

*Phaeocollybia*  
of

**Pacific Northwest North America**

Lorelei L. Norvell & Ronald L. Exeter

# ***Phaeocollybia* of Pacific Northwest North America**

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*Phaeocollybia kauffmanii* in Jackson State Forest, California  
Photograph courtesy of Scott Redhead, Agriculture & Agri-Food Canada

## Abstract

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As a result of the 1994 presidentially mandated Record of Decision, United States Bureau of Land Management (BLM) and Forest Service planning documents specified guidelines for surveying for 'rare' and 'uncommon' fungal species in United States forests within the range of the northern spotted owl. This document listed all but one of the described *Phaeocollybia* species then known to occur in the Pacific Northwest, believed to be the most highly diverse region for the genus in the world. Later taxonomic revision of the genus by the senior author — combined with data obtained from BLM-Pacific Northwest Mycology Service cooperative research and examination of hundreds of specimens collected by Northwest Forest Plan forest surveyors — led to the naming of ten new *Phaeocollybia* species. This publication offers a key to all described 25 *Phaeocollybia* species from Pacific Northwest United States (California, Idaho, Washington, Oregon) and Canada (British Columbia). Detailed summary descriptions are accompanied by color photos depicting each species in the field, in the lab, and under the microscope. Discussions of global distribution, ecology, development, biology, taxonomy, and suspected phylogenetic relationships offer essential background information to those working within and outside the Pacific Northwest region. A glossary and complete bibliography to the *phaeocollybia* literature are also provided.

Key words: *Phaeocollybia*, *Cortinariaceae*, *Agaricales*, fungi, Northwest Forest Plan

## Color Bar Key

A) **Distribution & Ecology**



B) **Development & Biology**



C) **Taxonomy & Phylogeny**



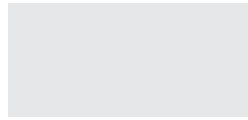
D) **Diagnostics**



E) **Conspectus & Keys to species**



F) **Species descriptions**



G) **Bibliography**



H) **Glossary**



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A photograph of a forest scene. A large tree trunk is covered in vibrant green moss. The forest floor is also covered in moss and small green plants. Several mushrooms with reddish-brown caps and stems are growing on the forest floor. The background is a misty forest with tall trees.

*Phaeocollybia*  
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## Introduction

*Phaeocollybia* is a genus of brown-spored agarics easily recognized in the field by their deeply rooting cartilaginous stipes and normally viscid conic-campanulate pilei. *Phaeocollybia* species were originally included among a heterogeneous assemblage of brown-spored species of *Agaricus* that Fries (1838) grouped within the subtribe *Gymnoti* in the Tribe *Naucoria*. Among eleven species placed together in an unnamed group characterized by gills that were narrowly attached ('nearly free') to the stipe were five that would form the core of *Phaeocollybia* a century later: two species first described by Fries in 1821 — *Agaricus lugubris* and *Agaricus hilaris* — and three also described by him in 1838 — *A. christinae*, *A. cidaris*, and *A. festivus*. When *Naucoria* was later elevated to generic level (Kummer 1871, Quélet 1872), the genus retained its essentially heterogeneous character.

Heim (1931) segregated *Phaeocollybia* from *Naucoria* for brown agarics with cartilaginous 'rooting' stipes, viscid to glutinous ('slimy') caps, brown ornamented spores, cheilocystidia (sterile cells on gill edges), and gelatinous tissues. Heim transferred the 'core' species named above to his new genus and suggested that four other species assigned to *Simocybe* by Karsten (1881, including *S. jennyae*) probably should be placed in *Phaeocollybia* as well. Heim did not select a type species for his genus, which another author (Konrad 1934) lectotypified by designating his recently neotypified *Phaeocollybia lugubris* as type species. After Heim and Konrad, the genus was critically revised by Kühner & Romagnesi (1957), Smith (1957b), Horak (1977), Singer (1970, 1986, 1987), Redhead & Malloch (1986), Bon (1992), Bandala (1994), Bandala et al. (1996), and Norvell (1998a).

## World distribution and ecology

Singer was the first to recognize distribution of *Phaeocollybia* species outside Europe when he transferred North American and Chinese naucorias (i.e., Smith's *N. kauffmanii* in 1940 and *N. radicata*, *N. attenuata*, and *N. similis* in 1951) to Heim's new genus. Since that time, new species have been recognized from forests on every continent except Africa and Antarctica. Distribution of currently recognized

*Phaeocollybia* species is provided in TABLES 1 and 2. The brief summary below provides an additional overview.

GREAT BRITAIN AND EUROPE — Although the genus was first described from Europe, *Phaeocollybia* is represented by only six currently accepted species reported from 13 countries (AUSTRIA: Moser 1950; CZECH REPUBLIC & SLOVAKIA: Vesely et al. 1972, Mann 1991; FINLAND: Karsten 1879, 1881; FRANCE: Bon 1979, 1992, Konrad & Maublanc 1948, Kühner 1980, Kühner & Romagnesi 1957, Labarre 1997, Robin 2007; GERMANY: Krieglsteiner 1991, Laber 1982, 1991; GREAT BRITAIN: Dennis & al. 1960, Watling & Gregory 1993; ITALY: Bresadola 1930; NORWAY: Reid 1972, Gulden 1983, 1992, 2008; ROMANIA: Pazmany & Laszlo 1987; SPAIN: Bandala & Montoya 2003, Olariaga & al. 2004; SWEDEN: Jacobsson & Stridvall 1983; SWITZERLAND: Horak 1968, Breitenbach & Kränzlin 2000; UKRAINE: Karpenko 1998. For the continent, see also Heim 1931; Singer 1951b, 1986; Bresinsky 1960; Lange & Hora 1963; Poelt & Jahn 1963; Horak 1977, 2005; Moser 1983; Moser & Jülich 1994.) Widely distributed throughout Europe, phaeocollybias are encountered only sporadically and are restricted to coniferous forests, particularly those containing spruce (*Picea*).

ASIA — Four European and five endemic species have been reported from eastern Asia and India (CHINA: Bresadola 1930, Keissler & Lohwag 1937, Liu 1995, Teng 1996, Zang 1996; INDIA: Horak 1974, 1980, Abraham 1992; JAPAN: Imai 1938, Imazeki & Hongo 1988; SIBERIA: Nezdoinnogo 1986, 1990. See also Horak 1977; Singer 1951b, 1986). Throughout Asia, phaeocollybias are reported only from boreal and temperate coniferous forests.

AUSTRALASIA — There are seventeen species reported from Australasia (AUSTRALIA: Fuhrer & Robinson 1992, Horak 1983, May & Wood 1997, Rees & Syme 1999, Rees & Wood 1996; MALAYSIAN ARCHIPELAGO: Corner 1994; NEW ZEALAND: Horak 1973, 1977. See also Singer 1986.) All species are endemics except for one possible exception. Horak (1977) placed his species *Phaeocollybia longipes* (Horak 1973) into synonymy with *P. festiva*, despite its association with *Sphagnum* and *Nothofagus*. Future type studies may show that *P. longipes* is also indigenous to New Zealand.



TABLE 1: World species of *Phaeocollybia*

SPECIES	SECTION	DISTRIBUTION
<i>P. amazonica</i> Singer (1961)	<i>Subattenuatae</i>	S. America: Bolivia
<i>P. ambigua</i> E. Horak & Halling (1991)	<i>Phaeocollybia</i>	C. & S. America: Costa Rica & Colombia
<i>P. ammiratii</i> Norvell (2000)	<i>Subattenuatae</i>	N. America: PNW—BC WA OR CA
<i>P. amygdalospora</i> Bandala & E. Horak (1996)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. arduennensis</i> Bon (1979)	<i>Radicatae</i>	Eurasia: Europe
<i>P. attenuata</i> (A.H. Sm.) Singer (1951)	<i>Phaeocollybia</i>	N. America: PNW—BC WA OR CA ID
<i>P. australiensis</i> B.J. Rees & AE Wood (1996)	<i>Versicolores</i>	Australasia: New South Wales
<i>P. benzokauffmannii</i> Norvell (2000)	<i>Phaeocollybia</i>	N. America: PNW—WA OR CA
<i>P. bicolor</i> E. Horak (1977)	<i>Radicatae</i>	Australasia: New Guinea
<i>P. brasiliensis</i> I.A. Araujo (1987)	<i>Subattenuatae</i>	S. America: Brazil
<i>P. californica</i> A.H. Sm. (1957)	<i>Versicolores</i>	N. America: PNW—OR CA, Mexico
<i>P. caudata</i> E. Horak & Halling (1991)	<i>Microspora</i>	C. & S. America: Costa Rica & Colombia
<i>P. christinae</i> (Fr.) Heim (1931).	<i>Phaeocollybia</i>	N. America & Eurasia: Mexico, Canada—ON QU, USA—MA ME & Europe, Siberia, Japan
<i>P. cidaris</i> (Fr.) Romagn. (1944)	<i>Versicolores</i>	Eurasia: Europe & Siberia
<i>P. columbiana</i> Singer (1970)	<i>Versicolores</i>	S. America: Colombia
<i>P. coniuncta</i> E. Horak (1980)	<i>Phaeocollybia</i>	Eurasia: China, India
<i>P. corneri</i> E. Horak (1977)	<i>Microspora</i>	Australasia: Borneo & Singapore
<i>P. dissiliens</i> A.H. Sm. & Trappe (1972)	<i>Radicatae</i>	N. America: PNW—OR, CA
<i>P. elaeophylla</i> Singer (1987)	<i>Subattenuatae</i>	S. America: Brazil
<i>P. fallax</i> A.H. Sm. (1957)	<i>Phaeocollybia</i>	N. America: PNW—BC WA OR CA ID & Mexico
<i>P. festiva</i> (Fr.) Heim (1931)	<i>Phaeocollybia</i>	N. America & Eurasia: USA—NC? & Europe, Siberia & Japan
<i>P. flava</i> I.A. Aguiar ex Singer (1987)	<i>Radicatae</i>	S. America: Brazil
<i>P. graveolens</i> B.J. Rees & K. Syme 1999	<i>Microspora</i>	Australasia: Western Australia
<i>P. gregaria</i> A.H. Sm. & Trappe (1972)	<i>Phaeocollybia</i>	N. America: PNW—OR
<i>P. guzmanii</i> Bandala & Montoya 1994	<i>Microspora</i>	N. America: Mexico
<i>P. herrerae</i> Bandala & Montoya (1996)	<i>Microspora</i>	N. America: Mexico
<i>P. hilaris</i> (Fr.) Romagn. (1944) [status in question]	<i>Phaeocollybia</i>	Eurasia: Europe—Sweden
<i>P. intermedia</i> Corner & Horak (1977)	<i>Phaeocollybia</i>	Australasia: Borneo
<i>P. jennyae</i> (P. Karst.) Romagn. (1944)	<i>Microspora</i>	N. America & Eurasia: Canada—NB ON QU, USA—MA MI VT & Europe Siberia
<i>P. kauffmannii</i> (A.H. Sm.) Singer (1940)	<i>Phaeocollybia</i>	N. America: PNW—BC WA OR CA ID, Mexico, neUSA—VT?
<i>P. latispora</i> Guzmán, Bandala & Montoya (1989)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. lilacifolia</i> A.H. Sm. (1957)	<i>Phaeocollybia</i>	N. America: PNW—WA OR CA
<i>P. longipes</i> E. Horak (1973)	<i>Phaeocollybia</i>	Australasia: New Zealand
<i>P. longistipitata</i> E. Horak & Halling (2008)	<i>Phaeocollybia</i>	C. America: Costa Rica
<i>P. lugubris</i> (Fr.) Heim (1931)	<i>Subattenuatae</i>	N. America & Eurasia: Mexico & Europe, Siberia, China
<i>P. luteosquamulosa</i> Norvell (2000)	<i>Versicolores</i>	N. America: PNW—WA OR CA
<i>P. martinicensis</i> Guzmán, Montoya & Bandala (1989)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. megalospora</i> I.A. Aguiar ex Singer (1987)	<i>Versicolores</i>	S. America: Brazil

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TABLE 1, World species concluded.

SPECIES	SECTION	DISTRIBUTION
<i>P. mexicana</i> Corner & E. Horak (1977)	<i>Subattenuatae</i>	N. America: Mexico
<i>P. minuta</i> Horak (1973)	<i>Versicolores</i>	Australasia: New Zealand
<i>P. moseri</i> Bandala & Guzmán (1996)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. muscicolor</i> E. Horak (1977)	<i>Versicolores</i>	Australasia: New Zealand
<i>P. neosimilis</i> Singer (1986)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. ochraceocana</i> Norvell & Exeter (2007)	<i>Phaeocollybia</i>	N. America: PNW—OR CA
<i>P. odorata</i> E. Horak (1977)	<i>Phaeocollybia</i>	Australasia: New Guinea
<i>P. oligoporpa</i> Singer (1987)	<i>Phaeocollybia</i>	C. & S. America: Mexico, Costa Rica & Colombia
<i>P. olivacea</i> A.H. Sm. (1957)	<i>Subattenuatae</i>	N. America: PNW—OR CA
<i>P. oregonensis</i> A.H. Sm. & Trappe (1972)	<i>Phaeocollybia</i>	N. America: PNW—BC OR
<i>P. parvispora</i> Corner & E. Horak (1977)	<i>Phaeocollybia</i>	Australasia: Malaysia, Singapore
<i>P. phaeogaleroides</i> Norvell (2002)	<i>Microsporae</i>	N. America: PNW—BC OR
<i>P. piceae</i> A.H. Sm. & Trappe (1972)	<i>Subattenuatae</i>	N. America: PNW—BC WA OR CA
<i>P. pleurocystidiata</i> Norvell & Redhead (2000)	<i>Phaeocollybia</i>	N. America: PNW—WA OR CA
<i>P. procera</i> E. Horak (1977)	<i>Versicolores</i>	Australasia: New Guinea
<i>P. pseudofestiva</i> A.H. Sm. (1957)	<i>Phaeocollybia</i>	N. America: PNW—BC WA OR CA
<i>P. pseudolugubris</i> Bandala & E. Horak (1996)	<i>Versicolores</i>	N. America: Mexico
<i>P. quercetorum</i> Singer (1987)	<i>Versicolores</i>	C. & S. America: Costa Rica & Colombia
<i>P. querqueti</i> Corner & E. Horak (1977)	<i>Phaeocollybia</i>	Australasia: Borneo
<i>P. radicata</i> (Murrill) Singer (1951)	<i>Microsporae</i>	N. America: PNW—OR CA
<i>P. rancida</i> E. Horak (1974)	<i>Radicatae</i>	Eurasia: India
<i>P. ratticauda</i> E. Horak (1973)	<i>Microsporae</i>	Australasia: New Guinea, New South Wales, Tasmania
<i>P. redheadii</i> Norvell (2000)	<i>Microsporae</i>	N. America: PNW—BC WA OR CA
<i>P. riplipes</i> Norvell (2000)	<i>Phaeocollybia</i>	N. America: PNW—WA OR CA
<i>P. rufipes</i> Bigelow (1963) (questionable)	<i>Phaeocollybia</i>	N. America: Canada—ON & USA—MA
<i>P. rufotubulina</i> Norvell (2004)	<i>Phaeocollybia</i>	N. America: PNW—CA
<i>P. scatesiae</i> A.H. Sm. & Trappe (1972)	<i>Versicolores</i>	N. America: PNW—WA OR CA
<i>P. similis</i> (Bresadola) Singer (1951)	<i>Versicolores</i>	Eurasia: China
<i>P. singeri</i> Guzmán, Bandala & Montoya (1989)	<i>Phaeocollybia</i>	N. America: Mexico
<i>P. singularis</i> E. Horak & Halling (1991)	<i>Phaeocollybia</i>	C. & S. America: Mexico & Colombia
<i>P. sipei</i> A.H. Sm. (1957)	<i>Versicolores</i>	N. America: PNW—OR ?WA
<i>P. smithii</i> Bandala & Montoya 1994	<i>Microsporae</i>	N. America: USA—MI
<i>P. spadicea</i> A.H. Sm. (1957)	<i>Radicatae</i>	N. America: PNW—WA OR CA
<i>P. sparsilamellae</i> P.G. Liu (1995)	<i>Versicolores</i>	Eurasia: China
<i>P. spoliata</i> E. Horak (1974)	<i>Phaeocollybia</i>	Eurasia: India
<i>P. subarduennensis</i> Singer (1987)	<i>Versicolores</i>	N. & C. America: Mexico & Costa Rica
<i>P. subattenuata</i> Singer (1962)	<i>Radicatae</i>	C. & S. America: Costa Rica & Bolivia
<i>P. tasmanica</i> B.J. Rees & A.E. Wood (1996)	<i>Subattenuatae</i>	Australasia: Tasmania
<i>P. tentaculata</i> E. Horak (1977)	<i>Microsporae</i>	Australasia: New Guinea
<i>P. tibiikauffmanii</i> Norvell (2004)	<i>Radicatae</i>	N. America: PNW—OR WA
<i>P. viridis</i> E. Horak (1977)	<i>Versicolores</i>	Australasia: New Guinea

In the Malaysian archipelago and New Zealand, phaeocollybias are generally found in hardwood (angiocarpous) forests dominated by the oak-related genera *Nothofagus*, *Quercus*, *Litchocarpus*, and *Castanopsis* (Horak 1977); in Australia they associate with *Eucalyptus*, *Leptospermum* and/or *Nothofagus* in sclerophyllic forests (Rees & Wood 1996).

**SOUTH AMERICA** — Twelve phaeocollybias have been reported for South America (BOLIVIA: Singer 1961, 1962; BRAZIL: Singer 1987; COLUMBIA: Horak & Halling 1991, Singer 1970, 1987; see also Horak 1977, Singer 1986). Six of these are found also in Central America or Mexico. The endemic species are found in 'virgin tropical rainforests' (Singer 1970) dominated by angiosperm associates. There appears a distinct group of phaeocollybias associated with *Quercus*, particularly at the higher elevations in Colombia and Costa Rica.

**CENTRAL AMERICA (COSTA RICA)** — Seven species have been reported from Costa Rica (Halling & Horak 2008, Halling & Mueller 2005, Horak & Halling 1991, Singer 1987), although that number is expected to increase (Norvell & Halling unpublished data). All are found in oak forests of the Talamanca Mountain Range. Five species are also known from South America and two species occur also in Mexico. The recently described *Phaeocollybia longistipitata* is thus far known only from a montane cloud oak forest in Costa Rica.

**NORTH AMERICA (MEXICO)** — Of the 18 species recognized from Mexico (Bandala 1994, Bandala & Montoya 1994, Bandala & al. 1989, 1996, Guzmán & al. 1987, Horak 1977, Singer 1961, 1970, 1986, 1987), ten are known only from the region, which also shares species with the Pacific Northwest (3), Eurasia and eastern North America (2), Costa Rica (1), and South America (3). In Mexico, phaeocollybias have been collected from coniferous (*Abies*, *Pinus*), angiocarpous (*Quercus*), and mixed (*Quercus-Pinus*) forests.

**NORTH AMERICA (EASTERN CANADA AND UNITED STATES)** — As in Europe, representatives of *Phaeocollybia* are rarely encountered in eastern North America where they are more or less restricted to the boreal and temperate coastal and Great Lake forests; no species are known from the interior continent from

Michigan west to the Rockies or south of Tennessee. Six species have been reported from east coast coniferous forests as far north as Quebec (Farlow & Burt 1929; Hesler 1949; Smith 1952, 1957b; Bigelow & Barr 1963, 1966; Pomerleau & Cooke 1964; Farr & Farr 1976; Pomerleau 1980; Redhead & Malloch 1986; Singer 1986; Bessette & Sundberg 1987; Minot 1989; Redhead & Norvell 1993; Bandala & Montoya 1994; Bessette & al. 1997; Barron 1999). More research is needed to determine whether collections identified as *P. festiva* and *P. kauffmanii* represent those species.

### ***Phaeocollybia* in western North America**

Home to approximately one-third of the world's known species, western North America has proven an exceptionally productive area for research into the taxonomy and biology of the genus. During his 1911 western expedition, New York Botanical Garden mycologist William A. Murrill collected the region's 'earliest' phaeocollybia from a second-growth oak and Douglas-fir forest near Glenbrook, Oregon, originally described as *Naucoria radicata* (Murrill 1917). Shortly thereafter, University of Michigan agaricologist C.H. Kauffman made several collections in Washington and Oregon that piqued the interest of his student, Alexander H. Smith (regarded as one of North America's foremost agaricologists until his death in 1986). After several collecting trips through Washington, Oregon, and California, Smith named fifteen more species from the region — *P. attenuata*, *P. californica*, *P. deceptiva*, *P. dissiliens*, *P. fallax*, *P. gregaria*, *P. kauffmanii*, *P. lilacifolia*, *P. olivacea*, *P. oregonensis*, *P. piceae*, *P. pseudofestiva*, *P. scatesiae*, *P. sipei*, *P. spadicea* (Smith 1937, 1957ab; Smith & Trappe 1972). Smith's 1957 monograph (with key) and Smith & Trappe's amended key served as the most reliable guides to western North American *Phaeocollybia* species until 1999.

No phaeocollybias were reported from western Canada, however, until 1991, when a mycological trek to British Columbia's Vancouver Island led by Agriculture & Agri-Food Canada agaricologist Scott Redhead (now curator of the Canadian National Mycological Collections in Ottawa) collected two phaeocollybias from the ancient spruce forest in the Upper Carmanah Valley. Redhead & Norvell (1993)

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TABLE 2: *Phaeocollybia* species according to region.

AUSTRALASIA	SOUTH AMERICA	NORTH AMERICA (MEXICO)	NORTH AMERICA (PNW)	EURASIA
<i>P. australiensis</i>	<i>P. amazonica</i>	<i>P. amygdalospora</i>	<i>P. ammiratii</i>	<i>P. arduennensis</i>
<i>P. bicolor</i>	<i>P. ambigua*</i>	<i>P. californica*</i>	<i>P. attenuata</i>	<i>P. christinae #</i>
<i>P. corneri</i>	<i>P. brasiliensis</i>	<i>P. christinae#</i>	<i>P. benzokauffmanii</i>	<i>P. cidaris</i>
<i>P. graveolens</i>	<i>P. caudata*</i>	<i>P. fallax*</i>	<i>P. californica*</i>	<i>P. coniuncta</i>
<i>P. intermedia</i>	<i>P. columbiana</i>	<i>P. guzmanii</i>	<i>P. dissiliens</i>	<i>P. festiva #</i>
<i>P. longipes</i>	<i>P. elaeophylla</i>	<i>P. herrerae</i>	<i>P. fallax*</i>	<i>P. hilaris</i>
<i>P. minuta</i>	<i>P. flava</i>	<i>P. kauffmanii*</i>	<i>P. gregaria</i>	<i>P. jennyae #</i>
<i>P. muscicolor</i>	<i>P. megalospora</i>	<i>P. latispora</i>	<i>P. kauffmanii*</i>	<i>P. lugubris</i>
<i>P. odorata</i>	<i>P. oligoporpa*</i>	<i>P. lugubris *</i>	<i>P. lilacifolia</i>	<i>P. rancida</i>
<i>P. parvispora</i>	<i>P. quercetorum*</i>	<i>P. martinicensis</i>	<i>P. luteosquamulosa</i>	<i>P. similis</i>
<i>P. procera</i>	<i>P. singularis*</i>	<i>P. mexicana</i>	<i>P. ochraceocana</i>	<i>P. sparsilamellae</i>
<i>P. querqueti</i>	<i>P. subattenuata*</i>	<i>P. moseri</i>	<i>P. olivacea</i>	<i>P. spoliata</i>
<i>P. ratticauda</i>		<i>P. neosimilis</i>	<i>P. oregonensis</i>	
<i>P. tasmanica</i>	CENTRAL AMERICA (COSTA RICA)	<i>P. oligoporpa*</i>	<i>P. phaeogaleroides</i>	NORTH AMERICA (EAST)
<i>P. tentaculata</i>		<i>P. pseudolugubris</i>	<i>P. piceae</i>	
<i>P. viridis</i>	<i>P. ambigua*</i>	<i>P. singeri</i>	<i>P. pleurocystidiata</i>	<i>P. christinae #</i>
	<i>P. caudata*</i>	<i>P. singularis*</i>	<i>P. pseudofestiva</i>	<i>P. festiva #?</i>
	<i>P. longistipitata</i>	<i>P. subarduennensis*</i>	<i>P. radicata</i>	<i>P. jennyae #</i>
	<i>P. oligoporpa*</i>		<i>P. redheadii</i>	<i>P. kauffmanii?*</i>
	<i>P. quercetorum*</i>		<i>P. riffipes</i>	<i>P. rufipes</i>
	<i>P. subarduennensis*</i>		<i>P. rufotubulina</i>	<i>P. smithii</i>
	<i>P. subattenuata*</i>		<i>P. scatesiae</i>	
			<i>P. sipei</i>	
			<i>P. spadicea</i>	
			<i>P. tibiikauffmanii</i>	

\* = widespread over contiguous regions; # = widespread with disjunct distributions; ? = possibly new species

described one as new — *P. carmanahensis* (now considered a synonym of *P. oregonensis*; see Norvell & Redhead 2000) — and with reservations referred the other to *P. kauffmanii*.

Following a two-month collecting expedition through British Columbia, Washington, Oregon, and California

in 1992, Norvell's examination of fresh material and reevaluation of herbarium specimens resulted in the referral of one type (*P. deceptiva*) to *Cortinarius* (Norvell 1998a, 2000), another (*P. carmanahensis*) to *Phaeocollybia oregonensis*, and the naming of ten new species — *P. ammiratii*, *P. benzokauffmanii*, *P. luteosquamulosa*, *P. ochraceocana*, *P. phaeogaleroides*,

*P. pleurocystidiata*, *P. redheadii*, *P. rifflipe*, *P. rufotubulina*, *P. tibiikauffmanii* (Norvell 1998ab, 2000, 2002, 2004; Norvell & Exeter 2007a; Norvell & Redhead 2000). Detailed descriptions, color photographs, and keys to the currently accepted twenty-five Pacific Northwest species comprise the major portion of this book.

### ***Phaeocollybia* and the Northwest Forest Plan**

The coniferous coastal forests of western North America support one of the richest concentrations of *Phaeocollybia* species in the world (Smith 1957b, Horak 1977, Redhead 1993, Redhead & Norvell 1993, Ammirati & al. 1993, 1994; Norvell 1992, 1995, 1998a,c). Perception of rarity prompted the United States government — the USDI-Bureau of Land Management (BLM) and USDA-Forest Service (FS) — to cite fourteen phaeocollybias (among 234 potentially endangered or threatened fungi in old-growth Pacific coast temperate rainforests) as species of concern in the Federal Ecosystem Management Assessment Team (FEMAT) report on Northern Spotted Owl habitats (USDA-USDI 1993). All fourteen were included in the Northwest Forest Plan (NWFP) and Record of Decision (ROD, USDA-USDI 1994; see also Castellano & al. 1999, 2003; Norvell 2000, 2002, 2004; Norvell & Exeter 2004, 2007a; Norvell & Redhead 2000) that contained the Resource Management Plan (RMP) to implement the NWFP (Molina 2008) and governed the survey and management of organisms on BLM and FS lands within the range of the Northern Spotted Owl.

The fourteen *Phaeocollybia* species of concern were: *P. attenuata*, *P. californica*, *P. carmanahensis* (now referred to *P. oregonensis*), *P. dissiliens*, *P. fallax*, *P. gregaria*, *P. kauffmanii*, *P. olivacea*, *P. oregonensis*, *P. piceae*, *P. pseudofestiva*, *P. scatesiae*, *P. sipei*, and *P. spadicea*. The NWFP required pre-disturbance surveys for many species of concern that eventually led to a huge field inventory for listed fungi from forest lands lying west of the crest of the Cascade Mountains in Oregon, with lesser numbers collected from western Washington and northwestern California forests. Because the government inventories were centered in Oregon and less dominant in western Washington and northern California, Oregon lists



FIGURE 1. Known *Phaeocollybia* sites in western North America (excluding Mexico).

more known sites for rare or rare-uncommon fungal species than the other two states.

In January of 2001, after the Government planning documents declared that fungal species of concern were “not practical to survey” (USDA-USDI 2001), the huge inventory effort within proposed projects abruptly slowed to a trickle. However, the already completed inventories provided valuable site and habitat data for not only targeted phaeocollybias but also the unlisted or newly named species. This was mostly due to the fact that while the genus is easily recognized in the field, few surveyors and field offices could identify specimens to the species level. This resulted in several hundred collections representing all phaeocollybias providing much needed distributional, habitat, and scientific information. Perhaps one of the greatest benefits from the government-sponsored regional plan has been the open exchange of large numbers of collections between forest managers and mycologists.

In addition, the Northwest Forest Plan provided an unusually rich opportunity to investigate *Phaeocollybia* for Norvell, who served both as one of six national taxonomic experts to review ‘the scientific literature and visited herbaria housing the major collections of fungi from western North America’ (Molina 2008; see also Castellano et al. 1999, 2003; Norvell 1995, 1998c) and as a professional taxonomist verifying and identifying collections of 60 epigeous basidiomycete species (including several hundred *phaeocollybia* collections) obtained by BLM and FS surveyors. The NWFP was particularly active in Oregon; for that reason we have more extensive and recent information about *Phaeocollybia* species distribution in Oregon than in British Columbia, Washington, or California. (British Columbia and Idaho were not included in the US government’s plan.) In addition, we personally collected over 350 collections from 2006–2008 in preparation for this publication.

The NWFP led to additional studies on rare and uncommon species. In 1998, the USDI-BLM Salem District (Oregon) Office also funded two five- to seven-year cost-share studies enabling Norvell and Exeter to research epigeous ectomycorrhizal basidiomycete species richness in Douglas-fir (*Pseudotsuga menziesii*) forests. The seven-year Green Peak Density Management Study monitored the impact of different timber-thinning regimes upon the fungal community in a 60-year old forest; the five-year Pedee Chronosequence Fungal Community Study compared species richness across different age-classes in a montane BLM reserve forest (Norvell & Exeter 2004). *Phaeocollybias* were found at both sites, and the information gained from the unusually large number of species (eleven in all) found in the 150–200 year old chronosequence stand (nicknamed ‘Oz’ by the authors) proved invaluable. The relatively small area (two 50×4 m transects) provided abundant collections of six species of concern as well as of five recently named species, additionally serving as the type locality for *P. tibiikauffmanii* (Norvell 2004) and *P. ochraceocana* (Norvell & Exeter 2007a).

### How ‘rare’ is *Phaeocollybia*?

At first glance, rarity seems to be relatively simple. If there are only a few individuals of a species in existence,

a species is usually considered rare. Conversely, a species represented by thousands of individuals over a wide range is usually regarded as common. Botanists customarily record their perception of rarity (rare, scattered, infrequent, abundant) in the field. This suggests that rarity is an obvious and logical condition, easily defined.

Unfortunately, fungi are not plants and their species abundance is less easily determined. In a recent review article on conserving rare fungi in Pacific Northwest forests, Molina (2008) noted, “Given that only about 5% of the estimated 1.5 [million] fungal species are currently described (Hawksworth 2001), most fungi are ‘little-known’. When a new species is recorded, it typically starts out as ‘rare’ and remains in that category until extensive inventories are performed.” In Oregon, for instance, threatened, endangered or rare fungi were not listed until the mid-1990’s; previously the Oregon Natural Heritage Program (ONHP) included only animals, vascular plants, lichens and bryophytes.

For the first time in 1998, ONHP included fungi on its Oregon ‘rare species’ list (ONHP 1998), among them four *Phaeocollybia* species: *P. gregaria*, *P. lilacifolia*, *P. oregonensis*, and *P. radicata*. These same four *phaeocollybias* were also included in the updated list in 2001 (ONHP 2001).

In 2002, the BLM and FS requested ONHP to rank approximately 160 fungal species of concern in Washington, Oregon, California, and globally; most of these were listed in the NWFP but not included in the then-current ONHP list. ONHP changed its name to Oregon Natural Heritage Information Center (ORNHIC) in 2004 and added nine more *phaeocollybias* to the Oregon rare and threatened species list: *P. attenuata*, *P. californica*, *P. dissiliens*, *P. olivacea*, *P. piceae*, *P. pseudofestiva*, *P. scatesiae*, *P. sipei*, and *P. spadicea* (ORNHIC 2004). The 13 *phaeocollybias* now listed were the same ‘species of concern’ as those listed in the NWFP except for the omission of *P. fallax* and *P. kauffmanii* and the addition of *P. lilacifolia* and *P. radicata* (ORNHIC 2004). The 2007 ORNHIC list includes only twelve *Phaeocollybia* species; *P. olivacea* has been dropped and noted as being ‘too common.’ However, *P. olivacea*

remains on the BLM and FS species of concern lists (Instruction Memorandum No. OR-2008-038, Final State Director's Special Status List).

As of 2007, no Pacific Northwest phaeocollybias are listed as threatened or endangered; all listed are considered rare (TABLE 3).

ORNHIC has not yet had an opportunity to rank most of the newly named phaeocollybias, and assigning rare or uncommon labels to any species is a difficult task. Often the number of sites is the only data available to permit rarity assessment; such data can easily mislead due to the local abundance of a species within a small area. The species range, existing potential habitat, habitat requirements, successional patterns, distribution patterns and threats also need to be considered. Nonetheless, if we follow ORNHIC's criteria and label each species with fewer than 20 known sites as rare, based on 18 years of intensive collecting data we would add *P. luteosquamulosa*, *P. ochraceocana*, *P. phaeogaleroides*, *P. ruffipes*, and *P. tibiikauffmannii* to the list of rare species. Additionally, were we to label all species with more than 20 known sites but fewer than 100 as rare-uncommon, only *P. kauffmannii* and (just barely) *P. olivacea* would be excluded from the Oregon list (TABLE 4). We should add that although two of the 25 *Phaeocollybia* species are listed with 100 known sites in the Pacific Northwest, neither can be considered as common or widespread.

Implementation of NWF plan policies overseeing fungal species of concern were conducted most rigorously in Oregon, which contributed more *Phaeocollybia* collections than elsewhere. That state also holds more USDI-BLM and USDI-FS administered lower elevation forests west of the Cascade crest, an area generally recognized as 'great fungal habitat.' There were no BLM-held Washington forest lands included in NWFP inventories, leaving only the Olympic, Gifford Pinchot, and Mt. Baker-Snoqualmie National Forests to provide inventory specimens for expert evaluation; likewise the Washington Natural Heritage Program has incorporated fungi only recently onto its working list, further limiting what we know about Washington state fungal distribution in general and *Phaeocollybia* in particular. Northern California

TABLE 3. Global and Oregon state rarity rankings (ORNHIC 2007 rankings explained below)

<i>Phaeocollybia</i> sp.	GLOBAL	OREGON	ONHIC LIST
<i>P. attenuata</i>	G3	S3?	4
<i>P. californica</i>	G2?	S2?	1
<i>P. dissiliens</i>	G2-3	S2-3	3
<i>P. gregaria</i>	G1-2	S1-2	1
<i>P. lilacifolia</i>	G2?	S1-2	3
<i>P. oregonensis</i>	G2?	S2?	1
<i>P. piceae</i>	G3?	S3?	4
<i>P. pseudofestiva</i>	G3	S3?	3
<i>P. radicata</i>	G2	S1	3
<i>P. rufotubulina</i>	G2	S1	3
<i>P. scatesiae</i>	G3?	S3?	3
<i>P. sipei</i>	G3?	S3?	3
<i>P. spadicea</i>	G3-4	S3?	3

G = global; s = state; ? = rank probably correct but provisional; documentation needed or ranking uncertainty.

G/S1 = critically imperiled due to extreme rarity or vulnerable to extinction; typically known from ≤ 5 occurrences. G/S2 = imperiled due to rarity or possibly vulnerable to extinction; typically known from 6–20 occurrences. G/S3 = rare, uncommon, or threatened, but not immediately imperiled; typically known from 21–100 sites. G/S4 = not rare, apparently secure, but with cause for long-term concern; typically known from > 100 occurrences.

ORNHIC lists: 1 = threatened/endangered throughout range [threatened with extinction or presumed extinct]; 2 = threatened/endangered/extirpated from Oregon, secure elsewhere; 3 = review [more information needed before status determined; may be threatened/endangered in Oregon]; 4 = watch [of concern, not currently threatened/endangered, but continued monitoring required]

likewise has delivered only limited information that has yet to be integrated in its entirety into the Northwest Forest Plan databases. (Forests east of the Cascades (including Idaho) and in British Columbia (in Canada) were not covered by the NWFP.)

### Impact of timber management on *Phaeocollybia* fruiting

In our density management study in the Green Peak BLM Research Forest in the Oregon Coast Range (Norvell & Exeter 2004), one mixed Douglas-fir+western hemlock stand with seven *Phaeocollybia* species was clear-cut in 1999. No phaeocollybias (or

## 10 ... Introduction — Distribution and ecology of *Phaeocollybia*

TABLE 4. Approximate number of known *Phaeocollybia* collection sites in Pacific Northwest North America

SPECIES*	KNOWN SITES					
	BRITISH COLUMBIA	WASHINGTON	OREGON	IDAHO	CALIFORNIA	NWFP AREA TOTAL <sup>^</sup> (BC & ID excluded)
<i>P. ammiratii</i>	3	~ 10	~ 30		~ 10	~ 50
<i>P. attenuata</i> +	2	~ 12	~ 50		~ 47	~ 79 [151]
<i>P. benzokauffmanii</i>		~ 10	~ 20		~ 5	~ 35
<i>P. californica</i> +			5		10	15 [38 <sup>3</sup> ]
<i>P. dissiliens</i> +			19		1	~ 20 [22]
<i>P. fallax</i> <sup>1</sup> +	2	~ 10	~ 55	1	~ 15	~ 80 [120]
<i>P. gregaria</i> +		1?	5			6 [4]
<i>P. kauffmanii</i> <sup>2</sup> +	4	~ 10	~ 80	1	~ 15	~ 105 [146]
<i>P. lilacifolia</i> +		1	3		1	5 [0]
<i>P. luteosquamulosa</i>		1	7		2	10
<i>P. ochraceocana</i>			5		1	6
<i>P. olivacea</i> +		1?	~ 65		~ 30	~ 100 + [114]
<i>P. oregonensis</i> +	2	1	9			12 [13]
<i>P. phaeogaleroides</i>	2		20			22
<i>P. piceae</i> +	2	4	~ 25		3	~35 [53]
<i>P. pleurocystidiata</i>		1	27		2	~30
<i>P. pseudofestiva</i> +	2	8	~25		~ 2	~ 35 [46]
<i>P. radicata</i>			7		2	9
<i>P. redheadii</i>	4	~ 15	~ 25		6	~ 50
<i>P. rifflipes</i>		2	7		1	~ 10
<i>P. rufotubulina</i>			2?		11	12
<i>P. scatesiae</i> +		2	25		3	30 [19 <sup>3</sup> ]
<i>P. sipei</i> +		1?	25			26 [51]
<i>P. spadicea</i> +		~ 5	~ 45		~ 5	55 [80]
<i>P. tibiikauffmanii</i>		1	14			15

\* Species in boldface are cited as rare by ORNHIC (2007); + denotes initial species of concern in the Northwest Forest Plan (NWFP).

<sup>^</sup> numbers enclosed in brackets represent USDA-FS 2006 tallies that include no longer producing sites (Molina 2008)

<sup>1</sup> also reported from northern Idaho and Mexico; originally listed as a species of concern in US planning documents

<sup>2</sup> also reported from northern Idaho, Mexico and eastern United States; originally listed as a species of concern in US planning documents

<sup>3</sup> ~15 collections reported for *P. californica* now referred to *P. scatesiae*.

other ectomycorrhizal fungi) fruited in the center of the 1-acre patch cut until five years after harvest. In 2004 *P. phaeogaleroides* (a suspected pioneer species) was collected near the bases of three 4- to 6-ft tall young western hemlocks (Norvell & Exeter 2007b). Although *P. phaeogaleroides* was recorded from the site through the final visit in 2006, none of the original seven phaeocollybias were retrieved during the first seven years after timber harvest (Norvell & Exeter 2008).

While clear-cutting (leaving no trees) and heavy thinning (e.g., leaving 40 trees/ac, 100 trees/ha) appear to affect phaeocollybia fruiting adversely, moderate to light thinnings (e.g., leaving 80-120 trees/ac, 200-300 trees/ha) do not appear to do so (Norvell & Exeter 2004, 2008). Pre-thinning inventories during the 1998 fall season included *P. attenuata* and *P. sipei* in the Green Peak stand scheduled for thinning to 120 trees/acres (300 trees/ha).



By completion of the fungal density management study, three more species — *P. ammiratii*, *P. fallax*, and *P. spadicea* — had been added to the phaeocollybias collected during 2000, 2001, and 2004 (Norvell & Exeter 2007b) in the light thinning treatment areas.

With respect to ectomycorrhizal species richness in general, Norvell & Exeter (2008) found that their data supported the conclusion that over the short term, the fungal community is not threatened by light to moderate thinning, with little difference between fungal species richness on the control (no-harvest) plot and species richness calculated for the light to moderate thinning plots. As noted above, removing all timber from a previously phaeocollybia-fruiting area depressed ectomycorrhizal species richness to virtually zero during the 9 years of this study; species richness in the heavily thinned stands (40 trees /ac) was also depressed during that period, although less drastically (Norvell & Exeter 2004, 2007b, 2008).

We believe that the smaller the size of the patch cut, the more swiftly the harvested area will reestablish itself with mycorrhizal fungi, as shown by the number of species that fruited at the base of reserved trees along the perimeter of the cut even after the first harvest year. Likewise, timber managers who protect seedlings/saplings (or wildlife trees) within patch cuts provide shelter for ectomycorrhizal fungi, as evidenced by the appearance of *Phaeocollybia phaeogaleroides* in the patch cut. Outside of this study area we have collected phaeocollybias in areas between mature or old growth forests and a younger (~10 years old) forest, and have collected phaeocollybias at the outer perimeter of older forests and inner perimeter of a band of younger trees that are encroaching on open meadow habitats. In both instances, the species continue to survive at the edge of two different habitat types.

### Forest age and *Phaeocollybia* fruiting

In the density management study, the fact that no phaeocollybias were ever recorded for the 60-year old control, moderate and high thinning plots during nine years of observation reflects the fruiting pattern characteristic for the genus. As noted in the paragraphs on rarity, *Phaeocollybia* is a notoriously “patchy” and “sociable” genus that is also thought to be associated

with old growth and ancient forests (Norvell 1995, 1998abc; Norvell & al. 1994). We observed this patchiness, sociability, and preference for older forest habitats first hand during our chronosequence fungal community study in the Oregon Coast Range Pedee (Polk County) BLM Reserve Forest (Norvell & Exeter 2004). For six years we regularly sampled two 200m<sup>2</sup> transects in each of three differently aged Douglas-fir+western hemlock stands. *Phaeocollybia* was never collected from the ~30-year old early succession transects, only once off-transect in the ~55-year old middle succession stand, yet it was represented by eleven species — 7.6% of the epigeous ectomycorrhizal basidiomycete species richness total — in the ~150–200-year old late successional stand (Norvell & Exeter 2004), an unexpectedly high number of phaeocollybias for so small an area.

Nonetheless, *Phaeocollybia* cannot be deemed an obligately old-growth genus. Data from our own studies and the Northwest Forest Plan’s intensive inventories show that phaeocollybias can be found in all forests, regardless of age, when their mycorrhizal associates are present and other biological requirements are met.

### Pacific Northwest phaeocollybia habitats

As evident in TABLE 2 (page 4), almost one-third of the currently named phaeocollybias occur within the coastal coniferous rainforests of the Pacific Northwest. This region extends from the Queen Charlotte Islands in British Columbia, Canada, and south to California’s Santa Cruz Mountains in the United States. *Phaeocollybia* species are more regularly found along the Coast and in the coast ranges in British Columbia, Washington, Oregon, and California, extending east to the western Cascade Range slopes in the north and the western Sierra Nevada coast slopes in California. Exceptionally, a few representatives have been collected from the moist coniferous forests of the ‘inland empire’ in southern British Columbia (Norvell 2006) and northern Idaho (Norvell 1998a).

Most Pacific Northwest species appear restricted to western North America, with only one immature (and thus unconfirmed) extralimital collection of *P. kauffmanii* reported from Vermont. Likewise,

no non-indigenous species are known to occur in the region. While generally somewhat uncommon, phaeocollybias are frequently locally abundant; perceived rarity may be explained by their patchy distribution within general forest habitats, with several species often fruiting together in a small area (Norvell 1998a).

Within the Pacific Northwest, phaeocollybias are most commonly found in the northwest temperate rainforest zone (sometimes termed the coastal coniferous forest; see Vankat 1980), dominated in the north by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) and in the south by coast redwood (*Sequoia sempervirens*). Although early workers (Smith 1957b, Smith & Trappe 1972, Redhead & Norvell 1993) suggested a close spruce-phaeocollybia association, it now appears that spruce is more an indicator of the moist habitats favored by *Phaeocollybia* species than an obligate associate (Norvell 1998a). Spruce dominates the Alaskan and northern British Columbian coniferous forests but is gradually supplanted southwards by western hemlock, Douglas-fir (*Pseudotsuga menziesii*) and western red cedar (*Thuja plicata*). *Phaeocollybia* sites on Vancouver Island, where Sitka spruce is restricted to flood plains and exposed beaches (Pojar & al. 1991), are dominated by western hemlock with silver fir (*Abies amabilis*) and western red cedar also present. Here, as elsewhere throughout the western hemlock zone, the shrubby huckleberry-salal (*Vaccinium-Gaultheria shallon*) understory is dense and bryophytes are common, but herbaceous ground covers are generally not well developed (Vankat 1980, Pojar & al. 1991). The same plant association (minus Sitka spruce) is also recorded for known phaeocollybia sites on mainland British Columbia (Gamiet & al. 1994).

Plant associations in the Washington and Oregon western hemlock zone mirror those described for British Columbia. Sitka spruce, often common in coastal forests, is infrequent or absent inland, while noble fir (*Abies procera*) supplants silver fir at higher elevations (Ammirati & al. 1994, Halverson & al. 1986). The herbaceous layer may or may not be more developed, with oxalis (*Oxalis oregana*), sword fern (*Polystichum munitum*), deer fern (*Blechnum spicant*), bunchberry (*Cornus cascadiensis*), and twinflower

(*Linnaea borealis*) common to frequent (Halverson & al. 1986, Henderson & al. 1989). A sub-climax species, Douglas-fir, is also often present. In coastal areas large concentrations of some phaeocollybias have been found in Douglas-fir plantations in areas previously inhabited by climax western hemlock-spruce forests (Norvell 1998a). *Phaeocollybia* is particularly species rich in mature and old-growth Douglas-fir/western hemlock forests of the Oregon Coast Range (Norvell & Exeter 2004).

From Oregon southwards, Sitka spruce and western hemlock are gradually replaced by coast redwood (Eyre 1968). Although not found in pure coast redwood stands, phaeocollybias do frequent mixed *Sequoia* forests where hemlock, true fir, Douglas-fir, western red cedar, and tan oak (*Lithocarpus densiflorus*) are also present. In these areas, the shrubby rhododendron (*Rhododendron macrophyllum*) - huckleberry - salal understory can be quite dense while bryophyte and herbaceous layers (except for frequently abundant sword fern) are poorly developed or absent. Phaeocollybias have also been collected inland within the oak-pine (*Quercus-Pinus*) zone just north of the California border in the Siskiyou mountain range (Smith 1957b).

CLIMATE — The coastal plant associations listed above share a common dependence on high ambient humidity. To the north, western hemlock, Sitka spruce, and western red cedar are all indicators of very humid environments (Vankat 1980) and the survival of coast redwood at the southern end of its range (which coincides with the southernmost occurrence of *Phaeocollybia* in California) depends on the ‘relatively high humidity and frequent fogs in the dry season’ (Eyre 1968). Most Pacific Northwest phaeocollybias typically fruit during the autumn cool rainy season, although some autumn species occasionally continue to fruit during and after mild wet winters. One species — *Phaeocollybia phaeogaleroides* — fruits in both autumn and spring while another — *P. pleurocystidiata* — is strictly vernal.

Although most species are restricted to the exceptionally moist coastal and inland coniferous rainforests, phaeocollybias can also be found in inland forests associated with dryer Mediterranean climates.

In northern California, scattered collections have been made from the Northwest Klamath Range, Cascade Range Foothill, and Sierra Nevada Foothill regions (Hickman 1993, Norvell 1998a) within the Douglas-fir series (cf. Sawyer & Keeler-Wolf 1995) where the dominant Douglas-fir occurs with oak, tan-oak, and pine. Numerous phaeocollybias have been collected in forests along the south fork of the Smith River (Del Norte Co) and in Castle Crags State Park (Shasta Co) where there is less ambient humidity and long hot dry summers precede the autumn rainy season when most of the annual 50-125 cm precipitation occurs.

**SOILS** — The relatively cool temperatures, high moisture, and coniferous vegetation combine with basalt or other volcanic parent material in British Columbia, Washington, and northern Oregon to produce the podzolic soils (Halverson & al. 1986) that tend to dominate most coastal phaeocollybia sites. Podzols, typically well drained and coarse textured, ‘undergo intense leaching of the clay, organic matter, iron, and aluminum from the upper to lower mineral horizons’ (Pojar & Meidinger 1991). In a well-developed podzol, this rapid leaching (*i.e.*, ‘podzolization’ or ‘base desaturation’ in Eyre 1968) leaves an albic horizon of whitish quartz sand at the base of the upper ‘A’ horizon that has been noted in numerous *Phaeocollybia* excavations (Norvell 1997b, 1998a). Podzols in which phaeocollybias occur have relatively thick top organic litter layers — mors or mor-mulls composed of needles, coarse woody debris and partly decomposed organic matter in which ericaceous shrubs (huckleberry, rhododendron) are also common (Ammirati & al. 1994, Halverson & al. 1986, Henderson & al. 1989). These podzols are acidic with 4.2–6 pHs (Donahue & al. 1977, Henderson & al. 1989).

In California, soils become more complex and less easily classified, ranging from volcanic to metamorphic in the northern portion to the schist-derived sandstone soils found toward the south (Sawyer & Keeler-Wolf 1995). Further inland mesic and well-drained granitic, schist-derived sandstone, serpentine, and volcanic soils are common (Sawyer & Keeler-Wolf 1995). Mixed sedimentary and older metamorphic soils occur in the oak-pine zone of the Klamath range (type locality of *P. olivacea*), while soils in the Douglas-fir-tanoak subseries are classified as gravelly to very gravelly loams or sandy loams that average a soil depth of 33–34”, 5–6” deep A horizon, and 6.2–6.3 pH (Jimerson & al. 1996).

Until recently, phaeocollybias were thought to occur primarily in closed canopy ancient or virgin forests (Norvell 1992, Norvell & al. 1994a, Smith 1957b). However, data from our own and abundant NWFP collections reveal that some species previously known only from undisturbed forests also occur in closed canopy mature second-growth forests, particularly those that have been ‘high-graded’ (thinned) rather than clear-cut. Other species (*e.g.* *P. scatesiae*, *P. olivacea*, *P. pleurocystidiata*) appear to flourish in recently thinned old-growth stands or mature ( $\geq 50$  year old) Douglas-fir plantations, at times in relatively open areas next to decaying stumps that presumably function as moisture reservoirs during the dry season (Norvell 1998a, Norvell & Exeter 2004). Reports of phaeocollybias collected from more open, less humid inland forests (Ammirati pers. com. 1996–1997) also show that they are not restricted to closed canopy forests.

A detailed microscopic cross-section of a plant root, likely Phaeocollybia redheadii, showing a central vascular cylinder surrounded by cortical cells. The image highlights the presence of fungal hyphae and rootlets, characteristic of ectomycorrhizal associations. The text is overlaid on the central part of the image.

# *Phaeocollybia*

## Development & Biology

Pseudorhizal origin & ectomycorrhizal rootlets in *Phaeocollybia redheadii*

## *Phaeocollybia* development and biology

*Phaeocollybia* was first characterized as a genus within the *Cortinariaceae* based on the formation of a pseudorhiza, brown ornamented spores, and the absence of a veil (Heim 1931; see also Norvell 1998b). The presence of 'tibiiform diverticula' on the mycelia and pseudorhiza first noted by Redhead & Malloch (1986) is now accepted as an additional generic feature (Norvell 1998b, Gulden 2008). Both Redhead & Malloch (1986) and Norvell (1998ab, 2000) successfully excavated the origins of the pseudorhiza to the host root systems, which provided the first evidence for biological strategy in the genus, which is outlined at the end of this section. Along with this, the study of many primordia revealed the existence of a universal veil (in *Phaeocollybia* usually called the primordial sheath or 'pellicular' veil), previously unknown for the genus (Norvell 1998ab). Examination of the primordial and pseudorhizal tissues also provided much-needed information to infer ontogeny within *Phaeocollybia*.

### Fruitbody initiation and early development

Norvell (1998b) observed that primordia originate at 30–300 mm below the soil surface in species-specific patterns, either from existing pseudorhizas or from mycelia concentrated within soil and decomposed humus surrounding rootlets with mycorrhizal tips. Fruitbody growth begins when an undifferentiated mycelial knot expands into an amorphous fungal mass that eventually gives rise to a stick-like primordium. This fruitbody initial consists of a compact context completely enclosed within a single universal veil that covers the gills until shortly before maturity (a condition called 'monovelangiocarpy'). The stipe elongates before the pileus begins to form, a developmental process referred to as 'stipitocarpy' (see also Reijnders 1979, Watling 1985).

### Tibiiform diverticula and the primordial sheath

Heim (1931) circumscribed *Phaeocollybia* as a 'non-velate' genus. In 1993, Norvell (1998ab) noticed a matted fibrillose veil covering several preserved primordia representing a new species (*P. rufotubulina*). Subsequent examination of primordia representing thirteen other species supported her hypothesis that

all phaeocollybian primordia are encased in gelatinous universal sheaths that eventually thin to agglutinated fibrils connecting stipe and cap as the fruitbody develops. Accordingly, Norvell (1998a) emended *Phaeocollybia* as a 'velate' genus, a view now accepted by other workers (Gulden 2008).

The primordial sheath is retained differently according to species, although vestiges (usually in the form of tibiiform diverticula) are usually found on the pseudorhizal surface. Elsewhere, many species retain only short fibrils or appressed fibrillose patches scattered around the upper stipe (usually at the apex) while others may display regular arrays of upraised fibrillose patches on the upper stipe like those found in *Phaeocollybia spadicea* (p. 195B–C). Two species — *P. luteosquamulosa* and *P. ochraceocana* — retain the sheath as a pigmented top layer on the caps, where they become visible as upraised scattered scaly patches when the cap becomes dry (p. 110A).

Microscopic secretory structures (FIG. 2.1) are found on the primordial sheath of all phaeocollybias. These highly refractive processes (termed 'tibiiform diverticula') emanate directly from surface hyphae without an intervening septum; they are usually quite small (5–30 × 1 μm) and taper from slightly wider bases upwards to slender necks. They are called 'tibiiform' because most have small spatula-shaped to (sub)globose heads ('capituli'). Tibiiform diverticula are found on the mycelial hyphae and fruitbody surfaces retaining remnants of the primordial sheath. Abundant on the surfaces of all primordia and equally abundant on the pseudorhizas, they have now been found on specimens representing 50 species within *Phaeocollybia* (Redhead & Malloch 1986; Laber 1991; Redhead & Norvell 1993; Rees & Wood 1996; Norvell 1998ab, 2000, 2002, 2004, unpub. data; Rees & Syme 1999; Norvell & Redhead 2000; Norvell & Exeter 2007; Halling & Horak 2008).

Tibiiform diverticula are a generically significant feature separating *Phaeocollybia* from the rest of the *Cortinariaceae* (i.e., *Cortinarius*, *Gymnopilus*, *Hebeloma*, *Inocybe*); they are similar in form to the septate caulocystidia found in some species of *Galerina*, which recent DNA sequence data (Matheny & al 2006) indicate may be the most closely related genus to *Phaeocollybia*. Their taxonomic utility was

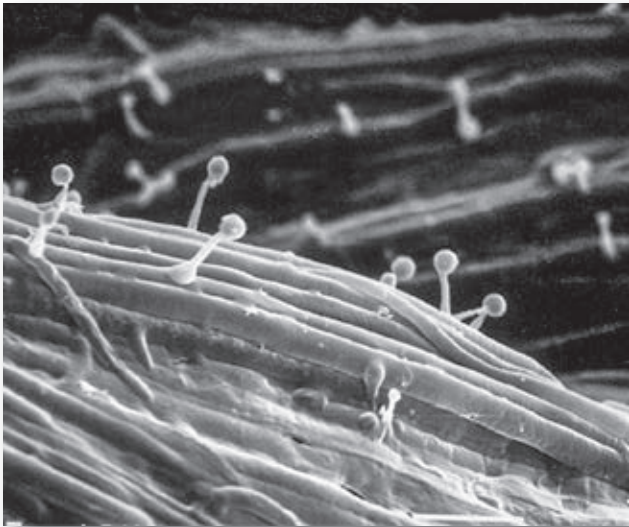


FIGURE 2.1 Scanning electron micrograph of tibiiform diverticula emerging from the surface hyphae of the pellicular sheath surrounding a *P. rufotubulina* pseudorhiza.

first demonstrated by Redhead & Smith (1986), who excluded *P. perplexa* from *Phaeocollybia*, transferring it to the monotypic *Stagnicola* in part because of the lack of diverticula, and recent DNA sequence analyses (Moncalvo & al. 2002) show that the excluded species is well separated from *Phaeocollybia*. The more scattered distribution of diverticula on aerial parts of the fruitbody is tied to differential retention of the primordial sheath, influenced in turn by the degree of abrasion the expanding primordium encounters during elongation. Watling & Largent (1976) noted that the disappearance of veils from mature basidiomes (in other genera) depends "... on the soil in which the primordia have developed... If the pileipellis commences to gelatinize early in development, the fragments of the veil can move easily and are pushed off by heavy clays." Both *P. luteosquamulosa* and *P. ochraceocana* lack a highly gelatinized pileipellis, and specimens with the scaliest caps were collected from soils with low clay content.

Diverticula have been observed on the mycelia of other agarics, and some that secrete repellent or toxic compounds have been linked to nitrogen-utilization in highly organic soils (Barron & Thorn 1987, Hutchison & al. 1996). Observing that insects rarely attack phaeocollybian pseudorhizas, Norvell (1998b) suggested that the diverticula may secrete antifeedants that protect the primordia and pseudorhiza from fungivory. More research is needed to determine the true function of the diverticula, however.

## Anatomy and development of the pseudorhiza

Pseudorhizal shapes are obviously influenced by soil composition, as seen by the twisted, coiled, curled or otherwise distorted pseudorhizas found in soils containing intact wood, roots, or stones around which fruitbodies twist in their upward path (e.g., FIG. p. 200G). Successful retrieval of complete pseudorhizas (including their origins), however, shows that there are two basic types: those that are continuous with the stipe, and those that are not. Norvell (1998ab) placed pseudorhizas in four categories based on their growth habit and tissue organization. The following paragraphs briefly outline the significant features of each category, while TABLE 5 (next page) provides an overview of pseudorhizal types for the 25 known Pacific Northwest phaeocollybias.

### Vertical-monopodial

Most phaeocollybias produce fleshy unbranched pseudorhizas that arise singly to gregariously from relatively blunt origins embedded in the 'albic' horizon of the mineral soil. In some species (e.g., *Phaeocollybia redheadii*, p. 166D–I), pseudorhizas emanate from small (2–3 mm diam) knots of undifferentiated fungal tissue, traveling upward sometimes more than 30 cm through the soil, gradually expanding to reach ~22 mm diam in larger fruitbodies. Firm interior pith (surrounded by 1–2 mm thick cartilaginous cortex) is present whether or not the aboveground stipe is stuffed (e.g., *P. kauffmanii*) or hollow (e.g., *P. fallax*).

Vertical-monopodial pseudorhizas arise from either fungal masses or mycelia (Norvell 1998b). Sometimes they have regenerative potential, as seen in young primordia that arise directly from an older pseudorhiza (see *P. piceae* FIG. p. 138A and *P. tibiikauffmanii* FIG. p. 200H–I). All pseudorhizas in this category exhibit the same gradual upwards expansion, tissue organization, and anatomy described for *P. redheadii*, and all appear continuous with the lower stipe. Because there is no one point where the stipe can be said to end and the pseudorhiza begin, for practical purposes we call the subterranean portion the pseudorhiza and the exposed portion the stipe. Fourteen PNW species are characterized by fleshy vertical-monopodial pseudorhizas (TABLE 5).

### Lateral-monopodial

*Phaeocollybia attenuata* produces small fruitbodies with slender (2–5 mm diam) polished stipes

attached to very thin, criniform (brittle and wire-like) pseudorhizas. Attempts to trace these thin pseudorhizas to their origins in the dense soil below the loose duff and humus layers have been frustrated by sudden lateral turns after which the wire-like portion travel distances greater than 10 cm from the lateral bend. Norvell (1998b) notes that some 'wires' narrowed to 125 µm before being accidentally broken. We have yet to retrieve the origins.

The wires consist of three zones. The ELONGATION ZONE lies closest to the origin and consists of a narrow pale cortex, a wider dark-brown cortex, a pale medulla, and an ill-defined central cavity. The intermediate EXPANSION ZONE displays a slightly different structure and the beginnings of sarcodimitic tissue construction (explained in detail on p. 20–21). The TRANSITION ZONE, closest to the upper fleshy pseudorhizal portion, contains a dark-brown single-layer cortex surrounding the central medulla of fully developed sarcodimitic tissues. Surface hyphae in all three zones are covered with tibiiform diverticula.

#### Sequential-racemose

Both *Phaeocollybia californica* and *P. rufotubulina* are characterized by short fleshy pseudorhizas (continuous with the lower stipe) arising from much longer rhizomorphic cords (Norvell 1998b, 2004). Mature fruitbodies are borne on tall tubular stipes that arise either from branching subterranean lateral 1-mm diam cords originating from the soil mycelium or from buried 'nurse' pseudorhizas of older fruitbodies. The cords run more or less horizontally through sandy or loamy soils for a distance before turning sharply upward (similar to *P. attenuata*) and usually travel vertically only a short distance before merging with the swollen fleshy stipe bases. Central cord tissue structure resembles that of the vertical-monopodial pseudorhiza except for an anatomical difference in the narrow dark pseudorhizal pellis (see Norvell 1998b for additional information). Five Pacific Northwest species are characterized by sequential-racemose pseudorhizas (TABLE 5).

#### Fasciculate-racemose

In *Phaeocollybia scatesiae*, masses of fruitbodies with hollow stipes erupt from umbellate fascicles, each subtended by a single cord-like pseudorhizal strand called a 'mother rhizomorph' (See FIG. 2.2D). The rhizomorphic strands give rise to large fascicles

TABLE 5. Pseudorhizal morphology in PNW phaeocollybias

CONTINUOUS WITH STIPE FLESHY	DISCONTINUOUS WITH STIPE CORDLIKE (CRINIFORM)
MONOPODIAL	MONOPODIAL
<i>P. ammiratii</i>	<i>P. attenuata</i> ^-LM
<i>P. benzokauffmanii</i>	<i>P. gregaria</i> *
<i>P. fallax</i>	<i>P. olivacea</i> *
<i>P. kauffmanii</i>	<i>P. phaeogaleroides</i> *^-VM
<i>P. lilacifolia</i>	RACEMOSE
<i>P. luteosquamulosa</i>	SEQUENTIAL
<i>P. ochraceocana</i>	<i>P. californica</i> +
<i>P. oregonensis</i>	<i>P. pseudofestiva</i> +
<i>P. piceae</i> +	<i>P. radicata</i> +
<i>P. pleurocystidiata</i>	<i>P. rufotubulina</i> +
<i>P. redheadii</i>	<i>P. sipei</i>
<i>P. rifflipe</i>	FASCICULATE
<i>P. spadicea</i> +	<i>P. dissiliens</i>
<i>P. tibiikauffmanii</i> +	<i>P. scatesiae</i>

+ = producing primordia near origin

\* = cord-like & pliable

^ = criniform (thread-like & brittle)

LM = lateral-monopodial

VM = vertical-monopodial

of primordia and variably aged fruitbodies, with some clusters containing more than 80 fruitbodies erupting from one point. We have not yet been successful in excavating the cord origins, but lengths up to 150 mm have been retrieved. (See *P. scatesiae* on pp. 181–186 and Norvell 1998b for more detail.)

Although *P. dissiliens* produces fruitbodies in twos and threes, we provisionally classify it as fasciculate-racemose based on the fact that the fruitbodies emerge from one point on the subtending strand.

NOTE: Our recent excavations revealed cord-like pseudorhizas for three species (*P. gregaria*, *P. olivacea*, *P. phaeogaleroides*) that Norvell (1998b, 2002) previously assigned to the vertical monopodial category. The retrieved cords were unbranched (each giving rise to only one fruitbody) and lack the lateral bends described for *P. attenuata*. Although we retain the 'vertical' versus 'lateral' terminology in our species descriptions, comparison between fleshy and cord-like is probably functionally more informative. The presence of a criniform portion below the subtending cord supports *P. phaeogaleroides* as being monopodial. However, as we were not able to retrieve the origins, we cannot rule out that the cords in *P. gregaria* and



Lorelei Norvell—A,C-D; Elizabeth Fox—B

FIGURE 2.2. Pseudorhizal types in *Phaeocollybia*. A. Vertical-monopodial (*P. ammiratii*). B. Lateral-monopodial with criniform origin (*P. attenuata*). C. Sequential-racemose from rhizomorphic cords & pseudorhizas (*P. radicata*). D. An umbellate fascicle (originally called a ‘fasciculate-starburst’) with subtending pseudorhizal cord (*P. scatesiae*).

*P. olivacea* may be branched. Given the gregarious to cespitose habit of those two species, it would not be surprising to discover that their pseudorhizal cords are, in fact, racemose.

Anatomically, all pseudorhizal tissues are composed of two distinct hyphal types — ‘vessel’ hyphae, which are fusoid, unbranched, long, wide, and thick-walled, and flexuous hyphae, which are cylindrical, branched, narrow, and thin-walled. This type of tissue, which Corner (1966) called ‘sarcodimitic’, is usually found within both pseudorhizas and lower stipes in *Phaeocollybia*, although its occurrence elsewhere in fruitbodies varies according to the species.

### Function of the pseudorhiza

The long unbranched ‘rooting’ stipe covered by a cartilaginous rind has long been the hallmark of *Phaeocollybia*. Fayod (1889), who felt that the term ‘rooting’ wrongly implied downward growth, introduced the term ‘pseudorhiza’ for *Collybia* (now *Xerula*) *radicata*. Buller (1934) confirmed that the primordia of that species elongated upwards through the soil from a buried substrate with the resultant pseudorhizal length dependent upon the amount of soil between the substrate and the soil surface. He described pseudorhizas for many different genera, distinguishing between perennial and annual types. Researchers regard the annual pseudorhizas found in most genera as simple stipe extensions. This opinion was shared for *Phaeocollybia* pseudorhizas until Norvell (1998b) recognized the different morphologies suggesting that they are more complex

than previously thought. Norvell, who observed that branching cords, primordia or pseudorhizas arising from older pseudorhizas, and multiple fruitbodies arising from the top of a solitary subtending strand imply localized meristematic activity, remarked upon the structural and functional similarity shared by rhizomorphs and some phaeocollybian pseudorhizas (Norvell 1998b).

Rhizomorphs, which are classified as belonging to the mycelium, extend the food-base of a fungus by traveling between and within substrates. Pseudorhizas, which are classified as belonging to the fruitbody, grow from the substrate to the surface (‘aerial interface’). Just as it is difficult to differentiate between pseudorhiza and stipe, it is equally difficult to draw a line separating what is regarded as a rhizomorph and what a pseudorhiza. Norvell (1998b) noted that that occurrence of highly differentiated pseudorhizas as found in *P. rufotubulina* and *P. scatesiae* imply ‘a gradual continuum from mycelium to mycelial strand to rhizomorph to pseudorhiza to stipe, further complicating determination of what belongs strictly to the mycelium and what to the basidiome.’ The term ‘rhizomorphic pseudorhiza’ refers to pseudorhizas that possess rhizomorphic characteristics (see Norvell 1998a or 1998b for further discussion).

### Cap differentiation, gill formation, cap expansion, and fruitbody emergence

In *Phaeocollybia*, caps generally do not expand or gill cavities develop until after the primordia extend



some distance from the origin, after which time cap constrictions begin to form at the primordium apices (FIG A. p. 179). Cap formation differs according to species. For example, the uniformly pale primordia in *P. attenuata* display a faint constriction line between the future cap and stipe when within 5 cm of the soil surface, at which point the gill cavities are formed. In other species, such as *P. kauffmanii*, gill cavities within fairly well developed caps are found much deeper in the soil (~20 cm from the surface), indicating that the cap develops before full stipe elongation. In *P. scatesiae* and *P. rufotubulina*, cavitation within the cap occurs simultaneously with cap constriction.

After cavitation, gill initials begin to form. With cap expansion, intervening ridges appear that will develop into lamellulae ('half gills' that do not reach the stipe). Phaeocollybias produce lamellulae in a 'polydymous' pattern of five or more tiers irregularly interspersed among the 'true' gills, or lamellae. As the gill cavity enlarges, the hymenium and basidia begin to form. Differentiation and development may vary somewhat according to species-specific patterns. (See Norvell 1998ab for developmental drawings.)

In species characterized by smaller or ephemeral fruitbodies (e.g., *P. attenuata*), caps expand only slightly while still well below ground, usually after partial hymenial development. The universal veil is ruptured at this time, leaving short fibrillose remnants adhering to the stipe apex. Complete expansion to the typically broadly campanulate shape is completed only after emergence. At that time, the stipe remains stuffed with loose fibrillose pith, but the pith does not proliferate as the rind elongates and broadens, so that the stipe eventually becomes hollow. In contrast, the *P. scatesiae* cap expands well below the surface and the stipe is hollow long before emergence, although it also possesses the fibrillose remnants of the primordial sheath at the stipe apex. In *P. attenuata* and *P. scatesiae*, the expanded cap appears to protect the fibrils from removal during final upward expansion through the soil. This also explains why such patches are usually confined to the stipe apex and rarely found at ground level.

Caps associated with larger and longer-lived fruitbodies do not fully expand until well above the soil surface. In *P. kauffmanii* separation of the veil into

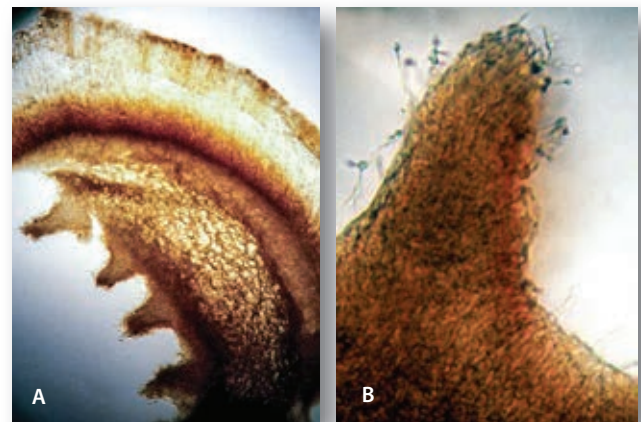


FIGURE 2.3 (*P. rufotubulina*). A. Radial section showing pileipellis, tramas, and gill initials. B. Thick-walled cystidia cover both edge and faces of gills before basidia develop.

matted fibrillose strands connecting cap and stipe precede gill ridge formation. In other species, the cap remains closely pressed over the stipe and does not expand until within a few cm of the surface, when most veil tissues rupture, leaving occasional fibrillose remnants on the stipe just below the still strongly inrolled pileus. Observation of two *P. kauffmanii* and *P. redheadii* clusters in place for one month (FIGS A–C, p. 166, see also Norvell 1998b, 2000) indicated that those species matured slowly. In such robust species, the cartilaginous rind surrounds a proliferating context that continues to grow during the final elongation and expansion phases so that stipes remain stuffed with a conspicuous firm pith even when fully mature.

### Cheilocystidial development

Cheilocystidia — the sterile cells confined to the gill edge — are present in all phaeocollybias and are secretory in nature. In *Phaeocollybia*, cheilocystidia belong to one of two types based on shape, wall-thickness, refractivity, and origin.

The first type — which we term 'thin-walled' — are variably shaped (but usually clavate), thin-walled, and not refractive. Examinations of primordia and young fruitbodies in species producing thin-walled cheilocystidia show that these elements originate from the central gill trama. Primordial examinations show that the clavate tramal ends extend beyond the edges of the gill ridges in the early developmental stages while the hymenium is still forming. As little more than terminal ends of central gill tramal hyphae, they exhibit 'indeterminate' growth and continue to

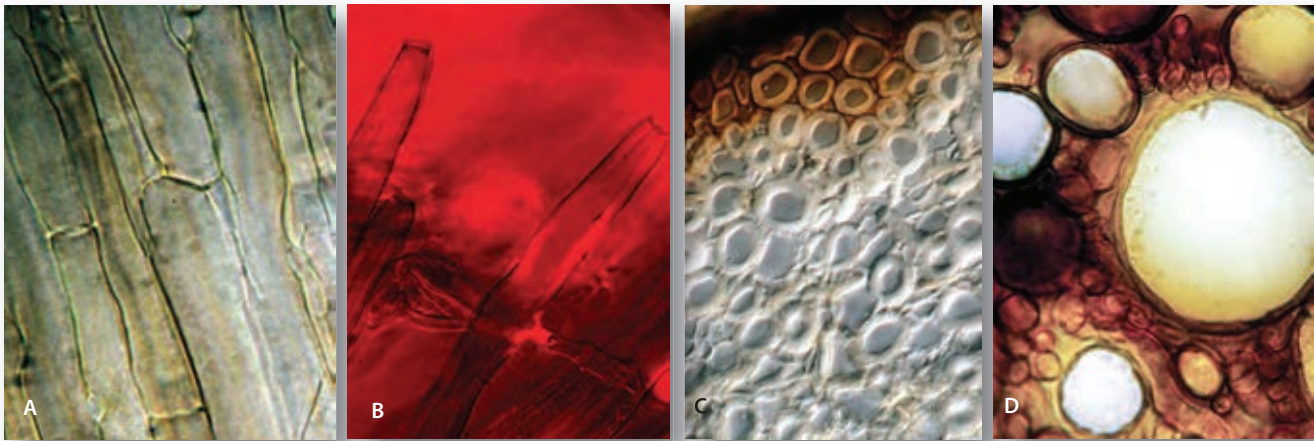


FIGURE 2.4 [Bright field: A,C,D; DIC: B.]. Sarcodimitic tissues consist of long fusoid thick-walled vessel hyphae and thin-walled branched flexuous hyphae. Here, longitudinal (A,B) and cross (C,D) sections demonstrate the dual-hypha system in pseudorhizal tissues. Width differences between vessel and flexuous hyphae are less marked in the *P. rufotubulina* rhizomorphic cord (C) than in the pseudorhiza (D).

extend apically, continually developing new septa throughout the life of the fruitbody, making length measurements taxonomically uninformative. Norvell (1998b) described examining what she believed to be the first successful *Phaeocollybia* tissue culture only to discover that the fuzzy whitish mat surrounding the explanted gill in the Petri disc consisted only of sterile cheilocystidia that had continued to elongate.

The other cheilocystidial type — which we term ‘thick-walled tibiiform’ — has wide and usually thin-walled bases and narrow thick-walled, refractive necks (with or without small globose heads). These arise from the same subhymenium that generates the fertile elements, the basidia. Here primordial examinations show tibiiform cystidia covering both gill edges and gill faces (FIG. 2.4B, p. 19). Whether the thick-walled cheilocystidia are derived from the tibiiform diverticula of the primordial sheath is still unclear, but their thick-walled necks and heads appear identical to (and possibly homologous with) the tibiiform diverticula that line the new gill cavity as soon as it is formed. True pleurocystidia (cystidia confined to the gill face) are rare in *Phaeocollybia* (although *P. pleurocystidiata* possesses them in abundance), so we suspect that the cheilocystidia are independent of the tibiiform diverticula seen in the earlier stages of gill development. Observations of mature gills (Norvell 1998ab) indicate that once formed, thick-walled tibiiform cheilocystidia cease further apical elongation, although they continue to function as secretory organs throughout the life of the fruitbody; here cheilocystidial length is taxonomically useful.

### Sarcodimitic tissue construction

Corner (1966) first introduced ‘sarcodimitism’ to describe certain cantharelloid tissues possessing a dual hyphal system composed of cylindrical narrow thin-walled highly branched flexuous elements and fusoid wide thick-walled rigid elements. The system has been recognized in several other genera, primarily those once placed in the white-spored *Xerulaceae* (Redhead 1987, Bas 1990, Corner 1991, Norvell & al. 1994b). Norvell (1998b) considered sarcodimitism as structurally significant in *Phaeocollybia* and noted that the unrelated *Caulorhiza*, *Termitomyces*, and *Xerula* pseudorhizas that travel through deep substrates also possess the tissue. She suggested that sarcodimitic construction develops the necessary resilient toughness that pushes a developing fruitbody “upwards through the soil a long distance from its origin” or enables one thin pseudorhiza to support multiple basidiomes.” (Norvell 1998b).

This existence of two different hyphal types interferes with determining whether the presence of clamps in sarcodimitic tissues. The rigid cylindrical elements with highly gelatinized thick walls prevent easy optical sections and so obscure the narrower thin-walled hyphae winding around and behind large elements. The vessel hyphae are so long that they are difficult to measure (particularly under oil). The flexuous hyphal branch ends frequently resemble clamp connections in size and appearance, particularly when seemingly bridging the septum of larger vessel hyphae. FIG. 2.4 (above) illustrates sarcodimitic tissue construction.

## Trophic status and ectomycorrhizae in *Phaeocollybia*

Although various biological hypotheses were proposed for *Phaeocollybia* species, few facts supported a saprotrophic, mycorrhizal, or parasitic status for the genus until Redhead & Malloch (1986) provided the first evidence for biotrophy from eastern Canada. Their excavation of an intact *P. christinae* arising from a senescent spruce rootlet sheathed in a mycorrhizal mantle and surrounded by diverticulate mycelia was the first successful retrieval of a phaeocollybia pseudorhiza attached to an associated host. They inferred a pathogenic relationship between host and fungus based on the degree of senescence of the rootlet, noting that the fruitbodies erupted ‘... through the cortical layers from a loosened vascular stele...’ through which nutrients were thought to flow from host to fungus (Redhead & Malloch 1986).

Norvell (1998b, 2000) published the first persuasive evidence that *Phaeocollybia* might be ectomycorrhizal after successful excavations of fruitbodies representing *P. redheadii*, *P. kauffmanii*, *P. benzokauffmanii*, *P. pseudofestiva*, and *P. spadicea*. Microscopical examinations of pseudorhizal origins showed them to be connected to ectomycorrhizal root-tips, as demonstrated by the presence of a Hartig net within the tips; both the mantle surfaces and surrounding mycelial hyphae bore the characteristic tibiiform diverticula diagnosing *Phaeocollybia*. No primordia or pseudorhizas erupted directly from rootlet cortex or invaded (or otherwise disrupted) the vascular stele as seen by Redhead & Malloch (1986), although pseudorhizas did associate with both healthy and senescent rootlets. Norvell (1998b) suggested that the rootlets retrieved by the Canadian excavation at the end of the active growing season were naturally senescent, observing that as both mycorrhizal and parasitic organisms penetrate their host substrates to some degree, a mycorrhizal status could not be ruled out for *P. christinae*.

Saprotrophy was previously suggested for phaeocollybias found in highly organic soils. For example, Smith & Trappe (1972), who were unaware that *P. scatesiae* forms fascicles subtended by long rhizomorphic pseudorhizas obviously originating elsewhere, suggested that one large mass of *P. scatesiae* fruitbodies originated from the remnants of a ‘long-decayed stump.’ Likewise, collection of phaeocollybias from highly organic substrates prompted Kühner (1980) to transfer *Phaeocollybia* from the mycorrhizal *Cortinariaceae* to the saprotrophic *Strophariaceae*. Allen (1991) and other mycorrhizal scientists now know that the presence of large quantities of organic matter in soils neither dictates saprotrophy nor excludes mycotrophy or parasitism. The fact that no one has yet succeeded in culturing *Phaeocollybia* via spore germination or tissue culture also suggests that the genus is not saprotrophic (Norvell 1998b).

Pacific Northwest phaeocollybias are found in forests containing *Tsuga*, *Picea*, *Abies*, *Pseudotsuga*, *Lithocarpus*, *Quercus* and/or *Pinus* — all genera known to form ectomycorrhizae (Allen 1991). Trudell & al. (2004) provided additional evidence for the mycorrhizal status of additional *Phaeocollybia* species by noting the high nitrogen isotope readings that *strongly* (italics ours) supported ectomycorrhizal status for *P. attenuata*, *P. benzokauffmanii*, *P. fallax*, *P. gregaria*, *P. kauffmanii*, *P. lilacifolia*, and *P. piceae*. While a parasitic strategy cannot be ruled out for at least some phaeocollybias, the combination of pseudorhizas emerging from fungal masses surrounding viable rootlets, the presence of a mantle on ectomycorrhizal tips, the existence of a Hartig net (considered by Wilcox, 1982, the most reliable index of mycorrhizal development), the connection of rootlets, tips, mantles, masses, and pseudorhizal surfaces by hyphae covered with the characteristic tibiiform diverticula, and the high nitrogen isotope readings offer the most persuasive evidence for accepting *Phaeocollybia* as an ectomycorrhizal genus.

## Taxonomy and phylogeny

### TECHNICAL DESCRIPTION OF THE GENUS

(adapted from emended description in Norvell, 1998a)

*Phaeocollybia* R. Heim, Encyclopedie mycologique 1. *Inocybe*: 70. 1931.

SYNONYM: *Quercella* Velen., Ceské Houby: 495.

TYPE SPECIES: *Phaeocollybia lugubris* (Fr. : Fr.) R. Heim, 1931.

BASIONYM *Agaricus lugubris* Fr. : Fr. *Typus conserv.* McNeill & al. p. 214. 2006.

PILEUS conic, obtusely conic or convex-campanulate, finally expanding to plano-umbonate in some, margin long remaining inrolled; the surface bald or sometimes bearing small squamulose remnants of the pellicular veil, typically glutinous to viscid to merely lubricous, rarely moist to dry; colors varied but tending toward ferruginous in age; characteristically developing dark brownish to blackish spots where injured; flesh cartilaginous.

LAMELLAE narrowly attached, deeply adnexed to practically free, close to crowded, typically polydymous with lamellulae irregularly interspersed between lamellae in three or more tiers, narrow to broad; variously colored when young (pallid, creamy, ochraceous, pinkish, orangish, violaceous, or greenish), darkening to cinnamon- or rusty brown in age from the spores; edges frequently uneven and often pallid under a lens even when mature but only rarely distinctly marginate.

STIPE cartilaginous, in some smaller species corneous, in others more flaccid, usually stiff and strict; surface bald (glabrous) except for short fibrillose patches or isolated fibrils scattered over the upper portion in some species, matte and closely longitudinally lined or naked and shining; the cortex cartilaginous, often thick and distinct, variously colored when young, developing ferruginous tones in age; the interior hollow or stuffed with a fibrillose to firm pallid context.

PSEUDORHIZA long and variably shaped; consistency fleshy and pliable or thin and brittle; frequently regenerative; belonging to one of the following types:

[i] ascending and giving rise to a single basidiome (vertical-monopodial), fleshy, continuous with the stipe and gradually narrowing downwards to a somewhat blunt origin, in age sometimes regenerating a new primordium; [ii] extending laterally through the substrate before turning upwards to give rise to a single basidiome (lateral-monopodial) and then a thin criniform wire differentiated from a fleshier stipe; [iii] cord-like and flexible, ascending or lateral, either [a] multiply branched with each branch giving rise to a single basidiome (sequential-racemose) or [b] apically umbellately branched giving rise to multiple basidiomes (fasciculate-racemose).

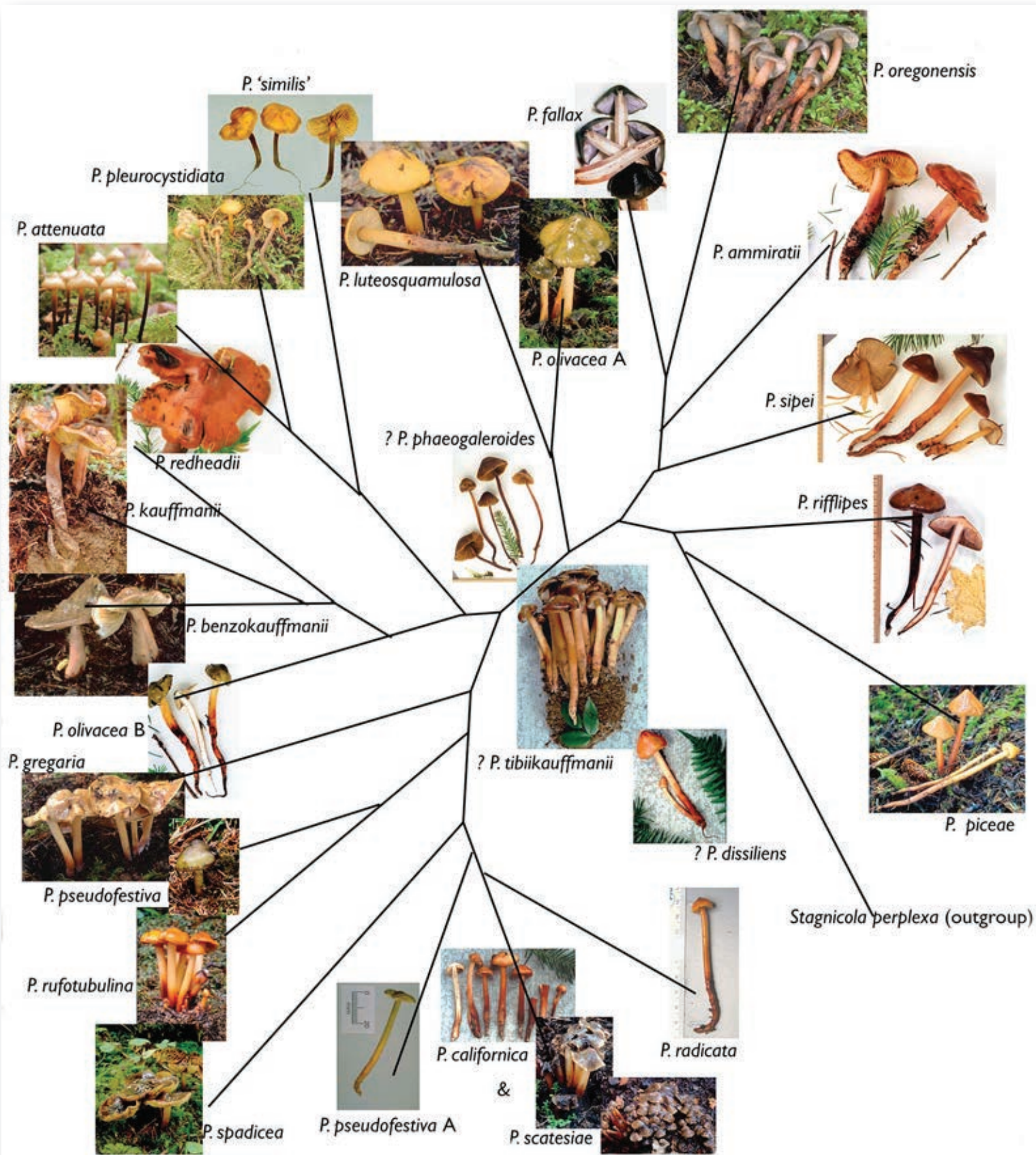
VEIL pellicular, sheathing the subterranean primordium but tearing during basidiome elongation and easily overlooked in mature basidiomes, often observed on the epigeous portion of mature basidiomes as irregularly to concentrically arrayed fibrillose patches on the aerial stipe, less frequently occurring as short appressed fibrillose patches over the pileus surface, often entirely absent on surfaces of emergent basidiomes but characteristically retained in part on the lower pseudorhizal surface.

BASIDIOSPORES in mass some shade of cinnamon or rusty brown; shape ranging from subellipsoid with inconspicuous apical callus to amygdaliform or limoniform with the apical callus projecting as a distinct beak; surface punctate-roughened to rugulose-warty ornamented except for smooth apex and apical callus; ornamentation often lower and less pronounced in the suprahilar area (as in a 'plage') but never completely smooth; color amber to brown in KOH, straw to amber in H<sub>2</sub>O, dextrinoid or not in Melzer's reagent.

BASIDIA clavate; 4-spored, rarely 2-spored.

CHEILOCYSTIDIA usually secretory, often gelatinized, colorless to very pale amber, terminal elements either [i] thin-walled and non-refractive, filamentous to clavate to sub-capitate, indeterminate and arising from the gill trama and frequently giving rise to filiform apical extensions in age or [ii] ventricose to equal below a narrow thick-walled highly refractive neck with or without a small rounded refractive head, determinate in growth and arising from the

FIGURE 3.1. The DNA-based phylotree (to the RIGHT, from Norvell 2005, adapted from Norvell 1998a) was the first DNA-based tree to depict molecular relationships among Pacific Northwest phaeocollybias. The unrooted Fitch-Margoliash + Neighbor-joining consensus tree derived from ITS rDNA length and restriction site data generated from 24 phaeocollybias and *Stagnicola perplexa* (the outgroup). (Fragmentary data from *P. dissiliens*, *P. phaeogaleroides*, and *P. tibiikauffmanii* were not included.) Current sequence analyses of DNA representing all 25 described species should provide better insights into the phylogeny of *Phaeocollybia* within the Pacific Northwest.



subhymenium; both types may be present in one species; occasional hyphidia may be interspersed.

PLEUROCYSTIDIA usually absent; when present either similar in shape to the accompanying cheilocystidia or filamentous and then termed hyphidia (paraphyses).

PILEIPELLIS typically a two layered ixocutis; the suprapellis usually colorless to faintly pigmented and with subgelatinous to highly gelatinized narrow hyphae, the subpellis pigmented and with gelatinous wide (often inflated) hyphae; rarely a three-layered ixocutis with pellicular veil then functioning as a pigmented suprapellis of narrow gelatinous hyphae over a colorless to faintly pigmented mediopellis and pigmented subpellis; in both types the highly gelatinized colorless layer either with loosened ascending hyphae embedded in a gel matrix or compactly radially aligned; pigments typically intraparietal and/or plasmatic, slightly to moderately encrusting pigments occasionally present; oleiferous hyphae often present.

TRAMAL TISSUES moderately to heavily gelatinized, hyphae forming a compact cartilaginous tissue, occasionally homogeneously monomitic but more often sarcodimitic and composed of two hyphal types (long, fusoid, wide, thick-walled fundamentals and branched, narrow, and thin-walled generatives), the highest degree of sarcodimitism within the pseudorhizal trama, sarcodimitism also often present to lesser degrees in the stipititrma, pileitrma, and lamellar trama; pileitrma continuous with but paler than the subpellis and gradually merging with the lamellar trama; lamellar trama more or less regular, with densely packed subparallel hyphae and rudimentary subhymenium.

CLAMP CONNECTIONS present or absent; when present frequent within the pileal suprapellis and at basidial and cheilocystidial bases; pseudoclamps occasional to frequent in some species.

TIBIIFORM DIVERTICULA aseptate, emergent from hyphae belonging to the mycelium and the pellicular veil (primordial sheath); consistently found on veil fibrils or patches remaining on the pseudorhizal pellis, less frequent elsewhere on the basidiome (stipitipellis, pileipellis) bearing fibrillose veil remnants.

DEVELOPMENT: (pileo)stipitocarpic monovelangiocarpy.

ECOLOGY: Solitary, scattered, gregarious, or cespitose, some in arcs where the basidiomes may be clustered or gregarious in the line of the arc. In western North America typically fruiting during the autumn (24 species) and/or spring (2 species) in moist mesic coniferous or coniferous-fagaceous forests. Known to be mycorrhizal; some species possibly parasitic.

### *Phaeocollybia* and other genera

When Heim (1931) described *Phaeocollybia*, he suggested a generic affinity with *Cortinarius* (same general aspect, basidiospore color, and morphology) and some European *Collybia* species with radicating stipes. Singer (1951b), Smith (1957b), and Horak (1977) accepted the genus within the *Cortinariaceae*. Kühner (1980) proposed a different classification in which he removed *Phaeocollybia* (along with *Galerina* and *Gymnopilus*) from the *Cortinariaceae*, a family he reserved only for mycorrhizal taxa, to the *Strophariaceae*, a family reserved for non-ectomycorrhizal genera. Kühner's classification has not been accepted by later *phaeocollybia* researchers.

Singer (1986) continued to classify *Phaeocollybia* as a cortinariaceous genus within the tribe *Cortinariae*, based on possession of rusty-brown thick-walled ornamented basidiospores lacking a germination pore. Those conducting primarily morphological and anatomical research (Gulden 1983; Jacobsson & Stridvall 1983; Redhead & Malloch 1986; Horak 1989; Nezdominogo 1990; Bon 1992; Watling & Gregory 1993; Bandala 1994; Rees & Wood 1996; Norvell 1998a) continued to place *Phaeocollybia* within the *Cortinariaceae*.

Recently, Matheny et al. (2006) proposed a molecular-based classification that limits the *Cortinariaceae* to a single genus (*Cortinarius*) and assigns the remaining genera to the *Tubariaceae*, *Inocybaceae*, or *Hymenogasteraceae*, noting, "The current configuration of lineages of the *Cortinariaceae* and *Strophariaceae* sensu Singer (1986) warrants the recognition of smaller monophyletic groups." This classification places *Phaeocollybia* within the *Hymenogasteraceae* (in the agaricoid clade) with *Flammula*, *Galerina*, *Hebeloma*, *Leucocortinarius*, and *Naucoria* (see also Gulden 2008). Although we tend to agree with this newly proposed taxonomy, we feel further molecular research is needed to refine relationships among the dark-spored agarics.

Historically, *Phaeocollybia* has been allied most closely to *Cortinarius*, *Galerina*, *Gymnopilus*, and *Pyrrhoglossum*. *Phaeocollybia* differs from these genera by having a pseudorhiza, a stipe with a cartilaginous cortex, and tibiiform diverticula on hyphae of the mycelium and pellicular veil. Recent DNA sequence analyses including north temperate phaeocollybias support *Phaeocollybia* either as a monophyletic genus of uncertain status ('*incertae sedis*') in the *Agaricales* (Moncalvo & al. 2002, who sequenced *P. attenuata*, *P. dissiliens*, *P. jennyae*, *P. redheadii*) or within the *Hymenogasteraceae* as noted above (Matheny & al. 2006, with *P. festiva*). Rees et al. (2002) included two southern hemisphere phaeocollybias (*P. ratticauda*, *P. graveolens*) in their preliminary phylogeny of *Gymnopilus* species and related genera, while Rees et al. (2003) included sequences from the south temperate *P. ratticauda* and the temperate *P. jennyae* in phylogenetic analyses of 78 species from brown-spored genera. Both phylogenies also imply monophyly for *Phaeocollybia*.

#### **Cortinarius**

As already noted, early researchers felt that *Phaeocollybia* was closely related to the genus *Cortinarius*. Smith (1957b) suggested a close relationship between *P. kauffmanii* and *Cortinarius* subg. *Myxadium* spp., based on similar stipe shape, viscid caps, thin-walled cheilocystidia, basidiospores, and rare clamp connections in the gelatinized pileipellis. *Cortinarius* differs morphologically in possessing a persistent cortina (remnants of an inner veil, which *Phaeocollybia* lacks); it also lacks a cartilaginous stipe cortex and the generically significant (for *Phaeocollybia*) tibiiform diverticula on universal veil and mycelium. Norvell (1998ab) suggested a biological similarity in that both *Phaeocollybia* and *Cortinarius* were mycorrhizal. Nevertheless, DNA sequence analyses (Moncalvo & al. 2002, Matheny & al. 2006) provide little support for a close phylogenetic relationship between the two genera.

#### **Galerina**

Except for similarly colored fruitbodies, *Phaeocollybia* seemingly shares little in common morphologically with *Galerina*, a saprophytic genus characterized by small fragile basidiomes with smooth or ornamented basidiospores and no pseudorhiza. Likewise, in *Galerina*, the typical ornamented basidiospore displays a well-delimited smooth plage, unlike the ill-defined roughened plage occasionally

found in *Phaeocollybia*. Smith (1957b), Singer (1986), and Bandala (1994) all felt that the two genera were not closely related, noting that rough-spored galerinas consistently lack clamp connections. Recent phylogenetic analyses (Rees & al. 2002, Matheny & al. 2006), however, do imply a close relationship between *Phaeocollybia* and *Galerina* and refer both genera together to a clade outside *Cortinarius* (= *Cortinariaceae* in the limited sense).

#### **Gymnopilus**

*Gymnopilus* basidiomes share similar stature and coloration (including drab to lilaceous caps and gills for some species), spore ornamentation, and cheilocystidia with *Phaeocollybia*. They are distinguished by attached lamellae, a stipe lacking a cartilaginous cortex, a saprophytic habit and preference for woody substrates, absence of pseudorhiza and tibiiform diverticula, ubiquitous clamp connections, bright brownish orange spore color, and pigments that are consistently soluble in KOH. Three recent phylogenetic analyses (Moncalvo & al. 2002, Rees & al. 2002, Matheny & al. 2006) do not support a close relationship between *Phaeocollybia* and *Gymnopilus*.

#### **Pyrrhoglossum**

Horak (1989) suggested that *Pyrrhoglossum* might be the genus most closely related to *Phaeocollybia*. As in *Phaeocollybia*, *Pyrrhoglossum* (unknown in the Pacific Northwest) also produces basidiomes with green or violet colors in addition to those that are strictly yellow to rusty brown. Pigments that are unstable in KOH, similar basidiospores, and similar cheilocystidia characterize both genera. The saprophytic and pleurotoid habit of *Pyrrhoglossum* differs from the mycorrhizal and pseudorhizal *Phaeocollybia*. None of the above cited phylogenetic studies include *Pyrrhoglossum*; DNA sequence analyses by Guzmán-Dávalos & al. (2003), which did not include *Phaeocollybia*, placed *Pyrrhoglossum* with *Cortinarius* and *Dermocybe* (treated as separate from *Cortinarius*) outside the *Gymnopilus*-*Psilocybe cubensis*-*Pholiota*-*Galerina* clade with a bootstrap value of 100%.

