

## Article

# *Coprinus leucostictus* Rediscovered after a Century, Epitypified, and Its Generic Position in *Hausknechtia* Resolved by Multigene Phylogenetic Analysis of Psathyrellaceae

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**Abstract:** About a century after the first finding in northern Vietnam (1908), *Coprinus leucostictus* is rediscovered on 12 localities in southern India and southern to southeastern China, growing in evergreen subtropical or tropical forests. It is morphologically a rather unique species with coprinoid basidiomata, strongly branched and diverticulate veil hyphae, and a hymeniderm pileipellis. The BLAST search of ITS and *tef-1 $\alpha$*  sequences showed its close relationship to *Hausknechtia floriformis*, which is not clear based on morphological characters. Multigene phylogenetic analysis of a concatenated dataset of ITS, LSU, *tef-1 $\alpha$* , and  $\beta$ -tubulin sequences, revealed *C. leucostictus* and *H. floriformis* as separate, but sister species. Molecular phylogenetic relationships within the family Psathyrellaceae (including 17 genera) are presented in the phylogram. The genera *Hausknechtia* and *Candolleomyces* formed two well-supported lineages and were recovered as a monophyletic group. A total of 27 sequences from the genus *Hausknechtia* were newly generated in this study. *Coprinus leucostictus* is combined as *Hausknechtia leucosticta*, its epitype is designated, and the hitherto monotypic genus *Hausknechtia* is emended. A detailed morphological description of *H. leucosticta* supplemented with colour photographs and line drawings is provided.

**Keywords:** Agaricales; Basidiomycota; biogeography; fungi; morphology; taxonomy

## 1. Introduction

From 2004 to 2022, 30 collections of the same coprinoid species (dry, plicate-sulcate pileus and dark basidiospores) were found at 12 localities in southern India and southern to eastern China. Its strongly branched and diverticulate veil hyphae (Alachuan-type) indicated that the species belongs to the genus *Coprinopsis* P. Karst. However, it was in contrast to its hymeniderm pileipellis, as all *Coprinopsis* species are characterized by having a cutis unlike all other *Psathyrellaceae* genera characterized by a hymeniderm [1]. The examination of the morphological characters of all known coprinoid species with this type of veil revealed that our collections match only *Coprinus leucostictus*, despite scarce original description, and revision of holotype which lacks data on pileipellis and cystidia.

*Coprinus leucostictus* Pat. [2] was described from northern Vietnam (Hanoi) in South-east Asia, based on a collection by V. Demange from 1908. Until this study, the species has not been recorded again. Yang [3] revised the holotype, made a description, and illustrated basidiomata (mainly based on Demange's colour plate), basidiospores, veil hyphae, and clamp-connections in line drawings. He was unable to observe the other microcharacters because of poor condition of the material (pers. comm.). Obviously based on the branched and diverticulate veil hyphae, he concluded that the species could be placed in the subsection *Alachuani* Singer of the section *Coprinus*. After the split of the large, polyphyletic genus *Coprinus* Pers. in four genera [4], species of the subsection *Alachuani* were transferred to the genus *Coprinopsis*, but *C. leucostictus* was never recombined. The part of the holotype of *C. leucostictus* we received on loan for morphological study confirmed Yang's [3] observations. The material was in very poor condition and only basidiospores and veil hyphae were preserved. Nevertheless, these elements, as well as the macromorphological characters of the basidiomata, agree well with those in our collections.

However, the morphology alone is insufficient to reveal the taxonomic position of *Coprinus leucostictus*. GenBank BLAST analysis of ITS and *tef-1 $\alpha$*  sequences from our collections showed their close relationship only with *Galerella floriformis* Hauskn. [5] (known only from the type locality in Vanuatu, South Pacific). That species settled among members of the family Psathyrellaceae Vilgalys, Moncalvo & Redhead [4] (where most coprinoid species belong), instead in the family Bolbitiaceae Singer as originally expected [6]. Until the study by Wächter and Melzer [1], a considerable number of unresolved phylogenetic and related taxonomic problems existed in Psathyrellaceae, including the status of *G. floriformis*. These authors carried out a taxon-rich multigene phylogenetic analysis which resulted in description of seven new genera and allowed a more natural taxonomic position for many species. They transferred *G. floriformis* in the newly described monotypic genus *Hausknechtia* D. Wächt. & A. Melzer, which formed a sister clade to the new genus *Candolleomyces* D. Wächt. & A. Melzer (accommodating *Psathyrella candolleana* (Fr.) Maire and related species from the section *Spintrigerae* (Fr.) Konrad & Maubl.).

Although the morphological characters of *Coprinus leucostictus* and *Hausknechtia floriformis* (Hauskn.) D. Wächt. & A. Melzer (especially the basidiospores) did not suggest their close relationship, four-gene phylogenetic study performed here confirmed that these two species are congeneric. Therefore, *C. leucostictus* was transferred to the genus *Hausknechtia* and its generic concept was emended. Also, an epitype of *C. leucostictus* was designated because of the very poor condition of the holotype (some important micro-characters were collapsed, e.g., pileipellis, cystidia, and basidia) and in this case the extraction of DNA from the holotype was not allowed by Farlow Herbarium, although the chance of success would be very low due to the age and condition of the sample.

## 2. Materials and Methods

### 2.1. Description of Sites

The Chinese specimens were collected in five provinces of southern and southeastern China: Anhui, Fujian, Jiangxi, Zhejiang, and Hainan. The first four mentioned provinces belong to the subtropical monsoon climate region with an average annual temperature of 13–20 °C and an average annual rainfall of (generally) 800–1500 mm. The vegetation type is subtropical evergreen broadleaf forest, mainly of Fagaceae trees (e.g., *Castanopsis* spp. and *Quercus* spp.). Hainan Province has a tropical monsoon climate with an average annual temperature of 22.5–25.6 °C and an annual precipitation of 1500–2500 mm, characterized by tropical vegetation composed mainly of Rhizophoraceae and Lauraceae trees (e.g., *Rhizophora* spp. and *Cinnamomum* spp.). The Indian specimens were collected in the southern part of Kerala State (southern India) in evergreen tropical forests, with an average rainfall of 3000 mm and an average temperature of 25–32 °C.

## 2.2. Sampling and Morphological Study

Thirty collections of *Coprinus leucostictus* were found between 2004 and 2022 on 12 localities, 17 collections in southern India (from two localities), and 13 collections in southern and southeastern China (from 10 localities). Collected basidiomata were preserved by drying. The Chinese specimens, including the epitype (designated below), were deposited in the Herbarium of Jiangxi Agricultural University (HFJAU), Nanchang, China, and in the Croatian National Fungarium (CNF), Zagreb, Croatia (isoeotype). The Indian specimens were deposited in the Mycological Herbarium of Tropical Botanic Garden and Research Institute (TBGT), Thiruvananthapuram, Kerala, India, and in the Croatian National Fungarium (one collection). Holotype of *C. leucostictus* is deposited in Farlow Herbarium (FH) of Harvard University, Cambridge, MA, USA. The holotype and paratype collections of *Hausknechtia floriformis* are deposited in Herbarium Universität Wien (WU), Vienna, Austria.

