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**Mallocybe africana** (Inocybaceae, Fungi), the first species of *Mallocybe* described from Africa

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**Abstract**

The family Inocybaceae has been poorly studied in Africa. Here we describe the first species of the genus *Mallocybe* from West African and Zambian woodlands dominated by ectomycorrhizal trees of Fabaceae and Phyllanthaceae. The new species *M. africana* is characterized by orange-brown fruitbodies, a fibrillose pileus, a stipe tapered towards the base and large ellipsoid basidiospores. It resembles many north and south temperate species of *Mallocybe* but is most closely related to the southeast Asian tropical species, *M. errata*. *M. africana* is widely distributed in West Africa (Benin, Togo, Burkina Faso and Ivory Coast) extending to South-eastern Africa in Zambia. Phylogenetic analyses based on 5.8S rDNA, nLSU and RPB2 sequence data confirm that *M. africana* is nested within *Mallocybe*. A complete morphological description and illustrations, including photographs and line drawings, are presented.

**Keywords:** African woodland, Agaricales, morphology, systematics, taxonomy

**Introduction**

Systematic studies of macrofungi in West Africa are increasing. However, despite taxonomic progress in some groups documented from West Africa during the last twenty years (Bâ et al. 2013, Maba et al. 2014, 2015, Rooij & Verbeken 2003, Yorou et al. 2011, Yorou & Agerer 2008) the tropical African ecozone, and particularly West Africa, remain poorly explored. In Soudano-Guinean forest ecosystems the family Inocybaceae Jüllichs (1982: 374) is among the least studied of the agaric fungi. Aside from some recent studies conducted in Africa (Matheny & Bougher 2006, Matheny et al. 2017) most identifications of African species of Inocybaceae (Buyck & Eyssartier 1999, Watling 2001) have been made based on morphology using literature from Europe. It is highly likely that Inocybaceae species from Africa differ from those of other continents and many collections are probably misidentified. The lack of taxonomic studies on the diversity of Inocybaceae in Africa has probably led to it being underestimated (Buyck & Eyssartier 1999, Hennings 1901, Watling 2001), therefore, it is essential to increase sampling efforts to identify and describe species of Inocybaceae in African ecosystems.

*Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav (2020:12) was first described as a subgenus of *Inocybe* (Fr.) Fr. (1863:346) but recently Matheny et al. (2020) elevated *Mallocybe* to one of seven genera in Inocybaceae. The genus is a monophyletic group of some 55 species (Matheny et al. 2020) distributed over much of the globe but predominantly occurs in north and south temperate regions and is not well-known outside of Europe and North America.
America (Matheny et al. 2009, 2020). A species of Malocybe was recorded from Sub-Saharan Africa, but it remains undescribed (Matheny et al. 2009, 2020).

Species of Malocybe are generally characterized by coarsely fibrillose, tomentose, or squamulose basidiomata, a dark reaction to weak alkaline solutions like 5% potassium hydroxide, the presence of necropigmented basidia, absence of pleurocystidia, and cheilocystidia present as, often short (<50 μm long), terminal elements of hyphae of the hymenophoral trama (Cripps et al. 2010, Jacobsson 2008, Kuyper 1986, Matheny et al. 2020).

In this paper we present the first species of Malocybe described from the African continent. Morphological and multigene molecular analysis of 5.8S rDNA, nLSU and RPB2 sequences data support Malocybe africana as a species new to science.

Material and methods

Study area and specimen sampling

Specimens were collected between 2013 and 2017 in Benin, Burkina Faso, Ivory Coast and Togo in woodland dominated by ectomycorrhizal trees such as Isoberlinia doka Craib & Stapf (1912: 94), Isoberlinia tomentosa Hutch. (1928: 203), Uapaca togoensis Pax (1904: 371) and Berlinia grandiflora Hutch. & Dalziel (1928: 398). Specimens were dried with an electric dryer (type Stöckli Dörrex) for 24 hours at 45° C. All studied materials, including the holotype, are deposited at the Mycological herbarium of Parakou University (UNIPAR).

FIGURE 1. Study area.