#### **Subgeneric classification in *Phaeocollybia***

Smith (1957b) was the first to classify *Phaeocollybia* at the subgeneric level, dividing the genus into two sections. Section *Phaeocollybia* contained species characterized by thin-walled cheilocystidia described as "... preponderantly clavate to elongate-capitate, the

TABLE 6. *Phaeocollybia* sections (Singer 1970, 1986)

SECTION	CHEILOCYSTIDIA	SPORE LENGTH	CLAMPS
<i>Phaeocollybia</i>	Thin-walled; clavate to cylindrical	> 6.5 µm	absent
<i>Subattenuatae</i>	Thin-walled; variable, non-capitate	> 6.5 µm	present
<i>Versicolores</i>	Thick-walled; acute or apically capitate	> 6.5 µm	absent
<i>Radicatae</i>	Thick-walled: (sub) capitate	< 6.5 µm	present
<i>Microsporae</i>	variable; oft clavate / cylindrical	< 6.5 µm	absent

tips 4–8 µm broad and the neck or shank regularly 3 µm or more thick; rarely a few hairs less than 3 µm...” (Smith 1957b). Section *Versicolores* contained species characterized by thick-walled, narrow-necked, lageniform to tibiiform cheilocystidia described as “... preponderantly with necks 1.5–2 µm thick, ending in an acute tip or a minute capitellum 2–3 µm in diam, the walls of the neck refractive and usually ochraceous in KOH, the basal portion usually enlarged somewhat (3–7 µm in diam); if hair like, the walls thickened somewhat in at least some of the individuals” (Smith 1957b).

After finding new species from the neotropics, Singer (1970, 1986) added basidiospore length and clamp connections as sectional characters and presented a new sectional classification, shown in TABLE 6. (See also TABLE 1 for classification of world *Phaeocollybia* species following Singer’s system.)

Bandala and Montoya (1994) next proposed two subgenera — subgenus *Phaeocollybia* (merging Singer’s “unclamped” sections *Phaeocollybia*, *Versicolores*, and *Microsporae*) and subgenus *Fibulophaeocollybia* (containing Singers “clamped” sections *Subattenuatae* and *Radicatae*).

Horak (1989) and Norvell (1998a, 2004) noted that assigning sections and subgenera to *Phaeocollybia* is premature, a conclusion supported by recent conflicting molecular analyses. Nonetheless, amplification and enzymatic digestion of the 5.8S ribosomal DNA (‘rDNA’) ITS (internally transcribed sequence) region from 22 Pacific Northwest *Phaeocollybia* species (Norvell 1998a, 2000, 2002, 2004; Norvell & Redhead 2000) suggested that cheilocystidial morphology was helpful in isolating monophyletic groups within the genus. Norvell (1998a)

extracted and amplified DNA from 160 specimens representing 24 putative PNW phaeocollybias (including 15 types) and seven out taxa to test traditional morphology-based species hypotheses with RFLP (random fragment length polymorphism) generated DNA profiles. FIGURE 3.1 shows the unrooted phylotree inferred by mapping restriction loci on ITS regions from PNW *Phaeocollybia* spp. and *Stagnicola perplexa* (Orton) Redhead & A.H. Sm. The preliminary tree shows partial support for sections based on cheilocystidial form as proposed by Smith (1957b) but little or no support for Singer’s 5-section classification (TABLE 6). Singer’s classification was not adequately tested, however, as the analyses included only one representative for each of two sections, *Subattenuatae* (*P. ammiratii*) and *Radicatae* (*P. radicata*).

The RFLP tree places species with thick-walled tibiiform cheilocystidia and racemose rhizomorphic pseudorhizas together in one clade; however, the inclusion of the small-spored, clamped *P. radicata* and exclusion of the thick-walled, vernal *P. pleurocystidiata* challenges both Smith (1957b) and Singer’s (1970, 1986) sections. Therefore, except for citing Singer’s sectional placement for each species in TABLE 1, we refer to them only rarely in the species descriptions.

Recent sequence analyses of DNA from the ITS region (Rees et al. 2002), the large ribosomal subunit (Moncalvo et al. 2002; Rees et al. 2003), and a six-gene region including rpb1, rpb-1intron 2, rpb2 and 18S, 25S, and 5.8S ribosomal genes (Matheny & al. 2006) each include only one to four *Phaeocollybia* species and thus offer little insight into subgeneric relationships within the genus. The phylogeny generated by Moncalvo et al. (2002) from 877 homobasidiomycete taxa (including four north temperate phaeocollybias) supports separation of subgenera *Phaeocollybia* and *Fibulophaeocollybia*, by showing the clampless *P. attenuata* & *P. redheadii* (Section *Phaeocollybia*) and *P. jennyae* (Section *Microsporae*) on a separate branch from the clamped *P. dissiliens* (Section *Radicatae*). Current DNA sequence analyses being conducted of isolates obtained from all 25 PNW species (by Matt Gordon under a USDI-BLM grant) should provide more reliable insights into phylogenetic relationships for *Phaeocollybia*, at least within the Pacific Northwest.



## Diagnostics: key characters and identification procedures



Forrest Norvell

### Macrocharacters

#### Color

Although *Phaeocollybia* is often characterized as a genus of yellow-brown to red-brown fruitbodies, PNW phaeocollybia caps display a number of other colors (ochraceous yellow, bright orange, olive green, purplish drab or blackish brown). The whitish, yellowish, pinkish, orange, or violet colors present in young gills also help contradict the designation of *Phaeocollybia* as a 'brown' genus. Nonetheless, most phaeocollybias do brown as they age, complicating identification using characters seen only in young specimens.

In particular, the two most striking colors — green and violet— change far too quickly. *Phaeocollybia fallax*, *P. olivacea*, and *P. pseudofestiva* caps usually lose the original green color after only one or two days. The initial green color may change to dark olive brown, cocoa colored, or dark brown with drab overtones; sometimes (particularly in *P. fallax*) an orange gluten obscures a green cuticle. Likewise, the purple to lilac gills of *P. fallax* and *P. lilacifolia* dull from 'striking' to barely detectable all too soon. Nonetheless, the diagnostic value of these colors, when present, is significant.

Technical descriptions typically include far too many color descriptors — with too much attention paid to subtle tone differences — to serve as quick

identification aids. After devoting many hours attempting to quantify colors for analytical purposes, the first author discovered that few color names are needed to convey taxonomic information; she found that even subtle color differences separating closely similar members of the *P. kauffmanii* complex could be expressed using the common color terms orange, tawny, drab, ochraceous yellow, tawny ochraceous, and red-brown (Norvell 1998a). Nonetheless, we suggest referring to some color standard when taking fresh notes because color perception is subjective. One NW Forest Plan surveyor used 'pumpkin pie' to describe *P. kauffmanii*, conveying the mature cap color beautifully and greatly shortening the identification process (Roux 1999 pers. comm.).

#### Cap (pileus)

After color, mature cap diameter and presence (or absence) of surface scales are more important than cap shape and degree of viscosity, although all provide good information. While taxonomically useful, shape is closely related to developmental stage, so the age of a specimen should be cited before noting whether an edge is inrolled or straight, a cap narrowly or broadly conic, or an umbo acute, blunt, or sharply papillate. Most phaeocollybias appear glutinous in the rain and shiny in dry weather, so it may be difficult to determine the degree of viscosity of caps under very wet or dry

conditions. Surface opaqueness and striation are also helpful key characters.

### Odor and taste

Smith (1949) discussed the subjective nature of odor and taste and noted that odor or taste ‘blindness’ — where a collector cannot detect bitter or sweet — is a problem. As one of us (Exeter) is odor and taste blind, we know the difficulty in using these character states in a key. We include them as supplementary qualifiers when helpful and include them in TABLE 7 for quick reference for those who can smell and/or taste.

Important PNW phaeocollybia odor/taste terms are farinaceous, ‘potato/pansy’, raphanoid or *Oxalis*-like, bitter, and not distinctive. The first three are explained below.

**FARINACEOUS** refers to the odor and taste of freshly ground flour (‘meal’). Today only those who grind their own wheat — or mushroomers taught to associate the term with certain *Tricholoma* species — recognize that descriptor. We use the term broadly, for both pleasant (‘sweetly’) and slightly unpleasant (‘bitter-cucumber’) farinaceous odors and tastes. Wood & al. (1994) identified the active ‘bitter cucumber’ component of several mushroom species as *trans*-2-nonenal. Strong farinaceous odors are found in *P. ammiratii*, *P. benzokauffmanii*, *P. kauffmanii*, *P. oregonensis*, *P. benzokauffmanii*, and *P. redheadii* — all also marked by strongly positive syringaldazine reactions and remarkably resistant to insect infestation, suggesting that the chemical source of the odor may function in a protective capacity.

**POTATO/PANSY** is a shorthand term introduced by Norvell (1998a) for a complex vegetable/floral odor that once learned is readily recalled but — like farinaceous — difficult to describe. The odor has variously been called ‘gebrenzlich’ (German for burnt hair; Horak 1996 pers. comm.), ‘musty raw potatoey’ (Barron, Redhead 1992 pers. comms.), and ‘slightly floral, like pansies’ (Fox 1992 pers. comm., Roger 1994 pers. comm.). Phaeocollybias with this faint but distinctive odor (e.g., *P. attenuata*, *P. fallax*, *P. scatesiae*, *P. sipei*, *P. spadicea*) are usually syringaldazine negative except on the pseudorhiza (the part of the fruitbody that rarely is smelled or tasted).

**RAPHANOID** (‘radish-like’) or **OXALIS-LIKE** is similar to ‘potato/pansy’ but, lacking a floral component, smells or tastes more acidic and pungent. Raphanoid phaeocollybias include *P. dissiliens*,

*P. phaeogaleroides*, and *P. radicata*, all of which are coincidentally syringaldazine negative.

### Gills (lamellae)

A narrow to nearly free gill attachment and presence of short gills that do not reach the stipe (‘lamellulae’) are the same for all PNW phaeocollybias and thus not used to differentiate species. Here, the most useful key character is the color of the young gills, particularly in the violet-gilled *P. fallax* and *P. lilacifolia* and the pinkish white- to rosy lilac-gilled *P. riffliipes*.

### Stipe (‘stem’)

The most significant stipe characters are width (at apex and broadest point) and the absence or presence and consistency of the stipe flesh, here called ‘pith.’ The thickness of the ‘rind’ (cartilaginous cortex) helps separate *P. californica* and *P. scatesiae* (with thick rinds) from *P. rufotubulina* (with a thin rind). Stipe color is also useful: a drab to gray stipe apex often helps differentiate a mature *P. fallax* with green cap but now brown gills from *P. olivacea* and *P. pseudofestiva* in the field. Stipe length and shape are generally too variable within each species to serve as key characters, although they should be noted in the description.

### Pseudorhiza (‘root’)

Pseudorhizal growth patterns detailed in previous chapters are important key features. Unfortunately, their taxonomic utility is considerably diminished by the difficulty in extracting intact pseudorhizas from rocky or root-filled soils, particularly as criniform wires and thin cords are easily broken.

### Spore print

Although spore print colors follow species-consistent patterns (e.g., dark blackish red-brown in *P. attenuata*, pinkish cinnamon in *P. fallax*), most color differences are too subtle to differentiate *Phaeocollybia* species. They should be taken, however, to provide mature spores for microscopical work.

### Fluorescence

The diagnostic potential of fluorescence, not particularly well explored for agarics, has been well researched in *Cortinarius* subg. *Leproclybe* (Moser 1969, Gill & Steglich 1987). Norvell (1998a), the first to research fruitbody fluorescence in *Phaeocollybia*, found that 16 phaeocollybias fluoresced under UV light. We have now tested all PNW phaeocollybias and confirm that all species fluoresce to some degree (see TABLE 7). The most intense fluorescence is provided by fresh gills, which typically appear brilliant

TABLE 7. Spore print color, fluorescence, syringaldazine reactivity, and odors in PNW phaeocollybias.

SPECIES	SPORE PRINT COLOR	FLUORESCENCE UNDER UV*		SYRINGALDAZINE REACTIVITY**			CAP ODOR (TASTE if impt)
		YOUNG GILLS	CONTEXT	CAP+ GILLS	STIPE	PSR	
<i>amm</i>	p cinn Br	brill pY > mustY	dp dullOr	0	0	+++	cuke far
<i>att</i>	dp red Br	brill yW > orY	0	0	0	+	raph / pot-pan
<i>ben</i>	drab Br	brill pY > wY	[not recorded]	+++	+++	+++	sw Far (cuke far)
<i>cal</i>	red Br	brill mustY	0	0 / +	0 / +	+++	pungent wild carrot
<i>dis</i>	y Cinn	(dull Och. / 0)	(0)	0	0	0	raph > oxalis
<i>fal</i>	pk Cinn	brill yW > dull Y	0	0	0	+	pot-pan
<i>gre</i>	gry cinn Br	0	dp mag > dull dp oY	0	0	0 / +	pot-pan
<i>kau</i>	cinn Br	brill W > Y > och	dp Red/ Mag cap occ Or	+++	+++	+++	far (occ bitter)
<i>lil</i>	pk cinn Br	brill wY	dp dull Purp	+++	0 (green)	0	pot-pan
<i>lut</i>	p cinn Br	wY > brill must Y	Or & dp Mag	0	0	0 / +	ND or raph
<i>och</i>	p cinn Br	brill Y	Mag / dull Purp	0 / +	0	0	ND, far, raph
<i>oli</i>	rust y Br	brill mustY	dp Mag & dp Or	0	0	0 / +	pot-pan
<i>ore</i>	dull y Cinn	brill violW > yW	(psr brill pY > pOr)	+++	+++	+++	cuke-far
<i>pha</i>	red Br	Ochre > yOr	dp dk Red, dp Purp	0	0	0	raph > oxalis
<i>pic</i>	dk cinn Br	brill yW > Dp yOr	dp mag Red > dull Purp	0	0	0	raph > sw farin, paint thinner
<i>ple</i>	dk red Br	brill W or Y > dull mustY	0	0	0	0	ND, sl cuke far, raph
<i>pse</i>	pk cinn Br	brill yW > dullY	dp dull Purp & Och, dp Red	0 (green)	0 (green)	+++	ND, nutty, pot-pan
<i>rad</i>	chest Br	ochOR	dull dp Mag, purp	0	0	0 / +	ND, raph, oxalis
<i>red</i>	cinn Br	violW > br pY	or Mag, dp Red	+++	+++	+++	cuke-far (far & bitter)
<i>rif</i>	cinn Br	brill yW	dull Or	0 / +	0	0	ND, pot-pan
<i>ruf</i>	dk red Br	(dull yOr)	0	0	0	0 / +	pot-pan
<i>sca</i>	med y Br	brill wY	0	0	0	(+)	pot-pan, ND (bitter, then ND)
<i>sip</i>	cinn Br	pY brill yW	dp Mag dp Or	0	0	+ / +++	ND, pot-pan, raph/far
<i>spa</i>	dk y Br	yW > mustY, dull Y	dp Purp	0	0	+++	ND, raph, pot-pan
<i>tib</i>	dull pk Br	Br Y > dull Y	Or & Purp	+++ / 0	0	+++	far, occ. pot-pan

COLOR abbreviations (modifiers in lower case): br = brown, brill = brilliant, cinn = cinnamon, chest = chestnut, dk = dark, dp = deep, mag = magenta, must = mustard, och = ochraceous, or = orange, p = pale, pk = pink, purp = purple, w = white, y = yellow

\* colors in brackets from dried specimens

\*\*0 = no reaction; + = pale magenta in 30 minutes; ++ = deep magenta in 30 minutes; +++ = deep magenta in 5–15 minutes

ODOR abbreviations: cuke = cucumber, far = farinaceous, oxalis = acidic, oxalis-like, ND = not distinctive, pot-pan = potato-pansy, raph = raphanoid, sw = sweetly

white to yellow when young and darken to bright to dull yellow, ochre, or orange when mature. Flesh in stuffed stipes generally exhibits a deep dark (but often intense) glow in the purple, magenta, red, or orange part of the spectrum. UV readings of dried gills yield similar (if muted) results. Although UV fluorescence is too consistent across species to serve as a key character, the one exception — non-fluorescent gills in *P. gregaria* (with flesh that does fluoresce) — is particularly helpful in distinguishing that species from *P. olivacea*.

### Syringaldazine

Marr & al. (1986), aware that a positive (magenta) syringaldazine response identified laccase production in growing cultures, tested fruitbodies (primarily in *Cortinarius*) for chemotaxonomic purposes, placing those with reactive tissues into ‘laccase dominant’ groups. Norvell (1998a), who spot-tested phaeocollybias using several different chemicals, found that syringaldazine had the greatest taxonomic potential. We have now tested all PNW phaeocollybias and find syringaldazine reactivity fairly consistent within species (see TABLE 7). Strongly positive syringaldazine reactions are those where tissue and/or leachate turns deep magenta within 5–15 minutes; moderately positive reactions are those that become deep magenta within 15–30 minutes; weakly positive are those turning pale magenta at 30 minutes. We consider syringaldazine one of the most valuable *Phaeocollybia* lab tools but include it only as a secondary entry in our keys, as the reagent is not readily available and must be used on fresh tissues.

## Microcharacters

### Cheilocystidia

Cheilocystidial type, clamp connections, and basidiospore size are the three most important key microcharacters in *Phaeocollybia*. Cheilocystidia are sterile cells found on the gill edges. As detailed in the previous two chapters, the two basic cheilocystidial types are represented by **thin-walled** filamentous to clavate elements (see FIG–pp. 123F, 134G–H, 139C, 163D, 164F, 189C–D, 190D–E) and refractive **thick-walled** tibiiform elements (see FIG–pp. 152E, 157A, 158K, 177B, 178A, 201D–F).

One type usually dominates, although some species have thin- and thick-walled elements intermixed. Additionally, the formation of filiform apical growths on thin-walled elements may be mistaken for narrow-

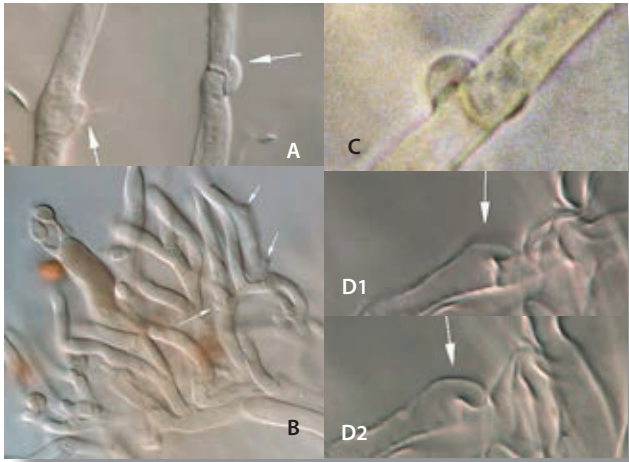
necked thick-walled elements. The apical outgrowths themselves can serve a diagnostic function by differentiating species with clavate cheilocystidia that never form them (notably *P. fallax*) from similar species that readily develop them (e.g., *P. olivacea*).

Thick-walled cheilocystidia are determinate; thus both lengths, which fall within a size-specific range, and widths help diagnose species. For thin-walled cheilocystidia (continually extending in length and thus indeterminate) width and general shape are more diagnostic. Thin-walled cheilocystidia are classified as mucronate (pointed), filamentous, cylindrical, irregularly cylindrical, narrowly clavate, broadly clavate, subcapitate, or inflated (sphaeropedunculate). Cheilocystidia are most easily found in healthy young or mature specimens. Gills in older fruitbodies are often so eroded that edges (and thus the cheilocystidia) are completely missing, so that it is easy to misinterpret immature basidia, hyphidia, or other elements on the gill faces as cheilocystidia.

### Clamp Connections

Clamp connections are hyphal outgrowths in basidiomycetes that connect the resulting two cells during cell division, forming a ‘by-pass’ channel at the septum (FIG 31A–D). *Phaeocollybia* is a genus where fruitbodies produce clamps only in some species, making clamps helpful in differentiating species. Among the 25 PNW phaeocollybias, only *P. ammiratii*, *P. dissiliens*, *P. phaeogaleroides*, and *P. radicata* have frequent clamp connections. Clamps occur also occasionally in the stipitipellis of *P. kauffmanii*, *P. redheadii*, and *P. rufotubulina*. The existence of clamps noted in numerous ‘*P. kauffmanii*’ collections drew Joe Ammirati’s attention to ‘el clampo,’ then a cryptic species now recognized as *P. ammiratii*.

Before sarcodimitism was recognized in *Phaeocollybia* (Norvell 1998a), artifacts caused by viewing a dual hyphal system were often misinterpreted as clamp connections. The erratic occurrence of such ‘false’ clamps no doubt prompted an exasperated Smith (1957b) to declare clamps absent ‘for all practical purposes’ when he described *P. spadicea*. Therefore, the monomitic pileipellis and gill hymenium are the safest tissues to search for clamps. Highly gelatinous tissues (particularly when rehydrated) also interfere with clamp detection. We recommend mounting thin fresh tissue sections in water or KOH with phloxine for best clamp detection. High-powered compound microscopes outfitted with Nomarski (DIC) optics or phase contrast particularly aid in finding clamps.



Lorelei Norvell

**BEWARE THE FALSE CLAMP.** After nuclear division, a clamp forms a channel around the septum so that one new nucleus can return to the 'mother' cell to reestablish its binucleate status. Arrows show true clamps in the pileipellis (A—*P. radicata*) and on basidia and cheilocystidia (B—*P. ammiratii*). The 'clamps' on the right are really a bubble on a convenient septum (C) and a short branch revealed as such by a twist of the focusing knob (D1 & D2).

Fortunately, the four PNW 'clamped' phaeocollybias do produce abundant clamps that are easily seen at septa of the narrow pileus suprapellis hyphae and at the terminal cells of the cheilocystidia. Although always present below the basidia, clamp connections there are seen with difficulty due to the dense congestion of basidioles, basidia, and other cells at the same site.

### Basidiospores

Basidiospore size, shape, ornamentation, and color are all key character states.

**BASIDIOSPORE SIZE** is strongly diagnostic. Unusually large limoniform spores were the first indication that a cryptospecies (*P. redheadii*) lurked under '*P. kauffmanii*' in the herbarium. Unusually small spores helped separate the cryptic *P. riflipes* (revealed first by rDNA RFLP analyses) from *P. fallax* and the cryptic *P. ochraceocana* from *P. luteosquamulosa*. Basidiospore size (and shape) immediately distinguish *P. oregonensis* from *P. benzokauffmanii*. Median basidiospore dimensions are surprisingly species constant. We cite medians rather than averages so as to discount the influence of large or small outliers on a dimension. PNW phaeocollybias have spore length medians that range from 5.8  $\mu\text{m}$  (*P. radicata*) to 10.5  $\mu\text{m}$  (*P. redheadii*) and spore width medians from 3.2  $\mu\text{m}$  (*P. radicata*) to 6  $\mu\text{m}$  (e.g., *P. luteosquamulosa*, *P. olivacea*, *P. redheadii*).

**BASIDIOSPORE SHAPE** here refers to the two basic *Phaeocollybia* categories: 'ellipsoidal' (more precisely

'inequilaterally ellipsoidal') and 'limoniform.' The latter broad category includes shapes also termed amygdaliform (almond-shaped), limoniform or citriform (lemon-shaped), and naviculate (fusoid or boat-shaped). The asymmetrical lemon and almond shapes make the length :: width ratio ('Q') less helpful than in other genera, so we do not cite 'Q' here. More significant is how gradually or abruptly the spore widens; thus we introduce 'big-bellied' to refer to the 'limoniform-globose' or 'rotund limoniform' shapes of the abruptly rounded *attenuata*-type spores and 'long-bellied' to refer to the elongated but full 'sublimoniform' *redheadii*-type spores. Also useful are the prominence of the apical callus ('apical beak') and its position related to the opposing apiculus (e.g., 'eccentric', 'tilted', 'straight').

**SPORE ORNAMENTATION** and **SPORE COLOR** are closely linked, as color is influenced by both spore wall thickness and degree of ornamentation. Basidiospores range from extremely pale amber with ornamentation barely discernible under oil when mounted in KOH (*P. oregonensis*) through very dark amber with coarsely rugulose-warty ornamentation clearly visible at low power (e.g., *P. attenuata*). The presence of a plage — here an area of lowered (but not smooth) ornamentation seen only under the high oil objective via optical sections — is less important in *Phaeocollybia* than in *Galerina*, primarily because phaeocollybia 'plages' are seen only with difficulty.

All phaeocollybia basidiospores are ornamented, even when appearing smooth under the high dry objective. (Scanning electron micrographs confirm that even the 'smoothest' *Phaeocollybia* spore — e.g., *P. oregonensis*, FIG-p.128j — is ornamented.) Terms describing ornamentation include (from lowest to highest roughness) punctate-roughened, verruculose, verrucose, and warty-rugulose. We use 'marbled' (cf. Gulden 1992) to refer to the undulating exosporium surface found in the *P. festiva* complex.

### Pileipellis

Norvell (1998a, 2000) was the first to focus on the taxonomic potential of pileipellis structure in *Phaeocollybia*. The presence of well-defined layers, differences in color and pigments, and variation in the degree of gelification and hyphal separation between species make the pileipellis an excellent key character, although admittedly it is a challenge to prepare good slide mounts of fresh tissues. Although topographical terms do not necessarily reflect tissue origins, we find them convenient and so use 'suprapellis', 'mediopellis'

and 'subpellis' to differentiate pileipellis layers (see also Bas 1969, Largent & Thiers 1977, Largent & Baroni, 1988).

**BILAMINATE VS. TRILAMINATE** — All but two PNW phaeocollybias are 'bilaminated' or two-layered, generally with a non-pigmented suprapellis (top layer) overlying a pigmented subpellis (bottom layer). There are several subgelatinous bilaminated PNW phaeocollybias (e.g., *P. attenuata*) that possess pigments in both pileipellis layers, but generally the suprapellis hyphae are colorless or only weakly colored beneath encrusting pigments; here the two layers are also distinguished by the presence of narrow cylindrical hyphae in the suprapellis and more inflated hyphae in the subpellis.

*Phaeocollybia luteosquamulosa* and *P. ochraceocana* are 'trilaminated' or three-layered, with a thin yellow-orange suprapellis resting above a compact highly gelatinized colorless mediopellis (middle layer) overlying an orange or tawny subpellis. Herbarium collections representing both species were found under the '*P. kauffmanii*' label; cap sections showing the brightly pigmented top layers quickly revealed the misidentification (Norvell 1998ab).

**COLOR AND PIGMENT TOPOGRAPHY** — Viewing pileipellis colors in both water mounts and in KOH is necessary to determine original color and pigment reactivity. Many green or brown pigments turn orange or orange brown in KOH, while others do not.

More useful taxonomically is location of pigments within a tissue (referred to as pigment topology). Important topological terms include: **incrusting** (pigments adhering to the inside hyphal wall), **encrusting** (those adhering to the outside wall), **(intra)parietal** (pigments contained between cell walls), **cellular** (pigments within a hyphal element), and **diffuse** (pigments located in the gel matrix surrounding the hypha).

**SUBPELLIS PIGMENTS** — Most PNW phaeocollybias contain parietal or cellular pigments in the subpellis that remain present (although the color may change) when placed in KOH. The bright orange pigment in the subpellis of *P. piceae*, however, is diffuse and soon disappears in KOH, over time leaving behind a completely clear tissue. Encrusting pigments are most easily seen in water mounts of fresh material; in dried material, encrusting pigments are sometimes visible only under the high oil immersion objective (as in *P. kauffmanii* and *P. redheadii*). Often a subpellis (as in *P. olivacea*) contains parietal, diffuse, and incrusting

pigments, but the tendency of some parietal pigments to coagulate within the hyphal walls in rehydrated tissues (and thus mimic a spottily distributed incrusting pigment) complicates determining which pigments are present and where.

**SUPRAPELLIS PIGMENTS** — Presence or absence of encrusting pigments within a suprapellis is an important key character. The closely allied species *P. scatesiae*, *P. californica* and *P. rufotubulina* can be microscopically differentiated by (respectively) (i) a lack of encrusting pigments, (ii) spirally aligned hyaline to pale amber gel encrustations, and (iii) spirally aligned dark reddish-orange gel encrustations. These distinctions are most obvious in water mounts of fresh tissues.

**GELATINIZATION** — Hyphal arrangement and degree of gelification within the suprapellis are also useful. Most viscid to glutinous PNW phaeocollybias have an ixocutis containing radially aligned, long, narrow, branched hyphae embedded within a gelatinous matrix. Smith (1957b) referred to a pellis containing well-separated hyphae floating in such a matrix as a 'collapsed ixotrichodermium.' Examination of *P. scatesiae* primordia, however, showed that the long narrow hyaline suprapellis hyphae are originally tightly packed in a radially aligned cutis beneath the pigmented primordial sheath; thereafter the suprapellis hyphae loosens and gelifies to produce a thick gelatinous matrix (Norvell 1998ab). Degree of gelification of the suprapellis at maturity appears consistent within species; the *P. scatesiae* suprapellis becomes so gelified that hyphal walls are obscured while walls remain clearly visible (although gel-encrusted) in *P. californica* and *P. rufotubulina*.

### Basidia

All PNW phaeocollybias are 4-spored, although they may be intermixed with occasional 2-spored basidia in some species. Phenetic analyses by Norvell (1998a) showed that the ratio of 4- to 2-spored basidia was not diagnostic and that basidial size was taxonomically less informative (and more difficult to measure) than spore size, so we do not refer to basidia in our keys. Nonetheless, basidial shape, color, and contents are secondarily diagnostic.

### Pleurocystidia

True pleurocystidia (not occasional cheilocystidial 'outliers' on gill faces) are rare in *Phaeocollybia*, so that the discovery of abundant thick-walled tibiiform

TABLE 8. Major key characters of Pacific Northwest phaeocollybias.

SPECIES	Spore size (median in $\mu\text{m}$ )	Cheilocystidia		Clamps present	Pileipellis		Young gills lilac to violet	Cap color green or drab	Mature stipe apex < 5 mm	Mature stipe hollow <sup>2</sup>	Pseudorhiza wire or cord <sup>3</sup>
		Thick- walled present	Thin- walled only		3- layers	Hyphae gel- or pigment- encrusted					
<i>att</i>	9 × 5.75		+			+	+ / -		+	+	W
<i>amm</i>	9 × 5.5		+	+							
<i>ben</i>	9 × 5.5		+					D			
<i>cal</i>	9 × 5.4	+				+				+	C
<i>dis</i>	6.2 × 4		+	+		+				+	C
<i>fal</i>	9 × 5		+				+	G		(+)	
<i>gre</i>	9.6 × 5.7		+					(D)			(C)
<i>kau</i>	8.8 × 5.2		+	rare		+					
<i>lil</i>	8 × 5		+			(+)	+				
<i>lut</i>	10 × 6		+		+	+					
<i>och</i>	7.4 × 4.7		+		+	+					
<i>oli</i>	10 × 6		+					G			(C)
<i>ore</i>	6.8 × 4		+					D			
<i>pha</i>	10 × 5.8		+	+		+			+	+	W
<i>pic</i>	9.4 × 6		+			(+)					
<i>ple</i>	9.25 × 6	+				+			+	(+)	
<i>pse</i>	8 × 5	+				+		G		(+)	C
<i>rad</i>	5.8 × 3.2	+							+	(+)	C
<i>red</i>	10.5 × 6		+	rare		+					
<i>rif</i>	7 × 4.5		+				+	(D)			
<i>ruf</i>	9 × 5	+		rare		+				+	C
<i>sca</i>	8.5 × 5	+								+	C
<i>sip</i>	6.5 × 3.8		+							+	C
<i>spa</i>	8 × 5	+						(D)			
<i>tib</i>	8 × 4.5	+				+					

+ = a character is present; + / - = a character is present or absent; (+) = <sup>1</sup>gel- but not pigment-encrusted, <sup>2</sup>fibril lined, <sup>3</sup>suspected or variable.  
C = cord; D = drab; G = green; W = wire; ( ) indicates that a feature is variable

elements covering the gill faces of one '*P. attenuata*' herbarium collection by Scott Redhead immediately flagged a potential new species. *P. pleurocystidiata* now represents western North America's only pleurocystidiata phaeocollybia. We do not treat the occasional to frequent narrow thin-walled paraphyses found in basidial clusters on *P. rillipes* gill faces (termed 'hyphidia' by Singer, 1986) as pleurocystidia, although we may do so in the future.

#### Tramal tissues and sarcodimitic construction

Sarcodimitism — the dual hyphal system composed of [i] thin-walled, narrow, branching flexuous hyphae and [ii] thick-walled, wide, rigid vessel hyphae (cf.

p. 20, FIG 2.4) — characterizes the pseudorhizal trama in all PNW phaeocollybias. Degree of sarcodimitism and distribution of the two hyphal types in gill, cap, and stipe tramas appears consistent within each species. Larger, robust fruitbodies (e.g., *P. benzokauffmannii*, *P. oregonensis*) possess a high degree of sarcodimitism with a fully developed dual hyphal system extending well up into the cap and gill tramas. In contrast, sarcodimitic tissues are present (but admittedly rudimentary) in species with more fragile fruitbodies such as *P. phaeogaleroides*, where they may be confined entirely to the pseudorhiza. In species that develop hollow stipes, sarcodimitic tissues are generally restricted to the tissues of

the pseudorhizal pith. Despite its importance to development within each species, we do not refer to the distribution of sarcodimitic tissues in our keys.

### Tibiiform diverticula

Distribution of the diverticula over the mature basidiome is directly correlated to the retention of the primordial sheath, which occurs in species-consistent patterns. In most species, diverticula are restricted to the pseudorhiza and accompanying mycelium; in others they also occur on sheath remnants on the apical stipitipellis and/or pileipellis. However, patience and experience is required to detect the small refractive diverticula, confined to broken sheath fibrils remaining on pellis hyphae that are easily flipped downward during mounting. Additionally, although these diverticula are diagnostic at the generic level, their morphology is relatively consistent, making them only secondarily diagnostic. The tibiiform diverticula found in *P. phaeogaleroides* are quite a bit larger (30–60+  $\mu\text{m}$  long) than those typically found (5–30  $\mu\text{m}$  long) in other PNW species.

### 'Setae'

During 2007, we made several excellent collections of *P. radicata* that included branched rhizomorphic pseudorhizas. Microscopical examination of the cords (FIGS 156-D–E, 158F–I) revealed thick-walled brown 'setae', previously unknown for *Phaeocollybia*. As all collections were made at one site, this character may not be constant for the species. It is also possible that the elements are present on other pseudorhizas and have simply been overlooked. Their function is unknown at the present time.

## *Phaeocollybia* identification procedures

### Field collection

#### Field gear

Important collecting gear includes a knife, small (but heavy duty) garden shears for clipping roots, folding hand saw for cutting larger roots, aluminum foil for wrapping specimens, a plastic 'fishing tackle' box with moveable dividers for smaller specimens, small notebook, blank field tags, pencils & markers, and collecting basket or backpack.

#### Collecting techniques

Unfortunately, the hallmark character associated with *Phaeocollybia* — the pseudorhiza — is all too often left behind in the field. To extricate this significant

subterranean part from unyielding substrates and heavy soils, gently dig slightly away from the stipe using a long narrow flat tool (e.g., a modified oyster knife or small hand trowel) before attempting to lift out the fruitbody. In loose soils, it may be easier to dig using the fingers, pulling the soil away from the base until it becomes necessary to use a digging implement. If the pseudorhiza disappears between rocks or hard roots at the bottom, do not pull directly up, but 'waggle' the fruitbody gently to retrieve as much of the trapped portion as possible. Generally, the best extractions are those accomplished by 'feel'.

In the field after collection, list important ephemeral characters (e.g., degree of viscosity, presence of green or lilac pigments, odor, and collection number) on the field tag to be wrapped or placed with the specimen. Also write the collection number into the photo log and/or place the tag at the edge of at least one photo when taking photographs. The tag is an excellent place to write a 'first' identification. (This usually proves highly amusing to the person at the microscope.)

Wrap each collection in aluminum foil and separate sample vegetation (leaves, cones, etc.) in crimped foil edges to serve as a reminder of the habitat. Smaller, more fragile specimens are best carried in plastic fishing tackle boxes with movable dividers.

## Identification

### Describing fresh specimens (macrocharacters)

It is best to describe a fresh *phaeocollybia* before attempting to key it to species. This forestalls 'forcing' specimens to fit a key (or photo) during the identification process. A good first step is to write a one- to two-sentence general impression summarizing stature, colors, viscosity, age, odors, surfaces, and other notable features. ('Notable' here means what **you** notice and not necessarily what an expert thinks *should* be noticed.)

The second step is to slice at least one specimen lengthwise to expose the flesh. Photograph or sketch both exterior and interior. Placing sliced fruitbodies onto a photocopier quickly produces excellent life-size photos on which annotations can be placed and from which measurements can be made.

Observe colors in diffuse daylight (on sunny days next to a window with a northern exposure) or under full-spectrum lamps (Ott® lamps are compact and work well), not under normal incandescent or fluorescent bulbs. A regular color standard (Ridgway 1912, Munsell 1986) is helpful but often unavailable.



Fortunately, any color reference — even paint chips or cosmetic charts — will train the eye to see colors that might otherwise be ignored. The advent of digital color photography has greatly simplified the description process, particularly when both ruler and neutral gray card are included in the photo.

To make spore prints (for spore measurements), place whole or halved caps gills downward on labeled microscope slides or white paper; keep at low room temperature (50–60°F) for 8 to 12 hours in loosely closed waxed paper packets or plastic boxes (with the lid slightly ajar). Air dry spore prints and retain the caps for microscopical examination.

Odors should be sampled from crushed cap tissues that have warmed to room temperature. Chew a small portion of the cap cuticle and flesh lightly (do not swallow; edibility is unknown!) to determine the taste (e.g., bitter, raphanoid, not distinctive, farinaceous).

Measure (in millimeters) the smallest and largest specimens in each collection. Record cap diameter & height, lengths of exposed stipe and combined stipe+pseudorhiza, stipe widths at apex and broadest point, and thickness of the cartilaginous stipe rind.

Record the following key macro-characters:

**CAP** — shape, degree of viscosity, edge (inrolled or not), surface (scaly, striate), colors, bruising reactions;

**GILLS** — color when young;

**STIPE** — consistency (fragile, tough, robust), surface (matte, shiny), pith (absent but for stray fibrils, loosely fibrillose, with central channel, densely fibrillose, cottony, firm); colors of surface at the apex, mid-stipe, and 'base' (ground level);

**VEIL** — location, type (isolated fibrils, fibrillose patches, scales), color;

**PSEUDORHIZA** — intactness (retrieved almost to origin, broken off during collection), type (fleshy, cord-like, criniform, unbranched, branching);

**SYRINGALDAZINE** (see FIG-p. 126; helpful, not essential; must be used on fresh tissues in good condition) — color of cap+gill tissues, upper stipe section, and pseudorhiza recorded at 0, 15, and 30 minutes; and

**FLUORESCENCE** (helpful, not essential) — color of gills and flesh under a UV 'black-light'.

### Drying the collections

Fresh specimens are best dried on low-heat forced-air dryers, such as home food dehydrators with low temperature settings. If possible, slice specimens

lengthwise only once. Dry every phaeocollybia until 'brittle' crisp to prevent moisture hidden in denser tissues from causing the collection to mold later in storage. Highly gelatinized tissues sometimes take longer (sometimes up to 1–2 days for larger specimens) before they are completely dry.

Spore prints should be air-dried, not placed in dehydrators. After drying, unite the spore print, all labels, and specimens and store in zip-lock freezer bags. Specimens should be frozen for 48 hours immediately after drying and again two weeks later to eliminate insect infestation.

### Under the compound microscope

During one pleasant 1996 collecting expedition through California and Oregon, Egon Horak — thus far the only researcher to attempt a world monograph of *Phaeocollybia* — remarked in passing that phaeocollybias were one of those genera where it was impossible to know what species you held in your hand until you looked at it under the microscope. Unfortunately, he is correct. There are exceptions — a pristine green-capped, lavender-gilled *P. fallax* being one — but for the most part, a microscope is absolutely essential for determining a phaeocollybia to species.

Examining fresh tissues microscopically is the best way to observe clamp connections, cheilocystidia, true colors, hyphal structure — actually, almost everything. Unfortunately, phaeocollybia tissues are so gelatinous that producing a thin fresh gill section with cheilocystidia still attached to the gill edge (and not to the razor blade) requires expertise lacked by most field mycologists; too often the 'section' placed in mountant on a microscope slide tiddly-winks across the room as soon as pressure is applied to the cover slip. For that reason alone, phaeocollybias are usually sectioned dry. Examination of dried material is also necessary because historical observations were made from rehydrated tissues, probably because researchers were too busy collecting and describing collections to have time to examine their material completely under the microscope during the field season.

**FRESH MATERIAL** — Unless a freezing microtome is available, it is best to examine fresh tissues using 'squash' mounts. These are small pieces of tissue placed into a liquid ('mountant') on a glass slide beneath a cover slip that is tapped gently to 'squash' the tissue thin enough so that it is easily seen under the compound microscope. To examine pigments and

clamp connections in the cap cuticle, remove a very small 'scalp' section from the cap margin (not the disc or edge), cutting deep enough to retrieve part of the cap context. To examine cheilocystidia, place a single gill flat onto a clean smooth surface; use a thin razor blade to slice the gill along the edge to obtain a long narrow edge lined by cheilocystidia.

Always prepare mounts using a dissecting microscope (if available) to ensure that they are not too thick. Water is the preferred mountant, although some workers add a coloring agent such as phloxine to view colorless elements. Melzer's reagent, used to determine whether basidiospores are dextrinoid (dark red), is also most easily used in fresh mounts.

Fresh mounts are best for locating clamp connections, cheilocystidia, pleurocystidia, tibiiform diverticula, and pileipellis pigments. Fresh spore measurements will differ from the dimensions published here. We reluctantly use dimensions obtained from rehydrated tissues for three reasons: (i) that is what mycologists before us have done, (ii) we also have not had time to record fresh spore measurements of all PNW phaeocollybias during our hectic field seasons, and (iii) many collectors not equipped with microscopes must dry their collections before they can have them microscopically examined.

**DRIED MATERIAL** — As noted above, gelatinous phaeocollybias are more easily sectioned dry. Cap tissues should be sliced radially from disc to edge to measure hyphal lengths, find clamp connections, and determine the approximate thickness of the top, middle (when present), and bottom pileipellis layers. Gills may be sliced along the edge (as in fresh mounts) to examine cheilocystidia, but it will be necessary to section the gill from edge to 'base' to expose the hymenium and tramal alignment.

Radial sections and squash mounts may be placed directly into 3-6% KOH aqueous solution on the microscope slide to rehydrate for ~15 minutes before examination, although rehydrating tissues slowly in a moist chamber before mounting in H<sub>2</sub>O, KOH, or Melzer's is definitely preferred. Those using our keys should make all measurements in KOH.

Basidiospore measurements should be obtained from spore print spores or — when spore prints are absent — spores collected from the stipe apex to ensure that only mature spores are measured. 'Gill' spores tend to be slightly smaller (immature) and highly variable; 'cap' spores — particularly those from

highly viscid caps — can become greatly enlarged and distorted, possibly because they have begun to germinate on the viscid cap surface. A minimum of 20 spores (selected at random in profile view) should be measured per specimen; optimally every specimen in the collection should be measured to determine the median length × width measurement that will most closely correspond to the reference dimension in our key. Throughout this text, we denote the median measurement by  $|x|$ .

### Keying

We present two keys on the following pages. One is a combination macro-/micro-key that attempts to present field (macro-) characters first; the second uses only microscopical characters. As noted earlier, there is — unfortunately — no way to identify phaeocollybias to species using only field or macrocharacters (even when we classify UV fluorescence and syringaldazine as 'macro').

To keep the keys to a reasonable length, we have eliminated size ranges and so cite only the median or uppermost dimensions. Because we publish these keys in a book accompanied by complete descriptions of each species, we expect users to refer to the descriptions where there are doubts about a choice. The combination key usually offers more than one alternative, and so the user is advised to read through each doublet entirely before making a selection.

We know that the microscopical key will be difficult for most users. The senior author uses a compound microscope with Nomarski optics that is particularly helpful for looking at highly gelatinized tissues. She also has been looking at phaeocollybias for almost two decades, so that interpreting pigment topographies, knowing the difference between cheilocystidia and basidioles, and differentiating clamp connections from bubbles or sarcodimitic tissue has become second nature. The junior author, while wistful at not having differential interference contrast (Nomarski) optics on his microscope, recently acquired phase contrast, which simplified finding clamps and other pesky items. Nonetheless, the microkey should be useful to anyone having no field data when confronting an unidentified, dried, dead phaeocollybia.

We suggest recording all the data listed on the previous page and Tables 7–8 before using either key. Keys are easiest to use when 'tracked' — so write down each lead as you work, to help you locate a confused selection. We welcome suggestions and encourage frustrated users to contact us. We understand.

## Conspectus of Pacific Northwest species of *Phaeocollybia*

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<i>Phaeocollybia attenuata</i> (A.H. Sm.) Singer 1951.....	51
<i>Phaeocollybia benzokauffmanii</i> Norvell 2000 .....	57
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### SYNONYMS AND MISAPPLICATIONS

### ACCEPTED SYNONYM

<i>Naucoria attenuata</i> Smith 1937 .....	see <i>P. attenuata</i>
<i>Naucoria festiva</i> sensu Smith (1937) .....	see <i>P. fallax</i>
<i>Naucoria kauffmanii</i> Smith 1937 .....	see <i>P. kauffmanii</i>
<i>Naucoria lugubris</i> sensu Smith (1937).....	see <i>P. spadicea</i>
<i>Phaeocollybia carmanahensis</i> Redhead & Norvell 1993 .....	see <i>P. oregonensis</i>
<i>Phaeocollybia similis</i> sensu Smith (1957b), Smith & Trappe (1972) ...	see <i>P. attenuata</i>

### EXCLUDED SPECIES

- Phaeocollybia perplexa* Orton 1960  
 See *Stagnicola perplexa* (Orton) Redhead & A.H. Sm. 1986
- Phaeocollybia deceptiva* A.H. Sm. & Trappe 1972  
 Not a phaeocollybia; believed to represent an unknown species of *Cortinarius*  
 (Norvell 1998a, Norvell & Exeter 2007)

## Key to the *Phaeocollybia* species of Pacific Northwest North America

- 1a. Fruitbody small; stipe apex usually  $\leq 4$  mm across, never drab apically;  
cap usually  $\leq 50$  mm broad, orange, tawny, or yellow-brown, but never green or drab . . . . . 2
- 1b. Fruitbody medium to large; stipe apex usually  $> 5$  mm across, color varied;  
cap usually  $\geq 50$  mm broad, varied in color, including green or drab . . . . . 5
- 2a.(1) Basidiospores ellipsoid, minutely punctate ornamentation and slightly pointed apical callus  
visible under high power oil immersion; clamp connections present . . . . . 3
- 2b. Basidiospores limoniform, verrucose to warty ornamentation and protruding apical beak  
visible without oil immersion lens; clamp connections absent . . . . . 4
- 3a.(2) Spores small,  $\sim 5.8 \times 3.2 \mu\text{m}$ ; cheilocystidia thick-walled, tibiiform with narrow necks,  
abundant but inconspicuous and difficult to see; fruitbody collybioid with stipe pliable,  
not easily broken; phenology autumnal (October–December) . . . . . *P. radicata*
- 3b. Spores large,  $\sim 10.3 \times 6 \mu\text{m}$ ; cheilocystidia thin-walled, narrowly clavate, extending well  
beyond hymenium; fruitbody mycenoid with stipe fragile and easily broken;  
phenology vernal (April–May) or autumnal (October–December) . . . . . *P. phaeogaleroides*
- 4a.(2) Stipe and pseudorhiza fleshy, not shiny or brittle; cheilocystidia thick-walled, tibiiform;  
pleurocystidia similar and frequent on gill faces; spores tapering to straight beaks,  
 $\sim 9.2 \times 6 \mu\text{m}$ ; phenology vernal (February–May) . . . . . *P. pleurocystidiata*
- 4b. Stipe polished, corneous; pseudorhiza brittle and wire-like (criniform); cheilocystidia  
thin-walled, clavate; pleurocystidia absent; spores big-bellied with abruptly tilted beaks,  
 $\sim 9 \times 5.75 \mu\text{m}$ ; phenology late autumn and winter (October–January) . . . . . *P. attenuata*
- 5a.(1) Young cap green, often aging brownish olive or brown; spores limoniform . . . . . 6
- 5b. Young cap ochre, orange, tawny, brownish, or drab (never green); spore shape varied . . . . . 8
- 6a.(5) Young gills violet; spores moderately beaked, in face view fusoid or naviculate, verrucose  
to marbled,  $\sim 9 \times 5.3 \mu\text{m}$ ; cheilocystidia thin-walled, clavate with swollen to subcapitate  
heads, rarely forming filiform apical outgrowths . . . . . *P. fallax*
- 6b. Young gills creamy to yellowish buff; spores with pronounced beaks, +/- ovate in face view,  
heavily rugulose warty roughened, size varied; cheilocystidia varied . . . . . 7
- 7a.(6) Spores  $\sim 8 \times 5 \mu\text{m}$ , with long, projecting beaks;  
cheilocystidia thick-walled, tibiiform with narrow refractive necks . . . . . *P. pseudofestiva*
- 7b. Spores  $\sim 10 \times 6 \mu\text{m}$ , 'turtle-backed' with abruptly protruding eccentric refractive beaks;  
cheilocystidia thin-walled, clavate, in age often with apical filiform outgrowths . . . . . *P. olivacea*
- 8a.(5) Spores ellipsoid or limoniform, length  $|x| = < 7.5 \mu\text{m}$ ; cheilocystidia uniformly thin-walled . . . . . 9
- 8b. Spores limoniform, length  $|x| = > 7.5 \mu\text{m}$ ; cheilocystidia walls thin or thick . . . . . 13
- 9a.(8) Spores limoniform, marbled to verrucose; clamps absent; pileipellis 2- or 3-layered . . . . . 10
- 9b. Spores ellipsoid, punctate-roughened; clamps present or not; pileipellis 2-layered . . . . . 11
- 10a.(9) Fruitbody small to medium, fragile (stipe  $\leq 7$  mm & cap  $\leq 60$  mm diam); cap bald, glutinous,  
tawny to dark brown; stipe polished, drab to violet (apex); stuffed to hollow,  
often insect-infested; pileipellis 2-layered with colorless top layer, dull brownish  
bottom layer; spores  $\sim 6.9 \times 4.3 \mu\text{m}$  . . . . . *P. riffsipes*
- 10b. Fruitbody large, robust (stipe  $\leq 28$  mm & cap  $\leq 120$  mm diam); cap appressed-scaly, subviscid  
(never glutinous), ochraceous tawny to tawny; stipe matte, tan to brown, firmly stuffed,  
never insect infested; pileipellis 3-layered with yellow-orange top and bottom layers,  
colorless middle layer; spores  $\sim 7.4 \times 4.7 \mu\text{m}$  . . . . . *P. ochraceocana*

- 11a.(9) Fruitbody overall drab to gray, robust with stout firmly stuffed pink to drab stipe ( $\leq 20$  mm diam) and fleshy pseudorhiza; taste and odor cucumber-farinaceous; all tissues soon deep magenta in syringaldazine; spores  $\sim 6.8 \times 4 \mu\text{m}$  ..... *P. oregonensis*
- 11b. Fruitbody overall orange, lacking drab colors, fragile with slender hollow tan stipe ( $\leq 13$  mm diam) and cord-like pseudorhiza; taste and odor mild; cap & gills syringaldazine negative ..... 12
- 12a.(11) Clamp connections abundant; cap bright to dull orange with yellowish margin; cheilocystidia irregularly filamentous to narrowly clavate; spores  $\sim 6.7 \times 4.3 \mu\text{m}$  ..... *P. dissiliens*
- 12b. Clamp connections absent; cap uniformly brownish orange to auburn; cheilocystidia narrowly clavate with long pedicels and swollen (subcapitate) heads; spores  $\sim 6.5 \times 3.8 \mu\text{m}$  ..... *P. sipei*
- 13a.(8) Pileipellis 3-layered with colorless gelatinized middle layer between yellow to yellow-orange top and bottom layers; cap minutely scaly (appressed), dry to subviscid (never glutinous), color ochre, ochraceous tawny, or tawny (never gray- or dark brown) ..... 14
- 13b. Pileipellis 2-layered, with colorless top layer and variously pigmented lower layer; cap bald, smooth, subviscid to glutinous and never appressed scaly, colors varied ..... 15
- 14a.(13) Spores large,  $\sim 10 \times 6 \mu\text{m}$ ; cap dry to greasy, generally ochre (yellow-ochre, ochre-gold); frequently associated with *Abies* ..... *P. luteosquamulosa*
- 14b. Spores small,  $\sim 7.4 \times 4.7 \mu\text{m}$ ; cap greasy to subviscid, tawny ochraceous or tawny; associated with *Pseudotsuga* or *Tsuga* ..... *P. ochraceocana*
- 15a.(13) Cheilocystidia tibiiform, with thin-walled broad bases and narrow, refractive, thick-walled necks and capituli; stipes hollow or stuffed; clamp connections absent ..... 16
- 15b. Cheilocystidia variably cylindrical to clavate, occasionally showing filamentous apical secondary growth in older specimens, but always lacking refractive thick-walled necks; stipes stuffed with firm pith; clamp connections present or absent ..... 20
- 16a.(15) Mature stipe tubular and hollow; fruitbodies closely gregarious to fasciculate, arising from a rooting branching rhizomorphic cord; spore median  $> 8.5 \mu\text{m}$  long ..... 17
- 16b. Mature stipe stuffed with firm compact pith; fruitbodies scattered to closely gregarious, arising from unbranched fleshy (not cord-like) pseudorhizas; spore median  $< 8 \mu\text{m}$  long ..... 19
- 17a.(16) Cap heavily glutinous, acutely conic-campanulate, yellow-brown to dark-brown; stipe rind thick (2–3 mm); habit in dense fasciculate mounds; suprapellis thick, colorless, hyphae not spirally pigment-encrusted with septa obscured by thick gel matrix; spores  $\sim 8.5 \times 5 \mu\text{m}$  ..... *P. scatesiae*
- 17b. Cap moist to viscid, obtusely convex-campanulate, red orange to tawny; stipe rind varied; habit in troops, arcs, or (rarely) fasciculate mounds; suprapellis compact, amber to orange, hyphae spirally pigment-encrusted with refractive septa; spores  $\sim 9 \mu\text{m}$  long ..... 18
- 18a.(17) Stipe with thick (2–2.5 mm) rind and fibril-lined cavity; cap viscid, orange-tawny (with amber margin when young); cheilocystidia occasional to infrequent; spores  $\sim 9 \times 5.4 \mu\text{m}$  ..... *P. californica*
- 18b. Stipe with thin (1–1.5 mm) rind and hollow cavity; cap moist to subviscid, uniformly reddish to tawny orange; cheilocystidia frequent; spores  $\sim 9 \times 5 \mu\text{m}$  (but read p. 180) ..... *P. rufotubulina*
- 19a.(16) Cap tawny orange to dark orange-brown; stipe apex +/- cinnamon colored; flesh soon insect infested; cheilocystidia abundant, forming a sterile gill edge; cap, gills, and stipe rind soon magenta in syringaldazine; spores  $\sim 8 \times 4.5 \mu\text{m}$  (but read p. 204) ..... *P. tibiikauffmanii*
- 19b. Cap gray-brown to dark chestnut brown; stipe apex pallid to drab; flesh rarely insect infested; cheilocystidia frequent, intermixed with basidia along gill edge; only pseudorhiza magenta in syringaldazine; spores  $\sim 8 \times 5 \mu\text{m}$  ..... *P. spadicea*

- 20a.(15) Clamp connections frequent throughout all tissues, most easily seen at septa of the pileus suprapellis hyphae and cheilocystidia; cap convex-campanulate with an acutely pointed or often papillate umbo, tawny ochraceous to tawny; cheilocystidia cylindrical to narrowly clavate; spores  $\sim 9 \times 5.5 \mu\text{m}$  ..... *P. ammiratii*
- 20b. Clamp connections lacking or rare (then only in stipe pellis); cap shape & color, cheilocystidial shape, and spore size varied ..... 21
- 21a.(20) Young gills whitish, smoky gray, or deep violet; young caps tawny, brownish-pink or drab; cap & gills magenta in syringaldazine ..... 22
- 21b. Young gills pinkish, orangish, or yellowish; young caps varied, but rarely pink or drab; cap & gills magenta or not in syringaldazine ..... 23
- 22a.(21) Young gills intensely bluish lilac to violet; cap tawny when young, soon darkening to dark brown; pseudorhiza syringaldazine negative; taste not farinaceous; spores  $\sim 8 \times 5 \mu\text{m}$  ..... *P. lilacifolia*
- 22b. Young gills white (occasionally pinkish) or ash gray, never lilac or violet; cap pinkish, drab, or purple-brown; all tissues soon deep magenta in syringaldazine; taste 'bitter cucumber' farinaceous; spores  $\sim 9 \times 5.5 \mu\text{m}$  ..... *P. benzokauffmanii*
- 23a.(21) Cap yellow tan, usually lacking orange colors and zonate with darker banded edge, soon chestnut- or coca brown (rarely grayish or drab); young stipe ivory tan, with lower stipe staining orange with orange band at ground level; habit fasciculate, densely gregarious; young gills dark under UV; all tissues syringaldazine negative; spores moderately large,  $\sim 9.5 \times 5.7 \mu\text{m}$  ..... *P. gregaria*
- 23b. Cap orangish to tawny, when young either overall orange, red-orange, or tawny or zonate with tawny to apricot-brown disc and pale amber margin; young stipe orange, buff, or pale cinnamon, lower stipe color varied; habit solitary, scattered, or gregarious; young gills fluoresce under UV; syringaldazine reactivity and spore size varied ..... 24
- 24a.(23) Fruitbody moderately small to large; stipe slender (apex  $\leq 12$  mm diam), stuffed but soon insect-eaten at ground level; cap subviscid, uniformly bright apricot- to peach-colored, with conic umbo; all tissues negative in syringaldazine; pileipellis hyphae colorless, spirally gel-incrusted, subpellis pigments diffuse, not encrusting; spores  $\sim 9.4 \times 6 \mu\text{m}$ , beaks short ( $\leq 5 \mu\text{m}$ ), straight ..... *P. piceae*
- 24b. Fruitbody moderately large to massive; stipe robust (apex  $\leq 25$  mm diam), stuffed with firm, insect-free pith; cap viscid to glutinous, orange, tawny, or orange-/red-brown or zonate with tawny disc, amber margin, tan edge, umbo obtuse; all tissues strongly magenta in syringaldazine; pileus subpellis hyphae pigment-encrusted; spores varied in size, beaks long ( $\leq 1.5 \mu\text{m}$ ), tilted or straight ..... 25
- 25a.(24) Spores medium ( $\sim 8.5 \times 5 \mu\text{m}$ ), lemon-shaped with tilted beak; cap +/- uniformly orange, tawny, or dark orange-brown; lower stipe and pith staining first orange, then orange-brown; cheilocystidia cylindrical or narrowly to broadly clavate, rarely pedicellate and subcapitate ..... *P. kauffmanii*
- 25b. Spores large ( $\sim 10.5 \times 6 \mu\text{m}$ ), almond-shaped with long 'belly' and slightly tilted beak; young cap zonate with reddish tawny umbo, amber margin and tan edge, aging to overall tawny brown to dark red-brown; lower stipe and pith staining red-brown; cheilocystidia usually pedicellate and catenulate, subcapitate with subglobose apices ..... *P. redheadii*

## Microscopical key to western North American *Phaeocollybia* species

The key below was developed using only characters that can be seen under the microscope, particularly useful in identifying dried specimens that are not accompanied by good (or any) field notes. Brief key macrocharacters or supplementary data are noted in italics.

- 1a. Cheilocystidia primarily thick-walled, lageniform to tibiiform capitulate with narrow refractive necks ..... 2
- 1b. Cheilocystidia only thin-walled, clavate, mucronate, or broadly subcapitate (*non-refractive filamentous apical outgrowths occasional to frequent in older material*) ..... 9
- 2a. Basidiospores small ( $\sim 5.8 \times 3.2 \mu\text{m}$ ), ellipsoidal, minutely punctate; clamp connections abundant (*small, stipe  $\leq 5 \text{ mm diam}$ , cap, gills, and stipe orange to tawny*) ..... *P. radicata*
- 2b. Basidiospores larger ( $> 6.5 \mu\text{m}$  long),  $\pm$  limoniform with apical beaks; clamp connections absent ..... 3
- 3a. Pleurocystidia abundant, thick-walled tibiiform (*vernal, stipe  $\leq 5 \text{ mm diam}$ , ochraceous to tawny*) ..... *P. pleurocystidiata*
- 3b. Pleurocystidia absent to rare (*autumnal, stipe  $> 5 \text{ mm diam}$* ) ..... 4
- 4a. Pileus suprapellis faintly pigmented, hyphae spirally gel-encrusted with refractive septa; spores  $\sim 9 \mu\text{m}$  long with  $\leq 0.5 \mu\text{m}$  long beak, heavily warted; tibiiform cheilocystidial base  $\sim 2\text{--}3 \mu\text{m}$  diam ..... 5
- 4b. Pileus suprapellis colorless, hyphae smooth; spores  $\sim \leq 8.5 \mu\text{m}$  long with  $\leq 1 \mu\text{m}$  long beak, verrucose; tibiiform cheilocystidial base wider,  $\sim 3\text{--}8 \mu\text{m}$  diam ..... 6
- 5a. Suprapellis encrusting pigments colorless to pale amber; thick-walled cheilocystidia infrequent; spores  $\sim 9 \times 5.4 \mu\text{m}$ , tawny in KOH (*stipe fibrillose lined, rind 2-2.5 mm thick; cap viscid, orange tawny*) ..... *P. californica*
- 5b. Suprapellis encrusting pigments orange to dark orange brown; thick-walled cheilocystidia frequent; spores  $\sim 9 \times 5 \mu\text{m}$ , dark orange amber in KOH (*stipe tubular, rind 1-1.5 mm thick; cap at most subviscid, reddish orange*) (see also p. 180) ..... *P. rufotubulina*
- 6a.(4) Pileus subpellis orange in KOH, encrusting pigments present ..... 7
- 6b. Pileus subpellis dull brown to dull orange-brown in KOH, encrusting pigments absent ..... 8
- 7a. Gill edge sterile; tibiiform cheilocystidial base  $3\text{--}7 \mu\text{m}$  diam; pileus subpellis tawny orange to orange-brown in KOH; spores  $\sim 8 \times 4.5 \mu\text{m}$  (*large; orange to tawny cap; cinnamon stipe apex  $\leq 20 \text{ mm diam}$ , matte*) (see also p. 180) ..... *P. tibiikauffmanii*
- 7b. Gill edge partly fertile; tibiiform cheilocystidium base  $2\text{--}3 \mu\text{m}$  diam ( $\leq 5 \mu\text{m}$  above septum); pileus subpellis bright orange in KOH; spores  $\sim 8 \times 5 \mu\text{m}$  (*medium; green cap; yellow buff gills; stipe apex  $\leq 13 \text{ mm diam}$ , polished*) ..... *P. pseudofestiva*
- 8a.(6) Pileus suprapellis hyphae curled with gel matrix obscuring septa and walls; spores  $\sim 8.5 \times 5 \mu\text{m}$ , pale tawny (*stipe hollow,  $\leq 12 \text{ mm diam}$ ; pseudorhiza a single cord subtending an umbellate fascicle of fruitbodies; cap heavily glutinous, conic, yellow-/black-brown*) ..... *P. scatesiae*
- 8b. Pileus suprapellis hyphae straight with septa and walls easily seen; spores  $\sim 8 \times 5 \mu\text{m}$ , medium dark amber (*stipe stuffed,  $\leq 20 \text{ diam}$ , pseudorhiza fleshy; cap viscid, obtusely umbonate, dark chestnut to dark (drab) brown*) ..... *P. spadicea*
- 9a.(1) Basidiospores inequilaterally ellipsoidal with low, rounded apical callus, punctate-roughened ..... 10
- 9b. Basidiospores limoniform to amygdaliform with projecting apical beaks, verruculose to warty ..... 13
- 10a. Spores  $\sim 10 \times 5.8 \mu\text{m}$ ; clamp connections abundant (*fruitbody mycenoid, fragile; stipe  $\leq 4 \text{ mm diam}$ , cap tawny*) ..... *P. phaeogaleroides*
- 10b. Spores  $< 7 \mu\text{m}$  long; clamp connections present or absent ..... 11

- 11a. Clamp connections abundant; cheilocystidia filamentous to narrowly clavate; spores  $\sim 6.7 \times 4.3 \mu\text{m}$   
(*cap viscid, orange; stipe hollow, rind thick, splitting; pseudorhiza cord-like*) ..... *P. dissiliens*
- 11b. Clamp connections absent; cheilocystidia and spores varied ..... 12
- 12a. Cheilocystidia broadly clavate, filamentous apical outgrowths frequent; spores  $\sim 6.8 \times 4 \mu\text{m}$   
(*cap drab to gray brown; stipe stuffed with firm pith, pseudorhiza fleshy*) ..... *P. oregonensis*
- 12b. Cheilocystidia narrowly clavate with long pedicels and swollen (subcapitate) heads, apical  
outgrowths rare; spores  $\sim 6.5 \times 3.8 \mu\text{m}$  (*cap dark orange to auburn; stipe hollow, rind thick,*  
*splitting; pseudorhiza cord-like*) ..... *P. sipei*
- 13a.(9) Pileipellis 3-layered, top and bottom layers yellow or orange; middle layer compact, colorless ..... 14
- 13b. Pileipellis 2-layered, top layer colorless to pale amber, bottom layer pigmented ..... 15
- 14a. Spores large,  $\sim 10 \times 6 \mu\text{m}$  (*cap at most greasy, yellow-ochre to ochre-gold;*  
*usually near Abies*) ..... *P. luteosquamulosa*
- 14b. Spores small,  $\sim 7.4 \times 4.7 \mu\text{m}$  (*cap at most subviscid, ochraceous to tawny;*  
*under Pseudotsuga or Tsuga*) ..... *P. ochraceocana*
- 15a.(13) Spores  $\sim 6.9 \times 4.3 \mu\text{m}$  (*gills rosy white to violet gray; stipe polished, drab to violet;*  
*cap tawny to brown,  $\leq 60$  mm diam; pseudorhiza fleshy*) ..... *P. riffliipes*
- 15b. Spores  $\geq 7.5 \times 4.5 \mu\text{m}$  ..... 16
- 16a. Clamp connections abundant, medallion-like; cheilocystidia cylindrical to narrowly clavate;  
spores  $\sim 9 \times 5.5 \mu\text{m}$  (*cap tawny, papillate; stipe wine-flushed; pseudorhiza fleshy,*  
*unbranched*) ..... *P. ammiratii*
- 16b. Clamp connections absent to rare (then only in stipe); cheilocystidia & spores varied ..... 17
- 17a. Pileipellis hyphae roughened by gel or pigment encrustations ..... 18
- 17b. Pileipellis hyphae smooth, lacking gel and pigment encrustations ..... 21
- 18a. Suprapellis thin ( $< 50 \mu\text{m}$  thick), hyphae gel- and/or pigment-encrusted; subpellis hyphae smooth  
or gel-encrusted, pigments diffuse or intracellular ..... 19
- 18b. Suprapellis thick ( $\leq 700 \mu\text{m}$ ), hyphae smooth; subpellis hyphae finely encrusted by orange to  
orange-brown gel deposits, intraparietal and intracellular pigments also present ..... 20
- 19a. Spores  $\sim 9 \times 5.7$ , 'big-bellied' with refractive abruptly protruding long ( $\leq 2.5 \mu\text{m}$ ) beaks,  
warty-rugulose; cheilocystidia abundant, forming a densely gelatinous sterile gill edge,  
filamentous to narrowly clavate; suprapellis hyphae  $1-2 \mu\text{m}$  diam, roughened and orange-  
encrusted (*small; stipe polished, corneous; pseudorhiza criniform; cap subviscid, tawny*) ... *P. attenuata*
- 19b. Spores  $\sim 9.4 \times 6 \mu\text{m}$ , limoniform with non-refractive short ( $\leq 5 \mu\text{m}$ ) straight beaks, verruculose;  
cheilocystidia frequent, intermixed with basidia, narrowly clavate, occasionally mucronate  
or subcapitate; suprapellis hyphae  $2-4 \mu\text{m}$  diam, colorless, spirally gel-incrusted (*fruitbody*  
*medium, orange to red-orange; cap subviscid; stipe  $\leq 12$  mm diam, stuffed, often insect-eaten at*  
*ground level; pseudorhiza fleshy*) ..... *P. piceae*
- 20a.(18) Spores  $\sim 10.5 \times 6 \mu\text{m}$ , almond-shaped with long 'belly' and slightly tilted beak; cheilocystidia  
subcapitate with broad ( $6-15 \mu\text{m}$ ) subglobose heads atop long  $2-4 \mu\text{m}$  diam pedicels ;  
(*large, robust; cap viscid, tawny to red-brown; stipe stuffed; pseudorhiza fleshy*) ..... *P. redheadii*
- 20b. Spores  $\sim 8.5 \times 5 \mu\text{m}$ , lemon-shaped with tilted beak; cheilocystidia cylindrical or  
narrowly to broadly clavate, rarely pedicellate and subcapitate  
(*large, robust; cap viscid, orange to tawny; stipe stuffed; pseudorhiza fleshy*) ..... *P. kauffmanii*



- 21a.(17) Spores  $\sim 8 \times 5 \mu\text{m}$ , pale amber; subpellis drab to pale dull brown in KOH; cheilocystidia cylindrical to narrowly clavate, apical outgrowths rare (*moderately large; bluish lilac to violet young gills and stipe; young tawny cap soon dark brown; pseudorhiza fleshy*) . . . . . *P. lilacifolia*
- 21b. Spores longer,  $\sim 9\text{--}10 \mu\text{m}$ , medium to dark amber; subpellis orange to orange brown in KOH; cheilocystidia usually with broader elements, apical outgrowths present or not . . . . . 22
- 22a. Spores  $\sim 10 \times 6 \mu\text{m}$ , 'turtle-backed' with eccentric apiculus and conic,  $\sim 1 \mu\text{m}$  wide, abruptly protruding refractive beak, dark tawny, warty-rugulose roughened; mature cheilocystidia usually with abundant filiform apical outgrowths (*medium-sized; cap green to olive brown; young gills yellow-buff; stipe tan to greenish, stuffed above 'rat-tail' pseudorhizal cord*) . . . . . *P. olivacea*
- 22b. Spores smaller, almond-shaped to fusoid-naviculate with tapered non-refractive beak, medium to dark amber, verruculose to marbled; cheilocystidial apical outgrowths absent to common, rarely abundant . . . . . 23
- 23a. Cheilocystidia with swollen to subcapitate heads, filiform apical outgrowths rare; spores  $\sim 9 \times 5.3 \mu\text{m}$ , almond-shaped in profile with evenly tapered  $0.5\text{--}1.5 \mu\text{m}$  straight beak, fusoid or naviculate in face view, medium amber brown, verrucose to marbled; pileus subpellis greenish to greenish brown in  $\text{H}_2\text{O}$ , orange in KOH (*small to medium; young gills violet; cap green; stipe polished, apex drab, lower stipe orange, stuffed to hollow; pseudorhiza fleshy*) . . . . . *P. fallax*
- 23b. Cheilocystidia rarely subcapitate, filiform apical outgrowths frequent in old material; spores broader, beaks shorter, medium amber, punctate to verrucose; pileus subpellis not greenish in  $\text{H}_2\text{O}$ , rarely orange in KOH . . . . . 24
- 24a. Spores  $\sim 9 \times 5.5 \mu\text{m}$ , sublimoniform with slightly tilted  $0.5 \mu\text{m}$  beak, verruculose to verrucose; pileus subpellis hyphae with dull orange brown contents; cheilocystidia narrowly to broadly ( $\leq 7 \mu\text{m}$  diam) clavate above  $2\text{--}3 \mu\text{m}$  diam pedicels (*large; cap pinkish, drab, or purple-brown, viscid; young gills white, pinkish, or ash gray; stipe stuffed with pink to drab apex; pseudorhiza fleshy*) . . . . . *P. benzokauffmanii*
- 24b. Spores larger,  $\sim 9.5 \times 5.7 \mu\text{m}$  almond-shaped with eccentric apiculus and straight beak, punctate to verruculose; pileus subpellis hyphae colorless, pigments diffuse, intercellular, dull brownish to orangish; cheilocystidia agglutinated, difficult to isolate in rehydrated material, variably clavate to occasionally mucronate, often with an irregularly sinuate outline (*densely gregarious; large; cap yellow tan, chestnut-brown, or cocoa; pale tan stipe stuffed, staining orange with orange band at ground level; pseudorhiza possibly cord-like*) . . . . . *P. gregaria*

## Species descriptions

**DESCRIPTION DATA** — The following technical descriptions, expanded from type descriptions so as to include the variability encountered in the field, have been drawn from type descriptions and our personal observations of fresh material identified only after thorough morphological and microscopical examination. The type descriptions augmented by descriptions of specimens confirmed by restriction digests of rDNA ITS regions form the core of most descriptions.

**COLORS** — General non-standardized color names in lower case are accompanied by italicized color standard references by Ridgway (1912). Often Ridgway colors have been extrapolated from comparisons made to Munsell (1976) using conversions developed by William Cibula (pers. com., now deceased) and adapted by Norvell (1997, unpub.).

**MICROSCOPIC EXAMINATIONS AND MEASUREMENTS** — Fresh tissues were examined in H<sub>2</sub>O or Meltzer's solution; dried tissues were rehydrated in 3-6 % aqueous KOH unless otherwise noted. Median measurements, determined by measuring at least 20–30 spores per specimen in each reference collection, were used to calculate the reference dimensions so

as to exclude uninformative outliers. The median dimension for all collections (denoted by  $|x|$ ) precedes the range of medians (in parentheses) for all examined collections; non-median outliers (in parentheses) are cited within the overall range when appropriate.

**SPECIMENS EXAMINED** — Illustration plate legends provide site, collection number and herbarium for each collection shown; herbarium acronyms follow Holmgren & al. (1990), with 'PNW-MS' denoting fungal collections now deposited in the Pacific Northwest Mycology Service herbarium. Norvell collection numbers include collection dates in YYYYMMDD-# format (*e.g.* Norvell1941006-18 = *November 6, 1994*, 18th collection); collections examined by Norvell as expert taxonomist for the Northwest Forest Plan are denoted either by LN+Norvell batch number+us+batch collection number [*e.g.*, LN18us123] or LN+us+surveyor collector number [*e.g.*, LNusSL4899cal]. Exeter collection numbers are numbered sequentially according to the year. Joint Norvell & Exeter date-based collection numbers preceded by 'a' [BLM Pedee chronosequence fungal community study] and 'g' [BLM Green Peak density management study] refer to collections obtained during those ecological studies.

*Phaeocollybia ammiratii*

Young *P. ammiratii* fruitbodies characteristically have ochraceous caps and burgundy flushed stipes.  
Mary's Peak, Benton County, Oregon — PNW-MS Exeter 2007-042

***Phaeocollybia ammiratii*** Norvell 2000, Can. J. Botany 78: 1061.

MISAPPLIED — Transparency labeled as *P. kauffmanii* in Smith 1949.

ETYMOLOGY — In honor of Joe Ammirati, who first noted the *kauffmanii*-like species with clamp connections in the Pacific Northwest.

HOLOTYPE — Wildcat Mountain, Mt. Hood National Forest (Clackamas County), OR, USA.  
28 October 1994 (WTU: LLNorvell 1941028-10<sub>amm6</sub>).

*Field summary* — Moderately large, fleshy mushrooms with a farinaceous odor, brownish yellow to butterscotch colored campanulate caps, orangish cream colored young gills, wine-tinged stuffed stipes, and deeply rooting unbranched pseudorhizas. Solitary to clustered during autumn from southern British Columbia to northern California in coastal to montane coniferous or coniferous-deciduous forests.

**PILEUS** — Up to 80 (115) mm diam, conic-convex to broadly campanulate with inrolled, incurved, and then straight outer margin; surface smooth, viscid to glutinous, non-striate; when young uniformly dull ochre to pale butterscotch (near *isabella color*, *ochraceous tawny*) or zoned with red-brown disc, tawny outer margin, and pale yellow-brown edge; in age tawny overall. — **FLESH** confluent in pileus and stipe, creamy pallid. — **ODOR** farinaceous when cut. — **TASTE** cucumber-farinaceous. — **DRIED PILEUS** metallic, pale or deep orange copper.

**LAMELLAE** — Orange-cream when young, later orange buff (*antimony yellow*) but increasingly obscured by cinnamon spores.

**STIPE** — Central to eccentric, fairly rigid,  $\leq 60$  (105) mm above the ground, combined length with pseudorhiza 300+ mm; apex 6-15 (18) mm diam, occasionally swollen and ventricose when young but usually slender and  $\pm$  equal to substrate when mature; surface dry, minutely longitudinally lined, otherwise smooth with occasional detached fibrils; young apex generally concolorous with gills, in age often flushed with orange; lower stipe grading to tawny but always burgundy flushed above and below ground level; stuffed with firm, pale cream to pinkish white pith; cartilaginous cuticle 2-4 mm thick. — *DRIED STIPE* dark burgundy.

**PSEUDORHIZA** — Vertical-monopodial, continuous with stipe,  $\leq 5/6$  overall stipe length, gradually tapering to fleshy narrow straight or loosely coiled blunt origin, vinaceous to tawny overall except at pale buff to salmon origin.

**VEIL REMNANTS** — Inconspicuous, as scattered patches on aerial stipe and occasional fibrils seen on young pileus margin.

**SYRINGALDAZINE REACTIVITY** — Positive (pale to deep magenta) on pseudorhiza after 5 to 30 minutes; pileus, gills, and stipe apex usually negative.

**FLUORESCENCE** — Under UV gills fluoresce an intense pale to mustard yellow and stipe pith a strong dull orange.

**SPORE PRINT** — Pale cinnamon brown (*pinkish cinnamon*).



Lorelei Norvell

Mature tawny fruitbodies are easily mistaken for *P. kauffmanii*.

The sharp, often papillate, umbo and burgundy stains on the stipe help identify *P. ammiratii*.  
Iron Mike, Gifford Pinchot National Forest, Washington — PNW-MS LLNorvell 2051018-1

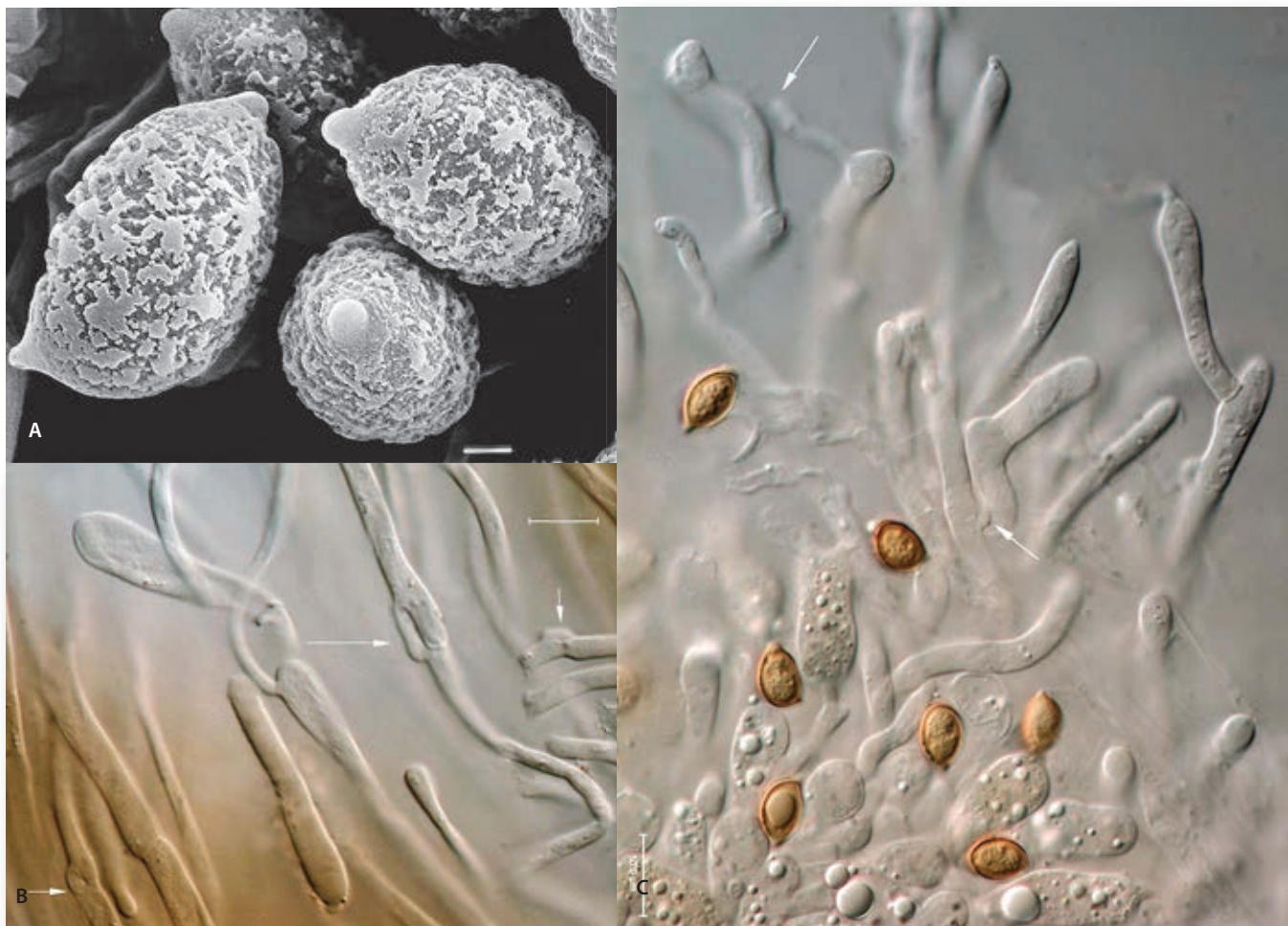
**Diagnostic characters** — Macroscopically, *P. ammiratii* can be recognized by the (1) conic viscid brownish yellow young pileus and butterscotch colored mature pileus with a straight outer edge, (2) orange-cream young gills and stipe apex, (3) deep burgundy blush over the middle stipe, and (4) cap & gills negative and pseudorhiza weakly magenta in syringaldazine.



*Phaeocollybia ammiratii*

HABIT (upper left; 1/2 actual size) — WTU HOLOTYPE Norvell 1951018-10  
Clockwise from upper right: cheilocystidia with clamps, basidia, basidiospores.

Important microscopical features detailed on the next page include (1) frequent clamp connections (best seen on the septa of the cheilocystidia and the colorless gelatinized hyphae of the pileus suprapellis), (2) large (~9 × 5.5 μm) moderately ornamented limoniform basidiospores, (3) narrow cylindrical thin-walled cheilocystidia, and (4) two-layered pileipellis lacking noticeably encrusting pigments.



Lorelei Norvell

*Phaeocollybia ammiratii* microcharacters [A—WTU Scates 5689a, B—PNW-MS Exeter2007-117, C—PNW-MS LLNorvell2071029-25].  
**BASIDIOSPORES** — The SEM micrograph (A) illustrates the limoniform shape and verruculose ornamentation common to basidiospores in the 'kauffmannii' complex. The roughened exosporium covers all but the 'snout' (callus) at spore apex and the apiculus where the spore attaches to the basidium. **CLAMP CONNECTIONS** — Photos B & C illustrate the looping clamp connections that led Joe Ammirati to refer to such puzzling 'kauffmanniis' as 'el clampo'. Clamps are most easily seen at the septa of narrow hyphae in the colorless pileus suprapellis (B) and cheilocystidia on the gill edges (C). **CHEILOCYSTIDIA** — Thin-walled narrowly clavate to cylindrical elements help diagnose the species; the top arrow in photo C points to an apical outgrowth often found in older specimens. Scales A = 1  $\mu$ m; B&C = 10  $\mu$ m.

**BASIDIOSPORES** —  $|x| = 9 \times 5.5$  [8.4-9.5(10.1)  $\times$  5-6(6.9)]  $\mu$ m, amygdaliform to limoniform with apical beak in profile, amygdaliform in face view, verruculose to verrucose except on 1-1.5  $\mu$ m long beak, pale amber (H<sub>2</sub>O) to orange-amber (KOH). — **BASIDIA** (2-)4-spored, projecting  $\leq 10$   $\mu$ m above immature hymenium, basally clamped, colorless.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, cylindrical to narrowly clavate, thin-walled, arising from the lamellar trama to form a distinct gelatinous layer, 2-5  $\mu$ m diam with apex usually only slightly swollen, lengths variable, from very short to  $>45$   $\mu$ m, often with medallion clamp connections, often developing long filamentous apical outgrowths in extreme age or after long storage, walls heavily gelatinized, usually hyaline but occasionally with pale yellowish oily contents. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelium and pseudorhizal pellis, frequent on stipe fibrillose patches,  $\leq 20 \times 1$   $\mu$ m, hyaline.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis with a thick ( $\sim 200$   $\mu$ m) colorless suprapellis of radially aligned, gelatinized, narrow (35  $\mu$ m) hyphae with medallion clamp connections overlying a subpellis with 5-12  $\mu$ m diam, thin-walled, often inflated hyphae, with intercellular and intraparietal orange pigments. — **STIPITIPELLIS** hyphal elements long ( $>200$   $\mu$ m), branched, cylindrical, highly gelatinized, thick-walled, brownish.

**TRAMAL TISSUES** — Uniformly gelatinized and hyaline; in the pseudorhiza strongly sarcodimitic with wide, thick-walled, cylindrical, rigid vessel hyphae intermixed with and supported by less conspicuous, thin-walled,



Ron Exeter

Darker mature *P. ammiratii* specimens are easily confused with *P. kauffmanii* or *P. redheadii* in the field.  
Boulder Creek TS, Polk County, Oregon — PNW-MS Exeter 2007-105

branched, flexuous hyphae; from stipe to pileus flexuous hyphae increasing in number as vessel hyphae become more narrow, thin-walled and distorted.

**CLAMP CONNECTIONS** — Frequent to abundant, medallion-like, readily visible on septa of suprapellicular hyphae and cheilocystidia, less visible but present at basidial bases; also present in tramal tissues and stipe tips.

**Ecology** — Terrestrial (mycorrhizal); solitary to clustered in autumn under conifers (*Picea*, *Tsuga*, *Abies*) or mixed conifers and angiosperms (*Pinus*, *Lithocarpus*, *Pseudotsuga*) in coastal to montane moist forests. — **PACIFIC NORTHWEST ENDEMIC** identified from ~50 localities from northwestern California to southwestern British Columbia.

**Similar species** — In the field, *P. ammiratii* could be confused with the other large brown-capped phaeocollybias with stuffed stipes: *P. kauffmanii*, *P. redheadii*, *P. luteosquamulosa*, *P. ochraceocana*, *P. gregaria*, and *P. tibiikauffmanii* and (rarely) *P. benzokauffmanii*.

*P. kauffmanii* and *P. redheadii* are usually more robust, have tightly inrolled pileus edges even when fully mature, lack the sharply papillate umbo, have a pinkish (not orange) tinge to the young gills, and have a less pronounced burgundy flush on the middle stipe.

Caps that are minutely squamulose and never viscid help separate the ochraceous *P. luteosquamulosa* or ochraceous-tawny *P. ochraceocana* from young ochre-colored forms of *P. ammiratii*.

A drab pileus, smoky white gills, and uniformly pale pink stipe usually distinguish *P. benzokauffmanii*.

Stipes frequently invaded by insect larva, lack of farinaceous odor, and densely gregarious habits help separate the golden to gray brown *P. gregaria* and orangish to orange-brown *P. tibiikauffmanii* from *P. ammiratii*.



Scott Redhead, Agriculture Canada

*Phaeocollybia ammiratii* caps become glutinous in wet weather at Barlow Pass  
Baker-Snoqualmie National Forest (Snohomish County) Washington — WTU LLNorvell1931020-02

The usually gold metallic coppery sheen of the dried pileus cuticle is distinctive to *P. ammiratii*; dried specimens of *P. gregaria*, while occasionally metallic, are generally a much duller brown.

The slow and mild reactivity of its pseudorhizal cuticle in syringaldazine separates *P. ammiratii* from *P. redheadii*, *P. benzokauffmanii*, and *P. kauffmanii*, where all tissues turn rapidly deep magenta.

Microscopically, *P. ammiratii* is easily separated from all the above species by its frequently looping clamp connections of the cheilocystidia and narrow hyphae of the pileus top layer.

See TABLE 11 (p. 96) and the species cited above for additional comparisons.

**Additional comments** — Another mushroom with clamps and large warty basidiospores, '*Phaeocollybia* *deceptiva*' A.H. Sm. & Trappe (1972), is now believed to represent an unknown species of *Cortinarius* subg. *Telamonia* (Norvell 1998a, 2000). This leaves *P. ammiratii*, *P. dissiliens*, *P. phaeogaleroides*, and *P. radicata* as the only consistently 'clamped' phaeocollybias in the Pacific Northwest.

*References with descriptions and /or illustrations of Phaeocollybia ammiratii* —

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [(as *P. ammiratii* nom. nov.) key; description pp. 138–142, 345; microdrawing & color photos pp. 228–229]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. (as *P. ammiratii* nom. nov.)
- Norvell LL. 2000. *Phaeocollybia* in western North America 1: The *Phaeocollybia kauffmanii* complex. *Can. Journ. of Botany* 78: 1055–1076. [key; type description, drawings & b&w photos, pp. 1061–1065]
- Smith AH. 1949. *Mushrooms in their natural habitats*. Sawyers, Inc., Portland. [stereoscopic color transparency of *P. 'kauffmanii'* represents *P. ammiratii*]



*Phaeocollybia attenuata*

*P. attenuata* fruitbodies showing typically scattered habit near Reese Creek  
Benton County, Oregon — PNW-MS Exeter2007-176

Ron Exeter

***Phaeocollybia attenuata*** (A. H. Sm.) Singer, *Lilloa* 22: 567. 1951.

≡ *Naucoria attenuata* A. H. Sm., *Mycologia* 29: 48. 1937.

ETYMOLOGY — From the Latin *attenuare*, meaning “to make thin” (referring to the thin stipe and thinner pseudorhiza).

HOLOTYPE — Quillayute River area near La Push (Clallam County), Washington, USA.

October 2, 1935 (MICH: A.H. Smith 3343).

MISAPPLIED — *Phaeocollybia similis* sensu Smith 1957b and Smith & Trappe 1972 (see discussion below)

*Field summary* — Small slender rooting mushrooms with moist orange-brown to tawny campanulate caps, pale violet to buff young gills, shiny cartilaginous tan stipes that darken from bases up and become hollow in age, and brownish black wire-like brittle pseudorhizas. Scattered to gregarious during autumn from southern British Columbia to northern California in coniferous forests.

**PILEUS** — Small, although occasionally reaching 50 mm diam, narrowly to broadly conic-campanulate with incurved outer margin, often with acute papillate umbo when young, moist to lubricous, glabrous, hygrophanous, edge often striatulate; color either uniformly brownish orange (*clay color, amber brown, ochraceous tawny*) or zonate with slightly darker brown disc (*warm sepia, tawny*), yellow- to orange-brown margin (*antimony yellow, clay color, snuff brown*) and paler yellow brown edge (*tawny olive*). — **FLESH** 1-2 mm thick on umbo, cartilaginous pliant, at first pallid (*cream color*), becoming duller and darker with age (*tawny olive*). — **ODOR** variably strong to not distinctive, raphanoid, slightly fishy smelling, or floral (like pansies) with complex undertones (similar to boiled potatoes or burnt hair). — **TASTE** slightly to strongly disagreeable, often bitter. — **DRIED PILEUS** matte, dark red brown.

**LAMELLAE** — Pinkish buff to lilac-colored when young, becoming moderately pinkish brown and aging to dark orange brown.

**STIPE** — Central to slightly eccentric, ≤ 70 mm above ground level, overall length (including pseudorhiza) ~220 mm long, 2-5 mm diam at the apex, equal, polished, cartilaginous when young and pale, soon corneous after darkening, initially stuffed with densely compacted to loose fibrillose pith but becoming hollow in age; at first overall pale yellowish brown (*ochraceous buff, cinnamon brown, pale pinkish cinnamon*), later gradually



Ron Exeter

Young *P. attenuata* fruitbodies near Reese Creek (left) display striatulate peaked caps and two-toned stipes. Older specimens near Trout Creek (right) show dark tawny umbonate caps and fully blackened stipes. Benton County, Oregon — PNW-MS Exeter2002-42 (left) & PNW-MS Exeter2008-109 (right)

ferruginous from ground upwards, often a narrow deep orange brown (*mikado brown*) band separating the pale yellowish brown apex from darker lower portion until entire stipe ages to dark reddish brown (*liver brown*, *Hay's russet*). — **DRIED STIPE** deep brown to black.

**PSEUDORHIZA** — Lateral-monopodial, cartilaginous upper portion continuous with the reddish brown lower stipe that gradually tapers below to a thin, brittle (criniform) brownish-black rhizomorphic pseudorhiza, wire-like portion often bending sideways below cartilaginous portion.

**VEIL REMNANTS** — Inconspicuous, evident as sparsely distributed short fibrillose patches on the stipe apex.

**SYRINGALDAZINE REACTIVITY** — Negative (no color change) on cap, gills, and stipe; positive (magenta) for wiry criniform pseudorhiza.

**FLUORESCENCE** — Young gills fluoresce brilliant yellow white to orange yellow under UV.

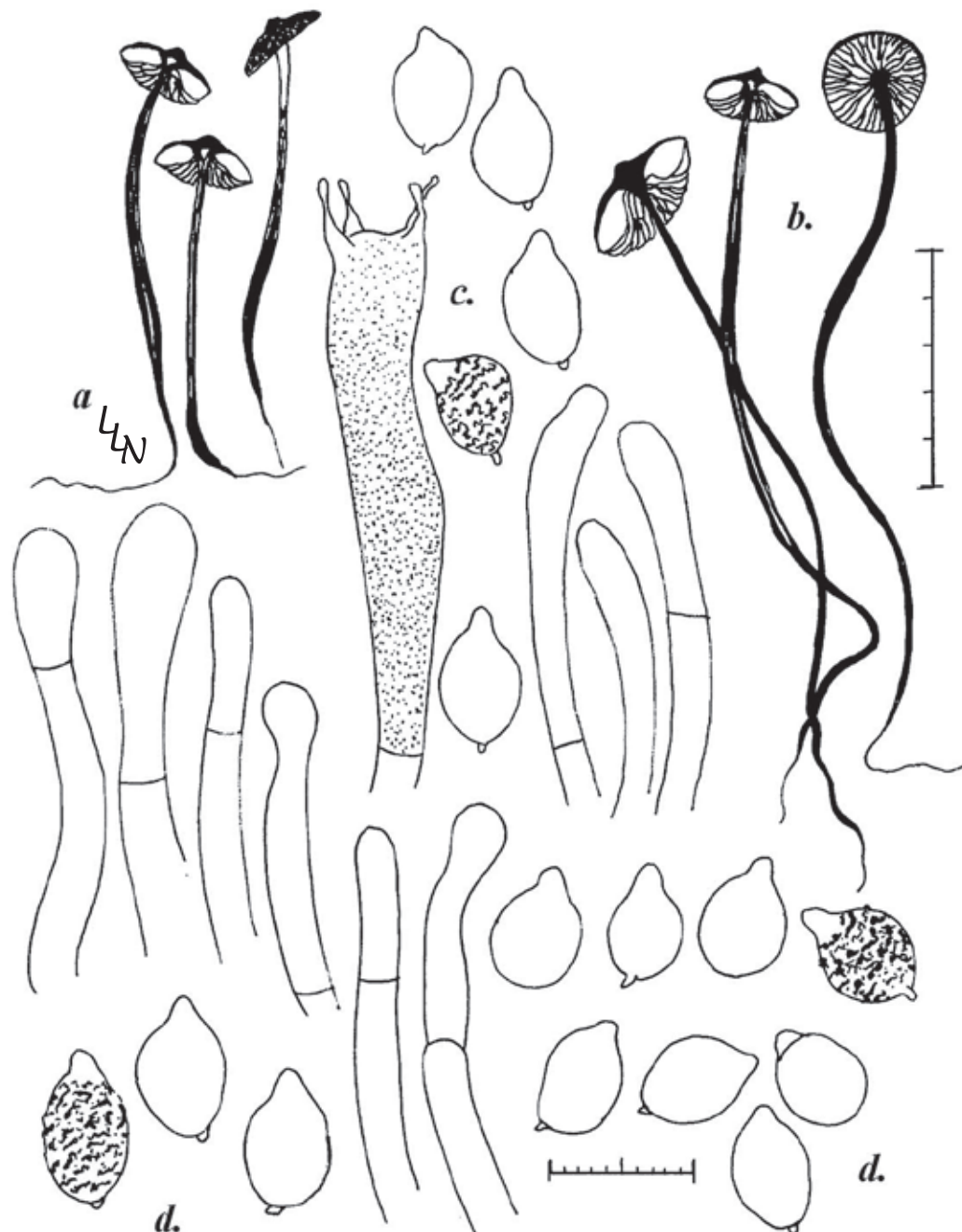
**SPORE PRINT** — Deep reddish brown (*Hay's brown*, *cameo brown*).



Elizabeth Fox (L), Lorelei Norvell (R)

Specimens from the Hoh Valley, Olympic National Park, Jefferson Co WA [left, wtU Norvell 1921015-04] & Saddlebag Mountain, Lincoln Co OR [right, PNW-MS Norvell 2071018-10] display shiny stipes that 'attenuate' (demonstrating the species name) to wiry criniform pseudorhizas.

**Diagnostic characters** — Macroscopically, *Phaeocollybia attenuata* can be recognized by its (1) small (~30–50 mm diam) cap and narrow (~5 mm diam) stem, (2) moist to subviscid brownish orange cap, (3) shiny ('corneous') tan stipe that ages dark reddish brown from the ground upwards, and (4) wiry & brittle brownish black pseudorhiza.



