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Geopyxis carolinae sp. nov. (Pezizomycetes, Ascomycota) from Mexico

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Abstract

Geopyxis is an ectomycorrhizal genus found in temperate forests. The members form yellow and orange to brown apothecia that range from 3–25 mm in diameter. Its ascospores are smooth to finely verrucous. The specimen collected from Mount Tlaloc, Texcoco, State of Mexico, was identified as *Geopyxis carolinae sp. nov*. This species typically forms sessile apothecia, cupuliform to discoid, and its ascospores are the largest [17–23(25) × 10–12 µm] within the genus. The species was found growing on a burnt ground associated with *Abies religiosa*. Multi-gene phylogenetic analyses inferred from ITS and LSU sequence data confirmed that *Geopyxis carolinae* is distinct from other *Geopyxis* spp. The new species is described, illustrated, and compared with similar taxa based on molecular and morphological data.

Key words: 1 new species, *Abies* forest, Ectomycorrhizal fungi, Pyronemataceae, Pyrophylls

Introduction

Geopyxis (Pers.) Sacc., belongs to the family Tarzettaceae (Pezizales, Pezizomycetes) (Ekanayaka *et al*. 2018). The genus was initially described as a subgenus of *Peziza* by Person (1822) and Fries (1822), and later it was recognized as a genus (Saccardo 1889) and placed within the family Pyronemataceae (Lumbsch and Huhndorf 2010). However, Ekanayaka *et al*. (2018) segregated the genera *Geopyxis*, *Hydnocystis* Tul. & C. Tul., *Hypotarzetta* Donadini, *Paurocotylis* Berk., *Stephensia* and *Tarzetta* (Cooke) Lambotte, from Pyronemataceae, to establish Tarzettaceae family. The taxa of *Geopyxis* are characterized by forming yellow and orange to brown cupuliform to discoid apothecia with the size of 3–25 mm in diameter. Eight-spored asci and hyaline ellipsoid ascospores are inamyloid and smooth to finely verrucous. This genus includes ectomycorrhizal fungi that grow and fructify in burned or disturbed soils (burnt ground) in coniferous or montane forests (Saccardo 1889, Kimbrough and Gibson 1990, Vralstad *et al*. 1998, Hansen *et al*. 2013, Wang *et al*. 2016).

According to the Index Fungorum (2024), the genus *Geopyxis* comprises 29 species. Sevaral of *Geopyxis* taxa are recorded from Mexico, *viz. Geopyxis vulcanalis* (Peck.) Sacc. was registered in the State of Mexico associated with *Abies religiosa* (Kunth) Schltdl. & Cham (Chacón and Guzmán 1985, Chio *et al*. 1988); *G. majalis* (Fr.) Sacc. was found in the state of Durango associated with *Cupressus arizonica* Greene and *Abies guatemalensis* Rehder in the State of Oaxaca (Raymundo *et al*. 2012, 2013). Recently, Madriz-Valdovinos *et al*. (2022) reported *G. deceptiva* X.H. Wang & K. Hansen in the State of Sonora; however, no mycorrhizal association was recorded.

Mount Tláloc is in the Municipality of Texcoco, north of the Sierra Nevada. This area belongs to the Iztaccihuatl-Popocatepetl National Park, which is part of the physiographic region of the Neovolcanic Transversal Axis. Mount

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Tláloc rises 4125 m a. s. L., and has a semi-cold climate (Sánchez-Sánchez *et al*. 2021, Sánchez-González and López-Mata 2003, Astudillo-Sánchez *et al*. 2017, Villanueva-Díaz *et al*. 2016). The dominant vegetation includes alpine plants such as *Quercus* L., *Pinus* L., and *Abies* Mill., and mixed forest vegetation such as *Abies religiosa, Alnus acuminata* Kunth*, Cupressus lusitanica* Mill.*, Juniperus monticola* Martínez*, Pinus hartwegii* Lindl.*, P. leiophylla* Schiede ex Schltdl. & Cham.*, P. montezumae* Lamb.*, P. pseudostrobus* Brongn.*, Quercus glabrescens* Benth.*, Q. laurina* Bonpl.*, Q. microphylla* Née*, Q. rugosa* Née*, Salix lasiolepis* Benth. and *S. paradoxa* Kunth (Sánchez-González y López-Mata 2003, Villanueva-Díaz *et al*. 2016, Astudillo-Sánchez *et al*. 2017). However, this forest has been in constant disturbance because of forest fires, dating back 15 years (Barrales-Brito *et al*. 2020).

