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# *Wynnea hypogaea* (Wynneaceae, Pezizales), a new species from Mexico

## *Wynnea hypogaea* (Wynneaceae, Pezizales), una especie nueva de México

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### Abstract:

**Background and Aims:** Sequestrate fungi form an artificial group characterized by their hypogeous habit; they are found within specific groups of Ascomycota and Basidiomycota. The family Wynneaceae was recently established, which includes the genera *Geodina* and *Wynnea*. The latter is characterized by forming spathuliform, auriculiform, otideoid to sparassoid apothecia, with ellipsoid to navicular ascospores bearing conspicuous longitudinal ridges. In Mexico, *W. americana*, *W. gigantea*, and *W. macrotis* have been reported. Molecular and morphological analyses recovered the specimens as a new hypogeous species of *Wynnea*, named here as *W. hypogaea*.

**Methods:** The specimens were collected in 2022 in a montane cloud forest in the municipality of Coscomatepec, Veracruz, Mexico. Morphological descriptions and studies were performed according to appropriate protocols. Morphological and molecular studies with ITS, nrLSU, 18S, *rpb2*, and *tef-1α* were performed to delimit the species. The studied material was deposited in the José Castillo Tovar Mycological Herbarium at the Instituto Tecnológico de Ciudad Victoria (ITCV) and the Escuela Nacional de Ciencias Biológicas (ENCB) of the Instituto Politécnico Nacional.

**Key results:** *Wynnea hypogaea* is described and illustrated. Based on its morphological, molecular, and ecological characteristics, this species is well-differentiated from other taxa in the genus. The new taxon is characterized by hypogeous ascomata with irregular glebal chambers, reddish brown peridium, and ascospores of 35–40 × 15–20(–22) μm, longitudinally striated. It grows under *Quercus lancifolia* in a montane cloud forest.

**Conclusions:** *Wynnea hypogaea* is the first species in the genus to exhibit a hypogeous and sessile habit. Phylogenetically, it is closely related to *W. macrotis* and *W. sparassoides*; however, both of these form a different clade from the one described here. The transition from epigeous to hypogeous life can be observed in some Pezizales. Therefore, further exploration and study of these organisms are required.

**Key words:** Ascomycota, *Quercus lancifolia*, montane cloud forest, sequestrate fungi.

### Resumen:

**Antecedentes y Objetivos:** Los hongos secuestrados forman un grupo artificial caracterizado por su hábito hipógeo; se ubican en un grupo determinado de Ascomycota y Basidiomycota. Recientemente se erigió la familia Wynneaceae, que incluye los géneros *Geodina* y *Wynnea*. Este último se caracteriza por formar apotecios espatuliformes, auriculiformes, otidioides a esparasoides, con ascosporas elipsoides a naviculares con crestas longitudinales conspicuas. En México se han citado *W. americana*, *W. gigantea* y *W. macrotis*. Los análisis moleculares y morfológicos muestran que los especímenes constituyen una especie nueva hipogea, aquí denominada *Wynnea hypogaea*.

**Métodos:** Los ejemplares se recolectaron en 2022 en un bosque mesófilo de montaña del municipio de Coscomatepec, Veracruz, México. La descripción y estudios morfológicos se realizaron bajo los protocolos adecuados. Se realizaron los estudios moleculares con ITS, nrLSU, 18S, *rpb2* y *tef-1α* para delimitar las especies. El material estudiado está depositado en el Herbario Micológico José Castillo Tovar del Instituto Tecnológico de Ciudad Victoria (ITCV) y Herbario de la Escuela Nacional de Ciencias Biológicas (ENCB) del Instituto Politécnico Nacional.

**Resultados clave:** *Wynnea hypogaea* se describe e ilustra. Por sus características morfológicas, moleculares y ecológicas, se distingue claramente de otros taxones del género. El taxón nuevo se caracteriza por los ascomas hipogeos con cámaras glebales irregulares, peridio marrón rojizo y ascosporas de 35–40 × 15–20(–22) μm, estriadas longitudinalmente. Crece bajo *Quercus lancifolia* en bosque mesófilo de montaña.

**Conclusiones:** *Wynnea hypogaea* es la primera especie del género con hábito hipogeo y sésil. Filogenéticamente es cercana a *W. macrotis* y *W. sparassoides*; no obstante, ambas forman un clado distinto del descrito. En algunos ascomicetos Pezizales, se puede observar la transición de epígeos a hipógeos. Por lo cual, la exploración y estudio de estos organismos deben continuar.

**Palabras clave:** Ascomycota, bosque mesófilo de montaña, hongos secuestrados, *Quercus lancifolia*.

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## Introduction

The sequestrate fungi (also called false truffles or truffle-like fungi) are an artificial group of fungi characterized by a hypogeous habit (Castellano et al., 1989, 2004). Several taxa of sequestrate fungi are well-known in temperate forests, but knowledge of this group in the tropics remains scarce. They form mycorrhizae with angiosperms and gymnosperms, but saprobic species are also known (Montecchi and Sarasini, 2000; Tedersoo et al., 2010). Most species enclose the fertile tissue (hymenium) in a persistent layer (peridium) and develop underground (Trappe et al., 2009). The sequestrate fungi cannot discharge their spores in the air, although several species have evolved mechanisms for dispersal through mycophagy; some species form an important part of the diet of small mammals, birds, insects, and invertebrates (Castellano et al., 1989; Guevara-Guerrero et al., 2014; Caiafa et al., 2021). Sequestrate forms have evolved in several groups within Ascomycota and Basidiomycota (Castellano et al., 2004; Kuhar et al., 2023). The hypogeous Ascomycetes produce ascocarp features that are homoplastic, resulting from the parallel evolution of independent lineages of epigeous/hypogeous fruit bodies during the evolutionary history of the Pezizales (Trappe, 1979; Borovička et al., 2024).

Pfister et al. (2020) described the family Wynneaceae to include the genera *Geodina* Denison and *Wynnea* Berk. & M.A.Curtis, based on morphological, molecular, and trophic interaction data. Currently, Wynneaceae is placed in the Pezizales, within the Class Pezizomycetes (Hyde et al., 2024). *Wynnea* is characterized by forming spathuliform, auriculiform, otideoid to sparassoid, rarely solitary apothecia, generally growing in groups, from a stem or a sclerotium, with a black, purplish, pinkish, dark orangish red or brownish hymenium. Ascospores are ellipsoid to naviculate, symmetrical or bilaterally asymmetrical, with conspicuous longitudinal ridges (Pfister, 1979). This

genus comprises eight species: *Wynnea americana* Thaxt., *W. gigantea* Berk. & M.A.Curtis, *W. intermedia* Waraitch, *W. macrospora* B.Liu, M.H.Liu & J.Z.Cao, *W. macrotis* (Berk.) Berk. & M.A.Curtis, *W. silvicola* Nannf., *W. sinensis* B.Liu, M.H.Liu & J.Z.Cao, and *W. sparassoides* Pfister. In Mexico, this genus is represented by *W. americana* in the states of Mexico, Michoacán, and Morelos (Valenzuela et al., 1981; Chacón and Bautista, 1988; Pompa-González and Cifuentes, 1991; Medel et al., 1995; Ortega-López et al., 2019); *W. gigantea* in the state of Veracruz (Berkeley, 1867); and *W. macrotis*, although data on the state in which it was collected is not shown (Berkeley, 1867). Furthermore, the genus *Geodina* has been observed in tropical Mexico and the Caribbean (Angelini et al., 2018; de la Fuente et al., 2020; Pfister et al., 2020). During mycological explorations in the Mexican state of Veracruz, some interesting truffle-like fungi were discovered growing under *Quercus* spp. Molecular and morphological analyses identified the specimens as a new hypogeous species, here named *Wynnea hypogaea*.

