Phytotaxa 709 (1): 001–104
https://www.mapress.com/pt/

Monograph

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

https://doi.org/10.11646/phytotaxa.709.1.1

PHYTOTAXA

709

The genus *Pluteus* (Basidiomycota, Agaricales, *Pluteaceae*) from Tafea Province, Republic of Vanuatu

JONATHAN A. DEL ROSARIO[1,2] & BRIAN A. PERRY[1]
[1]*Department of Biological Sciences, California State University East Bay, 25800 Carlos Bee Blvd., Hayward, California 94542, USA*
brian.perry@csueastbay.edu; https://orcid.org/0000-0002-0036-6032
[2]*U.S. Department of Energy Joint Genome Institute, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, CA, 94720, USA*
jonathdelrosario@gmail.com; https://orcid.org/0009-0009-1742-9421

Magnolia Press
Auckland, New Zealand

Accepted by Genevieve Gates: 1 Mar. 2025; published: 10 Jul. 2025

JONATHAN A. DEL ROSARIO & BRIAN A. PERRY
The genus *Pluteus* (Basidiomycota, Agaricales, *Pluteaceae*) from Tafea Province, Republic of Vanuatu
(*Phytotaxa* 709)
104 pp.; 30 cm.
10 July 2025
ISBN 978-1-77973-415-0 (paperback)
ISBN 978-1-77973-416-7 (Online edition)

FIRST PUBLISHED IN 2025 BY
Magnolia Press
P.O. Box 41-383
Auckland 1041
New Zealand
e-mail: magnolia@mapress.com
https://www.mapress.com/pt/

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

Table of Contents

Abstract

Twenty-three species of the genus *Pluteus* are newly reported from Tafea Province of the Republic of Vanuatu, a subtropical island archipelago country in the South Pacific located northeast of Australia and equidistant north of New Caledonia, southeast of the Solomon Islands, and west of Fiji. These taxa consist of seven new distributional reports, six tentative identifications, one *nom. prov.*, and nine species, including one form, that are new to science, *viz*., *Pluteus vanuatuensis*, *P. vanuatuensis* var. *ramacystidiatus*, *P. wahei*, *P. aureofuscus*, *P. ornatocystidiatus*, *P. eugraptoides*, *P. lalepiorum*, *P. presleyi*, and *P. tatafuensis*. Species level delimitations are based on comprehensive morphological analysis and phylogenetic reconstruction based upon DNA sequence data (ITS or *tef1*). Evolutionary and biogeographic relationships of the newly generated specimens were examined with molecular-based phylogenies of the three currently accepted infrageneric sections of *Pluteus*: sect. *Pluteus*, sect. *Hispidoderma*, and sect. *Celluloderma,* based on a global sampling. ITS, *tef1,* and combined molecular-based phylogenies were constructed to examine the species delimitations of one new species. Comprehensive descriptions, illustrations of relevant micromorphological features, color photographs, comparison to allied taxa, and a dichotomous key to aid in identification are provided.

Keywords: Taxonomy, systematics, phylogenetics, mushroom, fungal diversity, island funga

Introduction

The Republic of Vanuatu (formerly known as the New Hebrides) is a subequatorial South Pacific Ocean archipelago nation consisting of more than eighty islands. Vanuatu is situated almost equidistant from New Caledonia, Fiji, and the Solomon Islands, all of which are recognized as global hotspots for biodiversity (CEPF 2022, Conservation International 2022). Despite the region's importance for biodiversity studies, the funga (Kuhar *et al.* 2018) of Vanuatu and neighboring nations in Oceania has remained poorly documented in comparison to much of the Northern Hemisphere (Mueller *et al.* 2007). Published records of fungal species from Vanuatu date back to the late 1800's, with Berkeley (1877) being the first to report several species of Basidiomycota macrofungi from the island of Epi (*Schizophyllum commune* Fries (1821: 330), *Polyporus austalis* Fries (1828: 108) [= *Ganoderma australe* (Fries) Patouillard (1889: 65)], *Hirneola polytricha* (Montagne) Fries (1848: 146) [= *Auricularia nigricans* (Swartz) Birkebak, Looney & Sánchez-García in Looney, Birkebak & Matheny (2013: 12)]), from collections made in August, 1874, as part of the expedition of the H.M.S. Challenger. Pegler, in his monograph of the genus *Lentinus* Fries (1828: 45), studied a single collection of *Lentinus connatus* Berkeley (1842: 145) collected on the island of Aneityum by British entomologist Lucy Evelyn Cheesman during her final expedition to the South Pacific in 1954 (Pegler 1983b, Touzel & Garner 2018). McKenzie (1989) compiled a checklist for the country composed of approximately 370 species of mostly plant pathogenic fungi and excluding lichen-forming fungi. The list includes 61 species of basidiomycetous macrofungi from the islands of Ambae, Efate, Epi, Malekula, Tanna, and Espiritu Santo. More recently, Maekawa (2002) reported 31 species of corticoid basidiomycetes from Vanuatu that were collected during the Japan-Vanuatu Joint Scientific Expedition in 2000, all of which were new records for the country. These collections were made from the islands of Efate and Espiritu Santo, from the central and the northern provinces of Shefa and Sanma, respectively. Similarly, a group of French researchers conducted an expedition to Espiritu Santo in 2006 (Buyck 2011), but a detailed account of the fungal taxa encountered has not been published to our knowledge. On the island Efate, *Psathyrella floriformis* Hausknecht & Voto (2022: 9) [= *Galerella floriformis* Hausknecht in Hausknecht & Contu (2003: 34)] was first collected and described by Hausknecht and Contu (2003).

During 2017–2019, multiple expeditions were undertaken to document the macrofungal diversity of the southernmost Vanuatu province of Tafea, as part of a greater effort to document floristic and linguistic diversity of the region through the "*Plants mo Pipol blong Vanuatu* (Plants and People of Vanuatu)" collaborative program, initiated in 2013 by the Vanuatu National Herbarium (PVNH), Vanuatu and Tafea Kaljoral Sentas, and the New York Botanical Garden (NYBG). The islands of Aneityum, Tanna, and Futuna were sampled while the islands of Erromongo and Aniwa were unavailable for this investigation due to logistics and accessibility difficulties. Geologically, the islands of Aneityum and Tanna are volcanic in origin, while Futuna is a smaller raised coral atoll. The islands, between latitudes 18–20° S, experience a subtropical climate with a cooler, dry season from April–September and a warmer, wet season from October–March. Rainfall occurs year-round, however the leeward northwestern sides of the islands tend to be drier, while the windward southeastern sides tend to experience higher precipitation. Human settlement in coastal and lowland areas has resulted in interspersed mixed-use agroforests causing varying levels of forest fragmentation.

Generally, the islands' habitats are composed of coastal scrub, mangrove and littoral forest, inland lowland primary and sucessional broadleaf rainforest, and montane primary broadleaf and/or *Araucariaceae/Podocarpaceae* rainforest to cloud forest towards the summits (up to approximately 1000 m). In this first study, of what is expected to be several studies of taxa from Tafea Province, we treat twenty-three species of the genus *Pluteus* Fries (1835: 338) that were encountered during our collecting expeditions.

The genus *Pluteus*, the type genus of the family *Pluteaceae* Kotlaba & Pouzar (1972: 218) (Basidiomycota, Agaricales), is a relatively large genus with over 300 described species worldwide. Members of the genus are saprotrophic and associated with growth on wood or woody debris. This genus is generally characterized by medium to large basidiomes, a pink spore print, free lamellar attachment, the absence of an annulus or volva, smooth, hyaline, inamyloid, ellipsoid spores, the presence of cystidia, inverse lamellar tramal tissues, and inamyloid pileipellis, stipitipellis, and tramal tissues. The current infrageneric taxonomy of *Pluteus* is based primarily on morphological characteristics of the hymenial cystidia and the pileipellis. Singer recognized three sections: sect. *Pluteus* Fries (1836: 338) with metuloid (*i.e.*, thick-walled, mostly non-incrusted) pleurocystidia and a cutis pileipellis, sect. *Hispidoderma* Fayod (1838: 364) with non-metuloid pleurocystidia and a pileipellis composed of elongated filamentous elements arranged as a cutis, a hymeniderm or a trichoderm, and sect. *Celluloderma* Fayod (1838: 364) with non-metuloid pleurocystidia and a pileipellis composed of relatively short clavate or sphaeropedunculate elements organized as a hymeniderm or with transition to an epithelium (Singer 1956, 1986). Section *Celluloderma* was further divided into subsect. *Mixtini* Singer (1958: 257), characterized by a dimorphic pileipellis containing elongated elements or dermatocystidia, treated in this study as pileocystidia *sensu* Vellinga (1988), and subsect. *Eucellulodermini* Singer (1958: 274), characterized by a non-dimorphic pileipellis lacking such elongated cells (Singer 1986). Vellinga & Schreurs (1985) proposed a variation on Singer's classifications, dividing members of sect. *Hispidoderma* with non-metuloid pleurocystidia and a cutis pileipellis into sect. *Villosi* Vellinga & Schreurs (1985: 343), and relegating the other members of sect. *Hispidoderma* with non-metuloid pleurocystidia and a trichodermal or hymenidermal arranged pileipellis containing cylindrical or fusiform elements to a third subsection, *Hispidodermini* (1985: 349) in sect. *Celluloderma*. Later phylogenetic molecular studies (Justo *et al*. 2011b, Justo *et al*. 2011c) determined Vellinga and Schreurs's taxonomic arrangement to be unsupported based on both nuclear ribosomal internal transcribed spacer region (ITS) data alone and a multi-gene phylogeny containing ITS, nuclear large ribosomal subunit (nLSU), and small ribosomal subunit (nSSU). Instead, Singer's three sections *Pluteus*, *Hispidoderma*, and *Celluloderma* were supported with some caveats. Based on this, sect. *Pluteus* is characterized by these authors as containing species with metuloid (thick-walled, mostly non-incrusted) pleurocystidia and a cutis pileipellis, sect. *Celluloderma* is characterized by species with non-metuloid pleurocystidia and a pileipellis composed predominantly of short clavate or sphaeropedunculate cells (avQ $\leq$ 3) often intermixed with elongated cystidioid elements or as a cutis, and sect. *Hispidoderma* is characterized by species with non-metuloid pleurocystidia and a pileipellis composed mostly of long, elongated elements (avQ $\geq$ 3) arranged as a hymeniderm or trichoderm, with some taxa having clavate elements (avQ $\leq$ 3), however, they are not predominant (Justo *et al*. 2011b). This infrageneric classification scheme proposed by Justo *et al.* (2011b) will be followed in this treatment, although subsequent research and the current study have uncovered exceptions.

Materials and methods

Site description

Sampling took place in Tafea Province, Vanuatu on the islands of Aneityum, Tanna, and Futuna. Erromongo and Aniwa were unavailable due to logistic complications.

On the island of Aneityum, the coastal site of Umej was comprised of coastal scrub, mangrove forest, secondary littoral forest, and mixed-use agro tree garden containing *Annona muricata* (*Annonaceae*), *Artocarpus altillis* (*Moraceae*), *Bruguiera gymnorhiza* (*Rhizophoraceae*), *Cocos nucifera* (*Arecaceae*), *Macaranga tanarius* (*Euphorbiaceae*), *Magnifera indica* (*Anacardiaceae*), *Musa spp.* (*Musaceae*), and *Syzygium richii* (*Myrtaceae*). Aneityum's eastern Anecro/Mount Inhetiji area was composed of montane primary broadleaf rainforest to cloud forest containing *Balanops pedicellata* (*Balanopaceae*), *Diospyros sp.* (*Ebenaceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Ilex vitiensis* (*Aquifoliaceae*), *Melicope latifolia* (*Rutaceae*), *Metrosideros collina* (*Myrtaceae*), *Plerandra actinostigma* (*Araliaceae*), *Scaevola cylindrica* (*Goodeniaceae*), *Semecarpus tannaensis* (*Anacardiaceae*), and *Syzygium spp.* (*Myrtaceae*). Aneityum's central western Nethwanethervana area was composed of montane transitionary secondary to primary broadleaf-*Podocarpaceae* rainforest with *Burckella obovata* (*Sapotaceae*), *Cryptocarya tannaensis* (*Lauraceae*), *Dacrycarpus imbricatus* (*Podocarpaceae*), *Elaeocarpus floridanus* (*Elaeocarpaceae*), *Ficus smithii* (*Moraceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Melicope sp.* (*Rutaceae*), *Metrosideros vitiensis* (*Myrtaceae*), *Meryta neoebudica* (*Araliaceae*), and *Neuburgia corynocarpa* (*Loganiaceae*). The Noposjec/Anloulanelcau-Anatwojom area was composed of montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest with *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*).

The sites of the island of Futuna were along the slopes of the central tabletop mountain, Mount Tatafu. The lower slopes of Mount Tatafu were composed of montane primary broadleaf rainforest containing *Ascarina diffusa* (*Chloranthaceae*), *Claoxylon fallax* (*Euphorbiaceae*), *Diospyros ferra* (*Euphorbiaceae*), *Dillenia biflora* (*Dilleniaceae*), *Ficus storckii* (*Moraceae*), *Geissois denhamii* (*Cunoniaceae*), *Metrosideros vitiensis* (*Myrtaceae*), *Phyllanthus myrianthus* (*Phyllanthaceae*), *Plerandra actinostigma* (*Araliaceae*), *Schefflera neoebudica* (*Araliaceae*), and *Syzygium chanelii* (*Myrtaceae*). The upper slopes were composed of montane primary broadleaf cloud forest containing *Atractocarpus sezitat* (*Rubiaceae*), *Claoxylon psilogyne* (*Euphorbiaceae*), *Eumachia trichostoma* (*Rubiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Ficus septica* (*Moraceae*), *Neonauclea forsteri* (*Rubiaceae*), and *Schefflera neoebudica* (*Araliaceae*).

On the island of Tanna, the northern coastal site at Port Resolution was composed of lowland mixed-use agro tree garden and littoral secondary broadleaf forest containing *Annona muricata* (*Annonaceae*), *Artocarpus altilis* (*Moraceae*), *Barringtonia asiatica* (*Lecythidaceae*), *Cocos nucifera* (*Arecaceae*), *Cordia dichotoma* (*Boraginaceae*), *Euodia hortensis* (*Rutaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Musa sp.* (*Musaceae*). The northern site of Yakuwan was composed of lowland mixed-use agro tree garden and disturbed secondary broadleaf rainforest with *Cocos nucifera* (*Arecaceae*), *Cordia subcordata* (*Boraginaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium malaccense* (*Myrtaceae*). The eastern site of Kwaprapra/Iatukwei was composed of lowland mixed-use agro tree garden and primary broadleaf rainforest containing *Dysoxylum aneityense* (*Meliaceae*), *Ficus adenosperma* (*Moraceae*), *Hedycarya dorstenioides* (*Monimiaceae*), *Inocarpus fagifer* (*Fabaceae*), *Kermadecia lutea* (*Proteaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Myristica fatua* (*Myristicaceae*), and *Syzygium myriadenum* (*Myrtaceae*). The southern site of Kwamera/Yanemarei/ along the Numdretum River was composed of lowland mixed-use agro tree garden and secondary broadleaf rainforest with *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*). Another southern site on the lower slopes of Mount Kuning was composed of lowland-montane secondary broadleaf-*Podocarpaceae* rainforest consisting of *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Cryptocarya wilsonii* (*Lauraceae*), *Ficus wassa* (*Moraceae*), *Ixora aneityensis* (*Rubiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), and *Syzygium spp.* (*Myrtaceae*).

Field Sampling

Six collecting trips of four- to six-week periods were undertaken during the months of July–August and November–December in 2017–2019. Sampling in the field followed a general collecting approach and was designed to thoroughly survey each island within the time allotted.

For each collection, biotic and abiotic data were recorded, including habitat type, locality, elevation, and GPS coordinates. Macromorphological observations were recorded for each collection following the terminology of Largent *et al.* (1986) and Vellinga (1988). Color observations were standardized based on The Online Auction Color Chart™ (Online Color Chart Company, Palo Alto, CA) or the Methuen Handbook of Colour (Kornerup & Wanscher 1978). When possible, detailed photographs were made *in situ* and/or against a neutral backdrop under natural light using an Olympus Tough TG-5 or Olympus OM-D E-M1 MII digital camera. All collections were dried in silica gel and deposited in the California State University, East Bay Fungarium (HAY).

Light Microscopy

Hand-made radial or scalp sections were made from tissues of dried basidiomes and microstructures were examined at 1000× using an Olympus BX53 upright compound microscope (Olympus Life Sciences, Waltham, MA) with a drawing tube (*camera lucida*). These tissue sections were rehydrated in 95 % ethanol, followed by distilled water or 3 % KOH. Sections were stained with Melzer's reagent to test for amyloid, dextrinoid or negative (inamyloid) reactions, or Congo Red to improve visual contrast and assist with drawing the structures. Micromorphological description terminology is based on Largent *et al.* (1986) and Vellinga (1988). Basidiospores were observed in profile for shape, and a minimum of n = 50 spores were studied per collection. Size measurements were taken as length, including the hilar appendage, by width. Size is reported based on the observed minimum to maximum range with parentheses indicating a minority or outlier value. The following statistical values were calculated based on spore measurements: x_m = the arithmetic mean spore length by spore width (± standard deviation (SD)) for n spores in a single specimen; x_{mr} = the range of spore length and width means, and x_{mm} = the arithmetic mean of spore length and width means (± SD) when more than one specimen was available; Q = the quotient of spore length by width in any one spore, indicated as a range for n spores measured; Q_m = the arithmetic mean of all Q values (± SD); Q_{mr} = the range of Q value means, and Q_{mm} = the arithmetic mean of Q_m value means (± SD) when more than one specimen was available. For other pertinent cell types, a minimum of 10 individual cells per type was examined and measured. Measurements for size range were standardized by their length, defined from the cell's apex to its basal septa, and width, defined by the cell's widest median from end to end. Basidia and sterigmata were measured for size separately (length × width) and the number of spores per basidum was recorded. The tissue arrangements of the pileipellis, pileus trama, lamellar trama and stipitipellis were studied for hyphal cell diameter size range, cell shape, pigmentation, gelatinization presence/absence, wall-thickness, and Melzer's reaction. Specifically, for the pileipellis, terminal elements were characterized as the predominant terminating cell type constituting the uppermost layer, while pileocystidia were treated as a separate cell type if they distinctively differed in shape from the predominant terminal elements. The presence or absence of clamp connections was observed for all cell types and reported, particularly for pileipellis and stipitipellis cells.

Molecular Techniques

For each collection, total genomic DNA was extracted from dried material using the Extract-N-Amp Plant Tissue PCR Kit (Sigma-Aldrich, St. Louis, MO), according to the manufacturer's instructions. If poor quality sequence data was generated or polymerase chain reactions (PCR) failed multiple attempts, genomic DNA was re-extracted using the E.Z.N.A. Fungal DNA Mini Kit or E.Z.N.A. Forensic DNA Extraction Kit (Omega Bio-Tek, Norcross, GA), following the manufacturer's instructions. PCR amplification of extracted DNA was performed using FastStart™Taq DNA Polymerase (Sigma-Aldrich, St. Louis, MO) or PCR Master Mix (Promega, Madison, WI), according to the manufacturer's instructions. For each specimen, the ITS region was amplified using primer pairs ITS1-F and ITS4 (Gardes & Bruns 1993, White *et al.* 1990) or in segments with primer pairs ITS1-F with 5.8S and 5.8SR (Vilgalys & Hester 1990) with ITS4. For collections JAD 160, JAD 169, JAD 189, JAD 215, JAD 229, JAD 286, JAD 159, and JAD 285 the *tef1* gene was amplified using the primer pairs ef1-983F and ef1-1567R (Rehner & Buckley 2005). PCR protocols for amplifying ITS included an initial denature at 95 °C for 240 sec., followed by 35 cycles of 95 °C denaturation for 30 sec., annealing at 55 °C or 58 °C for 30 sec., extension at 72 °C for 120 sec., and a final extension at 72 °C for 7 min.. For amplifying *tef1*, a stepdown PCR protocol was used with an initial denaturation at 95 °C for 120 sec. followed denaturation for 10 cycles set at 95 °C for 30 sec., annealing first at 66 °C for 30 sec. and dropped incrementally by 1 °C over the next 9 cycles, and extension at 72 °C for 60 sec.. The step-down increments were followed by 36 additional cycles with denaturation at 94 °C for 30 sec., annealing at 56 °C for 30 sec., extension at 72 °C for 60 sec., and a final extension at 72 °C for 10 min.. Amplification products were cleaned using the Exo-SAPit kit (Affymetrix, Santa Clara, CA) and were sent to Elim Biopharmaceuticals (Hayward, CA) for Sanger sequencing utilizing the same primers used in PCR amplification. Sequencing products were edited and assembled using Geneious 9.0 (Biomatters, Ltd., Auckland, New Zealand). Due to the presence of multiple indels, collection JAD 286 and BAP 930 did not yield high quality ITS sequence data and were excluded from phylogenetic analyses. All generated sequences have been deposited into the National Center for Biotechnology Information GenBank database.

Phylogenetic Analyses

Sequence data generated from Vanuatu *Pluteus spp.* specimens were incorporated into a combination of existing datasets with additional selected sequences retrieved from GenBank. In order to delimit Vanuatu *Pluteus* species and better elucidate their evolutionary relationships to other species within their respective section, datasets using ITS sequences of each section were constructed to adequately reflect a broad sampling based on previous studies, *viz.*, *Pluteus* (Justo *et al.* 2014, Justo *et al.* 2011b), *Hispidoderma* (Justo *et al.* 2011b, Menolli *et al.* 2015c), *Celluloderma*

(Justo *et al*. 2011c, Menolli *et al*. 2015b), plus additional sequences retrieved from GenBank. The sampling for the *tef1* gene dataset was based on Menolli *et al*. (2014) and additional sequences from GenBank. These datasets were initially aligned using ClustalX 2.0 (Larkin *et al*. 2007) under default parameter settings. Sequences were then manually adjusted in Mesquite v. 3.5 (Maddison & Maddison 2016). For each dataset, Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed. ML analyses were run in RAxML 8.2.0 (Stamatakis 2014) under a GTRGAMMA nucleotide substitution model, and consisted of 100 alternative runs utilizing default parameters with node support estimated by 100 RAxML bootstrap replicates. Appropriate models of sequence evolution were determined via the Bayesian Information Criterion implemented in PAUP* 4.0a.169 (Wilgenbusch & Swofford 2003). BI analyses were performed on the CIPRES Science Gateway (Miller *et al*. 2010) utilizing Metropolis MCMC methods as implemented in MrBayes 3.2.7a (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) under a GTR+G (*albostipitatus*/*salicinus* clade; *tef1*), GTR+I+G (sect. *Pluteus*; ITS), HKY+G (*albostipitatus*/*salicinus* clade; ITS), or HKY+I+G (sects. *Hispidoderma* and *Celluloderma*; ITS) model of sequence evolution. The HKY+G and GTR+G model of sequence of evolution were applied accordingly to ITS+*tef1* data in the concatenated two-gene dataset of the *albostipitatus*/*salicinus* clade. Bayesian analyses consisted of two parallel searches, run for 1 million (*albostipitatus*/*salicinus* clade; ITS), 1.5 million (*albostipitatus*/*salicinus* clade; *tef1* and ITS+*tef1*) or 6 million (sects. *Pluteus, Hispidoderma,* and *Celluloderma;* ITS) generations and initiated with random starting trees. Swaps per generation and chain temperature parameters used default settings. Tracer v1.7.1 (Rambaut *et al*. 2018) was used to determine convergence of MCMC analyses and obtain estimates of the posterior parameter values, where results were accepted based on Effective Sample Size being above 200, and Potential Scale Reduction Factor close to 1. Trees sampled prior to runs reaching an average standard deviation of split frequencies of 0.01 were discarded as the burn-in, while remaining trees were used to calculate posterior probabilities of individual clades. Default settings were used in MrBayes to set unconstrained branch lengths and uninformative topology priors.

TABLE 1. List of *Pluteus spp.* sequenced (ITS1-5.8S-ITS2 and *tef1*) for this study.

Species	Section	Collection Number	GenBank Accession Number	
			ITS	*tef1*
Pluteus albostipitatus	*Pluteus*	BAP 930	–	–
Pluteus albostipitatus	*Pluteus*	BAP 968	OM060360	–
Pluteus petasatus	*Pluteus*	JAD 45	OM060373	–
Pluteus petasatus	*Pluteus*	JAD 47	OM060374	–
Pluteus petasatus	*Pluteus*	JAD 298	OM060375	–
Pluteus vanuatuensis	*Pluteus*	JAD 160	OM060388	OP094584
Pluteus vanuatuensis	*Pluteus*	JAD 169	OM060389	OP094585
Pluteus vanuatuensis	*Pluteus*	JAD 189, Holotype	OM060387	OP094586
Pluteus vanuatuensis	*Pluteus*	JAD 215	OM060390	OP094587
Pluteus vanuatuensis	*Pluteus*	JAD 229	OM060391	OP094588
Pluteus vanuatuensis	*Pluteus*	JAD 286	–	OP094590
Pluteus vanuatuensis f. *ramicystidiatus*	*Pluteus*	JAD 159, Holotype	OM060386	OP094583
Pluteus aff. *vanuatuensis*	*Pluteus*	JAD 285	OM060392	OP094589
Pluteus wahei	*Pluteus*	JAD 107	OM060380	–
Pluteus wahei	*Pluteus*	JAD 284, Holotype	OM060379	–
Pluteus aureofuscus	*Hispidoderma*	JAD 218	OM060385	–
Pluteus aureofuscus	*Hispidoderma*	JAD 342	OM060384	–
Pluteus aureofuscus	*Hispidoderma*	JAD 344, Holotype	OM060383	–
Pluteus chrysaegis	*Hispidoderma*	JAD 217	OM060364	–
Pluteus chrysaegis	*Hispidoderma*	JAD 248	OM060365	–
Pluteus chrysaegis	*Hispidoderma*	JAD 312	OM060366	–
Pluteus cf. *fastigiatus*	*Hispidoderma*	JAD 170	OM060361	–
Pluteus fernandezianus	*Hispidoderma*	JAD 331	OM060370	–
Pluteus cf. *haywardii*	*Hispidoderma*	JAD 346	OM060362	–

......*continued on the next page*

TABLE 1. (Continued)

Species	Section	Collection Number	GenBank Accession Number	
			ITS	*tef1*
Pluteus macrocystidiatus	*Hispidoderma*	JAD 302	OM060363	–
Pluteus neochrysaegis	*Hispidoderma*	JAD 17	OM060367	–
Pluteus neochrysaegis	*Hispidoderma*	JAD 244	OM060368	–
Pluteus neochrysaegis	*Hispidoderma*	JAD 245	OM060369	–
Pluteus neochrysaegis	*Hispidoderma*	JAD 265	OM060372	–
Pluteus ornatocystidiatus	*Hispidoderma*	JAD 167, Holotype	OM060381	–
Pluteus rimosellus	*Hispidoderma*	JAD 11	OM060376	–
Pluteus rimosellus	*Hispidoderma*	JAD 338/338B	OM060377	–
Pluteus rimosellus	*Hispidoderma*	JAD 343	OM060378	–
Pluteus aff. *semibulbosus*	*Hispidoderma*	JAD 166	OM060358	–
Pluteus aff. *semibulbosus*	*Hispidoderma*	JAD 197	OM060359	–
Pluteus velutinus	*Hispidoderma*	JAD 53	OM060396	–
Pluteus aff. *argentinensis*	*Celluloderma*	JAD 171	OM060355	–
Pluteus aff. *argentinensis*	*Celluloderma*	JAD 301	OM060356	–
Pluteus eugraptoides	*Celluloderma*	JAD 168, Holotype	OM060382	–
Pluteus lalepiorum	*Celluloderma*	JAD 12, Holotype	OM060371	–
Pluteus presleyi	*Celluloderma*	JAD 239, Holotype	OM060393	–
Pluteus presleyi	*Celluloderma*	JAD 251	OM060394	–
Pluteus aff. *riberaltensis* var. *missionensis*	*Celluloderma*	JAD 281	OM060357	–
Pluteus tatafuensis	*Celluloderma*	JAD 304, Holotype	OM060395	–

Results

A total of forty-three specimens belonging to the genus *Pluteus* were collected from Vanuatu during this study. These specimens generated forty-two ITS sequences and eight *tef1* sequences. From these collections, twenty-three distinct species were recognized based on a combination of morphological and molecular characters. Nine species including one additional form are described herein as new to science. One species is temporarily designated as *nom. prov.*. All of these collections are considered the first reports of *Pluteus* from Tafea Province and from Vanuatu. Of the Tafea Province Islands sampled, thirteen species are reported from Tanna, twelve species from Aneityum, and three species from Futuna.

The aligned ITS dataset of sect. *Pluteus* contained 169 sequences consisting of 1026 characters, with *P. chrysophlebius* (Berkeley & Curtis) Saccardo (1887: 678) (HM562064) and *P. cinereofuscus* Lange (1917: 9) (HM562018) of sect. *Celluloderma* as the outgroup. A total of 339 characters were considered too ambiguous for alignment and excluded from the analyses. The resulting topology is shown in Figure 1a–d. Six Vanuatu species are recognized and treated as belonging within sect. *Pluteus*.

The aligned ITS dataset of the *albostipitatus/salicinus* clade contained 28 sequences representing 13 taxa, consisting of 728 characters. Ambiguously aligned regions consisting of 85 characters were excluded from the analyses. A similar sampling based on aligned *tef1* data contained 29 sequences consisting of 618 characters. Of these, intron sequences were excluded from the analyses resulting in the exclusion of 78 characters. The concatenated ITS+*tef1* dataset with expanded sampling contained 42 sequences containing 1363 characters, of which 158 were excluded. The resulting topology is shown in Figure 6a–c.

The sect. *Hispidoderma* ITS dataset contained 162 sequences consisting of 1006 characters. Sequences of *P. diettrichii* Bresadola (1905: 160) (HM562143) and *P. seticeps* (Atkinson) Singer (1959: 272) (HM562199) of sect. *Celluloderma* were utilized as the outgroup. A total of 187 characters were considered too ambiguous for alignment and therefore excluded from the analyses. The resulting topology is shown in Figure 15a–c. Eleven Vanuatu species are recognized and treated as belonging within sect. *Hispidoderma*.

Fig. 1a

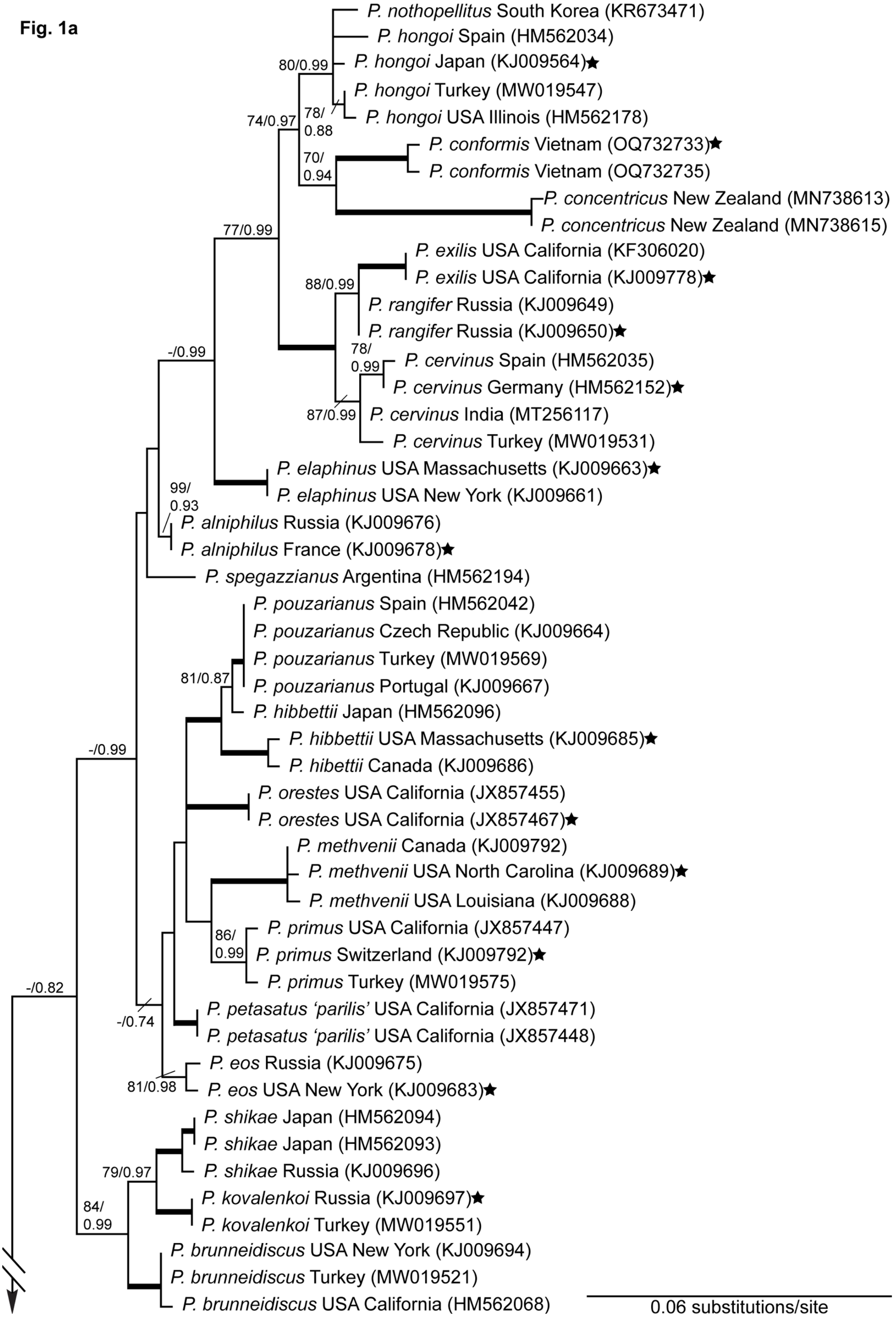

FIGURE 1a–d. Maximum Likelihood phylogeny of sect. *Pluteus* based on ITS sequence data (-lnL = 6609.645735). Sequences of specimens from Vanuatu are indicated in bold type. Stars indicate type specimens. Values separated by / refer to ML bootstrap proportions and Bayesian posterior probabilities, respectively. Only values greater than 70/0.70 are shown. Nodes receiving support values greater than 90/0.95 are highlighted in bold.

Fig. 1b

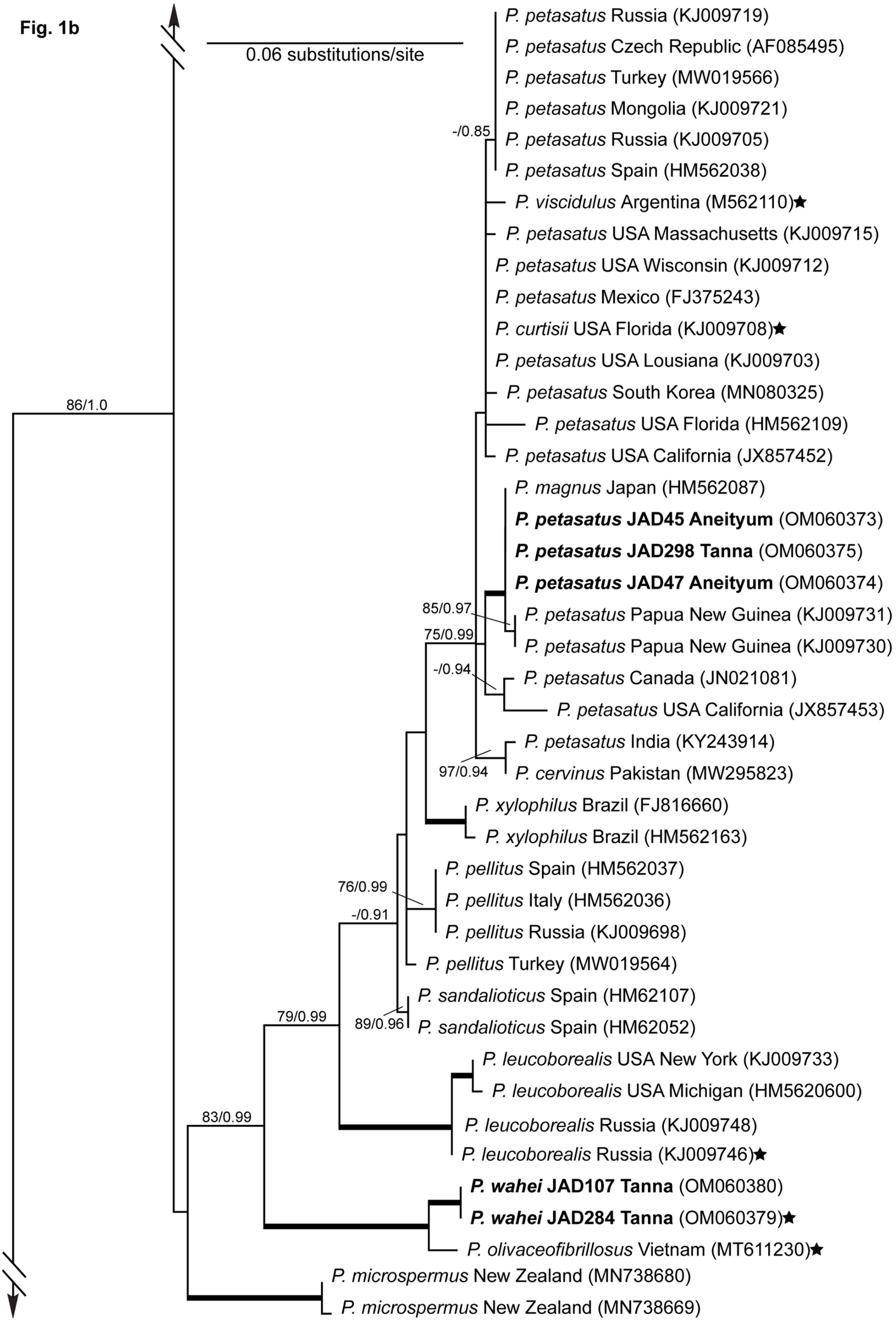

FIGURE 1. (Continued)

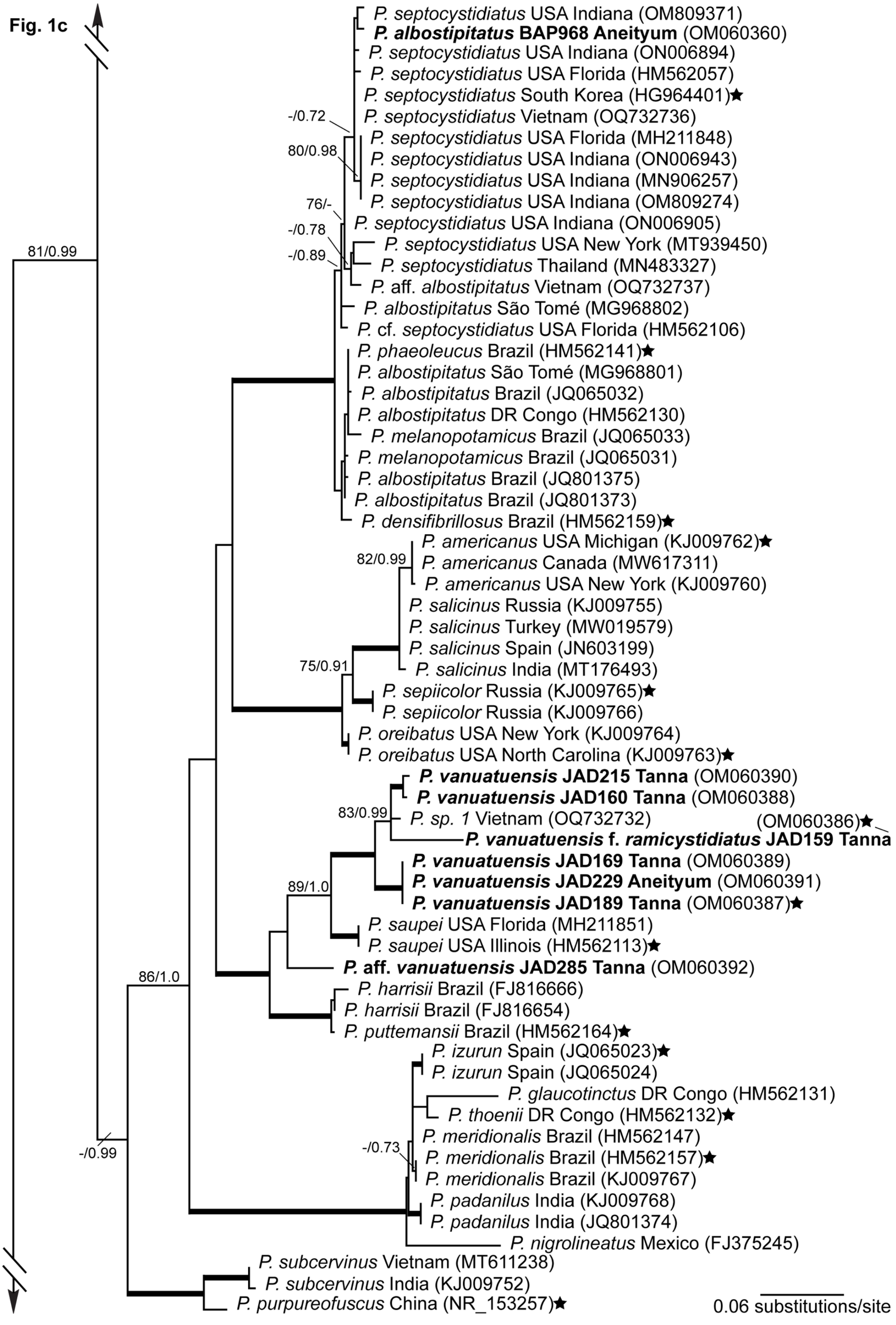

FIGURE 1. (Continued)

Fig. 1d

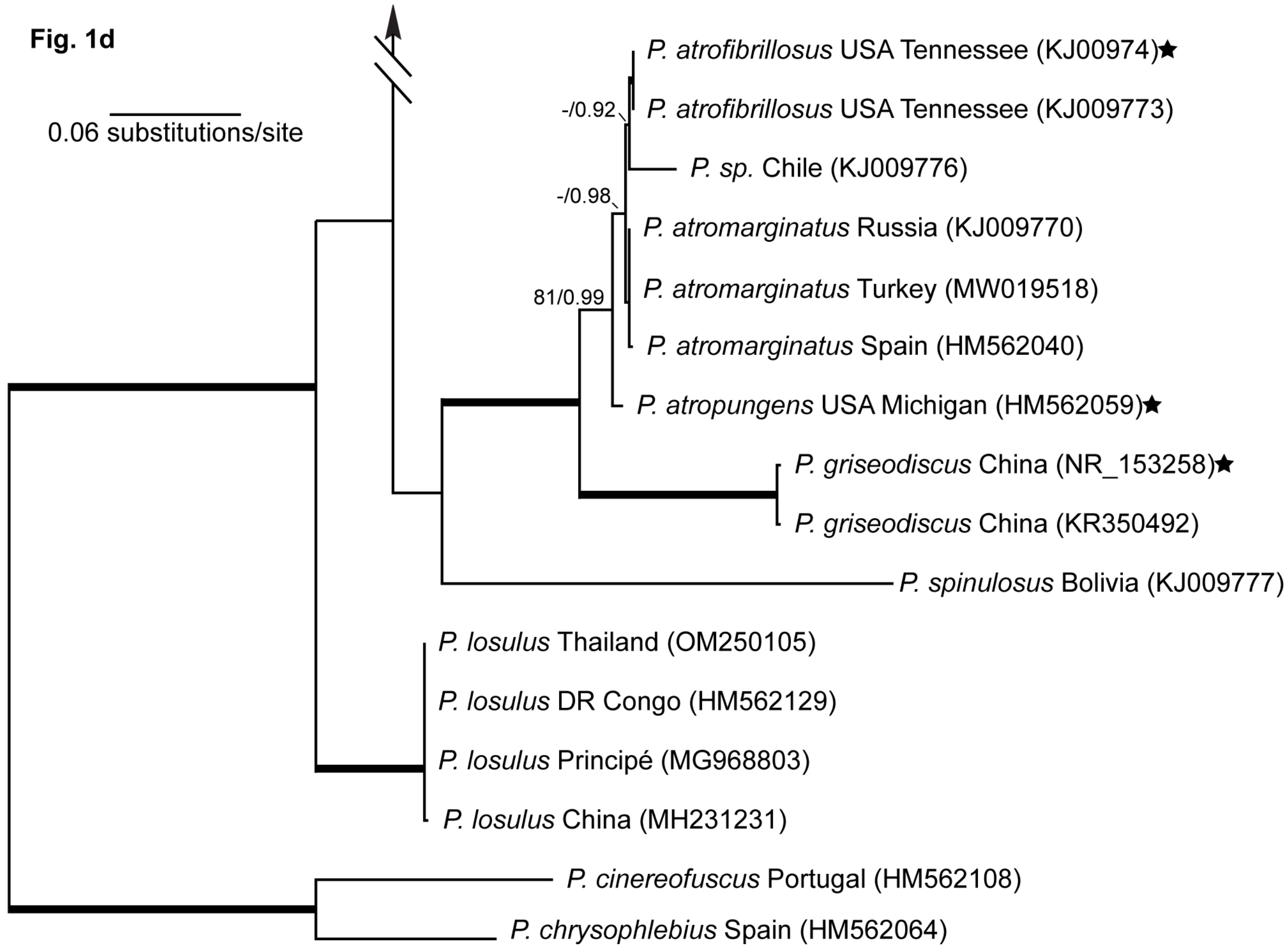

FIGURE 1. (Continued)

The ITS alignment for sect. *Celluloderma* contained 263 sequences consisting of 1039 characters. A sequence of *P. petasatus* (Fries) Gillet (1876: 395) (HM562038) of sect. *Pluteus* and *P. leoninus* (Schaeffer) Kummer (1871: 98) (HM562045) of sect. *Hispidoderma* were selected as the outgroup. A total of 214 characters were considered too ambiguous for alignment and therefore excluded from the analyses. The resulting topology is shown in Figure 37a–e. Six species of Vanuatu *Pluteus* are recognized and treated as belonging to sect. *Celluloderma*.

TABLE 2. List of sequences sampled in ITS, *tef1* and combined phylogenetic analyses of the *albostipitatus/salicinus* clade (See Fig. 6a–c).

Species	Collection Number	GenBank Accession Number	
		ITS	***tef1***
Pluteus albostipitatus	DED8220	MG968802	–
Pluteus albostipitatus	FK1973	JQ065032	KJ010046
Pluteus albostipitatus	GF5374	HM562130	–
Pluteus albostipitatus	FK1891	JQ801373	KJ010043
Pluteus albostipitatus	FK782	FJ816661	KJ010042
Pluteus americanus	MO145100	KJ009785	KJ010038
Pluteus americanus	AHS57842, holotype	KJ009762	KJ010037
Pluteus cf. *septocystidiatus*	AJ187	HM562106	KJ010040
Pluteus densifibrillosus	SP393696, holotype	HM562159	KJ010041
Pluteus glaucotinctus	GF5274, holotype	HM562131	–
Pluteus harrisii	SP393709	FJ816666	–

......continued on the next page

TABLE 2. (Continued)

Species	Collection Number	GenBank Accession Number	
		ITS	*tef1*
Pluteus harrisii	SP393698, holotype	HM562164	–
Pluteus izurun	ARAN3008424-1, holotype	JQ065023	KJ010047
Pluteus izurun	ARAN3008424-2	JQ065024	KJ010048
Pluteus meridionalis	FK1084	KJ009767	KJ010054
Pluteus meridionalis	MC4412, holotype	HM562157	KJ010052
Pluteus nigrolineatus	isolate 114	FJ375245	–
Pluteus oreibatus	AJ600	KJ009764	KJ010032
Pluteus oreibatus	ECV4183, holotype	KJ009763	KJ010033
Pluteus padanilus	Pradeep14418	KJ009768	KJ010050
Pluteus padanilus	Pradeep13844, holotype	JQ801374	KJ010049
Pluteus phaeoleucus	GF5102, type	HM562141	–
Pluteus puttemansii	SP393698	HM562164	–
Pluteus salicinus	LE202301	KJ009755	KJ010023
Pluteus salicinus	AJ349	JN603199	KJ010026
Pluteus saupei	ILLS42441	HM562113	–
Pluteus saupei	FLAS-F61275	MH211851	–
Pluteus sepiicolor	LE289365, holotype	KJ009765	KJ010030
Pluteus sepiicolor	LE289366	KJ009766	KJ010031
Pluteus septocystidiatus	BRNM761662, holotype	HG964401	–
Pluteus septocystidiatus	AJ154	HM562057	KJ010039
Pluteus sp. 1	LE F-313670	OQ732732	OQ772320
Pluteus thoenii	Thoen5546, type	HM562132	KJ010051

Taxonomy

Pluteus **section** ***Pluteus*** **Fr.**

Pluteus albostipitatus (Dennis) Singer, Lloydia 21: 240 (1959) (Figs. 2, 3)

≡ *Pluteus spilopus* var. *albostipitatus* Dennis, Bulletin de la Société Mycologique de France 69(2): 195 (1953)

Reported heterotypic synonyms:

= *Pluteus phaeoleucus* E. Horak, Bulletin du Jardin Botanique National de Belgique 47(1–2): 89 (1977)

= *Pluteus melanopotamicus* Singer, Fieldiana, Bot. 21: 96 (1989)

= *Pluteus densifibrillosus* Menolli & Capelari, Mycologia 102(2): 698 (2010)

Diagnosis:—Based on material from Aneityum, *P. albostipitatus* is characterized macroscopically by a gray-brown, variably fibrillose, centrally punctate pileus and a white stipe. Microscopically it is characterized by subglobose to broadly ellipsoid spores (8.1 × 6.2 µm), clavate cheilocystidia, fusoid, thin to thick-walled pleurocystidia with 2–6 apical hooks, a cutis pileipellis, and the absence of caulocystidia.

Description:—*Pileus* 35–37.5 mm diam., plano-convex to broadly plano-convex, margin entire or splitting; surface somewhat pearlescent, dry, disc pustulate or warted with agglutinated hairs, variably appressed-fibrillose; disc gray-brown (56E3–4), fibrils gray (5DE2–3) towards margin, underlying surface pallid gray. *Context* thin, pallid gray. *Lamellae* free, close with 2 tiers of lamellulae, moderately broad (3–4 mm), white-gray to pink-gray with brown tones (6–7B2–3), margin paler, slightly eroded. *Stipe* 32–47 × 2.5–3 mm, central, terete, cylindrical above a subbulbous base (4–6 mm), solid; surface pearlescent, dry, silky, pallid white-gray with brown tones towards base and where handled, context white. *Odor* indistinct. *Taste* not observed.

FIGURE 2. Basidiome of *Pluteus albostipitatus* (BAP 930). Scale bar = 10 mm. Photo by: Brian Perry.