The morphological description of *H. leucosticta* is based on Indian and Chinese collections. The macrocharacters were noted from fresh samples and photographs of basidiomata. The microcharacters were observed in 2.5–5% aqueous potassium hydroxide solution (KOH), water, 5% NH<sub>4</sub>OH and/or Congo Red, using optical microscope under the magnification up to 1500×. Basidiospores from dry, mature lamellae rehydrated in KOH were randomly selected and measured. Their length/width ratio is expressed as “Q” value (min.—av.—max.). The average basidiospore length, width, and Q value are shown in italics. Numbers in square brackets [X/Y/Z] denote X basidiospores measured in Y basidiomata from Z collections. Amyloid and dextrinoid reactions were tested in Melzer’s reagent [7].

## 2.3. DNA Extraction and Sequencing

Genomic DNA was extracted from dried specimens using the NuClean Plant Genomic DNA kit (CWBIO, Taizhou, China) (for *Hausknechtia leucosticta* specimens from China), and with EZNA<sup>®</sup> HP Fungal DNA Kit (Omega Bio-tek, Norcross, GA, USA) (for *H. leucosticta* specimen from India and *H. floriformis*) following the manufacturer’s protocols.

The sequences of internal transcribed spacer region (ITS), nuclear 28S rRNA gene (LSU), translation elongation factor 1 $\alpha$  (*tef-1 $\alpha$* ), and  $\beta$ -tubulin gene regions were amplified with ITS1F/ITS4 [8,9], LR0R/LR7 [10], EF983F/EF2218R [11] and B12r-psa/B36f-psa [12] primers, respectively. PCR amplification of ITS, LSU, and *tef-1 $\alpha$*  was performed using a touchdown program: 5 min at 95 °C; 1 min at 95 °C; 30 s at 65 °C (add –1 °C per cycle); 1 min at 72 °C; cycle 15 times; 1 min at 95 °C; 30 s at 50 °C; 1 min at 72 °C; cycle 20 times; 10 min at 72 °C [13]. PCR amplification of  $\beta$ -tubulin was performed under the following conditions: 5 min for 95 °C; 30 s at 95 °C, 30 s at 52 °C, 45 s at 72 °C, repeated for 35 cycles; 5 min at 72 °C (adapted from [12]). Successful PCR products were purified using ExoSAP-IT<sup>™</sup> (Thermo Fisher Scientific, Waltham, MA, USA) cleanup reagent and sent to MacroGen Europe (Amsterdam, The Netherlands) for Sanger sequencing in both directions using the same primers as for amplification.

A holotype of *H. floriformis* (WU22832) was newly sequenced and *H. floriformis* (WU22833) was resequenced for ITS, LSU, and *tef-1 $\alpha$*  marker genes and newly sequenced for  $\beta$ -tubulin.

## 2.4. Data Analyses

Sequence reads were assembled and edited using Geneious Prime 2021.2.2. (<https://www.geneious.com>, Biomatters, Auckland, New Zealand, accessed on 6 July 2022) and sequences were deposited at the National Center for Biotechnology Information (NCBI) GenBank database. Newly obtained ITS sequences of *Hausknechtia leucosticta* were BLAST searched against NCBI GenBank’s nucleotide database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi> (accessed on 14 June 2022)) resulting in *H. floriformis* (Accession number JX968254, [6]) as the only close hit (97.09–97.47% identity), taking in consideration sequences from published sources. Phylogenetic dataset comprised a total of 248 sequences

of four gene regions (ITS, LSU, *tef-1 $\alpha$* , and  $\beta$ -tubulin) from 64 taxa covering generic diversity of Psathyrellaceae, including 27 newly generated *Hausknechtia* sequences (Table 1). Sequences were aligned by each locus using MAFFT v7.450 [14,15] available as Geneious Prime plugin. Concatenation of ITS, LSU, *tef-1 $\alpha$* , and  $\beta$ -tubulin alignments was done using Geneious Prime 2021.2.2. After being aligned and trimmed, the combined dataset contained 3490 characters including gaps, with 786 characters for ITS, 1251 characters for LSU, 1034 characters for *tef-1 $\alpha$* , and 419 characters for  $\beta$ -tubulin alignment.

**Table 1.** Species included in this study, voucher numbers, countries of origin, and GenBank accession numbers. Newly generated sequences are in bold.

