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Cordyceps sensu lato: the current state of knowledge in Mexico

Estado actual del conocimiento de *Cordyceps sensu lato* en México

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RESUMEN

Antecedentes: *Cordyceps s.l.* es un grupo parafilético de hongos ascomicetes, principalmente parásitos de artrópodos. En México, estos hongos han sido poco estudiados y se desconoce el panorama actual de su diversidad.

Objetivo: Describir la historia de los registros de *Cordyceps s.l.* en México, así como realizar un listado de las especies, sus hospederos y distribución geográfica.

Métodos: Se realizó una revisión bibliográfica sobre *Cordyceps s.l.* citados en México de 1864 a 2022. Se elaboraron mapas de la distribución geográfica de las familias Clavicipitaceae, Cordycipitaceae y Ophiocordycipitaceae en el programa QGIS 3.18.1.

Resultados y conclusiones: El primer registro de *Cordyceps* en México data de 1864. A la fecha se han registrado 35 especies de *Cordyceps s.l.*, lo que equivale al 3.5% de la diversidad registrada para el género a nivel mundial. La distribución geográfica de estas especies está determinada en primer lugar por sus hospederos y consecuentemente por la vegetación. Las especies con mayor distribución geográfica fueron *Beauveria bassiana* y *Cordyceps militaris* de Cordycipitaceae; *Metarhizium anisopliae* de Clavicipitaceae; y *Tolypocladium capitatum* y *T. ophioglossoides* de Ophiocordycipitaceae. *Beauveria bassiana* y *Metarhizium anisopliae* son las especies con más estudios, debido a su patogenicidad en diferentes insectos plaga.

Palabras clave: entomopatógenos, Hypocreales, insectos, plagas, *Tolypocladium*

ABSTRACT

Background: *Cordyceps s.l.* is a paraphyletic group of Ascomycete fungi that parasitize mainly arthropods. In Mexico, these fungi have been little studied and the current state of their diversity is unknown.

Objective: To describe the history of the records of *Cordyceps s.l.* from Mexico, and to generate a checklist of the species, detailing their hosts and geographical distribution.

Methods: A literature review was conducted addressing on *Cordyceps s.l.* cited from Mexico from 1864 to 2022. Geographical distribution maps of Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae were created in the QGIS 3.18.1 Software.

Results and conclusions: The first record of *Cordyceps* in Mexico dates back to 1864. To date, 35 species of *Cordyceps s.l.* have been recorded, equivalent to 3.5% of the diversity of the genus recorded worldwide. The geographical distribution of these species is determined by their hosts and consequently by the vegetation. The species with the greatest geographical distribution were: *Beauveria bassiana* and *Cordyceps militaris* of Cordycipitaceae; *Metarhizium anisopliae* of Clavicipitaceae; and *Tolypocladium capitatum* and *T. ophioglossoides* of Ophiocordycipitaceae. *Beauveria bassiana* and *Metarhizium anisopliae* are the most studied species due to their pathogenicity to different crop pests.

Keywords: entomopathogens, Hypocreales, insects, pest, *Tolypocladium*

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INTRODUCTION

Cordyceps sensu lato (s.l.) is a paraphyletic group of Ascomycete fungi comprising approximately 1 000 species (Wei *et al*. 2020). The members of the group present multiple lifestyles, parasitizing arthropods, grasses, or hypogeous fungi (Sung *et al*. 2007a, 2007b) while some are saprotrophs or endophytes (Gazis *et al*. 2014), that includes fungal species of agricultural importance. Asexual stages are important as biological control of several pest and vector insects. *Metarhizium* has been used to control many groups of the insects in many countries, for example to control *Aeneolamia varia* ("salivazos"), which affects alfalfa and sugar cane cultivars in Brazil (Alves *et al*. 2008), and to control of *Anopheles* mosquitoes, which are vector of malaria (Scholte *et al*. 2005). *Akanthomyces sabanensis* (=*Lecanicillium sabanense*) parasitizes *Pulvinaria caballeroramosae* females that, in turn, parasitize *Ficus suatensis* in Colombia (Chiriví-Salomón *et al*. 2015). In Florida, USA, *Beauveria bassiana* has been used to control the whitefly *Bemisia tabaci* (Sani *et al*. 2020). This host species is considered by the International Union for Conservation of Nature (IUCN) as an invasive pest in North America that affects crops such as alfalfa, broccoli, cabbage, cotton, tomato, squash, peanut, and watermelon, among others (Quesada-Moraga *et al*. 2006; SEDECO 2014).

Cordyceps s.l. also comprises species with edible and medicinal properties. *Cordyceps militaris*, *C. pruinosa*, *C. tenuipes*, *Isaria cicadae*, *Ophiocordyceps sinensis*, and *Tolypocladium ophioglossoides*, among others are appreciated as edible and medicinal in Asia and are considered as functional foods since they produce metabolites beneficial to health (Ng and Wang 2005, Zhang *et al*. 2018). Different species of *Cordyceps s.l.* have antioxidant, anti-cancer, antihyperlipidemic, anti-diabetic, anti-fatigue, anti-aging, anti-depressant, and aphrodisiac properties, since they produce various biomolecules including nucleosides such as cordycepin, sterols, flavonoids, cyclic peptides, phenolic, bioxanthracenes, polyketides, and alkaloids (Das *et al*. 2021). Cordycepin (3´-deoxyadenosine), a nucleoside analogue of adenosine, is a well-studied metabolite, since it presents some of the properties described above. Its presence and quantity are considered indicators of the quality of the *Cordyceps* products (Lee *et al*. 2019).

Isaria cicadae is a species of great cultural importance, which has been used in China for about 1 600 years (Hsu *et al*. 2015). Another species of cultural, medicinal, and economic importance is *Ophiocordyceps sinensis*. Known in Tibet as "winter worm" or "summer grass", this species parasitizes larvae of the moths *Thitarodes/Hepialus* spp. (Wu *et al*. 2020). Its distribution is restricted to the Tibetan plateau in the Himalayas at over 5 000 m, and its overexploitation has led to a decline in its populations (Winkler 2009, Kumar *et al*. 2010, Shrestha 2011). *O. sinensis* currently has a high economic value worldwide, indeed it was marketed at up to $60 000 USD per kg in 2015 (Lei *et al*. 2015). Consequently, the IUCN has classed it as vulnerable (VU) (Yang 2020).

Artificial cultivation of *O. sinensis* is challenging; however, *C. militaris* can be used as a substitute for *O. sinensis* and is cultivated at industrial scale (Shrestha *et al*. 2010). *Cordyceps militaris* has biological activities, including as an antimalarial, hypoglycemic, anti-cancer, immunomodulatory, antidiabetic, and antiviral against severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) (Khan *et al*. 2010, Jedrejko *et al*. 2021).

In Mexico, there is a lack of knowledge regarding the diversity of species of *Cordyceps s.l.* and research topics have been mainly limited to list or records with descriptions using traditional taxonomy, doing little to facilitate their potential exploitation. Therefore, the objectives of this review were to analyze the records of these fungi cited in Mexico, and list the diversity, hosts, and geographical distribution of the *Cordyceps s.l.*

MATERIAL AND METHODS

This paper analyzes the published information pertaining to *Cordyceps s.l.* in Mexico. To achieve this, a list of the species recorded in the different states of the country was created through a review of the scientific literature published from 1864 to 2022. Bibliographic reviews as Chacón and Guzmán (1983), or those included in Rubio-Bustos *et al*. (1999) and Guzmán *et al*. (2001) were checked. The review of the first reports of entomopathogenic fungi was conducted in the Historical Collection of the Institute of Biology of the National Autonomous University of Mexico (UNAM).

