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First Mexican Records of Seven Soil *Penicillium* and *Talaromyces* Species with Insights into Their Biotechnological Potential

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Abstract

Penicillium and *Talaromyces* are among the most diverse genera of filamentous fungi and play important ecological roles in soil ecosystems. Despite their ecological and biotechnological relevance, the diversity of these genera remains insufficiently documented in many tropical regions of Mexico. This study aimed to identify species of *Penicillium* and *Talaromyces* isolated from soils in Veracruz, Mexico, using an integrative taxonomic approach and to evaluate selected functional traits associated with their biotechnological potential. Species identification was achieved through an integrative framework combining morphology and multilocus phylogenetic analyses. Functional characterization included qualitative assessments of laccase, manganese peroxidase, lignin peroxidase, cellulolytic activity, and phosphate-solubilizing capacity. Seven species were identified, all of which are reported here for the first time from Mexico: *Penicillium citreosulfuratum*, *P. citrinum*, *P. crustosum*, *P. mallochii*, *P. shanghaiense*, *Talaromyces albobiverticillius*, and *T. aculeatus*. Several isolates exhibited ligninolytic, cellulolytic, and phosphate-solubilizing activities, indicating their potential roles in organic matter decomposition, nutrient cycling, and sustainable agricultural applications. These findings expand the known distribution of *Penicillium* and *Talaromyces* in Mexico, contribute to the documentation of the country's fungal diversity, and demonstrate the value of integrative taxonomy for revealing previously unrecorded fungal taxa in tropical soil ecosystems.

Keywords: soil fungi; integrative taxonomy; multilocus phylogeny; Mexico; tropical soils; phosphate solubilization; ligninolytic enzymes; biodiversity

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1. Introduction

Penicillium represents one of the most diverse lineages within Aspergillaceae (Eurotiales, Ascomycota) and constitutes a taxonomically complex group whose delimitation has undergone substantial revisions in recent decades. Currently, more than 535 species are accepted worldwide [1], and this number continues to increase as a result of integrative studies combining morphological, molecular, and ecological evidence, particularly from still underexplored tropical regions.

Traditionally, the classification of *Penicillium* was based on morphological characters such as conidiophore structure, branching patterns, conidial morphology, and colony characteristics on culture media. However, morphological homoplasy and the presence of cryptic species complexes have highlighted the limitations of these criteria for reliable

species delimitation. The development of molecular phylogenetics has enabled the redefinition of infrageneric sections and the establishment of more precise species boundaries through multilocus analyses. The implementation of molecular markers such as the ITS region, β-tubulin (*benA*), and calmodulin (*cmdA*) has been fundamental for resolving phylogenetic relationships within the genus and strengthening species circumscription [2,3]. In particular, the combined use of these loci has been shown to provide robust resolution in closely related taxonomic complexes, enabling reliable and internationally comparable phylogenetic diagnoses.

Within this systematic framework, it is also important to consider *Talaromyces*, which was previously included within *Penicillium* (subgenus Biverticillium) and is now recognized as an independent lineage within Aspergillaceae. The segregation of *Talaromyces* was supported by multilocus phylogenetic evidence and consistent morphological differences, exemplifying the importance of integrative approaches for achieving a natural taxonomic classification [3]. Both genera are frequent components of soil mycobiota and share ecological affinities, although they follow distinct evolutionary trajectories.

Despite global advances in fungal taxonomy, the diversity of *Penicillium* and *Talaromyces* in Mexico remains poorly documented. Although the country is recognized for its high fungal diversity, systematic studies supported by multilocus phylogenetic data are still limited, particularly in tropical regions such as the state of Veracruz. Many historical records are based solely on morphological criteria, which hinder accurate assessments of species distributions and the detection of previously unrecorded taxa.

In addition to their systematic relevance, species of *Penicillium* and *Talaromyces* exhibit important ecological functions and considerable biotechnological potential. Various taxa have demonstrated the ability to produce extracellular ligninolytic and cellulolytic enzymes, solubilize insoluble phosphates, and synthesize secondary metabolites with applications in agriculture, industry, and bioremediation. In tropical soil ecosystems, these functional traits may confer adaptive advantages and contribute to nutrient cycling, decomposition of organic matter, and phosphorus mobilization. The integration of phylogenetic data with functional characterization not only strengthens species delimitation but also improves the ecological understanding and potential biotechnological relevance of the taxa involved.

Recent studies in Mexico have highlighted the importance of integrative taxonomy for documenting fungal diversity and revealing previously unrecognized fungal taxa. Multilocus approaches have enabled the discovery of new fungal species and previously unrecorded taxa, demonstrating their value for improving the knowledge of fungal biodiversity in the country [4].

In this context, the present study documents seven species of *Penicillium* and *Talaromyces* recorded for the first time in Mexico, supported by multilocus phylogenetic analyses (ITS, *benA*, and *cmdA*) and detailed morphological characterization. Additionally, functional traits associated with their biotechnological potential were evaluated through qualitative enzymatic assays and phosphate-solubilization tests. By integrating taxonomy, phylogeny, and functional characterization, this study contributes to expanding the national inventory of both genera and improving the understanding of their diversity, ecological roles, and potential applications in tropical soil ecosystems.

2. Materials and Methods

2.1. Penicillium and Talaromyces Isolates

For this study, isolates of *Penicillium* and *Talaromyces* obtained between August 2021 and July 2022 were selected from soil samples collected in Veracruz, Mexico. The strains originated from coffee plantation soils in Jilotepec [5] and from hydrocarbon-contaminated soil in Villa Hermosa, Alamo [6].

Briefly, 1 g of air-dried soil from each sample was washed with purified water through a series of stainless-steel micro-sieves (Bel-Art SP Scienceware, Mini-Sieve Micro Sieve Set) with mesh openings of 1 mm, 500, 250, and 150 µm, following the soil particle filtration technique described by Bills et al. [7]. Soil particles retained on the 150 µm sieve were dried at 25 °C and placed onto Petri dishes containing dichloran rose bengal chloramphenicol agar (DRBC; Becton, Dickinson and Company, Franklin Lakes, NJ, USA). Plates were incubated at 25 °C for 15 days. Emerging fungal colonies were transferred to potato dextrose agar (PDA; DIBICO S.A. de C.V., Cuautitlán Izcalli, Mexico) to obtain pure cultures. Pure cultures were subsequently lyophilized using a Benchtop Freeze Dryer (Cat. No. 77500-00, LABCONCO Corporation, Kansas, MO, USA). The isolates were maintained at 4 °C under refrigeration and at −80 °C in an ultra-freezer (Model 8809 7400A, Thermo Fisher Scientific Inc., Waltham, MA, USA). For experimental procedures, the strains were reactivated on PDA plates prior to use.

All strains were deposited in the Fungal Culture Collection of the Instituto de Ecología, A.C. (INECOL), Xalapa, Veracruz, Mexico. Permanent microscopic preparations were also prepared for each taxonomic voucher and deposited in the XAL Herbarium (Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico). The corresponding herbarium accession numbers are provided in the taxonomic treatments.

2.2. DNA Extraction, PCR and Sequencing

Genomic DNA was extracted from the biomass of *Penicillium* and *Talaromyces* cultures grown on PDA after seven days at 25 °C using the Wizard® Genomic DNA Purification Kit (Promega, Madison, WI, USA), according to the manufacturer's instructions. The ITS rDNA region (ITS1–5.8S–ITS2), partial fragments of the *benA* (β-tubulin) and *cmdA* (calmodulin) genes were amplified by PCR using the primer pairs ITS5/ITS4 [8], TIHV, Ben2f or Bt2a/Bt2b or BtHV2R [9–11], and CL1 or CMD5/CMD6 or CF4 [12–14], respectively. PCR amplifications were performed in 25 µL reaction mixtures containing 13.75 µL sterile distilled water, 5 µL 5× MyTaq Reaction Buffer, 1 µL of each forward and reverse primer (10 µM), 0.25 µL MyTaq™ DNA Polymerase (Meridian Life Science Inc., Memphis, TN, USA), and 2 µL template DNA. PCR reactions were carried out in a Bio-Rad C1000 thermocycler (Bio-Rad Laboratories, Hercules, CA, USA) under the following cycling conditions: an initial denaturation at 95 °C for 3 min; 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 35 s, and extension at 72 °C for 1 min; followed by a final extension at 72 °C for 7 min. PCR products were purified and sequenced in both directions by Macrogen Inc. (Seoul, Republic of Korea). Sequence editing and assembly were performed as described by Arias et al. [4].

2.3. Phylogenetic Analyses

The newly generated sequences were analyzed using BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi, accessed on 11 March 2026) searches against the NCBI database [15] to find the closest related species. Accordingly, ITS, *benA* and *cmdA* sequences from reference strains representing the most closely related species were selected based on published literature, and their corresponding sequences were retrieved from the NCBI database. Reference sequences representing *Penicillium* section Exilicaulis series Citreonigra, section Citrina series Citrina and Sumatraensia, section Fasciculata series Camembertiorum, and section Sclerotiorum series Sclerotiorum were selected [16–19] and from *Talaromyces* sections Talaromyces and Trachyspermi [20,21]. The NCBI GenBank accession numbers of all the strains used in this study are listed in Table S1 (Supplementary Materials). The matrices of sequences of each recovered group were aligned with the corresponding *Penicillium* and *Talaromyces* sequences obtained in this study (Table 1). Sequences matrices of each

gene were individually aligned using MAFFT v.7.310 online service [22], then manually improved and concatenated in PhyDE v.0.9971 (http://www.phyde.de/download.html, accessed on 5 January 2026). Phylogenetic reconstructions of concatenated sequences of ITS+*benA*+*cmdA* were conducted using both Maximum Likelihood (ML) and Bayesian Inference (BI) approaches. ML analyses were performed using IQ-TREE 3.0.1 [23] under the following substitution models: TN+G4 for *Penicillium* section Exilicaulis, TN+I for section Fasciculata, TIM2+G4 for section Citrina, TIM2+I+G4 for section Sclerotiorum and *Talaromyces* sections Talaromyces and Trachyspermi, which were selected via ModelFinder [24] according to Bayesian Information Criterion (BIC). Node support values were estimated by generating 1000 samples for ultrafast bootstrap [25]. BI analyses were carried out using MrBayes v.3.2.6 [26], under the general time-reversible model (rates = invgamma, nst = 6), with unlinked parameters and rate variation amongst sites. Phylogenetic trees were visualized and edited using FigTree v.1.4.4 [27].

Table 1. Fungal isolates included in this study, their origin, GenBank accession numbers, and molecular identification based on multilocus phylogenetic analyses.

