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A contribution to the diversity and distribution of the genus *Scleroderma* (Boletales: Sclerodermataceae) in Mexico

Contribución a la diversidad y distribución del género Scleroderma *(Boletales: Sclerodermataceae) en México*

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Abstract

The order Boletales is one of the most diverse and widespread groups of macromycetes globally, with the genus *Scleroderma* being a significant representative. Despite the ecological, medical, and biocultural importance of this genus, studies on its systematics and genetic diversity in Mexico are scarce. Here, we studied the diversity and distribution of *Scleroderma* in Mexico using all available information (voucher registers, voucher DNA, and environmental DNA). A total of 120 nrITS DNA sequences from different species were analyzed, including 27 from environmental samples, while the remaining sequences were obtained from public databases. In Mexico, 15 *Scleroderma* species have been cited by morphological taxonomy, while molecular evidence suggest around 24 taxa. Phylogenetic analyses divided the genus into 4 main clades. Clade A corresponds to section *Scleroderma* and includes *S. albidum* s.l., *S. areolatum*, and *S. cepa/laeve*; clade B includes species of section *Sclerangium* and *S. anomalosporum*; clade C includes only *S. dictyosporum*; and clade D corresponds to section *Reticulatae* and includes *S. bovista*, *S. citrinum* s.l., and *S. meridionale*. The presence of *S. capeverdeanum* s.l. and *S. venenatum* is reported for the first time in Mexico.

Keywords: Environmental DNA; Soil; Macromycetes; Biogeography

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Resumen

El orden Boletales constituye uno de los grupos de macromicetos más diversos y ampliamente distribuidos, con el género *Scleroderma* como un representante significativo. A pesar de su relevancia, los estudios sobre su sistemática y diversidad en México son escasos. En este trabajo analizamos la diversidad y distribución de *Scleroderma* en México a partir de toda la información disponible (registros de especímenes, DNA de esporomas y DNA ambiental). Se evaluaron 120 secuencias de DNA nrITS, de las cuales 27 corresponden a muestras ambientales; las restantes se obtuvieron de bases de datos públicas. Mientras que por taxonomía morfológica se han citado 15 especies de *Scleroderma* en el país, nuestros resultados sugieren aproximadamente 24 especies. Los análisis filogenéticos revelaron 4 clados principales: el clado A corresponde a la sección *Scleroderma* e incluye a *S. albidum* s.l., *S. areolatum* y *S. cepa*/*laeve*; el clado B incluye las especies de la sección *Sclerangium* y a *S. anomalosporum*; el clado C integra únicamente a *S. dictyosporum*; y el D corresponde a la sección *Reticulatae*, e incluye a *S. bovista*, *S. citrinum* s.l. y *S. meridionale*. Asimismo, se reporta por primera vez en México la presencia de *S. capeverdeanum* y *S. venenatum*.

Palabras clave: DNA ambiental; Suelo; Macromicetos; Biogeografía

Introduction

The estimation of the global diversity of fungi is still under debate, conservative authors propose a range between 1.5 and 3.8 million species (Hawksworth, 1991; Hawksworth & Lücking, 2017). However, current knowledge about fungal diversity is still insufficient, as many of the species have not been described or detected through their sporomes (Tedersoo et al., 2014). Furthermore, in Mexico the complex topography, strong habitat variability, and convergence of Nearctic and Neotropical biota contribute to a high fungal diversity characterized by many cryptic lineages (Cifuentes-Blanco et al., 1997; Sánchez-Ramírez, 2015). Consequently, morphological traits of fungi are insufficient in many taxa to detect hidden diversity.

In recent decades, tools such as metabarcoding have been used to improve species detection, particularly from environmental samples such as air, water, and soil (Heeger et al., 2018; Korpelainen et al., 2017; Tedersoo et al., 2014, 2022). Regarding macromycetes, these techniques have enhanced our understanding of the diversity of genera with medical, edible, economic, or cultural importance, such as *Suillus* and *Tuber* (Bonito et al., 2010; Tao et al., 2024) and have clarified ecological relationships between *Boletus* and the soil microbiota (Santolamazza-Carbone et al., 2023). However, the diversity of other groups such as *Scleroderma* remains underestimated.

The genus *Scleroderma* described by Persoon (1801) belongs to the family Sclerodermataceae within the Boletales (Binder & Bresinsky, 2002; Kirk et al., 2008). Species in this genus develop ectomycorrhizal associations with temperate and tropical plants such as *Coccoloba*, *Eucalyptus*, *Fagus*, *Pinus*, and *Quercus*, among others (Guzmán et al., 2013; Lu et al., 1998; Rincón et al., 2001; Sims et al., 1995). It has been estimated that the Sclerodermatineae originated 66 million years ago, at the end of the Cretaceous, while its main genera diversified around the middle Cenozoic. Consequently, *Scleroderma* is presumed to have originated approximately 38.37 million years ago, at the end of the Eocene (Wilson et al., 2012).