## Material and Methods

### Collection and morphological examination

The specimens were collected in the municipality of Coscomatepec, Veracruz, Mexico, in November 2022 (Fig. 1). The specimens were deposited in the mycological herbarium “José Castillo Tovar” of the Instituto Tecnológico de Ciudad Victoria (ITCV). The paratype was deposited in the herbarium of the Escuela Nacional de Ciencias Biológicas of the Instituto Politécnico Nacional (ENCB). The collected specimens were examined following the protocols of Castellano et al. (1989). All specimens were characterized in fresh condition, taking into account size, shape, color, texture, and host. The colors are indicated according to Kornerup and Wanscher (1978); likewise, the terminology was based on the Illustrated Dictionary of Mycology (Ulloa and Hanlin, 2006). Furthermore, the microscopic structures of peridi-

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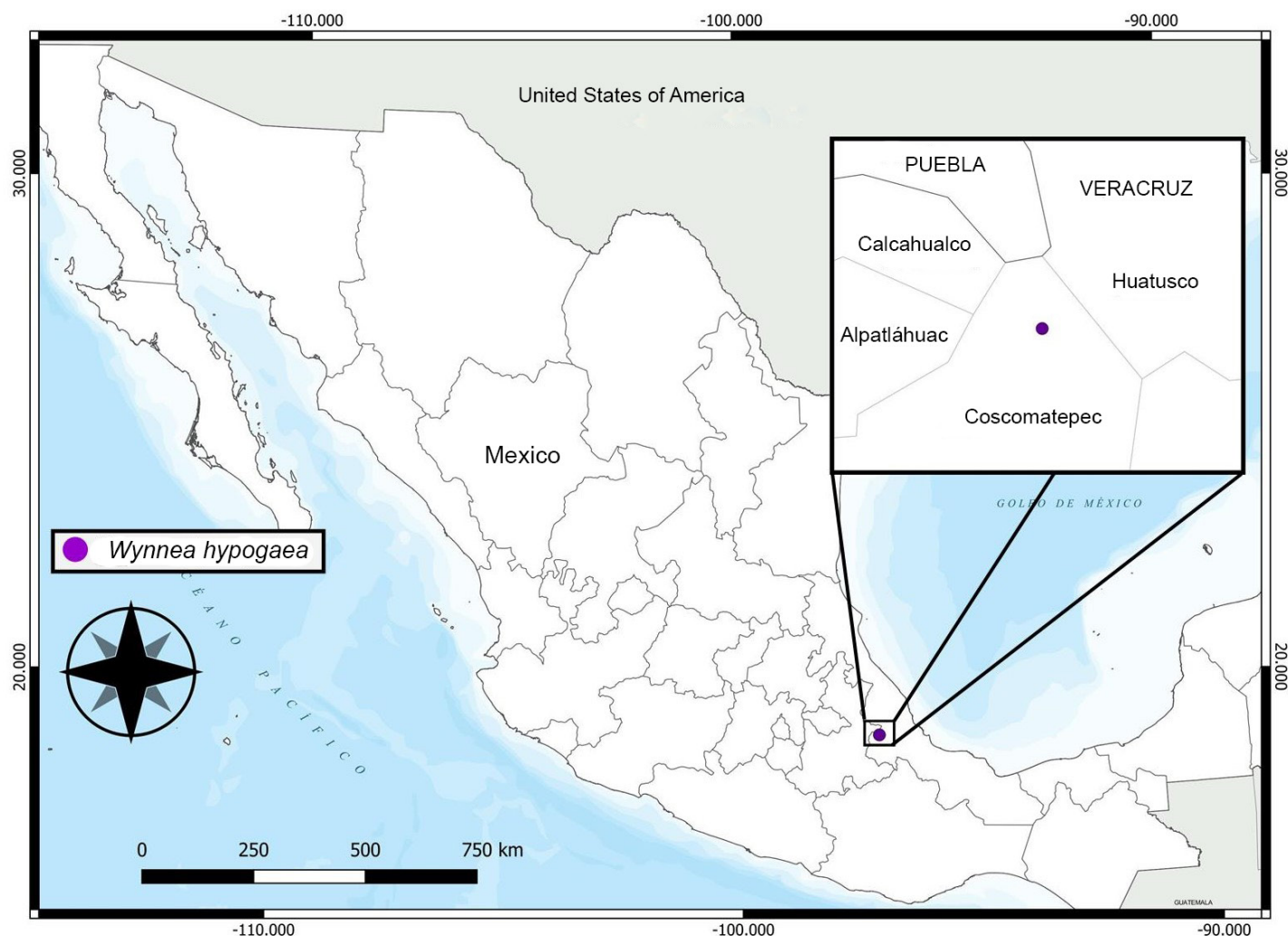


Figure 1: Map of the *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores locality.

um, medular excipulum, paraphyses, asci, and ascospores were analyzed and characterized using an optical microscope (OM) (Axiostar plus, Zeiss, Jena, Germany). Scanning electron microscopy (SEM) (SU1510, Hitachi High Technologies, Tokyo, Japan) was used to observe the ascospore ornamentation.

#### Extraction, amplification, and sequencing of DNA

Genomic DNA was extracted from ascomata using the modified CTAB method (Martínez-González et al., 2017). The DNA was quantified with a Nanodrop 2000c (Thermo Scientific, USA). Dilutions of each sample at 20 ng were prepared to amplify five genes. The Internal Transcribed Spacer (ITS) (primers ITS4-ITS5) (White et al., 1990), partial large sub-

unit rDNA gene region (nrLSU) (primers LROR-LR3) (White et al., 1990), small subunit ribosomal RNA gene (18S) (primers P6Fa-P7Ra), partial RNA polymerase II second largest subunit gene (*rpb2*) (RPB2-5F/RPB2-7cR) (Matheny et al., 2007) and translation elongation translation factor 1- $\alpha$  (*tef1*) (primer 983F-2218R) (Pfister et al., 2020) were amplified. The reaction mixture for PCR was prepared in a final volume of 13  $\mu$ l containing: 1 $\times$  Taq DNA polymerase buffer, 0.8 mM deoxynucleoside triphosphates (0.2 mM of each dNTP), 100 ng DNA, 20 pmol of each primer, and 2 units of GoTaq DNA (Promega, USA). Amplifications were performed with an initial denaturation cycle step at 96°C for 2 min.; followed by 35 cycles of denaturation at 94°C for 1 min., primer annealing at 57°C (Table 1) for 1 min., and