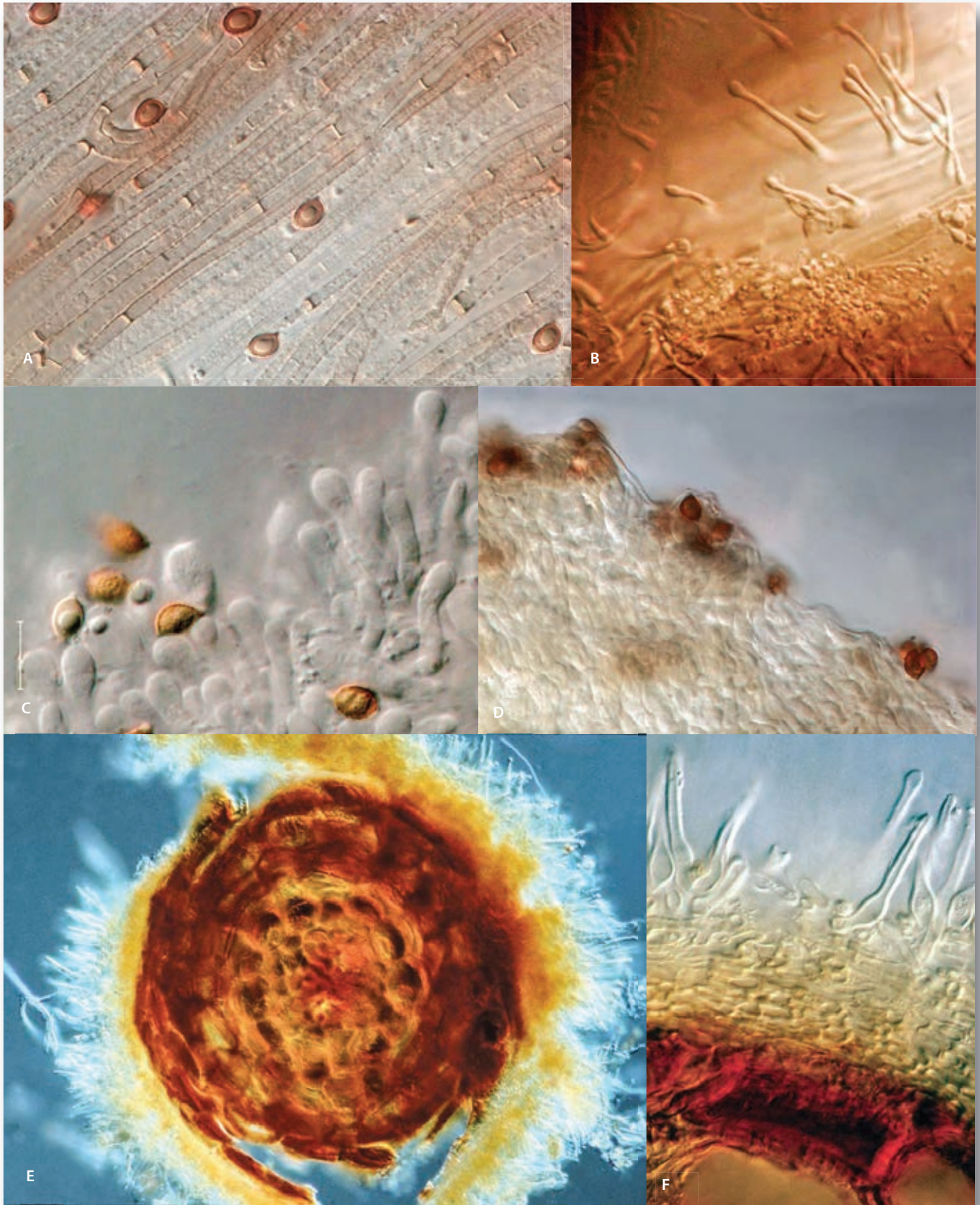
*Phaeocollybia attenuata*

A–B. HABIT. Fogarty Creek State Park, Lincoln Co., OR, wtU Norvell1951109-3 (A) & -13 (B)

C. BASIDIUM, BASIDIOSPORES & CHEILOCYSTIDIA — Cascade Head Exp. Forest, Tillamook Co, OR, wtU Norvell1941106-34

D. CHEILOCYSTIDIA & BASIDIOSPORES — La Push, Clallam Co, WA, MICH HOLOTYPE AHSmith3323

Important microscopical features detailed above and on the next page include (1) long beaked, heavily warted, broad lemon-shaped basidiospores that measure ~9 × 5.7 μm, (2) highly gelatinized, abundant, narrowly clavate cheilocystidia that usually aggregate in a gelatinous barrier along a sterile gill edge, (3) no clamp connections, and (4) a two-layered pileipellis with a thin sub-gelatinized colorless top layer above a thicker orange-brown layer.



*Phaeocollybia attenuata* — Diagnostic microscopic characters include heavily encrusting pigments on the pileus subpellis hyphae (A: OSC LNus8-166), thin-walled clavate cheilocystidia (C: PNW-MS LLNorvell2071029-1) that soon collapse into a gelatinous barrier on gill edges (D: PNW-MS Exeter2006-28), and fat, rough, beaked lemon-shaped spores (A,C). Tibiiform diverticula, diagnostic for the genus, are shown on fibrillose veil remnants from the upper stipe (B: OSC LNus11-75) and surrounding an ectomycorrhizal root tip obtained during excavation of a collection from a site near Otis, Oregon (F–G: WTU, PNW-MS LLNorvell1931104-08). Scale (c) = 10  $\mu$ m.

**BASIDIOSPORES** —  $|x| = 9 \times 5.75 \pm 0.5 \times 0.3 \mu\text{m}$  [range  $7 - 10 \times 4.5-7 \mu\text{m}$ ], subglobose-limoniform with a prominent central apical beak ( $\leq 2.5 \mu\text{m}$  wide and long) and short narrow apiculus in profile, broadly ovate to amygdaliform in face view, rugulose-warty except over the smooth apiculus and beak, the warts dark brown against a tawny ground (KOH) to paler ( $\text{H}_2\text{O}$ ). — **BASIDIA** 4-spored;  $25-35 \times 5-7 \mu\text{m}$ , colorless.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, but in mounts often collapsed together in an agglutinated barrier, filamentous to narrowly clavate, variable in length (usually  $20-30 \mu\text{m}$  long),  $2.5-3 \mu\text{m}$  diam. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelia and primordial and pseudorhizal pelli, frequent on vestiges of pellicular veil on stipe apex, rarely present on pileipellis.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis with a thin ( $25-50 \mu\text{m}$ ) suprapellis composed of radially aligned, long ( $40-60 \mu\text{m}$ ), narrow ( $1-2 \mu\text{m}$ ), gel-incrusted, colorless to pale orange-yellow hyphae overlying a much thicker ( $100-300 \mu\text{m}$ ) pale to dark orange-brown subpellis of inflated ( $4-8 \mu\text{m}$  wide) subgelatinous hyphae with intraparietal pigments. — **STIPITIPELLIS** composed of moderately wide ( $5-9 \mu\text{m}$  diam) highly gelatinized hyphae, pale orange brown near apex in young specimens but becoming increasingly darker orange brown toward rhizomorphic portion; pigments intraparietal.

**TRAMAL TISSUES** — Subgelatinized to gelatinized, strongly sarcodimitic in the pseudorhiza where wide ( $\leq 20 \mu\text{m}$ ), thick-walled ( $\leq 3 \mu\text{m}$ ), rigid hyphae are surrounded by numerous less conspicuous, thin-walled, branched, colorless flexuous hyphae, the rigid elements narrowing and becoming less thick-walled toward the base of the stipe and also present in the pileus as interwoven inflated ( $6-10 \mu\text{m}$  diam) gelatinized hyphae with slightly thickened walls. — **LAMELLAR TRAMA** subparallel, with central  $2.5-4 \mu\text{m}$  diam hyaline hyphae continuous with cheilocystidia and two to three outermost  $1-2.5 \mu\text{m}$  diam yellowish hyphae giving rise to a rudimentary subhymenium.

**CLAMP CONNECTIONS** — Absent.

**Ecology** — Terrestrial (mycorrhizal). Scattered to closely gregarious from mid to late autumn in highly humic soils in moist coniferous (*Picea sitchensis*, *Tsuga heterophylla*, *Abies*, *Pseudotsuga menziesii*) or mixed (*Sequoia*, *Tsuga heterophylla*, *Lithocarpus*) forests. — **PACIFIC NORTHWEST ENDEMIC** ~80 existing localities known west of the Cascade and Sierras Mountains from northern California to southern British Columbia; recorded most frequently from Oregon coastal forests.

**Similar species** — Small fruitbody size, tawny to 'clay' cap colors, and slender stipes separate *P. attenuata* from most other Pacific Northwest phaeocollybias except *P. radicata*, *P. pleurocystidiata*, and *P. phaeogaleroides*.

*Phaeocollybia radicata* differs by its brighter yellow-orange cap, less corneous stipe, lack of brittle wiry pseudorhiza, much smaller ( $\sim 5.8 \times 3.2 \mu\text{m}$ ) and almost smooth ellipsoid basidiospores, thick-walled lageniform or tibiiform cheilocystidia, and clamp connections.

*P. pleurocystidiata*, which fruits only in spring, is distinguished by its ochraceous conic-convex cap, and a slender but fleshy stipe that narrows to a non-criniform pseudorhiza. Its abundant thick-walled capitulate pleurocystidia and cheilocystidia and narrower more elongate basidiospores are microscopically diagnostic.

*P. phaeogaleroides*, which fruits in both autumn and spring, differs from *P. attenuata* in its more fragile and easily broken stipe, flexible and non-wiry pseudorhiza, larger ( $\sim 10 \times 5.8 \mu\text{m}$ ) finely punctate ellipsoid spores, and clamp connections.

Other species (e.g., *P. dissiliens*, *P. piceae*, *P. sipei*) that might be confused with *P. attenuata* in the field are more robust and have broader stipes. *P. dissiliens* and *P. sipei* have smaller and far less roughened ellipsoidal spores ( $\sim 7 \times 4 \mu\text{m}$ ), and *P. dissiliens* has abundant clamps. *P. piceae* has a consistently stuffed non-corneous stipe (with pith that is usually insect-infested at ground level) and less ornamented basidiospores with shorter, less prominent beaks.

**Additional comments** — Smith (1957b) and Smith & Trappe (1972) applied the name *P. similis* (proposed by Bresadola in 1930 for a Chinese species) to attenuata-like collections with longer, broader spores and a tendency to turn ferruginous (rusty brown) with age. Horak's (1977) comparison of Smith's material to Bresadola's holotype showed that the North American specimens did not represent the Chinese taxon. Nonetheless, preliminary molecular analyses (Norvell 1998a) divided sampled collections into two groups based on a 20 base pair length mutation in the rDNA ITS region, thus implying that there is a cryptic species closely related to *P. attenuata*. Subtle differences uniting the 'cryptic' group include a slightly smaller fruitbody, a brownish yellow to rusty brown cap with relatively low, broad umbo, young gills lacking blue



Ron Exeter

*Phaeocollybia attenuata* in situ on Old Blue Mountain, near Mary's Peak  
Benton County, Oregon — PNW-MS Exeter2007-134

tinges, a slightly more highly pigmented suprapellis & less highly pigmented subpellis, and cheilocystidia with dense oily amber contents. Ecology may prove helpful, as the preliminary DNA data divided samples with an '*attenuata*' DNA profile into one group collected from five Washington, Oregon, and California coastal forests and those with a different profile into another group collected from four British Columbia and Washington montane forests; unfortunately the 'montane' group also contained an interloper sampled from the same Oregon coastal forest that produced a collection with an '*attenuata*' DNA profile.

For the time being, we refer both groups to *P. attenuata*, preferring to wait for complete DNA sequence analyses and morphological reevaluations before naming a new species.

*References with descriptions and /or illustrations of Phaeocollybia attenuata —*

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- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. Sydowia 29: 28-70. [keys; *attenuata*: microdrawing p. 58; *similis*: microdrawings pp. 39a-e (with drawing of basidiome), 59]
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim. University of Washington PhD dissertation, Seattle. [key; pp. 15-19, 97, 142-145, 346-347; drawings and color photo pp. 230-231]
- Norvell LL. 1998b. Observations on the development, morphology, and biology of *Phaeocollybia*. Mycological Research 102: 615-630. [b&w drawing, photos p. 620-621]
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- Smith AH. 1957. A contribution toward a monograph of *Phaeocollybia*. Brittonia 9: 195-217. [key; *attenuata*: microdrawings p. 201, descr. pp. 206-7, b&w photo pl. 4; '*similis*': descr. pp. 207-8, microdrawings p. 210; b&w photo p. ]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. Mycologia. 64: 1141-1142 [Revised key].

*Phaeocollybia benzokauffmanii*

*P. benzokauffmanii* type collection in situ in Van Damme State Park  
Mendocino County, California — WTU HOLOTYPE (DAOM & PNW-MS ISOTYPES) LLNorvell1921120-05

***Phaeocollybia benzokauffmanii*** Norvell 2000, Can. J. Botany 78: 1065

ETYMOLOGY — From benzo- (for the color of the pileus, Ridgway *benzo brown*) + *kauffmanii* (a closely related species).

HOLOTYPE — Van Damme State Park (Mendocino County), CA, USA

20 November 1992 (WTU HOLOTYPE LLNorvell 1921120-01<sub>ben1</sub>).

*Field summary* — Medium to large fleshy mushrooms with pinkish to purplish brown, umbonate, glutinous caps, pale pinkish young gills, stuffed pink to drab stipes, and deeply rooting, unbranched fleshy pseudorhizas. Solitary, in small groups, or gregarious in autumn from northern Washington to northern California in coastal or montane coniferous or mixed forests.

PILEUS — up to 145 mm diam, convex to plano-umbonate with broad umbo, margin incurved and edge strongly inrolled at all times, surface smooth, heavily glutinous, non-striate; color either overall a mixture of pinkish to purplish brown (*benzo brown*, *wood brown*, (*cinnamon*) *drab*) or zoned with a dark disc, paler margin, and even paler drab (*light drab*) edge; in age frequently developing blackish spots and patches. —*FLESH* firm, confluent through stipe and pileus ( $\leq 11$  mm thick in disc), color purple-/pink-white (*light cinnamon drab*, *pale pinkish buff*); darker (*drab*) when water-soaked and often with a dark drab band next to the lamellae. —*ODOR* slightly floral or sweetly farinaceous. —*TASTE* 'bitter cucumber' farinaceous. —*DRIED PILEUS* blackish brown overall or dull winy to maroon metallic with blackish umbo.

LAMELLAE — White to pale pink or ash gray with violet tinges when very young, developing smoky drab tones before aging to dark yellowish gray.



Elizabeth Fox, Agriculture Canada

*Phaeocollybia benzokauffmanii* excavation [Rugged Ridge Trail, Olympic National Park, Clallam Co Washington, WTU, DAOM, PNW-MS LLNorvell 1921023-05]. Excavation sequence showing emergent fruitbodies (LEFT), partially excavated specimens arising from bleached granular soil ('albic' horizon; CENTER), and a detail of pseudorhizal origins and primordium arising from amorphous fungal mass (RIGHT).



Elizabeth Fox, Agriculture Canada

Excavated mature *P. benzokauffmanii* specimens from Rugged Ridge Trail (at top of page) photographed prior to microscopical examination and final processing.

**STIPE** — Central to slightly eccentric, rigid,  $\leq 35\text{--}100$  mm above the ground, combined length with pseudorhiza  $\leq 250$  mm; apex 7–30 mm diam, equal, slightly tapering, or ventricose and expanding to 42 mm diam at ground level; surface dry, minutely longitudinally lined, appressed fibrillose (hand lens) or with scattered purplish-brown fibrillose patches; apex pale pink to purple-gray (*buff pink*, (*light cinnamon drab*, *vinaceous fawn*), lower stipe grading to deep purple- or red-brown (*benzo brown*, *liver brown*); stuffed with firm, pallid pith, staining dark brown where bruised; cartilaginous cuticle 2–3 mm thick, occasionally splitting lengthwise to reveal proliferating pith.

**PSEUDORHIZA** — Vertical-monopodial, continuous with stipe, generally  $\leq 2/3$  overall stipe length, gradually tapering to a fleshy blunt or loosely curled origin, deep red-brown overall or paler at the origin.

**VEIL REMNANTS** — Inconspicuous, present as fibrillose patches on aerial stipe.

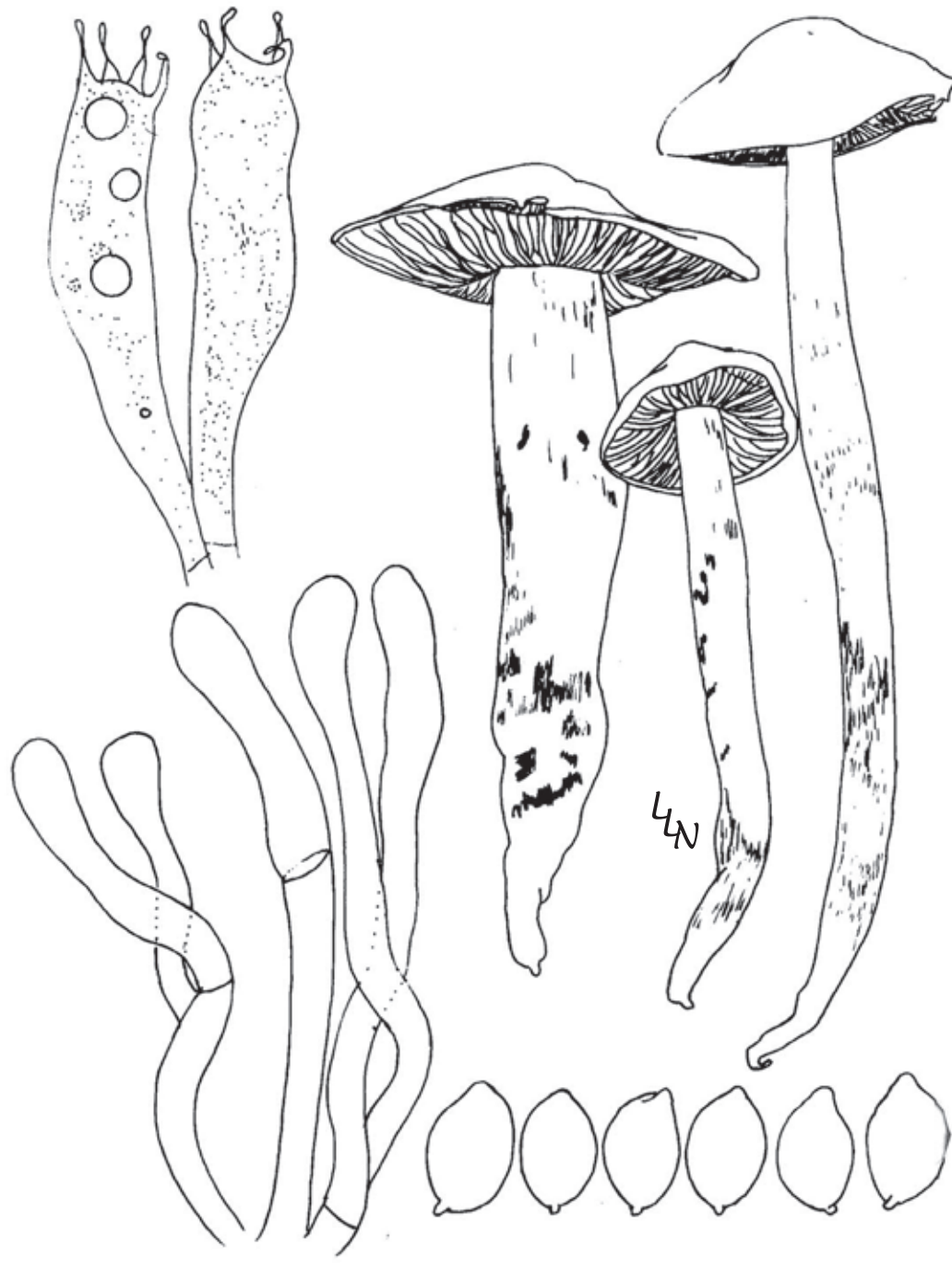
**SYRINGALDAZINE REACTIVITY** — Strong: gill, cap, stipe, and pseudorhizal tissues all soon deep magenta.

**FLUORESCENCE** — Under UV gills fluoresce brilliant pale yellow to whitish yellow.

**SPORE PRINT** — Pale purplish to dull yellowish brown (*drab*, *buckthorn brown*).



**Diagnostic characters** — Macroscopically, *P. benzokauffmanii* can be recognized by its (1) drab to pinkish brown coloration, (2) medium to large size, (3) heavily glutinous cap with incurved outer margin and inrolled edge, (4) pale pink to violaceous white gills, (5) stipe stuffed with firm solid pith, and (6) brownish black to dull maroon dried pileus.

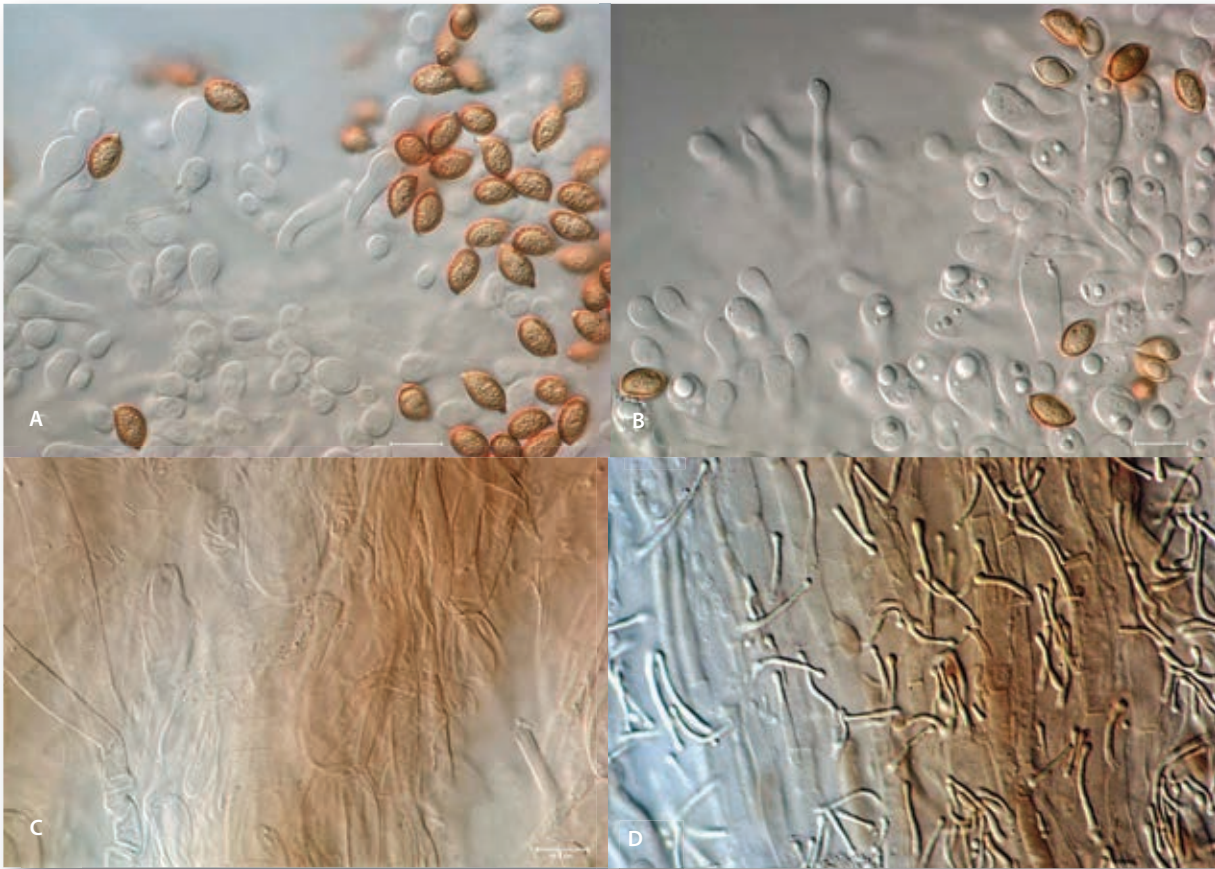


*Phaeocollybia benzokauffmanii*

HABIT. Robust (center, WTU Norvell1921120-1, HOLOTYPE) and slender (right, WTU Norvell1921023-5) forms.

MICROSCOPIC FEATURES: Limoniform basidiospores, narrowly clavate thin-walled cheilocystidia & basidia (HOLOTYPE).

Important microscopical features detailed on the next page include (1) moderately large (~9 x 5.5  $\mu\text{m}$ ) moderately ornamented limoniform basidiospores, (2) thin-walled clavate cheilocystidia, (3) absence of clamp connections, and (4) a two-layered pileipellis with the top-layer hyphae tightly compacted within a dense gelatinous matrix overlying a dull orange brown lower layer.



Lorelei Norvell

*Phaeocollybia benzokauffmanii*. A–B: BASIDIOSPORES & CHEILOCYSTIDIA [A—PNW-MS Exeter2007-013, B—OSC LNus17b78]. These roughened, sublimoniform ‘beaked’ spores are slightly longer than those in the closely related *P. kauffmanii*; apices of the thin-walled clavate elements vary from cylindrical or slightly inflated to almost subcapitate. C: PILEIPELLIS [OSC LNus17b127]: The pileus subpellis (shown here) contains diffuse intracellular pigments and lies under a highly gelatinized, colorless suprapellis. D. TIBIFORM DIVERTICULA [WTU HOLOTYPE LLNorvell1921120-9]: Abundant on remnant primordial sheath fibrils readily found on the stipe apex, tiny capitate refractive processes are best seen under high magnification in oil. Scales = 10  $\mu$ m.

**BASIDIOSPORES** —  $|x| = 9 \times 5.5 [8-10.6 \times 4.8-6.2]$   $\mu$ m, sub-limoniform in profile, fusoid-elliptical in face view, verruculose to verrucose except on 0.5  $\mu$ m long beak and eccentric apiculus, pale amber (H<sub>2</sub>O) to medium amber (KOH), dextrinoid in Melzer’s. —**BASIDIA** 4-spored, clavate above long, 2  $\mu$ m-wide pedicel, projecting  $\leq 5$   $\mu$ m above young hymenium, granular to vacuolate, colorless.

**CYSTIDIAL ELEMENTS** —**CHEILOCYSTIDIA** abundant, thin-walled, colorless; forming a dense, highly gelatinous layer (unpigmented gill edge visible to the naked eye), narrowly and broadly clavate elements intermixed, apices generally 3  $\mu$ m (young) to 5-7  $\mu$ m (mature) diam, pedicels variable in length and 2-3  $\mu$ m in diameter; long filamentous apical outgrowths frequent in very old or stored specimens. —**PLEUROCYSTIDIA** absent. —**TIBIFORM DIVERTICULA** abundant on mycelia and surfaces of primordia and pseudorhizas, also frequent on fibrillose stipe patches,  $\leq 20 \times 1$   $\mu$ m, colorless.

**CORTICAL TISSUES** —**PILEIPELLIS** a bilaminate ixocutis; the top 100–300  $\mu$ m thick suprapellis of radially aligned, sparingly branched, narrow (3–6  $\mu$ m), highly gelatinized colorless hyphae tightly compacted in a thick gelatinous matrix; the bottom 50–100  $\mu$ m thick subpellis with slightly thick-walled, 5–8  $\mu$ m diam, heavily gelatinized hyphae and dull orange brown intracellular pigments. —**STIPITYPELLIS** 70–150  $\mu$ m thick, hyphae parallel, sparingly branched, long and cylindrical, narrow (2–3  $\mu$ m), thick-walled, highly gelatinized, colorless to dark brown with refractive septa.

**TRAMAL TISSUES** — Highly gelatinized, colorless; in pseudorhiza and lower stipe strongly sarcodimitic: thick-walled ( $\leq 2$   $\mu$ m), wide ( $\leq 30$   $\mu$ m), slightly fusoid, rigid vessel hyphal elements intermixed with less conspicuous, highly branched, thin-walled (0.5  $\mu$ m), narrow (2–4  $\mu$ m), flexuous hyphal elements; in stipe apex flexuous hyphae dominate and widen ( $\leq 6$   $\mu$ m) and vessel hyphal walls thin to  $< 1$   $\mu$ m and diameters narrow; vessel hyphae absent in the pileus.

**CLAMP CONNECTIONS** — Absent in all tissues.



COMPARISON OF *P. BENZOKAUFFMANII* WITH SIMILAR SPECIES. A. ['Oz' (Polk Co) OR: PNW-MS a2061114o1-L(L) & -I(R)] — Two waterlogged *P. riffliipes* specimens with conic, tawny-tinged caps, lilac-tinged gills, and drab stipes (left) propped next to one young *P. benzokauffmanii* with convex, drab cap, whitish gills, and pale pink stipe (right). B. [Saddlebag Mtn (Lincoln Co) OR: PNW-MS LLNorvell2071018-8(L) & -7(R)] — *P. lilacifolia* with lilac gills and thin-fleshed cap (left) compared to *P. benzokauffmanii* with whitish gills and thick-fleshed cap (right).

**Ecology** — Terrestrial (mycorrhizal); solitary or scattered in small groups to gregarious, during autumn under conifers (*Abies*, *Tsuga*, *Pseudotsuga*) or mixed (*Pinus*, *Lithocarpus*) coastal to montane moist forests.

—PACIFIC NORTHWEST ENDEMIC collected from ~35 localities from northwestern California to northern Washington. (A slender stature and solitary to scattered habit common in the coniferous montane forests of Washington and Oregon contrasts with a robust stature and more gregarious habit in the mixed *Pinus*–*Lithocarpus* coastal forests of California.)

**Similar species** — *P. oregonensis* fruitbodies also are fairly robust and possess a drab pileus, smoky white young gills, consistently stuffed pale pink stipe, monopodial pseudorhizas, tissues that turn rapidly magenta in syringaldazine, and thin-walled clavate cheilocystidia. This species can be differentiated from *P. benzokauffmanii* in the field by the sharply conic to peaked campanulate cap with an edge that is straight (or only slightly incurved) when mature and colors that are generally less violaceous and more gray in tone. Microscopically, *P. oregonensis* is easily diagnosed by its much smaller ( $\sim 6.8 \times 4 \mu\text{m}$ ), almost smooth, ellipsoidal basidiospores.

*P. gregaria* produces similarly sized and shaped basidiospores and also lacks clamp connections. Earlier statements that 'only' *P. gregaria* is both macro- and microscopically close to *P. benzokauffmanii* (Norvell 1998a & 2000) were written before we had seen fresh young *P. gregaria* specimens. Immature *P. gregaria* basidiomes are golden brown, developing drab overtones only in age. Additionally, they fruit in tightly gregarious patches, never taste bitter or farinaceous, possess less firm and more pliant flesh and lower stipes that stain orange, and only the pseudorhizas turn slightly to moderately magenta in syringaldazine.

*P. lilacifolia* occasionally rivals *P. benzokauffmanii* in size but can be differentiated in the field by its conic-campanulate tawny to brown pileus and bright lilac gills. Its basidiospores are smaller ( $\sim 8 \times 5 \mu\text{m}$ ), less regularly ornamented, and more fusoid in shape.

Three other species in the region may exhibit drab to violaceous colors on gills and/or stipe. A mature *P. fallax* fruitbody that has lost its green cap color but retains its drab gills and upper stipe might be mistaken for a



*Phaeocollybia benzokauffmanii* drying in situ at Ipsut Creek (Mt. Rainier Park)  
Pierce County, Washington— wtu LLNorvell1930924-01

Scott Redhead, Agriculture Canada

small *P. benzokauffmanii*; smaller ( $\sim 8 \times 5 \mu\text{m}$ ) spores and the shiny, frequently hollow stipes will differentiate *P. fallax*. Small size, a tawny to dark brown pileus, and considerably smaller ( $\sim 7 \times 4.5 \mu\text{m}$ ) basidiospores distinguish the violet gilled, drab stiped *P. rifflipes*. Although *P. rufotubulina* specimens may have violet tinged stipes, the vivid orange-red fruitbodies with hollow stipes, racemose pseudorhizas, heavily ornamented spores, and thick-walled cheilocystidia are unlikely to be mistaken for the more massive and drab *P. benzokauffmanii*.

See TABLE 11 (p. 96) and species listed above for additional comparisons.

**Additional comments** — Due to its large size, prior to its naming, *Phaeocollybia benzokauffmanii* was usually referred to *P. kauffmanii*, a species with which it shares many microscopic features. *P. benzokauffmanii* lacks the orange colors in the pileus, produces slightly longer and broader basidiospores, and its pileipellis possesses a thinner, more compact pileus suprapellis and lacks encrusting pigments in the subpellis. Somewhat oddly, while *P. benzokauffmanii* specimens from California are generally far more massive than *P. kauffmanii* from the same vicinity, to the north this size discrepancy is reversed, with *P. kauffmanii* generally larger and more robust. The difference in coloration and the tendency of *P. benzokauffmanii* cap edges to remain more tightly inrolled help separate the two species in the field.

**References with descriptions and /or illustrations of *Phaeocollybia benzokauffmanii* —**

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (Agaricales, Cortinariaceae). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [(as *P. benzokauffmanii* nom. nov.) key; description pp. 146–150, 347; microdrawing & color photos pp. 33, 232–233]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. Mycol. Res. 102: 615–630. (as *P. benzokauffmanii* nom. nov.)
- Norvell LL. 2000. *Phaeocollybia* in western North America 1: The *Phaeocollybia kauffmanii* complex. Can. Journ. of Botany 78: 1055–1076. [key; type description, drawings & b&w photos, pp. 1065–68]
- Norvell LL, Exeter RL. 2007. *Phaeocollybia* in western North America 5: *P. ochraceocana* sp. nov. and the *P. kauffmanii* complex. Mycotaxon 102: 315–332. [key, comparison table]

*Phaeocollybia californica*

*Phaeocollybia californica* in situ at Blue Gulch  
Josephine County, Oregon—osc SLoring 4564 (LLNus7-3)

***Phaeocollybia californica*** A. H. Sm. 1957, Brittonia 9: 216.

ETYMOLOGY — From California, the state from which the species was first described.

HOLOTYPE — Crescent City, (Del Norte County), CA, USA.

23 November 1956 (MICH: AHSmith 55610).

*Field summary* — Medium-sized mushrooms with broadly campanulate yellowish brown to tawny viscid caps, pallid to pale buff gills, smooth, polished, hollow orange tan stipes with thick cartilaginous rinds, and umbellate rhizomorphic pseudorhizas. Fasciculate or gregarious in arcs in autumn from northern California and Oregon coastal coniferous (hemlock, Douglas-fir, true fir) or mixed (oak, madrone, hemlock, Douglas-fir, true fir) forests.

PILEUS — Usually 30–50 mm,  $\leq 80$  (105) mm diam, conic when young, soon campanulate with low, broad (papillate) umbo, inner margin usually downturned, outer margin sometimes strongly uplifted in age, edge inrolled when young to slightly incurved in age; surface smooth, viscid, hygrophanous and faintly striatulate; color yellowish brown to tawny orange (*amber brown*, *ochraceous orange*) when young, aging to uniformly butterscotch to dull reddish brown (*cinnamon brown*). — *FLESH* pallid in central disc, elsewhere cartilaginous and concolorous with cuticle, staining reddish when bruised or cut. — *ODOR* vaguely like ‘wild carrot’; pungent and chlorine-like when old. — *TASTE* not distinctive to slightly bitter, radish-like, or tart.  
*DRIED PILEUS* — metallic: brassy to reddish copper.

LAMELLAE — Initially whitish to pale orange buff, cinnamon-colored when mature, aging to rusty brown.



Lorelei Norvell

Technical photo (scale in millimeters) of a *P. californica* collection from Reese Creek Benton County, Oregon — PNW-MS Exeter 2007-177

**STIPE** — More or less central,  $\leq 90$  mm above ground level, combined length with pseudorhiza  $>200$  mm; apex 6–15 mm diam, equal, although sometimes swollen above ground level; surface polished beneath orange fibrillose patches; apex color at first watery tan to pale pinkish brown (*pale ochraceous salmon, cinnamon*), later becoming ferruginous from base up; soon hollow, with thick (2–3 mm) cartilaginous cortex surrounding central cavity lined with whitish long fibrils below solid pileus context.

**PSEUDORHIZA** — Rhizomorphic: arising from umbellate fascicles connected underground by long narrow thread-like cords ('mother rhizomorphs'); dark liver brown.

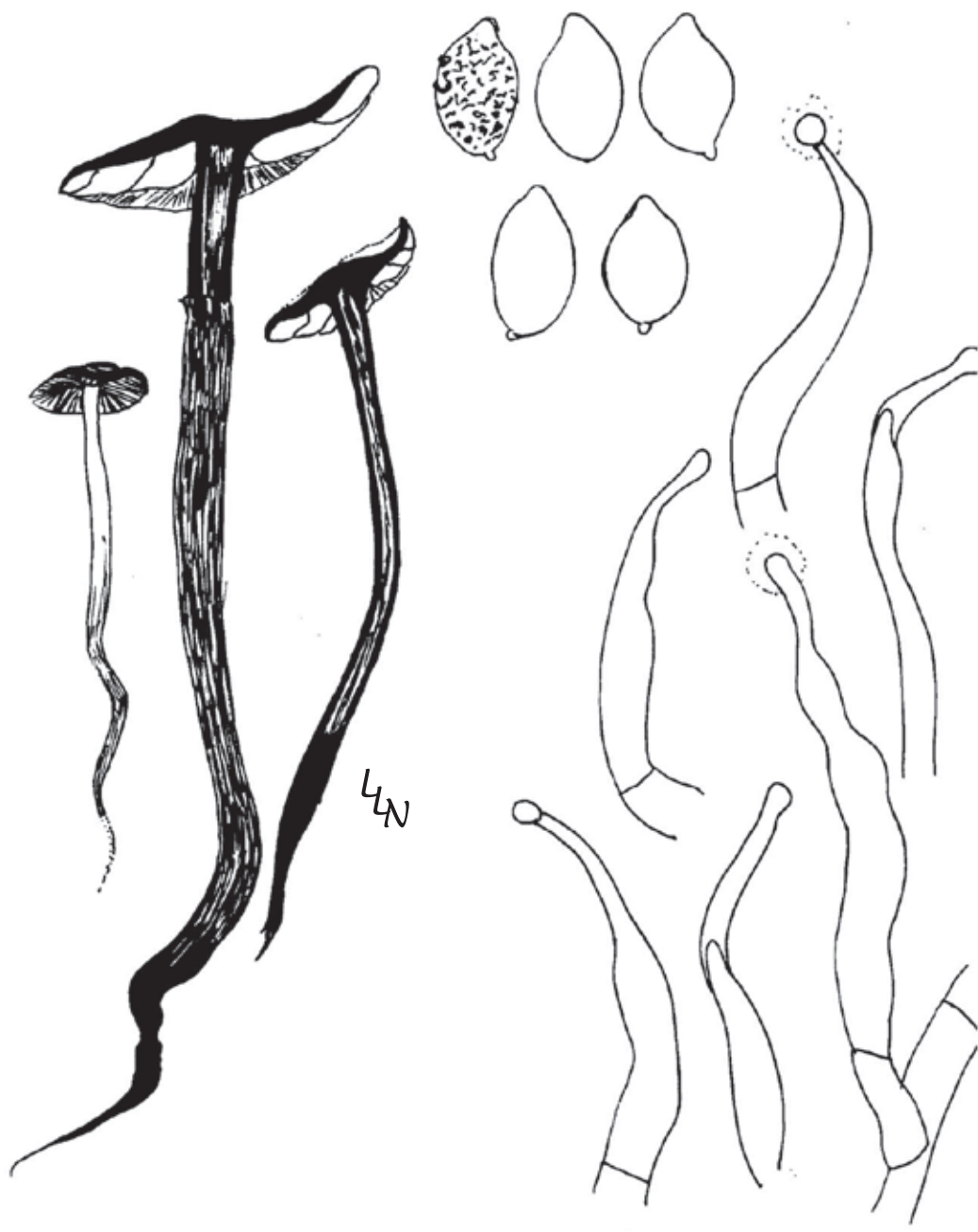
**VEIL REMNANTS** — Inconspicuous, seen as sparse reddish fibrils or fibrillose patches on stipe apex.

**SYRINGALDAZINE REACTIVITY** — Pseudorhiza immediately magenta; cap & gills variable, with gills from one population turning deep within 5 minutes but elsewhere inert (age of specimens important).

**FLUORESCENCE** — Young pileus margin and gills brilliant mustard yellow.

**SPORE PRINT** — Reddish brown (*sayal brown*).

**Diagnostic characters** — Macroscopically, *P. californica* can be recognized by its (1) medium size, slender aspect, and closely clustered to fasciculate habit, (2) broadly campanulate, viscid brownish-orange cap, (3) hollow stipe with thick cartilaginous rind, (4) stipe apex diameter averaging 5-10 mm, (5) young gills that sometimes turn magenta in syringaldazine.

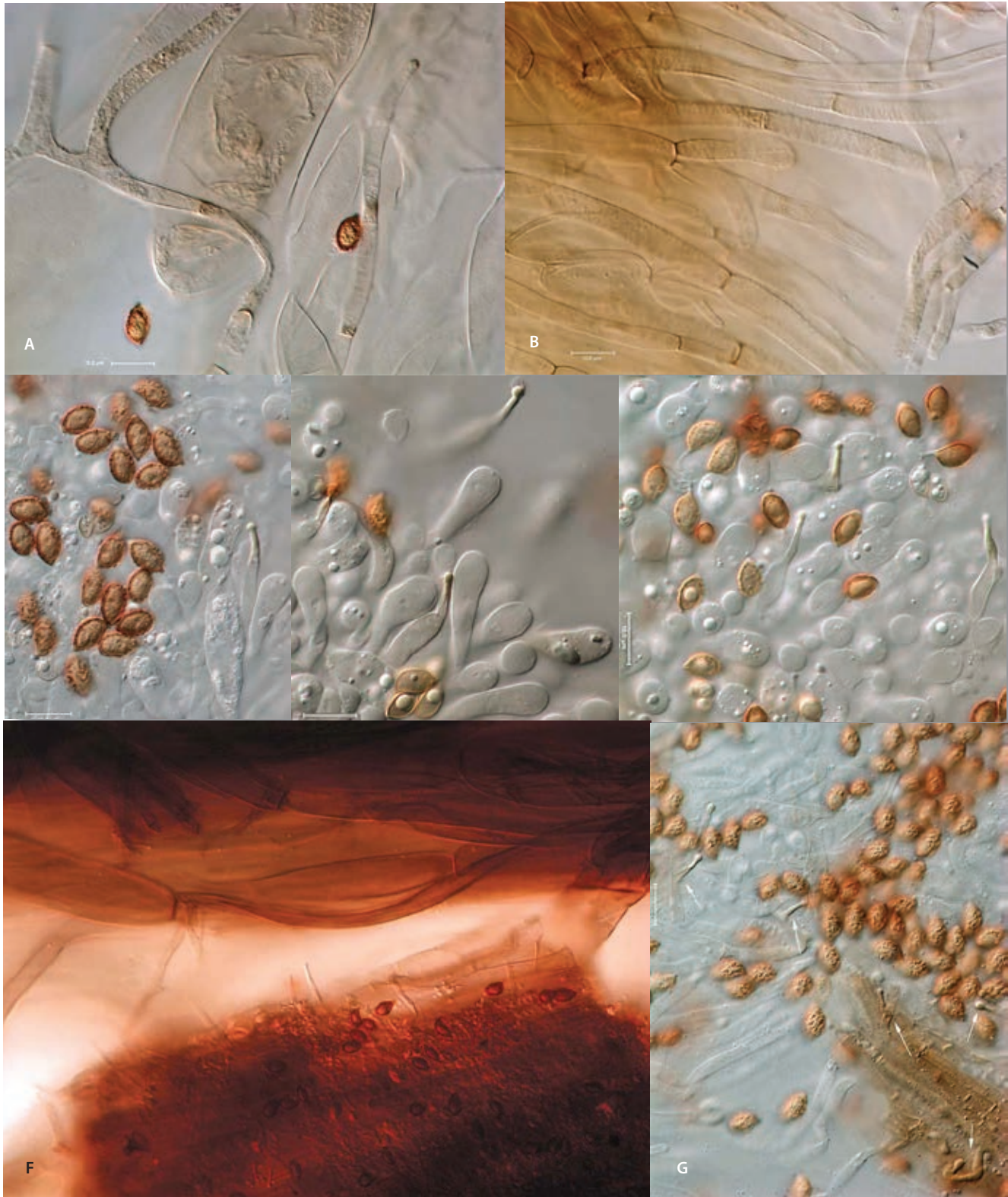


*Phaeocollybia californica*

HABIT (left) — WTU LLNorvell1951117-24

BASIDIOSPORES & CHEILOCYSTIDIA (right) — MICH HOLOTYPE AHSmith55610

Important microscopical features detailed on the next page include (1) long ( $\sim 9 \times 5 \mu\text{m}$ ) warty limoniform spores with short beaks, (2) infrequent thick-walled lageniform to tibiiform cheilocystidia with refractive necks and globose gel-secreting heads intermixed with thin-walled clavate elements and basidia, (3) a two-layered pileipellis with a thin yellowish top layer containing narrow hyphae spirally incrustated with colorless to amber gel overlying a thin brownish-orange lower layer, and (4) an absence of clamp connections.



*Phaeocollybia californica* [OREGON Benton Co—Old Blue, PNW-MS: Exeter2007-135 (D,F), Exeter2007-137 (E,G); Josephine Co—Grants Pass, OSC: Loring4563 (A), Loring4513 as LLNus8-4 (B), Loring4564 (C)]. A–B—SUPRAPELLIS HYPHAE are spirally encrusted with a colorless to dull amber gel; intraparietal orange pigments congregate at the septa. C–E—CHEILOCYSTIDIA & BASIDIOSPORES: Fertile gill edges have basidia and other thin-walled clavate elements that frequently obscure the infrequent tibiiform elements, making them difficult to detect. Tibiiform cheilocystidia with tall thin-walled bases, thick-walled narrow necks are usually topped by a little head (capitulum) with amber to orange oily contents. F–G—TIBIIFORM DIVERTICULA arise from mycelial and primordial sheath hyphae in all phaeocollybias. Mature specimens retain diverticula on pseudorhizal surfaces (F) or stipe apex fibrils (G). The optics used to reveal the diverticula in sharp focus (G) draw attention to roughened spores lying just below the focus plane. All scales = 10  $\mu$ m.





Lorelei Norvell (A), Ron Exeter (B-C)

*Phaeocollybia californica* [OREGON Benton Co—Old Blue, PNW-MS: Exeter2007-135]. This collection confirmed an umbellate habit for the species, with pseudorhizas found emerging from one point on a mother rhizomorph (A). The cross section (B) reveals a thick stipe cortex surrounding a fibrillose lined large central cavity. Not shown are the tibiiform diverticula surrounding the mantle and the Hartig net in an ectomycorrhizal tip that support a mycorrhizal strategy for the species.

**BASIDIOSPORES** —  $|x| = 9 \times 5.4$  [8–11  $\times$  5–6(–7)]  $\mu\text{m}$ , limoniform (inequilateral) in profile with eccentric short apiculus and 0.5–1  $\mu\text{m}$  long beak, ovate in face view; surface rugulose-roughened to heavily warted except over beak; tawny to rusty-brown in KOH, ornamentation distinctly darker (especially under low magnification), non-dextrinoid in Melzer's. **BASIDIA** — 4-spored.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** sparse; lageniform to capitulate tibiiform [with bases  $\leq 30 \times 5 \mu\text{m}$ , refractive necks  $\leq 2 \mu\text{m}$  diam, and capituli  $\leq 3 \mu\text{m}$  diam], often with droplets surrounding small globose heads difficult to see when bent over or obscured from view by surrounding clavate elements in hymenium; colorless or with oily amber to orange contents beneath the refractive neck walls. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on pseudorhizal pellis and occasional to frequent on fibrillose veil remnants on stipe apex,  $\leq 20 \times 1 \mu\text{m}$ , colorless.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis with a relatively thin (50–100  $\mu\text{m}$ ) colorless suprapellis overlying a dull orange to brown subpellis; suprapellicular hyphae radially aligned, narrow (1–4  $\mu\text{m}$ ), cylindrical, gelatinized, and spirally encrusted with colorless to pale brownish gel deposits; subpellicular hyphae inflated, thick-walled subpellicular hyphae with intraparietal pigments. — **STIPITIPPELLIS** a 50–100  $\mu\text{m}$  thick layer of parallel, cylindrical, narrow (2–4  $\mu\text{m}$ ), thick-walled highly gelatinized hyphae that widen increasingly toward the interior medulla.

**TRAMAL TISSUES** — Highly gelatinized, sarcodimitic in the pseudorhiza and lower stipe with wide ( $\leq 30 \mu\text{m}$  diam), thick-walled ( $\leq 3 \mu\text{m}$ ), cylindrical rigid yellowish vessel hyphal elements supported by less conspicuous, branched, thin-walled ( $< 0.5 \mu\text{m}$ ) flexuous hyphae; both hyphal types also present in the pileus but with vessel hyphae narrower ( $\leq 10 \mu\text{m}$  diam) and thinner ( $\leq 1 \mu\text{m}$ ) walled. Lamellar trama parallel, with hyphae highly gelatinized, 4–6  $\mu\text{m}$  diam, slightly thick-walled, pale amber and with refractive septa and intraparietal pigments, giving rise to a 10  $\mu\text{m}$  thick subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal). Fasciculate to gregarious in arcs during autumn in humic soils of moist coniferous (*Abies*, *Tsuga*, *Pseudotsuga*) and mixed (*Abies*, *Arbutus*, *Quercus*, *Pseudotsuga*, *Tsuga*) coastal and coastal montane forests. — **PACIFIC NORTHWEST ENDEMIC** collected from fewer than 15 sites (some no longer extant) in California and Oregon.



Ron Exeter

*Phaeocollybia californica* from Reese Creek, Benton County, Oregon [PNW-MS Exeter 2007-177]. This and several other recent collections greatly resemble the recently described *P. rufotubulina*. On-going sequence analyses will determine whether *P. rufotubulina* is an authentic separate species or conspecific with *P. californica*.

**Similar species** — *Phaeocollybia californica*, *P. rufotubulina*, and *P. scatesiae* all produce similarly sized, highly gregarious basidiomes with similar basidiospores and cheilocystidia. The smaller *P. rufotubulina* has a less viscid, intensely red-orange cap, a completely hollow stipe with a thinner rind, and cap suprapellis hyphae that have heavy orange gel spiral encrustations. The densely fasciculate, highly glutinous *P. scatesiae* fruitbodies, which erupt in dense fasciculate mounds rather than arcs, have broadly conic, sharply umbonate, yellow- to blackish brown caps, slightly paler and smaller spores, more abundant cheilocystidia, and non-encrusted smooth cap suprapellis hyphae that are so heavily gelatinized that septa are seen only with difficulty.

Both *P. californica* and *P. sipei* mature fruitbodies have broadly-campanulate tawny to dark orange caps and hollow stipes with thick cartilaginous rinds; *P. sipei* is easily microscopically differentiated by small ( $6.5 \times 3.8 \mu\text{m}$ ) punctate roughened ellipsoidal spores and exclusively thin-walled, subcapitate broad cheilocystidia.

In comparing *P. californica* to the northeastern American *P. laterarius* A.H. Sm. (now a synonym of *P. christinae* Fr.), Smith (1957) remarked on *P. californica*'s duller color (more yellow brown), odor so pungent as to be detectable even in dried specimens, stipe apex diameter up to 10 mm diam, and tendency to fruit in gregarious arcs. Recent collections suggest that younger fruitbodies are more brightly colored.

See TABLE 9 (on the opposite page), *P. rufotubulina*, and *P. scatesiae* for additional comparisons.

**Additional comments** — *P. californica* has not yet been verified north of Oregon or east of the Willamette Valley. Norvell's (1998a) preliminary molecular analyses supported the synonymy of *P. scatesiae* with *P. californica* as proposed by Horak (1977), and so she reported both species under the name *P. californica* during her 1995 Northwest Forest Plan evaluations. After further consideration of the obvious field and microscopical differences, Norvell reported the two as separate taxa (1998a, 2004). Castellano et al. (1999) correctly treat the two species as distinct, but the *P. californica* distribution discussion and map erroneously include *P. scatesiae* data. Recent DNA sequence data (M. Gordon 2009, unpubl.) challenge earlier RFLP-based analyses (Norvell 1998a, 2004) showing *P. californica* separate from *P. rufotubulina* but not *P. scatesiae*. These preliminary new data support *P. scatesiae* as independent from both *P. californica* and *P. rufotubulina* and suggest that the later two taxa may well be conspecific.



Ron Exeter

Young *P. californica* stipes and gills are usually pallid; when not covered by spore deposits. mature cap colors resemble butterscotch pudding.  
Old Blue Mountain near Mary's Peak (Benton County), Oregon — PNW-MS Exeter 2008-58 (L) & Exeter 2007-137 (R)

TABLE 9. Morphology and ecology in *Phaeocollybia californica*, *P. rufotubulina* and *P. scatesiae*

SPECIES	YOUNG PILEUS MOISTURE COLOR UMBO (shape)	YOUNG GILLS FRESH [UNDER UV]	STIPE RIND thickness (mm)	PSR CORD (rhizomorphic, racemose) & HABIT (all gregarious)	SPORE LENGTH (range) COLOR KOH mount (in print)	CHEILOS (refractive & thick-walled)	HYPHAE (pileus suprapellis) ENCRUSTS (color) SEPTA (prominence)	SYRING-ALDAZINE RXNS (tissues turning magenta)	HOST <sup>2</sup> TREES	RANGE (PNW NAM)
<i>P. CALIFORNICA</i>	Viscid. Tawny to tawny orange. Obtusely conic; often papillate.	Pallid to pale orange buff [fresh: mustard yellow]	2-2.5	PSR umbellate, sequential  Cespitose mounds in arcs	~9 µm (8-11)  Tawny ( <i>saya</i> brown)	Isolated, infrequent (never abundant; often difficult to find)	Gel spirals. (faint; colorless, pale brown) Refractive (easily seen)	Gills <sup>1</sup> (strong or negative)  PSR (rapid, strong)	Conifers PSME TSHE <i>Abies</i>  Angios ARME QUKE	Coast, Coast Range (to 3000')  w OR nw CA
<i>P. RUFOTUBULINA</i>	Subviscid. Red-orange. Convex; rarely papillate.	Pale orange ( <i>apricot</i> ) [dried: dull yellow-orange]	1-1.5	PSR sequential only  Loose bundles or troops	~9 µm (8.2-10)  Dark orange-amber ( <i>saya</i> brown)	Occasional to frequent, (rarely abundant; easily seen)	Gel spirals. (dense; yellow-orange, orange-brown) Refractive (easily seen)	PSR (slow, very faint)	Conifers PSME <i>Abies</i>  Angios LIDE	Coast (to 200')  nw CA
<i>P. SCATESIAE</i>	Glutinous. Pale to dark yellow-brown. Acutely conic.	Pale yellowish to buff [fresh: brilliant yellow-white]	2-3	PSR umbellate, rarely sequential Dense tightly packed mounds	~8.5 µm (7.2-9.5)  Pale tawny ( <i>pinkish cinnamon</i> )	Frequent to abundant (easily seen)	Not encrusted. (gelified) Obscured (by colorless gel matrix)	PSR (slow, weak)	Conifers PISI <i>Abies</i> PSME TSHE	Coast to Cascades (to 4000')  w WA w OR nw CA

<sup>1</sup>During 2007-2008, the gill and pseudorhizal cord tissues from different collections representing one Oregon population turned magenta in Syringaldazine. Results from other populations (from specimens held over several days after collection) were variably reactive.

<sup>2</sup>Suspected ectomycorrhizal host associations are not yet proven. ARME = *Arbutus menziesii*; LIDE = *Lithocarpus densiflora*; PISI = *Picea sitchensis*; PSME = *Pseudotsuga menziesii*; QUKE = *Quercus kelloggii*; TSHE = *Tsuga heterophylla*.

#### References with descriptions and /or illustrations of *Phaeocollybia californica* —

- Castellano MA, Smith JE, O'Dell T, Cázares E, Nugent S. October. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. USDA-FS. PNW-GTR-476. PNW Res. Stn., Portland. [descr. & color photo: s1 - 85].
- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. Sydowia 29: 28-70. [key; microdrawing p. 54].
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [key; description pp. 150-153, 348; microdrawing & color photos pp. 234-235]



Scot Loring

Cespitose *P. californica* clusters form a 'gregarious arc'  
Josephine County, Oregon — osc Loring4560 (LLNus7-3)

- Norvell LL. 2004. *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and Section *Versicolores* reconsidered. *Mycotaxon* 90(2): 241-260. [The 'californica' complex is discussed (including molecular analyses) in comparisons with *P. rufotubulina*; for molecular support for placement in section *Versicolores*: 254-256].
- Smith AH. 1957. A contribution toward a monograph of *Phaeocollybia*. *Brittonia* 9: 195-217. [key; descr. pp. 216-17, microdrawings p. 210; b&w photo pl. 6]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. *Mycologia*. 64: 1141-1142 [Revised key].

*Phaeocollybia dissiliens*

Ron Exeter

*Phaeocollybia dissiliens* 'leaping apart' near Reese Creek  
Benton County, Oregon — PNW-MS Exeter2007-169

***Phaeocollybia dissiliens*** A.H. Sm. & Trappe, Mycologia 64: 1143, 1972.

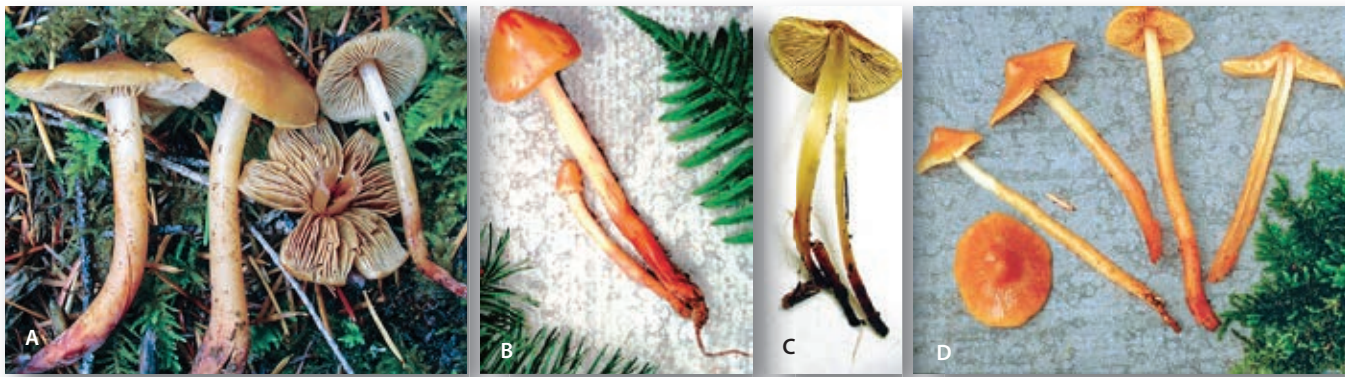
ETYMOLOGY — From '*dissilio*', Latin for 'to leap apart' or 'burst asunder', referring to fragile fruitbodies that split apart easily when handled or broken.

HOLOTYPE — Cape Lookout State Park (Tillamook County) OR, USA;  
October 23, 1970 (MICH HOLOTYPE 11608 AHSmith79252)

*Field summary* — Small to medium-sized fragile fruitbodies with viscid pale bright orange to pale tawny conic-umbonate caps, pale orange buff young gills, centrally hollow shiny cream colored stipes that split apart when broken, and deeply rooting cord-like pseudorhizas. Scattered to clustered under conifers during autumn in western Oregon and northwestern California.

PILEUS — ~20–80 mm diam, narrowly conic with incurved edge to broadly conic-campanulate with low sharply pointed umbo, straight margin, and incurved opaque to striatulate edge, surface subviscid to viscid, smooth, bald, hygrophanous with edge often paler than the disc; color when young bright orange to brownish orange (*orange cinnamon*, *antimony yellow*) with orange-brown disc (*raw sienna*), and yellow brown edge (*buckthorn brown*), developing cinnamon tones in age. —*FLESH* 2–4 mm thick, initially opaque and pallid but soon a translucent watery tan or concolorous with cap cuticle. —*ODOR* not distinctive, faintly raphanoid, or sharply pungent, like *Oxalis*. —*TASTE* not distinctive, faintly raphanoid, slightly bitter nutty. —*DRIED PILEUS* pale metallic copper or bronze, finally wrinkled radially.

LAMELLAE — Narrowly attached to free, pale orange yellowish white when young, dulling to orange cinnamon brown; edges finely serrulate even when young.



Exeter(A), Norvell(B,D), Sperling (C)

*Phaeocollybia dissiliens* [OREGON: Benton Co—Old Blue (Mary's Peak), PNW-MS Exeter2007-142 (A); —Green Peak, PNW-MS LLNorvell 1981028-1 (B); Coos Co—Myrtlewood RA osc F1js146 (C); Lincoln Co—Fogarty Crk SP, WTU Norvell1951109-16 (D)] — The fragile pale to bright orange cap with papillate to sharply pointed umbo and soon hollow stipe that splits apart when broken or cut help diagnose the species in the field. Careful excavation is needed to retrieve the narrow pseudorhizal cord (B) usually left behind in the soil.

**STIPE** — +/- central, rigid and tubular, ~40–80 mm above the ground, combined length with pseudorhiza >180 mm; apex 5–10 mm diam, upper stipe +/- equal, readily splitting lengthwise; dry to moist, polished; color of young apex pale pinkish buff (*pale* or *light pinkish cinnamon*), aging to deep orange-red (*raw sienna*) from ground upwards; stuffed with firm to loose silky pallid pith when young, but soon canaliculate (with fibrils surrounding 3–6  $\mu\text{m}$  diam cavity) then hollow; crisp cartilaginous rind 2–3 mm thick.

**PSEUDORHIZA** — (Fasciculate) racemose, abruptly tapering below underground stipe base to a cord-like origin; color dark rusty brown to liver red.

**VEIL REMNANTS** — Evident as scattered to frequent brownish orange fibrillose patches on upper stipe (almost annulate in one collection).

**SYRINGALDAZINE REACTIVITY** — Negative (no tissues turning magenta).

**FLUORESCENCE** — Fresh specimens not tested; dried gills dull ochraceous or not fluorescing (*i.e.*, black under UV).

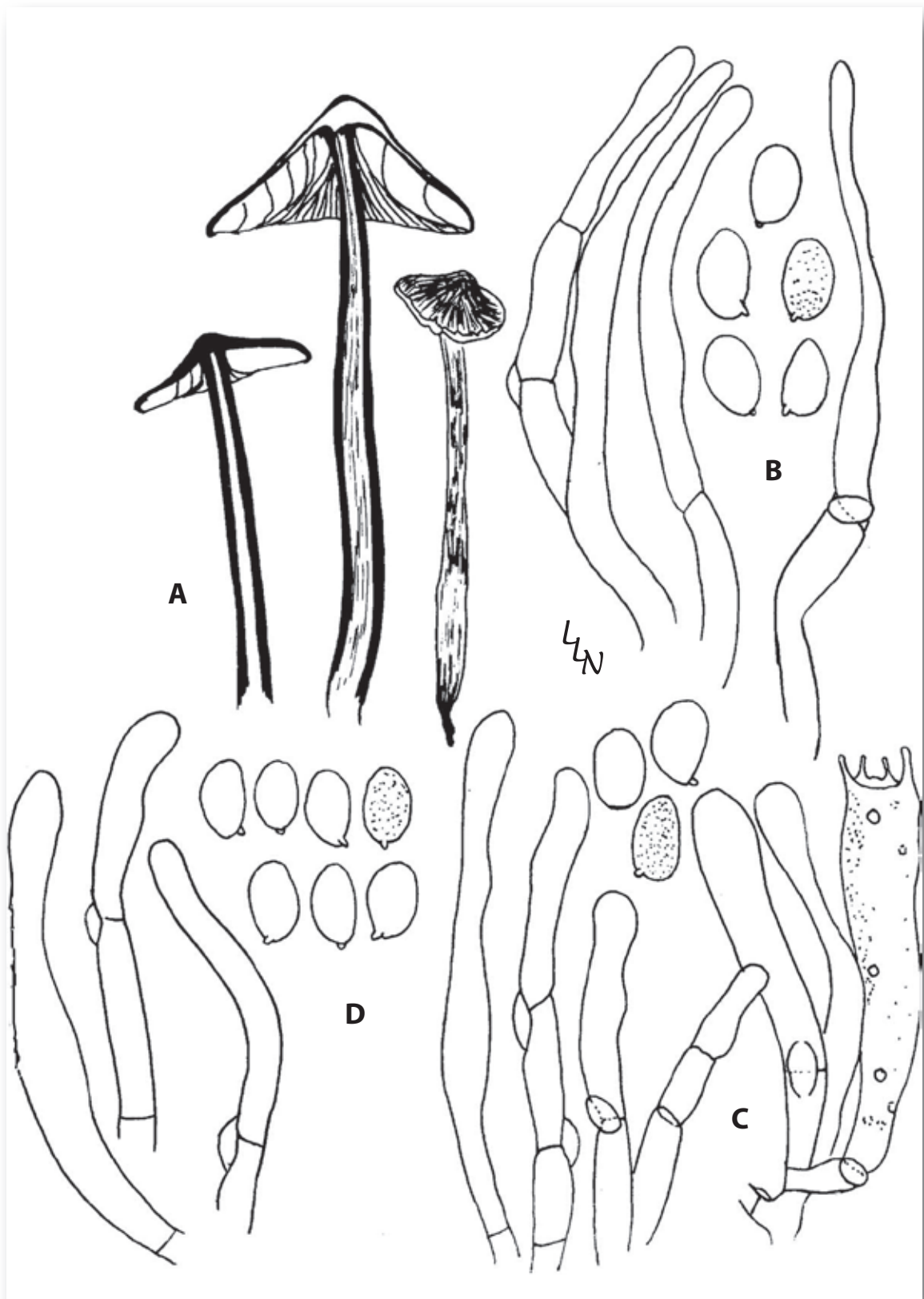
**SPORE PRINT** — Yellowish cinnamon.

**Diagnostic characters** — Macroscopically, *P. dissiliens* can be recognized by its (1) readily splitting (sub)viscid bright orange to pale butterscotch conic-campanulate cap with sharp umbo and orange creamy gills, (2) small to medium size, (3) shiny narrow (5–10 mm diam) buff to orange stipe that splits apart when cut or broken, and (4) negative syringaldazine reactivity.

Important microscopical features include (1) small (~6.7  $\times$  4.3  $\mu\text{m}$ ) ellipsoidal finely punctate roughened basidiospores with blunt apical beaks, (2) thin-walled filamentous to cylindrical cheilocystidia, (3) clamp connections frequent at septa in all tissues (constant at basidial bases), and (4) bilaminar pileipellis with orange to orange-brown diffuse and encrusting pigments.

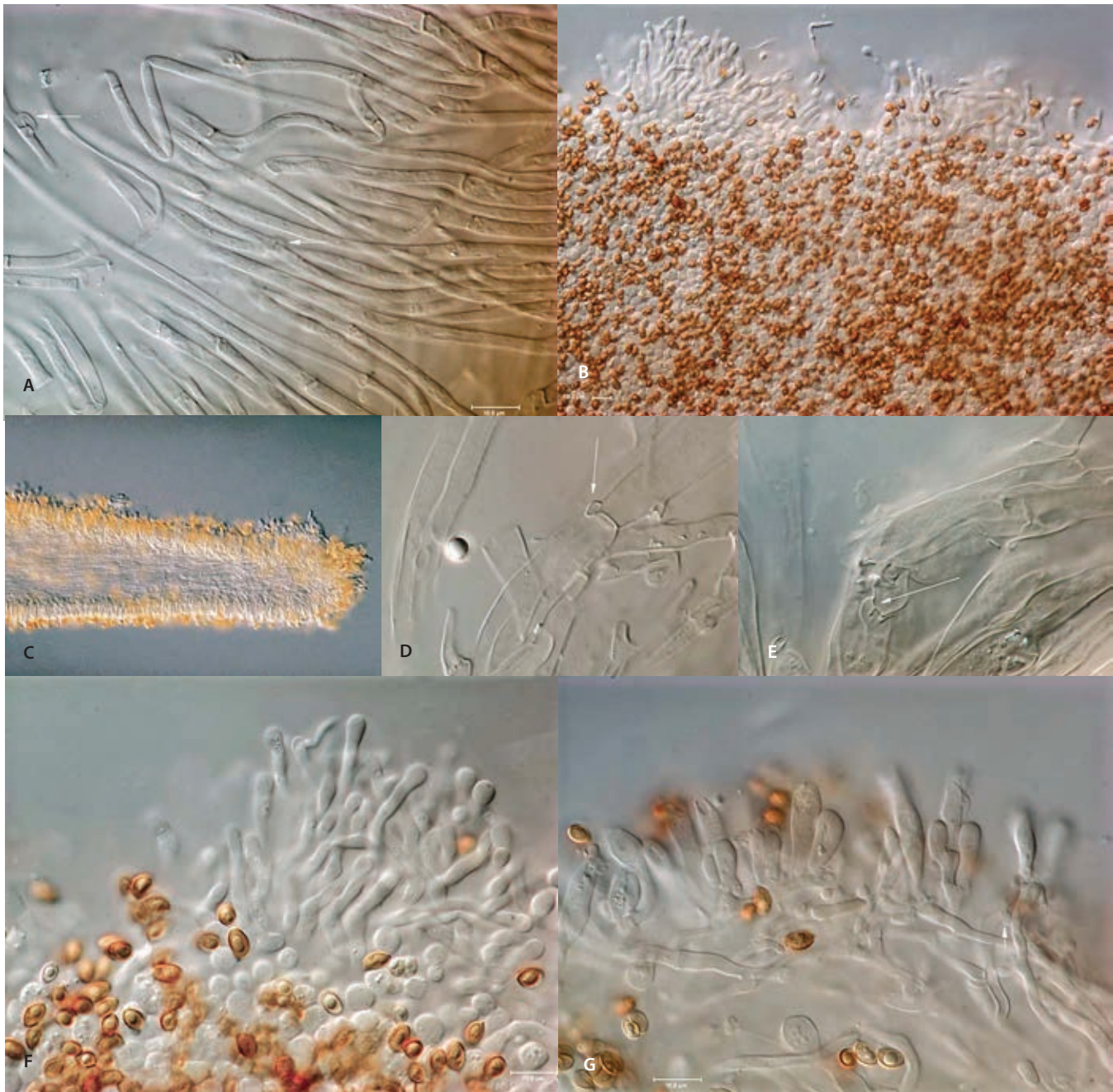
**BASIDIOSPORES** —  $|x| = 6.7 \times 4.3$  [(6)6.5–7.3(8)  $\times$  (3.7)3.9–4.3(4.8)]  $\mu\text{m}$ , subellipsoidal with a rounded back, small eccentric apiculus, and rounded to obscurely pointed apex in profile view, ovoid to subellipsoidal in face view, surface finely punctate-roughened under oil immersion; color in KOH pale medium amber, in H<sub>2</sub>O paler, in Melzer's inamyloid and non-dextrinoid. — **BASIDIA** 4-spored, clavate with clamp connections at bases, 24–30  $\times$  6–6.5  $\mu\text{m}$ , colorless to pale amber in KOH, granular and/or vacuolate.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a sterile layer occasionally intermixed with basidia; lengths variable and indeterminate (~28–45  $\mu\text{m}$ ), apices  $\leq$  3.5–4  $\mu\text{m}$  diam, filamentous, cylindrical to slightly irregular in outline, sometimes slightly inflated, subcapitate, or mucronate; clamp connections frequent at septa, apical extensions from senescent elements frequent in older tissues; colorless to pale straw-colored. — **PLEUROCYSTIDIA** as occasional filiform thin-walled hyphidia (not diagnostic). — **TIBIIFORM DIVERTICULA** abundant on pseudorhizal pellis, ~10  $\times$  1  $\mu\text{m}$  with/without (sub)globose head and/or apical droplet; highly refractive, colorless.



*Phaeocollybia dissiliens*

A-C. HABIT, CHEILOCYSTIDIA & BASIDIOSPORES — Fogarty Crk SP (Lincoln Co) OR: wtu Norvell1951109-1(b) &-16 (c).  
D. CLAMPED CHEILOCYSTIDIA & BASIDIOSPORES — Cape Lookout SP (Tillamook Co) OR: MICH HOLOTYPE11608 AHSmith69252.



Lorelei Norvell

*Phaeocollybia dissiliens* [OREGON: Benton Co—Old Blue (Mary's Peak), PNW-MS Exeter2007-142 (G), —Reese Creek, PNW-MS Exeter2007-169(A) & -171(B&D-F); Lincoln Co—Fogarty Crk SP, WTU Norvell1951106-1 (C)]— A. **PILEIPELLIS**. Clamp connections (arrows) are relatively easily seen at septa of the colorless relatively wide hyphae in the colorless gel matrix of the suprapellis; the orangish to orange-brown diffuse and encrusting pigments are confined to the subpellis below (at right). B–C. **HYMENIUM**. Abundant thin-walled narrow (sometimes 'strangulated') cheilocystidia are more easily found in a squash mount (B) of tissues sliced along the gill edge than in a longitudinal section (C) made to examine the gill trama. For all phaeocollybias such sections require extreme care (or a freezing microtome) to prevent gelatinized elements at the end of the gills from sticking to the blade. D–E. **CLAMP CONNECTIONS**. Inflated medallion-like clamps (arrows) are readily found throughout the pileus trama. F–G. **CHEILOCYSTIDIA & BASIDIOSPORES**. Thin-walled cylindrical to narrowly clavate cheilocystidia (many with swollen heads) form occasional apical outgrowths in older tissues (F). The small, ellipsoid basidiospores with blunt to pointed snouts appear almost smooth even under oil. Clamps (G, arrow), which do not occur on all cheilocystidia, are present (if difficult to see) at the bases of all basidia

Scales = 10  $\mu\text{m}$ .

**CORTICAL TISSUES** —**PILEIPELLIS** a bilaminar ixocutis: the top 70–100  $\mu\text{m}$  thick suprapellis with radially aligned, moderately narrow (3.5–4  $\mu\text{m}$  diam), smooth to gel-encrusted, occasionally clamped colorless hyphae in a gelatinous matrix; the bottom relatively narrow (50–75  $\mu\text{m}$  thick) subpellis with diffuse orange pigments and thin-walled, 5–8  $\mu\text{m}$  diam, frequently clamped hyphae encrusted by orange to dark orange-brown pigments.





The bright orange and yellow coloration in newly emerged *P. dissiliens* caps (L) fades on exposure and age (R).

LEFT: Fogarty Creek SP (Lincoln Co) OR — wtu LLNorvell1951106-2

RIGHT: Old Blue (Benton Co) OR — PNW-MS Exeter2007-169

Lorelei Norvell (L), Ron Exeter (R)

**TRAMAL TISSUES** — Highly gelatinized, sarcodimitic in the pseudorhizal cord with rigid thick-walled ( $\leq 1 \mu\text{m}$ ), wide ( $\leq 30 \mu\text{m}$  diam) vessel hyphae supported by less conspicuous branched thin-walled ( $\sim 0.5 \mu\text{m}$ ) narrow ( $2\text{--}4 \mu\text{m}$ ) flexuous hyphae; both types also present in the stipe base where rigid vessel hyphae become slightly thicker walled (to  $3 \mu\text{m}$ ) and wider (to  $40 \mu\text{m}$  diam); monomitic in the upper stipe and pileus with hyphae consistently thin-walled, wide, and colorless. Lamellar central hyphae parallel, highly gelatinized, cylindrical ( $4\text{--}8 \mu\text{m}$  diam), slightly thick-walled, colorless, and flanked by a narrow zone of  $2\text{--}3 \mu\text{m}$  diam colorless hyphae giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Present and relatively common in all tissues; easily seen on septa of the suprapellis hyphae and cheilocystidia; always present but difficult to see at the bases of the basidia.

**Ecology** — Terrestrial (mycorrhizal); scattered to gregarious during autumn in moist coniferous (*Picea*, *Tsuga*, *Pseudotsuga*, *Abies*) forests. — *PACIFIC NORTHWEST ENDEMIC* uncommon to rare, known from  $\sim 20$  sites in Oregon most along the coast and in the coast range (one collection from western slope of the Cascades; collected once under *Picea* from California's Redwood National Park).

**Similar species** — The similar *Phaeocollybia sipei* is also characterized by orange coloration, a readily splitting fibrillose-stuffed to hollow stipe with a thick rind, small ( $\sim 6.5 \times 3.8$ ) ellipsoidal basidiospores, and thin-walled narrow cheilocystidia. However, *P. sipei* produces larger, more robust fruitbodies with broader, more obtusely umbonate, less brightly colored (brownish orange) caps, wider and distinctly subcapitate cheilocystidia, and no clamp connections.

*P. ammiratii* and *P. phaeogaleroides*, also diagnosed by clamp connections and thin-walled cheilocystidia, are unlikely to be mistaken for *P. dissiliens*. Distinguishing characters for *P. ammiratii* include much larger stature, persistently firmly stuffed stipes, and large ( $\sim 9 \times 5.5 \mu\text{m}$ ) rough beaked limoniform basidiospores. *P. phaeogaleroides* produces much smaller (galerina-like) fruitbodies with tawny to red-brown convex caps and much larger ( $\sim 10 \times 5.8 \mu\text{m}$ ) punctate-roughened ellipsoidal basidiospores.

In the past, *P. dissiliens* was misidentified as *P. radicata*, a similarly colored small Pacific Northwest phaeocollybia diagnosed by clamps. *P. radicata* also produces bright orange fruitbodies and ellipsoidal basidiospores; however, it is distinguished by much smaller fruitbodies (similar in size to *P. phaeogaleroides*), small refractive lageniform to tibiiform cheilocystidia with thick-walled narrow necks, and much smaller ( $\sim 5.8 \times 3.2 \mu\text{m}$ ) basidiospores.

See discussions after the above species for additional comparisons.



Ron Exeter

*Phaeocollybia dissiliens* in situ near Trout Creek  
Benton County, Oregon — PNW-MS Exeter2008-138

**Additional comments** — Smith & Trappe (1972) cited pleurocystidia for *Phaeocollybia dissiliens* in their type description. However, as repeated examinations of type and other materials have not revealed sterile elements on gill faces away from the edge (Redhead pers. comm. 1992, Norvell 1998a), the presence of pleurocystidia is not considered a diagnostic character.

Horak (1977) treated *P. dissiliens* as a synonym of *P. radicata* before inspecting the holotype of *Naucoria radicata*. After examination of the type collection, he no longer regarded *P. dissiliens* and *P. radicata* as the same species (Horak. pers. comm. 1995, 1996).

**References with descriptions and /or illustrations of *Phaeocollybia dissiliens* —**

- Castellano MA, Smith JE, O'Dell T, Cázares E, Nugent S. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. PNW-GTR-476. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s1 – 86].
- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. *Sydowia* 29: 28–70. [(as '*Ph. radicata*') key to world species; line drawing, p. 67]
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales, Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [pp. 153–155; photos pp. 237]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. [B&W photo of gill section, p. 622]

*Phaeocollybia fallax*

Vivid green, violet, and orange colors immediately identify young *P. fallax* specimens on Old Blue Mountain. Mary's Peak, Benton County, Oregon — PNW-MS Exeter2007-140

***Phaeocollybia fallax*** A.H. Sm. 1957, Brittonia 9: 202.

ETYMOLOGY — From the Latin for 'false', alluding to the initial misuse of the name *P. festiva* for a distinct North American species.

HOLOTYPE — La Push (Clallam County), WA, USA;  
October 26, 1935 (MICH 11609 HOLOTYPE AHSmith3342)

MISAPPLIED — *Naucoria festiva* sensu A. H. Smith (1937)

*Field summary* — Small to medium-sized fruitbodies with conic-campanulate glutinous green caps, violet young gills, shiny finely stuffed to hollow drab and orange stipes, and deeply rooting fleshy unbranched pseudorhizas. Scattered to gregarious during autumn in Pacific Northwest coniferous forests.

PILEUS — ~15–65 (90) mm diam, at first conic-convex with acute conic umbo, incurved margin and inrolled edge, expanding to broadly campanulate with low to prominent conic umbo, plane margin, and incurved edge, viscid to glutinous, smooth, bald, hygrophanous with noticeably striate edge when moist; color when young some shade of light to dark olive-green (*olive buff*, *citrine drab*), often variably shaded with different greens in patches or zonate with darker disc (*dark olive*, *citrine drab*, *olive buff*) and paler edge (*buffy brown*), green



Elizabeth Fox (L), Scott Redhead (R)

Its green cap, violet gills, and drab & orange stipe make *P. fallax* the world's most beautiful phaeocollybia.

LEFT: Upper Carmanah Valley, Vancouver Island, British Columbia — wtU LLNorvell1921007-1

RIGHT: 'Oz,' BLM Reserve Forest, Polk County, Oregon — PNW-MS a1991202o1-1

at times obscured by dark orange or brown glutin; green fading with age to brownish olive. —*FLESH* thin at the margin,  $\leq 5$  mm at the disc, olive buff to deep olive, often consumed by insects. —*ODOR* not distinctive to complex with slight floral undertones (reminiscent of pansies, boiled potatoes, or burnt wet hair). —*TASTE* usually mild, occasionally raphanoid; glutin sometimes bitter in older specimens. —*DRIED PILEUS* greenish metallic bronze to satiny greenish to blackish brown; usually with striate edges.

*LAMELLAE* — Bluish violet when young, dulling to drab, orange cinnamon with ruffled whitish edges in age.

*STIPE* — +/- central, erect, ~30-100 mm above the ground, combined length with pseudorhiza >275 mm; apex ~3-8(12) mm diam, aerial portion usually slightly fusiform, occasionally equal or tapering; surface viscid to moist, smooth and +/- polished beneath short fibrillose patches, shiny; color of young apex grayish drab or dull olive buff, grading to deep orange to orange-brown at ground level; becoming uniformly orange to orange-brown in age; finely fibrillose stuffed when young, in age usually hollow but occasionally stuffed with fibrillose to firm pith; cartilaginous rind 1-2 mm thick.

*PSEUDORHIZA* — Vertical-monopodial, ~3/4 of overall length, continuous with stipe and gradually tapering to a curled or nipped origin; color deep orange to dark reddish brown.

*VEIL REMNANTS* — Present as irregularly arrayed short appressed orange or dark brown fibrillose patches on aerial stipe.

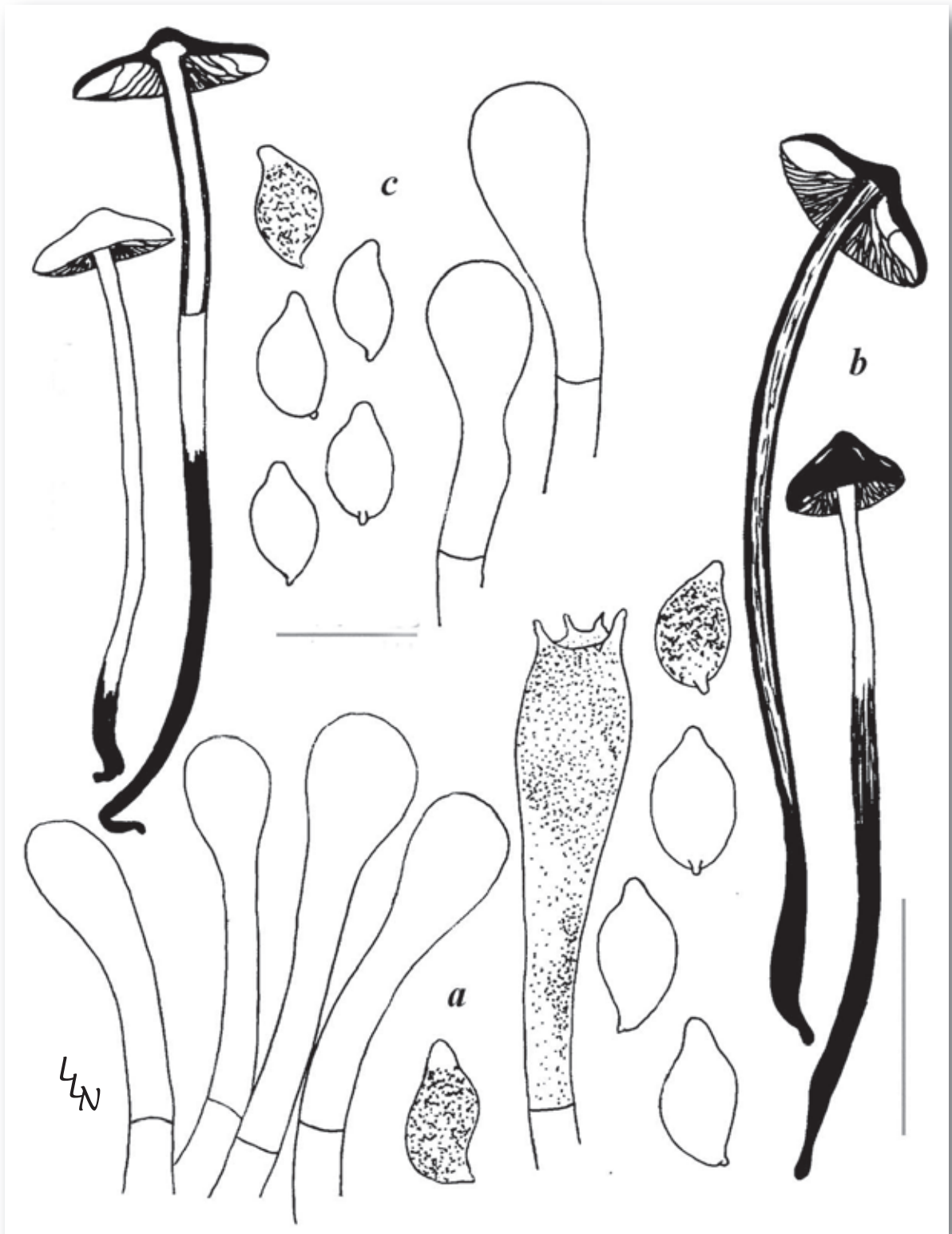
*SYRINGALDAZINE REACTIVITY* — Cap, gill, and upper stipe tissues negative; pseudorhiza sometimes faintly magenta after 30 minutes.

*FLUORESCENCE* — Under UV, gills fluoresce bright yellowish white (young) to dull yellow (mature).

*SPORE PRINT* — Pinkish cinnamon.

**Diagnostic characters** — Macroscopically, *P. fallax* can be recognized by its (1) viscid to glutinous olive green conic cap and violet young gills, (2) slender shiny stipe with drab apex and orange base, (3) small to medium size, and (4) gills that do not turn magenta in Syringaldazine.

Important microscopical features detailed on the next page include (1) large (~9 × 5 μm) verrucose-rugulose (marbled) almond-shaped beaked basidiospores that appear boat-shaped (naviculate) in face view, (2) a sterile gill edge composed of thin-walled predominantly subcapitate cheilocystidia that rarely form apical extensions in age, (3) a bilaminar pileipellis that turns orange in KOH, and (4) lack of clamp connections.



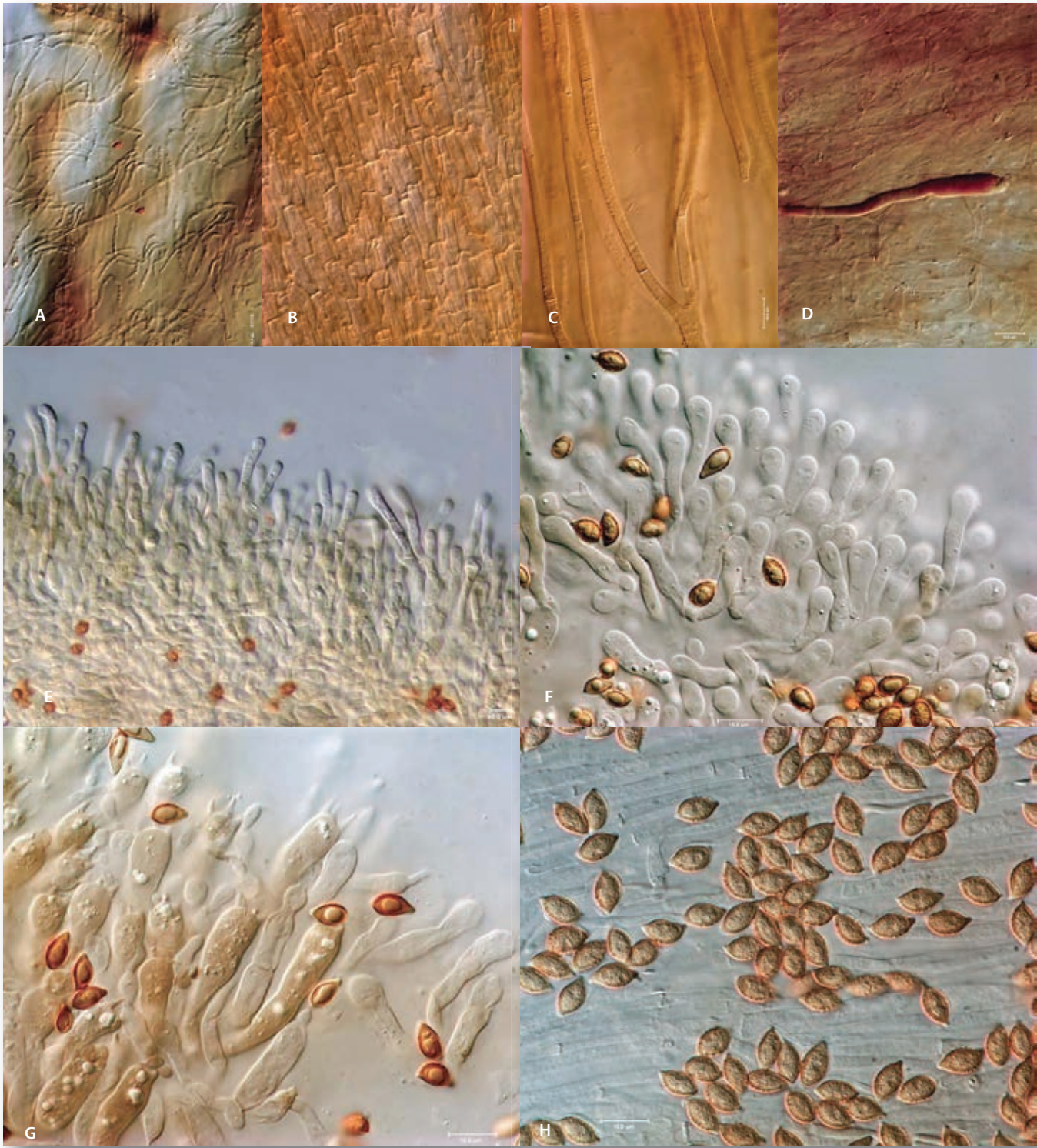
*Phaeocollybia fallax*

A-B. TYPICAL FORM. a: CHEILOCYSTIDIA, BASIDIUM, BASIDIOSPORES — MICH 11609 HOLOTYPE AHSmith 3342

b: HABIT — wtU LLNorvell1951022-1

C. SMALL-SPORED FORM: HABIT, BASIDIOSPORES, CHEILOCYSTIDIA — wtU LLNorvell1941011-16

Scales = 10  $\mu$ m & 5 cm



Lorelei Norvell

*Phaeocollybia fallax* [A,B,C,E — Saddlebag Mtn, Lincoln Co, OR: A&E—PNW-MS Norvell2071018-9, B&C—PNW-MS Exeter2007-66. D — Cascade Head Exper. Forest, Tillamook Co, OR: osc LLNus8-41. F — Reese Crk, Benton Co OR: PNW-MS Exeter2007-170. G — Fanno Pk, Polk Co OR: PNW-MS Exeter2007-109. H — Mary's Pk, Benton Co OR: PNW-MS Exeter2007-43]. A–D. PILEUS TISSUES. Pigments that appear dull green when mounted in H<sub>2</sub>O turn deep orange when mounted in 6% KOH. In the suprapellis, narrow curly colorless hyphae (A) are embedded in a colorless gelatinous matrix. The wider subpellis hyphae (B–C), which have slightly thickened walls and intraparietal pigments, can be seen as gel-encrusted (C) when viewed under oil. Oleifers with oily pigmented contents (D) are frequent throughout pileus pellis and trama. E–F. CHEILOCYSTIDIA. Thin-walled clavate elements form a sterile gelatinous barrier (E) along the gill edge. In most specimens, elements appear subcapitate with swollen heads atop narrower stems (F). G–H. BASIDIOSPORES. Although usually described as limoniform, *P. fallax* spores can also be termed 'naviculate' when the apiculus is hidden from view, with long pointed beaks forming the prows and blunted round bases forming the sterns of on the fusoid 'boats'. Basidia (G) A are typically 4-spored, clavate, and granular. When spore prints have not been taken, spores are best measured from the stipe apex (H). Scales = 10 µm.



Scott Redhead

Muted greens can make *P. fallax* difficult to spot. The inset highlights a 'hidden' arc in Oswald West State Park, Tillamook County, Oregon — wtu LLNorvell1921110-7

**BASIDIOSPORES** —  $|x| = 9 \times 5.3$  [7–10  $\times$  4–6]  $\mu\text{m}$ , limoniform-fusoid in profile view with eccentric apiculus and long central to slightly tilted tapered beak (to 1.5  $\mu\text{m}$ ), ovate with elongated apical beak and pointed apiculus in face view, verrucose-rugulose ('marbled'); color in KOH medium amber brown, in  $\text{H}_2\text{O}$  paler, in Melzer's dextrinoid. — **BASIDIA** 4-spored, 30–42  $\times$  7–9  $\mu\text{m}$ , clavate, granular, hyaline to yellowish.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a dense gelatinous sterile layer with individual elements frequently surrounded by apical gelatinous secretions in KOH; lengths variable and indeterminate, broadly clavate 7–9  $\mu\text{m}$  diam elements intermixed with long pedicelled subcapitate elements with apices 5–7  $\mu\text{m}$  diam; apical extensions from senescent elements rare; yellowish or hyaline in KOH. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelial and external primordial hyphae, also frequent on remnants of pellicular veil on stipe apex,  $\leq 20 \times 1 \mu\text{m}$  with no septum between base and hyphae, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** — **PILEIPELLIS** a well-delimited bilaminar ixocutis: the top ~500  $\mu\text{m}$  thick suprapellis a tangled turf of long branched narrow (2–4  $\mu\text{m}$ ) straight to curly highly gelatinized colorless hyphae in a thick gelatinous matrix; the bottom ~400  $\mu\text{m}$  thick subpellis with thicker walled, inflated ( $\leq 15$  from 6–10  $\mu\text{m}$  diam septa), gelatinized hyphae; subpellis intraparietal pigments orange in KOH, greenish in  $\text{H}_2\text{O}$ . — **STIPTIPELLIS** ~40  $\mu\text{m}$  thick, hyphae parallel, sparingly branched, long and cylindrical, narrow (2–4  $\mu\text{m}$ ), thick-walled, highly gelatinized, dull brownish in KOH and  $\text{H}_2\text{O}$ .

**TRAMAL TISSUES** — Highly gelatinized, strongly sarcodimitic in pseudorhiza, composed of long wide ( $\leq 20 \mu\text{m}$ ) thick-walled ( $\leq 2 \mu\text{m}$ ) pale brown rigid cylindrical hyphae intermixed with less conspicuous thin-walled branched flexuous hyphae; both hyphal types also present in the stipe apex where the long rigid elements narrow ( $\leq 10 \mu\text{m}$ ); bright orange (in KOH) oleifers frequent in pileal trama. Lamellar central hyphae parallel 3–5  $\mu\text{m}$  diam, thin-walled, colorless, and flanked by a narrow zone of 2–3  $\mu\text{m}$  diam colorless elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); scattered to gregarious, during autumn or (rarely) spring in coniferous (*Tsuga*, *Picea*, *Pseudotsuga*, *Abies*) forests. — **PACIFIC NORTHWEST ENDEMIC** known from ~100 sites (~75 believed extant) west of the Cascade/Sierra crests (in British Columbia, Washington, Oregon, and California) and in the Priest Lake area of Idaho. Also reported from Mexico.



Lorelei Norvell

LEFT — Two *P. fallax* collections from Wildcat Mountain (Clackamas Co., OR; WTU Norvell1951018-12 & -30) illustrate the contrast between the typical, smaller, hollow-stiped form (top) and more robust form with a swollen, firmly stuffed stipe (bottom). RIGHT — One collection from Mary's Peak (Benton Co., OR; PNW-MS Exeter2007-43) displays the dulled cap and gills typically observed in aging specimens.

**Similar species** — Basidiomes with glutinous olive-green caps, intense violet-blue gills, and slender drab and orange stipes are instantly identifiable as *Phaeocollybia fallax*. Unfortunately the green and violet colors so noticeable in fresh young specimens soon fade. The violet gills and olive-green cap rapidly dull and darken as they mature, with the green cap cuticle often covered by a brownish-orange to dark brown glutin, which can cause confusion with *P. lilacifolia* and *P. riffsipes*.

*Phaeocollybia lilacifolia* is distinguished macroscopically by its tawny to dark brown cap colors, large size and robust, densely stuffed stipe — all characters of the '*kauffmanii*' complex with which it is allied. *P. lilacifolia* is also differentiated by gills turning rapidly deep magenta in syringaldazine, smaller ( $\sim 8.3 \times 5.3 \mu\text{m}$ ) basidiospores, thin-walled clavate cheilocystidia that are predominantly narrow with subcapitate elements intermixed, and a pileipellis that is usually brown in both  $\text{H}_2\text{O}$  and KOH.

*Phaeocollybia riffsipes* resembles *P. fallax* in size, shape, lilac gill color, drab stipe apex, and negative syringaldazine reaction but is distinguished by its tawny to dark brown cap colors, pinkish to rosy lilac gills, much smaller ( $\sim 7 \times 4.5 \mu\text{m}$ ) basidiospores, and filiform hyphidia.

Two other western North American species — *P. olivacea* and *P. pseudofestiva* — produce olive-green colored basidiomes. *P. olivacea* possesses yellowish gills, consistently stuffed stipes, larger, rounder, and more heavily ornamented spores, and variably shaped clavate cheilocystidia that frequently develop apical outgrowths in older specimens. *P. pseudofestiva* basidiomes also lack violet lamellae and are easily differentiated microscopically by their refractive tibiiform thick-walled cheilocystidia and shorter ( $\sim 8 \mu\text{m}$ ) basidiospores.

