

# A new species and a new combination of truffle-like fungi in the *Geopora-Tricharina* lineage from North America: *Terracavicola echinospora* gen. et sp. nov. and *Geopora lateritia* comb. nov.

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**Abstract:** Molecular investigations into two truffle-like fungi within the *Pyronemataceae* (*Pezizales*, *Ascomycota*) revealed hidden diversity that required further clarification of generic and species boundaries of the hypogeous, ptychothecial members of this family. Here we describe *Terracavicola echinospora* gen. et. sp. nov. from Mexico and we transfer *Pachyphloides lateritia* from the western United States into the genus *Geopora* as *Geopora lateritia* comb. nov. We provide molecular phylogenetic evidence based on ITS and 28S ribosomal DNA for the placement of both taxa and provide detailed morphological analyses. We also discuss the taxonomy of other morphologically similar taxa in *Pyronemataceae* with an emphasis on the lineage that includes *Geopora*, *Hoffmannoscypha*, *Picoa*, and *Tricharina*.

**Keywords:** New genus, truffle systematics, *Pyronemataceae*, *Pachyphloeus*, *Pachyphloides*, *Pezizales*, 2 new sequestrate taxa.

## Introduction

The *Pyronemataceae* (*Pezizales*, *Ascomycota*) is a morphologically and ecologically diverse group of fungi that has proven taxonomically challenging (HANSEN *et al.*, 2013; PERRY *et al.*, 2007). The family includes taxa with a wide variety of nutritional modes, including ectomycorrhizae e.g. *Geopora*, *Genea*, and *Genabea* (FLORES-RENTERIA *et al.*, 2014; SMITH *et al.*, 2006), endophytes e.g. *Tricharina* (VAN VOOREN *et al.*, 2017) and putative saprobes e.g. *Anthracobia* (HANSEN *et al.*, 2013).

Ascoma morphology is also highly variable across the family and can sometimes be variable even within genera. Most *Pyronemataceae* species produce cupulate fruiting bodies on soil, but sequestrate, cleistothecial, or truffle-like ascomata have evolved several times within the family (HANSEN *et al.*, 2013). Some *Pyronemataceae* such as *Lasiobolidium* and *Orbicula* remain epigeous, but have evolved a cleistothecial form and lost forcible ascospore discharge (HANSEN *et al.*, 2005). Exclusively sequestrate hypogeous forms that have lost forcible ascospore discharge can be found in the genera *Densocarpa*, *Gelinipes* nom. prov., *Genea*, *Genabea*, *Hydnocystis*, *Myrmecocystis*, and *Picoa* (KUMAR *et al.*, 2017; PERRY *et al.*, 2007; ALVARADO *et al.*, 2018). Both cupulate and truffle-like forms are known to occur in the same genus, such as in *Geopora*, *Otidea*, and *Humaria* (GUEVARA *et al.*, 2012; SMITH & HEALY, 2009; ALVARADO *et al.*, 2018). Within the genus *Geopora*, species with the two different forms of ascomata were previously treated as two separate genera; truffle-like taxa were in *Geopora* whereas cupulate species were in *Sepultaria*. Although all of these taxa are currently treated within *Geopora*, some recent molecular analyses have suggested that both *Geopora* and *Sepultaria* should be recognized (GUEVARA *et al.*, 2012). One taxonomic complication that recent studies have shown is that members of the genus *Picoa* are nested within *Geopora* (SBISSI *et al.*, 2010; STIELOW *et al.*, 2013). *Picoa* is the oldest name for the species in this group, since the type species of *Picoa*, *P. juniperi* Vittad. (VITTADINI, 1831) predates that of the type species of *Geopora*, *G. cooperi* Harkn. (HARKNESS, 1885). However, it is outside the scope of this paper to resolve the taxonomic issues regarding *Geopora* and *Picoa*.

During revisions of herbarium specimens, we identified several Mexican collections of an unusual truffle-like taxon that did not fit well with any of the described genera of *Pyronemataceae*. The spec-

imens were tentatively identified as a *Genea* species based on the brown semi-hypogeous ascomata, extensive excipular hairs, and ornamented ascospores. However, the specimens also had large and obvious guttules in the ascospores and lacked a well-developed epithecium, so they were not a good fit morphologically in *Genea*. Other morphological features such as the hairy peridium and ascospores with one large guttule were similar to species of *Geopora*, although the ascospore ornamentation and weak epithecium did not fit well within that genus. Sequences of the Internal Transcribed Spacer region (ITS) and the large sub-unit of the 28S ribosomal DNA (28S) indicated an affinity with *Geopora*, *Hoffmannoscypha*, *Picoa* and *Tricharina*, hereafter referred to as the *Geopora-Tricharina* lineage.

We also studied a second sequestrate hypogeous species with affinities to the *Geopora-Tricharina* lineage, *Pachyphloides lateritia* (Fogel & States) Doweld. Studies of the type specimen, *Pachyphloeus lateritius* Fogel & States (FOGEL & STATES, 2002), revealed that this species was not closely related to the genus *Pachyphloides*, but had highest ITS and 28S sequence similarity to *Geopora* species (HEALY, 2013).

Accordingly, we initiated a molecular and morphological study of these two truffle-like species with morphological or molecular affinity with *Geopora* and compared them to related taxa from herbaria in the United States. Based on the unique molecular and morphological data generated in this study, we erect *Terracavicola echinospora* gen. et sp. nov. to accommodate the collections that superficially resembled a *Geopora* species. We also transfer *Pachyphloides lateritia* to *Geopora* as *Geopora lateritia* comb. nov. based on analyses of molecular data and a re-examination of morphological data.

## Materials and methods

Ascomata were collected by searching through leaf litter and soil using the methods of CASTELLANO *et al.* (1989). Samples were placed in plastic boxes and transported to the laboratory within eight hours. Macroscopic photographs of fresh specimens were taken in the lab. Samples were then dried on a forced-air dryer for approximately 24 hours and stored in herbarium packets. Specimens are accessioned in Mexico at the José Castillo Tovar (ITCV) and in the United States at the Florida Museum of Natural History at the Uni-

