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The Biology and Taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (Agaricales, Cortinariaceae)

by

Lorelei L. Norvell

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1998

Approved by _____
Chairman of Supervisory Committee

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Doctoral Dissertation

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Abstract

The Biology and Taxonomy of Pacific Northwest species of *Phaeocollybia* Heim (Agaricales, Cortinariaceae)

by Lorelei L. Norvell

Chairperson of the Supervisory Committee: Professor Joe F. Ammirati
Department of Botany

Investigation of the agaric genus *Phaeocollybia* (Cortinariaceae) in British Columbia, Washington, Oregon and California has led to a better understanding of the biology of the genus and resulted in a taxonomic revision of Pacific Northwest species. Discovery of mycelial and pseudorhizal connections to mantle-sheathed rootlet tips with Hartig nets offers the first good evidence in support of *Phaeocollybia* as an ectomycorrhizal genus. Basidiome development is traced from subterranean initiation to fully mature emergent basidiomes, and hypotheses on the monovelangiocarpic development of *Phaeocollybia* basidiomes are developed based on extensive observations of primordia and numerous field excavations. Generically significant new characters -- pellicular veil, tibiiform diverticula, and sarcodimitic tissues -- are examined in depth. Four different pseudorhizal morphologies (vertical-monopodial, lateral-monopodial, sequential-racemose, fasciculate-racemose) are fully explored together with evidence of pseudorhizal meristemoidal activity and rhizomorphic function. Developmentally dependent character variations (*e.g.*, apical extensions from senescent thin-walled cheilocystidia) are identified and discussed.

Diagnostic morphological, developmental and ecological characters subjected to computer-assisted multivariate and phenetic cluster analyses are evaluated. Problems caused by length variations of PCR-amplified ITS1+5.8S+ITS2 ribosomal DNA (obtained from 160 specimens representing twenty-six Pacific Northwest and extralimital Phaeocollybias and seven out-taxa) are outlined. Restriction fragment length polymorphisms and restriction site data produced by single digests with nine enzymes are discussed in detail. Phylogenies inferred from computer-assisted cladistic analyses of restriction site data show a high degree of support for previously formed morphologically-based species hypotheses and suggest that sections proposed by previous workers are probably polyphyletic.

Nine new species (*P. ammiratii, P. benzokauffmanii, P. luteosquamulosa, P. phaeogaleroides, P. pleurocystidiata, P. redheadii, P. rifflipes, P. rufotubulina,* and *P. tibiikauffmanii)* are proposed, *P. carmanahensis* is synonymized with *P. oregonensis,* and *P. deceptiva* (thought to represent Subgenus *Telamonia, Cortinarius)* is excluded from the

genus. Fully revised technical descriptions integrating morphological, ecological, developmental, macrochemical and molecular information for twenty-five currently recognized Pacific Northwest species are accompanied by dichotomous and synoptic keys, line drawings, and full color photographs. Placement of *Phaeocollybia* within the Cortinariaceae is discussed and an emended generic description presented. Supporting materials include a fully-annotated conspectus to eighty world species.

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CHAPTER 1. HISTORICAL AND DISTRIBUTIONAL BACKGROUND

Introduction

Phaeocollybia Heim (Cortinariaceae, Agaricales) is a biologically intriguing genus of brown-spored agarics for which 85 species have been reported worldwide (see Appendix D). *Phaeocollybia* species have been flagged in recent literature as an endemic component of old-growth Pacific coast temperate rainforests in the United States and Canada (Redhead, 1993; Redhead & Norvell, 1993; Ammirati *et al.*, 1993, 1994; USDA-USDI 1993, 1994; Norvell, 1995, 1997a; Castellano *et al.*, 1997; O'Dell *et al.*, 1997). Twenty-five species are currently recognized from British Columbia, Washington, Oregon and California where the genus appears to reach its highest level of diversity (Murrill, 1917; Smith, 1937, 1957a, 1957b; Smith & Trappe, 1972; Goetz, 1975; Goetz, Barnhart & Barnhart, 1986; Norvell & Redhead, 1992; Norvell & Ammirati, 1993, 1995, 1996; Redhead & Norvell, 1993; Norvell, Ammirati & Redhead 1994; Norvell 1997a, 1997b; Redhead, 1997).

Monographic treatments of *Phaeocollybia* have been few (Heim, 1931; Smith, 1957b; Singer, 1970; Smith & Trappe, 1972; Horak, 1977; Gulden, 1983, Jacobsson & Stridvall, 1983; Laber, 1991; Bon, 1992; Bandala, 1994), and only three (Smith, 1957b, Smith & Trappe, 1972; Horak, 1977) provide keys to Pacific Northwest taxa. Unfortunately, recognition of Pacific Northwest Phaeocollybias has been greatly complicated by the fact that many recently discovered species are not included in existing keys, and many published descriptions are based on single collections that do not reflect the full range of morphological variability encountered within a single taxon. Furthermore the biology, development, and genetics of *Phaeocollybia* have been, for the most part, ignored. These inadequacies have prompted the present investigation of the genus in the Pacific Northwest. It is hoped that the knowledge gained from the resulting field work, morphological and anatomical reevaluations, evidence of mycorrhizae in numerous species, investigation of the ITS1-5.8S-ITS2 rDNA region, discovery of new species and recognition of new generically significant characters will aid a future rigorous systematic treatment of the genus as a whole worldwide.

History of the genus

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 11 species placed together in an unnamed group characterized by nearly free lamellae were those that would form the core of *Phaeocollybia* a century later: two species earlier described by Fries in 1821 -- *Agaricus lugubris* Fr. and *A. hilaris* Fr.-- and three newly described

species -- *A. christinae* Fr., *A. cidaris* Fr. and *A. festivus* Fr. When *Naucoria* was later elevated to generic level (independently by Kummer in 1871 and by Quélet in 1872), the genus retained its essentially heterogeneous character.

Heim (1931) segregated *Phaeocollybia* from *Naucoria* as a genus for yellow-brown spored agarics with cartilaginous radicating stipes, viscid pilei, ornamented spores, cheilocystidia, and gelatinous tissues. At that time Heim transferred *Naucoria christinae, N. festiva, N. cidaris* and *N. lugubris* to *Phaeocollybia* and suggested that four other species placed into *Simocybe* by Karsten (1881, including *S. jennyae* Karsten) were probably congeneric.

Konrad (1934) later selected a neotype for *P. lugubris* (Fr.:Fr.) Heim and lectotypified *Phaeocollybia* with that species, at the same time treating *Phaeocollybia* as a subgenus of *Naucoria.* In 1951, Singer listed *P. festiva* (Fr.) Heim as the type species for *Phaeocollybia* the genus, but he did not discuss Konrad's earlier action. Kuyper and Bas (1986) subsequently rejected *P. festiva* as type of *Phaeocollybia*, citing Article 7.10 of the Botanical Code which suggested that Konrad's earlier lectotypification could not be superseded.

Acceptance of *P. lugubris* as type of *Phaeocollybia* was unfortunately complicated by the typification of *Simocybe,* another genus segregated from *Naucoria.* Karsten (1879) originally erected to accommodate the two Friesian subtribes, *Gymnoti* and *Phaeoti.* Subsequently, and in accordance with the American Code of Botanical Nomenclature, Earle (1909) lectotypified *Simocybe* with *A. lugubris,* the first listed species of the *Gymnoti* (Fries, 1838, 1874) and unfortunately the same species to be selected by Konrad 25 years later for *Phaeocollybia.* Lectotypification of *Simocybe* with *A. lugubris* was accepted by Donk (1962) and Horak (1968) but rejected by Singer and Smith (1946), Singer (1951b), and Kühner (1980), all of whom regarded *Simocybe centunculus* as the type of *Simocybe.* To settle this nomenclatural confusion, Kuyper and Bas (1986) formally proposed conservation of the genus *Phaeocollybia* (with *P. lugubris* as type) over *Simocybe;* their proposal was amended to include typification of *Simocybe* by *S. centunculus* and was subsequently accepted by the IAPT Committee for Fungi (Gams, 1994) and adopted in the International Code of Botanical Nomenclature (Greuter *et al.*, 1994). At the same time, a second genus with possible claim to Phaeocollybian taxa -- *Quercella* Velenovsky (1921) -- was rejected in favor of *Phaeocollybia* (Gams, 1994). In the latter instance a possible source of confusion revolved around the fact that Velenovsky (1921) had selected *Q. aurantiaca* as type for his genus; examination of the type specimen by Svrcek (1966) and a close reading of the protologue showed it to be probably conspecific with *Phaeocollybia christinae* (Kuyper & Bas, 1986).

Critical revisions of the genus have been made by Kühner & Romagnesi (1957), Smith (1957b), Horak (1977), Singer (1970, 1986, 1987), and Bandala (1994).

Distribution and Ecology

Singer was the first to recognize distribution of *Phaeocollybia* outside Europe when he transferred North American and Chinese Naucorias to the new genus (*i. e., N. kauffmanii* Smith in 1941; *N. radicata* Murrill, *N. attenuata* Smith and *N. similis* Bresadola in 1951). Since 1957 new species have been recognized from every continent except Africa and Antarctica. Distribution of currently recognized *Phaeocollybia* species is listed below (see also Appendix D).

Great Britain & Europe: Although *Phaeocollybia* was first described from Europe, there it is represented by only seven currently recognized species (*Austria* -- Moser, 1950; *Czechoslovakia* -- Vesely, Kotlaba & Pouzar, 1972; Mann, 1991; *Finland* -- Karsten, 1879, 1881; *France* -- Konrad & Maublanc, 1948; Kühner & Romagnesi, 1957; Kühner, 1980; Bon 1979, 1992; *Germany* -- Krieglsteiner, 1991; Laber, 1991; *Great Britain* -- Dennis, Orton & Hora, 1960; Watling & Gregory, 1993; *Italy* -- Bresadola, 1930; *Norway* -- Reid, 1972; Gulden 1983, 1992; *Romania* -- Pazmany & Laszlo, 1987; *Sweden* -- Jacobsson & Stridvall, 1983; *Switzerland* -- Horak, 1968; *Ukraine* -- Karpenko, 1988; *cf.* also Heim, 1931; Bresinsky, 1960; Lange & Hora, 1963; Poelt & Jahn, 1963; Horak, 1977; Moser, 1983; Singer, 1951b, 1986; Moser & Jülich, 1994). There Phaeocollybias, while widely distributed and only sporadically encountered (Horak, 1977, 1997 pers. comm.), are restricted to coniferous forests, particularly those containing *Picea*. (N.B.: The generic name '*Quercella*' is a Latinization of the maiden name of Velenovsky's wife name, Doubek (Slavic for 'oak'), and not an indication that the type species *Q. aurantiaca*, grew under oak).

Asia: Four European species 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, 1969; *Siberia* -- Nezdoimnogo 1986, 1990; see also Horak, 1977; Singer 1951b, 1986). Throughout Asia Phaeocollybias are found only in boreal and temperate coniferous forests.

Australasia: There are seventeen species reported from Australasia (*Malaysian archipelago* -- Corner, 1994 [who notes that a previous report of *Tricholoma thiochroum* Berk. & Br. represents a *Phaeocollybia*]; *Australia* -- Horak, 1983; Fuhrer & Robinson, 1992; Rees & Wood, 1996; May & Wood, 1997; *New Zealand* -- Horak, 1973, 1977; see also Singer, 1986). All species are endemics except possibly one (originally reported as *P. longipes* by Horak (1973), who placed it into synonymy with *P. festiva* (Horak, 1977) despite its association with *Sphagnum* and *Nothofagus*). Horak (1977) noted that in the Malaysian archipelago and New Zealand, Phaeocollybias are generally found in angiocarpous forests dominated by members of the Fagaceae (*i. e., Nothofagus, Quercus, Lithocarpus,* and *Castanopsis*). On the other hand, Rees & Wood (1996) report species from sclerophyllic forests associated with *Eucalyptus, Leptospermum* and/or *Nothofagus*.

South and Central America: Fourteen endemic Phaeocollybias have been reported from South and Central America (Singer 1961, 1970, 1986, 1987; Horak, 1977; Horak & Halling, 1991; Halling, 1997) from 'virgin tropical rainforests' (Singer, 1970) dominated by angiocarpous associates. There appears to be a distinct group of *Phaeocollybia* species associated with *Quercus*, particularly at the higher elevations in Colombia and Costa Rica (Singer, 1987; Horak & Halling, 1991).

Mexico: Bandala (1994) recently reevaluated the state of the genus in Mexico and currently recognizes 19 (most endemic) species (see also Singer 1970, 1986; Horak, 1977; Guzmán *et al.*, 1987, Bandala *et al.*, 1989, Bandala & Montoya, 1994; Bandala *et al.*, 1996). Representatives have been collected from coniferous (*Abies, Pinus*), angiocarpous (*Quercus*) and mixed (*Quercus-Pinus*) forests.

Northeastern North America: Representatives of *Phaeocollybia* are generally rarely encountered in eastern North America where they are more or less restricted to the boreal and temperate coastal or Great Lake areas. No species have yet been collected from the interior from Michigan west to the Rockies or south of Tennessee. Five species -- all known from Europe -- 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).

Northwestern North America: It now appears that almost one-third of the currently recognized Phaeocollybias occur within the coastal coniferous rainforests of the Pacific Northwest (here defined as including British Columbia, Washington, Idaho, Oregon, and northern California). Until 1993, only 17 species had been described from this region (Murrill, 1917; Smith, 1937, 1957a, 1957b; Smith & Trappe, 1972; Redhead & Norvell, 1993). During the current study additional collections and reevaluation of herbarium specimens have resulted in the transferral of one type to *Cortinarius*, synonymy of another, and discovery of nine additional taxa (see Chapter 6). 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 *et al.*, 1994a, Norvell 1995b). A high degree of endemism is suggested by the fact that most (if not all) of the Pacific Northwest species recognized to date appear restricted to western North America. Reports of Pacific Northwest endemics occurring outside this area have proved inaccurate (see Redhead & Norvell, 1993 regarding *P. kauffmanii*) or remain unconfirmed. Additionally, no non-indigenous species are known to occur within the Pacific Northwest where Phaeocollybias are for the most part confined to the coast east to the western slopes of the Cascade Range in the north and the Sierra Nevada range in the south. Exceptionally, a few representatives have also been collected from the moist mesic coniferous forests of northern Idaho.

Notes on Pacific Northwest *Phaeocollybia* habitats

Within the Pacific Northwest, *Phaeocollybia* is most commonly found in the northwest temperate rain-forest (sometimes called the coastal coniferous forest, *cf.* Vankat 1980), dominated in the north by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Gon.) Carr.) and in the south by coast redwood (*Sequoia sempervirens* (D. Don) Endl.). Although Smith (1957b), Smith & Trappe (1972), and Redhead & Norvell (1993) suggested a close *Picea-Phaeocollybia* association, it now appears that spruce is more an indicator of the moist habitats favored by *Phaeocollybia* species than an obligate associate (Norvell & Ammirati, 1993, 1997a, 1997b; Ammirati *et al.*, 1993; Norvell *et al.*, 1994a). Sitka spruce dominates the Alaskan and northern British Columbian coniferous forests but is gradually supplanted southwards by western hemlock and western redcedar (*Thuja plicata* Don.) (*cf.* Eyre 1968). *Phaeocollybia* sites on Vancouver Island, where Sitka spruce is restricted to flood plains and exposed beaches (Pojar *et al.*, 1991b), are dominated by western hemlock with silver fir (*Abies amabilis* (Dougl.) Forbes) and western redcedar also present. Here (as elsewhere throughout the western hemlock zone) the shrubby *Vaccinium-Gaultheria* understory is dense and mosses are common (*e. g.*, *Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregana* (Sull.) Ochyra, *Rhytidiadelphus loreus* (Hedw.) Warnst.), but herbaceous ground covers are generally not well developed (Vankat 1980, Pojar *et al.*, 1991b). The same plant association (minus Sitka spruce) is also recorded for the only *Phaeocollybia* site known thus far from mainland British Columbia (Gamiet *et 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* Rehder) supplants silver fir at higher elevations (*cf.* Halverson *et al.*, 1986, Ammirati *et al.*, 1994). The herbaceous layer may or may not be more developed, with *Oxalis oreganum* Nutt., *Polystichum munitum* (Kaulf.) Presl, *Blechnum spicant* (L.) Roth, *Cornus cascadensis* L., and *Linnaea borealis* L. common to frequent (*cf.* also Halverson *et al.*, 1986, Henderson *et al.*, 1989). A sub-climax species, Douglas-Fir (*Pseudotsuga menziesii* (Mirbel) Franco, is often also present. In coastal areas large concentrations of certain *Phaeocollybia* species have been found in Douglas-fir plantations in areas previously inhabited by climax western hemlock-spruce forests (Norvell, unpublished data).

From Oregon southwards, Sitka spruce and western hemlock gradually disappear from the coastal forests to be replaced by coast redwood (*cf.* Eyre, 1968). While absent from pure coast redwood stands, Phaeocollybias occur in mixed *Sequoia* forests where hemlock, fir, Douglas-fir, redcedar and tan oak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehder) are also present. Here the shrubby *Rhododendron-Vaccinium-Gaultheria* understory can be quite dense while moss and herbaceous layers (except for frequently abundant *Polystichum*) are poorly developed or absent. Phaeocollybias have also been collected inland from the *Quercus-Pinus* zone just north of the California border in the Siskiyou mountain range (Smith, 1957b).

The coastal plant associations and series listed above share a common dependence on high ambient humidity. To the north, western hemlock, Sitka spruce and western redcedar are all indicators of very humid environments (Vankat, 1980), and the survival of coast redwood at the southern end of its range (coincident with the southernmost range of *Phaeocollybia* in California) is said to depend on the "relatively high humidity and frequent fogs in the dry season" (Eyre, 1968). Almost all Pacific Northwest Phaeocollybias fruit typically during the late summer to early winter cool rainy season except for one new species that fruits only in the spring from March to May (see *P. pleurocystidiata*, Chapter 6). This innate phenology is moderated to a certain extent by weather patterns, with some species continuing to fruit during and after mild wet winters.

While most Pacific Northwest species have been reported from the exceptionally moist coastal and inland coniferous rainforests (Smith, 1957b; Smith & Trappe, 1972; Redhead & Norvell, 1993), they 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 (see Hickman, 1993) There Phaeocollybias can frequently be found in the Douglas-Fir Series (cf. Sawyer & Keeler-Wolf, 1995) where the dominant Douglas-fir is accompanied by *Quercus, Lithocarpus* and *Pinus*. Ammirati (pers. comm., 1995-1997) has made numerous *Phaeocollybia* collections along the South Fork of the Smith River (Six Rivers National Forest, Del Norte County) and near Castle Crags State Park (Shasta County). In these forests there is less ambient humidity and long hot dry summers are followed by the autumn rainy season when most of the annual 50-125 cm precipitation falls, typical of a Mediterranean regime.

