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#### **Research Article**

Julio Olguin, Patricia Velez\*, Vivianne Solís-Weiss, Alejandra Barrios, Allison K. Walker, Guadalupe Ponce-Vélez, María C. González, Mario Figueroa and Alfonso Botello

# An overview of fungal taxonomic, functional, and genetic diversity in coastal and oceanic biomes in megadiverse Mexico

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**Abstract:** A comprehensive literature review of mycodiversity in sandy beaches and oceanic environments in Mexico is presented through the analysis of published works from 1949 to early 2023. In addition, four unexplored sandy beaches in the Pacific Ocean and Gulf of California were sampled in order to fill knowledge gaps in terms of sampling biases. Marine fungi of Mexico were reported from water column, sediment, and debris samples collected in sandy beaches, open ocean, deep-sea plains, hydrothermal vents, and oxygen minimum zones in the Gulf of Mexico, the Pacific Ocean, the Gulf of California, and the Caribbean Sea. The taxonomic, functional, and genetic diversity, as well

as distribution patterns and potential use of marine fungal genetic resources are discussed. A list of 126 species in 83 genera, 40 families, 25 orders, 12 classes, three phyla and one subphylum (excluding non-cultured taxa) of marine fungi is documented from Mexico. Lastly, we identified areas that would benefit from additional research, including the exploration of further deep-sea biomes in the Pacific Ocean, and coastal areas covering ecoregions in the states of Sonora, Sinaloa, Nayarit, Michoacán, and Oaxaca.

**Keywords:** Ascomycota; fungal biodiversity; Halosphaeriaceae; marine biodiversity; marine mycobiota

## 1 Introduction

Marine fungi are delimited as an ecological, rather than a taxonomic group of chemoorganoheterotrophs, comprising obligate marine (those that grow and sporulate exclusively in a marine or estuarine habitat) and facultative taxa (those from freshwater or terrestrial milieus that are able to grow and possibly also to sporulate in the marine environment) (Kohlmeyer and Kohlmeyer 1979). This assemblage of species includes any fungus that is repeatedly recovered from a marine habitat because: (1) it can grow and/or sporulate (on substrata) in marine environments; (2) it forms symbiotic relationships with marine organisms; or (3) it is adapted and has evolved (or be metabolically active) in the marine environment (Pang et al. 2016). Marine fungi act at many trophic levels (Gladfelter et al. 2019; Hyde et al. 2000; Salcedo et al. 2023), occurring as saprobes, and parasites of algae (Raghukumar 1986), diatoms (Gutiérrez et al. 2016) and marine animals (Hyde et al. 1998; Pang et al. 2021). In addition, numerous symbiotic relationships between marine fungi and other marine biota have been reported including with algae (Kohlmeyer and Kohlmeyer 1979; Raghukumar et al. 2010), corals (Amend et al. 2012), Armeria maritima and other halophytic plants (Mason 1928), and marine lichens (Pérez-Ortega et al. 2016).

\*Corresponding author: Patricia Velez, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico, E-mail: pvelez@ib.unam.mx. https://orcid.org/0000-0002-4449-8977

Julio Olguin, Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico; and Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

**Vivianne Solís-Weiss**, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico, Puerto Morelos, 77580, Mexico

Alejandra Barrios, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico; and Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

**Allison K. Walker**, Department of Biology, Acadia University, 33 Westwood Avenue, Wolfville, Nova Scotia, B4P 2R6, Canada. https://orcid.org/0000-0002-5061-361X

**Guadalupe Ponce-Vélez and Alfonso Botello**, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

María C. González, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

Mario Figueroa, Facultad de Química, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

With more than 10,000 estimated species of marine fungi worldwide, only 1857 species have been described, representing merely ~19 % (http://www.marinefungi.org) (Iones et al. 2019). Most of these species are known for their worldwide distribution, yet certain taxa may be restricted to biogeographic groups sensu Hughes (1974, 1986): (1) Arctic-Antarctic or cold waters, (2) temperate, (3) sub-tropical, (4) tropical, and (5) cosmopolitan (Jones et al. 2022). Although marine fungi in tropical and temperate regions have been extensively studied (Jones and Pang 2012), diversity in tropical-temperate transitional regions remains to be fully explored.

Located in one such tropical-temperate transition region, Mexico is ranked within the top 17 megadiverse countries that harbor much of the Earth's biodiversity (CONABIO 2019; Mittermeier et al. 1999). Due to their environmental heterogeneity, Mexican marine biomes harbor highly productive regions of great biological importance that represent an ideal model to study marine fungal diversity on the tropical-temperate transition. Nonetheless, marine mycology can still be considered as an incipient discipline in this country (Pang et al. 2023).

Since the publication of the first obligate arenicolous species from a German beach in 1922 (Corollospora maritima) and the erection of the genus Corollospora (Werdermann 1922), the inventory of marine mycobiota in sandy beaches has progressed worldwide (revised in Velez et al. 2022b). In this regard, pioneer investigations across the globe laid the foundations for the development of marine mycology in Mexico (e.g., Höhnk 1955; Koch 1974; Kohlmeyer 1966, 1967, 1968, 1976, 1981, 1984; Kohlmeyer and Kohlmeyer 1971, 1977; Kohlmeyer and Volkmann-Kohlmeyer 1987a,b,c, 1991). The first fungus reported from the Mexican coastline (Pontogeneia codiicola) was collected in 1949 on the green algae Codium simulans on a rocky shore of the Guadalupe Island, Baja California (Kohlmeyer and Kohlmeyer 1979). Successive reports by Meyers (1957) documented Antennospora quadricornuta (originally Antennospora caribbea) in the intertidal zone of the Caribbean Sea. In the early 1990s sandy beaches emerged as the most extensively explored marine ecosystem for fungi in Mexico (González 2009; González and Herrera 1993, 1995, 2010; González et al. 1998, 2000, 2001, 2010; Velez et al. 2013, 2015a,b, 2016a,b, 2021). This trend might be attributed to two major phenomena: (1) Mexican sandy beaches developed as top-ranked tourist destinations during the late 1960s (e.g., the colonial port city of Acapulco on the Pacific and the border city of Tijuana) and in the 1980s (e.g., Caribbean beaches, and several destinations in the Pacific including Los Cabos, Ixtapa, and Huatulco) (Faber and Gaubert 2019), and (2) these systems represent priority areas for research in biodiversity, since

they face numerous anthropogenic stressors that jeopardize their sustainability.

The first marine fungus to be documented from a Mexican ocean was by Kohlmeyer (1984) who reported Lulworthia kniepii from the red alga Paragoniolithon solubile (now Neogoniolithon fosliei) in the Gulf of California, perhaps representing the first record (considering distribution of the host). However, it was not until early 2000s that the formal exploration of oceanic biomes was developed through investigation of deep-sea plains (González-Martínez et al. 2017, 2019; Vargas-Gastélum et al. 2019; Velez et al. 2020), hydrothermal vents (Hernández 2019; Velez et al. 2022a), and oxygen minimum zones (Posadas 2023).

In 2001, González et al. (2001) published the first checklist of Mexican marine fungi, reporting 62 species. mostly collected from beaches between 1949 and 2001. Subsequently, 50 further records of fungal taxa from marine habitats were listed for this country (Portillo-López and González-Martínez 2021). However, relevant data remained overlooked including: (1) updated figures on taxonomic (species-level), genetic and functional diversity; (2) reports from hydrothermal vents, and oxygen minimum zones; and (3) documentation of genetic lineages of the common arenicolous marine species, C. maritima sensu lato. Thus, the objective of this work is to present a thorough review and analysis of scientific literature reporting fungal diversity in Mexican marine environments from 1949 to 2023. In addition, records for unexplored sandy beaches in the Pacific Ocean and Gulf of California are provided to fill knowledge gaps in terms of sampling biases. We revised information on taxonomic, functional, and genetic diversity, as well as distribution patterns and the potential application of marine fungal genetic resources for bioprospecting, as bioindicators and in hydrocarbon bioremediation.

We provide a list of 126 species of marine fungi, including three genetic lineages of C. maritima sensu lato, occurring in a wide range of coastal and oceanic ecosystems (e.g., sandy beaches, wetlands, seagrass and algal beds, deep-sea plains, oceanic oxygen minimum zones, and hydrothermal vents; Table 1). This number excludes non-cultured taxa, and these species can be referred to 83 genera, 40 families, 25 orders, 12 classes, three phyla and one subphylum. The taxa contained in this checklist correspond to reports from the Gulf of Mexico, Pacific Ocean, Gulf of California, and Caribbean Sea.

