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ORIGINAL ARTICLE

Four new species and a new record of nodulose-spored *Inocybe* (*Inocybaceae*, *Agaricales*) from Benin, West Africa

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Abstract

Inocybe is a globally distributed genus of ectomycorrhizal fungi that occurs in temperate and tropical regions. However, species diversity of the genus in Africa remains underexplored. In this study, four new nodulose-spored *Inocybe* species, *I. arenosa*, *I. basialba*, *I. liliputiana*, and *I. luteofusca*, from tropical regions of Benin in West Africa, are described and illustrated based on comprehensive morphological and molecular analyses. In addition, *I. glaucodisca,* originally described from Zambia (Southeast Africa), is reported for the first time from West Africa (Benin). All five *Inocybe* species occur in association with *Berlinia grandiflora* (*Fabaceae*). Multilocus molecular analyses of the nuclear ribosomal internal transcribed spacer region (nrITS), a partial of the nuclear ribosomal large subunit (nrLSU), and a segment of the RNA polymerase II second-largest subunit (*RPB2*) gene, confirm the distinctiveness of these four novel species and indicate their phylogenetic placement within *Inocybe*.

Keywords African taxa · Biodiversity · Biogeography · Ectomycorrhizal fungi · Four new species · Molecular phylogeny · Taxonomy

Introduction

Inocybaceae Jülich is among the most species-rich families within the order *Agaricales* Underw. (*Basidiomycota*), encompassing approximately 1070 identified species (Matheny and Kudzma 2019; Matheny et al. 2020; Bandini et al. 2020, 2021; Kaygusuz et al. 2024a; Gao et al. 2025; Zhu et al. 2025). The species of this family engage in ectomycorrhizal (ECM) relationships with a wide array of angiosperms and gymnosperms across tropical and temperate regions (Kuyper 1986; Matheny and Kudzma 2019; Matheny et al. 2020). Traditionally, the family included the genera *Auritella* Matheny & Bougher ex Matheny & Bougher, *Inocybe* (Fr.) Fr., and *Tubariomyces* Esteve-Rav. & Matheny (Matheny and Bougher 2006; Alvarado et al. 2010). However, recent phylogenetic studies based on multigene datasets (nrITS, nrSSU, nrLSU, *RPB1*, *RPB2*, and *TEF1-α*) uncovered new relationships within the family (Matheny et al. 2020). Consequently, *Inocybaceae* now consists of seven genera: *Auritella*, *Inocybe*, *Inosperma* (Kühner) Matheny & Esteve-Rav., *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav., *Nothocybe* Matheny & K.P.D. Latha,

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Pseudosperma Matheny & Esteve-Rav., and *Tubariomyces* (Matheny et al. 2020).

Inocybe is the largest genus of *Inocybaceae* and comprises over 870 known species (Matheny et al. 2020; Bandini et al. 2022; Kaygusuz et al. 2024a; Gao et al. 2025; Zhu et al. 2025). The genus is distributed widely across different terrestrial biomes on every continent except Antarctica (Larsson et al. 2014; Matheny et al. 2020; Bandini et al. 2021). It is distinguished from other genera in the family by the presence of pleurocystidia and angular to nodulose or spinose basidiospores.

While *Inocybe* species have been extensively documented in temperate regions of Europe, North America, and parts of Asia and Australia, the species diversity of the genus in Africa remains profoundly understudied. The continent, particularly its tropical regions, shows a significant gap in our understanding of this ECM genus. To date, 15 species of *Inocybe*, so far known only from Africa, have been formally described: *I. beninensis* Aïgnon, Yorou & M. Ryberg, and *I. flavipes* Aïgnon, Yorou & M. Ryberg are known from Benin (Aïgnon et al. 2022), *I. fuscobrunnea* Aïgnon, Yorou & M. Ryberg and *I. pallidiangulata* Aïgnon, Yorou & M. Ryberg from Burkina Faso (Aïgnon et al. 2022), *I. bipindiensis* Henn. from Cameroon (Hennings 1901), *I. sclerotiicola* R. Heim & Gilles from Gabon (Heim 1969), *I. ghanaensis* Pegler from Ghana (Pegler 1969), *I. tulearensis* L.M. Dufour & Poiss. from Madagascar (Dufour and Poisson 1927), *I. cyaneovirescens* Henn. from Tanzania (Hennings 1900), and *I. conspicuispora* Buyck & Eyssart., *I. densifolia* nom. prov., *I. glaucodisca* Buyck & Eyssart., *I. hebes* Eyssart. & Buyck, *I. leucophaea* Eyssart. & Buyck, and *I. media* Eyssart. & Buyck from Zambia (Buyck and Eyssartier 1999; Matheny et al. 2009; Buyck et al. 2022). The sparse records of these described species indicate that the true extent of diversity remains unexplored. This situation is supported by mycological research metadata indicating that the currently documented fungal diversity of identified species across West African countries represents less than 2% of the estimated total number of fungi (Piepenbring et al. 2020).

We conducted field surveys in Benin in order to understand the species diversity of *Inocybaceae* in Africa and enhance our knowledge of their evolutionary history by expanding the pool of reliably annotated barcode reference sequences. These surveys also revealed several noteworthy species of nodulose-spored *Inocybe* not previously recorded from the African continent. An integrative approach, combining morphological characteristics with multilocus phylogenetic analyses (nrITS + nrLSU + *RPB2*), confirmed that several *Inocybe* specimens recently collected in Benin are morphologically and genetically distinct from all known species within the genus.

Materials and methods

Field sampling and morphological studies

Fungal material examined in this study was obtained during a mycological survey conducted across Benin from June to August 2022. Macromorphological descriptions were based on fresh basidiomata, with documentation comprising field notes and in situ images; colour was documented using Munsell Soil Color Charts (Munsell 1975). For micromorphological analysis, dried specimens were mounted in either 1% Congo red (w/v) or 5% potassium hydroxide KOH (w/v) and examined under a compound light microscope for imaging and measurement. A minimum of thirty basidiospores was measured per collection. Results are presented as the basidiospore length-to-width ratio (Q) and mean dimensions for basidiospores and cystidia, supplemented by the standard deviation (SD) of the length × width. The descriptive terminology for morphological and microscopic characteristics follows the conventions of Vellinga (1988) and Matheny & Bougher (2017). The holotypes of all examined specimens from Benin are stored in the fungarium of the Staatliches Museum für Naturkunde Stuttgart (STU), while the isotypes are deposited in the mycological herbarium of the University of Parakou (UNIPAR).

Molecular analyses

Genomic DNA extraction was conducted using the innuPREP Plant DNA Kit (Analytik Jena, Germany) according to the manufacturer's protocol. Amplification of targeted loci was achieved using specific primer pairs: the nuclear ribosomal internal transcribed spacer (ITS) region, encompassing ITS1-5.8S-ITS2, was amplified with primers ITS1F/ITS4 (White et al. 1990; Gardes and Bruns 1993); the 28S large subunit (LSU) ribosomal DNA with LR0R/LR5 (Vilgalys and Hester 1990; Rehner and Samuels 1994); and the second largest subunit of RNA polymerase II (*RPB2*) with *RPB2*−6F/*RPB2*−7.1R (Matheny 2005). Polymerase chain reaction (PCR) amplification was carried out following the protocols adopted by Matheny (2005) and Kaygusuz et al. (2020). After amplification, the PCR products were purified and subjected to bidirectional Sanger sequencing at a commercial facility (Microsynth Seqlab, Göttingen, Germany), using the same primer sets. After sequencing, the resulting chromatograms were edited and assembled using MEGA X v.10.0.5 (Kumar et al. 2018) and BioEdit (Hall 1999). The newly generated sequences were deposited in the GenBank database under respective accession numbers.

Novel nucleotide sequences generated in this study were queried against the GenBank (www.ncbi.nlm.nih.gov)

database using the BLASTn algorithm to identify closely related taxa within *Inocybe*. The top BLAST hits, exhibiting significant sequence similarity, were selected for inclusion in subsequent phylogenetic reconstruction (Table 1). *Pseudosperma beninense* Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr. (AR-22–037) and *P. indicum* K.P.D. Latha, Haridev & Manim. (DKP-SERB109) were used as outgroups. In the phylogenetic analyses, taxonomic labels (section, subclade, and group) were assigned according to Matheny and Bougher (2017), except for sect. *Umbraticae*, which follows Chen et al. (2024). The sequences were aligned using MAFFT 7 (https://mafft.cbrc.jp/alignment/server/) under the E-INS-i strategy for the nrITS and nrLSU loci, and the FFT-NS-i strategy for *RPB2* (Katoh et al. 2019). The resulting alignments were manually edited as necessary in AliView V.1.28 (Larsson 2014). Subsequently, ambiguous regions at the termini of each alignment were trimmed, and the individual locus alignments were concatenated using SeaView version 5.0.5 (Gouy et al. 2021) for multilocus phylogenetic analyses. The best-fit evolutionary models for each locus were estimated using MrModeltest 2.3 (Nylander 2004).

Phylogenetic reconstruction was performed on the concatenated dataset with Maximum Likelihood (ML) and Bayesian Inference (BI) frameworks. The ML analysis was executed in RAxML-HPC2 8.2.9 (Stamatakis 2014) on the CIPRES Science Gateway portal (Miller et al. 2010) under the GTRGAMMAI model, employing a rapid bootstrap algorithm with 1000 replicates to assess nodal support. Concurrently, BI analysis was conducted using MrBayes 3.2.5 (Ronquist et al. 2012), running two simultaneous Markov Chain Monte Carlo (MCMC) analyses over 3.0 million generations, with trees sampled every 1,000th generation. Stationarity and convergence were confirmed by ensuring the average standard deviation of split frequencies fell below 0.01. The resulting phylogenetic trees were visualized and arranged in FigTree v1.4.4 (Rambaut 2018).

Results

Phylogeny

The concatenated dataset of nrITS, nrLSU, and *RPB2* sequences, incorporating 17 novel sequences (six nrITS, six nrLSU, and five *RPB2*) from Benin specimens, encompasses 3381 nucleotide positions (including gaps) for 106 *Inocybe* specimens. Of these, 1004 characters were parsimony-informative, 247 were parsimony-uninformative, and 2130 were constant. The optimal substitution model, GTR + I + G, was applied to each genetic locus (nrITS, nrLSU, and *RPB2*). Phylogenetic reconstructions based on ML and BI yielded largely congruent topologies. The ML-derived topology was chosen for depiction, with statistical support indicated by Maximum Likelihood Bootstrap (MLB) and Bayesian Posterior Probability (BPP) values (Fig. 1).

Molecular analyses of the concatenated dataset revealed that the *Inocybe* specimens from Benin exhibit significant genetic divergence from other species within the genus represented in molecular sequence databases. These specimens cluster into four distinct evolutionary lineages, as illustrated in Fig. 1. The first phylogenetic lineage (MLB = 100%, BPP = 1.0) comprises the type sequence of *Inocybe glaucodisca* (EG96081) from Zambia, a sequence from Benin (AR-22–055) that constitutes a new geographical record for West Africa, and three previously undescribed and unpublished *Inocybe* sequences (d763c375, ASV_99, and ASV_463). The second lineage, with strong statistical support (MLB = 100%, BPP = 1.0), includes the novel species *I. arenosa* (AR-22–081) from Benin, as well as three undescribed and unpublished *Inocybe* sequences (ASV_211, ASV_516, and ASV_545). *Inocybe arenosa* and *I. glaucodisca* are nested in the same subclade and are sister species to each other. The third lineage (MLB = 99%, BPP = 1.0) consists of another new species *I. basialba* (AR-22–098) from Benin. It is phylogenetically sister to a subclade containing *I. densifolia* nom. prov. (EG96039) and *I. leucophaea* from Zambia. The fourth lineage (MLB = 100%, BPP = 1.0) consists of two collections of *I. luteofusca* from Benin (AR-22–003 and AR-22–004) and forms a distinct branch separate from other known *Inocybe* species. The final lineage comprises *I. liliputiana* from Benin (AR-22–042). It forms a distinct branch that is sister to the section *Calosporae*, which includes species such as *I. calospora* Quél., *I. hopeae* Raghoon. & Raspé, *I. spiniformis* Matheny & Bougher, and *I. thailandica* E. Horak, Matheny & Desjardin.

Taxonomy

Inocybe arenosa Kaygusuz, Bandini, Rühl & M. Piepenbr., sp. nov. (Figs. 2 and 3).

