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Review Article

Global Record, Distribution, Ectomycorrhizal, and Bioactivity Profile of the *Scleroderma* Mushrooms: A Review

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Abstract

Scleroderma, commonly known as "False truffles", is a sapotrophic-ectomycorrhizal fungus known as a poisonous puffball mushroom, displays interesting medicinal properties, and some species are traditionally consumed in different countries. This paper aims to synthesize and assess the distribution, edibility, ectomycorrhizal, cultivation, mycochemical, and bioactivities of *Scleroderma* mushrooms. In this review, a total of 73 species were recorded and studied, and *Scleroderma citrinum* was the most extensively studied and distributed in 16 countries. Significantly, Brazil and Mexico have the highest diversity of *Scleroderma*, with 21 identified species. The *Scleroderma* species, which has been reportedly edible in some countries, has a significant impact on socio-economic growth. Ecologically, *Scleroderma* mushrooms have ectomycorrhizal characteristics, which significantly increase plant health. Moreover, *Scleroderma* mushrooms are reported to be a source of bioactive compounds, and the most commonly detected are triterpenoids. This group of metabolites exhibits a range of biological activities such as antimicrobial, antioxidant, anti-inflammatory, antiproliferative, cytotoxicity, and antiprotozoan properties. These bioactivities highlight the potency of *Scleroderma* species as promising sources of therapeutic agents, despite existing limitations in cultivation and edibility. Furthermore, this review offers an in-depth examination and documentation of *Scleroderma* species, focusing on their ecological importance and exploring their prospective uses in medicine, bioremediation, environmental sustainability, and the eventual development of *Scleroderma*-based products.

Keywords: Bioactivities; Ectomycorrhizal; Metabolites; *Scleroderma*

Introduction

Fungi are the second-largest group of microorganisms, comprising approximately 11.7 to 13.2 million species; however, they have not been fully explored and studied, and only about 150,000 species have been examined (Wu *et al*. 2019). Mushrooms are classified as edible and non-edible, poisonous and non-poisonous, palatable and non-palatable. They are divided into Basidiomycotous and Ascomycotous macrofungi, wood-rotting or leaf-litter, or use a symbiotic relationship, such as parasitic, saprophytic, and mycorrhizal. Fungi can produce fruiting bodies, which are often called "mushrooms," and can be seen with the naked eye. These mushrooms have been used for over a thousand years in commercial food, medicine, and industrial applications. It contains a wide variety of proteins, fiber, carbohydrates, and minerals (Dulay *et al*. 2023).

One of the mechanisms of macrofungi is to establish symbiotic relationships with different host plants. Ectomycorrhizal fungi derive their carbon from host plants and, in exchange, assist the plants in absorbing water and nutrients from the soil (Karun *et al*., 2022). Aside from exchanging water, minerals, and salts, ectomycorrhizal fungi show a significant development in mycoremediation as they bind huge amounts of heavy metals and reduce the concentration before the host plant accumulates (Krupa and Kozdrój 2006). Different macrofungi display ectomycorrhizal (ECM) mechanisms, such as *Lactarius* sp., *Thelephora* sp., and, specifically, *Scleroderma* species (Kumar and Atri 2023).

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The *Scleroderma* genus, from the family Sclerodermataceae, is often called earthballs and is a class of ectomycorrhizal fungi. This genus is recognizable by its macroscopic sporocarp, which is a tough brown outer layer and dark or white, spore-filled interior; it differs from puffballs or *Lycoperdon* (Sebek 1953; Jeffries 1999). *Scleroderma* species typically grow in forests and woodlands, favoring acidic to neutral soils. Although not commonly consumed due to potential toxicity, they play a crucial ecological role in nutrient cycling and maintaining soil health.

The *Scleroderma* species offer a wide range of uses such as some species are edible, environmental management, biological activities, and applications for forestry. Among the species of *Scleroderma, Scleroderma citrinum* is widely studied with respect to distribution, ectomycorrhizal properties, edibility, cultivation, and biological activities. *S. citrinum* is reported to display different bioactivities such as antioxidant, antibacterial properties, antifungal activity, bioremediation strategies, antiviral activity, and cytotoxicity. Additionally, thrombolytic activity, low LC50 (edible), and plant protection activity are also present in some species of *Scleroderma* (Soytong *et al*. 2014; Łopusiewicz 2018; Culliao *et al*. 2020; Cullings *et al*. 2023).

Despite the abundance of studies on *Scleroderma* mushrooms, there is a significant gap in the scientific understanding of their full capabilities and potential as edible mushrooms and medicine. This article provides a compilation of existing and available information on *Scleroderma* mushrooms to present a comprehensive overview of the global status of these mushrooms, including their global distribution, ectomycorrhizal impact, cultivation, applications, and potential uses to answer sustainable development goals.

Species checklist, diversity, and distribution of *Scleroderma* species

Mushroom distribution is determined by a combination of nutritional and physical factors. They require specific substrates (like decaying wood or leaves) and are highly sensitive to temperature, humidity, substrate composition, elevation, and climate conditions. *Scleroderma* species grow in tropical and temperate climates and are mostly associated with host plants that form ectomycorrhizal symbiosis. Earthballs, or *Scleroderma* mushrooms, grow best in well-drained, organic-rich soils and commonly form symbiotic relationships with trees such as pines, oaks, and birches. They thrive in temperate areas with mild to warm temperatures, sufficient moisture, and stable weather conditions. They adapt to different elevations found in forests and woodlands and are most active during optimal seasons like late summer to fall, favoring soils with an acidic to neutral pH. The *Scleroderma* fruiting bodies develop as a ball-like structure resembling the truffles (*Tuber* sp.) called "False Truffles" (Fig. 1). The species distribution of *Scleroderma* across the different climatic regions is due to the varied environmental preferences of species within the genus. This adaptability is further enhanced by their morphological features, such as basidiospores, which facilitate efficient reproduction through wind dispersion, thereby improving their chances of survival and colonization. In this review article, a total of 73 species of *Scleroderma* were recorded from different authors and studies conducted around the world, such as identification, distribution, morphological study, and bioactivity profiling (Table 1).

Fig. 1: *Scleroderma* spp. specimen from the Philippines

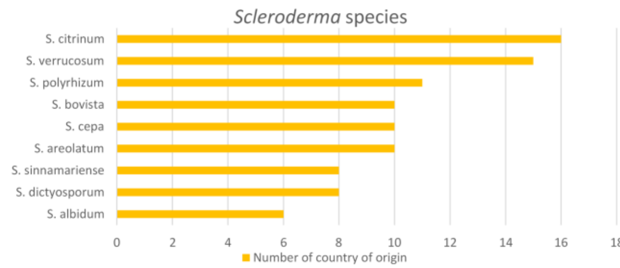


Fig. 2: Most widely distributed *Scleroderma* species worldwide

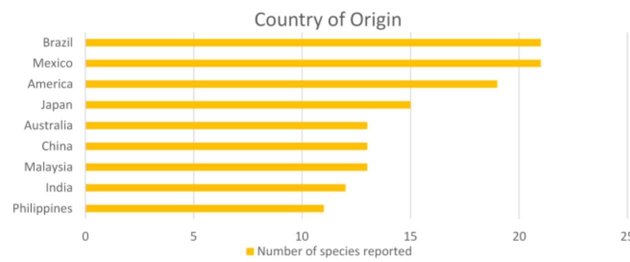


Fig. 3: The top countries with the greatest number of reported *Scleroderma* species

In Table 2, the list of *Scleroderma* species acquired from the Mycobank database with no reported studies was 38. In the Mycobank database, the total number of *Scleroderma* species was 111. In the reported species, *S. citrinum* or the "common earthball" was the most distributed (16 countries), followed by *S. verrucosum* (15 countries), *S. polyrhizum* (11 countries) and *S. cepa*, *S. bovista*, and *S. areolatum* (10 countries), *S. sinnamariense* and *S. dictyosporum* (8 countries) and *S. albidum* (6 countries) (Fig. 2-3).

Among the countries, the highest number of reported studies and recorded species was in Mexico and Brazil (21 species), followed by America (US) (19 species), Japan (15 species), Australia, China, Malaysia (13 species), India (12 species), and the Philippines (11 species). The distribution of *Scleroderma* species is shown in the geographical figure.

