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Four new nodulose-spored species of *Inocybe* (*Agaricales*) from West Africa

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Abstract: We describe four new nodulose-spored species of *Inocybe* from tropical regions of Africa: *I. beninensis, I. flavipes, I. fuscobrunnea* and *I. pallidiangulata.* The new species are recognised based on morphological data and phylogenetic analyses of ITS, 28S and *RPB2* sequences. Phylogenetic analyses indicated that *I. flavipes* and *I. beninensis* are part of a subclade leading to the *I. calida* group. *Inocybe fuscobrunnea* appears sister to the *I. asterospora* group. *Inocybe pallidiangulata* is nested within a clade of mainly tropical species from South Asia, Africa, and South America, close to the subclade of *I. lilacinosquamosa* and *I. ayangannae* from Guyana. Complete descriptions and illustrations, including photographs and line drawings, and a key to nodulose-spored taxa of tropical African species of *Inocybe* are provided.

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INTRODUCTION

Inocybe is the most diverse genus in the *Inocybaceae* with 850 species described worldwide (Matheny *et al*. 2020), but this number has increased as more areas are intensively studied and new species described (Matheny & Bougher 2017, Matheny & Kudzma 2019, Bandini & Oertel 2020, Caiafa *et al*. 2021). While competing infrageneric classification systems are available based on morphological analyses (Kuyper *et al.* 1986, Singer 1986, Bon 1997, 1998), these classifications are a poor representation of the phylogenetic relations within the group. For example, nodulose-spored species of the genus do not form a monophyletic group (Matheny *et al.* 2002, Matheny 2005, Kropp *et al*. 2010, Ryberg *et al.* 2010, Esteve-Raventós *et al*. 2016).

Anatomically, species of *Inocybe* are distinguished from those belonging to other genera of the family by possession of pleurocystidia and/or angular, nodulose, or spinose basidiospores, often with a distinct apiculus (Matheny *et al.* 2020). Some subgroups of *Inocybe* lack caulocystidia, whereas others possess them near the apex or along the entire length of the stipe correlated with the presence/absence of a partial veil (Kuyper 1986).

Despite progress to assess the diversity of *Inocybe* in many parts of the world, African regions remain poorly explored (Aïgnon *et al.* 2021a). To date, only four nodulose-spored species of *Inocybe* have been recorded from Africa. Hennings (1902) described *I. cyaneovirescens*, from what used to be called "German East Africa", which today encompasses the nations of Burundi, Rwanda and continental region of Tanzania. Pegler (1969) described *I. ghanaensis* from West Africa (Ghana). Lastly, Buyck & Eyssartier (1999) described two species *I. conspicuospora* and *I. glaucodisca* from Zambia. In addition to these, two studies published sequence data from several undescribed species from Zambia (Matheny *et al*. 2009, Tedersoo *et al.* 2011). In recent years, eight *Inocybe* species were recorded from Morocco (Ouabbou *et al*. 2014, Akil *et al.* 2015). Recently, Aïgnon *et al.* (2021b) estimated that approximately 62 species of *Inocybe* occur in Africa.

According to Matheny *et al.* (2020), certain regions such as Mediterranean types of habitats in North America and Australia are predominantly rich in species of *Inocybe* with smooth spores (Nishida 1989, Matheny & Bougher 2017), but tropical regions have accumulated a diverse assemblage of species with angular-nodulose spores (Matheny *et al.* 2003, Horak *et al.* 2015). This seems indeed to be the case in tropical Africa where we discovered four new species of *Inocybe,* all with angular-nodulose spores. Detailed descriptions and illustrations, as well as comparisons with closely related species, are provided. A key to nodulose-spored species of *Inocybe* from tropical Africa is also provided.

MATERIAL AND METHODS

Study area and specimen sampling

Specimens were collected between 2013 and 2018 in Benin, Burkina Faso, Ivory Coast and Togo. Collections were made

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in woodlands, with more than 10 % woody cover, including shrublands with a canopy only 2 m high, and that were dominated by ectomycorrhizal trees of *Euphorbiaceae, Fabaceae* and *Phyllanthaceae*. Colour codes of fresh specimens were recorded with the Online Auction Colour chart (2004). After labelling and recording morphological data, specimens were preserved by drying using an electric dryer (type Stöckli Dörrex) for 24 h at 45 °C. All studied materials, including the holotypes were deposited at the Mycological Herbarium of Parakou University, Benin Republic (UNIPAR).

Morphological and anatomical analyses

Fine sections from the dried basidiomata were rehydrated and examined in 3 % KOH and Congo Red for microscopic investigation. Drawings of microscopic characters were made with the aid of a drawing tube attached to a Leica DM2700 light microscope. Microscopic characters were drawn at 1000× magnification. For each species, spore measurements were made from 40 spores. We measured length (L) and width (W) of the basidiospores and calculated the ratio Q = L/W. Measurements of basidiospores and basidia excluded the apiculus and sterigmata, and spore dimensions included nodules. Spore measurements are given as (a–)b–c(–d), where (a) = extreme minimum value, range b–c contains minimum of 90 % of the calculated values and (d) = extreme maximum value following Aïgnon *et al*. (2021a, c).

Molecular analyses

DNA extraction, PCR and sequencing: Genomic DNA was extracted from dried specimens by a QIAGEN® plant mini kit. The ITS, parts of 28S, and *RPB2* were amplified. For the ITS region, we produced amplicons using primers pairs ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993). For the 28S region, we used the LR0R, LR7, LR5 and LR3R primers (Vilgalys & Hester 1990, Cubeta *et al.* 1991, Rehner & Samuels 1995) and for the *RPB2* region, primer pairs b6F and b7.1R (Matheny 2005) were used. PCR products were purified and sequenced at Macrogen Inc. (Netherlands) using the same primers as those used for PCR. We refer to Aignon *et al.* (2021a, c) for detailed methods of the DNA extraction and amplification.

Sequence alignment and phylogenetic analyses: New sequences derived in this study were compared with closely related *Inocybe* sequences that were retrieved from GenBank (Benson *et al*. 2010). Species of different groups, clades and sections of *Inocybe* such as *I. praetervisa* group, *I. mixtilis* group, *I. napipes* group, *I. xanthomelas* group, *I. diabolica* group, *I. lacera* group, *I. lanuginosa* group, *I. giacomi* group, Smooth-spored temperate boreal clade, Smooth-spored temperate boreal clade and Sect. *Inocybe* were selected on the basis of a literature survey (Ryberg *et al*. 2008, Horak *et al*. 2015, Matheny & Bougher 2017, Matheny *et al.* 2017, Latha & Manimohan 2017, Esteve-Raventós *et al*. 2018, Bandini *et al.* 2019, Cripps *et al*. 2019, Matheny *et al*. 2020). Sequences of the different regions (ITS, 28S and *RPB2*) were aligned separately using MAFFT v. 7.464 (Katoh *et al.* 2019), and a final concatenated data set of ITS, 28S and *RPB2* was generated using Geneious v. 7.0.2 software (Biometer, Auckland, New Zealand). The dataset was partitioned into ITS + 28S, *RPB2* codon position 1 + *RPB2* codon position 2 and *RPB2* codon position 3 + the intron in *RPB2* separately. For phylogenetic analyses, the substitution models and the best partitioning schemes were determined for both Maximum Likelihood (ML) and Bayesian Inference (BI). The substitution models for each locus were determined based on the AICc model selection criterion as implemented in PartitionFinder (Lanfear *et al*. 2016).

Maximum Likelihood analyses were performed with IQ-TREE v. 1.6.12 (Nguyen *et al.* 2015). Ultrafast bootstrapping (UFBoot) was done with 1 000 replicates (Hoang *et al*. 2017). BI analyses were performed in MrBayes v. 3.2.7a (Ronquist *et al*. 2012) using a GTR+I+G model at the Cipres Science Gateway (Miller *et al.* 2010). Two independent Markov Chain Monte Carlo (MCMC) were run in parallel, each with four chains for 20 M generations. Posterior probabilities (BPP) were calculated after discard the first 25 % samples from the cold chain by default. Sequences of *Nothocybe distincta* were used for rooting purposes based on Matheny *et al.* (2020). Nodes that received bootstrap proportions, ≥ 80 % of SHaLRT support, ≥ 95 % of UFBoot support and > 0.95 of BPP support were considered strongly supported, and nodes that met the criteria for strong support for at least one, but not all three of the methods, were considered moderately supported. Phylogenetic reconstructions for gene regions (ITS+28S, *RPB2*) was also performed separately with IQ-TREE v. 1.6.12.

RESULTS

Phylogenetic analysis

This study generated 17 new sequences submitted to GenBank (Table 1). The new species named *Inocybe beninensis* failed to yield any *RPB2* amplicons. In the dataset, the ITS partition included 150 taxa and 925 sites, the 28S partition included 163 taxa and 1 529 sites and *RPB2* included 85 taxa and 782 sites. Individual gene tree phylogenies (ITS+28S and *RPB2*) are shown in Supplementary Figs S1, S2. No strongly supported conflict was observed. Phylogenetic analyses of ITS, 28S and *RPB2* sequences data supported the distinction of four novel nodulose-spored *Inocybe* from tropical regions of Africa described below as *I. beninensis sp. nov., I. flavipes sp. nov., I. fuscobrunnea sp. nov*. and *I. pallidiangulata sp. nov*. All four new species were well-separated from sister species, and separate collections of the same species formed well supported clades with short internal branches in ML and BI analyses (Fig. 1).

Inocybe beninensis and *I. flavipes* were part of a subclade leading to the *I. calida* group, together with the specimen *Inocybe* sp. L4517e_Inoc_Zam11 from Zambia (belonging to what seems to be an undescribed species). *Inocybe beninensis* in turn was weakly supported (60 % SH-aLRT values, 75 % ML ultrafast bootstrap, 0.8 BPP) as sister to the common clade that they formed. The low sequence divergences (1.9 %) between the sequences of ITS of the collections MR00383, HLA0363, investigated here, and the sequence of the collection L4512_Inoc_Zam05 from Zambia, indicated that they may very well be conspecific, suggesting a wide distribution for *I. flavipes.*

Inocybe fuscobrunnea was moderately supported (88 % SH-aLRT values, 50 % ML ultrafast bootstrap, 0.6 BPP) as sister to the *I. asterospora* group including the European species *I. fibrosa* and *I. asterospora,* and Asian species *I. rekhankitha*, *I. silvana* and *I. pileosulcata.*

Inocybe pallidiangulata was weakly supported (54 % SH-aLRT values, 60 % ML ultrafast bootstrap, 0.7 BPP) as member of an inclusive clade with a major tropical component; including many species from India, Zambia, and Guyana.