**Table 1:** Primers used for amplification and sequencing of the DNA fragments.

| Loci/Segment | Primer | T(°C) | Reference            |
|--------------|--------|-------|----------------------|
| ITS          | ITS4   | 58    | White et al., 1990   |
|              | ITS5   | 58    | White et al., 1990   |
| nrLSU        | LROR   | 54    | White et al., 1990   |
|              | LR3    | 60    | White et al., 1990   |
| 18S          | P6Fa   | 56    | Hansen et al., 2005  |
|              | P7Ra   | 56    | Hansen et al., 2005  |
| <i>rpb2</i>  | 6F2    | 52    | Matheny et al., 2007 |
|              | 7R2    | 52    | Matheny et al., 2007 |
| <i>tef1</i>  | EF1BF1 | 53    | Pfister et al., 2020 |
|              | EF1BR  | 53    | Pfister et al., 2020 |

a final extension at 72°C for 5 min. All PCR reactions were performed in a Peltier Thermal Cycler PTC-200 (BIORAD, Mexico). The PCR products were verified by agarose gel electrophoresis. The gels were run for 1 h at 95 V in 1.5% agarose and 1× TAE buffer (Tris-Acetate-EDTA). The gel was stained with GelRed (Biotium, USA), and the bands were visualized using an Infinity 3000 transilluminator (Vilber Lourmat, Germany). The amplified products were purified using the ExoSAP Purification kit (Affymetrix, USA) according to the manufacturer's instructions. They were quantified and prepared for sequencing using BigDye Terminator v. 3.1 (Applied Biosystems). These products were sequenced in both directions using an Applied Biosystems model 3730XL (Applied Biosystems, USA). Sanger sequencing was carried out by MacroGen Inc. (Seoul, Korea).

## Sequence assembly

The sequences of both strands of each gene were analyzed, edited, and assembled using BioEdit v. 7.0.5 (Hall, 1999) to generate consensus sequences. These consensus sequences were compared with those deposited in GenBank (NCBI, 2026), using the BLASTN v. 2.2.19 tool (Zhang et al., 2000).

## Phylogenetic methods

Sequence data, retrieved from GenBank (NCBI, 2026) based on previous studies, are listed in Table 2. The sequences were analyzed using standard BLAST searches in GenBank (NCBI, 2026) to determine the primary identity of the fungal strains (Kirschner et al., 2023). To study phylogenetic

relationships, our newly generated sequences from two individuals of *Wynnea* were added to reference sequences of ITS, nrLSU, 18S, *rpb2*, and *tef1* deposited in the NCBI database (NCBI, 2026). Each region was independently aligned using the online version of MAFFT v. 7 (Katoh et al., 2002, 2017; Katoh and Standley, 2013). The alignments were revised in PhyDE v. 10.0 (Müller et al., 2005), followed by minor manual adjustments to ensure character homology between taxa. The matrices consisted for ITS of 13 taxa and 650 characters, nrLSU of 34 taxa and 600 characters, 18S of 29 taxa and 826 characters, *rpb2* of 26 taxa and 771 characters, and *tef1* of 26 taxa and 750 characters. Nine partition schemes were established: one for ITS, one for nrLSU, one for 18S, three to represent the three codon positions of the *rpb2* gene region, and three to represent the three codon positions of the *tef1* gene region, as determined using the option to minimize stop codons with Mesquite v. 3.2 (Maddison and Maddison, 2021).

The data were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Maximum parsimony analyses were carried out in PAUP\* v. 4.0b10 (Swofford, 2002) using the heuristic search mode, 1000 random starting replicates, and TBR branch swapping, with MULTREES and Collapse activated. Bootstrap values were estimated using 1000 bootstrap replicates under the heuristic search mode, each with 100 random starting replicates. Maximum likelihood analyses were carried out in RAXML v. 8.2.10 (Stamatakis, 2014) using a GTR + G nucleotide substitution model. To assess branch support, 10,000 rapid bootstrap replicates were run with the GTRGAMMA model. Bayesian inference was carried out in MrBayes v. 3.2.6 ×64 (Huelsenbeck and Ronquist, 2001) with four chains, and the best evolutionary model for the alignment was determined using PartitionFinder (Frandsen et al., 2015; Lanfear et al., 2014, 2016). Phylogenetic analyses were then performed using MrBayes v. 3.2.6 ×64 (Huelsenbeck and Ronquist, 2001). The information block for the matrix included two simultaneous Monte Carlo chain runs, with a temperature of 0.2 and 10 million sampled generations (standard deviation ≤0.1). Chain convergence was visualized in Tracer v. 1.6 (Rambaut et al., 2014). The remaining trees were used to calculate a 50% majority-rule consensus topology and posterior probabilities (PP). Trees were visualized and optimized in FigTree v.



**Table 2:** Details of the taxa used in the phylogenetic analysis of this study. The newly generated sequences are in bold.