The present study aims to describe a new species from Mount Tlaloc, Texcoco, State of Mexico. This study provides detailed morphological descriptions of *Geopyxis carolinae sp. nov*., supported by a phylogenetic tree with all available sequences of *Geopyxis* to infer the phylogenetic relationships of *Geopyxis carolinae*.

Material and methods

Collection and morphological examination

All the specimens were collected in the Municipality of Texcoco, State of Mexico, in the region located within the Transverse Neovolcanic Axis, 19°24’43.82” N, 98°44’58.86” W, 3559 m a. s. l., from September to January. The holotype was deposited in the mycological herbarium José Castillo Tovar of the Instituto Tecnológico of Ciudad Victoria (ITCV). The paratype was deposited in the herbarium of the Escuela Nacional de Ciencias Biológicas of the Instituto Politécnico Nacional (ENCB).

Macroscopic characteristics such as size, shape, colour, and host were described using fresh specimens. The illustrated dictionary of mycology (Ulloa and Hanlin 2006) was used as a guide during the taxonomic revision, and the colour determination was made using the colour chart of Kornerup and Wanscher (1978). Longitudinal sections were made for the apothecia and later were rehydrated with an alcohol solution (70%) and water. The apothecia were longitudinally sectioned. Sections were rehydrated with 70% alcohol, and 5% KOH and mounted on a glass slide with water to observe possible dehiscent ornamentation in ascospores. Melzer reagent was used to observe asci amyloidity. Further, the microscopic structures of exciples, paraphyses, asci, and ascospores were analyzed and characterized using an optical microscope (OM) (Axiostar plus, Zeiss, Jena, Alemania). Images were taken with a Rebel T-1i camera and a 100 mm macro lens (Canon, Tokyo, Japan). The species were differentiated following Wang *et al*. (2016).

A detailed morphological comparison of *Geopyxis* spp. distributed in America with *Geopyxis carolinae sp. nov*. was carried out, and the data are provided in Table 3.

PCR amplification and sequencing

The DNA was extracted from fresh specimens (Table 1) using the CTAB method (Martínez-González *et al*. 2017). The DNA was quantified with a Nanodrop 2000c (Thermo Scientific™, Wilmington, USA). We prepared dilutions from each sample at 20 ng/µl to amplify the two gene regions (Table 2): Internal transcribed spacer (ITS) and large subunit (LSU) ribosomal DNA. The reaction mixtures (25 µL) contained 5 µL PCR buffer 5x (Promega, Madison, WI, USA), 2.5 mM deoxynucleoside triphosphate (dNTP), 10 pmol/µL forward and reverse primers, 0.035U of Taq DNA Polymerase (GoTaq® DNA, 5U; 0.08 U/µL; Promega, Madison, WI, USA), and 100 ng template DNA. The PCR products were verified by agarose gel electrophoresis. The gels were run for 1 h at 95 V cm^{-3} in 1.5% agarose and 1× TAE buffer (Tris Acetate-EDTA). The gel was stained with GelRed (Biotium, USA) and the bands were visualized in an Infinity 3000 transilluminator (Vilber Lourmat, Eberhardzell, Germany). The amplified products were purified with the ExoSAP Purification kit (Affymetrix, USA), following the manufacturer’s instructions. They were quantified and prepared for the sequence reaction using a BigDye Terminator v.3.1 (Applied Biosystems, USA). These products were sequenced in both directions with an Applied Biosystem model 3730XL (Applied BioSystems, USA), at the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM). The sequences obtained were compared with the original chromatograms to detect and correct possible reading errors. The sequences of both strands of each of the genes were analyzed, edited, and assembled using BioEdit v. 7.0.5 (Hall 1999) to generate a consensus sequence which was compared with those deposited in GenBank (2022) using the tool BLASTN v. 2.2.19 (Zhang *et al*. 2000).

