North American Fungi

Volume 9, Number 4, Pages 1-10
Published August 26, 2014

A new hypogeous *Peziza* species that forms ectomycorrhizas with *Quercus* in California

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Smith, M. E. 2014. A new hypogeous *Peziza* species that forms ectomycorrhizas with *Quercus* in California. N*orth American Fungi* 9(4): 1-10. http://dx.doi.org/10.2509/naf2014.009.004

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Abstract: A new truffle species, *Peziza erini* sp. nov. (Pezizaceae, Pezizales), is described from xeric oak woodlands in northern California, USA. This fully enclosed and hypogeous *Peziza* is a member of the latex-producing *Peziza succosa* clade (the /galactinia ectomycorrhizal lineage). This new species is morphologically most similar to the sympatric species, *Peziza infossa,* but both morphological and molecular data conclusively show that *Peziza erini* is unique. Ribosomal internal transcribed spacer (ITS) sequence matches between fruiting bodies of *Peziza erini* and healthy ectomycorrhizal roots of *Quercus douglasii* definitively show that this new species is an ectomycorrhizal symbiont of oaks in California's Mediterranean woodlands.

Key words: truffles, hypogeous fungi, *Peziza*, Pezizaceae, ectomycorrhiza

Introduction: Hypogeous fungi, or "truffles," produce their fruiting bodies completely below the leaf litter or soil. Although hypogeous, truffle-like fungi have evolved many times in the Ascomycota, Basidiomycota, Zygomycota *sensu lato*, and Glomeromycota, the fungi known as the "true truffles" are hypogeous Ascomycota in the Pezizales (Læssøe & Hansen 2007, Tedersoo &

Smith 2013). The taxonomy of pezizalean truffles was traditionally challenging because the convergence in morphological traits (e.g. enhanced spore ornamentation, reduction in hymenium development, enhanced odor production) makes it difficult to deduce relationships between truffle species or to conclude which epigeous Pezizales may be close relatives of truffle-like taxa (Trappe et al. 2009). However, molecular techniques have clarified that truffles have evolved many times within Pezizales and phylogenetic methods have helped to determine the taxonomic placement of the truffles among epigeous relatives (Lœssøe & Hansen 2007). Furthermore, sequence matches between fruiting bodies and environmental samples have proven that a high proportion of these truffle-like Pezizales form ectomycorrhizal (ECM) associations with plants (Healy et al. 2013, Smith et al. 2007, Tedersoo et al. 2006).

Studies of ECM fungi in the oak-dominated woodlands at the University of California Sierra Research and Extension Center (SFREC) in northern California during 2000–2005 revealed high diversity and high frequency of truffle-like fungi both as sporocarps and as ECM symbionts (Morris et al. 2008, Smith et al. 2006, Smith et al. 2007, Smith et al. 2009). Although many of the truffle-like fungi from this site in Yuba County, California were described previously (e.g. Gilkey 1939, Harkness 1899), I encountered a unique, hypogeous *Peziza* species that could not be identified based on keys of truffle-like fungi or previously published species descriptions of Pezizales species (Trappe et al. 2009). This new *Peziza* is superficially similar to the sympatric species *Peziza infossa* (Fogel & States) Fogel & States but both morphological and molecular analyses clearly differentiate the two species. Here I describe this new species as *Peziza erini* sp. nov.

Materials and Methods: Hypogeous fungi were surveyed at the University of California Sierra Research and Extension Center (SFREC) in Yuba County, California from 2000–2005 (39° 15' 4.068" N, 121° 18' 47.274" W). The SFREC site is characterized as a Mediterranean savannah-woodland with dry, hot summers and cool, wet winters with an average annual precipitation of 71 cm (range 23–132 cm) (http://ucanr.edu/sites/sfrec/). Hypogeous fungi were located and collected using a truffle rake. Specimens were placed in wax paper bags and transported to the laboratory within 6 hours. Macroscopic photos of fresh specimens were captured with a Sony Mavica CD300 camera. Specimens were dried on a forced-air dryer for approximately 24 hours.