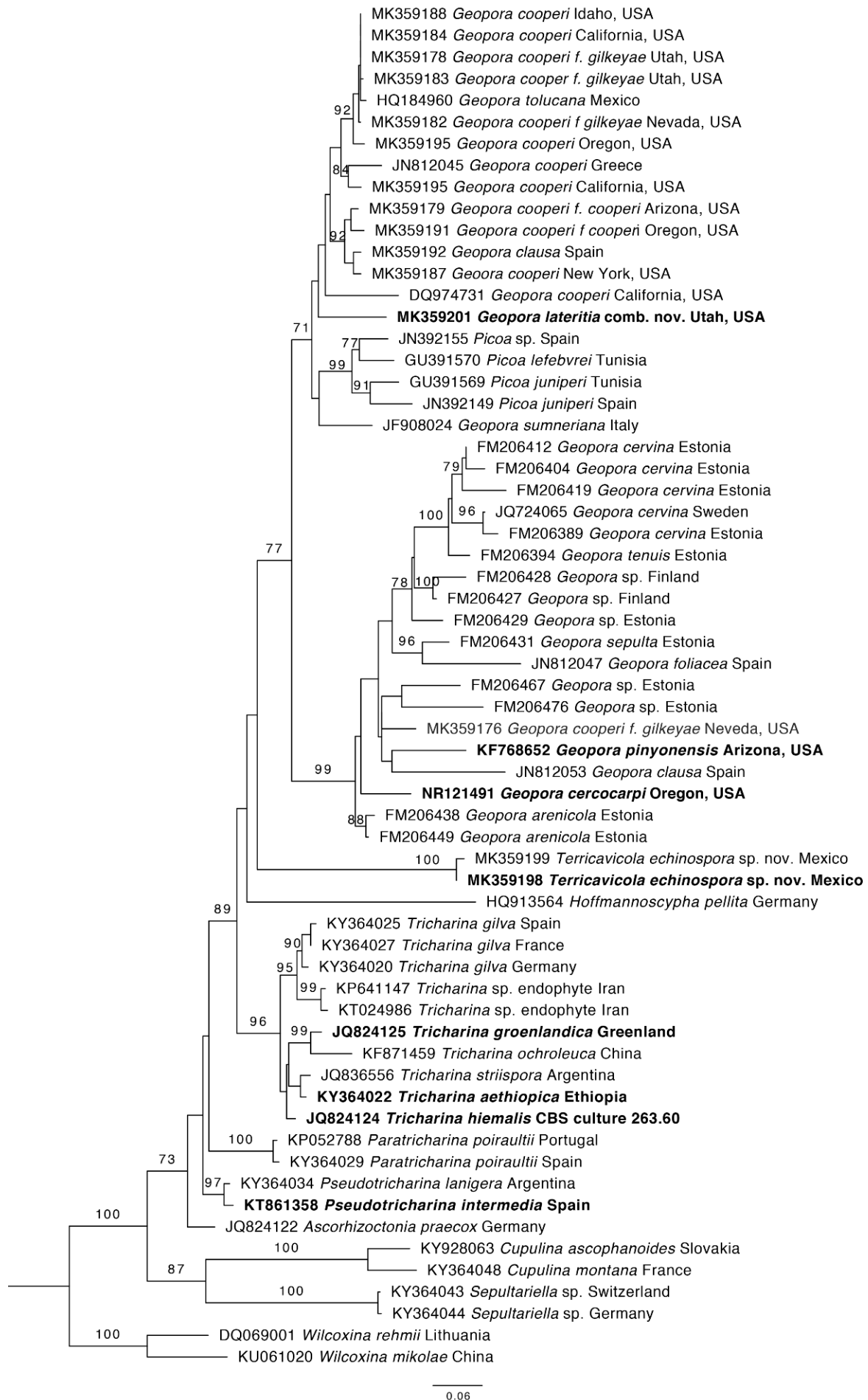
versity of Florida (FLAS) and Oregon State University (OSC). We also obtained loans of specimens identified as *Geopora cooperi sensu lato* and *Pachyphloes lateritia* for morphological examination and DNA sequencing from the following herbaria: University of Michigan (MICH), Oregon State University (OSC), University of British Columbia (UBC), Denver Botanical Garden (DBG), Utah State University (UTC), and University of Washington (WTU). For a list of all specimens sequenced for this project, their herbaria of origin, and GenBank accession numbers see Table 1.

Dried material was rehydrated, hand-sectioned with a razor blade, and mounted in water, 3% KOH, Cotton Blue in lactophenol, or Melzer's reagent. Relevant morphological characters, including hyphae, excipular setae (hairs), epitecium, paraphyses, asci, and as-

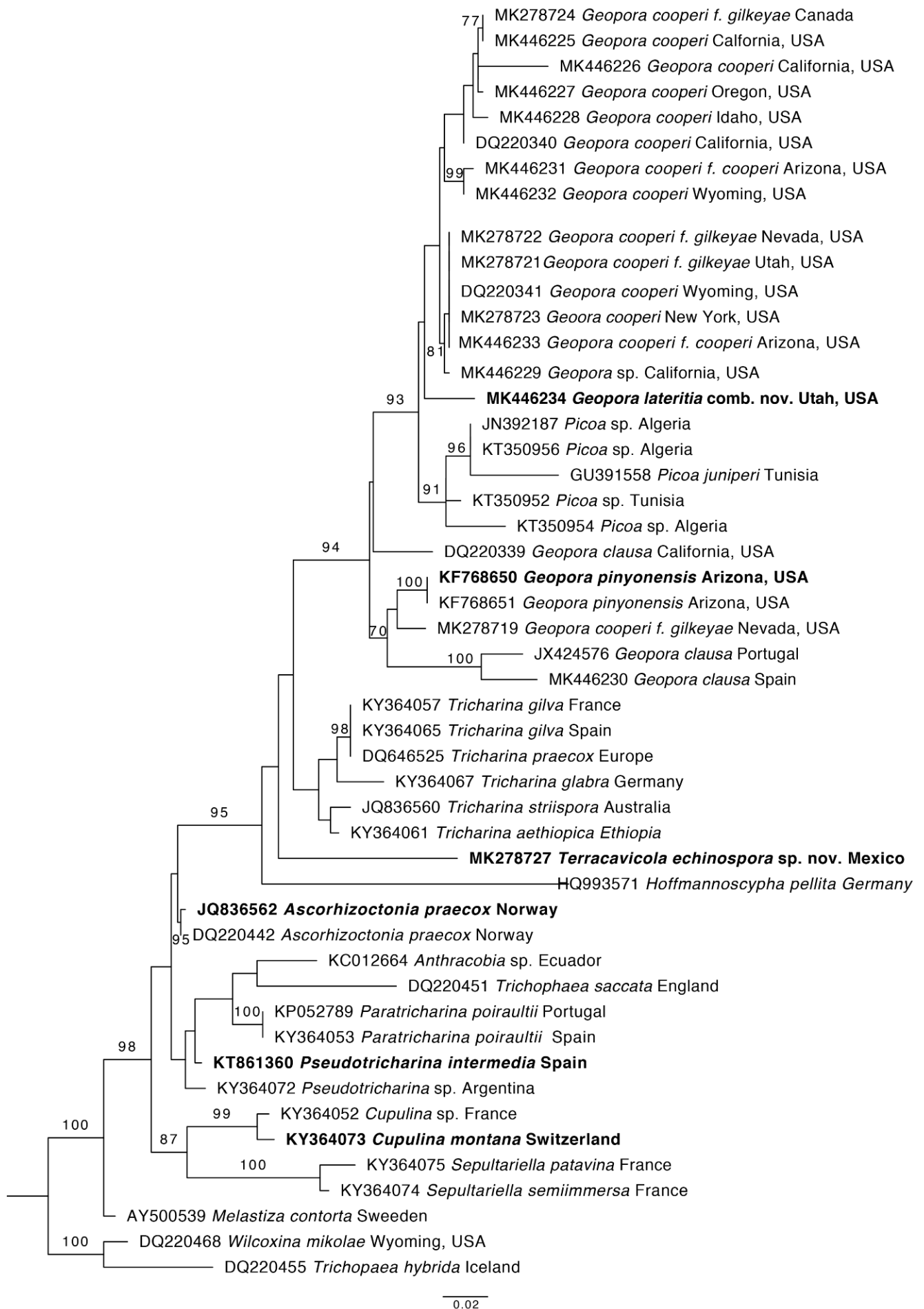
cospores, were studied and their sizes assessed based on 20 individual measurements at appropriate magnifications. Images were captured using a q-imaging micropublisher 3.3 RTV digital camera mounted on a Nikon Optiphot light microscope. For Scanning Electron Microscopy (SEM), dried sections of material were rehydrated in 3% KOH for 20 minutes, rinsed in water, dehydrated to 100% ethanol, critical point dried, fractured, and open halves mounted on silver tape on an aluminum stub, sputter coated with gold/palladium, and viewed on a Jeol 5800lv Sem (JEOL USA Inc., Peabody, MA) with 10 KV. Images were digitally captured. Microscopic features were compared with the known species of *Geopora* and related taxa based on original descriptions when available.