Basidiospores (5–) 6–11 (–13) × 5–8 (–9) µm [x_{mr} = 7.41–8.88 × 6.12–6.3 µm, x_{mm} = 8.15 ± 1.0 × 6.21 ± 0.62 µm, Q = 1–1.6 (–2.0), Q_{mr} = 1.21–1.42, Q_{mm} = 1.31 ± 0.25, n = 50, s = 2], subglobose to broadly ellipsoid, seldom globose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 15–35 × 6–11 µm, subclavate to cylindro-clavate, 4-spored, hyaline, thin-walled, sterigmata 2–5 × 0.5–1 µm. *Basidioles* 11–25 × 4–10 µm, clavate to subclavate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 24–60 × 8–22 µm, clavate to subclavate or fusoid-ventricose to sphaeropedunculate, obtuse or subcapitate to umbonate, hyaline, thin-walled. *Pleurocystidia* 53–110 × 6–22 µm, common, fusiform to fusoid-ventricose or seldom utriform to broadly clavate, obtuse to truncate without outgrowths, with 2–4 clefts, or infrequently corniculate with 2–6 whole or bifid, blunt, recurved poorly-developed apical hooks, rarely asymmetrical, hyaline, some with a guttule, thin to thick-walled (up to 2 µm thick) often thinning towards the base. *Pileipellis* a cutis of repent hyphae, composed of hyaline or pale to dark brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 4–20 (–25) µm diam.; terminal elements 35–111 × 7–22 µm, suberect to erect towards disc and repent elsewhere, cylindrical to clavate, obtuse or infrequently subcapitate. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 3–28 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–20 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–20 (–25) µm diam.. *Caulocystidia* absent. *Clamp connections* present sometimes in stipitipellis tissue, and absent in all other tissues.

Habitat and known distribution:—Solitary on decaying wood in subtropical coastal scrub, mangrove forest, secondary littoral forest, and mixed-use agro tree garden containing *Annona muricata* (*Annonaceae*), *Artocarpus altillis* (*Moraceae*), *Bruguiera gymnorhiza* (*Rhizophoraceae*), *Cocos nucifera* (*Arecaceae*), *Macaranga tanarius* (*Euphorbiaceae*), *Magnifera indica* (*Anacardiaceae*), *Musa spp.* (*Musaceae*), and *Syzygium richii* (*Myrtaceae*) or montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus*

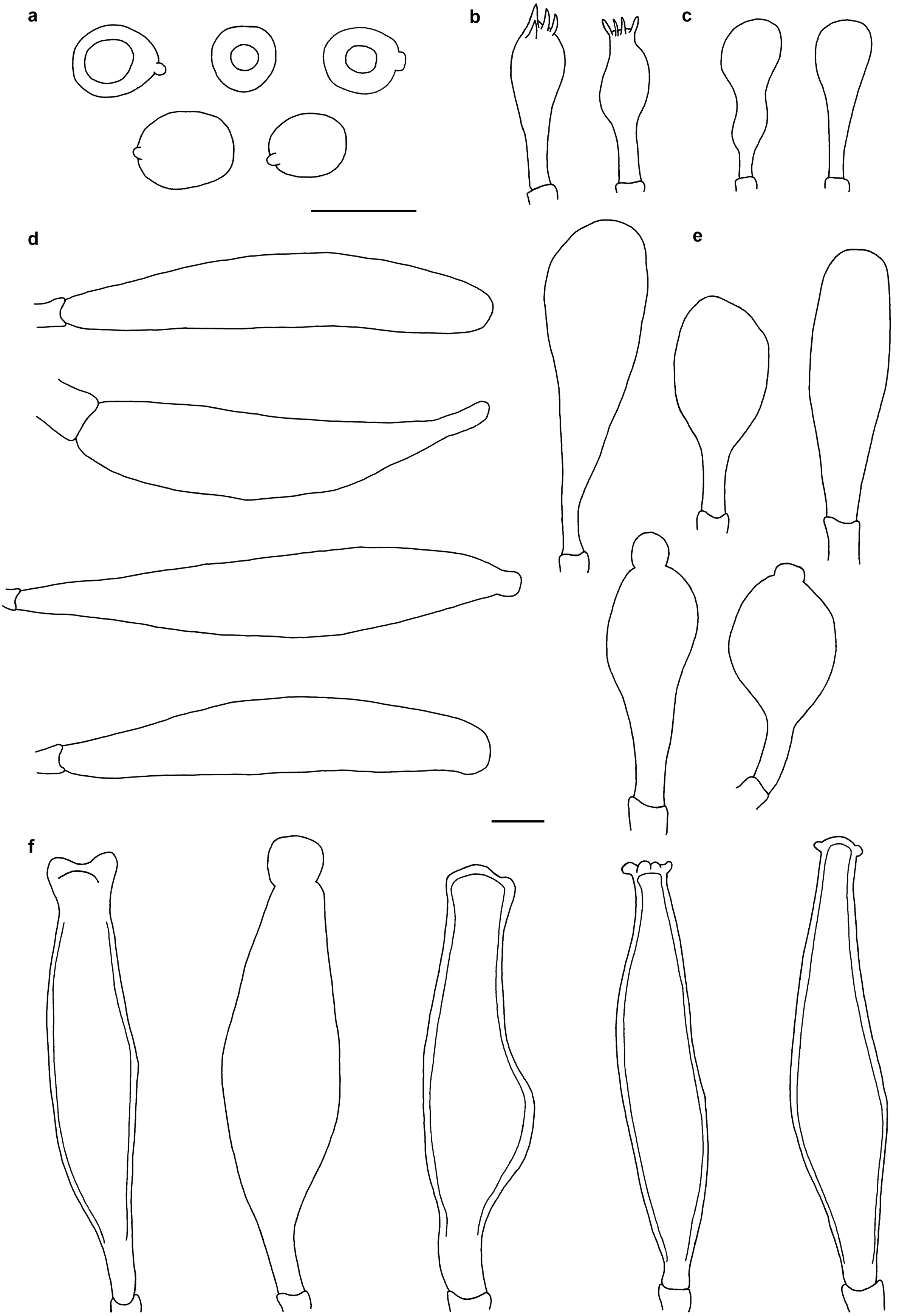

FIGURE 3. *Pluteus albostipitatus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

septica (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum). Also known from Africa (D.R. Congo, São Tomé), Asia (Thailand, Vietnam), Caribbean (Martinique, Trinidad), South America (Argentina, Bolivia, Brazil, French Guiana, Galapagos Islands), and North America (United States, Florida, Indiana).

Material examined:—VANUATU. Tafea Province: Aneityum, Anloulanelcau area, trail through mixed forest to transect 11, 20°13.066′S, 169°47.406′E, elev. 188 m, 29 July 2017, coll. *B.A. Perry, BAP 930* (HAY); Aneityum, along trail from Anelgauhat towards Umej, 20°14.202′S, 169°48.203′E, elev. 26 m, 7 August 2017, coll. *M.C. Aime, BAP 968* (HAY).

Notes:—A survey of multiple descriptions of *P. albostipitatus* (Dennis) Singer (1958: 240) reveals a morphologically cryptic species with wide macroscopic and microscopic variation, as also acknowledged by previous authors (Desjardin & Perry 2018, Menolli & Capelari 2010, Menolli *et al*. 2015a). Originally described from Trinidad as *P. spilopus* var. *albostipitatus* Dennis (1953: 195) before being elevated to species rank by Singer (1958), the species was initially placed in sect. *Hispidoderma* due to early collections generally displaying thin-walled pleurocystidia with truncate, hookless apices (Dennis 1953). Singer reported small apical outgrowths on pleurocystidia from Argentinean material, and both he and Pegler suspected that this atypical shape had an intermediate link to metuloid cystidia found in species of sect. *Pluteus* (Pegler 1983a, Singer 1958). Phylogenetic studies have confirmed the position of *P. albostipitatus* within sect. *Pluteus* as part of the *salicinus/albostipitatus* clade recognized by Justo *et al*. (2011b), which includes other species containing thin-walled pleurocystidia with poorly developed apical hooks that are considered atypical for the section (Justo *et al*. 2011b, Menolli & Capelari 2010). Recent descriptions of this species by Menolli *et al*. (2015a) and Desjardin and Perry (2018) display the extent of microcharacter variation within the species, and provide additional instances of pleurocystidia with poorly developed apical outgrowths and thin to thick walls similar to those seen in the Vanuatu specimens.

Based on multiple descriptions, the current concept of *P. albostipitatus* defines the pileus as morphologically variable, with the surface ranging from densely appressed-fibrillose to completely smooth and glabrous (Justo *et al*. 2011b, Menolli *et al*. 2015a, Singer 1956). Desjardin and Perry (2018) reported the pileus disc being appressed-fibrillose, but glabrous to subglabrous elsewhere, and Singer noted collections appearing subglabrous when wet, but typically "when fresh and dry more or less distinctly radially fibrillose with innate fibrils" (Singer 1956). Referring to a photo of Desjardin and Perry's São Tomé material (Fig. 7, 2018), the material appears older and wet, possibly similar to Singer's observations, and is an example of the influence of environmental factors on superficial appearance during collecting. The material from Aneityum appears as appressed-fibrillose with shades of gray to grayish brown, matching descriptions from multiple authors (Dennis 1953, Horak 1964, Menolli & Capelari 2010, Menolli *et al*. 2015a, Singer 1956). Species such as *P. phaeoleucus* Horak (1976: 89) from the D.R. Congo (Horak 1976) and *P. densifibrillosus* Menolli & Capelari (2010: 698) from Brazil (Menolli & Capelari 2010), that are recognized as synonymous with *P. albostipitatus* (Menolli *et al*. 2015a) were described with a non-striate pileus, similar to the Vanuatu material. In contrast, other authors have described the pileus as being striate to sulcate (Dennis 1953, Desjardin & Perry 2018, Horak & Heinemann 1978, Menolli *et al*. 2010, Pegler 1983a, Singer 1956). All prior mentioned accounts also describe the pileus center as punctate, nippled or some variation, and this occurs in the Aneityum material.

In *P. albostipitatus*, spore shape has been observed to range from globose to broadly ellipsoid, and the predominant shape and size may be dependent on the specimen. Overall, the Vanuatu material displays spore sizes within previously reported ranges, although collection BAP 968 was observed to consist of more broadly ellipsoid spores versus BAP 930 having predominantly subglobose spores. Size and morphological variation of microcharacters extends to the pleurocystidia and cheilocystidia in both Vanuatu specimens. Both collections contain thin to thick-walled (up to 2 μm thick) pleurocystidia that are predominantly fusiform to fusoid-ventricose in shape, matching previous accounts (Desjardin & Perry 2018, Horak 1964, Menolli & Capelari, 2010, Menolli *et al*. 2015a, Pegler 1983a, Singer 1958). Both Aneityum collections also contain apically obtuse pleurocystidia, but the predominant apex type on pleurocystidia differs between specimens. BAP 930 has more pleurocystidia with poorly developed outgrowths on the apices, like those described by Singer (1958), Menolli *et al*. (2015a), and Desjardin and Perry (2018). BAP 968 has more pleurocystidia with truncate apices, like those in Pegler (1983a), also in Desjardin and Perry (2018), and bifid apices as in Menolli & Capelari (2010), Menolli *et al*. (2015a), and Desjardin and Perry (2018). Both Aneityum collections also contain rarely observed broadly clavate to broadly utriform pleurocysitida, which appear to be the predominant type in descriptions by Horak (Horak & Heinemann 1978) and Menolli *et al*. (2015a). Cheilocystidia observed in the Vanuatu collections also match the size and shape from prior accounts, however in collection BAP 930 a subcapitate-umbonate apex type occurs that has not been previously reported. The clearly extensive morphological variation in the current concept of *P. albostipitatus* requires further inquiry and suggests that cryptic species could be hiding under this name.

Phylogenetic analysis of ITS data places one of the Vanuatu specimens, BAP 968, within a low supported clade (Fig. 1c, BS 69 %, PP 0.86) with poorly resolved internal topology comprised of sequences identified as *P. septocystidiatus* Ševčíková, Antonín & Borovička (2014: 230) from South Korea, Thailand, Vietnam, and the United States (New York, Indiana, and Florida), *P.* cf. *septocystidiatus* from Florida, U.S.A., *P.* aff. *septocystidiatus* from Vietnam, and *P. albostipitatus* from São Tomé. BAP 930 was not included in the analysis due to multiple failed attempts at sequencing ITS because of a high number of indels. *Pluteus septocystidiatus* is a recently described species from Korea and the U.S.A. (Florida) that is distinguished primarily by fusiform, relatively thick-walled pleurocystidia with distinctive medial septa (Ševčíková *et al*. 2014). Ševčíková *et al.* included two collections from Florida that were originally identified as *P. albostipitatus*. AJ154 (HM562057) contained distinctly thick-walled septate pleurocystidia as well as thin-walled pleurocystidia with obtuse projections similar to those known in *P. albostipitatus*. AJ187 (HM562106) was tentatively identified as *P.* cf. *septocystidiatus* due to having a minority of septate pleurocystidia never being distinctly thick-walled and being phylogenetically distant from the other collections of *P. septocystidiatus*. Singer noted in his description of *P. albostipitatus* that the pleurocystidia are characterized "exceptionally with a pseudo-[secondary] septum near the tip" (Singer 1958), which Ševčíková *et al.* considered when proposing *P. septocystidiatus* distinct from *P. albostipitatus*. In addition to septate pleurocystidia, the rare presence of clamp connections on the stipitipellis was also used as a distinct feature, and this character occurs in the Vanuatu material. The specimen of *P. septocystidiatus* from Thailand was described as having septate pleurocystidia, but lacking clamp connections in all tissues including the stipitipellis (Wannathes *et al*. 2022). The material from New York, U.S.A., provided a single photo with a septate pleurocystidia (iNaturalist 55850102). The Vietnamese material identified as *P. septocystidiatus* was described as predominantly having septate pleurocystidia while the specimen distinguished as *P.* aff. *septocystidiatus* was described as also having septate pleurocystidia, but to a lesser extent (Malysheva *et al*. 2023). Desjardin and Perry (2018) observed their São Tomé specimen of *P. albostipitatus* having non-septate, apically obtuse, thin-walled pleurocystidia and observed no clamp connections in the stipitipellis. Both Vanuatu specimens contain pleurocystidia ranging from thin to thick-walled with variable apex types but lack any septate pleurocystidia.

Considering the extensive morphology within the *P. albostipitatus* complex, further investigation of delimiting characters is necessary, including comparisons to specimens of *P. septocystidiatus*. Based on the description and photo of the Korean holotype of *P. septocystidiatus* (Fig. 1, Ševčíková *et al.* 2014), the dark brown, striate, and centrally rugulose characters of the pileus (perhaps comparable to punctate/warted/nippled) seem to be shared characters within the observed range of comprehensive descriptions of *P. albostipitatus*. Previous authors have acknowledged other taxonomically useful characters when distinguishing species in sect. *Pluteus* including the presence of clamp connections in the pileipellis and stipitipellis tissue (Justo *et al*. 2014, Singer 1956). Molecular studies of sect. *Pluteus* have also found the use of *tef1* gene data to provide better phylogenetic resolution compared to ITS alone (Justo *et al.* 2014, Menolli *et al.* 2014). Further study and intensive re-examination utilizing these characters and additional molecular markers could provide better resolution in the *P. albostipitatus* complex. For the sake of this study, identification of the Aneityum material better fits the wide range of morphological variation in *P. albostipitatus*. *Pluteus albostipitatus* appears to be a pantropical species known to occur throughout the subtropical and tropical Americas from Florida, U.S.A., through the Caribbean to Brazil and the Galapagos Islands, and tropical mainland Africa and its coastal islands. Interestingly, specimens of *P. septocystidiatus* have both a temperate distribution in the eastern to midwestern U.S.A. and South Korea and a subtropical to tropical occurrence in Florida, U.S.A., Vietnam, and Thailand. Although the Aneityum material is phylogenetically closer to *P. septocystidiatus,* the absence of septate pleurocystidia would separate them, but this septate character could just be an extension of the morphological variation within *P. albostipitatus* pending future studies.

Pluteus petasatus (Fr.) Gillet (*Hyménomycètes* (Alençon): 395 (1876) [1878] (Figs. 4, 5)

≡ *Agaricus petasatus* Fr., *Epicr. syst. mycol.* (Upsaliae): 142 (1838) [1836–1838]

≡ *Pluteus cervinus* var. *petasatus* (Fr.) Fr., Hymenomycetes europaei: 186 (1874)

Reported heterotypic synonyms:

= *Agaricus curtisii* Berk., Hooker's Journal of Botany and Kew Garden Miscellany 1: 98 (1849)

= *Agaricus patricius* Schulzer, Icones selectee Hymenomycetum Hungariae per Stephanum Schulzer et Carolum Kalchbrenner observatorum. Magyaroszág Hárta gombák váalogatott Képei 1: 20 (1873)

= *Pluteus viscidulus* Singer, Lilloa 25: 255 (1952)

= *Pluteus straminiphilus* Wichanský, Mykol. Sb., Praha: 119 (1968)

= *Pluteus australis* Murrill, Proceedings of the Florida Academy of Sciences 7 (2–3): 119 (1945)

= *Pluteus magnus* McClatchie, Proceedings of the Southern California Academy of Sciences 1: 383 (1897)

Diagnosis:—Based on material collected from Tafea Province, *P. petasatus* is characterized by a dry or viscid, ash brown fibrillose pileus and a white with sparse ash brown fibrils stipe with a subbulbous base. Basidiome variants include some that are white overall, as in JAD 45, or have ash brown floccules at the disc, as in JAD 47. Microscopic characters include broadly ellipsoid spores (7.0 × 4.6 µm), sparse clavate cheilocystidia, fusiform, thick-walled pleurocystidia with 2–4 apical hooks, similar thin-walled intermediate pleurocystidia, an ixo-cutis pileipellis, an absence of caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 35–80 mm diam., broadly convex, expanding to plano-convex, with or without a broad umbo, with or without a slight central depression; surface dull, dry to moist, the disc glabrous, appressed fibrillose or flocculose, glabrous towards the margin, cream, white to isabelline (oac815–oac816) or pale pink (oac675–oac676), fibrils if present ash brown (oac737–oac739), floccules if present dark ash brown (oac735–oac737). *Context* 2–4 mm thick, white. *Lamellae* free, crowded with many tiers of lamellulae, thin (1–2 mm thick), pale pink (oac682–oac683 or oac695–oac697), edges concolorous. *Stipe* 50–90 mm × 5–15 mm, central, terete, cylindrical above a subbulbous base, solid; surface dull, dry, glabrous to sparsely fibrous, white overall or with ash brown (oac737–oac739) fibrils that tend to become denser towards the base, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 6–9 (–10) × 4–6 (–8) µm [x_{mr} = 6.18–7.52 × 4.18–4.77 µm, x_{mm} = 6.95 ± 0.69 × 4.56 ± 0.33 µm, Q = 1.16–2.25, Q_{mr} = 1.48–1.59, Q_{mm} = 1.53 ± 0.59, n = 50, s = 3], broadly ellipsoid to subellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 16–26 × 5–10 µm, clavate, 4-spored, hyaline, thin-walled, sterigmata 2–5 × 0.5–1 µm. *Basidioles* 12–22 × 5–10 µm, clavate to subcylindrical, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 18–71 × 8–35 µm, sparse, infrequently forming a well-developed strip on lamellar edge, clavate to narrowly clavate or sphaeropedunculate, obtuse, hyaline, thin-walled. *Pleurocystidia*; *primary pleurocystidia* 60–92 × 12–24 µm, fusiform to narrowly utriform, cornuate with 2–4 whole, straight to recurved poorly or well-developed apical hooks, some acute, occasionally with 1–3 lateral hooks, hyaline, evenly thick-walled (up to 2.5 µm thick); *intermediate pleurocystidia* 38–61 × 8–13 µm, similar to primary pleurocystidia but smaller, fusiform to fusoid, acute or occasionally with 2–3 whole, recurved apical hooks, often with 1–3 lateral excrescences, hyaline, thin to thick-walled (up to 2 µm thick). *Pileipellis* an ixo-cutis of repent hyphae, embedded in a gelatinous matrix or a cutis with an external gelatinous layer of narrow hyphae, 2–6 µm diam., composed of hyaline or containing brown plasmatic pigment, non-incrusted, gelatinized or not, thin-walled, cylindrical hyphae, 4–18 µm diam.; terminal cells 30–150 × 7–20 µm, repent to erect towards disc, clavate, obtuse, sometimes strongly tapering, seldom with median constriction. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 9–25 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 4–13 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 5–29 µm diam.. *Caulocystidia* absent. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary on decaying wood in subtropical coastal scrub, mangrove forest, secondary littoral forest, and lowland mixed-use agro tree garden containing *Annona muricata* (*Annonaceae*), *Artocarpus altillis* (*Moraceae*), *Barringtonia asiatica* (*Lecythidaceae*), *Bruguiera gymnorhiza* (*Rhizophoraceae*), *Cocos nucifera* (*Arecaceae*), *Cordia dichotoma* (*Boraginaceae*), *Euodia hortensis* (*Rutaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Macaranga tanarius* (*Euphorbiaceae*), *Magnifera indica* (*Anacardiaceae*), *Musa spp.* (*Musaceae*), and *Syzygium richii* (*Myrtaceae*), Vanuatu (Aneityum, Tanna). Also known from Asia (Japan, Mongolia, Russia), Europe (Spain), North America (Canada, Mexico, United States), South America (Argentina, Paraguay), and Papua New Guinea.

Material examined:—VANUATU. Tafea Province: Aneityum, along trail from Anelgauhat towards Umej, 20˚14.208′S, 169˚47.940′E, elev. 26 m, 4 August 2017, coll. *M.J. Balick*, *JAD 45* (HAY); same location 4 August 2017, coll. *J.A. del Rosario & M.C. Aime*, *JAD 47* (HAY); Tanna, Port Resolution, trail between Tanna Horizon Bungalow and Ireupow, 19°31.310′S, 169°30.365′E, elev. 7 m, 16 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 298* (HAY).

Notes:—*Pluteus petasatus* is a species with one of the broadest known distributions within the genus as it has been recorded throughout Eurasia and North America, extending into the Southern Hemisphere. Justo *et al.* (2014) determined that *P. petasatus* produces basidiomes with morphologically variable pilei, ranging from dry to viscid, glabrous to variably fibrillose, and having color within a wide spectrum of cream, white, isabelline (pale gray-yellow or parchment-colored), and brown to dark gray. Based on molecular evidence and extensive examination of microscopic characters, Justo *et al.* (2014) proposed multiple species analogous to *P. petasatus*. The material collected from Aneityum and Tanna fits well within the range of macromorphological characters and consistent microscopic characters under the concept of *P. petasatus* as defined by Justo *et al.* (2014).

Phylogenetic analysis based on ITS data (Fig. 1b) places the Tafean material with collections from Papua New Guinea and Japan (originally identified as *P. magnus* McClatchie (1897: 383)) in a well-supported subclade (BS 90 %, PP 0.99) within a larger clade of a global sampling from material identified as *P. petasatus*. *Pluteus magnus* had been proposed as a synonym of *P. petasatus,* despite the absence of molecular data, due to the holotype having identical microcharacters (Justo *et al*. 2014). A comprehensive comparison of previous descriptions of *P. magnus* to the Tafean material reveals identical morphology, except for the Vanuatu specimen's ixo-cutis pileipellis, which has not been observed in previous accounts (Banerjee & Sundberg 1993, McClatchie 1897, Singer 1956, Takehashi & Kasuya 2009). Interestingly, the subclade contains collections distributed along the Pacific Ocean from East Asia to Australasia. Collections from Canada (JN021081) and the U.S.A. (JX857453) form a weakly supported subclade (BS 59 %, PP 0.94) sister to the preceding subclade, however this is unsupported. The specimen from the U.S.A. was collected from southern California in the same locality as the type specimen of *P. magnus* and may possibly serve as topotypical material. Whether or not either of these subclades are representative of *P. magnus*, and if it should be recognized as a separate species, requires further investigation. Current knowledge indicates that *P. petasatus* is a widely distributed species occurring in various environments, from disturbed habitats to natural and undisturbed forest, and in drastically different climates, from subtropical to tropical and Mediterranean to temperate. The Vanuatu collections were frequently collected in disturbed coastal forests and according to available records from GenBank, the Papua New Guinea material was collected on the University of Goroka campus. Both the Japanese and Californian collections appear to have been found in urban areas. In these instances, a possible explanation for such a wide distribution may be due to anthropogenic movement of fungal propagules or substrate.

FIGURE 4. Basidiome of *Pluteus petasatus in situ* (JAD 298). Scale bar = 10 mm. Photo by: Brian Perry.

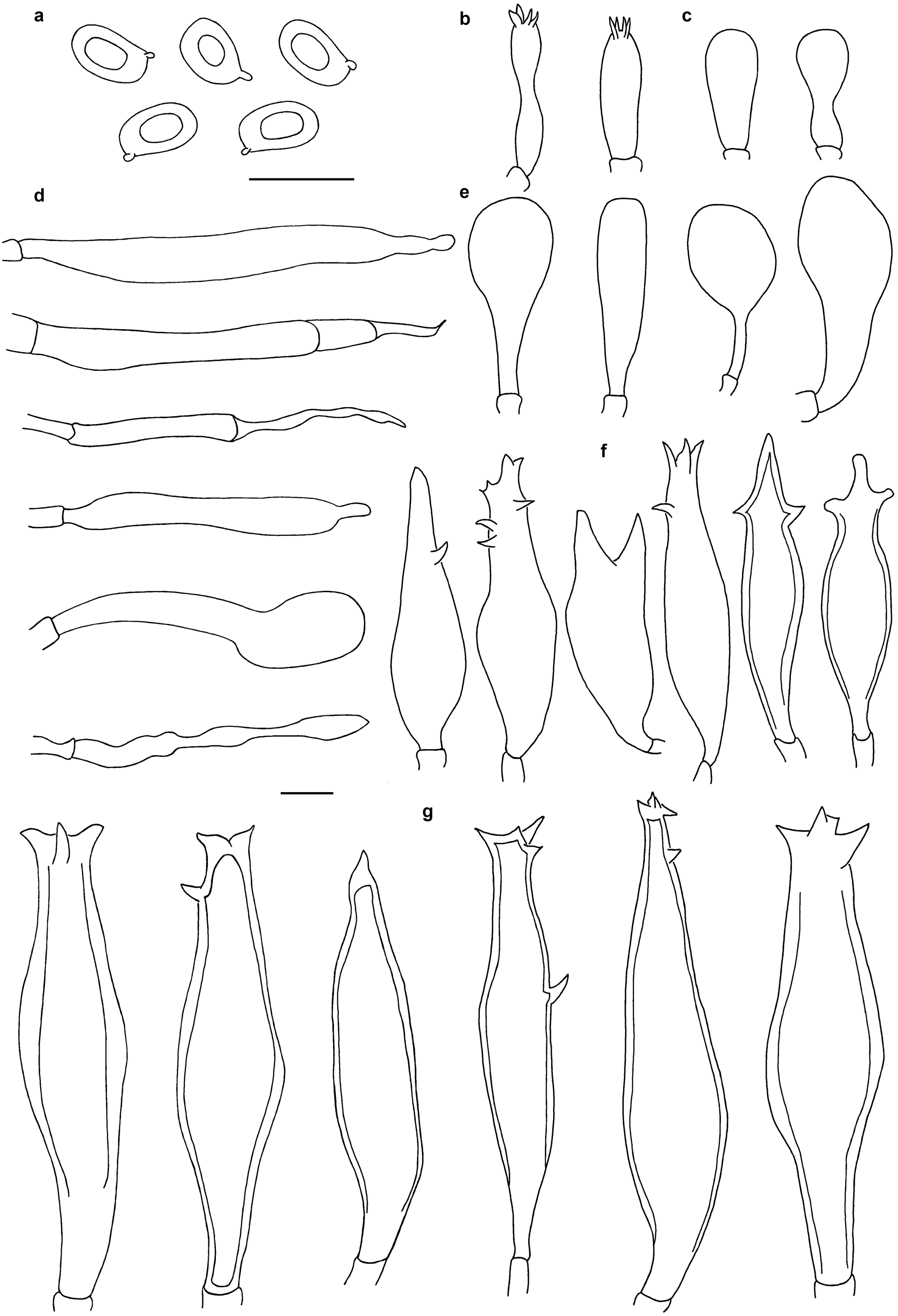

FIGURE 5. *Pluteus petasatus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Intermediate pleurocystidia. g. Primary pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

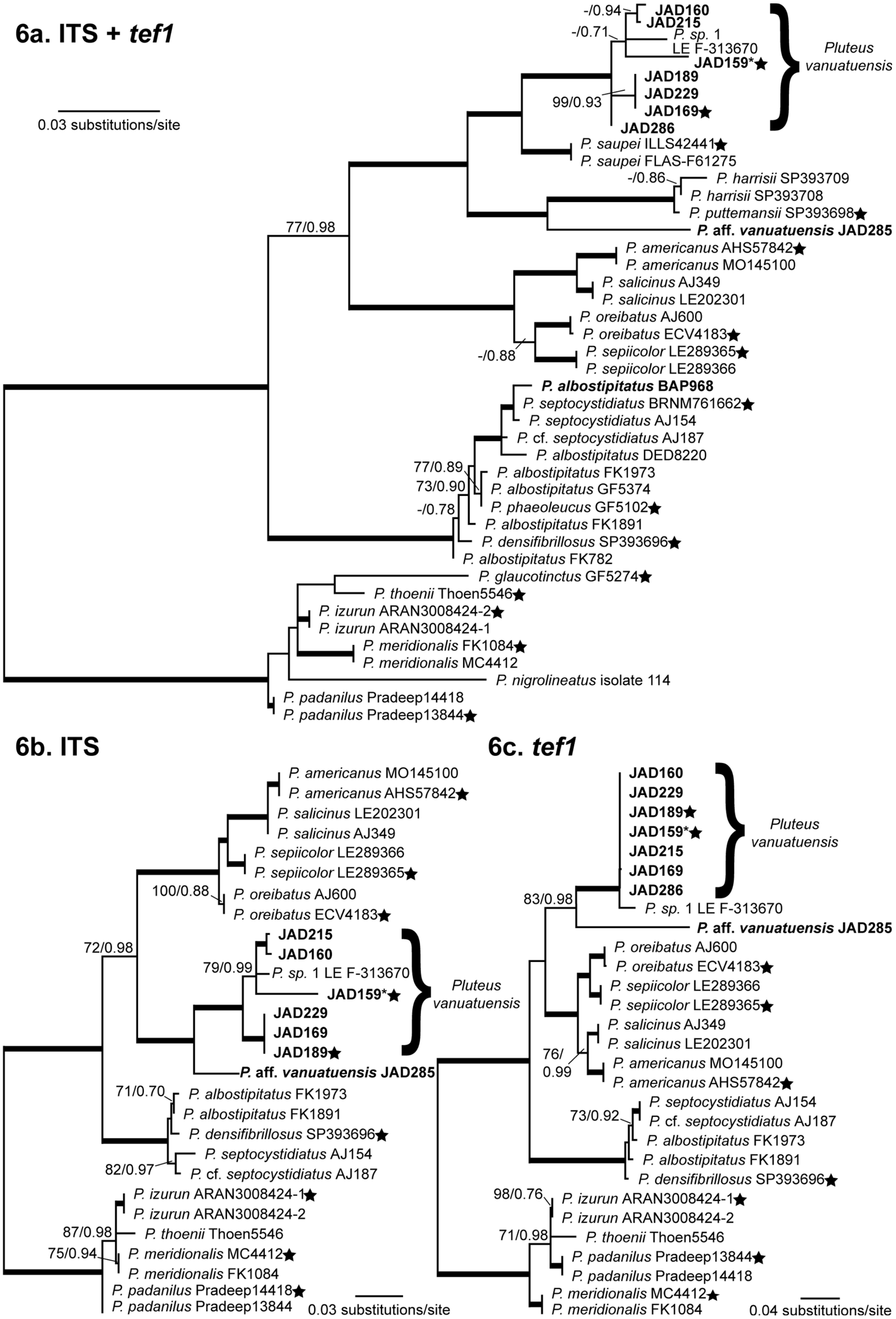

FIGURE 6a–c. Maximum Likelihood phylogenies of the *albostipitatus/salicinus* clade based on combined (Fig. 6a; -lnL = 4927.663337), ITS (Fig. 6b; -lnL 2206.25101), and *tef1* (Fig. 6c; -lnL = 2099.291416) sequence data. Sequences of specimens from Vanuatu are indicated in bold type. Stars indicate type specimens. Values separated by / refer to ML bootstrap proportions and Bayesian posterior probabilities, respectively. Only values greater than 70/0.70 are shown. Nodes receiving support values greater than 90/0.95 are highlighted in bold.

Pluteus vanuatuensis J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 7, 8)
MycoBank no.:—854222

Holotype:—VANUATU. Tafea Province: Tanna, Numdretum River, 19°38.246′S, 169°25.237′E, elev. 145 m, 4 December 2018, coll. *J.A. del Rosario, JAD 189* (HAY).

Etymology:—Refers to the Vanuatu islands where the holotype was collected.

Diagnosis:—*Pluteus vanuatuensis* from Tafea is distinguished by a grayish brown to hazel appressed-fibrillose, black floccose-pustulate disc, hygrophanous and sulcate pileus, and a white stipe with pale brown minute streaks and a bulbous base. All tissues bruise a faint bluish gray. Microcharacters include subglobose basidiospores (7.3 × 6.6 µm), clavate cheilocystidia, fusoid, thick-walled pleurocystidia with 2–5 apical hooks, similar but smaller intermediate pleurocystidia, a cutis pileipellis with erect clavate terminal elements at the disc, absent caulocystidia, and the presence of clamp connections in all tissue.

Description:—*Pileus* 25–70 mm diam., hemispherical to plano-convex with a slight centrally depressed umbo; surface dull to pellucid-striate up to half-way from margin, hygrophanous, finely appressed-fibrillose to subglabrous, disc floccose-pustulate; floccules/pustules/fibrils dark chocolate brown (oac639–oac641) to brown-black, underlying surface dull gray-brown (oac730–oac736/oac720–oac722) turning pallid brown (oac751–oac753) to pale hazel (oac646–648) towards margin. *Context* up to 1.5 mm thick, pallid gray-brown turning faintly bluish gray when exposed. *Lamellae* free, moderately close with 3 tiers of lamellulae, thin (up to 1 mm thick), light pink (oac632–oac634/oac696–oac697). *Stipe* 40–60 × 3–4 mm, central, terete, cylindrical above a subbulbous to bulbous base, hollow; surface pearlescent, dry, silky, white to off-white without or infrequently with tannish brown (oac672–oac675) tones mid-way towards the base, occasionally with bluish gray tones at the base, context white. Tissues turning bluish gray when disrupted or handled. *Odor* indistinct. *Taste* indistinct.

FIGURE 7. Basidiomes of *Pluteus vanuatuensis* (JAD 189 holotype). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

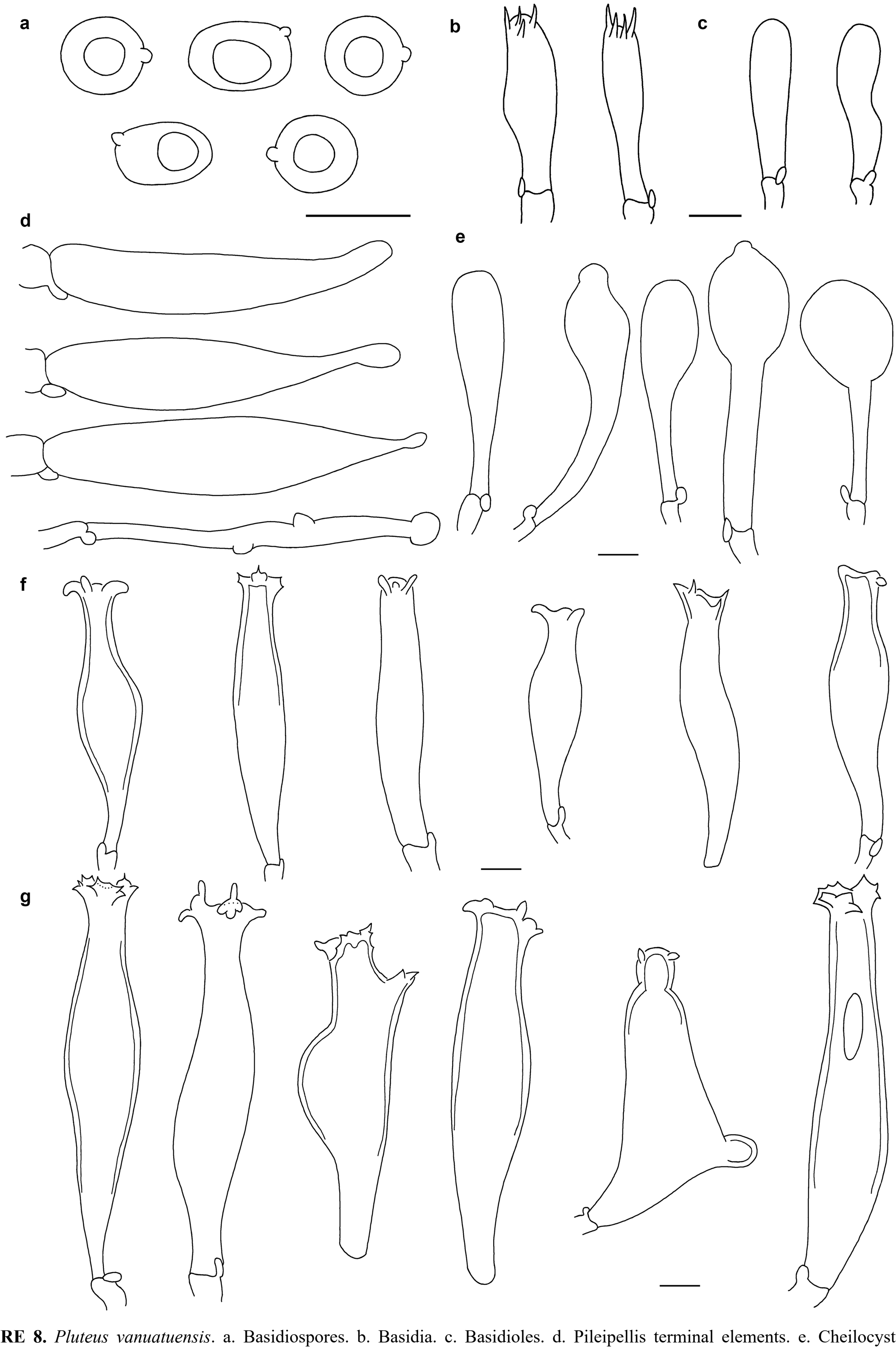

FIGURE 8. *Pluteus vanuatuensis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Intermediate pleurocystidia. g. Primary pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Basidiospores (5–) 6–8 (–9) × (5–) 6–7 (–8) µm [x_{mr} = 6.98–7.56 × 5.98–6.94 µm, x_{mm} = 7.26 ± 0.23 × 6.49 ± 0.35 µm, Q = 1–1.5, Q_{mr} = 1.04–1.18, Q_{mm} = 1.12 ± 0.04, n = 50, s = 6], globose to subglobose, rarely broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* (15–) 18–34 × 6–8 µm, clavate, 4-spored or rarely 2-spored, hyaline, thin-walled, sterigmata 2–3 × 0.5–1 µm. *Basidioles* 16–35 × 6–10 µm, clavate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 30–75 × (8–) 15–24 µm, clavate or seldom sphaeropedunculate or utriform, obtuse or seldom subcapitate, hyaline, thin-walled. *Pleurocystidia*; *primary pleurocystidia* 50–102 × 12–25 µm, fusoid to narrowly lageniform, apex variable, cornuate or corniculate with 2–4 (–5) whole to bifid, straight or recurved poorly or well-developed apical hooks, bifid frequency varying among specimens with acute, cornuate or corniculate arms, most with a guttule, rarely asymmetrical, hyaline, thin to thick-walled (up to 2 µm thick); *intermediate pleurocystidia* 33–66 × 11–25 µm, fusoid to lageniform or seldom utriform, obtuse, acute or corniculate to rarely cornuate with 1–4 whole, blunt, straight to recurved poorly developed apical hooks, with a guttule, hyaline, thin to thick-walled. *Pileipellis* a cutis of repent hyphae, composed of grayish brown plasmatic pigment or hyaline, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 5–20 µm diam.; terminal elements 45–135 (–180) × 11–18 µm, in erect fascicles at the disc, clavate or filiform, obtuse, rarely strongly tapering or subcapitate, rarely entirely nodulose (one collection), hyaline or with grayish brown plasmatic pigment, thin-walled. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 7–25 (–35) µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 5–22 µm diam.. *Stipitipellis* a cutis, composed of hyaline or sometimes with grayish brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–18 µm diam.. *Caulocystidia* absent. *Clamp connections* present in all tissues examined.

Habitat and known distribution:—Gregarious to solitary on decaying wood in subtropical lowland mixed-use agro tree garden and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*), Vanuatu (Aneityum, Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Numdretum River, 19°38.440′S, 169°25.385′E, elev. 131 m, 29 August 2018, coll. *J.A. del Rosario, JAD 160* (HAY); Tanna, Yanemarei, 19°38.511′S, 169°25.616′E, elev. 94 m, 30 August 2018, coll. *J.A. del Rosario, JAD 169* (HAY); Tanna, Numdretum River, 19°38.246′S, 169°25.237′E, elev. 145 m, 4 December 2018, coll. *J.A. del Rosario, JAD 189* (HAY); Tanna, Tangahuruti, 19°38.809′S, 169°26.382′E, elev. 66 m, 6 December 2018, coll. *J.A. del Rosario, JAD 215* (HAY); Aneityum, Nathaway, 20°14.245′S, 169°48.177′E, elev. 0 m, 10 December 2018, coll. *J.A. del Rosario, JAD 229* (HAY); Tanna, Yakuwan, 19°32.230′S, 169°28.911′E, elev. 84 m, 15 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 286* (HAY).

Notes:—The distinctive bluish gray bruising of disrupted tissue from this species requires comparison to similar species, such as *P. salicinus* (Persoon) Kummer (1871: 99), *P. saupei* Justo & Minnis (2011: 475), and *P. americanus* (Banerjee & Sunderberg) Justo, E.F. Malysheva & Minnis (2014: 180). The Eurasian *P. salicinus* differs in having a grayer pileus, smaller ellipsoid spores, less versiform pleurocystidia with developed apical hooks, intermediate pleurocystidia lacking apical hooks, and more clavate cheilocystidia (Justo *et al*. 2014). Known only from the state of Illinois in the U.S.A., *P. saupei* shares the outward appearance of *P. vanuatuensis*, but microscopically differs by having slightly larger ellipsoid spores, pleurocystidia with poorly developed hooks, and more lageniform cheilocystidia with elongated apices (Justo *et al*. 2011b). *Pluteus americanus* was originally described as a variety of *P. salicinus* before being elevated to species rank based on molecular data and geographic distinction by being known from the eastern United States and Russian Far East (Banerjee & Sundberg 1993, Justo *et al*. 2014). *Pluteus americanus* is also superficially very similar to the Vanuatu specimen, but differs with its lighter-colored pileus, more ellipsoid spores, less apically versiform pleurocystidia, non-apically hooked intermediate pleurocystidia, and the absence of utriform or umbonate cheilocystidia (Justo *et al*. 2014). Some additional tropical species share similarities to *P. vanuatuensis*, but fundamentally differ in lacking blue-gray bruising. From Papua New Guinea, *P. kobayasii* Hongo (1976: 100) is one of the few species of *Pluteus* known from Vanuatu's neighbouring region. Although this taxon has a similarly colored pileus and contains clamp connections in the hyphal tissue, it differs by lacking a floccose disc or a pellucid-striate margin, is slightly smaller in stature, has fusoid thick-walled cheilocystidia, and lacks apically variable pleurocystidia (Hongo 1976).

The type of *P. saupei* was originally identified as a specimen of *P. salicinus*, and the material from both species was used to demonstrate the presence of the psychotropic compound psilocybin for the first time in a species of *Pluteus* (Saupe 1981). Psilocybin expression and similar blue bruising reactions arose independently in multiple lineages throughout the evolutionary history of fungi (Guzmán *et al*. 1998). These same blue, gray, or sometimes green-toned bruising reactions have been shown to originate at least twice in the evolution of the genus *Pluteus*, as this character is known to occur in *P. cyanopus* Quélet (1883: 391) and *P. phaeocyanopus* Minnis & Sunderberg (2010: 44) of sect. *Celluloderma,* and members of the *P. glaucotinctus* Horak (1976: 88) complex, which falls in the *salicinus/albostipitatus* clade recognized by Justo *et al*. (2011b) (Justo *et al*. 2014, Minnis & Sundberg 2010). Currently, the presence of psilocybin has only been confirmed in certain species within the *salicinus/albostipitatus* clade, and not all members, such as the aforementioned *P. albostipitatus*, have been observed to exhibit a similar bruising reaction (Menolli *et al*. 2014).

Based on ITS molecular data (Fig. 1c), *P. vanuatuensis* is phylogenetically placed within the *salicinus*/*albostipitatus* clade recognized by Justo *et al*. (2011b). This relationship to other members of this group known to display a blue bruising reaction and produce psilocybin or allied compounds raises the question if the compound is produced by *P. vanuatuensis* as well. Among all the specimens made during this study, *P. vanuatuensis* is represented by the highest number of collections, and observations conclude that it is a morphologically variable species. Pleurocystidia display a wide variety of apical ornamentation without a distinct dominant type, ranging from well to poorly developed cornuate, corniculate, bifid, or obtuse. Phylogenetic analysis (Fig. 1c) places these collections in a well-supported clade with two distinct lineages: one is strongly supported (BS 100 %, PP 1.0) containing collections JAD 169, JAD 189, and JAD 229, another is moderately supported (BS 83 %, PP 0.99) containing collections JAD 160, JAD 215, JAD 159, and a Vietnamese specimen of *P. sp.* 1 (OQ732732). Comparison of the Vanuatu specimens with the description of the Vietnamese specimen (Malysheva *et al.* 2023) indicates that the collections of these two clades show no discernible morphological differences to clearly separate them, except collection JAD 159 which has enough different morphological features to warrant treatment as a separate taxonomic unit discussed in the following section. A pairwise analysis of the overlapping region of JAD 159 against both lineages showed a 90.37–90.75 % similarity when indels were included and a 93.06–94.03 % difference when indels are excluded. Unfortunately we were not able to produce ITS data for JAD 286 due to a high number of indels, but *tef1* data was successfully generated. The identity of JAD 286 as *P. vanuatuensis* is confirmed based on analysis of *tef1* data (Fig. 6c) and morphological similarity. One collection, JAD 285, is positioned outside of this clade in both analyses for the wider sampled ITS dataset, but this is weakly supported (ML 59 %, PP 0.66). The phylogenetic affinity of JAD 285 results in preference to treat it as a separate taxonomic unit, which will be discussed in the proceeding section as *P.* aff. *vanuatuensis*.

Pluteus vanuatuensis* f. *ramacystidiatus J.A. del Rosario & B.A. Perry, *f. nov.* (Figs. 9, 10)
MycoBank no.:—854230

Holotype:—VANUATU. Tafea Province: Tanna between Ienehepe and Lighthouse, along banks of Numdretum River, 19°38.558′S, 169°25.713′E, elev. 286 m, 29 August 2018, coll. *J.A. del Rosario, JAD 159* (HAY).

Etymology:—*rama* (L.) = branch, *cystidiatus* (L.) = cystidia; refers to the branching apices on the pleurocystidia.

Diagnosis:—*Pluteus vanuatuensis* f. *ramacystidiatus* is characterized by a glabrous and sulcate grayish brown pileus with a dark grayish brown rugose disc, and a white with fine pale brown fibrils hollow stipe with a subbulbous base. When disrupted, the tissues turn faintly grayish blue. Microcharacters include subglobose spores (7.4 × 6.4 µm), four or single-spored basidia, clavate cheilocystidia, fusoid, thick-walled pleurocystidia with variable apices being acute, hooked, or irregularly polychotomous branched, similar intermediate thinner-walled pleurocystidia with lateral hooks, an ixo-cutis pileipellis with brown plasmatic contents, and an absence of caulocystidia. Clamp connections are common in all tissues. It is differentiated from *P. vanuatuensis* which has a distinct floccose disc, lacks elongated branched pleurocystidia, and lacks lateral hooks on the intermediate pleurocystidia.

Description:—*Pileus* 30–40 mm diam., convex to hemispherical, with a slight umbo, disc rugose-warted, margin sulcate; surface pellucid-striate up to half-way from margin, hygrophanous, semi-viscid, glabrous; disc/warts dark gray-brown (oac639–oac641), surface grayish brown (oac646–oac648) with patches pale pink (oac674–oac676), margin slightly paler gray-brown (oac662). *Context* up to 5 mm thick, pale gray-brown (oac662). *Lamellae* free, moderately close with 3–4 tiers of lamellulae, thin (< 1 mm thick), pale pink, margin somewhat paler. *Stipe* 25–35 × 3–4 mm, central, terete, cylindrical above a subbulbous base, hollow; surface dull, dry, fibrous, white to cream white with minute pale gray fibrils. Tissues turning bluish gray when damaged or handled. *Odor* indistinct. *Taste* indistinct.