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Table 1. List of taxa used in the molecular analyses along with vouchers, GenBank accession numbers and geographic origin. The new species and their accession numbers are in bold.

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
Inocybe acanthosperma Matheny & Bougher	PBM3773	Australia	KJ729861	KJ729889	KJ729923	Matheny *et al.* (2017)
I. acuta Boud	TURA:5066	Finland	KP171102	KM197208	n/a	Unpublished
I. aff. *asterospora* Quél	PBM2453, PBM-2014	USA	DQ404390	AY702015	n/a	Kuo & Matheny (2015)
I. aff. *diabolica* Vauras	PBM2976	USA	n/a	KP170948	KM246001	Horak *et al.* (2015)
I. aff. *xanthomelas* Boursier & Kühner	PAM06060405, TENN063834	France	HQ586867	HQ641109	n/a	Horak *et al.* (2015)
I. alpinomarginata C.L. Cripps, E. Larss.& Vauras	CLC1303	USA	MK153644	MK153644	n/a	Cripps *et al.* (2019)
I. ambigua Romagn	BJ910730	Sweden	AM882800	AM882800	n/a	Ryberg *et al.* (2008)
I. angustifolia (Corner & E. Horak) Garrido	DED8139	Thailand	GQ892988	GQ892942	MH577422	Horak *et al.* (2015)
I. antoniniana E. Sesli, Bandini & Krisai	Fungi 4064	Turkey	MN988712	n/a	n/a	Bandini *et al.* (2020b)
I. appendiculata Kühner	SAT0026155	USA	n/a	JN974946	MH577432	Ryberg & Matheny (2012)
I. arctica E. Larss., Vauras & C.L. Cripps	JV2238	Norway	KY033843	KY033843	n/a	Larsson *et al.* (2017)
I. argenteolutea Vauras	EL9906	Sweden	FN550889	FN550889	n/a	Ryberg *et al.* (2010)
I. asterospora Quél	EL100-14	Sweden	MN296110	MN296110	n/a	Cripps *et al.* (2019)
I. ayangannae Matheny, Aime & T.W. Henkel	MCA 1232	Guyana	n/a	AY239018	AY337364	Matheny *et al.* (2009)
I. babruka K.P.D. Latha & Manim.	CAL 1344	India	KY440086	KY549116	KY553237	Latha & Manimohan (2017)
I. baltica Vauras & E. Larss.	EL50-09	Svalbard	KY033838	KY033838	n/a	Larsson *et al.* (2017)
***I. beninensis* Aïgnon, Yorou & Ryberg**	**HLA0390**	**Benin**	**MN096196**	**MN097888**	**n/a**	**This study**
	HLA0467	**Benin**	**MT994602**	**n/a**	n/a	
I. bombina Bandini & B. Oertel	KR-M-0043212	Germany	MK929261	n/a	n/a	Bandini *et al.* (2019)
I. botaurina Bandini & B. Oertel	DB1-6-12-1	Germany	MK929259	n/a	n/a	Bandini *et al.* (2019)
I. brevisquamulosa E. Horak, Matheny & Desjardin	ZT10102	Thailand	NR_153123	GQ892974	n/a	Horak *et al*. (2015)
I. brunneolipes Grund & D.E. Stuntz	DG1863	Canada	KY923032	NG_057289	n/a	Unpublished
I. cacaocolor Matheny & Bougher	PBM3790	Australia	KJ778845	KJ756464	KJ756422	Matheny *et al*. (2017)
I. calida Valen	TAA185175	Estonia	AM882760	AM882760	n/a	Ryberg *et al.* (2008)
I. calocephala Matheny & Bougher	PBM3600	Australia	n/a	NG 057234	KJ756413	Matheny & Bougher (2017)
I. calospora f. *pectinata* Guinb	PAM10082903	France	KP171112	KP170900	n/a	Unpublished
I. calospora Quél	PAM08092808	France	n/a	KP170899	n/a	Unpublished
I. calospora Quél	PAM99082905	France	HQ586871	HQ641114	n/a	Unpublished
I. calospora Quél	PAM10092501	France	KP171113	KP170901	n/a	Matheny *et al.* (2017)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
I. calospora Quél	PAM00073102	France	HQ586853	HQ641093	n/a	Unpublished
I. calospora Quél	PAM03082401	France	HQ586852	Q641094	n/a	Unpublished
I. calospora Quél	EL9505	Finland	AM882759	AM882759	n/a	Ryberg *et al.* (2008)
I. candidipes Kropp & Matheny	BK 24-July-99-7	USA	n/a	AY239019	AY337366	Kropp & Matheny (2004)
I. caprimulgi Vauras & E. Larss.	JV5808	Finland	KT958924	KT958924	n/a	Vauras & Larsson (2016)
I. cerasphora Singer	BSI 01/184	Chile	n/a	AY380370	AY337367	Matheny (2005)
I. ceskae Bandini	PBM 1315	USA	n/a	AY380387	AY337395	Matheny (2005)
I. cf. *intricata* Peck	TENN:063834	France	n/a	KP170914	KM245990	Matheny & Bougher (2017)
I. cf. *xanthomelas* Boursier & Kühner	EL3505	Norway	AM882989	AM882989	n/a	Ryberg *et al.* (2008)
I. chalcoceps Matheny & Bougher	TENN:068946	Australia	n/a	NG 057228	n/a	Matheny & Bougher (2017)
I. chondroderma D.E. Stuntz ex Matheny, Norvell & E.C. Giles	PBM1776	USA	GU949579	JN974967	MH249789	Matheny *et al.* (2013)
I. conspicuospora Buyck & Eyssart.	PC 96042	Zambia	n/a	EU555471	EU555470	Matheny *et al*. (2009)
I. corydalina Quél	TURA6488/ AM10687	Belgium/ Russia	AY038314	AY337370	n/a	Matheny *et al*. (2002)
I. curvipes P. Karst	PBM 2401	USA	n/a	AY239022	AY337414	Matheny (2005)
I. diabolica Vauras	EL9006	Sweden	FN550896	FN550896	n/a	Ryberg *et al.* (2010)
I. dunensis P.D. Orton	EL22906	France	FN550888	FN550888	n/a	Unpublished
I. epidendron Matheny, Aime & T.W. Henkel	MCA 1880, TH9186	Guyana	JN168725	EU569840	n/a	Matheny *et al*. (2009)
I. eriocaulis Matheny & Bougher	PBM2132	Australia	KJ778853	EU569843	EU569842	Matheny *et al*. (2009)
I. favrei Bon	JV30673	Norway	KY033798	KY033798	n/a	Larsson *et al.* (2017)
I. fibrosa (sowerby) Gillet	EL2599	Estonia	AM882846	AM882846	n/a	Ryberg *et al.* (2008)
***I. flavipes* Aïgnon, Yorou & Ryberg**	**MR00383**	**Togo**	**MN096197**	**MN097889**	**MW080915**	**This study**
	HLA0363	**Benin**	**MT994601**	n/a	n/a	
	L4512_Inoc_Zam05	Zambia	FR731552	n/a	n/a	Tedersoo *et al.* (2011)
I. flavoalbida Matheny & Bougher	PBM3768	Australia	KJ729873	KJ729901	KJ729932	Matheny & Bougher (2017)
I. flavobrunnescens Esteve-Rav., G. Moreno & Bizio	EL484-13	Spain	MK153642	MK153642	n/a	Esteve-Raventós *et al*. (2015)
I. flavosquamulosa C.K. Pradeep & Matheny	CAL 1353	India	KY440087	KY549117	KY553238	Latha & Manimohan (2017)
I. flavosquamulosa C.K. Pradeep & Matheny	CAL 1355	India	KY440088	KY549118	n/a	Latha & Manimohan (2017)
I. floccosistipitata K.P.D. Latha & Manim.	CAL 1256	India	KY440089	KY549119	KY553239	Latha & Manimohan (2017)
I. fuligineoatra Huijsman	PBM 2662	USA	EU523589	EU307831	EU307833	Matheny *et al.* (2009)
I. fuscata Singer	MES544	Chile	KP171120	KP170909	KM245986	Horak *et al*. (2015)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
I. fuscicothurnata Grund & D.E. Stuntz	PBM3980	USA	MF487844	KY990485	MF416408	Larsson *et al.* (2014)
***I. fuscobrunnea* Aïgnon, Yorou & Ryberg**	**MR00378**	**Burkina Faso**	**MN096201**	**MN097893**	**MW21933**	**This study**
	HLA0567	**Ivory Coast**	**MT994603**	n/a	n/a	
I. giacomi J. Favre	JV21543	Finland	MK153656	MK153656	n/a	Cripps *et al.* (2019)
I. glaucodisca Buyck & Eyssart.	PC 96081	Zambia	n/a	EU569853	n/a	Matheny *et al.* (2009)
I. godeyi Gillet	JV 14914F	Italy	n/a	AY038316	AY337378	Matheny *et al*. (2002)
I. gracilior E. Horak	PDD:72707	New Zealand	KY827277	KY827242	n/a	Horak (2018)
I. griseovelata Kühner	PBM2442	USA	KC305453	JN974938	KC305420	Ryberg & Matheny (2012), Braaten *et al.* (2014)
I. hirculus Vauras	JV30693	Finland	MK153643	MK153643	n/a	Cripps *et al.* (2019)
I. horakomyces Garrido	PDD:72491	New Zealand	KY827286	KY827251	n/a	Horak (2018)
I. humidicola Matheny & Bougher	PBM3719	Australia	KP171126	KJ801181	KJ811575	Matheny & Bougher (2017)
I. hydrocybiformis (Corner & E. Horak) Garrido	CAL 1376	India	KY440090	KY549120	KY553240	Latha & Manimohan (2017)
I. hystrix (Fr.) P. Karst.	SJ020824	Sweden	AM882810	AM882810	n/a	Ryberg *et al.* (2008)
I. impexa (Lasch) Kuyper	TAA172127	Finland	AM882821	AM882821	n/a	Ryberg *et al.* (2008)
I. insulana K.P.D. Latha & Manim.	CAL 1258	India	KY440092	KY549122	KY553241	Latha & Manimohan (2017)
I. iringolkavensis K.P.D. Latha & Manim.	K(M) 191731	India	KM924524	KM924519	KY553242	Latha & Manimohan (2017)
I. johannis-stanglii Bandini, Esteve-Rav. & G. Moreno	BAN959 KR M 0043321	Germany	KX290793	n/a	MH496019	Esteve-Raventós *et al*. (2018)
I. kapila K.P.D. Latha & Manim.	CAL 1346	India	KY440093	KY549123	n/a	Latha & Manimohan (2017)
I. kohistanensis Jabeen, I. Ahmad & Khalid	LAH 35001	Pakistan	NR_153155	n/a	n/a	Jabeen *et al.* (2015)
I. krieglsteineri Fern. Sas.	RFS031213-03	France	KT958914	KT958914	n/a	Kropp *et al.* (2010)
I. kurkuriya K.P.D. Latha & Manim.	CAL 1352	India	KY440095	KY549125	KY553245	Latha & Manimohan (2017)
I. kuruvensis K.P.D. Latha & Manim.	K(M) 191734	India	KM924522	KM924517	KY553246	Latha & Manimohan (2017)
I. lacera (Fr.) P. Kumm.	PBM2541	USA	KP171144	JN974993	KM245991	Ryberg & Matheny (2012)
I. lacunarum Vauras & E. Larss.	JV12244	Finland	KT958908	KT958908	n/a	Vauras & Larsson (2015)
I. lanuginosa (Bull.) P. Kumm	PBM3023/ PBM3719	USA	KP171126	KP170923	KM245992	Matheny *et al.* (2020)
I. lasseri Dennis	MCA 1971	Guyana	n/a	EU569857	EU569856	Matheny *et al.* (2009)
I. lasseroides (E. Horak) Garrido	PBM3749	Australia	KP171145	KP170924	KM245993	Horak *et al*. (2015)
I. leptospermi (E. Horak) Garrido	PBM3628	New Zealand	KP308758	KP170935	KJ811592	Matheny & Bougher (2017)
I. lilacinosquamosa Matheny, Aime & T.W. Henkel	MCA 1464	Guyana	n/a	AY380386	AY337389	Matheny *et al.* (2009)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
