

Three new species of *Psilocybe* (Strophariaceae, Basidiomycota) from Papua New Guinea

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Three new species of *Psilocybe* (Strophariaceae, Basidiomycota) from Papua New Guinea. *Sydowia* 58 (1): 3 – 14.

Three new species of *Psilocybe* (*Ps. fibrillosipes*, *Ps. megacystis*, *Ps. simplex*) collected in tropical-montane, broadleaf rain forests in Papua New Guinea are fully described, illustrated and discussed. A key is provided to identify the 8 species so far recorded from Papua New Guinea.

Key words: Basidiomycetes, fungal systematics, taxonomy, mycogeography.

The first report relating to Papua New Guinean species of *Psilocybe* was published by Heim (1967). In search of psychoactive mushrooms Heim discovered that the Waghi people in the Western Highlands traditionally use the blueing basidiomes of *Ps. kumaenorum* as drug prompting hallucinations due to the content of psilocibine (Thomas 2006a). The second and last contribution to the knowledge of Papuan representatives of *Psilocybe* was published by Guzmán & Horak (1979). In the present paper the following three additional new taxa of Papuan *Psilocybe* are presented viz. *Psilocybe brunneocystidiata*, *Ps. inconspicua*, and *Ps. nothofagensis*.

Based upon the macrocharacters of the non-blueing basidiomes the first three afore-mentioned species are expected to be devoid of psychoactive compounds. It is open to question, however, whether the olive-green but also non-blueing basidiomes of *Ps. papuana* actually contain psilocibines (Thomas 2006a, b).

Material and Methods

All specimens examined were originally collected and documented by E. Horak. – For microscopical analysis, the material was routinely mounted in 3 – 5 % KOH (and occasionally also in 1 % Congo Red in 5 % KOH). Holotypus or isotype material is kept in Herbarium ZT (Zurich, Switzerland) and XAL (Xalapa, Mexico).

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Key to Papuan species of *Psilocybe*

1. Basidiomes distinctly blueing (upon bruising or in old specimens). Pileus 5–7 mm, conical to campanulate, brown to purplish brown. Stipe 15–30 × 1.5–2 mm, cylindrical, equal or subbulbous at base, white to pale brown, covered with pale grey or lilac fibrils of veil. Distinctive cortina or annulus absent. Basidiospores 6.5–8 × 3.5–4.5 µm, ellipsoid in face view and side view, thin-walled. Cheilocystidia 11–17 × 3–3.5 µm, fusoid or lageniform. On soil among grass. 1. *Ps. kumaenorum*
- 1*. Basidiomes not blueing (upon bruising or in old specimens). 2
2. (1). Pileus conical or with distinctive conical papilla. 3
- 2*. Pileus convex, umbonate, campanulate or expanded-subdepressed in centre, ochre-brown or dark brown, veil remnants absent. Pleurocystidia absent. Odor and taste not distinctive. 6
3. (2). Pileus conical, 10–20 mm, deep olive to green-black. Lamellae often with purplish tinge, staining greenish when bruised. Stipe 35–50 × 1–1.5 mm, cylindrical, pale to dark brown, covered with white fibrils of veil, cortina or annulus absent. Odor and taste not distinctive. Basidiospores 5.5–7 × 4.5–6 × 4–4.5 µm, subrhombic in face view, amygdaliform in side view, thick-walled. Cheilocystidia 10–20 × 6–10 µm, vesiculate or broadly fusoid. On soil or among litter in tropical-montane broadleaf rain forest (dominated by *Castanopsis*, *Lithocarpus*, *Nothofagus*), 1000–2400 m a.s.l. 2. *Ps. papuana*
- 3*. Pileus with distinctive, acute and prominent papilla, yellow-brown or orange-brown. Distinctive, persistent cortina or annulus present or absent. Pleurocystidia present, pale brown or hyaline. Basidiospores thin-walled. 4
4. (3). Basidiospores in face view distinctly rhomboid, 5–6.5 × 5–6 × 3.5 µm. Pileus 10–40 mm, ochre to yellow-brown, with scattered white floccose veil remnants. Stipe 10–40 × 1–2 mm, cylindrical, with white, persistent, fibrillose to submembranaceous cortina. Odor and taste weakly farinaceous. Cheilocystidia 15–25(–30) × 4–5 µm, fusoid. Pleurocystidia 20–30 × 8–10 µm, fusoid with distinctive apical rostrate knob, hyaline or pale brown. On rotten wood in tropical-montane broadleaf rain forest (dominated by *Castanopsis*, *Nothofagus*), 500–2000 m alt. 3. *Psilocybe brunneocystidiata*
- 4*. Basidiospores ellipsoid, both in face view and side view. Odor and taste not distinctive. Pleurocystidia hyaline. 5
5. (4). Basidiospores 4.5–5(–5.5) × 3–3.5 µm. Pleurocystidia 25–45 × 12–18 (–20) µm, broadly utriform, thin-walled. Pileus 10–