We also looked for records of anamorphic states of *Cordyceps s.l.* used as biological controls. The

keywords used in the query were: entomopathogenic fungi, biological control, *Beauveria*, *Cordyceps*, *Isaria*, *Metarhizium*, *Paecilomyces*, *Paraisaria*, and *Tolypocladium*. Scientific names and their authors were standardized according to the nomenclature published in the Index Fungorum portal (http://www.indexfungorum.org). Geographic distribution maps of Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae were generated with QGIS 3.18.1 Software (QGIS 2021), using presence records from the studies listed in Tables 1, 2, and 3. The dataset for land use and vegetation cover, available from the Mexican National Institute of Statistics and Geography (INEGI 1992), was used with at scale 1:250,000. The coordinate system MEXICO ITRF 2008 LCC was used, along with the Lambert Conformal Conic and Datum projection (https://www.inegi.org.mx/app/biblioteca/ficha.html?upc=702825007020).

RESULTS

History of records of *Cordycesp s.l.* in Mexico

The first report of *Cordyceps* in Mexico was made by the physician and pharmacist Río de la Loza (1864), who analyzed an "animal-plant rare in nature" and determined it to be an "animal (*Cicada communis*) with animal excrescence" (Figure 1). In the same year, Milne-Edwards (1864) reviewed the "animal-plant" specimens from Mexico and mentioned that what looked like a plant and emerged from cicada larvae or nymphs was a fungus called *Sphaeria sobolifera* (=*Ophiocordyceps sobolifera*). Seventeen years later, Urbina (1881) supported the conclusions made by Milne-Edwards, corroborating that these specimens were insects parasitized by fungi. Then, seventy-seven years after the Milne-Edwards determination, the first species of entomopatogenous fungi was *Isaria cicadae* (= *Isaria sinclairii*) in Jalisco, Mexico were recorded in 1941-1942 (Petch 1941-1942)

Figure 1. Illustration of a "rare animal-plant" made by Río de la Loza in 1864. A. Larva-nymph, with ramifications that emerge from the head; B. Ramifications ending in a cauliflower formations, emerging from the anterior part of the thorax; C. Dissected lateral view of a larva-nymph; D. Serrated leg of the insect used to excavate the soil.

The taxonomic identification of herbarium material, collected material, and new records have been carried out mainly by Petch (1941-1942), Mains (1957, 1958), Guzmán (1958), Heim and Wasson (1958), Pérez-Silva (1977, 1978), and Rubio-Bustos *et al*. (1999). The regional taxonomic studies have been carried out mainly by Castro *et al*. (2012) and Pérez-Villamares *et al*. (2017). The most recent research described a new species, *Cordyceps mexicana*, in which morphology, host, and DNA data were analyzed (López-Rodríguez *et al*. 2022) (Figure 2).

Diversity of *Cordyceps s.l.* in Mexico

Currently, there are 35 *Cordyceps s.l.* species recorded in Mexico, belonging to the families Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae. These species represent 3.5 % of the entomopathogenic fungi worldwide. Most of the records have been made from Colima, Estado de México, Hidalgo, Jalisco, Morelos, and Oaxaca. Estado de México, with 13 species, represented the first place in terms of diversity. There were states, such as Aguascalientes, Baja California, Baja California Sur, Ciudad de México, Guerrero, Querétaro, Yucatán, and Zacatecas, in which no studies have been conducted (Figure 3).

Species and families recorded in Mexico

Clavicipitaceae

Clavicipitaceae in Mexico was the least recorded family, represented by eight entomopathogenic species: *Metarhizium acridum*, *M. anisopliae*, *M. brunneum*, *M. guizhaense*, *M. humberi*, *M. pemphigi*, *M. pinghaense*, and *M. robertsii*. These species have been found mainly in agricultural areas of maize and bean crops, in soil or parasitizing Coleoptera, Diptera, Hemiptera, Lepidoptera, Orthoptera, Thysanoptera, and acari (Arachnida) (Table 1). *Metarhizium anisopliae* had the highest number of records and the widest distribution (Figure 4), it has been isolated from soils and a wide range of insects. *Metarhizium acridum*, *M. brunneum*, and *M. humberi* have been found in a single order of insects, meanwhile *M. guizhaense*, *M. pinghaense*, and *M. robertsii* have been recorded parasitizing Coleoptera, Lepidoptera, and Orthoptera.

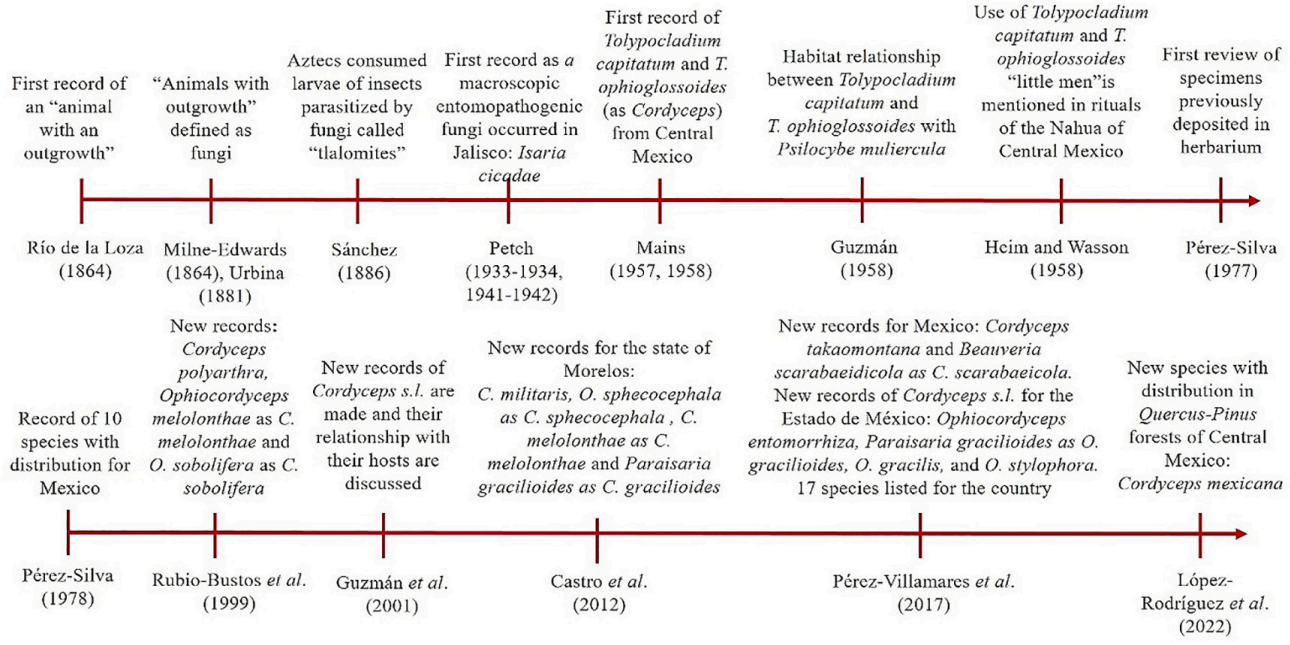

Figure 2. *Cordyceps s.l.* studies in Mexico time-line.