Basidiospores 6–8 (–9) × 5–8 µm, [x_m = 7.44 ± 0.78 × 6.38 ± 0.83 µm, Q = 1–1.6, Q_m = 1.17 ± 0.2, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 16–30 × 8–10 µm, clavate, 4-spored or 1-spored, guttulate, hyaline, thin-walled, sterigmata 1.5–3 × 0.5–1 µm. *Basidioles* 12–20 × 5–10 µm, clavate to cylindro-clavate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 20–80 × 12–18 µm, clavate to cylindro-clavate, or occasionally fusoid-ventricose to narrowly utriform, obtuse or occasionally capitate-umbonate, occasionally

FIGURE 9. a. Basidiomes of *Pluteus vanuatuensis* f. *ramacystidiatus in situ* (JAD 159 holotype). b. Basidiomes of *Pluteus vanuatuensis* f. *ramacystidiatus* (JAD 159 holotype). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

with a guttule, hyaline, thin-walled. *Pleurocystidia*; *primary pleurocystidia* 50–130 × 10–40 µm, fusoid to narrowly lageniform, or cylindro-clavate, apex variable, obtuse without outgrowths, corniculate or occasionally cornuate with 2–4 (–5) whole to bifid, acute to blunt, straight or recurved poorly or well-developed apical hooks, irregularly branched with 2–4 polychotomous branches, or sometimes bifid with 1–3 straight or recurved poorly or well-developed apical hooks per arm, majority with a guttule, hyaline, basally to apically or evenly thick-walled (up to 3 µm thick) to thin-walled; *intermediate pleurocystidia* 50–87 × 16–18 µm, fusoid to narrowly lageniform, apex variable, obtuse, acute,

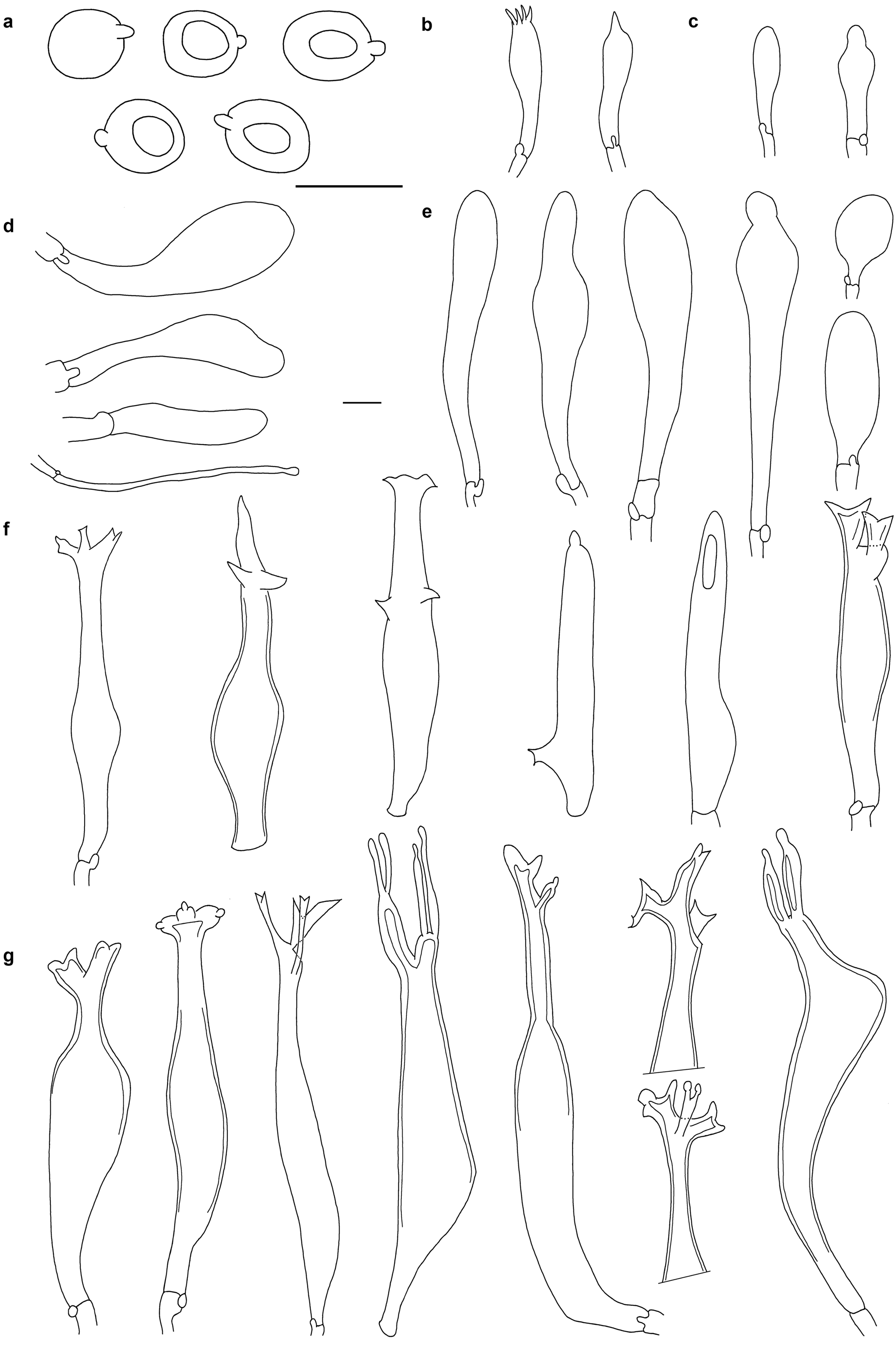

FIGURE 10. *Pluteus vanuatuensis* f. *ramacystidiatus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Intermediate pleurocystidia. g. Primary pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

rarely mucronate, seldom irregularly branched, or cornuate with whole or rarely bifid, straight or recurved poorly or well-developed apical hooks, occasionally with 1–2 lateral projections, some with a guttule, hyaline, thin to evenly or centrally thick-walled. *Pileipellis* an ixo-cutis of repent hyphae embedded in a gelatinous matrix, composed of hyaline or with brown plasmatic pigment, non-incrusted, gelatinized or not, thin-walled, cylindrical hyphae, 5–24 µm diam.; terminal cells 35–135 × 3–19 µm, repent to suberect towards the disc, clavate to cylindro-clavate, obtuse, rarely with tapering apices. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 5–38 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 4–18 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 4–24 µm diam.. *Caulocystidia* absent. *Clamp connections* present in all tissues examined.

Habitat and known distribution:—Gregarious on well-decayed wood in subtropical lowland mixed-use agro tree garden and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna between Ienehepe and Lighthouse, along banks of Numdretum River, 19°38.558′S, 169°25.713′E, elev. 286 m, 29 August 2018, coll. *J.A. del Rosario, JAD 159* (HAY).

Notes:—*Pluteus vanuatuensis* f. *ramacystidiatus* closely resembles the preceding newly described species, *P. vanuatuensis*, but has distinct morphological features that warrant treating it as a separate taxonomic unit. Notably, the pleurocystidia in JAD 159 display the same variation of apical ornamentation seen in all collections of *P. vanuatuensis*, but also contain a distinct type with elongated extensive branching elements. Phylogenetic analysis of ITS data sampling the *albostipitatus*/*salicinus* clade (Fig. 6b) places JAD 159 sister to collections JAD 160, JAD 215, and the Vietnamese *P. sp.* 1 within the *P. vanuatuensis* clade with moderate support (BS 79 %, PP 0.99) and identical internal topology compared to the broad sampled sect. *Pluteus* analysis (Fig. 1c). An identical sampling of taxa from this ITS analysis of the *albostipitatus*/*salicinus* clade using *tef1* data (Fig. 6c) collapses the internal branches of the *P. vanuatuensis* clade and unites all these collections, including JAD 159. An analysis of this two-gene data (Fig. 6a) with additional sampling of the *albostipitatus*/*salicinus* clade retrieves the internal branch topology of the *P. vanuatuensis* clade similar to the single gene ITS analysis (Fig. 6b) with JAD 159 on a long branch in both the likelihood and Bayesian analyses being in a weakly supported clade with the Vietnamese *P. sp.* 1, JAD 160, and JAD 215 (BS 33 %, PP 0.71). Based on the two-gene analysis, the phylogenetic affinity of JAD 159 indicates it to be *P. vanuatuensis*. Overall, the glabrous pileus, intermediate pleurocystidia with lateral hooks, and elongated, extended branching pleurocystidia show clear morphological differences in this single collection. These distinctive features, especially the elongated branching pleurocystidia that are rare in *Pluteus*, justify recognition of this specimen as a distinct form of *P. vanuatuensis*. It may well be that *P. vanuatuensis* is a highly variable morphological species, and it remains to be determined if this pleurocystidia type is exclusive to glabrous forms such as JAD 159.

Pluteus* aff. *vanuatuensis (Figs. 11, 12)

Diagnosis:—*Pluteus* aff. *vanuatuensis* from Tanna is characterized by a brown, glabrous pileus with a black squamulose disc and a white stipe with a subbulbous base. When disrupted, the tissues bruise bluish gray. Microcharacters include subglobose spores (7.2 × 5.8 µm), fusoid, thick-walled pleurocystidia with blunt conical protrusions at the apex, similar intermediate pleurocystidia with lesser developed apices, clavate cheilocystidia, a cutis pileipellis, an absence of caulocystidia, and clamp connections present in all tissues. Subtle differences compared to *P. vanuatuensis* are having a paler, glabrous, entirely pellucid-striate pileus and a more intense bruising reaction.

Description:—*Pileus* 50–58 µm diam., hemispherical to plano-convex, with a slight umbo, disc pustulate/rugose; surface pellucid-striate, dry to somewhat viscid, glabrous overall, disc pustulate to minutely appressed-fibrillose towards margin; squamules/fibrils dark chocolate brown, surface pale brown overall (oac720–oac722). *Context* up to 4 mm thick, white. *Lamellae* free, crowded with many tiers of lamellulae, thin, blush pink (oac695–oac697). *Stipe* 55–65 × 5–6 mm, central, cylindrical above a subbulbous base, hollow; surface pearlescent, dry, fibrous, white overall, context white. Tissues turning blue-gray (oac317–oac319) when damaged or handled. *Odor* indistinct. *Taste* indistinct.

Basidiospores 6–8 (–9) × (5–) 6–7 µm [x_m = 7.32 ± 0.68 × 5.78 ± 0.64 µm, Q = 1–1.3 (–1.7), Q_m =1.28 ± 0.18, n = 50, s = 1], subglobose, seldom globose or broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 16–32 × 6–11 µm, clavate, 4-spored, guttulate, hyaline, thin-walled, sterigmata 1.5–3 × 0.5–1 µm. *Basidioles* 15–26 × 5–11 µm, clavate, guttulate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* (25–) 32–52 × 10–18 µm, clavate, fusoid or utriform, obtuse or subcapitate-umbonate, hyaline, thin-walled. *Pleurocystidia*; *primary* *pleurocystidia* 55–100 × 13–24 µm, narrowly lageniform to fusoid, corniculate with 2–6 whole to bifid, blunt, poorly developed apical hooks, most with a guttule, hyaline, thick-walled (up to 3 µm thick); *intermediate pleurocystidia* (36–) 46–63 × 11–20 µm, similar to primary but smaller and thinner-walled, narrowly lageniform to fusoid, obtuse or corniculate with 1–4 blunt, poorly developed apical hooks, hyaline, thin to thick-walled. *Pileipellis* a cutis of repent hyphae, composed of hyaline or with brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 3–10 µm diam.; terminal cells 52–138 × 9–18 µm, repent or becoming suberect to erect towards disc, clavate to filiform, obtuse, flexuose or tapered. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 3–28 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3-12 µm diam.. *Caulocystidia* absent. *Clamp connections* present in all tissues examined.

FIGURE 11. Basidiomes of *Pluteus* aff. *vanuatuensis* (JAD 285). Scale bar = 10 mm. Photo by: Brian Perry.

Habitat and known distribution:—Gregarious on decayed wood in subtropical lowland mixed-use agro tree garden and disturbed secondary broadleaf rainforest containing *Cocos nucifera* (*Arecaceae*), *Cordia subcordata* (*Boraginaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium malaccense* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Yakuwan, 19°32.230′S, 169°28.911′E, elev. 84 m, 15 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 285* (HAY).

Notes:—Phylogenetic analysis sampling the *albostipitatus*/*salicinus* clade based on ITS (Fig. 6b) places JAD 285 sister to all collections of the *P. vanuatuensis* clade with strong support. Pairwise analysis of overlapping ITS sequences shows JAD 285 to have 87.12–90.75 % similarity to all collections of *P. vanuatuensis*. The identically sampled analysis based on *tef1* data retrieves the same relationship with moderate support (BS 85 %, PP 0.97). A concatenated analysis using both genes and expanded sampling of the *albostipitatus*/*salicinus* clade (Fig. 6a) places JAD 285 sister to a clade comprised of sequences of *P. harrisii* Murrill (1911: 277) and *P. puttemansii* Menolli Jr. & Capelari (2010: 701). It should be noted that *tef1* data is missing for many of the taxa in the expanded sampling. In the ITS analysis sampling all of sect. *Pluteus*, JAD 285 appears in a clade nested with *P. saupei* and *P. vanuatuensis*, however this is weakly supported (Fig. 1c). Morphologically, JAD 285 has both primary and intermediate pleurocystidia that appear to have a higher frequency of apices with lesser developed, more rounded corniculate outgrowths, rather than the more pointed hooks typically observed in *P. vanuatuensis.* However, *P. vanuatuensis* shows

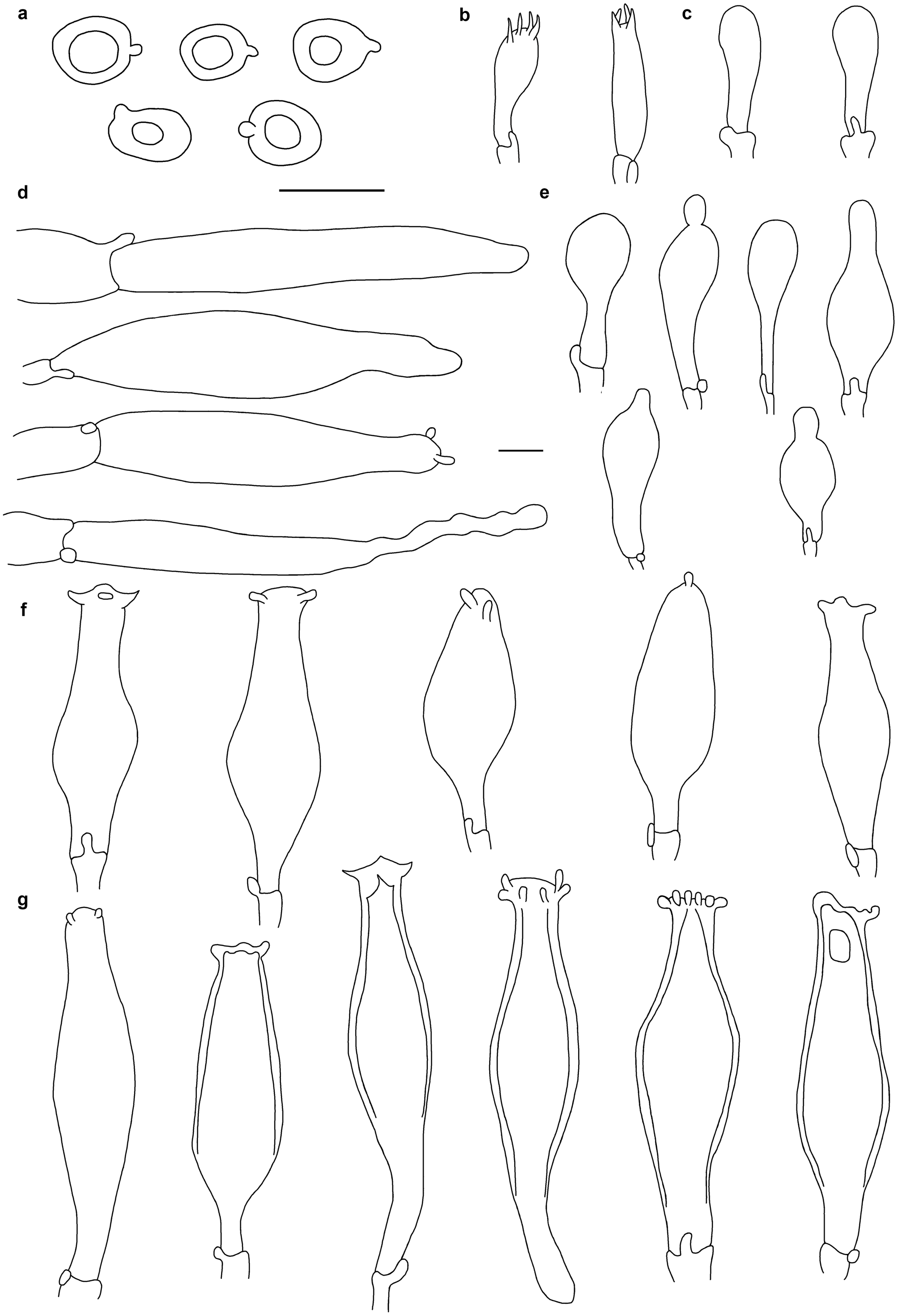

FIGURE 12. *Pluteus* aff. *vanuatuensis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Intermediate pleurocystidia. g. Primary pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

extensive pleurocystidia apex variability including this type found in JAD 285, thus hardly enough of a feature that can be used to distinguish between these taxa. JAD 285 can be distinguished from *P. vanuatuensis* f. *ramacystidiatus* by the lack of a rugose disc, lack of pleurocystidia with elongated branching apices, and the presence of intermediate pleurocystidia without lateral hooks. Based on molecular data, JAD 285 appears to be a phylogenetically distinct species, despite its morphological similarities to common forms of *P. vanuatuensis*. As this is based on a single collection, the identity of *P.* aff. *vanuatuensis* is maintained until additional material can be collected to clearly separate this taxon from *P. vanuatuensis*.

Pluteus wahei J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 13, 14)

MycoBank no.:—854223

Holotype:—VANUATU. Tafea Province: Tanna, Yakuwan, 19°32.230′S, 169°28.911′E, elev. 116 m, 19 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 284* (HAY).

Etymology:—Named in honor of Jean-Pascale Wahe, head of the Tafea Kaljoral Senta, for his long-time collaboration with the Plants mo Pipol blong Vanuatu project. Born and native to Tanna, this is reflected in the species' occurrence being known only from Tanna.

Diagnosis:—*Pluteus wahei* is characterized by a tawny brown appressed-fibrillose, dark umber disc, marginally sulcate pileus, and a silky white stipe. Some forms have a pileus that lack a distinct disc and are a paler shade of brown overall. Microcharacters include subglobose spores (5.8 × 4.5 µm), clavate cheilocystidia, fusoid-ventricose, thick-walled pleurocystidia with apical hooks, similar smaller intermediate pleurocystidia but with lateral outgrowths, a cutis pileipellis, absence of caulocystidia, and the presence of clamp connections in all tissues.

Description:—*Pileus* 30–45 mm diam., convex to broadly plano-convex, slightly umbonate with a small central depression, margin slightly sulcate; surface dull turning pellucid-striate at the margin, dry, densely appressed-fibrillose or glabrous, disc punctate or rugulose; disc dark umber, fibrils tawny brown (oac721–oac722), densest at disc becoming sparse towards margin, or some forms glabrous overall and pale gray-tan to almost off-white without a distinct disc. *Context* up to 5 mm thick, white. *Lamellae* free, moderately crowded with 3 tiers of lamellulae, thin, off-white to pale pink (oac696–oac697). *Stipe* 40–70 × 3–4 mm, central, terete, cylindrical, solid; surface pearlescent, dry, silky, white overall, context white. *Odor* indistinct. *Taste* indistinct.

FIGURE 13. Basidiomes of *Pluteus wahei* (JAD 284 holotype). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

Basidiospores 5–7 (–8) × 4–5 (–6) µm [x_{mr} = 5.62–5.94 × 4.1–4.84 µm, x_{mm} = 5.78 ± 0.22 × 4.47 ± 0.09 µm, Q = 1–1.6 (–2), Q_{mr} = 1.24–1.38, Q_{mm} = 1.31 ± 0.09, n = 50, s = 2], subglobose to broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 18–29 × 4–8 µm, clavate, 4-spored, hyaline, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 11–24 × 4–8 µm, clavate, hyaline, thin-walled. *Cheilocystidia* 28–58 × 8–22 µm, clavate to cylindro-clavate, seldom fusoid-ventricose, obtuse or rarely umbonate, hyaline, thin-walled. *Pleurocystidia*; *primary pleurocystidia* (56–) 65–80 (–96) × 14–20 µm, lageniform to fusoid-ventricose, cornuate with 2–4 whole, straight to recurved seldom poorly or well-developed apical hooks, rarely with 1–2 lateral excrescences, hyaline, thick-walled; *intermediate pleurocystidia* 31–56 (–70) × 10–16 µm, similar to primary but smaller and thinner-walled, lageniform to fusoid-ventricose, frequently corniculate with 1–3 blunt, poorly developed apical hooks or occasionally cornuate with 1–3 straight to recurved well-developed hooks, occasionally with 1–3 lateral excrescences, hyaline, thin to thick-walled. *Pileipellis* a cutis of repent hyphae, composed of hyaline or with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 8–22 µm diam.; terminal cells 50–112 × 7–16 µm, repent to suberect towards disc, clavate to filiform, obtuse to capitate, some entirely nodulose. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindro-clavate hyphae, 5–30 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 4–12 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 5–18 µm diam.. *Caulocystidia* absent. *Clamp connections* present in all tissues examined.

Habitat and known distribution:—Gregarious on decaying wood in subtropical lowland mixed-use agro tree garden and disturbed secondary broadleaf rainforest containing *Cocos nucifera* (*Arecaceae*), *Cordia subcordata* (*Boraginaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium malaccense* (*Myrtaceae*) and primary broadleaf rainforest containing *Dysoxylum aneityense* (*Meliaceae*), *Ficus adenosperma* (*Moraceae*), *Hedycarya dorstenioides* (*Monimiaceae*), *Inocarpus fagifer* (*Fabaceae*), *Kermadecia lutea* (*Proteaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Myristica fatua* (*Myristicaceae*), and *Syzygium myriadenum* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, at Transect 7, Kwaprapra, Iatukwei, 19°34.255′S, 169°27.093′E, elev. 252 m, 11 December 2017, coll. *J.A. del Rosario, JAD 107* (HAY); Tanna, Yakuwan, 19°32.230′S, 169°28.911′E, elev. 116 m, 19 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 284* (HAY).

Notes:—Historically there has been difficulty in identification and taxonomy of certain species in sect. *Pluteus*, especially when some pigmented species like *P. cervinus* (Schaeffer) Kummer (1871: 99) or *P. pouzarianus* Singer (1983: 283) are known to produce pure white or paler-colored morphotype variants (Justo *et al*., 2014). The use of microcharacteristics in combination with molecular data has been crucial for the taxonomy of this group. *Pluteus wahei* produces basidiomes with pale forms that may resemble a number of species. The Sri Lankan *P. aglaeotheles* (Berkeley & Broome) Saccardo (1887: 676) produces a pale basidiome and shares similarly sized and shaped spores and pleurocystidia with *P. wahei*, but differs significantly due to the lamellar edge containing metuloid cystidial elements, the pileipellis lacking nodulose elements, and clamp connections being absent (Pegler 1986, Singer 1956). *Pluteus brunneidiscus* Murrill (1917: 131) was noted to have lateral outgrowths on the terminal cells of the pileipellis, but compared to *P. wahei* has larger spores, seldom has lateral outgrowths on the cystidia, and has a superficially different squamulose pileus (Banerjee & Sundberg 1993, Justo *et al*. 2014, Singer 1956). The dark pigmented pileus form of *P. wahei* is comparable to tropical species such as *P. subcervinus* (Berkeley & Broome) Saccardo (1887: 666) and *P. fibulatus* Singer in Singer & Digilio (1952: 252). *Pluteus subcervinus* was originally described from Sri Lanka (Berkeley & Broome 1871) and since then has been reported from Tanzania (Pegler 1977), Indonesia (according to Pegler 1986), India (Pradeep *et al*. 2002), and recently Vietnam (Malysheva *et al*. 2020). *Pluteus subcervinus* differs from *P. wahei* in having a non-nodulose pileipellis, highly branched pleurocystidia, and in producing a paler camel brown pileus. *Pluteus fibulatus* tends to produce a darker brown pileus and stipe, has more apically variable pleurocystidia and non-nodulose pileipellis cells (Campi *et al*. 2019, Singer 1958, Singer & Digilio 1952).

Phylogenetic analysis of ITS data (Fig. 1b) places *P. wahei* on a supported branch, sister to the *petasatus* clade (BS 100 %, PP 1.0) with a recently described taxon *P. olivaceofibrillosus* E.F. Malysheva & A.V. Alexandrova (2020: 84). *Pluteus wahei* separates itself from species of Justo *et al.*'s (2014) *petasatus* clade by the presence of clamp connections on the pileipellis compared to a lack of clamp connections in *P. petasatus* and *P. leucoborealis* Justo, E.F. Malysheva, Bulyonkova & Minnis (2014: 58), a non-pigmented stipe, pleurocystidia with lateral hooks, nodulose pileipellis cells, and lack of a squamulose disc compared to *P. pellitus* (Persoon) Kummer (1871: 98). The pileus color of the pale morphotype of *P. wahei* strongly resembles the Vietnamese *P. olivaceofibrillosus*, but differs from this taxon in lacking a distinct disc. Both color variants of *P. wahei* share a sulcate margin and have a striate fibrillose pileus similar to *P. olivaceofibrillosus*, but the pigmented morphotype mainly differs in having a darker, tawny brown pileus. Micromorphologically, both species share multiple characters, but ultimately *P. wahei* is separated by the intermediate pleurocystidia having lateral hooks and a mix of poorly to well-developed apical hooks rather than being only mucronate, and the pileipellis terminal elements being nodulose and capitate (Malysheva *et al*. 2020). *Pluteus wahei* is recognized as a distinct species from *P. olivaceofibrillosus* and described as new due to the morphological differences in combination with phylogenetic data.

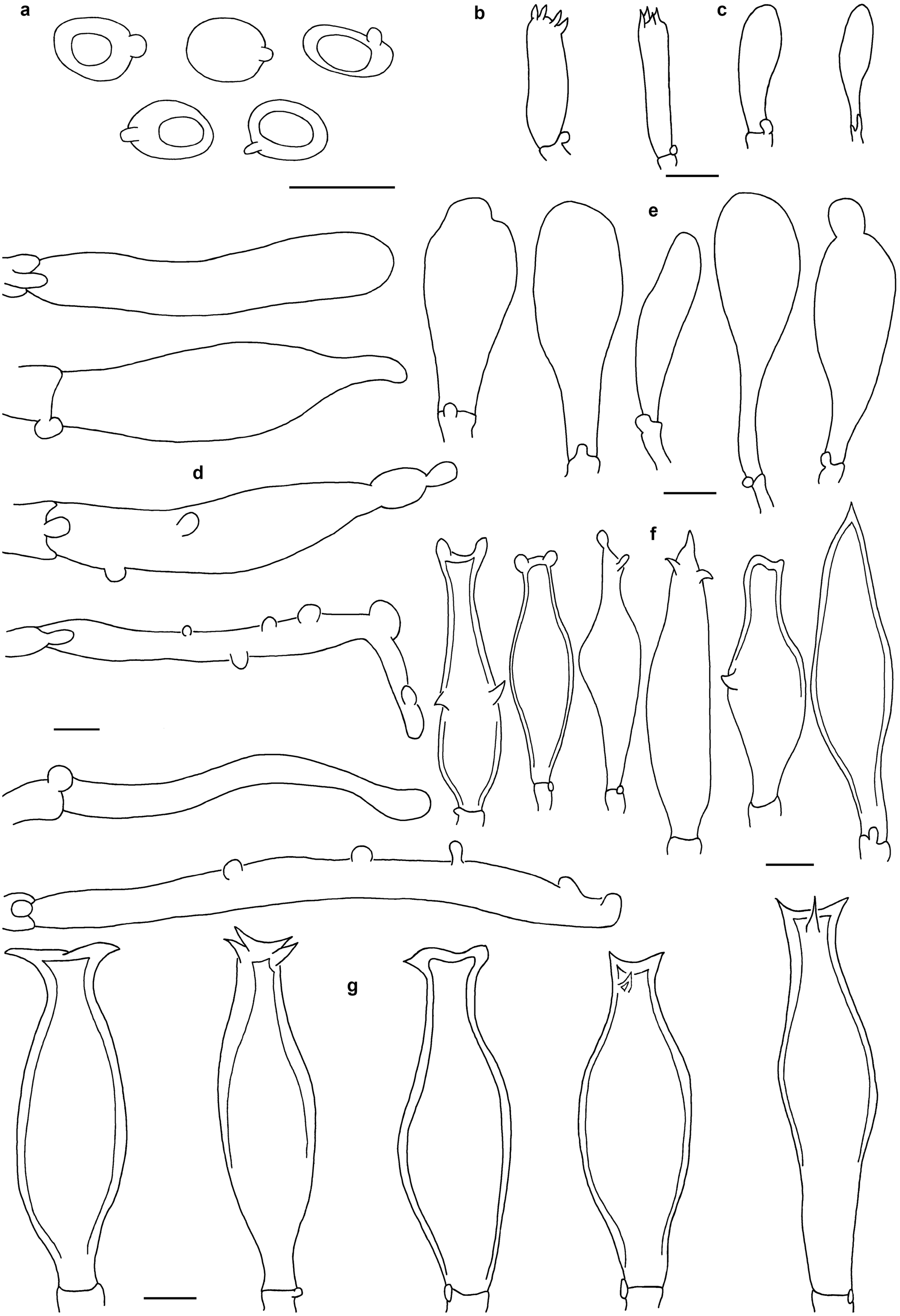

FIGURE 14. *Pluteus wahei*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Intermediate pleurocystidia. g. Primary pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

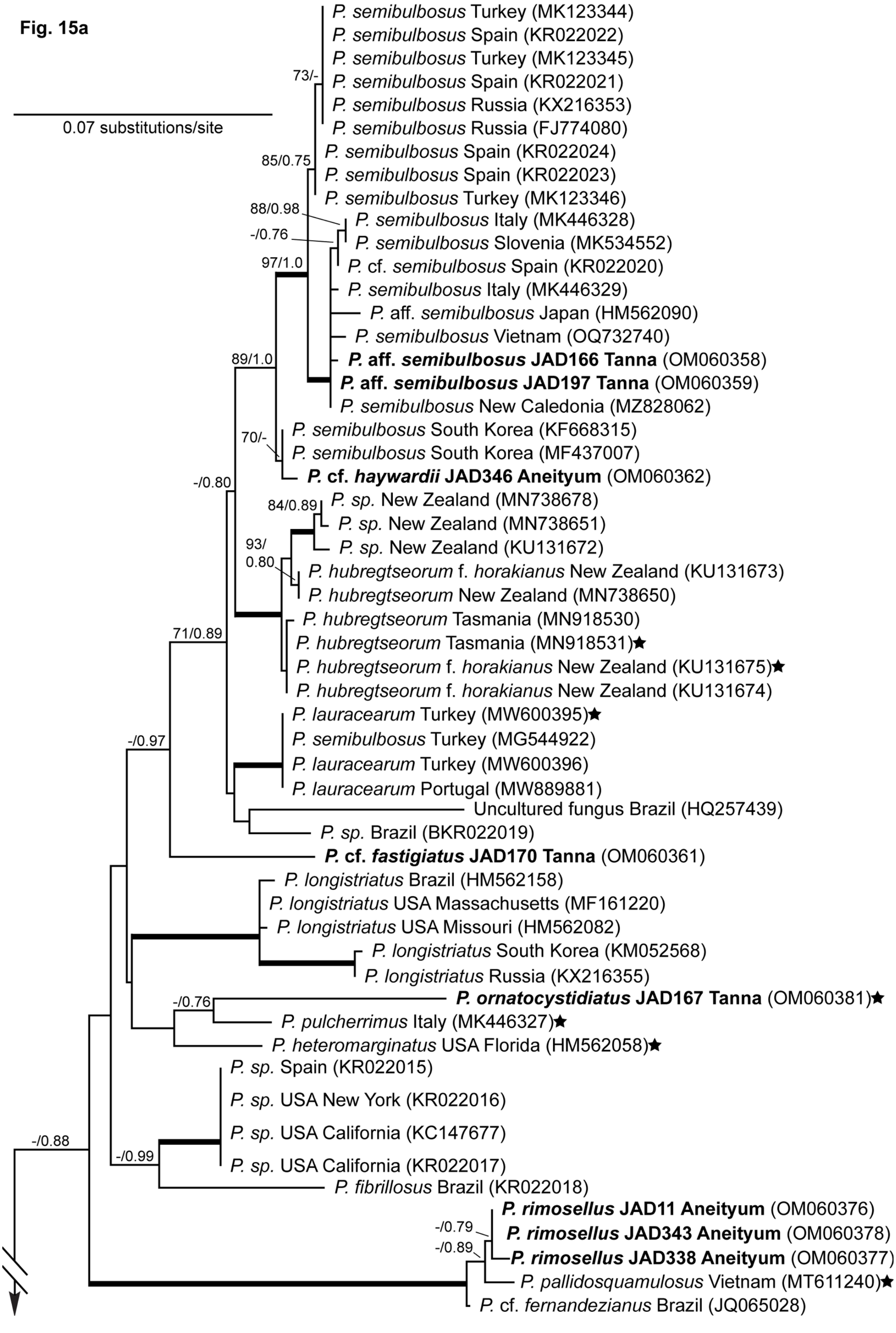

FIGURE 15a–c. Maximum Likelihood phylogeny of sect. *Hispidoderma* based on ITS sequence data (-lnL = 7783.640376). Sequences of specimens from Vanuatu are indicated in bold type. Stars indicate type specimens. Values separated by / refer to ML bootstrap proportions and Bayesian posterior probabilities, respectively. Only values greater than 70/0.70 are shown. Nodes receiving support values greater than 90/0.95 are highlighted in bold.

Fig. 15b

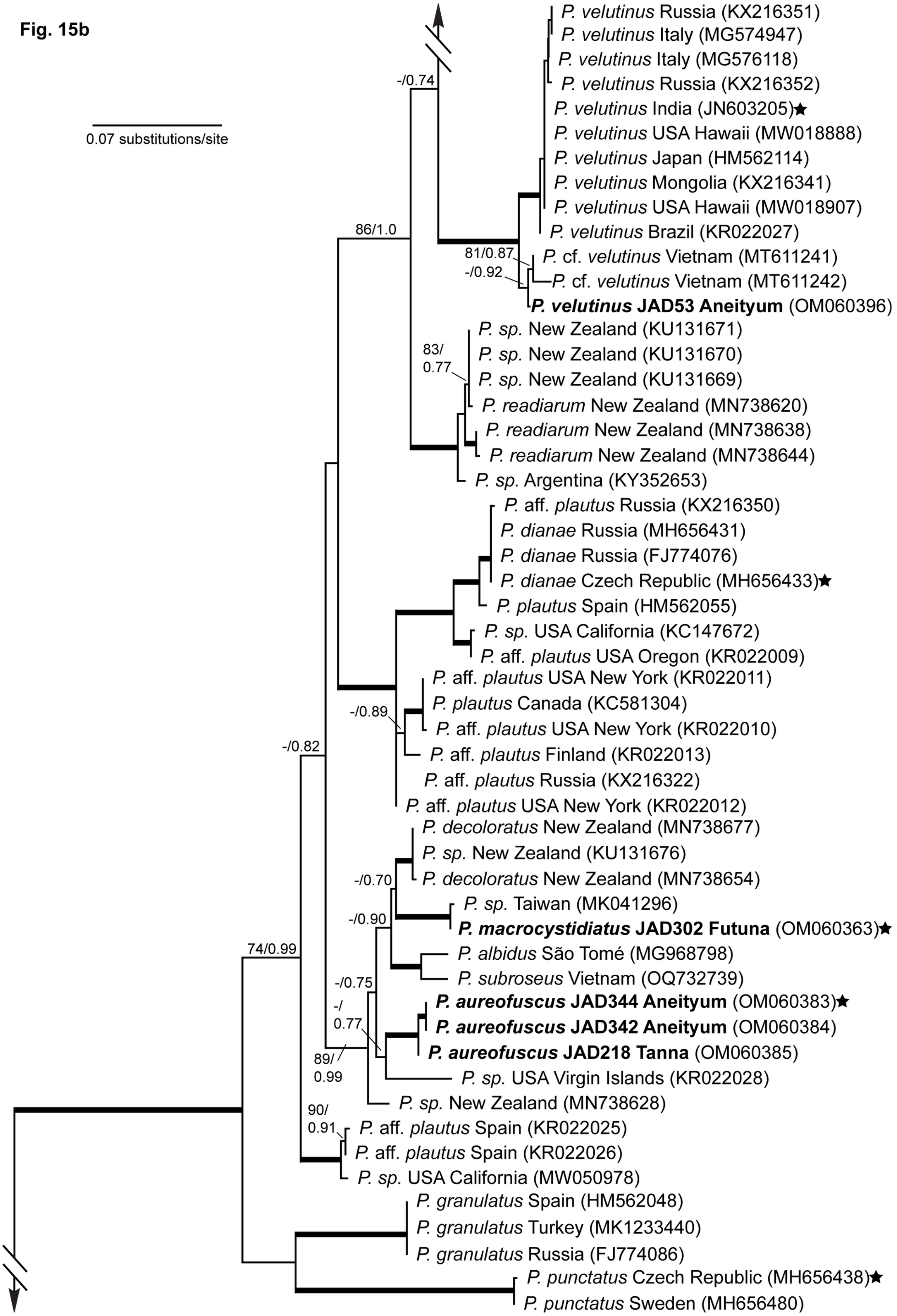

FIGURE 15. (Continued)

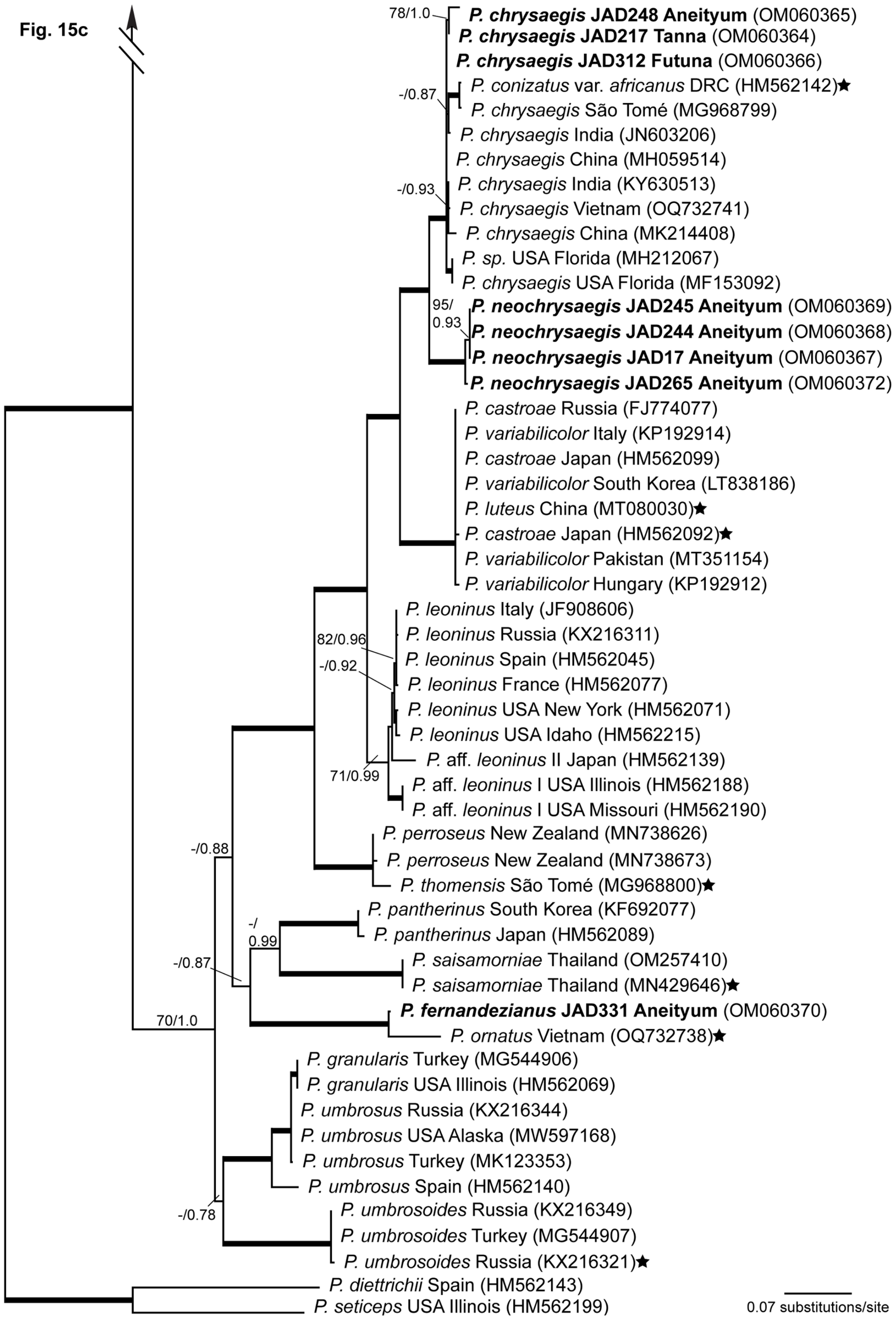

FIGURE 15. (Continued)

Pluteus section *Hispidoderma* Fayod

Pluteus aureofuscus J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 16, 17)
MycoBank no.:—854224

Holotype:—VANUATU. Tafea Province: Aneityum, Nopsjec. 19°12.444′S, 169°25.916′E, elev. 222 m, 11 December 2019, coll. *J.A. del Rosario, JAD 344* (HAY).

Etymology:—*aureo* (L.) = golden, *fuscus* (L.) = grayish brown; refers to the golden and gray-brown color of the pileus and stipe.

Diagnosis:—*Pluteus aureofuscus* from Tafea Province is characterized by a golden cream and pinkish brown to pale tan finely fibrillose-flocculose colored pileus with a sulcate margin, and a similarly colored and ornamented stipe with a bulbous base. Microcharacters include globose spores (7.0 × 6.3 µm), clavate cheilocystidia, fusoid-ventricose pleurocystidia with some having median or apical septa and small forms with an apical mucronate appendage, a pileipellis arranged as a euhymeniderm to trichoderm composed of broadly clavate to fusoid-ventricose cells mixed with subglobose to pyriform terminal elements overlaying a cutis subpelllis, and clavate caulocystidia.

Description:—*Pileus* 14–46 mm diam., hemispherical expanding to convex without or with a slight umbo, margin sulcate; surface dull becoming pellucid-striate in age, hygrophanous, finely appressed-fibrillose to finely flocculose, disc minutely pustulate becoming subtomentose in age; fibrils, floccules, and pustules pallid tan (oac709–oac711) with dull pinkish brown (oac667–oac669) tones becoming off-white in age, surface golden cream-colored, becoming gray to off-white in age. *Context* up to 1.5 mm, white. *Lamellae* free, crowded with 4 tiers of lamellulae, thin, cream white initially, turning pale pink (oac633–oac634) in age. *Stipe* 14–45 × 3–4 mm, central, solid, terete, cylindrical over a subbulbous to bulbous base; surface dull, dry, pallid tan (oac709–oac711) appressed-fibrillose to minutely flocculose over a cream-colored to off-white surface or glabrous in age, context white. *Odor* indistinct. *Taste* indistinct.

FIGURE 16. Basidiomes of *Pluteus aureofuscus* (JAD 344 holotype). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

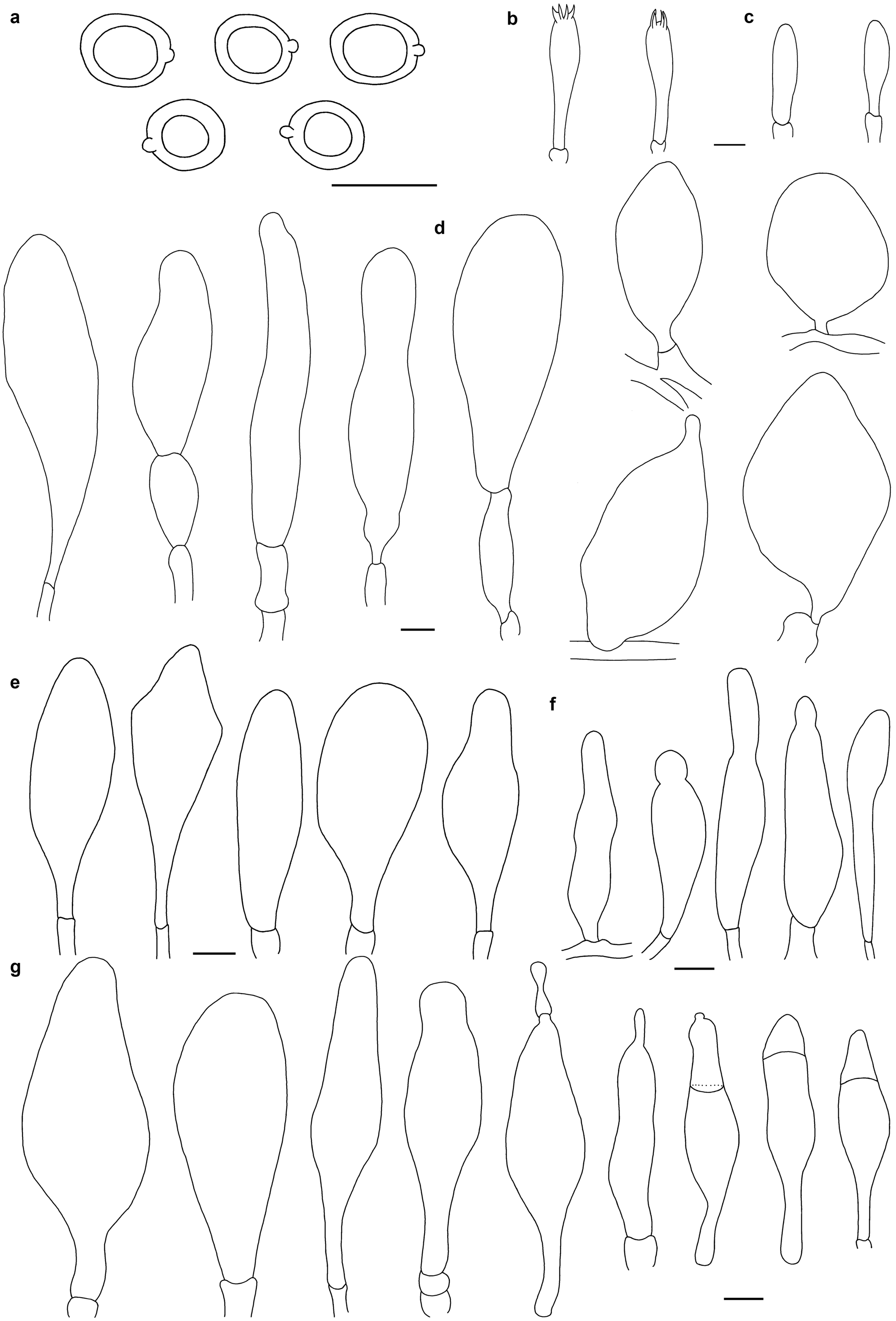

FIGURE 17. *Pluteus aureofuscus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Basidiospores 6–8 (–9) × 6–8 µm [x_{mr} = 6.78–7.24 × 6.02–6.68 µm, x_{mm} = 7.03 ± 0.23 × 6.32 ± 0.33 µm, Q = 1–1.6, Q_{mr} = 1.09–1.13, Q_{mm} = 1.12 ± 0.08, n = 50, s = 3], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 18–36 × 7–11 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 1.5–3 × 0.5–2 µm. *Basidioles* 18–30 × 6–9 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* (24–) 31–65 (–90) × (11–) 16–36 µm, narrowly to broadly clavate, fusoid or sphaeropedunculate, obtuse, hyaline, thin-walled. *Pleurocystidia* 60–92 (–120) × 18–36 (–40), uncommon to common, fusoid-ventricose to narrowly lageniform, obtuse, or (20–) 35–91 × 7–18 (–20) µm, lageniform to fusoid-ventricose, commonly to rarely mucronate (3–12 µm long), occasionally medially or apically septate in some collections or not, hyaline, thin-walled. *Pileipellis* a fragmented to complete ascending euhymeniderm to trichohymeniderm overlying a cutis subpellis, terminal elements typically 60–160 × 14–32 (–43) µm, scattered or in ascending fascicles, narrowly to broadly clavate, fusoid-ventricose or rarely filiform, obtuse, rarely acute, or capitate or sometimes 42–70 × 21–40 µm, sphaeropedunculate to pyriform, obtuse or occasionally capitate-mucronate, hyaline or with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled; *subpellis* a cutis of repent hyphae, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–16 µm diam.. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 2–25 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–12 µm diam.. *Stipitipellis* a cutis, composed of hyaline or with pale grayish brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Caulocystidia* 24–68 (–82) × 7–15 (–18) µm, scarce to abundant in fascicles, cylindro-clavate to broadly clavate, seldom fusoid, obtuse or capitate, with pale grayish brown plasmatic pigment or hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary to gregarious on decaying wood in subtropical montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Tanna, Aneityum).

Material examined:—VANUATU. Tafea Province: Tanna, Lighthouse area. 19°38.387′S, 169°25.923′E, elev. 155 m, 6 December 2018, coll. *J.A. del Rosario, JAD 218* (HAY); Aneityum, Noposjec. 20°12.649′S, 169°46.974′E, elev. 184 m, 11 December 2019, coll. *J.A. del Rosario, JAD 342* (HAY); Aneityum, Nopsjec. 19°12.444′S, 169°25.916′E, elev. 222 m, 11 December 2019, coll. *J.A. del Rosario, JAD 344* (HAY).

Notes:—The specimens of *P. aureofuscus* exhibit minor morphological variation. Collection JAD 344 consists of younger basidiomes with an overall golden cream-colored pileus surface and stipe streaked with pallid tan fibrils and floccules. JAD 342 contains more mature basidiomes with the same golden cream-colored pileus and stipe, however the fibrils and floccules turn gray with dull pinkish brown streaks. JAD 218 is well-aged, with the pileus turning entirely gray similar to JAD 342, however the dull pinkish brown tones remain. Microscopically, all three collections are similar with a few notable differences. JAD 218 and JAD 342 share a high frequency of apically mucronate pleurocystidia, while this cystidia type was only observed once in JAD 344. In particular, JAD 342 contains pleurocystidia with distinct singular septa, either towards the apex or at the median. Septate cystidia are rare in *Pluteus spp*., with *P. septocystidiatus* being a well-documented species that produces a fuscous pileus, contains thick-walled pleurocystidia, a cutis pileipellis, with the septate cell type occurring in both pleurocystidia and cheilocystidia (Ševčíková *et al*. 2014). Overall, the shared micromorphology between the collections of *P. aureofuscus* would be clavate or sphaeropedunculate cheilocystidia, a pileipellis consisting of clavate, fusoid-ventricose and subglobose elements, and clavate subcapitate caulocystidia.

The variable appearance of *P. aureofuscus* suggests comparison to species that physically encompass a similar range or are closer to one of the forms. *Pluteus sulcatus* Singer in Singer & Digilio (1952: 265) from Argentina is very close, but differs in having a more fuscous pileus, smaller cheilocystidia (21–23 × 12 µm), and lacks pyriform elements in the pileipellis (Singer 1956, 1958, Singer & Digilio 1952). Another similar Argentinean species, *P. hiemalis* Singer (1958: 248), differs microscopically in lacking mucronate pleurocystidia and pyriform pileipellis elements (Singer 1958). The Sri Lankan *P. glyphidiatus* (Berkeley & Broome) Saccardo (1887: 673) has a very similar stature, is yellow and translucent to grey and squamulose (Pegler 1986), but differs microscopically with smaller non-mucronate pleurocystidia, both pleurocystidia and cheilocystidia having incrustations, and the absence of pyriform pileipellis elements (Pegler 1986, Singer 1956). *Pluteus pelinus* (Berkeley & Broome) Saccardo (1887: 675) is another similar Sri Lankan species, but differs microscopically by having non-mucronate pleurocystidia, smaller pleurocystidia and cheilocystidia, and an overall repent cutis pileipellis (Pegler 1986).

Phylogenetic analysis based on ITS data (Fig. 14b) places the Vanuatu collections in a moderately supported clade (BS 89 %, PP 0.99) with weakly supported internal topology containing several unidentified species: *P. decoloratus* Horak (2008: 24), *P. subroseus* E.F. Malysheva (2023: 23), Vanuatu collection JAD 302, and *P. albidus* Beeli (1928: 82). *Pluteus decoloratus* described from New Zealand is similar macromorphologically to *P. aureofuscus*, but differs micromorphologically in having non-mucronate pleurocystidia, longer trichodermal pileipellis elements (100–270 × 24–30 µm) and lacking caulocystidia (Horak 2008). *Pluteus albidus* is very similar micromorphologically, especially in the clavate-mucronate pleurocystidia, but both the cheilocystidia (32–48 × 11–20 µm) and pleurocystidia (37–54 × 11–20 µm) are much smaller, lack septa, and the basidiome is white overall without contrasting colored fibrils/floccules (Desjardin & Perry 2018). *Pluteus subroseus* also shares similar micromorphology, but has smaller cheilocystidia (33–45 × 12–25 µm) and pleurocystidia (56–85 × 14–30 µm), thick-walled pileipellis elements, and an overall paler basidiome with a beige-red pileus disc (Malysheva *et al.* 2023).

Pluteus chrysaegis (Berk. & Broome) Petch, Annals of the Royal Botanic Gardens Peradeniya 5: 271 (1912) (Figs. 18, 19)

≡ *Agaricus chrysaegis* Berk. & Broome, Botanical Journal of the Linnean Society 11: 536 (1871)

≡ *Entoloma chrysaeges* (Berk. & Broome) Sacc., Sylloge Fungorum 5: 61 (1887)

Reported heterotypic synonym:

= *Pluteus conizatus* var. *africanus* E. Horak, Bulletin du Jardin Botanique National de Belgique 47(1–2): 89 (1977)

Diagnosis:—As represented by material from Tafea Province, *P. chrysaegis* is characterized by a sulfur yellow glabrous pileus with a light brown veined rugose-venose disc, and a tan brown longitudinally fibrillose stipe with a bulbous base. A second morphotype from Tanna Island exists with a pale brown pileus (Fig. 16b). Microcharacters include globose spores (6 × 5.4 µm), lageniform, acute, thin to thick-walled cheilocystidia, broadly lageniform, thick-walled pleurocystidia, a hymeniderm pileipellis composed of pyriform cells intermixed with fusoid pileocystidia arising from a cutis subpellis, and clavate to fusoid caulocystidia.