- 25 mm, yellow-brown to brown, veil remnants absent. Stipe 20–45 × 1.5–3 mm, densely covered with white fibrils from veil, cortina or annulus absent. On rotten wood in tropical-montane broadleaf rain forest (dominated by *Castanopsis*, *Lithocarpus*), 1100 m alt. 4. *Psilocybe fibrillosipes*
- 5*. Basidiospores 7–8 × 4–4.5 µm. Pleurocystidia 50–80 × 8–12 µm, slender lageniform, upper portion occasionally thick-walled. Pileus 10–45 mm, young specimens with appendiculate, pale ochre veil remnants on margin. Stipe 25–50 × 2–4 mm, young specimens with distinctive, fibrillose, non-persistent, pale ochre cortina. On rotten wood/bark in tropical-montane broadleaf rain forest (dominated by *Nothofagus*, *Castanopsis*, *Lithocarpus*), 2300 m alt. 5. *Psilocybe megacystis*
6. (2). Basidiomes rather robust. Pileus 20–45 mm, convex, centre depressed in old specimens. Stipe 20–40 × 2–3 mm, with persistent fibrillose or submembranaceous cortina, towards base densely covered with appressed, white fibrils from veil. Basidiospores 6–8 × 4–5 µm, ovoid in face view. Cheilocystidia 25–35 × 5–8 µm, fusoid. On rotten wood/bark in tropical-montane broadleaf rain forest (dominated by *Castanopsis-Lithocarpus* and rarely *Nothofagus* sp.), 2600 m alt. 6. *Psilocybe simplex*
- 6*. Basidiomes delicate. Pileus < 10 mm diam., convex, umbonate or campanulate. Stipe 10–25 × 0.5–1 mm. Basidiospores subrhomboid in face view, < 6 µm long. 7
7. (6). Pileus fuscous. Lamellae fuscous to deep chocolate brown. Veil remnants on stipe absent. Cheilocystidia 15–30 × 4.5–7 µm, slender fusoid. On rotten, moss-covered wood/bark in tropical-montane broadleaf rain forest (dominated by *Nothofagus*). 7. *Psilocybe nothofagensis*
- 7*. Pileus ochre to pale ochre-brown. Lamellae argillaceous. Stipe covered with white, fibrillose, non-persistent veil remnants. Cheilocystidia 20–30 × 7–14 µm, broadly fusoid or vesiculose. On soil among litter in tropical-montane conifer forest (dominated by *Araucaria cunninghamii*), 1100 m alt. 8. *Psilocybe inconspicua*

Enumeration and description of new and known Papuan species of *Psilocybe*

1. *Psilocybe kumaenorum* R. Heim, Revue de Mycologie 32: 206. 1967.

For full description and illustrations, cf. Heim (1967). In Papua New Guinea *Psilocybe kumaenorum* is the only representative of

Psilocybe with blueing basidiomes. Chemical analysis of recently collected specimens revealed that the basidiomes actually contain psilocybine and accordingly its psychoactive properties originally claimed by Heim have now been proven (Thomas 2006a).

2. *Psilocybe papuana* Guzmán & E. Horak, Sydowia 31: 49. 1979.

For full description and illustrations, cf. Guzmán & E. Horak (1979).

3. *Psilocybe brunneocystidiata* Guzmán & E. Horak, Sydowia 31: 45. 1979.

For full description and illustrations, cf. Guzmán & E. Horak (1979).