Species	Voucher	Substratum	GenBank Accession Number		
			ITS	*benA*	*cmdA*
Penicillium citreosulfuratum	IE7007	Hydrocarbon contaminated soil	PZ571754	PZ581615	PZ612837
Penicillium citrinum	IE7008	Hydrocarbon contaminated soil	PZ571755	PZ581616	-
Penicillium crustosum	IE7009	Coffee plantation soil	PZ571756	PZ581617	PZ612838
Penicillium crustosum	IE7014	Hydrocarbon contaminated soil	PZ571757	PZ581618	PZ612839
Penicillium crustosum	IE7012	Coffee plantation soil	PZ571758	PZ581619	-
Penicillium crustosum	IE7015	Coffee plantation soil	PZ571759	PZ581620	-
Penicillium crustosum	IE7010	Coffee plantation soil	PZ571762	-	-
Penicillium crustosum	IE7013	Coffee plantation soil	PZ571760	-	-
Penicillium crustosum	IE7011	Coffee plantation soil	PZ571761	-	-
Penicillium mallochii	IE7016	Coffee plantation soil	PZ571763	PZ581621	PZ612840
Penicillium shanghaiense	IE7017	Coffee plantation soil	PZ571764	-	-
Penicillium shanghaiense	IE7020	Coffee plantation soil	-	PZ581622	PZ612841
Talaromyces aculeatus	IE7019	Coffee plantation soil	PZ571765	PZ581623	PZ612842
Talaromyces albobiverticillius	IE7018	Coffee plantation soil	PZ571767	PZ581625	PZ612844
Talaromyces albobiverticillius	IE7021	Coffee plantation soil	PZ571766	PZ581624	PZ612843

2.4. Culture Conditions and Morphological Characterization

To evaluate colony morphology, each isolate was grown on Czapek Yeast Extract Agar (CYA), Malt Extract Agar (MEA), Potato Dextrose Agar (PDA), and Yeast Extract Sucrose Agar (YES). CYA medium contained (per liter of distilled water): K_2HPO_4 (1.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), laboratory-prepared Czapek concentrate (10 mL), yeast extract (5.0 g; EMD Millipore Corporation, Burlington, MA, USA), sucrose (30.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), and agar (15.0 g; Becton, Dickinson and Company, Franklin Lakes, NJ, USA). MEA contained malt extract (20.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), peptone (1.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), glucose (20.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), and agar (20.0 g). YES medium contained yeast extract (10.0 g), dextrose (15.0 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), and agar (20.0 g). PDA was prepared according to the manufacturer's instructions (Difco Laboratories, Detroit, MI, USA).

For each isolate, three independent replicate plates were prepared for each culture medium. Each 90 mm Petri dish was inoculated with three equidistant 5 mm diameter mycelial plugs obtained from the actively growing margin of seven-day-old colonies. The

three inoculation points within each plate were used to verify the consistency of colony development but were not considered independent experimental replicates. Plates were incubated at 25 °C in darkness for 7 days. Colony diameters were measured using a digital caliper, and the results are expressed as mean ± standard deviation (SD) based on the three independent replicate plates.

Macromorphological characteristics, including colony diameter, texture, surface and reverse coloration, production of exudates, soluble pigments, colony margin, and growth on CYA at 4 °C and 37 °C, were recorded following 7 days of incubation according to the taxonomic criteria of Visagie et al. [28]. Colony diameters are reported in the species descriptions as mean ± SD (mm).

Micromorphological observations were performed from colonies grown on MEA using slide preparations mounted in lactic acid (Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA). The morphology of conidiophores, stipes, metulae, phialides, conidia, and other diagnostic structures was examined and photographed using an Olympus BX53 light microscope equipped with an Olympus DP74 digital camera (Olympus Corporation, Tokyo, Japan). Taxonomic identification was based on the diagnostic morphological characters described for *Penicillium* and *Talaromyces* species by Visagie et al. [28].

2.5. Functional Characterization and Biotechnological Potential of the Strains

2.5.1. Phosphate-Solubilizing Activity

Phosphate-solubilizing activity was evaluated following the method of Sundara Rao and Sinha [29]. A modified Sundara Rao and Sinha agar medium containing (per liter of distilled water): glucose (10 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), tricalcium phosphate (5 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), ammonium sulfate (0.5 g; Realyt's Productos Químicos, Mexico City, Mexico), sodium chloride (0.2 g; Materiales y Abastos Especializados, S.A. de C.V., Mexico City, Mexico), potassium chloride (0.2 g; Fermont, Monterrey, NL, Mexico), magnesium sulfate·$7H_2O$ (0.1 g; Realyt's Productos Químicos, Mexico City, Mexico), manganese sulfate (0.002 g; Realyt's Productos Químicos, Mexico City, Mexico), ferrous sulfate (0.002 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), yeast extract (0.5 g; EMD Millipore Corporation, Burlington, MA, USA), and agar (15 g; Becton, Dickinson and Company, Franklin Lakes, NJ, USA) was prepared. The medium was sterilized by autoclaving and poured into 90 mm Petri dishes. Isolates were inoculated with 5 mm mycelial plugs taken from the actively growing margin of seven-day-old colonies. All assays were performed in triplicate using three independent replicate plates per isolate and incubated at 25 ± 2 °C for 7 days. Phosphate-solubilizing activity was assessed qualitatively based on the formation of a clear halo surrounding the colony due to the solubilization of tricalcium phosphate and was recorded as positive (+) or negative (−).

2.5.2. Cellulolytic Activity

Cellulolytic activity was evaluated using the carboxymethyl cellulose (CMC) hydrolysis method described by Mandels and Weber [30], with slight modifications. A modified Czapek medium containing (per liter of distilled water): yeast extract (2 g; EMD Millipore Corporation, Burlington, MA, USA), sodium nitrate (2 g; Realyt's Productos Químicos, Mexico City, Mexico), potassium chloride (0.5 g; Fermont, Monterrey, NL, Mexico), magnesium sulfate (0.5 g; Realyt's Productos Químicos, Mexico City, Mexico), ferrous sulfate (0.01 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), potassium phosphate (1 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), sodium carboxymethyl cellulose (20 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), and agar (20 g; Becton, Dickinson and Company, Franklin Lakes, NJ, USA) was used. The medium was

sterilized by autoclaving and poured into 90 mm Petri dishes. Isolates were inoculated with 5 mm mycelial plugs taken from the actively growing margin of seven-day-old colonies. All assays were performed in triplicate using three independent replicate plates per isolate and incubated at 25 ± 2 °C for 5 days. After incubation, the plates were flooded with 2% Congo red solution (Hycel de México, S.A. de C.V., Zapopan, Jalisco, Mexico) for 15 min and washed with 1 M NaCl (Materiales y Abastos Especializados, S.A. de C.V., Mexico City, Mexico) to remove excess Congo red. Cellulolytic activity was assessed qualitatively based on the formation of a clear or yellow hydrolysis zone surrounding the colony and was recorded as positive (+) or negative (−).

2.5.3. Ligninolytic Enzyme Activity

Ligninolytic enzyme activity was evaluated following the methodology of Rubilar-Araneda [31]. A basal medium containing (per liter of distilled water): glucose (10 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), KH_2PO_4 (2 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), agar (25 g; Becton, Dickinson and Company, Franklin Lakes, NJ, USA), ammonium tartrate (0.2 g; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA), $CaCl_2 \cdot 2H_2O$ (0.1 g; Materiales y Abastos Especializados, S.A. de C.V., Mexico City, Mexico), and $MgSO_4 \cdot 7H_2O$ (0.5 g; Realyt's Productos Químicos, Mexico City, Mexico) was prepared. All medium components were dissolved in distilled water and sterilized by autoclaving. Chromogenic substrates were sterilized separately by filtration when necessary and added aseptically to the medium after cooling to approximately 45–50 °C before pouring into 100 × 20 mm Petri dishes. All assays were performed in triplicate using three independent replicate plates per isolate. Plates were inoculated with 5 mm mycelial plugs taken from the actively growing margin of seven-day-old colonies and incubated at 25 ± 2 °C.

Laccase (Lac) activity was determined using ABTS (2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid); Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA) as the chromogenic substrate. Plates were incubated for 8 days, and positive activity was indicated by the development of an emerald-green coloration in the medium surrounding the colony due to ABTS oxidation.

Lignin peroxidase (LiP) activity was evaluated using Azure B (methylene azure B chloride; Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA) as the chromogenic indicator. Plates were incubated for 15 days, and positive activity was evidenced by decolorization of the medium, changing from blue-violet to colorless around the colony.

Manganese peroxidase (MnP) activity was evaluated using phenol red (Sigma-Aldrich Manufacturing LLC, St. Louis, MO, USA) as the chromogenic indicator. Plates were incubated for 15 days, and positive activity was evidenced by a color change in the medium from red to yellow-orange surrounding the colony.

For all three ligninolytic enzymes, activity was evaluated qualitatively according to the characteristic color changes in the indicator media and recorded as positive (+) or negative (−). No halo measurements or enzymatic indices were determined for these assays because enzyme activity was based on chromogenic reactions rather than substrate hydrolysis.

3. Results

3.1. Molecular Identification and Phylogenetic Analyses

DNA was successfully extracted from all 15 isolates representing the seven identified species. The ITS barcode region and partial fragments of the *benA* and *cmdA* genes were successfully amplified and sequenced, with additional loci obtained for representative isolates depending on amplification success. BLAST searches and multilocus phylogenetic analyses confirmed the placement of the isolates within the genera *Penicillium* and *Talaromyces*. The

phylogenetic trees revealed that all isolates clustered with the ex-type or reference strains of their respective species, with high bootstrap support and Bayesian posterior probabilities (Figures 1 and 2). The GenBank accession numbers and molecular identification results for all isolates are summarized in Table 1.

