



State of knowledge on the diversity, phylogeny and distribution of Inocybaceae in Africa

Aignon HL^{1*}, Acar İ², Naseer A³ and Yorou SN¹

¹ Research Unit Tropical Mycology and Plant-Soil Fungi Interactions, Faculty of Agronomy, University of Parakou, 03 BP 125, Parakou, Benin

² Yüzüncü Yıl University, Başkale Vocational High School, Organic Agriculture Department, Van, Turkey

³ Institute of Botany, University of the Punjab, Quaid-e-Azam Campus, 54590, Lahore, Pakistan

Aignon HL, Acar İ, Naseer A, Yorou SN 2021 – State of knowledge on the diversity, phylogeny and distribution of Inocybaceae in Africa. Asian Journal of Mycology 4(2), 56–66, Doi 10.5943/ajom/4/2/6

Abstract

Several recent taxonomic studies have been conducted on fungi in Africa but little is known about their taxonomy, ecology, occurrence, distribution and phylogenetic placement of certain families such as Inocybaceae. About 80 species of Inocybaceae are known from the African continent compared to against 1,100 species in the world. This review addresses the state of knowledge in relation to the taxonomy, ecology and collection sites of Inocybaceae taxa from Africa, as well as the aspects to be explored to better document Inocybaceae in Africa in general and particularly in West Africa.

Keywords – ecology – evolution – host tree – molecular phylogeny – origin

Introduction

Inocybaceae Jülich (Basidiomycota, Fungi) originated from Palaeotropics during the Cretaceous, 191 million years ago (Matheny et al. 2009). This family is considered among one of the most taxonomically diverse families of Agaricales (Matheny 2009). It is initially diversified in the world by symbiosis with angiosperms (Matheny et al. 2009). Unfortunately, the species of Inocybaceae have long been misplaced and classified in Cortinariaceae R. Heim ex Pouzar (Singer 1949, 1986, Malchol & Singer 1971, Horak 2005). Thereafter, Jülich (1982) elevated the Inocybeae tribe to the Inocybaceae family.

Previously, the identification of Inocybaceae species was based on only morphological characters (Matheny et al. 2002). Matheny et al. (2002) were the first to combine molecular approach and morphology characters of *Inocybe* (Fr.) Fr., which resulted in an increased number of new taxa (Matheny 2005, Garnica et al. 2007). In tropical regions (Alvarado et al. 2010, Matheny 2009, Pradeep et al. 2016), especially in tropical Africa, Inocybaceae is poorly known (Piepenbring et al. 2020), even though, *Auritella* Matheny & Bougher and *Tubariomyces* Esteve-Rav. & Matheny, two genera in Inocybaceae were recorded with few species in tropical Africa (Alvarado et al. 2010, Matheny & Bougher 2006, Matheny et al. 2017). In tropical Africa, the members of family Inocybaceae are one of the most dominant in the soil of the woodlands and gallery forests after Russulaceae Lotsy (Meidl et al. 2021).

In the present contribution, we are providing a state of knowledge on Inocybaceae in tropical Africa to document this hidden tropical diversity of Inocybaceae for our research orientation.

***Inocybe* and affiliated taxa**

Inocybe was accommodated within the Cortinariaceae family, which was considered a monogeneric tribe (Kühner 1980), together with *Hebeloma* (Fr.) P. Kumm., *Hebelomina* Maire and *Alnicola* Kühner in the tribe Inocybeae (Singer 1975). Indeed, the morphological resemblance between *Hebeloma* and *Inocybe* had been pointed out by Fries (1821, 1838). However, close relationships between *Hebeloma* and *Inocybe* appear unlikely because *Hebeloma* is characterized by the presence of ornamented basidiospores which are originated from the epitunica (Clemençon 1977), while *Inocybe* is characterized by smooth or nodulose/angular basidiospores (Pegler & Young 1972). Still, the wall of basidiospores of *Inocybe* species consists of a coriotunica and is immediately enveloped by the sporothecium without any myxosporium layer (tunica and epitunica), as reduction series from the more complex spores present in *Cortinarius* (Clemençon 1977). The different aspects of the spore wall in *Inocybe* have led to some doubts regarding its close relationship with the rest of Cortinariaceae, which prompts Jülich (1982) to propose the family Inocybaceae to accommodate *Inocybe*.

Phylogenetically, *Inocybe* is closely related to Crepidotaceae (Matheny 2005). But *Inocybe* affinity with Crepidotaceae was rather unexpected mainly due to the difference in the mode of nutrition. *Inocybe* is an ectomycorrhizal (EcM) genus, and Crepidotaceae is a saprotrophic family. In addition, there is a strong resemblance to species of *Phaeomarasmium* Scherff and several species of *Inocybe* (Horak 1977) due to their pileipelles, which form a trichodermis in the species of *Phaeomarasmium*.