Taxon	Voucher	Country	ITS	LSU	<i>tef-1<math>\alpha</math></i>	$\beta$ -Tubulin	Refs.
<i>Bolbitius excoriatus</i>	LO23-10	Sweden	KC456419	KC456419	KJ732834	-	[1,16]
<i>Bolbitius subvolvatus</i>	WU28379	Hungary	JX968248	JX968365	JX968454	-	[6]
<i>Britzelmayria multipedata</i>	LO237-04	Sweden	KC992888	KC992888	KJ732777	KJ664867.1	[17]
<i>Britzelmayria multipedata</i>	CNF 1/7263	Croatia	MK169241	-	-	-	[18]
<i>Britzelmayria supernula</i>	LO250-04	Sweden	KC992867	KC992867	KJ732763	KJ664849.1	[17]
<i>Candolleomyces badhyzensis</i> (type)	79478 (TAA)	Turkmenistan	KC992883	KC992883	-	-	[17]
<i>Candolleomyces badiophyllus</i>	SZMC-NL-2347	-	FN430699	FM876268	FN396261	FM897252	[12]
<i>Candolleomyces candolleanus</i> (type)	LAS73030	Hungary	KM030175	KM030175	-	-	[17]
<i>Candolleomyces candolleanus</i>	SZMC-NL-2937	Hungary	FN396114	FN396165	FN396220	FN396307	[12]
<i>Candolleomyces cladii-marisci</i> (type)	CLUF302	Italy	MK080112	-	-	-	[19]
<i>Candolleomyces eurysporoides</i> (type)	GLM-F126263	Germany	MT651560	MT651560	-	-	[20]
<i>Candolleomyces incanus</i>	BJTC Z777	China, Beijing	ON042759	ON042766	ON098508	ON098513	[21]
<i>Candolleomyces luteopallidus</i> (type)	Sharp20863 (MICH)	USA	KC992885	KC992885	KJ732775	KJ664865	[17]
<i>Candolleomyces luteopallidus</i>	HMJAU5148	China, Jilin	MG734736	MW301084	MW314056	MW314073	[22]
<i>Candolleomyces secotioides</i> (type)	UES2918	Mexico	KR003281	KR003282	-	KR003283	[23]
<i>Candolleomyces subcacao</i> (type)	HMJAU37807	China, Henan	NR_173317	NG_079683	MW314081	MW314063	[24]
<i>Candolleomyces subcacao</i>	HMJAU37808	China, Henan	MW301065	MW301093	MW314082	MW314064	[24]
<i>Candolleomyces subminutisporus</i>	HMJAU37916	China, Henan	MW301067	MW301095	MW314084	MW314066	[24]
<i>Candolleomyces subsingeri</i> (type)	HMJAU37811	China, Jilin	MG734715	MW301097	MW314085	MW314067	[22,24]
<i>Candolleomyces subsingeri</i>	HMJAU37913	China, Jilin	MG734725	MW301098	MW314086	MW314067	[22,24]
<i>Coprinellus disseminatus</i>	SZMC-NL-2337	Hungary	FM878017	FM876274	-	FN396282	[12]
<i>Coprinellus flocculosus</i>	SZMC-NL-1567	-	FN430683	JN159593	-	FN396345	[12]
<i>Coprinellus micaceus</i>	SZMC-NL-3656	-	JN159567	JN159588	-	JN159644	[25]
<i>Coprinellus truncorum</i>	SZMC-NL-1101	Sweden	JN159562	FM876262	FM897225	JN159629	[12,26]
<i>Coprinopsis afrocinerea</i> (type)	CNF 1/5838	Nigeria	MG662162	MG662158	-	-	[27]
<i>Coprinopsis annulopora</i>	CNF 1/4901	Croatia	MG662170	-	-	-	[27]
<i>Coprinopsis cerkezii</i> (type)	CNF 1/7253	Croatia	NR_173361	NG_068782	-	-	[28]
<i>Coprinopsis cineraria</i> (type)	CBM-FB-24142	Japan	KC992962	-	-	-	[17]

Table 1. Cont.

Taxon	Voucher	Country	ITS	LSU	<i>tef-1α</i>	β-Tubulin	Refs.
<i>Coprinopsis cinerea</i>	CNF 1/5242	Croatia	MG662167	-	-	-	[27]
<i>Coprinopsis musae</i> (type)	JV06-179	Denmark	NR_148070	KC992965	-	KJ664920	[17]
<i>Coprinopsis narcotica</i>	SZMC-NL-2342	Hungary	FM163180	FM160729	FN396244	FN396290	[29]
<i>Coprinopsis picacea</i>	SZMC-NL-3033	-	FN396119	FN396168	FN396223	FN396312	[12]
<i>Coprinopsis semitalis</i> (type)	CBS291.77	-	GQ249278	GQ249287	GQ249270	GQ249262	[12]
<i>Coprinopsis submicrospora</i> (type)	AH27055	Spain	KC992959	KC992959	-	KJ664918	[17]
<i>Coprinopsis udicola</i> (type)	AM1240	Germany	NR_148071	KC992967	KJ732831	KJ664922	[17]
<i>Cystoagaricus hirtosquamulosus</i>	Ramsholm800927	Finland	KC992945	KC992945	-	-	[17]
<i>Cystoagaricus olivaceogriseus</i> (type)	WK 8/15/63-5	USA	KC992948	KC992948	-	-	[17]
<i>Cystoagaricus silvestris</i>	LO191-92	Sweden	KC992949	KC992949	-	-	[17]
<i>Cystoagaricus strobilomyces</i>	30-V-1997	Japan	AY176347	AY176348	-	-	[30]
<b><i>Hausknechtia floriformis</i> (type)</b>	<b>WU22832</b>	<b>Vanuatu</b>	<b>ON745613</b>	<b>ON745616</b>	<b>ON746007</b>	<b>ON746008</b>	<b>This study</b>
<b><i>Hausknechtia floriformis</i></b>	<b>WU22833</b>	<b>Vanuatu</b>	<b>ON745619</b>	<b>ON745615</b>	<b>ON746009</b>	<b>ON746010</b>	<b>This study</b>
<b><i>Hausknechtia leucosticta</i></b>	<b>CNF 1/6900</b>	<b>India</b>	<b>ON745618</b>	<b>ON745617</b>	<b>ON746005</b>	<b>ON746006</b>	<b>This study</b>
<b><i>Hausknechtia leucosticta</i> (epitype)</b>	<b>HFJAU1486</b>	<b>China, Anhui</b>	<b>OL435561</b>	<b>OL435565</b>	<b>OL439896</b>	<b>ON677539</b>	<b>This study</b>
<b><i>Hausknechtia leucosticta</i></b>	<b>HFJAU1526</b>	<b>China, Fujian</b>	<b>OL435563</b>	<b>OL435566</b>	<b>OL439897</b>	<b>ON677541</b>	<b>This study</b>
<b><i>Hausknechtia leucosticta</i></b>	<b>HFJAU1730</b>	<b>China, Jiangxi</b>	<b>OL435562</b>	<b>-</b>	<b>OL439898</b>	<b>ON677540</b>	<b>This study</b>
<b><i>Hausknechtia leucosticta</i></b>	<b>HFJAU1751</b>	<b>China, Jiangxi</b>	<b>OL435564</b>	<b>OL435567</b>	<b>OL439899</b>	<b>ON677542</b>	<b>This study</b>
<i>Heteropsathyrella macrocystidia</i> (type)	HMJAU37802	China, Fujian	MW405102	MW413359	MW411004	-	[24]
<i>Heteropsathyrella macrocystidia</i>	HMJAU37803	China, Fujian	MW405101	MW413358	MW411003	-	[24]
<i>Homophron cernuum</i>	LO134-98	Sweden	DQ389726	DQ389726	KJ732828	KJ664915	[17,31]
<i>Homophron cernuum</i> ( <i>Psathyrella crenulata</i> type)	WK8/10/64-5	USA	KC992957	-	-	-	[17]
<i>Homophron spadiceum</i>	SZMC-NL-3996	Hungary	FN396132	FN396180	FN396231	FN396333.1	[12]
<i>Kauffmania larga</i>	LO223-90	Sweden	DQ389694	DQ389694	KJ732824	KJ664912.1	[17]
<i>Kauffmania larga</i>	LAS97-054	Sweden	DQ389695	DQ389695	-	-	[17]
<i>Lacrymaria glareosa</i>	LAS06-019	Sweden	KC992954	KC992954	KJ732827	KJ664914	[17]
<i>Lacrymaria hypertropicalis</i> (type)	Guzman29585	Mexico	KC992958	KC992958	-	KJ664916	[17]
<i>Lacrymaria pyrotricha</i>	CBS573.79	-	GQ249280	GQ249289	GQ249272	GQ249264	[12]
<i>Narcissea cordispora</i>	LO41-01	Sweden	DQ389723	DQ389723	-	KJ664910	[17,31]
<i>Narcissea patouillardii</i>	SZMC-NL-1687	Hungary	FM878009	FM876265	FM897238	FN396257	[26]
<i>Narcissea patouillardii</i>	SZMC-NL-1695	Hungary	FN430685	FN396196	-	FN396258	[26]
<i>Olotia codinae</i> (type)	AM1887/GLM-F112430	Spain	MG696611	MG674714	-	-	[32]
<i>Parasola conopilea</i> (type)	LO186-02	Sweden	DQ389725	DQ389725	-	-	[31]
<i>Parasola conopilea</i>	SZMC-NL-0285	Hungary	FM163225	FM160684	FM897237	FN396247	[29]

Table 1. Cont.