Several species of *Scleroderma* are considered edible, toxic, or medicinal. For instance, *S. citrinum*, *S. flavidum*, and *S. yunnanense* stand out as edible mushrooms in China (Wang et al., 2004; Zhang et al., 2013), while *S. citrinum*, *S. dictyosporum*, and *S. polyrhizum* are consumed in India (Karun et al., 2022). The edibility of *S. laeve* and *S. texense* has been documented for Mexico (Cortés-Pérez et al., 2021; De Ávila et al., 1980). Moreover, toxicity assays using *Artemia franciscana* larvae confirmed that Mexican specimens of *S. texense* do not exhibit toxic effects, supporting their local use as edible fungi (Ruiz-González et al., 2017). On the other hand, *S. areolatum*, *S. bovista*, *S. cepa*, *S. citrinum*, *S. flavidum*, *S. polyrhizum*, and *S. verrucosum* are considered medicinal in China (Dai & Yang, 2008). In Mexico, *S. areolatum*, *S. nitidum*, and *S. verrucosum* are used to stop bleeding from wounds (Guzmán et al., 2013). Conversely, some authors have classified species like *S. albidum*, *S. areolatum*, *S. cepa*, and *S. venenatum* as toxic (Guzmán, 1970; Sato et al., 2020; Yao et al., 2023; Zhang et al., 2020; Zhong et al., 2021).

In soil restoration projects, *Scleroderma* plays a significant role in maintaining and establishing ectomycorrhizal hosts. Its species improve the establishment, growth, and functional traits of their hosts (Bullaín-Galardis et al., 2024). For this reason, species such as *S. citrinum*, *S. polyrhizum*, *S. texense*, and *S. verrucosum* have been used to inoculate native trees during revegetation efforts in abandoned agricultural lands or arid soils (Pera & Parladé, 2005; Valdés-Ramírez et al., 2010). Even tropical species such as *S. bermudense* has been inoculated in *Coccoloba uvifera* to alleviate salinity stress and restore coastal dunes (Bandou et al., 2006; Bullaín-Galardis et al., 2024).

From a morphological perspective, *Scleroderma* was divided into 3 sections by Guzmán (1967, 1970) based on microscopic diagnostic characters such as basidiospore ornamentation and the structure of generative hyphae: section *Aculeatispora* characterized by the presence of echinulate basidiospores and the absence of clamp connections; section *Sclerangium* with subreticulate, subechinulate or echinulate basidiospores and abundant clamp connections; finally, section *Scleroderma* with reticulate basidiospores and few clamp connections. However, a change in the name of the sections *Aculeatispora* and *Scleroderma* to sections *Scleroderma* and *Reticulatae*, respectively, was later proposed (Guzmán et al., 2013). Some molecular studies partially agreed with this classification and reported new species based on some DNA regions such as nrITS (Nouhra et al., 2012; Phosri et al., 2009; Rusevska et al., 2014; Wu et al., 2023).

Scleroderma has around 100 species names registered in Index Fungorum (https://www.indexfungorum.org) and MycoBank (https://www.mycobank.org/). In *Scleroderma*, species complexes are not exclusively composed of cryptic taxa, while some species are morphologically indistinguishable and can only be separated using molecular data, many others can be reliably distinguished based on macroscopic and microscopic characters. However, some species such as *S. meridionale*, *S. polyrhizum*, and *S. septentrionale* represent species complexes that are being delimited through phylogenetic studies (Ortíz-Rivero et al., 2021). This highlights the importance of integrating morphological and molecular evidence to achieve accurate species delimitation within the genus.

Although phylogenetic and molecular studies for the genus exist worldwide (Nouhra et al., 2012; Phosri et al., 2009; Rusevska et al., 2014; Yang et al., 2025), only morphological studies have been carried out in Mexico, where 15 morphospecies have been reported: *S. albidum*, *S. areolatum*, *S. bermudense*, *S. bovista*, *S. cepa*, *S. citrinum, S. hypogaeum*, *S. mexicana*, *S. michiganense*, *S. nitidum*, *S. polyrhizum*, *S. pseudostipitatum*, *S. texense,* and *S. verrucosum* (Guzmán, 1970; Guzmán et al., 2013; Guzmán-Dávalos & Guzmán, 1985). Additionally, *S. guzmanii* was described by Ortíz-Rivero et al. (2021), and *S. cepa* s.l. was recently reported through phylogenetic analysis associated with *Carya illinoinensis* (Sánchez-Ledesma et al., 2023).

Due to the uncertainty regarding the diversity of *Scleroderma* species in Mexico, we conducted a comprehensive study integrating all genetic and geographic information available for the genus in the country. This approach is key to obtaining a more complete view of *Scleroderma* diversity in Mexico.

Materials and methods

Soil environmental DNA (eDNA) sampling was carried out in the northeast, center, south, and southeast of Mexico (Fig. 1C) from 2019 to 2021, as part of the Global Soil Mycobiome Consortium Project (Tedersoo et al., 2021). A total of 73 locations in the states of Aguascalientes, Campeche, Chiapas, Coahuila, Hidalgo, Jalisco, Mexico City, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Quintana Roo, Estado de Mexico, Tabasco, Tlaxcala, Veracruz, and Yucatán, were sampled. In each locality, we collected 40 soil cores around an area of 2,500 m^2. Each soil core was retrieved with a polyvinyl tube (5 cm diameter and 10 cm depth) to take the organic horizon and the first part of the mineral horizon, avoiding litter. Afterwards, these were combined and homogenized to form a composite sample (~ 1 kg). Composite samples were placed in Ziploc bags (~ 250 g), dried and stored at 5 °C.

DNA extraction was performed as described in Tedersoo et al. (2021). Polymerase chain reactions (PCR) were performed to amplify the internal transcribed spacer region of the nuclear ribosomal DNA (nrITS) with the universal eukaryotic primers ITS9mun and ITS4ngsUni, according to the methods and conditions in Tedersoo and Anslan (2019). PCR libraries were constructed and sequenced in the PacBio Sequel II platform at the University of Oslo. The resulting sequences were demultiplexed, quality filtered chimeric sequences were removed, OTUs clustered at 98% similarity, and taxonomically annotated as described in Tedersoo et al. (2021). The most abundant sequence of each OTU was selected as its representative sequence and used for further analysis.

