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NOTES ON GEOGRAPHIC DISTRIBUTION

Broadening the distribution of *Mattirolomyces mexicanus* Kovács, Trappe & Alsheikh (Pezizales, Ascomycota), a rare truffle-like fungus from Mexico

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Abstract. *Mattirolomyces mexicanus* Kovács, Trappe & Alsheikh is recorded for the first time from the Yucatan Peninsula, Mexico, based on morphological and molecular data. This species is characterized by the whitish membranous peridium with inflate hyphae over 100 µm in diameter, pale gleba, subreticulated ascospores of 15–21 µm, and the putative association with Fabaceae species. This is first record of a sequestrate Ascomycota from the Yucatan Peninsula and the second record of the species worldwide. A description, photographs, and a molecular analysis of two DNA markers (ITS and LSU) are presented.

Key words. Hypogeous fungi, macrofungi, Pezizaceae, tropical fungi

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INTRODUCTION

The genus *Mattirolomyces* E. Fisch. comprises hypogeous to subhypogeous species characterized by the pale peridium, pale cartilaginous gleba with sterile veins, inamyloid asci, and the nodulose-spinose to subreticulate ascospores (Trappe 1971; Castellano et al. 1989; Kovács et al. 2011). According to several authors, some species within this genus, like *M. terfezioides*, can form mycorrhizal association with members of Cistaceae and Fabaceae with or without forming mantle or Hartig net (Bratek et al. 1996; Healy 2003; Kovács et al. 2003). The genus has a wide distribution from Africa, North America, Asia, Europe, and Oceania (Trappe et al. 2008, 2010; Wang et al. 2017). Currently five species are known: *M. austroafricanus* (Marasas & Trappe) Kovács, Trappe & Claridge, *M. mexicanus* Kovács, Trappe & Alsheikh, *M. mulpu* Kovács, Trappe & Claridge, *M. spinosus* (Harkn.) Kovács, Trappe & Alsheikh, and *M. terfezioides* (Mattir.) E. Fisch. Furthermore, some of these species have been eaten since ancient times by Egyptians and tribal people from South Africa and Australia. These truffles are still sold in markets in Africa and Asia (Trappe 1971; Trappe et al. 2008; Kovács et al. 2009; Wang et al. 2017).

Mattirolomyces has been through several taxonomic changes. The type species, *M. terfezioides*, was described as *Choiromyces* Vittad. by Mattirolo (1887), and later Fischer (1938) coined the genus *Mattirolomyces* to acommodate Mattirolo's collection. Trappe (1971) considered *Mattirolomyces* as a subgenus of *Terfezia* (Tul. & C. Tul.) Tul. & C. Tul. Several authors pointed out the morphological and ecological differences between *Terfezia* and *Mattirolomyces*; while *Terfezia* has more turbinate ascomata and is distributed in arid zones, *Mattirlomyces* has more globose ascomata and grows in temperate zones (Healy 2003). Recent phylogenetic studies have shown evidence that these genera are distant from each other and confirmed their position within Pezizaceae (Norman and Egger 1999; Percudani et al. 1999; Diez et al. 2010; Healy and Kovács 2010). Kovács et al. (2011) placed the American species of *Terfezia* within *Mattirolomyces* and

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erected two new genera base on molecular and morphological evidence: *Temperantia* K. Hansen, Healy & Kovács and *Stouffera* Kovács & Trappe.

Several species of sequestrate Ascomycota can be found in the Mexican temperate forest, where they form mycorrhizas with angiosperms and gymnosperms species such as *Quercus* L., *Pinus* L., and *Abies* Mill. (Gómez-Reyes et al. 2018). Nevertheless, sequestrate fungi are scarce in tropical forests. Ascomycetes are very common in the tropical forest of the Yucatán Peninsula, and several articles have documented such diversity (Ju et al. 1997; San Martín et al. 1999; Barbosa-Resendiz et al. 2020; Cobos-Villagrán et al. 2020; Reyes et al. 2020). Nevertheless, no sequestrate ascomycetes have been recorded so far in the Yucatan Peninsula. During recent mycological explorations in the state of Quintana Roo, an interesting truffle was collected under *Lysiloma latisiliquum* (L.) Benth. (Fabaceae). Our molecular analysis of two DNA markers (ITS and LSU) and morphological evidence show that it belongs to *M. mexicanus*, a rare species only known from type locality in Nuevo León, Mexico. This is the second record of this species worldwide and the first record of a sequestrate ascomycete for the Yucatan Peninsula.