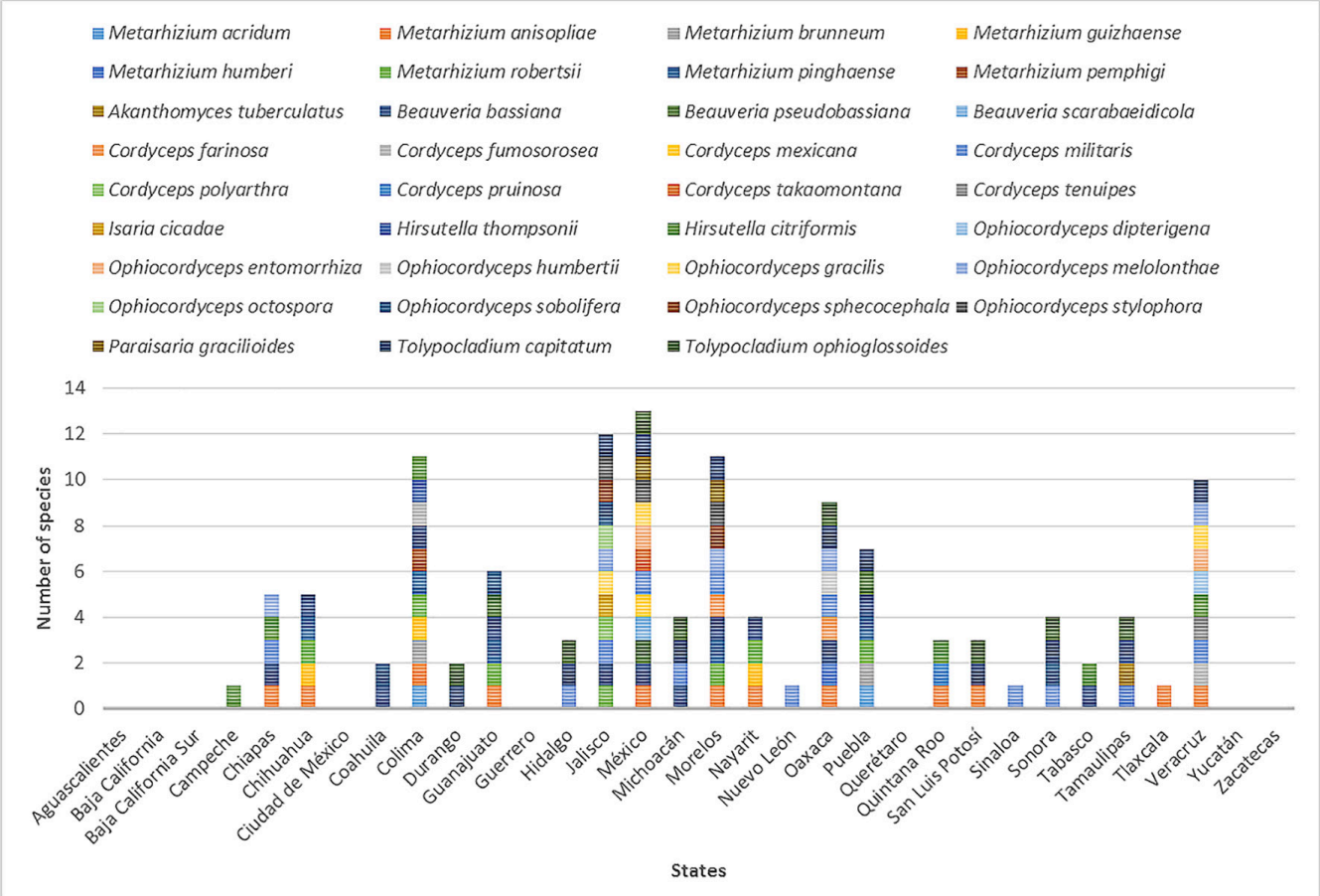

Figure 3. *Cordyceps s.l.* species registered by state in Mexico.

Cordycipitaceae

The Cordycipitaceae family was represented in Mexico by 13 species, eight of the genus *Cordyceps*, three of B*eauveria*, one of *Akanthomyces*, and one of *Isaria* (Table 2). *Cordyceps militaris* had the largest number of records and a wide geographic distribution (Figure 5). It has been recorded in 12 states, in various vegetation types including temperate forests, rainforests, grasslands, and agricultural areas. It grows on pupae and larvae of Lepidoptera of the families Geometridae, Noctuidae, and Sphingidae, and has only been reported once parasitizing Coleoptera (Table 2). *Isaria cicadae* was the first species cited in Mexico, however its ubication was not clear, therefore it is not shown on the figure 5.

Ophiocordycipitaceae

Ophiocordycipitaceae was the family with the greatest diversity recorded in Mexico, comprising 14 species and four genera. *Ophiocordyceps* had nine species distribuited in seven states. Of these, Estado de México, Jalisco, and Veracruz had the highest number of records. *Tolypocladium* was represented by two species, with the highest number of records and the largest geographic distribution, widely collected parasitizing *Elaphomyces* spp. in pine-oak forests. The genus *Hirsutella* was also represented by two species, while *Paraisaria* had presented only one species (Figure 6, Table 3).

Asexual states of Cordyceps s.l. recorded as agents of biological control of insect pests and disease vectors

In Mexico, the asexual states of *Beauveria bassiana*, *Cordyceps fumosorosea* (Table 2), *Hirsutella* sp. (Table 3), and *Metarhizium anisopliae* (Table 1) have been studied as biological control agents of insect pests that affect valuable crops such as beans, citrus, coffee, fruits, maize, and sugar cane. In addition, another application being investigated is its pathogenicity on insects or acarus vectors of bacteria, viruses, or parasites (Tables 1 and 2).

Figure 4. Geographic distribution of Clavicipitaceae in Mexico.

Figure 5. Geographic distribution of Cordycipitaceae in Mexico.

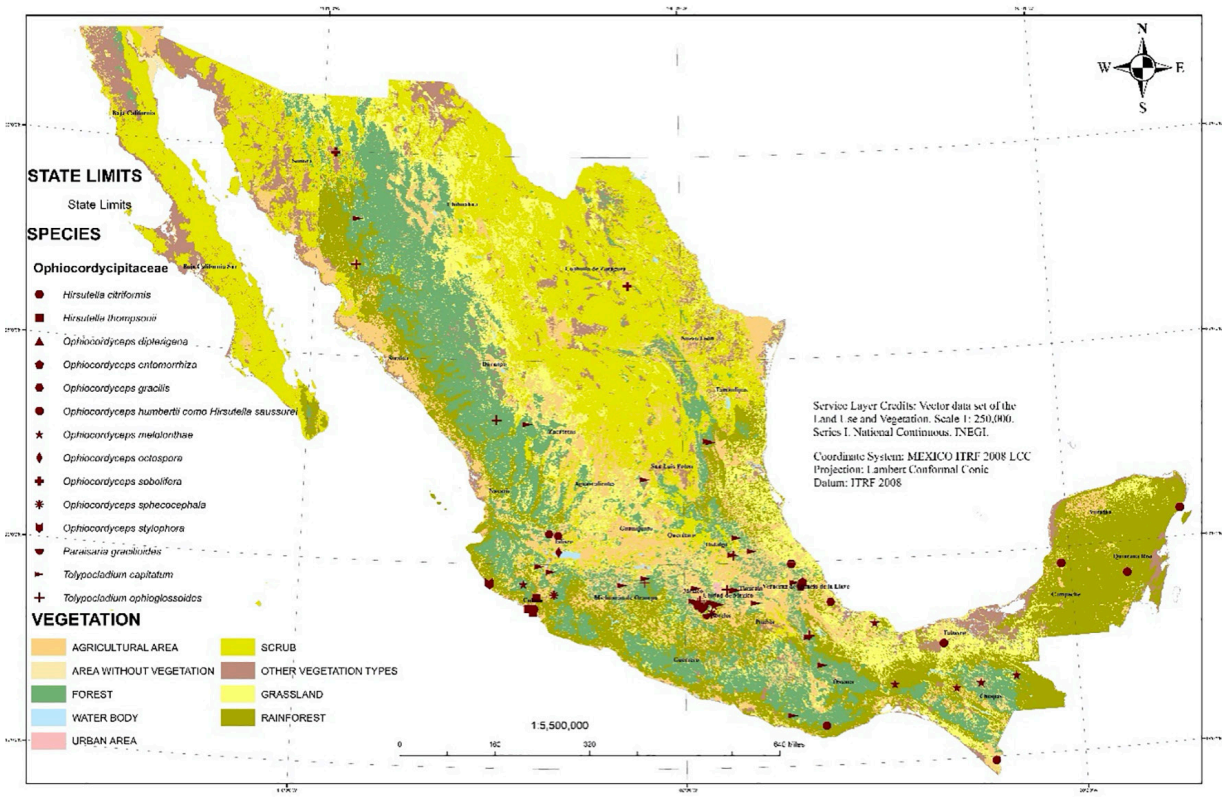

Figure 6. Geographic distribution of Ophiocordycipitaceae in Mexico.