While soil characteristics have not been evaluated in reference to *Phaeocollybia*, some information has been published on soil composition characteristic of the above vegetation zones. The relatively cool temperatures, high moisture, and coniferous vegetation of the temperate rain-forest combine with basalt or other volcanic parent material in the northernmost part of the range (British Columbia, Washington, and Oregon) to produce the podzolic soils (*cf.* "spodisols" in Steila, 1976; Halverson *et 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.*, "podzolisation" or "base desaturation" in Eyre 1968) leaves an "albic horizon" of whitish quartz sand (at the base of the upper "A" horizon) which has been noted in numerous *Phaeocollybia* excavations (Norvell, 1997b). Podzols in which Phaeocollybias are found have relatively thick top organic litter layers, either mors or mormulls composed of needles, coarse woody debris and partly decomposed organic matter in which ericaceous shrubs (*e. g., Vaccinium, Rhododendron)* are also common (Halverson *et al.*, 1986, Henderson *et al.*, 1989, Ammirati *et al.*, 1994). These podzols are acidic with pHs ranging from 4.2 to 6 (Donahue *et al.*, 1977, Henderson *et al.*, 1989). In California, soils become more

complex and less easily classified, ranging from volcanic to metamorphic in the northern portion, with 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). A mix of sedimentary and older metamorphic soils are found in the *Quercus-Pinus* zone of the Klamath range where Smith collected the type of *P. olivacea* (Sawyer & Keeler-Wolf, 1995). Jimerson *et al.* (1996) report that in the Douglas-fir-Tanoak subseries in the Six Rivers National Forests, soils are generally classified as gravelly to very gravelly loams or sandy loams with a mean soil depth of 33-34" (15-40" overall) with 5-6" (2-14") deep A horizons containing 34-52% coarse fragments with a pH of 6.2-6.3

While most Pacific Northwest species of *Phaeocollybia* can be found in undisturbed old growth, they are not necessarily restricted to ancient forests. Many of the species already described have been also collected from moist relatively undisturbed second-growth forests with dense closed canopies where "high-grading" (in lieu of "clear-cutting") has occurred (Ammirati *et al.*, 1993; Norvell *et al.*, 1994a; Norvell, 1997a). Other species *(e. g., P. olivacea, P. scatesiae)* appear to flourish in recently thinned old-growth stands or young mature (*ca.* 30 years old) Douglas-fir plantations (Norvell, unpublished data). Recent reports of Phaeocollybias collected from more open, less humid inland forests indicate that they are not necessarily restricted to closed canopy forests (Ammirati, pers. comm., 1996-1997). Researchers with the Bureau of Land-Management in Oregon (Exeter, pers. comm., 1997) have observed that Phaeocollybias are occasionally found in relatively open areas within mature Douglas-fir forests next to decaying stumps that presumably function as moisture reservoirs during the dry season.

Subgeneric Classification (Table 1.1)

Alexander H. Smith (1957b), the first to classify *Phaeocollybia* at the subgeneric level, divided the genus into two sections, Section *Phaeocollybia* for species characterized by thin-walled clavate cheilocystidia ("...cheilocystidia preponderantly clavate to elongate-capitate, the tips 4-8 µm broad and the neck or shank regularly 3 µm or more thick; rarely a few hairs less than 3 µm...."} and Section *Versicolores* for species producing basidiomes with thick-walled lageniform to tibiiform cheilocystidia ("...cheilocystidia 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 neck refractive and usually ochraceous in KOH, the basal portion usually enlarged somewhat (3-7 µm in diam.); if hairlike, the walls thickened somewhat in at least some of the individuals").

After discovering new species from the neotropic western hemisphere, Singer (1970) revised Smith's sections and added three new ones. Singer (1970, 1986, 1987) separated these five sections based on a combination of cheilocystidial morphology, the presence or absence of clamp connections and basidiospore length as follows: "...cheilocystidia in their majority clavate to +/-

cylindrical; spores >6.5 µm; clamp connections absent" (Section *Phaeocollybia*); "...non-capitate but versiform cheilocystidia, clamp connections [present], spores >6.5 µm" (Section *Subattenuatae*); "...attenuated to subacute and often apically capitate cheilocystidia; no clamp connections, spores >6.5 µm" (Section *Versicolores)*; "...subcapitate or capitate cheilocystidia, clamp connections [present], spores <6.5 µm" (Section *Radicatae)*; and cheilocystidia "...rather variable ... often clavate to cylindrical, no clamp connections, spores <6.5 µm" (Section *Microsporae).*

Recently Bandala and Montoya (1994) proposed the erection of two subgenera -- Subgenus *Phaeocollybia,* into which they placed the three sections characterized by an absence of clamp connections (Sections *Phaeocollybia, Versicolores,* and *Microsporae*), and Subgenus *Fibulo-phaeocollybia* into which are placed sections characterized by the presence of clamp connections (Sections *Subattenuatae* and *Radicatae*).

It should be noted that earlier Horak (1977) suggested that new sections of *Phaeocollybia* not be proposed until *Galerina, Gymnopilus,* and *Pyrrhoglossum* had been fully revised as well. Comparison of morphological and molecular characters during the current study (*q. v.* Chapters 4 & 5) suggest that taxonomic classification at the sectional and subgeneric levels is probably premature, although preliminary analyses of molecular data obtained from Pacific Northwest specimens confirm the diagnostic potential of cheilocystidial morphology for recognizing monophyletic groups of species within the genus. For the time being, however, classification between specific and generic levels would best be postponed until DNA sequence data can be obtained, fully analyzed and correlated with morphological and ecological data from a majority of world's species of *Phaeocollybia* and sister genera.

Taxonomic position of *Phaeocollybia* and related genera

When he described the genus *Phaeocollybia*, Heim (1931) suggested a generic affinity with *Cortinarius* (same general aspect and basidiospore color and morphology) and some European species of *Collybia* with radicating stipes. Since 1931 most agaricologists have placed *Phaeocollybia* in the Cortinariaceae, a family characterized by basidiomes with ornamented brown basidiospores lacking germ pores and having lamellae with parallel to sub-parallel gill trama (*cf.* Watling, 1996). The absence of a veil and the presence of a glabrous viscid umbonate pileus, cartilaginous stipe cortex, and pseudorhiza are considered the most important suite of characters delimiting *Phaeocollybia* from other members of that family (Singer 1951b, Smith 1957b, Horak 1977, Horak 1989, Gulden 1983, Jacobsson and Stridvall 1983, Redhead and Malloch 1986, Nezdominogo 1990, Bon 1992, Watling and Gregory 1993, Bandala 1994, Rees and Wood 1996). In his treatise *Les hymenomycetes agaricoïdes*, Kühner (1980) proposed a novel classification which included the presumably non-ectomycorrhizal Cortinariaceae -- *Phaeocollybia, Galerina,* and *Gymnopilus* -- in the Strophariaceae.

Smith (1957b) considered *Phaeocollybia* most closely related to *Cortinarius* but acknowledged the differences separating the two genera. In particular he alluded to the common ancestry implied by the similarity of certain representatives of *Cortinarius* Subgenus *Myxacium* and *P. kauffmanii* (Singer) Smith, pointing to the thin-walled cheilocystidia, absence of clamp connections in the cuticular hyphae of the pileipellis, general spore morphology and size and the overall stature of the stipe. He and other workers (Horak, 1977, Singer, 1986; Bandala, 1994) noted the absence of veil remnants and the cartilaginous stipe cortex found in *Phaeocollybia* as being the most significant characters separating it from *Cortinarius*. Smith (1957b) also noted the similarities between thin-walled long filamentous subcapitate cheilocystidia found in some species of *Phaeocollybia* to those found in *Hebeloma*, a cortinariaceous genus that was otherwise quite different.

More frequently cited are the similarities between *Phaeocollybia* on the one hand and *Galerina* and *Gymnopilus* on the other. Horak (1977) in particular mentions the similar deep-yellowish-brown to rusty brown coloration of the basidiomes shared by the majority of representatives in all three genera. While *Galerina* also shares numerous microscopical similarities, most authors state that because Galerinas with ornamented spores consistently lack clamp connections (Smith, 1957b; Singer, 1986; Bandala, 1994) and because the general aspect and habit of *Galerina* and *Phaeocollybia* basidiomes are so different, the two genera appear well separated from each other.

Phaeocollybia and *Gymnopilus* also share common basidiome coloration (including the lilac colored pileus and lamellae of some species in both genera), spore ornamentation, and cheilocystidia (Horak, 1977; Kühner, 1980; Bandala, 1994; Rees & Wood, 1996). The long list of characters distinguishing *Gymnopilus* from *Phaeocollybia* include ubiquitous clamp connections (Horak, 1977; Singer, 1986), consistently KOH-soluble pigments (Smith, 1957b; Horak, 1977; Bandala, 1994), woody substrates, lack of a pseudorhiza (Singer, 1986; Bandala, 1994), a bright orangish-brown spore print (Smith, 1957b; Singer, 1986), attached lamellae (Singer, 1986), and lack of cartilaginous stipe cortex (Smith, 1957b) found in *Gymnopilus*.

In his revision of the genus *Pyrrhoglossum*, Horak (1989) considered that genus to be the most closely related genus to *Phaeocollybia*, citing similarities in basidiome coloration, the instability of the pigments in KOH, spore types and cheilocystidial shape. Acknowledging the obvious differences in habit and stipe morphologies, he noted that '*Pyrrhoglossum* can be considered a conglomerate of ecotypes (form genus) which embraces taxa of *Phaeocollybia* with pleuropodial habit ecologically adjusted to decaying logs and trunks as substrate.'

Recent recognition of the existence of a pellicular veil in *Phaeocollybia* (Norvell, 1997a; *q. v.*, Chapter 2) has removed one of the most frequently cited differences separating *Phaeocollybia* from *Cortinarius* and *Gymnopilus* and supports inclusion of the genus within the Cortinariaceae. Likewise, the discovery of mycorrhizal species in the genus (Norvell, 1997; *q. v.*, Chapter 2)

would suggest that placing *Phaeocollybia* into the saprophytic Strophariaceae as earlier suggested by Kühner (1980) is ill advised. A full discussion of morphological and molecular characters, species concepts, and complete genus description is presented below in chapters 3-6.

Table 1.1 Historically proposed sectional and subgeneric classifications of *Phaeocollybia**

Section name:	**Section *Phaeocollybia:***	**Section *Versicolores:***	**Section *Microsporae:***	**Section *Subattenuatae:***	**Section *Radicatae:***
type species	*P. festiva*	*P. lugubris*	*P. jennyae*	*P. subattenuata*	*P. radicata*
Cheilo shape; Clamps; Spore length	clavate; absent, >6.5 µm	capitulate; absent; >6.5 µm	variable; absent; <6.5 µm	clavate; present; >6.5 µm	variable; present; <6.5 µm
Smith (1957)	*attenuata, fallax, festiva, kauffmanii, laterarius, lilacifolia, 'similis', sipei*	*californica, christinae, jennyae, lugubris, pseudofestiva, radicata, spadicea*	-----	-----	-----
Singer (1970, 1986)	*christinae, fallax, festiva, kauffmanii, lilacifolia, muscicolor, neosimilis, olivacea, quercetorum*	*californica, cidaris, columbiana, lugubris, mexicana, spoliata,*	*corneri, jennyae, rancida, ratticauda, sipei*	*amazonica, brasiliensis, elaeophylla, megalospora, oligoporpa, similis, subattenuata*	*arduennensis, flava, radicata*
Bandala & Montoya (1994) (Parentheses = no type examination)	*ambigua, attenuata, christinae, fallax, festiva, kauffmanii, muscicolor, neosimilis, odorata, piceae, procera, quercetorum, similis, singeri*	*californica, (cidaris), (columbiana), lugubris, martinicensis, olivacea**, *pseudofestiva*	*(caudata), (corneri), guzmani, jennyae, (parvispora), (querqueti), (ratticauda)*	*(brasiliensis), (deceptiva)*, (elaeophylla), latispora, (megalospora), oligoporpa, spoliata, subattenuata, viridis*	*arduennensis, (bicolor), (minuta), (oregonensis), radicata, smithii, (tentaculata)*

*PNW species underlined

CHAPTER 2: DEVELOPMENTAL AND BIOLOGICAL OBSERVATIONS[1]

As noted in Chapter 1, *Phaeocollybia* was first characterized as a genus within the Cortinariaceae by the formation of a pseudorhiza, rough-brown spores, and the absence of a veil (Heim, 1931; *cf. also* Smith, 1957b; Horak, 1977, 1989; Redhead & Malloch, 1986; Watling & Gregory, 1993; Bandala, 1994). The presence of tibiiform diverticula on the pseudorhizae has since been added as a reliable generic feature (Redhead & Malloch, 1986; Laber, 1991; Redhead & Norvell, 1993; Norvell, Ammirati & Redhead, 1994a). With the exception of the study by Redhead and Malloch (1986), no previous investigator has been able to trace the origins of *Phaeocollybia* basidiomes. Additionally, the difficulty of studying relatively rare fungi that form their initials deep underground and that have not yet been successfully cultured has forestalled developmental and biological studies.

The temperate rainforests of western North America support many *Phaeocollybia* species, some relatively common. This abundance of fruiting bodies has presented an opportunity to excavate basidiomes belonging to several species and then to trace their origins, locating numerous primordia in the process. These successful excavations have also revealed hitherto unanticipated variations in growth patterns and offered insights into the biology of the genus which are presented here for the first time.

Materials and Methods

Basidiomes of 24 *Phaeocollybia* species (out of 25 identified to date) were collected from temperate coniferous rainforests in British Columbia, Washington, Oregon and California (Tables 2.1-2.3). Intact pseudorhizae and rhizomorphic pseudorhizae were obtained from field excavations or from blocks of soil removed to the laboratory for extrication under a Wild dissecting microscope. Roots, rootlets, mycelia, and rhizomorphic pseudorhizae were teased apart with needles from the surrounding soil matrix and photographed or sketched free-hand before being sectioned for microscopical examination. Primordia and/or immature basidiomes discovered during the excavation process were either observed fresh immediately after excavation or preserved in FAA (formalin: glacial acetic acid: 50% ethanol --15 mL: 5 mL: 20 mL) or 90% ethanol or dried for later examination. Ecological and morphological observations were recorded, and fresh specimens were examined microscopically and photographed, photocopied, and/or sketched before low heat forced-air drying.

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[1]In press by Mycological Research under the title 'Observations on development, morphology and biology in *Phaeocollybia* (different format)

Primordia and immature basidiomes were first examined intact under a Wild or Zeiss dissecting microscope. Specimens were then hand-sectioned to produce longitudinal and transverse sections and mounted in water or 6% aqueous KOH for examination under Kohler illumination, differential interference contrast (DIC), or phase contrast using a Leitz DMRB or Zeiss standard light microscope. Some preserved primordia lost tissue integrity during storage, but good sections were obtained from dried specimens, which were sliced dry and not rehydrated before mounting in KOH. Informative features were photographed, drawn with the aid of a drawing tube, or sketched free-hand. SEM observations were made on dried specimens rehydrated in moist chambers, fixed in osmium tetroxide, dehydrated in an ethanol series, critically point dried in Freon TF, and sputter-coated with gold/palladium in a Hummer V Sputter Coater.

Results

Initiation and early primordial development

Primordia were observed to originate anywhere from 30-300 mm below the soil surface in species-specific patterns, either from existing pseudorhizae or from mycelia concentrated within soil and decomposed humus or around rootlets with mycorrhizal tips. Growth appeared to modify the initial undifferentiated prosenchymatous hyphal knot into a stipitiform primordium with a compact pseudoparenchymatous interior and an exterior completely sheathed by a pellicular veil composed of cylindrical, parallel-aligned, 1-2 µm wide, thick-walled highly gelatinous hyphae covered with tibiiform secretory diverticula. Examinations of 1-4 mm long initials in three different *Phaeocollybia* species suggest that proliferation of tissue within the mid-section precedes pilear differentiation and further elongation *(Fig. 2.1)*. Primordia observed thus far have pellicular veils enclosing the hymenium until shortly before maturity (indicative of monovelangiocarpy). Examination of primordia from 14 *Phaeocollybia* species suggests that development in the genus is (pileo)stipitocarpic; hyphae in most appeared to retain their parallel orientation until formation of the lamellar cavity and differentiation of the pileus.

Pellicular veil and tibiiform diverticula

In 1992, a matted fibrillose veil was first noticed on young basidiomes of *P. rufotubulina* (Norvell & Ammirati, 1993). Subsequent examination of unexpanded primordia from that and 13 other *Phaeocollybia* species has revealed that all appear to be covered by primordial sheaths which later thin to agglutinated fibrils connecting the stipes and pilei of expanding young basidiomes *(Figs 2.1-2.2)*. Additional comparisons of numerous basidiomes in all stages of development show that *Phaeocollybia* is demonstrably velate, although it does not produce a membranous or cottony veil. Pellicular veils formed by progressive differentiation of hyphae within the primordial cortices (*cf.* 'universal veil', Gilbert, 1947) were consistently observed enveloping entire

primordia and protecting the developing hymenia. These moderately to heavily gelatinized pellicular veils are thought to result from monovelangiocarpous development (*cf.* Reijnders, 1986).

Examinations of young to mature specimens imply differential retention of the pellicular veil after pileal expansion (Norvell et al. 1994a). While most species exhibit short scattered fibrillose patches only occasionally on the aerial stipes, others retain relatively regular arrays of fibrillose patches, as are found in *P. spadicea* (*Fig. 2.2*), *P. fallax*, and *P. pseudofestiva*. *Phaeocollybia luteosquamulosa*, first discovered in 1992, produces basidiomes with dry to moist pilei in which the silky appressed fibrils covering the pileus break up into scattered short fibrillose patches under dry or slightly humid conditions (*Fig. 2.2*).

Microscopic secretory structures (*Table 2.2; Figure 2.3*) were found on the pellicular veil in all *Phaeocollybia* basidiomes examined. These highly refractive diverticula, emanating directly from the cortical hyphae without intervening septa, are small (5-30 x 1 µm) and taper from slightly wider bases upwards to slender necks. Occasionally ligulate with only slightly inflated spathulate apices, most diverticula are tibiiform with minute capituli. Apical droplets are frequently visible surrounding the apices. Tibiiform diverticula were discovered anywhere on the basidiome retaining remnants of the pellicular veil, such as on pileus-stipe fibrils, fibrillose patches on stipe apices (*Fig. 2.3*) and pileal scales. They were abundant on all external surfaces of all primordia examined and equally abundant on the pseudorhizae of hundreds of basidiomes representing over 40 different species. They were also present on all *Phaeocollybia* mycelia identified (*Table 2.2*).