**Table 1** – List of specimens sequenced in this study with their corresponding species, herbarium code, ITS, and 28S accession numbers from GenBank.

Species	Herbarium Code	GenBank Accession Number	
		ITS	28S
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00026467	–	MK278718
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00071420	–	MK278719
<i>Geopora cooperi</i> f. <i>cooperi</i>	MICH 00026483	–	MK446231
<i>Geopora cooperi</i>	MICH 00067846	MK359172	MK446232
<i>Geopora cooperi</i>	UBC F28815	MK359173	–
<i>Geopora cooperi</i>	UBC F28213	MK359174	–
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00026471	MK359175	–
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00000078	MK359176	–
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00026478	MK359177	MK278720
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00026484	MK359178	–
<i>Geopora cooperi</i> f. <i>cooperi</i>	MICH 00067761	MK359179	–
<i>Geopora cooperi</i> f. <i>cooperi</i>	MICH 00067851	MK359180	–
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00071412	MK359181	MK278721
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00071413	MK359182	MK278722
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	MICH 00071414	MK359183	–
<i>Geopora cooperi</i> f. <i>cooperi</i>	MICH 00067858	–	MK446233
<i>Geopora cooperi</i>	OSC 80446	MK359184	MK446226
<i>Geopora cooperi</i>	OSC 111496	MK359185	–
<i>Geopora cooperi</i>	OSC 111416	MK359186	–
<i>Geopora cooperi</i>	OSC 80456	MK359187	MK278723
<i>Geopora cooperi</i>	OSC 79808	MK359188	MK446228
<i>Geopora cooperi</i>	OSC 111415	MK359189	MK446227
<i>Geopora cooperi</i> f. <i>cooperi</i>	OSC 80439	MK359190	–
<i>Geopora cooperi</i> f. <i>cooperi</i>	OSC 71357	MK359191	–
<i>Geopora clausa</i>	OSC 58245	MK359192	MK446230
<i>Geopora</i> sp.	OSC 58893	–	MK446229
<i>Geopora cooperi</i> f. <i>gilkeyae</i>	OSC 112404	MK359193	MK278724
<i>Geopora cooperi</i>	OSC 56085	MK359194	–
<i>Geopora cooperi</i>	OSC 127012	MK359195	–
<i>Geopora cooperi</i>	OSC 56168	MK359196	–
<i>Geopora cooperi</i>	OSC 149587	MK359197	MK446225
<i>Geopora cooperi</i> f. <i>gilkeyi</i>	UTC 00233166	–	MK278725
<i>Geopora cooperi</i> f. <i>cooperi</i>	OSC 111416	–	MK278726
<i>Terracavicola echinospora</i>	FLAS JT 19275 (Holotype)	MK359198	MK278727
<i>Terracavicola echinospora</i>	FLAS Guevara 1153	MK359199	–
<i>Pachyphloes lateritius</i>	MICH52896 (Paratype)	MK359200	MK446234
<i>Pachyphloes lateritius</i>	MICH52897 (Holotype)	MK359201	–



**Figure 1** – Phylogram of *Terricavicola echinospora* and related taxa (*Pyrenomataceae*) obtained from Maximum Likelihood analysis of ITS. Numbers above the nodes represent ML bootstrap values. Bootstrap values  $\geq 70\%$  are shown here. Type specimens are highlighted in bold.



**Figure 2** – Phylogram of *Terracavicola echinospora* and related taxa (*Pyrenomataceae*) obtained from Maximum Likelihood analysis of 28S. Numbers above the nodes represent ML bootstrap values. Bootstrap values  $\geq 70\%$  are shown here. Type specimens are highlighted in bold.

Clean fungal tissues were taken from the gleba of 32 dried specimens. DNA was extracted using a modified CTAB method (GARDES & BRUNS, 1993). Polymerase chain reactions (PCR) of the nuclear rDNA ITS region was performed using forward primer ITS1F and reverse primer ITS4 (WHITE *et al.*, 1990). Polymerase chain reactions of the 28S (LSU) region were performed using the same protocol but with forward primer LROR (HOPPLE & VILGALYS, 1994) and reverse primer LR5F (TEDERSOO *et al.*, 2008). Polymerase chain reaction products were visualized on 1.5% agarose gels stained with SYBR Green I (Molecular Probes, Eugene, Oregon). Amplicons were cleaned with EXO (Exonuclease I) and SAP (shrimp alkaline phosphatase) enzymes (WERLE *et al.*, 1994) and sequenced by Genewiz Sanger-sequencing service (South Plainfield, New Jersey) or Eurofins Genomics (Louisville, Kentucky). Additional sequences from TAMM *et al.* (2010) and VAN VOOREN *et al.* (2017) were downloaded from the GenBank NCBI database (CLARK *et al.*, 2016).

We generated an alignment for each locus in Mesquite 3.51 (MADDISON & MADDISON, 2018) with the aid of Muscle 3.8.31 (EDGAR, 2004). For 28S, ambiguously aligned positions were removed by Gblocks 0.91b (CASTRESANA, 2000) using the default parameters and “with-half-gap” option, which removes columns with characters missing in more than half of all the taxa. Ambiguously aligned positions in the ITS alignment were removed manually to include more nucleic acid sites than allowed by Gblocks. Both the 28S and ITS alignments were analyzed with Maximum Likelihood analysis (ML), which was performed in the Cyberinfrastructure for Phylogenetic Research Science Gateway (CIPRES) v. 3.1 (MILLER *et al.*, 2010). The analysis was run using RAxML 8.2.10 (STAMATAKIS, 2014) with 1,000 bootstrap iterations and the GTRGAMMA model for both loci. Resulting phylogenetic trees for both ITS and 28S were visualized and rooted in figtree 1.4.3 (RAMBAUT, 2016). *Wilcoxina* and *Trichophaea* species were selected as the outgroup taxa for both the ITS and 28S phylogenies (VAN VOOREN *et al.*, 2017).