4. *Psilocybe fibrillosipes* E. Horak, sp. nov. – Fig. 1: 1 – 6

Pileus 10–25 mm, persistenter conicus, luteobrunneus vel brunneus, hygrophanus, conspicue translucide striatus, siccus, velo nullo instructus. Lamellae adnatae vel subdecurrentes, argillaceae dein argillaceobrunneae. Stipes 20–45 × 1.5–3 mm, cylindricus, aequalis vel subattenuatus, ad apicem pileo concolor, basin versus fuscus vel nigrobrunneus, cortina fugacea, basim versus fibrillis albis e velo persistenter obtectus, siccus, cavus, solitarius vel fasciculatus. Caro fusca in stipite, tenax. Odor saporque nulli. Basidiosporae in cumulo brunneae, 4.5–5 (–5.5) × 3–3.5 µm, ovoideae vel leniter amygdaliformes, leves, pallide brunneae, poro germinativo instructae. Basidia 15–20 × 3–4.5 µm, 4-sporigera. Cheilocystidia polymorphica, clavatofusoidea (20–35 × 8–11 µm) vel fusioideolageniformia (30–45 × 4–9 µm), tenuitunicata, hyalina. Pleurocystidia 25–45 × 12–18 (–20) µm, obtuse fusioidea vel utriformia, tenuitunicata. Caulocystidia polymorphica, rara. Pileipellis ex hyphis cylindratis cutem formantibus, cellulis terminalibus distinctis instructis, membrana haud gelatinosa, tenuitunicata, e pigmento brunneo distincte incrustatis. Fibulae praesentes. Ad lignum putridum in silvis montanis fagaceis tropicalibusque. Holotypus. – Papua New Guinea, leg. E. Horak 73–207 (ZT).

Pileus 10–25 mm, in young and old specimens with distinctive, conical to sharply pointed papilla, strongly translucent-striate margin incurved, yellow-brown to dark brown if moist, strongly hygrophanous, pale ochre-brown upon drying, dry, smooth, veil remnants absent. – Lamellae 28–36 reaching stipe, lamellulae in 3–7 series, densely crowded, broadly adnate, often subdecurrent with short tooth, up to 2.5 mm wide, at first argillaceous brown gradually turning beige–brown, fimbriate edges whitish. – Stipe 20–45 × 1.5–3 mm, cylindrical, equal or gradually becoming broader towards base, upper portion concolorous with lamellae, fuscous or black-brown in lower portion, fibrillose cortina fugaceous, but with distinctive persistent white appressed fibrils towards base, with short