Pseudorhizal development and anatomy

The effort to collect and excavate specimens with as much care as possible produced a very large number of complete basidiomes with intact pseudorhizae. Individual shapes were influenced to a certain degree by substrate composition, and numerous twisted, coiled, curled or otherwise distorted pseudorhizae were collected from soils containing intact wood, roots, or stones around which the developing basidiomes presumably twisted in their upward path. However, pseudorhizae were found to have species-specific morphologies. Four primary fruiting patterns running the gamut from unbranched to occasionally branching to highly racemose were identified (*Table 2.3; Figs 2.4-2.5;* cf. also Norvell & Ammirati, 1993; Norvell *et al.*, 1994a).

[1] Vertical-monopodial (*Fig. 2.4*): Unbranched pseudorhizae were found to arise singly or gregariously from relatively blunt origins, usually located in the layer of quartz sand formed by leaching of clay, organic matter and certain minerals from the upper A to the lower B soil horizons (*i.e.* the 'albic' horizon, *cf.* Eyre, 1968). In some species pseudorhizae emanated from small (*ca.* 2-3 mm diam.) undifferentiated masses of fungal tissue. The pseudorhizae

gradually expanded upwards from their 1-2 mm diam. origins, reaching up to 300 mm in length and 15-20 mm in diameter at the soil surface in larger basidiomes. Firm interior piths, surrounded by 1-2 mm thick cartilaginous cortices, were present whether or not the aerial stipes were stuffed *(e. g. P. kauffmanii*) or hollow (*e. g. P. fallax).* Microscopical examination of the cortex revealed narrow, thick-walled, gelatinous dark brown hyphae, the outermost of which bore secretory tibiiform diverticula. Medullary tissues were composed of very long, wide, thick-walled rigid hyphae intermixed with branching, narrow, thin-walled flexuous hyphae; this dimorphism was noted over the entire pseudorhizal length, although the region of highest contrast between wall thicknesses appeared to vary in location according to species (see *Table 2.3*).

While most excavations of basidiomes of *P. spadicea* and *P. piceae* revealed pseudorhizae arising from either fungal masses or mycelium, the intact pseudorhiza of one *P. spadicea* basidiome (*cf.* LLN 92.10.15-12) was found attached to and confluent with a 30-mm long remnant of another pseudorhiza. Likewise, the characteristically upward-curled pseudorhiza of one young *P. piceae* specimen (*cf.* LLN 92.10.09-22) was found attached to the pseudorhiza of an older, still intact basidiome. In both instances the gross morphology (gradual upwards expansion from a 1-3 mm wide blunt tip), tissue organization, and anatomy parallels that described above for the solitary forms.

[2] Lateral-monopodial *[Figs 2.5,3,28]: Phaeocollybia attenuata* and *P. 'similis'* produce small basidiomes with 2-5 mm wide fistulose stipes attached to very thin, wire-like pseudorhizae. Attempts to trace these thin pseudorhizae to their origins in the denser soil below the loose moss and needle-duff were frequently frustrated by sudden lateral turns, after which the wire-like threads ran parallel to one another, frequently traveling distances greater than 100 mm from the lateral bends. Although these pseudorhizae sometimes appeared to merge with neighboring pseudorhizae, closer inspection revealed that each origin was in fact discrete, with one pseudorhiza terminating abruptly at the cortex of another pseudorhiza and not confluent with it. Numerous 'wires' were traced to 125-300 µm widths before being accidentally broken. Three longitudinal zones were noted for these pseudorhizal 'wires' (Table 1): [a] closest to the origin, an *elongation* zone with a narrow pale cortex composed of interwoven narrow hyphae and a wider dark brown sub-cortex composed of parallel-aligned, tapered, relatively wide, thick-walled gelatinous hyphae surrounding a pale medulla of slightly narrower, less thick-walled hyphae loosely encircling an ill-defined central cavity; [b] an intermediate *expansion* zone with wider sub-cortical hyphae and a slightly dimorphic medulla with thin-walled, wide unbranched and narrow branched hyphae intermixed with occasional long wide thick-walled hyphae; and [c] nearest the upper pseudorhiza, a *transition* zone in which the pale interwoven cortex disappeared, making the dark brown sub-cortical

zone the outer layer and pale medullary tissues now composed of cylindrical, long, wide, thick-walled rigid hyphae and narrow, branched, thin-walled flexuous hyphae. The outermost hyphae were diverticulate in all three zones.

[3] Sequential-racemose *[Figs 2.5, 3.29]*: In several collections of *P. rufotubulina* in which masses of moderately sized basidiomes in different stages of maturity were borne on tall tubular stipes, several to many pseudorhizae branched singly to successively from subterranean lateral pseudorhizae. Narrow 1 mm wide pseudorhizal threads, arising either from soil mycelia or 'nurse' pseudorhizae of older basidiomes, were observed running more or less horizontally through the sandy substrate distances above 60 mm before turning sharply upward (similar in manner to *P. attenuata*). The threads usually traveled vertically only 10-25 mm before merging with sharply swollen (to 5-10 mm diam) emergent stipes. The medullary regions of the thready portions of the pseudorhizae resembled those found in vertical-monopodial pseudorhizae. However the narrow dark cortices were composed of a tangle of interwoven and parallel-aligned elements: long fusoid to cylindrical thick-walled rigid hyphae with dark red-brown parietal pigments were intermixed with short narrow thin- to thick-walled branching flexuous hyphae and frequent collapsed inflated thin-walled hyphae that were 20-40 µm diam. 10-20 µm inward from 5-6 µm wide septa. Patches of interwoven pale mycelium frequently adhered to the outermost diverticulate cortical hyphae.

[4] Fasciculate-Racemose *[Figs 2.5, 3.20, 3.30]*: In *P. scatesiae*, masses of moderately-sized heavily glutinous basidiomes with 5-8 mm diam. hollow stipes and individual pseudorhizae were seen to emanate from the apices of subtending pseudorhizal strands. Here single 2-4 mm thick sparingly branched strands of indeterminate length gave rise to large fascicles of primordia and basidiomes (some 'starbursts' contained 80 differentially developed basidiomes erupting from one point, *cf.* Norvell *et al.*, 1994a). The subtending cords either attenuated within 2-3 cm or descended relatively long distances before appreciably narrowing in diameter. Efforts to excavate the subtending pseudorhizae to their ultimate origins were unsuccessful, but lengths up to 150 mm were retrieved. Each subtending strand was transversely zoned into a cortex of gelatinized moderately thick-walled dark hyphae and a medulla of long, cylindrical, wide, very thick-walled, rigid hyaline hyphae (intermixed with occasional branched, narrow, thin-walled, flexuous hyphae).

All pseudorhizae possessed medullary tissues composed of two distinct hyphal types: very long, inflated, unbranched thick-walled "vessel" hyphae were surrounded and supported by narrow, highly-branched, thin-walled flexuous hyphae. This distinctive mixture, highly reminiscent of 'sarcodimitic' tissue as described by Corner (1966), was generally found at some point within both pseudorhiza and lower stipe. Distribution of sarcodimitic tissue *(Fig. 2.6)* elsewhere in

mature basidiomes varied according to species. Often only vestiges were visible in the tramas of the pileus, lamellae, and the stipe apex (*e. g. P. attenuata)* where differences between wall thicknesses were less prominent, although there were robust specimens where sarcodimitism was well developed in all tramal tissues *(e.g. P. benzokauffmanii).*

Pilear differentiation and cavitation

Pilei generally did not expand nor lamellar cavities develop until after the primordia extended some distance from their points of origin and pileal constrictions had begun to form below the stipe apices. The stipitiform primordia differentiated in species-specific patterns as they approached the soil surface. For example, uniformly pale primordia of *P. 'similis' (Fig. 2.7)* collected within 5 cm of the surface displayed a faint constriction line between the future pileus and stipe; larger primordia with more swollen, darker apices above deeper constrictions developed a highly gelatinized, parallel-aligned cutis between the pellicular veil with its diverticulate hyphae and the internal medulla. Longitudinal sections revealed a sarcodimitic medulla with thick- and thin-walled hyphae gradually becoming equally thin-walled toward the central core; all hyphae were longitudinally parallel to well above the stipe apex, whereupon they turned outward around a small lamellar cavity lined with numerous diverticula, indicative of stipitocarpic development. On the other hand, pileostipitocarpy was inferred from examination of an 8-mm high primordium of *P. kauffmanii* found 20 cm below the surface: here longitudinally-aligned rigid hyphae within the fully-developed sarcodimitic medulla intercepted a zone of interwoven hyphae slightly above the newly-developed lamellar cavity (in which tibiiform diverticula -- present on all exterior surfaces except the highly gelatinized parallel-aligned pileipellis -- were noticeably absent) *(Fig. 2.7).* Examinations of primordia from *P. scatesiae* and *P. rufotubulina (Figs 2.7, 3.21-3.22)* suggest that cavitation and subapical constriction are synchronous; in the latter species tibiiform diverticula, abundant on all external surfaces, were found occasionally within the lamellar cavity. In *P. scatesiae* the primordial pileipellis was composed of the tangled mass of hyaline narrow hyphae within a dense gelatinous matrix characteristic of the mature pileipellis in this highly glutinous species.

Hymenial development, pileal expansion, and basidiome emergence

Lamellar initials generally appeared to form as centripetally radiating ridges within the lamellar cavity *(Fig. 2.8).* As the pileus expanded, intervening successive ranks of lamellular ridges appeared between these primary ridges, characteristically resulting in a polydymous pattern of five or more tiers of lamellulae irregularly interspersed among lamellae. Enlargement of the cavity and orientation of internal hyphae along the axes of the newly emergent ridges preceded formation of a parallel-aligned (*i.e.* 'regular') trama *(Fig. 2.9)* and emergence of the hymenium. A broad central trama (*i.e.* mediostratum) was generally observed; basidia and basidioles with occasional

filamentous 'paraphyses' usually arose from a rudimentary subhymenium consisting of the slightly narrower and more highly septate outermost tramal hyphae. A chronology for subsequent hymenial development, pileal expansion and rupture of the pellicular veil, and basidiome emergence has been developed based on species specific patterns observed in numerous primordia and immature basidiomes.

Some pilei (often in species producing smaller or ephemeral basidiomes) expand while still well below ground. In *P. attenuata* and *P. 'similis'*, pre-emergent pilear expansion occurs after partial hymenial development, rupturing the pellicular veil in such a way as to deposit short fibrillose patches at the apex of smooth shiny strict stipes; after emergence the pileus becomes fully broadly campanulate and the stipe, formerly stuffed with loose fibrillose pith, elongates and becomes hollow. However, numerous observations of primordia in another hollow-stiped species, *P. scatesiae*, suggest a different developmental sequence. After cavitation (but before full development of the lamellar ridges), the pileipellis is composed of three layers: a suprapellis (here the pellicular veil) of dark cortical hyphae overlying a mediopellis of hyaline hyphae embedded in a gelatinous matrix and a subpellis of wide pigmented hyphae. As the hyphae begin to align perpendicularly to the stipe axis in preparation for lamellar differentiation, sarcodimitic tissue is still visible in the medullary tissues of the upper stipe, and tibiiform diverticula can be seen on the pellicular hyphae remaining on the protected pileus edges. With pileal expansion (occurring well below the soil surface before complete basidial maturation), diverticulate hyphae can be found only in patches at the pileus edge and on the apical stipe. Unlike *P. attenuata* and *P. 'similis'*, the strict glutinous stipe of *P. scatesiae* becomes noticeably hollow well before emergence. In all three species, however, the expanded pileus appears to protect the fibrillose patches from removal on the smooth, polished stipe apex during final upward expansion through the soil.

Other pilei (generally associated with larger, longer-lived basidiomes in other species) do not fully expand until well above the soil surface. In *P. kauffmanii* separation of the veil into matted fibrillose strands connecting pileus and stipe preceded lamellar ridge formation in two primordia examined at this developmental stage. In basidiomes from other species, the pileus, long remaining closely appressed over the stipe apex, did not begin full expansion until within a few cm of the soil surface, after which most veil tissues were ruptured, leaving occasional fibrillose remnants of veil tissue on the stipe just below the still strongly inrolled pileus or beneath protrusions on the pseudorhizae. Mature basidia were observed in one pre-emergent *P. olivacea* specimen but were almost uniformly absent in pre-emergent (as well as some post-emergent) *P. kauffmanii* and *P. redheadii* basidiomes. Observation of two *P. kauffmanii* and *P. redheadii* clusters *in situ* over four weeks suggests that basidiomes in those species mature particularly slowly. Microscopical examination of numerous partially expanded post-emergent basidiomes in both species consistently revealed infrequent mature basidia projecting 10 μm above far more

numerous immature basidia and basidioles. Stipes in these more robust species remain stuffed with a conspicuous firm pith even when fully mature.

Cheilocystidial development

Two basic types of cheilocystidia were observed: those with thin-walled, more or less clavate apices *(Fig. 2.9)*, and those with thick refractive necks and secretory apices with or without small secretory capituli (*i.e.* 'tibiiform', *Fig. 2.9)*. Observations of mature lamellae indicate that the clavate cheilocystidia emanate directly from and are in fact the terminal ends of tramal hyphae. Examination of immature *P. attenuata, P. benzokauffmanii, P. kauffmanii, P. oregonensis* and *P. redheadii* lamellae show that clavate ends of the mediostratal hyphae extend beyond the edges of the lamellar ridges as the hymenium is forming on the lamellar faces.

Examinations of primordia in similar stages of development in two species that produce basidiomes with tibiiform cheilocystidia (*P. scatesiae* and *P. rufotubulina)* indicate a different developmental sequence *(Figs 2.8, 3.27)*. There is simultaneous development of hymenium and cystidia in *P. scatesiae*, but cystidial formation appears to precede hymenial development in *P. rufotubulina*. In both, however, tibiiform cystidia completely cover the faces and edges of the immature lamellae. The ultimate origin of these cystidia is unclear, for the refractive capitulate morphology is identical to (and possibly homologous with) that of the tibiiform diverticula earlier seen to line the newly formed lamellar cavity. True pleurocystidia are rare in *Phaeocollybia* (although the recently named *P. pleurocystidiata* does possess them in abundance), and while tibiiform pleurocystidia were found to co-exist with infrequent spore-bearing basidia on immature lamellae in both species, only basidia, basidioles and tibiiform cheilocystidia were present in mature basidiomes.

Observations of mature gill tissues in *Phaeocollybia* indicate that once formed, refractive tibiiform cheilocystidia cease further apical elongation, although they appear to function as secretory organs throughout the life of the basidiome. On the other hand, clavate cheilocystidia appear to exhibit indeterminate growth, continuing to extend apically unless ruptured, as inferred from comparisons between freshly collected specimens and those stored for long periods of time (in one instance cheilocystidial development was tracked over a two-week period). Close inspection of what initially was thought to be the only known successful *Phaeocollybia* tissue culture revealed that the fuzzy whitish mat surrounding the explanted lamellae was composed entirely of long senescing apical extensions from cheilocystidia and occasional basidioles and basidia. Such apical outgrowths *(Fig. 2.9)* have since been observed in freshly collected basidiomes as well, usually in mature or senescent individuals. Some species characterized by clavate cheilocystidia such as *P. fallax*, however, appear not to develop these developmental 'artifacts'.

Evidence of ectomycorrhizal associations

Examination of substrates associated with basidiomes of five different species has provided the first convincing evidence for mycotrophy in *Phaeocollybia*. In one instance, several small clusters of young *P. redheadii* basidiomes enclosed in soil were removed from their site under noble fir and western hemlock (LLN 93.11.05-1, *Fig. 2.11*). Careful separation of soil from pseudorhizal origins exposed primordia emanating from small compact 2-5 mm diam. masses of undifferentiated fungal tissue into which short rootlet branches protruded *(Fig. 2.11)*. Microscopical examination revealed fungal masses confluent with emergent pseudorhizae (eleven from one mass in one instance) completely surrounding one or more healthy and/or senescent rootlets *(Fig. 2.12a)*. The diverticulate gelatinized hyaline hyphae characteristic of *Phaeocollybia* mycelium were found leading to straw-colored mantles surrounding knob-like short branches *(Fig. 2.12b-d)*; the presence of Hartig nets *(Fig. 2.12c)* confirmed that these branches were in fact ectomycorrhizal tips. Similar undifferentiated fungal masses have also been retrieved with basidiomes of *P. kauffmanii* (LLN # 93.10.24-1) and *P. benzokauffmanii* (cf. LLN # 95.10.23-5), and the characteristic diverticulate hyphae leading to ectomycorrhizal tips with Hartig nets were noted for those species, as well for *P. pseudofestiva* (LLN # 92.11.21-1) and *P. spadicea* (LLN # 93.11.04-6). White cottony wefts of mycelium bearing tibiiform diverticula were also found running through the soil and surrounding small soil clumps around *P. pseudofestiva* and *P. spadicea* pseudorhizae. It should also be noted that all Pacific Northwest *Phaeocollybia* species described thus far have been found in forests containing *Tsuga, Picea, Abies, Pseudotsuga, Lithocarpus, Quercus* and/or *Pinus* -- all genera known to form ectomycorrhizae (*cf.* Allen, 1991)

Discussion

Ontogeny in Phaeocollybia

Phaeocollybia has long been a genus with an 'unknown' ontogeny (*cf. inter al.* Kühner, 1980; Singer, 1986; Watling & Gregory, 1993). Retrieval of primordia and immature basidiomes in the current study has enabled developmental observations to be made on representatives from 14 different species. All Phaeocollybian primordia examined appear to be monovelangiocarpic with a gelatinous pellicular veil; subsequent development follows either the 'stipitocarpic' or 'pileostipitocarpic' patterns demonstrated by most of the other Cortinariaceae genera already investigated by Reijnders (1979) and Watling (1985). (It is noteworthy that among closely related genera in the monovelangiocarpic Inocybeae, all 10 *Inocybe*, 3 out of 4 *Hebeloma*, all 4 *Galerina*, and all 5 *Gymnopilus* species studied were diagnosed by Reijnders or Watling as stipitocarpic). It appears at this time that a (pileo)stipitocarpic monovelangiocarpy may well be general throughout the genus *Phaeocollybia*, at least in western North America.