TABLE 1. Names, voucher numbers, and corresponding GenBank accession numbers of the sequences used in the phylogenetic analyses. The information of the new species is in black bold.

Species name	Voucher Number	GenBank Accession	
		ITS	LSU
Geopyxis aleurioides	CF 57391	KU932480	KU932535
Geopyxis aleurioides	TUR 078772 Type	NR154090	NG060674
Geopyxis aleurioides	TUR 075595	KU932481	KU932536
Geopyxis alpina	CF 56936	KU932457	KU932516
Geopyxis alpina	CF 57357	KU932455	KU932514
Geopyxis alpina	CF 57094	KU932456	KU932515
Geopyxis carbonaria	1941	Z96989	–
Geopyxis carbonaria	1942	Z96990	–
Geopyxis carbonaria	2217	Z96988	–
Geopyxis carolinae	**González-Sánchez 01 Type ITCV**	**OL851706**	**OL870613**
Geopyxis deceptiva	BAP 434	KU932471	–
Geopyxis deceptiva	BAP 501	KU932472	–
Geopyxis deceptiva	FLASMES 1393	MT156495	–
Geopyxis delectans	KH 0448	KU932498	NG068772
Geopyxis delectans	SF 274182	KU932504	KU932554
Geopyxis delectans	KH 0456a	KU932505	KU932555
Geopyxis korfii	HMAS 97506	KU932482	KU932537
Geopyxis korfii	HMAS 97508	KU932483	KU932538
Geopyxis majalis	SF 276561	KU932477	KU932529
Geopyxis majalis	SF 276573	KU932476	KU932528
Geopyxis majalis	2144	KU932475	KU932532
Geopyxis rehmii	CF 56486	KU932464	KU932525
Geopyxis rehmii	Rossbach 136a	KU932465	KU932527
Geopyxis rehmii	FLASMES 3254	MT156533	–
Geopyxis vulcanalis	DED 6280	–	DQ220350
Paurocotylis pila	JAC 16321	OL653036	–

TABLE 2. Primers used in the amplification and sequencing of the DNA fragments in this study.

Loci/Segment	Primer	Sequence 5'-3'	T(°C)	Reference
ITS	ITS5	GGAAGTAAAAGTCGTAACAAGG	57	White *et al.* 1990
	ITS4	TCCTCCGCTTATTGATATGC	57	White *et al.* 1990
LSU	LROR	ACCCGCTGAACTTAAGC	54	White *et al.* 1990
	LR5	GGTCCGTGTTTCAAGAC	60	White *et al.* 1990

Phylogenetic analyses

To explore the phylogenetic relationships of the new species, an alignment was made based on the taxonomic sampling employed by Wang *et al*. (2016). Each gene region was independently aligned using the online version of MAFFT v.7 (Katoh *et al*. 2002, 2017, Katoh and Standley 2013). Alignment was reviewed in PhyDE v. 10.0 (Müller *et al*. 2005), followed by minor manual adjustments to ensure character homology between taxa (Wang *et al.* 2016). The matrices were formed for ITS by 25 taxa (702 characters) and LSU by 18 taxa (910 characters). The aligned matrices were concatenated into a single matrix (26 taxa, 1612 characters). Phylogenetic inferences were estimated with maximum likelihood in RAxML v. 8.2.10 (Stamatakis, 2014) with a GTR + G model of nucleotide substitution. A 1000 rapid bootstrap replicates were run with the GTRGAMMA model to assess branch support. For Bayesian posterior probability, the best evolutionary model for alignment was sought using PartitionFinder (Frandsen *et al*. 2015, Lanfear *et al*. 2014, 2017). Phylogenetic analysis was performed using Mr Bayes v. 3.2.6 x 64 (Huelsenbeck and Ronquist 2001). The information block for the matrix includes two simultaneous runs, four Montecarlo chains, temperature set to 0.2, and sampling 10 million generations (standard deviation ≤0.1) with trees sampled every 1000 generations. The first 25% of samples were discarded as burn-in, and stationarity was checked in Tracer v. 1 (Rambaut *et al*. 2014). Trees were visualized and optimized in FigTree v. 1.4.4 (Rambaut 2014).