The resulting *Scleroderma* DNA sequences from soil were complemented with sequences retrieved from GenBank (Sayers et al., 2024) derived from voucher specimens and ectomycorrhizae. Our final dataset contained 120 nrITS sequences of which 27 correspond to eDNA and voucher specimens and 93 were retrieved from GenBank (Table 1). We used 2 sequences of *Tremellogaster surinamensis* (Wilson et al., 2011) as an outgroup to root the *Scleroderma* phylogeny. We aligned the DNA sequences with MAFFT with the FFT-NS-i algorithm with 1,000 repetitions implemented in Geneious

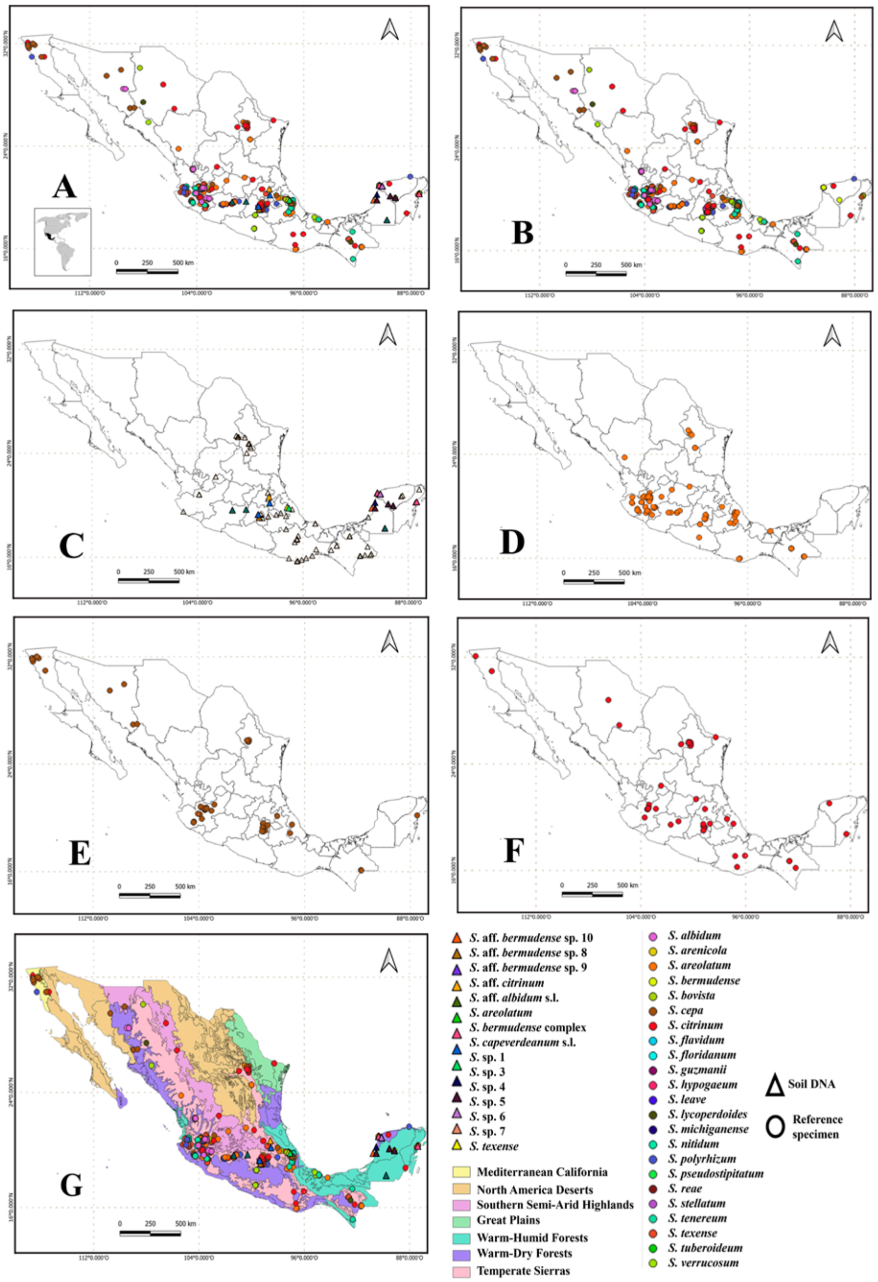

Figure 1. Geographic distribution of *Scleroderma* in Mexico. A, Colored circles correspond to reference specimen occurrences, taken from the Global Biodiversity Information Facility (GBIF) database; colored triangles indicate clades obtained by environmental DNA; B, taken from the GBIF database; colored circles correspond to reference specimen occurrences; C, *Scleroderma* DNA sequences; colored triangles indicate OTUS obtained by environmental DNA; open triangles correspond to sampling sites with no *Scleroderma* DNA sequences; D, distribution map of *S. areolatum*; E, distribution map of *S. cepa*; F, distribution map of *S. citrinum*; G, distribution map of *Scleroderma* in different bioregions of Mexico, colored circles correspond to reference specimen occurrences, taken GBIF database; colored triangles indicate clades obtained by environmental DNA.

Prime. The resulting alignment was manually edited and trimmed. The final alignment had 768 sites, including gaps.