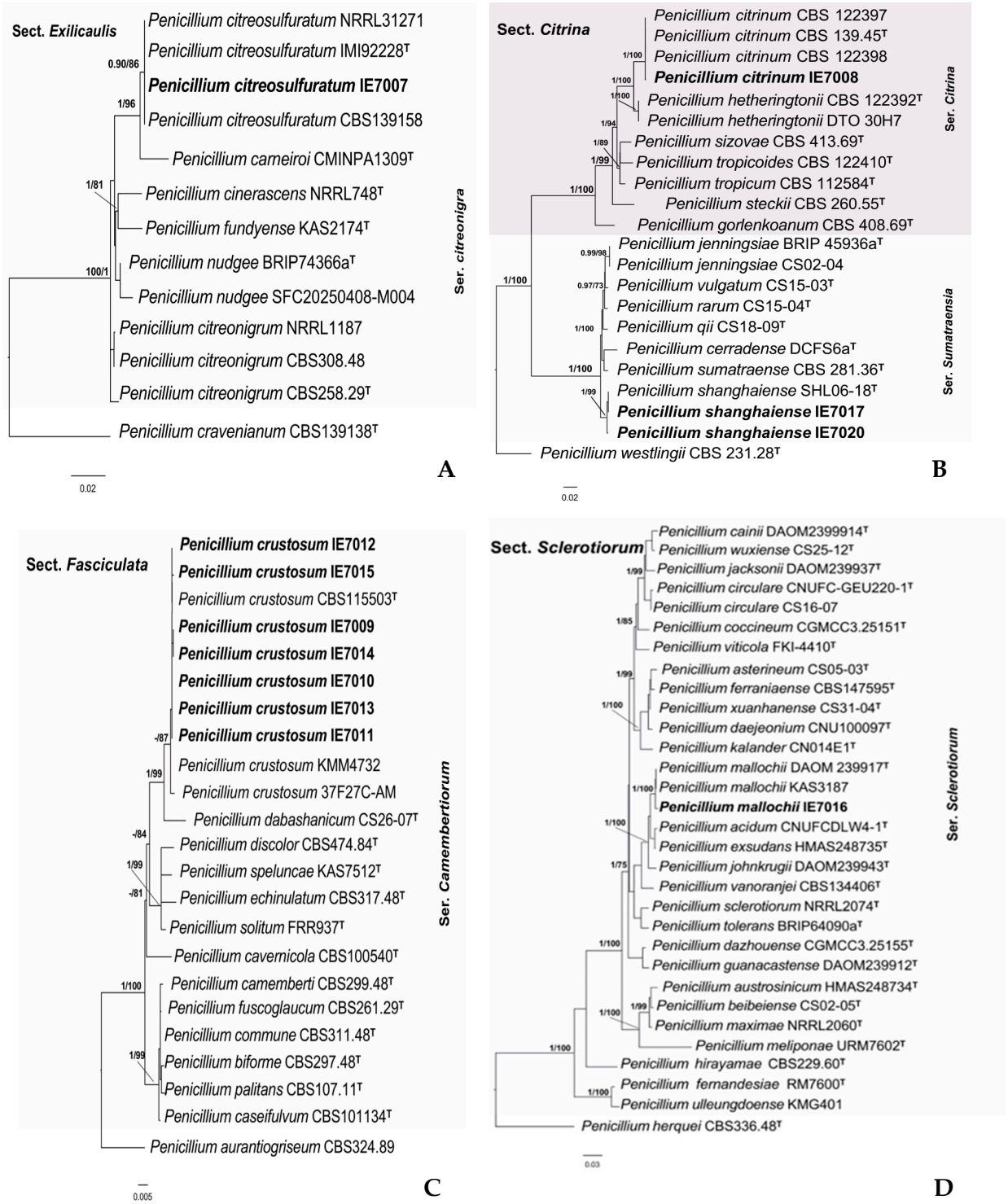

Figure 1. Maximum likelihood phylogenetic trees inferred by the combined ITS, *benA* and *cmdA* sequences of *Penicillium*. (**A**) Section Exilicaulis series Citreonigra, (**B**) Section Citrina series Sumatraensia and citrina, (**C**) Section Fasciculata series Camembertiorum and (**D**) Section Sclerotiorum Series Sclerotiorum. Bootstrap support values ≥70% and Bayesian posterior probabilities ≥0.90 are indicated at the nodes. Sequences from the studied material are indicated in bold. T = from type Material.

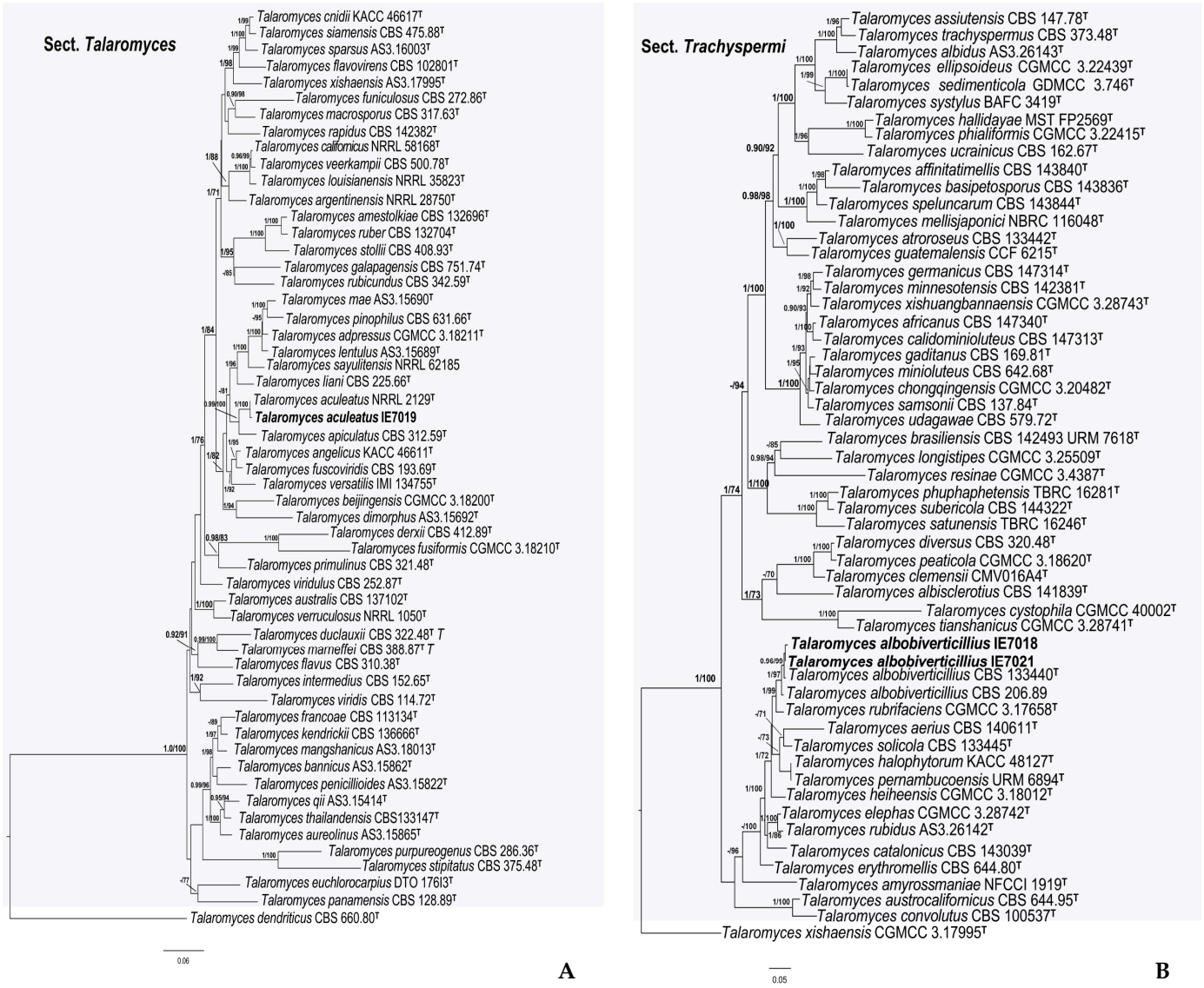

Figure 2. Maximum likelihood phylogenetic trees inferred by the combined ITS, *benA* and *cmdA* sequences of *Talaromyces* sections Talaromyces (**A**) and Trachyspermi (**B**). Bootstrap values ≥70% (left) and Bayesian posterior probability values ≥ 0.90 (right) are indicated at nodes. Sequences from the studied material are indicated in bold. T = from type Material.

3.2. Taxonomy

Based on the morphological and molecular evidence, seven species belonging to the genera *Penicillium* and *Talaromyces* were identified. Their taxonomic treatments are presented below.

Penicillium citreosulfuratum Biourge, *Cellule* 33: 285 (1923) (Figure 3).

Colony diameters after 7 d (mm) at 25 °C: YES, 12.6 ± 0.7; MEA, 18.0 ± 0.7; PDA, 20.3 ± 0.3; CYA, 5.2 ± 0.4. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies circular, floccose, white at the margins and yellow centrally, with slight radial sulcation and sparse sporulation; conidial masses white-green to dull green. Reverse pale to intense yellow, darker centrally. MEA: Colonies low to plane, velutinous to floccose, white at the margins and yellow elsewhere, with moderate sporulation and dull green to grey-green conidial masses; soluble yellow pigment weakly produced. Reverse greenish yellow to pale yellow, darker at the inoculation point. PDA: Colonies compact, velutinous to floccose, intense yellow to yellow-orange, with raised centers, distinct radial sulcation, and sparse sporulation. Reverse yellow-orange

to orange, darker centrally. CYA: Slow-growing colonies, floccose and yellowish, with radial sulcation, sparse to moderate sporulation, and grey to dark green conidial masses; soluble yellow pigment produced. Reverse yellow to yellow-orange, darker centrally.

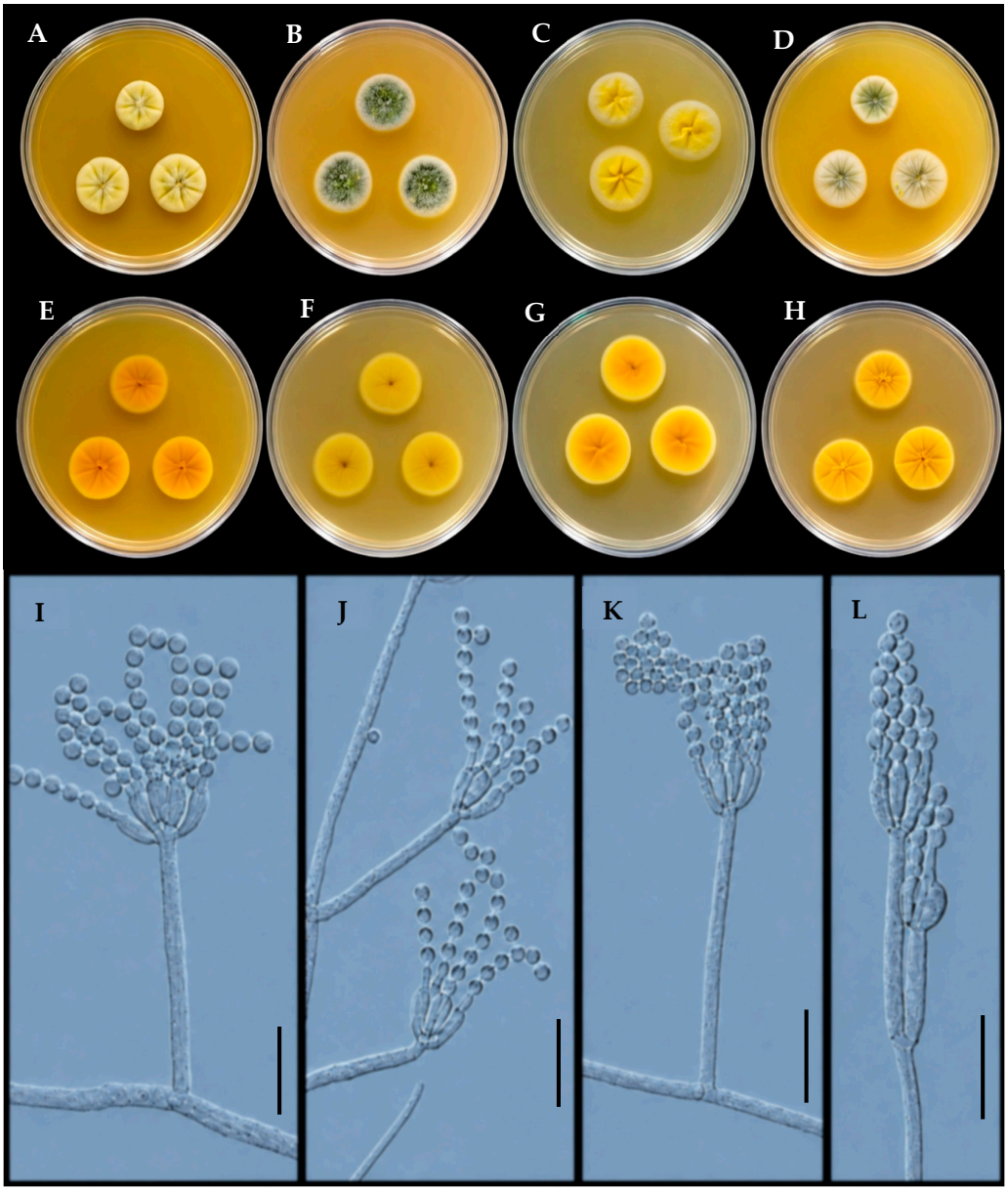

Figure 3. Morphology of *Penicillium citreosulfuratum*. Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**L**). Scale bars: 10 µm.

