Article received 12 July 2024 (pre-reviewed), accepted 18 July 2024

New data and update in the *Panaeolus papilionaceus* complex, first record of *P. punjabensis* and new finds of *P. sylvaticus* in the Dominican Republic

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Key words:
Basidiomycota
Agaricales
Galeropsidaceae
Caribbean
taxonomy
phylogeny

Abstract: *Panaeolus punjabensis*, recently described from Pakistan, is first documented from the Dominican Republic based on morphological description and molecular analyses (ITS sequence and phylogram). An updating on the *Panaeolus papilionaceus* complex is reported based on new molecular evidence on *P. papilionaceus* var. *parvisporus*. New finds of *P. sylvaticus* in the Dominican Republic are documented with photographs and morphological notes.

INTRODUCTION

In the family Galeropsidaceae, the genus *Panaeolus* has a cosmopolitan diffusion and is mainly composed of fimicolous to nitrophilous species (Voto & Angelini 2024). It is widely spread in the Dominican Republic where the habit of raising numerous herbivorous farm animals (such as cows, sheep, goats, horses and donkeys) exclusively on pasture in grassy unwooded spaces creates a particularly favourable habitat.

To the four Dominican species of *Panaeolus* (*P. antillarum*, *P. mexicanus*, *P. pantropicalis* sp. nov., *P. sylvaticus*) documented in previous works (Voto & Angelini 2021; Angelini & Voto 2023; Voto & Angelini 2024) we add now *P. punjabensis*.

In the second part of the work, following very recent new molecular evidence, we propose an update of our previous work regarding nomenclatural issues in the *Panaeolus papilionaceus* complex.

Finally, new photographs of *P. sylvaticus* are published showing more chromatic aspects of its pileus.

MATERIALS AND METHODS

Morphology

The collections of *Panaeolus punjabensis* and *P. sylvaticus* were photographed when fresh *in situ* by C. Angelini using a digital camera Nikon Coolpix 8400 and subsequently dried; macroscopic characters where observed by C. Angelini on fresh material; microscopic characters were studied, described and photographed by P. Voto on dried material revived with 10% NH4OH or 5% KOH and in some cases using Congo red as mounting medium for imaging. All collections are housed in C. Angelini's personal herbarium and will successively be transferred to the herbarium JBSD (Jardín Botánico Nacional Dr. Rafael M. Moscoso, Santo Domingo, Dominican Republic). The authors of the images in the figures are shown in square brackets.

DNA extraction, PCR and DNA sequencing

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 ºC. The primers ITS1F 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. Sequences were corrected to remove reading errors in chromatograms. An alignment of ITS rDNA

sequences related to the one obtained from the sample studied was assembled, using the dataset employed before (Voto & Angelini 2024) as well as selected sequences produced by Consiglio & Marchetti (2023).

Sequence alignment and phylogenetic analyses

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. Aligned sequences were loaded in MrBayes 3.2.6 (Ronquist *et al.* 2012) and subjected to Bayesian analysis (one partition, 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 14.55 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, GTRGAMMAI model, 2000 bootstrap replications). The significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP).

RESULTS

Phylogenetic analyses

Our phylogram demonstrates that *Panaeolus punjabensis* is a cosmopolitan species that, besides Asia (Pakistan) and Central America (Dominican Republic) is also present in Africa (Egypt and Namibia).

Concerning the *Panaeolus papilionaceus* complex, the results obtained in our previous work (Voto & Angelini 2024) are confirmed with the corrections, thanks to the inclusion of the holotype of *Panaeolus papilionaceus* var. *parvisporus*, that the clade there identified as *P. parvisporus* must be named *P. retirugis* and that this name must be treated as autonomous, not as a synonym of *P. papilionaceus*.

Table 1. 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 here or in Voto & Angelini (2024) 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), Epitype (E), Paratypes (P) and Lectotypes (L)

species name in GenBank	current name	voucher/origin	ITS
Galeropsis bispora T	***P. plantaginiformis****	LE 2863/Uzbekistan	MK397580
G. desertorum	***P. desertorum****	NL-1863/Hungary	JX968154
Gastrocybe iberica T	***P. desertorum****	AH 9990/Spain	MK397542
G. iberica P	***P. desertorum****	AH 9993/Spain	MK397543
G. iberica	***P. desertorum****	AH 10396/Spain	MK397544
G. iberica	***P. desertorum****	AH 42860/Spain	MK397545
G. iberica	***P. desertorum****	AH 10493/Spain	MK397546
Panaeolus acuminatus E		Gerhardt 83049 (B)/Germany	PP447476
P. acuminatus		CBS:270.47/?	MH856251
P. acuminatus		AMB 20065/Italy	PP447475
P. acuminatus		inaturalist.org/observations/141352004/USA	OQ372246
P. acuminatus		SGL09/China	OR035540
P. acuminatus		CBS 269.47/?	MH856250
P. acuminatus	*P. olivaceus*	PRM 935914/Czech Republic	MW352021
P. acuminatus	*P. fimicola*	4084/Italy	JF908518
P. alcis		Mushroom Observer #88085/Sweden	KM982723
P. alcis		SAT-14-239-20/USA(Alaska)	MW597122
P. antillarum		SFSU:DED7874/Thailand	MF497585
P. antillarum		PAD H0061942/Dominican Republic	PP590043

species name in GenBank	current name	voucher/origin	ITS
P. antillarum		CORT:013830/Dominican Republic	MF497586
P. antillarum		JL27/China	ON059337
P. antillarum		EGDA-N15/Egypt	ON024905
P. antillarum		BR5020167127933/Togo	OR035499
P. antillarum		WANG 140007/Taiwan	KR998382
P. antillarum		FLAS-F-69480/USA	OQ746434
P. antillarum		DQS36F/Philippines	MZ735416
P. antillarum		HYW22/Thailand	OR035522
P. antillarum		HYW21/Thailand	OR035520
P. antillarum	*P. semiovatus*	748/Italy	JF908515
P. axfordii T		MFLU:19-2367/China	NR_169700
P. bisporus	*P. cyanescens*	KaiR95/Benin	MT110229
P. bisporus	*P. cyanescens*	MushroomObserver.org/188954/USA	MG966283
P. bisporus	*P. cyanescens*	HYW197/China	OR035518
P. bisporus	*P. cyanescens*	T2507/China	OR035542
P. cambodginiens	*P. cyanescens*	NBRC-30222/Japan?	AB158633
P. campanulatus	*P. papilionaceus*	10141/Italy	JF908522
P. campanulatus	*P. papilionaceus*	Mushroom2/China	MT451920
P. campanulatus	*P. cinctulus*	/China	JF961376
P. castaneifolius	*P. foenisecii*	Mushroom Observer 90428/USA	KX010428
P. cinctulus E		Gerhardt 83052/Germany	PP447483
P. cinctulus		iNAT:56796374/USA	OQ147191
P. cinctulus		iNAT:126276059/USA	OP751540
P. cinctulus		S.D. Russell ONT iNaturalist 130442846/USA	OP549138
P. cinctulus		PRM 935916, Mushroom Observer 204889/Italy	MW352022
P. cinctulus		Mushroom Observer # 321948/USA	MH590045
P. cinctulus		OMDL K. Canan iNaturalist # 169757989/USA	OR987159
P. cinctulus		OMDL K. Canan iNaturalist # 170057671/USA	OR987260
P. cinctulus		MCVE 1084/Italy	PP447482
P. cinctulus		iNat86856915/USA	OQ389417
P. cinctulus		BR5020180462561/Netherlands	OR035501
P. cinctulus		HYW186/China	OR035517
P. cyanescens		AF163/China	OQ450458
P. cyanescens		D36/China	KT002152
P. cyanescens		MHHNU 31855/China	OP862802
P. cyanescens		SIV1/India	MK855517
P. cyanescens		FS1/India	MK855516
P. cyanescens		SIV2/India	MK855518
P. cyanescens		LAH37983_Panaeolus_cyanescens_sm38/PAK	OR668690
P. cyanescens		LAH37985_Panaeolus_cyanescens_sm40/PAK	OR668692
P. cyanescens		MES-4248/USA	OR664094
P. cyanescens		BP17M/Philippines	OR062405
P. cyanescens		1S/Croatia?	KU640168
P. cyanescens		18S/?	HM035084