MycoBank: MB861574.

Etymology: The specific epithet "*arenosa*" (Latin) refers to the sandy places where the specimens were found.

Holotype: Benin, Atakora, Kota Waterfall, on sandy ground in a gallery forest dominated by *Berlinia grandiflora* Hutch. & Dalziel, at 10°12′43.5"N, 001°26′36.6"E, 501 m a.s.l., 26 June 2022, leg. A. Rühl, D. Dongnima, F. Hampe, C. Manz & S. Sarawi (AR-22–081, STU, isotype in UNIPAR). GenBank accession numbers PX685950 (nrITS), PX685956 (nrLSU), and PX684958 (*RPB2*).

Diagnosis: Differs from all previously known nodulose-spored species in the African tropics by its strongly squamulose pileus becoming coarsely fibrillose with age, lamellae with pallid-fimbriate edges, pyriform caulocystidia,

Table 1 List of specimens of *Inocybe* considered for the molecular analyses, with voucher specimen numbers, country of origin, GenBank accession numbers of nrITS, nrLSU, and *RPB2* gene sequences, and corresponding literature references. Newly generated sequences are indicated in bold. In the table, the em dash (—) indicates that data are not available

Species	Voucher/strain number	Geographical origin	GenBank accession numbers			References
			nrITS	nrLSU	*RPB2*	
I. ailaoensis	FYG2015385	China	PP217739	PP230780	PP238456	Chen et al. 2024
I. angustifolia	DED8139 (SFSU)	Thailand	GQ892988	GQ892942	MH577422	Horak et al. 2015, Matheny and Kudzma 2019
I. arenosa	**AR-22–081**	**Benin**	**PX685950**	**PX685956**	**PX684958**	**This study**
I. arenosa	ASV_211	West Africa	LR993528	LR993528	—	Meidl et al. 2021
I. arenosa	ASV_516	West Africa	LR993833	LR993833	—	Meidl et al. 2021
I. arenosa	ASV_545	West Africa	LR993862	LR993862	—	Meidl et al. 2021
I. argenteolutea	EL9906	Sweden	FN550889	FN550889	—	Ryberg et al. 2010
I. asterospora	EL100-14	Sweden	KY440098	KY549128	—	GenBank, unpublished
I. aurea	EL14206	Sweden	FN550877	FN550877	—	Ryberg et al. 2010
I. australiensis	PBM3246	Australia	KJ756468	KJ756433	—	Matheny and Bougher 2017
I. avellaneifolia	PBM3648	Australia	KJ756475	KJ756440	KJ729951	Matheny and Bougher 2017
I. ayangannae	MCA 1232	Guyana	—	AY239018	AY337364	Matheny et al. 2009
I. basialba	**AR-22–098**	**Benin**	**PX685951**	**PX685957**	**PX684959**	**This study**
I. beninensis	HLA0390	Benin	MN096196	MN097888	—	Aïgnon et al. 2022
I. boreoaustralis	PBM3777	Australia	KF830044	KF808358	KF830060	Matheny and Bougher 2017
I. brevicula	NLB256	Australia	KJ756478	—	KJ729950	Matheny and Bougher 2017
I. brevisquamulosa	ZT10102	Thailand	GQ893019	GQ892974	PQ625751	Horak et al. 2015, GenBank, unpublished
I. calida	TAA185175	Estonia	AM882760	AM882760	—	Ryberg et al. 2008
I. calocephala	PBM3600	Australia	—	KJ756455	KJ756413	Matheny and Bougher 2017
I. calospora	JFA 12539	Sweden	—	AY038313	AY337365	Matheny et al. 2022
I. campestris	PBM3689	Australia	KJ778842	KJ756460	KJ756418	Matheny and Bougher 2017
I. castanea	Bau20140711	China	KU366499	—	—	GenBank, unpublished
I. cerasphora	BSI 01/184	Chile	—	AY380370	AY337367	Matheny 2005
I. chondroderma	PBM1776	USA	GU949579	JN974967	MH249789	Matheny et al. 2013
I. conspicuispora (as *conspicuospora*)	96042	Zambia	—	EU555471	EU555470	Matheny et al. 2009
I. dabaensis	YZ2023102844	China	PP993809	PP993852	PQ001020	Chen et al. 2024
I. densifolia nom. prov.	EG96039	Zambia	—	EU555474	EU555473	Matheny et al. 2009
I. diabolica	EL9006	Sweden	FN550896	FN550896	—	Ryberg et al. 2010
I. eburnea	PBM3367	Australia	KJ778851	KJ801162	KJ756424	Matheny and Bougher 2017
I. elata	HMJAU01	China	MG744559	—	—	Liu et al. 2018
I. emergens	NLB896	Australia	—	KJ729915	KJ729943	Matheny and Bougher 2017
I. epidendron	TH9186	Guyana	JN168725	EU569840	—	Matheny et al. 2009
I. flavipes	MR00383	Togo	MN096197	MN097889	MW080915	Aïgnon et al. 2022
I. flavoalbida	PBM3768	Australia	KJ729873	KJ729901	KJ729932	Matheny and Bougher 2017
I. flavosquamulosa	CAL1353	India	KY440087	KY549117	—	Latha and Manimohan 2017

Table 1 (continued)

Species	Voucher/strain number	Geographical origin	GenBank accession numbers			References
			nrITS	nrLSU	*RPB2*	
I. floccosistipitata	CAL1256	India	KY440089	KY549119	—	Latha and Manimohan 2017
I. fragilis	PBM3662	Australia	KF830029	KF808341	KF830047	Matheny and Bougher 2017
I. fulvilubrica	PBM3352	Australia	—	JQ085922	—	Bougher et al. 2012
I. fuscobrunnea	MR00378	Burkina Faso	MN096201	MN097893	MW219733	Aïgnon et al. 2022
I. giacomi	JV21543	Finland	MK153656	MK153656	—	Cripps et al. 2020
I. glaucodisca	**AR-22–055**	**Benin**	**PX685952**	**PX685958**	**—**	**This study**
I. glaucodisca	EG96081	Zambia	PQ526671	—	—	GenBank, unpublished
I. glaucodisca	d763c375	Benin	HG996250	HG996250	—	GenBank, unpublished
I. glaucodisca	ASV_99	West Africa	LR993416	LR993416	—	Meidl et al. 2021
I. glaucodisca	ASV_463	West Africa	LR993780	LR993780	—	Meidl et al. 2021
I. hopeae	OR1665	Thailand	—	ON831503	ON553692	Raghoonundon et al. 2023
I. insulana	CAL1258	India	KY440092	KY549122	—	Latha and Manimohan 2017
I. keteleeriicola	FYG2884	China	PP217732	PP230769	PP238448	Chen et al. 2024
I. kurkuriya	CAL1352	India	KY440095	KY549125	—	Latha and Manimohan 2017
I. lacera	PBM2541	USA	KP171144	JN974993	KM245991	Matheny and Bougher 2017, Ryberg and Matheny 2012
I. lacunarum	JV12244	Finland	KT958908	KT958908	—	Vauras and Larsson 2015
I. lanuginosa	PBM3023	USA	HQ232480	KP170923	KM245992	GenBank, unpublished
I. leptospermi	PBM3628	Australia	KP308758	KP170935	KJ811592	Matheny and Bougher 2017
I. leucophaea	EG96095	Zambia	—	EU569860	—	Matheny et al. 2009
I. lilacinosquamosa	MCA 1464	Guyana	—	AY380386	AY337389	Matheny 2005
I. liliputiana	**AR-22–042**	**Benin**	**PX685953**	**PX685959**	**PX684960**	**This study**
I. lineata	DED8048	Thailand	—	GQ892958	KM245999	Horak et al. 2015
I. luteofusca	**AR-22–003**	**Benin**	**PX685954**	**PX685960**	**PX684961**	**This study**
I. luteofusca	**AR-22–004**	**Benin**	**PX685955**	**PX685961**	**PX684962**	**This study**
I. lutosa	FYG2015298	China	PP993814	PP993851	—	Chen et al. 2024
I. media	96083	Zambia	—	EU600884	—	Horak et al. 2015
I. meirensongia	FYG3777	China	MZ322672	MZ322669	MZ336924	Bhunjun et al. 2022
I. melanopus	PBM3975	USA	—	MH220276	MH249807	Matheny and Kudzma 2019
I. meridionalis	PBM3413	Australia	KF977204	KF915281	KF991377	Matheny and Bougher 2017
I. mixtilis	ARAN-Fungi 4711	Spain	MH500842	MH500842	MH496022	Esteve-Raventós et al. 2018
I. multicoronata	DG1818A	Canada	MH578007	MH539763	—	GenBank, unpublished
I. muthangensis	K(M) 191735	India	KM924521	KM924516	KY553247	Latha and Manimohan 2017
I. nothomixtilis	AH 46558	Spain	KX290786	—	MH496025	Esteve-Raventós et al. 2018
I. obtusiuscula	PAM02081710	France	HQ586869	HQ641112	—	GenBank, unpublished
I. occulta	AH36443	Spain	KX290787	—	—	Esteve-Raventós et al. 2018
I. olivaceonigra	T. Bau & Y.G. Fan 2011131	China	JX025775	—	—	Fan and Bau 2013
I. pallidiangulata	MR00377	Burkina Faso	MN096202	MN097894	MW219732	Aïgnon et al. 2022

Table 1 (continued)

Species	Voucher/strain number	Geographical origin	GenBank accession numbers			References
			nrITS	nrLSU	*RPB2*	
I. paludinella	9774	Italy	JF908135	—	—	Osmundson et al. 2013
I. parvibulbosa	ZT10099	Thailand	GQ893000	GQ892955	—	Horak et al. 2015
I. parvifulva	PBM3783	Australia	KP308805	KP170972	—	Matheny and Bougher 2017
I. persicinipes	PBM2197	Australia	KF977215	EU600837	—	Matheny and Bougher 2017, Matheny et al. 2009
I. pileosulcata	CAL1362	India	KY440098	KY549128	—	Latha and Manimohan 2017
I. pingala	CAL:1345	India	KY440100	KY549130	KY553248	Latha and Manimohan 2017
I. pluppiana	STU:SMNS-STU-F-0901729	Netherlands	OP164088	OP164088	—	Bandini et al. 2022
I. pluvialis	PBM3227	Australia	KF871774	KF853398	KF891951	Matheny and Bougher 2017
I. pulchella	MCA 1122	Guyana	—	EU600842	—	Matheny et al. 2009
I. pygmaeformis	PBM3233	Australia	KF830036	KF808348	—	Matheny and Bougher 2017
I. relicina	HA15	Latvia	KR019846	—	—	Gaitnieks et al. 2016
I. rufobadia	NLB885	Australia	KF977213	KF915290	KF991385	Matheny and Bougher 2017
I. sejuncta	PERTH:08383103	Australia	—	KP171001	KM555102	Matheny and Bougher 2017
I. serrata	PBM3235	Australia	KP636810	KP171012	KM555111	Matheny and Bougher 2017
I. serratoides	PBM3422	Australia	KP636829	KP171033	KM555129	Matheny and Bougher 2017
I. sinuospora	E5980	Australia	JQ085936	EU600861	—	Bougher et al. 2012
I. snigdha	CAL1350	India	KY440105	KY549135	KY553250	Latha and Manimohan 2017
I. spiniformis	PBM3748	Australia	KP636868	KP171064	KM656103	Matheny and Bougher 2017
I. stellatospora	EL3004	Sweden	AM882747	AM882747	—	Ryberg et al. 2008
I. subangustifolia	BRI:794269	Australia	KP636870	KP171067	KM656112	Matheny and Bougher 2017
I. subcarpta	EL8905	Finland	AM882754	AM882754	—	Matheny et al. 2013
I. sylvicola	PBM3387	Australia	KP641630	JQ313576	KM656126	Horak et al. 2015, Matheny and Bougher 2017
I. tenax	PDD:72619	New Zealand	KY827285	KY827243	—	Horak 2018
I. thailandica	DED8049	Thailand	GQ893013	GQ892968	KM656129	Horak et al. 2015
I. torresiae	PBM 2157/E6978	Australia	—	EU600874	EU600873	Horak et al. 2015
I. aff. *torresiae*	MEL:2382851	Australia	KP012726	—	—	GenBank, unpublished
I. umbratica	BJ920804	Sweden	AM882799	—	—	Ryberg et al. 2008
I. viraktha	CAL:1357	India	KY440107	KY549137	KY553252	Latha and Manimohan 2017
I. viscata	PDD:27109	New Zealand	GU233318	—	—	GenBank, unpublished
I. xanthomelas	G00127626	France	ON227438	—	—	Esteve-Raventós et al. 2022
Inocybe sp.	REH7418	Costa Rica	KP636854	JN974931	—	Matheny and Bougher 2017

Table 1 (continued)

Species	Voucher/strain number	Geographical origin	GenBank accession numbers			References
			nrITS	nrLSU	*RPB2*	
Inocybe sp.	M:0138287	Papua New Guinea	KP636862	—	KM656100	Matheny and Bougher 2017
Pseudosperma beninense	AR-22–037	Benin	PP060393	PP060408	PP430968	Kaygusuz et al. 2024b
Pseudosperma indicum	DKP-SERB109 (CALI)	India	OR243200	OR243199	OR253891	Latha et al. 2023

and globose to ellipsoid cauloparacystidia, as well as by its unique nrITS, nrLSU, and *RPB2* sequences.