The traditional importance of Tolypocladium in Mexico

Tolypocladium capitatum (=*Cordyceps capitata*) and *T. ophioglossoides* (=*Cordyceps ophioglossoides*) were the only species recorded with an edible use in rituals of the indigenous of central Mexico. These were first recorded in the Estado de México (Table 3). The Nahuas attribute medicinal properties to both species (Heim and Wason 1958). Their consumption was first described in rituals of the nahua people of San Pedro Tlanixco and Tenango del Valle, where they were consumed together with *Psilocybe muliercula* and *Elaphomyces* spp. (Heim and Wason 1958). The common names of *T. capitatum* and *T. ophioglossoides* are "little men", while individuals of *Psilocybe muliercula* are known as "little women" and *Elaphomyces* spp. is called "great world". The ritual itself was described by Guzmán (2008); however, the use of *Tolypocladium* has not been recorded again.

Relationship with the hosts

In Mexico, we found that the members of Clavicipitaceae are mainly associated with nymphs or larvae of Coleoptera, Lepidoptera, and Orthoptera, although *Metarhizium anisopliae* has a very wide range of insect hosts and even parasitizes Arachnida (Table 1). Cordycipitaceae mainly presented an association with Lepidoptera. *Cordyceps militaris* and *C. takaomontana* were associated with Lepidoptera larvae and pupae. *Cordyceps farinosa* and *C. polyarthra* were found on Lepidoptera pupae, while only *Akanthomyces tuberculatus* was found on Lepidoptera adults. However, other species could be associated with Coleoptera, Hemiptera, and Orthoptera adults and *Beauveria bassiana* has also a very wide range of insect hosts (Table 2). In Ophiocordycipitaceae, *Tolypocladium* parasitizes *Elaphomyces* fungi, while *Ophiocordyceps* was found on Lepidoptera and Coleoptera larvae, on Diptera, Coleoptera, Hymenoptera, Homoptera, and Hemiptera adults, and only *Hirsutella thompsonii* parasitizes acari (Table 3).

Table 1. Clavicipitaceae species recorded in the literature from Mexico

Metarhizium acridum

(Driver & Milner) J.F. Bisch., S.A. Rehner & Humber

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Orthoptera, Acrididae, *Schistocerca piceifrons* in laboratory assays; Pyrgomorphidae, *Sphenarium purpurascens* (adults) in field experiments.

Vegetation

Agricultural areas with crops such as amaranth, beans, eggplant, maize, and squash, grass and soil.

State (references)

Without locality (Barrientos-Lozano *et al.* 2005), Puebla (Guerrero-Guerra *et al.* 2013), Colima (Serna-Domínguez *et al.* 2019).

M. anisopliae

(Metschn.) Sorokin

Host: Class, Order, family, species (larvae, pupae or adult).

Arachnida, Trombidiformes, Tetranychidae, *Tetranichus urticae*; Ixodidae, **Boophilus microplus* in field experiments with bovine; Coleoptera, Curculionidae, *Hypothenemus hampei* (adults); Scarabaeidae, *Anomala* sp., *Macrodactylus murinus, Paranomala* sp. (larvae), *Phyllophaga vetula* (larvae) in laboratory assays, *Phyllophaga* spp. (larvae) in laboratory assays; Tenebrinidae, *Tenebrio molitor* (larvae) in laboratory assays; Hemiptera; Aleyrodidae, **Bemisia tabaci* (nymph) in laboratory assays; Cercopidae, **Aeneolamia* spp., *A. postica*; Liviidae, **Diaphorina citri* (adults and nymphs) in field experiments; Reduviidae, **Meccus pallidipennis* (adults), **Triatoma dimidiata* (adults and nymphs) in laboratory assays; Triozidae, **Bactericera cockerelli* (nymph) in laboratory assays; Lepidoptera; Pyralidae, *Galleria mellonella* (larvae) in laboratory assays; Crambidae, *Diatraea saccharalis, D. magnifactella*; Noctuidae, *Spodoptera frugiperda* in laboratory assays; Orthoptera, Acrididae, *Schistocerca piceifrons*; Romaleidae, *Brachystola magna* (adults) in laboratory assays; Thysanoptera, Thripidae, *Frankliniella occidentalis* (larvae) in laboratory assays; Diptera, Culicidae, *Aedes aegypti* (eggs) in laboratory assays.

Vegetation

Agricultural areas with crops such as bean, citrus, ebo, maize, oatmeal and, wheat. Coffee and sugar cane plantations. Agroecosystem of *Citrus aurantifolia, C. grandis, Saccharum officinalis,* and *Mangifera indica*. Soil.

State (references)

Chiapas (De la Rosa *et al.* 2000; Bautista Gálvez *et al.* 2017; Torres-Estrada *et al.* 2020), Tabasco (Bautista-Gálvez and González-Cortes 2005; Hernández-Domínguez *et al.* 2016; Bautista-Gálvez *et al.* 2017; Brunner-Mendoza *et al.* 2017, 2018), Veracruz (Alonso-Díaz *et al.* 2007; Carrillo-Benítez *et al.* 2013; Hernández-Domínguez *et al.* 2016; Brunner-Mendoza et *al.* 2017, 2018; Navarro-Barranco *et al.* 2019), without locality (Lezama-Gutiérrez *et al.* 2012, Vázquez-Martínez *et al.* 2014), Colima (Carrillo-Benítez *et al.* 2013; Lezama-Gutiérrez *et al.* 2014; Serna-Domínguez *et al.* 2019; Ramírez-Milanes *et al.* 2022), Guanajuato (Carrillo-Benítez *et al.* 2013; Cabrera-Mora *et al.* 2019), Quintana Roo (Carrillo-Benítez *et al.* 2013), Chihuahua (Rios Velasco *et al.* 2014; Bustillos-Rodríguez *et al.* 2016), Nayarit (Bustillos-Rodríguez *et al.* 2016), San Luis Potosí (Flores-Villegas *et al.* 2016; Hernández-Domínguez *et al.* 2016; Brunner-Mendoza *et al.* 2017, 2018; Navarro-Barranco *et al.* 2019), Oaxaca (Hernández-Domínguez *et al.* 2016; Brunner-Mendoza *et al.* 2017, 2018; Navarro-Barranco *et al.* 2019), Morelos (Solis-Perez *et al.* 2016), Estado de México (Alcantara-Vargas *et al.* 2020)

* Considered vectors of bacteria, parasites or viruses.

