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## Studies in the *Panaeolus papilionaceus* complex (Agaricales, Galeropsidaceae): two new species discovered in the Dominican Republic and Australia

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**Abstract:** Dominican and Australian collections morphologically assignable to the “*Panaeolus papilionaceus* complex” were studied using morphological and molecular (nrITS) data. Two new species are described: *P. pantropicalis* from the Dominican Republic and Australia, and *P. detriticola* from Australia. A morphological and molecular revision of the holotype and three paratypes of *P. papilionaceus* var. *parvisporus* revealed that they do not all represent the same taxon. The holotype was revised morphologically but no usable sequences could be generated from it, the Brazilian paratype is molecularly conspecific with the species described here as *P. pantropicalis* and the two German paratypes are molecularly conspecific with several collections in GenBank identified as *P. retirugis*. These German paratypes, geographically and microscopically closest with the holotype, are accepted as reliable representative collections of *P. papilionaceus* var. *parvisporus* here combined at the species level. Our phylogenetic analysis identifies two major clades containing the “*P. papilionaceus* species complex”: *P. papilionaceus* clade and *P. parvisporus* clade. *P. campanulatus*, *P. retirugis* and *P. sphinctrinus* are treated as synonyms of *P. papilionaceus*, while the “small-spored” descriptions of *P. retirugis* are treated as *P. parvisporus* comb. nov. We also provide the first report of *P. antillarum* from the Dominican Republic and the first modern colour image of *P. nirimpii*.

## INTRODUCTION

The name *Panaeolus* was first introduced by Fries (1849) as *Agaricus* subgen. *Panaeolus* Fr. to accommodate species with black spores (Ser. V - *Coprinarius*), fleshy pileus and mottled lamellae (subgen. XXI - *Panaeolus*). This subgenus was later raised to the generic rank by Quélet (1872), *Panaeolus* (Fr.) Quél., currently a *nomen conservandum* against several other names treated as later synonyms (see Voto 2024). *Panaeolus* is typified by *Agaricus papilionaceus* Bull.

The genus *Panaeolus* has been classified in different families over time (Agaricaceae Chevall., Bolbitiaceae Singer, Panaeolaceae Locq. invalid, Psathyrellaceae Vilgalys, Moncalvo & Redhead and Strophariaceae Singer & A.H. Sm.) but recently Kalichman, Kirk & Matheny (2020) have proposed that *Panaeolus* should be classified in the family Galeropsidaceae Singer. Phylogenetic reconstructions (see, e.g., this study and Malysheva *et al.* 2019) demonstrate that *Galeropsis desertorum* Velen. & Dvořák [currently *Panaeolus desertorum* (Velen. & Dvořák) E.F. Malysheva] belongs to the genus *Panaeolus*; as this name is the type of the genus *Galeropsis* Velen., this genus is automatically reduced to synonymy with *Panaeolus* (Art. 11.3), and in turn, as *Galeropsis* is the type name of the family Galeropsidaceae, the genus *Panaeolus* must be included in this family (Art. 11.3).

*Panaeolus* comprises 4 subgenera and 56 species worldwide (Voto 2024) occurring in temperate, tropical and desert regions. It includes saprotrophic species growing in different habitats (coprophilous, lignicolous or grass-associated); agaricoid to secotioid habit; with or without a partial veil. Some species, mostly, but not only, in *P.* subg. *Copelandia* Ew., turn bluish on handling, as they contain psilocybin-like substances (see e.g. Voto & Angelini 2021). The microscopic characters of *Panaeolus* are very variable as well: pleurocystidia absent to present and then of the sulphidia type or metuloid; basidiospores large to very small, ellipsoid or rhomboid to hexagonal, terete or lenticular; germ pore flat to protruding, central to eccentric.

Within the genus, the “*Panaeolus papilionaceus* complex” is morphologically characterized mainly by absence of pleurocystidia, which includes it in *P.* subgen. *Panaeolus*, large three-dimensional spores (on average longer than 12  $\mu\text{m}$ ), a coprophilous habitat (with one lignicolous exception), non-bluing basidiomes and presence of velar remains at the pileus margin.

Collections of this complex made in the Dominican Republic had significantly smaller basidiospores than the typical *P. papilionaceus*. A morphological and molecular revision of *P. papilionaceus* var. *parvisporus* was consequently an obligate step to clarify the identity of the Dominican collections.

Gerhardt (1996), in his global compendium of the genus *Panaeolus* s.l., grouped all exannulate, small-spored collections of *P.* sect. *Panaeolus* under *P. papilionaceus* var. *parvisporus*. In the original description of this taxon Gerhardt listed collections from different geographical and climate areas of the world in the examined materials: Europe (from Germany, inclusive of the type), Africa (from Malawi and Zaire), North America (from Alabama, USA), South America (from Colombia and Brazil) and Australia (from South Australia). Of these, we have obtained to sequence and/or study those from Germany, Brazil and Colombia.

Based on our study the name *P. papilionaceus* var. *parvisporus* is raised to species-level as *P. parvisporus*, but, to current knowledge, this taxon is restricted to Europe. The examined Brazilian collection of *P. papilionaceus* var. *parvisporus* and new collections from the Dominican Republic and Australia represent a different species here described as *P. pantropicalis*.

During the revision of some Australian collections of *Panaeolus*, one more collection was found to represent an additional novel taxon, here described as *P. detriticola*.

## MATERIALS AND METHODS

### Morphology

*P. pantropicalis*. The Dominican collections were photographed when fresh *in situ* by C. Angelini using a digital camera Nikon Coolpix 8400 and subsequently dried; microscopic characters were studied, described and photographed by P. Voto on dried material revived with 10% NH<sub>4</sub>OH or 5% KOH and in some cases using Congo red as mounting medium for imaging. The microscopic characters of the Australian collection MDB5337 (in herb. PERTH 09605894) were studied, described and photographed by N.L. Bougher on dried material revived with 3% KOH.

*P. detriticola*. The basidiomes were photographed both when fresh *in situ* and in laboratory some hours after collecting by N.L. Bougher using a digital SLR camera Canon 450D. The microscopic characters were studied, described and photographed by N.L. Bougher on dried material revived with 3% KOH.

The measures of the three-dimensional spores are expressed with the formula  $a_1 - a_2 \times b_1 - b_2 \times c_1 - c_2$  where  $a_1 - a_2$  is the length interval,  $b_1 - b_2$  is the breadth interval as measured in front view,  $c_1 - c_2$  is the breadth interval as measured in side view; in parentheses the extreme values of measures with less than 10% occurrence.

The herbaria cited in this paper are: ZE Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Berlin (Germany), code B; Jardín Botánico Nacional Dr. Rafael M. Moscoso, Santo Domingo (Dominican Republic), code JBSD; The New York Botanical Garden, New York (USA), code NY; Università degli Studi di Padova, Padua (Italy), code PAD; Western Australian Herbarium, Perth (Australia), code PERTH. Their codes are taken from Index Herbariorum by Holmgren & Holmgren (1998).

The authors of the images in the figures are shown in square brackets.

### DNA extraction, PCR and DNA sequencing

The molecular study was performed employing ITS nrDNA sequences; the generation of new sequences from the Dominican materials were commissioned to Alvalab (Spain).

Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). PCR reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54°C. The primers ITS1F, ITS1 and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were employed to amplify the ITS rDNA region. PCR products were checked in 1% agarose gels, and amplicons were sequenced with one or both PCR primers.

### Sequence alignment and phylogenetic analyses

A data set consisting of a total of 197 ITS rDNA sequences from specimens, of which 185 retrieved from GenBank, 4 retrieved from UNITE and 9 newly generated from this study, was prepared for phylogenetic analysis. The samples' origin and their accession numbers are given in Table 1.

Sequences were corrected to remove reading errors in chromatograms. BLASTn (Altschul *et al.* 1990) was used to select the most closely related sequences from the International Nucleotide Sequence Database Collaboration public database (INSDC, Arita *et al.* 2021) and UNITE (Nilsson *et al.* 2018). Sequences first were aligned in MEGA 5.0 (Tamura *et al.* 2011) with its Clustal W application and then realigned manually as needed to establish positional homology.

The resulting alignment was loaded in MrBayes 3.2.6 (Ronquist *et al.* 2012), where a Bayesian analysis was performed (GTR+G+I model, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until the average split frequencies between the simultaneous runs fell below 0.01 after 4.32 M generations.

Finally, a full search for the best-scoring maximum likelihood tree was performed in RAxML 8.2.12 (Stamatakis 2014) using the standard search algorithm (same partitions, GTRCAT model, 2000 bootstrap replications). The significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP). *Panaeolus guttulatus* was chosen as outgroup due to its basal position to the remaining species of *Panaeolus*, as shown in Asif *et al.* (2023).

## RESULTS

### Phylogenetic analyses

Our study highlights that the morphology-based concept of the "*Panaeolus papilionaceus* complex" is not fully phylogenetically supported. In our phylogram all the species belonging to the complex are contained in a single well supported supra-clade (node A in fig. 1) including clades 2 to 6.

This supra-clade includes morphologically very different taxa: e.g. *P. punjabensis* (clade 3) which differs in the absence of a veil and non-lentiform spores with a non-protruding apex, and *P. desertorum* (clade 5) which differs in its secotioid habit, absence of a veil, non-lentiform spores with a non-protruding apex, and a non-coprophilic habitat.

However, a morphological subdivision is suggested in the topology of our phylogram. The supra-clade containing clades 2 to 6 comprises two blocks. One block is composed of clades 5 and 6 (*P. alcis*, *P. desertorum* and *P. papilionaceus*) which share large spores (on average more than 15 µm long and 8 µm wide in lateral view) and a temperate habitat. The second block is composed of clades 2 to 4 (*P. detriticola*, *P. pantropicalis*, *P. parvisporus*, *P. punjabensis* and three undetermined vouchers from China, Colombia and Lao) which share small spores (on average less than 15 µm long and 8 µm wide in lateral view) and usually a tropical to subtropical habitat.

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**Figure 1** (next page, divided in two parts): A 50% majority rule ITS rDNA consensus phylogram of the genus *Panaeolus* (with *P. guttulatus* as outgroup) obtained using MrBayes from 32400 sampled trees. Nodes were annotated if they were supported by  $\geq 0.95$  Bayesian posterior probability (left) or  $\geq 70\%$  maximum likelihood bootstrap proportions (right). Non-significant support values are exceptionally represented inside parentheses. Sequences newly generated in this study are in bold.







**Table 1** (page below): Data of specimens used in this study. The column 'Current name' is used for the current name of species which are synonymised (in bold) or vouchers which are misidentified (not in bold). Current names proposed in this paper are in red, those proposed by other authors are identified by asterisks (\*: Malysheva et al. 2019, \*\*: Asif et al. 2023). The accession numbers of the newly generated sequences are in bold blue. Bold capital letters after species names represent Holotype (T), Paratypes (P) and Lectotypes (L)

species name in GenBank	current name	voucher/origin	ITS
<i>Galeropsis bispora</i> T	<i>P. plantaginiformis</i> *	LE 2863/Uzbekistan	MK397580
<i>G. desertorum</i>	<i>P. desertorum</i> *	NL-1863/Hungary	JX968154
<i>Gastrocybe iberica</i> T	<i>P. desertorum</i> *	AH 9990/Spain	MK397542
<i>G. iberica</i> P	<i>P. desertorum</i> *	AH 9993/Spain	MK397543
<i>G. iberica</i>	<i>P. desertorum</i> *	AH 10396/Spain	MK397544
<i>G. iberica</i>	<i>P. desertorum</i> *	AH 42860/Spain	MK397545
<i>G. iberica</i>	<i>P. desertorum</i> *	AH 10493/Spain	MK397546
<i>Panaeolus acuminatus</i>		CBS:270.47/?	MH856251
<i>P. acuminatus</i>		inaturalist.org/observations/141352004/USA	OQ372246
<i>P. acuminatus</i>		SGL09/China	OR035540
<i>P. acuminatus</i>		CBS 269.47/?	MH856250
<i>P. acuminatus</i>	<i>P. olivaceus</i>	PRM 935914/Czech Republic	MW352021
<i>P. acuminatus</i>	<i>P. sp.</i>	4084/Italy	JF908518
<i>P. alcis</i>		Mushroom Observer #88085/Sweden	KM982723
<i>P. alcis</i>		SAT-14-239-20/USA(Alaska)	MW597122
<i>P. antillarum</i>		SFSU:DED7874/Thailand	MF497585
<i>P. antillarum</i>		PAD H0061942/Dominican Republic	<b>PP590043</b>
<i>P. antillarum</i>		CORT:013830/Dominican Republic	MF497586
<i>P. antillarum</i>		JL27/China	ON059337
<i>P. antillarum</i>		NSK 1017353/Russia	OR364524
<i>P. antillarum</i>		EGDA-N15/Egypt	ON024905
<i>P. antillarum</i>		BR5020167127933/Togo	OR035499
<i>P. antillarum</i>		WANG 140007/Taiwan	KR998382
<i>P. antillarum</i>		FLAS-F-69480/USA	OQ746434
<i>P. antillarum</i>		DQS36F/Philippines	MZ735416
<i>P. antillarum</i>		HYW22/Thailand	OR035522
<i>P. antillarum</i>		HYW21/Thailand	OR035520
<i>P. axfordii</i> T		MFLU:19-2367/China	NR_169700
<i>P. bisporus</i>	<i>P. cyanescens</i>	KaiR95/Benin	MT110229
<i>P. bisporus</i>	<i>P. cyanescens</i>	MushroomObserver.org/188954/USA	MG966283
<i>P. bisporus</i>	<i>P. cyanescens</i>	HYW197/China	OR035518
<i>P. bisporus</i>	<i>P. cyanescens</i>	T2507/China	OR035542
<i>P. cambodginiens</i>	<i>P. cyanescens</i>	NBRC-30222/Japan?	AB158633
<i>P. campanulatus</i>	<i>P. papilionaceus</i>	10141/Italy	JF908522
<i>P. campanulatus</i>	<i>P. papilionaceus</i>	Mushroom2/China	MT451920
<i>P. campanulatus</i>	<i>P. cinctulus</i>	/China	JF961376
<i>P. castaneifolius</i>	<i>P. foeniseccii</i>	Mushroom Observer 90428/USA	KX010428
<i>P. cinctulus</i>		iNAT:56796374/USA	OQ147191
<i>P. cinctulus</i>		iNAT:126276059/USA	OP751540
<i>P. cinctulus</i>		S.D. Russell ONT iNaturalist 130442846/USA	OP549138
<i>P. cinctulus</i>		PRM 935916, Mushroom Observer 204889/Italy	MW352022