METHODS

Sampling. The collection site is on the Yucatan Peninsula, in southern Quintana Roo. Dominant vegetation at the collecting site is a secondary evergreen tropical forest with *Lysiloma latisiliquum*, *Metopium brownei* (Jacq.) Urb., *Manilkara zapota* (L.) P. Royen, *Brosimum alicastrum* Sw., and *Bursera simaruba* (L.) Sarg. (Figure 1). The elevation in the study area was between 1 and 8 m above sea level. The climate is Ax′(w1) (i1) gw″, warm subhumid with an average annual temperature of 22–26 °C and with an autumn rainy season (García 1973; Balam et al. 1999). The collections were made during the rainy season (September–December). The classic protocols for collecting truffles were followed (Castellano et al. 1989). Hand cuts were made on dried specimens and mounted on KOH 5% and Melzer reagent to observe and measure ascospores, asci, and peridium thickness. The Q ratio was obtained for the ascospores. The scanning electron microscope (JEOL JSM-6010PLUS, LA, Tokyo, Japan) of El Colegio de la Frontera Sur (ECOSUR, Chetumal, Mexico) was utilized to observe ascospores. The voucher material is deposited at the mycological collections of Instituto Tecnológico de Ciudad Victoria (**ITCV**).

DNA extraction, amplification, and sequencing. DNA was extracted from dried specimens using a modification of the Murray and Thompson (1980) protocol. The PCR amplification was based on Mullis and Faloona (1987) and included 35 cycles with an annealing temperature of 54 °C and was carried out with the ITS5 and ITS4 primers (White et al. 1990; Gardes and Bruns 1993) for the ITS nrDNA region. The LR0R and LR5 primers (Vilgalys and Hester 1990; Cubeta et al. 1991) were used for the 28S nrDNA region (LSU). The PCR products were verified by agarose gel electrophoresis. The gels were run for 1 h at 95 V cm ^{3} in 1.5% agarose and 1× TAE buffer (Tris Acetate-EDTA). The gel was stained using GelRed (Biotium, USA) and the bands were visualized in an Infinity 3000 transilluminator (Vilber Lourmat, Germany). The amplified products were purified using the ExoSAP Purification kit (Affymetrix, USA), following the manufacturer's instructions. Products were quantified and prepared for the sequence reaction using a BigDye Terminator v. 3.1 (Applied Biosystems, USA). The products were sequenced in both directions with an Applied Biosystem model 3730XL (Applied BioSystems, USA), at the Instituto de Biología of the Universidad Nacional Autónoma de

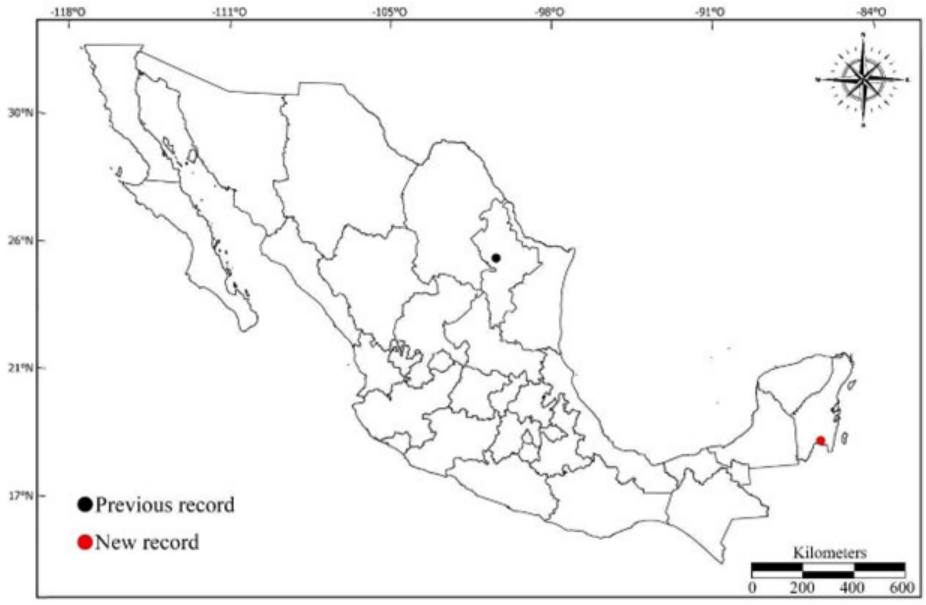

Figure 1. Known distribution of *Mattirolomyces mexicanus*.