M. brunneum

Petch

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera, Pyralidae, *Galleria mellonella* (larvae)

Vegetation

Agricultural areas with crop of bean and avocado plantations. Soil

State (references)

Colima (Serna-Domínguez *et al.* 2019), Puebla (Cabrera-Mora *et al.* 2019),

M. guizhaense

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleoptera, Lepidoptera, Pyralidae, *Galleria mellonella*; Noctuidae, *Spodoptera frugiperda*; Orthoptera, Romaleidae, *Brachystola magna* (adults) in laboratory assays.

Vegetation
Agricultural areas with crop of maize and avocado plantations. Soil.

State (references)
Chihuahua (Bustillos-Rodríguez *et al.* 2016), Colima (Brunner-Mendoza *et al.* 2017, 2018; Serna-Domínguez *et al.* 2019), Nayarit (Brunner-Mendoza *et al.* 2017, 2018).

M. humberi

C. Luz, L. Rocha & I. Delalibera

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Lepidoptera

Vegetation
Tropical gallery forest in a cerrado ecosystem and soil.

State (references)
Tamaulipas and Oaxaca (Luz *et al.* 2019)

M. pemphigi

(Driver & Milner) Kepler, Humber & S.A. Rehner

Host: Class, Order, family, species (larvae, pupae or adult).
Unspecified

Vegetation
Coffee plantations

State (references)
Colima (Serna-Domínguez *et al.* 2019)

M. pinghaense

Q.T. Chen & H.L. Guo

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleoptera, Scarabaeidae, Anomala cincta, Phyllophaga spp. (larvae) and white grubs; Lepidoptera, Pyralidae, *Galleria mellonella*; Orthoptera, Romaleidae, *Brachystola magna* (adults) in laboratory assays

Vegetation
Agricultural areas with crop as bean, and maize. Avocado plantations and soil

State (references)
Guanajuato (Guzmán-Franco *et al.* 2012; Carrillo-Benítez *et al.* 2013), Puebla (Guzmán-Franco *et al.* 2012), Chihuahua (Bustillos-Rodríguez *et al.* 2016), Morelos (Brunner-Mendoza *et al.* 2017, 2018), Colima (Serna-Domínguez *et al.* 2019)

M. robertsii

J.F. Bisch., S.A. Rehner & Humber

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Coleoptera, Scarabaeidae, *Phyllophaga* spp. (larvae) and white grubs; Lepidoptera, Pyralidae, Galleria mellonella; Orthoptera, Romaleidae, *Brachystola magna* (adults) in laboratory assays.

Vegetation

Agricultural areas with crop as bean, blackberry and, maize. Avocado plantations, tejocote orchard and soil

State (references)

Without locality (Carrillo-Benítez *et al*. 2013; Serna-Domínguez *et al*. 2019), Guanajuato (Pérez-González *et al*. 2014), Puebla (Muñiz-Reyes *et al*. 2014; Cabrera-Mora *et al*. 2019), Chihuahua and Nayarit (Bustillos-Rodríguez *et al*. 2016), Jalisco and Morelos (Brunner-Mendoza *et al*. 2017, 2018), Colima (Brunner-Mendoza *et al*. 2017, 2018; Serna-Domínguez *et al*. 2019)

Table 2. Cordycipitaceae species recorded in the literature from Mexico

Akanthomyces tuberculatus

(Lebert) Spatafora, Kepler & B. Shrestha

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera, Sphingidae (adults)

Vegetation

Agricultural areas with citrus

State (references)

Tamaulipas (Sánchez-Peña 1990)

Beauveria bassiana

(Bals. -Criv) Vuill.

Host: Class, Order, family, species (larvae, pupae or adult).

Arachnida, Ixodida, Ixodidae, **Rhicephalus microplus*; Insecta, Coleoptera, Scarabaeidae, *Anomala cincta, Phyllophaga polyphilla;* Curculionoidea, *Hypothenemus hampei, Scyphophorus acupunctatus* (larvae); Diptera, Tephritidae, *Rhagoletis pomonella* (larvae and pupae); Hemiptera, Triozidae, **Bactericera cockerelli*; Aleyrodidae, **Bemisia tabaci;* Liviidae,**Diaphorina citri*; Reduviidae,**Triatoma dimidiate*; Lepidoptera, Pyraloidea, *Galleria mellonella;* Noctuidae, *Spodoptera exigua* (larvae and pupae); Orthoptera, Romaleidae, *Brachystola magna* (adults); Thysanoptera, Thripidae, **Frankliniella occidentalis* (nymph and adults)

Vegetation

Agricultural areas with crops such as coffee, lemon, maize, and tejocote orchad, grassland and soil

State (references)

Chiapas (De la Rosa *et al*. 2000; Bautista Gálvez *et al*. 2017), Chihuahua (Barajas *et al*. 2011; Rios-Velasco *et al*. 2014; Bustillos-Rodríguez *et al*. 2016), Coahuila (Sánchez-Peña *et al*. 2011), Morelos (Hernández-Velázquez *et al*. 2011), Guanajuato (Guzmán-Franco *et al*. 2012; Pérez-González *et al*. 2014; Cabrera-Mora *et al*. 2019), Jalisco & Oaxaca (Carrillo-Benítez *et al*. 2013), Colima (Lezama-Gutiérrez *et al*. 2014), without locality (Lezama-Gutiérrez *et al*. 2012), Estado de México (Muñiz-Reyes *et al*. 2014), Puebla (Muñiz-Reyes *et al*. 2014; Cabrera-Mora *et al*. 2019), Michoacán (García-Munguía *et al*. 2015), Nayarit (Bustillos-Rodríguez *et al*. 2016), Tabasco (Bautista-Gálvez *et al*. 2017), Tamaulipas (Gandarilla-Pacheco *et al*. 2021)

*Considered vectors of bacteria, parasites or viruses

Beauveria pseudobassiana
S.A Rehner & Humber

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleoptera, Scarabaeidae, Cyclocephala, *Phyllophaga* spp., *Phyllophaga polyphilla*, and unidentified white grubs (larvae) in laboratory assays; Diptera, Tephritidae, *Rhagoletis pomonella* (larvae and pupae) in laboratory assays.

Vegetation
Agricultural areas with crops such as bean, maize,and tejocote orchard, grassland and soil

State (references)
Guanajuato (Carrillo-Benítez *et al*. 2013; Pérez-González *et al*. 2014; Cabrera-Mora *et al*. 2019), Puebla (Carrillo-Benítez *et al*. 2013; Muñiz-Reyes *et al*. 2014; Cabrera-Mora *et al*. 2019), Estado de México (Muñiz-Reyes *et al*. 2014)

Beauveria scarabaeidicola
(Kobayasi) S.A. Rehner & Kepler

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleoptera, Scarabaeidae, Melolonthinae, and Dynastinae (adults)

Vegetation
Quercus-Pinus forest, ecotone between shrubby secondary vegetation of Juniperus forest, agricultural zone and, secondary bushy vegetation of *Quercus* forest

State (references)
Estado de México (Pérez-Villamares *et al*. 2017, as *Cordyceps scarabaeicola*)

Cordyceps farinosa
(Holmsk.) Kepler, B. Shrestha & Spatafora

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Lepidoptera (pupae)

Vegetation
-

State (references)
Morelos (Pérez-Silva 1977; Guzmán *et al*. 2001, as *Isaria farinosa*), Oaxaca (Pérez-Silva 1977, 1979, Guzmán *et al*. 2001, as *Isaria farinosa*)

Cordyceps fumosorosea
(Wize) Kepler, B. Shrestha & Spatafora

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Orthoptera, Tetigonidae (adults); Hemiptera, Aleyrodidae, *Bermicia* sp.; Reduviidae, *Meccus pallidipennis* (nymphs) in laboratory assays

Vegetation
Agricultural areas with crops such as citrus and watermelon

State (references)
Veracruz (Pérez-Silva 1978, as *Paecilomyces fumoso-roseus*), Colima (Flores-Villegas *et al*. 2016, as *Isaria fumosorosea*), without locality (Lezama-Gutiérrez *et al*. 2012, as *Isaria fumosorosea*)

Cordyceps mexicana

L. López-Rodríguez, C. Burrola-Aguilar & R. Garibay-Orijel

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera; Hemileucinae, *Paradirphia* sp. (pupae)

Vegetation

Oak and mixed oak-pine forests

State (references)

Estado de México (López-Rodríguez *et al.* 2022)

Cordyceps militaris

(L.) Fr.