Identification of developmental stages has aided in identifying which morphological characters are less developmentally variable and thus more helpful in diagnosing species. The fact that dimensions, shape, and colour of a pileus change as a basidiome matures is well recognized. This is no less true anatomically. In *Phaeocollybia,* for example, while cheilocystidial morphology is considered a key character, lengths and widths may vary according to developmental stage, making dimensions less informative. While widths of clavate cheilocystidia in mature lamellae appear to follow species-specific ranges, lengths are highly variable and reflect the inherently indeterminate nature of these cells. This is not unique to *Phaeocollybia:* in the Bolbitiaceae, Watling (1975) observed proliferation and lengthening of cheilocystidia on lamellae tracked microscopically in a damp chamber, and in *Coprinus,* Moore (1996) found that all differentiated cells except basidia reverted to vegetative growth after gill explantation onto agar. The tendency of some mature or senescent clavate cheilocystidia to form apical outgrowths should be remembered when noting the cheilocystidial morphology of potentially new species. On the other hand, few tibiiform cheilocystidia have been observed with apical outgrowths. These cheilocystidia appear to exhibit determinate growth and may be derived from the tibiiform diverticula with which they are analogous, if not homologous. The presence of diverticula within newly formed lamellar cavities in immature basidiomes may be erroneously interpreted as cheilocystidial initials. Observation of tibiiform diverticula within the cavity of *P. attenuata,* a species with clavate cheilocystidia, suggests in that instance either proliferation of the pellicular veil into the cavity or formation of possible lipsanenchyma over the developing hymenium.

New generic concepts

Collection and comparison of hundreds of fresh basidiomes representing over 24 different species have provided a unique opportunity to evaluate the taxonomic importance of certain characters. Discovery of a pellicular veil and confirmation of secretory tibiiform diverticula in all Phaeocollybias thus far examined strongly imply that these are generic characters equal in importance to those traditionally used to delimit the genus (e. g. pseudorhizae, gelatinized tissues, brown ornamented basidiospores). Sarcodimitism, closely tied to development and present wherever support is structurally beneficial (*e. g.,* during the elongation phase in primordia), may likewise be generically significant. (That the differential retention of the dual hyphal system in mature individuals (from strongly developed in massive basidiomes such as *P. benzokauffmanii* to non-existent in the epigeous tramal tissues of more fragile individuals such as *P. phaeogaleroides.*) has already been noted above.)

Phaeocollybia has been treated as an 'evelate' member of the Cortinariaceae since Fries (1838) first described the subtribe that would later form the core of *Phaeocollybia* as having 'absolutely no veil' (*velum absolute nullum).* The fact that Heim (1931) made no mention of a veil in his

circumscription of *Phaeocollybia* implies that he considered this feature to be lacking in the genus. Some authors have alluded to its possible existence (*e.g.* "...veil rudimentary, pruinose, practically absent even in young specimens...." -- Singer 1986; *cf.* also Moser & Jülich, 1994), but none have had the opportunity to provide any evidence. Most other authors agree that there is no evidence for a fibrillose veil as occurs in *Cortinarius* or *Gymnopilus* (*e.g.*. Smith, 1957b; Kühner, 1980; Watling & Gregory, 1993), and in a comprehensive overview of 33 *Phaeocollybia* type specimens, Horak (1977) stated that "...so far none are known with persistent veiled remnants, either on the margin of the pileus or on the stipe...." The successful retrieval and examination of unexpanded primordia representing so many different species have substantially contributed to the hypothesis that all Phaeocollybias possess a pellicular veil. Once the existence of such a veil is acknowledged, other characters can be reinterpreted as differentially retained veil remnants (*e.g.* the short fibrillose patches on apical stipes in *P. fallax* and *P. spadicea* or the appressed short scales on the pilei in *P. luteosquamulosa).*

The existence of the pellicular veil has also been indicated by the presence of the tibiiform diverticula found on the pseudorhizae of all Phaeocollybias examined thus far. An integral part of the mycelium and the pellicular veil, tibiiform diverticula were first reported in 1986 by Redhead & Malloch (as 'caulocystidia'), who discovered them on pseudorhizal pelli on several North American and European Phaeocollybias (*e.g. P. christinae, P. jennyae).* Laber (1991) observed them on the pseudorhizae of other European species and concurred that they might be generically significant. Since then diverticula have been reported for western North American (Redhead & Norvell, 1993; Norvell & Ammirati, 1993; Norvell *et al.*, 1994a) and Australian *Phaeocollybia* species (Rees & Wood, 1996) as well. Redhead and Malloch (1986) also noted their occurrence on the mycelium surrounding the pseudorhizal origin of *P. christinae,* and diverticula have been observed on mycelia in eight western species in the current study (*Table 2.2*).

The tibiiform diverticula are in their own right a generically significant feature separating *Phaeocollybia* from the rest of the Cortinariaceae. Their taxonomic utility was first demonstrated by Redhead & Smith (1986), who excluded *P. perplexa* from the genus and placed it into the monotypic *Stagnicola* in part because of the absence of tibiiform diverticula. Their more scattered distribution on aerial portions of the basidiome is tied to differential retention of the pellicular veil and is undoubtedly influenced by the amount of abrasion to which the expanding primordium is exposed. 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 gelatinise early in development, the fragments of the veil can move easily and are pushed off by heavy clays." It is noteworthy that in *P. luteosquamulosa* the most visibly squamulose pilei were collected from highly humic soils that Watling and Largent (1976) indicated could supply moisture to the expanding pileus.

Diverticula have been reported on the mycelia of other agaric genera. Lamoure (1958) reported similarly sized aseptate diverticula on secondary mycelium of *Clitocybe senilis* Fr. (confirmed in a Pacific Northwest collection, Norvell, unpub. data) and noted their similarity to the putative conidia observed by Vandendries (1937) on the mycelium of *Agrocybe pediades* (Fr.) Fayod. (Examination of the latter elements convinced Lamoure (1958) that because they lacked basal septa and had permanently attached capituli, they were not conidial in nature.) Watling (1981) noted the presence of "diverticulae" of unknown function in cultures of *Schizophyllum commune* Fr. and two *Coprinus* species. Morphologically similar diverticula have also been reported on the mycelia of *Stigmatolemma* (Redhead, 1973), *Resupinatus* (Thorn & Barron, 1986), *Pleurotus* (Barron & Thorn, 1987), and *Conocybe lactea* (J. E. Lange) Métrod and *Panaeolina foenisecii* (Pers. : Fr.) Maire (Hutchison *et al.*, 1996). Some diverticula have been shown to secrete repellent or toxic compounds and have been linked to nitrogen-utilization in substrates with high C:N ratios (see Barron & Thorn, 1987; Hutchison *et al.* 1996). The specific function of Phaeocollybian diverticula, believed to operate in a glandular capacity of some sort, remains unknown.

Since Corner first introduced sarcodimitism to describe tissues found in cantharelloid genera in 1966, the system has been recognized in several other genera, primarily those in the white-spored Xerulaceae (Redhead, 1987; Bas, 1990; Corner, 1991; Norvell, Redhead & Ammirati, 1994b). The presence of sarcodimitism in *Phaeocollybia* is surprising when one considers its rarity within brown-spored genera. However, it may be structurally significant, for basidiomes in other unrelated pseudorhizal genera *(e.g. Caulorhiza, Termitomyces, Xerula)* that similarly must push through deep substrates also possess the tissue. The parallel, wide, thick-walled, rigid cylindrical hyphal 'vessels' are kept from separating under apical pressure by the many-branched, winding, thin-walled narrow hyphae, resulting in a resilient toughness that may help a developing basidiome to push upwards through the soil a long distance from its point of origin or enable one thin pseudorhiza to support multiple basidiomes as found in *P. scatesiae*. Sarcodimitic tissues have been noted in almost all *Phaeocollybia* basidiomes examined thus far, although often confined to the pseudorhizae. Whether sarcodimitism is taxonomically significant at a generic level remains to be seen.

The presence of this dual hyphal system can complicate interpretation of microscopic features, particularly when combined with the heavy gelatinous matrix present in most *Phaeocollybia* basidiomes. One difficulty encountered in the current study has been attempting to differentiate clamp connections from the thin-walled flexuous hyphae, particularly when clamp connections are not constant throughout all tissues. The rigid cylindrical elements with their highly gelatinized, very thick walls discourage easy optical sections and often obscure the highly branched, narrower thin-walled hyphae winding around and behind the larger elements. Branch termini *(Fig. 2.6)* of

the more flexuous hyphae frequently resemble clamp connections in both appearance and size, particularly when they appear at a septum of a larger vessel hypha. The use of differential interference contrast is particularly helpful in detecting whether a 'clamp' is genuine or an errant hyphal end.

Function of the pseudorhiza

Among the brown-spored agarics, the hallmark of the genus *Phaeocollybia* has been the long, unbranched, 'rooting' stipe sheathed in a cartilaginous cortex. Fayod (1889), who felt that the term 'rooting' wrongly implied downward growth, introduced the term 'pseudorhiza' in his treatment of *Collybia radicata* (now placed in *Oudemansiella* or *Xerula).* Buller (1934), who confirmed that primordia of *C. radicata* elongated upwards through the soil from a buried substrate with the resultant pseudorhizal length dependent upon the amount of soil between substrate and soil surface, described pseudorhizae for many different genera and differentiated between perennial and annual types. Although Singer (1986) suggested using 'sympodium' and 'geopodium' to distinguish between the perennial branching pseudorhiza found in *Gymnopus fusipes* (Bull.:Fr.) Gray (as *Collybia)* and the more common annual pseudorhiza, most authors (including Singer) refer to the latter as simply a 'pseudorhiza'.

Highly branching annual pseudorhizae have been described for *Coprinus* (*cf.* Brefeld, 1877; Buller, 1934), but most genera with annual pseudorhizae are said to possess simple unbranched extensions of the stipe (*cf.* Singer, 1986). All previous monographers have presumed that each *Phaeocollybia* basidiome is also borne by a single pseudorhiza that grows more or less directly upwards from its point of origin. However, recognition in the current work of four different pseudorhizal patterns indicates that these hallmark structures are highly evolved organs that obviously respond to different parameters than the strictly 'stipitomorphic' pseudorhizae previously thought to characterize *Phaeocollybia.* Additionally, observations of pseudorhizae emerging from other pseudorhizae and of multiple primordia arising from the apex of a solitary subtending pseudorhizal strand strongly suggest localized meristematic activity. It now appears that some Phaeocollybian pseudorhizae are both structurally and functionally similar to rhizomorphs.

Rhizomorphs, macroscopically visible compact strands of parallel hyphae that run through substrates, are highly differentiated, fully autonomous organs that grow apically and that can extend from food-bases into substrates that may not support their growth (*cf.inter. al.* Burnett, 1976; Singer, 1986; Moore, 1996). Rhizomorphic development and physiology have been intensively studied in numerous genera since Hartig (1874) first analyzed rhizomorphs of *Armillaria mellea* (Vahl.: Fr.) P. Kumm., although no rhizomorphs have been identified for

Phaeocollybia. Observation of rapid apical elongation and anatomical comparison of tissues in growing tips led Brefeld (1877) to hypothesize the existence of an apical meristem. The presence of rhizomorphic 'meristems' has since been generally accepted (Snider, 1959; Motta, 1969; Burnett, 1976; Garraway, Hütterman & Wargo, 1991; Hawksworth *et al.*, 1995), although Moore (1996), emphasizing that "...meristems do not occur in fungi..." strongly advocates use of Reijnder's 'meristemoids', which will be followed below.

In discussing the gross morphology of the basidiome, Singer (1986) used 'rhizomorph' only to refer to "...true, eventually black..." strands, employing 'thallorhizae' to refer to white mycelial strands. Most true rhizomorphs are assigned to one of four categories developed by Townsend (1954) based on degree of hyphal differentiation (*i. e.* (i) -- largely undifferentiated; (ii)-- zonate with similarly sized hyphae; (iii) -- zonate with differently-sized hyphae; (iv) -- zonate with differently sized hyphae with variously thickened walls), with most parasitic and ectomycorrhizal rhizomorphs exhibiting highly complex anatomies (*cf.* Zak, 1971; Agerer, 1988 *inter al.*). Rhizomorphs form or dedifferentiate in response to nutrient and stress factors (*inter al.* Gäumann, 1928; Burnett, 1976) and may follow either positive oxygen or positive water gradients (*cf.* Snider, 1959; Redfern & Filip, 1991). They are not food storage organs but "...serve rather to bring the fungus to new hosts or to new parts of the same host and thus widen or enlarge the area occupied...." (Heald, 1926). An adhesive function has also been suggested for rhizomorphs associated with litter- and canopy-inhabiting saprotrophs (Cairney & Chambers, 1991).

While rhizomorphs -- considered part of the mycelium -- can extend the potential food-base of a fungus by traveling between and among substrates, pseudorhizae -- ultimately pileate and considered part of the basidiome proper -- characteristically grow from a given substrate upwards or outwards to an aerial interface. However, the line between rhizomorph and pseudorhiza is not easily drawn. Szcepka and Sokól (1986) consistently refer to the 'appendix rhizomorpha' in their description of *Xerula melanotricha* Dörfelt, a sister species to the one for which the term 'pseudorhiza' was invented. Recalling Snider's (1959) observations that mycelial strands and rhizomorphs "...exist in a continuum from simple to complex...," the recognition of highly differentiated pseudorhizae in *Phaeocollybia* implies 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.

How different are Phaeocollybian pseudorhizae and rhizomorphs? Although anatomically as complex as *Paxillus involutus* (Bat. ex Fr.) Fr. rhizomorphs (*cf.* Agerer, 1988), unbranched vertical monopodial pseudorhizae appear more closely linked to basidiome than to mycelium, although pseudorhizae in *P. piceae* and *P. spadicea* have been found with secondary basidiomes attached. The sequential-racemose pseudorhizal cord in *P. rufotubulina*, with its ultimately pileate

branches on the one hand and its lateral orientation and rhizomorph-like anatomy (*cf. Lycoperdon* in Townsend, 1954) on the other, forms a peculiar bridge between pseudorhiza and rhizomorph. The primordial starbursts atop subtending fasciculate-racemose pseudorhizal cords in *P. scatesiae* also suggest the presence of localized rhizomorph-like meristemoids. Both sequential- and fasciculate-racemose pseudorhizae in *Phaeocollybia* recall Brefeld's (1877) illustrations of *C. ephemerus* in which secondary basidiomes were shown to emerge serially or in fascicles from solitary pseudorhizae. One can appreciate the difficulty in attempting to designate these structures as strictly rhizomorphs or pseudorhizae.

The criniform lateral-monopodial pseudorhizae, anatomically similar to *Armillaria mellea* and *Marasmius androsaceus* rhizomorphs (*cf.* Townsend, 1954), differ structurally from other Phaeocollybian pseudorhizae in that at the extreme origin, the cortical, sub-cortical and medullary zones are quite distinct from one another with no intermixing of hyphal types. Although virtually all pseudorhizae found thus far in *P. attenuata* and *P. 'similis'* have been pileate, it is possible that non-pileate, criniform threads were overlooked in the highly heterogeneous humus mix of needles, mosses, wood and debris. Singer (1986) reserved the term 'télèpode' for non-pileate criniform stipes (which he distinguished from 'true' rhizomorphs), although Redhead (1986) noted formation of occasional aborted pilei on the tips of similar *Crinipellis* rhizomorphs. (That pileal initiation does not necessarily preclude rhizomorphic function is suggested by Cairney & Chambers' (1991) observation on the function of the "aerial capitate organs" associated with the saprotroph *Mycena cystidiosa* (Stev.) Horak.) Given their structural and functional similarities, it would seem that 'télèpode' might apply equally to the wire-like 'pseudorhiza' of *P. attenuata* and to the criniform 'rhizomorph' of *Crinipellis*.

There is little question of the anatomical similarity between rhizomorphs and Phaeocollybian pseudorhizae, particularly in view of the "...cortex of narrow diameter hyphae ... surrounding a medulla containing ... vessel hyphae..." common to both (*cf.* Cairney, 1991). Furthermore, the atypical behavior of many of the pseudorhizae reflects a functional similarity as well -- whether implied by lateral growth through substrates in contradiction of the characteristic negative geotropism exhibited by basidiomes or by the production of secondary basidiomes indicative of meristemoidal activity. Although it seems premature to refer to Phaeocollybian pseudorhizae as rhizomorphs, the term 'rhizomorphic pseudorhizae' is introduced for pseudorhizae possessing rhizomorphic characteristics.

Consideration of trophic status in Phaeocollybia

In 1983 Horak, noting the still-unknown biological function of pseudorhizae in the genus, asked "...Does *Phaeocollybia* enter mycorrhizal symbiosis or is it a saprobe on buried wood?". In the

past 40 years, little evidence has been forwarded to support a single trophic status for the genus, although saprotrophic, mycorrhizal, and parasitic hypotheses have all been proposed (Smith, 1957b; Singer, 1970, 1987; Smith & Trappe, 1972; Horak, 1977, 1983; Redhead & Malloch, 1986; Norvell et al., 1994a). The recent excavations that have exposed primordia and pseudorhizae connected to ectomycorrhizal tips with Hartig nets offer the first hard evidence for mycotrophy in *Phaeocollybia.*

Biotrophy was earlier implied in Redhead & Malloch's 1986 report of an intact *P. christinae* attached to a senescent spruce rootlet sheathed in a mycorrhizal mantle and surrounded by diverticulate mycelia -- the only successful retrieval of a Phaeocollybian pseudorhiza attached to an associated host outside of the current study. The authors inferred a pathogenic rather than mycorrhizal relationship for that species, in part based on the degree of senescence of the attached rootlet and the fact that the basidiomes erupted "...through the cortical layers from a loosened vascular stele..." through which nutrients were thought to flow from host to basidiome (reexamination of their slide by this author confirms those observations). In the current study no basidiomes have been seen to erupt directly from rootlet cortex or invade (or otherwise disrupt) the vascular stele of the putative symbiont. Additionally pseudorhizae have clearly been closely associated with both healthy and senescent rootlets, leading to the speculation that the less healthy rootlets (found toward the end of the active growing season) were innately senescent. It can be quite difficult to identify the precise trophic status of a given fungus, for both mycorrhizal and pathogenic root fungi penetrate their hosts to some degree. The fact that mycelia have been found sheathing rootlets with ectomycorrhizal tips in five different western species does tend to support a mycorrhizal hypothesis, at least for those species. (The observation of diverticulate hyphae surrounding healthy to senescing hyphae of known mycorrhizal fungi such as *Cenococcum* (Norvell, unpublished data) might also suggest, however, parasitism on other fungi associated with the rootlets. In a recent discussion of his earlier findings, Redhead (pers. comm, 1996) notes that the mycorrhizal mantle greatly resembled that produced by *Cenococcum* species.) Singer (1987), building on Redhead and Malloch's observations, inferred a generalized non-ectomycorrhizal status for *Phaeocollybia* after noting that some South American Phaeocollybias were confined to 'anectrophic' tropical rainforests, although he provided no evidence that the forests were in fact fully non-ectomycorrhizal. However, in light of present observations and considering that some of the forests in question (*e.g.* Costa Rica, Columbia) are now recognized as containing ectomycorrhizae (Ammirati, pers. comm. 1996; Halling, pers. comm. 1996; Horak, pers. comm. 1996), the inference of a generalized non-ectomycorrhizal status for *Phaeocollybia* seems premature.