Table 1: Checklist of different species of *Scleroderma* and their country of origin

Scleroderma species	Country of origin	Reference
S. albidum Pat. & Trab.	Mexico	Guzmán *et al*. (2013)
	Brazil	Gurgel *et al*. (2008); Trierveiler-Pereira and Basaeia (2009); Montagner *et al*. (2015)
	Argentina	Nouhra *et al*. (2012)
	Japan	Yoshimi (2002); Sato *et al*. (2019)
	Australia	Chen (2006)
	America	Gibson (2003)
S. anomalosporum Baseia, B.D.B. Silva & M.P. Martín	Brazil	Baseia *et al*. (2016); Almeida *et al*. (2021)
S. arenicola Zeller	Mexico	Guzmán *et al*. (2013)
	Canada	Hutchison (1990)
S. areolatum Ehrenb	Argentina	Nouhra *et al*. (2012)
	China	Chen (2006); Wu *et al*. (2019)
	Australia	Chen (2006)
	Slovenia	Mrak *et al*. (2017)
	Oregon, America	Gibson (2003)
	Brazil	Giachini *et al*. (2000)
	Japan	Yoshimi (2002)
	Colombia	Pinzón-Osorio *et al*. (2018)
	Ghana	Annang *et al*. (2018)
	India	Karun *et al*. (2022)
S. aurantium (L.) Pers.	The Czech Republic	Vrkoč *et al*. (1976)
	Japan	Kardono *et al*. (2002)
	Indonesia	Khilafah and Widodo (2023)
	Malaysia	Chin (1988)
	India	Gardezi (2005)
S. aurantiacum Pers. ex Sacc.	Philippines	Reynolds (1967)
	Germany	Hartwich (1915)
	England	Lloyd (1905)
	Massachusetts, US	Lloyd (1905)
	Singapore	Chipp (1921)
S. bermudense Coker	Mexico	Guzmán *et al*. (2013)
	Bermuda, UK	Coker (1939)
	France	Bandou *et al*. (2006)
S. bougheri Trappe, Castellano & Giachini	Brazil	Giachini *et al*. (2000)
S. bovista Fr.	Mexico	Guzmán *et al*. (2013)
	Argentina	Nouhra *et al*. (2012)
	Philippines	Quimio and Capilit (1981)
	Brazil	Giachini *et al*. (2000); Gurgel *et al*. (2008)
	China	Chen (2006)
	Australia	Chen (2006)
	Germany	Hartwich (1915)
	United States	Dunaway *et al*. (2015)
	India	Patel and Rajput (2023)
	Japan	Yoshimi (2002); Ishida *et al*. (2008)
S. camassuense Martín, Baseia & Silva	Brazil	Baseia *et al*. (2016)
S.capeverdeanum Martín, Dueñas & Tellería	Cape Verde, Africa	Crous *et al*. (2016)
	Japan	Kasuya *et al*. (2022)
S. cepa Pers.	Mexico	Guzmán *et al*. (2013)
	China	Chen (2006)
	Sydney, Australia	Chen (2006)
	US	Lloyd (1905); Gibson (2003)
	New Zealand	Lloyd (1905)
	Brazil	Giachini *et al*. (2000)
	Pakistan	Yousaf *et al*. (2013)
	Japan	Yoshimi (2002)
	Philippines	Sims *et al*. (1997)
	India	Karun *et al*. (2022)
	Nepal	Jha and Thapa (2025)
S. citrinum G.W Martin	Mexico	Guzmán *et al*. (2013)
	South Africa	Rasalanavho (2021)
	Argentina	Nouhra *et al*. (2012)
	France	Huguet *et al*. (2022)
	Philippines	Leon *et al*. (2013, 2016); Culliao *et al*. (2020)
	Brazil	Giachini *et al*. (2000); Gurgel *et al*. (2008); Montagner *et al*. (2015)
	China	Chen (2006)
	Australia	Chen (2006)
	Germany	Loderer and Ansorge-Schumacher (2016)

Table 1: Continued

Table 1: Continued

	Indonesia	Sufaati *et al.* (2023)
	Malaysia	Chin (1988)
	Thailand	Kanokmedhakul *et al.* (2003); Soytong *et al.* (2014)
	WY, USA	Richter and Bruhn (1990); Gibson (2003); Cullings *et al.* (2023)
	India	Sindhu and Manorama (2014); Mohan *et al.* (2015); Borthakur and Joshi (2018)
	Poland	Łopusiewicz (2018)
	Japan	Yoshimi (2002)
S. columnare Berk. & Broome	Malaysia	Cesati (1879); Lee *et al.* (2002); Salleh *et al.* (2002); Lee (2005)
	Indonesia	Supriyanto (1999); Turjaman *et al.* (2006); Febriani *et al.* (2017); Kusuma *et al.* (2018)
	Thailand	Yomyart (2008)
	India	Kumar and Singh Atri (2023)
	Sri Lanka	Petch (1919)
	Philippines	Sims *et al.* (1997)
S. congolense Demoulin & Dring	Congo, Africa	Demoulin and Dring (1971)
S. cyaneoperidiatum Watling & Sims	Malaysia	Watling *et al.* (2004)
S. dictyosporum Pat.	Philippines	Reynolds (1967); Quimio and Capilit (1981); Sims *et al.* (1997)
	France	Sanon *et al.* (2010)
	Burkina Faso, Africa	Duponnois *et al.* (2006); Sanon *et al.* (2009)
	Tanzania	Maghembe and Redhead (1984)
	Malaysia	Lee (2005); Watling *et al.* (2004)
	Japan	Yoshimi (2002)
	India	Karun *et al.* (2022)
S. duckei Silva, Martín & Baseia	Brazil	Baseia *et al.* (2016)
S. dunense Silva, Sulzbacher, Grebenc, Baseia & Martín	Brazil	Crous *et al.* (2016); Lima and Baseia (2018)
S. echinatum (Petri) Guzmán	Borneo	Guzmán *et al.* (2004)
	Panama	Guzmán *et al.* (2004)
	Malaysia	Watling *et al.* (2004); Lee *et al.* (2002); Lee (2005)
S. echinosporites Rouse	Canada	Rouse (1962)
S. endoxanthum Petch	Sri Lanka	Petch (1919)
S. erubescens Ge, Wu & Zhou	Yunnan, China	Wu *et al.* (2023)
S. flavidum Ellis & Everh.	Melbourne, Australia	Lloyd (1905)
	Canada	Jones *et al.* (1988)
	Malaysia	Chipp (1921)
	Hokkaido, Japan	Kasuya (2024)
S. flavocrocatum Sacc. & De Toni	Philippines	Reynolds (1967); Quimio and Capilit (1981)
	Malaysia	Chipp (1921)
S. floridanum Guzmán	Oregon, America	Gibson (2003)
	Brazil	Gurgel *et al.* (2008)
S. franceschii Macchione	Italy	Macchione (2000)
S. furfuraceum Macchione	Russia	Rebriev and Zvyagina (2022)
S. furfurellum Zeller	Mississippi, US	Zeller (1947)
S. fuscum (Wallr.) Fisch.	Mexico	Guzmán *et al.* (2013)
	Brazil	Gurgel *et al.* (2008)
	Oregon and Washington America	Gibson (2003)
S. geaster Fr.	Spain	Ortiz-Rivero *et al.* (2021)
	Australia	Lloyd (1905)
	New Jersey, US	Lloyd (1905)
S. guzmanii Ortiz-Rivero, Watling, Guzm. Dáv. & M.P. Martín	USA	Ortiz-Rivero *et al.* (2021)
S. hakkodense Kobayasi	Japan	Kobayasi (1986)
S. hypogaeum Zeller	India	Tapwal *et al.* (2021)
	Mexico	Guzmán *et al.* (2013)
	Oregon, Idaho, and Washington America	Gibson (2003)
S. laeve Lloyd	Mexico	Guzmán *et al.* (2013); Cortés-Pérez *et al.* (2021)
	Oregon, Idaho, and Washington, America	Gibson (2003)
	Brazil	Pereira *et al.* (2014)
	Japan	Kasuya *et al.* (2002)
	South Korea	Cho *et al.* (2022)
S. leptopodium Pat. & Har.	Malaysia	Lee *et al.* (2002); Lee (2005)
	Philippines	Sims *et al.* (1997)
S. lycoperdoides Schwein.	Brazil	Bulmer and Beneke (1964)
	Indonesia	Kurnia (2014)