I. lineata E. Horak, Matheny & Desjardin	DED8048	Thailand	n/a	GQ892958	KM245999	Horak *et al.* (2015)
I. luteifolia A.H. Sm.,	PBM2642	USA	n/a	EU307814	EU307816	Kropp *et al.* (2010)
I. luteo-olivacea Matheny, Bougher & Halling	NY:01491109	Australia	KP308772	KP170946	KJ811603	Matheny & Bougher (2017)
I. melanopoda D.E. Stuntz 1954	PBM3975	USA	n/a	MH220276	MH249807	Matheny *et al.* (2020)
I. mendica E. Horak	PDD:97864	New Zealand	KP308780	KP170951	KM406193	Horak *et al.* (2015)
I. mixtilis (Britzelm.) Sacc.	ARAN-Fungi 4711	Spain	MH500842	MH500842	MH496022	Esteve-Raventós *et al.* (2018)
I. murina E. Larss., C.L. Cripps & Vauras	CLC1226	USA	MK153679	MK153679	n/a	Cripps *et al.* (2019)
I. muthangensis K.P.D. Latha & Manim.	K(M) 191735	India	KM924521	KM924516	KY553247	Latha & Manimohan (2017)
I. napipes J.E. Lange	PBM 2376	Norway	n/a	AY239024	AY337390	Matheny (2005)
I. nothomixtilis Esteve-Rav., Bandini & V. González	AH 46558, MC0003	Spain, Italy	MT384015	n/a	MH496025	Kropp & Matheny (2004)
I. oblectabilis (Britzelm.) Sacc.	BJ920908	Sweden	AM882831	AM882831	n/a	Ryberg *et al.* (2008)
I. obtusiuscula Kühner	PAM02081710	France	HQ586869	HQ641112	n/a	Matheny & Bougher (2017)
I. occulta Esteve-Rav., Bandini, B. Oertel & G. Moreno	AH 36443	Spain	NR_160564	n/a	MH496017	Esteve-Raventós *et al.* (2018)
I. ohenojae Vauras & E. Larss.	ohenojae02081975	Canada	KJ399955	KJ399955	n/a	Larsson *et al.* (2014)
I. olivaceohinnulea Matheny & Bougher	PBM3624	Australia	KP308797	KP170965	KM406205	Matheny & Bougher (2017)
***I. pallidiangulata* Aïgnon, Yorou & Ryberg**	**HLA0563**	**Burkina Faso**	**MZ605435**	n/a	n/a	**This study**
	MR00377	**Burkina Faso**	**MN096202**	**MN097894**	**MW21932**	
	MR00379	**Burkina Faso**	**MZ605434**	**n/a**	**n/a**	
	MR00384	**Burkina Faso**	**MZ605433**	**n/a**	**n/a**	
I. pallidicremea Grund & D.E. Stuntz	PBM2448	USA	HQ201357	HQ201357	MF416425	Matheny *et al.* (2020)
I. papilliformis C.K. Pradeep & Matheny	CAL 1372	India	KY440096	KY549126	n/a	Latha & Manimohan (2017)
I. paragiacomi E. Larss., C.L. Cripps & Vauras	EL64-11	Sweden	MK153670	MK153670	n/a	Cripps *et al.* (2019)
I. parvibulbosa E. Horak, Matheny & Desjardin	SFSU:DED8021	Thailand	GQ892999	GQ892954	KM555134	Horak *et al.* (2015)
I. persicinipes Matheny & Bougher	PBM2197/E7044	Australia	KF977215	EU600837	EU600836	Matheny *et al.* (2009), Matheny & Bougher (2017)
I. phaeocystidiosa Esteve-Rav., G. Moreno & Bon,	CLC1133	USA	MK153630	MK153630	n/a	Cripps *et al.* (2019)
I. phaeoleuca Kühner	EL297-08	Hungary	KJ399958	KJ399958	n/a	Seress *et al.* (2016)
I. phaeosticta Furrer-Ziogas	PAM05091310	France	HQ586859	HQ641102	MH577435	Unpublished
I. pileosulcata E. Horak, Matheny & Desjardin	CAL 1362	India	KY440098	KY549128	n/a	Latha & Manimohan (2017)
I. pileosulcata E. Horak, Matheny & Desjardin	CAL 1368	India	KY440099	KY549129	n/a	Latha & Manimohan (2017)
I. pingala K.P.D. Latha & Manim.	CAL 1345	India	KY440100	KY549130	KY553248	Latha & Manimohan (2017)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
I. pluppiana Bandini, B. Oertel & U. Eberh.	SMNS-STU-F-0901254	Netherlands	MN512327	MN512327	n/a	Bandini *et al.* (2020a)
I. pluvialis Matheny, Bougher & G.M. Gates	PBM3228	Australia	KF871777	KF853401	KF891954	Matheny & Bougher (2017)
I. populea Takah. Kobay. & Courtec.	TAKK15655	Japan	KT958911	n/a	n/a	Kobayashi & Courtecuisse (2000)
Inocybe praetervisa Quél	AH44415	Spain	KT203793	KT203793	n/a	Esteve-Raventós *et al.* (2015)
	SF229598	Italy	KT203792	n/a	n/a	
	UBC:F19322	Canada	HQ604397	HQ604397	n/a	
	UBC:F19334	Canada	HQ604401	HQ604401	n/a	
I. pseudodestricta Stangl & J. Veselský	JV061030	Italy	FN550908	FN550908	n/a	Unpublished
I. pulchella Matheny, Aime & T.W. Henkel	MCA 1122	Guyana	n/a	EU600842	n/a	Matheny *et al*. (2009)
I. purpureobadia Esteve-Rav. & A. Caball.	CLC 1205	USA	MK153689	MK153689	n/a	Cripps *et al.* (2019)
I. purpureoflavida K.B. Vrinda & C.K. Pradeep	CAL 1379	India	KY440101	KY549131	n/a	Latha & Manimohan (2017)
I. rekhankitha K.P.D. Latha & Manim.	CAL 1356	India	KY440102	KY549132	n/a	Latha & Manimohan (2017)
I. relicina (Fr.) Quél.	JV 10258	Finland	n/a	AY038324	AY333778	Matheny *et al.* (2002)
I. rivularis Jacobsson & Vauras	Weholt120818	Norway	KY033811	KY033811	n/a	Unpublished
I. roseifolia Murrill	CO5576	USA	n/a	MK421968	MH577441	Matheny *et al.* (2020)
I. rufobadia Matheny & Bougher	NLB885	Australia	KF977213	KF915290	KF991385	Matheny & Bougher (2017)
I. sambucina (Fr.) Quél.	SJ01002	Sweden	AM882757	AM882757	n/a	Ryberg *et al.* (2008)
I. scissa (E. Horak) Garrido	PDD:82757	New Zealand	KY827287	KY827239	n/a	Horak (2018)
I. sejuncta Matheny, Bougher & M.D. Barrett	PBM3752	Australia	n/a	KP171002	KM555103	Matheny & Bougher (2017)
I. serrata Cleland	PBM3235	Australia	KP636810	KP171012	KM555111	Matheny & Bougher (2017)
I. silvana K.P.D. Latha & Manim.	CAL 1259	India	KY440104	KY549134	n/a	Latha & Manimohan (2017)
I. snigdha K.P.D. Latha & Manim.	CAL 1350	India	KY440105	KY549135	KY553250	Latha & Manimohan (2017)
I. soluta Velen.	EL2904	Sweden	AM882755	AM882755	n/a	Ryberg *et al.* (2008)
Inocybe sp.	PC 96039	Zambia	n/a	EU555474	EU555473	Matheny *et al*. (2009)
Inocybe sp.	PC 96095	Zambia	n/a	EU569860	n/a	Matheny *et al*. (2009)
Inocybe sp.	PC 96111	Zambia	EU600875	EU600875	n/a	Matheny *et al*. (2009)
Inocybe sp.	MR00219	Australia	KF830031	KF808343	KF830049	Matheny & Bougher (2017)
Inocybe sp.	PERTH:08383235	Australia	KP636839	KP171043	KM555138	Matheny & Bougher (2017)
Inocybe sp.	3243F7	USA	KF618024	KF618024	n/a	Unpublished
Inocybe sp.	DPL12128	USA	MH578022	MT241843	MH618233	Unpublished
Inocybe sp.	D25 (WTU)	Argentina	n/a	AY380363	AY337361	Matheny (2005)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
Inocybe sp.	L4517e_Inoc_Zam11	Zambia	FR731548	n/a	n/a	Tedersoo *et al.* (2011)
Inocybe sp.	96083 (PC)	Zambia	n/a	EU600884	n/a	Matheny *et al*. (2009)
Inocybe sp.	ZT10031 (SFSU)	Thailand	GQ893020	GQ892976	n/a	Horak *et al.* (2015)
I. spadicea Matheny & Bougher	PBM2203	Australia	KP636866	EU600865	n/a	Matheny *et al*. (2009), Matheny & Bougher (2017)
I. spiniformis Matheny & Bougher	PBM3748	Australia	KP636868	KP171064	KM656103	Matheny & Bougher (2017)
I. splendens R. Heim	EL313-12	France	KJ399959	KJ399959	n/a	Larsson *et al.* (2014)
I. stellata E. Horak, Matheny & Desjardin	CAL 1369	India	KY440106	KY549136	KY553251	Latha & Manimohan (2017)
I. strickeriana Bandini, Anja Schneid. & M. Scholler	KR:KR-M-0044749	Germany	MG012477	MG551670	n/a	Bandini *et al.* (2018)
I. subcarpta Kühner & Boursier	EL8905	Finland	AM882754	AM882754	n/a	Ryberg *et al.* (2008)
I. subexilis (Peck) Sacc.	PBM2620/ACAD:11680	USA/Canada	MH578001	EU307845	EU307847	Esteve-Raventós *et al*. (2018)
I. subferruginea Matheny & Bougher	E7066 (PERTH)	Australia	n/a	EU600894	n/a	Matheny *et al*. (2009)
I. subfibrosoides Singer	FLAS:MES543	Chile	KP636879	KP171073	KM656117	Matheny & Bougher (2017)
I. subfulva Peck	PBM1482	USA	KP641623	JN974989	n/a	Ryberg & Matheny (2012), Matheny & Bougher (2017)
I. subgiacomi C.L. Cripps, Vauras & E. Larss	JV29938	Sweden	MK153665	MK153665	n/a	Cripps *et al.* (2019)
I. subporospora Kuyper	RP950618	Sweden	AM882931	AM882931	n/a	Ryberg *et al*. (2008)
I. substellata Kühner	EL52-13	France	KT958927	KT958927	n/a	Vauras & Larsson (2016)
I. subtrivialis Esteve-Rav., M. Villarreal & Heykoop	AH26789	Spain	KX354977	n/a	MH496024	Esteve-Raventós *et al*. (2018)
I. sylvicola Matheny, Bougher & G.M. Gates	TENN:065735	Australia	NR_153163	NG 057199	KM656126	Horak *et al*. (2015)
I. taxocystis (J. Favre & E. Horak) Senn-Irlet	Voucher358	Italy	JF908095	n/a	n/a	Osmundson *et al.* (2013)
I. tertia Matheny & Bougher	PBM3730, TENN:066951	Australia	KP641633	KP171086	KM656128	Matheny & Bougher (2017)
I. thailandica E. Horak, Matheny & Desjardin	DED8049	Thailand	GQ893013	GQ892968	KM656129	Matheny *et al.* (2009), Horak *et al.* (2015)
I. torresiae Matheny, Bougher & M.D. Barrett	PBM2157/E6978	Australia	KP641635	EU600874	EU600873	Matheny *et al.* (2009), Horak *et al.* (2015)
I. tubarioides G.F. Atk.	PBM 2570	USA	n/a	AY732210	n/a	Matheny & Moreau (2009)
I. tumidula Matheny & Bougher	PBM3770	Australia	KP641638	KP171090	KM656134	Horak *et al.* (2015), Matheny & Bougher (2017)
I. turbata E. Horak	PDD:82818	New Zealand	KY827281	KY827245	n/a	Horak (2018)
I. umbrosa E. Horak	PDD:106098	New Zealand	MN047364	MN047420	n/a	Unpublished
I. undinea Bandini, P.-A. Moreau, B. Oertel	FR-0246019	Germany	MK929265	n/a	n/a	Bandini *et al*. (2020b)

