Phytotaxa 230 (3): 201–238
www.mapress.com/phytotaxa/
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Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.230.3.1

The genus *Inocybe* (Inocybaceae, Agaricales, Basidiomycota) in Thailand and Malaysia

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Abstract

Twenty-five species of Inocybaceae are reported from Thailand and Malaysia. Thirteen are described as new from four different major clades of the family: *I. errata* from the Mallocybe clade, *I. bicolorata* and *I. proxima* from the Inosperma clade, *I. neglecta* from the Pseudosperma clade, and *I. brevisquamulosa, I. fragilissima, I. latibulosa, I. lineata, I. ornata, I. parvibulbosa, I. pileosulcata, I stellata* and *I. thailandica* from *Inocybe sensu stricto*. Nineteen species are documented in full, circumscribed by morphological and molecular (ITS and nLSU sequences) features. Six additional lineages are depicted in a molecular phylogenetic context but at present lack sufficient morphological data for complete description. Illustrations of anatomical features, photographs of basidiomes, and SEM images of basidiospores are presented. A key to 19 species of Inocybaceae from Thailand and Malaysia is provided.

Key words: Fungi, Ectomycorrhiza, Fagalean-dipterocarp-pine forests, SE-Asia, Taxonomy

Introduction

The diversity of basidiomycetous macrofungi in Thailand is high, but their documentation is still relatively limited. From 1902, when the first basidiomycetous fungi were reported from Thailand (Rostrup 1902), until 2004 only about 300 species had been reported, of which 55 were described as new species (Desjardin *et al.* 2004). Since that time a concerted effort has been made to collect and describe both ectomycorrhizal and saprotrophic macrofungi, resulting in numerous new species and new reports for the country (Desjardin *et al.* 2009; Kerekes & Desjardin 2009; Le *et al.* 2007a–c; Sanmee *et al.* 2008; Wannathes *et al.* 2004, 2007, 2009a–b; Van de Putte *et al.* 2010; Zhao *et al.* 2008, 2010).

The genus *Inocybe* (Fr.) Fr. has been studied in Southeast Asia only from Indomalaya and Australasia (Horak 1979, 1980) where 53 species have been reported. Of these, thirteen were reported from Malaysia (peninsular Malaysia and Sabah), of which nine were new species. Five species of *Inocybe* of questionable determination have been reported from Thailand (viz., *I. caesariata* (Fr.) P. Karst., *I. destricta* (Fr.) Quél., *I. infelix* Peck, *I. lutea* Kobayasi & Hongo, *I. splendens* R. Heim) in several mushroom field guides (Chandrasrikul *et al.* 2008; Ruksawong & Flegel 2001; Soytong 1994). We have conducted extensive fieldwork in peninsular Malaysia and Thailand over the past decade in which we encountered numerous species of *Inocybe*, thirteen of which are described as new species herein, and another six are reported for the first time from Thailand. Nineteen species are documented with comprehensive descriptions, line drawings, scanning electron micrographs of basidiospores, and discussion of their phylogenetic affinities. An additional six taxa are depicted as distinct lineages in a molecular phylogenetic context but at present lack sufficient morphological data for complete description. A key to aid in the diagnosis of the 19 species of Inocybaceae from Thailand and Malaysia is provided.

Accepted by Genevieve Gates: 6 Aug. 2015; published: 13 Oct. 2015

Material and methods

Morphometric methods

Dry material was rehydrated in KOH (5% aqueous solution) and Congo Red (5%). Basidiospore measurements include the spines or nodules. Color terms and notations are those of Kornerup & Wanscher (1978). Drawings of basidiomes are of natural size. Drawings of microscopical characters were made with the aid of a WILD-Drawing Tube. Acronyms referring to herbaria keeping holotype, isotype, and/or voucher material of the species enumerated in the present paper include the following abbreviations per Thiers [continuously updated]: BO: Herbarium Bogor, Bogor, Indonesia; E: Herbarium, Edinburgh, UK; FRIM: Herbarium Forest Research Institute, Kepong, Malaysia; SFSU: San Francisco State University; TENN: University of Tennessee.; and ZT: Herbarium, ETHZ, Zurich, Switzerland. An asterisk (*) indicates illustrations (figures, photographs) are found in publication(s) cited. Latin names of the Malayan forest trees mentioned in the text follow Gardner *et al.* (2000).

DNA extraction and Sanger sequencing

Genomic DNA was extracted from 58 collections using fungal DNA extraction kits manufactured by Omega Bio-Tek, Inc. (Norcross, Georgia). High performance (HP) DNA extraction kits were used for several collections with degraded DNA, namely collections of the ZT10000 series. PCR amplifications of the internal transcribed spacers and 5.8S ribosomal RNA (ITS) and the nuclear large subunit ribosomal RNA (LSU or 25S) were performed on a C1000 thermocylcer manufactured by Bio-Rad (Hercules, California). Reagents used for PCR included 5X buffer, Go Taq®, and mixes of dNTPs supplied by Invitrogen Corp (Carlsbad, California). Reagent concentrations for PCR followed manufacturer protocols. PCR and sequencing primers for ITS included ITS1F and ITS4 (White *et al.* 1990). LSU primers for PCR included LR0R and LR7 or LR0R and LR5 (Vilgalys & Hester 1990). LSU sequencing primers included LR0R, LR16, LR5, LR3R, and/or LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). Amplicons were purified using QIAGEN PCR purification columns (Valencia, California) and prepared for direct sequencing following Judge *et al*. (2010).

Cycle Sequencing Kits (Applied Biosystems, Foster City, California) were used to produce sequence reactions purified in 96-well Sephadex G-50 columns (General Electric Healthcare, Piscataway, New Jersey) using separator strips manufactured by Princeton Separations (Freehold, New Jersey). Sequencing was performed on an ABI 3730 48-capillary electrophoresis genetic analyzer using 96-well plates at the Molecular Biology Resource Facility (MBRF) at the University of Tennessee. Sequence chromatograms were annotated using Sequencher 4.8 software (Gene Codes Corp, Ann Arbor, Michigan). 95 new ITS and LSU sequences were submitted to NCBI. GenBank accession numbers for these include: GQ892935-GQ893026 and GQ906702-GQ906704.

Molecular sequence analysis

Fifty-three new LSU sequences were aligned manually in MacClade 4.08 (Maddison & Maddison 2005) with a dataset produced by Matheny *et al.* (2009). The merged dataset included 1581 nucleotide sites and 242 taxa. The alignment was exported as a PHYLIP formatted file for a Maximum Likelihood (ML) bootstrap analysis using RAxML 7.0.4 on the RAxML web-server (Stamatakis *et al.* 2008). All sites were included for analysis. RAxML performed 100 rapid bootstrap inferences and thereafter a thorough ML search. Sequences were established as a single partition, and a GTR substitution matrix was invoked following previous LSU model estimates (Matheny 2005). The following empirical base frequencies were utilized: pi(A): 0.280812, pi(C): 0.193987, pi(G): 0.281194, pi(T): 0.243007. All free model parameters were estimated by the program including a GTRCAT model for rapid bootstrapping. A GTRGAMMA model of rate heterogeneity and an ML estimate of the alpha-parameter were used for the final ML search. A second analysis was performed using the desktop version of RAxML 7.0.3 but employing 1000 bootstrap replicates to ensure consistency of results. *Pleuroflammula flammea* (Murrill) Singer (Crepidotaceae; Matheny *et al.* 2006) was used as an outgroup for rooting purposes. Forty-two ITS sequences were released to GenBank but were too divergent to align across the entire family for phylogenetic purposes. In some cases ITS sequence comparisons were performed in ClustalX 2.0.9 (Thompson *et al.* 1997) to estimate genetic divergence among selected collections.

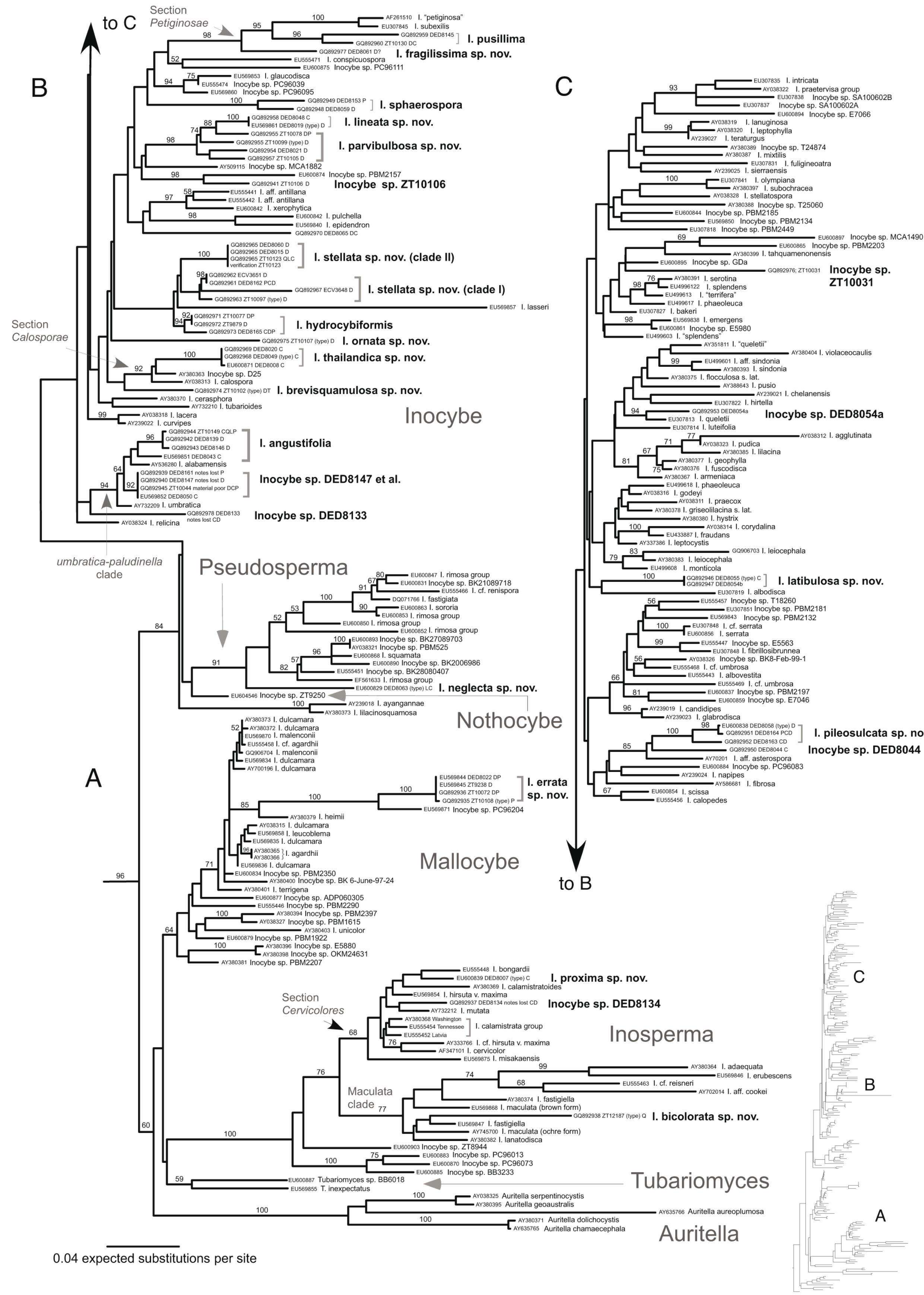


FIGURE 1. nLSU ML phylogeny of the Inocybaceae (with outgroups pruned) illustrating the autonomous placement and highly polyphlyetic nature of Thai and Malay species of *Inocybe* in bold (note that *I. petchii* and *I. gemina* are not present in the tree). Numbers above and below branches represent ML bootstrap values.

Results

Ecological observations of Inocybe species from Thailand and Malaysia

In the Indomayalan region, species of *Inocybe* are common in native tropical lowland and montane forests dominated by dipterocarp and fagalean broadleaf trees and the endemic conifer *Pinus kesiya*. In general, ascertaining ectomycorrhizal associations with specific plants is challenging in mixed broadleaf-conifer forest, especially so in tropical forests. However, based on available data, we can recognize several potential ecological alliances: (1) tropical lowland (<400 m elev.) species associated with Dipterocarpaceae (*I. brevisquamulosa*, *I. fragilissima*, and *I. ornata*); (2) tropical (sub)montane (>400 m elev.) species associated with a variety of Fagaceae, Dipterocarpaceae and Pinaceae, mainly *Castanopsis*, *Lithocarpus*, *Quercus*, and/or *Dipterocarpus* or *Pinus* (*I. bicolorata*, *I. latibulosa*, *I. neglecta*, *I. errata*, *I. proxima*, *I. petchii*, *I. gemina*, *I. thailandica*, *I. angustifolia*, and *I. lineata*); (3) species that have been collected in both lowland and montane habitats . (*I sphaerospora*, *I. hydrocybiformis*, *I. stellata*, *I. pusillima*, *I. pileosulcata*, and *I. parvibulbosa*); and (4) recently burned sites (*I. hydrocybiformis*, *I. brevisquamulosa*, and *I. parvibulbosa*). Of the species documented here, only *I. parvibulbosa* has been recorded in association with *Nothofagus*. These results are tentative and generally based on one or few collections for several species (e.g., *I. brevisquamulosa*, *I. ornata*) or broad morphological species concepts for others (e.g., *I. stellata*, *I. sphaerospora*, *I. parvibulbosa*), thus should be cautiously interpreted at this stage. More detailed data and information based on mycosociological observations can be retrieved in the following publications (with further references): Horak & Kobayasi (1978), Ingleby *et al.* (1998), Lee *et al.* (1997, 2008), Smith (1994), Thalisa *et al.* (2006), Watling & Lee (1995), Yuwa-Amornpitak *et al.* (2006). For more information of *Inocybe* occurring in (sub)tropical SE-Asia, see Bi *et al.* (1993) and Fan & Bau (2010).

Phylogenetic results

At least twenty-five species of Inocybaceae from Thailand and Malaysia are recovered by the ML analysis of LSU data (Fig. 1). The outgroup, *Pleuroflammula flammea* and other members of Crepidotaceae used in the analysis, have been pruned from the tree figure. The phylogram depicted is the best-scoring ML tree produced by RAxML. Bootstrap values and overall topology from two different runs were consistent except for the recovery of *Inocybe s. str*. as paraphletic by the RAxML BlackBox server. The position of the clade containing *I. ayangannae* and *I. lilacinosquamosa* is unstable. The desktop analysis using RAxML v7.0.3 recovered a monophyletic *Inocybe s. str*. (excluding the Pseudosperma and Nothocybe clades) but with low bootstrap support (57%). However, this latter topology is congruent with multigene phylogenetic studies of the Inocybaceae (Matheny 2005, Matheny *et al.* 2009, Ryberg *et al.* 2010). We present taxonomic descriptions or notes for nineteen of the twenty-five species below.

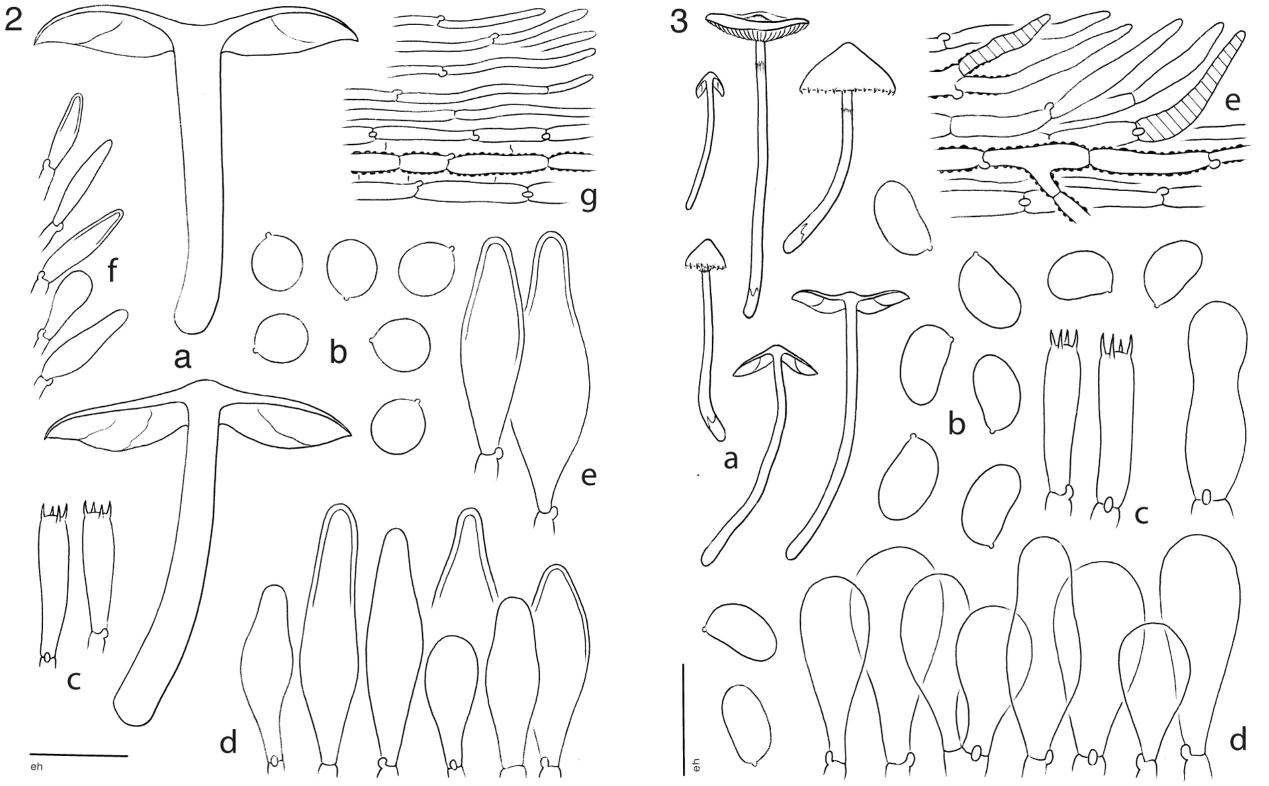
Taxonomic Part

Descriptions of Thai and Malaysian species of Inocybe

1. ***Inocybe sphaerospora*** Kobayasi (1952: 80) Fig. 2a–g; Pl. 1a–b

Pileus 45–60 mm wide, at first convex, expanded flat, center depressed or with shallow umbo in age, non-striate margin decurved with non-persisting fibrillose veil remnants, at disc subglabrous, towards margin radially appressed-fibrillose, dry, velipellis absent, splitting in age; deep (chrome) yellow (2A5–6) or pale (lemon) yellow (3A3) overall. *Lamellae* 42–60 reaching stipe, up to 15 lamellulae, adnexed to adnate, up to 10 mm wide, at first bright yellow, turning to greyish yellow (3–4B4–5) and finally dark greyish yellow (4C6–8) in age, entire edges concolorous. *Stipe* 45–60 × 8–9 mm, central, cylindrical, ± equal, bright yellow (2A5–6) overall, subpruinose (at apex), glabrous or fibrous towards base, dry, solid; cortina present in young specimens, absent in mature material; context 1–2 mm thick, pale yellow (2A2–3), unchanging on exposure. *Odor* not distinctive. *Taste* not distinctive.

Basidiospores 5.5–6 × 5–5.5 µm, subglobose, yellow-brown, smooth, brown in deposit. *Basidia* 24–30 × 6–8 µm, 4-spored, clavate. *Cheilocystidia* 30–65 (–75) × 10–18 (–20) µm, slender fusoid or lageniform, weakly metuloid, wall 0.5–1.5 µm thick at apex, hyaline, crystals absent or scattered; paracystidia absent. *Pleurocystidia* scattered, similar size and shape as cheilocystidia. *Caulocystidia* 30–60 × 8–12 µm, present at the apex only, shape ranging from subclavate to fusoid, hyaline, thin-walled, occasionally submetuloid at apex. *Pileipellis* a cutis of repent, cylindrical hyphae, 3–5 µm wide, terminal cells not differentiated, subgelatinized wall thin; subpellis hyphae cylindrical, 6–10 mm wide, minutely encrusted with pale yellow pigment; oleiferous hyphae absent. *Clamp connections* present.