**Additional comments** — Smith (1937) first reported his type collection as *Naucoria festiva*, originally described from Sweden by Fries in 1838. After comparing North American and European material, however, Smith (1957b) proposed the name *P. fallax* for the western species based on its narrower, violet-colored gills and more sharply conic caps. Although Smith & Trappe (1972) include *P. festiva* in their key to North American phaeocollybias, we do not recognize *P. festiva* from the Pacific Northwest.

Norvell (2002) assigned *P. fallax*, *P. lilacifolia*, and *P. riffsipes* to a *Phaeocollybia festiva* "complex" that includes species represented by relatively small, fragile, odorless/tasteless fruitbodies with conic-campanulate glutinous caps, rosy to violet gills, moderately rugulose-ornamented (best described as 'marbled') lemon-shaped to fusiform ('naviculate') basidiospores, thin-walled clavate cheilocystidia, and highly gelatinized tissues lacking clamp connections. Table 10 (next page) compares the diagnostic characters in the complex and should help key out specimens that have lost their original distinctive coloration.

The many anatomical similarities between the two types led Horak (1977) to place *P. lilacifolia* in synonymy with *P. fallax*. Norvell (1998a, 2002a), while admitting that the two were indeed microscopically quite close, withheld decision on the synonymy until fresh material could be examined, although she combined the two species under '*P. fallax*' during contract work from 1998–2006 (Norvell, 1998c, 2002





Ron Exeter

A wide color range — green to brown caps and lilac-white to cinnamon gills — is recorded for one *P. fallax* collection. BLM tract, Depoe Bay, Lincoln County, Oregon — PNW-MS Exeter2008-19

TABLE 10: Diagnostic differences among members of the *Phaeocollybia festiva* complex

	<i>P. FESTIVA</i> (Europe)	<i>P. FALLAX</i>	<i>P. LILACIFOLIA</i>	<i>P. RIFFLIPES</i>
YOUNG CAP COLOR	Olive-green/-brown	Olive-green	Tawny/ dark brown	Tawny / dark brown
YOUNG GILL COLOR	Buff to dull violet	Blue-violet	Deep lilac	Rosy lilac to drab
COLOR OR UPPER STIPE	Greenish	Drab or greenish	Pink to drab	Drab to violet
COLOR OF LOWER STIPE	Orange	Orange	Dull cinnamon	Dull cinnamon
STIPE CONTEXT	Hollow	Stuffed to hollow	Stuffed	Stuffed
CAP DIAMETER (in mm)	20-40 (60)	~20-65 (90)	~30-100	~20-60
STIPE DIAMETER (apex in mm)	3-10	3-9 (12)	8-15 (20)	4-9 (12)
SYRINGALDAZINE RXN	Unknown	Negative	Cap & gills magenta	Negative
BASIDIOSPORE (in $\mu\text{m}$ )	7-9 $\times$ 4.5-5	$ x  = 9 \times 5.3$	$ x  = 8 \times 5.3$	$ x  = 7 \times 4.5$
PILEIPELLIS (KOH)	Unknown	Orange	Brownish	Orange
CHEILOCYSTIDIA (clavate)	Broadly clavate	Subcapitate elements dominate	Narrow elements dominate	Broad elements dominate

unpub. report). The successful collection of many excellent representatives of *P. lilacifolia* during the 2007 autumn field season uncovered convincing evidence for the recognition of two independent taxa, and we now regard *P. lilacifolia* as distinct from *P. fallax*.

Some 'fallax' collections present anomalies that imply the possibility of more than one phaeocollybia producing conic green caps and lilac gills. Norvell (1998a, 2002) noted that Smith (1957b) referred to stipes as "tubular-hollow" in his type description, yet many specimens with firmly stuffed stipes now key to *P. fallax*. Likewise, while the majority of representatives collected are mild tasting specimens, some possess intensely



Ron Exeter

The sheltered gills in one *P. fallax* collection retain their violet colors even when caps display only a tinge of green.  
Trout Creek, Benton County, Oregon — PNW-MS Exeter2008-114

bitter-tasting cap cuticles or glutin. More significantly, many fruitbodies produce spores only slightly larger than those of the very small-spored *P. riffliipes*. Additional minor differences include convex versus conic caps and the presence or absence of striations on cap margins. Preliminary molecular sequence data (Matt Gordon, pers. comm. 2008) also imply the existence of additional cryptic taxa; we hope that additional molecular sampling will help establish which of the above deviations are taxonomically significant and which are simply ecologically influenced.

*References with descriptions and /or illustrations of Phaeocollybia fallax —*

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*Phaeocollybia gregaria*

Lorelei Norvell

Broadly campanulate viscid golden tan caps with darker wavy edges and orange staining lower stipes diagnose *P. gregaria*.  
The 'Oz' transect (BLM Reserve Forest, Polk County), Oregon — PNW-MS a2001018o1-20

***Phaeocollybia gregaria*** A. H. Smith & Trappe, Mycologia 64: 114. 1972.

ETYMOLOGY — From “gregarius” (Latin for ‘belonging to the herd’, gregarious).

HOLOTYPE — Cascade Head Experimental Forest, (Tillamook County), Oregon, USA;  
October 16, 1970 (MICH 11626 HOLOTYPE AHSmith79075)

*Field summary* — Medium sized fruitbodies with dark-rimmed, glutinous golden tan to chestnut- or light cocoa-brown conic-campanulate caps, creamy to smoky young gills, slender stuffed orange-banded tan to cinnamon colored stipes, and deeply rooting vertical-monopodial pseudorhizas. Closely gregarious during autumn in northern Oregon coast range coniferous forests.

**PILEUS** — ~30-100 mm diam, conic to convex to broadly campanulate with distinct umbo, uneven margin, and incurved to straight edges, viscid to glutinous, smooth, glabrous, opaque except for obscurely striatulate edges, hygrophanous; color golden to smoky tan (*wood brown*) when young, usually zonate with darker chestnut brown disc or banded edge, rapidly darkening to chestnut- or cocoa-brown, sometimes developing gray or drab overtones in age. —*FLESH* very thin over gills, ≤ 5 mm in disc, pallid. —*ODOR* not distinctive to complex with slightly floral undertones (reminiscent of pansies). —*TASTE* not distinctive. —*DRIED PILEUS* golden to dull bronze metallic.

**LAMELLAE** — Color smoky white to light cinnamon when young, darkening to dull cinnamon in age; edges serrulate in age.

**STIPE** — +/- central, erect, ~30–70 mm above the ground, combined length with pseudorhiza > 200 mm; apex ~8–11(15) mm diam, equal to tapering below, occasionally slightly ventricose; surface dry, matte and minutely longitudinally lined, sometimes becoming shiny or viscid from cap glutin, aerial portion with scattered isolated fibrils; color of young apex ivory to tan, grading to red-orange, orange-brown at ground



Lorelei Norvell

*P. gregaria* fruitbodies photographed after only a few hours after collection [PNW-MS Exeter 2006-6 (L) & PNW-MS a2021204o1-1 (R)] display the dark brown cap colors characteristic of harvested material. The hygrophanous caps become a brassy to bronze metallic after complete drying.

level, usually with a distinctive orange band on the lower portion above the darker pseudorhiza; stuffed with dense fibrillose pallid pith that separates when old or watersoaked; cartilaginous rind  $\leq 2$  mm thick.

**PSEUDORHIZA** — Vertical-monopodial,  $\sim 1/2$ – $2/3$  of overall length, continuous with stipe and gradually tapering to a slender (sometimes cord-like) origin; color dark red brown, staining red orange to maroon.

**VEIL REMNANTS** — Inconspicuous, as isolated brown fibrils or fibrillose patches on the aerial stipe.

**SYRINGALDAZINE REACTIVITY** — Negative on cap, gills, and stipe apex; pseudorhiza usually negative, but often turning faint to deep magenta after 30 minutes.

**FLUORESCENCE** — Under UV, gills do not fluoresce but cap/stipe pith appear deep magenta to a dull deep orange yellow.

**SPORE PRINT** — Smoky dark cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. gregaria* can be recognized by its (1) viscid zonate tan to cocoa colored broadly campanulate cap that dries to a metallic bronze; (2) medium size, slender stature, and densely gregarious habit; (3) tall, slender tan stipes with firm to stringy fibrillose pith and a orange band just above ground level; and (4) gills that do not fluoresce under UV and do not turn magenta in Syringaldazine.

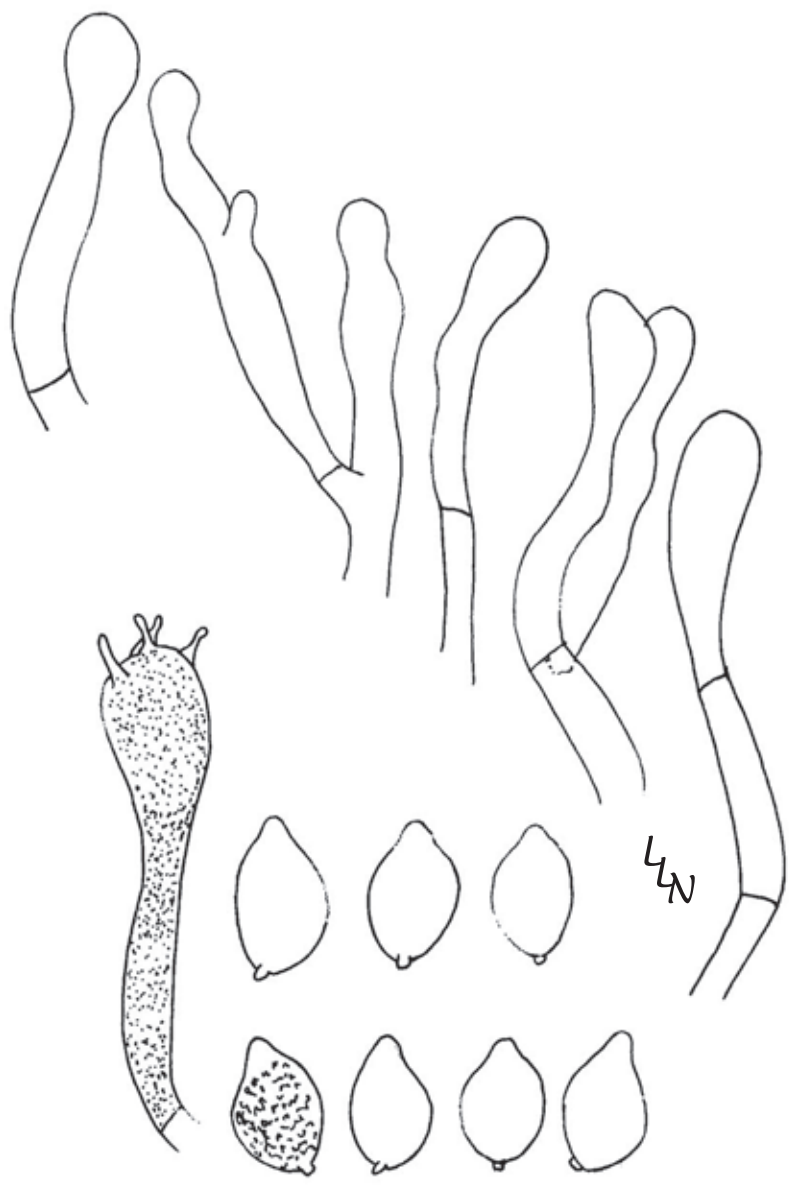
Important microscopical features detailed on the next pages include (1) large ( $\sim 9.6 \times 5.7$ ) punctate-roughened almond-shaped beaked basidiospores, (2) thin-walled variably clavate cheilocystidia, (3) a bilaminate gelatinized pileipellis that lacks encrusting pigments, and (4) lack of clamp connections.

**BASIDIOSPORES** —  $|x| = 9.6 \times 5.7$  [(8)8.9–10(11)  $\times$  5.3–6.1(7)]  $\mu\text{m}$ , ovate-pointed in end view, amygdaliform with eccentric apiculus and small to moderate ( $\leq 2$   $\mu\text{m}$ ) smooth beak in profile view, punctate to verruculose with ornamentation rarely projecting beyond spore outline; color in KOH pale to medium amber, in  $\text{H}_2\text{O}$  paler. — **BASIDIA** 4-spored, clavate and often with rounded upper portion above 2–4  $\mu\text{m}$  diam slender pedicel,  $\sim 30$ – $40 \times 6$ – $9$   $\mu\text{m}$ , colorless to sometimes orangish during spore development, granulose to vacuolate.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, but in rehydrated material usually agglutinated and difficult to separate into isolated elements, arising from the lamellar trama to form a partially sterile edge; terminal lengths variable and indeterminate, variably clavate with narrow, inflated, and mucronate elements intermixed, apical extensions common in old or stored material; all elements thin-walled, colorless.

— **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** occasional on stipe fibrils and abundant on pseudorhizal pellis,  $\leq 20 \times 1$   $\mu\text{m}$  with no septum between base and hyphae, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

CORTICAL TISSUES — *PILEIPELLIS* a bilaminate ixocutis; the top ~400  $\mu\text{m}$  thick suprapellis of uplifted narrow (1–2  $\mu\text{m}$ ), highly gelatinized colorless cylindrical hyphae loosely embedded in a gelatinous matrix; the bottom subpellis with wider (4–7  $\mu\text{m}$ ) gelatinized hyphae and dull brownish to orangish intercellular (diffuse) pigments; 4–6  $\mu\text{m}$  diam colorless oleifers present in both layers, and narrower (2–3  $\mu\text{m}$ ) oleifers with dark orange amber contents present in subpellis. — *STIPITIPELLIS* 20–40  $\mu\text{m}$  thick, hyphae parallel, sparingly branched, long and cylindrical, narrow (~1.5  $\mu\text{m}$ ), thick-walled, colorless.

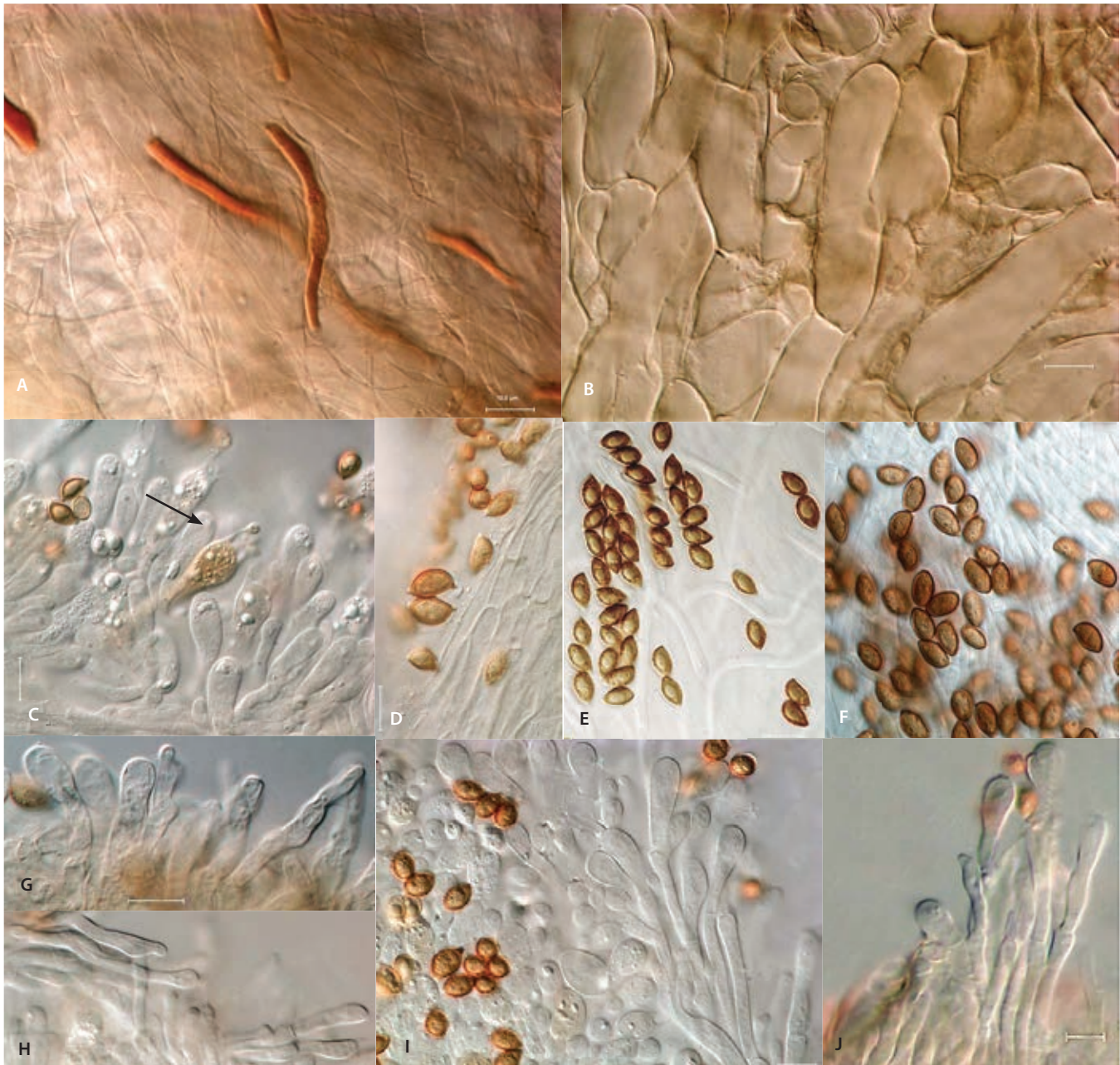


*Phaeocollybia gregaria*

CHEILOCYSTIDIA, BASIDIUM, & BASIDIOSPORES  
 Cascade Head Experimental Forest (Tillamook County), Oregon  
 MICH 11626 HOLOTYPE AHSmith79075

TRAMAL TISSUES — Moderately gelatinized, colorless to pale amber in cap and stipe, sometimes brownish in gills; in pseudorhiza and stipe strongly sarcodimitic, thick-walled (~1  $\mu\text{m}$ ), wide ( $\leq 10 \mu\text{m}$ ), fusoid, rigid vessel hyphal elements intermixed with less conspicuous, branched, thin-walled, narrow (~1.5  $\mu\text{m}$ ), flexuous hyphal elements. — *LAMELLAR* central hyphae parallel with 5–8  $\mu\text{m}$  diam, thin-walled hyphae flanked by a narrow zone of ~3  $\mu\text{m}$  diam elements giving rise to a closely interwoven subhymenium.

CLAMP CONNECTIONS — Absent in all pileus and hymenium tissues, occasionally present in the lower stipe.



Lorelei Norvell

*Phaeocollybia gregaria* [OREGON, PNW-MS. A–B&D–E: Polk Co. ‘Oz’ transect (A–Exeter2006-005, B–Exeter2007-056, D–Exeter2007-056, E–Exeter2006-004); C&F–G: Lincoln Co. Saddlebag Mtn (C–Exeter2007-061, F–Exeter2007-019, G–LLN2071018-14); H–J: Benton Co. Mary’s Pk (H–LLN2071029-27, I–J–LLN2071029-30)]. A–B. PILEUS TISSUES: A–Oleiferous hyphae containing oily colorless to orange pigments can be found in both pileipellis layers and pileus trama. The dull orange to orange brown diffuse pigments in the subpellis do not dissipate in KOH. B–Similar diffuse pigments in the top layer of the pileus trama are usually very faint. C. BASIDIA (arrow) are clavate but generally stand on straight pedicels and have swollen almost subglobose heads. D–F. BASIDIOSPORES [shown on gill trama (D), suprapellis (E), and stipitipellis (F)] are generally almond-shaped and have relatively low ornamentation and short straight beaks. These characters help to differentiate *P. gregaria* from the more lemon-shaped (but similarly verruculose) spores in *P. benzokauffmannii* and the much rougher ‘hump-backed’ spores with abrupt eccentric beaks in *P. olivacea*. G–J. Highly gelatinized CHEILOCYSTIDIA, frequent to abundant on the gill edges, tend to stick together in rehydrated tissues, making their detection difficult. As elsewhere in *Phaeocollybia*, gill sections rarely retain the cheilocystidia, which stick to the razor blade. In the absence of a freezing microtome, cheilocystidia are best revealed by rehydrating a single gill in 3% KOH, placing it flat on a slide, and slicing the edge off to view in a squash mount. The thin-walled *P. gregaria* cheilocystidia are variably clavate, and there are usually many strangulated irregular elements among them. Scales = 10 µm.

**Ecology** — Terrestrial (mycorrhizal); densely gregarious during autumn in Oregon coniferous (*Picea*, *Tsuga*, *Abies*) forests. — OREGON ENDEMIC uncommon to rare; known from only 5 sites within a ~60 square mile area in the coastal headlands and northern Oregon coast range in Benton, Lincoln, Polk, and Tillamook counties.



Ron Exeter

Dry weather young *P. gregaria* specimens already display the diagnostic orange band on the lower stipes.  
The 'Oz' transect (BLM Reserve Forest, Polk County), Oregon — PNW-MS Exeter2006-006

**Similar species** — *Phaeocollybia benzokauffmanii* and *P. olivacea* fruitbodies also have a gregarious habit and tall slender stuffed stipes; like *P. gregaria* they also produce thin-walled cheilocystidia and similarly sized basidiospores and lack clamp connections at basidial bases and cheilocystidial & pileipellis hyphal septa. Young representatives of the more robust *P. benzokauffmanii* also produce smoky white gills, but have drab to pinkish brown (never golden) caps that will help diagnose them in the field; although drying or older *P. gregaria* fruitbodies sometimes acquire a drab coloration. Microscopically, the two species are best differentiated by the pileus suprapellis (which is relatively thin and compact in *P. benzokauffmanii* vs. the thicker loose gelatinous matrix of *P. gregaria*) and the slightly smaller ( $\sim 9 \times 5.5 \mu\text{m}$ ) and more limoniform basidiospores in *P. benzokauffmanii*. Unlike *P. gregaria*, *P. benzokauffmanii* gills fluoresce a brilliant yellow under UV and all tissues turn rapidly magenta in syringaldazine.

Its olive green pileus usually separates *P. olivacea* from *P. gregaria* in the field; nonetheless, the gregarious habit, broadly campanulate caps, and tall stipes may cause dulled specimens that have lost their diagnostic green colors to be mistaken for *P. gregaria*. Basidiospore morphology helps distinguish the two species with a long abruptly protruding beak and dark rough ornamentation extending beyond the spore outline identifying *P. olivacea*.

*Phaeocollybia spadicea* and *P. tibiikauffmanii* also produce closely gregarious, similarly colored fruitbodies with stuffed stipes that could be easily mistaken for *P. gregaria*. A drab stipe apex covered with fairly dense orange fibrillose patches helps differentiate *P. spadicea* in the field. Both species are easily distinguished microscopically by their tibiiform cheilocystidia and smaller basidiospores ( $\sim 8 \times 5 \mu\text{m}$  in *P. spadicea*,  $\sim 8 \times 4.5 \mu\text{m}$  in *P. tibiikauffmanii*). Examination of numerous older *P. gregaria* fruitbodies, however, reveals many cheilocystidia with long hair-like apical extensions that might easily be misinterpreted as representing tibiiform cheilocystidia when viewed under lower magnification, so care must be taken to interpret the cheilocystidia properly before final determination.

See the species listed above and Table 1 in *P. kauffmanii* for additional comparisons.



Ron Exeter

These seven 'gregarious' *P. gregaria* specimens all arose from a single 1-2 cm block of mycelium below the duff. 'Oz' (BLM Reserve Forest, Polk County), Oregon — PNW-MS Exeter2008-26

**Additional comments** — Horak (1977) synonymized *P. gregaria* with *P. piceae* — a smaller, bright orange mushroom with a bitter taste — based on his microscopical comparison of the type collections. It is true that basidial, basidiospore and cheilocystidial morphology are very close in the two species. In fact, the only striking anatomical difference is an extensive ( $\leq 400 \mu\text{m}$  thick) suprapellis composed of a gelatinous matrix containing narrow hyphae that readily separate when rehydrated in *P. gregaria* versus a thinner ( $30\text{--}100 \mu\text{m}$  thick) suprapellis containing slightly wider hyphae 'interwoven in the basal area' (Smith & Trappe, 1972) that tend to retain their close parallel alignment in mountants in *P. piceae*. At the macroscopic level, this distinction is perceived as differences in degree of viscosity, with *P. gregaria* and *P. piceae* producing a viscid to glutinous pileus and moist to merely thinly viscid pileus respectively, although such differences might be attributed to age or environmental factors. The bright orange to red orange cap colors in *P. piceae* clearly differentiate that species from the tan to brown capped *P. gregaria* in the field. In the *P. piceae* pileus subpellis, these diffuse orange pigments rapidly dissolve in KOH, forming pigment pools that eventually dissipate from the mountant over time and individual suprapellis hyphae are often minutely spirally gel-encrusted; neither condition has been observed for *P. gregaria*. Although cap, gills, and stipe tissues are similarly inert in syringaldazine for both species, *P. gregaria* pseudorhizas occasionally do turn magenta. Further, *P. piceae* gills fluoresce bright to dull yellow, while *P. gregaria* gills remain dark under UV. In view of the above differences and the genetic separation implied by preliminary molecular analyses (Norvell 1998), we do not consider *P. gregaria* a synonym of *P. piceae*.

**References with descriptions and /or illustrations of *Phaeocollybia gregaria* —**

- Norvell LL. 1998. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (Agaricales, Cortinariaceae). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [discussion of x, pp. x]
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- Norvell LL, Exeter RL. 2007. *Phaeocollybia* in western North America 5: *P. ochraceocana* sp. nov. and the *P. kauffmanii* complex. Mycotaxon 102: 315–332. [key; comparison table].
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*Phaeocollybia kauffmanii*

*Phaeocollybia kauffmanii* excavation.  
 'Aleuria Glen', Jackson State Forest,  
 Mendocino County, California.  
 WTU LLNorvell 1921124-12  
 [also DAOM & PNW-MS]

Scott Redhead, Agriculture & Agri-Food Canada

*Phaeocollybia kauffmanii* (A.H.Sm.) Singer 1940, Rev. Mycol. 5:11.

≡ *Naucoria kauffmanii* [sic] A.H.Sm., Mycologia 29: 52. 1937.

ETYMOLOGY — In honor of Smith's mentor, C. H. Kauffman, an early 20<sup>th</sup> century agaricologist and author of the influential *AGARICACEAE OF MICHIGAN*.

HOLOTYPE — Lake Tahkenitch (Douglas County), Oregon, USA. 18 November 1935;  
 MICH HOLOTYPE 11572, AHSmith3523.

*Field summary* — Large fleshy fruitbodies with viscid orange to tawny convex-campanulate caps with inrolled edges, pinkish cream colored young gills, firmly stuffed pale pinkish buff to cinnamon stipes, deeply rooting fleshy unbranched pseudorhizas, and a farinaceous odor. Solitary to gregarious in autumn in British Columbia, Washington, Idaho, Oregon, and northern California coniferous rainforests.



Ron Exeter (L), Lorelei Norvell (R)

Orange colors, tightly inrolled cap edge, large stature, and firm stipe pith help identify *P. kauffmanii*.  
Boulder Creek (Polk County), Oregon — PNW-MS Exeter2007-074 (L) & PNW-MS Norvell2081113bc9 (R)

**PILEUS** — Up to 150(–195) mm diam, conic-convex (usually sharply minutely papillate) expanding to broadly campanulate with broad low umbo, margin incurved to upraised, edge strongly inrolled at all times; surface bald, smooth, viscid to heavily glutinous, non-striate; color often zonate with brownish orange to orange-brown disc (*tawny, hazel*), pale to bright brownish orange margin (*orange, ochraceous tawny, amber brown, chestnut*), and deep yellow- to orange-brown edge (*buckthorn brown, (ochraceous) tawny*), occasionally uniformly deep orange-brown or bright brownish orange, damaged areas blackish or deep brown. — **FLESH** firm, confluent through stipe and pileus ( $\leq 10$  mm thick in disc), color pale yellow cream or smoky pink (*pale ochraceous salmon, pinkish buff*) when young, darkening when water-soaked or in age and often with a brown band adjacent to the gills. — **ODOR** usually farinaceous, occasionally not distinctive. — **TASTE** farinaceous, occasionally slightly bitter. — **DRIED PILEUS** metallic dark red copper margin with burgundy colored pointed umbo.

**LAMELLAE** — Narrowly attached (almost free); pale buff when young, darkening as maturing to dull smoky golden brown in age.

**STIPE** — More or less central, rigid,  $\leq 40$ –110 mm above the ground, combined length with pseudorhiza  $\leq 400$  mm; apex 9–25 mm diam, slightly tapering or ventricose and swelling ( $\leq 37$  mm) at ground level before tapering downwards to the pseudorhiza; surface moist to dry, minutely longitudinally lined, appressed fibrillose (hand lens), rarely with fibrillose patches; color of young apex buff, light orange, or pale yellow-brown (*pale pinkish cinnamon, light ochraceous salmon*), aging to cinnamon (*pinkish buff, cinnamon*) above and darkening below to deep orange-brown (*army brown*), when cut staining first orange, then brown; cartilaginous rind 1–3 mm thick, sometimes splitting to reveal pith; stuffed with firm, pale light pink or dull ivory pith that turns deep orange-brown when crushed or cut.

**PSEUDORHIZA** — Vertical-monopodial,  $\leq 5/6$  of overall length, continuous with stipe and gradually tapering to a blunt origin; color uniformly deep red- to orange-brown or paler at the origin.

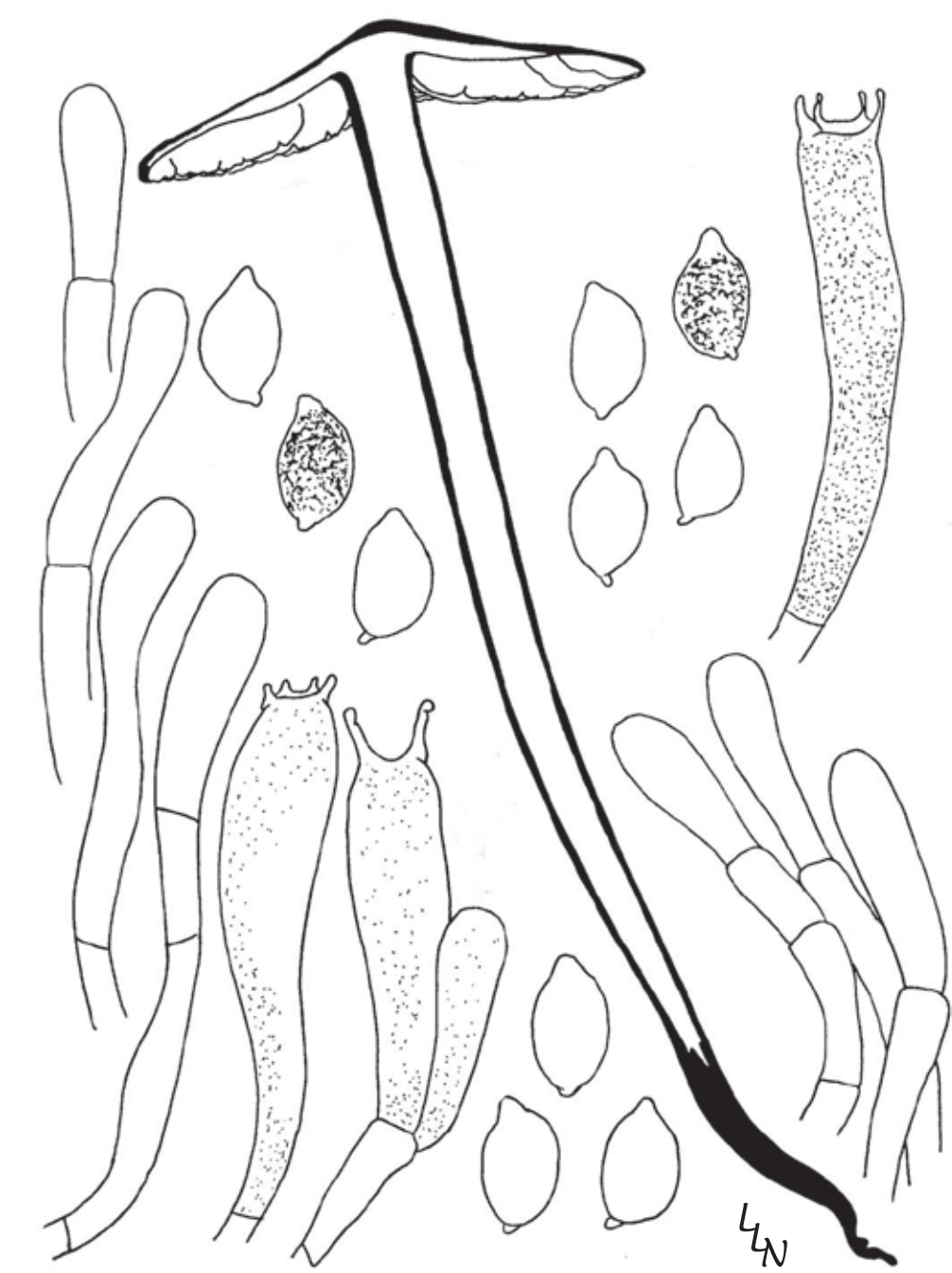
**VEIL REMNANTS** — Inconspicuous, present as scattered fibrils or scant fibrillose patches on stipe apex.

**SYRINGALDAZINE REACTIVITY** — Strongly positive: cap, gills, stipe, and pseudorhiza soon deep magenta.

**FLUORESCENCE** — Under UV gills usually whitish to pale/bright yellow to ochre; stipe pith deep dark red or magenta; cap context occasionally orange.

**SPORE PRINT** — Cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. kauffmanii* can be recognized by its (1) large size and robust stature, (2) viscid orange to ‘pumpkin pie’ colored fleshy cap with inrolled edge, (3) fleshy stipe (usually wider than 11 mm at the apex) stuffed with firm solid pith, (4) reddish copper dried cap with a dark burgundy pointed disc, and (5) all tissues usually magenta in syringaldazine.



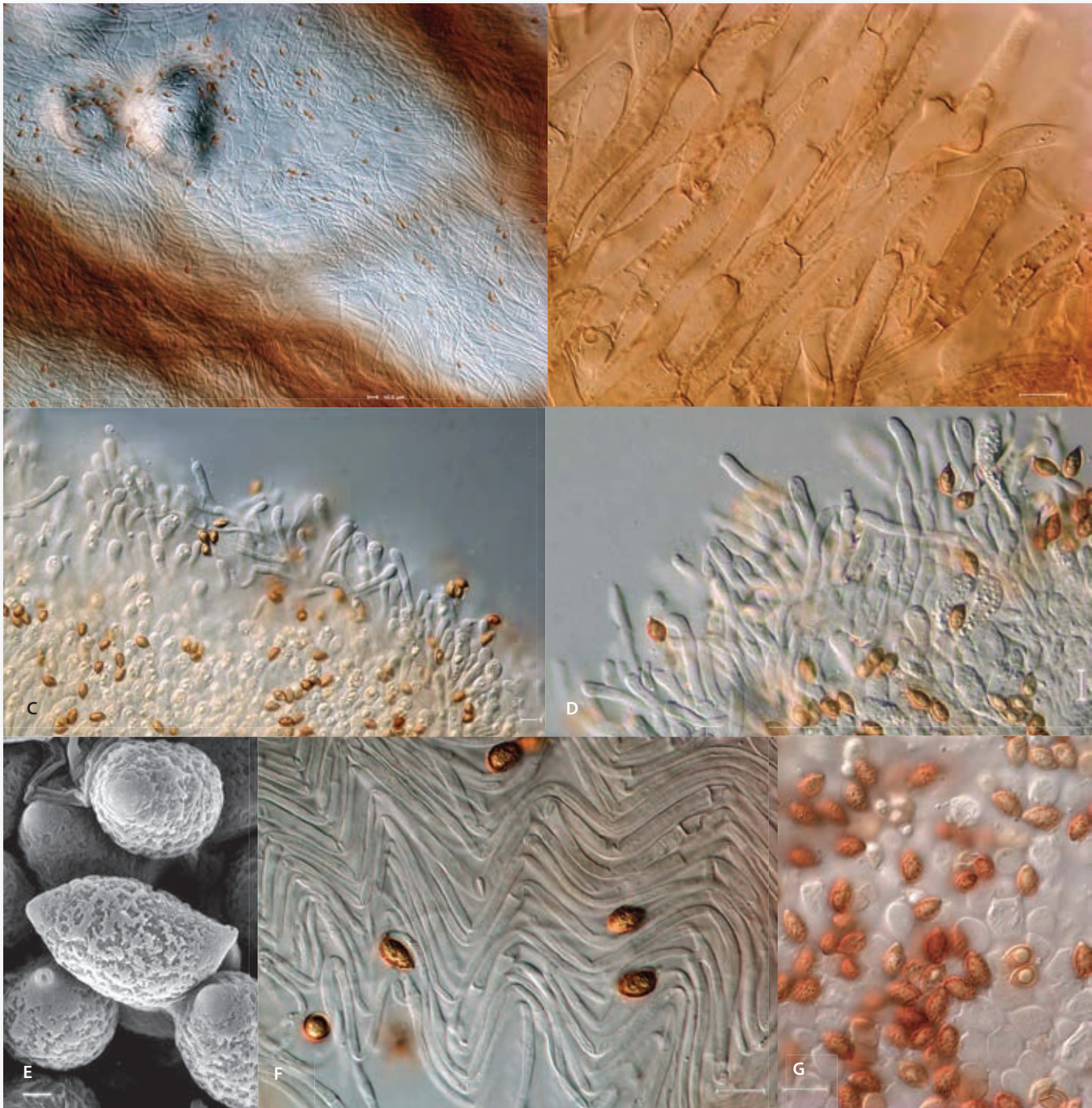
*Phaeocollybia kauffmanii*

A. HABIT. Tillamook County, Oregon — wtU Norvell1951106-4 (Scale = 5cm)

B-C. CHEILOCYSTIDIA, BASIDIA & BASIDIOSPORES (Scale = 10  $\mu$ m)

B: MICH HOLOTYPE AHSmith3523, C: wtU Norvell1941106-20.

Important microscopical features detailed on the next page include (1) large ( $\sim 8.5 \times 5 \mu\text{m}$ ) moderately roughened lemon-shaped basidiospores with pronounced beaks, (2) thin-walled narrowly clavate cheilocystidia, (3) occasional true and false clamp connections in stipitipellis and pseudorhiza, and (4) a two-layered pileipellis with top-layer hyphae loosely embedded in a thick colorless gelatinous matrix overlying a brownish orange subpellis with weakly encrusting pigments.



Lorelei Norvell

*Phaeocollybia kauffmanii*. A–B. PILEIPELLIS: A. [PNW-MS Exeter2007-126]— A squash mount of the cap cuticle seen under low power reveals a thick gel suprapellis with narrow colorless hyphae overlying a subpellis with wider orange hyphae. B. [osc LNus17a15]— High power (100×) oil objective exposes orange pigments encrusting the subpellis hyphae. C–D. CHEILOCYSTIDIA [C—PNW-MS Exeter2007-091; D—PNW-MS LLNorvell2071029-41]: Thin-walled narrowly clavate sterile elements crowd gill edges. E–G. BASIDIOSPORES: E. [MICH HOLOTYPE AHSmith3523]— A SEM of the gill surface displays the limoniform shape, smooth apical callus, and verruculose ornamentation found throughout the *kauffmanii* complex. The slightly downturned beak helps diagnose *P. kauffmanii*. (Scale = 1 μm). F. [PNW-MS Exeter2007-126]— When spore prints are lacking, measurements are taken from mature spores expelled onto the stipe apex, here ‘zig-zagged’ by a shifting cover slip. G. [osc LNus8-4CHj3-1]— Soft focus in oil immersion stresses surface ornamentation. All scales (except E) = 10 μm

**BASIDIOSPORES** —  $|x| = 8.8 \times 5.2$  [7.5–10 × 4–6] μm, terete to slightly compressed, inequilaterally amygdaliform or limoniform in profile, fusoid-elliptical (naviculate) in face view, apiculus prominent and eccentric; surface verruculose to verrucose except on tilted 0.5–1.5 μm long beak; color in KOH medium pale to dark amber, in H<sub>2</sub>O pale yellow-amber, in Melzer’s dextrinoid. —**BASIDIA** (2-)4-spored, clavate, vacuolate to granular, colorless.



*Phaeocollybia kauffmanii* in 'Oz' (Polk Co, OR) — PNW-MS Exeter2008-027

**CYSTIDIAL ELEMENTS** — *CHEILOCYSTIDIA* abundant, arising from the lamellar trama to form a dense highly gelatinous layer; irregularly cylindrical or narrowly clavate, isolated cheilocystidia sometimes catenulate, with terminal lengths variable ( $\leq 50 \mu\text{m}$ ) and often developing long filamentous apical outgrowths in very old or stored fresh material, septa 2–4  $\mu\text{m}$  diam, in mature basidiomes these elements intermixed with (occasionally) broadly clavate or (rarely) subcapitate ( $< 6 \mu\text{m}$  diam) pedicellate elements; all elements thin-walled, highly gelatinized, colorless or (in older basidiomes) with pale amber or brownish oily contents.

— *PLEUROCYSTIDIA* absent. — *TIBIIFORM DIVERTICULA* abundant on mycelia and surfaces of primordia and pseudorhizas, also frequent on veil remnants on stipe apex,  $\leq 20 \times 1 \mu\text{m}$  with no septum between base and hypha, with/without (sub)globose head and/or apical droplet; highly refractive, colorless to pale straw colored.

**CORTICAL TISSUES** — *PILEIPELLIS* a bilaminate ixocutis with very thick (200–700  $\mu\text{m}$ ) colorless gelatinous suprapellis containing long, branching, cylindrical, narrow (2–4  $\mu\text{m}$ ), thin-walled, highly gelatinized, colorless hyphae with refractive septa, this layer overlying a 60–180  $\mu\text{m}$  thick subpellis with inflated hyphae ( $\leq 12 \mu\text{m}$  from 3–5  $\mu\text{m}$  wide septa) and dull orange brown to yellow orange encrusting, intraparietal and intercellular pigments. — *STIPITIPELLIS* a compact 100–150  $\mu\text{m}$  thick layer of parallel, short-branched, narrow (2–4  $\mu\text{m}$ ), thick-walled, highly gelatinized, colorless hyphae slightly inflated at the septa and encrusted with dark brown gelatinous pigments.

**TRAMAL TISSUES** — Sarcodimitic to some degree, highly gelatinized, hyaline or pale amber, and with oleifers present throughout; in the pseudorhiza strongly sarcodimitic, with parallel, cylindrical, long ( $> 200 \mu\text{m}$ ), wide ( $\leq 30 \mu\text{m}$ ), thick-walled (3  $\mu\text{m}$ ), rigid vessel hyphal elements intermixed with less conspicuous, highly branched, narrow (2–3  $\mu\text{m}$ ), thin-walled ( $\leq 0.5 \mu\text{m}$ ) flexuous hyphae; in stipe apex flexuous hyphae widening to 3–4  $\mu\text{m}$  with vessel hyphae narrowing (7–15  $\mu\text{m}$ ) and thinner walled (1  $\mu\text{m}$ ); in the pileus both hyphal types also present. Lamellar central region hyphae parallel, long, 3–4  $\mu\text{m}$  diam, thick-walled hyphae intermixed with occasional highly branched, narrow, flexuous hyphae flanked by a narrow zone of 2–3  $\mu\text{m}$  wide elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Sporadic and rare in stipitipellis and pseudorhizal pellis, absent in all other tissues.

TABLE 11. Diagnostic characters within the *Phaeocollybia kauffmanii* complex (in the broad sense).  
(adapted from Norvell & Exeter, 2007)

SPP. *	PILEUS		SYRINGAL- DAZINE RXN ^	CLAMPS	SPORES		CHEILOCYSTIDIA		PILEIPELLIS		
	Color (yg)	Surface			Shape	Median (range)	Wall	Form	Layers	Suprapellis	# Pigment topography
AMM	ochr. > tawny	viscid smooth	PSR only magenta	present	limoniform beaked	9 × 5.5 μm (8.4-10 × 5-6.5)	thin	clavate: cylindrical > narrow	2	thick, loose in gel hyaline	SUB diff, parietal
BEN	drab > purp-brn	viscid smooth	rapidly magenta	absent	limoniform beaked	9 × 5.5 μm (8-10 × 4.9-6)	thin	clavate: narrow > medium	2	mod. thick, compact in gel, hyaline	SUB diff, cellular
GRE	tan > or-brown	viscid smooth	PSR weakly magenta	absent	limoniform beaked	9.8 × 6 μm (9-10.5 × 5-6)	thin	clavate: narrow, irregular	2	mod. thick, loose in gel hyaline	SUB diff, cellular
KAU	orange > or-brown	viscid smooth	rapidly magenta	rare	limoniform beaked	8.5 × 5 μm (7.5-10 × 4-6)	thin	clavate: narrow > medium	2	thick, loose in gel,hyaline	SUB encl, diff parietal
LIL	tawny > dk brown (gills lilac!)	viscid smooth	GILLS, CAP magenta	absent	limoniform beaked	8 × 5 μm (8-9 × 4.5-5.5)	thin	clavate: narrow > medium	2	thick, loose in gel,hyaline	SUB encl, diff parietal
LUT	ochre	dry, appressed scaly	negative	absent	limoniform beaked	9.8 × 6 μm (9-11 × 5-6.8)	thin	hyphidia & clavate	3	thin, compact, yellow, gel encrusted	SUB+SUP encl, diff, parietal
OCH	ochr. tawny	oily subvisc. scaly	negative	absent	limoniform beaked	7.4 × 4.7 μm (6.5-7.9 × 4.1-5.4)	thin	hyphidia & clavate	3	thin, compact, or-yellow, smooth	SUB+SUP encl, diff parietal
ORE	drab > gray	viscid smooth	rapidly magenta	absent	ellipsoid bullet-nosed	6.8 × 4 μm (6.3-7.2 × 3.6-4.1)	thin	hyphidia & narr. clavate	2	thick, loose in gel, hyaline	SUB encl, diff parietal
RED	pale red brown	viscid smooth	rapidly magenta	rare	limoniform beaked	10.5 × 6 μm (8.5-12 × 5-7)	thin	subglobose subcapitate pedicellate	2	thick, loose in gel, hyaline	SUB encl, diff parietal
SPD	gray-brn > dk brn	viscid smooth	PSR only magenta	absent	limoniform beaked	8 × 5 μm (6-9 × 4-5.5)	thick w thin	tibiiform & clavate	2	thick, loose in gel, hyaline	SUB cellular, parietal
TIB	orange > or-brown	viscid smooth	rapidly magenta	absent	limoniform beaked	8 × 4.5 μm (7.5-9 × 4-5.2)	thick w thin	tibiiform & clavate	2	thick, loose in gel, hyaline	SUB encl, diff

\*Species included are *P. ammiratii* (AMM), *P. benzokauffmanii* (BEN), *P. gregaria* (GRE), *P. kauffmanii* (KAU), *P. lilacifolia* (LIL), *P. luteosquamulosa* (LUT), *P. ochraceocana* (OCH), *P. oregonensis* (ORE), *P. redheadii* (RED), *P. spadicea* (SPD), *P. tibiikauffmanii* (TIB).

^A positive (magenta) syringaldazine reaction indicates laccase in the tissues. \* SUB = subpellis; SUP = suprapellis; encl = encrusting; diff = diffuse.

**Ecology** — Terrestrial (mycorrhizal); solitary to gregarious during autumn in coniferous (*Picea*, *Pseudotsuga*, *Abies*, *Tsuga*, *Pinus*) or mixed (*Tsuga*, *Abies*, *Pseudotsuga*, *Lithocarpus*, *Sequoia*) rainforests. In the PACIFIC NORTHWEST known from ~150 sites (90 believed still extant) from British Columbia, Washington, Oregon, California, and Idaho. Also reported from Mexico and the eastern United States.

**Similar species** — All representatives of the *P. kauffmanii* complex (*P. ammiratii*, *P. benzokauffmanii*, *P. gregaria*, *P. lilacifolia*, *P. luteosquamulosa*, *P. ochraceocana*, *P. redheadii*; see Norvell 1998ab, 2000; Norvell & Exeter 2007) produce medium to very large fleshy fruitbodies with solidly stuffed stipes, vertical-monopodial pseudorhizas, large amber-brown roughened lemon-shaped beaked basidiospores, and thin-walled clavate cheilocystidia. Together with *P. oligoporpa* Singer from Mexico and Central & South America, they represent the world's largest phaeocollybias.

*P. ammiratii*, long mistakenly referred to *P. kauffmanii*, produces less massive fruitbodies that lack pure orange cap coloration and have burgundy flushed stipes. The clamp connections easily seen in the top pileipellis layer and on cheilocystidia separate this species from other members of the complex.

*P. benzokauffmanii* is microscopically the closest to *P. kauffmanii*, with similarly shaped cheilocystidia and only slightly larger spores (~9 × 5.5 μm). Its pileipellis has a significantly thinner top layer and lacks encrusting pigments in the bottom layer. Drab to pinkish brown cap and whitish young gills readily distinguish *P. benzokauffmanii* in the field. Likewise, the dull tawny to dark brown cap and lilac gills readily differentiate *P. lilacifolia* from *P. kauffmanii*.



Lorelei Norvell (L), Ron Exeter (R)

*Phaeocollybia kauffmanii* at Boulder Creek (Polk Co, OR) — PNW-MS Norvell2081113bc9 (L) & PNW-MS Exeter2007-091 (R)

The ochre to yellow tawny *P. luteosquamulosa* and *P. ochraceocana* both produce dry to moist appressed scaly caps and are the only Pacific Northwest phaeocollybias having a three-layered pileipellis with a highly gelatinous colorless middle layer sandwiched between pigmented top and bottom layers. *P. ochraceocana* produces the smallest ( $\sim 7.4 \times 4.7 \mu\text{m}$ ) spores in the complex while the large *P. luteosquamulosa* ( $\sim 10 \times 6 \mu\text{m}$ ) spores are surpassed only by *P. redheadii* in size. The golden-capped *P. gregaria* that ages to drab brown produces similarly large ( $\sim 9.8 \times 6 \mu\text{m}$ ) basidiospores but is readily identified by the diffuse pigments in its bilaminate pileipellis and densely gregarious habit.

*P. redheadii* and *P. kauffmanii* can appear identical in the field, although an experienced phaeocollybia worker can identify *P. redheadii* from cap colors that are yellow brown when young and reddish brown when fully mature. Microscopically, large ( $\sim 10.5 \times 6 \mu\text{m}$ ) basidiospores and distinctive pedicellate (sub)catenulate subcapitate cheilocystidia clearly distinguish *P. redheadii*.

The similar tawny capped *P. tibiikauffmanii* is excluded from the restricted complex by virtue of its thick-walled tibiiform cheilocystidia. Unusually large representatives of *P. piceae* (generally much smaller than most complex species) have more intense red-orange coloration and slender fibrillose lined stipes that are usually so insect infested at ground level that they topple over when collected. Spores and cheilocystidia are very close in the two species, but *P. piceae* lacks incrusting pigments and when mounted in KOH, its diffuse orange pigments disappear entirely after an hour in the mountant.

See TABLE 11 on the opposite page for additional comparisons.

**Additional comments** — Norvell (2000) noted that the holotype of *P. kauffmanii* contained relatively few bulbous cheilocystidia depicted by Smith (1957b) and appeared instead to be dominated by a narrowly clavate cheilocystidia.

*P. kauffmanii* is the most widely reported and commonly collected species within the complex. Bandala (1994; see also Guzmán et al. 1987, Bandala-Muñoz et al. 1989) cites it as the most common *Phaeocollybia* in Mexico's pine-fir forests. The specimen identified as *P. kauffmanii* and cited by Farr & Farr (1976) as occurring in the Great Smokies National Park was determined by Norvell (1998b) to represent an unknown species. Additional collections are needed to determine whether the immature specimen reported from Vermont by Bigelow & Barr (1966) represents *P. kauffmanii*.

*References with descriptions and/or illustrations of Phaeocollybia kauffmanii* —

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Ron Exeter

*Phaeocollybia kauffmanii* in 'Oz'  
Polk County, Oregon — PNW-MS Exeter2008-027

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*Phaeocollybia lilacifolia*

Ron Exeter

*Phaeocollybia lilacifolia* in situ on Saddlebag Mountain  
Lincoln County, Oregon — PNW-MS Exeter2007-022

***Phaeocollybia lilacifolia*** A.H. Sm., 1957, Sydowia Beih. 1: 59.

ETYMOLOGY — From the Latin, meaning lilac 'leaves' (= gills).

LECTOTYPE (*designated here*) — Ipsut Creek Trail near the Carbon River, Mt. Rainier National Park, (Pierce County), WA, USA; September 16, 1952 .

[Large specimen (out of two) in AHSmith 39976 (MICH 11625 'HOLOTYPE'), a mixed collection also containing small specimen believed to represent *P. fallax*. See also Fig. B, p. 101, and discussion beginning on p. 106]

*Field summary* — Medium to moderately large fruitbodies with glutinous tawny to dark brown campanulate caps, lilac young gills, stuffed drab to dull cinnamon colored stipes, and deeply rooting fleshy-unbranched pseudorhizas. Scattered to gregarious during autumn near hemlock, spruce, or true fir in Washington, Oregon, and California forests.

**PILEUS** — ~30–100 mm diam, obtusely conic with an inrolled margin, expanding to plano-umbonate; slimy viscid (glutinous), smooth, bald, opaque, hygrophanous; color when young uniformly tawny or with dark brown umbo, soon after collection darkening, in age dark brown (*cinnamon brown, rood's brown*). —**FLESH** thin on the margins, ≤ 12 mm at the disc, cartilaginous, pallid when dry, drab brown when waterlogged. —**ODOR** complex with floral (pansy), boiled potato, radish, and burnt hair components; in age crushed flesh sharply pungent and less floral. —**TASTE** not distinctive to disagreeable. —**DRIED PILEUS** shiny dark brown or metallic bronze / dark copper.

**LAMELLAE** — Free or narrowly attached, lilac to pale violet (*lobelia violet*) when young, darkening to rusty brown in age.

**STIPE** — +/- central, rigid, ~40–65 mm above the ground, combined length with pseudorhiza >180 mm; apex 8–15(20) mm diam, aerial portion equal to ventricose and swollen at ground level; surface dry, fibrillose,



Lorelei Norvell (TOP), Ron Exeter (BOTTOM)



Two collections display the viscid chestnut brown caps & 'lobelia violet' gills that characterize *P. lilacifolia* in the field. The two photos showing an uncut (TOP-LEFT) and cut (TOP-RIGHT) large specimen highlight the robust stature and ventricose stuffed stipe with the relatively thick cortex also found in the species.

[Saddlebag Mountain, Lincoln County, Oregon, PNW-MS: LLNorvell2071018-12 (TOP), Exeter2008-13 (BOTTOM)]

matte and finely longitudinally lined; colors muted to dull with young apex pale pinkish cinnamon to drab, grading to dull cinnamon at ground level, old stipe more or less uniformly cinnamon drab; stuffed with firm, pallid to cinnamon colored pith; cartilaginous rind ~2-3 mm thick.

**PSEUDORHIZA** — Vertical-monopodial, ~1/2–2/3 of overall length, continuous with stipe and abruptly tapering beneath the swollen subterranean stipe base before narrowing to a relatively thick origin; color pale to dark cinnamon.

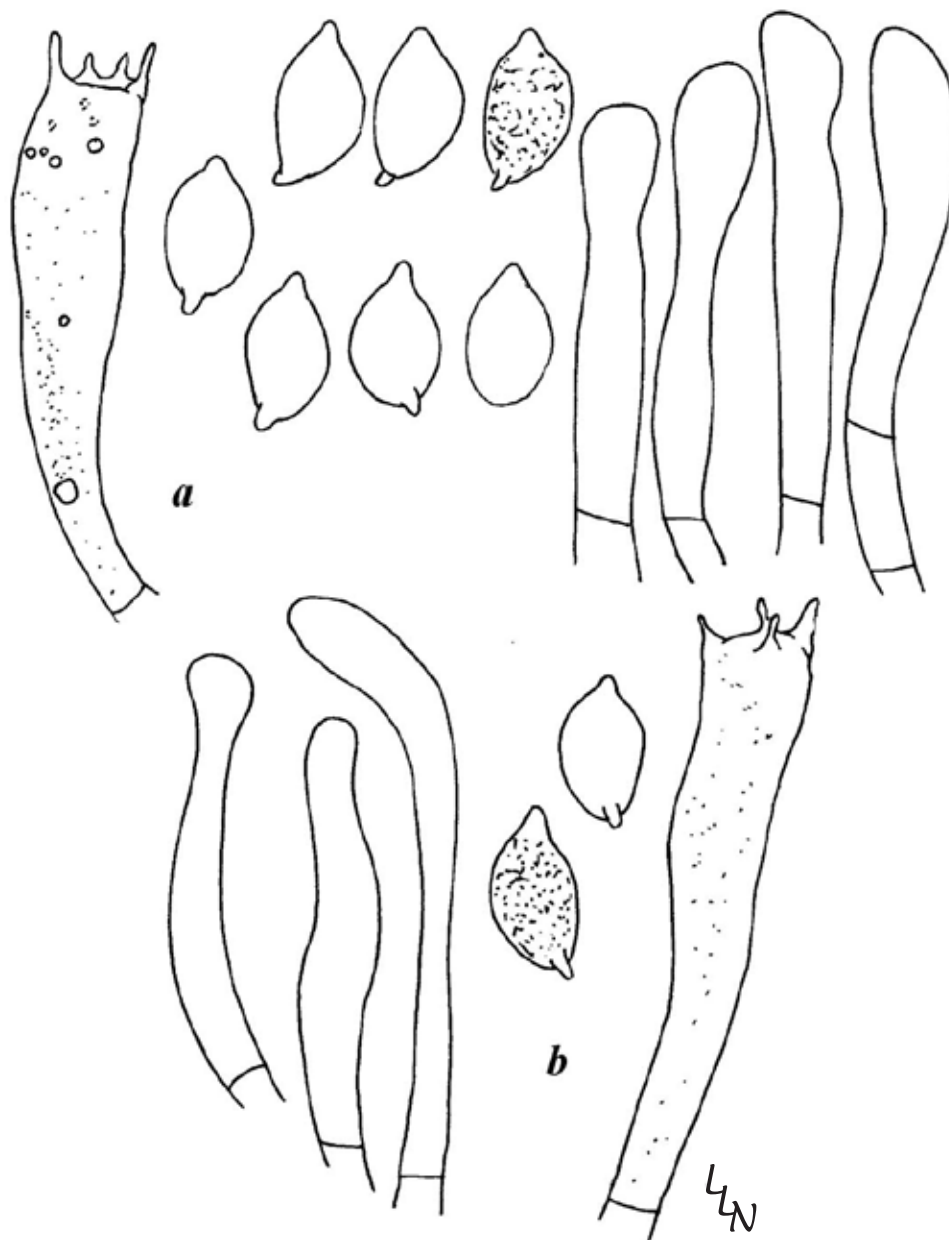
**VEIL REMNANTS** — Present as irregularly arrayed long fibrils or short appressed drab to dull cinnamon brown fibrillose patches on aerial stipe.

**SYRINGALDAZINE REACTIVITY** — Gills and cap turning deep magenta after 5–15 minutes; stipe occasionally producing a pale green exudate; pseudorhiza negative.

**FLUORESCENCE** — Under UV gills fluoresce whitish-yellow and cap & stipe deep dull purple.

**SPORE PRINT** — Pinkish cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. lilacifolia* can be recognized by its (1) viscid tawny to dark brown campanulate cap and lilac colored young gills, (2) robust stuffed drab to dull cinnamon colored stipe, (3) relatively large size, and (4) gills and cap that turn deep magenta in Syringaldazine.



*Phaeocollybia lilacifolia*

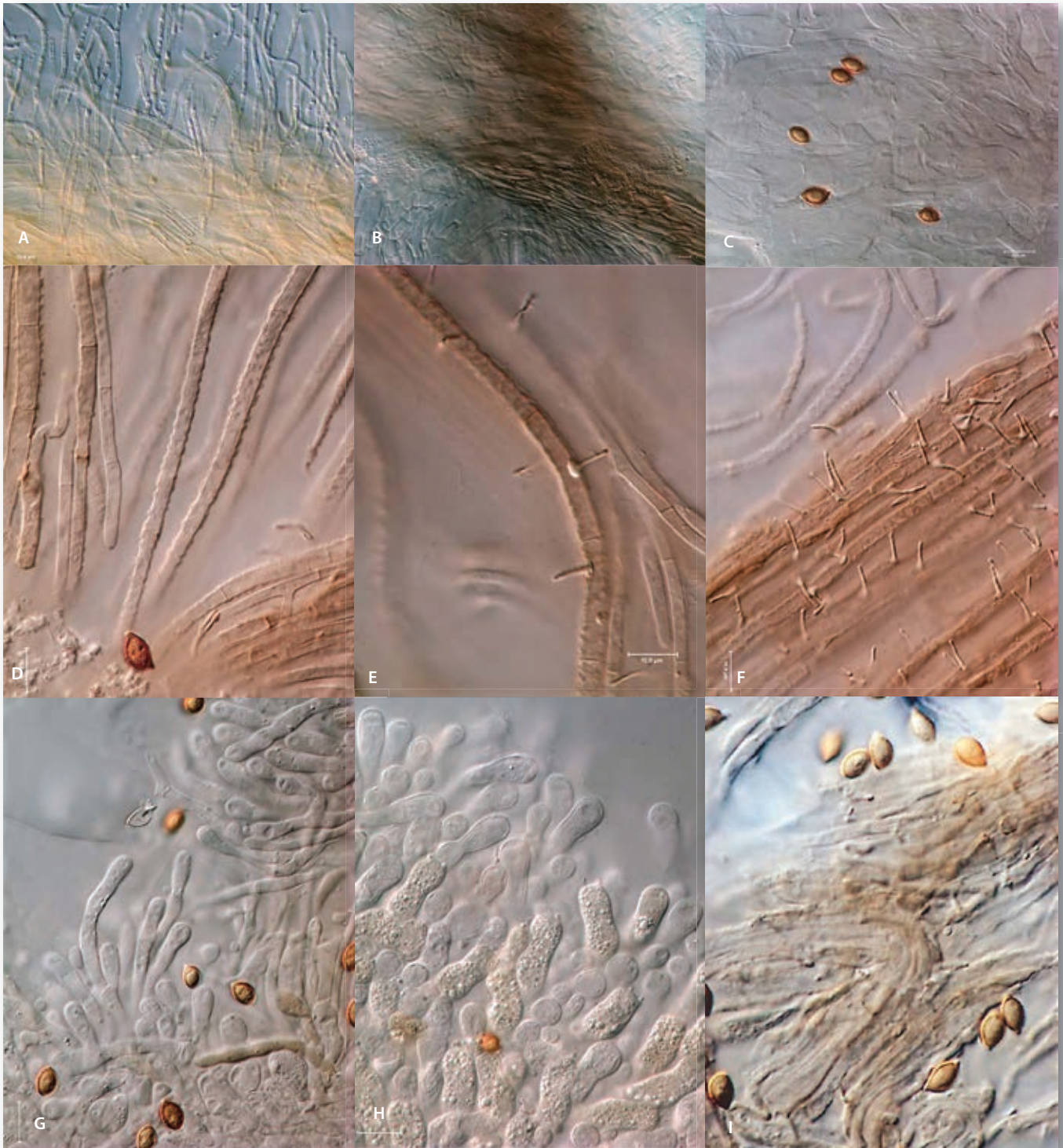
Ipsut Creek (Mt. Rainier National Park, Pierce County), Washington

[MICH 11625 HOLOTYPE AHSmith 39976 (mixed collection with one small & one large specimen)]

A. SMALLER SPECIMEN (= *P. fallax*) — Basidium, basidiospores, cheilocystidia.

B. LECTOTYPE (larger specimen) — Cheilocystidia, basidiospores, basidium.

Important microscopical features include (1) medium-sized (~8 x 5  $\mu\text{m}$ ) verrucose-rugulose (marbled) limoniform & fusoid beaked basidiospores, (2) a sterile gill edge composed of thin-walled, predominantly narrowly clavate cheilocystidia with occasional (sub)capitate elements intermixed, (3) a bilaminar pileipellis that remains brownish in KOH and lacks green pigments in  $\text{H}_2\text{O}$ , and (4) lack of clamp connections.



Lorelei Norvell

*Phaeocollybia lilacifolia* [Saddlebag Mountain, Lincoln Co. OR, PNW-MS: A-2071018-13, B—Exeter2007-23, C—Exeter2007-64, D—F—Exeter 2007-20, G—Exeter2007-22, H—Exeter2007-24; Ipsut Crk, Mt Rainier NP, Pierce Co, WA MICH11625; I—AHSsmith39976 LECTOTYPE]. A–C. PILEUS TISSUES. —A. Sparingly branched long narrow hyphae of the suprapellis within an immature specimen, where diffuse subpellis pigments (at the bottom) appear brownish-yellow (mounted in H<sub>2</sub>O). —B. In mature fruitbodies, diffuse subpellis pigments are drab brown in H<sub>2</sub>O. —C. Five floating spores display a typical 'festiva' shape; pileus pigments do not turn orange in KOH. D–F. VEIL REMNANTS & TIBIIFORM DIVERTICULA. —D. A basidiospore in profile view above gel-encrusted, diverticulate hyphal remnants. —E & F. Tibiiform diverticula, diagnostic of *Phaeocollybia*, emanate from brownish gel-encrusted 'mother' hyphae. Abundant within *P. lilacifolia*, diverticula are typically small (<10 µm long) and lack globose heads. G–H. CHEILOCYSTIDIA & BASIDIA. Most 'cheilos' are narrowly clavate with only slightly swollen heads; many elements have 'sinuous' walls. Prior to sporulation, basidia are highly granular (H). I. BASIDIOSPORES on stipe veil remnants. Typically limoniform spores (profile view) appear 'naviculate' in face view with prow-like pointed beaks and rounded 'sterns'.

Scales = 10 µm



*Phaeocollybia lilacifolia* — Saddlebag Mountain, Lincoln County, Oregon

Mature specimens [left, PNW-MS Exeter2007-23] have broadly campanulate caps with straight edges and dulled lilac gills. The caps and gills at right [PNW-MS Exeter2007-24] exhibit the convex shape with inrolled edges and brilliant lilac coloration characteristic of younger material.

**BASIDIOSPORES** —  $|x| = 8 \times 5$  [ $7.5-9 \times 4.9-5.5$ ]  $\mu\text{m}$ , limoniform to almond-shaped with a tapered apical beak in profile view, fusoid or boat-shaped in face view; the surface obscurely rugulose-verruculose (marbled) except over smooth projecting apical callus; color in KOH pale medium amber (paler in  $\text{H}_2\text{O}$ ). —**BASIDIA** 2- & 4-spored, clavate,  $\sim 35 \times 6-7$   $\mu\text{m}$ , colorless, highly granular.

**CYSTIDIAL ELEMENTS** —**CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a sterile layer; lengths variable and indeterminate ( $\sim 20-38$   $\mu\text{m}$ ), most narrowly clavate to cylindrical with apices  $\sim 3-5$   $\mu\text{m}$  diam intermixed with occasional broadly clavate to subcapitate elements with  $5-6$   $\mu\text{m}$  diam apices, surface often undulating and sinuously irregular, apical extensions from senescent elements rare; colorless or with dull (yellow-)brown contents. —**PLEUROCYSTIDIA** absent. —**TIBIIFORM DIVERTICULA** abundant on pellicular veil, apical stipitipellis and pseudorhizal pellis,  $\sim 10 \times 0.5$   $\mu\text{m}$  with no septum between base and hyphae, with/without (sub)globose head and/or apical droplet; highly refractive, colorless to amber.

**CORTICAL TISSUES** —**PILEIPELLIS** a well-delimited bilaminar ixocutis: the top layer a  $\sim 400$   $\mu\text{m}$  thick loosely tangled turf of long branched narrow ( $2-4$   $\mu\text{m}$ ) colorless hyphae in a thick gelatinous matrix; the  $\sim 400$   $\mu\text{m}$  thick subpellis comprising  $6-10$   $\mu\text{m}$  diam, gel-encrusted colorless hyphae and diffuse drab to pale brown pigments that do not change color in KOH. —**STIPITIPELLIS** composed of long wide ( $10$   $\mu\text{m}$  diam) lightly gel-encrusted hyphae with brownish walls.

**TRAMAL TISSUES** — pileus with occasional dull brown oleifers; pileus and stipe tramas composed of gelatinized thin-walled  $8-12$   $\mu\text{m}$  diam pale brown to drab to colorless hyphae. Lamellar central hyphae subparallel



Ron Exeter (r), Lorelei Norvell (n)

*P. lilacifolia* (A—LEFT: Exeter 2008-34, B—LEFT: Norvell2071018-8) vs. *P. benzokauffmanii* (A—RIGHT: Exeter2008-35, B—RIGHT: Norvell2071018-7) [Saddlebag Mountain, Lincoln Co, OR, PNW-MS]. Differentiating between the two ‘drab’ members of the *P. kauffmanii* complex is difficult, particularly when mature gills have lost their hallmark lilac or white coloration and old caps and stipes display similar colors. Subtle field distinctions for *P. lilacifolia* include mature caps that are tawny to orange-brown (lacking drab tones), thin-fleshed, and acutely conic-campanulate and orange-cinnamon lower stipes and pseudorhizas. *P. benzokauffmanii* has thick-fleshed convex-umbonate caps with persistently inrolled edges and onion pink to pinkish cinnamon stipes lacking orange hues. Although *P. benzokauffmanii* (to the right in both photos above) is usually much larger than *P. lilacifolia*, size alone is an unreliable field character, as is shown by the *P. lilacifolia* pseudorhizal remnant (B—LEFT) that dwarfs the young *P. benzokauffmanii* to the right.

3–5  $\mu\text{m}$  diam, thin-walled, colorless to faintly drab colored, flanked by a narrow zone of 2–3  $\mu\text{m}$  diam similarly colored elements giving rise to a compact subhymenium.

CLAMP CONNECTIONS — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to gregarious during autumn in *Abies*, *Piceae*, *Tsuga*, and other moist coniferous forests. —PACIFIC NORTHWEST ENDEMIC uncommon to rare, known from scattered locations in Washington (Mt. Rainier Park), Oregon (Clackamas, Lane, Lincoln, and Tillamook counties) and California (under spruce in Humboldt County’s Redwood National Park).

**Similar species** — *Phaeocollybia lilacifolia* overlaps into two different ‘complexes’, both represented by species possessing ‘beaked’ ornamented brown basidiospores and thin-walled clavate cheilocystidia. Within the *P. kauffmanii* complex, *P. lilacifolia* and *P. benzokauffmanii* share drab coloration, moderately large stature, strong syringaldazine reactivity, and narrowly clavate cheilocystidia; *P. benzokauffmanii* is distinguished by its whitish gills, convex drab pileus with persistently inrolled edges, stipe and pseudorhiza that turn deep magenta in syringaldazine, and larger ( $\sim 9 \times 5.5 \mu\text{m}$ ) sublimoniform basidiospores.

Its lilac gills and ‘marbled’ fusoid basidiospore morphology places *P. lilacifolia* with *P. fallax* and *P. riffliipes* in the *P. festiva* complex. *P. fallax* is easily distinguished by its smaller stature, green cap, shiny fragile loosely fibrillose stuffed to hollow stipe, gills that do not react in syringaldazine, a pileipellis that turns orange in KOH, and larger ( $\sim 9 \times 5.5 \mu\text{m}$ ) basidiospores. *P. riffliipes*, which shares tawny to dark brown cap colors and similarly drab stipe with *P. lilacifolia*, is differentiated by its smaller, fragile stature, negative syringaldazine reactivity, and smaller ( $\sim 7 \times 4.5 \mu\text{m}$ ) basidiospores.

See *P. benzokauffmanii*, *P. fallax*, *P. riffliipes* and TABLES 10 (p. 83) & 11 (p. 96) for additional comparisons.

**Additional comments** — Horak (1977) synonymized *P. lilacifolia* with *P. fallax* based on his microscopical examination of the holotype but unfortunately was sent only part of the type on loan (Horak, pers. comm. 1996). Norvell (1998a,c) was able to examine the entire type collection, AHSmith 39976. The collection,



*P. lilacifolia* in situ on Saddlebag Mountain  
Lincoln County, Oregon — pnw-ms Exeter2007-20

made by Smith in Mt. Rainier Park in 1952 (Smith 1957a), contained only one large specimen and one small specimen. Basidiospores from the large specimen averaged  $8 \times 5 \mu\text{m}$  (well within the  $7\text{--}8.5 \times 5.5 \mu\text{m}$  range cited in Smith's diagnosis) and the cheilocystidia were thin-walled and narrowly clavate. The smaller specimen, however, produced much longer and more elongate spores ( $\sim 9 \times 5 \mu\text{m}$ ) and a mix of subcapitate and capitate cheilocystidia, both characters more diagnostic of *P. fallax*, leading Norvell (1998a,c) to conclude that AHSmith 39976 represents a mixed collection.

Unfortunately while Smith (1957a) cited the smaller spore size for *P. lilacifolia* in his type description, he appears to have based his description of the cheilocystidia ("filamentous-subcapitate with the enlarged part  $4\text{--}9 \mu\text{m}$  or clavate and the broadest part  $6\text{--}9 \mu\text{m}$ ") on observations of tissues from the smaller specimen. His description of the stipe as 'hollow' also contradicts what we have observed in our own collections. Outside of those two anomalies, however, Smith's remaining description, as well as a watercolor by his wife, Helen V. Smith (now held in the library of Nancy Smith Weber), match what we refer to here as *P. lilacifolia*.

We infer that Horak received on loan the smaller specimen with the larger spores and more broadly clavate cheilocystidia, which we also refer to *P. fallax*. We believe that the larger specimen with the smaller spores and narrower cheilocystidia (not seen by Horak) represents the true *P. lilacifolia* type specimen. Therefore, in accordance with the International Code of Botanical Nomenclature (McNeil & al. 2006), we designate the larger specimen belonging to AHSmith 39976 (MICH) the **lectotype** of *Phaeocollybia lilacifolia*.

Our technical description (above, pp. 100–104) combines observations by Smith (1957a&b) and Norvell (1998a,c) with our own notes made from fourteen 2007 & 2008 collections from Saddlebag Mountain (Lincoln County) and Lobster Creek (Lane County) in Oregon, all of which conform microscopically to Smith's own collections from Washington (Pierce County) and Oregon (Tillamook County).



Ron Exeter (L), Lorelei Norvell (R)

*P. lilacifolia* [Saddlebag Mountain, (Lincoln Co), OR — PNW-MS Exeter2007-23]. Comparison of a collection photographed *in situ* (L) and twelve hours later (R) after the orange and lilac tones present in the field have begun to darken and dull.

*References with descriptions and /or illustrations of Phaeocollybia lilacifolia —*

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Smith AH. 1957a. Additional new or unusual North American agarics. Beih. Sydowia 1: 40-61. [type description, p. 59].

Smith AH. 1957b. A contribution toward a monograph of *Phaeocollybia*. Brittonia 9: 195-217. [key; microdrawings p. 201, descr. pp. 200 & 202.]



Ron Exeter

*P. lilacifolia* at Lobster Creek  
Lane County, Oregon — PNW-MS Exeter2008-47



*Phaeocollybia luteosquamulosa*

The type collection of *P. luteosquamulosa* in situ at 'Aleuria Glen'  
Jackson State Forest, Mendocino County, California — WTU HOLOTYPE (DAOM & PNW-MS isotypes) S.A.Redhead 7481

*Phaeocollybia luteosquamulosa* Norvell 2000, Can. J. Botany 78: 1068.

ETYMOLOGY — From the Latin for yellow (*luteo-*) + little scales (*squamulosa*)

HOLOTYPE — Jackson State Forest (Mendocino County), CA, USA;  
24 November 1992 (WTU holotype S.A.Redhead 7481; DAOM isotype).

*Field summary* — Large fleshy fruitbodies with dry to lubricous appressed scaly ochraceous to peach colored convex-campanulate caps with strongly inrolled edges, yellowish young gills, firmly stuffed ochre- to salmon-colored robust stipes, and deeply rooting fleshy unbranched pseudorhizas. Solitary to scattered during autumn in California, Oregon, and Washington coniferous and mixed rainforests.

**PILEUS** — Up to 110 mm diam, convex expanding to conic-umbonate or broadly campanulate with incurved margin and tightly inrolled edge; surface moist to dry, sparsely silky with short appressed scales on outer margin and edge, non-striate, hygrophanous; color some shade of ochre yellow overall (*ochraceous tawny*, *ochraceous buff*, *antimony yellow*), often with disc darker (*russet*, *dresden brown*), outer margin brighter or paler (*antimony yellow*, *buckthorn brown*), damaged areas darker (*russet*, *sudan brown*), and scales tawny to pale orange (*tawny*, *ochraceous orange*). — **FLESH** firm, confluent through stipe and pileus ( $\leq 11$  mm thick in disc); color creamy. — **ODOR** not distinctive to faintly raphanoid when cut or crushed. — **TASTE** not distinctive or (more often) bitter. — **DRIED PILEUS** brown, often with a dull orange margin.

**LAMELLAE** — Yellowish white to orange cream when young, ochraceous to yellow brown in age.

**STIPE** — More or less central, rigid, ~30–80(–100) mm above the ground, combined length with pseudorhiza  $\leq 400$  mm; apex 8–20 mm diam, equal, tapered, or ventricose; surface matte, finely longitudinally lined, dry,



Lorelei Norvell

Young and mature *P. luteosquamulosa* specimens display the characteristic ochraceous to peach colors in pileus and stipe. Brownish areas develop in exposed specimens; note the cartilaginous stipe cortex splitting to expose inner pith of the largest specimen [Mary's Peak summit meadow (Benton County), OR, PNW-MS LLN2071029-33].

appressed fibrillose (hand lens), apex occasionally bearing scattered orange brown fibrillose patches; color of apex some shade of buff (*orange / (light) ochraceous / warm / pinkish buff*) or ochre (*antimony yellow*), grading to pale orange brown (*orange cinnamon, cinnamon rufous*) at ground level, where bruised staining orange (*zinc orange*); stuffed with firm, cream-colored pith; cartilaginous rind 2-3 mm thick.

**PSEUDORHIZA** — Vertical-monopodial,  $\leq 5/6$  of overall length, continuous with stipe and gradually tapering to a loosely coiled or straight blunt origin; color dark red-brown above a paler or darker origin.

**VEIL REMNANTS** — Inconspicuous, evident (i) on unexpanded specimens as isolated fibrils connecting cap margin to stipe and (ii) in mature basidiomes as scattered, small appressed pileal scales (more conspicuous when dry) and scattered fibrillose patches on the exposed stipe; color yellow-orange.

**SYRINGALDAZINE REACTIVITY** — All tissues negative, except (rarely) extreme pseudorhizal pellis turning magenta after 30 minutes.

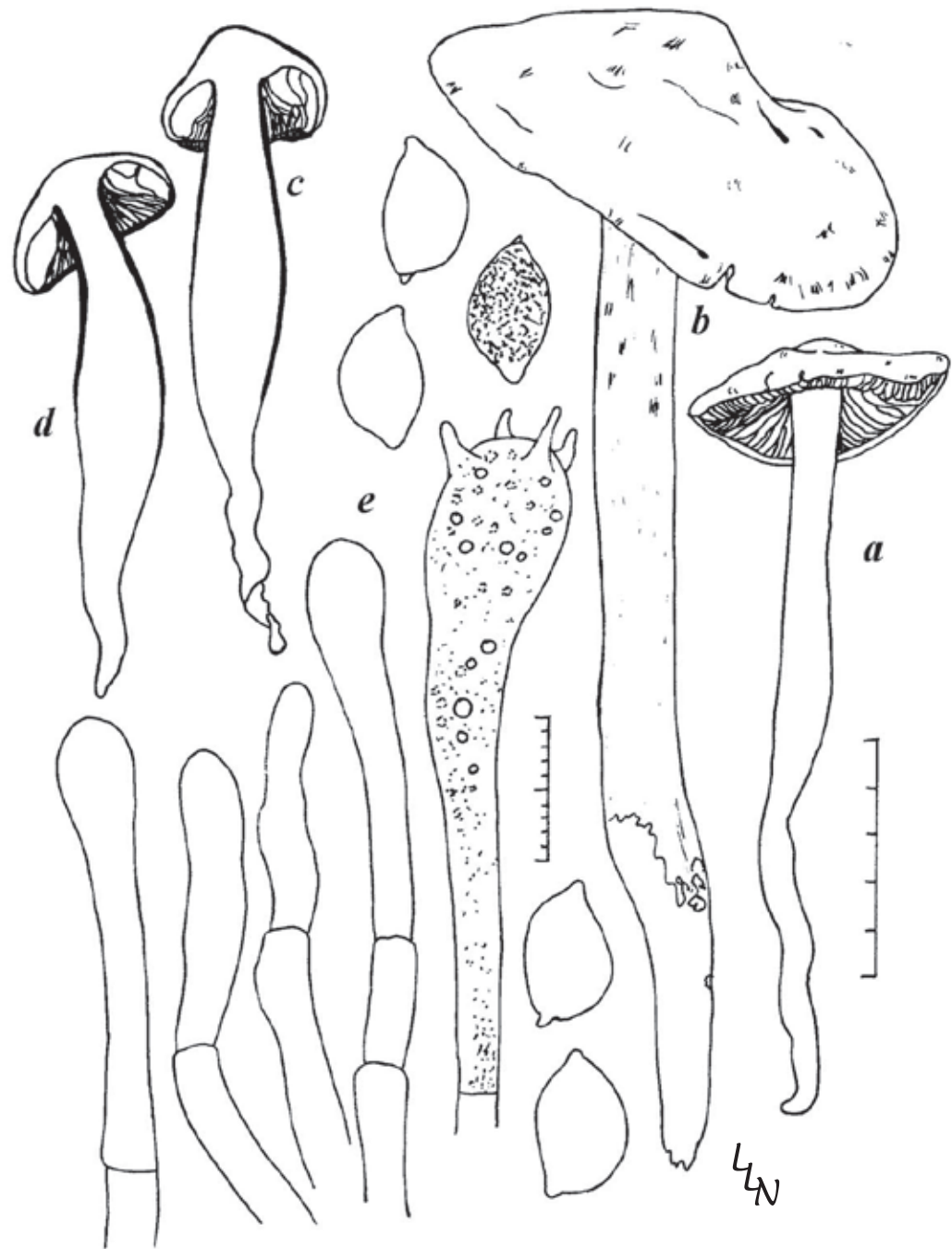
**FLUORESCENCE** — Gills whitish yellow (young) to brilliant mustard yellow (mature); context orange to deep dark magenta.

**SPORE PRINT** — Pale cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. luteosquamulosa* can be recognized by its (1) appressed scaly, dry to moist, yellow-ochre convex to campanulate cap with inrolled edge, (2) medium to large size, and (3) stuffed stipe and thick vertical-monopodial pseudorhiza.

Important microscopical features detailed on the next page include (1) large ( $\sim 10 \times 6 \mu\text{m}$ ) roughened almond- to lemon-shaped spores, (2) broadly clavate thin-walled cheilocystidia that are often gel-incrusted,

(3) absence of clamp connections, and — most important — (4) a three-layered pileipellis with a compact gelatinous colorless middle layer sandwiched between yellow pigmented top and bright orange bottom layers with gel encrusted hyphae in all three layers.

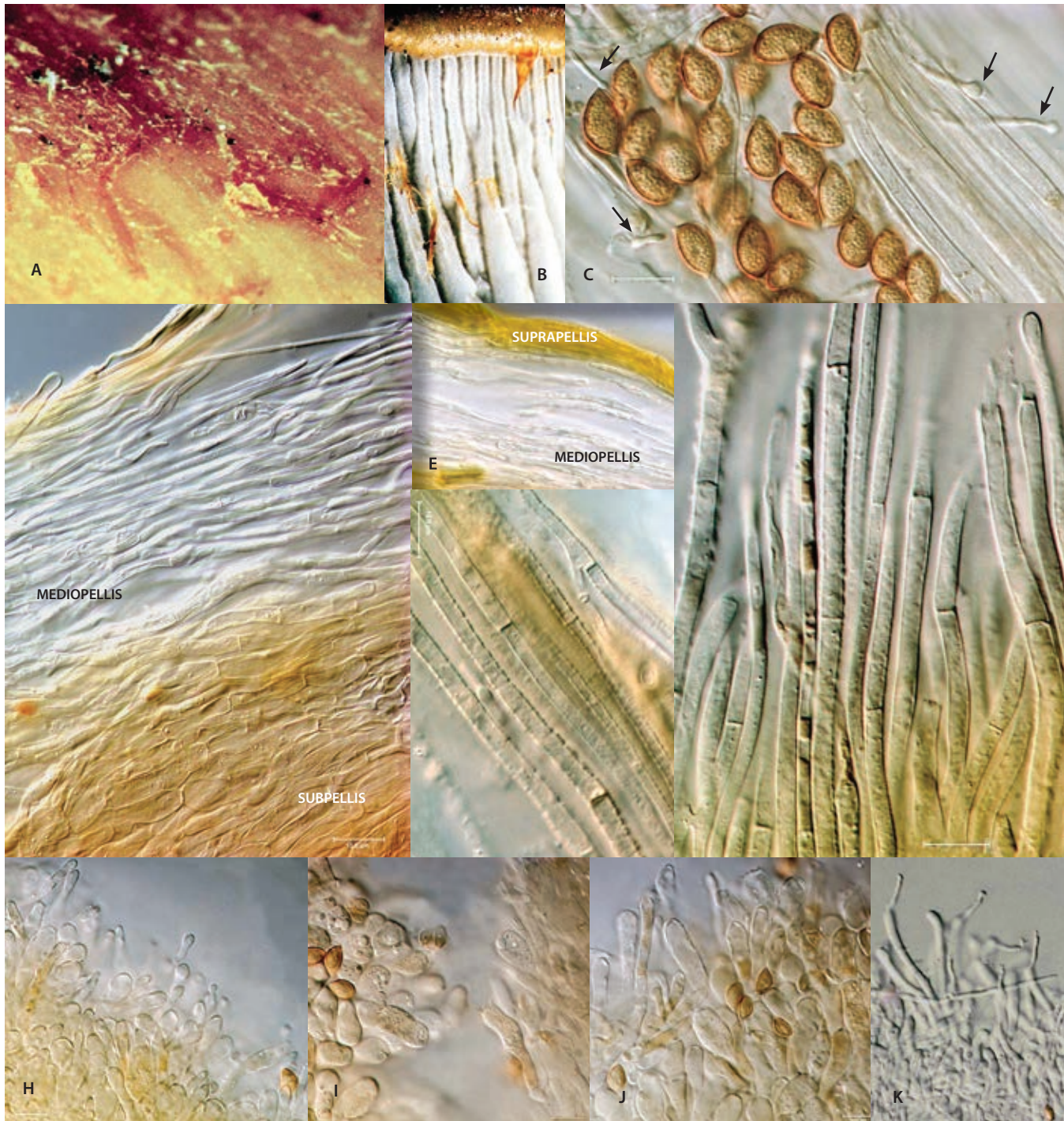


*Phaeocollybia luteosquamulosa*

A-D. HABIT — A: WTU HOLOTYPE SAREdhead7481, B: WTU LLN1921124-1,  
C: WTU LLN1940907-1, D: WTU LLN1931105-9.

E. BASIDIOSPORES, BASIDIUM, CHEILOCYSTIDIA — WTU LLN1931024-10.

BASIDIOSPORES —  $|x| = 10 \times 6$  [8.7–12  $\times$  5–7.2]  $\mu\text{m}$ , terete in end view, broadly amygdaliform to limoniform in profile, verruculose with exosporium irregularly projecting beyond outline except on 1–1.5  $\mu\text{m}$  long mammiform apex and distinct eccentric apiculus; color in KOH medium amber, in  $\text{H}_2\text{O}$  paler, in Melzer's inamyloid and nondextrinoid. — BASIDIA 4-spored, clavate, granular to vacuolate, colorless to yellowish.



Lorelei Norvell

*Phaeocollybia luteosquamulosa* [CA: Mendocino Co, Jackson SF, Aleuria Glen — E: WTU LLN1921124-1. OR: Benton Co, Mary's Pk — C: PNW-MS Exeter2007-051, D: PNW-MS Exeter2007-125, G: PNW-MS LLN1071029-24; Lincoln Co, Saddle Bag Mtn — F: PNW-MS Exeter2007-016; Multnomah Co, Larch Mtn — A: WTU LLN1931105-9, B: WTU LLN1931024-6, H-J: PNW-MS LLN2001105-9, K: LLN1941011-18]. A-G. THE PELLICULAR SHEATH: A, D-G—PILEIPELLIS. Appressed fibrillose patches (A) on mature pileus surfaces and remnants of the pellicular sheath across the gills (B) are visible to the naked eye; the sheath comprises the thin top layer (D-E) of the trilaminar pileipellis. *P. luteosquamulosa* hyphae are gel-encrusted in the mediopellis (E) and both gel- and pigment-incrusted in the top and bottom layers (G) where KOH-soluble diffuse orange pigments are also found. C—BASIDIOSPORES & TIBIFORM DIVERTICULA (arrows) on pellicular sheath hyphae from the stipe apex. H-K. CHEILOCYSTIDIA AND BASIDIA: Colorless to yellowish oily contents usually coat the inside walls (H, J) of the abundant clavate sterile elements on the gill edge; basidia (I) are usually granular to vacuolate. Cheilocystidial apical outgrowths (K) are common in older specimens. Scales = 10  $\mu$ m.

**CYSTIDIAL ELEMENTS** —CHEILOCYSTIDIA abundant, arising from the lamellar trama to form a distinct gelatinous layer; terminal lengths variable ( $\leq 38 \mu$ m), septa  $\sim 3 \mu$ m diam with apices either cylindrical and not appreciably inflated or broadly clavate/slightly subcapitate  $\leq 9 \mu$ m diam, often developing long filamentous



Lorelei Norvell

Ochraceous colors and tiny cap scales diagnose this *P. luteosquamulosa* collection [PNW-MS Exeter2007-050] from a noble fir stand below Mary's Peak summit in Benton County.

apical outgrowths in very old or stored fresh materials; all elements thin-walled, highly gelatinized, colorless to amber gel-incrusted. —*PLEUROCYSTIDIA* absent or present only (and not diagnostic) as occasional hyphidia (1-2  $\mu\text{m}$  diam) in mature specimens. —*TIBIIFORM DIVERTICULA* rare to occasional on pileal scales, frequent on stipe fibrillose patches, and prolific on the pseudorhizal surface,  $\leq 30 \times 2 \mu\text{m}$  with no septum between base and hypha, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** —*PILEIPELLIS* a trilaminar ixocutis with brilliant orange yellow oleiferous hyphae running throughout; the suprapellis consisting of 1-4 pellicular sheath remnant hyphae that are radially aligned, each 5  $\mu\text{m}$  wide, slightly gelatinized, rarely diverticulate, with KOH-soluble brilliant yellow-orange encrusting pigments and yellow intraparietal pigments that congregate at the refractive septa; the 75–110  $\mu\text{m}$  thick, colorless mediopellis of unbranched, cylindrical, 2-5  $\mu\text{m}$  wide, highly gelatinized hyphae that are usually gel-encrusted; and the ~100  $\mu\text{m}$  thick orange-yellow to orange subpellis of thin-walled, ventricose and inflated (to 15  $\mu\text{m}$  diam), gelatinized hyphae with intraparietal, diffuse, and encrusting pigments. —*STIPITIPELLIS* a compact layer of parallel, long, cylindrical, thick-walled, narrow (4  $\mu\text{m}$  wide), highly gelatinized hyphae with orange-yellow pigments that may form tiny crystals in KOH mountants.

**TRAMAL TISSUES** — Moderately gelatinized throughout; in the pseudorhiza strongly sarcodimitic, with long (>200  $\mu\text{m}$ ), wide ( $\leq 15 \mu\text{m}$ ), thick-walled ( $\leq 2 \mu\text{m}$ ), rigid, colorless vessel hyphal elements intermixed with and supported by highly branched, narrow (2–3  $\mu\text{m}$ ), thin-walled (~0.25  $\mu\text{m}$ ), colorless flexuous hyphae; in stipe apex both types widening (vessel to 30  $\mu\text{m}$ , flexuous to 6  $\mu\text{m}$  diam) and vessel hyphal walls thinning to 1  $\mu\text{m}$ ; in the pileus not noticeably sarcodimitic, hyphae inflated, thin-walled, orange. Lamellar central region hyphae parallel, cylindrical, 3-6  $\mu\text{m}$  diam, thin-walled, colorless; center flanked by a narrow zone of 2–3  $\mu\text{m}$  diam hyaline elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to clustered during early autumn in highly humic soils in inland mature or old-growth coniferous (*Abies*, *Tsuga*) forests in Washington and Oregon or mixed (*Tsuga*, *Abies*, *Lithocarpus*, *Sequoiadendron*) forests in coastal northern California. **PACIFIC NORTHWEST ENDEMIC** — Uncommon to rare; known from 9 sites in Washington, Oregon, and California.

**Similar species** — Of the known phaeocollybias, only *P. ochraceocana* combines the robustness, ochraceous coloration, and non-viscid, scaly cap that diagnose *P. luteosquamulosa* in the field. We place both Pacific Northwest endemics, which share an unusual three-layered pileipellis structure, in the *P. kauffmanii* complex for medium to large fleshy mushrooms characterized by firmly stuffed stipes, unbranched fleshy pseudorhizas, large roughened lemon-shaped amber-brown spores, and thin-walled clavate cheilocystidia that form long apical extensions in age. Except for slightly paler young gills and a slightly darker pileus, *P. ochraceocana* appears virtually identical to *P. luteosquamulosa* in the field. Microscopically, *P. ochraceocana*



Ron Exeter

*P. luteosquamulosa* specimens from a noble fir stand near Mary's Peak summit (Benton Co, OR, PNW-MS Exeter2007-016) show appressed cap squamules.

is easily distinguished by its much smaller ( $\sim 7.8 \times 4.9 \mu\text{m}$ ) spores, lack of encrusted hyphae in the mediopellis, and non-incrusted cheilocystidia. *P. luteosquamulosa* occurs most frequently in forests where *Abies* is present, while *P. ochraceocana* thus far appears restricted to *Pseudotsuga*/*Tsuga* forests.

Before it was described (Norvell 2000), *P. luteosquamulosa* was erroneously referred to *P. kauffmanii*, which has a viscid to glutinous pileus, never develops squamules on the cap surface, has smaller spores ( $8.5 \times 5$ ), and a two-layered pileipellis.

See *P. ochraceocana* and TABLE 11 (p. 96) for additional comparisons.

**Additional comments** — *Phaeocollybia luteosquamulosa* helped establish that all *Phaeocollybia* basidiomes develop within a universal veil (see pp. 15–16). The diagnostic 3-layered pileipellis comprises a narrow bright yellow orange top layer, a compact colorless gelatinized middle layer, and an orange bottom layer (p. 110, FIGS D–E). Most other phaeocollybias retain only the colorless mediopellis (then termed the ‘suprapellis’) and the pigmented subpellis, as the top pellicular sheath sloughs off into the soil during upward growth.

The non-viscid *P. luteosquamulosa* cap can lead to problems in recognizing it as a phaeocollybia in the field, particularly in dry weather. During a field excursion in California's Jackson State Forest, fellow collectors handed Norvell what they thought represented another pseudorhizal species, the white-spored *Caulorhiza umbonata*. Pleased at the prospect of comparing two different pseudorhizal types, she examined the dry ‘caulorhiza’ later that evening, only to discover that the non-viscid specimen represented an as-yet undescribed new phaeocollybia. Scott Redhead and George Barron photographed and collected the type specimens the next day.

**References with descriptions and /or illustrations of *Phaeocollybia luteosquamulosa* —**

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales, Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [key; description pp. 170173, 362–363; microdrawing & color photos pp. 31, 41, 246–247]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. [photos pp. 617, 622]
- Norvell LL. 2000. *Phaeocollybia* in western North America 1: The *Phaeocollybia kauffmanii* complex. *Can. Journ. of Botany* 78: 1055–1076. [key; type description, drawings and b&w photos, pp. 1068–1071]
- Norvell LL, Exeter RL. 2007. *Phaeocollybia* in western North America 5: *P. ochraceocana* sp. nov. and the *P. kauffmanii* complex. *Mycotaxon* 102: 315–332. [key, comparison table, b&w photo (p. 325)].

*Phaeocollybia ochraceocana*

Complete type collection of *P. ochraceocana* in situ in 'Oz'  
BLM Research Forest, Polk County, Oregon — wtU Exeter 2007-033

***Phaeocollybia ochraceocana*** Norvell & Exeter 2007, Mycotaxon 102: 315–332.

ETYMOLOGY — From the Latin *ochraceo-* + *-cana* for the canescent sheen that develops as the drying ochraceous top pileus layer lifts slightly up from the lower tissues.

HOLOTYPE — Pedee old growth chronosequence transect, BLM Reserve Forest, Pedee (Polk County), OR, USA; 11 October 2007 (MYCOBANK 511266. WTU HOLOTYPE Exeter2007-033; PNW-MS, OSC isotypes.).

*Field summary* — Large fleshy fruitbodies with lubricous to subviscid orange tawny convex–campanulate caps, creamy buff young gills, stuffed buff colored stipes, and deeply rooting thick unbranched salmon-colored pseudorhizas. Solitary to gregarious during autumn in Oregon and California hemlock, Douglas-fir, and spruce forests.