Description: Pileus 10–27 mm wide, convex when young, then expanded to nearly plane, without an umbo; margin decurved, often eroded on older specimens; velipellis absent; surface strongly squamulose, sometimes with coarsely fibrillose, covered with soil particles, not translucent-striate; colour brownish yellow to pale brown (2.5Y 7/6, 7.5YR 6/6–10). *Lamellae* L = 32–46, I = 1–3, moderately close to close, ventricose, up to 3 mm broad, adnexed, very light brown to pale straw yellow, with more or less pallid-fimbriate, whitish edge. *Stipe* 15–40 × 3–6 mm, cylindrical to slightly widened towards the base, pale straw or very light brown, pruinose on the upper half but rather sparse towards the middle. *Cortina* not observed. *Context* fibrillose, white or whitish in stipe and pileus, unchanging upon exposure. *Colour of exsiccata* pileus whitish, lamellae and stipe with brownish tinge, no darkening when dried. *Smell* (sub)spermatic. *Taste* not distinctive.

Basidiospores 7.0–10.5 µm (av. 8.3 µm, SD 0.7 µm) × 4.8–6.8 µm (av. 5.6 µm, SD 0.2 µm), Q = 1.1–2.0 (av. 1.5, SD 0.2) (n = 85 of 1 coll.), heterodiametric, with nodulose profile, each spore with 6–10, obtuse, rounded to broadly conical knobs on one side of its surface, pale yellowish brown in 5% KOH. *Basidia* 20–30 × 7.5–9.5 µm, clavate, generally 4-spored, rarely 2-spored, hyaline. *Pleurocystidia* 45–55 µm (av. 50 µm, SD 2.1 µm) × 10–14 µm (av. 11.5 µm, SD 3.5 µm), Q = 3.8–5.5 (av. 4.5, SD 0.4) (n = 48 of 1 coll.), mostly (sub)utriform, (sub)fusiform and (sub)lageniform, usually without a neck or with a rather short neck, crystalliferous, bases often rounded, walls up to 4.0 µm thick, light yellow-green in 5% KOH. *Lamellar edge* with cheilocystidia and paracystidia. *Cheilocystidia* 40−55 × 12−22 µm (n = 45 of 1 coll.), (sub)fusiform, (sub)lageniform or (sub)utriform, base truncate or with short pedicel, often with curved neck, apex usually crystalliferous, thick-walled, light yellow-green in 5% KOH. *Paracystidia* numerous, 10−17 × 6−8 µm (n = 30 of 1 coll.), oblong to ellipsoid, sometimes subglobose, hyaline, thin-walled. *Pileipellis* a cutis consisting of narrow cylindrical hyphae, 4–10 µm wide, terminal elements fusiform with mucronate apex, without incrusted walls, brownish yellow intracellular pigment in 5% KOH. *Oleiferous hyphae* not observed. *Caulocystidia* only near the apex of the stipe, 65–85 × 12–35 µm, mostly pyriform with a very obtuse base, with crystals, thick-walled, light yellow-green in 5% KOH. *Cauloparacystidia* numerous, occurring in dense clusters, 8.5−15 × 7−15 µm, mostly globose, subglobose to ellipsoid, thin-walled, very light yellow-green in 5% KOH. *Clamps* present at all septa.

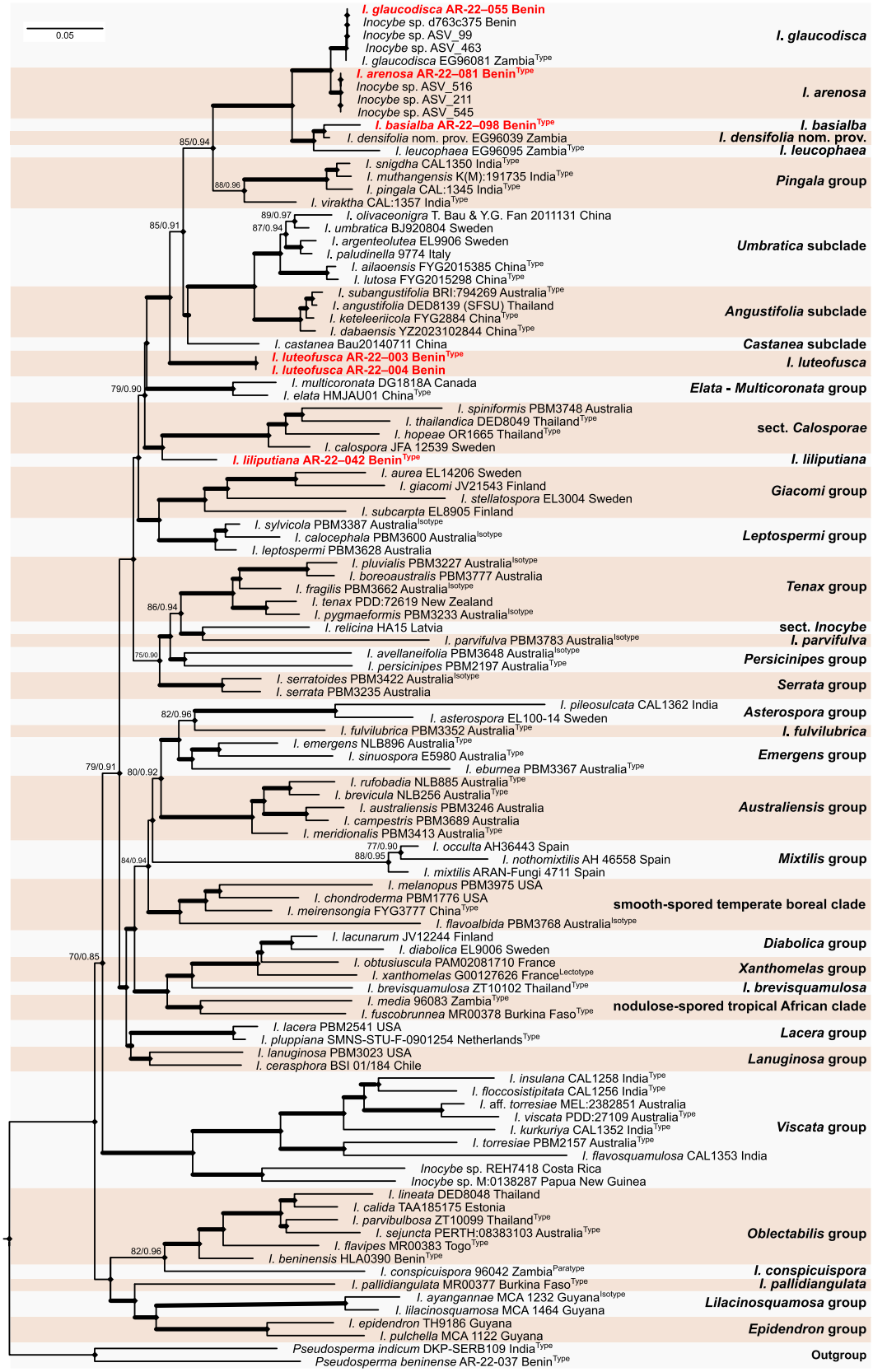
Habit, habitat, and distribution: Basidiomata subgregarious, usually terrestrial, on wet and sandy soils, under *Berlinia grandiflora*. Hitherto only known from Benin and from environmental sequences (ASV_211, ASV_516, and ASV_545) deposited in GenBank. The sequences were obtained from a set of soil samples collected in West Africa (Meidl et al. 2021).

Remarks: Inocybe arenosa is characterised by the following combination of features: small basidiomata with a strongly squamulose pileus that becomes coarsely fibrillose with age, lamellae with pallid-fimbriate edges, basidiospores adorned with numerous hemispherical knobs, each with 6–10 distinct nodules on one side, pyriform caulocystidia restricted to the stipe apex, and the presence of globose to ellipsoid cauloparacystidia.

The nrITS sequence of *I. arenosa* from Benin is identical (99.85–100% similarity) to three sequences (ASV_211, ASV_516, and ASV_545) stored in GenBank. These sequences were derived from West African soil samples (Meidl et al. 2021).

Multigene phylogenetic analyses reveal that *I. arenosa* is most closely related to *I. glaucodisca,* originally described from Zambia, with strong support (MLB = 100%, BPP = 1.0, Fig. 1). Although closely related, *I. arenosa* differs from *I. glaucodisca* by 26 nucleotide positions in the nrITS region, corresponding to a 96% sequence similarity. Morphologically, *I. glaucodisca* differs from *I. arenosa* by the pileus typically with a glaucous grayish umbo, an entirely pruinose stipe with a marginate bulb, slightly smaller basidiospores (7.0–9.0 × 5.0–7.5 µm), and subcylindrical to sublageniform caulocystidia (Buyck and Eyssartier 1999). *Inocybe glaucodisca* was found in open areas of miombo woodland (Buyck and Eyssartier 1999).

Phylogenetic analyses generated from the combined nrITS, nrLSU, and *RPB2* dataset indicate that *Inocybe arenosa* is closely related to two additional African species, i.e., *I. leucophaea* and *I. basialba*, with high statistical