species name in GenBank	current name	voucher/origin	ITS
P. cyanescens		0709305/JG/France	PP447485
P. cyanescens		AMB 20070/Italy	PP447484
P. cyanescens var.	*P. cyanescens*	n. 6576 AQUI/Italy	EU834287
P. desertorum		LE 313090/Russia	MK397566
P. desertorum		LE 313250/Russia	MK397568
P. desertorum		LE 313091/Greece	MK397567
P. desertorum		B. Dima BG-2022-10-19-1/Hungary	PP447487
P. desertorum		GB-0073426/Hungary	PP447486
P. desertorum	*P. plantaginiformis*	LE 2864/Uzbekistan	MH055384
P. desertorum	*P. plantaginiformis*	LE 2865/Uzbekistan	MH055383
P. dunensis		AMB 20210/France	PP447489
P. dunensis		AMB 20211/Italy	PP447490
P. fimicola E		Gerhardt 75349 (B)/Germany	PP447491
P. fimicola E		Gerhardt 75349 (B)/Germany	PP447492
P. fimicola	*P. semiovatus*	NSK 1017274/Russia	OR242695
P. fimicola	*P. semiovatus*	Mushroom6/China	MT451924
P. fimicola	*P. semiovatus*	20180624002/China	MT347601
P. fimicola	*P. semiovatus*	474/Italy	JF908514
P. fimicola	*P. semiovatus*	HMJAU66147/China	OQ927089
P. foenisecii		T-790/USA	KC176293
P. foenisecii		S.D. Russell MycoMap # 5430/USA	ON561649
P. foenisecii		S.D. Russell ONT iNaturalist # 141290781/USA	OQ297023
P. foenisecii		iNAT:21657597/USA	OM212934
P. foenisecii		S.D. Russell MycoMap # 5431/USA	ON561650
P. foenisecii		OMDL K. Canan iNaturalist # 172543719/USA	OR732083
P. foenisecii		OMDL K. Canan iNaturalist # 169180865/USA	OR825597
P. foenisecii		OMDL K. Canan iNaturalist # 171232504/USA	OR785929
P. foenisecii		S.D. Russell ONT iNaturalist 118906067/USA	OP749347
P. foenisecii		S.D. Russell ONT iNaturalist # 121782791/USA	OP470404
P. foenisecii		OMDL K. Canan iNaturalist # 170924896/USA	OR732074
P. foenisecii		JLF9301 iNaturalist # 81665784/USA	OQ859921
P. foenisecii		S.D. Russell MycoMap # 5536/USA	ON561653
P. foenisecii		S.D. Russell ONT iNaturalist 127360021/USA	OP549249
P. foenisecii		GS6/China	OR035507
P. foenisecii		M8/Hungary	OQ029266
P. foenisecii		AMB 20071/Italy	PP447493
P. foenisecii		AMB 20072/Italy	PP447494
P. foenisecii		OTA:71571/New Zealand	OQ064958
P. foenisecii		6643/Italy	JF908520
P. foenisecii		K(M):250281/United Kingdom	MZ159698
P. foenisecii		BR5020160357160/Belgium	OR035496
P. foenisecii		CBS 142.40/?	MH856067
P. foenisecii		CBS 143.40/?	MH856068

species name in GenBank	current name	voucher/origin	ITS
P. foenisecii	*P. sp.*	CBS 251.37/?	MH855904
P. foenisecii	*P. antillarum*	NSK 1017353/Russia	OR364524
P. foenisecii	*P. antillarum*	UOC-KAUNP-MK62/Sri Lanka	KP764810
P. foenisecii	*P. antillarum*	UOC KAUNP K01/Sri Lanka	KR867660
P. foenisecii	*P. antillarum*	PC14/Philippines	OK446756
P. fraxinophilus	*P. dunensis*	OMDL K. Canan iNaturalist # 170758482/USA	OR987324
P. fraxinophilus	*P. dunensis*	MushroomObserver.org/455364/USA	OL629088
P. desertorum		LE 313090/Russia	MK397566
P. desertorum		LE 313250/Russia	MK397568
P. desertorum		LE 313091/Greece	MK397567
P. desertorum		B. Dima BG-2022-10-19-1/Hungary	PP447487
P. desertorum		GB-0073426/Hungary	PP447486
P. desertorum	*P. plantaginiformis*	LE 2864/Uzbekistan	MH055384
P. desertorum	*P. plantaginiformis*	LE 2865/Uzbekistan	MH055383
P. dunensis		AMB 20210/France	PP447489
P. dunensis		AMB 20211/Italy	PP447490
P. fimicola E		Gerhardt 75349 (B)/Germany	PP447491
P. fimicola E		Gerhardt 75349 (B)/Germany	PP447492
P. fimicola	*P. semiovatus*	NSK 1017274/Russia	OR242695
P. fimicola	*P. semiovatus*	Mushroom6/China	MT451924
P. fimicola	*P. semiovatus*	20180624002/China	MT347601
P. fimicola	*P. semiovatus*	474/Italy	JF908514
P. fimicola	*P. semiovatus*	HMJAU66147/China	OQ927089
P. foenisecii		T-790/USA	KC176293
P. foenisecii		S.D. Russell MycoMap # 5430/USA	ON561649
P. foenisecii		S.D. Russell ONT iNaturalist # 141290781/USA	OQ297023
P. foenisecii		iNAT:21657597/USA	OM212934
P. foenisecii		S.D. Russell MycoMap # 5431/USA	ON561650
P. foenisecii		OMDL K. Canan iNaturalist # 172543719/USA	OR732083
P. foenisecii		OMDL K. Canan iNaturalist # 169180865/USA	OR825597
P. foenisecii		OMDL K. Canan iNaturalist # 171232504/USA	OR785929
P. foenisecii		S.D. Russell ONT iNaturalist 118906067/USA	OP749347
P. foenisecii		S.D. Russell ONT iNaturalist # 121782791/USA	OP470404
P. foenisecii		OMDL K. Canan iNaturalist # 170924896/USA	OR732074
P. foenisecii		JLF9301 iNaturalist # 81665784/USA	OQ859921
P. foenisecii		S.D. Russell MycoMap # 5536/USA	ON561653
P. foenisecii		S.D. Russell ONT iNaturalist 127360021/USA	OP549249
P. foenisecii		GS6/China	OR035507
P. foenisecii		M8/Hungary	OQ029266
P. foenisecii		AMB 20071/Italy	PP447493
P. foenisecii		AMB 20072/Italy	PP447494
P. foenisecii		OTA:71571/New Zealand	OQ064958
P. foenisecii		6643/Italy	JF908520