The best nucleotide substitution model for our alignment (HKY + I + Gama) was selected based on the corrected Akaike information criterion (AICc; Burnham & Anderson, 2002) inferred in jModelTest (Darriba et al., 2012). We inferred phylogenetic relationships based on Bayesian and Maximum likelihood approaches. Both analyses were performed in MrBayes 6.1 and PHYML implemented in Geneious Prime. Maximum likelihood support was estimated with 1,000 bootstrap pseudo-replicates (MLB) (Felsenstein, 1985), leaving the rest of parameters as default. For the Bayesian inference, we ran 4 simultaneous Monte Carlo Markov Chains (MCMC) for 10 M generations, sampling every 1,000 trees.

Table 1
nrITS DNA sequences obtained from environmental soil samples and GenBank used for phylogenetic analysis.

Species	GenBank access code	Country	Reference
Scleroderma albidum	PP582969	India	Unpublished**
Scleroderma albidum	OR656734	Spain	Unpublished**
Scleroderma albidum	KJ676532	Brazil	Montagner et al., 2015
Scleroderma albidum s.l.*	PV232154	Mexico	This study
Scleroderma albidum s.l.*	PV232155	Mexico	This study
Scleroderma albidum s.l.*	PV232156	Mexico	This study
Scleroderma anomalosporum Type	NR147662	Brazil	Baseia et al., 2016
Scleroderma areolatum	FM213352	USA	Phosri et al., 2009
Scleroderma areolatum	EU784407		Brock et al., 2009
Scleroderma areolatum	HF933231	Macedonia	Rusevska et al., 2014
Scleroderma areolatum	KC152224	Mexico	Unpublished**
Scleroderma areolatum	KY574379	Mexico	Unpublished**
Scleroderma areolatum	PV211138	Mexico	Unpublished**
*Scleroderma areolatum**	PV232141	Mexico	This study
*Scleroderma bermudense**	PV232132	Mexico	This study
*Scleroderma bermudense**	PV232133	Mexico	This study
*Scleroderma bermudense**	PV232142	Mexico	This study
*Scleroderma bermudense**	PV232143	Mexico	This study
*Scleroderma bermudense**	PV232144	Mexico	This study
Scleroderma bermudense	OQ351731	Cuba	Unpublished**
Scleroderma bermudense	OQ351725	Cuba	Unpublished**
Scleroderma bermudense	OQ351721	Cuba	Unpublished**
Scleroderma bermudense	KJ209672	Senegal	Unpublished**
Scleroderma bermudense	KJ209674	France	Unpublished**
Scleroderma aff. *bermudense* sp. 8*	PV232136	Mexico	This study
Scleroderma aff. *bermudense* sp. 8*	PV232137	Mexico	This study
Scleroderma aff. *bermudense* sp. 8*	PV232138	Mexico	This study
Scleroderma aff. *bermudense* sp. 9*	PV232134	Mexico	This study
Scleroderma aff. *bermudense* sp. 10*	PV232135	Mexico	This study

Table 1. Continued

Species	GenBank access code	Country	Reference
Scleroderma bovista	KU739419	Spain	Fernández-Miranda, 2014
Scleroderma bovista	FM213340	Spain	Phosri et al., 2009
Scleroderma bovista	HF933235	Macedonia	Rusevska et al., 2014
Scleroderma bovista	HF933242	Serbia	Rusevska et al., 2014
Scleroderma cf. *bovista*	FM213339	USA	Phosri et al., 2009
Scleroderma camassuense Type	NR147663	Brazil	Baseia et al., 2016
Scleroderma capeverdeanum Type	NR164545	Cape verde	Crous et al., 2016
Scleroderma capeverdeanum	KU747111	Cape verde	Crous et al., 2016
Scleroderma capeverdeanum s.l.*	PV232145	Mexico	This study
Scleroderma capeverdeanum s.l.*	PV232157	Mexico	This study
Scleroderma cepa	OR882638	USA	Unpublished**
Scleroderma cepa	EU784411		Brock et al., 2009
Scleroderma cepa	OP743680	USA	Unpublished**
Scleroderma cepa s.l.	MZ092921	Mexico	Sánchez-Ledesma et al., 2023
Scleroderma citrinum	FM213344	USA	Phosri et al., 2009
Scleroderma citrinum	KJ679575	Brazil	Montagner et al., 2015
Scleroderma citrinum	KJ679576	Brazil	Montagner et al., 2015
Scleroderma aff. *citrinum**	PV232139	Mexico	This study
Scleroderma columnare	AB459519	Thailand	Ruankaew-Disyatat et al., 2016
Scleroderma columnare	AB459512	Thailand	Ruankaew-Disyatat et al., 2016
Scleroderma dictyosporum	FJ840444	Burkina Faso	Sanon et al., 2009
Scleroderma dictyosporum	FJ840442	Burkina Faso	Sanon et al., 2009
Scleroderma dictyosporum	FJ840443	Burkina Faso	Sanon et al., 2009
Scleroderma dictyosporum	FJ840449	Burkina Faso	Sanon et al., 2009
Scleroderma duckei	KX792086	Brazil	Baseia et al., 2016
Scleroderma duckei Type	NR147664	Brazil	Baseia et al., 2016
Scleroderma dunensis Type	NR147646	Brazil	Crous et al., 2016
Scleroderma dunensis	KU747112	Brazil	Crous et al., 2016
Scleroderma dunensis	KU747114	Brazil	Crous et al., 2016
Scleroderma erubescens Type	OQ554978	China	Wu et al., 2023
Scleroderma erubescens	OQ554976	China	Wu et al., 2023
Scleroderma geaster	MT270642	Spain	Ortiz-Rivero et al., 2021
Scleroderma geaster	MT270640	Portugal	Ortiz-Rivero et al., 2021
Scleroderma guzmanii	MT270647	Mexico	Ortiz-Rivero et al., 2021
Scleroderma guzmanii Type	NR176725	USA	Ortiz-Rivero et al., 2021
Scleroderma furfuraceum Type	NR186993	Russia	Rebriev & Zvyagina, 2022
Scleroderma laeve	EU718117		Wilson et al., 2011
Scleroderma laeve	ON212388	South Korea	Cho et al., 2022
Scleroderma meridionale	HF933238	Macedonia	Rusevska et al., 2014