| Species name                                                                              | Isolate                     | GenBank Accessions |                 |                 |                 |                 |
|-------------------------------------------------------------------------------------------|-----------------------------|--------------------|-----------------|-----------------|-----------------|-----------------|
|                                                                                           |                             | ITS                | nrLSU           | 18S             | <i>rpb2</i>     | <i>tef1</i>     |
| <i>Chorioactis geaster</i> (Peck) Kupfer ex Eckblad                                       | DHP02497                    | -----              | KC012672        | AF104340        | DQ017609        | KC109211        |
| <i>Cookeina tricholoma</i> (Mont.) Kuntze                                                 | IDD5                        | -----              | AY945860        | AF006311        | MN103428        | MN103423        |
| <i>Desmazierella acicola</i> Lib.                                                         | RK9512                      | -----              | AY945854        | AF104341        | DQ017603        | LN794774        |
| <i>Donadinia nigrella</i> (Seaver) M.Carbone, Agnello & P.Alvarado                        | FLASF69550                  | -----              | AY945853        | -----           | DQ017592        | KC109214        |
| <i>Galiella rufa</i> (Schwein.) Nannf. & Korf                                             | h101                        | -----              | AY945850        | AF004948        | DQ017594        | KC109213        |
| <i>Geodina guanacastensis</i> Denison                                                     | FH                          | MN096939           | MN096940        | MN096941        | MN103424        | MN090946        |
| <i>Geodina salmonicolor</i> Angelini & Medardi                                            | JBSD127408                  | MG597289           | MG597287        | -----           | -----           | -----           |
| <i>Geodina salmonicolor</i> Angelini & Medardi                                            | JBSD127409                  | MG597290           | MG597288        | -----           | -----           | -----           |
| <i>Gyromitra californica</i> (W.Phillips) Raitv.                                          | AFTOLID176                  | -----              | AY544673        | AY544717        | DQ470891        | DQ471059        |
| <i>Komposcocypha phylogena</i> (Seaver) Pfister                                           | DHP10690                    | -----              | JQ260810        | JQ260820        | MN103430        | MN103416        |
| <i>Morchella elata</i> Fr.                                                                |                             | -----              | U42667          | U42641          | AF107810        | HM756737        |
| <i>Neournula pouchetii</i> (Berthet & Riousset) Paden                                     |                             | -----              | AY307940        | AF104666        | DQ017601        | -----           |
| <i>Phillipsia carnicolor</i> Le Gal                                                       | DHP7126                     | -----              | JQ260811        | JQ260821        | MN103426        | MN090948        |
| <i>Pithya cupressina</i> (Batsch) Fuckel                                                  | MH208                       | -----              | JQ260818        | AF006316        | MN103429        | MN103415        |
| <i>Plectanua melastoma</i> (Sowerby) Fuckel                                               | TURA195784                  | -----              | JX669850        | MN102128        | MN103434        | MN103422        |
| <i>Pseudopithyella minuscula</i> (Boud. & Torrend) Seaver                                 | mh675                       | -----              | AY945849        | AF006317        | DQ017600        | FJ238387        |
| <i>Pseudoplectania nigrella</i> (Pers.) Fuckel                                            | KH9728                      | -----              | AY945852        | MN096942        | MN103433        | MN103421        |
| <i>Pseudosarcosoma latahense</i> (Paden & Tylutki) M.Carbone Agnello & P.Alvarado         | AFTOLID954                  | -----              | FJ176860        | FJ176806        | -----           | FJ238392        |
| <i>Rickiella edulis</i> (Speg.) Pfister                                                   | BAFC51697                   | -----              | JQ260809        | JQ260819        | MN103425        | MN090947        |
| <i>Sarcoscypha austriaca</i> (Beck ex Sacc.) Boud.                                        | mh670                       | -----              | AY945856        | AF006318        | MN103427        | KC109210        |
| <i>Sarcosoma globosum</i> (Sacc.) Casp.                                                   | KH0704                      | -----              | FJ499393        | U53386          | JX943753        | KC109215        |
| <i>Urnula craterium</i> (Schwein.) Fr.                                                    | DHP04511                    | -----              | AY945851        | AF104347        | DQ017595        | KC109216        |
| <i>Wolfina aurantiopsis</i> (Ellis) Seaver ex Eckblad                                     | DHP04599                    | -----              | AY945859        | AF104664        | DQ017605        | KC109212        |
| <i>Wynnea americana</i> Thaxt.                                                            | SNFH                        | MK599141           | AY945848        | MK592785        | MN103435        | MN103417        |
| <i>Wynnea americana</i> Thaxt.                                                            | FLASF61957                  | -----              | MZ018899        | -----           | -----           | -----           |
| <i>Wynnea americana</i> Thaxt.                                                            | FH00445978                  | MK599141           | MK599148        | -----           | -----           | -----           |
| <i>Wynnea gigantea</i> Berk. & M.A.Curtis                                                 | Brazil 2013                 | MK335782           | MK335802        | -----           | -----           | -----           |
| <i>Wynnea gigantea</i> Berk. & M.A.Curtis                                                 | Brazil 1993                 | MK335781           | MK335801        | MK335790        | -----           | -----           |
| <b><i>Wynnea hypogaea</i> J.García, Gallardo-Yobal, de la Fuente &amp; Sánchez-Flores</b> | <b>SGY 77 ITCV Holotype</b> | <b>PZ839274</b>    | <b>PZ834822</b> | <b>PZ834854</b> | <b>PZ852167</b> | <b>PZ852169</b> |
| <b><i>Wynnea hypogaea</i> J.García, Gallardo-Yobal &amp; Sánchez-Flores</b>               | <b>SGY 78 ITCV Paratype</b> | <b>PZ839275</b>    | <b>PZ834823</b> | <b>PZ834855</b> | <b>PZ852168</b> | <b>PZ852170</b> |
| <i>Wynnea macrospora</i> B.Liu, M.H.Liu & J.Z.Cao                                         | FH00445975                  | MK335784           | MK335803        | MK335793        | MN103432        | MN103419        |
| <i>Wynnea macrospora</i> B.Liu, M.H.Liu & J.Z.Cao                                         | WZ2130                      | MK335785           | -----           | MK335794        | -----           | -----           |
| <i>Wynnea macrotis</i> (Berk.) Berk. & M.A.Curtis                                         | CUP2864                     | -----              | MK335804        | MK335795        | -----           | MN103420        |
| <i>Wynnea</i> sp.                                                                         | N. 153                      | -----              | MG871342        | -----           | MG980708        | -----           |
| <i>Wynnea sparassoides</i> Pfister                                                        | FH 00445986                 | -----              | EU360917        | MK335796        | MN103431        | MN103418        |
| <i>Wynnea sparassoides</i> Pfister                                                        | NYBG024800                  | MK335787           | -----           | MK335797        | -----           | -----           |
| <i>Wynnea sparassoides</i> Pfister                                                        | FLASF68409                  | OM672767           | -----           | -----           | -----           | -----           |



1.1.4 (Rambaut, 2014) and edited in Adobe Illustrator (Adobe Systems, Inc., San Jose, California, USA).

## Results

### Molecular phylogenetic analyses

The dataset of combined ITS, nrLSU, 18S, *rpb2*, and *tef1* comprises 37 taxa with 3597 characters, including gaps. The three phylogenetic analyses, MP, ML, and BI, recovered similar topologies (Fig. 2). No significant conflicts (bootstrap values >80%) were detected among the topologies obtained from the separate phylogenetic analyses. The parsimony analysis of the alignment found 11485 trees of 371 steps (CI= 0.5952, HI= 0.1350, RI= 0.2901, RC= 0.1088). The best RAxML tree with a final likelihood of -20842.006371 is presented. The matrix had 1071 distinct alignment patterns, with 4.12% undetermined characters or gaps. Estimated base frequencies were as follows: A= 0.190241, C= 0.195100, G= 0.105247, T= 0.103407; substitution rates AC= 1.000683, AG= 1.003401, AT= 1.00957, CG= 1.002740, CT= 4.001954, GT= 1.141004; gamma distribution shape parameter  $\alpha$ = 0.001007. In the Bayesian analysis, the standard deviation between the chains stabilized at 0.001 after 3 million generations. No significant changes in tree topology, trace plots, or cumulative split frequencies of selected nodes were observed after about 0.25 million generations, which were discarded as the 25% burn-in. The analysis produced a phylogenetic tree in which *Wynnea hypogaea* is shown to be a sister group of *W. gigantea* (BS= 100%, BS= 100%, BI p= 1) and a separate taxon.

## Taxonomy

### Ascomycota

### Pezizomycetes

### Pezizales

### Wynneaceae

***Wynnea hypogaea*** J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores sp. nov. Figs. 3, 4, 5, 6, 7.

TYPE: MEXICO. Veracruz, Coscomatepec municipality, Japalma bridge, in montane cloud forest, 1389 m, 19.106627°N, 97.039096°W, 7.XI.2022, S. Gallardo-Yobal 77 (holotype: ITCV! [SGALLARDOYOBAL-77-ITCV]).

GenBank: ITS: PZ839274; 28S: PZ834822; 18S: PZ834854; *rpb2*: PZ852167; *tef1*: PZ852169.