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Table 1. (Continued).

Species	Voucher	Country	GenBank accession no.			References
			ITS	28S	RPB2	
I. villosa Bandini, B. Oertel & U. Eberh.	BAN1420	Germany	MG012478	n/a	n/a	Esteve-Raventós *et al.* (2018)
I. viraktha K.P.D. Latha & Manim.	CAL 1357	India	KY440107	KY549137	KY553252	Latha & Manimohan (2017)
I. vulpinella Bruyl.	NI250904	Canada	n/a	EU307834	n/a	Matheny *et al.* (2009)
I. wayanadensis K.P.D. Latha & Manim.	K(M) 191737	India	KM924520	KM924515	KY553254	Latha & Manimohan (2017)
I. xanthomelas Boursier & Kühner	PAM08082901	France	HQ586856	HQ641097	n/a	Esteve-Raventós *et al.* (2015)
I. xerophytica Pegler	GUA242	British Virgin Islands	n/a	EU600880	n/a	Matheny *et al.* (2009)
Nothocybe distincta (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha,	CAL 1310	India	KX171343	NG_057278	KX171345	Matheny *et al.* (2009), Latha *et al.* (2016)
	ZT 9250	India	n/a	EU604546	EU600904	

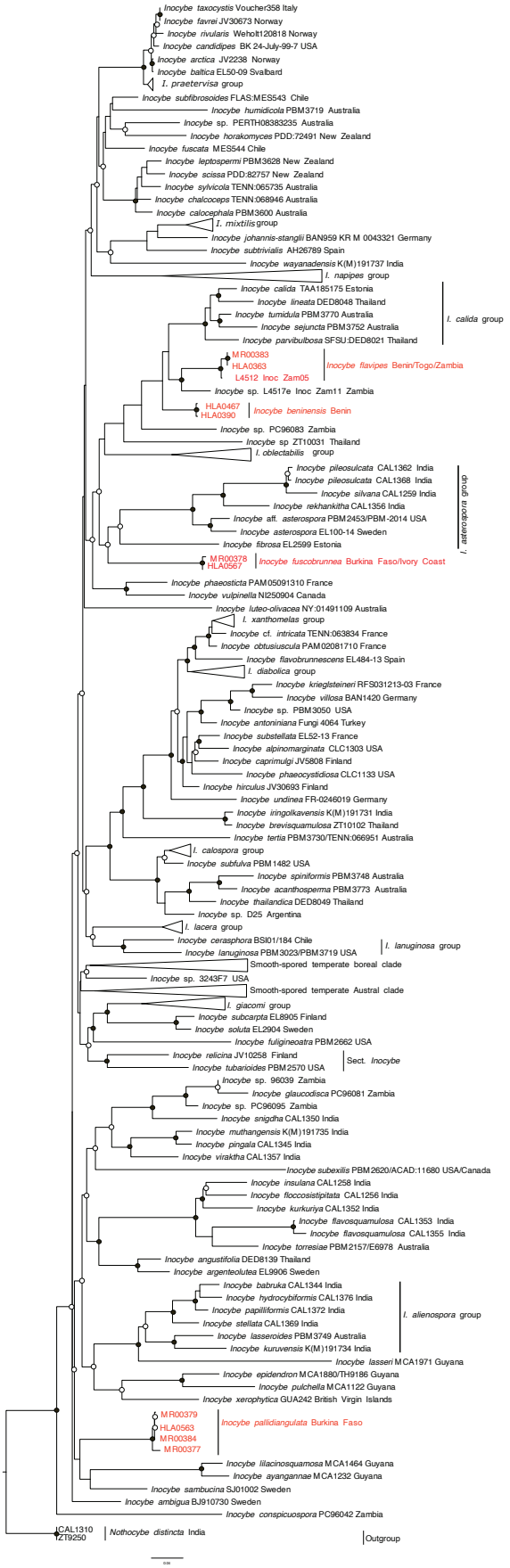

Fig 1. ML tree of ITS, 28S and *RPB2* sequences showing the placement of four new species described from tropical regions of Africa: *Inocybe beninensis*, *I. flavipes I. fuscobrunnea* and *I. pallidiangulata*. Filled circles indicate internodes that are strongly supported (bootstrap proportions SHaLRT support ≥ 80 % / ultrafast bootstrap support ≥ 95 % / Bayesian posterior probabilities > 0.95). Empty circles indicate internodes with moderate support where at least one, but not all, support statistics meet the criteria for strong support). The geographic origin of each tip is given after the species name.

Taxonomy

Inocybe beninensis Aïgnon, Yorou & Ryberg, ***sp. nov.*** MycoBank MB 837971. Figs 2, 3, 10A, B.

Etymology: *beninensis* (L.), referring to the type locality of Benin.

Diagnosis: *Inocybe beninensis* is morphologically similar to *I. flavipes* from Benin and Togo but differs from it by the larger basidiospores on average (10.4 × 8.8 µm *vs*. 8.6 × 5.3 µm) and whitish yellow stipe.

Typus: **Benin**, Collines region, Toui-Kilibo forest reserve, 8.545722N, 2.67375E, on soil in woodlands dominated by *Isoberlinia doka* and *I. tomentosa,* 22 Jun. 2017, *leg*. *H.L. Aïgnon* (**holotype** HLA0390, deposited at UNIPAR). GenBank accessions: ITS (MN096196) and 28S (MN097888).