Morpho-anatomical analyses

Specimens were photographed with a Sony FE digital camera. Color codes were described according to Kornerup & Wanscher (1978). Samples of the dried specimens were rehydrated and examined in 3% KOH and Congo Red. Drawings of microscopic characters were made with the aid of a drawing tube attached to a Leica DM2700. Microscopic characters were drawn at 1000× magnification. For each microscopic element observed, 40 measurements were made from three samples from three collections. 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 respectively. Spore measurements are given as (a–)b–c(–d), where (a) = extreme minimum value, range b–c contains the minimum of 90% of the calculated values and (d) = extreme maximum value, as indicated by Jabeen & Khalid (2020).

DNA extraction, PCR and sequencing

Genomic DNA was extracted from dried specimens using a QIAGEN® plant mini kit. Three nuclear gene regions, internal transcribed spacer (ITS), portions of the large subunit ribosomal RNA gene (nLSU) and RNA polymerase II subunit (RPB2), were amplified using the following primers: ITS1F and ITS4 for ITS (Gardes & Bruns 1993, White et al. 1990), LR0R, LR7, LR5 and LR3R for nLSU (Cubeta et al. 1991, Rehner & Samuels 1995, Vilgalys & Hester 1990) and bRPB2-6F, bRPB2-7.1R for the most variable region of RPB2 (Matheny 2005). PCR products were cleaned and sequenced at Macrogen Inc. (Macrogen Europe B.V., Amsterdam, Netherlands) using the same primers as those used for PCR.
We generated fourteen new sequences that have been submitted to GenBank (Table 1), but the accession numbers MT458693, MT509392, MT458692 and MT476161 are not presented in Table 1 because they contain only short fragments of ITS or LSU and were excluded from the phylogenetic analysis. The new sequences were subjected to a BLAST search and relevant related sequences retrieved from GenBank (Benson et al. 2010). These ITS, LSU and RPB2 sequences were aligned separately using MAFFT V7.464 (Katoh et al. 2019). The ITS1 and ITS2 regions of the internal transcribed spacer (ITS) contained highly variable sites, which were difficult to align correctly and were excluded. For phylogenetic analysis, we used 5.8S rDNA, LSU and RPB2. Thus, the 5.8S rDNA partition included 29 taxa with 156 sites, the LSU partition included 49 taxa with 1524 sites and RPB2 included 27 taxa with 772 sites. The final concatenated data set of 5.8S rDNA, LSU and RPB2 was generated using Geneious 7.0.2 (Kearse et al. 2012) and included 49 taxa and 2452 sites.

The dataset was partitioned in 5.8S rDNA, LSU, RPB2 codon position 1, RPB2 codon position 2, RPB2 codon position 3 and the intron in RPB2 separately. We tested for the best partitioning scheme and best model for each partition using ModelFinder (Kalyaanamoorthy et al. 2017). It indicated that keeping all the partitions was the best. Maximum Likelihood (ML) analysis was performed with IQTREE 1.6.12 (Nguyen et al. 2015). Bootstrap support was assessed with 1000 replicates of ultrafast bootstrap resamplings (Hoang et al. 2017). Sequences from Tubariomyces sp. BB6018, T. hygrophoroides Esteve-Rav., P.-A. Moreau & C.E. Hermos (2010: 1394), T. inexpectatus (M. Villarreal, Esteve-Rav., Heykoop & E. Horak) Esteve-Rav. & Matheny (2010: 1390) and T. similis Della Magg., Tolaini & Vizzini (2013: 377) were used as outgroup taxa based on Matheny et al. (2020).

For Bayesian Inference (BI) analyses, GTR models with gamma distributed rate heterogeneity and a proportion of invariant sites parameter were assigned to each partition as indicated above, using MrBayes 3.2.7 (Ronquist et al. 2012), set as follows: Iset applyto = (all), nst = 6, rates = invgamma, ngammacat = 4, sampling frequency = 1000, and the command “unlink” was used to unlink parameters across characters on partitioned datasets. Two independent Markov Chain Monte Carlo (MCMC) processes were executed, each in 4 chains for 20 million generations. Posterior probabilities (BPP) were calculated after burning the first 25% of the posterior sample and ensuring that this threshold met the convergence factors described above.