FIGURES 2–3. **2**. Macroscopic and anatomical features for *Inocybe spherospora* (DED8059). a. Basidomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Pleurocystidia. f. Caulocystidia. g. Pileipellis. **3**. Macroscopic and anatomical features for *I. bicolorata* (ZT12187, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Habitat: On soil in tropical lowland or submontane forest (dominated by *Dipterocarpus, Anisoptera, Quercus*) and tropical montane forest (dominated by *Castanopsis, Lithocarpus, Quercus*, with scattered *Pinus kesiya*), 750–1050 m elev.

Known distribution: Japan (type), Papua New Guinea (Horak 1981), Singapore (Horak 1981), Malaysia (Turnbull 1995), Thailand.

Specimens examined: THAILAND. Chiang Mai Prov.: Hwy 1095, at 22 km marker, N19°07.570‘, E98°45.647‘, 750 m elev., on soil in tropical submontane or montane forest (dominated by *Dipterocarpus*), 11 Jun. 2006, leg. R. Zhao & D.E. Desjardin (DED8059, SFSU; ZT13024) GenBank accession no. GQ892993, GQ892948 (Fig. 1); Doi Inthanon National Park, Hwy 109, at 25 km marker, N18°32‘19.5“, E98°33‘42.5“, 1050 m elev., on soil in tropical montane broadleaf forest, under *Pinus kesiya*), 28 Jun. 2007, leg. D.E. Desjardin (DED8153, SFSU) GenBank accession no. GQ892994, GQ892949 (Fig. 2). MALAYSIA. Selangor: Kepong, Bukit Hari, trail to Waterfall, 200 m elev., tropical lowland forest (dominated by *Castanopsis, Quercus*), 30 Aug. 2009, leg. E. Horak (ZT13248). PAPUA NEW GUINEA. Morobe District: Bulolo, Manki, on soil in tropical montane rain forest (dominated by *Castanopsis, Lithocarpus*), 28 Mar. 1972, leg. E. Horak (ZT72-333). SINGAPORE. Singapore: Singapore Botanical Garden, in tropical lowland dipterocarp forest, leg. E.J.H. Corner s.n. (E, ZT 80-176).

Notes: *Inocybe sphaerospora* is an unique species characterized by yellow, medium-sized basidiomes and (rarely observed in the genus) subglobose basidiospores (Horak 1981). It is widely distributed in southeast and east Asia (Turnbull 1995), predominantly in dipterocarp and less often in fagalean forests where it was recorded from sea level to 1400 m elevation (Papua New Guinea). The tricholomatoid yellow basidiomes of *I. sphaeropora* can be mistaken for *I. lutea* Kobayasi & Hongo (Kobayasi 1952), which both in Japan (type) and Papua New Guinea is considered to be in ectomycorrhizal association with *Castanopsis* and *Lithocarpus*. However, *I. lutea* is distinctly separated by the smaller yellow-orange basidiomes, the marginate stipe base and nodulose basidiospores (Horak 1980). Kobayashi (2002) includes reference to *I. hinoana* Yukawa & Katum., known only from its type locality in Japan, which differs by its larger (7–8.5 × 5–6.5 µm) ellipsoid spores.

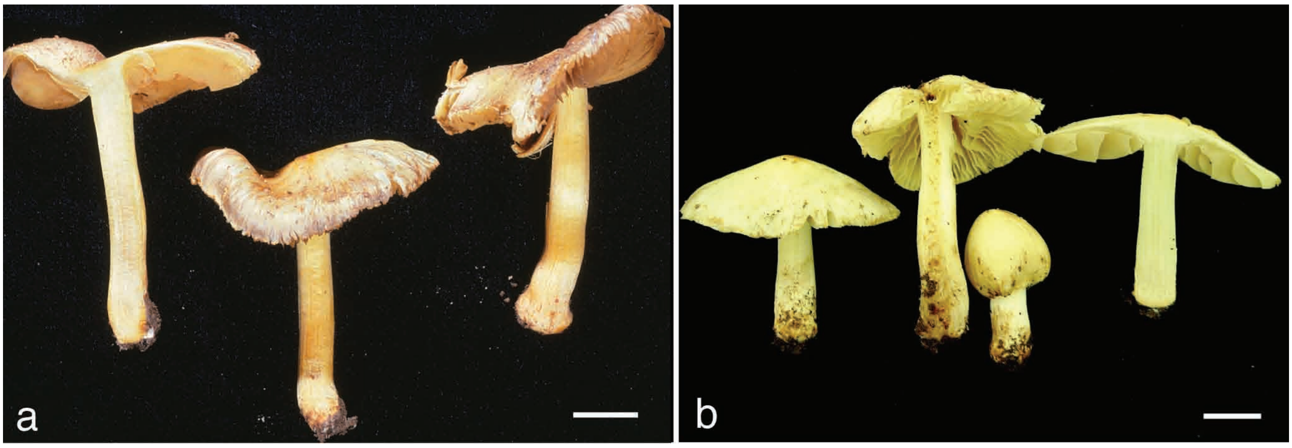


PLATE 1. a. *Inocybe sphaerospora* (DED8059). b. *Inocybe sphaerospora* (DED8153). Scale bars = 10 mm. Photos by Dennis Desjardin.

We observed a large number of unambiguous LSU nucleotide differences (22) between the two Thai exemplars identified as *I. sphaerospora* based on morphology. These are visualized on the tree figure (Fig. 1). DED8153 (Pl. 1b) also possesses a unique 27-bp insert in the LSU region. This sequence differentiation could correspond with ecological differences: DED8153 is a *Pinus*-associate, whereas DED8059 (Pl. 1a) is a dipterocarp-associate. Additional collections are needed to determine consistency of these genetic and ecological differences.

2. ***Inocybe bicolorata*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 3a–e.
MycoBank: MB 519910

Etymology: *bi* (Lat.), two; *coloratus* (Lat.), colored.

Diagnosis: Pileus bicolorus with a dark fuscous disc and deep chestnut brown margin, non-scaly. Stipe smooth, non-pruinose, with lilac at the apex at least when young. Odor distinctly spermatic. Basidiospores phaseoliform. Pleurocystidia absent. Cheilocystidia short, clavate-vesiculose or subutriform, thin-walled. In tropical montane forest dominated by *Quercus*, Malayasia.

Holotype:—MALAYSIA. Pahang: Frazer‘s Hill, Bishop Trail, on soil in tropical montane rain forest (dominated by *Quercus* spp.), N 03°42‘950‘, E 101°44‘43“, 15 Jan. 2004, leg. E. & A. Horak ZT12187 (SFSU, holotype; ZT, isotype) GenBank accession no. GQ892984, GQ892938.

Pileus 6–20 (–25) mm wide, at first conical, in age hemispherical to convex with obtuse umbo, finally umbonate-expanded, at first deep chestnut brown, disc gradually becoming dark fuscous, radially innate-fibrillose to minutely fibrillose, margin weakly splitting in old specimens, dry, young with distinctive pale fibrils from veil; KOH (5%) negative on pileus surface. *Lamellae* 20–28 reaching stipe, up to 5 lamellulae, adnate, ventricose, at first distinctly lilac or lilac-grey, becoming umber to pale fuscous in age, entire or minutely fimbriate edges concolorous. *Stipe* 20–50 × 1.5–3 mm, cylindrical, equal with slightly swollen at base, lilac at non-pruinose apex (at least in young specimens), towards base concolorous with pileus, smooth, (apart from cortina) velar fibrils present towards base of stipe, base often with whitish mycelial pad, dry, solid; cortina only distinctive in young specimens, usually present as remnants or occasionally forming submembranaceous non-persisting funnel-shaped annulus; context distinctly lilac-violet in upper half of stipe, old concolorous. *Odor* and *taste* distinctly spermatic.

Basidiospores (6.5–) 7–7.5 × 4–5 µm, phaseoliform (in side view), pale brown, smooth, thin-walled, germ pore absent, brown in deposit. *Basidia* 24–30 × 7–8 µm, 4-spored, subclavate or cylindrical. *Cheilocystidia* 20–35 × 12–20 µm, clavate-vesiculose or subutriform, hyaline, thin-walled, pigment absent. *Pleurocystidia* absent. *Caulocystidia* absent or scattered, shape and size like cheilocystidia. *Pileipellis* a cutis (or trichoderm) of repent (or semierect) cylindrical hyphae, 4–6 µm wide, terminal cells slender fusoid, non-gelatinized wall encrusted with yellow-brown (in 5% KOH) pigment, occasionally also with yellow-brown plasmatical pigment; subpellis hyphae cylindrical, 6–10 µm wide, entangled, wall encrusted with pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On soil among litter in tropical montane rain forest (dominated by *Quercus* spp.), 1400 m elev.

Known distribution: Malaysia.

Notes: The present species is characterized by distinctive macroscopic (in young basidiomes lilac colors both on lamellae and at the stipe apex, strong spermatic odor) and microscopic features (phaseoliform basidiospores and clavate-vesiculose, thin-walled cheilocystidia). The Malaysian taxon, reported from tropical montane oak forests, is readily identified by the comparatively small basidiospores measuring 7–7.5 × 4–5 µm. Phylogenetically, *I. bicolorata* is nested in the Inosperma clade (Fig. 1; Kropp *et al.* 2013) with strong support. This tropical *Quercus*-associated species appears related among north temperate species *I. fastigiella* G.F. Atk., *I. lanatodisca* Kauffman, and *I. maculata* Boud. but with weak support. This latter mixture corresponds to a subgrouping of the Maculata clade of Larsson *et al.* (2009).

3. ***Inocybe latibulosa*** E. Horak, Matheny & Desjardin, *spec. nov*. Fig. 4a–h; Pl. 2a

MycoBank MB 519914

Etymology: *latibulosus* (Lat.), hiding.

Diagnosis: Fruitbodies very small. Pileus 3–5 mm wide, conspicuously velutinous all over, texture soft. Lamellae distant. Stipe 8–12 × 0.5–1 mm, subpruinose at apex, cortina absent. Odor not distinctive. Basidiospores amygdaliform, smooth. Cheilocystidia and pleurocystidia thin-walled. On soil in tropical montane forest dominated by *Castanopsis* in Thailand.

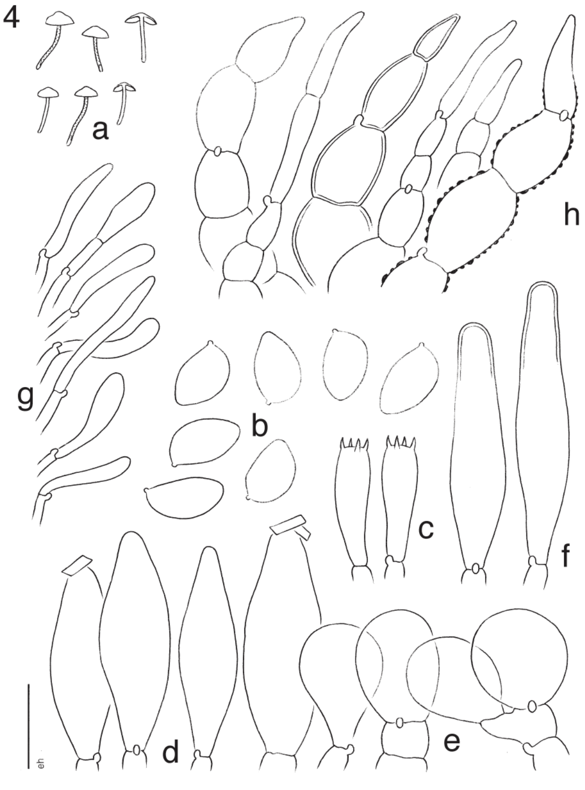


FIGURE 4. Macroscopic and anatomical features for *Inocybe latibulosa* (DED8055, holotype). a. Basidiomes. b. Basidiosores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Pleurocystidia. g. Caulocystidia. h. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Holotype:—THAILAND. Chiang Mai Prov.: Mae Sae, Hwy 1095, at 55 km marker, N19°14‘32.6“, E98°38‘29.4“, 990 m elev., on soil in tropical montane forest (dominated by *Castanopsis*), 10 Jun. 2006, leg. T. Osmundson & D.E. Desjardin (DED8055, holotype, SFSU; isotype ZT13026) GenBank accession no. GQ892992, GQ892946.

Pileus 3–5 mm wide, obtusely conical, convex or convex with a low and broad umbo, conspicuously velutinous all over, dark brown (6F5–8), dull, dry, veil remnants absent; context < 0.5 mm thick, unchanging on exposure, soft (not *Inocybe*-like). *Lamellae* (16–) 20–28 reaching stipe, 1–3 lamellulae, adnexed, rather distant, up to 1.5 mm wide, pale brown (7D4), fimbriate edges concolorous or whitish. *Stipe* 8–12 × 0.5–1 mm, central, cylindrical, equal, pale brown (7D5–6) overall, subpruinose at apex, minutely fibrillose towards base, dry, solid; cortina absent. *Odor* and *taste* not distinctive.

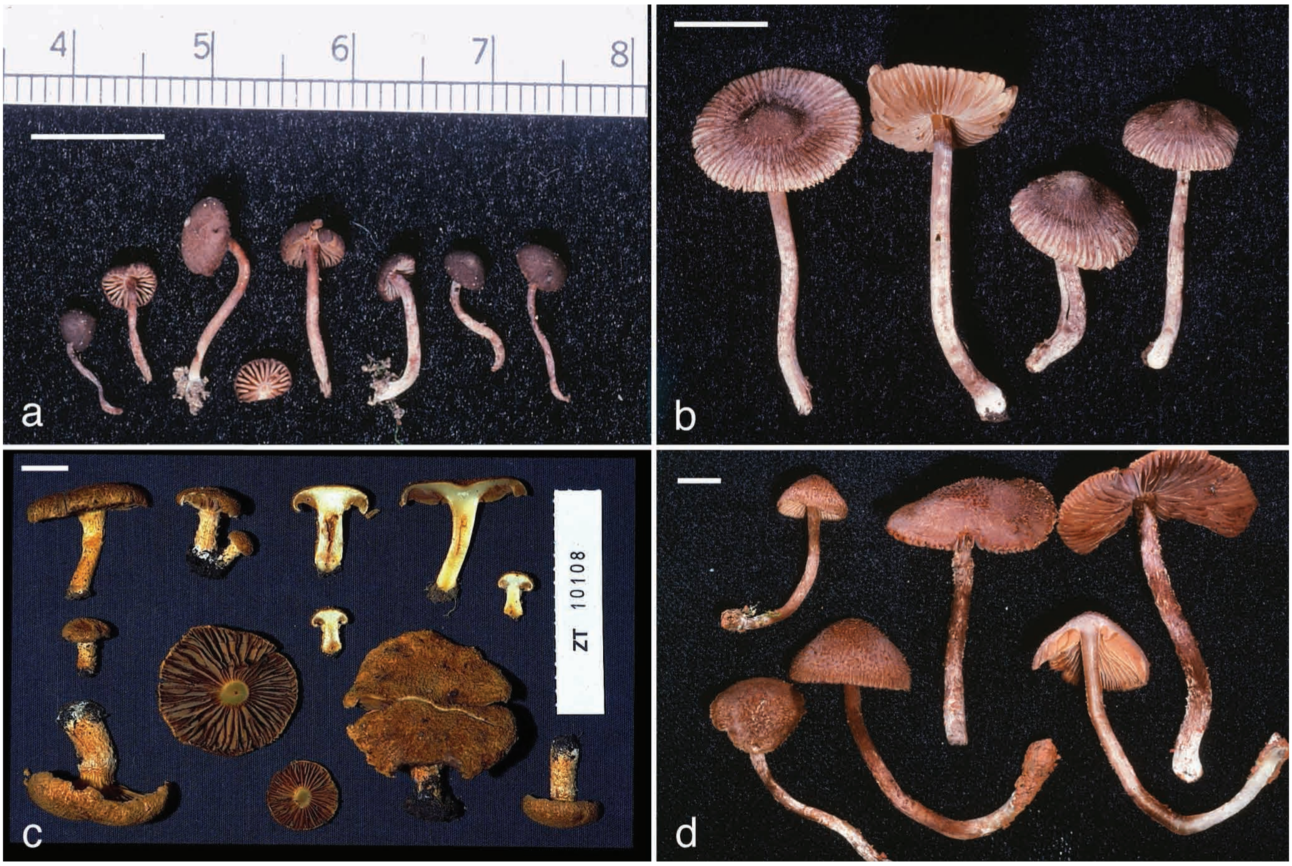


PLATE 2. a. *Inocybe latibulosa* (DED8055, holotype). b. *Inocybe neglecta* (DED8063, holotype). c. *Inocybe errata* (ZT10108, holotype). d. *Inocybe proxima* (DED8007, holotype). Scale bars = 10 mm. Photos a, b, d, by Dennis Desjardin, c, by Egon Horak.

Basidiospores 7.5–9 × 5–5.5 µm, distinctly amygdaliform, brown, smooth, occasionally with obscure germ pore, brown in deposit. *Basidia* 24–30 × 7–9 µm, 4-spored (occasionally 2-spored), clavate. *Cheilocystidia* 45–55 (–60) × 12–20 µm, subfusoid or lageniform, wall thin (< 0.5 µm thick), hyaline, crystals absent or scattered; paracystidia 20–35 × 15–22 µm, broadly clavate or subglobose, conspicuous, wall thin, hyaline. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* 35–65 × 6–12 µm, polymorphic, shape ranging from cylindrical to subfusoid, wall thin, occasionally encrusted with brown pigment. *Pileipellis* a distinctive trichoderm of suberect chains of short-globose or ovoid cells, 20–34 µm wide; terminal cells 20–50 × 6–10 µm, slender fusoid or conical, non-gelatinized wall strongly encrusted with dark brown pigment; subpellis hyphae globose or ovoid, wall occasionally up to 1 µm thick; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On soil in tropical montane forest (dominated by *Castanopsis*), 990 m elev.

Known distribution: Northwest Thailand.

Other specimen examined: THAILAND. Chiang Mai Prov.: same location as holotype, 10 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8054b, SFSU; ZT13027) GenBank accession no. GQ906702, GQ892947.

Notes: The basidiomes of *Inocybe latibulosa* are remarkably small and thus macroscopically the habit is reminiscent of a species of *Flammulaster* or *Phaeomarasmius*. Microscopical analysis, however, reveals distinctive and for *Inocybe* typical features, viz., pleurocystidia occasionally encrusted with crystals and large hyaline vesiculose paracystidia at the lamellar edges. In addition, this species is well characterized by the trichodermal pileipellis composed of suberect chains of short-globose or ovoid cells with distinctive slender fusoid or conical terminal cells.

Inocybe latibulosa is only one of two smooth-spored species with pleurocystidia that we describe from Thailand. A portion of DED8054 (DED8054b) is conspecific with the type. The phylogenetic position of *I. latibulosa* is not strongly placed, but the ML tree (Fig. 1) suggests the species is related to other smooth-spored species of *Inocybe*, as well as the weakly nodulose-spored *I. albodisca* Peck recorded from the west coast of North America.

4. ***Inocybe neglecta*** E. Horak, Matheny & Desjardin, *spec. nov*. Fig. 5a–g; Pl. 2b
MycoBank MB 519916

Etymology: *neglectus* (Lat.), neglected.

Diagnosis: Pileus dark brown on the disc and minutely scaly, brown or greyish brown and rimose-sulcate towards the margin, surface dry. Stipe greyish brown to pale brown, minutely pruinose at the apex, base subbulbous. Odor not distinctive. Basidiospores pruniform, smooth. Pleurocystidia absent. Cheilocystidia present but inconspicuous, broadly lageniform to subutriform, thin-walled, hyaline. On soil in tropical montane forest dominated by *Lithocarpus* and *Castanopsis* in Thailand.

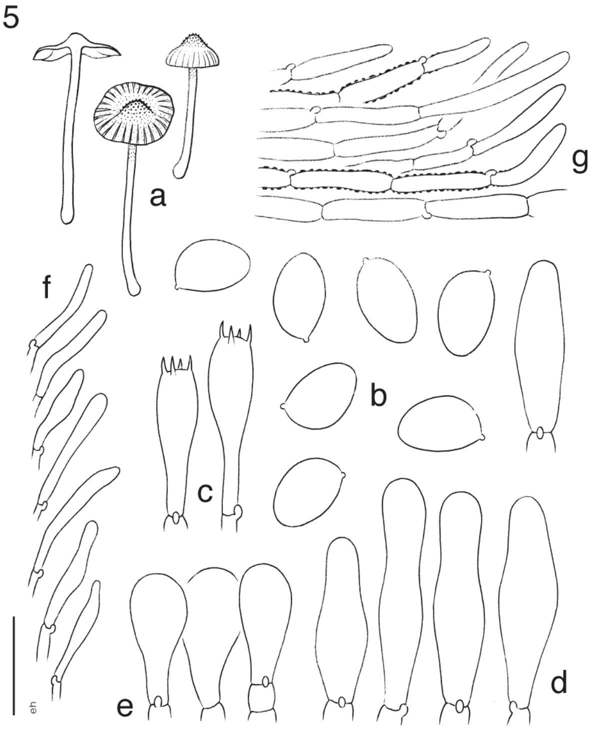


FIGURE 5. Macroscopic and anatomical features for *Inocybe neglecta* (DED8063, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Caulocystidia. g. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 μm, basidia and cystidia = 20 μm, pileipellis = 40 μm. Drawings by Egon Horak.