PILEUS — Up to 120 mm diam, conic-convex expanding to broadly campanulate with low broad umbo, inner margin straight to downcurved, outer margin downturned to uplifted with inrolled to incurved sinuous edge; surface moist to subviscid, sparsely squamulose on disc and margin, nonstriate, hygrophanous; color some shade of orange to tawny overall (*deep chrome, antimony yellow, chestnut brown*), disc sometimes darker (*buckthorn brown, dresden brown*), outermost edge brighter (*apricot yellow, antimony yellow, warm buff*) or darker (*chestnut brown*), damaged areas darker (*russet, sudan brown*), and scales concolorous with pileus when wet but lighter yellow (*apricot yellow, ochraceous buff*) in dry conditions. —*FLESH* firm, confluent through stipe and pileus (~7 mm thick in disc); color pinkish, whitish with a brownish or cinnamon cast (*cartridge buff, pale pinkish buff, pale ochraceous salmon*). —*ODOR* not distinctive or mildly farinaceous/



Orange tawny cap with inrolled edge, pale orange cream gills, and stuffed stipe in *P. ochraceocana*  
'Oz,' Polk County, Oregon — WTU HOLOTYPE Exeter2007-033

raphanoid when crushed. — *TASTE* slightly farinaceous/raphanoid or bitter. — *DRIED PILEUS* uniformly dull brown with light yellow brown edge or metallic ochraceous orange, depending on age and condition of specimen when dried.

*LAMELLAE* — Pale tan (*pale cinnamon buff*, *pale ochraceous buff*) when young, darkening to yellow-brown (*buckthorn brown*) with serrulate edges in age.

*STIPE* — Slightly eccentric, rigid, ~30–90 mm above the ground, combined length with pseudorhiza ~200 mm; apex 15–28 mm diam, aerial portion usually equal or tapering downwards but occasionally swelling just above ground level; surface dry, appressed to shaggy fibrillose, with short yellow fibrillose patches often present; color of young apex pale buff with a cinnamon to ochraceous cast (*pale ochraceous salmon*, *pale ochraceous buff*, *pale pinkish cinnamon*), grading to *drab* or brown at ground level, bruising orange to brown; stuffed with firm, pinkish buff (*pale pinkish cinnamon*, *cartridge buff*) pith; cartilaginous rind 1–2 mm thick.

*PSEUDORHIZA* — Vertical-monopodial, ~3/5 of overall length, continuous with stipe and gradually tapering to a blunt origin; color *drab* brown to salmon colored (*drab*, *salmon*), staining brown (*carob brown*).

*VEIL REMNANTS* — Frequent and visible in young fresh material (even without hand lens) as sparsely scattered to numerous squamules on pileus, stipe, and pseudorhiza; color ochraceous to orange-yellow.

*SYRINGALDAZINE REACTIVITY* — Usually negative (gills of one specimen tinged slightly magenta after 30 minutes).

*FLUORESCENCE* — Intense pale yellow young gills, cap flesh occasionally purplish pink or stipe pith dull purple.

*SPORE PRINT* — Pale cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. ochraceocana* can be recognized by its (1) scaly, lubricous, tawny campanulate cap, (2) medium to large size, and (3) stuffed salmon stipe and thick vertical-monopodial pseudorhiza.

Important microscopical features detailed below include (1) medium-sized (~7.4 × 4.7 μm) roughened broad lemon-shaped spores, (2) clavate thin-walled non-incrusted cheilocystidia that rarely generate apical





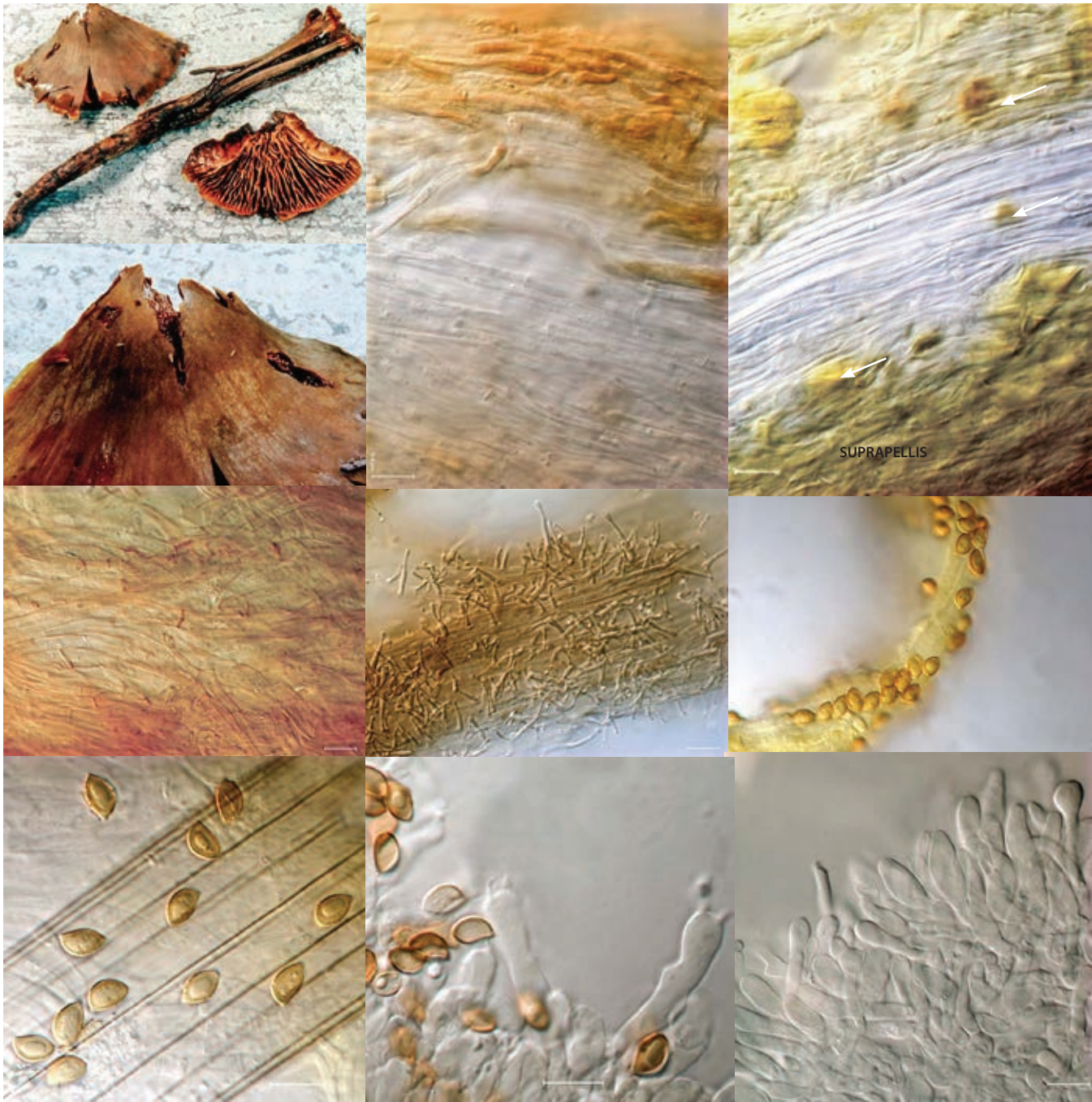
Lorelei Norvell

*Phaeocollybia ochraceocana*

BLM Research Forest, Polk County, Oregon — WTU HOLOTYPE Exeter2007-033

outgrowths even in very old specimens, (3) absence of clamp connections, and — most importantly — (4) a three-layered pileipellis with a highly gelatinous colorless middle layer sandwiched between yellow to orange top and dull orange-amber bottom layers.

**BASIDIOSPORES** —  $|x| = 7.4 \times 4.7$  [5.8–8.9  $\times$  3.8–5.6]  $\mu\text{m}$ , slightly compressed in end view, limoniform in profile view, inequilaterally amygdaliform in face view, verruculose with ornamentation irregularly projecting beyond outline except on short (0.5  $\mu\text{m}$ ) apical beak and eccentric apiculus; color in KOH medium amber, in  $\text{H}_2\text{O}$  paler amber, in Melzer's inamyloid and nondextrinoid. — **BASIDIA** 4-spored, clavate, 18–36  $\times$  5–8.3  $\mu\text{m}$ , colorless to dull amber, vacuolate.



Lorelei Norvell

*Phaeocollybia ochraceocana* [Pedee BLM Research Forest, Polk County, Oregon — A–C: PNW-MS a199120101-2; D: PNW-MS a200101801-19; E–I: PNW-MS a200110102-31-19; H: PNW-MS a200111502-1; G: PNW-MS a201101701-2; J: PNW-MS Exeter2007-009.]. A–E. PILEUS & TRILAMINATE PILEIPELLIS STRUCTURE. A–B—Canescence (B, arrows) in an old cap while drying led to the discovery of a trilaminar pileipellis in a specimen with small spores. C—Subpellis with encrusting, KOH-soluble diffuse, and intraparietal orange pigments. D–E—Squash mounts of the pileus scalp. Diffuse suprapellis pigments dissolve into drops (E, arrows) in KOH. F. TIBIFORM DIVERTICULA emerge by the hundreds from the primordial sheath retained on the pseudorhiza, where they are found in all phaeocollybias. In *P. ochraceocana* they are also common (but less abundant) on loose fibrils and sheath patches on upper stipe and cap surfaces. G–I. BASIDIOSPORES & BASIDIA: When spore prints are lacking, dimensions are best taken from spores on the stipe apex (G, clinging to fibril) or cap surface (H, with insect wing fragment), not the gills, which usually contain many immature spores. *P. ochraceocana* spores (G,H) and basidia (I) are similar to, but smaller than, those found in *P. luteosquamulosa*. J. CHEILOCYSTIDIA. The thin-walled colorless ‘clavate’ elements that form a sterile gill edge are variably shaped, but apical outgrowths (arrow) are only rarely encountered. Scales = 10 μm.

**CYSTIDIAL ELEMENTS** —*CHEILOCYSTIDIA* abundant, arising from the lamellar trama to form a distinct sterile barrier; terminal lengths variable and indeterminate, narrow (~2 μm) hyphidia intermixed with variably inflated clavate elements (sometimes with subglobose heads atop long narrow pedicels), apical extensions



Jennie Sperling (A) &amp; D. Roediger (B-C), USDI-BLM Coos Bay Office

Since 1998, Northwest Forest Plan surveyors have sent specimens, photos, and notes to mycological experts, contributing greatly to what we know about all macrofungi. Collections field identified as *P. kauffmanii* (A-C) uncovered a productive *P. ochraceocana* site in the Myrtlewood RNA (Coos County, Oregon). One mixed collection contained *P. redheadii* (c-left) and *P. ochraceocana* (c-right).

from senescent elements extremely rare; all elements thin-walled, colorless. —*PLEUROCYSTIDIA* present only as occasional filamentous hyphidia. —*TIBIIFORM DIVERTICULA* abundant on pileal scales, stipe fibrillose patches, and pseudorhizal surfaces,  $\leq 25 \times 2.5 \mu\text{m}$  with no septum between base and hypha, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** —*PILEIPELLIS* a trilaminar ixocutis; the thin ( $\sim 60 \mu\text{m}$ ) compact suprapellis consisting of narrow (2–3  $\mu\text{m}$  diam) compact hyphae that are radially aligned, equal (2–3  $\mu\text{m}$  diam), heavily gelatinized but not gel-encrusted, occasionally diverticulate, with encrusting and KOH-soluble, diffuse orange-yellow to pale orange pigments, the suprapellis separating in squash mounts to reveal colorless the mediopellis below (p. 116, FIG. E); the slightly thinner ( $\sim 40 \mu\text{m}$ ) compact hyaline mediopellis composed of hyphae that are unbranched, cylindrical, equal (2–3  $\mu\text{m}$  diam), highly gelatinized with refractive septa, smooth and never gel-encrusted; the subpellis consisting of hyphae 4–8  $\mu\text{m}$  diam, both incrusting and encrusted with sordid pale yellow brown pigments in KOH that congregate at the septa. —*STIPITIPPELLIS* a compact layer of parallel, long, cylindrical, thick-walled, narrow (4  $\mu\text{m}$  wide), highly gelatinized hyphae with pale yellow pigments.

**TRAMAL TISSUES** — Gelatinized throughout; in the pseudorhiza and stipe sarcodimitic, with long, wide ( $\leq 25 \mu\text{m}$ ), thick-walled ( $\leq 2 \mu\text{m}$ ), rigid, colorless to dull orange vessel hyphal elements intermixed with flexuous, thin-walled, highly branched, narrow (2–3  $\mu\text{m}$ ) colorless hyphae; in the pileus not noticeably sarcodimitic, hyphae inflated  $< 40 \mu\text{m}$  diam, walls variably thickened up to 1  $\mu\text{m}$ , incrusting with dull golden orange pigments.

—Lamellar central hyphae parallel, 4–6  $\mu\text{m}$  diam, thin-walled, colorless, and flanked by a narrow zone of 2–3  $\mu\text{m}$  diam colorless elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); gregarious during autumn in old-growth coniferous forests (*Tsuga*, *Picea*, *Pseudotsuga*) in Oregon and northern California. —*PACIFIC NORTHWEST ENDEMIC* thus far known only from 22 collections from one California and five Oregon sites.

**Similar species** — *Phaeocollybia ochraceocana* has previously been mistaken for *P. kauffmanii* and belongs to a group of 11 western phaeocollybias exhibiting a robust stature, solidly stuffed stipe, fleshy unbranched



Ron Exeter

Mature tawny *P. ochraceocana*  
in situ in 'Oz' [Polk Co, OR]  
— PNW-MS Exeter2008-23.

pseudorhiza, roughened lemon-shaped brown spores, and thin-walled clavate cheilocystidia. The dry to moist scaly cap and three-layered cap cuticle serve to distinguish *P. ochraceocana* from all other species in this *P. kauffmanii* complex except the also uncommon *P. luteosquamulosa*.

*P. luteosquamulosa* produces similarly ochraceous fruitbodies possessing minutely squamulose, non-glutinous 'tri-layer' caps. *P. luteosquamulosa* specimens are usually paler and more uniformly ochre in color with moist to dry caps that are never subviscid and have more sparsely scattered and closely appressed squamules. *P. luteosquamulosa* is easily differentiated microscopically by its much larger ( $\sim 10 \times 6 \mu\text{m}$ ) basidiospores, pigment incrustated cheilocystidia that regularly produce apical extensions in age, and gel-encrusted pileipellis hyphae. All but one *P. luteosquamulosa* collection have been made in forests containing *Abies*, while *P. ochraceocana* appears restricted to *Pseudotsuga*, *Tsuga*, or *Picea* forests where *Abies* is absent.

See *P. luteosquamulosa* and TABLE 11 (p. 96) for additional comparisons.

**Additional comments** — Even old, waterlogged specimens can provide needed taxonomic data. In 1999, while processing one over-the-hill December transect collection (p. 116, FIGS. A–B), we noticed canescent areas on a drying cap unusual for *Phaeocollybia*. Examination of the cap tissues under the compound microscope revealed three distinct layers previously observed only in *P. luteosquamulosa*: a compact suprapellis containing bright yellow-orange pigments, an equally compact gelatinized colorless mediopellis, and a subpellis with orange diffuse and encrusting pigments. The next year we collected younger material that also displayed the same tri-layer structure in better condition at the same site. Norvell (2000) excluded these and one California collection from *P. luteosquamulosa* based on the small spore size (see also Norvell 1998a). After examining twelve additional collections, we concluded that the lack of incrustated cheilocystidia and encrusted mediopellis hyphae, the thicker suprapellis, and the smaller spore size were significant enough to justify naming *P. ochraceocana* as a new species (Norvell & Exeter 2007a).

*References with descriptions and /or illustrations of Phaeocollybia ochraceocana* —

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [discussion of lut-x, pp. 173–174]
- Norvell LL. 2000. *Phaeocollybia* in western North America 1: The *Phaeocollybia kauffmanii* complex. *Can. Journ. of Botany* 78: 1055–1076. [graph showing spore dimensions of lut-x compared to rest of complex, p. 1057; brief discussion, p. 1071]
- Norvell LL, Exeter RL. 2007a. *Phaeocollybia* in western North America 5: *P. ochraceocana* sp. nov. and the *P. kauffmanii* complex. *Mycotaxon* 102: 315–332. [key; type description & b&w photos].

*Phaeocollybia olivacea*

Scott Redhead

*Phaeocollybia olivacea* in situ in Van Damme State Park  
Mendocino County, California — WTU Norvell1921120-2

*Phaeocollybia olivacea* A.H. Smith Brittonia 9: 204. 1957.

ETYMOLOGY — From the Latin for olive, referring to the yellow-green to greenish brown colors of the fruitbody.

HOLOTYPE — Grants Pass, Josephine County, OR, USA; November 17, 1956 (MICH HOLOTYPE 11627 AHSmith55767)

*Field summary* — medium-sized fruitbodies with glutinous olive green to olive brown convex-campanulate caps, pallid buff to yellowish young gills, fibrillose stuffed green stipes with red bases, and long thread-like pseudorhizas. Densely gregarious and often in arcs during autumn under oaks and conifers in coastal Pacific Northwest forests.

**PILEUS** — ~30-120 mm diam, obtuse to convex with inrolled edge when young, broadly campanulate with low umbo when mature, surface glutinous, smooth, bald, hygrophanous; color uniformly or irregularly mottled some shade of olive green to brown (*buffy brown, citrine drab, olive brown*) or zonate with a darker disc (*dark olive brown, ivy green*) and distinct paler edge (*deep olive buff, isabella color, buckthorn brown*). — **FLESH** 3–6 mm at disc, evenly tapering to edge, cartilaginous, color varying from pallid, greenish yellow to olive. — **ODOR** fleeting, complex with floral, cucumber, or boiled potato components. — **TASTE** mild and not distinctive, gluten occasionally bitter. — **DRIED PILEUS** metallic greenish yellow bronze.

**LAMELLAE** — Free to nearly free, pale yellow cream colored when young, darkening to dull gold or olive, with eroded edges in age.

**STIPE** — +/- central, rigid, ~40–100 mm above the ground, combined length with pseudorhiza >220 mm; apex 6–15 (20) mm diam, aerial portion equal or swelling towards base to 15–20(35) mm, frequently narrowing abruptly below ground level to a cord-like pseudorhiza; surface moist to lubricous, smooth beneath fibrillose veil patches; color of young apex watery green or gold (*chamois, olive buff, isabella color*) above a red or orange-red (*Mikado brown, Kaiser brown*) base, red tones eventually extending upwards turning entire aerial portion red-brown, staining orange (*zinc orange*) to brown where bruised; stuffed when young with firm white pith that becomes silky fibrillose and yellow, greenish, or pale cinnamon in age; cartilaginous rind 1–2 mm thick.

**PSEUDORHIZA** — Sequential-racemose, cord-like and easily broken (and consequently rarely retrieved), generally uniformly liver brown except for paler (*light pinkish cinnamon*) origin.



Ron Exeter (L), Lorelei Norvell (R)

Photos taken of the same specimens in field and lab show how green caps dull and stipes redden even after collection.  
 Conner's Camp on Mary's Peak, Benton County, Oregon — PNW-MS Exeter2007-122

**VEIL REMNANTS** — Visible as olive brown fibrillose patches on the upper stipe.

**SYRINGALDAZINE REACTIVITY** — Negative in cap, gill and stipe tissues; pseudorhiza rarely turning faintly magenta.

**FLUORESCENCE** — Under UV, gills fluoresce brilliant mustard yellow; stipe pith glow dark magenta to deep orange.

**SPORE PRINT** — Rusty brown to yellowish brown.

**Diagnostic characters** — Macroscopically, *P. olivacea* can be recognized by its (1) glutinous convex-campanulate green cap and pallid to yellowish gills, (2) stuffed green stipe with reddish base turning uniformly orange-red in age, (3) cord-like dark brown pseudorhiza, (4) gregarious fruitbodies growing in arcs or rings, (5) tissues that do not turn magenta in syringaldazine, and (6) gills that fluoresce brilliant mustard yellow under UV.

Important microscopical features include (1) large (~10 × 6 μm) 'turtle-backed' (broadly limoniform with abruptly protruding eccentric refractive beaks) rough dark brown basidiospores, (2) thin-walled clavate cheilocystidia that often generate long filiform extensions in older specimens, (3) a bilaminate pileipellis with a lower layer containing encrusting and intraparietal pigments, and (4) absence of clamp connections.

**BASIDIOSPORES** —  $|x| = 10 \times 6 [(8)9-10(11) \times 5-6(7)] \mu\text{m}$ , broadly inequilateral ('turtle-backed') with dorsally eccentric apiculus and abrupt, conspicuous beak in profile view, broadly ovate with an abruptly projecting snout in face view, rugulose-warty roughened with dark ornamentation projecting well beyond outline except on the smooth (1–1.5 μm) apical beak; in KOH tawny, in H<sub>2</sub>O amber, in Melzer's inamyloid and non-dextrinoid. — **BASIDIA** 4-spored, clavate, ~25–40 × 7–9 μm, colorless in KOH.

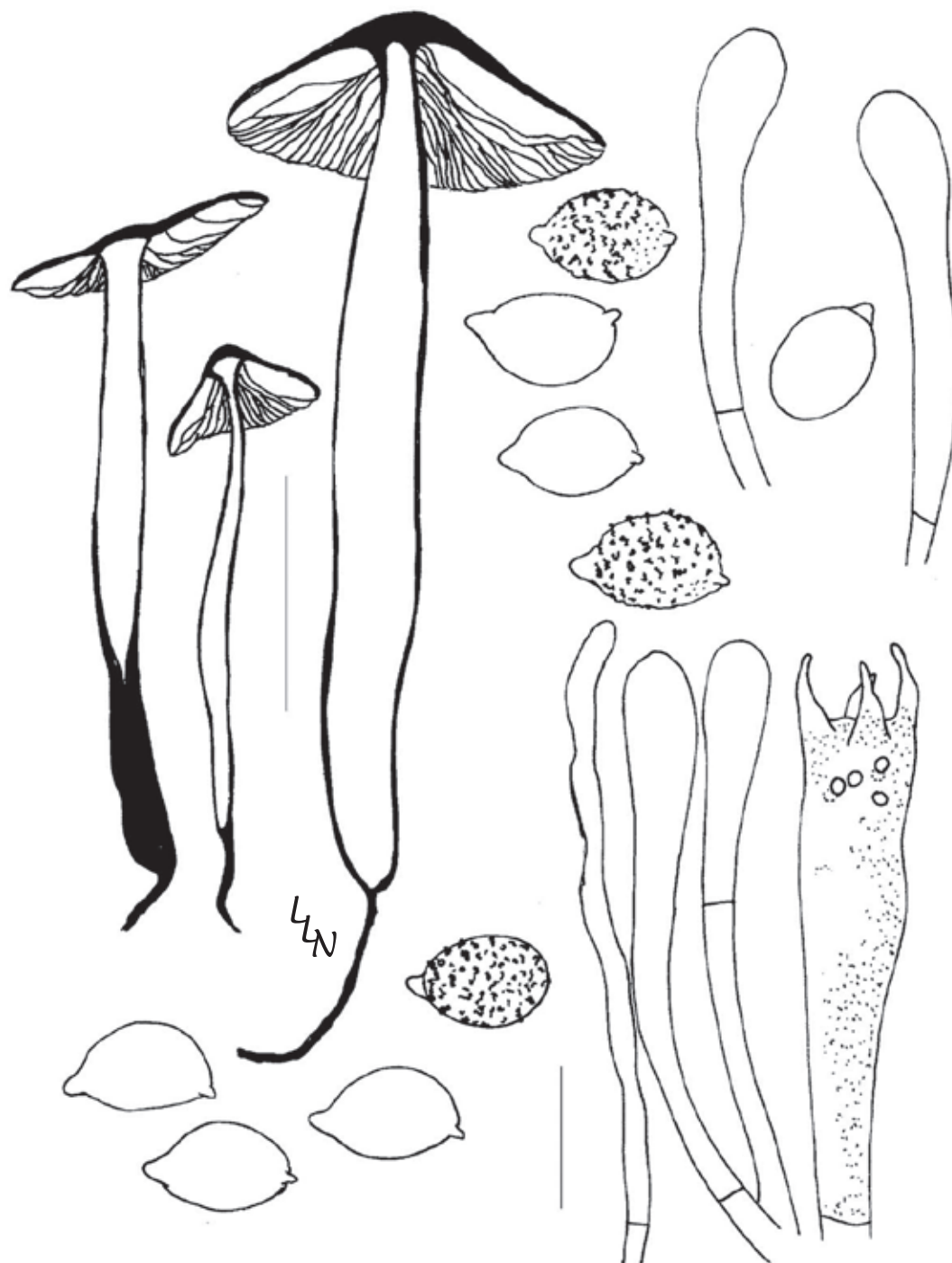
**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a sterile layer; lengths variable and indeterminate with elements occasionally septate, variably clavate with narrow (~3–4 μm diam) elements intermixed with wider (5–7 μm diam) elements; in older specimens often generating thin-walled filamentous (rarely capitulate) apical extensions, sometimes surrounded by a gelatinous matrix or collapsed in an agglutinated barrier, colorless to yellowish in KOH. — **PLEUROCYSTIDIA** Absent. — **TIBIIFORM DIVERTICULA** abundant on mycelia, primordial and pseudorhizal surfaces, also frequent on pellicular veil remnants on stipe apex, infrequently observed on pileipellis of mature basidiomes, ≤ 20 × 2 μm, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis: the ~400 μm thick suprapellis comprising a thick gelatinous matrix surrounding radially aligned, cylindrical (1–2 μm diam) to inflated (3–4 μm diam) colorless hyphae with the uppermost hyphae slightly separating and often slightly curled or kinked; the bottom ~400 μm thick subpellis composed of thin-walled, wider (5–10 μm diam) hyphae with intraparietal pale to dark orange-brown pigments that may coagulate irregularly within the walls in older specimens, oleifers containing oily amber to dark orange pigments intermixed. — **STIPITIPELLIS** a thick layer of 5–8 μm diam gelatinized gel-encrusted colorless hyphae intermixed with oleifers containing oily pale greenish amber contents.

**TRAMAL TISSUES** — Dark orange-amber to brown oleifers occasional throughout, hyphae highly gelatinized, strongly sarcodimitic in pseudorhiza with occasional thick-walled broad cylindrical colorless rigid vessel elements intermixed with slightly thinner-walled narrow flexuous colorless elements, both hyphal types

becoming less differentiated near the stipe apex with the wide rigid elements becoming less frequent and the wall thicknesses of both types approaching  $0.5\text{--}1\ \mu\text{m}$ ; the pileus trama +/- monomitic, resembling that of the subpellis. Lamellar central hyphae parallel  $3\text{--}7\ \mu\text{m}$  diam, thin-walled, yellowish, and flanked by a narrow zone of  $2\text{--}3\ \mu\text{m}$  diam elements giving rise to a compact subhymenium.

CLAMP CONNECTIONS — Absent in all tissues.



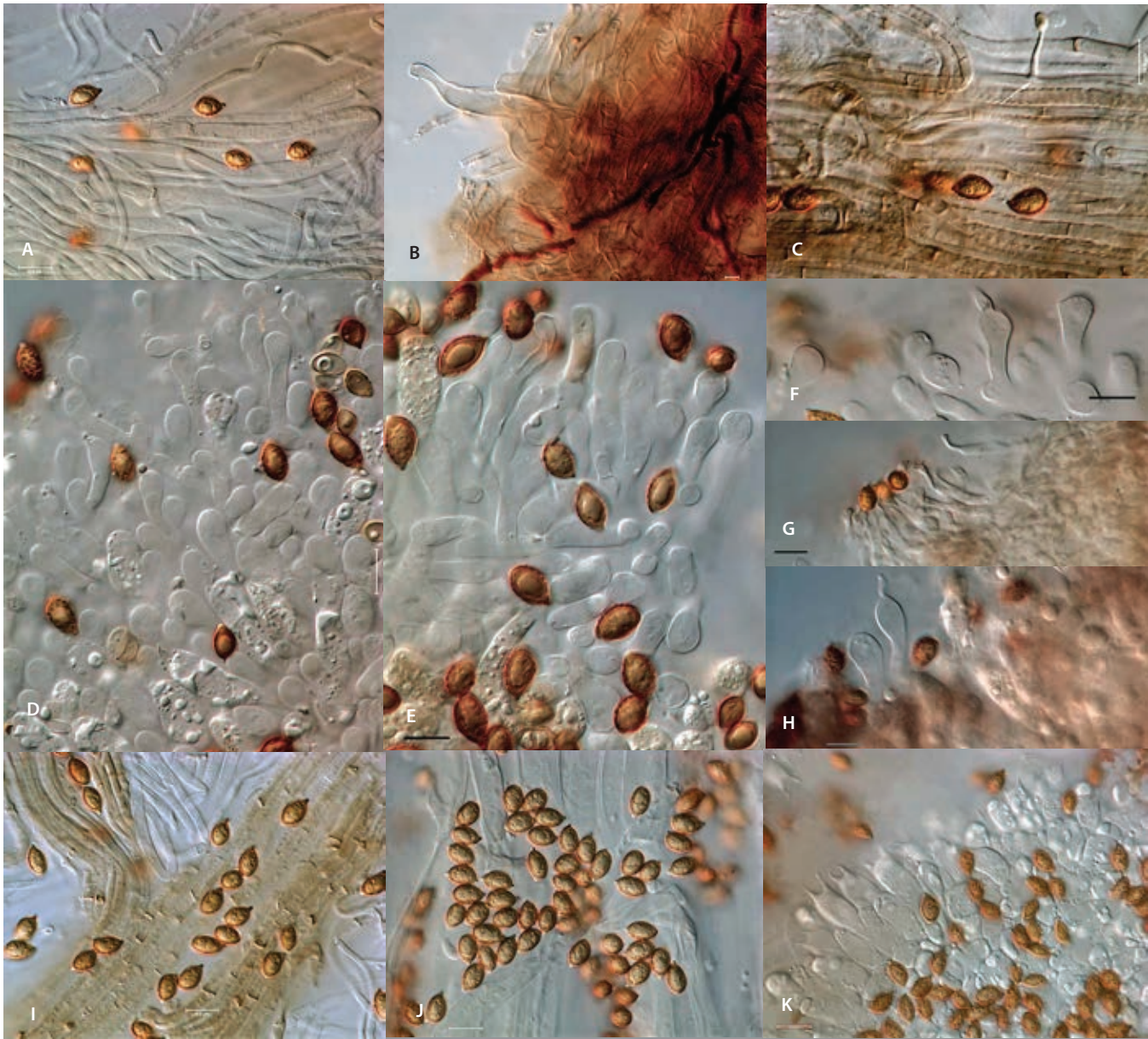
*Phaeocollybia olivacea*

A. HABIT. (L)—Shasta Co CA, wtU Norvell1961129-6; (R)—Benton Co OR, wtU Norvell1951117-6.

B. BASIDIOSPORES & CHEILOCYSTIDIA—Josephine Co OR, MICH HOLOTYPE 11627 AHSmith55767.

C. BASIDIOSPORES, HYPHIDIUM, CHEILOCYSTIDIA, BASIDIUM—Clackamas Co OR, wtU Norvell1941128-1.

Scale bars = 5 cm & 10  $\mu\text{m}$



Lorelei Norvell

*Phaeocollybia olivacea* [OREGON: Benton Co—Mary's Pk, PNW-MS: Exeter2007--119 (I), -122 (C&F), -155 (A&J); Coos Co—Medford RA, osc: LNus17b122 (F); Josephine Co—Limpy Crk, osc: LNus8(4)-4589sl (D) & -4602sl (B); Lane Co—Lobster Valley, PNW-MS: Exeter2007-133 (4K); Linn Co—Keel Flats, osc: LNus5-157 (E), —McCully Mtn, osc LNus8-4MCM2cn6 (G)]. A–B. PILEIPELLIS. Gelatinized narrow (2–4 µm diam) colorless suprapellis hyphae (A) separate and coil toward the surface, remaining relatively compact below; wider hyphae, encrusting and parietal pigments, and oleifers are found within the subpellis (B). C. TIBIFORM DIVERTICUA (arrow) are frequent on the encrusted remnants of the primordial sheath usually found on the stipe apex. D–H. CHEILOCYSTIDIA. Thin-walled narrowly to broadly clavate cheilocystidia (D–E) that crowd gill edges when young frequently collapse into an agglutinated gelatinous barrier in age (not shown). Thin-walled long apical extensions (F–H), commonly found in old or improperly dried specimens, sometimes produce small 'heads' above narrow 'necks' (G) leading to confusion with tibiiform thick-walled cheilocystidia of other species; the absence of the refractive thick-walls of neck and 'capitellum' is helpful in separating *P. olivacea* from *P. pseudofestiva*. I–K. BASIDIOSPORES & BASIDIA. The eccentric apiculi and abruptly protruding beaks of the large, broadly limoniform, very rough, dark brown basidiospores are key to identifying *P. olivacea*. The raised focal plane in (K) illustrates the typical roughened spore surfaces. Scale bars = 10 µm.

**Ecology** — Terrestrial (mycorrhizal); clustered to gregarious (in arcs) during autumn in mixed (*Quercus-Pinus*, *Pseudotsuga/Abies/Tsuga-Lithocarpus*) or coniferous (*Tsuga*, *Pseudotsuga*) forests. —PACIFIC NORTHWEST ENDEMIC known from over 100 sites in Oregon and California.

**Similar species** — Smith (1957b), who described *Phaeocollybia olivacea* based on abundant material he collected from an oak-pine forest near Oregon's Grants Pass, cited the large size, olive-colored cap, pallid young gills, silky stipe pith, and orange-red mature stipe as constant field characters. Nonetheless, *P. olivacea* is





*P. olivacea* drying in situ at Conner's Camp  
Benton County, Oregon — PNW-MS Exeter2008-129

often confused with the similarly green-capped *P. fallax* and *P. pseudofestiva*, both often found growing intermingled with *P. olivacea*. Norvell (1998a,c) discovered numerous herbarium collections identified as *P. olivacea* (including three designated as *P. olivacea* paratypes by Smith) that either represented *P. fallax* or *P. pseudofestiva* or were mixed with representatives of those species.

*P. pseudofestiva*, which also produces large gregarious to cespitose clusters, is easily microscopically diagnosed by its abundant thick-walled lageniform / tibiiform cheilocystidia and smaller ( $\sim 8 \times 5 \mu\text{m}$ ), less highly ornamented basidiospores. Its smaller basidiomes with stipes that may become hollow in age may help distinguish *P. pseudofestiva* from *P. olivacea* in the field.

*P. fallax* basidiomes with stuffed stipes and gills that have lost their diagnostic violet color are less easily separated from *P. olivacea*, especially if the drab *P. fallax* stipe apex is not noted. Here, basidiospore shape is key to separating *P. olivacea* from *P. fallax*. Smaller and narrower ( $\sim 9 \times 5 \mu\text{m}$ ), *P. fallax* spores have long tapered beaks. *P. olivacea* spore beaks are among the most prominent of all Pacific Northwest phaeocollybias; the rounded 'turtle-backed' spore shape prevents the dorsally eccentric apiculus from being seen when 'the plane of focus includes the beak, which itself resembles a nose viewed directly from above a head' (Redhead, in Norvell 1998a). Both species produce thin-walled clavate cheilocystidia; however, although the subcapitate *P. fallax* cheilocystidia may broaden in age, they rarely (if ever) develop the thin filamentous apical extensions commonly found in older *P. olivacea* specimens.

Differentiating *P. olivacea* from *P. gregaria* can be extremely difficult, as both species exhibit a gregarious habit, similar size, caps that swiftly dull to brown, stuffed stipes, thin-walled cheilocystidia that readily develop apical outgrowths in age, and equally large, broadly limoniform basidiospores. Comparison of abundant material from both species during the 2007 & 2008 field seasons convinces us that older *P. gregaria* specimens are most easily differentiated by their symmetrical verruculose basidiospores with tapering, slightly shorter (usually  $< 1 \mu\text{m}$ ), less highly refractive beaks and gills that do not fluoresce under UV.



Scott Redhead

*P. olivacea* — Small clusters and gregarious arcs in Mendocino County, California  
In situ at 'Mushroom Corners' [wrtu Norvell1921116-4] & Van Damme State Park [wrtu Norvell1921123-12]

**Additional comments** — Proliferation of cheilocystidial apical outgrowths occurs to such an unusual degree in *P. olivacea* that they can be mistaken for thick-walled capitulate cheilocystidia (see plate 4G). Bandala & Montoya (1994) erroneously placed *P. olivacea* into Section *Versicolores* based on Bandala's discovery of 'tibiiform' elements in the type. Norvell's subsequent microscopical examination using oil immersion and Nomarski optics showed that although numerous capitulate appendages did occur in one type specimen, they were developmental outgrowths on thin-walled clavate cheilocystidia, not thick-walled capitulate cheilocystidia characteristic of Section *Versicolores*. Norvell (2004) concluded that *P. olivacea* properly belongs in Section *Phaeocollybia* as originally proposed by Smith (1957b).

For the time being we hold a broad species concept for *P. olivacea*. Early DNA analysis of eight *P. olivacea* collections (including the type) proved inconclusive, showing two different RFLP profiles that could not be separated by morphological, chemical or ecological characters. Recent misidentifications of *P. gregaria* as *P. olivacea* suggests that one DNA profile may represent that species. Current DNA sequence analyses will help clarify remaining taxonomic ambiguities to determine whether 'hidden' taxa lurk within our current species concept.

*References with descriptions and /or illustrations of Phaeocollybia olivacea* —

- Arora D. 1986. Mushrooms demystified. Ten Speed Press: Berkeley (CA). (description, b&w photo pp. 414–415).
- Castellano MA, Cázares E, Fondrick B, Dreisbach T. 2003. Handbook to additional fungal species of special concern in the Northwest Forest Plan. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s3 – 84].
- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. Sydowia 29: 28-70. [key; microdrawing p. 54].
- Kibby G. 1993. An illustrated guide to mushrooms and other fungi of North America. Longmeadow Press: Stamford CT. (description & watercolor (lacking reddish stipe base and pseudorhizal cord, p. 123)
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [description 174–178, color photos & line drawing 248–249]
- Norvell LL. 2004. *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and Section *Versicolores* reconsidered. Mycotaxon 90(2): 241-260. [explanation for transferring *P. olivacea* back to Section *Phaeocollybia*].
- Smith AH. 1957. A contribution toward a monograph of *Phaeocollybia*. Brittonia 9: 195-217. [key; type description 204–205, microdrawings 201, b&w photo pl. 3]
- Smith AH. 1975. A field guide to western mushrooms. University of Michigan Press, Ann Arbor. [description, color photo 190–191]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. Mycologia. 64: 1141–1142 [Revised key].

*Phaeocollybia oregonensis*

Ron Exeter

*Phaeocollybia oregonensis* in situ in Lobster Valley  
Lane County, Oregon — PNW-MS Exeter2006-16

***Phaeocollybia oregonensis*** A.H. Sm. & Trappe, Mycologia 64: 1145, 1972.

= *Phaeocollybia carmanahensis* Redhead & Norvell, Mycotaxon 46: 343-359. 1993

ETYMOLOGY — from the state where the first specimen was found.

HOLOTYPE — Larch Mountain Summit, Mt. Hood National Forest (Multnomah County), OR, USA;  
October 30, 1947, by W.B. Gruber (MICH 11628 AHSmith28420)

*Field summary* — Medium to moderately large fruitbodies with viscid drab convex-campanulate caps, smoky white young gills, stuffed pinkish cinnamon stipes, and deeply rooting thick unbranched pseudorhizas. Solitary to gregarious during autumn in British Columbia, Washington, and Oregon coniferous forests.

**PILEUS** — ~30–110 mm diam, conic-convex with inrolled edges when young, expanding to broadly conic-campanulate with subacute conic umbo and incurved to straight edges when mature; viscid to glutinous, smooth, bald, opaque; color some shade of drab to pinkish or purplish brown (*drab, benzo brown, fawn, wood brown*). —**FLESH** relatively thick over gills, ≤ 7 mm over disc, pallid when young, cartilaginous and concolorous with cap surface in aged or waterlogged fruitbodies. —**ODOR** farinaceous or cucumber-like when fresh, unpleasantly pungent when dried. —**TASTE** usually farinaceous and bitter. —**DRIED PILEUS** matte red- to orange-brown.

**LAMELLAE** — Almost free, smoky white (*mouse gray, drab gray*) when young, darkening to yellow buff to yellow brown, edges even when young, serrulate or eroded in age.

**STIPE** — +/- central, firm, ~40-80 mm above the ground, combined length with pseudorhiza >210 mm; apex ~7–20 mm diam, aerial portion equal, tapered, or ventricose from proliferating pith; surface dry, matte and finely longitudinally striate; color of young apex grayish pink or drab (*avellaneous, vinaceous buff*), grading



Lorelei Norvell

*P. oregonensis* [OREGON (Lane Co) Lobster Valley, PNW-MS Exeter2007-130] — A robust stature, pinkish brown to drab-brown colors, farinaceous odor, stuffed stipe (inset), and strong syringaldazine reactivity are key characters shared with the larger spored *P. benzokauffmanii* (not shown). The right photo shows tissues submerged in syringaldazine for 15 minutes: the three syringaldazine wells — containing (from top down) gill, stipe, and pseudorhiza tissues — contrast with the H<sub>2</sub>O control (containing the same tissues) at bottom. Magenta tones develop swiftly, with gills deep at 3 minutes; after additional reagent was added, the pseudorhizal well was also deep magenta at 30 minutes.

to grayish reddish brown (*cacao brown*) at ground level, bruising orange brown; persistently stuffed with firm pallid pith that turns orange-brown on exposure; cartilaginous rind ~2 mm thick.

**PSEUDORHIZA** — Vertical-monopodial, ~1/2-3/4 of overall length, continuous with stipe and gradually tapering to a blunt origin; color dark gray- to red-brown.

**VEIL REMNANTS** — Evident as scattered short drab fibrillose patches on aerial stipe.

**SYRINGALDAZINE REACTIVITY** — Strongly positive, all tissues soon (5 minutes) deep magenta.

**FLUORESCENCE** — Under UV, young gills and stipe pith fluoresce brilliant violet- to yellow-white, pseudorhizal pellis brilliant pale yellow to dull orange.

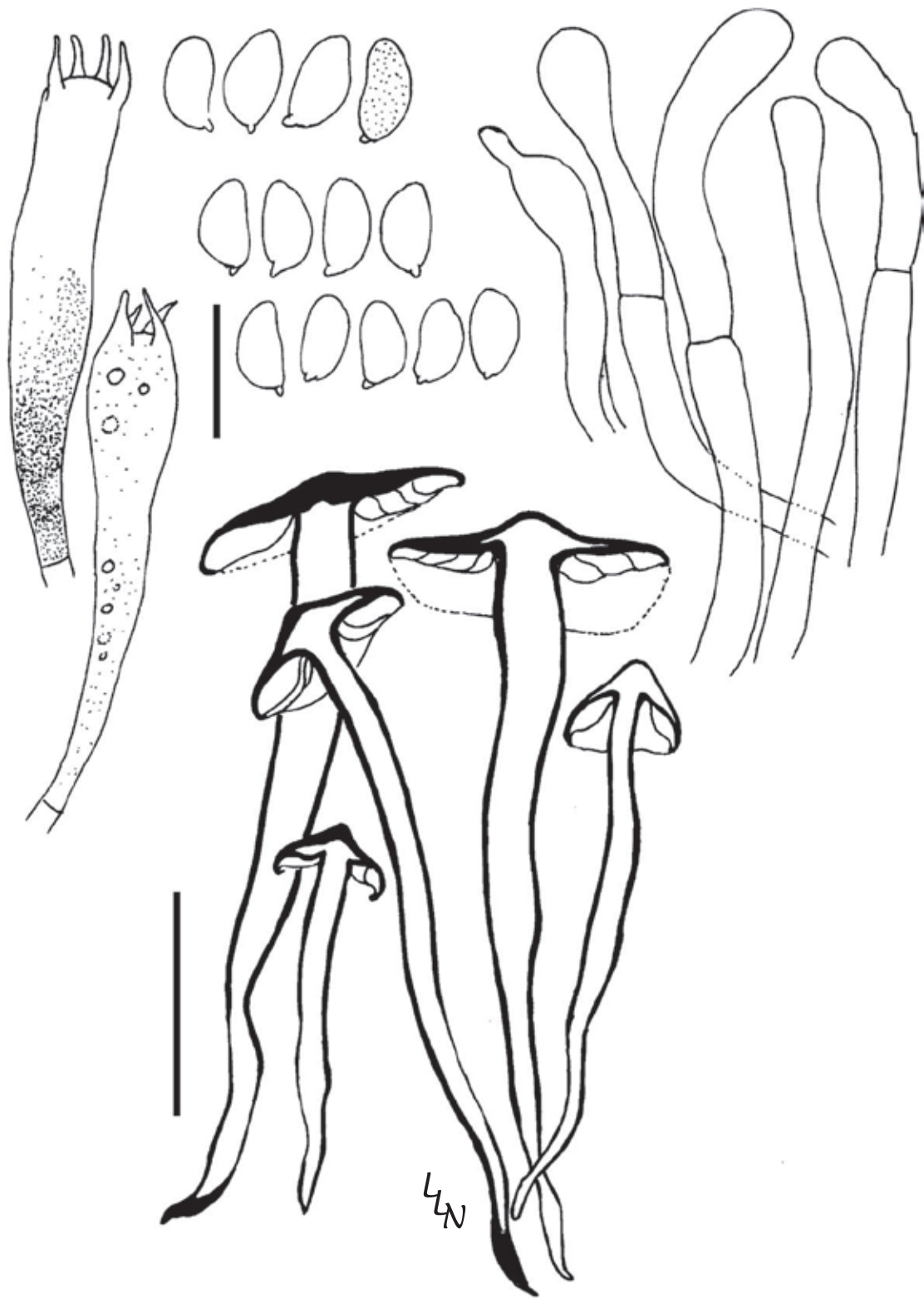
**SPORE PRINT** — Dull yellow cinnamon.

**Diagnostic characters** — Macroscopically, *P. oregonensis* can be recognized by its (1) viscid drab to dull brown convex-campanulate cap and smoky white young gills, (2) robust stature and medium size, (3) pinkish brown to drab stuffed stipe, and (4) tissues that quickly turn deep magenta in syringaldazine.

Important microscopical features detailed below include (1) small (~6.8 × 4 μm) punctate-roughened bullet-nosed basidiospores, (2) thin-walled narrowly clavate cheilocystidia, (3) a bi-laminar pileipellis with a relatively thick colorless top layer and bottom layer with incrusting/intraperietal pigments, and (4) lack of true clamp connections (but see note below).

**BASIDIOSPORES** —  $|x| = 6.8 \times 4 [5.4-7.5 \times 3.5-5] \mu\text{m}$ , relatively (for *Phaeocollybia*) thin-walled, ellipsoidal with small rounded blunt apical callus in profile view, bullet-nosed (elliptical to slightly obovate tapering to the bluntly rounded apex) in face view, punctate roughened with ornamentation visible only under oil at high magnification; color in KOH golden brown, in H<sub>2</sub>O paler, in Melzer's reddish-brown (dextrinoid). — **BASIDIA** 4-spored, clavate, ~34 × 6.5 μm, colorless to slightly brown at the base in older specimens, granular.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a sterile layer with basidia occasionally intermixed; length variable and indeterminate [~12-36 μm], apices ≤ 5-6 (8) μm diam above ~2-4 μm diam pedicels with penultimate elements often swelling below terminal septa, apical extensions occasional in senescent elements; colorless. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on primordia, pseudorhiza, and veil remnants on stipe apex, ≤ 20 × 1.8 (bases) μm, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

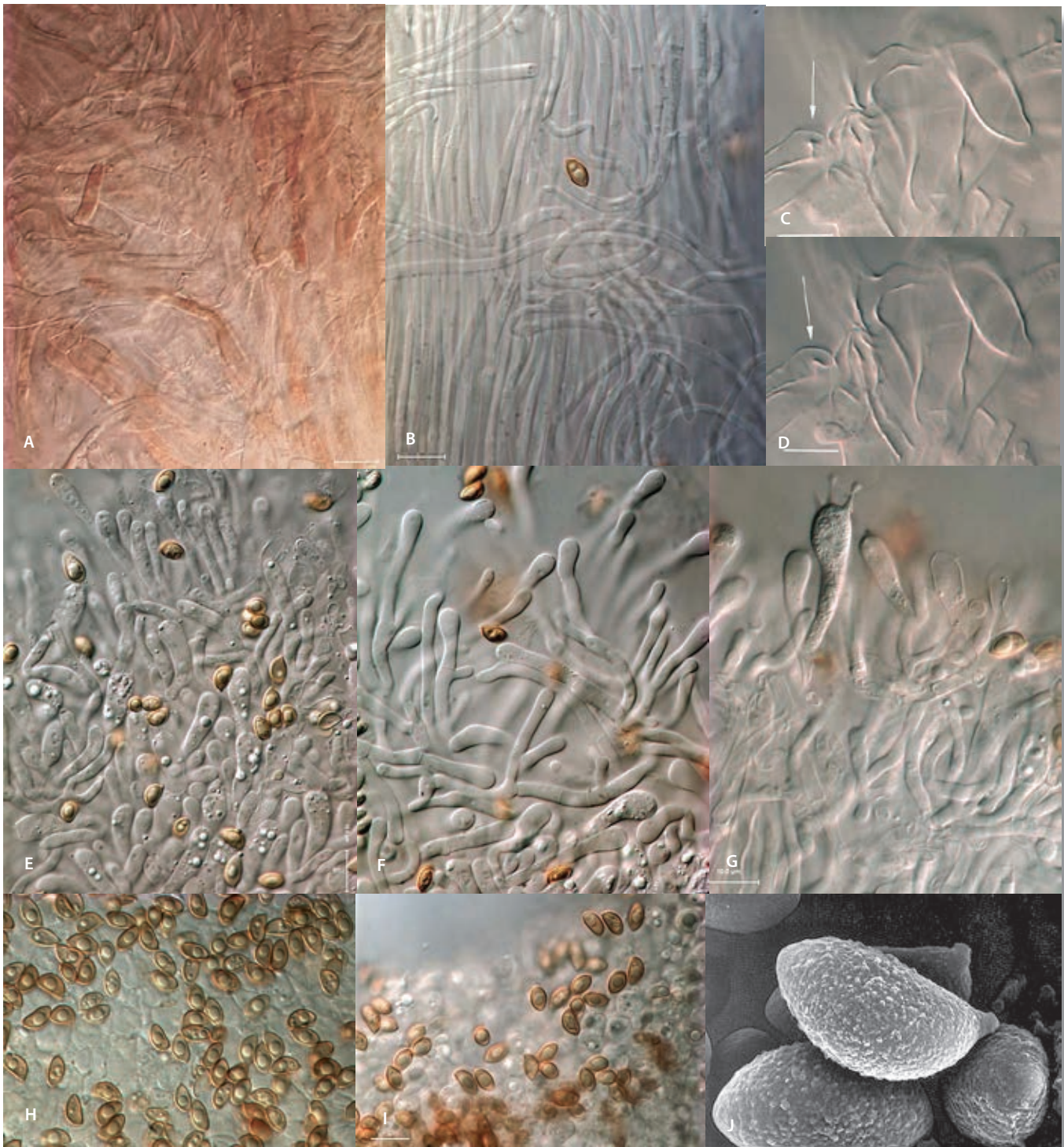


*Phaeocollybia oregonensis*

A. BASIDIA, BASIDIOSPORES, CHEILOCYSTIDIA (scale = 10  $\mu$ m).

Larch Mountain, Oregon — MICH HOLOTYPE 11628 AHSmith28420.

B-C. HABIT (scale = 5 cm). B: Larch Mountain (Mt Hood NF, Multnomah Co, OR) — wtU Norvell1921104-5.  
c: Wildcat Mountain (Mt Hood NF, Clackamas Co, OR) — wtU Norvell194-1018-22.



Lorelei Norvell

*Phaeocollybia oregonensis* [OREGON: (Lane Co) Lobster Valley, PNW-MS A-B&I—Exeter2006-16, C-D&F-G—Exeter2007-130; (Tillamook Co) Cascade Head ExpFor, osc E—usCH2jp3; (Josephine Co) GlendaleRA 32-7W-29, osc H—LNus32.7.29m3b; (Multnomah Co) Larch Mtn, J—MICH HOLOTYPE 11628 AHSmith28420] — A. PILEIPELLIS. A thick subpellis composed of relatively wide gelatinized hyphae incrustated with pigments that are orange in KOH lies under an equally thick colorless suprapellis (not shown) containing narrow hyphae floating in a dense gelatinous matrix. B. STIPITPELLIS. Loosely arrayed narrow surface hyphae (right) lie above tightly packed parallel hyphae that make up the cartilaginous stipe 'rind'. C-D. PSEUDOCAMPS. A 'clamp connection' (C) found in the pileus trama is revealed as an aborted branchlet (D) when the microscope objective is moved up and down. Such branchlets and flexuous hyphal ends (common in fruitbodies with sarcodimitic tissues) may mislead researchers into seeing clamps where none exist. E-G. CHEILOCYSTIDIA & BASIDIA. Thin-walled narrowly clavate cheilocystidia usually have distinctly swollen apices; long (sometimes refractive) filiform extensions (not shown) may grow from the tips in aging specimens. The colorless granular basidia are usually 4-spored (G). H-J. BASIDIOSPORES. The small bullet-snouted spores with the small, blunted callus apices appear almost smooth, even under oil. A SEM of the holotype spores (J) reveal the finely punctate ornamentation. Species with completely smooth spores lacking any ornamentation are excluded from *Phaeocollybia*. Scale bars = 10  $\mu$ m.



Scott Redhead(A) Lorelei Norvell(B) Ron Exeter(C)

Comparison of the only photo taken of *Phaeocollybia carmanahensis* (A) with Oregon material (B–C) supports the synonymy of the British Columbian species with *P. oregonensis*. All fresh specimens lacked clamp connections and exhibited drab colors, features not noted in the original *P. oregonensis* type description. [A—Carmanah Valley, BC, Canada (DAOM HOLOTYPE 2156071 & WTU ISOTYPE Norvell1911024-3); B—Wildcat Mountain (Clackamas County, Mt Hood NF) OR (WTU Norvell1951018-4); C—Lobster Valley (Lane County) OR (PNW-MS Exeter2006-16).]

**CORTICAL TISSUES** — *PILEIPELLIS* a bilaminar ixocutis: the moderately thick ( $\leq 200 \mu\text{m}$ ) suprapellis containing radially aligned, narrow (2–5  $\mu\text{m}$  diam), colorless hyphae with refractive septa embedded in a thick gelatinous matrix; the similarly thick subpellis with slightly thicker walled, wider (6–10  $\mu\text{m}$  diam) gelatinized elements with incrusting and intraparietal dull brown to brownish orange (in KOH) pigments. — *STIPITPELLIS* a thin layer of loose, filiform (1–3.5  $\mu\text{m}$  diam) colorless hyphae over a compact layer of 2–4  $\mu\text{m}$  diam elements sheathing a compact dull drab rind of 5  $\mu\text{m}$  diam hyphae.

**TRAMAL TISSUES** — Highly gelatinized throughout, strongly sarcodimitic in pseudorhiza, stipe, and pileus with long cylindrical thick-walled (1–2  $\mu\text{m}$ ), wide ( $\leq 15 \mu\text{m}$  diam) vessel hyphae intermixed with less conspicuous, thin-walled, narrow (2–4), branched elements. Lamellar trama also containing a mix of hyphal types, with primarily 3–8  $\mu\text{m}$  diam, colorless central hyphae parallel and flanked by narrow colorless zones of 2–3  $\mu\text{m}$  diam elements, each giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — True clamps absent in all tissues; ‘pseudoclamps’ near septa — such as variously oriented short branchlets, flexuous hyphal ends, and thin-walled broad diverticula — also absent in cortical tissues but frequent throughout all tramal tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to gregarious during autumn in coniferous forests under *Abies*, *Tsuga*, and *Pseudotsuga*. — *PACIFIC NORTHWEST ENDEMIC* uncommon to rare, known from 12 sites in British Columbia (2), Washington state (1), and Oregon (9).

**Similar species** — *Phaeocollybia oregonensis*, *P. benzokauffmanii*, *P. lilacifolia*, and *P. rifflipes* characteristically all have drab coloration. The two most similar — *P. benzokauffmanii* and *P. oregonensis* — share brownish drab caps and pale gray young gill colors, robust firmly stuffed stipes with pinkish-drab apices, a farinaceous odor, and strong magenta syringaldazine reactivity. Its generally larger size and persistently inrolled convex cap edge is only slightly helpful in identifying *P. benzokauffmanii* in the field. Tawny caps and violet to lilac colored young gills help distinguish *P. lilacifolia* and *P. rifflipes* while smaller size and narrow shiny stipe further differentiates *P. rifflipes*. Fortunately, larger —  $\sim 9 \times 5.5 \mu\text{m}$ ,  $\sim 8 \times 5 \mu\text{m}$ ,  $\sim 6.9 \times 4.3 \mu\text{m}$  for *P. benzokauffmanii*, *P. lilacifolia*, and *P. rifflipes* respectively — and visibly ornamented limoniform basidiospores with pronounced apical beaks are sufficient to separate the look-alikes from *P. oregonensis*, with its small ( $\sim 6.8 \times 4 \mu\text{m}$ ), bullet-nosed, virtually smooth spores.

Small, ellipsoid bullet-nosed basidiospores are also key features for *P. sipei* and *P. dissiliens*. These species are unlikely to be confused with *P. oregonensis*, however, due to their bright to dark orange caps, hollow shiny orange stipes, and thread-like pseudorhizas; cheilocystidial shape and pigmentation also differ, and *P. dissiliens* fruitbodies are further distinguished by having abundant true clamp connections throughout.



Lorelei Norvell

This 1992 *P. oregonensis* collection was the first gathered from the type locality since Gruber collected the holotype in 1947.  
Larch Mountain, Multnomah County, Oregon — WTU & PNW-MS LLNorvell1921104-05

**Additional comments** — Smith & Trappe (1972) described *Phaeocollybia oregonensis* — from a solitary specimen collected by Gruber in 1947 — as having rare (‘very rare’) clamp connections. Repeated examination of the holotype by later workers (Norvell 1998ac, Norvell & Redhead 2000) revealed only ‘pseudoclamps’ — small branchlets or balloon-like diverticula (cf. Fig. 4C–D) — within the gill and pileus tramas that the original authors probably misinterpreted as true clamp connections. These pseudoclamps are best understood as such when viewed under oil through a compound microscope equipped with differential interference contrast (Nomarski) optics. (See p. 31 for additional information on clamp connections.)

Redhead & Norvell (1993) originally named a small, drab, small-spored, clampless phaeocollybia from British Columbia as *Phaeocollybia carmanahensis*, believing that the similar *P. oregonensis* possessed clamp connections. They differentiated their new species by its lack of clamps, smaller size, and drab cap colors that contrasted with the ‘dark reddish brown to dull liver brown’ originally described for *P. oregonensis*. Subsequent collections from British Columbia, Washington, and Oregon led to re-evaluation of both type collections. After Norvell (1998a) determined that all specimens shared similar morphologies and identical RFLP DNA profiles, Norvell & Redhead (2000) declared *P. carmanahensis* a synonym of *P. oregonensis*.

*References with descriptions and /or illustrations of Phaeocollybia oregonensis —*

- Castellano MA, Smith JE, O’Dell T, Cázares E, Nugent S. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. PNW-GTR-476: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s1 – 89, written before *P. carmanahensis* placed in synonymy].
- Horak E. 1977 (‘1976’). Further additions towards a monograph of *Phaeocollybia*. Sydowia 29: 28-70. [key; microdrawing p. 66].
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [emended *P. oregonensis* type description 178-182; color photos, drawing 250-251]
- Norvell LL, Redhead SA. 2000. *Phaeocollybia* in western North America 2: the vernal *P. pleurocystidiata* sp. nov. and *P. carmanahensis* reconsidered. Mycologia 92: 984-991 [fdescription, B&W photos 988–990]
- Redhead SA, Norvell LL. 1993. *Phaeocollybia* in western Canada. Mycotaxon 46:343-359. [*P. carmanahensis* type description with B&W comparison photos, line drawings]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon’s Cascade Head Experimental Forest and vicinity I. The genus *Phaeocollybia* (Aragicales) and notes and descriptions of other species in the *Agaricales*. Mycologia 64:1138-1153 [key, *P. oregonensis* type description]



*Phaeocollybia phaeogaleroides*

Ron Exeter

*Phaeocollybia phaeogaleroides* at Boulder Creek  
Polk County, Oregon — PNW-MS Exeter2007-93

*Phaeocollybia phaeogaleroides* Norvell, Mycotaxon 81: 96, 2002.

ETYMOLOGY — ‘*Phaeogalera*-like,’ derived from *Phaeogalera*, another brown-spored agaric that produces similar basidiospores and fruitbodies.

HOLOTYPE — Finley Hill BLM Reserve Forest (Mary’s Peak RA, Benton County), OR, USA;  
December 7, 1999 (OSC HOLOTYPE RLExeter199-64, WTU & PNW-MS isotypes)

*Field summary* — Small, fragile mycenoid fruitbodies with hygrophanous dark brownish orange to chestnut brown convex-campanulate caps that soon fade to tan, pallid to tan young gills, deeply rooting fragile cartilaginous equal tan stipes, and unbranched criniform pseudorhizas. Solitary to loosely scattered during spring and autumn in Pacific Northwest coniferous forests.

PILEUS — ~20–50 mm diam, when young conic-convex with prominent to obscure obtuse umbo, when mature broadly campanulate, moist to subviscid, smooth or sometimes radially rugulose, bald, striate, hygrophanous; when moist dark red-brown to brownish orange (*clay color, chestnut brown*), when dry honey tan (‘cardboard brown’). —*FLESH* ~2 mm at disc and rapidly thinning over gills, pallid to pale tan. —*ODOR* not distinctive to slightly raphanoid or vaguely acidic (like *Oxalis*). —*TASTE* not distinctive. —*DRIED PILEUS* copper to golden metallic.

LAMELLAE — Free to narrowly sinuate attached; pallid to pale honey tan (*warm buff*) when young, darkening to pale rusty brown with serrulate edges in age.

STIPE — Central, terete, slender, cartilaginous rigid but fragile (mycenoid), ~30–90 mm above the ground, combined length with pseudorhiza to >205 mm; apex 1.5–4 (5) mm diam, upper stipe equal, lower stipe equal or tapering gradually to pseudorhiza, sometimes swelling slightly at ground level; dry, slightly polished; color of young apex honey tan (*warm buff*), grading to vinaceous brown at ground level, darkening to uniformly dark brown in age; when young stuffed with silky, pallid to pale yellow pith, in age fistulose;



Ron Exeter (A), Lorelei Norvell (B-H)

Gills, stipes, & pseudorhizas in *P. phaeogaleroides*. — A–D. LAMELLAE. Gill attachment [usually described as ‘almost free’ in young (A–C) but ‘adnate’ in mature expanded caps (D)] is rarely diagnostic in *Phaeocollybia*. E–G. STIPE MORPHOLOGY. Fragile long equal stipes (E) arise from rarely retrieved criniform attenuata-like ‘threads’, as illustrated by an unusually long 205 x 2 mm stipe (F) lacking the pseudorhizal cord presumably snapped off when collected. Cartilaginous rinds on exposed upper stipes may curl back from the underlying pith like wood-shavings (F–G) in dry weather. H. The similar size and color of two spring fruiting phaeocollybias — *P. pleurocystidiata* (left) and *P. phaeogaleroides* (right) — make the microscope the best identification option. All scales in millimeters.

[OREGON. ~Benton Co: Alesia Falls PNW-MS Exeter2007-3(A), PNW-MS Exeter2008-4(H)&-5(D&H); Finley Hill BLM Reserve OSC HOLOTYPE RLExeter199-64(B); Mary’s Peak summit PNW-MS Norvell2071029-40(C); Klickitat Rd, Old Blue PNW-MS Norvell2071029-19(H)&-20(G). ~Polk Co: Boulder Crk PNW-MS Exeter2007-99(F)]

cartilaginous rind ~0.5 mm thick, in dry weather sometimes curling in concentric patches away from the context.

PSEUDORHIZA — Vertical-monopodial, continuous with lower stipe and gradually tapering to a criniform thread; concolorous with lower stipe except for pale tan origin.

VEIL REMNANTS — Inconspicuous, occasionally evident as scattered pale fibrillose patches on the upper stipe.

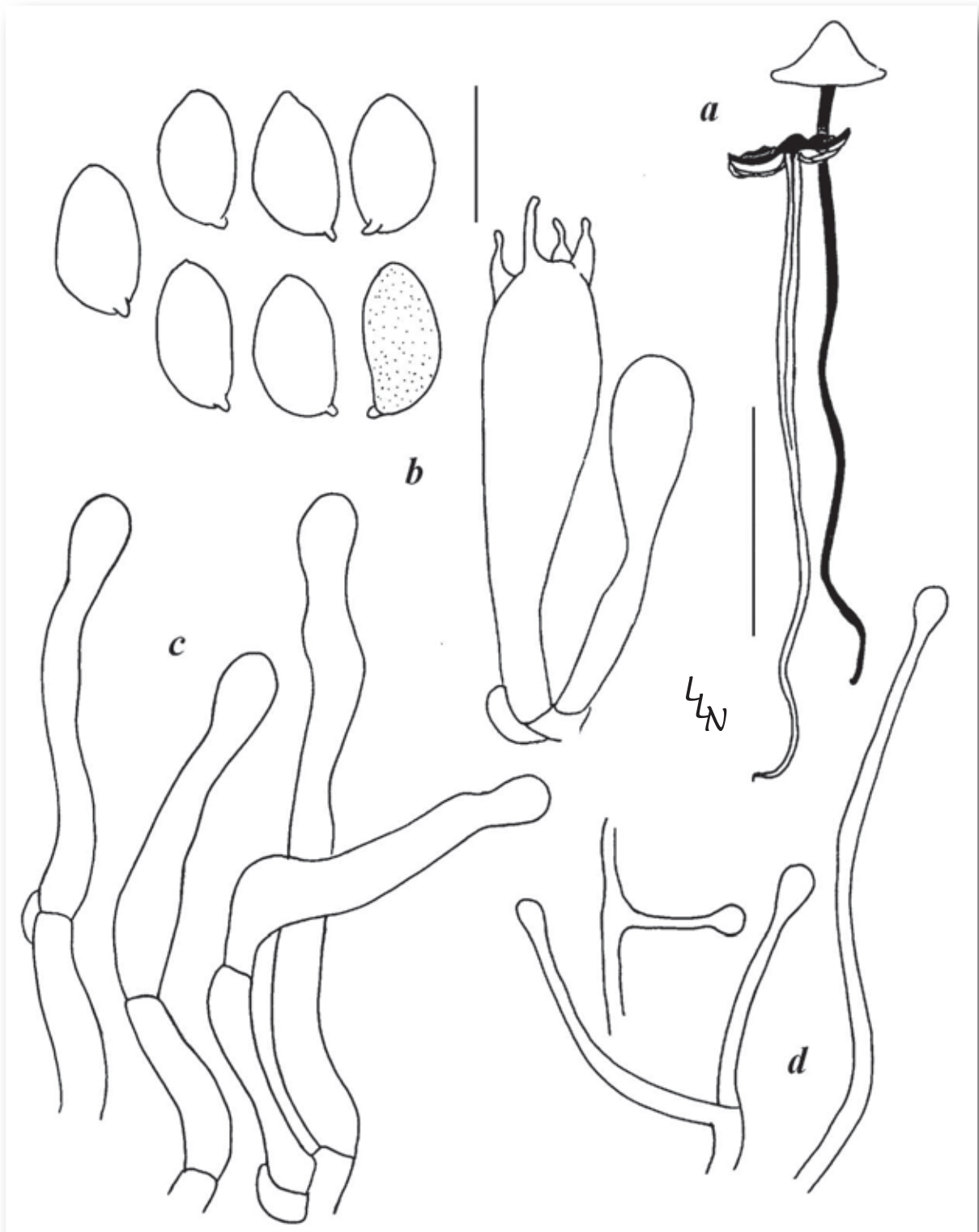
SYRINGALDAZINE REACTIVITY — All tissues negative.

FLUORESCENCE — Under UV, gills fluoresce ochre to yellow-orange; context glows a deep dark red to purple.

SPORE PRINT — Reddish brown.

**Diagnostic characters** — Macroscopically, *P. phaeogaleroides* can be recognized by its (1) small, fragile mycenoid to galerinoid stature, (2) thin-fleshed cap with striate edge that rapidly dulls from chestnut brown or tawny to ‘cardboard brown’ when drying, (3) long, thin (~2-4 mm diam), equal, tan stipe and criniform pseudorhiza, and (4) tissues that do not turn magenta in syringaldazine.

Important microscopical features detailed on the next page include (1) large ( $10.3 \times 6 \mu\text{m}$ ), ellipsoidal finely punctate-roughened brown basidiospores with bullet-shaped snouts that appear smooth under lower magnifications, (2) long, slender, cylindrical to subcapitate cheilocystidia that extend well beyond (~30-40  $\mu\text{m}$ ) the hymenium; (3) frequent to abundant clamp connections, and (4) a bilaminar pileipellis with a subpellis with encrusting and intracellular pigments that turn deep red-brown in KOH.



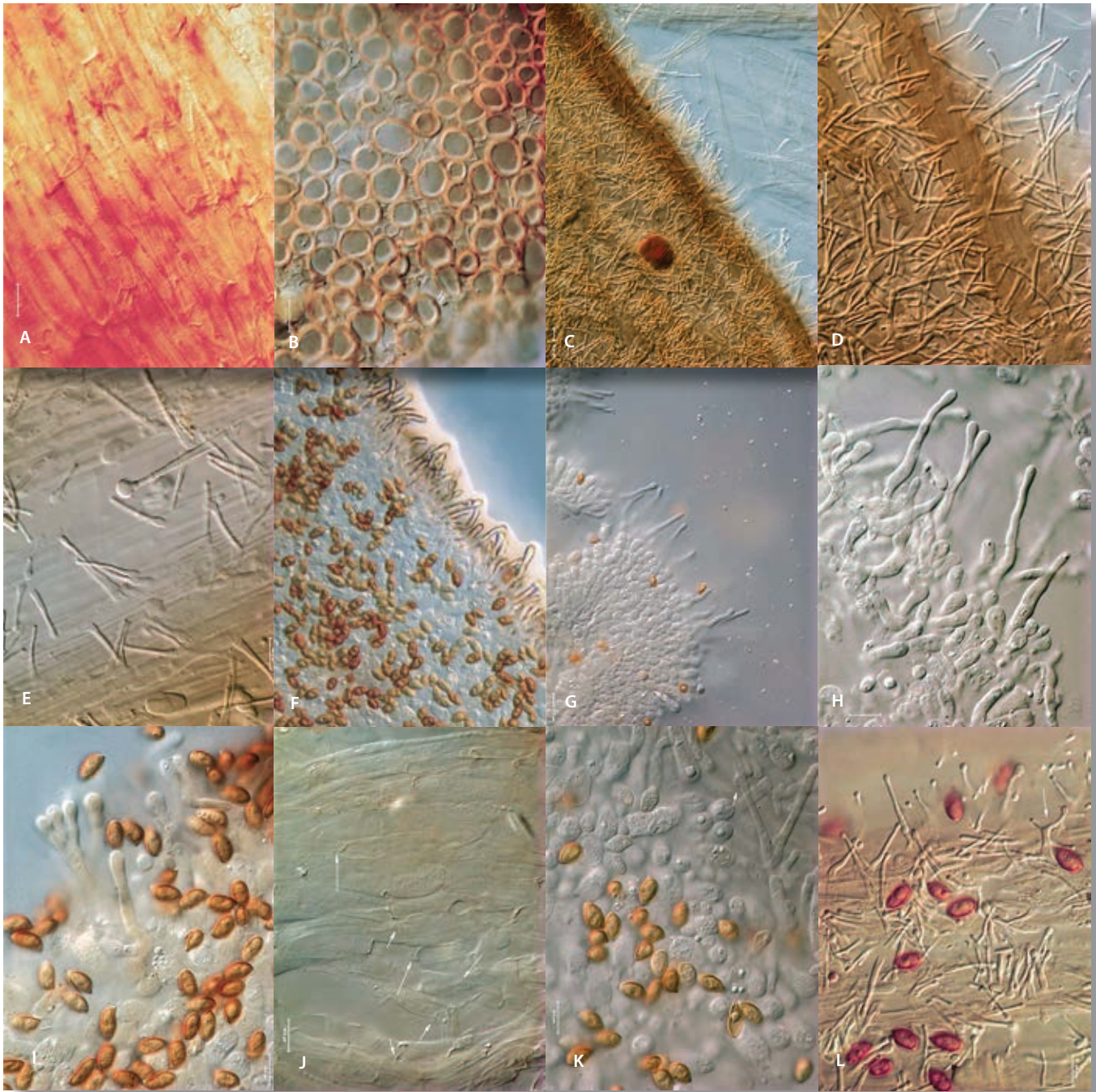
*Phaeocollybia phaeogaleroides*

A. HABIT. *Left*: Drift Creek, Lincoln County, OR — wtU Norvell1961106-1. *Right*: Vancouver Island, BC — DAOM Outerbridge298.

B-D. ANATOMICAL CHARACTERS. Drift Creek, Lincoln County, OR — wtU Norvell1961106-1 by NSWeber.

B—Basidiospores, basidium, and basidiole. C—Cheilocystidia with clamp connections. D—Tibiiform diverticula.

Scale bars = 10  $\mu$ m and 5 cm.



Lorelei Norvell

*Phaeocollybia phaeogaleroides* — A. PILEUS SUBPELLIS. Orange-yellow encrusting and intracellular pigments turn deep red-orange in KOH. B. SARCODIMITIUM. Thick-walled vessel hyphae (in cross section) predominate in the sarcodimitic tissues within the criniform pseudorhizal thread. C–E. TIBIFORM DIVERTICULA. Abundant diverticula, present by the thousands on lower stipe and pseudorhizal surfaces, may reach 50  $\mu\text{m}$  in length. F–I. CHEILOCYSTIDIA. F: The gelatinous matrix surrounding refractive cylindrical elements is highlighted under the 40 $\times$  objective. G: Slender cheilocystidia project 30–40  $\mu\text{m}$  above the hymenium. H–I: Swollen cheilocystidial heads and oily contents are visible under oil immersion. J. CLAMP CONNECTONS (arrows) occur at the septa of all elements and are numerous even in gelatinized tramal tissues. K–L. BASIDIOSPORES. Large ellipsoid basidiospores with snubbed ‘bullet-nosed’ snouts ( $\kappa$ —with basidia on the gill; L— with tibiiform diverticula on the stipe) have ornamentation so fine that it can be detected only under oil immersion. Scales = 10  $\mu\text{m}$ .

[OREGON — ~Benton Co: Alsea Falls PNW-MS Exeter2007-3(J); Mary’s Peak summit PNW-MS Norvell2071029-40(F)&-53(I); Klickitat Rd, Old Blue PNW-MS Norvell2071029-19(K)&-22(H). ~Polk Co: Boulder Crk PNW-MS Exeter2007-93(A), -99(B), -100(L), -101(C,D,G)&-102(E)]

BASIDIOSPORES —  $|x| = 10.3 \times 6$  [(8)9–12(13.3)  $\times$  (5)5.8–6.3(7.4)]  $\mu\text{m}$ , terete to slightly compressed in end view, ellipsoidal with eccentric apiculus and rounded to slightly pointed (‘bullet-nosed’) snout in profile view,



*Phaeocollybia phaeogaleroides* from Mary's Peak Summit in Benton County, Oregon [PNW-MS Exeter2007-045] — The above sequence showing the same specimens photographed immediately after collection (A), two hours later (B), and in the lab the next day (C) illustrates the rapid fading that can occur in hygrophanous caps and demonstrates why good field notes are needed to describe a new species.

very finely punctate roughened; color in KOH dark amber, in H<sub>2</sub>O yellowish, in Melzer's inamyloid and nondextrinoid. —*BASIDIA* (2-)4-spored, clavate, 28–32 × 8–12 μm, colorless, granular, basally clamped.

**CYSTIDIAL ELEMENTS** —*CHEILOCYSTIDIA* frequent to abundant, arising from the subhymenium with basidia occasionally intermixed; long (≤ 80 μm) and rising ~30–40 μm above the hymenium, cylindrical with sinuous sides and ~2–4 μm diam apices or subcapitate with heads swollen to 3–5 μm, walls slightly thickened and refractive, septa with frequent medallion-like clamps, apical extensions from senescent elements not seen; colorless to pale orange-yellow in KOH. —*PLEUROCYSTIDIA* occasional to infrequent, filamentous or sparsely forked, readily collapsing in mounts. —*TIBIIFORM DIVERTICULA* frequent on primordial sheath remnants and stipe surface, unusually abundant (densely crowded) on pseudorhizal surface; relatively large (15–50 × 1–2 μm), with/without 2–3 μm diam subglobose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** —*PILEIPELLIS* a bilaminar ixocutis: the top 50–100 μm thick suprapellis of radially aligned, narrow (2–4 μm), thin-walled (sub)gelatinized colorless hyphae and the bottom 150–200 μm thick subpellis with thin-walled, 4–12 μm diam, gelatinized hyphae at times encrusted by orange-yellow pigments that turn deep red-orange in KOH; clamp connections frequent in both tissues. —*STIPIPELLIS* also bilaminar with a colorless top layer of tightly packed, long and cylindrical, narrow (2–4 μm), (sub)gelatinized, and colorless hyphae overlying a pale orange-yellow (in H<sub>2</sub>O) zone of wide (10–15 μm) heavily gelatinized hyphae.

**TRAMAL TISSUES** — gelatinized and with occasional oleifers throughout; in the criniform pseudorhiza sarcodimitic with long (~80 μm), fusoid, wide (10–15 μm) thick-walled (~1 μm) pale amber, rigid vessel hyphae intermixed with less frequent thin-walled, narrow (2–4 μm) colorless flexuous hyphae; the number of vessel hyphae decreasing in the fleshy upper pseudorhiza and lower stipe; in upper stipe and pileus composed of uniformly thin-walled 4–6 μm diam, pale amber hyphae. Lamellar central hyphae parallel, 3–7 μm diam, moderately thick-walled (0.5 μm), pale orange-yellow, and flanked by a narrow subhymenium of 2–3 μm diam colorless elements.

**CLAMP CONNECTIONS** — Medallion-like, present in all tissues on the septa of most elements, including the basidia, cheilocystidia, and suprapellis hyphae.

**Ecology** — Terrestrial (mycorrhizal); solitary, scattered, or loosely gregarious from spring through late autumn in coniferous (*Abies*, *Picea*, *Pseudotsuga*, *Tsuga*) forests. —*PACIFIC NORTHWEST ENDEMIC* (inconspicuous and probably not commonly collected) known from ~20 sites in Benton, Coos, Lane, Lincoln, and Polk counties in Oregon and near Fairy Lake on Vancouver Island, British Columbia.

**Similar species** — In the field *P. phaeogaleroides* might be mistaken for a fragile *P. attenuata* or *P. pleurocystidiata*, species that generally produce more robust fruitbodies with smaller, roughly ornamented, prominently beaked basidiospores and lack clamp connections. Paler pigments and thick-walled capitate tibiiform



Ron Exeter

Spring *P. phaeogaleroides* at Alsea Falls  
Benton County, Oregon — PNW-MS Exeter2007-3

cheilocystidia and pleurocystidia further separate *P. pleurocystidiata*, while *P. attenuata* (which does not fruit in the spring) possesses broadly clavate, non-refractive cheilocystidia.

*Phaeocollybia radicata* is a similar small fragile phaeocollybia also characterized by clamp connections and almost smooth ellipsoid spores. Its less abundant and smaller lageniform cheilocystidia with narrow highly refractive necks, and much smaller ( $\sim 5.8 \times 3.2 \mu\text{m}$ ) basidiospores easily distinguish *P. radicata*.

See discussion after the above species for additional comparisons.

**Additional comments** — *Phaeocollybia phaeogaleroides* was first discovered in the Michigan herbarium during examination of a mislabeled *P. radicata* collection. Its small fragile aspect, scattered habit, coniferous associations, generally tan coloration, and large ellipsoidal non-dextrinoid basidiospores recall the genus *Phaeogalera* for which the species is named. Unless observed under high magnification with oil immersion, the spores appear smooth and the blunt apical callus could easily be misinterpreted as a pore, a diagnostic feature for *Phaeogalera*. Recent collections have since revealed that when fresh, fruitbodies are much more deeply colored than first thought.

Clamp connections within *P. phaeogaleroides* are among the most conspicuous in the genus and its tibiiform diverticula are among the largest and most abundant of any phaeocollybia.

*P. phaeogaleroides* is thus far the only western phaeocollybia that regularly fruits in both spring and autumn. Current DNA sequencing by Matt Gordon (pers. comm. 2009) suggests that this difference in phenology reflects a taxonomic difference.

*References with descriptions and /or illustrations of Phaeocollybia phaeogaleroides —*

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [as *P. phaeogaleroides* nom. prov. pp. 182–184; color photos pp. 253]
- Norvell LL. 2002. *Phaeocollybia* in western North America 3: New species *P. phaeogaleroides* and *P. riffsipes*, with notes on the *P. festiva* complex. *Mycotaxon* 81: 95–112.

*Phaeocollybia piceae*

Ron Exeter

*Phaeocollybia piceae* at Trout Creek  
Benton County, Oregon — PNW-MS Exeter2008-112

***Phaeocollybia piceae*** A.H. Sm. & Trappe, Mycologia 64: 1145, 1972.

ETYMOLOGY — From the Latin genitive for *Picea*, the tree (Sitka spruce) associated with the type collection.

HOLOTYPE — Cascade Head Experimental Forest (Tillamook County), OR, USA.

October 16, 1970(MICH HOLOTYPE AHSmith 79085)

*Field summary* — Usually small- to medium-sized fruitbodies with moist to subviscid orange convex-complanate caps, yellow buff young gills, slender pale orange cartilaginous stipes stuffed with frequently insect-infested pith, and deeply rooting unbranched regenerating pseudorhizas. Solitary to scattered in small groups during autumn in Pacific Northwest coniferous forests.

**PILEUS** — ~15–60 (90) mm diam, obtusely conic-convex with tall umbo, young incurved margin and inrolled edge expanding to broadly campanulate with straight to down-turned margin and incurved edge that is often sinuate on one side; moist to thinly viscid, smooth, bald, occasionally striate, hygrophorous; color uniformly some shade of bright to dull orange (*ochraceous orange, zinc orange, ochraceous tawny, tawny, orange rufous*) or zonate with darker or duller disc and edge. —**FLESH** ~2–3(5) mm at disc, rapidly thinning over gills; firm and pallid (*pale pinkish buff*) when young, but soon translucent and concolorous with cuticle. —**ODOR** vaguely raphanoid to sweetly farinaceous or not distinctive when young, occasionally pungent ('like paint solvent') in very old specimens. —**TASTE** usually bitter, occasionally mild or raphanoid. —**DRIED PILEUS** with striate edges: young caps pale orange copper; older caps dark red or rufous brown.

**LAMELLAE** — Ascending-adnexed to almost free; yellow buff when young, darkening to cinnamon or rusty brown with serrulate edges in age.

**STIPE** — +/- central, rigid, ~40–80 mm above the ground, combined length with pseudorhiza ≤ 225 mm; apex 4–12 mm diam, upper stipe equal or gradually narrowing, characteristically swelling slightly at ground level; surface dry to lubricous, typically bald, matte to occasionally longitudinally striate; color of young apex



Elizabeth Fox(A), Lorelei Norvell(B,D), Ron Exeter(C)

*Phaeocollybia piceae* [BRITISH COLUMBIA, Vancouver Isl, Lower Carmanah: wtU Norvell1921009-22(A). OREGON, PNW-MS. Lincoln Co, Saddle Bag Mtn: Exeter2007-27(B) & 2008-14(C); Polk Co, Fanno Pk: Exeter2007-107(D)]. —A. The younger fruitbody arising from the origin of an older pseudorhizal remnant illustrates the regenerative nature of *P. piceae* pseudorhizas. —B–D. Although most *P. piceae* fruitbodies are relatively small (A–C), robust exceptions (D) can be large enough to be confused with *P. kauffmanii*. Bitter taste, negative syringaldazine reactivity, and insect-consumed stipe pith at mid-stipe causing the fruitbody to topple over when touched help identify such as *P. piceae*.

orange to pinkish buff (*light orange, orange cinnamon, zinc orange*), grading to deeper orange or orange-red (*xanthine orange, hay's russet, chestnut*) at ground level, staining or bruising bright orange (*mars yellow, tawny*); stuffed with firm to spongy, pinkish orange pith that characteristically is consumed by insects at ground level; cartilaginous rind 1–2 mm thick, ascending from the origin in a gradually twisting spiral.

**PSEUDORHIZA** — Vertical-monopodial and regenerative, continuous with lower stipe and gradually tapering down to an upwards curled origin that is often found attached to older pseudorhizae or pseudorhizal remnants; color dark reddish to orangish brown, staining bright orange.

**VEIL REMNANTS** — Infrequent on upper stipe as inconspicuous short reddish brown short fibrils.

**SYRINGALDAZINE REACTIVITY** — All tissues negative.

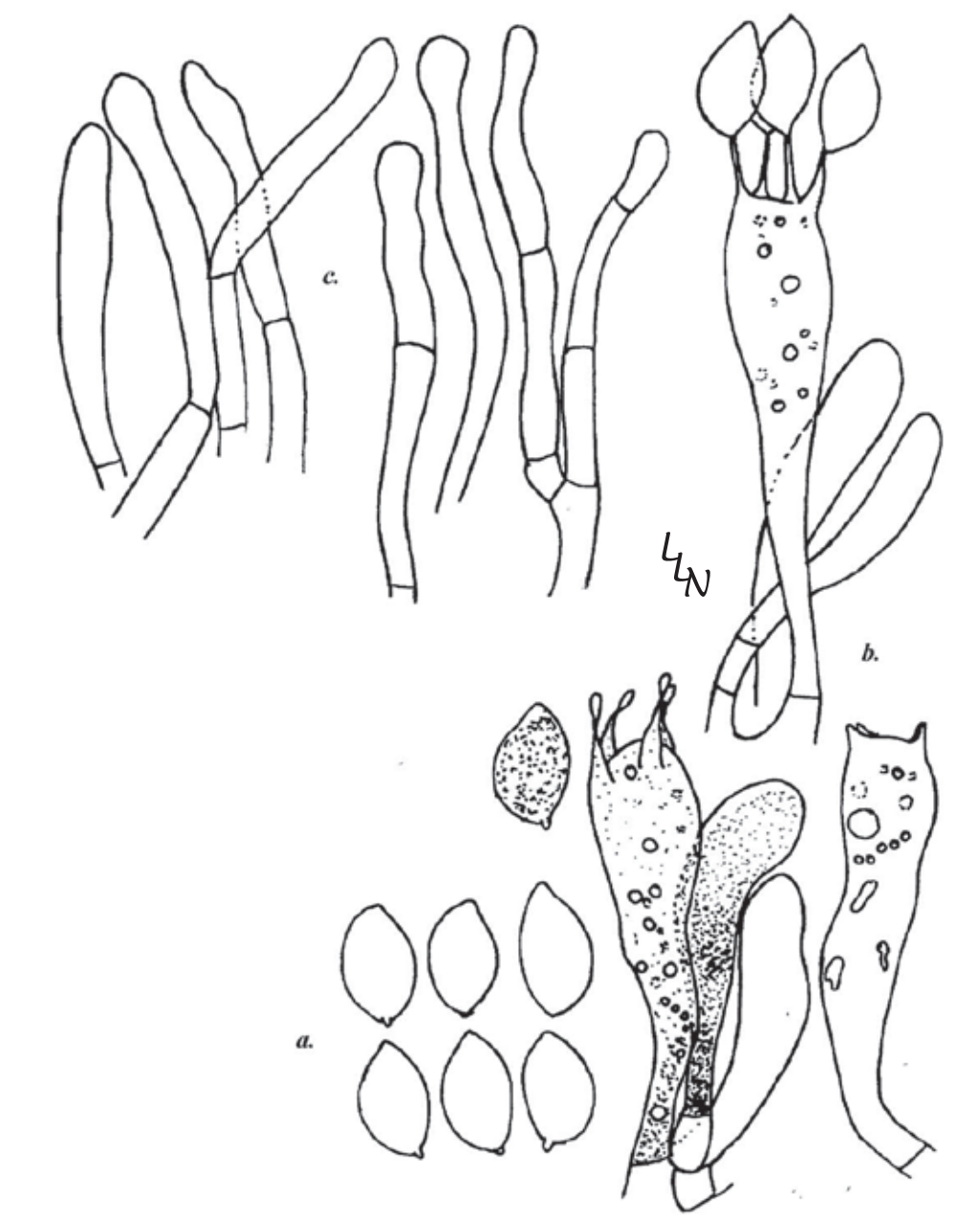
**FLUORESCENCE** — Under UV, gills fluoresce brilliant yellow white (young) to deep yellow orange; stipe pith glows a deep magenta red to dull purple.

**SPORE PRINT** — Dark cinnamon brown.

**Diagnostic characters** — Macroscopically, *P. piceae* can be recognized by its (1) (usually) small size, overall orange coloration and tendency to fruit in small groups, (2) (sub)viscid, bitter tasting convex-campanulate cap with an edge that becomes striate after drying, (3) orange to orange-cinnamon stipe with a rind that spirals slightly and a pith often insect-infested at ground level, causing it to topple over when touched, and (4) negative syringaldazine reactivity.



Important microscopical features include (1) large ( $\sim 9.4 \times 6 \mu\text{m}$ ), broadly almond-shaped to limoniform basidiospores with rounded to slightly pointed beaks, (2) narrow filamentous to cylindrical cheilocystidia with rounded or slightly swollen heads, (3) a bilaminar pileipellis with spirally gel-encrusted hyphae and KOH-soluble diffuse pigments, and (4) usual lack of clamp connections.



*Phaeocollybia piceae*

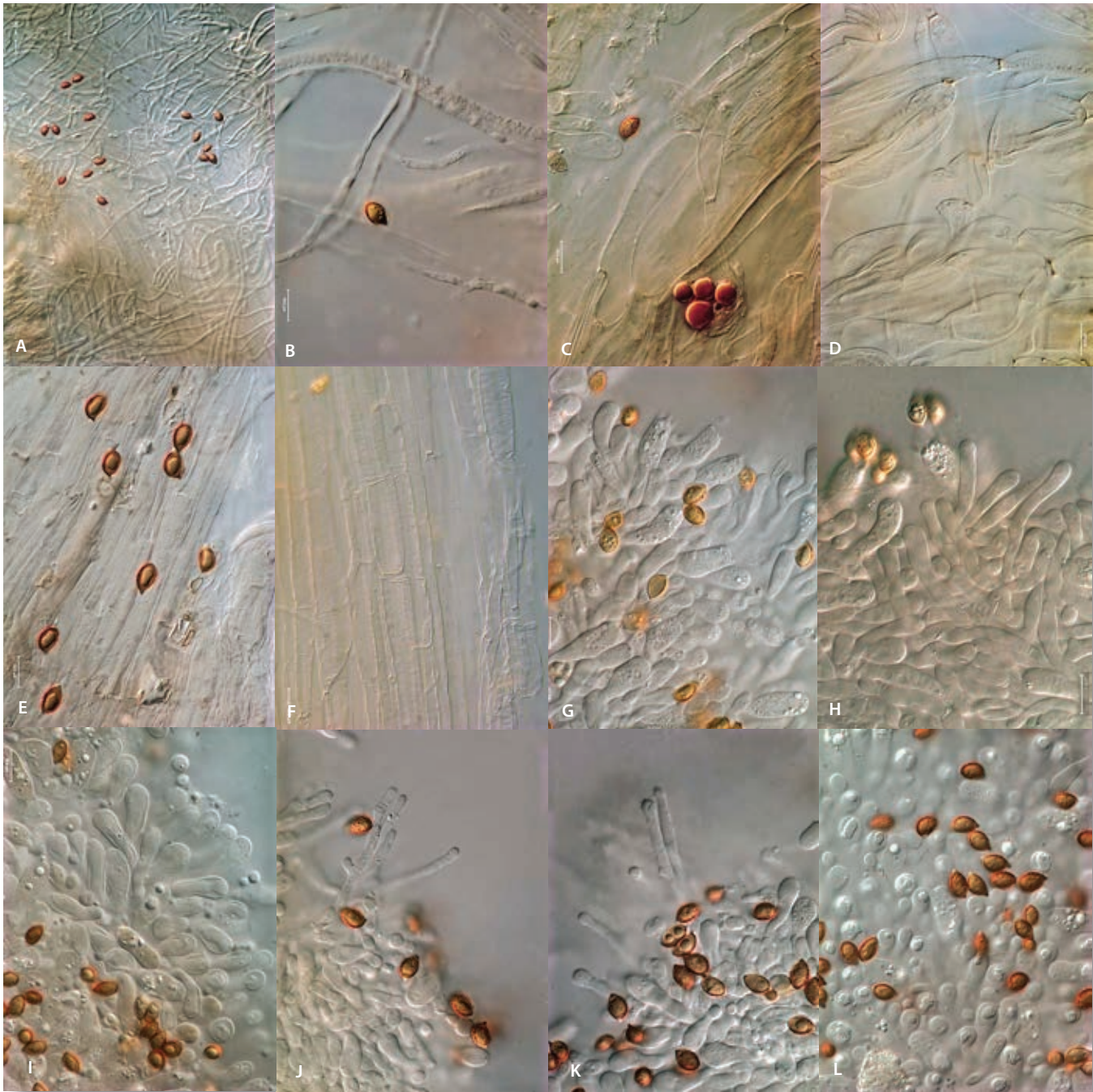
A–B. BASIDIOSPORES, BASIDIA, BASIDIOLES.

A—MICH HOLOTYPE AHSmith79085 & B—WTU LLNorvell1941106-1

C. CHEILOCYSTIDIA: MICH HOLOTYPE AHSmith79085 (L) & WTU Norvell1941022-4 (R).

OREGON: A, B & C (L) — Tillamook Co (type locality). C (R) — Clackamas Co.

**BASIDIOSPORES** —  $|x| = 9.4 \times 6 [(8)9-10.2(11) \times (5)5.3-6.3(6.5)] \mu\text{m}$ , broadly limoniform with rounded apical beak and distinct eccentric apiculus in profile view, broadly almond-shaped with small apical snout in face view, verruculose with ornamentation only occasionally projecting beyond spore outline, apical beak smooth; color in KOH medium orange amber, in  $\text{H}_2\text{O}$  paler, in Melzer's dextrinoid. — **BASIDIA** (2–)4-spored, clavate above long 2–3  $\mu\text{m}$  diam pedicels, 30–45  $\times$  6.5–8.5  $\mu\text{m}$ , colorless, contents granular.



Lorelei Norvell

*Phaeocollybia piceae*. A–D. PILEIPELLIS. A–B—Colorless narrow hyphae of the suprapellis are spirally encrusted with a faintly yellow gel. C–D—The subpellis contains brilliant orange diffuse pigments that rapidly dissolve into pigment drops (c) or eventually dissipate in KOH mounts; the orange intraparietal pigments are best seen at the septa of the inflated gel-encrusted thin-walled hyphae. E–F. STIPITIPPELLIS. E—The highly gelatinized thick-walled surface hyphae form a compact parallel suprapellis. F—Thinner walled lightly gel encrusted hyphae of the second layer gradually merge with the sarcodimitic tissues in the interior pith (not shown). G–I. BASIDIA & BASIDIOLES. G–H—Basidia are typically granular, becoming vacuolate after sporulation. I—It can be difficult to distinguish between ‘basidioles’ (immature basidia or basidia-like sterile elements) and true cheilocystidia in mounts where filamentous cheilocystidia are not visible. I–K. CHEILOCYSTIDIA. The typically filamentous to cylindrical cheilocystidia frequently collapse into an agglutinated mass, making them difficult to find in rehydrated tissues. L. BASIDIOSPORES are limoniform, faintly to coarsely roughened on the surface and have a short, but sometimes protruding, apical beak.

[OREGON, PNW-MS or OSC\*. Benton Co, ~Conner’s Camp (Mary’s Pk) Exeter2007-156(A); ~Reese Crk Exeter2007-173(G),-174(B). Coos Co, Myrtlewood RA: \*LNus17b86(J,K). Lane Co, Lobster Valley: Exeter2007-131(I,L). Lincoln Co, Saddle Bag Mtn: Exeter2007-27(F), -73(H), Norvell2071018-3(C–D),-4(E)] Scales = 10  $\mu$ m.

CYSTIDIAL ELEMENTS —CHEILOCYSTIDIA frequent to abundant, thin-walled, arising from the subhymenium and often intermixed with basidia; lengths variable and indeterminate ( $\leq 50 \mu\text{m}$  long), narrowly cylindrical with apices swelling occasionally to 4  $\mu\text{m}$  diam above narrow 2–3  $\mu\text{m}$  diam bases; some specimens also contain



Lorelei Norvell (L), Ron Exeter (R)

The 'moist to subviscid' *P. piceae* as fruitbodies appear in wet (left) and dry (right) weather. [LEFT—Type locality, Cascade Head Exp F, Tillamook Co OR, wtU Norvell1941106-1. RIGHT—Boulder Crk, Polk Co OR, PNW-MS Exeter2008-29].

large broadly basidiolate-like elements, apical extensions from senescent narrow elements occasional; colorless. —*PLEUROCYSTIDIA* absent. —*TIBIIFORM DIVERTICULA* abundant on primordial and pseudorhizal surfaces,  $\leq 20 \times 1 \mu\text{m}$  usually capitulate with 1.5–2  $\mu\text{m}$  diam subglobose heads, secretory with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** —*PILEIPELLIS* a bilaminar ixocutis: the top 20–50  $\mu\text{m}$  thick suprapellis of radially aligned, narrow (2–3  $\mu\text{m}$ ), gelatinized colorless hyphae that are frequently spirally-gel encrusted; the bottom subpellis with long (~85  $\mu\text{m}$ ), inflated (6–8  $\mu\text{m}$  diam) sausage-shaped hyphae that narrow abruptly to highly refractive septa, diffuse KOH-soluble orange pigments soon dissipating or concentrating in large brilliant orange drops with intraparietal orange pigments concentrated at the septa; occasional orange and colorless oleifers also present. —*STIPITIPELLIS* also bilaminar, thin surface layer parallel with sparingly branched, long and cylindrical, narrow (2–3  $\mu\text{m}$ ) gel-encrusted hyphae overlying wider (6–10  $\mu\text{m}$ ) thick-walled elements.

**TRAMAL TISSUES** — Subgelatinized, colorless; sarcodimitic in the pseudorhiza and weakly sarcodimitic in the upper stipe and pileus, where long (~150  $\mu\text{m}$ ), wide (8–15  $\mu\text{m}$ ), rigid, thick-walled (1  $\mu\text{m}$ ) hyphae predominate, intermixed with inconspicuous thin-walled, narrow (2–3  $\mu\text{m}$ ), branched, flexuous hyphae. Lamellar central hyphae parallel 2–4  $\mu\text{m}$  diam, thin-walled, colorless, and flanked by a narrow zone of 1–2  $\mu\text{m}$  diam colorless elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Found only rarely in the outer stipitipellis layer; elsewhere absent.