Taxon	Voucher	Country	ITS	LSU	<i>tef-1α</i>	β-Tubulin	Refs.
<i>Parasola kuehmeri</i> (type)	Ulje 31-V-1987	Netherlands	KY928608	KY928633	-	-	[33]
<i>Parasola plicatilis</i>	SZMC-NL-0295	Hungary	FM163216	FM160693	FM897242	FN396253	[29]
<i>Parasola plicatilis</i> (type)	SZMC-NL-0075a	Hungary	FM163213	FM160696	-	-	[29]
<i>Psathyrella amygdalinospora</i> (type)	HMJAU37952	China, Sichuan	NR_173320	MW413361	MW410999	MW410991	[24]
<i>Psathyrella fagetophila</i> (type)	LO210-85 (M)	Sweden	NR_167955	KC992902	-	KJ664879	[17]
<i>Psathyrella fennoscandica</i> (type)	LO484-05	Sweden	KC992903	KC992903	KJ732790	KJ664881	[17]
<i>Psathyrella pertinax</i> (type)	LO259-91	Sweden	DQ389701	DQ389701	KJ732809	-	[17]
<i>Psathyrella piluliformoides</i> (type)	HMJAU37923	China, Zhejiang	MW405106	MW413362	MW411002	-	[24]
<i>Psathyrella rybergii</i> (type)	LÖ373-06	Sweden	KC992893	KC992893	KJ732781	KJ664872	[17]
<i>Psathyrella truncatisporoides</i> (type)	HMJAU37947	China, Zhejiang	MW405107	MW413363	MW410990	MW410998	[24]
<i>Punjabia pakistanica</i> (type)	LAH35323	Pakistan	MH366736	-	-	-	[34]
<i>Punjabia pakistanica</i>	LAH35324	Pakistan	MH366737	-	-	-	[34]
<i>Tulosesus callinus</i>	SZMC-NL-1931	Hungary	FN396105	FN396158	FN396213	FN396299	[12]
<i>Tulosesus cinereopallidus</i> (type)	SZMC-NL-0177	Hungary	HQ847001	HQ847090	-	HQ847149	[25]
<i>Tulosesus pallidus</i> (type)	SZMC-NL-1556	Hungary	HQ846989	HQ847076	-	HQ847155	[25]
<i>Tulosesus radicellus</i> (type)	SZMC-NL-3168	Sweden	GU227719	HQ847077	-	GU227737	[25,35]
<i>Typhrasa gossypina</i>	Schumacher024	Germany	KC992946	KC992946	KJ732825	-	[17]
<i>Typhrasa nanispora</i> (type)	Barta980706	Austria	KC992947	KC992947	-	-	[17]
<i>Typhrasa polycystis</i> (type)	HFJAU1454	China, Zhejiang	MW466538	MW466544	MW475280	-	[36]

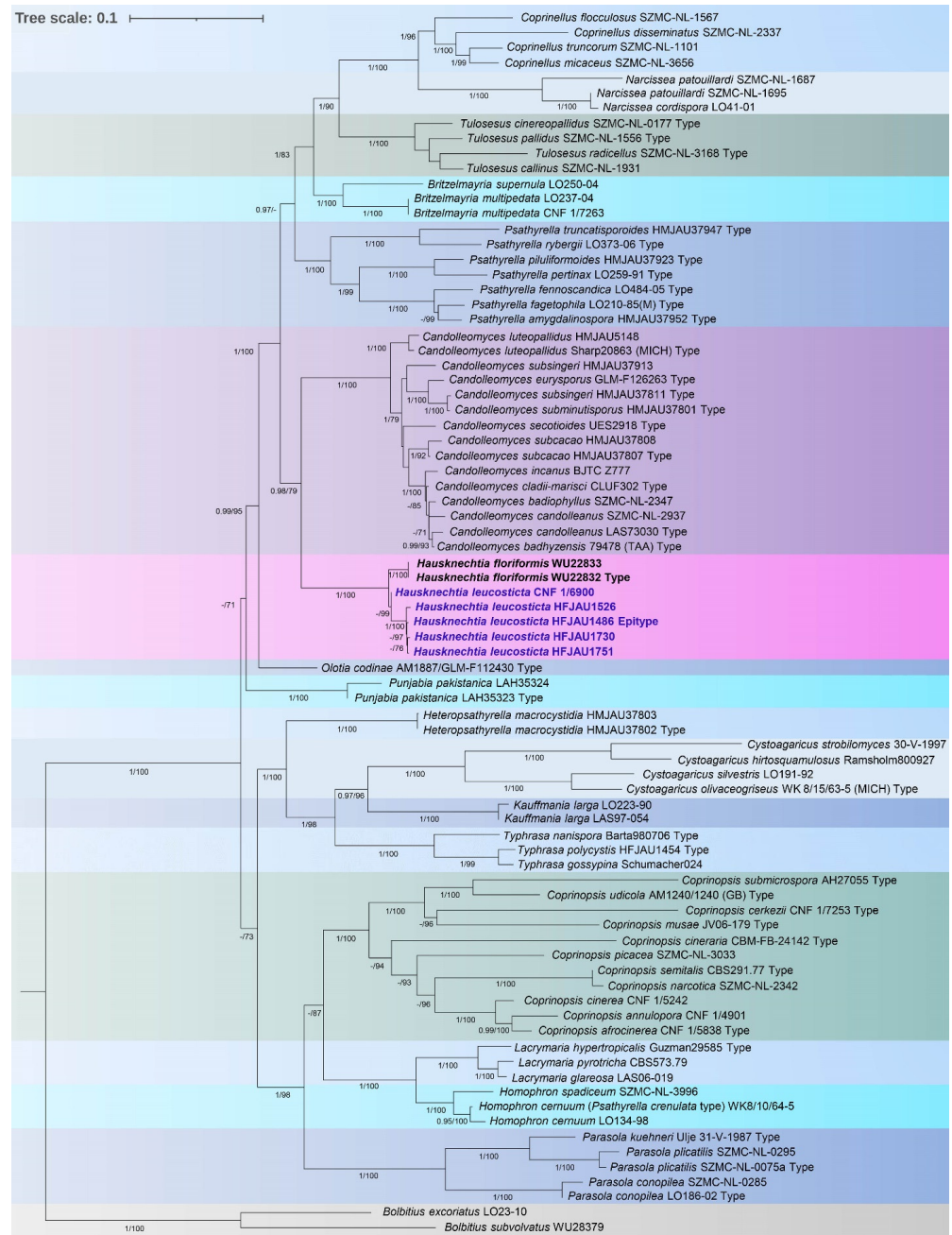
Phylogenetic analyses of concatenated four-gene (ITS, LSU, *tef-1α*, β-tubulin) sequence alignment were conducted using Maximum Likelihood (ML) analysis in IQTREE v1.6.12 [37,38] and a Bayesian Inference (BI) analysis in MrBayes 3.2.6 (Geneious plugin, [39]). The best model (GTR + F + I + G4) was selected by ModelFinder implemented in IQ-TREE considering separately the corrected Akaike, and Bayesian Information Criterion (cAIC, BIC). ML analysis was executed by applying the ultrafast bootstrap approximation with 1000 replicates. BI analysis was executed for 10,000,000 generations, sampling trees and other parameters every 10,000 generations. The default number of chains (four) and heating parameters were used. Posterior probabilities (BPP) were calculated after burning the first 25% of the posterior sample. The outgroup taxa (*Bolbitius subvolvatius* (WU28379) and *B. excoriatius* (LO23-10)) were selected following [1]. Phylogenetic tree was visualized and annotated using iTOL v6.5.4 [40] and FigTree 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/> (accessed on 6 July 2022)).