Microscopic characters are described based on razor-blade sections of dried specimens mounted in water, 3% KOH, and Melzer's reagent. Microscopic images were captured using a Qimaging Micropublisher 3.3 RTV digital camera mounted on a Nikon Optiphot light microscope. Measurements of spore dimensions are based on 20 randomly selected spores examined at 1000X magnification.

Clean fungal tissue was taken from the gleba of fresh or dried specimens and DNA was extracted using a modified CTAB (cetyltrimethylammonium bromide) method (Gardes and Bruns 1993). PCR of the ribosomal internal transcribed spacer (ITS) and 28S ribosomal DNA was performed with two primer combinations according to published protocols: ITS1F and LR3 (Smith et al. 2007) and LROR and LR5F (Tedersoo et al. 2008). DNA sequences from ECM roots were obtained as part of the Smith et al. (2007) study on ectomycorrhizal fungi communities associated with *Quercus douglasii*. PCR products were visualized on 1.5% agarose gels stained with SYBR Green I (Molecular Probes, Eugene, OR, USA). Amplicons were cleaned with EXO (Exonuclease I) and SAP (shrimp alkaline phosphatase) enzymes (Werle et al. 1994) and sequenced by the University of Florida Interdisciplinary Center for Biotechnology Research (ICBR)

(www.biotech.ufl.edu/). Sequences were edited with Sequencher v.5.0.1 (Gene Codes Inc., Ann Arbor, MI, USA). Maximum parsimony analysis was performed with PAUP* (Swofford 2001) using the default settings. I then performed bootstrap analysis using 1000 replicate heuristic searches each with 10 random addition sequence replicates, stepwise addition, and tree bisection and reconnection (TBR) branch swapping. Maximum likelihood (ML) analysis was performed using the Garli v. 0.951 software package (Zwickl 2006). The GTR+I+G model was selected. ML boostrap support values were calculated based on 500 replicate searches with both the model and rates estimated by Garli.

Results: The ITS rDNA dataset analyzed here consisted of 614 characters and included 25 taxa. After 69 ambiguous positions were excluded, maximum parismony (MP) and ML analyses produced equivalent phylogenetic results. Of the 544 analyzed characters, 377 characters were constant whereas 143 characters were parsimony informative. MP analysis generated 232 equally parsimonious trees, each with a length of 198 steps. Since MP and ML phylogenies were congruent and almost identical, Figure 1 depicts only the ML phylogeny (-ln l 1717.164) with both ML and MP bootstrap support shown. Holotype src696 and paratype src682 are identical across the entire ITS-28S rDNA region but are only approximately 91% similar to ITS sequences of *Peziza infossa* and other members of the *P. succosa* group (*Peziza succosa, P. succosella, P. infossa,* and *P. michelii*). Sequences derived from *P. erini* fruiting bodies are nested in a well-supported clade with two ITS sequences derived from ECM roots of *Quercus douglasii* that originated at the same research site where the two fruiting bodies were collected. As suggested by both morphology and initial BLAST searches, *Peziza erini* is most closely related to *Peziza infossa* and *P. succosa* and only more distantly related to *P. michelii*. BLAST and preliminary phylogenetic analyses of 28S rDNA (DQ974739) also corroborate the placement of *P. erini* within the *Peziza succosa* clade and suggest that *Peziza erini* is more closely related to *P. succosa* than to *P. michelii* (data not shown). Furthermore, two sizeable introns (11 nucleotides and 15 nucleotides in length) and several smaller introns clearly separate the *Peziza erini–infossa–succosa* clade from *P. michelii* in the ITS alignment (data not shown). We also detected significant molecular diversity within the *Peziza succosa–succosella* complex. This group was divided into at least three lineages and includes named specimens of *P. succosa* and *P. succosella* as well as soil clones, ectomycorrhizal roots, and orchid mycorrhizas from across Europe, Asia, and North America. In contrast, the only available sequences from the *P. michelii* group (including named specimens of *P. michelii* and *P. irina*) were from Europe and Asia. All new sequences have been deposited in GenBank.