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<i>P. cinctulus</i>		Mushroom Observer # 321948/USA	MH590045
<i>P. cinctulus</i>		OMDL K. Canan iNaturalist # 169757989/USA	OR987159
<i>P. cinctulus</i>		OMDL K. Canan iNaturalist # 170057671/USA	OR987260
<i>P. cinctulus</i>		iNat86856915/USA	OQ389417
<i>P. cinctulus</i>		BR5020180462561/Netherlands	OR035501
<i>P. cinctulus</i>		HYW186/China	OR035517
<i>P. cyanescens</i>		AF163/China	OQ450458
<i>P. cyanescens</i>		D36/China	KT002152
<i>P. cyanescens</i>		MHHNU 31855/China	OP862802
<i>P. cyanescens</i>		SIV1/India	MK855517
<i>P. cyanescens</i>		FS1/India	MK855516
<i>P. cyanescens</i>		SIV2/India	MK855518
<i>P. cyanescens</i>		LAH37983_Panaeolus_cyanescens_sm38/Pakistan	OR668690
<i>P. cyanescens</i>		LAH37985_Panaeolus_cyanescens_sm40/Pakistan	OR668692
<i>P. cyanescens</i>		MES-4248/USA	OR664094
<i>P. cyanescens</i>		BP17M/Philippines	OR062405
<i>P. cyanescens</i>		1S/Croatia?	KU640168
<i>P. cyanescens</i>		18S/?	HM035084
<i>P. cyanescens</i> var. <i>bisporus</i>	<i>P. cyanescens</i>	n. 6576 AQU1/Italy	EU834287
<i>P. desertorum</i>		LE 313090/Russia	MK397566
<i>P. desertorum</i>		LE 313250/Russia	MK397568
<i>P. desertorum</i>		LE 313091/Greece	MK397567
<i>P. desertorum</i>	<i>P. plantaginiformis</i>	LE 2864/Uzbekistan	MH055384
<i>P. desertorum</i>	<i>P. plantaginiformis</i>	LE 2865/Uzbekistan	MH055383
<i>P. fimicola</i>		NSK 1017274/Russia	OR242695
<i>P. fimicola</i>		Mushroom6/China	MT451924
<i>P. fimicola</i>		20180624002/China	MT347601
<i>P. fimicola</i>		474/Italy	JF908514
<i>P. fimicola</i>		HMJAU66147/China	OQ927089
<i>P. foenisecii</i>		T-790/USA	KC176293
<i>P. foenisecii</i>		S.D. Russell MycoMap # 5430/USA	ON561649
<i>P. foenisecii</i>		S.D. Russell ONT iNaturalist # 141290781/USA	OQ297023
<i>P. foenisecii</i>		iNAT:21657597/USA	OM212934
<i>P. foenisecii</i>		S.D. Russell MycoMap # 5431/USA	ON561650
<i>P. foenisecii</i>		OMDL K. Canan iNaturalist # 172543719/USA	OR732083
<i>P. foenisecii</i>		OMDL K. Canan iNaturalist # 169180865/USA	OR825597
<i>P. foenisecii</i>		OMDL K. Canan iNaturalist # 171232504/USA	OR785929
<i>P. foenisecii</i>		S.D. Russell ONT iNaturalist 118906067/USA	OP749347
<i>P. foenisecii</i>		S.D. Russell ONT iNaturalist # 121782791/USA	OP470404
<i>P. foenisecii</i>		OMDL K. Canan iNaturalist # 170924896/USA	OR732074
<i>P. foenisecii</i>		JLF9301 iNaturalist # 81665784/USA	OQ859921
<i>P. foenisecii</i>		S.D. Russell MycoMap # 5536/USA	ON561653
<i>P. foenisecii</i>		S.D. Russell ONT iNaturalist 127360021/USA	OP549249
<i>P. foenisecii</i>		705-2/China	DQ403253
<i>P. foenisecii</i>		GS6/China	OR035507
<i>P. foenisecii</i>		M8/Hungary	OQ029266
<i>P. foenisecii</i>		OTA:71571/New Zealand	OQ064958

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<i>P. foeniseccii</i>		6643/Italy	JF908520
<i>P. foeniseccii</i>		K(M):250281/United Kingdom	MZ159698
<i>P. foeniseccii</i>		BR5020160357160/Belgium	OR035496
<i>P. foeniseccii</i>		CBS 142.40/?	MH856067
<i>P. foeniseccii</i>		CBS 143.40/?	MH856068
<i>P. foeniseccii</i>	<i>P. sp.</i>	CBS 251.37/?	MH855904
<i>P. foeniseccii</i>	<i>P. antillarum</i>	UOC-KAUNP-MK62/Sri Lanka	KP764810
<i>P. foeniseccii</i>	<i>P. antillarum</i>	UOC KAUNP K01/Sri Lanka	KR867660
<i>P. foeniseccii</i>	<i>P. antillarum</i>	PC14/Philippines	OK446756
<i>P. fraxinophilus</i>		MushroomObserver.org/455364/USA	OL629088
<i>P. fraxinophilus</i>		OMDL K. Canan iNaturalist # 170758482/USA	OR987324
<i>Panaeolus guttulatus</i>		STA5/Iraq	LC458688
<i>Panaeolus guttulatus</i>		AMB n. 18101/Italy	KU725993
<i>Panaeolus guttulatus</i> var. <i>merrisiani</i>		AMB n. 18102/Italy	KU725994
<i>P. mexicanus</i>		ANGE1557/Dominican Republic	MZ856314
<i>P. olivaceus</i>		139/Iran	MH593015
<i>P. olivaceus</i>		Pan.Olivaceus-ITS1/USA	OQ318238
<i>P. olivaceus</i>		MushroomObserver.org/89608/USA	MH285992
<i>P. olivaceus</i>	<i>P. fraxinophilus?</i>	UBC F-32268/Canada	MF955153
<i>P. cf. olivaceus</i>		MushroomObserver.org/158389/USA	MF629829
<i>P. pantropicalis</i> T		JBSD 130972/Rep. Dominicana	PP590037
<i>P. pantropicalis</i> P		PAD H0061940/Rep. Dominicana	PP590036
<i>P. pantropicalis</i> P		PAD H0061941/Rep. Dominicana	PP590038
<i>P. pantropicalis</i> P		PERTH 09605894/Australia	PP590039
<i>P. papilionaceus</i>		iNAT:22477730/USA	OM338968
<i>P. papilionaceus</i>		MushroomObserver.org/312080/USA	MH100727
<i>P. papilionaceus</i>		MushroomObserver.org/312173/USA	MH100681
<i>P. papilionaceus</i>		Mushroom Observer 428579/USA	MW633031
<i>P. papilionaceus</i>		S.D. Russell MycoMap # 5533/USA	ON245337
<i>P. papilionaceus</i>		Montri-76/Switzerland?	MK028487
<i>P. papilionaceus</i>		Mushroom Observer # 114447/Mexico	MF628989
<i>P. papilionaceus</i>		GSX/China	OR035509
<i>P. papilionaceus</i>		MHHNU31392/China	MK439503
<i>P. papilionaceus</i>		HNL501769/Lao	UDB033926
<i>P. papilionaceus</i>		STA2/Iran	LC458685
<i>P. papilionaceus</i>		RA400/Iraq	MH632116
<i>P. papilionaceus</i> T	<i>P. detriticola</i>	PERTH 08944954/Australia	MT571659
<i>P. papilionaceus</i>	<i>P. foeniseccii</i>	CIRM BRFM 715/?	OL739389
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	Mushroom Observer # 288725/Mexico	MH169580
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	FLAS-F-69055/USA	OP163246
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	FLAS-F-69481/USA Florida	OQ746433
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	DNA1940/USA Florida	KF830093
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	D15/China	KC414234
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	HFJAU0032/China	MN258670
<i>P. papilionaceus</i>	<i>P. pantropicalis</i>	MHHNU 31396/China	OP862800
<i>P. papilionaceus</i>	<i>P. punjabensis</i>	Shelly024/Namibia	UDB0800254
<i>P. papilionaceus</i>	<i>P. sp.</i>	EGDA-Pan228/Egypt	MW915589
<i>P. papilionaceus</i>	<i>P. sp.</i>	SR024/Namibia	UDB0800254

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<i>P. papilionaceus</i>	<i>P. parvisporus</i>	ECO-TA-HO 7877/Mexico	MF156263
<i>P. papilionaceus</i>	<i>P. parvisporus</i>	iNAT:69899192/USA	MZ666372
<i>P. papilionaceus</i>	<i>P. parvisporus</i>	NAMA 2017-161/USA	MH979305
<i>P. cf papilionaceus</i>	<i>P. parvisporus</i>	MushroomObserver.org/312079/USA	MH101639
<i>P. papilionaceus</i> var. <i>capitatoscystis</i>	<i>P. parvisporus</i>	TUF118728/Estonia	UDB019537
<i>P. papilionaceus</i> var. <i>parvisporus</i> P	<i>P. parvisporus</i>	B700108103/Germany	PP590041
<i>P. papilionaceus</i> var. <i>parvisporus</i> P	<i>P. parvisporus</i>	B700108102/Germany	PP590042
<i>P. papilionaceus</i> var. <i>parvisporus</i> P	<i>P. pantropicalis</i>	B700108104/Brazil	PP590040
<i>P. papilionaceus</i> var. <i>retirugis</i>	<i>P. parvisporus</i>	iNAT:21623086/USA	OM212937
<i>P. plantaginiformis</i>		LE 313092/Russia	MK397573
<i>P. plantaginiformis</i>		LE 2869/Russia	MK397572
<i>P. plantaginiformis</i> L		LE 2862/Russia	MK397577
<i>P. plantaginiformis</i>		LE 2870/Uzbekistan	MK397576
<i>P. plantaginiformis</i>		LE 2867/Uzbekistan	MK397575
<i>P. punjabensis</i> T		LAH 36793/Pakistan	NR189851
<i>P. punjabensis</i>		LAH37417/Pakistan	OP681142
<i>P. punjabensis</i>		BWN_45/Pakistan	MZ265143
<i>P. retirugis</i>	<i>P. parvisporus</i>	CBS:272.47/France	MH856253
<i>P. retirugis</i>	<i>P. parvisporus</i>	CBS:273.47/France	MH856254
<i>P. retirugis</i>	<i>P. parvisporus</i>	CBS:274.47/France	MH856255
<i>P. retirugis</i>	<i>P. parvisporus</i>	CBS:324.34/?	MH855549
<i>P. retirugis</i>	<i>P. parvisporus</i>	7070/Italy	JF908521
<i>P. rickenii</i>	<i>P. acuminatus</i>	KA16-1041/Kyrgyzstan	MK351680
<i>P. rickenii</i>	<i>P. acuminatus</i>	TENN:054965/Argentina	KY559329
<i>P. rickenii</i>	<i>P. acuminatus</i>	749/Italy	JF908516
<i>P. rickenii</i>	<i>P. papilionaceus</i>	12446/Italy	JF908523
<i>P. rickenii</i>	<i>P. sp.</i>	4474/China	OR035489
<i>P. semiovatus</i>		4083/Italy	JF908517
<i>P. semiovatus</i>		GL-13/India	MK386836
<i>P. semiovatus</i>		GS2/China	OR035506
<i>P. semiovatus</i>		Mushroom Observer 377584/USA	MT712776
<i>P. semiovatus</i>		UBC F-23942/Canada	MF955154
<i>P. semiovatus</i>		CBS 388.50/France	MH856675
<i>P. semiovatus</i>	<i>P. parvisporus</i>	CBS:276.39/?	MH856012
<i>P. sp.</i>		BR5020211847626V/Belgium	OR035504
<i>P. sp.</i>		iNat72986889/USA	OQ383438
<i>P. sp.</i>		LAH05071008/Pakistan	MZ825207
<i>P. sp.</i>		JLF9258/USA	OQ740139
<i>P. sp.</i>		ubco14/Canada	OP456264
<i>P. sp.</i>	<i>P. antillarum</i>	biocode08-94/French Polynesia	MZ997244
<i>P. sp.</i> P	<i>P. punjabensis</i> **	S1 (LAH36792)/Pakistan	KY636363
<i>P. sp.</i>	<i>P. papilionaceus</i>	PDD: 105318/New Zealand	MH380188
<i>P. sphinctrinus</i>	<i>P. papilionaceus</i>	CBS:582.79/?	HM035081
<i>P. sphinctrinus</i>	<i>P. papilionaceus</i>	CBS:582.79/France	MH873000
<i>P. sphinctrinus</i>	<i>P. papilionaceus</i>	TFB8627/Argentina	KY559331
<i>P. sphinctrinus</i>	<i>P. papilionaceus</i>	AFTOL-ID 1499/USA	DQ182503
<i>P. sphinctrinus</i>	<i>P. papilionaceus</i>	HMAS 290139/China	MK966651



<i>P. sphinctrinus</i>	<i>P. parvisporus</i>	232/Italy	JF908513
<i>P. sphinctrinus</i>	?	UOC SIGWI S47/Sri Lanka	KP826787
<i>P. aff. sphinctrinus</i>	<i>P. sp.</i>	NY04449017/Colombia	<a href="#">PP590035</a>
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	UBC F-23948/Canada	MF955155
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	OMDL K. Canan iNaturalist # 148029993/USA	OR987162
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	iNAT:16440988/USA	MZ197976
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	CBS 326.34/USA	MH855550
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	CBS 327.34/USA	MH855551
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	HFJAU-ND146/China	MN622762
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	4/China	MW192454
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	NX180911-04/China	MN960188
<i>P. subbalteatus</i>	<i>P. cinctulus</i>	/China	JF961370
undetermined (Uncultured)	clade 9	54A2/Colombia	MW380834
undetermined (fungal endophyte)	clade 9	C111L/USA	KT202838

## TAXONOMY

*Panaeolus pantropicalis* Voto, Angelini & Barrett *sp. nov.* [MB 853142] (Fig. 2-9)



Fig 2: *P. pantropicalis*. JBSD130972, holotype [C. Angelini]



*Typus*. Dominican Republic, Puerto Plata, Sosúa, Sea Horse Ranch locality, on horse dung, 13 January 2023, *legit* C. Angelini, Holotype: JBSD 130972; GenBank PP590036 - ITS.