### 3. Results

#### 3.1. Molecular Phylogenetic Analysis

A total of 27 sequences from seven *Hausknechtia* specimens (five *H. leucosticta* and two *H. floriformis*) were newly generated in this study. Sequence identity analysis between *H. floriformis* WU22832 (holotype) and *H. floriformis* WU22833 (paratype) revealed 100% identity for each of the four gene regions. Based on the BLAST results, *H. leucosticta* (five collections) shared identity with *H. floriformis* (newly generated sequences) of 97.67–97.95% for ITS, 99.40–99.78% for LSU, 95.22–97.29% for *tef-1α*, and 95.83–96.69% for β-tubulin gene region. A total of 17 branches (BI-PP ≥ 0.95, ML-BP ≥ 70), representing 17 genera within the family Psathyrellaceae, are formed in the phylogenetic tree (Figure 1). The two well supported lineages (BI-PP = 0.98, ML-BP = 79), corresponding to the genera

*Hausknechtia* and *Candolleomyces*, were recovered as a monophyletic group. At the species level, *H. leucosticta* formed a distinct lineage separated from *H. floriformis* with high support (BI-PP = 1, ML-BP = 100).



**Figure 1.** Concatenated phylogenetic tree of *Psathyrellaceae* species based on Bayesian interference (BI) and Maximum Likelihood (ML) analyses of four-gene (ITS, LSU, *tef-1α*,  $\beta$ -tub) sequence alignment. BI and ML analyses were performed using MrBayes v. 3.2.6 and IQ-TREE 1.6.12, respectively. Significant branch support values, Bayesian posterior probability (BI-PP  $\geq$  0.95) and ultrafast bootstrap support (ML-BP  $\geq$  70%), are presented at the nodes. Species with newly generated sequences are marked in bold and recombined species is marked in colour and bold.

### 3.2. Taxonomy

*Hausknechtia* D. Wächt. & A. Melzer [1], emend. Tkalčec, J.-Q. Yan, C. Nie & C.K. Pradeep.

Type species: *Hausknechtia floriformis* (Hauskn.) D. Wächt. & A. Melzer, Mycol. Progr. 19(11): 1234 (2020).

Transfer of *Coprinus leucostictus* in hitherto monotypic genus *Hausknechtia* required emendation of the concept of the genus, which is given below.

*Emended description:* Basidiomata thin-fleshed and fragile. Pileus dry, plicate-sulcate, later deeply, strongly radially splitted and ragged or not, with veil (at least when young). Lamellae adnexed to adnate, deliquescent (easily collapsing) when old or not. Stipe slender. Basidiospores smooth, ellipsoid, ovoid or cylindrical (in frontal view), yellowish-hyaline or brown in maturity, thin- to moderately thick-walled; germ-pore present or absent. Hymenophysalides (pseudoparaphyses) present or not. Cheilocystidia absent or present. Pleurocystidia absent. Pileipellis a hymeniderm. Veil hyphae septate, occasionally to strongly branched, diverticulate or not. Clamp-connections present.

*Hausknechtia leucosticta* (Pat.) Tkalčec, J.-Q. Yan, C. Nie & C.K. Pradeep, comb. nov. (Figures 2–4).

Mycobank MB 844448.

Basionym: *Coprinus leucostictus* Pat., Bull. Soc. Mycol. Fr. 33: 61 (1917).

Holotype: Vietnam, Hanoi, on soil, 1908, *leg.* V. Demange (287), FH 4457 (barcode 00258859).

Epitype (designated here): China. Anhui Province: Chizhou Guliujiang Nature Reserve, *leg.* Jun-Qing Yan, on soil, 8 June 2020, HFJAU1486, MBT 10007586; CNF 1/8787 isoeotype.

*Description:* Pileus (10–)15–60 mm broad, ellipsoid to paraboloid when young, later  $\pm$  convex, conical, obtusely conical, broadly conical, plano-conical, plano-convex or appanate to plano-concave with a broad obtuse umbo; margin mostly straight, sometimes moderately deflexed or reflexed (when fully mature); surface dry, distinctly to strongly radially plicate-sulcate up to 85% of the radius (except when young), central disc smooth; at first light to medium orangish- to orange-brown or  $\pm$  dark reddish-brown, uniformly coloured or paler towards the margin, later light to medium orangish-brown, orange-brown or brown in the central part and on the ribs, gradually paler towards the margin, between the ribs and sometimes throughout the whole narrower or wider outer zone pale grey(ish) to pale brownish-greyish, non-deliquescent. Veil white, thin, felty, covering the whole pileus in primordial stage only, very soon splitting up in small, flat,  $\pm$  concentrically arranged patches, becoming scattered over the pileus at maturity and can fall off during the rain or on handling. Lamellae adnexed to adnate, moderately crowded to crowded, L = ca. 30, l = 1–7, up to 6 mm wide, white at first, becoming light yellowish-brown, greyish-brown, then brownish-grey, grey or dark grey-brown, with whitish, entire edge, non-deliquescent. Stipe 23–132  $\times$  1.4–5 mm, central,  $\pm$  cylindric with slightly broadened base (up to 6 mm) or gradually thickening downwards, white to cream, finely pruinose in the upper part, below smooth or mottled with small white fibrils, often white strigose at the very base, dry, hollow. Context thin, fragile, whitish, greyish or orangish-brownish. Odour mild, not characteristic. Spore print black.