## 2 Materials and methods

The bibliographic search was conducted on main scientific databases including PubMed (591 records), Scopus (53 records), ScienceDirect (4760 records), and Scielo (three records). Reference works written prior

**Table 1:** List of marine fungi reported in Mexico from 1949 to 2023, presenting information on their distribution, ecology, and putative functional guilds.

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota	Sordariomycetes	Hypocreales	Incertae sedis	Acremonium sp. <sup>FA, SA a</sup>	Ver, GM Jal, Nay, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Hypocreales	Incertae sedis	Acremonium murorum. (Corda) W. Gams 1971 FA, SA a	Gue, PO	González et al. (2000)
Ascomycota	Sordariomycetes	Hypocreales	Incertae sedis	Acremonium rutilum. W. Gams 1971 <sup>FA, SA a</sup>	Ver, GM	González et al. (1998)
Ascomycota	Sordariomycetes	Hypocreales	Stachybotryaceae	Albifimbria verrucaria (Alb. et Schwein.) L. Lombard et Crous. 2016 <sup>FA, SA a</sup>	Jal, PO Ver, GM	González and Herrera (1993), González et al. (1998)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Alternaria sp. <sup>FA, SA, PA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Alternaria sp. <sup>FA, SA, PA a</sup>	Ver, Cam, GM Nay, PO	Romero-Hernández et al. (2021)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Alternaria sp. <sup>FA, SA, PA a</sup>	Bac, GC	This study
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	<i>Alternaria alternata</i> (Fr.) Keissl. 1912 <sup>FA, SA, PA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	<i>Alternaria citri</i> Ellis <i>et</i> N. Pierce 1902 <sup>FA, SA, PA a</sup>	Ver, GM	González et al. (1998)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Alternaria longipes (Ellis et Everh.) E.W. Ma- son. 1928 <sup>FA, SA, PA a</sup>	Qro, CS	González et al. (1998)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Antennospora quadricornuta (Cribb et J.W. Cribb) T.W. Johnson. 1958 MA, SA a	Oax, Jal, PO Bcs, GC	Kohlmeyer (1968, 1984), González and Herrera (1995)
Ascomycota	Eurotiomycetes	Onygenales	Gymnoascaceae	<i>Arachniotus dankaliensis</i> (Castell.) J.F.H. Beyma 1942 <sup>FA, SA a</sup>	Qro, CS Ver, GM Gue, PO	González et al. (2000)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Arenariomyces majusculus Kohlm. et VolkmKohlm. 1989 MA, SA a	Ver, GM	Velez et al. (2013)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Arenariomyces parvulus</i> Jørg. Koch 1986 <sup>MA, SA a</sup>	Qro, CS Ver, GM	González et al. (1998, 2001), Velez et al. (2013, 2015a)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Arenariomyces triseptatus Kohlm. 1984 <sup>MA, SA a</sup>	Qro, Yuc, CS Cam, GM	Kohlmeyer (1984), Kohlmeyer and Kohl- meyer (1971),
						Velez et al. (2013, 2015a)
Ascomycota	Eurotiomycetes	Onygenales	Arthrodermataceae	<i>Arthroderma curreyi</i> Berk. 1860 <sup>FA, SA a</sup>	Qro, CS	González et al. (2000)
Ascomycota	Dothideomycetes	Incertae sedis	Eremomycetaceae	Arthrographis kalrae (R.P. Tewari et Macph.) Sigler et J.W. Carmich. 1976 <sup>FA PA a</sup>	Bac, GC	Velez et al. (2021)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Ascosacculus heteroguttulatus (S.W. Wong, K.D. Hyde et E.B.G. Jones) J. Campb., J.L. Anderson et Shearer 2003 MA, SA a	Tab, GM	Velez et al. (2015b)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus sp. <sup>FA, SA a</sup>	Yuc, CS	Fajardo-Hernández et al. (2022)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus sp. <sup>FA, SA a</sup>	Gue, PO	Aparicio-Cuevas et al. (2019)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus sp. <sup>FA, SA a</sup>	Gue, PO	Aparicio-Cuevas et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus sp. <sup>FA, SA a</sup>	Bcs, GC	González-Martínez et al. (2017)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota Ascomycota	Eurotiomycetes Eurotiomycetes	Eurotiales Eurotiales	Aspergillaceae Aspergillaceae	Aspergillus sp. <sup>FA, SA a</sup> Aspergillus sp. <sup>FA, SA a c</sup>	Bcs, GC Ver, GM Chi, Nay, PO	This study Valderrama et al. (2016)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus amstelodami</i> (L. Mangin) Thom <i>et</i> Church 1926 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus auricomus</i> (Guég.) Saito. 1939 <sup>FA, SA a</sup>	Ver, GM	González et al. (2000)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus chevalieri</i> (L. Mangin) Thom <i>et</i> Church 1926 <sup>FA. SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus costiformis H.Z. Kong et Z.T. Qi 1995 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus cristatus</i> Raper <i>et</i> Fennell 1965 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus fumigatus</i> Fresen. 1863 <sup>FA, SA a</sup>	Ver, GM Gue, PO	González et al. (2000)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus flavo-furcatus Bat. et H. Maia. 1955 <sup>FA, SA a</sup>	Gue, PO	González et al. (2000)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus flavus link. 1809 <sup>FA, SA a</sup>	Jal, Col, PO Ver, GM Qro, CS Bac, GC	González and Herrera (1993), González et al. (1998)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus loretoensis S. González-Martínez et A. Portillo- López. 2019 <sup>MA, SA b</sup>	GC	González-Martínez et al. (2019)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus nidulans (Eidam) G. Winter 1884 <sup>FA, SA a</sup>	Ver, GM Col, PO Qro, CS	González and Herrera (1993), González et al. (1998)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus niger</i> Tiegh. 1867 <sup>FA, SA a</sup>	Ver, GM Qro, CS Jal, Col, Nay PO	González and Herrera (1993), González et al. (1998)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus pulverulentus (McAlpine) Thom 1926 FA, SA a	Ver, GM	González et al. (1998)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus recurvatus Raper et Fennell 1965. FA, SA a	Gue, PO	González et al. (2000)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus repens (Corda) Sacc. 1882 <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus ruber (Jos. König, Spieck. et W. Bremer) Thom et Church 1926 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus salinarum (Greiner, Peršoh, Weig et Rambold) Zalar et Greiner 2017 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus tamarii</i> Kita 1913 <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus terreus Thom 1918 <sup>FA, SA a</sup>	Bac, GC Ver, GM Qro, CS Col, Gue, Nay, PO	González et al. (1998, 2000), Velez et al. (2021)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Aspergillus tonophilus</i> Oht- suki. 1962 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Aspergillus violaceus Fennell et Raper. 1955 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Dothideomycetes	Dothideales	Saccotheciaceae	Aureobasidium pullulans (De Bary et Löwenthal) G. Arnaud. 1917 <sup>FA, PA a</sup>	Qro, CS Col, Nay, PO Bac, GC	González et al. (1998)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota	Dothideomycetes	Pleosporales	Camarosporiaceae	Camarosporium roumeguerei Sacc. 1880 <sup>FA, PA a</sup>	Son, PO	Kohlmeyer and Kohlmeyer (1979)
Ascomycota	Saccharomycetes	Saccharomycetales	Incertae sedis	Candida sp. FA, SA C	Tam, GM	Valderrama et al. (2016)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Ceriosporopsis capillacea Tab, GM Kohlm. 1981 <sup>MA, SA a</sup>		Velez et al. (2015b)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Ceriosporopsis halima</i> Linder 1944 <sup>MA, SA a</sup>	Tab, Ver, GM	González et al. (2001), Velez et al. (2013, 2015b)
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	Chaetomium sp. <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	<i>Chaetomium globosum</i> Kunze 1817 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Eurotiomycetes	Onygenales	Onygenaceae	<i>Chrysosporium tropicum</i> J.W. Carmich. 1962 <sup>FA, SA a</sup>	Qro, CS	González et al. (2000)
Ascomycota	Sordariomycetes	Diaporthales	Cryphonectriaceae	Chrysoporthe sp. <sup>FA, SA c</sup>	Chi, PO	Valderrama et al. (2016)
Chytridiomycota	Chytridiomycetes	Chytridiales	Chytriomycetaceae	Chytriomyces sp. <sup>FA, SA c</sup>	Tam, GM	Valderrama et al. (2016)
Mucoromycota	Mucoromycetes	Mucorales	Syncephalastraceae	<i>Circinella mucoroides</i> Saito 1907 <sup>FA, SA a</sup>	Tab, GM	González and Herrera (2010)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Cirrenalia pseudomacrocephala</i> Kohlm. 1968 <sup>MA, SA a</sup>	Ver, GM	Kohlmeyer (1968)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium sp. <sup>FA, SA b</sup>	GM PO	Velez et al. (2020)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium sp. <sup>FA, SA b</sup>	CS	Fajardo-Hernández et al. (2022)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium cladosporioides (Fresen.) G.A. de Vries 1952 <sup>FA, SA a</sup>	Qro, CS Ver, GM Jal, Col, Nay, PO	González and Herrera (1993), González et al. (1998)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium cucumerinum Ellis et Arthur 1889 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium halotolerans Zalar, de Hoog et Gunde-Cim. 2007 <sup>FA, SA b</sup>	GM	Romero-Hernández et al. (2021)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium herbarum (Pers.) link. 1815 <sup>FA, SA a b</sup>	Qro, CS Col, PO Ver, GM GC	González et al. (1998), González-Martínez et al. (2017)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium ramotenellum K. Schub., Zalar, Crous et U. Braun 2007 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium sphaer- ospermum Penz. 1882 <sup>FA, SA a</sup>	Jal, Col, PO Ver, GM Qro, CS	González and Herrera (1993), González et al. (1998)
Ascomycota	Saccharomycetes	Saccharomycetales	Metschnikowiaceae	<i>Clavispora lusitaniae</i> Rodr. Mir. 1979 <sup>FA, SA a</sup>	Qro, CS	González et al. (1998)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Cochliobolus geniculatus R.R. Nelson 1964 <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora angusta Nakagiri et Tokura 1987 <sup>MA, SA a</sup>	Ver, GM	González et al. (1998)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora gracilis Nakagiri et Tokura 1987 <sup>MA, SA a</sup>	Qro, CS Tab, Ver, GM	González et al. (1998), Velez et al. (2015a,b, 2020, 2021)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora intermedia I. Schmidt 1970 <sup>MA, SA a</sup>	Bac, GC Jal, PO	González and Herrera (1993)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora maritima sensu lato Werderm. 1922 <sup>MA, SA a</sup>	Bac, Bcs, GC Col, Jal, Oax, PO Ver, Tab, Yuc, GM Qro, CS	Kohlmeyer (1968, 1984), Kohlmeyer and Kohlmeyer (1971), González and Herrera (1993), González et al. (1998, 2001, 2010), Velez et al. (2015a,b, 2021)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora maritima lineage 1 <sup>MA, SA a</sup>	Son, PO Yuc, CS Tam, Cam, GM Bac, GC	Velez et al. (2016)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora maritima lineage 4 <sup>MA, SA a</sup>	Qro, CS	Velez et al. (2016)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Corollospora maritima</i> lineage 5 <sup>MA, SA a</sup>	Ver, Tab, Tam, GM Jal, Gue, PO	Velez et al. (2016)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora pseudopulchella Nakagiri et Tokura 1987 <sup>MA, SA a</sup>	Tab, GM Qro, CS	González et al. (2001), Velez et al. (2015b)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora pulchella Kohlm., I. Schmidt et N.B. Nair 1967 <sup>MA, SA a</sup>	Tab, Cam, GM Qro, Yuc, CS Col, Oax, PO	Kohlmeyer (1968, 1969, 1984), Hyde (1992), González et al. (1998), Velez et al. (2013, 2015b)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora ramulosa (Meyers et Kohlm.) E.B.G. Jones et Abdel-Wahab 2016 <sup>MA, SA a</sup>	Ver, Tab, GM Yuc, Qro, CS	Kohlmeyer (1984), Kohlmeyer and Kohl- meyer (1971), González et al. (1998), Velez et al. (2013)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Corollospora trifurcata (Höhnk) Kohlm. 1962 <sup>MA, SA a</sup>	Tab, Cam, GM Oax, PO Qro, Yuc, CS	Kohlmeyer (1968, 1984), Kohlmeyer and Kohlmeyer (1971), Velez et al. (2013, 2015b)	
Ascomycota Ascomycota Mucoromycota	Sordariomycetes Sordariomycetes Mucoromycetes	Microascales Microascales Mucorales	Halosphaeriaceae Halosphaeriaceae Cunninghamellaceae	Corollospora sp. MA, SA a Corollospora sp. MA, SA a Cunninghamella echinulata (Thaxt.) Thaxt. ex Blakeslee 1905 FA, SA a	Tab, GM Bac, GC Jal, PO	Velez et al. (2015b) This study González and Herrera (1993)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia intermedia Boedijn 1933 <sup>FA SA a</sup>	Ver, GM	González et al. (1998)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia eragrostidis (Henn.) J.A. Mey. 1959 FA, SA a	Jal, PO	González and Herrera (1993)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia lunata (Wakker) Boedijn 1933 <sup>FA, SA a</sup>	Jal, Col, PO	González and Herrera (1993), González et al. (1998)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia pallescens Boedijn 1933 FA, SA a	Ver, GM	González et al. (1998)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia senegalensis (Speg.) Subram. 1956 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Curvularia tuberculata B.L. Jain 1962 FA, SA a	Ver, GM	González et al. (1998)	
Ascomycota	Saccharomycetes	Saccharomycetales	Dipodascaceae	Dipodascus geotrichum (E.E. Butler et L.J. Petersen) Arx 1977 <sup>FA, SA a</sup>	Jal, PO Qro, CS	González and Herrera (1993), González et al. (2000)	