Origin, geographic distribution and ecological importance of Inocybaceae

The palaeotropical area seems to be the "center of origin" or the most probable ancestral area of Inocybaceae (Matheny et al. 2009). The species in the family were involved in EcM associations with angiosperms from Palaeotropical region (Matheny et al. 2009) and probably older than Hymenogastraceae Vittad and Suillaceae Besl & Bresinsky (Matheny et al. 2009). The family Inocybaceae is cosmopolitan, and its species are distributed within four major biogeographic zones, Palaeotropics, Neotropics, Northern Temperate zone and Southern temperate zone (Matheny et al. 2009).

Inocybaceae is an EcM forming fungal family (Kuyper 1986, Ryberg et al. 2008) and are associated with 23 families of angiosperm host plants (Matheny et al. 2020). Approximately 80% of the species in this family form symbiotic associations with EcM plants (Matheny et al. 2012a). However, many species are not always associated with a single plant family (Kuyper 1986, Ryberg et al. 2010). Several other species are well known for their association with gymnosperms like Cupressaceae and Pinaceae (Matheny et al. 2012a) or angiosperms, including Betulaceae, Casuarinaceae, Cistaceae, Dipterocarpaceae, Ericaceae, Fabaceae, Fagaceae, Malvaceae and Myrtaceae (Kuyper 1986, Matheny et al. 2009, Ryberg et al. 2009). Besides *Mallocybe errata* (E. Horak, Matheny & Desjardin) Haelew, all species described in the tropics are associated with angiosperms (Matheny et al. 2009). The host specificity is examined at different levels as some species are limited to a single plant family, a single plant species or any other taxonomic level (Bruns et al. 2002, Tedersoo et al. 2008, Geml et al. 2017). *Inocybe dunensis* P.D. Orton probably has a saprophytic lifestyle or a possible mycorrhizal association with *Ammophila arenaria* (L.) (Kuyper 1986). Also, many species of Inocybaceae prefer soil rich in nutrients (Latha & Manimohan 2017). Nevertheless, some species of the northern temperate region prefer calcareous soils (Kuyper 1986, Jacobsson 2008). In contrast, *Inocybe sambucina* (Fr.) Quél. and *I. lacera* (Fr.) P. Kumm is found exclusively on acidic nutrients-poor soil. Otherwise, other species grow between mosses and bryophytes, but this relationship may seem occasional (Latha & Manimohan 2017). Similarly, some species of Inocybaceae are xerophyte species such as *I. impexa* (Lasch) Kuyper and *I. viridumbonata* Pegler, which adapt to underground growth in order to resist very severe xeric conditions (Kuyper 1986). In natural forests, Inocybaceae species play a fundamental role in forest ecology and agroforestry due to the considerable importance of the EcM association, which governs the species preference in terms of habitat. Thus, many species of Inocybaceae colonize

disturbed habitats in order to promote the growth of partner trees, thanks to the EcM symbiosis while ensuring their health (Horak 1977). In tropical Africa, the species of Inocybaceae are mainly associated with woodlands and gallery forests dominated by *Isoberlinia doka* Craib & Stapf, *I. tomentosa* (Harms) Craib et Stapf, *Uapaca togoensis* Pax, *Berlinia grandiflora* (Vahl) Hutch, *Uapaca* ssp. and *Monotes kerstingii* Gilg.

Morphological and anatomical characteristics of Inocybaceae

The species of Inocybaceae are characterized by brownish basidiomata often lilac or purplish, with a pileus of coarsely fibrous or minutely squamous texture and a stipe of uniform thickness with a clearly bulbous base and sometimes fibrillose or pruinose apex with brownish lamellae (Kuyper 1986, Matheny et al. 2020). The shapes of the spores are ellipsoid, ovoid, thin conical or cylindrical, sometimes phaseoliform, nodular or angular (Kuyper 1986, Ryberg et al. 2010, Pradeep et al. 2016). Many species in the family have thick-walled cheilocystidia but some only have thin-walled cheilocystidia, completely lacking metuloids (Table 1).

Table 1 Some anatomical characteristics for different genera of Inocybaceae

Genera	Spore shape	Cheilocystidia	Pleurocystidia	References
<i>Auritella</i>	- Globose - Cylindrical	Present /long thick walled	Present/rely absent	Matheny et al. (2020)
<i>Inocybe</i>	- Amygdaliform - Elliptic - Subcylindrical - Angular - Nodulose - Spinose	Present	Absent	Horak et al. (2015), Matheny et al. (2020)
<i>Inosperma</i>	Smooth/ellipsoid to phaseoliform	Present	Absent	Latha & Manimohan (2016), Naseer et al. (2017)
<i>Mallocybe</i>	Smooth/cylindrical, subphaseoliform or subamygdaliform	Short /if present	Absent	Matheny et al. (2020)
<i>Nothocybe</i>	Smooth/phaseoliform, ovo-ellipsoid	Versiform	Absent	Latha et al. (2016), Matheny et al. (2020)
<i>Pseudosperma</i>	Smooth/elliptical to phaseoliform	Cylindrical to clavate	Absent	Larsson et al. (2009), Saba et al. (2020)
<i>Tubariomyces</i>	Smooth/cylindrical, cylindrical-fusiform to suballantoid	Elongate, thin- walled, subcylindrical to subclavate or sublageniform to narrowly clavate	Absent	Alvarado et al. (2010), Matheny et al. (2012b), Vizzini et al. (2013)