Description:—*Pileus* 30–60 mm diam., hemispherical expanding to plano-convex, with a slightly depressed broad umbo; surface pellucid-striate up to half-way from margin, dry to viscid, glabrous, disc rugose-venose radiating towards the margin; tan-brown (oac686–oac687) in age, or if not, disc veins and wrinkles light to dark brown (oac690–oac691/oac721–oac722), fading towards margin, surface sulfur to pale yellow (oac896–oac897) turning pale (oac898–899) towards disc with translucent patches exposing underlying white context tissue. *Context* up to 3 mm thick, white. *Lamellae* free, crowded with 4 tiers of lamellulae, thin, pink-brown (oac619–oac620). *Stipe* 28–65 × 4–6 mm, central, terete, cylindrical with a subbulbous base, solid; surface dull, dry, tannish brown (oac643–oac645) longitudinally fibrillose over an off-white base, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 5–7 (–8) × 4–6 (–7) µm [x_{mr} = 5.55–6.7 × 4.94–5.38 µm, x_{mm} = 6.11 ± 0.59 × 5.19 ± 0.22 µm, Q = 1–1.6, Q_{mr} = 1.12–1.28, Q_{mm} = 1.18 ± 0.09, n = 50, s = 3], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 18–28 × 5–8 µm, clavate, 4-spored, guttulate, hyaline, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 15–28 × 5–8 µm, clavate, guttulate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 28–62 × 5–18 µm, lageniform or fusoid, acute or capitate, hyaline, thin to thick-walled (up to 2 µm thick) especially at the apex. *Pleurocystidia* typically 50–110 × 13–34 µm, broadly clavate to narrowly lageniform, obtuse or truncate, hyaline, thin to thick-walled (up to 2 µm thick); rarely 35–56 × 8–18 µm, fusoid to lageniform, obtuse with 2–4 poorly developed apical outgrowths or capitate, hyaline, thin-walled. *Pileipellis* an epithelioid hymeniderm with pileocystidia over a subpellis, composed of a majority of cells 8–30 × 8–15 µm, subglobose to pyriform or sphaeropedunculate, obtuse, some capitate or mucronate, hyaline or sometimes with pale amber brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled; *pileocystidia* 26–75 × 8–22 µm, fusoid to lageniform, acute, capitate or mucronate, hyaline or sometimes with pale amber brown plasmatic pigment, thin-walled; *subpellis* a cutis of repent hyphae, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 3–18 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–20 µm diam.. *Stipitipellis* a cutis, composed of hyaline or often with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Caulocystidia* 14–45 × 8–15 µm, scattered to clustered, clavate or fusoid to lageniform, acute or mucronate, hyaline or sometimes with pale brown plasmatic pigment, thin-walled. *Clamp connections* absent in all tissues examined.

FIGURE 18. Basidiome morphotypes of *Pluteus chrysaegis*. a. Typical morphotype basidiome of *Pluteus chrysaegis* (JAD 248). b. Secondary morphotype basidiomes of *Pluteus chrysaegis* (JAD 217). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

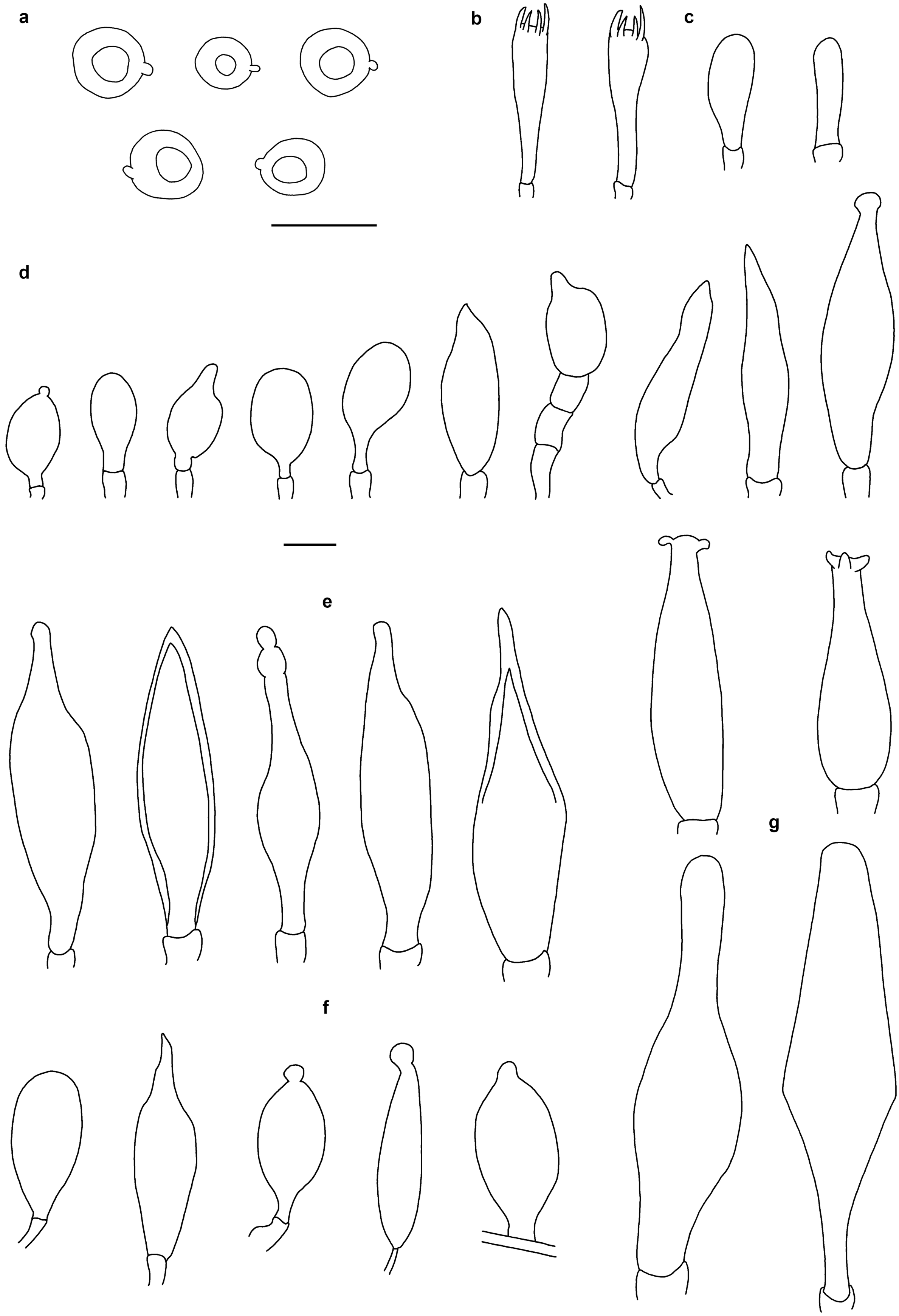

FIGURE 19. *Pluteus chrysaegis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Habitat and known distribution:—Solitary on decaying wood in subtropical montane primary broadleaf rainforest to cloud forest containing *Balanops pedicellata* (*Balanopaceae*), *Diospyros sp.* (*Ebenaceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Ilex vitiensis* (*Aquifoliaceae*), *Melicope latifolia* (*Rutaceae*), *Metrosideros collina* (*Myrtaceae*), *Plerandra actinostigma* (*Araliaceae*), *Scaevola cylindrica* (*Goodeniaceae*), *Semecarpus tannaensis* (*Anacardiaceae*), and *Syzygium spp.* (*Myrtaceae*); montane transitionary secondary to primary broadleaf-*Podocarpaceae* rainforest containing *Burckella obovata* (*Sapotaceae*), *Cryptocarya tannaensis* (*Lauraceae*), *Dacrycarpus imbricatus* (*Podocarpaceae*), *Elaeocarpus floridanus* (*Elaeocarpaceae*), *Ficus smithii* (*Moraceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Melicope sp.* (*Rutaceae*), *Metrosideros vitiensis* (*Myrtaceae*), *Meryta neoebudica* (*Araliaceae*), and *Neuburgia corynocarpa* (*Loganiaceae*); and montane primary broadleaf cloud forest containing *Atractocarpus sezitat* (*Rubiaceae*), *Claoxylon psilogyne* (*Euphorbiaceae*), *Eumachia trichostoma* (*Rubiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Ficus septica* (*Moraceae*), *Neonauclea forsteri* (*Rubiaceae*), and *Schefflera neoebudica* (*Araliaceae*), Vanuatu (Tanna, Aneityum, Futuna). Also known from Africa (D.R. Congo, São Tomé) and Asia (China, India, Sri Lanka, Vietnam).

Material examined:—VANUATU. Tafea Province: Tanna, coastal forest near Kwamera, 19°38.467′S, 169°26.078′E, elev. 110 m, 6 December 2018, coll. *J.A. del Rosario, JAD 217* (HAY); Aneityum, Mount Inhetiji, lowland forest in former taro terraces, 20°12.552′S, 169°51.107′E, elev. 140 m, 12 December 2018, coll. *J.A. del Rosario & B. Nasawman, JAD 248* (HAY); Futuna, Mount Tatafu, upper slopes, 19°31.759′S, 170°12.683′E, elev. 645 m, 22 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 312* (HAY).

Notes:—*Pluteus chrysaegis* (Berkeley & Broome) Petch (1912: 271) was described and known only from Sri Lanka (Berkeley & Broome, 1871) until material was collected and re-described from India (Pradeep *et al*. 2012, Pradeep & Vrinda 2006). Additional recent reports have expanded its known distribution to include equatorial coastal Central Africa (Desjardin & Perry 2018), southern China (Hosen *et al*. 2018), and Vietnam (Malysheva *et al.* 2023). Molecular data retrieved from GenBank (MF153092 and MH212067) of additional material included in ITS phylogenetic analysis suggest the presence of the species in Florida, U.S.A.. The material collected throughout Tafea Province matches well with descriptions from previous regional accounts with minor exceptions being that the basidiospores and pleurocystidia are both slightly larger than previously reported size ranges. One feature observed in the Tafean collections is an additional form of pleurocystidia that differs by being smaller, thin-walled, and with capitate or mucronate apical projections. This pleurocystidia type has not been not observed in other reports until recently reported in a study by Malysheva *et al.* (2023).

Pluteus conizatus var. *africanus* Horak (1977: 89) was originally described from the Democratic Republic of the Congo (Horak & Heinemann 1978) and considered to be a synonym of *P. chrysaegis* by Pradeep *et al*. (2012) based on Horak's basidiome descriptions being identical to their newly collected material. Pradeep *et al.* (2012) commented on the similarity of the microscopic features from Horak's description with those of their material, but this is not made immediately obvious as previous authors emphasized different characters when describing the microstructures. Desjardin and Perry (2018) noted in their São Tomé collection, identified as *P. chrysaegis*, the absence of apically thick-walled, acutely fusiform cheilocystidia seen in *P. conizatus* var. *africanus,* a trait that is observed in the Vanuatu material. One notable feature in the Aneityum material is the presence of pale brown plasmatic granular contents found sparsely in pileipellis terminal cells and in patches throughout the stipitipellis, typically at the base of the caulocystidia. Horak is the only author to note the presence of pigments in *P. conizatus* var. *africanus*, but this pigmentation was described as 'yellowish' and only in the pileipellis terminal cells (Horak & Heinemann 1978).

Phylogenetic analysis of ITS molecular data (Fig. 16c) places the Tafean specimens within a supported clade (BS 91 %, PP 0.99). Sister to this *P. chrysaegis* clade is a well-supported branch (BS 98 %, PP 1.0) consisting of other Vanuatu collections determined to be *P. neochrysaegis* Menolli & de Meijer in Menolli, de Meijer & Capelari (2014: 135), with both of these species positioned in the *leoninus* clade *sensu* Justo *et al.* (2011b). Distinction of *P. chrysaegis* from other yellow pigmented species within the *leoninus* clade, such as *P. leoninus* or *P. variabilicolor* Babos (1973: 38), is primarily through the prominent brown veins on the pileus, thick-walled cheilocystidia and pleurocystidia, and its distribution being mostly restricted to the tropics (Lezzi *et al*. 2014).

The presence of another morphotype of an entirely brown rather than yellow pileus, additional form of pleurocystidia, and varying thickness of the cheilocystidia indicates a broader known morphological variation in *P. chrysaegis*. The differing observations of pigmentation in the pileipellis and stipitipellis is another example of this variability, but combined with molecular data this also presents a strong case that *P. conizatus* var. *africanus* is likely conspecific with *P. chrysaegis*.

Pluteus* cf. *fastigiatus Singer in Singer & Digilio, Lilloa 25: 259 (1952) (Figs. 20, 21)

Diagnosis:—*Pluteus* cf. *fastigiatus* from Tanna is characterized by a campanulate, marginally sulcate dark brown fibrillose-rimose pileus with a dark brown squamulose disc, and a white stipe finely covered with gray fibrils. Microcharacters include subglobose spores (6.2 × 5.0 µm), broadly clavate, acute cheilocystidia, lageniform pleurocystidia, a euhymeniderm pileipellis of broadly clavate cells mixed with fusiform, sometimes thick-walled cells containing brown plasmatic pigment, fusoid-ventricose caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 45 mm diam., campanulate to convex with a slight umbo, slightly sulcate up to a quarter from margin; surface dull, dry, densely appressed-fibrillose and radially slightly splitting to expose the underlying white context, disc squamulose; squamules and fibrils dark brown (oac638–oac640), darkest and densest at the disc, fading towards margin, underlying surface white to off-white. *Context* up to 2 mm thick, white. *Lamellae* free, close with 3–4 tiers of lamellulae, thin, undulate, white to off-white. *Stipe* 45 × 5 mm, central, terete, cylindrical over a subbulbous base, solid; surface pearlescent, dry, fibrous, fine gray fibrils over a white to off-white surface, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores (5–) 6–7 × (4–) 5–6 µm [x_m = 6.2 ± 0.49 × 4.96 ± 0.53 µm, Q = 1–1.5, Q_m = 1.26 ± 0.14, n = 50, s = 1], subglobose to broadly ellipsoid, smooth, with a guttule, inamyloid, thick-walled. *Basidia* 20–30 × 6–10 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 16–25 × 5–10 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 40–68 × 13–26 µm, broadly clavate to fusoid-ventricose, obtuse, occasionally acute or subcapitate, hyaline, thin-walled. *Pleurocystidia* 35–78 × 15–28 µm, scattered, fusiform to lageniform, obtuse, rarely centrally strangulate, hyaline, thin-walled. *Pileipellis* a euhymeniderm with pileocystidia, composed of a majority of cells 50–90 × 8–28 µm, erect to suberect, clavate to broadly clavate or cylindro-clavate, obtuse or rarely subcapitate, erect to suberect, hyaline or with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled; *pileocystidia* 60–112 × 10–18 µm, abundant, erect to suberect, fusiform to lageniform, obtuse or seldom capitate, hyaline or with brown to pale brown plasmatic pigment, thin to sometimes thick-walled. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled hyphae, 8–30 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 4–16 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 5–13 µm diam.. *Caulocystidia* 40–80 × 8–24 µm, solitary to clustered, fusiform to fusoid-ventricose or clavate, obtuse or occasionally subcapitate to capitate, hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

FIGURE 20. Basidiome of *Pluteus* cf. *fastigiatus* (JAD 170). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

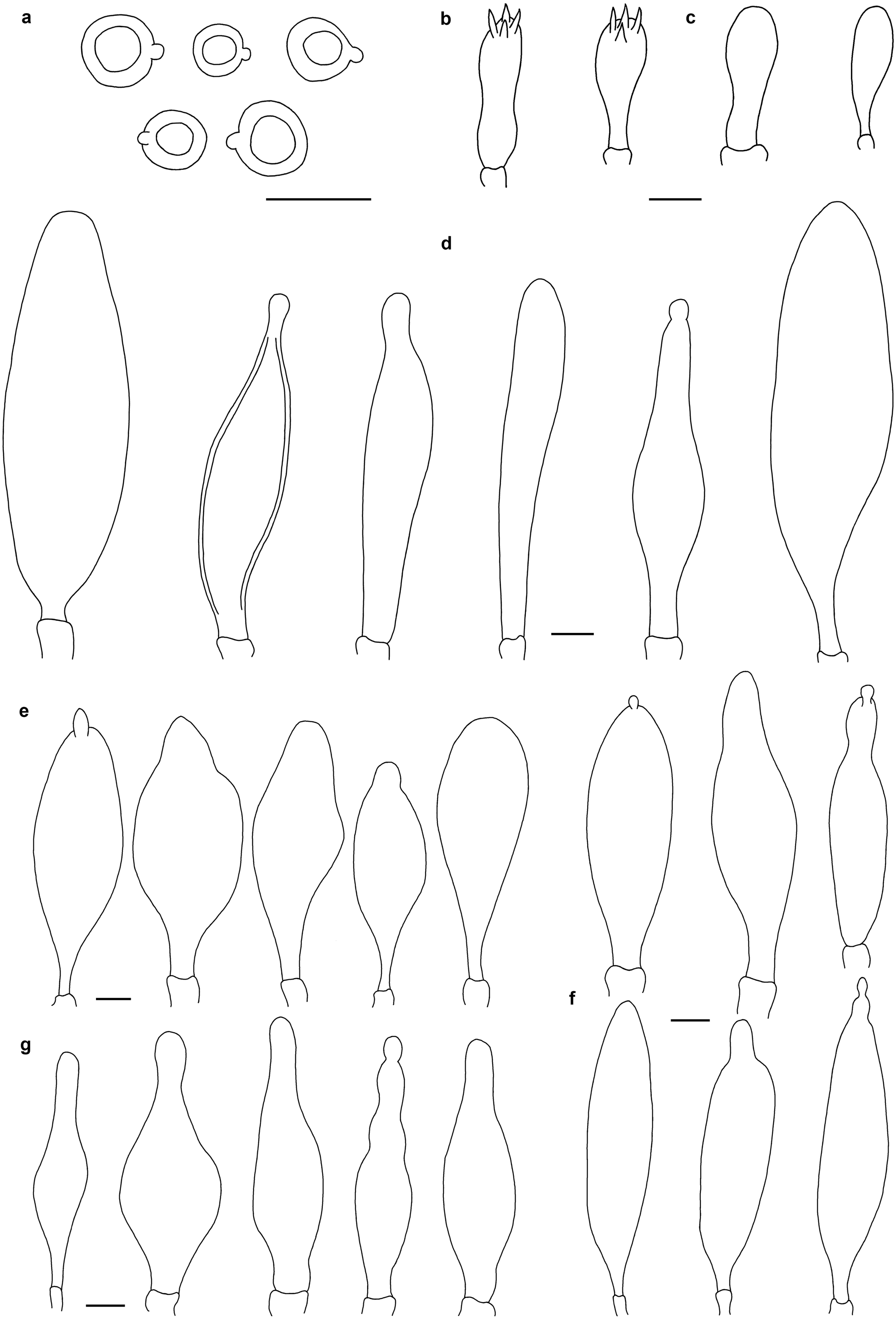

FIGURE 21. *Pluteus* cf. *fastigiatus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Habitat and known distribution:—Solitary on decayed wood in subtropical lowland mixed-use agro tree garden and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, along banks of Numdretum River, 19°38.661′S, 169°25.708′E, elev. 115 m, 30 August 2018, coll. *J.A. del Rosario, JAD 170* (HAY).

Notes:—*Pluteus fastigiatus* Singer in Singer & Digilio (1952: 259) is a species currently known only from Argentina (Singer & Digilio 1952), and although the Vanuatu specimen matches well with many of its characters, the ambiguity of the original description and similarity to other species prevents a conclusive identification. Macromorphologically, the Vanuatu material shares the dark brownish gray fibrillose-rimose pileus with an appressed-squamulose disc. Micromorphologically, the pleurocystidia match in shape, size, and absence of incrustation, the cheilocystidia are similarly shaped and only slightly shorter (21.5–80 × 11.3–30 µm), and the spores are similar in size, but lack "macrospores" (9–11 × 7–8.5 µm) that Singer stated only occurred in carpophores with 1–3-spored basidia (Singer 1956, 1958, Singer & Digilio 1952). The main differing and ambiguous character is the pileipellis, which based on a compilation of descriptions appears to be a cutis with ascending terminal cells transitioning to a palisade at the disc. This may somewhat resemble the arrangement in the Vanuatu material, which this study prefers to treat as a euhymeniderm as the terminal elements are all erect, or at the least suberect, resembling a palisade throughout the pileipellis. Overall, these terminal elements arise from the interwoven pileus trama with one to two basal septate cells, and are not so much in chains with multiple elongate basal septate cells such as in a typical trichoderm. *Pluteus fastigiatus* also apparently has no obvious cutis that this study treats as a subpellis or what Singer typically describes as a "hypodermium" (Singer 1958). From all the descriptions, Singer only provides one illustration of a pileipellis cell (Fig. 12e, Singer 1956), which is similar to one aspect of the pileipellis elements from the Vanuatu material. Singer emphasized two cell types: broader cells having smaller basal elements and narrow cells being the terminal elements of a longer chain, both being apically rounded. Compared to the Vanuatu material, this may parallel the clavate-fusoid and narrowly lageniform elements, respectively. Even the size of these terminal elements in *P. fastigiatus* are ambiguous, although Singer does not provide measurements in the original circumscription, a misprint from different re-descriptions appears as "53–80 × 16–0 µm" (Singer 1956) and "43–117 × 8–4.3 µm" (Singer 1958). Nevertheless, the pileipellis cell length for both overlaps, and it could be assumed that the width of these elements reach at most up to 16 µm, which are both within the Vanuatu material's size range. A re-examination of the type and additional material to clearly categorize the pileipellis with other characters and sampling for molecular analysis may aid in confirming the identity of this material. For now, it is preferred to tentatively identify the Vanuatu specimen as *P.* cf. *fastigiatus*.

Singer considered the predominantly attenuate cheilocystidia, which also occur in the Vanuatu material, in *P. fastigiatus* to separate it from *P. spilopus* (Berkeley & Broome) Saccardo (1887: 669). *Pluteus spilopus* shares a similar stature to the Vanuatu specimen, but the stipe has distinct black dots that Singer compares to *Gomphidius maculatus* (Scopoli) Fries (1838: 319), which may be interpreted as being squamose (Singer 1956). *Pluteus spilopus* also differs microscopically due to slightly shorter obtuse cheilocystidia, broadly clavate pleurocystidia, and a repent cutis pileipellis (Pegler 1986, Singer 1956). The Vanuatu material's tapered lageniform pileipellis elements may be interpreted as subacute, suggesting comparison to similar taxa with this trait that Singer considered important in establishing his morphological stirps. The Bolivian *P. pluvialis* Singer (1958: 234) was initially considered for the identity of the Vanuatu material due to similar basidiome stature and similar pileipellis elements. According to the original description, this species also has an ambiguous pileipellis that appears to be a cutis with ascending terminal elements in bunches, but Singer later categorized the species in stirps *Fuliginosus* which is characterized by a trichodermium type pileipellis with subacute or acuminate terminal cells (Singer 1958, 1986). Nevertheless, *P. pluvialis* ultimately differs in the presence of a tomentose pileus, abruptly bulbous stipe, incrusted lamellar cystidia, less lageniform pleurocystidia, and significantly larger pileipellis elements (82–165 × 16.5–19.5 µm) (Singer 1958). Menolli and Capelari (2016) determined a specimen from Brazil as *P.* cf. *fastigiatus*, and this differs from the Vanuatu material by the slightly smaller spores, more clavate incrusted pleurocystidia, lack of caulocystidia, and a cutis pileipellis without obtuse elements.

Pluteus fernandezianus Singer, Lloydia 21: 220 (1959) (Figs. 22, 23)

Diagnosis:—*Pluteus fernandezianus* from Aneityum is characterized by a pileus with a disc composed of radiating dark brown pustules fading towards the margin over a pallid tan surface, marginate lamellae with a grayish brown edge, and a white stipe with minute grayish brown fibrils concentrating at the bulbous base. Microcharacters include broadly ellipsoid basidiospores (7.8 × 6.1 µm), clavate pale brown pigmented cheilocystidia, lageniform infrequently pale brown pigmented pleurocystidia, a trichodermal pileipellis made up of filiform pale brown pigmented terminal elements, narrowly clavate capitate pale brown pigmented caulocystidia, and an absence of clamp connections.

FIGURE 22. Basidiome of *Pluteus fernandezianus* (JAD 331). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

Description:—*Pileus* 45–50 mm diam., hemispherical to plano-convex with a minute flattened umbo, disc somewhat rugulose; surface dull, dry, velutinous to pruinose at the disc, radiating outwards and appearing as dense pustules under a hand-lens, glabrous elsewhere; pustules dark brown (oac734–oac736), surface pallid tan (oac688–oac689). *Context* up to 3 mm thick, white. *Lamellae* free, close, with 3–4 tiers of lamellulae, some bifurcate, thin, pale pink (oac758–oac760), margin pallid tan (oac688–oac689). *Stipe* 45–48 × 4–5 mm, central, terete, hollow; surface dull, dry, finely fibrillose especially at the base, grayish brown fibrils over a white to off-white surface, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 7–8 (–9) × 5–7 µm [x_m = 7.8 ± 0.45 × 6.1 ± 0.52 µm, Q = 1.14–1.4, Q_m = 1.28 ± 0.09, n = 50, s = 1], subglobose to broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 20–36 × 5–8 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 15–22 × 6–8 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 28–60 (–80) × 12–23 µm, narrowly to broadly clavate or rarely fusoid-ventricose, obtuse, with pale brown plasmatic pigment or sometimes hyaline, thin-walled. *Pleurocystidia* 70–98 (–103) × 15–30 µm, broadly to narrowly lageniform or sometimes fusoid, obtuse or sometimes nodulose-capitate, hyaline or occasionally with pale brown plasmatic pigment, thin-walled. *Pileipellis* a trichoderm to trichohymeniderm with erect fascicles, especially towards the disc, terminal elements 64–105 × 8–25 µm, clavate to cylindro-clavate or narrowly filiform, obtuse or rarely subcapitate, with pale brown plasmatic pigment or hyaline, non-incrusted, non-gelatinous, thin-walled. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 3–20 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–14 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Caulocystidia* 40–75 × 6–12 µm, uncommon, solitary to clustered, narrowly clavate to filiform, obtuse or frequently mucronate-capitate, typically with brown plasmatic pigment or hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

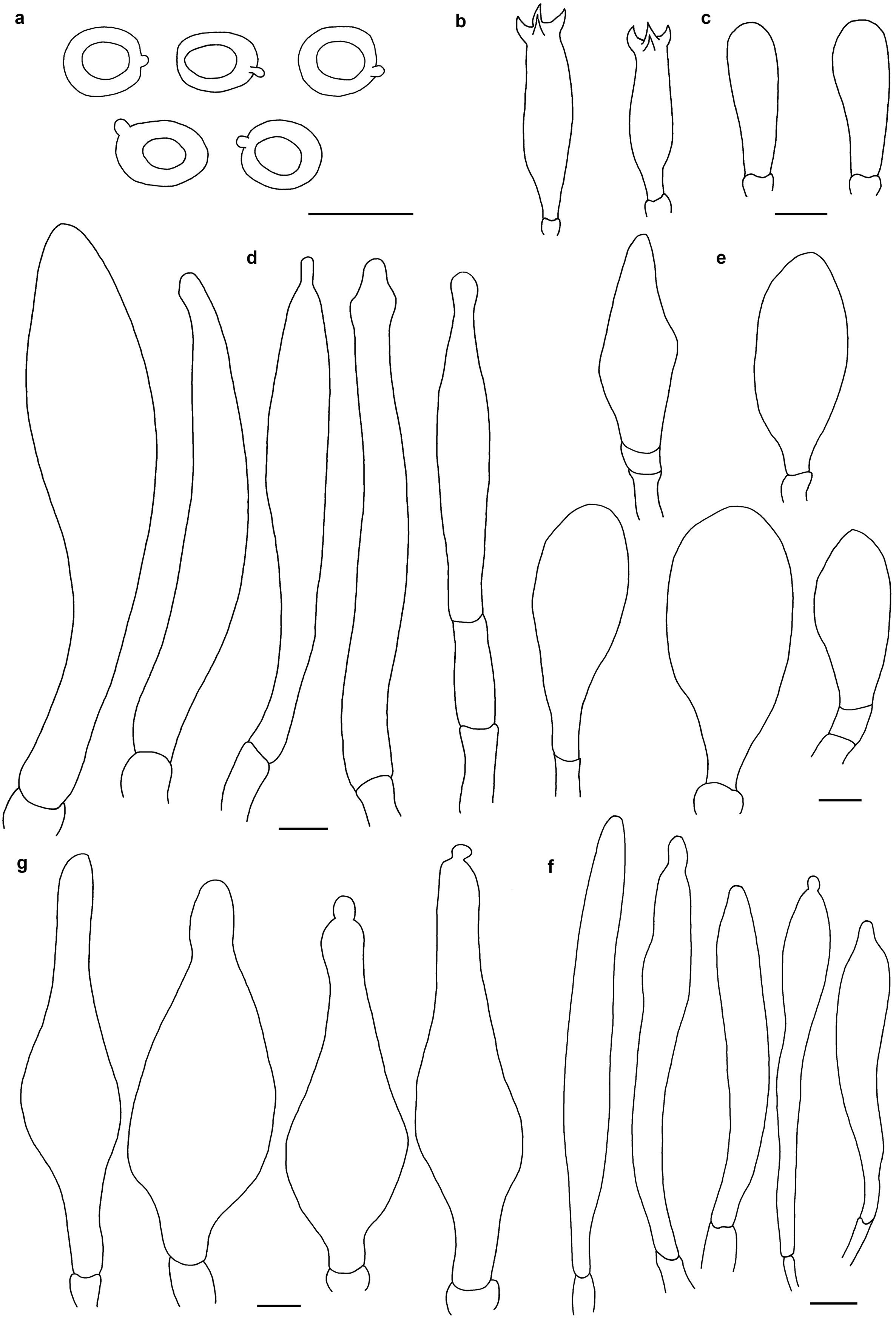

FIGURE 23. *Pluteus fernandezianus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Habitat and known distribution:—Gregarious on wood in subtropical montane transitionary primary to secondary broadleaf-*Podocarpaceae* rainforest containing *Burckella obovata* (*Sapotaceae*), *Cryptocarya tannaensis* (*Lauraceae*), *Dacrycarpus imbricatus* (*Podocarpaceae*), *Elaeocarpus floridanus* (*Elaeocarpaceae*), *Ficus smithii* (*Moraceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Melicope sp.* (*Rutaceae*), *Metrosideros vitiensis* (*Myrtaceae*), *Meryta neoebudica* (*Araliaceae*), and *Neuburgia corynocarpa* (*Loganiaceae*), Vanuatu (Aneityum). Also known from Chile (Juan Fernandez Islands) and Argentina.

Material examined:—VANUATU. Tafea Province: Aneityum, Nethwanethervana, 20°12.027′S, 169°47.727′E, elev. 317 m, 10 December 2019, coll. *J.A. del Rosario, JAD 331* (HAY).

Notes:—*Pluteus fernandezianus* Singer (1958: 220) was originally described by Singer (1958) from the Juan Fernandez Islands located off the western coast of Chile and was placed in stirps *Plautus* and then in stirps *Umbrosus* (Singer 1986). According to Niveiro and Albertó (2012) the species has also been reported in Argentina by Raithelhuber (1991). A study by Menolli and Capelari (2013) of Brazilian *Pluteus spp.* collections by P.C. Hennings and J. Rick, concluded *P. velatus* Rick (1961: 417) should be considered a *nomen dubium* based on their observations that the type material is inconsistent with the type description. According to Menolli and Capelari, the pileus and lamellae edge color from the type description combined with their examination led them to suggest the possible identity of *P. fernandezianus*, however its presence in Brazil remains unconfirmed.

The Vanuatu specimen would fit well compared to the original protologue description of *P. fernandezianus*, but with a few caveats. The Vanuatu material displays very similar pileus features, but are larger than what was originally described by Singer. Singer (1958) noted the pileus being 14 mm broad when dried, which may lead to the assumption many of these observations were on dried material that may have been larger when fresh. Singer described the stipe as being pallid white and maybe darkening towards the base, but noted it as not being any sort of fuscous or fuliginous fibrillose, but rather somewhat pubescent-subpruinose. The Vanuatu specimen, also at first glance has an overall white stipe, however with the aid of a hand-lens it is possible to see that there are very fine grayish brown fibrils which are easily overlooked. Singer's observations based on dried material may suggest this character is less distinctive in old material. Regarding microscopic characters, the Vanuatu specimen matches in the size and shape of the spores, and the shape and pigmentation of the pleurocystidia, cheilocystidia, and pileipellis terminal cells. The Vanuatu material's pleurocystidia shape and apex ornamentation especially match the pleurocystidia of Singer's Chilean material described as "…the tip sometimes short apiculate in the center, sometimes sinuate or nodulose at the apex," (Singer 1958). The main difference is that Singer's specimens have slightly shorter cheilocystidia (33–48 × 8.7–19 µm) and pleurocystidia (46–65 × 8.7–23.3 µm) compared to this material. Singer also did not include caulocystidia in the original description, which may indicate re-examination of the holotype is necessary.

Menolli *et al*. (2015c) also acknowledged that Singer (1969) considered *P. brunneoolivaceus* Horak (1964: 165) a synonym of *P. fernandezianus*, but without elaboration. Based on a comprehensive comparison of the type descriptions of these species, Singer may have related the two due to the similarities of the basidiomes and the marginate lamellae. Horak described the pleurocystidia of *P. brunneoolivaceus* as having an apex "subcapitata, cornuis nullis, saepissmime verruciformibus vel digitiformibus…" (Horak 1964) compared to Singer's *P. fernandezianus* pleurocystidia being "…sometimes short apiculate in the center, sometimes sinuate or nodulose" (Singer 1958). Based on Horak's accompanying plate illustrations (Tab. 1, 1a–g; Horak 1964) and a re-description of the holotype (Horak 1980b) the pleurocystidia on *P. brunneoolivaceus* appear to be digitate or cornuate and have apically thickened walls similar to metuloids in sect. *Pluteus*, which in the protologue (Horak 1964) are comparable to the metuloids in *P. cervinus*. Confusingly, in the re-description of *P. brunneoolivaceus* the thick-walled pleurocystidia are not mentioned but illustrated (Lamina XXV, v; Horak 1980b). Re-examinations of these type specimens in addition to analysis with molecular data are necessary to clarify the relationships between these taxa. Nevertheless, based on the type descriptions, none of these species conform with the material from Vanuatu.

Menolli *et al.* (2015c) tentatively identified specimen "RSPF330" deposited in the RSPF Herbarium at the Universidade de Passo Fundo in Brazil as *P.* cf. *fernandezianus*. This Brazilian collection was originally identified as *P*. *beniensis* Singer (1958: 285), a species in sect. *Celluloderma*, and was revised due to their observations of a euhymeniderm pileipellis mixed with clavate-fusiform and sphaeropedunculate elements, rather than an epithelial type pileipellis. In addition, their molecular analysis placed the specimen in sect. *Hispidoderma*. Due to an absence of macromorphological data, they related "RSPF330" to *P. fernandezianus* because of the shape and pigmentation of the pleurocystidia and cheilocystidia. The combination of larger, more utriform pleurocystidia, presence of sphaeropedunculate cells in the pileipellis, and molecular data separates "RSPF330" from the Vanuatu specimen. Interestingly, in part due to molecular and morphological data, "RSPF330" may be compared to the Vanuatu collections in the following section identified as *P. rimosellus* Singer in Singer & Digilio (1952: 262).

Phylogenetic analysis of ITS data (Fig. 15c) places the Vanuatu material of *P. fernandezianus* sister to a recently described species from Vietnam, *P. ornatus* E.F. Malysheva (2023: 20) (Malysheva *et al.* 2023). Both the Vanuatu specimen and *P. ornatus* share a superficial resemblance to the well-known species of *P. umbrosus* (Persoon) Kummer (1871: 98) and its allies. However, the two species can be separated due to some significant differences between them. *Pluteus ornatus* produces a much larger pileus (80–100 mm diam.) and stipe (70–90 × 6–13 mm). The Vanuatu material of *P. fernandezianus* has a stipe that is white overall with fine longitudinal gray fibrils, rather than the beige-toned stipe described in *P. ornatus*. *Pluteus ornatus* specimens also have distinctly marginate, serrate lamellae while those in the Vanuatuan *P. fernandezianus* have a whole margin. Micromorphologically, both specimens share the same shaped cystidia, but there are subtle significant differences. *Pluteus ornatus* has larger cheilocystidia (47–110 × 17–43), and pleurocystidia with 2–4 apical excrescences compared to the seldom observed single capitate pleurocystidia in the Vanuatu material. The latter difference may be significant, but it is noteworthy that variation in this form exists within known species of *Pluteus* or is easily overlooked as in the instance with *P. chrysaegis*. However, these traits in addition to phylogenetic distance in the analyses warrants treating them as separate taxa.

Pluteus* cf. *haywardii Singer, Transactions of the British Mycological Society 39: 147 (1956) (Figs. 24, 25)

Diagnosis:—*Pluteus* cf. *haywardii* from Aneityum is characterized by a grayish brown appressed-fibrillose, slightly marginally sulcate pileus, and a similarly colored stipe with a subbulbous base. Microcharacteristics include globose spores (6.7 × 6.1 µm), fusoid cheilocystidia, fusoid pleurocystidia, an ixo-cutis pileipellis with clustered, ascending clavate terminal elements, clavate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 10–15 mm diam., convex, margin slightly sulcate; surface dull, somewhat moist, variably appressed-fibrillose typically fading towards the margin or faded at the disc; fibrils pallid tan to grayish brown (oac702–oac704), surface cream-white. *Context* up to 2 mm thick, white. *Lamellae* free, moderately close with 2–3 tiers of lamellulae, thin, cream. *Stipe* 24–30 × 3–4 mm, central, cylindrical over a straight to subbulbous base, hollow; surface dull, dry, fibrous, cream to off-white, with minute streaks concolorous with the pileus surface, context white. *Odor* not observed. *Taste* not observed.

Basidiospores 6–7 (–8) × (5–) 6–7 µm [x_m = 6.67 ± 0.46 × 6.09 ± 0.44 µm, Q = 1–1.3, Q_m = 1.1 ± 0.07, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 20–30 × 7–9 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 18–25 × 7–9 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 32–63 × 7–26 µm, narrowly fusoid to fusoid, or narrowly utriform, obtuse, hyaline, thin-walled. *Pleurocystidia* 36–63 (–73) × 11–30 µm, narrowly to broadly fusoid-ventricose, or narrowly lageniform to narrowly utriform, obtuse, hyaline, thin-walled. *Pileipellis* an ixo-cutis of repent hyphae with ascending terminal elements embedded in a gelatinous matrix or gelatinized, composed of hyaline or with pale brown plasmatic pigment, non-incrusted, gelatinized or not, thin-walled, cylindrical hyphae, 12-20 µm diam.; terminal elements (55–) 68–105 × 18–24 µm, typically in fascicles, suberect to erect, clavate to fusoid-ventricose, obtuse, with pale brown plasmatic pigment. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical hyphae, 3–26 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–14 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–12 µm diam.. *Caulocystidia* 22–46 × 8–20 µm, in fascicles or sometimes in trichoderm-like chains, clavate or rarely fusoid, obtuse, sometimes with one to three basal cells, hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on wood in subtropical montane primary broadleaf-*Araucariaceae*/*Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum).

Material examined:—VANUATU. Tafea Province: Aneityum, Noposjec, 20°12.420′S, 169°46.795′E, elev. 252 m, 11 December 2019, coll. *J.A. del Rosario, JAD 346* (HAY).

Notes:—Singer (1956) decided that Patouillard's species, *P. alborubellus* (Montagne) Patouillard (1899: 196), from the Lesser Antilles was erroneously applied to the Montagne species *Agaricus alborubellus* Montagne (1854: 96) as he found the type to not represent a member of the genus *Pluteus*. Instead, Singer found Patouillard's material to match his collection from Argentina, and decided to describe the taxon as *P. haywardii* Singer (1956: 147). Additional material has been reported from Martinique and Guadeloupe (Pegler 1983a) and recollected in Argentina (Horak 1964, Singer 1961). The Vanuatu material matches closely with the descriptions of *P. haywardii,* but some morphological discrepancies with the type and very similar morphology to other species prevents a conclusive identification. Singer originally described the pleurocystidia and cheilocystidia together (Singer 1956, 1958), which are similar in shape but slightly smaller in size (37–55 × 13.7–29 µm equally) compared to the Vanuatu material. Singer also collected additional material close to the type locality, but only observed some of the spores to be more subglobose, with the overall majority still globose compared to the type, and illustrations of the pleurocystidia were provided to include more lageniform-shaped elements (Singer 1961). The type of *P. haywardii* also differs from the Vanuatu material by significantly smaller pileipellis elements (37–55 × 13.7–29 µm) and the presence of granules in the form of small fibrils on the pileus surface. Pegler's material from the Lesser Antilles is more micromorphologically similar to the Vanuatu material, having similarly shaped and sized pileipellis elements and spores, and although the pleurocystidia and cheilocystidia match in shape and size, these are also larger than those of the type (Pegler 1983a). The additional material reported from Horak (1964) has slightly larger spores and similarly sized pleurocystidia and cheilocystidia, however the pleurocystidia are differently shaped from the cheilocystidia, appearing to be more lageniform with a tapering apex compared to the type, Antillean, and Vanuatu material. Overall, there may be morphological variation within the species, but additional molecular data is necessary to determine this. While Singer describes small fibrils forming granules on the pileus surface, Pegler describes his material as containing squamules at the disc and throughout the pileus, while the surface of the Vanuatu material is glabrous overall, or at least minutely appressed-fibrillose. It must be acknowledged that the basidiomes of the Vanuatu material were not fully expanded when collected, so it is uncertain if expansion may have revealed a similar character or if this trait is important in the taxonomy of *P. haywardii*.

In the ITS phylogenetic analysis (Fig. 15a) the Vanuatu specimen falls in a poorly supported lineage (BS 70 %, PP 0.51) basal to other members of the supported *P. semibulbosus* (Lasch) Gillet (1876: 395) complex (BS 87 %, PP 1.0). On this branch, JAD 346 falls out with two collections from South Korea identified as *P. semibulbosus* (MF437007, KF668315). Pairwise analysis of overlapping ITS regions shows the Vanuatu sequence having 99.64 % similarity to the two South Korean specimens. Superficially, the two share similar basidiome stature, with the South Korean material having a wider pileus (10–25 mm diam.) (Park *et al*. 2017). Microscopically, these collections share similarly sized and shaped spores and similarly shaped cheilocystidia, pleurocystidia, and caulocystidia. All three cystidia types are similar in length, but the Vanuatu material generally has broader pleurocystidia and cheilocystidia. Based on micromorphology, JAD 346 is much more similar to the European material identified as *P. semibulbosus* compared to two other Vanuatu collections identified in this study as *P.* aff. *semibulbosus* (see below). Overall, JAD 346 differs in its colored stipe from European collections, and there is little to clearly separate this taxon morphologically from the current concept of *P. semibulbosus*. The basidiomes of the South Korean material are described with white to cream-colored stipes, but it is unclear if this character is enough to separate them as distinct species from *P. semibulbosus*.

FIGURE 24. Basidiomes of *Pluteus* cf. *haywardii* (JAD 346). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

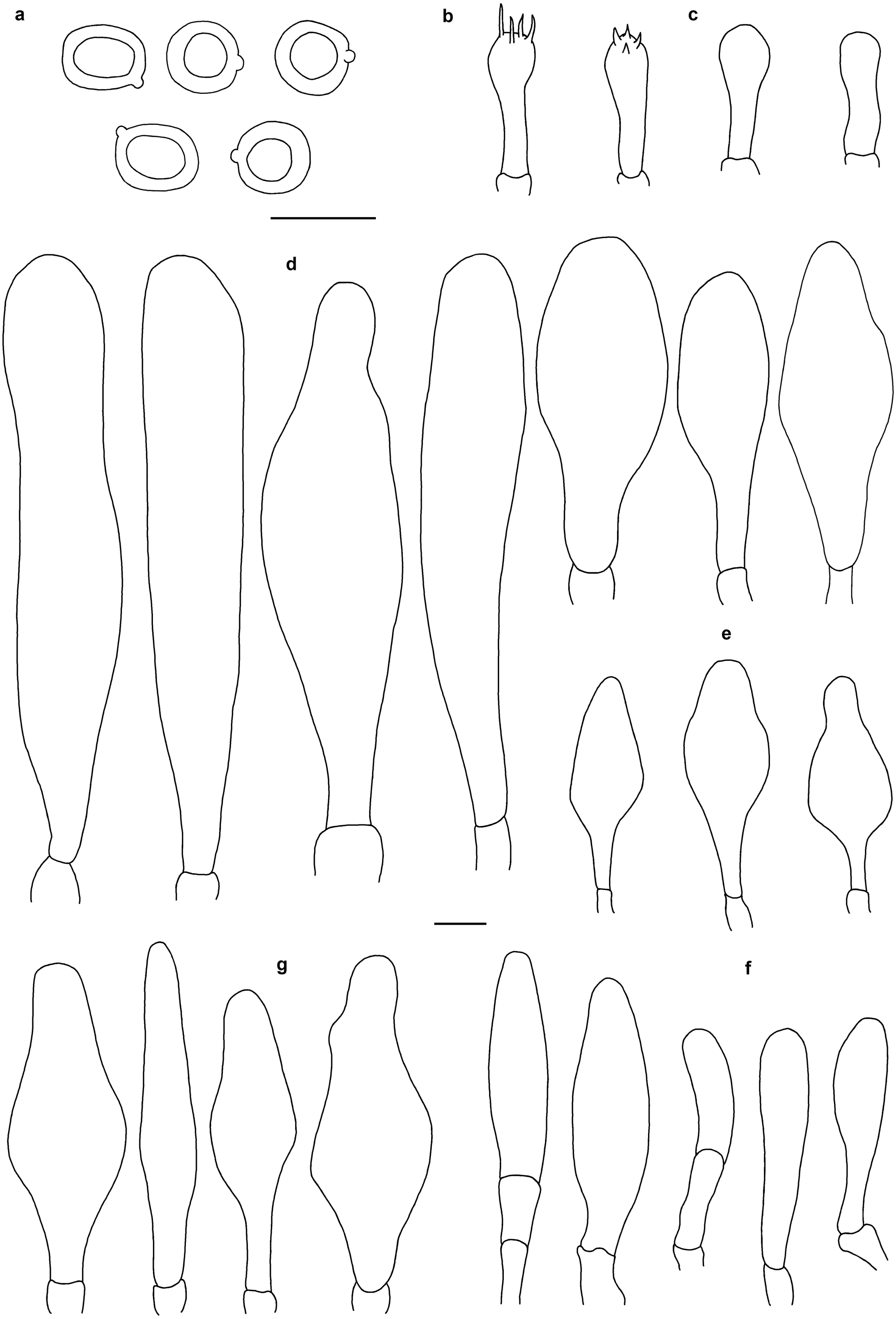

FIGURE 25. *Pluteus* cf. *haywardii*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Due to morphological similarity and overlap among species within Singer's (1986) stirps, *Semibulbosus* and the general *P. semibulbosus* complex, the identity of this Vanuatu species is inconclusive. Clear delimitations need to be established for *P. semibulbosus* to clearly separate this Vanuatu material. The same can be said for *P. haywardii*, as contemporary collections, molecular sampling, and re-examination are necessary to refine the concept for this species. *Pluteus aquosus* Singer (1956: 148) differs based on a white stipe, smaller spores, smaller cheilocystidia, and has subcapitate pleurocystidia (Singer 1956, 1958). There has been disagreement regarding the concept of *Pluteus niveus* Murrill (1917: 131). from the U.S.A. and the type has been re-examined in multiple studies. Smith and Stuntz (1958) and Banerjee and Sundberg (1993) assumed Singer's (1956) description to be a composite of the type material and a different collection. Based on their concept, *P. niveus* clearly differs based on a white stipe, more ellipsoid spores, slenderer pleurocystidia, and smaller cheilocystidia (Banerjee & Sundberg 1993, Smith & Stuntz 1958).

Pluteus macrocystidiatus *nom. prov.* (Fig. 26)

Diagnosis:—*Pluteus macrocystidiatus* from Futuna is characterized by a small, cream, convex, fibrillose, marginally eroded pileus, serrated lamellae, and a similarly ornamented and colored stipe with a bulbous base arising from a white tomentum. Microcharacteristics include subglobose to broadly ellipsoid spores (8.6 × 7.7 µm), rare sphaeropedunculate cheilocystidia, scattered fusiform to lageniform pleurocystidia, clustered and distinctly large broadly clavate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 15 mm diam., convex, margin slightly sulcate, slightly eroded; surface hygrophanous, dry, appressed-fibrillose; fibrils off-white to cream (oac815), densest at the disc, less dense towards the margin, underlying surface pale pink to pink-brown (oac793). *Context* up to 2 mm thick, pale pink to pink-brown (oac793). *Lamellae* free, crowded with 5 tiers of lamellulae, thin, pink-brown (oac793), margin slightly serrate-eroded. *Stipe* 10 × 1.5 mm, central, cylindrical over a bulbous base arising from a white tomentum (upwards 2 mm from base), hollow; surface dry, dull, fibrous, flocculose at base; white fibrils over a tan (oac795) surface, context white. *Odor* indistinct. *Taste* not observed.

Basidiospores (7–) 8–10 × (6–) 7–9 µm [x_m = 8.62 ± 0.75 × 7.63 ± 0.8 µm, Q = 1–1.5, Q_m = 1.1 ± 0.1, n = 50, s = 1], subglobose to occasionally broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* not observed. *Basidioles* 16–22 × 8–10 µm, clavate, hyaline, thin-walled. *Cheilocystidia* 26–52 × 14–25 µm, rare, seldom forming a well-developed strip on the lamellar edge, sphaeropedunculate to broadly clavate, obtuse, hyaline, thin-walled. *Pleurocystidia* 42–76 × 8–22 µm, scattered, fusiform to lageniform, obtuse to truncate or capitate, hyaline, thin-walled. *Pileipellis* ambiguous (due to weathered nature of specimen), possibly a cutis, composed of cylindrical, hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–12 µm diam.; terminal elements 32–115 × 5–11 µm, repent or occasionally suberect, clavate to cylindro-clavate, obtuse. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical hyphae, 3–24 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–9 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–9 µm diam.. *Caulocystidia* 25–106 × 8–27 µm, common, solitary to clustered, clavate to broadly clavate, obtuse, hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary on decaying wood in subtropical montane primary broadleaf rainforest containing *Ascarina diffusa* (*Chloranthaceae*), *Claoxylon fallax* (*Euphorbiaceae*), *Diospyros ferra* (*Euphorbiaceae*), *Dillenia biflora* (*Dilleniaceae*), *Ficus storckii* (*Moraceae*), *Geissois denhamii* (*Cunoniaceae*), *Metrosideros vitiensis* (*Myrtaceae*), *Phyllanthus myrianthus* (*Phyllanthaceae*), *Plerandra actinostigma* (*Araliaceae*), *Schefflera neoebudica* (*Araliaceae*), and *Syzygium chanelii* (*Myrtaceae*), Vanuatu (Futuna).