**Ecology** — Terrestrial (mycorrhizal). Solitary to scattered in small groups during autumn in coniferous (*Picea*, *Tsuga*, *Pseudotsuga*, *Abies*) forests. —*PACIFIC NORTHWEST ENDEMIC* known from ~35 sites in British Columbia, Washington, Oregon, and California.

**Similar species** — Although *Phaeocollybia piceae* fruitbodies are typically small (similar in size to *P. dissiliens*), we have encountered many robust specimens that rival the similarly orange-capped *P. kauffmanii* in size. The two species can be particularly difficult to differentiate microscopically, as they share similar basidiospore and cheilocystidial morphologies and both lack clamp connections except for the rare clamps in the stipe pellis. Features that differentiate *P. kauffmanii* in the field include a farinaceous taste, a paler solid stipe with firm pith that has not yet been seen as insect infested, and a strong magenta syringaldazine reactivity. The safest way to differentiate the two species is microscopically in the pileipellis from the non-KOH-soluble encrusting orange-brown pigments in *P. kauffmanii* and diffuse KOH-soluble orange pigments in *P. piceae*.

*P. radicata* and *P. dissiliens* are two other orange to yellow-orange species that might be mistaken for *P. piceae* in the field. Both species are easily distinguished microscopically by abundant clamp connections in all tissues and small ( $\leq 6.5 \mu\text{m}$ ) ellipsoid punctate-roughened basidiospores. Possession of hair-like to lageniform cheilocystidia with thin refractive necks further differentiates *P. radicata*.

See the discussion after the above species for additional comparisons.



Ron Exeter

*Phaeocollybia piceae* on Saddlebag Mountain  
Lincoln County, Oregon — PNW-MS Exeter2008-11 (in situ) & -12 (cut)

**Additional comments** — *Phaeocollybia piceae* was collected only once by Smith and Trappe (1972), who considered it rare. Recent collections have considerably extended its known range. Locally abundant in 1992 on a sandy flood plain under ancient spruce in Vancouver Island's 'Heaven's Grove', the species elsewhere exhibits a much more scattered habit. Numerous recent collections suggest that only rarely are more than four fruitbodies found close together, although 'twins' are frequent. Observation of younger fruitbodies arising from 'nurse' pseudorhizas of older specimens (Norvell 1998a,b) confirms the cespitose habit reported by Smith & Trappe (1972), but thus far no branched pseudorhizal cords have been collected.

In addition to the size variability noted above, there is also some variation in basidiospore ornamentation and color, ranging from minutely warty pale amber in Oregon materials to a more coarsely roughened medium orange-amber found in Californian and British Columbian specimens. Eight isolates obtained from specimens sampled from different sites generated identical RFLP profiles, implying that the above cited basidiospore variability probably is not taxonomically significant (Norvell 1998a).

Although *P. piceae* was originally described from a Sitka spruce forest, the numerous collections made from forests lacking spruce suggest the species is not host specific.

*References with descriptions and /or illustrations of Phaeocollybia piceae* —

- Castellano MA, Smith JE, O'Dell T, Cázares E, Nugent S. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. PNW-GTR-476. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s1 – 90].
- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. *Sydowia* 29: 28–70. [key to world species; line drawing, p. 59]
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [description 184–187; color photos pp. 255]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. [drawing of pseudorhizal regeneration, p. 620]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. *Mycologia* 64: 1138–1153. [key; type description 1145–1146]

*Phaeocollybia pleurocystidiata*

Scott Redhead

*Phaeocollybia pleurocystidiata* along the Bogachiel River Trail  
Olympic National Forest, Jefferson County, Washington — WTU HOLOTYPE Norvell1940330-2

***Phaeocollybia pleurocystidiata*** Norvell & Redhead, Mycologia 92: 985, 2000.

ETYMOLOGY — Based on possession of abundant pleurocystidia, unusual for *Phaeocollybia*.

HOLOTYPE — Bogachiel River Trail, Olympic National Forest (Jefferson County), WA, USA.

March 30, 1994 by L.L. Norvell & S.A. Redhead (WTU HOLOTYPE (DAOM ISOTYPE) LLNorvell1940330-2)

*Field summary* — Small fruitbodies with subviscid frequently mottled yellow to tawny convex–campanulate caps, pale yellow buff young gills, slender equal stuffed salmon colored stipes, and deeply rooting unbranched pseudorhizas. Scattered to gregarious during spring in Pacific Northwest coastal or coast range coniferous forests.

**PILEUS** — ~10–30 (60) mm diam, convex-umbonate with incurved margin and edge when young, expanding to broadly campanulate in age, umbo frequently with a small sharp papilla; moist to thinly viscid, smooth, opaque, hygrophanous; color when moist uniformly bright yellow brown (*buckthorn brown, sayal brown*), under dry conditions zonate with tawny to foxy brown (*tawny*) disc and papilla, ochraceous yellow (*yellow ochre, ochraceous buff, apricot yellow*) margin and yellow brown edge, in aged frequently rust mottled or spotted. —*FLESH* ~2 mm at the disc; pale buff. —*ODOR* not distinctive to slightly cucumber-farinaceous or raphanoid when crushed. —*TASTE* slightly raphanoid or cucumber-farinaceous. —*DRIED PILEUS* dark copper metallic with striate edge.

**LAMELLAE** — Almost free; pale yellow buff when young, darkening to rusty brown (*clay color*) in age.

**STIPE** — +/- central, rigid, ~50–80 mm above the ground, combined length with pseudorhiza >200 mm; apex 2–5 mm diam, upper stipe equal; surface moist, longitudinally lined to slightly polished, smooth; color of upper



Lorelei Norvell (A&amp;C), Ron Exeter (B)

Long slender pseudorhizas of the spring-fruiting *P. pleurocystidiata* narrow only gradually to deeply buried origins.

A–B—Bummer Ridge near Alsea (Benton Co, OR) [PNW-MS Exeter2008-02(A),-04(B)]

C—Green Peak (Benton Co, OR) [PNW-MS Norvell1980403-4(c)]

stipe pinkish brown (*light pinkish cinnamon*), soon darkening from base upwards to dark reddish brown (*liver brown*), upper and lower portions sometimes separated by an orange-brown (*mikado brown*) band; stuffed with compact pith that becomes loose and stringy in older specimens; cartilaginous rind moderately thin (~1 mm).

**PSEUDORHIZA** — Vertical monopodial, ~1/2–2/3 of overall length, continuous with stipe, equal and only gradually tapering to a slightly blunt origin; color salmon-colored to dark red brown.

**VEIL REMNANTS** — Inconspicuous, occasionally seen as isolated brownish (*mikado brown*) fibrils on cap edge and upper stipe.

**SYRINGALDAZINE REACTIVITY** — Negative (rarely faintly magenta after 45 minutes).

**FLUORESCENCE** — Under UV, gills fluoresce intensely white to brilliant yellow when young and dull mustard yellow in age.

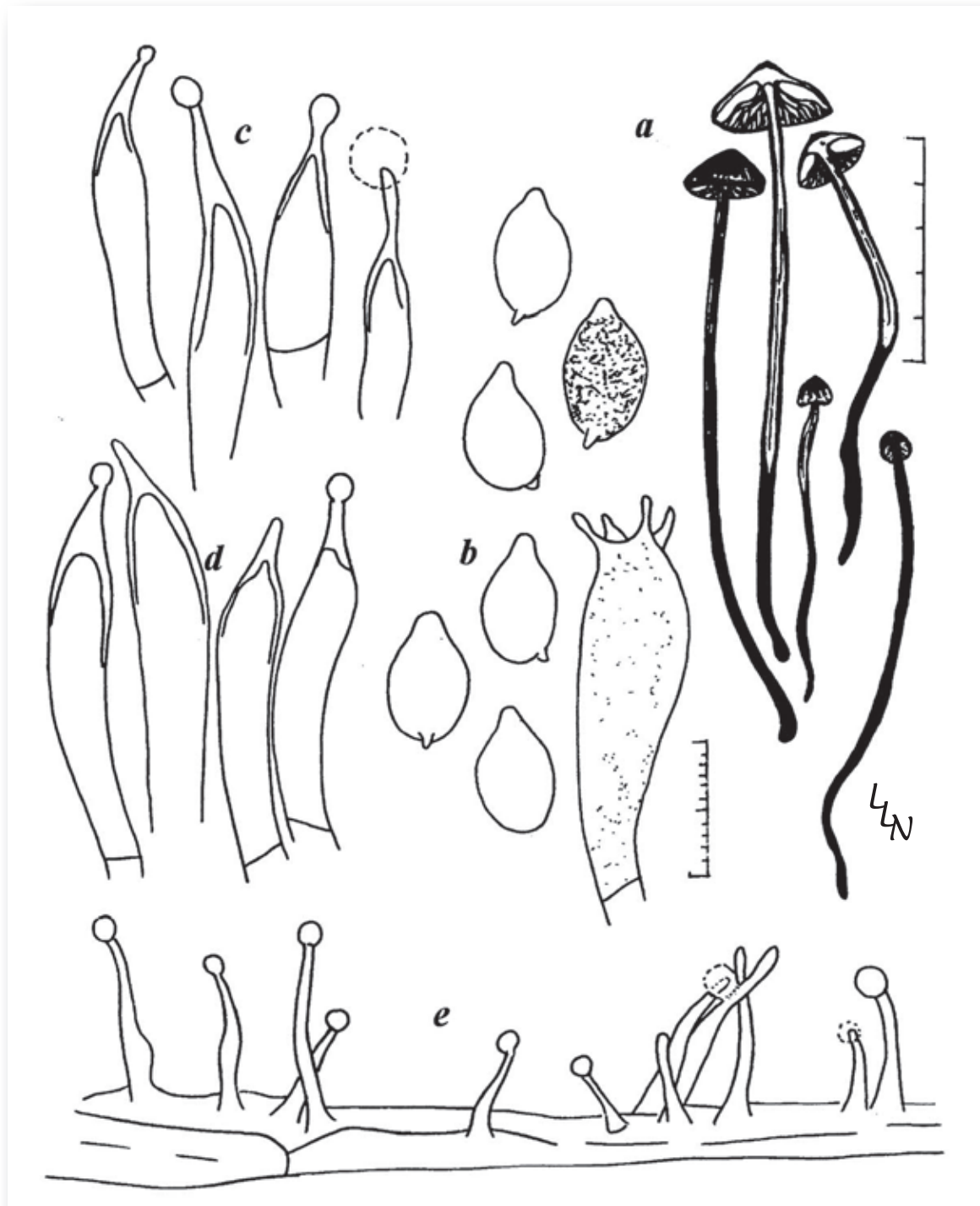
**SPORE PRINT** — Dark red brown.

**Diagnostic characters** — Macroscopically, *P. pleurocystidiata* can be recognized by its (1) small size and spring fruiting habit, (2) frequently mottled tawny yellow to tawny convex-campanulate caps, (3) long slender equal stipe and pseudorhiza, and (4) tissues that are negative to tardily faintly magenta in syringaldazine.

Important microscopical features include (1) thick-walled lageniform to tibiiform colorless to pale amber cystidia on both gill face and gill edge, (2) large (~9.2 × 6 μm) rough broadly limoniform beaked orange-brown basidiospores, (3) bilaminar pileipellis with encrusting orange pigments in both top and bottom layers, and (4) lack of clamp connections.

**BASIDIOSPORES** —  $|x| = 9.2 \times 6$  [8–11 × 5–7] μm, broadly limoniform with medium eccentric apiculus and rounded or tapered ~0.5 μm long beak in profile view, ovate to slightly almond-shaped in face view, verrucose to finely rugulose roughened with ornamentation usually projecting beyond spore outline except on smooth apical beak; color in KOH dark orange-brown, in H<sub>2</sub>O paler. — **BASIDIA** 4-spored, clavate, ~30 × 6–8 μm, colorless to dull pale amber, granular.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant and tightly packed, arising from the subhymenium to form a sterile layer; lageniform to tibiiform, lengths 17–30 μm, ventricose basal portion swelling above 2–3 μm diam basal septum to 4–6 μm before sharply narrowing to highly refractive thick-walled narrow (1–1.5 μm diam) neck, some with a 1–2 μm diam capitulum, with/without a surrounding secretory apical droplet, colorless. —

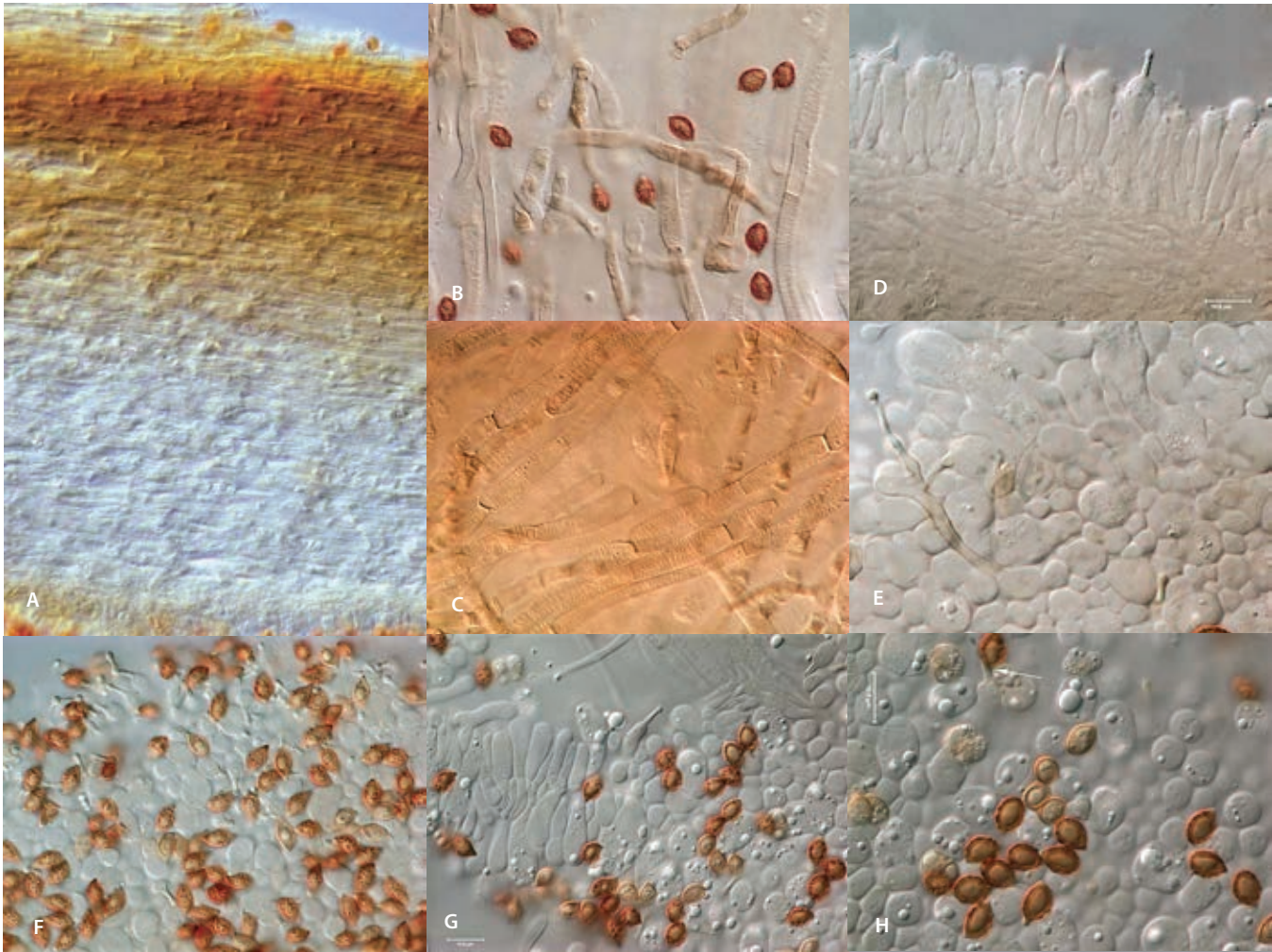


*Phaeocollybia pleurocystidiata*

Bogachiel River Trail, Olympic National Park, Jefferson County, Washington  
 WTU Norvell1940330-2 (HOLOTYPE) & -1 (PARATYPE) — Scales = 5 cm & 10  $\mu$ m

A — Habit. B — Basidia and basidiospores. C — Cheilocystidia.  
 D — Pleurocystidia. E — Tibiiform diverticula on pseudorhizal pellis.

*PLEUROCYSTIDIA* frequent, scattered, similar to cheilocystidia, refractive necks often with dull medium amber contents and then visible under a strong hand lens on fresh gill faces. — *TIBIIFORM DIVERTICULA* abundant on primordial and pseudorhizal surfaces, 5–15  $\times$  1–2  $\mu$ m, with/without head and/or apical droplet; highly refractive, colorless to pale amber.



Lorelei Norvell

*Phaeocollybia pleurocystidiata* [WASHINGTON: Jefferson Co, Olympic NP, Bogachiel Riv Tr WTU HOLOTYPE Norvell1940330-2(A). OREGON: ~Benton Co, Reese Crk PNW-MS Exeter2007-001(D,G&H); ~Coos Co, Myrtlewood RA osc LNus5-149(c) & -150(B); ~Lane Co, Siuslaw NF osc LNus12-66(E) & -75(F)] — A–C. *PILEIPELLIS*. Encrusting pigments coat the subgelatinized hyphae in both layers of pileus cuticle. —A. Radial section shows the compact narrow orange yellow suprapellis and wider orange subpellis overlying the colorless pileal trama at bottom. —B. Spores and gel-encrusted hyphae in the suprapellis. —C. Encrusting, diffuse, and intraparietal pigments (orange in KOH) are all present in the subpellis. D–H. *CHEILOCYSTIDIA*, *PLEUROCYSTIDIA*, AND *BASIDIOSPORES*. —D. Refractive thick-walled heads protrude only slightly above thin-walled bases. —E. A loose pleurocystidium with amber oily contents demonstrates entire element; generally only the pleurocystidial heads can be seen above the hymenium. —F–G. Pleurocystidia, although frequent, may be misinterpreted as representing basidial sterigmata. The easiest way to confirm their presence is by looking at an unmounted gill face under a dissecting microscope or strong hand lens. —G–H. Cystidial elements, basidioles, basidia and spores are readily detected in two gill 'squash' mounts. The dark orange-brown basidiospores have a rough ornamentation that extends beyond the spore outline. Scales — 10  $\mu$ m.

**CORTICAL TISSUES** —*PILEIPELLIS* a bilaminare ixocutis: the rudimentary top ~20–50  $\mu$ m thick suprapellis of radially aligned, narrow (1–3  $\mu$ m), spirally gel-encrusted pale amber hyphae; the bottom ~120  $\mu$ m thick subpellis with 2–6  $\mu$ m diam, gelatinized hyphae with brownish encrusting pigments and orange intraparietal and diffuse pigments; occasional orange oleifers also present. —*STIPITPELLIS* hyphae predominantly 1–2  $\mu$ m diam, gelatinized, with dull grayish orange encrusting and orange intraparietal pigments, occasional bright orange oleifers intermixed.

**TRAMAL TISSUES** — Moderately to highly gelatinized, strongly sarcodimitic in the pseudorhiza with long (95–200  $\mu$ m), wide (15–20  $\mu$ m), thick-walled ( $\leq$  4  $\mu$ m) rigid vessel hyphae intermixed with inconspicuous branched narrow (4–6  $\mu$ m), thin-walled (0.5  $\mu$ m) flexuous hyphae that become less numerous in the upper stipe where the thick-walled (1  $\mu$ m) wider (10–15) vessel hyphae predominate. In the pileus, interwoven, moderately thick-walled elements predominate. Lamellar central hyphae parallel 4–6  $\mu$ m diam, thin-walled, colorless, and flanked by a narrow zone of 1–2  $\mu$ m diam colorless elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.





Young and mature caps in one *P. pleurocystidiata* collection exhibit all hues in the typically 'tawny' spectrum  
 Bummer Ridge near Alsea, Benton County, Oregon — PNW-MS Exeter2008-002

**Ecology** — Terrestrial (mycorrhizal); scattered to loosely gregarious during early to late spring in coastal coniferous (*Tsuga*, *Picea*, *Abies*, *Pseudotsuga*) forests. — *PACIFIC NORTHWEST ENDEMIC* known from ~30 sites from northern Washington south to northern California, relatively frequent in coastal Oregon's lowland and montane western hemlock forests.

**Similar species** — *Phaeocollybia pleurocystidiata* is distinguished by its diagnostic pleurocystidia, spring fruiting habit, small slender stature, ochraceous yellow to tawny pileus, and large rough limoniform basidiospores. In the field it might be confused with the equally small *P. radicata*, *P. attenuata*, and *P. phaeogaleroides*.

Neither *P. attenuata* nor *P. radicata* fruit in the spring or produce pleurocystidia. *P. radicata* is further distinguished by its much smaller ( $\sim 5.8 \times 3.8 \mu\text{m}$ ), almost smooth, punctate-roughened ellipsoidal basidiospores and clamp connections. *P. attenuata* is additionally separated based on its thin-walled broadly clavate cheilocystidia and criniform wire-like pseudorhizas.

*P. phaeogaleroides*, which does fruit in the spring and frequently grows near or among *P. pleurocystidiata*, can usually be separated in the field by its darker red-brown to chestnut-brown often striate cap. It is easily separated microscopically by its longer ( $\sim 10 \times 6 \mu\text{m}$ ), paler, punctate-roughened ellipsoidal basidiospores with low snubbed apical beaks, abundant clamp connections, and cylindrical to filamentous cheilocystidia.

See notes under the above species for additional comparisons.

**Additional comments** — The existence of *P. pleurocystidiata* was first noted by finding abundant pleurocystidia in one 1965 herbarium collection misdetermined as *P. attenuata*. Subsequent herbarium finds suggested that



Ron Exeter

One *Phaeocollybia pleurocystidiata* collection dangles from a convenient moss-covered branch.  
 Bummer Ridge near Alsea, Benton County, Oregon — PNW-MS Exeter2008-006

the species was collected only in the spring, confirmed when Norvell & Redhead (2000) encountered fresh specimens during 1994 in late March to April on the Olympic Peninsula and western Oregon. Subsequent spring surveys have shown that the previously rarely collected species is relatively common along the northern Pacific coast and coast range forests, fruiting as early as January in the southern part of the range until mid-May in the north.

Following Singer's (1970, 1986) sectional classification system, *P. pleurocystidiata* should be referred to section *Versicolores* based on its cheilocystidial form, spore size, and lack of clamp connections. However, its relatively long (740 bp, cf. Norvell 1998a) ITS region gives a unique RFLP profile that separates it from the 5 other tested representatives of that section. Preliminary molecular data imply a close relationship with *P. attenuata*, which Singer (1986) referred to section *Phaeocollybia*. DNA sequencing will help determine its true phylogenetic affinities.

*References with descriptions and /or illustrations of Phaeocollybia pleurocystidiata —*

- Norvell LL. 1998. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales, Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [pp. 188–191; color photos 257]
- Norvell LL, Redhead SA. 2000. *Phaeocollybia* in western North America 2: the vernal *P. pleurocystidiata* sp. nov. and *P. carmanahensis* reconsidered. *Mycologia* 92: 984–991. [type description with B&W photos and line drawing]

*Phaeocollybia pseudofestiva*

Ron Exeter

*Phaeocollybia pseudofestiva* in situ on Saddlebag Mountain  
Lincoln County, Oregon — PNW-MS Exeter2007-69

***Phaeocollybia pseudofestiva*** A.H. Sm., Brittonia 9: 213, 1957

ETYMOLOGY — From the Latin for ‘false’ (*pseudo-*) + ‘festiva’, for its resemblance to the European species, *P. festiva*.  
HOLOTYPE — Crescent City (Del Norte), CA, USA; October 31, 1937 (MICH HOLOTYPE 11632 AHSmith8272)

*Field summary* — Small to medium-sized fruitbodies with glutinous dark green conic caps, pale dull yellow young gills, silky stuffed to hollow greenish stipes, and deeply rooting unbranched pseudorhizal cords. Solitary to gregarious during autumn in Pacific Northwest coniferous forests.

**PILEUS** — ~25–75(100) mm diam, acutely convex with incurved to slightly inrolled edge to conic-campanulate with slightly incurved to straight edge, viscid to glutinous, smooth, bald, faintly striatulate, hygrophanous; color when young uniformly to mottled dark olive-green (*citrine drab*, *dark olive*) or zonate with darker disc (*dark/deep olive*, *olive brown/black*) and brighter yellowish green margin (*citrine drab*, *honey yellow*, *isabella color*, *dark olive buff*), often with a duller greenish olive to greenish brown edge, in age darkening to dark olive to olive-brown. —**FLESH** 2–6 mm thick at disc, gradually thinning over the gills, cartilaginous, dull yellow to pale greenish white. —**ODOR** not distinctive, mild, occasionally sweetly nutty or complex with subtle floral-boiled potato components. —**TASTE** mild, not distinctive. —**DRIED PILEUS** metallic orange-brown, frequently with dark reddish brown disc.

**LAMELLAE** — Free to deeply adnexed, pale yellow or greenish buff when young, dark greenish brown with eroded edges in age.

**STIPE** — +/- central, rigid, ~30–70 mm above the ground, retrieved length with pseudorhiza up to 235 mm before breaking off in soil; apex 4–13 mm diam, upper portion equal or slightly narrowing/widening to ground level; dry to moist, shiny beneath short fibrillose patches; color of young apex greenish to pinkish buff (*deep olive buff*, *tea green*, *light cinnamon buff*) darkening in age (*olive buff*, *buffy brown*, *cinnamon*), grading to



*Phaeocollybia pseudofestiva* – This composite showing two collections from Oregon’s Saddle Bag Mountain details the pallid context and dark ivy green cap colors typical in young specimens (left) as well glutinous conic caps, dense concentrations of dark green short fibrillose patches on stipes with red bases, and hints of pseudorhizal cords left behind in the soil. Although the caps now appear brown, the longitudinal section at left reveals the diagnostic blue-green color noted in the field when the specimens were collected earlier the same day. [PNW-MS: Norvell2071029-35 (A) & Exeter2007-70 (B–D)]

dark green to yellow-/red-brown at ground level, often staining brown where bruised; when young stuffed with closely compacted silky pale greenish to pinkish-buff pith, in age sometimes hollow or insect-infested; cartilaginous rind ~2 mm thick.

**PSEUDORHIZA** — Unbranched or sequential-racemose (see comments below), continuous with stipe and tapering (sometimes abruptly) to an easily broken cord-like origin; color dark orange to red-brown.

**VEIL REMNANTS** — Usually evident as abundant short gold or greenish brown fibrillose patches on the upper stipe.

**SYRINGALDAZINE REACTIVITY** — Pseudorhiza usually strongly magenta, cap, gills and stipe not magenta but often exuding a bright yellow-green color that fades after 15 minutes.

**FLUORESCENCE** — Under UV, gills brilliant yellow white to dull yellow; context deep dull purple at stipe apex, elsewhere ochraceous to deep red.

**SPORE PRINT** — Pinkish cinnamon brown.

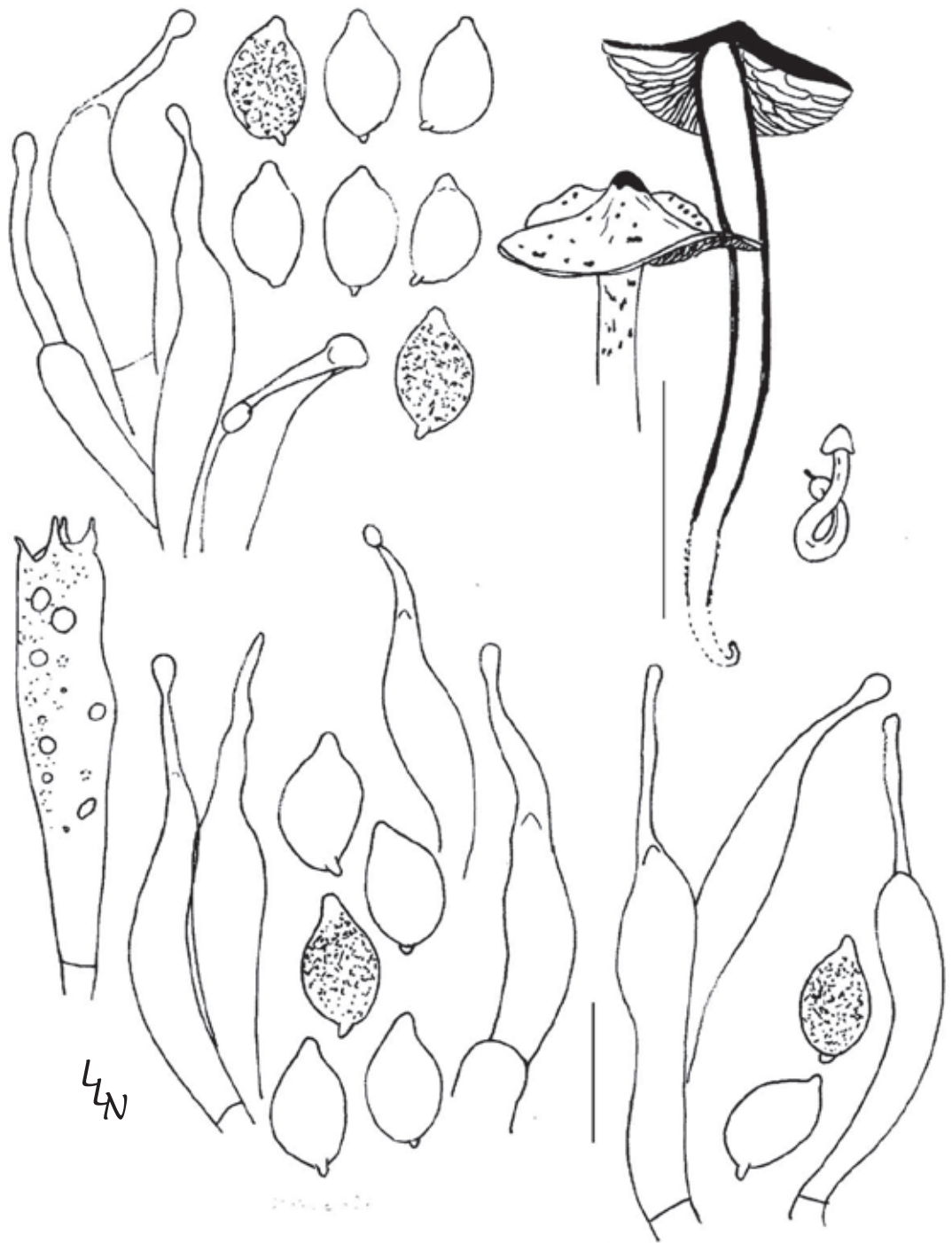
**Diagnostic characters** — Macroscopically, *P. pseudofestiva* can be recognized by its (1) viscid to glutinous green conic-campanulate cap, (2) dull yellow gills, (3) usually stuffed greenish buff stipe with orange-red base that narrows (sometimes abruptly) to a pseudorhizal cord, (4) medium stature, and (5) pseudorhiza that rapidly turns deep magenta in syringaldazine.

Important microscopical features include (1) abundant lageniform to minutely capitulate tibiiform cheilocystidia with long narrow thick-walled refractive necks, (2) medium-sized (~8 × 5 μm) rough limoniform basidiospores with pronounced pointed apical beaks, (3) a bilaminar pileipellis with a subpellis with diffuse and encrusting pigments that immediately turn orange in KOH, and (4) absence of clamp connections.

**BASIDIOSPORES** —  $|x| = 8 \times 5 [(6.5)7-9(9.5) \times (4)4.5-5.5] \mu\text{m}$ , inequilaterally limoniform central beak and eccentric apiculus in profile view, ovate with long narrow beak in face view, verrucose to rugulose warty roughened except on smooth long (0.5–1.0 μm) apical beak; color in KOH medium amber, in H<sub>2</sub>O paler, in Melzer’s inamyloid and non-dextrinoid. — **BASIDIA** 4-spored, clavate, ~25–32 × 6–9 μm, granular, colorless to pale amber in KOH.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, arising from the subhymenium and intermixed with basidia; lengths 25–80 μm, with thin-walled 3–7 μm diam hyaline bases subtending long (12–20 μm) thick-walled

narrow (0.5–2.0  $\mu\text{m}$  diam) necks with or without slightly wider ( $\leq 2.5$   $\mu\text{m}$  diam) capitula, apices or capitula often either obscured by gelatinous secretory drops or gel-encrusted; the thin-walled bases usually colorless, and highly refractive necks and capitula usually pale greenish in  $\text{H}_2\text{O}$  and ochraceous in KOH. —*PLEUROCYSTIDIA* absent. —*TIBIIFORM DIVERTICULA* abundant on mycelia, primordial and pseudorhizal surfaces, and fibrillose patches on upper stipe; tibiiform, 5–20  $\times$  1  $\times$  0.5  $\mu\text{m}$ ; colorless to pale ochraceous.

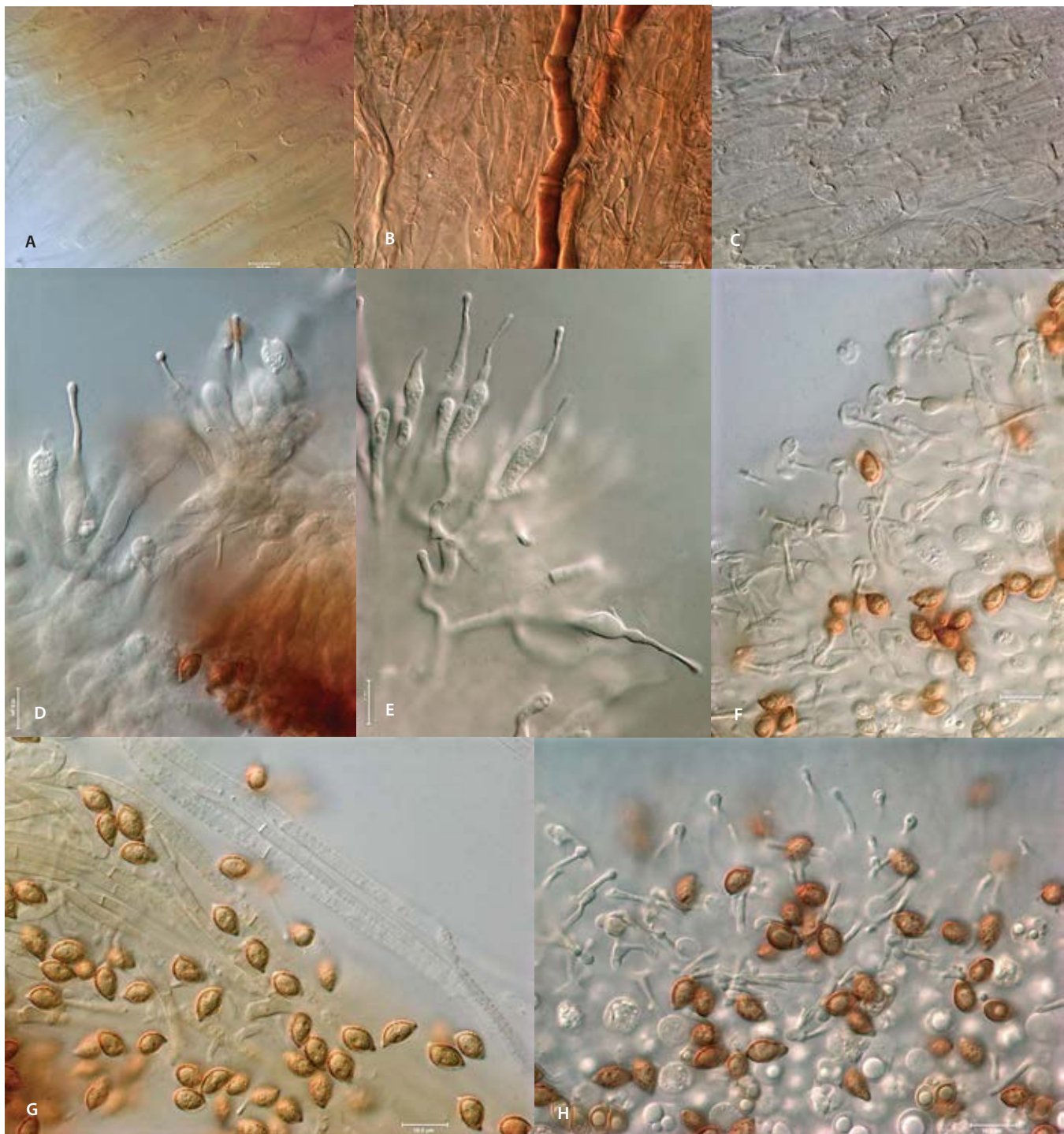


*Phaeocollybia pseudofestiva*

A. HABIT (scale = 5 cm) — Jackson SF & Van Damme SP, Mendocino County, California  
Mature specimen (WTU Norvell1921116-2) & Primordium (WTU Norvell1921121-1)

B–D. CHEILOCYSTIDIA & BASIDIOSPORES (scale = 10  $\mu\text{m}$ ).

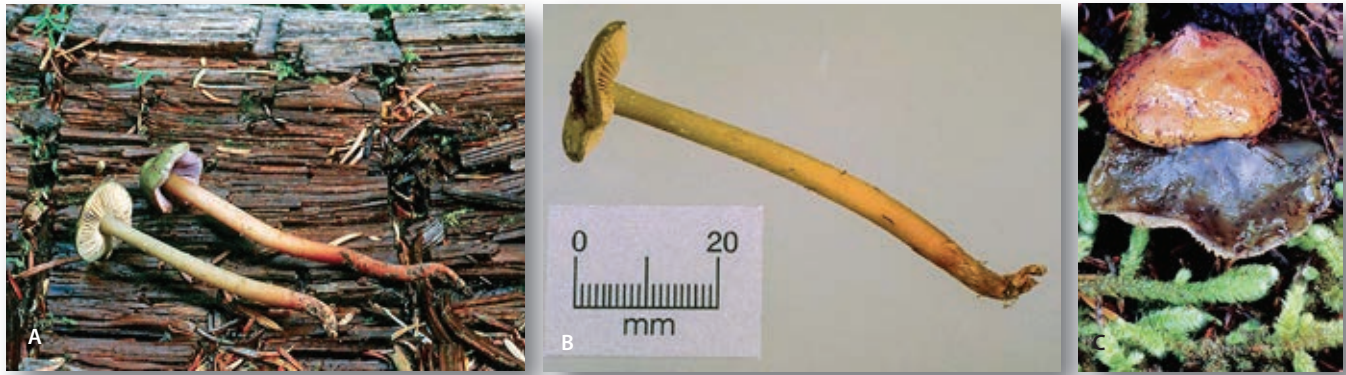
B: Vancouver Isl, BC—WTU Norvell1921007-6, c: Clallam Co, WA—WTU Norvell1921023-28,  
d: Del Norte Co, CA—MICH HOLOTYPE 11632 AHSmith8274.



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*Phaeocollybia pseudofestiva* [OREGON: Coos Co—Medford RA, osc: LNus17b91 (B) & 95 (B); Lincoln Co—Saddlebag Mtn, PNW-MS: Exeter2007-70 (A, D–G)]. A–C. PILEUS TISSUES. Diffuse and encrusting pigments of the subpellis (A–B) and oleifers (B) turn bright deep orange in KOH, while inflated hyphae of the pileus trama (C) remain colorless. D–F. CHEILOCYSTIDIA. Although abundant and relatively large, the sterile lageniform and tibiiform elements with narrow necks and minute capitula frequently obscured by gelatinous secretions arise from the subhymenium and share the gill edge with the granular basidia. The secretory cheilocystidia are similar in form and function to the tibiiform diverticula found on all phaeocollybian mycelia, primordia, and pseudorhizas. G–H. BASIDIOSPORES. The limoniform basidiospores with long protruding beaks share a similar roughness with *P. olivacea* spores. The narrower shape and smaller size of *P. pseudofestiva* spores help separate the two species, which often fruit together in gregarious clusters. Scale bars = 10 μm.

CORTICAL TISSUES —PILEIPELLIS a bilaminare ixocutis: the 100–250 μm thick suprapellis of radially aligned, narrow (1–3 μm diam), highly gelatinized colorless hyphae in a thick gelatinous matrix overlies a diffusely pigmented subpellis with wide (8–15 μm diam), gelatinized hyphae encrusted by pale greenish amber



*Phaeocollybia pseudofestiva* and associates [A&B—Upper Carmanah Valley, Vancouver Island BC WTU&DAOM: Norvell1921007-6 (A&B), Norvell1921007-1 (A); c—Wildcat Mtn, Clackamas Co WA, WTU: Norvell1951018-10 (top) & -11 (bottom)]. A—Two pristine green-capped specimens collected within a few meters of each other were quickly separated based on the violet gills of *P. fallax* (top) and the buff gills & green stipe of *P. pseudofestiva* (bottom). B—The green-colored cap and upper stipe, buff colored gills, and reddish stipe bases are also key characters for *P. olivacea* (not shown), which often grows in the same clusters as *P. pseudofestiva*. Smaller stature, abundant tibiiform cheilocystidia and smaller basidiospores will identify *P. pseudofestiva*. C—A tawny *P. ammiratii* (top) and green *P. pseudofestiva* (bottom) occupy the same site in a recently thinned noble fir stand.

pigments that turn pale to deep orange in KOH: amber to orange oleifers also present. —*STIPITIPPELLIS* a thick layer of sparingly branched, long cylindrical narrow (2–4  $\mu\text{m}$  diam) colorless to greenish amber hyphae.

TRAMAL TISSUES — gelatinized, +/- thin-walled and wide ( $\leq 20$   $\mu\text{m}$  diam) throughout pileus and stipe; oleifers occasional throughout. Lamellar central hyphae parallel, thin-walled, narrow (2–3  $\mu\text{m}$  diam), colorless, with similar outer elements giving rise to a compact subhymenium.

CLAMP CONNECTIONS — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to densely gregarious during autumn in coniferous (*Picea*, *Abies*, *Tsuga*, *Pseudotsuga*) and mixed (*Lithocarpus* included in the southern part of the range) forests. —*PACIFIC NORTHWEST ENDEMIC* uncommon, known from ~35 sites in British Columbia, Washington, Oregon, and northern California.

**Similar species** — Key characters for *Phaeocollybia pseudofestiva* are the conic viscid greenish cap and dull to ochraceous yellow gills. In stature, pileus shape and color, basidiomes greatly resemble those of *P. fallax*, which is differentiated by its violet colored young gills and drab upper stipe. Thin-walled, broadly subcapitate cheilocystidia that form a sterile gill edge microscopically distinguish *P. fallax*.

In the field, *P. pseudofestiva* has been most often mistaken for the larger, more robust *P. olivacea*, a frequent close associate throughout the southern part of its range in Oregon and California. Fruitbodies of both species share similarly colored green caps and yellowish to pallid gills. Possession of thin-walled clavate cheilocystidia within a sterile gill edge serves to separate *P. olivacea* from *P. pseudofestiva*, although long filiform extensions emerging from cheilocystidia in older specimens may sometimes be misinterpreted as tibiiform elements; there the larger, more broadly limoniform basidiospores will diagnose *P. olivacea*.

See comments after *P. fallax* and *P. olivacea* for additional comparisons.

**Additional comments** — In his type description, Smith (1957b) described *P. pseudofestiva* as having ‘hollow’ stipes and a ‘fleetingly pungent’ odor, emphasizing the former as key field characters for differentiating *P. pseudofestiva* from *P. olivacea*, which he described with persistently stuffed stipes. Relatively few of the *P. pseudofestiva* stipes we have examined proved to be hollow, however, with most stipes stuffed with pith that ranged from pale and firm (in young material) to spongy and stringy (in mature or saturated material). Care should be taken in slicing older specimens lengthwise, as frequently the stringy pith may catch on the edge of the blade and be dragged down during the cut, making stipes appear hollow when they are not. The odor can at best be described as ‘not distinctive’, and we have not encountered the ‘fleetingly pungent’ odor noted by Smith. We have detected a pleasant sugary sweet odor (vaguely reminiscent of maple syrup and not uncommon in dried phaeocollybias) in dried specimens.

As in *P. olivacea*, there is wide morphological variation found in *P. pseudofestiva*. The typically small fruitbody size has helped separate *P. pseudofestiva* from *P. olivacea* in mixed herbarium collections prior to



Elizabeth Fox (L), Ron Exeter (R)

Short greenish brown fibrils ring the *P. pseudofestiva* stipe apex in Carmanah Valley (L) and Saddlebag Mountain (R).  
LEFT: Vancouver Island, BC—WTU&DAOM Norvell1921009-1. RIGHT: Lincoln Co, OR—PNW-MS Exeter2007-070.

microscopic examination (Norvell 1998a, c), but some *P. pseudofestiva* specimens have had surprisingly large (up to 100 mm diam) caps. Furthermore, while most basidiomes produce relatively narrow spores, median spore widths of 5.5  $\mu\text{m}$  have been noted for several collections. Additionally, in Washington and British Columbia, numerous solitary fruitbodies were identified as *P. pseudofestiva*, contradicting the gregarious/cespitoso habit noted by Smith (1957b) for the type collection.

After having observed two pseudorhizal types for *P. pseudofestiva* — with some pseudorhizas arising from vertical-monopodial blunt origins continuous with the stipe and others originating from narrow cords — Norvell (1998a) noted that solitary specimens tended to be monopodial and gregarious fruitbodies tended to have cord-like pseudorhizas. Finding only short severed unbranched lengths or cords within the latter group, Norvell inferred a racemose (branched) pattern for the complete pseudorhizas. Based on recent numerous collections from in northern Oregon, we suspect that a great many previously ‘vertical-monopodial’ specimens were broken off during collection, leaving the pseudorhizal cord behind in the soil. For that reason, we provisionally place *P. pseudofestiva* in the ‘sequential-racemose’ pseudorhizal category.

Preliminary molecular analyses of seven ‘pseudofestiva’ collections (Norvell 1998a) implied the existence of three closely allied but geographically separated taxa. We still have not yet identified consistent key characters to support separate molecular ‘taxa’, and so for the purposes of this field guide, we refer all green-capped phaeocollybias with lageniform to tibiiform thick-walled cheilocystidia to *P. pseudofestiva*.

#### References with descriptions and /or illustrations of *Phaeocollybia pseudofestiva* —

- Castellano MA, Cázares E, Fondrick B, Dreisbach T. 2003. Handbook to additional fungal species of special concern in the Northwest Forest Plan. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [description s3 – 85].
- Horak E. 1977 (‘1976’). Further additions towards a monograph of *Phaeocollybia*. Sydowia 29: 28–70. [key to world species; line drawing, p. 54]
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [discussion of x, pp. x]
- Norvell LL. 2002. *Phaeocollybia* in western North America 3: New species *P. phaeogaleroides* and *P. rifflipes*, with notes on the *P. festiva* complex. Mycotaxon 81: 95–112. [comparison with *P. fallax*]
- Norvell LL. 2004. *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and Section *Versicolores* reconsidered. Mycotaxon 90(2): 241–260. [comparison with other members of sect. *Versicolores*].
- Smith AH. 1957b. A contribution toward a monograph of *Phaeocollybia*. Brittonia 9: 195–217. [key; microdrawings p. 210, type descr. pp. 213–214]



*Phaeocollybia radicata*

Ron Exeter

*Phaeocollybia radicata* (resting on a cracked *Boletus chrysenteron* cap)  
Old Blue near Mary's Peak, Benton County, Oregon — PNW-MS Exeter2007-79

***Phaeocollybia radicata*** (Murrill) Singer, Lilloa 22: 567, 1951.

= *Naucoria radicata* Murrill, N. Amer. Flora 10: 181, 1917.

ETYMOLOGY — From the Latin 'radix' meaning root, for the rooting stipe.

HOLOTYPE — Glenbrook (Benton County), OR, USA; November 7, 1911 (NY HOLOTYPE Murrill 775).

*Field summary* — Small fruitbodies with moist orange convex-campanulate caps, orangish to pale cinnamon young gills, slender loosely fibrillose stuffed orange to chestnut brown stipes, and deeply rooting branching pseudorhizas. Solitary to loosely gregarious during autumn in western hemlock & Douglas-fir forests in Oregon and California.

**PILEUS** — ~15–40 mm diam, convex to campanulate with an inconspicuous to prominent (occasionally papillate) umbo and downturned margin, smooth, bald, lubricous to subviscid, hygrophanous and slightly striatulate when wet; color when young overall orange to tawny or zonate with a dark reddish brown disc and orange to ochraceous tawny margin, fading to orange or yellow tan (*buckthorn brown*, *apricot buff*). — **FLESH** ~2 mm at disc, thinning over gills; pale orange or concolorous with cap cuticle. — **ODOR** not distinctive or vaguely raphanoid or *Oxalis*-like. — **TASTE** not distinctive. — **DRIED PILEUS** bright gold or copper metallic, occasionally red-brown shiny to matte, frequently striate on edges.

**LAMELLAE** — Almost free, pale orange to pale cinnamon buff when young, darkening to cinnamon brown to rust brown (*cinnamon rufous*) with serrulate edges in age.

**STIPE** — +/- central, upright, cartilaginous and slightly fragile, ~40 mm above the ground, combined length with pseudorhiza exceeding 180 mm; apex 2–4(5) mm diam, upper stipe equal or swelling slightly at ground level; dry to lubricous, smooth, slightly polished to matte; color of young apex similar to cap cuticle (orange to orange tan), grading to brown (*chestnut brown*) at ground level, bruising orange; when young stuffed with silky pale orange pith, often hollow in age; cartilaginous rind ~1 mm thick.



Lorelei Norvell

Development in *P. radicata* [OREGON. Benton Co, Old Blue (Klickitat Rd), PNW-MS: Exeter2007-079(A); Norvell2071029-6(C),-10(B&G) & -11(B-F)] — It can be difficult to know where the lower stipe ends and the pseudorhiza begins, particularly when most specimens (A&C) snap loose from the recently discovered pseudorhizal cord during collection. The remaining photos (b & d-g) show the branching rhizomorphic cords (or 'mother pseudorhizas') and lower pseudorhizas that give rise to primordia (arrows). Both the cord and pseudorhiza exhibit 'meristemoidal' (regenerating) activity. Scales in millimeters

**PSEUDORHIZA** — Rhizomorphic and racemose (branching to give rise to many fruitbodies); upper portion continuous with lower stipe, gradually narrowing to origin from ~2 mm diam cord-like 'mother pseudorhiza', both fleshy and cord-like pseudorhizas giving rise to primordia; dark red-brown (*chestnut brown*).

**VEIL REMNANTS** — Infrequent, evident as isolated fibrillose patches on upper stipe; color pale orange-yellow.

**SYRINGALDAZINE REACTIVITY** — Variable; gills, cap, and upper stipe negative; lower pseudorhiza and cord negative or positive (after 30 minutes).

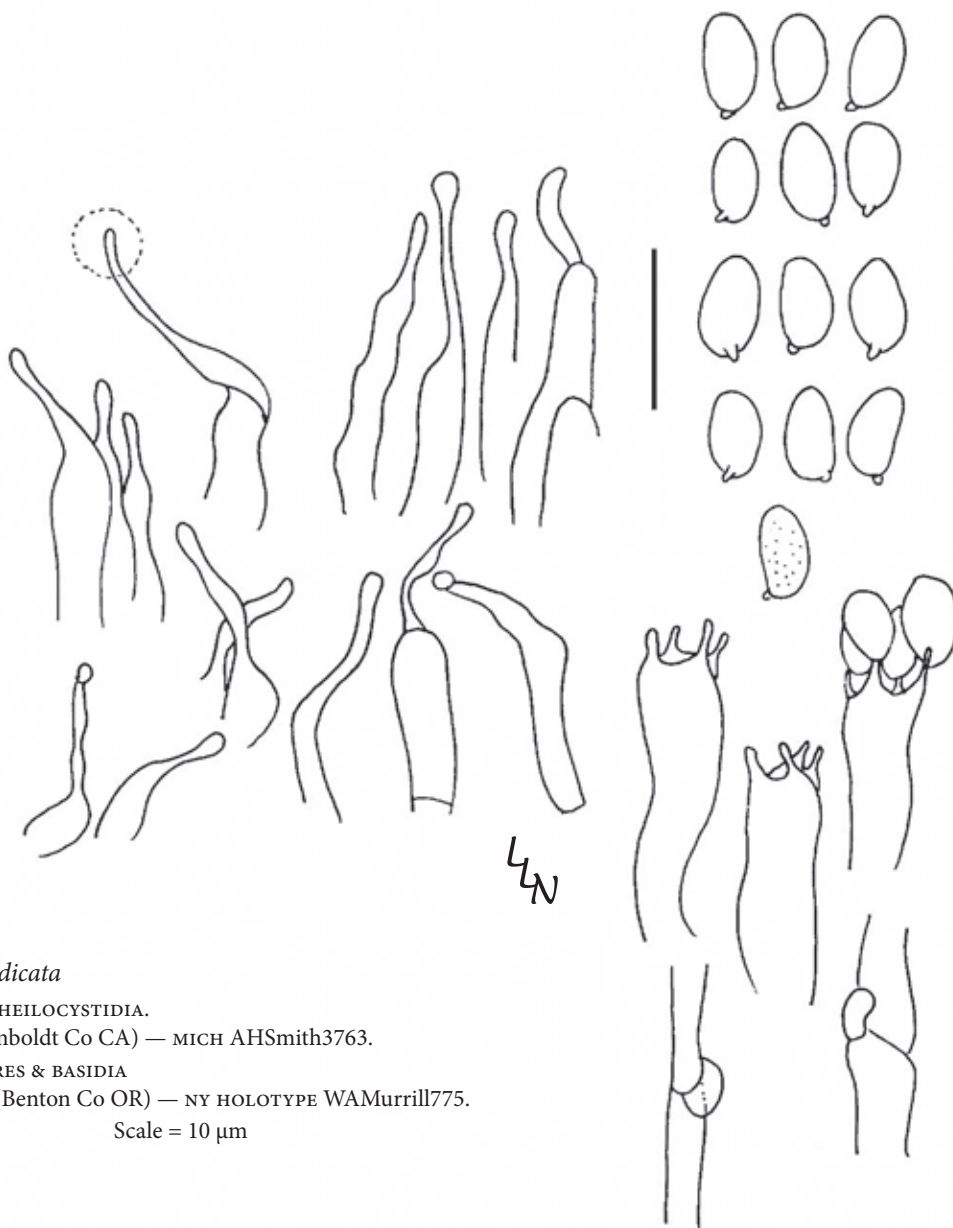
**FLUORESCENCE** — Under UV, gills fluoresce ochraceous orange; other surfaces glow dull deep magenta to purple.

**SPORE PRINT** — Chestnut brown.

**Diagnostic characters** — Macroscopically, *P. radicata* can be recognized by its (1) small (~25 mm diam) moist convex-campanulate orange to tawny cap, (2) long, narrow (2–4 mm) pale orange to brown fibrillose stuffed to hollow stipe, (3) regenerating upper pseudorhiza and pliable branching rhizomorphic cord (excavation necessary), and (4) scattered solitary to gregarious habit.

Important microscopic features include (1) small (~5.8 × 3.2 μm), faintly ornamented ellipsoidal basidiospores with rounded to slightly pointed apices, (2) frequent to abundant clamp connections, (3) small tibiiform to lageniform cheilocystidia with thin-walled swollen bases and hair-like thick-walled refractive neck with/without globose heads, and (4) the presence of thick-walled orange-brown setae, refractive tibiiform diverticula, and thin-walled caulocystidia on the lower stipe and pseudorhizal surfaces.

BASIDIOSPORES —  $|x| = 5.8 \times 3.2$  [4.7–6.2(6.3)  $\times$  2.8–4.1]  $\mu\text{m}$ , inequilaterally ellipsoidal with small eccentric apiculus and rounded to subtly pointed apex in profile view, ovate in face view, minutely punctate roughened ornamentation visible only under oil immersion; color in KOH pale amber, in  $\text{H}_2\text{O}$  very pale amber, in Melzer's dextrinoid. —BASIDIA 4-spored, clavate,  $17\text{--}27 \times 4\text{--}7$   $\mu\text{m}$ , colorless, contents slightly granular.



*Phaeocollybia radicata*

A. BASIDIA & CHEILOCYSTIDIA.

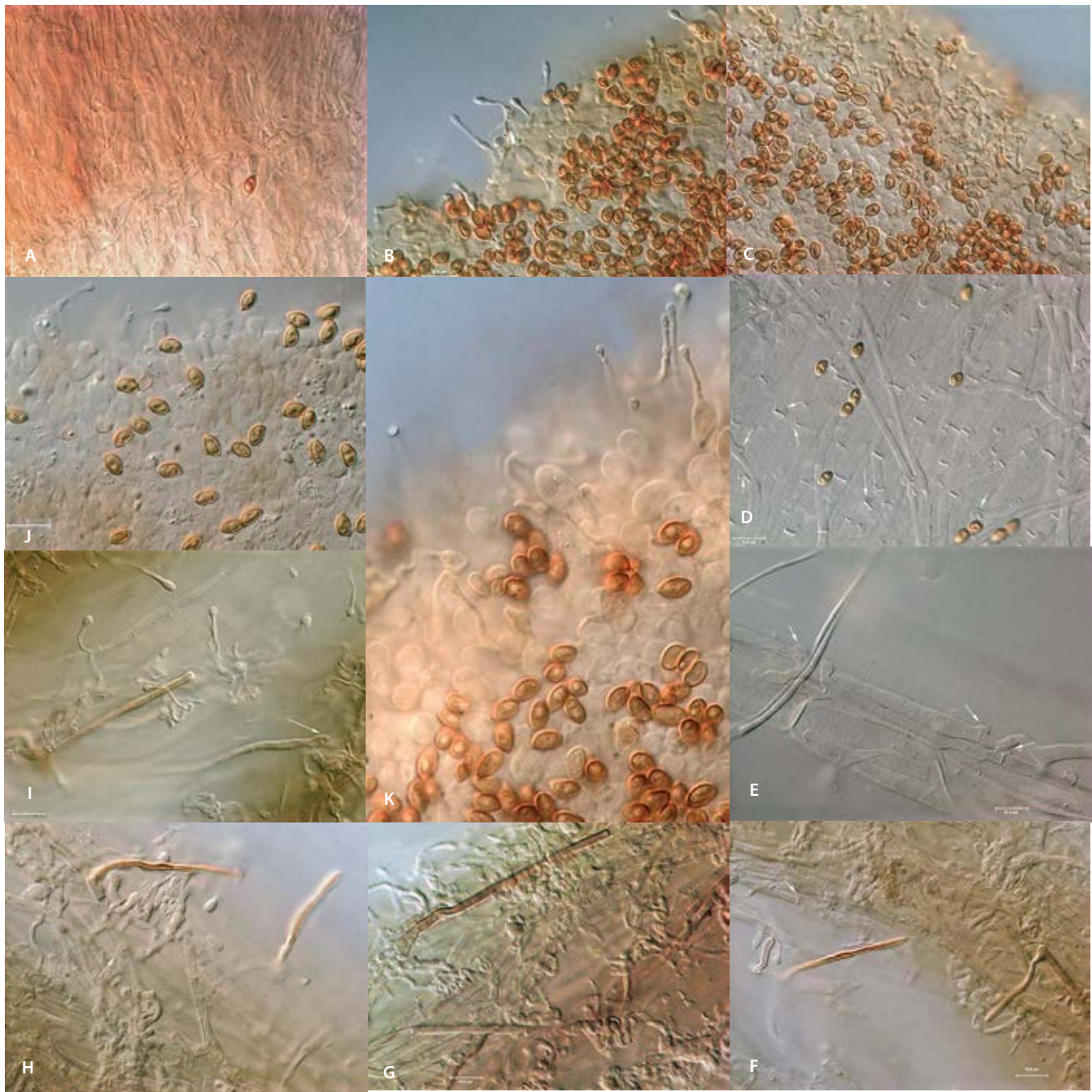
Orick (Humboldt Co CA) — MICH AHSmith3763.

B. BASIDIOSPORES & BASIDIA

Glenbrook (Benton Co OR) — NY HOLOTYPE WAMurrill775.

Scale = 10  $\mu\text{m}$

CYSTIDIAL ELEMENTS —CHEILOCYSTIDIA abundant but often collapsed or turned under in mounts and thus difficult to see, arising from the subhymenium; lengths 18–35  $\mu\text{m}$ , lageniform to tibiiform with thin-walled ventricose (2–4  $\mu\text{m}$ ) bases and thick-walled narrow ( $\leq 1$   $\mu\text{m}$ ) refractive necks, with/without minute capituli and/or apical secretory droplets; colorless to pale amber. —PLEUROCYSTIDIA absent. —TIBIIFORM DIVERTICULA frequent on pseudorhizal pellis,  $\leq 20 \times 2$   $\mu\text{m}$ , basally aseptate, refractive, lageniform to tibiiform, thick-walled, with/without minute capitulum and/or secretory droplet, colorless. —CAULOCYSTIDIA abundant but confined to lower stipe and upper pseudorhiza,  $\leq 20 \times 1$   $\mu\text{m}$ , +/- flexuous, thin-walled, basally septate, ligulate to tibiiform, contents colorless to pale amber. —SETAE occasional to frequent on surfaces of rhizomorphic cord and lower pseudorhiza, long ( $\leq 100$   $\mu\text{m}$ ), thick-walled ( $< 2$   $\mu\text{m}$ ), apices mucronate to rounded, often broken off; thick-walled; brown.



Lorelei Norvell

*Phaeocollybia radicata* [OREGON: ~Benton Co, Old Blue, Klickitat Rd, PNW-MS: Exeter2006-19(A), Exeter2007-83(B) & -89(D), Norvell2071029-6(J) & -13(E) ~Coos Co, Myrtlewood RA, Bronson Crk, osc: LN12us83 (C&F-I); ~Lane Co, Siuslaw NF, osc: LN8us170(K)] (clockwise from upper left) — A. PILEUS SUBPELLIS in KOH. B–C&J–K. BASIDIOSPORES AND CHEILOCYSTIDIA. The faintly roughened exosporium of the basidiospores may appear smooth even under high oil immersion unless the focus is shifted up and down to expose the finely punctate ornamentation. Although highly gelatinized tibiiform cheilocystidia stick together in agglutinated clumps (c) in poorly rehydrated gill tissues, it is better to section dry tissues, as fresh secretory elements usually stick to the blade. D–E. CLAMP CONNECTIONS — abundant throughout all tissues— are most easily seen in the slightly less gelatinized stipe surface tissues. F–I. TIBIIFORM DIVERTICULA, CAULOCYSTIDIA, & SETAE are found on pseudorhizal surfaces. The function of the recently discovered orange-brown ‘setae’ is not known. Scales = 10  $\mu$ m.

**CORTICAL TISSUES** — *PILEIPELLIS* a bilaminar ixocutis: the top 25–50  $\mu$ m thick compact suprapellis of radially aligned, narrow (1–3  $\mu$ m), gelatinized colorless hyphae; the bottom ~100  $\mu$ m thick subpellis with inflated (4–8  $\mu$ m) gelatinized hyphae and brown pigments that turn orange in KOH; orange oleifers also present. — *STIPITIPPELLIS* a bilaminar ixocutis: the compact top layer containing parallel, narrow (2–4  $\mu$ m), subgelatinized colorless hyphae; the subpellis with thinner-walled, inflated (to 6  $\mu$ m) colorless hyphae.



*Phaeocollybia radicata* versus *P. attenuata* on Old Blue Mountain [OREGON. Benton County, PNW-MS — A&B: Exeter2007-83, C: Exeter2007-89, D: Exeter2007-90]. A fleshy, non-corneous stipe and more robust stature help separate an orange-yellow *P. radicata* (A–C) from the also small, slender, tawny *P. attenuata* (D).

**TRAMAL TISSUES** — Highly gelatinized, relatively thin-walled, (sub)parallel, inflated (5–12  $\mu\text{m}$  diam), colorless to dull ochraceous. Lamellar central hyphae parallel 3–6  $\mu\text{m}$  diam, thin-walled, colorless, and flanked by a narrow zone of 1–2  $\mu\text{m}$  diam hyphae giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Abundant in all tissues but most easily observed in the less pileipellis and stipitipellis.

**Ecology** — Terrestrial (mycorrhizal); solitary to loosely gregarious in autumn in coastal montane conifer (*Tsuga*, *Pseudotsuga*) forests. — *PACIFIC NORTHWEST ENDEMIC* rare, known only from seven Oregon and two California sites and has not been reported from California since 1965. Murrill, who described the type from dense second-growth conifers mixed with occasional oaks, is alone in noting an association with hardwoods. The recent Oregon sites occur in multi-age conifer stands or in 40–60 year old western hemlock and/or Douglas-fir stands with large diameter woody debris, thick duff, and/or scattered remnant old-growth trees.

**Similar species** — *Phaeocollybia radicata* shares small size and characteristic orange to tawny coloration with *P. attenuata*, *P. dissiliens*, *P. phaeogaleroides*, *P. piceae*, and *P. pleurocystidiata*.

The larger stature of *P. dissiliens* and *P. piceae* usually help distinguish them from the other species in the field. Microscopically *P. piceae* is easily separated by much larger (9.4  $\times$  6  $\mu\text{m}$ ) limoniform basidiospores, thin-walled clavate cheilocystidia, and lack of clamp connections. *P. dissiliens*, which — like *P. radicata* — is characterized by clamp connections and obscurely punctate-roughened ellipsoidal basidiospores produces thin-walled narrowly clavate cheilocystidia and larger (6.7  $\times$  4.3  $\mu\text{m}$ ) basidiospores.

A different fruiting season separates the vernal *P. pleurocystidiata* from the autumnal *P. radicata*; in the herbarium, abundant pleurocystidia, much larger (9.2  $\times$  6  $\mu\text{m}$ ) rough beaked limoniform spores, and absence of clamps easily distinguish *P. pleurocystidiata*.

Spore size alone easily differentiates the small-spored *P. radicata* from *P. attenuata* (9  $\times$  5.7  $\mu\text{m}$ ) and *P. phaeogaleroides* (10.3  $\times$  6  $\mu\text{m}$ ), fortunate because all three species fruit in the same season, have overlapping ranges, and occur in the same habitat.

**Additional comments** — Until 2000, only six *P. radicata* collections — the 1911 holotype from Oregon and five 1935–1965 Orick, California, collections — had been recorded (Norvell 1998a). Recent Northwest Forest Plan (USDA-USDI 1994) fungal surveys have added 30 collections and 4 new Oregon sites (from Benton, Coos, and Lane counties) to that total, but *P. radicata* is still regarded as rare to very uncommon.

Spore size, cheilocystidial form, and presence of clamps place the species in section *Radicatae*. Smith (1957b) noted that although the spores may appear smooth under lower magnifications, when viewed under high-powered oil immersion, they appear ‘minutely warty-rugulose;’ even so, it is necessary to move the objective up and down to see the ornamentation. Although not particularly viscid in the field, the highly gelatinized tissues prompted one exasperated researcher to write:

“In the field I thought perhaps I had found *P. radicata*.... What fits are the very small ellipsoid spores of 5.5-6(7)  $\times$  3.5-4  $\mu\text{m}$ . Seven microns is a huge one! However, the hyphae are so gelatinous I cannot get any hyphae separated to look at the tissues. The gill edge is so gelatinous that nothing can get through.



Ron Exeter

*Phaeocollybia radicata* in age and youth under hemlock above Klickitat Road  
Old Blue, Benton County, Oregon —PNW-MS Exeter2007-78

I don't see any basidia or cheilos. Actually, I did find two or three very nice capitulate cheilos but not much else through the gel barrier. Same with a fine slice of the cap, fat short cells (only twice as long as wide) but I don't see any clamps and when you try to spread it with an eraser it breaks into an amoeba. This fungus is an organized [slime]ball with small spores!"

Fortunately, the basidiospore size, among the smallest of all *Phaeocollybia* species, is usually sufficient to diagnose *P. radicata* when clamps or cheilocystidia cannot be seen in a fresh mount.

An unusually productive 2007 fall season enabled us to retrieve 13 *P. radicata* collections (including three with intact pseudorhizal cords and primordia) from one site approximately ten miles from the type locality of Glenbrook, Oregon. Our observation of so many fruitbodies in various developmental stages allowed us to determine previously unknown diagnostic characters, including a negative to variably positive syringaldazine reactivity, gills that fluoresce ochraceous orange under UV, existence of a regenerating pseudorhiza and branched rhizomorphic cord, and the presence of setae on the pseudorhiza. The last character, not previously seen in other *Phaeocollybia* species, was found in five different collections with intact pseudorhizas and may prove helpful when the rhizomorphic cord is present.

*References with descriptions and /or illustrations of Phaeocollybia radicata —*

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*Phaeocollybia redheadii*

Ron Exeter

*Phaeocollybia redheadii*, one of the world's largest phaeocollybias (inset reveals its fleshy, unbranched pseudorhiza).  
The Polk County 'Oz' transect in Oregon — PNW-MS Exeter2006-008

***Phaeocollybia redheadii*** Norvell 2000, Can. J. Botany 78: 1071

ETYMOLOGY — In honor of Scott Redhead, who first noted a *kauffmanii*-like species with large basidiospores from western Canada.

HOLOTYPE — Upper Carmanah Valley, Vancouver Island, British Columbia, Canada.

24 October 1991 (wtu holotype LLNorvell1911024-02, DAOM & PNW-MS isotypes)

MISAPPLIED — *P. kauffmanii* sensu Norvell (1992), Norvell & Redhead (1993), Redhead & Norvell (1993).

*Field summary* — Large fleshy fruitbodies with heavily viscid orange- to red-brown campanulate caps with strongly inrolled edges, pinkish or yellowish buff young gills, robust firmly stuffed pinkish buff stipes, deeply rooting fleshy unbranched pseudorhizas, and a 'cucumber' farinaceous odor. Solitary to densely clustered in autumn in British Columbia, Washington, Oregon and northern California coniferous temperate rainforests.

**PILEUS** — Up to 140 mm diam, conic-convex expanding to broadly campanulate with broad low umbo, incurved margin, and inrolled edge; surface bald, smooth, viscid to heavily glutinous, non-striate; color either uniformly warm orange-/red-brown (*verona /sayal brown, warm sepia*) or zonate with deep orange- to dark brown disc (*verona /bone /snuff /clove brown*), lighter brown margin (*sayal /cinnamon /mikado brown, russet*), and darker edge (*warm sepia, verona / snuff brown*), older specimens blackish or purplish brown overall, moldy or frost-exposed specimens frequently developing dull purplish or greenish brown tones, damaged areas generally blackish. —**FLESH** firm, confluent through stipe and pileus ( $\leq 15$  mm thick in disc), color pale yellow cream or buff (*cartridge buff, (pale) pinkish buff*) when young, staining orange or deep orange-brown when cut, when watersoaked or in age darkening and often with a brown band next to the gills. —**ODOR** strongly farinaceous, often slightly floral when cut or crushed. —**TASTE** strongly farinaceous (cucumber-like), glutinous cap cuticle slightly to extremely bitter. —**DRIED PILEUS** metallic dark copper to bronze with blackish umbo (from younger, merely viscid material) or shiny ('shellacked') to satiny mahogany brown (from older and/or heavily glutinous material).



Two views of *P. redheadii* collected from the type locality one year after the first collections confirmed the genus for western Canada. Upper Carmanah Valley, Vancouver Island, British Columbia, Canada — DAOM & WTU LLNorvell1921007-4

**LAMELLAE** — Pinkish white or yellow cream when young, dark brownish yellow when mature, becoming deep yellow brown in age.

**STIPE** — Central, rigid, ~40–100 mm above the ground, combined length including pseudorhiza sometimes exceeding 340 mm, apex 10–23 mm diam, occasionally equal or tapering downward, usually ventricose and swelling ( $\leq 30$  mm) slightly above ground level before tapering downwards to the pseudorhiza; surface moist to dry, matte and minutely lined lengthwise, smooth or appressed fibrillose (hand lens); surface color of young apex pale to medium pinkish buff ([light] pinkish cinnamon), deepening in age (cinnamon, cinnamon drab, avellaneous) above and darkening below to deep orange-brown (ferruginous, kaiser /mikado /verona brown), staining deep red-brown; 2–4 mm thick cartilaginous rind surrounding firm pith that often proliferates to split the cortex lengthwise; context concolorous with cap context (unless waterlogged) throughout development.

**PSEUDORHIZA** — Vertical-monopodial,  $\leq 5/6$  of overall length, continuous with stipe and gradually tapering to a blunt fleshy origin arising from an amorphous fungal mass surrounding ectomycorrhizal rootlets; color either uniformly deep rusty to red-brown (liver brown, kaiser brown) or with a salmon colored origin.

**VEIL REMNANTS** — Inconspicuous; when present as scattered fibrils or sparse fibrillose patches on stipe apex.

**SYRINGALDAZINE REACTIVITY** — All tissues strongly positive: cap, gills, stipe, and pseudorhiza rapidly turning deep magenta.

**FLUORESCENCE** — Primordia dull orange; young gills violet-white; mature fruitbodies with brilliant (pale) yellow gills and orange magenta to deep red stipe pith.

**SPORE PRINT** — Cinnamon brown.



**Diagnostic characters** — Macroscopically, *P. redheadii* is diagnosed by its (1) large size, (2) viscid orange- to dark red-brown fleshy cap with inrolled edge, (3) mature stipe >11 mm at apex (often swelling below) and stuffed with firm solid pith, (4) bronze metallic or brown shellacked dried cap, and (5) all tissues turning magenta rapidly in syringaldazine.



*Phaeocollybia redheadii*

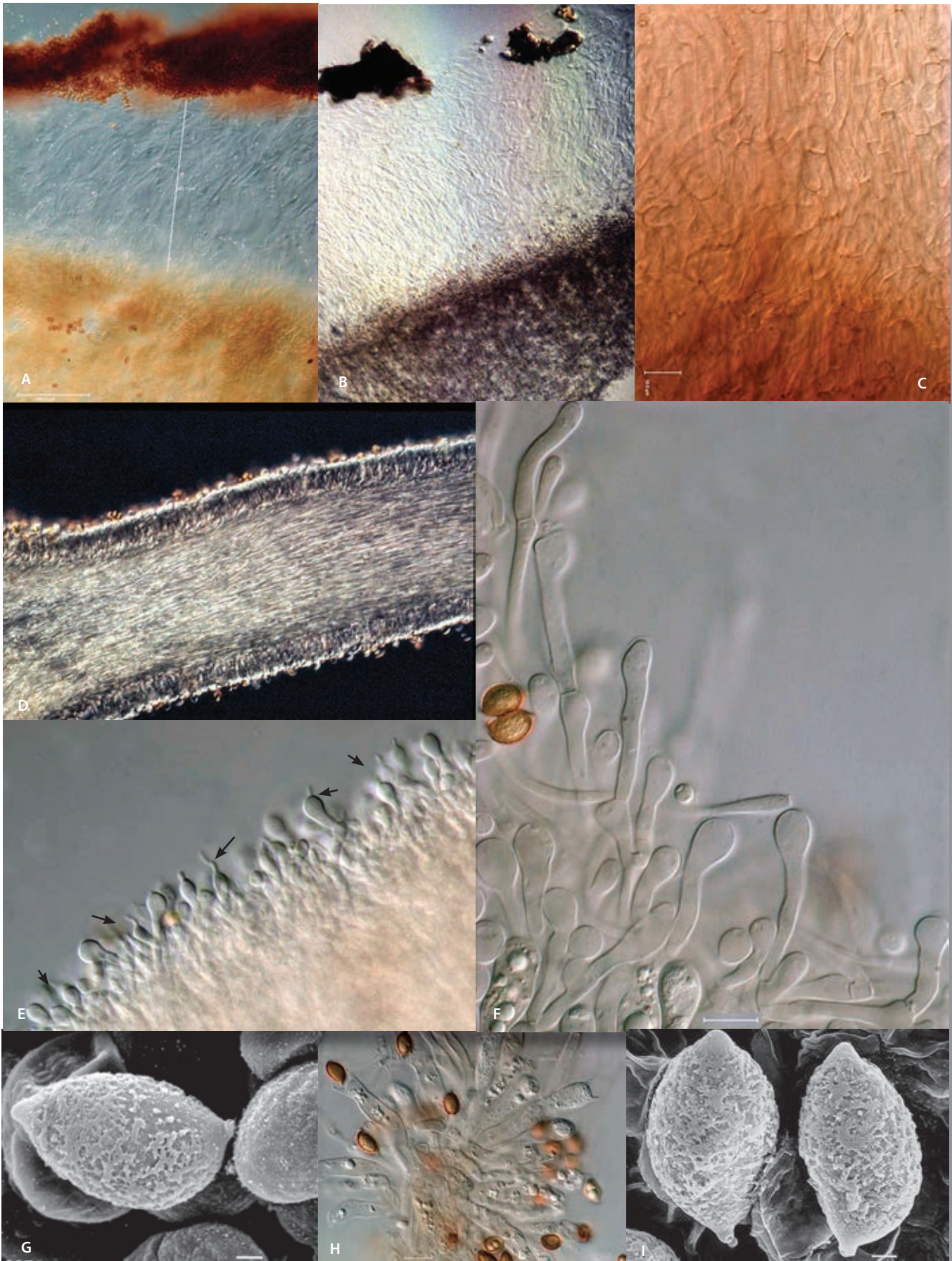
A-C. HABIT — young (c, WTU HOLOTYPE LLNorvell1911024-2); mature (A&B, WTU LLN1921009-20).

D. BASIDIOSPORES — WTU LLN1931024-16. BASIDIUM — WTU LLN1951018-18.

CHEILOCYSTIDIA — WTU LLN1921009-20.

Scales = 5 cm & 10  $\mu$ m

Important microscopical features detailed on the next page include (1) large ( $\sim 10.5 \times 6 \mu\text{m}$ ), moderately roughened, elongate, almond-shaped basidiospores with tilted beaks, (2) thin-walled, long, pedicellate, broadly clavate to subcapitate cheilocystidia with subglobose heads, (3) occasional true and false clamp connections in stipe and pseudorhiza, and (4) a two-layered pileipellis with an extensive colorless gelatinous suprapellis and orange-brown subpellis containing both encrusting and interparietal pigments.



Lorelei Norvell (A,D,E-I), Scott Redhead (B,C)

**BASIDIOSPORES** —  $|x| = 10.5 \times 6 [(8)9 - 10.7(13) \times (4.9)5.3 - (6.5)7.3]$   $\mu\text{m}$ , terete to almost angular in end view, elongated inequilaterally amygdaliform in profile, elongate-elliptical in face view, verruculose to verrucose except on the 1- $\mu\text{m}$  long tilted beak and eccentric prominent apiculus; color in KOH orange- to medium amber, in  $\text{H}_2\text{O}$  paler, in Melzer's dextrinoid. — **BASIDIA** (2-)4-spored, clavate with pedicel tapering to a 1.5–3  $\mu\text{m}$  septum, colorless.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, arising from the lamellar trama to form a dense, highly gelatinous layer; terminal lengths variable ( $\leq 35 \mu\text{m}$ ), apically often developing long filamentous outgrowths in very old or stored fresh specimens; broadly clavate elements intermixed with subcapitate elements with 6–15  $\mu\text{m}$  diam globose heads atop 2–4  $\mu\text{m}$  wide pedicels, at times catenulate with penultimate elements swelling before the top septa; all elements thin-walled, highly gelatinized, colorless. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelia and surfaces of primordia and pseudorhizas, also frequent on veil remnants on stipe apex,  $\leq 25 \times 1.5 \mu\text{m}$ , with no septum between base and hypha, with/without (sub)globose head and/or apical droplet; highly refractive, colorless to slightly straw colored.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis with a very thick (200–600  $\mu\text{m}$ ) suprapellis containing long, branching, cylindrical, narrow (2–6  $\mu\text{m}$ ), thin-walled, highly gelatinized, colorless hyphae embedded within a clear gelatinous matrix and overlying a thinner (75–200  $\mu\text{m}$ ), yellow-orange to dull orange-brown subpellis of unbranched, 5–8  $\mu\text{m}$  diam (inflated to 14  $\mu\text{m}$ ), thick-walled hyphae with refractive septa and encrusting, intraparietal and diffuse pigments; oleiferous hyphae present in both layers. — **STIPITIPELLIS** a compact layer of parallel hyphae gradually intergrading with the stipe trama, hyphae 4–9  $\mu\text{m}$  diam, walls thick and colorless to orange-brown, infrequent to rare clamp connections also present. — **PSEUDORHIZAL PELLIS**  $\leq 200 \mu\text{m}$  thick, hyphae 20  $\mu\text{m}$  diam, coarsely encrusted with dark brown pigments, often with coagulated brownish contents, outermost hyphae bearing tibiiform diverticula; clamp and pseudoclampe connections rare.

**TRAMAL TISSUES** — Gelatinized and colorless to pale amber, dark amber oleifers occasional throughout; in the pseudorhiza strongly sarcodimitic, with parallel, rigid, long ( $\leq 200 \mu\text{m}$ ), wide ( $\leq 40 \mu\text{m}$ ), thick-walled ( $\leq 4 \mu\text{m}$ ) vessel hyphae intermixed with less noticeable flexuous, branched, thin-walled (0.5  $\mu\text{m}$ ), narrow (2–3  $\mu\text{m}$ ) hyphae; in the stipe both hyphal types with thick (1–2  $\mu\text{m}$ ) walls and vessel hyphae narrowing to 20  $\mu\text{m}$ ; in the pileus not noticeably sarcodimitic, hyphae loosely radially arranged, inflated to 15–20  $\mu\text{m}$  diam, walls variably thickened up to 1  $\mu\text{m}$ . Lamellar central region 200–400  $\mu\text{m}$  across, parallel, with parallel, relatively thick-walled ( $>1.0 \mu\text{m}$ ), 3–10  $\mu\text{m}$  diam hyphae occasionally intermixed with highly branched, narrow, thin-walled flexuous hyphae; the central region flanked by a narrow zone of 2–3  $\mu\text{m}$  diam colorless elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Sporadic and rare in stipitipellis and pseudorhizal pellis, absent in all other tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to closely gregarious during autumn in loamy humic soils in old growth and mature moist coniferous (*Tsuga*, *Pseudotsuga*, *Abies*, *Picea*) forests. — **PACIFIC NORTHWEST ENDEMIC** known from ~40 localities in British Columbia, Washington, Oregon, and northern California.

**Similar species** — The obviously clamped *P. ammiratii* and the essentially unclamped *P. kauffmanii* 'sensu stricto' and *P. redheadii* — all sharing similar size, habit, and tawny coloration — are easily confused. Its usually more slender stature and burgundy-flushed stipes may help to identify *P. ammiratii* in the field, although

LEFT: *P. redheadii* diagnostic microcharacters [CANADA—BC, Vancouver Isl: DAOM ISOTYPE LLN1911024-2(B,D,I), WTU HOLOTYPE LLN1911024-1(G). USA—CA, Humboldt Co: PNW-MS LLN2041118-1(A). OR, Benton Co, PNW-MS: Exeter2006-13(C), LLN2071029-29(H); Lincoln Co, OSC LNus8-125(E), PNW-MS LLN207101819-2(F)]. A–C. **PILEIPELLIS** — Radial sections under Nomarski (A) and dark field (B) display the extensive suprapellis composed of narrow colorless branching hyphae submerged in a thick (here ~250  $\mu\text{m}$ ) gelatinous matrix. The encrusting and diffuse pigments characteristically found in the subpellis (C) are brightest in mature specimens. D. **GILL TRAMA** — A gill section in dark field displays the regular gill trama typical for most phaeocollybias. The gill edge where the cheilocystidia are found is not shown. E–F. **CHEILOCYSTIDIA** — Abundant thin-walled elements with globose heads on long stems crowd edges of immature gills. Finger-like extensions on cheilocystidial apices (E–arrows) can develop even in young material when kept too long before drying. Typical for the species are the multiply septate ('catenulate') cheilocystidial stalks (F). G–I. **BASIDIA & BASIDIOSPORES** — SEMs of gill sections from the paratype (G) and holotype (I) show the 'long-bellied' limoniform shape and tilted beak characteristic of *P. redheadii*. Most basidia are 4-spored, but 2-spored basidia (H) are not uncommon. Scales = 100  $\mu\text{m}$  (A), 10  $\mu\text{m}$  (C,E,F,H), and 1  $\mu\text{m}$  (G,I).



Scott Redhead (A–D); Lorelei Norvell (E–K)

DEVELOPMENT. A productive site in Oregon's Larch Mountain summit old growth *Abies-Tsuga* forest overlooking the Columbia provided developmental and biological breakthroughs for both *P. redheadii* and *Phaeocollybia*. [A–WTU LLN1921104-13; B, D–K WTU LLN1931105-1; C–WTU LLN1931113-1]. A— The extreme age of the slimy fruitbodies collected during the first 1992 visit prevented a firm species determination. B— One year later, young specimens from the same site were verified as *P. redheadii*. C— Eight days later, the excellent condition and unchanged size of two uncollected specimens (B, black arrow) suggested that *P. kauffmanii* complex species probably remain viable for several weeks. D. Excavation of fruitbodies (B, white arrow) on the first 1993 visit exposed a caespitose cluster of mature and primordial mushrooms with roots and ectomycorrhizal tips. E–K. ANATOMICAL EVIDENCE FOR ECTOMYCORRHIZAL ASSOCIATIONS. E— Attachment of rootlet with mycorrhizal tips to soil-covered mass with emergent pseudorhiza after dissection. F— Longitudinal section shows a pseudorhiza arising from an undifferentiated fungal mass with the dark pseudorhizal pellis extending over upper mass; bottom two rootlets encased in mycorrhizal sheath. G— Fungal mass giving rise to primordium. H–J: Sections of rootlet and ectomycorrhizal tips found embedded in fungal mass. Close inspection of (J) shows barely discernible tibiiform diverticula (arrow) attached to mycelial hyphae emerging from an ectomycorrhizal mantle that provide support for ectomycorrhizal status of *P. redheadii*. K— Longitudinal section showing Hartig net within ectomycorrhizal tip cortex.



*Phaeocollybia redheadii*. COLOR. The darker or more intense colors restricted to the central disc in young caps (A) gradually extend to the cap edge in more mature fruitbodies (B–C) before deepening to dark red–brown in fully mature, expanded specimens (D–E); stipe colors also deepen from the pseudorhiza upward as the fruitbody ages. CONTEXT. Cap flesh usually thins and darkens as the cap expands, but although the usually firm stipe pith may also darken or become spongy in age, the stipe never hollows, remaining stuffed (E) even in very old material.

[CANADA, BC, Vancouver Isl, Carmanah Valley: A—WTU HOLOTYPE LLNorvell1911024-2; C—WTU LLNorvell1921009-20. UNITED STATES, OR: B—Laurel Mtn (Polk Co), PNW-MS Norvell2031024-3 by RLE; D—Saddlebag Mtn (Lincoln Co) PNW-MS Norvell2071018-02]

more reliable key characters — the looping to medallion clamp connections on pileus suprapellis hyphae and cheilocystidia— require microscopic confirmation.

The difference between the distinctly orange young pileus of *P. kauffmanii* and the yellow-orange to darker apricot-brown young *P. redheadii* is even more subtle, and the fact that *P. redheadii* caps usually pass through an orange-brown ‘pumpkin pie’ color phase (Fig. p. 167 B–C) before turning deep brown or red-brown in age greatly complicates distinguishing these two ‘giants’ in the field. Microscopically, *P. kauffmanii* is easily separated by its smaller ( $\sim 8.5 \times 5 \mu\text{m}$ ) basidiospores and cylindrical to clavate cheilocystidia. The distinctive pedicellate subcapitate catenulate cheilocystidia with subglobose heads are particularly helpful in assigning immature fruitbodies to *P. redheadii*, as these are at their most noticeable before basidiospore formation.

Although *P. redheadii* basidiospores are the largest in the *kauffmanii* complex, spores from three other members — *P. benzokauffmanii*, *P. luteosquamulosa*, *P. gregaria* (all averaging  $\sim 10 \times 6 \mu\text{m}$ ) — come close. This spore-size overlap can complicate separating *P. redheadii* from *P. benzokauffmanii*, particularly when *P. redheadii* pilei acquire a purplish-brown cast due to frost or advanced age. As *P. benzokauffmanii* also produces occasional inflated subcapitate cheilocystidia, that species is most easily diagnosed — again microscopically — by its lack of encrusting pileus subpellis pigments and compact, relatively thin suprapellis.

See TABLE 11 (p. 96) under *P. kauffmanii* for additional comparisons.

**Additional comments** — The authors who referred the first Canadian collections of *P. redheadii* to *P. kauffmanii* (Norvell 1992, Norvell & Redhead 1992, Redhead & Norvell 1993) were aware that their Vancouver Island collections might represent a cryptic species. Nonetheless, in reporting the first two phaeocollybias collected from western Canada, they did not anticipate that spore size comparisons of *P. kauffmanii* herbarium



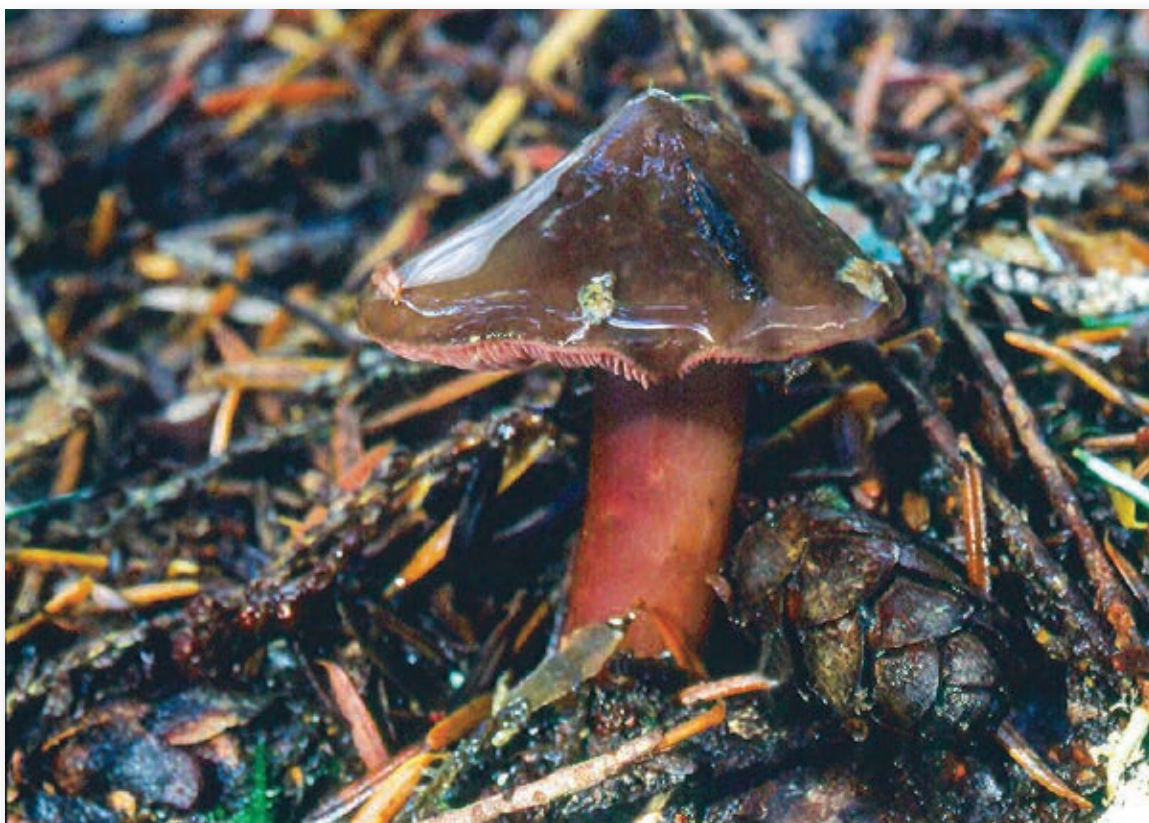
Ron Exeter

*Phaeocollybia redheadii*, uncharacteristically pale — but still massive — in dry weather.  
 Cascade Head Experimental Forest, Tillamook-Lincoln county line, Oregon — PNW-MS Exeter2008-038

collections would uncover five new cryptic *P. kauffmanii* look-alikes. Additional collections sparked by the Upper Carmanah Valley discoveries eventually led to a thorough taxonomic reevaluation of *Phaeocollybia* accompanied by preliminary DNA analyses and observation of development and biological strategies of the genus. Norvell and Redhead's excavation of one *P. redheadii* collection from Oregon's Larch Mountain (see p. 166; also Norvell 1998ab, Norvell 2000) provided the first solid evidence of a mycorrhizal status for a genus previously thought either saprophytic (Singer 1970) or parasitic (Redhead & Malloch 1986).

*References with descriptions and /or illustrations of Phaeocollybia redheadii —*

- Norvell LL. 1992. A Canadian Odyssey: The search for the elusive *Phaeocollybia*. *Mushroom, The Journal* 10(2): 9-12.
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales, Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [key; description (as nom. prov.) pp. 197-202, 374; microdrawing & color photos pp. 43-44, 261-262]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615-630. [(as nom. prov.) evidence for mycorrhizal association & b&w photos pp. 625]
- Norvell LL. 2000. *Phaeocollybia* in western North America 1: The *Phaeocollybia kauffmanii* complex. *Can. Journ. of Botany* 78: 1055-1076. [key & comparison tables; type description, drawings & b&w photos, pp. 1057, 1071-1074]
- Norvell LL, Exeter RL. 2007. *Phaeocollybia* in western North America 5: *P. ochraceocana* sp. nov. and the *P. kauffmanii* complex. *Mycotaxon* 102: 315-332.
- Redhead SA, Norvell LL. 1993. *Phaeocollybia* in western Canada. *Mycotaxon* 46: 343-359. [(as *P. kauffmanii*) description, b&w photos pp. 349-355]

*Phaeocollybia rifflipes*

Scott Redhead

The *P. rifflipes* holotype in situ at Barlow Pass, Mt. Baker-Snoqualmie National Forest  
Snohomish County, Washington, USA —WTU HOLOTYPE LLNorvell1931020-1

*Phaeocollybia rifflipes* Norvell, Mycotaxon 81: 102, 2002

ETYMOLOGY — From RFLP (the abbreviation for Random Fragment Length Polymorphism), the molecular analytical technique that first implied the existence of a previously undiagnosed phaeocollybia.

HOLOTYPE — Barlow Pass, Mt. Baker-Snoqualmie National Forest, Snohomish County, WA, USA;  
20 October 1993, WTU HOLOTYPE LLN1931020-01 (DAOM ISOTYPE) by LLNorvell, SAREdhead & GLBarron

*Field summary* — Small to medium-sized fruitbodies with heavily glutinous tawny to dark brown convex-campanulate caps, pinkish young gills, fibrillose-stuffed drab stipes, and rooting fleshy unbranched pseudorhizas. Solitary to scattered during autumn under western hemlock and true fir in PNW montane coniferous forests.

PILEUS — ~ 20–60 mm diam, initially conic-convex with acute papillate umbo, soon broadly campanulate with low broad umbo and downturned margin with inrolled to incurved edge; surface heavily glutinous, smooth, bald, faintly striate, hygrophanous; color when young uniformly tawny or obscurely zonate with darker disc (*verona brown, russet*), and red-yellow-brown edge (*army brown, cinnamon brown*), in age usually uniformly dark brown (*olive brown*) with *dark olive* edge. —FLESH thin over the gills, 1–4 mm over the disc, color pallid buff when young, brownish drab in age. —ODOR not distinctive to obscurely complex with floral and pungent chemical components. —TASTE mild to faintly bitter. —DRIED PILEUS dark brassy metallic to dull blackish brown, edges frequently noticeably striate.

LAMELLAE — Pinkish, pale rosy lilac, or pale bluish gray (*pale vinaceous drab, pale brownish drab*) with even edges when young, darkening to drab brown (*wood brown, drab, avellaneous*) with uneven to eroded edges in age.

STIPE — +/- central, fleshy, ~30–50 mm above the ground, combined length with pseudorhiza close to 165 mm; apex 4–7(9) mm diam, aerial portion usually tapering to pseudorhiza but sometimes thickening slightly at ground level; surface viscid, smooth and shiny beneath fibrillose patches; color of young apex pale drab to violet (*deep quaker, cinnamon drab, benzo brown*), increasingly darkening in hue towards ground level (*duky*



Lorelei Norvell

Relatively small and fragile, *P. riffliipes* has a heavily glutinous tawny to brown cap and pinkish to pale rosy lilac gills. Young (LEFT: PNW-MS a2061114o1-D) and older (RIGHT: PNW-MS a2021204o1-7) collections from the BLM ‘Oz’ transect in Polk County, Oregon, are compared above. Scale in millimeters.

*drab, fawn color, army brown*); when young stuffed with firmly packed fibrils that in age may loosen and split to form a central hollow (‘canaliculate’), the pallid pith darkening when waterlogged and often insect infested; cartilaginous rind ~1.5 mm thick.

**PSEUDORHIZA** — Vertical-monopodial, ~2/3 of overall length, continuous with stipe and gradually tapering to a narrow curled or ‘nippled’ origin; dark red-brown (*liver brown, verona brown*) above a brownish drab origin.

**VEIL REMNANTS** — Evident as scattered to abundant short fibrillose patches on the stipe apex and occasional scattered fibrils overlying young gills; color brownish drab.

**SYRINGALDAZINE REACTIVITY** — Cap, stipe, and pseudorhiza negative; gills variable, ranging from no reaction (older material) to faint to strongly magenta.