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera, Geometridae, Noctuidae, and Sphingidae (larvae and pupae) Coleoptera (adults) (only one record by Castro *et al.*, 2012)

Vegetation

Quercus forest, *Quercus-Pinus* forest, mesophytic and *Abies-Pseudotsuga* mixed forests, deciduous forest, agricultural zone, grassland and, secundary bushy vegetation of *Quercus* forest

State (references)

Jalisco (Mains 1958; Guzmán-Dávalos and Nieves 1984; Guzmán-Dávalos 1992, as *Cordyceps sobolifera*; Rubio-Bustos *et al*. 1999; Guzmán *et al*. 2001; Gándara *et al*. 2014), without locality (Guzmán 1977), Hidalgo (Pérez-Silva 1977), Morelos (Pérez-Silva 1977; Rubio-Bustos *et al.* 1999; Castro *et al*. 2012), Oaxaca (Pérez-Silva 1977; Rubio-Bustos *et al.* 1999), Veracruz (Pérez-Silva 1977; Rubio-Bustos *et al*. 1999), Chiapas (Chacón and Guzmán 1984; Rubio-Bustos *et al*. 1999; Guzmán *et al*. 2001), Estado de México (Frutis *et al*. 1985; Rubio-Bustos *et al*. 1999; Pérez-Villamares *et al*. 2017), Michoacán (Díaz-Barriga *et al*. 1988; Rubio-Bustos *et al*. 1999, based on the literature), Sonora (Pérez-Silva *et al*. 1996), Sinaloa (Rubio-Bustos *et al*. 1999), Nuevo León (Guzmán *et al*. 2001)

Cordyceps polyarthra

Möller

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera (pupae)

Vegetation

Tropical forest with some *Quercus* and deciduous tropical forest

State (references)

Jalisco (Rubio-Bustos *et al*. 1999)

Cordyceps pruinosa

Petch

Host: Class, Order, family, species (larvae, pupae or adult).

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Vegetation

Tropical rain forest

State (references)

Quintana Roo (Guzmán *et al*. 2001)

Cordyceps takaomontana

Yakush. & Kumaz.

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Lepidoptera (larvae and pupae)

Vegetation

Quercus-Pinus forest, secundary bushy vegetation of *Quercus* forest, ecotone between shrubby secondary vegetation of *Juniperus* forest and agricultural zone

State (references)

Estado de México (Pérez-Villamares *et al*. 2017)

Cordyceps tenuipes

(Peck) Kepler, B. Shrestha & Spatafora

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, unidentified (pupae)

Vegetation

Mesophyll forest

State (references)

Veracruz (López and García 2002b)

Isaria cicadae

Miq. 1838

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Hemiptera, Cicadidae (pupae)

Vegetation

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State (references)

Jalisco (Petch 1934, 1941-1942)

Table 3. Ophiocordycipitaceae species recorded in the literature from Mexico

Hirsutella citriformis

Speare 1920

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Hymenoptera, Liviidae, **Diaphorina citri* (adults and nymphs)

Vegetation

Citrus agricultural areas

State (references)

Campeche, Chiapas, Colima, Quintana Roo, Tabasco, Veracruz, and Yucatán (Pérez-González *et al*. 2015)

* Considered vectors of bacteria, parasites or viruses.

Hirsutella thompsonii

F.E. Fisher 1950

Host: Class, Order, family, species (larvae, pupae or adult).

Arachnida, Trombidiformes, Tetranychidae, *Tetranychus urticae*; Tenuipalpidae, *Aceria guerreronis* and *Brevipalpidos phoenicics*; Eriophyidae, *Phyllocoptruta oleivora*

Vegetation

Low rainforest, scrub, and mangrove

State (references)

Without locality (Mier *et al*. 1989, 1992; Sampedro and Rosas 1989; Guzmán *et al*. 2001), Colima (Rosas-Acevedo and Sampedro-Rosas 2006)

Ophiocordyceps dipterigena
(Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Diptera, Calliphoridae, *Eucalliphora* and *Lucilia sericata* (adults)

Vegetation
Mesophytic forest and coffee plantations

State (references)
Veracruz (Guzmán *et al*. 2001, as *Cordyceps dipterigena* Berk. & Broome; López and García 2009, as *C. dipterigena*; Medel 2013)

Ophiocordyceps entomorrhiza
(Dicks.) G.H Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Lepidoptera, Noctuidae (larvae); Coleoptera (larvae)

Vegetation
Secondary bushy vegetation of *Quercus* forest, coffee plantations, mesophytic forest, *Cupressus* forest

State (references)
Veracruz [Pérez-Silva 1978; Chacón and Guzmán 1983, 1995; Chacón *et al.* 1995; Rubio-Bustos *et al.* 1999; López and García, 2002a, all the previous as *Cordyceps entomorrhiza* (Dicks.) Fr.; Medel 2013], Estado de México (Pérez-Villamares *et al*. 2017).
Note: Revision of the collections of *C. entomorrhiza* reported by Chacón and Guzmán 1983, 1995, Chacón *et al*. 1995 and Rubio-Bustos *et al.* 1999, belong to *Ophiocordyceps gracilis* (Guzmán *et al*. 2001)

Ophiocordyceps gracilis
Grev.) G.H. Sung, J.M. Sung, Hywel-Jones and Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Lepidoptera, Noctuidae (larvae)

Vegetation
Deciduous tropical forest, mesophytic forest, ecotone between shrubby secondary vegetation of *Juniperus* forest and agricultural zone

State (references)
Jalisco [Rodríguez *et al*. 1993; Medel *et al*. 1999, all the previous as *Cordyceps gracilis* (Grev.) Durieu & Mont; Medel 2013], Veracruz (Chacón and Guzmán 1995; Chacón *et al*. 1995; Guzmán *et al*. 2001), Estado de México (Pérez-Villamares *et al*. 2017)

Ophiocordyceps humbertii
(C.P. Robin) Petch 1935

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Hymenoptera, Vespidae, *Polistes* (adults)

Vegetation
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State (references)
Oaxaca [Ulloa and Benavides 1991, as *Hirsutella saussurei* (Cooke ex Sacc.) Speare]

Ophiocordyceps melolonthae
(Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleoptera, Melolonthidae, *Enema endymion, Strategus aloeus* (larvae), and *Phyllophaga* spp. (adults)

Vegetation
Quercus-Pinus forest, subtropical humid forest, rainforest, subdeciduous tropical forest, agricultural zone with coffee plantations

State (references)

Chiapas (Pérez-Silva 1977; Robles-Porras *et al.* 2006, Jalisco (Rubio-Bustos *et al.* 1999, without locality (Herrera and Ulloa 1998), Oaxaca [Guzmán *et al.* 2001, all the previous as *Cordyceps melolonthae* var. *rickii* (Lloyd) Mains], Veracruz (Guzmán *et al.* 2001), Morelos [Castro *et al.* 2012, as *C. melolonthae* (Tul. & C. Tul.) Sacc.]