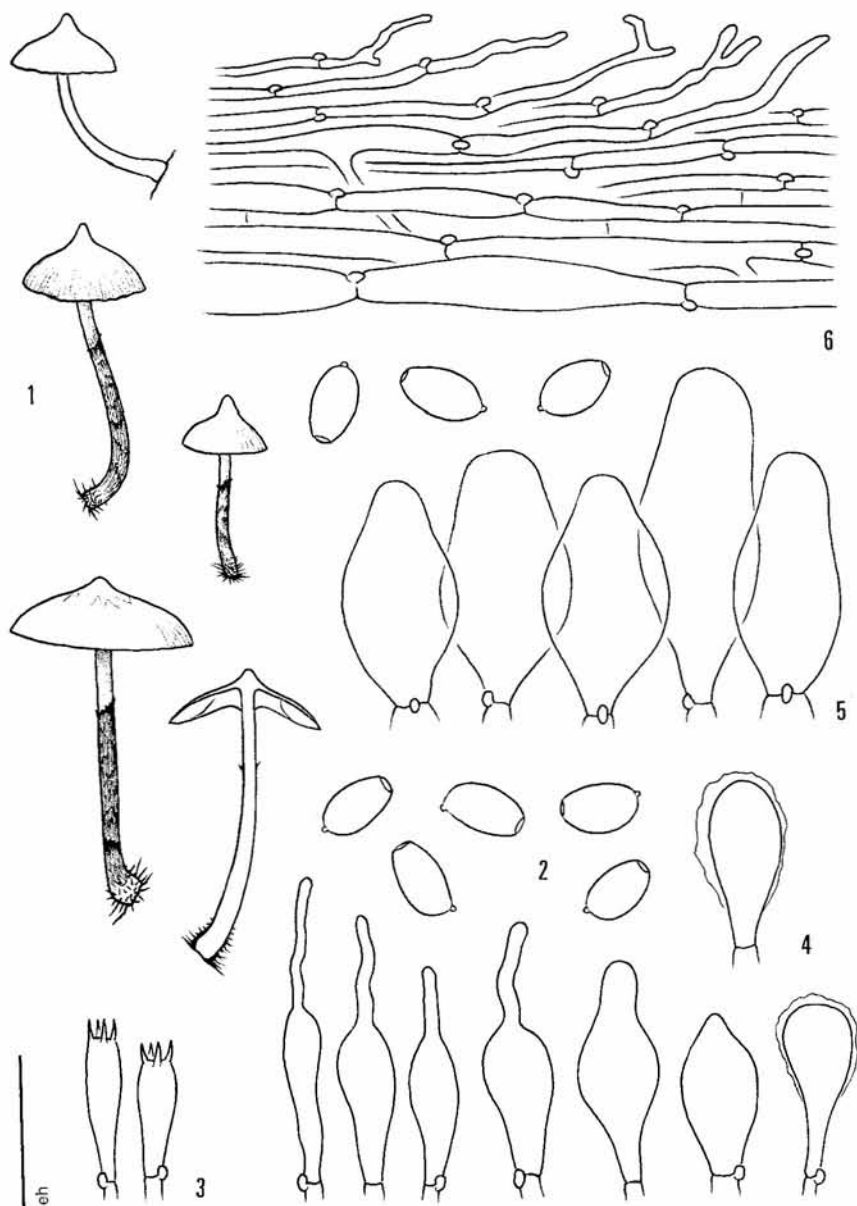


Fig. 1. 1–6: *Psilocybe fibrillosipes* (Holotypus): 1. Basidiomes. – 2. Basidiospores. – 3. Basidia. – 4. Cheilocystidia. – 5. Pleurocystidia. – 6. Pileipellis. – Scale bar: 10 mm (1), 5 μ m (2), 10 μ m (3, 4, 5), 20 μ m (6).

concolorous rhizoids, dry, hollow, tough, solitary or fasciculate. – Context pale yellow-brown in pileus, fuscous in stipe, unchanging. – Odor and taste not distinctive. – Chemical reactions on pileus: KOH – negative.

Spore print brown (lilac tints absent). – Basidiospores $4.5 - 5 (-5.5) \times 3 - 3.5 \mu\text{m}$, ovoid in face view, weakly amygdaliform in side view, brown (in KOH), thin-walled, smooth, germ pore small but distinctive. – Basidia $15 - 20 \times 3 - 4.5 \mu\text{m}$, 4-spored, sterigma up to $3 \mu\text{m}$ long, clamped. – Cheilocystidia polymorphic, shape ranging from clavate or fusoid ($20 - 35 \times 8 - 11 \mu\text{m}$) to distinctly fusoid with elongate neck ($30 - 45 \times 4 - 9 \mu\text{m}$), hyaline, thin-walled, occasionally covered with resinous or gelatinous incrustation, plasmatic pigment absent. – Pleurocystidia $25 - 45 \times 12 - 18 (-20) \mu\text{m}$, broadly and obtusely fusoid or utriform, hyaline, thin-walled. – Caulocystidia $20 - 40 \times 4 - 6 \mu\text{m}$, scattered, polymorphic, mostly cylindrical to slender fusoid, with short mucronate or finger-like projections, hyaline. – Pileipellis a cutis composed of repent, cylindrical hyphae, $2 - 4 (-5) \mu\text{m}$ diam., terminal cells differentiated, slender fusoid, rarely with irregular finger-like projections, non-gelatinized walls hyaline, thin, encrusted with brown pigment. Subpellis composed of regular cylindrical hyphae, $5 - 15 \mu\text{m}$ diam. Oleiferous hyphae absent. – Clamp connections present.

Etymology: *fibrillosus* (Lat.) – fibrillose; *pes* (Lat.) – foot.

Specimen examined: PAPUA NEW GUINEA: Morobe District, Bulolo, Watut, 10 May 1973, leg. Horak 73-207 (Holotypus, ZT).

Habitat and Ecology: Saprobic. – On rotting wood/bark of fagalean trees (*Castanopsis-Lithocarpus*), in tropical-montane rain forest, 1100 m a.s.l.

Distribution: Papua New Guinea.

Discussion: According to the keys published by Guzmán (1983, 1995) *Psilocybe fibrillosipes* can readily be accommodated in sect. *Singerianae*. Macroscopically this Papuan species is recognized by its conical pileus and the conspicuous white fibrillose veil remnants covering the lower portion of the fuscous stipe. The most distinctive features of *Ps. fibrillosipes* are, however, the polymorphic cheilocystidia, the broadly fusoid or utriform pleurocystidia and the remarkably small, ovoid basidiospores measuring only $4.5 - 5 (-5.5) \times 3 - 3.5 \mu\text{m}$.