Micromorphology: Conidiophores predominantly monoverticillate, occasionally biverticillate, smooth-walled and hyaline. Stipes septate, 20–30 × 1.5–2.0 µm. Phialides ampulliform to lageniform, 5.2–8.2 µm long, arranged in compact verticils. Metulae short and poorly differentiated. Conidia globose to subglobose, smooth-walled, formed in basipetal chains, 1.1–2.4 µm diam.

Notes: The BLASTn analysis of the ITS, *benA* and *cmdA* sequences of the strain IE7007 indicated 99.82%, 99.55% and 99.78% sequence identity, respectively with the sequences of the ex-type strain of *P. citreosulfuratum* IMI 92228 [16]. Phylogenetic analyses of *P. citreosulfuratum* and related species with concatenated ITS + *benA* + *cmdA* sequences showed that the Mexican specimen was placed in the same clade with high support (PP = 0.90 and

BS = 86) as the sequence of the ex-type strain of *P. citreosulfuratum* IMI 92228 (Figure 1A). This isolate was consistent with the original description of *P. citreosulfuratum*, particularly in the compact yellow colonies, soluble pigment production and sparse sporulation. *P. citreosulfuratum* is morphologically similar to *P. cinerascens*, *P. citreonigrum* and *P. fundyense*, but differs in its ability to grow on CYA at 37 °C.

Material examined: Mexico, Veracruz, Villa Hermosa, Alamo, 20°57′54.0″ N, 97°35′47.9″ W, 41 m a.s.l., from hydrocarbon-contaminated soil, 27 July 2022, R. Fernandez RN9; IE7007 (living culture, INECOL); XAL CB2315 (permanent microscopic preparation).

Penicillium citrinum Thom, U.S.D.A. Bur. Animal Industr. Bull. 118: 61 (1910) (Figure 4).

Figure 4. Morphology of *Penicillium citrinum*. Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**L**). Scale bars: 10 µm.

Colony diameters after 7 d (mm) at 25 °C: YES, 19.0 ± 0.9; MEA, 18.1 ± 0.5; PDA, 25.1 ± 0.8; CYA, 11.3 ± 1.9. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies circular, compact, velutinous to slightly floccose, white to cream, with sparse sporulation and soluble yellow pigment production. Reverse intense yellow to golden yellow, darker centrally. MEA: Colonies slow to moderately growing, with bluish-green conidial masses produced mainly in the colony center; peripheral mycelium white and sparse. Reverse pale cream to yellowish. PDA: Colonies compact, white to cream, with umbonate centers, conspicuous radial sulcation,

and sparse sporulation. Reverse pale to light yellow, darker centrally. CYA: Colonies moderately growing, slightly elevated, with moderate sporulation and orange-red to yellow-orange conidial masses; soluble yellow pigment produced. Reverse intense yellow with characteristic orange areas in the colony center.

Micromorphology: Conidiophores arising from superficial or submerged hyphae; stipes smooth-walled, 100–300 µm long, terminating in verticils of 3–5 divergent metulae; branches and subterminal or intercalary metulae occasionally present. Metulae 12–15 µm long, commonly spatulate to terminally vesiculate, up to 5 µm wide. Phialides ampulliform, 7–8(–12) µm long. Conidia globose to subglobose, 2.2–3.0 µm diam, smooth-walled to very finely roughened, produced in long, well-defined columns, usually one per metula.

Notes: The BLASTn analysis of the ITS and *benA* sequences of strain IE7008 against those of the ex-type strain of *P. citrinum* CBS 139.45 [17] supported 100% and 99.77% identity, respectively. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of related *Penicillium* species demonstrated that the Mexican strain was placed in the same clade as reference sequences of *P. citrinum*, including the sequence of the ex-type (Figure 1B) with the highest support (PP = 1; BS = 100). *P. citrinum* was characterized by fast-growing colonies, yellow-green sporulation and production of soluble yellow pigments, distinguishing it from species such as *P. citreosulfuratum*, which typically forms predominantly yellow colonies with sparse sporulation. Pitt [32] recognized *P. citrinum* by its penicilli composed of 3–5 divergent, usually vesiculate metulae bearing long columns of conidia.

Material examined: Mexico, Veracruz, Villa Hermosa, Alamo, 20°57′54.0″ N, 97°35′47.9″ W, 41 m a.s.l., from hydrocarbon-contaminated soil, 27 July 2022, R. Cruz RO10; IE7008 (living culture, INECOL); XAL CB2316 (permanent microscopic preparation).

Penicillium crustosum Thom, The Penicillia: 399 (1930) (Figure 5).

Colony diameters after 7 d (mm) at 25 °C: YES, 28.9 ± 0.7; MEA, 32.7 ± 0.6; PDA, 28.0 ± 1.5; CYA, 21.6 ± 0.7. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies moderately fast growing, velutinous, white at the margins with sparse grey-green conidial masses centrally and faint radial zonation. Reverse bright to intense yellow, darker centrally. MEA: Colonies fast growing, velutinous to slightly granular, with abundant bluish-green to deep green sporulation. Reverse pale yellow to yellow, more intense centrally. PDA: Colonies moderately growing, velutinous, with abundant grey-green sporulation, well-developed white peripheral mycelium, and radially sulcate centers. Reverse pale yellow to yellow, darker centrally, with weakly diffusible pigment. CYA: Colonies moderately growing, velutinous, with abundant grey-green to bluish-green conidial masses and radial zonation. Reverse pale cream to yellowish, with weak pigmentation.

Micromorphology: Conidiophores predominantly terverticillate, rarely biverticillate; stipes smooth-walled, septate, hyaline, 80–250 × 2.5–4 µm, arising directly from vegetative hyphae. Metulae in well-developed verticils, usually 3–5 per branch, cylindrical to slightly divergent, 7–12 µm long. Phialides ampulliform to subcylindrical, arranged in compact verticils, 4–8 per metula, 6–10 × 2–3 µm. Conidia globose to subglobose, smooth-walled to finely roughened, formed in compact basipetal chains, 1.7–2.7 µm diam, predominantly 1.9–2.5 µm; conidial masses grey green to dark green.

Notes: The BLASTn analysis of the ITS sequences of strains IE7012, IE7011, IE7015, IE7010, IE7013, IE7014 and IE7009 sequences confirmed 99.82–100% identity with the ex-type strain of *P. crustosum* CBS 115503 [19]. From these strains the four *benA* and two *cmdA* obtained sequences showed both 100% identity with the ex-type specimen. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of the related *Penicillium* species placed these strains in the same clade with high support (BS = 87) as the

reference sequences of *P. crustosum* including the ex-type strain CBS 115503 (Figure 1C). The isolate corresponded well with *P. crustosum* in its penicillus structure, abundant blue-green sporulation, and conidial morphology. Although the conidiophores were slightly shorter than those reported in the original species description, these differences have been documented among strains from different substrates and culture conditions and do not affect species delimitation when morphological and molecular evidence are considered together [19,33].

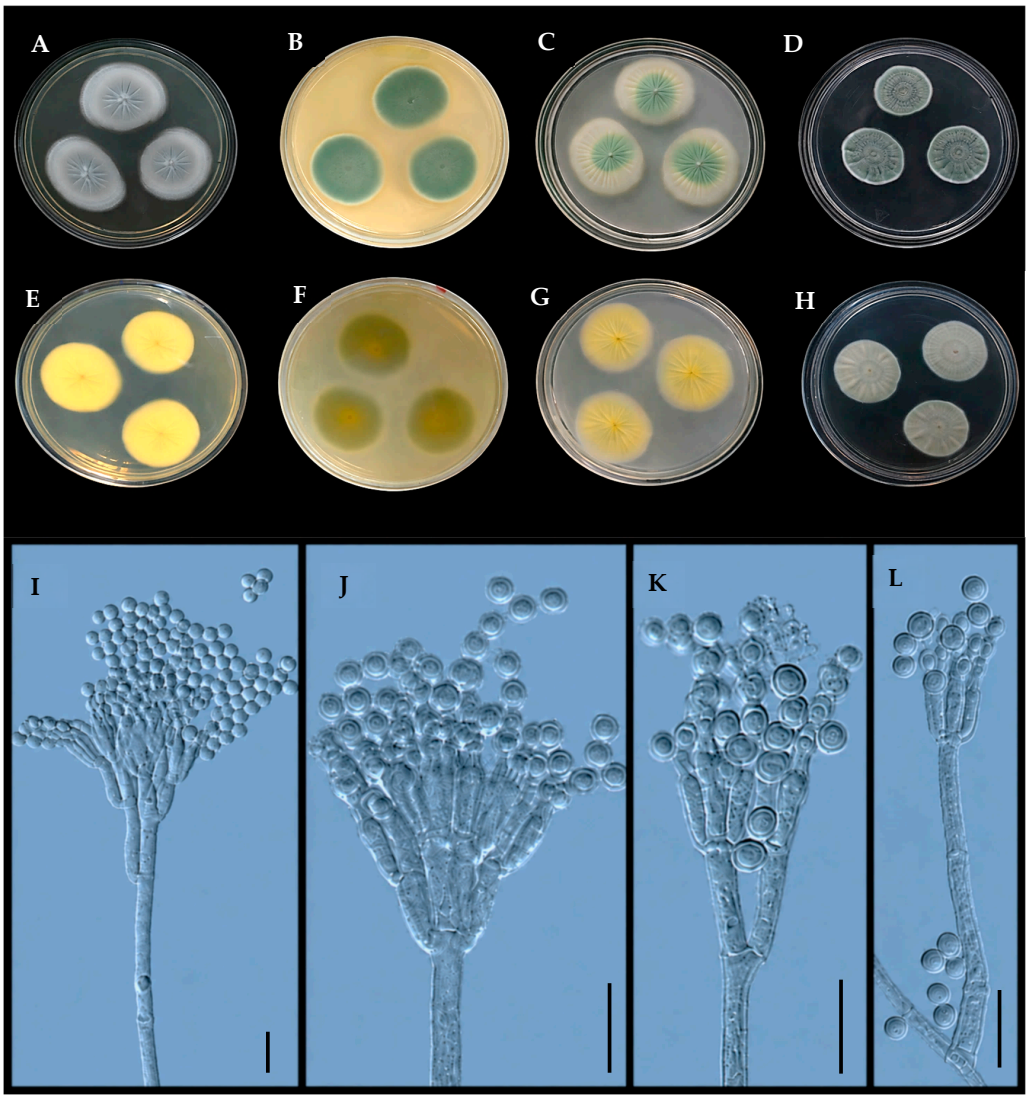

Figure 5. Morphology of *Penicillium crustosum.* Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**L**). Scale bars: 10 µm.

Material examined: Mexico, Veracruz, Jilotepec, Los Bambus, 19°36′44″ N, 96°00′16.5″ W, 1370 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA25 (living culture IE7012; permanent microscopic preparation XAL CB2317). Jilotepec, San Isidro, 19°36′11″ N, 96°54′46″ W, 1412 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA5 (living culture IE7011; permanent microscopic preparation XAL CB2318) and RA15 (living culture IE7015; permanent microscopic preparation XAL CB2319). Jilotepec, La Barranca, 19°36′40″ N, 96°55′40.5″ W, 1484 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA34 (living culture IE7010; permanent microscopic preparation XAL CB2320), RA50 (living culture IE7013; permanent microscopic preparation XAL

CB2321), and RA103H (living culture IE7009; permanent microscopic preparation XAL CB2322). Mexico, Veracruz, Villa Hermosa, Alamo, 20°57′54.0″ N, 97°35′47.9″ W, 41 m a.s.l., from hydrocarbon-contaminated soil, 27 July 2022, R. Cruz RO12 (living culture IE7014; permanent microscopic preparation XAL CB2323).