Saprotrophy has been occasionally proposed for *Phaeocollybia* because its basidiomes are usually found in highly humic soils. For example, Smith and Trappe (1972), who were unaware that *P.*

scatesiae forms fascicles on the ends of long rhizomorphic pseudorhizae obviously originating elsewhere, indicated that a "gigantic loose cluster" of *P. scatesiae* basidiomes probably originated from the "remains of a long-decayed stump". The collection of Phaeocollybias from highly organic substrates appears to have prompted Kühner (1980) to transfer the presumably non-mycorrhizal *Phaeocollybia* from the mycorrhizal Cortinariaceae to the saprotrophic Strophariaceae. However, Allen (1991) notes the frequent distribution and association of mycorrhizae within decomposing organic matter and speculates that many mycorrhizal fungi may be able to "...survive on organic substrates, at least for a short time...." It appears that substrates containing even unusually large amounts of dead roots, woody debris and other organic matter neither dictate saprotrophy nor exclude mycotrophy or parasitism. Although the primary focus of the current research has been the collection, identification, and taxonomy of Pacific Northwest species, attempts have been made to cultivate *Phaeocollybia* via both spore germination and tissue culture. No spores have yet been successfully germinated. All tissue cultures -- whether on potato, malt, Marx-Melin-Norkrans or water media (with or without streptomycin) -- have been likewise unsuccessful (Norvell, unpublished data; Trappe, pers. comm. 1996; *cf.* also Kühner, 1980). These failures suggest that the genus is probably not saprotrophic (Trappe, pers. comm.1996).

As it now stands, the combination of pseudorhizae emerging from a fungal mass surrounding viable rootlets, the presence of a mantle on ectomycorrhizal tips, the existence of a Hartig net -- considered by Wilcox (1982) to be the most reliable index of mycorrhizal development -- and the connection of rootlets, tips, mantles, masses, and pseudorhizae by hyphae covered with the characteristic tibiiform diverticula offers the most persuasive evidence for accepting *Phaeocollybia* as an ectomycorrhizal genus. While there is little evidence supporting saprotrophy in Pacific Northwest species, the possibility that *Phaeocollybia* may be facultatively parasitic (as suggested by the eastern *P. christinae*, also linked to mycorrhizal rootlets) is still open. The differences and similarities between parasitism and mycotrophy and the degree to which ectomycorrhizal fungi alternate between beneficial and destructive states must be further explored before a single trophic strategy can be assumed for the genus. In the interim, the identification of mycorrhizal species and the discovery of a universal veil throughout the genus imply a much closer affinity between *Phaeocollybia* and the ectomycorrhizal velate cortinariaceous genera (*e.g. Cortinarius, Inocybe,* and *Hebeloma)* than has been previously demonstrated.

Table 2.1 Developmentally informative reference collections: geographical origin, collector, and informative features

Species	Geographical Origin	LLN Coll. No. (WTU)	Primary Collector	Feature(s) studied
P. ammiratii	California (HC-B)	92.11.19-1	L. Norvell	psr, veil
P. ammiratii	Oregon (MHNF-L)	93.11.13-3	L. Norvell	veil
P. attenuata	Washington (ONP-H)	92.10.15-4	L. Norvell	psr
P. benzokauffmanii	Washington (ONP-R)	92.10.23-5	L. Norvell	prim, psr, veil
P. benzokauffmanii	California (MC-J)	92.11.20-9	L. Norvell	veil
P. fallax	Washington (ONP-H)	92.10.15-24	L. Norvell	veil
P. kauffmanii	Washington (BSNF-BP)	92.09.21-3	L. Norvell	prim, psr
P. kauffmanii	California (MC-J)	92.11.24-12	S. Redhead	prim, psr
P. kauffmanii	Oregon (MHNF-L)	94.10.11-6	L. Norvell	psr
P. luteosquamulosa	Oregon (MHNF-L)	92.11.04-9	L. Norvell	veil
P. luteosquamulosa	California (MC-J)	92.11.24-1	R. Halling	veil
P. luteosquamulosa	Oregon (MHNF-L)	93.10.24-6	L. Norvell	veil
P. luteosquamulosa	Oregon (MHNF-L)	93.11.05-9a	L. Norvell	veil
P. luteosquamulosa	Oregon (MHNF-L)	94.10.11-18	L. Norvell	psr
P. olivacea	Oregon (CC-E)	94.11.28-1	J. Roger	prim
P. oregonensis	Oregon (MHNF-L)	92.11.04-6	S. Redhead	veil
P. oregonensis	Oregon (MHNF-W)	95.10.18-4	L. Norvell	psr, prim
P. piceae	British Columbia (VI-LC)	92.10.09-22	L. Norvell	psr, veil
P. redheadii	Oregon (MHNF-L)	93.10.24-13	L. Norvell	prim, psr
P. redheadii	Oregon (MHNF-L)	93.11.05-1,5	L. Norvell	prim, psr, veil
P. redheadii	Oregon (MHNF-L)	94.10.06-12	L. Norvell	prim, psr
P. rufotubulina	California (MC-J)	92.11.16-1	L. Norvell	prim, psr, veil
P. rufotubulina	California (MC-J)	92.11.24-2,6,9	L. Norvell	prim, psr, veil
P. scatesiae	Washington (ONP-H)	92.10.15-19	R. Petersen	prim, psr
P. scatesiae	Oregon (MHNF-L)	92.11.04-15	L. Norvell	prim, psr
P. scatesiae	Oregon (TC-VD)	92.11.10-4	L. Norvell	psr
P. scatesiae	California (MC-V)	92.11.23-1	S. Redhead	psr
P. scatesiae	Oregon (TC-VD)	93.11.04-9	L. Norvell	prim, psr, veil
P. scatesiae	Oregon (MHNF-W)	95.10.14-4	J. Roger	psr
P. scatesiae	Oregon (TC-CH)	95.11.09-27	L. Norvell	prim, psr, veil
P. 'similis'	British Columbia (VI)-LC	92.10.09-23	L. Norvell	psr,
P. 'similis'	British Columbia (VI)-UC	93.10.30-25	S. Redhead	psr, prim, veil
P. 'similis'	Oregon (LC-CH)	93.11.04-8	L. Norvell	psr, prim
P. 'similis'	Oregon (LC-CH)	93.11.14-12	L. Norvell	psr, prim
P. sipei	Oregon (LC-CH)	93.11.04-1	S. Redhead	psr
P. spadicea	Washington (ONP-H)	92.10.15-12	S. Redhead	myc, psr, veil
P. spadicea	Oregon (TC-OW)	92.11.02-3	L. Norvell	psr, veil
P. spadicea	Oregon (TC-OW)	93.10.23-6	L. Norvell	veil
P. spadicea	Washington (ONP-R)	93.10.12-1	L. Norvell	veil
P. spadicea	Oregon (LC-CH)	93.11.04-6	L. Norvell	veil
P. tibiikauffmanii	Oregon (LC-CH)	95.11.09-19	L. Norvell	dev

BSNF-BP: Baker-Snoqualmie National Forest, Barlow Pass, Snohomish County
CC-E: Clackamas County, Estacada
HC -B: Humboldt County, Big Lagoon State Park
LC: Lincoln County. -VD: Van Duzer State Wayside; -CH: Cascade Head Experimental Forest
MC: Mendocino County. -J: Jackson State Forest; -V: Van Damme State Park
MHNF: Mt. Hood National Forest. -L: Larch Mountain, Multnomah County; -W: Wildcat Mountain,Clackamas County
ONP: Olympic National Park. -R: Rugged Ridge Trail, Clallam County; -H: Hoh Valley, Jefferson County
TC: Tillamook County. -CH: (Cascade Head Experimental Forest), -OW: (Oswald West State Park)
VI : Vancouver Island. -LC: (Lower Carmanah Valley); -UC: (Upper Carmanah Valley)

dev = developmental sequence
myc = mycelium
prim = primordium
psr = pseudorhiza

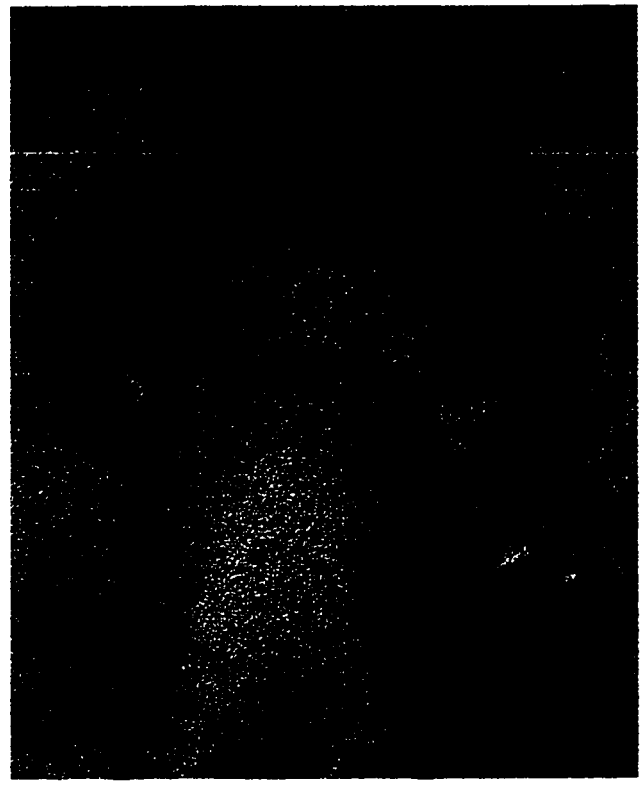


Figure 2.1 Pellicular veil in *P. rufotubulina* (LLN 92.11.16-1). **(a)** Primordium with pellicular veil covering developing pileus, stipe, pseudorhiza, and pseudorhizal cord. Scale = 1 mm. **(b)** Longitudinal section showing gelatinized pellicular veil and pileipellis and lamellar cavities. Scale = 50 μm.

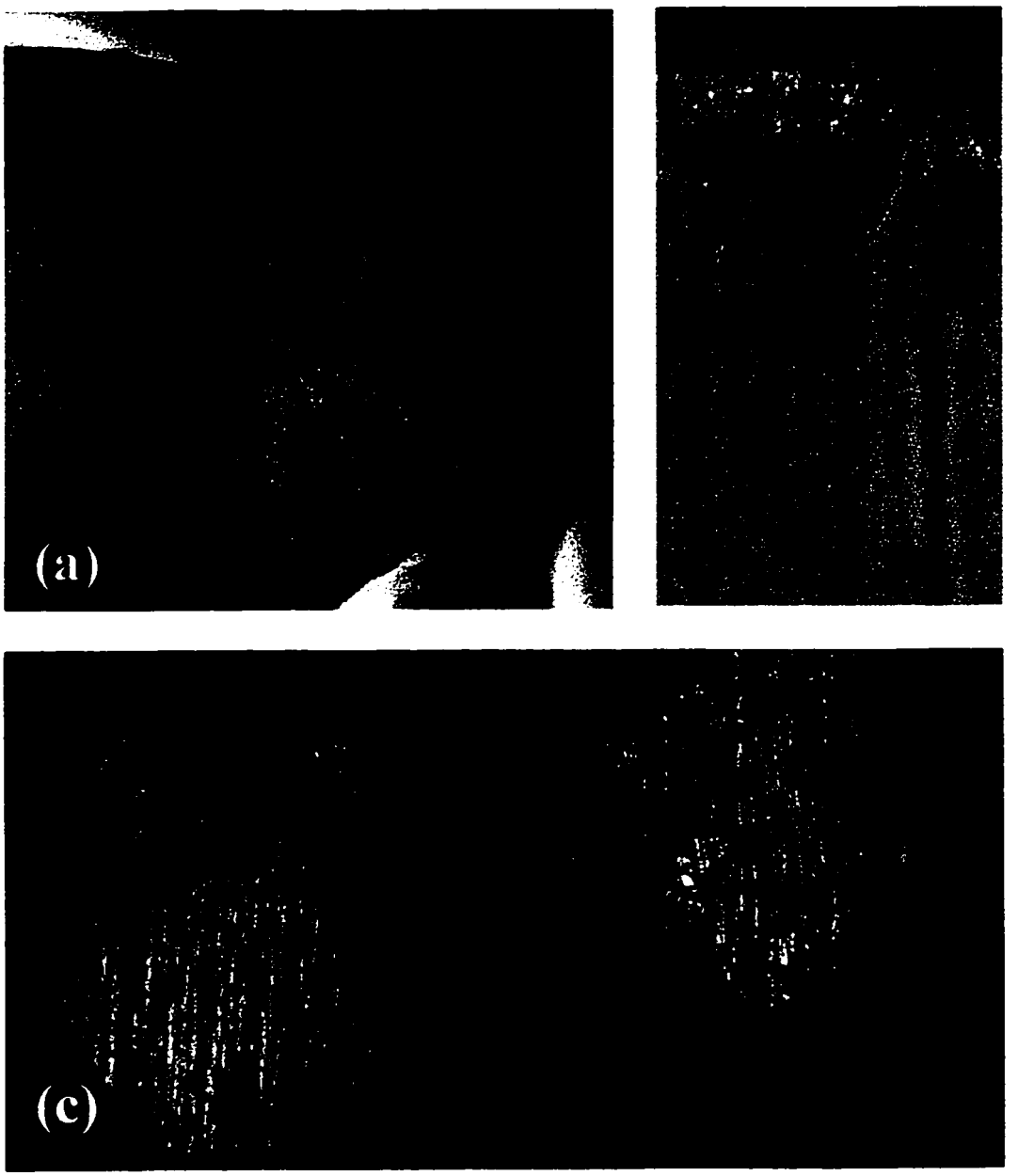


Figure 2.2 Pellicular veil remnants on mature basidiosomes. **(a)** Fibrillose patches on pileus in *P. luteosquamulosa* (LLN 93.11.05-9a). Scale = 5 mm. **(b)** Fibrillose remnant (arrow) trailing across young lamellae in *P. luteosquamulosa* (LLN 93.10.23-6). Scale=0.1 mm. **(c)** Aerial stipe bearing large fibrillose patches (arrows) in *P. spadicea* (LLN 93.10.23-6). Scale = 1 mm.

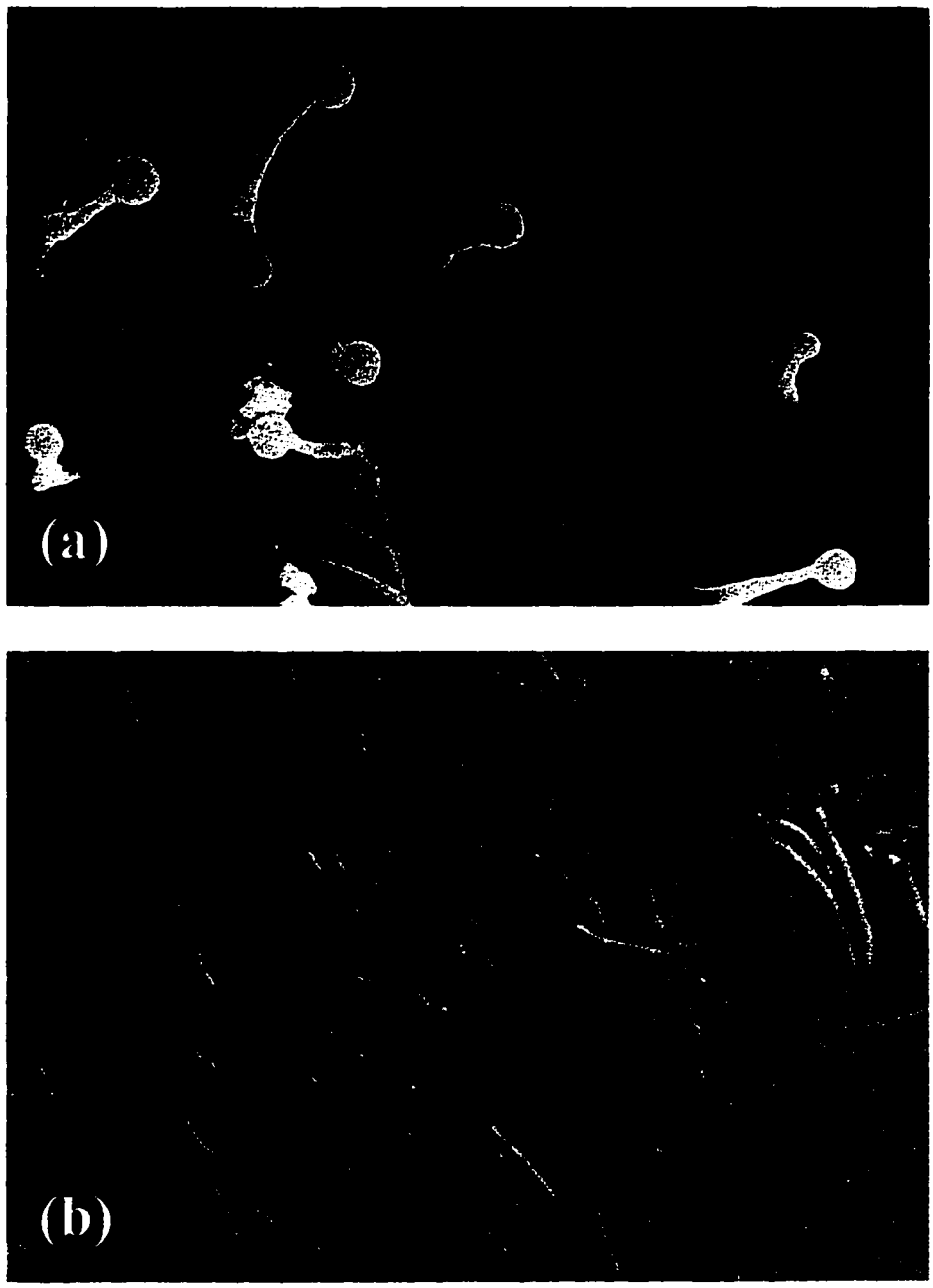


Figure 2.3 Secretory tibiiform diverticula. Scale = 10 μm. **(a)** 10 kV SEM of pseudorhizal pellis on mature specimen in *P. rufotubulina* (LLN 92.11.16-1d). **(b)** Light micrograph (DIC, oil immersion) of fibrillose veil adhering to aerial stipe of mature basidiome in *P. benzokauffmanii* (LLN 92.11.20-9).