- *P. papilionaceus* var. *parvisporus* Ew. Gerhardt p.p. (paratype de Meijer 1992 from Brazil, Paraná, Curitiba, Marumbi Park);

Non *P. papilionaceus* var. *parvisporus* Ew. Gerhardt p.p. (Holotype Gerhardt 5.7.1988 from Germany = *P. parvisporus*);

Non *P. papilionaceus* var. *parvisporus* Ew. Gerhardt p.p. (paratypes Enderle 24.6.1987 - MTB 7527 and Enderle 4.7.1990 from Germany = *P. parvisporus*);

?- *P. papilionaceus* sensu Pegler (1977) (collection Pegler 673 from Tanzania, West Usambara Mts.);

?- *P. papilionaceus* var. *parvisporus* Ew. Gerhardt p.p. (paratypes Cleland 17.1.1920 from Australia, Sydney, Neutral bay; Dumont 4605 from Colombia, Boyacá); Goossens-Fontana 5001, 5309, 5589 from Zaire (currently Democratic Republic of the Congo);

?- *P. retirugis* sensu Singer (1969) (collection S 341, from Argentina, Sierra de la Ventana);

?- *P. sphinctrinus* sensu Pegler (1977) (collections Polhill 65a from Kenya, Lake Naivasha, and Pegler 1127 from Tanzania, Mt. Meru)

*Etymology*. The name refers to the worldwide distribution in tropical and subtropical areas.



Fig 3: *P. pantropicalis*. PAD H0061940, paratype [C. Angelini]

Fig 4 (next page): *P. pantropicalis*. A-C: PAD H0061940, holotype; D: PAD H0061940, paratype; E-G: PAD H0061940, paratype; H: PAD H0061941, paratype [C. Angelini]







### Macroscopic characters

*Pileus* (10) 15 – 40 (52) mm diam., broadly paraboloid to conical-hemispheric, then conical to conical-campanulate or convex, normally dry but frequently slightly greasy when very fresh, initially smooth, eroded at margin and possibly concentrically wrinkled towards the margin or grossly cracked overall with age and in dry weather; at first dark brownish-grey, quickly discolouring to pale (brownish) grey often with a beige shade at centre and a brownish shade at extreme margin, finally whitish overall or with brownish-beige shades at centre; veil whitish, powdery, especially abundant towards the margin, often appendiculate to the margin.

*Lamellae* ascending-adnexed to narrowly adnate, distant, approx. 18 – 20 with 3 – 7 lamellulae, ventricose, 1.0 – 1.8 mm broad, fawn to olivaceous brownish grey, mottled black to dark brown; edge whitish.

*Stipe* 33 – 80 (120) × 2 – 3 (4) mm, straight to flexuous, occasionally eccentric, cylindrical with an enlarged to slightly bulbous base and sometimes with an enlarged apex, striate or minutely white pruinose at apex; violaceous- grey to greyish brownish or sometimes pale orange-brown to dark reddish brown, below an initial thick whitish covering; sometimes a small annular line is visible in the upper half highlighted by the deposit of blackish spore powder; hollow.

*Context* whitish to sub concolorous.

### Microscopic characters

*Basidiospores* (n=140, 4 collections) lenticular, (11.0) 11.7 – 14.5 (15.0) × 8.0 – 10.3 (10.5) × 6.2 – 8.1 (9.0) μm, on average 12.7 – 13.0 × 8.7 – 9.2 × 6.9 – 7.2 μm, Q = 1.36 – 1.59 × 1.60 – 2.03, on average 1.43 – 1.47 × 1.78 – 1.83; in front view citriform to broadly elliptic or hexagonal, base obtuse to broadly conical, apex mostly more or less papillate, in side view narrowly elliptic to less frequently amygdaliform; smooth, thick-walled, dark brown to blackish brown in water, darker in 3% and 5% KOH; germ pore approx. 2 μm broad, central.

*Basidia* 15.0 – 31.0 × 8.5 – 15.0 μm, sterigmata up to 6.0 × 2.5 μm; cylindrical to utriform or thickly ululiform, sometimes (saccate-) clavate, sessile to short pedunculate (peduncle up to 5 μm long), 4-spored.

*Pleurocystidia* not observed.

*Cheilocystidia* 20.0 – 37.0 (40.0) × 5.5 – 10.0 μm, apex (3.0) 5.0 – 9.5 μm broad, clavate, utriform, lageniform or cylindrical, often more or less irregular to flexuous, apex equal or sometimes swollen; smooth, thin-walled; numerous but sometimes locally scattered and then mixed with basidia. Paracystidia 13.0 – 44.0 × 7.0 – 17.5 μm. clavate to sphaeropedunculate, scattered to numerous.

*Pileipellis* a hymeniderm of clavate to pyriform-sphaeropedunculate elements approx. 18 – 30 × 12 – 38 μm. Subpellis a cutis of brown-encrusted hyphae.

*Pileocystidia* 25.0 – 51.0 × 4.0 – 10.0 μm at the swollen apex, 7.0 – 13.0 μm broad at base, projecting or recumbent, lageniform-clavate to lageniform-capitate or cylindrical, sometimes fusoid-ventricose or capitate-pedunculate to clavate, often flexuous; smooth, thin-walled, apex sometimes with adhering mucous material, hyaline to glassy greyish-greenish in 3% and 5% KOH; scattered to locally abundant and entangled.

*Clamp connections* found in the pileus tissue.

**Habitat:** gregarious to fasciculate, on horse dung (Dominican Rep.), on buffalo dung (Brazil) and on cow dung (Australia).

### Additional material examined.

Dominican Republic, Puerto Plata, Sosúa, locality Sea Horse Ranch, on horse dung, 13 January 2023, *legit* C. Angelini (PAD H0061940); GenBank PP590037 - ITS;

Dominican Republic, Puerto Plata, Sosúa, Puerto Chiquito, on cow dung, 2 February 2021, *legit* C. Angelini (PAD H0061941); GenBank PP590038 - ITS;

Australia, Western Australia, Waterfall Yard Mound Spring (TEC), Central Kimberley, north side of Hann River, Mt Elizabeth Station, Lat.: -16.280833, Long.: 126.105555555556, on cow dung in savannah woodland, 17 June 2016, *legit* M.D. Barrett (PERTH 09605894); GenBank PP590039 - ITS;

Brazil, Parana State, Curitiba, Marumbi Park, on buffalo dung, de Meijer 1992 (in herb. B 700108104) (as *P. papilionaceus* var. *parvisporus*, paratype), GenBank PP590040 - ITS.

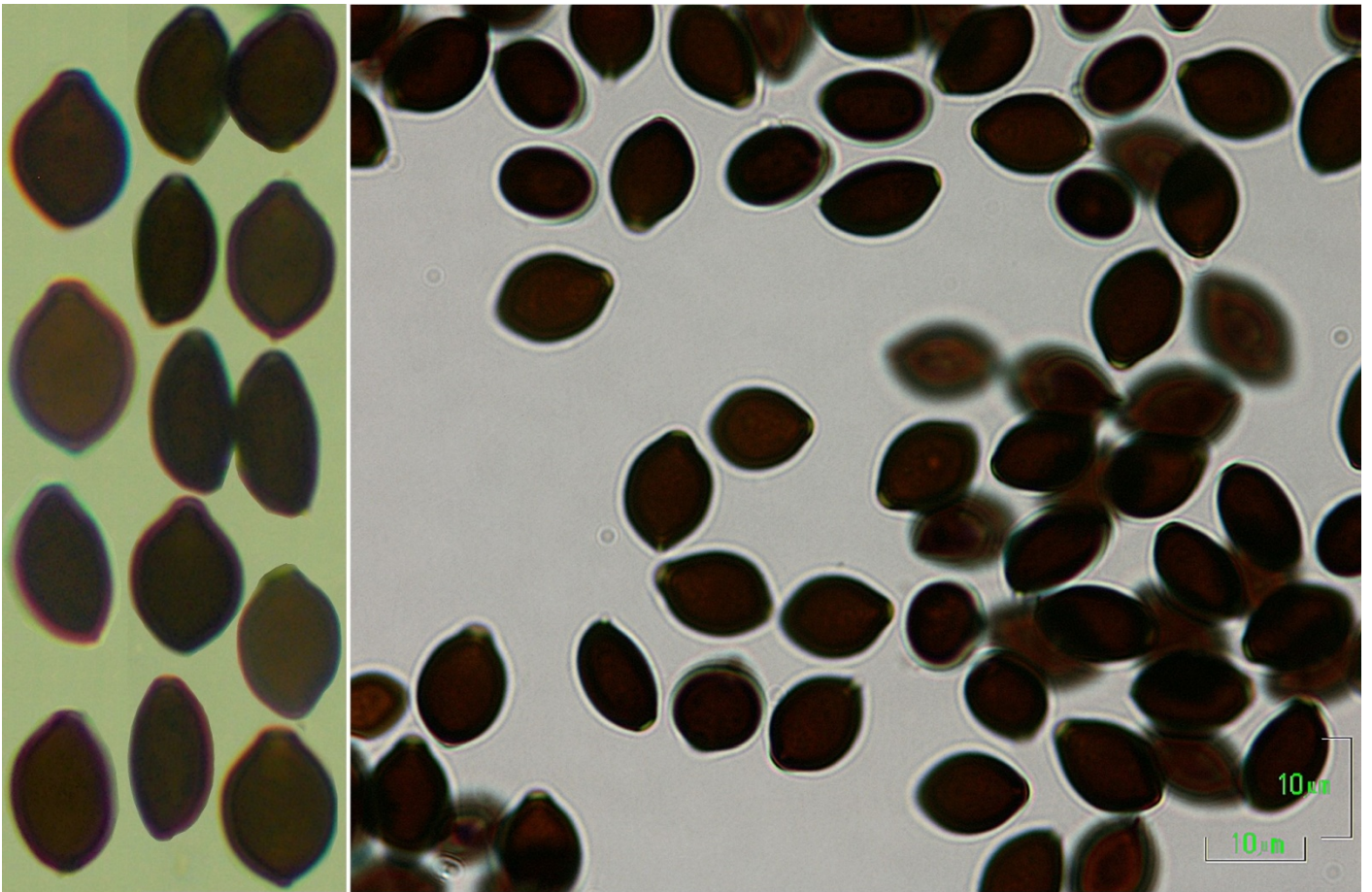


Fig 5: *P. pantropicalis*. Spores. Left: in water (type) [P. Voto]; right: in 3% KOH (PERTH 09605894) [N.L. Bougher]