Penicillium mallochii Rivera, Urb & Seifert, Mycotaxon 119: 322 (2012) (Figure 6).

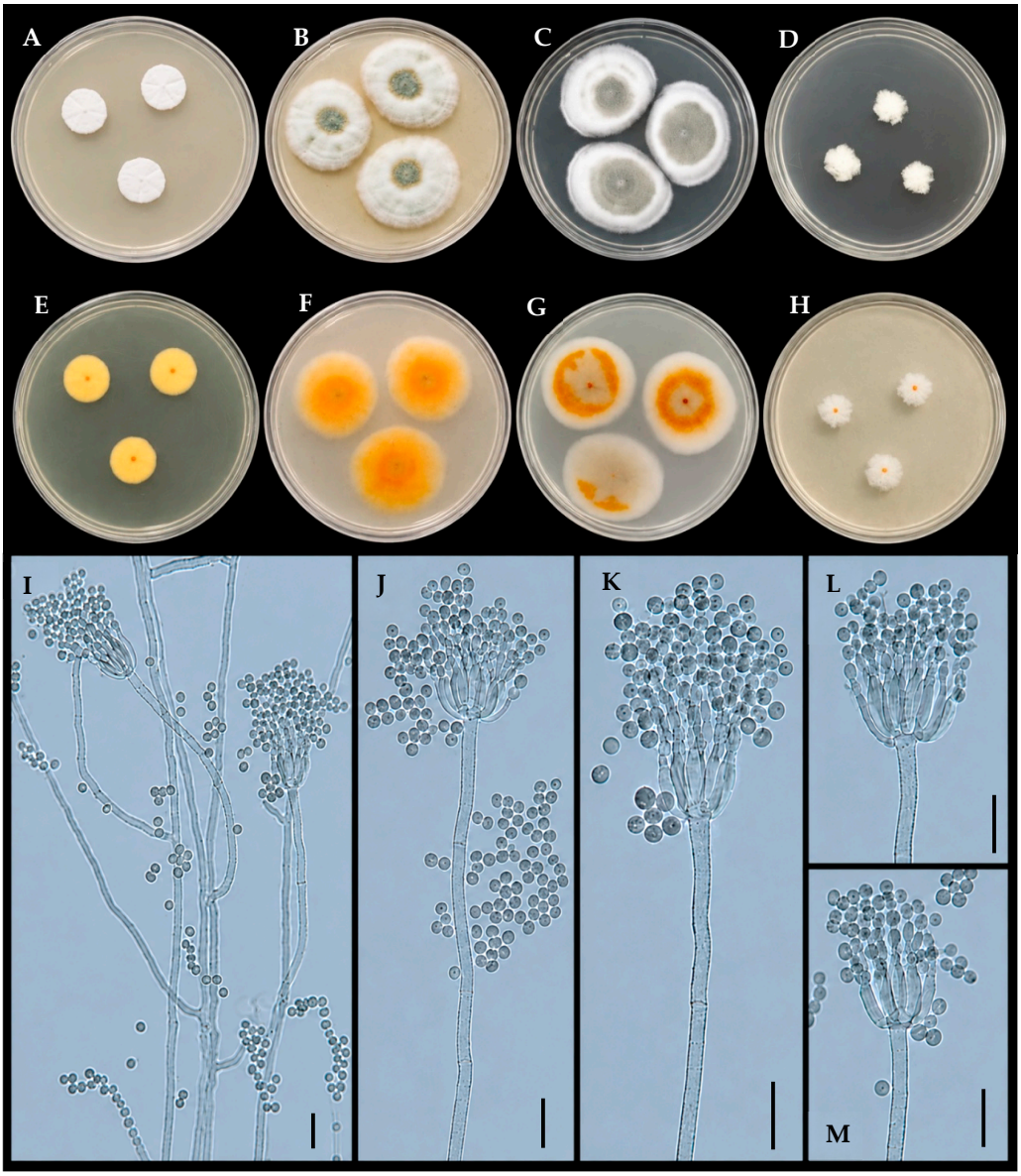

Figure 6. Morphology of *Penicillium mallochii*. Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**M**). Scale bars: 10 µm.

Colony diameters after 7 d (mm) at 25 °C: YES, 14.2 ± 1.0; MEA, 33.3 ± 1.0; PDA, 30.4 ± 1.1; CYA, 8.9 ± 1.9. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies slow to moderately growing, compact, white to cream, floccose to slightly velutinous, with very sparse sporulation. Reverse pale yellow, darker centrally. MEA: Colonies moderately growing, floccose, with grey-green conidial masses developing centrally and evident radial zonation. Reverse yellow to yellow-orange, more intense centrally and diffusing toward the periphery. PDA: Colonies moderately growing, with abundant white mycelium, moderate central sporulation, grey-green conidial masses, and slightly umbonate centers. Reverse yellow-orange to orange,

darker centrally, with slight pigment diffusion. CYA: Colonies slow growing, compact, elevated, and white, with sparse or absent sporulation. Reverse pale cream with slight yellowish tones centrally.

Micromorphology: Conidiophores monoverticillate, hyaline, smooth-walled to slightly roughened, simple or rarely branched, 49–82(–100) × 1.7–2.9 µm; apex slightly vesiculate. Phialides ampulliform to lageniform, arranged in terminal verticils, (7.8–)8.3–10.3(–12) × 1.7–2.8 µm. Conidia globose to subglobose, smooth-walled to finely roughened, hyaline, 1.3–2.7 µm diam, produced in terminal mucilaginous masses.

Notes: The BLASTn analysis of the ITS, *benA* and *cmdA* sequences of the strain IE7016 with the reference sequences of *P. mallochii* [34] indicated 99.63–99.81%, 98.89–99.78%, and 98.95–99.37% sequence identity. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of related *Penicillium* species supported that the Mexican strain was placed in the same clade as reference sequences including the ex-type strain DAOM 239917 of *P. mallochii* (Figure 1D) with the highest support (PP = 1 and BS = 100). Morphologically, the isolate corresponded well to *P. mallochii* as originally described by Rivera et al. [34], although the material exhibited somewhat shorter conidiophores, less conspicuous vesicles and slightly smaller conidia. These differences are considered within the expected phenotypic variability of the species, particularly because multilocus sequence analyses demonstrated high sequence similarity with reference sequences of *P. mallochii*.

Material examined: Mexico, Veracruz, Jilotepec, La Barranca, 19°36′40″ N, 96°55′40.5″ W, 1484 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA26P; IE7016 (living culture, INECOL); XAL CB2324 (permanent microscopic preparation).

Penicillium shanghaiense X.C. Wang & W.Y. Zhuang, J. Fungi 10 (5, no. 342): 9 (2024) (Figure 7).

Colony diameters after 7 d (mm) at 25 °C: YES, 25.4 ± 0.2; MEA, 24.6 ± 0.8; PDA, 21.4 ± 0.4; CYA, 21.9 ± 1.0. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies slow growing, compact, white, velutinous to slightly floccose, with sparse to moderate central sporulation. Reverse pale yellow to light orange, darker centrally. MEA: Colonies moderately growing, velutinous to slightly floccose, with abundant grey-green conidial masses and evident concentric zonation. Reverse bright to deep orange, more intense centrally. PDA: Colonies moderately growing, with abundant white mycelium, moderate to abundant grey-green sporulation, slight radial sulcation, and somewhat umbonate centers. Reverse orange-brown to amber, darker centrally, with slight pigment diffusion. CYA: Colonies slow growing, compact to pulvinate, with moderate central sporulation and grey-green conidial masses. Reverse cream to pale yellow with slight orange tones centrally.

Micromorphology: Conidiophores biverticillate to terverticillate; stipes smooth-walled, 85–415 × 2.0–3.0 µm; branches 21.5–32.5 × 2.0–3.0 µm; metulae 9.5–17.5 × 2.0–5.0 µm; phialides ampulliform, 6.0–9.0 × 2.0–3.0 µm; conidia subglobose, smooth-walled, 2.0–3.0 µm diam.

Notes: The BLASTn analysis of the ITS, *benA*, and *cmdA* sequences of strains IE7017 and IE7020 showed 100% identity with those of the ex-type strain of *P. shanghaiense* SHL06-18 [35]. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of related species of *Penicillium* confirmed the identity, placing the Mexican strain in the same clade as the ex-type strain of *P. shanghaiense* with high support (PP = 1 and BS = 99) (Figure 1B). Micromorphologically, the isolate corresponded well with the original description in possessing biverticillate to terverticillate conidiophores, smooth-walled stipes, metulae arranged in verticils, ampulliform phialides with narrow necks, and smooth-walled subglobose conidia. The observed differences, mainly denser conidial heads, more compact penicilli

and slightly larger conidia, are considered within the expected intraspecific variability or attributable to culture and observation conditions.

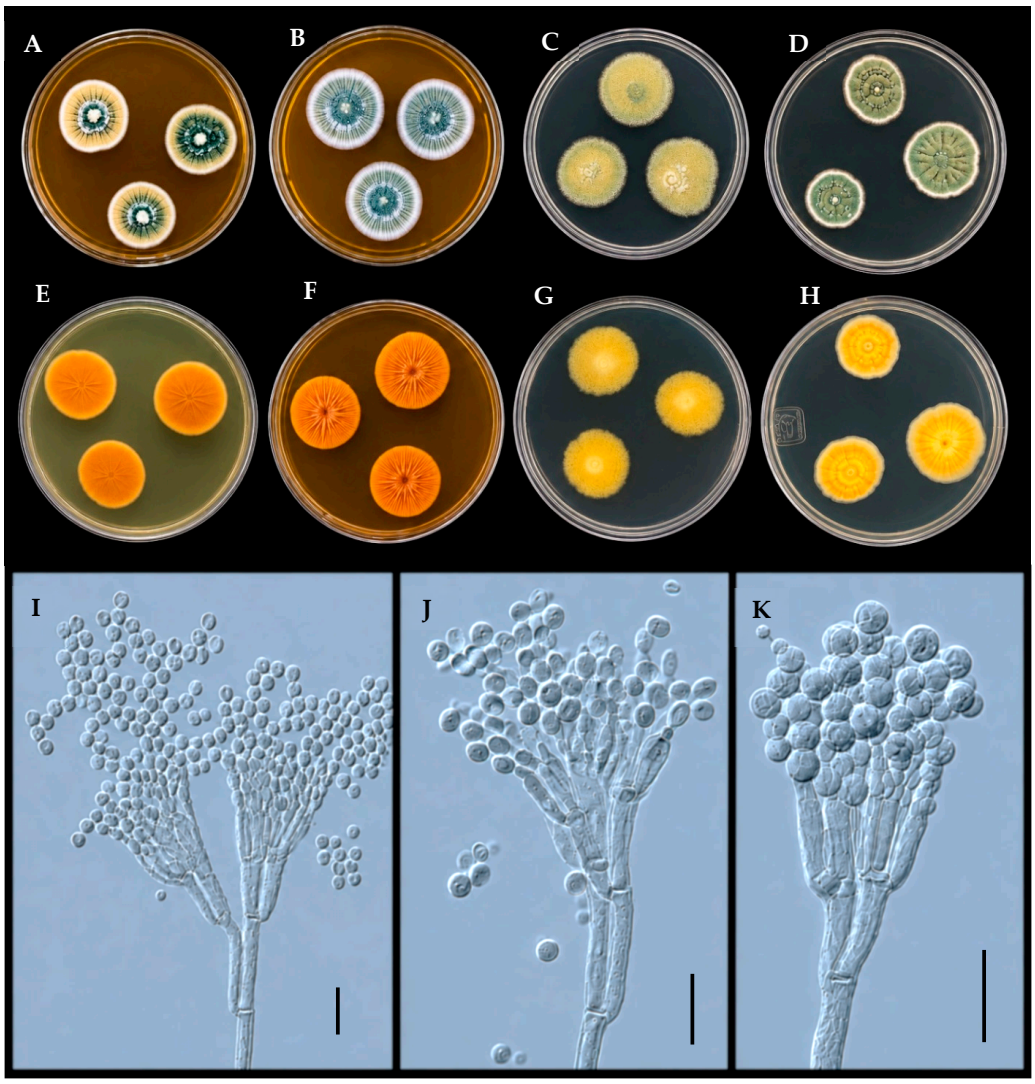

Figure 7. Morphology of *Penicillium shanghaiense.* Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**K**). Scale bars: 10 µm.