México (UNAM). The sequences obtained were compared with the original chromatograms to detect and correct reading errors.

Phylogenetic analysis. Bayesian-inference (BI) and maximum-likelihood (ML) analyses of a concatenated matrix of LSU and ITS markers were performed of the sequences of one specimen of *M. mexicanus* collected in Quintana Roo (J. de la Fuente 492) and sequences of *Mattirolomyces* with both markers, available in NCBI GenBank (https://www.ncbi.nlm.nih.gov/nuccore), with two specimens of *Elderia arenivaga* (Cooke & Massee) McLennan (GenBank accession numbers OSC111641 and OSC111751) used for the outgroup. The alignment of the individual matrices of LSU and ITS was performed using the MUSCLE algorithm (Edgar 2004) through MEGA 11 (Tamura et al. 2021) and afterwards inspected and trimmed in BioEdit v. 7.2.5 (Hall et al. 1999). The nucleotidic substitution model of each marker was evaluated in jModelTest v. 2.1.7 (Darriba et al. 2012) following the Akaike Information Criterion (AIC), which were HKY+I for LSU and HKY+G for ITS. The matrices were concatenated with Mesquite v. 3.70 (Maddison & Maddison 2021). The BI analysis was done in MrBayes v. 3.2.6 (Ronquist and Huelsenbeck 2003; Ronquist et al. 2012) treating each marker as an independent partition, unlinking the following parameters: statefreq, revmat, shape, and pinvar; the overall rate was allowed to vary across partitions setting ratepr = variable. The substitution model of each marker was set according to the results obtained in jModelTest. The parameters of the MCMC were set as follows: 10 million generations, sampling frequency every 1000 generations, burn-in fraction 0.25, and all other values as default. The ML analysis was performed in RAxML v. 8.2.12 (Stamatakis 2014) using 100 replicates of bootstrap to test the phylogeny and all other parameters as default. Both BI and ML analyses were implemented through the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). The trees were visualized and exported in FigTree v. 1.4.4 (Rambaut 2014) and edited for publication in Adobe Photoshop Elements 10 (Adobe Systems, Inc., San Jose, CA).

RESULTS

***Mattirolomyces mexicanus* Kovács, Trappe & Alsheikh, Mycologia 103(4): 835 (2011)**
Figures 2–4

New record. MEXICO – Quintana Roo • Calderitas town, Rivadeneira Ranch; 18.5721, −088.2450; 6 m elev.; 25.XII.2020, J de la Fuente & L. Ibarra-Garibay leg.; JID-ITCV-492; GenBank: PP680778 (ITS), PP693088 (LSU).

Identification. The concatenated matrix of LSU and ITS consisted of 1267 characters, of which 240 were variable (18.9%) and 205 parsimony-informative (16.2%). The genus *Mattirolomyces* appears as monophyletic with high support (PP = 1, BS = 100), with the three specimens of *M. terfezioides* forming a clade (PP = 1, BS = 100) and being sister to the rest of the species of the genus. The studied specimen of *M. mexicanus*