Ophiocordyceps octospora

(M. Blackw. & Gilb.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Blattoidea, Termitidae, *Tenuirostritermes tenuirostris* (adults)

Vegetation

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State (references)

Jalisco (Blackwell and Gilbertson 1984, as *Cordycepioideus octosporus* M. Blackw. & Gilb)

Ophiocordyceps sobolifera

(Hill ex Watson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Hemiptera, Cicadidae (nymphs)

Vegetation

Xerophilous forest with oak, subtropical scrub

State (references)

Without locality (Urbina 1881, Petch 1934, Mains 1951, 1955; Pérez-Silva 1979), Guanajuato (Duges 1924; Guzmán *et al.* 2001), Jalisco (Mains 1958; Guzmán and García-Saucedo, 1973; Guzmán-Dávalos 1992, based on specimens of *C. militaris* because the host was confused with a nymph of Cicadidae), Coahuila (Rubio-Bustos *et al.* 1999), Sonora [Méndez-Mayboca *et al.* 2008, all the previous as *Cordyceps sobolifera* (Hill ex Watson) Berk. & Broome].

Ophiocordyceps sphecocephala

(Klotzsch ex Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Hymenoptera, Vespidae, *Polistes* (adults)

Vegetation

Tropical rainforest, oak forest in transition to tropical deciduous forest

State (references)

Jalisco (Pérez-Silva 1977; Rodríguez *et al.* 1993; Rubio-Bustos *et al.* 1999; Guzmán *et al.* 2001), Morelos [Castro *et al.* 2012, all the previous as *Cordyceps sphecocephala* (Klotzsch ex Berk.) Berk. & M.A. Curtis]

Ophiocordyceps stylophora

(Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 2007

Host: Class, Order, family, species (larvae, pupae or adult).

Insecta, Coleoptera (larvae), also in Hymenoptera, Vespidae, *Polistes instabilis* (adults) by mistake

Vegetation

Deciduous forest, *Quercus-Pinus* forest

State (references)

Jalisco (Pérez-Silva 1978, as *Cordyceps stylophora* and *Hirsutella stylophora*; not this species according to Rubio-Bustos *et al.* 1999; Estado de México (Pérez-Villamares *et al.* 2017)

Paraisaria gracilioides
(Kobayasi) C.R. Li, M.Z. Fan & Z.Z. Li 2004

Host: Class, Order, family, species (larvae, pupae or adult).
Insecta, Coleptera (larvae)

Vegetation
Ecotone between shrubby secondary vegetation of *Juniperus* forest, agricultural zone, and deciduous forest

State (references)
Estado de México [Pérez-Villamares *et al.* 2017, as *Ophiocordyceps gracilioides* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora], Morelos (Castro *et al.* 2012)

Tolypocladium capitatum
(Holmsk.) C.A. Quandt, Kepler & Spatafora 2014

Host: Class, Order, family, species (larvae, pupae or adult).
Hypogeal fungi, Ascomycota, Eurotiales, *Elaphomyces granulatus* and *E. muricatus*

Vegetation
Pinus-Quercus forest and *Quercus forest*

State (references)
Estado de México (Heim 1957; Guzmán 1958, 1977, 2008; Heim and Wason 1958; Pérez-Silva 1977), San Luis Potosí (Guzmán 1958; Pérez-Silva 1977), Hidalgo (García-Romero *et al.* 1970, as *C. canadensis* Ellis & Everth; Pérez-Silva 1977), Jalisco (Pérez-Silva 1977; Gándara *et al.* 2014), Morelos (Pérez-Silva 1977), Oaxaca (Pérez-Silva 1977), Puebla (Martínez *et al.* 1983), Durango (Quintos *et al.* 1984), Veracruz (Guzmán and Villareal 1984), Michoacán (Díaz-Barriga *et al.* 1988), Sonora (Pérez-Silva *et al.* 1996). In all cases as *Cordyceps capitata* (Holmsk.) Fr., except when indicated.

Tolypocladium ophioglossoides
(J.F. Gmel.) C.A Quandt, Kepler & Spatafora 2014

Host: Class, Order, family, species (larvae, pupae or adult).
Hypogeal fungi, Ascomycota, Eurotiales, *Elaphomyces granulatus* and *E. muticatus*

Vegetation
Pinus-Quercus forest and *Quercus* forest

State (references)
Estado de México (Heim and Wason 1958; Trappe and Guzmán 1971; Pérez-Silva 1977; Guzmán *et al.* 2001), Durango (Pérez-Silva 1977), Hidalgo (Pérez-Silva 1977), Michoacán (Díaz-Barriga *et al.* 1988), Oaxaca (Pérez-Silva 1977), Sonora (Pérez-Silva *et al.* 1996), San Luis Potosí (Guzmán 1958; Guzmán *et al.* 2001), Tamaulipas (García-Jiménez and Valenzuela 2005)
All recorded as *Cordyceps ophioglossoides* (J.F. Gmel.) P. 1818

Discussion

Diversity of *Cordyceps* in Mexico

Currently, Mexico presents 3.5 % of *Cordyceps s.l.* entomopathogen, considering an overall world diversity of 1 000 species (Wei *et al.* 2020). However, we assume that the existing records are underestimates, since few studies have focused on these fungi, the studies are mainly regional and involve classic taxonomy, the intervals between investigations are usually long, and there are numerous geographic areas where no studies have been conducted.

Regarding distribution maps, we found that the vegetal stratum has changed from 1980 to 2018. We observed that some temperate and tropical forests have changed to human settlements, suggesting possible biodiversity loss over time. For example, *Ophiocordyceps octospora* was recorded in Jalisco by Blackwell and Gilbertson (1984), from an agricultural zone that is now occupied by an human settlement. Of the family Cordycipitaceae, at least one record from the forest of *Beauveria scarabaeidicola*, *Cordyceps militaris*, and *C. takaomontana*, now the localities correspond to human settlements. On the other hand, the locations of some records of *Hirsutella citriformis, Ophiocordyceps gracilis, O. melolonthae, O. sphecocephala,* and *Paraisaria gracilioides* in agricultural areas now correspond to human settlements.

Fungal biodiversity loss in this group of fungi is a little studied global problem, with few evaluations conducted (Yang 2020). However, it has been recorded that the main factors responsible for this loss are agriculture and aquaculture, biological resource use, comercial-residential development, modifications of natural systems, and others (Lughadha *et al.* 2020). We recommended investment of time and funds in further research of aspects of the biology of *Cordyceps s.l.* in Mexico, particularly to explore the genetics, anatomy, and ecology of the group, which would allow the proposal of suitable conservation strategies.

Species recorded in Mexico

Clavicipitaceae

Metarhizium anisopliae is the most dominant species of Clavicipitaceae in Mexico (Pérez-González *et al.* 2014). We therefore recommend further studies to explore its utility as substitute for chemical insecticides. This species has the highest number of records, being isolated from soils and a wide range of insects, from tropical and temperate regions. It is considered to be generalist (Bischoff *et al.* 2009) and mesophilic, since it grows at temperatures of 10-40 °C (Roberts and Campbell 1977), and it has been used in the management of crop pests and malaria vectors (Scholte *et al.* 2005).

Cordycipitaceae

Cordyceps militaris is the most dominant species of Cordycipitaceae in Mexico. This species can be considered cosmopolitan, since it has been reported widely distributed in Asia, Europe, and North America (Mains 1958). Its distribution is not determined by vegetation or climate, but rather by the distribution of its insect hosts (Shrestha *et al.* 2016). In Asia, it is consumed for its attributed medicinal properties, since it produces secondary metabolites, such as cordycepin, with anticancer, antibiotic, and antifungal activities (Ng and Wang 2005, Shrestha *et al.* 2016). Despite its importance as food and medicine, studies addressing these aspects have yet to be conducted in Mexico.