Diversity and classification within Inocybaceae

Most species in the family Inocybaceae have not yet been described and are poorly known (Matheny & Bougher 2006, Ryberg et al. 2008, Horak et al. 2015). The family was organized into seven major clades, *Auritella*, *Inocybe*, *Inosperma*, *Mallocybe*, *Nothocybe*, *Pseudosperma* and *Tubariomyces* (Matheny et al. 2009). Later, *Auritella*, *Inocybe* and *Tubariomyces* are recognized as distinct genera (Matheny & Bougher 2006, Alvarado et al. 2010). The clades *Inosperma*, *Mallocybe*, *Nothocybe* and *Pseudosperma* were included in the genus *Inocybe* (Larsson et al. 2009, Matheny et al. 2009). Matheny et al. (2020) raised *Inosperma*, *Mallocybe*, *Nothocybe* and *Pseudosperma* to generic rank. Recently, several studies have described new Inocybaceae species, and the estimate given by Matheny & Kudzma (2019) of 1050 species is already known and reached more than 1100 species (Table 2).

Table 2 Currently richness of Inocybaceae

Genera	Species richness	Distribution	Reference
<i>Auritella</i>	15	Temperate regions of Australia, India and tropical Africa	Matheny et al. (2020)
<i>Inocybe</i>	874	Africa, Australasia, Asia, Europe, North America, Oceania, and northern and southern South America	Matheny et al. (2020) Cervini (2021) Mešić et al. (2021)
<i>Inosperma</i>	61	Africa, Australasia, Asia, Europe, and North America	Aignon et al. (2021b), Cervini et al. (2020a)
<i>Mallocybe</i>	60	Africa, Asia, Australia, Europe, New Zealand, and North America	Aignon et al. (2021a)
<i>Nothocybe</i>	01	Tropical India	Latha et al. (2016) Matheny et al. (2020)
<i>Pseudosperma</i>	83	Africa, Asia, Australia, Europe, North America and northern South America	Cervini et al. (2020b), Saba et al. (2020)
<i>Tubariomyces</i>	06	Sub-Saharan Africa, northern Australia and southern Europe	Matheny et al. (2020)

Based on these revisions, an in-depth exploration of the diversity in the tropics could well enhance the diversity of Inocybaceae, and new genera may emerge. In Africa, there are hitherto 80 recorded species of Inocybaceae (Hennings 1901, Eichelbaum 1906, Heim 1931, Maire & Werner 1937, Pegler 1969, Thoen 1974, Malençon & Bertault 1975, Morris 1990, Buyck & Eyssartier 1999, Matheny & Watling 2004, Matheny & Bougher 2006, El Akil et al. 2015, Ouabbou et al. 2014a, b, Matheny et al. 2017, Piepenbring et al. 2020, Aignon et al. 2021a, b). Still, the estimation of the exact diversity of Inocybaceae in Africa is controversial and the lack of studies in Inocybaceae cause confusion with exotic species (Watling 2001). Table 3 presents the current diversity of Inocybaceae in Africa.

Table 3 Diversity and distribution of the family Inocybaceae from Africa

Species	Countries	References
<i>Auritella aureoplumosa</i> (Watling) Matheny & Bougher	Cameroon	Matheny & Bougher (2006)
<i>A. erythroxa</i> (De Seynes) Matheny & Bougher	Gabon, Cameroon	Matheny & Bougher (2006)
<i>A. hispida</i> Matheny & T.W. Henkel	Cameroon	Matheny et al. (2017)
<i>A. spiculosa</i> Matheny & T.W. Henkel	Cameroon	Matheny et al. (2017)
<i>Inocybe abjecta</i> P. Karst	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. amblyospora</i> Kühner	Morocco	Maire & Werner (1937)
<i>I. asterospora</i> Quél.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. bipindiensis</i> Henn.	Zambia	Hennings (1901)
<i>I. boltoni</i> sensu NCL	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. bresadolae</i> Masee	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. brunnea</i> Quél	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. calospora</i> Quél	Morocco	Ouabbou et al. (2014b)
<i>I. cincinnatula</i> Kühner	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. conspicuispora</i> Buyck & Eyssart	Zambia	Buyck & Eyssartier (1999)

Table 3 Continued.