Material examined: Mexico, Veracruz, Jilotepec, Los Bambus, 19°36′44″ N, 96°00′16.5″ W, 1370 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA59; IE7017 (living culture, INECOL); XAL CB2325 (permanent microscopic preparation). Jilotepec, La Barranca, 19°36′40″ N, 96°55′40.5″ W, 1484 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA28; IE7020 (living culture, INECOL); XAL CB2326 (permanent microscopic preparation).

Talaromyces aculeatus (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, Stud. Mycol. 70: 174 (2011) (Figure 8).

Colony diameters after 7 d (mm) at 25 °C: YES, 26.8 ± 0.4; MEA, 28.7 ± 0.6; PDA, 25.2 ± 0.2; CYA, 35.3 ± 1.0. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies moderately fast growing, densely floccose with abundant white aerial mycelium and sparse to moderate central sporulation, developing pale salmon to pinkish tones. Reverse bright yellow to orange-yellow with a darker reddish-orange center and slightly diffusible pigment production. MEA: Colonies moderately fast growing, floccose, with pronounced radial furrows, pinkish to salmon

centers, and greenish sporulation in mature areas. Reverse deep orange to amber, darker centrally, with slight pigment diffusion. PDA: Colonies moderately growing, compact, with dense white mycelium, sparse to moderate sporulation, and pale salmon to light pink shades; centers slightly umbonate. Reverse pale yellow-orange with reddish-brown central pigmentation. CYA: Colonies moderately growing, densely floccose, with moderate central sporulation and grey-green to pale olive conidial masses in older portions. Reverse yellow to orange-yellow with darker reddish-brown central areas.

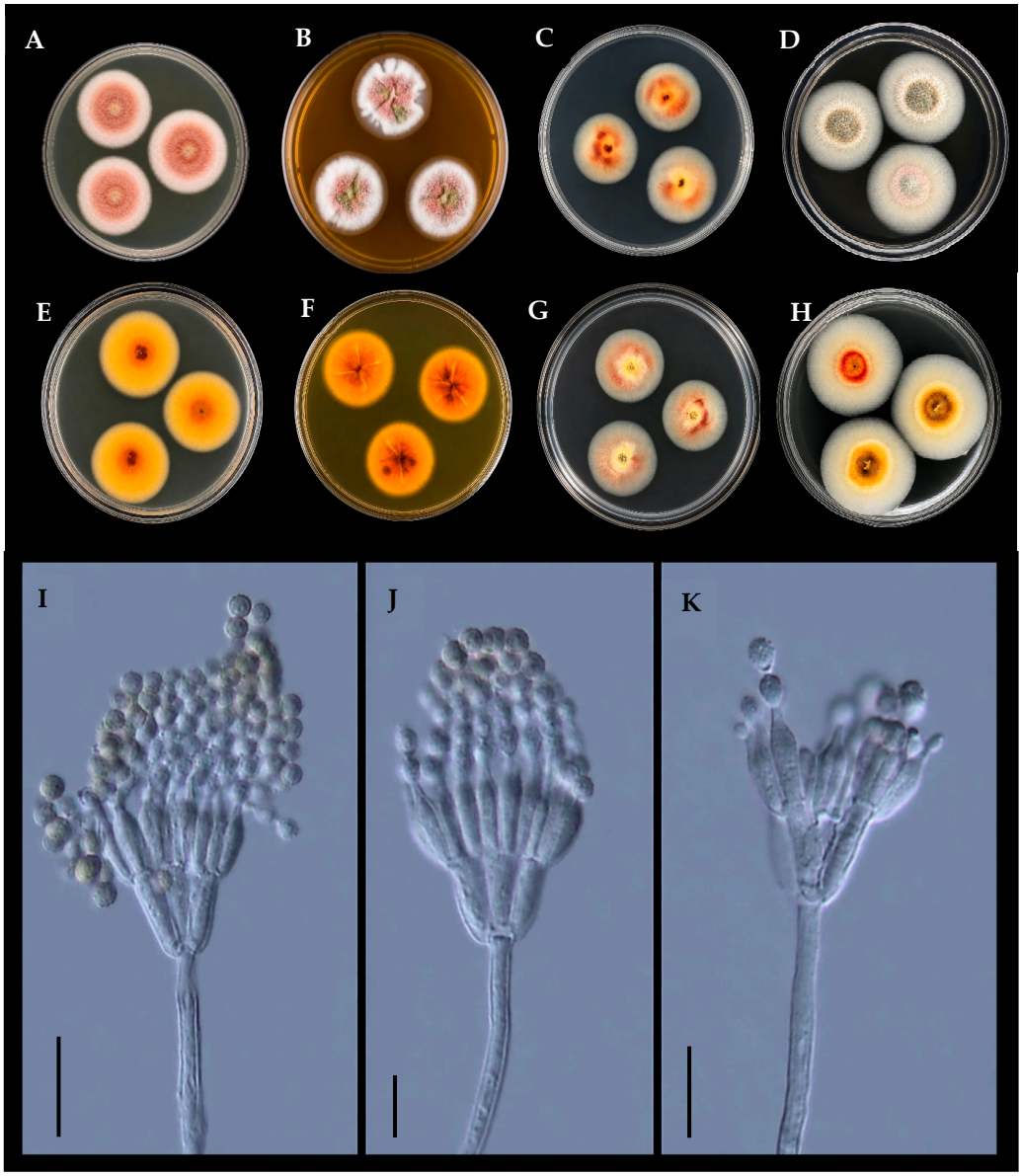

Figure 8. Morphology of *Talaromyces aculeatus*. Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**K**). Scale bars: 10 µm.

Micromorphology: Conidiophores predominantly biverticillate, rarely terverticillate, arising from smooth-walled hyaline hyphae; stipes smooth-walled, hyaline, septate, straight to slightly flexuous, 80–300 × 2.0–3.5 µm. Metulae arranged in verticils of 3–6, cylindrical to slightly clavate, 8–15 × 2.5–4.0 µm. Phialides ampulliform to lageniform, tapering into a distinct neck, 4–8 per metula, 7–12 × 2.0–3.0 µm. Conidia globose to subglobose, borne in dry compact chains, 2.5–4.0 µm diam., finely roughened to echinulate. Conidial

heads compact, radiate to slightly columnar. Vegetative hyphae hyaline, smooth-walled and septate.

Notes: The BLASTn analysis of the ITS, *benA* and *cmdA* sequences of the IE7019 revealed 99.82%, 100%, 99.78% identity, with the ex-type strain of *T. aculeatus* NRRL 2129 [36]. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of related species of *Talaromyces* showed that the Mexican strain was placed in the same clade as the ex-type strain with the highest support (PP = 1 and BS = 100) (Figure 2A). The morphology observed was consistent with the classical description of *T. aculeatus*, particularly due to the presence of robust biverticillate penicilli, ampulliform phialides, and finely ornamented ("aculeate") conidia, which represent a diagnostic feature of the species.

Material examined: Mexico, Veracruz, Jilotepec, Los Bambus, 19°36′44″ N, 96°00′16.5″W, 1370 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA90; IE7019 (living culture, INECOL); XAL CB2327 (permanent microscopic preparation).

Talaromyces albobiverticillius (H.M. Hsieh, Y.M. Ju & S.Y. Hsieh) Samson, Yilmaz, Frisvad & Seifert, Stud. Mycol. 70: 174 (2011) (Figure 9).

Colony diameters after 7 d (mm) at 25 °C: YES, 21.6 ± 0.8; MEA, 20.2 ± 1.3; PDA, 19.9 ± 1.0; CYA, 15.9 ± 0.8. Growth on CYA at 37 °C. No growth on CYA at 4 °C.

Colony characteristics (25 °C, 7 d): YES: Colonies moderately growing, velutinous, with abundant dark green to bluish-green sporulation and faint radial zonation. Reverse reddish-brown to dark brown on a pale-yellow background, with evident diffusible pigment. MEA: Colonies moderately growing, with abundant and uniform dark green sporulation and sparse white peripheral mycelium. Reverse yellow to yellow-orange with darker reddish-brown central areas and diffusible pigmentation. PDA: Colonies moderately growing, compact, with white to cream mycelium, sparse to moderate central sporulation, and slightly raised cream to beige centers. Reverse intense reddish-brown centrally, becoming paler toward the margins. CYA: Colonies moderately growing, with moderate to abundant reddish-orange to reddish-brown sporulation and soluble yellow pigment production. Reverse yellow with conspicuous dark red central pigmentation.

Micromorphology: Conidiophores hyaline, smooth-walled, predominantly biverticillate, simple to slightly branched; stipes long, septate, up to 190 × 3.5 µm. Metulae arranged in terminal verticils, supporting ampulliform to lageniform phialides, 7–9 × 1.5–2.5 µm. Conidia globose to subglobose, smooth-walled, formed in basipetal chains, 2–3.5 µm diam. Conidial heads compact to loosely columnar, frequently dense and divergent.

Notes: The BLASTn analysis of the ITS, *benA* and *cmdA* sequences of the IE7018 and IE7021 confirmed 99.82%, 100%, 98.64% identity, with the ex-type strain of *T. albobiverticillius* CBS 133440 [1]. Phylogenetic analyses with concatenated ITS + *benA* + *cmdA* sequences of related species of *Talaromyces* indicated that both Mexican strains were grouped in the same clade as the reference strains including the ex-type strain of *T. albobiverticillius* with the highest support (PP = 1 and BS = 100) (Figure 2B). Colonies were characterized by the production of reddish-orange diffusible pigments in reverse combined with green sporulation on the obverse, particularly on YES and MEA, features characteristic of the genus *Talaromyces* and consistent with *T. albobiverticillius*.

Material examined: Mexico, Veracruz, Jilotepec, Los Bambus, 19°36′44″ N, 96°00′16.5″ W, 1370 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA114; IE7018 (living culture, INECOL); XAL CB2328 (permanent microscopic preparation). Jilotepec, La Barranca, 19°36′40″ N, 96°55′40.5″ W, 1484 m a.s.l., from coffee plantation soil, 15 August 2021, R. Arias RA147; IE7021 (living culture, INECOL); XAL CB2329 (permanent microscopic preparation).

