

Third report of coprinoid fungi (Psathyrellaceae, Agaricales) in the Dominican Republic with notes on *Coprinopsis clastophylla*, rhacophylloid taxa and the *Coprinopsis afronivea* complex

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Abstract: New combined morphological and phylogenetic studies in coprinoid fungi from the Caribbean have revealed some interesting novelties in the genus *Coprinopsis*. New reports from the Dominican Republic in this article include *Coprinopsis flamboyani* sp. nov. belonging to the *Coprinopsis alnivora* complex and having teleomorphic and anamorphic states. Comments on dimorphic species of *Coprinopsis* and *Rhacophyllus lilacinus* are included, demonstrating that *Coprinopsis clastophylla* must be considered a synonym of *Coprinopsis sclerotiger* and that dimorphism in the genus *Coprinopsis* is more developed than previously thought, spanning more than one section. Also newly reported from the Dominican Republic are *Coprinopsis variispora* sp. nov., and *Coprinopsis caribaeonivea* sp. nov. (the latter previously reported as a *nomen provisorium*) both belonging to the *Coprinopsis nivea* complex. Also reported herein is the first record of *Coprinopsis calospora* from the Dominican Republic. In addition to those Dominican species, *Coprinopsis sinonivea* sp. nov. is formally described from Chinese collections previously identified as *Coprinopsis nivea*.

INTRODUCTION

Following on from Angelini, Voto & Alvarado (2023) and Voto & Angelini (2024), this third report of coprinoid taxa of the Dominican Republic adds more knowledge with the formal description and naming of three new species of *Coprinopsis* P. Karst.

Coprinopsis flamboyani sp. nov. belongs to the complex of *Coprinopsis alnivora* (Bogart) Voto in *Coprinopsis* sect. *Coprinopsis*, characterized by a filamentous veil of forked to nodulose hyphae. *Coprinopsis variispora* sp. nov. and *Coprinopsis caribaeonivea* sp. nov. belong to the complex of *Coprinopsis nivea* (Pers.) Redhead, Vilgalys & Moncalvo in *Coprinopsis* sect. *Niveae* (Citérin) D.J. Schaf., characterized by a globose veil and smooth spores. This report also presents the first confirmation in the Dominican Republic of *Coprinopsis calospora* (Bas & Uljé) Redhead, Vilgalys & Moncalvo, belonging to *Coprinopsis* sect. *Lanatulae* (Fr.) D.J. Schaf. s.l. (phylogenetically to *C.* sect. *Cinereae* D. Wächt. & A. Melzer), characterized by a filamentous veil of smooth hyphae.

The morphological and phylogenetic comparison, between our Dominican collections and species already described in some cases did not seem to outline a clear line of convergence or divergence, especially when it came to evaluating whether the geographic isolation in some areas may have favoured the speciation or simply the production of local forms.

For example, in the case of our voucher ANGE1831, previously published as *Coprinopsis nivea* (Voto & Angelini 2024), despite the phylogenetic analysis nests it (sequence PP349937) in a separate branch (Fig. 2), due to the fact that we could not find relevant morphological differences with the sister species *C. nivea*, we maintain a conservative approach considering it a local breed falling within the intraspecific variability of *C. nivea*. For

considering this voucher a new cryptic sister species, broader molecular analyses on more collections will be necessary.

On the contrary in some other cases we encountered stronger convincing evidence. For example, *C. variispora* sp. nov. and *C. flamboyani* sp. nov. are phylogenetically well supported and also morphologically different from the closest species. Similarly, our collection of *C. calospora* matches the type material on both a morphological and molecular basis.

In the case of *C. caribaeonivea* sp. nov., previously published in Angelini, Voto & Alvarado (2023) as *nom. prov.*, following a morphological re-examination and the results of the new phylogenetic analysis (Fig. 2), we consider it to be an autonomous taxon distinct from *Coprinopsis afronivea* Desjardin & B.A. Perry.

The description of *C. flamboyani* sp. nov. is of particular significance because it is shown to be a dimorphic species that possesses both a teleomorphic state (typically coprinoid) and an anamorphic state (of the rhacophylloid type). This characteristic has directed us towards an analysis of *Coprinopsis clastophylla* (Maniotis) Redhead, Vilgalys & Moncalvo, described in both states, and *Coprinopsis lilacina* (Berk. & Broome) Redhead, described only in the rhacophylloid state. The specification that the anamorphic stage treated in this paper is of the rhacophylloid type is due to the fact that another kind of anamorph stage, of a conidiogenous morph, is also known in the family Psathyrellaceae [see the anamorph genus *Hormographiella* Guarro & Gené having teleomorphic stages in *Coprinellus* P. Karst. and *Coprinopsis* (Cáceres *et al.* 2006; Stalpers *et al.* 2021; Surmont *et al.* 2022)].

In the case of *C. clastophylla* we confirm a clear phylogenetic separation from our *C. flamboyani*. We also demonstrate that *C. clastophylla* is synonymous with *Coprinopsis sclerotiger* (Watling) Redhead, Vilgalys & Moncalvo (Fig. 3) and, consequently, that it belongs to a different section [*Coprinopsis* sect. *Narcoticae* (Uljé & Noordel.) D.J. Schaf.] to *C. flamboyani* (*Coprinopsis* sect. *Coprinopsis*). This, in turn, leads us to postulate that several *Coprinopsis* species may have a dimorphic (coprinoid-rhacophylloid) condition. Therefore, we contend that, in the absence of a simultaneous collection of both morphs for morphological and molecular comparison all collections identified as *Rhacophyllus lilacinus* Berk. & Broome (basonym of *C. lilacina*) must be considered unidentifiable. Until sequences from the holotype of *R. lilacinus* or a neotype from the *locus typicus* (Sri Lanka) are available, the taxon must be treated as a *nomen collectivum* and the description of more new *Coprinopsis* species with a dimorphic state must be considered inevitable.

MATERIALS AND METHODS

Samples analyzed

Morphological and molecular analyses were attempted on a total of 6 *Coprinopsis* samples from the Dominican Republic. They are deposited in the herbaria of the Jardín Botánico Nacional Dr. Rafael M. Moscoso, Santo Domingo, Dominican Republic (herbarium code JBSD) and of the Padova Botanical Garden at the University of Padova, Italy (herbarium code PAD). All additional sequences used in the phylogenetic analyses were retrieved from GenBank excluding one from UNITE. The analysis is divided into three phylograms, while all samples analysed are collectively listed in Table 1.

Morphology

As in Angelini, Voto & Alvarado (2023), with photographs in habitat by C. Angelini, and microscopy and imagery by P. Voto. When spores are three-dimensional their measurement is expressed as length × width in front view × width in side view; similarly, the ratio length/width (quotient, Q) is expressed as quotient in front view × quotient in side view.

Phylogeny

DNA extraction, amplification and 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 °C. The primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were employed to amplify the ITS rDNA region, and EF1-983F, EF1-1567R and EF1- 2218R (Rehner & Buckley 2005) for the translation elongation factor 1a (*tef1*)

gene. 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.

Phylogenetic analysis

Three different datasets of ITS rDNA sequences were built and analyzed separately: 1) *Coprinopsis* sect. *Cinereae*, 2) *Coprinopsis* sect. *Niveae*, and 3) *Coprinopsis* sects. *Coprinopsis* and *Narcoticae*. 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). The sequences retrieved are listed in Table 1. 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 loci were loaded in MrBayes 3.2.6 (Ronquist *et al.* 2012), where a Bayesian analysis was performed (single partition, 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 0.22 M (*Coprinopsis* sect. *Cinereae*), 0.15 M (*Coprinopsis* sect. *Niveae*) and 0.94 M (*Coprinopsis* sects. *Coprinopsis* and *Narcoticae*) 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

Phylogeny

The analysis of ITS rDNA sequences of *Coprinopsis* sect. *Cinereae* (Fig. 1) showed seven major clades: *C. afrocinerea*, *C. annulopora*, *C. calospora*, *C. cinerea*, *C. neocinerea* and two undetermined clades. One of the samples analyzed in the present work, ANGE1704, is significantly similar to those identified as *C. calospora* in public databases, including the type. On the basis of genetic results available, this is therefore the most suitable name for this sample.

The analysis of ITS data of *Coprinopsis* sect. *Niveae* (Fig. 2) showed a great variability, with significant structures inside *C. nivea* and *C. afronivea*. One of the samples analyzed in the present work (ANGE 1831, sequence PP349937) is subsignificantly related to *C. nivea*, maybe representing a deviant lineage of this species, while *C. pseudonivea*, *C. igarashi* and a *species nova* (paper in progress, pers. comm. from the author) are less significantly related to it. An infraspecific differentiation seems to occur in the *C. afronivea* complex wherein the two clades represented by the new taxa *C. caribaeonivea* and *C. sinonivea* show varying degrees of significant relationship with each other and with *C. afronivea*. The new taxon *C. variispora* could prudentially be considered sister to this group.

Finally, the analysis of ITS rDNA sequences of *Coprinopsis* sects. *Coprinopsis* and *Narcoticae* (Fig. 3) showed that the teleomorphic and anamorphic samples of *C. flamboyani* are genetically identical. Both form a significantly distinct clade related to *C. alnivora*, *C. palaciosii*, and multiple samples identified as *C. clastophylla*. However, the holotype of *C. clastophylla* (CBS:470.73) belongs to *Coprinopsis* sect. *Narcoticae*, being apparently conspecific with several collections identified as *C. sclerotiger* and *C. lilacina*. As a result, the samples identified as *C. clastophylla* in *Coprinopsis* sect. *Coprinopsis* must belong to a different species. The actual taxonomic status of these clades and the species names proposed for some of them should be revisited with the aid of additional information (sequences from other loci or even genomic data). The pair comparison between the *tef1* sequence obtained from *C. flamboyani* and those of *C. palaciosii* (PP907119 and PP910696), of unpublished homologous sequences of N.L. Bougher BOU911 and N.L. Bougher NLB 1393 (a new species in publication), and of M.D. Barrett F214/10 and PERTH:08733635 (a new species in publication) revealed an average 94.68% similarity. Between these clades mutations are present in both exons and introns without intraspecific variation. As a result, these lineages are independent species.

Table 1. Compliant with the subdivision of the analysis into three separate phylograms, all samples analysed in this study are listed first by section and then in alphabetic order. Species treated in this study are written in bold. The letters T and P in bold after a species name stand for Type and Paratype respectively. The origin of the vouchers is reported in the phylograms.

Section	species	voucher	ITS
<i>Cinereae</i>	<i>C. afrocinerea</i> T	CNF1/583	NR_159796
<i>Cinereae</i>	<i>C. annulopora</i> T	Enderle 3071987	NR_158291
<i>Cinereae</i>	<i>C. calospora</i> T	Bas8795a	JX118675
<i>Cinereae</i>	<i>C. calospora</i> T	CBS 612.89	MH862284
<i>Cinereae</i>	<i>C. calospora</i> T	CBS 612.90	MH873965
<i>Cinereae</i>	<i>C. calospora</i> T	CBS 612.91	NR_154762
<i>Cinereae</i>	<i>C. calospora</i>	JBSD130796 (ANGE1704)	PQ998501
<i>Cinereae</i>	<i>C. calospora</i>	iNaturalist # 129888756	OP470607
<i>Cinereae</i>	<i>C. cinerea</i>	O27	KX610168
<i>Cinereae</i>	<i>C. cinerea</i>	NBRC100011	AB097563
<i>Cinereae</i>	<i>C. cinerea</i>	NBRC30628	AB097562
<i>Cinereae</i>	<i>C. cinerea</i>	Gr159	FJ904826
<i>Cinereae</i>	<i>C. cinerea</i>	CNRMA/F 07-32	GQ131575
<i>Cinereae</i>	<i>C. cinerea</i>	HN08	JQ796875
<i>Cinereae</i>	<i>C. cinerea</i>	KACC49356	AF345819
<i>Cinereae</i>	<i>C. cinerea</i>	BM-FB37260	LC105653
<i>Cinereae</i>	<i>C. cinerea</i>	LVPEI.H726 10	JX868672
<i>Cinereae</i>	<i>C. cinerea</i>	NCCPF:660001	MG547964
<i>Cinereae</i>	<i>C. cinerea</i>	LA2	KU844325
<i>Cinereae</i>	<i>C. cinerea</i>	C2	KX468975
<i>Cinereae</i>	<i>C. cinerea</i>	C3	PP989445
<i>Cinereae</i>	<i>C. cinerea</i>	A2S3-5	KJ780765
<i>Cinereae</i>	<i>C. cinerea</i>	UTHSCSA DI 14-207	KM272006
<i>Cinereae</i>	<i>C. aff. cinerea</i>	SZMC-NL-0799	HQ847019
<i>Cinereae</i>	<i>C. neocinerea</i> T	CBM-FB39575	LC107784
<i>Cinereae</i>	<i>C. sp.</i>	YM71	FJ548835
<i>Cinereae</i>	uncultured	MAT-FV1-4	JX436235
<i>Cinereae</i>	uncultured	R3M5c31P	EU144583
<i>Coprinopsis</i>	<i>C. alnivora</i>	WTU-F-018318	MK169326
<i>Coprinopsis</i>	<i>C. alnivora</i>	WU 41009	MT828909
<i>Coprinopsis</i>	<i>C. alnivora</i>	SNMH529	MZ364343
<i>Coprinopsis</i>	<i>C. alnivora</i>	WU 43426	MZ407758
<i>Coprinopsis</i>	<i>C. alnivora</i>	HFRG_RW220928_1	OQ133586
<i>Coprinopsis</i>	<i>C. brunneofibrillosa</i>	Pegler2704	JX118664
<i>Coprinopsis</i>	<i>C. clastophylla</i>	FLAS-F-60004	KY654717
<i>Coprinopsis</i>	<i>C. clastophylla</i>	JZ41	MG719298
<i>Coprinopsis</i>	<i>C. clastophylla</i>	M. van der Walt:VDW1581	MT304660
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	N.L Bougher BOU911	MT537037
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	N.L. Bougher NLB 1393	MT537072
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	M.D. Barrett F214/10	PV090787
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	M.D. Barrett F86/06	PV090786
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	PERTH:08733635	PV090788
<i>Coprinopsis</i>	<i>C. aff. clastophylla</i>	MEL 2382611	KP012971
<i>Coprinopsis</i>	<i>C. cf. clastophylla</i>	iNat93090585	OP651758

