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Diversity, Ecology, and Conservation of Truffle Fungi in Forests of the Pacific Northwest

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Authors

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Cover art:

This photographic collage displays the species diversity, ecosystem function, human use, and beauty of truffle fungi in the Pacific Northwest. Clockwise: High magnification of *Hysterangium* spp. truffle attached via an umbilical-like fungal cord (rhizomorph) to ectomycorrhizae on Douglas-fir roots (photo by B. Zak). Northern flying squirrel eating a truffle (photo by Jim Grace). Surface and interior tissue of the ascomycete truffle *Hydnotrya cubispora* (photo by Michael Castellano). Basket of commercially harvested Oregon black truffles, *Leucangium carthusianum*, displayed at the Orgeon Truffle Festival in Eugene, 2007; a chocolate truffle candy is also shown in the upper left of basket (photo by David Pilz). Bright lemon-yellow truffles of the basidiomycete *Rhizopogon truncatus* found under pines in southwest Oregon (photo by Randy Molina).

Abstract

Trappe, James M.; Molina, Randy; Luoma, Daniel L.; Cázares, Efren; Pilz, David; Smith, Jane E.; Castellano, Michael A.; Miller, Steven L.; Trappe, Matthew J. 2009. Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-772. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 194 p.

Forests of the Pacific Northwest have been an epicenter for the evolution of truffle fungi with over 350 truffle species and 55 genera currently identified. Truffle fungi develop their reproductive fruit-bodies typically belowground, so they are harder to find and study than mushrooms that fruit aboveground. Nevertheless, over the last five decades, the Corvallis Forest Mycology program of the Pacific Northwest Research Station has amassed unprecedented knowledge on the diversity and ecology of truffles in the region. Truffle fungi form mycorrhizal symbioses that benefit the growth and survival of many tree and understory plants. Truffle fruit-bodies serve as a major food souce for many forest-dwelling mammals. A few truffle species are commercially harvested for gourmet consumption in regional restaurants. This publication explores the biology and ecology of truffle fungi in the Pacific Northwest, their importance in forest ecosystems, and effects of various silvicultural practices on sustaining truffle populations. General management principles and considerations to sustain this valuable fungal resource are provided.

Keywords: Mycorrhiza, mycophagy, small mammals, biodiversity, conservation, fungi, mushrooms, truffles.

Summary

Pacific Northwest (PNW) forests harbor over 350 truffle species in 55 genera. Unlike their mushroom cousins that fruit aboveground, most truffle species fruit belowground (hypogeously) producing small, potato-like structures that bear the reproductive spores. Truffles are thus more difficult to find than mushrooms; collectors must rake away some of the forest duff to reveal the truffle fruit-bodies that reside at the mineral soil-organic layer interface. As truffles mature, their aromas intensify and attract animals that excavate and eat them. As the animals digest the truffle tissues, the spores pass through the digestive track unharmed and are released in fecal pellets and dispersed throughout the forest. Many small mammals strongly depend on truffles as a major part of their diets. Most truffle species also form mutually beneficial symbioses with plant roots called ectomycorrhizae. Ectomycorrhizal fungi receive their primary energy source from host photosynthate (sugars) sent from leaves to roots; in return, the fungus takes up minerals and water from soil and transports them into the fine feeder roots for use by the host plant. Plants absolutely depend on this functioning symbiosis for their growth and survival in natural ecosystems. Approximately 120 plant species from 19 families and 41 genera are documented as ectomycorrhizal hosts in the PNW, with members of the Pinaceae, Fagaceae, Betulaceae, and Salicaceae acting as the major tree hosts. This rich assembledge of ectomycorrhizal hosts, together with diverse forest habitat and climatic conditions, has created a unique confluence of biological and environmental conditions for the explosive evolution and diversity of truffle species in the PNW. As ectomycorrhizal fungi, truffle species also perform many important ecosystem functions including organic matter decomposition, nutrient cycling and retention, soil aggregation, and transferring energy through soil food webs. These functions contribute to the overall health, resiliency, and sustainability of forest ecosystems. Conserving these fungal communities and maintaining their functions are keys to wise management of our forest resources. This publication summarizes the knowledge accumulated over the last five decades by the Forest Mycology Team, Corvallis, Oregon, on the diversity, ecology, and management of truffle fungi. Descriptions and keys to genera, and photos of over 130 species provide a practical means to identify and appreciate these diverse and cryptic species. Effects of various silvicultural practices on truffle populations and community dynamics are discussed, so that managers can understand how truffle species respond to disturbance. We provide 12 summary management principles and considerations to help managers integrate truffle conservation into sustainable ecosystem management plans. Although this review is specific to the Pacific Northwest, many of the ecological concepts and management principles are applicable to other forested regions of the world where truffles occur.

Contents

Introduction

The forests of the Pacific Northwest (PNW) USA (fig. 1) are well known for their bounty of mushroom species; several regional mushroom clubs and societies dedicate themselves to the study and enjoyment of these fungi (Molina et al. 1993). Truffle fungi are likewise bountiful in PNW forests, but they remain poorly known to the region's mycophiles and forest managers. Unlike their showy mushroom cousins, truffles are challenging to find because their small, potato-like fruiting structures lie hidden beneath the forest litter layer. With a bit of training, however, most mushroom collectors readily master the hunt for truffles. After such training, "trufflers" are every bit as enthusiastic as "shroomers" in collecting and studying these cryptic truffle fungi. Indeed, the North American Truffling Society, based in Corvallis, Oregon (http://www.natruffling.org/), has about 300 members and enjoys an active program that promotes truffle forays and education.

Approximately 350 truffle species are presently recognized from PNW forests (table 1). After 70 years of extensive collection and study, Corvallis-based mycologists have acquired an unparalleled understanding of these species. This paper taps that extensive knowledge and explores the fascinating evolution, diversity, and ecology of truffle fungi in the Pacific Northwest. Our primary objective is to educate the public, resource managers, and other scientists about the diversity and importance of fungi that form truffles in forest ecosystems. We begin by briefly describing the primary characteristics of truffles, where they occur, and the history of their discovery. Then we explore the evolution of the hypogeous (belowground) fruiting habit and discuss truffle diversity in the PNW. Next come detailed descriptions and keys to genera, so that readers can appreciate and discern differences among the major species groups. Color photographs of many of the species we have collected are provided on CD-ROM. We discuss in detail the ecology, community structure, and ecosystem function of truffles followed by effects of various silvicultural practices on truffle populations. We also discuss the culinary uses of wild truffles that are commercially harvested in PNW forests and sold as gourmet fungi to restaurants and the public. We conclude with a section that integrates our ecological knowledge and addresses approaches to conserve and manage this valuable resource.

(text continues on page 16)

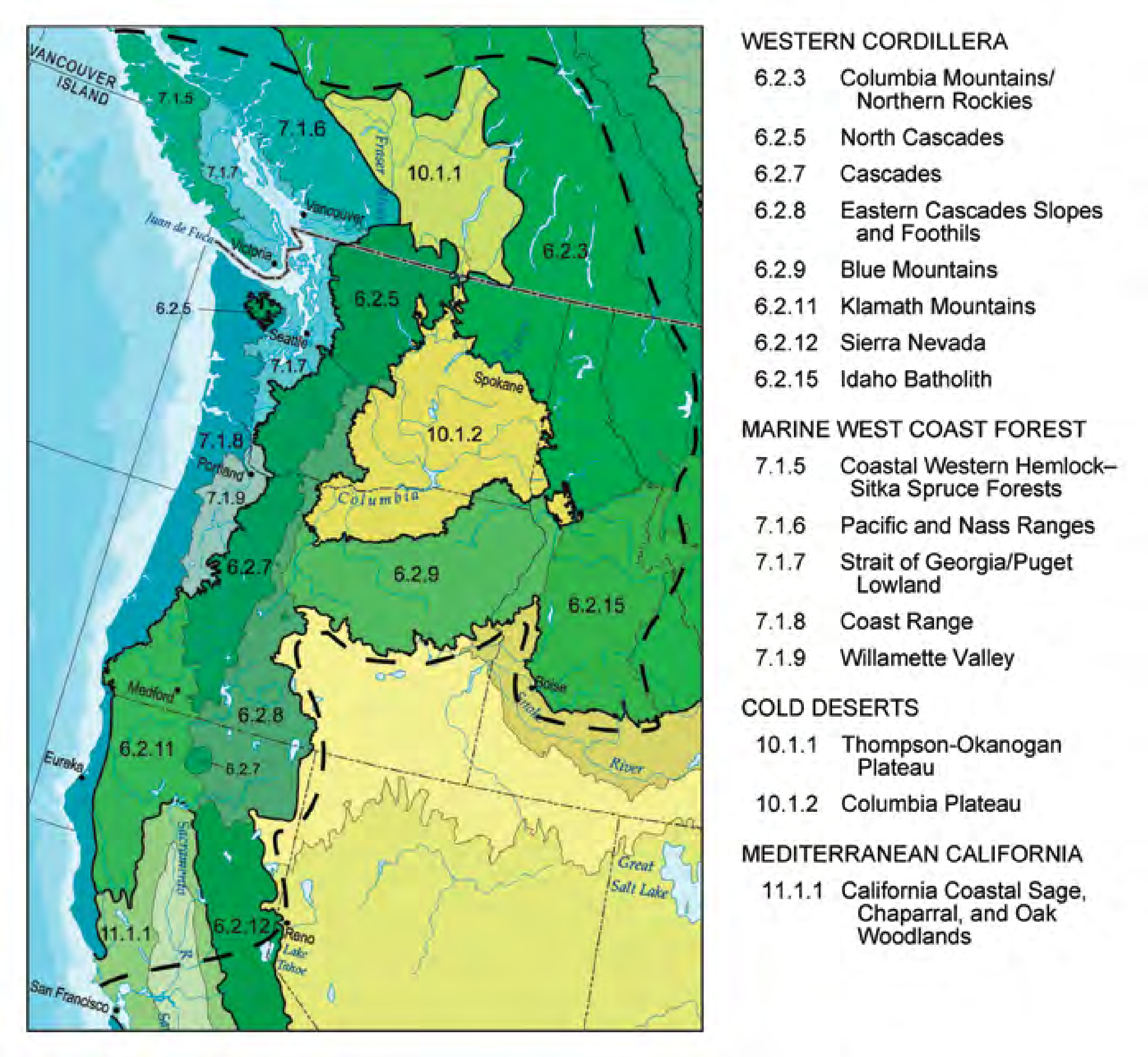


Figure 1—The Pacific Northwest region. The geographical extent of the most complete species coverage is contained within the bold dashed line. The legend refers to the level II and III classifications of Ecological Regions of North America. Map source: Commission for Environmental Cooperation. (1997) (see also http://www.epa.gov/wed/pages/ecoregions/na_eco.htm).

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Zygomycota			
Endogone acrogena Gerd., Trappe & Hosford	Rare	Western Washington	Pinaceae
Endogone flammicorona Trappe & Gerd.[b]	Abundant	North America and Europe	*Pseudotsuga, Pinus*
Endogone lactiflua Berk.[b]	Abundant	North America and Europe	*Pseudotsuga, Pinus, Quercus*
Endogone oregonensis Gerd. & Trappe	Rare	Northwest Oregon coast and Coast Ranges	Pinaceae
Endogone pisiformis Link[b]	Abundant	North America and Europe	Saprotroph on decayed wood and old polypores
Youngiomyces stratosus (Trappe, Gerd. & Fogel) Y.J. Yao	Rare	Benton County, Oregon	*Pseudotsuga*
Glomeromycota			
Glomus caledonium (T.H. Nicolson & Gerd.) Trappe & Gerd.[b]	Common	Widespread in Northern Hemisphere	Forms arbuscular mycorrhizae with many plants
Glomus convolutum Gerd. & Trappe	Common	Washington, Oregon, and California at high elevations	Probably saprobic
Glomus fasciculatum (Thaxt.) Gerd. & Trappe[b]	Abundant	Worldwide, common	Forms arbuscular mycorrhizae with many plants
Glomus macrocarpum Tul. & C. Tul.[b]	Abundant	Worldwide, locally common	Forms arbuscular mycorrhizae with many plants
Glomus melanosporum Gerd. & Trappe	Infrequent	Washington, California, and Oregon in mountains	Unknown
Glomus microcarpum Tul. & C. Tul.[b]	Abundant	Worldwide, locally common	Forms arbuscular mycorrhizae with many plants
Glomus radiatum (Thaxt.) Trappe & Gerd.	Infrequent	Oregon and Washingon in the Cascade Mountains	*Chamaecyparis nootkatensis*
Glomus rimosipagina C. Walker, Trappe & Colgan nom. prov.	Rare	Thurston County, Washington, in *Pseudotsuga* forests	Unknown
Ascomycota			
Balsamia alba Harkn.	Rare	Western Oregon to southern California	*Pseudotsuga, Pinus, Quercus*
Balsamia magnata Harkn.	Common	Oregon to southern California and Colorado	*Pseudotsuga, Pinus, Quercus*
Balsamia nigrens Harkn.	Infrequent	Oregon and northern California	*Pseudotsuga, Pinus, Quercus*
Balsamia vulgaris Vittad.[b]	Rare	Western Washington and Oregon to southern California	*Pseudotsuga, Pinus*
Barssia oregonensis Gilkey	Abundant	Western Washington to Idaho and northern California	*Pseudotsuga*
Cazia flexiascus Trappe	Infrequent	Western Oregon to southern California	*Quercus*
Choiromyces alveolatus (Harkn.) Trappe	Infrequent	Southwestern Washington to northern California	Pinaceae
Choiromyces meandriformis Vittad.[b]	Rare	Lane County, Oregon; widespread in Europe	*Pseudotsuga*
Elaphomyces anthracinus Vittad.[b]	Rare	Deschutes County, Oregon	*Pinus*

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Elaphomyces decipiens Vittad.[b]	Infrequent	Oregon, northern California	Pinaceae
Elaphomyces granulatus Fr.[b c]	Abundant	Northern Hemisphere, widespread	Pinaceae, Fagaceae
Elaphomyces asperulus Vittad.[b]	Common	Northern Hemisphere, widespread	Pinaceae, Fagaceae
Elaphomyces muricatus Fr.[b c]	Abundant	Northern Hemisphere, widespread	Pinaceae, Fagaceae
Elaphomyces reticulatus Vittad.[b]	Rare	Western Oregon, Europe	*Pinus*
Elaphomyces subviscidus (Zeller) Trappe & Guzmán	Rare	Western Oregon, Idaho	Pinaceae
Fischerula subcaulis Trappe	Rare	Southwestern Washington, western Oregon	*Pseudotsuga*
Genabea cerebriformis (Harkn.) Trappe	Common	Western Washington and Oregon to southern California	Pinaceae, *Quercus*
Genea arenaria Harkn.	Common	Western Oregon to southern California and Mexico	*Quercus*
Genea compacta Harkn.	Rare	Marin County, California	Unknown
Genea harknessii Gilkey	Common	Western Washington and Oregon to northern California	Pinaceae, *Quercus*
Geopora cooperi Harkn.	Abundant	Throughout the Pacific Northwest	Pinaceae
Geopora cooperi f. gilkeyae Burdsall	Abundant	Alaska to Mexico, mostly east of Cascade and Sierra mountains	
Gilkeya compacta (Harkn.) M.E. Sm. & Trappe	Common	Western Oregon to Idaho, southern California and Mexico	Pinaceae, *Quercus*
Hydnobolites californicus E. Fisch.	Infrequent	Western Oregon to southern California	*Pseudotsuga, Pinus, Quercus*
Hydnotrya cubispora (E.A. Bessey & B.E. Thomps.) Gilkey	Infrequent	Western Washington and Oregon to eastern United States	Pinaceae
Hydnotrya inordinata Trappe & Castellano	Rare	Oregon, Cascade Mountains at relatively high elevations	*Abies, Tsuga*
Hydnotrya michaelis (E. Fisch.) Trappe[b]	Infrequent	Oregon and Washington Cascade Mountains to Rocky Mountains	Pinaceae
Hydnotrya subnix Trappe & Castellano	Rare	Washington, Skamania County, Cascade Mountains	*Abies*
Hydnotrya tulasnei (Berk.) Berk. & Broome[b]	Infrequent	Western Oregon, Europe, and Japan	*Pseudotsuga*
Hydnotrya variiformis Gilkey	Common	Southern British Columbia to northern California and the Rocky Mountains	Pinaceae
Leucangium brunneum Trappe et al.	Common	Northwestern Oregon	*Pseudotsuga*
Leucangium carthusianum (Tul.) Paol.[b]	Common	Southern British Columbia to western Oregon at low elevations; southern Europe	*Pseudotsuga*
Pachyphloeus citrinus Berk. & Broome[b]	Infrequent	Western California at low elevations; eastern United States	*Quercus, Lithocarpus*
Pachyphloeus thysellii Colgan & Trappe	Rare	Thurston County, Washington	*Pseudotsuga*
Pachyphloeus virescens Gilkey	Rare	California, San Francisco Bay area	Unknown
Peziza ellipsospora (Gilkey) Trappe	Infrequent	Western Oregon to southern California	*Quercus*
Stephensia bynumii Trappe, Bushnell & Castellano	Rare	Marion and Clackamas Counties, Oregon	*Pseudotsuga*

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Tuber anniae W. Colgan & Trappe	Infrequent	Southwestern Washington to northwestern Oregon and Idaho	*Pseudotsuga*
Tuber argenteum Gilkey	Rare	California, San Francisco County	Unknown
Tuber bellisporum Trappe & Bonito, nom. prov.	Rare	Northern California Sierra Nevada Mountains	Pinaceae
Tuber californicum Harkn.	Abundant	Southwestern Washington to southern California	Pinaceae
Tuber candidum Harkn.	Abundant	Western Oregon to southern California	*Quercus*
Tuber castellanoi Bonito & Trappe, nom. prov.	Rare	Southwestern Oregon	*Pseudotsuga*
Tuber citrinum Harkn.	Rare	Marin County, California	Unknown
Tuber gardneri Gilkey	Common	Western Washington to California and Mexico	Pinaceae
Tuber gibbosum Harkn.	Abundant	Western Washington and Oregon to northern California	*Pseudotsuga*
Tuber irradians Gilkey	Infrequent	Oregon and northern California	*Pseudotsuga*
Tuber levissimum Gilkey	Rare	Southwestern Oregon and California	Unknown
Tuber monticola Harkn.	Common	British Columbia to northern California and Idaho	Pinaceae
Tuber oregonense Trappe & Bonito, nom. prov.	Abundant	Western Washington and Oregon to northern California	*Pseudotsuga*
Tuber pacificum Trappe, Castellano & Bushnell	Rare	Western coastal Oregon	Pinaceae
Tuber phlebodermum (Gilkey) Trappe	Rare	Benton County, Oregon	Unknown
Tuber quercicola J.L. Frank, Southworth & Trappe	Common	Western Oregon and northern California	*Quercus*
Tuber separans Gilkey	Infrequent	Western Oregon, northern California, eastern United States	Pinaceae
Tuber shearii Harkn.	Infrequent	Western Oregon, eastern United States	*Pseudotsuga*
Tuber sphaerosporum Gilkey	Rare	Benton County, Oregon	*Pseudotsuga*
Tuber whetstonense J.L. Frank, Southworth & Trappe	Rare	Jackson County, Oregon	*Quercus*
Basidiomycota			
Agaricus inapertus Vellinga	Common	Western Oregon to northern California and Idaho	Saprobic
Alpova alexsmithii Trappe	Infrequent	British Columbia south to Cascade Mountains of Oregon	*Tsuga*
Alpova diplophloeus (Zeller & C.W. Dodge) Trappe & A.H. Sm.	Abundant	British Columbia south to northern California and east to the east coast; Europe	*Alnus*
Alpova trappei Fogel	Common	Oregon to northern California in Cascade Mountains	Pinaceae
Amogaster viridigleba Castellano	Rare	Sierra County, California, and Douglas County, Oregon	Mixed forests of conifers and *Populus*
Arcangeliella alveolata (Singer & A.H. Sm.) J.M. Vidal	Infrequent	Western Oregon	*Quercus*
Arcangeliella gardneri (Zeller & C.W. Dodge) J.M. Vidal	Infrequent	Western Oregon to northern California	*Pseudotsuga*, *Quercus*

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Arcangeliella oregonensis (Singer & A.H. Sm.) J.M. Vidal	Infrequent	Western Oregon	*Pseudotsuga*
Arcangeliella papyracea (Singer & A.H. Sm.) J.M. Vidal	Rare	Northern coastal California	Unknown
Arcangeliella scissilis (Zeller & C.W. Dodge) J.M. Vidal	Abundant	Southwestern Oregon to northern California	Pinaceae
Brauniellula albipes (Zeller) A.H. Sm. & Singer	Infrequent	Washington to Idaho, northern California and Nevada	*Pinus*
Chamonixia ambigua (Zeller & C.W. Dodge) A.H. Sm. & Singer	Rare	Western California	*Quercus*
Chamonixia brevicolumna A.H. Sm. & Singer	Rare	Northern Idaho	Pinaceae
Chamonixia caudata (Zeller & C.W. Dodge) A.H. Sm. & Singer	Rare	Southwestern Oregon and northern California	*Quercus*
Chamonixia caespitosa Rolland[b]	Infrequent	Southwestern British Columbia to northern California, Colorado	Pinaceae
Chroogomphus loculatus Trappe & O.K. Miller	Rare	Oregon, central Cascade Mountains	Pinaceae
Cortinarius magnivelatus Dearness	Infrequent	Southwestern Oregon, northern California, Nevada	Pinaceae
Cortinarius bigelowii Thiers & A.H. Sm.	Rare	Cascade Mountains of Oregon and Washington to central Idaho	Pinaceae
Cortinarius verrucisporus Thiers & A.H. Sm.	Infrequent	Idaho, northern California and Colorado	Pinaceae
Cortinarius wiebeae Thiers & A.H. Sm.	Rare	Clackamas County, Oregon	Pinaceae
Cystangium echinosporum (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano	Rare	Northern California	*Quercus*
Cystangium idahoensis (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Infrequent	Western Oregon to Idaho	*Abies*
Cystangium lymanensis (Cázares & Trappe) Trappe, T. Lebel & Castellano	Rare	Chelan County, Washington	*Abies*
Cystangium maculatum (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Common	Western Washington and Oregon	Pinaceae
Cystangium medlockii (Trappe & Castellano) Trappe, T. Lebel & Castellano	Rare	Linn County, Oregon	*Pseudotsuga*
Cystangium oregonense (Zeller) Trappe, T. Lebel & Castellano	Infrequent	Western Oregon, Idaho	Pinaceae
Cystangium vesiculosum (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Common	Washington to Idaho and northern California	Pinaceae
Destuntzia fusca Fogel & Trappe	Rare	Western Oregon to northern California	Pinaceae
Destuntzia rubra (Harkn.) Fogel & Trappe	Infrequent	Northwestern Oregon to northern California	*Pseudotsuga*
Destuntzia saylorii Fogel & Trappe	Rare	Northern Sierra Mountains, California	Unknown
Destuntzia subborealis Fogel & Trappe	Rare	Northern Idaho	*Tsuga*
Fevansia aurantiaca Trappe & Castellano	Rare	Oregon Cascade Mountains	Pinaceae
Gastroboletus amyloideus Thiers	Rare	Sierra County, California	Unknown
Gastroboletus brunneus Thiers	Rare	Sierra County, California	Unknown
Gastroboletus citrinobrunneus Thiers	Rare	Tehama County, California	*Abies*
Gastroboletus dinoffii Nouhra & Castellano	Rare	California, Fresno County and south	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Gastroboletus molinai Nouhra, Castellano & Trappe	Rare	Butte County, California	*Quercus*
Gastroboletus ruber (Zeller) Cázares & Trappe	Common	Washington and Oregon in Cascade Mountains	*Tsuga*
Gastroboletus subalpinus Trappe & Thiers	Common	Southwestern Washington, Oregon and northern California in the Cascade Mountains	*Pinus*, *Abies*
Gastroboletus turbinatus (Snell) A.H. Sm. & Singer	Common	Western Washington to Idaho and northern California; Eastern United States and Mexico	Pinaceae
Gastroboletus vividus Trappe & Castellano	Infrequent	Southern Oregon Cascade Mountains to northern California	*Abies*, *Tsuga*
Gastroboletus xerocomoides Trappe & Thiers	Rare	California, Yuba County	*Abies*
Gastrolactarius camphoratus (Singer & A.H. Sm.) J.M. Vidal	Infrequent	Southwestern British Columbia to southwestern Oregon	*Pseudotsuga*
Gastrolactarius crassus (Singer & A.H. Sm.) J.M. Vidal	Infrequent	Northern Oregon to northern California in mountains	Pinaceae
Gastrolactarius desjardinii (Thiers) J.M. Vidal	Rare	California, Mendocino County	*Pseudotsuga*
Gastrolactarius lactarioideus (Zeller) J.M. Vidal	Infrequent	Southwestern Oregon to northern California in mountains	*Abies*
Gastrolactarius parvus (Thiers) J.M. Vidal	Rare	Plumas County, California	Pinaceae
Gastrolactarius pilosus (Zeller & C.W. Dodge) J.M. Vidal	Rare	Santa Clara County, California	Unknown
Gastrolactarius saylorii (Thiers) J.M. Vidal	Rare	El Dorado County, California	Pinaceae
Gastrolactarius tenax (A.H. Sm. & Wiebe) J.M. Vidal	Rare	Clackamas County, Oregon	Pinaceae
Gastrolactarius variegatus (Thiers) J.M. Vidal	Rare	Northern California coast	Pinaceae
Gastrosuillus amaranthii Thiers	Rare	California, Tehama County	*Pinus*
Gastrosuillus imbellus (Trappe) Thiers	Rare	Lane County, Oregon	Pinaceae
Gastrosuillus umbrinus Trappe & Castellano	Rare	Siskiyou County, California	*Pinus*
Gautieria angustispora States & Fogel, nom. prov.	Common	Washington and Oregon in Cascade Mountains	Pinaceae
Gautieria borealis States, Fogel & Hosford nom. prov.	Infrequent	Washington and Oregon in Cascade Mountains	Pinaceae
Gautieria caudata (Harkn.) Zeller & C.W. Dodge	Rare	California, Marin County and south	*Quercus*
Gautieria coralloides States & Fogel, nom. prov.	Infrequent	Southwest Oregon to the Rocky Mountains	Pinaceae
Gautieria crassa States & Fogel, nom. prov.	Infrequent	Washington to California	Pinaceae
Gautieria ellipsospora States & Fogel	Rare	Northern California	Unknown
Gautieria fragilis States & Trappe, nom. prov.	Infrequent	Washington to Oregon and Idaho	Pinaceae
Gautieria fusispora States & Fogel	Rare	Southwestern Oregon, Idaho	Pinaceae
Gautieria gautierioides (Lloyd) Zeller & C.W. Dodge var. *gautierioides*	Infrequent	Northwestern Oregon to northern California	Pinaceae
Gautieria gautierioides var. *candida* States & Trappe, nom. prov.	Infrequent	Western Washington to northern California	Pinaceae
Gautieria hespera States & Fogel, nom. prov.	Infrequent	Washington to southern California	Unknown

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Gautieria minilocularis States & Trappe, nom. prov.	Rare	Polk County, Oregon	*Pseudotsuga*
Gautieria monticola Harkn.	Abundant	British Columbia to northern California	Pinaceae
Gautieria ochraceispora States & Fogel, nom. prov.	Infrequent	Washington to northern California	Pinaceae
Gautieria otthii var. *odora* (Solheim & A.H. Sm.) States & Fogel, nom. prov.	Infrequent	British Columbia to Idaho and northern California	Pinaceae
Gautieria ovalis States & Fogel	Rare	California, Amador County	Mixed forest
Gautieria parksiana Zeller & C.W. Dodge	Infrequent	Southern Washington to southern California	Broad spectrum of hosts
Gautieria parvispora States & Fogel	Rare	Southern Washington to northern California in the Cascade Mountains	Unknown
Gautieria plumbea Zeller & C. W. Dodge	Rare	British Columbia to Idaho and northern California	Pinaceae
Gautieria pterosperma States, Trappe & E.L. Stewart, nom. prov.	Infrequent	Western Oregon to northern California	Pinaceae
Gautieria ramarioides States & Fogel, nom. prov.	Infrequent	Southwestern Oregon to southern California	*Quercus*
Gautieria rubescens States, Trappe & Fogel, nom. prov.	Rare	Western Oregon to northern California	Pinaceae
Gautieria saximontana States & Fogel, nom. prov.	Abundant	Eastern Oregon to the Rocky Mountains	Pinaceae
Gautieria striata States & Fogel, nom. prov.	Infrequent	Western Oregon to northern California	Pinaceae
Gautieria tenuispora States & Trappe, nom. prov.	Rare	Oregon, Cascade Mountains	Pinaceae
Gautieria thiersii States & Fogel, nom. prov.	Rare	Western Oregon to northern California	Pinaceae
Gomphogaster leucosarx (A.H. Sm. & Singer) O.K. Miller	Rare	Northern Idaho	Pinaceae
Gymnomyces abietis Trappe & Castellano	Common	Washington to Idaho and northern California in mountains	*Abies*
Gymnomyces brunnescens (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Infrequent	Southwestern British Columbia to Northern California	Pinaceae
Gymnomyces californicus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Infrequent	Northern California	Pinaceae, *Quercus*
Gymnomyces cinnamomeus Singer & A.H. Sm.	Rare	Western Oregon to northern California	Unknown
Gymnomyces compactus Singer & A.H. Sm.	Rare	Western Oregon	Unknown
Gymnomyces cremea (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano	Rare	Western Oregon	*Quercus*
Gymnomyces ellipsosporus (Zeller) Trappe, T. Lebel & Castellano	Infrequent	Western Oregon	Pinaceae
Gymnomyces fallax (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Infrequent	Western Oregon to southern California	Pinaceae
Gymnomyces ferruginascens Singer & A.H. Sm.	Infrequent	Northern Idaho	Pinaceae
Gymnomyces foetens (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Southwestern Washington	Pinaceae
Gymnomyces fragrans (A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Central Idaho	*Abies*

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Gymnomyces fulvisporus (A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Central Idaho	Pinaceae
Gymnomyces gilkeyae (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano	Infrequent	Northwestern Oregon	*Pseudotsuga*
Gymnomyces monosporus E.L. Stewart & Trappe	Rare	Western Oregon	*Pseudotsuga*
Gymnomyces monticola (Harkn.) Trappe, T. Lebel & Castellano	Infrequent	Southwestern Washington to northern California in mountains	Pinaceae
Gymnomyces nondistincta Trappe & Castellano	Rare	Oregon to northern California in mountains	Pinaceae
Gymnomyces parksii Singer & A.H. Sm.	Rare	Northern Idaho	*Quercus*
Gymnomyces rogersii (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Western Oregon	*Pseudotsuga*
Gymnomyces rolfalexii Trappe, T. Lebel & Castellano	Common	Western Oregon	Pinaceae
Gymnomyces setigerus (Zeller) Trappe, T. Lebel &Castellano	Rare	Northeastern Washington and western Oregon	Pinaceae
Gymnomyces subalpinus (A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Central Idaho	*Abies*
Gymnomyces subfulvus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Common	Southwestern British Columbia to northern California	Pinaceae
Gymnomyces subochraceus (A.H. Sm.) Trappe, T. Lebel & Castellano	Common	Washington to northern California and Idaho	*Pseudotsuga*, *Tsuga*
Hymenogaster alnicola A.H. Sm.	Infrequent	Idaho to western Oregon and northern California	*Alnus*
Hymenogaster boozeri Zeller & C.W. Dodge	Common	Western Washington and Oregon	*Corylus*, *Pseudotsuga*
Hymenogaster brunnescens A.H. Sm.	Rare	Central Idaho	*Picea*
Hymenogaster gardneri Zeller & C.W. Dodge	Infrequent	Western Oregon to northern California	Unknown
Hymenogaster gilkeyae Zeller & C.W. Dodge	Common	Southwestern Washington to northern California	*Pseudotsuga*
Hymenogaster glacialis Cázares & Trappe	Rare	Chelan County, Washington	*Salix*
Hymenogaster nigrescens A.H. Sm.	Rare	Northern Idaho	Pinaceae
Hymenogaster occidentalis Zeller & C.W. Dodge	Rare	Western Oregon to northern California	*Quercus*
Hymenogaster subalpinus A.H. Sm.	Abundant	Southern Washington to northern California and northern Idaho	Pinaceae
Hymenogaster subborealis A.H. Sm.	Rare	Northern Idaho	Pinaceae
Hymenogaster subochraceus A.H. Sm.	Rare	Idaho	*Picea*
Hysterangium coriaceum R. Hesse[b]	Abundant	Widespread in western North America	Broad spectrum of hosts
Hysterangium crassirhachis Zeller & C.W. Dodge	Common	British Columbia to southern California and Idaho	Pinaceae
Hysterangium occidentale Harkn.	Infrequent	Western Oregon to northern California	Pinaceae, *Quercus*
Hysterangium separabile Zeller	Common	Oregon to southern California and Arizona	*Quercus*
Hysterangium setchellii Fischer	Abundant	Washington to southern California	Pinaceae
Kjeldsenia aureispora Colgan, Castellano & Bougher	Rare	Mendocino County, California	Unknown

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Leucogaster candidus (Harkn.) Fogel	Infrequent	Western Washington to northern California	*Pseudotsuga*
Leucogaster citrinus (Harkn.) Zeller & C.W. Dodge	Infrequent	Western Washington to northern California and Idaho	Pinaceae
Leucogaster gelatinosus Fogel nom. prov.	Infrequent	Western Washington to northern California	*Pseudotsuga, Tsuga*
Leucogaster microsporus Fogel nom. prov.	Infrequent	Southwestern Washington to Idaho and northern California	*Pseudotsuga, Tsuga*
Leucogaster odoratus (Harkn.) Zeller & C.W. Dodge	Rare	Western Oregon to northern California	*Pseudotsuga, Quercus*
Leucogaster rubescens Zeller & C.W. Dodge	Abundant	Washington to northern California and Idaho; Rocky Mountains, Northeastern United States	Pinaceae
Leucophleps levispora (Mattir.) Fogel[b]	Rare	Western Oregon, southern California	Pinaceae
Leucophleps magnata Harkn.	Abundant	Washington to northern California and east to Montana	Pinaceae
Leucophleps spinispora Fogel	Infrequent	Eastern Washington to Idaho, Oregon, northern California, Arizona, Mexico	Pinaceae
Macowanites acris Singer & A.H. Sm.	Rare	Central Idaho	*Picea*
Macowanites albidigleba Singer & A.H. Sm.	Rare	Northern Idaho	*Abies*
Macowanites chlorinosmus A.H. Sm. & Trappe	Infrequent	Coastal Oregon, California and Alaska	*Picea, Tsuga*
Macowanites citrinus Singer & A.H. Sm.	Rare	Central Idaho	*Pinus*
Macowanites fulvescens Singer & A.H. Sm.	Rare	Southwestern British Columbia to central Idaho	Pinaceae
Macowanites fuscoviolaceous Singer & A.H. Sm.	Rare	Northern Idaho	*Abies*
Macowanites iodiolens A.H. Sm. & V.L. Wells	Rare	Coastal Oregon	Pinaceae
Macowanites lilacinus A.H. Sm.	Rare	Idaho	Pinaceae
Macowanites luteolus A.H. Sm. & Trappe	Common	Western Oregon, Alaska	Pinaceae
Macowanites magnus H.E. Parks	Rare	Northern California	Unknown
Macowanites mollis Singer & A.H. Sm.	Rare	Southwestern Washington to northwestern Oregon	Pinaceae
Macowanites nauseosus A.H. Sm.	Rare	Central Idaho	Pinaceae
Macowanites odoratus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Southwestern Washington	Unknown
Macowanites olidus A.H. Sm.	Rare	Central Idaho	Pinaceae
Macowanites pinicola A.H. Sm.	Rare	Central Idaho	*Pinus*
Macowanites pseudoemeticus A.H. Sm.	Rare	Northern Idaho	*Picea*
Macowanites roseipes (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Northwestern California	*Picea*
Macowanites russuloides (Setchell) Trappe, T. Lebel & Castellano	Rare	California, San Francisco Bay region	*Quercus*
Macowanites setchellianus Singer & A.H. Sm.	Rare	Contra Costa County, California	Unknown
Macowanites subolivaceus A.H. Sm.	Rare	Idaho	*Picea*
Macowanites subrosaceus A.H. Sm.	Rare	Central Idaho, western Montana	Pinaceae
Macowanites vinicolor A.H. Sm.	Rare	Central Idaho	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Macowanites zellerianus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano	Rare	Grays Harbor County, Washington	Pinaceae
Melanogaster ambiguus (Vittad.) Tul. & C. Tul.[b]	Infrequent	Western Washington, western Oregon and Idaho, widespread in Europe	Broad spectrum of hosts
Melanogaster euryspermus (Zeller & C.W. Dodge) Zeller	Common	Washington to southern California	Broad spectrum of hosts
Melanogaster natsii Y. Wang nom. prov.	Common	Western Washington to southern California	Pinaceae
Melanogaster intermedius (Berk.) Zeller & C.W. Dodge	Infrequent	Western Oregon, northern California	Pinaceae
Melanogaster tuberiformis Corda[b]	Abundant	Washington to northern California, Idaho and Montana	Broad spectrum of hosts
Melanogaster variegatus (Vittad.) Tul. & C. Tul.[b]	Common	Western Washington to southern California	Broad spectrum of hosts
Mycolevis siccigleba A.H. Sm.	Common	Washington to southern California and east to Montana	Pinaceae
Nivatogastrium nubigenum (Harkn.) Singer & A.H. Sm.	Common	Eastern Washington, Idaho, Oregon and northern California in mountains	Saprobe on well-decayed logs
Octaviania cyanescens Trappe & Castellano	Rare	Oregon to northern California, in mountains	*Tsuga*, Fagaceae
Protogautieria lutea A.H. Sm.	Rare	Northeastern Washington	Unknown
Protogautieria substriata Thiers	Rare	Sierra Nevada Mountains of Fresno County, California	Pinaceae
“Protoglossum” (Hymenogaster) idahoensis A.H. Sm.	Rare	Central Idaho	Pinaceae
“Protoglossum” (Hymenogaster) sublilacinus A.H. Sm.	Common	Washington to southern California and east to Idaho	Pinaceae
Radiigera bushnellii L.S. Domínguez & Castellano	Rare	Tillamook and Yamhill Counties, Oregon	Probable saprobe
Radiigera fuscogleba Zeller	Common	Washington south to Mexico and east to Idaho and Colorado	Probable saprobe
Radiigera taylorii (Lloyd) Zeller	Common	Southwestern Washington to northern California, New Mexico	Probable saprobe
Rhizopogon abietis A.H. Sm.[e]	Infrequent	Oregon to northern California and Idaho	Pinaceae
Rhizopogon albidus A.H. Sm.	Infrequent	Southwest Oregon, cental Idaho	Pinaceae
Rhizopogon albiroseus A.H. Sm.	Rare	Northern Idaho	Pinaceae
Rhizopogon alkalivirens A.H. Sm.	Rare	Southwestern Washington to Idaho	Pinaceae
Rhizopogon anomalus A.H. Sm.	Rare	Northwest Oregon to Idaho and New Mexico	Pinaceae
Rhizopogon arctostaphyli A.H. Sm.	Infrequent	Southwestern Oregon and northern California	*Arbutus*, *Arctostaphylos*
Rhizopogon argillaceus A.H. Sm.	Rare	Washington and Idaho	Pinaceae
Rhizopogon argillascens A.H. Sm.	Rare	Northern Idaho	*Pinus*
Rhizopogon ater Trappe & Grubisha	Infrequent	Southwestern Washington and northwestern Oregon	*Pseudotsuga*
Rhizopogon atroviolaceus A.H. Sm.	Infrequent	Western Oregon and Washington to Idaho	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Rhizopogon aurantiacus A.H. Sm.	Infrequent	Idaho	Pinaceae
Rhizopogon avellaneitectus A.H. Sm.	Rare	Northeastern Washington	Pinaceae
Rhizopogon bacillisporus A.H. Sm.	Common	Oregon to Idaho and Wyoming	Pinaceae
Rhizopogon brunneicolor A.H. Sm.	Infrequent	Idaho	Pinaceae
Rhizopogon brunneifibrillosus A.H. Sm	Rare	Wasco County, Oregon	*Pseudotsuga*
Rhizopogon brunneiniger A.H. Sm.	Infrequent	Western Oregon to northern California	Pinaceae
Rhizopogon brunnescens Zeller	Rare	Northern California	Pinaceae
Rhizopogon burlinghamii A.H. Sm.	Rare	Eastern Oregon to southern California	Pinaceae
Rhizopogon butyraceus A.H. Sm.	Rare	Southern Washington, Idaho and southern California	*Pinus, Pseudotsuga*
Rhizopogon chamaleontinus K.A. Harrison & A.H. Sm.	Rare	Northern Idaho, southwestern Oregon	*Pseudotsuga*
Rhizopogon cinerascens A.H. Sm.	Infrequent	Western Oregon, northern Idaho	Pinaceae
Rhizopogon clavitisporus A.H. Sm.	Infrequent	Western Oregon to Idaho	*Pseudotsuga*
Rhizopogon cusickiensis A.H. Sm.	Rare	Southwestern Oregon, northeastern Washington	Pinaceae
Rhizopogon cylindrisporus A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon deceptivus A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon defectus A.H. Sm.	Rare	Northern Idaho	Pinaceae
Rhizopogon diabolicus A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon ellenae A.H. Sm.	Abundant	Western Washington to northern California and Idaho	Pinaceae
Rhizopogon ellipsosporus Trappe, Castellano & Amar.	Infrequent	Western Oregon	Pinaceae
Rhizopogon evadens var. *evadens* A.H. Sm.	Abundant	Washington, Oregon, northern California, Idaho, eastern North America	Pinaceae
Rhizopogon evadens var. *subalpinus* A.H. Sm.	Common	Oregon Cascade Mountains and central Idaho in mountains	Pinaceae
Rhizopogon exiguus Zeller	Infrequent	Western Washington and Oregon	*Pseudotsuga*, *Tsuga*
Rhizopogon fallax A.H. Sm.	Infrequent	Idaho and Wyoming	*Pinus*
Rhizopogon flavofibrillosus A.H. Sm.	Infrequent	Southwestern Oregon to northern California, Idaho and Montana	Pinaceae
Rhizopogon florencianus A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon fragmentatus A.H. Sm.	Rare	Klickitat County, Washington	Pinaceae
Rhizopogon fragrans A.H. Sm.	Rare	Central Idaho	*Pseudotsuga*
Rhizopogon fuscorubens A.H. Sm.	Common	Coastal Oregon and northern California, Montana, eastern North America	*Pinus*
Rhizopogon griseovinaceus A.H. Sm.	Rare	Lane County, Oregon	*Pseudotsuga*
Rhizopogon hawkerae A.H. Sm.	Abundant	Southern British Columbia to northern California and Idaho	*Pseudotsuga*
Rhizopogon hysterangioides A.H. Sm.	Rare	Northern California to Idaho and Colorado	Pinaceae
Rhizopogon idahoensis A.H. Sm.	Common	Southwestern Oregon to northern California and Idaho	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Rhizopogon inquinatus A.H. Sm.	Rare	Western Oregon to northern Idaho	Pinaceae
Rhizopogon isabellinus A.H. Sm.	Rare	Western Oregon to Idaho	Pinaceae
Rhizopogon kauffmanii A.H. Sm. & Zeller	Rare	Idaho	Pinaceae
Rhizopogon libocedri A.H. Sm.	Rare	Western Oregon, Northern California	Pinaceae
Rhizopogon luteoalboides A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon luteoalbus A.H. Sm.	Rare	Idaho	*Pinus*
Rhizopogon luteoloides A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon luteorubescens A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon lutescens A.H. Sm.	Rare	Southwestern British Columbia to Idaho	*Pseudotsuga*
Rhizopogon maculatus Zeller & C.W. Dodge	Rare	Northern California	Pinaceae
Rhizopogon masoniae A.H. Sm.	Rare	Clackamas County, Oregon	Pinaceae
Rhizopogon milleri A.H. Sm.	Infrequent	Western Oregon to Idaho	Pinaceae
Rhizopogon molallaensis A.H. Sm.	Rare	Clackamas and Polk Counties, Oregon	Pinaceae
Rhizopogon molligleba A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon monticola A.H. Sm.	Rare	Southwestern Oregon, central Idaho, New Mexico	Pinaceae
Rhizopogon nitens A.H. Sm.	Infrequent	Southwestern Washington to northwestern Oregon	Pinaceae
Rhizopogon obscurus A.H. Sm.	Rare	Northwestern Oregon, northern California and Idaho	Pinaceae
Rhizopogon occidentalis Zeller & C.W. Dodge	Abundant	Washington, Oregon, northern California, Idaho	*Pinus*
Rhizopogon ochraceisporus A.H. Sm.	Common	Washington, Idaho and Oregon	*Pseudotsuga*
Rhizopogon ochraceobrunnescens A.H. Sm.	Rare	Northern California, northern Idaho	*Pinus*
Rhizopogon ochraceorubens A.H. Sm.	Abundant	Washington to southern California, Idaho and Colorado	*Pinus*
Rhizopogon ochroleucoides A.H. Sm.	Infrequent	Washington and Idaho	Pinaceae
Rhizopogon ochroleucus A.H. Sm.	Rare	Southwestern Oregon, Idaho	*Pinus*
Rhizopogon olivaceofuscus A.H. Sm.	Infrequent	Western Oregon to northern Idaho	Pinaceae
Rhizopogon olivaceoluteus A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon olivaceotinctus A.H. Sm.	Infrequent	Southwestern Oregon to southern California	*Abies*
Rhizopogon oregonensis A.H. Sm.	Rare	Southwestern Oregon and northern California	Pinaceae
Rhizopogon oswaldii A.H. Sm.	Rare	Western Oregon and Washington	Pinaceae
Rhizopogon pachysporus Hosford	Rare	Western Washington	Pincaeae
Rhizopogon pannosus Zeller & C.W. Dodge	Rare	Northern California	Pinaceae
Rhizopogon parksii A.H. Sm.	Abundant	Southwestern British Columbia to northern California and Idaho	*Pseudotsuga*
Rhizopogon parvulus A.H. Sm.	Rare	Northern Idaho	Pinaceae
Rhizopogon pedicellus A.H. Sm.	Infrequent	Western Oregon to eastern Washington and Idaho	Pinaceae
Rhizopogon ponderosus A.H. Sm.	Rare	Western Oregon to southern California	*Pseudotsuga*
Rhizopogon proximus A.H. Sm.	Rare	Northern Idaho	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Rhizopogon pseudoaffinis A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon pseudoalbus A.H. Sm.	Rare	Southwest Oregon, cental Idaho	Pinaceae
Rhizopogon pseudoroseolus A.H. Sm.	Rare	Southwestern Washington to Idaho	Pinaceae
Rhizopogon pseudovillosulus A.H. Sm.	Infrequent	Washington to southern Oregon and Idaho	*Pseudotsuga*
Rhizopogon quercicola A.H. Sm.	Rare	Clackamas and Wasco Counties, Oregon	*Pseudotsuga*
Rhizopogon reaii A.H. Sm.	Rare	Southwestern Oregon to southern California	Pinaceae
Rhizopogon rogersii A.H. Sm.	Infrequent	Southwestern Washington and Oregon	*Pseudotsuga*
Rhizopogon roseolus (Corda) Th. Fr.[b]	Abundant	Southern British Columbia to northern California and the Rocky Mountains	Pinaceae
Rhizopogon rudus A.H. Sm.	Rare	Oregon, Idaho, and New Mexico	Pinaceae
Rhizopogon salebrosus A.H. Sm.	Abundant	Western Oregon to Washington and Idaho	Pinaceae
Rhizopogon semireticulatus A.H. Sm.	Infrequent	Washington and Oregon east to Colorado	*Abies, Pinus, Pseudotsuga*
Rhizopogon semitectus A.H. Sm.	Infrequent	Oregon and northern Idaho in mountains	Pinaceae
Rhizopogon separabilis Zeller	Rare	Oregon, Cascade Mountains	Pinaceae
Rhizopogon sepelibilis A.H. Sm.	Rare	Washington, Pierce County	*Pseudotsuga*
Rhizopogon sipei A.H. Sm.	Rare	Oregon, Linn County	Pinaceae
Rhizopogon smithii Hosford	Infrequent	Western Oregon and northern California	Pinaceae
Rhizopogon sordidus A.H. Sm.	Rare	Northern Idaho	*Pinus*
Rhizopogon subareolatus A.H. Sm.	Abundant	Southwestern British Columbia to northern California and east to Colorado	*Pseudotsuga*
Rhizopogon subbadius A.H. Sm.	Infequent	Western Oregon to Idaho and Wyoming	Pinaceae
Rhizopogon subcaerulescens A.H. Sm.	Abundant	Washington to northern California and east to the Rocky Mountains	Pinaceae
Rhizopogon subcinnamomeus A.H. Sm.	Rare	Western Oregon to northern Idaho	Pinaceae
Rhizopogon subcitrinus A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon subclavitisporus A.H. Sm.	Rare	Northwestern Oregon to northern Idaho	*Pseudotsuga*
Rhizopogon subcroceus A.H. Sm.	Rare	Idaho	*Pinus*
Rhizopogon subgelatinosus A.H. Sm.	Infrequent	Western Oregon to northern California and Idaho	Pinaceae
Rhizopogon sublateritius A.H. Sm.	Rare	Northern California to northern Idaho	Pinaceae
Rhizopogon subolivascens A.H. Sm.	Rare	Central Idaho	Pinaceae
Rhizopogon subpurpurascens A.H. Sm.	Infrequent	Western Oregon to Idaho and Wyoming	Pinaceae
Rhizopogon subsalmonius A.H. Sm.	Common	Washington to northern California, Idaho and Arizona	*Abies*
Rhizopogon truncatus Linder	Common	Western Oregon to northern California; Eastern North America	Pinaceae
Rhizopogon tsugae A.H. Sm.	Rare	Northwestern Oregon	*Pseudotsuga*
Rhizopogon udus A.H. Sm.	Rare	Idaho	Pinaceae
Rhizopogon umbrinoviolascens A.H. Sm.	Rare	Eastern Washington and Idaho	*Pseudotsuga*
Rhizopogon variabilisporus A.H. Sm.	Rare	Southwestern Oregon to northern California and Idaho	Pinaceae

Table 1—Truffle species native to the Pacific Northwest, with generalized categorization of relative frequency, known distribution, and mycorrhizal hosts in the Pacific Northwest (continued)

Phylum, genus, and species	Frequency in PNW[a]	Known distribution	Mycorrhizal hosts in Pacific Northwest
Rhizopogon ventricisporus A.H. Sm.	Rare	Northern California and Idaho	Pinaceae
Rhizopogon vesiculosus A.H. Sm.	Common	Washington, Oregon and Idaho	*Pseudotsuga*
Rhizopogon villescens A.H. Sm.	Infrequent	Washington to southwestern Oregon and Idaho	*Pseudotsuga*
Rhizopogon villosulus Zeller	Abundant	Rocky Mountains, southern British Columbia to northern California, Mexico	*Pseudotsuga*
Rhizopogon vinicolor A.H. Sm.	Abundant	Southwestern British Columbia to northern California, Colorado	*Pseudotsuga*
Rhizopogon viridis Zeller & C.W. Dodge	Rare	Northern Idaho	*Pseudotsuga*
Rhizopogon vulgaris (Vittad.) M. Lange[b]	Abundant	Pacific Northwest; widespread in the United States and Europe	Pinaceae
Rhizopogon zelleri A.H. Sm.	Infrequent	Western Oregon to Idaho and the Rocky Mountains	*Pseudotsuga*
Schenella simplex T. MacBride	Abundant	British Columbia to northern California, Idaho, Colorado	Probable saprotroph
Schenella pityophilus (Malençon & Riousset) Estrada & Lado[b]	Common	Southwestern Oregon and northern Colorado, Mexico, France	Probable saprotroph
Scleroderma hypogaeum Zeller	Common	Southern Washington to southern California	Pinaceae
Sclerogaster pacificus Zeller & C.W. Dodge	Rare	Southern British Columbia, coastal Oregon	Unknown
Sedecula pulvinata Zeller	Rare	Idaho, northern California, Colorado	Pinaceae
Thaxterogaster pavelekii Trappe, Castellano & P. Rawl.	Infrequent	Northwestern Oregon coast	*Pinus, Picea*
Thaxterogaster pinguis (Zeller) Singer & A.H. Sm.	Abundant	British Columbia to northern California and east to Colorado	*Abies*
Thaxterogaster thiersii Calhoun	Infrequent	Marin County, California and south	*Pinus, Picea*
Trappea darkeri (Zeller) Castellano	Common	Eastern Washington, Idaho, Oregon to southern California and east to South Dakota	Pinaceae
Trappea phillipsii (Harkn.) Castellano	Infrequent	Eastern Oregon to southern California and Nevada	Pinaceae
Truncocolumella citrina Zeller	Abundant	British Columbia to northern California to the Rocky Mountains	*Pseudotsuga*

Note: Species that are rare in the PNW may be common or abundant elsewhere.