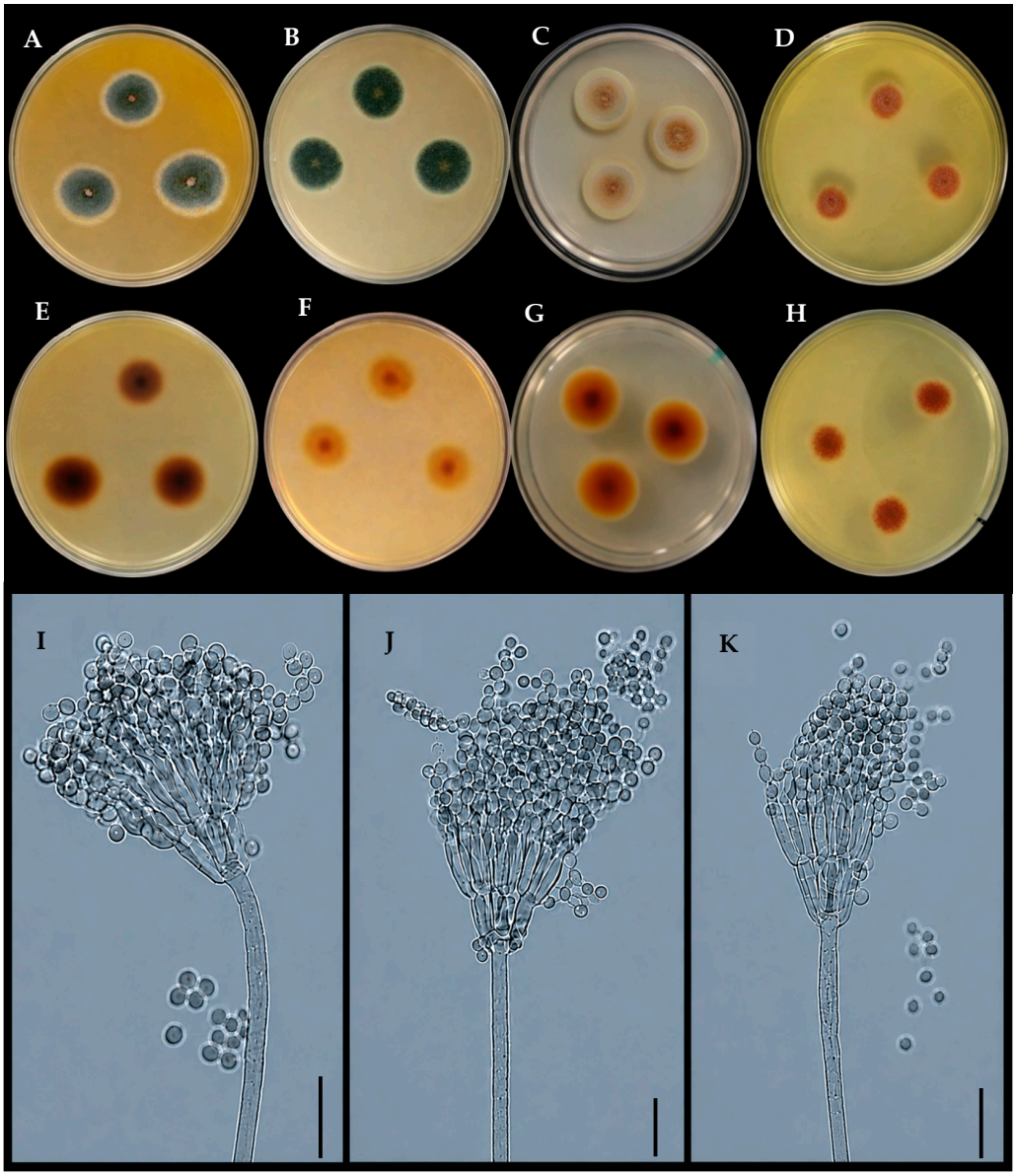

Figure 9. Morphology of *Talaromyces albobiverticillius.* Colonies top row left to right, obverse (**A**) YES, (**B**) MEA, (**C**) PDA, and (**D**) CYA; bottom row left to right, reverse (**E**) YES, (**F**) MEA, (**G**) PDA, and (**H**) CYA. Conidiophores, phialides and conidia (**I**–**K**). Scale bars: 10 µm.

3.3. Functional Characterization of the Strains

The functional heatmap (Figure 10) revealed distinct enzymatic and physiological profiles among the evaluated strains. Most isolates exhibited positive activity for manganese peroxidase and phosphate solubilization.

Penicillium citrinum, *P. mallochii*, and *Talaromyces albobiverticillius* exhibited the broadest functional profiles, showing positive responses for all evaluated traits, including ligninolytic enzymes and cellulolytic activity. These species showed the largest number of positive reactions among the evaluated traits.

Conversely, *P. citreosulfuratum* and *P. shanghaiense* displayed more restricted enzymatic profiles, lacking lignin peroxidase and laccase activities, although both maintained phosphate-solubilizing and cellulolytic capacities. *T. aculeatus* confirmed positive activity for all evaluated traits except cellulolytic activity, while *P. crustosum* lacked laccase activity but exhibited positive ligninolytic and phosphate-solubilizing activities.

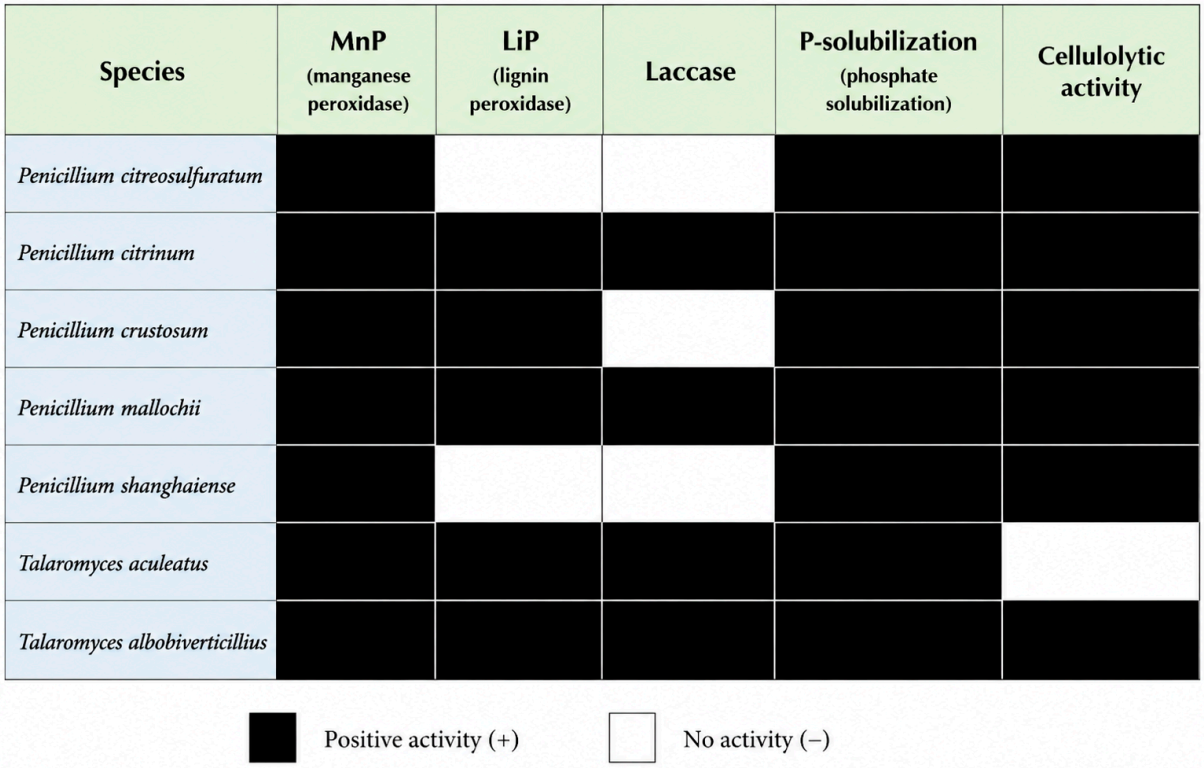

Figure 10. Functional heatmap of enzymatic activities and phosphate-solubilizing capacity of *Penicillium* and *Talaromyces* strains isolated from soils in Veracruz, Mexico. Black cells indicate positive activity (+), whereas white cells indicate absence of activity (−). Evaluated traits included manganese peroxidase (MnP), lignin peroxidase (LiP), laccase activity, phosphate solubilization, and cellulolytic activity.

Overall, the evaluated isolates exhibited distinct qualitative functional profiles, differing in the combination of ligninolytic, cellulolytic, and phosphate-solubilizing activities.

4. Discussion

4.1. Diversity of Penicillium and Talaromyces in Mexico

This study documents seven species of *Penicillium* and *Talaromyces* as new records for Mexico, expanding the known distribution of these genera in tropical soils. Although Mexico is recognized as one of the world's megadiverse countries, the diversity of soil microfungi remains insufficiently documented, particularly in tropical and subtropical ecosystems. *Penicillium* is currently one of the most species-rich genera of filamentous fungi, comprising more than 535 accepted species worldwide [1]. However, only a small fraction of this diversity has been recorded in Mexico, and many historical records were based exclusively on morphological identifications.

Despite the ecological importance of Veracruz and the availability of numerous studies on macrofungi and plant-associated fungi, information on soil-inhabiting species of *Penicillium* and *Talaromyces* remains limited. The discovery of *Penicillium citreosulfuratum*, *P. citrinum*, *P. crustosum*, *P. mallochii*, *P. shanghaiense*, *Talaromyces aculeatus*, and *T. albobiverticillius* demonstrates that Mexican soils harbor a considerable amount of undocumented fungal diversity. These findings contribute to updating the national inventory of both genera and highlight the need for continued surveys of soil fungal communities in tropical ecosystems.

The documentation of new species and records of *Penicillium* and *Talaromyces* continues to increase worldwide as a result of integrative taxonomic approaches. Recent studies conducted in Asia, Europe, and other regions have revealed numerous previously unknown species and significantly expanded the known distribution of both genera [1,35]. These

findings suggest that a substantial proportion of the diversity of *Penicillium* and *Talaromyces* remains undocumented, particularly in tropical regions where systematic studies are still limited.

The findings are consistent with a growing number of studies showing that integrative taxonomy remains fundamental for documenting fungal diversity in tropical regions. In Mexico, the recent description of *Talaromyces oaxaquensis* from Oaxaca [37] and two new *Trichoderma* species from coffee plantation soils in Veracruz [4] illustrates how multilocus phylogenetic analyses continue to uncover previously unrecognized taxa. These studies, together with the new records reported here, suggest that the diversity of soil microfungi in Mexico remains substantially underestimated and that further exploration of tropical ecosystems will likely reveal additional undocumented species and distribution records.

4.2. Importance of Integrative Taxonomy for Species Delimitation

Species identification within *Penicillium* and *Talaromyces* is often challenging because of the occurrence of morphologically similar taxa and cryptic species complexes. Although the ITS region is widely accepted as the universal fungal barcode, its resolution is frequently insufficient for distinguishing closely related species within these genera [2]. Consequently, species delimitation based solely on ITS sequences may result in ambiguous identifications.

In the present study, the integration of morphological observations with multilocus phylogenetic analyses based on ITS, *benA*, and *cmdA* provided robust support for species identification. The congruence between morphological characters and phylogenetic placement allowed all isolates to be reliably assigned to previously described taxa. These results reinforce the value of integrative taxonomy as an effective approach for documenting fungal diversity and generating reliable distribution records.

