

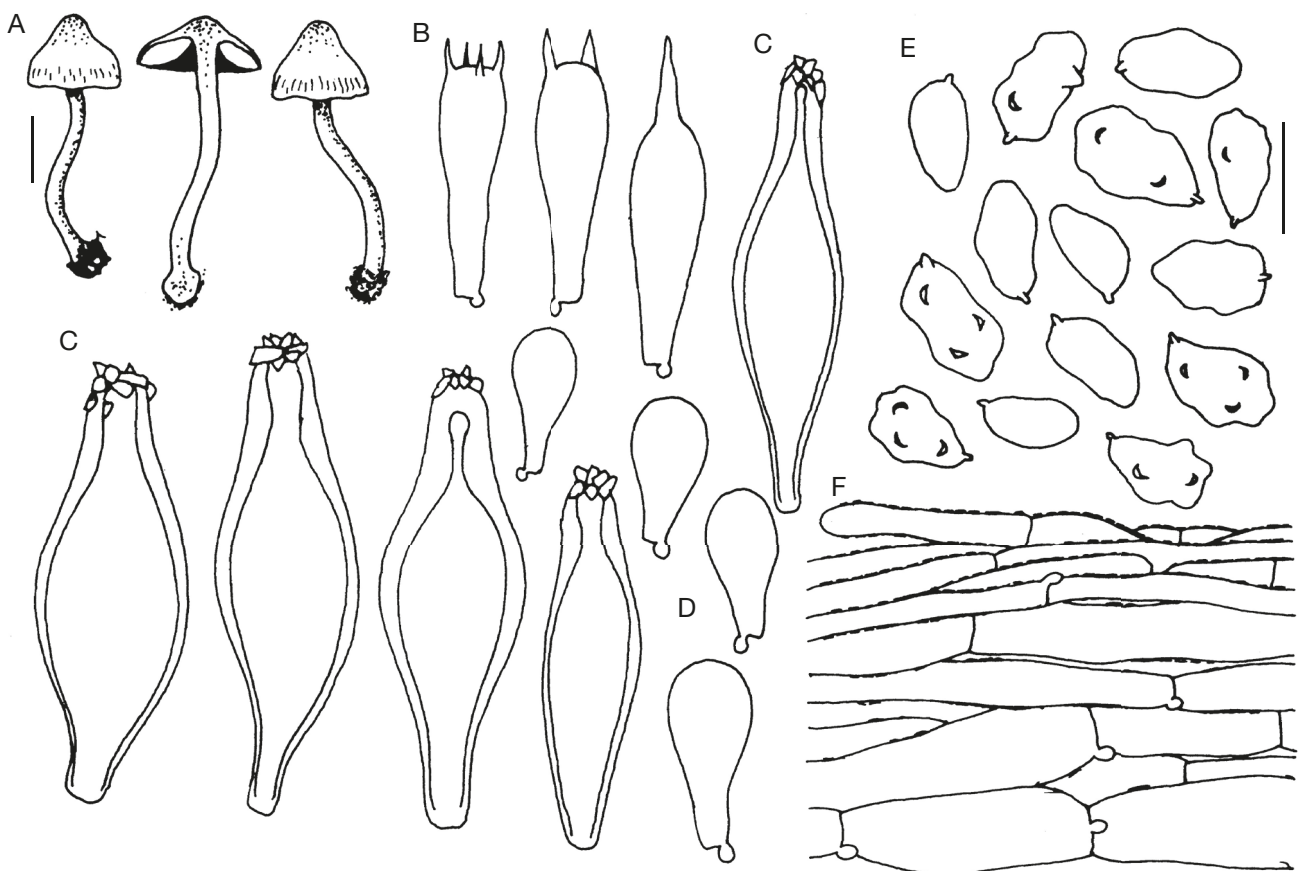


FIG. 10. — *Inocybe media* Eyssart. & Buyck, sp. nov. (holotype): **A**, fruiting bodies; **B**, basidia; **C**, cystidia; **D**, marginal cells of the gill edge; **E**, spores; **F**, pileipellis in section (detail). Scale bars: **A**, 1 cm; **B-E**, 10  $\mu$ m. Drawings by G. Eyssartier.

*Paracystidia*

Clavate, (13)15–20(25) × 7–8(10) µm.

*Hymenial cystidia*

Very similar on sides and edge of gills, lageniform to broadly lageniform, (45)50–60(65) × 15–20(25) µm, with very thickened walls, (2)3–4 µm, up to 5 µm in the upper part; colourless or almost so in 10 % ammonia.

*Pileipellis*

A cutis of subcylindrical or slightly inflated hyphae, 3–8 µm broad, broadened to 12–15 µm towards the underlying layer. Pigment brown yellowish, distinctly incrusting.

*Clamp connections*

Present in all parts.

NOTES

Although only a LSU sequence has been published for *Inocybe media* sp. nov., the species was part of multigene phylogenetic analyses (Matheny *et al.* 2009) where it is placed in a terminal clade with *I. pileosulcata* E. Horak, Matheny & Desjardin from Thailand, and with the European *I. napipes* J. E. Lange (Horak *et al.* 2015). *Inocybe pileosulcata* is associated with *Dipterocarpus* and is morphologically similar to the European *Inocybe asterospora* Quél., with which it was once confused (Horak 1979) and both species probably belongs to the same clade. All the abovementioned *Inocybe* have clearly gibbose spores with prominent knobs: *Inocybe media* sp. nov. is thus distinguished by its singular spores, of intermediate form between the smooth and gibbose type.

116. *Inocybe leucophaea*

Eyssart. & Buyck, sp. nov.  
(Figs 11; 12)

DIAGNOSIS. — Differs from *Inocybe subclavata* in its larger spores with less prominent knobs, its distinctly thicker-walled cystidia and its association with trees from the African miombo woodland.

HOLOTYPE. — **Zambia**. Near Lusaka, gregarious, in strongly degraded miombo woodland, 08.II.1996, Eyssartier 96095 (holo-, P[PC0088783]).

INDEX FUNGORUM. — IF558793.

GENBANK. — EU569860 (LSU), EU569859 (*rpb1*).

ETYMOLOGY. — Named after the general colors of the basidiomata, from ancient greek *leukos*, “white”, and *phaios*, “dusky”.

DESCRIPTION

*Pileus*

Measuring (8)12–20(30) mm in diam., conical obtuse with inflexed margin or conico-campanulate, often with a broad umbo topped by another very small and obtuse one, sometimes totally absent, the young very pale by a white veil, sometimes greyish, then the margin becomes beige, slightly

ochraceous but always pale, even in the young stages, soon fibrillose slightly rimose towards the margin, which is a little bit incised and paler by the veil.

*Lamellae*

Quite close, (1.5)2–3 mm broad, emarginate, white in the young stages then ochraceous greyish, ochraceous beige, quite pale.

*Stipe*

35–60(65) × 3–4(6) mm, bulbous, marginate, whitish, pale beige to straw-yellow, pruinose.

*Flesh*

Pale, whitish.

*Odor*

Slightly honey-like.

*Taste*

Mild, slightly herbaceous.

*Spores*

Nodulose, with (6)7–8(9) obtuse swellings, (7)8–9(10.5) × (5)6–7(8) µm, few spores quite larger, up to 12–14 × 8–9 µm (possibly from 2-spored basidia ?).

*Basidia*

4-spored, clavate, (18)20–25 × 8–9 µm.

*Paracystidia*

Clavate, small, 15–20 × 8–9 (10) µm.

*Cheilocystidia*

Pyriiform with a very obtuse base, or broadly lageniform, with very thickened walls, up to 4 (–4.5) µm, very slightly coloured in 10 % ammonia.

*Pleurocystidia*

Similar to cheilocystidia.

*Pileipellis*

A cutis of cylindrical hyphae, (3)5–7(10) µm broad, without clear pigment, very slightly incrusting.

*Clamp connections*

Present in all parts.

NOTES

*Inocybe leucophaea* sp. nov. was part of the multigene phylogenetic analyses published by Matheny *et al.* (2009) where it was part of a highly supported African clade together with two other species collected by us: *I. glaucodisca* Buyck & Eyssart. (Buyck & Eyssartier 1999) for which the LSU sequence is 98.2 % similar for 100 % coverage, while it was placed sister to *I. densifolia* nom. prov. (similarity 99 % for 100 % coverage). This African clade was placed sister with high support to a neotropical clade composed of *I. antillana* Pegler and





FIG. 11. — *Inocybe leucophaea* Eyssart. & Buyck, sp. nov. Photo: B. Buyck.

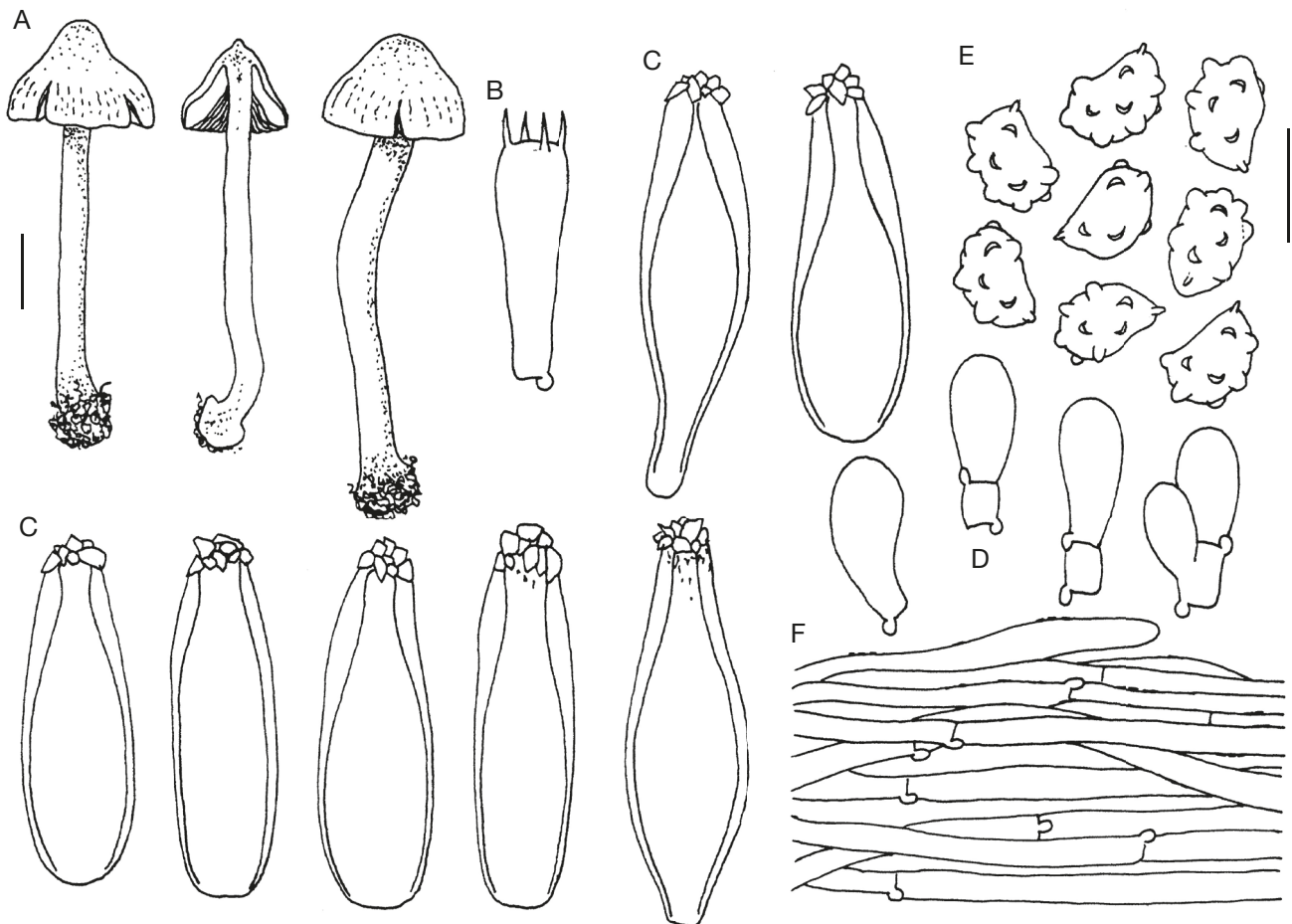


FIG. 12. — *Inocybe leucophaea* Eyssart. & Buyck, sp. nov. (holotype): **A**, fruiting bodies; **B**, basidia; **C**, cystidia; **D**, marginal cells of the gill edge; **E**, spores; **F**, pileipellis in section (detail). Scale bars: A, 1 cm; B-E, 10  $\mu$ m. Drawings by G. Eyssartier.

*I. xerophytica* Pegler (see Pegler 1983). The phylogenetic analyses based on LSU sequences in Horak *et al.* (2015) still grouped with high support *I. glaucodisca*, *I. densifolia* nom. prov. and *I. leucophaea* sp. nov., but lacked support for the deeper nodes that suggested close affinities with other *Inocybe* from the African miombo woodlands such as *I. conspicuospora* Buyck & Eyssart or the still undescribed *I. velatorimosa* nom. prov. *Inocybe subclavata* (E. Horak) Garrido closely resembles *Inocybe leucophaea* sp. nov., particularly in general habit, colour and presence of an abundant veil, but differs in its marginate stipe, and the smaller spores with less numerous and more prominent knobs, its distinctly thinner-walled cystidia and the association with *Nothofagus* in New Zealand (Horak 2018).

Order POLYPORALES Gäum  
Family LAETIPORACEAE Jülich  
Genus *Phaeolus* (Pat.) Pat

117. *Phaeolus sharmae*

Hembrom, A. Parihar, K. Das & A. Ghosh, sp. nov.  
(Figs 13–15)

DIAGNOSIS. — Differs from other *Phaeolus* by its habitat as it grows in the upper part of its host tree *Abies densa* Griff. at high altitude in the Himalayas, also by its basidiomata with pinkish orange tainted hymenophore when young, duplex context, larger basidia (16–53 × 7–12 µm) and basidiospores (6–11 × 6–7.8 µm).

HOLOTYPE. — **India**. Sikkim, North district, Yumthang valley Shingba Rhododendron sanctuary, attached to the bark of a living tree trunk of *A. densa* Griff., 3470 m, 27°46'53.2"N, 88°42'34.8"E, 19.VII.2019, K. Das & M. E. Hembrom, KMA-19-014 (holo-, CAL[CAL1843]).

MYCOBANK. — MB840191.

GENBANK. — MT762941 (nrITS, holotype), MT762940 (nrITS, paratype); MT764209 (nrLSU, holotype), MT764236 (nrLSU, paratype).

ETYMOLOGY. — Named in honour of J. R. Sharma for his contribution to Indian macrofungi.

ADDITIONAL MATERIAL STUDIED. — **India**. Sikkim, North district, Dombang valley, on living tree trunk of *A. densa* Griff. attached to bark, 3540 m, 27°46'06.2"N, 88°48'21.3"E, 20.VII.2019, K. Das, M. E. Hembrom & A. Parihar, KMA-19-026 (CAL 1844).