Holotype:—THAILAND. Chiang Mai Prov.: Hwy 1095 near 27 km marker, next to Buddhist temple, N19°06‘ 28.8“, E98°44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Lithocarpus* and *Castanopsis*), 12 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8063, holotype, SFSU; isotype, ZT13022) GenBank accession no. EU600829.

Pileus 12–18 mm wide, at first obtusely conical, becoming broadly umbonate or campanulate in age, at disc dark brown (7F4–8), brown (7E6–7) or greyish brown (7D3–4) towards the conspicuously rimose-sulcate and splitting margin, umbo felty or appressed-tomentose, with a few tiny squamules on the ridges towards margin, dry, veil remnants absent; context <1 mm thick, white, unchanging upon exposure. *Lamellae* 40–48 reaching stipe, up to 7 lamellulae, adnexed, up to 2 mm wide, greyish brown (6D3) to brown (7E4–5), entire edges concolorous. *Stipe* 25–35 × 1–2 mm, central, cylindrical, ± equal, but base subbulbous, greyish brown (6–7D3) to pale brown (7D4), minutely pruinose at apex only, glabrous towards paler or white base, dry, solid; cortina absent. *Odor* and *taste* not distinctive.

Basidiospores 7.5–8.5 × 5.5–6 μm, pruniform (in side view), broadly ovoid (in front view), brown, smooth, occasionally with obscure germ pore, brown in deposit. *Basidia* 24–32 × 9–10 μm, 4-spored, clavate. *Cheilocystidia* 30–45 × 8–14 μm, inconspicuous, broadly lageniform or subutriform, wall thin, hyaline, crystals absent; paracystidia 18–25 × 10–15 μm, scattered, broadly clavate, thin-walled and hyaline. *Pleurocystidia* absent. *Caulocystidia* 30–50 × 5–8 μm, scattered, shape ranging from cylindrical to subfusoid, hyaline, thin-walled, crystals absent. *Pileipellis* a cutis (or trichoderm at squamules) of repent or suberect, cylindrical hyphae, 5–8 μm wide, terminal cells not differentiated, non-gelatinized wall with pale brown incrusting and parietal pigment; subpellis hyphae cylindrical, 6–10 μm wide, encrusted with brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On soil in tropical montane forest (dominated by *Lithocarpus* and *Castanopsis*), 1050 m elev.

Known distribution: Northwest Thailand.

Notes: The most distinctive macromorphological characters of *I. neglecta* are the strongly rimose margin of the pileus, the subbulbous base of the mostly glabrous stipe and the lack of odor. Microscopically, this species is readily recognized by the rather large pruniform-ovoid basidiospores and the scattered, inconspicuous, thin-walled cheilocystidia. Typical for sect. *Rimosae* (Pseudosperma clade) pleurocystidia are absent. In Thailand, the type locality of this unique *Inocybe* is situated in tropical montane forest dominated by *Lithocarpus* and *Castanopsis*.

A multigene relaxed molecular clock analysis by Matheny *et al.* (2009) placed *I. neglecta* sister to the remaining Pseudosperma clade with significant support (Bayesian posterior probability). A similar arrangement is recovered here but with weak support (Fig. 1, see also Kropp *et al.* 2013).

5. ***Inocybe errata*** E.Horak, Matheny & Desjardin, *spec. nov*. Fig. 6a–e; Pl. 2c
MycoBank MB 519912

Etymology: *erratus* (Lat.), deceiving, false.

Diagnosis: Pileus warm brown, hazel brown, pale golden brown or orange-brown, covered all over with fibrillose squamules or minute scales, dry. Lamellae adnate. Stipe equal, not longer than pileus diameter, surface not pruinose in any part; cortina conspicuous, persistent, annulate, present as belts and scaly zones of veil tissue towards base. Odor not distinctive. Basidiospores amygdaliform, smooth. Pleurocystidia absent. Cheilocystidia broadly clavate or vesiculose. On lateritic soil in tropical submontane conifer forest dominated by *Pinus kesiya, P. merkusii* and dipterocarp forest dominated by *Dipterocarpus obtusifolia*, Thailand and India.

Holotype:—THAILAND. Chiang Mai Prov.: Orb Luang, on lateritic soil in tropical submontane conifer forest (*Pinus merkusii,* pure stand in plantation), 2 Jul. 2002, leg. E. & A. Horak (ZT10108, holotype) GenBank accession no. GQ892935.

Pileus 10–40 mm wide, at first hemispherical or convex with incurved non-striate margin, becoming expanded in age, disk subdepressed with or without low umbo, warm brown, hazel brown (6E6–8), pale golden brown or orange-brown, all over covered with small, concolorous, fibrillose squamules or minute scales, dry, in young specimens with whitish, non-persisting fibrillose veil remnants at margin. *Lamellae* close, 36–48 reaching stipe, 3 (–7) lamellulae, adnate, broadly adnate or marginate-decurrent, up to 6 mm wide, at first greyish yellow (4B5), umber brown (6E6–8) to chocolate brown, with faint rust tinge, entire or subfimbriate edges paler; context whitish or greyish yellow (4B4–5), orange at frass holes and upon exposure. *Stipe* 10–35 × (3–) 4–8 mm, cylindrical, equal, concolorous with pileus, at base with white tomentum, strongly innate-fibrillose all over, apex not pruinose; cortina conspicuous, persistent, annulate, composed of whitish or pale cinnamon fibrils; towards base velar remnants as numerous woolly-fibrillose concolorous belts and scaly zones, dry; context solid becoming fistulose. *Odor and taste* not distinctive.

Basidiospores 8.5–10 × 4.5–5 µm, amygdaliform (in side view) or obovoid (in front view), pale yellow-brown, smooth, germ pore absent, brown in deposit. *Basidia* (25–) 30–38 × 6–7 µm, 4-spored (rarely 2-spored), cylindrical-clavate, becoming necropigmented. *Cheilocystidia* 15–35 (–40) × 12–22 µm, conspicuous, broadly clavate or vesiculose, thin-walled, hyaline, crystals absent. *Pleurocystidia* absent. *Caulocystidia* absent. *Pileipellis* a trichoderm of erect, tightly fasciculate, cylindrical hyphae, 6–10 µm wide, terminal cells not differentiated, hyaline or yellowish, non-gelatinized wall, strongly encrusted with (yellow-) brown pigment; subpellis hyphae cylindrical, 8–14 µm wide, encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on lateritic soil in tropical submontane conifer forest (dominated by *Pinus kesiya, P. merkusii*) and dipterocarp forest (dominated by *Dipterocarpus obtusifolia*), 500–600 m elev.

Known distribution: Northwest Thailand (type), India (Kerala).

Other specimens examined: THAILAND. Hwy 1095, at 22 km marker, N19˚07.570‘, E98˚45.647‘, 4 Jun. 2006, leg. D.E. Desjardin (DED8022, SFSU; ZT13034) GenBank accession no. EU569844. Mae Hong Son Prov.: south of Mae Hong Son, Hwy. 108, at 235 km marker, road to TV Station 3–9, on lateritic soil (in recently burned) tropical submontane mixed broadleaf conifer forest (dominated by *Dipterocarpus obtusifolia, Pinus kesiya*), 29 Jun. 2002, leg. E. & A. Horak (ZT10072) GenBank accession no. GQ892936.

Notes: *Inocybe errata* belongs to subgen. *Mallocybe* (Mallocybe clade) and is affiliated with the *I. dulcamara*-complex that encompasses numerous closely related taxa. The occurrence and geographical distribution of *I. errata* is not only restricted to Thailand, but this distinctive species is also known from India (Kerala) in association with dipterocarps (ZT9238; EU569845). *Inocybe errata* is sister to an undescribed species from Zambia (PC 96204) and appears to have diverged from the African species relatively recently (Matheny *et al.* 2009). Both are phylogenetically related to a Mediterranean species, *I. heimii* Bon.

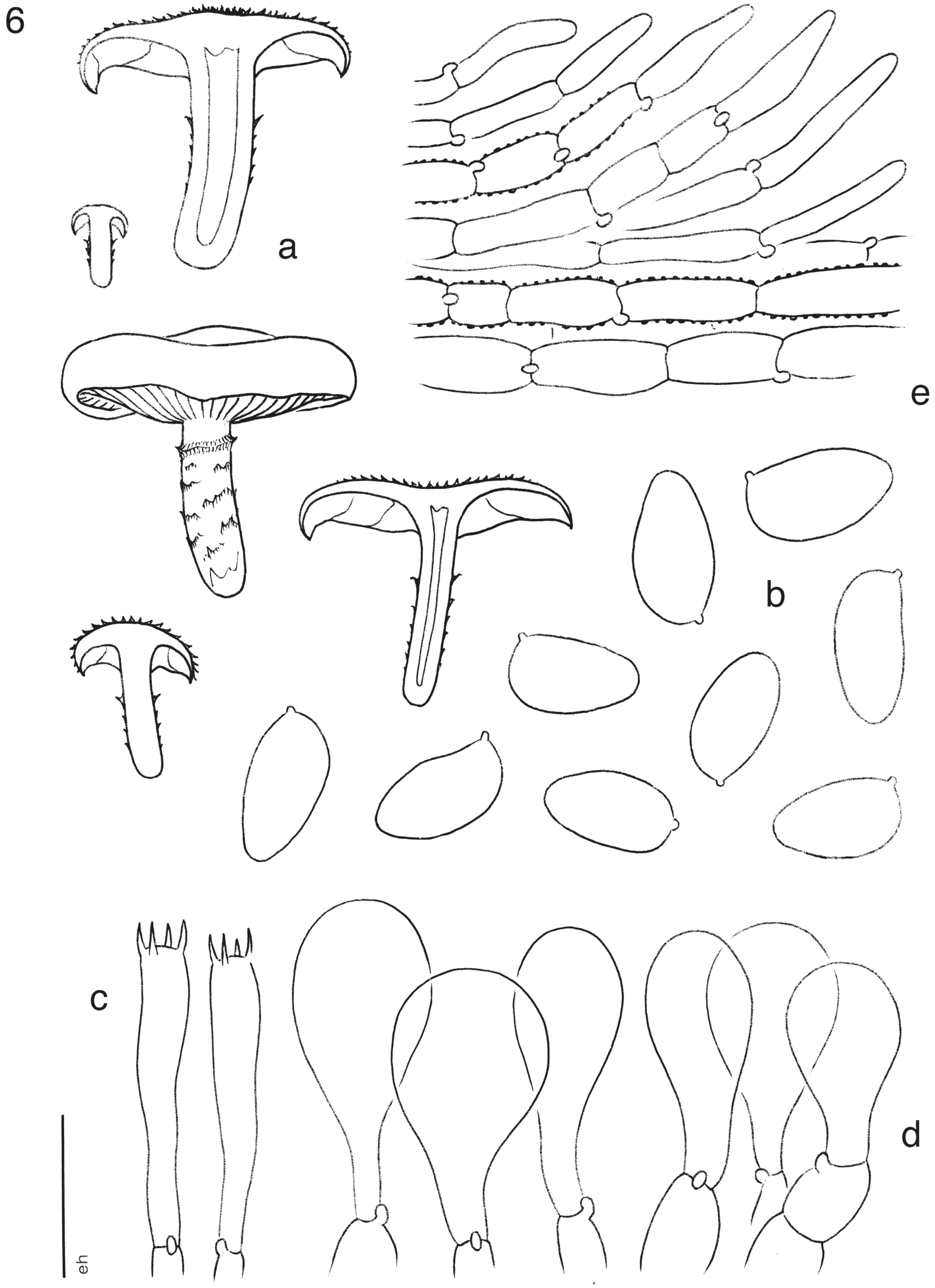


FIGURE 6. Macroscopic and anatomical features for *Inocybe errata* (ZT10108, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

6. ***Inocybe proxima*** E. Horak, Matheny & Desjardin, *spec. nov*. Fig. 7a–e; Pl. 2d
MycoBank MB 519920

Etymology: *proximus* (Lat.), close to, next to.

Diagnosis: Pileus dark brown, disc with numerous small but conspicuous tufts of erect fibrils, context unchanging upon exposure. Stipe covered with concolorous loose fibrils and small scales, not pruinose anywhere, stipe base olive grey, cortina evanescent. Odor not distinctive. Basidiospores ovoid-elliptical. Cheilocystidia present. Pleurocystidia and caulocystidia absent. In tropical montane forest dominated by *Castanopsis* in Thailand.

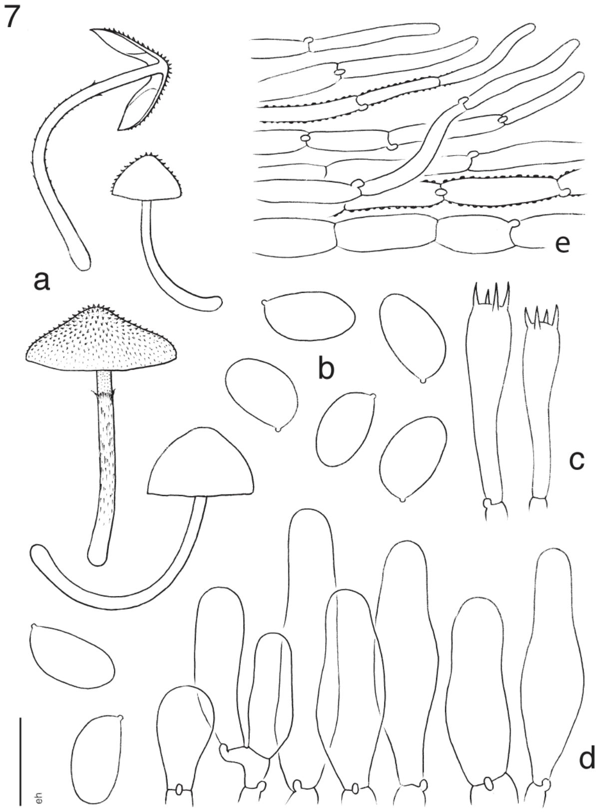


FIGURE 7. Macroscopic and anatomical features for *Inocybe proxima* (DED8007, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Holotype:—THAILAND. Chiang Mai Prov.: Mae Sae on Hwy 1095, at 55 km marker, N19°14‘32.6“, E98°38‘29.4“, on soil in tropical montane forest (dominated by *Castanopsis*), 990 m elev., 3 Jun. 2006, leg. D.E. Desjardin (DED8007, SFSU, holotype; ZT13015, isotype) GenBank accession no. EU600839, EU600840.

Pileus 20–40 mm wide, at first broadly and obtusely conical with decurved margin, becoming distinctly campanulate in age, not expanding, dark brown (6–7F6–8) overall, at disc with numerous small but conspicuous, conical and concolorous spines (formed from tufts of erect fibrils), towards margin with smaller scales and fibrils, at non-striate margin glabrous, dry, veil remnants absent; context 1–2 mm thick, watery white, unchanging upon exposure. *Lamellae* 28–36 reaching stipe, 7 (–15) lamellulae, adnexed, up to 5 mm wide, at first beige, becoming brown (6E6–8), entire edges concolorous. *Stipe* 35–70 × 2–5 mm, central, cylindrical, ± equal, covered with concolorous, loose fibrils and scattered small scales, apex not pruinose, brown (6E5–8) above, at base olive grey, dry; cortina present in young specimens, not persisting; context solid or stuffed, with olive grey tinge in base. *Odor* not distinctive. *Taste* not recorded.

Basidiospores 8.5–10 × 5–5.5 µm, ovoid-elliptical (in side and face view), brown, smooth, germ pore absent, brown in deposit. *Basidia* 35–42 × 8–10 µm, 4-spored, clavate. *Cheilocystidia* 20–55 × 10–15 µm, polymorphic, shape ranging from clavate to broadly fusoid, thin-walled, hyaline, crystals absent. *Pleurocystidia* absent. *Caulocystidia* absent. *Pileipellis* a cutis of suberect or repent, cylindrical hyphae, 6–8 µm wide, terminal cells not differentiated, non-gelatinized wall hyaline, encrusted with yellow-brown pigment; subpellis hyphae cylindrical or slender subfusoid, 12–20 µm wide, wall encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on soil in tropical montane forest (dominated by *Castanopsis*), ca. 1000 m elev.

Known distribution: Northwest Thailand.

Notes: The olive grey colored context in the base of the stipe indicates that *I. proxima* belongs to the intricate group of species related to *I. calamistrata* (Fr.) Gillet, a common species complex with a wide distribution in the Northern Hemisphere (Stangl 1989, Horak 2005) which usually have a reddening context in stipe. To date this reddening of context has not been observed in *I. proxima*. In the Southern Hemisphere the related *I. calamistratoides* E. Horak (1977) is reported from New Zealand where it is frequently encountered in *Nothofagus* forests. Molecular results (Fig. 1; Kropp *et al.* 2013) support placement of *I. proxima* in the Inosperma clade where it is closely related to *I. bongardii* (Weinm.) Quél. and other members of *Inocybe* sect. *Cervicolores*. At present *I. proxima* is known only from the type collection.

7. ***Inocybe hydrocybiformis*** (Corner & E. Horak) Garrido (1988: 17) Fig. 8a–g; Pl. 8a

Basionym: *Astrosporina hydrocybiformis* Corner & E. Horak in Horak (1979: 170).

Pileus 10–20 mm wide, at first obtuse-conical becoming convex or expanded with more or less distinctive umbonate or acute papilla (habit is reminiscent of *Cortinarius* subgen. *Hydrocybe-Telamonia*), center smooth but scurfy, minutely squamulose or covered with small recurved conical scales, innate-fibrillose towards often rimose or sulcate, non-striate margin, deep umber brown or fuscous, dry, veil remnants at margin absent, velipellis absent; context concolorous, unchanging upon exposure; 5% KOH negative on pileus surface. *Lamellae* (18–) 24–32 reaching stipe, 3 (–7) lamellulae, adnexed to adnate, ventricose, up to 2 mm wide; at first fuscous cinnamon, very dark umber brown with rusty tinge in age; fimbriate edges white. *Stipe* 25–35 (–40) × 1–1.5 mm, cylindrical, equal, base rarely swollen (up to 3.5 mm diam), concolorous with pileus all over, fibrillose (but not pruinose) at apex, smooth towards base, dry; cortina not observed; context solid. *Odor* and *taste* not distinctive.