Taxonomy

Peziza erini M.E. Sm. sp. nov. Figs. 1–2
Mycobank no.: 808474

Holotype: United States, California, Yuba County, University of California Sierra Foothill Research and Extension Center, Koch Natural Area, in woodland dominated by *Quercus* spp. and *Pinus sabiniana*, 24 April 2003, coll. M. E. Smith, src696, FLAS 58918, GenBank DQ974739.

Diagnosis: Differs from all other species of *Peziza* due to a combination of morphological features that include fully enclosed and hypogeous ascomata without any obvious openings, lactiferous hyphae that produce yellowish latex, a yellow-orange spongy gleba composed of small, irregular folds of tissue creating a labyrinthine appearance, immature asci that are strongly dextrinoid but upon maturity are more-or-less amyloid over the ascus

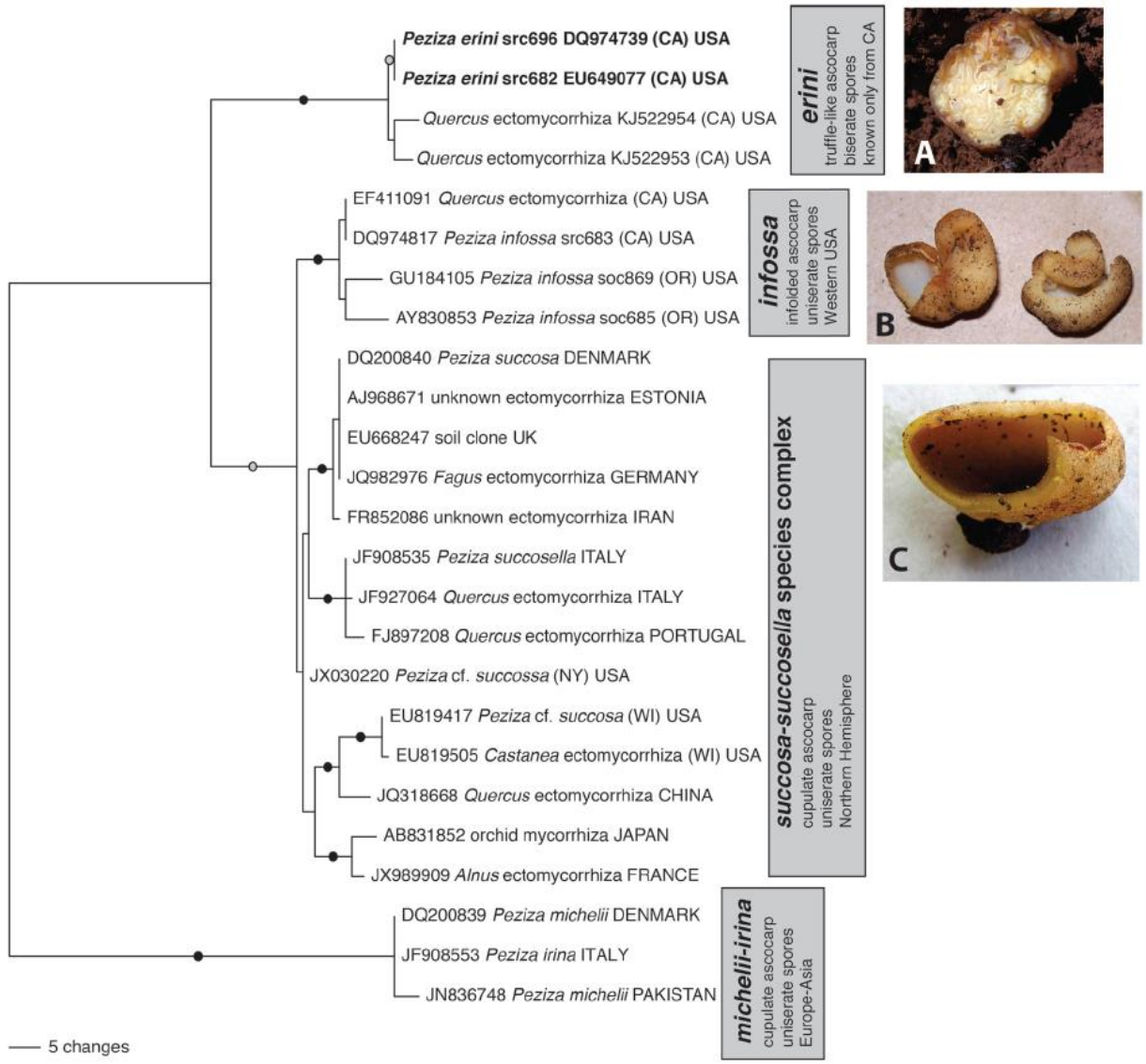

Figure 1. Maximum likelihood phylogeny depicts the distinct position of *Peziza erini* sp. nov. within the *Peziza succosa-michelii* clade based on ITS ribosomal DNA sequences. Black circles indicate nodes with ML and MP bootstrap support >70 whereas grey circles indicate nodes with bootstrap support >70 for only one of the two methods. Images contrast (A) the fully enclosed ascomata with highly chambered gleba of *Peziza erini* with (B) the infolded yet hollow ascomata of *Peziza infossa* and (C) the open, cupulate, apothecial fruiting bodies of *Peziza succosa*.

apex, and finely ornamented ascospores that are biserately to irregularly arranged within the asci.

Ascomata hypogeous, subglobose, ptychothecial, slightly lobed, 1.5–2.5 cm in diameter, basal tuft of hyphae notable but easily broken off during collection, no obvious openings in the peridium. **Gleba** yellowish-orange, spongy, composed of small, irregular folds of tissue creating a labyrinthine system of small to minute chambers, the light yellow hymenium notably lighter in color than the darker,

yellowish-orange subhymenium and light brown peridium. **Peridium** light brown with yellow to yellow-orange tints, soft, brittle, smooth, hygrophanous, many surfaces encrusted with adhering soil particles. Variable in height but mostly 200–500 µm thick, composed of two indistinct layers, outer peridial layer 30–100 µm in height, composed of a pseudoparenchyma with cells 5–30 µm in diameter, cells often flattened with the