Species	Countries	References
<i>I. corydalina</i> Quél	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. curvipes</i> P. Karst	Congo-Kinshasa	Thoen (1974)
<i>I. cyaneovirescens</i> Henn.	Burundi, Rwanda and Tanzania	Hennings (1901)
<i>I. decemgibbosa</i> (Kühner) Vauras	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. decipientoides</i> Peck	Congo-Kinshasa	Thoen (1974)
<i>I. decipientoloides</i> Peck	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. descissa</i> sensu NCL	Zambia	Eichelbaum (1906)
<i>I. dolichospora</i> Malençon	Morocco	Malençon & Bertault (1975)
<i>I. dulcamara</i> Sacc	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. erinaceomorpha</i> Stangl & J. Veselský	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. eutheles</i> (Fr.) Quél	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. flocculosa</i> Sacc.	Morocco	Ouabbou et al. (2014a)
<i>I. fuscidula</i> Velen	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. geophylla</i> (Bull.) P. Kumm.	Zambia	Eichelbaum (1906)
<i>I. ghanaensis</i> Pegler	Ghana	Pegler (1969)
<i>I. glaucodisca</i> Buyck & Eyssart.	Zambia	Buyck & Eyssartier (1999)
<i>I. grammocephala</i> Malençon	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. grammopodia</i> Malençon	Morocco	Malençon & Bertault (1975)
<i>I. griseovelata</i> Kühner	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. haemacta</i> (Berk. & Cooke) Sacc.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. halophila</i> R. Heim	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. incarnata</i> Bres	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. lacera</i> (Fr.) P. Kumm.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. lanuginella</i> (J. Schröt.) Konrad & Maubl.	Tanzania	Maghembe & Redhead (1980)
<i>I. maculata</i> Boud.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. margaritispora</i> (Berk.) Sacc.	Morocco	Ouabbou et al. (2014a)
<i>I. mixtilis</i> (Britzelm.) Sacc.	Malawi	Morris (1990)
<i>I. muricellata</i> Bres	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. nitidiuscula</i> (Britzelm.) Lapl.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. oblectabilis</i> (Britzelm.) Sacc.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. obscura</i> Gillet	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. ochrofulva</i> Malençon	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. orbata</i> Malençon	Morocco	Malençon & Bertault (1975)
<i>I. pallida</i> Velen	Morocco	Ouabbou et al. (2014a)
<i>I. paludinella</i> (Peck) Sacc.	Morocco	Ouabbou et al. (2014b)

Table 3 Continued.

Species	Countries	References
<i>I. praetervis</i> Carteret	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. pyriodora</i> (Pers.) P. Kumm.	Tanzania and Morocco	Eichelbaum (1906), Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. queletii</i> Konrad	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. rhodella</i> Matheny, Aime & M.E. Sm.	Morocco	Ouabbou et al. (2014a)
<i>I. roseipes</i> Malençon	Morocco	Malençon & Bertault (1975)
<i>I. rufula</i> Malençon	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. rufuloides</i> Bon	Morocco	El Akil et al. (2015)
<i>I. sambucina</i> (Fr.) Quél.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. scabelliformis</i> Malençon	Morocco	Malençon & Bertault (1975)
<i>I. sclerotiicola</i> R. Heim & Gilles	Gabon	Hennings (1901)
<i>I. squarrosa</i> Rea	Morocco	El Akil et al. (2015)
<i>I. tigrina</i> R. Heim	Morocco	Ouabbou et al. (2014a)
<i>I. tristis</i> Hruby	Morocco	Malençon & Bertault (1975)
<i>I. tulearensis</i> L.M. Dufour & H. Poiss.	Madagascar	Heim (1931)
<i>I. valida</i> Malençon	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. whitei</i> (Berk. & Broome) Sacc.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>Inosperma africanum</i> Aignon, Yorou & Ryberg	Benin, Burkina Faso, Guinea, Ivory Coast and Togo	Aignon et al. (2021b)
<i>I. adaequatum</i> (Britzelm.) Matheny & Esteve-Rav.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. bongardii</i> (Weinm.) Matheny & Esteve-Rav.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. bulbomarginatum</i> Aignon, Yorou & Ryberg	Benin and Zambia	Aignon et al. (2021b)
<i>I. flavobrunneum</i> Aignon, Yorou & Ryberg	Benin	Aignon et al. (2021b)
<i>I. hirsutum</i> (Lasch) Matheny & Esteve-Rav.	Tanzania	Eichelbaum (1906)
<i>I. cookei</i> (Bres.) Matheny & Esteve-Rav.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>I. misakaense</i> (Matheny & Watling) Matheny & Esteve-Rav.	Zambia	Matheny & Watling (2004)
<i>Mallocybe africana</i> Aignon, Yorou & Ryberg	Benin, Burkina Faso, Ivory Coast, Togo and Zambia	Aignon et al. (2021a)
<i>M. gymnocarpa</i> (Kühner) Matheny & Esteve-Rav.	Morocco	Maire & Werner (1937), Malençon & Bertault (1975)
<i>Pseudosperma cerinum</i> (Malençon) Matheny & Esteve-Rav.	Morocco	Malençon & Bertault (1975)
<i>P. curreyi</i> (Berk.) Matheny & Esteve-Rav.	Morocco	Ouabbou et al. (2014b)
<i>P. orbatum</i> (Malençon) Matheny & Esteve-Rav	Morocco	Ouabbou et al. (2014b)
<i>P. rimosum</i> (Bull.) Matheny & Esteve-Rav.	Morocco and Madagascar	Heim (1931), Maire & Werner (1937), Malençon & Bertault (1975)