**FLUORESCENCE** — Under UV, young gills fluoresce intensely yellow white and stipe pith a dull orange.

**SPORE PRINT** — Cinnamon brown.

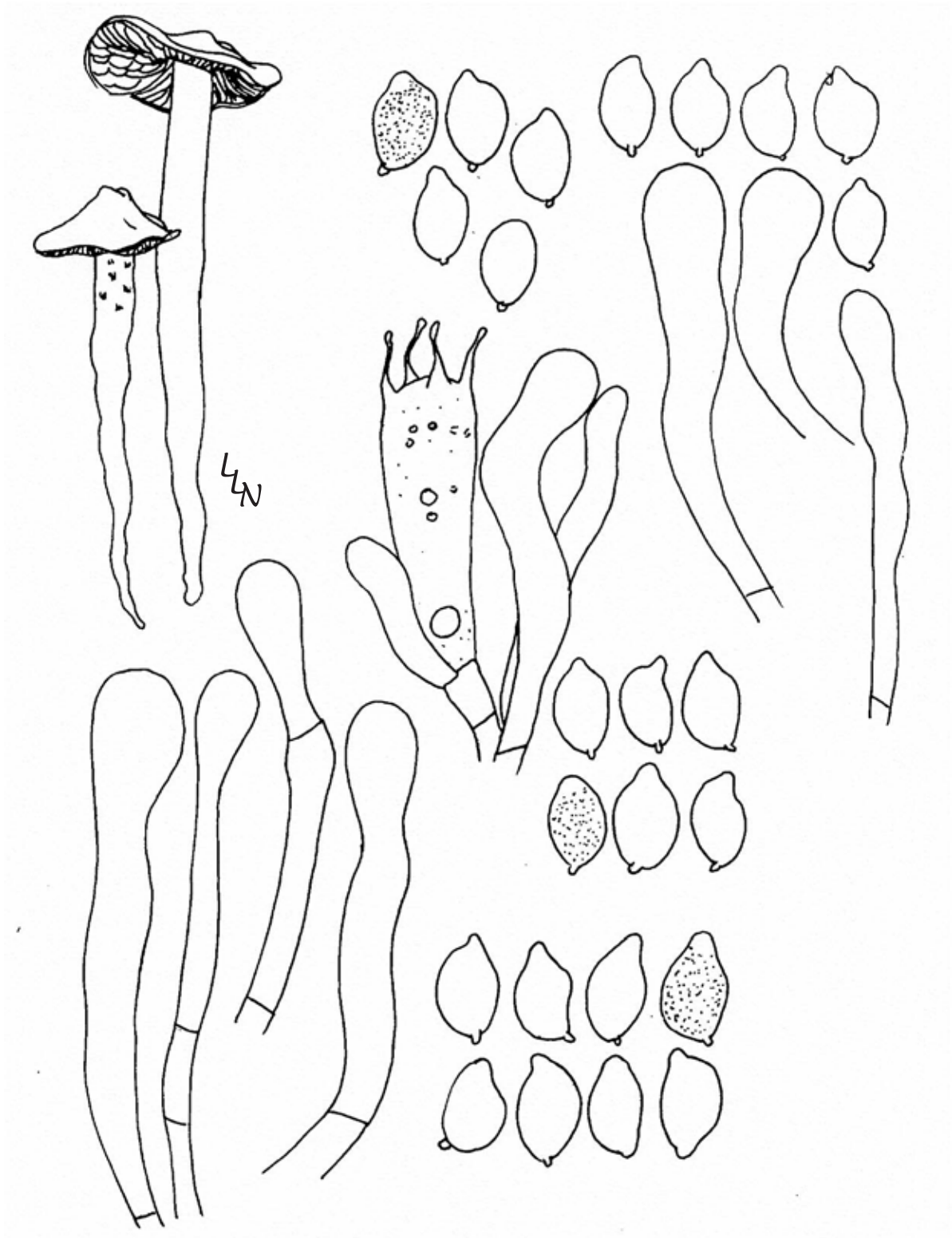
**Diagnostic characters** — Macroscopically, *P. riffliipes* can be recognized by its (1) fragile stature and small to medium size, (2) heavily glutinous tawny to dark brown conic-campanulate cap and pinkish to rosy lilac gills, (3) stuffed to partially hollow shiny drab to violet stipe, and (4) syringaldazine negative cap and stipe.

Important microscopical features include (1) ~6.9 × 4.3 μm finely roughened brown limoniform basidiospores, (2) thin-walled broadly clavate (at times sphaeropedunculate) cheilocystidia, usually within a gelatinous sterile barrier, (3) bilaminar pileipellis with dull /orange-brown (in KOH) diffuse pigments, and (4) absence of clamp connections.

**BASIDIOSPORES** —  $|x| = 6.9 \times 4.3$  [(6)6.5–7.5 × (3.8)4–4.8(5)] μm, limoniform with low to moderate beak and small apiculus in profile view, fusoid to vaguely naviculate in face view, verruculose to irregularly marbled



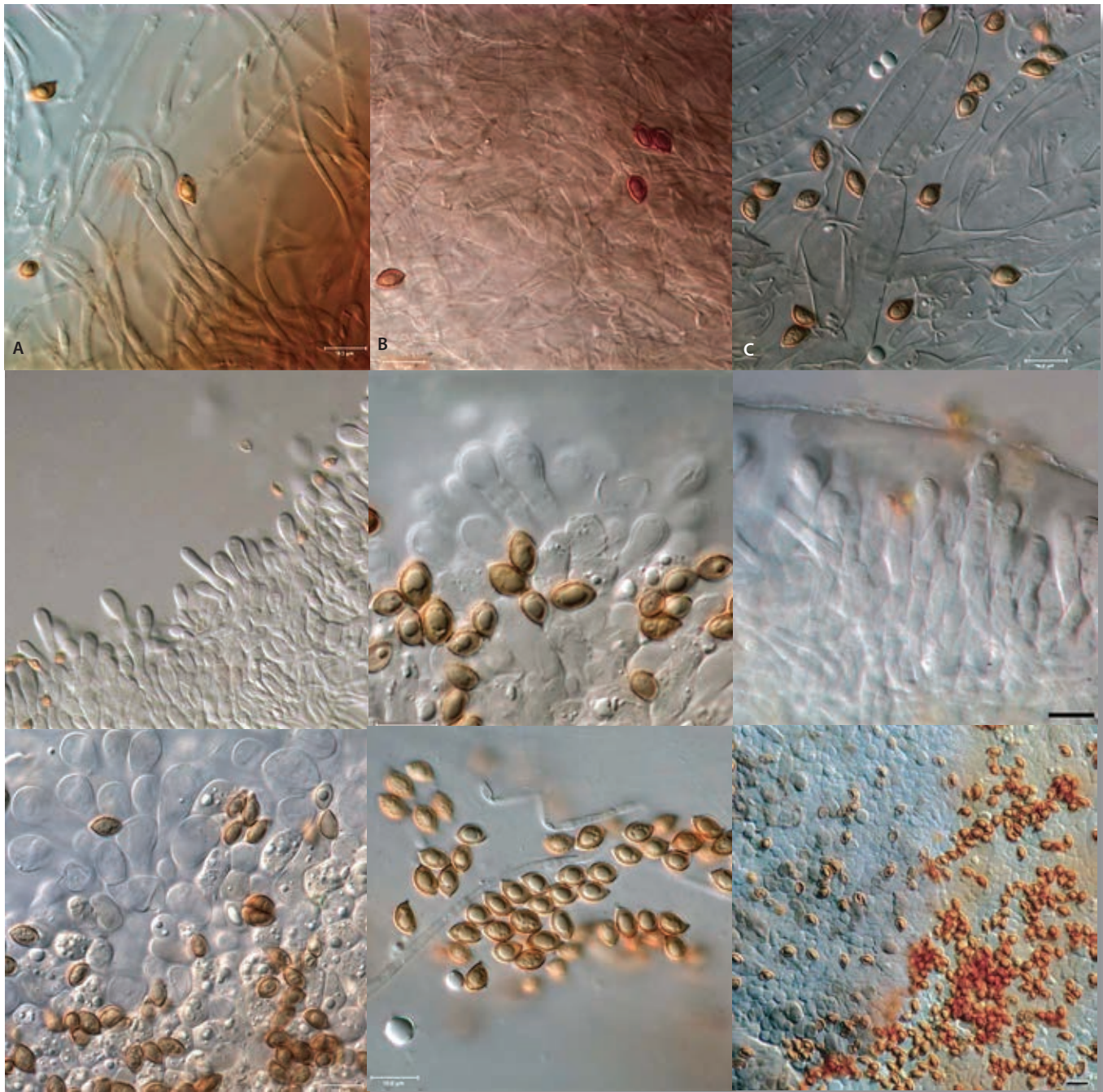
except on smooth apical beak; color in KOH pale amber, in H<sub>2</sub>O pale straw-colored. —BASIDIA (2-)4-spored, clavate, 26–36 × 6–7.5 μm, hyaline to dull brown.



*Phaeocollybia rifflipes*

A. HABIT. Left: WTU HOLOTYPE Norvell1931020-1 (Snohomish Co, WA). Right: WTU Norvell1921023-8 (Clallam Co, WA).

B–D. BASIDIOSPORES (B–D), CHEILOCYSTIDIA (B,D), BASIDIUM (C) — All in WTU  
 B: HOLOTYPE. C: Norvell1921023-8. D: Norvell1921104-5 (Multnomah Co, OR).



Lorelei Norvell

*Phaeocollybia rifflipes* [CANADA, BC: A—PNW-MS Kroeger3159b (Campbell River). UNITED STATES, OR: PNW-MS B—Exeter 2006-43, D—a2021113o1-2, F—a2061114o1-E (Oz transect, Polk Co); C,E,H—PNW-MS Exeter 2007-132 (Lobster Creek, Lane Co); G—OSC11625 LNus17b98 (Medford BLM lands, Coos Co). WA: I-LEFT—WTU HOLOTYPE Norvell1931020-1 (Barlow Pass, Snohomish Co)].

A–C. PILEUS TISSUES — Long, 2–3  $\mu\text{m}$  diam suprapellis hyphae and spores in a colorless gel matrix (A) float above wider hyphae of the diffusely pigmented subpellis (B). Tramal tissues contain only thin-walled hyphae (C). D–G. CHEILOCYSTIDIA — Thin-walled & variably clavate in young fruitbodies (D, 40 $\times$  objective), the sterile elements broaden (E), often secreting such abundant gel that they are obscured by a thick gelatinous layer (F) along the gill edge; often becoming sphaeropenduculate in age (G). H–I — BASIDIOSPORES. Spore shape and ornamentation resembles that produced by other '*P. festiva*' complex species, but small spore size sets *P. rifflipes* apart. Two gill tissues within a single mount (I) compare the small *P. rifflipes* holotype basidiospores (I-left) to those obtained from a *P. fallax* small-spored variant from Oregon's Wildcat Mountain [I-RIGHT: WTU Norvell1951018-23]. Scale bars = 10  $\mu\text{m}$ .

CYSTIDIAL ELEMENTS — CHEILOCYSTIDIA abundant and crowded, thin-walled, arising from the lamellar trama to form a sterile layer; lengths variable and indeterminate [ $\sim$ 15–45  $\mu\text{m}$ ], broadly clavate with most apices  $\sim$ 5–7  $\mu\text{m}$  diam above  $\sim$ 3–4  $\mu\text{m}$  diam bases, in age expanding to  $\sim$ 10  $\mu\text{m}$  and becoming almost spherical in shape, narrower 2–3  $\mu\text{m}$  diam elements occasionally intermixed, filiform apical outgrowths sometimes found in aged or poorly preserved material; colorless or (in age) filled with oily brownish contents. — PLEUROCYSTIDIA



Heavily glutinous rosy-tawny caps, pinkish gills, and drab stipes with fibrillose pith help diagnose these specimens as *P. riffliipes*.  
 Pedee Old Growth Chronosequence transect, Polk County, Oregon — PNW-MS a2061114o1-H (left, *in situ*) & -E (right).

absent, but 2- $\mu\text{m}$  diam filiform hyphidia ('paracystidia') frequent within basidial clusters. — *TIBIIFORM DIVERTICULA* abundant on remnants of the pellicular sheath on pseudorhiza and stipe, 5–12 (20)  $\times$  2 (base)  $\times$  0.5 (neck)  $\mu\text{m}$  with no septum between base and hyphae, with/without 1–2- $\mu\text{m}$  diam (sub)globose head and/or apical droplet; highly refractive, colorless.

**CORTICAL TISSUES** — *PILEIPELLIS* a bilaminar ixocutis: the top 150–350  $\mu\text{m}$  thick suprapellis of radially aligned, long, branched, narrow (1–3  $\mu\text{m}$ ), straight or curling highly gelatinized colorless hyphae in a thick gelatinous matrix; the subpellis hyphae thin-walled, inflated to 5–10  $\mu\text{m}$  diam from 3–5  $\mu\text{m}$  diam septa, amber-orange intraparietal pigments congregating at the septa, diffuse pigments dull green-brown in  $\text{H}_2\text{O}$  and orange-brown to deep orange in KOH. — *STIPITPELLIS* hyphae parallel, long, ~10  $\mu\text{m}$  diam, lightly gelatinized with brownish walls. Pellicular veil remnant hyphae diverticulate and coated with greenish encrusting pigments in KOH.

**TRAMAL TISSUES** — Pileus and stipe hyphae thin-walled, ~8–12  $\mu\text{m}$  wide; colorless to watery brownish drab in KOH. Lamellar central hyphae subparallel, 3–5  $\mu\text{m}$  diam, thin-walled, colorless, and flanked by narrow (2–3  $\mu\text{m}$  diam) colorless hyphae giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to scattered under *Abies* and *Tsuga* during autumn in montane old-growth coniferous forests. — *PACIFIC NORTHWEST ENDEMIC* known from ~10 sites west of the Cascade crest in British Columbia, Washington, Oregon, and California.

**Similar species** — *Phaeocollybia riffliipes* appears closely related to *P. fallax* and *P. lilacifolia* and, with them, is referred to the *P. festiva* complex based on possession of drab colors in stipe and gills and obscurely marbled limoniform-naviculate basidiospores.

Green caps, more intensely colored bluish violet young gills, and orange stipe bases easily diagnose young *P. fallax* in the field. Older fruitbodies that have lost this distinctive coloration can be separated microscopically from *P. riffliipes* by the larger (~9  $\times$  5  $\mu\text{m}$ ) spores and absence of filiform hyphidia in basidial clusters.

In addition to sharing drab to violet tinged stipes and lilac colored gills, *P. lilacifolia* and *P. riffliipes* both produce glutinous tawny to dark brown convex-campanulate caps. *P. lilacifolia*, however, is usually much larger and more robust and has more intensely colored bluish-lilac gills lacking the pink to rosy tones that characterize *P. riffliipes*. Microscopically, *P. lilacifolia* is differentiated by its larger (~8  $\times$  5  $\mu\text{m}$ ) and slightly more heavily ornamented spores and less heavily gel-secreting narrowly clavate cheilocystidia.

Two other species — *P. benzokauffmanii* and *P. oregonensis* — also produce drab fruitbodies. Both produce more robust fruitbodies with firm (never fibrillose) stipe pith and viscid (rarely heavily glutinous) convex-campanulate caps with strongly inrolled edges, white to smoky white (not pinkish or rosy white) gills, and



Ron Exeter

*Phaeocollybia rifflipes* at Lobster Creek  
Lane County, Oregon — PNW-MS Exeter2008-044

strong and rapid magenta syringaldazine reactions for all tissues. *P. benzokauffmanii* is further differentiated by its much larger ( $\sim 9 \times 5.5 \mu\text{m}$ ) basidiospores. *Phaeocollybia oregonensis*, also occurring under *Abies* and *Tsuga* in montane forests, has slightly smaller ( $\sim 6.8 \times 4 \mu\text{m}$ ) spores that are obscurely punctate-roughened, bullet-nosed, ellipsoid, and lack the obtusely projecting snout that characterizes *P. rifflipes*.

See comments after the above species and TABLE 10 (p. 83) for additional comparisons.

**Additional comments** — *Phaeocollybia rifflipes* was first recognized as a distinct species during RFLP analyses of 160 *Phaeocollybia* collections. Four isolates – extracted from one 1993 Washington collection initially referred to *P. fallax* due to its small size and violet tinged gills and three 1992 Oregon ‘unknowns’ with tawny caps and drab gills — produced the same distinct DNA profile originally interpreted as a contaminant. Subsequent research revealed that all four collections shared the same diagnostic characters not found in any already described species.

We were fortunate to be able to observe one population for seven years during our chronosequence study in a 200-year old *Pseudotsuga menziesii* / *Tsuga heterophylla* stand. The collections there, as well as those gathered at six other sites in Oregon and Washington, were all found in montane regions (650–1350 m elev.) under *Tsuga* or *Abies*. The additional observations presented here modify the original *P. rifflipes* description (Norvell 2002). Special emphasis is now placed on the pinkish to rosy lilac gill coloration, previously incorrectly described as more bluish violet in hue .

**References with descriptions and /or illustrations of *Phaeocollybia rifflipes* —**

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (Agaricales, Cortinariaceae). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [*P. rifflipes*, pp. 202–206, color photos p. 264]
- Norvell LL. 2002. *Phaeocollybia* in western North America 3: New species *P. phaeogaleroides* and *P. rifflipes*, with notes on the *P. festiva* complex. Mycotaxon 81: 95-112.

*Phaeocollybia rufotubulina*

*P. rufotubulina* at 'Mushroom Corners'  
Jackson State Forest, Mendocino County, California  
WTU HOLOTYPE LLNorvell 1921116-1

Scott Redhead, Agriculture & Agri-food Canada

***Phaeocollybia rufotubulina*** Norvell 2004, Mycotaxon 90: 243.

ETYMOLOGY — From the Latin *rufus* = “reddish” + *tubulus* = “little pipe.”

HOLOTYPE — Jackson State Forest (Mendocino County), CA, USA.

16 November 1992 (WTU: LLNorvell1921116-01).

*Field summary* — Small to medium sized colorful mushrooms with reddish orange, convex-campanulate, subviscid caps, pale orange young gills, strict, tubular pale orange to purplish red stipes with matte to polished very thin rinds, and long, cord-like branching pseudorhizas. Densely gregarious in troops in autumn from northern Californian coastal mixed (live oak, Douglas or true fir, coast redwood) forests.

**PILEUS** — Up to 62 mm diam, convex with acute umbo and incurved margin when young, later broadly campanulate with acute to low broad umbo, incurved to straight margin, and incurved edge; surface smooth, oily to subviscid, non-striate; bright red- to brown-orange (*xanthine* or *ochraceous orange*, *mars yellow*), often with slightly darker (*tawny*) disc and edge, brown streaks or spots occasionally present. —**FLESH** ≤ 6 mm thick at the disc, pale orangish cream (*pale ochraceous salmon*). —**ODOR** faintly floral to vegetable-like (e.g., of pansies, cooked potatoes, or green corn silk). —**TASTE** mild and not distinctive to slightly bitter (e.g., of raw potatoes). —**DRIED PILEUS** metallic, usually copper or burgundy bronze.

**LAMELLAE** — Initially pale orange cream (*apricot*, *ochraceous buff*), maturing to foxy brown (*clay color*, *tawny*) with bright rusty orange streaks.

**STIPE** — Central to slightly eccentric; ≤ 140 mm above soil, combined length with pseudorhiza > 180 mm; apex ≤ 12 mm diam, strict, terete, uniformly equal except for slight bulbous swelling at ground above sharply attenuating cord-like pseudorhiza; surface smooth and bald or covered with fine short reddish orange fibrils; dry to lubricous; apex at first slightly paler than pileus (*xanthine orange*, *light ochraceous buff*, *cinnamon*), later



Scott Redhead, Agriculture & Agri-food Canada

*P. rufotubulina* holotype specimens grew in bundled troops (TOP)  
on long, erect ('strict') hollow stipes (BELOW).

gradually turning dark reddish to purplish brown (*kaiser* or *liver brown*) from the base upwards; hollow, with thin (1-1.5 mm) cartilaginous rind surrounding cavity that extends from pileus to rhizomorphic pseudorhiza.

**PSEUDORHIZA** — Rhizomorphic: sequential-racemose (branching to give rise to many fruitbodies); cord-like,  $\leq 2$  mm thick diam, full length unknown (55 mm long strands were retrieved before breaking); dark reddish brown (*liver brown*, *clay color*).

**VEIL REMNANTS** — Inconspicuous, seen as connective fibrils between immature cap and stipe or as occasional, densely scattered, fine, dark red-brown fibrils on mature stipe apex.

**SYRINGALDAZINE REACTIVITY** — Negative to very slightly positive (slight blackening after 15 minutes with magenta tinge noticeable on pseudorhiza after one hour).

**FLUORESCENCE** — Fresh material not tested; dried gills dull yellow-orange.

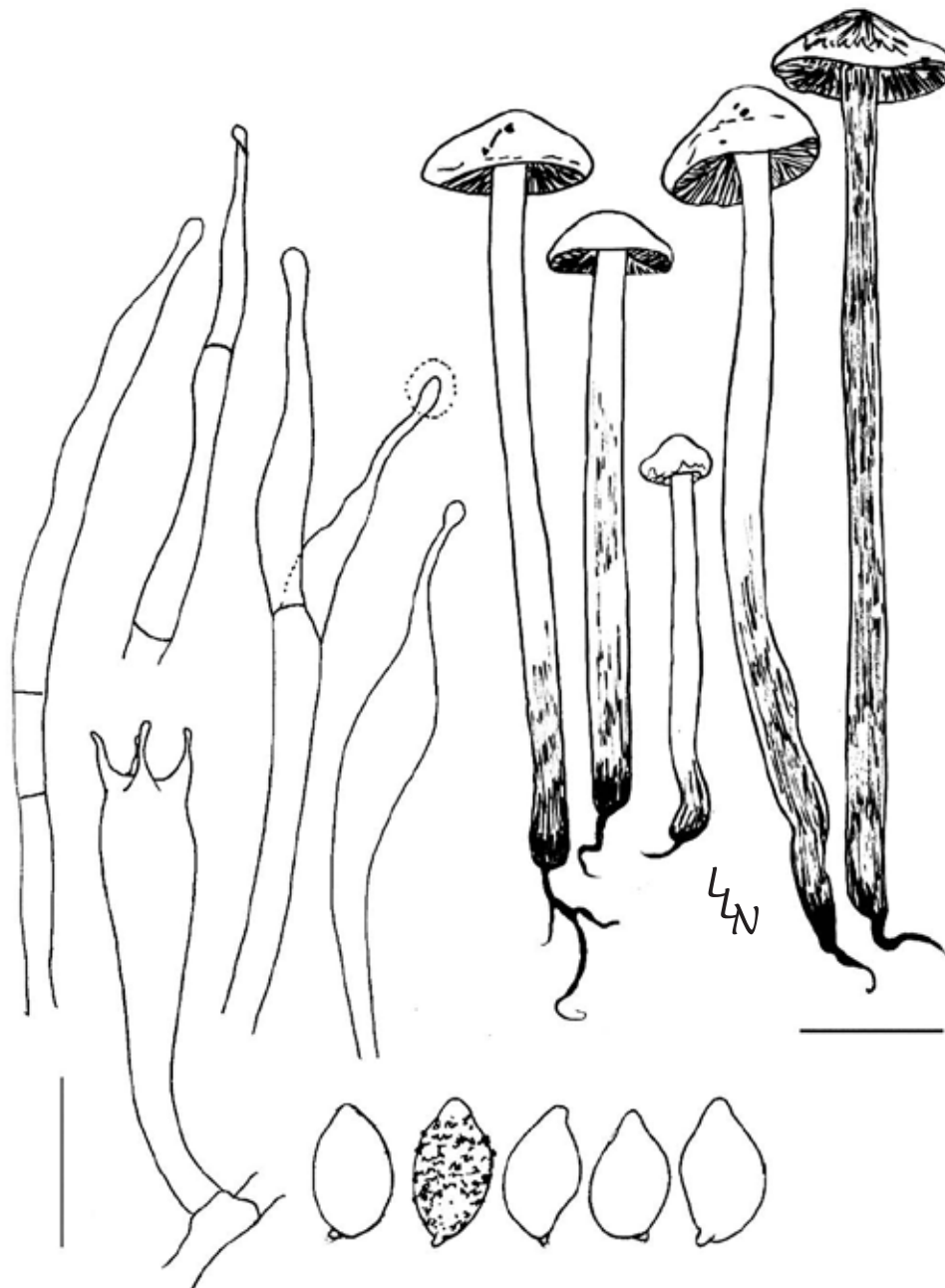
**SPORE PRINT** — Dark reddish brown (*saya* brown).

**Diagnostic characters** — Macroscopically, *P. rufotubulina* can be recognized by its (1) striking reddish orange color, medium size, and densely gregarious habit with fruitbodies assembled in rows or troops, (2) convex campanulate, incurved, moist, brightly colored cap that dries to a metallic copper or purplish bronze, and (3) strict tubular stipe with a thin rind that splits longitudinally to curl back onto itself when sliced crosswise (similar to a dandelion stem).



Scott Redhead, Agriculture & Agri-food Canada

Important microscopical features detailed below include (1) long & narrow ( $\sim 9 \times 5 \mu\text{m}$ ), heavily warty limoniform spores with short beaks, (2) both narrow-necked, thick-walled tibiiform and thin-walled clavate cheilocystidia intermixed on the gill edge, (3) a moderately thick two-layered pileipellis with narrow hyphae (spirally encrusted with orange to brown gel) embedded in the amber top layer above a brownish orange lower layer, and (4) an absence of clamp connections.

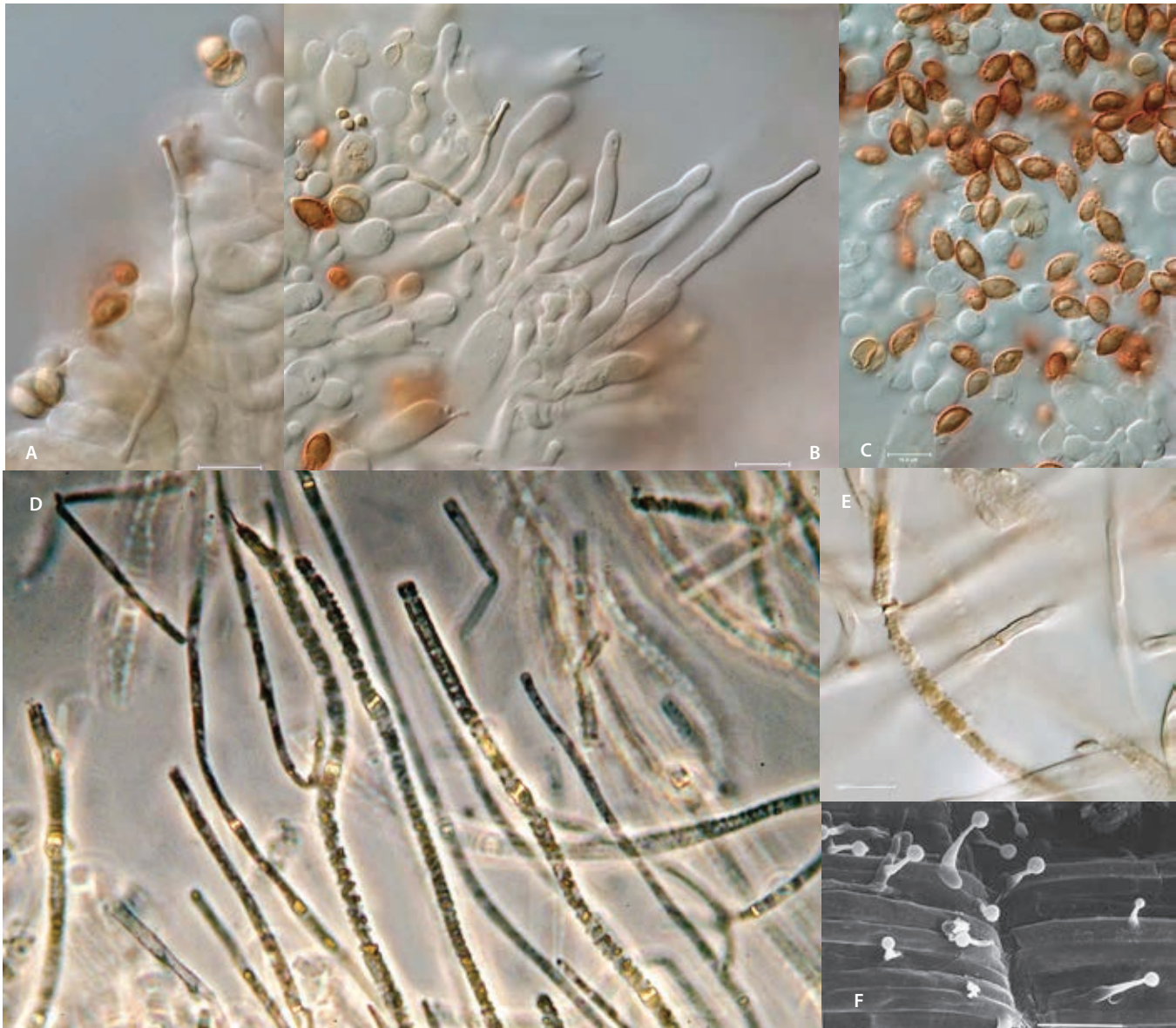


*Phaeocollybia rufotubulina*

a — Habit (LLNorvell, WTU holotype). Scale = 5 cm.

b — Tibiiform cheilocystidia, basidium, basidiospores. Scale = 10  $\mu\text{m}$ .

**BASIDIOSPORES** —  $|x| = 9 \times 5$  [ $8.2\text{--}10 \times 4.5\text{--}6$ ]  $\mu\text{m}$ , limoniform with a prominent straight to slightly tilted beak in profile, ovate in face view; surface coarsely rugulose roughened except over the beak; dark to deep orange amber in KOH; non-dextrinoid in Melzer's. — **BASIDIA** 4-spored; sterigmata long ( $\leq 8\text{-}\mu\text{m}$ ), colorless to straw colored.



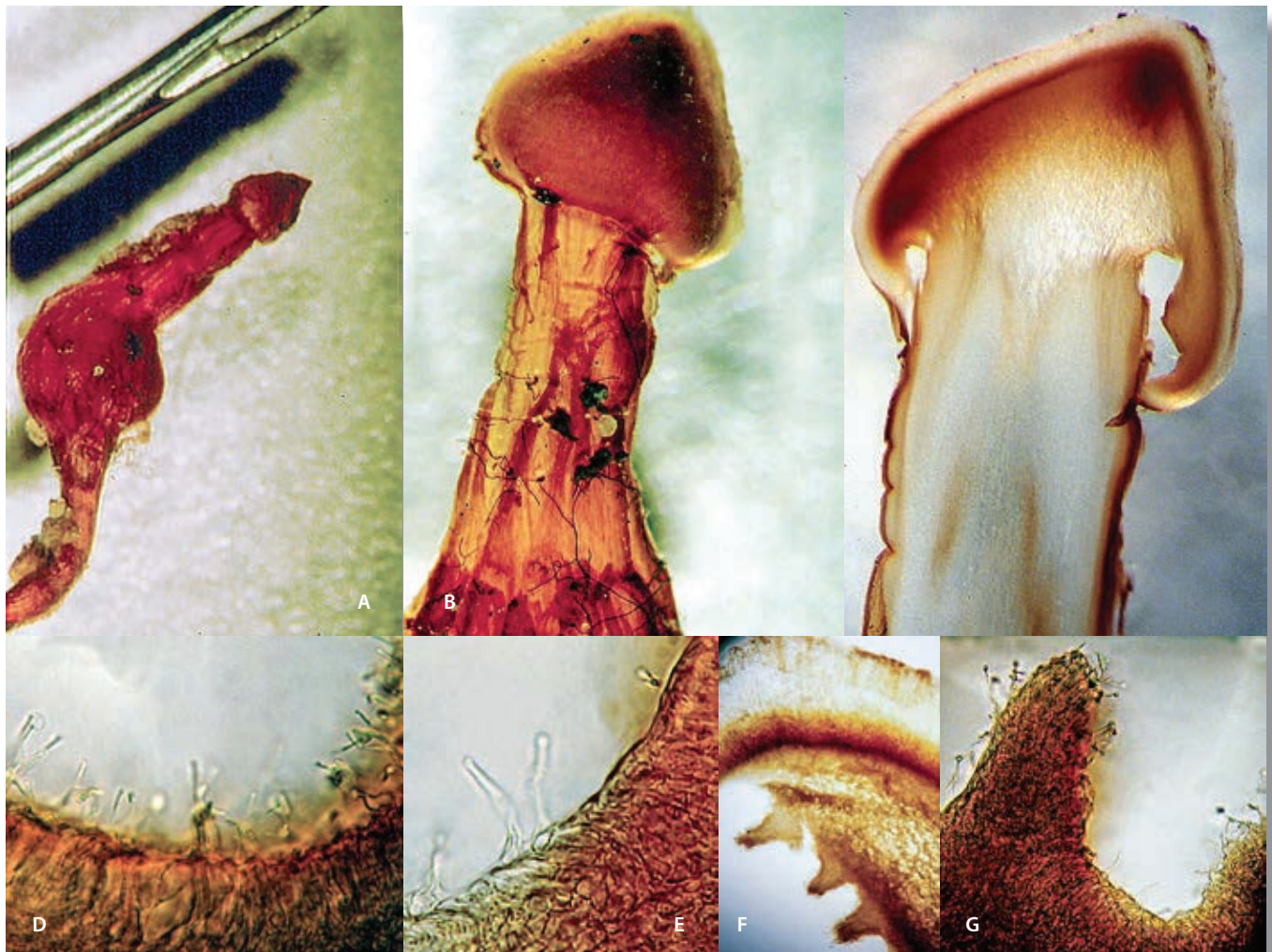
Lorelei Norvell

*Phaeocollybia rufotubulina* [WTU HOLOTYPE LLNorvell1921116-1]— A–C. HYMENIUM. A–B: Occasional secretory tibiiform elements with narrow, thick-walled necks (usually capitulate) and more abundant thin-walled clavate elements intermix with basidia on the partially fertile gill edge; 4-spored basidia often display orange granules during sporulation. C: The rough limoniform basidiospores are dark orange-amber. D–E. SUPRAPELLIS. Spiral encrustations on hyphal surfaces as seen under the compound microscope using phase (D) and DIC (E) optics. Refractive septa and gel encrustations occur on the suprapellicular hyphae in both *P. rufotubulina* and *P. californica*, but the considerably darker encrustations in *P. rufotubulina* (shown here) help separate the two species. F. Tibiiform diverticula arise from the pseudorhizal pellis in this scanning electron micrograph of a mature specimen. All scales = 10  $\mu\text{m}$ .

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** thick-walled tibiiform/mucronate cystidia occasional to frequent,  $\leq 30$  (60)  $\mu\text{m}$  long with 3  $\mu\text{m}$  diam ventricose bases containing viscous pale to dark amber contents below narrow (1  $\mu\text{m}$ ) refractive necks, usually topped by small ( $\leq 1.5$   $\mu\text{m}$  diam) globose heads; also present are more frequent thin-walled elements that are narrowly to variably clavate, heavily gelatinized, colorless, and which develop long filamentous apical outgrowths in age or in storage. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelium, primordial surfaces, and pseudorhizal pellis; also frequent on vestiges of pellicular veil on stipe apex.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis; the top layer a moderately thin suprapellis composed of long, branched, narrow (2–4  $\mu\text{m}$  diam) gelatinized hyphae roughened by spirally encrusting yellow-orange to orange-brown gel and embedded within an orange-yellow gelatinous matrix; intraparietal pigments that concentrate at the septa also present; the 300–450  $\mu\text{m}$  thick subpellis composed of wider ( $\leq 15$   $\mu\text{m}$  diam) hyphae with highly gelatinized, thick, orange-yellow (deep orange in KOH) walls.





ONTOGENY IN *P. RUFOTUBULINA* [WTU HOLOTYPE LLNorvell1921116-1] — A-C. The PELLICULAR SHEATH covering primordia in the type collection helped establish monovelangiocarpic development for *Phaeocollybia*. A longitudinal section of the 'pinhead' primordium in (A) and (B) reveals the dark orange pellicular sheath connecting pileus & stipe and exposes the empty lamellar cavity (C). D-G. CHEILOCYSTITIAL FORM in the species echoes that of the tibiiform diverticulum found on the mycelium and primordial sheath in all phaeocollybias. Tibiiform elements lining the surfaces of the 'empty' lamellar cavity (D & E) in the primordium are also found on lamellar initials (F & G) of a more mature specimen. A longitudinal section (F) shows the dark gel-encrusted hyphae of the suprapellis lying above the subpellis, pileus & gill trama, and gill layers prior to basidial development.

—*STIPITIPPELLIS* a longitudinal ixocutis, hyphae narrow (2-4  $\mu\text{m}$  diam), cylindrical, thick-walled, highly gelatinized, incrustated with medium to dark orange-amber to orange-red pigments.

TRAMAL TISSUES — Moderately to highly gelatinized, strongly sarcodimitic in the pseudorhiza and lower stipe with long ( $\leq 200 \mu\text{m}$ ), wide ( $\leq 20 \mu\text{m}$ ), thick-walled ( $\leq 3 \mu\text{m}$ ), cylindrical, rigid yellowish vessel hyphal elements supported by less conspicuous, branched, shorter ( $\sim 20 \mu\text{m}$ ), narrower ( $\leq 6 \mu\text{m}$ ), thin-walled ( $< 0.5 \mu\text{m}$ ) flexuous hyphal elements; in the pileus both hyphal types also present with vessel hyphal walls thinning to  $1 \mu\text{m}$ . Lamellar trama parallel, with hyphae highly gelatinized, 4-6  $\mu\text{m}$  diam, slightly thick-walled, with refractive septa and pale amber intraparietal pigments, giving rise to a compact ( $\leq 6 \mu\text{m}$  thick) subhymenium.

CLAMP CONNECTIONS — Absent in all tissues of mature fruitbodies but occasionally present in primordial pellis.

**Ecology** — Terrestrial (mycorrhizal). Densely gregarious in loose bundles or troops from mid to late autumn in sandy loam under needle duff in moist mature mixed (*Abies*, *Lithocarpus*, *Pseudotsuga*, *Sequoia*) forests, generally also with *Rhododendron* and/or *Vaccinium* (particularly *V. ovatum*) present in the understory.

*PACIFIC NORTHWEST ENDEMIC* — known from 12 sites in north central California coastal lowlands from Humboldt to Marin counties.



Scott Redhead, Agriculture &amp; Agri-food Canada

*Phaeocollybia rufotubulina*  
DAOM SAREdhead 7500  
Russian Gulch State Park  
Mendocino County, California

**Similar species** — *Phaeocollybia rufotubulina* is included in a complex with *P. californica* and *P. scatesiae* based on anatomical similarities (basidiospore form and size, cheilocystidia) and possession of hollow stipes and racemose rhizomorphic pseudorhizae. *P. californica* produces larger less colorful fruitbodies, hollow stipes with thicker (2-3 mm) rinds that are generally lined with long white fibrils, gills that sometimes turn magenta in syringaldazine, less strongly ornamented spores, wider and colorless suprapellicular hyphae spirally encrusted with paler (often colorless) gel encrustations, and less abundant tibiiform cheilocystidia. Both *P. californica* and *P. scatesiae* produce fruitbodies that erupt in gregarious to fasciculate heaps from single points along subtending pseudorhizal cords. *P. scatesiae* is further diagnosed by its highly glutinous, brownish pileus, paler basidiospores, and smooth hyaline hyphae floating in a massively thick gelatinous suprapellis.

See *P. californica*, *P. scatesiae*, and TABLE 9 (p. 69) for additional comparisons.

**Additional comments** — Preliminary molecular analyses (RFLP profiles of the 5.8s rDNA ITS region) by Norvell (1998a, 2004) of two holotypes and one paratype originally supported separation of *P. rufotubulina* from *P. californica* and *P. scatesiae*. However, new (although still preliminary) sequence data (Matt Gordon, 2009 unpub. data) cluster *P. californica* and *P. rufotubulina* as one species that is well separated from *P. scatesiae*. If complete molecular analyses do support this recent inference, we intend to declare *P. rufotubulina* a synonym of *P. californica*. In the interim, we retain the species as independent in this book.

*P. rufotubulina* appears to be coastally restricted to Humboldt, Mendocino, and Marin Counties in California, while *P. californica* ranges north from Humboldt County in California to Benton County in Oregon. *P. scatesiae* is the most widely distributed of the three species, extending from California's Mendocino County the furthest north (to Washington's Olympic Peninsula) and farthest inland (to Oregon's Mt. Hood in the Cascades).

**References with descriptions and /or illustrations of *Phaeocollybia rufotubulina* —**

- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [as *P. rufotubulina* nom. prov. — key; description pp. 206–209, 375–76; microdrawing & color photos pp. 265–266]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. [as *P. rufotubulina* nom. prov. — development; b&w photos, p. 617]
- Norvell LL. 2004. *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and Section *Versicolores* reconsidered. *Mycotaxon* 90(2): 241–260. [descr. pp. 243–248, microdrawing p. 247; b&w photos p. 245; molecular support for placement in section *Versicolores*: 254–256].

*Phaeocollybia scatesiae*

Slimy yellow-brown caps with peaked umbos and a fasciculate habit characterize *Phaeocollybia scatesiae*.  
Running Bear TS, Benton County, Oregon — PNW-MS Exeter2007-151

***Phaeocollybia scatesiae*** A. H. Sm. & Trappe 1972, Mycologia 64: 1146.

ETYMOLOGY — In honor of Catherine ‘Kit’ Scates, founder of the Pacific Northwest Key Council, who collected the holotype.

HOLOTYPE — Cascade Head Experimental Forest (Tillamook County), OR, USA.  
24 October 1970 (MICH: AHSmith 79286).

*Field summary* — Medium-sized heavily glutinous mushrooms with yellow- to dark brown broadly conic caps, dingy ivory to pale gold young gills, hollow polished tan to ferruginous stipes with thick cartilaginous rinds, and long cordlike salmon-colored pseudorhizas subtending umbellate ‘starbursts’ of immature and mature fruitbodies. Densely fasciculate in erumpent mounds during late autumn from Washington, Oregon, and California coastal or montane coniferous (spruce, true or Douglas fir, hemlock) forests.

**PILEUS** — Up to 65 mm diam, conic with inrolled margin and incurved edge, becoming broadly campanulate with straight margin and edge, umbo often acute and occasionally sharply papillate, edge rarely even, often irregularly sinuate; surface bald, smooth, glutinous, and striatulate at the edge; color yellowish brown (*snuff brown, tawny olive*) when young, soon aging to deep reddish or blackish brown (*chestnut brown, bister*), disc often darker (*bone brown*) than reddish to orange-brown (*bay, auburn*) margin and yellow-brown (*buckthorn brown, dresden brown*) edge; hygrophanous, developing radial furrows and dark brown spots over grayish brown ground color during drying. —**FLESH** thin, buff (*pale pinkish buff, tilleul buff*), often with dark (*mummy brown, light grayish olive*) cartilaginous band near gills. —**ODOR** mildly floral (pansy-like) when young; later not distinctive (occasionally raphanoid or slightly farinaceous), rarely pungent. —**TASTE** faintly bitter when very young, later generally mild or very slightly raphanoid or farinaceous. —**DRIED PILEUS** grayish smoky brown to yellowish copper with metallic glints.



Elizabeth Fox, Agriculture &amp; Agri-Food Canada

*Phaeocollybia scatesiae* fruitbodies and primordium from Twin Creek Olympic National Park, WA — WTU LLN1921015-19 (McCleneghan)

**LAMELLAE** — Initially pale dingy yellowish or pale pinkish white (*light buff*, (*pale*) *pinkish buff*), cinnamon to dull brownish yellow (*pinkish cinnamon*, *isabella color*) when mature, aging to dingy yellow-brown (*tawny olive*).

**STIPE** — More or less central, terete,  $\leq 65$  mm above ground level ( $<100$  mm in unusually large specimens), combined length with pseudorhiza  $> 250$  mm; apex 4–12 mm diam, equal; surface naked and shining, dry to lubricous (often viscid from pileus); color overall initially pinkish to orangish buff (*pinkish buff*, *cinnamon buff*, *pale ochraceous salmon*) but staining orange (*zinc orange*, *orange red*), aging gradually orange cinnamon to dark orange-brown (*mikado brown*, *orange cinnamon*) from ground upwards; hollow, with thick (2–3 mm) cartilaginous cortex surrounding central cavity lined with whitish long fibrils.

**PSEUDORHIZA** — Rhizomorphic: fasciculate-racemose and cord-like; often with scores of differentially developed fruitbodies erupting from one point (fasciculate ‘starburst’) above a solitary subtending rhizomorphic pseudorhizal strand; the stipe+pseudorhiza junction pallid and the 1–2 mm diam subtending cord salmon colored.

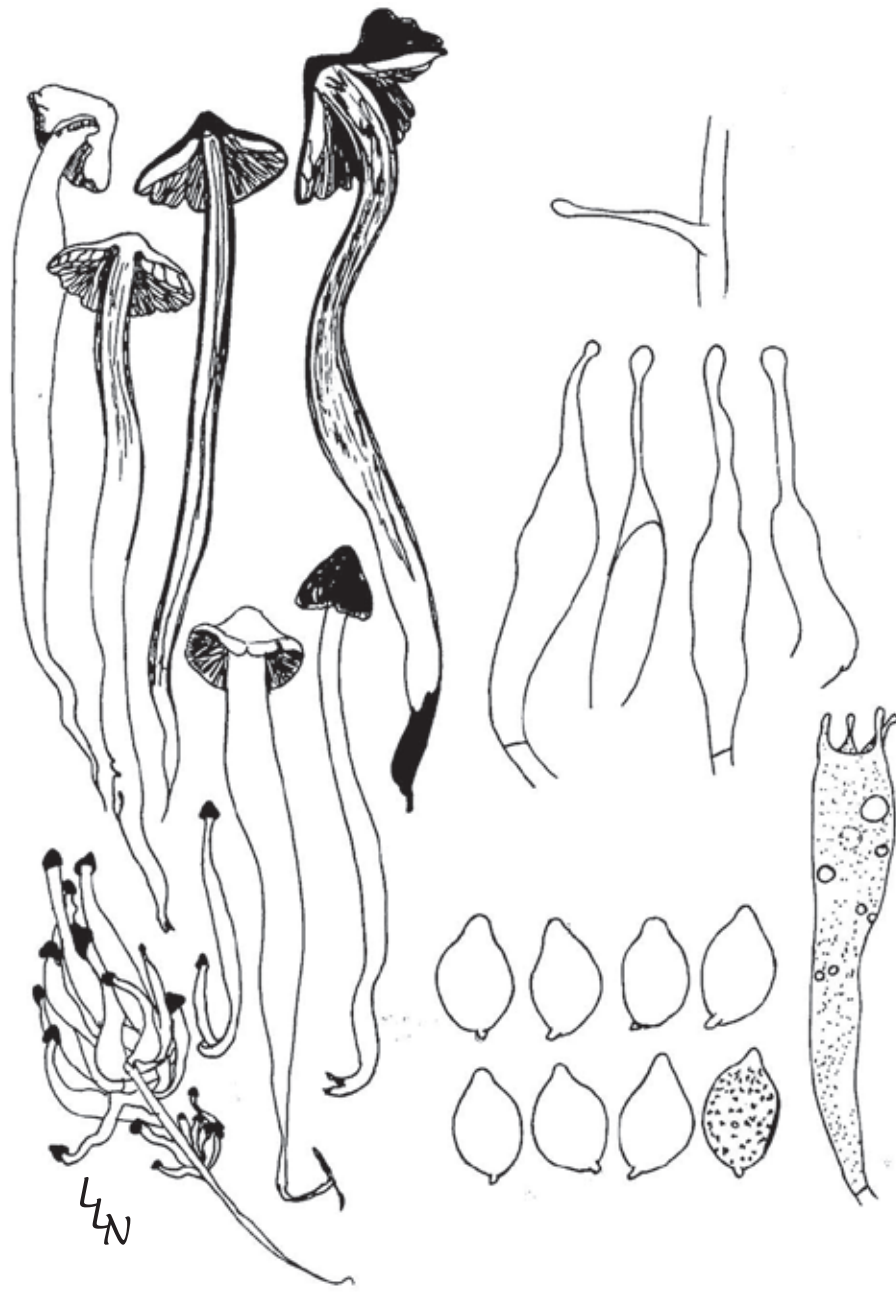
**VEIL REMNANTS** — Inconspicuous, present as short brownish fibrillose patches on stipe apex.

**SYRINGALDAZINE REACTIVITY** — Slowly magenta on pseudorhizal pellis; negative elsewhere.

**FLUORESCENCE** — Young gills brilliant whitish yellow under UV.

**SPORE PRINT** — Medium yellowish brown (close to *pinkish cinnamon*).

**Diagnostic characters** —Macroscopically, *P. scatesiae* can be recognized by its (1) densely fasciculate fruiting habit with scores of differently aged fruitbodies emerging from one point on a subtending rhizomorphic cord, often producing over 100 fruitbodies in one single mound, (2) highly glutinous, pale to dark yellow-brown caps, (3) hollow stipes with thick (2-3 mm) cartilaginous rinds that split lengthwise and recurve when cut, and (4) orangish red stains on lower stipe.



*Phaeocollybia scatesiae*

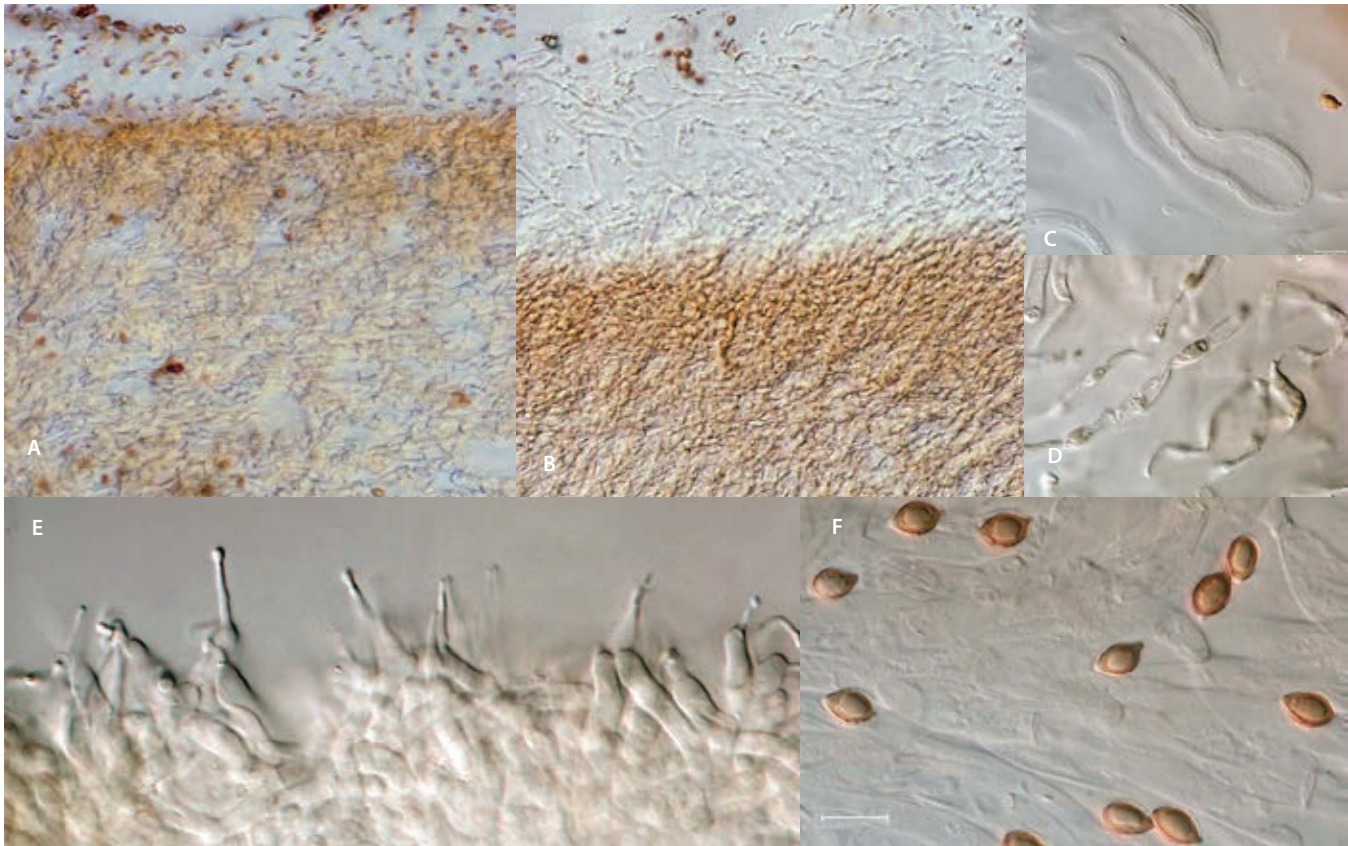
A. HABIT —Mature specimens (a) and primordia & rhizomorph (b)

(A—WTU LLN1951109-27; B—WTU LLN1941019-4).

C-E. TIBIIFORM DIVERTICULUM (C), CHEILOCYSTIDIA & BASIDIOSPORES (D), BASIDIUM (E).

(C—WTU LLN1951018-2; D—MICH HOLOTYPE AHSmith79826; E—WTU LLN 1951109-25)

Important microscopical features detailed on the next page include (1) large (~ 8.5 × 5µm) verruculose limoniform spores with short beaks, (2) secretory lageniform and tibiiform cheilocystidia with narrow, thick-walled, refractive necks with/without small globose heads, (3) a bilaminar pileipellis with a thick top layer composed of narrow 'curly' smooth colorless hyphae embedded within a thick colorless gel matrix overlying a thin pale dull brownish lower layer, and (4) an absence of clamp connections.



Lorelei Norvell

A-D. BILAMINATE SUPRAPELLIS. A-B — Brightfield (200x) comparisons of pileipelli in *P. californica* [A: MICH HOLOTYPE AHSmith55610] and *P. scatesiae* [B: MICH HOLOTYPE AHSmith79286 MICH] display the more highly gelatinized suprapellis of *P. scatesiae* (B); the relatively straight hyphae immersed in colorless gelatinous matrix in a young suprapellis [C: PNW-MS Exeter2007-111] become kinked in a mature suprapellis [D: PNW-MS Exeter2007-151]. E. TIBIIFORM CHEILOCYSTIDIA [PNW-MS Evergreen2003-6] are relatively abundant along the partially fertile gill edge in *P. scatesiae*. F. LIMONIFORM BASIDIOSPORES [PNW-MS Exeter2007-111] with a typically short apical callus (snout). Scales = 10  $\mu$ m.

**BASIDIOSPORES** —  $|x| = 8.5 \times 5$  [7.2–9.5  $\times$  4.5–5.6]  $\mu$ m, limoniform in profile with eccentric short apiculus and central 1  $\mu$ m long beak, ovate in face view; surface verrucose-roughened to warty except over beak; color in KOH pale tawny to pale rusty-brown, in Melzer's non-dextrinoid. **BASIDIA** — 4-spored; colorless (but with orange amber contents during spore formation).

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** relatively abundant; lageniform to capitulate tibiiform [bases  $\sim 20 \times 5$   $\mu$ m, refractive necks  $\leq 3$   $\mu$ m diam, capituli  $\leq 2$   $\mu$ m diam], with or without apical secretory droplets; with colorless or pale amber oily contents surrounded by thick refractive walls. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on primordial and pseudorhizal surfaces and frequent on fibrillose veil remnants on stipe apex,  $\leq 20 \times 1$   $\mu$ m, colorless.

**CORTICAL TISSUES** — **PILEIPELLIS** a bilaminate ixocutis with a moderately thick (100–300  $\mu$ m) suprapellis of colorless radially aligned, uplifted and frequently 'curly', narrow (1–3)  $\mu$ m, highly gelatinized, smooth hyphae embedded in an extensive gelatinous matrix that overlies a subpellis composed of increasingly wider (4–15  $\mu$ m), thick-walled, gelatinized hyphae with brownish to brownish-orange walls (KOH). — **STIPITIPPELLIS** hyphae parallel, long, cylindrical, narrow (1–3  $\mu$ m), thick-walled, highly gelatinized, colorless to pale amber.

**TRAMAL TISSUES** — Very highly gelatinized; in the rhizomorphic pseudorhiza strongly sarcodimitic, dominated by vessel hyphal elements [parallel, cylindrical to slightly fusoid, long (200  $\mu$ m), wide ( $\leq 14$   $\mu$ m), rigid and extremely thick-walled (3–9  $\mu$ m), colorless] around which weave occasional thin-walled flexuous hyphae; at the pseudorhizal junction with stipe base, vessel hyphae less numerous and with thinner (2  $\mu$ m) walls, more abundant supporting flexuous hyphae highly branched, narrow (4–5  $\mu$ m), and thin-walled (0.5  $\mu$ m). Lamellar trama parallel; central hyphal elements (long, cylindrical to slightly inflated, 3–5  $\mu$ m diam, highly gelatinized, colorless) narrowing toward the edges to 1–2  $\mu$ m and giving rise to a compact subhymenium.

**CLAMP CONNECTIONS:** Absent in all tissues.



Lorelei Norvell

Rhizomorphs and pseudorhizas in *Phaeocollybia scatesiae* [wtu LLNorvell 1931104-9, Van Duzer Wayside, Lincoln Co, Oregon] — Excavation of one ‘fasciculate starburst’ (A) exposed 55 mature fruitbodies and 17 primordia arising from a subtending ‘mother’ rhizomorphic cord (B). Magnification of the rhizomorph + pseudorhiza junction under the dissection microscope (C) shows all fruitbodies emanating from a single site.

**Ecology** — Terrestrial and mycorrhizal. Densely cespitose in erumpent mounds during late autumn in woody humus in coastal and montane ( $\leq 4000'$ ) coniferous (*Picea*, *Abies*, *Pseudotsuga*, *Tsuga*) forests. *PACIFIC NORTHWEST ENDEMIC* — collected from 30 sites west of the Cascades and Sierras from northern Washington (Jefferson County) south to northern California (Mendocino County); most (24) sites occur in Oregon.

**Similar species** — *Phaeocollybia scatesiae*, *P. californica*, and *P. rufotubulina* all produce similar sized, highly gregarious fruitbodies with hollow stipes, cord-like pseudorhizas, large rough limoniform spores, and refractive necked tibiiform or lageniform cheilocystidia.

The densely fasciculate habit, slightly smaller stature and highly glutinous yellowish to dark blackish brown pilei in *P. scatesiae* readily distinguishes it from *P. californica*, which produces generally more robust, tawny to orange brown fruitbodies arranged in close to crowded bundles or gregarious arcs. While usually viscid, *P. californica* caps are rarely glutinous. Subtle microscopical differences for *P. californica* include slightly larger ( $\sim 9 \times 5 \mu\text{m}$ ) and more coarsely ornamented darker basidiospores, less frequent cheilocystidia, and a much thinner suprapellis containing spirally gel-encrusted straight (not curly) hyphae. Additionally, in *P. scatesiae* the conical caps open while still underground (Norvell 1998b); this early expansion may explain why mature stipes retain veil remnants covered with tibiiform diverticula, as the expanded pileus may protect the upper stipe surface from abrasion by the surrounding substrate during elongation. *P. californica* also has a narrower range, extending only to low elevations in the coast range to the east and confined to an area south from Oregon’s Benton County to California’s Humboldt County.



Ron Exeter (l), Lorelei Norvell (r)

Kit Scates was unimpressed with having *P. scatesiae* named in her honor. Noting its tendency to burst forth in large heaps, trapping mud & debris in the thick cap glutin, she remarked in her characteristic Alabaman drawl, "It's such an ugly thang!" [OREGON. *Left*—Running Bear TS, Benton Co, PNW-MS Exeter2008-76; *Right*—Wildcat Mtn, Clackamas Co, wru LLNorvell1951018-1]

*Phaeocollybia rufotubulina* differs from *P. scatesiae* in its thinner cartilaginous stipe rind, sequential-racemose pseudorhiza, and subviscid bright reddish orange cap. *P. rufotubulina* has not yet been confirmed for Oregon.

Darker *P. scatesiae* fruitbodies may be confused with unusually small and closely gregarious forms of *P. spadicea*, which generally produces scattered large, robust fruitbodies. *P. spadicea* stipes are never shiny (polished) or hollow, always stuffed with firm solid pith; the pseudorhizas are vertical-monopodial, its tibiiform cheilocystidia are larger, and its basidiospores are slightly smaller (~8 x 5).

See TABLE 9 (p. 69), *P. californica*, *P. rufotubulina*, and *P. spadicea* for additional comparisons.

**Additional comments** — In 1977 Horak synonymized *P. scatesiae* with *P. californica*, a synonymy supported by the identical RFLP profiles of the ITS rDNA region for the two species (Norvell 1998a, 2004). Macroscopical and microscopical comparisons of numerous fresh and dried collections, however, support the existence of two species, which we recognize here. As noted earlier for *P. californica*, Norvell's decision to accept *P. scatesiae* as a separate species was made after she submitted her first evaluation of the species to the Northwest Forest Plan; here, however, the data for *P. scatesiae* are shown correctly in both distribution map and site data in Castellano et al. (1999).

*References with descriptions and /or illustrations of Phaeocollybia scatesiae:*

- Castellano MA, Smith JE, O'Dell T, Cázares E, Nugent S. October. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. USDA-FS. PNW-GTR-476. PNW Res. Stn., Portland. [descr. & color photo: s1 - 91].
- Horak E. 1977 ('1976'). Further additions towards a monograph of *Phaeocollybia*. *Sydowia* 29: 28-70. [note placing *P. scatesiae* into synonymy with *P. californica*: p. 37 & 40].
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [key; description pp. 209-212, 376; microdrawing & color photos pp. 267-268]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615-630. [pseudorhizal morphology & development pp. 623-624; b&w photos p. 620 & 622].
- Norvell LL. 2004. *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and Section *Versicolores* reconsidered. *Mycotaxon* 90(2): 241-260. [The 'californica' complex is discussed (including molecular analyses) in comparison with *P. rufotubulina*].
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. *Mycologia*. 64: 1138-1153 [Revised key; type description 1146-1148; b&w photo p. 1147].



*Phaeocollybia sipei*

*Phaeocollybia sipei* at Reese Creek  
Benton County, Oregon — PNW-MS Exeter2007-167

Ron Exeter

*Phaeocollybia sipei* A.H. Sm., Brittonia 9: 207, 1957.

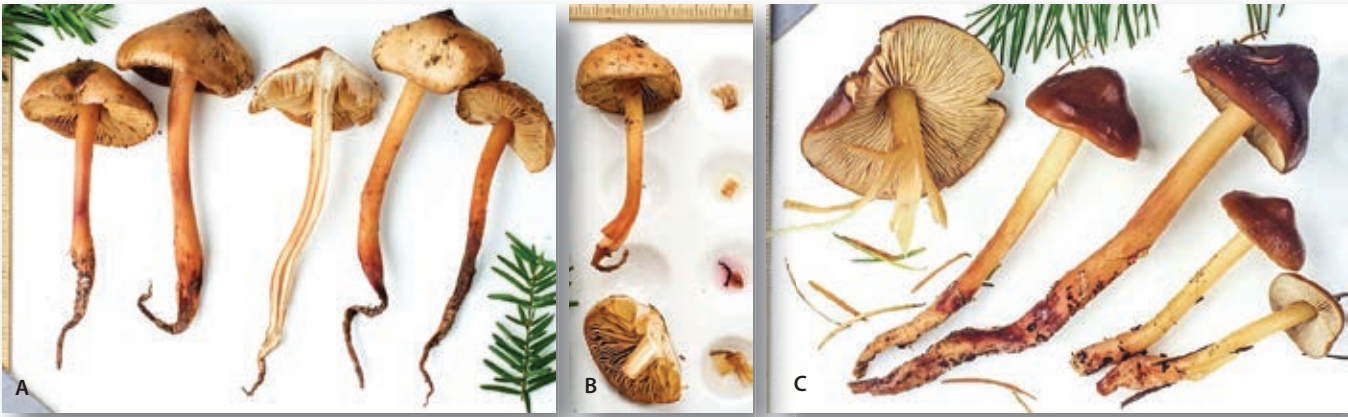
ETYMOLOGY —In honor of Dr. Frank P. Sipe, collector of the holotype.

HOLOTYPE — Eugene (Lane County), OR, USA; October, 1937 (MICH HOLOTYPE FPSipe s.n.)

*Field summary* — Medium-sized fruitbodies with subviscid brownish-orange broadly campanulate caps, pale yellowish young gills, watery tan to orange polished fibrillose stuffed to hollow stipes with thick splitting cartilaginous rinds, and deeply rooting pseudorhizal cords. Closely gregarious during autumn under Douglas-fir, western hemlock, and spruce in Oregon and Washington.

**PILEUS** — ~25–120 mm diam, acutely or obtusely umbonate with down-curved margin and inrolled edge when young, expanding to broadly campanulate with down-turned edge, surface (sub)viscid, smooth, bald, often splitting radially in age; color either uniformly deep brownish orange to orange-brown (*chestnut*, *auburn*, *orange cinnamon*, *russet*) or zonate with darker auburn disk and edge and foxy orange (*burnt sienna*, *mikado brown*, *orange cinnamon*) margin. —**FLESH** 3–8 mm and buff colored in the umbo, rapidly narrowing over the gills and concolorous with the cuticle. —**ODOR** when young, not distinct, vaguely farinaceous, or complex with floral (pansy) and burnt hair components; when old sometimes strongly pungent and unpleasant. —**TASTE** not distinctive to slightly raphanoid or farinaceous. —**DRIED PILEUS** finely concentrically wrinkled, flat dark orange-brown to (rarely) dark copper metallic.

**LAMELLAE** — Free to narrowly attached, relatively broad, color pale yellowish buff (*cartridge buff*, *ivory yellow*) when young, pinkish buff when mature, deep yellow–brown (*buckthorn brown*) with serrulate edges in age.



*Phaeocollybia sipei* — Diagnostic characters include an umbonate subviscid pale to dark orange-brown cap, broad gills, a thready pseudorhiza giving a weak (B) to strong magenta reaction in syringaldazine, and a hollow stipe with a thick rind that splits apart (C) when cut crosswise. OREGON, Benton Co: A&B—Conner's Camp (Mary's Peak), PNW-MS Exeter2007-123; C—Green Peak, PNW-MS g2041027h2-5.

**STIPE** — +/- central, ~40–80 mm above the ground, combined length with pseudorhiza up to 210 mm before breaking; apex 5–13 mm diam, upper stipe equal to slightly fusiform, subterranean base often swelling before abruptly tapering to thread-like pseudorhiza; surface moist to polished, smooth beneath scattered veil remnants; young apex watery tan (*cartridge buff*, *cream buff*) above a pale orange (*apricot buff*) to cinnamon lower stipe, in age darkening to deep orange-red to reddish brown (*cacao brown*) from the base upwards; at first stuffed with a firm silky pallid pith, soon canaliculate with 3–4 mm diam cavity, in age completely hollow but for stray pale orange fibrils; cartilaginous rind ~3 mm thick, frequently splitting apart when cut or broken crosswise.

**PSEUDORHIZA** — (Sequential) racemose and cord-like, either continuous with lower stipe and gradually narrowing to a thin narrow origin or abruptly tapering beneath a swollen stipe base to a thread-like 'rat-tail'; color above cord dark red to liver brown, cord paler (salmon colored) toward tip.

**VEIL REMNANTS** — Inconspicuous, evident as scattered orangish appressed fibrillose patches on upper stipe.

**SYRINGALDAZINE REACTIVITY** — Cap, gill, and upper stipe tissues negative, pseudorhiza weakly to strongly magenta.

**FLUORESCENCE** — Under UV, young gills fluoresce pale light to brilliant yellow while the stipe context glows deep magenta and orange.

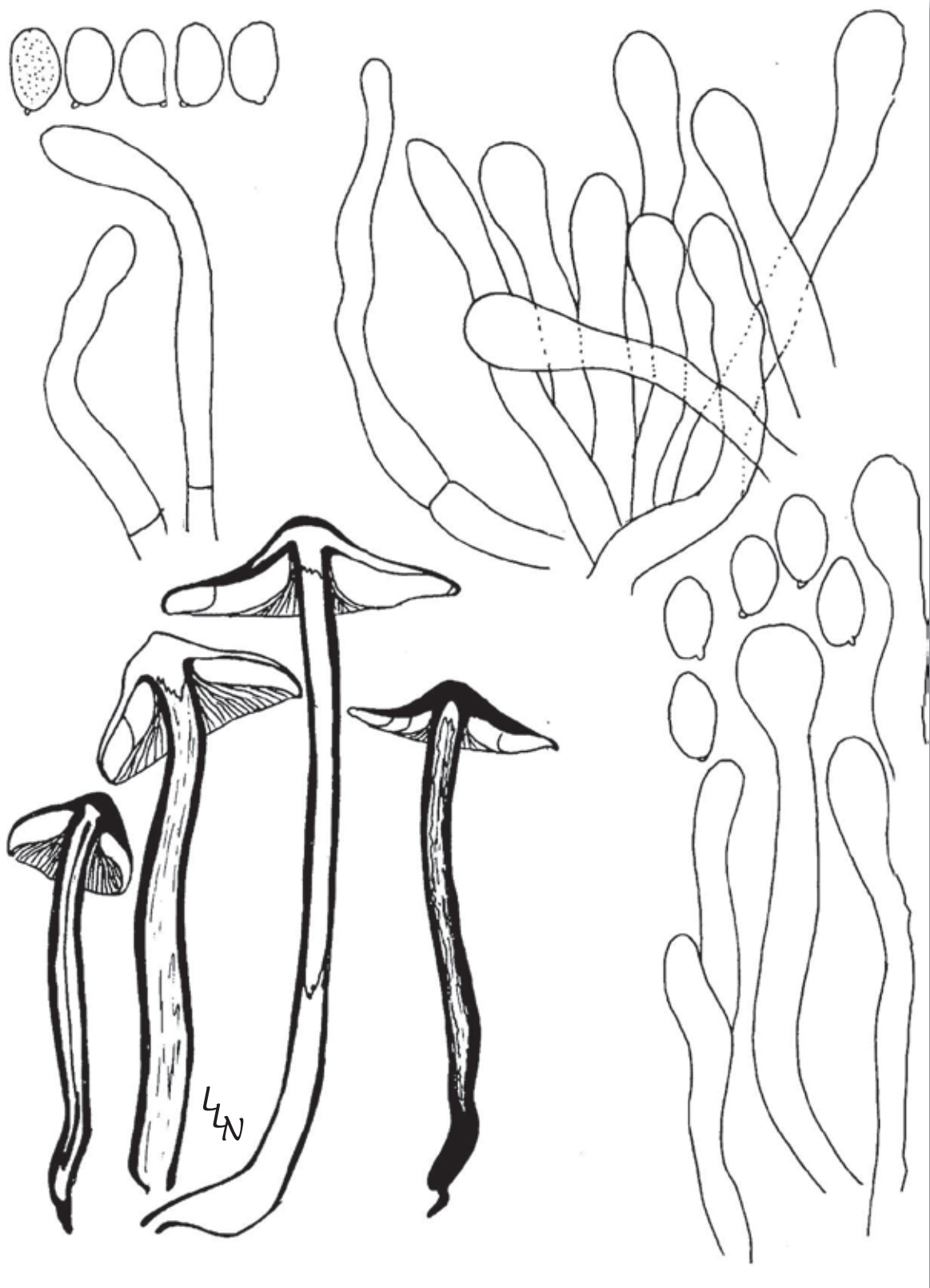
**SPORE PRINT** — Cinnamon brown (*buckthorn brown*).

**Diagnostic characters** — Macroscopically, *P. sipei* can be recognized by its (1) viscid convex-campanulate brownish orange to orange-brown cap with an acute to broad umbo, (2) yellowish to buff young gills, (3) usually hollow tan to orange stipe with thick cartilaginous rind and cord-like pseudorhiza, and (4) pseudorhiza weakly to strongly magenta in syringaldazine.

Important microscopical features include (1) small (~6.5 × 3.8 μm) punctate roughened basidiospores with blunt bullet-nosed apical snouts, (2) thin-walled, long cylindrical to pedicellate colorless cheilocystidia with swollen subglobose heads, (3) bilaminate pileipellis with a subpellis that turns deep red-orange in KOH, and (4) lack of clamp connections.

**BASIDIOSPORES** —  $|x| = 6.5 \times 3.8$  [5.8–7.5 × 3.3–5] μm, subellipsoidal, ventrally rounded with small eccentric apiculus and rounded bullet-nosed snout in profile view, ovoid to subellipsoidal in face view, finely punctate roughened under oil immersion; color in KOH pale medium amber, in H<sub>2</sub>O paler, in Melzer's inamyloid and nondextrinoid. — **BASIDIA** 4-spored, clavate, 22–28 × 6–9 μm, colorless, granular to vacuolate.

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, thin-walled, arising from the lamellar trama to form a sterile layer; lengths variable and indeterminate (~30–40 μm long), variably filamentous to clavate, often subcapitate with long 2–4 μm diam pedicels and swollen subglobose (≤ 8 μm diam) heads, apical extensions from senescent elements rare; colorless. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on



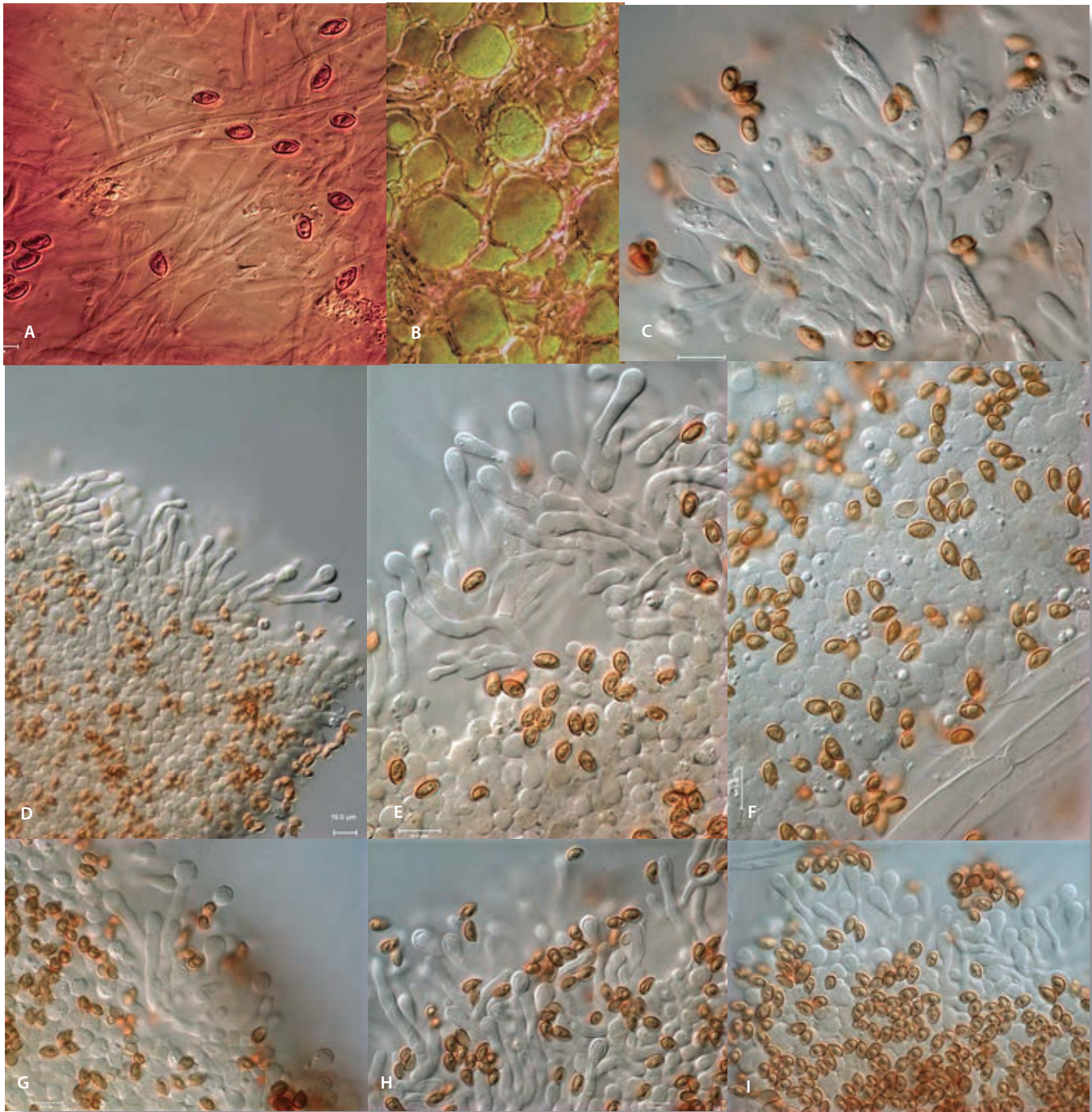
*Phaeocollybia sipei*

A. HABIT. Fogarty Creek State Park (Lincoln Co), OR — WTU Norvell1951109-2(left), -7(middle), -6(right)].

B-D. CHEILOCYSTIDIA & BASIDIOSPORES.

B: Eugene (Lane Co) OR — MICH HOLOTYPE FPSipe Oct1937.

c-d: Fogarty Creek State Park (Lincoln Co), OR — WTU Norvell1951109-2(c) & -6(D).



Lorelei Norvell

*Phaeocollybia sipei* [OREGON. Benton Co, Conner's Cmp (Mary's Peak) PNW-MS—Exeter2007-123(c); Ernest Crk PNW-MS—Exeter2007-163(g); Reese Crk PNW-MS—Exeter2007-166(d)&-167(a&f); Coos Co, OCS—Myrtlewood RA LNus17b61DRoediger (e), LN17b118JSperling(h); Lincoln Co, Cascade Head Exp F Norvell1931104-1(b), OSC—LN8US127(i)] — A. PILEIPELLIS. The diffuse brownish pigments of the subpellis turn a deep reddish-orange when mounted in KOH. B. STIPE TRAMA. A cross-section illustrates the two different hyphal diameters that distinguish wide rigid vessel elements and narrow flexuous 'binders' that make up the sarcodimitic tissues found in the pseudorhiza. The similar wall thicknesses in the stipe, however, keep that tissue from being classified as 'sarcodimitic'. C. BASIDIA are clavate, granular, colorless, and 4-spored. D–I. CHEILOCYSTIDIA AND BASIDIOSPORES. Microscopically, the most reliable diagnostic characters for *P. sipei* are the lack of clamp connections, a sterile gill edge lined with abundant thin-walled tall elements with swollen subglobose heads and long narrow pedicels, and the small minutely roughened bullet-nosed spores. Scales = 10  $\mu$ m.

primordial and pseudorhizal surfaces,  $\sim 10 \times 1 \mu\text{m}$ , with/without (sub)globose head and/or apical droplet; highly refractive, colorless.

CORTICAL TISSUES — PILEIPELLIS a bilaminar ixocutis: the suprapellis with interwoven, narrow (2–3  $\mu\text{m}$ ), gelatinized colorless hyphae in a colorless gelatinous matrix; the pigmented subpellis with inflated



*Phaeocollybia sipei* at Ernest Creek (Benton County), Oregon

Left [PNW-MS Exeter2008-042] —Young fruitbodies with incurved subviscid brownish-orange caps and pallid stipes.

Right [PNW-MS Exeter2007-24] —Older specimens with campanulate glutinous tawny caps and darkening stipes.

(8–30  $\mu\text{m}$  diam), gelatinized hyphae and diffuse ochraceous-brown pigments turning deep red-orange in KOH. —*STIPITIPPELLIS* hyphae parallel, sparingly branched, long and cylindrical, narrow, relatively thick-walled, gelatinized, colorless when young, orange-brown to brown in age.

TRAMAL TISSUES — Gelatinized, sarcodimitic in the pseudorhizal cord with rigid thick-walled ( $\leq 1 \mu\text{m}$ ), wide ( $\leq 30 \mu\text{m}$  diam) vessel hyphae supported by less conspicuous branched thin-walled ( $\sim 0.5 \mu\text{m}$ ), narrow (2–4  $\mu\text{m}$ ) flexuous hyphae; in stipe and pileus wide and narrow hyphae both present but with walls similarly ( $\sim 0.5 \mu\text{m}$ ) thick, colorless. Lamellar central hyphae parallel, colorless, and flanked by a narrow zone of 2–3  $\mu\text{m}$  diam colorless elements giving rise to a compact subhymenium.

CLAMP CONNECTIONS — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); closely gregarious (often in arcs) during autumn under *Tsuga*, *Picea*, and *Pseudotsuga*. —PACIFIC NORTHWEST ENDEMIC known from 25 sites in Oregon and one site in Washington (based on a single old specimen collected in Olympic National Park's Hoh Rainforest).

**Similar species** — *Phaeocollybia dissiliens* shares striking similarities with *P. sipei*, including stature, orange coloration, cheilocystidial form, and small, almost smooth, bullet-nosed basidiospores. *P. dissiliens* can be differentiated by its smaller size, brighter orange colors, pale orange copper metallic dried cap that wrinkles radially (not concentrically), abundant clamp connections, and cheilocystidia that only occasionally produce subglobose heads but frequently develop apical outgrowths in old tissues.

Other species that might be mistaken for *P. sipei* in the field include *P. californica*, *P. rufotubulina*, and *P. gregaria*. Like *P. sipei*, both *P. californica* and *P. rufotubulina* produce large gregarious clusters of hollow-stiped fruitbodies from cord-like pseudorhizas, but they are easily distinguished by their large rough limoniform basidiospores and thick-walled tibiiform cheilocystidia.

*P. sipei* fruitbodies with paler caps could be confused with the typically yellow-brown to tawny capped *P. gregaria*, which also produces dense gregarious clusters of broadly campanulate basidiomes. The presence of persistent pith, lack of pseudorhizal cord, and large rough limoniform basidiospores help distinguish *P. gregaria*.

Refer to comments after the above species for additional comparisons.

**Additional comments** — Horak (1977) treated *P. sipei* as a synonym of *P. californica* based his examination of one type specimen; he later (Horak pers. comm. 1995, 1996) discovered that the specimen sent him from the mixed type collection represented *P. scatesiae* (which he considered conspecific with *P. californica*). His initial



Lorelei Norvell

*Phaeocollybia sipei* in Fogarty Creek State Park  
Lincoln County, Oregon — WTU Norvell1951109-2

confusion was compounded by the fact that in the paper containing the type description, Smith (1957) described *P. sipei* spores as small and faintly ornamented but referred to drawings depicting large, heavily ornamented beaked basidiospores. Norvell's (1998a) later examination of the entire holotype confirmed that the spores — which are not rough but only finely punctate under high-power oil immersion, lack prominent apical beaks, and are more or less bullet-nosed — closely resemble those found in *P. dissiliens* and *P. oregonensis*.

*References with descriptions and /or illustrations of Phaeocollybia sipei —*

- Castellano MA, Smith JE, O'Dell T, Cázares E, Nugent S. 1999. Handbook to Strategy 1 fungal species in the Northwest Forest Plan. PNW-GTR-476. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s1 – 92].
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales, Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [description 217–219; color photos 272]
- Smith AH. 1957b. A contribution toward a monograph of *Phaeocollybia*. *Brittonia* 9: 195-217. [key; type descr. 207, microdrawing of cheilocystidia p. 210 (the basidiospore drawings represent *P. scatesiae*)]



Ron Exeter

*Phaeocollybia sipei* on Old Blue near Mary's Peak  
Benton County, Oregon — PNW-MS Exeter2007-086

*Phaeocollybia spadicea*

*Phaeocollybia spadicea* at Ernest Creek  
Benton County, Oregon — PNW-MS Exeter2008-040

***Phaeocollybia spadicea*** A.H. Sm., Brittonia 9: 215, 1957

ETYMOLOGY — From the Latin for ‘date-colored’, a deep reddish brown.

HOLOTYPE — Near Mora on the Quillayute River (Clallam), WA, USA;  
October 26, 1935 (MICH HOLOTYPE 11634 AHSmith3339)

*Field summary* — Medium to large fruitbodies with viscid dark brown convex-campanulate caps, pale to buff young gills, dull pinkish to cinnamon drab stuffed stipes often covered with cinnamon veil patches, and deeply rooting fleshy unbranched pseudorhizas. Scattered to gregarious during autumn in Washington, Oregon, and California coniferous or mixed forests.

**PILEUS** — ~25-120 mm diam, convex-campanulate with a low broad umbo, straight margin and slightly incurved to upturned non-striate edge, surface bald, smooth, viscid to glutinous, slightly hygrophanous; color either uniformly some shade of dark to chestnut brown (*chestnut/ bone/ clove/ snuff brown*) or with darker disc (*fuscous, bister, bone/ clove/ hair/ brown*), brownish drab to brown margin (*wood/ buffy/ clove/ snuff brown, avellaneous, drab, saccardo’s umber*), and paler edge (*cinnamon, sayal/ snuff/ natal/ wood brown, tawny olive, vinaceous buff, avellaneous*). —**FLESH** 3–8 mm thick at the disc and tapering evenly to the edge, pallid when young, dull brown in age. —**ODOR** not distinctive to radish-like or complex with subtle floral and boiled potato components. —**TASTE** usually mild or radish-like, occasionally bitter. —**DRIED PILEUS** metallic dull copper to bronze, often with purplish tinges, black spots, or satiny patches.

**LAMELLAE** — Narrowly attached (nearly free), pale tan when young, darkening to pinkish to yellowish brown, dark yellow brown when mature.

**STIPE** — +/- central, rigid and robust, ~50–120 mm above the ground, combined length with pseudorhiza up to 250 mm; apex ~6–20 mm diam, equal, tapering gradually or expanding slightly to ground level before narrowing below; surface dry, matte, roughened, finely longitudinally lined; color of young apex pinkish



Scott Redhead (A-C), Lorelei Norvell (D-E)

*Phaeocollybia spadicea* is best diagnosed in the field by its light to dark brown cap (A&D) and the firmly stuffed (E) fleshy drab stipe frequently covered by abundant short cinnamon colored veil remnants (B&C). [OREGON, Tillamook County: A—WTU Norvell1921102-3, B&C—WTU Norvell1931023-6 [Oswald West State Park]; Benton County: D—PNW-MS Exeter2007-52 (Mary's Peak); E—PNW-MS Norvell2071029-3 (Old Blue Mtn).]

brown to drab (*pinkish buff, light pinkish cinnamon, cinnamon buff, drab*) becoming dark yellow-brown (*tawny olive, wood brown, cinnamon color*) in age, grading to dark pink- to red-brown (*fawn color, mikado/ kaiser brown, saccardo's umber*) at ground level; stuffed with firm pale buff pith that turns orange to brownish when sliced or crushed; cartilaginous rind 1–2 mm thick.

**PSEUDORHIZA** — Vertical-monopodial, more or less continuous with stipe and tapering gradually downwards to a blunt origin; rhizomorphic and occasionally regenerating, giving rise to primordia; color dark red-brown (*liver/ kaiser brown, saccardo's umber*).

**VEIL REMNANTS** — Usually frequent to abundant (occasionally inconspicuous) as fibrillose patches on exposed stipe; color cinnamon to yellow-brown.

**SYRINGALDAZINE REACTIVITY** — Pseudorhiza deep magenta within 15 minutes; other tissues usually negative.

**FLUORESCENCE** — Under UV, gills fluoresce intense yellow-white when young and mustard to dull yellow when spore-covered; cap/stipe pith fluoresce deep purple.

**SPORE PRINT** — Dark yellow-brown.

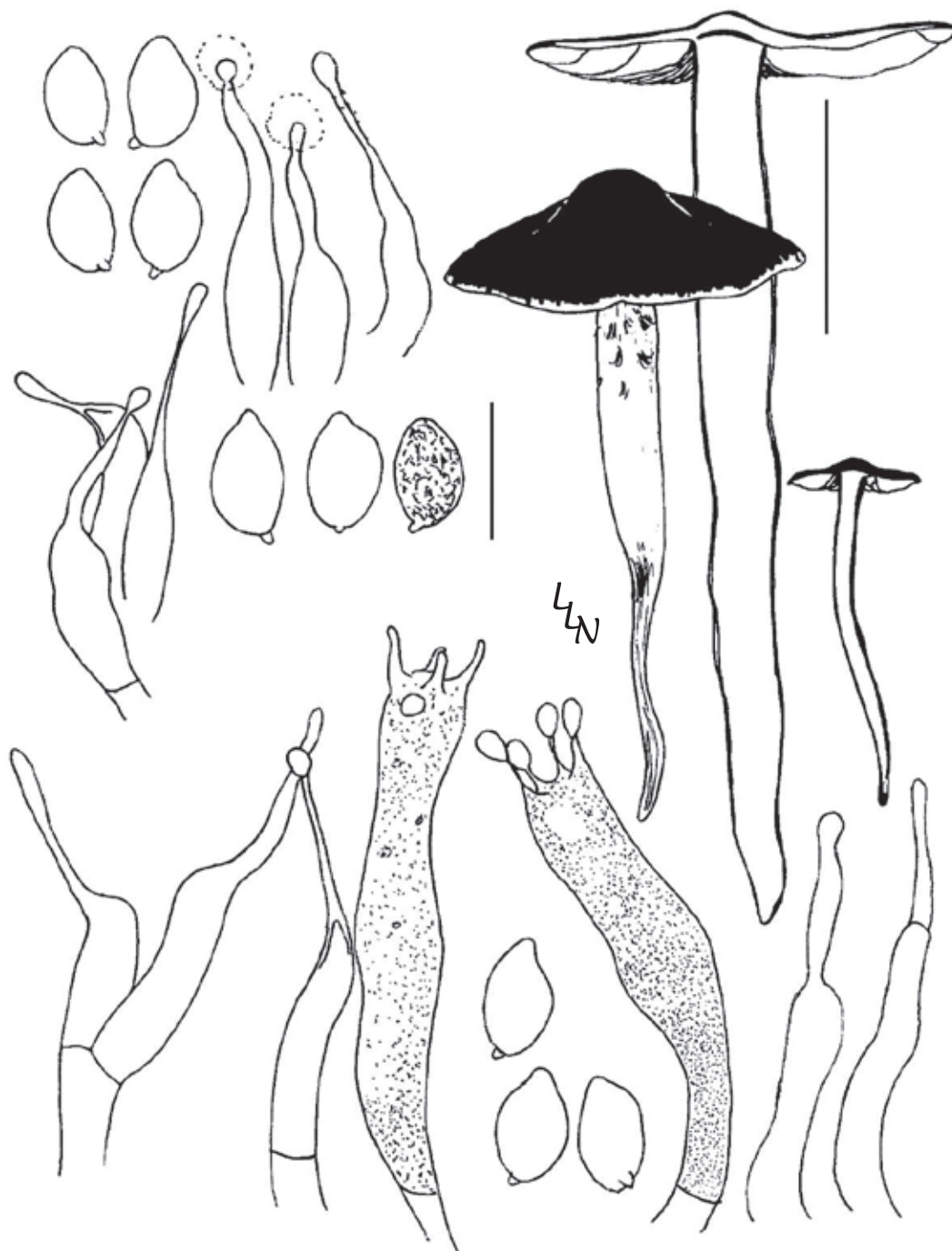
**Diagnostic characters** — Macroscopically, *P. spadicea* can be recognized by its (1) viscid to glutinous dark brown campanulate cap, (2) dry matte robust stuffed stipe with cinnamon fibrillose patches that contrast with the pinkish tan to drab surface, (3) medium to large stature, and (4) pseudorhiza that turns deep magenta in syringaldazine.

Important microscopical features include (1) medium-sized ( $\sim 8 \times 5 \mu\text{m}$ ) roughened limoniform spores with tapered short apical beaks, (2) tibiiform to lageniform cheilocystidia with narrow thick-walled colorless to amber refractive necks, (3) a bi-laminate pileipellis with diffuse brown subpellis pigments, and (4) absence of clamp connections.

**BASIDIOSPORES** —  $|x| = 8 \times 5 [6-9 \times 4-5.5] \mu\text{m}$ , limoniform with a short slender eccentric apiculus and gradually tapering  $\leq 0.5 \mu\text{m}$  long central apical beak in profile view, broadly ovate to almond-shaped in face view; verruculose roughened with ornamentation slightly projecting beyond outline except on beak and ill defined less roughened plage; color in KOH medium dark amber, in  $\text{H}_2\text{O}$  paler, in Melzer's dextrinoid. — **BASIDIA** 4-spored, clavate,  $33-40 \times 6-9 \mu\text{m}$ , colorless to orange amber in older tissues, granular.



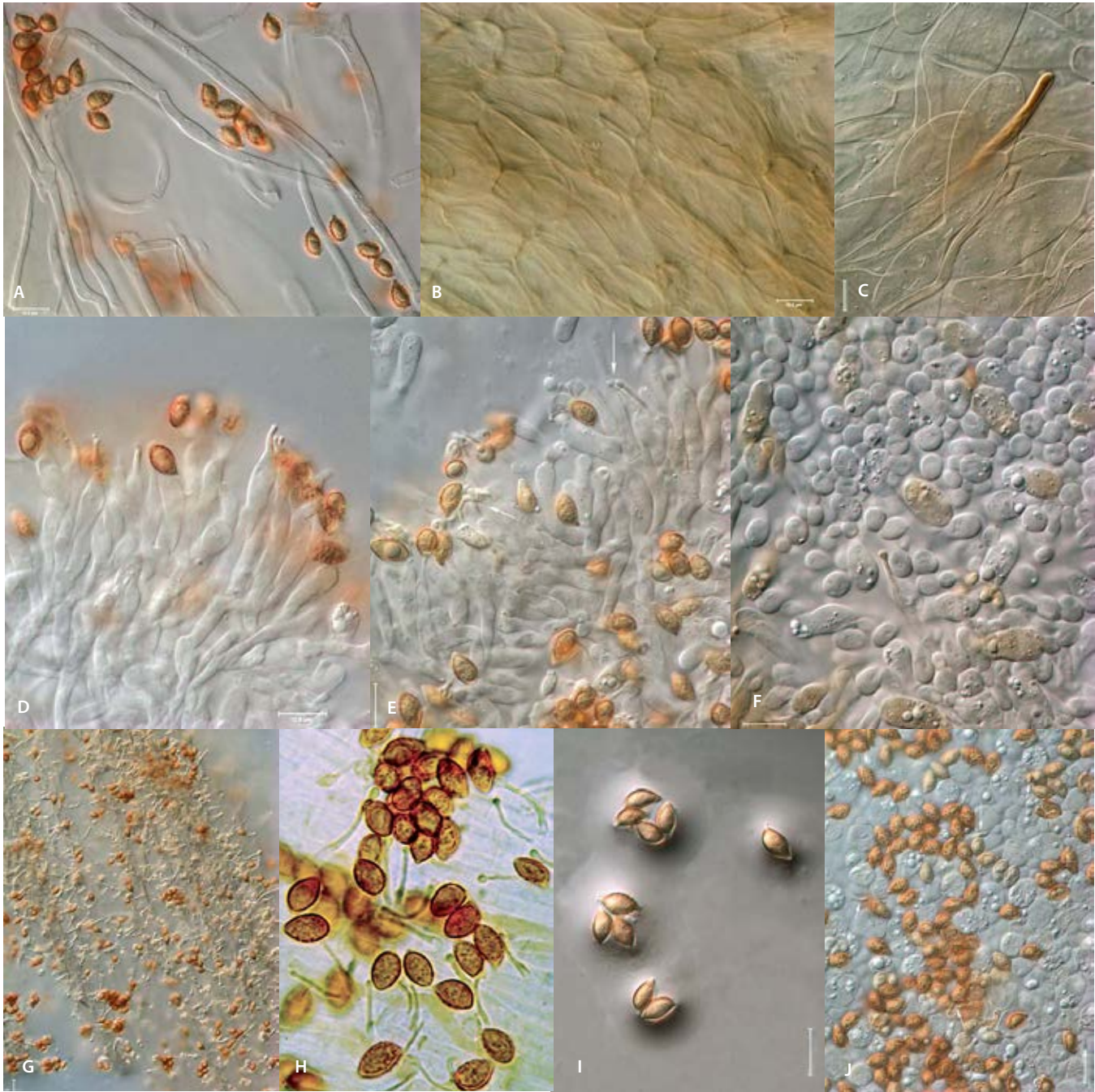
CYSTIDIAL ELEMENTS —*CHEILOCYSTIDIA* abundant, arising from the subhymenium and intermixed with basidia, lageniform to tibiiform elements 23–40  $\mu\text{m}$  long and with  $\sim 3\text{--}5\ \mu\text{m}$  diam bases subtending narrow ( $1\text{--}1.5\ \mu\text{m}$  diam), thick-walled, refractive, colorless to amber necks and capitula ( $\leq 2\ \mu\text{m}$  diam) surrounded by apical secretory droplets; occasionally intermixed with lageniform or capitate elements with thin-walled wider ( $\sim 2\ \mu\text{m}$  diam) watery amber necks and thin-walled wide ( $4\text{--}8\ \mu\text{m}$  diam) colorless bases. —*PLEUROCYSTIDIA* absent. —*TIBIIFORM DIVERTICULA* abundant on mycelium and surfaces of the primordial sheath remnants on the pseudorhiza and stipe,  $5\text{--}15 \times 1 \times 0.5\ \mu\text{m}$  with no septum between base and hyphae, with/without (sub) globose head and/or apical droplet; highly refractive, colorless.



*Phaeocollybia spadicea*.

A. HABIT (Scale = 5 cm). B–C. BASIDIOPORES, CHEILOCYSTIDIA & BASIDIA (Scale = 10  $\mu\text{m}$ ).

Cascade Head ExpF (Lincoln Co OR)—A: wtU LLN1931114-6&7, LLN1951109-20; c: wtU LLN1941106-28a  
Quillayute River (Clallam Co WA)—B: MICH HOLOTYPE11634 AHSmith 3339



Lorelei Norvell

*Phaeocollybia spadicea* [OREGON: Benton Co—Botkin Rd, PNW: Exeter2007-39 (I); Old Blue, PNW: Exeter2007-141 (B,D,G); Running Bear, PNW: Exeter2007-145 (E). Coos Co—Myrtlewood RNA, osc: LNus17b112 (F). Josephine Co—Limpy Creek, osc LNus8-4 (A,C,I). Lincoln Co—Cascade Head Exp For, WTU: Norvell1931114-9 (H)]. A–C. *PILEIPELLIS*. A—Basidiospores float within a loose gel matrix amid narrow colorless hyphae of the suprapellis. B & C—Hyphae are widely inflated in the subpellis, where diffuse dull brown pigments turn slightly tawny in KOH; oleifers with brown to orange (C) contents are also present. D–F. *CHEILOCYSTIDIA*. Elements with tall moderately thin-walled bases, narrow thick-walled refractive necks often below minutely globose heads are frequent along the partially fertile gill-edge. Colorless in young material, cheilocystidia and granular basidia may develop yellow-orange hues in older tissues (F). G–H. *TIBIFORM DIVERTICULA*. The abundant primordial sheath patches on the upper stipe are here densely covered by refractive 10- $\mu$ m long tibiiform diverticula, shown in Nomarski under the high dry objective (G) and under oil in bright field with the characteristic limoniform spores (H). I–J. *BASIDIOSPORES*. Brown coloration, presence of an apical callus (I), and a roughened outer spore wall (J) are exhibited by all *Phaeocollybia* basidiospores. Size, shape, beak length, and degree of ornamentation are helpful in diagnosing species. Scale bars = 10  $\mu$ m.