TABLE 1. List of taxa used in the molecular analyses along with vouchers, accession numbers and geographic origin. The new species is in bold.

| Species | Voucher | Country | ITS | LSU | RPB2 | References |
|---------|---------|---------|-----|-----|------|------------|
| Malloxybe africana Aïgnon, Yorou & Ryberg | BRF4123 | Benin | MK908842 | Unpublished |
| | HLA0462 | Benin | MT458691 | MT456364 |
| | MR00369 | Burkina Faso | MT476162 | MT509361 |
| | MR00385 | Togo | MN096194 | MT465593 |
| | MR00358 | Benin | MT476160 | MT509360 | MT628398 |
| | PC 96204 | Zambia | EU569871 | Matheny et al. 2009 |
| | PC:0088767 | Zambia | MN178510 | Unpublished |
| M. agardhii (N. Lund) Matheny & Esteve-Rav. | JV 7485 | Finland | AY380365 | Matheny 2005 |
| M. althoffiae (E. Horak) Matheny & Esteve-Rav. | ZT:72/495 | Papua New Guinea | NR_163748 | ESI55444 | Matheny et al. 2009 |
| M. arenaria (Bon) Matheny & Esteve-Rav. | EL25008 | France | FN550937 | Matheny et al. 2019 |
| M. arthrocystis (Kühner) Matheny & Esteve-Rav. | PBM 2397 | Norway | AY380394 | Matheny 2005 |
| M. crassivelata Ferisin, Bizio, Esteve-Rav., Vizzini & Dovana | MCVE2956 | Slovenia | MN536812 | Crous et al. 2020 |

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### TABLE 1. (Continued)

| Species (Author) | Voucher | Country | ITS | LSU     | RPB2   | References                  |
|------------------|---------|---------|-----|---------|-------|----------------------------|
| M. errata (E. Horak, Matheny & Desjardin) Haellew | DED8022 | EU569844 | Matheny et al. 2009 |
|                  | ZT10072 | GG892936 | Horak et al. 2015 |
|                  | ZT 9238 | EU569845 | Matheny et al. 2009 |
|                  | ZT10108 | GG892935 | Horak et al. 2015 |
| M. fibrillosa (Peck) Matheny & Esteve-Rav. | LVK14390 | MN178527 | Matheny et al. 2019 |
| M. fulvipes (Kühner) Matheny & Esteve-Rav. | EL8307 | FN550935 | Cripps et al. 2010 |
| M. fuscomarginata (Kühner) Matheny & Esteve-Rav. | BJ890718 | GU980656 | Cripps et al. 2010 |
| M. gymnocarpa (Kühner) Matheny & Esteve-Rav. | SJ980707 | AM882866 | Ryberg et al. 2008 |
| M. heimii (Bon) Matheny & Esteve-Rav. | JV 14932F | AY380379 | Matheny 2005 |
| M. isabellina (Matheny & Bouger) Matheny & Esteve-Rav. | PERTH:07712758 | MN178501 | Matheny et al. (2019) |
| M. latispora (Bon) Matheny & Esteve-Rav. | JV19640F | MN178503 | Matheny et al. 2019 |
| M. leucoblema (Kühner) Matheny & Esteve-Rav. | PBM1522 | MN178533 | Cripps et al. 2010 |
| M. leucoloma (Kühner) Matheny & Esteve-Rav. | CLC1869 | GU980618 | Cripps et al. 2010 |
| M. malenconii (R. Heim) Matheny & Esteve-Rav. | JV5498A | EU569870 | Horak et al. 2015 |
| M. multispora (Murrill) Matheny & Esteve-Rav. | CO4248 | MN178509 | Matheny et al. 2019 |
| M. myriadophylla (Vauras & E. Larss.) Matheny & Esteve-Rav. | JV19652F | AY700196 | Matheny et al. 2009 |
| M. pygmaea (J. Favre) Matheny & Esteve-Rav. | EL48-05 | GU980628 | Cripps et al. 2010 |
| M. pyrrhopoda (Matheny & Bouger) Matheny & Esteve-Rav. | PERTH:08557764 | KP308815 | Horak et al. 2015 |
| M. subalosa (Matheny & Bouger) Matheny & Esteve-Rav. | PERTH:07680775 | KP308823 | Horak et al. 2015 |
| Mallocybe sp. | ADP060305 | EU600877 | Matheny et al. 2009 |
| Mallocybe sp. | BK 6-June-97-24 | MN178541 | Matheny 2005 |
| Mallocybe sp. | PBM 1922 | MN178543 | Unpublished |
| Mallocybe sp. | PBM 2290 | EU555446 | Matheny et al. 2009 |
| M. siciliana (Brugaletta, Consiglio & M. Marchetti) | AMB 18274 | MG757417 | Brugaletta et al. 2018 |
| M. squarrosoannulata (Kühner) Matheny & Esteve-Rav. | SJ84030 | GU980609 | Cripps et al. 2010 |
| M. subdecurrens (Ellis & Everh.) Matheny & Esteve-Rav. | REH10168 | MH024886 | Matheny et al. 2020 |