Table 2.2 Western North American *Phaeocollybia* species: Observations of tibiiform diverticula on basidiomes.

Species	Known geographic distribution	Mycelium	Primordium	Pseudorhiza	Aerial stipe	Mature pileus
P. ammiratii nom. prov.	BC,WA,OR,CA	+	+	+	+	-
P. attenuata (A. H. Sm.) Sing.	BC,WA,OR,CA	+	+	+	+/-	(+)
P. benzokauffmani nom. prov.	WA,OR,CA	+	+	+	+	-
P. californica A. H. Sm.	OR,CA			+	-	-
P. carmanahensis Redhead & Norvell	BC		(+)	+	-	-
P. dissiliens A. H. Sm. & Trappe	OR			+	-	-
P. fallax A. H. Sm.	BC,WA,OR,CA	+	+	+	+	-
P. gregaria A. H. Sm. & Trappe	OR			+		-
P. kauffmanii (A. H. Sm.) Sing.	BC,WA,ID,OR,CA	+	+	+	-(+)	-
P. lilacifolia A. H. Sm.	WA,,OR			+	+	-
P. luteosquamulosa nom. prov.	WA,OR,CA			+	+/-	+
P. olivacea A. H. Sm.	WA,OR,CA	+	+	+	+	-
P. oregonensis A. H. Sm. & Trappe	BC, OR		+	+	-(+)	-
P. phaeogaleroides nom. prov.	OR			+	-	-
P. piceae A. H. Sm. & Trappe	BC,WA,OR,CA			+	-	-
P. pleurocystidiata nom. prov.	WA,OR,CA			+	-	-
P. pseudofestiva A. H. Sm.	BC,WA,OR,CA	+	+	+	+	-
**P. radicata* (Murrill) Sing.	OR, CA			+	-	-
P. redheadii nom. prov.	BC,WA,OR	+	+	+	-	-
P. rifflipes nom. prov.	OR, WA			+	+	-
P. rufotubulina nom. prov.	CA	+	+	+	-	-(+)
P. scatesiae A. H. Sm. & Trappe	WA,OR,CA		+	+	+	-
†P. similis sensu. A. H. Sm.	BC,WA	+	+	+	+/-	-
P. sipei A. H. Sm.	OR		+	+	-	-
P. spadicea A. H. Sm.	WA,OR,CA	+	+	+	+++	-
P. tibiikauffmanii nom. prov.	OR			+	-	-

*no fresh specimens collected 1991-1996
†may represent new undescribed species

Table 2.3 Pseudorhizal patterns and comparative pseudorhizal anatomy of selected Phaeocollybias.

	[1] Vertical-monopodial*		[2] Lateral-monopodial§	
	Lower pseudorhiza	Upper pseudorhiza	Upper rhizomorphic pseudorhiza ['wire' transition zone]	Lower rhizomorphic pseudorhiza ['wire' elongation zone]
Cortex		~10 µm thick layer	~50 µm thick layer*	~10 µm thick layer
arrangement	parallel	interwoven	parallel	interwoven
hyphal dimensions	20-40 x 2-3 µm	2-3 µm wide	80-110 x 8-20 µm	2-3 µm wide
wall thickness	1 µm	1-2.5 µm	1-2 µm	2-3 µm
shape	cylindrical	cylindrical	cylindrical	cylindrical
colour	dark (melanized)	non-pigmented	dark (melanized)	non-pigmented
Subcortex	ill-defined zone containing cortical and medullary elements	~50 µm thick layer	lacking*	~50 µm thick layer
arrangement		parallel		parallel
hyphal dimensions		80-110 x 8-20 µm		10 µm wide
wall thickness		1-2 µm		2 µm
shape		cylindrical		fusoid
colour		dark (melanized)		dark (melanized)
Medulla				
tissue type	sarcodimitic	sarcodimitic	sarcodimitic	monomitic
color	non-pigmented	non-pigmented	non-pigmented	non-pigmented
Hyphal type (1)	vessel	vessel	vessel	generative
arrangement	parallel	parallel	parallel	parallel
abundance	abundant	occasional	frequent	abundant
dimensions	(80) 150-250 x 10-30 µm	100-600 x 15-30 µm	180-200 x 15-25 µm	6-8 µm wide
wall thickness	2-3 (5) µm	1-2 µm	1-2 µm	0.5 - 1 µm
shape	cylindrical to fusoid	cylindrical to fusoid	cylindrical to fusoid	cylindrical, slightly inflated
Hyphal type (2)	flexuous/generative	flexuous/generative	flexuous/generative	lacking
arrangement	woven about vessels	woven about vessels	lwoven about vessels	
abundance	numerous	numerous	occasional	
dimensions	~20-30 x 1-4 (7) µm	6-12 µm wide	3-5 µm wide	
wall thickness	<0.5 µm	<0.5 µm	0.5 µm	
shape	cylindrical, branched	cylindrical, branched	cylindrical, branched	

*Vessels with thicker walls (3- 5 µm) in *P. benzokauffmanii, P. kauffmanii, P. oregonensis & P. redheadii;* Vessels' shorter (80 µm) in *P. sipei;* Flexuous hyphae sometimes wider (to 7 µm) in *P. spadicea*

§Cortex in the upper transition zone corresponds to the subcortices of the upper pseudorhiza and wire elongation zone and is anatomically identical to the subcortex of the former; Representatives: *P. attenuata, P. 'similis'*

Table 2.3 (Pseudorhizal patterns continued)

	[3] Sequential-racemose†	[4] Fasciculate-racemose‡	
	Rhizomorphic pseudorhiza ['thread']	Upper pseudorhiza	Rhizomorphic pseudorhiza [subtending strand]
Cortex	complex**		
arrangement		parallel	parallel
hyphal dimensions		2-3 µm wide	25 x 4-6 µm
wall thickness		1 µm	1.5-2 µm
shape		cylindrical	cylindrical
colour	dark (melanized)	dark (melanized)	dark (melanized)
Subcortex	lacking**	ill-defined zone containing cortical and medullary elements	ill-defined zone containing cortical and medullary elements
arrangement			
hyphal dimensions			
wall thickness			
shape			
colour			
Medulla			
tissue type	sarcodimitic	sarcodimitic	sarcodimitic
color	occasionally pigmented	non-pigmented	non-pigmented
Hyphal type (1)	vessel	vessel	vessel
arrangement	parallel	parallel	parallel
abundance	abundant	abundant	abundant
dimensions	150 x 10 µm	150 x 15 µm	200 x 14 µm
wall thickness	2-3 µm	2 µm	3-5 µm
shape	cylindrical to fusoid	cylindrical to fusoid	cylindrical to fusoid
Hyphal type (2)	flexuous/generative	flexuous/generative	flexuous/generative
arrangement	woven about vessels	woven about vessels	woven about vessels
abundance	frequent	frequent	occasional
dimensions	~20 x 2-3 µm	15-30 µm x 4-5 µm	~20 x 2-4 µm
wall thickness	< 1 µm	<0.5 µm	<0.5 µm
shape	cylindrical, branched	cylindrical, branched	cylindrical, branched

†Cortex complex with long, medium, and short narrow thick- or thin-walled elements intermixed with heteromorphic inflated thin-walled elements (see text); Representative species: *P. rufotubulina.*
‡Representative species: *P. scatesiae*

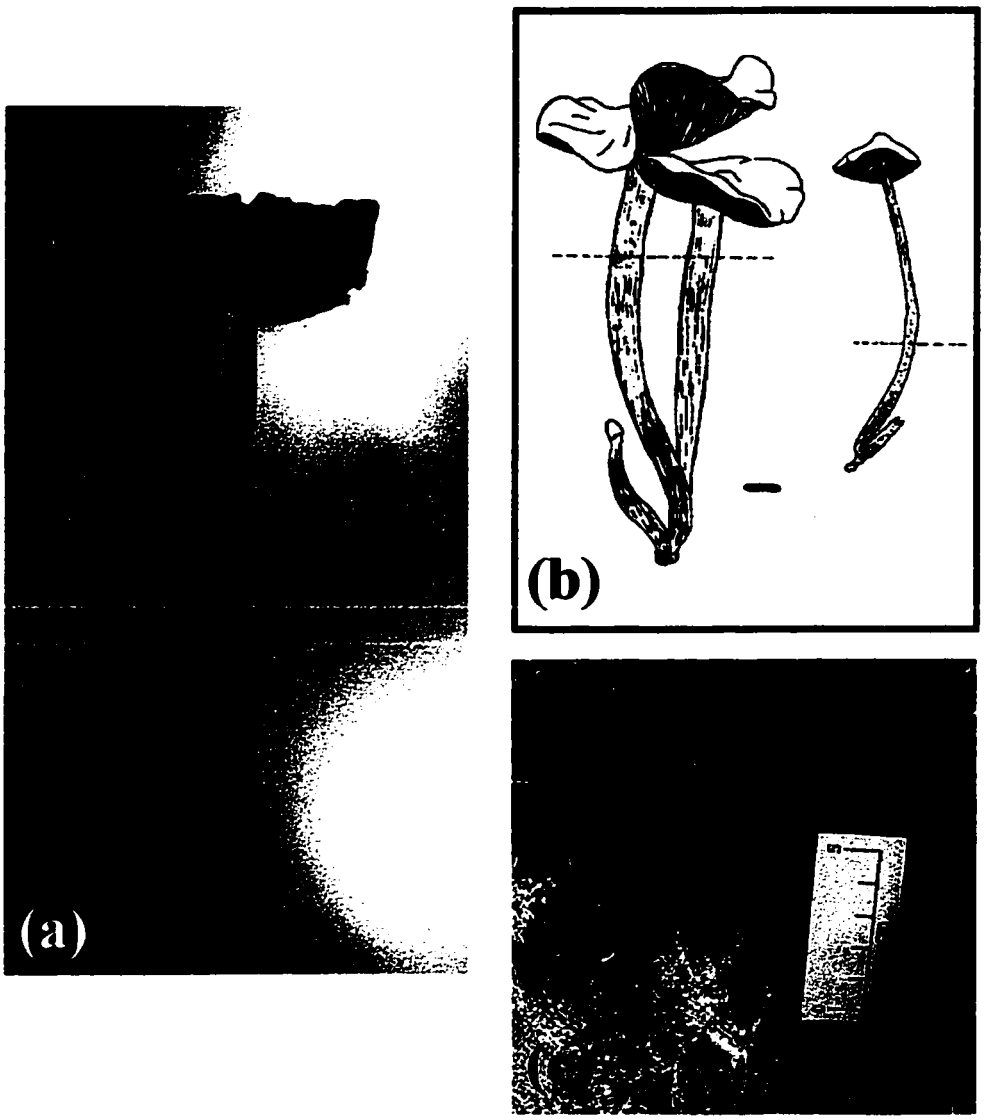


Figure 2.4 Vertical-monopodial pseudorhizae. **(a)** Solitary soil-covered pseudorhiza in *P. spadicea* (LLN 92.11.02-3). **(b)** Depictions of pseudorhizae in (left) *P. kaufmanii* (*cf.* LLN 92.11.24-12) and (right) *P. piceae* (shown attached to older pseudorhizal remnant, *cf.* LLN 92.10.09-22). Soil surface represented by dotted line. Scale = 5 cm. **(c)** Two mature *P. benzokauffmanii* pseudorhizae and one promordium [pr] *in situ* at albic horizon [a]. (LLN 92.10.23-5). Scale = 10mm.

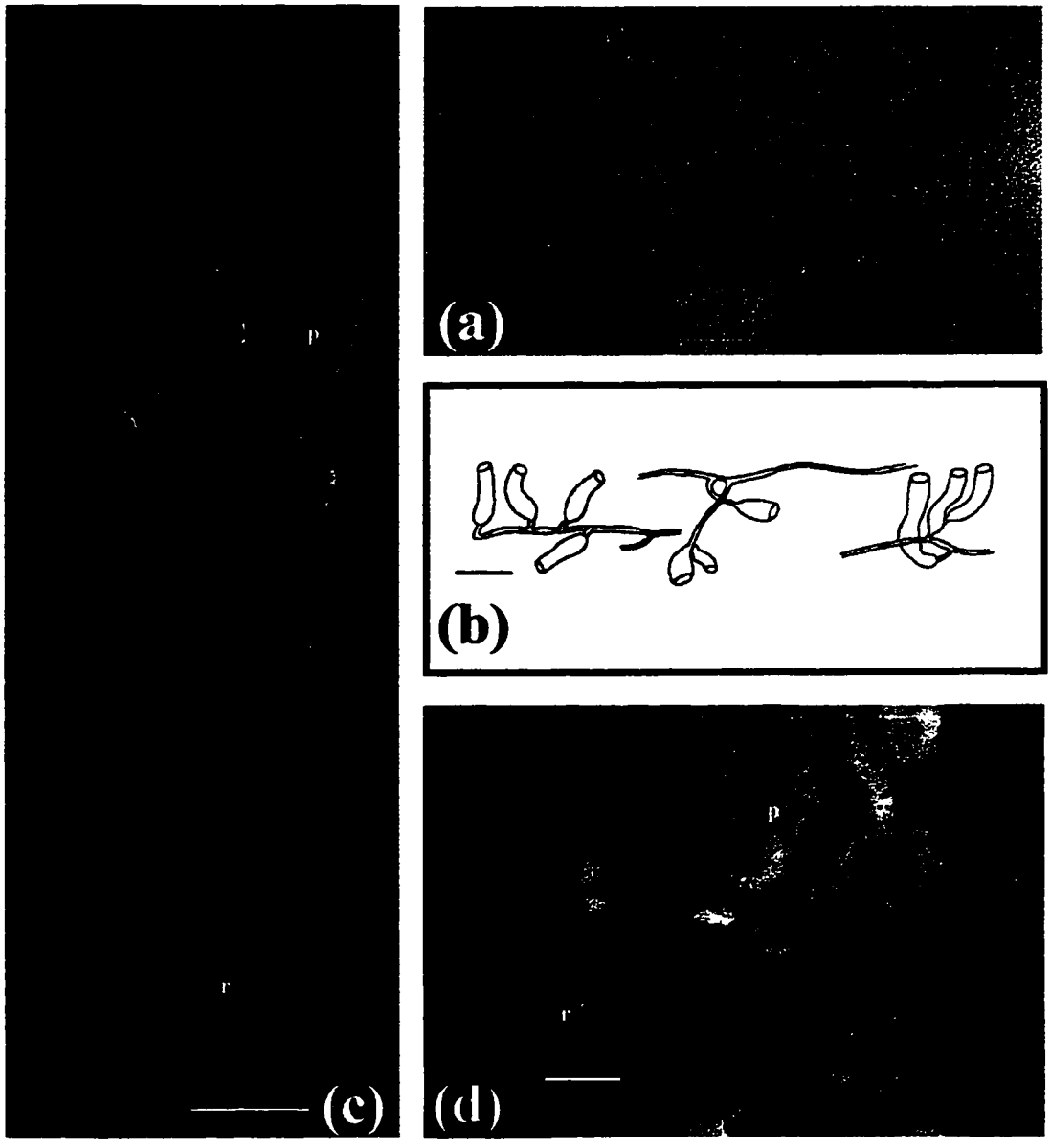


Figure 2.5 Rhizomorphic pseudorhizae. **(a)** Criniform lateral-monopodial pseudorhizae subtending solid pseudorhizae and hollow corneous stipes of *P. attenuata* (LLN 92.10.15-4). **(b)** Sequential-racemose pseudorhizae giving rise to primary and secondary basidiomes in *P. rufotubulina* (*cf.* LLN 92.11.16-1, LLN 92.11.24-2). Individiual pseudorhizae arise either from different points on one ultimately capitate rhizomorph-like cord or from primary pseudorhizae. Scale = 10 mm. **(c)** Fasciculate-racemose pseudorhizae with 55 basidiomes and 17 primordia (p) in *P. scatesiae* (LLN 93.11.04-9) emergent from single site on subtending rhizomorph-like cord (r). Scale 10 mm. **(d)** Detail of pseudorhizal-'rhizomorph' junction. Scale = 1 mm.

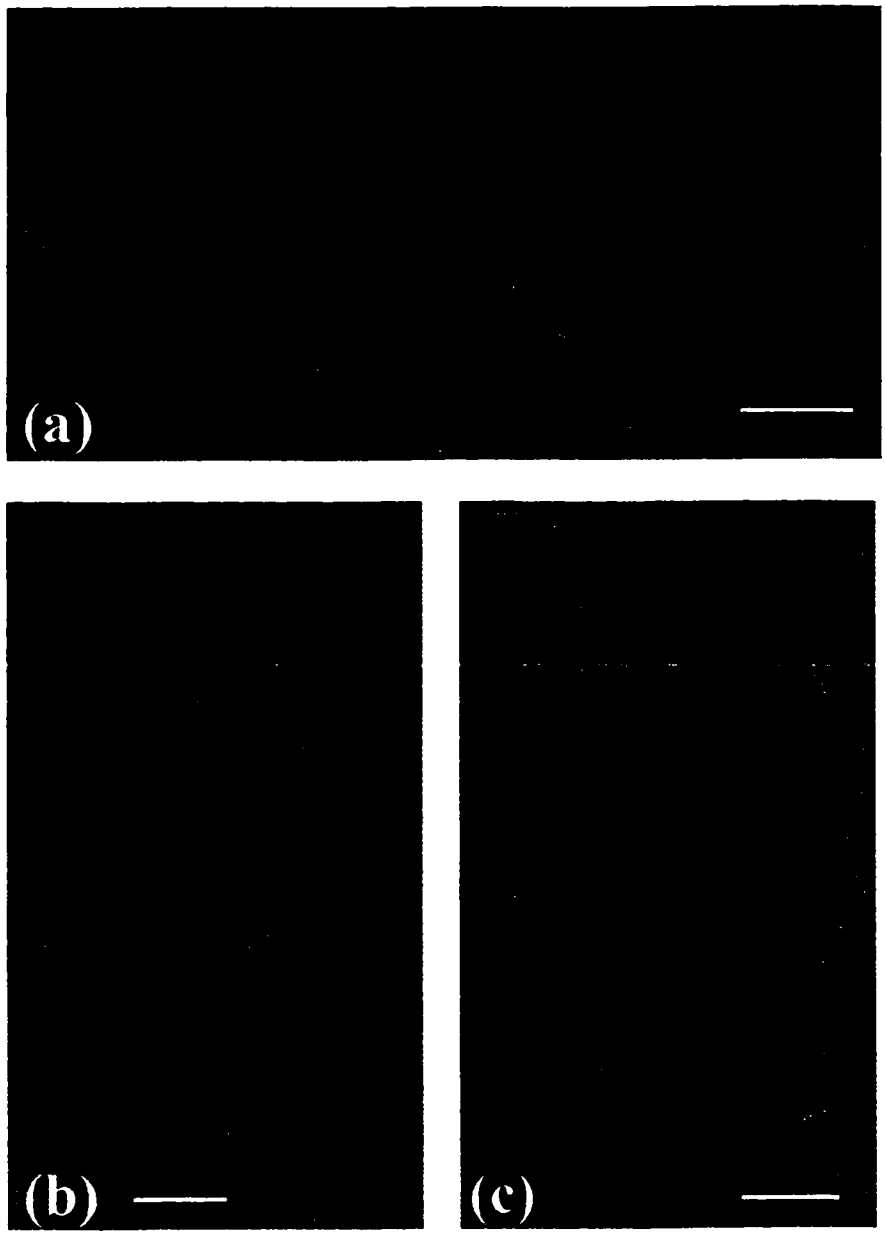


Figure 2.6 Sarcodimitism in *Phaeocollybia*. *Scales* = 10 μm. Bright field, oil immersion (100x). **(a)** Transverse section of pseudorhizal trama in *P. sipei* (LLN 93.11.04-1). **(b)** Longitudinal section of pseudorhizal trama in *P. rufotubulina* (LLN 92.11.16-1). Long thick-walled rigid hyphae conceal all but branch termini (arrows) of flexuous hyphae. **(c)** Longitudinal section of pseudorhizal trama in *P. scatesiae* (LLN 93.11.04-9).