DESCRIPTION

*Basidiomata*

Annual, lignicolous, narrowly and loosely attached to host, single or imbricate, up to 100 mm broad, 150 mm wide and 20–50 mm thick, spongiose watery to leathery and heavy when fresh, rigid to brittle and lightweight when dry.

*Pileus*

70–190 × 70–320 mm, 8–20 mm thick near base, sessile, spathulate to applanate when young, then gradually becoming semicircular to almost dimidiate; upper surface covered with dense hispid hairs forming a thick tomentum in actively

growing regions, glabrous and rough in older parts, concentrically zonate, weakly sulcate, mustard yellow to olive yellow (3B6–C7) when young, turning light brown to brown (7D5–E6) when mature; finally, becoming pale reddish brown to blackish with age.

*Margin*

Sterile, up to 3 mm wide, acute to obtuse, entire to more or less undulating, sometimes forming narrow lobes, distinctly incurved when dry, lemon yellow or yellowish when actively growing, turning concolorous to pileus surface at maturity.

*Hymenophore*

Poroid to irpicoid to often daedaleoid near base; pores 1–2 per mm, often widening up to 3–4 mm in mature parts while staying minute towards pileus margin, glancing, pinkish orange to ochraceous orange when young, then gradually changing into almost yellowish brown to sulphur yellow, finally becoming darker coffee brown with age, turning charcoal black when bruised.

*Context*

5–10 mm wide, divided in a compact lower and loose upper part that are not separated by a black demarcation line, spongy to cheese-like when fresh, often fibrillose, becoming hard and brittle on drying, light brown to brown (7D5–E6) to dark reddish brown in the lower compact part, upper loose part and tomentum light brown (7D4–6).

*Tubes*

3–10 mm long, distinct from context, yellowish brown or concolorous with the context, brittle on drying, orange to dark blonde (5C5–D4) when young, then turning brown to dark brown (7E3–F4) when mature; dissepiments thin, entire to lacerate.

*Hyphal system of context*

Monomitic, generative hyphae 3–15 µm wide, simple septate, frequently to occasionally branched, thin- to thick-walled (<1.5 µm), hyaline or pale yellowish to dark brownish, becoming collapsed when old; walls smooth or sometimes with crystal deposits.

*Hymenophoral trama*

Composed of parallel and compactly arranged, thin- (mostly) to moderately thick-walled generative hyphae mixed with submerged gloeocystidial hyphae; generative hyphae 2–6 µm wide; submerged gloeocystidial hyphae 40–105 × 4–10 µm, septate, unbranched (mostly) to rarely branched, thin-walled, smooth, pale coffee brown to dark brown, filled with dense cytoplasmic contents.

*Hymenial gloeocystidia*

Measuring 10–105 × 4–15 µm, clavate to cylindrical, irregularly capitate, thin- to moderately thick-walled, smooth, projected up to 55 µm beyond hymenial layer, filled with dense pale yellowish contents before becoming empty in older specimens.



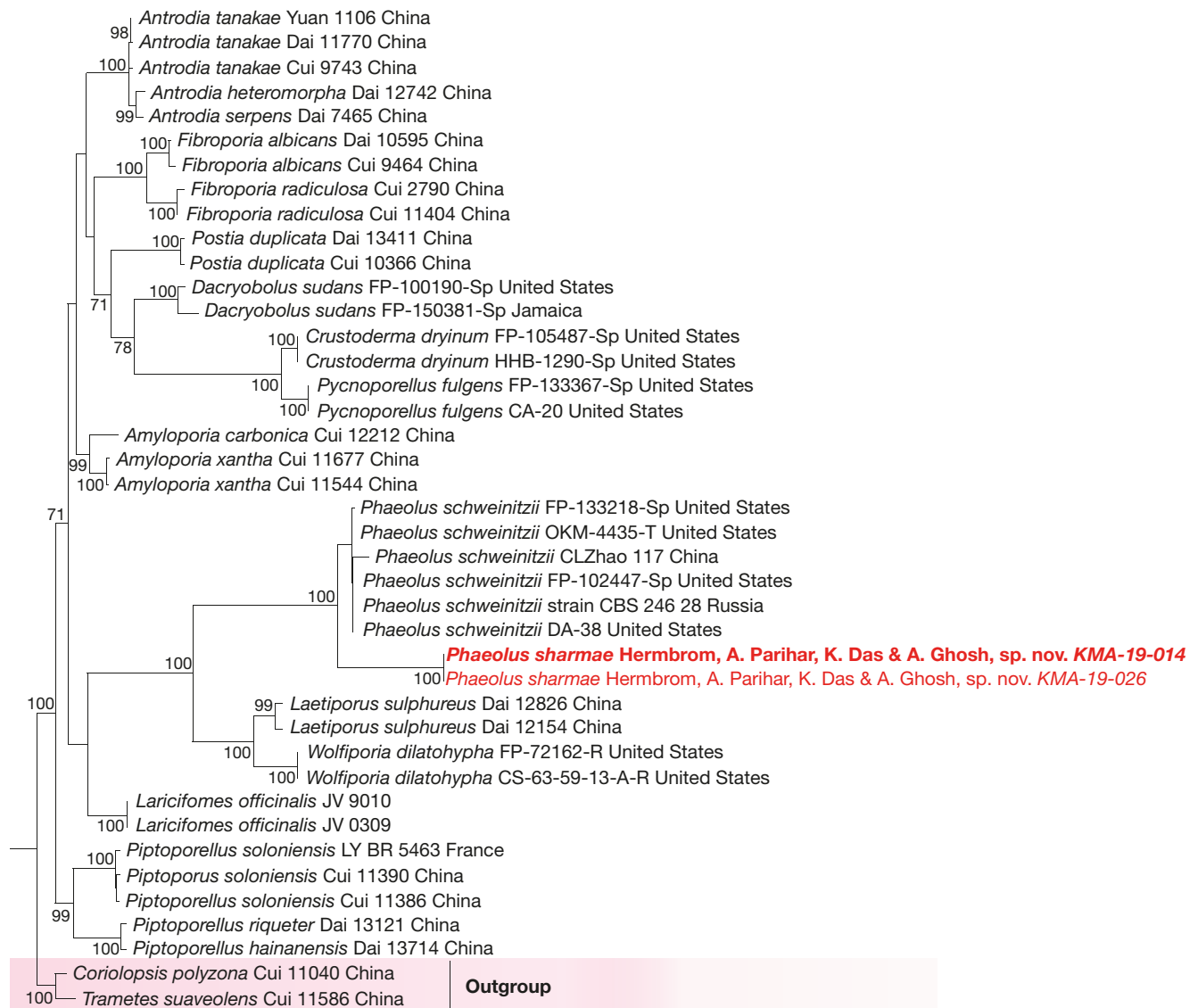


FIG. 13. — A Maximum Likelihood (ML) phylogram inferred from raxmlGUI 2.0 (Edler *et al.* 2021) on a concatenated dataset of nrITS and nrLSU sequence data of *Phaeolus* and related genera. One thousand bootstrap replicates were analyzed to obtain nodal support values. Bootstrap support values (>70 %) obtained from ML analysis are shown above or below the branches at nodes. Two collections of our novel Indian species are shown in red and the holotype in **bold** in the phylogram. See Table 1 for details on used vouchers for the phylogenetic analysis.

### Basidia

16–53 × 7–12 µm, clavate to pedicellate-clavate, thin-walled, smooth, 4-spored; sterigmata 6–8 µm long, hyaline.

### Basidiospores

6–(8.97)–11 × 6–(6.75)–7.8 µm,  $Q = 1$ –(1.32)–1.57, ellipsoid to ovoid, thin-walled, smooth, distinctly apiculate, hyaline, acyanophilic, inamyloid.

### NOTES

During fungal forays to the North district of Sikkim in 2018 and 2019, three of us (KD, MEH and AP) repeatedly came across populations of an unknown species growing on bark of standing trees of *Abies densa*. This species is quite distinct based on phylogenetic analyses including obtained ITS & LSU

sequences that place it sister to *Phaeolus schweinitzii*, a species widely distributed in the northern hemisphere (Gilbertson & Ryvarden 1987; Ryvarden & Gilbertson 1994; Núñez & Ryvarden 2001; Sharma 2012; Prasher 2015).

Within Polyporales, species of *Phaeolus* (Pat.) Pat. are easily confused with various xanthochoric polypores but the genus is phylogenetically distinct and causes a brown rot. Within family Laetiporaceae, *Phaeolus* can be separated from *Laetiporus* Murrill and *Wolfiporia* Ryvarden & Gilb. because these lack gloeoplerous elements. Also *Inonotus hispidus* (Bull.) P. Karst., which lacks hymenial setae and forms lightweight, brittle basidiocarps with a strongly hispid pileus surface and large hymenial pores, may resemble our species in the field. Yet, it equally lacks gloeoplerous elements in context and hymenium.



TABLE 1. — A list of species used in the phylogeny for *Phaeolus*, giving specimen and GenBank accession numbers together with bibliographic references for used sequences.

Species name	Specimen no.	GenBank accession no.		Reference
		nrITS	nrLSU	
<i>Amyloporia carbonica</i>	Cui 12212	KR605816	KR605755	Han <i>et al.</i> 2015
<i>A. xantha</i>	Cui 11544	KR605817	KR605756	Han <i>et al.</i> 2015
<i>A. xantha</i>	Cui 11677	KR605818	KR605757	Han <i>et al.</i> 2015
<i>Antrodia heteromorpha</i>	Dai 12742	KP715319	–	Chen & Cui 2015
<i>A. serpens</i>	Dai 7465	KR605813	KR605752	Han <i>et al.</i> 2015
<i>A. tanakae</i>	Cui 9743	KR605814	KR605753	Han <i>et al.</i> 2015
<i>A. tanakae</i>	Dai 11770	KR605815	KR605754	Han <i>et al.</i> 2015
<i>A. tanakae</i>	Yuan 1160	KP715313	KP715329	Han <i>et al.</i> 2015
<i>Corioloopsis polyzona</i>	Cui 11040	KR605824	KR605767	Han <i>et al.</i> 2015
<i>Crustoderma dryinum</i>	FP-105487-Sp	KC585321	KC585145	Ortiz-Santana <i>et al.</i> 2013
<i>C. dryinum</i>	HBB-1290-Sp	KC585321	KC585146	Ortiz-Santana <i>et al.</i> 2013
<i>Dacryobolus sudans</i>	FP-100190-Sp	KC585332	KC585157	Ortiz-Santana <i>et al.</i> 2013
<i>D. sudans</i>	FP-150381-Sp	KC585333	KC585158	Ortiz-Santana <i>et al.</i> 2013
<i>Fibroporia albicans</i>	Cui 9464	KC456250	KR605758	Chen <i>et al.</i> 2015
<i>F. albicans</i>	Dai 10595	KC456249	KR605759	Chen <i>et al.</i> 2015
<i>F. radiculosa</i>	Cui 2790	KC456248	KR605761	Chen <i>et al.</i> 2015
<i>F. radiculosa</i>	Cui 11404	KP145011	KR605760	Chen <i>et al.</i> 2015
<i>Laetiporus sulphureus</i>	Dai 12154	KF951295	KF951302	Song <i>et al.</i> 2014
<i>L. sulphureus</i>	Dai 12826	KR605819	KR605762	Han <i>et al.</i> 2015
<i>Laricifomes officinalis</i>	JV 0309	KR605821	KR605764	Han <i>et al.</i> 2015
<i>L. officinalis</i>	JV 9010	KR605822	KR605765	Han <i>et al.</i> 2015
<i>Phaeolus schweinitzii</i>	DA-38	EU402585	–	Lindner & Banik 2008
<i>P. schweinitzii</i>	CLZhao 117	MH114833	–	GenBank
<i>P. schweinitzii</i>	CBS 246.28	MH855001	–	GenBank
<i>P. schweinitzii</i>	FP-102447-Sp	KC585368	KC585197	Ortiz-Santana <i>et al.</i> 2013
<i>P. schweinitzii</i>	FP-133218-Sp	KC585369	KC585198	Ortiz-Santana <i>et al.</i> 2013
<i>P. schweinitzii</i>	OKM-4435-T	KC585370	KC585199	Ortiz-Santana <i>et al.</i> 2013
<i>P. sharmae</i> sp. nov.	KMA-19-014	MT762941	MT764209	In this study
<i>P. sharmae</i> sp. nov.	KMA-19-026	MT762940	MT764236	In this study
<i>Piptoporellus soloniensis</i>	Cui 11386	KR605802	KR605741	Han <i>et al.</i> 2015
<i>P. soloniensis</i>	Cui 11390	KR605803	KR605742	Han <i>et al.</i> 2015
<i>P. soloniensis</i>	LY BR 5463	KR605805	KR605744	Han <i>et al.</i> 2015
<i>P. hainanensis</i>	Dai 13714	KR605806	KR605745	Han <i>et al.</i> 2015
<i>P. triqueter</i>	Dai 13121	KR605807	KR605746	Han <i>et al.</i> 2015
<i>Postia duplicata</i>	Cui 10366	KF699124	KJ684975	Shen <i>et al.</i> 2015
<i>P. duplicata</i>	Dai 13411	KF699125	KJ684976	Shen <i>et al.</i> 2015
<i>Pycnoporellus fulgens</i>	CA-20	KC585385	KC585218	Ortiz-Santana <i>et al.</i> 2013
<i>P. fulgens</i>	FP-105487-Sp	KC585386	KC585219	Ortiz-Santana <i>et al.</i> 2013
<i>Wolfiporia dilatohypha</i>	CS-63-59-13-A-R	KC585400	KC585234	Ortiz-Santana <i>et al.</i> 2013
<i>W. dilatohypha</i>	FP-72162-R	EU402556	KC585235	Ortiz-Santana <i>et al.</i> 2013

*Phaeolus* harbours six species, half of these described by Patouillard, from which *P. sharmae* sp. nov. can be distinguished by its combination of having broadly attached basidiomata with rough pilear surface forming irregular papillae, a shiny pinkish orange young hymenophore and larger basidia and basidiospores. Berkley's (1845), Lévillé's (1844) and Patouillard's (1900) descriptions for *P. tabulaeformis* (Berk.) Pat., *P. javanicus* (Pat.) Henn., and the description of *P. rigidus* (Lév.) Pat. lack microscopic details to compare these with our species. Moreover, *P. tabulaeformis* has been considered as synonym of *P. schweinitzii* (Overholts 1953; Bakshi 1971). The African *Phaeolus manihotis* R. Heim has stipitate (6–7 × 3–4 mm) basidiomata and minute basidia (11–14 × 6–8 µm) and smaller spores (5.5–7 × 3.2–4.3 µm) (Heim 1931). The medium sized (up to 60 × 50 × 10 mm), laterally stipitate (40 × 20 mm) basidiomata with whitish yellow context and smaller basidiospores (5–6 × 4–4.3 µm) of *P. amazonica* M. A. De Jesus & Ryvarden (De Jesus & Ryvarden 2010) separate it from our novel species, while

*P. subbulbipes* (Henn.) O. Fidalgo & M. Fidalgo possesses much smaller spores (3.5–4 µm).