Material examined:—VANUATU. Tafea Province: Futuna, low slopes of Mount Tatafu from Natangi, 19°31.309′S, 170°13.536′E, elev. 281 m, 16 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 302* (HAY).

Notes:—Unfortunately, sparse material and the poor condition of the Vanuatu specimen prevented a clear characterization of the pileipellis, which may be a cutis. Because of this missing character and closeness to a number of similar species, a provisional identification is proposed for this study. The small stature of the Vanuatu specimen suggests comparison to a number of *Pluteus* species. *Pluteus delicatulus* C.K. Pradeep & Vrinda (2006: 95) is a similarly small, fragile species from India, however it differs due to the darker basdiomes, smaller spores, smaller non-lageniform pleurocystidia, absence of caulocystidia, and an epithelioid pileipellis (Pradeep *et al*. 2006). *Pluteus aquosus* has similar micromorphology, but differs by lacking a serrate lamellar edge, having a pure white stipe lacking a bulbous base stipe, lacking white basal tomentum, having smaller spores, and ventricose cheilocystidia (Singer 1956, 1958,

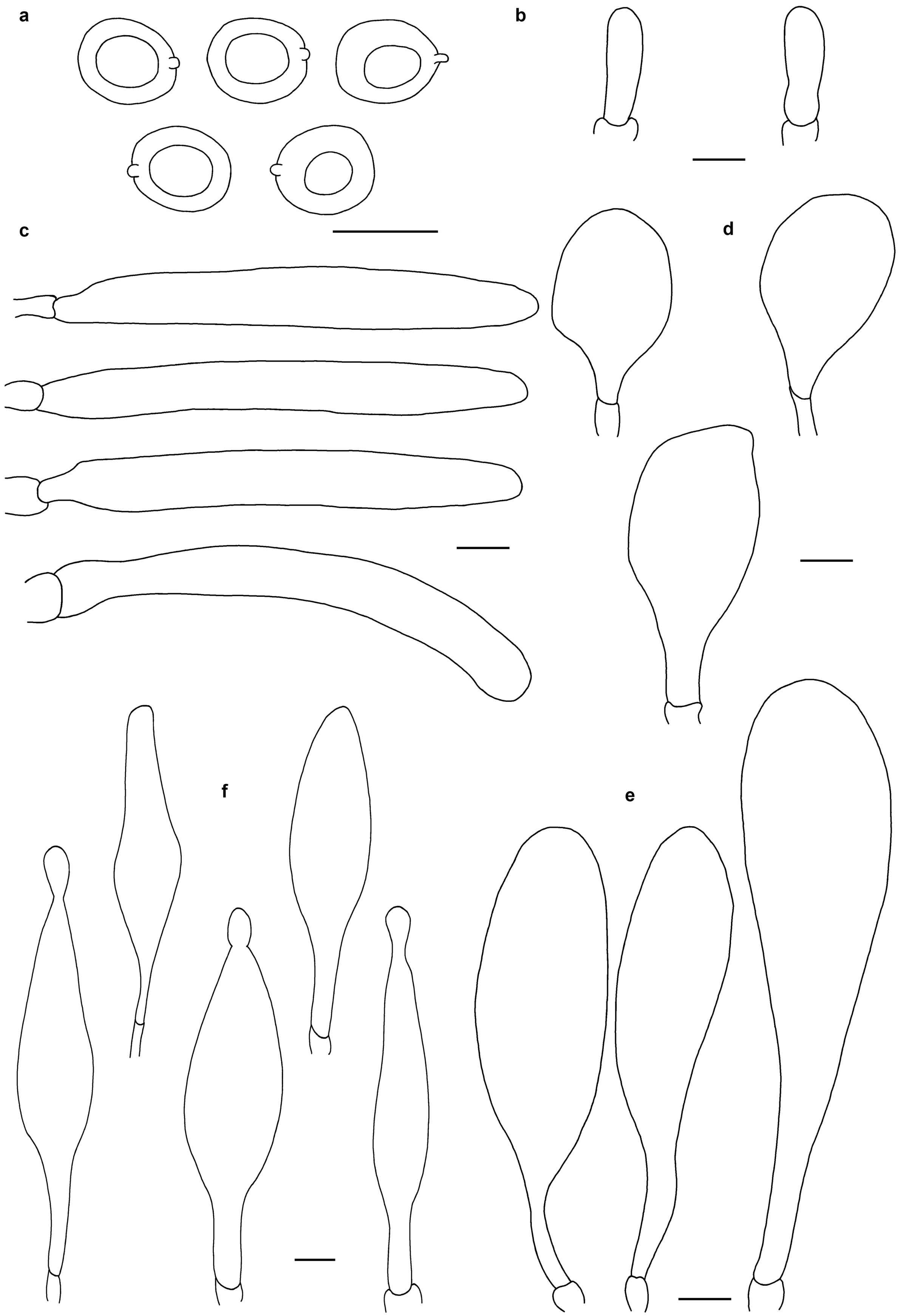

FIGURE 26. *Pluteus macrocystidiatus*. a. Basidiospores. b. Basidioles. c. Pileipellis terminal elements. d. Cheilocystidia. e. Caulocystidia. f. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

1961). *Pluteus albidus* shares many morphological similarities, but differs slightly by its smaller subglobose spores, versiform cheilocystidia, smaller caulocystidia, and lacks serrate gill edges (Desjardin & Perry 2018). *Pluteus espeletiae* Singer (1961: 120) from Venezuela (Singer 1961) similarly shares a crenate gill edge, large spores (8–8.8 × 6.8–7.5 µm), and pleurocystidia shape, but differs due to having a scaly disc, ventricose cheilocystidia, pigmented cystidia, and lacking caulocystidia.

ITS data phylogenetic analysis (Fig. 15b) places *P. macrocystidiatus* with an undetermined *Pluteus* species from Taiwan (MK041296) within the general *plautus*/*longistriatus* clade recognized by Justo *et al.* (2011b). A pairwise comparison of the two aligned, overlapping ITS sequences reveals a 99.84 % similarity suggesting these may be conspecific. Currently, the Taiwanese material has not been studied and unfortunately morphological data is currently unavailable for comparison. Regardless, assuming these two are the same taxon there is a wide gap in a distribution between Taiwan and Vanuatu's island of Futuna. Similarity between Taiwan's range of northern subtropical climates to southern tropical and Vanuatu's subtropical climate may explain the species' preferred conditions. This species possibly occurs elsewhere throughout the Pacific, but incomplete regional records of this group combined with its general small stature suggest it is easily overlooked. The particular combination of the serrate lamellar edge, sparse cheilocystidia, and rather large spores and caulocystidia (hence the epithet *macrocystidiatus*) may be distinct enough to describe the species as new. It would be ideal to compare the Taiwanese specimen to the Futuna material and determine if these specific characters are shared consistently in both. Due to incomplete data and for the sake of the study, the Vanuatu specimen is tentatively identified with a *nom. prov.* pending further investigation of additional material.

Pluteus neochrysaegis Menolli & de Meijer in Menolli Jr., de Meijer & Capelari, *Nova Hedwigia* 100(1–2): 135 (2014) [2015] (Figs. 27, 28)

Diagnosis:—*Pluteus neochrysaegis* from Aneityum is distinguished by a grayish tan fading to white plano-convex pileus with a pellucid-striate margin and a rugose-venose uplifted white context disc. The bulbous based stipe is variably pallid tan fibrillose-flocculose. Microscopic characters include subglobose spores (6.3 × 5.6 µm), fusoid, thin to thick-walled acute cheilocystidia and obtuse pleurocystidia, an epithelioid hymeniderm pileipellis of pyriform cells with fusoid terminal cells over a cutis subpellis, fusoid-ventricose caulocystidia, pale grayish brown pigments throughout the cutis subpellis, stipitipellis, and caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 27–42 mm diam., broadly plano-convex with a broad slight central depression, slightly to broadly umbonate, margin minutely plicate in some; surface dull, dry, glabrous to appressed-fibrillose with minute exposed rivulose-pulverulent patches, disc absent or radially rugose-venose up to three-fourths the pileus width towards margin, veins splitting to expose and uplift the white context, margin pellucid-striate; surface overall pallid tan (oac690, oac710–oac711, oac730–oac732) with slight dull yellowish gray (oac723–oac725) tinges fading to white or grayish tan (oac674–oac676) towards the margin. *Context* 1.5–3 mm thick, white. *Lamellae* free, crowded, with 3–4 tiers of lamellulae, thin, dull pink (oac610–oac612). *Stipe* 20–50 × 3–5 mm, central, terete, cylindrical over a subbulbous to bulbous base, solid to hollow; surface dull, dry, longitudinally fibrillose-striate and/or minutely flocculose, pale tan (oac653–oac655) over a white surface, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 5–7 (–8) × 5–7 µm [x_{mr} = 6.22–6.5 × 5.52–5.62 µm, x_{mm} = 6.3 ± 0.14 × 5.57 ± 0.1 µm, Q = 1.0–1.5, Q_{mr} = 1.11–1.18, Q_{mm} = 1.1 ± 0.14, n = 50, s = 4], subglobose to broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 20–35 × 6–8 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 12–26 × 5–8 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 35–83 × 6–25 µm, lageniform to broadly lageniform or fusoid-ventricose, obtuse, acute, or occasionally capitate, hyaline, thin to evenly or apically thick-walled (up to 3 µm thick) especially in larger cystidia. *Pleurocystidia* 35–90 × 15–25 (–35) µm, scattered to common, fusiform to narrowly lageniform, obtuse or rarely mucronate, hyaline, thin to thick-walled (up to 3 µm thick) especially in larger cystidia; rarely 34–46 × 10–18 mm, fusoid-ventricose, acute or corniculate with 2–4 poorly developed hooks, hyaline, thin to thick-walled. *Pileipellis* an epithelioid hymeniderm with pileocystidia over a subpellis, majority of terminal elements 12–30 × 5–12 µm, sphaeropedunculate to clavate, obtuse or rarely mucronate, hyaline, non-incrusted, non-gelatinous, thin-walled; *pileocystidia* 28–55 (–71) × 8–16 µm, scattered to abundant especially at the disc, fusiform to narrowly lageniform, obtuse, acute, infrequently capitate or rarely mucronate (up to 50 µm long), hyaline, thin to evenly or apically thick-walled especially in lageniform elements; *subpellis* a cutis of repent hyphae, composed of pale brown plasmatic pigmented, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 µm diam.. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 4–23 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–18 µm diam.. *Stipitipellis* a cutis, composed of hyaline or with patches of plasmatic pale brown pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–14 µm diam.. *Caulocystidia* 20–62 × 6–16 µm, solitary or often clustered, lageniform to fusoid-ventricose, acute or rarely subcapitate, hyaline or with pale brown plasmatic pigment, thin to thick-walled especially in larger cystidia. *Clamp connections* absent in all tissues examined.

FIGURE 27. Basidiomes of *Pluteus neochrysaegis*. a. Non venose-rugose forms of *Pluteus neochrysaegis* (JAD 244). b. Venose-rugose form of *Pluteus neochrysaegis* (JAD 265). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

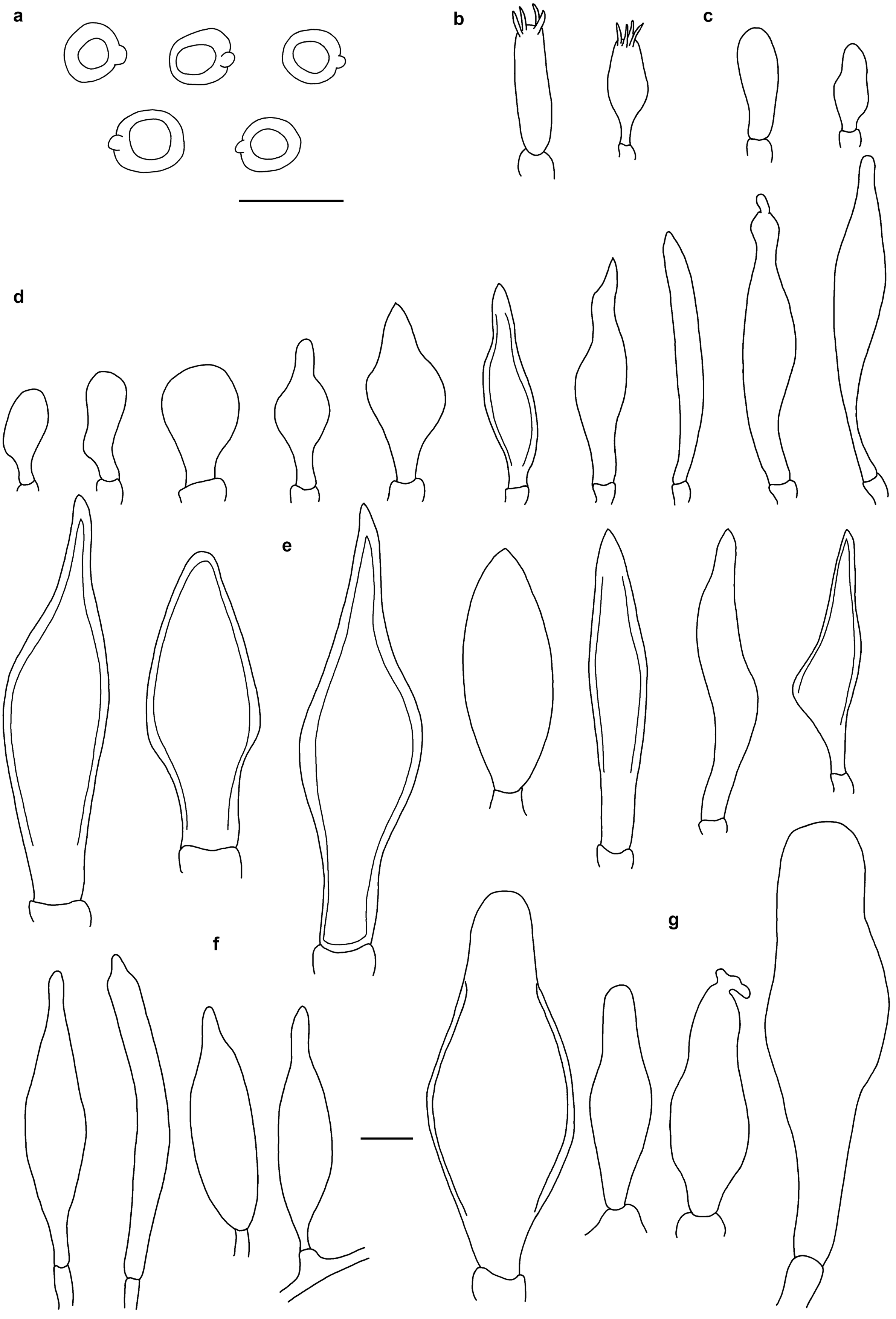

FIGURE 28. *Pluteus neochrysaegis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Habitat and known distribution:—Solitary to gregarious on decayed wood in subtropical montane primary broadleaf rainforest to cloud forest containing *Balanops pedicellata* (*Balanopaceae*), *Diospyros sp.* (*Ebenaceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Ilex vitiensis* (*Aquifoliaceae*), *Melicope latifolia* (*Rutaceae*), *Metrosideros collina* (*Myrtaceae*), *Plerandra actinostigma* (*Araliaceae*), *Scaevola cylindrica* (*Goodeniaceae*)*, Semecarpus tannaensis* (*Anacardiaceae*), and *Syzygium spp.* (*Myrtaceae*) and montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum). Also known from Brazil (Paraná).

Material examined:—VANUATU. Tafea Province: Aneityum, Anloulanelcau area, trail to Transect 11, 20°13.066′S, 169°47.406′E, elev. 188 m, 29 July 2017 coll. *J.A. del Rosario, JAD 17* (HAY); Aneityum, Mount Inhetiji, lowland forest in former taro terraces close to Anecro, 20°12.567′S, 169°51.102′E, elev. 145 m, 12 December 2018, coll. *J.A. del Rosario, JAD 244* (HAY); same location, 12 December 2018, coll. *P. Dovo, JAD 245* (HAY); Aneityum, Anecro, footpath to river near Chief Nicolas's house, 20°12.490′S, 169°51.983′E, elev. 76 m, 14 December 2018, coll. *J.A. del Rosario, JAD 265* (HAY).

Notes:—*Pluteus neochrysaegis* is currently known and originally described from Paraná state of Brazil (Menolli *et al*. 2015a). The material collected from Aneityum Island fits well with the original description with minor caveats. Coloration in the pileus is slightly paler, albeit across collections variation occurs likely due to environmental conditions. In collection JAD 265, the distinct uplifted white context veins radiate from the disc, however multiple specimens in this collection show that the magnitude of this rugose-venose ornamentation varies as this is significantly reduced in the smallest basidiome and does not occur in the other collections.

Menolli *et al*. (2015a) distinguished *P. conizatus* (Berkeley & Broome) Saccardo from *P. neochrysaegis* by its pale yellow stipe, however this trait may not necessarily be consistent as the Vanuatu material has a similarly colored pale yellow stipe that varies but occurs across all specimens. Menolli *et al*. also discussed pileipellis similarity between *P. neochrysaegis* and *P. chrysaegis,* and distinguished *P. neochrysaegis* as different in having shorter pleurocystidia, dimorphic cheilocystidia, both lamellar cystidia types being pigmented, and ellipsoid spores. The Vanuatu material recognized as *P. neochrysaegis* shares similarly sized and shaped hyaline pleurocystidia compared to the Tafean collections and other regional accounts of *P. chrysaegis*. Between the Brazilian and Vanuatu material of *P. neochrysaegis*, the Brazilian specimen has smaller pleurocystidia (30–44 × 6.2–11.2 µm). The Vanuatu specimens lack pigmented cheilocystidia, which is present in the Brazilian material, but shares similarly sized and dimorphic thick-walled cheilocystidia. All the Vanuatu specimens of *P. chrysaegis* share this dimorphic variety of cheilocystidia with intermediate elements as well, so it is uncertain if this trait proposed by Menolli *et al*. as distinctive should be considered an exclusive feature of *P. neochrysaegis*. For the most part, the micromorphology between these species is nearly homogenous. One exception, that was also recognized by Menolli *et al*., could be the ellipsoid spores in *P. neochrysaegis*, while *P. chrysaegis* has typically subglobose spores. The primary means of distinguishing among these species would be through their pileus coloration as *P. neochrysaegis* has a dull grayish brown pileus fading to white without or with white veins, and *P. chrysaegis* typically has a brilliant to dull yellow pileus with brown veins.

Pluteus amphicystis Singer (1958: 213) from Bolivia is a superficially similar species (Singer 1958). Pegler reported a collection from Martinique and provided a line drawing that strongly resembles the stature of *P. neochrysaegis* (Fig. 58, Pegler 1983a). Both Singer and Pegler reported the rugose-venose elements of the pileus and described this as 'scrobiculate'. Singer described the pileus as "yellow, center watery melleous…finely tomentose or subfibrillose…" (Singer 1958), while Pegler described the color as light ochraceous-buff with yellow ocher granules and the marginal edge being transparent (Pegler 1983a). Both authors described the presence of metuloid pleurocystidia and cheilocystidia like those of *P. neochrysaegis*. The important distinction between these taxa is in regard to Singer's emphasis of the metuloids being similar to those of *Inocybe spp.* that includes the presence of apical crystals, which Pegler also observed in the Martinique material. The presence of these apical crystals on the pleurocystidia were confirmed and imaged via electron microscopy during a re-examination of the type and with supplementary material from Mexico (Fig. 2, Rodríguez & Guzmán-Dávalos 2007). *Pluteus amphicystis* can also be distinguished based on its pileipellis, which Singer described as consisting of elongated hyphae with terminal elements having broadly rounded tips and additional forms similar to the metuloid cystidia (Singer 1958). Pegler (1983a) describes this as a repent epicutis with dermatocystidia (60–160 × 5–24 µm) forming erect fascicles at the disc, and Rodríguez and Guzmán-Dávalos (2007) illustrated a filamentous pileipellis, noting some of the elements with thick walls and becoming suberect near the pileus center. As mentioned, pileipellis interpretation has caused difficulty in the taxonomy of *Pluteus spp.*. Overall, the hymeniderm pileipellis and lack of cystidia with apical crystals separates the Vanuatu material from *P. amphicystis* and better identifies it as *P. neochrysaegis*.

Pluteus ornatocystidiatus J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 29, 30)
MycoBank no:—854225

Holotype:—VANUATU. Tafea Province: Tanna, Yanemari/Lighthouse and Mount Kuning area, 19°37.602′S, 169°25.870′E, elev. 286 m, 30 August 2018, coll. *J.A. del Rosario, JAD 167* (HAY).

Etymology:—*ornato* (L.) = ornate, *cystidiatus* (L.) = cystidia; in reference to the abundant apically ornamented cystidia on all tissues.

Diagnosis:—*Pluteus ornatocystidiatus* from Tanna is characterized by a dark fading to pale tan areolate-squamulose disc, tan glabrous pileus with a pellucid-striate margin and a white stipe with tan floccules and a broadened base. Microcharacters include subglobose spores (6.1 × 4.9 µm), clavate sometimes mucronate cheilocystidia, lageniform mucronate or clavate pleurocystidia, a trichohymeniderm pileipellis comprised of lageniform, broadly clavate mucronate terminal elements that occasionally have thickened walls and brown pigmentation, fusoid mucronate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 25–55 mm diam., convex to plano-convex, margin slightly sulcate or not; surface dull to pellucid-striate up to half-way from margin, hygrophanous, disc areolate-squamulose in expansion, glabrous with pulverulent patches towards the margin; disc and squamules dark tan (oac646–oac647) fading to tan (oac668–oac669) turning cream (oac696–oac697) at the margin. *Context* up to 3 mm thick, pale pinkish brown. *Lamellae* free, close to crowded with 3 tiers of lamellulae. *Stipe* 30–55 × 4–6 mm, central, terete, cylindrical over a broadened base, hollow; surface pearlescent, dry, minutely flocculose or appressed-fibrillose, white overall with some tan floccules becoming most dense at the base. *Odor* indistinct. *Taste* indistinct.

FIGURE 29. Basidiomes of *Pluteus ornatocystidiatus* (JAD 167 holotype). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

Basidiospores 5–7 × 4–6 µm [x_m = 6.08 ± 0.48 × 4.84 ± 0.5 µm, Q = 1–1.75, Q_m = 1.26 ± 0.15 µm, n = 50, s = 1], subglobose to ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 16–24 × 4–7 µm, clavate, 4-spored or 2-spored, guttulate, hyaline, thin-walled, sterigmata 2–3 × 0.5–1 µm. *Basidioles* 15–28 × 5–10 µm, clavate, guttulate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 30–65 × 8–22 µm, clavate to narrowly lageniform or fusoid, obtuse or occasionally mucronate to subcapitate, hyaline, thin-walled. *Pleurocystidia* 30–68 × 8–32 µm, lageniform to fusoid-ventricose or narrowly utriform, mucronate with regular to irregular or strangulate

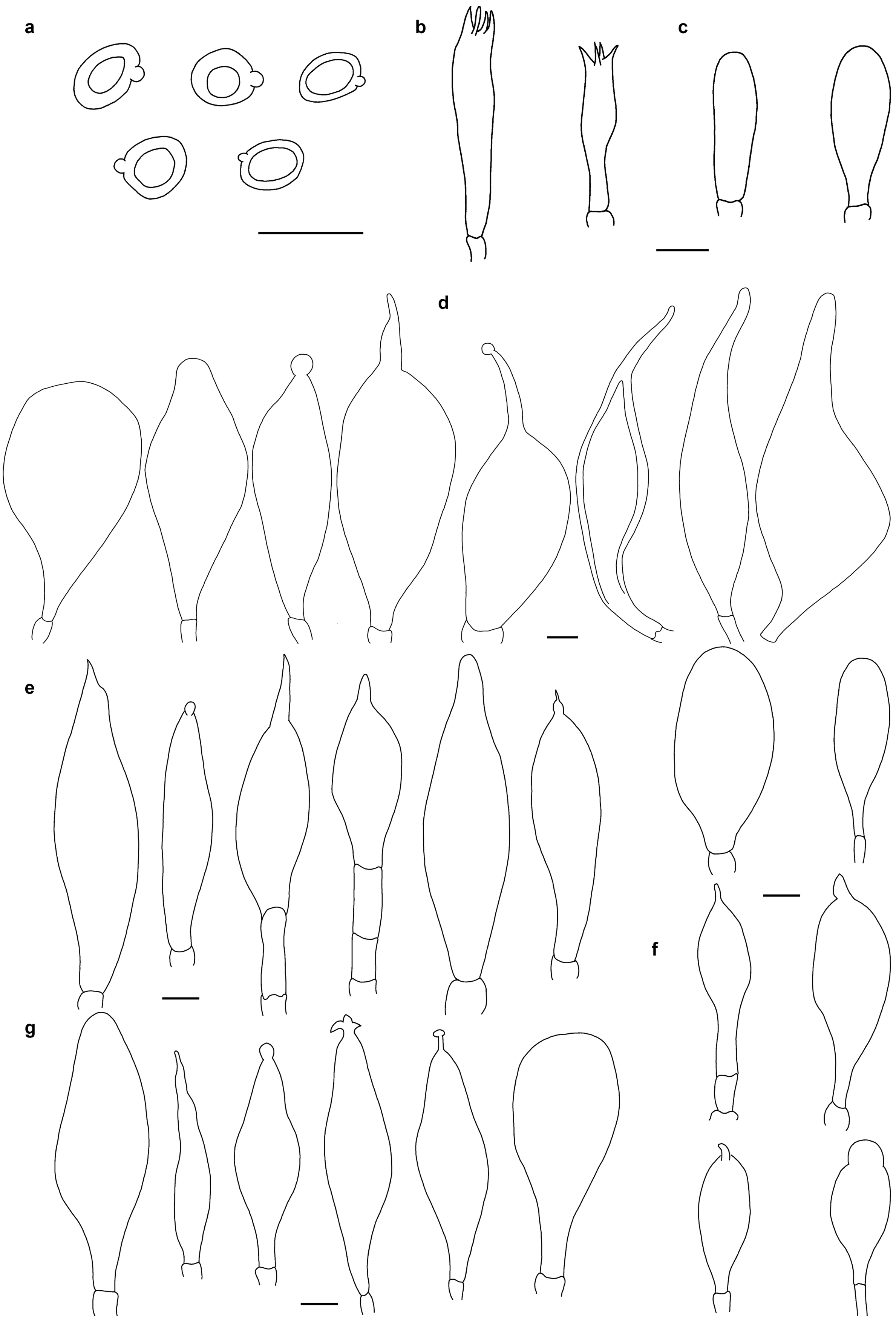

FIGURE 30. *Pluteus ornatocystidiatus* a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

apical projections, hyaline, thin-walled; some 50–78 × 25–36 µm, ovoid to broadly clavate, obtuse without apical projections, hyaline, thin-walled. *Pileipellis* a trichohymeniderm with pileocystidia, composed of a majority of cells 50–140 × 13–42 µm, clavate to broadly clavate, fusiform to fusoid-ventricose or lageniform, obtuse or frequently capitate or mucronate, typically with brown plasmatic pigment or occasionally hyaline, non-incrusted, non-gelatinous, thin-walled; *pileocystidia* 110–210 × 12–45, common, fusiform to fusoid, frequently mucronate with an elongated appendage (up to 85 µm long) or obtuse, with brown plasmatic pigment or occasionally hyaline, thin to evenly or apically thick-walled (up to 3 µm thick). *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, cylindrical hyphae, 5–28 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–20 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 4–12 µm diam.. *Caulocystidia* 30–120 × 13–22, clustered or scattered, clavate to broadly clavate or fusoid, capitate or mucronate, hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on decaying wood in subtropical lowland-montane secondary broadleaf-*Podocarpaceae* rainforest containing *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Cryptocarya wilsonii* (*Lauraceae*), *Ficus wassa* (*Moraceae*), *Ixora aneityensis* (*Rubiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Yanemari/Lighthouse and Mount Kuning area, 19°37.602′S, 169°25.870′E, elev. 286 m, 30 August 2018, coll. *J.A. del Rosario, JAD 167* (HAY).

Notes:—In comparison to *P. ornatocystidiatus*, the species *P. heteromarginatus* Justo (2011: 472) from the U.S.A. is close macromorphologically, but differs primarily by lacking a flocculose stipe. Micromorphologically it differs by having slightly smaller pleurocystidia, smaller cheilocystidia lacking apical appendages, narrower pileipellis terminal elements without thick walls or elongated apical appendages, and narrower caulocystidia (Justo *et al*. 2011b). *Pluteus aeolus* (Berkeley & Broome) Saccardo (1887: 666), a tropical species from Sri Lanka, also has macromorphological similarities, but differs due to a lack of clavate or thick-walled pileipellis terminal elements, lack of mucronate cheilocystidia, and no pleurocystidia (Pegler 1986). *Pluteus longistriatus* Peck (Peck) (1835: 137) reported from North and South America is also superficially similar, but fundamentally differs in the absence of apical appendages on the pleurocystidia, cheilocystidia and caulocystidia, lacking apical appendages or thickened walls in the pileipellis terminal elements, and having less lageniform and non-mucronate caulocystidia (Menolli & Capelari 2010, Singer 1956, 1958). Based on ITS phylogenetic analysis (Fig. 15a) *P. ornatocystidiatus* is placed on an unsupported branch (BS 39 %, PP 0.76) sister to the Italian species *P. pulcherrimus* Ferisin & Dovana (2019: 24). *Pluteus pulcherrimus* is macromorphologically much closer to the Vanuatu specimen, but this species differs by slightly smaller pleurocystidia, slightly smaller cheilocystidia lacking apical appendages, and generally larger caulocystidia that are apically acute (Ferisin & Dovana 2019). Importantly, *P. pulcherrimus* is distinguished by the presence of brown veins on the pileus disc, which are absent in the Vanuatu material.

Pluteus rimosellus (Singer), Singer & Digillio, Liloa 25: 262, 1952 (Figs. 31, 32, 33)

Reported heterotypic synonyms:

= *Pluteus subfibrillosus* Singer, Transactions of the British Mycological Society 39: 187 (1956)

Probable heterotypic synonyms:

= *Pluteus pallidosquamulosus* E. Malysheva, V. Malysheva, A. Alexandrova, & O. Morozova, Phytotaxa 461.2: 85–86 (2020)

Diagnosis:—*Pluteus rimosellus* from Aneityum is characterized by a convex, slightly umbonate, marginally sulcate pileus with a grayish tan tomentose surface with patches exposing the off-white context and a venose-rugose or appressed squamulose disc composed of reddish brown pustules. The stipe is pale brown and minutely flocculose with a bulbous base. Microcharacters include broadly ellipsoid basidiospores with a mean size of 7.0 × 5.7 µm, fusoid-ventricose cheilocystidia and pleurocystidia both typically obtuse or infrequently with mucronate appendages, a euhymeniderm pileipellis with terminal elements comprised of pale brown pigmented, clavate-mucronate cells, sphaeropedunculate mucronate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 12–45 mm diam., convex to campanulate expanding to hemispherical in age with a moderate umbo, disc finely to coarsely venose-rugose, margin sulcate; surface dull, dry, veins composed of pustules-subtomentum radiating and diminishing towards margin, appressed-fibrillose elsewhere with rimulose patches exposing the underlying off-white to gray context; pustules/tomentum dark reddish brown (oac734–oac737) fading to pallid brown (oac771–oac773) in age and away from the disc, fibrils and surface pallid grayish tan (oac779–oac781 or oac800–oac802). *Context* up to 4 mm thick, off-white to pale gray. *Lamellae* free, close with 2 tiers of lamellulae, thin, margin turning serrate in age, white turning dull pink (oac767) in age. *Stipe* 20–48 × 3–5 mm, central, terete, cylindrical over a subbulbous to bulbous base, solid; surface dull, dry, glabrous or finely appressed-fibrillose to finely flocculose towards the apex, cream (oac794–oac795) to white with pale brown (oac771–oac773) fibrils and floccules, context white. *Odor* indistinct. *Taste* indistinct.

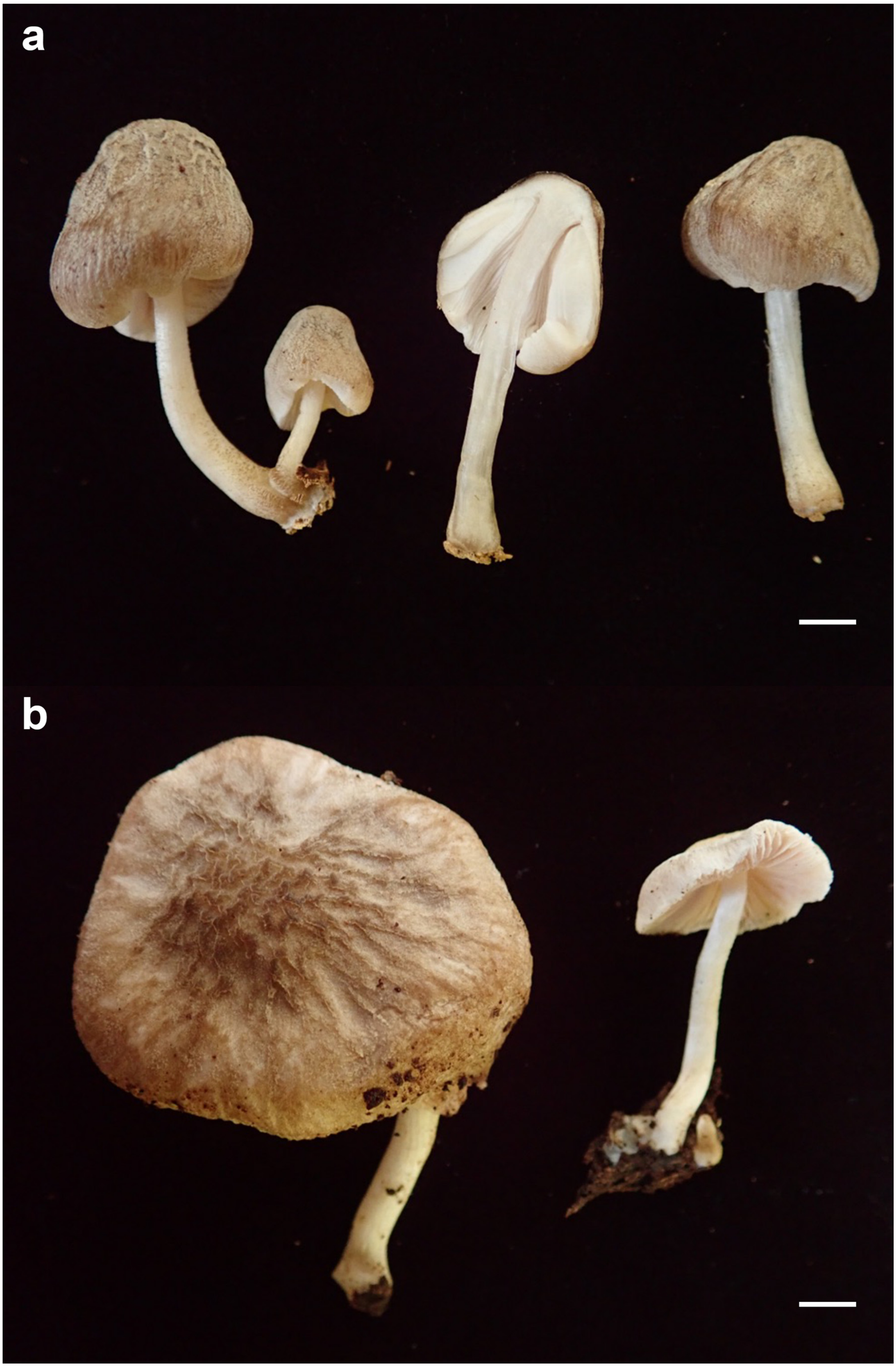

FIGURE 31. Basidiomes of *Pluteus rimosellus*. a. Immature basidiomes of *Pluteus rimosellus* (JAD 338-B). b. Mature basidiomes of *Pluteus rimosellus* (JAD 338). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

FIGURE 32. Squamulose morphotype basidiome form of *Pluteus rimosellus in situ* (JAD 343). Scale bar = 10 mm. Photo by: Jonathan del Rosario.

Basidiospores 5–8 (–9) × 5–8 µm [x_{mr} = 6.64–7.0 × 5.37–6.2 µm, x_{mm} = 7.02 ± 0.29 × 5.73 ± 0.42 µm, Q = 1–1.6, Q_{mr} = 1.21–1.25, Q_{mm} = 1.23 ± 0.02, n = 50, s = 3], subglobose to broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 20–30 (–36) × 7–9 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–2 µm. *Basidioles* 13–28 × 7–12 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* heterogenous. *Cheilocystidia* 38–78 (–92) × 14–28 (–40) µm, in fascicles or forming a well-developed strip on the lamellar edge, versiform, clavate to broadly clavate, fusoid-ventricose, or seldom sphaeropedunculate, obtuse or in some collections mucronate with an appendage (up to 10 µm long) or digitate-capitate with 1–2 appendages or nodules, rarely with apical incrustations, hyaline, thin-walled. *Pleurocystidia* (38–) 53–72 (–86) × (10–) 16–30 (–38) µm, scattered to abundant, fusoid-ventricose to lageniform, obtuse or in some collections frequently mucronate with an appendage or digitate-capitate with 1–2 appendages/nodules, rarely with apical incrustations, hyaline, thin-walled. *Pileipellis* an intricate trichoderm to euhymeniderm over a cutis subpellis, composed of terminal elements 56–92 (–115) × 14–26 µm, in erect to suberect fascicles, narrowly to broadly clavate or narrowly lageniform, obtuse, in some collections occasionally mucronate with an appendage (up to 17 µm long) or capitate with 1–2 nodules, with pale brown plasmatic pigment or hyaline, non-incrusted, non-gelatinous, thin or apically thick-walled (in one collection); *subpellis* a cutis, composed of hyaline or some with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–12 µm diam.. *Pileus trama* composed of interwoven, hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 3–24 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–20 µm diam.. *Stipitipellis* a cutis, composed of hyaline or sometimes with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 3–16 µm diam.. *Caulocystidia* 34–60 (–73) × 8–19 (–38) µm, scattered in fascicles, clavate to sphaeropedunculate, obtuse, in some collections frequently mucronate with an appendage (up to 22 µm long) or capitate with 1–2 nodules, hyaline or sometimes with pale brown plasmatic pigment, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary to gregarious on decayed wood in subtropical montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest with *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum). Also known from Argentina, Brazil, Vietnam.

Material examined:—VANUATU. Tafea Province: Aneityum, trail through Antowojon area, 20°13.142′S, 169°47.788′E, elev. 119 m, 28 July 2017, coll. *J.A del Rosario & B.A. Perry, JAD 11* (HAY); Aneityum, Noposjec, 20°12.710′S, 169°46.990′E, elev. 192 m, 11 December 2019, coll. *J.A. del Rosario, JAD 338/338B* (HAY); Aneityum, Noposjec, 20°12.420′S, 169°46.795′E, elev. 184 m, 11 December 2019, coll. *J.A. del Rosario, JAD 343* (HAY).

Notes:—*Pluteus rimosellus* was originally described by Singer from Argentina (Singer & Digilio 1952) and recently an isotype was re-examined and accompanied with a modern Brazilian collection (Menolli *et al*. 2015a). Unfortunately, a recent re-examination of a paratype by Rodríguez (2024) found the specimen to be in poor condition and only spores were observable. Singer (1956) commented that *P. fibrillosus* Murrill (1917: 134), had a close relationship with both *P. rimosellus* and *P. subfibrillosus* Singer (1956: 187), but did not clarify how to distinguish between these taxa. *Pluteus fibrillosus* was described from Louisiana by Murrill (1917) and since then the holotype since then has been examined by multiple authors (Banerjee & Sundberg 1993, Menolli *et al*. 2015a, Singer 1956, Smith & Stuntz 1958). The observations of Menolli *et al.* (2015a) are consistent with previous examinations, including distinct incrustations in the pileipellis, but the same accounts were unable to confirm Singer's observations of pigmented cystidia. Despite Singer's observed similarities in *P. fibrillosus* to *P. rimosellus* and *P. subfibrillosus*, Menolli *et al.* treated *P. fibrillosus* as a separate species. In addition, Menolli *et al.* compared an isotype of *P. rimosellus* plus additional Brazilian material against the holotype of *P. subfibrillosus*, and due to similar micromorphology concluded that *P. subfibrillosus* should be considered a synonym of *P. rimosellus*.

Extensive comparison of the protologues of both *P. rimosellus* and *P. subfibrillosus* reveals a wide range of macrocharacters that are also present and varied between the Vanuatu specimens. Specimens JAD 338 and JAD 338-B were initially collected on the same piece of rotten wood; however, it was uncertain at the time if they were the same species. JAD 338-B was composed of less mature and more venose fruiting bodies while JAD 338 had more mature, slightly paler basidiomes with one venose and a smaller one not (Fig. 31). Micromorphological comparison confirmed JAD 338-B as being a less mature form of JAD 338. These more venose forms of the Vanuatu specimens place them closer to the descriptions of *P. subfibrillosus* (Singer 1956, 1958). The other Vanuatu specimens of this taxon, JAD 11 and JAD 343, have a pileus disc that is more appressed-squamulose to subtomentose (Fig. 32), and much more similar to *P. rimosellus*, which has not been described as venose (Singer 1958, Singer & Digilio 1952). Overall, consistent macrocharacters for this species would include the pileus with a sulcate margin, a grayish tan appressed-fibrillose rimulose surface with a disc being either squamulose to rugose-venose comprised of reddish brown subtomentum, and a white stipe covered with pale brown minute floccules. This would strengthen the case for Menolli *et al.* synonymizing *P. subfibrillosus* under *P. rimosellus* (Menolli *et al*. 2015a). Based on both type descriptions of *P. rimosellus* and *P. subfibrillosus* plus the re-examinations by Menolli *et al.* (2015a), the specimens from Vanuatu fit closer to the concept of *P. rimosellus* with some discrepancies. None of the Vanuatu material has pigmented pleurocystidia observed by previous authors. Both the cheilocystidia and pleurocystidia are slightly longer compared to the type collections being closer in size to the Brazilian collection made by Menolli *et al.* (2015a), but this slightly varies between specimens. Otherwise, the size and shape of the globose to ellipsoid spores and the pileipellis elements fit well based on all other accounts, despite caulocystidia not being reported as in this material. The disc variation being either a reduced squamulose to a developed rugose-venose and the variously ornamented cystidia between specimens clearly point to a species with broad morphological variation.

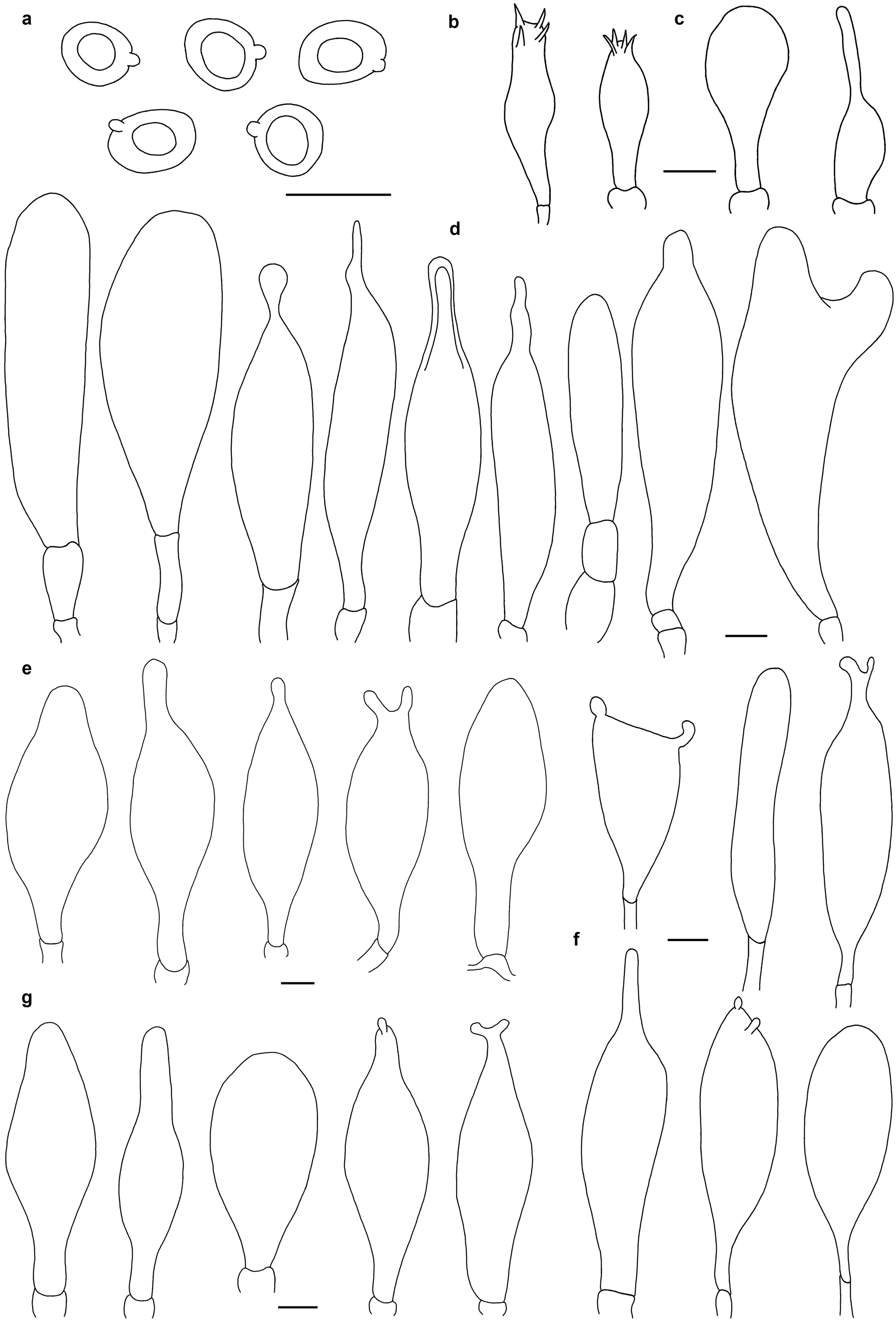

FIGURE 33. *Pluteus rimosellus*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Comparisons among the Vanuatu specimens reveal minor differences in micromorphology regarding cystidia apical ornamentation, although these traits are not predominant among cell types. For example, the well matured basidiomes in JAD 338 had some pleurocystidia that were infrequently observed with mucronate-digitate apices, while the less matured basidiomes in collection JAD 338-B occasionally has similar ornamentation on the cheilocystidia, and both share this on a minority of the pileipellis terminal cell apices. This particular trait would suggest comparison to *P. jaffueli* (Spegazzini) Singer (1954: 123) from Chile and Argentina, but this species differs primarily in having marginate lamellae and significantly larger pileipellis elements (66–150 × 13.8–30.8 µm) (Horak 1964, Singer 1954, 1956, 1958). In addition, a type of incrustation was sometimes observed on the cheilocystidia in JAD 338 and on the pleurocystidia of JAD 338-B. Even the caulocystidia of JAD 338 had a higher degree of apical variation compared to the other collections. With regards to JAD 11 and JAD 343, none of these traits were observed, except the pileipellis elements of JAD 343 were infrequently observed with apically thickened walls. While these characteristics may not be considered consistent enough to be taxonomically informative it is still worth noting and does suggest a high level of micromorphological variation within this species. Despite this minor variation, these collections can be united through ITS molecular data and tentatively identified to *P. rimosellus* in combination with matching physical characters from the type descriptions and matching the overall shape and size range of the spores, cheilocystidia, pleurocystidia, and pileipellis arrangement and elements.

In the phylogenetic analysis of ITS data (Fig. 15b) a recently described Vietnamese species, *P. pallidosquamulosus* E.F. Malysheva & A.V Alexandrova (2020: 85), falls within the strongly supported branch with the Vanuatu specimens of *P. rimosellus* and the Brazilian *P.* cf. *fernandezianus* specimen. The study did not include ITS data for the Brazilian specimen nor was it mentioned or noted in the protologue (Malysheva *et al.* 2020). Pairwise analysis of overlapping ITS regions shows that the sequence for *P. pallidosquamulosus* ranges from 97.18–97.83 % similarity to the Vanuatu specimens, and 97.06–99.05 % similarity to the Brazilian sequence. As mentioned in the commentary of the Aneityum material identified as *P. fernandezianus*, Menolli *et al.* (2015c) had revised collection "RSPF330", initially identified as *P. beniensis*, to *P.* cf. *fernandezianus* due to an absence of macromorphological data. Microscopic comparison between the Vanuatu material and the observations provided by Menolli *et al.* (2015c) match up well, however their material contained slightly longer pleurocystidia and pigmented pleurocystidia and cheilocystidia. Despite the absence of macromorphological data in "RSPF330", similarity in micromorphology combined with ITS (JQ065028) molecular data analysis places it with the Vanuatu specimens on a well-supported branch and suggests the identity of *P. rimosellus*. The micromorphology of *P. pallidosquamulosus* compared to the Vanuatu collections is practically a perfect match, with a minor exception of having slightly narrower pleurocystidia. *Pluteus pallidosquamulosus* even shares the minor variation seen throughout all the Vanuatu specimens, such as some pileipellis cells being slightly thick-walled, some cheilocystidia being apically papillate, or some pleurocystidia being subcapitate. The photo provided in the description bears a strong likeness to the Vanuatu specimens JAD 11 and JAD 343 suggesting similarity to *P. rimosellus*, and is dissimilar from the rugose-venose forms of the other collections and *P. subfibrillosus* (Figure 4A, Malysheva *et al.* 2020). Comparing the type description of *P. pallidosquamulosus* to the type descriptions and re-examinations of *P. rimosellus* and *P. subfibrillosus* suggests they are the same species due to high morphological similarities (Menolli *et al.* 2015a, Singer 1956, 1958, Singer & Digilio 1952). Therefore, it is unlikely *P. pallidosquamulosus* should be treated as a new species and may be better identified as *P. rimosellus*. Unfortunately, ITS data is unavailable for any of the types or additional collections of *P. rimosellus* or *P. subfibrillosus*, and this would be particularly useful in unifying these collections. However, this extensive literature comparison can confidently conclude this identity, and determines *P. rimosellus* as a morphologically variable species.