species name in GenBank	current name	voucher/origin	ITS
P. foenisecii		K(M):250281/United Kingdom	MZ159698
P. foenisecii		BR5020160357160/Belgium	OR035496
P. foenisecii		CBS 142.40/?	MH856067
P. foenisecii		CBS 143.40/?	MH856068
P. foenisecii	*P. sp.*	CBS 251.37/?	MH855904
P. foenisecii	*P. antillarum*	NSK 1017353/Russia	OR364524
P. foenisecii	*P. antillarum*	UOC-KAUNP-MK62/Sri Lanka	KP764810
P. foenisecii	*P. antillarum*	UOC KAUNP K01/Sri Lanka	KR867660
P. foenisecii	*P. antillarum*	PC14/Philippines	OK446756
P. fraxinophilus	*P. dunensis*	OMDL K. Canan iNaturalist # 170758482/USA	OR987324
P. fraxinophilus	*P. dunensis*	MushroomObserver.org/455364/USA	OL629088
P. guttulatus		STA5/Iraq	LC458688
P. guttulatus		AMB n. 18101/Italy	KU725993
P. guttulatus		AMB 20073/Italy	PP447495
P. guttulatus var.		AMB 18102/Italy	KU725994
P. mediterraneus T		AMB 20075/Italy	PP447497
P. mediterraneus P		AMB 20074/Italy	PP447496
P. mexicanus		ANGE1557/Dominican Republic	MZ856314
P. cf. *olivaceus*	*P. olivaceus*	MushroomObserver.org/158389/USA	MF629829
P. olivaceus		inaturalist.org/observations/141678308/USA	OQ318240
P. olivaceus		Pan.Olivaceus-ITS1/USA	OQ318238
P. olivaceus		MushroomObserver.org/89608/USA	MH285992
P. olivaceus	*P. dunensis*	UBC F-32268/Canada	MF955153
P. olivaceus	*P. sp.*	AMB 20076/Italy	PP447498
P. olivaceus	*P. sp.*	139/Iran	MH593015
P. pantropicalis T		JBSD 130972/Rep. Dominicana	PP590037
P. pantropicalis P		PAD H0061940/Rep. Dominicana	PP590036
P. pantropicalis P		PAD H0061941/Rep. Dominicana	PP590038
P. pantropicalis P		PERTH 09605894/Australia	PP590039
P. papilionaceus E		Gerhardt 87085 (B)/Germany	PP447500
P. papilionaceus E		Gerhardt 87085 (B)/Germany	PP447499
P. papilionaceus		iNAT:22477730/USA	OM338968
P. papilionaceus		MushroomObserver.org/312080/USA	MH100727
P. papilionaceus		MushroomObserver.org/312173/USA	MH100681
P. papilionaceus		Mushroom Observer 428579/USA	MW633031
P. papilionaceus		S.D. Russell MycoMap # 5533/USA	ON245337
P. papilionaceus		Montri-76/Switzerland?	MK028487
P. papilionaceus		Mushroom Observer # 114447/Mexico	MF628989
P. papilionaceus		STA2/Iran	LC458685
P. papilionaceus		RA400/Iraq	MH632116
P. papilionaceus	*P. detriticola* T	PERTH 08944954/Australia	MT571659
P. papilionaceus	*P. sp.*	MHHNU31392/China	MK439503
P. papilionaceus	*P. sp.*	HNL501769/Lao	UDB033926

species name in GenBank	current name	voucher/origin	ITS
P. papilionaceus	*P. foenisecii*	CIRM BRFM 715/?	OL739389
P. papilionaceus	*P. pantropicalis*	Mushroom Observer # 288725/Mexico	MH169580
P. papilionaceus	*P. pantropicalis*	FLAS-F-69055/USA	OP163246
P. papilionaceus	*P. pantropicalis*	FLAS-F-69481/USA Florida	OQ746433
P. papilionaceus	*P. pantropicalis*	DNA1940/USA Florida	KF830093
P. papilionaceus	*P. pantropicalis*	D15/China	KC414234
P. papilionaceus	*P. pantropicalis*	HFJAU0032/China	MN258670
P. papilionaceus	*P. pantropicalis*	MHHNU 31396/China	OP862800
P. papilionaceus	*P. punjabensis*	Shelly024/Namibia	UDB080025
P. papilionaceus	*P. punjabensis*	EGDA-Pan228/Egypt	MW915589
P. papilionaceus	*P. retirugis*	ECO-TA-HO 7877/Mexico	MF156263
P. papilionaceus	*P. retirugis*	iNAT:69899192/USA	MZ666372
P. papilionaceus	*P. retirugis*	NAMA 2017-161/USA	MH979305
P. cf papilionaceus	*P. retirugis*	MushroomObserver.org/312079/USA	MH101639
P. papilionaceus var. *capitatocystis*	*P. retirugis*	TUF118728/Estonia	UDB019537
P. papilionaceus var. *parvisporus* T	*P. papilionaceus*	Gerhardt 5.7.1988 (B)/Germany	PP447501
P. papilionaceus var. *parvisporus* P	***P. retirugis***	B700108103/Germany	PP590041
P. papilionaceus var. *parvisporus* P	***P. retirugis***	B700108102/Germany	PP590042
P. papilionaceus var. *parvisporus* P	*P. pantropicalis*	B700108104/Brazil	PP590040
P. papilionaceus var. *retirugis*	***P. retirugis***	iNAT:21623086/USA	OM212937
P. plantaginiformis		LE 313092/Russia	MK397573
P. plantaginiformis		LE 2869/Russia	MK397572
P. plantaginiformis L		LE 2862/Russia	MK397577
P. plantaginiformis		LE 2870/Uzbekistan	MK397576
P. plantaginiformis		LE 2867/Uzbekistan	MK397575
P. plantaginiformis		TAAM120547/Uzbekistan	PP447502
P. plantaginiformis		TAAM120647/Uzbekistan	PP447503
P. punjabensis T		LAH 36793/Pakistan	NR189851
P. punjabensis P		LAH37417/Pakistan	OP681142
P. punjabensis P		BWN_45/Pakistan	MZ265143
P. punjabensis		ANGE1898/Dominican Republic	PP998475
P. retirugis		CBS:272.47/France	MH856253
P. retirugis		CBS:273.47/France	MH856254
P. retirugis		CBS:274.47/France	MH856255
P. retirugis		CBS:324.34/?	MH855549
P. retirugis		7070/Italy	JF908521
P. retirugis		AMB 20077/Italy	PP447508
P. retirugis		AMB 20078/Italy	PP447505
P. rickenii	***P. acuminatus***	KA16-1041/Kyrgyzstan	MK351680
P. rickenii	***P. acuminatus***	TENN:054965/Argentina	KY559329
P. rickenii	***P. acuminatus***	749/Italy	JF908516
P. rickenii	*P. papilionaceus*	12446/Italy	JF908523

species name in GenBank	current name	voucher/origin	ITS
P. rickenii	*P. sp.*	4474/China	OR035489
P. semiovatus		AMB 20084/Italy	PP447509
P. semiovatus		AMB 20082/Italy	PP447511
P. semiovatus		4083/Italy	JF908517
P. semiovatus		GL-13/India	MK386836
P. semiovatus		GS2/China	OR035506
P. semiovatus		Mushroom Observer 377584/USA	MT712776
P. semiovatus		UBC F-23942/Canada	MF955154
P. semiovatus		CBS 388.50/France	MH856675
P. semiovatus	*P. retirugis*	CBS:276.39/?	MH856012
P. sp.	*P. fimicola*	BR5020211847626V/Belgium	OR035504
P. sp.	*P. foenisecii*	705-2/China	DQ403253
P. sp.		iNat72986889/USA	OQ383438
P. sp.	*P. semiovatus*	LAH05071008/Pakistan	MZ825207
P. sp.	*P. semiovatus*	JLF9258/USA	OQ740139
P. sp.	*P. semiovatus*	ubco14/Canada	OP456264
P. sp.	*P. antillarum*	biocode08-94/French Polynesia	MZ997244
P. sp.	*P. punjabensis* P**	S1 (LAH36792)/Pakistan	KY636363
P. sp.	*P. papilionaceus*	PDD: 105318/New Zealand	MH380188
P. sphinctrinus	***P. papilionaceus***	CBS:582.79/?	HM035081
P. sphinctrinus	***P. papilionaceus***	CBS:582.79/France	MH873000
P. sphinctrinus	***P. papilionaceus***	TFB8627/Argentina	KY559331
P. sphinctrinus	***P. papilionaceus***	AFTOL-ID 1499/USA	DQ182503
P. sphinctrinus	***P. papilionaceus***	HMAS 290139/China	MK966651
P. sphinctrinus	*P. retirugis*	232/Italy	JF908513
P. sphinctrinus	*P. sp.*	UOC SIGWI S47/Sri Lanka	KP826787
P. aff. *sphinctrinus*	*P. sp.*	NY04449017/Colombia	PP590035
P. subbalteatus	***P. cinctulus***	UBC F-23948/Canada	MF955155
P. subbalteatus	***P. cinctulus***	OMDL K. Canan iNaturalist # 148029993/USA	OR987162
P. subbalteatus	***P. cinctulus***	iNAT:16440988/USA	MZ197976
P. subbalteatus	***P. cinctulus***	CBS 326.34/USA	MH855550
P. subbalteatus	***P. cinctulus***	CBS 327.34/USA	MH855551
P. subbalteatus	***P. cinctulus***	HFJAU-ND146/China	MN622762
P. subbalteatus	***P. cinctulus***	4/China	MW192454
P. subbalteatus	***P. cinctulus***	NX180911-04/China	MN960188
P. subbalteatus	***P. cinctulus***	/China	JF961370
P. sylvaticus		ANGE1393/Dominican Republic	OQ311002
undetermined	*P. sp.*	54A2/Colombia	MW380834
undetermined (fungal endophyte)	*P. sp.*	C111L/USA	KT202838