[a] Rare = known only from a very restricted range, e.g., two adjacent counties, or only a very few sites; infrequent = known from a wider range than "rare" but not often found; common = known from a relatively wide range, e.g., California to British Columbia west of the coastal mountains, and regularly collected; abundant = throughout the PNW where appropriate host trees occur, frequently collected.

[b] European name applied to North American species; recent molecular evidence indicates many North American fungi given European names are in fact separate species and require new names. Accordingly, such species in this table may receive new names as new data become available.

[c] Current research by M. Castallano and J. Trappe (unpublished data) indicates that these species, designated by European names, are species complexes; none in the PNW are identical with European species.

[d] Some are likely to be developmental stages of other species, but molecular data are needed to determine this. Taxa that have been identified as new but are not yet formally published are designated as "nom. prov.," i.e., "provisional name."

[e] The genus *Rhizopogon* has many "rare" species. Some are likely to be developmental stages of other species, but molecular data are needed to determine this.

What Are Truffles?

Forest floor fungi exist primarily as microscopic filaments (hyphae) that permeate soil and organic substrates (litter, wood). The main body or thallus of the fungus is composed of millions of hyphae collectively called a mycelium. When conditions are right, the fungal mycelium enters its reproductive stage to produce fleshy, spore-bearing structures (mushrooms, truffles, conks, cups, etc.) These spore-bearing structures (sporocarps) are commonly called fruit-bodies because they are analogous to fleshy plant fruits that bear seeds. Like seeds, the microscopic spores disperse and germinate to propagate new fungal individuals or fuse into established colonies of the species to contribute new genetic diversity. Truffles are in many ways like mushrooms, and, indeed, the truffle form has evolved many times from mushroom ancestors. Truffle fruit-bodies differ from mushrooms, however, in how they produce and disperse their spores. Mushrooms typically have a stem that pushes their caps up through the forest floor where they open to expose and release their spores to the air; air movement carries many spores away. Truffles no longer have a stem robust enough to push the fruit-body up and out of the soil. Truffle spores remain enclosed within the interior of the fruit-body. As truffles mature, they produce odors that are sensed by animals, which excavate and consume them. The spores pass unharmed through the animal's digestive tract and are later dispersed when the animal defecates. Truffles provide a key food resource for many forest animals (Fogel and Trappe 1978, Luoma et al. 2003, Maser et al. 2008, Trappe and Claridge 2005).

For simplicity, we use the colloquial term "truffle" to refer to this diverse fungal group. Many other terms are used in the scientific literature, so we provide some brief explanations of their uses. Truffles have been refered to as "hypogeous fungi" in reference to their belowground fruiting habit. However, the mycorrhizae (fungus root symbioses) and mycelium of many nontruffle fungi are "hypogeous," so the phrase "hypogeous fruit-bodies" may be preferred. Additionally, not all truffles fruit completely belowground; some emerge through the soil surface, either partially or completely depending on the species and environmental conditions. Truffles have recently been called "sequestrate" fungi. This term accurately reflects how the spores are isolated or hidden away (sequestered) within the enclosing tissue.

Old mycological literature often refers to "true" and "false" truffles. True truffles are formed by a phylum of fungi called Ascomycota (fungi that bear their spores in small sacs or asci), which are also referred to as ascomycetes. The black and white European truffles highly prized by gourmets are ascomycetes, hence the emphasis on calling this group “true” truffles. False truffles are formed by basidiomycetes (fungi that bear their spores on microscopic, club-like structures termed basidia); most mushroom-forming fungal species belong to this group. Some truffle species are called “truffle-like” because they have some but not all of the traits typical of truffles; for example, some species retain a vestigial stem. Finally, there are chocolate truffles! Of course, these sweet confectionaries are not fungi at all but draw upon similarities to the dark, round, appearance of European culinary black truffles.

Where Do We Find Truffles?

Truffle species occur around the world in almost exclusive association with trees and other plants that form ectomycorrhizae. Ectomycorrhizae are mutualistic, beneficial symbiotic associations between the roots of many plants (primarily trees) and specialized soil fungi. The fungi act as extensions of the root system, taking up nutrients and water and translocating them to the plant in return for plant sugars to fuel their growth (see later section “Mycorrhizal Symbiosis” for more details). Only a minority of the world’s tree species form ectomycorrhizae, but those species are often dominant components in temperate forest ecosystems, particularly species in the Pinaceae, Betulaceae, Fagaceae, and Myrtaceae (pine, birch, oak, and myrtle families).

Approximately 120 plant species from 19 families and 41 genera are documented as ectomycorrhizal hosts in the PNW (table 2). As more plants are investigated, the list will grow. On a regional scale, this assemblage of ectomycorrhizal host genera and species is one of the larger in the world. Forests in the PNW are also extremely diverse in terms of species composition, structure, and soil types; climates range from cool and wet in coastal and high-elevation forests to hot and dry in interior forests (Barbour and Major 1977, Franklin and Dyrness 1973, Krajina 1965). These forests have existed for millennia as shifting mosaics of different seral stages, shaped by complex disturbance patterns and processes brought by fire, volcanism, insects, and disease (Wimberly et al. 2000). Many of the dominant tree species can live for hundreds of years, and extensive stands of old-growth forest habitat have been common features of the landscape. This diversity in ectomycorrhizal tree hosts, forest habitat, and climatic conditions created a unique confluence of biological and environmental conditions for the explosive evolution and diversity of truffle species in the PNW.

Table 2—Known ectomycorrhizal host genera and species for the Pacific Northwest

Family	Genus	Species	Common name
Gymnosperms			
Pinaceae	*Abies*	*amabilis* (Douglas ex Louden) Douglas ex Forbes	Pacific silver fir
		concolor (Gord. & Glend.) Lindl. ex Hildebr.	white fir
		grandis (Douglas ex D. Don) Lindl.	grand fir
		lasiocarpa (Hook.) Nutt.	subalpine fir
		magnifica A. Murray	California red fir
		procera Rehder	noble fir
	Larix	*lyallii* Parl.	subalpine larch
		occidentalis Nutt.	western larch
	Picea	*engelmannii* Parry ex Engelm.	Engelmann spruce
		sitchensis (Bong.) Carrière	Sitka spruce
	Pinus	*albicaulis* Engelm.	white bark pine
		attenuata Lemmon	knobcone pine
		balfouriana Balf.	foxtail pine
		contorta Douglas ex Louden	lodgepole/shore pine
		flexilis James	limber pine
		jeffreyi Balf.	Jeffrey pine
		lambertiana Douglas	sugar pine
		monticola Douglas ex D. Don	western white pine
		muricata D. Don	bishop pine
		ponderosa C. Lawson	ponderosa pine
		sabiniana Douglas ex Douglas	grey pine
	Pseudotsuga	*menziesii* (Mirb.) Franco	Douglas-fir
	Tsuga	*heterophylla* (Raf.) Sarg	western hemlock
		mertensiana (Bong.) Carrière	mountain hemlock
Angiosperms			
Asteraceae	*Anaphalis*	*margaritacea* (L.) Benth.	pearly-everlasting
Betulaceae	*Alnus*	*incana* (L.) Moench ssp. *tenuifolia* (Nutt.)	mountain alder
		rhombifolia Nutt.	white alder
		rubra Bong	red alder
		viridis (Chaix) DC. ssp. *sinuata* (Regel) A. Löve & D. Löve	Sitka alder
		viridis (Chaix) DC. ssp. *fruticosa* (Rupr.) Nyman	Siberian alder
	Betula	*glandulosa* Michx.	resin birch
		occidentalis Hook	water birch
		papyrifera Marsh.	paper birch
	Corylus	*cornuta* Marsh. ssp. californica (A. DC.) E. Murray	California hazel
Caprifoliaceae	*Sambucus*	*racemosa* L.	elderberry
Caryophyllaceae	*Silene*	*acaulis* (L.) Jacq.	moss campion
Cyperaceae	*Kobresia*	*myosuroides* (Vill.) Fiori	Bellard's kobresia
Elaeagnaceae	*Shepherdia*	*canadensis* (L.) Nutt.	soapberry
Ericaceae	*Arbutus*	*menziesii* Pursh	Pacific madrone
	Arctostaphylos	*canescens* Eastw.	hoary manzanita
		columbiana Piper	hairy manzanita
		glandulosa Eastw.	Eastwood's manzanita
		hispidula Howell[a]	Gasquet manzanita
		klamathensis S.W. Edwards, Keeler-Wolf & W. Knight[a]	Klamath manzanita
		malloryi (W. Knight & Gankin) P.V. Wells[a]	Mallory's manzanita
		manzanita Parry	whiteleaf manzanita
		mendocinoensis P.V. Wells[a]	pygmy manzanita
		nevadensis A. Gray	pinemat manzanita
		nummularia A. Graya	glossyleaf manzanita
		patula Greene	greenleaf manzanita
		stanfordiana Parry[a]	Stanford's manzanita

Table 2—Known ectomycorrhizal host genera and species for the Pacific Northwest (continued)

Family	Genus	Species	Common name
		uva-ursi (L.) Spreng	kinnikinnick, bearberry
		viscida Parry	sticky manzanita
	Chimaphila	*umbellata* (L.) W. Bartram	prince’s-pine
	Gaultheria	*shallon* Pursh	salal
	Ledum	*glandulosum* Nutt.	western Labrador tea
	Monotropa	*hypopithys* L.	pinesap
		uniflora L.	Indian pipe
	Rhododendron	*macrophyllum* D. Don ex G. Don	western rhododendron
	Sarcodes	*sanguinea* Torr.	snow plant
	Vaccinium	*myrtillus* L.	dwarf bilberry
		ovatum Pursh	evergreen huckleberry
		parvifolium Sm	red blueberry
		scoparium Leiberg ex Coville	grouseberry
		uliginosum L.	bog blueberry
Fagaceae	*Chrysolepis*	*chrysophylla* (Douglas ex Hook.) Hjelmqvist	chinquapin
		sempervirens (Kellogg) Hjelmqvist	bush chinquapin
	Lithocarpus	*densiflorus* (Hook. & Arn.) Rehder	tanoak
	Quercus	*chrysolepis* Liebm.	canyon live oak
		douglasii Hook. & Arn.	blue oak
		garryana Douglas ex Hook.	Oregon white oak
		kelloggii Newberry	California black oak
		sadleriana R. Br.	deer oak
		vacciniifolia Kellogg	huckleberry oak
Myricaceae	*Myrica*	*californica* (Cham.) Wilbur	wax-myrtle
Polygonaceae	*Polygonum*	*bistortoides* Pursh	American bistort
		davisiae W.H. Brewer ex A. Gray	Davis’ knotweed
		viviparum L.	alpine bistort
Ranunculaceae	*Clematis*	*vitalba* L.	travelers-joy
Rhamnaceae	*Rhamnus*	*purshiana* (DC.) Cooper	cascara
Rosaceae	*Cercocarpus*	*ledifolius* Nutt.	curl-leaf mountain mahogany
	Crataegus	*douglasii* Lindl	black hawthorne
	Dryas	*drummondii* Richardson ex Hook.	yellow mountain-avens
		integrifolia Vahl	white mountain-avens
		octopetala L.	white dryas
	Prunus	*emarginata* (Douglas ex Hook.) D. Dietr.	bittercherry
		virginiana L.	common chokecherry
	Rosa	*gymnocarpa* Nutt.	baldhip rose
	Rubus	*lasiococcus* A. Gray	dwarf bramble
	Sorbus	*sitchensis* M. Roem.	Sitka mountain ash
Rubiaceae	*Galium*	*oreganum* Britton	Oregon bedstraw
Salicaceae	*Populus*	*angustifolia* James	willow cottonwood
		tremuloides Michx.	quaking aspen
		trichocarpa Torr. & A. Gray ex Hook.	black cottonwood
	Salix	About 30 species plus additional hybrids	willows
Scrophulariaceae	*Pedicularis*	*groenlandica* Retz.	pink elephant’s head
Pteridophyte			
Pteridaceae	*Adiantum*	*pedatum* L.	northern maidenhair

Note: Many, if not most, may also form vesicular-arbuscular mycorrhizae or, in the case of the Ericaceae, ericoid mycorrhizae.

[a] These are less widespread but locally important species of *Arctostaphylos*; the other manzanita species are widespread in the area covered, rare species are not listed. Many hybrids have been documented.

History of Truffle Science in the Pacific Northwest


Figure 2—Carlo Vittadini, 1800–1865.

The PNW has a unique and interesting history of professional mycologists who have dedicated themselves to unraveling the mysteries surrounding this group of cryptic fungi. Before we discuss them, however, homage is due to a 19th-century Italian mycologist who specialized in the study of truffle taxonomy: Carlo Vittadini (fig. 2). In the 1820s, the Swedish mycologist Elias Magnus Fries (fig. 3) had established the beginnings of modern fungal taxonomic science, but Fries paid relatively scant attention to truffles. He named and classified the genus *Rhizopogon* (Fries 1817), the most diverse and abundant genus in the PNW. Otherwise, his descriptions of truffles (Fries 1821–1832) were based more on what he gleaned from writings of earlier mycologists than from his own observations. Given the knowledge of the time, Fries did a remarkable job of classifying the few truffle species known, but he also made some mistakes that muddied the truffle taxonomic waters.


Figure 3—Elias M. Fries, 1794–1878.

In 1831, however, Vittadini provided the much-needed clarification that hitherto had been lacking. A professor of botany at the University of Torino, he published that year his superb *Monographia Tuberaceum,* or “Monograph of the Truffles” (Vittadini 1831), followed 11 years later by his *Monographia Lycoperdineorum,* or “Monograph of the Lycoperdaceae” (Vittadini 1842). In these works, Vittadini established the classification system ancestral to that used today, albeit now much expanded and modified to cover discoveries over the many decades since. Vittadini (1842) also has the distinction of being the first to recognize the importance of mycorrhizal fungi to the nutrition of their host trees.


Figure 4—Harvey W. Harkness, 1821–1901.

Meanwhile, the few North American mycologists who were contemporaries of Vittadini had little to say about truffles. But in 1821, the same year that gave birth to Fries’ epic work on fungal classification, Harvey W. Harkness (fig. 4) was born in Pelham, Massachusetts (Werner 2006). In 1847, he apprenticed as a physician and in the following year made his way to California to join the gold rush. For a year or so he mined gold but discovered an even more lucrative source of fortune. Physicians were scarce in the California goldfields, and miners were constantly getting sick or injured and paid for medical care with gold.

A canny businessman, Harkness saved his earnings, and in 1850 he established a medical practice in Sacramento. As a now well-to-do and educated man, he was welcomed into Sacramento society, becoming friends of Govenor Leland Stanford and businessmen such as Mark Hopkins. He became president of Sacramento's first Board of Education in 1850. In ensuing years he made shrewd investments in real estate during Sacramento's boom years, became a millionaire, and somehow developed an interest in fungi. He began collecting fungi of all kinds and in 1868 retired from his medical practice to devote himself to mycological science. As a sign of his prominence, he was one of the selected speakers at the joining of the transcontinental railroad tracks at Promontory Point, Utah: at the end of his speech, he was the one who handed the golden spike to Leland Stanford to join the rails from east and west. In 1869 Harkness moved to San Francisco, devoting much of his time to collecting and describing fungi. A member of the California Academy of Sciences, he was elected to its presidency, an office he held from 1887 to 1896.

Well into his years of studying fungi, Harkness began collecting truffles. How he arrived at this mycological pursuit is not recorded, but he developed skill in finding them. He collected in the Sierra goldfield country as well as the San Francisco Bay Area. In 1899, Harkness published his treatise, *California Hypogeous Fungi* (Harkness 1899). This was the first extensive publication on truffles in North America. Although his collecting was confined to a small geographic area in California, many of his new species occur northward as far as British Columbia, including *Tuber gibbosum*, the spring form of the Oregon white truffle of commerce today. Altogether, Harkness described nearly 60 new species, of which about 40 are still recognized as valid. He illustrated many of the species in watercolor paintings reproduced in his paper. Readers will see his name cited as the naming authority for many of the species we discuss, abbreviated as "Harkn."

Harkness died in 1901, a multimillionaire celebrated for being the first American mycologist to focus on truffles and for establishing the west coast as a center of excellence in truffle research. His herbarium at the California Academy of Sciences was transferred to Stanford University and, some years later, donated to the National Fungus Collections in Beltsville, Maryland, where it resides today.

Not long after Harkness died, a young woman enrolled in Oregon Agricultural College to study botany, Helen Margaret Gilkey (fig. 5) (Trappe 1975a). She earned a Bachelor of Science degree and, in 1911, was awarded a Master of Science in botany. A highly skilled and artistic botanical illustrator, she was employed in that capacity by the Department of Botany. She had become fascinated with fungi, however, and was accepted into a Ph.D. program at the University of California, Berkeley. There she studied mycology under Professor W.A. Setchell, who had

Figure 5—Helen M. Gilkey, 1886–1972.

collected truffles from under eucalyptus trees in and around Berkeley, California. Setchell suggested that she continue the work of Harkness by restudying his collections and collecting additional specimens. As Gilkey related many years later (about 1970, Trappe, unpublished conversation), Professor Setchell told her that any specimens she collected that did not fit Harkness' species were surely new: it was self-evident that truffles could not have migrated from Europe or Asia because they could not discharge their spores to the air. Gilkey followed his advice but later chuckled at his naivety when relating the story, because by 1940 several "European" species had been found in North America. However, since then, the new science of molecular biology has emerged; accumulating data now indicate that many, perhaps all, of the North American collections labeled with European names are, in fact, genetically different from their European analogs. So, Setchell and Gilkey were right initially.

Gilkey was the first woman to be awarded a Ph.D. in botany at Berkeley. Her thesis was published in 1916: *A Revision of the Tuberales of California*. Most of the species she included occur in the Pacific Northwest. In 1918, she joined the faculty of Oregon Agricultural College (now Oregon State University, OSU) as curator of the Botany Herbarium. Meanwhile, another young mycologist, Sanford Myron Zeller (fig. 6), was finishing his Ph.D. program in botany at Washington University, St. Louis (Gilkey 1949). A year after Gilkey's appointment, Zeller accepted a position as plant pathologist at Oregon Agricultural College. Neither was hired as a truffle taxonomist, but both had a vigorous, even joyous interest in truffle fungi, and they quickly developed a warm friendship and collaboration. Like the fungi and plants they studied, Zeller and Gilkey formed a symbiosis: Gilkey specialized in the "true" truffles, i.e., the ascomycetes, whereas Zeller worked with the basidiomycetes, sometimes called the "false" truffles. When they would go collecting singly or together, they sorted out the "catch of the day"; the ascomycetes went to Gilkey, the basidiomycetes to Zeller. Because of this division of the spoils, they each published on their respective groups but, oddly enough, they never wrote a joint paper. Perhaps that is how they maintained their friendship and otherwise close working relationship.

Figure 6—Sanford M. Zeller, 1884–1948.

Zeller published many papers on taxonomy of hypogeous fungi, starting with his first find, a *Rhizopogon* species (Zeller 1918) later transferred to the genus *Alpova* (Trappe 1975c). That event aroused a curiosity and enthusiasm for truffle-like fungi that endured for the rest of Zeller's career; after that first find, he rushed to a hardware store to purchase a four-tined garden fork, which he converted to a truffle rake by sawing off the long handle to a comfortable length for use in the woods. He published many papers on truffles and other fungi over the ensuing 30 years, many appearing in the Annals of the Missouri Botanical Garden in collaboration with C.W. Dodge (Gilkey 1949). The new species he described or revised number more than 300. He loved collecting fungi in the field and availed himself of every opportunity to do so. When Zeller became incapacitated, he gave his truffle rake to Gilkey. In 1965, when Jim Trappe came to OSU as a project leader in the forest mycology group of the USDA Forest Service, Pacific Northwest Research Station, Gilkey gave Zeller's rake to Trappe. He used it for another 30 years, by which time the tines had worn down so much that he retired it to a place of honor as "the Heritage Truffle Rake."

Because Gilkey was employed as herbarium curator and plant taxonomist, and Zeller as plant pathologist with a specialty in tree fruit diseases, their pleasure in truffle taxonomy was pursued as a quasiprofessional hobby. Their symbiotic relationship flourished for 30 years until Zeller died at the age of 64 from acute asthma. Gilkey expanded her 1916 monograph of California truffles to include all of North America (Gilkey 1939) and updated that 15 years later (Gilkey 1954a). In the course of her studies, she described or revised nearly 70 species and greatly expanded knowledge of their distributions and ecology. She retired in 1951 but continued publishing on truffle taxonomy until 1963. She continued sharing her knowledge on these fungi with students and younger colleagues until she died at age 86 (Trappe 1975a). Together, Gilkey and Zeller established the now OSU as a renowned center of truffle taxonomy in North America, a reputation it retains to this day.


Figure 7—Alexander H. Smith, 1904–1986.

As the era of Gilkey and Zeller waned, Professsor Alexander H. Smith (fig. 7) of the University of Michigan began his amazingly productive studies of western fungi. Initially he focused on mushrooms, but he became increasingly fascinated with truffles. Although he had published papers on mushroom taxonomy from the early 1930s, his first publication on truffle species came out in 1958 in collaboration with another prolific mycologist, Rolf Singer (Singer and Smith 1958a). These two mycologists laid the foundation of understanding for the fungi that are intermediate between epigeous mushrooms and hypogeous truffles, i.e., fungi that have evolved from mushroom producers to the belowground fruiting habit and ecology but still retain some morphological features of mushrooms, such as a vestigial stem. Such fungi especially abound in the Pacific Northwest. During his many field seasons spent in Idaho and Oregon, Smith more and more looked for belowground fungi. He discovered that the genus *Rhizopogon* is especially diverse and abundant in western conifer forests. He also realized that it posed some extraordinarily difficult taxonomic problems. Zeller had already described a number of species from Oregon, and Smith and his students and collaborators made many hundreds of additional collections. Smith published the results of his studies in his tome *A Preliminary Account of the North American Species of Rhizopogon,* generously recognizing the early work of Zeller, who had died 18 years earlier, by listing him as a posthumous co-author (Smith and Zeller 1966). By placing the word "preliminary" in the title of this treatise, Smith signalled to his successors that much remained to be done to thoroughly understand the genus and its species. He had established, however, that *Rhizopogon* is the world's largest and most complex of all the truffle genera. In recent years, molecular phylogenetic methods have been used to clarify many of the taxonomic puzzles encountered by Smith, but new species keep turning up and much more research is needed to fully understand the genus. After publication of a few additional papers on truffle fungi, Smith turned his attention back to mushroom taxonomy. By his death in 1986, he had established a legacy of advancing our knowledge of Pacific Northwestern truffle fungi.

Figure 8—Harry D. Thiers, 1919–2000.

Students were among Alexander Smith's special legacies, and one of these, Harry D. Thiers (fig. 8), is especially noteworthy in the saga of Pacific Northwestern truffles. After earning his Ph.D. in Mycology under Alexander Smith, Thiers taught in Texas until accepting a professorship at San Francisco State College (now University) in 1959, where he stayed until his retirement in 1989. He was expert in many families of mushrooms, but his particular love was the Boletaceae. He soon became interested in truffles related to boletes, i.e., those that had evolved from mushroom ancestors to a hypogeous fruiting habit. The PNW, including northern California, has a considerable diversity of these; in collaboration with James Trappe, Thiers published a paper in which this diversity was revealed by description of five new species (Thiers and Trappe 1969). Thiers continued his studies on these interesting mushroom-to-truffle transitional forms. He described additional new species and ultimately published a seminal paper that explored their evolution on a worldwide basis (Thiers 1984b). At his death in 2000, Thiers, like Smith, left a legacy not only of solid mycological research but also of students who continue his tradition at many different universities.


Figure 9—Albert B. Frank, 1839–1900.

In 1885, as H.W. Harkness was pursuing his interest in hypogeous fungi in California, the German botanist A.B. Frank (fig. 9), Professor of Plant Pathology at the Royal College of Agriculture, Berlin, published a paper that would radically alter our understanding of how trees get their nutrients from the soil (Trappe 2005a, 2005b). Frank had been commissioned by the King of Prussia to discover how to grow truffles in that northern kingdom. Knowing that truffles were produced among the rootlets of certain trees, Frank first carefully examined the tiny feeder rootlets of various tree species. He quickly perceived that the rootlets were enclosed in fungal tissue; indeed the root surfaces had no direct contact with the soil.

Several other researchers had reported this phenomenon earlier, but most had interpreted it either as a diseased condition of the rootlets or as a curiosity (Trappe and Berch 1985). In 1841, the brothers Louis-René and Charles Tulasne noted that the rootlets “embrace so intimately” the fruit-bodies of truffles in the genus *Elaphomyces* that the fungus must be parasitizing the roots (Trappe and Berch 1985), but they did not mention that the rootlets were mantled by the fungus. Only Vittadini (1842) correctly interpreted the meaning of this fungus-root association in his studies of *Elaphomyces*. He observed that the proliferated rootlets enclosing fruit-bodies become mantled by mycelium growing out from the fruit-bodies. Vittadini wrote (English translation from the original Latin), “It is our decided opinion, that beyond all doubt the higher plants absorb nutrients from the fungus by their feeder rootlets.” It was Frank, however, who established that a mutualistic relationship occurred between fungus and root: he termed it “mycorrhiza.”

Although some of Frank’s insights about the mutualistic symbiosis of mycorrhizae were not confirmed for several decades after his original paper, by the mid-20th century nearly all his hypotheses had become accepted. Mycorrhiza research was underway in many parts of North America by the 1930s, but the first reference to the phenomenon in the PNW was by Slipp and Snell (1944), who posited mycorrhizal associations between various fungi in the family

Boletaceae and conifers in Idaho and Washington. The first reports of truffle fungi as mycorrhizal associates of Pacific Northwestern tree species were *Rhizopogon roseolus* (as *R. rubescens*) with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarge) (Trappe 1960) and *Truncocolumella citrina* with Douglas-fir (Trappe 1961). Trappe (1965) also described a unique, tuberculate mycorrhiza of Douglas-fir, which subsequently proved to be formed with *Rhizopogon vinicolor* (Zak 1971). The first pure culture syntheses of Douglas-fir mycorrhizae with cultures of identified fungi included *Rhizopogon villosulus* (as *R. colossus*) (Trappe 1967).

Figure 10—James M. Trappe, 1931–

The "modern era" of truffle research in the PNW begins with the arrival of James M. Trappe (fig. 10) to Corvallis in 1965. After receiving his masters in forestry at Syracuse University in 1955, Trappe returned to his native state of Washington and entered in the Ph.D. program in forestry at the University of Washington. Although a forestry major, Trappe's real interest was in forest fungi, particularly mycorrhizal fungi and symbioses. So he honed his early mycological skills under the tutelage of botany Professor Daniel Stuntz, a world expert on the ectomycorrhizal genus *Inocybe*. Trappe would pick up much of his passion for the collection and description of fungi from Dr. Stuntz. Trappe completed his Ph.D. in 1962 with a thesis on the ecology of the widely distributed *Cenococcum graniforme* (*geophilum*) (Trappe 1962a); *Cenococcum geophilum* forms mycorrhizae with nearly all ectomycorrhizal hosts it encounters. Trappe also published at this time the first comprehensive, worldwide compilation of ectomycorrhizal fungus-host associations (Trappe 1962b); that pioneering publication has been one of the more cited papers in mycorrhizal research.

Upon arriving in Corvallis as project leader of the PNW mycology program in 1965, Trappe soon headed over to the Botany and Plant Pathology Department at OSU to meet Professor Gilkey who was long retired but was just then vacating her office. Little did he know the historical significance of this meeting for himself and the future of truffle research in the PNW. As Trappe tells of the encounter (as told to R. Molina), upon arriving in Gilkey's office and introducing himself, he noticed that Gilkey was packing her entire dried truffle collection for shipment to the New York Botanical Garden for deposit and curation. Because there was no longer an active mycology program at OSU, she felt the specimens could best be preserved and studied at the garden's internationally acclaimed herbarium. Halfway through their discussion, Trappe noticed that she began to unpack the same boxes. When he asked her why she was doing so, she replied that she had hoped to leave her collection at OSU but feared that they'd be neglected, perhaps put in a closet where insects would eat them or a janitor would throw them out. Recognizing Trappe's interest and passion for these organisms, she now had the proper person to leave them with. This was a great honor for Trappe, and together with receiving Zeller's truffle rake from Dr. Gilkey, these events set him on a path to becoming the world-recognized truffle scientist that he is today.

Trappe's passion for studying truffles and publishing his findings quickly led to his recognized leadership in this field. In 1967 he traveled to Torino, Italy, for a year to study the earliest truffle specimens on which modern truffle taxonomy was based. After returning to Corvallis, Trappe received a National Science Foundation grant to monograph genera of truffles. His first Ph.D. student under that funding was Elwin Stewart, who worked on the genus *Gautieria* (Stewart 1974). Then came Robert Fogel to specialize in the genera *Leucogaster* and *Leucophleps* for his Ph.D. project (Fogel 1975). Both found new species in the PNW and reevaluated and redescribed previously named species.

Although truffle taxonomy and ecology has always been his primary interest, Trappe also understood early on the importance of forest fungi for tree growth, seedling survival, and forest ecosystem function. So in the 1970s and 1980s he focused much of the program's research on the ecology of mycorrhizal fungi and applying this knowledge to forestry practices, particularly reforestation. This research effort brought many graduate students to his tutelage and attracted other mycorrhizae scientists to OSU. The rapid growth of Trappe's mycology program put Corvallis on the mycological world map as a center of excellence. Indeed, visiting scholars from over 20 countries traveled to and trained in Corvallis, bringing new knowledge to the Corvallis group and taking home fresh ideas and techniques to apply in their research programs.

Trappe's pioneering contributions to truffle and mycorrhizal research included many firsts. In 1974, for example, he and J.W. Gerdemann published the first modern monograph of the Endogonaceae, a family containing the ancient group of mycorrhizal fungi that enabled the earliest land plants to exploit soil resources (Gerdemann and Trappe 1974). That monograph set the stage for countless taxonomic works on this important group of fungi. Trappe also wrote a comprehensive treatise on the application of mycorrhizae in forestry (Trappe 1977); it contains general principles on selecting beneficial mycorrhizal fungi for seedling inoculation that are still in use today. His active collaboration with Chris Maser in 1978 (Maser et al. 1978) documented the importance of truffles in the diets of many small forest mammals and dispersal of truffle fungi by these animals. Many truffle mycophagy studies ensued in the PNW and later in Australian forests, culminating in a book written with C. Maser and A.W. Claridge titled *Trees, Truffles, and Beasts: How Forests Function* (Maser et al. 2008) (see later section on truffle mycophagy).

Trappe began active collaboration with Australian colleagues in 1978 on truffle fungi that are mycorrhizal with *Eucalpytus*, and that collaboration continues today. Since 1978, Trappe has made over 20 visits to Australia to collect truffle specimens and conduct ecological studies. This collaboration has resulted in the discovery of hundreds of new species and dozens of genera. Australia is now recognized, along with the PNW, as one of the great epicenters for truffle evolution and diversity.

As a Forest Service employee, and later as an OSU forestry professor, Trappe developed and maintained strong working relationships with forest managers, hosting forest mycology workshops and lecturing around the region on the importance of forest fungi. In 1993, his expertise—along with others—was called upon to help develop a list of potentially rare and at-risk truffle fungi that needed protection under the Northwest Forest Plan (USDA and USDI 1994). That listing would become the first for truffles in the United States. Trappe was also instrumental in setting up the North American Truffling Society (NATS) that promotes truffle collection and education by its membership. He continues to act as the society's scientific advisor. Members of NATS have collected many new truffle species over the years throughout the PNW. Trappe's publication record is unparalleled in the fields of truffle and mycorrhiza science. He has described and named (with co-authors) a new order, two families, 35 new genera, 140 new species or varieties, and 130 new combinations of fungi, and that endeavor continues. He has also published some 200 papers on mycorrhizae.

Trappe retired from the Forest Service in 1985 and handed over the mycology program leadership to Randy Molina. Molina did his Ph.D. research under Trappe on host specificity of ectomycorrhizal fungi in the PNW, including many truffle fungi (Molina 1980). Molina led the Forest Mycology team until his retirement in 2007, and published over 100 papers on mycorrhizal symbioses, including seminal papers on host specificity (Molina et al. 1992), the truffle genus *Rhizopogon* (Molina et al. 1999), and conservation of rare forest fungi (Molina 2008). He also expanded the team's scope to include research on the ecology and management of the several wild, edible fungus species that had come to be commercially harvested. As an internationally recognized lead scientist in developing principles of conservation and management of wild fungi, Molina has left an indelible mark on the science and applications in these activities (Molina 2008, Molina et al. 2001, Raphael and Molina 2007).

Mike Castellano, another student and Forest Service employee in Trappe's group, did his dissertation on the truffle genus *Hysterangium* (Castellano 1988). Although Castellano also did pioneering work on the use of truffle spores to inoculate tree seedlings in nurseries (Castellano and Molina 1989), he has maintained his interest and expertise in truffle taxonomy and continues this tradition in Forest Service research. The last 20 years also witnessed an increased focus on the community ecology of truffle fungi from scientists such as Daniel Luoma (Luoma et al. 1991) and Jane Smith (Smith et al. 2002). Results from their studies and others are highlighted in the sections that follow on truffle ecology and silviculture.

Much additional taxonomic and ecological research on truffle fungi continues today in the Pacific Northwest. The foundation laid by past mycologists serves as an ever-increasing body of knowledge aided by new methods such as DNA analyses. Despite the regions's 100+ years of history in this discipline, new species are regularly being discovered and described. New insights regarding the relationships of truffles to their ancestors are being revealed, and research on their ecology, applications in forestry, and use as valuable food products have greatly expanded. This age of exploration is maturing, but it is far from over.

Evolution of the Hypogeous Habit

Darwinian Theory, Molecular Phylogenetics, and Plate Tectonics

The forms and distributions of today's truffle fungi are best understood via classical Darwinian theory as elaborated by molecular phylogenetics and plate tectonics. Vesicular-arbuscular mycorrhizae (VAM), or at least mycorrhiza-like structures, appear along with the first root-forming plants in the fossil record from some 460 million years ago (Redecker et al. 2000). The fungal spores associated with these fossils are remarkably similar to those of certain present-day fungi, including sporocarp-forming, hypogeous species such as *Glomus fasciculatum*. Random mutations occasionally alter a species genetically. The process of selection that follows in a given environment, however, is nonrandom. A mutated individual may be more fit or less fit to survive and compete in that environment, or the mutation may not alter its fitness there. The many, successful genera and species of today that have not been found in the fossil record attest that many mutations in VAM fungi have enabled diversification. Molecular phylogenies show these lineages and their relationships quite nicely, so that one can infer in general the successive mutants that proved fittest for survival (Schüssler et al. 2001).

It is surprising, however, that some spore types have been reproduced almost without morphological change over hundreds of millions of years to the present. Evolution's early experiments in spore morphology have succeeded in VAM fungi far better than one might expect, although the fossil evidence reveals nothing about physiological and ecological characteristics. Plate tectonics further evidence the success of these living but very active and successful "fossils." *Archeospora trappei, Glomus fasciculatum,* and *G. macrocarpum* or their minor morphological variants are associated with diverse plants in both Northern and Southern Hemispheres. As these fungi are dispersed by soil movement or transport by animals, one attractive hypothesis about how they came to be distributed from North America to Australia entails their early presence in the supercontinent Pangaea (pronounced "Pan-GAI-ah"): they are not adapted well to transport over large expanses of water. Pangaea separated into the northern Laurasia (including North America, Europe, and much of Asia) and the southern Gondwana (Africa, South America, Australia, Antarctica, and southeastern parts of Asia) continents some 200 million years ago (Hallam 1983, Olsen 1997). By that time, these ancient VAM fungi were likely widely distributed and accompanied their respective land masses in that stately, supercontinental separation. Subsequently, a similar breakup of Laurasia into Eurasia and North America and of Gondwana into Antarctica (which was subtropical and forested at the time), Africa, South America, Australia, and the Indian subcontinent provided the VAM fungi further isolated distributions. Not enough is known about the distribution of other, seldom collected fossil VAM fungi to speculate which had been present in the supercontinents and which evolved in what is essentially their present continents. However, some, such as the truffle-like *Acaulospora sporocarpia* of Southwestern United States deserts, may well be endemic products of relatively recent evolution.

The evolutionary story of ectomycorrhizal fungi is even more speculative. Most being fleshy and ephemeral, fruit-bodies of ectomycorrhizal fungi normally rot before they can fossilize. The earliest ectomycorrhizal fungi in the fossil record date back about 50 milliion years (Lepage et al. 1997), but plant families that are presently ectomycorrhizal show up in the fossil record 150 to 200 million years ago. Some distinctive truffle fungi with unique structures such as the complex peridium of the *Elaphomyces granulatus* group occur on both Laurasian and Gondwanan continents, e.g., Australia and North America. Hypothetically, the early common ancestors of these could have evolved and spread widely in Pangaea before its breakup. The genus *Tuber*, in contrast, is native only to the Northern hemisphere, so its ancestors seem likely to have originated in Laurasia after the Pangaean separation and did not evolve in Gondawana. At the other end of the evolutionary scale are narrowly endemic genera, several of which are confined to the Pacific Northwest, for example *Sedecula*. Table 3 shows the truffle genera of the PNW by overall present range; worldwide can be inferred to mean hypothetically evolved from Pangaean ancestors, hence the most ancient lineages; Northern Hemisphere from Laurasian ancestors, North American from American ancestors, and Pacific Northwestern from regional ancestors, accordingly the most recent lineages. This is an oversimplification of complex processes, but it is a general hypothesis that can be tested by molecular methods such as the molecular clock hypothesis and dispersal-vicariance analysis (Ronquist 1997, Tajima 1993).

The molecular evidence indicates that, with some exceptions, truffles have been derived from mushroom ancestors. Many species have a morphology intermediate between truffles and mushrooms. They may have a vestigial stem, not enough to lift them out of the ground, a cap that does not open to expose the gills, and the gills may be crowded and distorted or even replaced by chambers (fig. 11). Such fruit-bodies have been referred to as "secotioid" in reference to the genus *Secotium*, which displays these modifications (Singer 1958). A further evolution to hypogeous morphology is represented by loss of cap and stem, the latter being reduced to a columella, i.e., a "little column," through the center of a now-rounded fruit-body that is enclosed by an outer skin. Finally, as evolution trends toward economy to improve fitness, the vestigial stem or columella is lost, having been left over from mushroom ancestry but no longer functional (fig. 11). Bruns et al. (1989) documented that such morphological divergence (from mushroom to truffle) can proceed relatively rapidly, possibly as a result of selective pressures on a small number of developmental genes.

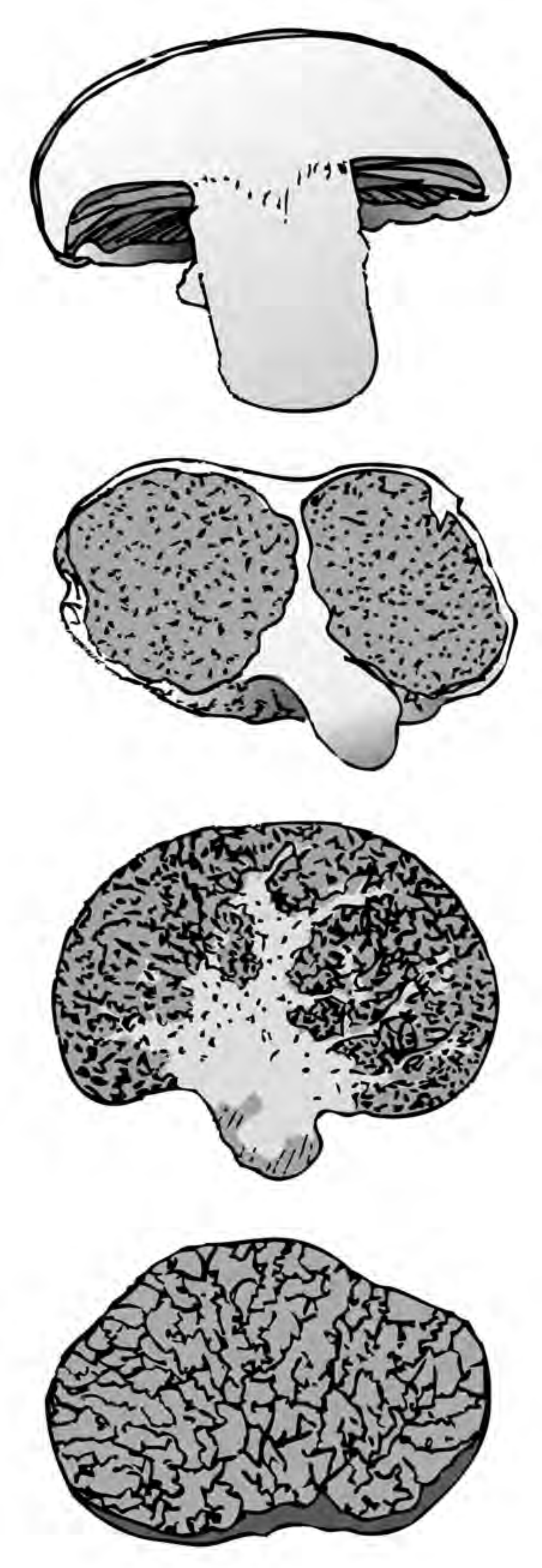


Illustration by Gretchen Bracher

Figure 11—Evolution of the hypogeous truffle morphology. From top to bottom, the original mushroom shape is lost as the cap and stipe become reduced until finally the reproductive tissue is completely enclosed.