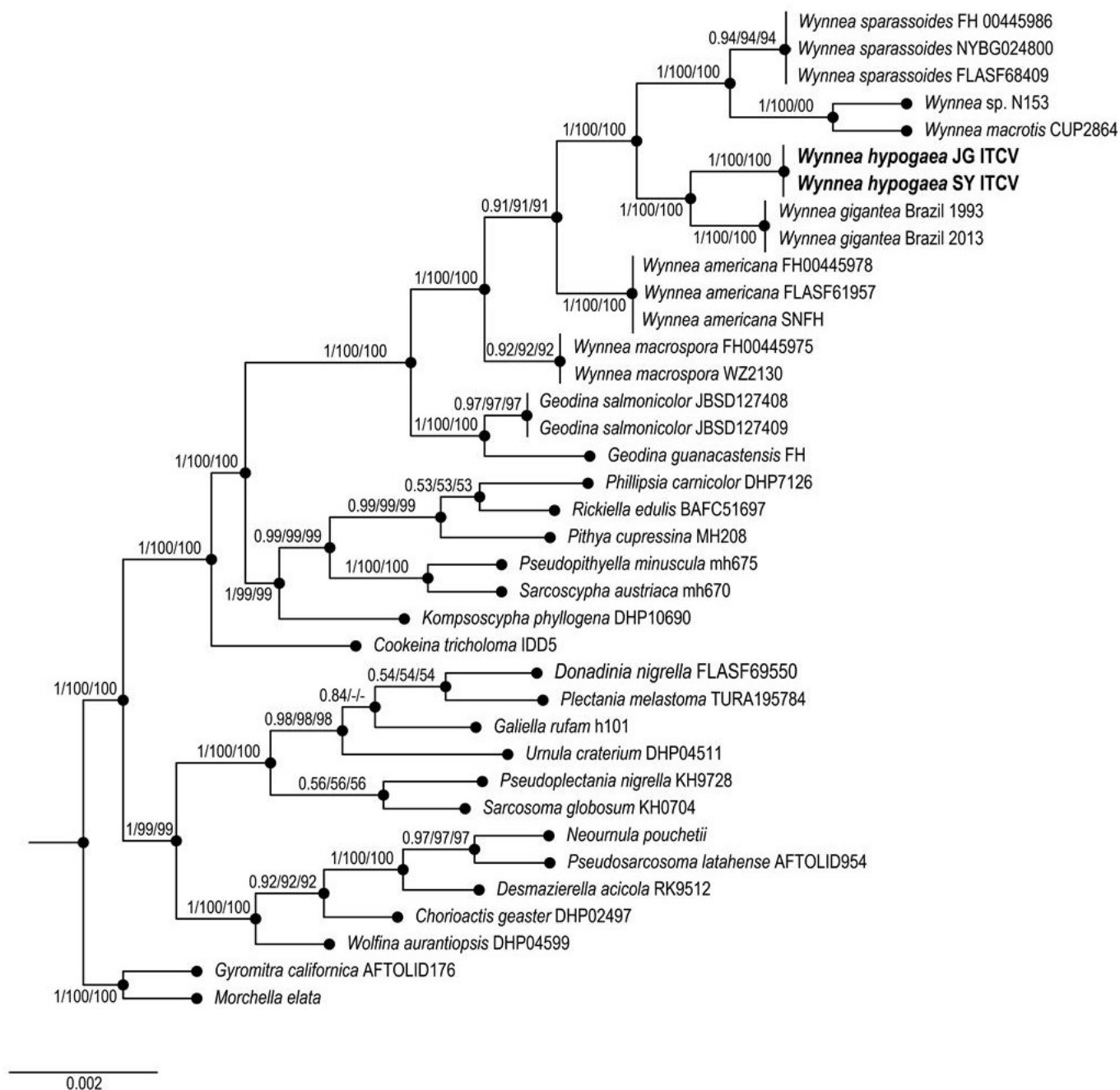
MycoBank: 856887 (MycoBank, 2025).

*Wynnea hypogaea* differs from other species within the genus by its hypogeous, turbinate ascomata, irregular, empty, pinkish locules, ascospores 35-40 × 15-22 µm, and grows below *Quercus lancifolia*.

Ascomata 20-25 mm in diameter, hypogeous, turbinate, irregularly lobulate, solitary to scattered, garnet red (11E8) to violet brown (11F8), texture rough to slightly tomentose, with a wide columella, becoming thinner at the base and dendroid in the hymenium, forming irregular to elongate locules, purplish pink (14A4), purplish grey (14B2), reddish lilac (14B5), becoming greyish magenta (14C7) near the locules, locules sometimes become exposed near the peridium, sclerotium not observed; peridium 120-170 µm thick, composed of pseudoparenchymatous tissue, with globose to subglobose cells of 15-47 × 10-32 µm, hyaline with purplish cell walls, inamyloid, thick-walled (1-3 µm), with clavate to cylindrical terminal cells of 36-100 × 15-32 µm, septate, thick-walled; medullary excipulum 125-340 µm in diameter, textura intricata, composed of tubulose hyphae of 7-9 µm in diameter; hymenium 300-410 µm in diameter; paraphyses 7-10 µm in diameter, branched, widening at the apex, hyaline, thin-walled; asci 284-406 × 20-27 µm, hyaline, 8-spored, uniseriate, without croziers, stipe 60-90 µm long, inamyloid, thin-walled; ascospores 35-40 × 15-22 µm, n= 100, X= 37.15 × 17.29 µm, Q= 1.81-2.53, Qm= 2.148, bilaterally symmetric, hyaline, with four conspicuous longitudinal ridges joined by small ribs between the ridges, disappearing with 5% KOH.

Habitat: on soil, below *Quercus lancifolia* Schltdl. & Cham.