Table 1. Continued

Species	GenBank access code	Country	Reference
Scleroderma meridionale	MG367369	Italy	Leonardi et al., 2018
Scleroderma meridionale	MG264160	Italy	Leonardi et al., 2018
Scleroderma meridionale	EU718121	USA	Unpublished**
Scleroderma michiganense	FM213348	USA	Phosri et al., 2009
Scleroderma michiganense	FM213347	USA	Phosri et al., 2009
Scleroderma michiganense	FM213346	USA	Phosri et al., 2009
Scleroderma nastii	ON212391	South Korea	Cho et al., 2022
Scleroderma nitidum	KU759906	Brazil	Baseia et al., 2016
Scleroderma nitidum	KU759908	Brazil	Baseia et al., 2016
Scleroderma patagonicum	KY462453	Argentina	Truong et al., 2017
Scleroderma patagonicum	HQ688789	Argentina	Noura et al., 2012
Scleroderma polyrhizum	MT270661	USA	Ortiz-Rivero et al., 2021
Scleroderma polyrhizum	MT270662	Spain	Ortiz-Rivero et al., 2021
Scleroderma separatum	OQ554975	China	Wu et al., 2023
Scleroderma separatum	OQ554973	China	Wu et al., 2023
Scleroderma septentrionale	FM213338	USA	Phosri et al., 2009
Scleroderma septentrionale	FM213336	Sweden	Phosri et al., 2009
Scleroderma cf. *septentrionale*	FM213337	USA	Phosri et al., 2009
Scleroderma sinnamariense	FM213358	Thailand	Phosri et al., 2009
Scleroderma sinnamariense	AB908177	India	Unpublished**
Scleroderma sinnamariense	HQ687222	Thailand	Unpublished**
Scleroderma squamulosum	OQ554980	China	Wu et al., 2023
Scleroderma squamulosum Type	OQ554979	China	Wu et al., 2023
Scleroderma suthepense Type	NR132871	Thailand	Kumla et al., 2013
Scleroderma texense	MT270650	USA	Ortiz-Rivero et al., 2021
Scleroderma texense	MT270649	USA	Ortiz-Rivero et al., 2021
*Scleroderma texense**	PV232140	Mexico	This study
Scleroderma venenatum	OQ750238	China	Unpublished**
Scleroderma venenatum	JF273540	China	Zhang et al., 2020
Scleroderma venenatum	KC52225	Mexico	Unpublished**
Scleroderma venenatum	MH513631	China	Zhang et al., 2020
Scleroderma venenatum	OM874611	Russia	Rebriev & Zvyagina, 2022
Scleroderma venenatum	OM874613	Russia	Rebriev & Zvyagina, 2022
Scleroderma venenatum	MH513632	China	Zhang et al., 2020
Scleroderma verrucosum	EU784415	England	Brock et al., 2009
Scleroderma verrucosum	HF933241	Macedonia	Rusevska et al., 2014
Scleroderma vinaceum	OQ554986	China	Wu et al., 2023
Scleroderma vinaceum Type	OQ554987	China	Wu et al., 2023
Scleroderma yunnanense	JQ639046	China	Wu et al., 2023

Table 1. Continued

Species	GenBank access code	Country	Reference
Scleroderma yunnanense	JQ639045	China	Wu et al., 2023
Scleroderma yunnanense	JQ639041	China	Wu et al., 2023
Scleroderma sp. 1*	PV232153	Mexico	This study
Scleroderma sp. 2	PV211140	Mexico	Unpublished **
Scleroderma sp. 3*	PV232158	Mexico	This study
Scleroderma sp. 4*	PV232149	Mexico	This study
Scleroderma sp. 4*	PV232150	Mexico	This study
Scleroderma sp. 4*	PV232151	Mexico	This study
Scleroderma sp. 4*	PV232152	Mexico	This study
Scleroderma sp. 5*	PV232146	Mexico	This study
Scleroderma sp. 6*	PV232147	Mexico	This study
Scleroderma sp. 7*	PV232148	Mexico	This study
Tremellogaster surinamensis	KT724170	Colombia	Unpublished **
Tremellogaster surinamensis	EU718127		Wilson et al., 2011

* Sequences obtained from environmental soil samples. ** Unpublished GenBank sequences.

We visually assessed sampling stationarity in Tracer ver. 1.7 (Rambaut et al., 2018) and by the observed average standard deviation of split frequencies (< 0.01). Finally, we discarded 20% of the sampled trees as burn-in, resulting in a collection of 7,510 trees. A majority rule consensus tree and Bayesian posterior probabilities (BPP) were calculated with the post-burn-in trees. We visually compared topological congruence between replicates and inference methods and edited the final tree in FigTree ver 1.4.4 (Rambaut, 2018).

To determine the distribution and species richness of *Scleroderma* in Mexico, we used the occurrence of the clades in the 73 sampling sites (Fig. 1C). This information was complemented with the 2,349 records of *Scleroderma* for Mexico in the GBIF public database (GBIF.org, August 27, 2024) (Fig. 1B). Records at the genus level were excluded. Since the political division of the country is not suitable for understanding patterns and processes of biodiversity, a distribution map of the genus was created using the level IV ecoregions of Mexico (Conabio, 2008).