Table 1: Continued

Table 1: Continued

S. macrosporum (Cunn.) Cooper	New Zealand	Cunningham (1931a)
S. mcalpinei (Rodway) Castellano	Australia	Sheedy *et al*. (2016)
S. meridionale Demoulin & Malençon	Australia	Chen (2006)
	Oregon, America Mississippi, America	Guzman and Ovrebo (2000); Gibson (2003)
	America (Southeast)	Dunaway *et al*. (2015)
	Italy	Leonardi *et al*. (2018)
S. mexicana Guzmán & Tapia	Mexico	Guzmán *et al*. (2013)
S. michiganense (Guzmán) Guzmán	Mexico	Guzmán *et al*. (2013)
	India	Sindhu and Manorama (2014)
	Africa	Rasalanavho (2021)
S. minutisporum Baseia, Alfredo & Cortez	Brazil	Alfredo *et al*. (2012)
S. multiloculare Dring & Rayss	Egypt	Mouchacca (2016)
	Israel	Dring and Rayss (1963)
S. nastii Raut	Nepal	Raut *et al*. (2020)
S. nitidum Berk.	Mexico	Guzmán *et al*. (2013)
	Brazil	Gurgel *et al*. (2008); Nascimento *et al*. (2012)
	South Korea	Cho *et al*. (2022)
S. pantherinum Mattir.	Congo, Africa	Mattirolo (1923); Dissing and Lange (1962)
S. paradoxum Beaton	Australia	Chen (2006); Beaton and Weste (1982)
	Russia	Burtsev (2014)
S. patagonicum Nouhra & Hernández Caffot	Argentina	Nouhra *et al*. (2012)
S. polyrhizum (J.F. Gmel.) Pers.	Spain	Ortiz-Rivero *et al*. (2021); Díez *et al*. (2000)
	Mexico	Guzmán *et al*. (2013)
	Brazil	Baseia and Milanez (2000)
	Australia	Chen (2006)
	China	Xianling *et al*. (2005); Chen (2006)
	Oregon, America	Gibson (2003)
	America (Southeast)	Dunaway *et al*. (2015)
	Japan	Yoshimi (2002)
	India	Tapwal *et al*. (2021); Karun *et al*. (2022)
	Nepal	Christensen *et al*. (2008)
	Philippines	Paderes and Bernal (2020)
S. pseudostipitatum Petch	Mexico	Guzmán *et al*. (2013)
	Sri Lanka	Petch (1919)
S. radicans Lloyd	India	Harsh *et al*. (1996)
	Australia	Cunningham (1931b)
	Japan	Yoshimi (2002)
S. reae Guzmán	Mexico	Guzmán *et al*. (2013)
	Japan	Yoshimi (2002)
S. schmitzii Demoulin & Dring	Africa	Demoulin and Dring (1971)
S. separatum Ge, Wu & Zhou	Yunnan, China	Wu *et al*. (2023)
S. septentrionale Jeppson	Finland, Denmark, Sweden, Iceland	Jeppson (1998)
	Poland	Jeppson and Piątek (2005)
	Australia	Chen (2006)
	Massachusetts and Michigan, USA	Guzman and Ovrebo (2000)
S. sinnamariense Mont.	Mexico	Guzmán *et al*. (2013)
	Costa Rica	Guzman and Ovrebo (2000)
	Thailand	Siri-in *et al*. (2014)
	Indonesia	Khastini *et al*. (2022); Sufaati *et al*. (2023)
	Malaysia	Chipp (1921); Lee *et al*. (2002); Lee (2005)
	Philippines	Sims *et al*. (1999)
	Nepal	Christensen *et al*. (2008)
	Japan	Yoshimi (2002)
S. squamulosum Ge, Wu & Zhou	Yunnan, China	Wu *et al*. (2023)
S. stellatum Berk.	Mexico	Guzmán *et al*. (2013)
	Brazil	Guzmán *et al*. (2004)
S. suthepense Kumla, Suwannarach & Lumyong	Thailand	Kumla *et al*. (2013a)
	Indonesia	Sufaati *et al*. (2023)
	China	Zhang *et al*. (2020)
S. tenerum Berk. & Curtis	Mexico	Guzmán *et al*. (2013)
	Australia	Lloyd (1905)
S. texense Berk.	Mexico	Cortés-Pérez *et al*. (2021)
	Germany	Stump *et al*. (2001)
	Pennsylvania, US	Lloyd (1905)
	India	Karun *et al*. (2022)
S. torrendii Bres.	Portugal	Bresadola (1902)
S. tuberoideum Speg.	São Paulo, Brazil	Bononi *et al*. (1981)

Table 1: Continued

Table 1: Continued

S. uruguayense (Guzmán) Guzmán	Brazil	Giachini *et al*. (2000); Mamede (2012)
S. venenatum Zhang, Sun & Hai	China	Zhang *et al.* (2020)
S. verrucosum (Bull.) Pers.	Mexico	Guzmán *et al.* (2013)
	Philippines	Reynolds (1967); Quimio and Capilit (1981); Tadiosa and Lubos (2019)
	Brazil	Giachini *et al*. (2000); Montagner *et al*. (2015)
	Australia	Chen (2006)
	China	Chen (2006)
	France	Sanon *et al*. (2010)
	Malaysia	Lee (2005)
	Turkey	Yayli *et al.* (2007)
	New Zealand	Lloyd (1905)
	Idaho, US	Gibson (2003)
	Chile, America (Southeast)	Machuca *et al.* (2007); Dunaway *et al.* (2015)
	India	Karun *et al.* (2022)
	Tunisia, Africa	Ali and Aschi-Smiti (2013)
	Japan	Yoshimi (2002)
	Nepal	Christensen *et al*. (2008)
S. vinaceum Ge, Wu & Zhou	Yunnan, China	Wu *et al*. (2023)
S. vulgare Fr.	Mexico	Guzmán *et al*. (2013)
	Malaysia	Chipp (1921)
S. xanthochroum Watling & Sims	Malaysia	Watling *et al.* (2004)
	Indonesia	Sufaati *et al*. (2023)
S. yunnanense Wang	Yunnan, China	Zhang *et al*. (2013)
	Japan	Kasuya *et al.* (2023)
	India	Tudu *et al*. (2024)

Table 2: List of *Scleroderma* species in MycoBank Database with no reported studies

S. ambiguum Petri	*S. pandanaceum* F. Muell.
S. anomalum Ces.	*S. patens* Lloyd
S. arrhizum (Scop.) Pers.	*S. pedunculatum* Link
S. aureum Massee	*S. phaeotrichum* (Berk.) De Toni
S. australe Massee	*S. pileolatum* Kalchbr.
S. bulla R. Heim	*S. pisiforme* Henn.
S. caespitosum Lloyd	*S. poltaviense* Sosin
S. callostoma Pers.	*S. pyramidatum* Kalchbr.
S. capensis Lloyd	*S. radicatum* (Durieu) De Toni
S. cervinum Pers.	*S. rhodesicum* Verwoerd
S. chevalieri Guzmán	*S. sapidiforme* Sosin
S. chrysastrum G.W. Martin	*S. spinulosum* (Peck) De Toni
S. chrysosporum Opiz	*S. squamatum* Chevall.
S. dugesii De Seynes	*S. stellenbossiense* Verwoerd
S. hemisphaericum Lázaro Ibiza	*S. tuberosum* Spreng.
S. lanosum Pat.	*S. umbrinum* Cooke & Massee
S. macrorrhizon Wallr.	*S. venosum* Boud.
S. martinicense Pat.	*S. violaceum* Lloyd
S. mayama Grgur.	*S. zenkeri* Henn.

Furthermore, 47 out of 195 countries around the world show recorded sightings of *Scleroderma* species, which gives 24.10% of the world's land countries. The distribution of *Scleroderma* species is shown in the geographical map (Fig. 4).

In some studies, such as Chua *et al.* (2012), only recorded distribution in one country, like Malaysia, with different species of *Scleroderma*. The different studies suggest only one to three countries of distribution, while in this review, the species of *Scleroderma* around the world were reviewed and allocated. *Scleroderma* species are widely distributed, especially in regions with tropical and temperate regions. The top countries with the highest number of reported *Scleroderma* mushrooms are in the tropical to temperate zones.