Section	species	voucher	ITS
<i>Coprinopsis</i>	<i>C. episcopalis</i>	SZMC-NL-3032	FN396118
<i>Coprinopsis</i>	<i>C. friesii</i>	AM954	MK072829
<i>Coprinopsis</i>	<i>C. gonophylla</i>	ST-R-9	KU258651
<i>Coprinopsis</i>	<i>C. palaciosii</i> P	AH:49300	PP907119
<i>Coprinopsis</i>	<i>C. palaciosii</i> T	AH:49301	PP907120
<i>Coprinopsis</i>	<i>C. phaeopunctata</i> T	AH18881	HQ847042
<i>Coprinopsis</i>	<i>C. pseudofriesii</i>	SZMC-NL-2631	HQ847016
<i>Coprinopsis</i>	<i>C. rhombisporoides</i> T	BR DDCOFRI	NR_191198
<i>Coprinopsis</i>	<i>C. sclerotiorum</i>	SZMC-NL-0564	HQ847039
<i>Coprinopsis</i>	<i>C. flamboyani</i> T	JBSD130794 (ANGE1942)	PQ998502
<i>Coprinopsis</i>	<i>C. flamboyani</i> P	JBSD130795 (ANGE1943)	PQ998503
<i>Coprinopsis</i>	<i>C. sp.</i>	Vega512	EF687929
<i>Coprinopsis</i>	<i>C. sp.</i>	HG-5-1	KF438021
<i>Coprinopsis</i>	<i>C. sp.</i>	S.L 16	KF578439
<i>Coprinopsis</i>	<i>C. sp.</i>	ARF-4598	OP580268
<i>Coprinopsis</i>	<i>C. sp.</i>	S.D. Russell ONT iNaturalist # 130014767	OP643316
<i>Coprinopsis</i>	<i>C. alcobae</i> (as <i>Coprinus alcobae</i>)	SZMC-NL-0767	HQ847037
<i>Coprinopsis</i>	<i>C. sp.</i> (as <i>Coprinus comatus</i>)	KACC49373	AF345823
<i>Coprinopsis</i>	<i>C. spilospora</i>	15273	JF907840
<i>Coprinopsis</i>	<i>C. subdomesticus</i> T	Murrill459	HQ847038
<i>Coprinopsis</i>	<i>C. urticicola</i>	SZMC-NL-0170	HQ847015
<i>Coprinopsis</i>	<i>C. urticicola</i>	42108111MF0003	OQ174488
<i>Coprinopsis</i>	<i>C. vermiculifer</i>	CBS132.46	GQ249279
<i>Coprinopsis</i>	uncultured	BF-OTU86	AM901943
<i>Coprinopsis</i>	uncultured	HATFD14-17	KU712516
<i>Narcoticae</i>	<i>C. clastophylla</i>	isolate 2	EU375239
<i>Narcoticae</i>	<i>C. clastophylla</i>	isolate 3	EU375240
<i>Narcoticae</i>	<i>C. clastophylla</i>	isolate 4	EU375241
<i>Narcoticae</i>	<i>C. clastophylla</i> T	CBS 473.70	NR_154756
<i>Narcoticae</i>	<i>C. clastophylla</i>	HFRG_SR240526_1_FRDBI_36793323	PP992751
<i>Narcoticae</i>	<i>C. clastophylla</i>	OMDL K. CananiNaturalist # 223263258	PQ678643
<i>Narcoticae</i>	<i>C. foetidella</i>	SZMC-NL-3187	HQ847014
<i>Narcoticae</i>	<i>C. laanii</i>	CBS:476.70	GQ249276
<i>Narcoticae</i>	<i>C. laanii</i>	AJ1896	OR269905
<i>Narcoticae</i>	<i>C. lilacina</i>	I_16_B2	PQ114346
<i>Narcoticae</i>	<i>C. lilacina</i>	II_10_A3	PQ114347
<i>Narcoticae</i>	<i>C. lilacina</i>	II_23_A8	PQ114348
<i>Narcoticae</i>	<i>C. martinii</i>	O50524	GU234126
<i>Narcoticae</i>	<i>C. narcotica</i>	SZMC:NL:2342	FM163180
<i>Narcoticae</i>	<i>C. narcotica</i>	CBS:171.39	MH855976
<i>Narcoticae</i>	<i>C. sclerotiger</i>	CBS:596.80	GQ249277
<i>Narcoticae</i>	<i>C. sclerotiger</i>	TEP19c	KR869759
<i>Narcoticae</i>	<i>C. sclerotiger</i>	UT-Co3	MF161091
<i>Narcoticae</i>	<i>C. sclerotiger</i>	25P1	MZ413261

Section	species	voucher	ITS
<i>Narcoticae</i>	<i>C. sclerotiger</i>	FLAS-F-68796	OM672956
<i>Narcoticae</i>	<i>C. semitalis</i>	CBS:291.77	GQ249278
<i>Narcoticae</i>	<i>C. sp.</i>	CBM-FB-42015	LC425103
<i>Narcoticae</i>	<i>C. sp.</i> (as <i>Coprinus sp.</i>)	O73607	GU234153
<i>Narcoticae</i>	<i>C. stercorea</i>	SFSU MRK37	AY461839
<i>Narcoticae</i>	<i>C. stercorea</i>	SFSU DEH2074A	AY461828
<i>Narcoticae</i>	<i>C. stercorea</i>	CBS 470.70	FJ386439
<i>Narcoticae</i>	<i>C. stercorea</i>	SZMC-NL-2343	FM878028
<i>Narcoticae</i>	<i>C. sp.</i> (as <i>Gymnopus alkalivirens</i>)	GG85	GU234034
<i>Narcoticae</i>	<i>C. trispora</i>	MR180722	MN227299
<i>Narcoticae</i>	uncultured	MBP53-36	FJ237086
<i>Narcoticae</i>	uncultured	BF-OTU683	FR682426
<i>Narcoticae</i>	uncultured	LX042233-122-012-C10	GQ999406
<i>Narcoticae</i>	uncultured	LX042233-122-012-F01	GU054169
<i>Narcoticae</i>	uncultured	112_NA9_P32_M23	KC966135
<i>Narcoticae</i>	uncultured	15y-10	KU534610
<i>Narcoticae</i>	uncultured	15y-137	KU534729
<i>Narcoticae</i>	uncultured	consensus02974	OU941681
<i>Niveae</i>	<i>C. afronivea</i> T	SFSU BAP 619	NR_148105
<i>Niveae</i>	<i>C. caribaeonivea</i> T	JBSD130971 (ANGE1390)	OQ275140
<i>Niveae</i>	<i>C. igarashi</i> T	CBM-FB39186	AB854626
<i>Niveae</i>	<i>C. igarashi</i> P	CBM-FB38829	AB854625
<i>Niveae</i>	<i>C. nivea</i>	ANGE1831	PP349937
<i>Niveae</i>	<i>C. nivea</i>	SZMC-NL-0847	HQ847032
<i>Niveae</i>	<i>C. nivea</i>	TUF118721	UDB019531
<i>Niveae</i>	<i>C. nivea</i>	LO27613	MT889691
<i>Niveae</i>	<i>C. nivea</i>	4585	JF907848
<i>Niveae</i>	<i>C. nivea</i>	iNAT:18020138	OM212924
<i>Niveae</i>	<i>C. nivea</i>	iNAT:6625315	OM212943
<i>Niveae</i>	<i>C. nivea</i>	DM113-40512	OM212954
<i>Niveae</i>	<i>C. pseudonivea</i>	SZMC-NL-2340	FM163181
<i>Niveae</i>	<i>C. sinonivea</i> T (as <i>C. afronivea</i>)	HMJAU46372	MW822049
<i>Niveae</i>	<i>C. sinonivea</i> P (as <i>C. afronivea</i>)	HMJAU46459	OL355163
<i>Niveae</i>	<i>C. sp.</i>	337914	OK649901
<i>Niveae</i>	<i>C. sp. nov.</i> (paper in progress)	CBM-FB42007	LC259498
<i>Niveae</i>	<i>C. sp. nov.</i> (paper in progress)	CBM-FB41367	LC259499
<i>Niveae</i>	<i>C. variispora</i> T	JBSD13798 (ANGE1712)	PQ998504

Figure 1. A 50% ITS rDNA majority rule consensus phylogram of *Coprinopsis* section *Cinereae* (with *C. rhombisporoides* from *C. sect. Coprinopsis* as outgroup) obtained using MrBayes from 1650 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or $\geq 70\%$ maximum likelihood bootstrap proportions (right). Nonsignificant support values are exceptionally represented inside parentheses. Sequences newly generated in this study are in red. The letter T in bold after a species name stands for Type.

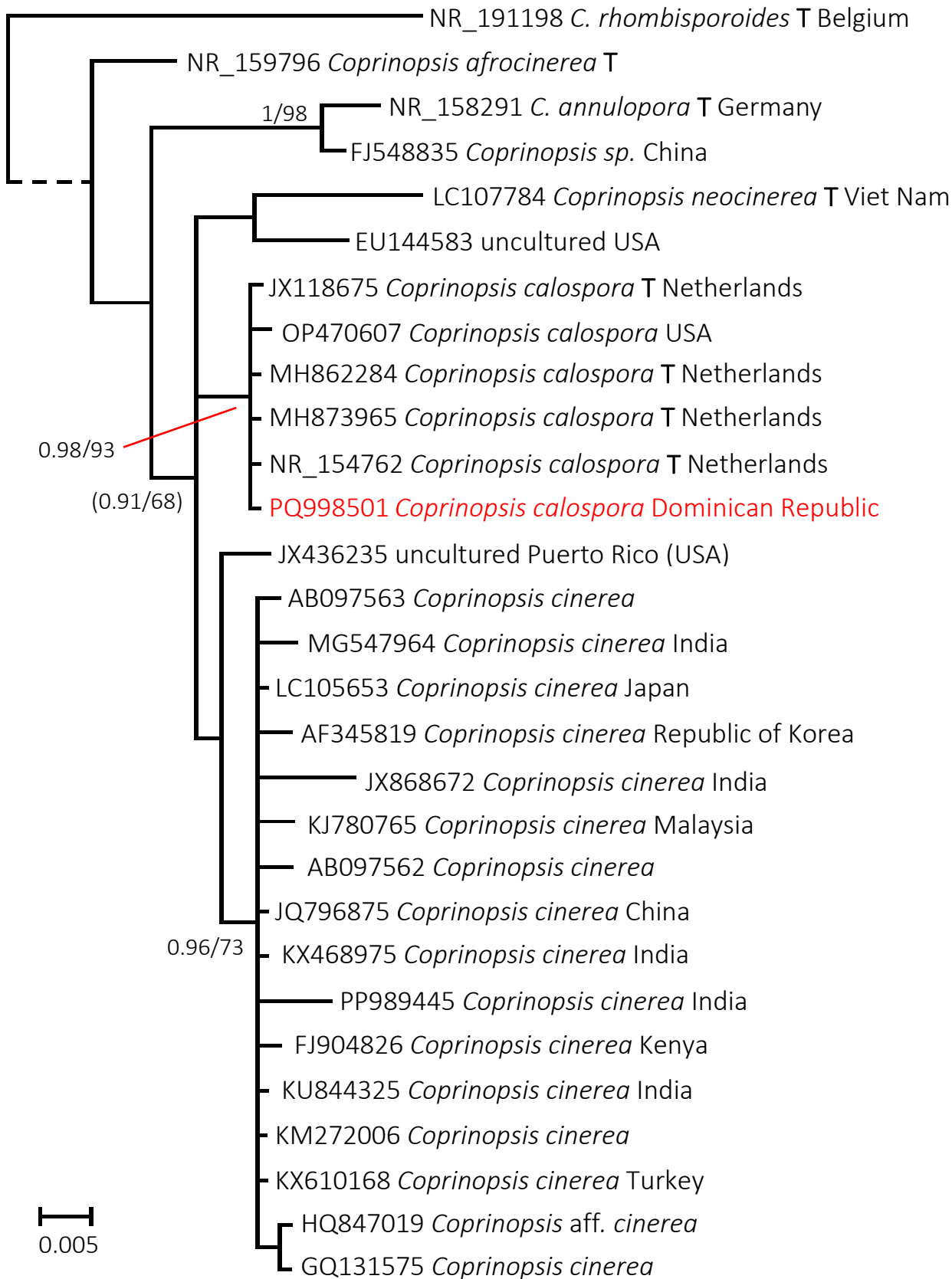


Figure 2. A 50% ITS rDNA majority rule consensus phylogram of the *Coprinopsis afronivea* and *C. nivea* complexes inside *Coprinopsis* section *Niveae* (with *C. rhombisporoides* from *C. sect. Coprinopsis* as outgroup) obtained using MrBayes from 1125 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or $\geq 70\%$ maximum likelihood bootstrap proportions (right). Nonsignificant support values are exceptionally represented inside parentheses. Sequences newly generated and species names treated in this study are in red. The letters T and P in bold after a species name stand for Type and Paratype respectively.