0.05
I. glaucodisca AR-22–055 Benin
Inocybe sp. d763c375 Benin
Inocybe sp. ASV_99
Inocybe sp. ASV_463
I. glaucodisca EG96081 Zambia Type
I. glaucodisca
I. arenosa AR-22–081 Benin Type
Inocybe sp. ASV_516
Inocybe sp. ASV_211
Inocybe sp. ASV_545
I. arenosa
I. basialba AR-22–098 Benin Type
I. basialba
I. densifolia nom. prov. EG96039 Zambia
I. densifolia nom. prov.
I. leucophaea EG96095 Zambia Type
I. leucophaea
I. snigdha CAL1350 India Type
I. muthangensis K(M):191735 India Type
I. pingala CAL:1345 India Type
I. viraktha CAL:1357 India Type
Pingala group
I. olivaceonigra T. Bau & Y.G. Fan 2011131 China
I. umbratica BJ920804 Sweden
I. argenteolutea EL9906 Sweden
I. paludinella 9774 Italy
I. ailaoensis FYG2015385 China Type
I. lutosa FYG2015298 China Type
Umbratica subclade
I. subangustifolia BRI:794269 Australia Type
I. angustifolia DED8139 (SFSU) Thailand
I. keteleeriicola FYG2884 China Type
I. dabaensis YZ2023102844 China Type
Angustifolia subclade
I. castanea Bau20140711 China
Castanea subclade
I. luteofusca AR-22–003 Benin Type
I. luteofusca AR-22–004 Benin
I. luteofusca
I. multicoronata DG1818A Canada
I. elata HMJAU01 China Type
Elata - Multicoronata group
I. spiniformis PBM3748 Australia
I. thailandica DED8049 Thailand Type
I. hopeae OR1665 Thailand Type
I. calospora JFA 12539 Sweden
sect. Calosporae
I. liliputiana AR-22–042 Benin Type
I. liliputiana
I. aurea EL14206 Sweden
I. giacomi JV21543 Finland
I. stellatospora EL3004 Sweden
I. subcarpta EL8905 Finland
Giacomi group
I. sylvicola PBM3387 Australia Isotype
I. calocephala PBM3600 Australia Isotype
I. leptospermi PBM3628 Australia
Leptospermi group
I. pluvialis PBM3227 Australia Isotype
I. boreoaustralis PBM3777 Australia
I. fragilis PBM3662 Australia Isotype
I. tenax PDD:72619 New Zealand
I. pygmaeformis PBM3233 Australia Isotype
Tenax group
I. relicina HA15 Latvia
sect. Inocybe
I. parvifulva PBM3783 Australia Isotype
I. parvifulva
I. avellaneifolia PBM3648 Australia Isotype
I. persicinipes PBM2197 Australia Type
Persicinipes group
I. serratoides PBM3422 Australia Isotype
I. serrata PBM3235 Australia
Serrata group
I. pileosulcata CAL1362 India
I. asterospora EL100-14 Sweden
Asterospora group
I. fulvilubrica PBM3352 Australia Type
I. fulvilubrica
I. emergens NLB896 Australia Type
I. sinuospora E5980 Australia Type
I. eburnea PBM3367 Australia Type
Emergens group
I. rufobadia NLB885 Australia Type
I. brevicula NLB256 Australia Type
I. australiensis PBM3246 Australia
I. campestris PBM3689 Australia
I. meridionalis PBM3413 Australia Type
Australiensis group
I. occulta AH36443 Spain
I. nothomixtilis AH 46558 Spain
I. mixtilis ARAN-Fungi 4711 Spain
Mixtilis group
I. melanopus PBM3975 USA
I. chondroderma PBM1776 USA
I. meirensongia FYG3777 China Type
I. flavoalbida PBM3768 Australia Isotype
smooth-spored temperate boreal clade
I. lacunarum JV12244 Finland
I. diabolica EL9006 Sweden
Diabolica group
I. obtusiuscula PAM02081710 France
I. xanthomelas G00127626 France Lectotype
Xanthomelas group
I. brevisquamulosa ZT10102 Thailand Type
I. brevisquamulosa
I. media 96083 Zambia Type
I. fuscobrunnea MR00378 Burkina Faso Type
nodulose-spored tropical African clade
I. lacera PBM2541 USA
I. pluppiana SMNS-STU-F-0901254 Netherlands Type
Lacera group
I. lanuginosa PBM3023 USA
I. cerasphora BSI 01/184 Chile
Lanuginosa group
I. insulana CAL1258 India Type
I. floccosistipitata CAL1256 India Type
I. aff. torresiae MEL:2382851 Australia
I. viscata PDD:27109 Australia Type
I. kurkuriya CAL1352 India Type
I. torresiae PBM2157 Australia Type
I. flavosquamulosa CAL1353 India
Inocybe sp. REH7418 Costa Rica
Inocybe sp. M:0138287 Papua New Guinea
Viscata group
I. lineata DED8048 Thailand
I. calida TAA185175 Estonia
I. parvibulbosa ZT10099 Thailand Type
I. sejuncta PERTH:08383103 Australia Type
I. flavipes MR00383 Togo Type
I. beninensis HLA0390 Benin Type
Oblectabilis group
I. conspicuispora 96042 Zambia Paratype
I. conspicuispora
I. pallidiangulata MR00377 Burkina Faso Type
I. pallidiangulata
I. ayangannae MCA 1232 Guyana Isotype
I. lilacinosquamosa MCA 1464 Guyana
Lilacinosquamosa group
I. epidendron TH9186 Guyana
I. pulchella MCA 1122 Guyana
Epidendron group
Pseudosperma indicum DKP-SERB109 India Type
Pseudosperma beninense AR-22-037 Benin Type
Outgroup
85/0.94
88/0.96
89/0.97
87/0.94
85/0.91
79/0.90
82/0.96
86/0.94
75/0.90
79/0.91
80/0.92
77/0.90
88/0.95
84/0.94
70/0.85
82/0.96

◂**Fig. 1** Phylogenetic position of the Beninese collections of *Inocybe* based on a Maximum Likelihood (ML) and Bayesian Inference (BI) analyses of combined nrITS, nrLSU, and *RPB2* sequences. The tree is rooted with *Pseudosperma beninense* (AR-22–037) and *P. indicum* (DKP-SERB109). Maximum Likelihood Bootstrap (MLB) ≥ 70% and Bayesian Posterior Probabilities (BPP) ≥ 0.85 values are indicated on the branches. Branches with significant support (MLB ≥ 90% and BPP ≥ 0.95) in both analyses are thickened. Beninese collections are highlighted in red-boldface

support (MLB = 100%, BPP = 1.0). Morphologically, *Inocybe leucophaea* differs from *I. arenosa* by a darker pileus colour, presence of an abundant veil, marginate stipe, basidiospores with less prominent knobs, and pileipellis with incrusted hyphae (Buyck et al. 2022). The novel species *I. basialba* (see below) has slender basidiomata, brownish-orange to yellow-ochre pileus with a distinctly conical umbo, considerably longer basidiospores (on av. 10.1 × 8.0 µm), fusiform pleurocystidia, oleiferous hyphae, and caulocystidioid hairs.

Two other tropical African *Inocybe* species are somewhat similar to *I. arenosa* in having a brown-toned pileus and nodulose basidiospores. One of these, *I. ghanaensis,* first described from Ghana, is distinguished by the larger basidiomata (pileus up to 45 mm wide), a slender longitudinally silky-striate stipe, slightly shorter basidiospores (on av. 8.0 × 5.2 µm) with less prominent knobs, and cylindrical to lageniform caulocystidia (Pegler 1969). The second species, *I. sclerotiicola*, originally described from the rainforests of Gabon, differs from the new species presented here by the stipe with a marginate basal bulb, shorter basidiospores (6.5–8.0 × 5.2–7.6 µm), and predominantly subcylindrical to ellipsoid pleuro- and cheilocystidia (Heim 1969).

Inocybe cyaneovirescens, a species originally described from Tanzania, is easily distinguished by its blue pileus that turns green when injured, an olive-brown basidiospores print, and markedly longer, subglobose basidiospores measuring 10.0–13.0 × 9.0–12.0 µm (Hennings 1900). Another African species, *I. bipindiensis,* described from Cameroon, is characterized by a chestnut-brown pileus with a tomentose-scaly surface, a grey-brown stipe, and significantly shorter basidiospores (5.0–7.0 × 3.5–4.0 µm) (Hennings 1901).

Inocybe basialba Kaygusuz, Bandini, Rühl & M. Piepenbr., sp. nov. (Figs. 4 and 5).

MycoBank: MB861575.

Etymology: The specific epithet "*basialba*" refers to the white base of the stipe.

Holotype: Benin, Bassila gallery forest, on the ground in forest dominated by *Berlinia grandiflora*, at 09°00′04.8"N, 001°38′57.4"E, 363 m a.s.l., 02 June 2022, leg. A. Rühl, D. Dongnima, C. Manz, F. Hampe & S. Sarawi (AR-22–098, STU, isotype in UNIPAR). GenBank accession numbers PX685951 (nrITS), PX685957 (nrLSU), and PX684959 (*RPB2*).

Diagnosis: Most similar to *I. conspicuispora* but differing by a more conical pileus, a distinctly longer stipe with a white base, lamellae with decurrent teeth, basidiospores with 8–15 distinct conical nodules, predominantly fusiform to broadly fusiform pleurocystidia, oleiferous hyphae with encrusted walls, differently shaped caulocystidioid hairs, and distinct nrITS, nrLSU, and *RPB2* sequences.

Description: Pileus 40–50 mm wide, highly conical to broadly conical, becoming almost broadly conico-campanulate with age and developing a pronounced bluntly conical umbo; margin initially inflexed, later reflexed; velipellis absent or with an inconspicuous to conspicuous brownish area over the disc when young; surface dry, smooth to minutely innately fibrillose at the margin with age; margin radially cracked, margin somewhat excoriated and therefore appearing striate; colour brownish orange to yellow-ochre (2.5Y 7/8–10, 5YR 5/8–10, 4/8). *Lamellae* L = 60–80, I = 1(–3), rather crowded, emarginate to emarginate with decurrent teeth, uniformly brownish orange; edges entire, whitish. *Stipe* 75–100 × 4–8 mm, cylindrical or broadened at the apex and somewhat thinner at the basis, somewhat swollen to subbulbous at the base; surface dry, pruinose, especially in the upper part, light greyish orange to very light yellow brown, white at the basis. *Cortina* not observed. *Context* solid, whitish in stipe and pileus, unchanging upon exposure. *Colour of exsiccata* pileus and stipe pallid, lamellae very light yellowish brown, with no darkening when dried. *Smell* spermatic. *Taste* not remarkable.

Basidiospores 8.0–13.0 µm (av. 10.1 µm, SD 0.7 µm) × 7.0–10.0 µm (av. 8.0 µm, SD 0.6 µm), Q = 1.0–1.5 (av. 1.3, SD 0.1) (n = 100 of 1 coll.), heterodiametric, distinctly nodulose with mostly 8–12(–15) large conical nodules on each side, to 2–3 µm high, yellowish brown in 5% KOH. *Basidia* 25–30 × 8.0–10 µm, clavate, 4-spored, hyaline, thin-walled. *Pleurocystidia* numerous, 50–60 µm (av. 55 µm, SD 2.0 µm) × 11–16 µm (av. 14 µm, SD 2.1 µm), Q = 2.9–4.6 (av. 3.5, SD 0.5) (n = 55 of 1 coll.), mostly fusiform to broadly fusiform, apex crystalliferous, often with broadly truncate base, walls up to 5.5 µm thick near the apex, intensely yellow-green in 5% KOH. *Lamellar edge* sterile, with cheilocystidia and paracystidia. *Cheilocystidia* abundant, 40−55 × 12−25 µm (n = 60 of 1 coll.), mainly lageniform with predominantly rounded base, apex crystalliferous, walls up to 4.0 µm thick, light yellow-green in 5% KOH. *Paracystidia* numerous, 12−28 × 7−13 µm (n = 35 of 1 coll.), highly variable in shape, clavate, ovoid, utriform, subglobose, fusiform, thin-walled, hyaline or very light yellow-green in 5% KOH. *Pileipellis* a cutis of radially arranged, elongated cylindrical or fusoid-cylindrical, 15−45 µm wide hyphae, terminal elements narrowly fusiform, with or without incrusted walls, intracellular pigment brownish yellow in 5% KOH. *Oleiferous hyphae* present in pileus and stipe trama, 2–6 µm in diameter, with incrusted walls, bright green in 5% KOH. *Caulocystidia*



Fig. 2 Basidiomata of *Inocybe arenosa* (AR-22–081, holotype). Bar = 10 mm

only near the apex of the stipe, 45–65 × 12–18 µm (n = 40 of 1 coll.), lageniform with a rounded base or fusiform with a short, narrow pedicel, apex crystalliferous, thick-walled, light yellow-green in 5% KOH. *Cauloparacystidia* numerous, occurring in clusters, 20–35 × 10–15 µm, mostly fusiform to clavate, sometimes oblong or obovate, thin- to slightly thick-walled, hyaline or very light yellow-green in 5% KOH. *Caulocystidioid hairs* 30–75 × 5–13 µm, very variable in shape, narrowly cylindrical to cylindrical, cylindrical-fusiform, subulate or narrowly lageniform with broad basal part and tapering, curved apical part, thin- to thick-walled, very light yellow-green in 5% KOH. *Clamps* present at all septa.

Habit, habitat, and distribution: In small groups, terrestrial, on sandy soils, under *Berlinia grandiflora*. Known only from the type locality.

Remarks: Inocybe basialba is characterized by a conical pileus with a blunt conical umbo, a stipe typically with a long, thin, white base, emarginate lamellae often with decurrent teeth, basidiospores with 8–15 distinct conical nodules, usually lageniform cheilocystidia with rounded bases, oleiferous hyphae with incrusted walls, and diverse caulocystidioid hairs.

In phylogenetic analyses of the concatenated nrITS-nrLSU-*RPB2* (Fig. 1), *I. basialba* is placed within a clade of five species known only from tropical Africa. *Inocybe basialba* is in a position close to *I. densifolia* nom. prov. (EG96039) and *I. leucophaea* (EG96095), both from Zambia, and clustered together with *I. arenosa* and *I. glaucodisca*. Based on pairwise nucleotide comparisons of the nrLSU region, the sequences most similar to *Inocybe basialba* were those of *I. densifolia* nom. prov. and *I. leucophaea*, with sequence similarities of 99% (10 nucleotide differences) and 98.6% (16 nucleotide differences), respectively. Despite these genetic affinities, *I. basialba* is morphologically distinct. *Inocybe leucophaea* differs from *I. basialba* by the shorter stipe (up to 65 cm long), shorter basidiospores (7.0–10.5 × 5.0–8.0 µm) with less prominent nodules, and the presence of pyriform to broadly lageniform pleurocystidia (Buyck et al. 2022). *Inocybe densifolia* nom. prov. is not yet formally described and is known only from sequence data (Matheny et al. 2009).