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota Ascomycota	Dothideomycetes Dothideomycetes	Pleosporales Pleosporales	Didymellaceae Didymellaceae	Didymellaceae sp. <sup>FA, SA a</sup> Epicoccum nigrum link 1815 <sup>FA, SA b</sup>	Bac, GC GC	This study González-Martínez et al. (2017)
Ascomycota Ascomycota	Eurotiomycetes Dothideomycetes	Chaetothyriales Pleosporales	Herpotrichiellaceae Pleosporaceae	Exophiala sp. <sup>FA, SA a</sup> Exserohilum rostratum	Bac, GC Ver, GM	Velez et al. (2021) González and Herrera
				(Drechsler) K.J. Leonard <i>et</i> Suggs 1974 <sup>FA, SA a</sup>	Jal, PO	(1993), González et al. (1998)
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	<i>Fusarium fujikuroi</i> Niren- berg 1976 <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Fusarium incarnatum (Desm.) Sacc. 1886 <sup>FA, SA a</sup>	Jal, Col PO, Ver, GM Qro, CS	González and Herrera (1993), González et al. (1998, 2000)
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Fusarium neocosmosporiellum O'Donnell et Geiser 2013 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Fusarium oxysporum Schltdl. 1824 <sup>FA, SA a</sup>	Ver, GM Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	Fusarium solani (Mart.) Sacc. 1881 <sup>FA, SA a</sup>	Jal, Col. PO Ver, GM Qro, CS Bac, GC	González and Herrera (1993), González et al. (1998, 2000), Velez et al. (2021)
Ascomycota	Incertae sedis	Incertae sedis	Incertae sedis	Gilmaniella humicola G.L. Barron 1964. <sup>FA, SA a</sup>	Ver, GM	González et al. (1998)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Graphium penicillioides</i> Corda 1837 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Eurotiomycetes	Onygenales	Gymnoascaceae	Gymnascella hyalinospora (Kuehn, G.F. Orr et G.R. Ghosh) Currah 1985 <sup>FA, SA a</sup>	Gue, PO	Aparicio-Cuevas et al. (2019)
Ascomycota	Eurotiomycetes	Onygenales	Gymnoascaceae	Gymnoascus sp. <sup>FA, SA a</sup>	Ver, GM Gue, PO	González et al. (2000)
Ascomycota	Eurotiomycetes	Onygenales	Gymnoascaceae	Gymnoascus hyalinosporus Kuehn, G.F. Orr et G.R. Ghosh) M. Solé, Cano et Guarro 2002 <sup>FA, SA a</sup>	Gue, PO	Aparicio-Cuevas et al. (2019)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Haiyanga salina</i> (Meyers) K.L. Pang <i>et</i> E.B.G. Jones 2008 <sup>MA, SA a</sup>	Oax, Chi, PO Qro, CS Cam, Ver, GM	Kohlmeyer (1968, 1969, 1984), González et al. (1998), Velez et al (2013)
Ascomycota	Leotiomycetes	Helotiales	Tricladiaceae	Halenospora varia (Anastasiou) E.B.G. Jones 2009 FA, SA a	Tab, Cam, GM	González and Herrera (1995), Velez et al. (2015b)
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	Humicola alopallonella Meyers et R.T. Moore 1960 MA, SA a	Qro, CS Jal, PO	Kohlmeyer (1984), González and Herrera (1995)
Ascomycota	Sordariomycetes	Lulworthiales	Halosphaeriaceae	<i>Hydea pygmea</i> (Kohlm.) K.L. Pang <i>et</i> E.B.G. Jones 2010 <sup>MA, SA a</sup>	Chi, PO	Kohlmeyer (1968)
Ascomycota	Dothideomycetes	Botryosphaeriales	Botryosphaeriaceae	<i>Lasiodiplodia theobromae</i> (Pat.) Griffon <i>et</i> Maubl. 1909 <sup>FA, SA a</sup>	Jal, Col, PO	González and Herrera (1993), González et al. (1998)
Ascomycota Ascomycota	Sordariomycetes Dothideomycetes	Sordariales Pleosporales	Lasiosphaeriaceae Phaeosphaeriaceae	Lasiosphaeria sp. <sup>FA, SA a</sup> Leptosphaerella sp. <sup>FA, SA a</sup>	Bac, GC Mer, Tab, GM Yuc, CS	Velez et al. (2021) Velez et al. (2013)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Lignincola laevis</i> Höhnk. 1955 <sup>MA, SA a</sup>	Col, PO Ver, Cam, GM	Velez et al. (2013)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Lignincola tropica</i> Kohlm. 1984 <sup>MA, SA a</sup>	Qro, CS	Kohlmeyer (1984)
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	<i>Lindra crassa</i> Kohlm. <i>et</i> Volkm Kohlm. 1991 <sup>MA, SA a</sup>	Mer, Ver, GM Qro, Yuc, CS	Kohlmeyer (1984), Velez et al. (2013)
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	<i>Lindra thalassiae</i> Orpurt, Meyers, Boral <i>et</i> Simms 1964 <sup>MA, SA a</sup>	Cam, Ver, GM Qro, Yuc, CS Col, PO Bcs, GC	Kohlmeyer (1984), Kohlmeyer and Kohl- meyer (1971), Gonzá- lez et al. (1998), Velez et al. (2013, 2015a)
Ascomycota	Dothideomycetes	Lineolatales	Lineolataceae	<i>Lineolata rhizophorae</i> Kohlm. et E. Kohlm. 1990 MA, SA a	Bcs, GC Ver, GM	Kohlmeyer (1984), Velez et al. (2013)
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	Lulworthia sp. <sup>MA, SA a</sup>	Jal, PO	González and Herrera (1995)
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	<i>Lulworthia</i> sp. <sup>MA, SA a</sup>	Ver, GM Oax PO Qro, CS	Kohlmeyer (1968)
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	<i>Lulworthia</i> sp. <sup>MA, SA a</sup>	Tab, Ver, Cam, Yuc, Tam, GM	Velez et al. (2013)
Ascomycota Ascomycota	Sordariomycetes Sordariomycetes	Lulworthiales Lulworthiales	Lulworthiaceae Halosphaeriaceae	Lulworthia sp. MA, SA a Matsusporium tropicale (Kohlm.) E.B.G. Jones et K.L. Pang. 2010 MA, SA a	Tab, GM Col, PO	Velez et al. (2015b) González et al. (1998)
Ascomycota	Dothideomycetes	Mycosphaerellales	Niessliaceae	<i>Melanopsamma balani</i> (G. Winter) Meyers. 1957 <sup>MA, SA a</sup>	Son, PO	Kohlmeyer and Kohl- meyer (1979)
Ascomycota	Saccharomycetes	Saccharomycetales	Debaryomycetaceae	<i>Meyerozyma guilliermondii</i> (Wick.) Kurtzman <i>et</i> M. Suzuki. 2010 <sup>FA, SA a</sup>	Bac, GC	Velez et al. (2021)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus</i> sp. <sup>MA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus brevicaulis</i> S.P. Abbott 1998 <sup>FA, SA a</sup>	Jal, Col, PO Qro, CS	González and Herrera (1993), González et al. (1998, 2000)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus cinereus</i> Curzi 1931 <sup>MA, SA a</sup>	Gue, PO	González et al. (2000)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus manginii</i> (Loubière) Curzi 1931 <sup>MA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus melanosporus</i> (Udagawa) Woudenb. <i>et</i> Samson 2017 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Microascus trigonosporus</i> C.W. Emmons <i>et</i> B.O. Dodge 1931 <sup>FA, PA, SA a</sup>	Jal, PO Ver, GM	González and Herrera (1993), González et al. (1998)
Mucoromycota	Mucoromycetes	Mucorales	Mucoraceae	<i>Mucor hiemalis</i> Wehmer. 1903 <sup>MA, SA a</sup>	Jal, PO	González and Herrera (1993)
Ascomycota Ascomycota	Dothideomycetes Dothideomycetes	Mycosphaerellales Mycosphaerellales	Mycosphaerellaceae Mycosphaerellaceae	<i>Mycosphaerella</i> sp. <sup>FA, SA a</sup> <i>Mycosphaerella salicorniae</i> (Auersw.) Lindau 1903 <sup>FA, SA a</sup>	Ver, GM Yuc, CS Bcs, GC	Velez et al. (2013) Kohlmeyer (1980, 1984)
Basidiomycota	Agaricomycetes	Agaricales	Niaceae	Nia sp. MA, SA a	Bac, GC	Velez et al. (2021)
Basidiomycota	Agaricomycetes	Agaricales	Niaceae	<i>Nia vibrissa</i> R.T. Moore <i>et</i> Meyers 1959 <sup>MA, SA a</sup>	Qro, CS	Kohlmeyer (1984)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota	Sordariomycetes	Incertae sedis	Incertae sedis	<i>Nigrospora oryzae</i> (Berk. <i>et</i> Broome) Petch 1924 <sup>FA, SA a</sup>	Jal, Col, PO Ver, GM Qro, CS	González and Herrera (1993), González et al. (1998)
Ascomycota	Sordariomycetes	Sordariales	Sordariaceae	<i>Neurospora sitophila</i> Shear <i>et</i> B.O. Dodge 1927 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Okeanomyces cucullatus Oax, PO (Kohlm.) K.L. Pang et E.B.G. Jones 2004 MA, SA a		Kohlmeyer (1969)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Paecilomyces sp. <sup>FA, SA c</sup> Tam, GM Nay, Chi, PO		Valderrama et al. (2016)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Paradendryphiella arenariae (Nicot) Woudenb. et Crous 2013 <sup>MA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Sordariomycetes	Hypocreales	Stachybotryaceae	Paramyrothecium roridum (Tode) L. Lombard et Crous 2016 <sup>FA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Parengyodontium album (Limber) C.C. Tsang, J.F.W. Chan, W.M. Pong, J.H.K. Chen, A.H.Y. Ngan, M. Cheung, C.K.C. Lai, D.N.C. Tsang, S.K.P. Lau et P.C.Y. Woo 2016 FA SA a	Bac, GC	Velez et al. (2021)
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Parengyodontium album (Limber) C.C. Tsang, J.F.W. Chan, W.M. Pong, J.H.K. Chen, A.H.Y. Ngan, M. Cheung, C.K.C. Lai, D.N.C. Tsang, S.K.P. Lau et P.C.Y. Woo 2016 FA SA a	Bcs, GC	This study
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Penicillium sp. FA, SA a	Ver, GM	Velez et al. (2020)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Penicillium sp. <sup>FA, SA a</sup>	Bac, GC	Velez et al. (2021)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Penicillium sp. <sup>FA, SA a</sup>	Ver, GM	Romero-Hernández et al. (2021)
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Penicillium brevicompactum</i> Dierckx 1901 <sup>FA, SA b</sup>	GM	Velez et al. (2020)
Basidiomycota	Agaricomycetes	Russulales	Peniophoraceae	<i>Peniophora</i> sp. <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Basidiomycota	Agaricomycetes	Russulales	Peniophoraceae	<i>Peniophora incarnata</i> (Pers.) P. Karst. 1889 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Basidiomycota	Agaricomycetes	Russulales	Peniophoraceae	<i>Peniophora pini</i> (Schleich. Ex DC.) Boidin 1956 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)
Ascomycota	Leotiomycetes	Helotiales	Mollisiaceae	Phialocephala sp. <sup>FA, SA b</sup>	GM	Velez et al. (2020)
Ascomycota Ascomycota	Dothideomycetes Sordariomycetes	Pleosporales Incertae sedis	Pleosporaceae <i>Incertae sedis</i>	Pleospora sp. <sup>FA, SA a</sup> Pontogeneia codiicola	Col, PO Bac, GC	Velez et al. (2021) Dawson (1949)
,	,			(Dowson) Kohlm. <i>et</i> E. Kohlm. 1979 <sup>FA, SA a</sup>	,	, ,
Ascomycota	Sordariomycetes	Incertae sedis	Incertae sedis	<i>Pontogeneia padinae</i> Kohlm. 1975 <sup>FA, SA a</sup>	Son, PO	Kohlmeyer (1975)
Ascomycota	Sordariomycetes	Microascales	Chaetomiaceae	<i>Pseudothielavia terricola</i> (J.C. Gilman <i>et</i> E.V. Abbott) X. WeiWang <i>et</i> Houbraken 2019 <sup>MA, SA a</sup>	Col, PO	González et al. (1998)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Pyrenophora biseptata (Sacc. et Roum.) Crous. 2013 <sup>FA, SA a</sup>	Jal, PO Qro, CS	González and Herrera (1993), González et al. (1998)