Figure 1 (next page). Best scoring ITS rDNA phylogram of genus *Panaeolus* (with *P. guttulatus* as outgroup) obtained using RAxML. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or ≥ 70% maximum likelihood bootstrap proportions (right). Nonsignificant support values are exceptionally represented inside parentheses. Sequences newly generated in this study are in bold.


LC458688 Panaeolus guttulatus var. guttulatus
KU725994 Panaeolus guttulatus var. merrisianoi
KU725993 Panaeolus guttulatus var. guttulatus
PP447495 Panaeolus guttulatus var. guttulatus
OQ311002 Panaeolus sylvaticus
Panaeolus cinctulus
Panaeolus fimicola
Panaeolus antillarum
Panaeolus semiovatus
Panaeolus olivaceus
Panaeolus acuminatus
OR035489 Panaeolus rickenii
Panaeolus cyanescens
Panaeolus plantaginiformis
Panaeolus foenisecii
PP447497 Panaeolus mediterraneus
PP447496 Panaeolus mediterraneus
P. mediterraneus
MW915589 Panaeolus papilionaceus
MZ265143 Panaeolus punjabensis
OP681142 Panaeolus punjabensis
NR 189851 Panaeolus punjabensis - HOLOTYPE
KY636363 Panaeolus sp.
PP998475 Panaeolus punjabensis
UDB0800254 Panaeolus papilionaceus
P. punjabensis
MT571659 Panaeolus papilionaceus
P. detriticola
MN258670 Panaeolus papilionaceus
OP862800 Panaeolus papilionaceus
MH169580 Panaeolus papilionaceus
KC414234 Panaeolus papilionaceus
OP163246 Panaeolus papilionaceus
KF830093 Panaeolus papilionaceus
PP590037 Panaeolus pantropicalis
PP590036 Panaeolus pantropicalis - HOLOTYPE
PP590038 Panaeolus pantropicalis
P590039 Panaeolus pantropicalis
Q746433 Panaeolus papilionaceus
PP590040 Panaeolus papilionaceus var. parvisporus
P. pantropicalis
KP826787 Panaeolus sphinctrinus
PP447508 Panaeolus retirugis
PP590042 Panaeolus papilionaceus var. parvisporus
MH856253 Panaeolus retirugis
MH101639 Panaeolus cf. papilionaceus
MH856254 Panaeolus retirugis
PP447505 Panaeolus retirugis
PP590041 Panaeolus papilionaceus var. parvisporus
MH856012 Panaeolus semiovatus
JF908521 Panaeolus retirugis
OM212937 Panaeolus papilionaceus var. retirugis
MH856255 Panaeolus retirugis
MH979305 Panaeolus papilionaceus
MH855549 Panaeolus retirugis
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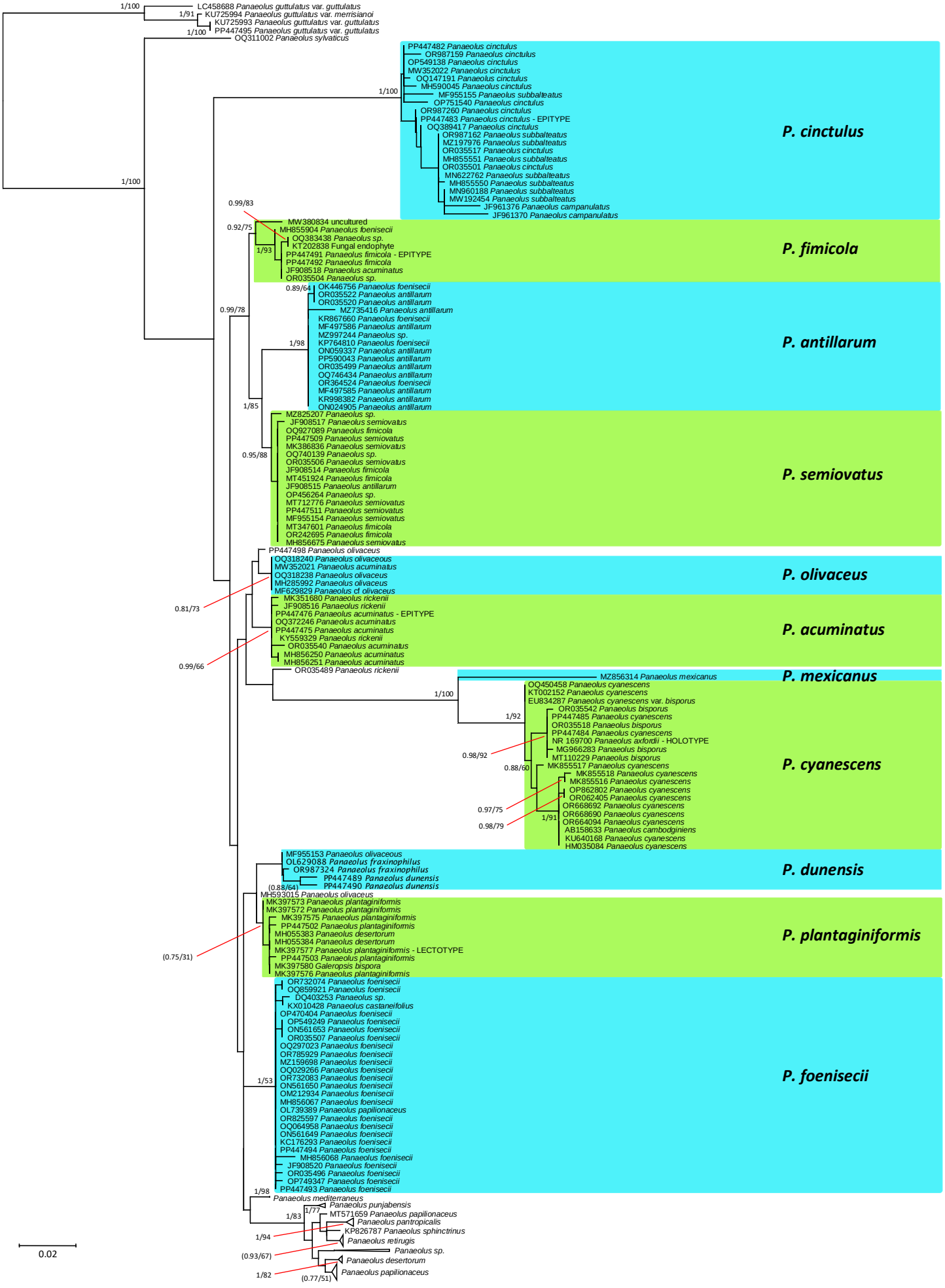
MF156263 Panaeolus papilionaceus
UDB019537 Panaeolus papilionaceus
MZ666372 Panaeolus papilionaceus
P. retirugis
PP590035 Panaeolus aff. sphinctrinus
MK439503 Panaeolus papilionaceus
UDB033926 Panaeolus papilionaceus
P. sp.
MK397544 Gastrocybe iberica
MK397542 Gastrocybe iberica - HOLOTYPE
MK397543 Gastrocybe iberica
MK397566 Panaeolus desertorum
PP447487 Panaeolus desertorum
MK397567 Panaeolus desertorum
JX968154 Galeropsis desertorum
MK397545 Gastrocybe iberica
MK397568 Panaeolus desertorum
PP447486 Panaeolus desertorum
MK397546 Gastrocybe iberica
P. desertorum
= Gastrocybe iberica
MH632116 Panaeolus papilionaceus
MK966651 Panaeolus sphinctrinus
MF628989 Panaeolus papilionaceus
ON245337 Panaeolus papilionaceus
HM035081 Panaeolus sphinctrinus
JF908523 Panaeolus rickeni
MH380188 Panaeolus sp.
PP447500 Panaeolus papilionaceus - EPITYPE
MK028487 Panaeolus papilionaceus
JF908523 Panaeolus rickenii
PP447499 Panaeolus papilionaceus
DQ182503 Panaeolus sphinctrinus
PP447501 Panaeolus papilionaceus var. parvisporus - HOLOTYPE
MH100727 Panaeolus papilionaceus
MH100681 Panaeolus papilionaceus
MW633031 Panaeolus papilionaceus
JF908522 Panaeolus campanulatus
KY559331 Panaeolus sphinctrinus
LC458685 Panaeolus papilionaceus
MT451920 Panaeolus campanulatus
MH873000 Panaeolus sphinctrinus
OM338968 Panaeolus papilionaceus
MW597122 Panaeolus alcis
KM982723 Panaeolus alcis
P. papilionaceus
= P. campanulatus
= P. papilionaceus var. parvisporus
= P. sphinctrinus
0.02