longer dimension running parallel to the peridium, intergrading with an inner peridium layer that is composed of compressed hyphae that intergrades with the subhymenium. **Ascospores** broadly ellipsoid, 15–16 (18) x (11) 12–13 µm (mean = 16 x 12 µm), Q = 1.2–1.4, spore walls 0.5 – 1 µm thick, with minute warts less than 0.3 µm in height and diameter scattered across the spore surface and becoming more prominent as spores mature, most spores with a single guttule but occasional spores with two guttules. **Asci** 8-spored, lacking an operculum, cylindrical to clavate, 20–30 µm thick at their widest point toward the ascus apex, usually 7–13 µm in width toward the ascus base, mostly 100–180 µm long but with occasional asci extending beyond the irregular hymenium up to 220 µm in length, arranged in a loose palisade layer in some parts of the ascomata but convoluted and compressed in other parts, with biserrate to irregularly uniserate spore arrangement at maturity, amyloid reaction weak and diffuse but noticeable in both fresh and dried specimens without KOH pretreatment. Immature asci strongly dextrinoid in Melzer's reagent, with irregular to biserrate spore arrangement and with young ascospores concentrated in a constricted point in the middle of the ascus and surrounded by conglomerations of cytoplasm toward the ascus base and apex, cytoplasm in the apices of young asci riddled with specks of unknown cellular contents that are less obvious in more mature asci. **Paraphyses** infrequent, irregular but when present typically 3–6 (10) µm in width. **Odor** none detected. **Taste** not determined.

Etymology: This new species is dedicated to my wife, Erin Colleen Smith, in recognition of her stalwart support of me and my ongoing mycological research. This name is especially appropriate because, like *Peziza erini,* she is a unique and beautiful California native.

Ecology, Habitat, and Distribution: Specimens and ECM sequences of *Peziza erini* are thus far only known from *Quercus douglasii* (blue oak) woodlands at the UC Sierra Foothill Research and Extension Center near Marysville, California. Although the species has only been collected twice, I suspect that this new truffle species may be common (but fruit erratically) with oaks in low-elevation, Mediterranean woodland habitats across California.