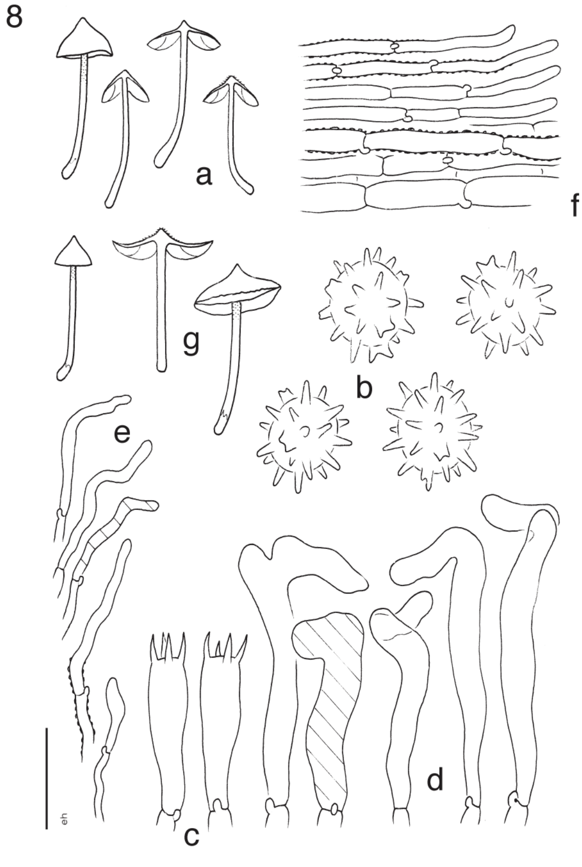


FIGURE 8. Macroscopic and anatomical features for *Inocybe hydrocybiformis* (ZT10077). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Caulocystidia. f. Pileipellis. g. Basidiomes (ZT78-47, holotype). Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Basidiospores 8–10 × 7.5–8.5 µm, ovoid, slender conical or cylindrical, occasionally also with saddle-shaped projections up to 2.5 µm long, brown, brown in deposit. *Basidia* 25–36 × 7–8 µm, 4-spored, clavate. *Cheilocystidia* 40–70 × (8–) 10–20 µm, polymorphic, mostly cylindrical or clavate-capitate, often with blunt, forked or irregular finger-like projections at apex, in 5% KOH filled with conspicuous, strongly refringent, granular, yellow or orange content, thin-walled, crystals absent; paracystidia absent. *Pleurocystidia* absent or scattered (size and shape like cheilocystidia). *Caulocystidia* shape and size like cheilocystidia. *Pileipellis* a cutis (or trichoderm) of cylindrical hyphae, 3–5 µm wide, terminal cells not differentiated, non-gelatinized thin wall, coarsely encrusted with dark brown pigment, often also brown plasmatical pigment present; subcutis hyphae cylindrical or slender ovoid, 8–16 µm wide, encrusted with pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on lateritic soil (in recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis* or *Pinus kesiya*) and in tropical submontane forest (dominated by *Castanopsis*, with scattered *Pinus kesiya*), 425–1050 m elev.

Known distribution: Thailand, Malaysia, Singapore (type).

Specimens examined: SINGAPORE. Singapore: Singapore Botanical Garden, Gardens Jungle, 5 Sep. 1940, leg. E.J.H. Corner (E, holotype of *I. hydrocybiformis*; ZT78-47, isotype). THAILAND. Mae Hong Son Prov.: S of Mae Hong Son, Hwy. 108, 235 km marker, road to TV Station 3–9, ca. 580 m elev., on lateritic soil (in recently burned) tropical submontane forest (*Dipterocarpus obtusifolia*, *Pinus kesiya*), 29 Jun. 2002, leg. E. & A. Horak (ZT10077) GenBank accession no. GQ892971; south of Mae Hong Son, Hwy. 108, 247 km marker, ca. 425 m elev., on lateritic soil in (recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia,* mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT9879) GenBank accession no. GQ892972. Chiang Mai Prov.: Hwy 1095 near 27 km marker, Pathummikaram Temple area near Ban Pha Deng, N19˚06‘28.8“, E98˚44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*), 27 Jun. 2007, leg. D.E. Desjardin (DED8144, SFSU); Hwy 1095, 22 km marker, N19˚07‘570 ,‘, E98˚45‘647“, 750 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*, *Castanopsis*, mixed with *Pinus kesiya*), 30 Jun. 2007, leg. D.E. Desjardin (DED8165, SFSU) GenBank accession no. GQ892973. MALAYSIA. Negri Sembilan: Pasoh, FRIM Field station, on soil in tropical lowland forest (dominated by *Shorea*), 2 Mar. 1992, leg. R. Watling 25436 (E, holotype of *Inocybe aurantiocystidiata*). SINGAPORE. Singapore: Singapore Botanical Garden, Gardens Jungle, 4 Sep. 1937, leg. E.J.H. Corner (E, holotype of *Astrosporina alienospora*; ZT78-50, isotype).

Notes: *Inocybe hydrocybiformis* is readily recognized both by macroscopic and microscopic characters. The pileus of the rather fragile and small basidiomes measures less then 20 mm wide, and the acute, conical (rarely umbonate) papilla is a significant feature to recognize this taxon that is probably widely distributed in southeast Asian tropical lowland and montane forests. In addition, *I. hydrocybiformis* is well distinguished by the peculiar cheilocystidia (and pleurocystidia) rarely encountered in *Inocybe*: the thin-walled, cylindrical or clavate-capitate cystidia are filled with a conspicuous, yellow, strongly refringent content. Crystals at the apex of the cystidia are absent. Note that Horak (1979) reported pleurocystidia as absent from material collected in Singapore and Malayasia but present though scattered in Thai material.

Two other *Inocybe* species with yellow colored cheilocystidia and similar basidiospores as observed in *I. hydrocybiformis* occur in the general region. The first taxon is the Malayan *I. aurantiocystidiata* Turnbull & Watling (1995), which differs from *I. hydrocybiformis* by the marginate stipe base and violaceous context. The second species reminiscent of *I. hydrocybiformis* due to the golden yellow cheilocystidia is *I. alienospora* (Corner & E. Horak) Garrido (Horak 1980) reported from Singapore. Microscopically, this latter species is distinctly separated from the two aforementioned taxa by basidiospores with nodulose or flange-like projections. Similar cheilocystidia with yellow plasmatic pigment have been observed in Australian collections of *I. lasseroides* (E. Horak) Garrido (Matheny & Bougher, pers. comm.). Horak (1979) did not report this feature from material collected in Papua New Guinea.

Sequences of this species from Thailand form a robust monophyletic group (Fig. 1). *Inocybe hydrocybiformis* may be most closely related to *I. stellata* groups I and II (see below) and *I. lasseri* Dennis, the latter described from the neotropics. However, this arrangement is weakly supported.

8. ***Inocybe petchii*** Boedijn (1951: 223)

Basionym: *Inocybe umbonata* Petch, *Ann. R. bot. Gdns Peradenyia* 6: 202, 1917 (syn. post., non *Inocybe umbonata* Quél., *Bull. Soc. mycol. France* 2: 4, 1876).

Synonym: *Astrosporina petchii* (Boedijn) E. Horak, *Persoonia* 10: 164, 1979.

Misappl.: *Astrosporina gemina* E. Horak, *Persoonia* 10: 166, 1979.

Habitat: On soil in tropical montane rain forest dominated by *Castanopsis, Lithocarpus*, *Quercus*, also in tropical dipterocarp forest.

Known distribution: Sri Lanka (type), Papua New Guinea, Malaysia.

Specimens examined: SRI LANKA. Peradenyia, Jul. 1912, leg. T. Petch 3499 (holotype, as *Inocybe umbonata* Petch, K); same locality, 15 Oct. 1914, leg. T. Petch 4173 (K). PAPUA NEW GUINEA. Morobe District: Bulolo, Manki, 1400 m elev., on soil in tropical montane rain forest (dominated by *Castanopsis-Lithocarpus*), 25 Apr. 1972, leg. E. Horak (ZT72-408); Western Highlands: Mt Hagen, Baiyer River Forest Reserve, on soil in montane rain forest (dominated by *Lithocarpus*), 22 May 1972, leg. E. Horak (ZT72-476). INDONESIA. Java: Cibodas, trail to Mt Gede, 1800 m elev., on soil in tropical montane fagalean forest, 11 Apr 1972, leg. E.J.H. Corner, J-5 (E, ZT); same locality and habitat, on soil in tropical montane fagalean forest (dominated by *Castanopsis-Lithocarpus*), 14 Mar 1977, leg. E. Horak (ZT77-188); same locality and habitat, on soil in tropical montane rain forest (dominated by *Quercus* and *Castanopsis*), 30 Dec. 1998, leg. E. Horak (ZT6457); same locality and habitat, on soil in tropical montane rain forest (dominated by *Quercus* and *Castanopsis*), 22 Jan. 1999, leg. D.E. Desjardin (DED6962, SFSU; BO99-361; ZT7331); same locality and habitat, 31 Dec. 1999, leg. E. Horak (ZT8322, BO001). MALAYSIA. Johor: Gunong Panti, 500 m elev., on soil in tropical dipterocarp forest, 7 Sep. 1930, leg. E.J.H. Corner (ZT78-44).

Notes: *Inocybe petchii* is probably widely distributed in southeast Asia. To date this species with eye-catching basidiomes has not been recorded in Thailand. However, its occurrence can be expected (Horak 1980). Macroscopically, the basidiomes are similar to large specimens of *I. gemina*. However, these two taxa are readily distinguished by microscopical features. DNA sequence data have yet to be produced from any samples of *I. petchii*.

9. ***Inocybe gemina*** (E. Horak 1979: 166) Garrido (1988: 176). Pl. 3a

Habitat: On soil in tropical montane rain forest dominated by *Castanopsis, Lithocarpus*.

Known distribution: Papua New Guinea (type), Malaysia.

Specimens examined: PAPUA NEW GUINEA. Morobe District: Bulolo, Watut, ca. 1100 m elev., on soil in tropical montane rain forest (dominated by *Castanopsis-Lithocarpus*), 28 Apr. 1972, leg. E. Horak (ZT72-425, holotype!). MALAYSIA. Sabah: Mt Kinabalu, Mesilau River, 1600 m elev., on soil in tropical montane rain forest, 18 Jan 1964, leg. E.J.H. Corner RSNB 5007 (E, ZT78-45).

Notes: The type locality of the conspicuous *I. gemina* is situated in tropical montane forests dominated by *Castanopsis* and *Lithocarpus* in Papua New Guinea. This species is probably widely distributed in southeast Asia, but to date it has not been recorded in Thailand or in peninsular Malaysia. However, various habitats indicate that its occurrence can be expected (Horak 1980). Recently, this taxon was found in Indonesia (Bali, Lombok: Horak, unpubl.).

The sharply pointed pileus of *Inocybe gemina* is a reliable macroscopical character, which is reminiscent of small specimens of *I. petchii* or *I. hydrocybiformis*. However, these three taxa are readily distinguished by distinctive microscopical features. No sequence data are yet available for *I. gemina*.

10. ***Inocybe stellata*** E. Horak, Matheny & Desjardin, *spec. nov*. Fig. 9a–g; Pl. 3b–d, 8b
MycoBank MB 519921

Etymology: *stellatus* (Lat.), star-like, referring to the shape of the basidiospores.

Diagnosis: Pileus conical or cuspidate, expanding with a distinctive papilla, dark brown or fuscous brown, papilla drying yellow-brown or pale ochre, center of surface with recurved scales, veil remnants appendiculate on the margin but not persisting with age, context tough, not changing upon exposure. Stipe slender, base equal or slightly swollen; surface dry, densely covered with conspicuous whitish or concolorous fibrils often forming appressed belts or zones. Odor not distinctive. Basidiospores 12–16 µm wide, globose to subglobose, with distinct conical and/or saddle-shaped projections. Cheilocystidia and pleurocystidia 35–50 × 15–20 µm, utriform or broadly fusoid, walls 1–2 µm thick, apices with crystals. In tropical lowland forest dominated by Dipterocarpaceae and in tropical montane forest dominated by *Quercus, Lithocarpus, Castanopsis*, with scattered *Pinus kesiya*, Thailand and Bangladesh.

Holotype:—THAILAND. Mae Hong Son Prov.: south of Mae Hong Son, Hwy. 108, at 247 km marker, ca. 425 m elev., on lateritic soil (in recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak ZT10097 (SFSU, holotype; ZT, isotype) GenBank accession no. GQ893008, GQ892963.

PLATE 3. a. *Inocybe gemina* (ZT72-425, holotype). b. *Inocybe stellata* clade II (ZT10123). c. *Inocybe stellata* clade I (ZT10097, holotype). d. *Inocybe stellata* clade II (DED8060). Scale bars = 10 mm. Photos a, b, c, by Egon Horak, d, by Dennis Desjardin.

Pileus 8–25 (–35) mm wide, at first distinctly conical or cuspidate, gradually expanding with distinctive conical or cuspidate papilla; dark brown (6E–F5–8) or fuscous brown (6E5–8) overall, on drying papilla turning yellow-brown or pale ochre, occasionally with faint reddish tinge; with small recurved, concolorous squamules or small scales at center, with radial, appressed whitish fibrils or appendiculate, non-persisting veil remnants towards rimose margin, dry, veil remnants absent in old specimens; context tough, concolorous or buff, unchanging upon exposure. *Lamellae* 32–40 reaching stipe, 3–7 (–15) lamellulae, adnexed or sinuate, ventricose, up to 3.5 mm wide; at first pale grey-brown (5C3), becoming dark brown (6E7–8) or chocolate brown in age, occasionally with rusty tinge; edges subfimbriate, concolorous or whitish. *Stipe* 35–70 (–120) × 1.5–2 mm, central, cylindrical, slender, equal or base slightly swollen (up to 5 mm diam); surface dry, densely covered with conspicuous whitish or concolorous fibrils often forming appressed belts or zones, subpruinose at apex only, pale grey-brown (6C3) or brown (6E5–8), reddish tinge absent, with white tomentum covering base; cortina present in youth; context solid or hollow. *Odor* not distinctive (or mildly rancid or astringent). *Taste* not distinctive.

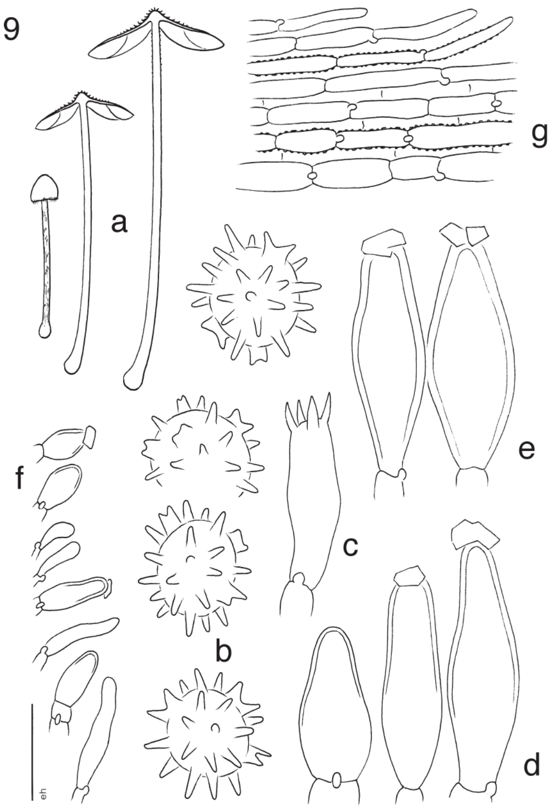


FIGURE 9. Macroscopic and anatomical features for *Inocybe stellata* clade II (DED8060). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Pleurocystidia. f. Caulocystidia. g. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Basidiospores (10–) 12–16 µm (including conical and/or saddle-shaped projections, up to 3 µm long), globose or subglobose, brown, also brown in deposit. *Basidia* (25–) 30–40 × 10–13 µm, 4-spored, clavate or subcylindrical. *Cheilocystidia* (30–) 35–50 × 15–20 µm, utriform or broadly fusoid, metuloid, wall thick (1–2 µm) or thin, hyaline, crystals present; paracystidia 14–25 × 10–15 µm, clavate or vesiculose, thin-walled, hyaline. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* scattered, similar to cheilocystidia, present at stipe apex only. *Pileipellis* a trichoderm or cutis of cylindrical hyphae, 4–7 µm wide, terminal cells not differentiated, non-gelatinized wall encrusted with brown pigment; subpellis of cylindrical, short-celled hyphae, 8–12 µm wide, encrusted with brown pigment; oleiferous hyphae scattered. *Clamp connections* present.

Habitat: Singly on lateritic soil in tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*) and in tropical montane forest (dominated by *Quercus, Lithocarpus, Castanopsis*, with scattered *Pinus kesiya)*, 425–1200 m elev.

Known distribution: Northwest Thailand (type), Bangladesh.

Other specimens examined: BANGLADESH. Rangpur Division: Dinajpur, Birganj, Singra Forest, N25°52‘33.04“, E88°33‘347.28“, 4 Jul. 2013, M.I. Hosen 746 (SHAF 6). THAILAND. Chiang Mai Prov.: Doi Suthep, Sangasabhasri Lane, 1200 m elev., on lateritic soil in tropical montane forest (dominated by *Quercus, Lithocarpus, Castanopsis*), 4 Jul. 2002, leg. E. & A. Horak (ZT10123) GenBank accession no. GQ893009, GQ892965; Hwy 1095, at 22 km marker, N19˚07‘57.0“, E98˚45‘64.7“, on soil in tropical submontane forest (dominated by *Dipterocarpus*), 4 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8015, SFSU; ZT13028) GenBank accession no. GQ893011, GQ892966; same locality and habitat, 4 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8060, SFSU; ZT13029) GenBank accession so. GQ893010, GQ892965; Hwy 1095, at 22 km marker, N19˚07‘570“, E98˚45‘647“, 750 m elev., on soil in tropical submontane forest (dominated by *Dipterocarpus*, *Castanopsis*, with scattered *Pinus kesiya*), 30 Jun. 2007, leg. D.E. Desjardin (DED8162, SFSU) GenBank accession no. GQ893006, GQ892961; Hwy 1095 near 27 km marker, Pathummikaram Temple area, Ban Pha Deng, N19˚06‘28.8“, E98˚44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*), 19 Jul. 2007, leg. E.C. Vellinga 3648 (SFSU) GenBank accession no. GQ893012, GQ892967; same locality and habitat, 19 Jul. 2007, E.C. Vellinga 3651 (SFSU) GenBank accession no. GQ893007, GQ892962.

Notes: *Inocybe stellata* is frequently encountered in tropical lowland and tropical montane forests in northwest Thailand and Bangladesh dominated by *Dipterocarpus* and fagalean trees (*Quercus, Lithocarpus, Castanopsis*). The identification of *I. stellata* must be supported by a molecular analysis as the morphological features (macroscopic and microscopic) of the basidiomes are not sufficient. Indeed, two separate clades of *I. stellata* are recovered as weakly supported sister taxa: clade I [DED8162, ECV3651, ECV3648, ZT10097 (type; Pl. 3c)]; and clade II [DED8015, ZT10123 (Pl. 3b), DED8060 (Pl. 3d)]. Unpublished sequences of *rpb2* from DED8015, DED8060 and DED8162, ECV3651 also support the distinction between the two clades (data not shown). At this point we prefer to label these as two distinct lineages (similar to treatment of *Paxillus involutus* by Vellinga *et al.* 2012) within the morphological species *I. stellata*. Additional collections and future work will be necessary to determine the extent of morphological, ecological, and genetic variation within *I. stellata.* Large basidiomes of *I. stellata* are readily confused with small specimens of *I. petchii, I. gemina* and/or *I. echinosimilis* (E. Horak) Garrido (Horak 1980), which are already recorded or expected to occur either in Thailand or Malaysia.

11. ***Inocybe thailandica*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 10a–i; Pl. 4a–b, 8c
MycoBank MB 519922

Etymology: *thailandicus* (Lat.), referring to the type locality situated in Thailand.

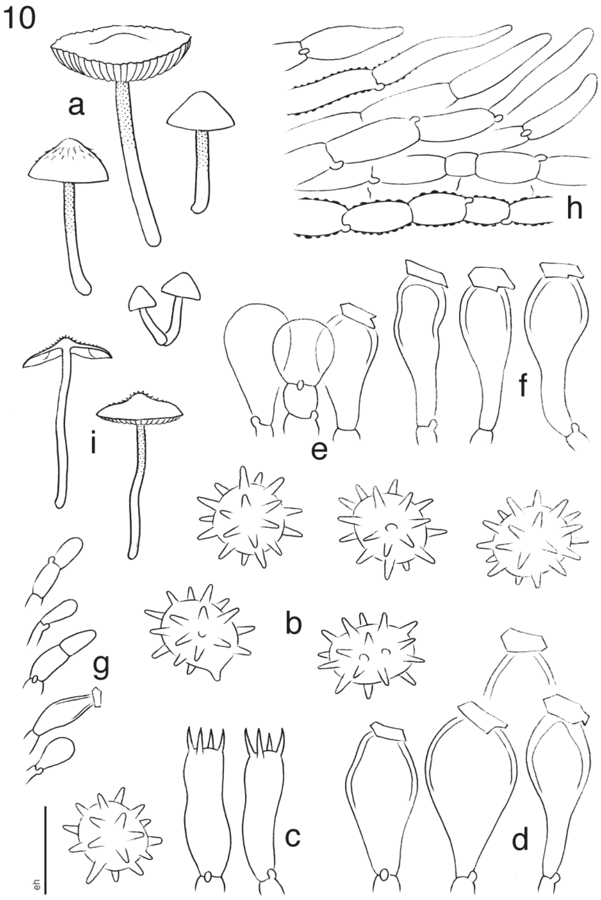


FIGURE 10. Macroscopic and anatomical features for *Inocybe thailandica* (DED8049, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia and cheilocystidium. f. Pleurocystidia. g. Caulocystidia. h. Pileipellis. i. Basidiomes (ZT13017). Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Diagnosis: Pileus dark brown at the center, pale brown towards the margin, disc velvety or with small, recurved scales. Stipe slender, base equal or slightly enlarged, pruinose at the apex, glabrous elsewhere, light brown above, brown or dark brown below. Odor not distinctive. Basidiospores 10–12 µm wide, spinose, globose or broadly ovoid. Cheilocystidia, pleurocystidia, and caulocystidia 20–40 (–45) × 6–17 (–20) µm, broadly clavate or utriform, walls hyaline, up to 1.5 µm thick at apex. In tropical montane forest dominated by *Castanopsis*, 950–1100 m elev., Thailand.