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports	
Ascomycota Basidiomycota	Sordariomycetes Microbotryomycetes	Microascales Sporidiobolales	Halosphaeriaceae Sporidiobolaceae	<i>Remispora</i> sp. <sup>MA, SA a</sup> <i>Rhodotorula mucilaginosa</i> (A. Jörg.) F.C. Harrison 1928 <sup>FA, SA a</sup>	Tab, GM Qro, CS	Velez et al. (2015b) González et al. (1998)	
Choanozoa	Rozellidea	Rozellidea	Rozellidae	Rozella sp. <sup>FA, SA c</sup>	Nay, Jal, PO	Valderrama et al. (2016)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	Saagaromyces abonnis (Kohlm.) K.L. Pang et E.B.G. Jones 2003 <sup>MA, SA, PA a</sup>	Tam, GM Bcs, GC	Kohlmeyer (1984)	
Ascomycota	Saccharomycetes	Saccharomycetales	Saccharomycetaceae	Saccharomyces sp. FA, SA a	Jal, PO	González and Herrera (1993)	
Ascomycota	Sordariomycetes	Lulworthiales	Lulworthiaceae	Sammeyersia grandispora (Meyers) S.Y. Guo, E.B.G. Jones et K.L. Pang 2017 MA, SA a	Qro, CS Tab, Cam, GM Jal, Col, PO Bcs, GC	Kohlmeyer (1984), González and Herrera (1995), Velez et al. (2015a,b)	
Ascomycota	Sordariomycetes	Savoryellales	Savoryellaceae	Savoryella lignicola E.B.G. Jones et R.A. Eaton 1969 MA, SA a	Tab, GM Col, PO	Velez et al. (2015b)	
Ascomycota	Sordariomycetes	Microascales	Microascaceae	Scopulariopsis sp. FA, SA, a b	Bac, GC Nay, PO	González-Martínez et al. (2017), Velez et al. (2021)	
Ascomycota	Sordariomycetes	Microascales	Microascaceae	<i>Scopulariopsis brumptii</i> Salv Duval 1935 <sup>FA, SA a b</sup>	Jal, PO Ver, GM GC	González and Herrera (1993), González et al. (2000), González-Mar- tínez et al. (2017)	
Ascomycota	Sordariomycetes	Microascales	Microascaceae	Scopulariopsis sphaerospora Zach 1934 <sup>FA, SA b</sup>	GC	González-Martínez et al. (2017)	
Ascomycota	Sordariomycetes	Hypocreales	Stachybotryaceae	Stachybotrys sp.	Yuc, CS	Fajardo-Hernández et al. (2022)	
Ascomycota	Sordariomycetes	Hypocreales	Stachybotryaceae	Stachybotrys chartarum (Ehrenb.) S. Hughes 1958 <sup>FA, SA a</sup>	Ver, Cam, GM	González et al. (1998)	
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	Stemphylium sp. <sup>FA, SA a</sup>	Jal, PO	González and Herrera (1993), Romero-Her- nández et al. (2021)	
Mucoromycota	Mucoromycetes	Mucorales	Syncephalastraceae	Syncephalastrum racemosum Cohn ex J. Schröt. 1886 FA, SA a	Jal, PO	González and Herrera (1993)	
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Talaromyces sp. MA, SA b	GM GC	González-Martínez et al. (2017)	
Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	<i>Talaromyces assiutensis</i> Samson <i>et</i> Abdel-Fattah 1978 <sup>MA, SA b</sup>	GC	González-Martínez et al. (2017)	
Ascomycota	Sordariomycetes	Torpedosporales	Torpedosporaceae	Torpedospora radiata Meyers 1957 MA, SA a	Tab, Ver, Cam, GM Col, PO Yuc, Qro, CS	González et al. (1998), Velez et al. (2015b)	
Ascomycota	Sordariomycetes	Hypocreales	Hypocreaceae	Trichoderma sp. <sup>FA, SA a</sup>	Ver, GM Jal, PO	González and Herrera (1993)	
Ascomycota	Sordariomycetes	Hypocreales	Hypocreaceae	<i>Trichoderma viride</i> Pers. 1794 <sup>FA, SA a</sup>	Ver, GM Qro, CS Col, PO	González et al. (1998)	
Ascomycota	Sordariomycetes	Microascales	Halosphaeriaceae	<i>Tubakiella galerita</i> (Tubaki) Sakay., K.L. Pang <i>et</i> E.B.G. Jones 2011 <sup>MA, SA a</sup>	Yuc, GM	Kohlmeyer and Kohlmeyer (1971)	