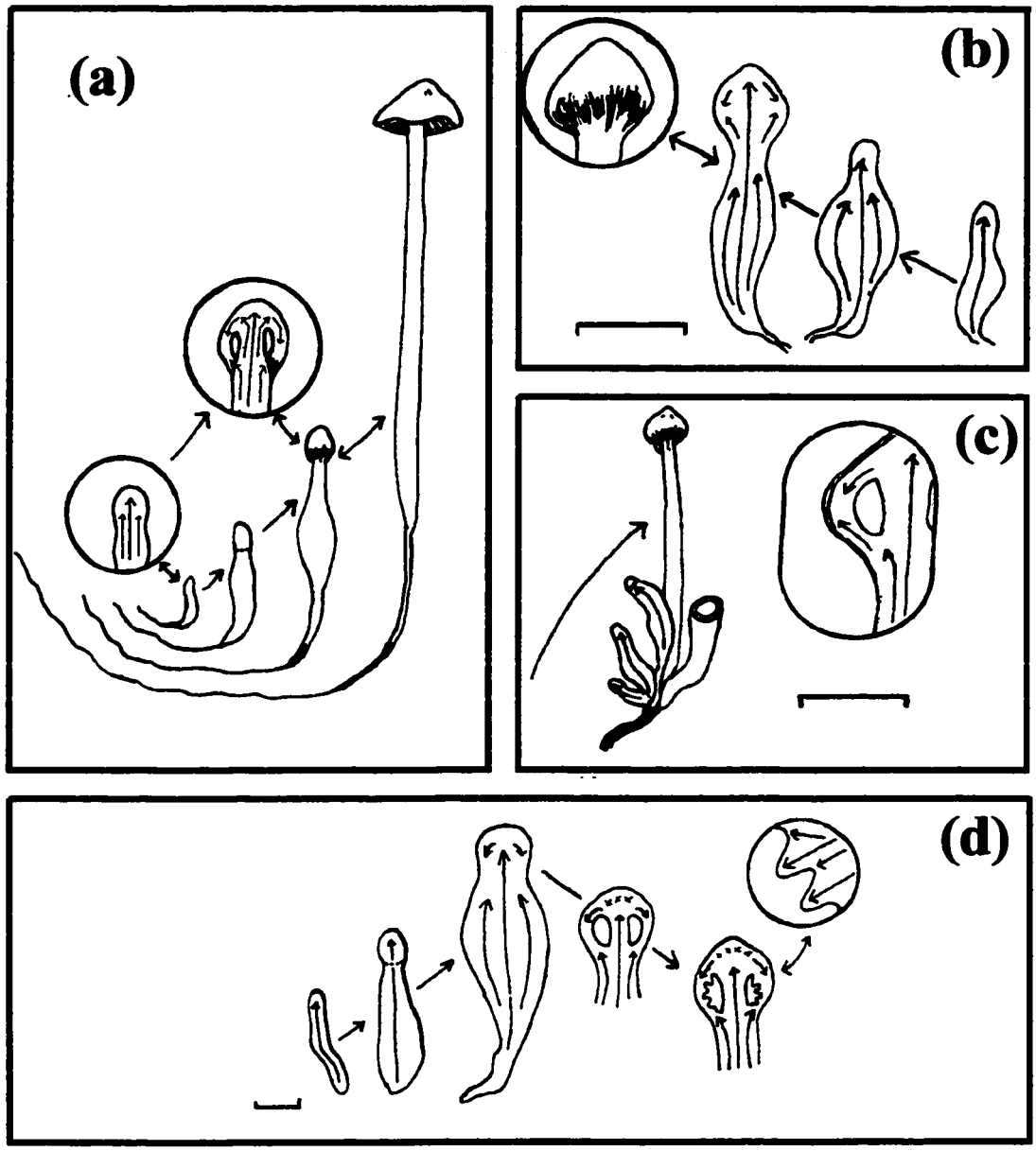


Figure 2.2 Ontogeny in four *Phaeocollybia* species. Scales = 1 mm. **(a)** Primordial development in *P. 'similis'* (*cf.* LLN 93.11.04-12, LLN 93.10.30-25). *[Inset]* Cavitation (tibiiform diverticula present on all external surfaces and stipe surface in newly formed lamellar cavity). **(b)** *P. rufotubulina* (*cf.* LLN 92.11.16-1). *[Inset]* Disruption of pellicular veil on pre-emergent basidiome. **(c)** Stipitiform development from primordium to pre-emergent basidiome on rhizomorph-like cord in P. scatesiae *(cf.* LLN 93.11.04-9). *[Inset]* Cavitation prior to lamellar ridge development. (Tibiiform diverticula present on external surfaces and within lamellar cavity). **(d)** *P. kauffmanii* (*cf.* LLN 92.11.24-12, LLN 93.10.24-1, LLN 93.10.11-13). Longitudinal sections showing subterranean primordial development with cavitation and lamellar ridge formation preceding hymenial development (tibiiform diverticula present on all external surfaces but absent within cavity).

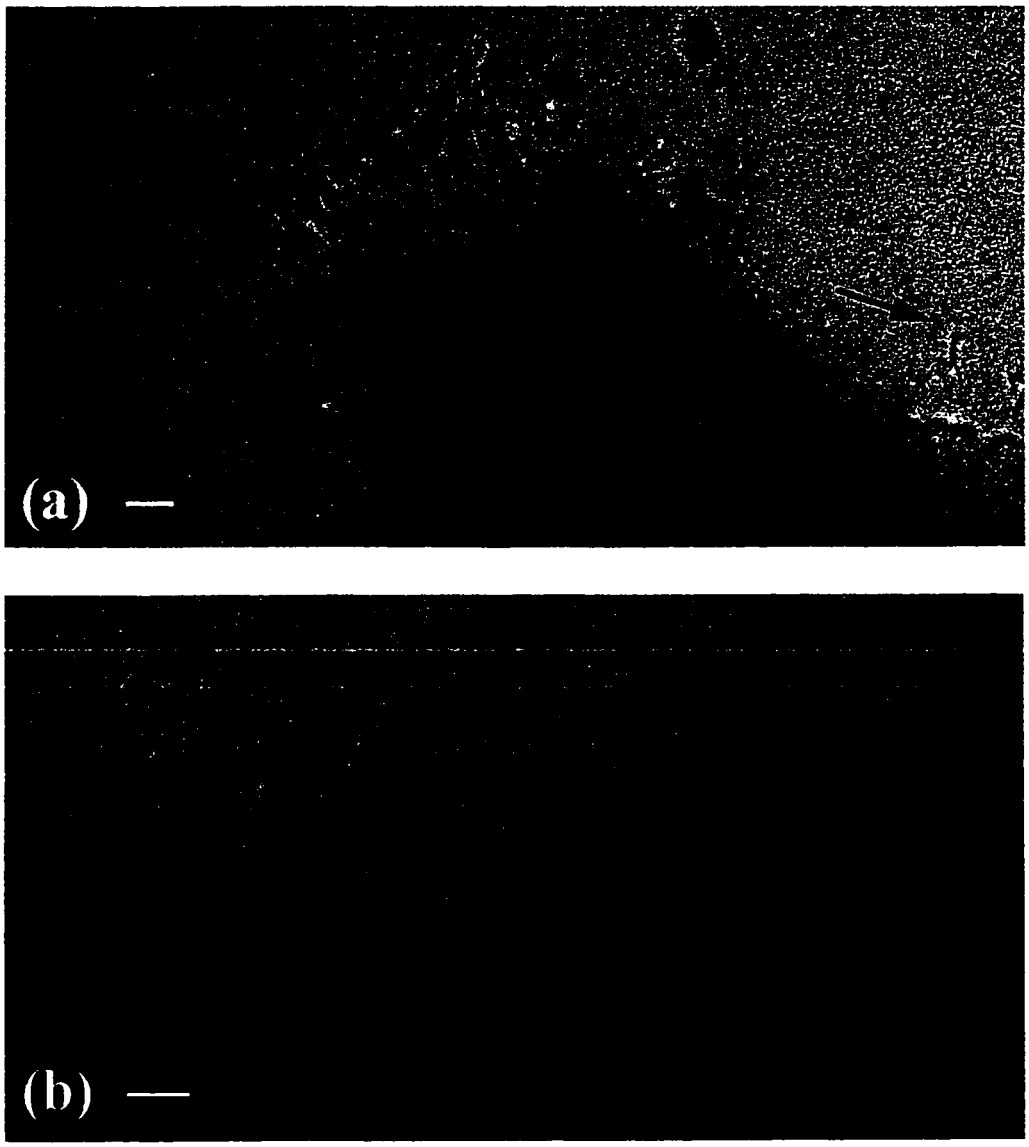


Figure 2.8 Lamellar development in *P. rufotubulina* (LLN 92.11.16-1). Kohler, Brightfield. Scale = 10 μm. **(a)** Developing lamellar ridges covered with tibiiform cystidia (arrows); other hymenial cells still rudimentary. Low power (20x). **(b)** Tibiiform cystidia present on gill faces within developing lamellar cavity. Secretory droplets surrounding capituli (arrows). High dry (40x).

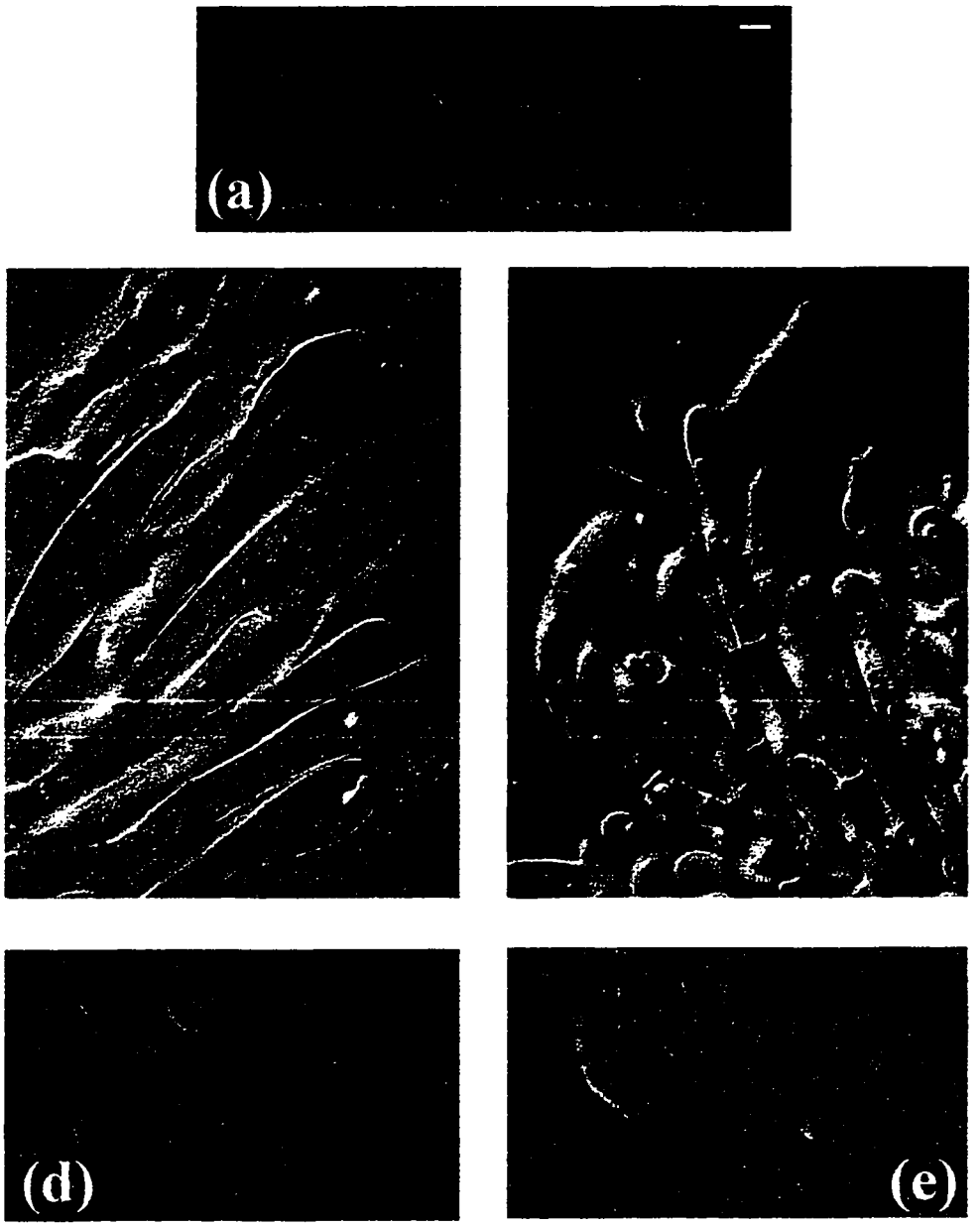


Figure 2.9 Lamellar structure in *Phaeocollybia* (DIC). Scales = 10 μm. **(a)** Regular (parallel) trama and mature hymenium in *P. dissiliens* (LLN 95.11.06-1). Low dry (20x). **(b)** Thin-walled clavate cheilocystidia in *P. luteosquamulosa* (LLN 92.11.04-9). Oil immersion (100x). **(c)** Developmental apical outgrowths (arrows) on clavate cheilocystidia of mature *P. luteosquamulosa* basidiome (LLN 94.10.11-18). Oil immersion (100x). **(d)** Tibiiform cheilocystidia in *P. tibiikauffmanii* (LLN 95.11.09.19). Oil immersion (100x). **(e)** Tibiiform cheilocystidia in *P. rufotubulina* (LLN 92.11.16-1). Oil immersion (100x).

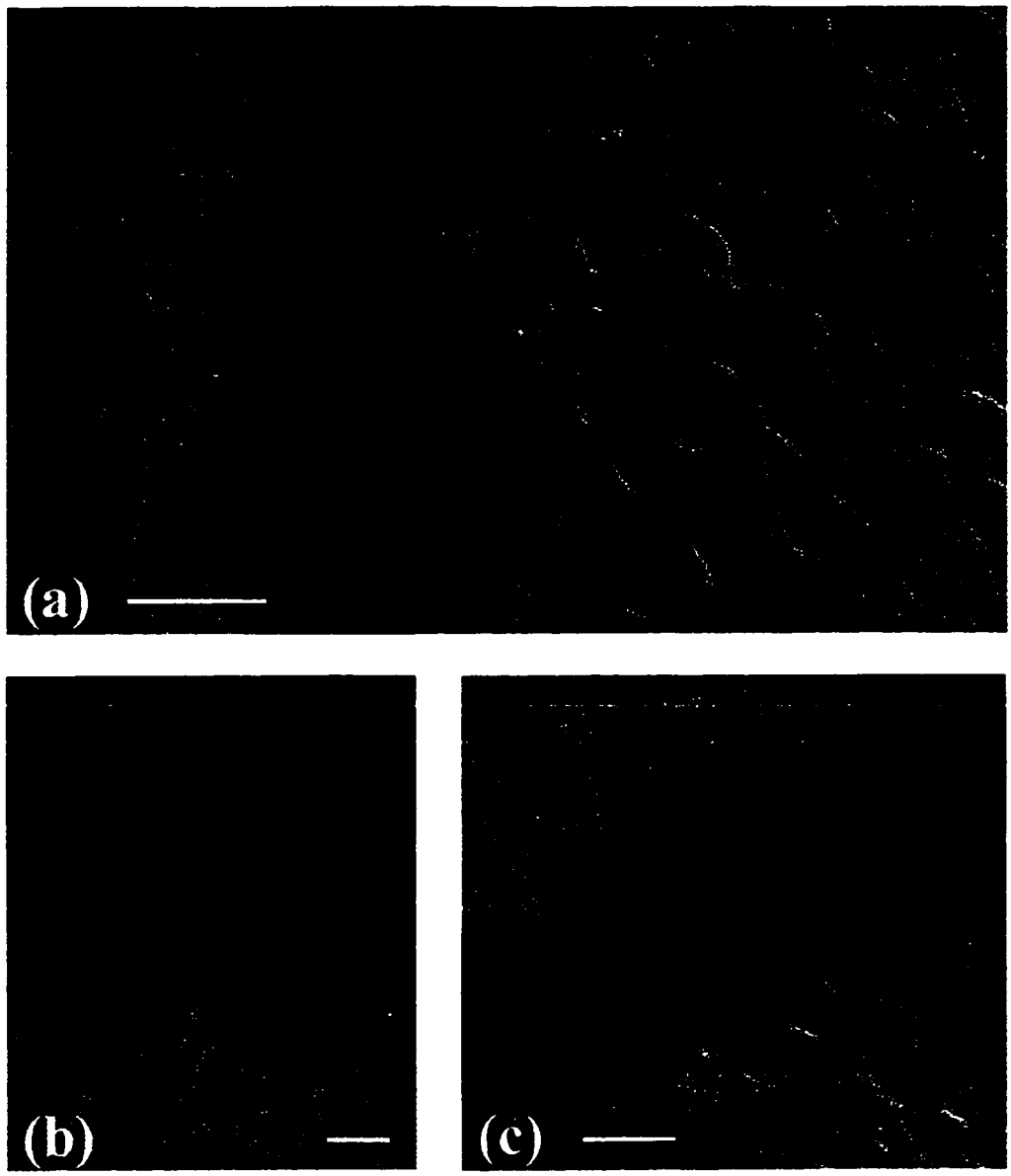


Figure 2.10 Comparisons of transverse sections of rhizomorphic pseudorhizae (oil immersion, DIC). Scales = 10 μm. **(a)** Criniform thread (*i.e.* telepode) in *P. 'similis'* (LLN 93.10.30-25) showing pale interwoven cortex, melanized sub-cortex of parallel-aligned, thick-walled hyphae, and medulla of hyaline hyphae. **(b)** Rhizomorph-like cord in *P. rufotubulina* (LLN 92.11.16-1) showing interwoven cortex of slightly melanized hyphae and sarcodimitic medulla composed of wide thick-walled hyphae intermixed with thin-walled elements. Diverticula present on cortical hyphae. **(c)** Subtending rhizomorphic pseudorhiza in *P. scatesiae* (LLN 93.11.04-9) showing darkened parallel-aligned cortical elements surrounding medulla consisting of primarily thickened elements.