Additional specimens examined:
Peziza erini – United States, California, Yuba County, University of California Sierra Foothill Research and Extension Center, Koch Natural Area, in woodland dominated by *Quercus* spp. and *Pinus sabiniana*, 7 April 2003, coll. M. E. Smith, src682 (Paratype), FLAS 58919, GenBank EU649077. ***Peziza infossa*** – United States, California, Yuba County, University of California Sierra Foothill Research and Extension Center, Koch Natural Area, 7 April 2003, coll. M. E. Smith, src683; OSC.

Discussion: Based on both morphological and molecular evidence, *Peziza erini* is a new member of the *Peziza succosa-michelii* clade that includes *Peziza succosa, P. succosella, P. infossa, P. michelii* and possibly other species (Hansen et al. 2001, Hansen et al. 2005, Tedersoo & Smith 2013). Taxa in this group are united by several morphological and ecological features, including irregular spore ornaments, asci that are more-or-less amyloid over the ascus apex, lactiferous hyphae that produce yellowish latex that stains fruiting bodies with yellow to orange-yellow colors when they are cut or broken, and a fruiting

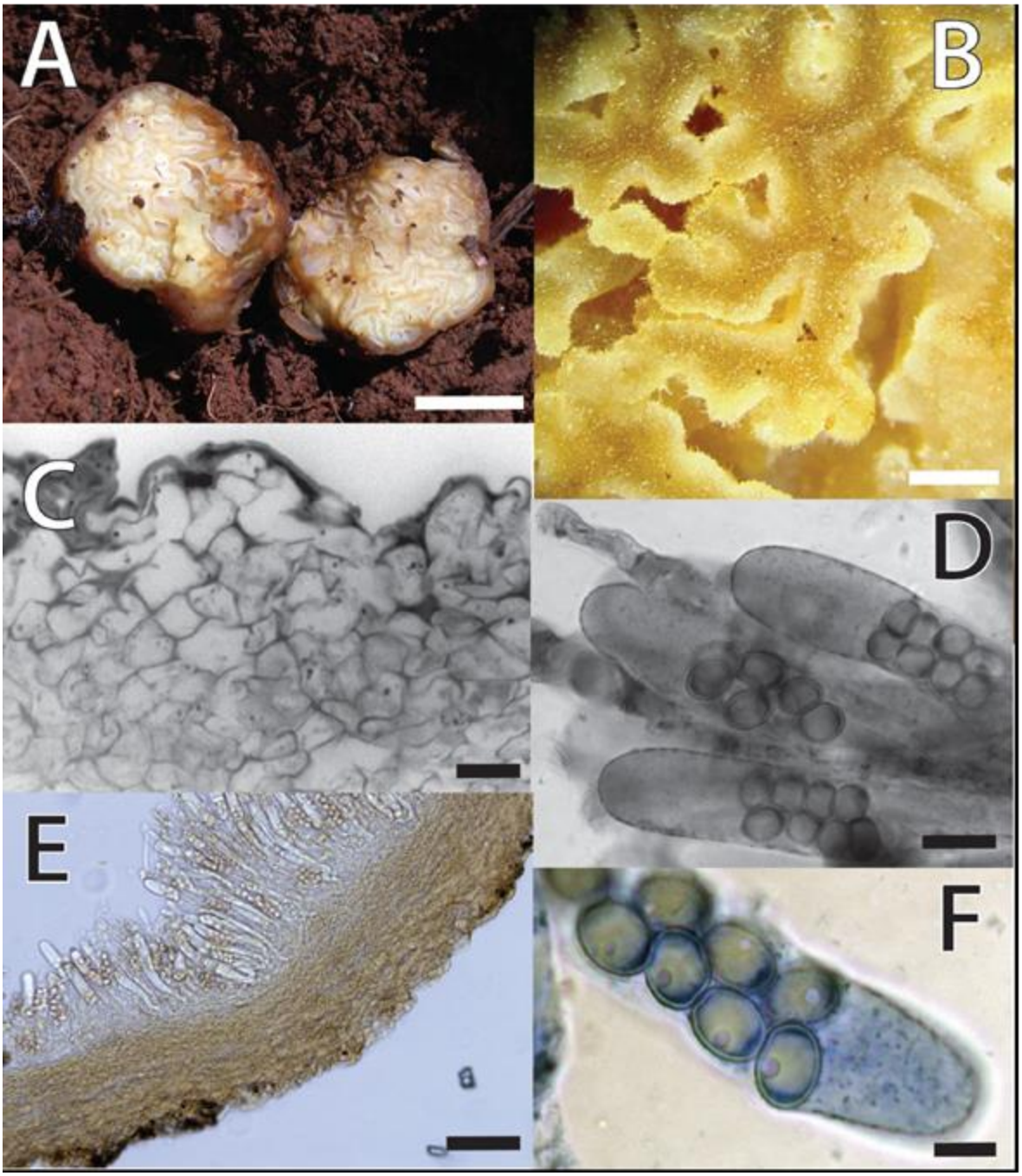

Figure 2. Morphology of *Peziza erini* src696 (Holotype) – (A) fresh ascomata in the field (scale = 1 cm), (B) close up photograph of gleba morphology (scale = 1 mm), (C) pseudoparenchymetous cellular structure of peridium (scale = 20 µm), (D) biserate spore arrangement in young asci (scale = 20 µm), (E) side view of the convoluted hymenial layer and thick, compressed peridium (scale = 100 µm), and (F) thick-walled, uniguttulate ascospores (scale = 10 µm).

habit directly on or in soil near ECM plants (Hansen et al. 2005, Trappe et al. 2007).

Although the exact phylogenetic position of this lineage remains uncertain within Pezizaceae, this

clade was strongly supported by phylogenetic analyses of three different genes (beta-tubulin, RPB2, and LSU rDNA)(Hansen et al. 2005).

Peziza succosa (Berk.) Sacc. has been accepted by some authors as the type species of the genus *Galactinia* (Rifai 1968) and was therefore referred to as the /galactinia lineage by Tedersoo et al. (2010) and Tedersoo and Smith (2013). Members of this monophyletic /galactinia lineage are usually found fruiting in association with angiosperms and molecular studies have confirmed their presence as ECM symbionts on roots (Figure 1, Smith et al. 2007, Tedersoo et al. 2006, Valentine et al. 2004). This group has been referred to as the /galactinia lineage in order to more