Results

Molecular phylogenetic analyses

The two simultaneous Bayesian runs continued until the convergence parameters were met, and the standard deviation fell below 0.001 after 10 million generations. No significant changes in tree topology trace or cumulative split frequencies of selected nodes were observed after about 0.25 million generations, which were discarded as 25% burn-in.

The analysis of ITS and LSU produced a phylogenetic tree in which *Geopyxis carolinae* is found in a terminal branch, with a subsequent 1 Bayesian Posterior Probability (PP) and 100% bootstrap proportion (BP) for Maximum Likelihood (Figure 1).

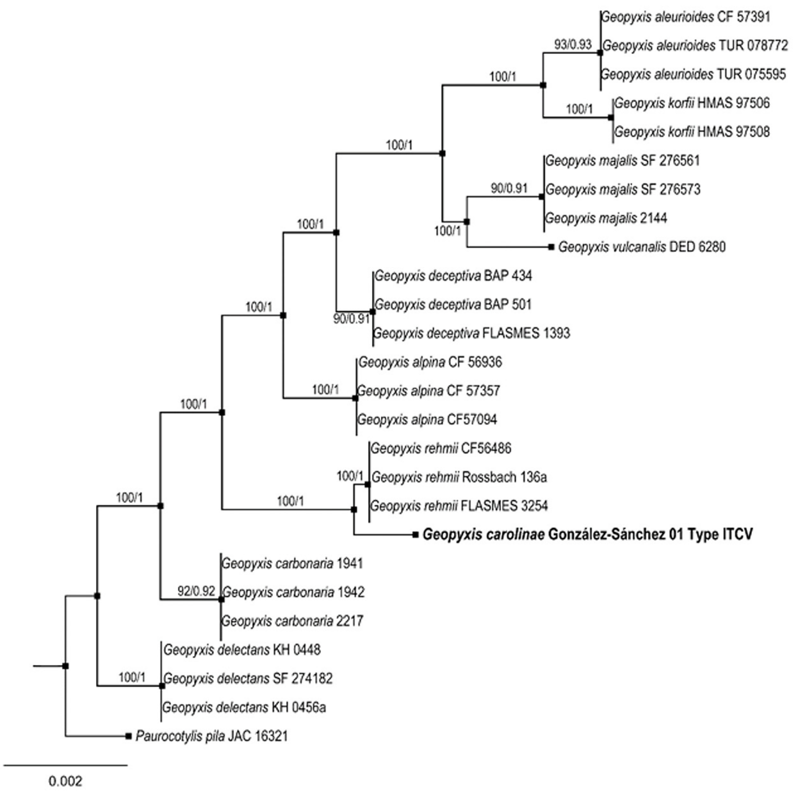

FIGURE 1. Maximum-likelihood phylogenetic tree based on combined ITS and nrLSU nucleotide sequences (Wang *et al*. 2016). Bootstrap values (BP) ≥ 90% from ML analysis and Bayesian posterior probabilities (BPP) ≥ 0.90 are shown on the branches. The new species *Geopyxis carolinae* is shown in black bold.

Taxonomy

Geopyxis carolinae Sánchez-Flores, García-Jiménez, C. Martínez-González, Ekanayaka & Raymundo *sp. nov.* (Figures 2–3)
Mycobank no. MB 842941

Etymology: dedicated to D. Carolina González-Sánchez, who collected the species for the first time.

FIGURE 2. *Geopyxis carolinae* (Holotype: DCGONZÁLEZSÁNCHEZ-01-ITCV). A, B. Gregarious apothecia. C. Mature apothecia. D, E. Young apothecia.

Type: MEXICO, State of Mexico, Texcoco Municipality, Canoas Altas, Mount Tlaloc, 19°24'43.82" N, 98°44'58.86" W, 3559 m a. s. l., 06 July 2020, D. C. González-Sánchez 01 (holotype: ITCV! [DCGONZÁLEZSÁNCHEZ-01-ITCV]).

Diagnosis: *Geopyxis carolinae* differs from the other species by having asci sizes of 260–310 × 12–14 (15) µm and the largest ascospores of 17–23 (25) × 10–12 µm within the genus.