## Results

### Phylogenetic analysis

The ITS alignment was comprised of 63 sequences with a total of 510 nucleic acid sites, whereas the 28S alignment was comprised of 44 sequences with a total of 596 nucleic acid sites. Phylogenetic trees based on Maximum Likelihood analysis (ML) of both alignments placed the newly discovered species *Terracavicola echinospora* inside the *Geopora-Tricharina* clade with high support values (Figs. 1 and 2).

The ITS phylogeny indicates that the genus *Geopora* is divided into two sub-clades (Fig. 1). The first sub-clade is strongly supported and consists mostly of cupulate epigeous *Geopora* species such as *Geopora cervina* (Velen.) T. Schumach. (SCHUMACHER, 1979), *G. tenuis* (Fuckel) T. Schumach. (SCHUMACHER, 1979), *G. cercocarpi* D. Southworth & J.L. Frank (SOUTHWORTH & FRANK, 2011), *G. arenicola* (Lév.) Kers (KERS, 1974), and *G. sepulta* (Fr.) Korf & Burds. (BURDSALL, 1968), but also some truffle-like species such as *G. clausa* (Tul. & C. Tul.) Burds. (BURDSALL, 1968) and *G. pinyonensis* Flores-Rentería & Gehring (FLORES-RENTERÍA *et al.*, 2014). The second sub-clade is weakly supported and includes mostly specimens identified as *Geopora cooperi* Harkn. (HARKNESS, 1885) and one cupulate species, *G. sumneriana* (Cooke) M. Torre (TORRE & CALONGE, 1976). Interestingly, the second sub-clade also includes *Picoa* species and *Pachyphloeus lateritius* Fogel & States (FOGEL & STATES, 2002). Bootstrap support for the ITS analysis (Fig. 1) was moderate and the 28S analysis (Fig. 2) was high for *P. lateritius* within *Geopora*. Accordingly, below we transfer *Pachyphloides lateritia* ( $\equiv$  *Pachyphloeus lateritius*) to the genus *Geopora* as *G. lateritia* comb. nov. In both the ITS and 28S analyses, the exact position of *Terracavicola echinospora* relative to the other genera in the *Geopora-Tricharina* lineage is not resolved.

Despite the difficulties in resolving the exact placement of *T. echinospora*, the genus *Geopora* (including *Picoa*) is supported as a

monophyletic group in both the ITS and 28S analyses and there is strong support for the placement of *P. lateritius* within *Geopora*.

### Taxonomy

***Terracavicola*** A. Grupe, Kraisit., Guevara & M.E. Sm., *gen. nov.*

Mycobank: MB828994

Diagnosis: A hypogeous, creamy-tan to light brown truffle-like ascoma with a roughened peridium that is covered with copious brown hairs (setae), the presence of a weak epithecium which covers the hymenium and prevents active discharge of the ascospores, and unique ITS and 28S DNA sequences.

Type species: *Terracavicola echinospora* A. Grupe, Kraisit., Guevara & M.E. Sm.

Etymology: “*terra*” in reference to the Latin word for earth; “*cavum*” in reference to the Latin word for hollow; “*incola*” in reference to the Latin word for inhabiting. Taken together “*Terracavicola*” means “dweller in a hole in the earth”.

***Terracavicola echinospora*** A. Grupe, Kraisit., Guevara & M.E. Sm., *sp. nov.* – Mycobank: MB828995 (Fig. 3 A–B, Fig. 4 A–F)

Diagnosis: A hypogeous, creamy-tan to light brown truffle-like ascoma with a roughened peridium that is covered by copious brown hairs (setae) that are branched and textured microscopically, the presence of a weak epithecium which covers the hymenium and prevents active discharge of the ascospores, ascospores that are weakly spinose, and unique ITS and 28S DNA sequences.

GenBank: ITS: MK359198; 28S: MK278727

Holotype: Specimen Trappe 19275 at the Oregon State University Herbarium (OSC).

Etymology: “*echinospora*” in reference to the spines that are easily visible on the ascospores of this species.

**Ascoma** ptychothecium, hypogeous, sessile, 8–15 × 5–12 × 3–5 mm, creamy-tan to dark brown, subglobose or lobed, irregular, covered with warts or small verrucae (5–8 warts/mm) and ochre brown, brittle, papillate, with an irregular apical opening 5 mm wide that has irregular setae on the edges, opening leads to an irregular hollow chamber that is covered by the thin, white epithecium layer, excipular setae on the outside up to 2 mm long (Fig. 3). Odor and taste not recorded. **Peridium** 0.25–0.5 mm thick, mostly light brown. **Epithecium** thin, white to cream, tomentose, covering the glebal tissue (Figs. 3A, 4F).

**Peridium** 200–350  $\mu$ m wide, two layered; epicutis (outer layer) 125–270  $\mu$ m wide, pseudoparenchymatous, versiform, angular or isodiametric cells, 12–52  $\mu$ m in diameter, thick walled, reddish brown in KOH and cotton blue, forming fine warts that give rise to hairy, branched hyphae (setae) (Fig. 4A). **Setae** 62–750 × 10–15  $\mu$ m, single or cespitose, branched, brittle, tapering at the tip or sometimes claviform, with punctuations or incrustations on the cell wall, thick walled (2.5  $\mu$ m), septate, reddish brown to ochre in KOH (Fig. 4B). **Subcutis** 32–125  $\mu$ m wide, pseudoparenchymatous gradually changing toward subhymenium to interwoven and prostrate, hyphae 6–7  $\mu$ m wide, thin walled, hyaline in KOH. Subhymenium of interwoven to prostrate hyphae, 6–7  $\mu$ m in diam. thin walled, hyaline in KOH or bluish in cotton blue. **Paraphyses** claviform or capitate, 5–8  $\mu$ m wide at tips, exceeding the hymenial layer and forming a narrow epithecium 25–125  $\mu$ m wide, thin walled, hyaline in KOH (Fig. 4D). **Asci** 150–237 × 15–23  $\mu$ m, cylindrical, claviform with tapering stalk, arising from croziers, 8-spored, hyaline in KOH, thin walled (1  $\mu$ m) (Fig. 4C). **Ascospores** uniseriate, 16–24 × 14–16  $\mu$ m, broadly ellipsoid to subglobose, thin walled, hyaline in KOH, bluish in cotton blue, with an intracellular oil droplet, ornamented with spines 1.5–2.0  $\mu$ m high with rounded or knobby tips, rounded spines soluble in KOH, varying in sizes on width and length in the same ascospore (Figs. 4C, 4E).

**Distribution and habit** hypogeous, solitary or in clusters in *Pinus-Quercus* and *Pinus-Juniperus* forests of central and northeastern Mexico.