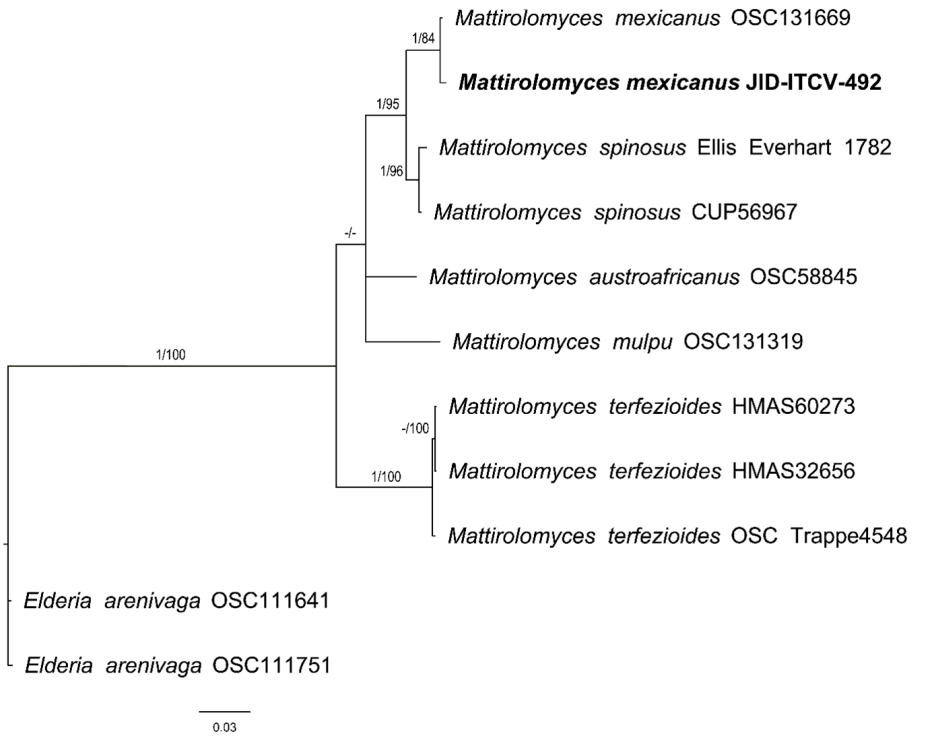

Figure 2. Majority rule consensus tree obtained from the Bayesian-inference analysis of LSU and ITS of the nrDNA of specimens of the genus *Mattirolomyces*. *Elderia arenivaga* was used as outgroup. The posterior probability and the bootstrap values of the maximum-likelihood analysis are shown above the branches (only values >0.9 and >50, respectively, are shown). In bold, the specimen studied of *Mattirolomyces mexicanus* (JID-ITCV-482) from the Yucatan Peninsula.

Figure 3. *Mattirolomyces mexicanus* (JID-ITCV-492). Scale bar: 20 mm.

(JID-ITCV-492) groups together with the other specimen of *M. mexicanus* (OSC131669) (PP = 1, BS = 84). *Mattirolomyces mexicanus* appears as sister to the clade of *M. spinosus* (PP = 1, BS = 95). *Mattirolomyces austroafricanus* and *M. mulpu* are in a trichotomy with the clade of *M. mexicanus/M. spinosus*, but this relationship shows a low support (Figure 2).

Ascomata 25 × 16 mm, subglobose, flattened at tip and bottom, white to yellowish white, with membranous peridium, sometimes absent or thinner at some zones, especially at the base, without rhizomorphs. Gleba viscid and cartilaginous, cream colored when fresh, orange when dry, with scattered white veins, more conspicuous in dried specimens. Odor similar to fresh tomatoes; taste none.

Peridium composed of two layers. Epicutis 40–63 µm in diameter, composed of tubulose prostrate or loosely interwoven hyphae, yellowish or hyaline in KOH and Melzer reagent, 3.9–6.6 µm in diameter, thick, and septa, with terminal cells clavate to cylindrical, thin-walled. Subcutis 298–600 µm in diameter, composed of irregular, globose, isodiametrical and tubulose hyphae, 9–21 µm in diameter, with scattered globose hyphae reaching more than 100 µm in diameter, becoming smaller and compacted near the gleba, hyaline to yellowish in KOH and Melzer reagent, thick-walled. Vein hyphae 12–23 µm in diameter, tubulose or rarely inflated, septate, parallel or slightly interwoven, compact, hyaline, thin-walled. Asci 48–117 × 43–52 µm, ellipsoid, subglobose to irregular, when immature the asci can be clavate, sometimes biseriate or randomly occurring within the asci, eight-spored, rarely four-spored, sometimes pedicellate, hyaline to yellowish, negative in Melzer reagent, thick-walled. Ascospores 15–21 µm (Q = 1.04–1.13, *N* = 30) excluding the ornamentation, subglobose, rarely collapsed, ornamented with spines of 3–5 µm long, up to 3 µm in diameter, with obtuse tips, sometimes forming a poorly developed reticulum projecting less than 1 µm (visible in SEM), hyaline to yellowish in KOH and Melzer reagent, thick-walled.