Results

The consensus tree shows that *Scleroderma* is divided into 4 main clades (A, B, C, and D) with medium to high MLB and BPP support values. The topology of the inferred phylogenetic trees was similar in both analyses. The Mexican species were distributed in clades A, B, and D (Fig. 2). Morphologically, 15 species reported in the literature are recognized for Mexico, 9 from GBIF records only. *Scleroderma capeverdeanum* s.l. and *S. venenatum* complex are recorded for the first time along with several unnamed clades from soil samples. Of the total number of species, the clades corresponding to *S. areolatum*, the *S. bermudense* complex and the *S. capeverdeanum* s.l. are recognized from specimen vouchers and eDNA sampling, which leads us to consider that the number of species for Mexico is around 24.

Clade A (MLB: 92% and BPP: 1) contains species such as *S. areolatum*, *S. cepa*/*laeve*, and *S. verrucosum*. Several species from soil samples are also grouped together. Among the species sequenced from specimen vouchers, mycorrhizae, and eDNA from Mexico is *S. areolatum*. The grouping of Mexican sequences within the *S. capeverdeanum* s.l. clade (MLB: 75% and BPP:0.70) stands out, as well as sequences within *S. venenatum* (MLB: 100% and BPP: 1). Clade B (MLB: 62%, BPP: 0.99) includes species such as *S. guzmanii* and *S. polyrhizum*. Its most diverse subclade comprises the *S. bermudense* complex (MLB: 56%, BPP: 0.8), which is sister to *S.* aff. *bermudense* (MLB: 80%, BPP: 0.99), along with numerous soil DNA sequences associated with these 2 taxa. Clade C (MLB: 100% and BPP: 1) only contains *S. dictyosporum*, a species distributed in Africa and Southeast Asia. Clade

D (MLB: 81%, BPP: 1) includes the Mexican taxon *S.* aff. *citrinum* from soil DNA*,* which is sister to *S. citrinum* s.l.

Species of *Scleroderma* occur throughout Mexico (Fig. 1A, Table 2); however, there are no records for the states of Baja California Sur and Zacatecas (Fig. 1B). The records obtained from soil eDNA are mainly concentrated in the central states of the country such as Estado de México, Hidalgo, and Michoacán; as well as the Yucatán Peninsula (Fig. 1C).

Regarding the clades obtained by eDNA, we found that they are distributed in 3 main vegetation types that correspond to tropical broadleaf forest, subtropical broadleaf forest, and tropical coniferous forest (Table 3). The clades of *S.* aff. *bermudense* and *S. bermudense* complex are mainly distributed in tropical broadleaf forest and subtropical broadleaf forest, while *S. capeverdeanum* distributes in tropical coniferous forest and subtropical coniferous forest. In the case of *S. areolatum*, it was only sequenced tropical broadleaf forests soil. The Transmexican Volcanic Belt is the physiographic province with the highest diversity of *Scleroderma*, being *S. areolatum*, *S. cepa*, and *S. citrinum* the most common species (Fig. 1D, E, F). Meanwhile, the largest number of records corresponds to *S. bermudense* complex from the Yucatán Peninsula.

There are clades of Neotropical distribution that include basidiomes and eDNA sequences such as those found within the *S. bermudense* complex; both, its basidiomes and soil DNA come mainly from the Yucatán Peninsula. Some OTUs of *S. bermudense* complex were found abundantly in the soil, such as *S.* aff. *bermudense* sp. 8 with 3,877 sequences. However, *S.* aff. *bermudense* sp. 9 and *S.* aff. *bermudense* sp. 10, have small distribution areas, apparently restricted to Mexico (Table 2).

Regarding the distribution of *Scleroderma* in Mexican ecoregions, there are more reports in the temperate sierras and less in the warm-dry forests. The ecoregions corresponding to the great deserts of Mexico remain among the least explored (Fig. 1G). In the southeast there are more records of *S. bermudense* found in the warm-humid forests of the Yucatán Peninsula, and in smaller numbers in warm-humid forests of Chiapas, Tabasco, and Veracruz.

Discussion

Our phylogenetic analysis matches partially with the results obtained in former molecular studies reporting that *Scleroderma* is divided into 2 main clades (Phosri et al., 2009; Rusevska et al., 2014). However, it is more consistent with current phylogenies including a larger number of species such as those of Wu et al. (2023) and Yang et al. (2025), who also found 4 main clades. It also does not fully correspond with the sections proposed by Guzmán (1967, 1970).

Our phylogeny and that of Yang et al. (2025) are similar across all major clades; even while our study includes only ITS sequences. Clade A corresponds to section *Scleroderma* and includes *S. albidum* s.l., *S. areolatum*, and *S. cepa*/*laeve*. Guzmán (2013) proposed *S. laeve* as a synonym of *S. albidum*; however, our results suggest that, instead, it may be a synonym of *S. cepa*. This section also comprises *S. erubescens*, *S. separatum*, *S. squamulosum*, and *S. vinaceum*, which cluster with species assigned to section *Scleroderma*, traditionally characterized by echinulate basidiospores and the absence of clamp connections. Nevertheless, Wu et al. (2023) reported that both *S. erubescens* and *S. separatum* possess clamp connections. This suggests that section *Scleroderma* may not be exclusively composed of species without clamp connections.