Infrageneric classifications, molecular and phylogenetic analyses of Inocybaceae

Inocybaceae has undergone many infrageneric classifications (Kuyper 1986, Singer 1986, Bon 1997, 1998). Kuyper (1986) argued that the existence of paraphyletic taxa could not be excluded from *Inocybe* and the knowledge on the premature development and taxonomy of *Inocybe* would most certainly promote taxonomic and nomenclatural instabilities (Kuyper 1986). The application of molecular data in the taxonomy of Inocybaceae is recent but has increasingly evolved (Matheny et al. 2020). The genes initially used were nuclear small and large subunit ribosomal DNA (nucSSU, nucLSU); mitochondrial small subunit ribosomal DNA (mitSSU rDNA); RNA polymerase subunit, RPB1 and RPB2 (Matheny et al. 2002, Lutzoni et al. 2004). Some studies have shown the sufficiency of the majority of these genes. However, Internal Transcribed Spacer (ITS), considered as the reference gene by taxonomists for the identification of fungal species (Raja et al. 2017), is also essential but its sequences hardly align across all genera of Inocybaceae (Matheny et al. 2020) and a part of this gene is very conserved in the majority of fungal species. Many genes have been assembled to reconstruct the phylogenetic relationships between the species of Inocybaceae. Recent studies used the combination of two, three or more genes (Horak et al. 2015, Pradeep et al. 2016, Matheny et al. 2017, 2020). However, the phylogenetic inference of single-gene trees is not as robust as the combined data. Matheny (2005) proved that the nLSU dataset generates the least robust phylogenetic estimate for *Inocybe* and outgroup taxa compared to RPB1 and RPB2 genes. Also, the combination of at least three loci increases the nonparametric priming environment, the Bayesian Posterior Probabilities (BPP) and the resolution of many clades compared to separate gene analyses (Matheny 2005). Nevertheless, the lack of sequences in the GenBank of African taxa of Inocybaceae generates incomplete taxonomy resolutions within Inocybaceae (Rehner & Buckley 2005, Vizzini et al. 2013). Moreover, Inocybaceae contains a large number of wrongly identified or unidentified sequences in the GenBank (Ryberg et al. 2008). Unfortunately, this does not contribute to a better understanding of the phylogenetic position of the species of Inocybaceae.

Phylogeography

Inocybaceae receive a lot of attention in evolutionary research (Matheny & Bougher 2006, Matheny et al. 2009). Although research has been conducted using recent advances, Matheny et al. (2009) and Matheny & Bougher (2006) used phylogenetic dating to study the biogeographic patterns underlining the evolutionary histories of Inocybaceae. Despite this progress, biogeographical patterns and knowledge related to the understanding of the evolution of Inocybaceae in Africa remain poorly assessed. However, few taxa from tropical Africa have been analyzed in most of these biogeographic areas, and their dispersion has not been deduced with a less complete disjunctive distribution effect compared to other taxa of Inocybaceae. It is preferable to understand the reasons and causes of the disjoint distribution between African taxa and those from other regions.

Discussion

Inocybaceae is a monophyletic, EcM forming family that occurs in all continents except Antarctica (Matheny & Kudzma 2019, Matheny et al. 2020). In Africa, the diversity of Inocybaceae is high, and about 80 species have been recorded (Pegler 1969, Buyck & Eyssartier 1999, Watling 2001, Matheny & Bougher 2006, Matheny et al. 2017, Aïgnon et al. 2021a, b). The species of this family are generally characterized by the occurrence of fruiting bodies on soil with distinctive odours, nonglutinous pileus, brownish mature lamellae, smooth or angular or nodulose basidiospores with the presence of cheilocystidia and/or pleurocystidia (Matheny et al. 2020). According to current data, four species in the genus *Auritella*, 62 species in *Inocybe*, eight species in *Inosperma*, two in *Mallocybe* and four in *Pseudosperma* are known from Africa (Pegler 1969, Buyck & Eyssartier 1999, Watling 2001, Matheny & Bougher 2006, Matheny et al. 2017, Aïgnon et al. 2021a, b). This diversity should be considered with careful observations. For example, *I. curvipes* was noted from Congo-Kinshasa and is an exotic species restricted to *Pinus* L. (Buyck &

Eyssartier 1999). So, if the samples are still available, a molecular analysis could help to clarify the taxonomic reliability of this taxon, and many samples of Inocybaceae from Africa are described based only on morphology. Although the species of Inocybaceae are relatively common in Africa, a taxonomic monograph is not available yet (Buyck & Eyssartier 1999).

To contribute to a clear hiatus of species limits within Inocybaceae and a better understanding of the evolution, the combination of morphology studies and DNA sequencing from type collections seems necessary as convincingly applied for numerous fungal taxa from Africa (Yorou et al. 2011, Maba et al. 2015) and elsewhere (Kuo & Matheny 2015, Yangdol 2016). The inclusion of African taxa in any phylogenetic studies will undoubtedly increase sampling effort and provide a more accurate interpretation of evolutionary and biogeographic conclusions within fungal taxa. Recent sampling in West Africa (Benin, Burkina Faso, Guinea, Ivory Coast, Mali and Togo) have reported four new species for science such as *Inosperma africanum*, *I. bulbomarginatum*, *I. flavobrunneum* and *Mallocybe africana* with a large number of sequences of Inocybaceae generated (Aignon et al. 2021a, b) and deposited in the international Genbank to facilitate future phylogeographic studies.