In our combined (nrITS+nrLSU) phylogenetic analysis (Fig. 1), our species appeared as sister to the American, European and Asian samples of *P. schweinitzii* (Fr.) Pat. But *P. sharmae* sp. nov. always occupies upper parts of living tree trunks and branches rather than growing on the ground or on bases of trees as found in *P. schweinitzii* (Overholts 1953; Gilbertson & Ryvarden 1987; Zhao & Zhang 1992; Sharma 2012). The distinctly shiny pinkish orange hymenophore that changes on bruising, observed in young specimens of our species, is also worth mentioning, along with its non-decurrent tubes attached to a duplex context, thus clearly distinguishing it from *P. schweinitzii* (Overholts 1953; Ryvarden & Gilbertson 1994; Sharma 2012; Ryvarden & Melo 2014) where context is homogeneous and continuous with tube layer. Microscopically, the larger basidiospores (6–11 × 6–7.8 µm) and basidia (16–53 × 7–12 µm) distinguish our species from *P. schweinitzii* (usually with spores 5.5–9 × 2–5.6 µm and basidia





FIG. 14. — *Phaeolus sharmae* Hembrø, A. Parihar, K. Das & A. Ghosh, sp. nov. (from holotype): **A, B**, habitat; **C**, habit; **D**, gloeoplerous hyphae; **E, G**, cystidia; **H**, basidioles and basidia; **I**, basidiospores. Scale bars: 10  $\mu$ m.



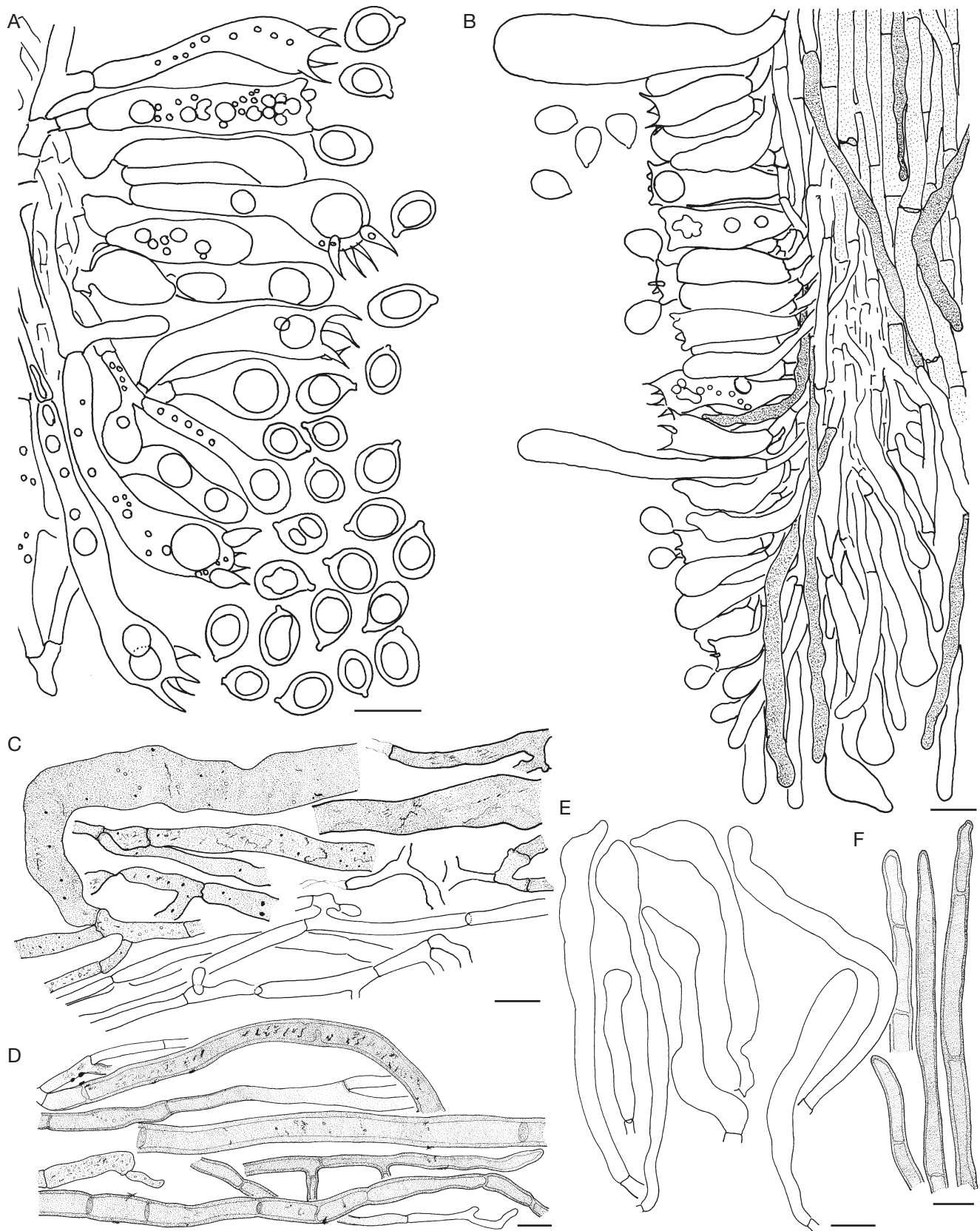


FIG. 15. — *Phaeolus sharmae* Hembrom, A. Parihar, K. Das & A. Ghosh, sp. nov. (holotype): **A**, basidia, basidioles and basidiospores; **B**, section through trama showing gloeoplerous hyphae, basidia, basidioles and cystidia; **C**, hyphae from loose upper part of context; **D**, hyphae adjacent to tube regions of context; **E**, cystidia; **F**, hyphae from pileus surface. Scale bars: 10 µm.



20-30 × 6-8 µm) known from India and abroad (Overholts 1953; Bakshi 1971; Ryvarden & Johansen 1980; Gilbertson & Ryvarden 1987; Zhao & Zhang 1992; Ryvarden & Gilbertson 1994; Sharma 2012; Ryvarden & Melo 2014). Another Indian report of *P. schweinitzii* made by Prasher (2015) from Shimla Himachal Pradesh should be recollected and re-examined under the light of phylogenetic estimations as sizes of basidiospores (6-11.5 × 4-6.8 µm) and clavate basidia (12.4-15.3 × 5-6.8 µm) are deviating from report of similar kind of standard Indian and extralimital materials (Overholts 1953; Bakshi 1971; Ryvarden & Johansen 1980; Gilbertson & Ryvarden 1987; Zhao & Zhang 1992; Ryvarden & Gilbertson 1994; Sharma 2012; Ryvarden & Melo 2014).

### Order RUSSULALES

Kreisel ex P. M. Kirk, P. F. Cannon & J. C. David

Family RUSSULACEAE Lotsy

Genus *Russula* Pers.

#### 118. *Russula ferruginea*

Corrales & Vera, sp. nov.

(Figs 16A; 17-20)

DIAGNOSIS. — *R. ferruginea* sp. nov. differs from the European *R. praetervisa* Sarnari or the North American *R. amerorecondita* Avis & Barajas in the combination of the relatively delicate stature, dark brown pileus centre contrasting to its pale yellowish brown margin, almost mild taste and especially its conspicuous color change from light brown to reddish brown or rusty on wounded places especially apparent on the stipe base and the lamellae. It is defined also by combination of narrow hymenial cystidia up to 8 µm and spores with warts connected by fusions and short fine lines.

HOLOTYPE. — **Colombia**. Cundimarca Depart., Mosquera, Chicaque Natural Reserve, 4°36'22"N, 74°18'17"W, alt. 2130 m, in forest dominated by *Quercus humboldtii*, terrestrial, 17.X.2019, A. Corrales 944 (HUA, SAV).

MYCOBANK. — MB841769.

GENBANK. — [MZ604288](#) (ITS), [MZ604283](#) (nrLSU), [MZ553923](#) (*rpb2*), [MZ553926](#) (*tef1a*), all from holotype.

ETYMOLOGY. — The name refers to reddish spots on the base of the stipe and colour change of the wounded context from light brown to reddish brown, resembling iron rusting.

ADDITIONAL MATERIAL STUDIED. — **Colombia**. Cundimarca Depart., Mosquera, Chicaque Natural Reserve, 4°36'22"N, 74°18'17"W, alt. 2130 m, in forest dominated by *Quercus humboldtii*, terrestrial, multiple collections of different mycelia distant approximately hundred meters apart, 17.X.2019, A. Corrales 914, A. Corrales 935, A. Corrales 1019 (all deposited in HUA).

SPECIMENS STUDIED FOR COMPARISON. — *Russula austromontana* (Singer B 12402 (F), holotype); *Russula cf. austromontana/crucensis*: Costa Rica, 3.5 km W of Empalme, 2200 m asl., in montane *Quercus seemannii* forest, 2.VI.2001, leg. B. Buyck, BB 01.023 (PC); ±5 km SW of Cerro de la Muerte, Albergue de la Montana, Savegre, 2200 m asl., in montane *Quercus seemannii* forest, 6.VI.2001, leg. B. Buyck, BB 01.076 (PC).

### DESCRIPTION

#### *Pileus*

Small to medium sized, 24-48 mm in diam., when young convex, mature plane with depressed centre; margin strongly tuberculate-striate to c. half of the radius (7-13 mm); cuticle slimy especially near the center, shiny, margin peeling or radially cracking, color near margin light brown turning to light yellowish brown or beige, near the center dark brown, deep blackish brown to almost black, discoloring to yellowish brown.

#### *Lamellae*

Moderately distant, c. 8-12/1 cm near the pileus margin, 1.5-4 mm broad, pale yellowish-brownish to almost white, lamellulae rare, furcations frequent especially near the stipe, edge even and concolorous.

#### *Stipe*

28-33 × 5-7.4 mm, cylindrical and straight, longitudinally striate, light brown, darker and with reddish spots at the base, cortex 1-2 mm thick, interior cavernate.

#### *Context*

2-3 mm thick at the middle of the pileus radius, fragile, light brown, flesh turning reddish brown when cut and getting more red spots at the base when bruised, taste slightly bitter and spicy, odour fishy and fetid.

#### *Spore print*

Not observed.

#### *Spores*

(6.4-)6.8-7.5-8.1(-8.6) × (5.4-)5.7-6.2-6.7(-7) µm, subglobose to broadly ellipsoid Q = (1.07-)1.13-1.21-1.28(-1.34); ornamentation of moderately large, moderately distant [(4-7(-8) in a 3 µm diam. circle] amyloid, obtuse warts, (0.3)0.4-0.8(-1) µm high, mainly fused in small groups or short chains ([0-]1-4[-5] fusions in the circle), connected by occasional and usually short line connections ([0-]1-3[-5] in the circle); suprahilar spot not amyloid, relatively large, smooth or covered by few small low warts.

#### *Basidia*

(22-)35-43.7-53 × (5.5-)7-9.2-11(-12) µm, narrowly clavate, occasionally pedunculate, 4-spored; basidiola cylindrical or clavate, c. 5-9 µm wide.

#### *Hymenial cystidia*

Mostly numerous, c. 1800-2100/mm<sup>2</sup>, (50-)56-67.8-79(-86) × 6-7.1-8(-9) µm, mainly fusiform or lanceolate, rarely narrowly lageniform or subcylindrical, apically mainly acute and sometimes pointed, occasionally obtuse, often moniliform, mainly with small, pearl-like, 1-3(-6) µm long appendage, thin-walled; contents weakly heteroformous, with fine, dispersed granulations usually near the apex, sometimes optically empty, often in Congo red with pale yellow pigment, turning almost black in sulfovanillin; near the lamellae edges

smaller, (35-)38-48.4-58(-66) × 6-6.8-8 µm, similar in shape and contents.

#### *Marginal cells*

Similar to basidiola but smaller, (12-)14-17-20(-21) × 5-6.5-7.5 µm, cylindrical or clavate, apically obtuse, mixed with occasional basidia.

#### *Pileipellis*

Orthochromatic in Cresyl Blue, sharply delimited from the underlying context, 150-240 µm deep; suprapellis strongly gelatinized, verrucose-bumpy in vertical section, irregularly 15-35 µm deep, composed of more or less repent, loose or clustered hyphae; gradually passing to 120-220 µm thick subpellis formed by loose, gelatinised, irregularly oriented but near trama horizontally oriented, dense, 2-4 µm wide hyphae.

#### *Acid-resistant incrustations*

Absent.

#### *Hyphal terminations*

Near the pileus margin composed mainly of one or two cells, flexuous, thin walled, frequently branched, occasionally nodulose or angulose; terminal cells (9-)12.5-19.7-27(-34) × 2.5-3.8-5(-5.5) µm, mainly cylindrical or clavate, often apically obtuse and sometimes slightly narrowed; subterminal cells usually as wide as long, frequently branched or with lateral projections. Hyphal terminations near the pileus centre similar, (12-)14-23.8-33(-41) × 3-4.3-5(-6) µm, more frequently angulose-nodulose.

#### *Pileocystidia*

Near the pileus margin always 1-celled, subulate, narrowly fusiform or lanceolate, variable in length and often long and originating deep in the subpellis, thin-walled, (24-)29-40.4-51(-76) × 3-4.2-5 µm, apically mainly acute, with a small appendage or knob; contents dispersed, finely granulous, weakly greying in sulfovanillin. Pileocystidia near the pileus centre similar in shape but usually shorter (22-)28-36.6-42.5(-47) × (3-)3.6-4.4-5.2(-6.5) µm, more frequently apically constricted than acute, with contents located in diverse places, usually in apical parts.

#### *Cystidioid hyphae*

Dispersed in subpellis but more frequent near the context, sometimes similar to cystidia but longer, contents often more conspicuous, oleiferous and turning dark brown in sulfovanillin and red after carbolfuchsin treatment.

#### *Clamp connections*

Absent from all tissues.

#### NOTES

The multilocus phylogenetic reconstruction based on nrLSU, *rpb2* and *tefla* (Fig. 5) clearly places our Colombian and Panamanian collections in one monophyletic clade with strong support values concerning bootstrap (MLbs = 100 %) and

Bayesian posterior probability (BPP = 1). This clade is recognised in this study on the rank of species as *R. ferruginea* sp. nov. It belongs to section *Ingratae* Quél. of the subgenus *Heterophyllidinae* Romagn. The rusty-spotted North American *R. pulverulenta* Peck is the sister species of *R. ferruginea* sp. nov. (MLbs = 61 %, BPP = 0.96), although with poor support. The collection BPL276, labelled as *R. pectinatoides* Peck, is placed on the higher rank node with moderate support (ML = 68, BI = 0.96). In the ITS analyses (see sample with GenBank accession number KT933975 in Fig. 6), however, this collection forms part of the species clade of *R. amerorecondita*.