Ophiocordycipitaceae

Worldwide, Ophiocordycipitaceae comprises about 160 species that infect 11 orders of insects (Evans *et al.* 2011, Araújo and Hughes 2016). *Ophiocordyceps* is considered the most diverse genus of the Hypocreales (Sung *et al.* 2007a). Below, we review some of the important species of this genus present in Mexico.

Ophiocordyceps melolonthae has been found in different vegetation types including evergreen forests, pine-oak forest and subtropical humid forests, as well as agroecosystems such as coffee plantations. It is always found parasitizing larvae and adults of Coleoptera of the family Melolonthidae (Pérez-Silva 1977, Rubio-Bustos *et al.* 1999), and its distribution is therefore considered to be related to that of its host.

Ophiocordyceps dipterigena has been recorded only in the humid subtropical forest of the state of Veracruz, where it parasitizes species of Diptera (Guzmán *et al.* 2001, Medel 2013). This species has biotechnological importance since it produces an exobiopolymer that induces the production of the interleukin IL-8 for fibroblasts (Kocharin *et al.* 2010). This is useful as a healing material, while its high viscosity and moisturizing properties allows its use as a substitute for

hyaluronic acid in the pharmaceutical industry.

Ophiocordyceps entomorrhiza is a species similar to *Paraisaria gracilis*; indeed, it is difficult to taxonomically distinguish between the two species (Guzmán *et al.* 2001). *Paraisaria gracilis* and *O. entomorrhiza* have been reported on Lepidoptera in various types of vegetation (Chacón and Guzmán 1983, 1995; Chacón *et al.* 1995, Pérez-Silva 1978, Rubio-Bustos *et al.* 1999, López and García 2002a, Medel 2013); however, Pérez-Villamares *et al.* (2017) stated that *O. entomorrhiza* has only been found parasitizing Coleoptera larvae, and *P. gracilis* has only been found parasitizing Lepidoptera, so it is probably, each species is restricted to an insect order, respectively. The morphological difference between both species is mainly the coloration of the fertile part and stipe of the stromata, in *O. entomorrhiza* the fertile part is wine-colored, violet gray or grayish brown and the stipe is brown, in contrast *P. gracilis* has the fertile part red, orange or ocher and the stipe is yellowish (Pérez-Villamares *et al.* 2017), both species have been recorded in Mexico (Table 3). *Paraisaria gracilioides* is a rare species that specializes in parasitizing Coleoptera larvae (Kobayasi 1941, Castro *et al*. 2012, Pérez-Villamares *et al*. 2017). *Ophiocordyceps sphecocephala* has been recorded in Mexico as a parasite of the wasp of the genus *Polistes,* but in China, Japan, Korea, and Nepal, it has been found parasitizing *Aphrophora* wasps (Shrestha 2011).

In Mexico, *O. stylophora* has been described as parasitizing larvae of Coleoptera (Pérez-Villamares *et al.* 2017) and also on Hymenoptera (Pérez-Silva 1978); however, their identification on Hymenoptera was considered erroneous by Rubio-Bustos *et al.* (1999), who mentioned that *O. stylophora* grows on coleopterans, additionally they examined the specimen of Pérez-Silva (1978) and observed a different morphology with respect to *O. stylophora*, therefore, they suggested it could be a new species. *Ophiocordyceps sobolifera* has been reported on cicada nymphs and it is probably the species that was first recorded as a "rare plant-animal" (Guzmán *et al.* 2001).

Unlike the genera described above, *Tolypocladium* does not parasitize insects but rather hypogeous fungi of the genus *Elaphomyces* and, some nymphs of Cicadidae. It was hypothesized that, given the same belowground habitat of Cicadas and *Elaphomyces*, *Tolypocladium* has performed a host switch (Nikoh and Fukatsu 2000). *Tolypocladium ophioglossoides* has been reported with a wide distribution in the northern hemisphere: Japan, Russia, and USA, as well as Mexico (Mains 1957, Pérez-Silva 1977). This species is of pharmaceutical importance because it produces ophiocordin with antibiotic and antifungal properties (Kneifel *et al.* 1997), and ophiosetin with antibiotic properties (Putri *et al.* 2010).

Asexual states of Cordyceps s.l.

Beauveria bassiana and *Metarhizium anisopliae* are pathogens of *Brachystola magna* and *Phyllophaga* spp., two pests that affect bean *(Phaseolus vulgaris)* and maize (*Zea mays*) crops (Lezama *et al.* 2005, Barajas *et al.* 2011, Hernández-Velázquez *et al.* 2011). These fungi are also found on insects in coffee (*Coffea* spp.) crops (De la Rosa *et al.* 2000) and have been used to treat sugar cane crop pests (SAGARPA 1999). The pest control properties of these fungi have also been tested in the dengue vector *Aedes aegypti* (García-Munguía *et al*. 2015) and in *Meccus pallidipennis* and *Triatoma dimidiata*, two vectors of Chagas disease (Vázquez-Martínez *et al*. 2014, Flores-Villegas *et al.* 2016). *Cordyceps fumosorosea* (as *Paecilomyces fumosorosea* or *Hirsutella* sp.), has also been used to control *Diaphorina citri*, an insect that transmits viruses to citrus fruits (Lezama-Gutiérrez *et al*. 2012, Pérez-González *et al*. 2015).

Hosts

The main hosts of *Cordyceps s.l.* have been reported as immature stages of Coleoptera and Lepidoptera (Shrestha *et al.* 2016), as well as spiders (Shrestha *et al.* 2019). In this review, the main hosts were in order of importance, Lepidoptera, Coleoptera, and Orthoptera. These host associations are informative taxonomic characters in *Cordyceps s.l.*, since the hosts are probably drivers for speciation (Sanjuan *et al.* 2015). Lopez-Rodríguez *et al.* (2022) also suggested that host identification to species or genera level is substancial, as well as analysis in conjunction with morphology and phylogenetic analysis of multilocus DNA sequences. We therefore suggest that future studies should place an emphasis on the taxonomic identification of hosts at species level.

Conclusions

In Mexico, the history of the study of the *Cordyceps s.l.* dates back to 1864, but the research has advanced sporadically, leaving lapses of up to 77 years with no research at all. Currently, *Cordyceps s.l.* diversity is represented by 35 species, where the family Ophiocordycipitaceae is the most diverse, followed by Cordycipitaceae, and finally Clavicipitaceae. These species are associated with the distribution of their hosts, as observed mainly in *Ophiocordyceps dipterigena*, *O. entomorrhiza*, and *O. melolonthae*. Most species are associated with a genus or family of the class Insecta and in the case of fungal parasites have only been reported in the genus *Elaphomyces*. Only *Beauveria bassiana, C. militaris,* and *M. anisopliae* have been recorded in more than one order of insects. *Beauveria bassiana* and *M. anisopliae* are species with agricultural importance because they are utilized in the control of pest insects and disease vectors that affect animals, humans, and plants. Despite their global agricultural importance, there has been no specific research of specialized entomopathogenic species in Mexico, and the studies that have been conducted to date did not address any effects on other insects, including pollinators or other ecologically important insects. *Tolypocladium capitatum* and *T. ophioglossoides* are the only species recorded with ritual use by indigenous people in Mexico. Some of the listed species have medicinal, nutritional or pharmacological importance, such as *C. dipterigena, C. militaris, C. pruinosa*, and *T. ophioglossoides.* Given the great taxonomical diversity and nutritional and pharmaceutical importance of these fungi, we consider it crucial to initiate research on integral taxonomy, its in vitro culture and metabolites in order to elucidate the taxonomic identity of the species and evaluate its possible use.

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