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TABLE 1. (Continued)

| Species                        | Voucher | Country | ITS          | LSU           | RPB2          | References                |
|-------------------------------|---------|---------|--------------|---------------|---------------|---------------------------|
| *M. subflavospora* (Matheny & Bougher) Matheny & Esteve-Rav. | E5880   | Australia | AY380396     | AY337404      | Matheny 2005             |
| *M. substriaminipes* (Kühner) Matheny & Esteve-Rav. | CLC1731 | USA     | GU980603     | GU980603      | Cripps et al. 2010       |
| *M. subtilior* (Matheny & Bougher) Matheny & Esteve-Rav. | OKM 24631 | Australia | AY380398     | AY337406      | Matheny 2005             |
| *M. terrigena* (Fr.) Matheny, Vizzini & Esteve-Rav. | JV 16431 | Sweden   | AY380401     | AY333309      | Matheny 2005             |
| *M. tomentosula* Matheny & Esteve-Rav. | PBM4138 | USA | MG773814     | MK421969      | Matheny et al. 2020      |
| *M. unicolor* (Peck) Matheny & Esteve-Rav. | TENN:06355 | USA | MN178525     | MN178554      | Matheny et al. 2019      |
| *Tubariomyces sp.*          | BB6018  | Zambia   | MK421965     | EU600887      | Matheny et al. 2009      |
| *T. hygrophoroides* Esteve-Rav., P.-A. Moreau & C.E. Hermos. | P05112008 | France | GU907097     | GU907094      | Alvarado et al. 2010     |
| *T. inexpectatus* (M. Villarreal, Esteve-Rav., Heykoop & E. Horak) Esteve-Rav. & Matheny | AH25500 | Spain | GU907095     | GU907091      | Alvarado et al. 2010     |
| *T. similis* Della Magg., Tolaini & Vizzini | RFS0805 | Spain | GU907096     | GU907092      | Alvarado et al. 2010     |

Results

Phylogenetic analyses

The ML and BI phylogenies show the placement of the investigated specimens within *Mallocybe* (Fig 2). The eight African collections clustered together with strong support (96% ML bootstrap, 1 BPP) to form a unique lineage, which we recognize as a new species, *M. africana*. Within *Mallocybe*, the new species *M. africana* formed a subgroup with the southeast Asian tropical species, *M. errata* (E. Horak, Matheny & Desjardin) Haelew (2020: 24), with strong support (99% ML bootstrap, 1 BPP).

Taxonomy

*Mallocybe africana* Aïgnon, Yorou & Ryberg *sp. nov.* Figures 3 & 4
MycoBank No:—835658

Diagnosis:—*Mallocybe africana* is most closely related to *M. errata* from southeast Asia but differs from it by the smaller size of the basidiomata, larger basidiospores, and ecological association with Fabaceae Lindley (1836: 148) and/or Phyllanthaceae Martynov (1820: 369). *Mallocybe errata* is associated with Pinaceae Spreng. ex F. Rudolphi, (1830: 35) and Dipterocarpaceae Blume (1825: 222).

Holotype:—BENIN. Borgou, North region: Village Gando, 09°45'43.8"N, 002°19'56.2"E, 08 July 2013, on soil in woodland dominated by *Isoberlinia doka* and *I. tomentosa*, M. Ryberg (MR00358), deposited in Parakou University, GenBank accession: ITS (MT476160), LSU (MT509360) and RPB2 (MT628398).
Etymology:—africana, refers to the distribution in Africa.