Acknowledgements

We gratefully acknowledge Martin RYBERG for valuable recommendations and the reviewers for their valuable time to assess this paper despite the COVID-19 pandemic. The authors are highly indebted to IDEA WILD for providing office and field equipment.

References

- Aignon HL, Naseer A, Matheny PB, Yorou NS, Ryberg M. 2021a – *Mallocybe africana* (Inocybaceae) the first species of *Mallocybe* described from Africa. *Phytotaxa* 478, 049–060.
- Aignon HL, Jabeen S, Naseer A, Yorou NS, Ryberg M. 2021b – Three new species of *Inosperma* (Agaricales, Inocybaceae) from Tropical Africa. *MycologyKeys* 77, 97–116.
- Alvarado P, Manjón JL, Matheny PB, Esteve-Raventós F. 2010 – *Tubariomyces*, a new genus of Inocybaceae from the Mediterranean region. *Mycologia* 102, 1389–1397.
- Bon M. 1997 – Clé monographique du genre *Inocybe* (Fr.) Fr. *Documents Mycologiques* 27, 1–51.
- Bon M. 1998 – Clé monographique du genre *Inocybe* (Fr.) Fr. (3ème partie : espèces gibbosporées, = Ss.-g. *Clypeus* Britz. 5 genre *Astrosporina* Schroet.). *Documents Mycologiques* 28, 1–45.
- Bruns T, Bidartondo M, Taylor D. 2002 – Host specificity in ectomycorrhizal communities: what do the exceptions tell us? *Integrative and Comparative Biology* 42, 352–359.
- Buyck B, Eyssartier G. 1999 – Two new species of *Inocybe* (Cortinariaceae) from African woodland. *Kew Bulletin* 54, 675–681.
- Cervini M. 2021 – *Inocybe messapica* (Inocybaceae, Agaricales, Basidiomycota), a new species in section *Splendentes*, from Mediterranean oak woods. *Phytotaxa* 480, 174–184.
- Cervini M, Carbone M, Bizio E. 2020a – *Inosperma vinaceum*, una nuova specie distinta da *I. rhodiolum* e *I. adaequatum*. *RdM* 63, 215–241
- Cervini M, Bizio E, Alvarado P. 2020b – Quattro nuove specie italiane del Genere *Pseudosperma* (Inocybaceae) con odore di miele. *RdM* 63, 3–36.
- Clemençon H. 1977 – Die Strukturen der Basidiosporenwand und des Apikulus, und deren Beziehung zur Exogenisation der Spore. *Persoonia* 9, 363–380.
- Eichelbaum F. 1906 – Beiträge zur Kenntnis der Pilzflora des Ostusambaragebirges. *Verh. Naturwiss. Vereins Hamburg* 3, 1–92.
- El Akil M, Khouader M, Chliyah M, Douiri EM et al. 2015 – A new species of Basidiomycetes for the fungal diversity of Morocco: *Inocybe squarrosa* and *I. rufuloides*. *International Journal of Pure & Applied Bioscience* 3, 27–34.
- Fries EM. 1821 – *Systema Mycologicum*. Lund, Sweden, Pp. 520.
- Fries EM. 1838 – *Epicrisis Systematis Mycologici*. Typographia Academica, Uppsala, Pp. 610.