Moreover, the geographical map shows that the Asian regions have the most widespread distribution. It can be seen that they are most prevalent in Southeast Asia, which is known for having a tropical climate. However, *Scleroderma* species can also thrive in other temperate regions like Japan and China, since *Scleroderma* species were reported to withstand different temperatures (Jeffries 1999). Therefore, one factor that influences the distribution and diversity of *Scleroderma* species is the climatic conditions of their geographic origin. The most crucial factor to take into consideration is the number of mycologists and taxonomists in different countries. The majority of *Scleroderma* species are known to exist in Brazil due to the extensive studies conducted specifically on *Scleroderma* species and mushroom puffball biodiversity, specifically its usage in different indigenous groups. Based on the list of species presented in this paper, studies on the identification and morphology of *Scleroderma* species and their distribution

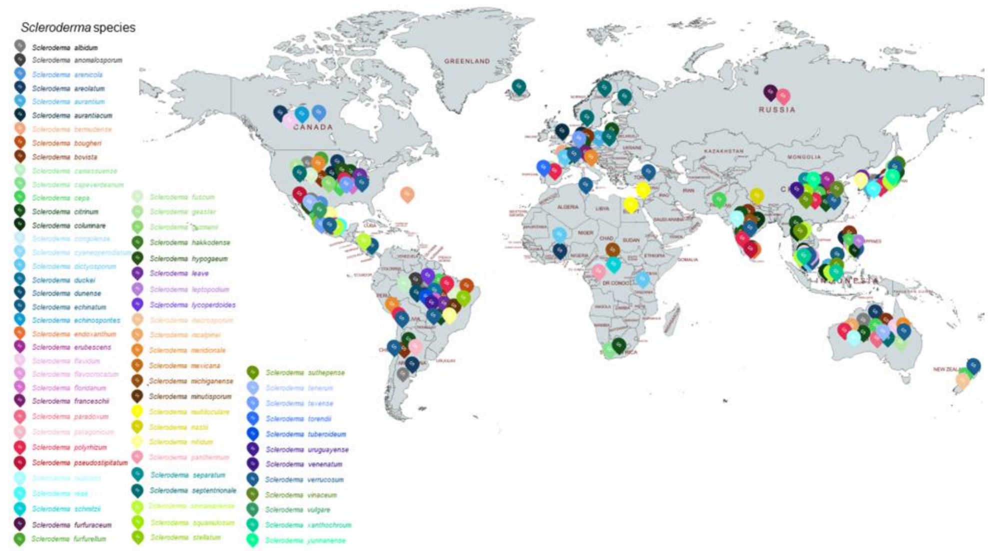


Fig. 4: Geographical distribution of *Scleroderma* species worldwide

have already started in the year 1870, and newly discovered species are being identified. Furthermore, *Scleroderma* studies progress over the years and more precise identification and characterization methods are being developed. Most importantly, the identification of edible species is being studied in Asian regions, enabling the establishment of updated species listings.

Table 3 shows the re-ordered species of *Scleroderma* to different genera or renamed species due to their similar morphological and molecular identification. Genera such as *Lycoperdon* (6 species), *Mycenastrum* (6 species), *Pisolithus*, (2 species), *Sclerangium* (2 species), *Bovista* (2 species), *Podaxis* (2 species), *Actigea* (2 species), *Phellorinia* (2 species), *Hydnangium* (2 species), *Veligaster* (2 species), and *Elaphomyces* (2 species) were species that were re-ordered to different genera. These species were re-ordered due to similarities in structure that were identified at first. The difficulty of identification through the years led to the re-ordering of *Scleroderma* since these species appeared similarly as ball-like morphology. Additionally, the availability of a molecular approach to construct a phylogenetic analysis of *Scleroderma* sp. is still developing up to the present.

Edibility and socio-economic impact

Scleroderma mushrooms are generalized to be poisonous; however, it also a delicacy in some countries, particularly in rural or developing areas in some countries, and offer a socio-economic factor as they become a sustainable source of food and nutrition in low-income populations and marginalized groups due to their convenience. It also supports environmental sustainability, as one of the bioactivities of *Scleroderma* mushrooms is bioremediation and an ectomycorrhizal role. In different countries, the *Scleroderma* species are considered to be inedible or poisonous, but different reports of this species are being edible in other countries, such as the new species including *S. yunnanense* in China and India (Zhang *et al*. 2023; Tudu *et al*. 2024), *S. texense* in Mexico (Cortés-Pérez *et al*. 2021), and *S. cepa* (Jha and Thapa 2025) as edible in Nepal. However, Ávila *et al*. (1980) reported *S. laeve* as edible in Morelos, but Cifuentes *et al*. (1993) stated that all species in Guerrero, Mexico, are toxic. In a confusing report, Christensen *et al.* (2008) considered *S. sinnamariense*, *S. polyrhizum*, and *S. verrucosum* to be edible. Sebek (1953) reported that early stages of *Scleroderma* were used to adulterate truffles. Cases of *Scleroderma* poisoning were reported in Japan with *S. albidum* that contains sclerocitrin, which induces muscarinic effects and is toxic to the central nervous system (Sato *et al*. 2019) when consumed in significant amounts. In recent years, the appearance of *S. yunnanense* has contributed significantly to the study of *Scleroderma*, revealing that this species is edible in parts of China (Zhang *et al*. 2013) and India (Tudu *et al*. 2024). In some regions of the Philippines, edible *S. citrinum* species or "buo" (Leon *et al*. 2016) are foraged and sold in the local community, providing an additional source of income for rural populations, particularly during rainy seasons from the month of June to December.

These species form symbiotic relationships with forest trees that improve soil quality and plant growth, aiding a sustainable forestry that enhances forest productivity and biodiversity, which indirectly supports local economies. Although not as widely cultivated as other domesticated mushrooms, *Scleroderma* species holds potential in niche markets where they are traditionally consumed. Moreover, ongoing research into their use in biotechnology and microbiology, such as biofertilizers and natural compounds, suggests possible future industrial applications. Overall, *Scleroderma* contributes both ecologically and economically, especially in sustainable land use, rural and socio-cultural development.

Table 3: List of re-ordered *Scleroderma* species from MycoBank

Scleroderma species	Current Name
S. arhizum	*Pisolithus arhizus* (Scop.)
S. aurantium	*Lycoperdon aurantium* L.
S. aurantium var. *macrorhizum*	*S. vulgare var. macrorhizum* Fr.,
S. aurantium var. *spadiceum*	*Lycoperdon spadiceum* Schaeff.
S. beccarii	*Mycenastrum beccarii* Pass.
S. bermudense	*Sclerangium bermudense* (Coker) D.A.
S. bovistoides	*Bovista bovistoides* Cooke & Massee
S. bovonei	*Corditubera bovonei* Mattir.
S. bresadolae	*Lycoperdon pyriforme* Schaeff.
S. carcinomale	*Podaxis carcinomalis* (L. f.) Fr.
S. cepa var. *maculatum*	*S. maculatum* (Peck) Lloyd
S. cepioides	*S. cepa* Pers.
S. chilense	*Mycenastrum chilense* Mont.
S. coelatum	*Glyptoderma coelatum* (Pat. ex R. Heim) R. Heim & Perr.-Bertr.
S. cookei	*Bovista paludosa* Lév.
S. corium	*Mycenastrum corium* (Guers.) Desv.
S. dunensis	*S. dunense* B.D.B. Silva, Sulzbacher, Grebenc, Baseia & M.P. Martín
S. echinatum	*Caloderma echinatum* Petri
S. flavidum f. multifidum	*Actigea multifida* Raf.
S. flavidum f. *macrosporum*	*S. macrosporum* (G. Cunn.) J.A. Cooper
S. fragile	*Gastropila fragilis* (Lév.)
S. fuscum	*Tuber excavatum* Vittad.
S. geaster	*S. polyrhizum* (J.F. Gmel.) Pers.
S. geaster var. *siculum*	*Actigea sicula* Raf.
S. herculaneum	*Phellorinia herculeana* (Pers.)
S. leiospermum	*Mycenastrum lejospermum* Mont.
S. lycoperdoides	*S. areolatum* Ehrenb
S. lycoperdoides var. *reticulatum*	*S. citrinum* var. *reticulatum*
S. macalpinei	*Hydnangium macalpinei* Rodway
S. mcalpinei	*Hydnangium macalpinei* Rodway
S. michelii	*Sclerangium michelii* Lév.
S. michiganense	*S. hypogaeum* var. *Michiganense* Guzmán
S. nitidum	*Veligaster nitidus* Berk.
S. ohiense	*Mycenastrum ohiense* Ellis & Morgan
S. olivaceum	*Mycenastrum olivaceum* Cooke & Massee
S. oregonense	*Bovista pila* Berk. & M.A.
S. pistillare	*Podaxis pistillaris* (L.) Fr.
S. polyrhizon	*Scleroderma polyrhizum* (J.F. Gmel.) Pers.
S. pteridis	*Astraeus pteridis* (Shear) Zeller
S. sapidum	*Pompholyx sapidum* Corda
S. septentrionalis	*S. septentrionale* Jeppson
S. spadiceum	*Lycoperdon spadiceum* Schaeff.
S. strobilinum	*Phellorinia herculeana* Pers.
S. subviscidum	*Elaphomyces subviscidus* Zeller
S. tenerum	*Veligaster nitidus* (Berk.) Guzmán & Tapia
S. texense	*S. bovista* Fr.
S. tinctorium	*Pisolithus arhizus* Scop.
S. uruguayense	*S. citrinum* var. *uruguayense* Guzmán

Nutritional prospects

Beyond their pharmaceutical potential, mushrooms play a crucial dietary role, offering low-fat, high-protein, and low-energy nutritional profiles (Khatun *et al*. 2012). *Scleroderma* species are well-known for being inedible mushrooms due to the dangerous toxins they contain, which can cause harm to individuals who consume their fruiting bodies. Almost all of the species are identified as inedible, but in some cases, such as *S. yunnanense*, *S. texense* and *S. cepa*, have been revealed to be edible and show a significant nutritional value when consumed (Leon *et al*. 2013; Zhang *et al*. 2013). The edibility of *Scleroderma* from different regions varies depending on the origin of the *Scleroderma* species.