The new species *Inocybe arenosa* is characterized by a small, strongly squamulose pileus, a shorter stipe (up to 40 cm long), shorter basidiospores (on av. 8.3 × 5.6 µm), typically (sub)utriform, (sub)fusiform to (sub)lageniform pleurocystidia, oblong to ellipsoid paracystidia, a lack of oleiferous hyphae, pyriform caulocystidia, and globose, subglobose to ellipsoid cauloparacystidia. *Inocybe glaucodisca*, initially discovered from Zambia and later reported from Benin in the present study, has a small pileus (up to 20 mm diam.) with a glaucous, grayish umbo, a shorter stipe (up to 30 mm long) that is entirely pruinose, considerably smaller basidiospores (7.0–9.0 × 5.0–7.5 µm), and subcylindrical to sublageniform pleuro- and cheilocystidia (Buyck and Eyssartier 1999).

Another Zambian species, *Inocybe conspicuispora*, is morphologically somewhat similar to *I. basialba*, mainly due to the conical pileus and often slender stipe. However, *I. conspicuispora* differs from it by the non-bulbous, entirely pruinose and dark brown stipe, minutely shorter basidiospores (10.0–12.0 × 7.5–11.0 µm) with 8–10 nodules, and subcylindrical, utriform to broadly lageniform pleurocystidia (Buyck and Eyssartier 1999).

Inocybe liliputiana Kaygusuz, Bandini, Rühl & M. Piepenbr., sp. nov. (Figs. 6 and 7).

MycoBank: MB861577.

Etymology: The specific epithet refers to the very small basidiomata.

Holotype: Benin, Borgou Department, Tchatchou Gokana, on the ground in a gallery forest dominated by *Berlinia grandiflora*, at 09°01′32.5"N, 002°35′18.7"E, 361 m a.s.l., 20 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–042, STU, isotype in UNIPAR). GenBank accession numbers PX685953 (nrITS), PX685959 (nrLSU), and PX684960 (*RPB2*).

Diagnosis: Similar to *I. glaucodisca*, but differing in the combination of very small basidiomata, a dull brown pileus, absence of a velipellis, a very light yellowish-brown stipe lacking a bulbous base, distinctly larger basidiospores (7.0–11.5 × 6.1–8.8 µm), pleurocystidia that are often (sub) utriform with long, slightly undulate necks and predominantly lageniform or (sub)utriform caulocystidia, as well as distinct nrITS, nrLSU, and *RPB2* sequences.

Description: Pileus 5–7 mm wide, convex, plano-convex to applanate; with or without rather low broad umbo, margin straight; surface dry, shiny; velipellis absent, typically with small almost appressed scales in the centre and around the disc, giving it a furfuraceous appearance; fibrillose to smooth towards the margin, not translucent-striate;

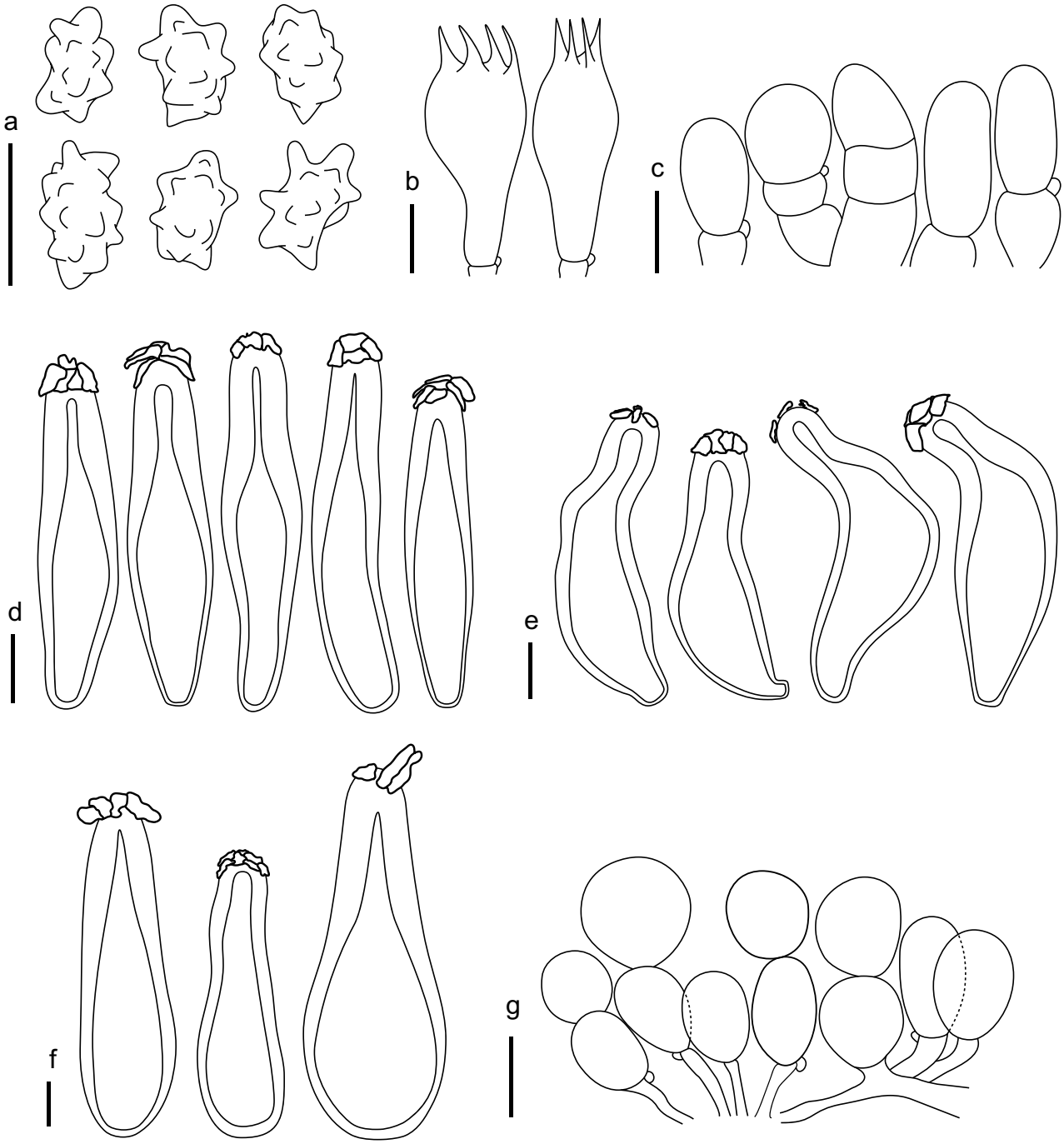


Fig. 3 Microscopic features of *Inocybe arenosa* (AR-22–081, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Pleurocystidia. **e** Cheilocystidia. **f** Caulocystidia. **g** Cauloparacystidia. Bars = 10 µm

colour light umber or almost dull brown (2.5Y 7/6, 7.5YR 6/6–10, 5/8, centre 4/4), umbo dark brown, usually paler towards the edge. *Lamellae* L = 35–45, I = 1–3, moderately distant, subventricose, up to 3.5 mm broad, nearly free to adnexed, white to dirty white, with entire or more or less fimbriate, whitish edge. *Stipe* 8–10 × 2–5 mm, slender, straight or curved, sometimes widening somewhat towards the apex, white cream at the apex, gradually very light yellowish brown towards the base, pruinose, especially in the upper part. *Cortina* not observed. *Context* fibrillose, whitish in stipe and pileus, unchanging upon exposure. *Colour of exsiccata* pileus white beige, lamellae and stipe dirty white to light beige, no darkening when dried. *Smell* not distinctive or weakly spermatic. *Taste* not distinctive.



Fig. 4 Basidiomata of *Inocybe basialba* (AR-22–098, holotype). Bar = 10 mm

Basidiospores 7.0–11.5 µm (av. 8.9 µm, SD 0.6 µm) × 6.1–8.8 µm (av. 7.1 µm, SD 0.5 µm), Q = 1.0–1.5 (av. 1.3, SD 0.1) (n = 90 of 1 coll.), heterodiametric, with 5–7 obtuse nodules on one side of a spore, rather pale yellow–brown in 5% KOH. *Basidia* 25–35 × 8.5–10 µm, clavate, generally 4-spored, rarely 2-spored, hyaline. *Pleurocystidia* 60–80 µm (av. 67 µm, SD 4.4 µm) × 11–20 µm (av. 16 µm, SD 1.2 µm), Q = 3.3–5.3 (av. 4.2, SD 0.6) (n = 68 of 1 coll.), mostly (sub)utriform, also (sub)lageniform, often with rather long and somewhat undulated neck, usually with short pedicel, sometimes with truncate base, apex crystalliferous, walls up to 2.5–3.0 µm thick, very pale yellowish-brownish in 5% KOH. *Lamellar edge* sterile, with cheilocystidia and paracystidia. *Cheilocystidia* 40−70 × 15−27 µm (n = 55 of 1 coll.), fusiform or (sub) utriform, base tapered or with short to long pedicel, some with short neck, with or without crystals at apex, thick-walled, intermixed with numerous colourless cells in 5% KOH. *Paracystidia* frequent, 10−20 × 8−10 µm (n = 30 of 1 coll.), clavate to ellipsoid, hyaline, thin-walled. *Pileipellis* a cutis consisting of cylindrical hyphae, 10–30 µm wide, terminal elements narrowly fusiform to fusiform with subcapitate to rostrate apex, with incrusted walls, brownish yellow intracellular pigment in 5% KOH. *Oleiferous hyphae* not observed. *Caulocystidia* only near the apex of the stipe, 50–90 × 8–20 µm, mostly lageniform or (sub)utriform with an undate neck, sometimes narrowly fusiform, without or with crystals, thick-walled, pale yellowish-greenish in 5% KOH. *Cauloparacystidia* numerous, occurring in clusters, 20−35 × 10−15 µm, mostly oblong, clavate to fusiform, hyaline, thin-walled. *Clamps* present at all septa.

Habit, habitat, and distribution: Basidiomata gregarious, usually terrestrial, on wet and sandy soils, under *Berlinia grandiflora*. Hitherto only known from Benin.

Remarks: Inocybe liliputiana is characterised by the tiny basidiomata, dull brown pileus with minute appressed scales, absence of a velipellis, very light yellowish-brown stipe, basidiospores with 5–7 nodules on one side, often (sub)utriform pleurocystidia with long and slightly undulated necks, and predominantly lageniform or (sub)utriform caulocystidia.

Phylogenetic analyses of the combined nrITS-nrLSU-*RPB2* dataset (Fig. 1) indicate that *Inocybe liliputiana* forms a distinct monophyletic lineage and is sister to a clade containing species of sect. *Calosporae*, e.g. *I. calospora*, *I. hopeae*, *I. spiniformis*, and *I. thailandica*. Despite this genetic affinity, *I. liliputiana* is microscopically distinct from other members of the sect. *Calosporae* because the basidiospores are nodulose and not spinose as it should be the case in species of sect. *Calosporae* (Singer 1986).

Among recently described nodulose-spored species from Benin and Burkina Faso, *I. beninensis*, *I. flavipes*, and *I. fuscobrunnea* are somewhat similar to *I. liliputiana*, especially concerning the color of their basidiomata. However, morphologically, *I. beninensis* differs from *I. liliputiana* by the presence of a veil on the stipe, longer basidiospores (on av. 10.4 × 8.8 µm), subclavate cheilocystidia, shorter pleurocystidia (up to 44 µm in length), and pyriform to clavate caulocystidia (Aïgnon et al. 2022). *Inocybe flavipes* differs from *I. liliputiana* by the somewhat larger basidiomata (up to 13 mm in length), slightly shorter basidiospores (on av. 8.6 × 5.3 µm) with 3–5 nodules, and obovoid cheilocystidia (Aïgnon et al. 2022). *Inocybe fuscobrunnea* is characterized by the larger basidiomata (pileus up to 40 mm wide) with a flocculose-tomentose or slightly rimose surface and shorter pleurocystidia (up to 52 µm in length) (Aïgnon et al. 2022). The nrITS sequences of *I. liliputiana* show pairwise dissimilarities of 13.4%, 18.3%, and 6.9% with corresponding sequences of *I. beninensis*, *I. flavipes*, and *I. fuscobrunnea*, respectively.