Table 3—Evolutionary origins of Pacific Northwestern hypogeous fungal genera and genera with only some hypogeous species as inferred from present distributions

Present distribution and inferred origin	Genera by class (Ascomycota, Basidiomycota, Glomeromycota, Zygomycota)
Worldwide (Pangaea)	Ascomycota: *Elaphomyces*, *Genea*, *Hydnoplicata*
	Basidiomycota: *Arcangeliella*, *Cystangium*, *Endoptychum*, *Gastroboletus*, *Gautieria*, *Gymnomyces*, *Hymenogaster*, *Hysterangium*, *Leucogaster*, *Macowanites*, *Nivatogastrium*, *Octaviania*, *Radiigera*, *Scleroderma*, *Secotium*, *Thaxterogaster*, *Weraroa*
	Glomeromycota: *Glomus*
	Zygomycota: *Endogone*
Northern Hemisphere (Laurasia)	Ascomycota: *Balsamia*, *Choiromyces*, *Fischerula*, *Genabea*, *Geopora*, *Hydnobolites*, *Hydnotrya*, *Leucangium*, *Pachyphloeus*, *Stephensia*, *Tuber*
	Basidiomycota: *Alpova*, *Chamonixia*, *Melanogaster*, *Pyrenogaster*, *Rhizopogon*
Western North America	Basidiomycota: *Brauniellula*, *Mycolevis*, *Trappea*, *Truncocolumella*
Pacific Coastal North America	Ascomycota: *Cazia*, *Hydnotryopsis*
	Basidiomycota: *Gastrosuillus*
Pacific Northwestern North America	Ascomycota: *Barssia*, *Destuntzia*
	Basidiomycota: *Fevansia*, *Kjeldsenia*, *Sedecula*

Note: The narrower the present distribution, the more recently the genus has evolved.

We can't know the specific habitat where truffles first evolved, but we can infer some of the selection pressures that increased the fitness of hypogeous-fruiting mutants of mushrooms. To do that on a broad scale, we can look to the continent that has the greatest diversity of truffles: Australia, estimated to have about a third of the world's species (Mueller et al. 2007). Australia epitomizes the evolution of organisms specially adapated to ancient, much-leached soils and hot, dry seasons (Flannery 1995). Most truffles and truffle-like fungi form ectomycorrhizae with trees, and the ectomycorrhizal genus *Eucalyptus* has diversified to occupy all but the most arid parts of Australia. Even *Eucalyptus* rain forests are subject to seasonal or periodic drought. During soil-wetting rainy times, truffles form and mushrooms emerge to discharge their spores. It often happens, however, that the storms that wetted the soil are soon followed by dry, warm, and often windy weather. Emergent mushrooms are caught dead in their tracks, as it were. Having little structural defense against desiccation, they may shrivel and die before their spores have matured. The hypogeous fruiters, meanwhile, insulated from heating and drying in the cool, moist soil, continue to mature their spores (Claridge and Trappe 2005, Maser et al. 2008).

Similar conditions prevail in much of western North America, including the Pacific Northwest, which also has a great diversity of truffles. Thiers (1984b) proposed that in the Mediterranean and semiarid climates of the Western United States, high summer temperatures combined with extended drought stress were primary drivers in the evolution of hypogeous fruit-body formation (i.e., the truffle form). Kretzer and Bruns (1997) found that secotioid forms derived from the important ectomycorrhizal mushroom genus *Suillus* evolved at least twice and have persisted for evolutionarily significant times over a wide range of summer-dry habitats in the Western United States. But other selection pressures can also be at play. In the Cascade Mountains and east, hard frosts or snow are common soon after the summer and autumn dry seasons. Mushrooms may get frozen before they can mature spores, but the insulation provided by soil and leaf litter under which truffles nestle enables them to continue maturing.

On a more local scale, in their study of effects of gaps created in a contiguous forest, Luoma et al. (2004) presented the first experimental evidence to support Thiers' hypothesis. Even gaps of only 1 ha significantly reduced fall production of ectomycorrhizal mushrooms in the surrounding uncut forest. Those same gaps, however, did not significantly reduce truffle production. The formation of gaps likely influenced the thermal properties, humidity, and evapotranspiration of the remaining intact forest (Zheng and Chen 2000). Luoma and Eberhart (2005) extended Thiers' hypothesis to encompass the influence of fire in the broader context of forest disturbance in the summer-dry climates of the Western United States. Fire is an important agent for producing the patterns of forest fragmentation (Heyerdahl et al. 2001) that would select for hypogeous fruit-body production via the "secotioid syndrome," i.e., the evolution of epigeous fruiting to hypogeous fruiting patterns.

However, even in places with mild, moist climates, such as the coastal fog belt of northern California, Oregon, and Washington, truffles flourish. Hibbett et al. (1994) presented a case in which a simple secotioid phenotype, arising from a mutation at one locus, has persisted over a wide geographic range in wet environments that do not exert the selective pressures that drive the secotioid syndrome toward evolution of more strongly traditional truffle morphology. Baura et al. (1992) speculated that such mutations will not persist long in a population. That might be the case if the hypogeous habit improved fitness only by protecting the fungus from vagaries of weather. Because truffle speciation through mutation has succeeded in the coastal fog belt of the PNW and the wet forests of New Zealand, for example, other factors might enhance the fitness of truffle fungi. One of these is likely the effectiveness of spore dispersal through mycophagy (fungus eating) (Maser et al. 2008). Aerial dispersal of spores discharged from mushrooms is not necessarily the most effective means of spore dispersal. Under usual circumstances of mushrooms fruiting in forests, the great majority of spores alight on the ground directly under the mushroom, and most of the others come to rest on the soil within a few meters (Allen et al. 1999). Some of those that do get carried farther may land in lakes or on rocks or rooftops, never to contact a rootlet to form mycorrhizae. Spores in fecal pellets of mycophagists, in contrast, will nearly always be deposited in habitats similar to where the mycophagist ate the truffles, because that is where the mycophagists live. Moreover, those spores will be concentrated in the fecal pellets and hence in great numbers where they are weathered into the soil and root zone of host trees (Maser et al. 2008). Of course, mushroom spores also are carried into the soil by water, but except for under the parent mushroom they are much diluted. So the truffles go for limited but concentrated dispersal sites, the mushrooms for widespread but diluted deposits. Clearly, both strategies succeed well in the big picture.

In evolving to a hypogeous habit where their fitness and chances of producing spores are increased, truffles must also evolve a means of attracting animal mycophagists. The answer to this challenge is the production of aromas. We can only speculate on the multitude of mutational events that failed before a given species produced a truffle morphology along with successful biochemical pathways for attractants. The animals, in turn, had to adapt to locating, extracting, and using the truffle resource effectively. Many would already have evolved to detect food sources in the soil. Some evolved even further to specialize as truffle mycophagists. A good example in North America is the coastal subspecies of the California redbacked vole (*Clethrionomys californicus*) that is native to the fog belt of the northern California and Oregon coasts. It seems to exemplify a true coevolution with truffles. It spends most of its time belowground, apparently tunneling from one truffle to the next. It has fragile teeth that, unlike those of most rodents, do not grow continually, so it must eat only nonabrasive foods or its teeth will wear out. Its diet consists exclusively of truffles or occasional hair lichens that blow from tree crowns to the ground during storms (Ure and Maser 1982). And its habitat is confined to places with high rainfall and summer fog drip, one of the few regions of the world that produce truffles throughout the year. We explore truffles and animal mycophagy in more detail later.

Diversity of Hypogeous Fungi in the Pacific Northwest

Trappe (in Mueller et al. 2007) estimated that 4,500 to 5,500 species of truffle fungi, all but a few being hypogeous, presently exist worldwide. About 1,200 of these occur in North America (Mueller et al. 2007), and about 350 named species are accepted for the PNW (table 1). Perhaps as many remain to be found and described. In any event, such estimates cannot be taken literally, for several reasons. Many habitats remain to be explored, and many of those where mycologists have collected truffle fungi have been visited only once. Another problem lies in the difficulty of identifying many species by morphology alone, because as a given species passes through developmental stages from juvenile to senescent, it may change in several ways, such as color, size, odor, or spore onrnamentation, as it matures. In that instance, a single species may have been given more than one name. On the other hand, because of morphological similarities between some species, more than one species may have been classified under a single name (Bidartondo and Bruns 2002). Analyses of DNA have been valuable in resolving such ambiguities.

Naming Fungi

The names of some truffles in table 1 will be changed from what may have been familiar names to some readers. People tend to feel comfortable with the familiar, so name changes by taxonomists often annoy and even cause disdain or outright resistance from people used to an earlier name. This problem has intensified with the advent of molecular phylogeny, which reveals that relationships between species, genera, and families are not always as obvious as suggested by morphology alone. Roughly a century ago, botanists recognized that as additional evidence accumulated over time, some species turned out to have been named more than once, and that some early species concepts actually embodied more than one species. Codes were devised to deal with these conflicting names in an orderly manner, and eventually these codes were amalgamated into what is now called the International Code of Botanical Nomenclature. It is periodically updated and amended by International Botanical Congresses, and the updated code is posted on the Web. The most recent one is termed the "Vienna" Code (http://ibot.sav.sk/icbn/main.htm) from the Vienna Congress of 2005.

The code also establishes the "principle of priority," by which the first validly published name bestowed on a species, genus, or family has priority over later names applied to that same species or group. This may seem simple, but it can take many twists and turns over the years, all of which the code attempts to anticipate. Readers interested in these processes can browse the code's Web site to get a feel for such complications.

The tale of the genus *Schenella* exemplifies the convoluted naming history undergone by many fungi over the years. Mycological detective work is often needed to sort out the identity of fungi described long before electron microscopy and DNA analysis became available tools in mycological research. The *Schenella* mystery stems from the character of its mature sporocarp, which has a thick peridium enclosing a powdery spore mass loosely held by intertwining hyphae. Small mammals eat the peridium but discard the spore powder, which then can be dispersed by wind; *Radiigera, Elaphomyces*, and several Australian truffle genera have a similar mode of spore dispersal (Maser et al. 2008). Squirrels that collect these often take them to eat on a log or stump or up in a tree, where they discard the spore powder after consuming the peridium (Trappe and Maser 1977). Here is a chronology of the Schenella saga.

> **1911**: Early in the 20th century, Thomas Macbride, a specialist on slime molds, examined a clump of spores and hyphae found on a log in Yosemite Valley, California. He judged it to be a possibly undescribed genus and species of slime mold, which he published as *Schenella simplex*. However, he expressed uncertainty about it actually being a slime mold. This fungus received little attention over ensuing decades.
>
> **1944**: S.M. Zeller collected an unusual hypogeous puffball in Oregon with a thick peridium and powdery spore mass. He named it *Radiigera atrogleba* and described two other new *Radiigera* species as well, one of which (*R. fuscogleba*) being designated as the type of the genus.
>
> **1977**: Malençon and Riousset reported another unusual, hypogeous puffball, which they named *Pyrenogaster pityophylus*. It appeared to be related to *Radiigera* but differed in its spore-bearing structures.
>
> **1996**: Dominguez de Toledo and Castellano discovered that *Radiigera atrogleba* really belonged in *Pyrenogaster* and appropriately transferred the species to that genus, resulting in the new name *Pyrenogaster atrogleba*. Neither Zeller, Malençon and Riousset, nor Dominguez de Toledo and Castellano had any reason to equate these thick-skinned puffballs with slime molds.
>
> **2005**: Arturo Estrada-Torres and his students collected what seemed to be the slime mold *Schenella simplex* in Mexico. It was lying loose on logs or conifer needles or mosses. Some of the collections had fragments of a thick peridium, and some fragments that were not fully mature had structures identical to those of the genus *Pyrenogaster*. This alerted Estrada-Torres to the probability that *Schenella* was not a slime mold at all. Later *Pyrenogaster atrogleba* was found intact at a site where *Schinella simplex* had been collected, and since then it has been found to be common in similar Mexican forests (Estrada-Torres and Trappe, unpublished data). The Mexican sporocarps, fragments of sporocarps, and powdery

masses of spores were compared to the original "slime mold" *S. simplex* from Yosemite in great detail by light and electron microscopy and DNA analysis. All were found to be identical (Estrada-Torres et al. 2005). Hence the name *Pyrenogaster atrogleba* (formerly *Radiigera atrogleba*) gave way to its original name *Schenella simplex*, which was moved from the slime molds to the puffballs. *Pyrenogaster pityophilus* joined it under the name *Schenella pityophilus.*

2006. Hosaka et al. awarded *Schenella* (as *Pyrenogaster*) its own family as a result of molecular phylogenetic studies. Now, however, it must be Schenellaceae, rather than Pyrenogastraceae.

Given the careful studies of Estrada-Torres and his colleagues, the confusing history of these fungi has finally been straightened out. Those used to the previously coined names may find this annoying, but the first name validly applied to an organism is the correct one, according to the International Code of Botanical Nomenclature. It's rather like the name Robert given to an infant. He may later be called Bob, Bobby, Rob, Red, or Shorty, but Robert takes priority in all matters of legal identification.

Species Richness in Relation to Habitat and Mycorrhizal Hosts

The richness of truffles lavished upon the Pacific Northwest, which contains more known species than all of Europe, seems related to its geologic history and great diversity of habitats, ectomycorrhizal hosts, and mycophagous animals. Most of North America's mountain ranges run north and south. This allowed organisms to migrate north and south as the ice age cold periods waxed and waned in alternation with the interglacial warm periods. In Europe, major mountain ranges—the Pyrenees, Alps, Carpathians, and Caucasus—trend east and west. During advance of the glaciers, populations of organisms north of these ranges could be driven to extinction by climatic conditions too extreme for their survival, their southward migration thwarted by the mountains. During interglacial warming periods, the organisms south of the mountains faced formidable barriers to northward migration. These phenomena would particularly affect movement of truffle fungi, which depend on animal mycophagy for spore dispersal. The result can be seen today in Italy, which contains many species and several genera not found in areas with similar current climates on the northern side of the Alps.

In the Pacific Northwest, the Klamath Mountains of northern California and southwestern Oregon appear to have served as a refugium for many organisms during the ice ages. Although not very high compared to the Cascades and Sierras, they have enough topographic and edaphic variation to include a huge diversity of habitats. Today they combine elements of northern and southern truffle populations, including numerous species that are rare or absent to the north and others that are rare or absent to the south.

The coasts of Washington, Oregon, and northern California, the Coast Ranges, and the Cascades also contribute to habitat diversity and thus to truffle diversity. The coastal fog belt, with its spruce-hemlock wet forests, has a relatively low diversity but contains some species, such as *Macowanites chlorinosmus*, known only from that habitat. In the Coast Ranges to the east, Douglas-fir becomes more common and truffle diversity increases with increases of elevational variation and added host species: many *Rhizopogon* species associate only with Douglas-fir. Additional host species appear in subalpine and treeline habitats in the Cascade Mountains to the east. There, pines (*Pinus* spp.), true firs (*Abies* spp.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) are more prominent forest components, and each has its own specific truffle associates: numerous *Rhizopogon* species specific to pines; *Thaxterogaster pinguis*, *Gymnomyces abietis*, and *Rhizopogon subsalmonius* to true firs; and *Gastroboletus ruber* to mountain hemlock. Still farther east, increasingly drier habitats prevail in the rainshadow of the Cascades. The genus *Rhizopogon* diversifies particularly in pine forests, and genera rarely known from west of the Cascades appear, for example, *Mycolevis*.

Much of this overall truffle diversity would not likely have evolved without the co-evolution and adaptation of animal mycophagists to disperse spores. From mites and millipedes to slugs, rodents, deer, and bear, the dispersers contribute to the success of truffle fungi around the world.

Diversity by Taxonomic Groups

Of the six phyla currently recognized in Kingdom Fungi (Blackwell et al. 2006), four (67 percent) contain truffle fungi in the Pacific Northwest, as do 5 of the approximately 26 classes (19 percent), and 11 of the approximately 129 orders (9 percent). Only 31 of the hundreds of families and 50 of the many hundreds of genera have truffle-like sporocarps. These numbers indicate that truffle taxa occur broadly across the higher taxonomic ranks, but within those, the lower the rank the less common the habit. The same pattern occurs with mycorrhizal fungi: except for a few species in the genus *Endogone* plus the genus *Nivatogastrium* in the Strophariaceae and the three families in the order Geastrales, the truffle fungi are mycorrhiza formers. Moreover, except for the Glomeromycetes, which form vesicular-arbuscular mycorrhizae, the great majority of truffle species form ectomycorrhizae. All this informs us that mycorrhiza formation and the hypogeous habit have evolved in most of the phyla but in only a relatively few orders and families within the Kingdom Fungi. Why natural selection operated in this way is unknown, but future molecular and phylogenetic research may clarify our understanding of the evolutionary pathways.

The 4 phyla, 5 classes, 7 subclasses, 11 orders, 31 families, and 57 genera of truffle members of Kingdom Fungi in the Pacific Northwest are outlined below. Proper placement of two genera, *Fevansia* and *Protogautieria,* is currently uncertain, so "(?)" follows those names. Pacific Northwestern members currently assigned to the genus *Hymenogaster* actually belong to two different families, according to the molecular data (Peintner et al. 2001). *Hymenogaster sublilacinus* is related to the mushroom genus *Cortinarius* in the Cortinariaceae, the other *Hymenogaster* spp. to the mushroom genus *Hebeloma* in the Hymenogastraceae. Until the infrageneric relationships of the huge genus *Cortinarius* are sorted out by further molecular scrutiny, name changes are premature. Accordingly, *Hymenogaster* appears twice in the listing: once in the Cortinariaceae for *H. sublilacinus* and once in the Hymenogastraceae for other *Hymenogaster* spp.

- Phylum Glomeromycota (Redecker and Raab 2006)
  - Class Glomeromycetes
    - Subclass Glomeromycetidae
      - Order Glomerales
        - Family Glomeraceae
          - Genus *Glomus*

- Phylum Zygomycota (White et al. 2006)
  - Class Mucoromycetes
    - Subclass Mucoromycetidae
      - Order Endogonales
        - Family Endogonaceae
          - Genus *Endogone*
          - Genus *Youngiomyces*

- Phylum Ascomycota
  - Class Eurotiomycetes (Lumbach and Huhndorf 2007)
    - Subclass Eurotiomycetidae
      - Order Eurotiales
        - Family Elaphomycetaceae
          - Genus *Elaphomyces*

- Class Pezizomycetes (Hansen and Pfister 2006)
  - Subclass Pezizomycetidae
    - Order Pezizales
      - Family Discinaceae
        - Genus *Hydnotrya*
      - Family Helvellaceae
        - Genus *Balsamia*
        - Genus *Barssia*
      - Family Morchellaceae
        - Genus *Fischerula*
        - Genus *Leucangium*
      - Family Pezizaceae
        - Genus *Cazia*
        - Genus *Hydnobolites*
        - Genus *Hydnotryopsis*
        - Genus *Pachyphloeus*
        - Genus *Peziza*
      - Family Pyronemataceae
        - Genus *Genabea*
        - Genus *Genea*
        - Genus *Geopora*
        - Genus *Gilkeya*
        - Genus *Stephensia*
      - Family Tuberaceae
        - Genus *Choiromyces*
        - Genus *Tuber*

- Phylum Basidiomycota
  - Class Agaricomycetes
    - Subclass Agaricomycetidae
      - Order Agaricales (Hibbett 2006, Matheny et al. 2006)
        - Family Agaricaceae
          - Genus *Agaricus*
        - Family Cortinariaceae
          - Genus *Cortinarius*
          - Genus *Hymenogaster*
          - Genus *Protoglossum*
          - Genus *Thaxterogaster*
        - Family Hymenogastraceae
          - Genus *Hymenogaster*

- Family Strophariaceae
  - Genus *Nivatogastrium*
- Family Tricholomataceae
  - Genus *Amogaster*

- Order Boletales (Binder and Hibbett 2006)
  - Family Boletaceae
    - Genus *Alpova*
    - Genus *Chamonixia*
    - Genus *Fevansia* (?)
    - Genus *Gastroboletus*
    - Genus *Octaviania*
  - Family Gomphidiaceae
    - Genus *Brauniellula*
    - Genus *Chroogomphus*
    - Genus *Gomphogaster*
  - Family Paxillaceae
    - Genus *Melanogaster*
  - Family Rhizopogonaceae
    - Genus *Rhizopogon*
  - Family Sclerodermataceae
    - Genus *Scleroderma*
  - Family Suillaceae
    - Genus *Gastrosuillus*
    - Genus *Truncocolumella*

- Subclass Phallomycetidae (Hibbett 2006, Hosaka et al. 2006)
  - Order Geastrales
    - Family Geastraceae
      - Genus *Radiigera*
    - Family Schenellaceae
      - Genus *Schenella*
    - Family Sclerogastraceae
      - Genus *Sclerogaster*
  - Order Gomphales
    - Family Gautieriaceae
      - Genus *Gautieria*
    - Family Gomphaceae
      - Genus *Destuntzia*
      - Genus *Protogautieria* (?)
  - Order Hysterangiales
    - Family Hysterangiaceae
      - Genus *Hysterangium*

- Order Phallales
  - Family Claustulaceae
    - Genus *Kjeldsenia*
  - Family Trappeaceae
    - Genus *Trappea*

Subclass uncertain

- Order Russulales (Miller et al. 2006)
  - Family Albatrellaceae
    - Genus *Leucogaster*
    - Genus *Leucophleps*
    - Genus *Mycolevis*
  - Family Russulaceae
    - Genus *Arcangeliella*
    - Genus *Cystangium*
    - Genus *Gastrolactarius*
    - Genus *Gymnomyces*
    - Genus *Macowanites*

Descriptions of Truffle Genera

Many characters are used to describe fungal genera. Below we focus on key aspects of fruit-body shape and size, peridium (the outer skin of a truffle), gleba (the inner, spore-bearing tissue), odor, spores, and reactions to Melzer's reagent (an iodine solution that produces diagnostically useful orange to red, purple, blue, or green coloration on spores or tissues of species of certain genera). We also note distribution and available keys to identify Pacific Northwestern species and provide photographs of a representative species for each genus when available. Photos of additional species are provided on the accompanying CD-ROM. Readers interested in European species in the same genera as found in the Pacific Northwest will find Montecchi and Sarasini (2000) to be the most complete and best illustrated treatment presently available; although its title is in Italian, the text is in both Italian and English.

Agaricus (Phylum Basidiomycota, Order Agaricales, Family Agaricaceae) (fig. 12)

Name derivation: Greek *agarikon*, "a mushroom."

Fruit-bodies of hypogeous species 2–10 cm tall, 1–7 cm broad, with a cap and short stem, the cap center typically depressed and the cap edges turned under to connect with the stem. **Peridium** white to pale tan, becoming brown at maturity, dry, obscurely fibrillose to slightly scaly. **Gleba** with contorted and anastomosed gills, which become black and powdery from spores by maturity. **Odor** not distinctive to somewhat pungent-acrid by senescence. **Spores (for *Agaricus inapertus* only)** ellipsoid, 6–10 × 5–8 µm, smooth, dark brown from a pigmented middle layer sandwiched between two colorless layers, lacking an apical pore, with a short, straight to angled point of attachment. **Reaction to Melzer's reagent** not distinctive.

Number of species: *A. inapertus* is the only North American hypogeous representative of this otherwise large mushroom genus.

Distribution: *Agaricus inapertus* occurs from middle to high elevations in mountains of the Pacific Northwestern United States in forests of Pinaceae. Several other hypogeous *Agaricus* species are known from Australia.

James Trappe

Figure 12—*Agaricus inapertus*.

Season: Late summer and autumn.

Keys and descriptions: Singer and Smith (1958b) described A. *inapertus* as *Endoptychum depressum*.

Comments: *Agaricus inapertus* was originially named *Endoptychum depressum*. DNA evidence, however, shows that it relates to the genus *Agaricus*, whereas the type species for *Endoptychum* relates to the mushroom genus *Chlorophyllum*. Accordingly, the species was moved to *Agaricus*, but because the species name *depressum* was already occupied in *Agaricus*, Vellinga et al. (2003) coined the new name *A. inapertus*. The three-layered spore wall of *A. inapertus* is distinctive for truffle-like fungi in north temperate forests.

Alpova (Phylum Basidiomycota, Order Boletales, Family Boletaceae) (fig. 13)

Michael Castellano

Figure 13—*Alpova diplophloeus*.

Name derivation: Named by Dodge (1931) in honor of Dr. Alfred H. Povah of the Isle Royale Lake Superior Survey, the collector of the specimens on which the new genus was based.

Fruit-bodies globose to slightly irregular, rarely exceeding 2.5 cm broad. **Peridium** yellow to reddish brown, often with large rounded cells and clamp connections. **Gleba** yellow to ochraceous in youth, in some staining reddish brown when exposed, later darkening to brown, gelatinous and sticky to the touch, the spores being borne in a gelatinous matrix that fills the chambers that are walled off by meandering veins. **Odor** fruity to unpleasant. **Spores** mostly longitudinally symmetrical and cylindrical to fusoid, 4–10 × 2–5 µm, smooth, colorless to pale brownish yellow, the walls ± 0.5 µm thick, the attachment straight, inconspicuously cupped; spores that are individually colorless are often yellow to brownish yellow in mass. **Reaction to Melzer's reagent** not distinctive, or in some species spores yellow to orange or brown.

Number of species: Three have been described from north temperate forests.

Distribution: Greenland, northern South America, North America, and Europe in lowland to montane forests. Most species are obligate associates of *Alnus* spp. (Clemençon 1977; Molina 1979, 1980, 1981; Trappe 1975c).

Season: Spring through autumn.

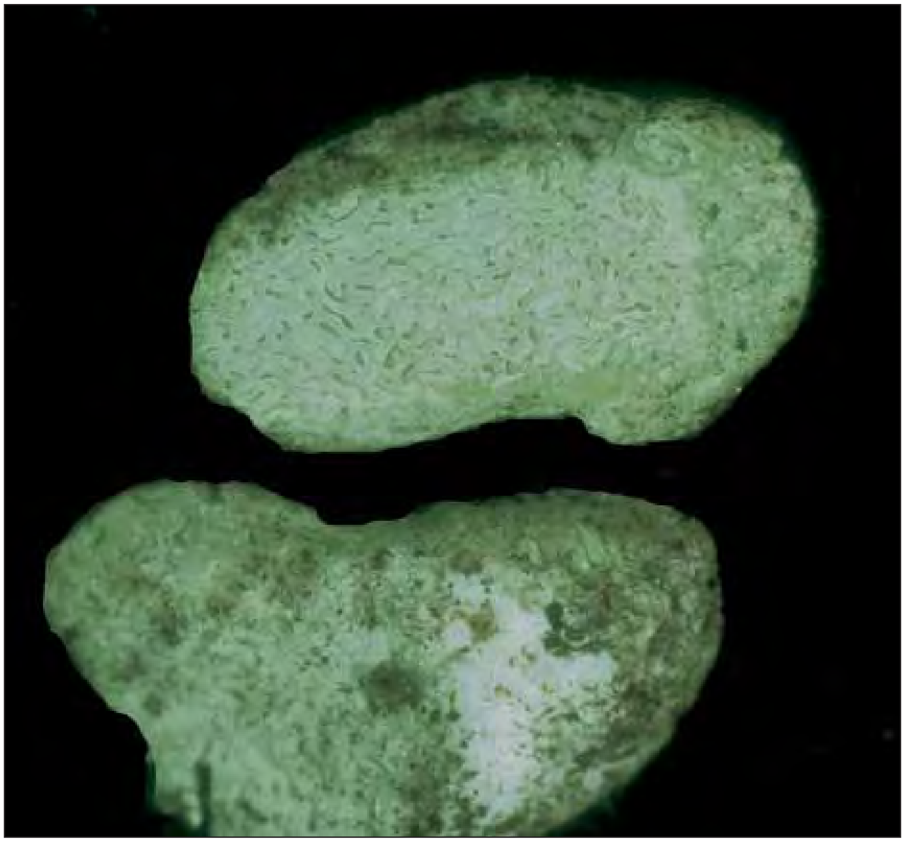
Keys and descriptions: Several species in the monograph by Trappe (1975c) are now more correctly placed in *Rhizopogon* on the basis of molecular evidence. Fogel (1977a) emended the monograph and renamed one species. M. Trappe et al. (2007) described and illustrated *A. diplophloeus* and *A. trappei*. *Alpova alexsmithii* and *A. olivaceotinctus* as described and illustrated by Castellano et al. (1999) belong in *Rhizopogon*.

Comments: Molecular data indicate that most of the present *Alpova* species need transferring to *Rhizopogon*. In the PNW, *Alpova diplophloeus* is strictly an *Alnus* associate. Spores of *Gastroboletus*, *Trappea*, and *Truncocolumella* spp. are similar, so other characters must be used to separate *Alpova* from these genera.

Amogaster (Phylum Basidiomycota, Order Agaricales, Family Tricholomataceae) (fig. 14)

Name derivation: Coined by Castellano (1995) in honor of Dr. Michael P. "Amo" Amaranthus, collector of the holotype, plus Greek, -*gaster* (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs), hence "Amo's puffball."

Fruit-bodies subglobose to irregular, 1.25 × 0.75 cm. **Peridium** thin, composed of loosely interwoven nearly parallel hyphae, white to pale green. **Gleba** pale green when fresh, pale to medium yellow when dried, composed of multiple empty chambers. Columella small, cartilaginous, dendroid when fresh, becoming indistinct when dried. **Odor** not distinct. **Spores** ellipsoid, subglobose, to subfusiform, 9–14 (-15) × 4–6 µm, the apex blunt, smooth; walls up to 0.5 µm thick, pale yellowish brown; sterigmal attachment present. **Reaction to Melzer's reagent:** spores orange to deep orange-brown.



Herb Saylor

Figure 14—*Amogaster viridigleba*.

Number of species: One described from north temperate forests, *Amogaster viridigleba*.

Distribution: Under Pinaceae and *Populus* spp. in the Californian Sierra Nevada and under *Pseudotsuga menziesii* in the Cascade Mountains of southwest Oregon.

Season: June.

Keys and descriptions: Castellano (1995).

Comments: Resembles *Rhizopogon* but differs from it in spore characteristics. *Amogaster* spores are larger than those of all but a very few *Rhizopogon* spp., asymmetrical, and turn orange to orange brown in Melzer's reagent. The gleba of *Amogaster* lacks olive or brown hues, which are common in *Rhizopogon* fruit-bodies (Castellano 1995).

Arcangeliella (Phylum Basidiomycota, Order Russulales, Family Russulaceae) (fig. 15)

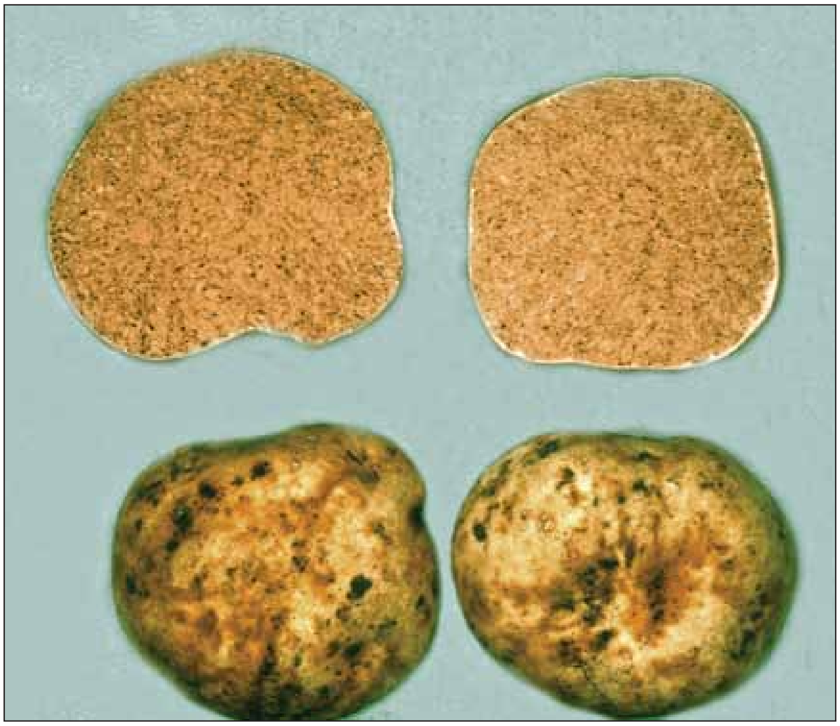


Figure 15—*Arcangeliella scissilis*.

Name derivation: Named by Cavara (1910) in honor of the Italian botanist G. Arcangeli. The species in this genus had been placed in the genus *Zelleromyces* by Singer and Smith (1960), but Cavara's *Arcangeliella* is the earlier name.

Fruit-bodies globose to ellipsoid or irregular, up to 6 cm broad. **Peridium** generally smooth, white to cream color, yellow, orange, or reddish brown. **Gleba** white to orange or brown, when moist exudes a watery to white, yellow or orange latex from cut surfaces. **Spores** globose to ellipsoid, up to 15 μm broad excluding the ornamentation of spines or a reticulum. **Reaction to Melzer's reagent:** spore ornamentation purple to black, either entirely or in spots; the most common species in the Pacific Northwest, *Arcangeliella scissilis*, has only infrequent and inconspicuous black spots on its spores.

Number of species: Ten from north temperate forests, eight described and two undescribed.

Distribution: Ectomycorrhizal forests of conifers and hardwoods in Europe, North America, Australia, and Asia.

Season: Autumn and early winter.

Keys and descriptions: Past authors treated *Arcangeliella* spp. as *Zelleromyces* spp. Singer and Smith (1960) covered most described species; M. Trappe et al. (2007) described and illustrated two species; Pegler and Young (1979) and Miller (1988) described and illustrated representative spores.

Comments: *Arcangeliella* is the stemless truffle genus that, along with the stemmed truffle genus *Gastrolactarius,* is derived from the mushroom genus *Lactarius.* These three genera produce a latex from specialized, latex-bearing hyphae and have a similar array of spiny to reticulate spore ornamentation that turns purple to black in Melzer's reagent. Formerly known as *Zelleromyces,* its name was corrected to *Arcangeliella* by Vidal (2004), who also transferred species formerly placed in *Arcangeliella* to the new genus *Gastrolactarius.* This may seem confusing, but it corrects errors made by earlier taxonomists.

Balsamia (Phylum Ascomycota, Order Pezizales, Family Helvellaceae) (fig. 16)


Matthew Trappe

Figure 16—*Balsamia nigrens*.

Name derivation: Coined by Vittadini (1831) in honor of the 19th-century Italian botanist Giuseppi Balsamo.

Fruit-bodies subglobose to irregular, with a basal or lateral cavity, 1–4 cm broad. **Peridium** verrucose, the warts small and rounded to prominent and angular, brown to orange brown or black, usually with a basal tuft of mycelium. **Gleba** solid, white to pale yellow, with narrow, meandering, open or hypha-stuffed veins or labyrinthine chambers that generally radiate from the fruit-body cavity. **Odor** not distinctive to pungent or garlicky. **Spores** borne in cylindric to ellipsoid asci, ellipsoid to subcylindric, 13–42 × 10–21 µm, smooth or, in one species, with nearly submicroscopic peripheral lines, colorless, the walls thin to ± 1 µm thick. **Reaction to Melzer's reagent** not distinctive.

Number of species: Five have been reported from north temperate forests.

Distribution: Common in the Northern Hemisphere in association with Pinaceae and Fagaceae; infrequent to rare.

Season: Spring, summer, and autumn.

Keys and descriptions: Trappe (1979) described the genus as a whole and illustrated a spore of *B. alba*. Gilkey (1954a) monographed the American species (as two genera, *Balsamia* and *Pseudobalsamia*); Castellano et al. (1999) and M. Trappe et al. (2007) each described and illustrated two Pacific Northwestern species.

Comments: Some North American species have been regarded as the same as some European species, but molecular studies are needed to confirm that this is indeed the case. **Spores** of some *Balsamia* spp. are difficult to differentiate from those of *Barssia* and *Geopora* species. *Barssia* occurs only in spring and early summer, so it is eliminated from consideration of autumn or winter specimens. *Geopora* species have spore walls ± 1 µm thick, rather thicker than those of most *Balsamia* species.

Barssia (Phylum Ascomycota, Order Pezizles, Family Helvellaceae) (fig. 17)


Matthew Trappe

Figure 17—*Barssia oregonensis*.

Name derivation: Coined by Gilkey (1925) in honor of the Oregon botanist who first collected the genus, Professor H.P. Barss.

Fruit-bodies subglobose to irregular with a basal or lateral cavity or numerous, scattered pits, 1-4 cm broad. **Peridium** smooth, pink to pinkish brown or orange brown. **Gleba** white, solid except for narrow veins that emerge at the fruit-body cavity or pits. **Odor** not distinctive. **Spores** borne in cylindric to narrowly clavate asci, oblong, 24–36 × 12–21 µm, smooth, colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: Three are known from north temperate forests, one of these undescribed.

Distribution: *Barssia oregonensis* is associated with *Pseudotsuga menziesii* in Pacific Northwestern North America. *Barssia yezo-montana* is known from only one collection in Japan, and an undescribed species has been collected once under *Quercus* spp. near San Francisco, California.

Season: Spring and summer.

Keys and descriptions: *Barssia* is described by Trappe (1979); *B. oregonensis* is described by Gilkey (1925, 1954b) and M. Trappe et al. (2007).

Comments: *Barssia oregonensis* is among the more common spring truffles in the Pacific Northwest. Its delicate pinkish color and smooth, clean surface are particularly attractive, and its cavity distinguishes it from *Tuber* spp. of the region.

Brauniellula (Phylum Basidiomycota, Order Boletales, Family Gomphidiaceae) (fig. 18)

Michael Castellano

Figure 18—*Brauniellula albipes*.

Name derivation: Named for its purported resemblance to the South American fungal genus *Brauniella* with the added diminutive Latin suffix -*ula*, literally "little Brauniella" (A.H. Smith and Singer 1958). As it happens, *Brauniellula* is only distantly related to *Brauniella*.

Fruit-bodies 0.5–5 cm broad, with an irregular to flat, convex or depressed cap and a distinct stem, appearing as an unopened mushroom. **Peridium** yellowish brown to reddish brown, blackish brown, or dark red, dry and fibrillose or slightly slimy in wet weather. **Stem** color similar to cap or paler. **Gleba** with convoluted and anastomosed gills or chambers, grayish brown at maturity, usually totally enclosed by the inturned margin of the cap, which is connected to the stem by a generally persistent veil. **Odor** not distinctive. **Spores** symmetrical to longitudinally asymmetrical, ellipsoid to narrowly ellipsoid, 14–20 × 6–10 µm, smooth to faintly wrinkled, smoky yellowish brown to pale brown, the walls ca 1 µm thick, the attachment conspicuous, straight to offset from the longitudinal axis of the spore. **Reaction to Melzer's reagent:** spores pale to deep reddish brown, flesh of fruit-bodies purple to black.

Number of species: The genus contains two species in North America, *Brauniellula albipes* being the only one in the Pacific Northwest.

Distribution: Mountains of western North America in association with 2- to 3-needled pines.

Season: Summer and autumn.

Keys and descriptions: A.H. Smith and Singer (1958).

Comments: *Brauniellula* is derived from the mushroom genus *Chroogomphus* but is hypogeous and the cap remains enclosed. As originally conceived, the genus contained three species, but one has been transferred to the genus *Gomphogaster* (Miller 1973), while the second is a synonym of *B. albipes*. *Brauniellula* cannot be differentiated from other genera of the Gomphidiaceae by spores alone. This family has spores that also may be difficult to distinguish from those of some Boletaceae. The smoky tinge and large size of the spores of Gomphidiaceae, however, generally suffice to separate them from those of most Boletaceae. The instant blackening of *Brauniellula* and *Chroogomphus* fruit-bodies in reaction to a drop of Melzer's reagent is unique to these genera.

Cazia (Phylum Ascomycota, Order Pezizales, Family Pezizaceae) (fig. 19)

James Trappe

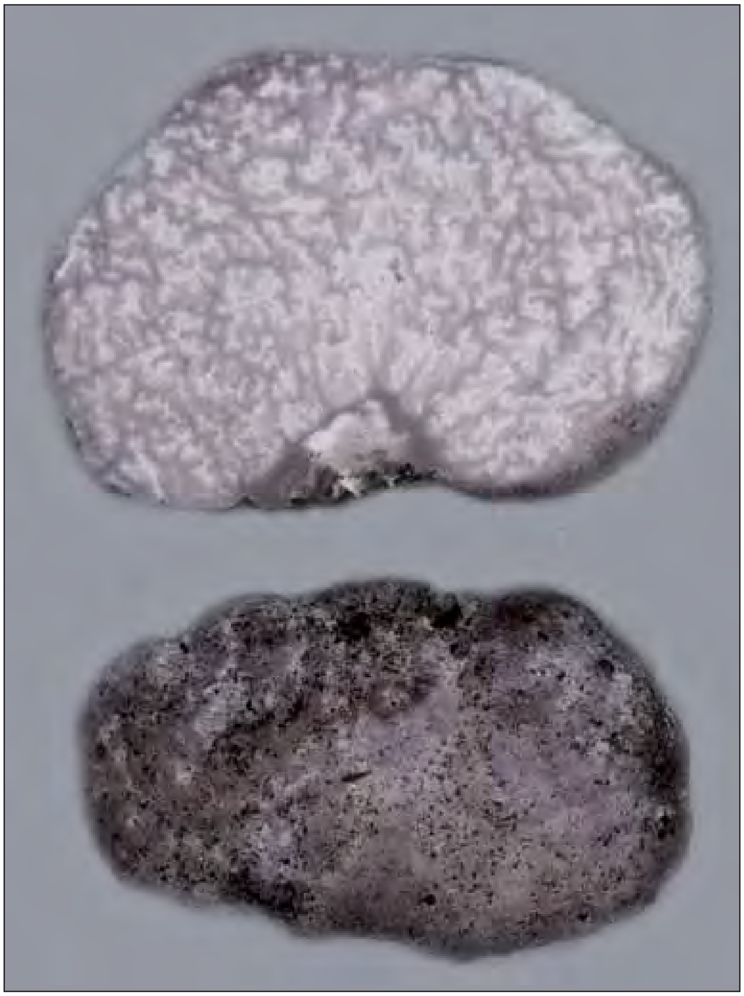


Figure 19—*Cazia flexiascus.*

Name derivation: Named after the collector of the holotype, Michael "Caz" Castellano (Trappe 1989).

Fruit-bodies subglobose with minor lobes and furrows, 3–5 cm broad, sometimes emergent from the soil. **Peridium** white with faint yellowish brown tones, glabrous, darkening when exposed. **Gleba** solid, pale purplish gray, marbled with white veins radiating from a basal pad; a drop of potassium hydroxide (KOH) produces a strong yellow reaction. **Odor** faintly pungent. **Spores** borne in cylindric but crooked asci, globose, subglobose to ellipsoid, 11–16 × 10–12 µm excluding the irregularly warty-reticulate ornamentation, colorless, the walls 1–1.5 µm thick. **Reaction to Melzer's reagent:** immature spores orange, asci in occasional specimens very faintly blue.

Number of species: Two from north temperate forests, *Cazia flexiascus* being the only one in the Pacific Northwest.

Distribution: Oregon, California, and Colorado.

Season: Autumn.

Keys and descriptions: Trappe (1989) described and illustrated *C. flexiascus* and Fogel and States (2002), *C. quericola*.

Comments: This genus differs from *Fischerula, Hydnotrya,* and *Dingleya* by its colorless, minutely ornamented spores, crooked asci, and strong reaction of the fresh gleba to KOH. The crooked asci of *Cazia* are novel (Trappe 1989). Its asci usually do not turn blue in Melzer's reagent, or when they do the reaction is very faint, in contrast to the pronounced reaction by most genera in the Pezizaceae.

Chamonixia (Phylum Basidiomycota, Order Boletales, Family Boletaceae) (fig. 20)

Name derivation: From Chamonix, France, near where the first species was initially discovered (Rolland 1899).

Fruit-bodies subglobose to pyriform, sometimes with a short, stem-like basal projection, 1–5 cm broad. **Peridium** white to brown in most species, soon changing to green, blue, or vinaceous when exposed or bruised, sometimes later becoming black; surface smooth to felty. **Gleba** chambered, usually with a basal pad of sterile tissue; columella ranging from absent to well developed; the cinnamon to dark brown color of the spores in mass dominates the color of the mature gleba. **Odor** not distinctive or lemony. **Spores** longitudinally symmetrical, ellipsoid to ovate or obovate, 9–20 × 9–15 µm excluding the ornamentation of even to irregular, longitudinal, coarse ridges that neither fork nor regularly spiral and are 0.5–2 µm high, rusty cinnamon to dark brown, the walls 0.5–1.0 µm thick; attachment prominent. **Reaction to Melzer's reagent** not distinctive or spores somewhat more reddish brown than in KOH.

Number of species: Four described from north temperate forests.

Distribution: *Chamonixia caespitosa* occurs in Europe and North America. The three other species are endemic to western Oregon and California.

Season: June through November, depending on species.

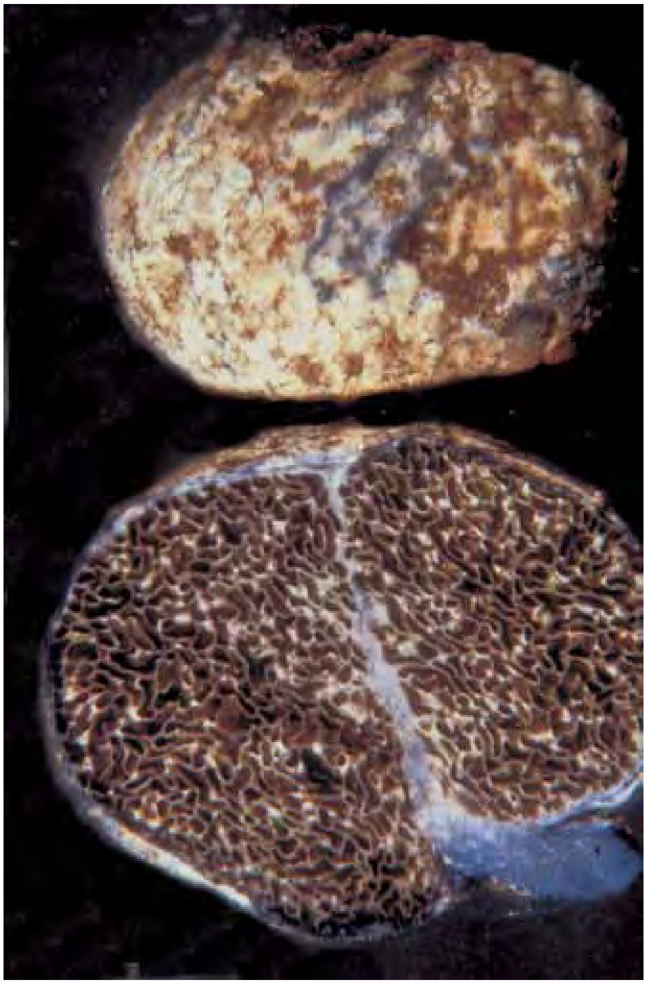

Michael Castellano

Figure 20—*Chamonixia caespitosa*.