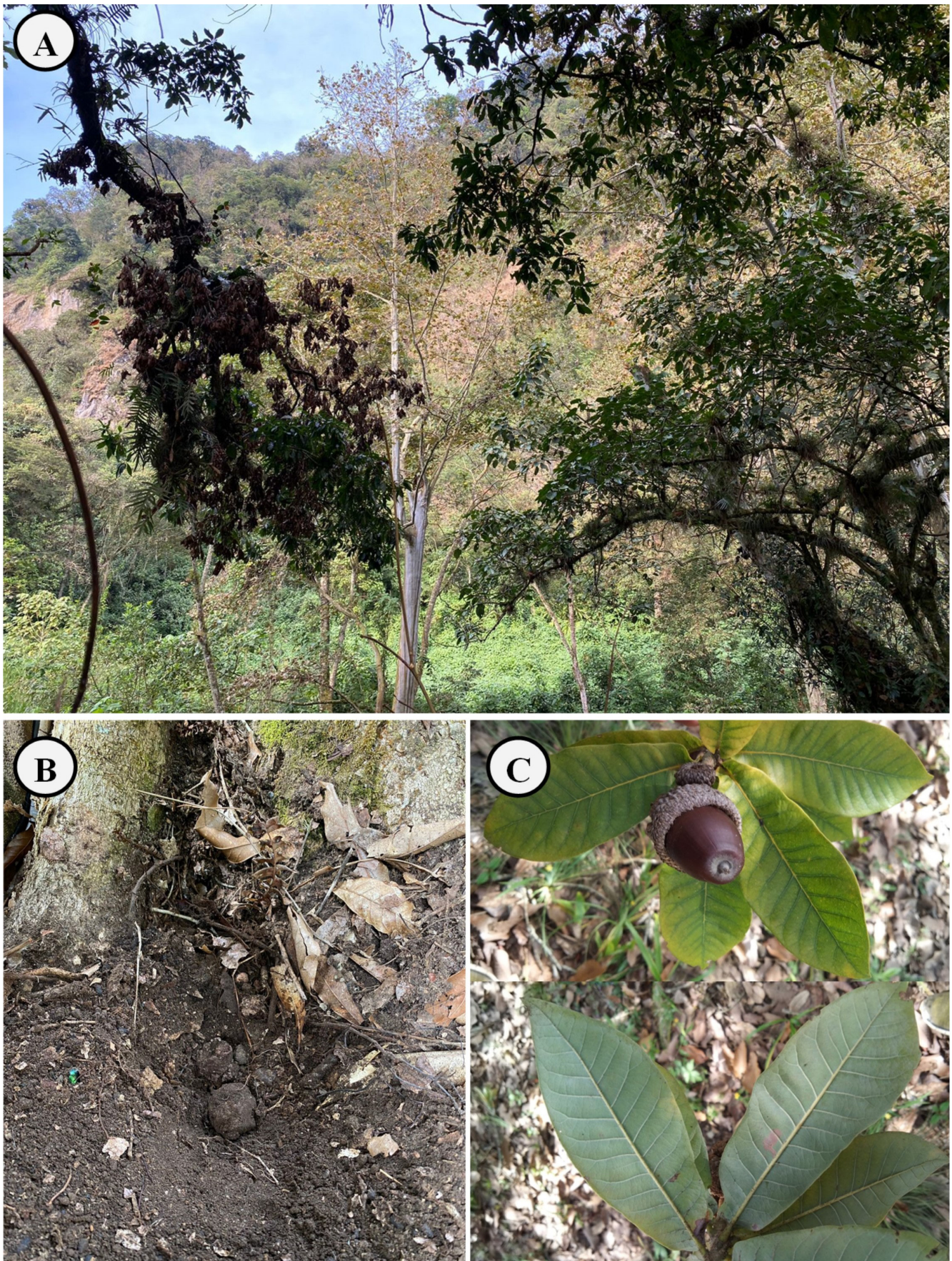
**Figure 2:** Maximum likelihood phylogeny based on the concatenated ITS, nrLSU, 18S, *rpb2* and *tef1* sequence alignment. Maximum parsimony and Bayesian analyses recovered identical topologies for the relationships among the main clades of *Wynnea* Berk. & M.A.Curtis. For each node, the following values are provided: posterior confidence (p-value) / maximum parsimony bootstrap (%), and maximum likelihood bootstrap (%). The scale bar represents the expected number of nucleotide substitutions per site. The new species is shown in bold.

Distribution: known from the type locality, Veracruz, Mexico.

Etymology: the name refers to the formation of the first hypogaeal ascomata within the genus *Wynnea*.

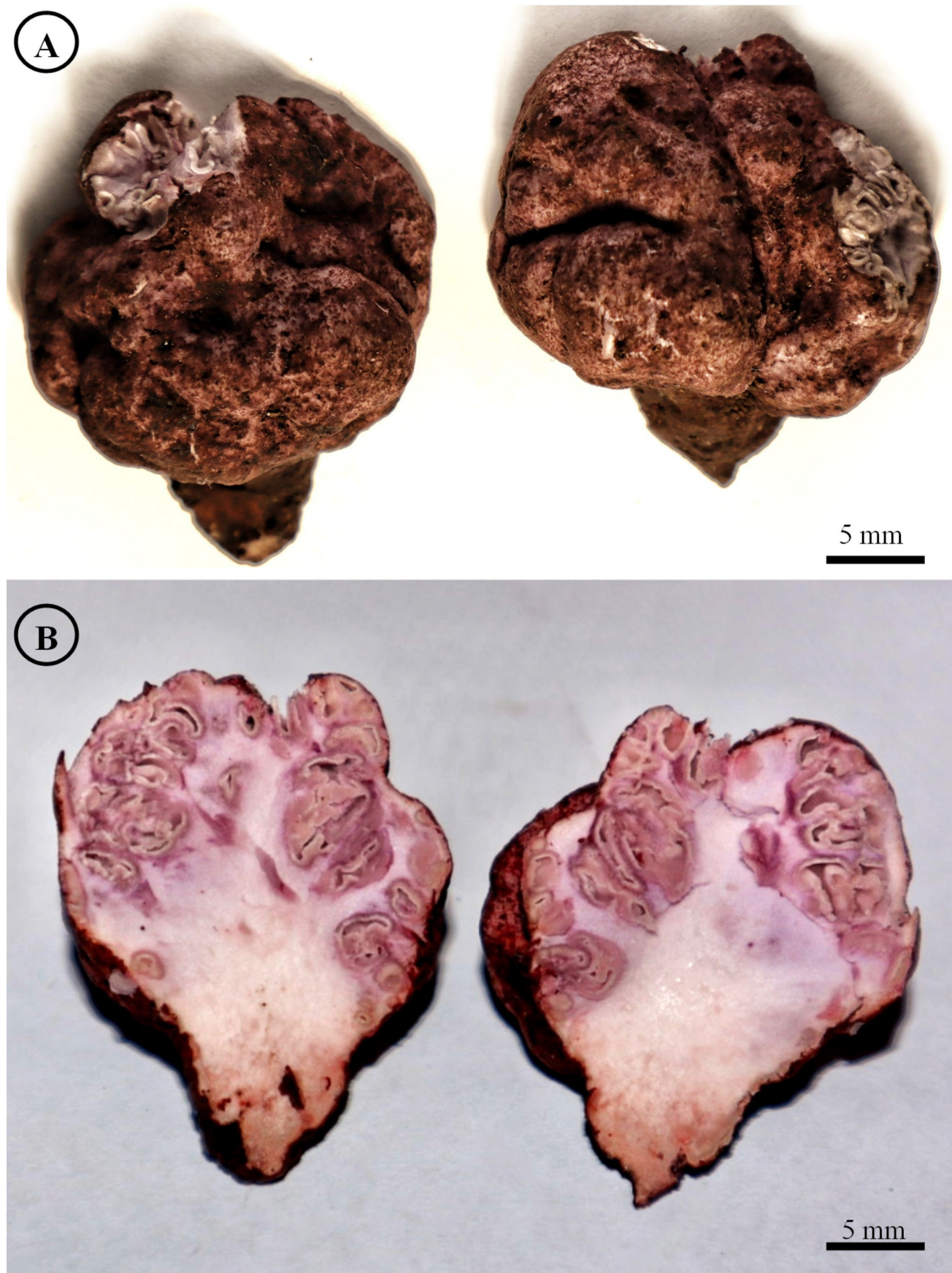
Additional specimens examined: MEXICO. Veracruz, municipality Coscomatepec, Japalma bridge, in montane cloud forest, 1389 m, 19.106627°N, 97.039096°W, 14.XI.2022, S. Gallardo-Yobal 78 (ENCB, ITCV).