Pluteus* aff. *semibulbosus (Lasch) Gillet, Les Hymenomycetes ou Description de tous les Champignons qui croissent en France: 395 (1876) (Figs. 34, 35)

≡ *Agaricus semibulbosus* Lasch ex Fr., Epicrisis Systematis Mycologici: 140 (1838)

Diagnosis:—*Pluteus* aff. *semibulbosus* from Tanna is characterized by a hygrophanous, pale pink to off-white glabrous, pellucid-striate pileus and a white stipe with a subbulbous base arising from a white tomentum. Microcharacters include subglobose basidiospores (8.0 × 7.1 µm), versiform cheilocystidia being broadly clavate to fusoid-ventricose, fusiform pleurocystidia, a euhymeniderm pileipellis consisting of clavate cells, clavate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 20–34 mm diam., convex expanding to hemispherical in age with or without a slight central depression, sulcate up to half-way from margin, disc rugulose or smooth; surface dull at the disc when dry becoming pellucid-striate when moist, hygrophanous, dry to moist, glabrous when moist, to minutely appressed-fibrillose/subtomentose when dry; surface overall pale to dull pink (oac669/oac597–oac599) typically turning white from the disc outwards in age or when drying, or white overall. *Context* 1–3 mm thick, white. *Lamellae* free, subdistant with 2–3 tiers of lamellulae, thin (1–1.5 mm thick), pale pink (oac667–oac669). *Stipe* 25–30 × 3–4 mm, central, terete, cylindrical with a subbulbous base arising from a white tomentum, solid; surface shiny, dry, longitudinally fibrous, white to off-white, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 7–9 (–10) × 6–9 µm [x_{mr} = 7.84–8.14 × 7.06 µm, x_{mm} = 7.99 ± 0.21 × 7.06 ± 0.02 µm, Q = 1–1.33, Q_{mr} = 1.11–1.15, Q_{mm} = 1.13 ± 0.01, n = 50, s = 2], globose to subglobose or rarely broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 19–30 × 6–12 µm, clavate to broadly clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 18–26 × 7–10 µm, clavate, guttulate, hyaline, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 36–80 × 15–28 µm, versiform, clavate to broadly clavate, fusoid-ventricose to narrowly lageniform, obtuse or short to long capitate, hyaline, thin-walled. *Pleurocystidia* 47–103 × 14–41 µm, fusiform to fusoid-ventricose, or narrowly lageniform to broadly utriform, obtuse or sometimes truncate, sometimes basally septate, hyaline, thin-walled. *Pileipellis* a euhymeniderm, composed of a majority of cells 25–110 × 6–28 µm, cylindro-clavate to broadly clavate or rarely fusoid-ventricose, obtuse, hyaline, non-incrusted, non-gelatinous, thin-walled. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 3–22 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–19 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–14 µm diam., commonly with excrescences. *Caulocystidia* 20–60 × 6–18 µm, scattered to clustered, cylindro-clavate to clavate, obtuse or rarely capitate, sometimes with basal septae, hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

FIGURE 34. Basidiomes of *Pluteus* aff. *semibulbosus* (JAD 166). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

Habitat and known distribution:—Gregarious on decayed wood in subtropical lowland mixed-use agro tree garden and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*) and lowland-montane secondary broadleaf-*Podocarpaceae* rainforest containing *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Cryptocarya wilsonii* (*Lauraceae*), *Ficus wassa* (*Moraceae*), *Ixora aneityensis* (*Rubiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Tanna).

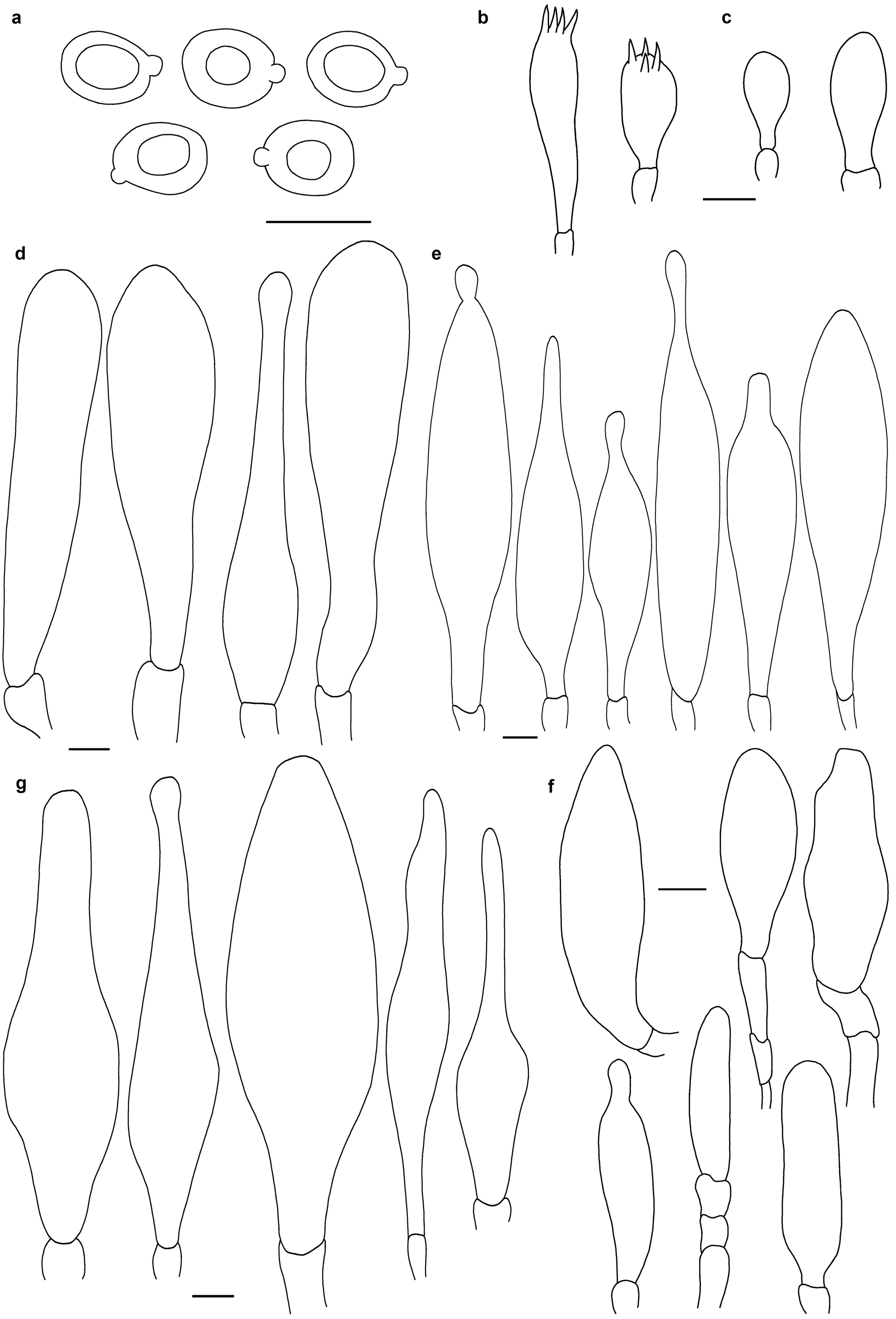

FIGURE 35. *Pluteus* aff. *semibulbosus* a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Materials examined:—VANUATU. Tafea Province: Tanna, base of Mt. Kuning, 19°37.602′S, 169°25.870′E, elev. 286 m, 30 August 2018, coll. *J.A. del Rosario, JAD 166* (HAY); Tanna, along banks of Numdretum River, 19°37.482′S, 169°25.928′E, elev. 267 m, 5 December 2018, coll. *J.A. del Rosario, JAD 197* (HAY).

Notes:—There has been disagreement among multiple authors about the species concept of *P. semibulbosus*, as some have described the pileipellis to consist of subglobose elements (Lange 1936, Orton 1960, 1986), while others recognize this taxon and others as conspecific within the *P. plautus* (Weinmann) Gillet (1876: 394) species complex (Vellinga 1990, Vellinga & Schreurs 1985). The original circumscription "pileo carnosulo hemisphaerico obtuso atomoto-molli sulcato…" (Fries 1838) was interpreted by Vellinga and Schreurs (1985) and Ferisin and Dovana (2019) to represent a species with a pileus cuticle comprised of particles, which when viewed microscopically is a trichodermal pileipellis containing elongated elements typical for sect. *Hispidoderma*. Both Vanuatu specimens fit this description, but their appearance slightly varies based on environmental conditions during collection. JAD 166 contains one basidiome with a pure white pileus and the other is an overall pinkish brown. The pilei of both collections are pellucid-striate, glabrous to minutely fibrillose/subtomentose and slightly rugulose at the disc (Fig. 34). JAD 197 had drier basidiomes, being a similarly colored pinkish brown around the pileus margin while the center is off-white and minutely fibrillose. Both specimens contain a pileipellis composed of elongated clavate terminal elements. The stipe of *P. semibulbosus* was originally described as "…subtiliter fistuloso pubescente, basi bullato" (Fries 1838), which could be interpreted as being fibrillose/pubescent with a bulbous base and a match to both Vanuatu specimens.

Phylogenetic analysis by Justo *et al.* (Justo *et al.* 2011b) determined the broad morphological concept of *P. plautus* by Vellinga and Schreurs (1985) comprising multiple species did not include *P. semibulbosus*, and concluded this taxon is a separate species requiring wider sampling for molecular and morphological distinction. For this study's phylogenetic analysis of ITS data (Fig. 15a), the two Vanuatu collections are positioned in a strongly supported clade representing sequences of *P. semibulbosus* (BS 95 %, PP 1.0) with low to moderately supported internal topology. The two Vanuatu specimens fall within a well-supported lineage (BS 98 %, PP 1.0) with a Japanese collection identified as *P.* aff. *semibulbosus* (HM562090), a Spanish collection of *P.* cf. *semibulbosus* (KR022020), a Slovenian (MK534552), Vietnamese (OQ732740), and two Italian (MK446329, MK446328) specimens identified as *P. semibulbosus*. Pairwise analysis of overlapping ITS regions of the two Vanuatu specimens compared to these sequences indicates a range of 99.11–99.82 % similarity to the previously mentioned taxa. Unfortunately, morphological data for the Japanese and Spanish collections is unavailable for comparison. Compared to the Italian/Slovenian collections, the Vanuatu specimens are distinguished macroscopically by having a pinkish brown pileus rather than white with a pale brown disc, and microscopically through larger spores, pleurocystidia and cheilocystidia, and more variable cheilocystidia with tapered to capitate apices (Ferisin & Dovana 2019). Compared to the Vietnamese material, the overall morphological descriptions fit quite well with each other (Malysheva *et al.* 2023). Phylogenetically, this lineage may be considered a separate species, but it is worth extensively comparing the Vanuatu specimens to the better-defined descriptions determined to be *P. semibulbosus* from South Korea (Park *et al.* 2017) and Turkey (Kaygusuz *et al.* 2019), which are placed in the adjacent lineages. Overall, the Vanuatu specimens' microcharacters are also distinct in significantly larger spores, pleurocystidia and cheilocystidia compared to the South Korean and Turkish accounts. The versiform-shaped cheilocystidia of the Vanuatu specimens are closer to those in the Turkish material, while the others seem less variable and overall clavate. Pairwise analysis of the Vanuatu specimens to sequences of *P. semibulbosus* representative of the other two lineages shows 98.76–98.93 % similarity to those from Turkey (MK123344, MK123344) and 98.05–98.23 % similarity to those from South Korea (KF668315, MF437007). A separate Vanuatu collection made in Aneityum, collection JAD 346 as *P.* cf. *haywardii* (discussed above), is placed in a basal clade with the two South Korean collections. Between the Vanuatu collections of *P.* aff. *semibulbosus* and *P.* cf. *haywardii*, the main superficial differences are that the Vanuatu *P.* cf. *haywardii* has a white cap with tan streaks and a cream stipe. Microscopic differences include *P.* aff. *semibulbosus* having larger spores, larger pleurocystidia, and larger more versiform and lageniform cheilocystidia. Pairwise analysis of overlapping ITS data shows that the sequence from *P.* cf. *haywardii* is 97.7–97.90 % similar to the Vanuatu collections of *P.* aff. *semibulbosus* (JAD 166 and JAD 197). Because of these features combined with molecular evidence it is preferred to maintain them as separate units until wider sampling and in-depth study can better define species limits. Undoubtedly, there is some overlap between the specimens and the size range of the microcharacters in the Vanuatu specimens is likely of taxonomic importance. Further studies including a new type designation, intensive re-examination of existing specimens, and additional molecular data are necessary in order to clearly delimit *P. semibulbosus* and others within this broad complex. For now, the Vanuatu specimens will be treated as *P.* aff. *semibulbosus*.

Pluteus velutinus Pradeep, Justo & Vrinda, Mycological Progress 11: 871 (2012) (Fig. 36)

Diagnosis:—*Pluteus velutinus* from Aneityum is characterized by a brown pruinose pileus with pulverulent patches exposing a white context, and a tan fibrillose stipe with a subbulbous base. Microcharacters include subglobose spores (6.5 × 5.5 µm), clavate cheilocystidia, clavate or fusoid-ventricose pleurocystidia, a trichohymeniderm pileipellis comprised of fusoid terminal cells containing brown pigment, similarly pigmented clavate caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 35 mm diam., hemispherical; surface pruinose or somewhat pearlescent, dry, finely areolate-reticulate with pulverulent patches exposing the underlying context; surface uniformly brown-toned (oac722–oac723). *Context* 1.5 mm thick, white. *Lamellae* free, somewhat subdistant with 2–3 tiers of lamellulae, regular, dark pinkish brown (oac659–oac660). *Stipe* 55 × 5 mm, central, terete, cylindrical over a subbulbous base, solid; surface pearlescent, dry, longitudinally fibrillose, overall tan (oac653–oac655). *Taste* indistinct. *Odor* indistinct.

Basidiospores (4–) 5–7 (–8) × (4–) 5–7 µm [x_m = 6.2 ± 0.82 × 5.8 ± 0.66 µm, Q = 1–1.33, Q_m = 1.07 ± 0.09, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 15–20 (–27) × 5–8 µm, clavate, 4-spored, hyaline, with a guttule, thin-walled, sterigmata 1.5–4 × 0.5–1 µm. *Basidioles* 10–20 × 5–8 µm, clavate, hyaline, with a guttule, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 32–80 × 8–25 µm, clavate to broadly clavate, fusoid to narrowly utriform or sphaeropedunculate, obtuse, hyaline, thin-walled. *Pleurocystidia* 38–96 × 10–55 µm, clavate to ovoid or fusoid-ventricose to narrowly utriform, obtuse, seldom truncate or rarely with a mucronate appendage (up to 8 µm long), one observed with a median constriction, hyaline, thin to rarely thick-walled especially in larger ovoid elements. *Pileipellis* a trichohymeniderm, composed of a majority of cells 80–200 × 8–16 µm, clavate to cylindro-clavate mixed with 28–75 × 8–14 µm lageniform to fusoid or occasionally globose, obtuse or seldom capitate, with brown plasmatic pigment or hyaline, non-incrusted, non-gelatinous, thin-walled. *Pileus trama* interwoven, composed of hyaline or occasionally with brown plasmatic pigment, non-gelatinous, thin-walled, cylindrical to inflated hyphae, 3–17 (–28) µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–24 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–24 µm diam.. *Caulocystidia* 25–48 (–80) × 8–20 µm, abundant, solitary to clustered, clavate to cylindro-clavate or seldom fusoid-ventricose, obtuse, with brown plasmatic pigment or hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary on decayed wood in subtropical montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum). Also known from Asia (Japan, India, Mongolia, Russia, South Siberia, Vietnam), Europe (Italy), U.S.A. (Hawaii).

Material examined:—VANUATU. Tafea Province: Aneityum, area around and within transect 11, 20°12.622′S, 169°47.578′E, elev. 294 m, 8 August 2017, coll. *J.A del Rosario & B.A. Perry*, *JAD 53* (HAY).

Notes:—The original description of *P. velutinus* Pradeep, Justo & Vrinda (2012: 871) is based on an Indian holotype and collections originating from Japan (Pradeep *et al.* 2012). Additional reports have extended the species' distribution to Brazil (Menolli *et al*. 2015c), Vietnam (Malysheva *et al*. 2020, 2023), across Russia (Malysheva *et al*. 2016), and to Italy and Slovenia (Ferisin & Dovana 2016, 2019). According to ITS data (MW018888, MW018907) in this study's phylogenetic analysis (Fig. 15b), the species may also occur in Hawaii, U.S.A..

The specimen from Aneityum matches well in comparison to previous descriptions of *P. velutinus*, but with some minor differences. The Vanuatu material diverges based on rarity of pleurocystidia with digitate apical projections (observed once) versus other descriptions that report this trait to be common. The absence of apical digitate projections on pleurocystidia appears to have been observed in recently described material from Vietnam by Malysheva *et al.* (2023), but they have also observed it as common in collected material from a previous study (Malysheva *et al.* 2020). However, this particular pleurocystidia ornamentation does not seem readily consistent based on line drawings from the protologue, as the Indian holotype lacks pleurocystidia with apical projections while the Japanese material's pleurocystidia are ornamented (Fig. 3 e2, Pradeep *et al*. 2012). According to the holotype description, the species is distinguished by this character, although they are rarer on the cheilocystidia and common on the pleurocystidia. Based on other reports of *P. velutinus* the frequency and variation of apical ornamentation does not appear to be only restricted to pleurocystidia, but occurs on other taxonomically informative structures, suggesting a high degree of morphological diversity within the species. The pileipellis terminal elements have been described as

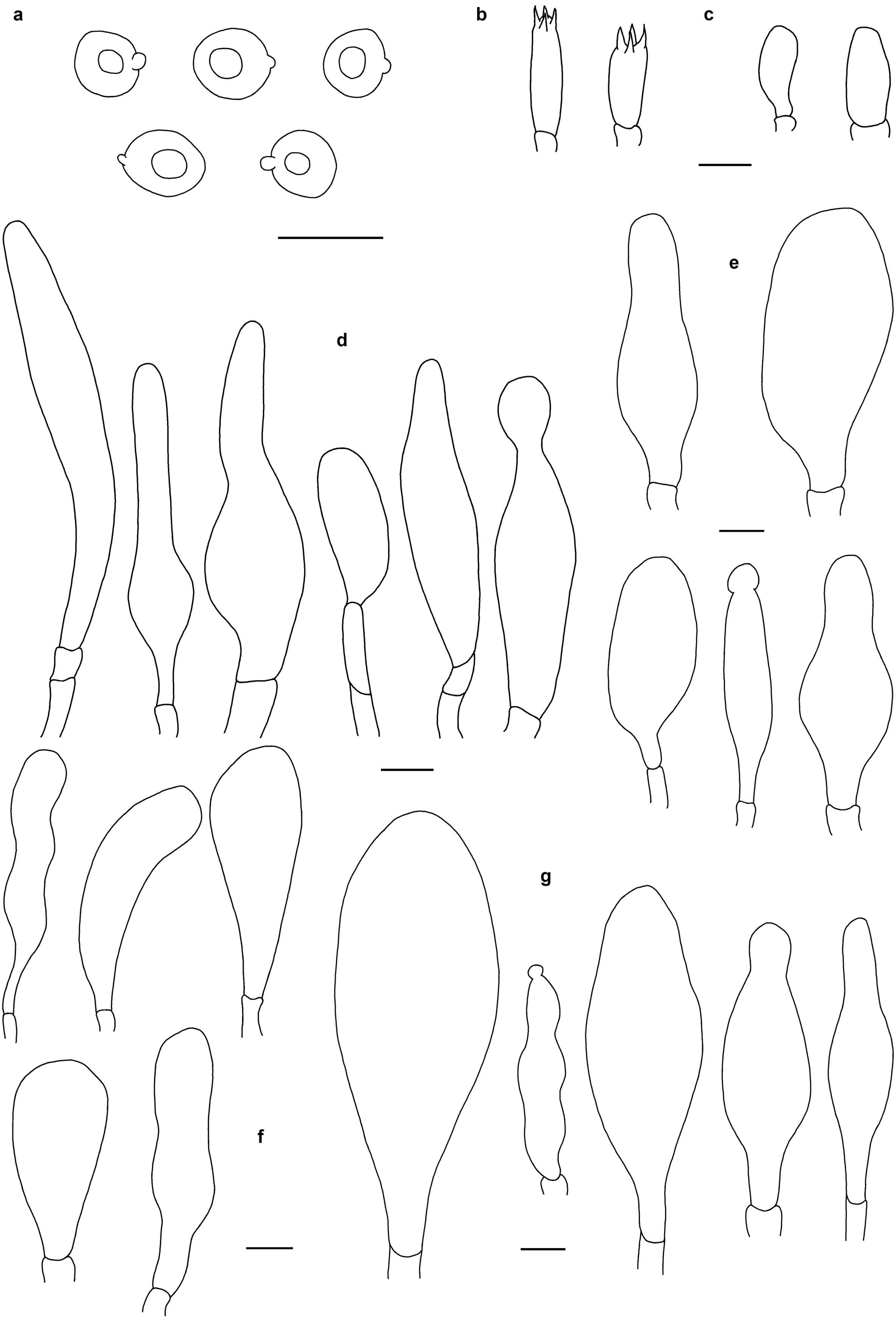

FIGURE 36. *Pluteus velutinus* a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Fig. 37a

FIGURE 37a–e. Maximum Likelihood phylogeny of sect. *Celluloderma* based on ITS sequence data (-lnL = 18618.671374). Sequences of specimens from Vanuatu are indicated in bold type. Stars indicate type specimens. Values separated by / refer to ML bootstrap proportions and Bayesian posterior probabilities. Only values greater than 70/0.70 are shown. Nodes receiving support values greater than 90/0.95 are highlighted in bold.

Fig. 37b

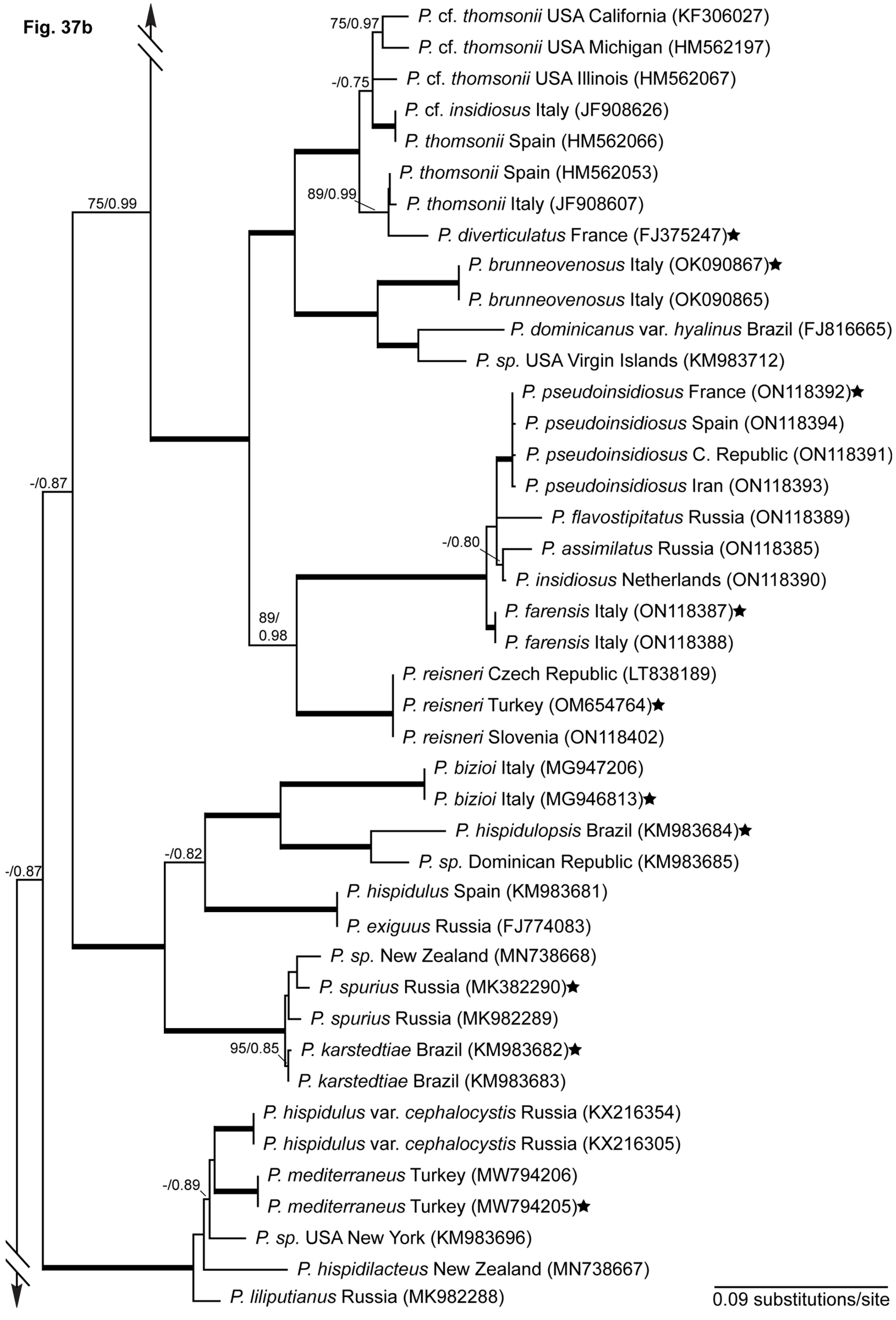

FIGURE 37. (Continued)

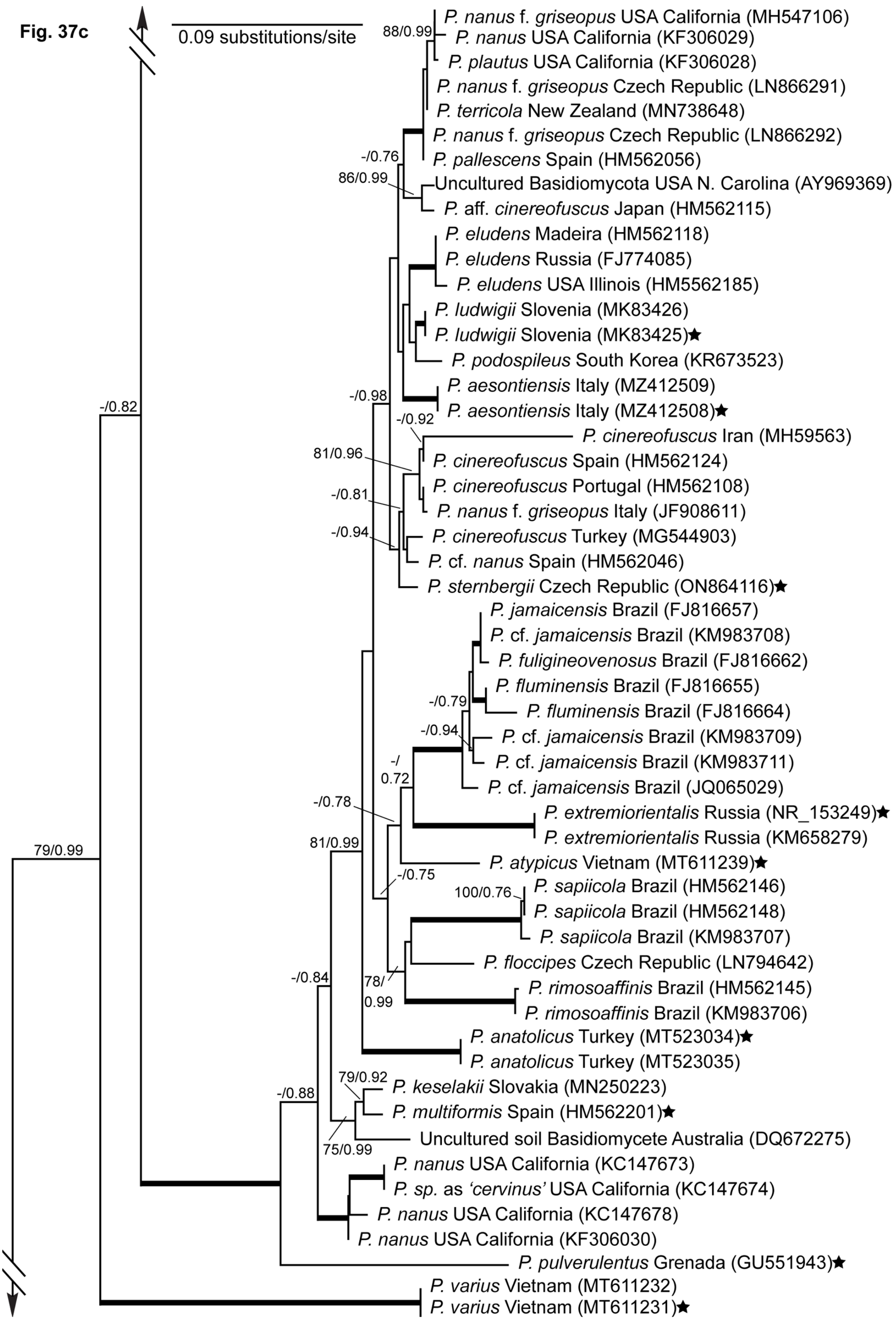

FIGURE 37. (Continued)

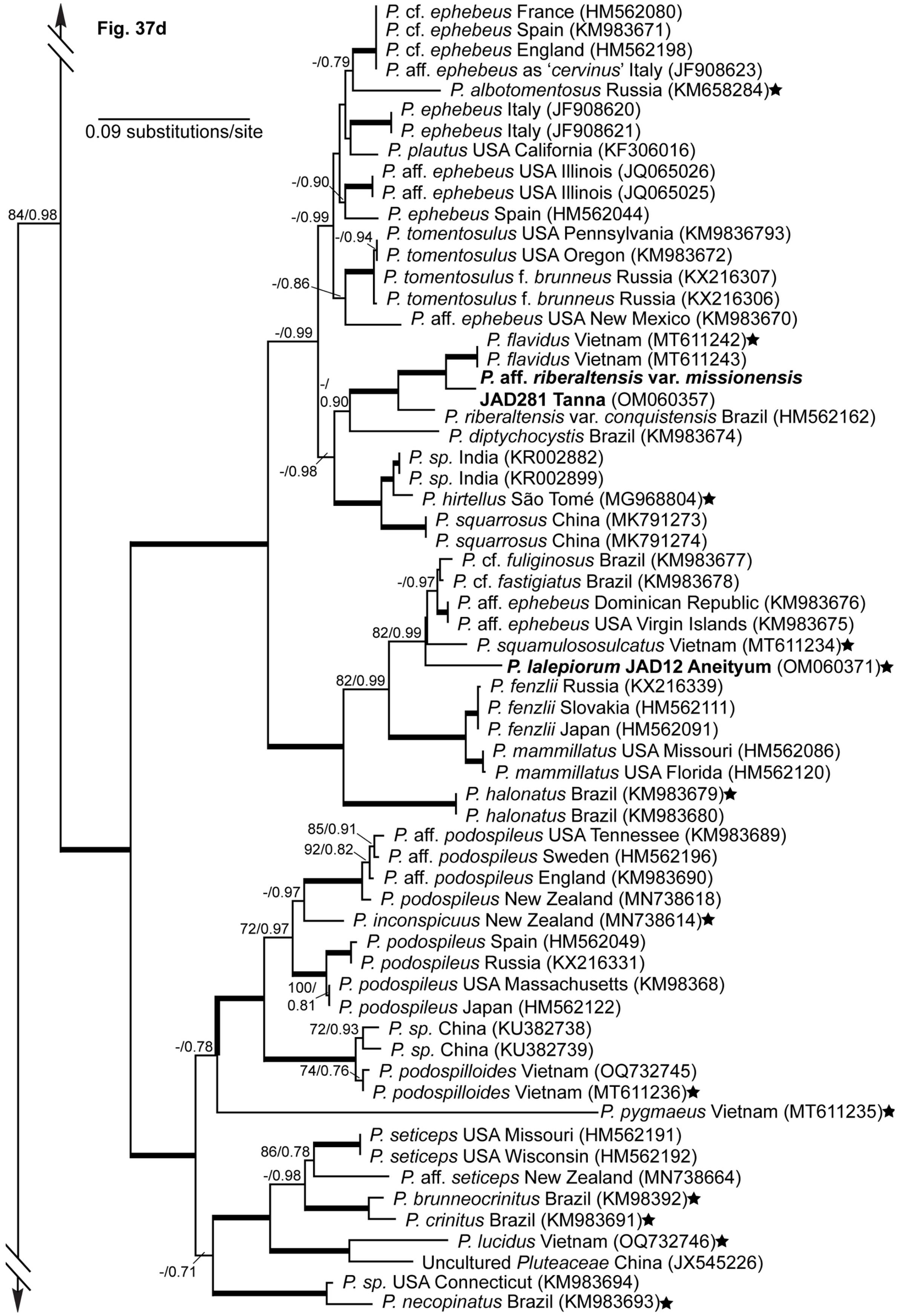

FIGURE 37. (Continued)

Fig. 37e

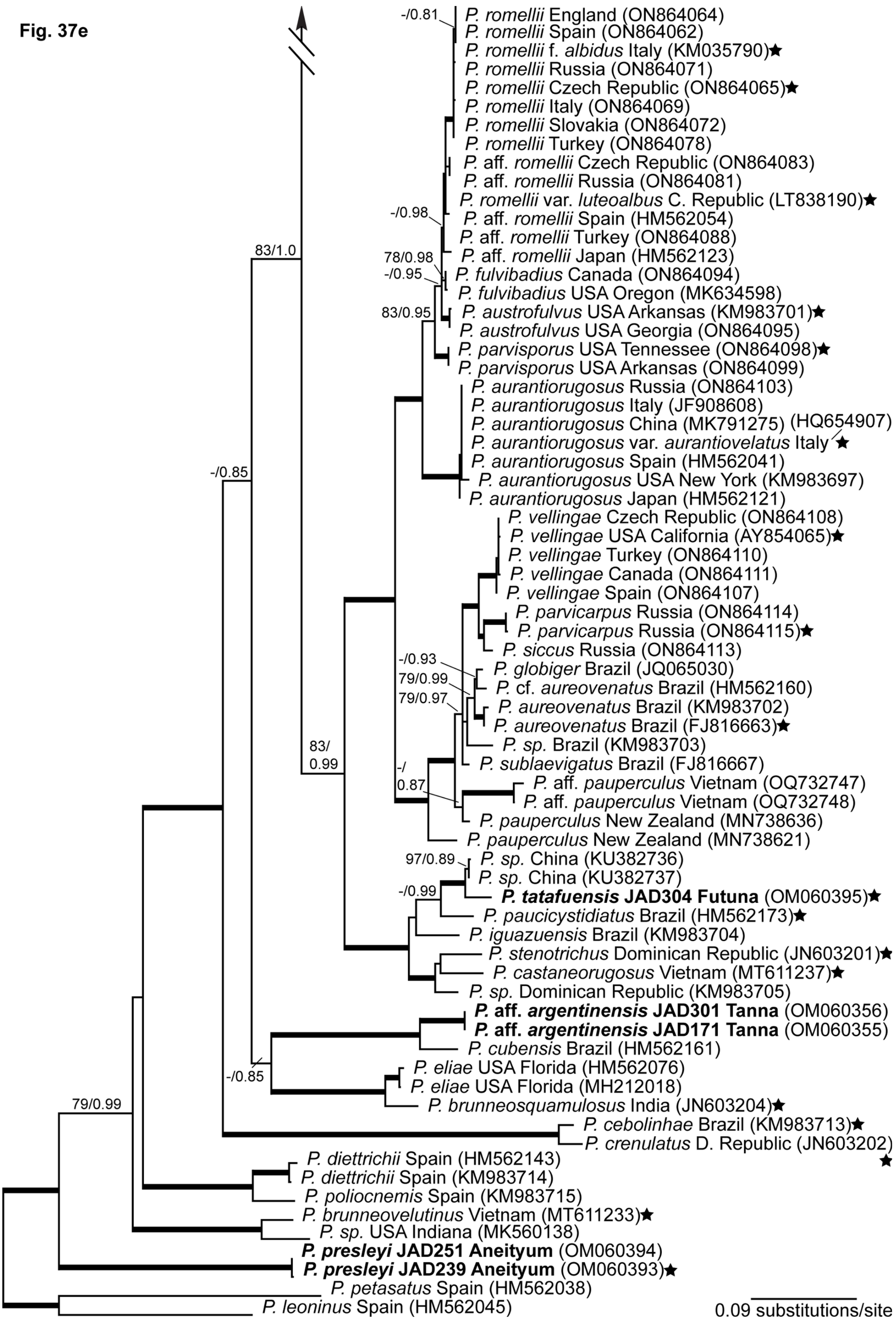

FIGURE 37. (Continued)

being irregularly shaped or having apical projections, as seen in material from Russia, Japan, and Italy, but less so in Brazilian, Indian, Vietnamese, or the Vanuatu material (Ferisin & Dovana 2016, Malysheva *et al*. 2016, 2020, 2023, Menolli *et al*. 2015c, Pradeep *et al*. 2012). A lesser emphasized cystidia character has been described as "undulating" (Menolli *et al*. 2015c) or "strangulated" (Ferisin & Dovana 2016) in caulocystidia of the Brazilian and Indian material, appearing as a median constriction in the Vanuatu specimen's caulocystidia and pleurocystidia, and occurring in the cheilocystidia and pileipellis terminal cells of the Brazilian and Russian material respectively. Pleurocystidia with pale brown plasmatic pigment have been reported from Brazilian, Russian, and Vietnamese material, but not in the others nor the Vanuatu specimen. The Vanuatu specimen does share the presence of brown plasmatic pigment in caulocystidia and pileipellis hyphae, and this does appear consistent with all other accounts. Spore size and shape appears to vary across specimens, as the Vanuatu and Russian material appear to have more globose/subglobose spores while the others are more ellipsoid.

Phylogenetic analysis of ITS data (Fig. 15b) places the Vanuatu specimen in a weakly supported clade (BS 69 %, PP 0.93) with Vietnamese specimens of *P.* cf. *velutinus* (MT611241, MT611242) that subtends the other *P. velutinus* sequences within the stronger supported clade encompassing them. Pairwise analysis of overlapping regions of the ITS data show the Vietnamese specimen is 99.29 % similar to the Vanuatu sequence, whereas the Indian holotype is 97.26 % similar and the remaining sequences are 97.35 % similar. Malysheva *et al.* (2020, 2023) did not firmly identify their material due to it being phylogenetically different from the other *P. velutinus* specimens, and not having additional material from the Indochinese Peninsula region for comparison to propose a separate species. Malysheva *et al.* considered their material close to the Russian specimens based on spore size, but differing based on paler pileus color and cheilocystidia pigmentation. As the Vanuatu specimen is phylogentically closer to the Vietnamese specimen, it is worth noting that although spore size is similar to both the Russian and Vietnamese material (not typically exceeding a length of 7.5 µm according to Malysheva *et al.*) the pigmentation is absent in the cheilocystidia, and this character may not be enough to warrant a separate species.

Early reports of *P. velutinus* considered it to be a pantropical species (Menolli *et al*. 2015c) with the Japanese material being an exception, until additional records from temperate Italy and Russia surfaced (Ferisin & Dovana 2016, Malysheva *et al*. 2016). The species is better known now to be cosmopolitan as it has been found to occur in tropical, temperate, and subtropical climates across multiple continents and both hemispheres. Pradeep *et al.* (2012) and Menolli *et al*. (2015c) note the difficulty in explaining this distribution pattern or distinguishing a center of origin for the species. This raises the question of how highly variable climates may have influenced the establishment of the species. Menolli *et al*. (2015c) compared climatic data of the areas during the time of fructification for each collection among Japan, Brazil, and India and found similar relative humidity and slightly similar average temperatures between the Japanese and Indian collections, while the Brazilian material was collected during a tropical rainy season with much warmer temperatures. Similarly, the Vanuatu specimen was collected during the dry season of a subtropical climate country. The case for a new record from isolated islands such as Vanuatu may further complicate things or provide a stronger case for anthropic dispersal.

***Pluteus* section *Celluloderma* Fayod**

Pluteus* aff. *argentinensis Singer, Lloydia 21: 230 (1958) (Figs. 38, 39)

Diagnosis:—*Pluteus* aff. *argentinensis* from Tanna is characterized by a pileus with a fuliginous longitudinally-striate fibrillose surface and dark gray disc surface, and a gray longitudinally-striate fibrillose stipe with basal tan floccules. Microcharacters include subglobose basidiospores (6.4 × 6.1 µm), fusoid-ventricose cheilocystidia and pleurocystidia sometimes covered apically or entirely with mucilage, a cutis pileipellis with suberect dark brown pigmented fusoid terminal elements, and an absence of caulocystidia and clamp connections.

Description:—*Pileus* 55–75 mm diam., convex expanding to plano-convex with a slight to deep (8–10 mm) central depression, margin slightly sulcate, eroded; surface pellucid-striate towards margin, dull elsewhere, dry, strongly longitudinally appressed-fibrillose or silky; fibrils fuliginous to ash brown (oac624–oac627) densest and darkest at disc fading towards margin, underlying surface pallid tan. *Context* up to 2 mm thick, colored pallid tan (oac661–oac662). *Lamellae* free, crowded with 3–4 tiers of lamellulae, thin, white to cream-white. *Stipe* 52–80 × 5–8 mm, central, terete, cylindrical sometimes arising from a white tomentum, hollow; surface pearlescent, dry, silky, off-white to gray overall, context off-white. *Odor* indistinct. *Taste* indistinct.

FIGURE 38. Basidiomes of *Pluteus* aff. *argentinensis* (JAD 301). Scale bar = 10 mm. Photos by: Brian Perry.

Basidiospores 5–7 (–8) × 5–7 µm, [x_{mr} = 6.36–6.5 × 6.02–6.18 µm, x_{mm} = 6.43 ± 0.09 × 6.1 ± 0.11 µm, Q = 1–1.2, Q_{mr} =1.05–1.06, Q_{mm} = 1.05 ± 0.01, n = 50, s = 2], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 24–38 (–50) × 6–10 µm, clavate to cylindro-clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 20–25 × 5–8 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 25–80 × 10–24 µm, clavate to broadly clavate or fusoid-ventricose to narrowly utriform, obtuse or rarely umbonate, often with apical mucilage sometimes adhering spores that obscure view, hyaline, thin-walled. *Pleurocystidia* 42–100 (–140) × 12–42 (–50) µm, scattered, broadly clavate to fusoid-ventricose, narrowly lageniform, or sometimes broadly sphaeropedunculate, obtuse, some with apical or completely enveloped in mucilage sometimes with adhering spores that obscure view, hyaline, thin-walled. *Pileipellis* a cutis of repent hyphae, composed of dark brown plasmatic pigment or hyaline, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 4–16 µm diam.; terminal elements 40–90 (–155) × 8–20 (–35) µm, mostly repent becoming suberect in fascicles especially at the disc, cylindro-clavate to fusiform, obtuse or seldom subcapitate. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 4–22 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 5–16 µm diam.. *Stipitipellis* a cutis, composed of hyaline or infrequently with pale brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled hyphae, 8–16 µm diam.. *Caulocystidia* absent. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on rotted wood in subtropical coastal mixed-use agro tree garden and secondary littoral broadleaf forest containing *Annona muricata* (*Annonaceae*), *Artocarpus altilis* (*Moraceae*)*,* *Barringtonia asiatica* (*Lecythidaceae*), *Cocos nucifera* (*Arecaceae*), *Cordia dichotoma* (*Boraginaceae*), *Euodia hortensis* (*Rutaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*)*,* and *Musa sp.* (*Musaceae*) and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Yanemari, 19°28.511′S, 169°25.616′E, elev. 146 m, 30 August 2018, coll. *J.A. del Rosario, JAD 171* (HAY); Tanna, Port Resolution near Tanna Horizon Bungalow, 19°31.391′S, 169°30.371′E, elev. 7 m, 16 August 2019, coll. *J.A. del Rosario, M. Wahe & G.M. Plunkett, JAD 301* (HAY).

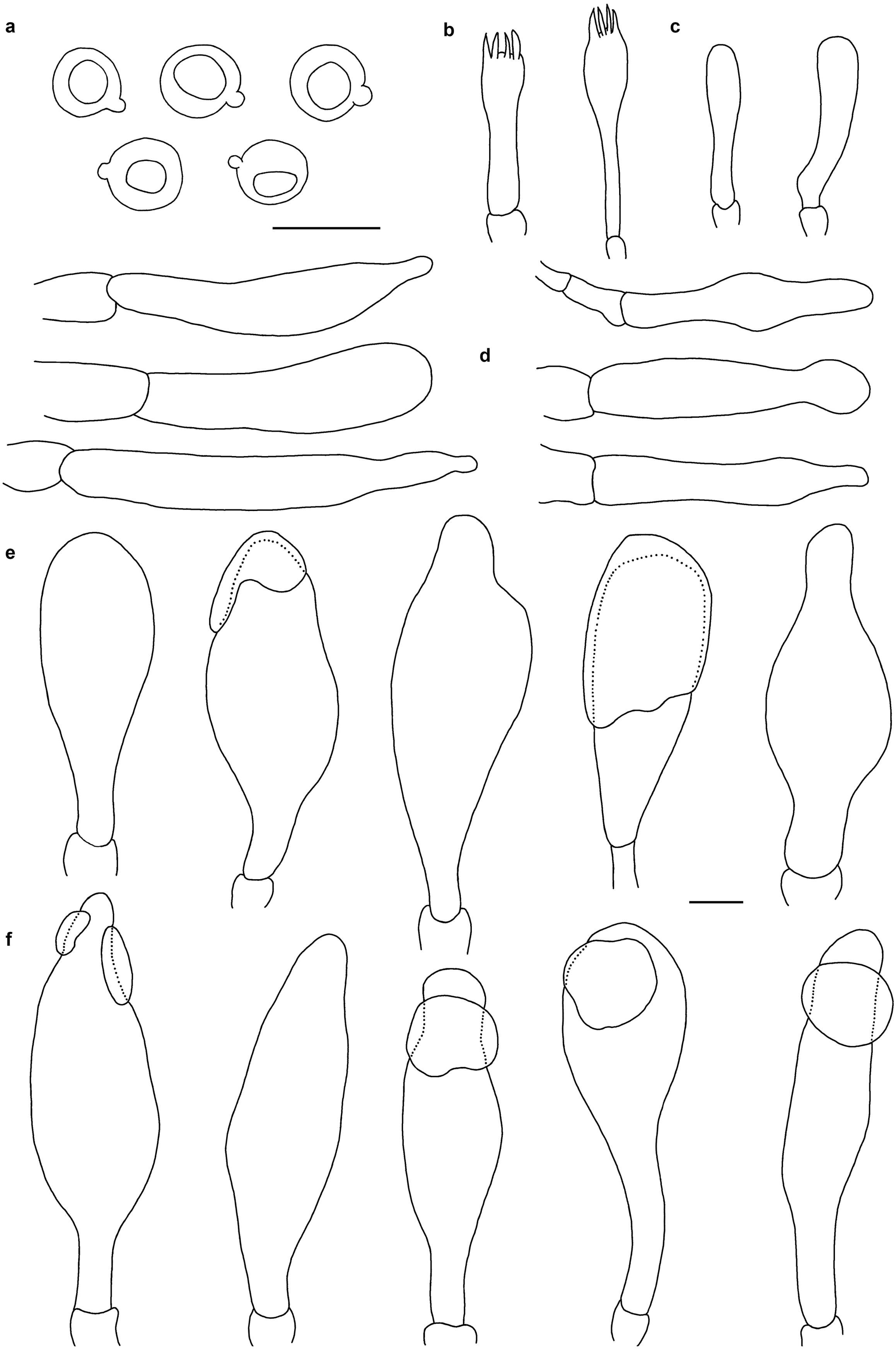

FIGURE 39. *Pluteus* aff. *argentinensis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Notes:—*Pluteus argentinensis* Singer (1958: 230) was originally described by Singer based on two collections from Argentina, one (Singer T 929) was initially identified as *P. plautus* (Singer & Digilio 1952) and the other (Singer T 2139) was designated as the holotype (Singer 1958). Since then, *P. argentinensis* has been reported from Mexico (Rodríguez & Guzmán-Dávalos 1999, 2001) and Brazil (Dias & Cortez 2013). According to Dias and Cortez, a report by Wright and Albertó (2002) from Buenos Aires may be misidentified based on the presence of clamp connections in that material.

The Vanuatu specimens fit well within previous descriptions of *P. argentinensis*, however there are some discrepancies. Macroscopically, the Vanuatu material matches the holotype description, except that the pileus size is significantly larger than the type (25–35 mm diam.) and slightly larger compared to the other reports. In the original description, Singer described the pleurocystidia and cheilocystidia together by generalizing the size as "34–68 × 14–25 µm, mostly 42–54 × 14–19 µm" and shape "ventricose below and ampullaceous or mucronate above", and differentiated the cystidia on the lamellar edge by "some ventricose-vesiculose or ampullaceous-subcapitate" (Singer 1958). Singer also observed the presence of an inconspicuous resinous incrustation on these cystidia. Both lamellar cystidia in the Vanuatu material fit these criteria, except for being slightly larger. The presence of any type of incrustation/mucilage on cystidia was not reported from either the Mexican or the Brazilian material (Rodríguez & Guzmán-Dávalos 1999, 2001, Dias & Cortez 2013). Compared to the Vanuatu collections, the Mexican material would be closer in pleurocystidia and cheilocystidia shape variety (Rodríguez & Guzmán-Dávalos 1999), while the Brazilian material is similar in size, but the pleurocystidia were described only as ventricose and lack lageniform or clavate elements (Dias & Cortez 2013). The orientation of the pileipellis is not clearly categorized in the original description of *P. argentinensis*, and Singer only provided measurements, an illustration and emphasized the terminal elements as "fusoid to ventricose with strongly attenuate apex" (Singer 1958). Singer's collection T 929, originally identified as *P. plautus*, described the pileipellis as a trichoderm with the majority of the elements depressed (Singer & Digilio 1952). Pileipellis interpretation has varied in concepts of *P. argentinensis* as Rodríguez and Guzmán-Dávalos (1999) described their material as a trichoderm and suberect, while Dias and Cortez described "filamentous and elongated hyphae" providing a photo similar to a repent cutis with terminal elements appearing as ascending (Fig. 4, Dias & Cortez 2013). Rodríguez and Guzmán-Dávalos did re-examine a portion of the holotype, but due to the poor condition of the material were unable to measure elements of the pileipellis and could only provide spore measurements (Rodríguez & Guzmán-Dávalos 2001). Singer placed *P. argentinensis* in his morphological stirps *Fuliginosus*, which he characterized by the pileipellis terminal cells being subacute or acuminate-subacute and part of a trichoderm (Singer 1958, 1986). Regarding the Vanuatu material, the pileipellis is overall a cutis with the terminal elements sometimes turning to erect clusters with the shape and size of the terminal elements fitting well with all previous described material, but the ambiguity of the pileipellis arrangement from the protologue requires clarity. Singer did not originally describe the shape of the spores, but the Vanuatu material matches in size and matches the shape and size in the other material. The absence of caulocystidia was noted in the Mexican material (Rodríguez & Guzmán-Dávalos 1999), but other authors omitted its presence or absence. Overall, the Vanuatu specimen's pleurocystidia and cheilocystidia closely resemble those in the Mexican material, while the Brazilian material lacks clavate cystidia. Both the Mexican and Brazilian material lack mucilage/incrustation on their cystidia, but this character is shared with the holotype according to the original description. Interestingly, the accompanying picture of the Brazilian specimen bears a resemblance to the Vanuatu material (Fig. 1, Dias & Cortez 2013), and the pileipellis shares some similarity as well. The slight difference in cystidia shape from the Brazilian material may be just minor variation and both might be the same species, but molecular data is unavailable for further confirmation. Regardless, clarification of pileipellis arrangement and molecular sampling would be preferred to confirm this material as *P. argentinensis*. Observations of the presence of mucilage/incrustation and the arrangement of the pileipellis in the other material would also be necessary to confirm their identities and strengthen the concept of *P. argentinensis*. In agreement with Menolli and Capelari (2016), a revision of the holotype is necessary to refine the concept of *P. argentinensis* and ideally a re-examination of these collections would unite them.