Description: *Pileus* 7–20 mm wide, conical to plane, sometimes umbonate, fibrillose to tomentose, yellowish (oac715) to orange-brown (oac719); margin dentate. Flesh white, 2 mm thick at umbo, wider towards the edges, margin smooth. *Lamellae* 2–4 mm deep, regular, adnexed to adnate, moderately close, white when young becoming yellowish orange (oac768) with age, edge slightly crisped. Lamellulae multi-tiered. *Stipe* 18–20 × 1.5–3 mm, hollow, flocculose, yellowish white (oac717), central, cylindrical, straight or curved, pruinose, surface slightly fibrillose at the base, veil present. Odour and taste not distinctive. *Basidiospores* (8.0–)8.7–12.0(–12.1) × (6.0–)6.6–10.9(–11.0) µm, avl × avw = 10.4 × 8.8 µm, Q = (1–)0.9–1.4(–1.5), avQ = 1.1, globose, distinctly nodulose with mostly 4–6 conic nodules, brown in KOH under the microscope. Basidia 27–40 × 9–12 µm, 4–spored, clavate to cylindric. *Cheilocystidia* 24–55 × 11–18 µm, subclavate, sometimes thin-walled, with apex sometimes crystalliferous. *Pleurocystidia* 32–44 × 10–15 µm, utriform, thick-walled. *Caulocystidia* 42–45 × 11–25 µm, pyriform to clavate, thin-walled, observed only at the apex of the stipe. *Pileipellis* a trichoderm of filamentous hyphae; subpellis of compact hyphae 3–8 µm wide, thin-walled. *Stipitipellis* a cutis of subcylindrical hyphae 5–20 µm wide, hyaline, thick-walled, with differentiated terminal cells.

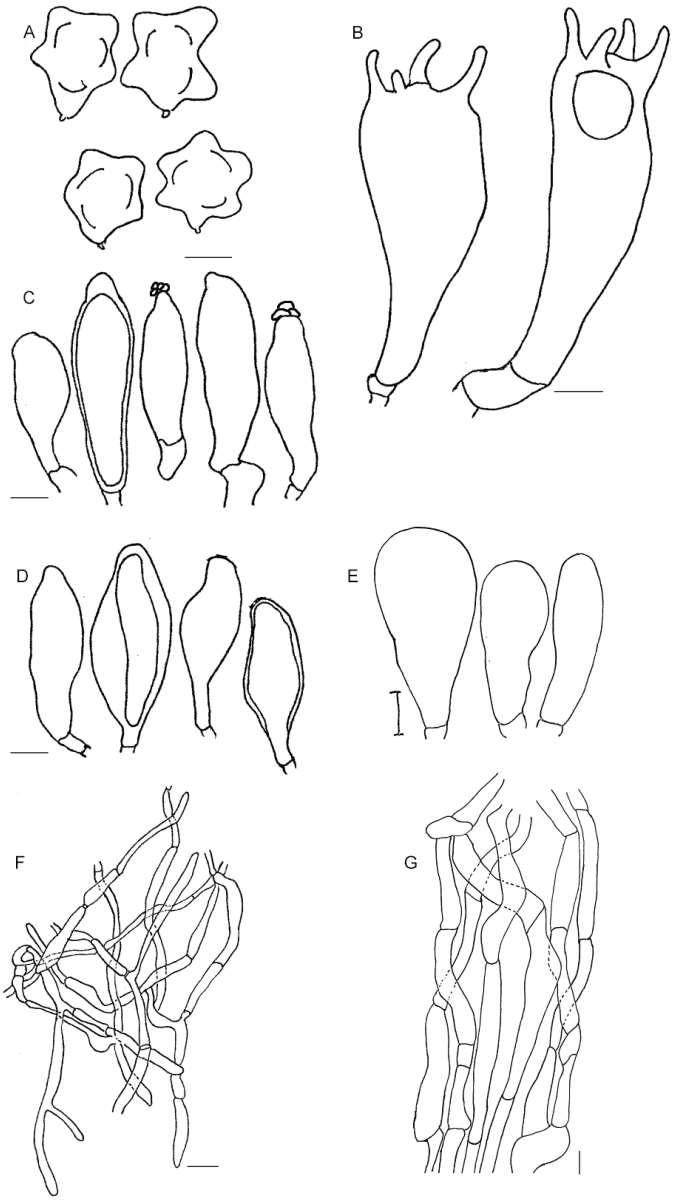

Fig. 2. Micromorphology of *Inocybe beninensis* (HLA0390). **A.** Basidiospores. **B.** Basidia. **C.** Cheilocystidia. **D.** Pleurocystidia. **E.** Caulocystidia. **F.** Pileipellis. **G.** Stipitipellis. Scale bars: A = 3 µm, B = 5 µm; C–G = 10 µm.

Habit: Solitary or in groups, scattered on soil.

Habitat: In woodland dominated by *Isoberlinia doka* and *I. tomentosa.* Occurring June to September.

Geographical distribution: Hitherto known from Benin only.

Additional specimen examined: **Benin**, Borgou Province, N'dali forest reserve, 9.74279N, 2.6929277E, on soil in woodlands dominated by *Isoberlinia doka* and *I. tomentosa,* 1 Sep. 2017, *leg*. *H.L. Aïgnon*, Specimen voucher (HLA0467). GenBank accession: ITS (MT994602).

Inocybe flavipes Aïgnon, Yorou & Ryberg, ***sp. nov.*** MycoBank MB 837975. Figs 4, 5, 10C.

Etymology: *flavipes* (L.), referring to the yellow stipe.

Diagnosis: *Inocybe flavipes* is most similar to *I. beninensis* from Benin but differs from it by the absence of a veil on the stipe, stipe light yellow to light orange, and smaller basidiospores on average (8.6 × 5.3 µm *vs.* 10.4 × 8.8 µm).

Typus: **Togo**, Central region, prefecture of Assoli, Aledjo forest reserve, 9.340278N, 1.251944E, on soil in gallery forest dominated by *Isoberlinia tomentosa*, 17 Jul. 2013, *leg*. *M. Ryberg* (**holotype** MR00383, deposited at UNIPAR). GenBank accessions: ITS (MN096201), 28S (MN097893) and *RPB2* (MW080915).

Description: *Pileus* 6–13 mm wide, hemispherical, conical to conical with broad umbo, surface fibrillose to minutely scaly, yellow brown (oac734) to orange-brown (oac755). Flesh white, 1mm thick at umbo, margin smooth. *Lamellae* 2.5 mm deep, adnexed, lamellulae in tiers, brown (oac734). *Stipe* 14–24 × 1–1.5 mm, surface fibrillose, pruinose in the upper part, more or less equal but with a basal rounded bulb, whitish remnants of a velipellis in lower parts, light yellow (oac716) to light orange (oac718). Odour and taste not distinctive. *Basidiospores* (6–) 6.3–10(–10.9) × (3.7–)4–10(–10.4) µm, avl × avw = 8.6 × 5.3 µm, Q = (1–)1.1–2.2(2.5) µm, avQ = 1.6, elongate, with 3–5, obtuse nodules, prominent and distinct. *Basidia* 20–32 × 6–10 µm,

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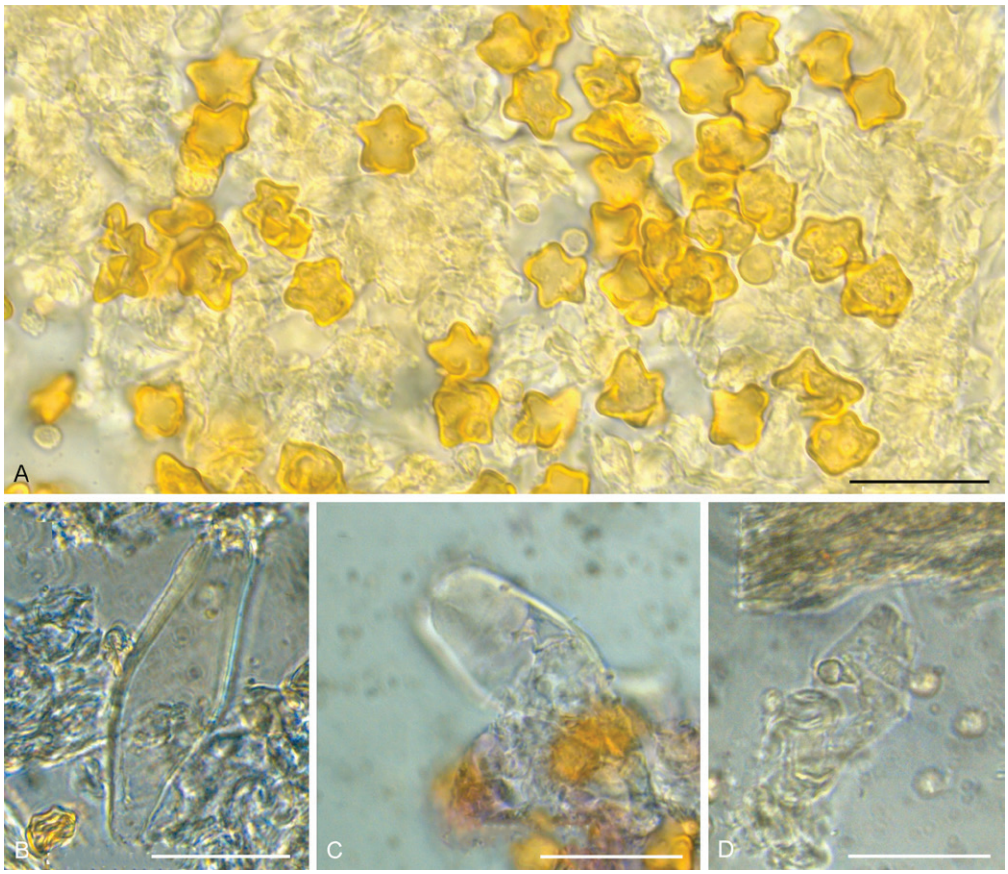
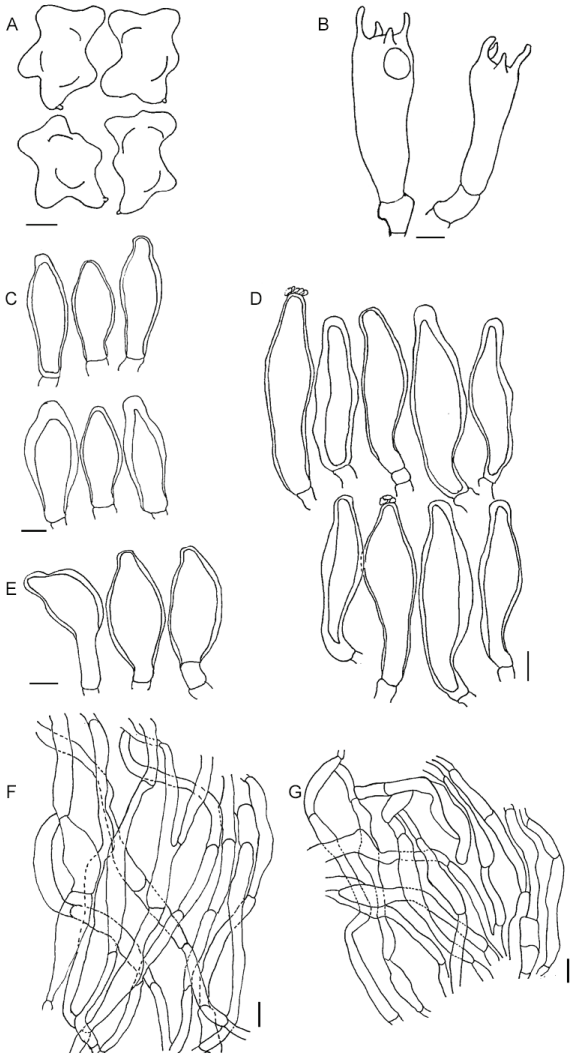