Keys and descriptions: A.H. Smith and Singer (1959) detailed all described species in the Northern Hemisphere; Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated *C. caespitosa*.

Comments: The brown, mature spores of *Chamonixia* spp. are readily distinguishable from the colorless to pale yellow or yellow-brown spores of *Gautieria* spp. (Gomphales). The pigment chemistry of *Chamonixia* spp. relates it to the Boletales (Gill and Steglich 1987). It is not clear at present that the three species endemic to Oregon and California belong in *Chamonixia*: molecular studies are needed. Species ascribed to *Chamonixia* in Australasia need to be put in a new, separate genus, as evidenced by DNA sequences (T. Lebel, personal communication, mycologist, The National Herbarium of Victoria, Birdwood Avenue, South Yarra, Victoria 3141, Australia).

Choiromyces (Phylum Ascomycota, Order Pezizales, Family Tuberaceae) (fig. 21)

James Trappe

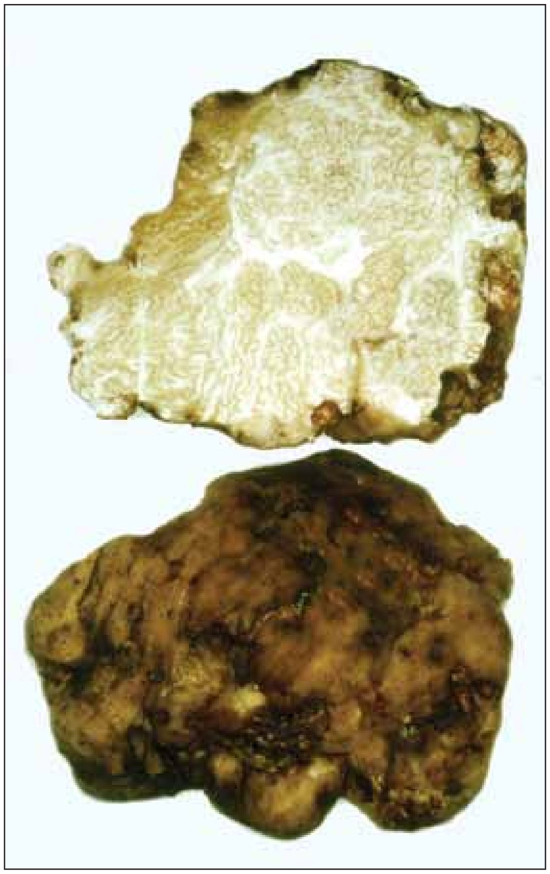


Figure 21—*Choiromyces meandriformis.*

Name derivation: Coined by Vittadini (1831) from Greek *choer-* (pig) and *-myces* (fungus), hence "pig fungus," perhaps referring to the avid searching for this truffle by pigs.

Fruit-bodies subglobose to irregular, 1–10 cm broad. **Peridium** pale yellow to dark brown, smooth to uneven. **Gleba** white to pale yellow or brown marbled with narrow, pale yellow to yellowish brown or brown veins, solid. **Odor** garlicky, pungent, or nauseous. **Spores** borne in cylindric to clavate or saccate asci, globose, 10–30 µm broad excluding the ornamentation of pits or sinuous rods up to 5 µm tall, colorless to pale brown, the walls 0.5–2 µm thick. **Reaction to Melzer's reagent** not distinctive.

Number of species: Three species have been described from north temperate forests.

Distribution: Europe and North America.

Season: Spring, summer, and autumn.

Keys and descriptions: Trappe (1979) described the genus and illustrated spores of *C. meandriformis* (as *C. venosus*) and *C. alveolatus*. Montecchi and Sarasini (2000) described *C. meandriformis*, which occurs both in Europe and North America. *Choiromyces alveolatus* of the Pacific Northwest is described by Gilkey (1939, as *Piersonia alveolata* Harkn.) and Castellano et al. (1999).

Comments: The ornamentation of spores of *Choiromyces* species in the Northern Hemisphere is distinctive to the genus. The pitted spores of *C. alveolatus* resemble micro golf balls. *C. meandriformis* Vittad., common in Europe and present but rare in North America, has spores ornamented with sinuous rods that vary greatly in length on a given spore and have a rimmed depression in the tip. *C. echinulatus* was described from South Africa, but molecular data support its transfer to the new genus *Eremiomyces.*

Chroogomphus (Phylum Basidiomycota, Order Boletales, Family Gomphidiaceae) (fig. 22)

Thom O'Dell

Figure 22—*Chroogomphus loculatus*.

Name derivation: Greek, *chroo-* (skin-colored) and *-gomphus* (a club), coined presumably in reference to the pink to orange hues of the club-shaped fruit-bodies of some species.

Fruit-bodies of *C. loculatus* (the only hypogeous species) hypogeous to partly emergent, with a contorted cap 2.5–7 mm broad, fully expanding on some specimens, remaining closed on others, dry, with smoky olive scales over a pale orange to yellowish ground color. Context pale orange. **Gills** irregular, loculate owing to folds and interconnections, pinkish in youth, becoming brownish orange with age, decurrent. **Stem** 2.5–8 cm long, 1.5–3.5 cm broad, tapering to a narrowed base, often the stems of two or several fused together to form clusters. **Spores** spindle-shaped, (15-) 19–30 × 6–9 µm, smooth, smoky black in spore print, brown to smoky or brownish black in KOH. **Reaction to Melzer's reagent:** spores red, flesh of fruit-bodies purple to black.

Number of species: About 18 known in the Northern Hemisphere, but only *C. loculatus* is hypogeous.

Distribution: *Chroogomphus loculatus* is known so far only from the Lamb Butte Scenic Area of the Cascade Mountains of Lane County, Oregon.

Season: October.

Keys and descriptions: Miller and Trappe (1970) and Castellano et al. (1999) described and illustrated the single hypogeous species.

Comments: *Chroogomphus loculatus* is a mushroom that discharges it spores; it is included here because it represents mushrooms that are trending toward a hypogeous habit. Although hypogeous more often than not, it still forcibly discharges its spores and retains a mushroom form, albeit much contorted. A truly hypogeous descendent of *Chroogomphus* mushrooms, *Brauniellula albipes,* has a chambered gleba and remains closed and underground throughout its development (see its description on page 49).

Cortinarius (Phylum Basidiomycota, Order Agaricales, Family Cortinariaceae) (fig. 23)

Michael Castellano

Figure 23—*Cortinarius verrucisporus*.

Name derivation: An early name from Latin *cortina* (literally "curtain," but in mycology referring to the cortina, the web-like veil that connects the edge of the cap of some mushrooms to the stem) and *-arius* (possessive suffix), hence "possessing a cortina."

Fruit-bodies (hypogeous species only) with stem and cap, resembling an unopened mushroom with a persistent veil of cobwebby to membranous tissue enclosing the gills; stem too short to lift the cap out of the humus; 1–9 cm tall, 2–15 cm broad. **Peridium** smooth to silky or tomentose, dry to viscid, white to pale yellow to brownish yellow, brown, or purplish brown. **Stem** fibrillose, white or similar in color to cap, penetrating through the gleba to the cap but poorly developed and vestigial in hypogeous species. **Gleba** regular to uneven gills that forcibly discharge spores that deposit on the inner side of the persistent veil. **Odor** not distinctive to radish-like or pungent. **Spores** sub-globose to ellipsoid or fusoid, 10–30 × 8–20 µm, ornamented with warts and ridges, often with a detectable outer membrane that collapses on the spore surface to form the ornamentation. **Reaction to Melzer's reagent** not distinctive or spores reddish.

Number of species: Three PNW species are truly hypogeous and thus depend on animals for spore dispersal.

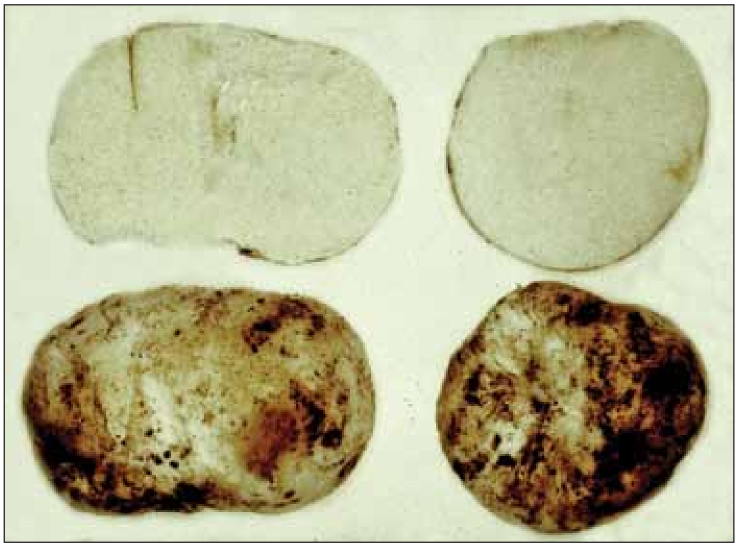
Distribution: Beneath ectomycorrhizal shrubs and trees; the hypogeous species of the Northern Hemisphere are known only from coniferous forests of mountains in western North America. Several hypogeous species occur in Australia.

Season: Late spring to early autumn for the hypogeous species; the genus as a whole occurs throughout the year.

Keys and descriptions: The hypogeous species of north temperate forests are treated by Thiers and Smith (1969), Watling (1980), and M. Trappe et al. (2007).

Comments: *Cortinarius* contains perhaps 2,000 species in the Northern Hemisphere; it has been thoroughly studied only in Europe, and even there many taxonomic questions remain unresolved. The hypogeous species are few and thus more easily identified with confidence, at least in North America. Some species of *Thaxterogaster*, a hypogeous genus derived from *Cortinarius*, resemble hypogeous *Cortinarius* species but have a gleba with much contorted, interconnected gills. The evolutionary boundary between these two groups thus is ambiguous. In those intermediates, species that forcibly discharge their spores could be assigned to *Cortinarius*, those lacking that ability to *Thaxterogaster*. Most *Thaxterogaster* spp., however, have a distinctly chambered gleba and are readily distinguished from hypogeous *Cortinarius* spp.

Cystangium (Phylum Basidiomycota, Order Russulales, Family Russulaceae) (fig. 24)



James Trappe

Figure 24—*Cystangium vesiculosum*.

Name derivation: From Greek, *cystis*- (bladder), and -*angium* (a vessel, a term used by 19th-century mycologists to mean "fruit-body"), hence "a bladder-like fruit-body" (Singer and Smith 1960).

Fruit-bodies globose to irregular with or without stipe-columella, up to 40 mm broad. **Peridium** smooth to pubescent, white to yellow or brown, sometimes with reddish to purplish patches, often developing brown stains, totally enclosing the gleba or sometimes leaving a small area of gleba exposed at the base; peridium with a surface layer of globose cells, sometimes with an overlay of scattered to abundant hyphal tips that produce the pubescence. **Gleba** white to yellow or brown, with small chambers or contorted, compressed and fusing gills; columella present or absent, when present sometimes extended below the gleba as a short stem. **Spores** globose to ellipsoid, sometimes laterally asymmetric, 7–15 × 5–15 µm excluding the ornamentation of warts or spines, in many species these connected by reticulate lines, colorless to brown, the walls ±0.5 µm thick; sterigmal attachment straight to offset in relation to its longitudinal axis. **Reaction to Melzer's reagent:** spore walls colorless to gray or purplish, spore ornamentation purple to black in spots or overall.

Number of species: About 20 species have been described from north temperate forests.

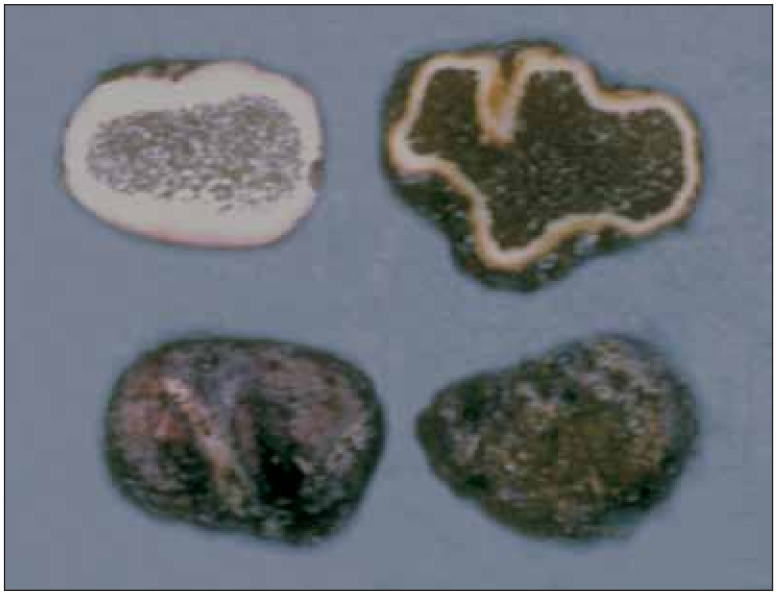
Distribution: Worldwide under ectomycorrhizal woody plants.

Season: Spring, summer, and autumn.

Keys and descriptions: Singer and Smith (1960) covered the genus as known at that time but placed some *Cystangium* species in *Martellia*, a genus no longer accepted. Later, A.H. Smith (1963) described new species and revised the key to the species, again with some in *Martellia*. Pegler and Young (1979) and Miller (1988) described and illustrated representative spores. Castellano et al. (1999) described *C. maculatum* (as *Martellia maculata*) and M. Trappe et al. (2007) described and illustrated *C. vesiculosum*. Lebel and Trappe (2000) redefined the genus. Trappe et al. (2002) corrected the nomenclature.

Comments: *Cystangium* differs from *Gymnomyces* and *Macowanites* by having a layer of one to many tiers of rounded and often inflated cells at the peridial surface or sometimes immediately below a turf of hyphal tips. All three are derived from the mushroom genus *Russula*.

Destuntzia (Phylum Basidiomycota, Order Gomphales, Family Gomphaceae) (fig. 25)



Michael Castellano

Figure 25—*Destuntzia rubra*.

Name derivation: Named by Fogel and Trappe (1985) in honor of the eminent Pacific Northwestern mycologist Professor Daniel E. Stuntz.

Fruit-bodies pulvinate to irregular or subglobose, 0.8–2.5 cm broad. **Peridium** felty to fibrillose, white to dingy, often staining yellow or pink where bruised or exposed. **Gleba** solid, with more or less gel-filled chambers, often sticky to the touch, the chambers olive to dark brown and separated by narrow, pale veins; columella lacking but sterile pad often present. **Odor** not distinctive to strongly fishy. **Spores** ellipsoid to subglobose, 8–11 × 5–9 µm excluding the ornamentation of warts or wrinkles up to 2 µm tall, dark grayish yellowish brown, the walls 0.5 µm thick; sterigmal attachment present. **Reaction to Melzer's reagent** not distinctive.

Number of species: Five from north temperate forests, four being endemic to the Western States.

Distribution: From the coast to middle elevations in the mountains in coniferous forests of northern California, Oregon, and Idaho plus a single collection of one species from Massachusetts.

Season: Spring through autumn.

Keys and descriptions: Fogel and Trappe (1985) described all species in detail and provided a key. Castellano et al. (1999) described and illustrated *D. fusca* and *D. rubra*.

Comments: Spores of *Destuntzia* species cannot be separated easily from those of the small-spored *Hymenogaster* species. The two genera are distinguished primarily by fruit-body characters.

Elaphomyces (Phylum Ascomycota, Order Eurotiales, Family Elaphomycetaceae) (fig. 26)


Matthew Trappe

Figure 26—*Elaphomyces muricatus*.

Name derivation: An early name from Greek, *elapho-* (deer) and *-myces* (fungus), the “deer fungus” in reference to deer digging up and eating these fungi. The origin of the name may be the earliest scientific recognition of mycophagy by wild animals.

Fruit-bodies subglobose to globose, 5–40 mm broad, enclosed in a crust of mycelium, dirt, and proliferated ectomycorrhizae of associated trees or shrubs. **Peridium** brownish yellow to brown, dark blue or black, smooth to ornamented with hard, rounded warts, pyramids or cones, often tomentose, crisp-fleshy to leathery to carbonaceous, 2–5 mm thick. **Gleba** hollow in youth, becoming stuffed with asci and cottony hyphae; at maturity the hollow becomes filled with a yellow to brown, olive, brownish black, bluish black, or black spore powder. **Odor** not distinctive to metallic or garlicky. **Spores** borne in round asci, globose to subglobose, 8–48 µm broad including the ornamentation of spines, warts, a reticulum, or spiralling ridges up to 2+ µm tall as seen by light microscopy, or a complex architecture visible only by scan electron microscopy; some species produce spores of two size groups within a single fruit-body, e.g., 10–15 µm and 25–35 µm; bluish gray to gray, olive, brown, or black, the wall single, 0.5–2 µm thick, lacking an attachment. **Reaction to Melzer’s reagent** not distinctive.

Number of species: About 30 from north temperate forests, but scan electron microscopy of spores reveals the number to be considerably higher than those described to date (Castellano and Trappe, unpublished data).

Distribution: Associated with ectomycorrhizal trees and shrubs in Northern Hemisphere forests from sea level to timberline. Undescribed taxa have been found in South America, Australia, New Zealand, and Papua New Guinea.

Season: Throughout the year; fruit-bodies require many months, perhaps up to a year, to mature.

Keys and descriptions: Trappe (1979) described the genus, and Castellano et al. (1999) and M. Trappe et al. (2007) illustrated five Pacific Northwestern species between them. No modern monographs or keys to *Elaphomyces* spp. are available, but the entire genus is being investigated and revised by M. Castellano.

Comments: *Elaphomyces* spores can be difficult to differentiate by light microscopy from the globose, reticulate spores of some species of *Scleroderma*, *Ruhlandiella*, or *Tuber*, or the globose, spiny spores of certain species of *Genabea* or *Hydnotrya*. The asci that contain *Elaphomyces* spores disintegrate at early maturity, so spores found within intact asci in mammal stomach contents will generally not be those of *Elaphomyces.* Scan electron microscopy reveals the spore ornamentation to be often much more complex than perceived by light microscopy, and many of the past species names may represent complexes of several undescribed species (M. Castellano, unpublished data). Of the genera mentioned above, only *Elaphomyces* includes species with bluish gray, olive, or nearly black spores as seen under the microscope. The description here omits characters of the southern European *E. leucosporus* Vittad., which differs in so many ways from other species in the genus that it may well deserve a separate genus of its own. The peridium of *Elaphomyces* is eaten by small mammals, which discard the powdery spore mass of the gleba (Trappe and Maser 1977). They thereby release the spores to the air for dispersal.

Endogone (Phylum Zygomycota, Order Endogonales, Family Endogonaceae) (fig. 27)

James Trappe

Figure 27—*Endogone flammicorona*.

Name derivation: Coined by Link (1809) from Greek *endo*- (inside) and -*gone* (reproductive organs), hence “with reproductive organs inside.”

Fruit-body subglobose to irregular, 3–20 mm broad. **Peridium** absent or, when present, white to bright yellow or brown, smooth to cottony or felty. **Gleba** solid gray to bright yellow or brown, in most species a mass of spores and mycelium without an organized structure. **Odor** garlicky or not distinctive. **Spores** ellipsoid to globose or irregular, 41–200 × 52–150 µm excluding the mantle of adherent hyphae found on some species, colorless to yellow or brown, the walls one- to three-layered and 2–11 µm thick. **Reaction to Melzer’s reagent** mostly not distinctive, but in some species one or more spore wall layers becoming deep orange to red.

Number of species: Eight species have been described from north temperate forests, seven of which occur in the Pacific Northwest.

Distribution: Common in forests of the Northern Hemisphere; saprobic or etomycorrhizal with Pinaceae and some broad-leaved families. *E. lactiflua* and *E. flammicorona* are common in tree nurseries.

Season: Throughout the year.

Keys and descriptions: Gerdemann and Trappe (1974). Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated three species between them.

Comments: The large, smooth or hypha-mantled spores of *Endogone* species separate them readily from all others except *Youngiomyces* and *Glomus* species. *Endogone* spores either show no attachments by maturity or arise from two, fused suspensors. The two suspensors of *Youngiomyces* are not fused but separated from each other. *Glomus* spores of species included in this paper have one attachment. *Endogone pisiformis* and related species with smooth, bright yellow spores are saprobic and form the core of the genus. Species such as *E. lactiflua* and *E. flammicorona* are ectomycorrhizal and probably need a separate genus of their own.

Fevansia (Phylum Basidiomycota, Order Boletales, Family Boletaceae [placement uncertain pending DNA analysis])

Name derivation: Named by Trappe and Castellano (2000) in honor of the collector of the holotype, Frank Evans of the North American Truffling Society.

Fruit-bodies subglobose-lobed with much adherent soil and debris, up to 2.5 cm broad. **Peridium** smooth, sticky, pale brownish orange to orange brown. **Gleba** firm, sticky, with locules filled with spores, pale pinkish orange to orange brown. **Odor** strongly oily-fruity. **Spores** longitudinally symmetrical, fusoid, 10–13 × (3.5-) 4–5 µm, smooth; walls 0.5 µm thick, colorless singly, grayish yellow in mass; sterigmal attachment indistinct. **Reaction to Melzer's reagent** not distinctive.

Number of species: Only one species is known for the genus, *F. aurantiaca*.

Distribution: Endemic to western Oregon.

Season: August.

Keys and descriptions: *F. aurantiaca* has been described by Trappe and Castellano (2000), Castellano et al. (1999), and M. Trappe et al. (2007).

Comments: Spores of *Fevansia* are similar to those of *Rhizopogon* spp. but grayish yellow rather than olivaceous to brown in mass. *Fevansia* is perhaps the rarest truffle in the Pacific Northwest, but it is easily identified in the field by its distinctly orange color and sticky gleba.

Fischerula (Phylum Ascomycota, Order Pezizales, Family Morchellaceae)

Name derivation: Coined by Mattirolo (1928) in honor of the early 20th-century Swiss mycologist, Eduard Fischer, who devoted much study to truffle-like fungi.

Fruit-bodies subglobose to turbinate to irregular, with a basal tuft of hyphae, often with a short stem 0.8–2.5 cm broad. **Peridium** yellowish pink to brown, scabrous. **Gleba** solid, at maturity brown marbled with white to grayish yellow veins that more or less radiate outward from the base of the columella to emerge through the peridium; columella when present grayish reddish brown. **Odor** not distinctive. **Spores** borne in clavate to reniform or ellipsoid asci, ellipsoid, 40–77 (-101) × 25–29 µm excluding the ornamentation of conic warts, broad ridges, or agglutinated, flexuous spines; walls 1–2 µm thick, dark brown. **Reaction to Melzer's reagent:** spores dark reddish brown.

Number of species: Two species have been described from north temperate forests.

Distribution: *Fischerula subcaulis* occurs on the coast and in the coastal mountains of Oregon and Washington in association with *Pseudotsuga menziesii*. The only other species, *F. macrospora*, occurs in central and southern Italy.

Season: Late spring through late autumn

Keys and descriptions: Trappe (1975d) described and illustrated both species.

Comments: Only *Fischerula* species combine warty, ridged, or agglutinated-spiny spore ornamentation with extra large spores (i.e., spores commonly longer than 50 µm). It is rarely collected, but where found can be locally abundant.

Gastroboletus (Phylum Basidiomycota, Order Boletales, Family Boletaceae) (fig. 28)

Name derivation: From Greek, *gaster*- (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs) and Latin -*boletus* (literally "a superior mushroom," referring to the genus *Boletus*), hence, in the sense of Lohwag (1926), who coined the name, "a puffball-like *Boletus*."

Fruit-bodies hypogeous, misshapen, 3–10 cm broad, with a flat to convex or irregular cap and a short, usually stout stem. **Peridium** dingy white to brown, in some species with yellow or red tones, dry to moist, smooth to felty or scaly-tomentose, some species bruising blue where handled. **Gleba** a layer of very long, usually curved or contorted, olive to brown tubes on the underside of the cap; tube mouths are often covered or stuffed with cottony or membranous tissues, and the tubes often have cross-walls. **Odor** mild and pleasant to pungent or unpleasant. **Spores** ellipsoid, fusoid, oblong, subovate, pyriform, often slightly inequilateral, 6–18 × 2.5–8 µm, smooth; walls 0.5–2 µm thick, colorless to yellow or brown. **Reaction to Melzer's reagent** not distinctive in most species, but spores of some turn brown and one becomes purple.

Number of species: Nine have been described from north temperate forests.

Distribution: Most species are restricted to coniferous forests of the Pacific coastal states, but *G. turbinatus* extends from the Pacific coast to the Midwest and Mexico. The original species of the genus, *Gastroboletus boedijnii* Lohwag, was described from China. Two other species occur in the Southern Hemisphere.

Michael Castellano

Figure 28—*Gastroboletus subalpinus*.

Season: Generally summer through autumn.

Keys and descriptions: Thiers and Trappe (1969) provided a key and descriptions for most species, five of which were described and illustrated by Castellano et al. (1999, 2003) and M. Trappe et al. (2007) between them. Thiers (1989) proposed two new *Gastroboletus* species and segregated two new genera, *Gastrosuillus* and *Gastroleccinum*, on the basis of distinctive fruit-body tissues and provided a comprehensive key. Some mycologists combine the genus *Gastroboletus* into the mushroom genus *Boletus*. Nouhra et al. (2002) provided a key to all known species of *Gastroboletus*.

Comments: *Gastroboletus* species represent evolutionary progression from mushrooms to belowground forms. They have tubes, but the tubes are contorted and are blocked by tissues covering their mouths and often by inner cross-walls. Moreover, the fruit-bodies are usually entirely belowground. Clearly they cannot discharge spores to the air and thus rely on animals for dispersal. Their spores resemble those of closely related mushroom genera in the family Boletaceae (*Boletus*, *Leccinum*, *Suillus*) as well as belowground genera such as *Rhizopogon*.

Gastrolactarius (Phylum Basidiomycota, Order Russulales, Family Russulaceae) (fig. 29)

Michael Castellano

Figure 29—*Gastrolactarius camphoratus*.

Name derivation: Named by Vidal (2004) from Greek *gastero-* (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs) and Latin -*lactarius* (in this case referring to the mushroom genus *Lactarius*), hence a "puffball-like *Lactarius*" to accommodate hypogeous species formerly placed in *Arcangeliella* but having a stem and columella somewhat akin to *Lactarius* spp.

Fruit-bodies globose to irregular, 1–4 cm broad, with a stem and prominent columella, appearing as an unopened mushroom. **Peridium** white to orange or brownish, smooth, moist to slimy. **Gleba** loculate, white to orange, exuding a watery to white or yellow latex from the cut tissue of moist, fresh specimens. **Spores** ellipsoid to subglobose, 7–15 × 6–10 µm excluding the ornamentation of warts, spines, or a reticulum; walls 0.5 µm thick, colorless to pale yellowish brown; sterigmal attachment present but often inconspicuous, **Reaction to Melzer's reagent:** spore walls sometimes gray to purple, spore ornamentation purple to black.

Number of species: Eight from north temperate forests; more have been found in the Southern Hemisphere.

Distribution: Hypogeous to emergent under ectomycorrhizal shrubs and trees in Oregon, California, Europe, Australia, New Zealand, and Thailand.

Season: Summer and autumn.

Keys and descriptions: The following authors treat *Gastrolactarius* species as *Arcangeliella* species: Singer and Smith (1960) covered most described species; Thiers (1984a) keyed and described species found in the Western United States, and Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated several species. Pegler and Young (1979) and Miller (1988) described and illustrated representative spores.

Comments: *Gastrolactarius* is derived from the mushroom genus *Lactarius* and represents the evolutionary progression from mushrooms toward a truffle habit. It is intermediate between *Lactarius* spp. and the stemless, hypogeous *Arcangeliella* spp. All three genera produce a latex when fresh and moist. If no latex appears when a specimen is cut open, for example in dry conditions, the latex-producing capability can be confirmed by checking cap tissue under the microscope for conspicuous, latex-producing hyphae scattered through the tissues. It is helpful to record latex production in the field when specimens are collected, because they may dry enough in a few hours to stop production. Vidal (2004) updated the nomenclature of the genus.

Gastrosuillus (Phylum Basidiomycota, Order Boletales, Family Suillaceae) (fig. 30)

Name derivation: Coined by Thiers (1989) from Greek *gastero-* (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs) and Latin *-suillus* (for the species formerly in *Gastroboletus* but instead related to the mushroom genus *Suillus*).

Fruit-bodies 10–35 mm, convex to irregular or depressed, stipe and columella present, sometimes with glandular dots. **Peridium** glabrous and slightly slimy or sometimes scaly or tomentose, yellowish brown to brown. **Gleba** composed of contorted tubes, yellow, olive, or brown, sometimes with a purple reaction to KOH. **Odor** mild. **Spores** ellipsoid to subcylindric, 6–10 × 3–4 µm, smooth; walls thin, colorless to pale brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: Five from north temperate forests.

Distribution: North America.

Keys and descriptions: Thiers (1989) described and keyed four species, and Trappe and Castellano (2000) added a fifth. Two species are described and illustrated by Castellano et al. (1999).

James Trappe

Figure 30—*Gastrosuillus umbrinus*.

Comments: *Gastrosuillus*, like *Gastroboletus,* represents the evolutionary progression from mushrooms toward a truffle form. It is hypogeous, and its spores are not discharged to the air. Its spores are not easily differentiated from those of *Gastroboletus*. Many mycologists place the species of *Gastrosuillus* in the mushroom genus *Suillus*.

Gautieria (Phylum Basidiomycota, Order Gomphales, Family Gautieriaceae) (fig. 31)

Matthew Trappe

Figure 31—*Gautieria monticola*.

Name derivation: Named by Vittadini (1831) in honor of the natural historian Joseph Gautier.

Fruit-bodies 1–8 cm broad, globose to subglobose or irregular, usually with a prominent rhizomorph emerging from the base. **Peridium** lacking or fragile and ephemeral in most species, when present dingy white to brown, felty and fragile or membranous. **Gleba** with small to prominent, labyrinthine chambers and a poorly to strongly developed, usually cartilaginous columella; the cinnamon to dark cinnamon color of the spores in mass dominate the color of the gleba of mature specimens. **Odor** not distinctive or merely mushroomy in young specimens but by full maturity (and especially at warm temperatures) often becoming offensive, ranging from nauseous to sweet-oily to sewer-gaseous. **Spores** longitudinally symmetrical, ellipsoid to ovoid, obovoid, or globose, 10–32 × 6–18 µm including the ornamentation of longitudinal, often slightly spiraled and forked ridges up to 4.5 µm tall with rounded to humped margins; walls 0.5–1 µm thick, nearly colorless to pale brownish yellow or yellowish brown; sterigmal attachment prominent. **Reaction to Melzer's reagent** not distinctive in most species, but in some orange to reddish orange.

Number of species: About 36 have been described from north temperate forests, of which 22 occur in the Pacific Northwest (J. States, personal communication, Professor Emeritus, Biological Sciences Department, Northern Arizona University, Flagstaff, Arizona 86011).

Distribution: Common in ectomycorrhizal forests of the Northern Hemisphere. Several species also occur in the Southern Hemisphere.

Season: Throughout the year, often the most abundant genus in early spring; *G. monticola* may fruit under melting snow.

Keys and descriptions: North American species are keyed and described by Dodge and Zeller (1934), but that paper is seriously out of date: several undescribed species have been discovered since. Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated five species between them. A new monograph of the genus is in preparation by J. States et al. (personal communication).

Comments: *Gautieria* is a close relative of coral fungi in the genus *Ramaria* subgen. *Ramaria*. Indeed, if one were to take a *Ramaria* and compress it into a tight ball, it might even suggest a *Gautieria*. *Gautieria* spores are similar those of some species of *Ramaria*.

Genabea (Phylum Ascomycota, Order Pezizales, Family Pyronemataceae) (fig. 32)


James Trappe

Figure 32—*Genabea cerebriformis*.

Name derivation: Coined by Tulasne and Tulasne (1845) for the locality in which the first material was collected, Genabum, an ancient name for present-day Orleans, France.

Fruit-bodies subglobose to convoluted or ridged, often with an opening to the convoluted, hollow interior, 0.2–2 cm broad. **Peridium** yellowish gray to brown or black, verrucose, lacking surface hairs. **Gleba** of irregular chambers with a warty lining similar to the peridium; the lining overlies white to gray or grayish yellow flesh with pockets of asci in an irregular palisade. Each pocket is separated from the others by sterile tissue. **Odor** not distinctive to garlicky. **Spores** borne in clavate to ellipsoid asci, ellipsoid to globose, 26–53 (-70) µm × 20–53 (-70) µm excluding the ornamentation of prominent spines; walls 2–5 µm thick, grayish yellow to brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: Five from north temperate forests.

Distribution: *Genabea cerebriformis* (Harkness) Trappe is widely distributed in the Western United States and Mexico. The other species, found in eastern North America and southern Europe, are rare.

Season: Spring through autumn; *G. cerebriformis* occurs only in spring in the Western United States and in summer in Mexico.

Keys and descriptions: Gilkey (1954b) described and keyed the North American species (including the synonymous genus *Myrmecocystis*); Trappe (1979) described the genus and illustrated a spore of *G. fragilis.* M.E. Smith et al. (2006) and M. Trappe et al. (2007) described *Genabea cerebriformes* in detail.

Comments: *G. cerebriformis* is common in its distribution zone. All other species appear to be infrequent to rare.

Genea (Phylum Ascomycota, Order Pezizales, Family Pyronemataceae) (fig. 33)

Matthew Smith

Figure 33—*Genea arenaria*.

Name derivation: Coined by Vittadini (1831) to honor the 19th-century Italian zoologist, Giuseppi Gene, for his studies of fungicolous insects.

Fruit-bodies subglobose to irregular, 0.3–3 cm broad, with an apical opening to a single chamber and a basal tuft of mycelium. **Peridium** brown or black, verrucose, often with guard hairs at the margin of the apical opening, in some species tomentose in part or overall. **Gleba** a single, uniform to irregular chamber with a verrucose lining similar to the peridium; the lining overlies white to gray flesh, which contains a generally continuous, embedded palisade of asci. **Odor** fungoid to strongly garlicky or pungent. **Spores** borne in cylindric to clavate asci, ellipsoid to subglobose, 20–45 × 12–34 µm excluding the ornamentation of colorless, rounded warts or pointed, truncate or forked cones that dissolve in KOH; walls 1–3 µm thick, colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 25 identified from north temperate forests, including some as yet undescribed.

Distribution: Associated with ectomycorrhizal hosts in the Northern Hemisphere; infrequently collected, but sometimes locally abundant.

Season: Spring through early winter.

Keys and descriptions: Trappe (1979) described the genus and illustrated spores of three species. Gilkey (1939, 1954b) and M.E. Smith et al. (2006) covered the North American species described so far, three also being described and illustrated by M. Trappe et al. (2007).

Comments: *Genea* is probably fairly common, but the small, brown to black fruit-bodies are difficult to see in the soil. The colorless, KOH-soluble ornamentation of spores of *Genea* spp. and *Gilkeya compacta* (described below) does not occur in other hypogeous genera of the Northern Hemisphere. *Genea intermedia* Gilkey, the only species with globose spores, has been transferred to the new genus *Gilkeya* as *Gilkeya compacta* on the basis of DNA evidence (M.E. Smith et al. 2006).

Geopora (Phylum Ascomycota, Order Pezizales, Family Pyronemataceae) (fig. 34)


Matthew Trappe

Figure 34—*Geopora cooperi f. gilkeyae.*

Name derivation: Coined by Harkness (1885) from Greek, *geo-* (earth) and *-pora* (pore), hence an "earth pore."

Fruit-bodies subglobose to cerebriform, 1–7 (-10) cm broad. **Peridium** brown, tomentose. **Gleba** white to gray and usually with some brownish veins, hollow and simple or of complex, infolded trama and empty chambers that open inconspicuously to the surface and are lined by a hymenium of asci. **Odor** fungoid to radish-like. **Spores** borne in cylindrical, operculate asci, subglobose to ellipsoid, 20–30 × 13–24 µm, smooth; walls ≤ 1 µm thick, colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: Twelve species from north temperate forests, including those formerly assigned to the genus *Sepultaria*.

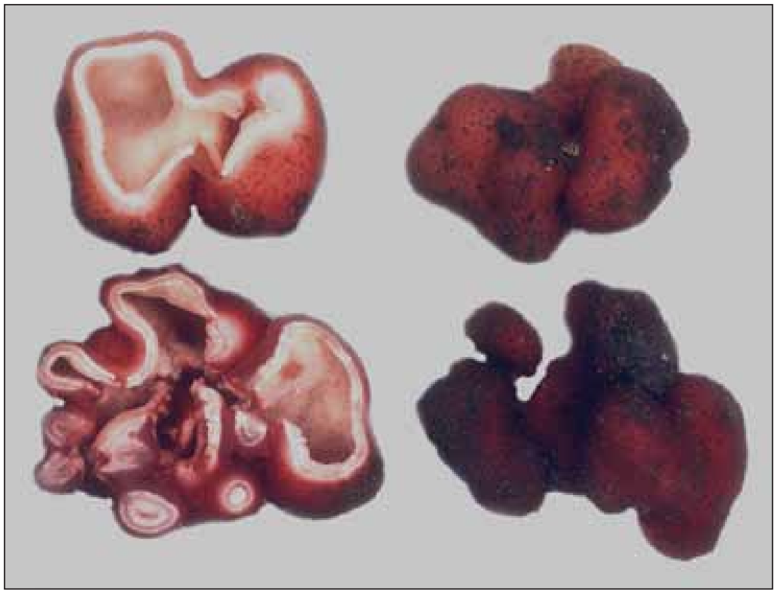
Distribution: Widely distributed in the Northern Hemisphere in association with ectomycorrhizal host trees and shrubs. *Geopora cooperi* is the most common species; its two forms are mostly associated with members of the Pinaceae. *Geopora clausa* occurs in semi-arid regions, often in association with Salicaceae in oases or riparian zones.

Season: Throughout the year as weather conditions permit.

Keys and descriptions: Trappe (1979) described the genus. Burdsall (1968) covered its hypogeous species worldwide. M. Trappe et al. (2007) described and illustrated the common, hypogeous *G. cooperi*.

Comments: Most *Geopora* spp. are not strictly hypogeous; rather, they are hollow spheres that are largely immersed within the soil but open to the soil surface as a little hole, "earth pores." *G. cooperi* is the much infolded species that assumes a typical, truffle shape, but even it has operculate asci that forcibly discharge the spores. The spores cannot escape the intact, infolded, belowground fruit-body for dispersal by moving air. However, if its fruit-body is broken open, as when eaten by a squirrel, the spores can puff out and become airborne (Burdsall 1965). The cover of the book by Montecchi and Sarasini (2000) features a most attractive cross-sectional view of the gleba of *G. cooperi*.

Gilkeya (Phylum Ascomycota, Order Pezizales, Family Pyronemataceae) (fig. 35)



Michael Castellano

Figure 35—*Gilkeya compacta*.

Name derivation: In honor of Professor Helen Gilkey (1886–1972), pioneering taxonomist at OSU and internationally recognized expert on taxonomy of hypogeous Ascomycota.

Fruit-bodies subglobose to convoluted, 5–20 mm broad, hollow, with a small, hairless apical opening; base lacking a tuft of hyphae. **Peridium** pink to vinaceous or vinaceous brown, verrucose, of inflated, thick-walled cells; lacking hairs. **Gleba** lined with a tissue similar to the peridium. **Odor** not distinctive. **Spores** borne in cylindrical asci, subglobose to globose, 28–43 × 25–38 mm excluding the ornamentation of rounded warts 2–3 (-7) mm tall and 2–6 (-15) mm broad, the spore surface between with smaller warts and granules; the ornamentation dissolves in KOH; spore walls colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: *Gilkeya* contains only one species, *G. compacta*.

Distribution: Northern Oregon to southern California, rare in Idaho, apparently disjunct in central Mexico, from near sea level to 1600 m elevation in the Oregon Cascades, 1900 m in the Sierra Nevada and San Gabriel Mountains of California, and up to 3200 m in Mexico; associated with *Quercus, Abies, Pinus,* and *Pseudotsuga* spp. in pure or mixed stands.

Season: March through August but mostly May and June.

Keys and descriptions: M.E. Smith et al. (2006) named and described this new genus. M. Trappe et al. (2007) described and illustrated *G. compacta*.

Comments: *Gilkeya compacta* has been bounced around in different genera since Harkness originally described it (see M.E. Smith et al. 2006 for the historical references). In morphology it didn't quite fit in the older genera, but it didn't quite differ from them either. So it was originally named *Hydnocystis compacta,* then over years of additional morphological study transferred to *Genea,* then to *Myrmecocystis*, then back to *Genea*. Finally, the advent of DNA analysis enabled M.E. Smith et al. (2006) to confirm that it didn't fit genetically with any of those or other genera and deserved a genus of its own.

Glomus (Phylum Glomeromycota, Order Glomerales, Family Glomeraceae) (fig. 36)

Name derivation: Coined by Tulasne and Tulasne (1845) from Latin *Glomus* (a ball of yarn), possibly in reference to the rounded, wooley appearance of some fruit-bodies.

Fruit-bodies (only truffle-like species included in this description) globose to convoluted or irregular, 3–20 mm broad, in a few species hollow. **Peridium** absent or present and white to yellow or brown, smooth to felty or cottony. **Gleba** white to bright yellow or brown, a mass of spores randomly placed or aligned in rows radiating from the base. **Odor** generally not detectable. **Spores** globose to ellipsoid or pyriform, 20–470 µm excluding ornamentation when present, smooth or ornamented with spines or warts or enclosed in a mantle of adherent hyphae, colorless to yellow-brown or brownish black, the wall one- to three-layered and 2–18 µm thick. **Reaction to Melzer's reagent** not distinctive in most species, but spores orange to red in some.

Number of species: 10 to 20 truffle-like species from north temperate forests.

Distribution: Truffle-like species may occur in any forest with vesicular-arbuscular mycorrhizal host plants.

Season: Throughout the year.

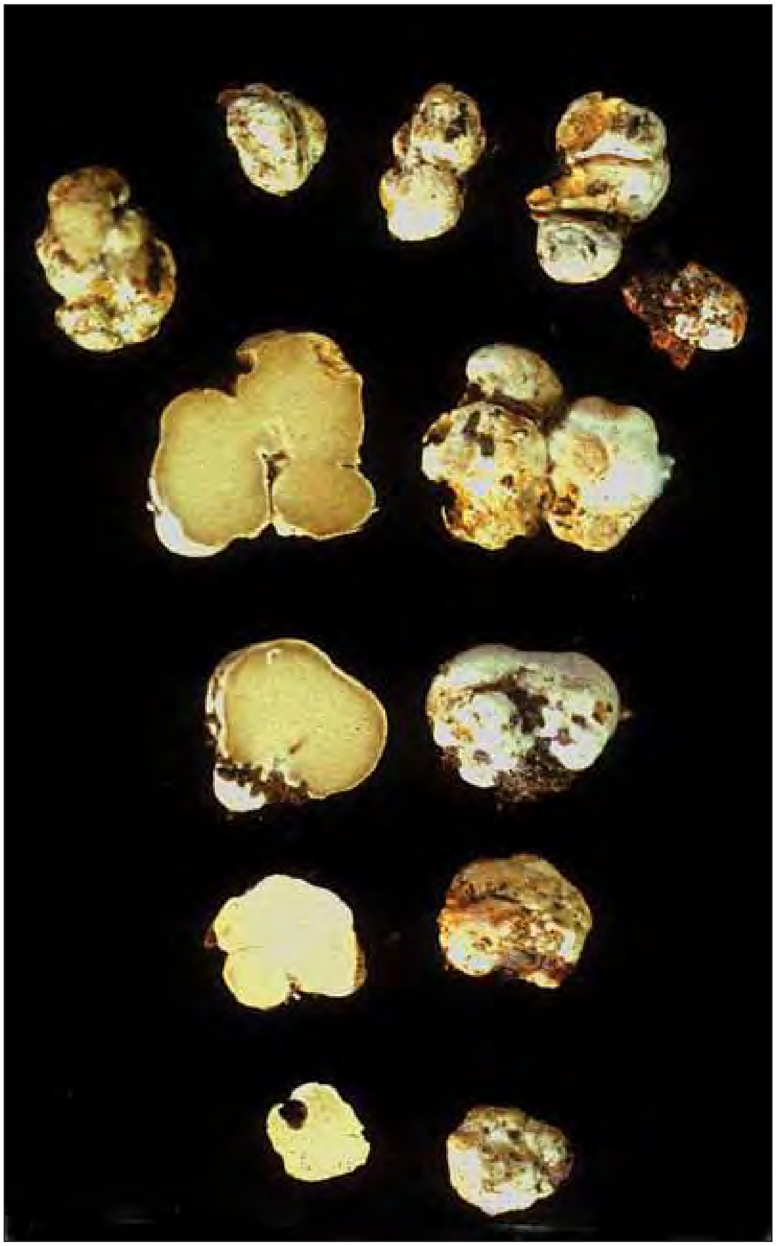

James Trappe

Figure 36—*Glomus microcarpum*.

Keys and descriptions: Gerdemann and Trappe (1974) monographed the Pacific Northwestern species, and Trappe (1982) provided keys to species. However, many new species have been described since, and no up-to-date monographs or keys are available for the PNW. Castellano et al. (1999) described and illustrated *G. radiatum*, as did M. Trappe et al. (2007) for *G. microcarpum*.

Comments: Most species form spores individually in soil or mycorrhizae. Spores of all species form at the tips of hyphae, a trait that is restricted to *Glomus* among the hypogeous fungi.

Gomphogaster (Phylum Basidiomycota, Order Boletales, Family Gomphidiaceae)

Name derivation: Greek *gompho-* (a club) and *-gaster* (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs), indicating its more-or-less club shape and spore-bearing tissue enclosed like that of a puffball.

Fruit-bodies club-shaped to irregular, the cap up to 15 cm broad and stem 12 mm tall and 6 mm broad. **Peridium** pale vinaceous, soon becoming blackish spotted, smooth, with much adherent debris. Stem tissue initially white, slowly becoming tinged pale vinaceous brown when exposed, lemon yellow at the base. **Gleba** brownish gray, with minute chambers. **Odor** not recorded. **Spores** ovoid to ellipsoid, slightly bilaterally asymmetric, 17–22 × 8.5–10 µm, smooth; walls slightly thickened, smoky brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: One, *Gomphogaster leucosarx*.

Distribution: Known only from northern Idaho.

Season: Early summer.

Keys and descriptions: The sole species was described as *Brauniellula leucosarx* by A.H. Smith and Singer (1958) and later by O.K. Miller (1973) as *Gomphogaster leucosarx*.

Comments: This fungus is related to the mushroom genus *Gomphidius*. It being very rare, little is known about its ecology.