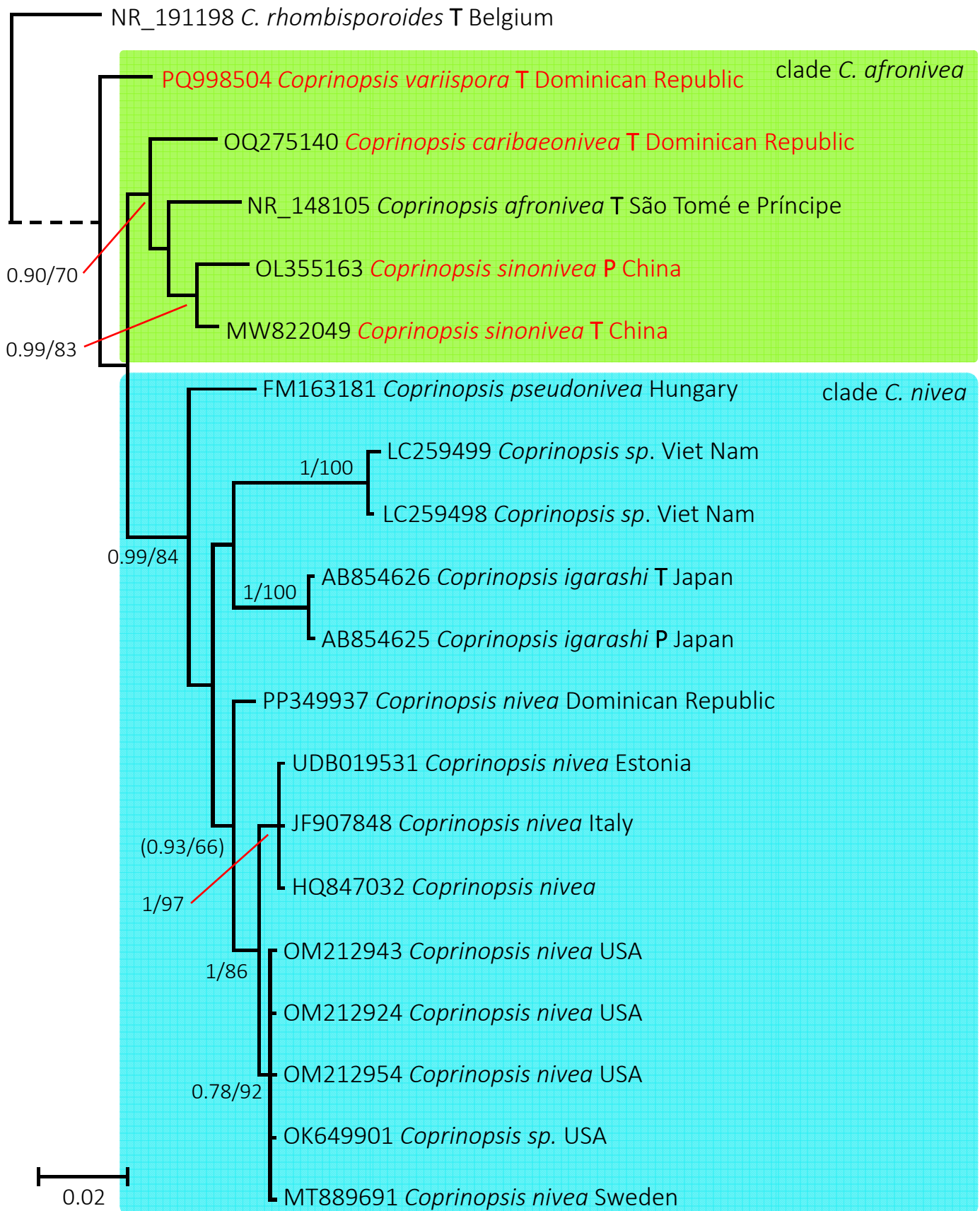


Figure 3. A 50% ITS rDNA majority rule consensus phylogram of *Coprinopsis* sections *Coprinopsis* and *Narcoticae* (with *C. nivea* from *C. sect. Niveae* as outgroup) obtained using MrBayes from 7050 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or $\geq 70\%$ maximum likelihood bootstrap proportions (right). Nonsignificant support values are exceptionally represented inside parentheses. Sequences newly generated in this study or still unpublished are in red. The letters T and P in bold after a species name stand for Type and Paratype respectively.

Taxonomy***Coprinopsis flamboyani* Voto & Angelini sp. nov.** [MycoBank 857603]

Typus. Dominican Republic, Puerto Plata, Sosúa, Playa, gregarious and moderately caespitose on the bark of a standing dead flamboyant tree trunk (*Delonix regia*), 18 December 2023, *legit* C. Angelini ANGE1942 (Holotype: JBSD 130794); GenBank PQ998502 - ITS, PV101184 - tef1.

Etymology. The name refers to the tree *Delonix regia*, widely diffused and appreciated for the bright colours of its flowers in the Dominican Republic where it is popularly called flamboyan.

Description of the teleomorphic state (collection number ANGE1942) [Fig. 4-10]



Fig. 4: *Coprinopsis flamboyani* ANGE1942, Holotype - coprinoid state

Macroscopic characters

Pileus when young 10 – 22 mm high, 8 – 20 mm broad, cylindrical to sub conical, then conical to narrowly conical-campanulate, finally approx. up to 35 mm broad, through broadly conical to umbonate-applanate with margin rolled upward and deeply radially lacerate; white to whitish, discoloring beige-alutaceous and lastly taking on a marked grey-lilac necropigment. Veil of fibrillose patches divided in two layers: upper layer grey and covering all pileus in button stage, then lilaceous-brownish grey, discoloring to ochre-brown, very fugacious; lower layer white and immutable, persistent.

Lamellae free, crowded; white, then though the maturation of the spores from grey to blackish; edge white; slowly deliquescing.

Stipe 22 – 50 × 4 – 5 mm, equal or progressively tapering to 1.7 – 3 mm broad at apex, base equal, often with a volva-like line at the point of detachment of the opening pileus; whitish, covered by two-layered fibrils pigmented like the veil on the pileus; hollow.

Context very thin from margin to centre of pileus; white in the stipe, greyish at the pileus centre.



Fig. 5 (top) and 6 (bottom): *Coprinopsis flamboyani* ANGE1942, Holotype - coprinoid state



Fig. 7 (top) and 8 (bottom): *Coprinopsis flamboyani* ANGE1942, Holotype - coprinoid state

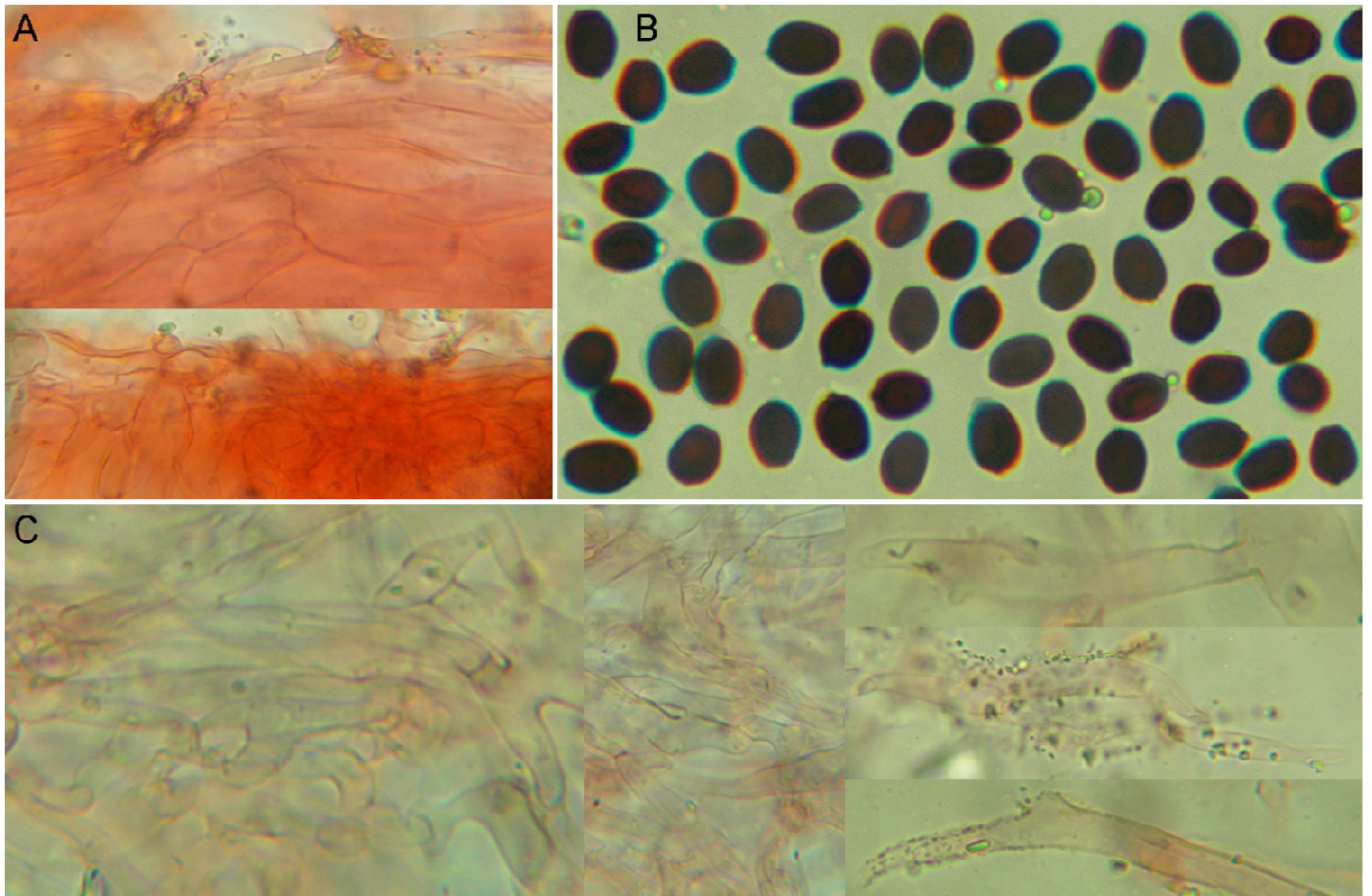


Fig. 9: *Coprinopsis flamboyani*. A) pileipellis in Congo red; B) spores in water; C) veil hyphae in Congo red