- Garnica S, Weis M, Walther G, Oberwinkler F. 2007 – Reconstructing the evolution of agarics from nuclear gene sequences and basidiospore ultrastructure. *Mycological Research* 111, 1019–1029.
- Geml J, Morgado LN, Semenova-Nelsen TA, Schilthuizen M. 2017 – Changes in richness and community composition of ectomycorrhizal fungi among altitudinal vegetation types on Mount Kinabalu in Borneo. *New Phytologist* 215, 454–468.
- Heim R. 1931 – Le genre *Inocybe*, encyclopédie mycologique 1. Paris: Paul Lechevalier & Fils, Pp. 429.
- Hennings P. 1901 – Fungi camerunenses novi. III. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 30, 39–57.
- Horak E. 1977 – Fungi Agaricini Novazelandiae. VI. *Inocybe* (Fr.) and *Astrosporina* Schroeter. *New Zealand Journal of Botany* 15, 713–747.
- Horak E, Matheny PB, Desjardin DE, Soyong K. 2015 – The genus *Inocybe* (Inocybaceae, Agaricales, Basidiomycota) in Thailand and Malaysia. *Phytotaxa* 230, 201–238.
- Horak E. 2005. Röhrlinge und Blätterpilze in Europa. Heidelberg, Germany: Spektrum Akademischer Verlag, Pp. 575.
- Jacobsson, S. 2008 – Key to *Inocybe*. In: Knudsen H. & Vesterholt J. (Eds.) *Funga Nordica. Agaricoid, boletoid and cyphelloid genera*. Nordsvamp, Copenhagen, Pp. 868–906.
- Jülich W. 1982 – Higher taxa of Basidiomycetes. *Bibliotheca Mycologica* 85, 1–485.
- Kühner R. 1980 – Les Hyménomycètes agaricoïdes (Agaricales, Tricholomatales, Plutéales, Russulales). *Etude générale et classification* 49, 1–1927.
- Kuo M, Matheny PB. 2015 – Contemporary documentation of the rare eastern North American species *Inocybe insignis* (Inocybaceae, Agaricales). *MycKeys* 11, 23–31.
- Kuyper TW. 1986 – A revision of the genus *Inocybe* in Europe I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia* 3, 1–247.
- Larsson E, Ryberg M, Moreau PA, Mathiesen ÅD, Jacobsson S. 2009 – Taxonomy and evolutionary relationships within species of section *Rimosae* (*Inocybe*) based on ITS, LSU and mtSSU sequence data. *Persoonia* 23, 86–98.
- Latha KPD, Manimohan, P. 2016 – *Inocybe gregaria*, a new species of the *Inosperma* clade from tropical India. *Phytotaxa* 286, 107–115
- Latha KPD, Manimohan P, Matheny PB. 2016 – A new species of *Inocybe* representing the *Nothocybe* lineage. *Phytotaxa* 267, 40–50.
- Latha KPD, Manimohan P. 2017 – *Inocybe* of Kerala. *SporePrint Books, Calicut*, Pp. 181.
- Lutzoni F, Kauff F, Cox CJ, McLaughlin D et al. 2004 – Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *American Journal of Botany* 91, 1446–1480.
- Maba D, Guelly AK, Yorou NS, Agerer R. 2015 – Diversity of *Lactifluus* (Basidiomycota, Russulales) in West Africa: 5 new species described and some considerations regarding their distribution and ecology. *Mycosphere* 6, 737–759.
- Maghembe JA, Redhead JF. 1980 – A survey of ectomycorrhizal fungi in pine plantations in Tanzania. *East African Agricultural and Forestry Journal* 45, 203–206.
- Maire R, Werner RG. 1937 – Fungi Marocani, catalogue raisonné des champignons connus jusqu'ici au Maroc. *Mémoires de la Société des Sciences Naturelles du Maroc*, Pp. 143.
- Malchol RE, Singer R. 1971 – Bayesian analysis of generic relations in Agaricales. *Nova Hedwigia* 21, 753–787.
- Malençon G, Bertault R. 1975 – Flore des champignons supérieurs du Maroc, Tome I. *Travaux de l'Institut Scientifique Cherifien de la Faculté des Sciences, Rabat*, 33, Pp. 540.
- Matheny PB, Liu YJ, Ammirati JF, Hall BD. 2002 – Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *American Journal of Botany* 89, 688–698.
- Matheny PB, Watling R. 2004 – A new and unusual species of *Inocybe* (Inosperma clade) from tropical Africa. *Mycotaxon* 89, 497–503.