easily distinguish the *P. succosa* group from other ECM-forming lineages that also contain *Peziza* species (e.g. *Peziza gerardi* in the /hydnobolites lineage, *Peziza depressa*, *P. badia,* and other *Peziza* species in the /terfezia-peziza depressa lineage – Tedersoo & Smith 2013). In contrast, members of *Peziza* sensu stricto (e.g. the clade containing the type species *Peziza vesiculosa*) are saprobic (Hansen et al. 2002).

Morphologically, *Peziza erini* is strikingly different from the described species in the *Peziza succosa-michelii* clade (Figure 2). All of the described species in this group form cupulate, epigeous sporocarps that fruit directly on top of exposed soils (Beug et al. 2014, Seaver 1928) except for the sympatric species, *P. infossa,* which forms truffle-like ascomata that are superficially similar to *P. erini*. *Peziza infossa* was first described from oak-dominated habitats in the Great Basin of the Western USA (Fogel & States 2003) but is also common in oak woodlands across California and Oregon, including at the UC Sierra Research and Extension Center (Arora 1986, Frank et al. 2006, Smith et al. 2007, Trappe et al. 2007). Although *P. erini* and *P. infossa* have similar spores, form mycorrhizas with oaks, and are found in the same habitat, they are quite different from one another upon close inspection. *Peziza erini* forms fully enclosed fruiting bodies with a more brownish colored peridium and a highly infolded gleba that has only small, air-filled pockets. The asci of *Peziza erini* are clavate with biserate to irregular spore arrangement and no opercula. This highly infolded gleba and irregular hymenium combined with the more clavate-shaped asci suggest that *P. erini* is not capable of forcible spore discharge. In contrast, *P. infossa* has a widely varying fruiting body morphology that ranges from partially infolded to almost cupulate. However, even the most contorted sporocarps of *P. infossa* retain large air pockets with a recognizable hymenium and have uniserate asci with identifiable opercula (Fogel & States 2003, Trappe et al. 2007, M. E. Smith personal observation). The morphology of *P. infossa* suggests that, despite its hypogeous or semi-hypogeous fruiting habit, the spores of this truffle-like species may be forcibly ejected from the asci. Similar cases of truffle-like fungi that forcibly discharge their spores have been previously documented in both Ascomycota and Basidiomycota (e.g. *Geopora cooperi* – Burdsall 1965, *Lactarius rubriviridis* – Desjardin 2003).