The macroscopical characters of *Psilocybe fibrillosipes* are recalling the closely related *Ps. washingtonensis* A.H. Sm. (Smith &

Hesler 1946), reported from the Pacific North West, USA. This taxon, however, is clearly separated from the Papuan species by the shape and size both of the pleurocystidia and the basidiospores.

5. *Psilocybe megacystis* E. Horak, sp. nov. – Fig. 2: 1 – 6

Pileus 10–45 mm, primo conicus dein campanulatus vel applanatus papilla conica semper instructus, brunneus vel ochraceobrunneus, translucide striatus, ad marginem e velo appendiculato instructus. Lamellae late adnatae vel subdecurrentes, ex argillaceo ochraceae. Stipes 25–50 × 2–4 mm, cylindricus, aequalis vel subbulbosus, fuscus basim versus, cortina et fibrillis pallide ochraceis obtectus. Caro in pileo et in stipite concolor. Odor sapor nulli. Basidiosporae in cumulo pallide brunneae, 7–8 × 4–4.5 µm, ovoideae vel subamygdaliformes, tenuitunicatae, poro germinativo instructae. Basidia 30–40 × 7–10 µm, 4-sporigera. Cheilocystidia 30–40 × 7–10 µm, fusioidea, hyalina. Pleurocystidia 50–80 × 8–12 µm, elongatofusioidea vel lageniformia, apicem versus subincrassata, hyalina. Caulocystidia nulla. Pileipellis ex hyphis cylindraceis cutem formantibus, pigmento luteobrunneo incrustatis et impletis, membrana haud gelatinosa. Fibulae praesentes. Ad terram et ad lignum putridum in silvis montanis fagaceis tropicalibusque. Holotypus. – Papua New Guinea, leg. E. Horak 71–468 (ZT).

Pileus 10–45 mm, at first conical becoming campanulate, finally expanded with distinctive, conical papilla, centre depressed in old specimens, dark brown or pale orange-brown if moist, hygrophanous, turning ochre-brown if dry, smooth, innately fibrillose in centre, in young specimens margin with non-persisting, pale ochre, appendiculate veil remnants, velar remnants absent in mature specimens. – Lamellae 20–28 reaching stipe, lamellulae in 3–7 series, crowded, broadly adnate or subdecurrent with short tooth, up to 5 mm wide, at first pale beige-ochre becoming argillaceous-beige with age, even edges concolorous. – Stipe 25–50 × 2–4 mm, cylindrical, equal or slightly swollen at base, upper portion concolorous with lamellae, brown to fuscous towards base, young specimens with distinctive, fibrillose, non-persistent, pale ochre cortina, towards base with scattered, appressed, pale ochre fibrils of veil, dry, hollow, solitary. – Context concolorous in pileus and stipe, tough in stipe. – Odor and taste not distinctive. – Chemical reactions on pileus: KOH – negative.

Spore print pale brown (lilac tints absent). – Basidiospores 7–8 × 4–4.5 µm, ovoid-ellipsoid in face view, weakly amygdaliform in side view, pale brown, smooth, thin-walled, germ pore distinctive. – Basidia 16–20 × 4–6 mm, cylindrical, 4-spored, sterigmata up to 3 µm long, clamped. – Cheilocystidia 30–40 × 7–10 µm, fusoid, apex rounded, hyaline, thin-walled, pigment absent. – Pleurocystidia 50–80 × 8–12 µm, slender fusoid or lageniform, apex rounded, hyaline, walls in upper portion often 1–1.5 µm thick, thin towards base, occasionally with hyaline, resinous incrustation. –