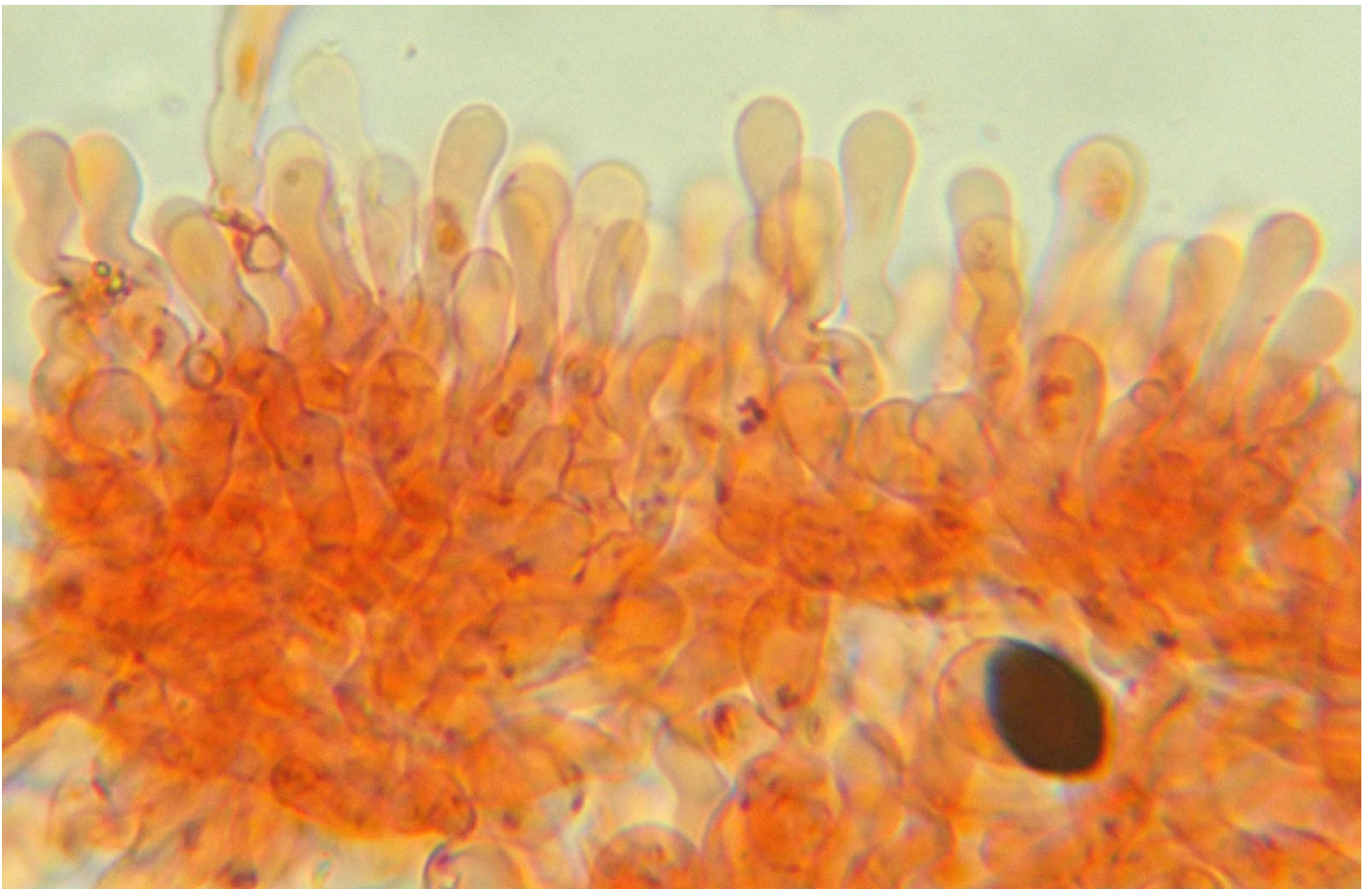


Fig 6: *P. pantropicalis*. Cheilocystidia in Congo red (PAD H0061940) [P. Voto]



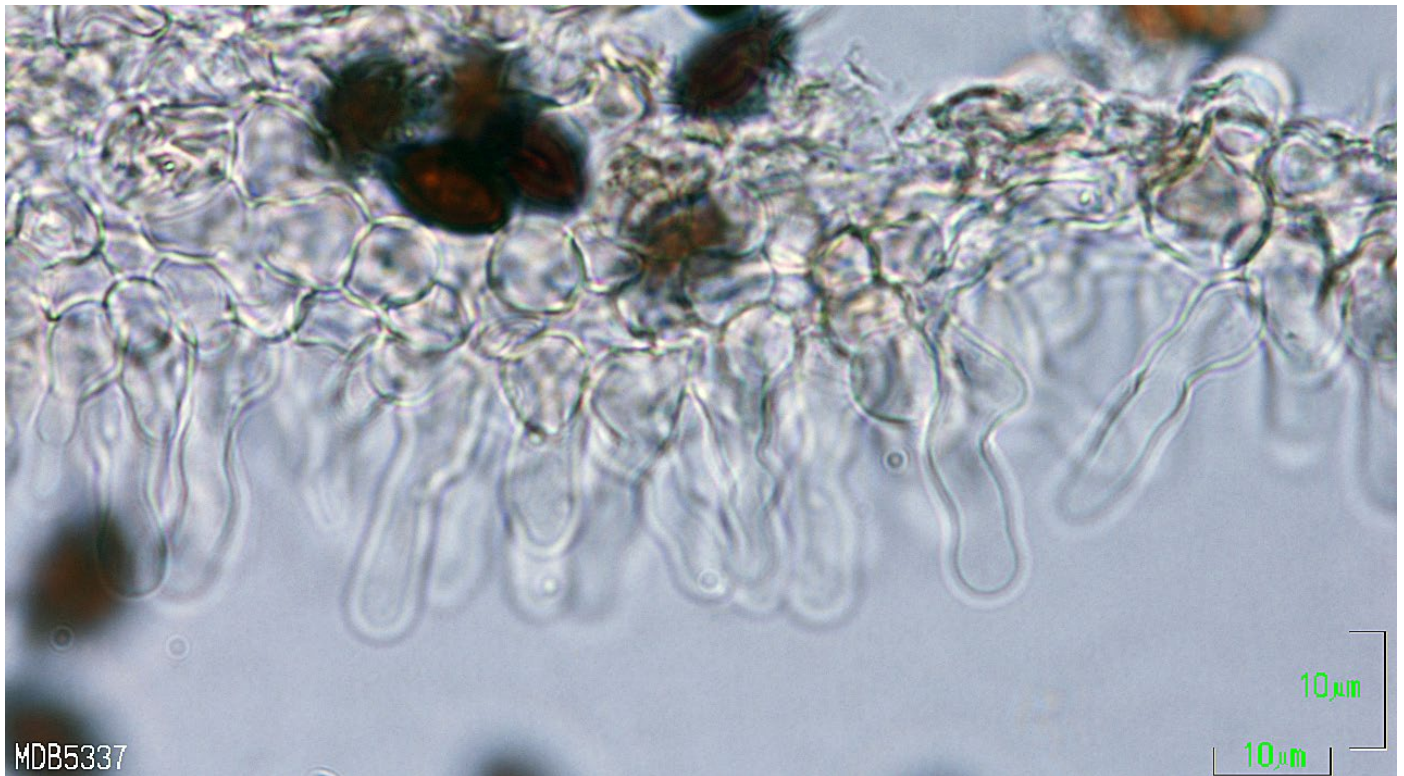


Fig 7: *P. pantropicalis*. Cheilocystidia in 3% KOH (PERTH 09605894) [N.L. Bougher]

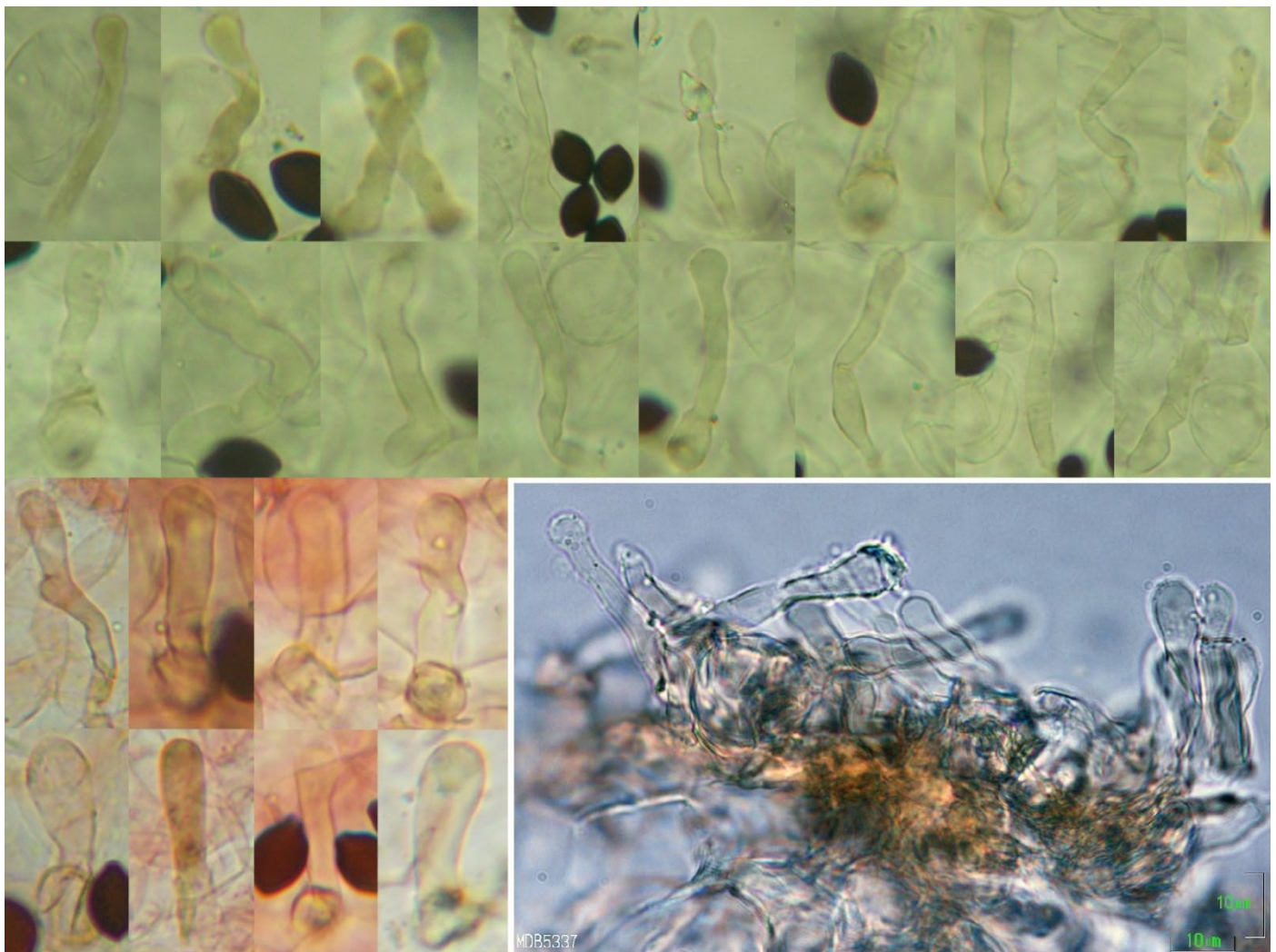


Fig 8: *P. pantropicalis*. Pileocystidia. PAD H0061940: in 5% KOH (top) and in Congo red (bottom left) [P. Voto]; PERTH 09605894: in 3% KOH (bottom right) [N.L. Bougher]



**Notes.**

*P. pantropicalis* is characterized by the size and three-dimensionality of the spores, a central and more or less protruding germ pore, absence of pleurocystidia, an appendiculate veil at the pileus margin, and coprophilous habitat in tropical and subtropical regions.

*P. papilionaceus* has considerably larger spores,  $13.0 - 18.5 (19.0) \times 8.5 - 13.0 \times 7.0 - 10.0 \mu\text{m}$ . *P. parvisporus* differs by its longer spores that also are broader in side view,  $10.8 - 16.5 \times 7.9 - 10.5 \times 7.0 - 8.5(9) \mu\text{m}$ . Basing on the vouchers in our phylogram, we consider it likely that these two species predominantly occur in temperate regions and are not strictly linked to tropical and subtropical vegetation, e.g. Europe, China, Iraq, Iran, New Zealand, USA, Mexico, Argentina for *P. papilionaceus*, and Europe, Mexico, USA for *P. parvisporus*.

The revision of materials of *P. papilionaceus* var. *parvisporus* (see below) revealed further relevant information. In particular the conspecificity of the Brazilian paratype led us to suppose that also the other Neotropical and tropical materials cited by Gerhardt (1996) could be conspecific (see above, list of synonyms of *P. pantropicalis* preceded with a question mark).

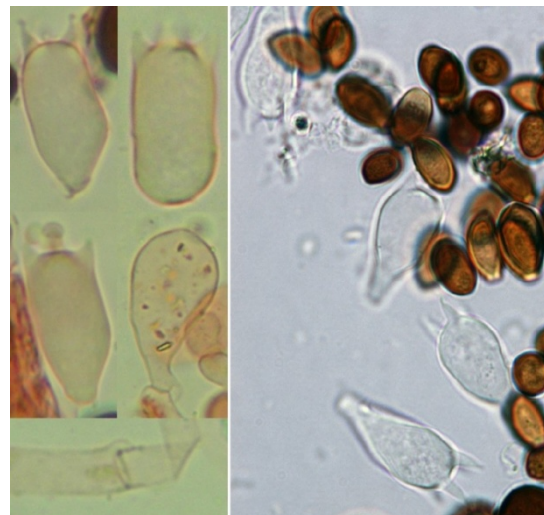


Fig 9: *P. pantropicalis*. Left: basidia and a clamp in the pileus trama in Congo red (type) [P. Voto]; right: basidia in 3% KOH (PERTH 09605894) [N.L. Bougher]

***Panaeolus detriticola* Voto & Bougher sp. nov. [MB 853143] (Fig. 10-15)**



Fig 10: *P. detriticola*. PERTH 08944954. Left: in habitat; right: in laboratory [N.L. Bougher]





Fig 11: *P. detriticola*. PERTH 08944954. Left: detail of lamellae and upper stipe; right: young pileus [N.L. Bougher]

*Typus*. Australia, Western Australia, Kings Park, fungi survey site 4, Forrest Drive, Lat.: 31° 58' 6.6'' S, Long.: 115° 50' 2.5'' E, in woody mulch, 25 July 2017, *legit* N.L. Bougher (Holotype: PERTH 08944954); GenBank MT571659 - ITS+nLSU.

*Etymology*. The name refers to the habitat in woody mulch.

### Macroscopic characters

*Pileus* 17 – 35 mm broad; ovoid-parabolic when young becoming campanulate-convex; margin entire, clasping inwards close to the stipe in young specimens, later the margin becomes duller, not expanding outwards; surface smooth, dry, brown, darkest centrally and paler towards the margin in young specimens, then greyish-brown with some blackish flecks developing with age. Veil scarce, briefly appearing as pale very small appendiculate flaps at pileus margin of young specimens.

*Lamellae* adnate to sometimes broadly adnexed, slightly ventricose, lower and less developed at the pileus margin; mottled dark grey becoming increasingly darker and with a whitish minutely fimbriate edge; about 40 lamellae with 36 lamellulae in at least 3 tiers.

*Stipe* 50 – 100 × 1.7 – 3.5 mm, cylindrical, equal or slightly widened at base, finely densely pruinose along entire length, longitudinally finely striate in upper part due to smooth narrow zones alternating with broader pruinose zones; concolorous to the pileus; basal mycelium white. Annulus not observed (primordia not seen).