Because sequence data are not yet available for many species of the section *Ingratae*, our multilocus analysis is undersampled. To trace close relationships and to eliminate coidentity with some taxa published earlier, we analysed also the ITS region based on a set of sequences (Fig. 6) representing the described diversity of American species of the section *Ingratae*. The topology of this tree is not consistent with the topology obtained in the multilocus analyses and good bootstrap support is usually limited to terminal nodes. *Russula ferruginea* sp. nov. is placed in a strongly supported clade on a long branch, but there is no support for a more precise placement within the section *Ingratae*. Colombian and Panamanian collections of the new species received good support (MLbs = 97 % and MLbs = 94 % respectively), but they are recognised on the rank of subspecies as discussed below (see comment under subsp. *panamensis*).

The field appearance of *R. ferruginea* sp. nov. with a relatively fragile stature, dark brown pileus centre contrasting to its pale yellowish brown margin and almost mild taste resembles the European species *R. praetervisa* or the North American *R. amerorecondita*. A remarkable feature of *R. ferruginea* sp. nov. is its conspicuous color change, of the trama becoming reddish brown or rusty on wounded places, especially apparent at the base of the stipe and at the lamellae. This distinct rusty aspect of bruised surfaces is known in several other species of *Ingratae* such as *R. illota* Romagn. or *R. pulverulenta*. With different intensity, however, this color change also occurs in many other species of *Ingratae*.

Among the 78 *Russula* species described from Latin America (Vera *et al.* 2021), only some are known from subtropical and tropical montane oak forests and, among these, four are described from Costa Rica as members of the section *Ingratae*: *R. arcyospora* Singer, *R. austromontana* Singer, *R. cruceensis* Gómez and Alfaro and *R. quercusoleoides* Singer *et al.* *Russula arcyospora* is similar to *R. foetens* Romagn. but has odour components of bitter almond and a prominent spore ornamentation composed of high ridges (Singer 1990). *Russula austromontana* (Singer 1989) is similar to *R. ferruginea* sp. nov., but has broader hymenial cystidia and more prominent spore ornamentation composed of mostly isolated warts, according to our personal (BB) observations of the type. We sequenced two recent collections collected at or near the type locality in Costa Rica with macroscopical and microscopical characteristics similar to the type collection of



TABLE 2. — Vouchers and sequences used for the multilocus phylogenetic analyses. Newly generated sequences are marked in **bold**.

Species	Specimen voucher	Country	nrLSU	rpb2	tef1a
<i>R. aeruginea</i>	AT2003017	Sweden	DQ421999	DQ421946	
<i>R. aff. crustosa</i>	PC0124665	Canada	KU237461	KU237747	KU237896
<i>R. aff. delica</i>	PC0142529	Italy	KU237594	KU237879	KU238020
<i>R. aff. palidospora</i>	PC0142404	Spain	KU237580	KU237866	KU238007
<i>R. aff. virescens</i>	PC0142406	New Caledonia	KU237582	KU237868	KU238009
<i>R. ammophila</i>	46370 (AH)	Spain	—	MK102748	MK102724
<i>R. amoenolens</i>	PC0124771	Italy	KU237562	KU237848	—
<i>R. cf. annulata</i>	PC0124641	Madagascar	KU237470	KU237756	KU237902
<i>R. atroglaucia</i>	SAV F-20375	Sweden	MT738250	MT732158	—
<i>R. aff. brunneoannulata</i>	PC0124638	Madagascar	KU237452	KU237738	KU237887
<i>R. cerolens</i>	UBC:F30282	Canada	KX812865	KX813648	KX813617
<i>R. columbicolor</i>	2010BT108A	Germany	JN389003	JN375606	—
<i>R. cyanoxantha</i>	UPS: UE29.09.2002-2	France	DQ422033	DQ421970	—
<i>R. elastica</i>	PC0124636	Madagascar	KU237451	KU237737	—
<b><i>R. ferruginea</i> subsp. <i>ferruginea</i> subsp. nov.</b>	<b>HUA (Corrales935)</b>	<b>Colombia</b>	<b>MZ604284</b>	—	—
<b><i>R. ferruginea</i> subsp. <i>ferruginea</i> subsp. nov.</b>	<b>HUA (Corrales1019)</b>	<b>Colombia</b>	<b>MZ604286</b>	—	—
<b><i>R. ferruginea</i> subsp. <i>ferruginea</i> subsp. nov.</b>	<b>HUA (Corrales944)</b>	<b>Colombia</b>	<b>MZ604283</b>	<b>MZ553923</b>	<b>MZ553926</b>
<b><i>R. ferruginea</i> subsp. <i>ferruginea</i> subsp. nov.</b>	<b>HUA (Corrales914)</b>	<b>Colombia</b>	<b>MZ604285</b>	<b>MZ553924</b>	<b>MZ553927</b>
<b><i>R. ferruginea</i> subsp. <i>panamensis</i> subsp. nov.</b>	<b>UCH (A28)</b>	<b>Panama</b>	<b>MZ604287</b>	<b>MZ553925</b>	<b>MZ553928</b>
<i>R. flavobrunnea</i> var. <i>violaceotincta</i>	PC0124643	Madagascar	KU237468	KU237754	KU237901
<i>R. floriformis</i>	Corrales943	Colombia	MT023729	MT02175	—
<i>R. foetens</i>	GENT:FH-12-277	Germany	KT933877	KT933948	—
<i>R. granulata</i>	TENN:067622	United States	KT933832	KT933903	—
<i>R. grisea</i>	PC0124678	Slovakia	KU237509	KU237795	KU237939
<i>R. herrerae</i>	PC0124763	Mexico	KU237486	KU237772	KU237915
<i>R. heterophylla</i>	UPS: UE20.08.2004-2	Sweden	DQ422006	DQ421951	—
<i>R. ilicis</i>	PC0142534	Italy	KU237595	KU237880	KU238021
<i>R. cf. illota</i>	PC0124650	Mexico	KU237464	KU237750	KU237898
<i>R. ionochlora</i>	PC0124712	Slovakia	KU237508	KU237794	KU237938
<i>R. langei</i>	PC0124720	France	KU237510	KU237796	KU237940
<i>R. aff. laurocerasi</i>	PC0124663	Canada	KU237458	KU237744	KU237893
<i>R. madagassensis</i>	PC0142535	Madagascar	KU237456	KU237742	KU237891
<i>R. aff. madecassensis</i>	PC0124647	Madagascar	KU237475	KU237761	KU237906
<i>R. maguaensis</i>	XHW4765	China	MH714537	MH939989	MH939983
<i>R. mariae</i>	PC0124668	United States	KU237538	KU237824	KU237968
<i>R. medullata</i>	PC0124690	Slovakia	KU237546	KU237832	KU237976
<i>R. mustelina</i>	PC0142537	Slovakia	KU237596	KU237881	KU238022
<i>R. ochrospora</i>	UPS: Donelli20.07.2004	Italy	DQ422012	DQ421953	—
<i>R. oleifera</i>	PC0124730	Tanzania	KU237490	KU237776	KU237919
<i>R. orientipurpurea</i>	HCCN18725	South Korea	KF361810	KF361710	—
<i>R. ornateps</i>	PC0124733	Mexico	KU237466	KU237752	—
<i>R. parazurea</i>	UPS: MF01.10.2003	Sweden	DQ422007	DQ421944	—
<i>R. pectinatoides</i>	TENN:067626	United States	KT933836	KT933907	—
<i>R. prolifica</i>	PC0124781	Madagascar	KU237455	KU237741	KU237890
<i>R. cf. pseudocarmesina</i>	PC0124639	Madagascar	KU237453	KU237739	—
<i>R. "pseudociliata"</i>	PC0124721	Madagascar	KU237537	KU237823	KU237967
<i>R. cf. pseudolepida</i>	TENN:067297	United States	KT933821	KT933892	—
<i>R. pulverulenta</i>	PC0124777	United States	KU237563	KU237849	—
<i>R. redolens</i>	TENN:067593	United States (TN)	KT933825	KT933897	—
<i>R. redolens</i>	TENN:069923	United States (TN)	KT933808	KT933879	—
<i>R. cf. roseoalba</i>	PC0124645	Madagascar	KU237472	KU237758	—
<i>R. substriata</i>	XHW4766	China	MH714540	MH939992	MH939986
<i>R. tsokae</i>	KD-KVP1283	India	JN389006	JN375608	—
<i>R. variata</i>	TENN:067302	United States (TN)	KT933818	KT933889	—
<i>R. vesca</i>	PC0124658	Mexico	KU237465	KU237751	KU237899
<i>R. violeipes</i>	PC0124694	Slovakia	KU237534	KU237820	KU237964
<i>Russula</i> sp.	170722Z7	China	MK748175	MK764531	MK764523
<i>Russula</i> sp.	180808C23	China	MK748169	MK764525	MK764518

*R. austromontana*. These specimens proved to be unrelated to *R. ferruginea* sp. nov. in our phylogeny. *Russula crucensis*, originally classified in sect. *Pelliculariae* R. Heim subsect. *Discopodinae* R. Heim, is another member of the section *Ingratae* (Buyck 1992) and differs from *R. ferruginea* sp. nov. exactly in the same features as *R. austromontana*, from which

it is difficult to distinguish at this moment. *R. quercusoleoideis* was originally placed in sect. *Ingratae* (Singer *et al.* 1983), but according to Buyck (1992) it is a member of subsect. *Griseinae* Jul. Schäff. and both, pileipellis structure and hymenial cystidia, are different from the corresponding structures in *R. ferruginea* sp. nov.



FIG. 16. — Basidiomata of *Russula ferruginea* Corrales & Vera, sp. nov. **A**, basidiomata of *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, subsp. nov. in the field (HUA Corrales935); **B**, **C**, basidiomata of *Russula ferruginea* subsp. *panamensis* Corrales & Vera, subsp. nov. in the field (ARIZ Corrales099); **D**, basidiomata of *Russula ferruginea* subsp. *panamensis* Corrales & Vera, subsp. nov. (UCH Anna Gießel A28). Scale bars: 1 cm.



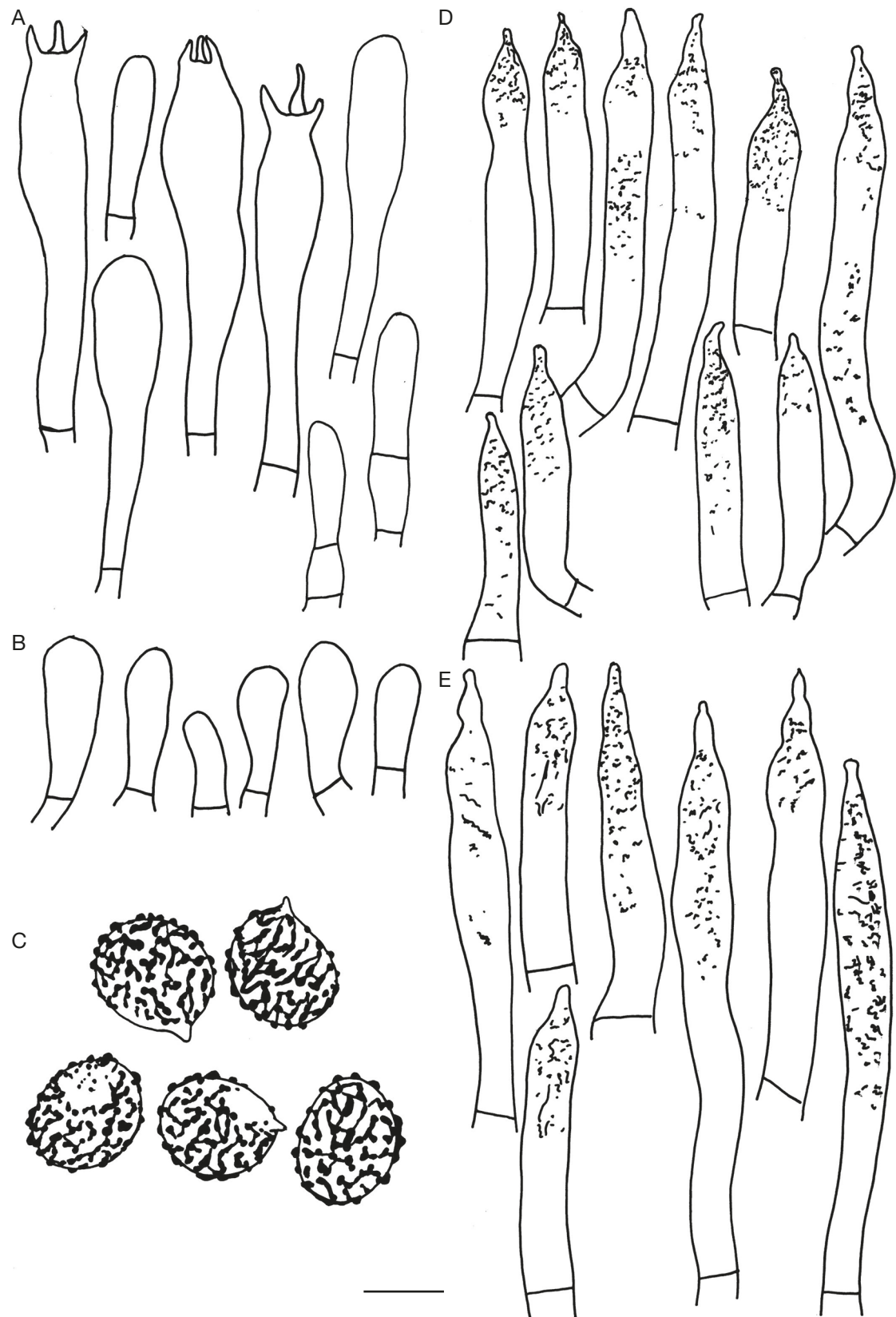


FIG. 17. — *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, subsp. nov. (HUA Corrales 944, holotype). Elements of the hymenium drawn as seen by light microscopy. **A**, basidia and basidiola; **B**, marginal cells near the edges of lamellae; **C**, basidiospores in Melzer's reagent; **D**, hymenial cystidia near the edges of lamellae; **E**, hymenial cystidia on the sides of lamellae. Cystidia with contents as observed in Congo Red. Scale bars: A, B, D, E, 10 µm; C, 5 µm. Drawings by Michelle Vera.