The majority of *Scleroderma* species, though not commonly consumed due to concerns about toxicity, show promising nutritional potential based on different studies. These ectomycorrhizal fungi, specifically *S. yunnanense*, contain rich levels of proteins, including essential amino acids, complex carbohydrates, fats, minerals, and beneficial polysaccharides, as well as dietary fiber that support digestive health (Zhang *et al*. 2013; Tudu *et al*. 2024). They are generally low in fat but may include healthy fatty acids such as oleic and linoleic acids.

Mineral content is notable, with high levels of potassium, calcium, phosphorus, magnesium, iron, and zinc, along with B-complex vitamins and potential vitamin D precursors like ergosterol. Moreover, *Scleroderma* species

Table 4: Reported ectomycorrhizal studies of *Scleroderma* species

Species	Tree species	ECM activity	Reference
S. areolatum	*Eucalyptus* spp. *Fagus sylvatica* L.	Host specificity on conifers and *Quereus* spp.	Giachini *et al*. (2000); Mrak *et al*. (2017)
S. bougheri	*Eucalyptus* spp.	Associated only with the eucalyptus strand in Australia	Giachini *et al*. (2000)
S. bovista	*Eucalyptus* spp., *Pinus elliottii, Pinus taeda*	n.d.	Giachini *et al*. (2000)
	Corylus heterophylla *Corulys avellana*	Auxin biosynthesis, transport, and signaling, and the transport of nutrients, may contribute to root development regulation in hazel ectomycorrhiza.	Cheng *et al*. (2024)
S. cepa	*Eucalyptus dunnii*	Prevalent	Giachini *et al*. (2000)
	Eucalyptus globulus, Eucalyptus urophylla	Promotes ECM effectively using spores	Chen (2006)
S. citrinum	*Pinus elliottii, Pinus taeda*	Produce more mycorrhizal roots by using spores	Giachini *et al*. (2000)
	Eucalyptus globulus, Eucalyptus urophylla *Pinus Sylvestris L.*	Significantly reduced translocation of Zn (II), Cd (II), or Pb (II)	Chen (2006) Krupa and Kozdrój (2006)
	n.d.	Tolerance to and Accumulation of Cadmium by the Mycelia	Carrillo-González and González-Chávez (2012)
S. columnare	*Hopea odorata*	Only a fruiting body was found.	Salleh *et al*. (2002)
	Shorea javanica	Sand and soil enhanced ECM colonization and growth;	Febriani *et al*. (2017)
	Shorea seminis	Soil conditioner (BN-50) increased ECM colonization in the roots of *S. javanica*	Turjaman *et al*. (2006)
	Dipterocarpus alatus	Increased shoot nitrogen and phosphorus uptake.	Yomyart (2008)
S. distysporum	*Acacia holosericea*		Duponnois *et al*. (2006)
S. flavidum	*Betula papyrijera*	The ectomycorrhizal fungus enhanced nickel tolerance	Jones (1988)
S. floridanum	*Eucalyptus spp., Pinus elliottii, Pinus taeda*	n.d.	Giachini *et al*. (2000)
S. fuscum	*Pinus elliottii, Pinus taeda*	n.d.	Giachini *et al*. (2000)
S. leptopodium	n.d.	n.d.	Lee *et al*. (2002)
S. meridionale	*Halimium halimifolium*	Mycorrhizal symbiosis	Leonardi *et al*. (2018)
S. polyrhizum	*Quercus suber*	*in vitro* mycorrhization	Díez *et al*. (2000)
	Pinus gerardiana		Tapwal *et al*. (2021)
S. sinnamariense	n.d.	n.d.	Lee *et al*. (2002)
S. uraguayense	*Pinus elliottii, Pinus taeda*	n.d.	Giachini *et al*. (2000)
S. verrucosum	*Eucalyptus spp., Pinus elliottii*	n.d.	Giachini *et al*. (2000)

Note: no data (n.d.) recorded

Table 5: Culture media used in cultivating the mycelia of *Scleroderma*

Species	Substrate and Optimal Conditions	Reference
Scleroderma sp.	Murashige and Skoog medium	Ramos and Tad-awan (2018)
S. areolatum	Potato Dextrose Agar + Sucrose for mycelia; Potato Dextrose Agar + Fructose for exopolysaccharide	Wu *et al*. (2019)
S. bovista	Modified Merlin-Norkran (MMN)	Cheng *et al*. (2024)
S. citrinum	Modified Melin-Norkrans + 5–10 g/L of di-ammonium hydrogen orthophosphate concentration; Potato Dextrose Broth	Yan and Shuang-hong (2005); Itoo and Reshi (2014)
	Pachlewski growth medium	Krupa and Kozdrój (2006)
S. verrucosum	Modified Melin-Norkrans + nitrate	Putra *et al*. (1999)
S. sinnamariense	Fungal-host agar; 30°C; pH 5.0	Siri-in *et al*. (2014)
	Modified Merlin-Norkran (MMN) + Ammonium	Bechem (2012)
	MMN + Peptone + Pi for maximum mycelial yield	Bechem (2012)

have demonstrated bioactive properties, including antioxidant, antimicrobial, and anti-inflammatory activities, primarily attributed to their phenolic compounds and flavonoids (Huguet *et al*. 2022; Yang and Zhang 2023). While some species are considered mildly toxic or inedible when raw or improperly prepared, controlled cultivation and processing methods could open their value as a functional food or nutraceutical source. As such, further studies are needed to fully evaluate their safety, edibility, and application in the food and pharmaceutical industries.

Ectomycorrhizal importance

Studies on macrofungi often focus on their use in food and pharmaceuticals, neglecting the critical role of the ectomycorrhizal (ECM) relationship. This relationship, which involves certain mushroom species forming a mutually beneficial symbiotic association with host trees in the ecosystem, is crucial for the health and survival of both the fungi and the plants. The morphological structures of *Scleroderma* mushrooms, such as the special fungal roots, rhizomorphs, or external hyphae, have various functions: a site for storing or storing and exchanging salts and water (Krupa and Kozdrój 2006).

Different studies and articles on *Scleroderma* species portray a good symbiotic relationship between tree species. The *S. bovista* and *S. citrinum* recorded the highest ECM activities in different trees (Table 4).

Cultivation of the *Scleroderma* mushroom

In different studies, sightings of *Scleroderma* species have been reported and identified as being associated with the roots of different tree species (ECM). In this review, the cultivation of *Scleroderma* species is complicated due to the required nutrients, substrates, and host plants (Siri-in *et al*. 2014). *Scleroderma* species are not commercially cultivated due to their complexity in producing viable fruiting bodies, especially the edible species.

The main challenge in the commercial cultivation of ectomycorrhizal mushrooms, especially *Scleroderma* species, lies in the absence of established protocols, techniques, and sufficient information about the culture medium needed to produce viable inoculants, which are essential for growing the mushrooms. In different studies, *Scleroderma* sp. was cultivated using different synthetic culture media with different compositions for maximum yield of mycelia and polysaccharides. Table 5 shows the different media used for cultivating the mycelia of *Scleroderma* species. The different media show different optimizations. In different studies, the media substrate consists of commercialized potato dextrose agar, Modified Merlin-Norkran with supplementation of various sugars and chemicals, Murashige and Skoog medium, and Fungal-host agar (Putra *et al*. 1999; Bechem 2012; Siri-in *et al*. 2014).