*Context* not studied, odour none. Spore print black.

### Microscopic characters

*Basidiospores* (n=46, 1 collection) 12.0 – 15.4 × 9.0 – 11.3 × 7.0–9.5 µm, on average 13.7 – 14.1 × 9.9 × 7.8 µm, Q = 1.28 – 1.56 × 1.58–1.95, on average 1.42 × 1.76 (occasionally, very large spores were noted as measured in face view: e.g. 18.7 × 11.7 µm, 19.2 × 11.5 µm, 17.7 × 11.6 µm, Q = 1.53 – 1.67); in front view broadly limoniform to sometimes (the smaller ones) subhexagonal, base shallowly triangular, apex distinctly attenuated, in side view elliptic to subamygdaliform; rich reddish-brown in 3% KOH, smooth, thick-walled; germ pore central, protruding, up to 2.5 µm wide.

*Basidia* (n=16, length of sterigmata included) 24.8 – 35.0 × 9.0 – 13.1 µm, on average 28.4 × 11.0 µm, Q = 2.11 – 3.50, on average 2.62, sterigmata up to 7.0 × 3.5 µm at base; 4-spored; cylindrical to ventricose and centrally constricted with an absent to short pedicel or clavate with usually an up to 15.0 µm long pedicel; sometimes with brown contents. *Basidioles* 15.0 – 17.0 × 7.5 – 9.0 µm, clavate.

*Cheilocystidia* 20.0 – 65.0 × 4.0 – 7.0 µm at apex, 3.0 – 6.0 µm broad at mid height, cylindric-flexuous, with or without a slightly swollen apex, smooth, thin-walled; crowded, forming a sterile gill edge.

*Pleurocystidia* not observed.

*Pileipellis* a hymeniderm of clavate to pyriform-sphaeropedunculate elements 12.0 – 40.0 × 7.0 – 32.0 µm, subpellis of repent, brown-encrusted hyphae 3.0 µm to sometimes swollen to over 20.0 µm broad.

*Pileocystidia* up to 40.0 × 6.0 µm, cylindric-flexuous, rarely lageniform, usually without swollen apex; smooth, thin-walled, mostly hyaline, sometimes with a brown amorphous cytoplasm; mostly recumbent on the pellis, sometimes projecting outwards beyond the pellis for part of their length; rare in some parts but more abundant in some other parts such as at the pileus margin. Velar tissue: none observed.

*Clamp connections* present.

**Habitat:** scattered singly in woody mulch along road verge area in which woodchips and woody material had been laid a year or two before (Fig. 16).

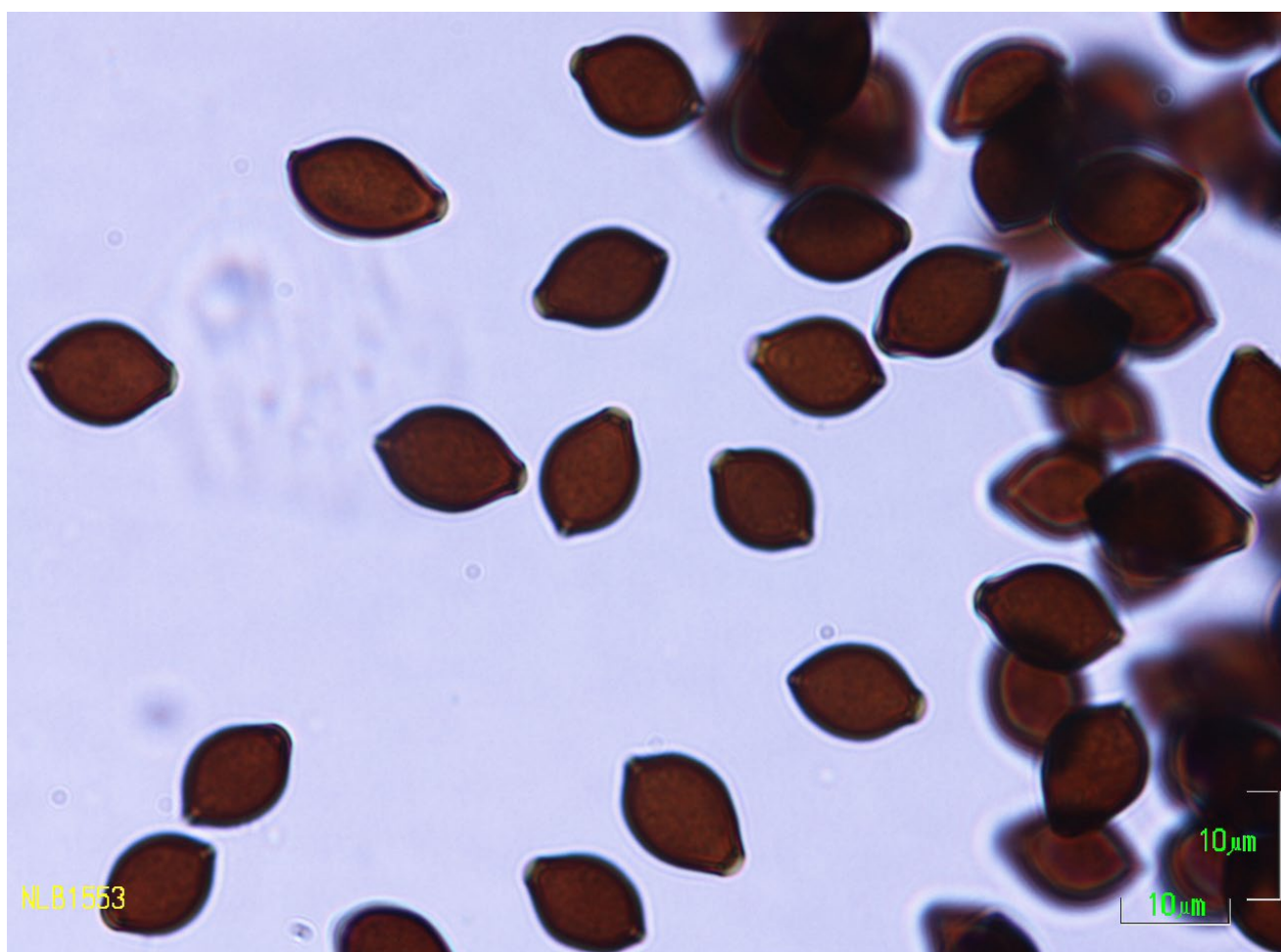


Fig 12: *P. detriticola*. PERTH 08944954. Spores in 3% KOH [N.L. Bougher]



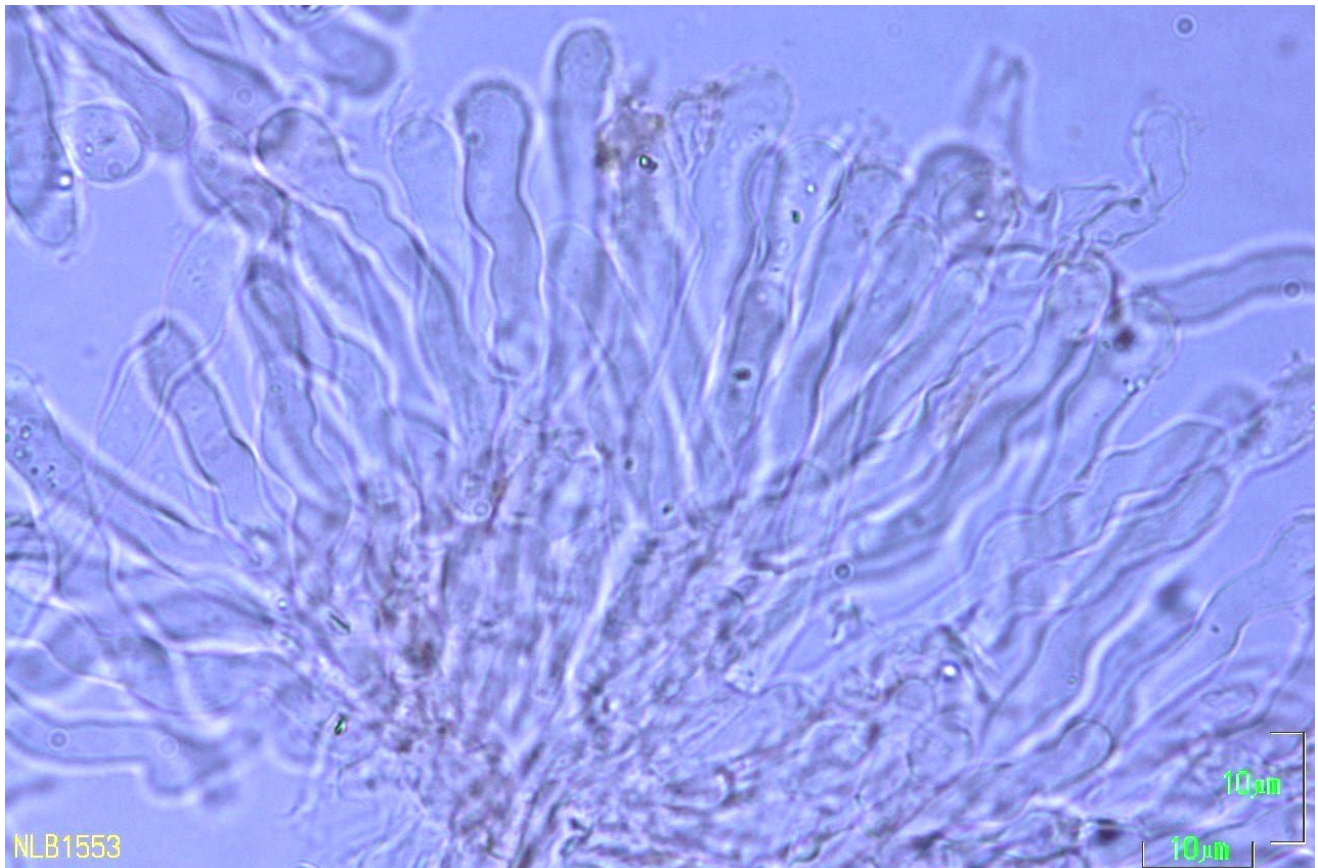


Fig 13: *P. detriticola*. PERTH 08944954. Cheilocystidia in 3% KOH [N.L. Bougher]

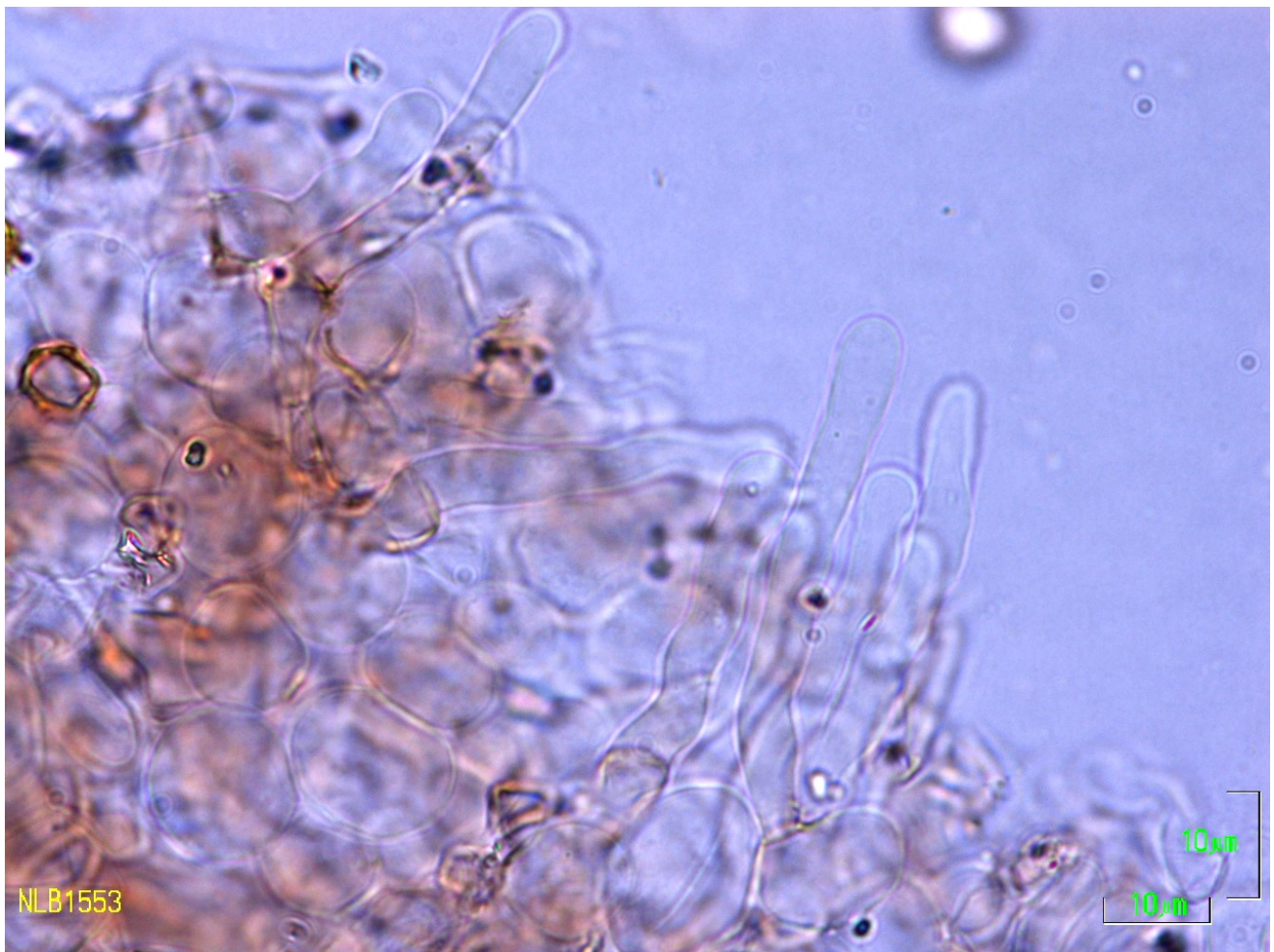


Fig 14: *P. detriticola*. PERTH 08944954. Pileocystidia near pileus margin in 3% KOH [N.L. Bougher]