Gymnomyces (Phylum Basidiomycota, Order Russulales, Family Russulaceae) (fig. 37)

Name derivation: From Greek, *gymno-* (naked) and *-myces* (fungus), "naked fungus" (Massee and Rodway in Massee 1898). The type species lacked a peridium, so the gleba was uncovered (Singer and Smith 1960).

Fruit-bodies subglobose to turbinate or irregular, 0.5–5 cm. **Peridium** lacking to thick, smooth to felty or pubescent, when present white to orange yellow or brown, sometimes rose to red-spotted, composed of interwoven hyphae and, in many species, with a turf of cystidia or hyphal tips on the surface but lacking a layer of inflated cells. **Gleba** with small to prominent,

Matthew Trappe

Figure 37—*Gymnomyces brunnescens*.

labyrinthine chambers; columella lacking or present as a few, narrow, sterile veins or as a basal pad; color white to pink, yellow, orange yellow, or brown; scattered to abundant sphaerocysts present in some species. **Odor** not distinctive or pungent. **Spores** longitudinally symmetrical, globose to ellipsoid, 7–20 × 6–16 µm excluding the ornamentation of rods, spines, ridges, a partial to complete reticulum, or any combination of the above; rods and spines 0.5–2.5 (-5) µm tall, lines and ridges are usually less than 1 µm tall; walls up to 2 µm thick, colorless to brown; attachment straight, prominent on many species. **Reaction to Melzer's reagent:** spore ornamentation strongly gray to purple, black or black-spotted; spore walls range from nonreactive to gray or purple; one rare species has nonreactive ornamentation with only a pale purple reaction in the spore wall.

Number of species: Twenty or more from north temperate forests, including several as yet undescribed.

Distribution: In forests of ectomycorrhizal conifers and hardwoods in both Northern and Southern Hemispheres.

Season: Throughout the year when not limited by dry or cold weather.

Keys and descriptions: Singer and Smith (1960) covered most species described from the Northern Hemisphere at that time, but they placed most in *Martellia*. Trappe et al. (2002) corrected the nomenclature, Lebel and Trappe (2000) redefined the genus and presented a complete list of all species at that time, and Trappe and Castellano (2000) added two new species; Castellano et al. (1999) described four species (including *M. fragrans* and *M. idahoensis*) and M. Trappe et al. (2007) described and illustrated two species. Pegler and Young (1979) and Miller (1988) described and illustrated representative spores.

Comments: *Gymnomyces* cannot be distinguished from other members of the Russulaceae by spore characters alone; they are separated on the basis of fruit-body morphology. *Gymnomyces* is derived from the mushroom genus *Russula* but is totally truffle-like in lacking a stem, having a chambered gleba rather than cap and gills, and fruiting belowground. For differences from *Cystangium*, see the comments for that species.

Hydnobolites (Phylum Ascomycota, Order Pezizales, Family Pezizaceae) (fig. 38)

James Trappe

Figure 38—*Hydnobolites californicus*.

Name derivation: Coined by Tulasne and Tulasne (1843) from Greek *hydno*- (fungus), -*bol*- (a lump) and -*ites* (having the nature of), hence “ a fungus having the nature of a lump.”

Fruit-bodies subglobose to irregular, furrowed, 0.3–3 cm broad. **Peridium** white to brown, glabrous to scabrous. **Gleba** gray to brown, marbled with white veins lined with peridium-like tissue. **Odor** mild to pungent. **Spores** borne in rounded asci randomly distributed in glebal tissue, globose to broadly ellipsoid, 12–24 (-30) µm broad excluding the ornamentation of a broad-meshed, honeycomb-like reticulum 3–4 µm tall; walls 0.5–1 µm thick, colorless to pale brown. **Reaction to Melzer’s reagent** not distinctive.

Number of species: Two known from north temperate forests. DNA analyses suggest additional, as yet undescribed species exist (M.E. Smith, personal communication, postdoctoral research fellow, Farlow Herbarium, Harvard University, Cambridge, Massachusetts 02138).

Distribution: North America and Europe. This genus is infrequently encountered and is usually localized.

Season: Summer and autumn.

Keys and descriptions: Trappe (1979) described the genus. Gilkey (1939, 1954b) described *H. californicus* Fischer, known only from California and Oregon. Montecchi and Sarasini (2000) described *H. cerebriformis* Tul. and Tul. from Europe; it, or a similar species, occurs in eastern North America.

Comments: Spores of *Hydnobolites* spp. resemble those of *Terfezia spinosa* Harkn., *T. longii* Gilkey, and *Mattirolomyces terfezioides* (Mattir.) E. Fisch. Its pale-colored spores readily distinguish it from genera with globose, reticulate, but dark brown spores (*Elaphomyces*, *Scleroderma*, and *Tuber*). *Hydnobolites* differs from all these genera by having the gleba marbled with veins lined with inflated cells similar to those of the peridium. The veins open to the fruit-body surface and are essentially narrow insertions of the peridium into the gleba.

Hydnotrya (Phylum Ascomycota, Order Pezizales, Family Discinaceae) (fig. 39)

Matthew Trappe

Figure 39—*Hydnotrya variiformus* var. *pallidus.*

Name derivation: Coined by Berkeley and Broome (1846) from Greek, *hydno-* (fungus) and *-trya* (a hole or opening), in reference to the openings from the gleba to the surface of the fruit-body.

Fruit-bodies irregular and infolded, 0.5–8 cm broad. **Peridium** ivory to pink, orange brown or dark purplish brown, smooth or minutely scurfy. **Gleba** hollow to fleshy-firm, concolorous with the peridium and permeated with small to large, labyrinthine chambers formed by complex infolding and fusing of the fruit-body walls. **Odor** not distinctive to strongly garlicky. **Spores** borne in cylindric to clavate asci in a hymenium, ellipsoid to globose, 16–34 × 16–35 µm excluding ornamentation of spines, warts, or an amorphous epispore; wall 1–3 µm thick, colorless in youth, becoming yellow to brown at maturity. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 12 described from north temperate forests; more remain to be described.

Distribution: North temperate forests.

Season: Spring through autumn, although individual species tend to occur either only in spring or only in autumn.

Keys and descriptions: Gilkey's (1954b) treatment is the best available, but the genus is in serious need of revision and updating. Trappe and Castellano (2000) described two new species. Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated five species between them.

Comments: The spores of most *Hydnotrya* spp. are distinctive enough to permit species identifications from spores alone, although those with globose, spiny spores are difficult to distinguish from certain *Elaphomyces* or *Genabea* spp. For overlap with species of *Hydnotryopsis*, see comments under that genus. *Hydnotrya cubispora* is particularly distinctive, in that its spores have a thick epispore that appears almost rectangular in optical longitudinal section when viewed through a compound microscope.

Hydnotryopsis (Phylum Ascomycota, Order Pezizales, Family Pezizaceae)

Name derivation: Coined by Gilkey (1916) from the Greek generic name *Hydnotrya* and *-opsis* ("resemblance"), hence "resembling a *Hydnotrya*."

Fruit-bodies subglobose to irregular, deeply furrowed, 1–4 cm broad. **Peridium** white to yellowish brown or pink, smooth to roughened. **Gleba** nearly white to yellow or pink, solid, with meandering veins stuffed with asci, spores, and hyphae. **Odor** not recorded. **Spores** ellipsoid, 11–22 × 10–18 µm excluding the ornamentation of warts, pits, or ridges; walls ± 1 µm thick, colorless to brownish yellow. **Reaction to Melzer's reagent:** the asci turn blue.

Number of species: Two are known from north temperate forests, but others remain to be described.

Distribution: Pacific coastal states of the United States.

Season: Spring and early summer.

Keys and descriptions: Trappe (1975c) discussed the two species keyed and described by Gilkey (1954b) as *Choiromyces setchellii* Gilkey and *C. compactus* Gilkey.

Comments: The bluing asci of *Hydnotryopsis* spp. in Melzer's reagent relates them to the Pezizaceae rather than the Discinaceae, which contains the genus *Hydnotrya*. *Hydnotrya* spp. with spores similar to those of *Hydnotryopsis* spp. occur in conifer forests throughout the Western United States, especially at the higher elevations. *Hydnotryopsis*, in contrast, is known only from the Pacific coastal states and appears to be usually associated with oaks and other hardwoods.

Hymenogaster (Phylum Basidiomycota, Order Agaricales, Family Hymenogastraceae) (fig. 40)

Name derivation: Coined by Vittadini (1831) from Greek, *hymeno-* (membrane or thin skin) and *-gaster* (literally "stomach" but in mycology referring generally to gasteromycetes, i.e., puffballs), hence "thin-skinned puffball."

Fruit-bodies subglobose to globose or irregular, 4–50 mm broad. **Peridium** white to yellow or brown, in some species staining dark brown where bruised or exposed, smooth or felty or wrinkled, often thin and fragile. **Gleba** dark brown, often with a basal pad, sometimes with a prominent, dendroid columella. **Odor** not distinctive or of green corn, cheese, pine pitch, or unpleasant. **Spores** ellipsoid to ovoid, obovoid, fusoid, citriform, or subcylindrical with an obscure to prominent apical hump, 13–40 × 4.5–18 µm including the ornamentation of wrinkles, irregular ridges, warts, or pegs; walls mostly one-layered, 0.5–1 µm thick, pale yellow-brown to cinnamon or dark brown; symmetrical sterigmal attachment usually broad; apical hump smooth, thin-walled, colorless to light brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: Unknown; the genus needs critical revision. Some Southern Hemisphere species have been introduced to the Northern Hemisphere as "hitchhikers" on roots of imported *Eucalyptus* seedlings.


Matthew Trappe

Figure 40—*Hymenogaster subalpinis*.

Distribution: Beneath ectomycorrhizal shrubs and trees in both Northern and Southern Hemispheres.

Season: Individual species may be strongly seasonal, others fruit throughout the year. In the Pacific Northwest, *Hymenogaster subalpinus* is the most common hypogeous fungus in winter.

Keys and descriptions: The most complete work on *Hymenogaster* (Dodge and Zeller 1934) is out of date. Less inclusive keys and descriptions are to be found in A.H. Smith (1966) and Fogel and Trappe (1985) for North America. M. Trappe et al. (2007) described and illustrated *H. subalpinus*. With the present state of knowledge, attempts to identify species are frustrating as often as not.

Comments: *Hymenogaster* is related to the mushroom genus *Hebeloma* (Peintner et al. 2001), the two genera being in the family Hymenogastraceae (Matheny et al. 2006). Some hypogeous species related to the genus *Cortinarius* in the Cortinariaceae were assigned to *Hymenogaster* before molecular data were available. Species from two different families cannot be put in a single genus, however, so here we informally assign the *Cortinarius* relatives to the genus *Protoglossum* for the moment. The differences between *Hymenogaster* and *Protoglossum* are discussed below under the latter genus.

Hysterangium (Phylum Basidiomycota, Order Hysterangiales, Family Hysterangiaceae) (fig. 41)

Matthew Trappe

Figure 41—*Hysterangium coriaceum*.

Name derivation: Named by Vittadini (1831) from the Greek *hyster*- (womb) and -*angion* (a vessel, a term used by the 19th-century mycologists to mean "fruit-body"). Hence, a "womb-vessel," a redundant way of saying "spore-bearing vessel" or fruit-body.

Fruit-bodies subglobose to globose or irregular, 0.5–3 cm broad, often with a large rhizomorph emanating from the base. **Peridium** thin and membranous to 1 mm thick, often readily separable from the gleba, white to pink, yellow, or brown, many species staining pink to brown where cut or bruised; some species are enclosed by numerous, outgrowing hyphae and rhizomorphs on the base and sides of fruit-bodies or overall. **Gleba** pink to gray, green, olive, or pale brown, with small to prominent, usually labyrinthine chambers and a weak to prominent, dendroid, gelatinous to cartilaginous, gray to reddish brown columella. **Odor** not distinctive to fruity, wine-like, chlorine-like or nauseous-sweet. **Spores** rod-shaped to narrowly ellipsoid or fusoid, 10–30 × (3-) 4–8 µm, smooth to minutely ornamented, usually enveloped in a wrinkled to inflated outer membrane, longitudinally symmetric; wall up to 0.5–1.5 µm thick, colorless to pale brownish yellow. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 25 from north temperate forests, with more described from the Southern Hemisphere.

Distribution: Worldwide except for Africa and Antarctica.

Season: Throughout the year; many species are not strongly seasonal.

Keys and descriptions: The most comprehensive treatment of the genus is that of Castellano (1988). North American species were keyed and described by Zeller and Dodge (1929). Both of these papers are out of date. M. Trappe et al. (2007) described and illustrated three Pacific Northwest species.

Comments: *Hysterangium* and *Trappea* bear some resemblance macroscopically, but the tiny spores of *Trappea* barely overlap in size with any *Hysterangium* species. Most *Hysterangium* species have a distinct, often wrinkled outer layer, a character that separates them from *Rhizopogon* species having spores of the same size.

Kjeldsenia (Phylum Basidiomycota, Order Phallales, Family Claustulaceae) (fig. 42)

Name derivation: Coined by Colgan et al. (1995) in honor of Dr. C.K. Kjeldsen, professor of Botany at Sonoma State University, California.

Fruit-bodies subglobose to irregular, 0.4–2 cm broad. **Peridium** slightly pubescent, white, turning yellow upon handling and reddish brown when exposed for long periods. **Gleba** brown to dark brown, of empty locules and a reduced columella. **Odor** not recorded. **Spores** ellipsoid, 7.5–10.5 × (4-) 4.4–4.5 µm excluding the ornamentation of irregularly shaped warts mostly < 1 µm tall; wall ± 1 µm thick, pale yellow to golden. **Reaction to Melzer's reagent** not distinctive.

Number of species: One, *Kjeldsenia aureispora*.

Distribution: The only known collection was gathered in Mendocino County, California, at 500-ft elevation in a mixed stand of *Abies grandis*, *Lithocarpus densiflora*, and *Pseudotsuga menziesii* (Colgan et al. 1995).

Season: April.

Keys and descriptions: Colgan et al. (1995).

Michael Castellano

Figure 42—*Kjeldsenia aureispora*.

Comments: *Kjeldsenia* macroscopically resembles *Sclerogaster* Hesse (Fogel 1977b) but differs in peridial structure, locules, and spore characters. *Kjeldsenia* differs from *Hymenogaster* by having thin-walled, ellipsoid spores lacking a cup-like sterigmal appendage and apical hump. *Kjeldsenia* locules are empty and lined with a hymenium in contrast to the gel-filled locules and disorganized hymenium of *Destuntzia* (Colgan et al. 1995).

Leucangium (Phylum Ascomycota, Order Pezizales, Family Morchellaceae) (fig. 43)

Matthew Trappe

Figure 43—*Leucangium carthusianum*.

Name derivation: Named by Quélet (1883) from Greek, *leuco-* (white) and *-angion* (vessel, receptacle), possibly in reference to the white color of the immature gleba.

Fruit-bodies subglobose to ellipsoid, 2–8 cm broad. **Peridium** brown and smooth or black and warty. **Gleba** solid, initially white, then developing gray to dark gray pockets of spore-bearing asci separated by white veins. **Odor** fruity to garlicky. **Spores** fusoid-citriform to ellipsoid, 60–75 (-90) × 20–35 µm, smooth, the walls 1–2 µm thick, colorless to smoky olive. **Reaction to Melzer's reagent** not distinctive.

Number of species: One species described, *L. carthusianum*, plus at least one other, *L. brunneum*, as yet undescribed.

Distribution: In PNW forests mostly with *Pseudotsuga*, but *Abies* and *Picea* often present.

Season: Autumn and winter.

Keys and descriptions: Trappe (1979) described the genus. M. Trappe et al. (2007) described and illustrated both species.

Comments: Once assigned to the genus *Picoa*, *Leucangium* spp. can be differentiated by size and shape of its spores. *L. carthusianum* has distinctive, eye-shaped spores. It occurs in France with beech (*Fagus* spp.) and oaks (*Quercus* spp.); although very similar, its Pacific Northwest representatives may be a different species. Both Pacific Northwest species are harvested commercially and prized by gourmets.

Leucogaster (Phylum Basidiomycota, Order Russulales, Family Albatrellaceae) (fig. 44)

Name derivation: From Greek, *leuco*- (white) and -*gaster* (literally "stomach," but in mycology referring to gasteromycetes, i.e., puffballs). Hence, the "white puffball" as coined by Hesse (1882) in reference to the white gleba and generally overall pale coloration of the fruit-body.


Matthew Trappe

Figure 44—*Leucogaster citrinus.*

Fruit-bodies globose to irregular, 1–5 cm broad. **Peridium** white to yellow, often staining red when dried, felty, with sparse to abundant rhizomorphs appressed on the base and sides. **Gleba** white, when moist exudes a sticky, white fluid from the rounded, spore-filled chambers 1–2 mm broad. **Odor** pleasant (often fruity) to oily. **Spores** globose to broadly ellipsoid, 6–19 µm broad excluding the ornamentation of a honeycomb reticulation with spines at the junction of the ridges, 0.5–2 µm tall; the entire spore is enclosed in a loose, smooth, thin-walled membrane; walls 1–3 µm thick, colorless; attachment inconspicuous, straight. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 15 from north temperate forests.

Distribution: North America and Europe in forests of ectomycorrhizal hosts from sea level to high elevations in the mountains. One species is known from Australia (Beaton et al. 1985).

Season: Spring through autumn, often in summer in the mountains.

Keys and descriptions: The 60-year-old monograph by Zeller and Dodge (1924) was revised by Fogel (1975), who included a key to species. Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated three species between them.

Comments: *Leucogaster* spp. are distinctive in having colorless, reticulate spores enclosed in a loose-fitting membrane exuding a sticky fluid when moist and cut open.

Leucophleps (Phylum Basidiomycota, Order Russulales, Family Albatrellaceae) (fig. 45)

James Trappe

Figure 45—*Leucophleps magnatus*.

Name derivation: From Greek, *leuco-* (white) and *-phleps* (vein), named by Harkness (1899) in reference to the white veins of the gleba. **Fruit-bodies** globose to irregular, 1–3 cm broad. **Peridium** white to pale yellow or pale brown, often with clusters of rhizomorphs. **Gleba** white, in moist conditions exudes a sticky white fluid from the spore-filled, labyrinthine chambers ± 0.5 mm broad. **Odor** not distinctive to pleasant; when dried, some species have an aroma of celery salt. **Spores** globose to ellipsoid and longitudinally symmetric, 8–19 (-22) × 7–17 (-22) µm excluding the ornamentation of minute, mucilage-embedded spines 0.1–2 µm tall; walls 1–2 µm thick, colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: Four described from north temperate forests.

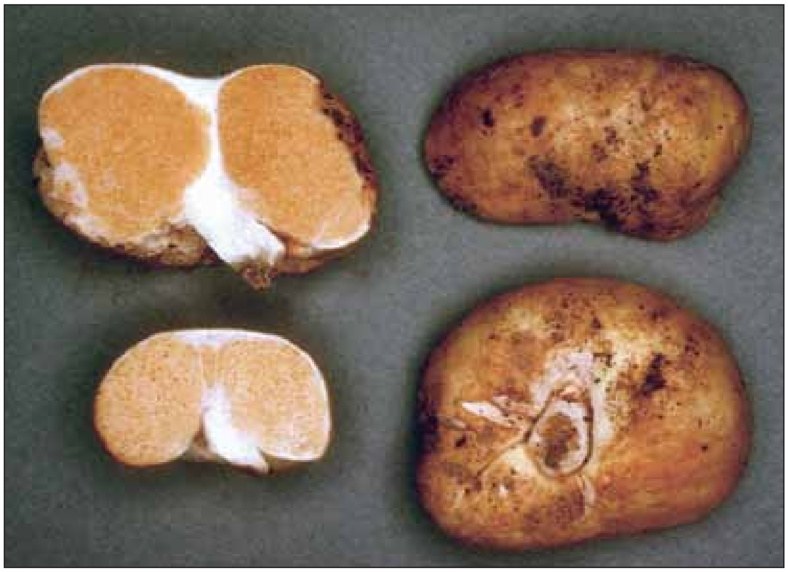
Distribution: Ectomycorrhizal forests from sea level to high mountains of western North America (Fogel 1979), Mexico, and central Europe.

Season: Spring through autumn.

Keys and descriptions: Fogel (1979); M. Trappe et al. (2007) described and illustrated *L. spinispora*.

Comments: *Leucophleps* is distinctive in exuding a sticky fluid when moist and cut open and having spores ornamented with crowded, minute, colorless, mucilage-embedded spines that do not react to Melzer's reagent.

Macowanites (Phylum Basidiomycota, Order Russulales, Family Russulaceae) (fig. 46)



James Trappe

Figure 46—*Macowanites chlorinosmus*.

Name derivation: In honor of the botanist Peter MacOwan, who collected the type species in South Africa (Kalchbrenner 1876). The Greek suffix *-ites* (indicating a close connection) was appended to differentiate its generic name from *Macowania*, a genus in the aster family.

Fruit-bodies similar to *Gymnomyces* but with a prominent columella and stem. **Peridium** smooth, dry to slimy, white to yellow, reddish or purplish, enclosing the gleba, leaving a narrow opening between the gleba and stem, or in a few species expanding belowground; lacking an outer layer of inflated cells. Stem usually vestigial and protruding only a few millimeters below the gleba, white or sometimes rose tinted. **Gleba** of contorted and intergrown or compressed lamellae or of small chambers, white to deep yellow. **Odor** mild or in some species strongly chlorinaceous or of iodine. **Spores** ellipsoid to globose, 6–15 µm broad excluding an ornamentation of warts, spines, or a reticulum 0.1–2.5 µm tall. **Reaction to Melzer's reagent:** spore walls faintly gray to purplish, ornamentation unevenly to evenly purple to black.

Number of species: About 20 from north temperate forests and many more from the Southern Hemisphere.

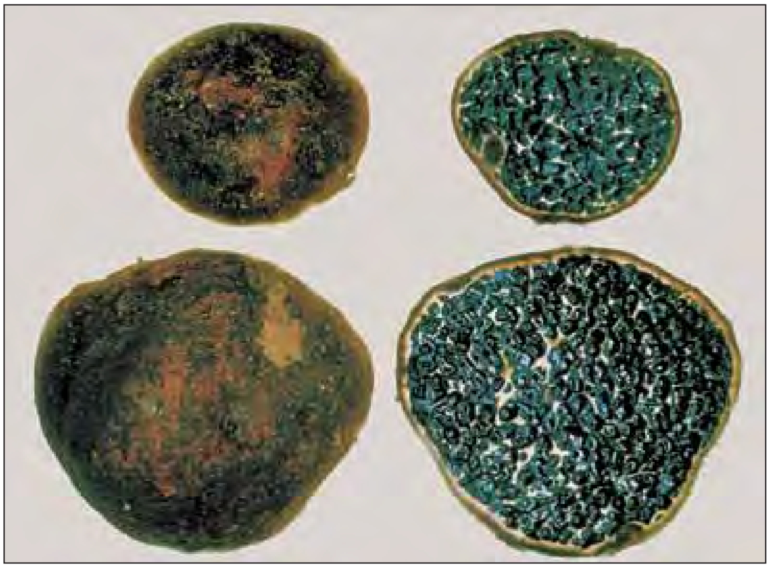
Distribution: Hypogeous under ectomycorrhizal conifers and hardwoods in western and southeastern North America, South America, Russia, South Africa, and Australasia. In the Pacific Northwest they are particularly abundant in wet forests such as the spruce-hemlock stands of the coastal fog belt.

Season: Summer and autumn.

Keys and descriptions: Singer and Smith (1960) covered the genus as conceived at that time. Later, A.H. Smith (1963) described new species and revised the key to the species; Pegler and Young (1979) and Miller (1988) described and illustrated representative spores. Trappe et al. (2002) presented a complete list of all species then known and have corrected the nomenclature for the entire genus. Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated four species between them.

Comments: *Macowanites* spp. externally resemble small *Russula* mushrooms that have a stem too reduced to lift them out of the soil. Mycologists often used to discard them in the field as "aborted *Russula* specimens."

Melanogaster (Phylum Basidiomycota, Order Boletales, Family Paxillaceae) (fig. 47)



James Trappe

Figure 47—*Melanogaster euryspermus.*

Name derivation: From Greek, *melano-* (black), and *-gaster* (literally "stomach" but in mycology generally referring to gasteromycetes, i.e., puffballs), hence "black puffball" in reference to the black gleba common to most species (Corda 1831). It is not a puffball, however; the gleba is gelatinous rather than powdery.

Fruit-bodies globose, ellipsoid, or irregular, 1–6 cm broad, with some species occasionally reaching up to 10 cm. **Peridium** dark brown to brownish black, felty, usually with robust rhizomorphs appressed onto the bottom and sides, in wet weather often beset with drops of brown liquid. **Gleba** dark brown to black, gel-filled chambers separated by white to pale yellowish brown veins. **Odor** fruity to garlicky, metallic, or sweet-oily. **Spores** ellipsoid to ovoid, obovoid, fusoid, ventricose, or subcitriform, 6–22 × 3.5–13 µm, longitudinally symmetrical, smooth, with a truncate base; wall one- to two-layered, 0.5–1.5 µm thick, pale brown to dark brown, purple-brown, dark purple, or nearly black. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 19 from north temperate forests; species concepts are currently being defined in a new monographic treatment of the genus (Wang Yun, personal communication, research scientist, New Zealand Crop and Food Research, Ltd., Invermay Agricultural Center, Private Bag 50034, Mosgiel, New Zealand).

Distribution: Common in the Northern Hemisphere in association with ectomycorrhizal conifers and hardwoods from sea level to high-elevation forests; introduced into the Southern Hemisphere on roots of ornamentals such as oaks.

Season: Most species fruit either in spring or in autumn, but fruit-bodies of some can be found throughout the year except in very dry or cold weather.

Keys and descriptions: No recent treatments of the genus have been published. The most comprehensive treatments and keys for North American species are those of Zeller and Dodge (1936). A new world monograph of the genus is currently in preparation (Wang Yun, personal communication).

Comments: The black, gelatinous gleba and dark brown to deep purple spores of *Melanogaster* spp. are distinctive among the smooth-spored hypogeous fungi. Spores of some species in the mushroom genus *Coprinus* may resemble those of *Melanogaster* but usually show an apical pore, which is lacking in *Melanogaster* spores.

Mycolevis (Phylum Basidiomycota, Order Russulales, Family Albatrellaceae) (fig. 48)

James Trappe

Figure 48—*Mycolevis siccigleba*.

Name derivation: Named by A.H. Smith (1965) from Greek, *myco-* (fungus) and Latin, *-levis* (light weight) in reference to the relatively light weight of the fruit-body.

Fruit-bodies subglobose to irregular, 1–5 cm broad. **Peridium** minutely pubescent, white in youth but developing pale yellow to greenish yellow or olive hues with age. **Gleba** white in youth, in age becoming pale olive, with empty, globose chambers, more or less dry. Columella occasionally present. **Odor** fruity to unpleasant. **Spores** globose to ellipsoid, 8–14 (-18) × 9–12 (-16) µm excluding the ornamentation of crowded spines 1–2 µm tall that project from an inner wall layer 1–2 µm thick into an outer surface layer, colorless; basal attachment with a collar. **Reaction to Melzer's reagent:** spines and collar of basal attachment of spores turn purple.

Number of species: The genus contains only one species, *M. siccigleba*.

Distribution: Hypogeous beneath ectomycorrhizal conifers in mountains of the Western United States and Mexico.

Season: Spring and autumn.

Keys and descriptions: The single species is detailed by Fogel (1976).

Comments: These spores are distinctive in their strongly amyloid, crowded spines and basal collar; Fogel (1976) described and illustrated the spores in elegant detail, including electron microscopic photos of the structure of the ornamentation that shows it to be much more complex than what appears by the light microscope to be spines. The fruit-bodies are light weight for their size; Smith (1955) noted the gleba was "like styrofoam."

Nivatogastrium (Phylum Basidiomycota, Order Agaricales, Family Strophariaceae) (fig. 49)


James Trappe

Figure 49—*Nivatogastrium nubigenum*.

Name derivation: From Latin *nivato-* (snowy) and Greek *-gaster* (literally "stomach" but in mycology generally referring to gasteromycetes, i.e., puffballs). The first part of the name refers to the type locality (Sierra Nevada) and at the same time to the fact that "the mature carpophores fade to white" (Singer and Smith 1959). Coincidently, the species also fruits in spring under or adjacent to melting snowbanks.

Fruit-bodies appearing as an unopened mushroom, 3–6 cm tall, 2–6 cm broad, with an obvious stem. **Peridium** yellowish, often with darker brown streaks, fading to whitish with age, smooth, slimy when wet, shiny when dry, usually the margin connected to the stem to enclose the gleba. **Stem** color similar to that of cap. **Gleba** irregularly chambered or with contorted and anastomosed gills, dull cinnamon to bright cinnamon brown at maturity, the stem continuous as a columella through the center of the gleba to the cap. **Odor** fruity, of bubblegum. **Spores** ellipsoid to almond-shaped, 7–13 × 5–8 µm, smooth, longitudinally asymmetric, the attachment nipple angled to the spore axis; wall three-layered, but appearing single-layered at all but the highest magnification, with a narrow, apical pore; walls pale golden brown.
Reaction to Melzer's reagent not distinctive.

Number of species: One known for the genus.

Distribution: Mountains of California and Oregon; epigeous or hypogeous on well-rotted logs, sticks, etc.

Season: *Nivatogastrium nubigenum* Singer and Smith fruits in spring, often under snow, and early summer toward the end of the snowmelt period in high mountain forests.

Keys and descriptions: Singer and Smith (1959) fully described *N. nubigenum,* which is described and illustrated by Castellano et al. (1999).

Comments: *Nivatogastrium* is related to the mushroom genus *Pholiota* in the family Strophariaceae; the two cannot be differentiated by spores alone; however, *Nivatogastrium* depends on animal mycophagy for spore dispersal because, unlike *Pholiota*, it cannot discharge its spores into the air. It is not strictly epigeous, although it can be enclosed in the rotted wood of logs.

Octaviania (Phylum Basidiomycota, Order Boletales, Family Boletaceae)

Name derivation: Named by Kuntze (1893) in honor of the Italian botanist, Vincento Octaviani.

Fruit-bodies globose to irregular, 1–4 (-8) cm broad. **Peridium** white overall to mottled with brown or brown overall, some species becoming red to green, blue or blackish where bruised; felty; rhizomorphs lacking or inconspicuous. **Gleba** white in youth, with age becoming yellow to brown, in some species reddening where cut, with small, empty or spore-filled chambers; columella lacking or rudimentary. **Odor** not distinctive. **Spores** globose to ellipsoid, 9–23 × 9–19 µm excluding the ornamentation of large, conic to blunt warts composed of agglutinated spines 1–3.5 µm long; wall one- to two-layered, 0.5–3 µm thick, yellow to pale yellow-brown, the ornamentation colorless to brown. **Reaction to Melzer's reagent:** spore walls orange red.

Number of species: Nine described from north temperate forests, but most of these belong to other genera (Trappe et al. 2002; J. Trappe and M. Castellano, unpublished data). Several additional, undescribed species have been found in western North America.

Distribution: Widely distributed in temperate zones of the Western Hemisphere as well as Australia and New Zealand, but infrequently collected in the PNW; associated with ectomycorrhizal conifers and hardwoods.

Season: Mostly autumn, but occasionally spring or summer.

Keys and descriptions: Singer and Smith (1960) covered all North American species described to date; Pegler and Young (1979) described and illustrated representative spores. Castellano et al. (1999) described and illustrated three species from the Pacific Northwest.

Comments: Species originally assigned to *Octaviania* later proved to include both ornamented and smooth-spored ones. For reasons detailed by Singer and Smith (1960), the species with ornamented spores had been assigned to a new genus, *Octavianina* (*Octaviania* with the Latin suffix -*ina* denoting the resemblance, hence "*Octaviania* resembler"). The smooth-spored *Octaviania* species were all assigned to the genus *Melanogaster. Octaviania* and *Melanogaster,* as it happens, bear little resemblance to each other. The International Code of Botanical Nomenclature gives priority to the name *Octaviania* for the species with ornamented spores.

Pachyphloeus (Phylum Ascomycota, Order Pezizales, Family Pezizaceae) (fig. 50)

James Trappe

Figure 50—*Pachyphloeus austro-oregonensis.*

Name derivation: Coined by Tulasne and Tulasne (1845) from Greek, *pachy*- (thick) and -*phloe* (bark) in reference to the thick peridium of the fruit-bodies.

Fruit-bodies subglobose, often with a cavity or cluster of grooves. **Peridium** greenish yellow to orange, reddish brown or black, scabrous to coarsely verrucose. **Gleba** yellow to green, gray or nearly black, marbled with pale veins that tend to converge near the fruit-body cavity, solid. **Odor** not distinctive to pungent. **Spores** ornamented with free or mucilage-embedded warts or spines 1–3 µm tall, globose, 14–21 µm broad, excluding ornamentation, wall 1–2 µm thick, colorless to brown. **Reaction to Melzer's reagent:** asci of some species turn faintly green to blue.

Number of species: Six from north temperate forests.

Distribution: Europe, North America, Japan, and undescribed species from Australia and South America.

Season: Spring and autumn.

Keys and descriptions: Trappe (1979) described the genus. Gilkey (1954a, 1954b) covered the North American species known at that time.

Comments: *Pachyphloeus* is notable for its warty peridium, glebal veins that radiate from a cavity, and often lively colors. A much needed revision of the genus is now underway (R. Healy, personal communication, graduate student, Department of Plant Biology, University of Minnesota, St. Paul, MN 55108).

Peziza (Phylum Ascomycota, Order Pezizales, Family Pezizaceae) (fig. 51)

James Trappe

Figure 51—*Peziza ellipsospora*.

Name derivation: An ancient name from Greek, *pezis* (a stalkless mushroom).

Fruit-bodies cerebriform to cup shaped, 0.5–5 cm broad. **Peridium** white to grayish yellow, pink, vinaceous brown or violet, smooth to scabrous or warty. **Gleba** open or with one or a few hymenium-lined chambers, pale yellow to yellow-brown. **Odor** not distinctive to pungent or chlorinaceous. **Spores** globose to ellipsoid, 8–18 × 4–14 µm when smooth, or when ornamented, excluding warts, ridges, or a reticulum; wall single, thin to 1 µm thick, colorless to brown. **Reaction to Melzer's reagent:** asci or tips of asci turn blue.

Number of species: A large genus with at least three truffle-like species from north temperate forests.

Distribution: Worldwide, but hypogeous species have been reported only from western North America and Australia. The hypogeous Australian genus *Hydnoplicata* has been synonymized with *Peziza* by some taxonomists.

Season: Spring through autumn.

Keys and descriptions: Korf (1973) presented a key to species, with additions and comments by Trappe (1979).

Comments: The hypogeous species of *Peziza* have open chambers and sometimes forcible spore discharge, as opposed to the essentially solid, veined ascocarps that lack forcible spore discharge in *Hydnotryopsis*. Some of these taxa may be widely distributed but infrequent and only locally abundant.

Protogautieria (Phylum Basidiomycota, Order Gomphales, Family Gomphaceae [placement uncertain pending DNA analysis])

Name derivation: Coined by A.H. Smith (1965) from Greek *proto* (original) + *Gautieria* (a truffle genus) hence “the original *Gautieria*” to indicate the hypothesis that *Protogautieria* is ancestral to *Gautieria*.

Fruit-bodies ovoid to subglobose or irregular, 1.5–2.5 cm broad. **Peridium** white when young, dull brown or discolored when mature, dry, glabrous to slightly tomentose. **Gleba** chambered, white to yellow, sometimes turning pale red when exposed. **Odor** not recorded. **Spores** ovoid to obovoid or subglobose, 12.5–17 × 7.5–9.5 µm, smooth; wall 1–2 µm thick, colorless. **Reaction to Melzer’s reagent:** longitudinal folds or striations not readily visible in water become reddish orange in KOH.

Number of species: Two from north temperate forests.

Distribution: Western North America in subalpine habitats in soil under *Abies* spp. and mixed conifers, rare.

Keys and descriptions: A.H. Smith (1965).

Comments: One species, *P. lutea*, has cystidia that stain red and a yellow peridium that stains purple with application of KOH. The family and order placement of *Protogautieria* need clarification by DNA analysis.

“Protoglossum” (Phylum Basidiomycota, Order Agaricales, Family Cortinariaceae) (fig. 52)

Name derivation: from Greek *proto-* (first or original) + *-glossum* (tongue). The intent of Massee (1890) in coining this name is obscure, except the peridium of the original species is slimy.


David Largent

Figure 52—“*Protoglossum*” (*Hymenogaster*) *sublilacinus*.

Fruit-bodies globose to irregular, 1–5 cm broad. **Peridium** smooth to felty, often slimy when fresh, whitish to yellow, brown, cinnamon, lilac, violet, or purple. **Gleba** cinnamon to brown, chambered, usually with a white to brownish basal pad and often with a dendroid to truncate columella. **Odor** mild or resinous, in some becoming obnoxious by maturity. **Spores** of PNW species ovoid to ellipsoid, 8–16 × 5–10 µm excluding the ornamentation of fine warts or wrinkles ≤ 1 µm tall; walls < 1 µm thick, ochraceous to brown or cinnamon; sterigmal appendage prominent. **Reaction to Melzer's reagent:** spores not distinctive to reddish orange.

Number of species: Two in the PNW, possibly some in Europe, and several in Australia.

Distribution: In the Pacific Northwest, in mountain forests of *Abies*, *Picea*, *Pinus,* and *Tsuga*.

Season: Spring and summer.

Keys and descriptions: The two Pacific Northwest species have been placed in the genus *Hymenogaster* by past workers. Smith (1966) described and keyed them as *H. idahoensis* and *H. sublilacinus*. He also separated out several other species, which Fogel (1985) synonymized with *H. sublilacinus*.

Comments: DNA analyses indicate that *Protoglossum* is related to the huge mushroom genus *Cortinarius* in the family Cortinariaceae, whereas *Hymenoaster* is related to the mushroom genus *Hebeloma* in the Hymenogastraceae (Peintner et al. 2001). The preliminary phylogenetic tree of *Cortinarius* and its hypogeous relatives demonstrates that past taxonomy of this group based on morphology has not produced a coherent organization within *Cortinarius* or between it and its hypogeous relatives. One solution is to dump all hypogeous species of the complex into *Cortinarius,* despite their obvious morphological and ecological differences, as Peintner et al. (2002) did with the genus *Thaxterogaster*. We regard this as premature, because it drowns a few dozen distinct hypogeous species in an ocean of perhaps 2,000+ *Cortinarius* mushroom species, many of which are at best poorly known. Accordingly, we have informally placed the two PNW species into the only described genus that is based on stemless, hypogeous *Cortinarius*-related truffles, *Protoglossum*. This at least separates them from *Hymenogaster* and places them into the family Cortinariaceae. Because the PNW species differ substantially from the original *Protoglossum* species, however, this is just an interim step until a large amount of additional molecular data become available to sort out this huge complex of fungi.

Radiigera (Phylum Basidiomycota, Order Geastrales, Family Geastraceae) (fig. 53)

James Trappe

Figure 53—*Radiigera fuscogleba*.

Name derivation: From Latin *radii-* (radii) and the suffix *-gera* (bearing), hence "bearing radii." Named by Zeller (1944) in reference to the straight glebal hyphae that radiate from the columella of the fruit-body to its peridium.

Fruit-bodies subglobose to globose with indented base and a basal attachment, 2–8 cm broad. **Peridium** white to pale brown, often staining pink to olive where exposed, bruised, or cut, 3–8 mm thick with a thin, felty outer layer over a thick, crisp-fleshy layer; some species have a third, thin, innermost membrane. **Gleba** white in youth, with a prominent, soft, capitate, white columella, from which straight hyphae radiate to connect with the peridium, becoming pale brown to black from maturation of the pigmented spores, which at full maturity form a powdery mass. **Odor** usually mushroom-like or not distinctive, sometimes metallic-disagreeable at maturity. **Spores** globose to broadly ellipsoid, 2.5–6.5 µm broad including the ornamentation of minute warts or spines; walls thin, nearly colorless to brown; attachment not evident or sometimes prominent as a scar. **Reaction to Melzer's reagent** not distinctive.

Number of species: Four described from north temperate forests.

Distribution: Western North America and northern Europe at low to midlevel elevations; associated with species of *Populus*, *Quercus*, and the Pinaceae.

Season: Spring, summer, or early autumn.

Keys and descriptions: Zeller (1944) initially described three North American species, then added a fourth (Zeller 1948). Kers (1976) reported European finds. Dominquez de Toledo and Castellano (1996) presented a modern treatment of all species.

Comments: Related to the earthstar genus *Geastrum* in the family Geastraceae but remaining closed and belowground. *Radiigera* and its relative *Schenella* have the smallest ornamented spores of all hypogeous fungi. The two differ primarily in the arrangement of spore-bearing tissue of the gleba. These genera do not separate out from small-spored *Sclerogaster* species in a spore key.

Rhizopogon (Phylum Basidiomycota, Order Boletales, Family Rhizopogonaceae) (fig. 54)


James Trappe

Figure 54—*Rhizopogon ochraceorubens.*

Name derivation: From Greek, *rhizo-* (root) *-pogon* (beard), "root-beard," coined by Fries (Fries and Nordholm 1817) in reference to the copious rhizomorphs that often "beard" fruit-bodies of the type species, *R. luteolus* Fr.

Fruit-bodies globose to top-shaped, flattened or irregular, 1–9 cm broad, with some species occasionally reaching up to 15 cm. **Peridium** white to yellow, salmon, red, or brown, often darker on top than at the base, many species staining pink to red, violet, or brown where bruised or cut, 0.5–2 mm thick, smooth or felty or composed of interwoven rhizomorphs, mostly with rhizomorphs appressed at least around the base and sides; KOH solution applied to fresh peridia usually produces a gray to olive, blue, purple, red, brown, or black reaction. **Gleba** white to yellow in youth, with small chambers that are usually empty but in some species filled with spores, at maturity becoming olive, olive-gray, olive-brown, orange-brown, or blackish brown. **Odor** fruity, wine-like, cheesy, or spicy-pungent. **Spores** mostly longitudinally symmetrical and cylindrical to fusoid (spindle-shaped), but some species have ellipsoid or irregularly shaped spores 5–15 (-20) × 2–8 µm, smooth; walls thin except for a few species with walls up to 2 µm thick, individually colorless to pale yellow or pale brown, in mass yellow to olive or brown; attachment straight, inconspicuous or a basal, cupped truncation of the spore. **Reaction to Melzer's reagent** not distinctive in most species, but several in subgenus *Amylopogon* turn gray to deep purple.

Number of species: Over 150 species have been described from north temperate forests, but many probably represent developmental stages of a single species.

Distribution: Throughout the Northern Hemisphere in association with Pinaceae from lower to upper tree lines; abundant in the Southern Hemisphere where Pinaceae have been introduced.

Season: Most fruit only in spring or only in autumn through early winter, but fruit-bodies of some can be found throughout the year except in very dry or very cold weather.

Keys and descriptions: The most comprehensive treatment is that by A.H. Smith and Zeller (1966), as supplemented by additional descriptions of North American species by A.H. Smith (1968), Harrison and Smith (1968), Hosford (1975), Hosford and Trappe (1980), Castellano et al. (1999, as *Alpova* spp.; 2003) and M. Trappe et al. (2007)

Comments: The genera *Alpova*, *Gastroboletus, Gastrosuillus*, and *Truncocolumella* have spores similar to those of some *Rhizopogon* spp., so these genera must be separated on the basis of other structures. Early taxonomists were not aware that *Rhizopogon* fruit-bodies usually change drastically in color and reaction to chemicals such as KOH as they age, so many described species may actually be developmental stages of one or another single species. Molecular analyses are much needed to sort out these and other sources of confusion in species concepts. Distinct, undescribed species are nonetheless still turning up regularly in the PNW, which appears to be a center of evolution for the genus.

Schenella (Phylum Basidiomycota, Order Geastrales, Family Schenellaceae) (fig. 55)

James Trappe

Figure 55—*Schenella pityophilus*.

Name derivation: Coined by Macbride (1911). Schenell is a family surname, but Macbride did not indicate for whom he named the genus.

Fruit-bodies subglobose to ellipsoid with indented base and basal attachment, 1.5–2.5 cm broad. **Peridium** white to rose-colored, 1.5–3 mm thick, with a thin, felty outer layer over a thick, crisp-fleshy layer and a thin, innermost membrane. **Gleba** white in youth, with a prominent, soft, capitate, white columella from which radiate narrow separable cones or tubes within which the spores are formed; at full maturity the spores form a brown to black, powdery mass. **Odor**: not distinctive. **Spores** ellipsoid, 4–8 × 3.5–7 µm including the finely warty ornamentation < 1 µm tall; walls thin, brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: Two species in north temperate forests.

Distribution: Known only from southern France, Mexico, and southwestern Oregon.

Season: Spring and autumn.

Keys and descriptions: Electron micrographs are presented by Jülich (1982) and Jülich and Starr (1983). Dominquez de Toledo and Castellano (1996) produced a modern treatment of the genus as *Pyrenogaster,* later corrected to *Schenella* by Estrada-Torres et al. (2005).

Comments: The reasons for replacing the name *Pyrenogaster* with *Schenella* are outlined on pages 35–37, "The virtues of rules." Binder and Bresinsky (2002) provided evidence for placement of the genus (as *Pyrenogaster*) in the order Geastrales. Molecular phylogenetic studies by Hosaka et al. (2006) evidenced that it should have its own family Pyrenogastraceae. As the name with priority for the type genus of the family is *Schenella*, however, the family name must be Schenellaceae.

Scleroderma (Phylum Basidiomycota, Order Boletales, Family Sclerodermataceae) (fig. 56)

Michael Castellano

Figure 56—*Scleroderma hypogaeum*.

Name derivation: An early name from Greek, *sclero-* (hard) and *-derma* (skin), "hard skin" or "tough skin" in reference to the thick, crisp to leathery peridium characteristic of the genus.

Fruit-bodies (of *S. hypogaeum*) subglobose to irregular, with a cluster of rhizomorphs at the base, 2–6 cm broad. **Peridium** pale brown to pale yellow or brownish yellow in youth with a rosy blush where bruised and pink where cut, smooth to slightly scaly, 0.5–6 mm thick. **Gleba** white and solid in youth, at maturity an olivaceous black to purplish black, powdery spore mass. **Odor** not distinctive to fishy or rancid or otherwise unpleasant. **Spores** of *S. hypogaeum* globose and 15–30 µm broad including the honeycomb-reticulate ornamentation up to 4 µm tall; dark brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 20 species described from north temperate forests, but only one, *Scleroderma hypogaeum* Zeller, is hypogeous. At least 11 as yet undescribed truffle-like species occur in Australia (J. Trappe, unpublished data).

Distribution: The genus is worldwide, most species being epigeous puffballs and not likely used as food by mammals. Truffle-like species have been found only in ectomycorrhizal forests of western North America, South America, and Australia.

Season: Summer through autumn.

Keys and descriptions: Guzmán (1970) monographed the genus *Scleroderma* on a worldwide basis. *Scleroderma hypogaeum* is described in detail by Zeller (1922) and Guzmán (1970).