Further nodulose-spored species described from Zambia are *I. conspicuispora*, *I. glaucodisca*, *I. hebes*, *I. leucophaea,* and *I. media*. *Inocybe conspicuispora* is characterized by the dark chestnut-brown pileus, which is almost black at the papilla; a slender, entirely pruinose, dark brown stipe; and slightly larger basidiospores (10.0–12.0 × 7.5–11.0 µm) with 8–10 nodules (Buyck and Eyssartier 1999). *Inocybe glaucodisca* is recognised by the chestnut-brown to reddish-brown pileus, a bulbous and entirely pruinose stipe, and smaller basidiospores (7.0–9.0 × 5.0–7.5 µm) (Buyck and Eyssartier 1999). *Inocybe hebes* is characterized by a notably vivid brown pileus, which is fibrillose to coarsely fibrillose, a non-pruinose stipe, and lageniform (often subcapitate) pleuro- and cheilocystidia (Buyck et al. 2022). *Inocybe leucophaea* differs from *I. liliputiana* by the larger basidiomata (pileus up to 30 mm wide), the presence of a velipellis, and pyriform pleuro- and cheilocystidia (Buyck et al. 2022). *Inocybe*

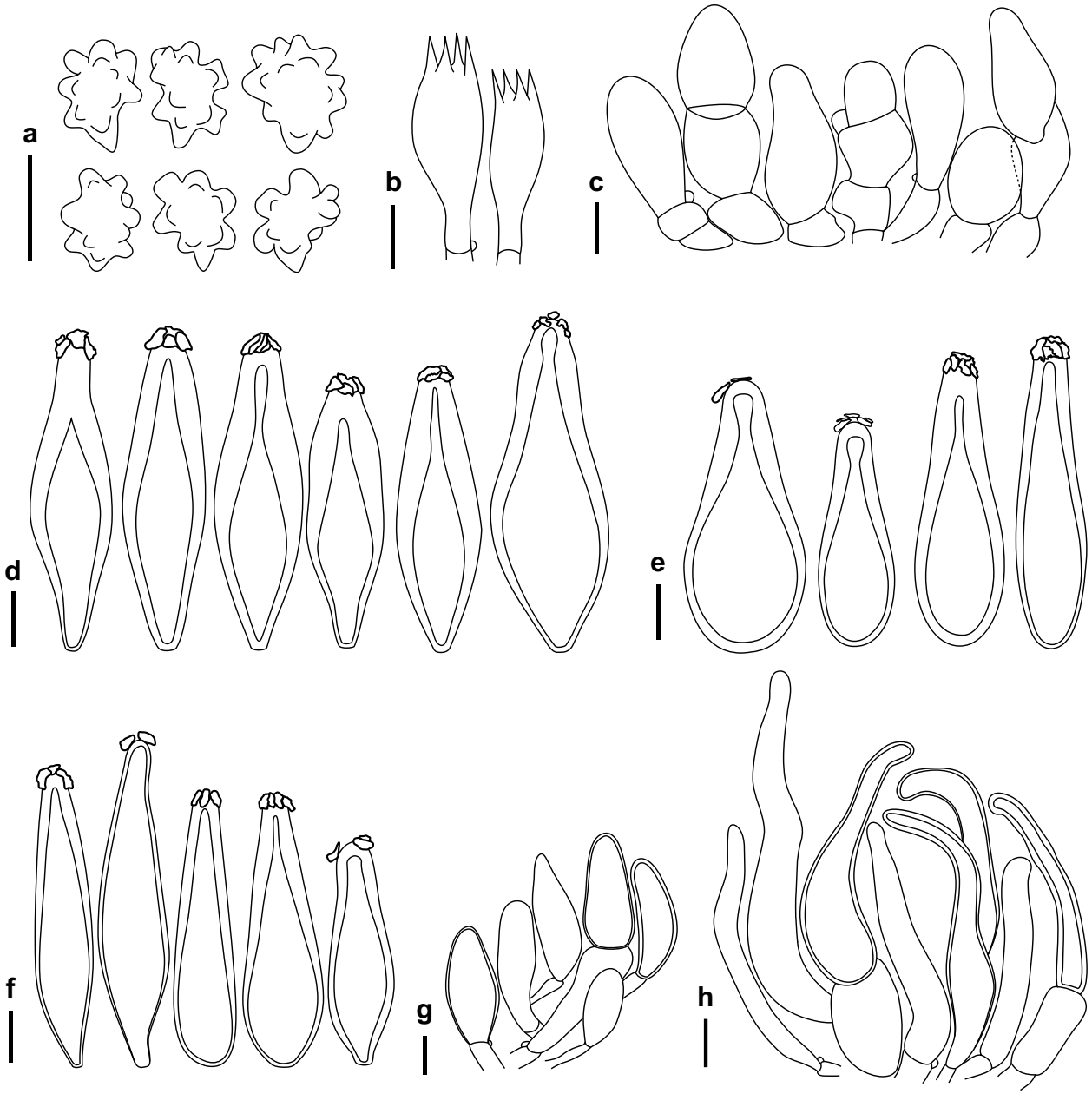


Fig. 5 Microscopic features of *Inocybe basialba* (AR-22–098, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Pleurocystidia. **e** Cheilocystidia. **f** Caulocystidia. **g** Cauloparacystidia. **h** Caulocystidioid hairs from the apex of the stipe. Bars = 10 µm

media features a pileus that is pruinose by a white veil, a stipe with bulbous-marginate base, and basidiospores that are only slightly nodulose (Buyck et al. 2022).

Inocybe luteofusca Kaygusuz, Bandini, Rühl & M. Piepenbr., sp. nov. (Figs. 8 and 9).

MycoBank: MB861578.

Etymology: The specific epithet refers to the dull brownish-yellow colour of the pileus and stipe.

Holotype: Benin, Littoral, Jardin Botanique de l'Université d'Abomey-Calavi, on the ground, under *Berlinia grandiflora*, at 06°25′06.8"N, 002°20′36.1"E, 51 m a.s.l., 21 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–003, STU, isotype in UNIPAR). GenBank accession numbers PX685954 (nrITS), PX685960 (nrLSU), and PX684961 (*RPB2*).

Diagnosis: Differs from *I. beninensis* by a pileus with a velutinous surface, the presence of a velipellis, a yellowish-brown stipe with a silky-fibrillose surface, predominantly cylindrical to narrowly utriform pleurocystidia, broadly fusiform to oblong cheilocystidia, differently shaped caulocystidia and caulocystidioid hairs, and unique nrITS, nrLSU, and *RPB2* sequences.



Fig. 6 Basidiomata of *Inocybe liliputiana* (AR-22–042, holotype). Bar = 10 mm

Description: Pileus 6–18 mm wide, hemispherical to convex, becoming almost applanate with age, usually with a small and broad obtuse umbo; margin reflexed, eroded; velipellis present, distinct in young fruitbodies, as a very thin whitish coating over the entire pileus, but also around the disc in older specimens; surface dry, generally smooth and velutinous; colour dull brownish yellow to light brown (2.5Y 7/6–10, 6/8, 7.5YR 6/4–6, centre 7.5YR 5/6), umbo, at times darker than the rest of the pileus centre. *Lamellae* L = 40–55, I = 1–2(–3), moderately crowded to crowded, ventricose, up to 3 mm broad, nearly free to adnexed, pale yellow to very light yellowish brown; edges entire, whitish. *Stipe* 15–60 × 2–6 mm, cylindrical, weakly or distinctly broadened at the base, with soil tightly attached to the base; surface of the stipe dry, pruinose only near the apex, pale yellow to light yellowish brown, with silky-fibrillose covering at the base. *Cortina* not observed. *Context* solid, whitish in stipe and pileus, unchanging upon exposure. *Colour of exsiccata* pileus pale yellow, lamellae and stipe dirty pale yellow to very light yellowish brown, not darkening when dried. *Smell* and *taste* not remarkable.

Basidiospores 8.0–11.0 µm (av. 9.2 µm, SD 0.7 µm) × 5.4–7.9 µm (av. 6.5 µm, SD 0.1 µm), Q = 1.2–1.8 (av. 1.4, SD 0.1) (n = 125 of 2 coll.), heterodiametric, with 5–7 obtuse nodules, rather pale yellow–brown in 5% KOH. *Basidia* 20–35 × 8.5–13 µm, clavate, 4-spored, hyaline. *Pleurocystidia* numerous, 45–55 µm (av. 50 µm, SD 3.1 µm) × 10–17 µm (av. 12.5 µm, SD 2.3 µm), Q = 3.3–5.5 (av. 4.2, SD 0.7) (n = 60 of 2 coll.), mostly cylindrical or narrowly utriform, sometimes narrowly fusiform, apex crystalliferous, rarely scattered crystals, walls up to 1.5(2.0) µm thick but generally thinner towards the base, very pale yellowish-brownish in 5% KOH. *Lamellar edge* sterile, with cheilocystidia and paracystidia. *Cheilocystidia* 40−60 × 15−28 µm (n = 55 of 2 coll.), broadly fusiform to oblong, base tapering into the short pedicel, apex crystalliferous, walls up to 1–1.5 µm thick, very pale yellowish-brownish in 5% KOH. *Paracystidia* frequent, 15−25 × 8−12 µm (n = 25 of 2 coll.), clavate to subglobose, hyaline, thin-walled. *Pileipellis* a cutis consisting of parallel-arranged hyphae, 6.0–12 µm wide, with incrusted walls, light brownish yellow intracellular pigment in 5% KOH. *Oleiferous hyphae* not observed. *Caulocystidia* present only near the apex of the stipe, 60–80 × 12–25 µm, generally (sub)clavate, lageniform or (sub)cylindrical, crystalliferous at apex, slightly thick-walled, very pale yellowish-greenish in 5% KOH. *Caulocystidioid hairs* especially present on the lower part of the stipe, 35−50 × 7−15 µm, largely subclavate to narrowly lageniform, sometimes cylindrical, without or with crystals, hyaline, slightly thick-walled. *Cauloparacystidia* not observed. *Clamp connections* present.

Habit, habitat, and distribution: Basidiomata gregarious, usually terrestrial, on wet and sandy soils, under *Berlinia grandiflora*. Hitherto only known from Benin.

Additional specimen examined: Benin, Littoral, Jardin Botanique Calavi, on the ground, under *Berlinia grandiflora*, at 06°25′06.8"N, 002°20′36.1"E, 51 m a.s.l., 26 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–004, STU).

Remarks: Sequences of the two collections of *I. luteofusca* from Benin form a distinct and statistically highly-supported clade (MLB = 100%, BPP = 1.0), separate from all other known nodulose-spored *Inocybe* species (Fig. 1). *Inocybe luteofusca* is macroscopically characterized by a dull brownish-yellow pileus with a velutinous surface, the presence of a velipellis, evident as a whitish coating, a light yellowish-brown stipe with a silky-fibrillose covering at the base, predominantly cylindrical to narrowly utriform pleurocystidia, and caulocystidia and caulocystidioid hairs that are highly variable in shape.