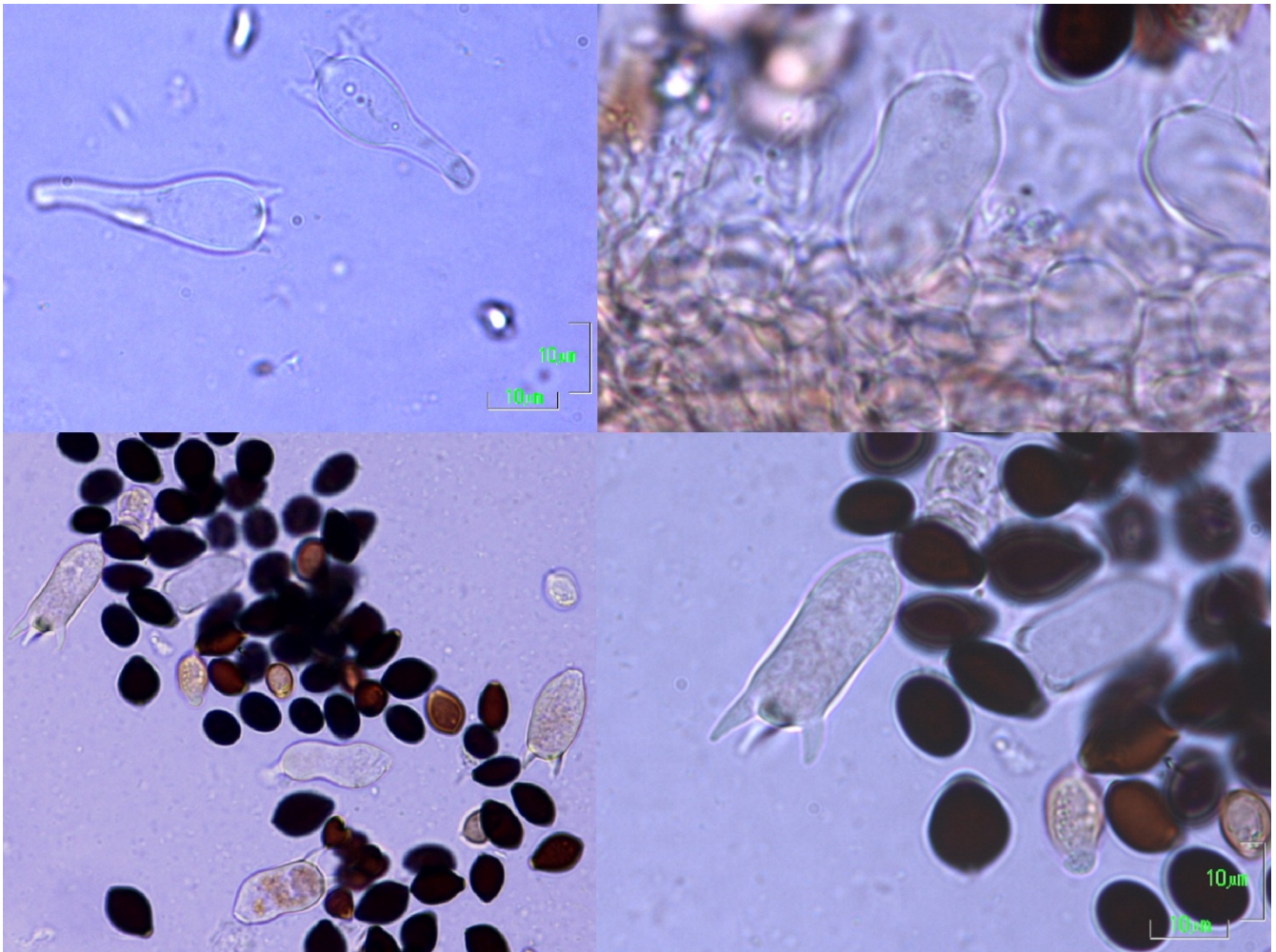


Fig 15: *P. detriticola*. PERTH 08944954. Basidia in 3% KOH [N.L. Bougher]



Fig 16: General view typical of the detriticolous habitat in which the type of *P. detriticola* was collected. Shown in this image is *Coprinellus velatopruinatus*, NLB1489 (in herb. PERTH 8944237), which was collected close to *P. detriticola*, PERTH 08944954, in the same habitat [N.L. Bougher]



## Notes

*P. detriticola* is characterized by the size and three-dimensionality of the spores, a central and more or less protruding germ pore, absence of pleurocystidia, presence of an appendiculate veil, and detriticolous habitat.

In the exact same collecting patch other typically detriticolous species have been found: *Bolbitius titubans* var. *olivaceus* (Gillet) Arnolds, *Coprinellus velatopruinatus* (Bender) Redhead, Vilgalys & Moncalvo (Fig. 16), *Cyathus stercoreus* (Schwein.) De Toni and *Parasola conopilea* (Fr.) Örstadius & E. Larss.

While both the relatively small spore size and the phylogenetic evidence locate this taxon in */parvisporus* s.l., the woody, not coprophilic habitat clearly separates it from the sister species.

*P. fraxinopilus* A.H. Sm., another wood-inhabiting species of subgen. *Panaeolus* reported from North America, has distinctly smaller spores, only up to  $12 \times 8 \times 6 \mu\text{m}$ , and lacks veil remains (Smith 1948).

### ***Panaeolus parvisporus* Voto & Angelini comb. nov. [MB 853144]**

Basionym: *Panaeolus papilionaceus* var. *parvisporus* Ew. Gerhardt, *Bibliotheca Botanica* **147**: 58. 1996

## Notes

According to our proposal and interpretation, this taxon groups "small-spored" descriptions of *P. papilionaceus*, *P. sphinctrinus* and, above all, of *P. retirugis* sensu Ola'h (1970) and Bon & Courtecuisse (2003) (see Discussion below) together.

### **Revision of some material of *Panaeolus papilionaceus* var. *parvisporus* from Gerhardt's (1996) list (Fig. 17)**

We obtained four vouchers from the Berlin herbarium (B): the holotype, B 700108101, from Germany, and three collections from Gerhardt's list of additional material examined, one from Brazil, de Meijer 1992, and two from Germany, Enderle 24.6.1987 and Enderle 4.7.1990. We also tried to study the collection K.P. Dumont 4605 from Colombia, housed at NY 04449016.

- Collection Gerhardt 5.7.1988, Germany, B 700108101 (holotype)

Morphology (on fragments of the stipe): spores (n=40)  $11.0 - 14.5 (15.7) \times (7.7) 8.2 - 10.0 (10.4) \times 7.0 - 9.0 \mu\text{m}$ , on average  $13.4 \times 9.3 \times 7.9 \mu\text{m}$ ; caulocystidia numerous, similar to the cheilocystidia in Enderle 4.7.1990.

Phylogeny: ITS sequence failed after several attempts.

- Collection Enderle 4.7.1990, Germany, B 700108103

Morphology (on lamella): spores (n=25)  $12.0 - 15.0 (16.7) \times (8.2) 8.5 - 10.0 (10.5) \times (6.8) 7.0 - 8.1 \mu\text{m}$ , on average  $13.5 \times 9.3 \times 7.5 \mu\text{m}$ ; cheilocystidia  $27.0 - 35.0 \times 5.0 - 9.3 \mu\text{m}$  at apex, apex cylindrical to often capitate, base often little to distinctly ventricose, central body often flexuous, abundant.

Phylogeny: GenBank ITS sequence PP590041.

- Collection Enderle 24.6.1987, Germany, B 700108102

Morphology (on lamella): spores (n=25)  $12.2 - 15.6 (17.0) \times 9.0 - 10.0 (11.6) \times (6.8) 7.0 - 8.0 \mu\text{m}$ , on average  $13.8 \times 9.6 \times 7.6 \mu\text{m}$ ; cheilocystidia as in Enderle 4.7.1990.

Phylogeny: GenBank ITS sequence PP590042.

- Collection de Meijer 1992, Brazil (Paraná, Curitiba, Marumbi Park), B 700108104

Morphology (on lamella): spores (n=25)  $10.5 - 14.3 (14.8) \times (7.7) 8.0 - 9.8 (10.2) \times 5.8 - 7.8 \mu\text{m}$ , on average  $12.7 \times 9.0 \times 6.9 \mu\text{m}$ .

Phylogeny: GenBank ITS sequence PP590040.

- Collection K.P. Dumont 4605 as *P. aff. sphinctrinus*, Colombia, Boyacá, on the Chocontá-Aguaclara road, in the vicinity of km post 94, on dung, 10 June 1976, NY 04449016

Morphology: not available.

Phylogeny: ITS sequence failed.

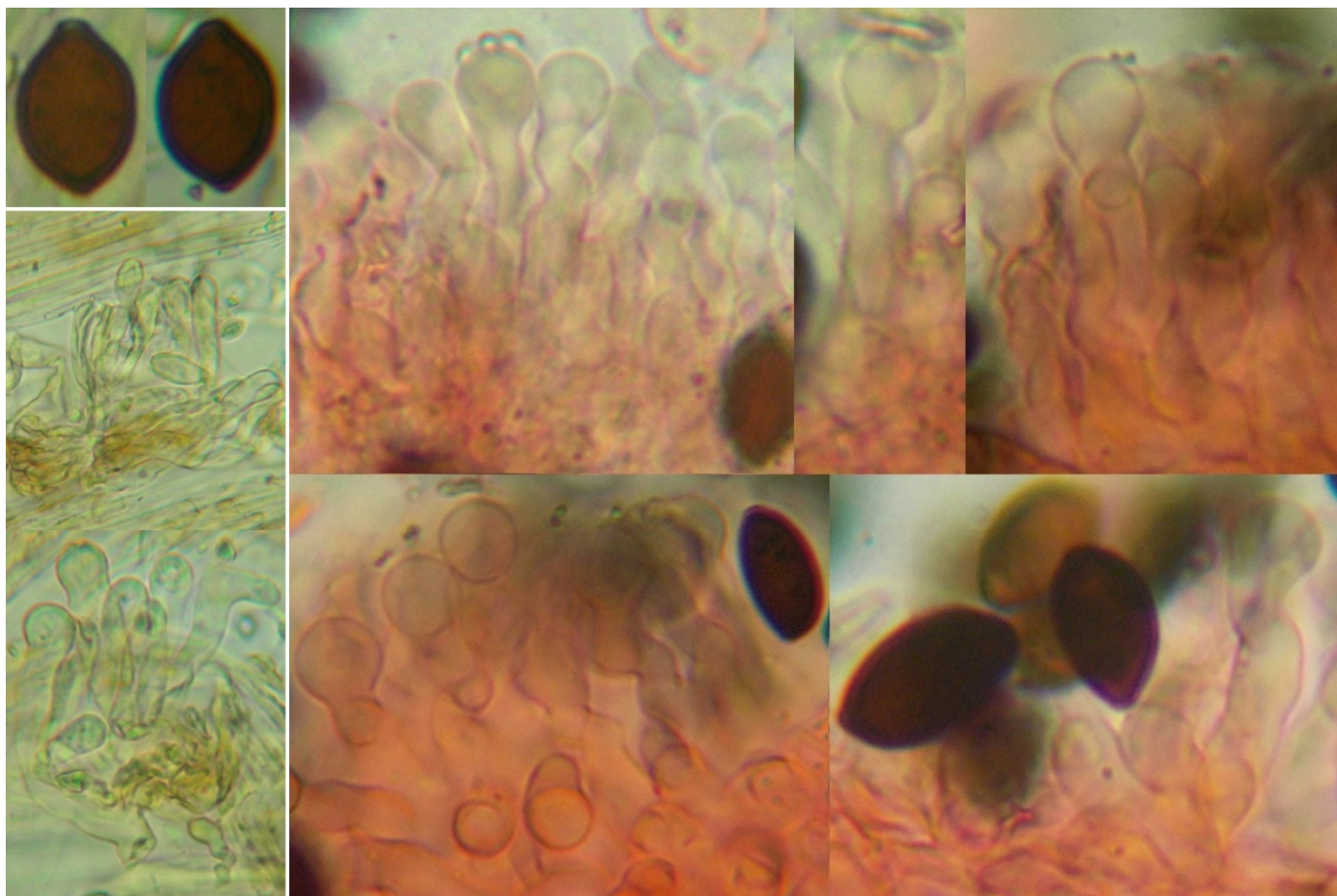


Fig 17: *P. papilionaceus* var. *parvisporus*. Left. Gerhardt 5.7.1988 (holotype). Top: spores in ammonia, bottom: caulocystidia in ammonia. Right. Enderle 4.7.1990 (paratype). Cheilocystidia in Congo red [P. Voto]

## Notes

Another voucher in NY, K.P. Dumont 4606 (NY04449017), collected in the same date and place of K.P. Dumont 4605, was sequenced but came out to represent a different, undetermined taxon (GenBank ITS sequence PP590035).