These mushrooms are cultivated in the wild, where they grow on soil. Different species have been studied to identify the conditions needed for mycelial growth and fruiting bodies. In the study of Siri-in *et al*. (2014), *S. sinnamariense* successfully observed its growth on optimized media of Fungal-host agar at 30°C temperature and pH 5.0.

Ethnomedicinal importance of *Scleroderma*

Mushrooms have long been valued for their culinary and nutritional benefits globally, but they are now gaining significant recognition for their medicinal properties and potential to prevent various diseases. This medicinal application is not new, as ethnic tribes and indigenous people have traditionally used diverse wild mushrooms as both food and alternative medicine since ancient times, providing a wealth of traditional knowledge that can help identify and validate their medicinal potential. *Scleroderma* species, historically, were used as ethnomedicinal antiseptics in afflicted physical wounds (Lahiri *et al*. 2010). *Scleroderma* was widely used in different countries such as India, Brazil, Mexico, and the Philippines, which became a significant ethnomedicine. The records of being used as ethnomedicines in different countries were studied, revealing the significant appearance of a wide variety of bioactive compounds and bioactivity shows different profiles such as antibacterial, antioxidant, anticancer, antiprotozoan, antiproliferative, and antifungal properties, which provided concrete evidence as effective ethnomedicines

Mycochemical constituents and bioactivity profiling of *Scleroderma*

The bioactivity profiling of mushrooms is a growing area of study due to the significant pharmaceutical potential of their mycochemical composition, which includes compounds like phenols, terpenoids, polysaccharides, and alkaloids. Specifically, bioactive polysaccharides found in the fungal cell walls are recognized for their diverse functional properties, including anti-tumor, immune-boosting, antioxidant, and hypoglycemic effects (Kumar *et al*. 2021). However, the precise mechanism of bioactive compounds present in *Scleroderma* and their underlying effects remains incompletely understood in some countries. The mycochemical constituents and their bioactivities of *Scleroderma* species are presented in Table 6.

Several species within the genus *Scleroderma* exhibit diverse mycochemical profiles and bioactivities that could be significant to human health, although their pharmaceutical potential must be weighed against the toxicity risks portrayed by *Scleroderma* mushrooms. Different compounds were extracted and identified from different *Scleroderma* species. Seventeen out of 73 recorded species were studied for their bioactivity. Among *Scleroderma* species, *S. citrinum* was the most evaluated for the biological activities, with 14 studies. The biological activities of *S. citrinum* were identified, such as antioxidant, antibacterial, antifungal, insecticidal, bioremediation, antiviral, antimycobacterial, cytotoxicity, thrombolytic activity, and antagonistic activity. The extraction of *Scleroderma* was also identified using mostly the following: ethanol, methanol, ethyl acetate, and chloroform. Furthermore, different notable mycochemicals have been successfully isolated and identified as sclerocitrin, dimethoxymethyl vulpinate (DMV), dimethoxyvulpinic acid (DMVA), indole-3-acetic acid (IAA), peptide texenomycins A and B, and new triterpenes. The chemical structure of the mycochemical compound groups is presented in Fig. 5. These compounds demonstrate antiprotozoal, antiviral activity against herpes simplex virus, antimycobacterial activity against *Mycobacterium tuberculosis*, antifungal, and cytotoxicity in *S. citrinum* (Stump *et al.* 2001; Kanokmedhakul *et al.* 2003).

Scleroderma species possess notable antimicrobial activity, primarily against Gram-positive bacteria such as *Staphylococcus aureus*, *Escherichia coli*, *Enterococcus faecalis*, and *Pseudomonas aeruginosa* (Łopusiewicz 2018; Paderes and Bernal 2020; Huguet *et al.* 2022), to a lesser extent against Gram-negative bacteria and different pathogenic fungi such as *Phytophthora palmivora* and *Colletotrichum gloeosporoides* (Soytong *et al*. 2014). These bioactivities are attributed to secondary metabolites such as phenols, terpenoids, and alkaloids, which disrupt microbial membranes or interfere with metabolic pathways.

Some of the organic solvent extraction, particularly ethanol and methanol, generally exhibit stronger effects than aqueous extracts due to enhanced solubility and separation of non-polar compounds. Bioactivity may vary according to species, growing conditions, and extraction procedures. Despite their potential as natural antibacterial sources, the toxicity of several *Scleroderma* species demands extensive

Table 6: Solvent extraction, bioactive compounds, and biological activities of *Scleroderma* species

Species	Solvent Extraction	Mycochemical Compounds	Bioactivity	Reference
S. albidum	n.d.	Sclerocitrin	Mushroom poisoning	Sato *et al*. (2019)
S. areolatum	Ethanol	Exopolysaccharide (EPS)	Antiproliferative activity	Wu *et al*. (2019)
	n.d.	EPS	Antioxidant activity	Xi *et al*. (2024)
	Methanol	Triterpenes	Antiprotozoan activity (against *Plasmodium falciparum* 3D7 and against *Trypanosoma cruzi*).	Annang *et al*. (2018)
S. aurantium	Ethanol	Palmitic acid, linoleic acid, ergosterol peroxide, and mannitol	n.d.	Vrkoč *et al*. (1976)
	ethyl acetate-methanol	3,25-dihydrocy-22-acetoxyl-lanosta-8,23-diene, new triterpene	n.d.	Kardono *et al*. (2002)
S. bermudense	n.d.	n.d.	Enhances salt stress	Bandou *et al*. (2006)
S. bovista	Methanol	Ergostane, lanostane, and ceramide derivative	Antiproliferative property	Kovacs *et al*. (2018)
S. citrinum	ethanol, methanol, chloroform, ethyl acetate, acetone and DMSO	Melanin	Antioxidant and light barrier, Antibacterial properties (*E. facealis* and *P. aeruginosa*)	Łopusiewicz (2018)
	Methanol	Dimethoxymethyl vulpinate (DMV) and Dimethoxyvulpinic acid (DMVA)	Antifungal activity (against *Phytophthora palmivora* and *Colletotrichum gloeosporioides*)	Soytong *et al*. (2014)
	chloroform-methanol petroleum ether	n.d.	Insecticidal activity (against *Mythimna*)	Yan and Shuang-hong (2005)
	Methanol	Unusual Pulvunic Acid	n.d.	Winner *et al*. (2004)
	de-ionized H_2O	silica, sulfur, and zinc	Bioremediation strategies	Cullings *et al*. (2023)
	Methanol	lanostane-type triterpenoid, 4,4'-dimethoxyvulpinate, 4,4'-dimethoxyvulpinic acid	Antiviral activity (against Herpes simplex type 1), Antimycobacterial activity (against *Mycobacterium tuberculosis*), and Cytotoxicity (against the NCI-H187 cell line)	Kanokmedhakul *et al*. (2003)
		n.d.	Antifungal Activity (against *Pythium* sp. and *Phytophthora* sp.)	Mohan *et al*. (2015)
	Triethanolamine (TEA) buffer and Isopropyl Alcohol	n.d.	Useful carbonyl reductases (KREDs)	Loderer and Ansorge-Schumacher (2016)
	n.d.	Zinc	Inedible/toxicity (High concentration of Zn)	Rasalanavho (2021)
	Ethanol and Chloroform	n.d.	High phenolic compound (Ethanol Extract), Thrombolytic Activity, Low LC50 (Edible)	Culliao *et al*. (2020)
	Pachlewski growth medium	n.d.	Plant protection (against heavy metals)	Krupa and Kozdrój (2006)
		n.d.	Antagonistic activity	Yang and Zhang (2023)
	Heptane, ethyl acetate (EtOAc), and methanol (MeOH)	n.d.	Antibacterial Activity against *S. aureus* and *E. coli.*	Huguet *et al*. (2022)
	Ethanol		Effective EC50 of total phenolic compounds	Culliao *et al*. (2020)
S. columnare	n.d.	n.d.	Increase in root chitinase kinetic properties	Darusman (1998)
	Ethanol (95%)	n.d.	Antioxidant Activity, Anti-inflammatory, Antituberculosis	Stanikunaite *et al*. (2007)
S. lycoperdoides	n.d.	Mycochemical (Ethyl−β-D galactopyranoside), Ethyl−β−D glucopyranoside, Nicotinic acid, Caffeic Acid	n.d.	Kurnia (2014)
S. michiganense	n.d.	Lead	Inedible/Toxicity (High concentration of Pb)	Rasalanavho (2021)
S. nitidum	80% Acetone	Polysaccharide Sclerodol A Sclerodol B lanostane tripenoid	Anti-inflammatory activity	Nascimento *et al*. (2012)
S. polyrhizum	Ethanol Ethyl Acetate H_2O	Steroids and 5a,8a-epidoxyergosta-6,22-dien-3B-o1, and also palmitic and oleic acids.	n.d.	Gonzalez *et al*. (1983)
	Methanol	Phenols	Antioxidant activity and antimicrobial activity	Borthakur *et al*. (2023)
	n.d.	Ergosterol	Anti-inflammatory activity.	Zhang *et al*. (2015)