Clade B includes species in Section *Sclerangium* and *S. anomalosporum*, a species with smooth basidiospores (Baseia et al., 2016). Clade C remains the same, including only *S. dictyosporum*. This species was formerly placed in section *Scleroderma*, now recognized as section *Reticulatae*; however, in our analysis it forms an independent clade. Clade D corresponds to section *Reticulatae.*

Similarly, Yang et al. (2025) concluded that basidiospore ornamentation is not a reliable character for distinguishing section *Scleroderma* from section *Sclerangium*. Many species in section *Scleroderma* may also produce subreticulate basidiospores (e.g., *S. areolatum*, *S. cepa*, and *S. nastii*), whereas several new species in section *Sclerangium* can produce echinulate basidiospores (e.g., *S. navigatum*, *S. xanthochroum*, and *S. zengchengense*). The authors further proposed that peridium thickness may serve as an additional distinguishing feature.

Our results suggest that the number of *Scleroderma* species in Mexico is greater than the 15 previously reported (Guzmán et al., 2013; Ortíz-Rivero et al., 2021; Sánchez-Ledesma et al., 2023). We reported for the first time *S. capeverdeanum* s.l. and *S. venenatum*, as well as 10 clades that do not match with species previously sequenced. Conservatively the diversity of *Scleroderma* for Mexico is around 24 taxa. The discrepancy between species richness in voucher specimens versus DNA sequences may be explained due to scarce formation of basidiomes or because most of the described species have not been sequenced (Tedersoo et al., 2014).

In the case of some OTUs of the *S. bermudense* complex, they could be considered endemic to Mexico, as they were only recorded at 1 sampling site. Other

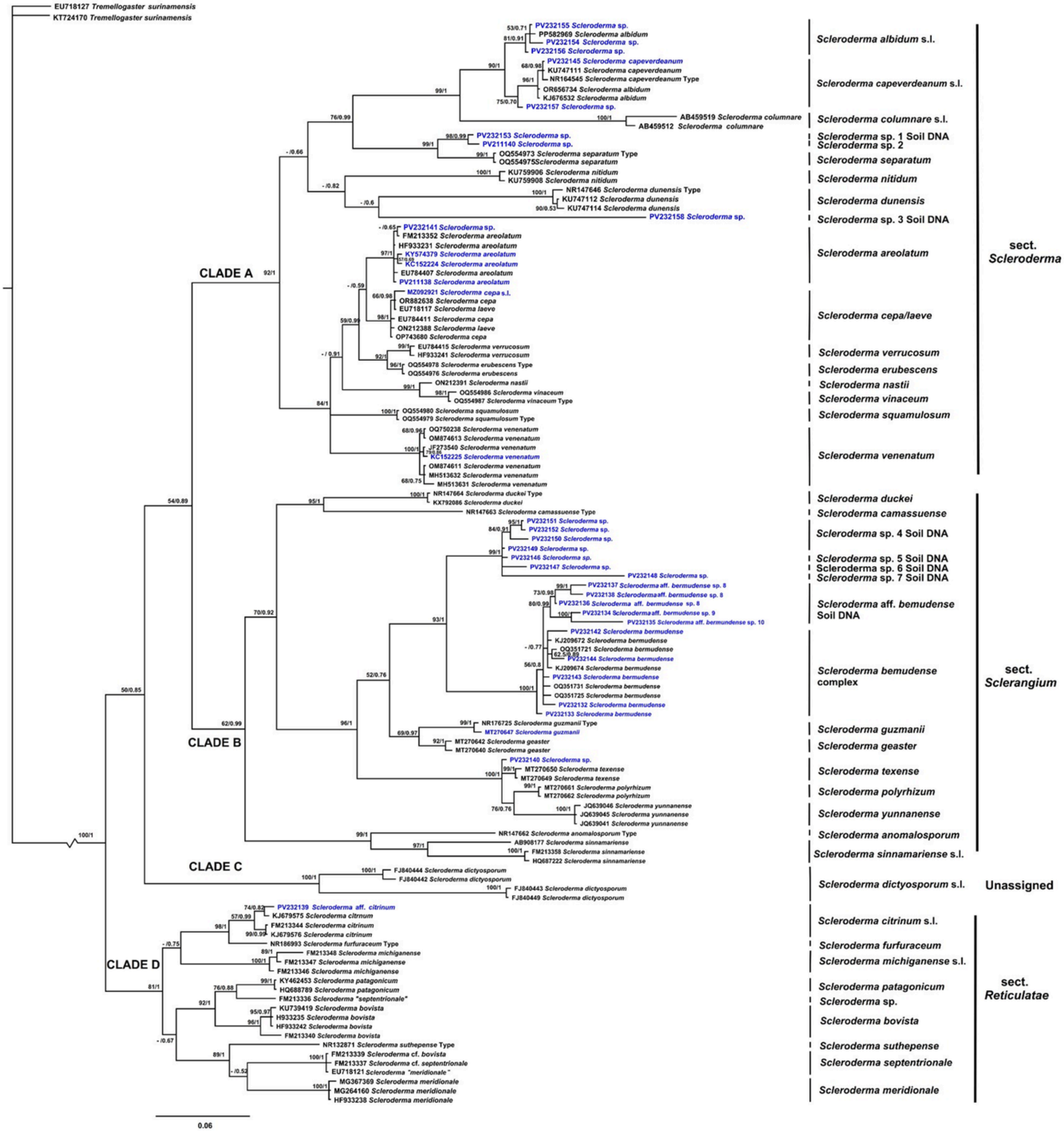

Figure 2. Phylogenetic analysis of the nrITS DNA sequences of *Scleroderma* obtained through ML and Bayesian analysis. The dash (-) indicates likelihood values less than 50 and posterior probabilities less than 0.5. Names in blue represent sequences of Mexican specimens or environmental DNA.