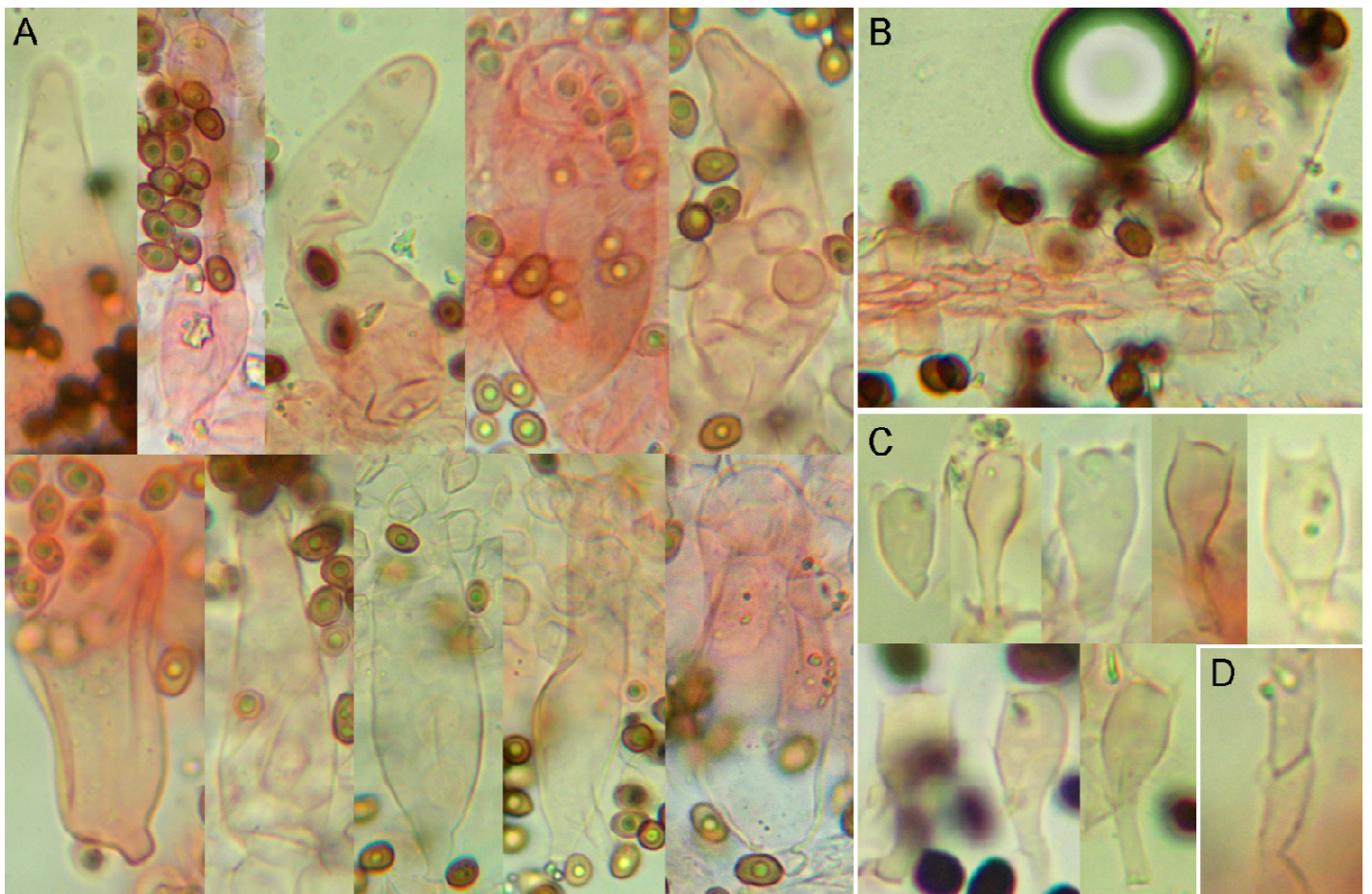


Fig. 10: *Coprinopsis flamboyani*. A) pleurocystidia; B) hymenium; C) basidia; D) a clamp. All images in Congo red

Microscopic characters

Basidiospores [33/1/1]: (5.4) 6.5 – 8.0 (9.0) × (4.2) 4.5 – 5.3 (5.8) μm , on average 7.3 × 5.0 μm , Q = (1.15) 1.30 – 1.50 (1.60), on average 1.4, smooth; in front view elliptic to narrowly/broadly oval or subglobose, sometimes slightly asymmetric, base mostly broadly rounded, apex not papillate; in side view mostly elliptic to adaxially flattened; blackish brown in water and in 5% KOH; germ pore 1.7 – 2.2 μm broad, truncate, central.

Basidia 7.5 – 30.0 × 7.5 – 8.0 (10.0) μm ; of three types: sessile to shortly clavate, narrowly clavate, cylindrical to subululiform; 4-spored, surrounded by 4 – 6 hymenophysalides.

Pleurocystidia 42 – 86 × 16 – 30 μm , ellipsoid to utriform or obconical, sometimes strangled in the middle, apex obtuse to broadly rounded; smooth, thin-walled.

Cheilocystidia 40 – 55 × 21 – 30 μm , similar to the pleurocystidia.

Pileipellis a very thin cutis of filamentous hyphae; subpellis of ellipsoid to subglobose elements.

Veil lower layer composed of 3 – 12 μm broad, forked, nodulose, sometimes anastomosed, thin-walled hyphae; pigment incrustated.

Caulopellis a cutis composed of 2 – 8 μm broad hyphae with a heavy incrustated pigment.

Clamp connections commonly present.

Description of the anamorphic (rhacophylloid) state (collection ANGE1943) [Fig. 11-16]



Fig. 11: *Coprinopsis flamboyani* ANGE1943, Paratype - rhacophylloid state

Macroscopic characters

Pileus primordia ovoid to ellipsoid and completely covered by the same veil as described for the agaricoid state; then from oblong to narrowly and obtusely conic, sometimes bent toward the apex, with the margin inflexed and starting to be radially lacerate, in this phase 5 – 15 mm high and 2 – 9 mm broad; finally more opened or uplifted at margin and deeply radially lacerate like narrow tongues starting from the centre; cuticle pure violet to red-violet or more greyish, striate.



Fig. 12: *Coprinopsis flamboyani* ANGE1943, Paratype - rhacophylloid state



Fig. 13 (top) and 14 (bottom): *Coprinopsis flamboyani* ANGE1943, Paratype - rhacophylloid state



Fig. 15: *Coprinopsis flamboyani* ANGE1943, Paratype - rhacophylloid state

Fertile zone composed of gills. Gills crowded not ventricose, violet, smooth at the beginning and then cracked in several small irregular cells (referred to as ‘bulbils’ or ‘loculoments’), not deliquescing but loculoments in age disaggregating and falling apart; edge concolorous.

Stipe 4 – 23 × 0.7 – 2.3 mm, central, equal or progressively tapering toward apex, base equal to often somewhat swollen; surface white, covered with fugacious fibrils, with a mycelial matt at the base, no volva-like line noted.

Microscopic characters

Loculoments: irregularly shaped, in exsiccata avellaneous with a pinkish-lilac shade, composed of strongly packed cells (‘loculospores’). *Loculospores*: 7.0 – 12.5 (13.0) × 6.7 – 8.0 (11.0) μm, mostly irregularly polygonal. *Cystidia*: absent. *Pileipellis*, *caulopellis* and *veil*: as in the teleomorph state. Some gelification was noted in the pileal and stipital tissues. *Clamp connections*: present but rare.

Additional material examined: on the same tree trunk of the type collection and close to it, same habit, same date, *legit C. Angelini* ANGE1943 (JBSD130795), containing only anamorphic carpophores; GenBank PQ998503 - ITS. *Ibidem*, 16 December 2023, *legit C. Angelini* ANGE1900 (PADH0062320), containing both teleomorphic and anamorphic carpophores.

Notes

Coprinopsis flamboyani has forked to nodulose veil hyphae and, on that basis, belongs to *Coprinopsis* sect. *Coprinopsis*. The main diagnostic characters of *C. flamboyani* include smooth and two-dimensional spores of an average size, a two-layered veil, a volva-like zone often present on the lower portion of the stipe, and a woody habitat in the Neotropics.

Due to the presence of an anamorphic state, *C. flamboyani* reminds the only other congeneric dimorphic species so far known, *C. clastophylla*.

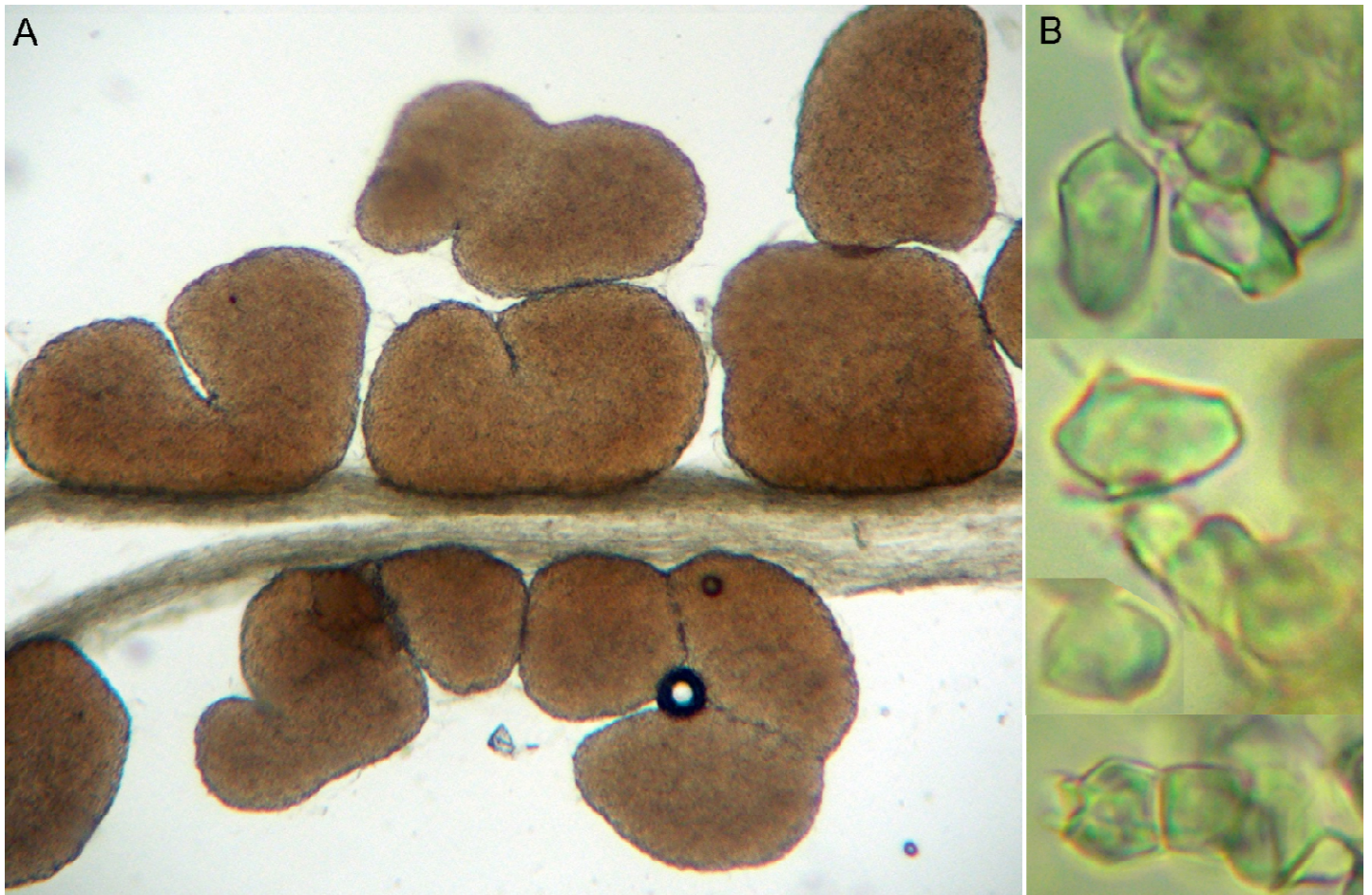


Fig. 16: *Coprinopsis flamboyani* - rhacophylloid state. A) loculoments in water; B) loculospores in water

However, *C. clastophylla* has two main problematic taxonomic issues. First, Maniotis (1964) described it as the teleomorph state of *R. lilacinus* but, actually, this author obtained its coprinoid basidiomes from a culture of a North American rhacophylloid material that he only assumed to be conspecific with the ancient, still unsequenced, original Sri Lankan anamorphic material of *R. lilacinus* (Berkeley & Broome 1871). Secondly, we have found that the ITS sequence NR_154756 (voucher CBS:473.70) obtained from the culture material of the type of *Coprinus clastophyllus* Maniotis (basonym of *C. clastophylla*) is similar to those of several vouchers identified as *C. sclerotiger* (Fig. 3) and, therefore, *C. clastophylla* must be considered conspecific with this species. However, *Coprinus clastophyllus* was described with a filamentous and forked to nodulose veil (typical of *Coprinopsis* sect. *Coprinopsis*) and smooth spores while *C. sclerotiger* belongs to *Coprinopsis* sect. *Narcoticae* (Uljé & Noordel.) D.J. Schaf. whose members are characterized by warty globose veil cells and a myxosporium coating the spores. Two of these differences may be explained taking into account that *C. sclerotiger* has a smooth, easily unperceivable myxosporium [for instance, when observed in water (Cacialli, Caroti & Doveri 1999)]; while the warty to forked veil hyphae detected by Maniotis (1964) on his material may correspond to the connecting cells of the globose veil. Conversely, the absence of reports of warty globose veil cells remains unexplained.