Fig. 3. *Inocybe beninensis* (HLA0390), microscopical characters in KOH. **A.** Basidiospores. **B.** Cheilocystidia. **C.** Pleurocystidia. **D.** Caulocystidia. Scale bars = 20 µm.



generally 4–spored, sometimes 2 or 3-spored. *Cheilocystidia* 32–51 × 11–22 µm, obovoid, apex sometimes crystalliferous, thick-walled. *Pleurocystidia* 35–60 × 12–22 µm, utriform, sometimes obovoid, with short pedicel, sometimes with rounded or truncate base, thick-walled, apex usually crystalliferous. *Caulocystidia* 23–45 × 10–22 µm, sometimes crystalliferous, in upper part of the stipe only, pale brown apex usually. *Pileipellis* a cutis made up of subparallel hyphae 3–12 µm wide. *Stipitipellis* a trichoderm of dense, compact hyphae 4–12 µm wide and thick-walled.

Habit: Solitary, in pairs or in small groups, scattered on soil.

Habitat: In gallery forest dominated by *Isoberlinia tomentosa* or *Isoberlina doka.* Occurring in June to July.

Geographical distribution: Until now known from West Africa: Benin and Togo.

Additional specimen examined: **Benin**, Borgou Province, Commune of Tchaourou, 9.2446277 N, 2.7262333E, on soil in Okpara forests dominated by *Isoberlina doka*, 10 Jun. 2017, *leg*. *H.L. Aïgnon*, Specimen voucher (HLA0363), GenBank accession: ITS (MT994601).

Inocybe fuscobrunnea Aïgnon, Yorou & Ryberg, ***sp. nov.*** MycoBank MB 837976. Figs 6, 7, 10D.

Etymology: *fuscobrunnea* (L.), referring to the dark brown pileus.

Fig. 4. Micromorphology of *Inocybe flavipes* (MR00383). **A.** Basidiospores. **B.** Basidia. **C.** Cheilocystidia. **D.** Pleurocystidia. **E.** Caulocystidia. **F.** Pileipellis. **G.** Stipitipellis. Scale bars: A = 3 µm; B = 5 µm; C–G = 10 µm.

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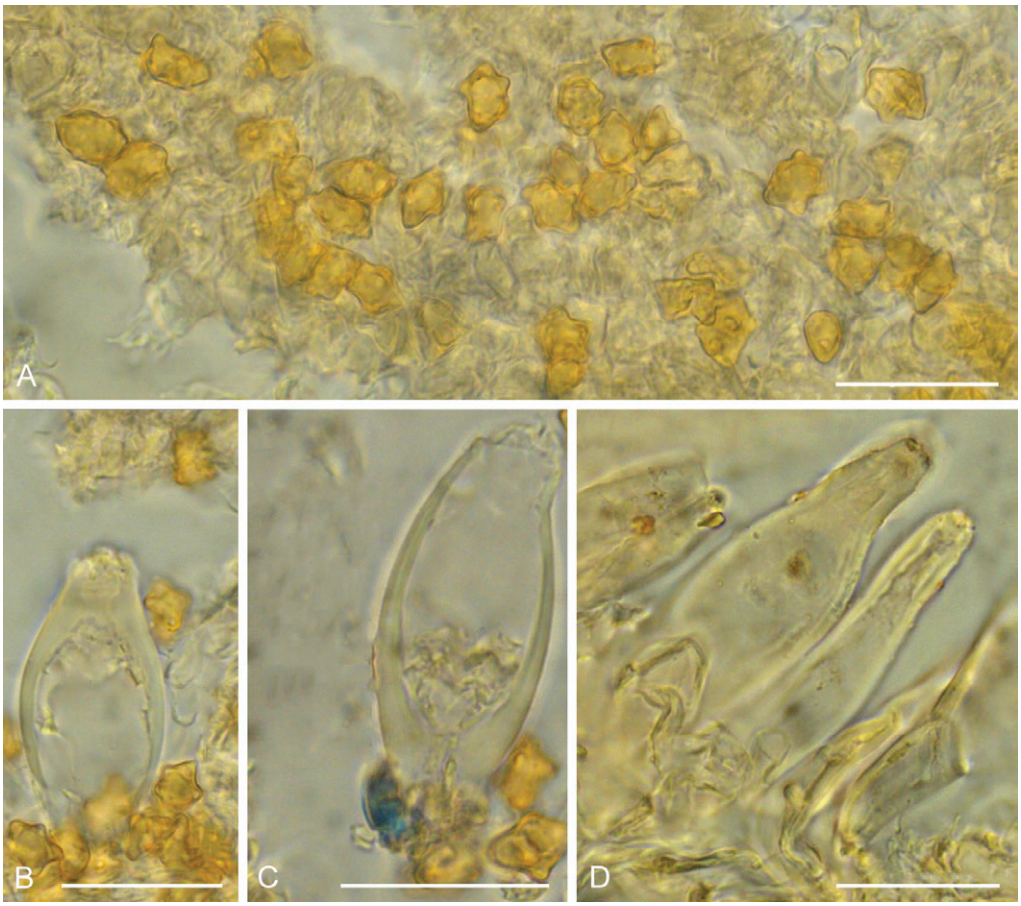

Fig. 5. *Inocybe flavipes* (MR00383), microscopical characters in KOH. **A.** Basidiospores. **B.** Cheilocystidia. **C.** Pleurocystidia. **D.** Caulocystidia. Scale bars: A–D = 20 µm.

Diagnosis: *Inocybe fuscobrunnea* has a dark brown, slightly rimose pileus, nodulose spores measuring 7–12 × 6–10.4 µm, similar to *I. pallidiangulata* in size, but differs from it by the dark reddish brown pileus and larger basidiospores (9.5 × 8.3 µm *vs.* 7.0 × 5.2 µm).

Typus: **Burkina Faso**, Bobo-Dioulasso region, forest reserve of Kou, 11.188027N, 4.440556W, on soil in gallery forests dominated by *Berlinia grandiflora*, 13 Jul. 2013, *leg*. *M. Ryberg* (**holotype** MR00378, deposited at UNIPAR). GenBank accessions: ITS (MN096201), 28S (MN097893) and *RPB2* (MW21933).

Description: *Pileus* 19–40 mm wide, wide conical to plane with obtuse umbo, surface flocculose/tomentose to smooth rimose, brown (oac646) to dark reddish brown (oac836-838), margin smooth, slightly rimose. Flesh white, 2 mm thick under the disc, thinner towards edges, margin rimose. *Lamellae* 3–5 mm deep, adnexed, pale grey (oac809) turning brown with age (oac807), 34 reaching stipe. Lamellae alternate with lamellulae, multi-tiered. Stipe 32–72 × 2.5–4 mm, subclavate, mostly silky greyish yellowish white (oac857), smooth to longitudinally substriate, pruinose in the upper 1/3 part. Odour and taste not distinctive. *Basidiospores* (7–)7.6–11.4(–12) × (6–)6.2–10(–10.4) µm, avl × avw = 9.5 × 8.3 µm, Q = 0.9–1.4 µm, avQ = 1.1, globose, with 3–6 obtuse nodules. *Basidia* 25–38 × 9–14 µm, ventricose, 4-spored. *Cheilocystidia* 30–47 × 12–20 µm, utriform sometimes obovoid, hyaline crystals on the top, often short pedicels, thin-walled. *Pleurocystidia* 35–52 × 11–27 µm, utriform, apex sometimes crystalliferous, rounded or truncate base, thin-walled. *Caulocystidia* 38–51 × 12–17 µm, thin-walled, sometimes crystalliferous, observed only near of the stipe's apex. *Pileipellis* a cutis composed of parallel hyphae 4–31 µm wide. *Stipitipellis* a cutis of subparallel hyphae 6–17 µm wide, hyaline and thick-walled.

Habit: Solitary or in small groups, scattered on soil.

Habitat: In gallery forest dominated by *Berlinia grandiflora.* Occurring in July.

Geographical distribution: Known from West Africa: Burkina Faso and Ivory Coast.

Additional specimen examined: **Ivory Coast**, Koudianikro, gbeke region, Bouake, 7.629444N, 4.746667W, on soil in woodland dominated by *Berlinia grandiflora*, 11 Jul. 2018, *leg*. *L.H. Aïgnon*, Specimen voucher (HLA0567), deposited at UNIPAR. GenBank accession: ITS (MT994603).

Inocybe pallidiangulata Aïgnon, Yorou & Ryberg, ***sp. nov.*** MycoBank MB 837977. Figs 8, 9, 10E, F.

Etymology: *pallidiangulata* (L.), referring to the pale pileus and angular spores.