Some of the recently described *Inocybe* species with nodulose spores from tropical African countries are *Inocybe beninensis*, *I. flavipes*, *I. fuscobrunnea,* and *I. pallidiangulata*. Beninese species *I. beninensis,* though comparable to *I. luteofusca*, is distinctive by virtue of the fibrillose to tomentose pileus, slightly longer basidiospores (on av. 10.4 × 8.8 µm), subclavate cheilocystidia, and pyriform to clavate caulocystidia (Aïgnon et al. 2022). *Inocybe flavipes*, also described from Benin, can be distinguished from the new species by the slightly shorter basidiomata (up to 13 mm in length) and obovoid cheilocystidia (Aïgnon et al. 2022). *Inocybe fuscobrunnea*, initially described from Burkina Faso, differs from *I. luteofusca* by the larger basidiomata (pileus up to 40 mm wide), dark reddish-brown pileus, globose basidiospores (Q = 1.1), and utriform pleuro- and cheilocystidia (Aïgnon et al. 2022). *Inocybe pallidiangulata*, first described from Burkina Faso,

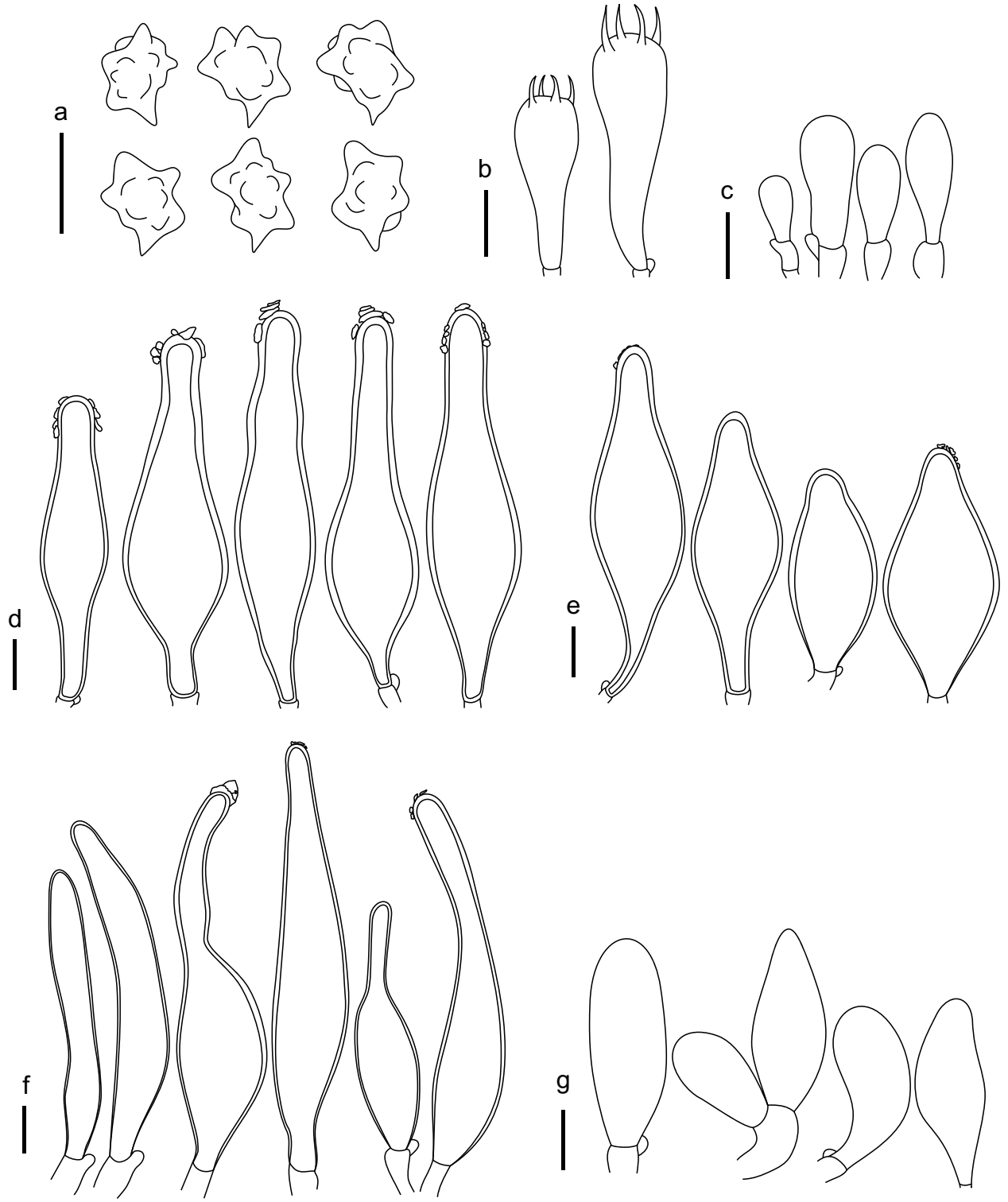


Fig. 7 Microscopic features of *Inocybe liliputiana* (AR-22–042, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Pleurocystidia. **e** Cheilocystidia. **f** Caulocystidia. **g** Cauloparacystidia. Bars = 10 µm

differs markedly from *I. luteofusca* by the paler pileus, extremely shorter basidiospores (on av. 7.0 × 5.2 µm) with less protruding nodules, utriform cheilocystidia, and obovoid caulocystidia (Aïgnon et al. 2022). Genetically, the percentage of dissimilarity of nrITS sequences between *Inocybe luteofusca* and *I. beninensis*, *I. flavipes*,



Fig. 8 Basidiomata of *Inocybe luteofusca*. **a** Collection AR-22–003 (holotype). **b** Collection AR-22–004. Bars = 10 mm

I. fuscobrunnea, and *I. pallidiangulata* is 19.2%, 19.4%, 6.4%, and 11.9%, respectively.

Inocybe luteofusca is morphologically similar to *I. castanea* Peck, a species originally discovered under spruce and balsam fir in the USA (Peck 1904) and later reported in northern Europe and northeast Asia (Ferrari 2006; Jacobsson 2008; Chen et al. 2024). However, *I. castanea* can be distinguished by the brown to reddish brown pileus, a whitish, furfuraceous-pruinose stipe, notably shorter basidiospores (on av. 7.3 × 5.1 µm) with 10–18 weak nodules, and lageniform cheilocystidia (Chen et al. 2024). Furthermore, *I. castanea* occurs in a variety of habitats, including coniferous forests, mixed forests, and alpine communities (Chen et al. 2024). Despite this similarity, our phylogenetic analyses confirm they represent distinct evolutionary lineages.

New record for Western Africa.

Inocybe glaucodisca Buyck & Eyssart., Kew Bull. 54(3): 677 (1999) (Figs. 10 and 11).

Description: Pileus 3–8 mm wide, hemispherical to convex when young, then expanding to plano-convex with a small obtuse umbo; margin initially inflexed, later straight; at first around the disc and most of the surface covered by abundant remnants of a pale greyish velipellis; surface non-hygrophanous, surface smooth to slightly felty, towards the margin rubbed somewhat off probably due to water or wind; colour when moist very light brown at the centre, glaucous greyish around umbo, pale brown to brown elsewhere (7.5YR 5/4–10, 4/4, centre 7.5YR 8/2, 2.5Y 8/2). *Lamellae* L = 34–48, I = 1(–3), moderately crowded, ventricose to broadly ventricose, up to 3.7 mm deep, nearly free to adnexed, light brown to light yellowish brown; edges entire, whitish. *Stipe* 10–30 × 2–4 mm, cylindrical with a marginate bulb, with tightly bound soil; surface, dry, pruinose its entire length, silky-fibrillose below, more densely fibrillose above the base, pale whitish brown to light yellow brown, darker when touched. *Cortina* not observed. *Context* solid, becoming hollow, yellowish brown to brown. *Colour of exsiccata* pileus beige brown, lamellae and stipe creamish, no darkening when dried. *Smell* spermatic and *taste* not remarkable.

Basidiospores 7.3–10.7 µm (av. 8.8 µm, SD 0.5 µm) × 5.0–7.7 µm (av. 6.1 µm, SD 0.4 µm), Q = 1.2–1.9 (av. 1.4, SD 0.1) (n = 85 of 1 coll.), heterodiametric, mostly with 8–11 nodules, sometimes one or more nodules larger than the other nodules, yellowish brown in 5% KOH. *Basidia* 20–30 × 8.0–12.0 µm, clavate, 4-spored, hyaline, thin-walled. *Pleurocystidia* abundant, 45–60 µm (av. 47 µm, SD 3.1 µm) × 10–14 µm (av. 12 µm, SD 1.3 µm), Q = 3.3–6.0 (av. 4.0, SD 0.6) (n = 50 of 1 coll.), mostly narrowly fusiform, sometimes narrowly utriform, often with short pedicel, mostly with large crystals at the apex, walls up to 4.5 µm thick near the apex, slightly yellow-green in 5% KOH. *Lamellar edge* sterile, with cheilocystidia and paracystidia. *Cheilocystidia* numerous, 30−45 × 11−13.5 µm (n = 65 of 1 coll.), fusiform, clavate or lageniform, with crystals at the apex, walls up to 3.7 µm thick, light yellow-green in 5% KOH. *Paracystidia* scarce, 10−17 × 8−10 µm (n = 30 of 1 coll.), clavate to ellipsoid, hyaline, thin-walled. *Pileipellis* a trichoderm of suberect chains of cylindrical to ovoid cells, 10–55 µm wide, terminal elements narrowly cylindrical to narrowly conical or conical, with incrusted walls, brown intracellular pigment in 5% KOH. *Oleiferous hyphae* not observed. *Caulocystidia* only near the apex of the stipe, 40–60 × 12–24 µm, mostly lageniform, often with a rounded or urceoliform base, crystalliferous at the apex, thick-walled, pale yellowish-greenish in 5% KOH. *Cauloparacystidia* numerous, occurring in clusters, 8−20 × 5−10 µm, mostly narrowly clavate to clavate, sometimes ellipsoid, thin-walled, hyaline. *Clamps* present at all septa.

Specimen examined: Benin, Collines, forest close to Kilibo, on the ground in a gallery forest dominated by *Berlinia grandiflora*, at 08°36′57.3"N, 002°39′54.7"E, 320 m a.s.l., 21 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–055, STU).

Habit, habitat, and distribution: Basidiomata gregarious, usually terrestrial, found on wet and sandy soils under *Berlinia grandiflora* in Benin and in miombo woodland

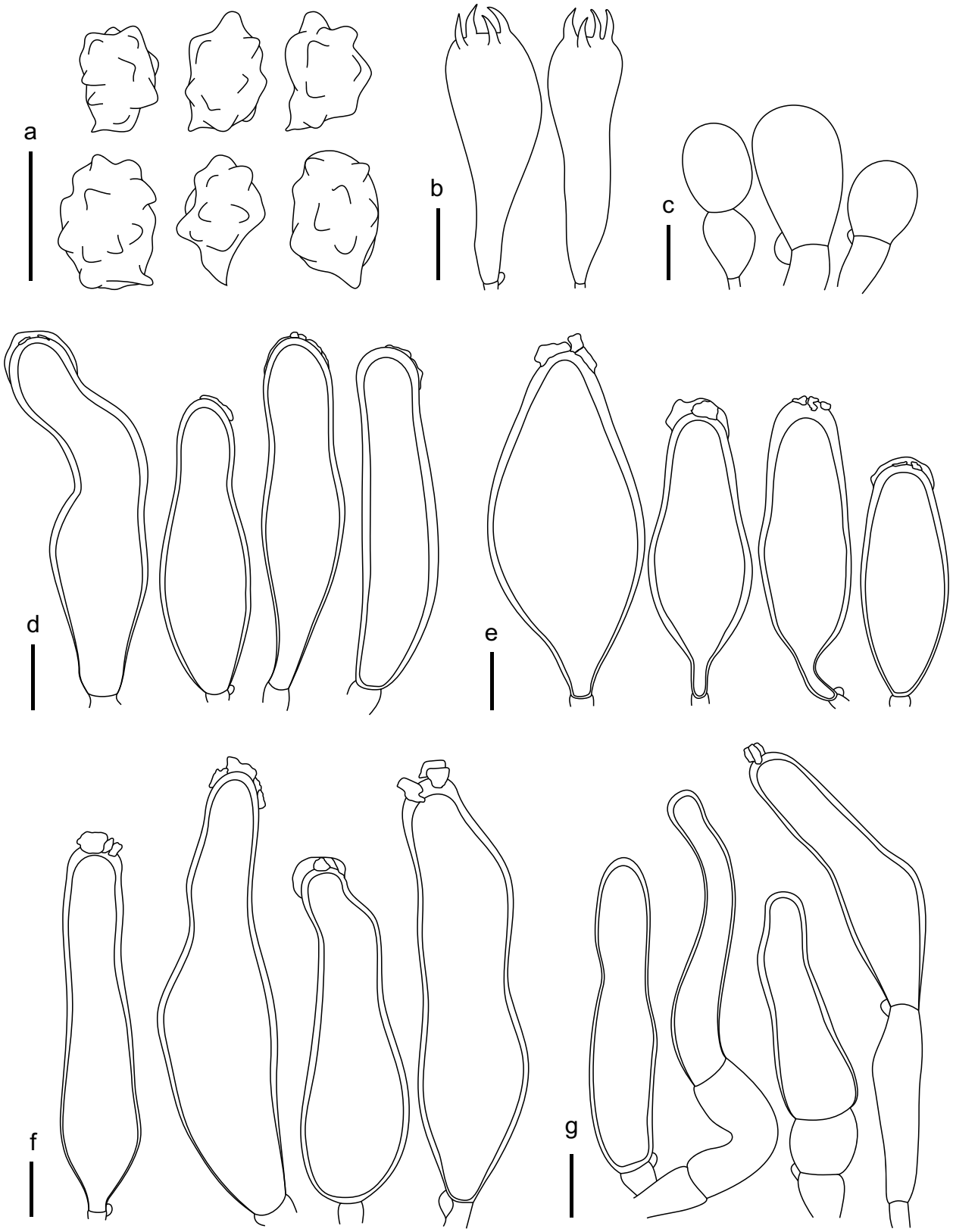


Fig. 9 Microscopic features of *Inocybe luteofusca* (AR-22–003, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Pleurocystidia. **e** Cheilocystidia. **f** Caulocystidia. **g** Caulocystidioid hairs from stipe apex. Bars = 10 µm



Fig. 10 Basidiomata of *Inocybe glaucodisca* (AR-22–055). Bar = 5 mm

dominated by *Uapaca* sp. (*Phyllanthaceae*) in Zambia (Buyck and Eyssartier 1999). This species was previously known only from the type locality in Zambia and is now also reported from Benin.