- Matheny PB. 2005 – Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution* 35, 1–20.
- Matheny PB. 2009 – A phylogenetic classification of the Inocybaceae. *McIlvainea* 18, 11–21.
- Matheny PB, Aime MC, Smith ME, Henkel TW. 2012a – New species and reports of *Inocybe* (Agaricales) from Guyana. *Kurtziana* 37, 23–39.
- Matheny PB, Aime MC, Bougher NL, Buyck B et al. 2009 – Out of the Palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *Journal of Biogeography* 36, 577–592.
- Matheny PB, Bougher NL. 2006 – The new genus *Auritella* from Africa and Australia (Inocybaceae, Agaricales): Molecular systematics, taxonomy and historical biogeography. *Mycological Progress* 5, 2–17.
- Matheny PB, Henkel TW, Séné O, Korotkin HB, Dentinger BTM, Aime MC. 2017 – New species of *Auritella* (Inocybaceae) from Cameroon, with a worldwide key to the known species. *IMA Fungus* 8, 287–298.
- Matheny PB, Kudzma LV. 2019 – New species of *Inocybe* (Inocybaceae) from eastern North America. *The Journal of the Torrey Botanical Society* 146, 213–235.
- Matheny PB, Hobbs AM, Esteve-Raventós F. 2020 – Genera of Inocybaceae: New skin for the old ceremony. *Mycologia* 112, 83–120.
- Matheny PB, Pradeep CK, Vrinda KB, Varghese SP. 2012b – *Auritella foveata*, a new species of Inocybaceae (Agaricales) from tropical India. *Kew Bulletin* 67, 119–125.
- Morris B. 1990 – An annotated check-list of the macrofungi of Malawi. *Kirkia* 13, 323–364.
- Meidl P, Furneaux B, Tchan KI, Kluting K, Ryberg M, Guissou M-L, Soro B, Traoré A, Konomou G, Yorou NS, Rosling A. 2021 – Soil fungal communities of ectomycorrhizal dominated woodlands across West Africa. *MycKeys* 81, 45–68.
- Mešić A, Haelewaters D, Tkalčec Z, Liu J, Kušan I, Aime MC, Pošta A. 2021 – *Inocybe brijunica* sp. nov., a New Ectomycorrhizal Fungus from Mediterranean Croatia Revealed by Morphology and Multilocus Phylogenetic Analysis. *Journal of Fungi* 7, 1–12.
- Naseer A, Khalid AN, Smith ME. 2017 – *Inocybe shawarensis* sp. nov. in the *Inosperma* clade from Pakistan. *Mycotaxon* 132, 909–918.
- Ouabbou A, Touhami AO, Benkirane R, Douira A. 2014a – Study of some new species of the *Inocybe* genus with gibbous spore for the Morocco's fungal flora. *International Journal of Recent Scientific Research* 5, 1464–1467.
- Ouabbou A, Touhami AO, Benkirane R, Douira A. 2014b – Etude de quelques nouvelles espèces du genre *Inocybes* à spores lisses rencontrées au Maroc, *Nature & Technologie* 10, 21–28.
- Pegler DN. 1969 – Studies on African Agaricales II. *Kew Bulletin* 23, 219–249.
- Pegler DN, Young TWK. 1972 – Studies on African Agaricales II. *Kew Bulletin* 23, 219–249.
- Piepenbring M, Maciá Vicente J, Codija EJ, Glatthorn C, Kirk P, Meswaet Y, Minter D, Olou BA, Reschke K, Schmidt M, Yorou NS. 2020 – Mapping mycological ignorance – checklists and diversity patterns of fungi known for West Africa. *IMA Fungus* 11, 1–22.
- Pradeep CK, Vrinda KB, Varghese SP, Korotkin HB, Matheny PB. 2016 – New and noteworthy species of *Inocybe* (Agaricales) from tropical India. *Mycological Progress* 15, 1–25.
- Raja HA, Miller AN, Pearce CJ, Oberlies NH. 2017 – Fungal Identification Using Molecular Tools: A Primer for the Natural Products Research Community. *Journal of Natural Products* 80, 756–770.
- Rehner SA, Buckley E. 2005 – A *Beauveria* phylogeny inferred from nuclear ITS and EF1-sequences: evidence for cryptic diversification and links to *Cordyceps teleomorphs*. *Mycologia* 97, 84–98.
- Ryberg M, Larsson E, Jacobsson S. 2010 – An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). *Molecular Phylogenetics and Evolution* 55, 431–442.

- Ryberg M, Larsson E, Molau U. 2009 – Ectomycorrhizal diversity on *Dryas octopetala* and *Salix reticulata* in an Alpine Cliff Ecosystem. *Arctic, Antarctic, and Alpine Research An Interdisciplinary Journal* 41, 506–514.
- Ryberg M, Nilsson RH, Kristiansson E, Töpel M et al. 2008 – Mining metadata from unidentified ITS sequences in GenBank: A case study in *Inocybe* (Basidiomycota). *BMC Evolutionary Biology* 8, 1–14.
- Saba M, Haelewaters D, Pfister DH, Khalid AN. 2020 – New species of *Pseudosperma* (Agaricales, Inocybaceae) from Pakistan revealed by morphology and multi-locus phylogenetic reconstruction. *MycKeys* 69, 1–31.
- Singer R. 1949 – The Agaricales (mushrooms) in modern taxonomy. *Lilloa Revista de Botánica* 22, 5–832.
- Singer R. 1975 – The Agaricales in modern taxonomy (3rd Eds.). J. Cramer, Vaduz, Pp. 912
- Singer R. 1986 – The Agaricales in modern taxonomy, (4th Eds.). Koeltz Scientific Books, Koenigstein, Pp. 981.
- Tedersoo L, Jairus T, Horton BM, Abarenkov K et al. 2008 – Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytologist* 180, 479–490.
- Thoen D. 1974 – Premières indications sur les mycorrhizes et les champignons mycorrhiziques des plantations d'exotiques du Haut-Shaba (Republique du Zaïre). *Bulletin de l'Institut Agronomique de l'Etat et des Stations de Recherches de Gembloux* 9, 215–227.
- Vizzini A, Maggiora MC, Tolaini F, Ercole E. 2013 – A new cryptic species in the genus *Tubariomyces* (Inocybaceae, Agaricales). *Mycological Progress* 12, 375–381.
- Watling R. 2001 – An unusual *Inocybe* sp. from West Africa. *Czech Mycology* 52, 329–334.
- Yangdol R. 2016 – Two species of *Inocybe* from Trans-Himalayan Ladakh (J&K), India. *Current Research in Environmental & Applied Mycology* 6, 305–311.
- Yorou NS, Diabaté M, Agerer R. 2011 – Phylogenetic placement and anatomical characterization of two new West African *Tomentella* (Basidiomycota, Fungi) species. *Mycological Progress* 11, 171–180.