**Studied collections:** MÉXICO, Nuevo Leon state, Municipality of Zaragoza, in a *Pinus-Quercus* forest, *leg.* G. Guevara, 24 June 1985, Guevara 1153 (ITCV, FLAS 63748); Municipality of Zaragoza, *leg.* J. García, 17 October 1985, García 4808 (ITCV, FLAS 63749); Querétaro State, Cadereyta de Montes, South of Chavarrías in a *Pinus-Juniperus* forest, 2926 m elevation, *leg.* M. Castellano & J. Trappe, 23 September 1996, Trappe 19275 (Holotype FLAS 63750, Isotype OSC).

***Geopora lateritia*** (Fogel & States) Healy & M.E. Sm., *comb. nov.* – MycoBank: MB81742 (Fig. 5 A–F)  
Basionym: *Pachyphloeus lateritius* Fogel & States, *Mycotaxon*, 81: 84 (2002).

≡ *Pachyphloides lateritia* (Fogel & States) Doweld, *Index Fungorum*, 32: 1 (2013) [as *P. lateritius*].

Diagnosis emended from the original by FOGEL & STATES (2002).

Ascoma, ptychothecia up to 33 × 28 mm, subglobose and fissured. Peridium smooth, brick-colored. Interior white. Asci, four to eight-spored, inamyloid. Ascospores globose to sub-globose, hyaline, uniguttulate, 18–27 µm including minute ornaments that are rounded and isolated, <0.5 µm diam. Paraphyses 4 µm in diameter, rounded at the tip, extending beyond asci to intertwine with others in the canals.

GenBank: ITS: MK359201; 28S: MK446234 (Paratype).

Holotype: Specimen Fogel F4887 at the University of Michigan Herbarium (MICH).

Illustrations: FOGEL & STATES (2002: 84).

**Ascoma** ptychothecium, hypogeous, up to 33 × 28 mm, light yellow brown to deep brown with reddish undertones, verrucose with small warts, sparsely tomentose, with apical opening, and a single 0.5 mm rhizomorph. Odor and taste not recorded. **Peridium** 0.2 mm thick, outermost part reddish brown. **Gleba** white consisting of meandering irregular hymenium separated by sterile veins.

**Peridium** 180–200 µm wide, two layered (Fig. 5A). **Epicutis** 48–100 µm thick, of *textura angularis*, with large cells vertically elongated (perpendicular to surface), outermost layers of cells 17–35 µm long × 12–30 µm wide, with light yellow to medium brown pigmented walls in water, turning dark brown in KOH, up to 3 µm thick

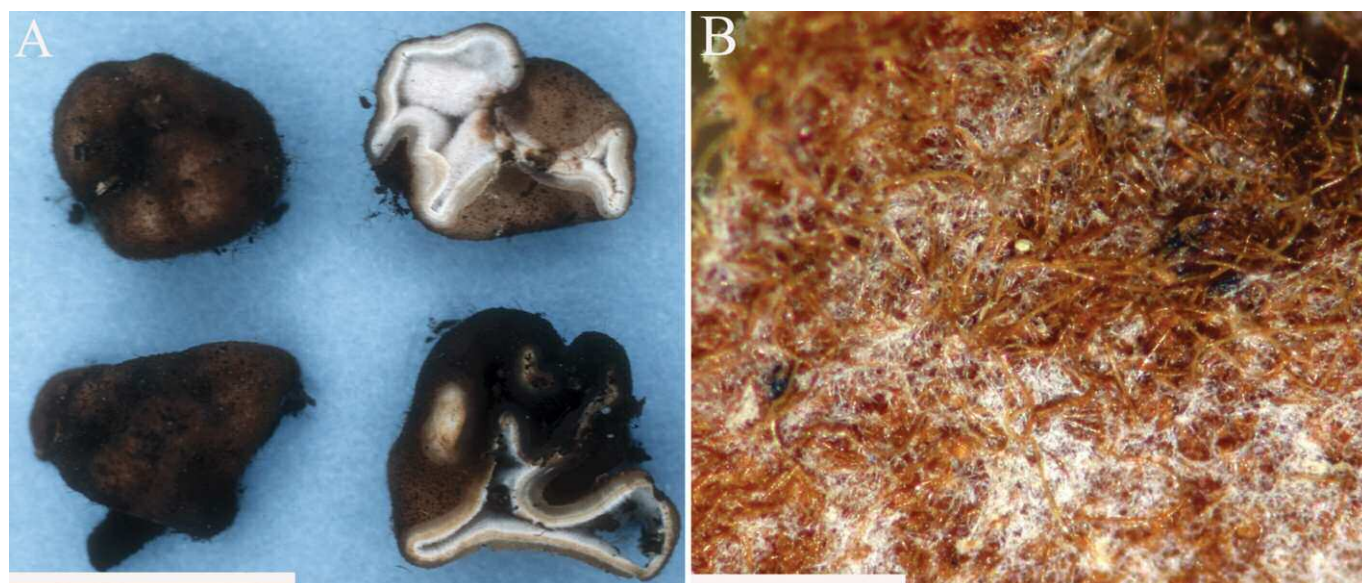
(Fig. 5B). **Tomentum** extending from surface cells, generally straight, thick-walled, pigmented brown, and smooth in water, unchanging in KOH (Fig. 5C). **Innermost cells of outer excipulum** hyaline, smaller, with thinner cell walls compared to outermost cells. **Subcutis** up to 100 µm thick, hyaline, composed of *textura intricata* horizontally elongate, generally uninflated, 5–6 µm diam, but with occasional cell inflated to 8 µm (Fig. 5A). **Paraphyses** septate, rounded, not swollen at the tips, 4 µm diam., extending beyond the ascus tips, and intertwining to stuff the cavities formed by folded hymenia. **Asci** 85–120 × 35–45 µm, broadly clavate, with 4–8 ascospores, cylindrical, claviform with tapering stalk, arising from croziers, immature asci dextrinoid, mature asci inamyloid in Melzer's solution, arranged in an irregular palisade. **Ascospores** irregularly biseriolate, 18–26 µm diam, or 18–26 × 22–27 µm, globose to subglobose, with primary and secondary wall which together are 2 µm thick, hyaline in water, blue in cotton blue, filled with one large oil body (guttule) at maturity, minutely warted, warts < 0.5 µm diam, dissolving in KOH, not easily viewed with light microscopy, but can be observed when focusing on the outer wall in plane view. The ascospore ornaments are most effectively visible with SEM (Fig. 5D); they appear to be isolated, and unencumbered, not embedded in mucilage.