The two basionymic names, *Coprinus clastophyllus* and *Coprinus sclerotiger* Watling, were both combined in *Coprinopsis* by Redhead, Vilgalys, Moncalvo *et al.* (2001). Due to the aforementioned taxonomic ambiguities of *Coprinus clastophyllus*, we propose that *Coprinopsis sclerotiger* be treated as the prior name.

Our discovery of another dimorphic *Coprinopsis* species morphologically and phylogenetically different from *C. clastophylla* leads us to believe that there is a well-founded possibility that some other species have the same dimorphism and that the various reports of anamorphic collections from all over the world identified as *Rhacophyllus lilacinus* based on morphological characters alone, may represent multiple different species.

These reports of *R. lilacinus* can be divided into two groups. Those that originated from the Indian and South East Asian area have a good possibility to be conspecific with the true *R. lilacinus* which was described from Sri Lanka. Some examples of reports belonging to this group are Pegler (1986), from Sri Lanka (treating two very old

collections, the holotypical one dated 1868 and one by Petch dated 1916); Petch (1926), from Sri Lanka (as Ceylon); Vrinda, Pradeep & Varghese (2012), from India; and Patouillard (1913), from Northern Vietnam.

The second group from outside of that area contains reports from North Africa such as Patouillard (1901), Tunisia, and Malençon & Bertault (1970), Morocco (it could be useful to compare these two collections with the recently described *Coprinopsis palaciosii* A. Ruiz, G. Moreno & P. Alvarado from Spain); from the Caribbean by Patouillard (1901), Guadeloupe [in this case a dried agaricoid specimen was also observed but the author only reports his general morphological impression that it resembles '*Psathyra gyroflexa*' (this material could correspond to *C. flamboyani*)]; from East Europe by Gorovoy (1977), Ukraine (as *Zerovaemyces copriniformis* Gorovij, a genus recognized as a synonym of *Rhacophyllus* by Redhead *et al.* 2001). Since none of the aforementioned reports are described with both morphs (to allow a morphological comparison between the teleomorphic basidiomes) and as long as no phylogenetic data are available on them, it is not currently possible to evaluate which teleomorphic state they, including the original *R. lilacinus*, are associated with nor to predict how many coprinoid species may possess a dimorphic state. The scope of further investigations may need to be broadened in view of the confirmation herein of dimorphic *Coprinopsis* species representing more than one section of the genus.

***Coprinopsis caribaeonivea* Voto & Angelini sp. nov.** [MycoBank 857604] [Fig. 17-18]

Typus. Dominican Republic, Puerto Plata, Sosúa, Playa, gregarious, on a strongly rotten fallen trunk of deciduous tree in a coastal forest, 8 November 2019, *legit C. Angelini ANGE1390* (Holotype: JBSD 130971); GenBank OQ275140 - ITS.

Etymology. The name refers to the Caribbean geographic location and to the likeness with *C. nivea*.

The images and the description are taken from Angelini, Voto & Alvarado (2023)

Macroscopic characters

Pileus 11.3 – 13.5 mm broad, at first paraboloid, then convex, light grey; veil first woolly to floccose, white, abundantly covering the pileus and appendiculate from the margin, later reduced to a powdery-flocculose cover on the pileus, more tenacious at the margin, not or scarcely fading to pale yellowish grey in the pileus center.

Lamellae free, moderately crowded (approx. 20), with 1 – 3 lamellulae; first pale grey, finally blackish; deliquescing.

Stipe 16 – 54 × 1.4 – 2.4 mm at the base, cylindrical or slightly tapering upwards (0.9 – 1.5 mm thick at the top), white; with a veil at the basal half similar to that on the pileus.

Context almost inexistent in the pileus, with the gills almost directly attached below the pileipellis.

Microscopic characters

Basidiospores [88/2/1] (4.5) 5.1 – 6.7 (7.7) × (3.0) 3.3 – 4.3 (5.0) × 3.0 – 3.8 μm, on average 5.75 × 3.72 × 3.40 μm, Q = (1.34) 1.44 – 1.65 (1.79) × (1.50) 1.59 – 1.86 (2.03), on average 1.55 × 1.74, smooth; in front view more or less oval and angular (pentagonal, hexagonal, rarely rhomboid-mitriform and then sometimes asymmetric), sometimes oblong or elliptic, base triangular to rounded, apex not papillate; in side view slightly narrower, subphaseoliform to subphaseoliform-subamygdaliform or subelliptic; brown with a reddish shade in water, greyish brown in KOH; germ pore 0.7 – 1.3 μm broad, central.

Basidia 8.0 – 20.0 × 5.0 – 6.5 μm, claviform to ululiform, 4-spored, surrounded by 4 – 5 hymenophysalides.

Pleurocystidia not found.

Cheilocystidia not observable (gill edge already consumed by deliquescence).

Pileipellis a very thin and difficult to observe cutis composed of 2.5 – 7.5 μm broad filamentous, smooth hyphae.

Veil composed of abundant, subglobose (40 – 50 × 30 – 40 μm) to ellipsoid (25 – 45 × 10 – 27 μm), thin-walled elements intermixed with some elongate, sometimes branched hyphae 3 – 5 μm broad.

Caulocystidia not found.

Clamp connections found on some septa in the stipe tissue.



Fig. 17: *Coprinopsis caribaeonivea* ANGE1390, Holotype

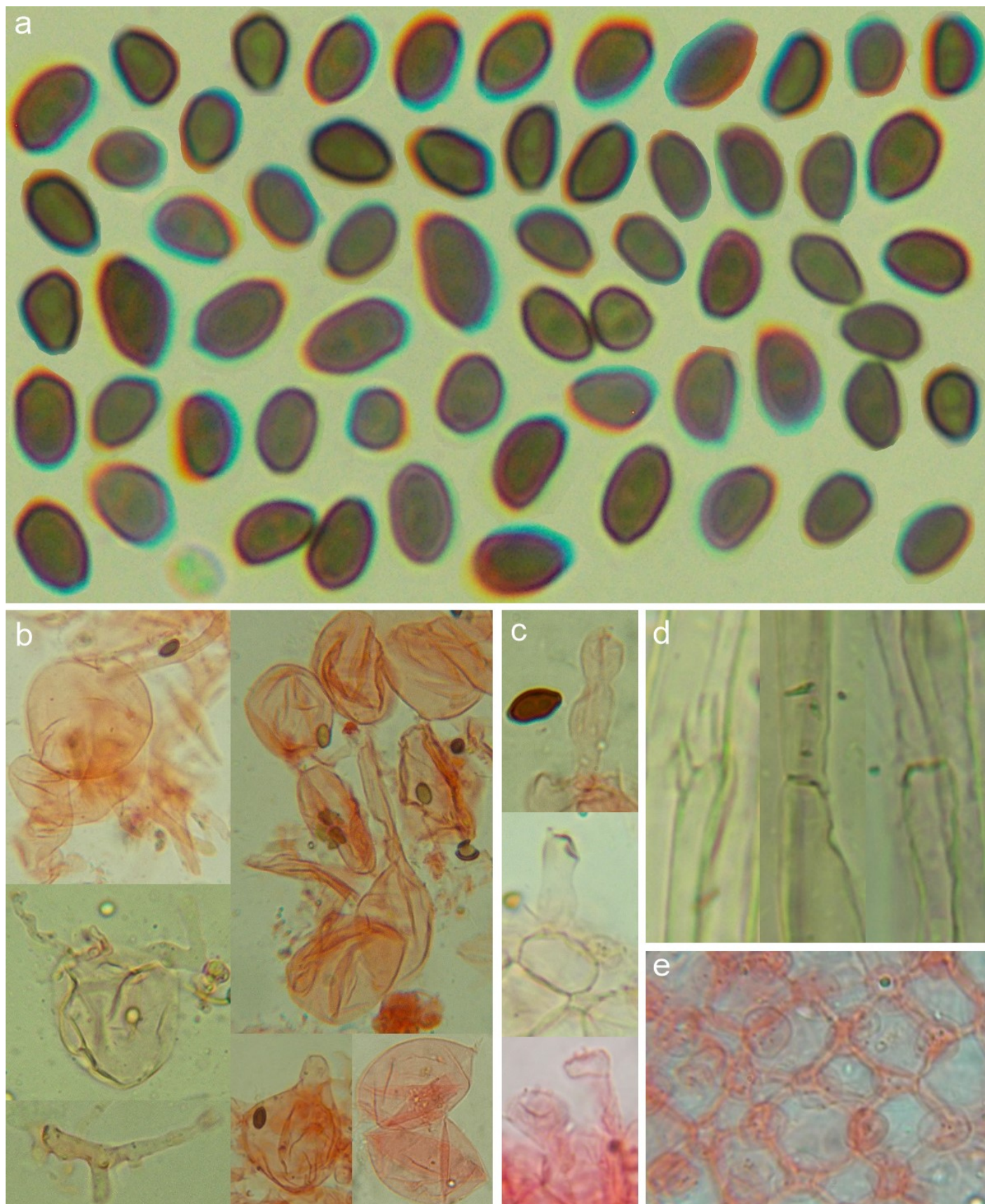


Fig. 18 *Coprinopsis caribaeonivea*: a) basidiospores, b) veil cells, c) basidia, d) clamp connections, e) hymenophysalides. Image a) in KOH, images b-e) in Congo red

Notes

The main diagnostic features of *Coprinopsis caribaeonivea* are smooth cellular veil elements; absence of pleurocystidia; clavate to ululiform basidia; very small, partly angular to irregular spores which are differently shaped in front and side views but only weakly three-dimensional; and a lignicolous habitat in the Neotropics.

Phylogenetically it belongs to a cluster of species gathered in the subclade *C. afronivea* (see Fig. 2). All the species in that clade are characterized by three-dimensional spores or, when the widths in the two views barely differ, by the distinct difference in shape which is more or less angular or mitriform in front view and simply flattened-elliptic or subphaseoliform to subamygdaliform in side view.

Notwithstanding distinctly different spores and low identity percentages compared to the closest vouchers in GenBank (all identified as *C. afronivea*, including the type), Angelini, Voto & Alvarado (2023) had preferred a cautious approach to this collection. With the new phylogenetic analysis developed in this paper it has warranted treatment as an autonomous species. More detailed observations can be found below, in the notes to *C. variispora* *sp. nov.*

***Coprinopsis variispora* Voto & Angelini *sp. nov.* [MycoBank 857605] [Fig. 19-21]**

Typus. Dominican Republic, Puerto Plata, Sosúa, Puerto Chiquito, gregarious on a very rotten fallen trunk of a deciduous tree, 5 February 2022, *legit C. Angelini ANGE1712* (Holotype: JBSD 13798); GenBank PQ998504 - ITS.

Etymology. The name refers to the characteristic of the spores of being variously shaped in front view.

Macroscopic characters

Pileus 14 – 15 mm broad, paraboloid then conical; scarcely striate; grey; veil first woolly to floccose, white, abundantly covering the pileus and appendiculate from the margin, later reduced to a powdery-flocculose cover on the pileus, more tenacious at the margin.

Lamellae subfree to adnexed, moderately close, with lamellulae; grey then blackish; deliquescing.

Stipe 38.0 – 65.0 × 1.5 – 1.7 mm in the median part, tapering to 1.2 mm at apex and to 1.3 – 1.4 mm at base; light grey; covered with abundant white flocci of veil more coarse from the median part downwards where, coupled with the grossly flocci appendiculate from the pileus margin, they give the impression of a fragmented diffuse annular zone.

Context almost inexistent in the pileus, with the gills almost directly attached below the pileipellis and the hymenial mat between gills thinly separated from the pileipellis.