PLATE 4. a. *Inocybe thailandica* (DED8049, holotype). b. *Inocybe thailandica* (DED8008). c. *Inocybe angustifolia* (DED8043). d. *Inocybe angustifolia* (ZT10149). Scale bars = 10 mm. Photos a, b, c, by Dennis Desjardin, d, by Egon Horak.

Holotype:—Thailand. Chiang Mai Prov.: Hwy 1095, near Buddhist temple, at 27 km marker, N19˚06‘ 28.8“, E98˚44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Castanopsis*), 8 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8049, SFSU, holotype; ZT13018, isotype) GenBank accession no. GQ893013, GQ892968.

Pileus 10–25 mm wide, at first obtusely conical, becoming broadly campanulate or plano-convex umbonate, finally plano-umbonate; dark brown (6F5–8), pale brown (6E5–8) towards margin; disc velvety or with small, recurved squamules and scales, fibrillose towards striate and fibrillose-streaked margin, dry, veil remnants absent; context rather tough, 1–1.5 mm thick, whitish, unchanging upon exposure. *Lamellae* 36–42 reaching stipe, 3–5 lamellulae, close, adnexed to adnate, up to 4 mm wide; at first pale brown (6D3, 6D4–5) or greyish brown, becoming brown (6E5–6–8) in age; edges entire or subfimbriate, concolorous. *Stipe* 30–50 × 1.5–2 mm, central, cylindrical, equal or with weakly enlarged base; surface dry, minutely pruinose at apex, glabrous or sericeous elsewhere, light brown (7D4) above, brown (7E5–7) or dark brown (6–7F6–8) towards base; cortina absent; context solid or fistulose in age. *Odor* and *taste* not distinctive.

Basidiospores (9–) 10–12 µm (including rather isolated, conical-spinose projections, up to 2 µm long), globose or broadly ovoid, brown, also brown in deposit. *Basidia* 28–36 × 7–9 µm, 4-spored, clavate. *Cheilocystidia* 30–40 (–45) × 10–17 (–20) µm, broadly clavate or utriform, metuloid, walls up to 1.5 µm thick at apex, hyaline, crystals present but scattered; paracystidia 14–30 × 7–15 µm, clavate or vesiculose, walls hyaline, submetuloid at apex or thin, rarely with crystals. *Pleurocystidia* similar to cheilocystidia, scattered. *Caulocystidia* 20–36 × 6–12 µm, polymorphic, shape ranging from clavate to fusoid, hyaline, thin-walled, rarely thick at apex, crystals absent or rare. *Pileipellis* a trichoderm or cutis of erect or repent, cylindrical hyphae, 6–16 µm wide, terminal cells distinctly conical or fusoid, non-gelatinized wall encrusted with yellow-brown pigment; subpellis hyphae short-ovoid, 10–20 µm wide, encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on soil in tropical montane forest dominated by *Castanopsis*, 950–1100 m elev.

Known distribution: Northwest Thailand (type).

Other specimens examined: THAILAND. Chiang Mai Prov.: Mae Sae on Hwy 1095, at 55 km marker, N19˚14.326‘, E98˚38.294‘, 990 m elev., on soil in tropical montane forest (dominated by *Castanopsis*), 3 Jun. 2006, leg. D.E.

Desjardin (DED8008, SFSU; ZT13016) GenBank accession no. EU600871; Mae Sae on Hwy 1095, at 22 km marker, N19˚07.570‘, E98˚45.647‘, on soil in montane forest (dominated by *Castanopsis*), 4 Jun. 2006, leg. D.E. Desjardin (DED8020, SFSU; ZT13017) GenBank accession no. GQ893014, GQ892969.

Notes: The basidiospores and the general habit of the basidiomes of *I. thailandica* recall several other species recorded from localities in tropical lowland and montane habitats situated in the Malayan Region, e.g. *I. aurantiocystidiata* Turnbull & Watling (1995) from Malaysia, *I. hydrocybiformis* (Horak 1979) from Malaysia and Singapore, and *I. pahangi (*Corner & E. Horak) Garrido (Horak 1979) from Malaysia. Micromorphologically, *I. thailandica* is distinctly characterized by its rather short, broadly clavate or utriform cheilocystidia and pleurocystidia and ecologically by association in stands dominated by *Castanopsis*. In combination with the small habit of the basidiomes, this new Thai species is closely related to *I. calospora* Quél. (sect. *Calosporae*: Vauras 1989, Matheny *et al.* 2009). In temperate zones of Eurasia, *I. calospora* usually occurs in association with broadleaf trees with *Alnus* and *Betula* as its most frequent host partner (Horak 1980, Peintner & Horak 2002, Horak 2005). In addition, the spinose basidiospores of *I. thailandica* are also similar or larger than the following North American taxa also belonging to the *I. calospora* complex, viz., *I. echinocarpa* Ellis & Everh. (1889), *I. rigidipes* Peck (1898), and *I. subfulva* Peck (1888). Furthermore, in the montane zone of northern Argentina, a yet undescribed record of *Inocybe* with spinose basidiospores is found in close association with the native host partner *Alnus jorullensis* (Singer, BAFC T4069; Horak, ZT66-569, ZT66-571, unpublished data).

Molecular results confirm a robust alliance between *I. thailandica* (putative *Castanopsis* associate) together with Betulaceae-associates from Sweden (*I. calospora*) and Argentina (*Inocybe* sp. D25). We refer to this clade as section *Calosporae* (Fig. 1).

12. ***Inocybe angustifolia*** (Corner & E. Horak) Garrido (1988: 120). Fig. 11a–g; Pl. 4c–d, 8d

Basionym: *Astrosporina angustifolia* Corner & E. Horak in Horak (1979: 195).

Pileus 10–35 mm wide, at first obtuse conical, becoming convex with obtuse papilla, campanulate or expanded with low obtuse umbo in age, at first whitish to very pale ochre (4A3), turning yellowish (4B5–6) or pale ochre yellow in age, weakly viscid if moist, at first smooth, in age becoming innate-fibrillose and distinctly rimose at non-striate margin, occasionally with appressed squamules at disc, veil remnants absent; context whitish or pale yellow, slowly turning rust orange on bruising and on exposure. *Lamellae* 28–36 reaching stipe, up to 15 lamellulae, adnate (to subdecurrent), up to 4 mm wide, at first whitish or greyish yellow (4B4), becoming very pale beige brown (6D4) in age, entire edges concolorous. *Stipe* 20–65 × 2–3 (–4) mm, cylindrical, slender, equal, base sometimes swollen; surface dry, pruinose all over, white or pale yellowish (3–4A2–3), staining rust ochre on bruising; cortina absent; context solid, whitish or pale yellow, slowly turning rust orange on bruising and on exposure. *Odor* strongly spermatic. *Taste* spermatic or bitter-raphanoid.

Basidiospores (6.5–) 7–9 × 4.5–5.5 (–6) µm, distinctly nodulose, ovoid, yellow-brown, germ pore absent, brown in deposit. *Basidia* 22–28 × 6–9 µm, 4-spored, slender clavate. *Cheilocystidia* (35–) 40–60 (–70) × 12–18 µm, fusoid, metuloid, walls up to 2.5 µm thick at apex, hyaline, crystals present; paracystidia 15–25 × 8–12 µm, clavate to vesiculose, hyaline, thin-walled. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* similar to cheilocystidia, intermixed with clavate cells. *Pileipellis* a cutis (ixocutis), composed of repent, cylindrical hyphae, 3–5 µm wide, terminal cells not differentiated, weakly gelatinized wall, hyaline, thin-walled, pigment absent; subcutis hyphae short-cylindrical, 5–10 µm wide, wall occasionally up to 1.5 µm wide, weakly encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on (lateritic) soil in tropical montane forest dominated by *Dipterocarpus, Castanopsis*, *Quercus, Lithocarpus*, with scattered *Pinus kesiya*, 950–1260 m elev.

Known distribution: Papua New Guinea (type), Indonesia, Malaysia, northwest Thailand.

Specimens examined: PAPUA NEW GUINEA. Morobe District: Bulolo, Manki, on soil in tropical montane forest (dominated by *Lithocarpus* sp.), 1400 m elev., leg. E. Horak (ZT72-406, holotype!). THAILAND. Chiang Mai Prov.: Chiang Mai, Doi Suthep, 19 km marker, 1260 m elev., on lateritic soil in tropical montane forest (dominated by *Castanopsis, Quercus, Lithocarpus,* with scattered *Pinus kesiya*), 6 Jun. 2002, leg. E. & A. Horak (ZT10149) GenBank accession no. GQ892990, GQ892944; Doi Suthep National Park, Sangasabhasri Lane to Huai Kok Ma Village, N18˚48.68‘, E98˚54.60‘, on soil in tropical montane forest (dominated by *Castanopsis*), 7 Jun. 2006, leg. D.E. Desjardin (DED8043, SFSU; ZT13031) GenBank accession no. EU569851; same locality and habitat, 4 Jul. 2002, leg. D.E. Desjardin (DED8139, SFSU) GenBank accession no. GQ892988, GQ892942; Hwy 1095 near 27 km marker, Pathummikaram Temple area near Ban Pha Deng, N19˚06‘28.8“, E98˚44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*), 27 Jun. 2007, leg. D.E. Desjardin (DED8146, SFSU) GenBank accession no. GQ892989, GQ892943.

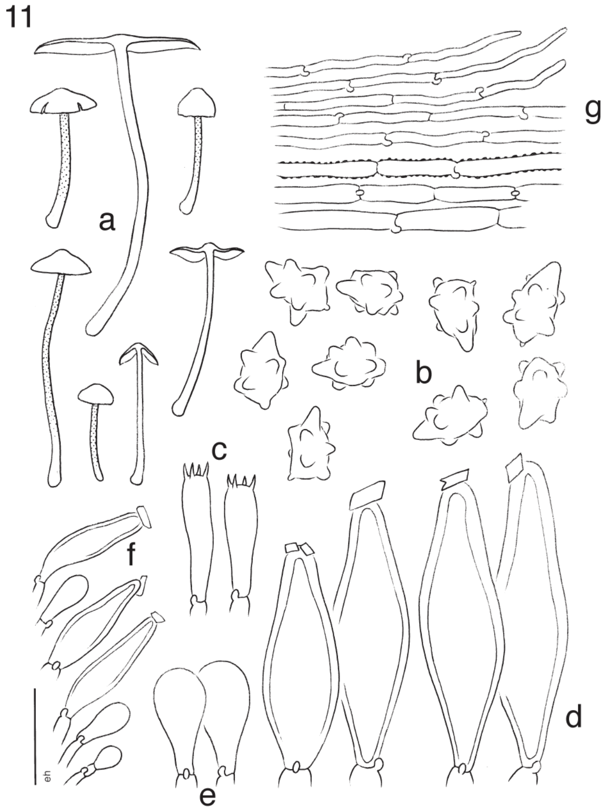


FIGURE 11. Macroscopic and anatomical features for *Inocybe angustifolia* (ZT10149). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Caulocystidia. g. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Notes: The taxonomic description is presented from Thai specimens. The most distinctive characters of *I. angustifolia* are: a pileus (and stipe) at first whitish, pale yellow or fawn in age, narrow, densely crowded lamellae, and an entirely pruinose stipe that is cylindrical-equal or with a swollen to submarginate base. The basidiospores are relatively small, with numerous subconical or hemispherical nodules. Cheilocystidia and pleurocystidia often have yellowish parietal pigment (in 5% KOH). This species is widely distributed in Australasia and southeast Asia (Turnbull & Watling 1999) where it is encountered in association with *Dipterocarpus* or *Castanopsis*, *Lithocarpus* and *Quercus* with scattered *Pinus* in tropical montane rain forest (Horak 1980). It has been reported in association with *Shorea* in Malaysia (Turnbull & Watling 1999).

Two LSU sequences correspond well with collection ZT10149. The sequence of DED8043 appears sister to this core group. *Inocybe angustifolia* shares pale yellow coloration and small size with *I. alabamensis* Kauffman, known from the southeast USA but which may be conspecific with *I. paludinella* (Peck) Sacc. Together with *I. umbratica* Quél. and a second unclarified Thai species, for which our morphological data are incomplete, these four lineages form a robust monophyletic group (91% MLBP).

13. ***Inocybe brevisquamulosa*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 12a–f; Pl. 8e

MycoBank MB 519911

Etymology: *brevis* (Lat.), short; *squamulosus* (Lat.), squamules.

Diagnosis: Basidiomes very small and delicate. Pileus 6–10 mm wide, papilla or umbo absent, surface densely covered with suberect to scurfy scales, cinnamon brown to pale umber brown. Stipe 12–18 × 1 mm, equal with a slightly swollen base, concolorous with the pileus, minutely fibrillose all over (not pruinose), veil remnants absent. Odor not distinctive. Basidiospores 8.5–10 × 5.5–6 µm, distinctly nodulose. Cheilocystidia and pleurocystidia 30–50 × 12–17 µm, utriform, with hyaline walls up to 2.5 µm thick. Caulocystidia absent. In lowland tropical forest dominated by Dipterocarpaceae, Thailand.

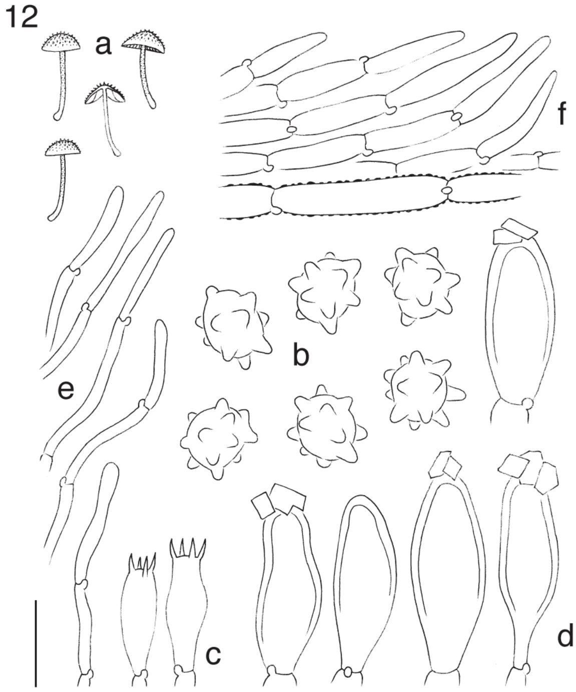


FIGURE 12. Macroscopic and anatomical features for *Inocybe brevisquamulosa* (ZT10102, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia and pleurocystidia. e. Caulocystidia. f. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Holotype:—THAILAND. Mae Hong Son Prov.: S of Mae Hong Son, Hwy. 108, at 247 km marker, 425 m elev., on lateritic soil in (recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT10102, holotype) GenBank accession no. GQ893019, GQ892974.

Pileus 6–10 mm wide, at first hemispherical, convex in age, papilla or umbo absent; cinnamon brown to pale umber brown; disc densely covered with rather coarse, concolorous, suberect to scurfy squamules, coarsely innate-fibrillose towards non-striate margin, dry, veil remnants absent. *Lamellae* 24–32 reaching stipe, 3 (–7) lamellulae, adnexed, ventricose, up to 1.5 mm wide, cinnamon brown to umber brown, edges white and fimbriate. *Stipe* 12–18 × 1 mm, cylindrical, equal, base slightly swollen (up to 1.5 mm diam), concolorous or paler as pileus, also at base, minutely fibrillose all over (not pruinose), dry, solid; veil remnants absent; context concolorous, not reddening. *Odor* and *taste* not distinctive.

Basidiospores 8.5–10 × 5.5–6 µm, ovoid, distinctly nodulose, yellow-brown, brown in deposit. *Basidia* 20–26 × 7–8 µm, 4-spored, clavate or urniform. *Cheilocystidia* 30–50 × 12–17 µm, utriform, metuloid, walls up to 2.5 µm thick at apex, hyaline, crystals present; paracystidia absent. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* absent, surface covered with loose, hyaline, thin-walled, cylindrical hyphae, 4–6 µm wide, terminal cells gradually tapering towards blunt apex, hyaline wall encrusted. *Pileipellis* a trichoderm of erect, cylindrical hyphae, 6–14 µm wide, terminal cells distinctly conical towards apex, non-gelatinized, thin-walled, strongly encrusted with yellow-brown pigment; subcutis hyphae cylindrical, 10–20 µm wide, encrusted with pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on lateritic soil in (recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 425 m elev.

Known distribution: Northwest Thailand.

Notes: The basidiomes of *I. brevisquamulosa* are very small and delicate. Accordingly, this rarely encountered taxon is easily overlooked or can be mistaken readily for one of the two other phenetically similar Thai representatives of *Inocybe*, viz., *I. pusillima* or *I. fragilissima*. Macroscopically, however, *I. brevisquamulosa* can be identified in the field by the minutely squamulose pileus. Furthermore, this taxon is characterized by rather large nodulose basidiospores (the largest of the three aforementioned sympatric taxa) and the broadly utriform metuloid cheilocystidia and pleurocystidia. No distinctive caulocystidia occur on the stipe. *Inocybe brevisquamulosa* was discovered only once occurring on soil among ashes and charcoal after a recent forest fire under dipterocarps.

Phylogenetic analysis (Fig. 1) places *I. brevisquamulosa* (type) sister to sect. *Calosporae* but with poor bootstrap support. *Inocybe brevisquamulosa*, unlike members of sect. *Calosporae*, lacks a pruinose stipe and has distinctly nodulose spores, rather than globose spinose spores.

14. ***Inocybe pusillima*** (Corner & E. Horak) Garrido (1988: 77). Fig. 13a–f; Pl. 8f

Basionym: *Astrosporina pusillima* Corner & E. Horak in Horak (1979: 163).

Etymology: *pusillimus* (Lat.), very small.

Pileus 3–8 mm wide, at first conical, becoming convex and plane-umbonate in age; surface dry, veil remnants absent, disc tomentose, radially fibrillose, with tiny scales near the non-striate margin; at first beige, becoming dark brown (6F6–8) at disc, brown (6E5–6) elsewhere, margin (in young specimens) with distinctive, persisting, whitish, bristle-like fibrils. *Lamellae* 20–24 reaching stipe, 3 (–7) lamellulae, subdistant, ascending or adnexed, up to 1 mm wide, pale brown or umber (6D4); edges entire or subfimbriate, concolorous. *Stipe* 5–8 (–12) × 0.5–1 mm, central, cylindrical, equal, curved; surface dry, pruinose overall, pale brown or dark brown (6F5–8) overall, weakly reddening on bruising; cortina absent; context extremely thin, concolorous, unchanging or weakly reddening upon exposure. *Odor* not distinctive. *Taste* not recorded.