**Figure 2.** *Hausknechtia leucosticta*; basidiomata. (A) Original painting of the holotype by V. Demange (1908), from the Farlow Reference Library of Cryptogamic Botany at Harvard University. (B) HFJAU1486 (epitype). (C) HFJAU1200. (D–F) HFJAU3631. (G) HFJAU2076. (H) HFJAU2822. (I–K) TBGT13589 & CNF 1/6900. (L) TBGT14823. (M) TBGT16390.

Basidiospores [540/7/6] (8.8–)9.2–10.8–13.0(–13.7)  $\times$  (4.9–)5.2–6.2–7.3(–7.7)  $\mu\text{m}$ , averages of different collections 10.5–11.2  $\times$  5.8–6.5  $\mu\text{m}$ , Q = (1.46–)1.53–1.74–2.00(–2.23), Q av. = 1.65–1.81, ellipsoid, narrowly ellipsoid or ovoid in frontal view, ellipsoid, narrowly ellipsoid or subamygdaliform in side view, rarely ovoid, not or only insignificantly flattened, smooth, moderately thick-walled (up to 0.8(–1)  $\mu\text{m}$ ), with distinct and central germ-pore (0.8–1.5  $\mu\text{m}$  wide inner diameter, 1.4–2.4  $\mu\text{m}$  wide outer diameter), rusty brown to dark red brown in  $\text{H}_2\text{O}$  and  $\text{NH}_4\text{OH}$ , medium to dark brown in  $\text{KOH}$  (become more greyish over time), non-amyloid and non-dextrinoid. Basidia (13–)16–25(–32)  $\times$  (9.5–)10–13  $\mu\text{m}$ , clavate to broadly clavate, 4-spored, occasionally 2- or 3-spored, thin-walled, hyaline, mostly with refractive guttules, surrounded by 3–6 hymenophysalides (pseudoparaphyses). Hymenophysalides 10–20  $\times$  6–20  $\mu\text{m}$ , subglobose, broadly clavate, ellipsoid, broadly cylindrical or cuboid, thin-walled, hyaline; fully developed only in mature basidiomata. Lamellar edge sterile with rather crowded cheilocystidia. Cheilocystidia 12–50  $\times$  8–30(–40)  $\mu\text{m}$ , de-

velop to the full maturity of the lamellae; versiform, predominantly  $\pm$  utriform (with  $\pm$  broadened apex or not), (broadly) clavate, subglobose, spheropedunculate, obovoid or  $\pm$  ellipsoid; thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular to subregular, composed of 1.5–15(–20)  $\mu\text{m}$  broad, thin-walled, hyaline hyphae. Pileipellis a hymeniderm, composed of clavate, broadly clavate, ellipsoid, spheropedunculate or subglobose elements, 18–70  $\times$  11–45  $\mu\text{m}$ , thin- to moderately thick-walled (up to 1  $\mu\text{m}$ ), hyaline or with pale brown, intracellular pigment. Pileal trama composed of 3–25  $\mu\text{m}$  broad, thin- to thick-walled (up to 1.2  $\mu\text{m}$ ), hyaline or brown pigmented hyphae; pigment partially encrusted, mostly present in upper part. Veil composed of 2–12  $\mu\text{m}$  broad, septate, strongly branched and diverticulate (excrescences with rounded tip, 1–30  $\mu\text{m}$  long), thin- to moderately thick-walled (up to 1  $\mu\text{m}$ ), hyaline to pale brown hyphae (pigment intracellular). Stipitipellis a cutis of repent hyphae, 1.5–10  $\mu\text{m}$  broad, thin- to moderately thick-walled (up to 0.8  $\mu\text{m}$ ), hyaline. Stipe trama composed of parallel and longitudinal hyphae, often somewhat swollen and constricted at septae, 1.5–24  $\mu\text{m}$  broad, thin- to moderately thick-walled (up to 0.8  $\mu\text{m}$ ), hyaline. Caulocystidia present in the upper part of the stipe, 20–105  $\times$  6–25  $\mu\text{m}$ , variously shaped:  $\pm$  utriform, narrowly to broadly clavate, ellipsoid, subcylindric or irregular; thin- to thick-walled (up to 2.8  $\mu\text{m}$ ), hyaline. Clamp-connections present, abundant.