Table 1: (continued)

Phylum	Class	Order	Family	Species	Localities	Reports
Ascomycota	Sordariomycetes	Microascales	Pleuroascaceae	Venustampulla parva (A.H.S. Br. et G. Sm.) Unter. et Réblová 2019 <sup>FA, SA a</sup>	Qro, CS	González et al. (2000)
Ascomycota	Dothideomycetes	Pleosporales	Pleosporaceae	<i>Verruculina enalia</i> (Kohlm.) Kohlm. <i>et</i> VolkmKohlm. 1990 FA, SA a	Ver, GM	Kohlmeyer (1968)
Ascomycota	Sordariomycetes	Microascales	Microascaceae	Yunnania carbonaria (F.J. Morton et G. Sm.) Woudenb., Houbraken et Samson 2017 FA, SA a	Gue, PO	González et al. (2000)
Ascomycota	Sordariomycetes	Xylariales	Zygosporiaceae	<i>Zygosporium masonii</i> S. Hughes 1951 <sup>FA, SA a</sup>	Jal, Col, PO	González and Herrera (1993), González et al. (1998)

SA, saprotrophic; PA, pathogen; FA, facultative marine species; MA, obligate marine species. The environment is indicated as follows: asandy beach/ intertidal zone; bdeep-sea plain; water column (hypersaline sea). Data from high-throughput amplicon sequencing are not considered. The abbreviations of the states from where the isolates were obtained are listed as: Bac, Baja California; Bcs, Baja California Sur; Cam, Campeche; Chi, Chiapas; Gue, Guerrero; Jal, Jalisco; Nay, Nayarit; Qro, Quintana Roo; Son, Sonora; Tab, Tabasco; Tam, Tamaulipas; Ver, Veracruz; Yuc, Yucatán; the nomenclature denoting littorals is denoted as: PO, Pacific Ocean; GM, Gulf of Mexico; CS, Caribbean Sea; GC, Gulf of California.

to 2001 were examined to retrieve relevant elements on fungal distribution and ecology. Furthermore, we focused on works coming sandy beaches, deep-sea plains, open sea, and hydrothermal vents on morphological, culturable, genetic and metabarcoding diversity studies.