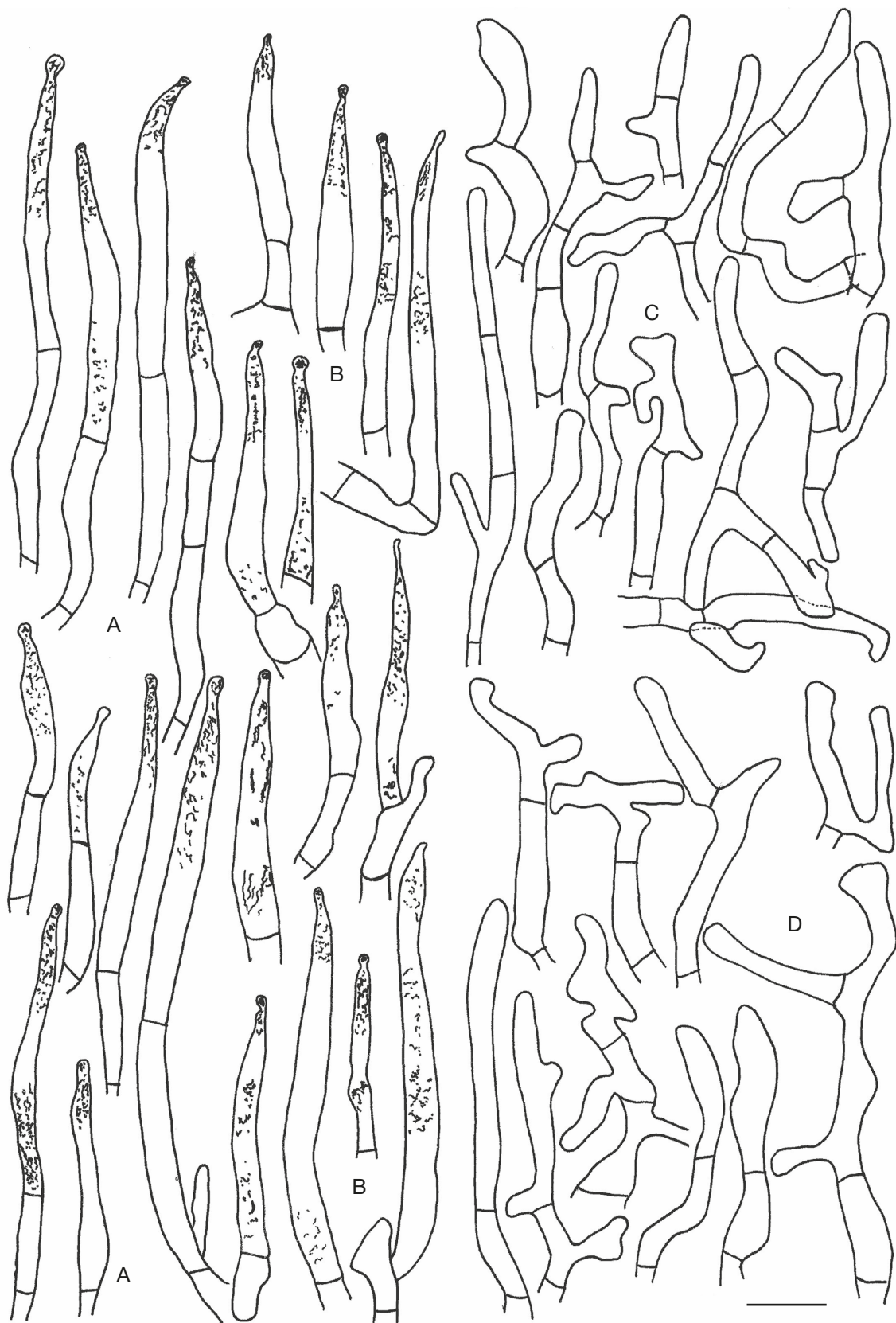


FIG. 18. — *Russula ferruginea* subsp. *ferruginea* Corrales & Vera, subsp. nov. (HUA Corrales 944, holotype). Elements of the pileipellis drawn as seen by light microscopy. **A**, pileocystidia near the pileus margin; **B**, pileocystidia near the pileus center; **C**, hyphal terminations near the pileus margin; **D**, hyphal terminations near the pileus center. Cystidia with contents as observed in Congo Red. Scale bar: 10  $\mu$ m. Drawings by Michelle Vera.



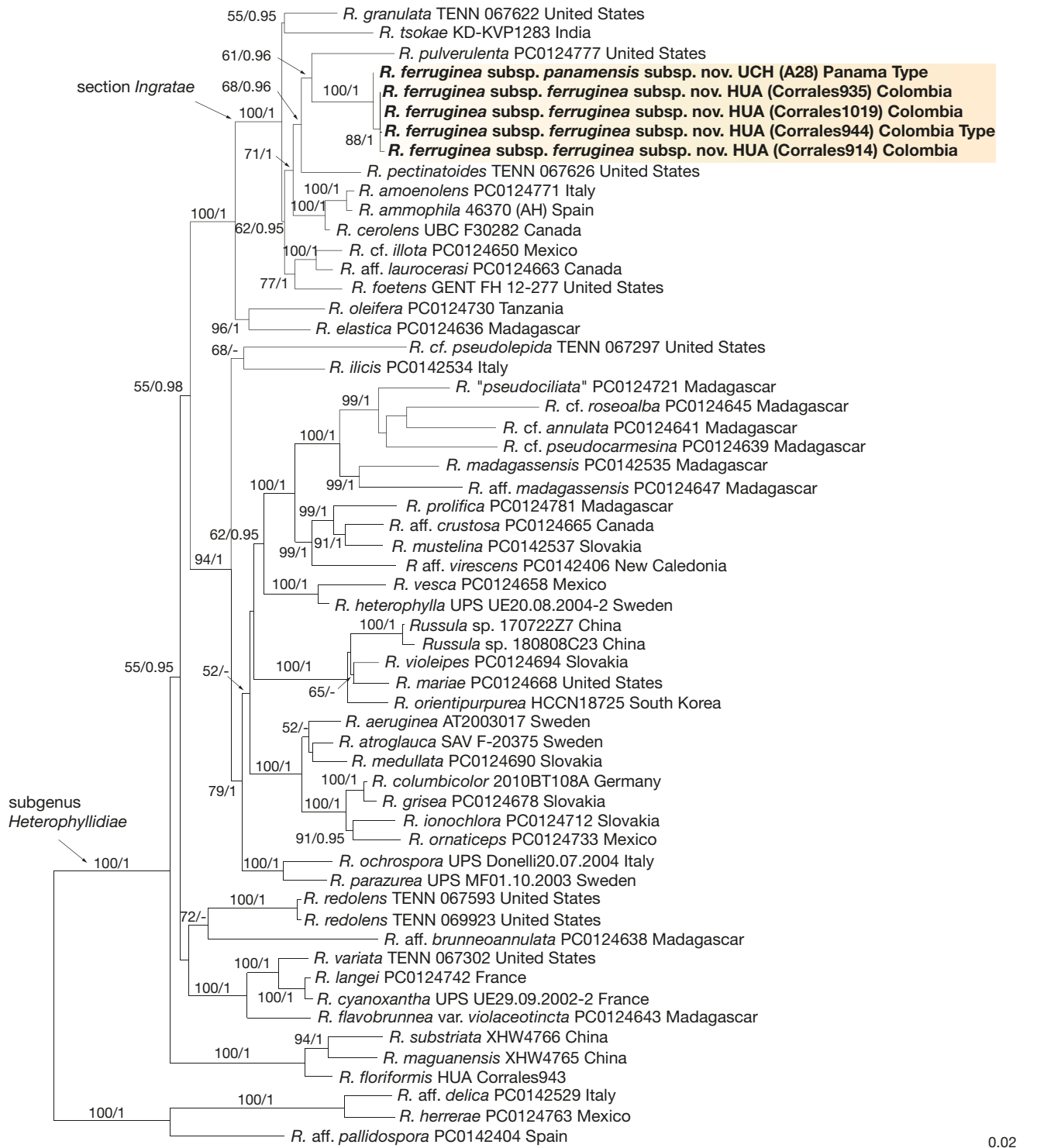


FIG. 19. — Maximum likelihood (ML) tree of *Russula* subgenus *Heterophyllidia* based on combined sequence data of nrLSU, *rpb2* and *tef1a*. Bootstrap values from ML analysis  $\geq 50\%$  and Posterior probabilities from Bayesian inference (BPP)  $\geq 0.95$  are shown at branch nodes. The newly generated sequences of *R. ferruginea* sp. nov. are highlighted in **boldface** and on coloured background. Data of sequences used for the tree are listed in Table 2. Protocols for DNA extraction, PCR and sequencing followed Vera *et al.* (2021). Sequences were edited in the BioEdit 7.2.5 sequence alignment editor (Hall 2013) and Geneious R10 (Kearse *et al.* 2012). Intra-individual polymorphic sites having more than one signal were marked with NC-IUPAC ambiguity codes. The datasets were aligned in MAFFT 7 using the E-INS-i strategy (Katoh & Standley 2013) and manually improved in Geneious R10 (Kearse *et al.* 2012). Divergent and ambiguously aligned positions in the nrLSU were removed with Gblocks (Castresana 2000) using the least stringent parameters. Intronic positions of *rpb2* and *tef1a* were manually removed. For the BI analysis, the data set was divided into five partitions: 28S, the 1st+2nd, and 3rd codon positions of *tef1*, the 1st+2nd, and 3rd codon positions of *rpb2*. The best substitution model for each partition was computed jointly in PartitionFinder 1.1.1 (Lanfear *et al.* 2012). BI runs were computed twice in MrBayes 3.2.6 (Ronquist *et al.* 2012) with four Markov chain Monte Carlo (MCMC) chains for 10 million iterations until the standard deviation of split frequencies fell below the 0.01 threshold. Convergence of runs was visually assessed using the trace function in Tracer 1.6 (Rambaut *et al.* 2013). For the ML analysis, the concatenated alignment was loaded as a fasta file to CIPRES Science Gateway (Miller *et al.* 2010) and analyzed using RAXML-HPC2 on XSEDE (8.2.12) as a partitioned data set (as in the BI analysis) under the GTR+GAMMA model with 1000 bootstrap iterations as recommended by the RAXML user manual (Stamatakis 2014).

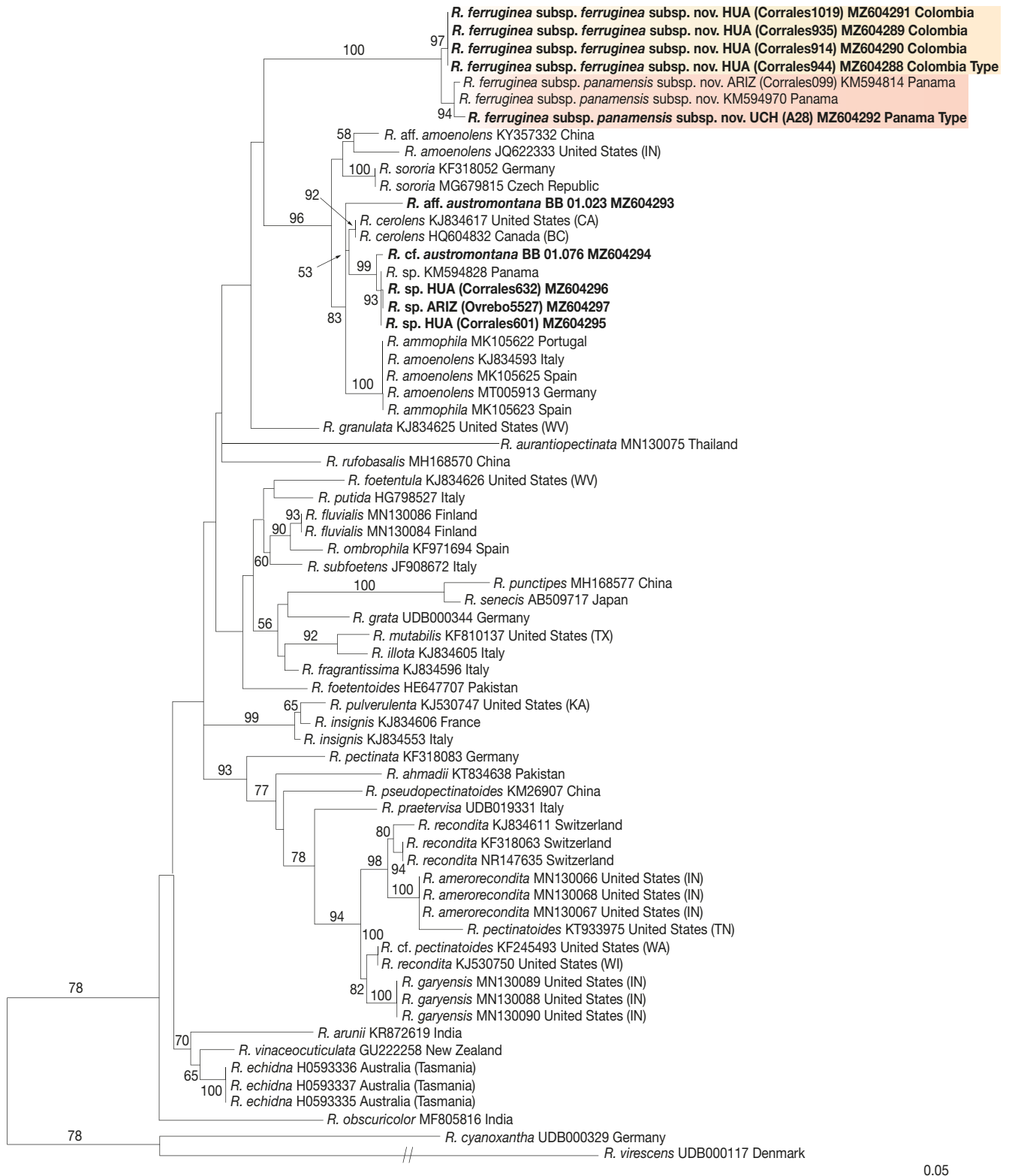


FIG. 20. — Maximum likelihood tree of *Russula* sect. *Ingratae* based on sequence data of the ITS region. The newly generated sequences are in **boldface**, two subspecies of *R. ferruginea* sp. nov. are highlighted by different colour backgrounds. Names of taxa are followed by GenBank accession numbers and country of origin of samples, newly generated sequences are annotated with collection numbers. Protocols for DNA extraction, PCR and sequencing followed Vera *et al.* (2021). Sequences were edited in the BioEdit 7.2.5 sequence alignment editor (Hall 2013) and Geneious R10 (Kearse *et al.* 2012). The data set was analyzed on the CIPRES Science Gateway (Miller *et al.* 2010) under the GTR+GAMMA model with 1000 bootstrap iterations (Stamatakis 2014).



119. *Russula ferruginea* subsp. *panamensis*

Corrales &amp; Manz, subsp. nov.

(Figs 16B-D; 19-22)

DIAGNOSIS. — *Russula ferruginea* subsp. *panamensis* Corrales & Manz, subsp. nov. differs from Colombian subsp. *ferruginea* Corrales & Vera, subsp. nov. by terminal cells of hyphae in the pileipellis that are not occasionally to frequently inflated close to their bases, they are shorter on average and slightly narrower. These differences are most evident near the centre of the pileus, where average values of Colombian terminal cells are  $18.5\text{--}32 \times 4.1\text{--}4.6 \mu\text{m}$  and of Panamanian ones  $13.5\text{--}15.5 \times 3.4\text{--}3.5 \mu\text{m}$ .