**Distribution and habit** hypogeous in oak and pine woodlands of the mountains in the Great Basin of the western U.S.A.

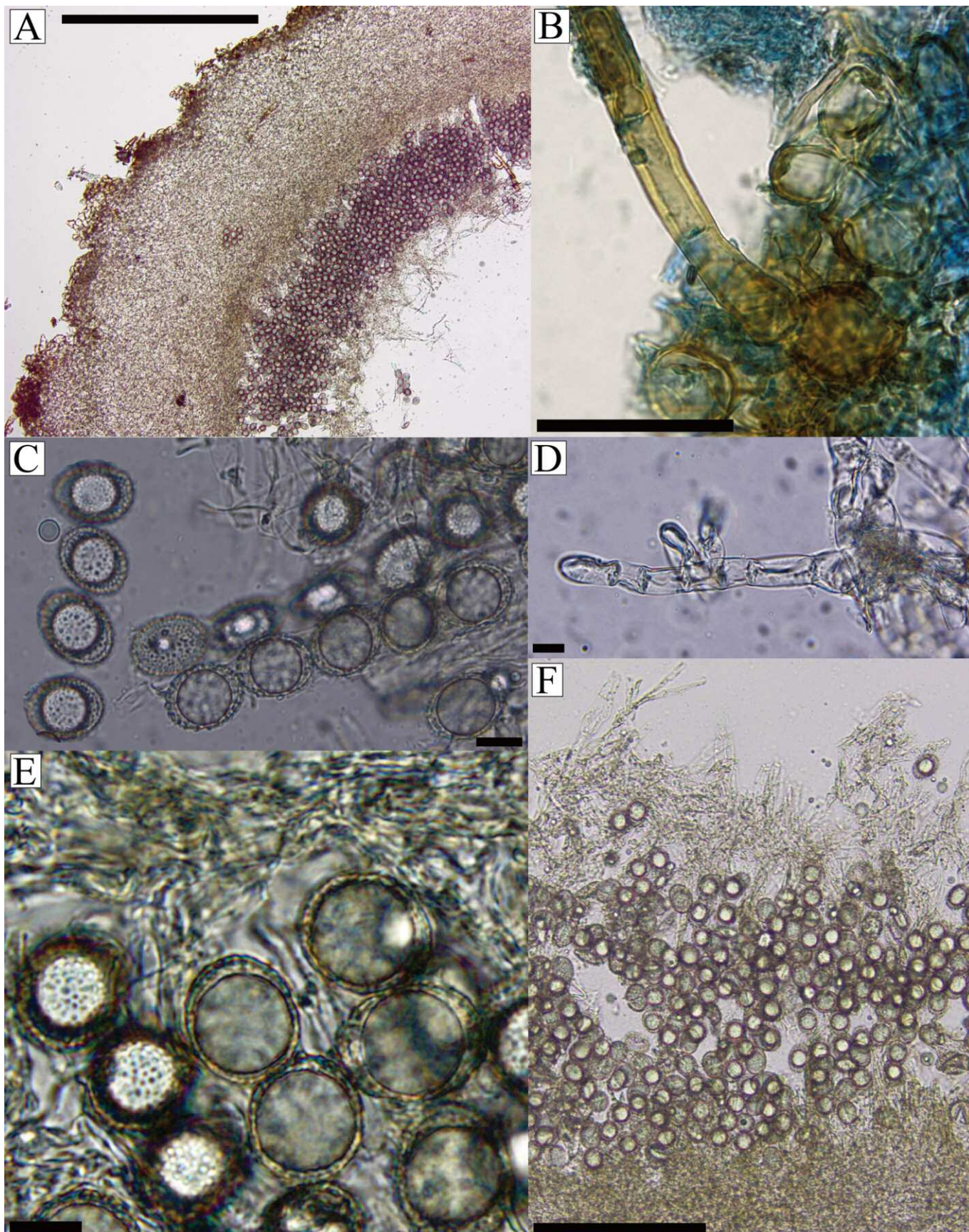
**Studied collections:** USA, Utah, Washington Co., N of Gunlock, Tobin Wash Road, 3.4 mi NW of junction with Route 3184, 37°20.58' N, 113°47.47' W, *leg.* R. Fogel, 13 May 1995, R. Fogel F4887 (Holotype MICH 52897). Utah, Washington Co., Grapevine Spring Road, 1 mile from junction with Tobin Wash Road, 37°21.41' N, 113°47.76, *leg.* R. Fogel, 30 June 1995, R. Fogel F4981 (Paratype, MICH 52895); Kane Co., outside E side of Zion National Park on road to Navajo Lake, 3.6 mi N of junction with Route 9, 37°16.02' N, 112°51.85' W, *leg.* R. Fogel, 29 June 1995, R. Fogel F4969 (Paratype, MICH 52896).

## Discussion

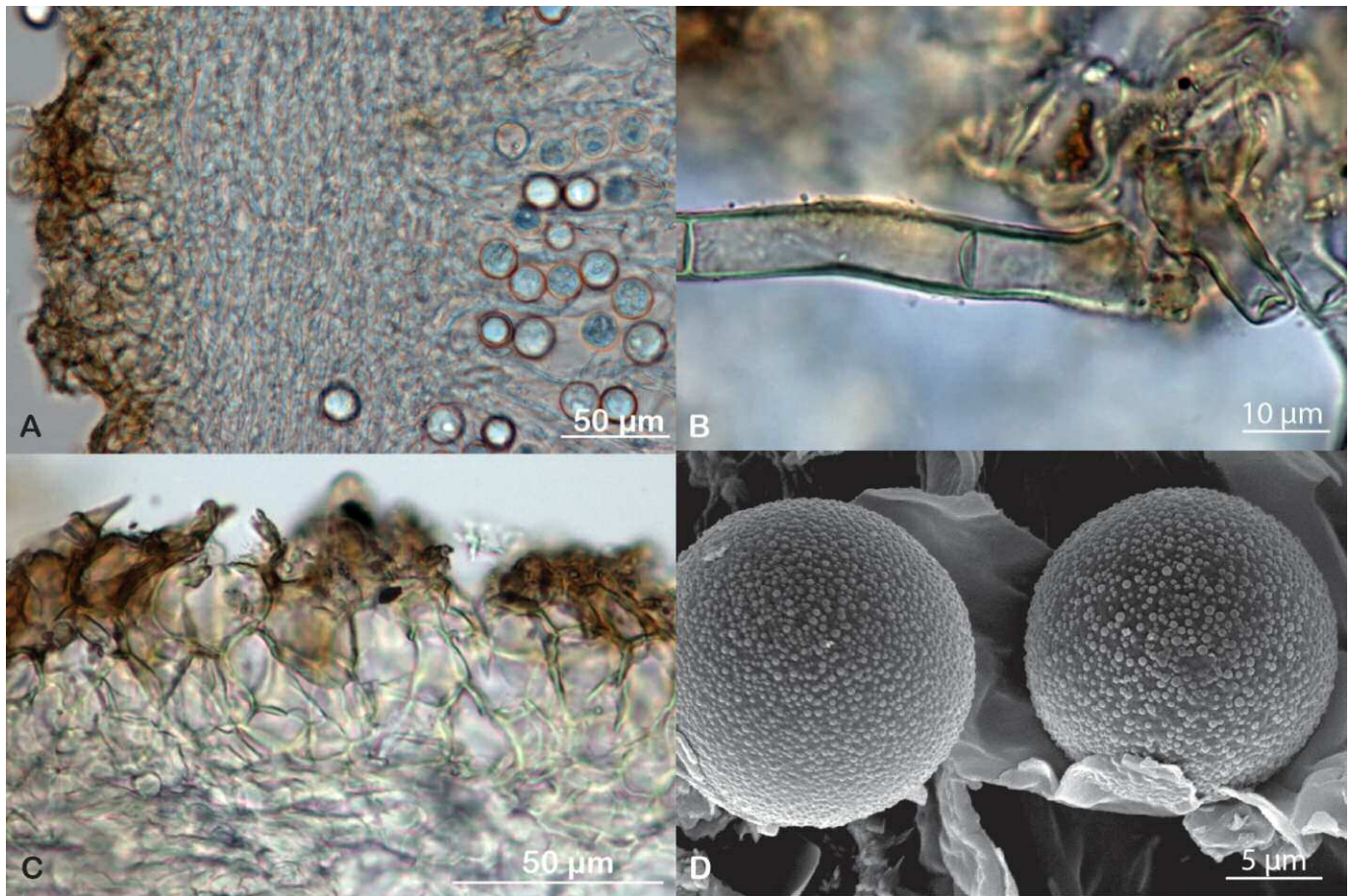
*Terracavicola echinospora* is unique from all other described fungi due to a combination of characters including ornamented, subglobose ascospores, an enclosed truffle-like fruiting body, textured, brown, branching, excipular setae, and the presence of a weak epithecium which covers the hymenium and prevents active as-