Comments: The spores are difficult to distinguish from those of some *Elaphomyces* spp., because the size, color, and ornamentation can be similar for the two genera. Indeed, *Elaphomyces subviscidus* was originally described as a *Scleroderma* sp.

Sclerogaster (Phylum Basidiomycota, Order Geastrales, Family Sclerogastraceae)

Name derivation: From Greek, *sclero*- (hard) and -*gaster* (literally "stomach" but in mycology generally referring to gasteromycetes, i.e., puffballs) hence, "hard puffball" in reference to the very firm consistency of some species.

Fruit-bodies globose to irregular, 3–20 mm broad, often in crowded clusters in humus or soil. **Peridium** white to pale yellowish brown, sometimes staining rose where bruised; surface smooth to floccose and bound to surrounding organic matter, often easily separable from the gleba. **Gleba** pale yellow to deep yellow, yellow-brown, or brown, with small chambers filled with spores embedded in gel at maturity; chamber walls narrow and paler than the spore mass; columella absent to moderately developed. **Odor** not distinctive or of vitamin B. **Spores** globose, 4–10 µm broad excluding the ornamentation of spines, warts, or cones 0.2–2 µm tall; walls 0.5–1 µm broad, colorless to yellow or pale brown; sterigmal attachment straight, prominent to inconspicuous. **Reaction to Melzer's reagent** not distinctive.

Number of species: Ten described from north temperate forests, with at least one more undescribed.

Distribution: Western North America and western Europe.

Season: Late spring through autumn.

Keys and descriptions: The monograph by Dodge and Zeller (1936) has been supplemented with a description of a new species by Fogel (1977b).

Comments: The largest *Sclerogaster* spores barely overlap the smallest *Octaviania* spores. The small-spored *Sclerogaster* species will not separate readily from *Radiigera* species in a spore key. The genus is poorly known and needs revision and updating.

Stephensia (Phylum Ascomycota, Order Pezizales, Family Pyronemataceae)

Name derivation: Named by Tulasne and Tulasne (1851) in honor of the English physician and collector of truffle-like fungi, H.O. Stephens.

Fruit-bodies subglobose to irregular, 1–7 cm broad. **Peridium** brown, pubescent to tomentose. **Gleba** solid, white to pale brownish yellow, with veins or chambers lined with asci and loosely stuffed with cottony hyphae. **Odor** strong, unpleasant. **Spores** globose to ellipsoid and 12–26 µm broad or ellipsoid and 28–40 × 15–18 µm, smooth; walls 0.5–1 µm thick, one- to two-layered, colorless. Reaction to Melzer's reagent not distinctive.

Number of species: Four described from north temperate forests, including one undescribed species from Oregon.

Distribution: North America, Europe, and west Asia, infrequent and usually very localized.

Season: Summer and autumn.

Keys and descriptions: Trappe (1979) described the genus. *S. bynumii* is described by Trappe et al. (1997), who provided a key to the species of the genus.

Comments: *Stephensia* is rare in the PNW; *S. bynumii* is known only from Clackamas and Marion Counties of northwestern Oregon.

Thaxterogaster (Phylum Basidiomycota, Order Agaricales, Family Cortinariaceae) (fig. 57)

James Trappe

Figure 57—*Thaxterogaster pinguis*.

Name derivation: Named by Singer (1951) in honor of the eminent American mycologist, Roland Thaxter (1858–1932); "Thaxter" and *-gaster* (Greek, literally "stomach" but in mycology generally referring to the gasteromycetes, i.e., puffballs), hence "Thaxter's puffball."

Fruit-bodies with stem and cap, resembling an unopened mushroom with its margin at most only slightly separated from the stem, 1–10 cm tall, 0.5–8 cm broad. **Peridium** roughened to silky or smooth and shiny, dry to slimy, white to olive, brown, purple-brown, violet, or purple; the margin of the cap remaining attached to the stem or seceding slightly to expose a sliver of gleba. **Stem** smooth to silky or viscid, white to pale brown, violet, or purple, penetrating through the gleba. **Gleba** of chambers or contorted and anastomosed gills, brown to rusty brown. **Odor** not distinctive to faintly fragrant. **Spores** subglobose to ellipsoid or obovoid, 8–25 × 5–15 µm excluding the ornamentation of warts and wrinkles up to 2 µm tall; wall ≤ 1 µm thick, brown; sterigmal attachment straight in some species, angled to the longitudinal axis of the spore in others, or a mix of both in still others. **Reaction to Melzer's reagent** not distinctive.

Number of species: Three from north temperate forests, but several dozen occur in the Southern Hemisphere.

Distribution: Associated with ectomycorrhizal trees and shrubs. Of the three known North American species of *Thaxterogaster*, the most widely distributed is *T. pinguis* (Zeller) Singer and Smith; it fruits abundantly under *Abies* spp. in the mountains of western North America. *Thaxterogaster pavalekii* and *T. thiersii* Calhoun in Oregon and California, respectively, are associated with coastal forests.

Season: Late summer and autumn.

Keys and descriptions: Singer and Smith (1958a, 1963) provided the most complete coverage at that time, but their monoraphs are now out of date. Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated *T. pavelekii* and *T. pinguis.*

Comments: Peinter et al. (2002) transferred all *Thaxterogaster* spp. to the closely related genus *Cortinarius*, but we retain the name *Thaxterogaster* because it separates the hypogeous, ecologically distinct species from the epigeous *Cortinarius* species. See also the comments under *Protoglossum* (p. 89).

Trappea (Phylum Basidiomycota, Order Phallales, Family Trappeaceae) (fig. 58)

James Trappe

Figure 58—*Trappea darkeri*.

Name derivation: Named by Castellano (1990) in honor of J.M. Trappe for his contributions to knowledge of truffle-like fungi.

Fruit-bodies subglobose to irregular, 1–5 cm broad, with one or several rhizomorphs emerging from the base. **Peridium** generally thin, in one species evanescent, white but slowly becoming yellow-brown to pink where handled or exposed, with an underlying layer of sterile chambers. **Gleba** olive to brown-olive, olive-green, dark green, or bright green. With small, empty chambers and a well-developed, dendroid, gelatinous to cartilaginous columella. **Odor** not distinctive or of gasoline. **Spores** ellipsoid to oblong, 3–6 × 1–3.5 µm, smooth; walls less than 0.5 µm thick, colorless to green-tinged. **Reaction to Melzer's reagent** not distinctive.

Number of species: *Trappea darkeri* is described from north temperate forests; DNA analysis of *T. phillipsii* and *T. pinyonensis* indicates they should be given a genus of their own in the family Gallaceae (Hosaka et al. 2006).

Distribution: Western North America, Spain, India, and Australia.

Season: Throughout the year.

Keys and descriptions: *Trappea darkeri* is described in detail by M. Castellano (1990) and M. Trappe et al. (2007).

Comments: *Trappea* species have the smallest spores of all the truffle-like fungi. The largest of the *Trappea* spores barely overlap in length with the smallest *Rhizopogon* species spores.

Truncocolumella (Phylum Basidiomycota, Order Boletales, Family Suillaceae) (fig. 59)

Matthew Trappe

Figure 59—*Truncocolumella citrina*.

Name derivation: From Latin, *trunc*- (trunk) and -*columella* (little column), named by Zeller (1922) in reference to the "tree-like column" of sterile tissue (columella) that penetrates the gleba from the base.

Fruit-bodies 2–8 cm broad, often with a basal projection. **Peridium** bright yellow and felty when freshly collected, soon fading to dull yellow. **Gleba** gray to olive or brown, with empty chambers and a prominent, pale yellow to yellow, dendroid columella penetrating the gleba from the fruit-body base. **Odor** fruity to mushroomy. **Spores** ellipsoid, 6–10 × 3.5–5 µm, smooth, longitudinally symmetrical; walls thin, colorless. **Reaction to Melzer's reagent** not distinctive.

Number of species: One.

Distribution: *T. citrina* is commonly associated with *Pseudotsuga menziesii* (Mirb.) Franco in the PNW but occasionally occurs in the Great Basin and the Rocky Mountains.

Season: Summer and early autumn.

Keys and descriptions: A.H. Smith and Singer (1959). M. Trappe et al. (2007) described and illustrated *T. citrina*.

Comments: *Truncocolumella* resembles *Rhizopogon* except for having a dendroid columella. It sometimes occurs in bright yellow clusters that always please the collector who finds them.

Tuber (Phylum Ascomycota, Order Pezizales, Family Tuberaceae) (fig. 60)

Matthew Trappe

Figure 60—*Tuber gibbosum*.

Name derivation: The ancient Latin word for truffle.

Fruit-bodies subglobose to irregular and deeply lobed and furrowed, some species with a pronounced cavity, 0.5–12+ cm broad. **Peridium** white to yellowish brown, reddish brown or black, often mottled with one or more of these hues, smooth to scurfy or strongly verrucose, usually with furrows of paler color where internal veins of tissue emerge from the gleba. **Gleba** solid, white to gray in youth but gradually becoming brown to black as spores mature, with meandering white to grayish yellow veins that often emerge through the peridium. **Odor** usually prominent at maturity, pungent, garlicky, cheesy, or wine-like. **Spores** borne in randomly distributed asci, globose to ellipsoid, 32–88 × 21–54 µm excluding the ornamentation of spines or an irregular to honeycomb-like reticulum 2–5 (-8) µm tall; walls single, 2–5 µm thick, pale brown to dark brown. **Reaction to Melzer's reagent** not distinctive.

Number of species: About 60 described from north temperate forests and numerous others undescribed.

Distribution: In forests and woodlands of ectomycorrhizal hosts in the Northern Hemisphere; introduced to the Southern Hemisphere as accidental "hitchikers" on exotic ectomycorrhizal host species such as oak, hazel (*Corylus* spp.), pine, or Douglas-fir or purposely inoculated on oaks or hazels to establish commercial truffle orchards.

Season: Most species have well-defined fruiting seasons, e.g., spring or autumn.

Keys and descriptions: Gilkey (1939, 1954b) treated what was known at that time of the North American species. Trappe (1979) described the genus. Additional North American species have been described by Colgan and Trappe (1997), Trappe and Castellano (2000), and Frank et al. (2006). Castellano et al. (1999) and M. Trappe et al. (2007) described and illustrated 12 species between them.

Comments: This large and important genus has never been satisfactorily monographed for North America. It is the most widespread of the North American hypogeous ascomycetes, and it contains PNW species commercially harvested for table use: *T. gibbosum* and *T. oregonense*. These two species are detailed to good advantage by M. Trappe et al. (2007) for use by truffle harvesters.

Youngiomyces (Phylum Zygomycota, Order Endogonales, Family Endogonaceae)

Name derivation: In honor of British mycologist T.W.K. Young.

Fruit-bodies of the only species known from the PNW, *Y. stratosus,* ± 1 mm thick by 3–6 mm broad. **Peridium** white and cottony or absent. **Gleba** white to gray. **Odor** not distinctive. **Spores** ellipsoid to globose, ovoid, obovoid, pyriform, or irregular, 113–177 × 82–150 µm excluding the enclosing mantle 8–13 µm thick of tightly adherent hyphae; gametangia spaced apart from each other; walls two-layered, each 4–8 µm thick, colorless. **Reaction to Melzer's reagent** not recorded.

Number of species: Of the two species described from north temperate forests, only *Y. stratosus* has been found in the PNW.

Distribution: *Youngiomyces stratosus* is known only from the type collection in Benton County, Oregon, possibly not rare but certainly inconspicuous and easily overlooked.

Season: Early summer.

Keys and descriptions: Gerdemann and Trappe (1974), as *Endogone stratosa*.

Comments: The large, hypha-mantled spores of *Youngiomyces stratosa* together with their separated gametangia distinguish them readily from *Endogone* spp.

Keys to Genera

Truffles have a limited number of macroscopic characters for use in keys. Having evolved the belowground fruiting habit, they often lack distinctive features such as stems or brightly colored caps. Many resemble small potatoes or dirt clods more than a mushroom or cup fungus. Consequently, a key based solely on macroscopic characters has limitations. We present a macroscopic key and have tried to use common words in lieu of technical terms when possible. The first challenge is to determine whether a specimen is a member of the Ascomycota, Basidiomycota, Glomeromycota, or Zygomycota. No single macroscopic character differentiates the two groups. Accordingly we present **Key 1** for this first determination. If the specimen is in the Ascomycota, one can turn to **Key 2**. **Key 3** covers the Basidiomycota, and **Key 4** the Glomeromycota and Zygomycota. In Keys 3 and 4, some choices depend on the specimen being mature, which can be determined in some cases by the application of a drop of iodine to see if the specimen gives a blue or black reaction. It often won't unless it is at least partially matured, but how does someone without a microscope check whether asci are filled with spores? We have not determined a way around such a dilemma. Fortunately, most collections will include some mature specimens.

In some cases a particular genus keys out in two or more places. The genus *Tuber*, for example, does so because it is diverse in form and color and yet difficult to describe in a readily understood way without recourse to microscopic characters.

Use of macroscopic characters to determine a genus is a first approximation. With experience, one learns to recognize many genera on sight. Truffles are full of surprises, however, and even the most experienced collector can mistake a generic identification before using the microscope. Fortunately, spores are very diagnostic for identification of truffles, so one can in most cases confirm the genus of a specimen by combining macrocharacters with spore or other microscopic characters. For that reason, we have provided references to keys of species for each genus discussed in the preceeding generic discussions. The user of those resources will soon realize, however, that many genera are poorly known. Progress is happening in the taxonomy of these wonderful fungi, but it is slow because so few mycologists work with them.

Key 1: Differentiating Pacific Northwestern Genera of Ascomycota, Basidiomycota, Glomeromycota, and Zygomycota Truffles by Macroscopic Characters

1. Truffle surface ± evenly covered with round to angular warts (use hand lens) .... **Ascomycota, Key 2**
1. Truffle surface not warty **2**
    2. Truffle solid in cross section (use hand lens) **3**
    2. Truffle with one to many empty or spore-filled canals or chambers **6**
3. Truffle interior gelatinous or exuding a sticky fluid **4**
3. Truffle interior firm to crisp, not exuding a sticky fluid **5**
    4. Interior consisting of large spores visible with a hand lens as whitish or brown dots; fruit-bodies < 15 mm broad .... **Zygomycota, Key 4**
    4. Spores too small to be seen with a hand lens, in brown to black pockets separated by paler veins or the fruit-body interior white to pale yellow overall .... **Basidiomycota, Key 3**
5. Interior consisting of large spores visible with a hand lens as brown to black dots; spores massed or embedded in white, cottony hyphae; fruit-bodies < 15 mm broad ...... **Glomeromycota and Zygomycota, Key 4**
5. Interior with spores borne in rounded to irregular or meandering groups separated by meandering, white veins of generally firm (not cottony) tissue .... **Ascomycota, Key 2**
    6. (from 2) Chambers single to many, > 3 mm broad .... **Ascomycota, Key 2**
    6. Chambers or canals numerous, < 3 mm broad **7**
7. Truffle with a stem or stemlike tissue in vertical cross section .... **Basidiomycota, Key 3**
7. Truffle lacking a stem or stemlike tissue in vertical cross section **8**
    8. Truffle with rootlet-like strands (rhizomorphs) at base or appressed on surface ..... **Basidiomycota, Key 3**
    8. Truffle lacking rhizomorphs **9**
9. Truffle interior with long, meandering canals .... **Ascomycota, Key 3**
9. Truffle interior with rounded to slightly elongate or irregular chambers **10**
    10. Truffle flesh soft, white to yellow or brown .... **Basidiomycota, Key 3**
    10. Truffle flesh firm to crisp, gray to brown or purple .... **Ascomycota, Key 2**

Key 2: Ascomycota Truffle Genera in the Pacific Northwest

1. Truffle with one to many empty or spore-filled chambers **2**
1. Truffle solid or nearly solid, often marbled with veins or narrow canals **9**
    2. Truffle with a single chamber **3**
    2. Truffle with multiple chambers or open canals **5**
3. Chamber in youth rounded, containing cottony hyphae, at maturity filled with spore powder .... ***Elaphomyces***
3. Chamber hollow, often convoluted, lined with peridium-like tissue **4**
    4. Truffle brown or black, with a basal tuft of mycelium .... ***Genea***
    4. Truffle pink to wine colored, lacking a basal tuft of mycelium .... ***Gilkeya***

5. (from 2). Truffle warty **6**

5. Truffle smooth, roughened, or minutely hairy (check with hand lens) **7**

    6. Truffle ≤ 1 cm broad, yellowish .... ***Genabea***

    6. Truffle generally > 1 cm broad, brown to wine-colored or purple .... ***Peziza***

7. (from 5) Surface smooth or roughened, not hairy but sometimes with a basal tuft of hyphae **8**

7. Surface minutely hairy (check with hand lens) .... ***Geopora***

    8. Drop of iodine on cross-sectional cut of mature truffle yellow to orange brown; basal tuft of hyphae lacking .... ***Hydnotrya***

    8. Drop of iodine on cross-sectional cut through mature truffle blue to black (it may be yellow to orange on immature specimens); basal tuft of hyphae often present .... ***Peziza***

9. (from 1) Surface minutely hairy; interior whitish to pale brown .... ***Stephensia***

9. Surface smooth, roughened, or warty **10**

    10. Surface warty **11**

    10. Surface smooth or roughened but not warty **14**

11. Truffle with an irregular cavity or rounded and wrinkled zone on one side; the interior with veins that radiate from the cavity or wrinkled zone **12**

11. Truffle even to irregular but lacking a distinct cavity or wrinkled zone **13**

    12. Truffle with a distinct cavity; interior white .... ***Balsamia***

    12. Truffle with a cavity or rounded and wrinkled zone; interior yellowish, greenish, or brown .... ***Pachyphloeus***

13. (from 11) Surface brown to black; interior white in youth, by maturity with olive to gray or black pockets of spores separated by white tissue .... ***Leucangium***

13. Surface grayish yellow, brown or black; interior with meandering veins, white in youth, by maturity brown to dark brown with white veins .... ***Tuber***

    14. (from 10) Truffle with an irregular cavity on one side; interior white, with veins that radiate from the cavity .... ***Barssia***

    14. Truffle rounded to irregular but lacking a cavity on one side **15**

15. Drop of iodine on cross-sectional cut through mature truffle interior blue to black (it may be yellow to orange on immature specimens) **16**

15. Drop of iodine on cross-sectional cut of mature truffle yellow to orange brown **17**

    16. Truffle surface nearly white, the interior pale violaceus gray marbled with white veins .... ***Cazia***

    16. Truffle surface white to dirty yellow, the interior grayish yellow to brownish yellow .... ***Hydnotryopsis***

17. (from 15) Truffle pink to yellowish pink, with a sterile basal pad or vestigial stem giving rise to a tuft of mycelium that attaches to the soil .... ***Fischerula***

17. Truffle white to yellowish, orange or brown, lacking a basal pad or vestigial stem ***18***

    18. Truffle interior with a few white, meandering veins intermingled with gray to yellowish veins that enclose canals lined with a palisade of asci (use hand lens) .... ***Choiromyces***

    18. Truffle interior with meandering white, filamentous veins or veins lined with white globose cells ***19***

19. Truffle interior at maturity brown to very dark brown and marbled with white, filamentous veins (i.e., veins stuffed with hyphae—use hand lens) ..... ***Tuber***

19. Truffle interior at maturity pale brownish, marbled with white, nonfilamentous veins, sometimes open but all lined with globose cells similar to those of peridium (use hand lens) ..... ***Hydnobolites***

Key 3: Basidiomycota Truffle Genera in the Pacific Northwest

1. Fruit-bodies lacking an obvious external stem, stem-columella, or well-formed, large sterile base **2**

1. Fruit-bodies with a stem, stem-columella, or sterile base that is evident before sectioning, often resembling a contorted or unopened mushroom **38**

    2. Fruit-bodies when cut to a true vertical section with a small or large columella or small sterile basal pad within the gleba but lacking a stem **3**

    2. Fruit-bodies when cut with true vertical section lacking a columella or sterile basal pad within the gleba **24**

3. Gleba surrounding a central globose columella from which radiate hyphae or elongated, spore-filled chambers to the peridium **4**

3. Gleba composed of numerous, small or large chambers, occasionally requiring a hand lens to be visible **6**

    4. Gleba with elongated, spore-filled chambers or tubes radiating from a central globose columella to the peridium, not becoming powdery or only at full maturity ..... ***Schenella***

    4. Gleba with hyphae radiating from a central globose columella to the peridium, rapidly becoming powdery as spores mature **5**

5. Gleba with persistent central columella; hyphae radiating from a globose central columella to the peridium ..... ***Radiigera***

5. Gleba lacking a columella and composed of small, subglobose, spore-filled chambers evident in young fruit-bodies, but disintegrating into a powdery spore mass by maturity ..... **Hypogeous *Scleroderma***

6. (from 3) Gleba brown, pink, yellow, orange, green, or blue-green **7**

6. Gleba typically white or off-white **22**

    7. Gleba gray-brown, brown, red-brown to dark brown **8**

    7. Gleba variously colored, occasionally olive to olive brown but not brown **16**

8. Fruit-body lacking peridium; iodine on tissues gives a deeper orange to red reaction ..... ***Protogautieria***

8. Fruit-body entirely enclosed in a peridium; reaction to iodine various but usually not deep orange to red **9**

    9. Glebal chambers filled with gel-like material ..... ***Destuntzia***

    9. Glebal chambers containing spores but not filled at maturity with gel-like material **10**

10. Columella well developed, central, dendritic or percurrent **11**

10. Columella poorly developed or lacking; sterile basal pad may be present **13**

    11. Fruit-bodies usually soft to rubbery; chambers radiating asymmetrically from a reduced columella; gleba brown to dark brown ..... ***Kjeldsenia***

    11. Fruit-bodies usually cartilaginous, tough or rubbery; columella usually much branched, never columnar **12**

12. Fruit-bodies usually > 2 cm broad; peridium lacking in many species; gleba grayish brown, cinnamon, brown, or dark brown .... ***Gautieria***

12. Fruit-bodies usually < 2 cm broad; peridium white when first collected, smooth or with many emanating hyphae and rhizomorphs, white, often bruising pink to red or brown; gleba pink to gray, olive or green .... ***Hysterangium***

13. (from 10) Iodine solution produces a blue to purple or black reaction on gleba .... ***Gymnomyces***

13. Iodine producing orange to red or not reacting on gleba **14**

14. Peridium white to brown or mottled, often staining red, green, blue, or black where bruised; gleba firm, the chambers small and often spore-filled .... ***Octaviania***

14. Peridium white to yellow or violet, not staining or staining brown where bruised. Gleba usually soft, the chambers large and not filled with spores **15**

15. Peridium white to yellow; gleba dark brown .... ***Hymenogaster***

15. Peridium yellow with areas of lilac or violet; gleba cinnamon .... ***Protoglossum***

16. (from 7) Gleba gray, green, yellowish green, or olive **17**

16. Gleba pink, yellow, orange, or gray-blue **19**

17. Peridium bright yellow, sometimes staining smudgy where bruised; columella yellow, much branched through the gray to brown, fleshy gleba; basal pad present, yellow .... ***Truncocolumella***

17. Peridium white to brownish, in many species staining pink to orange or yellow where bruised; columella absent or gray-translucent and much branched; glebal tissues gray to green, cartilaginous or gelatinous; basal rhizomorphs abundant, conspicuous **18**

18. Gleba with scattered to abundant sterile locules contained in a white gelatinized zone just beneath the peridium, which stains yellow to orange where bruised .... ***Trappea***

18. Gleba lacking sterile locules beneath the peridium, which stains pink to red or brown or not at all .... ***Hysterangium***

19. (from 16) Fresh, moist gleba when cut exuding a watery to white or colored latex .... ***Arcangeliella***

19. Fresh, moist gleba when cut not exuding a latex **20**

20. Gleba bluish gray at maturity .... ***Gautieria***

20. Gleba yellow or orange **21**

21. Iodine solution on gleba produces blue, purple, or black reaction .... ***Cystangium and Gymnomyces***

21. Iodine solution on gleba produces little or no reaction .... ***Sclerogaster***

22. (from 6) Iodine solution on gleba produces blue, purple, or black reaction **23**

22. Iodine solution on gleba produces little or no reaction .... ***Octaviania***

23. Fresh, moist fruit-bodies exuding latex when cut .... ***Arcangeliella***

23. Fresh, moist fruit-bodies not exuding latex when cut .... ***Cystangium and Gymnomyces***

24. (from 2) Glebal chambers filled with thick, colored, gelatinous material, these separated by pale colored veins **25**

24. Glebal chambers empty, filled with thin, white latex or with powdery content **26**

25. Glebal chambers filled with black gel at maturity and separated by pale veins; usually with a strong latex paint or oily-metallic odor; peridium dark brown .... ***Melanogaster***

25. Glebal chambers filled with yellow, brown, olive, or reddish gel at maturity, or if black or nearly black then the peridium is bright yellow; usually with little or no odor (see also *Destuntzia*, no. 9) .... ***Alpova***

26. (from 24) Gleba white when fresh and mature, and with a scant or profuse white latex **27**

26. Gleba usually not white at maturity, with or without latex, or if white then latex absent **28**

27. Gleba with copious latex in fresh specimens; chambers round, ≥0.5–3.0 mm broad .... ***Leucogaster***

27. Gleba with scant latex in fresh specimens, this drying rapidly into a chalky, white surface, often obscuring the chambers; chambers narrow and vein-like, ≤0.3–0.5 mm broad .... ***Leucophleps***

28. (from 26) Iodine solution on gleba produces blue, purple, or black reaction **29**

28. Iodine solution not producing a distinctive reaction **33**

29. Gleba white or off-white at maturity **30**

29. Gleba more darkly colored at maturity **31**

30. Fruit-body very light in weight and gleba dry when fresh .... ***Mycolevis***

30. Fruit-body denser and gleba moist when fresh .... ***Cystangium and Gymnomyces***

31. Fresh fruit-bodies exuding a copious latex .... ***Arcangeliella***

31. Fresh fruit-bodies moist but not exuding a copious latex **32**

32. Fresh peridium quickly turning red to purple or bluish black in KOH .... ***Rhizopogon***

32. Fresh peridium not affected by KOH .... ***Cystangium and Gymnomyces***

33. (from 28) Gleba at first composed of filled chambers separated by pale-colored veins but at maturity becoming powdery; peridium 1–5 mm thick .... ***Scleroderma***

33. Gleba not composed of filled chambers separated by pale-colored veins, and not powdery at maturity **34**

34. Gleba gray-brown, brown, to dark brown; often with a strong, penetrating, unpleasant odor .... ***Hymenogaster***

34. Gleba variously colored; with a variety of odors but not strong **35**

35. Peridium pale pinkish orange to orange brown, not bruising a different color .... ***Fevansia***

35. Peridium usually white, yellow, green, or brown, frequently bruising black, blue, orange, or red **36**

36. Gleba cinnamon to dark brown at maturity, discoloring on exposure; peridium white to pink at maturity, discoloring to red, brown, or blue where bruised; scanty latex sometimes present .... ***Octaviania***

36. Gleba with various colors, rarely discoloring on exposure; peridium various colors, frequently discoloring on bruising, latex absent **37**

37. Peridium thin, evanescent, white to pale green from underlying gleba when fresh, bruising orange to pale red; associated with *Populus* .... ***Amogaster***

37. Peridium well developed, usually not evanescent; associated with Pinaceae .... ***Rhizopogon***

38. (from 1) Gleba chocolate brown, dark purple brown, smoky gray, or black at full development from the color of the spores in mass **39**

38. Gleba white, yellow, orange, green, vinaceous (pale purple brown) or olive yellow, yellow brown, red brown to rusty brown at full development owing to coloration of the spores in mass **42**

39. Trama of gleba and stem-columella pale orange to pale red, turning purple to purplish black with application of iodine soluion .... ***Brauniellula***

39. Trama of gleba and stem-columella yellow, white, or very pale, at most brusing vinaceous near the base of the stem-columella but not turning purple to purplish black with application of iodine solution **40**

40. Base of stem bright yellow; gleba or gills smoky brown **41**

40. Base of stem white or brownish .... ***Agaricus inapertus***

41. Fruit-body cap not expanding; solitary and nearly always hypogeous .... ***Gomphogaster***

41. Fruit-body cap expanding like a typical mushroom; two to several fruit-bodies often joined at the base; hypogeous to barely emergent .... ***Chroogomphus loculatus***

42. (from 38) Spores in mass in the glebal chambers white, pale yellow, or orange at full development; iodine solution applied to the gleba produces a purple to purplish black reaction **43**

42. Spores in mass in the chambers olive yellow, gray, olive brown, yellow brown, red, brown rusty brown, or vinaceous; iodine solution nonreactive on gleba **45**

43. Fresh gleba and/or peridium exuding latex when cut; resembling contorted or unopened *Lactarius* .... ***Gastrolactarius***

43. Neither fresh gleba nor peridium exuding latex when cut **44**

44. Stem-columella continues through the gleba to the top of the fruit-body; gleba loculate, labyrinthiform, or sublamellate, may or may not be exposed; resembling contorted or unopened *Russula* .... ***Cystangium and Macowanites***

44. Sterile base or at most a small columella present; gleba usually loculate or at most labyrinthiform, not exposed .... ***Cystangium and Gymnomyces***

45. (from 42) Peridium bright yellow .... ***Truncocolumella***

45. Peridium white to brown, olive brown, or dark brown, or reddish brown **46**

46. Gleba of contorted tubes **47**

46. Gleba of chambers or contorted gills **48**

47. Either cap or stem or both white or with bright yellow, orange, or red colors; peridium dry, smooth; stem lacking glandular dots .... ***Gastroboletus***

47. Cap or stem dull yellow or brown; peridium sometimes slimy or scaly; stem sometimes with glandular dots .... ***Gastrosuillus***

48. (from 46) On twigs or logs in spring, often as snowbanks melt or even under snow; cap whitish or brown streaked .... ***Nivatogastrium***

48. Hypogeous or partly emergent from soil in forests **49**

49. Fruit-bodies rounded; peridium white to brown, quickly staining blue or green when exposed; gleba grayish brown to dark brown, chambered; stem small, vestigial, easily breaking off .... ***Chamonixia***

49. Fruit-bodies in the form of mushrooms with distinct stem; gleba cinnamon from spore color **50**

50. Fruit-bodies in the form of small mushrooms with expanded caps and a stem so short that it cannot lift the cap out of the soil; gills cinnamon brown from spores that are discharged onto a persistent, membranous veil that connects the cap margin with the stem .... ***Cortinarius***

50. Fruit-bodies in the form of small, unexpanded mushrooms; gleba chambered, cinnamon from spores; cap slimy when wet .... ***Thaxterogaster***

Key 4: Glomeromycota and Zygomycota Truffle Genera in the Pacific Northwest

1. Fruit-bodies gray, a mix of pale spores, hyphae, and soil, 1–2 mm thick and variable length and width .... ***Youngiomyces stratosus***

1. Fruit-bodies rounded to irregular, 3–20 mm broad, brown to yellow **2**

    2. Fruit-bodies bright yellow in cross section when moist **3**

    2. Fruit-bodies white to brown or brownish black in cross section when moist **4**

3. Fruit-bodies rounded or somewhat convoluted, smooth .... ***Endogone***

3. Fruit-bodies much convoluted, the surface bumpy from large spores (use hand lens) .... ***Glomus convolutum***

    4. Fruit-bodies containing black spores (use hand lens) .... ***Glomus melanosporum***

    4. Fruit-bodies containing brown spores **5**

5. Individual spores shiny (use hand lens) .... ***Glomus***

5. Individual spores dull from being enclosed in hyphal mantles .... ***Endogone***

Ecology of Truffles

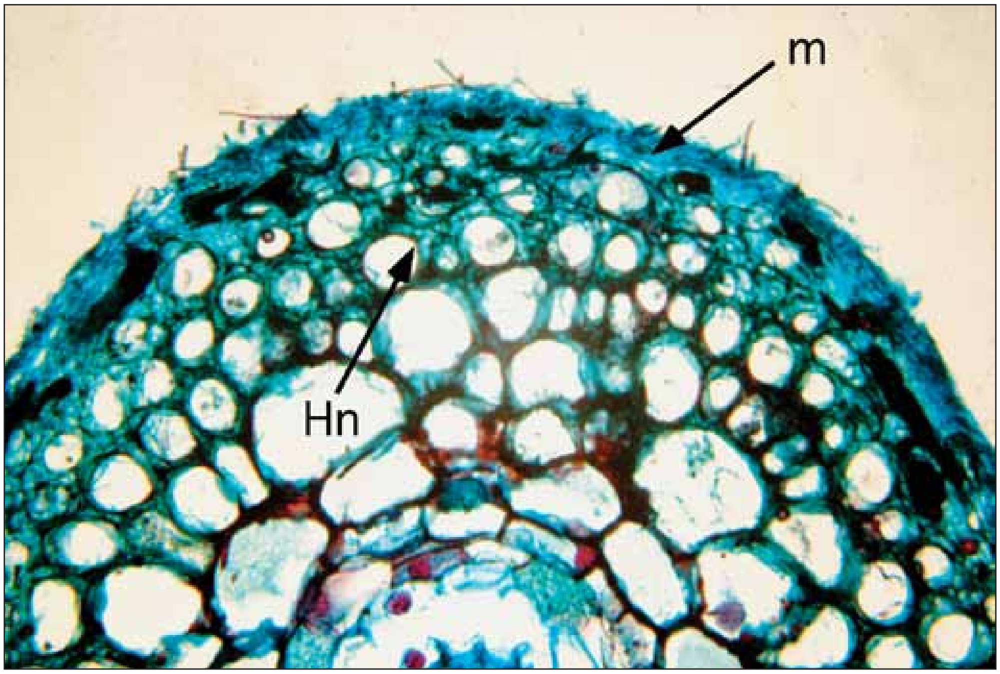
Mycorrhizal Symbiosis

As noted previously, most truffle fungi are ectomycorrhizal, although a few may be decomposers. Because mycorrhizal symbioses play essential roles in the life history of these fungi, survival and growth of the plant hosts, and ecosystem function, we discuss this symbiosis in detail.

"Mycorrhiza" literally translates as "fungus-root." The mycorrhizal fungus serves as an extension of the root system, exploring soil far beyond the roots' reach and transporting water and nutrients to the plant. Mycorrhizal fungi are particularly efficient in taking up inorganic phosphorus and nitrogen and releasing bound forms of these nutrients otherwise unavailable to the roots. In return, the plant provides the primary energy source for the fungus in the form of simple sugars produced in photosynthesis and transported to the roots and then the fungus (Allen 1991, Marks and Kozlowski 1973, Smith and Read 1997).

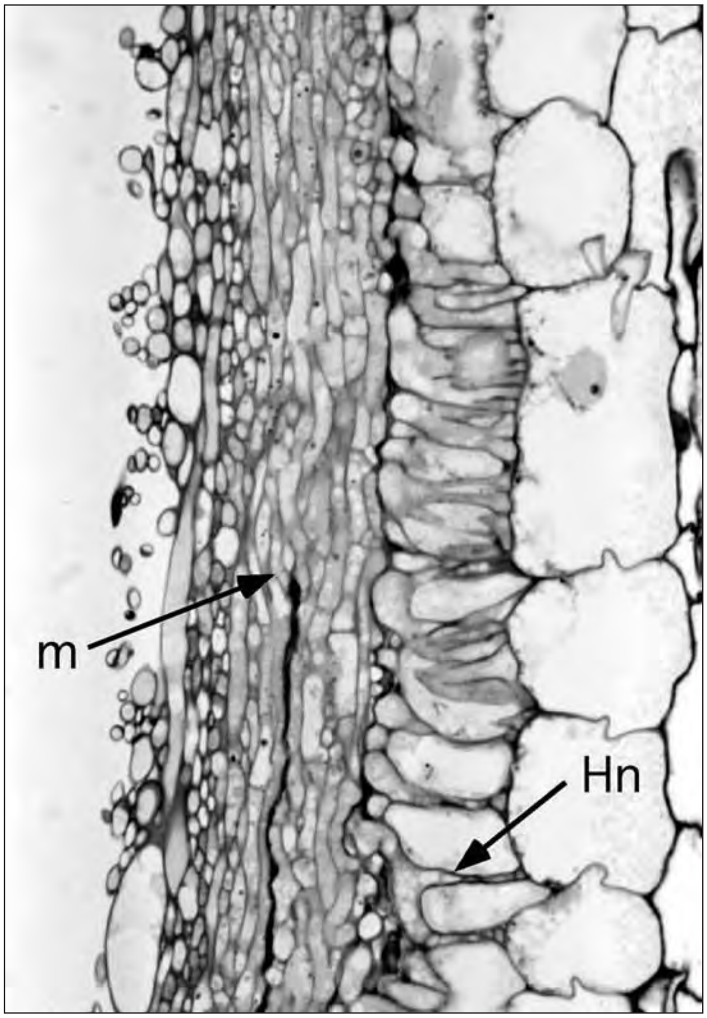
There are several types of mycorrhizae (see Molina et al. 1992), and truffle fungi form ectomycorrhiza (plural, ectomycorrhizae). Ectomycorrhizae develop on the fine feeder roots of conifers and angiosperms and are distinguished by development of a sheath or mantle of fungus mycelium around the root tip. Mantle mycelium is sometimes white or brightly colored, so ectomycorrhizae may be visible to the unaided eye when fine roots are excavated from the soil. Ectomycorrhizal mantles range from one to several hyphal diameters in thickness and serve as storage tissue for nutrients received from the mycelium in the soil. Mantle tissue can also protect fine roots from soil pathogens and desiccation. Mantle characteristics (color, surface texture, hyphal structure, width) differ depending on fungus and host and provide key diagnostics in identifying the fungal partner of ectomycorrhizae collected in field studies (Agerer 1987–1993, Goodman et al. 1996). The fungus also grows into colonized fine roots, penetrating the epidermal and cortical cell layers to form a network of fungus tissue called the Hartig net (figs. 61 and 62). Nutrient and carbohydrate exchange between fungus and root occurs within this extensive contact zone.

The branching patterns of ectomycorrhizae formed by different host-fungus combinations also differ widely and provide additional characteristics to distinguish different ectomycorrhizal types. Some branching patterns are characteristic to particular hosts. For example, pine (*Pinus*) ectomycorrhizae typically have a forked or bifurcate branching pattern; they begin as simple cylindrical structures and then branch dichotomously at their tips, often repeatedly so (figs. 63 and 64). Ectomycorrhizae of other hosts, such as Douglas-fir and many angiosperms, have simple, unbranched to pinnate or variously branched patterns, at times resembling



Randy Molina

Figure 61—Cross section of ectomycorrhizae formed between Douglas-fir and *Rhizopogon parksii*. M = mantle; Hn = Hartig net.



Hugues Massicotte

Figure 62—Longitudinal section of ectomycorrhiza formed between red alder and *Alpova diplopholeus*. M = mantle; Hn = Hartig net.

James Trappe

Figure 63—Ectomycorrhizae and hyphae of *Rhizopogon idahoensis* on pondersa pine. Note the extensive colonization by mycelia and rhizopmorphs into the substrate.

Hugues Massicotte

Figure 64—Ectomycorrhizae synthesized by spore inoculation between *Rhizopogon flavofibrillosus* and ponderosa pine.

coral-like (coralloid) structures (figs. 65 through 68). Many ectomycorrhizal fungi produce phytohormones such as auxins and gibberellins that influence and promote the branching seen in ectomycorrhizae. This promotion of branching greatly increases the root surface area and provides an extensive contact zone between fungus, root, and soil.

Randy Molina

Figure 65—Ectomycorrhiza synthesized in pure culture between *Alpova diplopholeus* and red alder.

Michael Castellano

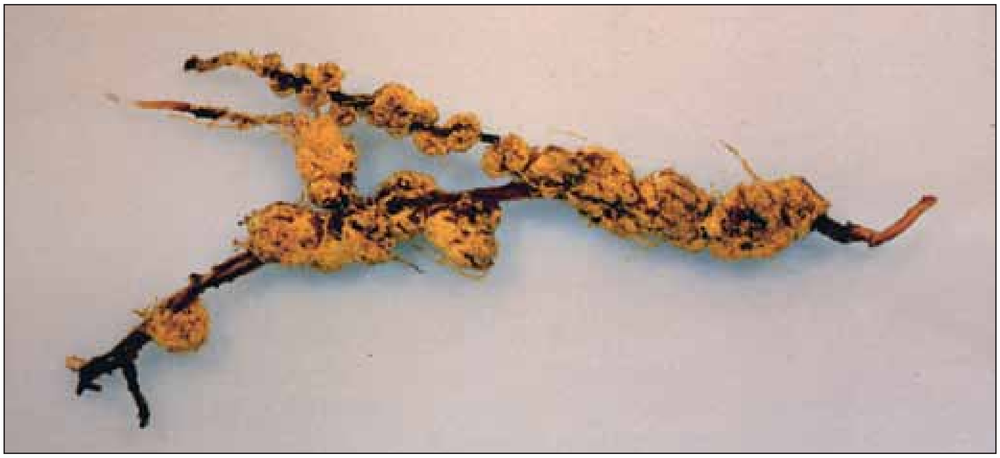
Figure 66—Ectomycorrhizae synthesized by spore inoculation between *Rhizopogon vinicolor* and Douglas-fir on nursery seedlings.

Randy Molina

Figure 67—Ectomycorrhiza synthesized in pure culture between *Melanogaster intermedius* and Pacific madrone (*Arbutus menziesii*).

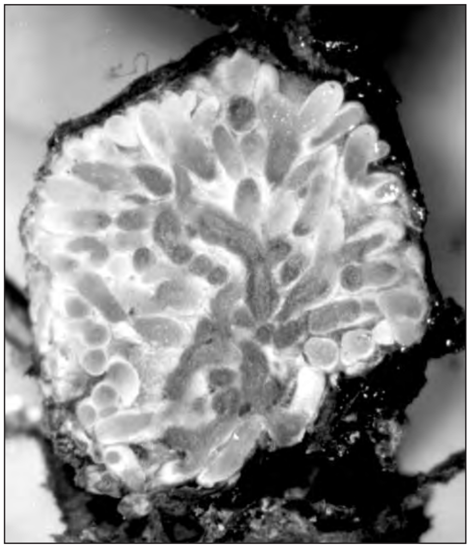
Randy Molina

Figure 68—Ectomycorrhizae synthesized by spore inoculation between bearberry (*Arctostaphylos uva-ursi*) and *Rhizopogon subcaerulescens*.



B. Zak

Figure 69—Tuberculate ectomycorrhizae of *Rhizopogon truncatus* on *Tsuga mertensiana*.



Hugues Massicotte

Figure 70—Tuberculate ectomycorrhiza of *Rhizopogon vinicolor* with Douglas-fir. Note the dark outer surface of the tubercle, and the white, multibranched ectomycorrhizae within.

Given the diversity of truffle fungi and hosts, it is not surprising that truffle ectomycorrhizae show a wide range in morphology (such differences are termed “morphotypes”). Some truffle species in the genus *Rhizopogon* form a unique morphotype called tuberculate ectomycorrhizae (figs. 69 through 72). Tuberculate ectomycorrhizae resemble small, tuber-like nodules on lateral roots that can reach up to 2 cm diameter. The root tips branch repeatedly to form a tight cluster of ectomycorrhizae that is often enveloped by mycelial tissue over the entire nodular structure. In *Rhizopogon vinicolor* + Douglas-fir tubercles, the outer covering is formed by thick, darkly pigmented hyphae. This outer rind of hyphae is thought to further protect the ectomycorrhizae from desiccation and insect feeding and may harbour nitrogen-fixing bacteria. Given their large size and unique structure, tuberculate ectomycorrhizae are easily extracted from soil for detailed ecological study (Kretzer et al. 2003, 2005; Trappe 1965; Twieg et al. 2007).

The quantity and structure of hyphae that emanate from ectomycorrhizae also distinguish morphotypes formed by different fungal species. Some fungi may only grow a few centimeters from their ectomycorrhizae into the soil whereas others can grow several meters. Emanating hyphal types range from lone hyphae to dense

B. Zak

Figure 71—Tuberculate ectomycorrhizae of of *Rhizopogon vinicolor* with Douglas-fir as seen along the main lateral root. Some of the tubercle rind has been removed to reveal the interior of crowded ectomycorrhizal root tips.

Hugues Massicotte

Figure 72—Scan electron micrograph of the interior of a tubercle formed by *Rhizopogon vinicolor* on Douglas-fir. Note the thick outer rind that encases the ectomycorrhizae. The rind protects the fine roots from desiccation as soils dry, and predation by small soil organisms.

wefts of hyphae or rope-like strands of bundled hyphae (figs. 63, 73). Some strands differentiate into vessel-like tissue called rhizomorphs wherein nutrients and carbohydrates can be rapidly transported between fungus and plant root. Many truffle fungi such as in the genera *Rhizopogon* and *Hysterangium* produce abundant rhizomorphs. In addition to spreading mycelial colonization in the soil, rhizomorphs can also function as efficient conduits for water transport, and some *Rhizopogon* species provide drought tolerance to seedlings or allow seedlings to quickly recover after drought (Parke et al. 1983).

Several truffle species develop dense hyphal mats composed of rhizomorphs and wefts of mycelium that strongly bind the soil and organic matter surrounding the ectomycorrhizae. If the mycelium is white or brightly colored, these extensive mats are readily visible when a bit of the upper organic layer is removed (figs. 74 and 75). Some fungi produce colorless or dark mycelia that are difficult to see with the unaided eye, but their growth into the soil can likewise be extensive.

B. Zak

Figure 73—Ectomycorrhizae and truffle formed by *Hysterangium* on Douglas-fir. Note the large rhizomorphs that emanate from the mycorrhizae.

Specificity Between Fungus and Host

Ectomycorrhizal fungi differ in ability to form mycorrhizae with various plant hosts. We refer to this phenomenon as host-fungus specificity or compatibility. For example, many ectomycorrhizal fungi form mycorrhizae only with a single plant genus or family (e.g., the genus *Pinus* or the family Pinaceae). Other fungi can form ectomycorrhizae with plants from many different genera and families (e.g., different genera of gymnosperms or angiosperms). Host plants, on the other hand, typically form ectomycorrhizae with many fungi at any one time. There are examples, however, of hosts such as alders (*Alnus* spp.) that form ectomycorrhizae with far fewer fungal species than do adjacent conifer hosts (Molina 1979, 1981).

Compared to mushroom-forming ectomycorrhizal fungi, truffle fungi typically display a more narrow host range, most commonly a single host genus (Molina et al. 1992). The largest truffle genus in the PNW, *Rhizopogon,* has many species that form ectomycorrhizae and produce fruit-bodies primarily in association with a single genus in the Pinaceae such as *Pseudotsuga* or *Pinus.* Truffle fungus specificity also occurs with some angiosperm hosts. For example, *Alpova diplophloeus* is restricted to the genus *Alnus.* Although most truffle fungi display a narrow host range, we suspect that several species can form ectomycorrhizae with a wide array of host species in different genera or families. The truffle *Melanogaster*

Matt Trappe

Figure 74—Sporocarps of *Hysterangium coriaceum*. Note the extensive colonization of the soil and organic matter (right side) by fungal hyphae and rhizomorphs. Many *Hysterangium* species form extensive mats of mycelium and rhizomorphs as part of their colony's growth in vivo.