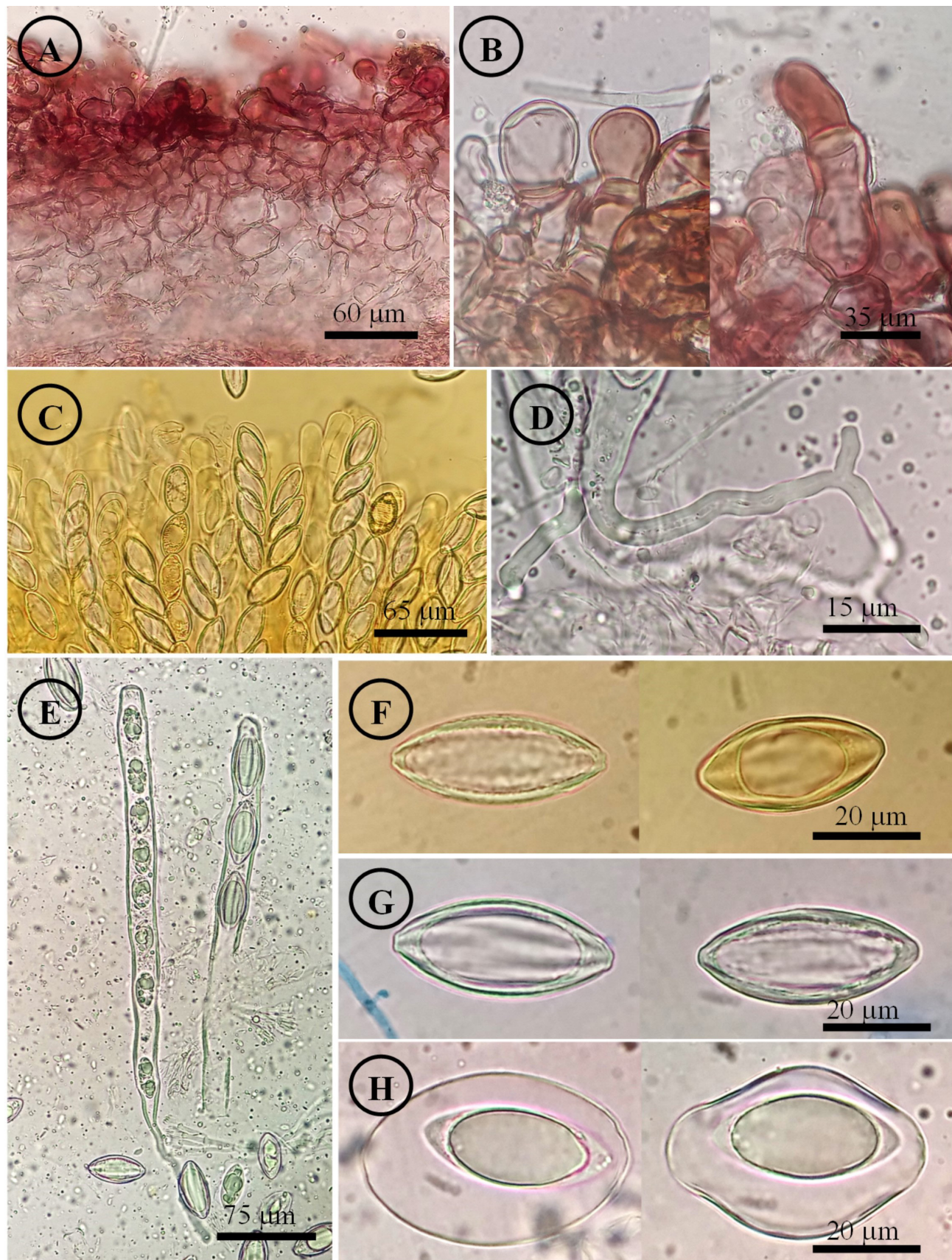


**Figure 3:** A. type locality of *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores; B. ascomata of *Wynnea hypogaea*; C. *Quercus lancifolia* Schltdl. & Cham.

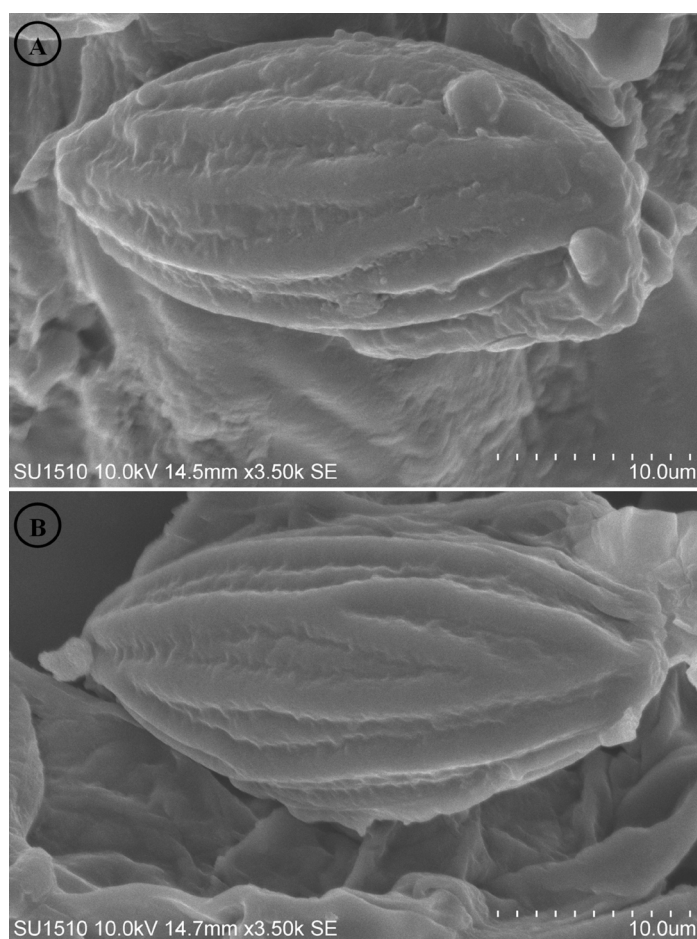




**Figure 4:** *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores. A, B. apothecia.



**Figure 5:** *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores. A. peridium; B. terminal cells; D. asci base; E. asci; F. ascospores in Melzer reagent; G. ascospores in blue cotton; H. ascospores in KOH.