A number of species from Singer's morphological stirps (Singer 1986), such as *Diptychocystis, Fuliginosus*, or *Spilopus*, resemble the Vanuatu specimens, but their micromorphological characters can subtly distinguish them. *Pluteus diptychocystis* Singer (1954: 123) was described from Argentina (Singer 1954) and has been reported from Chile (Singer 1969) and Brazil (Menolli & Capelari 2016). Macromorphologically, *P. diptychocystis* differs in having a tomentose to squamulose pileus and micromorphologically differs by having slightly larger ellipsoid spores (6.8–9.6 × 5.3–7 µm), more lageniform or "ampullaceous with broad neck" and less cylindro-clavate pleurocystidia and cheilocystidia, and more apically rounded pileipellis terminal elements (Singer 1954, 1956, 1958, Menolli & Capelari 2016). *Pluteus striatocystis* Pegler (1977: 268) was originally described from east Africa (Pegler 1977) and reported from re-identified material from Brazil (Menolli *et al.* 2015a). This species primarily differs micromorphologically with more ellipsoid spores, smaller pleurocystidia (40–70 × 15–25 µm) with a characteristic distinct striate collar, smaller cheilocystidia (36–46 × 11.2–20 µm) absent of mucilage/incrustation, and longer pileipellis terminal elements (–214 × 17.5 µm) (Pegler 1977, Menolli *et al*. 2015a). The Bolivian *P. pluvialis* Singer (1958: 234) may be interpreted as similar by sharing a pubescent "margined" bulbous base, although the Vanuatu material here is described as cylindrical with a white tomentum (Singer 1958). Regardless, *P. pluvialis* would differ through being smaller in stature, having granular punctations on the pileus, slightly smaller cheilocystidia (40–55 × 7–21 µm), smaller pleurocystidia, and larger pileipellis elements (82–165 × 16.5–19.5 µm) with more attenuate apices.

Pluteus cubensis (Murrill) Dennis (1953: 155) is a morphologically variable species distributed throughout the tropical Americas (Murrill 1911, Dennis 1953, Singer 1956, 1958, Pegler 1983, 1997, Menolli *et al.* 2015a). Phylogenetic analysis of ITS data (Fig. 37e) places the Vanuatu *P.* aff. *argentinensis* in a well-supported sister relationship (BS 100 %, PP 1.0) to a Brazilian specimen of *P. cubensis* (HM562161). A recent re-examination of the type specimen of *P. cubensis* by Menolli *et al.* (2015a) resulted only in the measurement of two cheilocystidia and ellipsoid basidiospores, and they were unable to report the presence of granular incrustation or nodulose excrescences that were observed by Singer (Singer 1956, 1958). A survey of the literature of *P. cubensis* leaves it uncertain if Singer's cystidia incrustation observations should be included in the current concept of this species, and its absence may be taxonomically informative. Therefore, *P. cubensis* can be distinguished from the Vanuatu specimen in having more ellipsoid basidiospores, smaller pleurocystidia (43–55 [–77] × ([12.5–] 13.7–20 [–22] µm), smaller cheilocystidia ([20–] 31–47 [–56] × [8.7–] 10.0–21 [–25]) lacking mucilage/incrustation, and more rounded to obtuse pileipellis terminal elements (Singer 1956, 1958, Pegler 1983a, Menolli *et al.* 2015a). The two taxa are phylogenetically placed on a branch sister to *P. brunneosquamulosus* Pradeep & Vrinda (2012: 870) and *P. eliae* Singer (1958: 290), but this is unsupported. The Indian *P. brunneosquamulosus* and Bolivian *P. eliae* are completely different from the Vanuatu specimen due to paler brown, non-fuliginous basidiomes and an epithelioid or hymeniderm type pileipellis (Pradeep *et al.* 2012; Singer 1958).

Pluteus eugraptoides J.A. del Rosario & B.A. Perry, *sp. nov*. (Figs. 40, 41)

MycoBank no:—854226

Holotype:—VANUATU. Tafea Province: Tanna, Yanemari, 19°38.294′S, 169°25.568′E, elev. 146 m, 30 August 2018, coll. *J.A. del Rosario*, *JAD 168* (HAY).

FIGURE 40. Basidiomes of *Pluteus eugraptoides* (JAD 168 holotype). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

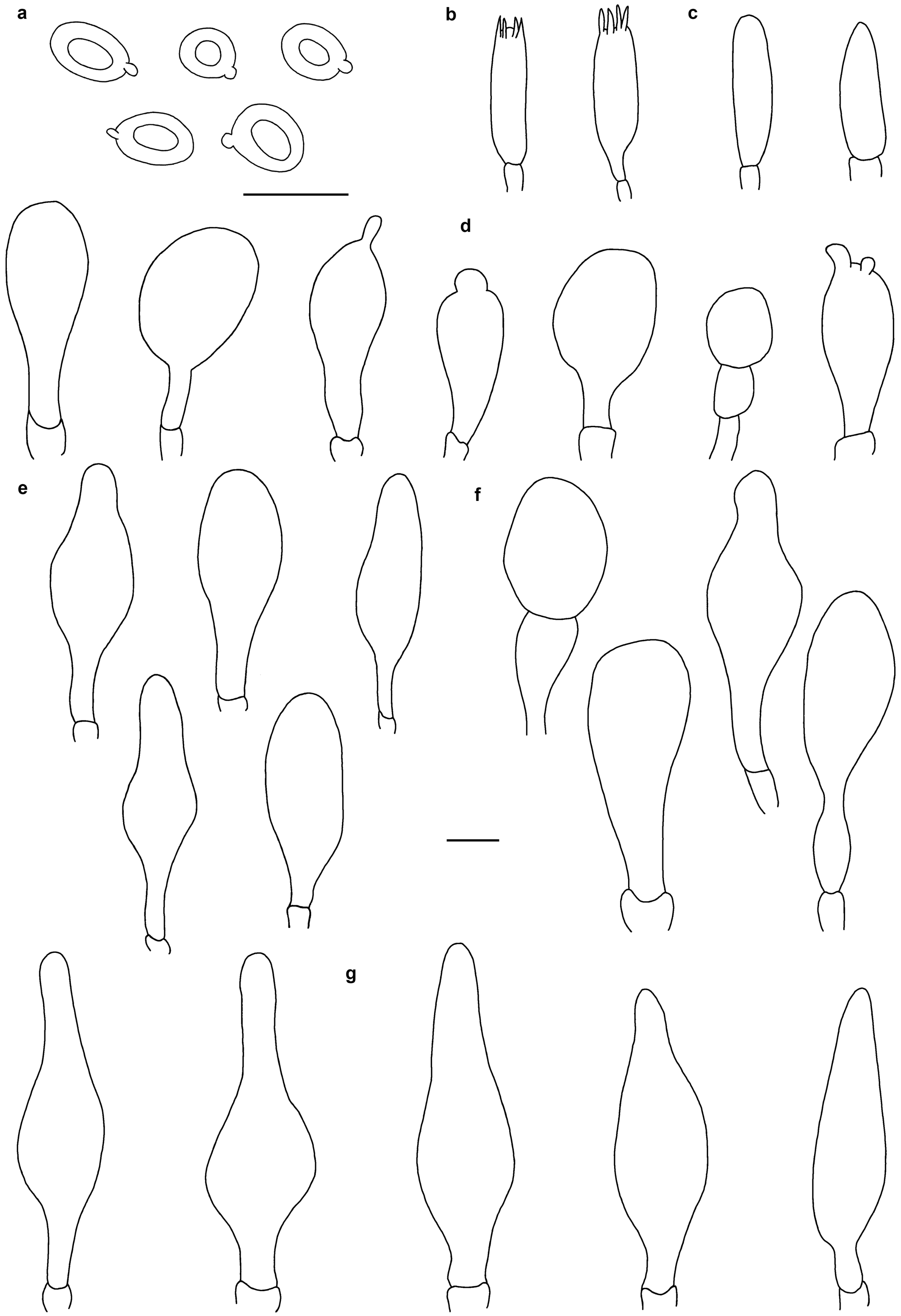

FIGURE 41. *Pluteus eugraptoides*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Etymology:—refers to morphological similarities to *P. eugraptus*.

Diagnosis:—*Pluteus eugraptoides* from Tanna is characterized by a pale brown hygrophanous pileus with maroon-brown veins radiating from the disc, and a gray stipe with a subbulbous base. Microcharacteristics include subglobose spores (6.7 × 5.5 µm), fusoid-ventricose, cheilocystidia and pleurocystidia, a euhymeniderm pileipellis composed of brown pigmented clavate or sphaeropedunculate, sometimes mucronate cells, clavate or fusoid-ventricose caulocystidia, and an absence of clamp connections. *Pluteus eugraptoides* closely resembles *P. eugraptus* (Berkeley & Broome) Saccardo (1887: 678), but fundamentally differs by lacking marginate lamellae.

Description:—*Pileus* 15–35 mm diam., hemispherical to plano-convex and papillate; surface dull becoming pulverulent-pellucid-striate, dry, glabrous, disc venose-rugulose, radiating up to one-half of pileus towards margin; veins/wrinkles maroon-brown (oac621–oac623) or concolorous with the surface, surface dull brown (oac722) fading to pale tan (oac675–oac676) towards the margin. *Context* 3 mm thick, pale tan. *Lamellae* free, close with 2–3 tiers of lamellulae, slightly thick (up to 2 mm thick), tan (oac675–oac676). *Stipe* 25–35 × 3–5 mm, central, terete, cylindrical over a subbulbous base, hollow; surface dull, dry, silky, gray to pale tan (oac675–676), context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 5–7 (–8) × 5–6 µm [x_m = 6.71 ± 0.79 × 5.51 ± 0.49 µm, Q = 1–1.6, Q_m = 1.22 ± 0.15, n = 50, s = 1], subglobose or seldom broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 22–28 × 5–8 µm, clavate to cylindro-clavate, 4-spored or rarely 2-spored, hyaline, guttulate, thin-walled, sterigmata 1.5–3 × 0.5–1 µm. *Basidioles* 16–28 × 5–8 µm, clavate to cylindro-clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 32–46 (–56) × 8–14 (–20) µm, abundant, often clustered, clavate or occasionally lageniform to fusoid-ventricose, obtuse, hyaline, thin-walled. *Pleurocystidia* (25–) 40–65 (–72) × 12–20 µm, lageniform to fusoid-ventricose, obtuse, hyaline, thin-walled. *Pileipellis* a euhymeniderm to epithelioid hymeniderm, composed of a majority of cells 25–50 × 10–22 µm, clavate to sphaeropedunculate, obtuse, sometimes mucronate (up to 5 µm long) or rarely nodulose-capitate with 1–2 nodules, with brown plasmatic pigment or sometimes hyaline, non-incrusted, non-gelatinous, thin-walled. *Pileus trama* interwoven, composed of hyaline, non-incrusted, non-gelatinous, thin-walled, clavate to inflated hyphae, 4–25 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 5–14 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 5–15 µm diam.. *Caulocystidia* 30–70 × 13–25 µm, clustered to solitary, fusoid-ventricose to clavate, obtuse, hyaline or with brown plasmatic pigment, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on rotted wood in subtropical lowland mixed-use agro tree garden and secondary broadleaf rainforest containing *Bischofia javanica* (*Phyllanthaceae*), *Burckella obovata* (*Sapotaceae*), *Claoxylon gillisonii* (*Euphorbiaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Didymocheton spp.* (*Meliaceae*), *Ficus spp.* (*Moraceae*), *Garcinia pseudoguttifera* (*Clusiaceae*), *Homolanthus nutans* (*Euphorbiaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Syzygium nomoa* (*Myrtaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Yanemari, 19°38.294′S, 169°25.568′E, elev. 146 m, 30 August 2018, coll. *J.A. del Rosario, JAD 168* (HAY).

Notes:—*Pluteus eugraptoides* has some macroscopic features similar to multiple species, however there are microscopic differences. *Pluteus variipes* Singer (1956: 218) was collected from Argentina (Horak 1964, Singer 1956, 1958) and Bolivia (Singer 1956, 1958) and has a similarly colored pileus, but is overall non-venose, has smaller spores and slightly larger pleurocystidia (34.7–67 × 16–37.5 µm). The Mexican species *P. neotropicalis* Rodríguez-Alcántar (2008: 274) is also superficially similar, but differs in having slender fusoid cheilocystidia with a long cylindrical projection, narrow subcylindrical pleurocystidia, and narrow fusoid pileipellis elements (Rodríguez *et al.* 2008). *Pluteus chusqueicola* Horak (1964: 180) from Argentina is similar in stature, and shares capitate/mammillate pileipellis elements, but these cells tend to have slightly thickened walls and this species also has slightly larger pleurocystidia (60–75 × 16–30 µm) (Horak 1964).

Pluteus eugraptus is a species originally described from Sri Lanka and later reported from Argentina (Singer 1956), Bolivia (Singer 1958), and Tanzania (Pegler 1977). The type specimen was re-examined (Justo *et al*. 2011a) and a collection from Japan (TNSF 12042), was identified as *P*. cf. *eugraptus* due to having slightly longer pleurocystidia and cheilocystidia than the holotype, and the lack of additional topotypical material for morphological and molecular comparison. The Japanese material of *P*. cf. *eugraptus* differs from the Vanuatu specimen by having longer pleurocystidia and cheilocystidia, pigments in most cheilocystidia and some pleurocystidia, and a lack of caulocystidia. Phylogenetic analysis of ITS data (Fig. 37a) places this specimen sister to the Vanuatu material, but with moderate support (BS 74 %, PP 0.98). Compared to the Vanuatu material, *P. eugraptus* primarily differs by distinct marginate lamellae, slightly shorter pleurocystidia and cheilocystidia, brown pigmented cheilocystidia, lacking a mucronate-nodulose pileipellis, and according to the type re-examination and other studies, an absence of caulocystidia (Singer 1956, Pegler 1977, Justo *et al.* 2011a). The lack of pigments on the lamellar edge, pileipellis with apical ornamentation, and presence of caulocystidia clearly separate the Vanuatu material from *P*. *eugraptus* and the Japanese *P*. cf. *eugraptus*, as well as being molecularly distinct from the latter. In addition, a closely related species in *P. pseudeugraptus* Horak (1967: 187) of Argentina is microscopically close with similarly shaped cheilocystidia and pleurocystidia, however this species was not reported with caulocystidia, has slightly wider pleurocystidia, pigmented cheilocystidia, a unicolored darker brown pileus, and marginate lamellae (Horak 1964).

Pluteus eugraptoides appears to share a relationship with *P. phlebophorus* (Ditmar) Kummer (1871: 98) and its allies, which is a taxonomically difficult group due to a high degree of morphological variability and the absence of type specimens. Phylogenetic analysis (Fig. 38a) places the Vanuatu specimen within the *chrysophlebius*/*phlebophorus* clade *sensu* Justo *et al*. (2011b). Based on current knowledge of *P. phlebophorus* the species appears to have a widespread temperate distribution throughout Eurasia and the northeastern United States and is otherwise morphologically distinct in having larger pleurocystidia and cheilocystidia, and lacking a mucronate-capitate pileipellis (Breitenbach & Kränzlin 1995, Homola 1972, Minnis & Sundberg 2010, Orton 1986). *Pluteus hendersoniensis* Singer (1989: 793) is one of the few *Pluteus spp.* reported from the South Pacific, being from Henderson Island (Pitcairn Islands), and exhibits close features comparable to members of the *chrysophlebius*/*phlebophorus* clade and the Vanuatu specimen (Singer 1989). Compared to *P. eugraptoides*, the pileus color and ornamentation of *P. hendersoniensis* is similar, but differs based on the white stipe and smaller stature (pileus 7.5–15 mm, stipe 11 × 0.5 mm). Additionally, the terminal elements of the pileipellis are non-mucronate and significantly smaller (20–30 × 11.5–25 µm), and both cheilocystidia and pleurocystidia are much smaller compared to the Vanuatu material, which Singer described as undifferentiated in size and the same as that of the pileipellis (Singer 1989).

Pluteus lalepiorum J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 42, 43)
MycoBank no:—854227

Holotype:—VANUATU. Tafea Province: Aneityum, trail through Antowojon area, 20°13.142′S, 169°47.788′E, elev. 119 m, 28 July 2017, coll. *J.A. del Rosario & B.A. Perry, JAD 12* (HAY).

FIGURE 42. Basidiomes of *Pluteus lalepiorum* (JAD 12 holotype). Scale bar = 10 mm. Photo by: Brian Perry.

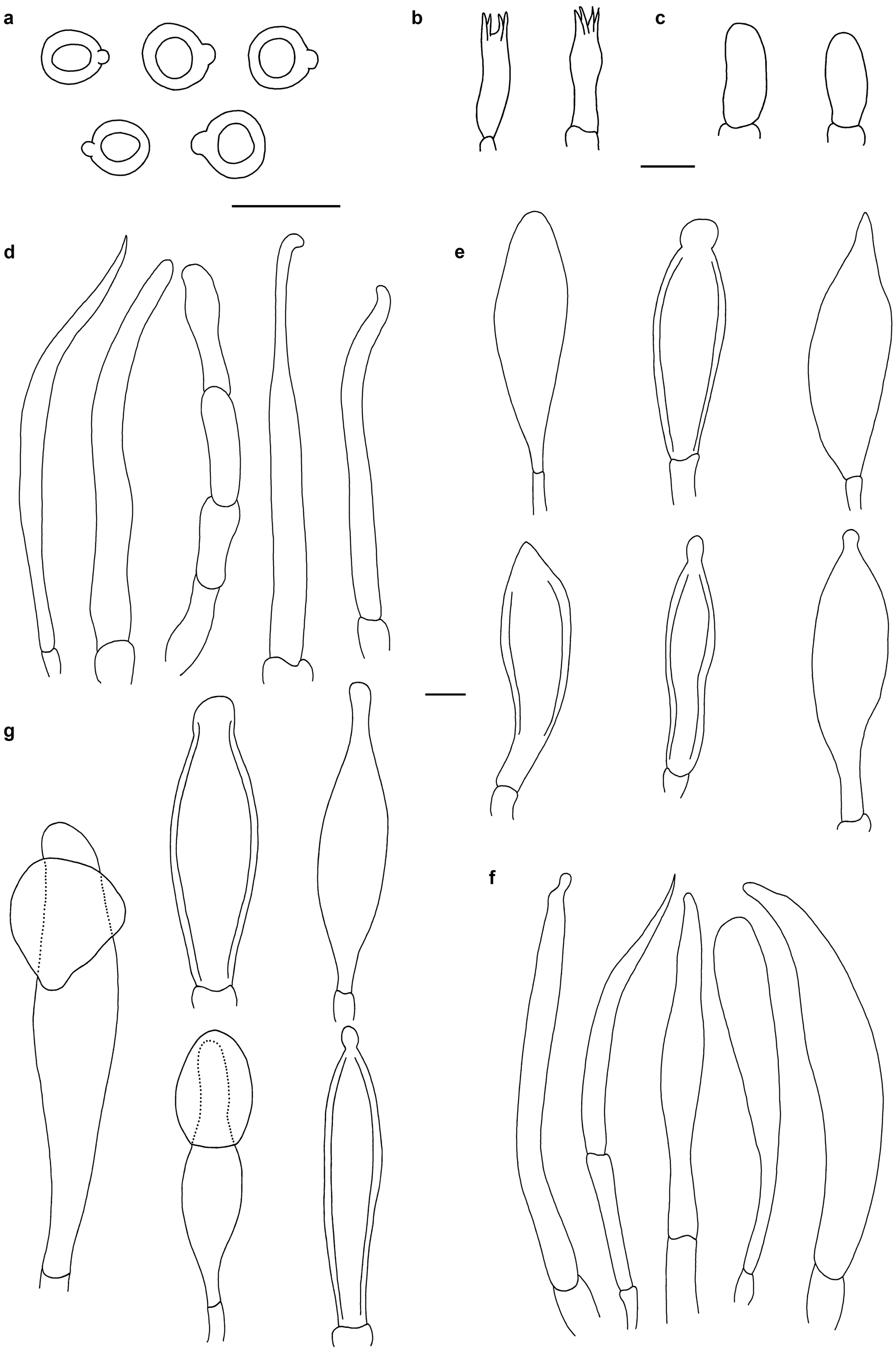

FIGURE 43. *Pluteus lalepiorum*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Etymology:—Named in honor of the Lalep family and for their contributions of the language and natural knowledge of Aneityum to the Plants mo Pipol blong Vanuatu project. In memory of Titya Kelly Lalep, who was one of the earliest contributors.

Diagnosis:—*Pluteus lalepiorum* from Aneityum is characterized by a hygrophanous, cream colored pileus with sooty brown floccules at the disc and a white stipe typically with similar floccules towards the base. Microcharacters include subglobose basidiospores (6.1 × 5.5 µm), fusoid-ventricose thick-walled cheilocystidia and pleurocystidia with mucilage coating some pleurocystidia, a cutis pileipellis with fragmented erect filiform brown pigmented terminal elements, similarly shaped and pigmented caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 40–45 mm diam., hemispherical to plano-convex with an umbo, some slightly centrally depressed, margin entire or undulate; surface dull turning pellucid-striate at margin, hygrophanous, appressed-fibrillose turning glabrous at margin, disc finely flocculose; floccules and fibrils sooty brown (oac778–oac780) dense at disc, diminishing towards margin, fibrils turning cream to off-white with minute sooty brown streaks, surface pale off-white. *Context* 5 mm thick, white to off-white. *Lamellae* free, crowded with 3 tiers of lamellulae, thin, pallid tan to pale pink (oac709–oac711). *Stipe* 25–40 × 2.5–4 mm, central, terete, cylindrical over a bulbous base, solid; surface dull, dry, fibrous, some finely flocculose towards the base, white overall with sooty brown floccules, context white, arising from a white tomentum or not. *Odor* indistinct. *Taste* indistinct.

Basidiospores 5–7 × 5–7 µm [x_m = 6.1 ± 0.54 × 5.42 ± 0.57 µm, Q = 1.0–1.4, Q_m = 1.13 ± 0.13, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 16–25 × 6–8 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 11–19 × 6–8 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 30–78 × 8–16 µm, clavate to fusoid-ventricose, obtuse or mucronate, hyaline, thin to thick-walled (up to 2 µm thick). *Pleurocystidia* 40–80 × 11–30 µm, fusoid-ventricose to narrowly lageniform or narrowly utriform, obtuse or sometimes capitate-truncate, some with apical lateral mucilage sometimes with adhering spores that obscure view, hyaline, thin to thick-walled. *Pileipellis* a cutis of repent hyphae with fragmented erect terminal elements (pileocystidia), composed of hyaline or brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 3–11 µm diam.; *pileocystidia* 30–110 × 5–10 µm, repent to erect, solitary to clustered in fascicles especially at the disc, filiform to fusoid, acute, obtuse or subcapitate, sometimes with one to multiple basal cells, typically with brown plasmatic pigment or occasionally hyaline. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate to inflated hyphae, 3–25 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–16 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 4–18 µm diam.. *Caulocystidia* 50–110 × 6–16 µm, similar to pileipellis terminal elements, clustered to solitary, filiform to narrowly lageniform, acute, obtuse or sometimes capitate, some with one to multiple basal cells, with brown plasmatic pigment or sometimes hyaline, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on decayed wood in subtropical montane primary broadleaf-*Araucariaceae/Podocarpaceae* rainforest containing *Agathis macrophylla* (*Araucariaceae*), *Balanops pedicellata* (*Balanopaceae*), *Calophyllum neoebudicum* (*Calophyllaceae*), *Dendrocnide latifolia* (*Urticaceae*), *Ficus septica* (*Moraceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Hernandia moerenhoutiana* (*Hernandiaceae*), *Macaranga dioica* (*Euphorbiaceae*), *Podocarpus vanuatuensis* (*Podocarpaceae*), *Polyscias cissondendron* (*Araliaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum).

Material examined:—VANUATU. Tafea Province: Aneityum, trail through Antowojon area, 20°13.142′S, 169°47.788′E, elev. 119 m, 28 July 2017, coll. *J.A. del Rosario & B.A. Perry, JAD 12* (HAY).

Notes:—The distinctly thick-walled cystidia are unusual for members of sect. *Celluloderma* suggesting immediate comparison to only one other known species with this trait in the section: *P. crassocystidiatus* Menolli & de Meijer (2014: 114). This Brazilian species is known only from the protologue (Menolli *et al*. 2015a) and compared to *P. lalepiorum* shares similarly shaped thick-walled pleurocystidia and cheilocystidia that contain apical mucilage, but has much longer cheilocystidia (44–110 × 11.2–24 µm). The pileipellis in *P. crassocystidiatus* is also different, being a euhymeniderm of smaller clavate-vesiculose cells (23–41 × 17.5–24 µm). *Pluteus crassocystidiatus* is also not known to have caulocystidia and has a different colored olive brown to yellowish brown pileus.

Pluteus maculosipes Singer (1961: 122) from Venezuela (Singer 1961) and Brazil (Menolli *et al*. 2015c) is micromorphologically similar in pileipellis structure and caulocystidia, but differs by lacking pleurocystidia, having thin-walled cheilocystidia without mucilage, and producing a darker pigmented basidiome. The Sri Lankan *P. glyphidiatus* has similar pileipellis elements and mucilaginous lamellar cystidia, but differs by its yellow colored basidiome, and less lageniform, non-thick-walled cheilocystidia and pleurocystidia (Pegler 1986, Singer 1956). A recently described species from Thailand, *P. saisamorniae* Wannathes, J. Kumla & N. Suwannarach (2022: 9), similarly shares thick-walled pleurocystidia and cheilocystidia, and has similarly shaped pileipellis terminal cells, however *P. saisamorniae* is phylogenetically distinct by belonging in sect. *Hispidoderma*, lacks mucilage on the cystidia, and has a brown basidiome.

ITS phylogenetic analysis (Fig. 37d) places *P. lalepiorum* on a moderately supported branch (BS 82 %, PP 0.99) within the *ephebeus* clade recognized by Justo *et al*. (2011b). Within this clade, the Vanuatu species is morphologically close to the Brazilian *P. halonatus* Menolli, Justo & Capelari (2015: 1213), with which it shares a similar pileipellis structure and mucilaginous pleurocystidia. *Pluteus lalepiorum* differs from this species as the latter forms shorter non-thick-walled-pleurocystidia and cheilocystidia, and has a distinct brown fibrillose pileus (Menolli *et al*. 2015b). *Pluteus lalepiorum* is positioned on a branch with low internal node statistical support containing *P. squamulososulcatus* E.F. Malysheva & O.V. Morozova (2020: 99) (MT611234) and specimens identified as *P.* aff. *ephebeus* (KM983675, KM983676), *P.* cf. *fastigiatus* (KM983678) and *P.* cf. *fuliginosus* (KM983677). Recently described from Vietnam, *P. squamulososulcatus* differs in having a sulcate, gray-pink squamulose pileus, non-thick-walled and non-mucilaginous pleurocystidia and cheilocystidia, a cutis pileipellis without pileocystidia, and lacks caulocystidia (Malysheva *et al.* 2020). The Brazilian specimen tentatively identified as *P.* cf. *fastigiatus* shares similarly sized mucilaginous pleurocystidia and cheilocystidia, but differs due to the cystidia not being thick-walled, the basidiome being dark pigmented, having a different pileipellis, and lacking caulocystidia (Menolli & Capelari 2016). *Pluteus* cf. *fuliginosus* shares with *P. lalepiorum* a similar pileipellis structure and mucilaginous pleurocystidia and cheilocystidia, and although the pleurocystidia are also apically thick-walled, they differ due to having apical prongs; a dark pigmented pileus, thin-walled cheilocystidia, and lacking caulocystidia (Menolli & Capelari 2016).

Pluteus presleyi J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 44, 45)
MycoBank no:—854228

Holotype:—VANUATU. Tafea Province: Aneityum, lowland in former taro terraces, Mount Inhetiji, 20°12.531′S, 169°51.071′E, elev. 116 m, 12 December 2018, coll. *J.A. del Rosario, JAD 239* (HAY).

Etymology:—Named in honor of Presley Dovo for his extensive contributions to the Plants mo Pipol blong Vanuatu project as far back as the earliest 2006 expeditions on the island of Santo.

FIGURE 44. Basidiome of *Pluteus presleyi* (JAD 239 holotype). Scale bar = 10 mm. Photos by: Jonathan del Rosario.

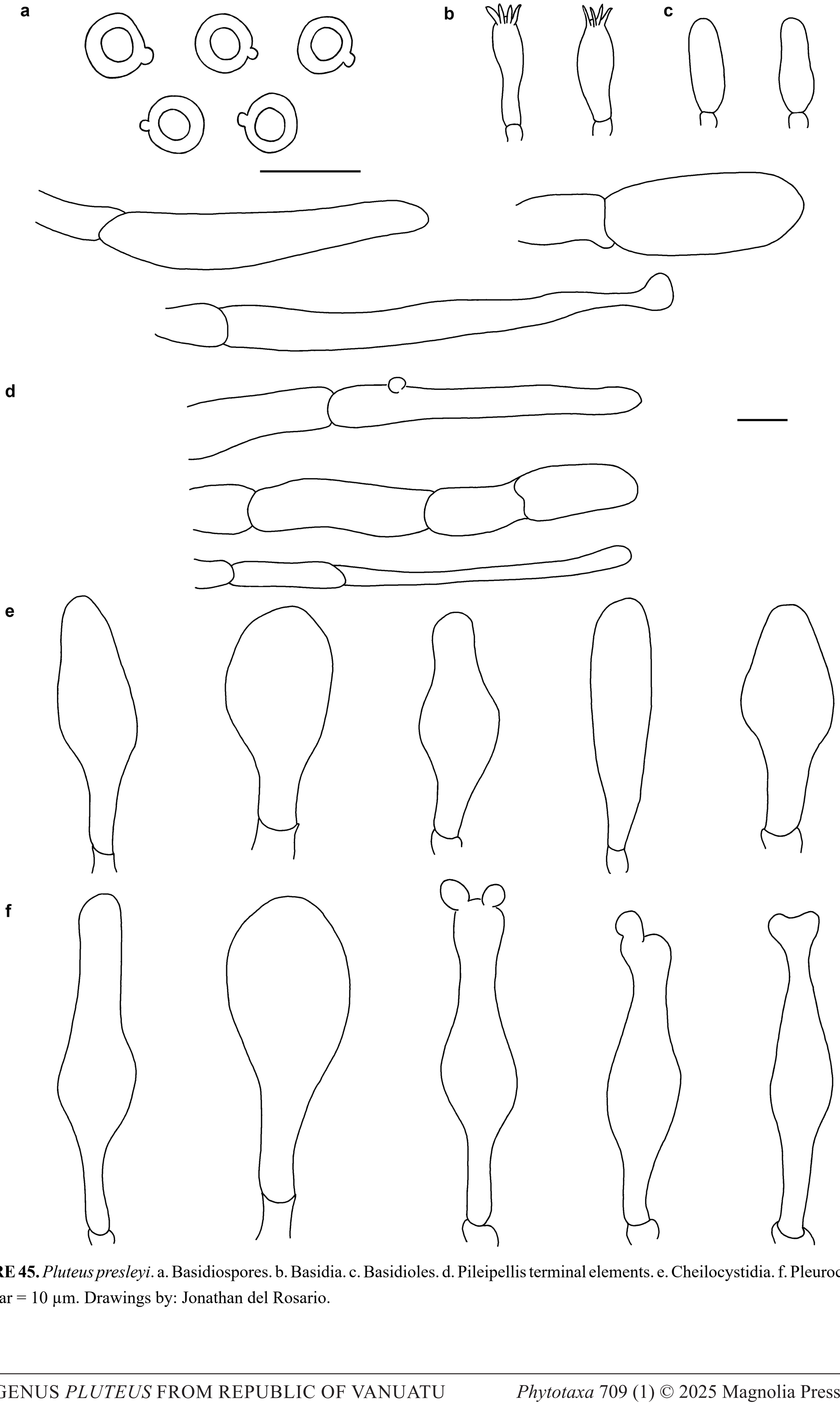

FIGURE 45. *Pluteus presleyi*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Diagnosis:—*Pluteus presleyi* from Aneityum is characterized by a light tan pileus covered with gray fibrils and floccules-spinules at the disc spreading outwards, and a cylindrical white stipe. Microcharacteristics include subglobose basidiospores (5.7 × 5.2 µm), fusoid-ventricose cheilocystidia, fusoid-ventricose pleurocystidia occasionally apically nodulose, a cutis pileipellis with suberect clustering clavate or filiform brown pigmented terminal elements, an absence of caulocystidia, and a lack of clamp connections.

Description:—*Pileus* 20–30 mm diam., convex with a slight umbo, with or without a slight central depression; surface dull, dry, densely longitudinally appressed-fibrillose turning into erect clusters and splitting to expose the context underneath, disc rugose or pustulate-spinulose to floccose; fibrils and pustules/spinules/floccules pallid gray-brown (oac723–oac725), underlying surface isabelline/grayish brown (oac730–oac732). *Context* 1 mm thick, white. *Lamellae* free, subdistant to close with 1–2 tiers of lamellulae, thin, dark tan (oac660/oac667). *Stipe* 20–40 × 3–4 mm, central, terete, cylindrical, solid; surface pearlescent, dry, silky, white, context white. *Odor* indistinct. *Taste* indistinct.

Basidiospores 5–7 × 4–6 µm [x_{mr} = 5.58–5.86 × 5.14–5.28 µm, x_{mm} = 5.72 ± 0.18 × 5.21 ± 0.09 µm, Q = 1.0–1.5, Q_{mr} = 1.08–1.1, Q_{mm} = 1.1 ± 0.02, n = 50, s = 2], globose to subglobose, rarely broadly ellipsoid, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 14–22 × 4–6 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 13–22 × 4–8 µm, clavate, hyaline, guttulate, thin-walled. *Cheilocystidia* (21–) 28–46 × 8–17 (–24) µm, clavate to fusoid-ventricose, obtuse or rarely capitate (observed once), hyaline, thin-walled. *Pleurocystidia* 44–70 × 9–18 (–28), common to scattered, lageniform to fusoid-ventricose, obtuse to umbonate or occasionally nodulose-capitate with 1–2 nodules, hyaline, thin-walled. *Pileipellis* a cutis with ascending terminal elements typically in fascicles, composed of cylindrical, with pale brown plasmatic pigment or sometimes hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–20 µm diam.; terminal elements 24–125 × 2–30 µm, ellipsoid to broadly clavate, cylindro-clavate or occasionally filiform, obtuse to somewhat tapering, seldom subcapitate or with a medial nodule. *Pileus trama* interwoven, composed of hyaline, non-gelatinous, thin-walled, clavate hyphae, 3–26 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 2–12 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–16 µm diam.. *Caulocystidia* absent. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Solitary on decaying wood in subtropical montane primary broadleaf rainforest to cloud forest containing *Balanops pedicellata* (*Balanopaceae*), *Diospyros sp.* (*Ebenaceae*), *Ficus smithii* (*Moraceae*), *Garcinia platyphylla* (*Clusiaceae*), *Ilex vitiensis* (*Aquifoliaceae*), *Melicope latifolia* (*Rutaceae*), *Metrosideros collina* (*Myrtaceae*), *Plerandra actinostigma* (*Araliaceae*), *Scaevola cylindrica* (*Goodeniaceae*), *Semecarpus tannaensis* (*Anacardiaceae*), and *Syzygium spp.* (*Myrtaceae*), Vanuatu (Aneityum).

Material examined:—VANUATU. Tafea Province: Aneityum, lowland in former taro terraces, Mount Inhetiji, 20°12.531′S, 169°51.071′E, elev. 116 m, 12 December 2018, coll. *J.A. del Rosario, JAD 239* (HAY); Aneityum, lowland in former taro terraces, Mount Inhetiji, S20°12.567’, E169°51.206, elev. 140 m, 12 December 2018, coll. *J.A. del Rosario, JAD 251* (HAY).

Notes:—*Pluteus presleyi* is comparable to several species that are macromorphologically superficially similar. The Sri Lankan *P. spilopus* tends to be larger in stature (4–10 cm), has non-lageniform pleurocystidia and more obtuse and non-tapering pileipellis terminal elements (Pegler 1986). Another Sri Lankan species, *P. escharites* (Berkeley & Broome) Saccardo (1887: 670) is similar in stature, but differs based on lacking pleurocystidia, and having a disrupted trichoderm pileipellis with fundamentally different fusoid terminal elements (Pegler 1986). *Pluteus hispidilacteus* Horak (2008: 20) from New Zealand has a somewhat similar pileus, but differs in the hispid stipe, absent pleurocystidia, non-ovoid and non-capitate pileipellis terminal elements, and the presence of caulocystidia (Horak 2008). The European species *P. hispidulus* (Fries) Gillet (1887: 391) is similar in stature with a slightly more squamulose pileus surface, but differs microscopically in rare to absent pleurocystidia, narrowly clavate cheilocystidia, and non-capitate and non-filliform pileipellis terminal elements (Kühner & Romagnesi 1956, Vellinga & Schreurs 1985). The Chinese *P. squarrosus* Iqbal Hosen & T.H. Li (2019: 3) has similar pileus coloration, somewhat similar surface characteristics and similarly shaped cheilocystidia and pleurocystidia, but differs in having a more squamose-areolate pileus surface, larger pleurocystidia (45–80 × 13–28 µm), having caulocystidia, and a trichoderm pileipellis (Hosen *et al*. 2019).

Phylogenetic analysis of the ITS data (Fig. 37e) resolves *P. presleyi* in a basal grade to sect. *Celluloderma.* The general cutis pileipellis and non-metuloid lamellar cystidia would conform with the current concept of sect. *Celluloderma*. Interestingly, among the variable elongated clavate and filiform pileipellis cells there are occasionally terminal elements that are chains consisting of short cylindrical cells, ending in short ellipsoid cells. These chains almost resemble epithelioid cells and are perhaps similar to a kind of intermediate form between the cells typical in a hymeniderm or epithelium. Nevertheless, the morphological differences and phylogenetic placement are enough to recognize this species as new.

Pluteus* aff. *riberaltensis* var. *missionensis Singer, *Sydowia* 15 (1-6): 123–124, 131 (1962) (Figs. 46, 47)

Diagnosis:—Based on material from Tanna, *P.* aff. *riberaltensis* var. *missionensis* is characterized by an ash brown fibrillose-rimulose pileus with a squamulose disc, and a white basally ash gray flocculose stipe with a subbulbous base. Microcharacteristics include globose basidiospores with a mean size of (5.7 × 4.6 µm), lageniform capitate cheilocystidia, fusoid-ventricose pleurocystidia without or with mucilage, a euhymeniderm-trichoderm pileipellis with brown pigmented lageniform terminal cells overlying a cutis subpellis, narrowly fusiform caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 28–35 mm diam., convex with a slight umbo with or without a slight central depression, margin slightly sulcate or not; surface dull, dry, densely appressed-fibrillose, disc squamulose-areolate turning radially rimose; squamules, pustules and fibrils ash brown (oac723–oac725) densest and darkest at disc, fading to brown-gray (oac701–oac704) towards the margin with minute streaks of the underlying white context. *Context* 2–3 mm thick, white. *Lamellae* free, close, with 2–3 tiers of lamellulae, regular, off-white, turning pale pink (oac760) in maturity. *Stipe* 42–50 × 3–5 mm, central, cylindrical over a subbulbous base, hollow; surface pearlescent, dry, fibrous, minutely flocculose at the base, surface white to off-white, floccules pale tan (oac760), context white. *Odor* indistinct. *Taste* indistinct.

FIGURE 46. Basidiomes of *Pluteus* aff. *riberaltensis* var. *missionensis* (JAD 281). Scale bar = 10 mm. Photos by: Brian Perry.

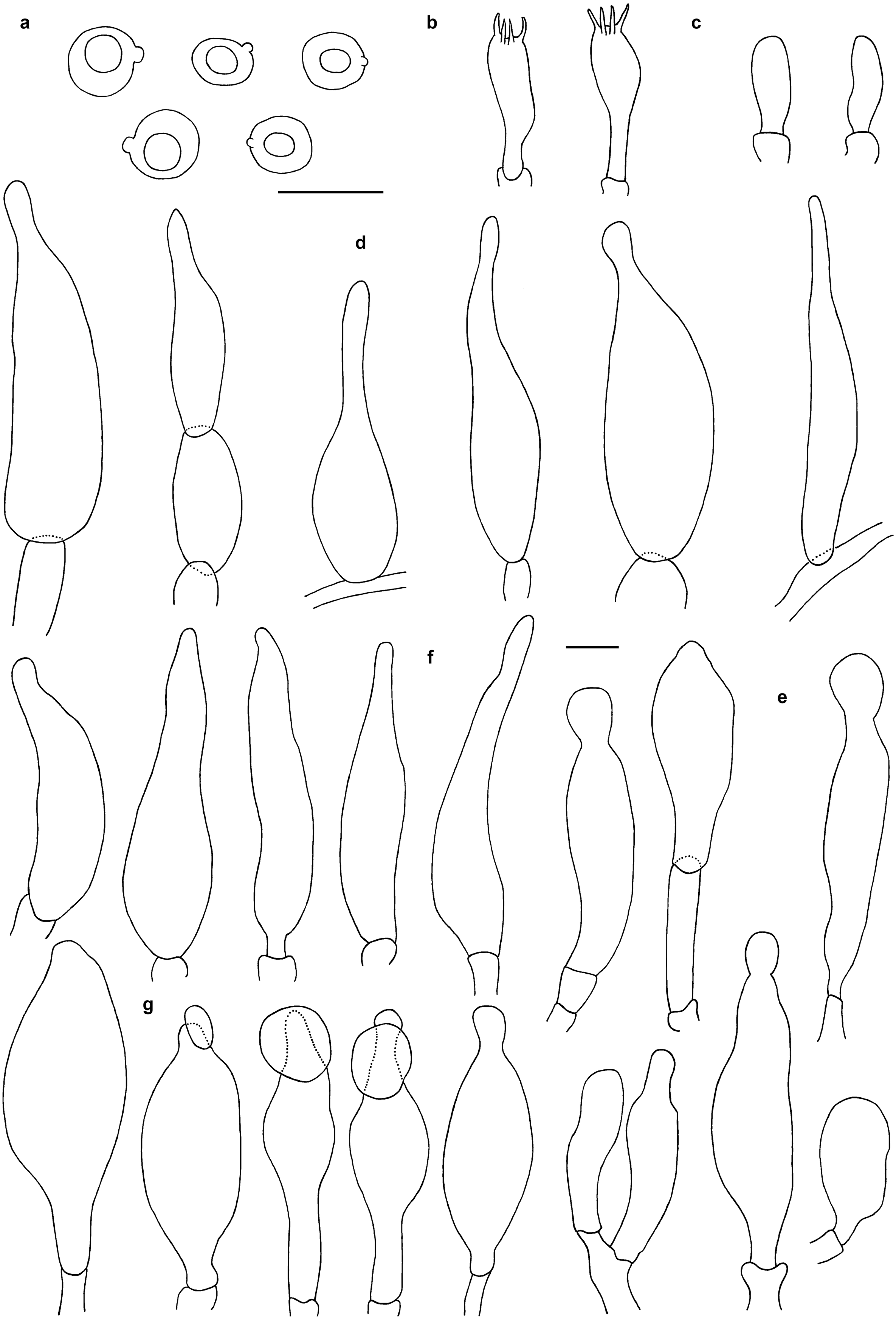

FIGURE 47. *Pluteus* aff. *riberaltensis* var. *missionensis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Basidiospores 5–6 × 4–6 µm [$x_m = 5.66 \pm 0.47 \times 4.62 \pm 0.56$ µm, Q = 1–1.5, $Q_m = 1.24 \pm 0.17$, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. *Basidia* 23–32 × 6–8 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 18–23 × 5–8 µm, cylavate to cylindro-clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 30–64 × 8–13 µm, fusiform to fusoid or clavate, obtuse or capitate, hyaline, thin-walled. *Pleurocystidia* 35–66 (–80) × 10–20 (–25) µm, fusiform to fusoid-ventricose or narrowly lageniform, some with apical or completely enveloped in mucilage sometimes with adhering spores that obscure view, obtuse or capitate, hyaline, thin-walled. *Pileipellis* a transition from a euhymeniderm to a trichoderm over a subpellis, composed of a majority of terminal elements 40–69 × 8–12 µm, erect in clusters, especially at the disc, narrowly to broadly lageniform or narrowly fusoid, acute or subcapitate, arising directly from the subpellis or some with one to multiple basal cells, hyaline or with brown plasmatic pigment, non-incrusted, non-gelatinous, thin-walled; *subpellis* a cutis of repent hyphae, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–8 µm diam.. *Pileus trama* interwoven, composed of hyaline, non-incrusted, non-gelatinous, thin-walled, cylindrical to clavate hyphae, 3–22 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae, 3–12 µm diam.. *Stipitipellis* a cutis of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–8 µm diam.. *Caulocystidia* 22–74 × 8–16 µm, often clustered, fusiform to fusoid or lageniform, obtuse or acute, hyaline or with brown plasmatic pigment, thin-walled. *Clamp connections* absent in all tissues examined.

Habitat and known distribution:—Gregarious on rotted wood in subtropical coastal mixed-use agro tree garden and secondary littoral broadleaf forest containing *Annona muricata* (*Annonaceae*), *Artocarpus altilis* (*Moraceae*), *Barringtonia asiatica* (*Lecythidaceae*), *Cocos nucifera* (*Arecaceae*), *Cordia dichotoma* (*Boraginaceae*), *Euodia hortensis* (*Rutaceae*), *Leucaena leucocephala* (*Fabaceae*), *Macaranga dioica* (*Euphorbiaceae*), and *Musa sp.* (*Musaceae*), Vanuatu (Tanna).

Material examined:—VANUATU. Tafea Province: Tanna, Port Resolution. 19°31.459′S, 169°30.340′E, elev. 62 m, 14 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 281* (HAY).

Notes:—The type variety, *P. riberaltensis* var. *riberaltensis* Singer (1958: 255), is only known from the original protologue based on Bolivian material (Singer, 1958). Based on this original description, the type variety differs from the Vanuatu material by having smaller cheilocystidia (33–44 × 11–16.5 µm), slightly wider pleurocystidia (41–86 × 12.5–39 µm) without mucilage, lacking caulocystidia, and having a cutis pileipellis consisting of cylindrical, rarely attenuate cells. In the same description, Singer proposed *P. riberaltensis* var. *conquistensis* Singer (1958: 255) from additional material he acknowledged differed based on the presence of black stripes on the stipe (Singer 1958). Recently, multiple *Pluteus spp.* type specimens were re-examined by Rodríguez (2024), including the type *P. riberaltensis* var. *riberaltensis*, which differs from this Vanuatu material by having Singer's observed cutis type pileipellis, lacking the presence of mucilage on any cystidium, and lacking caulocystidia. A specimen of var. *conquistensis* was reported from Brazil (Menolli *et al.* 2010) differing based on having moderately longer pleurocystidia closer in size to the type variety. Based on phylogenetic analysis of ITS data (Fig. 37d) the Vanuatu material diverges with strong support from the Brazilian specimen of *P. riberaltensis* var. *conquistensis*. Comparing the Vanuatu specimen to Singer (1958) and Menolli *et al.*'s (2010) material, *P. riberaltensis* var. *conquistensis* differs by having shorter and wider cheilocystidia ([27–] 30–47 [–57] × [12.5–] 17.7–27 µm), slightly wider pleurocystidia ([44–] 48–69 [–78] × [15–] 17.5–28 [–35] µm) without mucilage, lacking caulocystidia, a pileipellis arranged as a cutis, and is phylogenetically distinct. The presence of dark fibrils on the stipe was considered exclusive to var. *conquistensis*, and as this occurs in the Vanuatu specimen, although inconsistently, the reliability of this character is questionable.

Singer proposed another variety, *P. riberaltensis* var. *missionensis* Singer (1961: 123) from Argentina (Singer 1961) that he classified as having a white stipe like the type variety, but differing by the presence of incrustation on cystidia and lacking size differentiation between the pleurocystidia and cheilocystidia. Additional material of *P. riberaltensis* var. *missionensis* has also been reported from Mexico (Cifuentes & Guzmán 1981, Rodríguez 2013). Singer (1961) described the pleurocystidia and cheilocystidia together, regarding their sizes equal (41–69 × 12–22 µm), and by comparison both lamellar cystidia in the Vanuatu material are similarly shaped and roughly equal in length, but the cheilocystidia are slightly narrower. A brief description of Mexican material from the state of Chiapas also describes both the pleurocystidia and cheilocystidia together as equal (67.5–75 × 30–37.5 µm), and these differ from the Vanuatu specimen mainly by being slightly broader and mucilage was not observed (Cifuentes & Guzmán 1981). Rodríguez re-examined the Chiapas material and provided additional Mexican material from Veracruz and the state of Morelos, but only provided an illustration without a description (Fig. 10, Rodríguez 2013). Based on this, compared to the Vanuatu specimen the pileipellis terminal cells appear similarly shaped and arranged, and both lamellar cystidia types appear similarly shaped with both having a type of incrustation/mucilage. Apparently, Rodríguez also re-examined the type variety for comparison, but unfortunately did not provide additional information. Pileipellis terminal elements were not measured or detailed from any of the Mexican material, but Singer's Argentinean specimen was reported as longer in size (45–160 × 13–26 µm) and described as "appressed…the terminal members often combining to form bunches of ascending hyphae or pyramids which form the fibrils of the pileus" (Singer 1961). Even navigating Singer's key from that study requires classifying the pileipellis as a trichoderm to conclude at *P. riberaltensis* var. *missionensis* (Singer 1961). Based on this, Singer's pileipellis description is slightly ambiguous and may be loosely interpreted as arranged similar to that in the Vanuatu material. Singer described the type var. *riberaltensis* as a cutis without specifying the ornamentation of the terminal elements, and var. *conquistensis* as "…consisting of cylindric hyphae, the terminal members and the cylindric elements anteceding them fuscous and often ascendant," (Singer 1958). The Brazilian material of *P. riberaltensis* var. *conquistensis* characterized the pileipellis as a cutis "…sometimes with the terminal elements slightly inflated and often ascendant," (Menolli *et al*. 2010). Assuming var. *conquistensis* and var. *missionensis* were established due to being closely analogous to the type variety, it may be their pileipellis is simply a cutis. The pileipellis arrangement in the Vanuatu material tends to have abundant, erect terminal elements, sometimes with one to multiple basal cells forming a chain, being the predominant feature of the surface and arising from a distinct cutis second layer, and here classified as a euhymeniderm-trichoderm. This contrasts with what this study interprets as a typical cutis arrangement, where the terminal elements may still be repent and integrate themselves into an overall parallel orientation, and sometimes ascending into erect clusters. The Vanuatu specimen is clearly closest to *P. riberaltensis* var. *missionensis* based on microscopic similarity with the other descriptions and the mucilaginous cystidia, which may be considered consistent a character for distinction. Singer's consideration of equal pleurocystidia and cheilocystidia size as a defining feature of var. *missionensis* may be useful, but the overall defined size range for the variety is unclear as that of Mexican material is slightly larger compared to the Argentinean material, and within the Vanuatu material the cheilocystidia are typically slimmer than the pleurocystidia. The subtly fibrillose stipe, although sparse in some material, would make it closer to var. *conquistensis*, but this species is phylogenetically distinct and neither account mentions caulocystidia nor cystidia mucilage. Due to Singer's ambiguous pileipellis classification for *P. riberaltensis* var. *missionensis* and vague descriptions from other material, this study prefers to maintain the Vanuatu specimen's identity as *P.* aff. *riberaltensis* var. *missionensis*. An in-depth re-examination for morphological comparison and molecular sampling for all the varieties, especially the type, are necessary to clarify the relationships and delimitations among the varieties of *P. riberaltensis*.