The three German vouchers share a similar spore size; in particular, the average length in the range 13.4 – 13.8  $\mu\text{m}$  and the average breadth in side view in the range 7.5 – 7.9  $\mu\text{m}$ . The Brazilian voucher, on the contrary, has spores on average shorter than 13  $\mu\text{m}$  and narrower than 7.5  $\mu\text{m}$  in side view. These comparative data are in agreement with the phylogenetic results and confirm the status of two distinct species. Both series of measures, in turn, show values distinctly lower than the spore size of *P. papilionaceus* [(13.0 – 18.5 (19.0)  $\times$  8.5 – 13.0  $\times$  7.0 – 10.0  $\mu\text{m}$ )] where the average length is greater than 15  $\mu\text{m}$  (Bon & Courtecuisse 2003; Gerhardt 1966, 2012; Oláh 1970) and the average width in side view is greater than 8  $\mu\text{m}$  (Gerhardt 1966, 2012).

Therefore the three sympatric vouchers of *P. papilionaceus* var. *parvisporus* represent an autonomous taxon raised to species-level, *P. parvisporus*, while the Brazilian paratype is conspecific with our new taxon *P. pantropicalis*.

## HISTORICAL OVERVIEW

### Original descriptions

The concepts of all four main species involved in the “*Panaeolus papilionaceus* species complex” date back to the 18<sup>th</sup> and 19<sup>th</sup> century and lack any detail of microscopic morphology. Below are their original descriptions and Fries’ sanctioning when it occurs.

*Panaeolus campanulatus* (Fr.) Quél. (Quélet 1872)

Basionym and sanctioning name *Agaricus campanulatus* Fr. (Fries 1821: 295) (based on the illustration of *Agaricus campanulatus* Bull. (Bulliard 1792: pl. 552 fig. 1, here reproduced in Fig. 18, without text description), non *A. campanulatus* L. (Linnaeus 1753) which refers to a white-gilled fungus:

“16. *A. campanulatus*, pileo submembranaceo campanulate lævi brunneo, lamellis liberis ferrugineis, stipite lævi obsolete annulate. *Bull. t.* 552. *f.* 1. *Dec. fr.* 2. *p.* 154. *Pers. syn. p.* 426. *Fries Obs.* 2. *p.* 173.

Stipite fistulosus, 4 unc. longus, tenuis, lævis. Pileus siccus pro more lutescens, uncialis usque. Lamellæ perlatæ. *Ad terram in silvis. Aug. Sept.* (v. v.)”.

*Panaeolus papilionaceus* (Bull.) Quél. (Quélet 1872)

Basionym *Agaricus papilionaceus* Bull. (Bulliard 1782: t. 58 here reproduced in Fig. 19):

“*Agaricus papilionaceus*. On trouve ce CHAMPIGNON en Juin et Juillet, dans les bois, parmi les fouilles pourries, il vient aussi dans les Prairies, dans les Jardins, sur les couches, &c. CHAPEAU regulierement arrondi, plus ou moins conique, frangé à son bord, n’ayant presque point de chair. FEUILLETS très larges, très minces, parsemés de taches approchantes de celles qu’on rencontre sur les ailes de certains papillons, ils acquierent en vieillissant une couleur noire comme de l’encre. PÉDICULE creusé, d’un très petit canal dès sa jeunesse, il n’est pas continu avec la chair du chapeau, mais seulement contigu; il n’a ni bulbe ni collet”.

Sanctioned as *Agaricus papilionaceus* by Fries (1821:301):

“3 *A. papilionaceus*, pile subcarnoso campanulato sicco nigrescente-fuligineo expallente, lamellis adnatis cinereo-atris, margine albis, stipite longo rufescente, apice striato atro-pulverulento.

*Fung. buf. sp. l. Clus. p.* 278. *Bauh. l. c. c.* 73. *ic.* *Fungus parvus galericulatus, striis lividis &c. Raji Hist.* II. *p.* 98. *Vaill. par. p.* 65. — *Buxb. Cent. IV. t.* 13. *f.* 2. *A. acuminat. Schæff. t.* 202. *A. papilionac. Bull. t.* 58, 561. *f.* 2. *Dec. fr. 2 p.* 152. *Pers. syn. p.* 410. *A. carbon. Batsch. f.* 6. *A. semiovat. b. Schum. l. c. A. varius. Pers. ic. & descr. p.* 40. *b. minor. Buxb. C. V. t.* 48. *f.* 2. *A. equinus. Abb. d. Sch. 3.*

*c. stipite guttulis aqueis. Fries Obs. 2. p.* 184.

Stipes 3 unc. longus, æqualis, 1-2 lin. crassus, rufescens. Pileus demum, convexus, exsiccatus subrufescens, lævis, ½-1 uncialis, nunquam viscosus. Lamellæ adscendentes, confertæ, integerrimæ. Velum fugacissimum. *In fimetis, silvaticis pinguibus &c. Majo-Nov.* (v. v.)”.

*Panaeolus retirugis* (Fr.) Gillet (Gillet 1878)

basionym *Agaricus retirugis* Fr., based on *Agaricus carbonarius* var. “ $\delta$ ” Batsch Batsch (1786:107 and fig. 91 here reproduced in Fig 20):

“*Pileo pallido ochraceo - carneo, rugoso - venuloso, glabro; stipite carneo - fulvello.*

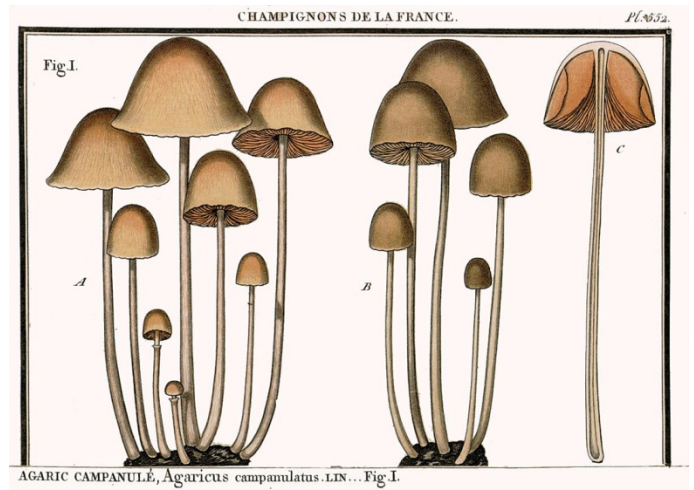


Fig 18: Iconography of *Agaricus campanulatus* from Bulliard (1792)



Fig 19: Iconography of *Agaricus papilionaceus* from Bulliard (1792)



*Pileus* convexus, subumbonatus, vertice acutiusculo, margine valde incurvatus, inique frustulis latiusculis a velo remanentibus fimbriatus, superficie opaca, alutaceo - glabrata, tota rugulis linearibus, levibus, crebris, anastomosantibus venulosus.

*Stipes* elongatus, linearis, tamen validus, carneus; totus pruina carneo - fulva subtilissima infectus, basi infima tegmine albo obvelatus.

Stercori cervino adnatum inveni in praedicta sylvula autumnno 1783. semel tantum. Icon. 91. fungum integrum sistit floccis veli superne in pileo, particulis fimi cervini termino infero adhaerentibus".

Fries (1838:234-235):

XXVII. PANAEOLUS. Velum contextum, saepe deficiens. Stipes politus, firmulus. Pileus *carnosulus, exstrius, margine primo excedente*. Lamellae in conii fundum adscendens, «papilionaceae» i. e. *variegatae*; jove sicco juniores passim subgilvae. *Vulgo fimicolae*, Clusio *pern. gen. XVI. sp. 1.*

\*\**pileo (humido) udo opaco bibulo, sicco subflocculoso.*

"960. A. RETIRUGIS, pileo carnosulo e globoso hemisphaerico subumbonato *costis elevatis reticulato atomato-opaco*, velo lacero appendiculato, stipite aequali pruinoso carneo purpurascete, lamellis adfixis adscendentibus cinereo-nigricantibus. — *Batsch. f. 91.*! In fimo cervino B., in lepirino nos legimus var. minorem.

*Pileus* carneo-alutaceus, facie omnino A. *corrugis*".



Fig 20: Iconography of *Agaricus carbonarius* var. "d" from Batsch (1786)

*Panaeolus sphinctrinus* (Fr.) Quél. (Quélet 1872)

Basionym *Agaricus sphinctrinus* Fr. (Fries 1838:234-235) [the Buxbaum's (1740) figure referred to by Fries (1838) is here reproduced in Fig. 21]:

XXVII. PANAEOLUS. Velum contextum, saepe deficiens. Stipes politus, firmulus. Pileus *carnosulus, exstrius, margine primo excedente*. Lamellae in conii fundum adscendens, «papilionaceae» i. e. *variegatae*; jove sicco juniores passim subgilvae. *Vulgo fimicolae*, Clusio *pern. gen. XVI. sp. 1.*

\*\**pileo (humido) udo opaco bibulo, sicco subflocculoso.*

"962. A. SPHINCTRINUS, pileo carnosulo parabolico obtuso opaco laevi udo, sicco subsericeo, velo albo primitus appendiculato, stipite aequali stricto *fuligineo-griseo apice laevi pruinoso*, lamellis adnatis confertis cinereo-nigricantibus acie concoloribus. *Weinm. n. 427* ut apparet. — b. *Batt. t. 27. L. hujus loci omnino videtur.*

*Stipes* 2 — 3 unc. l., 1 lin. cr. fragilis, basi tantum rufescens. Pileus udus glaber, fuligineo-nigricans, siccus lividus; carne tenui umbrina. In forma pumila stip. unc., lamellae lineares: *Buxb. C. V. t. 48, f. 2*".



Fig 21: Buxbaum (1740: tab 48, fig. 2)

### Interpretations over time

The following brief chronological selection of authors shows these four names have been differently treated over time.

- Romagnesi (1937) cites *P. campanulatus* and *P. papilionaceus*, separately; without any description;
- Hora FB (1957) keeps all four names separate. The dichotomous steps in his key are based on macrocharacters;



- Singer (1960) describes *P. sphinctrinus* with *P. campanulatus* as a synonym (pileus smooth or reticulate-venose, spores  $12.5-14.5 \times 8 - 10 \mu\text{m}$ );
- Ola'h (1970) treats three names separately synonymising *P. papilionaceus* with *P. campanulatus*. In his informal non dichotomous key these names are treated on the basis of spore size and other macrocharacters (he does not differentiate the spore width by side- and front-view):  
a5, Sp.  $10.8 - 16.4 \times 7.9 - 10.5 \mu\text{m}$  *P. retirugis*  
...  
a7, Sp.  $14.5 - 18.5 \times 10.5 - 12.6 \mu\text{m}$ . Marge du chapeau avec des franges crénelées, blanchâtres, débordantes, formant un étranglement marginal surtout chez les jeunes. Chapeau gris verdâtre, olivâtre, campanulé, élevé, obtus. Revêtement piléique du type « B et E ». *P. sphinctrinus*  
a8, Sp.  $13.5 - 18.0 \times 7.5 - 12 \mu\text{m}$ . Marge du chapeau débordante, droite à récurvée, appendiculée par de petites franges blanc-gris. Chapeau campanulé brun-gris, rouge-carné, rose briquette. Revêtement piléique du type « A-C » et « D ». *P. campanulatus*
- Watling & Gregory (1987) and Bon & Courtecuisse (2003) keep all four names separate. The dichotomous steps in their keys are based on macrocharacters of the pileus (shape, colour, cuticle surface);
- Gerhardt (1996) treats all four names as one species, *P. papilionaceus* [pileus smooth or reticulate-venose, spores (13)  $15 - 18$  (19)  $\times$  (9.5)  $10 - 12$  (13)  $\times$  (7)  $8 - 9.5$  (11)  $\mu\text{m}$ ], and introduces *P. papilionaceus* var. *parvisporus* differentiated by smaller spores ( $13 - 16 \times 8 - 10 \times 6 - 8 \mu\text{m}$ ) in the protolog and in the key;
- Gerhardt (2012) confirms Gerhardt (1996).

## DISCUSSION

As seen above, there is considerable objective taxonomic and nomenclatural complexity in interpreting and separating species in the "*P. papilionaceus* complex". This is reflected by the ITS sequences currently available in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) where several collections identified as *P. campanulatus* (Bull.) Quél., *P. papilionaceus* (Bull.) Quél., *P. retirugis* Fr. and *P. sphinctrinus* (Fr.) Quél., together with some collections unidentified ("*Panaeolus* sp.") or prefixed with "*Panaeolus* cf." or "*Panaeolus* aff.", appear scattered in the phylogram.

The fact that these species were described without elements of micromorphology, especially the spore size, has generated two lines of interpretations: most authors primarily have used differential macrocharacters of the pileus (e.g. Bon & Courtecuisse 2003; Hora 1957; Watling & Gregory 1987), while others have prioritized the relevance of differences in spore size (Ola'h 1970; Gerhardt 1966, 2012).

We accept Gerhardt's (1996, 2012) concept and observations on this complex. Based on numerous collections and specimens that he personally observed, he concludes that *P. papilionaceus*, *P. sphinctrinus* and *P. campanulatus* simply represent different aspects of a single variable species. Also, he argues that a species of *Panaeolus* specifically based on a corrugated pileus is not acceptable as this particular morphology can occur in almost all species of this genus therefore he also synonymises *P. retirugis* with the three aforementioned species. On the contrary, he rightly focuses his attention on spore size and distinguishes "large-spored" and "small-spored" collections. He then admits that, due to the lack of any micromorphological data in the protologs, it is impossible to assign a confident name to these two entities. He therefore adopts, as a traditionally established concept, the association between the name *P. papilionaceus* and "large" spores (e.g. Hora 1957; Ola'h 1970; Watling & Gregory 1987), about  $15 - 18 \mu\text{m}$  long. He suggests that an epitype should be proposed to stabilize this concept and institutes the new name *P. papilionaceus* var. *parvisporus* for the small-spored collections. However, it must be commented that, unlike the two sympatric paratypes, the Brazilian paratype of *P. papilionaceus* var. *parvisporus* is conspecific with our new tropical taxon, *P. pantropicalis*. This demonstrates that Gerhardt's (1996) concept of conspecificity, based only on the approximate similarity of microcharacters among collections from very different geographical and climate regions, was not entirely correct in all cases.