Description: Sexual morph: Ascomata apothecial. *Apothecia* 3–11 mm diameter [= 7.2 mm, n= 24], cupuliform when young to discoid at maturity stage, solitary to gregarious, sessile to subsessile, with a stipe up to 1. 5 mm high, greyish orange (5B4) to melon (5A7), entire margin to slightly lobed, crenulate, dentate to serrate, cracking at maturity, white colour at the beginning and becoming light brown (6D6) at maturity stage, the exterior of apothecium concolorous smooth to finely pruinose, at base forming folds that unite with a stipe, smooth hymenium. *Ectal exciple* 65–125 µm thick, consisting of cells 15–25 × 10–17 µm, angular to subglobose in texture, subhyaline, thin wall 1–1. 5 µm wide. *Medullary exciple* 60–133 µm thick, formed by hyphae 3–5 µm, intricate texture, subhyaline. *Subhymenium* 25–50 µm thick. *Hymenium* 260–328 µm thick. *Paraphyses* 2–3 µm diameter, filiform, hyaline, septate, sparsely branched. *Asci* 260–310 × 12–14 (15) µm [= 284 × 12.8 µm, n = 20], cylindrical, clavate, octospored, inamyloid. *Ascospores* 17–23 (25) × 10–12 µm [= 19. 9 × 11.1 µm, n = 74], Q = 1.5-2 (2.3), Qm = 1.7, elliptical to oblong-elliptical, hyaline, smooth, multigutulate. **Asexual morph:** Unknown.

Distribution: Known from the type locality, State of Mexico, Mexico.