**Figure 3** – Morphological characteristics of *Terracavicola echinospora*. A) Sectioned ascomata showing the dark-colored tomentum of the peridium and the white epithecium. B) Dense brown tomentum of the peridium. Scale bars: A = 15 mm, B = 1 mm.



**Figure 4** – Morphological characteristics of *Terracavicola echinospora*. A) Overview of section of ascoma showing thick peridial layer with warts on exterior surface. The thin, hyphal epithecium is visible at the bottom right-hand side of the section. B) Close-up of peridial surface with brown, rounded to angular, thick-walled cells and the base of a peridial hair. C) Subglobose to ellipsoid ascospores with small, rounded spore ornaments. Ascospores on the left are floating free whereas the spores on the right are partially encased in an ascus. Note the large singular guttule present in most spores. D) Example of thin-walled hyphae that comprise the epithecium. E) Ascospores encased by the layer of thin-walled hyphal elements that comprise the epithecium. F) Close up of ascospores encased between the epithecium (top) and the subhymenium (bottom). Scale bars: A = 500  $\mu\text{m}$ , B = 600  $\mu\text{m}$ , C = 24  $\mu\text{m}$ , D = 5  $\mu\text{m}$ , E = 8  $\mu\text{m}$ , F = 170  $\mu\text{m}$ .



**Figure 5** – *Geopora lateritia* (Holotype MICH 52897). A-C in 3% KOH, brightfield. A) Section through ascoma showing low wart of peridium, outer layer of peridium composed of *textura angularis*, inner layer of peridium composed of *textura intricata*, palisade of asci and paraphyses in hymenium, and globose to subglobose spores. B) Smooth, thick-walled, equal excipular hairs. C) Higher magnification of outer layer of peridium showing longitudinally elongate, thick walled, pigmented cells. D. SEM of spores showing minute unconnected warts. Scale bars: A, B = 50 µm, C = 10 µm, D = 5 µm.

cospore discharge. While the relationship between *T. echinospora* and other genera within the *Geopora-Tricharina* lineage is unresolved within the ITS and 28S phylogenies, there is moderate support for the monophyletic group that includes all species of *Geopora* (including *Picoa*). Taken together, these analyses support a monophyletic *Geopora-Picoa* and place *T. echinospora* and *Hoffmannoscypha pellita* outside of this monophyletic group in uncertain positions (Figs. 1 and 2). *Tricharina* is clearly supported as a unique lineage with high support in the ITS analysis but there is no bootstrap support for this clade in the 28S analysis, potentially due to the difference in species and isolates used between the two analyses.

It is significant to note that species of *Geopora* and *Picoa* have been shown to form ectomycorrhizas with plants whereas *Tricharina* species are generally considered non-mycorrhizal (TEDERSOO & SMITH, 2013). However, the ECM status of many species in both genera, including *T. echinospora*, *G. lateritia*, and *H. pellita* remain untested. Because the best ML trees in both the ITS and 28S phylogenies infer *T. echinospora* outside of *Geopora* and always on a long branch, we conclude that this new species should be recognized in a unique genus. The trophic status of *T. echinospora* is not yet known.

The *Geopora-Tricharina* lineage contains a number of other species of truffle-like fungi but all of them are distinct from *T. echinospora* in either morphology or geographic distribution or both. For example, *Geopora cooperi* and *Geopora clausa* both have truffle-like ascomata but both species have smooth ascospores and lack an epithecium. *Geopora cooperi* and *G. lateritia* are from North America, while *Geopora clausa* is described from Europe. There are two accepted species of *Picoa* and both form truffle-like ascomata.

The first is the type species *Picoa juniperi* Vittad. (VITTADINI, 1831). The second is *Picoa lefebvrei* (Pat.) Maire, which MAIRE (1906) recombined from the basionym *Phaeangium lefebvrei* Pat. (PATOULLARD, 1894). Molecular evidence indicates that the genus *Picoa* includes at least five phylogenetic species, some of which have ornamented ascospores (ZITOUNI-HAOUAR *et al.*, 2015). However, these taxa are known from the Mediterranean and the Middle East and are primarily found in association with ECM host plants in the Cistaceae (ZITOUNI-HAOUAR *et al.*, 2015). Both *P. juniperi* and *P. lefebvrei* have solid glebas and irregularly shaped asci that are not formed in a hymenium. Three additional taxa (*Imaia gigantea*, *Leucangium carthusianum* and *Tuber melosporum*) were originally named in *Picoa* but do not fall into that genus based on molecular phylogenetic evidence (KOVÁCS *et al.*, 2008; ALVARADO *et al.*, 2012; TRAPPE *et al.*, 2010).

*Terracavicola echinospora* is also phylogenetically related to species of *Tricharina sensu stricto*. However, *T. echinospora* differs morphologically from *Tricharina*. For example, *Tricharina gilva* (Boud.) Eckblad (ECKBLAD, 1968) has a cupulate ascoma, lacks an epithecium, and has smooth, eguttulate ascospores (VAN VOOREN *et al.*, 2017) whereas *T. echinospora* makes ptychothelial ascomata, has an epithecium and has ascospores that are minutely spinose containing a single, large guttule.

*Hoffmannoscypha* is a monotypic genus of brightly colored, cupulate apothecia, closely related to *Tricharina* and *Geopora* (STIELOW *et al.*, 2013). Our phylogenetic trees reveal that it is sister to *Terracavicola echinospora* with low support (Figs. 1 and 2). However, *Hoffmannoscypha pellita* (Sacc.) Stielow, Hensel, Göker & Klenk (STIELOW *et al.*, 2013) differs from *T. echinospora* in several major characteristics, including the yellow-orange hymenium and the ascospores



that are smooth when viewed with light microscopy (STIELOW *et al.*, 2013).