Table 6: Continued

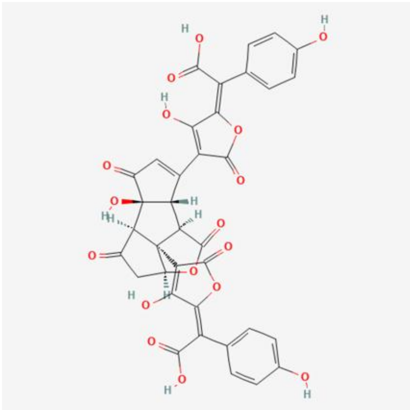
Table 6: Continued

	Ethanol	n.d.	Antibacterial activity against *S. aureus* and *E. coli*.	Paderes and Bernal (2020)
	n.d.	N,N-dimethylphenylalanine; 2-N,N, N-trimethyl-phenylalanine and 2-trimethyl-ammonio-3-(3-indolyl)propionate	n.d.	Xianling *et al*. (2005)
S. sinnamariense	Ethyl acetate	Indole-3-acetic acid	IAA production, solubilization of insoluble metal minerals, and metal tolerance abilities *in vitro*.	Kumla *et al*. (2013b)
	Methanol	Methyl 4,4'-dimethoxyvulpinate and 4,4'-dimethoxyvulpinic acid.	Antimicrobial activity	Putra *et al*. (2011)
	Petroleum ether, Ethyl acetate, methanol	Three pigments, *i.e*., methyl 4,4' -di-0-rnethylatrornentate, rnethyl per-0-methylatrornentate, and rnethyl 2',5'-dichloro-4,4'-di-O-methylatrornentate	n.d.	Arnold *et al*. (1996)
	Modified universal buffer (MUB)	n.d.	The absence of phosphorus in the assay medium stimulated cell-bound acid phosphatase activity.	Bechem (2012)
	n.d.	n.d.	Utilize some organic and inorganic nitrogen (N) for growth	Bechem (2012)
S. suthepense	Ethyl acetate Methanol	Indole-3-acetic acid	IAA biosynthesis *via* the indole-3-pyruvic acid pathway	Kumla *et al*. (2020)
S. texense	Sea water	n.d.	Toxicity activity	Ruiz-González *et al*. (2023)
	Methanol	Peptide texenomycins A and B	Antifungal activity and antimycotics	Stump *et al*. (2001)
S. verrucosum	Ethanol	alkaloids, flavonoids, phenolics, triterpenoids, steroids, tannins, organic acids, reducing sugars, aromatic compounds and carboxylic acids	Phytochemical composition; Antioxidant activity	Filho *et al*. (2022)
	Crude essential oil	Essential oils, 3-octanone	-	Yayli *et al*. (2007)
	Ethanol	Phenolic	Antioxidant activity	He *et al*. (2021)
	n.r.	n.r.	Inedible; dMn, Cu, Co, and Ni content	Sarikurkcu *et al*. (2020)
	Petroleum ether DTPA extracting solution	n.d.	High in Mg and Ca, permissible limits in heavy metals	Naik and Naika (2022)
	n.d.	Polyphenolic	Antioxidant activity	Gevorgyan (2022)
	Distilled and deionized water	Oxalic, citric, succinic and malonic acids	Produced metal-chelating compounds, the highest CAS reaction in the absence of iron	Machuca *et al*. (2007)
S. vulgare	Hexane	ergosterol, (S)-23 hydroxylanosterol, linolenic ester, ergosterol endoperoxide; 9,11-dehydroergosterol endoperoxide, (23E)-lanosta-8,23-dien-3β,25-diol	Highest antiproliferative activity against the cells of the HL-60 cell line	Szumny *et al*. (2009)
S. yunnanense	n.d.	DOPA-melanin Polysaccharide	12 biosynthetic gene clusters, 13 key mevalonate (MVA) pathway enzymes, a key tyrosinase enzyme in the 3,4-dihydroxyphenylalanine (DOPA), 16 enzymes involved in uridine diphosphate glucose biosynthesis.	Zhang *et al*. (2023)

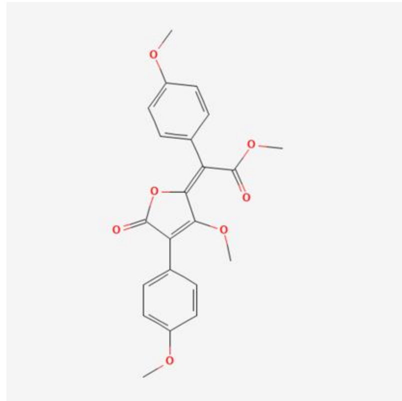
Note: no data (n.d.) recorded

safety and pharmacological testing. Future research should concentrate on isolating active constituents, understanding mechanisms of action, and investigating synergistic effects with conventional antimicrobials to combat rising antibiotic resistance.

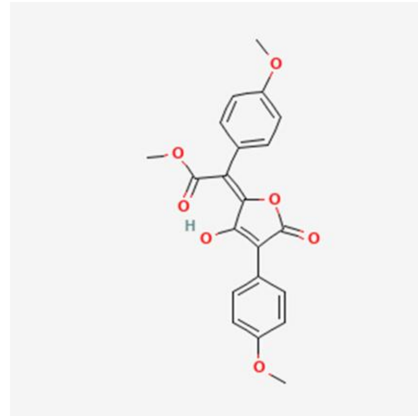
Around the world, *S. citrinum* contains rich and diverse bioactive compounds, including alkaloids, flavonoids, phenolics, triterpenoids, tannins, steroids and organic acids. Its exceptionally high phenolic content correlates with strong free radical scavenging capacity, suggesting significant antioxidant potential that may have implications for conditions characterized by oxidative stress. *S. texense* also displays promising nutraceutical attributes as it contains peptide texenomycin A and B (Stump *et al*. 2001).



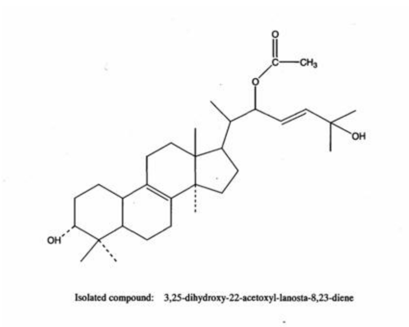
Sclerotinin
PubChem CID: 56928143



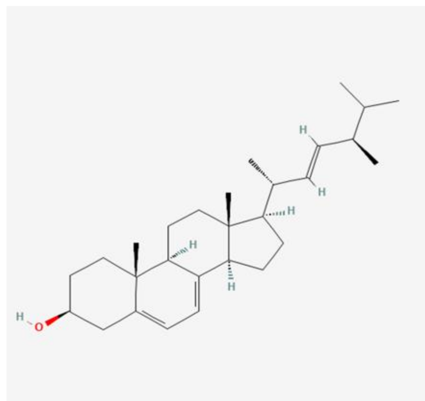
4,4'-Dimethoxymethyl vulpinate (DMV)
PubChem CID: 54718139



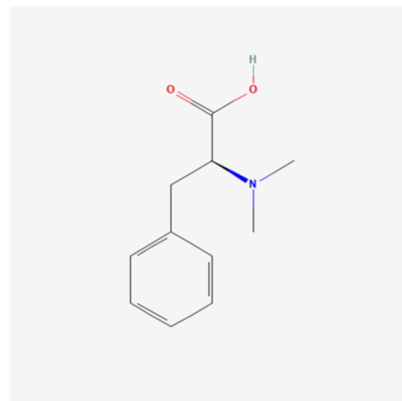
4,4'- Dimethoxyvulpinic acid (DMA)
PubChem CID: 54718139