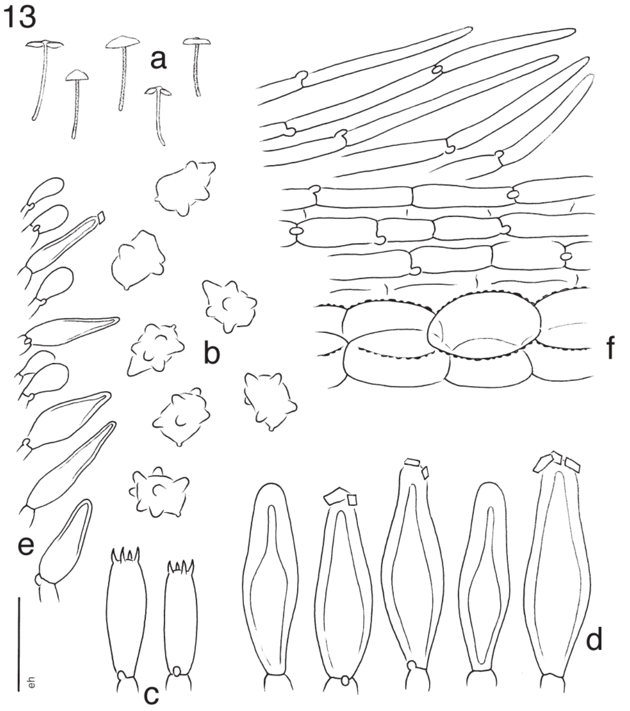


FIGURE 13. Macroscopic and anatomical features for *Inocybe pusillima* (ZT10130). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia and pleurocytidia. e. Caulocystidia. f. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Basidiospores 5.5–7 × 4.5–5 µm, nodulose, yellow-brown. *Basidia* 18–24 × 6–7 µm, 4-spored, clavate or subcylindrical. *Cheilocystidia* (32–) 40–50 × 9–15 µm, fusoid, metuloid, walls up to 2.5 µm thick at apex, hyaline, crystals present; paracystidia 10–15 × 7–9 µm, clavate or vesiculose, with thin, hyaline walls. *Pleurocystidia* size and shape like cheilocystidia. *Caulocystidia* 20–40 × 10–14 µm, shape like cheilocystidia, intermixed with clavate-vesiculose cells. *Pileipellis* a cutis of stiff, repent, cylindrical hyphae, 2–5 µm wide, terminal cells not differentiated, with non-gelatinized hyaline thin walls, pigment absent; subpellis hyphae slender fusoid or ovoid, 16–25 (–30) µm wide, wall encrusted with brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: Singly on soil in tropical montane forest (dominated by *Dipterocarpus, Castanopsis*, with scattered *Pinus kesiya*), 1000–1200 m elev.

Known distribution: Papua New Guinea (type), Singapore, northwest Thailand.

Specimens examined: PAPUA NEW GUINEA. Eastern Highlands: Ayura, on soil in tropical montane rain forest (dominated by *Castanopsis*), 27 May 1973, leg. E. Horak 73-273 (ZT, holotype!). SINGAPORE. Bukit Timah: Fern Valley, on rotten wood in tropical lowland dipterocarp and fagalean forest, 19 Apr. 1941, leg. E.J.H. Corner s.n.

(E; ZT78-043). THAILAND. Mae Hong Son Prov.: S of Mae Hong Son, Hwy. 108, near 235 km marker, road to TV Station 3–9, ca. 1125 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus obtusifolia*, with scattered *Pinus kesiya*), 30 Jun. 2002, leg. E. & A. Horak (ZT10093). Chiang Mai Prov.: Doi Suthep, Sangasabhasri Lane, 1200 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*, *Castanopsis*), 4 Jul. 2002, leg. D.E. Desjardin & E. Horak (ZT10130) GenBank accession no. GQ893005, GQ892060; Hwy 1095 near 27 km marker, Pathummikaram Temple area near Ban Pha Deng, N19°06‘28.8“, E98°44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Dipterocarpus*), 27 Jun. 2007, leg. D.E. Desjardin (DED8145, SFSU) GenBank accession no. GQ893004, GQ892959.

Notes: *Inocybe pusillima* was first described from tropical montane fagalean rain forest in Papua New Guinea, and subsequently specimens collected in Singapore were discovered in the herbarium of E.J.H. Corner kept in Edinburgh, U.K. (Horak 1980). We now report the species from Thailand. In both Papua New Guinea and Thailand, *I. pusillima* was gathered several times in tropical dipterocarp and fagalean forests, thus suggesting this *Inocybe* may be widely distributed in various habitats in southeast Asia and Australasia.

The most distinctive macroscopical character of *I. pusillima* is the silvery coarse fibrils on the pileus that are responsible for the conspicuous strigose „hairs“ along its margin. Further distinctive features of the basidiomes are the entirely pruinose stipe and the remarkably small nodulose basidiospores. The combination of an equal pruinose stipe, small size, and small nodulose basidiospores is consistent with other species of *Inocybe* section *Petiginosae*. Indeed, LSU sequence analysis strongly supports a phylogenetic relationship between *I. pusillima*, *I. subexilis* (Peck) Sacc., and a sequence that is mislabeled *I. petiginosa* from North Carolina. Unpublished results that include French and Swedish representatives of *I. petiginosa* (Fr.) Gillet corroborate these findings. LSU sequences of two samples of *I. pusillima* exhibit substantial heterogeneity (Fig. 1). Sequences of this species from elsewhere in southeast Asia, especially the type locality of Papua New Guinea, require comparison.

15. ***Inocybe fragilissima*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 14a–h; Pl. 5a, 8g

MycoBank MB519913

Etymology: *fragilissimus* (Lat.), most fragile.

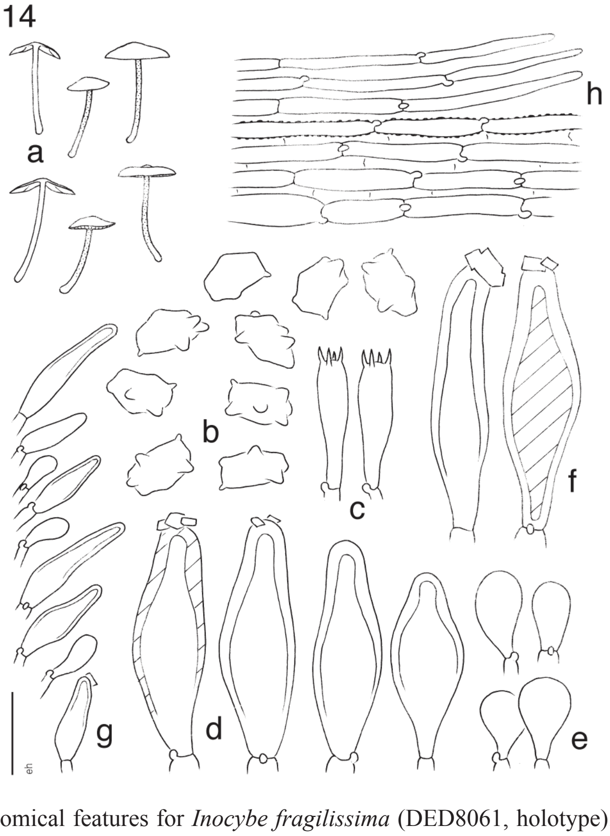


FIGURE 14. Macroscopic and anatomical features for *Inocybe fragilissima* (DED8061, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Pleurocystidia. g. Caulocystidia. h. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Diagnosis: Basidiomes very small. Pileus 7–13 mm wide, developing a low umbo or small obtuse-conical papilla with age, surface minutely innately fibrillose, distinctive velipellis absent, margin not splitting, cinnamon brown to argillaceous brown. Lamellae adnexed to almost free, pale cinnamon when young, gradually becoming dark fuscous or dark chocolate brown. Stipe 15–25 × 1 mm, pallid or paler than the pileus, base not bulbous, upper part distinctly pruinose, lower half appressed fibrillose, cortina absent. Basidiospores 5.5–7 × 4–4.5 µm, nodulose or irregularly angled with few inconspicuous nodules. Cheilocystidia, pleurocystidia, and caulocystidia 35–60 × 10–17 µm, fusoid, walls up to 2.5 µm thick, ochre brown or yellowish. In tropical lowland forest dominated by Dipterocarpaceae, Thailand.

Holotype:—THAILAND. Chiang Mai Prov.: Hwy 1095, at 22 km marker, N19°07‘57.0“, E98°45‘64.7“, on soil in tropical submontane forest (dominated by *Dipterocarpus*), 11 Jun. 2006, leg. D.E. Desjardin (DED 8061, SFSU, holotype) GenBank accession no. GQ893021, GQ892977.

PLATE 5. a. *Inocybe fragilissima* (DED8061, holotype). b. *Inocybe pileosulcata* (DED8058). c. *Inocybe parvibulbosa* (ZT10099, holotype). d. *Inocybe parvibulbosa* (DED8021). Scale bars = 10 mm. Photos a, b, d, by Dennis Desjardin, c, by Egon Horak.

Pileus 7–13 mm wide, at first convex, becoming expanded with low umbo or small obtuse-conical papilla in age, cinnamon brown to argillaceous brown (6E5–6, with pale ochre tinge), minutely innate-fibrillose all over, non-striate margin not splitting, if moist slightly viscid (covered with soil particles), soon dry, distinctive velipellis absent. *Lamellae* 32–40 reaching stipe, 3 (–7) lamellulae, moderately close, adnexed to almost free, up to 1.5 mm broad, narrow, at first pale cinnamon (6D4) but gradually becoming dark fuscous or dark chocolate brown; edges subfimbriate, concolorous. *Stipe* 15–25 × 1 mm, cylindrical, equal or gradually enlarging into base, sometimes slightly swollen; surface dry, upper portion distinctly pruinose, lower half appressed fibrillose, pallid or paler concolorous with pileus, basal tomentum absent; cortina absent; context solid, concolorous, unchanging upon exposure. *Odor* not distinctive or weakly acidulous to spermatic. *Taste* similar to odor.

Basidiospores 5.5–7 × 4–4.5 µm, nodulose or irregularly angled with few inconspicuous nodules, pale yellow-brown, germ pore absent, brown in deposit. *Basidia* 24–30 × 6–7 µm, 4-spored, slender clavate. *Cheilocystidia* 35–60 × 10–17 µm, fusoid, metuloid, with ochre brown or yellowish walls up to 2.5 µm thick at apex, occasionally also with ochre brown, plasmatic pigment, scattered crystals or resinous matter present; paracystidia 12–23 × 8–12 µm, clavate to vesiculose, hyaline, thin-walled, scattered. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* similar to cheilocystidia, often in clusters, intermixed with numerous clavate-vesiculose, hyaline cells. *Pileipellis* a cutis of repent, cylindrical hyphae, 3–4 µm wide, terminal cells not differentiated, non-gelatinized or weakly gelatinized, encrusted with pale yellow-brown pigment; subcutis hyphae cylindrical, 6–14 µm wide, encrusted with pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On lateritic soil in tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*) forest, 425 m elev.

Known distribution: Northwest Thailand.

Notes: As pointed out in the key, *I. fragilissima* is the third Thai species (cf. *I. brevisquamulosa*, *I. pusillima)* with remarkably small basidiomes. It is recognized, in particular, by the predominantly brown basidiomes, innately fibrillose pileus, pruinose stipe in its upper portion only and the small weakly nodulose or angular basidiospores. The species is placed phylogenetically in sect. *Petiginosae* (Fig. 1) with strong support.

16. ***Inocybe ornata*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 15a–h; Pl. 8h
MycoBank MB 519917

Etymology: *ornatus* (Lat.), ornate.

Diagnosis: Pileus 20–45 mm wide, pale cinnamon, argillaceous or pale ochre, disc with umber brown tinge; surface smooth, viscid when moist; margin non-striate and not splitting, with persistent whitish appendiculate veil remnants. Lamellae pallid at first, slowly becoming cinnamon to beige brown. Stipe 20–60 × 3.5–5 mm, with a marginate basal bulb up to 10 mm wide, surface entirely pruinose, whitish, cortina absent, margin of base covered by conspicuous whitish persisting fibrillose appendiculate volva-like veil remnants. Basidiospores 6–8 × 4.5–5.5 µm, ovoid, with low hemispheric nodules. Cheilocystidia, pleurocystidia, and caulocystidia 45–65 × 11–17 µm, fusoid, walls up to 3 µm thick, hyaline. In tropical lowland forest dominated by Dipterocarpaceae, Thailand.

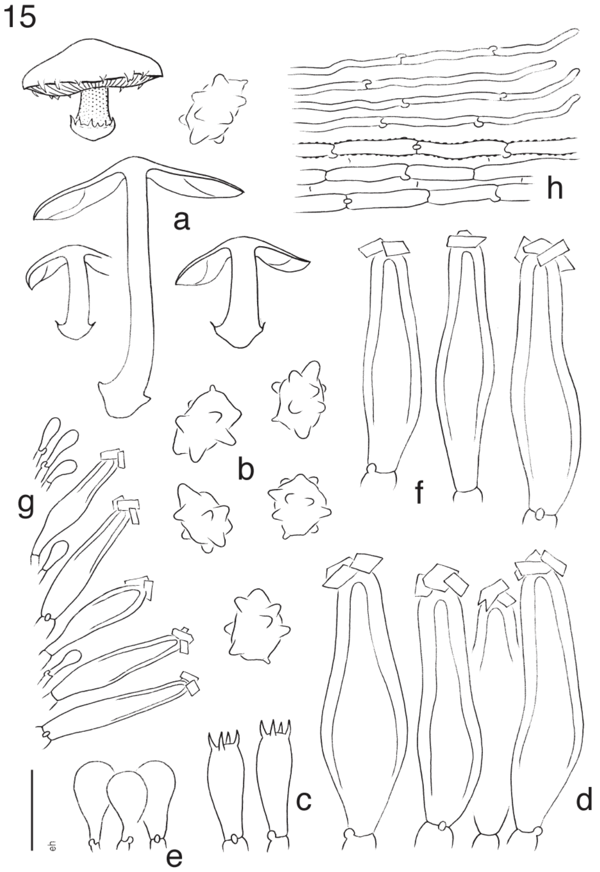


FIGURE 15. Macroscopic and anatomical features for *Inocybe ornata* (ZT10107, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Pleurocystidia. g. Caulocystidia. h. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Holotype:—THAILAND. Mae Hong Son Prov.: S of Mae Hong Son, Hwy. 108, 247 km marker, ca. 425 m elev., on lateritic soil in tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT10107, holotype) GenBank accession no. GQ892975.

Pileus 20–45 mm wide, at first hemispherical to convex with incurved margin, in age becoming campanulate to umbonate-expanded; pale cinnamon, argillaceous or pale ochre, disc with umber brown tinge; surface smooth, viscid if moist, non-striate and non-splitting margin with conspicuous, appendiculate whitish or pallid, fibrillose, persisting veil remnants. *Lamellae* 32–40 reaching stipe, 3–7 lamellulae, moderately close to close, adnexed to short-marginate, ventricose, up to 5 mm broad; at first pallid slowly becoming cinnamon to beige-brown in mature specimens, edges white and fimbriate. *Stipe* 20–60 × 3.5–5 mm, cylindrical, equal then gradually enlarging into distinctive bulbous-marginate base (up to 10 mm wide), whitish; surface dry, pruinose all over, margin of base covered by conspicuous whitish persisting fibrillose appendiculate volva-like veil remnants; cortina absent; context solid, whitish, unchanging upon exposure. *Odor* weakly spermatic. *Taste* like odor.

Basidiospores 6–8 × 4.5–5.5 µm, ovoid, nodulose, hemispherical projections (nodules) rather inconspicuous, up to 1.5 µm high, yellow-brown, brown in deposit. *Basidia* 20–26 × 7–8 µm, 4-spored, slender clavate. *Cheilocystidia* 45–65 × 11–17 µm, fusoid, metuloid, walls up to 3 µm thick at apex, hyaline, crystals present; paracystidia 15–20 × 8–10 mm, clavate to vesiculose, hyaline, thin-walled. *Pleurocystidia* size and shape like cheilocystidia. *Caulocystidia* similar to cheilocystidia, intermixed with paracystidia-like cells. Hyphae of stipe 4–12 µm wide, encrusted with pigment. *Pileipellis* an (ixo)cutis of repent, cylindrical hyphae, 2–4 µm wide, terminal cells not differentiated, weakly gelatinized hyaline and smooth thin wall; subcutis hyphae cylindrical, 5–10 µm wide, encrusted with pale yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On lateritic soil in tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), ca. 425 m elev.

Known distribution: Northwest Thailand.

Notes: Among all representatives of *Inocybe* recorded so far in Thailand and Malaysia, *I. ornata* is outstanding due to the significant cup-shaped and marginate base of the stipe, the margin of which is appendiculate from volva-like, persistent, white velar remnants. In fresh specimens the pileus surface is densely covered with innately fibrillose and weakly gelatinized hyphae from the universal veil (velipellis), and the whitish stipe is pruinose over the entire length. The microscopical characters are insignificant except for the medium-sized basidiospores with rather low hemispherical nodules. The LSU sequence of the type (ZT10107) is poorly placed and divergent from other sequences in the *Inocybe* clade. Affiliation with other species is not well-known at this time.

17. ***Inocybe pileosulcata*** E. Horak, Matheny & Desjardin, *spec. nov*. Fig. 16a–g; Pl. 5b
MycoBank MB 519919

Etymology: *pileus* (Lat.), pileus; *sulcatus* (Lat.) sulcate, split.

Diagnosis: Basidiomes medium- to large-sized. Pileus 35–55 mm wide, conspicuously sulcate and splitting (plicate) from the margin to the smooth umbo, veil remnants absent, brownish orange to light yellowish brown, elsewhere more or less greyish white to yellowish grey. Stipe 40–55 × 3–4 mm, with a conspicuous marginate basal bulb up to 10 mm wide, lacking appendiculate veil remnants, surface entirely pruinose, white or pale orange. Basidiospores 10–12 × 8.5–10 µm, stellate. Cheilocystidia, pleurocystidia, and caulocystidia 55–70 × 18–26 µm, fusoid or utriform, with hyaline walls up to 5 µm thick. In tropical lowland and montane forests dominated by *Dipterocarpus, Castanopsis, Shorea*, intermixed with *Pinus kesiya*, Thailand and Malaysia.

Holotype:—THAILAND. Chiang Mai Prov.: Hwy 1095, at 22 km marker, N19˚07.570‘, E98˚45‘647“, 750 m elev., on soil in tropical submontane forest (dominated by *Dipterocarpus*), 750 m elev., 11 Jun. 2006, leg. A. Neves & D.E. Desjardin (DED8058, holotype, SFSU; ZT13025, isotype) GenBank accession no. EU600838.

Misappl.: *Inocybe asterospora* Quél. sensu Horak, *Persoonia* 10: 202, 1979. — *Inocybe asterospora* Quél. sensu Turnbull, *Edinb. J. Bot.* 52: 353, 1995.

Pileus (30–) 35–55 mm wide, at first convex becoming broadly plano-convex with low but distinct umbo, conspicuously sulcate and splitting (plicate) from margin to glabrous umbo, radially appressed-fibrillose on ridges of plicae; surface dry, veil remnants absent; umbo and plicae pale brownish orange (5C3) to light yellowish brown (5D4), elsewhere pale dingy greyish white to yellowish grey (4B2); context in pileus up to 1 mm thick, white, unchanging upon exposure. *Lamellae* 32–44 reaching stipe, 3–7 lamellulae, close, adnexed, up to 5 mm wide, pale brownish orange (5C3) becoming greyish brown (6D3), entire or subfimbriate edges concolorous. *Stipe* 40–55 × 3–4 mm, central, cylindrical, equal until a distinctive marginate bulb up to 10 mm wide at base, margin of bulb devoid of appendiculate volva-like veil remnants, pruinose all over, white or pale orange (5A2), dry, hollow; cortina absent. *Odor* and *taste* not distinctive.