Fig. 19: *Coprinopsis variispora* ANGE1712, Holotype

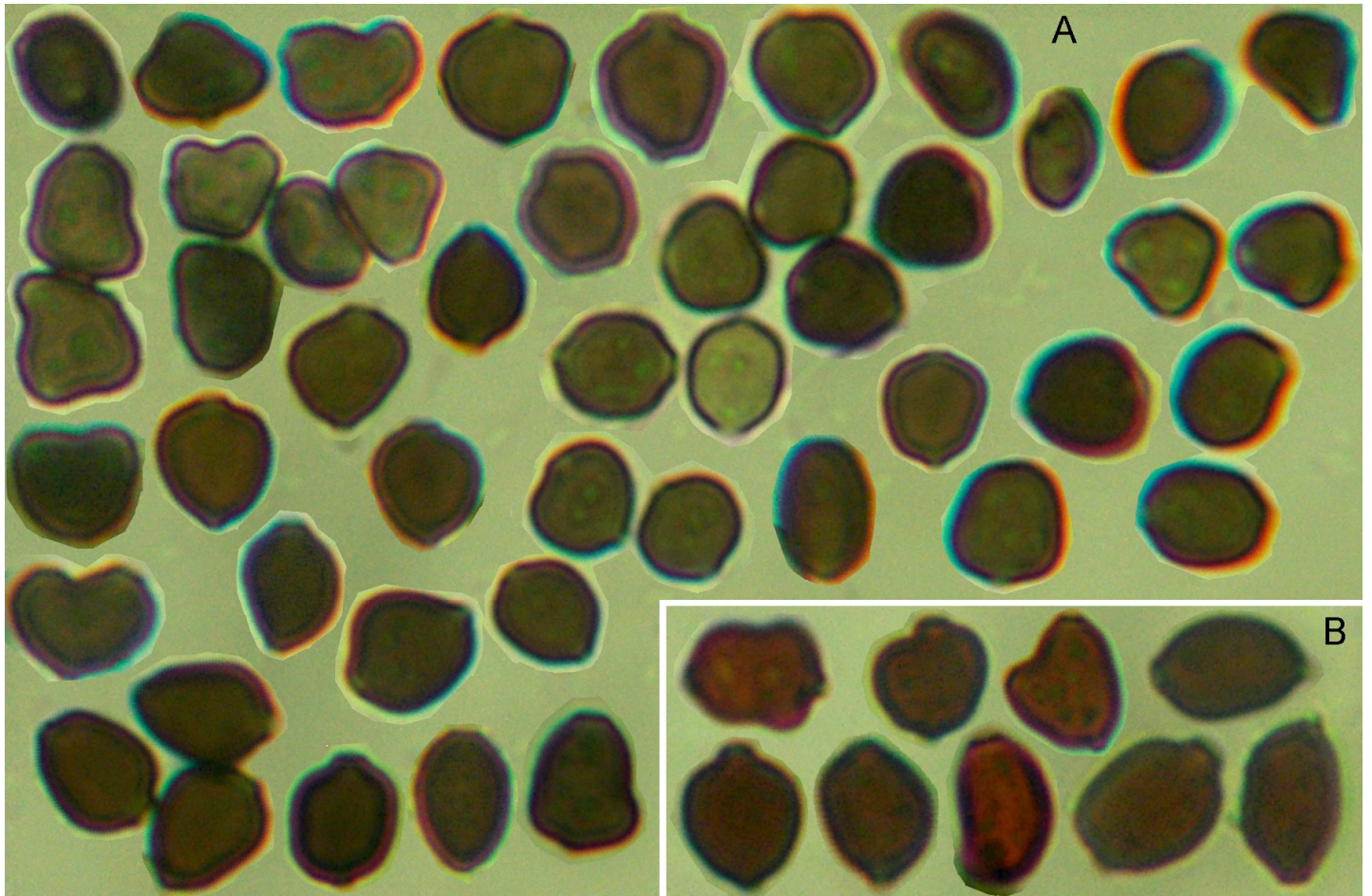


Fig. 20: *Coprinopsis variispora*. Basidiospores. A) in 5% KOH; B) in Congo red

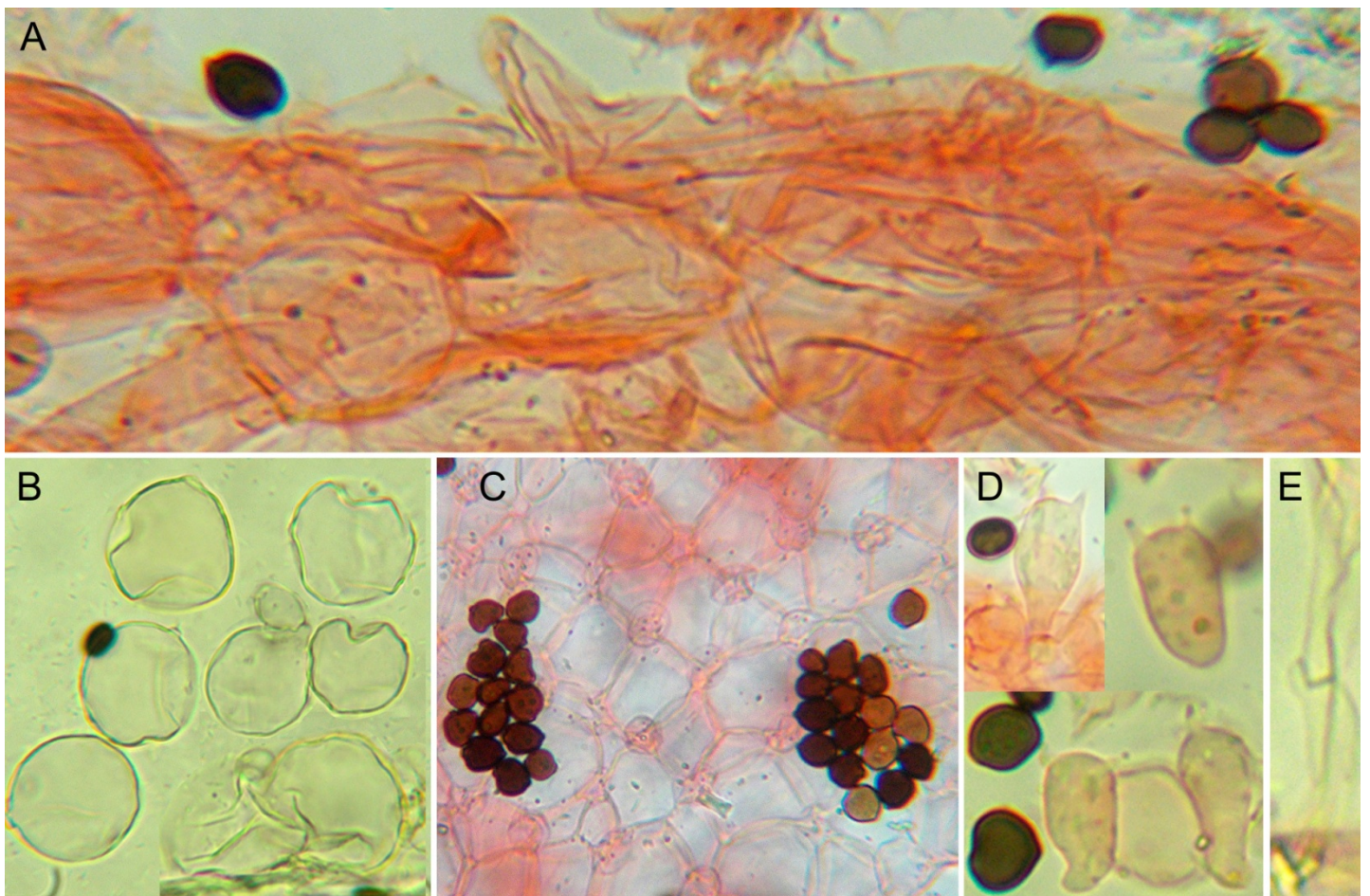


Fig. 21: *Coprinopsis variispora*. A) pileipellis; B) Veil cells; C) hymenophysalides; D) basidia; E) clamp. In Congo red

Microscopic characters

Basidiospores [70/2/2] (7.5) 8.0 – 9.0 (9.6) × (5.5) 6.5 – 8.0 (9.0) × 5.0 – 5.5 μm, Q = (0.83) 1.04 – 1.25 (1.36) × 1.45 – 1.73, in front view hexagonal, oval-hexagonal, oval-pentagonal, oval- subtriangular, mitriform, often asymmetric or deformed, occasionally with median constriction, base broadly rounded to broadly triangular or sometimes (sub) truncate, in side view oblong to elliptic, not or rarely angular, apex not or only slightly protruding; in water dark brown with a more or less appreciable reddish tint, in 5% KOH dark grey-brown; germ pore 1.0 – 1.5 μm broad.

Basidia 14.5 – 22.0 × 8.0 – 10.5 μm, short to long clavate, 4-spored, peduncle absent to slenderly elongate or stocky; surrounded by 3 – 5 hymenophysalides.

Pleurocystidia not found.

Cheilocystidia not observable because of the deliquesced gill edge.

Pileipellis made of a thin layer of about a couple of hyphae 2.5 – 5.0 μm broad; subpellis of swollen repent cells.

Veil (examined on pileus) of smooth, hyaline to slightly pigmented, thin- to slightly thick-walled, globose to subglobose cells (12) 15 – 30 × (9) 14 – 28 μm.

Clamp connections present.

Notes

Coprinopsis variispora shares similar morphological characteristics to those of *C. afronivea* and *C. caribaeonivea* as well as two Chinese vouchers, HMJAU46372 and HMJAU46459 (in GenBank as *C. afronivea*), described in Zhu, Huang & Bau (2022) and nested beside *C. afronivea* in the phylogram (Fig. 2). These Chinese collections are recognized here as *Coprinopsis sinonivea* sp. nov. All BLAST cross-comparisons with each other of these four taxa show low, 95.66% to 97.14%, pairwise similarities.

Morphologically, these four species are characterized by a veil of globose cells smooth or with encrustations easily dissolving in hydrochloric acid (HCl) and by spores without a myxosporium (the combination of these two characters are univocally typical of *Coprinopsis* sect. *Niveae*). Moreover, these species share lentiform (or differently shaped in front and side views if weakly lentiform) spores 5 – 9 μm long, 4-spored basidia, absence of pleurocystidia, and presence of clamp connections. A fifth species, *Coprinopsis iocularis* (Uljé) La Chiusa & Boffelli, known from Europe, shares all the same morphological parameters but, since there is no sequence of it in the genetic databases yet, its relation with the aforementioned non-European species is unknown.

The following key extracted from Voto (2024) best highlights the main reciprocal morphological differences among them.

1) Spores hexagonal and often constricted in the middle, apex papillate, 5.9 – 9.0 × 4.8 – 6.0 × 4.0 – 4.5 μm, Q in front view 1.05-1.5; cheilocystidia utriform to clavate; habitat on lawn. Distribution: Europe

C. iocularis

1) Spores not or rarely constricted in the middle; habitat on wood or litter. Distribution: not in Europe ... **2**

2) Spores on average smaller than 8.0 × 6.5 μm, not papillate; basidia clavate to (utriform-) ululiform ... **3**

2) Spores on average larger than 8.0 × 6.5 μm, at least in part papillate; basidia only clavate ... **4**

3) Spores 6.1 – 7.8 long, up to 6.6 μm broad and suboval (-triangular) in front view, subamygdaliform to subelliptic in side view; cheilocystidia rare, subglobose to broadly clavate. Distribution: east China

C. sinonivea

3) Spores (4.5) 5.1 – 6.7 (7.7) × (3.0) 3.3 – 4.3 (5.0) × 3.0 – 3.8 μm, oval, pentagonal, hexagonal, some rhomboid - mitriform or asymmetric; cheilocystidia not described. Distribution: Central America (Caribbean)

C. caribaeonivea

4) Spores (7.5) 8.0 – 9.0 (9.6) × (5.5) 6.5 – 8.0 (9.0) × 5.0-5.5 μm, Q in front view (0.83) 1.04 – 1.25 (1.36), hexagonal to oval-hexagonal/-pentagonal/-subtriangular or mitriform, often asymmetric to strongly deformed; cheilocystidia not described. Distribution: Central America (Caribbean)

C. variispora

4) Spores 8.5 – 9.6 × 6.4 – 7.0 × 5.5 – 6.2 μm, Q in front view presumably higher than 1.2, subhexagonal to mitriform, not or rarely deformed; cheilocystidia globose to broadly clavate. Distribution: Central Africa

C. afronivea

***Coprinopsis sinonivea* Voto sp. nov.** [MycoBank 857606]

Typus. China, Jilin, Jilin Agricultural University, scattered on litter, 22 July 2017, *legit M. Huang*, Holotype: HMJAU 46372; GenBank: MW822049 - ITS, OL376316 LSU.

Paratype. China, Liaoning, Benxi City, Wunu Mountain, 1 September 2018, *legit M. Huang*, HMJAU46459, GenBank: OL355163 - ITS, OL376336 LSU.

Etymology. The name refers to the Chinese geographic location and to the likeness with *C. nivea*.

Macroscopic characters

Basidiomes small to very small.

Pileus subcampanulate to subconical when young, hemisphaerical when mature, not striate, pale grey; veil of dense pale grey to brownish grey squamules on the pileus and fringed curtained remains at the margin.

Lamellae crowded, with lamellulae; greyish white then dark grey.

Stipe grey to brown-grey; covered with powdery to flocculose scales of veil.