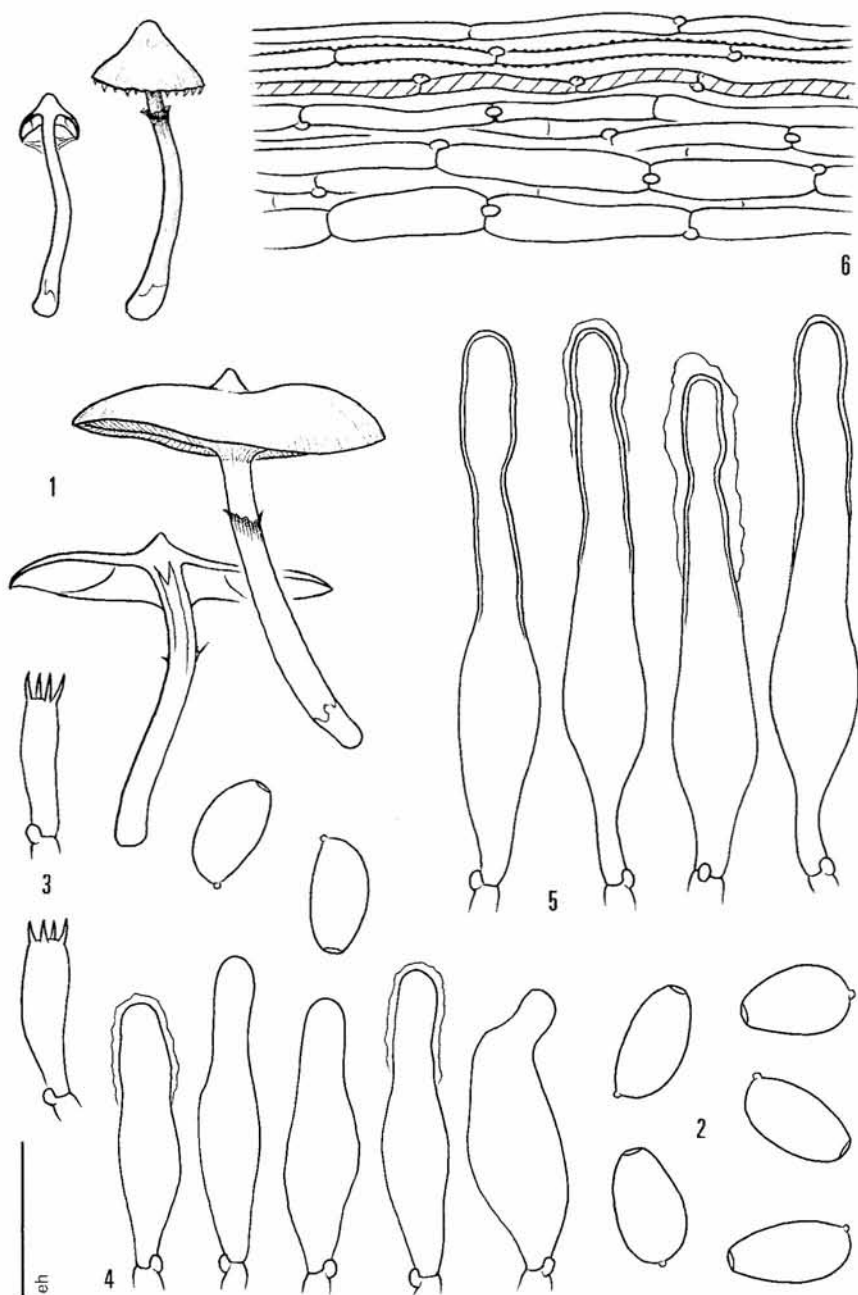


Fig. 2. 1–6: *Psilocybe megacystis* (Holotypus): 1. Basidiomes. – 2. Basidiospores. – 3. Basidia. – 4. Cheilocystidia. – 5. Pleurocystidia. – 6. Pileipellis. – Scale bar: 10 mm (1), 5 μ m (2), 10 μ m (3, 4, 5), 20 μ m (6).

Caulocystidia absent. – Pileipellis a cutis composed of repent, cylindrical hyphae, 2–8 mm diam., terminal cells not differentiated, non-gelatinized walls encrusted with yellow-brown pigment but also yellow-brown plasmatic pigment present. Oleiferous hyphae absent. – Clamp connections present.

Etymology: *mega* (Greek) – large; *cystis* (Greek): vesica, cystidium.

Specimen examined: PAPUA NEW GUINEA: Eastern Highlands, Kainantu, Mt. Michael, Frigano, Hut Track, 31 Dec 1971, leg. E. Horak 71–468 (Holotypus. – ZT).

Habitat and Ecology: Saprobic. – On rotten, moss-covered log of fagalean tree (*Castanopsis-Lithocarpus* spp., rarely *Nothofagus* sp.), in tropical-montane rain forest, 2300 m a. s. l.

Distribution: Papua New Guinea.

Discussion: Both macroscopically and microscopically *Psilocybe megacystis* is a remarkable species belonging to sect. *Singerianae* (Guzmán 1995). The taxon is characterized by rather large basidiomes with distinctly conical pileus and the presence of persistent veil remnants both on the pileus margin and the stipe. Based upon these features *Ps. megacystis* can readily be mistaken for the sympatric *Ps. eximia* Guzmán & E. Horak (1979). The two taxa, however, are distinctly separated by their microscopic features. The basidiospores in *Ps. megacystis* are slender ovoid-ellipsoid as compared to the mitriform-rhomboid basidiospores in *Ps. brunneocystidiata* which in addition is defined by the occurrence of chrysocystidia-like pleurocystidia.