**CORTICAL TISSUES** —*PILEIPELLIS* a bilaminar ixocutis: the top 200–450  $\mu$ m thick suprapellis a thick gelatinous matrix containing loosely radially aligned, narrow (1–2  $\mu$ m), highly gelatinized colorless hyphae; the subpellis composed of gelatinous hyphae inflating to 15  $\mu$ m diam from 4–5  $\mu$ m diam septa and with thin pale to dark



Elizabeth Fox (L), Scott Redhead (R)

*Phaeocollybia spadicea* in the Hoh Rainforest (L) and the Cascade Head Experimental Forest (R)

LEFT: Olympic National Park, Jefferson County, Washington — WTU Norvell1921019-1

RIGHT: Lincoln County, Oregon — WTU Norvell1931104-4

rusty brown walls, oleifers with bright tawny contents and diffuse brownish (H<sub>2</sub>O) to dull tawny (KOH) pigments also present.

**TRAMAL TISSUES** — Brown to tawny orange oleifers present throughout; all hyphae highly gelatinized and colorless. Strongly sarcodimitic in the pseudorhiza and lower stipe with long fusoid rigid white vessel hyphae intermixed with narrow branched thin-walled flexuous hyphae; both hyphal types often also present in the stipe apex. Lamellar central hyphae parallel 3–5 μm diam, thin-walled and flanked by a narrow zone of 2–3 μm diam elements giving rise to a compact subhymenium.

**CLAMP CONNECTIONS** — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary, closely gregarious to occasionally cespitose during autumn in moist coniferous (*Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Pinus contorta*) or mixed (*Tsuga*, *Pinus*, *Pseudotsuga*, *Lithocarpus*, *Quercus*) forests. — **PACIFIC NORTHWEST ENDEMIC** known from ~55 sites along the Pacific coast from Washington's Olympic Peninsula south to California's Santa Cruz Mountains and east to the western Cascade slope of Oregon's Willamette Valley and eastern slope of California's Coast Range.

**Similar species** — Macroscopically, *Phaeocollybia spadicea* shares similar coloration and/or robust stature with *P. scatesiae*, *P. tibiikauffmanii*, *P. gregaria*, *P. redheadii*, and *P. benzokauffmanii*. Under the microscope, the presence of uniformly thin-walled clavate cheilocystidia and much larger basidiospores easily separate *P. benzokauffmanii*, *P. gregaria*, and *P. redheadii* from *P. spadicea*. *Phaeocollybia benzokauffmanii* can be further distinguished macroscopically by its drab to dark purple-brown pileus, strong farinaceous odor, and immediate magenta reaction of all tissues in Syringaldazine. The usually more massive stature, convex cap with tightly inrolled edges, and warmer brown tones of pileus and stipe will help diagnose *P. redheadii* in the field, while *P. gregaria* has a more slender aspect, more fibrillose stipe pith, and caps that are golden-brown when young.

*Phaeocollybia scatesiae* shares a dark brown glutinous pileus, pallid to cinnamon gill coloration, similarly shaped and only slightly longer (~8.5 μm) basidiospores, and thick-walled refractive tibiiform cheilocystidia with *P. spadicea*. In the field, *P. scatesiae* is easily identified by its viscid, polished consistently hollow stipes and fasciculate-racemose rhizomorphic pseudorhizae; furthermore, although *P. spadicea* may exhibit a gregarious to cespitose habit, it does not produce the dense masses of fruitbodies arising from one point that characterize *P. scatesiae*. Highly gelatinized, 'kinky' subpellis hyphae, shorter cheilocystidia, and slightly longer and slightly paler spores help differentiate *P. scatesiae* under the microscope.

Older *P. tibiikauffmanii* specimens that have darkened and thus easily mistaken for *P. spadicea* can be identified by the orange to tawny cap, salmon colored stipe apex with tawny veil patches, less abundant and



Ron Exeter

*Phaeocollybia spadicea* along Klickitat Road on Old Blue Mountain  
Benton County, Oregon — PNW-MS Exeter2007-141

more stringy stipe pith that is soon maggot infested (particularly near the apex), narrower ( $\sim 8 \times 4.5 \mu\text{m}$ ) limoniform basidiospores with slightly longer beaks, encrusting orange-brown to tawny pigments in the pileus subpellis, and cap and gill tissues that turn rapidly magenta in syringaldazine.

Refer to comments after *P. tibiikauffmanii* and *P. scatesiae* for additional comparisons.

**Additional comments** — Smith, who initially reported *Phaeocollybia spadicea* from Oregon as representing the European *Naucoria lugubris* (Smith 1937), later proposed it as a new species based on absence of caulocystidia and color and basidiospore differences (Smith 1957). Horak (1977) synonymized *P. spadicea* with *P. lugubris* based on his early type studies but later rejected his synonymy in Bandala & al. (1998). The uniformly drab to dark brown cap colors and distinctly apically beaked limoniform spores in the western American *P. spadicea* contrast with the olivaceous cap colors and rounded basidiospores lacking a developed apical beak found in the European *P. lugubris*. Norvell (1998a, 2004) confirmed that both *P. spadicea* and *P. lugubris* possess abundant tibiiform diverticula (earlier interpreted as ‘caulocystidia’ by many workers) on the veil remnants on the stipe apex.

*References with descriptions and /or illustrations of Phaeocollybia spadicea* —

- Castellano MA, Cázares E, Fondrick B, Dreisbach T. 2003. Handbook to additional fungal species of special concern in the Northwest Forest Plan. PNW-GTR-572: USDA-FS Pacific Northwest Research Station, Portland OR. [descr. & color photo: s3 – 86].
- Norvell LL. 1998a. The biology and taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (*Agaricales*, *Cortinariaceae*). Ph. D. dissertation, Department of Botany, University of Washington, Seattle. 391 pp. [pp. 220–224; photos pp. 31, 36, 273–274]
- Norvell LL. 1998b. Observations on development, morphology, and biology in *Phaeocollybia*. *Mycol. Res.* 102: 615–630. [discussion of stipe, tibiiform diverticula, pseudorhiza 618–619; b&w photos pp. 617, 620]
- Smith AH. 1957. A contribution toward a monograph of *Phaeocollybia*. *Brittonia* 9: 195–217. [key; microdrawings p. 210, descr. pp. 215–217, b&w photo pl. 6]
- Smith AH, Trappe JM. 1972. The higher fungi of Oregon's Cascade Head Experimental Forest and vicinity. I. The genus *Phaeocollybia* (*Agaricales*) and notes and descriptions of other species in the *Agaricales*. *Mycologia*. 64: 1138–1153 [Key 1146–1148].

*Phaeocollybia tibiikauffmanii*

Ron Exeter

*Phaeocollybia tibiikauffmanii* at Conner's Camp below Mary's Peak  
Benton County, Oregon — PNW-MS Exeter2008-055

*Phaeocollybia tibiikauffmanii* Norvell, Mycotaxon 90: 248, 2004

ETYMOLOGY — From “tibia” (Latin for thigh-bone), relating to the ‘bone-shaped’ cheilocystidia + “kauffmanii” for similarities to *P. kauffmanii* fruitbodies.

HOLOTYPE — Old Growth Chronosequence Transect [‘Oz’], BLM Reserve Forest (Polk Co.), OR, USA;  
October 31, 2001 by LLNorvell & RLExeter (OSC HOLOTYPE a2011031ox-01; ISOTYPES WTU PNW)

*Field summary* — Moderately tall slender fruitbodies with viscid tawny orange to orange brown broadly campanulate caps, pale orange-yellow to buff young gills, slender fibrillose-stuffed salmon colored stipes, and deeply rooting fleshy unbranched regenerating pseudorhizas. Solitary to fasciculate during autumn in coastal and coast range coniferous (hemlock, Douglas-fir, spruce) forests in Oregon and Washington.

PILEUS — ~40–120 mm diam, broadly campanulate with conic low umbo, upturned margin and down-turned straight edge, surface viscid, bald, nonstriate, opaque to slightly hygrophanous; color overall brownish orange or foxy brown (*tawny, orange cinnamon*) or with tawny disc and orange-cinnamon edge zone, darkening to uniformly brown (*verona/ snuff brown*) in age. — *FLESH* 4–6 mm at the disc and confluent with the stipe pith; color when young pale orangish white, in age drab brown. — *ODOR* faintly floral with farinaceous overtones. — *TASTE* mild, not distinctive. — *DRIED PILEUS* metallic copper to orange bronze.

LAMELLAE — Nearly free, pale orangish buff (*warm buff*) when young, darkening to dull pinkish brown (*fawn color*) in age.

STIPE — +/- central, rigid, ~100 mm above the ground, combined length with pseudorhiza may exceed 240 mm; apex 5–20 mm diam, terete above, gradually narrowing below toward pseudorhiza; surface dry, bald except for occasional fibrils or fibrillose patches, matte, finely longitudinally lined; color of young apex pale to deep pinkish orange (*pinkish/ orange cinnamon, warm buff*), grading to dull pinkish brown (*fawn color*) at ground level; cartilaginous rind 1.5–2 mm thick, splitting longitudinally in age; stuffed with compact fibrillose orangish white pith that is often insect infested in the upper stipe.



*Phaeocollybia tibiikauffmanii* is best diagnosed in the field by its orange tawny cap (A) that darkens to dark orange-brown in age (B–D), slender cartilaginous salmon orange stipe (E), easily insect infested cap and stipe context (F), long thick pseudorhiza that occasionally winds around buried obstacles (G) and that gives rise to young primordia (H–I) near its base. [The ‘Oz’ old-growth transect (Polk Co, OR): osc HOLOTYPE a20110331ox-1 (A,I); PNW-MS a2061114 colls. o2-O(B), o2-M(C), o1-2a(D), o1-C(G); also a201103o2-3(E), a2021113o2-o1(F), a2001018o2-27(H)] Scales in millimeters.

**PSEUDORHIZA** — Vertical-monopodial, ~2/3 of overall length, continuous with stipe and gradually tapering to a pointed origin; color ferruginous to dark brown.

**VEIL REMNANTS** — Seen as isolated fibrils and scattered fibrillose patches on the exposed stipe; color concolorous with or slightly darker than stipe surface.

**SYRINGALDAZINE REACTIVITY** — Pseudorhiza (always) and cap and gills (often) soon deep magenta; cap and/or gills sometimes not reactive.

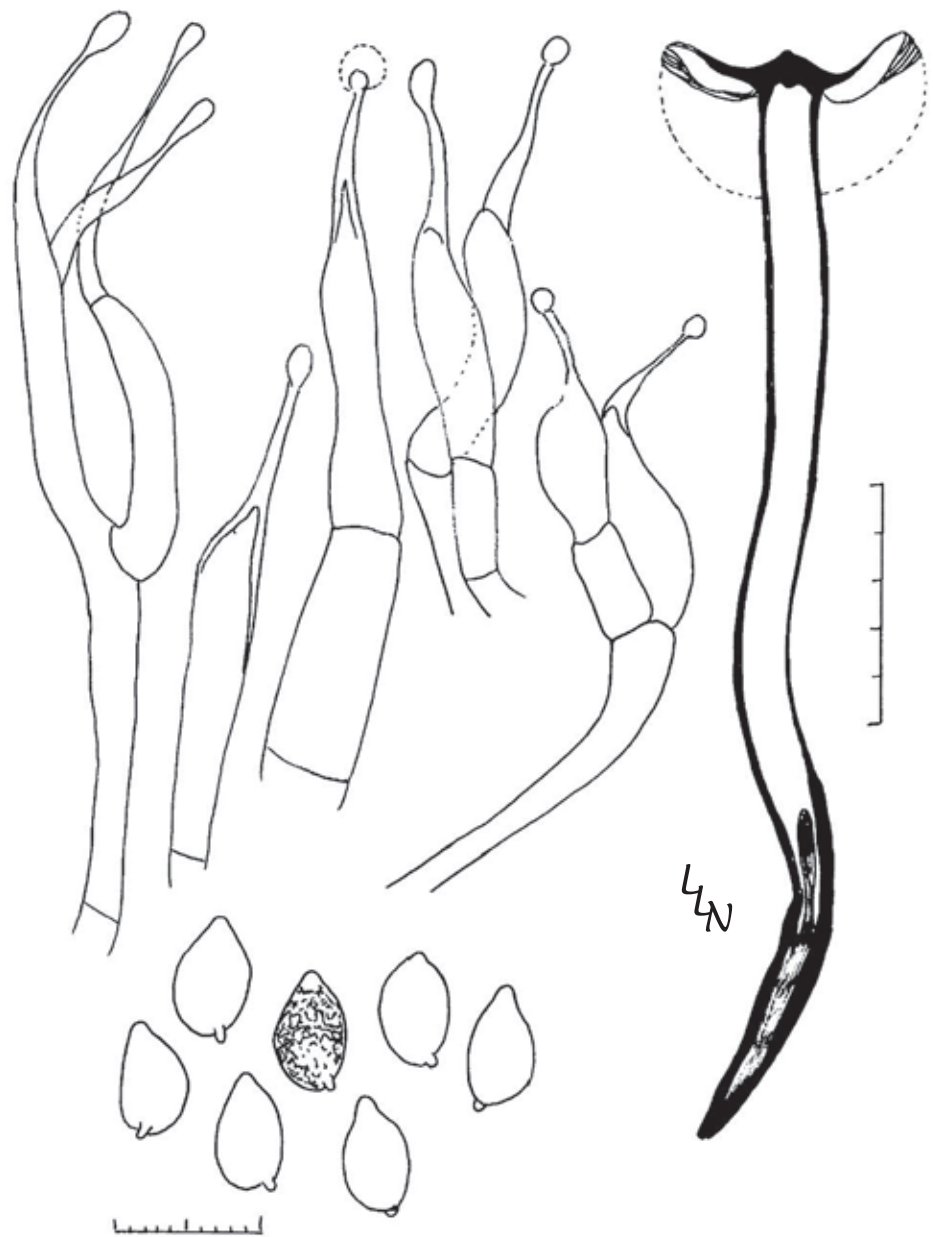
**FLUORESCENCE** — Under UV gills fluoresce brilliant to dull yellow and flesh displays a mix of deep orange and purple.

**SPORE PRINT** — Dull pinkish brown (*fawn color, cocoa brown*).

**Diagnostic characters** — Macroscopically, *P. tibiikauffmanii* can be recognized by its (1) broadly campanulate viscid to glutinous orange tawny to orange brown cap, (2) slender dry matte salmon to cinnamon-colored stipe stuffed with often maggot infested pith, (3) tall slender stature, and (4) cap (usually), stipe, and pseudorhiza surface tissues that turn deep magenta in syringaldazine.

Important microscopical features include (1) a bilaminar pileipellis with 2–6 gel-encrusted suprapellis hyphae and a subpellis with encrusting and diffuse orange pigments, (2) medium-sized narrow (~8 × 4.5 μm) limoniform basidiospores with tapered apical beaks, (3) abundant tall capitulate tibiiform colorless cheilocystidia, some refractive with narrow thick-walled necks and some with narrow thin-walled necks, and (4) absence of clamp connections.

**BASIDIOSPORES** —  $|x| = 8 \times 4.5 [7.5-9(10) \times 4-5.5] \mu\text{m}$ , limoniform with a short eccentric apiculus and 0.5–1.0  $\mu\text{m}$  long central apical beak in profile view, fusoid-elliptical in face view, verruculose to punctate roughened except on beak, plage an indistinctly bordered area of lowered ornamentation visible under oil; color in KOH orange-amber, in  $\text{H}_2\text{O}$  ochraceous, in Melzer's inamyloid (immature spores attached to basidia faintly dextrinoid). — **BASIDIA** 4-spored, clavate,  $27-35 \times 7-9 \mu\text{m}$ , colorless, granular.

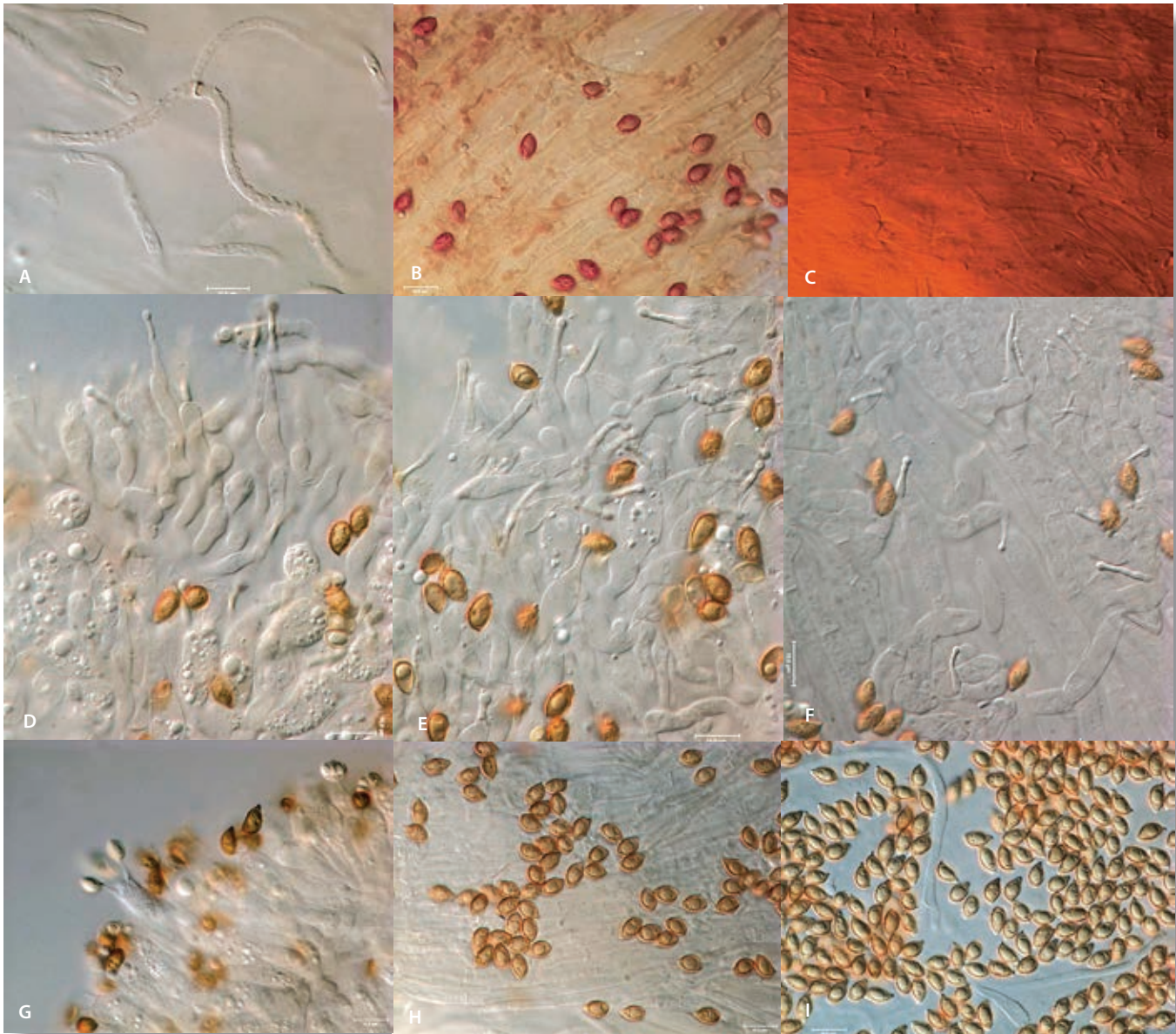


*Phaeocollybia tibiikauffmanii*

Cascade Head Experimental Forest, Lincoln Co, OR — wtU Norvell1951109-19

CHEILOCYSTIDIA & BASIDIOSPORES (scale = 10  $\mu\text{m}$ ). HABIT (scale = 5 cm).

**CYSTIDIAL ELEMENTS** — **CHEILOCYSTIDIA** abundant, arising from the subhymenium to form a sterile layer; tibiiform colorless elements ~20–50  $\mu\text{m}$  long, occasionally branching at or above ultimate and penultimate 2–3  $\mu\text{m}$  diam septa, often swelling above septum to 3–5  $\mu\text{m}$  before narrowing to  $8-15 \times 0.5-2 \mu\text{m}$  at the necks that are either thick-walled and refractive or thin-walled, capitula when present 1.5–3  $\mu\text{m}$ ; occasional thin-walled clavate elements intermixed. — **PLEUROCYSTIDIA** absent. — **TIBIIFORM DIVERTICULA** abundant on mycelium and pseudorhizal pellis, less frequent on primordial sheath remnants on upper stipe,  $4-20 \times 0.5-1 \mu\text{m}$ , aseptate at base, with/without (sub)globose head and/or apical droplet; highly refractive, colorless.



Lorelei Norvell

*Phaeocollybia tibiikauffmanii* [OREGON, PNW: Benton Co—Ernest Crk Exeter2007-165 (I); Lane Co—Lobster Valley Exeter2007-129 (A&E); Lincoln Co—Cascade Head Exp. For. Exeter2007-74 (D&G); Polk County—Pedee OG trsect 'Oz' a2061114o1B (B&C), Exeter2007-60 (F), a2061114o1Q (H)]. A–C. *PILEIPELLIS*. A—Gel-encrusted colorless narrow hyphae float in the gelatinous matrix of the suprapellis. B—Orange encrusting pigments adhere to the hyphal walls within the subpellis of a mature specimen. C—Orange diffuse pigments of the subpellis become more intensely colored when mounted in KOH. D–F. *CHEILOCYSTIDIA*. Abundant tibiiform and occasional thin-walled clavate elements crowd out granular basidia along a sterile gill edge (D&E). Minutely capitulate tibiiform elements with long thin-walled bases may have either thin-walled or thick-walled necks. F—Tibiiform cheilocystidia occurring on the stipe that might called 'caulocystidia' are confined to a narrow zone at the top of the apex. G–I. *BASIDIA & BASIDIOSPORES*. Mature 4-spored basidia (G) extend beyond the hymenium. Lemon-shaped rough basidiospores with long tapered beaks crowd the stipitipellis (H&I). Scales = 10  $\mu$ m.

**CORTICAL TISSUES** — *PILEIPELLIS* a bilaminar ixocutis: the 100–120  $\mu$ m thick suprapellis of radially aligned, 2–6  $\mu$ m diam, highly gelatinized colorless hyphae, the uppermost elements narrower (~2  $\mu$ m diam), cylindrical, closely compacted and collapsed while elements closer to the subpellis inflated to 6  $\mu$ m diam; the 170–200  $\mu$ m thick tawny orange (in KOH) to orange brown subpellis with thin-walled hyphae inflating to 8  $\mu$ m diam from 2  $\mu$ m diam refractive septa, orange pigments diffuse and (often) encrusting; occasional orange oleifers intermixed. — *STIPITIPELLIS* hyphae loosely parallel, subgelatinized, thin-walled, long, 2–6  $\mu$ m diam, pale brownish green (diffuse pigments soluble in KOH).

**TRAMAL TISSUES** — Oleifers present throughout; slightly sarcodimitic in the pseudorhiza with infrequent fusoid, long, 10–20  $\mu$ m diam, only slightly thick-walled ( $\leq 0.5$   $\mu$ m thick) vessel hyphae interspersed among abundant





*Phaeocollybia tibiikauffmanii* in situ in 'Oz' (left, type locality) and near Ernest Creek (right)  
 LEFT: 'Oz,' Polk Co, OR — PNW-MS a2061114o2O &. RIGHT: Benton Co, OR — PNW-MS Exeter2007-16.

thin-walled, branched, 2–6  $\mu\text{m}$  wide flexuous hyphae; tissues monomitic in upper stipe and pileus with only thin-walled inflated hyphae present. Lamellar central hyphae parallel, 3–6  $\mu\text{m}$  diam, thin-walled, inflated, subgelatinized, colorless, and flanked by a narrow zone of 2–3  $\mu\text{m}$  diam colorless elements giving rise to a rudimentary subhymenium.

CLAMP CONNECTIONS — Absent in all tissues.

**Ecology** — Terrestrial (mycorrhizal); solitary to fasciculate during autumn in coniferous (*Tsuga*, *Pseudotsuga*, *Picea*) forests. — PACIFIC NORTHWEST ENDEMIC known from 14 sites (~60 collections) along the central Oregon coast and Coast Range and from one collection on Washington's Olympic peninsula.

**Similar species** — *Phaeocollybia kauffmanii* shares slender stature, large size, overall coloration, tapering stuffed stipe, and vertical-monopodial pseudorhiza; the presence of thin-walled clavate cheilocystidia (and lack of thick-walled elements), heavily gelatinized, strongly sarcodimitic tissues in the pileal trama, and larger (~8.5  $\times$  5  $\mu\text{m}$ ) basidiospores clearly differentiates it from *P. tibiikauffmanii*. In the field *P. kauffmanii* can be distinguished by its more robust aspect, strong farinaceous odor, strongly inrolled pileus edge, clustered instead of fasciculate habit, and the absence of any sort of insect infestation in older specimens.

Older collections of *Phaeocollybia spadicea* and *P. tibiikauffmanii* are easily confused. In the field, young *P. spadicea* fruitbodies can usually be distinguished by their brown to brownish drab cap colors that contrast with the orange to tawny caps that identify *P. tibiikauffmanii*. Drab to dull brownish diffuse colors and lack of encrusting pigments in the pileus subpellis help diagnose *P. spadicea* microscopically. However, recent preliminary molecular data (M. Gordon, 2009 unpub.; see p. 204, following) suggest that we may currently hold a mixed species concept that will soon need clarification.

Similar sized basidiospores and tibiiform cheilocystidia, positive syringaldazine reactivity, and a bilaminar pileipellis with a subpellis containing both diffuse and encrusting pigments that immediately turn bright orange in KOH are produced by both *P. pseudofestiva* and *P. tibiikauffmanii*. However, in the field its olive-green coloration and smaller size readily identify *P. pseudofestiva*, which is further distinguished by more prominently beaked basidiospores.

*Phaeocollybia ammiratii*, *P. piceae*, *P. sipei*, and *P. californica* also produce moderately large orange to tawny colored fruitbodies. A strong farinaceous odor, larger (9  $\times$  5.5  $\mu\text{m}$ ) basidiospores, cylindrical thin-walled cheilocystidia, and clamp connections easily diagnose *P. ammiratii*. *P. piceae*, with a stipe that also suffers from insect infestation (but only at ground level), is differentiated by its smaller size, more brilliant orange colors, bitter taste, negative syringaldazine reactivity, much larger (~9.4  $\times$  6  $\mu\text{m}$ ) basidiospores, uniformly thin-walled cheilocystidia, and diffuse KOH-soluble subpellis pigments. In the field, hollow stipes and thick



Ron Exeter

Two *P. tibiikauffmanii* collections from 'Oz' (the type locality)  
BLM Pedee old growth chronosequence transect, Polk Co, OR — PNW a2061114o2M (left) & A (right)

cartilaginous rinds readily diagnose *P. sipei* and *P. californica*; small ( $\sim 6.5 \times 3.8 \mu\text{m}$ ) ellipsoid basidiospores and uniformly thin-walled cheilocystidia further distinguish *P. sipei*, while longer ( $\sim 9 \times 5 \mu\text{m}$ ), darker, rougher basidiospores and threadlike sequential-racemose pseudorhizal cords additionally diagnose *P. californica*.

See the discussions of the above species and TABLE 11 (p. 96) for additional comparisons.

**Additional comments** — Fragmented molecular data obtained from a solitary old specimen from Washington's Olympic Peninsula first suggested an unnamed 'spadicea-like' species. Subsequent 1995 collections of solitary 'kauffmanii-like' specimens with tibiiform cheilocystidia from two Oregon coast sites led to the proposal of '*Phaeocollybia tibiikauffmanii* nom. prov.' (Norvell 1998). Numerous 1998–2008 collections of a caespitose orange 'spadicea' from our BLM density management and chronosequence transects (Norvell & Exeter 2003) eventually led to the formal description of *P. tibiikauffmanii* (Norvell, 2004). Recent (but still preliminary) DNA sequence data (M. Gordon, 2009 unpub.), however, reveal two widely separated 'tibiikauffmanii' clades — one represented by coastal collections with larger solitary specimens and basidiospores, pileipellis hyphae that are heavily gel-encrusted, and brilliant subpellis orange pigments and another by caespitose montane specimens with smaller basidiospores, rare gel encrustations, and duller orange pigments. Although we have suspicions, we cannot resolve them until all the data are in. Thus our book goes to press possibly presaging Thomas Huxley's rueful dictum, "Science — the slaying of a beautiful hypothesis by ugly fact." Stay tuned.

*References with descriptions and /or illustrations of Phaeocollybia tibiikauffmanii* —

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We dedicate this book to the memory of Alexander Hanchett Smith (1904–1986), who did the first difficult taxonomic work and left most of the fun for us.

—The Authors,  
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Lorelei Norvell &  
Ron Exeter

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## Glossary of symbols, terms, and abbreviations

The definitions below have been written by the authors, who adapted liberally from Kirk et al. (2001), Snell & Dick (1971), and other sources as needed. Eight symbols are listed first, followed by terms and abbreviations in alphabetical order.

### Symbols

~ — approximately.

= — the equality sign, which in formal nomenclators designates a taxonomic synonym of a name in current use.

≡ — the identity sign, which in formal nomenclators designates the basionym of a name in current use.

≤ — less than or equal to.

≥ — greater than or equal to.

♠ — and; the italicized ampersand as it appears in Minion Pro, the font used in this publication.

|x| — the median measurement that represents the mid-point (not average) of all measurements taken.

μm — microns, micrometers (unit of measurement); 1000 μm = 1 mm.

### Terms & abbreviations

**acute** — (*adj.*) a sharp angle (less than 90°), usually with a peak or sharp apex

**adnate** — (*adj.*) referring to gills attached broadly to the stipe apex.

**adnexed** — (*adj.*) referring to gills attached narrowly to the stipe apex.

**agaricology** — (*n.*) the study of gilled mushrooms (agarics); **agaricologist** — (*n.*) one who studies agarics.

**agglutinated** — (*adj.*) firmly attached, as if glued together; used for individual elements (such as cheilocystidia) isolated only with difficulty, particularly in rehydrated tissues.

**aggregate** — (*n.*) a crowded mass.

**albic horizon** — (*n.*) a pale (whitish) subsurface soil layer from which clays and other oxides have been leached.

**ambient** — (*adj.*) surrounding, encircling, atmospheric (as in 'ambient humidity').

**amorphous** — (*adj.*) lacking shape, having no definite form.

**amygdaliform** — (*adj.*) almond-shaped (here referring to basidiospore shape).

**amyloid** — (*adj.*) staining blue to dark violet in Melzer's reagent (containing a clearing agent) or other iodine-based solutions (e.g., IKI) that identifies the presence of starch. This reaction has little taxonomic significance in *Phaeocollybia*, although immature spores of some species do turn dark red

(‘pseudoamyloid,’ more commonly termed dextrinoid) in microscopical mounts containing Melzer's.

**anatomy** — (*n.*) the structural organization of a fruitbody; here referring primarily to elements and tissues seen under the microscope; **anatomical** (*adj.*).

**ancient forest** — (*n.*) a forest older than 200 years in age that has never been harvested; i.e., virgin.

**angiocarpous forest** — (*n.*) a ‘hardwood’ forest containing only angiosperms (see below).

**angiosperm** — (*n.*) a plant that produces both seeds and flowers; **angiospermous** (*adj.*).

**annulus** — (*n.*) a ring of veil tissue or fibrils left on the stipe after cap expansion; **annulate** — (*adj.*) possessing an annulus.

**apical beak, apical snout** — (*n.*) the smooth callus visibly projecting at a basidiospore apex (the end opposite the apiculus). See also **callus**.

**apical callus** — (*n.*) exosporium (spore outer wall) accumulating at the spore apex to form a variably rounded to pointed mound of wall tissue; when low sometimes misinterpreted as a pore unless viewed under a high oil-immersion objective. See also **callus**.

**apical outgrowth** — (*n.*) a filiform extension from the apex of a cell, here generally a thin-walled cheilocystidium; an artifact caused by continued hyphal extension of indeterminate cells in old age or during storage of a fresh fruitbody after collection; found in many phaeocollybias with thin-walled clavate cheilocystidia (e.g., *P. olivacea*, *P. redheadii*; FIGS 122G–H, 164E) but absent in others (e.g., *P. fallax*).

**apiculus** — (*n., pl. apiculi*) the short projection (peduncle) at the base of a basidiospore that attaches to a basidium sterigma prior to spore discharge.

**appressed** — (*adj.*) closely flattened down; here referring to scales and fibrils seen on the cap surface in *P. luteosquamulosa* and *P. ochraceocana* as well as remnants of the pellicular sheath on the upper stipes in most species.

**aseptate** — (*adj.*) lacking a septum, referring to long hyphae that lack cross walls or tibiiform diverticula that have no basal membrane separating them from the mother hypha.

**attached (gills)** — (*adj.*) referring to gills connected (either broadly or narrowly) to the stipe apex.

- attenuate** — (*v.*) to narrow or taper gradually from a broader point, sometimes to a thread; **attenuating** (*adj.*).
- bald** — (*adj.*) referring to a surface (usually cap) lacking scales, fibrils, or other surface decoration; here used instead of the more technically correct **glabrous**.
- basidiocarp** — (*n.*) fruitbody, basidiome.
- basidiole** — (*n.*) a basidium-like cell on a hymenium; a general basidiomycete term for paraphysis or young and/or aborted basidia.
- basidiome** — (*n., pl. basidiomata*) fruitbody in the *Basidiomycota* characterized by bearing basidia that produce sexual spores.
- basidiomycete** — (*n.*) a fungus that produces sexual spores on a basidium.
- Basidiomycota* — (*n.*) the formal phylum name for basidiomycetes in kingdom *Fungi*.
- basidiospore** — (*n.*) the sexual spore produced by a basidium (see also pp. 22, 31).
- basidium** — (*n., pl. basidia*) a sac-like terminal cell in which karyogamy followed by meiosis produces haploid nuclei that are transmitted through apical extensions (sterigmata) into spores (see also pp. 24, 32); **basidial** (*adj.*).
- basionym** — (*n.*) the earliest valid name proposed for a species; e.g., the *basionym* of *Phaeocollybia attenuata* (A.H. Sm.) Singer is *Naucoria attenuata* A.H. Sm.; similarly, the *basionym* of *P. olivacea* A.H. Sm. (which has no synonym) is *P. olivacea* A.H. Sm.
- BC — (*abbrev.*) the province British Columbia (Canada), currently the northernmost known range for *Phaeocollybia* in western North America
- beak** — (*n.*) the smooth, projecting snout formed by an accumulation of exosporium material (i.e., callus) on the basidiospore apex (the end opposite the apiculus).
- bilaminate, bi-laminate** — (*adj.*) here referring to the two-layered pileipellis composed of one top layer ('suprapellis') and one bottom layer ('subpellis'); see also p. 32.
- BLM — (*abbrev.*) Bureau of Land Management.
- boreal forest** — (*n.*) a northern forest of the higher latitudes, in Canada, northern Europe, and Asia.
- BPI — (*abbrev.*) the U.S. National Fungus Collections (Beltsville, Maryland) herbarium acronym.
- bright-field** — (*n.*) the simplest (and thus most common) microscopic illumination system in which transmitted light passes through a condenser and then a sample before reaching the objective lens, illuminating only translucent tissues and structures in the sample.
- buff** — (*adj.*) pale creamy gray to creamy yellow; occasionally with pinkish overtones (e.g., 'pale pinkish buff' in Ridgway 1912).
- CA — (*abbrev.*) the state California (USA).
- caespitose, cespitose** — (*adj.*) aggregated in tufts (like grass), sometimes arising from a central point but not grown together.
- callus** — (*n.*) the smooth rounded to pointed exospore wall accumulation concentrated at the basidiospore apex that characterizes all *Phaeocollybia* spores, often called the 'beak' or 'snout.' In this publication we reserve 'callus' for the rounded, low accumulation found in ellipsoid basidiospores (e.g., *P. oregonensis*, *P. phaeogaleroides*), using 'beak' or 'snout' for the pointed, more prominent accumulations found in limoniform spores.
- campanulate** — (*adj.*) bell-shaped, including the following variations: **broadly campanulate** is wider than tall; **conic-campanulate** has a peaked or sharply pointed disc that remains conical when fully expanded; **convex-campanulate** has an obtuse umbo and incurved/inrolled margin, remaining bluntly umbonate when fully expanded; **narrowly campanulate** is taller than wide; and **plano-campanulate** has flat disc (or very low umbo) and flat margins when fully expanded.
- canaliculate** — (*adj.*) referring to pith with a hollow channel running through the stipe from cap downwards.
- canescent** — (*adj.*) covered with a hoary down; here referring to the frosted appearance sometimes seen as a hygrophanous cap dries and the top cuticle layer separates from the bottom layer; see *P. ochraceocana*, p. 116.
- cantharelloid** — (*adj.*) chanterelle-like.
- cap** — (*n.*) the popular term (used here) for pileus; see pp. 18–19, 22, & 27–28.
- capitate** — (*adj.*) having a well-formed and rounded head.
- capitellum** — (*n., pl. capitella*) a 'little' or 'minute' head; see also **capitulum**.
- capitulate** — (*adj.*) having a small globose head.
- capitulum** — (*n., pl. capitula*) a small, rounded globose head, here used to refer to the apices of tibiiform cheilocystidia and diverticula; see also **capitellum** (often used interchangeably).
- cartilaginous** — (*adj.*) firm, tough, and pliant (readily bent); here distinguishing the tough, pliant outer stipe rind (cortex) from the softer internal stipe flesh (context).
- catenate** — (*adj.*) in chains.
- catenulate** — (*adj.*) formed in parts united or linked as in a chain.

- caulocystidium** — (*n.*, *pl.* **caulocystidia**) a cystidium found on the stipe; differentiated from a diverticulum by possessing a basal septum that separates it from the mother hypha.
- cavitation** — (*n.*) the process during which cavities are formed, either a gill cavity between stipe and cap within a primordium or a hollow developing in a young or mature stipe.
- cheilocystidium** — (*n.*, *pl.* **cheilocystidia**) a sterile cell (cystidium) found on the gill edge; see pp. 19–20, 22–24, 30.
- chronosequence** — (*n.*) time sequence; here referring to our comparison of fungal communities in early-, mature-, and old-growth forests.
- clamp, clamp connection** — (*n.*) in basidiomycetes, the small, semicircular, hollow outgrowth connecting two adjoining cells and arching over the septum to permit reestablishment of a binucleate state in the older cell; see also pp. 22, 30–31.
- clavate** — (*adj.*) club-like, with narrow base and obtusely rounded apex; here the typical shape exhibited by basidia and thin-walled cheilocystidia.
- clear cut** — (*n.*) now called regeneration cut; a timber-harvesting method in which all trees are cut and removed from an area prior to reforestation.
- climax species** — (*n.*) species that exist in equilibrium within a climax community, the final and most stable of a series of communities in a succession, remaining relatively unchanged as long as environmental conditions remain constant. Within the PNW rainforests, ectomycorrhizal climax species include true fir (*Abies amabilis*, *A. procera*), Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). Coast redwood (*Sequoia sempervirens*) and western red cedar (*Thuja plicata*) are climax species that do not form ectomycorrhizae. Western hemlock, which occupies the majority of the PNW rainforests, is usually regarded as the dominant climax species.
- clustered** — (*adj.*) grouped together closely.
- cm** — (*abbrev.*) centimeter (unit of measurement: 100 cm = 1 m).
- Co., Co.** — (*abbrev.*) county (used in figure captions only).
- collapsed ixotrichodermium** — (*n.*) a term referring to the loose aggregation of hyphae floating within a gelatinous matrix within an **ixotrichodermium** (defined below).
- collybioid** — (*adj.*) collybia-like, characterized by a slightly fleshy cap with an initially inrolled edge, attached gills, and stipe with a cartilaginous cuticle.
- concentric** — (*adj.*) having rings or zones within one another in a series; **concentrically** (*adv.*).
- concolorous** — (*adj.*) having the same hue (color) as something else, although the color intensity (brightness, dullness) may vary; here generally referring to the gills or stipe having the same color as the cap.
- confluent** — (*adj.*) continuous and lacking change; here referring to pileus and stipe context that have the same color and consistency.
- conic, conical** — (*adj.*) cone-shaped; referring to caps that narrow to a more or less pointed disc.
- conifer** — (*n.*) a gymnosperm within the order *Coniferales* that produces naked seeds in ‘cones,’ e.g., true fir (*Abies*), hemlock (*Thuja*), Douglas-fir (*Pseudotsuga*), spruce (*Picea*), pine (*Pinus*), and coast redwood (*Sequoia*).
- context** — (*n.*) the inner cap, stipe, and pseudorhiza tissue (flesh) covered by a surface layer (or cuticle); microscopically referred to as the **trama**.
- continuum** — (*n.*) an unbroken series in which change proceeds in imperceptible increments.
- convex** — (*adj.*) regularly rounded or broadly obtuse; **convex-campanulate** — (*adj.*) bell-shaped with obtuse umbo and incurved/inrolled margin, remaining bluntly umbonate when fully expanded.
- corneous** — (*adj.*) having a horn-like texture; smooth and tough.
- cortex** — (*n.*) rind; the densely interlaced and more or less sclerotized outer layer of a fruitbody, the hyphal elements of which are usually more or less modified; microscopically referred to as a **pellis**.
- cortical** — (*adj.*) belonging to the surface cortex or rind.
- criniform** — (*adj.*) hair-like, thin and brittle; here referring to the thin hair-like pseudorhizas found in *P. attenuata* and *P. phaeogaleroides*; see pp. 16–17, FIG 2.2B.
- Crk** — (*abbrev.*) Creek (used only in figure captions).
- cryptic** — (*adj.*) hidden, secret, unknown or concealed.
- cryptospecies** — (*n.*) undescribed species resembling and thus ‘hidden’ within a previously described species and so often filed in herbaria under a misleading name. *Phaeocollybia ammiratii*, *P. benzokauffmanii*, *P. luteosquamulosa*, *P. ochraceocana*, and *P. redheadii* are previous cryptospecies long referred to *P. kauffmanii*.
- cuticle** — (*n.*) cortex, the differentiated surface tissue (on cap and stipe) comprising the outermost hyphal layer; analogous (but not homologous) to the same term used for plants.
- cutis** — (*n.*) a layer covering the cap formed by compressed hyphae running periclinally (parallel to the surface), thus giving a smooth or bald appearance macroscopically.
- cylindrical** — (*adj.*) having the same diameter throughout a length (used for both stipe and cystidia).

- cystidium** — (*n., pl. cystidia*) a large colorless or pale sterile cell; in *Phaeocollybia* frequently gel-secreting and located on the gill hymenium among the basidia and often projecting beyond them; **cystidial** (*adj.*). See also **caulocystidium**, **cheilocystidium**, **pleurocystidium**.
- DAOM** — (*abbrev.*) the National Mycological Herbarium of Canada maintained by Agriculture & Agri-food Canada (Ottawa).
- dark field microscopy**— (*n.*) an illumination technique used to enhance contrast of a specimen in which light entering a microscope is blocked in the center, leaving an outer ring of light that is focused toward the sample by a condenser lens; the light scattered from the sample enters the objective lens. (See p. 164D).
- deciduous** — (*adj.*) (trees or shrubs) vascular plants (angiosperms) that shed their leaves seasonally; e.g., alder (*Alnus*), maple (*Acer*), oak (*Quercus*).
- dextrinoid** — (*adj.*) sometimes referred to as pseudoamyloid (e.g., Singer 1949, 1986); here referring to basidiospores becoming dark red in Melzer's reagent; **non-dextrinoid** (*adj.*) indicates a negative reaction.
- diam** — (*abbrev.*) diameter
- DIC optics** — (*abbrev.*) differential interference contrast microscopy (also known as Nomarski microscopy) uses a polarizer to separate a light source into two beams that follow slightly different paths through a sample to produce an image with the object appearing black to white on a gray background; similar to phase contrast but lacking the bright diffraction halo. This illumination technique enhances contrast in unstained, transparent samples, thus yielding an almost 3-dimensional image and particularly helpful when studying highly gelatinized, transparent tissues, such as those found in *Phaeocollybia*. (The senior author refers to her Leica DMRB microscope as 'the Lab Goddess,' while the junior author refers to it as the 'Mothership.')
- dingy** —(*adj.*) dull, not brightly colored, slightly dirty looking.
- disc** — (*n.*) the central portion of a cap (pileus).
- diverticulum** — (*n., pl. diverticula*) a pocket-like side branch.
- diverticulate** —(*adj.*) possessing diverticula.
- diverticulate mycelium** — (*n., pl. — mycelia*) a mycelium composed of individual hyphae that are diverticulate; mycelial hyphae possessing tibiiform diverticula are considered a generic constant and diagnostic of *Phaeocollybia*.
- DNA** — (*abbrev.*) deoxyribonucleic acid, composed of phosphoric acid, sugar, and nitrogenous bases; occurring primarily on chromosomes in nuclei of living cells.
- downcurved, down-turned** — (*adj.*) referring here to the orientation of the outer cap margin or edge.
- drab** —(*adj.*) a dull brownish color, often with dull purple or pinkish-brown tones.
- duff** — (*n.*) partly decayed organic material (needles, leaves, twigs, etc.) forming the top soil layer on the forest floor.
- eccentric** — (*adj.*) off-centered; here referring either to the position of a stipe in relation to a cap or to the basidiospore apiculus and/or beak offset from the longitudinal spore axis.
- ectomycorrhiza** — (*n., pl. ectomycorrhizae* or *-s*) a symbiotic association in which a fungus colonizes the roots of a host plant forming a hyphal sheath ('mantle') covering a root tip and a Hartig net of hyphae surrounding the plant cells within the root cortex. The mycelial network within the soil and leaf litter transports moisture to the host plant and extends the root system. See also p. 21 & FIG-p. 166; **ectomycorrhizal** (*adj.*).
- element** — (*n.*) an individual hyphal cell.
- elev.** — (*abbrev.*) elevation.
- ellipsoid, ellipsoidal** — (*adj.*) ellipse-shaped, as in some basidiospores; see also p. 31.
- emanate** — (*v.*) to emerge or rise out of.
- emergent** —(*adj.*) rising out of or emerging from.
- encrusting** — (*adj.*) forming a crust-like coating; here referring to gel or pigments deposited on outside cell wall surfaces; see also p. 32.
- endemic** — (*adj.*) native to a given region.
- endemism** — (*n.*) the condition of being confined to a certain region or locality.
- ephemeral** — (*adj.*) transient, lasting only a short time.
- epigeous** — (*adj.*) above-ground; here referring to the portion of a phaeocollybia fruitbody not buried in the soil.
- ericaceous** — (*adj.*) pertaining to plants in the heath family (*Ericaceae*), such as huckleberry, rhododendron, madrone.
- eroded** — (*adj.*) eaten away; here referring to gill edges that appear gnawed.
- erumpent** — (*adj.*) breaking through, emerging abruptly.
- etymology** — (*n.*) the origin of a word and the historical development of its meaning.
- evanescent** — (*adj.*) transitory, fleeting; lasting only a short time.
- excavation** — (*n.*) the action of removing a phaeocollybia (carefully) by digging or brushing away the soil and rocks to expose (and extract) the buried pseudorhizal origin; see also p. 166 for an excavation sequence.
- exosporium** — (*n. pl., exosporia*) also exospore, outer spore wall; the surface layer that covers the 'epispore'

- (inside spore wall) after dissipation of the perispore (peripheral envelope).
- Exp** — (*abbrev.*) Experimental (as in Cascade Head Experimental Forest).
- extant** — (*adj.*) still in existence; surviving.
- extralimital** — (*adj.*) occurring outside a given area of study; here referring to areas outside the Pacific Northwest region (Alaska, British Columbia, Washington, Idaho, Oregon, California) of North America.
- exudate** — (*n.*) an exuded substance, such as a gel secretion.
- F** — (*abbrev.*) Forest; used only in figure captions, as in CHEF (Cascade Head Experimental Forest), ONF (Olympic National Forest).
- F** — (*abbrev.*) Field Museum of Natural History (Chicago) herbarium acronym.
- false clamp** — (*n.*) pseudoclamp; a clamp-like hyphal branch that appears to join two cells but does not form a by-pass channel to reestablish the dikaryotic nuclear status in the mother cell; such false clamps usually are not connected at both ends; see also p. 31.
- farinaceous** — (*adj.*) referring to the odor of freshly ground meal (either wheat or corn); see also p. 28.
- fascicle** — (*n.*) a little group or bundle.
- fasciculate** — (*adj.*) crowded together or growing in close bundles.
- fasciculate starburst** — (*n.*) the term originally used to refer to the umbellate attachment of a fascicle of scores of fruitbodies in different developmental stages attached to a single point on a subtending rhizomorphic pseudorhizal cord; see also pp. 17, 28, 185.
- FEMAT** — (*abbrev.*) Forest Ecosystem Management Assessment Team, the scientists and agency officials who evaluated all organisms as potential species of concern during the preliminary stages of the Northwest Forest Plan (NWFP).
- ferruginous, ferrugineous** — (*adj.*) rust-colored.
- fertile gill edge** — (*n.*) a gill edge bearing spore-producing basidia.
- fibril** — (*n.*) a narrow, hair-like fiber; **fibrillose** — (*adj.*) having fine hairs or fibers.
- filament** — (*n.*) a thread; here referring to a hypha or other simple, thread-like element.
- filamentous** — (*adj.*) thread-like, generally long, narrow; may be hollow or solid.
- filiform** — (*adj.*) thread-like.
- fistulose** — (*adj.*) tubular; hollow.
- flaccid** — (*adj.*) flabby, limp; soft and limber; lacking firmness or elasticity.
- flanked (by)** — (*adv.*) in the middle between two similar entities; here often referring to the central gill trama *flanked by* subhymenium hyphae.
- fleeting** — (*adj.*) brief, transitory; here used to refer to the instability of certain pigments in KOH; also used to refer to an odor that may be strong at first, but then rapidly disappears.
- flexuous** — (*adj.*) easily pliable, elastic.
- flexuous hyphae** — (*n., pl.*) narrow, branched, thin-walled hyphae that make up part of the dual-hyphal system found in *Phaeocollybia*, with vessel hyphae representing the other hyphal form; see also **sarcodimitism, vessel hypha**, p. 20.
- fluoresce** — (*v.*) to shine or glow brightly due to fluorescence.
- fluorescence** — (*n.*) the visible or invisible radiation emitted by certain substances as a result of incident radiation of a shorter wavelength (found in X-rays or under ultraviolet light). See also p. 28.
- flush** — (*n.*) a wash of color, often subdued; in *P. ammiratii* referring to the burgundy-colored wash extending from mid-stipe to below ground level.
- For** — (*abbrev.*) Forest (used only in figure captions).
- free** — (*adj.*) gills that do not touch the stipe; **nearly free** refers to gills that do touch the stipe, but only by the very tip of the gill.
- fruitbody** — (*n.*) the spore-producing portion of a fungus (mushroom, toadstool).
- FS** — (*abbrev.*) Forest Service.
- fungivory** — (*n.*) eating of fungi; **fungivore** — (*n.*) an organism that uses fungi for food.
- furrow** — (*n.*) little rut, wrinkle, line – used to refer to slightly roughened lines on an unpolished (**matte**) stipe.
- fusiform** — (*adj.*) tapering at both ends; spindle-shaped.
- fusoid** — (*adj.*) swollen in the middle and tapering more or less evenly toward each end; **fusoid-elliptical** — (*adj.*) a basidiospore that is swollen in the middle and tapers more or less evenly to a straight apiculus and apical beak or callus.
- galerina-like, galerinoid** — (*adj.*) resembling a *Galerina* fruit-body, i.e. small, relatively fragile, yellow-brown.
- gebrenzlich** — (*adj.*) a German expression used to evoke the odor of burned hair; see p. 28.
- gelatinous** — (*adj.*) jelly-like, slimy; applied to tissues where the hyphae partly dissolve or become glutinous (slimy) in wet weather or with moisture; when mounted in water under the microscope, hyphae

- appear more transparent and generally align more loosely than in non-gelatinous tissues (see also p. 32); **gelatinized** — coated with gelatin.
- gelification** — (*n.*) the process of becoming jellified or gelatinous; changing from a more or less solid state to a gel state.
- genitive** — (*adj.*) of or pertaining to the grammatical case (in Latin) that expresses possession or source; in English, the genitive case is generally translated as 's or "of" (e.g., the *gill's* color; the color *of the gills*).
- gill** — (*n.*) the popular term (used here) for the more technically correct **lamella**, the vertical radial plate (or blade) on the underside of the cap bearing the hymenium where spores are produced; see also pp. 19, 22, 23.
- glabrous** — (*adj.*) smooth, lacking ornamentation (usually referring to the cap).
- gluten** — (*n.*) as used here, the clear slime or sticky substance occurring on cap and stipe surfaces, particularly noticeable in wet or rainy weather.
- glutinous** — (*adj.*) slimy, covered with gluten; sticky or glue-like in texture.
- grading** — (*adv.*) gradually becoming, gradually changing; referring to the gradual changing of one color to another across cap or down stipe.
- granular (granulate)** — (*adj.*) resembling or consisting of small grains or particles.
- gregarious** — (*adj.*) in companies or groups but not joined together; scattered loosely or closely within a small area.
- gymnosperm** — (*n.*) a plant, such as a conifer, that produces seeds but no flowers ('naked' seeds); **gymnospermous** (*adj.*).
- H<sub>2</sub>O** — (*abbrev.*) the chemical formula for water.
- habit** — (*n.*) the general, external, and characteristic appearance or manner of growth of a fungus.
- Hartig net** — (*n.*) a complex network of fungal hyphae that is the site of nutrient exchange between fungus and host on the surface of an ectomycorrhizal plant rootlet; see also **ectomycorrhiza**.
- head** — (*n.*) here referring to the rounded apex or top of a hyphal element, usually a cystidium or diverticulum; the opposite of 'base.'
- herbaceous** — (*adj.*) relating to flowering plants that perish down to the roots at the end of the growing season; the opposite of 'woody.'
- heterogeneous** — (*adj.*) of unlike structure or tissues.
- holotype** — (*n.*) the single collection of specimens or other element used or designated by an author as the item to which the name of a taxon is permanently attached.
- homologous** — (*adj.*) corresponding in type, structure and origin but not necessarily in function; thought to reflect evolutionary relatedness.
- HSC** — (*abbrev.*) the Humboldt State University (Arcata, CA) herbarium acronym.
- humic (soils)** — (*adj.*) soils that have a high organic component (opposed to 'clay')
- hyaline** — (*adj.*) colorless (used here); usually referring to tissues or elements as seen under the microscope.
- hygrophanous** — (*adj.*) watery in appearance, with moisture disappearing rapidly and color fading or otherwise changing markedly when dried. See FIG-p. 135
- hymenium** — (*n.*) the spore-producing layer; in agarics, the cell layer covering the gills and containing the fertile basidia.
- hypha** — (*n., pl.* hyphae) a single filament or microscopic thread that comprises the mycelium or fruitbody of a fungus.
- hyphidia** — (*n., sing.* hyphidium) slightly to strongly modified terminal hyphae interspersed throughout a hymenium; phaeocollybian hyphidia are simple and filiform.
- ID** — (*abbrev.*) the state of Idaho (USA).
- in situ** — (*n.*) Latin for 'in its original place,' used here to specify photographed specimens that either have not yet been excavated or that are shown above the substrate after excavation.
- inamyloid** — (*adj.*) inert in Melzer's reagent (e.g., the element does not turn blue, black, violet, or red).
- incrusting** — (*adj.*) here referring to gel or pigments deposited on or coating internal cell wall surfaces inside a hyphal element, often in patches.
- incurved** — (*adj.*) curved inward (usually referring to the outer cap margin).
- indeterminate** — (*adj.*) displaying indefinite growth, here referring to the origin of the thin-walled 'cheilocystidia' from the central gill trama (rather than from the hymenium) that continue to extend apically for the life of the fruitbody, thus making length measurements taxonomically uninformative. Opposed to **determinate** growth exhibited by the tibiiform cystidia (and possibly also hyphidia) originating from the subhymenium where length measurements fall within a certain definite range.
- inequilaterally** — (*adv.*) off-centered, usually used in describing basidiospore shape to modify 'ellipsoidal' or 'amygdaliform' and so indicate that the apiculus and apical callus do not both fall on the spore's long axis.
- inrolled** — (*adj.*) rolled (tightly) inward, similar to a young fern frond; usually referring to the outermost



cap edge, particularly in fleshy capped species such as *P. kauffmanii* and *P. redheadii*.

**intercellular** — (*adj.*) occurring between cells, such as diffuse pigments occurring within the matrix outside cell walls.

**intracellular** — (*adj.*) occurring within a cell, such as intracellular contents confined within a cystidium, basidium, or hyphal cell.

**intraparietal** — (*adj.*) within a wall or walls; usually referring to pigments trapped between hyphal walls that are most easily seen within the septa.

**isolate** — (*n.*) used here to refer to the DNA isolated from a specimen for use in molecular analysis.

**isotype** — (*n.*) the portion of the original collection containing the holotype but separated from it, usually held in a different herbarium. A type collection may have several isotypes, and distribution of type specimens among many herbaria is encouraged to help ensure the continued existence of valuable reference material.

**ITS (region)** — (*abbrev.*) Internally Transcribed Spacer; a non-coding region of DNA flanked by the 5.8s and 18s ribosomal genes successfully used by mycologists to explore phylogenetic relationships among fungi. See also RFLP, restriction digest.

**ixocutis** — (*n.*) the slimy cap cuticle formed by hyphae with interlaced ends lying parallel to the cap surface that later gelify into a gelatinous matrix that makes the surface viscid, viscous, or glutinous.

**ixotrichodermium** — (*n., pl. ixotrichodermia*) the slimy cap cuticle formed by more or less erect, somewhat wavy, and more or less interlaced hyphal ends of some length that later gelify to such an extent that the surface becomes viscid, viscous, or glutinous.

**kinky** — (*adj.*) tightly crimped, curly, not straight and even.

**KOH** — (*abbrev.*) chemical formula for potassium hydroxide; here used as a 3–6% aqueous solution mounting medium for microscopical examinations.

**lageniform cheilocystidia** — (*n.*) cystidia along the gill edge that are flask-shaped, having broad bases and narrow necks and pointed or narrow apices (non-capitulate).

**lamella** — (*n., pl. lamellae*) the technically correct term for gill, the vertical radial plate (or blade) on the underside of the cap that bears the fertile hymenium.

**lamellar** — (*adj.*) belonging to the lamella or gill; **lamellar trama** — (*n.*) the internal hyphal system that makes up the central portion of the gills; the tissues between the hymenium layers; **lamellar initial** — (*n.*) a young or not-yet fully formed lamella (gill).

**lamellula** — (*n., pl. lamellulae*) a short gill that does not reach the stipe; common to most phaeocollybias.

**lateral-monopodial** — (*adj.*) unbranched with a basal lateral bend; used here to categorize the thread-like unbranched brittle (criniform) pseudorhiza in *P. attenuata* that turns laterally below the corneous stipe somewhere in the duff or top soil layer and runs horizontally just below the duff layer away from the stipe base. Due to its extremely thin diameter, the ultimate origin has never been found, despite numerous attempts to trace the origin under the dissecting microscope. See also pp. 16–17.

**lectotypify** — (*v.*) to typify a species by selecting an element or collection described in a work later than the original work that does not select or directly specify a holotype; **lectotypification** (*n.*).

**length mutation** — (*n.*) insertion or deletion of DNA within a DNA region; an insertion-deletion ('indel') may result from a one-time mutation, so that RFLP analyses may imply a greater difference between original and mutated sequences than really exists, making DNA sequence analysis more reliable in determining relationships among species.

**limoniform** — (*adj.*) lemon-shaped, citriform; used here exclusively for basidiospores with pointed apical beaks as seen in profile view; **limoniform-fusoid** — (*adj.*) lemon-shaped with and narrowing to points at both ends. See also p. 31.

**loamy** — (*adj.*) referring to rich soils with well-decomposed organic matter.

**longitudinally lined** — (*adj.*) here referring to the faint surface grooves that run from the cap downwards seen on unpolished stipes.

**lubricous** — (*adj.*) smooth and slippery, slightly greasy; similar to but slightly drier and less slippery than **subviscid**.

**m** — (*abbrev.*) meter (standard unit of measurement).

**mammiform** — (*adj.*) conical with a rounded apex.

**mantle** — (*n.*) a compact layer of hyphae enclosing short feeder rootlets of ectomycorrhizal plants connected to the Hartig net on the inside and to the mycelial hyphae on the outside; said to act as a nutrient sink. See also **ectomycorrhiza**.

**marbled** — (*adj.*) stained with irregular streaks of color; in spores also referring to the varying thicknesses of the outer spore wall (exosporium) that causes the color streaks.

**matrix** — (*n.*) the mucilaginous (gelatinous) material comprising the extracellular environment surrounding hyphae within tissues, as in **dense gelatinous matrix** within the suprapellis of a two-layered **pileipellis**.

**matte** — (*adj.*) dull, slightly roughened, unpolished; used to describe fresh stipe or dried cap surfaces and contrasting with polished or shiny (stipe) and metallic (dried cap).

**mature forest** — (*n.*) here referring to forests between (60)80–120 years old.

**medallion clamp** — (*n.*) a clamp connection with a space between the primary hypha and the channel or ‘hook’.

**mediopellis** — (*n.*) in a three-layered (trilaminar) pileipellis, the middle layer.

**Melzer’s** — (*n.*) a reagent (mixture) developed to reveal spore ornamentation in *Russula* spores caused by the presence of starch in the spore wall; formulated by dissolving 1.5 g potassium iodide (KI) and 0.5 g iodine (I) in 20 mL water (H<sub>2</sub>O) and 20 mL chloral hydrate (within the US a controlled substance). Purplish colors indicate a positive (amyloid) reaction; partially positive (dextrinoid) reactions are indicated by dark red to reddish brown. Rarely taxonomically informative in *Phaeocollybia*.

**meristematic** — (*adj.*) in plants, the tissue found primarily at the growing tips of roots and shoots and in the cambium that consists of cells actively dividing to form new tissue. In fungi, the term ‘meristemoid’ is preferred to indicate the region where new growth occurs.

**mesic** — (*adj.*) moist; in ecology referring to regions with high humidity or rainfall; usually used in conjunction with **rain forest**.

**metallic** — (*adj.*) used here to refer to the slightly reflective, foil-like sheen found in some dried *phaeocollybia* cap surfaces (e.g., *P. ammiratii*, *P. californica*); opposed to ‘matte’, a cap cuticle that is dull and non-reflective.

**metamorphic** — (*adj.*) in geology, referring to rock that was formed (and thus transformed) by heat, pressure, or folding of geological layers or intrusion of adjacent igneous (heat formed) rock.

**MICH** — (*abbrev.*) the University of Michigan (Ann Arbor) herbarium.

**microtome** — (*n.*) an instrument for cutting extremely thin sections of tissue prior to microscopical examination.

**misapplied** — (*adj.*) an identification in which the name of one species is wrongly applied to another, most frequently caused by a confused species concept.

**mixed forest** — (*n.*) containing conifers (gymnosperms) and angiosperms; sometimes referred to as mixed coniferous & deciduous, however, the presence of live oaks, rhododendrons, and madrones (none of which lose their leaves seasonally) makes ‘deciduous’ less precise in the PNW region.

**mm** — (*abbrev.*) millimeter (a term of measurement); 1,000 millimeters = 1 meter.

**moist** — (*adj.*) here referring to a cap’s innate moisture in the *Phaeocollybia* moisture gradient: dry, moist, lubricous, subviscid, viscid, glutinous. The fact that cap moisture noted in the field depends greatly upon ambient humidity at the time of collection makes it a less reliable field character and thus less taxonomically informative; however, moisture can be determined microscopically by the degree of gelatinization in the pileipellis.

**monomitic** — (*adj.*) possessing a single hyphal system (usually uniformly thin-walled).

**monopodial pseudorhiza** — (*n.*) an unbranched pseudorhiza.

**monovelangiocarpy** — (*n.*) development of a fruitbody within a single veil or sheath.

**montane** — (*adj.*) higher elevational, occurring in the mountains; in contrast to ‘low-land’ or ‘alpine.’

**mor** — (*n.*) acidic humus-rich soil characteristic of coniferous forests, particularly in cold regions or at high latitudes.

**mor-mull** — (*n.*) sometimes called *moder* (European), a raw humus condition in soils containing few microorganisms to decompose the surface organic matter that lies on the soil surface.

**morphology** — (*n.*) the biological study of form and structure; ‘shape science.’

**mother rhizomorph** — (*n.*) a regenerating rhizomorph (usually cord-like) giving rise to primordia.

**mountain cloud forest** — (*n.*) also called a montane rainforest or ‘fog’ forest; an evergreen montane moist forest occurring in the tropics or subtropics.

**mountant** — (*n.*) a fluid mounting medium used for microscopic examinations that may contain stains, clearing agents; usually stored in dark reagent bottles to protect from light exposure. The most common mountants used for *phaeocollybias* are distilled water (to which one to two drops of dish detergent or contact lens solution are added as a wetting agent), 3–6% aqueous KOH solution (to which sometimes phloxine or Congo red is added to reveal cell contents or walls), and Melzer’s reagent. Water is the preferred mountant for viewing fresh tissues; all key measurements were made from rehydrated tissues mounted in 3–6% KOH.

**Mt, Mtn** — (*abbrev.*) mountain (used only in figure captions).

**mucronate** — (*adj.*) ending in a sharp point; pointed.

**mull** — (*n.*) a non-acidic humus that eventually integrates into the underlying soil layer; characteristic of

hardwood forests, deciduous forests, or grasslands in warm, humid climates.

- mutation**— (*n.*) alteration of a gene structure that may be transmitted to subsequent generations; caused by single DNA base substitutions or by the deletion, insertion, or rearrangement of longer chromosomal DNA sequences. See also **length mutation**.
- mycelium** — (*n., pl. mycelia*) an aggregation of hyphae (fungus filaments) within a substrate that constitutes the vegetative (asexual) state or thallus of a fungus.
- mycenoid** — (*adj.*) resembling a *Mycena* (small, fragile, white-spored agaric); having a straight young cap margin and cartilaginous, tubular stipe.
- mycology** — (*n.*) the formal study of fungi; **mycologist** — (*n.*) a scientist who studies fungi.
- mycorrhiza** — (*n., pl. mycorrhizae*) a mutually beneficial symbiotic association between plant roots and fungi. See also **ectomycorrhiza**.
- mycotroph** — (*n.*) a organism (including another fungus) that obtains nutrients from a fungus; sometimes also mycoparasitic.
- mycotrophy** — (*n.*) plant nutrition with the aid of mycorrhizae.
- naviculate** — (*adj.*) boat-like in form, with one end tapered and the other blunt or squared off or keeled, like the stern of a boat; inequilaterally fusiform.
- neotypify** — (*v.*) to select a specimen to replace a holotype after the original type material has been lost or destroyed; **neotypification** (*n.*).
- nippled** — (*adj.*) here referring to a pseudorhizal base displaying a short, rounded, abruptly raised portion at the ultimate origin.
- Nomarski optics** — (*n.*) another name for differential interference contrast microscopy; see **DIC optics**.
- nurse pseudorhiza** — (*n.*) based on *nurse log*, also ‘mother’ pseudorhiza; a regenerating pseudorhiza that gives rise to a primordium near its origin.
- NWFP** — (*abbrev.*) Northwest Forest Plan (1998–2008); the ten-year joint USDA & USDI planning document for government forest lands within the range of the Northern Spotted Owl. A portion of this plan administered the inventory (‘survey & manage’) of species of concern in California, Oregon, and Washington.
- NY** — (*abbrev.*) the New York Botanic Garden (Bronx) herbarium acronym.
- O** — (*abbrev.*) the Oslo (Norway) herbarium acronym.
- obscure** — (*adj.*) used here to refer to a barely perceptible feature, such as a small, rounded callus ‘beak’ on an ellipsoidal basidiospore.

**obtuse** — (*adj.*) rounded, blunt.

**ochre** — (*n.*) a reddish yellow color; **ochraceous** (*adj.*).

**oil immersion lens** — (*n.*) an objective used for high magnifications requiring high resolution. The special lens is placed directly into oil on top of the cover slip; the similar refractive indices of oil, glass slide, and cover slip permit light to pass from source through objective, thus increasing the resolution. Best resolution is achieved with oil placed also between condenser lens and slide bottom. All measurements here were taken using oil immersion placed only on the cover slip using a 100× oil objective.

**old growth** — (*n.*) any forest (even technically second growth) older than 120 years old. We distinguish between ancient (or virgin) and old growth forests, reserving the term ‘ancient’ for stands older than 200 years in age.

**oleifer** — (*n.*) a hypha containing oily, resinous (sometimes refractive) contents.

**oleiferous** — (*adj.*) oily, resinous; producing oil, hence secretory in nature.

**ONHC** — (*abbrev.*) Oregon Natural Heritage Center.

**ontogeny** — (*n.*) development of a fruitbody from primordium to mature individual; once erroneously believed to represent the evolutionary pathway, as written by Ernst Haeckel (1866), “Ontogeny recapitulates phylogeny.”

**opaque** — (*adj.*) the opposite of transparent; dull and unable to be seen through; **opaqueness** — (*n.*) the degree to which a surface is opaque.

**OR** — (*abbrev.*) the state of Oregon (USA).

**origin** — (*n.*) the beginning, start; **pseudorhizal origin** — (*n.*) the base of the buried pseudorhiza from which the fruitbody develops upward or outward, depending on the pseudorhizal type.

**ornamented** — (*adj.*) opposite of smooth; relating to markings, lines, wrinkles, striations, ridges, warts, scales, etc. on surfaces; here primarily referring to basidiospore surface decorations.

**ORNHC** — (*abbrev.*) Oregon Natural Heritage Information Center (2004–present).

**OSC** — (*abbrev.*) the Oregon State University (Corvallis) herbarium acronym.

**Oz** — (*n.*) derived from ‘O2’, designating one old-growth transect in our five-year chronosequence study where eleven *Phaeocollybia* species were tallied within a 400 m<sup>2</sup> area. The authors’ favorite phaeocollybian collecting site, they regard Oz (with Oregon’s Larch Mountain and Mary’s Peak) as a phaeocollybian Garden of Eden.

- pallid** — (*adj.*) usually unspecified, but representing a pale, whitish, or pale color.
- papilla** — (*n., pl. papillae*) a small rounded to pointed projection, usually on the central disc of a mushroom cap; **papillate** — (*adj.*) possessing a papilla.
- paraphysis** — (*n., pl. paraphyses*) an upward growing, basally attached, sterile hyphal element in the hymenium; see **hyphidium**.
- parasitic** — (*adj.*) living in or on another organism to obtain nourishment, usually at the host organism's expense.
- paratype** — (*n.*) any fungal collection cited in and used to prepare the original description of a new species, other than the type collection.
- parietal** — (*adj.*) contained between walls, here especially pigments between the inner and outer cell walls of a hypha.
- pedicel** — (*n.*) the long, slender, usually cylindrical, base found in some cheilocystidia, basidia, or other cells; **pedicellate** — (*adj.*) possessing a pedicel.
- pellicle** — (*n.*) a detachable, skin-like cap cuticle.
- pellicular** — (*adj.*) possessing a pellicle, a viscid 'cuticle' that peels easily; filmy, cuticular, skin-like.
- pellicular (primordial) sheath** — (*n.*) the outside tissue that envelops or encases a primordium.
- pellicular (primordial) veil** — (*n.*) derived from the pellicular sheath, used here to refer to remnants left on cap, stipe, or pseudorhiza after the sheath thins and ruptures during the elongation phase.
- pellis** — (*n., pl. pelli*) the cortical layer of the fruitbody that does not belong to the primordial sheath.
- penultimate element** — (*n.*) the next to last hyphal element in a series; e.g., a hyphal element subtending a cheilocystidium, basidium, and hyphidium or the element below the apical cell in a multiply septate (catenulate) thin-walled, clavate cheilocystidium.
- phase (contrast) optics** — (*n.*) an optical system using special condensers and lenses adjusted to use differences in the phase of light transmitted (or reflected) by an object to form distinct, contrasting images. Phase optics, which are particularly useful for finding clamps in highly gelatinous, low-contrast tissues, can cause distortions that may interfere with taking accurate measurements.
- phenetic analysis** — (*n.*) analysis using numerical taxonomy (taximetrics) to classify items based on overall similarity, regardless of evolutionary relationships. Phenetics includes clustering and ordination techniques to determine 'like' individuals.
- phenology** — (*n.*) the study of weather- or seasonal fruiting patterns — e.g., vernal (spring) or autumnal (fall) — exhibited by species. Note: Because the range of 'phaeocollybian' latitudes extends from northern British Columbia to Santa Cruz County in California, we have avoided using such modifiers as 'early,' 'mid-', or 'late', although many species (e.g., *P. luteosquamulosa*) typically fruit earlier than others (e.g., *P. oregonensis*) within a given region.
- phylogeny** — (*n.*) the evolutionary relationships among taxa, usually emphasizing descent from a common ancestor.
- pileipellis** — (*n., pl. pileipelli*) referring to the cap (pileus) cuticle as seen under the microscope. Usually divided into different layers, such as the epicutis (top layer) and hypodermium (bottom layer). In *Phaeocollybia* we use terms that reflect location ('suprapellis,' 'mediopellis,' 'subpellis') rather than homology. See also pp. 22 & 31–32.
- pileus** — (*n., pl. pilei*) the technical (and more proper) term for a fungus (mushroom) cap. 'Cap' and 'pileus' are interchangeable in meaning; both terms are used as such here. We use 'cap' more often because all readers (regardless of training) immediately understand its meaning.
- pique** — (*v.*) to stimulate, as in interest.
- pith** — (*n.*) the soft tissue in the stipe interior; stipe context or flesh; often present in immature fruitbodies but in many species fibrillose and not proliferating during stipe elongation and/or expansion, so that mature or old stipes appear virtually hollow.
- Pk** — (*abbrev.*) Peak (used in figure captions only).
- plage** — (*n.*) the smoothed area just above the apiculus on the 'belly' of a basidiospore formed by the pressing together of two spores during spore development.
- plano-umbonate** — (*adj.*) similar to broadly campanulate, referring to a cap with a broad flat margin and edge and obtuse central umbo.
- plasmatic** — (*adj.*) referring to the extracellular matrix surrounding the hyphae.
- pleurocystidium** — (*n., pl. pleurocystidia*) a hymenial cystidium (sterile cell) that is distributed over the entire gill face; usually (but not always) similar to the cheilocystidia confined to the gill edge (see also pp. 24 & 32–33); **pleurocystidiate** — (*adj.*) possessing pleurocystidia.
- pliable** — (*adj.*) movable, bending readily without breaking, elastic.
- pliable pseudorhiza** — (*n.*) a fleshy or cordlike pseudorhiza that bends easily; the opposite of a brittle & wire-like ('criniform') pseudorhiza.
- pliant** — (*adj.*) see pliable; here referring to flesh that bends and turns without shattering.

- PNW** — (*abbrev.*) Pacific Northwest; here used broadly to incorporate the northwestern North American Pacific Coast rain forest regions including Alaska, British Columbia, Washington, Idaho, Oregon, and California. (No *phaeocollybias* have yet been collected from Alaska.)
- PNW-MS** — (*abbrev.*) the Pacific Northwest Mycology Service herbarium herbarium (not yet registered).
- podzolic soil** — (*n.*) a soil of temperate to cold moist regions usually found under conifers or ericaceous vegetation; generally containing an organic mat above a gray leached ('albic horizon') soil layer.
- polished** — (*adj.*) smooth and shiny, generally referring to the stipe (see *P. fallax*, *P. scatesiae*).
- polydymous** — (*adj.*) a term introduced by Singer (1949) to describe the multi-tiered distribution of lamellulae ('short gills') that stop variably distant from the stipe, thus forming different sized 'wedges' (when viewed from the edge) between two 'full' gills (lamellae).
- primordial pellis, primordial sheath** — the tissue forming the outermost surface layer enclosing a developing fruitbody (primordium); see also **pellicular sheath**; pp. 15 ff & 24).
- primordium** — (*n.*) the earliest stage of development of a fruitbody; the 'pinhead'; see also FIG—pp. 166G, 179A); **primordial** — (*adj.*).
- proliferating pith** — (*n.*) stipe flesh that accumulates throughout fruitbody development to such a degree that the stipe becomes ventricose or fusoid ('big-bellied'); such pith is always firm and may contain darker and lighter streaks, with the darker tissues strongly reminiscent of the cartilaginous rind usually restricted to the stipe surface.
- prominent** — (*adj.*) protruding, dominating; usually referring to the cap umbo or basidiospore beak.
- pseudorhiza** — (*n.*) a subterranean (and thus root-like) extension of the stipe regarded as the union (or 'interface') between the stipe and soil mycelium that has both storage and conductive functions. The pseudorhiza may be regarded either as part of the fruitbody or a transition between fruitbody and mycelium that may or may not possess regenerating abilities. The pseudorhiza is considered the 'hallmark' of *Phaeocollybia*, where it has been classified into four types: vertical-monopodial, lateral-monopodial, fasciculate-racemose, and sequential-racemose. It may or may not be rhizomorphic in nature. See also pp. 16ff, 22, & 28.
- pseudorhizal pellis** — (*n., pl.* —pellis) the outermost surface (rind) of the pseudorhiza.
- punctate (roughened)** — (*adj.*) here referring to the small dot-like roughening of the outer basidiospore wall
- pungent** — (*adj.*) penetrating, referring here to odors.
- RA** — (*abbrev.*) Resource Area (used only in figure captions).
- racemose** — (*adj.*) branching; here referring both to sequential (where branches emerge in series along the pseudorhizal cord) or fasciculate (where all branches emerge from one point on the cord).
- radial** — (*adj.*) referring to a line from the disc to cap edge (along the radius).
- rainforest, rain forest** — (*n.*) a lush, dense forest rich in biodiversity due to a consistently heavy rainfall; globally 40–75% of all species occur in rainforests, with the warmer tropical rain forest usually more species-rich than the temperate. Rainforests (including those in the PNW) comprise four layers: an 'emergent' layer with tall trees (e.g., coast redwood, Sitka spruce) rising above the general canopy, the *canopy* with large trees (e.g., western red cedar, hemlock, true fir, Douglas-fir), a shrubby *understory* (e.g., vine maple, huckleberry), and forest *floor* on which ferns, *phaeocollybias*, and other plants adapted to low light conditions are found.
- raphanoid** — (*adj.*) radish-like, referring to odor or taste; see also p. 28.
- Rd** — (*abbrev.*) Road (used only in figure captions).
- rDNA ITS** — (*abbrev.*) the internally transcribed sequence of the ribosomal DNA; see also ITS.
- reagent** — (*n.*) a substance, mixture, or compound used for chemical analysis or other reactions.
- refractive** — (*adj.*) refringent; an optical term referring to the scattering or bouncing back of light waves (here noted under the microscope) after light passes through a denser material (as in thick-walled hyphae) to glow brightly when viewed from above.
- regenerating** — (*adj.*) here referring to pseudorhizas that replace or give rise to new primordia. We speculate that such pseudorhizas may resemble sclerotia and lie dormant for a period of time before giving rise to new fruit-bodies during the next active fruiting season. See also pp. 16–18.
- restriction digest** — (*n.*) a process in which DNA is 'cut' into shorter lengths by restriction enzymes that digest short DNA sequences, thus dividing the original DNA sequence into shorter segments. In the 1990's this technique was used with PCR (Polymerase Chain Reaction) amplification for analytical purposes. It has since been replaced by DNA sequence analysis that is now less expensive and thus more accessible to researchers with a limited budget.
- RFLP** — (*abbrev.*) Restriction Fragment Length Polymorphism; a molecular analytical technique used by Norvell on nuclear ribosomal DNA (ITS1 region) obtained from 160 different *Phaeocollybia*

- specimens using 9 restriction enzymes to produce DNA fragments that were then separated by gel electrophoresis. The resulting **RFLP profiles** (DNA 'fingerprints') followed species-consistent patterns, helpful in testing species hypotheses and inferring relationships among the 21 tested *phaeocollybia* species. Helpful a decade ago, RFLP analysis has been supplanted by the now affordable and more precise DNA sequence methodology.
- rhizomorph** — a root-like aggregation of hyphae formed into a well-defined mycelial cord; a visible strand or cord of compacted mycelium; **rhizomorphic** — (*adj.*) pertaining to a rhizomorph.
- rhizomorphic pseudorhiza** — a pseudorhiza that functions in a rhizomorphic capacity, thought to connect the *phaeocollybia* fruitbody to its food source (see also p. 16–18; **nurse pseudorhiza**).
- rhizopellis** — (*n., pl. rhizopelli*) the outermost cartilaginous tissue comprising the rind (pellis) of a pseudorhiza.
- rind** — (*n.*) the outermost cartilaginous tissue; here used only to refer to outer tissues of the stipe.
- robust** — (*adj.*) a fleshy stature that is firm and stocky, sometimes large, but never fragile, pliant or easily broken.
- ROD** — (*abbrev.*) Record of Decision for implementation of governmental planning documents.
- rudimentary** — (*adj.*) not fully developed; generally basic to the earliest developmental stages.
- rufous** — (*adj.*) reddish to dull red; *fulvous*.
- rugulose** — (*adj.*) undulating, wrinkled (here referring to the outer basidiospore wall).
- saprophyte** — an organism that feeds on dead organic material; saprotroph (preferred).
- saprotrophic** — (*adj.*) living on or obtaining nourishment from dead organic material; saprophytic; **saprotrophy** — (*n.*) the utilization of dead organic matter for nutrition; the opposite of biotrophy.
- sarcodimitic** — (*adj.*) possessing a dual-hyphal system composed of two types of generative hyphae: wide vessel **hyphae** that are non-septate, fusoid, and thick-walled and narrow **flexuous hyphae** (sometimes called binding hyphae) that are thin-walled, sinuous, and branched.
- sarcodimitism** — (*n.*) possession of a generative dual hyphal system; see also pp. 20, 22–24, & 33–34.
- scalp** — (*n.*) a small slice across the cap disc to show the orientation of the pileipellis tissues under the microscope; usually viewed in 'squash' mounts.
- scape** — (*n.*) botanically, the leafless stem of a flower; here in particular the dandelion flower stem that curls back on itself when sliced cross-wise.
- scattered** — (*adj.*) referring to the distribution of fruitbodies in a seemingly random loose pattern; contrasting with 'solitary' on the one hand and 'gregarious' or 'caespitose' on the other.
- schist** — (*n.*) foliated metamorphic rock, usually containing mica.
- sclerophyll(ic) forest** — (*n.*) a forest composed of non-deciduous angiosperms with thick-cuticled leaves (e.g., madrones, live-oaks, evergreen rhododendrons, magnolia).
- second growth forest** — (*n.*) broadly, a forest that has grown up (or been planted) after harvest of the original forest; narrowly a forest less than 100 years old.
- secretory** — (*adj.*) here referring to microscopic elements (oleifers, cystidia, tibiiform diverticula) that secrete gel or other compounds.
- sedimentary** — (*adj.*) rock formed over geologic time by the gradual accumulation of silt and organic matter, usually at the bottom of a large body of water (ocean, lake).
- SEM** — (*abbrev.*) Scanning Electron Microscopy; a technique permitting high magnification imaging of surface features with a very high depth of field in which a sample is coated with a thin gold layer to expose characters using a scanning electron beam; see photos on pp. 16, 48, 94, 128, 164, and 178.
- senescent** — (*adj.*) over-mature, aged.
- senescent element** — (*n.*) an over-mature, aging hyphal cell.
- septum** — (*n., pl. septa*) the cross-wall separating one hyphal cell from another.
- sequential racemose pseudorhiza** — (*n.*) the *Phaeocollybia* pseudorhiza category characterized by a rhizomorphic cord that branches in a series, each branch giving rise to a single fruitbody. See also p. 17.
- serrulate** — (*adj.*) referring to the minutely saw-toothed gill edges found in younger fruitbodies as well as mature eroded gill edges.
- seta** — (*n., pl. setae*) a bristle or bristle-shaped body, typically deep yellow or brown (dark brown or black when mounted in KOH); here referring to the thick-walled dark brown pointed or broken elements seen on the pellis of the subtending pseudorhizal strand in *P. radicata*. See also pp. 34 & 158E–J.
- SFSU** — (*abbrev.*) the San Francisco (CA) State University herbarium acronym.
- sinuate** — (*adj.*) referring to either cap or gill edge displaying one or more concave indentations.
- sinuous** — (*adj.*) wavy, serpentine.
- snout** — (*n.*) also called the 'beak;' the pronounced callus projection at a basidiospore apex (the end opposite the apiculus).

- snubbed** — (*adj.*) referring to the low profile of some basidiospore beaks (snouts) or accumulation of callus at the apex of an ellipsoidal basidiospore in *Phaeocollybia*.
- solitary** — (*adj.*) growing alone, not in the immediate vicinity of other fruitbodies representing the same species.
- sphaeropedunculate** — (*adj.*) referring to cystidia having a large, spherical apex resting on a short pedicel (peduncle).
- spirally encrusting** — (*adj.*) referring to the helical distribution of surface gel or pigment encrustations upon the outside hyphal wall.
- spore print** — (*n.*) the spore mass obtained by placing a mushroom cap flat with the gills perpendicular to the plane of the paper or glass slide. (See also p. 28.)
- sporulation** — (*n.*) the process during which spores form and are forcibly discharged from the sterigmata of a basidium.
- squamule** — (*n.*) a small scale (in *Phaeocollybia* derived from the primordial sheath remaining on stipe or cap); **squamose** — (*adj.*) scaly; **squamulose** — (*adj.*) minutely scaly. See also FIG-p. 110A–B.
- squash mount** — (*n.*) a microscope mount in which a tissue placed into a mountant (usually KOH) under a cover slip is firmly tapped and ‘squashed’ to display individual elements; contrasted to a section prepared by carefully slicing a tissue (usually radially) to display all layers without distortion. Although careful sectioning is preferred, the high gel content of most phaeocollybias makes a squash mount the quickest and easiest way to view fresh tissues to verify field species identifications.
- starburst** — (*n.*) here referring to the umbellate ‘explosion’ of many fruitbodies (with primordia) from a single point on a subtending rhizomorphic pseudorhizal cord. See also figures on page 17 & 185.
- sterigma** — (*n., pl. sterigmata*) the tiny ‘spicule-like’ pedicel upon which a basidiospore is borne and from which it is forcibly discharged.
- sterile gill edge** — (*n.*) a gill edge on which only sterile elements (i.e. cheilocystidia, hyphidia) occur.
- stipe** — (*n.*) the technically correct term for mushroom stem; see also pp. 22 & 28.
- stipitipellis** — (*n.*) microscopically, the stipe cuticular layer, the rind.
- stipitipith** — (*n.*) the stipe flesh, context.
- stipitocarp** — (*n.*) development of a primordium first by stipe elongation and then by cap formation. See also p. 15.
- strangulated** — (*adj.*) here referring to cheilocystidia with sinuous walls that contract and expand in an irregular fashion (see *P. gregaria*).
- striate** — (*adj.*) bearing lines or minute furrows, here referring to radial lines at the cap margin and/or edge that appear when the cap cuticle becomes so thin that the gills become visible beneath the cap cuticle; **striation** — (*n.*) a line or minute furrow.
- striatulate** — (*adj.*) similar to striate, but with less pronounced, fainter lines.
- strict** — (*adj.*) straight, upright, usually equal (referring to the stipe).
- subcapitate** — (*adj.*) slightly capitate; here referring to thin-walled cheilocystidia with ~2–4 µm diam long pedicels swelling to a broader (~4–8 µm diam) subglobose to globose head. See also *P. redheadii*.
- subglobose** — (*adj.*) almost spherical.
- subhymenium** — (*n.*) in *Phaeocollybia*, a tissue composed of three or more hyphae flanking the gill trama and giving rise to the basidia and true cystidia.
- sublimoniform** — (*adj.*) as in limoniform, lemon-shaped, but more elongated (less rotund) and thus seemingly more narrow overall.
- subpellis** — (*n.*) the lower layer of a pellis; here referring to the bottom layer of either a bilaminar or a trilaminar pileipellis. See also pp. 24 & 32.
- subviscid** — (*adj.*) tacky to slightly slimy; more viscous than ‘lubricous’ and less slimy than ‘viscid’ or ‘glutinous.’
- suprapellis** — (*n.*) the top layer of a pellis (elsewhere sometimes termed the ‘epicutis’); here referring to the top layer of either a bilaminar or a trilaminar pileipellis; see also pp. 24 & 32); **suprapellicular** (*adj.*).
- synonym** — (*n.*) another name for a taxon (or group), usually a later name that has been determined to represent an earlier named taxon (e.g., *P. carmanahensis* is a synonym of *P. oregonensis*).
- syringaldazine** — (*n.*) a chemical reagent used to test for the presence of laccase in cultures or tissues, compounded from 0.1 g syringaldazine made to 100 mL with 95% ethanol heated to dissolve the solute (Marr et al. (1986; see also Lennox 1979). In *Phaeocollybia* syringaldazine has proved an especially helpful diagnostic tool. See also p. 30, FIG-p. 126, FIG-p. 188B.
- tardily** — (*adv.*) slowly, in a delayed fashion (referring to a delayed reaction to syringaldazine).
- tawny** — (*adj.*) dull orangish to yellowish brown.
- taxonomy** — (*n.*) the science of classification; in biology the arrangement of organisms into a classification scheme or matrix; **taxonomic** — (*adj.*) of or pertaining to taxonomy; **taxonomically** (*adv.*).
- temperate** — (*adj.*) referring to the climate of the middle latitudes, generally with warm dry summers and cool wet autumns, winters, and springs.

**temperate rainforest** — (*n.*) a vegetation class in temperate areas with high and more or less evenly distributed rainfall characterized by comparatively few species with large populations of each species. PNW rainforests — which occur on west-facing coastal mountains along the Pacific coast from Alaska to northern California, in Washington and Oregon inland west of the Cascade crest, and in Idaho along the western slope of the Rockies in sheltered areas with high annual precipitation — are predominantly coniferous, sometimes with an understory of broadleaved trees and shrubs.

**TENN** — (*abbrev.*) the University of Tennessee (Knoxville) herbarium acronym.

**terete** — (*adj.*) round (like a broom handle), not irregular (pertaining to the stipe).

**terrestrial** — (*adj.*) growing on the ground.

**thick-walled** — (*adj.*) referring to hyphal walls measuring 0.5(1)–10 µm across and readily seen under the high dry and oil immersion objectives.

**thin-walled** — (*adj.*) referring to hyphal walls measuring below 0.5(1) µm across and appearing linear and thin under the high-powered oil immersion objective.

**thready** — (*adj.*) another term for ‘cord-like’, referring to a thin pliable pseudorhiza.

**tibiiform** — (*adj.*) bone-shaped; here referring to cheilocystidia or diverticula with a wide thin-walled base, narrow thick-walled refractive neck, and small spherical (globose) minute head (capitellum, capitulum). The term ‘tibiiform’ here incorporates both tibiiform and lageniform elements, both bearing thick-walled narrow necks.

**tibiiform diverticulum** — (*n., pl. tibiiform diverticula*) a diverticulum arising from a hypha of the primordial (pellicular) sheath and found throughout *Phaeocollybia* (hence a generic constant). See also pp. 15 ff, 24, 34 and FIG 2.1

**tiddly-wink** — (*v.*) derived from the children’s game ‘Tiddly-Winks’ in which pressure applied to a plastic disc flips the disc below a distance away toward a target cup. A gelatinous tissue that does not compress below a cover slip is said to ‘tiddly-wink’ across the room when too much pressure is applied. (Particularly frustrating to a microscopist who must prepare a new mount to view the tissue.)

**trama** — (*n.*) a tissue from the context of cap, stipe, and pseudorhiza, usually referring to the central gill tissue beneath the hymenium and subhymenium; see also p. 22; **tramal** — (*adj.*) pertaining to the trama.

**translucent** — (*adj.*) semi-transparent, permitting the passage of light that is so diffuse that distinct images cannot be clearly identified.

**trilaminate, tri-laminate** — (*adj.*) three-layered (referring to the pileipellis structure).

**troop** — (*n.*) a mass of individual fruit-bodies, sometimes occurring in ranks or phalanxes.

**trsect, trst** — abbreviation for transect (used only in figure captions).

**tubular** — (*adj.*) hollow; referring to a strict (straight) stipe that lacks pith except for a few stray fibrils.

**UBC** — (*abbrev.*) the University of British Columbia (Vancouver) herbarium acronym.

**UC** — (*abbrev.*) the University of California (Berkeley) herbarium acronym.

**umbellate** — (*adj.*) derived from ‘umbel,’ a flat-topped or rounded flower cluster in which the individual flower stalks arise from about the same point, as in Queen Anne’s Lace (*Umbelliferaeae*); here referring to all fruitbodies within a fascicle emerging from one point on a subtending strand. In *Phaeocollybia* an umbellate fascicle contains fruitbodies in different developmental stages and with stipes of different lengths.

**umbo** — (*n.*) a raised, conical to convex knob or mound on the center.

**undulating** — (*adj.*) wavy; rolling and uneven.

**universal veil** — (*n.*) the enveloping veil in agarics formed by the progressive differentiation of the peripheral layer of the primordium, beneath which the fruitbody tissues form and develop; see also **primordial sheath, pellicular veil**.

**uplifted, upturned** — (*adj.*) used here to refer to the outer cap margin or edge after full expansion.

**USDA** — (*abbrev.*) United States Department of Agriculture.

**USDI** — (*abbrev.*) United States Department of the Interior.

**USFS** — (*abbrev.*) United States Forest Service (more correctly abbreviated USDA-FS).

**UV** — (*abbrev.*) ultraviolet; used here to refer to the ‘black light’ under which fluorescent gills and tissues glow in a blacked-out room.

**vacuolate** — (*adj.*) possessing vacuoles (empty regions); here referring to basidia that form vacuoles after sporulation.

**vascular stele** — (*n.*) the central tissue core of a vascular plant root.

**veil** — (*n.*) here referring to the fibrils, scales, and fibrillose patches remaining on cap, stipe, and/or pseudorhiza after disruption of the primordial sheath; see also **universal veil, pellicular veil**, and p. 22.

**velate** — (*adj.*) possessing a veil.



- ventricose** — (*adj.*) referring to a stipe or spore swollen or enlarged in the middle; similar to ‘fusoid’ except that one end is more tapered than the other.
- verrucose** — (*adj.*) basidiospore ornamentation consisting of small rounded ‘warts’ or processes covering the outer spore wall (exosporium).
- verrucose-rugulose** — (*adj.*) basidiospore ornamentation combining a small rounded warts and an irregular wavy spore outer wall surface.
- verruculose** — (*adj.*) basidiospore ornamentation consisting of fine rounded warts covering the outer spore wall (less rough than verrucose, but more noticeable than punctate).
- vertical-monopodial pseudorhiza** — (*n.*) a fleshy, unbranched pseudorhiza that may or may not possess regenerative properties; see also pp. 16, 22, & 28.
- vessel hypha** — (*n., pl. vessel hyphae*) wide, non-septate, fusoid, unbranched, thick-walled hyphae that make up one part of the dual-hyphal system found in *Phaeocollybia*, with ‘flexuous hyphae’ representing the other hyphal form. See also **flexuous hypha**, **sarcodimitism**, and pp. 24, 28, & 33–34.
- vestige** — (*n.*) remnant, fragment, relic.
- vinaceous** — (*adj.*) wine-colored.
- virgin forest** — (*n.*) a native forest that has not been logged or otherwise manipulated by humans and thus shaped only by the environment (including wildfire).
- viscid** — (*adj.*) tacky, sticky, slippery when moist; more slippery than sub-viscid and less slimy than glutinous.
- viscidity** — (*n.*) the degree to which a fruitbody is sticky or slimy; terms used here (from driest to slimiest) are: dry, moist, lubricous, subviscid, viscid, glutinous.
- viscous** — (*adj.*) thickly viscid, gluey, glutinous; slimy.
- VTMH** — (*abbrev.*) the Virginia Polytechnic Institute and State University (Blacksburg) herbarium acronym.
- WA** — (*abbrev.*) the state of Washington (USA).
- wart** — (*n.*) a rounded process or bump confined to the outer basidiospore wall.
- warty-verrucose** — (*adj.*) basidiospore ornamentation combining small and large warts on the outer spore surface.
- WTU** — (*abbrev.*) the University of Washington (Seattle) herbarium acronym.
- zonate** — (*adj.*) possessing fairly well delineated zones or regions; used to designate cap regions (disc, inner margin, outer margin, edge), usually with respect to color.



Ron Exeter

### Oz (BLM Reserve Forest, Polk County, Oregon)

The name 'Oz' is derived from 'O2,' the code we used to designate one old-growth transect in our five-year chronosequence study in the Oregon coast range near Pedee, Oregon. The tall trees, resident Northern Spotted Owl, and heavy moss and fern ground cover soon made the virgin 'emerald' forest our favorite place to survey. An added bonus was the fact that we tallied eleven *Phaeocollybia* species within the 400 m<sup>2</sup> transect area, including the type collections of *Phaeocollybia ochraceocana* and *P. tibiikauffmanii*. The authors have designated Oz as an official phaeocollybian Garden of Eden.

## Back Cover:

Top: *P. ammiratii*, *P. attenuata*, *P. benzokauffmanii*, *P. californica*

2nd row: *P. dissiliens*, *P. fallax*, *P. gregaria*, *P. lilacifolia*

3rd row: *P. luteosquamulosa*, *P. ochraceocana*, *P. olivacea*, *P. oregonensis*

4th row: *P. phaeogaleroides*, *P. piceae*, *P. pleurocystidiata*, *P. pseudofestiva*

5th row: *P. radicata*, *P. redheadii*, *P. rifflipes*, *P. rufotubulina*

Bottom: *P. scatesiae*, *P. sipei*, *P. spadicea*, *P. tibiikauffmanii*

Photographs by R.L. Exeter, E. Fox, S. Loring, L.L. Norvell, S.A. Redhead

Cover design by L.L. Norvell



Senior Systems Administrator