Table 2

Distribution and abundance of *Scleroderma* species obtained from soil samples.

Species	Distribution	Abundance (Number of sequences)	Number of sites in Mexico
Scleroderma albidum s.l.	Estado de México	5	1
Scleroderma areolatum	Michoacán	5	1
Scleroderma bermudense	Quintana Roo and Yucatán	164	2
Scleroderma aff. *bermudense* sp. 8	Morelos, Estado de México, Quintana Roo, and Yucatán	3,877	5
Scleroderma aff. *bermudense* sp. 9	Yucatán	1	1
Scleroderma aff. *bermudense* sp. 10	Yucatán	10	1
Scleroderma capeverdeanum s.l.	Hidalgo and Estado de México	74	2
Scleroderma aff. *citrinum*	Hidalgo	1	1
Scleroderma texense	Veracruz	35	2
Scleroderma sp. 1	Veracruz	3	1
Scleroderma sp. 3	Campeche and Quintana Roo	3	2
Scleroderma sp. 4	Campeche, Michoacán and Yucatán	33	8
Scleroderma sp. 5	Campeche and Yucatán	33	5
Scleroderma sp. 6	Yucatán	1	1
Scleroderma sp. 7	Campeche and Yucatán	5	3

Table 3

Distribution of *Scleroderma* species in different types of vegetation.

Species	Type of vegetation
Scleroderma albidum s.l.	Tropical coniferous forest
Scleroderma areolatum	Tropical broadleaf forest
Scleroderma bermudense	Subtropical broadleaf forest
Scleroderma aff. *bermudense* sp. 8	Tropical broadleaf forest, subtropical broadleaf forest and tropical coniferous forest
Scleroderma aff. *bermudense* sp. 9	Subtropical broadleaf forest
Scleroderma aff. *bermudense* sp. 10	Subtropical broadleaf forest
Scleroderma capeverdeanum s.l.	Tropical coniferous forest and subtropical coniferous forest
Scleroderma aff. *citrinum*	Subtropical broadleaf forest
Scleroderma texense	Tropical coniferous forest
Scleroderma sp. 1	Tropical coniferous forest
Scleroderma sp. 3	Tropical broadleaf forest and subtropical broadleaf forest
Scleroderma sp. 4	Tropical broadleaf forest, subtropical broadleaf forest, and tropical coniferous forest
Scleroderma sp. 5	Tropical broadleaf forest and subtropical broadleaf forest
Scleroderma sp. 6	Subtropical broadleaf forest
Scleroderma sp. 7	Tropical broadleaf forest and subtropical broadleaf forest

studies have reported that *S. bermudense* represents one of the most abundant endemic taxa in the Caribbean, mainly associated with *Coccoloba uvifera* (Bâ et al., 2024; Põlme et al., 2017). This association is mediated by the environmental stress of the coastal dunes where they develop, which causes a high specificity of the symbiosis (Bâ et al., 2024; Põlme et al., 2017). We found several clades of *S. bermudense* s.l. with high genetic differentiation not associated with *Coccoloba* species. Thus, there is a species complex associated with *S. bermudense* with an unsolved taxonomy and ecology in the Yucatán Peninsula.

Species such as *S. areolatum* and *S. cepa* have been recorded throughout the country through their basidiomes (Guzmán & Herrera, 1973; Guzmán et al., 2013). *Scleroderma areolatum* was reported from Durango, Guerrero, Hidalgo, Jalisco, México City, Michoacán, Nuevo León, Oaxaca, Puebla, and Veracruz (Guzmán & Herrera, 1973). Through ITS analysis it has been confirmed that *S. cepa* s.l. is an ectomycorrhizal symbiont of pecan trees in Chihuahua and Coahuila and that it is possibly a species complex (Sánchez-Ledesma et al., 2023). However, the type specimens of both species have not been sequenced, so it is important to carry out their type studies given the importance they can have in agroecosystems. In fact, species complexes indicating cryptic lineages in fungi are common (Sánchez-Ramírez, 2015) and may include taxa that can be morphologically distinguished, as well as cryptic species that are only discernible through molecular data, as this study found for the *S. albidum*, *S. bermudense*, and *S. cepa* complexes.

We recorded for the first time *S. venenatum* in Mexico, a species considered toxic in China (Zhang et al., 2020). The presence of this species in the country is particularly relevant given that some *Scleroderma* species are traditionally consumed in Mexico. For example, the consumption of *S. laeve* has been reported in Morelos and *S. texense* in Oaxaca (Cortés-Pérez et al., 2021; De Ávila et al., 1980). In contrast, *S. venenatum* was recorded in Querétaro and can be distinguished from edible species by its sessile, brown to grayish brown basidiomes and well-developed rhizomorphs (Zhang et al., 2020). Regarding the identity of the species that have been reported as edible in Mexico, their identification was only carried out with morphology and given their importance in cultural contexts, it would be advisable to obtain molecular data from the basidiomes to corroborate their identity.

A higher diversity of *Scleroderma* in the Transmexican Volcanic Belt shows that, while for other organisms the system represents a barrier or a filter, fungi use it as a corridor (Gómez-Reyes et al., 2018). In this region, the complex topography, habitat variability, and the convergence between Nearctic and Neotropical biota contribute to a higher diversity of fungal species in general (Cifuentes-Blanco et al., 1997) and in particular for *Scleroderma*.

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