Randy Molina

Figure 75—Sporocarps and fungal mycelium of *Rhizopogon truncatus*. The brightly colored sporocarps and extensive mycelium are easily seen when encountering this truffle species.

intermedius, for example, can form ectomycorrhizae with seven different host genera in the Pinaceae and also with angiosperms in the genera *Arctostaphylos* (manzanita) and *Arbutus* (madrone) (Molina and Trappe 1982).

In one of the more intriguing recent findings on specificity among truffle fungi and different plants, some *Rhizopogon* species previously thought to form mycorrhizae only with hosts in the Pinaceae also develop mycorrhizae with chlorophyll-lacking plants in the Monotropodieae such as *Pterospora andromedea* (pine drops) and *Sarcodes sanguinea* (snow plant) (fig. 76). These fungus-root associations are unique anatomically and ecologically. Most monotropoid plants form a root ball with strongly ramified root tips (fig. 77). Their monotropoid mycorrhizae are characterized by thick mantles and Hartig nets restricted to the epidermis, but they also intrude a "fungal peg" into epidermis cells (Robertson and Robertson 1982). Because these plants lack chlorophyll and thus provide no photosynthate to

Daniel Luoma

Figure 76—The chlorophyll-lacking plant *Sarcodes sanguinea* forms mycorrhizae specifically with the truffle fungus *Rhizopogon ellenae*, which is ectomycorrhizal with the neighboring trees. These plants are thus considered hyperparasites on the fungus and trees.

Daniel Luoma

Figure 77—The root ball of *Pterospora andromedea* has few extending roots and is in essence a mass of mycorrhizal roots that obtain carbon (sugar) from their connections to ectomycorrhizal fungi associated with the overstory trees.

the fungus, they are considered trophic parasites on the fungus and the overstory ectomycorrhizal tree host. In these unique monotropoid mycorrhizal interactions, the plant forms mycorrhizae predominantly with a single truffle species: *Sarcodes sanguinea* with *Rhizopogon ellenae* and *Pterospora andromedea* with *Rhizopogon salebrosus* (Bidartondo and Bruns 2002). Because of this extreme specialization, these achlorophyllous plants strongly depend on the presence and mycorrhizal functioning of these specific fungi to receive their carbohydrate nutrition from forest trees. As we shall explore in a later section, the ability of plants to be linked by compatible, shared ectomycorrhizal fungi influences plant community dynamics and ecosystem function.

Community Ecology of Truffle Fungi

We suspect that just as plants and animals reside in or develop “communities” based on those species regularly found living together, truffle species and ectomycorrhizal fungi do so too. Truffle communities are typically described based on fruit-body presence within certain forest types, and are often included as part of the total ectomycorrhizal fungus community. Ectomycorrhizal fungus communites are measured in several ways, including mushroom and truffle presence, production, species diversity, and, more recently, based on morphological and genetic DNA identification of ectomycorrhizal root tips sampled from soil. In this section we review general findings on the communities of ectomycorrhizal fungi in a variety of PNW forest settings. In a later section we focus on silviculture effects on truffle communities.

Comparison of fungal communities based on the occurrence of mushrooms and truffles with communities from DNA identification of ectomyorrhizal species on root tips has shown that the dominant ectomycorrhizal fungi of a site are not the most prolific mushroom and truffle producers (Brandrud and Timmermann 1998, Dahlberg et al. 1997, Gardes and Bruns 1996, Kårén and Nylund 1996, Yamada and Katsuya 2001). However, truffle abundance and mycorrhiza abundance of some individual species correspond (Luoma et al. 1997). Truffle and mushroom abundance can reveal changes in the fungal community that are related to environmental gradients (Luoma 1988, O’Dell et al. 1995b) and thereby serve as an indicator of the overall ectomycorrhizal fungus community response to environmental conditions.

Studies assessing mushroom and truffle communities in North America often focus on differences between vegetation types or forest age classes (e.g., Bills et al. 1986, Luoma 1988, Smith et al. 2002, Villeneuve et al. 1989). Miller (1983) presented data on ectomycorrhizal mushroom species richness in stands of different ages of western white pine (*Pinus monticola*); diversity was substantially higher in

175-year-old stands than in 15-year-old stands. Kranabetter et al. (2005) found strong differences between 20- and 225-year-old stands, including 12 late-seral-dependent species. They suggested that ectomycorrhizal fungus succession largely represents an accumulation of species with little species replacement as host stands age.

In the PNW, several studies of truffle communities have been reported (Colgan et al. 1999; Fogel 1976; Hunt and Trappe 1987; Luoma et al. 1991, 2004; North et al. 1997; Smith et al. 2002; Waters et al. 1994). In two studies (Fogel and Hunt 1979, North et al. 1997), mushroom biomass was compared with that of truffle biomass: the contribution of truffle biomass averaged from about half to more than twice as much as the mushroom biomass. At the H.J. Andrews Experimental Forest, over a range of stand-age classes, J. Smith et al. (2002) found that truffle biomass was about twice as much as mushroom biomass. Because epigeous mushrooms include substantial amounts of stems and caps whereas truffles are made up largely of spore-bearing tissue, the reproductive tissue in truffles would generally equal or exceed that in mushrooms.

Luoma (1988) and Luoma et al. (1991) described the community structure of truffle species along age and moisture gradients in the H.J. Andrews Experimental Forest. Maximum number of species was found in the mesic mature (≈175-year-old) stands. Although some species of truffles were restricted to the oldest stands, the truffle community changed more along the moisture gradient than by stand age class.

In a followup study, J. Smith et al. (2002) examined truffle and mushroom fruit-body production in stands of three age classes at the H.J. Andrews Experimental Forest: unmanaged old-growth (400+ yr), managed rotation-age (50 yr), and managed young (35 yr) Douglas-fir stands. About a third of the species were unique to an age class, and truffle biomass was more evenly distributed among species in old-growth stands.

Young managed stands may have a different composition of truffle species than old-growth or natural mature stands. Among western-hemlock-dominated forests of various ages studied across northwest Washington by North et al. (1997), the number of truffle species was highest in the old-growth stands. The total truffle biomass was much higher in the natural mature and old-growth stands than in the young managed stands. This was largely due to the presence of large clusters of the truffle *Elaphomyces granulatus* in the older natural stands. A similar trend was found in Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) stands of western Washington. The annual production of truffles was only 1 kg/ha per year dry weight in 23-year-old stands, whereas in the 180-year-old stands, production was 380 kg/ha per year (Vogt et al. 1981).

Evidence of ectomycorrhizal fungus succession has also been drawn from observations of fruit-body occurrence as young stands age (Termorshuizen 1991). Generally, few species are present initially and species number gradually increases with stand age. Several studies of ectomycorrhizal fungus succession in birch (*Betula* spp.), spruce (*Picea* spp.), pine, and other types of forests (Deacon et al. 1983, Fleming et al. 1984, Fox 1986) indicate that some genera and species of ectomycorrhizal fungi consistently appear earlier in stand development than others (e.g., *Thelephora* spp. and *Hebeloma* spp. often appear before *Russula* spp. and *Amanita* spp.).

Accurate baseline estimates of ectomycorrhizal fungus productivity and species diversity are necessary to effectively assess population changes over time. For example, Arnolds (1991) reported a serious decline in fruit-body production of mycorrhizal fungi over the preceding three decades. Mushrooms have been consumed in Europe for centuries, yet no prolonged decline had been noted previously. Now accumulated experimental and field data show that a large number of ectomycorrhizal fungi were in decline owing to indirect effects of air pollution, particularly nitrogen, as well as loss of habitat (Arnolds 1991, Arnolds and Jansen 1992, Termorshuizen 1993).

The weight of truffles produced in a forest can be useful for interpreting roles of fungal species as a food source for animals or measuring the energy expended in an ecosystem for truffle reproduction. The sampled weight of truffles may underestimate actual truffle productivity because animals consume a portion of the fruit-bodies (Luoma et al. 2003). The degree of underestimation is most pronounced at periods of low productivity, when consumptive pressure on the available food resource is proportionally high (North et al. 1997).

Clearly, studies of sporocarp production of ectomycorrhizal fungi are incomplete without comparable data for both truffle and mushroom taxa. When both mushroom and truffle species are simultaneously assessed, new understanding of overall diversity phenomena emerges. For example, our region has similar truffle production in spring and fall (Luoma et al. 2004, Smith et al. 2002). This constancy of truffle production has important implications to mycophagous mammals. Fungal diversity in the diet of such animals is nutritionally important (Claridge et al. 1999, Luoma et al. 2003, Maser et al. 1978). During spring in our region, mushroom production is often far less than truffle production (Cázares et al. 1999, Luoma et al. 2004, Smith et al. 2002). Animals that depend on fungi as major food items (Maser et al. 1978) could not rely on mushroom fungi for diet diversity during the spring. Quite possibly, population decline of some mycophagous animals could relate to decline in diversity of the fungal populations owing to habitat disturbance or climate change (Claridge et al. 1996, Jacobs and Luoma in press). Disturbance, whether natural or from managment, can drastically alter populations of ectomycorrhizal fungi (Amaranthus et al. 1994, 1996; Colgan 1997; Pilz and Perry 1984; Schoenberger and Perry 1982).

The functional importance of ectomycorrhizal fungus diversity is little explored, but different ectomycorrhizal fungus species differ in their response to substrate pH (Hung and Trappe 1983), seasonal or environmental change, providing benefits to their hosts (Trappe 1987) or nutritional value to mycophagists (Claridge and Cork 1994, Claridge and Trappe 2005, Fogel and Trappe 1978). Ectomycorrhizal fungus diversity can thus be inferred to provide resilience to forest systems: different species enhance fitness and growth of host trees at different seasons, in different niches in the soil, or in response to different perturbations, and provide necessary nutritional diversity to the diet of mammal mycophagists. High levels of ectomycorrhizal fungus diversity may provide both tree and forest with the functional diversity necessary to cope with changes in season, habitats, or climate. This belowground functional diversity may be linked to the ability of Douglas-fir to grow well over decades and centuries. Thus, maintenance of ectomycorrhizal fungus diversity is important for ecosystem health and resilience (Amaranthus and Luoma 1997, Perry et al. 1990).

Ecosystem Functions of Truffle Fungi

In addition to important functions performed as ectomycorrhizal fungi that influence plant establishment and growth, truffle fungi are key players in many other important forest ecosystem processes. For example, they perform critical soil processes that sustain ecosystem productivity. Most importantly, they serve as key biological links that connect complex food webs between belowground and aboveground organisms as illustrated in figure 78.

Nutrient Cycling and Soil Structure

Although hidden from our view, microscopic members of the soil ecosystem live in much the same way as larger more familiar, and perhaps more charismatic, aboveground creatures. They must find space to live and food to eat. In so doing, they carry out life-sustaining functions for themselves and all life aboveground.

Beneath our feet, the soil teems with an extremely diverse array of soil fungi (including mycorrhizal fungi), micro-organisms, and arthropods. The numbers of these organisms in a single gram of soil defy comprehension: 10 million to 100 million bacteria and actinomycetes, 1,000 to 100,000 fungal propagules, and several kilometers of fungal hyphae (Trappe and Bollen 1979). The soil of an

Illustration by Gretchen Bracher

Figure 78—Illustration of truffle ecosystem functions and their interconnecting roles in forest food webs. Truffle fungi form symbiotic root associations (ectomycorrhizae) with host plant roots, taking up and releasing soil nutrients to the host and receiving photosynthates (sugars) in return to fuel their growth. Small ground-dwelling and arboreal mammals (pictured) consume truffles as major parts of their diets and disperse the fungal spores throughout the forest. Birds such as the northern spotted owl (pictured) prey on the small mammals, and so are intimately linked to the fungi both by way of their prey's food base and their roost trees that are nourished by mycorrhizae. Achlorophyllous plants like *Sarcodes sanguinea* (pictured in center with erect stalks) obtain their carbon (photosynthate) from the overstory trees via their shared mycorrhizal truffle fungus connections. Hence, truffles and other mycorrhizal fungi have been referred to as "the ties that bind" in forest ecosystems.

old-growth Douglas-fir forest stand in Oregon has been estimated to contain 3,700 lb/acre (4200 kg/ha) dry weight of fungal mycelium, 4,800 lb/acre (5400 kg/ha) of mycorrhizal root tips, and 36,500 lb/ac (41 000 kg/ha) of woody roots (Fogel et al. 1973). The combined efforts of these organisms perform the complex biological and chemical processes that render essential nutrients available for the healthy growth of forest plants (Maser et al. 2008). This cycling of nutrients from forms not usable by plants to forms readily assimilated is a life-sustaining function of these mostly hidden organisms that directly influences soil fertility and soil structure in forest ecosystems. In terms of biomass, but not numbers, fungi generally dominate over bacteria in forest soil ecosystems (Kilham 1994). Fungal hyphae exude polysaccharides (sugars) that stabilize soil. In this process they form the fabric of soil by creating and increasing soil aggregation and soil micropores, thus facilitating soil aeration and water movement–essential benefits for myriad oxygen-requiring soil organisms and plants (Chotte 2005). These soil functions are considered keystones to maintaining soil health and long-term productivity.

Mycorrhizal Networks

As noted previously, ectomycorrhizal plants generally associate with numerous species of mycorrhizal fungi. For example, Douglas-fir throughout its range and growth stages may associate with as many as 2,000 species of ectomycorrhizal fungi (Trappe 1977). Similarly, many fungi form mycorrhizae with diverse host species. The belowground world is thus a complex network of mycorrhizal hyphae linking plants of the same or different species, and, in so doing, the fungal network provides a conduit for interplant transfer of nutrients and energy (Simard et al. 1997). Indeed, multiple plant species may be linked by the hyphae of multiple species of mycorrhizal fungi in what is termed a “common mycorrhizal network” (Simard and Durall 2004). Common mycorrhizal networks have the potential to improve seedling establishment, reduce or increase plant competition, and reduce or increase plant community diversity (Simard and Durall 2004, Wardle 2002). We discuss the practical importance of maintaining these functioning networks in the final sections of “Management Considerations.”

Soil Food Webs

The importance of soil fungi to ecosystems goes beyond nutrient cycling and soil aggregation. Fungi are active participants in forest food webs and biodiversity pathways (Maser et al. 1978). Soil bacteria are often intimately associated with fungal mycelia, feeding on exudates and proliferating around mycorrhizae (Reddy and Satyanarayana 2006). A significant soil food web pathway is the consumption of fungal mycelium by the countless microscopic soil arthropods (mites and insects); in fact, nearly 80 percent of forest soil arthropods feed on fungi (Moldenke 1999). Soil arthropods act as the primary biological machinery that shred the vast quantity of organic matter in forest soils and prepare it for the final mineralization processes carried out by bacteria and fungi. In the absence of fungal grazing by soil arthropods, release of plant-available nitrogen in soil would be significantly reduced (Kilham 1994). Given the large amount of fungal hyphae in forest soil noted previously (Fogel et al. 1973, Trappe and Bollen 1979), the magnitude of this soil food web process and its importance to soil nutrient mobilization becomes readily apparent.

Truffle fungi are a vital food source for aboveground organisms. Truffles are consumed by numerous forest animals including deer, elk, bear, small mammals, slugs, and insects (Claridge and Trappe 2005; Fogel and Trappe 1978; Maser et al. 1978, 2008). These animals are important in transporting truffle spores. Truffles provide animals with an essential source of minerals, amino acids, and vitamins (see “Small Mammal Mycophagy”). In the following sections we explain why it is critical to understand the role of fungi as a basis for important wildlife food webs (Maser et al. 2008, Molina et al. 2001). Given the particular importance of small mammal mycophagy in truffle evolution, biology, and forest food webs, we discuss this ecosystem process in more detail.

Small Mammal Mycophagy

Observations of mammal mycophagy have been recorded since at least the 1800s. Reess and Fisch (1887) addressed the dissemination of spores of *Elaphomyces* (stag truffle) by animals (both wild and experimental) and concluded that spores pass through the animals unchanged. Fogel and Trappe (1978) reviewed the literature and documented a general trend of mycophagy in the diets of many small mammal species. They also posed several questions relevant to the life histories and ecosystematic functions of fungi and animals. Claridge and Trappe (2005) updated the literature on mycophagy and added more considerations. They categorized mycophagists thus: (1) **obligate**—entirely or almost entirely dependent on fruit-bodies; (2) **preferential**—prefer fruit-bodies over other food sources, but regularly or seasonally eat other types of food as well; (3) **casual or opportunistic**—occasionally feed on fruit-bodies as available and attractive; and (4) **accidental**—ingest fruit-bodies or spores accidently in the course of eating other food sources (table 4).

Moving beyond simple observations of mycophagy, many important aspects of the interdependencies among fungi, mycophagists, and forest trees have been

Table 4—Mammals and birds of the Pacific Northwest recorded as eating fungi

Mycophagy category[a]	Class	Order	Family	Species	Common name	References
Obligate	Mammalia	Rodentia	Arvicolidae	*Myodes californicus californicus*	Western redbacked vole	Maser et al. 1978, Ure and Maser 1982
Preferential	Mammalia	Rodentia	Geomyidae	*Thomomys bulbivorus*	Camas pocket gopher	Maser et al. 1978
			Arvicolidae	*Microtus oregoni*	Creeping vole	Maser et al. 1978
				Myodes californicus mazama	Mazama redbacked vole	Hayes et al. 1986, Maser et al. 1978, Ure and Maser 1982
				Myodes gapperi	Southern red-backed vole	Maser et al. 1978, Ure and Maser 1982
				Phenacomys intermedius	Heather vole	Maser et al. 1978
			Sciuridae	*Glaucomys sabrinus*	Northern flying squirrel	Maser et al. 1985, Maser et al. 1978, McKeever 1960
				Sciurus griseus	Western gray squirrel	Maser and Maser 1988, Maser et al. 1978, Steinecker and Browning 1970
				Spermophilus lateralis	Mantled ground squirrel, Oregon	Maser and Maser 1988, Maser et al. 1978, Tevis 1952, Tevis 1953
				Spermophilus saturatus	Mantled ground squirrel, Washington	Cork and Kenagy 1989
				Tamias amoenus	Yellowpine chipmunk	Maser and Maser 1988, Maser et al. 1978, Tevis 1952, Tevis 1953
				Tamias quadrimaculatus	Long-eared chipmunk	Tevis 1952, Tevis 1953
				Tamias speciosus	Lodgepole chipmunk	Tevis 1953
				Tamias townsendi	Townsend chipmunk	Cázares and Trappe 1994, Jones et al. 1976, Maser and Maser 1988, Maser et al. 1978, Tevis 1952
				Tamiasciurus douglasi	Douglas squirrel, chickaree	Maser and Maser 1988, Maser et al. 1978
				Tamiasciurus hudsonicus	Red squirrel	Maser and Maser 1988, Maser et al. 1978
Opportunistic	Aves	Galliformes	Phasianidae	*Callipepla californica*	California quail	Trappe unpublished data
				Meleagria gallopavo	Wild turkey	Trappe unpublished data
		Passeriformes	Corvidae	*Cyanocitta stelleri*	Steller's jay	Trappe unpublished data
				Perisoreus canadensis	Gray jay	Trappe unpublished data
	Mammalia	Artiodactyla	Bovidae	*Oreamnos americanus*	Mountain goat	Cázares and Trappe 1994
			Cervidae	*Cervus elaphus*	Wapiti or North American elk	Maser et al. 2008
				Odocoileus hemionus	Mule deer	Maser et al. 2008

Table 4—Mammals and birds of the Pacific Northwest recorded as eating fungi (continued)

Mycophagy category[a]	Class	Order	Family	Species	Common name	References
		Carnivora	Mustelidae	*Martes pennanti*	Fisher	Trappe unpublished data
			Ursidae	*Ursus americana*	Black bear	Maser et al. 2008, Trappe unpublished data
				Ursus arctos	Grizzly bear	Mattson et al. 2002
		Didelphimorpha	Didelphidae	*Didelphis virginianus*	Virginia opossum	Fogel and Trappe 1978
		Insectivora	Soricidae	*Sorex pacificus*	Pacific shrew	Jones et al. 1976
				Sorex trowbridgii	Trowbridge shrew	Jones et al. 1976, Maser et al. 1978
				Sorex vagrans	Wandering shrew	Jones et al. 1976
				Sorex yaquinae	Yaquina shrew	Jones et al. 1976
		Lagomorpha	Leporidae	*Sylvilagus nuttalli*	Mountain cottontail	Maser et al. 1978
			Ochotonidae	*Ochotona princeps*	Pika or rock rabbit	Cázares and Trappe 1994, Maser et al. 1978
		Rodentia	Cricetidae	*Neotoma cinerea*	Bushy-tailed woodrat	Maser et al. 1978
				Peromyscus crinitus	Canyon mouse	Maser et al. 1978
				Peromyscus maniculatus	Deer mouse	Maser et al. 1978
				Peromyscus truei	Pinyon mouse	Maser et al. 1978
			Geomyidae	*Thomomys mazama*	Mazama pocket gopher	Maser et al. 1978
				Thomomys talpoides	Northern pocket gopher	Maser et al. 1978
				Thomomys townsendi	Towsend pocket gopher	Maser et al. 1978
			Arvicolidae	*Lemmiscus curtatus*	Sage vole	Maser et al. 1978
				Microtus longicaudus	Long-tailed vole	Maser et al. 1978
			Sciuridae	*Marmota caligata*	Hoary marmot	Cázares and Trappe 1994
			Zapodidae	*Zapus trinotatus*	Pacific jumping mouse	Jones et al. 1978, Maser et al. 1978
Accidental	Aves	Strigiformis	Strigidae	*Strix occidentalis*	Northern spotted owl	Claridge and Trappe 2005, Maser et al. 2008

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[a] Obligate = entirely or almost entirely dependent on sporocarps; preferential = prefer sporocarps over other dietaries, but regularly or seasonally eat other types of food as well; opportunistic = occasionally feed on sporocarps as available and attractive; and accidental = ingest sporocarps or spores accidentally in the course of eating other dietaries, especially in reference to predators that eat small mammal mycophagists whole.

explored by researchers during the last 20 years. Truffle fungi are primarily dispersed by small mammals that eat the fruit-bodies and subsequently disperse spore-packed fecal pellets (Claridge et al. 1992, Fogel and Trappe 1978, Kotter and Farentinos 1984a, Lamont et al. 1985, Maser and Maser 1988, Maser et al. 2008, Trappe and Claridge 2005). Spores of a few truffle species, particularly in the genus *Elaphomyces*, also are disseminated by air. The edible outer layer of *Elaphomyces* encloses a powdery spore mass that may be discarded while a small mammal is perched above the ground, resulting in the release of spores into the airstream (Ingold 1973, Trappe and Maser 1977).

Spores can germinate to form new fungal mycelia or fuse with an existing mycelium of the same species, thus colonizing new areas or increasing the genetic diversity of existing fungus populations (Fogel and Trappe 1978, Miller et al. 1994). Forest-dwelling small mammals that depend on fruit-bodies of ectomycorrhizal fungi as a major part of their diet have spores from a diverse array of truffle genera in their feces (Carey et al. 2002; Colgan et al. 1999; Jacobs and Luoma, in press; Maser et al. 1978, 1985).

As truffles mature, they produce strong, chemically complex odors that attract many small mammals (Donaldson and Stoddart 1994, Trappe and Claridge 2005, Trappe and Maser 1977). The truffle scent may contain compounds similar to certain animal hormones. Odor trials suggest that males and females may respond to these odors differently (Marin and McDaniel 1987). Responding to these olfactory cues, small mammals are adept at uncovering mature fruit-bodies (Pyare and Longland 2001a). With consumption of the truffle, many fungal spores are ingested; these spores remain viable after passage through the animal's digestive tract (Kotter and Farentinos 1984b, Trappe and Maser 1976). The spores of some truffle species may actually require passage through an animal's digestive tract before they will germinate (Claridge et al. 1992, Lamont et al. 1985). Claridge et al. (1992) found that when spores obtained directly from fruit-bodies of the Australian truffle, *Andebbia pachythrix* (as *Mesophellia pachythrix*), were applied to eucalyptus trees they did not form ectomycorrhizae, whereas *A. pachythrix* spores that came from fecal pellets did. However, they could not determine whether it was passage through the gut or some other factor that allowed the spores to germinate in natural forest soil conditions.

As prey for raptors (e.g., goshawks (*Accipter gentilis*) and northern spotted owls (*Strix occidentalis caurina*)) and mammalian carnivores (e.g., coyotes (*Canis latrans*), martens (*Martes americana*) and fishers (*Martes pennanti*)), small mammals form important links in the trophic structure of forest ecosystems (Carey 1991, Hayes et al. 1986). The potential for indirect consumption of truffles by predators of small mammals has been recognized, but there is also evidence that fishers consume truffles directly (Grenfell and Fasenfest 1979, Zielinski et al. 1999). A wide variety of animals and trophic relationships, then, are instrumental in distributing mycorrhizal fungi to new tree roots. The animals at the same time depend on the trees for cover and reproductive sites (Aubry et al. 2003). Disruption of any part of this interdependent web of organisms will inevitably affect the others. Improved understanding of these relationships can lead to improved approaches to management of forest ecosystems (Amaranthus and Luoma 1997; Carey 2000, 2001; Carey and Harrington 2001; Carey and Wilson 2001; Colgan et al. 1999; Jacobs and Luoma, in press; Laurance 1997; Maser et al. 2008; Wilson and Carey 2000).

The interactions of trees, fungi, small mammals, and predators in North America are epitomized in the mature conifer forests of the Pacific Northwestern United States. In the following paragraphs, we use the northern flying squirrel (*Glaucomys sabrinus*) (figs. 79 and 80) and its use of truffles to exemplify small mammal preferential mycophists, and arthropods and molluscs to represent non-mammalian mycophists.

Over much of its range, the threatened northern spotted owl feeds primarily on northern flying squirrels (Carey 1991, Forsman et al. 1984, Thomas et al. 1990) with

Jim Grace

Figure 79—Northern flying squirrel digging for truffles in Alaska.

Jim Grace

Figure 80—Northern flying squirrel eating a truffle in Alaska.

the exception of the Klamath Province in northern California and southwest Oregon (Zabel et al. 1995). The squirrels, in turn, consume truffles as their primary food source (Carey 1995; Colgan 1997; Hall 1991; Jacobs and Luoma, in press; Maser et al. 1985; Pyare and Longland 2001b; Waters and Zabel 1995; Zabel and Waters 1997). Spring-captured northern flying squirrels from the southern Coast Range of Oregon ate a wider diversity of food items than fall-captured squirrels, although the diet in each season was dominated by fungi (Carey et al. 1999).

Data on stomach contents of northern flying squirrels led McKeever (1960) to conclude that when the snow cover was deep, lichens (also fungal) were the squirrels' principal food. With a decrease in snow cover in the spring, they consumed some truffles. In summer, their entire diet consisted of fungi. In the fall, lichens appeared again, but fungi constituted over half the diet. Despite the availability of various seed crops in the three forest types of McKeever's study (*Pinus ponderosa, P. contorta,* and mixed *Abies*), no seeds were found in the stomachs. Rosentreter et al. (1997) found a similar seasonal pattern in northern flying squirrel food habits in central Idaho. In contrast, Currah et al. (2000) working in the boreal forest of northeast Alberta, found that flying squirrels consumed substantial amounts of mushrooms and no lichens during the winter. They attributed this result to the ability of flying squirrels to raid the caches of red squirrels (*Tamiasciurus hudsonicus*). However, R. Mowrey (personal communication, retired wildlife biologist, 1941 7th Avenue SE, Olympia, Washington 98501) observed flying squirrels drying and caching truffles in mistletoe brooms of spruce in Alaskan boreal forests.

In one study, the squirrel dietary composition of *G. sabrinus* tended to parallel the seasonal availability of fruit-bodies, suggesting that in general it did not prefer particular truffle species under those field conditions (Maser et al. 1986). The notable exception was the consumption of *Rhizopogon* fruit-bodies, which did not change with likely seasonal abundance (Maser et al. 1986). This may have been an artifact of sample technique, use of dried and cached fruit-bodies, or an actual disproportional consumption of *Rhizopogon*. Subsequent trials under laboratory conditions showed that northern flying squirrels did prefer certain species of truffles over other truffle and nonfungal foods (Zabel and Waters 1997). The basidiomycete truffles of *Gautieria monticola* and *Alpova trappei* and the lichen *Bryoria fremontii* were the top-ranked food items in a comparison of fruit-bodies, lichen, and seeds. *Rhizopogon* truffles were not included in the experiment, however (Zabel and Waters 1997). Flying squirrels consumed significantly more *Gautieria* fruit-bodies than chipmunks (*Tamias townsendii* and *T. siskiyou*) or voles (*Clethrionomys gapperi* and *C. californicus*) in western Oregon and Washington, although the diets of all three groups were dominated by *Rhizopogon* spores (Jacobs and Luoma, in press). Because some fungal spores may be retained in the gut of flying squirrels up to 11 days, wide dispersal of spores is possible (Pyare and Longland 2001b).

Knowledge of northern flying squirrels' food habits provided insight to a formerly puzzling aspect of their biology. Bobcats (*Lynx rufus*) and coyotes prey effectively on flying squirrels, yet to do so they must capture the squirrels on the ground. Biologists had wondered what drew "arboreal" squirrels away from the relative safety of the tree crowns. In this case, of course, they descend to the ground to dig out their primary food, truffles (Maser et al. 1985, Wells-Gosling and Heaney 1984). While digging, they are particularly vulnerable to predation.

Northern flying squirrels use a wide range of forest habitats and have a home range of 3 to 6 ha (Martin and Anthony 1999, Witt 1992). Thus, management practices that cause local reductions in fungal diversity and abundance may not affect this species as much as species with smaller home ranges (Jacobs and Luoma, in press). In one study, thinning treatments applied to young stands (35 to 45 years old) showed no strong effect on squirrel density, but squirrel density increased with the amount of truffles available as food (Gomez et al. 2003).

Most information on mycophagy involves mammals, but arthropods and molluscs play a role as well. Anyone who has collected many truffles will have frequently observed insect larvae and occasional slugs in specimens. Arthropods are known dispersers of fungal spores, both by mycophagy and by carrying spores on their exoskeletons (Lilleskov and Bruns 2005, Maser et al. 2008). Senescent, nonharvested truffles are common at the peak of the fruiting season, when the crop exceeds the needs of the small mammal mycophagists (North et al. 1997). These leftover truffles decay in situ into a slimy mass of spores. We suspect that insects, centipedes, millipedes, etc. feed on the spore slime and travel through it, catching spores on their exoskeletons en route and depositing them elsewhere. Lilleskov and Bruns (2005) demonstrated that spores of an ectomycorrhizal fungus, ingested and then defecated by a millipede, were capable of germinating and then initiating mycorrhiza formation on pine roots. Although their test fungus was not a truffle, we suppose that this would happen with truffles as well.

Truffle spores occur in the feces of slugs (McGraw et al. 2002). Although these have not been tested for capability of germinating and forming mycorrhizae, it seems reasonable to suppose that they could do so. Given the speed at which slugs travel, the dispersal distance would not be large. Over time, however, dispersal could spread considerably and, in any event, the spread of spores even a short distance from the truffle would contribute to evening out of the soil spore bank.

Nutritional value of truffles—

Fruit-bodies of ectomycorrhizal fungi generally contain much higher concentrations of minerals than do leaves and fruits of plants (Maser et al. 2008, Trappe and Claridge 2005). Phosphorus and zinc, for example, are 20 to 50 times more concentrated in fruit-bodies than in leaves of plants commonly browsed by animals (Stark 1972). Trace elements, too, can be concentrated at relatively high rates in fungi, for example copper and selenium. Large animals such as bear (*Ursus* spp.), deer (*Odocoileus* spp.), and wallabies (*Macropus* spp.) may ingest fruit-bodies more for the mineral content than for other nutritional needs, using the fungi as a type of salt lick (Fogel and Trappe 1978, Maser et al. 2008, Trappe and Claridge 2005).

In contrast, small mammals that depend strongly on truffles for nourishment appear to do so to meet most of their nutritional needs, and mycophagist specialists such as California red-backed voles, northern flying squirrels, and long-footed potoroos (*Potorous longipes*) have little else in their diet (Trappe and Claridge 2005). Stomach content and fecal analyses reveal that such specialists almost always feed on diverse species in a given day. This is true even of the very small rodents. The typical volume of a single *Rhizopogon* sporocarp, for example, would exceed the stomach capacity of a California red-backed vole, yet those voles invariably have pieces of about 3 and sometimes as many as 12 species in their stomachs at any given time (Maser et al. 1978). We can infer, then, that this diversity in their diets reflects a nutritional imperative.

Reviews of the nutritional value of fungi reveal that truffles and mushrooms have been underrated (Claridge and Trappe 2005, Maser et al. 2008). The following paragraphs on nutrition summarize these reviews, in which the original references for each type of nutrient are cited. Because mushrooms average about 90 percent water by weight when fresh and truffles about 80 percent, mycophagists use them to meet part or all of their water requirements: small mammals do not need additional water when dining on fungi. Accordingly the nutrient contents of fungi are best evaluated on a dry-weight basis.

Of the macroelements, nitrogen, phosphorus, potassium, calcium, magnesium, sodium, and sulphur vary markedly in concentration among fungal species and habitats. The ectomycorrhizal fungi, including truffles, are particularly effective in taking up phosphorus from soil, and their fruit-bodies tend to contain it in abundance. Microelements essential for many physiological processes in animals, for example copper, manganese, selenium, and zinc, are often concentrated in fruit-bodies. Thus fungi are particularly important to animals where the soil is deficient in one or another of these microelements.

Total carbohydrates in fruit-bodies are not a good measure of energy available to mycophagists, because many are not readily digestible, for example cellulose. Accordingly, sugar and sugar alcohol contents of fruit-bodies are more meaningful in terms of animal nutrition. Few analyses of these compounds are reported for fungi, and those show huge variability among fungi species. Fats and fatty acids, on the other hand, show up in truffles and other fungi more than in mushrooms. In one unidentified truffle, the peridium had negligible fats, but the gleba contained about 22 percent by weight, low compared to whole milk or eggs but much higher than most vegetables. Spores of *Glomus* and *Endogone* species are full of lipids. Eleven to 13 fatty acids were found in two truffle species.

Although much of the nitrogen in fungi is a constituent of the relatively indigestible chitin in cell walls, fungi have a good array of proteins and amino acids essential for life, ranging from 6 to 42 percent of dry weight, depending on species. Proteins are broken down into amino acids during digestion by mycophagists, and truffles can be especially rich in them. Seventeen to 29 amino acids have been detected in various truffles and mushrooms, including most to all of those essential for good nutrition. The amino acid content of the gleba of several truffles was reasonably well balanced and made up more than 9 percent of dry weight; the amino acid content of the peridium, in contrast, was negligible.

Fungi are excellent sources of vitamins, and various species are rich in vitamins A, B complex, C, D, and K. Vitamin D is particularly interesting, because it is only produced by animals and fungi. Vitamin D is produced when precursors are exposed to ultraviolet light, hence animals get it by exposure to sunlight. But most mycophists are covered with fur that limits exposure of skin to the sun, and the small species tend to prefer shady cover, are nocturnal, or live belowground. Their vitamin D requirement in many, if not most, cases is met by eating fungi. All fungi have a substantial content of ergosterol, also known as provitamin D, a compound produced only by fungi. Experiments by Stamets (2005) demonstrated that only a few hours of exposure to sunlight of fresh or dried fruit-bodies alike produces astounding concentrations of vitamin D. This in itself may account for mycophagy by opportunistic mycophagists. Truffles, however, normally fruit with no exposure to sunlight; at first thought, they would not appear to be good vitamin D sources for most mycophagists. However, caching animals such as squirrels collect and dry truffles in the sun for later use. Thus a nocturnal, northern flying squirrel female may store sun-dried truffles in her nest, or the diurnal Douglas squirrel (*Tamiasciurus douglasii*) will cache them for winter use.

In addition to the nutrients discussed in the preceding paragraphs, truffles can contain an array of other compounds of potential value to animal health: steroids, triterpenes, amines, indoles, and phenols that could potentially benefit mycophagous animals (Catalfomo and Trappe 1970).

The digestibility of two species of truffles, *Elaphomyces granulatus* and *Rhizopogon vinicolor*, has been studied in detail. In a feeding trial, Cork and Kenagy (1989) fed captive mantled ground squirrels (*Spermophilus lateralis*) the fruit-bodies of *Elaphomyces granulatus*, a common truffle. They compared digestibility of the fungus to digestibility of the leaves of various plant species eaten naturally by the squirrels, as well as cones, pine nuts, leguminous foliage, and grass. A high-quality food, rodent laboratory chow, was used as a reference diet. Squirrels were offered pre-weighed amounts of the different foods. During the experiment, squirrels maintained or gained body mass on two of the food types: pine nuts and rodent chow. Squirrels consuming a high daily intake of only *Elaphomyces* lost weight. The digestibility of nitrogen and energy from *Elaphomyces* was lower than that recorded for nearly all the other diets. Although chemical analyses revealed that the nitrogen content of fruit-bodies was relatively high, 80 percent of it was bound in totally indigestible spores that the squirrels rarely ate. Of the remaining 20 percent, only half was present as protein nitrogen. Sources of energy were tied up in complex, relatively indigestible cell-wall tissue.

The digestible energy requirement of the squirrels was also estimated (Cork and Kenagy 1989). The overall digestibility of *E. granulatus* fruit-bodies fell just below the critical threshold for the squirrels to maintain energy balance. For these squirrels, with a relatively simple digestive tract, *E. granulatus* was seen as a marginal but important dietary item when no alternative was available. Moreover, the truffles were readily detectable and required minimal processing time prior to consumption, unlike some foods such as seeds extracted from cones. The truffles, therefore, yielded more energy and nutrients in relation to foraging effort. They suggested that if squirrels cannot maintain normal energy balances by eating truffles, then the minor incorporation of less abundant, higher quality foods may be all that is needed to achieve a positive energy balance.

Feeding experiments by Claridge et al. (1999) in Oregon with captive northern flying squirrels and western red-backed voles, revealed that neither of the animals could maintain their weight when fed only a single species of truffle (*Rhizopogon vinicolor*). The digestibilities of *R. vinicolor* fruit-bodies were lower than those of other food types eaten by other mammals of similar size. Voles digested the various fruit-body components as well as the squirrels did, although average vole body mass was one-sixth that of the squirrels. This supports the hypothesis that western red-back voles, like other microtine rodents, have morphological and physiological adaptations of the digestive system to permit greater digestion of fibrous diets than predicted on the basis of body size. Neither of the animals drank water during the experiments. Fresh truffles are >70 percent water by weight (Claridge et al. 1999), evidently enough to meet the water requirements of the mycophagists. Nonetheless, individual species of truffle fungi appear to be of only moderate nutritional value for many small mammals. Again, this may account for the animals' habit of eating relatively small amounts of several different species within a day, a behavior that may compensate for differences in digestibility and nutritional quality among truffle species.

Silviculture, Mycorrhizae, and Truffles

Studies from the PNW indicate that forest management activities can reduce ectomycorrhizal fungus populations and forest regeneration success (Amaranthus and Perry 1987, 1989; Amaranthus et al. 1990; Wright and Tarrant 1958). In these studies, the abundance and rapidity of ectomycorrhiza formation was critical to seedling survival and growth, especially on harsh sites. However, across the PNW the degrees of reduction of ectomycorrhizal fungi and resultant impacts on forest regeneration differ widely and depend on many factors. As noted, species differ in their abilities to provide particular benefits to their hosts, and presence and abundance of ectomycorrhizal fungus species change during forest succession (Mason et al. 1983; Trappe 1977, 1987; Visser 1995). The abundance and composition of truffle production may also change following natural disturbance (Luoma 1988, Luoma et al. 1991, Waters et al. 1997).

Douglas-fir forests undergo many vegetational and structural changes during succession (Franklin et al. 1981, Spies et al. 1988). Yet, despite the importance of ectomycorrhizal fungi to ecosystem processes, we are only beginning to understand their community structure and dynamics in managed stands. Such data are essential to predicting impacts of disturbance and management on ecosystem productivity. Integration of vegetation, wildlife, and landscape responses with knowledge of ectomycorrhizal fungi and underground functions is needed to elucidate critical aspects of the ecology of ectomycorrhizal fungi that have strong management implications. Only integrated research can provide a sufficiently comprehensive perspective needed to produce information on interactions among mycorrhizal fungi, small mammals, and a range of forest management practices.

Clearcutting

Ectomycorrhizal fungi and the production of truffles are closely linked to host trees. When the trees are removed or the composition of a stand changes, the composition, species richness, or abundance of truffles in the stand change as well (Amaranthus et al. 1994, Clarkson and Mills 1994, Colgan et al. 1999, North et al. 1997). Clearcutting forests is especially detrimental to ectomycorrhizal fungus diversity and abundance because all potential hosts are removed. Removal of the host tree cuts off the supply of energy to the fungus and prevents it from producing truffles (Amaranthus et al. 1994). Byrd et al. (2000) noted an overall reduction of ectomycorrhizal fungus species richness and significant changes in species composition after clearcutting. Changes in species composition of ectomycorrhizal fungi after clearcutting are influenced by the soil environment as well as by loss or change in fungal inoculum (Jones et al. 2003). Additionally, soil temperature or moisture changes and soil compaction will heavily impact the production of truffles (Cázares et al. 1998, Fogel 1976, Waters and Zabel 1995).

Thinning

Thinning is a common silvicultural practice throughout the world. Unlike clearcutting, thinning retains residual trees that can act as refugia for ectomycorrhizal fungi. However, thinning still alters the community structure, diversity, and composition of ectomycorrhizal fungi in a stand (Colgan et al. 1999, Waters et al. 1994). The effects of variable-density thinning on truffle production during the first years following thinning was examined by Colgan et al. (1999). Douglas-fir stands comprised a mosaic of patches thinned to different densities of standing live trees. The total weight of truffles was significantly lower in thinned stands compared to control stands. The abundance of *Gautieria* and *Hysterangium* species was lower in thinned stands, whereas the number of species of *Melanogaster* and their productivity were highest in thinned stands.

Initial effects of thinning appear to include truffles becoming less common and shifts in abundance among species (Colgan et al. 1999). Total truffle production may recover 10 to 17 yrs. after thinning, but shifts in species relative abundance persist longer (Waters et al. 1994). The shifts in truffle species composition may affect mycophagous animals by altering the nutritional balance of their diets.

Green-Tree Retention

Retention of green trees during commercial timber harvest can moderate the impact of host loss by providing a refuge for ectomycorrhizal fungus diversity. Under the auspices of the Demonstration of Ecosystem Management Options (DEMO) study, Luoma et al. (2006) examined the initial response of ectomycorrhizae to a 15-percent basal-area retention treatment. Ectomycorrhizal root tips beneath the crown of retained trees and in open areas away from the retained trees were evaluated. Ectomycorrhizal fungus richness was reduced by an average of 50 percent in open areas compared to areas within the dripline of retention trees. Species composition also differed between the open areas and areas within the canopy dripline. These results provide evidence that green trees act as refugia for legacy species (i.e., species that remain on a site following disturbance) and are important in maintaining ectomycorrhizal fungus diversity in managed stands.

Presence of the ectomycorrhizae does not ensure reproductive success, however. Truffle species fruiting was reduced 55 to 65 percent and truffle biomass production was reduced 65 to 95 percent in the 15-percent retention treatment (Luoma et al. 2004). Those results supported the use of dispersed retention around aggregated retention. This mix was proposed as an alternative to clearcutting when a goal is to maintain higher levels of fruit-body production in the aggregate retention areas. Continuing study of these relationships is important for development of scientifically sound silvicultural techniques for use in the pursuit of ecosystem-based forest management. In the longer term, the DEMO project will enable examining the role of green-tree retention in the recovery of truffle production after disturbance (Cázares et al. 1999, Luoma and Eberhart 2005, Luoma et al. 2004).

Fire Effects and Site Preparation

Currently, little information exists on fire-plant-fungus interrelationships, making it difficult to generalize about fire effects on populations and fruiting of fungi (Hart et al. 2005, Trappe et al. 2006). Nevertheless, studies suggest that ectomycorrhizal fungus community composition is not substantially altered by low-intensity wildfires (Jonsson et al. 1999) or by restoration thinning and burning (Korb et al. 2003) if the organic layer of the soil remains relatively undamaged. A short-term reduction in fruiting or in numbers of ectomycorrhizal fine roots is a finding common to numerous studies examining the effects of thinning and/or broadcast burning (Colgan et al. 1999; Gomez et al. 2003; Harvey et al. 1980; Herr et al. 1994; Meyer and North 2005; Pilz and Perry 1984; Stendell et al. 1999; Smith et al. 2004, 2005; Trappe et al. 2006; Waters et al. 1994).

High-intensity, stand-replacing fires that cause total combustion of soil organic layers severely affect populations of ectomycorrhizal fungi (Bruns et al. 2002, Dahlberg 2002). In dry pine-dominated forests in the inland PNW, managers are striving to reduce the risk of stand-replacing wildfires through low-intensity prescribed underburning and thinning. Knowledge about how ectomycorrhizal fungi respond to prescribed fire and thinning is essential to forest managers for selecting fuel-reducing restoration treatments that maintain critical soil processes and site productivity.

Fire and disturbance effects on ectomycorrhizal fungi are no doubt directly related to the severity of the event and to the particular species of fungi. In a study of prescribed burning, Dahlberg (2002) reported that the abundance and diversity of ectomycorrhizal fungi decreased with increasing depth of burn. Similarly, J. Smith et al. (2004) reported that prescribed fire in the dry season of year (autumn in this PNW ecosystem) largely removed live root biomass to a depth of 10 cm and significantly reduced ectomycorrhizal species richness for at least 2 years, whereas prescribed fire in a more moist season (spring) did not significantly affect either root biomass or species richness as compared to an unburned control. Perry et al. (1989) showed that aboveground ecosystem recovery after timber harvest and site preparation burning is linked directly to the survival of ectomycorrhizal fungi that reside mainly in the surface layers of soil and organic matter. Fruiting of some species of truffles may be promoted by fire, whereas others are suppressed (Trappe et al. 2006). Fire-adapted species may fruit deeply enough in the soil to escape lethal soil temperatures (Claridge and Trappe 2004).

McIntire (1984) examined effects of slash burning on mycophagy within a shelterwood-logged coniferous forest in southwest Oregon. The slash burning treatment was associated with a reduction of truffle spores in fecal samples from Siskiyou chipmunks (*Eutamias siskiyou*) on the site. Waters and Zabel (1995) found that heavy logging (shelterwood stands) and intensive site preparation in northeastern California negatively affected flying squirrel populations and truffle frequency. North and Greenburg (1998) found that stands that had been altered by management prescriptions such as slash burning and soil scarification showed marked reductions in their ability to provide truffles for small mammals when compared to unmanaged stands.