Additionally, in order to fill knowledge gaps in terms of sampling biases across the Baja California Peninsula (Pacific Ocean and Gulf of California), sampling of four sandy beaches (De Los Angeles Bay, Loreto Bay, Santa Rosalia, Beach Alfredo) was conducted in August 2017 following the field sampling procedures described in Velez et al. (2016b). Briefly, washed-up organic detritus covered with moist sand was collected at each site, placed in Ziploc® plastic bags and incubated for eight months under laboratory conditions (23 °C with a 12-h photoperiod) to induce production of fungal reproductive structures. The material was analyzed for mycelia and reproductive structures. Morphological observations were made, and axenic isolates were obtained on potato dextrose agar (PDA; Sigma-Aldrich, St. Louis, MO, USA) supplemented with artificial seawater (salinity 31.4; Fluval Sea, Montreal, Canada). Fungi were identified based on morphology of their reproductive structures using the taxonomic keys of Kohlmeyer and Kohlmeyer (1979) and Kohlmeyer and Volkmann-Kohlmeyer (1991).

In addition, the universal DNA barcode marker for fungi (nuclear ribosomal internal transcribed spacer region, ITS rDNA; Schoch et al. 2012) was sequenced and analyzed as well as the beta-tubulin gene (benA). Mycelium was harvested from liquid cultures, and DNA was extracted using the protocol described by Doyle and Doyle (1987). The ITS rDNA region was amplified and sequenced using ITS1 and ITS4 primers (White et al. 1990), and the beta-tubulin gene was amplified using the primers Bt2A and Bt2b (Glass and Donaldson 1995). Sanger sequencing reactions were performed in both directions using a 3730xl DNA Analyzer (Applied Biosystems™) at LANABIO, Biology Institute, National Autonomous University of Mexico (UNAM). Dehydrated specimens, cultures, and genomic DNA were deposited at the laboratory headed by Dr. Patricia Velez in the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), and are available for research upon request (Table 2).

# 3 Sandy beaches

Mexico has a long coastline that covers around 15,069 km (considering the insular surface; CONABIO 2019) and includes tropical and temperate zones that sustain several economic activities (Martínez et al. 2006). This dynamic ecotone, characterized by strong environmental shifts in temperature, salinity, UV radiation, and substratum availability, harbors rich biotic assemblages which include a native fungal community represented mostly by arenicolous marine fungi that coexist with numerous facultative marine species (González and Herrera 1993; Walker and Robicheau 2021).

In terms of marine fungal diversity in beaches, few studies were carried out in Mexico before 2001, including Hyde (1992), Kohlmeyer (1968, 1969, 1983, 1984), Kohlmeyer and Kohlmeyer (1979), González and Herrera (1995) and González et al. (1998). Since 2001, investigation of arenicolous marine fungi has extended to 32 localities (including both impacted and pristine sites), in the Gulf of California (Velez et al. 2016a), the Caribbean Sea (González and Hanlin 2010; Velez et al. 2015a, 2016a), and the Gulf of Mexico (González et al. 2010; Velez et al. 2013, 2015b, 2016a,b). As a result, 27 species of fungi have been reported from Mexican coasts.

During the last two decades, beaches have been intensively explored for marine fungi. Particularly, the Gulf of Mexico stands as the top investigated region with 62 records (within the Ascomycota, Rozellomycota, Mucoromycota, and

Table 2: Top five ITS (internal transcribed spacer regions 1 and 2 of rDNA) and beta-tubulin gene hit reference sequences retrieved from the NCBI GenBank database through a BLAST search considered for taxonomic assignation of fungal isolates obtained from Mexican sandy beaches.

Isolate		Assigned OTU	Accession			
	Reference accession	ID	% Identity	Coverage		
BA20	OM965340	Alternaria angustiovoidea	100	100	Alternaria sp.	OQ675147
	OP699757	Alternaria alternata	100	100		
	OP482359	Alternaria alstroemeriae	100	100		
	MZ742813	<i>Alternaria</i> sp.	100	100		
	MW474911	Alternaria tenuissima	100	100		
BA23	MG664756	Didymella glomerata	100	100	Didymellaceae sp.	OQ675148
	MK020673	Epicoccum sorghinum	99.79	100		
	NR_158278	Epicoccum keratinophilum	99.79	100		
	KY587324	Epicoccum nigrum	99.79	100		
	OP796486	Didymella keratinophila	99.79	100		
L14	MT582757	Aspergillus tennesseensis	100	100	Aspergillus sp. 1	OQ675149
	MT582748	Aspergillus jensenii	100	100	,	
	MT549678	Aspergillus versicolor	100	100		
	MK140695	Aspergillus versicolor	100	100		
	T102669	Aspergillus sp.	100	100		
SR13	MK027304	Aspergillus versicolor	99.82	100	Aspergillus sp. 2	OQ675150
	OW988460	Aspergillus austroafricanus	99.82	100	, 3	•
	MH911388	Asperaillus tabacinus	99.63	100		
	ON008181	Aspergillus versicolor	99.63	100		
	LN898709	Aspergillus protuberus	99.45	100		
SR2	MN944461	Parengyodontium album	100	100	Parengyodontium album	OQ675151
	KP269065	Parengyodontium album	100	100		
	ON527249	Parengyodontium album	100	100		
	JF779670	Parengyodontium album	100	99		
	MT626052	Parengyodontium album	99.83	100		
BA22, BAPA3	NR_175013	Corollospora portsaidica	81.39	95	Corollospora sp.	OQ675152
2, 122, 2, 11, 10	AB361031	Corollospora portsaidica	81.39	95	coronospora sp.	0 (0/0.02
	JN943387	Corollospora maritima	82.79	87		
	JN943386	Corollospora gracilis	87.15	87		
	MT569593	Corollospora gracilis	86.67	86		
	1111303333	Beta-tubulin	00.07	00	Assigned OTU	Accession
BA23	EU552932	Epicoccum plurivorum	96.48	100	Didymellaceae sp.	OR351937
	EU552931	Epicoccum plurivorum	96.48	100	- 1	
	OM164105	Similiphoma crystallifera	96.14	100		
	KP185125	Didymella curtisii	95.42	100		
	LT593016	Epicoccum sp.	98.39	87		
SR2	MN944461	Parengyodontium album	100	100	Parengyodontium album	OR351939
3112	KP269065	Parengyodontium album	100	100	r arengyouomann aibann	01.551555
	ON527249	Parengyodontium album	100	100		
	JF779670	Parengyodontium album	100	99		
	MT626052	Parengyodontium album	99.83	100		
BA22, BAPA3	NR_175013	Corollospora portsaidica	81.39	95	Corollospora sp.	OR351938
טו ובב, טחר חט	AB361031	Corollospora portsaidica	81.39	95 95	coronospora sp.	005 ا دریاں
	JN943387	Corollospora maritima	82.79	93 87		
	JN943386	Corollospora gracilis	87.15	87 87		
		Corollospora gracilis				
	MT569593	coronospora graciiis	86.67	86		

Chytridiomycota), followed by the Caribbean with 42 records (within the Ascomycota and Basidiomycota). Overall, these works point to the Caribbean and east beaches in the Gulf of Mexico as rich biodiverse spots, in contrast to the southern portion of the Gulf of Mexico where lower diversity levels might be explained by the presence of major polluted rivers and industrial complexes. Nevertheless, numerous coastal regions of the country remain unexplored, especially in the Pacific Ocean, which represents 68 % of the Mexican coastline. Further unexplored priority areas include natural reserves, sanctuaries, or heavily impacted zones, in the states of Oaxaca (La Escobilla and Morro Ayuta), Baja California (National Park Bahía de Loreto, and the biosphere reserve El Vizcaíno), Nayarit (Bahía de Banderas), and Colima (Revillagigedo Islands) (PROFEPA 2016; SEMARNAT 2021). As a result of our exploration of four localities in the Baja California Peninsula in August 2017, six taxa were discovered including a partially identified Corollospora sp. (Table 1). This fungus, previously reported by Velez et al. (2021) from Ensenada, Baja California, considerably diverges (morphologically and genetically) from all the described species within the genus, and perhaps represents a new species that should be further investigated (Figure 1).

Regional distribution patterns have been reported for fungal communities in the Gulf of Mexico by Velez et al. (2013), identifying taxa with: (1) wide distribution (C. maritima sensu lato); (2) restricted to the Yucatán Peninsula (Arenariomyces triseptatus); (3) associated with the occurrence of the seagrass Thalassia testudinum (Lindra thalassiae); and (4) restricted to the south of the state of Veracruz (Corollospora gracilis and Lignincola laevis). Moreover, local patterns have been described for Cozumel Island in the Caribbean (Velez et al. 2015a), and Tabasco State in the Gulf of Mexico (Velez et al. 2015b), suggesting that neighboring ecosystems represent an important source of assorted substrata, which promotes fungal proliferation.