Due to the ascoma shape, the hairy peridium, the uniseriate asci, and the ornamented ascospores, *Terracavicola echinospora* might at first glance be confused with one of the brown, hairy species of *Genea*. The two *Genea* species that most resemble *T. echinospora* are *Genea hispidula* Berk. ex Tul. & C. Tul. (TULASNE & TULASNE, 1851) and *Genea arenaria* Harkn. (HARKNESS, 1899); both species have been found across large parts of the USA and are probably present in Mexico (ALVARADO *et al.*, 2016; SMITH *et al.*, 2006). However, both of these *Genea* species have darker and thicker epithelial layers and ascospores with less conspicuous guttules than in *T. echinospora*.

Our phylogenetic analysis also revealed that the truffle-like species previously described as *Pachyphloides lateritia* was resolved within the genus *Geopora* (Figs. 1 and 2). We recombined this species as *Geopora lateritia* comb. nov. The original description is accurate in most details, but re-examination revealed some new details about excipular cells and ascospores. The excipular cell walls are much thicker than originally described and the ascospores are not exclusively globose but instead range from globose to subglobose. Additionally, the ascospore wall is thicker than described. Molecular analyses were not commonly used in new fungal taxon descriptions at the time *Pachyphloeus lateritius* was described in 2002 (later transferred to *Pachyphloides* as *P. lateritia* by DOWELD, 2013). Now genetic evidence resolves *P. lateritia* in the *Geopora* lineage.

The type description of *P. lateritius* did not match well with other species in the genus *Pachyphloides* (as *Pachyphloeus*), and the authors did not make any comparisons with other *Pachyphloides* species. Presumably the large pigmented cells of the exciple, combined with ornamented ascospores interpreted as globose reminded the authors of *Pachyphloides*. Re-examination of the type material indicates that the ascospores range from globose to subglobose. This variation is seen in Fig. 5A as well as in a figure from the original description that depicts asci with ascospores (FOGEL & STATES, 2002: 85, Fig. 3). All known species of *Pachyphloides* have ascospores that are strictly globose (BERKELEY, 1844; BERKELEY & BROOME, 1846; FRANK *et al.*, 2007; GILKEY, 1939; HEALY *et al.*, 2015; HEALY *et al.*, 2018; TULASNE & TULASNE, 1851). Furthermore, the ascospore ornaments of *Pachyphloides* species do not dissolve in KOH whereas those of *G. lateritia* rapidly dissolve in KOH, similar to the KOH soluble ascospore ornaments of *Terracavicola echinospora* and *Genea* species (TRAPPE & GUZMÁN, 1971). PFISTER (1970) reviewed the earlier literature on which species of *Pezizales* have ascospore ornaments that dissolve or are altered in KOH solution. Most taxa that undergo this change belong to *Pyronemataceae*, including species of *Cheilymenia*, *Scutellinia* and *Trichophaea*, but also *Discina* (*Discinaceae*). An excipular feature of longitudinally elongate cells perpendicular to the gleba is another characteristic found in *G. lateritia* that does not fit any known species of *Pachyphloides*. Instead, the excipular cells in *Pachyphloides* species are typically isodiametric or slightly wider (latitudinally elongated cells). The morphological characteristics that tie *G. lateritia* to *Geopora* include: 1) pychothelial ascoma, 2) excipular hairs that are smooth and originate from the surface excipular cells, 3) a two-layered excipulum with outer excipulum composed of *textura angularis* of large yellow-brown longitudinally elongate, thick walled cells, and inner excipulum composed of *textura intricata* that is hyaline, 4) inamyloid, cylindrical asci and 5) hyaline ascospores with one large oil droplet at maturity. *Geopora lateritia* is unusual among *Geopora* species in that it has finely warted globose to subglobose ascospores while most other species have smooth subglobose to ellipsoid ascospores. However, ornamented, globose to subglobose ascospores are characteristic of the related North African and Middle Eastern desert truffle species *Picoa lefebvrei* (ALSHEIKH & TRAPPE, 1983). The original description of *Phaeangium lefebvrei*, perhaps due to studying immature material, reported the ascospores as smooth (PATOILLARD, 1894), but this description was later emended (ALSHEIKH & TRAPPE, 1983). *Geopora*

*lateritia* is also unusual in having a brighter, brick red-brown peridium (as compared to the typical greyish brown of other *Geopora* species) and an excipulum that is only sparsely covered by excipular hairs (as compared to the dense tomentum in other *Geopora* species). This variation among species within a *Pyronemataceae* genus is also seen in *Genea*, where the range of hairiness among ascomata is from densely to sparsely tomentose to nearly smooth except for the basal tuft (ALVARADO *et al.*, 2016; GILKEY, 1939; GILKEY, 1954; SMITH *et al.*, 2006). Lastly, *Geopora lateritia* is distinguished by its irregular hymenium with paraphyses that extend beyond the tips of the asci whereas most other *Geopora* species are reported to have uniseriate asci and paraphyses that do not extend beyond the asci (BURDSALL, 1968; FLORES-RENTERÍA *et al.*, 2014; GILKEY, 1916; GILKEY, 1954). Exceptions include *G. toluhana* and *G. cercocarpi* which have paraphyses that exceed the asci in length (GUEVARA *et al.*, 2012; SOUTHWORTH & FRANK, 2011).

Under transmitted light, the pigmented excipular cell walls of *Geopora lateritia* match those described for *Geopora* by BURDSALL (1968). Among the above delineated differences between *G. lateritia* and most other species of *Geopora*, the most outstanding are the nearly globose ornamented ascospores and lack of dense tomentum. Molecular markers (ITS and 28S) firmly place this species within *Geopora*, which suggests that these are relatively minor differences at the generic level. Some of these same variabilities are seen within the closely allied genus *Picoa*, where ascospores may be smooth or warted.

In addition to the taxonomic novelties outlined above, our analyses highlight the high diversity of truffle-like taxa in the *Geopora-Tricharina* lineage. For example, new ITS sequences generated in this study from specimens of *Geopora cooperi sensu lato* were resolved in at least six different clades (Fig. 1). In some cases these clades contain specimens from a wide geographic range (e.g. the *Geopora toluhana* clade contains specimens from Mexico, Nevada, California, and Utah). These findings suggests that specimens currently treated in herbarium collections as "*Geopora cooperi*" should be critically re-evaluated to determine the appropriate phylogenetic placement and species epithets to use. In particular, it will be important to evaluate the many *Geopora* species that were named from California and Oregon by HARKNESS (1899) and GILKEY (1916, 1939), including *Geopora annulata* Gilkey (GILKEY, 1916), *G. brunneola* Harkn. (HARKNESS, 1899), *G. harknessii* (E. Fisch.) Gilkey (GILKEY, 1916), *G. magnata* Harkn. (HARKNESS, 1899), *G. magnifica* Gilkey (GILKEY, 1916), and *G. mesenterica* Harkn. (HARKNESS, 1899).

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