Trappe et al. (2006) studied effects of prescribed burning on production of truffle fungi in a Eucalyptus woodland in Australia. The results are striking and are likely meaningful in other forests such as those of the PNW. A year after the burn, truffle fungi abounded in nonburned plots but were nearly absent from burned plots. Two years later, the burned plots showed recovery in truffle production, but species richness was still lower on burned than nonburned plots. In the third postburning year, the burned plots came close to equaling nonburned plots in richness and number of fruit-bodies except for one fleshy species that tended to be a very shallow fruiter.

Truffles and Coarse Wood Remnants

Several researchers report a positive relationship between truffle production and coarse wood (CW) remnants on the forest floor (Amaranthus et al. 1994, Luoma

1988, Waters et al. 1997) (note: much of the forestry literature refers to these coarse wood remants, e.g., large logs laying on or buried in the forest floor and standing snags, as coarse woody debris; current literature has moved away from calling this valuable ecosystem resource "debris" to avoid a negative trash-like connotation). Many forest management practices impact the amount and decay class of CW in a stand. In turn, this may affect truffle production, abundance, or diversity. Older forests tend to have more CW in the later stages of decomposition than younger or recently clearcut stands (Harmon et al. 1986). Late-seral forest remnants in southwestern Oregon had 20 to 40 times the fruit-bodies of the surrounding 10- to 27-year-old clearcuts (Clarkson and Mills 1994). Out of the 80 sample plots placed within clearcuts, only one truffle was found. Within the late-seral stands, truffles were four times as numerous in plots with CW than without.

When comparing the numbers of truffles and truffle dry weight between Douglas-fir forest fragments and the clearcuts surrounding them, Amaranthus et al. (1994) also found an association between stand age, amount of CW, and truffle production. A greater number, diversity, and total dry weight of truffles were found in the mature stands than in the plantations. Thirteen of the 21 truffle species were found only in the mature stands and 8 species were found only under CW. The effect of CW upon truffle production was evident only in the mature stands. In the mature forest fragments, there were more truffles and greater truffle biomass in CW than in soil (Amaranthus et al. 1994). Because well-decayed CW retains water, truffle production may be limited to areas in and around well-decayed CW during dry times of drought. Retention of mature forest fragments in the managed landscape can help maintain a diverse food source for small mammals, one that may not be available in younger stands during critical times (Amaranthus et al. 1994). Alhough Amaranthus et al. (1994) demonstrated that previously clearcut young stands produce fewer fruit-bodies than intact mature forest fragments, only limited information is currently available for a range of partial forest harvests and silvicultural systems.

Implications for Wildlife

As the diversity, composition, and abundance of truffles in a forest change, the ability of small mammals to find an adequate amount and diversity of food may be affected. This, in turn, may affect small mammal population numbers or species composition. Pyare and Longland (2001b) suggested that different small mammal species may disperse fungal spores in "ecologically nonredundant ways." Thus, a change in small mammal population composition may reduce dispersal or change dispersal patterns for various fungi. An example of this in the PNW is the contrast between the western redbacked vole and northern flying squirrel (Maser et al. 2008). The vole spends much of its time tunneling belowground. The distance over which it disperses spores in its fecal pellets is thus limited, but it deposits those spores in the feeder root zone in the soil, close at hand for ectomycorrhiza formation when host trees produce new rootlets. The flying squirrel, in contrast, spends most of its time in tree crowns except when foraging for truffles. They may travel several kilometers in a night, scattering spores in a "fecal pellet rain" as they go, but the pellets would not be deposited in the fine root zone of host trees as those of the vole.

Evidence also suggests that different species of small mammals compete with each other for the truffle food base (Pyare and Longland 2001b). As truffle abundance is reduced or species become less diverse, animals that rely heavily on fungi in their diet may have difficulty finding adequate numbers of truffles. If the small mammal community then changes, predators dependent on small mammals as prey may be affected (Pyare and Longland 2001b). During periods of low truffle production or when other food sources are not available, the effects of clearcutting and thinning on the food supply of small mammals may be more severe (Tevis 1952). These effects may resonate throughout the tightly knit relationship among trees, truffles, small mammals, and predators.

Spore Inoculation of Nursery Seedlings

Inoculation of tree seedlings with specifically selected mycorrhizal fungi, particularly spores of some truffle fungi, can improve survival and growth of various tree species in the nursery and upon outplanting in many parts of the world. In the PNW, the practical application of mycorrhizal fungus inoculation in nurseries dates back to the mid-1970s. Typically, either vegetative inoculum (i.e., mycelium grown and added in a carrier such as vermiculite) or spore inoculum from fruit-bodies has been used.

Spore inoculum is relatively inexpensive and can yield more success than vegetative inoculum for some fungal species. Massive amounts of spores can be economically obtained from specific ectomycorrhizal fungi that fruit as puffballs (*Pisolithus* spp., *Scleroderma* spp.) or truffles (*Rhizopogon* spp.), because most of the spores remain within the fruit-body until maturity. The spores are subsequently suspended in water for storage; the spore suspension is inexpensive to apply through fertilizer or water delivery systems in the nursery or in the field. Spore inoculum has two additional advantages over vegetative inoculum. First, the genetic variability within the inoculum allows for potential genetic expression in response to diverse local abiotic and biotic conditions. Second, the incidental inclusion of associated micro-organisms, such as nitrogen-fixing bacteria, in the inoculum can benefit seedling growth and survival. Castellano and Molina (1989) detailed procedures for spore inoculum production, handling, and inoculation.

Spore inoculation of forest tree seedlings has proven successful for many tree genera and species worldwide, including species of *Abies, Cedrus, Pinus, Pseudotsuga,* and *Quercus.* In the Pacific Northwest, spore inoculation of container and bare-root seedlings nurseries has succeeded with several pine species and Douglas-fir. Several commercial products of spore inoculum are available. By far the most successful use of truffe fungi for spore inoculation has been with species of *Rhizopogon* on Douglas-fir and pines. *Rhizopogon* spores accumulate in forest soils, persist, and quickly colonize seedling roots to form ectomycorrhizae in disturbed forest settings, for example, following fire or tree harvest (Luoma et al., in press; Molina et al. 1999). A related truffle species, *Alpova diplophloeus,* has been used to successfully inoculate red alder seedlings (Molina et al. 1994). Spores from some commercially harvested edible, culinary truffles are used to inoculate tree seedlings for cultivating these highly valuable fungi. We explore this topic next.

Culinary Truffles

History

Although many people think of chocolate candies when they hear the word “truffles” (fig. 81), others immediately remember the aroma of expensive, exotic meals. Not all truffles smell good to humans and not all humans like the odor of culinary truffles. But among the individuals who do like the fragrance of such truffles, reactions can range from appreciative to rapturous. So much so, that the truffles used to prepare gourmet meals are among the most valuable of harvested fungi and expensive foods.

Certain types of truffles have been harvested in Europe since Roman times (Vehling 1977) and likely earlier than that in Africa, Australia, Greece, and the Middle East. In Europe today, the two most valuable truffle species are the Italian white truffle, *Tuber magnatum*, and the French or Périgord black truffle, *Tuber melanosporum*. The common names are a bit misleading because both types of truffles are native to several countries. Other species, such as *T. aestivum* syn. *T. uncinatum* (Wedén et al. 2005) (the Burgundy or summer truffle), and *T. borchii* (the white bianchetto truffle), among others, are also harvested in Europe.

Italian white truffles retail for $1,500 or more per pound and Périgord black truffles for more than $800 per pound. Such high prices reflect, in part, limited supplies. Changes in land use patterns and vegetation cover throughout many parts

David Pilz

Figure 81—Black truffles and a chocolate truffle.

of southern Europe have diminished the extent of native truffle habitat, and truffle crops declined 80 to 90 percent during the 20th century. Efforts to cultivate truffles in orchards have, until the last 20 years, been hampered by inadequate quality control in the production of inoculated tree seedlings and lack of information about ideal ecological conditions and plantation management regimes. These difficulties are now being surmounted so successfully that truffle plantations are being established around the world in temperate climates.

Lefevre and Hall (2001) provided a summary of global truffle cultivation. The general history of culinary truffles is a fascinating topic. Interested readers can delve into it with recent and comprehensive English-language books by Hall et al. (2007) and Renowden (2005).

Truffle Gastronomy

Culinary truffles are obviously edible, but they are predominantly used for flavoring. Their aroma differs by species and they must be smelled to be appreciated. Adjectives such as “fungal,” “musky,” ”garlicky,” “cheesy,” “earthy,” and even “fruity,” all provide hints. Actually, they add more fragrance than flavor to a dish, and their scent is easily destroyed with cooking, so truffles are often added just before the dish is served; truffle-flavored products are minimally cooked. Some aromatic compounds of truffles cling to fat molecules, so any dish with fat in it can be enhanced with truffles. Olive oil, butter, eggs, meat, cheese, and cream are often infused with the flavor of truffles to add savor to pasta dishes, soups, omelets, dips, and spreads. Indeed, many people even find truffle-flavored vanilla ice cream to be surprisingly delicious.

Truffles mature slowly underground and exude strong scents only when they have fully ripened. The period of maturity when they emit intense bouquets can be short because their shelf life is limited. So truffles must be harvested as they reach their peak of ripeness, then marketed and used quickly. Growing underground as they do, dirt clings to them, and because they are minimally cooked, they should be thoroughly cleaned. However, when water is used to clean them, it can hasten decay and shorten their shelf life, particularly if the outer surface is broken. Hence, truffles are usually brushed clean for market and then washed only immediately before use.

Various storage methods are used to allow truffles to "breathe" without becoming too wet or dry. Examples include placing them in waxed paper bags or nestling them in uncooked rice in jars. Microporous plastic bags designed for long-term storage of vegetables would likely also work. If truffles are stored in breathable containers, their aroma is likely to infuse any fatty food product also stored in the same refrigerator, even eggs in their shells.

A variety of "truffle oils" can be found in specialty stores. Virtually all are flavored with one or a few synthesized chemicals known to be in truffle scents, not the full suite of aromatic compounds found in real truffles. Therefore, most truffle oils do not impart the complex fragrance of actual truffles. Olive oil is often infused with fresh truffles for immediate use such as dipping bread (fig. 82) or drizzling on pasta. Controlling bacterial growth can be a challenge when oil that has been in direct contact with fresh or inadequately cleaned truffles is bottled, stored, and marketed later. Irradiation might solve this problem, but presents marketing challenges in the United States.

Although native truffles with potential culinary value have been discovered in temperate forest habitats around the northern hemisphere, Europe, China, and the PNW are three centers of diversity for the especially aromatic truffle species prized by humans. Each species has distinctive characteristics. Odor, habitat, range, size, color, surface texture, interior marbling of the fertile spore-bearing tissues (gleba), maturation season, and handling and storage characteristics all differ. Many chefs esteem truffles native to the PNW as highly as European truffles. However, PNW truffles are not as valuable on the market yet, and the reasons for this discrepancy will be discussed below.

David Pilz

Figure 82—Truffles shaved in olive oil for dipping bread.

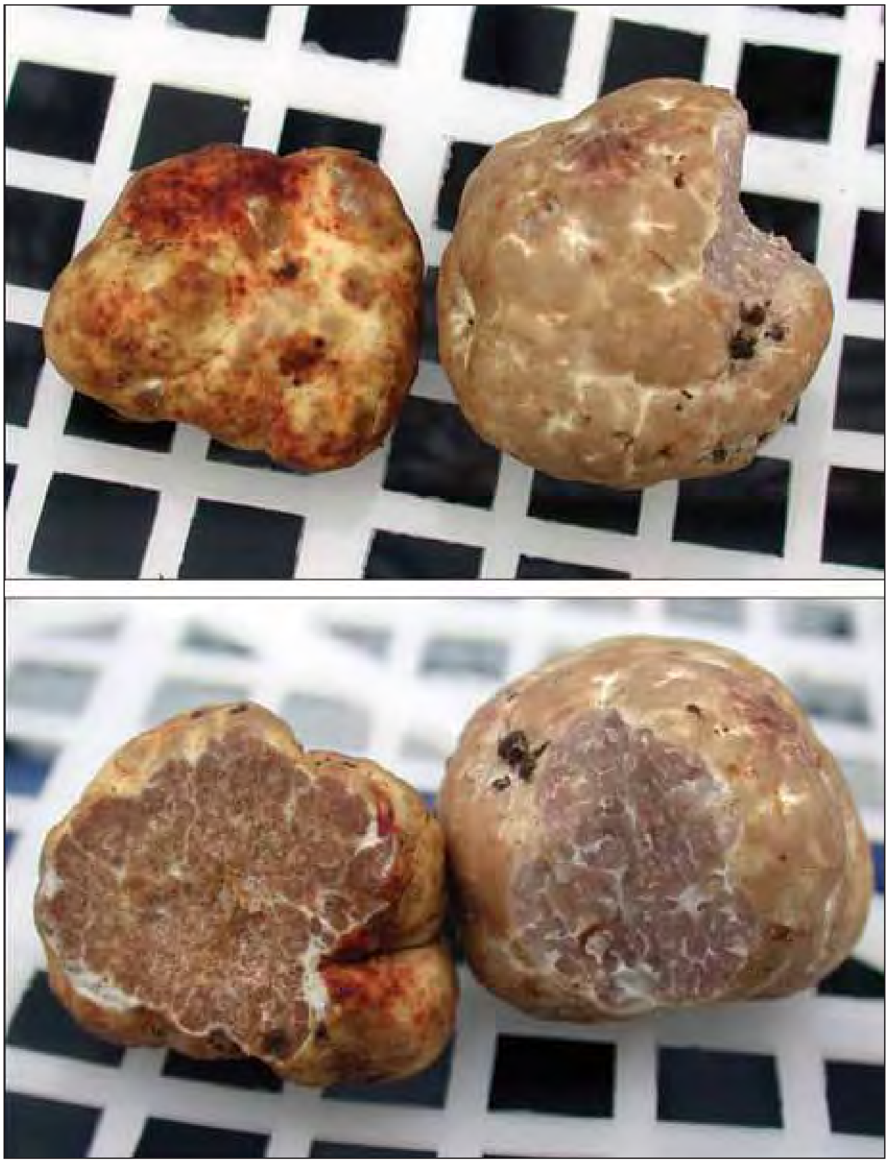
Native Culinary Truffles of the Pacific Northwest

Three types of truffles are currently being harvested in the Pacific Northwest; white, black, and brown truffles. Additional species with culinary potential might still be discovered, but we discuss the most common. For the major commercially harvested species, we briefly describe their appearance, habitat, fruiting seasons, and odors. Further details are available in the Field Guide to North American Truffles (M. Trappe et al. 2007).

White truffles—

The white truffles of the PNW (called "Oregon" white truffles) are related to the culinary truffles of Europe by virtue of being in the same genus, *Tuber*. All the commercially harvested PNW white truffles were originally considered one species, *T. gibbosum*. Further investigation showed morphological differences between those fruiting in the autumn versus spring (Lefevre et al. 2001). DNA analysis now reveals four similar but separate species (G. Bonito, personal communication, Ph.D. candidate, Department of Biology, Duke University, 344 Biological Sciences Building, Durham NC 27708). The autumn white truffle (*T. oregonense* Trappe & Bonito nom. prov.) fruits from October to January, and the spring white truffle (*T. gibbosum* Harken.) fruits from January to June.

Although they can both be found in midwinter, most *T. oregonense* sporocarps are ripening then and most *T. gibbosum* sporocarps are just beginning to grow. These are the two main truffles of commerce. The two other species, provisionally named *Tuber castellanoi* and *T. bellisporum*, are rare and occur in the central Sierra Nevada Mountains of California and far southwestern Oregon, respectively. Figure 83 shows how the exterior and interior appearances of *T. oregonense* and *T. gibbosum* differ. The illustrated truffles are not yet fully ripe. Their interior spore-bearing tissue will darken further, but the distinctive patterns of marbling are currently visible and the differences in exterior coloration are evident.



Charles Lefevre

Charles Lefevre

Figure 83—The exterior and interior of the autumn white truffle (*Tuber oregonense*) on the left of both images and the spring white truffle (*Tuber gibbosum*) on the right of each.

Tuber oregonense and *T. gibbosum* grow as ectomycorrhizal associates of coastal Douglas-fir. They fruit from northern California to southern British Columbia, west of the Sierra and Cascade Ranges at elevations from sea level to 2,000 ft (approximately 610 meters). They occur abundantly with Douglas-fir, ranging from 5 to 60 years of age and growing in monoculture plantations established on former agricultural or pastureland (Charles Lefevre, personal communication, owner, New World Truffieres, P.O. Box 5802, Eugene, Oregon 97405). They are commonly found in Christmas tree farms and fruit abundantly in dense young timber stands, especially those growing in the foothills of the mountains surrounding the Willamette Valley of Oregon and other western interior valleys of California, Oregon, Washington, and British Columbia. Figure 84 shows classic white truffle habitat.

Charles Lefevre

Figure 84—Ideal white truffle habitat. Young, dense Douglas-fir stands growing in the foothills of the Willamette Valley of Oregon.

Several other *Tuber* species fruit in the PNW (for instance *T. californicum* Harken., *T. gardneri* Gilkey, and *T. quercicola* J. Frank et al.) but these are also either seldom found or not very fragrant, so they are not harvested commercially. All currently recognized PNW *Tuber* species are listed in table 1.

Black and brown truffles—

The commercially harvested black truffle of the PNW, *Leucangium carthusianum*, was originally called *Picoa carthusiana*. It is usually larger than Oregon white truffles (fig. 85), has a black, warty surface (fig. 86), and fruits from September to February. It was originally described from France but is more common in the PNW.

Michael Castellano

Figure 85—Oregon white truffles are commonly an inch (2.54 cm) in diameter at maturity, black truffles 2 or more inches (although the size of both can vary considerably—see figure 89).

James Trappe

Figure 86—A closeup of the Pacific Northwest black truffle, *Leucangium carthusianum*. Specimen courtesy of Rita Claremont.

The PNW black truffle grows in much the same habitat as the white truffle. They are ectomycorrhizal associates of coastal Douglas-fir and are as common as white truffles in very young stands. Whereas white truffles occur near the interface of the litter layer and mineral soil, black truffles are usually a bit deeper in the soil profile, often 4 to 10 inches down into the mineral soil. Distribution studies would be useful because harvesters report greater abundance in coastal valleys than interior valley foothills. The scent of black truffles is not as powerful as white truffles nor are they garlicky: rather they exude a “fruity” or “pineapple-like” fragrance.

A second *Leucangium* species is also commercially harvested in the Pacific Northwest, but less frequently. Its provisional name is *Leucangium brunneum*, or the brown truffle. Figure 87 shows the two harvested *Leucangium* species side by side. The brown truffle fruits in the same places and times as the black truffle but is known only from western Oregon and northern California in lowland or foothill forests. Its odor is garlicky.

Charles Lefevre

Figure 87—*Leucangium brunneum* (brown truffle) on the left and *L. carthusianum* (black truffle) on the right.

Harvesting and Management of Pacific Northwest Truffles

The world-famous chef James Beard gave the nascent PNW truffle industry a boost when he sampled a local white truffle at the 1977 Mushrooms and Man Symposium at Linn Benton Community College near Corvallis, Oregon (Walters 1977) and declared it as good as Italian white truffles. The North American Truffling Society (NATS), was organized in 1978. Its mission is to enhance the scientific knowledge of North American truffles and truffle-like fungi and promote educational activities related to these fungi. This all-volunteer organization has collaborated enthusiastically with professional mycologists at OSU, the USDA Forest Service PNW Research Station, and other research organizations. Although its mission is broader than focusing merely on culinary truffles, the society has contributed extensively to general understanding of the habitat, range, fruiting seasons, and characteristics of commercially harvested truffles. Importantly, NATS members are trained in careful data collection, the data are subject to review, and the information they collect is in the public domain rather than held as proprietary business secrets.

As commercial harvesting of truffles and other wild edible forest mushrooms increased in the 1980s and early 1990s, federal scientists and land managers became more involved in understanding and regulating the expanded harvest and associated impacts. In 1991, a workshop was held in Springfield, Oregon, "Biology and Management of Wild Edible Mushrooms in Pacific Northwest Ecosystems." Afterward Molina et al. (1993) published the first report on managing the commercial harvest of wild edible forest mushrooms (including culinary truffles). Much has subsequently been published on the topic of wild mushroom harvesting by the Pacific Northwest Research Station, USDA Forest Service, but because culinary truffles grow predominantly on lower elevation private forest lands, they have not been a primary focus. Pilz and Bondi (2005) prepared a pamphlet on Oregon's forest truffles, especially culinary truffles.

As mentioned earlier, PNW truffles do not fetch the same high prices as European truffles, although many chefs find them just as desirable. Much of the price differential has to do with reputation. As the "original" culinary truffles, European species have a premier reputation. Additionally, PNW white truffles seem to have a shorter period of peak ripeness, a shorter shelf life, and more exacting storage requirements than European truffles. Rectifying these issues will entail educating chefs about the unique characteristics of PNW truffles.

But the difference in reputation for quality also relates to harvesting methods. European truffles are typically harvested individually, near full maturity, by use of dogs to sniff them out (fig. 88). The PNW truffles, in contrast, are usually sought by raking aside the litter layers of the forest floor. Because truffles require a long time to mature and all specimens do not mature at the same rate, raking results in the harvest of many unripe truffles that lack their full mature aroma. The sale of such unripe truffles to chefs has resulted in lackluster demand and low prices for PNW truffles. Raking for truffles is also unsightly and disrupts the mycorrhizae and truffle colonies in the soil. The sooner PNW truffle harvesters train and use dogs to harvest only ripe truffles, the sooner prices for premium Oregon truffles will approach their full potential, but overcoming a reputation for poor quality will take time.

Currently, most profit from harvesting native PNW truffles is realized by the harvesters and sellers, but if harvesting practices and prices improve, landowners


David Pilz

Figure 88—Stella, one of Oregon’s first truffle dogs, hunts in a young truffle plantation near Corvallis.

also stand to realize income from harvests in their forests. As in Europe, trespass and unauthorized harvesting are issues that must be addressed to insure that all parties benefit equitably from the growing PNW truffle industry.

The Future

Cultivating Pacific Northwest truffles—

Although some truffle harvesters and landowners claim success at establishing new truffle patches by spreading spores on the forest floor, no one has yet demonstrated with prior sampling and replicated trials that the truffles were not there already or that the method actually works. Anecdotal evidence, however, suggests that such trials would be worthwhile. Additionally, a Christmas tree farm that was accidentally limed very heavily produced some of the largest native white truffles on record (James Trappe, personal observation). The white truffle in figure 89, although not from this farm, illustrates how large PNW white truffles can grow. Liming experiments might prove useful for improving production. Similarly, irrigation is a standard method for enhancing truffle production in plantations of European truffles and might work well with our native truffles too.

Although some attempts have succeeded, methods for consistent inoculation of PNW truffles onto the roots of Douglas-fir seedlings in nurseries have not yet been developed. Additional experiments with growing media or nursery conditions may

David Pilz

Figure 89—Potential size of Pacific Northwest white truffles.

yield reliable methods, but, so far, plantations of Douglas-fir seedlings inoculated with PNW truffles remain a future prospect. If perfected, this technology could vastly expand native culinary truffle production.

Plantations of European truffles—

The Périgord black truffle is the most valuable and easiest truffle to cultivate. Two other species native to Europe, the Burgundy or summer truffle and the white bianchetto truffle, are also readily cultivated but a little less valuable. The spores of the Périgord black truffle can readily be used to inoculate hazel or oak roots under nursery conditions, and the truffle ectomycorrhizae formed in the nursery then persist after planting if the soil, moisture, pH, and temperature conditions in the plantation are appropriate. Périgord black truffles are large and command good prices. Orchards can start producing within 5 to 10 years and may become profitable shortly thereafter. In the Pacific Northwest, Périgord black truffles can be grown on sites with moderate climate, irrigation, and well-drained soils that have been heavily limed to raise the pH. Lefevre and Hall (2001) discussed current trends in truffle cultivation. Hall et al. (2007) provided a detailed, up-to-date manual for establishing and managing truffle orchards.

One company in the Pacific Northwest, New World Truffières (http://www.truffletrees.com/; 6 June 2008), currently sells tree seedlings inoculated with the Périgord black truffle and provides information about site selection and plantation management on its Web site. Seedlings from this company are now growing in

California, Oregon, Washington, elsewhere in the United States, and in British Columbia. California has at least one plantation producing, and, although Canada is relatively chilly, the Truffle Association of British Columbia (http>//www.bctruffles.org/index.html; 6 June 2008) is promoting trufficulture in British Columbia, especially the south coastal and Okanagan areas. Cultivated European truffles likely will compete with native PNW truffles in the market, but there is little chance of such truffles escaping cultivation and becoming established as ecological competitors of native truffles; European truffles are adapted to alkaline soils, and most soils in the PNW are naturally acidic. This requirement of the Périgord black truffle for alkaline soils also gives it a competitive ecological advantage in heavily limed soils in plantations in the PNW, because most native ectomycorrhizal fungi in the surrounding forests are adapted to acidic soils and are unlikely to compete well in alkaline soils.

A truffle industry—

The growing harvest of truffles in the PNW is leading to the development of a truffle industry that will certainly complement the local wine industry. The Oregon Truffle Festival (http://www.oregontrufflefestival.com; 6 June 2008) has been held annually in Eugene (fig. 90). The weekend event emphasizes both native and cultivated truffles. It includes cultivation seminars, forays into surrounding forests to hunt native truffles, winery tours, truffle meals prepared by local restaurants, cooking expositions, a demonstration of training dogs to hunt truffles, a marketplace of Oregon food and wine products (including truffles), a lecture series about truffles, and a grand truffle dinner (fig. 91). Culinary truffles may grow underground in the dark, but their future looks bright in the Pacific Northwest.

Conservation and Management of Truffle Fungi and the Fungal Resource

The PNW truffle species exhibit complex natural histories and ecologies. Although we have broad knowledge on truffle community dynamics and ecosystem functions, we lack detailed information for most individual species, particularly regarding unique habitat preferences, ecological amplitudes, and response or adaptation to various types of forest disturbance. Without species-specific knowledge, it is difficult to tailor management recommendations aimed at conserving individual species. There are also too many species to take a species-by-species approach to conservation and management. For these reasons, Molina et al. (2001) emphasized use of holistic ecosystem management concepts to sustain the diversity and function of forest fungi. Within this management paradigm, truffle ecosystem functions, community dynamics, and response to disturbance are taken into account when

David Pilz

Figure 90—Banner for the Oregon Truffle Festival.

David Pilz

Figure 91—Participant contemplates black truffles at the Oregon Truffle Festival grand truffle dinner, 2006.

developing management plans. Planning is often done at large spatial and long temporal scales to account for broad, landscape patterns of disturbance and their effects on the recovery and dispersal of different species. Managers also consider the importance of maintaining biological legacies such as green trees, standing snags, coarse wood on the forest floor, and understory vegetation to enable natural recovery following disturbance. The Northwest Forest Plan (USDA and USDI 1994) exemplifies an ecosystem management approach that conserves species, including fungi, while producing the goods and services desired by the public.

In this final section we reflect on some of the major challenges managers face in integrating truffle conservation into management plans, including rare species management, monitoring, and habitat restoration. Some of the concepts we present are specific to truffles, and others pertain more generally to forest fungi, particularly ectomycorrhizal fungi. We conclude by providing guiding principles for managing the fungal resource.

Understanding Fungal Rarity

New truffle species are discovered and described nearly every year from Pacfic Northwest forests. Given that mycologists have been searching for truffles for a hundred years in the region, do these newly described truffles represent rare species or simply reflect an expanding area of search with more collectors? We expect that both explanations are valid. To protect rare truffle species in a conservation context, how does one determine if a fungus is truly rare or just undercollected? Botanists have answered this question for plants simply by conducting extensive statewide surveys and inventories, particularly on public lands. Availability of comprehensive species keys, cadres of trained professionals and amateurs, and inclusion of plants in state and federal conservation plans aid in this pursuit. Plant inventories done over decades throughout the PNW have yielded comprehensive lists of rare plant species and support placement of many species onto various protection status lists. Unfortunately, comprehensive identification keys and cadres of trained professionals do not exist for macrofungi, and fungi are not routinely included in species inventory programs. Thus we lack extensive data sets from systematic surveys to gauge rarity. Nevertheless, mycologists do not lack resources to address the rarity question, and significant progress has occurred in the PNW.

In 1994, the federal land agencies in the PNW implemented the Northwest Forest Plan (USDA and UDSI 1994) to meet a variety of species conservation and timber harvest objectives. Protection of old-growth forests and rare species associated with those forests was a primary conservation objective. As part of plan development, 527 fungal species were assessed to answer whether the plan's system of reserves and other management guidelines provided ample protection for their persistence. In the final analysis, 234 fungi were listed for protection under the Survey and Manage Program guidelines (Molina et al. 2006). The mycologists who did this analysis (Professors Joseph Ammirati, William Denison, and James Trappe) based their findings on herbarium collections, personal records, and expert knowledge (together they had over 90 years of collecting experience in the region). The Survey and Manage Program species list included about 60 truffle species. Because of the uncertainty regarding species rarity status, habitat association, and distribution in reserves, the program proposed 10 years of survey to learn more about those attributes and inform decisionmakers about conservation needs (e.g., Do these species need protection of known locations?). This unique conservation program was the first in the United States to include fungi on a federally protected species list.

After 8 years of various types of surveys throughout the region, new data are available to address the original uncertainties regarding fungal rarity. About half the 60 presumed rare truffle species were found to be rare, having been documented from 10 or fewer locations (Molina 2008). A few truffle species proved to be common and were removed from the program. The remaining species displayed intermediate rarity designations (see Molina 2008 for additional data regarding rarity and distribution of Survey and Manage Program fungi). These data represent the first comprehensive evaluation of fungal rarity based on systematic surveys at a regional scale in the United States.

Two important lessons emerge from the Survey and Manage Program experience. First, given adequate resources (funds and personnel) and time (years), practical surveys can be conducted for forest fungi, including truffle species, and those data can be applied to issues of rarity and habitat association. Secondly, the use of expert knowledge and records by established mycologists, together with herbarium records, can serve as a reliable starting point to address fungal conservation issues. When such expert knowledge is used, it is important to view early assessments as hypotheses that need testing with systematic surveys. For example, based on collection records and expert knowledge, we estimate that nearly 50 percent of truffles in the PNW are rare and an additional 25 percent are infrequent (table 1). This first approximation of rarity designations for the region's truffle species now calls for systematic surveys to test these hypotheses.

Our difficulty in detecting fungi based on fruit-body presence creates the greatest challenge to assembling the data required to declare species rarity or abundance. Detection is particularly difficult for truffles because of their cryptic reproduction with fruit-bodies mostly hidden beneath the soil surface. Regardless of that, researchers have developed methods to sample truffle populations and address detectability issues. The next section summarizes our knowledge on this important issue and provides tools to improve truffle inventories.

Inventory, Sampling, and Detection Considerations

Many researchers have addressed the problems of sampling fruit-bodies to estimate the diversity and standing crop of ectomycorrhizal fungi (Arnolds 1981; Claridge et al. 1993, 2000b; Colgan 1997; Fogel 1981; Horton and Bruns 2001; Luoma 1991; North et al. 1997; O'Dell et al. 1995a; Pilz and Molina 1996; Smith et al. 2002). Some of the difficulties are (1) in many cases, fungal species concepts are poorly understood and defined; (2) collections are difficult to identify morphologically and often require considerable research to reach independent taxonomic decisions; (3) fruit-body production is strongly seasonal, subject to yearly variation caused by variable weather patterns, and exhibits varying, largely unknown rates of decay and predation; (4) fruit-bodies are regularly consumed by mammals, thereby potentially masking our abililty to quantify true productivity in the field; (5) fruit-body production is not necessarily related to the vegetative abundance or to the activity of the mycelial colony or mycorrhizae; and (6) autecological research is lacking both in the field, where it is hampered by the concealed nature of the fungal colonies, and in the laboratory, where it is constrained by the investigators' inability to confidently relate findings to field situations.

The more frequently an area is sampled during the year and the more years such sampling is conducted, the better the estimates represent ecosystem conditions. Although axiomatic for any sampling, this conclusion pertains especially to fungal fruit-bodies, which are extremely weather dependent and variable in their fruiting, temporally and spatially. Luoma et al. (2004) provided a particularly well-documented example by tracking the presence or absence of fruit-bodies on 4,500 individual square-meter plots on forest soil, twice yearly, for 3 years. Of those, only 1,246 (28 percent) ever contained a fruit-body of any ectomycorrhizal species. Yet we know from studies of ectomycorrhizal fungi that the forest soil of our study area has highly diverse and abundant populations of ectomycorrhizal fungi (Luoma et al. 2006). Some of that peculiar problem can be overcome by use of large plots (e.g., 1000 m^2) sampled for a fixed time (e.g., 100 person-minutes), such as used by Claridge et al. (2000a, 2000b). This approach overcomes the patchiness typical of fungal colonies.

For reasons noted above, it becomes clear that studies of effects of forest management practices on the fruiting of ectomycorrhizal fungi must be relatively long term and involve frequent sampling. Such studies can be costly and, if sampling is inadequate, may miss treatment effects. Alternative approaches to answer questions about populations of ectomycorrhizal fungi entail estimation of their actual occupation of rootlets in the soil. This can be based on ectomycorrhiza morphotypes and on DNA analysis of ectomycorrhizae (Agerer et al. 1996; Eberhart and Luoma 1996, 1997; Eberhart et al. 1996; Gardes and Bruns 1996; Goodman et al. 1996; Horton and Bruns 2001; Izzo et al. 2005; Luoma et al. 2006). These approaches are presently costly, but are becoming less so as the technology develops. When combined with sampling of the fruiting of ectomycorrhizal fungi, they hold promise to greatly improve methods to determine effects of natural or anthropogenic disturbance on populations of ectomycorrhizal fungi in forests (Dahlberg 2001).

Readers are referred to Claridge et al. (2000a, 2000b) and Castellano et al. (2004) for detailed discussion of sampling strategies for truffle fungi.

Protection and Restoration of Habitat

Protecting and retoring habitat for truffle fungi populations and productivity requires both a broad consideration of disturbance effects on truffle fungi and general principles of ecosystem restoration. In this section we bring forward some of the ecological and silvicutural findings discussed previously and relate these to restroration activities.

Federal land management agencies in the PNW are concerned about effects of forest management practices on conservation of fungal species, particularly species associated with diminishing old-growth forests. Therefore, forest management strategies in this region currently emphasize protecting biodiversity while sustaining site productivity by maintaining old-growth components, such as coarse wood (CW) on the forest floor, in managed stands (Molina et al. 2006). This conservation approach seems prudent, particularly in forests west of the Cascade Range, given the results of Amaranthus et al. (1994) that brown-cubical rotted CW left in plantations acted as refugia for fruiting of truffe fungi, and of Elliott et al. (2007) that ectomycorrhizal communities in CW were similar between young and old-growth stands. It was hypothesized that this would be the case, although little was known about whether the decay patterns and physical and chemical properties of CW in young, managed stands resembled those in old-growth stands. Again, these results highlight the importance of CW in advanced decay stages in providing habitat critical to some species of ectomycorrhizal fungi in both old-growth and young, managed stands (Amaranthus et al. 1994, Elliott et al. 2007). In addition, the presence of decaying logs influences the abundance of truffles for some species (Amaranthus et al. 1994, Meyer and North 2005, North and Greenberg 1998).

Numerous factors other than CW influence the abundance of truffles in forests of the PNW and must be considered when protecting habitat for truffle species. Forest stand structure (Luoma et al. 2004, North et al. 1997, Smith et al. 2002), canopy cover (States and Gaud 1997), stand density (Colgan et al. 1999, Luoma et al. 2004), moisture gradients (O'Dell et al. 1995b), and fire history (Claridge et al. 2000a) have all been shown to influence truffle abundance. Much of the information about ecological factors influencing truffle production has come out of studies conducted in wet forest ecosystems of the Pacific Northwest. In contrast, relatively few studies have examined truffle abundance or species occurrence in drier interior forests of the PNW (Lehmkuhl et al. 2004; Meyer and North 2005; Smith et al. 2004, 2005). The variety of forest ecosystems within the region is vast, so it must be emphasized how difficult it is to directly apply study findings conducted in one habitat type to that of another, even within the same geographic region.

Public land managers in the PNW are being confronted with ecosystem management planning that incorporates increasing complexity and goals that can seem contradictory. For example, in the dry pine-dominated forests of this region, fire suppression over the past century, combined with insect infestations, climate change, and logging of the largest trees, has resulted in increased stand densities, unusually high fuel loads, and changes in plant species composition (Hessburg and Agee 2003, Hessburg et al. 2005). In some areas on the east side of the Cascade Range, these densely wooded, multistoried forests now extend the range of, and provide habitat suitable for, the northern spotted owl. Public land managers require a landscape-level perspective to develop and balance management approaches to reduce fuels and the imminent risk of stand-replacing wildfire, while also maintaining owl habitat (Rapp 2005).

Ecosystem approaches to forest management provide an avenue for integrating our understanding of the biological and functional diversity of forest fungi into current forest management objectives (Molina et al. 2001). Forest management has the potential to degrade soil productivity. Productive soils are the foundation of productive forest ecosystems. Effects of management (short-rotation nutrient removals, soil erosion and compaction, nutrient losses by fire, and fertilization) on growth of crop trees have been a focus of policy concern for many years (Ballard and Gessel 1983, Bormann and Gordon 1989). Emerging concerns, in addition to long-term growth of crop trees, focus on restoring and maintaining habitat.

Adopting management approaches that "tread lightly" on the soil ecosystem are the most effective and least costly approach to maintaining forest soils in a productive condition. Nevertheless some level of disturbance is inevitable with most management activities and may require action to restore productivity to soils.

Although several terms, with sometimes contradictory meanings, are employed in the vast literature in restoration ecology, it is generally accepted that rehabilitation seeks to repair ecosystem functions but may also seek to develop an ecosystem generally similar to one previously on the site (restoration in the broad sense) or re-create an ecosystem previously present (restoration in the narrow sense) (Walker and del Moral 2003). In forest management, soil conservation seeks to maintain forest soils in a productive condition and soil rehabilitation aims to restore productivity to degraded soils.

Approaches for restoring productivity to degraded soils after forest management actions are diverse, depending on interactions among a variety of factors including site characteristics (e.g., steepness, soil type, and soil texture), the management activity, and the intended future use or objective for the site. For example, if a road, log-landing, or trail is intended for re-use at a future time, then no action other than erosion control may be needed; in areas where trees and shrubs readily encroach (e.g., Willamette Ecological Province), then active removal of vegetation may be necessary (Anderson et al. 1997). In most areas, if the objective is to restore the site so that it supports trees and vegetation, then measures such as subsoiling or tillage, topsoil recovery, site organic matter enhancement, and reforestation may be appropriate and beneficial (B.C. Ministry of Forests 2002). Reforestation may or may not be improved by outplanting seedlings inoculated with ectomycorrhizal fungus species, depending on host and fungus species, site conditions, and their interactions (Castellano 1996, Jones et al. 2003, Trappe 1977). Indeed, as the review of the role of ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging by Jones et al. (2003) showed, rehabilitation cannot be accomplished by following a set formula. Instead, it requires considerable site-specific information combined with general principles, and ecosystem and economic constraints.

Summary of Management Principles and Considerations

The following 12 principles and considerations will help managers integrate truffle conservation into ecosystem management plans where appropriate. These principles are not mutually exclusive; several overlap in concept and practice. Many of the principles are elaborated by Maser et al. (2008).

1. **Maintain habitat diversity at landscape scales.** Truffle species have evolved within the shifting mosaic of forest age classes, plant community dynamics, and periodic disturbances that have occurred in the PNW over many thousands of years. Thus, truffles occur in a wide variety of forest types from young to old growth, wet to dry, and frequently to infrequently

disturbed. Maintain, protect, or restore these various large-scale habitat elements at the landscape scale. For example, old-growth forest habitat likely covered 25 to 75 percent of the PNW forest landscape over the last few thousand years, yet only about 10 percent of the landscape is currently old growth, and much of that is high-elevation forest that is less productive for timber. Maintaining and restoring old-growth forest habitat will be important for the many truffle species associated with that habitat (Molina 2008). Franklin et al. (2006) provided general principles for restoring old-growth forest habitat. Pattern these elements on the landscape to provide for truffle dispersal and population establishment.

2. **Maintain habitat diversity within forest stands.** Truffle fungi often fruit in patches scattered throughout forest stands, a likely response to different habitat niches, microclimatic differences, and fungal species competition. Maintaining or developing habitat diversity at the stand level will provide ample latitude for truffle populations to flourish. Habitat attributes to consider include plant and animal species composition, organic matter, coarse wood on the forest floor, openings to promote shade-tolerant plants and tree age diversity, and soil quality (see below).

3. **Maintain or restore tree (host) diversity.** Nearly all truffles form ectomycorrhizae and often do so with a broad diversity of tree and shrub hosts (table 2). Stands with a high diversity of host plants therefore have higher truffle diversity than stands with one or few hosts (e.g., monocultures of Douglas-fir or pine). For example, in Crater Lake National Park, stands with noble fir (*Abies procera* Rehd.), mountain hemlock, and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) had about 20 percent more ectomycorrhizal fungus species than those with only fir and hemlock (M. Trappe 2008). Ectomycorrhizal shrubs or trees that quickly sprout after fire (e.g., *Arbutus, Arctostaphylos, Quercus*) provide biological legacies to maintain truffle species until later seral, dominant trees return. Allow some portion of these legacy plants to remain active in the natural recovery process to benefit truffle populations.

4. **Integrate truffle conservation and wildlife management principles.** Truffles are dispersed mostly by mammals, particularly small mammals, and many such animals depend largely or exclusively on truffles in their diet. Joint consideration of wildlife and truffle habitat in forest management plans will lead to the best conservation of both species groups.

5. **Provide habitat connectivity for wildlife populations.** Healthy wildlife populations strongly depend on their ability to explore and disperse into suitable habitat. Maintaining or building appropriate habitat connectivity is crucial to these processes. Positive effects on animal dispersal will also positively affect dispersal of truffle fungi.
6. **Use prescribed fire to improve wildlife habitat.** Prescribed fire is usually applied as a hazard reduction tool, but it can damage wildlife habitat if not carefully applied. To avoid damage or even to improve habitat, Trappe et al. (2006) recommend these: (1) do not burn too frequently; allow restoration of litter layers and shrub cover needed by many small mammals; (2) keep burns small and not intense; (3) whenever possible, leave nonburned islands within the burn; (4) design the burn to have maximum edge so that even very small mammals can move between burned and nonburned areas. These principles will also maintain diverse habitats for diverse truffles.
7. **Maintain or restore coarse wood on the forest floor.** Both buried wood in and CW on the forest floor provide important microhabitat for truffles and small mammals. Ectomycorrhizae often proliferate in buried wood, and a few truffle species fruit abundantly in well-decayed logs (e.g., *Rhizopogon vinicolor, R. truncatus,* and *Hydnotrya variiformis*). Small mammals often travel beneath or along the edges of logs and are thus protected from predation. The Northwest Forest Plan (USDA and USDI 1994) provided excellent guidelines for CW management in PNW forests and an online model, DecAid (https://wwwnotes.fs.fed.us/pnw/DecAID/DecAID.nsf), provides tools to guide CW management for maintaining biodiversity.
8. **Maintain soil health.** Ectomycorrhizal fungi are aerobic soil organisms, i.e., they require oxygen for respiration and thus good soil aeration. Avoid soil compaction and hot fires that destroy soil structure, particularly the stable microaggregates that allow for air and water movement. Ectomycorrhizal fungi are also efficient scavengers of soil nutrients, and many directly decompose and mobilize nutrients from organic matter. Maintaining natural organic matter accumulation and decomposition processes is essential for thriving truffle populations and overall ecosystem health. This is a particularly challenging principle when prescribed burning is used for fire hazard reduction.

9. **Limit size of clearcut timber harvests and maintain live legacy trees and shrubs.** Truffle fungi cannot live without their ectomycorrhizal hosts. Thus, retain green trees in harvest units, or consider leaving sizable patches of healthy trees to serve as refugia for fungi and other forest organisms. Integrate concepts of habitat connectivity in designing harvests at watershed and landscape scales.

10. **Protect known locations of rare truffle species or truffle hotspots.** The Survey and Manage Program of the Northwest Forest Plan (Molina 2008, Molina et al. 2006) provides extensive data on known locations and distribution maps for several rare, old-growth forest-associated truffle species. Protect these known locations and maintain habitat conditions. Castellano and O'Dell (1997) provided detailed management recommendations on how to do so. Consider forest stands with high truffle species diversity, particularly of rare species, for extra protection or even designate them as fungal reserves. Similarly, when stands are known to produce highly productive populations of commercially harvested truffles such as *Tuber oregonense*, *T. gibbosum*, or *Leucangium carthusianum*, prioritize the management of these stands to sustain this valuable nontimber forest product. If several locations of rare species are known, sampling and modeling as done by Claridge et al. (2000a, 2000b) to define the habitat requirements would be good for maintaining populations or finding additional locations.

    Except for mature old-growth species, protecting specific locations may only provide a short-term solution. Providing habitats of the right age class of trees in the vicinity of known locations is an important strategy because it will contribute to the establishment of future fungal populations.

11. **Monitor truffle populations.** Key to sustaining any biological resource is having adequate baseline data to detect population trends. Therefore include truffle fungi in long-term biodiversity monitoring programs. Establish permanent monitoring locations in representative forest types, hot spots, or rare species locations around the region. Use citizen volunteers to help with data collection in partnership with resource managers (Pilz et al. 2006).

12. **Develop and nurture partnerships between mycologists, resource managers, and the public.** Promote workshops and field trips to educate resource managers and the public on the intricacies of truffle ecology and ecosystem function, and forge partnerships to study, monitor, and manage the truffle resource.

Concluding Remarks

Mycologists at times lament that it is difficult to recommend management approaches to conserve fungi because we have limited knowledge on the taxonomy, natural history, and ecology for the thousands of species. Although our knowledge may indeed be meager on a species-by-species basis, it is broad in a general sense as seen in this publication. This general knowledge provides more than enough background to appreciate the diversity and critical ecosystem function of truffles and move forward with plans to conserve and manage this resource. This cryptic group of soil fungi has been studied and documented in more detail in the PNW than in any other forested region of the world. Most importantly, mycologists associated with the Forest Service's Pacific Northwest Research Station in Corvallis, Oregon, have worked for decades with managers to incorporate an ecosystem understanding of fungi in forest ecosystem management plans. We hope that this synthesis will provide the underpinning for conserving this fascinating and important group of forest organisms.

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Metric Equivalents

When you know	Multiply by:	To find:
Microns, micrometers (µm)	25,400	Inches
Millimeters (mm)	25.4	Inches
Centimeters (cm)	2.54	Inches
Meters (m)	3.28	Feet
Kilometers (km)	.62	Miles
Hectares (ha)	2.47	Acres
Kilograms (kg)	2.205	Pounds
Metric tons (t)	1.102	Short (U.S.) tons
Metric tons (t)	2,222	Pounds
Kilograms per ha	.893	Pounds per acre
Celsius (°C)	(1.8 × °C) + 32	Fahrenheit (°F)

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Appendix (CD-ROM)

What's On the CD-ROM: We have provided photographs for 111 species of PNW truffles and a short movie featuring James Trappe on a truffle hunt.

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