Globally, C. maritima sensu lato has been accounted as a ubiquitous and most abundant species complex in Mexican beaches (González et al. 1998; Velez et al. 2013, 2015a,b). In this regard, the effect of environmental variables (e.g., temperature, average rainfall and salinity) on the occurrence of isolates from Tamaulipas, Veracruz, Tabasco, and Campeche was explored (Velez et al. 2013), describing particularities such as the ability of some species to grow and produce mature ascomata over a broad range of salinities. Transcriptomic data has demonstrated that isolates from Tabasco and Veracruz displayed high tolerance towards salinity fluctuations, upregulating GPI-anchored putative glucosidase and the aspartic-type endopeptidase genes when grown under freshwater conditions (Velez et al. 2015c). Furthermore, variables such as temperature, radiation, and moisture have been identified as key environmental parameters associated with the occurrence of one of the genetic lineages, which was distributed in Sonora, Yucatán, Tamaulipas, Baja California Sur, and Campeche (Velez et al. 2016a), confirming early observations on ecotypes (Bebout et al. 1987).

The presence of facultative marine fungi in beaches has been repeatedly reported, including potentially human pathogenic species (Velez et al. 2022b; Whitman et al. 2014). Numerous opportunistic human pathogenic fungi including Arthrographis kalrae, Parengyodontium album, Neocosmospora solani, Scopulariopsis sp., and Exophiala sp. have been reported from Mexican sandy beaches. This is a health risk in impacted beaches of Ensenada City, evidencing coastal wastewater contamination (Velez et al. 2021). In this sense, sand may act as a reservoir for potentially allergenic fungi and opportunistic human pathogenic fungi (Yee et al. 2016).

Unfortunately, beaches are increasingly impacted by anthropogenic pressures, mostly owing to urban and tourism development (Martínez et al. 2006; Tanahara

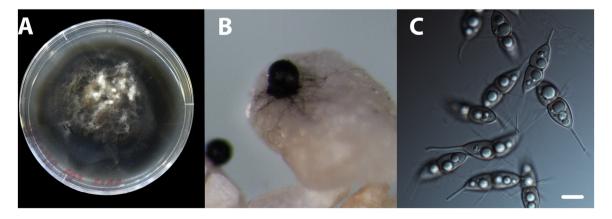


Figure 1: Corollospora sp. isolated from sand samples in Baja California, Mexico. (A) Axenic isolate on potato dextrose agar. (B) Ascoma attached to a sand grain. (C) One-septate, pigmented ascospores, scale bar = 17 μm.

et al. 2021), which poses major challenges to inventorying biodiversity. Nonetheless, recent studies have demonstrated that the new environmental setting resulting from the COVID-19 lockdown may restore the biological community of beaches previously impacted by human activity, hinting to their impressive resilience capacities (Soto et al. 2021). The potential application of intertidal autochthonous species as bioindicators has been proposed for an urban tourist beach in the Caribbean Sea, with high anthropogenic activities (González and Hanlin 2010; Ocaña et al. 2020). Long-term investigations incorporating arenicolous fungi could provide valuable data to confirm observations on the rapid recovery of Mexican tourist beaches in the Caribbean during the COVID-19 lockdown.

# 4 Deep-sea, brackish, and hypersaline coastal lagoons

Fungi in deep-sea ecosystems have developed adaptations to cope with extreme conditions such as high hydrostatic pressure, low temperature and pH, nutrient limitations, and high salinity (Raghukumar et al. 2010). Exploration of fungal diversity in the deep-sea is recent in Mexico. The first report from a vent field resulted as a peripheral finding from the evaluation of benthic eukaryotic diversity from sediments in the Guaymas Basin (27°1'388"N, 111°24'112"W), identifying fungal taxa based on nuclear small subunit rDNA (SSU) amplicon sequencing (Edgcomb et al. 2002). Data obtained from the ITS rDNA region hinted at high diversity levels (4421 OTUs) in deep-sea sediments from the Gulf of Mexico at depths between 1000 and 3500 m, where Penicillium, Rhodotorula and Cladosporium occurred as the dominant genera (Vargas-Gastélum et al. 2019). Subsequent efforts include the description of 2653 ITS amplicon sequence variants (ASVs) from hydrothermal vents in the Guaymas Basin, suggesting that fungal taxa were not linked with specific sample areas as Chytridiomycota (54 % of the total ASVs) and Agaricomycetes were widely distributed across the sample set (Ramírez et al. 2021). Recently, sediment samples from low- and high-temperature vent systems at the Pescadero Basin, Pescadero Transform Fault, and the Alarcón Rise, as well as an oxygen minimum zone in the southern Gulf of California were explored, where 102 ASVs principally affiliated with the Ascomycota and Basidiomycota were documented. The FUNGuild analysis of these data revealed characteristic assemblages in each ecosystem, which could be linked to site-specific processes

that should be further investigated (Velez et al. 2022a). Likewise, 353 fungal ASVs from an oxygen minimum zone in the Mexican Tropical Pacific were reported with the Ascomycota as the most abundant phylum, followed by Basidiomycota. This work demonstrated both a bathymetric diversity pattern (nearshore subsamples showed higher diversity values) and a vertical diversity pattern (subsurface subsamples showed higher diversity values) in fungal diversity (Posadas 2023). Remarkably, all the abovementioned culture-independent studies agree with the occurrence of a high proportion of widely distributed, uncultured phylotypes awaiting description. This represents a research orientation that needs to be further advanced.

A culture-independent study documented sequences recovered from different water bodies including marine water column (depths of 134 m) and surface water in brackish and hypersaline coastal lagoons in Tamaulipas, Jalisco, Navarit, and Chiapas. The data derived from this investigation identified Ascomycota (89.1%) as the most frequently recovered phylum, followed Chytridiomycota (8.1%), Basidiomycota (2.8%) and subphylum Mucoromycotina (1.3%). The authors of this contribution highlighted the lack of culture-independent information on aquatic fungi for Mexico, and suggested that the occurrence of rare taxa could be explained by local adaptations (specialization) (Valderrama et al. 2016).

Culture-dependent investigations have also been conducted, revealing the occurrence of a new species Aspergillus loretoensis in sediments at 275 m depth in Baja California (González-Martínez et al. 2017). Also, fungi from deep-sea sediments in oil reserves in the Gulf of Mexico have been isolated, including: Aureobasidium sp., Cladosporium sp., Penicillium spp., and Phialocephala sp. (Velez et al. 2020); and Alternaria sp., Aureobasidium sp., Cladosporium spp., Penicillium spp., Phialocephala sp., and Stemphylium sp. (Romero-Hernández et al. 2021).

# 5 Marine fungal genetic resources

Although the universal definition of a "marine genetic resource" remains elusive, this concept represents a new frontier for genetic and biochemical information (Eugui and Meyer 2019). Marine fungi produce a variety of unique and biologically potent natural products including alkaloids, terpenoids, steroids, peptides, polyketides, and others (Arrieche et al. 2023). Hence, bioprospecting of marine fungi has emerged for their antitumor, anticancer, antimicrobial,

and enzymatic activities, bioremediation potential, as well as in the production of several therapeutically bioactive agents (Devi and Thakur 2021). Mexican fungal isolates from the marine environments produce an array of fascinating natural products, displaying a remarkable metabolic plasticity. Secondary metabolites and bioactive compounds obtained from these fungi include N-methyl cyclic pentapeptides and dioxomorpholines with unique chemical structures and antimicrobial properties (Aparicio-Cuevas et al. 2017, 2019).

Population genetic analyses of C. maritima sensu lato based on the amplification of inter-simple sequence repeats suggested that Mexican beaches (mainly the Caribbean Sea) harbored a high genetic diversity and exclusive genetic clusters (Velez et al. 2016b). This result was subsequently confirmed by ITS sequencing, delimiting the occurrence of five genetic lineages with distinctive environmental preferences and an overlapping geographic distribution (Velez et al. 2016a). This remarkable genetic diversity within one obligate marine fungal species might offer interesting prospects for bioprospecting and natural product discovery.

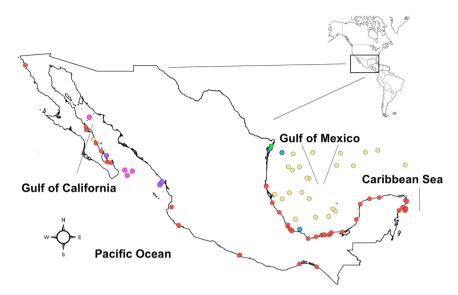
Data obtained under the "one strain, many compounds" approach for a collection of fungal isolates obtained from deep-sea sediments of the Gulf of Mexico revealed that over 50 % of the tested extracts showed antimicrobial activity, particularly those grown at 4°C in darkness. This finding confirmed that culture temperature is one of the primary factors driving variation of metabolomes, and a key to explore deep-sea fungal chemical diversity and antimicrobial potential (Nagano and Nagahama 2012; Villanueva-Silva et al. 2021).