As the epithet of *Ps. megacystis* indicates, this species is at once identified by its unique, comparatively large lageniform or slender fusoid pleurocystidia which occasionally are covered with a resin-like incrustation (cf. *Psilocybe largicystidata* E. Horak & Desjardin from Indonesia, described in present issue of *Sydowia*).

6. *Psilocybe simplex* E. Horak, sp. nov. – Fig. 3: 1–5

Pileus 20–45 mm, primo convexus dein subcampanulatus in disco subdepressus, brunneus vel ochraceobrunneus, conspicue et translucide striatus, unguinosus, velum nullum. Lamellae densae, adnatae, pallide ochraceobrunneae, ad aciem concolores. Stipes 20–40 × 2–3 mm, centralis, cylindricus, obscure brunneus, cortina pallida, fibrillosa vel submembranacea instructus, basim verse dense fibrillis albis e velo obtectus, siccus. Caro in stipite fusca. Odor saporque nulli. Basidiosporae 6–8 × 4.5–5 × 4–4.5 µm, frontaliter ovoideae, lateraliter subamygdaliformes, brunneae, leves, tenuitunicatae, poro germinativo instructae, in cumulo brunneae. Basidia 20–25 × 6 µm, cylindrica, 4-sporigera. Cheilocystidia

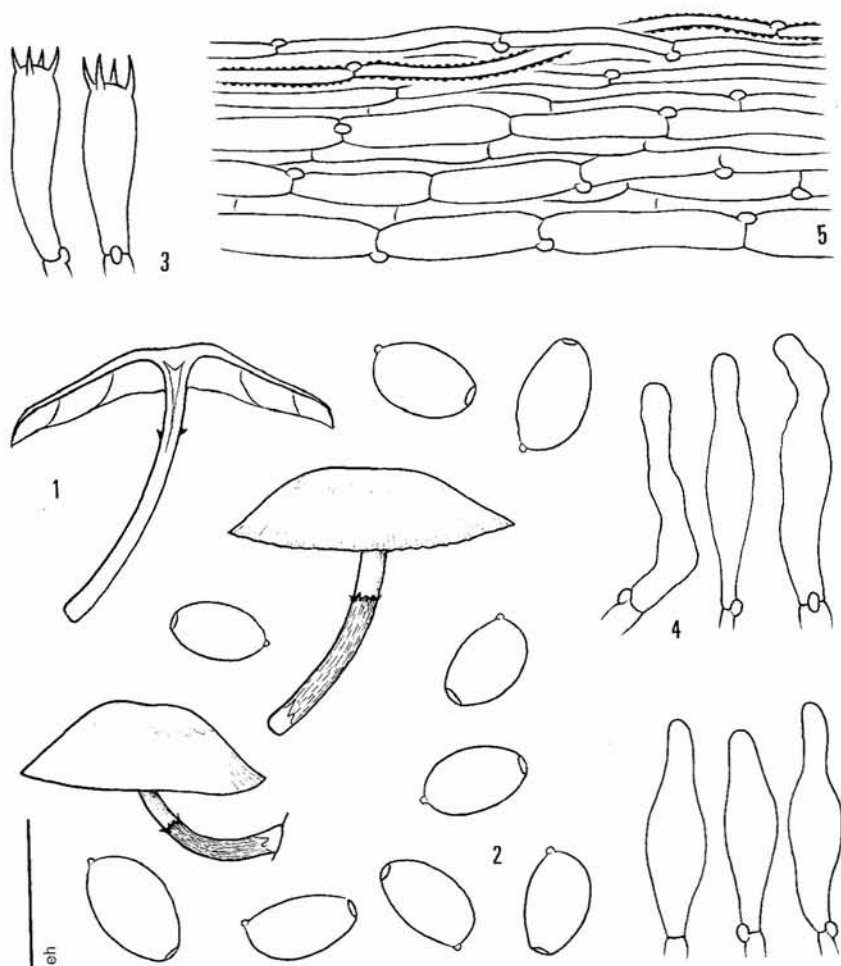


Fig. 3. 1–5: *Psilocybe simplex* (Holotypus): 1. Basidiomes. – 2. Basidiospores. – 3. Basidia. – 4. Cheilocystidia. – 5. Pileipellis. – Scale bar: 10 mm (1), 5 μ m (2), 10 μ m (3, 4), 20 μ m (5).