Context white, extremely thin.

Microscopic characters

Basidiospores 6.1 – 7.8 μm long, sub lenticular, up to 6.6 μm broad in front view; in front view suboval to oval-triangular, in side view subamygdaliform; reddish brown to dark brown; germ pore central.

Basidia dimorphic, clavate to ululiform, 4-spored; surrounded by 3-5 hymenophysalides.

Pleurocystidia not found.

Cheilocystidia subglobose to broadly clavate; rare.

Pileipellis a cutis.

Veil composed of smooth globose cells and hyphal elements in the marginal fringes; pigment pale yellowish brown to sub hyaline.

Notes

The above description was extracted and translated from Chinese from Zhu, Huang & Bau (2022) which also contains a figure (no. 2, F to H) showing basidiomes, and a figure (no. 7) of the main microscopic characters. These authors report two sequenced vouchers, HMJAU46372 and HMJAU46459, and three more unsequenced collections (HMJAU59030, HMJAU59031, HMJAU59032); although noticing an evident difference in the spore size, they identify these collections as *C. afronivea*. *Coprinopsis sinonivea* is well characterized by its main characters which distinguish it from the sister taxa of the *C. afronivea* complex. However, a more detailed description is required to fully characterise this species.

***Coprinopsis calospora* (Bas & Uljé) Redhead, Vilgalys & Moncalvo (Fig. 22-25)**

Taxon 50(1): 226 (2001)

Microscopic characters

Pileus when still closed up to 1.8 mm high and 0.8 – 1.8 mm broad, ellipsoid, when mature 35 – 45 mm broad, convex with revolute margin; grey; wholly covered with abundant, white, elongate-triangular squamules of veil with more or less upturned tips persisting in mature specimens.

Lamellae free, close, narrow; pale grey before blackening; deliquescent; some lamellulae present.

Stipe 57.5 – 60.0 \times 3.1 – 3.3 mm broad towards base, tapering to 2.25 – 2.50 mm at apex; white; covered with abundant white flocci of veil which are more conspicuous in the lower half.

Microscopic characters

Basidiospores [30/1/1] 7.6 – 10.0 (12.7) \times 6.0 – 7.2 (9.3) μm with ornamentation, Q (1.21) 1.37 – 1.51 (1.55), in front view elliptic to sometimes oval, in side view amygdaliform and sometimes with a smooth trait above the apiculus, base more or less conical in both views, apex protruding and terminating in an up to 2.3 μm broad truncate germ pore; surface ornamented with coarse obtusely conical warts; blackish in water.

Basidia 14.0 – 22.0 \times 7.5 – 9.5 μm , clavate to short clavate, and utriform to sub ululiform, 4-spored, surrounded by (3) 4 – 5 (6) hymenophysalides.



Fig. 22: *Coprinopsis calospora* ANGE1704

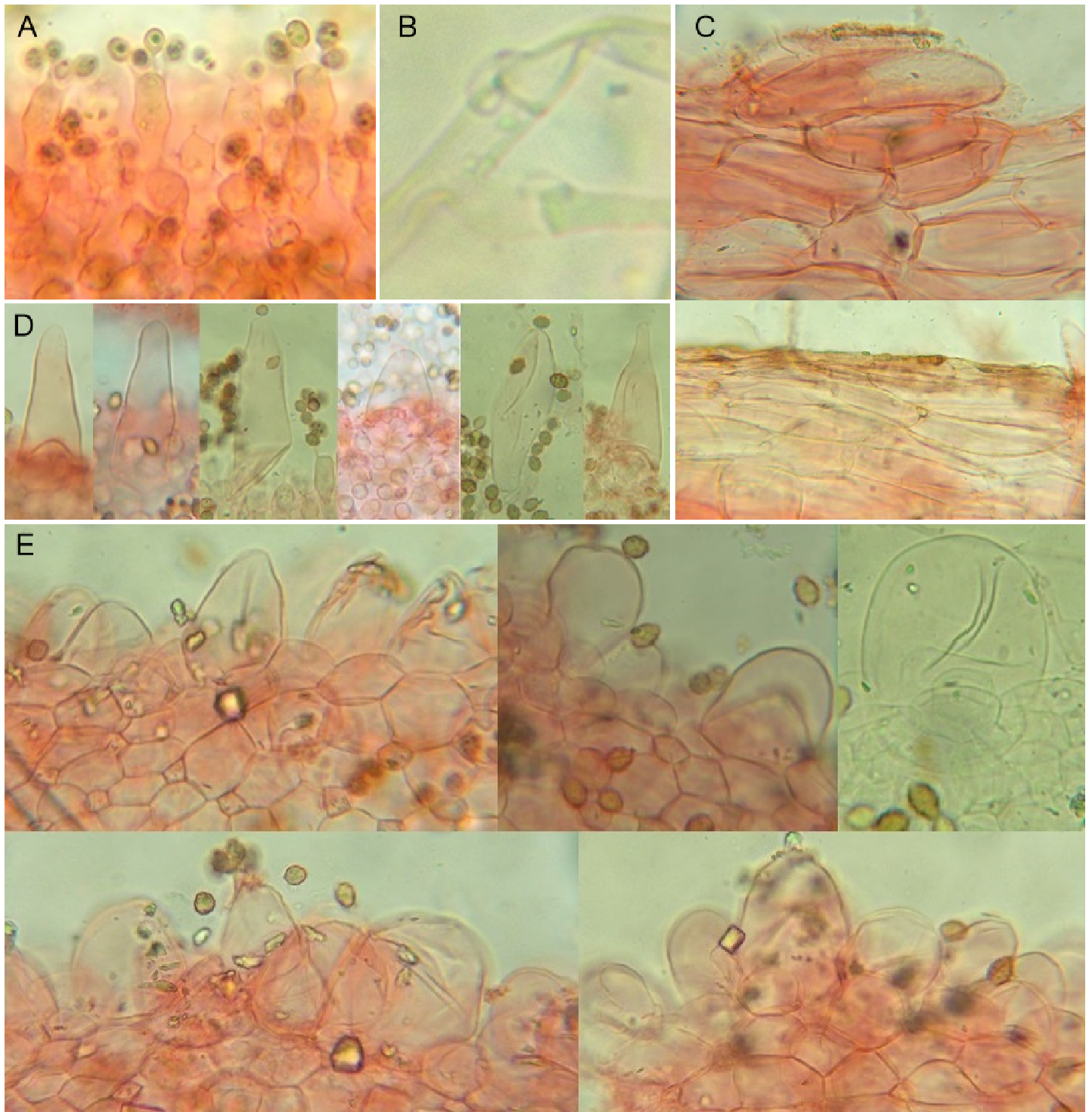


Fig. 23: *Coprinopsis calospora*. A) basidia; B) clamp connections; C) pileipellis; D) pleurocystidia ; E) cheilocystidia. All images in Congo red

Pleurocystidia 50 – 95 × 22 – 33 μm, obconical to lageniform or ovoid, scattered.

Cheilocystidia 14 – 52 × 14 – 39 μm, ellipsoid to subglobose or pruniform; sometimes incrustated at apex, numerous.

Pileipellis a cutis externally composed of 4 – 8 μm broad hyphae and with a conspicuous parietal incrusting pigment.

Veil composed of septate, elongate, 5 – 15 μm broad hyphae with last element tapering; septa not or scarcely tapering.

Caulopellis (immature specimen examined) an approx. 50 μm broad outer layer composed of aeriferous hyphae 3 – 15 μm broad, forked to diverticulate or nodulose, septate, smooth, hyaline (remembering the veil cells of species in *Coprinopsis* sect. *Coprinopsis*), remains of these hyphae also found on the gill edge.

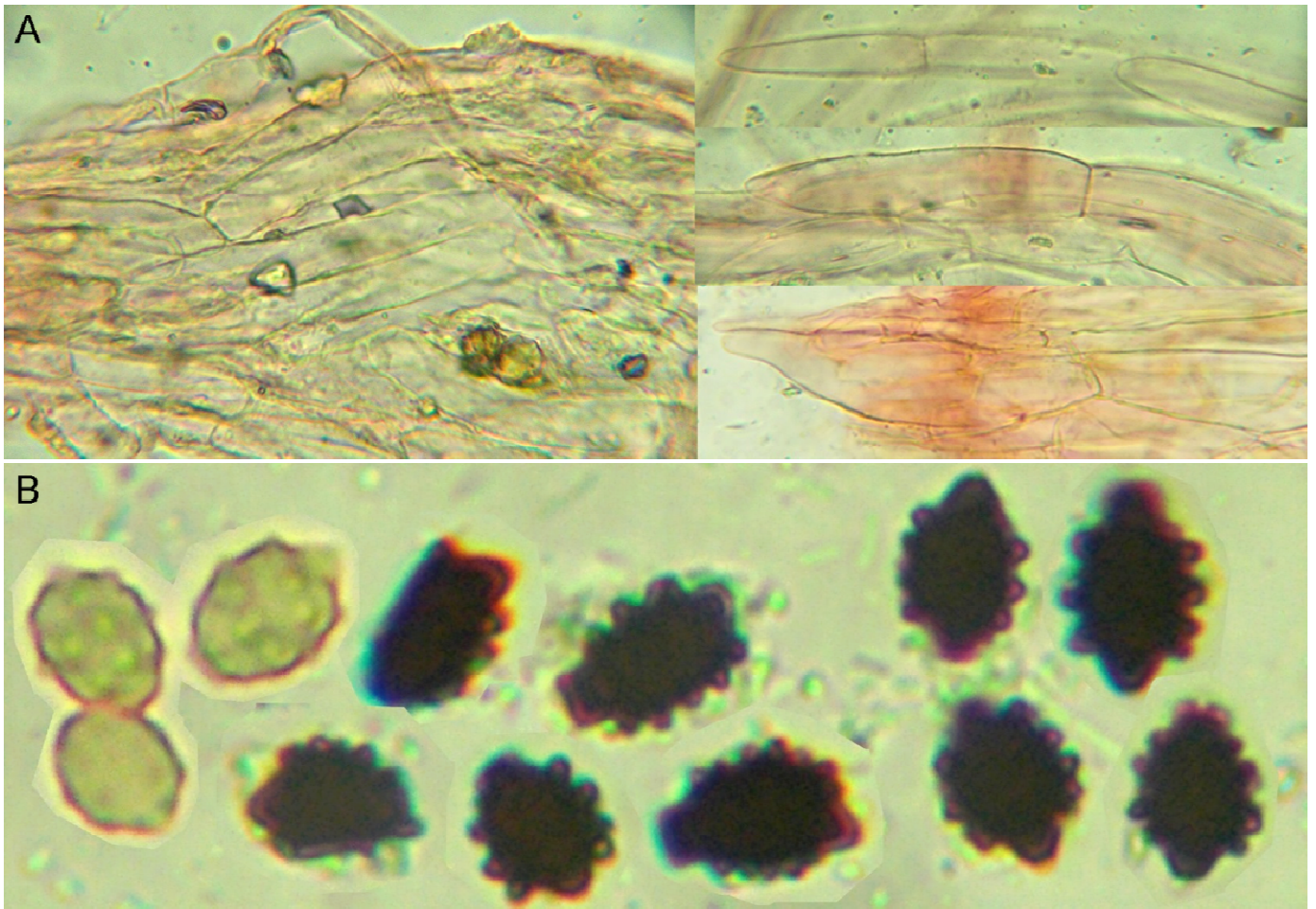


Fig. 24: *Coprinopsis calospora*. A) veil hyphae in Congo red; B) spores in water