Remarks: Inocybe glaucodisca is reported here for the first time from West Africa, thousands of kilometers from its type locality in Southeast Africa. The identity of the Benin specimen as *Inocybe glaucodisca* is confirmed by its concordance with the original description (Buyck and Eyssartier 1999) and by the nrITS sequence match with the corresponding sequence of the Zambian holotype. We provide additional nrLSU sequence data for this species. Nearly 25 years after its original description, *I. glaucodisca* is redescribed here and illustrated for the first time with colour photographs of fresh basidiomata from Benin. These new molecular and morphological data significantly extend the known range of *I. glaucodisca* in Africa and provide a critical foundation for future studies on its biogeographic distribution and ecology across the continent.

Discussion

Previous studies have proposed that the ancestors of *Inocybaceae* began to broaden their range across vast areas of northern and southern South America, Australia, and New Zealand, as well as Africa, during the Palaeogene or subsequent geological periods (Matheny 2009; Matheny et al. 2009). This ancient dispersal helps to explain the distinct biogeographical patterns observed today. Mediterranean-type habitats in regions such as Europe, North America, and Australia are dominated by abundant *Inocybe* species with smooth spores (Kuyper 1986; Nishida 1989; Matheny and Bougher 2017; Matheny et al. 2020; Bandini et al. 2021, 2023; Caiafa et al. 2021; Kaygusuz et al. 2024a). In contrast, tropical regions harbor a rich diversity of species with angular-nodulose spores (Singer et al. 1983; Buyck and Eyssartier 1999; Matheny et al. 2003, 2009, 2012; Horak et al. 2015; Latha and Manimohan 2017; Matheny and Bougher 2017; Aïgnon et al. 2022; Buyck et al. 2022; Chen et al. 2024; Zhu et al. 2025). Here, we contribute to this known diversity by describing four new nodulose-spored *Inocybe* species from tropical Benin, thereby confirming the observed prevalence of species with nodulose-angular to tuberculate-sinuose spores in tropical Africa. Phylogenetic analyses reveal that nodulose ornamentation of *Inocybe* evolved independently multiple times, rather than from a single ancestor. This characteristic has a mosaic distribution, with smooth spores generally being ancestral (Kuyper 1986; Nishida 1989; Matheny 2009; Matheny et al. 2009, 2020).

The dominance of nodulose-spored species in African tropics may be due to an adaptive advantage conferred by local environmental pressures (Pringle et al. 2015). Specifically, the complex ornamentation of spores may have facilitated zoochorous dispersal by enhancing spore adhesion to arthropods. Consistently, Halbwachs et al. (2015) suggested that spore ornamentation in ectomycorrhizal fungi may promote zoochory by soil invertebrates, thereby transporting spores closer to plant roots. These adaptations in spore morphology likely enable *Inocybe* species to colonize new substrata and consequently disperse into the rich ecological niches of tropical regions.

Phylogenetically, *Inocybe basialba*, *I. arenosa*, and *I. glaucodisca* cluster within a clade of tropical African species that also includes *I. densifolia* nom. prov. and *I. leucophaea* (Fig. 1). The species in this tropical African clade are associated with species of the family *Fabaceae*, while species in its sister clade belonging to the *I. pingala* group are linked to *Hopea ponga* (Dennst.) Mabb. (*Dipterocarpaceae*), a tree species endemic to India (Latha and Manimohan 2017). In the three-gene phylogeny, *I. luteofusca* forms a distinct, monophyletic lineage among nodulose-spored *Inocybe* species. Furthermore, *I. liliputiana* is discovered as a sister to the species of sect. *Calosporae,* which are characterized by spinose basidiospores (Jacobsson and Larsson 2012).

The earliest scientifically documented ectotrophic mycorrhizal association involving fungi in tropical Africa is believed to be an *Inocybe* sp. linked to *Afzelia bella* Harms (as *Afzelia bella* var. *bella*, *Fabaceae*) in the Benin province of Nigeria, West Africa (Redhead 1968). This same *Inocybe* sp. was later found in a woodland ecosystem primarily composed of *Brachystegia eurycoma* Harms and *B. nigerica* Hoyle & A.P.D. Jones, both of which are members of the *Detarioideae* (*Fabaceae*) recognized for including several species with ECM relationships (Redhead 1968). Subsequently, some new or unidentified apparently endemic

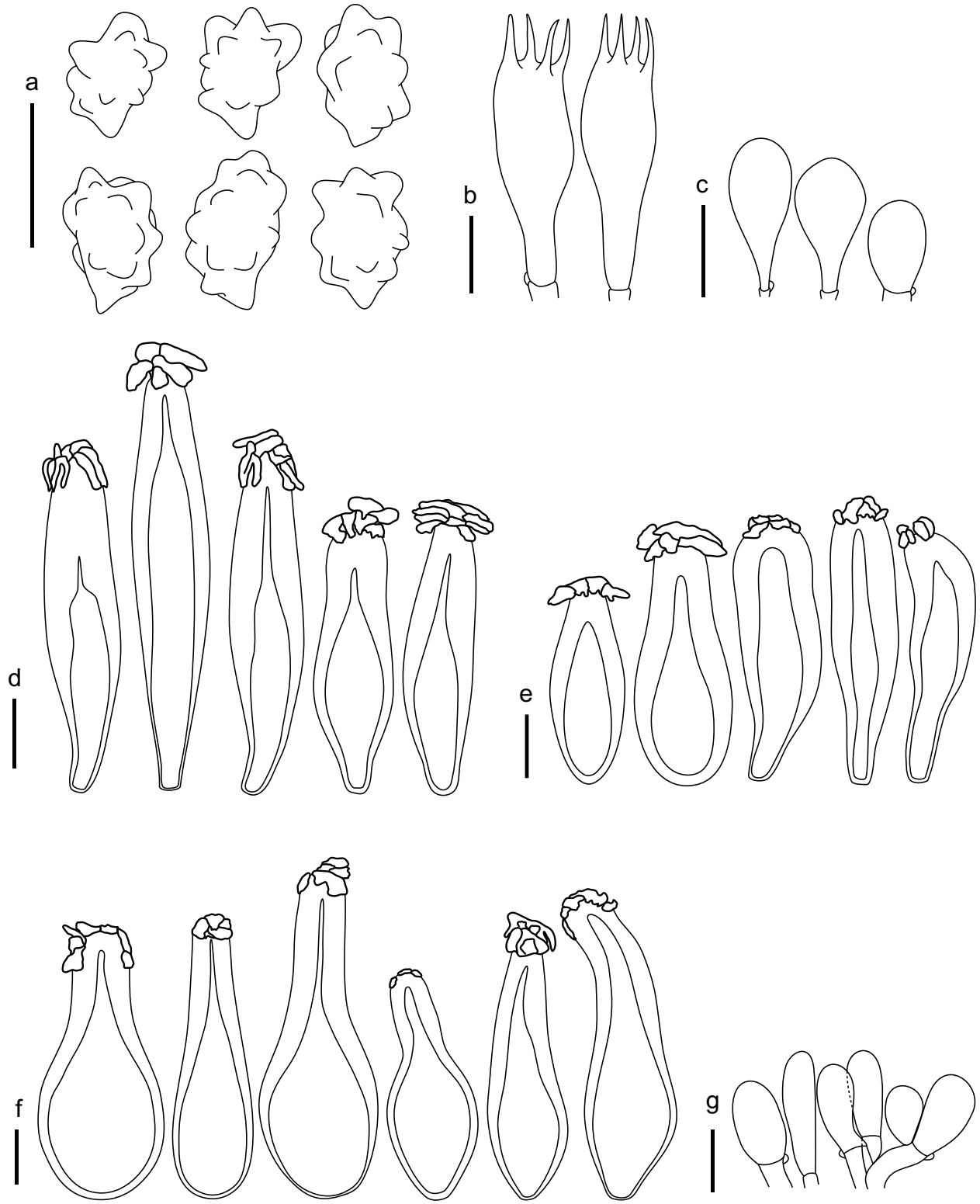


Fig. 11 Microscopic features of *Inocybe glaucodisca* (AR-22–055). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Pleurocystidia. **e** Cheilocystidia. **f** Caulocystidia. **g** Cauloparacystidia. Bars = 10 µm

Inocybe species have been reported from Benin (Aïgnon et al. 2022), Burkina Faso (Aïgnon et al. 2022), Cameroon (Hennings 1901; Buyck et al. 1996), the Democratic Republic of the Congo (Buyck et al. 1996), Gabon (Heim 1969), Ghana (Pegler 1969), Guinea (Thoen and Ducousso 1989), Ivory Coast (Aïgnon et al. 2022), Nigeria (Redhead 1968), Senegal (Thoen and Ba 1989; Thoen and Ducousso 1989), Tanzania (Hennings 1900), Togo (Aïgnon et al. 2022), and Zambia (Buyck 1994; Buyck et al. 1996; Buyck and Eyssartier 1999; Buyck et al. 2022). In the miombo woodlands and gallery forests of Africa, such macrofungi are associated with ECM tree species of the *Fabaceae* and *Phyllanthaceae*, forming relationships with hosts such as *Afzelia africana* Sm. ex Pers., *Anthonotha crassifolia* Baill., *Berlinia grandiflora*, *Isoberlinia doka* Craib & Stapf ex Holland, *I. tomentosa* (Harms) Craib & Stapf, *Uapaca chevalieri* Beille, *U. kirkiana* Müll.Arg., and *U. pilosa* Hutch (Wang and Qiu 2006; Codjia et al. 2022). All four of the new and newly recorded *Inocybe* species from Benin were discovered in tropical forests dominated by *Berlinia grandiflora* (*Fabaceae*). The distribution of this host tree is restricted to the tropical African phytochorion, which stretches from West Africa through Central Africa, including the Cameroon Highlands (Keay 1989; Arbonnier 2004).

The current understanding of *Inocybe* species in Africa is limited because the region is not well-studied compared to other continents, and these fungi are challenging to identify; therefore, many more species are anticipated to be discovered with future, targeted research. Nearly all of the fifteen species of *Inocybe* recorded so far are endemic to Africa. With the addition of the four nodulose-spored *Inocybe* species presented in this study, the total number of species in the region has now increased to nineteen.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11557-026-02127-1.

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Author contribution All authors contributed to the conception and design of the study. Adrian Rühl, Sepas Sarawi, Nourou Soulemane Yorou, and Meike Piepenbring contributed to data collection. Morphological characteristics were examined by Oğuzhan Kaygusuz, Ditte Bandini, and Meike Piepenbring. Molecular lab work and phylogenetic analyses were conducted by Oğuzhan Kaygusuz, Adrian Rühl, Sepas Sarawi, and P. Brandon Matheny. The first draft of the manuscript was written by Oğuzhan Kaygusuz and Meike Piepenbring, which was then improved by changes, edits, suggestions, and comments from P. Brandon Matheny, Ditte Bandini, Nourou Soulemane Yorou, Adrian Rühl, and Sepas Sarawi. All authors have read and agreed to the publication of the final manuscript.

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Data availability The DNA sequences produced in this study are available on NCBI GenBank (https://www.ncbi.nlm.nih.gov). The alignments are provided in the supplementary information.

Code availability Not applicable.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Informed consent was obtained from all individual participants included in the study.

Competing interests The authors declare no competing interests.

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