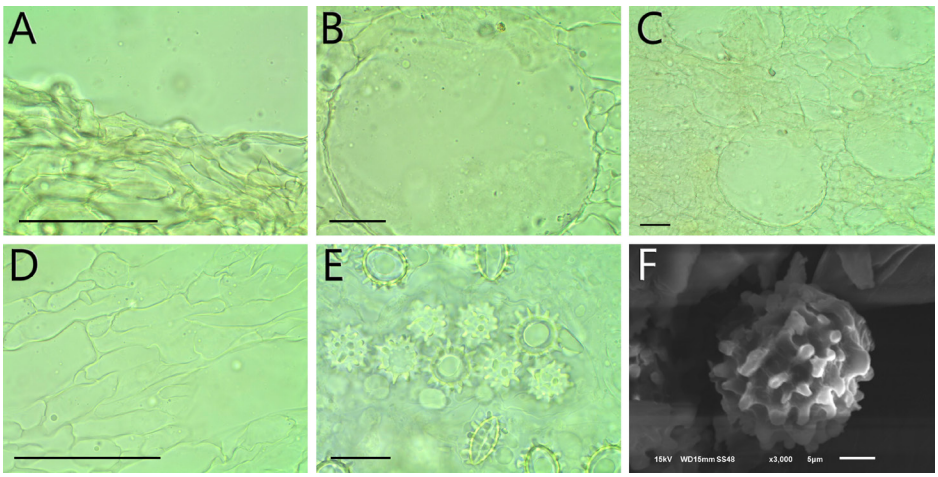

Figure 4. *Mattirolomyces mexicanus* (JID-ITCV-492), microscopic features. **A.** Epicutis. **B, C.** globose hyphae of the epicutus. **D.** Trama. **E.** Ascospores. **F.** Details of ascospore ornamentation under SEM. Scale bars: A–E = 20 µm; H = 5 µm.

DISCUSSION

The genus *Mattirolomyces* has a wide distribution including semiarid zones and temperate and tropical forests. Most species seem to be associated with Fabaceae and Cistaceae (Kovács et al. 2003). Although the genus seems common in some countries, *Mattirolomyces* species are seldom observed in Mexico (Kovácks et al. 2011). So far only three collections have been made, which correspond to three different species. The Mexican *Mattirolomyces* species are considered here to be endemic and rare until more collections are made and studied. Although *Mattirolomyces* is considered edible by many cultures, there is no information on the use as food of this genus in Mexico. Furthermore, there are few data on the fungi used by the Maya people of Yucatán, so we discard the idea that the ancient Maya consumed *M. mexicanus*.

Mattirolomyces mexicanus is characterized mainly by the wide hyphae in the subcutis that are up to 100 µm wide and the habit in secondary tropical forest dominated by *Lysiloma latisiliquum*. Our material agrees with the description of the species by Kovács et al. (2011), but there are there some differences in the structure of the peridium. In our specimen, the globose hyphae in the peridium are bigger, up to 100 µm. *Matirolomyces spinosus* differs in having a pubescent peridium, thicker peridium (up to 800 *µm), and smaller globose hyphae of the subcutis*, which reaching up to 35 µm wide. The ascospore size and peridium thickness is similar to *M. mulpu* Kovács, Trappe & Claridge from Africa, but it differs in the smaller hyphae of the subcutis (40 µm) and the more developed reticulum of the ascospores (Trappe et al. 2009).

Our specimen was found in a secondary evergreen tropical forest near *Lysiloma latisiliquum*, a common member of Fabaceae in the Yucatan Peninsula (Figure 5). Although the specimen was found near *Lysiloma*, we have no evidence of a mycorrhizal association between the fungus and the tree. It is interesting to note that *M. terfezioides* and *M. spinosus* are also found growing near members of Fabaceae, such as *Robinia pseudoacacia* L. and *Enterolobium cyclocarpum* (Jacq.) Griseb. Mycorrhizal association have been observed between *R. pseudoacacia* and *M. terfezioides* (Bratek et al. 1996; Kóvács et al. 2003), but studies on mycorrhizal association with other members of Fabaceae are needed. So far, studies of the mycorrhizal fungi of *Lysiloma latisiliquum* have focused mainly on Glomeromycota (Rodríguez-Rodríguez et al. 2014; Oros-Ortega et al. 2020). We recommend more studies to understand the mycorrhizal associations in the Mexican tropical forests.

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Figure 5. Representative vegetation at the sampling area.

ADDITIONAL INFORMATION

Conflict of interest
The authors declare that no competing interests exist.

Ethical statement
No ethical statement is reported.

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Author contributions
JIF and LEIG collected the specimens. JIF, GGG, and JGJ identified the species. JPP made the phylogenetic analyses. MSF and JIF made the taxonomic description. All authors contributed to the final draft.

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Data availability
All data that support the findings of this study are available in the main text.

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