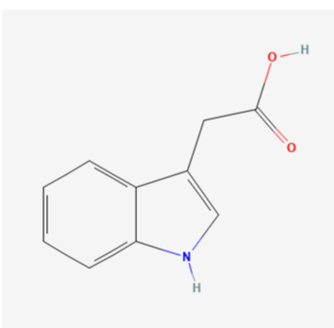
3,25-dihydroxy-22-acetoxyl-lanosta-8,23-diene*,* new triterpene (Kardono *et al.* 2002)



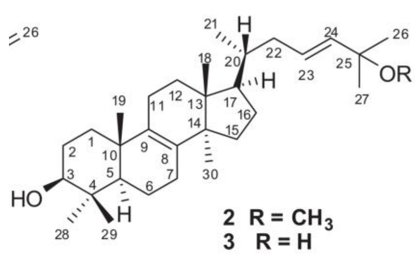
Ergosterol
PubChem CID: 444679



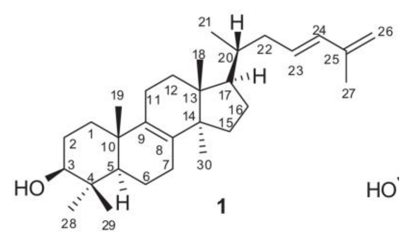
N,N-dimethylphenylalanine
PubChem CID: 53749380



Indole-3-acetic acid PubChem CID: 802

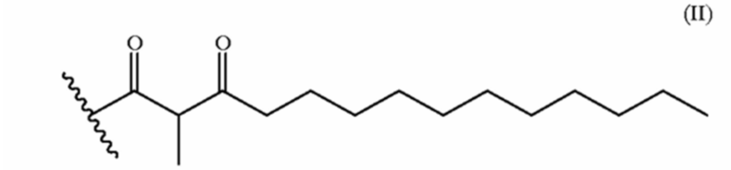


Sclerodol B, Lanostane (Morandini *et al*. 2016)



Sclerodol A (Morandini *et al*. 2016)

(II)



Peptide texenomycin (Stump *et al*. 2001)

Fig. 5: Chemical structure of bioactive compounds present in *Scleroderma*

It is notable for its high protein content, different minerals, elevated flavonoid concentration, and potent dietary antioxidant source. In contrast, other members of the genus, such as *S. albidum* and *S. citrinum*, are known to be toxic in some countries, linked to muscarinic effects, central nervous system toxicity, and, in some cases, shock or visual disturbances, underscoring the importance of accurate species identification in any medicinal or dietary context (Sato *et al.* 2019).

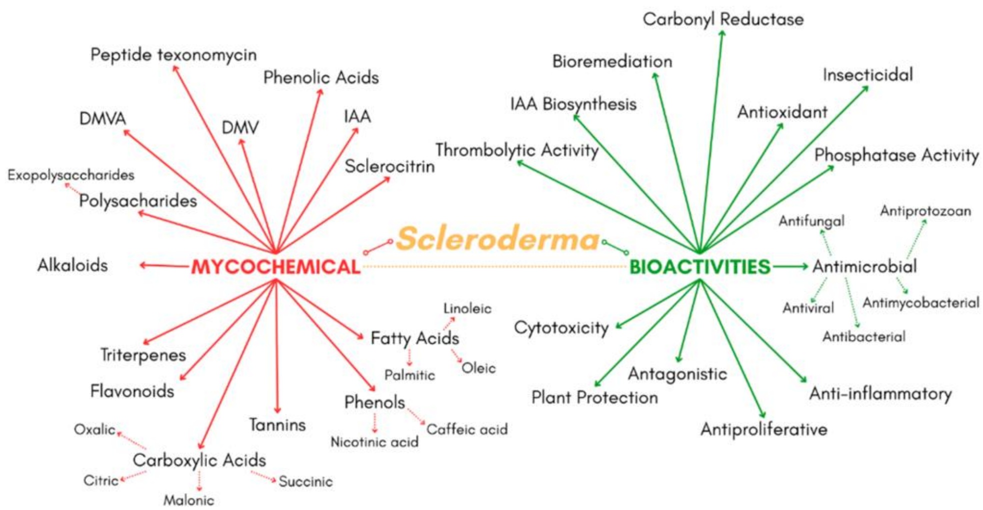


Fig. 6: Summary of biological activities of *Scleroderma*

Whereas *S. polyrhizum* was used in traditional Chinese medicine for reducing swelling and promoting hemostasis, it contains steroidal compounds and fatty acids such as palmitic and oleic acid, which may contribute to its bioactivity (Zhang *et al*. 2015). Furthermore, the antioxidant and possible anti-inflammatory properties of selected *Scleroderma* species could or may mitigate oxidative and inflammatory pathways, though rigorous toxicological assessment and targeted mechanistic studies are essential before any therapeutic application can be considered (Fig. 6).

Application of *Scleroderma* species

The *Scleroderma* species is worth noting for its application in forestry and biotechnology. The application of *Scleroderma* species revolves around the bioremediation, plant protection, and enhancing stress tolerance, which highlights in ecological importance of this ectomycorrhizal species.

Based on different studies, *S. bermudense* on seagrape (*Coccoloba uvifera*), saline stress tolerance has been considerably enhanced, which gives high osmoregulating capacity, where ECM plants could be important salt-alleviating mechanisms for seagrape seedlings growing in soils with saline concentrations (Bandou *et al*. 2006).

Scleroderma species also portrays important bioremediation activities and plant protection on tree seedlings. *S. citrinum* shows an important reduction in the translocation of zinc, cadmium, and lead from its root to the shoots of the tree seedlings (*Pinus sylvestris*). It also identified an ectomycorrhizal-associated bacterium (*Pseudomonas* sp.), which is another component for inoculating pine seedlings (Krupa and Kozdrój 2006). These findings show as a potential candidate for use in bioremediation projects, especially for polluted soils with different heavy metals.

Moreover, this allows fungi to gain traction as promising bioremediation alternatives, owing to their inherent capacity to metabolize complex molecules that are commonly resistant to conventional treatment methods. *Scleroderma* mushrooms offer significant applications across three communities, utilizing their ectomycorrhizal properties for bioremediation and aiding climate change. For the scientific community, its ability to translocate and accumulate heavy metals and enhance tree health provides a sustainable method for cleaning polluted soils and boosting carbon absorption. The general community benefits from a low-cost, natural solution for local environmental cleanup and land restoration. Lastly, indigenous groups provide crucial Traditional Ecological Knowledge (TEK) regarding the role of these species in healthy forest ecosystems, enabling the effective, sustainable application of *Scleroderma* in land management and conservation efforts through biotechnology and microbiology.

Summary and future research

This review article successfully provides a comprehensive global synthesis of *Scleroderma* species, summarizing their worldwide checklist, distribution, morphology, ectomycorrhizal status, cultivation, chemistry, and bioactivities. The analysis compiled a global checklist of 73 *Scleroderma* species and confirmed their significant potential for pharmaceutical applications due to a wide range of bioactive compounds; *S. citrinum* was identified as the most well-studied species. Beyond medicinal uses, the review highlighted their crucial ecological role as ectomycorrhizal fungi and their potential for bioremediation activities, noting that some new species, like *S. yunnanense,* are traditionally edible.

In this review, the compiled data on *Scleroderma* species clearly mandate a sustained, multi-disciplinary approach in future studies to fully exploit their potential. The key research priorities can be summarized across six significant areas: (a) mapping and identification through conducting extensive field and molecular studies to accurately define the worldwide distribution and identification of *Scleroderma*, focusing particularly on areas with optimal growth conditions, (b) genomic profiling by implementing advanced taxonomic and phylogenetic investigations to establish the unique genomic profile of each species using molecular technology, which is essential for updating global databanks, (c) optimization, developing, and refining methods for commercial cultivation to fully understand their growth potential and promote their utilization across various industrial applications, (d) further studies of the isolation, characterization, and identification of the complete mycochemical composition of different *Scleroderma* species, specifically to those traditionally edible, (e) evaluating their biological activities using different models to precisely determine their underlying mechanism of action, (f) Finally, capitalizing on their edibility and bioactive compounds to create a potential *Scleroderma*-based products, such as dietary supplements or pharmaceutical drugs.

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Author Contributions

MADCT and RMRD conceptualized the article review. MADCT drafted and edited, and RMRD, NCC, and SPK contributed to the revision and reviewed the article manuscript. All authors reviewed and approved the final version of the article review manuscript.

Conflict of Interest

All authors declare no conflict of interest

Data Availability

The data presented in this study were compiled from different studies, and a list of available compiled data will be given upon request to the corresponding author.

Ethics Approval

Not applicable to this paper.

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