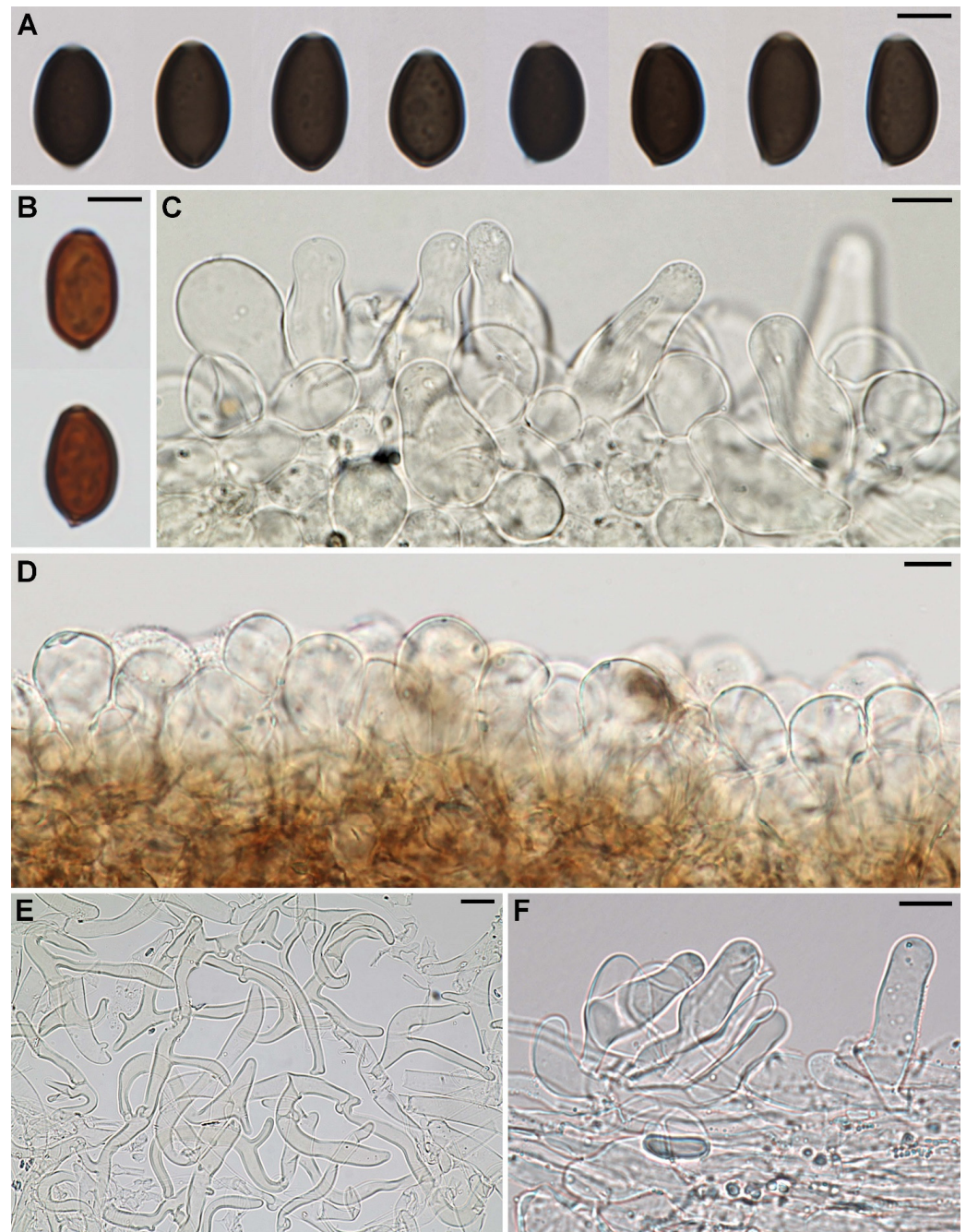
The macro- and micromorphological characters of the epitype (designated above) fit well with the above comprehensive description of the Indian and Chinese collections. The particular measures of the epitype are as follows: pileus 16–43 mm broad; stipe 25–53  $\times$  1.4–3.2 mm (1.7–5 mm at the base); basidiospores (8.8–)9.3–10.8–12.5(–13.5)  $\times$  (5.0–)5.2–6.0–7.0  $\mu\text{m}$ ,  $Q = 1.50\text{--}1.80\text{--}2.00\text{(–}2.14\text{)}$ .

*Habit, habitat, and phenology:* Solitary, scattered or in groups on soil, soil litter or decaying wood, in evergreen subtropical or tropical forests; basidiomata occurred from April to October.

*Distribution:* Known so far from Northern Vietnam (Hanoi Province), southern India (southern part of Kerala State), southern and southeastern China (Anhui, Fujian, Hainan, Jiangxi, and Zhejiang provinces). Based on BLAST search of ITS sequences data against GenBank (0.44–1.10% difference to our *H. leucosticta* sequences), the species was also found in Thailand (MN483260) and Brazil (MK881745).

*Specimens examined:* Vietnam. Hanoi Province: *leg.* V. Demange, on soil, 1908, FH 4457 (barcode 00258859; holotype).

China. Anhui Province: Chizhou Guliujiang Nature Reserve, ca. 30.1008° N, 117.4975° E, *leg.* J.Q. Yan, on soil, 8 June 2020, HFJAU1486 (epitype, designated above), CNF 1/8787 (isoepitype); Fujian Province: Wuyishan Reserve, ca. 27.6181° N, 117.9939° E, *leg.* J.Q. Yan, 13 June 2020, HFJAU1526; Hainan Province: Parrot Ridge Nature Reserve, ca. 18.9136° N, 109.6881° E, *leg.* Y. Fan, 4 July 2020, HFJAU2349; 5 July 2020, HFJAU2350.

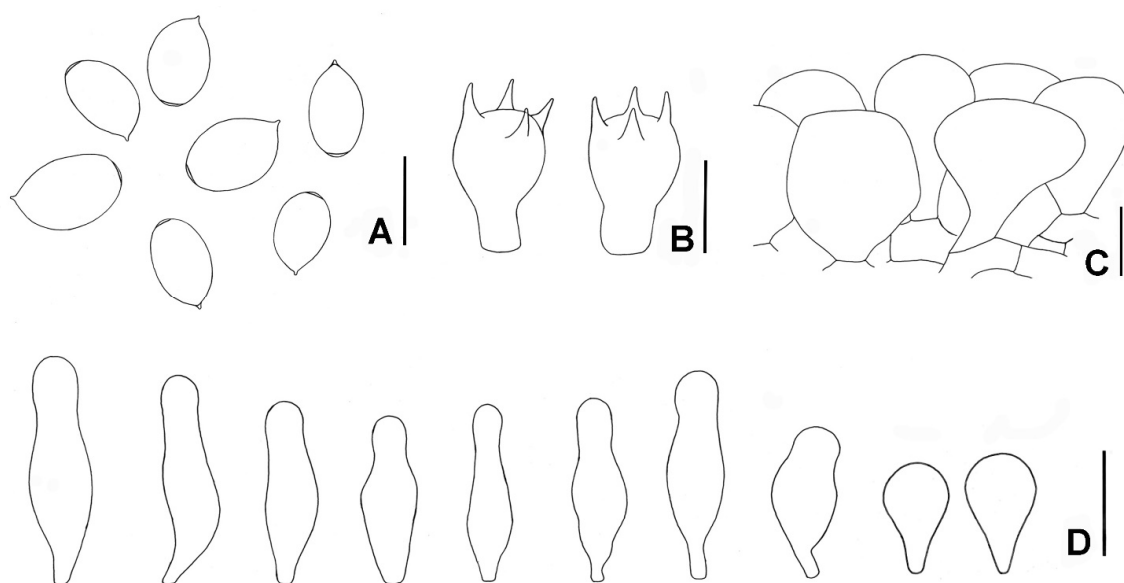


**Figure 3.** *Hausknechtia leucosticta*, TBGT13589 & CNF 1/6900. (A) Basidiospores in KOH. (B) Basidiospores in H<sub>2</sub>O. (C) Cheilocystidia. (D) Pileipellis. (E) Veil on the pileus. (F) Caulocystidia. Bars: (A,B) = 5  $\mu$ m, (C–F) = 10  $\mu$ m.