The importance of combining morphological and molecular evidence has been widely recognized in recent studies of both genera. During the last decade, the delimitation of numerous newly described species has required the combined use of phenotypic characters and multilocus analyses due to intraspecific morphological variation and the presence of cryptic species complexes. Consequently, polyphasic approaches are currently regarded as the standard for modern taxonomy of *Penicillium* and *Talaromyces* [1–3].

Recent studies conducted in Mexico have similarly demonstrated the importance of multilocus approaches for revealing previously undocumented fungal taxa and improving knowledge of fungal biodiversity. Continued application of integrative taxonomic methods will therefore be essential for refining national fungal inventories and achieving a more accurate understanding of fungal diversity in the country.

4.3. Distribution, Ecology, and Known Substrates of the Recorded Species

The seven species identified in this study exhibit contrasting geographic distributions and ecological preferences, ranging from cosmopolitan taxa with broad environmental adaptability to species that have been only rarely reported worldwide. Most species have been isolated from terrestrial environments, particularly soils, decaying plant material, agricultural substrates, and the rhizosphere, whereas others have also been recovered from marine habitats or in association with insects. The present records expand the known distribution of these fungi in Mexico and provide additional information on their occurrence in coffee-growing soils.

Among the species identified, *P. citrinum* and *P. crustosum* are well-known cosmopolitan fungi with broad ecological amplitudes. *P. citrinum* has been reported from agricultural and forest soils, stored foods, cereals, spices, decaying plant material, citrus fruits, indoor environments, and as an endophyte associated with plant roots [17,38,39], demonstrating its remarkable capacity to colonize diverse habitats. Likewise, *P. crustosum* has been isolated

from soils, air, dust, stored grains, fruits, coffee, dairy products, cheeses, meat products, and animal feed [18,19,33], reflecting its saprobic lifestyle and high ecological adaptability. The recovery of both species from coffee-growing soils in Veracruz is therefore consistent with their cosmopolitan distribution and broad ecological tolerance previously documented, confirming that agricultural soils constitute important reservoirs for these fungi.

In contrast, *P. citreosulfuratum* has been reported less frequently and is known from terrestrial habitats associated with soils and plants, as well as from marine environments, including marine sand in South Korea [16,40]. Its isolation from coffee-growing soils in Veracruz expands its known ecological occurrence and demonstrates its capacity to colonize contrasting terrestrial habitats. Similarly, *P. mallochii* has been reported mainly from tropical and subtropical environments associated with insects, fruits, soils, and plant material. Since its original description from caterpillars in Costa Rica [34], it has also been recovered from marine sediments in South Korea, fruits of *Spondias mombin*, insects associated with strawberry crops, and postharvest sweet orange (*Citrus sinensis*) fruits in Brazil [39,41]. The present isolation from coffee-growing soil further supports the ecological plasticity of this species and suggests that its distribution in tropical agroecosystems may be broader than currently recognized.

Particularly noteworthy is *P. shanghaiense*, which had previously been reported only from soil associated with *Cinnamomum camphora* in Shanghai, China [35]. Therefore, this study represents the first record of this species in Mexico and, to our knowledge, only the second report worldwide. This finding substantially extends its known geographic distribution and suggests that the apparent rarity of this species may reflect limited sampling rather than a truly restricted distribution. The discovery of *P. shanghaiense* in a coffee agroecosystem also highlights the importance of exploring understudied tropical environments using integrative taxonomic approaches to reveal previously undocumented fungal diversity.

Both *Talaromyces* species identified in this study also exhibit broad ecological associations. *T. aculeatus* has been reported from rhizosphere soils, lignocellulosic residues, composts, agricultural environments, decaying plant material, and marine environments as an endophyte of the red alga *Laurencia obtusa* [3,42,43], reflecting its ability to colonize a wide range of ecological niches. Likewise, *T. albobiverticillius* has been recorded from decaying broadleaf litter in Taiwan, postharvest pomegranate fruits in Italy, and marine ascidians in Indonesia [3,43–45], demonstrating its occurrence in both terrestrial and marine ecosystems. The recovery of both species from coffee-growing soils is consistent with previous reports describing *Talaromyces* species as common saprobes in plant-associated substrates and agricultural environments.

Overall, the ecological information available for these species indicates that they are predominantly saprobic fungi with broad substrate preferences and the capacity to colonize both natural and managed ecosystems. The occurrence of all seven species in coffee-growing soils of Veracruz agrees with previous studies identifying agricultural soils and plant-associated habitats as important reservoirs of *Penicillium* and *Talaromyces* diversity. However, the detection of both cosmopolitan species and rarely reported taxa, particularly *P. shanghaiense*, demonstrates that coffee agroecosystems can harbor fungal communities that remain incompletely documented. These findings contribute to expanding the known geographic distribution of several *Penicillium* and *Talaromyces* species in North America and reinforce the importance of coffee agroecosystems as valuable reservoirs of fungal biodiversity. Furthermore, they highlight the need for continued surveys integrating morphological characterization with multilocus phylogenetic analyses to improve our understanding of fungal diversity, ecology, and biogeography in tropical agricultural ecosystems.

4.4. Functional Traits and Biotechnological Potential

The qualitative functional characterization performed in this study indicated that the seven fungal species possess traits associated with key ecological processes in soil ecosystems and with potential biotechnological applications. The evaluated isolates exhibited different combinations of ligninolytic, cellulolytic, and phosphate-solubilizing activities, indicating substantial functional diversity among the *Penicillium* and *Talaromyces* species recovered from coffee-growing soils. These functional traits are associated with organic matter decomposition, nutrient cycling, and soil fertility, highlighting the ecological relevance of these fungi within tropical coffee agroecosystems.

Among the evaluated traits, positive ligninolytic activity was detected in several isolates through the production of laccase, manganese peroxidase (MnP), and lignin peroxidase (LiP). These oxidative enzymes play fundamental roles in the degradation of lignin and other complex aromatic compounds, contributing to carbon cycling and the mineralization of plant residues. Previous studies have shown that species of *Penicillium* and *Talaromyces* are important producers of oxidative enzymes involved in lignocellulose degradation and have considerable potential for applications in bioremediation, biomass conversion, and industrial enzyme production [16,40,42,46,47]. The qualitative detection of ligninolytic activity in this study is consistent with these reports and further demonstrates that coffee-growing soils harbor fungi with important degradative capabilities.

Positive cellulolytic activity was also detected in several isolates, indicating their ability to degrade cellulose-rich plant residues. The simultaneous occurrence of cellulolytic and ligninolytic activities suggests that these fungi participate in complementary stages of lignocellulose decomposition, facilitating nutrient release and organic matter turnover in soil ecosystems. Similar enzymatic capabilities have previously been reported for *T. aculeatus* [46,47] and for several *Penicillium* species [16,33], supporting the ecological significance of these fungi as decomposers in agricultural soils.

Another important functional trait identified in this study was phosphate solubilization. Because phosphorus frequently limits plant productivity in tropical agricultural systems, microorganisms capable of mobilizing insoluble phosphate compounds contribute to nutrient availability. Several isolates exhibited positive phosphate-solubilizing activity, suggesting that they may contribute to phosphorus mobilization in soil and therefore deserve further evaluation as potential plant growth-promoting fungi. The widespread occurrence of manganese peroxidase activity together with phosphate-solubilizing activity suggests that several of the evaluated fungi may contribute to nutrient mobilization and the degradation of complex organic compounds in coffee plantation soils. In contrast, lignin peroxidase and laccase activities were more variable among species, indicating a certain degree of functional specialization within the fungal community. Similar activities have previously been documented in species of *Talaromyces*, particularly *T. aculeatus*, as well as in several representatives of *Penicillium* [46–49]. The present findings reinforce the ecological relevance of these genera and support their potential for future studies focused on sustainable agricultural applications.

Although several of the evaluated species are already recognized as producers of valuable secondary metabolites, the functional characterization performed in this study provides additional evidence supporting their ecological and biotechnological relevance. *P. citrinum* is well known for producing bioactive metabolites such as citrinin, quinolactacins, and compactin, together with antioxidant and antimicrobial compounds [50–53]. Likewise, *P. citreosulfuratum* produces extracellular pigments and metabolites of industrial interest [16,40,54], whereas *P. crustosum* synthesizes secondary metabolites including penitrem A and roquefortine C, in addition to extracellular enzymes involved in organic matter degradation [8,55]. *P. mallochii* has recently attracted attention because of its production

of pigments with antioxidant and antimicrobial activities and its potential as a biological control agent [39,41,56]. Similarly, *T. aculeatus* has been recognized as a producer of lignocellulolytic enzymes and bioactive metabolites with applications in sustainable agriculture and environmental biotechnology [42,46,47], while *T. albobiverticillius* produces azaphilone pigments and secondary metabolites with promising pharmaceutical potential [43,55]. In contrast, little information is currently available regarding the ecological functions or biotechnological applications of *P. shanghaiense*, making the functional characterization presented here the first evidence of its potential ecological relevance.

Among the evaluated species, *P. mallochii*, *P. citrinum*, and *T. albobiverticillius* exhibited the broadest functional profiles, showing positive reactions for ligninolytic, cellulolytic, and phosphate-solubilizing activities. The remaining species also displayed at least one of the evaluated functional traits, demonstrating considerable functional diversity within the fungal community associated with coffee-growing soils. These complementary metabolic capabilities suggest that different fungal taxa contribute simultaneously to organic matter decomposition and nutrient mobilization, thereby supporting soil functioning in coffee agroecosystems.

Overall, the combination of taxonomic novelty and functional diversity identified in this study highlights the importance of coffee-growing soils as reservoirs of fungal resources with ecological and biotechnological value. Although this study provides a qualitative assessment of selected functional traits, the observed activities indicate that these newly recorded species constitute promising candidates for future research. Further studies should focus on quantitative enzyme assays, characterization of secondary metabolites, genome-based analyses, and plant–fungus interaction experiments to better understand their ecological roles and evaluate their potential applications in sustainable agriculture, industrial biotechnology, and environmental remediation.

5. Conclusions

This study documents seven species of *Penicillium* and *Talaromyces* as new records for Mexico, contributing to the knowledge of fungal diversity in tropical soils and expanding the known distribution of these taxa. The integration of morphological characterization and multilocus phylogenetic analyses based on ITS, *benA*, and *cmdA* provided robust species identification and demonstrated the value of integrative taxonomy for documenting soil fungal diversity.

The occurrence of these species in both coffee plantation and hydrocarbon-contaminated soils highlights the ecological versatility of *Penicillium* and *Talaromyces* and emphasizes the importance of exploring different soil environments to improve fungal inventories. Several isolates exhibited ligninolytic, cellulolytic, and phosphate-solubilizing activities, suggesting potential roles in organic matter decomposition, nutrient cycling, and soil fertility.

Among the species evaluated, *Penicillium mallochii*, *P. citrinum*, and *Talaromyces albobiverticillius* displayed the broadest functional profiles, indicating their potential relevance for future studies on sustainable agriculture and environmental biotechnology. Overall, these findings reinforce the importance of tropical soils as reservoirs of poorly documented fungal diversity and highlight the need for continued taxonomic, ecological, and functional investigations of soil fungi using integrative approaches. These findings demonstrate that tropical soils of Mexico remain an important source of undocumented fungal diversity and represent promising reservoirs of taxa with potential ecological and biotechnological value.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/taxonomy6030047/s1, Table S1. Section/Series, species, voucher specimens, GenBank accession numbers of the sequences used in this study.

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