LC458688 Panaeolus guttulatus var. guttulatus
KU725994 Panaeolus guttulatus var. merrisianoi
KU725993 Panaeolus guttulatus var. guttulatus
PP447495 Panaeolus guttulatus var. guttulatus
OQ311002 Panaeolus sylvaticus
PP447482 Panaeolus cinctulus
OR987159 Panaeolus cinctulus
OP549138 Panaeolus cinctulus
MW352022 Panaeolus cinctulus
OQ147191 Panaeolus cinctulus
MH590045 Panaeolus cinctulus
MF955155 Panaeolus subbalteatus
OP751540 Panaeolus cinctulus
OR987260 Panaeolus cinctulus
PP447483 Panaeolus cinctulus - EPITYPE
OQ389417 Panaeolus cinctulus
OR987162 Panaeolus subbalteatus
MZ197976 Panaeolus subbalteatus
OR035517 Panaeolus cinctulus
MH855551 Panaeolus subbalteatus
OR035501 Panaeolus cinctulus
MN622762 Panaeolus subbalteatus
MH855550 Panaeolus subbalteatus
MN960188 Panaeolus subbalteatus
MW192454 Panaeolus subbalteatus
JF961376 Panaeolus campanulatus
JF961370 Panaeolus campanulatus
P. cinctulus
MW380834 uncultured
MH855904 Panaeolus foenisecii
OQ383438 Panaeolus sp.
KT202838 Fungal endophyte
PP447491 Panaeolus fimicola - EPITYPE
PP447492 Panaeolus fimicola
JF908518 Panaeolus acuminatus
OR035504 Panaeolus sp.
P. fimicola
OK446756 Panaeolus foenisecii
OR035522 Panaeolus antillarum
OR035520 Panaeolus antillarum
MZ735416 Panaeolus antillarum
KR867660 Panaeolus foenisecii
MF497586 Panaeolus antillarum
MZ997244 Panaeolus sp.
KP764810 Panaeolus foenisecii
ON059337 Panaeolus antillarum
PP590043 Panaeolus antillarum
OR035499 Panaeolus antillarum
OQ746434 Panaeolus antillarum
OR364524 Panaeolus foenisecii
MF497585 Panaeolus antillarum
KR998382 Panaeolus antillarum
ON024905 Panaeolus antillarum
P. antillarum
MZ825207 Panaeolus sp.
JF908517 Panaeolus semiovatus
OQ927089 Panaeolus fimicola
PP447509 Panaeolus semiovatus
MK386836 Panaeolus semiovatus
OQ740139 Panaeolus sp.
OR035506 Panaeolus semiovatus
JF908514 Panaeolus fimicola
MT451924 Panaeolus fimicola
JF908515 Panaeolus antillarum
OP456264 Panaeolus sp.
MT712776 Panaeolus semiovatus
PP447511 Panaeolus semiovatus
MF955154 Panaeolus semiovatus
MT347601 Panaeolus fimicola
OR242695 Panaeolus fimicola
MH856675 Panaeolus semiovatus
P. semiovatus
PP447498 Panaeolus olivaceus
OQ318240 Panaeolus olivaceus
MW352021 Panaeolus acuminatus
OQ318238 Panaeolus olivaceus
MH285992 Panaeolus olivaceus
MF629829 Panaeolus cf olivaceus
P. olivaceus
MK351680 Panaeolus rickenii
JF908516 Panaeolus rickenii
PP447476 Panaeolus acuminatus - EPITYPE
OQ372246 Panaeolus acuminatus
PP447475 Panaeolus acuminatus
KY559329 Panaeolus rickenii
OR035540 Panaeolus acuminatus
MH856250 Panaeolus acuminatus
MH856251 Panaeolus acuminatus
P. acuminatus
OR035489 Panaeolus rickenii
MZ856314 Panaeolus mexicanus
P. mexicanus
OQ450458 Panaeolus cyanescens
KT002152 Panaeolus cyanescens
EU834287 Panaeolus cyanescens var. bisporus
OR035542 Panaeolus bisporus
PP447485 Panaeolus cyanescens
OR035518 Panaeolus bisporus
PP447484 Panaeolus cyanescens
NR 169700 Panaeolus axfordii - HOLOTYPE
MG966283 Panaeolus bisporus
MT110229 Panaeolus bisporus
MK855517 Panaeolus cyanescens
MK855518 Panaeolus cyanescens
MK855516 Panaeolus cyanescens
OP862802 Panaeolus cyanescens
OR062405 Panaeolus cyanescens
OR668692 Panaeolus cyanescens
OR668690 Panaeolus cyanescens
OR664094 Panaeolus cyanescens
AB158633 Panaeolus cambodginiens
KU640168 Panaeolus cyanescens
HM035084 Panaeolus cyanescens
P. cyanescens
MF955153 Panaeolus olivaceus
OL629088 Panaeolus fraxinophilus
OR987324 Panaeolus fraxinophilus
PP447489 Panaeolus dunensis
PP447490 Panaeolus dunensis
P. dunensis
MH593015 Panaeolus olivaceus
MK397573 Panaeolus plantaginiformis
MK397572 Panaeolus plantaginiformis
MK397575 Panaeolus plantaginiformis
PP447502 Panaeolus plantaginiformis
MH055383 Panaeolus desertorum
MH055384 Panaeolus desertorum
MK397577 Panaeolus plantaginiformis - LECTOTYPE
PP447503 Panaeolus plantaginiformis
MK397580 Galeropsis bispora
MK397576 Panaeolus plantaginiformis
P. plantaginiformis
OR732074 Panaeolus foenisecii
OQ859921 Panaeolus foenisecii
DQ403253 Panaeolus sp.
KX010428 Panaeolus castaneifolius
OP470404 Panaeolus foenisecii
OP549249 Panaeolus foenisecii
ON561653 Panaeolus foenisecii
OR035507 Panaeolus foenisecii
OQ297023 Panaeolus foenisecii
OR785929 Panaeolus foenisecii
MZ159698 Panaeolus foenisecii
OQ029266 Panaeolus foenisecii
OR732083 Panaeolus foenisecii
ON561650 Panaeolus foenisecii
OM212934 Panaeolus foenisecii
MH856067 Panaeolus foenisecii
OL739389 Panaeolus papilionaceus
OR825597 Panaeolus foenisecii
OQ064958 Panaeolus foenisecii
ON561649 Panaeolus foenisecii
KC176293 Panaeolus foenisecii
PP447494 Panaeolus foenisecii
MH856068 Panaeolus foenisecii
JF908520 Panaeolus foenisecii
OR035496 Panaeolus foenisecii
OP749347 Panaeolus foenisecii
PP447493 Panaeolus foenisecii
P. foenisecii
Panaeolus mediterraneus
Panaeolus punjabensis
MT571659 Panaeolus papilionaceus
Panaeolus pantropicalis
KP826787 Panaeolus sphinctrinus
Panaeolus retirugis
Panaeolus sp.
Panaeolus desertorum
Panaeolus papilionaceus
0.02