The oil industry in Mexico represents a crucial economic activity (with a daily production of 1622 million barrels, Comisión Nacional de Hidrocarburos 2023) that unfortunately poses an imminent environmental risk. During spills, oil displays dynamic characteristics in the sea, spreading from coastal areas to deep-sea sediments (IARC 1989). Under this scenario, the identification of hydrocarbon degraders is mandatory to enhance the implementation of efficient bioremediation actions. Hydrocarbon tolerant fungi from deep-sea sediments in the Gulf of Mexico have been proposed as potential candidates for bioremediation. These fungi were proved to use aliphatic hydrocarbons as the sole carbon source (Velez et al. 2020), as well as heavy and extra-heavy crude oil (Romero-Hernández et al. 2021). Also, microbial biofouling and biocorrosion on a marine oil pipeline in the Gulf of Mexico were studied, identifying fungi (Pucciniaceae, Clavariaceae, and Onygenaceae) as important components of marine corrosion processes (Avelino-Jiménez et al. 2023). This presents a formidable challenge in terms of marine materials damaged by the action of microbial consortia.

# 6 Functional diversity

The intertidal zone accumulates assorted organic debris consisting mainly of lignin, cellulose, and chitin (Kohlmeyer and Kohlmeyer 1979). Accordingly, fungal diversity on Mexican beaches largely consists of saprobiotic species such as Corollospora pseudopulchella, C. gracilis, Leptosphaerella sp., L. thalassiae, Lineolata rhizophorae and Lulworthia sp. (González et al. 2001; Velez et al. 2013, 2015c); as well as terrestrial borne opportunistically pathogenic fungi such as A. kalrae, P. album, N. solani, Scopulariopsis sp., and Exophiala sp. (Velez et al. 2021). Interestingly, substrata specificity in arenicolous species has been documented including L. thalassiae (T. testudinum) and C. gracilis (Sargassum sp.) (Velez et al. 2013, 2021). The ecological implications of beach wrack cleaning (directional selection of species with no substrata specificity) have been discussed by Velez et al. (2021).

Hydrothermal vents are frequently associated with endemic faunal assemblages fulfilling unique functions (Desbruyères et al. 2001). However, fungal functional roles in this ecosystem remain poorly explored. Velez et al. (2022a) inferred functional guilds from ITS-amplicon dataset in deep-sea hydrothermal vents and an oxygen minimum zone, as animal pathogens, endophytes, plant pathogens, among others, and documented an uncultured fungal group with a putative limited distribution to deep-sea environments, such as methane cold-seeps, anoxic bacterial mats, and deep-sea sediments. The results presented in this work evidenced that a diverse and functionally multifaceted microfungal community inhabited these deep-sea extreme ecosystems, and that the conserved core of fungal taxa across ecosystems comprised barely 3.9 % of the total community. A subsequent investigation approached the analysis of stable isotopes of carbon ( $\delta^{13}$ C), nitrogen ( $\delta^{15}$ N), and sulfur ( $\delta^{34}$ S) in isolates obtained from these deep-sea vent systems, showing that 60 % of the isolates relied on mixed carbon sources fixed by the Calvin-Benson-Bassham and the reductive Tricarboxylic Acid (rTCA) cycles, whereas the remaining 40 % relied exclusively on rTCA carbon (Salcedo et al. 2023). The  $\delta^{15}$ N and δ<sup>34</sup>S values in this work suggested a dependence on local and external nitrogen sources and the assimilation of chemosynthetic and photosynthetic inputs. Remarkably, fungal  $\delta^{13}$ C and  $\delta^{15}$ N overlapped with those of primary and secondary vent macroconsumers, implying the assimilation of bacterial and invertebrate necromass and their ecological role as parasites (Salcedo et al. 2023). More research is needed to obtain a full picture of fungal diversity in this habitat, and to understand compositional differences across ecosystems.



**Figure 2:** Coastal and oceanic localities explored for marine fungi in Mexico from 1992 to 2023, including deep-sea plains (yellow circles), hypersaline sea (green circle), oxygen minimum zones (purple circles), sandy beaches (red circles), water column (blue circles), hydrothermal vents (pink circles).

## 7 Conclusions

Over the past ~75 years the investigation of marine fungal diversity in Mexico has focused on the exploration of coastal environments; however, recent studies in deep-sea plains, oxygen minimum zones, hydrothermal vents, and water columns have proved that these environments are fertile niches for fungi (Figure 2). Mexican marine mycodiversity reflects the heterogeneous environmental settings resulting from its neotropical biogeographical region influenced by two oceans, Atlantic and Pacific, and two internal seas, the Gulf of California and the Gulf of Mexico, all with different ecological conditions (CONABIO 2019). Culture-dependent approaches are needed to determine fungal tolerance towards shifts in key marine conditions, including changes in physicochemical variables, climate change and anthropogenic pressures.

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**Author contributions:** PV designed the work. PV, JO and AB generated the data. All the authors contributed to the analysis and interpretation of the data, drafting the work and approved the version to be published. The authors have accepted responsibility for the entire content of this manuscript and approved its submission.

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**Data availability:** The generated sequences are publicly available under the accession numbers OQ675147- OQ675152 and OR351937- OR351938 in the NCBI GenBank database.

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## **Bionotes**



#### Julio Olguin

Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

Julio Olguin received his B.S. (2017) and M.S. (2022) degrees from UNAM, Mexico. Currently, he is a PhD student in the Graduate School in Marine Sciences and Limnology, National Autonomous University of Mexico under the mentorship of Professor Patricia Velez. His research focuses on the bioremediation of Mexican marine ecosystems contaminated with hydrocarbons and crude oil, studying fungi obtained from the intertidal zone, hydrothermal vents, and beaches.



#### Patricia Velez

Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico pvelez@ib.unam.mx https://orcid.org/0000-0002-4449-8977

Dr. Patricia Velez earned her B.S. (2008), M.S. (2010), and Ph.D. (2014) degrees in Biological Sciences from the UNAM for her work on arenicolous marine fungi. Next, she performed two postdoctoral stays at the UNAM and the CICESE studying molecular ecology of freshwater and deep-sea fungi respectively. She is now a faculty member and full-time researcher at the Institute of Biology, UNAM where her work aims to explore the diversity, ecology and potential utilization of fungal communities, particularly in marine ecosystems.



#### Vivianne Solís-Weiss

Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico, Puerto Morelos, 77580, Mexico

Vivianne Solís-Weiss holds a PhD in Oceanography (1975, France). Postdocs: Israel 1975–1977, Trieste 2002–2004; sabbaticals: DC-USA (1986), Trieste (2000), Paris (2003). She is a Mexican Academy of Sciences member since 1993, Senior Professor and Researcher, and Head of Lab. She has over 220 publications and supervised 55 theses. Dr. Solís-Weiss is Head of Research projects in marine ecosystems in Mexican seas and coasts (cenotes to Deepsea). She has described more than 65 new species of invertebrates, is a co-discoverer of seagrasses pollination by invertebrates and presently involved in Sargassum, microplastics and marine fungi. She is fluent in 5 languages.



#### Allison K. Walker

Department of Biology, Acadia University, 33 Westwood Avenue, Wolfville, Nova Scotia, B4P 2R6, Canada

https://orcid.org/0000-0002-5061-361X

Professor Allison K. Walker trained at the University of Toronto, Canada and the USDA Systematic Botany and Mycology Laboratory, USA. She completed her graduate training in marine fungi at the University of Southern Mississippi, followed by postdoctoral research with David Miller and Keith Seifert (Ottawa) studying fungal endophytes. Now Full Professor at Acadia

University, she serves as Director of the E.C. Smith Herbarium. She and her students study intertidal fungal biodiversity and ecology, focusing on salt marshes and endophytic fungi.



María C. González

Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, Mexico City, 04510, Mexico

Dr. María C. González is a faculty member and full-time researcher at the Institute of Biology-National Autonomous University of Mexico. She is a mycologist interested in studying the Mexican marine and freshwater Ascomycota diversity that inhabits ecotones of coastal and lentic ecosystems, respectively. She has published more than 55 articles in peerreviewed journals and has served as the advisor for more than 15 graduate theses.