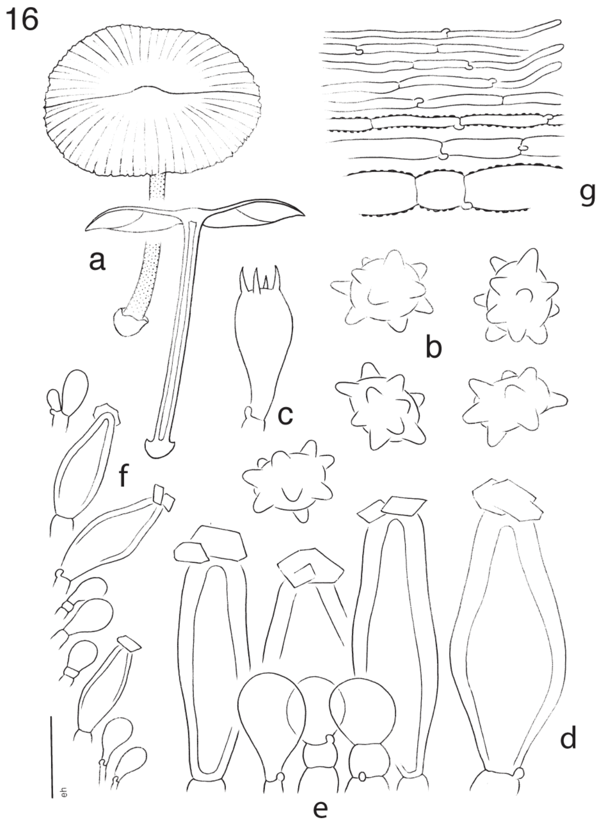


FIGURE 16. Macroscopic and anatomical features for *Inocybe pileosulcata* (DED8058, holotype). a. Basidiomes. b. Basidiospores. c. Basidium. d. Cheilocystidia. e. Paracystidia. f. Caulocystidia. g. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Basidiospores 10–12 × 8.5–10 µm, ovoid, conspicuously nodulose (stellate), covered with rather large, conspicuous, obtuse-conical nodules, yellow-brown, brown (7E–F6) in deposit. *Basidia* 30–34 x 10–13 µm, 4-spored, clavate. *Cheilocystidia* 55–70 × 18–26 µm, fusoid or utriform, metuloid, walls up to 5 µm thick at apex, hyaline, crystals present; paracystidia 15–25 × 10–15 µm, vesiculose or subglobose, walls thin and hyaline. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* similar to cheilocystidia, intermixed with clavate, thin-walled, hyaline cells. *Pileipellis* a cutis of repent, cylindrical hyphae, 2–4 µm wide, terminal cells not differentiated, non-gelatinized wall, thin, hyaline; subpellis hyphae cylindrical or broadly ovoid, 8–14 µm wide, encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat On soil in tropical lowland and montane forest (750–1700 m elev.) dominated by *Dipterocarpus, Castanopsis, Shorea*, intermixed with *Pinus kesiya*.

Known distribution: Malaysia (Selangor, Pahang, Sabah), Northwest Thailand (type).

Other specimens examined: MALAYSIA. Selangor: Kepong, Forest Research Institute (FRIM), on soil in tropical lowland forest (under *Shorea sumatrana*), 19 Mar. 1993, leg. E. Turnbull 27 (E). Pahang: Tembeling, 8 Nov. 1930, leg. E.J.H. Corner (ZT 78-066). Sabah: Mt Kinabalu, Mesilau River, on soil in tropical montane forest, 1700 m elev., 19 Jan. 1964, leg. E.J.H. Corner RSNB 5015 (E, ZT 78-067); same locality and habitat, 21 Apr. 1964, leg. E.J.H. Corner RSNB 8387 (E; ZT 78-065). THAILAND. Chiang Mai Prov.: same locality as the type, on soil in tropical submontane forest (dominated by *Dipterocarpus*, *Castanopsis*, with scattered *Pinus kesiya*), 30 Jun. 2007, leg. D.E. Desjardin (DED8164, SFSU) GenBank accession no. GQ892996, GQ892951.

Notes: Based on present collections, *I. pileosulcata* is reported from tropical lowland and montane forests both in Thailand and Malaysia. The medium-sized to large-sized basidiomes of this spectacular species are characterized by the deeply and radially sulcate-splitting pileus, the pruinose stipe with distinctly marginate basal bulb, the large, thick-walled cheilocystidia and pleurocystidia and the large basidiospores with distinctive conical projections. All macroscopic and microscopic characters are similar to the European *I. asterospora* Quél. (Stangl 1989, Horak 2005), and thus it is not surprising that earlier records of this taxon were erroneously filed under this name (Horak 1979, Turnbull 1995).

LSU sequences of this species form two distinct sister lineages apart from a North American *I.* aff. *asterospora*. Together with *Inocybe* sp. DED8044, also from Thailand but for which morphological data are insufficent, these sequences form a robust *asterospora*-like clade.

18. ***Inocybe parvibulbosa*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 17:a–i; Pl. 5c–d, 8i
MycoBank MB 519918

Etymology: *parvus* (Lat.), small; *bulbosus* (Lat.), bulbous.

Diagnosis: Similar to *Inocybe lineata* but *I. parvibulbosa* differs by the smaller basidiomes (pileus 6–18 mm wide, stipe 15–30 × 1–1.5 mm), broader basidiospores, and the pileipellis structure: a cutis of non-gelatinized or weakly gelatinized hyphae in *I. parvibulbosa*, a trichoderm or cutis of erect or repent, non-gelatinized hyphae in *I. lineata*. Pileus smooth or minutely scaly over the disc, weakly splitting or rimose towards the margin. Stipe slender, entirely pruinose, with a distinct marginate bulb, cortina absent. Basidiospores 8.5–10.5 × 8–9.5 µm, ovoid, distinctly nodulose, with hemispherical or obtuse-conical projections. Cheilocystidia, pleurocystidia, and caulocystidia 40–60 (–70) × 12–20 (–24) µm, broadly fusoid or utriform; walls mostly hyaline, up to 4–5 µm thick. In tropical lowland and montane mixed dipterocarp, fagalean, conifer forests, Thailand and Papua New Guinea.

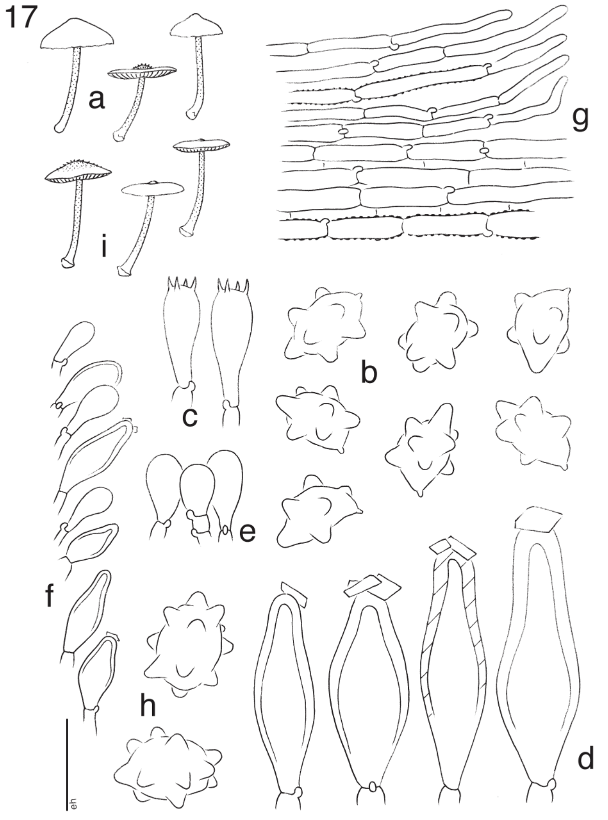


FIGURE 17. Macroscopic and anatomical features for *Inocybe parvibulbosa* (ZT10099, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Caulocystidia. g. Pileipellis. h. Basidiospores (ZT13033). Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Holotype:—THAILAND. Mae Hong Son Prov.: S of Mae Hong Son: Hwy. 108, 247 km marker, ca. 425 m elev., on lateritic soil (in recently burned) tropical submontane forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT10099, holotype) GenBank accession no. GQ893000, GQ892955.

Pileus 6–18 mm wide, at first obtuse-conical, becoming convex, campanulate or plane with depressed obtuse umbo in age, cinnamon brown, dark hazel brown (6E5–6) or fuscous, paler towards margin, smooth or minutely squamulose at disk, coarsely innately fibrillose towards weakly splitting or rimose margin, young specimens occasionally with greyish velipellis over disk, subviscid if moist, veil remnants at margin absent. *Lamellae* 36–52 reaching stipe, 3–7 lamellulae, close to crowded, adnate to adnexed, ventricose, up to 2 mm broad; at first greyish brown, cinnamon brown, becoming dark brown with rusty tinge or umber brown in age; edges fimbriate and white. *Stipe* 15–30 × 1–1.5 (–2) mm, cylindrical, equal above, but base with distinctive marginate, cup-shaped bulb, up to 3.5 mm wide; surface dry, pruinose all over, whitish to pallid brown, dark brown in old specimens; cortina absent; context solid, whitish, not reddening upon exposure. *Odor* not distinctive or weakly spermatic. *Taste* not distinctive.

Basidiospores 8.5–10.5 × 8–9.5 µm, ovoid, distinctly nodulose, hemispherical or obtuse-conical projections (nodules) 2–2.5 µm high, yellow-brown, brown in deposit. *Basidia* 20–34 × 7–10 µm, 4-spored, clavate. *Cheilocystidia* 40–60 (–70) × 12–20 (–24) µm, broadly fusoid or utriform, with hyaline or sometimes yellow-brown metuloid walls, up to 4–5 µm thick at apex, crystals present; paracystidia (10–) 15–30 × 7–15 µm, vesiculose or clavate, numerous, with hyaline thin walls, pigment absent. *Pleurocystidia* size and shape like cheilocystidia. *Caulocystidia* size and shape like cheilocystidia, but less metuloidal, intermixed with clavate, thin-walled cells. *Pileipellis* an (ixo)cutis of repent (or suberect) cylindrical hyphae, (2–) 4–8 (–10) µm wide, terminal cells not differentiated, non-gelatinized or weakly gelatinized wall encrusted with yellow-brown pigment; subcutis hyphae cylindrical, 6–12 µm wide, encrusted with pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On lateritic soil, in (recently burned) tropical lowland and montane mixed dipterocarp, fagalean, conifer forests (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*, *Castanopsis* spp*, Pinus kesiya*), 425–1000 m elev.

Known distribution: Papua New Guinea, Northwest Thailand (type).

Other specimens examined: THAILAND. Mae Hong Son Prov.: S of Mae Hong Son, Hwy. 108, 235 km marker, road to TV Station 3–9, ca. 580 m elev., on lateritic soil in tropical submontane mixed dipterocarp and conifer forest (*Dipterocarpus obtusifolia*, *Pinus kesiya*), 29 Jun. 2002, leg. E. & A. Horak (ZT10078) GenBank accession no. GQ893001, GQ892956; S of Mae Hong Son, Hwy. 108, 247 km marker, ca. 425 m elev., on lateritic soil (in recently burned) tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT10103) GenBank accession no. GQ893002. Chiang Mai Prov.: S of Mae Hong Son, Hwy. 108, at 247 km marker, ca. 425 m elev., on lateritic soil tropical lowland forest (dominated by *Dipterocarpus obtusifolia*, mixed with *Tectona grandis*), 1 Jul. 2002, leg. E. & A. Horak (ZT10105) GenBank accession no. GQ893003, GQ892957; Hwy. 1095, at 22 km marker, N19°07‘570“, E98°45‘647“, on soil in tropical lowland forest (dominated by *Dipterocarpus)*, 4 Jun. 2006, leg. D.E. Desjardin (DED8021, SFSU; ZT13033) GenBank accession no. GQ892999, GQ892954. PAPUA NEW GUINEA. Morobe District: Wau, Mt Kaindi, on soil in tropical montane rain forest under *Nothofagus carrii*, 2300 m elev., 3 Jun. 1973, leg. E. Horak 73-299 (ZT).

Notes: The epithet of *I. parvibulbosa* refers to the distinctive marginate bulb at the base of the slender and entirely pruinose stipe. To date the species has been recorded six times and it can be speculated that in the Malayan tropical lowland and montane forests *I. parvibulbosa* is an obligate ectomycorrhizal partner of *Dipterocarpus* spp. and probably also *Castanopsis* spp.

Inocybe parvibulbosa represents a complex of genetically distinct lineages. The name is conservatively applied here as four different LSU sequences labeled *I. parvibulbosa* form a paraphyletic entity that gives rise to *I. lineata* (described below). All four are found in dipterocarp associations or in forests with dipterocarps present. Together, LSU sequences of *I. parvibulbosa* and *I. lineata* form a strongly supported clade. More field data and sequences from alternative loci, we believe, are required to better interpret the extent of morphological and genetic variation in this complex. For further discussion refer to *I. lineata*.

19. ***Inocybe lineata*** E. Horak, Matheny & Desjardin, *spec. nov.* Fig. 18a–h; Pl. 6a–b
MycoBank 519915

Etymology: *lineatus* (Lat.), striate, streaked.

Diagnosis: Similar to *Inocybe parvibulbosa* but *I. lineata* differs by the larger basidiomes (pileus 18–26 mm wide, stipe 25–50 × 2–3 mm), narrower basidiospores, and the non-gelatinized trichoderm or cutis-like pileipellis. Pileus center scurfy or with small scales, margin conspicuously splitting and sulcate-plicate. Stipe entirely pruinose, with a distinct marginate bulb, cortina absent. Basidiospores 8.5–10 × 6–7.5 µm, distinctly nodulose, with hemispherical or broadly conical projections. Cheilocystidia, pleurocystidia, and caulocystidia 45–60 × 15–20 µm, broadly fusoid or lageniform, with hyaline walls up to 3.5 µm thick at the apex. In tropical montane forest dominated by *Dipterocarpus*, *Castanopsis*, Thailand.

Holotype:—THAILAND. Chiang Mai Prov.: Hwy 1095, at 22 km marker, N19°07‘570“, E98°45‘647“, on soil in tropical montane forest (dominated by *Dipterocarpus*), 4 Jun. 2006, leg. T.J. Baroni & D.E. Desjardin (DED8019, holotype, SFSU; ZT13019, isotype) GenBank accession no. EU569861.

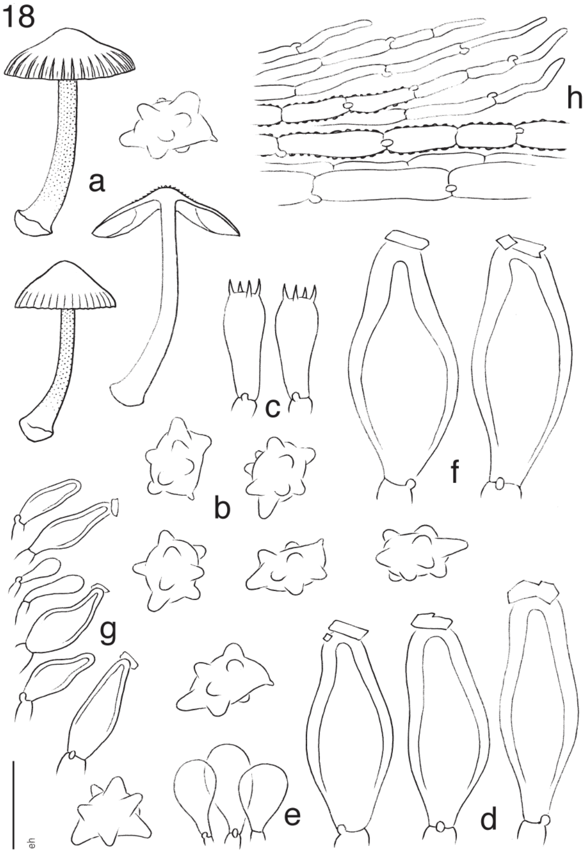


FIGURE 18. Macroscopic and anatomical features for *Inocybe lineata* (DED8019, holotype). a. Basidiomes. b. Basidiospores. c. Basidia. d. Cheilocystidia. e. Paracystidia. f. Pleurocystidia. g. Pileipellis. Scale bars: basidiomes = 20 mm, basidiospores = 10 µm, basidia and cystidia = 20 µm, pileipellis = 40 µm. Drawings by Egon Horak.

Pileus 18–26 mm wide, at first conical, campanulate or umbonate expanded in age; surface dry, veil remnants absent, with small, scurfy also recurved squamules at disk (and between radial streaks), fibrillose towards conspicuously splitting and sulcate-plicate margin; dark brown (7F5–7) or fuscous, pale olive brown (7E4–5) towards the margin, exposed subpellis greyish yellow (4B3). *Lamellae* 36–42 reaching stipe, (3–) 7 lamellulae, close, ascending or adnexed, up to 4 mm wide, brown (6–7E4); edges entire or subfimbriate, concolorous or whitish. *Stipe* 25–50 × 2–3 mm, central, cylindrical, equal but with distinctive cup-shaped marginate bulb, up to 6 mm wide; surface pruinose all over, dry, pale brown or greyish brown or brownish orange (6B3) over whole length, occasionally with faint incarnate tint, edge of basal bulb white; cortina absent; context solid, white, weakly incarnate upon exposure. *Odor* not distinctive or faintly sour. *Taste* not recorded.

Basidiospores 8.5–10 × 6–7.5 µm, ellipsoid, distinctly nodulose, hemispherical or broadly conical projections up to 3 mm high, yellow-brown, brown in deposist. *Basidia* 20–28 × 8–10 µm, 4-spored, clavate. *Cheilocystidia* 45–60 × 15–20 µm, broadly fusoid or lageniform, metuloid, with hyaline walls up to 3.5 µm thick at apex, crystals present; paracystidia 15–20 × 8–9 µm, clavate, hyaline, thin-walled. *Pleurocystidia* similar to cheilocystidia. *Caulocystidia* similar to cheilocystidia, intermixed with clavate, hyaline, thin-walled cells. *Pileipellis* a trichoderm or cutis of erect or repent, cylindrical hyphae, 3–4 µm wide, terminal cells not differentiated, non-gelatinized wall encrusted with (yellow-) brown pigment; subpellis composed of short cylindrical hyphae 8–15 µm wide, walls hyaline, encrusted with yellow-brown pigment; oleiferous hyphae absent. *Clamp connections* present.

Habitat: On soil in tropical montane forest (dominated by *Dipterocarpus*, *Castanopsis*), 1050–1150 m elev.

Known distribution: Northwest Thailand.

Other specimens examined: THAILAND. Chiang Mai Prov.: Hwy 1095, near 27 km marker, N19˚06‘28.8“, E98˚44‘47.3“, 1050 m elev., on soil in tropical montane forest (dominated by *Castanopsis*), 8 Jun. 2006, leg. T.J. Baroni & D.E. Desjardin (DED8048, SFSU; ZT13020) GenBank accession no. GQ892958.

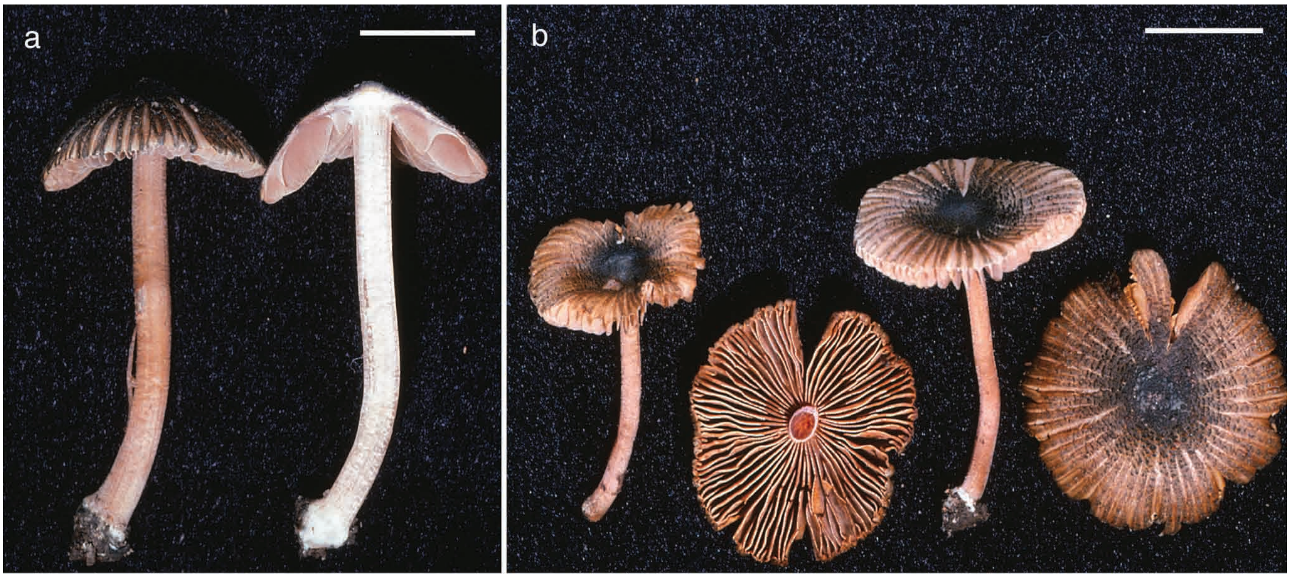


PLATE 6. a. *Inocybe lineata* (DED8019, holotype). b. *Inocybe lineata* (DED8048). Scale bars = 10 mm. Photos by Dennis Desjardin.

Notes: In the field the brown or fuscous colored basidiomes of *I. lineata* resemble those of the closely related *I. parvibulbosa*, although the basidiomes of *I. lineata* are larger. The two sympatric Thai species are distinguished by the size of the basidiomes and the surface structure of the pileipellis. Morphotaxonomically, the two species share similar basidiospores and distinctly metuloid cystidia.