Description:—Pileus 7–20 mm diam, hemispherical when young, expanding to convex or planate when mature, margin inflexed, surface dry, fibrillose to tomentose, at times scaly, disc occasionally with a grayish velipellis, otherwise orange-brown (5B4) to brown, sometimes yellowish (5B2) towards the margin when young, flesh yellowish white (4A2), pale brown (4C4) to grayish white, 1–2 mm thick. Lamellae adnate, close, with 30–40 L and several tiers of lamellulae, dark yellowish brown to dark brown (6B5), 2–4 mm deep, edges paler and fimbriate. Stipe 11–25 × 2–4 mm, tapered towards the base, dry, woolly or felt from veil remnants, becoming coarsely fibrillose or developing appressed fibrillose scales, almost cinnamon to orange-brown (5B4), buff to brown, paler yellow at top, flesh pale yellow to white, becoming hollow.

Basidiospores (8–)8.9–13.5(–14) × (4–)4.5–7.3(–8) μm, avl × avw = 11.2 × 5.6 μm Q: (1.4–)1.6–2.6(–3), avQ = 2.0, ellipsoid, smooth, thick-walled, yellowish brown.

Basidia 20–47 × 5–14 μm, usually with 4 sterigmata, cylindrical to slenderly clavate, hyaline becoming ochraceous (necropigmented). Cheilocystidia (25–42 × 10–25 μm, clavate, some almost pyriform or cylindrical and attenuated, thin-walled, clamped. Pleurocystidia absent. Pileipellis a cutis of dense layers of branched hyphae, with fusiform terminals, granular internal pigment brown, 5–12 μm wide, hyphae internally incrusted, clamped. Stipitipellis a cutis made up of filamentous, branched, septate clamped hyphae 5–15 μm wide, thin- or thick-walled, hyaline. Caulocystidia 32–45 × 10–12 μm, cylindrical to bacilliform, walls hyaline, scattered at stipe apex, infrequent, clamped.

Habitat:—Solitary, scattered or in small clusters on soil.

Habitat:—Woodland dominated by Isoberlinia doka, I. tomentosa, Uapaca guineensis Müller Argoviensis. (1864: 517), U. togoensis or Berlinia grandiflora. Occurring from June to September.

FIGURE 2. ML tree of 5.8S rDNA, LSU and RPB2 sequences showing the placement of Malloacybe africana. Values above or below branches indicate bootstrap proportions. BS values ≥70%/Bayesian posterior probabilities >0.95 are shown. Origin of species is given after the name of each taxon. The new species is in red.
Geographical distribution: West Africa–Benin, Togo, Burkina Faso, Ivory Coast, and in south-eastern Africa–Zambia.

Additional specimens examined: BENIN. Collines, central region: Forest reserve of Toui-Kilibo, 8°33'38.15" N, 002°36'5.44" E, 12 August 2017, on soil in woodland dominated by Isoberlinia doka, L.H. Aignon (HLA0378), GenBank accession: ITS (MT458692). Borgou, North region: Forest reserve of N’dali, 09°44'55.73" N, 002°41’40.51" E, 30 August 2017, on soil in woodland dominated by Isoberlinia doka and J. tomentosa, L.H. Aignon (HLA0462), GenBank accession No.: ITS (MT458691) and nLSU (MT456364). Donga region, Igbeke village: Wari- Marou forest reserve, 8°59’36.1” N, 1°58’10.4” E, 30 August 2018, on soil in woodland dominated by Isoberlinia doka and Uapaca togoensis, L.H. Aignon (HLA0623). BURKINA FASO. Bobo-Dioulasso: Forest reserve of Dan, 10°53’39.7” N, 004°50’17.6” W, 12 July 2013, on soil in woodlands and gallery forests dominated by Berlina grandiflora and Uapaca guineensis, M. Ryberg (MR00369), GenBank accession: ITS (MT458691) and nLSU (MT509361). IVORY COAST. Bouake, Gbêkê region: District of Bandama Valley, 7°40’31.4” N, 004°54’29.2” W, 11 July 2018, on soil in woodland dominated by Berlina grandiflora, L.H. Aignon (HLA0561), GenBank accession: ITS (MT476161). TOGO. Central region, prefecture of Assoli: reserve forest of Aledjo, 09°20’25.1” N, 001°14’66.6” E, 17 July 2013, on soil in Woodland dominated by Isoberlinia tomentosa, M. Ryberg (MR00385), GenBank accession: ITS (MN096194), LSU (MN097886) and RP2 (MT465593). ZAMBIA. 6 kilometers before the Gibbon’s farm, 17 November 1996 on soil in miombo woodland (Phyllanthaceae, Fabaceae), 08 February 1996, G. Eyssartier (EG96012ter!). (Phyllanthaceae, Fabaceae), G. Eyssartier (EG96012!). Luanshya-Ibenga road, on soil in miombo woodland, 03 February 1996, G. Eyssartier (EG96012bis!). Lusaka, on soil in miombo woodland dominated by species of Phyllanthaceae and Fabaceae.