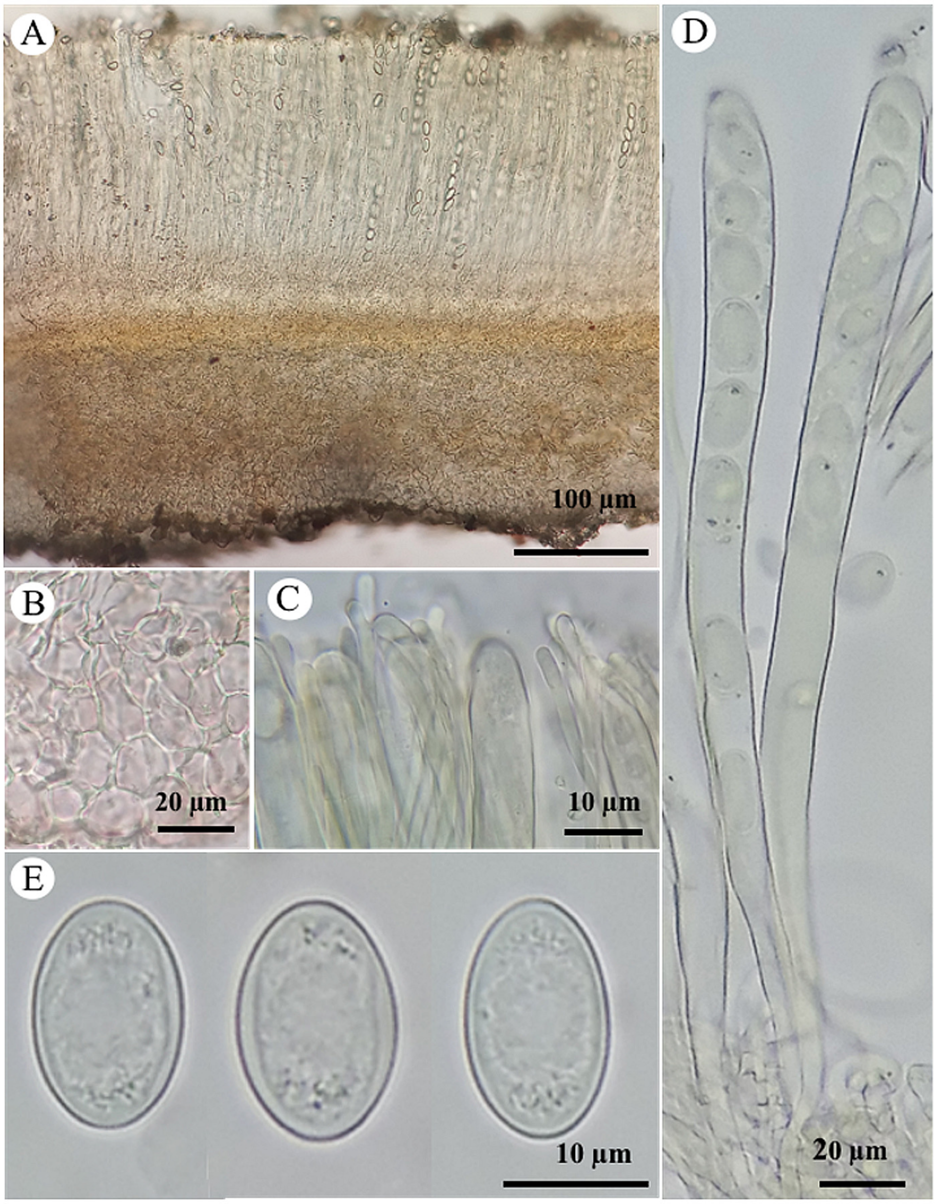

FIGURE 3. *Geopyxis carolinae* (Holotype: DCGONZÁLEZSÁNCHEZ-01-ITCV). A. Longitudinal section of the apothecium. B. Ectal excipulum. C. Paraphyses. D. Asci. E. Ascospores in 5% KOH.

Notes: *Geopyxis carolinae* is characterized by greyish orange to orange apothecia up to 11 mm in diameter, cylindrical and inamyloid asci, and elliptical to oblong-elliptical, smooth ascospores of 17–23 (25) × 10–12 µm. Phylogenetically, it is closely related to *G. rehmii* Turnau; however, it has verrucous and smaller ascospores 10–19 × 9–10 µm (Turnau 1985). Another related species is *G. carbonaria* (Alb. & Schwein) Sacc., which differs from *G. carolinae* by its smaller ascospores 12–18 × 6.5–11 µm, like *G. korfii* W. Y. Zhuang 12–15 × 8–10 µm. Conversely, the ascospores of both species have a verrucous wall (Wang *et al*. 2016, Zhuang and Liu 2006), but the ascospores of *G. carolinae* are smooth (Table 3).

Additional specimens examined: MEXICO. State of Mexico, Municipality of Texcoco, Mount Tlaloc 19°24’43.82” N, 98°44’58.86” W, 3559 m a. s. l., 14 November 2021, D.C. González-Sánchez 02 (Paratype: ENCB), M. Sánchez 2573 (ITCV), 2575 (ITCV), 2580 (ITCV), 2582 (ITCV), 2591 (ITCV), 2602 (ITCV), 2605 (ITCV), 2608 (ITCV), 2612 (ITCV), 2615 (ITCV), and 2620 (ITCV). Loc. cit., 16 January 2022, M. Sánchez 2687 (ITCV) and 2690 (ITCV). Loc. cit., 18 September 2020, M. Sánchez 2981 (ITCV). Loc. cit., 21 September 2022, M. Sánchez 2995 (ITCV). Loc. cit., 25 September 2022, M. Sánchez 3040 (ITCV) and 3049 (ITCV).

TABLE 3. Morphological comparisons of Geopyxis that are distributed in America.