TAXONOMY

Panaeolus punjabensis M. Asif, Q. Firdous, A. Izhar, Niazi & Khalid (Fig. 2-7)

European Journal of Taxonomy 888: 85 (2023)

=? *Panaeolus alcis* (as '*alcidis*') sensu Kaur, Atri & Kaur (2014)

Macroscopic characters

Pileus (primordia and young specimens not observed): 12 – 18 mm broad, paraboloid-convex; off-white to pale grey, at centre with a pale ochraceous-pinkish shade; cuticle dry, cracking and eroded with age, margin not striate; veil absent.

Lamellae adnate, spaced, approx 18 – 20, intermixed with 1-3 lamellulae, adnate, ventricose; at first olivaceous, then violaceous-bluish grey with blackish spots ("salt and pepper" appearance); edge pale.

Stipe 110 – 130 × 3 – 4.5 mm, base swollen up to 6.6 mm, cylindric, flexuous, straight to twisted; surface pale brownish with an olivaceous shade at apex, medium to darkish brown to reddish-violaceous brown elsewhere, distinctly covered in white pruina at apex and white fibrils elsewhere, base covered with white mycelial felt and floccules; bruising blue towards base; annulus absent.

Context not examined.

Fig. 2: *P. punjabensis*. ANGE188 [C. Angelini]

Fig. 3: *P. punjabensis*. ANGE188 [C. Angelini]

Fig. 4: *P. punjabensis*. ANGE188 [C. Angelini]

MIcroscopic characters

Fig. 5: *P. punjabensis*. ANGE1898. Stipe base with bluish tints [C. Angelini]

Basidiospores (n=20) (14.0) 15.0 – 17.6 (19.2) × 9.0 – 10.2 (12.0) × 7.7 – 9.5 µm, Q 1.50 – 1.73 × 1.65 – 1.94; in front view broadly elliptic to broadly fusiform or subhexagonal, base obtuse to conical-obtuse, in side view elliptic-oblong; apex not or little protruding; dark brown to blackish brown in 5% KOH, distinctly thick-walled; germ pore distinct, 2.0 – 2.5 µm broad.

Basidia 24.0 – 34.0 × 10.0 – 13.7 µm, stoutly cylindric to stoutly subululiform, rarely clavate, 4-spored; hyaline.

Cheilocystidia 35.0 – 50.0 µm long, base 5.0 – 11.5 µm broad, apex (3.0) 5.0 – 11.0 µm broad, lageniform, lageniform-clavate, clavate- to capitate-pedicellate, rarely cylindric or tapering at apex, usually when swollen at apex then little ventricose at base; mostly hyaline and smooth, thin-walled, abundant. *Pleurocystidia* absent.

Pileipellis cellular composed of up to 30 µm broad elements.

Pileocystidia approx. 35 – 45 × 7 – 13 µm, lageniform, scattered.

Clamp connections found in pileus trama and at base of cheilocystidia.

Collection examined and habitat: Dominican Republic, P.to Plata, Cabarete, on grassy, heavily horse grazed ground of back dunes among shrubs of *Coccoloba uvifera*, 12 November 2023, *legit C. Angelini* (pers. herb. ANGE1898), GenBank: PP998475 - ITS.

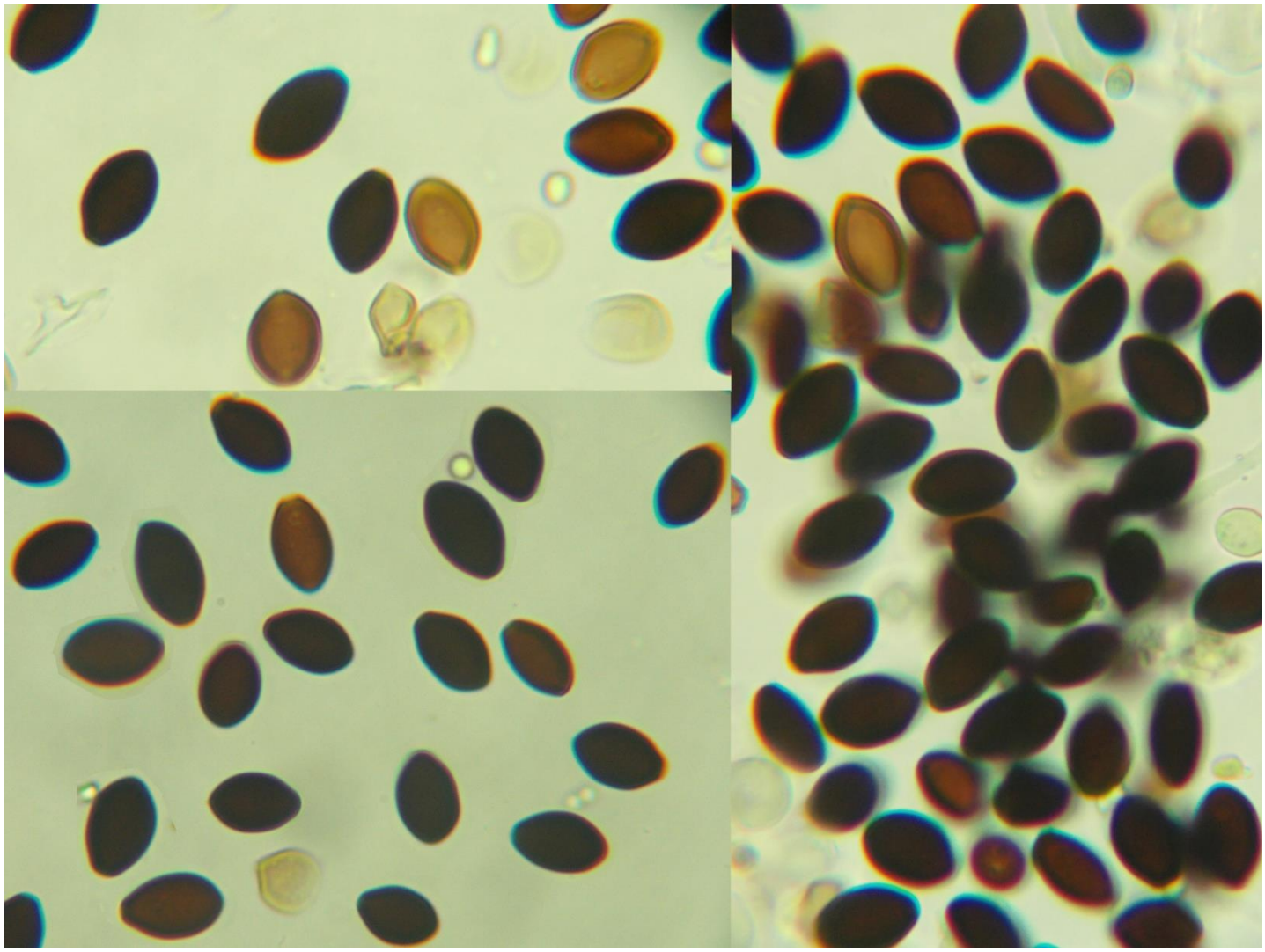


Fig 6: *P. punjabensis*. ANGE1898. Spores in 5% KOH [P. Voto]