As Gerhardt (1996, 2012) has so far only proposed his concept on the basis of morphology alone, we have been able to demonstrate here, supported by our phylogenetic analysis, the autonomy of his new variety. In

fact, *P. papilionaceus* var. *parvisporus* has a distinct position in our phylogram, inside clade 4, based on our examination of the two small-spored German paratypes. Furthermore, we can reasonably assume that the large clade 6 containing several vouchers mostly identified as *P. papilionaceus*, *P. sphinctrinus* and *P. campanulatus* represents the common, widely distributed, large-spored taxon *P. papilionaceus*.

The number of species included in the morphological “*P. papilionaceus* species complex” would be even greater if some had not been reduced to synonyms before the advent of the phylogenetic analysis: *P. atratus* Dvořák, *P. niveus* Velen. and *P. semilanceatus* Peck were synonymised with *P. papilionaceus* by Gerhardt (1996), *P. linnaeanus* S. Imai was synonymised with *P. papilionaceus* by Singer (1960), and *P. carbonarius* Batsch was synonymised with *P. retirugis* (→ *P. papilionaceus*) by Morgan (1907).

Some varieties and forms have been also published.

- *P. papilionaceus* f. *squarrosus* Kavina

Bon & Courtecuisse (2003) suppose it represents a *P. papilionaceus* with a cracked pileus.

- *P. papilionaceus* var. *capitatocystis* E. Ludw.

Ludwig (2001) differentiates it from *P. papilionaceus* and *P. papilionaceus* var. *parvisporus* by shorter (up to 30 µm) and broader, capitulate at apex (up to 8 µm) cheilocystidia; he does not provide data for the exact spore size, simply reporting it as in the autonym variety treated by the author in the broad sense of Gerhardt (1996). Unfortunately, Ludwig’s concept is not correct. The cheilocystidia of *P. papilionaceus* var. *parvisporus* are exactly of the same dimensions, 25 – 35 × 5 – 8 µm (see Gerhardt 1996 and our revision of the German paratypes), and also of the same shape with an often capitate apex as observed in our revision. As the reliable difference between *P. papilionaceus* and *P. parvisporus* is the spore size, and as this datum was not specified by Ludwig (2001), the doubt remains whether to synonymise Ludwig’s variety to one or the other species. However, Hausknecht & Krisai-Greilhuber (2009) report several Austrian capitate-cystidiate collections under *P. papilionaceus* var. *capitatocystis* with a spore size of 12.5 – 17.5 × 8.5 – 12.0 × 6.5 – 10.0 µm, on average 14.8 – 16.3 × 9.3 – 11.4 × 7.2 – 9.5 µm; these spore measurements are more well-matched to *P. papilionaceus*.

- *P. sphinctrinus* var. *minor* (Fr.) Singer (basonym *Agaricus campanulatus* var. *minor* Fr.)

In the original sense of Fries (1878) it is considered as having a small habit similar to *P. papilionaceus* by Gerhardt (1996), while for sensu Singer (1960), based on a small-spored collection from Mexico, Gerhardt (1996) commented as follows (authors’ translation from German):

‘Singer describes the Fries variety with smaller spores than usual for *sphinctrinus* (= *papilionaceus*). It has not been possible to obtain the material that he reports from Mexico, Oaxaca, Huautla de Jimenez, Casa del Cure, July 11, 1957, Singer M 1546 (MICH, LIL), despite repeated attempts to borrow it. This leaves the identity of this mushroom uncertain. There is probably no correspondence with the fungus described by Fries, especially since Singer’s material comes from South America. According to Singer’s drawing of the cheilocystidia and the small size of the spores, 12-13,3 × 9-9,3 × 7,5-8 µm, which are even smaller than those of *Panaeolus papilionaceus* var. *parvisporus*, it should be treated as a deviant taxon’.

Contrary to Gerhardt’s (1996) opinion, we note that the spore size falls well within the spore range of *P. parvisporus*. In particular the width in side view is better matched to *P. parvisporus* than to *P. pantropicalis*.

Finally, we mention two of the several doubtful identifications published over time.

- Singer (1969) describes a collection of *P. retirugis* from Argentina, Sierra de la Ventana, among herbaceous vegetation, with spore size 10.8 – 13.3 × 7.2 – 9.0 × 6.5 – 7.5 µm; we do not know if the collecting area is a tropical/subtropical region, however, by the spore size in side view, this collection could be *P. pantropicalis*.

- Pegler (1983), in describing the mycoflora of the Lesser Antilles, reports a description of *P. papilionaceus* identical to the one he (Pegler 1977) previously published from East Africa (one of our putative morphological synonyms of *P. pantropicalis*) but without citing any collecting site, thus leaving doubt as to whether he had actually found that species in the southern part of the Caribbean or simply assumed its possible presence there too.

An updated morphology-based worldwide key to species of *Panaeolus* by P. Voto is available open access at [https://www.ameronlus.it/chiavi\\_micologia.php](https://www.ameronlus.it/chiavi_micologia.php).



## ADDITIONAL SPECIES TREATED

### *Panaeolus antillarum* (Fr.) Dennis (Fig. 22-25)

*Kew Bulletin* 15(1): 124 (1961)

Basionym: *Agaricus antillarum* Fr., *Elench. fung.* 1: 42 (1828)

= *P. albellus* Masee, *Bot. Tidsskr.* 24: 366 (1902) [fide Gerhardt (1996)];

= *P. bolombensis* Beeli, *Bull. Soc. R. Bot. Belg.* 61(1): 96 (1928) [fide Gerhardt (1996)];;

= *P. eburneus* Sacc., *Syll. fung. (Abellini)* 9: 147 (1891) [fide Young (1989)];

= *P. ovatus* Sacc., *Syll. fung. (Abellini)* 9: 147 (1891) [fide Pegler (1983)];

= *P. sepulchralis* (Berk.) Sacc. [as 'sepulcralis'], *Syll. fung. (Abellini)* 5: 1119 (1887) [fide Pegler (1983)];

= *P. solidipes* (Berk.) Sacc., *Syll. fung. (Abellini)* 5: 1123 (1887) [fide Pegler (1983)].

### Macroscopic characters

*Pileus* 20-42 mm, at first hemisphaerical with involute margin, then conical to convex with margin not fully extended; surface viscid, smooth then cracked or broken in small patches with somewhat split margin, white to pale grey, sometimes turning to brownish in small spots; veil absent.

*Lamellae* crowded with several tiers of lamellulae, ascending-adnexed, 6-13 mm high, ventricose, grey and dotted then greyish black; edge whitish.

*Stipe* 60-120x3-7 mm, cylindrical, base equal to tapering or swollen; mostly finely striate, decorticating with age or on handling, apex finely flocculose or not, base strigulose or not, white to somewhat dirty ochraceous with age; solid to fistulose.

*Context* whitish to dirty ochraceous.



Fig 22: *P. antillarum*. PAD H0061942 [C. Angelini]





Fig 23: *P. antillarum*. PAD H0061942 [C. Angelini]



Fig 24: *P. antillarum*. PAD H0061942 [C. Angelini]



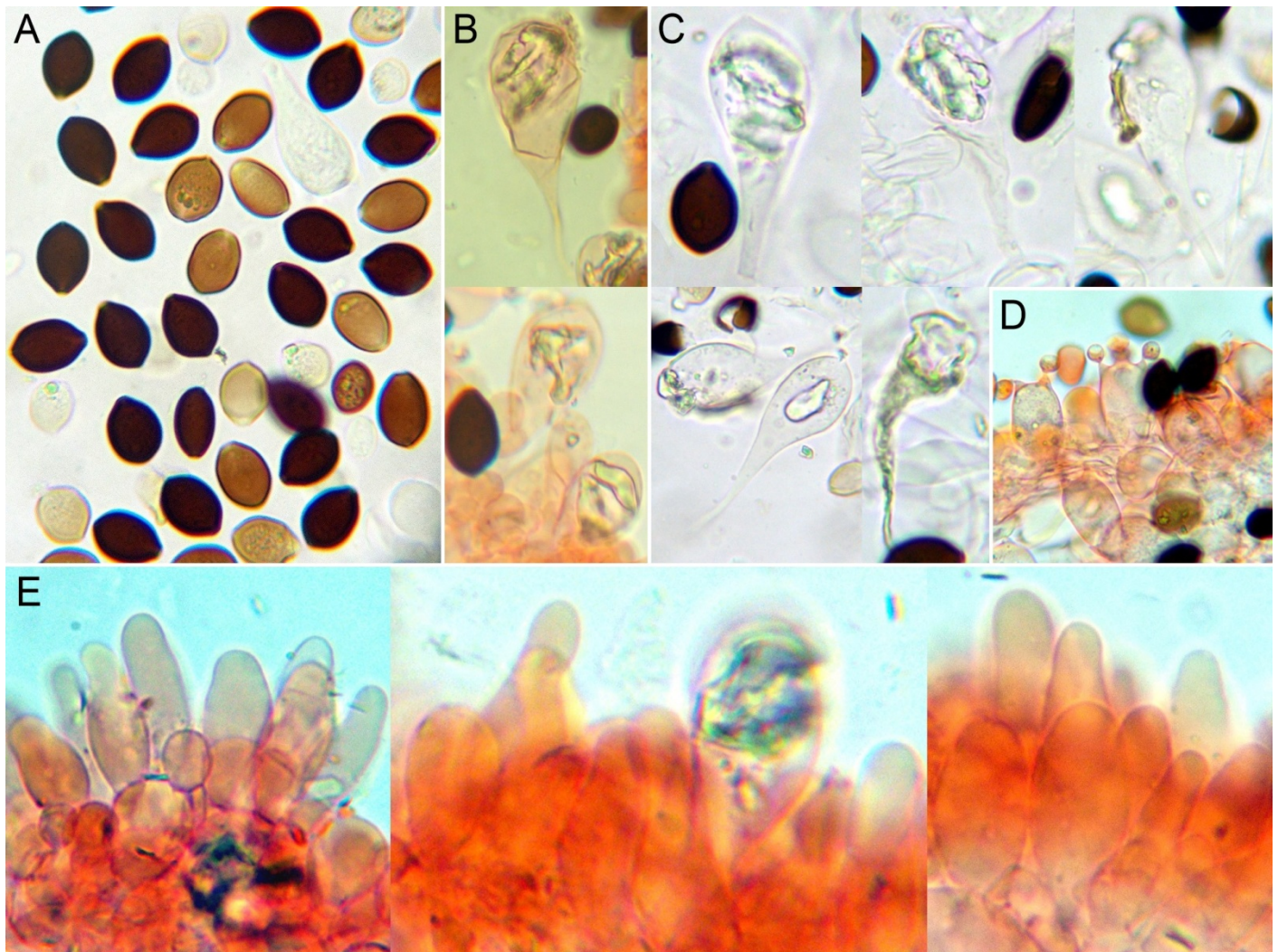


Fig 25: *P. antillarum*. PAD H0061942. A: spores in 5% KOH, B: sulphidia in Congo red, C: sulphidia in 5% KOH, D: basidia in Congo red, E: cheilocystidia in Congo red [P. Voto]

### Microscopic characters

*Basidiospores* (n=30) 14.0-17.5x11.2-12.5x7.7-10(11.5)  $\mu\text{m}$ , in front view hexagonal to broadly elliptic, apex often a little protruding, in side view narrowly elliptic; dark brown in water and in 5% KOH; germ pore central, distinct.

*Basidia* 28-36x15-23  $\mu\text{m}$ , 4-spored, short clavate.

*Cheilocystidia* 20-40x8.5-13  $\mu\text{m}$ , utriform, hyaline.

*Pleurocystidia* of the sulphidia type, 30-60x16-20  $\mu\text{m}$ , clavate to papillate-clavate, with long peduncle.

**Habitat and collection examined:** Dominican Republic, Puerto Plata, Sosua, Sea Horse Ranch, gregarious, on horse dung, 13 January 2023, *legit* C. Angelini (PAD H0061942); GenBank ITS PP590043.

### Notes

*Panaeolus antillarum* has a worldwide distribution in tropical to subtropical climate and is easily recognizable in the field, because of its coprophilous habitat in tropical regions and a greasy, pale and often cracked pileus lacking a veil. It is recognizable microscopically due to its sulphidia-type pleurocystidia and large hexagonal spores with a central germ pore and a protruding apex.

*P. semiovatus* (Sowerby) S. Lundell & Nannf. is another cosmopolitan coprophilic whitish species which sometimes may have been misidentified as *P. antillarum*. However *P. semiovatus* usually occurs in temperate regions, has velar remains either at the pileus margin as appendiculate flaps or on the stipe as an annulus, and it has been treated as such by some authors (e.g. Gerhardt 1996) in their descriptions and keys. Therefore, in some cases when collections of *P. semiovatus* are presented with their velar remains already completely lost, it



is possible that they maybe misidentified as *P. antillarum*. Such cases may account for incongruent reports of the tropical *P. antillarum* in temperate areas [Gerhardt 1996 synonymised with it *P. solidipes* (Peck) Sacc., from Albany, New York, and referred of adventitious presence in temperate zones in warm, humid years].

Misidentifications may be lessened by taking into consideration that *P. semiovatus* is distinguished also by a non-ovoid pileus shape and slightly larger spores often with an eccentric germ pore.

***Panaeolus nirimbi*** (Watling & A.M. Young) Voto

*Mycological Observations* 6: 28 (2023)



Fig 26: *P. nirimbi*. Australia, Western Australia, Perth, gregarious, in a park (grass playing field), 25 March 2005, N.L. Bougher E8142 (in herb. PERTH 7680368) [N.L. Bougher]

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