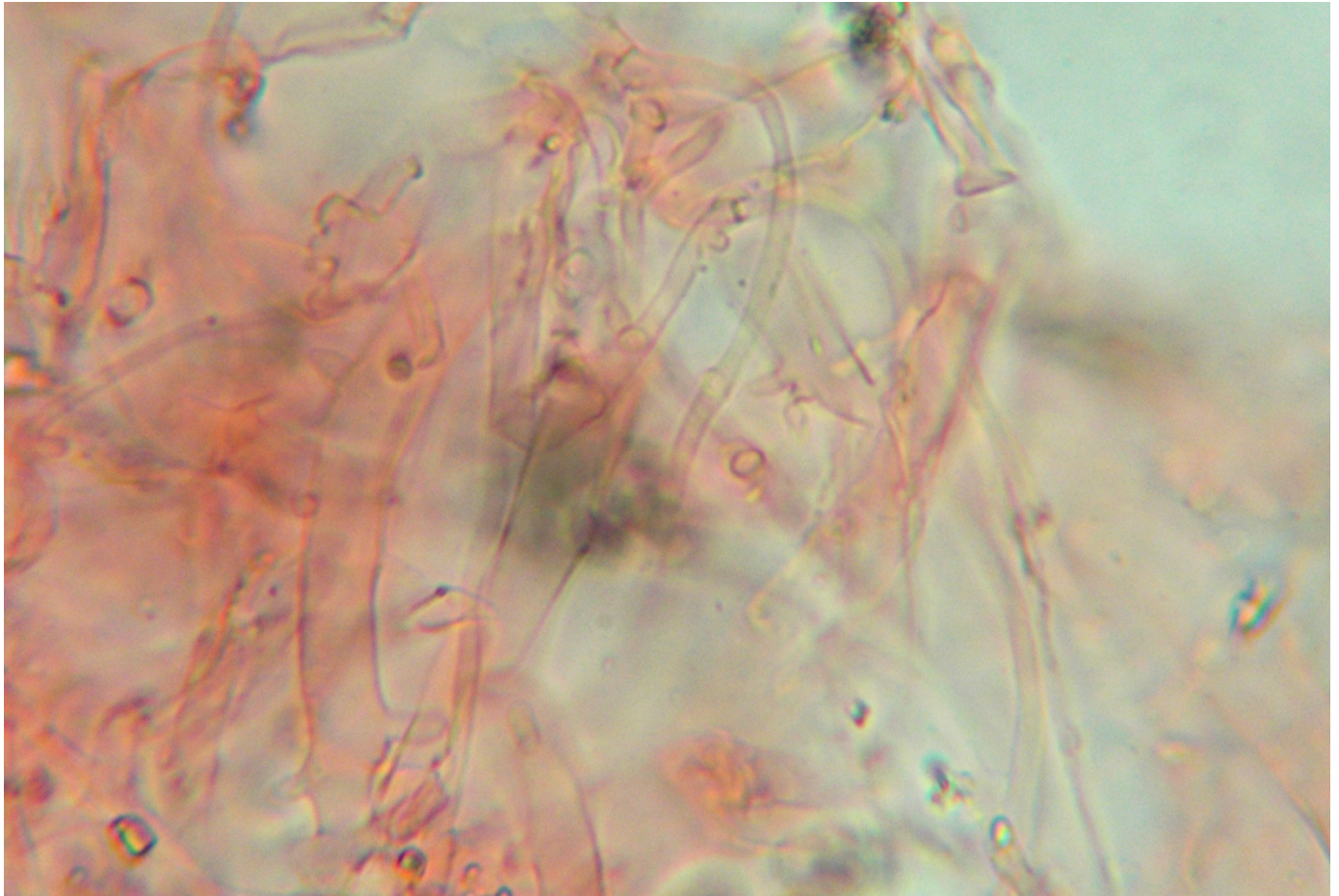


Fig. 25: *Coprinopsis calospora*. Hyphae of the stipe surface in Congo red

Stipe context composed of thick-walled hyphae; pigment strongly intraparietal and epiparietal (hyphae almost appearing minutely warty).

Clamp connections present everywhere.

Habitat and collection examined: gregarious and caespitose on a rotting wood building plank, Dominican Republic, Puerto Plata, Sosúa, Puerto Chiquito, 11 January 2022, *legit* C. Angelini ANGE1704 (JBSD130796); GenBank PQ998501 - ITS.

Notes

The morphology of the Dominican collection conforms well to the original diagnosis of *Coprinopsis calospora*. The spore measurements reported in the protologue for *C. calospora* (Uljé & Bas (1993) did not take into account the considerable size of the warts. Consequently, the spore breadth reported (4.6 – 5.8 µm, on average 5.0 – 5.4 µm, Q = 1.35 – 1.75, on average 1.60) is narrower than for the Dominican collection.

Currently, there are only two other known species of *Coprinopsis* worldwide characterized by a filamentous veil of smooth hyphae and by ornamented spores (*Coprinopsis* sect. *Narcoticae*). *Coprinopsis insignis* (Peck) Redhead, Vilgalys & Moncalvo, from temperate areas of North America, Asia and Europe, and *Coprinopsis karwinicola* (Grgur.) J.A. Simpson & Grgur. from South Australia. Those species differ from *C. calospora* phylogenetically, and by having spores longer than 10 µm.

Since its first description from the Netherlands at the base of a *Yucca* plant growing in an indoor flowerpot (Uljé & Bas 1993), the natural geographical and climatic distribution of *C. calospora* has remained dubious. Uljé & Noordeloos (1999) suspected that the *locus typicus* was adventitious and that the species belonged to warmer regions than the Netherlands.

To date, we are unaware of any other described and verified collection of this species, apart from an ITS-sequenced collection on the iNaturalist website (see ref.), voucher 129888756. This voucher lacks morphological data, except for photos of the basidiomes in a natural woody habitat with leaves and needles from a temperate region of North America (Indiana, USA). This record may imply spontaneous diffusion in boreal temperate areas. The ITS sequence of this voucher, OP470607, is 99.85% identical to the type sequences generated by Nagy *et al.* (2013).

Our Dominican collection grew on rotten wooden construction planks probably imported from USA. Therefore, our collection cannot definitively support the presence of *C. calospora* in tropical areas. In fact, at the current state of knowledge, only its diffusion in temperate areas is documented with certainty and a possible connection with warm climates or wet habitats, unless adventitious, remains unconfirmed.

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REFERENCES

- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* **215**:403–410
[https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Angelini C, Voto P, Alvarado P (2023) First report of coprinoid fungi (Psathyrellaceae, Agaricales) in the Dominican Republic. *MycolObs* **6**:54–76
- Arita M, Karsch-Mizrachi I, Cochrane G (2021) The international nucleotide sequence database collaboration. *Nucleic Acids Research* **49**:D121–D124
 DOI: 10.1093/nar/gkaa967
- Berkeley MJ, Broome CE (1871) The fungi of Ceylon. (Hymenomycetes, from *Agaricus* to *Cantharellus*). *Botanical Journal of the Linnean Society* **11**:494–567
- Boonmee S, Wanasinghe DN, Calabon MS, *et al.* (2021) Fungal diversity notes 1387–1511: taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity* **111**:1–335
 DOI: <https://doi.org/10.1007/s13225-021-00489-3>

- Cáceres O, Kirschner R, Piepenbring M, Schöfer H, Gené J (2006) *Hormographiella verticillata* and an Ozonium stage as anamorphs of *Coprinellus domesticus*. *Antonie Van Leeuwenhoek* **89**(1):79–90
- Cacialli G, Caroti V, Doveri F (1999) *Contributio ad Cognitionem Coprinorum*. A.M.B. Monografie di Pagine di Micologia. Tomo Primo. Brescia
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for *Basidiomycetes* – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**:113–118
- Gorovoy LF (1977) Loculose type of sex sporogenesis in Hymenomycetes. *Dopov. Akad. Nauk Ukrajin's'k RSR, Ser. B* **39**:742–746 (In Ukrainian)
- Hussain S, Usman M, Afshan NS, Ahmad H, Khan J, Khalid AN (2018) The genus *Coprinellus* (Basidiomycota; Agaricales) in Pakistan with the description of four new species. *Mycokeys* **39**:41–61
<https://doi.org/10.3897/mycokeys.39.26743>
- iNaturalist: <https://www.inaturalist.org/observations/129888756> (last visited 6 September 2024)
- Keirle MR, Hemmes DE, Desjardin DE (2004) Agaricales of the Hawaiian Islands. 8. Agaricaceae: *Coprinus* and *Podaxis*; Psathyrellaceae: *Coprinopsis*, *Coprinellus* and *Parasola*. *Fungal Diversity* **15**:33–124
- Malençon G, Bertault R (1970) Flore des champignons du Maroc. Tome I. *Trav. Inst. sci. chérifien, Sér. Bot. Biol. Vég.* **32**:1–604
- Maniotis J (1964) The Coprinoid state of *Rhacophyllus lilacinus*. *American Journal of Botany* **51**:485–494
- Mullis K, Faloona FA (1987) Specific synthesis of DNA in vitro via a polymerase-catalyzed chain reaction. *Methods in Enzymology* **155**:335–350
- Murray MG, Thompson WF (1980) Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* **8**(19):4321–4325
- Nagy LG, Desjardin DE, Vágvölgyi C, Kemp R (2013) Phylogenetic analyses of *Coprinopsis* sections *Lanatulii* and *Atramentarii* identify multiple species within morphologically defined taxa. *Mycologia*, **105**(1):112–124
 DOI: <https://doi.org/10.3852/12-136>
- Nilsson RH, Larsson K, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, Kennedy P, Picard K, Glöckner FO, Tedersoo L, Saar I, Kõljalg U, Abarenkov K (2018) The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Research* **47**:D259–D264
<https://doi.org/10.1093/nar/gky1022>
- Noordeloos ME (2005) Coprinaceae Overeem. In: Noordeloos ME, Kuyper TW, Vellinga EC (Eds) *Flora agaricina Neerlandica*. Critical monographs on families of agarics and boleti occurring in the Netherlands, vol 6. Taylor & Francis Group, Boca Raton, pp. 21–109
- Patouillard N (1901) Champignons Algéro-Tunisiens nouveaux ou peu connus. La bulbillose des lames chez les Agarics. *Bull. Soc. Mycol. Fr.* **17**:182–188
- Patouillard N (1913) Quelques champignons du Tonkin. *Bull. Soc. Mycol. Fr.* **29**:206–228
- Pegler DN (1966) Tropical African Agaricales. *Persoonia* **4**(2):73–124
- Pegler DN (1977) A preliminary Agaric flora of East Africa. *Kew Bulletin Additional Series* **6**:1–615
- Pegler DN (1983) Agaric flora of the Lesser Antilles. *Kew Bull. Add. Ser.* **9**:1–668
- Pegler DN (1986) Agaric flora of Sri Lanka. *Kew Bulletin Additional Series* **12**:1–519
- Pegler DN (1997) The Agarics of São Paulo: An Account of the Agaricoid Fungi (Holobasidiomycetes) of São Paulo State, Brazil. Royal Botanic Gardens, Kew
- Petch T (1926) *Rhacophyllus* B. & Br. *Trans. Brit. Mycol. Soc.* **11**:238–251
- Redhead SA, Seifert KA, Vilgalys R, Moncalvo J-M (2001) *Rhacophyllus* and *Zerovaemyces*. Teleomorphs or Anamorphs? *Taxon* **49**(4):789–798
- Redhead SA, Vilgalys R, Moncalvo J-M, Johnson J, Hopple JS Jr (2001) *Coprinus* Persoon and the disposition of *Coprinus* species sensu lato. *Taxon* **50**(1):203–241
<https://doi.org/10.2307/1224525>
- Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98
 DOI:10.3852/mycologia.97.1.84

- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**(3):539–542
doi.org/10.1093/sysbio/sys029
- Stalpers JA, Redhead SA, May TW, Rossman AY, Crouch JA, Cubeta MA, Dai Y-C, Kirschner R, Langer GJ, Larsson K-H, Mack J, Norvell LL, Oberwinkler F, Papp V, Roberts P, Rajchenberg M, Seifert KA, Thorn RG (2021) Competing sexual-aseexual generic names in Agaricomycotina (Basidiomycota) with recommendations for use. *IMA Fungus* **12**(22):1–31
https://doi.org/10.1186/s43008-021-00061-3
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9):1312–1313
DOI: 10.1093/bioinformatics/btu033
- Surmont I, Van Aelst F, Verbanck J, De Hoog GS (2002) A pulmonary infection caused by *Coprinus cinereus* (*Hormographiella aspergillata*) diagnosed after aneutropenic episode. *Medical Mycology* **40**:217–219
https://doi.org/10.1080/mmy.40.2.217.219
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**(10):2731–2739
https://doi.org/10.1093/molbev/msr121
- Uljé CB, Bas C (1993) Some new species of *Coprinus* from the Netherlands. *Persoonia* **15**(3):357–368
- Uljé CB, Noordeloos ME (1999) Studies in *Coprinus* V - *Coprinus* section *Coprinus*. Revision of subsection *Lanatulii* Sing. *Persoonia* **17**(2):165–199
- Voto P (2020b) [continuously updated] Key to Psathyrellaceae. A.M.E.R. Associazione Micologica Ecologica Romana (last accessed 21 November 2024)
Available from: https://www.ameronlus.it/chiavi_micologia.php
- Voto P, Angelini C (2024). Second report of coprinoid fungi (Psathyrellaceae, Agaricales) in the Dominican Republic. *MycolObs* **8**:19–23
- Vrinda KB, Pradeep CK, Varghese SP (2012) *Rhacophyllus lilacinus* – a remarkable fungal morph from Western Ghats of Kerala, India. *Österr. Z. Pilzk.* **21**:79–82
- White TJ, Bruns TD, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky J, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, London, 482 pp
<http://dx.doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Zhu LY, Huang M, Bau T (2022) Taxonomy of coprinoid fungi in China. *Mycosystema* **41**(6):878–898
DOI: 10.13346/j.mycosystema.210398