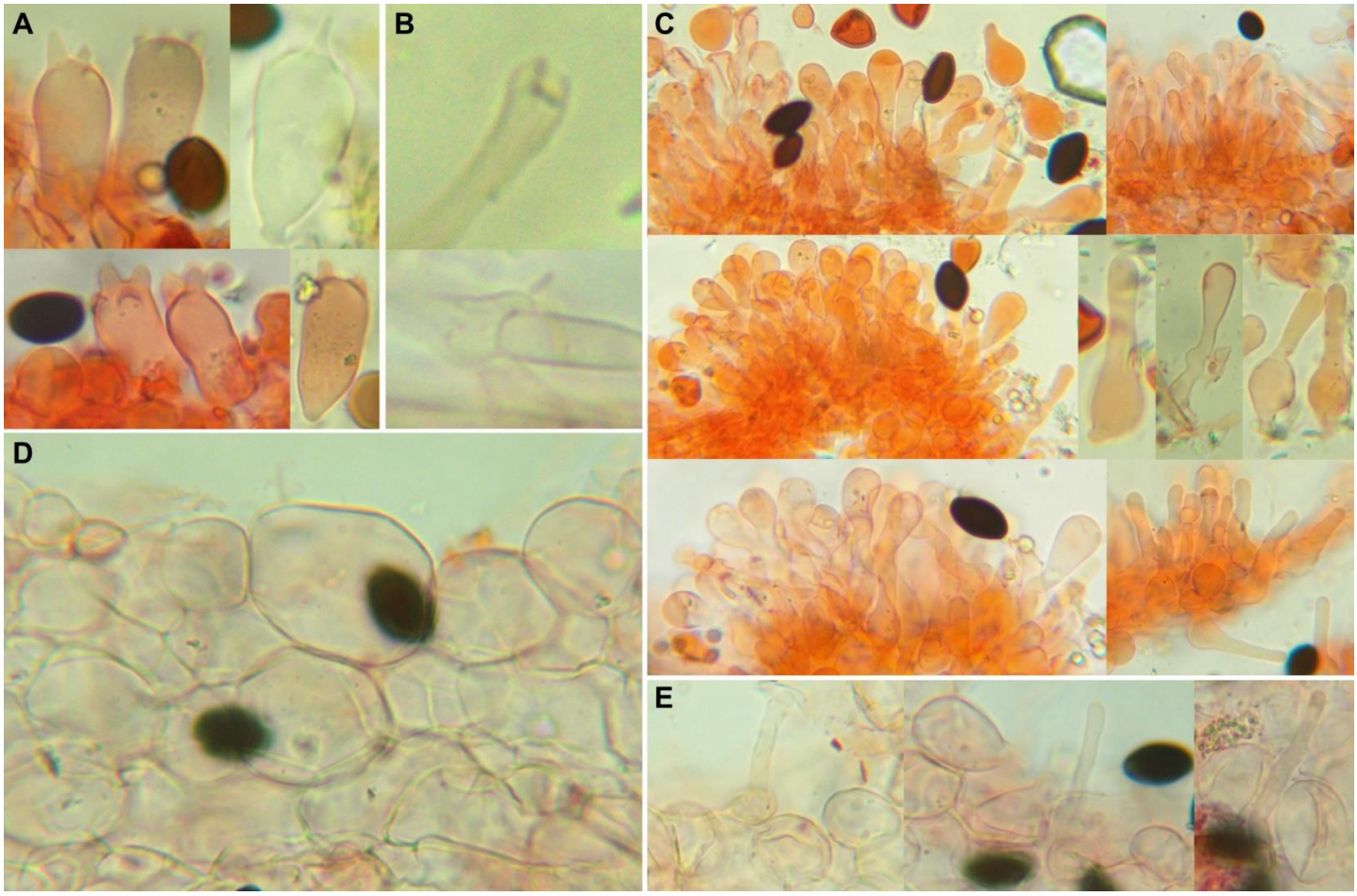


Fig 7: *P. punjabensis*. ANGE1898. A) Basidia, B) Clamps, C) Cheilocystidia, D) Pileipellis, E) Pileocystidia. All images in Congo red [P. Voto]

Notes

Our description offers new relevant data integrating those reported in the protolog (Asif *et al*. 2023).

In particular we have noticed in our collection a not striate margin of pileus, a partial lentiform shape of the spores, narrower and 4-spored basidia, lageniform and scattered pileocystidia, presence of clamps.

Panaeolus punjabensis is characterized by absence of pleurocystidia (subgenus *Panaeolus*), agaricoid habit, absence of veil, whitish to pale grey pileus with ochraceous shades only at centre, and tending to crack and peel off, bluish tints on handling or bruising (we have not performed chemical tests attesting the presence of hallucinogenic substances), a mixture of lageniform to lageniform-clavate or claviform-capitate cheilocystidia, large elliptic-subfusiform, scarcely hexagonal-lentiform spores, habitat on nitrogenous soil with herbivorous dung present or directly on dung in tropical/subtropical climate.

Beyond the Indian region and the Caribbean, the taxon is also present, based on Genbank ITS sequences, in Egypt and in Namibia, evincing a broad diffusion.

Morphologically, the closest taxon seems to be *Panaeolus moellerianus* Singer, typified from the Macquarie Island in Oceania on humus among graminaceous plants, unsequenced. The pileus is defined as scrobiculate to reticulate-wrinkled (Singer 1960).

There are other unveiled, large-spored species in subgenus *Panaeolus*, they all differ by distinctly lentiform spores: *P. cinctulus* (Bolton) Sacc. (with also a partially eccentric germ pore), *P. acuminatus* (P. Kumm.) Quél., *P. paludosus* Cleland and *P. goossensiae* Beeli.

Finally, we report an unsequenced collection identified as *P. alcis* (as '*alcidis*') by Kaur, Atri & Kaur M (2014), from India. This material features all characteristics we found in our collection. The authors report having noticed a bluing also on the pileus and in the context. We are convinced this represents a misidentification of *P. punjabensis*.

NEW DATA IN THE *PANAEOLUS PAPILIONACEUS* COMPLEX

An ITS sequence of the holotype of *Panaeolus papilionaceus* var. *parvisporus* has very recently become available (it was repeatedly and unsuccessfully tried by Voto & Angelini 2024). Since the phylogram demonstrates that it nests in the clade *Panaeolus papillionaceus* s.str. (see Fig. 1), the systematics of the *Panaeolus papilionaceus* complex as proposed in Voto & Angelini (2024) needs to be reassessed.

Voto & Angelini (2024) had phylogenetically demonstrated the presence in Europe of two taxa in the *P. papilionaceus* complex (ignoring the galeroid taxa).