HOLOTYPE. — **Panama**. Chiriquí province, Quebrada Honda watershed, Fortuna forest reserve,  $80^{\circ}45'09.4''\text{N}$ ,  $82^{\circ}14'23.6''\text{W}$ , 1191 m asl., associated with *Oreomunnea mexicana*, *Quercus* sp., 19.XII.2012, Anna Gießel & Meike Piepenbring A28 (UCH, PMA).

MYCOBANK. — MB841771.

GENBANK. — MZ604292 (holotype).

ETYMOLOGY. — Referring to the distribution area of the subspecies, which is so far only known from Panama.

ADDITIONAL MATERIAL STUDIED. — **Panama**. Chiriquí province, Zarcadero site near Bocas del Toro Road, Fortuna Forest Reserve,  $8^{\circ}45'24''\text{N}$ ,  $82^{\circ}16'47''\text{W}$ , alt. 1000 m, in forest dominated by *Oreomunnea mexicana*, terrestrial, 19.IV.2012, A. Corrales 099 (ARIZ).

## DESCRIPTION

*Pileus*

Small to medium sized, 45–46 mm in diam., when mature plane with depressed centre; margin strongly tuberculate-striate to *c.* half of the radius; cuticle near centre shiny when wet, rugulose, near margin radially cracking, color near margin light brown turning to light yellowish brown or beige, near the center dark grey-brown, deep blackish brown to almost black.

*Lamellae*

Moderately distant, up to 4 mm broad, pale cream-white, lamellulae and furcations occasional, edge even and concolorous.

*Stipe*

$35 \times 7$  mm, cylindrical, longitudinally striate, near lamellae greyish white, towards base light brown, with darker reddish-brown spots at the base, interior hollow.

*Context*

2 mm thick at the middle of the pileus radius, fragile, greyish brown, flesh turning reddish brown when cut and getting more red spots at the base when bruised, taste and odour not observed.

*Spore print*

White.

*Spores*

$(6.8\text{--})7.1\text{--}7.4\text{--}7.7\text{--}(8.2) \times (5.3\text{--})5.6\text{--}6.4\text{--}(6.8) \mu\text{m}$ , mainly broadly ellipsoid,  $Q = (1.09\text{--})1.18\text{--}1.24\text{--}1.29\text{--}(1.4)$ ; ornamentation of moderately large, dense [(4-)6-8 in a  $3 \mu\text{m}$  diam. circle] amyloid, low, obtuse warts,  $(0.3\text{--})0.5\text{--}0.8\text{--}(0.9) \mu\text{m}$

high, fused in pairs or short chains [(0-)1-4 fusions in the circle], connected by occasional to frequent line connections [(0-)1-3 in the circle], isolated warts absent; suprahilar spot not amyloid, smooth, relatively large.

*Basidia*

$(29\text{--})32\text{--}35.4\text{--}39\text{--}(45) \times (5.5\text{--})7.5\text{--}8.9\text{--}10\text{--}(11) \mu\text{m}$ , fusiform or clavate, 4-spored; basidiola first cylindrical or ellipsoid, then clavate, *c.*  $5\text{--}9 \mu\text{m}$  wide.

*Hymenial cystidia*

Numerous, *c.*  $1800\text{--}2400/\text{mm}^2$ ,  $(37\text{--})54\text{--}63.7\text{--}74\text{--}(90) \times (5.5\text{--})6.5\text{--}7.7\text{--}9\text{--}(11) \mu\text{m}$ , mainly fusiform or lanceolate, pedunculate, apically acute, with 1–6  $\mu\text{m}$  long appendage, thin-walled, often originating deeply in the subhymenium; contents almost homogenous, yellowish, with few faint dispersed granulations, turning dark brown in sulfovanillin; near the edges of lamellae smaller,  $(30\text{--})32.5\text{--}40.3\text{--}48\text{--}(64) \times 5\text{--}6.4\text{--}7\text{--}(8.5) \mu\text{m}$ , clavate, rarely lanceolate or fusiform, acute, occasionally also apically obtuse, apically with small, 1–3  $\mu\text{m}$  long appendage.

*Marginal cells*

$(7\text{--})10\text{--}13.1\text{--}16\text{--}(19) \times 4\text{--}5.9\text{--}7\text{--}(8.5) \mu\text{m}$ , similar to basidiola but shorter, occasionally mixed with some basidia.

*Pileipellis*

Orthochromatic in Cresyl Blue, sharply delimited from the underlying context, 70–130  $\mu\text{m}$  deep; suprapellis very thin, up to 30  $\mu\text{m}$  deep, near margin disrupted and absent on some parts, composed of more or less horizontally oriented or repent and sometimes clustered hyphae; vaguely delimited from the thick, gelatinized subpellis formed by loose, irregularly oriented, 2–4  $\mu\text{m}$  wide hyphae, that are denser and horizontally oriented near the trama.

*Acid-resistant incrustations*

Absent.

*Hyphal terminations*

Near the pileus margin loose or in dispersed clusters, composed of one or two cells, thin walled; terminal cells  $(8\text{--})10\text{--}15.8\text{--}21\text{--}(31) \times 2.5\text{--}3.4\text{--}4\text{--}(5) \mu\text{m}$ , mainly cylindrical, occasionally clavate, apically obtuse; subterminal cells branched or not, of constant width and usually as long as wide. Hyphal terminations near the pileus centre similar, terminal cells  $(6\text{--})10\text{--}14.6\text{--}19\text{--}(28) \times (2\text{--})2.5\text{--}3.4\text{--}4\text{--}(5) \mu\text{m}$ , frequently distinctly flexuous-nodulose.

*Pileocystidia*

Near the pileus margin dispersed, always 1-celled, mainly subulate, occasionally fusiform or lanceolate, thin-walled,  $(21\text{--})32\text{--}60.9\text{--}89\text{--}(165) \times (3\text{--})3.5\text{--}4.6\text{--}5.5\text{--}(6) \mu\text{m}$ , apically acute-pointed, mostly with a 1–2  $\mu\text{m}$  long, pearl-like appendage; contents slightly yellowish with indistinct granulations, hardly reacting in sulfovanillin. Pileocystidia near the pileus centre relatively frequent,  $(20\text{--})23\text{--}30.7\text{--}40\text{--}(65.5) \times (3\text{--})3.5\text{--}4.5\text{--}5.5\text{--}(7) \mu\text{m}$ , usually subulate or lageniform, otherwise similar to those near the margin of the pileus.

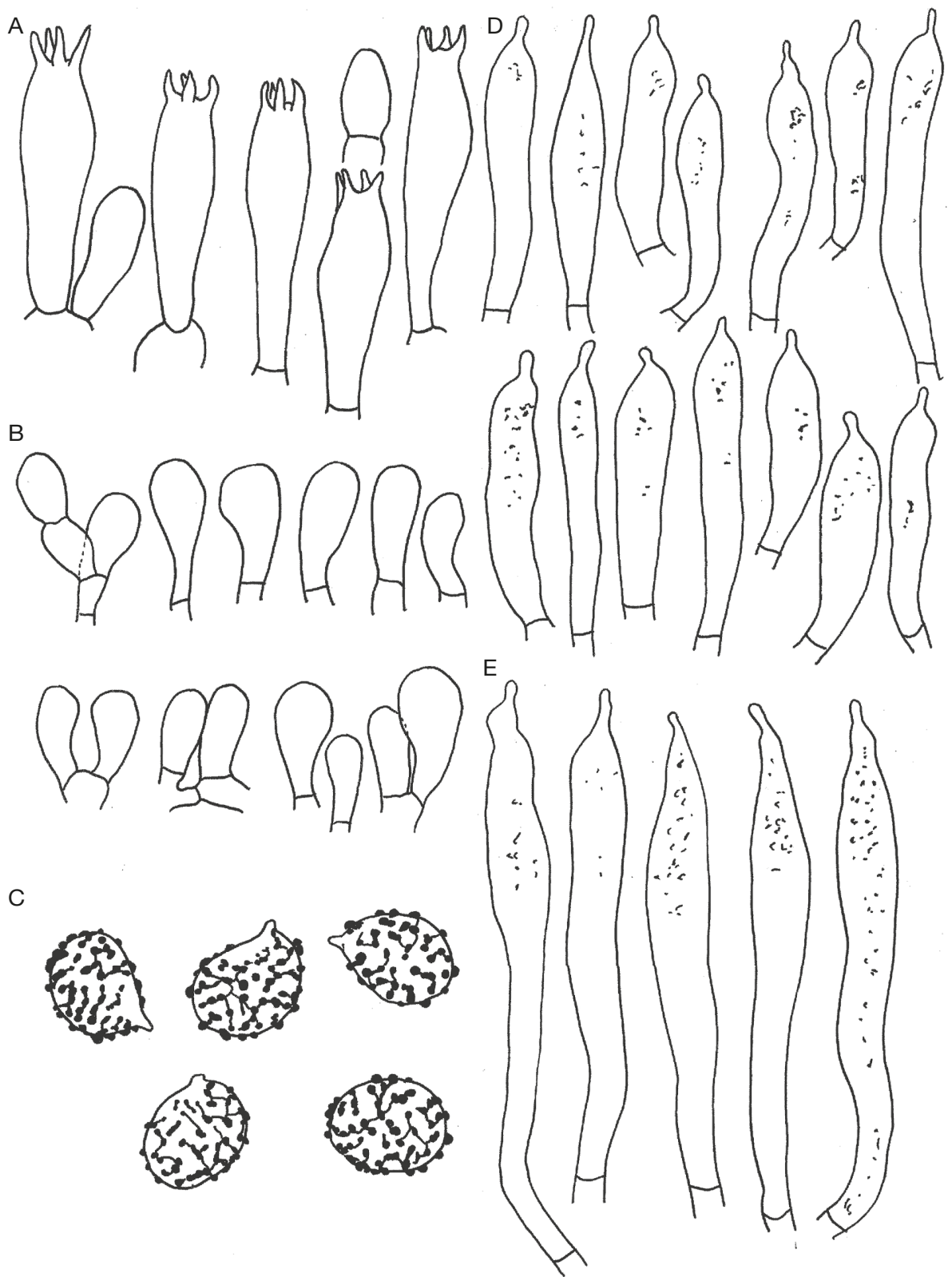


FIG. 21. — *Russula ferruginea* subsp. *panamensis* Corrales & Manz, subsp. nov. (ARIZ Corrales 99, holotype). Elements of the hymenium drawn as seen by light microscopy. **A**, basidia and basidiola; **B**, marginal cells near the edges of lamellae; **C**, basidiospores in Melzer's reagent; **D**, hymenial cystidia near the edges of lamellae; **E**, hymenial cystidia on the sides of lamellae. Cystidia with contents as observed in Congo Red. Scale bar: A, B, D, E, 10  $\mu$ m; C, 5  $\mu$ m. Drawings by Michelle Vera.

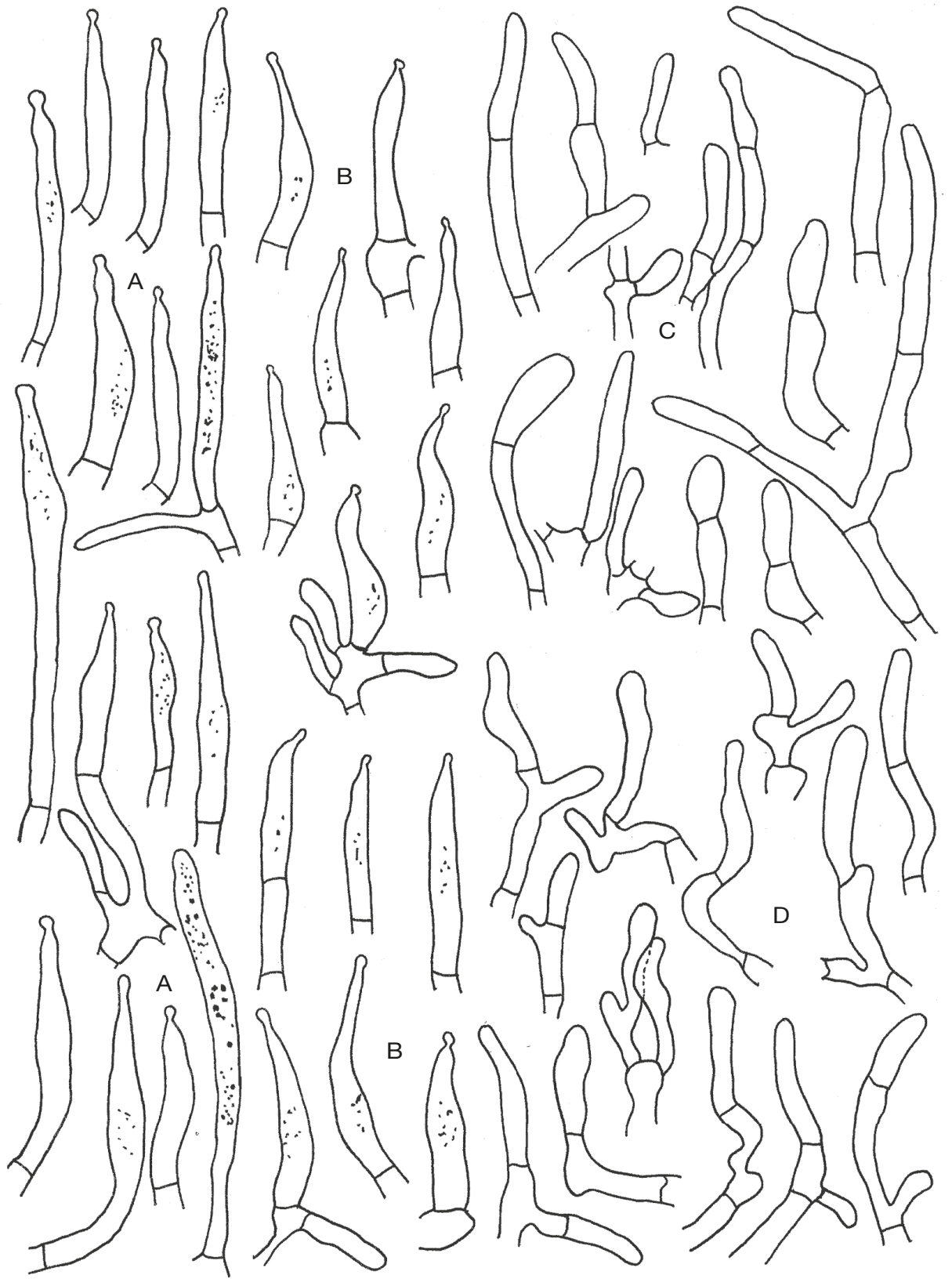


FIG. 22. — *Russula ferruginea* subsp. *panamensis* Corrales & Manz, subsp. nov. (ARIZ Corrales 99, holotype). Elements of the pileipellis drawn as seen by light microscopy. **A**, pileocystidia near the margin of the pileus; **B**, pileocystidia near the center of the pileus; **C**, hyphal terminations near the margin of the pileus; **D**, hyphal terminations near the center of the pileus. Cystidia with contents as observed in Congo Red. Scale bar: 10  $\mu$ m. Drawings by Michelle Vera.