NW from Changfeng town, ca. 18.8478° N, 110.2550° E, leg. Y. Fan, on soil, 1 May 2021, HFJAU3631; Jianxi Province: Jiu Lian Shan National Nature Reserve, ca. 24.6772° N, 114.5775° E, leg. J.Q. Yan, 22 August 2020, HFJAU1730; HFJAU1751; Jianxi Agricultural University, ca. 50 m a.s.l., ca. 28.7614° N, 115.8325° E, leg. Z. Yi, on soil/litter, 18 May 2019, HFJAU1200; leg. J.Q. Yan, 26 June 2019, HFJAU1295; Zhejiang Province: Suichang County Ramishang village, ca. 28.6689° N, 119.0444° E, leg. J.Q. Yan & Y. Chen, on soil litter, 14 July 2020, HFJAU2076; vicinity of Lishui city, ca. 28.4933° N, 119.6917° E, leg. J.Q. Yan & Z. Liu, on soil, 3 August 2021, HFJAU2683; ca. 220 m a.s.l., ca. 28.4300° N, 120.0535° E, leg. Q. Na, B. Ke & Z. Zeng, on decaying wood, 5 August 2021, HFJAU2836; vicinity of Qingtian County Grid Rossi village, ca. 28.3797° N, 119.9733° E, leg. Q. Na, B. Ke & Z. Zeng, on soil, 5 August 2021, HFJAU2822.

India. Kerala State: Kollam district, Thenmala, 190 m a.s.l., 8.9632° N, 77.0651° E, leg. C.K. Pradeep, on soil, 16 September 2004, TBGT7860; Thiruvananthapuram district, Palode, JNTBGRI campus, ca. 120 m a.s.l., ca. 8.7244° N, 77.0248° E, leg. C.K. Pradeep, on soil, 14 May 2009, TBGT12452; 11 May 2010, TBGT13214; 24 May 2010, TBGT13261; 27 April 2011, TBGT13573; 4 May 2011, TBGT13589, CNF 1/6900; 5 May 2011, TBGT13592; 18 May 2011, TBGT 13595; 23 May 2011, TBGT13599; 30 May 2011, TBGT13607; 31 May 2011, TBGT13608; 13 June 2011, TBGT13646; 10 May 2013, TBGT14472; 3 October 2013, TBGT14823; 5 May 2014, TBGT14983; 11 July 2016 TBGT16390; 6 April 2022, TBGT18769.

*Specimens of Hausknechtia floriformis examined:* Vanuatu. Efate island, Blue Water beach, leg. I. Hausknecht, on sandy soil near *Pandanus* sp., 8 April 2003, WU 22832 (holotype); leg. A. Hausknecht, 10 April 2003, WU 22833 (paratype).



**Figure 4.** *Hausknechtia leucosticta*. (A) Basidiospores. (B) Basidia. (C) Pileipellis. (D) Cheilocystidia. Bars: (A–C) = 10  $\mu$ m, (D) = 20  $\mu$ m.

#### 4. Discussion

Although *Hausknechtia leucosticta* (*Coprinus leucostictus*) is rediscovered after almost a century, the number of its collections and localities found within this study showed that it is not a rare species. For example, during the study of Chinese psathyrelloid species, *H. leucosticta* was frequently collected during field research in the eastern and southern regions of the country. An insufficient level of fungal diversity research in southern and southeastern Asia is the most likely reason that the species has not been found again for so long.

Based on only one collection, a scarce original description, and a redescription of the holotype in very poor condition, knowledge of the morphology of *H. leucosticta* (especially microcharacters) was limited. The present study revealed morphological characters of *H. leucosticta* in detail. It is a rather unique taxon. The combination of coprinoid basidiomata, a veil consisting exclusively of strongly branched and diverticulate hyphae (Alachuanitype), and a hymeniderm pileipellis is not known in other species. The morphological characters of *H. leucosticta* collections studied (including the holotype) were not very variable. The same is true for ITS and  $\beta$ -tubulin gene regions. Based on the BLAST results, the identities among our five ITS sequences are 99.35–100%, and among our  $\beta$ -tubulin sequences are 99.37–100%. The homogeneity among four Chinese sequences is even higher: identities of 99.84–100% for ITS and 99.79–100% for  $\beta$ -tubulin. However, the identities between the Indian *tef-1 $\alpha$*  sequence on the one side and the Chinese *tef-1 $\alpha$*  sequences on the other are 96.66–96.93%. The homogeneity among Chinese *tef-1 $\alpha$*  sequences is much higher:

identities of 99.40–99.90%. Despite that, due to the high identity of ITS and  $\beta$ -tubulin gene regions, as well as the concordance of morphological characters, we consider that the Indian and Chinese collections belong to the same species characterized by somewhat greater *tef-1 $\alpha$*  variability.

Phylogenetic analysis showed that *H. leucosticta* and *H. floriformis* are closely related species. However, their morphological characters do not indicate such close relationship. Although both possess a dry, plicate-sulcate pileus with veil (at least when young), hymeniderm pileipellis, and lack pleurocystidia, there are many morphological differences. Among others, *H. floriformis* differs from *H. leucosticta* by strongly radially splitted and ragged pileus at maturity, deliquescent (easily collapsing) lamellae when old, elongated ellipsoid to cylindrical and yellowish-hyaline basidiospores without germ-pore, the absence of cheilocystidia and hymenophysalides, and by only occasionally branched, non-diverticulate veil hyphae [3,5].

The genus *Psathyrella* was treated in a broader sense by Voto [41]. He disagreed with Wächter & Melzer [1] who transferred members of *Psathyrella* section *Spintrigerae* in the new genus *Candolleomyces* and *Galerella floriformis* in the new genus *Hausknechtia*. Accordingly, he proposed a new combination *Psathyrella floriformis* (Hauskn.) Voto [41]. However, our multigene phylogenetic analysis recovered the two well supported monophyletic lineages (*Hausknechtia* and *Candolleomyces*) distant from the genus *Psathyrella* s. str., in agreement with study by Wächter & Melzer [1].

**Author Contributions:** Conceptualization, J.-Q.Y. and Z.T.; methodology, J.-Q.Y., Z.T., C.N., A.M. and A.P.; formal analysis, J.-Q.Y., Z.T., C.N., S.-N.W. and A.P.; investigation, J.-Q.Y., Z.T., C.N., A.P. and C.K.P.; resources, J.-Q.Y., Q.N., H.Z., Y.H., H.D., Y.G., G.H. and C.K.P.; data curation, Z.T., C.N., A.P. and C.K.P.; writing—original draft preparation, Z.T., J.-Q.Y., C.N., A.M. and A.P.; writing—review and editing, J.-Q.Y., Z.T., C.N. and A.M.; visualization, Z.T., J.-Q.Y. and A.P.; supervision, J.-Q.Y., Z.T., C.N. and A.M.; project administration, J.-Q.Y. and Z.T.; funding acquisition, A.M. and C.N. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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