Unclarified species of *Inocybe* from Thailand

While we were able to produce and release genetic data for six additional autonomous species of *Inocybe* from Thailand, morphological data for the following species are insuffcent (data lost) for complete documentation. However, we would like to provide collection details and brief phylogenetic results in case these species are detected in the future.

20. ***Inocybe sp***. DED8050, DED8147, DED8161, ZT10044 Pl. 7c

This species is nested strongly in the *umbratica-paludinella* clade and potentially affiliated with a broad range of host trees: *Pinus*, *Castanopsis*, and *Dipterocarpus*. It is closely related to *I. angustifolia*.

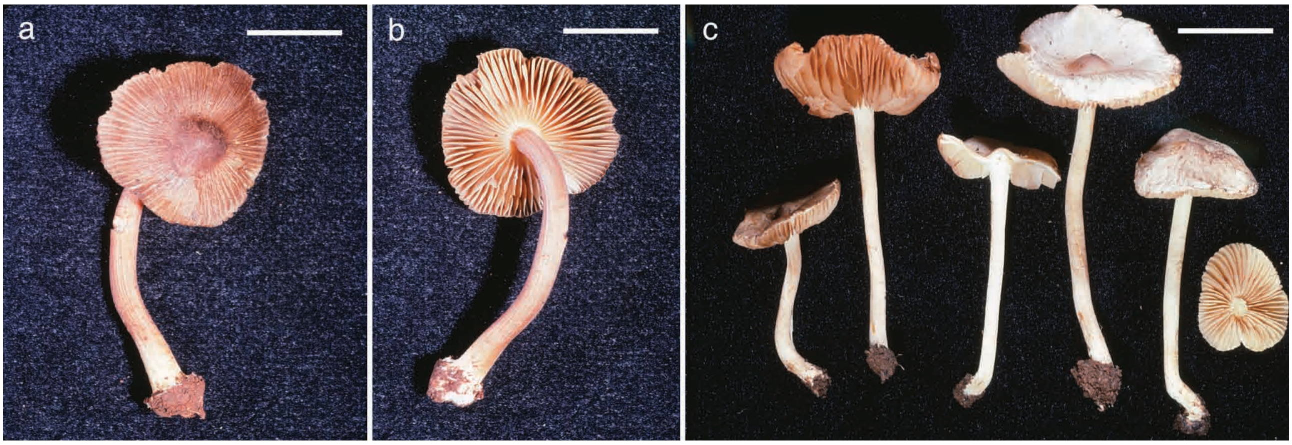


PLATE 7. a. *Inocybe* sp. DED8044 (pileus view). b. *Inocybe* sp. DED8044 (lamellae view). c. *Inocybe* sp. DED8050. Scale bars = 10 mm. Photos by Dennis Desjardin.

Specimens examined: THAILAND. Chiang Mai Prov.: near Buddhist temple along Hwy 1095 near 27 km marker, N19˚06'28.8", E98˚44'47.3", 1050 m elev., in soil under *Castanopsis* sp, 8 Jun. 2006, leg. R. Zhao & D.E. Desjardin (DED8050, SFSU; ZT13032) GenBank accession no. EU569852; same location, in soil under *Dipterocarpus* spp, 27 Jun. 2007, leg. D.E. Desjardin (DED8147, SFSU) GenBank accession no. GQ892986, GQ892940; Doi Inthanon National Park, Hwy 1009 at 25 km marker, N18˚32‘19.5“, E98˚33‘42.5“, 950 m elev., in soil under *Pinus kesiya*, 28 Jun. 2007, leg. D.E. Desjardin (DED8161, SFSU) GenBank accession no. GQ892985, GB892939; same location, in soil under *Dipterocarpus* spp, *Castanopsis* sp and *Pinus kesiya*, 25 Jun. 2002, leg. E. Horak (ZT10044) GenBank accession no. GQ892991, GQ892945.

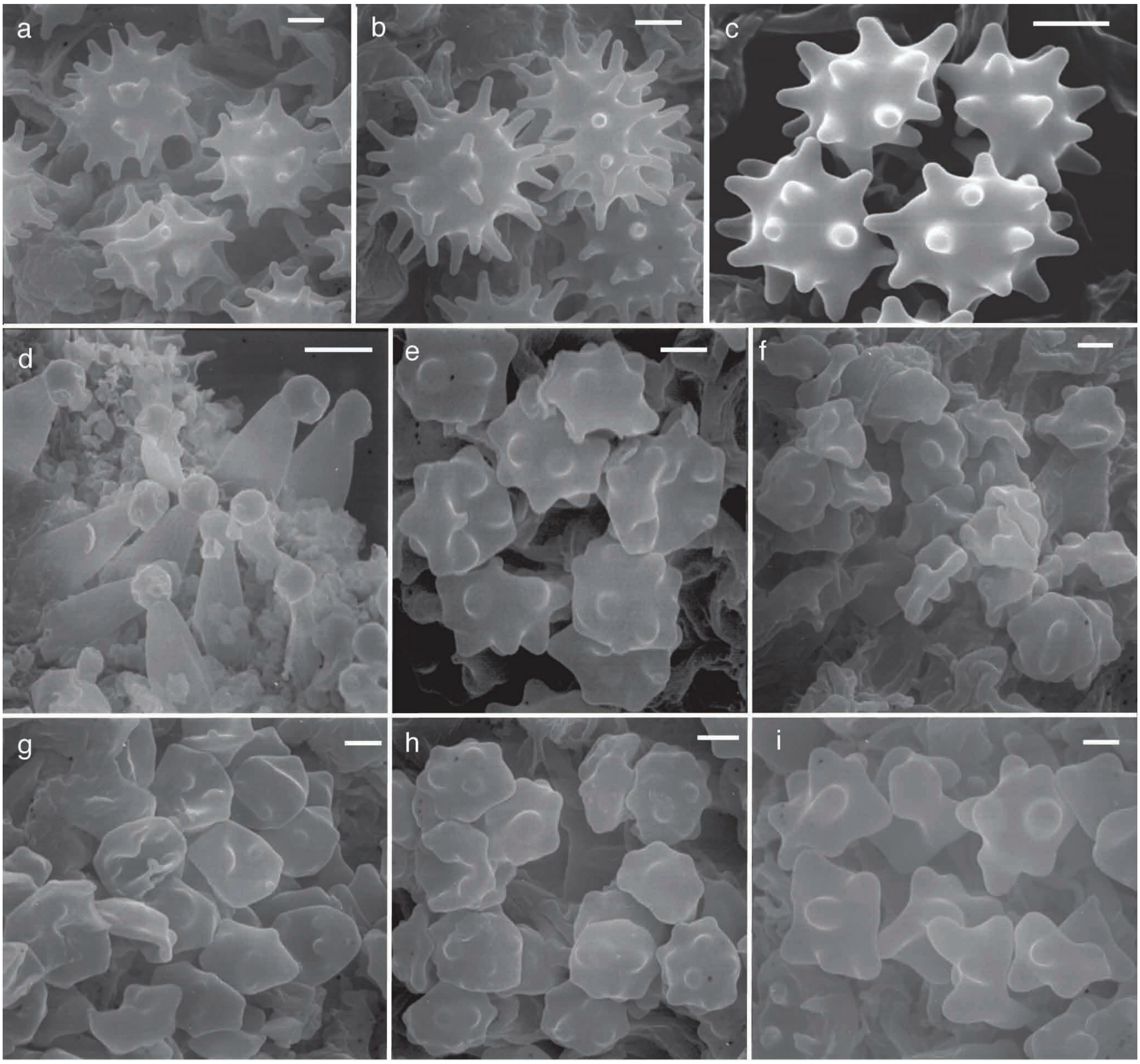


PLATE 8. SEM images. a. Basidiospores of *Inocybe hydrocybiformis* (ZT10077); scale bar = 2 µm. b. Basidiospores of *Inocybe stellata* (ZT10097, holotype); scale bar = 2 µm. c. Basidiospores of *Inocybe thailandica* (DED8049, holotype); scale bar = 5 µm. d. Hymenial cystidia of *Inocybe angustifolia* (ZT10149); scale bar = 10 µm. e. Basidiospores of *Inocybe brevisquamulosa* (ZT10102, holotype); scale bar = 2 µm. f. Basidiospores of *Inocybe pusillima* (ZT10130); scale bar = 2 µm. g. Basidiospores of *I. fragilissima* (DED8061, holotype); scale bar = 2 µm. h. Basidiospores of *Inocybe ornata* (ZT10107, holotype); scale bar = 3 µm. i. Basidiospores of *Inocybe parvibulbosa* (ZT10099, holotype). Scale bar = 2 µm. Photos by U. Jauch & M Kirchmair.

21. ***Inocybe sp*.** DED8133

This unique species appears sister to the *umbratica-paludinella* clade but with poor support.

Specimen examined: THAILAND. Chiang Mai Prov.: Doi Suthep National Park, Sangasabhasri Lane to Huai Kok Ma Village, N18˚48.68‘, E98˚54.60‘, 1140 m elev., in soil under *Dipterocarpus* and *Castanopsis*, 26 Jun. 2007, leg. D.E. Desjardin (DED8133, SFSU) GenBank accession no. GQ893022, GQ892978.

22. ***Inocybe sp***. DED8054a

We are uncertain about the status of the LSU sequence attached to this specimen, which joins *I. queletii*, a north temperate species, with robust support.

Specimen examined: THAILAND. Chiang Mai Prov.: Mae Sae, Hwy. 1095, at 55 km marker, N19˚14‘32.6“, E98˚38‘29.4“, 1000 m elev., on soil in tropical submontane forest (dominated by *Castanopsis*), 10 Jun. 2006, leg. H.T. Le & D.E. Desjardin (DED8054a, SFSU) GenBank accession no. GQ892998, GQ892953.

23. ***Inocybe sp***. DED8044 Pl. 7a–b

The LSU sequence from this collection represents yet another lineage in the *I. asterospora* group.

Specimen examined: THAILAND. Chiang Mai Prov.: Doi Suthep National Park, Sangasabhasri Lane to Huai Kok Ma Village, N18˚48.68‘, E98˚54.60‘, 1140 m elev., solitary in soil under *Castanopsis*, 7 Jun. 2006, leg. H.T. Le & D. E. Desjardin (DED8044, SFSU) GenBank accession no. KM656121, GQ892995, GQ892950.

24. ***Inocybe sp***. DED8134

The LSU sequence from the collection suggests it may be an autonomous species in the *I. calamistrata* group. It appears to be most closely relatedly to *I. mutata* from eastern North America.

Specimen examined: THAILAND. Chiang Mai Prov.: Doi Suthep National Park, Sangasabhasri Lane to Huai Kok Ma Village, N18˚48.68‘, E98˚54.60‘, 1140 m elev., in soil under *Dipterocarpus* and *Castanopsis*, 26 Jun. 2007, leg. D.E. Desjardin (DED8134, SFSU) GenBank accession no. GQ892983, GQ892937.

25. ***Inocybe sp***. ZT10031

The LSU sequence for this species is distinct but poorly resolved in our LSU-only phylogenetic estimate.

Specimen examined: THAILAND. Chiang Mai Prov.: Doi Suthep National Park, 17 km marker, 1180 m alt., on lateritic soil in tropical montane fagalean rain forest (dominated by *Castanopsis*, *Quercus*, *Lithocarpus*), 24 Jun. 2002, leg. E. & A. Horak (ZT10031) GenBank accession no. GQ893020, GQ892976.

Artificial Key to Thai and Malaysian species of *Inocybe*

1.	Basidiospores smooth	2
-	Basidiospores spinose, irregularly warted, or nodulose	7
2.	Basidiospores subglobose	1. *Inocybe sphaerospora*
-	Basidiospores phaseoliform, ± amygdaliform, pruniform or ovoid-elliptical (in side view)	3
3.	Basidiospores phaseoliform (in side view). Lamellae and context of stipe distinctly lilac	2. *Inocybe bicolorata*
-	Basidiospores ± amygdaliform, pruniform or ovoid-elliptical (in side view). Lamellae and context of stipe not lilac	4
4.	Basidiomes very small. Pileus 3–5 mm. Stipe 8–12 × 0.5–1 mm. Basidiospores amygdaliform (in side view), Pleurocystidia present	3. *Inocybe latibulosa*
-	Basidiomes small to medium-sized. Pileus and stipe larger than above. Basidiospores pruniform or ovoid-elliptical. Pleurocystidia absent	5
5.	Basidiomes small. Pileus 12–18 mm. Basidiospores pruniform (in side view)	4. *Inocybe neglecta*
-	Basidiomes medium-sized (pileus >20 mm diam). Basidiospores ovoid or ovoid-elliptical (in side view)	6
6.	Stipe with distinctive ring and coarsely fibrillose zones of veil, concolorous with the hazel, golden brown or orange brown pileus. Basidiospores amygdaliform (in side view). Tropical lowland and submontane dipterocarp and *Pinus* forest	5. *Inocybe errata*
-	Stipe without distinctive veil remnants, but fibrillose or minutely scaly, dark brown and concolorous with pileus, base of stipe with olive-grey tinge. Basidiospores ovoid-elliptical. Tropical montane fagalean forest	6. *Inocybe proxima*
7(1).	Basidiospores with spinose, saddle-shaped and/or irregularly warted projections	8
-	Basidiospores distinctly nodulose	12
8.	Cheilocystidia filled with strongly refringent, yellow content, cylindrical or slender clavate, non-metuloid, crystals (encrustations) absent	7. *Inocybe hydrocybiformis*
-	Cheilocystidia hyaline (yellow refringent content absent), wall thin or distinctly metuloid, crystals absent or present	9

9. Basidiomes robust. Stipe distinctly pruinose all over, veil remnants on stipe and margin of pileus absent; 120–200 × 5–9 mm, base distinctly bulbous and submarginate. Basidiospores 15–20 µm wide (incl. conical rarely saddle-shaped projections)........ 8. *Inocybe petchii*

\- Basidiomes medium-sized or small. Stipe (and margin of pileus) densely covered with distinctive persisting fibrillose belts or squamules from veil remnants or smooth (pruinose at apex only); <4 mm wide, base equal or bulbous. Basidiospores (incl. projections) <15 µm wide........ 10

10. Basidiospores 14–17 (–18) µm (incl. conical rarely saddle-shaped projections, up to 3.5 µm long). Stipe 60–125 × 2.5–4 mm (cf. 10. *Inocybe stellata*)........ 9. *Inocybe gemina*

\- Basidiospores and size of basidiomes distinctly smaller........ 11

11. Basidiospores (10–) 12–16 µm (including conical and/or saddle-shaped projections up to 3 µm long). Pileus distinctly conical or cuspidate. Stipe covered with whitish or concolorous fibrils forming appressed belts and zones. Tropical lowland and montane dipterocarp and fagalean forest. (cf. 8. *I petchii*)........ 10. *Inocybe stellata*

\- Basidiospores (9–) 10–12 µm, (including rather isolated, conical-spinose projections up to 2 µm long). Pileus obtusely conical or umbonate. Stipe subpruinose at upper half only, smooth towards base. Tropical montane fagalean forest........ 11. *Inocybe thailandica*

12(7). Base of stipe equal, not enlarged, or at most swollen........ 13

\- Base of stipe distinctly marginate (cup-shaped), less often only bulbous........ 16

13. Basidiomes whitish, pale yellow, yellow or fawn. Pileus 10–35 mm. Stipe 25–65 × 2–3 (–4) mm. Odor raphanoid or spermatic........ 12. *Inocybe angustifolia*

\- Basidiomes pale brown or dark brown. Pileus <15 mm. Stipe up to 25 × ca. 1 mm. Odor not distinctive........ 14

14. Basidiospores 8.5–10 × 5.5–6 µm. Metuloid caulocystidia absent. Pileipellis dry, a trichoderm of cylindrical hyphae 6–14 µm wide, terminal cells distinctly conical, encrusted with brown pigment........ 13. *Inocybe brevisquamulosa*

\- Basidiospores 5.5–7 × 4–5 µm. Metuloid caulocystidia present. Pileipellis subviscid (in young and moist specimens), innately fibrillose, a cutis of weakly gelatinized hyphae 3–4 µm wide, terminal cells not differentiated, not encrusted with pigment........ 15

15. Pileus 3–8 mm. Stipe 5–8 (–12) × 0.5–1 mm. Cheilocystidia walls hyaline. Tropical montane dipterocarp and fagalean forest with scattered *Pinus kesiya*........ 14. *Inocybe pusillima*

\- Pileus 7–13 mm. Stipe 15–25 × 1 mm. Cheilocystidia walls ochre brown or yellowish. Tropical lowland dipterocarp forest........ 15. *Inocybe fragilissima*

16(12). Pileus 20–55 mm. Stipe >3 mm wide........ 17

\- Pileus 10–26 mm. Stipe <3 mm wide........ 18

17. Pileus with a non-striate margin, not splitting, beige or pale ochre, with umber brown tinge at disc, viscid, margin with whitish, persisting, appendiculate veil remnants. Stipe whitish, margin of bulb with appendiculate veil remnants. Odor weakly spermatic. Basidiospores 6–8 × 4.5–5.5 µm, nodules rather inconspicuous. Tropical lowland dipterocarp forest (mixed with *Tectona*)........ 16. *Inocybe ornata*

\- Pileus conspicuously sulcate-splitting (plicate) from disc to margin, pale grey, pale yellow or orange at disc, dry, veil remnants absent. Stipe white or pale orange, margin of bulb devoid of appendiculate veil remnants. Odor not distinctive. Basidiospores 10–12 × 8.5–10 µm, nodules large and conspicuous. Tropical montane dipterocarp and fagalean forest with scattered *Pinus kesiya*........ 17. *Inocybe pileosulcata*

18(16). Pileus 6–18 mm. Stipe 15–30 × 1–1.5(–2) mm, cinnamon brown or dark brown, marginate or cup-shaped base up to 3.5 mm wide. Odor not distinctive or weakly spermatic. Basidiospores ovoid, 8–9.5 µm broad........ 18. *Inocybe parvibulbosa*

\- Pileus 18–26 mm. Stipe 25–50 × 2–3 mm, pale brown, often with orange incarnate tinge, base up to 6 mm wide. Odor not distinctive or faintly. Basidiospores ellipsoid, 6–7.5 µm broad........ 19. *Inocybe lineata*

Acknowledgments

E. Horak is grateful to S. S. Lee (Forest Research Institute, Kepong, Malaysia) for the invitation and local support during several collecting trips in Malaysia and to R. Watling (Herbarium, Edinburgh, UK) for the loan of specimens kept in E.J.H. Corner's herbarium. E. Horak expresses his gratitude to the expert help by the two SEM-operators: Mr. U. Jauch (Electron Microscopy Laboratory, Zurich, Switzerland) and Dr. M. Kirchmair (Institute of Microbiology, University, Innsbruck, Austria). Support for funds to P. B. Matheny was provided by National Science Foundation (NSF) award DEB-0949517 and funds from the University of Tennessee. Technical support was provided by A. D. Wolfenbarger at the University of Tennessee. Support for funds to D.E. Desjardin was provided by NSF awards DEB-9705083 and DEB-0118776. We are most grateful Dr. Morakat Tanticharoen and the National Center for Genetic Engineering and Biotechnology (BIOTEC, Bangkok, Thailand) and Dr. S. Vikineswary and the University of Malaya (Kuala Lumpur, Malaysia) for providing Material Transfer Agreements that allowed us to remove fungal specimens from their countries for examination and duplicate storage in the USA and Switzerland. We are thankful to Dr. Kevin Hyde and the Mushroom Research Centre (Thailand) for providing excellent facilities from which to work. During fieldwork both in Thailand and Malaysia several persons actively supported the Project and greatly enhanced the yield of specimens: Almut Horak (Austria), Else Vellinga, (USA), Amy Honan (USA), Jennifer Kerekes (USA), Tim Baroni (USA), Roy Halling (USA), Wipapat Kladwang (Thailand/USA), Kevin Hyde (Thailand), Nopparat Wannathes (Thailand), Huyen T. Le (Vietnam), Yee Shin Tan (Malaysia), S. Vikineswary (Malaysia), Ruilin Zhao (China), Annemieke Verbeken (Belgium) and Ruben Walleyn (Belgium). Iqbal Hosen (China) kindly shared sequence data of material sampled in Bangladesh.

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