Basing on the ITS sequences obtained from two German paratypes of *P. papilionaceus* var. *parvisporus*, they assumed that these two taxa could be separated on the base of the spore length: a large-spored (more than 15 µm long on average) taxon identified as *P. papilionaceus* (= *P. campanulatus* = *P. retirugis* = *P. sphinctrinus*) and a small-spored (at most 15 µm long on average) taxon they named *P. parvisporus* comb. nov. (the choice of the names followed the systematics proposed by Gerhardt 1996, 2012).

With the new molecular evidence of a small-spored collection occurring in the clade of *P. papilionaceus* s. str., the separation based on the spore length would become incorrect. The only morphological difference between these two taxa would therefore be based on the tendency towards a smooth and more greyish pileus in *P. papilionaceus* compared to a corrugated and more brownish pileus in *P. retirugis*.

However, we have examined the three following considerations.

a) Over time, several authors (e.g. Hora 1957; Ola'h 1970; Watling & Gregory 1987; Bon & Courtecuisse 2003) having treated the *Panaeolus papilionaceus* complex never reported small-spored collections combined with a smooth, non-corrugated pileus;

b) In all descriptions of the above mentioned authors the pileus breadth of *P. papilionaceus* falls in the range 20-45 mm. Therefore, a pileus 8-15 mm broad, as described by Gerhardt (1996) for *P. papilionaceus* var. *parvisporus*, is unusually very small;

c) In Bulliard's (1782, table 58) iconography of *Agaricus papilionaceus* (see reproduction in Voto & Angelini 2024 figure 19) mature pilei are drawn conical-convex to convex, and in Fries's (1821) sanction they are defined convex. On the contrary, Gerhardt (1996) defines the pileus of *P. papilionaceus* var. *parvisporus* as thimble-shaped to campanulate.

Ultimately, basing on these observations, we propose to treat the type collection of *P. papilionaceus* var. *parvisporus* as consisting of still immature specimens and therefore with spores not yet of the definitive size.

On this assumption, we confirm Voto & Angelini's (2024) proposal of using the spore length for separating the two taxa, we add to it the pileus characteristics and we renounce the use of the epithet '*parvisporus*' instead of '*retirugis*'.

The two European non-galeroid taxa of the *P. papilionaceus* complex are therefore:

- ***P. papilionaceus*** (= *P. campanulatus* = *P. sphinctrinus*) with spores on average more than 15 µm long, and pileus smooth and mostly in the greyish tones;

- ***P. retirugis*** (= *P. papilionaceus* var. *parvisporus* = *P. parvisporus*) with spores on average at most 15 µm long, and pileus corrugated and mostly in the brownish tones.

Pileus colour and corrugation of course may depend on environmental conditioning and the freshness of the basidiomata.

The tree used in Voto & Angelini's (2024) is here reproduced expanded with the sequence of the typus of *P. papilionaceus* var. *parvisporus* and some others and with the names of the species updated.

Panaeolus sylvaticus Silva-Filho & Cortez (Fig. 8-10)

Edinburgh Journal of Botany 76(2): 303 (2019)

Collections examined and habitat. Dominican Republic, P.to Plata, Cabarete, Sea Horse Ranch, gregarious on woody debris between piles of decaying plant material (landfill of material from pruning) in an almond forest near the beach, 4 February 2024, *legit C. Angelini*, pers. herb. ANGE1992; ibid, pers. herb. ANGE1993.

Fig. 8: *P. sylvaticus*. ANGE1992 [C. Angelini]

Fig. 9: *P. sylvaticus*. ANGE1993 [C. Angelini]

Notes

Our two new collections feature morphological data fully correspondent to those already reported in Angelini & Voto (2023). We can only add that we found occasional larger spores attaining to 11.1x8.1x5.8 µm and somewhat more evident greenish-yellowish mucus or content of cheilocystidia (Fig. 10). The photographs here published show the colours in discoloring pilei.

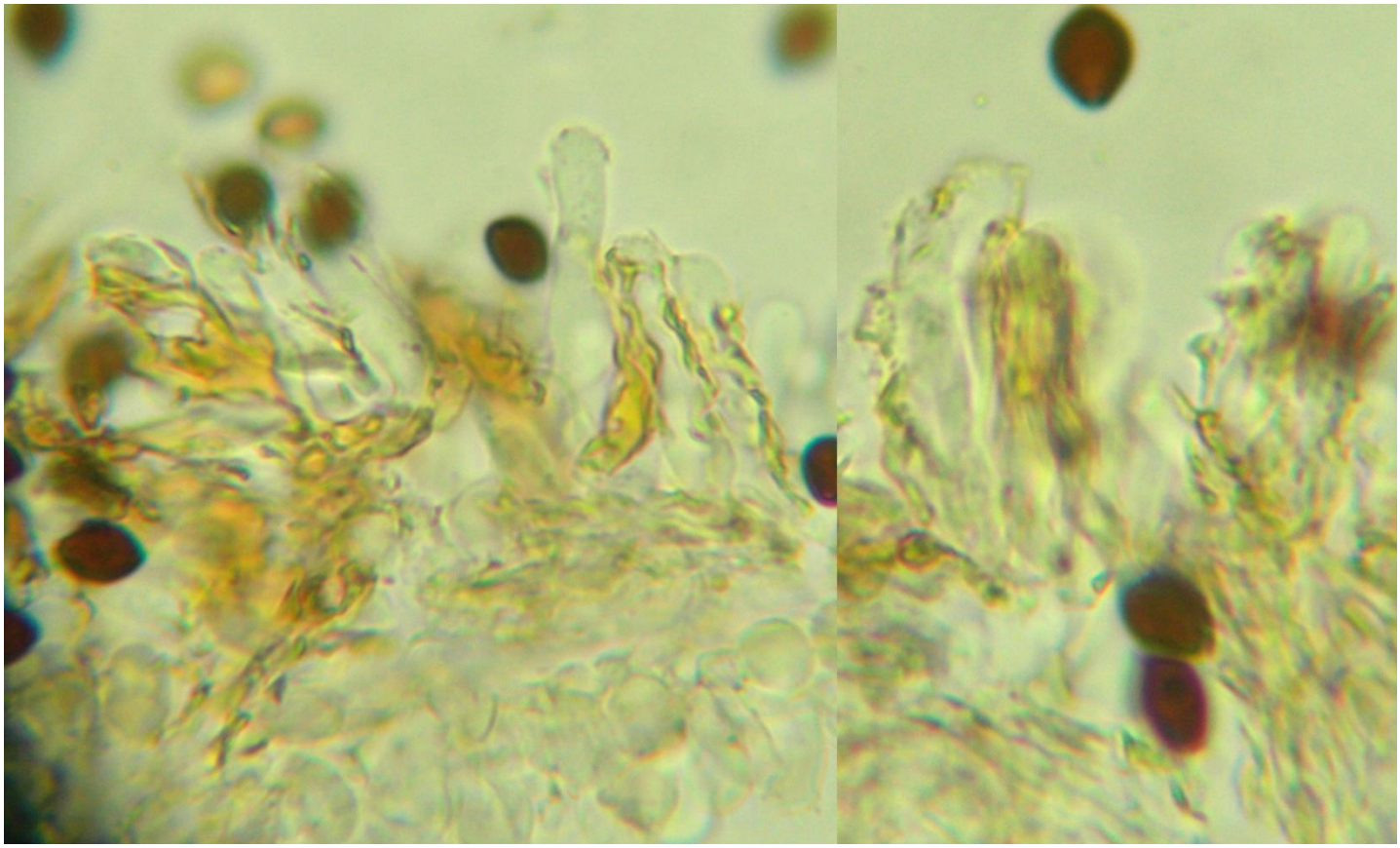


Fig. 10: *P. sylvaticus*. ANGE1992. Cheilocystidia in 5% KOH

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