Diagnosis: *Inocybe pallidiangulata* is characterised by a pale brown to honey-yellow pileus, nodulose spores measuring 6–9 × 3–6.4 µm, caulocystidia only at the apex of the stipe, and apparent ectomycorrhizal association with tropical *Fabaceae* and/or *Phyllanthaceae*. It is superficially similar to *I. fuscobrunea* by being rimose pileus, similar in size, and occurring in the same habitat but differs from it by the paler pileus and smaller basidiospores with very inconspicuously protruding nodules.

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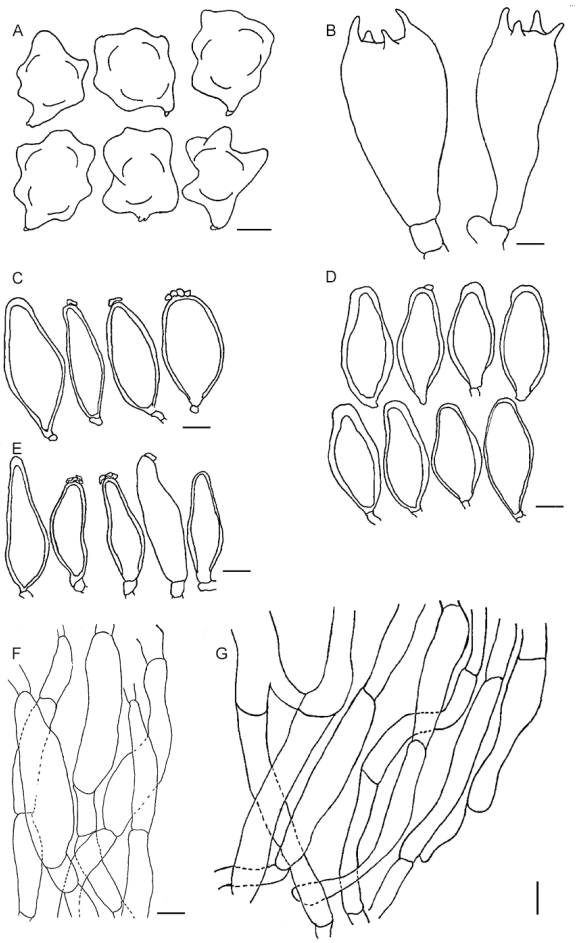

Fig. 6. Micromorphology of *Inocybe fuscobrunnea* (MR00378). **A.** Basidiospores. **B.** Basidia. **C.** Cheilocystidia. **D.** Pleurocystidia. **E.** Caulocystidia. **F.** Pileipellis. **G.** Stipitipellis. Scale bars: A = 3 µm, B = 4 µm, C–G = 10 µm.

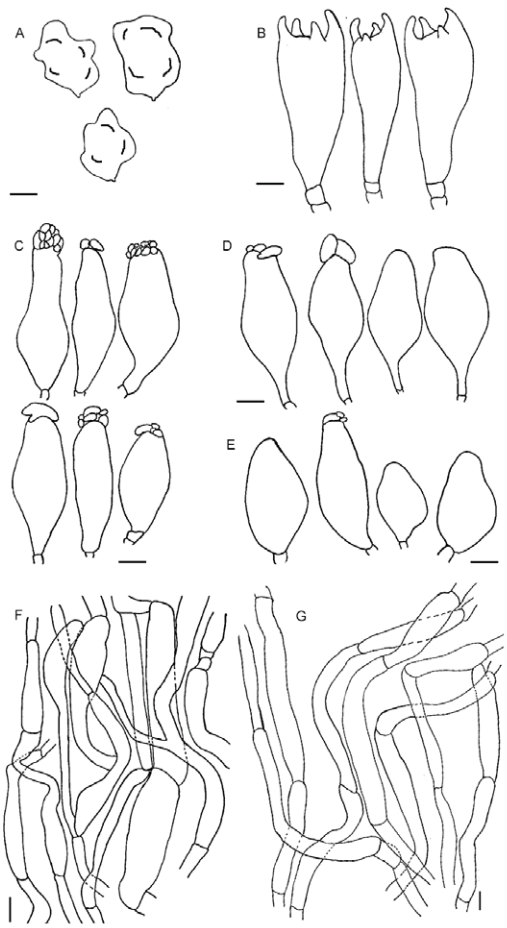

Fig. 8. Micromorphology of *Inocybe pallidiangulata* (MR00377). **A.** Basidiospores. **B.** Basidia. **C.** Cheilocystidia. **D.** Pleurocystidia. **E.** Caulocystidia. **F.** Pileipellis. **G.** Stipitipellis. Scale bars: A = 3 µm, B = 5 µm; C–G = 10 µm.

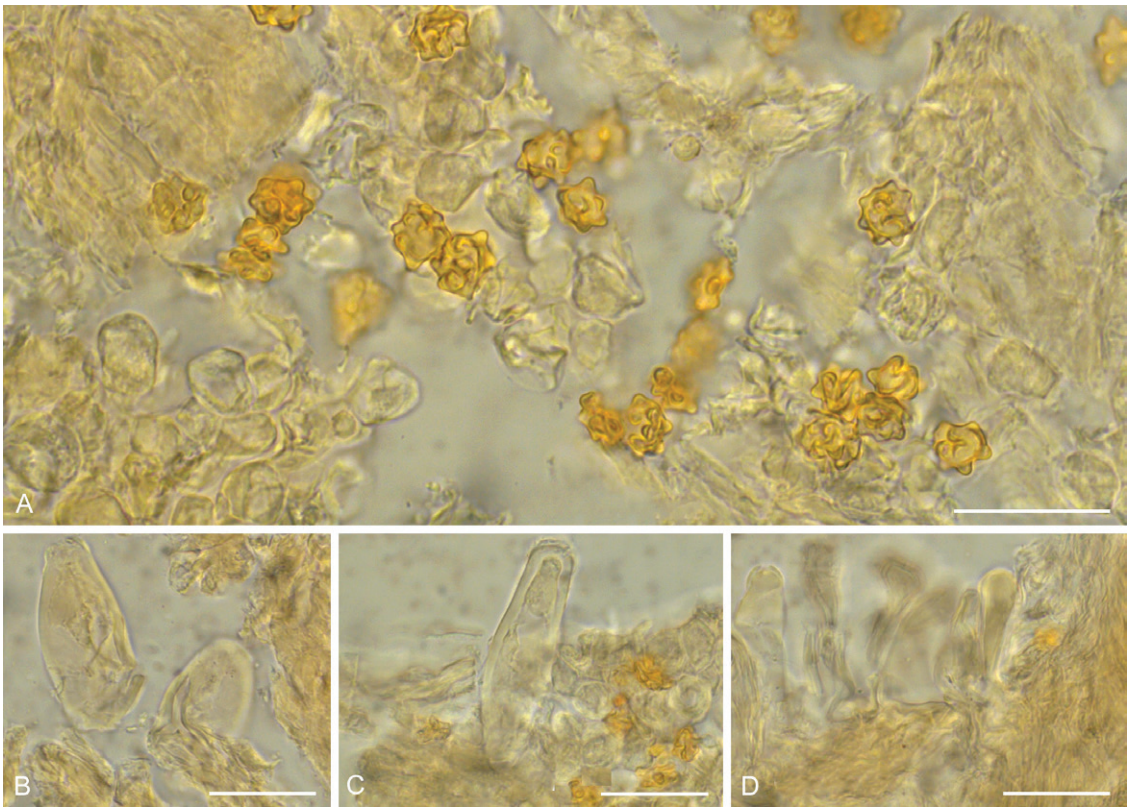

Fig. 7. *Inocybe fuscobrunnea* (MR00378), microscopical characters in KOH. **A.** Basidiospores. **B.** Cheilocystidia. **C.** Pleurocystidia. **D.** Caulocystidia. Scale bars: A–D = 20 µm.

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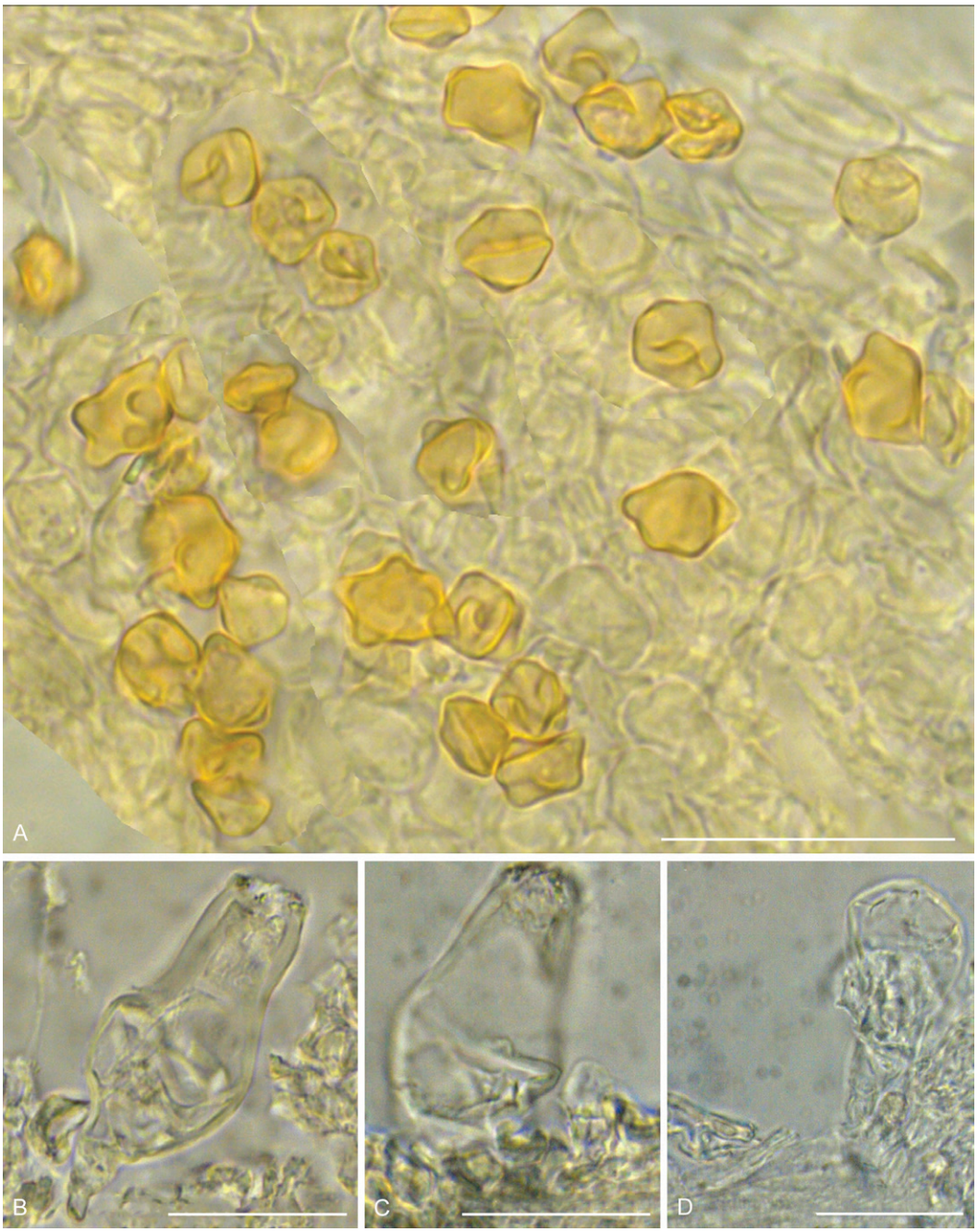

Fig. 9. *Inocybe pallidiangulata* (MR00377), microscopical characters in KOH. **A.** Basidiospores. **B.** Cheilocystidia. **C.** Pleurocystidia. **D.** Caulocystidia. Scale bars: A–D = 20 µm.