I suspect that small mammals may regularly consume both *P. erini* and *P. infossa* and disperse their spores. I regularly witnessed evidence of soil disturbance by animals at the UC Sierra site and Frank et al. (2006) observed direct evidence of mammal mycophagy in the form of teeth marks in fruiting bodies of Pezizales truffles (including *P. infossa*) at an ecologically similar site in southern Oregon. Frank et al. (2006) also noted that scats from both *Microtus californicus* (California Vole) and *Peromyscus maniculatus* (Deer Mouse) contained spores of *P. infossa*. The regular consumption of *P. erini* by mycophagous mammals may partly explain why *P. erini* was so rarely encountered during surveys of hypogeous fungi. *Peziza erini* was only collected twice over the course of four years of regular truffle surveys, suggesting that it may be quite rare.

In addition to the morphological features, the uniqueness of *P. erini* is further corroborated by the phylogenetic analysis based on ITS rDNA (Figure 1) and the unique 28S rDNA sequence (GenBank DQ974739), both of which convincingly place *P. erini* in the *Peziza succosa-michelii* clade. Although *P. erini* is morphologically most similar to *P. infossa*, *Peziza erini* is resolved as sister to a clade that includes *Peziza succosa, P. succosella,* and *P. infossa* whereas the Eurasian species *P. michelii* appears to be more distinct based on ITS and 28S rDNA. Matches between ITS rDNA sequences from fruiting bodies and sequences from ECM roots of *Quercus douglasii* also confirm that *Peziza erini* forms ECM associations with California oaks (Figure 1 and Smith et al. (2007) as "*Peziza* 'hypogeous' sp. src696").

Although several other hypogeous *Peziza* species have been described, all of these taxa are morphologically distinct from *Peziza erini*. *Peziza whitei* (Gilkey) Trappe is an Australian species that is more or less white in color and is found in association with *Eucalyptus* and other Australasian trees (Trappe and Claridge 2006). *Peziza stuntzii* Trappe is known only from Washington state (USA) and is readily distinguished by its pink flesh and brown veins of sterile tissue (Trappe 1979). Another species, *Peziza ellipsospora* (Gilkey) Trappe, has also been found at the UC Sierra site (in Smith et al. (2007) as '*Hydnoplicata* sp.'). However, *P. ellipsospora* has dark purplish ascomata, distinct spore ornaments, and is phylogenetically affiliated with the/terfezia-peziza depressa lineage (Smith et al. 2007, Trappe 1979).

Acknowledgements: I thank the University of Florida's Institute for Food and Agricultural Sciences (IFAS), the Farlow Fellowship from Harvard University, and National Science Foundation grant DEB-99-81711 (to DM Rizzo) for funding that contributed to this work. I am indebted to Dr. James Trappe and Dr. Donald Pfister for their continuing mentorship and guidance in my studies of hypogeous fungi and Pezizales. Dr. David Rizzo was a stellar Ph.D. mentor and provided advice, resources, laboratory space, and funding that contributed to this work. Lastly, I would like to thank my wife, Erin Colleen Smith, for her continued support of me and my research – my contributions to fungal biology would truly not be possible without her assistance.

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