Species	Apothecia	Paraphyses diameter	Asci	Ascospores	Country	Vegetation	Citations
G. aleuriodes	4–17 mm diameter, sessile to stipitate, stipe 5 × 2 mm, cupuliform, reddish brown to reddish orange.	2.5–3.5 (4) µm diameter, widening toward the apex.	200–230 × 10–13 µm	13.5–18.5 × 7–9 µm, subfusiform, smooth	Canada (Type), Switzerland	*Pinus*	Wang *et al*. (2016)
G. carolinae	3–11 mm diameter, sessile to subsessile, 1.5 mm high, cupuliform to discoid, greyish orange to melon.	2–3 µm diameter, filiform, not widening towards the apex.	260–310 × 12–14 (15) µm	17–23 (25) × 10–12 µm, ellipsoidal to oblong-ellipsoidal, smooth	Mexico	*Abies religiosa*	In this study
G. carbonaria	3–25 mm diameter-18 mm high, cupuliform, funnel-shaped, ochraceous-brown to brownish-orange.	2.5–5 (6) µm diameter, filiform, slightly widening towards the apex,	190–230 (250) × 9–13 µm	12–18 × 6.5–11 µm, subfusiform to fusiform, finely verrucose	Germany, Czech Republic, Canada, Denmark, Finland, India, Norway, Poland, Sweden, USA	Coniferous forest	Wang *et al*. (2016)
G. deceptiva	3–11 mm diameter, stipe 0.5–3 mm high, cupuliform to discoid, pale orange, brownish yellow, grayish orange, ochraceous yellow.	2–4 µm diameter, filiform, widening towards the apex.	230–270 (300) × 10–15 (17) µm	13.5–18.5 × 7.5–11 µm, ellipsoidal to subfusiform, smooth	USA (Type)	*Abies-Pinus*	Wang *et al*. (2016)
G. delectans	8–17 mm diameter, sessile to stipitate, stipule 1.5 × 1 mm, cupuliform to discoid, bright orange to orange brown.	2.5–4 (5) µm, clavate or capitate, widening towards the apex.	(165) 180–200 × 10–12 µm	11–15 × 6–9.5 µm, ellipsoidal, smooth	Sweden (Lectotypo), Finland, Norway, USA	Coniferous forest	Wang *et al*. (2016)
G. majalis	7.5–25 mm diameter, sessile to subsessile stipitate 2.5 × 1.5 mm, subglobose, cupuliform to discoid, pale yellow to pale orange.	2.5–4 µm diameter, filiform, slightly widening towards the apex, nodulous.	220–260 × 10–13 (15) µm	13–18.5 × 7–10.5 µm, subfusiform to fusiform, smooth	Sweden (Type), Cyprus, Greece, India, Spain, Mexico	*Cupressus*, *Pinus, Abies guatemalensis*	Wang *et al*. (2016), Raymundo *et al.* (2012, 2013)
G. vulcanalis	1–1.5 mm diameter, sessile to subsessile, yellow-orange.	2–3 (4) µm diameter, filiform, curved towards the apex.	200–250 × 8–11 µm	14–16 (18) × 7–9 µm, ellipsoid to subfusoid	Mexico	*Abies religiosa* forest	Chacón and Guzmán 1985.

Discussion

Geopyxis carolinae, described in the present study, is a species that presents the largest ascospores within the genus. Phylogenetically close to *G. rehmii* but differentiated by the size of its ascospores ornamented (verrucose, size: 10–19 × 9–10 µm), and by the diameter of its wider paraphyses (6–8 µm) (Wang *et al.* 2016). The species *G. majalis* and *G. korfii* are morphologically close but phylogenetically far because they are in different clades. *Geopyxis majalis* has smooth sub-fusiform ascospores (13–18.5 × 7–10.5 µm), with slightly wider paraphyses (2.5–4 µm); *G. korfii* has ornamented (verrucose), ellipsoid ascospores (12–15 × 8–10 µ), and narrower paraphyses (1.5–2 µm) (Wang *et al.* 2016).

The genus *Geopyxis* is little known in Mexico. Only a few species have been reported in the country. For example, *G. majalis* has been described with ornamented rough (Raymundo *et al.* 2012) and smooth ascospores (Wang *et al*. 2016). Their distribution reports include the States of Durango and Oaxaca growing in association with *Cupressus arizonica*, *Abies guatemalensis,* and *A. religiosa* (Raymundo *et al*. 2012, 2013). Rifai (1968) synonymized *Geopyxis vulcanalis* under *G. carbonaria* (Index Fungorum 2023). *Geopyxis carbonaria* was initially described in local studies as a species with considerably large ascospores (14–16 (18) × 7–9 µm), but data on its ornamentation is missing; Chacón y Guzmán (1985), associated the distribution with coniferous forests in the South and East of the Estado de México; Chio *et al*. (1988) reported its presence in the *Pinus-Quercus* forests of the entity but without providing a specific locality. Recently, *G. decpetiva* was described with smooth ascospores growing in the soil of disturbed forest. The information provided here contemplates a locality for *G. carolinae*, contributing to broadening knowledge of the genus in the country. Due to the richness of coniferous forests in Mexico, it would be relevant to carry on future studies of this genus.

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