Typus: **Burkina Faso**, Bobo Dioulasso, forest reserve of Kou, 11.186861N, 4.4415277W, on soil in gallery forest dominated by *Berlinia grandiflora*. 17 Jul. 2013, *leg*. *M. Ryberg* (**holotype** MR00377, deposited at UNIPAR). GenBank accession: ITS (MN096202), 28S (MN097894) and *RPB2* (MW21932).

Description: *Pileus* 11–29 mm wide, oval, obtuse, conical when young, becoming plane with age, umbo wide, surface fibrillose, fibrils, pale brown (oac825), almost honey-yellow (oac826). Flesh white to greyish white (oac847), 5 mm thick at centre, thinner at edges, margins serrate and slightly rimose. *Lamellae* 3 mm deep, adnexed, 36 reaching stipe, grey white (oac816). *Lamellulae* multi-tiered. *Stipe* 14–45 × 4.5–6 mm, equal to slightly wider at the centre, base bulbous having marginate bulb in young specimens, not obvious in old specimens, stipe surface longitudinally striated, white when young becoming yellow (oac858) with age, possible remnants of veil. Odour and taste not distinctive. *Basidiospores* (6–)5.6 –8.5(–9) × (3–) 4–6(–6.4) µm, avl × avw = 7.0 × 5.2 µm, Q = (1–)1.1–1.7(–1.8) µm, avQ = 1.4, ellipsoid with 2–3, very inconspicuously protruding nodules. *Basidia* 20–35 × 7–12 µm, generally 4–spored, seldom 2–spored, clavate. *Cheilocystidia* 25–52 × 11–25 µm, utriform, truncate base or sometimes rounded, apex usually crystalliferous. *Pleurocystidia* 33–63 × 12–22 µm, obovoid sometimes utriform with long pedicel truncate base, apex usually crystalliferous wall thickness. *Caulocystidia* 35–40 × 16–27 µm obovoid, present at stipe apex only, pale brown apex sometimes crystalliferous. *Pileipellis* a cutis made up of compact hyphae, subparallel 4–12 µm wide. *Stipitipellis* a cutis often disrupted, composed of parallel hyphae 6–15 µm wide, thick-walled, encrusted, brownish pigment.

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Fig. 10. Macro-morphology. **A, B.** *Inocybe beninensis* (A = HLA0390, B = HLA0462). **C.** *Inocybe flavipes* (MR00383). **D.** *Inocybe fuscobrunnea* (MR00378). **E, F.** *Inocybe pallidiangulata* (E = MR00377, F = HLA0565). Bar = 1 cm.

Habit: Solitary on soil.

Habitat: In gallery forest dominated by *Berlinia grandiflora.* Occurring in July.

Geographical distribution: West Africa: Burkina Faso, Ivory Coast and Togo.

Additional specimens examined: **Burkina Faso**, Bobo-Dioulasso region, forest reserve of Kou, 11.18694N, 4.441667W, on soil in gallery forest dominated by *Berlinia grandiflora*, 13 Jul. 2013, *leg. M. Ryberg*, specimen voucher (MR00379), deposited at UNIPAR. **Ivory Coast**, Kekrekouakoukro, Gbeke, Bouake region, 7.675388N, 4.908111W, on soil in woodland dominated by *Berlinia grandfifolia* 11 Jul. 2018, *leg. H.L. Aïgnon*, specimen voucher (HLA0565). **Togo**, Central region, prefecture of Assoli, forest reserve of Aledjo, 9.276944N, 1.225556E, on soil in gallery forest dominated by *Berlinia grandiflora* and *Uapaca guineensis*, 17 Jul. 2013, *leg. M. Ryberg*, specimen voucher (*MR00384*).

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Taxonomic key to nodulose-spored *Inocybe* species from tropical Africa

1a. Basidiomata blackish blue and becoming green with a stipe slightly thickened at the base, basidiospores subglobose-quandrangular, 10–13 × 9–12 um, from Tanzania ..... ***Inocybe cyaneovirescens***
1b. Basidiomata not blackish blue and not turning green, stipe base bulbous or not, basidiospores smaller than above if similar in size then basidiomata not turning green 2

2a. Stipe pruinose along entire length 3
2b. Stipe pruinose over the upper part or apex only 4

3a. Stipe robust with a marginate bulb, pale brown to subconcolourous with the pileipellis ..... ***I. glaucodisca***
3b. Stipe remarkably slender, base not bulbous, dark brown but paler and more or less honey-brown in the upper part, with some reddish-brown tinges towards the base ..... ***I. conspicuospora***

4a. Pileus margin rimose, straight, stipe surface longitudinally silky-striate, lacking smell when fresh ..... ***I. ghanaensis***
4b. Pileus margin not rimose, stipe surface not silky-striate, smell present when fresh 5

5a. Pileus margin dentate or serrate 6
5b. Pileus margin smooth 7

6a. Pileus fibrillose to tomentose, margins dentate, stipe hollow, flocculose, yellowish white, surface slightly fibrillose at the base, caulocystidia pyriform to clavate ..... ***I. beninensis***
6b. Pileus conical to conical with broad umbo, surface fibrillose to minutely scaly, stipe surface fibrillose, more or less equal but with a bulb, light yellow to light orange, caulocystidia crystalliferous ..... ***I. flavipes***

7a. Stipe wider, white to yellow, base bulbous having marginate bulb in young specimens ..... ***I. pallidiangulata***
7b. Stipe slender, mostly silky greyish yellowish white, base not bulbous ..... ***I. fuscobrunnea***

DISCUSSION

Four species with nodulose-spores; *Inocybe conspicuospora, I. cyaneovirescens, I. ghanaensis* and *I. glaucodisca* have been described from tropical Africa before this study (Hennings 1902, Pegler 1969, Buyck & Eyssartier 1999), but many undescribed species with nodulose-spores are known from Zambia (Matheny *et al.* 2009, Tedersoo *et al*. 2011). Most of these species have a restricted distribution and so that what is found in tropical Africa is not likely to be the same species as something from other parts of the world (Buyck & Eyssartier 1999). Here we describe four additional new species of *Inocybe*; *I. beninensis, I. flavipes, I. fuscobrunnea* and *I. pallidiangulata* from tropical African regions. Our phylogenetic analyses show that *I. conspicuospora* and *I. glaucodisca* are distinct from the species described here by their distinct positions in the phylogenetic tree. *Inocybe cyaneovirescens* is distinguished by its colour and *I. ghanaensis* differs from the others by the presence of a marginate bulb. In the phylogenetic tree, as none of the new describe species belong in the *I. praetervisa* group, *I. mixtilis* group, *I. napipes* group, *I. oblectabilis* group, *I. xanthomelas* group, *I. diabolica* group, *I. calospora* group, *I. lacera* group, *I. giacomi* group, Smooth-spored temperate boreal clade and Smooth-spored temperate Austral clade, these groups or clades have been reduced without violating the result (Fig. 1). While all the species of these groups used in the phylogenetic analyses are shown in Supplementary Fig. S3. The new species described here emerge as sister to other groups, either by themselves or together with undescribed species from Zambia, or as even more isolated in the phylogeny (Fig.1).

The autonomy of the new species is supported by morphological and molecular data. The new species are currently known from Benin, Burkina Faso, Ivory Coast, Togo and/or Zambia and are associated with *Isoberlinia doka*, *I. tomentosa, Berlinia grandiflora* and/or *Uapaca guineensis* in West Africa and associated with the species of the family *Phyllanthaceae* and/or *Fabaceae* in miombo woodlands. All species described here have pleurocystidia with crystals and nodulose basidiospores, typical characteristics that support their placement in *Inocybe* (Matheny *et al.* 2020).

This study doubles the described diversity of the nodulose-spored species from tropical Africa, but we expect the actual number of species of *Inocybe* from Africa to be higher given the extent and diversity of ectomycorrhizal habitats, ectomycorrhizal tree species, and paucity of previous studies in this group.

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Conflict of interest: The authors declare that there is no conflict of interest.

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Supplementary Material: http://fuse-journal.org/

Fig. S1. ML tree of ITS+28S sequences showing the placement of *Inocybe beninensis*, *I. flavipes I. fuscobrunnea* and *I. pallidiangulata*. For each node, the ML ultrafast bootstrap support ≥ 95 % is presented above or in front of the branch leading to that node.
Fig. S2. ML tree of *RPB2* sequences showing the placement of *Inocybe flavipes, I. fuscobrunnea* and *I. pallidiangulata*. For each node, the ML ultrafast bootstrap support ≥ 95 % is presented above or in front of the branch leading to that node.
Fig. S3. ML tree showing the placement of four new species described from tropical regions of Africa: *Inocybe beninensis*, *I. flavipes I. fuscobrunnea* and *I. pallidiangulata* based on phylogenetic analyses of ITS, 28S and *RPB2* data set.

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