### *Cystidioid hyphae*

Dispersed in subpellis but more frequent near the context, sometimes similar to cystidia but longer, contents often more conspicuous, oleiferous and turning dark brown in sulfovanillin and red after carbolfuchsin treatment.

### *Clamp connections*

Absent from all tissues.

### NOTES

The Colombian collections described here as *R. ferruginea* sp. nov. are very similar to the Panamanian collections ARIZ (Corrales 99) and UCH (A28). We were unable to find any differences in the field, but this might be caused by the lack of details in field descriptions of the Panamanian samples. Under the microscope, Colombian collections have terminal cells of hyphae in the pileipellis occasionally to frequently inflated near bases that are on average longer and also slightly wider than terminal cells in the pileipellis of Panamanian collections. These differences are especially apparent near the pileus centre, where average values of Colombian terminal cells are  $18.5\text{--}32 \times 4.1\text{--}4.6 \mu\text{m}$  and of Panamanian ones are  $13.5\text{--}15.5 \times 3.4\text{--}3.5 \mu\text{m}$ . Our multi-loci analysis shows support to distinguish the Panamanian samples as different taxa from the Colombian samples but this was not supported by the individual gene analysis of LSU or *rpb2*. The fixed nucleotide differences between them are three in ITS, five in coding parts of *tefla* and three in *rpb2* region. Because of few morphological differences and very close phylogenetic proximity, we decided to follow the criteria used by Vera *et al.* (2021) and assign the rank of subspecies to populations of *R. ferruginea* sp. nov. separated by the disjunction at the Isthmus of Panama. The clade of *R. ferruginea* subsp. *panamensis* subsp. nov. based on sequences of the ITS region (Fig. 6) also includes the sequence KM594970, that was obtained from an ectomycorrhizal root tip of *Oreomunnea mexicana* from Panama (Corrales *et al.* 2016).

Order CORTICIALES K. H. Larss  
Family VUILLEMINIACEAE Maire  
Genus *Vuilleminia* Maire

### 120. *Vuilleminia tropica*

Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov.  
(Figs 23–25)

**DIAGNOSIS.** — Differs from other species because of its tropical distribution, lemon yellow hymenophore delimited by a white floccose margin when actively growing and its erumpent nature with a tendency to grow on bark of dead wood, further also by the smaller basidiospores ( $11\text{--}16 \times 5\text{--}8 \mu\text{m}$ ), basidia ( $45\text{--}75 \times 7\text{--}9 \mu\text{m}$ ) and rare dendrohyphidia in the hymenium, the thin- to distinctly thick-walled generative hyphae with clamped septae.

**HOLOTYPE.** — India, Jharkhand, Rajmahal hills, Sahibganj district, Brindaban Panchayat, Joshkuti, on dead fallen branch of *Bauhinia vahili* Wight & Arn., 63 m,  $25^{\circ}01'50.9''\text{N}$ ,  $87^{\circ}42'17.2''\text{E}$ , 29.VIII.2013, *M. E. Hembrom*, MEH-70133 (holo-, CAL[CAL1845]!).

MYCOBANK. — MB840192.

GENBANK. — MZ314343 (nrITS, holotype), MZ314344 (nrITS, paratype); MZ314347 (nrLSU, holotype), MZ314346 (nrLSU, paratype).

**ETYMOLOGY.** — *Tropica* (Lat.) refers to the tropical distribution of the taxon.

**ADDITIONAL MATERIAL STUDIED.** — India, Bihar, Valmiki National Park, West Champaran district, Valmiki Nagar, on the fallen branch (un-barked wood) of *Shorea robusta* Gaertn.,  $27^{\circ}26'26.1''\text{N}$ ,  $83^{\circ}56'10.4''\text{E}$ , 141 m, 2019, *M. E. Hembrom*, MEH-19; West Bengal, Howrah district, AJCBIBG, Div.: VIII near Kyd monument, on dead branch of *Psidium guajava* L., 5 m,  $22^{\circ}33'25.4''\text{N}$ ,  $88^{\circ}17'30.1''\text{E}$ , 30.VII.2020, *M. E. Hembrom*, KMA-20-26; Bihar, West Champaran, Valmiki National Park, Ganouli Forest Range, on the decorticated log of unidentified tree, 180 m,  $27^{\circ}22'33.6''\text{N}$ ,  $83^{\circ}59'38.5''\text{E}$ , 01.VIII.2020, *A. V. Kisku*, MEH-20-50 (CAL1846).

### DESCRIPTION

#### *Basidiomata*

Annual, widely effused ( $5\text{--}200 \times 5\text{--}100 \text{ mm}$  or even much larger), up to 0.3 mm thick, growing on bark and more or less separable when fresh, but becoming closely adnate when dried, initially starting to form as small round patches with white margin that quickly merge to form large, effused, crusty basidiomata, leathery and slightly sticky when fresh, brittle and waxy on drying. Margin up to 1 mm wide when actively growing, distinct to indeterminate in older specimens, sterile, floccose, chalky-white (1-2A1) to pale yellow (3A3).

#### *Hymenophore*

Smooth, glabrous, pale yellow to pastel yellow (3A3–4) when young then yellow to lemon yellow (3B5–8), becoming bright yellow to almost egg yellow at maturity, finally ochraceous in older dried specimens.

#### *Flesh*

Papery thin, waxy, yellowish white (1-2A2).

#### *Hyphal system*

Monomitic, generative hyphae septate, clamped at most septa, thin- to moderately thick-walled, branched, with smooth, hyaline, acyanophilic walls (but contents cyanophilic) and not amyloid.

#### *Subhymenium & subiculum*

Composed of compactly arranged vertical elements ending with indistinct subiculum with crystal elements; basal hyphae  $3\text{--}5 \mu\text{m}$  wide, thin to moderately thick-walled, loosely interwoven, cytoplasmic contents cyanophilic; hyphae in the middle part  $2\text{--}4 \mu\text{m}$  wide, towards subhymenium less interwoven and less branched, more or less parallel, thin-walled.

#### *Hymenium*

Composed of hyphoid elements, rare delicate dendrohyphidia, basidia and basidioles; hyphoid elements  $30\text{--}45 \times 3\text{--}4 \mu\text{m}$ ,

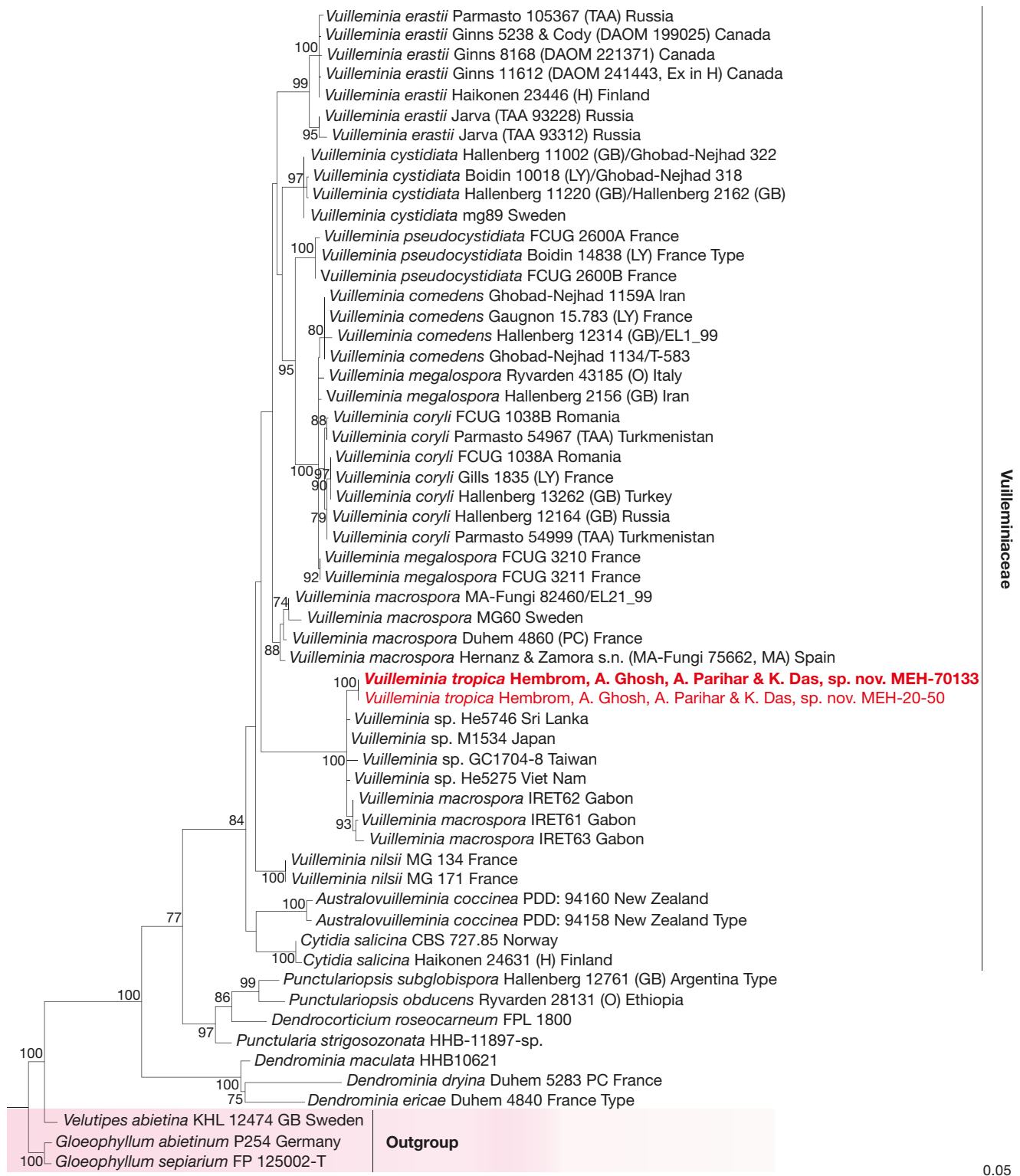


FIG. 23. — A Maximum Likelihood (ML) phylogram inferred from raxmlGUI 2.0 (Edler *et al.* 2021) on a concatenated dataset of nrITS and nrLSU sequence data of *Vuilleminia* and related genera. One thousand bootstrap replicates were analyzed to obtain nodal support values. Bootstrap support values (>70 %) obtained from ML analysis are shown above or below the branches at nodes. Two collections of our novel Indian species are shown in red and the holotype in **bold** in the phylogram. See Table 3 for details on used vouchers for the phylogenetic analysis.

embedded to projecting up to 16  $\mu\text{m}$  beyond the hymenium, cylindrical, smooth. Dendrohyphidia often difficult to observe,

up to 2  $\mu\text{m}$  wide, less branched, thin-walled, smooth, hyaline. Basidia 45–75  $\times$  7–9  $\mu\text{m}$ , clavate to elongated cylindri-

TABLE 3. — Species used in the molecular analyses, voucher data and their GenBank (ITS and LSU) accession numbers. Numbers in **bold** were generated for this study.

Species name	Voucher specimen/isolate/strain	GenBank accession no.		Reference
		nrITS	nrLSU	
<i>Australovuilleminia coccinea</i>	PDD: 94158	HM046875	HM046930	Ghobad-Nejhad & Duhem 2013
<i>A. coccinea</i>	PDD: 94160	HM046876	HM046931	Ghobad-Nejhad & Duhem 2013
<i>Cytidia salicina</i>	CBS 727.85	—	DQ915478	Ghobad-Nejhad & Duhem 2013
<i>C. salicina</i>	Haikonen 24631 (H)	GU590881	HM046921	Ghobad-Nejhad & Duhem 2013
<i>Dendrocorticium roseocarneau</i>	FPL1800	—	AF393053	Ghobad-Nejhad & Duhem 2013
<i>Dendrominia dryina</i>	Duhem 5283 (PC)	JX892936	JX892937	Ghobad-Nejhad & Duhem 2013
<i>D. ericae</i>	Duhem 4840	JX892938	JX892939	Ghobad-Nejhad & Duhem 2013
<i>D. maculata</i>	HHB10621	—	AY586652	Ghobad-Nejhad & Duhem 2013
<i>Gloeophyllum abietinum</i>	P254	—	AJ583431	Ghobad-Nejhad & Duhem 2013
<i>G. sepiarium</i>	FP 125002-T	—	AY333806	Ghobad-Nejhad & Duhem 2013
<i>Punctularia strigosozonata</i>	HHB-11897-sp.	—	AF518642	Ghobad-Nejhad & Duhem 2013
<i>Punctulariopsis obducens</i>	Ryvarden 28131 (O)	HM046918	HM046933	Ghobad-Nejhad & Duhem 2013
<i>P. subglobispora</i>	Hallenberg 12761 (GB)	HM046917	HM046932	Ghobad-Nejhad & Duhem 2013
<i>Veluticeps abietina</i>	KHL 12474 GB	—	EU118619	Ghobad-Nejhad & Duhem 2013
<i>Vuilleminia comedens</i>	Ghobad-Nejhad 1134/T-583	HM046882	AF518666	Ghobad-Nejhad & Duhem 2013
<i>V. comedens</i>	Gaugnon 15.783 (LY)	HM046891	—	Ghobad-Nejhad & Duhem 2013
<i>V. comedens</i>	Hallenberg 12314 (GB)/EL1_99	HM046898	AY586725	Ghobad-Nejhad & Duhem 2013
<i>V. comedens</i>	Ghobad-Nejhad 1159A	HM046880	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	Hallenberg 13262 (GB)	HM046908	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	FCUG 1038A	HM046903	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	Gills 1835 (LY)	HM046901	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	Hallenberg 12164 (GB)	HM046906	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	Parmasto 54967 (TAA)	JN387995	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	FCUG 1038B	HM046904	—	Ghobad-Nejhad & Duhem 2013
<i>V. coryli</i>	Parmasto 54999 (TAA)	JN387996	JN388005	Ghobad-Nejhad & Duhem 2013
<i>V. cystidiata</i>	Boidin 10018 (LY)/Ghobad-Nejhad 318	HM046909	HM046923	Ghobad-Nejhad & Duhem 2013
<i>V. cystidiata</i>	Hallenberg 11002 (GB)/Ghobad-Nejhad 322	HM046911	HM046924	Ghobad-Nejhad & Duhem 2013
<i>V. cystidiata</i>	Hallenberg 11220 (GB)/Hallenberg 2162 (GB)	HM046912	HM046925	Ghobad-Nejhad & Duhem 2013
<i>V. cystidiata</i>	mg89	—	HM100715	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	Jarva (TAA 93312)	JN387997	JN388006	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	GINNS 5238 & Cody (DAOM 199025)	JN387998	JN388007	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	Haikonen 23446 (H)	JN387999	JN388008	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	GINNS 8168 (DAOM 221371)	JN388000	JN388009	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	Parmasto 105367 (TAA)	JN388001	—	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	Jarva (TAA 93228)	JN388002	—	Ghobad-Nejhad & Duhem 2013
<i>V. erastii</i>	GINNS 11612 (DAOM 241443, Ex in H)	JN388003	JN388010	Ghobad-Nejhad & Duhem 2013
<i>V. macrospora</i>	MG60	HM046885	HM046927	Ghobad-Nejhad & Duhem 2013
<i>V. macrospora</i>	Duhem 4860 (PC)	JX892940	JX892941	Ghobad-Nejhad & Duhem 2013
<i>V. macrospora</i>	Hernanz & Zamora s.n. (MA-Fungi 75662, MA)	JX892942	JX892943	Ghobad-Nejhad & Duhem 2013
<i>V. macrospora</i>	MA-Fungi 82460/EL21_99	JX892944	AY586726	Ghobad-Nejhad & Duhem 2013
<i>V. macrospora</i>	IRET61	KY449402	—	GenBank
<i>V. macrospora</i>	IRET62	KY449403	—	GenBank
<i>V. macrospora</i>	IRET63	KY449404	—	GenBank
<i>V. megalospora</i>	FCUG 3210	HM046913	—	Ghobad-Nejhad & Duhem 2013
<i>V. megalospora</i>	FCUG 3211	HM046914	—	Ghobad-Nejhad & Duhem 2013
<i>V. megalospora</i>	Hallenberg 2156 (GB)	HM046886	—	Ghobad-Nejhad & Duhem 2013
<i>V. megalospora</i>	Ryvarden 43185 (O)	HM046887	—	Ghobad-Nejhad & Duhem 2013
<i>V. nilsii</i>	MG134	JX892945	JX892946	Ghobad-Nejhad & Duhem 2013
<i>V. nilsii</i>	MG171	JX892947	JX892948	Ghobad-Nejhad & Duhem 2013
<i>V. pseudocystidiata</i>	FCUG 2600A	HM046915	—	Ghobad-Nejhad & Duhem 2013
<i>V. pseudocystidiata</i>	FCUG 2600B	HM046916	—	Ghobad-Nejhad & Duhem 2013
<i>V. pseudocystidiata</i>	Boidin 14838 (LY)	HM046888	HM046928	Ghobad-Nejhad & Duhem 2013
<i>V. sp.</i>	GC1704-8	MK874059	—	GenBank
<i>V. sp.</i>	He5275	MK874057	—	GenBank
<i>V. sp.</i>	He5746	MK874058	—	GenBank
<i>V. sp.</i>	M1534	LC327047	LC322152	GenBank
<b><i>V. tropica</i> sp. nov.</b>	<b>MEH-70133</b>	<b>MZ314343</b>	<b>MZ314347</b>	<b>In this study</b>
<b><i>V. tropica</i> sp. nov.</b>	<b>MEH-20-50</b>	<b>MZ314344</b>	<b>MZ314346</b>	<b>In this study</b>