**FIGURE 3.** A–D= Basidiomes of *Mallocybe africana*, A = MR00358, B = HLA0462 C = HLA0399 and D = HLA0561. Bar = 1 cm. Photos by: H.L. Aignon.

**Discussion**

Previously, *M. africana* was provisionally referred to as “Inocybe microdulcamara” in Matheny et al. (2009) based on collections made by Bart Buyck and Guillaume Eyssartier in Zambia. Here we have detected the same species from other regions of tropical Africa, where it is widely distributed in different habitats including woodlands dominated by Fabaceae (*Isoberlinia doka, I. tomentosa* and *Berlinia grandiflora*) and of Phyllanthaceae (*Uapaca togoensis* and *U. guineensis*).

On the basis of our multi-gene (5.8S rDNA, LSU and RP2) phylogenetic analyses (Fig. 2), *M. africana* is subdivided into two subclades, with separation of the samples from West Africa from those in Zambia. However, the
low sequences divergence in ITS and LSU between the clades (0.4% and 0.5% respectively) leads to us conclude that they belong to the same species.

In the phylogenetic tree, *M. africana* is most closely related to *M. errata* with strong bootstrap support. *M. errata* is a species from northwest Thailand and India (Kerala) found in tropical forests mainly dominated by *Pinus kesiya* subsp. *szemaoensis* Silba (2009:52) and dipterocarp forest dominated by *Dipterocarpus obtusifolius* Teijsm. ex Miq. (1864: 214) reported by Horak et al. (2015). The phylogenetic affinities of the Zambian collections of *M. africana* with *M. errata* have long been recognized, and, according to Matheny et al. (2009) and Horak et al. (2015), both were strongly supported as phylogenetically related to *M. heimii*. However, our phylogeny reveals that *M. africana* and *M. errata* may be more closely related to *M. althoffiae* (E. Horak) Matheny & Esteve-Rav (2020: 105), *M. unicolor* (Peck) Matheny & Esteve-Rav. (2020: 109) and *M. multispora* (Peck) Matheny & Esteve-Rav. (2020: 107).

**FIGURE 4A–F.** Micromorphology of *Mallocybe africana*. A. Basidiospores B. Basidia C. Cheilocystidia D. Caulocystidia E. Pileipellis F. Stipitipellis. Scale bars: **A**=3 μm, **B**=5 μm, **C, D, E, F** = 10 μm. Drawings by: H.L. Aignon.
**FIGURE 5. A–F. Malloxybe africana**, microscopical characters in Congo Red (MR00358), A. Basidiospores B. Basidia C. Cheilocystidia D. Caulocystidia E. Pileipellis F. Stipitipellis. Scale bars: A–F = 10 μm. Photos By: H.L. Aignon.

*Malloxybe africana* shares some morphological similarities with *M. errata* as both have a brown to orange-brown pileus with radially fibrous, fibrilllose squamules or scales (Horak et al. 2015). However, *M. africana* differs from *M. errata* by the larger basidiospores (8–14 × 4–8 μm for *M. africana* and 8.5–10 × 4.5–5 μm for *M. errata*), plant association and geographic distribution. During this study, *M. africana* has been collected from tropical Africa and associated with Fabaceae and Phyllanthaceae species while *M. errata* is distributed in tropical Asia and associates with Dipterocarpaceae and *Pinus* (Horak et al. 2015). *Malloxybe africana* appears to be a common and widespread species in African woodland savannas, and its description may therefore potentially resolve the identification of many collections. Additional surveying is needed though, to determine exactly how widespread and common it is.

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