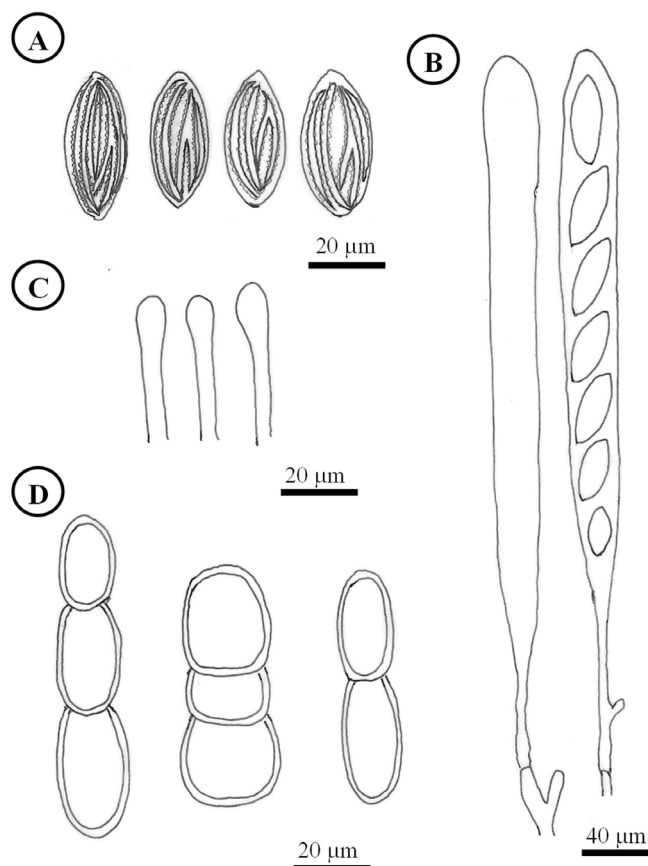


**Figure 6:** *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores. A, B. ascospores under SEM.

**Notes:** The new species is characterized by hypogaeous ascomata and ascospores measuring  $35\text{--}40 \times 15\text{--}22\text{ }\mu\text{m}$ . It differs from *W. sparassoides* by its epigeous ascomata, with a cartilaginous stalk, asci  $350\text{--}375 \times 16\text{--}20\text{ }\mu\text{m}$ , and ascospores  $32\text{--}36 \times 12\text{--}15\text{ }\mu\text{m}$  (Pfister, 1979) vs. *W. hypogaea* with hypogaeous ascomata, asci  $284\text{--}406 \times 20\text{--}27\text{ }\mu\text{m}$ , and ascospores  $35\text{--}40 \times 15\text{--}22\text{ }\mu\text{m}$ . According to the phylogeny, the new species is close to *W. macrotis*. However, that species shows long, oblique, auriform apothecia emerging from a stipe and smaller, asymmetric ascospores of  $28\text{--}32 \times 12\text{--}13\text{ }\mu\text{m}$ .

## Discussion

The genus *Wynnea* is described as having epigeous, elongated-cupped, spatulate, auriculiform, otideoid to secotioid apothecia (Thaxter, 1905; Pfister, 1979; Ekanayaka et al., 2018; Pfister et al., 2020), among which *W. hypogaea* is



**Figure 7:** *Wynnea hypogaea* J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores. A. ascospores; B. asci; C. paraphyses; D. terminal cells.

the first species within the genus to form hypogaeous ascomata. This genus is reported to be saprobic (Ekanayaka et al., 2018), despite our species being often collected under *Q. lancifolia*. The new species is phylogenetically close to *W. macrotis* and *W. sparassoides*. However, *W. hypogaea* forms a clade with *W. gigantea*, which, despite its distinct morphological characteristics, is separate from the other species, justifying the erection of a new taxon. Due to its morphology, the new species described here resembles *W. sparassoides*. Both species show stipitate ascomata. The fertile tissue remains closed in *W. hypogaea*; nevertheless, some specimens of *W. sparassoides* show slightly irregular apothecia, similar to those of some sequestrate taxa. Another characteristic of *Wynnea* species is the presence of a sclerotium. This structure can even develop symbiotic relationships with other fungi, such as *Armillaria* (Fr.) Staude



(Xu et al., 2019; Pfister et al., 2020). According to our data, no sclerotia are formed in *W. hypogaea*, but more sampling is recommended. Morphological comparisons are shown in Table 3.

Several hypogeous forms are known in Ascomycota, mainly in Pezizales. Those taxa are distributed in several genera, some of them composed only of sequestrate forms (Castellano et al., 1989; Trappe et al., 2009). The transition between epigeous and hypogeous ascomata has already been observed within the Pezizales. Despite morphological differences between the two types of ascomata, some sequestrate species retain features shared with their epigeous relatives, such as tissue structure and ascospore shape and ornamentation (Smith and Healy, 2009; Smith, 2014). Still, classification of pezizalean hypogeous taxa and evidence of a link with their epigeous relatives can be challenging (Smith, 2014). In *W. hypogaea*, the species still retains features of the genus, such as ascospore ornamentation and peridial structure (Pfister, 1979). Due to *W. hypogaea*'s current hypogeous habit, its dispersal by zoochory is suspec-

ted (Castellano et al., 1989). Unfortunately, data about their aroma and taste were not recorded. Furthermore, data about its dispersers are lacking. Further studies will fill the gaps in our understanding of the ecology of this outstanding new species.

This transition to a sequestrate lifestyle has been studied by Thiers (1984), who proposed that climate change could stimulate the progression to a hypogeous habit. Furthermore, some studies have suggested that the sequestrate form is a recessive feature expressed under endogamy (Hibbett et al., 1994). Also, paedomorphosis and neoteny have been proposed to explain the gasteromycetization phenomenon (Kuhar et al., 2023).

## Author contributions

Conceptualization: JGJ, TR ILV, MSF, and JIF; Data curation: JGJ, SGY, JIF, and MSF; Formal analysis: CRMG; Funding acquisition: ILV; Resources: JGJ, TR, FGO, and ILV; Visualization: JGJ, SGY, JIF MSF, and FGO; Writing – original draft: JGJ, SGY, JIF, and MSF; Writing – review & editing: JGJ, SGY, MSF, JIF, CRMG, TR, FGO, and ILV.

**Table 3:** Morphological comparison of the known species of *Wynnea* Berk. & M.A.Curtis.

| Species                                                                    | Ascomata size (mm) | Ascomata habit | Ascospore size (µm) | Asci size (µm)      | Sclerotium   | Distribution           | Reference         |
|----------------------------------------------------------------------------|--------------------|----------------|---------------------|---------------------|--------------|------------------------|-------------------|
| <i>W. americana</i> Thaxt.                                                 | 130 × 60           | epigeous       | 35-40 × 12-18       | 330-400 × 16-20     | present      | Costa Rica, Japan, USA | Pfister (1979)    |
| <i>W. gigantea</i> Berk. & M.A.Curtis                                      | >80                | epigeous       | 30-35 × 13-16       | 300-325 × 14-18     | not recorded | Brazil, Mexico, Peru   | Pfister (1979)    |
| <i>W. hypogaea</i> J.García, Gallardo-Yobal, de la Fuente & Sánchez-Flores | 20-25              | hypogeous      | 35-40 × 15-22       | 284-406 × 20-27     | not recorded | Mexico                 | This study        |
| <i>W. intermedia</i> Waraitch                                              | 180-40             | epigeous       | 25-32 × 11.5-14.5   | 360-435 × 13.5-19.5 | present      | India                  | Waraitch (1976)   |
| <i>W. macrospora</i> B.Liu, M.H.Liu & J.Z.Cao                              | 45-65 × 23-50      | epigeous       | 40-47 × 17-18       | 320-350 × 19-22     | present      | China                  | Liu et al. (1987) |
| <i>W. macrotis</i> (Berk.) Berk. & M.A.Curtis                              | 180 × 40           | epigeous       | 28-32 × 12-13       | 320-360 × 15-18     | present      | India, Tibet           | Pfister (1979)    |
| <i>W. sinensis</i> B.Liu, M.H.Liu & J.Z.Cao                                | 80-90 × 50-60      | epigeous       | 26-30 × 13-14       | 300-320 × 13-14     | not recorded | China                  | Liu et al. (1987) |
| <i>W. sparassoides</i> Pfister                                             | 60-80              | epigeous       | 32-36 × 12-15       | 350-375 × 16-20     | not recorded | USA                    | Pfister (1979)    |



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## Declaration of use of Artificial Intelligence

The authors confirm that no artificial intelligence tools were used in the preparation of this manuscript.

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