cal, 4-sterigmate with sterigmata 3-10 × 1-3 µm, clamped at base with clamps often delicate and difficult to observe, thin-walled, when young filled with dense and globular contents, becoming empty and collapsed with maturity, smooth, hyaline, when older with occasionally transverse septa.

#### Basidiospores

11-13.6-16 × 5-6.35-8 µm, Q = 1.7-2.15-2.76, cylindrical to narrowly ellipsoid, moderately thick-walled with walls up to 1 µm thick, smooth, hyaline and acyanophilic; contents cyanophilic, inamyloid.



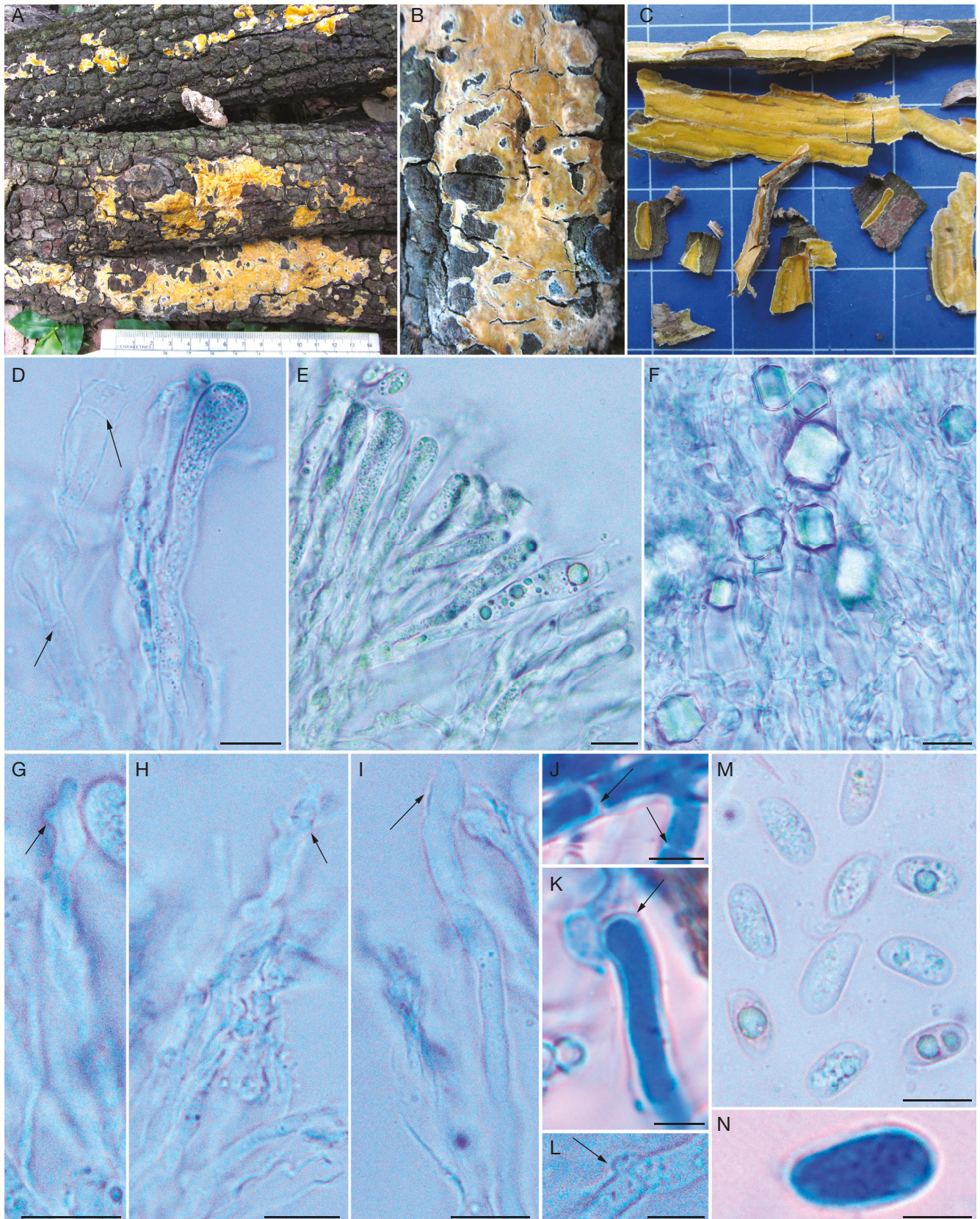


FIG. 24. — *Vuilleminia tropica* Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov. (from holotype): **A, B**, basidiomata showing decorticate tendency of growth on bark; **C**, habit; **D**, basidiomata filled with dense globules in cytoplasm and empty septate basidia; **E**, section through hymenium showing basidia, basidioles and hyphidia; **F**, indistinct subiculum with crystalline contents; **G, H**, dendrohyphidia; **I**, hyphidia; **J**, septate, moderately thick-walled hyphae in indistinct subiculum; **K**, clamped moderately thick-walled hyphae with cyanophilic cytoplasmic contents; **L**, delicate thin-walled clamped hyphae; **M**, basidiospores in phloxine; **N**, basidiospore in cotton blue showing thick-wall and cyanophilic cytoplasmic contents. Scale bars: D-I, M, 10  $\mu$ m; J-L, N, 5  $\mu$ m.



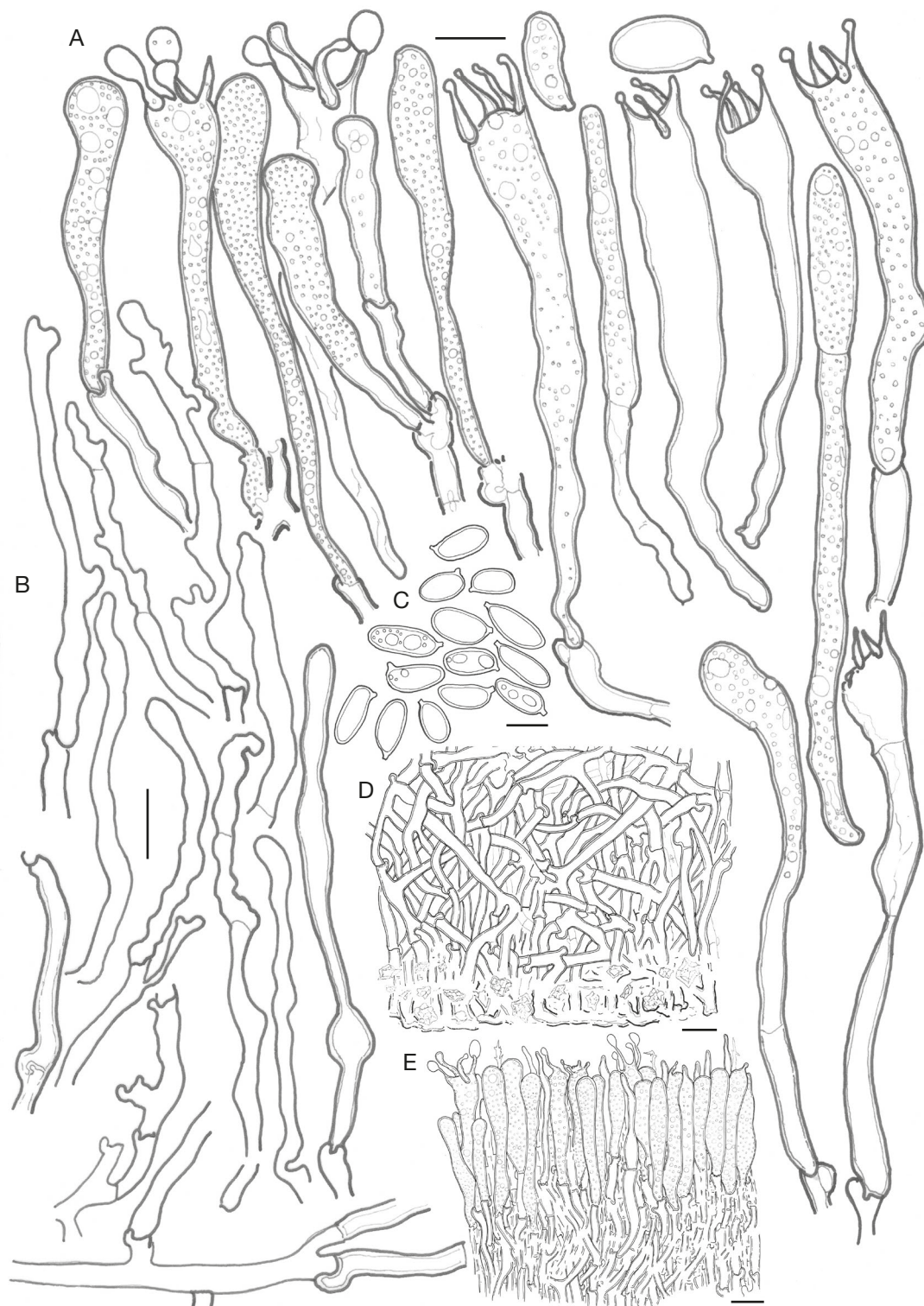


FIG. 25. — *Vuilleminia tropica* Hembrom, A. Ghosh, A. Parihar & K. Das, sp. nov. (holotype): **A**, basidia and basidioles; **B**, dendrohyphidia, hyphidia and thin to thick-walled hyphae; **C**, thick-walled basidiospores; **D**, part of indistinct subiculum below subhymenial layer; **E**, section through hymenium and subhymenium. Scale bars: 10  $\mu$ m.

## NOTES

*Vuilleminia* Maire is mostly confined to Europe with few exceptions (Bernicchia & Gorjón 2010; Ghobad-Nejhad *et al.* 2010). Very recently, one of us (MEH) came across some

specimens in eastern tropical India growing on bark as well as invading the xylem vessels below the bark. Morphological features and molecular phylogeny place these specimens

in the genus *Vuilleminia*, but none of the described species matches the present collections.

The genus *Vuilleminia* fits the morphological features of our species, including the gelatinous (when fresh) to ceraceous basidiomata with monomitic hyphal system and clamped hyphae, pedicellate-clavate basidia producing large basidiospores and presence of dendrohyphidia (Hjortstam *et al.* 1988; Bernicchia & Gorjón 2010; Ghobad-Nejhad *et al.* 2010; Ghobad-Nejhad & Duhem 2013).

Growing in the tropics and forming basidiomata (up to 300 µm thick) with lemon yellow hymenial surface and whitish floccose margin on fallen wooden logs, make it easy to identify our species in the field. The more or less thick-walled basidiospores with cyanophilic cytoplasmic contents are unrecorded from other *Vuilleminia*, viz. *V. alni* Boidin, Lanq. & Gilles; *V. comedens* (Nees) Maire; *V. corticola* Parmasto, *V. coryli* Boidin, Lanq. & Gilles; *V. cystidiata* Parmasto; *V. erastii* Ghob.-Nejh., *V. macrospora* (Bres.) Hjortstam; *V. megalospora* Bres.; *V. nilsii* Ghob.-Nejh. & Duhem, *V. oyensis* Duhem & M. Gérard, and *V. pseudocystidiata* Boidin, Lanq. & Gilles. (Hjortstam *et al.* 1988; Gorjón 2009; Bernicchia & Gorjón 2010; Ghobad-Nejhad *et al.* 2010, 2012; Ghobad-Nejhad & Duhem 2013). Many *Vuilleminia* have numerous dendrohyphidia, but in the present species dendrohyphidia are very few and become difficult to trace in older specimens and usually lack any side branching.

Our phylogeny places this novel species sister to *V. macrospora*, which differs morphologically in its white basidiomata with abundant dendrohyphidia, and capitate, thick-walled, tubular cystidia, and it also has a temperate distribution (Bernicchia & Gorjón 2010; Ghobad-Nejhad *et al.* 2010). *Vuilleminia nilsii* shares the creamish to yellowish white hymenial surface and basidiospores with cyanophilic contents (Ghobad-Nejhad & Duhem 2013), but its spores are thin-walled and longer (14.5–18 µm).

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