25–35 $\times$ 5–8 μ m, fusoidea, tenuitunicata, hyalina. Pleurocystidia et caulocystidia nulla. Pileipellis ex hyphis cylindraceis cutem formantibus, 3–8 μ m diam., membrana haud gelatinosa conspicue e pigmento luteobrunneo incrustatis. Fibulae praesentes. Ad lignum putridum in silvis montanis, fagaceis tropicalibusque. Holotypus. – Papua New Guinea, leg. E. Horak 72–460 (ZT).

Pileus 20–45 mm, at first convex becoming subcampanulate, finally expanded with subdepressed centre, dark brown (moist) at disk, paler or yellow-brown towards strongly striate-subsulcate margin, strongly hygrophanous, turning pale ochre upon drying, fatty (but not viscid), pellicle not peeling off, veil remnants absent. –

Lamellae 32–40 reaching stipe, lamellulae in 7–15 series, densely crowded, broadly adnate, occasionally subdecurrent with short tooth, up to 4 mm broad, at first pale yellow-brown, ochre-brown in mature specimens, often with pale red-brown tinge, even edges concolorous. – Stipe 20–40 × 2–3 mm, central, cylindrical or gradually tapering towards base, curved, dark brown, apex smooth, persistent cortina fibrillose or submembranaceous, towards base densely covered with appressed, white, persistent fibrils from veil, dry, hollow, gregarious but solitary. – Odor and taste not distinctive. – Context concolorous in pileus, dark brown in stipe, rather tough in stipe. – Chemical reactions on pileus: KOH – negative.

Spore print brown (lilac tinge absent). – Basidiospores 6–8 × 4.5–5 × 4–4.5 µm, ovoid in face view, subamygdaliform in side view, brown (in KOH), thin-walled, smooth, germ pore distinctive. – Basidia 20–25 × 6 µm, cylindrical, 4-spored, sterigmata up to 5 µm long, clamped. – Cheilocystidia 25–35 × 5–8 µm, fusoid, scattered, thin-walled, hyaline, incrustations or plasmatic pigment absent. – Pleurocystidia absent. – Caulocystidia absent. – Pileipellis a cutis composed of repent, cylindrical hyphae, 3–8 µm diam., distinctive terminal cells absent, non-gelatinized walls thin, strongly encrusted with yellow-brown pigment (in KOH). Hyphae in regular subcutis cylindrical, 8–14 µm diam. – Clamp connections present.

Etymology: *simplex* (Lat.) – simple.

Specimen examined: PAPUA NEW GUINEA: Western Highlands, Mt. Hagen, Tomba, trail to Mt. Hagen, 2300 m a.s.l., 19 May 1972, leg. E. Horak 72–460 (Holotypus, ZT).

Habitat and Ecology: Saprobic. – On rotten wood/bark of fagalean trees (*Castanopsis-Lithocarpus*, rarely *Nothofagus* sp.), in tropical-montane rain forest, 2600 m a.s.l.

Distribution: Papua New Guinea.

Discussion: The rather inconspicuous diagnostic characters of *Psilocybe simplex* support its taxonomic position in sect. *Pratenses* (Guzmán 1995). The most distinctive features of the present *Psilocybe* growing on rotten fagalean wood are the convex or depressed-expanded pileus lacking a separable pellicle, the broadly attached lamellae and the conspicuous, white fibrillose veil remnants covering the stipe from the submembranaceous cortina downwards. In addition *Ps. simplex* is defined by ovoid and thin-walled basidiospores and fusoid cheilocystidia measuring 25–35 × 5–8 µm. Pleurocystidia are absent.

Taxonomically, the present Papuan *Psilocybe* is close to *Ps. subhyperella* Singer (1973) described from Colombia (Guzmán 1983). The two species, however, can be distinguished by the shape and size of the pileus and the smaller size of the cheilocystidia. It is noteworthy that the Colombian species is also reported to grow on rotten, fagalean wood in temperate-montane forest dominated by *Quercus*.

7. *Psilocybe nothofagensis* Guzmán & E. Horak, Sydowia 31: 47. 1979.

For full description and illustrations, cf. Guzmán & E. Horak (1979).

8. *Psilocybe inconspicua* Guzmán & E. Horak, Sydowia 31: 50. 1979.

For full description and illustrations, cf. Guzmán & E. Horak (1979).

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