Phylogenetic analysis of ITS molecular data (Fig. 37d) places the Vanuatu specimen within the general *ephebeus* clade *sensu* Menolli *et al.* (2015b) with a well-supported sister taxon *P. flavidus* E.F. Malysheva & A.V. Alexandrova (2020: 96). This recently described Vietnamese species is close to the Vanuatu specimen, particularly in the very similar pileipellis arrangement with fusiform or needle-shaped terminal elements connected to basal cells (Malysheva *et al.* 2020). *Pluteus flavidus* was classified with a hymeniderm with transitions to an epithelium type pileipellis, which may subtly differ from *P.* aff. *riberaltensis* var. *missionensis* as it appears there are more pyriform or epithelioid cells compared to more elongate cells in the Vanuatu specimen. Even so, *P. flavidus* differs due to more sphaeropedunculate cheilocystidia, lacking mucilaginous pleurocystidia, irregularly shaped caulocystidia, and producing a paler pileus (Malysheva *et al.* 2020). The phylogenetically distantly related *P. hirtellus* Desjardin & B.A. Perry (2018: 612) from São Tomé is superficially similar, but differs by a paler shade of brown, lack of brown fibrils towards the stipe base, smaller more clavate non-capitate cheilocystidia (25–48 × 10–20 µm), more clavate non-mucilaginous pleurocystidia, longer pileipellis elements (48–115 × 8–16 µm), and lack of caulocystidia (Desjardin & Perry 2018). The Chinese *P. squarrosus*, shares similar pileipellis terminal elements, but these tend to be longer (50–120 × 7–13 µm) and the species differs in having non-mucilaginous pleurocystidia, shorter cheilocystidia (35–42 × 9–18 µm), and a more grayish brown pileus (Hosen *et al.* 2019).

Pluteus tatafuensis J.A. del Rosario & B.A. Perry, *sp. nov.* (Figs. 48, 49)
MycoBank no:—854229

Holotype:—VANUATU. Tafea Province: Futuna, upper slopes of Mount Tatafu. 19°31.422′S, 170°13.433′E, elev. 485 m, 19 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 304* (HAY).

Etymology:—Named in honor of Mount Tatafu on Futuna Island, where the holotype specimen was collected, and the fact that the pileus surface resembles the furrowed flanks of Mount Tatafu.

Diagnosis:—*Pluteus tatafuensis* from Futuna is characterized by a dark chocolate brown rugose-venose, fuliginous appressed-fibrillose, rimose, marginally sulcate pileus and a white stipe with fuliginous floccules towards the base. Microcharacters include subglobose basidiospores (6.4 × 5.8 µm), broadly clavate cheilocystidia, clavate pleurocystidia sometimes with mucilaginous coating, a transition between a hymeniderm and epithelium pileipellis consisting of globose and lageniform, frequently mucronate brown pigmented cells, fusoid capitate brown pigmented caulocystidia, and an absence of clamp connections.

Description:—*Pileus* 28 mm diam., convex to hemispherical with a slight centrally depressed umbo, margin sulcate; surface dull, dry, appressed-fibrillose splitting radially in a rimose pattern exposing white context beneath, disc densely rugose-venose; veins dark chocolate brown to black, fibrils fuliginous to pallid brown (oac730–oac732). *Context* 3 mm thick, white. *Lamellae* free, crowded with 3+ tiers of lamellulae, thin, dull pinkish brown. *Stipe* 35 × 3 mm, central, cylindrical over a straight base, hollow; surface dull, dry, silky, minutely flocculose at the base, white to off-white, floccules colored fuliginous to pallid brown, context white. *Odor* indistinct. *Taste* indistinct.

FIGURE 48. Basidiome of *Pluteus tatafuensis* (JAD 304 holotype). Scale bar = 10 mm. Photos by: Brian Perry.

Basidiospores (5–) 6–7 × 5–7 µm µm [x_m = 6.34 ± 0.55 × 5.84 ± 0.42 µm, Q = 1–1.2, Q_m = 1.08 ± 0.08, n = 50, s = 1], globose to subglobose, smooth, hyaline, with a guttule, inamyloid, thick-walled. Basidia 23–30 × 9–10 µm, clavate, 4-spored, hyaline, guttulate, thin-walled, sterigmata 2–4 × 0.5–1 µm. *Basidioles* 18–24 × 6–11 µm, clavate, hyaline, guttulate, thin-walled. *Lamellar edge* sterile. *Cheilocystidia* 30–118 × 11–70 µm, clavate to broadly clavate or sphaeropedunculate to inflated, obtuse, hyaline, thin-walled. *Pleurocystidia* 43–90 × 14–30 µm, clavate to broadly clavate, obtuse or seldom mucronate, some with apical or completely enveloped in mucilage sometimes with adhering spores that obstruct view, hyaline, thin-walled. *Pileipellis* a transition between a hymeniderm and epithelium to a euhymeniderm overlaying a subpellis; majority of terminal elements 35–85 × 6–56 µm, globose to broadly clavate or narrowly lageniform to filliform, obtuse, frequently mucronate or rostrate (up to 40 µm long), with brown plasmatic pigment or sometimes hyaline, non-incrusted, non-gelatinous, thin-walled; *subpellis* a cutis of repent hyphae, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–8 µm diam.. *Pileus trama* interwoven, composed of hyaline, non-incrusted, non-gelatinous, thin-walled, cylindrical hyphae, 3–20 µm diam.. *Lamellar trama* inverse, composed of hyaline, non-gelatinous, thin-walled hyphae 3–12 µm diam.. *Stipitipellis* a cutis, composed of hyaline, non-incrusted, non-gelatinous, thin-walled hyphae, 3–10 mm diam.. *Caulocystidia* 35–110 × 5–25 µm, common, solitary to clustered, clavate to cylindro-clavate or narrowly fusoid, some strangulate, infrequently forming trichoderm-like chains, obtuse or capitate, hyaline or pale brown plasmatic pigment, thin-walled. *Clamp connections* absent in all tissues examined.

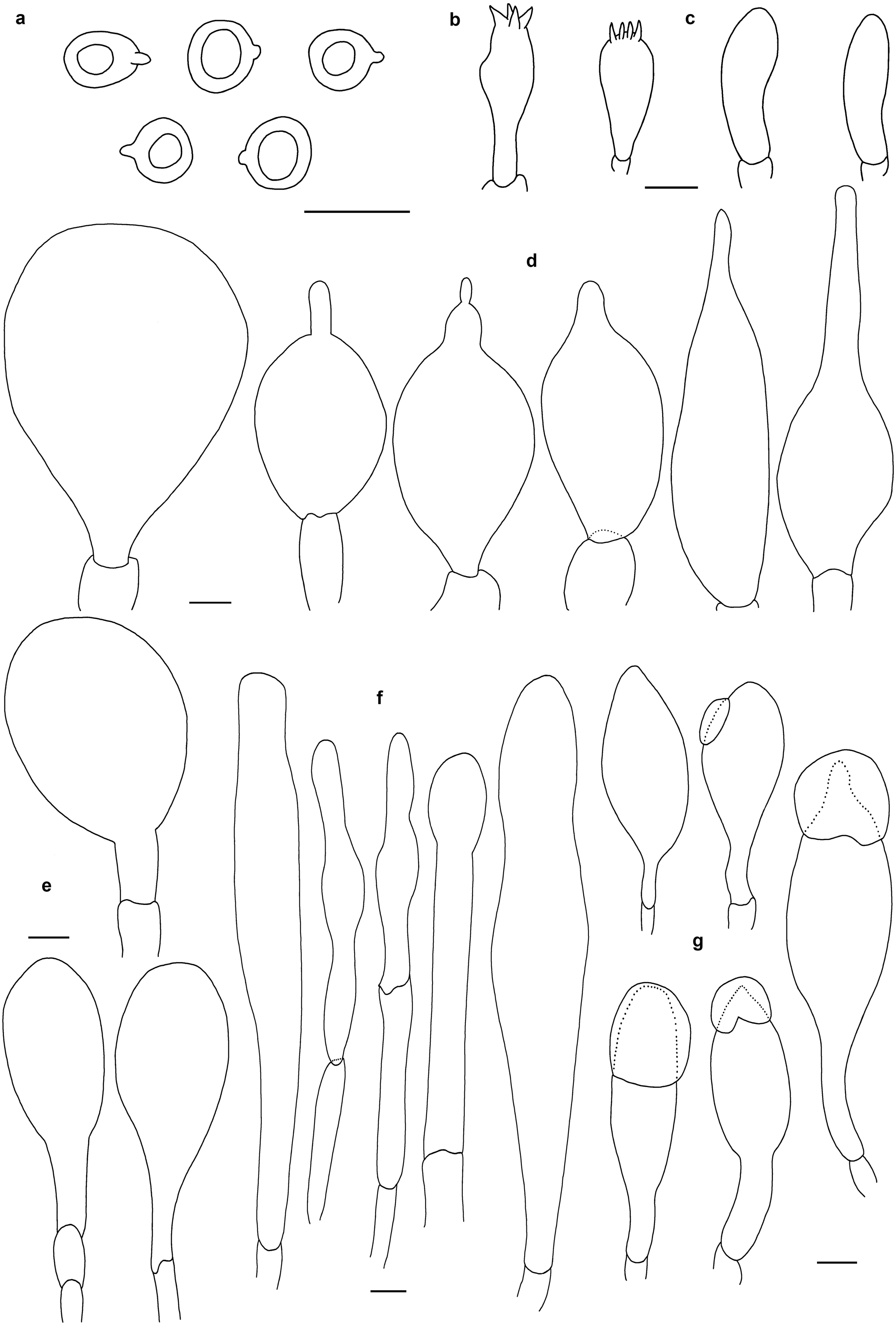

FIGURE 49. *Pluteus tatafuensis*. a. Basidiospores. b. Basidia. c. Basidioles. d. Pileipellis terminal elements. e. Cheilocystidia. f. Caulocystidia. g. Pleurocystidia. Scale bar = 10 µm. Drawings by: Jonathan del Rosario.

Habitat and known distribution:—Solitary on rotted wood in subtropical montane primary cloud broadleaf rainforest containing *Atractocarpus sezitat* (*Rubiaceae*), *Claoxylon psilogyne* (*Euphorbiaceae*), *Eumachia trichostoma* (*Rubiaceae*), *Geissois denhamii* (*Cunoniaceae*), *Ficus septica* (*Moraceae*), *Neonauclea forsteri* (*Rubiaceae*), and *Schefflera neoebudica* (*Araliaceae*), Vanuatu (Futuna).

Material examined:—VANUATU. Tafea Province: Futuna, upper slopes of Mount Tatafu. 19°31.422′S, 170°13.433′E, elev. 485 m, 19 August 2019, coll. *J.A. del Rosario & B.A. Perry, JAD 304*, (HAY).

Notes:—The combination of the rugose-venulose, rimose, marginally sulcate, and fuliginous pileus of *P. tatafuensis* suggests comparison to a number of similar looking species. The Bolivian *P. substigmaticus* Singer (1958: 273) produces very similar basidiomes, shares a similarly shaped pileipellis, pleurocystidia and cheilocystidia cells, but differs by the pileus lacking a venose disc and has significantly smaller cheilocystidia and pleurocystidia (15.5–42 × 10.3–16.5 µm equally), which lack mucilage (Singer 1958). *Pluteus rimosoaffinis* Singer (1956: 211), an Argentinean (Singer 1956) and confirmed Brazilian species (Pegler 1997, de Meijer 2006; Menolli & Capelari, 2016), has similarly sized and shaped pleurocystidia with apical mucilage, but this species tends to be larger in stature, is not known to have caulocystidia, lacks mucronate or filiform pileipellis elements, and has more utriform non-sphaeropedunculate cheilocystidia. Other similar dark venose species include the tropical American *P. jamaicensis* Murrill (1911: 278) (Dennis 1953, Menolli & Capelari 2010, Murrill 1911, Pegler 1983a, Singer 1956, 1958, Singer & Digilio 1952), *P. fluminensis* Singer (1958: 292) from Brazil, Bolivia and the U.S.A. (Singer 1958, Menolli *et al*. 2010), and the Chilean *P. fuligineovenosus* Horak (1964: 190) (Horak 1964), but these all differ due to more lageniform non-mucilaginous pleurocystidia, non-sphaeropedunculate cheilocystidia, lack of rostrate and lageniform pileipellis elements, and are phylogenetically distinct.

Phylogenetic analysis of ITS data (Fig. 37e) places *P. tatafuensis* within the *romelli*/*aurantiorugosus* clade recognized by Justo *et al*. (2011b), and sister to an undetermined species of *Pluteus* from China (KU382737, KU382736) with strong support (BS 97 %, PP 0.99). These taxa are placed on a well-supported branch containing additional superficially similar species *P. paucicystidiatus* Menolli, Justo & Capellari (2015: 1218), *P. stenotrichus* Justo, Battistin & Angelini (2012: 17), *P. castaneorugosus* E.F. Malysheva & A.V. Alexandrova (2020: 461), *P. iguazuensis* Singer (1956: 201), and an unidentified *Pluteus sp.* from the Dominican Republic (KM983705). Compared to *P. tatafuensis* the Brazilian *P. paucicystidiatus* shares similarly shaped cheilocystidia and pileipellis elements, but these are smaller and the species differs by not having (or only sometimes) pleurocystidia, differently shaped shorter caulocystidia, and a paler brown pileus (Menolli *et al*. 2015b). From the Dominican Republic, *P. stenotrichus* differs in producing a paler brown non-sulcate pileus, smaller cheilocystidia (25–50 × 14–20 µm), pleurocystidia lacking mucilage, differently shaped non-mucronate pileipellis elements, and similarly shaped but shorter caulocystidia (31–63 × 12–24 µm) (Justo *et al*. 2012). *Pluteus castaneorugosus* from Vietnam differs in having smaller spores (5–6 × 4.5–5.5 µm), smaller non-mucilagenous pleurocystidia (35–55 × 15–22 µm), smaller thick-walled cheilocystidia (25–43 × 14–20 µm), and a differently shaped non-mucronate pileipellis (Malysheva *et al.* 2020). Finally, *P. iguazuensis* from Argentina (Singer 1958) and Brazil (Menolli & Capelari 2016) differs in having a non-rugose, non-rimose pileus, shorter cheilocystidia, non-mucilaginous pleurocystidia, lack of caulocystidia, and lack of lageniform or mucronate elements in the pileipellis.

Discussion

This monograph represents the first detailed account of any macrofungal group for Vanuatu and Tafea Province. A literature search reveals *Pluteus* species occurring in the following neighboring countries: New Zealand (Horak 1983, 2008, Stevenson 1962), Papua New Guinea (Hongo 1976. Horak 1983), New Caledonia (Eyssartiere *et al*. 2011), Bonin Islands (Ito 1939), Pitcairn Islands (Singer 1989), and Australia (Cooke 1888, Grgurinovic 1998. Horak 1980a, 1983, Hubregtse & Hubregtse 2011, Massee 1899, Saccardo 188, Ševčíkovâ *et al*. 2021). Surprisingly, none of the species reported from these areas were observed to occur in Tafea Province during this project. Prior to this study, members of the genus *Pluteus* were virtually unknown from Tafea Province or greater Vanuatu. The twenty-three species described here are represented by a total of forty-three collections. Of these collections, twenty-one were made from Aneityum, twenty from Tanna, and three from Futuna. Aneityum and Tanna produced a similar number of species at twelve and thirteen species respectively, whereas Futuna had the least with only three species recorded. Only one species, *P. chrysaegi*s, was observed to occur on all three islands and has previously been suggested to have a pantropical distribution (Desjardin & Perry 2018, Horak & Heinemann 1978, Hosen *et al.* 2018, Pradeep &

Vrinda 2006, Pradeep *et al.* 2012). Phylogenetic analysis from this study also indicates this taxon's occurrence in North America, in the southeastern (Florida) United States (Fig. 15c). The Vanuatu specimens are the first to extend the range of *P. chrysaegis* as far south as the Oceania region, providing additional evidence to its likely pantropical distribution. As Tafea Province is the southernmost province of Vanuatu, it may imply that the species likely occurs in the understudied northern provinces and on Aniwa and Erromongo. Reasons for this ubiquitous distribution are unclear, but not entirely unexpected as other *Pluteus* species are understood to have cosmopolitan distributions (*e.g.*, *P. petasatus*). Similarly, two of the nine newly proposed species in this study, *P. vanuatuensis* and *P. aureofuscus*, were found on more than one island (Tanna and Aneityum). Based on these observations, these taxa likely also occur on the other islands given their close geographic proximity (all within 90 kilometers of each other). Interestingly, the occurrence of *P. vanuatuensis* may span outside of Vanuatu to Vietnam based on a preliminary identification of a specimen by Malysheva *et al.* (2023) as "*Pluteus* sp. 1," suggesting a potentially wider distribution for this species across Asia and Australasia. Of the other seven taxa proposed as new here, four species are currently known only from Tanna, two species are only known from Aneityum, and one new taxon is exclusive to Futuna. It should be addressed that based on the documented nature of many *Pluteus* species having broad geographic ranges, the distributions of the new species reported herein may well be much greater than currently known. A general absence of data from the country and surrounding areas prevents establishing endemism for any of the newly described species.

Multiple Vanuatu specimens studied here were given tentative identifications, often from older names and poorly understood species. For many of these names, their species concepts require refinement due to the brevity of the original descriptions. Re-examination of the type material or new material from the type locality, paired with molecular data for phylogenetic analysis, is warranted for many taxa. The case may be that these Vanuatu specimens also represent new species, but rather than risk generating superfluous species names, a prudent approach has been taken here to utilize existing names until additional data to suggest otherwise is presented. The biogeographic relationships of the funga between these islands are still not fully explored, as this work represents a preliminary study for not only Tafea Province, but the rest of Vanuatu. Despite logistical difficulties in studying the islands of Aniwa and Erromongo, the total six-month window of fieldwork during the course of this study shows a high density of biodiversity richness for such a small landmass of subtropical islands. Continued effort in this region over time in both the unexplored islands and unsampled areas of the visited islands will undoubtedly uncover additional new species and more specimens to refine our taxonomic understanding of those documented here. The products of this study will hopefully provide a baseline understanding for future surveys in Tafea Province and extend to the rest of the Vanuatu archipelago.

Artificial key to the *Pluteus spp.* from Tafea Province, Vanuatu

1. Lamellar edge marginate, colored gray to dark brown .... ***Pluteus fernandezianus***
- Lamellar edge concolorous 2
2. Basidiome bruising blue or bluish-gray when handled or disrupted 3
- Basidiome not bruising blue or bluish-gray when handled 4
3. Pileus disc floccose-pustulate, thick-walled pleurocystidia apices varying from poorly to well-developed cornuate/corniculate with straight to recurved hooks .... ***Pluteus vanuatuensis/Pluteus*** **aff.** ***vanuatuensis***
- Pileus disc rugose-warted, thick-walled pleurocystidia apex with 2–4 extending polychotomous branches .... ***Pluteus vanuatuensis*** **f.** ***ramacystidiatus***
4. Pileus disc pigmented venose to venose-rugose 5
- Pileus disc floccose, fibrillose, pustulate, pruinose, tomentose, non-pigmented venose-rugose, or glabrous 7
5. Veins colored dark brown to black, pileus surface grayish-brown rimose, pileipellis elements 35–85 × 6–56 µm, some rostrate up to 40 µm long .... ***Pluteus tatafuensis***
- Veins colored a shade of pale tan to brown, pileus paler colored 6
6. Pileus surface yellow or to dull brown, stipe tannish brown, pileipellis an epithelioid hymeniderm with distinct cystidia elements 8–75 × 8–22 µm .... ***Pluteus chrysaegis***
- Pileus surface tan, veins reddish brown, stipe white to gray, pileipellis a euhymeniderm with more homogenous elements 25–50 × 10–22 µm, some mucronate up to 5 µm long .... ***Pluteus eugraptoides***
7. Pileus primarily white, off-white, cream, pale gray, or pink 8
- Pileus primarily a shade of brown or darker gray 10
8. Pileus surface glabrous, pink or white .... ***Pluteus*** **aff.** ***semibulbosus***
- Pileus surface fibrillose, tomentose, rimose or squamose, variously colored 9
9. Pileus surface white, disc with brown floccules, pleurocystidia and cheilocystidia thick-walled and mucilaginous .... ***Pluteus lalepiorum***
- Pileus surface pale gray fibrillose-tomentose, rimose, disc squamulose or rugose-tomentose, margin sulcate, pleurocystidia and cheilocystidia thin-walled and lack mucilage .... ***Pluteus rimosellus***
10. Pileus fuliginous, dark gray, ash brown, or sooty 11
- Pileus tan, isabelline, tawny brown, gray-brown, chestnut brown, olive brown, or yellowish brown 14

11.	Pileipellis a cutis	12
-	Pileipellis a hymeniderm	13
12.	Pleurocystidia semi to thick-walled with cornuate or corniculate apices	***Pluteus albostipitatus***
-	Pleurocystidia thin-walled, some mucilaginous	***Pluteus*** **aff.** ***argentinensis***
13.	Pileipellis a trichohymeniderm of lageniform cells (40–69 × 8–12 µm) arising directly or in chains from a cutis subpellis	***Pluteus*** **aff.** ***riberaltensis*** **var.** ***missionensis***
-	Pileipellis a euhymeniderm of fusoid and lageniform cells (50–112 × 8–28 µm), some thick-walled	***Pluteus*** **cf.** ***fastigiatus***
14.	Pileus pruinose to glabrous, areolate with pulverulent patches	***Pluteus velutinus***
-	Pileus fibrillose, floccose, squamulose, pustulate	15
15.	Pileus fibrillose-floccose	16
-	Pileus appressed-fibrillose, squamulose, venose-rugose	17
16.	Pileus isabelline, stipe white, pileipellis a cutis with brown pigmented cells	***Pluteus presleyi***
-	Pileus and stipe yellowish brown, pileipellis a hymeniderm intermixed with clavate and globose cells	***Pluteus aureofuscus***
17.	Pleurocystidia and/or cheilocystidia a mix of thin or thick-walled cells	18
-	Pleurocystidia and cheilocystidia thin-walled	20
18.	Pileipellis an epithelioid hymeniderm intermixed with elongate terminal elements, cheilocystidia mostly thick-walled	***Pluteus neochrysaegis***
-	Pileipellis a cutis, pleurocystidia thick-walled with cornuate or corniculate apices	19
19.	Cheilocystidia rare to absent, seldom forming a well-developed strip on the lamellar edge, clamp connections absent on pileipellis and stipitipellis	***Pluteus petasatus***
-	Cheilocystidia common, clamp connections present on pileipellis and stipitipellis.	***Pluteus wahei***
20.	Basidiome robust, pileipellis a trichohymeniderm, cystidia and pileipellis cells apically ornamented	***Pluteus ornatocystidiatus***
-	Basidiome small, pileipellis a cutis	21
21.	Lamellar edge serrate, spores 8–10 × 7–9 µm, caulocystidia 25–106 × 8–27 µm	***Pluteus macrocystidiatus***
-	Lamellar edge entire, spores 6–7 × 6–7 µm, caulocystidia 22–46 × 8–20 µm	***Pluteus*** **cf.** ***haywardii***

Acknowledgements

This work was funded by a grant from the National Science Foundation to B.A. Perry (1555802). We thank Drs. Gregory M. Plunkett and Michael J. Balick at the New York Botanical Gardens for leading the surveys, access to the Vanuatu National Herbarium (PVNH) records, and their continued botanical and ethnobotanical work throughout Vanuatu and the South Pacific region. We would like to acknowledge our collaborators from the larger Plants mo Pipol blong Vanuatu project from University of Hawai'i at Manoa, Swarthmore College, and the University of the South Pacific. We are grateful to Presley Dovo at the Vanuatu Forestry Department and Jean-Pascale Wahe of the Tafea Kaljoral Senta for their contributions and accommodations as liaisons. We are indebted to the many Ni-Vans of Aneityum, Futuna, and Tanna for their hospitality and guidance through their lands, particularly Kenneth Keith†, Mary Michelle, and Titiya Kelly Lalep†. We would also like to acknowledge Sean Thackurdeen, Thomas Doro, Frazer Alo, Stephanie Sali, Martial Wahe, Tony Keith, Wopa Nasauman, Thomas Japansei Lalep, and Benjamin Nasauman for their aid in the field. We would also like to thank Dr. Konstanze Bensch for her corrections on the new species epithets, Dr. Alfredo Justo for his discussions and sharing data on the current species concept of *P. conizatus*, and Dr. Nelson Menolli Jr. for his insights on *P. neochrysaegis*, which improved this manuscript.

References

Babos, M.G. (1978) *Pluteus* studies, I. (Basidiomycetes, *Pluteaceae*). *Annales Historico-Natureles Musei Nationalis Hungarici* 70: 93–97.

Banerjee, P. & Sundberg, W.J. (1993) Reexamination of *Pluteus* type specimens: types housed at the New York Botanical Garden. *Mycotaxon* 49 (1): 413–435.

Berkeley, M.J. (1842) Enumeration of fungi, collected by H. Cuming, Esq. F.L.S. in the Philippine Islands. *London Journal of Botany* 1 (3): 142–157.

Berkeley, M.J. (1877) Contributions to the Botany of HMS 'Challenger.'XXXVIII. Enumeration of the Fungi collected during the Expedition of HMS 'Challenger.'1874–75. *Botanical Journal of the Linnean Society* 16 (89): 38–54.

Berkeley, M.J. & Broome, C.E. (1871) The fungi of Ceylon (Hymenomycetes, from *Agaricus* to *Cantharellus*). *The Journal of the Linnean Society Botany* 11: 494–567.

Breitenbach, J. & Kränzlin, F. (1995) *Fungi of Switzerland. Vol 4. Agarics, 2nd Part. 'Entolomataceae, Pluteaceae, Amanitaceae,* *Agaricaceae, Coprinaceae, Bolbitiaceae, Strophariaceae.'* Verlag Mykologia, Lucerne.

Bresadola, G. (1905) Hymenomycetes novi vel minus cogniti. *Annales Mycologici* 3 (2): 159–164.

Buyck, B. (2011) Fungi the Forgotten Kingdom. *In*: Bouchet, P., Le Guyader, H. & Pascal, O. (Eds.) *The Natural History of Santo*, Marseilles: Pro-Natura international, pp. 113–115.

Campi, M.G., Maubet, Y., Cristaldo, E., Grassi, E. & Menolli Jr., N. (2019) *Pluteus* Fr. (*Pluteaceae*, Agaricales) in Paraguay: morphological studies and new records. *Check List* 14 (6): 313–322. https://doi.org/10.15560/15.2.313

Cifuentes, J. & Guzmán, G. (1981) Descripcion y distribucion de hongos tropicales (Agaricales) no conocidos previamente en Mexico. *Boletín de La Sociedad Mexicana de Micología* 16: 41–43.

Conservation International (2021) Asia-Pacific webpage. Available from: https://www.conservation.org/places/asia-pacific/ (accessed 14 August 2022)

Cooke, M.C. (1888) Australian fungi. *Grevillea* 16 (79): 146.

Critical Ecosystem Partnership Fund (CEPF) (2022) East Melanesian Islands webpage. Available from: http://www.cepf.net/our-work/biodiversity-hotspots/east-melanesian-islands/ (accessed 14 August 2022)

de Meijer, A.A.R. (2006) Preliminary list of the macromycetes from the Brazilian State of Paraná. *Boletim Do Museu Botânico Municipal* 68: 1–55.

Dennis, R.W.G. (1953) Les Agaricales de l'Île de la Trinité: Rhodosporae-Ochrosporae. *Bulletin de La Société Mycologique de France* 69 (2): 145–198.

Desjardin, D.E. & Perry, B.A. (2018) The genus *Pluteus* (Basidiomycota, Agaricales, *Pluteaceae*) from Republic of São Tomé and Príncipe, West Africa. *Mycosphere* 9 (3): 598–617. https://doi.org/https://doi.org/10.5943/mycosphere/9/3/10

Dias, R.L. & Cortez, V.G. (2013) New records of *Pluteus* (Agaricales) from Paraná State, Brazil. *Mycosphere* 4 (5): 937–943. https://doi.org/10.5943/mycosphere/4/5/6

Eyssartiere, G., Ducousso, M. & Buyck, B. (2011) Les *Entolomes* blancs de Nouvelle-Calédonie. *Bulletin de La Société Mycologique de France* 127 (1–2): 81–98.

Fayod, V. (1889) Prodrome d'une histoire naturelle des Agaricinés. *Annales des Sciences Naturelles, Botanique, VII. 9* 181–411.

Ferisin, G. & Dovana, F. (2016) *Pluteus velutinus* prima segnalazione in Italia. *Micologia e Vegetazione Mediterranea* 31 (1): 45–52.

Ferisin, G. & Dovana, F. (2019) Il genere *Pluteus*, sezione *Hispidoderma*. *Rivista Micologica Romana. Bollettino Dell'Associazione Micologica Ecologica Romana* 106 (1): 23–51.

Fries, E.M. (1815) *Observationes mycologicae*. G. Bonnieri, Havniae.

Fries, E.M. (1821) *Systema Mycologicum: sistens fungorum ordines, genera et species, huc usque cognitas, quas ad normam methodi naturalis determinavit*. Ex Officina Berlingiana, Lundae.

Fries, E.M. (1828) *Elenchus Fungorum, sistens Commentarium in Systema Mycologicum*. Sumtibus Ernesti Mauritii, Gryphiswaldiae.

Fries, E.M. (1835) *Corpus florarum provincialium Sueciae. I. Floram scanicam*. Typis Palmblad, Sebell & Co., Upsaliae, 4–394.

Fries, E.M. (1838) *Epicrisis systematis mycologici seu synopsis Hymenomycetum*. Typographia Academica, Uppsala.

Fries, E.M. (1849) Fungi Natalenses, quos annis 1839-41 collegit J. A. Wahlberg, adjectis quibusdam Capensibus. *Kungl. Svenska vetenskapsakademiens handlingar ser. 3* 121–154.

Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes, application to the identification of mycorrihiza and rusts. *Molecular Ecology* 2 (2): 113–118. https://doi.org/10.1111/J.1365-294x.1993.Tb00005.X

Gillet, C.C. (1876) *Les Hyménomycètes ou Description de tous les Champignons (Fungi) qui Croissent en France avec l'indication de leurs propriétés utiles ou vénéneuses*. Ch. Thomas, Alençon, 177–560.

Grgurinovic, C. (1998) *Larger Fungi of South Australia*. Botanic Gardens of Adelaide and State Herbarium, Adelaide.

Guzmán, G., Allen, J.W. & Gartz, J. (1998) A worldwide geographical distribution of the neurotropic fungi, an analysis and discussion. *Annali Dei Museo Civico, Rovereto* 14: 189–290.

Hausknecht, A. & Contu, M. (2003) The genus *Galerella*. A world-wide survey. Österr. *Z. Pilzk* 12: 31–40.

Homola, R. (1972) Section *Celluloderma* of the Genus *Pluteus* in North America. *Mycologia* 64 (6): 1211–1247. https://doi.org/10.1080/00275514.1972.12019374

Hongo, T. (1976) Agarics from Papua-New Guinea III. *Reports of the Tottori Mycological Institute* 14: 95–104.

Horak, E. (1964) Fungi austroamericani II. *Pluteus* Fr. *Nova Hedwigia* 8: 163–199.

Horak, E. (1976) Neue zairische Arten der Gattung *Pluteus*. *Bulletin Du Jardin Botanique National de Belgique* 47 (1–2): 87–89.

Horak, E. (1980a) *Entoloma* (Agaricales) in Indomalaya and Australasia. *Beihefte Zur Nova Hedwigia* 65: 317.

Horak, E. (1980b) Fungi, Basidiomycetes. Agaricales y Gasteromycetes secotioides. *Flora Criptogámica de Tierra Del Fuego* 11 (6): 110–111.

Horak, E. (1983) Mycogeography in the south Pacific region: Agaricales, Boletales. *Australian Journal of Botany Supplementary Tiers* 13 (10): 1–42.
https://doi.org/10.1071/BT8310001

Horak, E. (2008) *Agaricales of New Zealand 1: Pluteaceae - Entolomataceae (Fungi of New Zealand/Nga Harore o Aotearoa, Volume 5)*. Fungal Diversity Press, Hong Kong.

Horak, E. & Heinemann, P. (1978) *Flore illustrée des Champignons d'Afrique centrale Fascicule 6*. Ministère de l'agriculture, Jardin botanique national de Belgique, Bruxelles.

Hosen, M.I., Liang, X., Xu, J. & Li, T. (2019) *Pluteus squarrosus sp. nov.* (*Pluteus* sect. *Celluloderma*, *Pluteaceae*) from northeast China. *Nordic Journal of Botany* 37 (8): 1–7.
https://doi.org/10.1111/njb.02427

Hosen, M.I., Xu, J., Liang, X. & Li, T.H. (2018) *Pluteus umbrosoides* and *P. chrysaegis*, new records from China. *Mycotaxon* 133 (4): 559–568.
https://doi.org/10.5248/133.559

Hubregtse, J. & Hubregtse, V. (2011) Preliminary Observations on an Undescribed Yellow *Pluteus* Species. *The Victorian Naturalist* 128 (3): 111–115.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
https://doi.org/10.1093/bioinformatics/17.8.754

Ito, S. (1939) Fungi of the Bonin Islands, IV. *Transactions of the Sapporo Natural History Society* 16: 45–56.

Justo, A., Battistin, E. & Angelini, C. (2012) Two new species of *Pluteus* section *Celluloderma* from the Dominican Republic. *Mycotaxon* 120 (1): 1–21.

Justo, A., Caballero, A., Muñoz, G., Minnis, A.M. & Malysheva, E.F. (2011a) Taxonomy of *Pluteus eugraptus* and morphologically similar taxa. *Mycologia* 103 (3): 646–655.
https://doi.org/10.3852/10-280

Justo, A., Malysheva, E.F., Bulyonkova, T., Vellinga, E.C., Cobian, G., Nguyen, N., Minnis, A.M. & Hibbett, D.S. (2014) Molecular phylogeny and phylogeography of Holarctic species of *Pluteus* section *Pluteus* (Agaricales: *Pluteaceae*), with description of twelve new species. *Phytotaxa* 180: 1–85.
https://doi.org/10.11646/phytotaxa.180.1.1

Justo, A., Minnis, A.M., Ghignone, S., Menolli Jr., N., Capelari, M., Rodríguez, O., Malysheva, E.F., Contu, M. & Vizzini, A. (2011b) Species recognition in *Pluteus* and *Volvopluteus* (*Pluteaceae*, Agaricales): Morphology, geography and phylogeny. *Mycological Progress* 10 (4): 453–479.
https://doi.org/10.1007/s11557-010-0716-z

Justo, A., Vizzini, A., Minnis, A.M., Menolli Jr., N., Capelari, M., Rodríguez, O., Malysheva, E.F., Contu, M., Ghinone, S. & Hibbett, D.S. (2011c) Phylogeny of the *Pluteaceae* (Agaricales, Basidiomycota): Taxonomy and character evolution. *Fungal Biology* 115 (1): 1–20.
https://doi.org/10.1016/j.funbio.2010.09.012

Kaygusuz, O., Türkekul, I., Knudsen, H. & Çolak, Ö.F. (2019) New records of *Pluteus* section *Hispidoderma* in Turkey Based on Morphological Characteristics and Molecular Data. *Phytotaxa* 413 (3): 175–206.
https://doi.org/10.11646/phytotaxa.413.3.1

Kornerup, A. & Wanscher, J.H. (1978) *Methuen Handbook of Colour* (3rd ed.). Eyre Methuen, London.

Kotlaba, F. & Pouzar, Z. (1972) Taxonomic and nomenclatural notes on some Macromycetes. *Česká Mykologie* 26 (4): 217–222.

Kuhar, F., Furci, G., Drechsler-Santos, E.R. & Pfister, D.H. (2018) Delimitation of Funga as a valid term for the diversity of fungal communities: The Fauna, Flora & Funga proposal (FF&F). *IMA Fungus* 9 (2): 71–74.
https://doi.org/10.1007/bf03449441

Kühner, R. & Romagnesi, H. (1956) Compléments à la "Flore analytique". VIII. Espèces nouvelles, critiques ou rares de Volvariacées. *Bulletin de La Société Mycologique de France* 72 (3): 181–239.

Kummer, P. (1871) *Der Führer in die Pilzkunde*. C. Luppe, Zerbst, 1–146.

Lange, J.E. (1917) Studies in the Agarics of Denmark. Part III. *Pluteus*, *Collybia*, *Inocybe*. *Dansk botanisk Arkiv* 2 (7): 1–50.

Lange, J.E. (1936) *Flora Agaricina Danica* (Vol. 1–2). Copenhagen, Copenhagen.

Largent, D., Johnson, D. & Watling, R. (1986) *How to Identify Mushrooms to Genus III: Microscopic Features*. Mad River Press, Eureka.

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, L.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W & Clustal X version 2.0. *Bioinformatics* 23: 2947–2948.

Lezzi, T., Vizzini, A., Ercole, E., Migliozzi, V. & Justo, A. (2014) Phylogenetic and morphological comparison of *Pluteus variabilicolor* and *P. castri* (Basidiomycota, Agaricales). *IMA Fungus* 5 (2): 415–423.

https://doi.org/10.5598/imafungus.2014.05.02.06

Looney, B.P., Birkebak, J.M. & Matheny, P.B. (2013) Systematics of the genus *Auricularia* with an emphasis on species from the southeastern United States. *North American Fungi* 8 (6): 1–25.

Maddison, W.P. & Maddison, D.R. (2016) Mesquite: a modular system for evolutionary analysis. Version 3.10. Available from: http://mesquiteproject.org

Maekawa, N. (2002) Corticioid fungi (Basidiomycota) collected in Vanuatu. *Annals of the Tsukuba Botanical Garden* 21: 119–126.

Malysheva, E.F., Malysheva, V.F. & Justo, A. (2016) Observations on *Pluteus* (*Pluteaceae*) diversity in South Siberia, Russia: morphological and molecular data. *Mycological Progress* 15 (8): 861–882.
https://doi.org/10.1007/s11557-016-1215-7

Malysheva, E.F., Malysheva, V.F., Alexandrova, A. & Morozova, O. (2020) Observations on *Pluteaceae* in Vietnam. 2. One new record and ten new species of *Pluteus*. *Phytotaxa* 461 (2): 79–107.
https://doi.org/10.11646/phytotaxa.461.2.2

Malysheva, E.F., Popov, E., Morozova, O., Dudka, V., Pham, T.H.G. & Malysheva, V.F. (2023) Observations on *Pluteaceae* in Vietnam: Four New Species and New Records of *Pluteus*. *Journal of Fungi* 9: 584.
https://doi.org/10.3390/jof9050584

Massee, G.E. (1899) Fungi Exotici, II. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 1899 (153/154): 178.
https://doi.org/10.2307/4111355

McClatchie, A.J. (1897) Seedless plants of southern California. *Proceedings of the Southern California Academy of Sciences* 1: 338–395.

McKenzie, E.H.C. (1989) *The fungi, bacteria and pathogenic algae of Vanuatu*. Plant Diseases Division, DSIR, Auckland.

Menolli Jr., N., Asai, T. & Capelari, M. (2010) Records and new species of *Pluteus* from Brazil based on morphological and molecular data. *Mycology* 1 (2): 130–153.
https://doi.org/10.1080/21501203.2010.493531

Menolli Jr., N. & Capelari, M. (2010) Notes on *Pluteus* (*Pluteaceae*, Agaricales) from Brazil including two new species and a new record. *Mycologia* 102 (3): 697–707.
https://doi.org/10.3852/09-200

Menolli Jr., N. & Capelari, M. (2013) One hundred fourteen years of *Pluteus* in Brazil: collections studied by Hennings and Rick. *Mycotaxon* 126 (1): 191–226.
https://doi.org/10.5248/126.191

Menolli Jr., N. & Capelari, M. (2016) *Pluteus* section *Celluloderma* (*Pluteaceae*, Agaricales) in Brazil: additional morphological studies and an annotated checklist of all named taxa. *Iheringia Serie Botanica* 71 (3): 316–330.

Menolli Jr., N., de Meijer, A.A.R. & Capelari, M. (2015a) The genus *Pluteus* (*Pluteaceae*, Agaricales) from the state of Paraná, Brazil. *Nova Hedwigia* 100 (1–2): 101–157.
https://doi.org/10.1127/nova_hedwigia/2014/0224

Menolli Jr., N., Justo, A., Arrillaga, P., Pradeep, C.K., Minnis, A.M. & Capelari, M. (2014) Taxonomy and phylogeny of *Pluteus glaucotinctus* sensu lato (Agaricales, Basidiomycota), a multicontinental species complex. *Phytotaxa* 188 (2): 78–90.
https://doi.org/10.11646/phytotaxa.188.2.2

Menolli Jr., N., Justo, A. & Capelari, M. (2015b) Phylogeny of *Pluteus* section *Celluloderma* including eight new species from Brazil. *Mycologia* 107 (6): 1205–1220.
https://doi.org/10.3852/14-312

Menolli Jr., N., Justo, A. & Capelari, M. (2015c) *Pluteus* Section *Hispidoderma* in Brazil with New Records Based on Morphological and Molecular Data. *Cryptogamie, Mycologie* 36 (3): 331–354.
https://doi.org/10.7872/crym/v36.iss3.2015.331

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In: 2010 Gateway Computing Environments Workshop, GCE 2010.*
https://doi.org/10.1109/GCE.2010.5676129

Minnis, A.M. & Sundberg, W.J. (2010) *Pluteus* section *Celluloderma* in the U.S.A. *North American Fungi* 5: 1–107.
https://doi.org/10.2509/naf2010.005.001

Montagne, J.P.F.C. (1854) Cryptogamia Guyanensis seu plantarum cellularium in Guyana gallica annis 1835-1849 a cl. Leprieur collectarum enumeratio universalis. *Annales des Sciences Naturelles Botanique* 1: 91–144.

Mueller, G.M., Schmit, J.P., Leacock, P.R., Buyck, B., Cifuentes, J., Desjardin, D.E., Halling, R., Hjortstam, K., Iturriaga, T., Larsson, K.H., Lodge, D.J., May, T.W., Minter, D., Rajchenberg, M., Redhead, S.A., Ryvarden, L., Trappe, J.M., Watling, R. & Wu, Q. (2007) Global diversity and distribution of macrofungi. *Biodiversity and Conservation* 16 (1): 37–48.
https://doi.org/10.1007/s10531-006-9108-8

Murrill, W.A. (1911) The *Agaricaceae* of tropical North America–IV. *Mycologia* 3 (6): 271–282.

Murrill, W.A. (1917) *Agaricaceae* subtribe Pluteanae. *North American Flora* 10 (2): 77–144.

Niveiro, N. & Albertó, E. (2012) Checklist of the Argentine Agaricales I. *Amanitaceae*, *Pluteaceae* and *Hygrophoraceae*. *Mycotaxon* 119: 493–494.

Orton, P.D. (1960) New checklist of British agarics and boleti 3. Notes on genera and species in the list. *Transactions of the British Mycological Society* 43: 159–439.

Orton, P.D. (1986) *British Fungus Flora. Agarics and Boleti 4: Pluteaceae: Pluteus and Volvariella*. Royal Botanic Garden, Edinburgh.

Park, M.S., Cho, H.J., Kim, N.K., Park, J.Y., Lee, H., Park, K.H., Kim, M., Kim, C. & Lim, Y.W. (2017) Ten New Recorded Species of Macrofungi on Ulleung Island, Korea. *Mycobiology* 45 (4): 286–296.

Patouillard, N.T. (1889) Le Genre *Ganoderma*. *Bulletin trimestriel de la Société mycologique de France* 5 (2,3): 54–80.

Peck, C.H. (1885). Report of the Botanist (1884). *Annual Report on the New York State Museum of Natural History* 38:77-138.

Pegler, D.N. (1977) A Preliminary Agaric Flora of East Africa. *Kew Bulletin Additional Tiers* 6 (1): 264–277.

Pegler, D.N. (1983a) Agaric flora of the Lesser Antilles. *Kew Bulletin Additional Tiers* 9: 1–668.

Pegler, D.N. (1983b) The genus *Lentinus*: a world monograph. *Kew Bulletin Additional Tiers*.

Pegler, D.N. (1986) Agaric flora of Sri Lanka. *Kew Bulletin Additional Tiers* 12: 1–519.

Pegler, D.N. (1997) *The agarics of São Paulo: an account of the agaricoid fungi (Holobasidiomycetes) of São Paulo State, Brazil*. Royal Botanic Gardens Kew.

Petch, T. (1912) Revisions of Ceylon fungi (Part III). *Annals of the Royal Botanic Gardens Peradeniya* 5: 265–301.

Pradeep, C.K., Justo, A., Vrinda, K.B. & Shibu, V.P. (2012) Two new species of *Pluteus* (*Pluteaceae*, Agaricales) from India and additional observations on *Pluteus chrysaegis*. *Mycological Progress* 11 (4): 869–878.
https://doi.org/10.1007/s11557-011-0801-y

Pradeep, C.K. & Vrinda, K.B. (2006) New and noteworthy species of *Pluteus* (*Pluteaceae*, Agaricales) from Kerala State, India. *Persoonia: Molecular Phylogeny and Evolution of Fungi* 19 (1): 95–99.

Pradeep, C.K., Vrinda, K.B. & Abraham, T.K. (2002) *Pluteus* section *Pluteus* (*Pluteaceae*, Agaricales) from Kerala State, India. *Mycotaxon* 83: 59–66.

Quélet, L. (1883) Quelques espèces critiques ou nouvelles de la Flore Mycologique de France. *Comptes Rendus de l'Association Française pour l'Avancement des Sciences* 11: 387–412.

Raithelhuber, J. (1991) *Flora mycologica Argentina. Hongos III*. Mycosur, Stuttgart.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67 (5): 901–904.

Rehner, S.A. & Buckley, T.R. (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97 (1): 84–98.

Rick, J. (1961) Basidiomycetes eubasidii in Rio Grande do Sul – Brasilia. 5. *Agaricaceae*. *Iheringia, Série Botánica* 8: 301–449.

Rodríguez, O. (2013) El género *Pluteus* (Agaricales, *Pluteaceae*) en México. *Revista Mexicana de Biodiversidad* 84: 128–151.

Rodríguez, O. (2024) Type studies of *Pluteus* (Fungi, Agaricales, *Pluteaceae*). *Darwiniana, nueva serie* 12 (1): 75–106.

Rodríguez, O. & Guzmán-Dávalos, L. (1999) Nuevos registros del género *Pluteus* Fr. (*Pluteaceae*) en México. *Documents Mycologiques* 114: 67–78.

Rodríguez, O. & Guzmán-Dávalos, L. (2001) Clave Dicotómica de las Especies del Género *Pluteus* Fr. (*Pluteaceae*) Conocidas de la Región de Nueva Galicia y Algunas Áreas Aledañas, México. *Acta Botanica Mexicana* (57): 23–36.

Rodríguez, O. & Guzmán-Dávalos, L. (2007) Nuevos registros de *Pluteus* Fr. (Basidiomycetes, Agaricales, *Pluteaceae*) en Mexico. *Acta Botánica Mexicana* 80: 21–39.

Rodríguez, O., Guzmán-Dávalos, L. & Horak, E. (2008) *Pluteus neotropicalis* (*Pluteaceae*, Agaricales) a new species from tropical-subtropical Mexico. *Mycotaxon* 103: 273–278.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Saccardo, P.A. (1887) Sylloge Hymenomycetum, Vol. I. Agaricineae. *Sylloge Fungorum* 5: 1–1146.

Saupe, S.G. (1981) Occurrence of psilocybin/psilocin in *Pluteus salicinus* (*Pluteaceae*). *Mycologia* 73: 781–784.

Ševčíková, H., Antonín, V. & Borovička, J. (2014) *Pluteus septocystidiatus*, a new species with unique pleurocystidia. *Sydowia* 66 (2): 229–239.
https://doi.org/10.12905/0380.sydowia66(2)2014-0229

Ševčíková, H., Borovička, J. & Gates, G. (2021) *Pluteus hubregtseorum* (*Pluteaceae*), a new species from Australia and New Zealand. *Phytotaxa* 496 (2): 147–158.
https://doi.org/10.11646/phytotaxa.496.2.4

Singer, R. (1954) Agaricales von Nahuel Huapi. *Sydowia* 8: 100–157.

Singer, R. (1956) Contributions towards a monograph of the genus *Pluteus*. *Transactions of the British Mycological Society* 39 (2): 145–232.
https://doi.org/10.1016/S0007-1536(56)80001-6

Singer, R. (1958) Monographs of South American Basidiomycetes, especially those of the east slope of the Andes and Brazil. 1. The genus *Pluteus* in South America. *Lloydia* 21: 195–299.

Singer, R. (1961) Monographs of South American Basidiomycetes, especially those of the East Slope of the Andes and Brazil. 4. Inocybe in the Amazon region with a Supplement to part 1 (*Pluteus* in South America). *Sydowia* XV (4): 112–132.

Singer, R. (1969) Mycoflora australis. *Beihefte Zur Nova Hedwigia* 29: 153–159.

Singer, R. (1984) Weiss-und rosasporige Agaricales (Tricholomatales und Pluteaceae) aus Österreich. *Sydowia* 36: 277–287.

Singer, R. (1986) *The Agaricales in Modern Taxonomy*. Koeltz Scientific Books, Chicago.

Singer, R. (1989) Agaricales from Henderson Islands (South Pacific). *Mycologia* 81: 793.

Singer, R. & Digilio, R.P.L. (1952) Pródomo de la flora Agaricina Argentina. *Lilloa* 25: 5–461.

Smith, A.H. & Stuntz, D.E. (1958) Studies on the genus *Pluteus* I. Redescriptions of American species based on a study of type specimens. *Lloydia* 21: 115–136.

Stamatakis, A. (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*.
https://doi.org/10.1093/bioinformatics/btu033

Stevenson, G. (1962) The Agaricales of New Zealand: II. *Kew Bulletin* 16 (1): 65–74.

Takehashi, S. & Kasuya, T. (2009) *Pluteus magnus* and *Pluteus podospileus* f. *podospileus*, two agaric species new to Japan. *Mycoscience* 50 (1): 74–77.
https://doi.org/10.1007/s10267-008-0446-0

Touzel, G. & Garner, B. (2018) "The Person Herself is not Interesting": Lucy Evelyn Cheesman's Life Dedicated to the Faunistic Exploration of the Southwest Pacific. *Collections* 14 (4): 497–531.

Vellinga, E.C. (1988) Glossary. *In*: Bas, C. (Ed.) *Flora Agaracina Neerlandica: critical monographs on families of agarics and boleti occurring in the Netherlands Vol. 1*, Rotterdam: Taylor & Francis, pp. 54–64.

Vellinga, E.C. (1990) *Pluteus*. *In*: Bas, C., Kuyper, T.W., Noordeloos, M.E. & Vellinga, E.C. (Eds.) *Flora Agaricina Neerlandica, Vol. 2*. A.A. Balkema Publishers.

Vellinga, E.C. & Schreurs, J. (1985) Notulae ad Floram agaricinam neerlandicam — VIII. *Pluteus* Fr. in West-Europe. *Persoonia* 12 (4): 337–373.

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. *Journal of bacteriology* 172 (8): 4238–4246.

Voto, P. (2022) Novelties in the Family *Psathyrellaceae*. Part VI. *Mycological Observations* 2: 9.

Wannathes, N., Suwannarach, N., Khuna, S. & Kumla, J. (2022) Two Novel Species and Two New Records within the Genus *Pluteus* (Agaricomycetes, Agaricales) from Thailand. *Diversity* 14 (3): 156.

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In*: *PCR protocols: a Guide to Methods and Applications*, Academic Press, San Diego, pp. 315–322.

Wilgenbusch, J.C. & Swofford, D. (2003) Inferring Evolutionary Trees with PAUP*. *In*: *Current Protocols in Bioinformatics*.
https://doi.org/10.1002/0471250953.bi0604s00

Wright, J.E. & Albertó, E. (2002) *Guía de hongos de la región pampeana. I. Hongos con laminillas* (1st ed.). L.O.L.A. (Literature for Latin America), Buenos Aires.