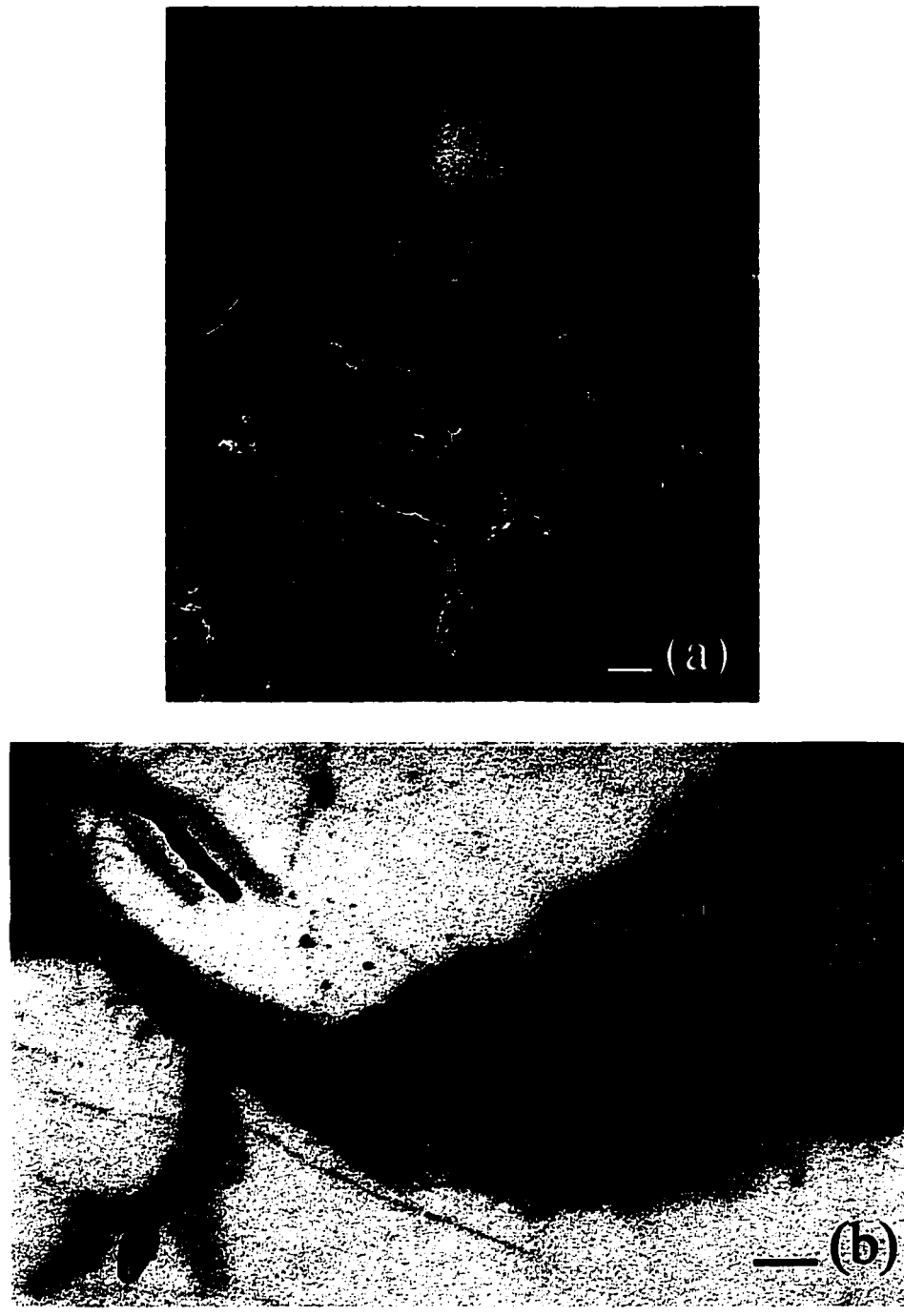


Figure 2.11 Morphological evidence for ectomycorrhizal association in *P. redheadii* (Larch Mountain, Oregon; LLN 93.11.05-1). **(a)** Cluster of young basidiomes *in situ* during excavation before removal of soil block and exposure of pseudorhizal origins with dissecting needles. (Scale = 10 mm) **(b)** Attachment of rootlet (r) with mycorrhizal tips (t) to soil-covered mass (m) with emergent pseudorhiza (psr) after dissection. (Scale = 1 mm)

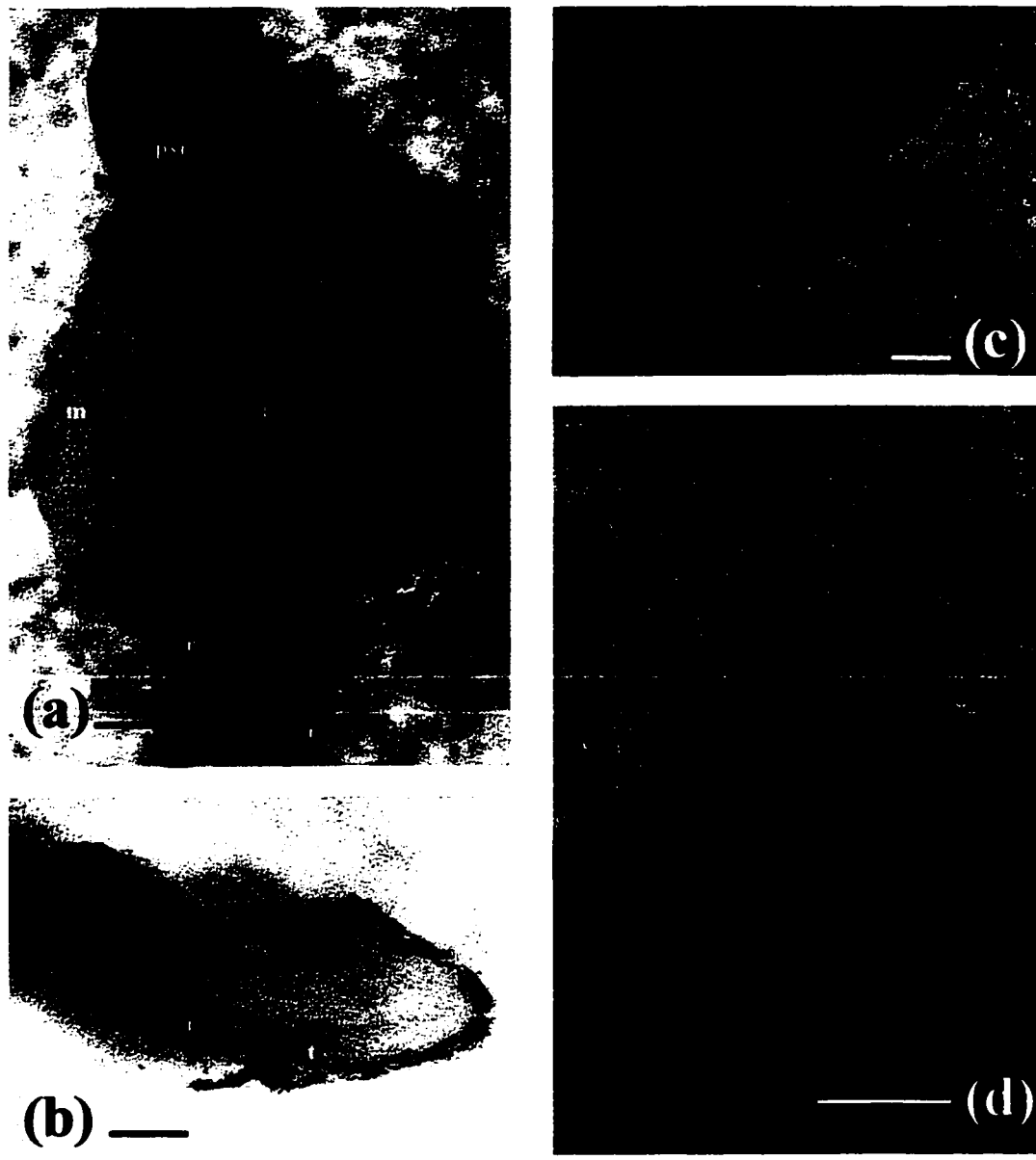


Figure 2.12 Anatomical evidence for ectomycorrhizal associations in *P. redheadii.* **(a)** Longitudinal section of pseudorhiza (psr) originating from undifferentiated fungal mass (m) with dark pseudorhizal pellis extending over upper portion of mass; bottom two rootlets (r) encased in mycorrhizal sheath. Scale = 1 mm. **(b)** Transverse section of rootlet (r) and longitudinal section of ectomycorrhizal tip (t) found embedded in fungal mass. Scale= 0.5 mm. **(c)** Longitudinal section showing evidence of Hartig net within cortex of ectomycorrhizal tip surrounded by diverticulate mycelia. **(d)** Tibiiform diverticulum (arrow) attached to mycelial hypha emergent from mantle on ectomycorrhizal tip. (**c & d** -- Scale = 10 μm. Light microscope, Brightfield, oil immersion 100x).

CHAPTER 3 -- MORPHOLOGY, ANATOMY AND MACROCHEMICAL REACTIVITY

Materials and Methods

Preparatory work -- Morphological and ecological characters from all known *Phaeocollybia* species were obtained from the literature (see Bibliography) and entered into informational matrices using either WingZ Version 1.1 (Informix, 1989; Macintosh-compatible) or MS Excel Version 5.0 (Microsoft, 1994; IBM-compatible) spread-sheet computer applications. Slightly under 600 collections of *Phaeocollybia* exsiccati including 22 types and holotypes were received on loan from the following fungal herbaria: United States National Fungus Collections (BPI), National Mycological Herbarium of Canada (DAOM), Field Museum of Natural History (F), Humboldt State University (HSC), University of Innsbruck (IB), University of Michigan at Ann Arbor (MICH), New York Botanical Gardens (NY), University of Oslo (O), Oregon State University (OSC), San Francisco State University (SFSU), University of Tennessee (TENN), University of California at Berkeley (UC), Virginia Polytechnic Institute (VTMH), and Herbarium Vadense (WAG-W). Approximately 60 additional collections were examined at five herbaria (DAOM, HSC, MICH, OSC, and SFSU). Data from herbarium labels and written materials accompanying the collections entered into a WingZ database included scientific name, herbarium name and number, collector name and number, determiner name, collection location (country, state/province, county, locality), habit, habitat, elevation, presence of spore print or photograph. Color transparencies and prints previously donated to the University by the photographers (J. Ammirati, C. Ardrey, D. Grund, D. Largent, K. Scates, J. Spurr, B. Woo) were consulted, as were photographs donated or lent by Dr. Joe Ammirati (WTU), Ms. Catherine Ardrey, Mr. Richard Gaines, Mr. Paul Kroeger, Dr. David Largent (HSC), Dr. Orson Miller, Jr. (VTMH), Mr. Buck McAdoo, Dr. Scott Redhead and Ms. Elizabeth Fox (DAOM), and Ms. Judy Roger. A catalogue of known *Phaeocollybia* localities and phenology was made in advance of the second field season to determine the itinerary for a two-month field expedition through British Columbia to California (1992) and to facilitate collecting activities during subsequent field seasons.

Field work -- Over 730 collections of *Phaeocollybia* basidiomes were made in British Columbia, Washington, Oregon and California from 1991-1996. At the same time potential outgroup taxa including *Caulorhiza umbonata* (Peck) Lennox, *Cortinarius vanduzerensis* Smith & Trappe, *Gymnopilus spectabilis* (Fr.) A. H. Smith, *Galerina autumnalis* (Peck) Smith & Singer, and *Stagnicola perplexa* (Orton) Redhead & Smith were also collected.

Because of the subterranean nature of the pseudorhizae, all Phaeocollybias were excavated using a long narrow blade (a modified oyster knife) or small hand trowel. In addition to the basidiomes,

soil, roots, and plant material vouchers were collected with or without the use of tweezers and dissecting needles, after which all remaining soil and organic materials were carefully returned to the original site to minimize site disturbance. Most intact pseudorhizae and rhizomorphic pseudorhizae were obtained during field excavations; occasional blocks of soil containing a large number of specimens were taken to the laboratory for dissection (see Chapter 2). Habitat and prime specimens were photographed, and important ephemeral characters (*e. g.*, degree of viscidity, presence of green or lilac pigments) and ecological data were recorded at the time of collection.

Laboratory examination of fresh material -- In addition to photographs taken *in situ*, specimens were also photographed or drawn after longitudinal sectioning to expose key characters. Photocopying collections (begun in 1993) proved particularly helpful when a large number of specimens were collected at once, for measurements of fresh material could be taken from the photocopies after the specimens were dried.

Colors of the pileus, lamellae, stipe, pseudorhizae, contexts, and veil remnants were compared to standards (Ridgway, 1912 (1991-1995); Munsell, 1976 (1995-1996) under diffuse daylight or a full-spectrum Vita-Lite and recorded. A color standard converter was developed during the research which greatly facilitated comparison of and translation between Ridgway and Munsell standards.

The odor of the sliced or crushed pileus and taste of a small portion of the pileus context and cuticle were recorded.

Measurements in millimeters were recorded for all specimens, including height and diameter of the pileus, breadth of the lamellae, overall (including pseudorhiza) and aerial lengths of the stipe, width of the stipe at the apex and the widest point, and width and height of primordia. Numbers of lamellae and lamellulae at the edge of the pileus and midway between the edge and disc were recorded for representative specimens.

The context and exterior surfaces of selected specimens were exposed to a Raytech BS-8 ultraviolet light and notations made of the location and color of fluorescent areas.

Selected reagents (alpha-Naphthol, $FeSO_4$, Guaiac, Guaiacol, 3% KOH, L-Tyrosine, 10% NH4OH, Para-Cresol, PDAB, and syringaldazine) were dropped directly onto small portions of the pileus, lamellae, stipe and pseudorhiza in porcelain or plastic spot plates, compared to a H_2O control after 15 and 30 minutes, and color changes noted.

Small to medium-sized (preferably mature) pilei were sliced cross-wise just below the stipe apex and placed individually into loosely covered small petri dishes; care was used to place the lamellar

edges perpendicular to a microscope slide, cover slip, or square of white paper to ensure a maximum spore deposit. Larger (or unusually fleshy) pilei were sliced in pie-shaped wedges or otherwise trimmed to fit the dishes and propped up to keep the lamellae perpendicular. When possible these were stored at temperatures as close as possible to those at the collection site, preferably outside in a protected area. (Good spore prints were generally obtained after eight hours, although younger basidiomes from longer-lived fleshy species such as *P. kauffmanii* often produced only faint prints.) The prints were then air-dried and after removing small portions of the pilei and stipe apices for microscopical examination of fresh material, the spore-print voucher specimens were force-air dried at low temperatures and placed with the spore prints and the rest of the collection.

Selected fresh specimens were closely examined for informative surface features under using a 16x Bausch & Lomb hand lens or Wild or Zeiss dissecting microscope; photographs of significant characters were made using either a camera equipped with a macrolens (either Olympus OM-1 or Canon Eos-Elan) or a Nikon camera mounted on the Wild dissecting microscope. Portions of the pilei, lamellae, stipe apex and pseudorhizae were placed in H20+soap and/or (time permitting) KOH and Melzer's reagent and examined under the light microscope (Zeiss or Leitz DMRB) to note the pigmentation of fresh tissues, existence of encrusting or plasmatic pigments, and to record the general spore size, cheilocystidial types, and presence or absence of clamp connections. Because the highly gelatinous nature of most fresh tissues prevented easy sectioning, only squash mounts were examined of fresh material.

As noted in Chapter 2, primordia, pseudorhizal origins, and/or immature basidiomes discovered during the excavation process were either observed fresh immediately after excavation or preserved in formalin-glacial acetic acid-5-% ethanol (FAA) or 90% ethanol or dried for later examination.

After fresh data were recorded, specimens were placed on low-heat forced-air dryers. Portable home food dehydrators (Sigg, American Harvest FD 50/30, or Waring 11DF10) were used in the field; otherwise the large dryers provided by the University of Washington herbarium were used. After 1995 dried lamellae from selected specimens were placed in glassine envelopes or small Eppendorf tubes and stored in silica gel for later molecular analysis. All Norvell collections cited in Appendix B are stored wholly or in part in WTU; some collections are also divided between DAOM and/or the Norvell personal herbarium (PNWMS).

In writing the collection descriptions, a brief 'general impression' containing general references to stature, colors, and important or unusual features was found to be exceedingly helpful; this non-technical paragraph generally preceded a full technical description incorporating the more precise data noted above.

Examination of dried material -- At the beginning of the study, small portions of the basidiomes were placed into moist chambers to be rehydrated before sectioning. It was soon discovered, however, that the highly gelatinous tissues common to *Phaeocollybia* were much more easily sectioned dry. Thereafter exsiccati were hand-sectioned without rehydrating and the sections placed either directly into 3-6% KOH aqueous solution or rehydrated in a moist chamber before mounting in Melzer's reagent. Sections from selected specimens were also mounted in Acetocarmine solution (following the guidelines outlined in Grund & Marr, 1965) to determine the nuclear state of various tissues.

Sections and squash mounts were examined under Kohler illumination, differential interference contrast (DIC), or phase contrast using a Leitz DMRB or Zeiss standard light microscope. Informative features were photographed through a microscope-mounted Zeiss or Contax 167MT camera or drawn with the aid of a drawing tube mounted on a standard Zeiss light microscope elevated 6 1/2 inches above the drawing plane. Scanning electron micrographs of spores and tibiiform diverticula were made on a JEOL scanning microscope from rehydrated samples fixed in osmium tetroxide, dehydrated in an ethanol series, critically point dried in Freon TF, and sputter-coated with gold/palladium in a Hummer V Sputter Coater. Basidiospores were measured from spore prints or (when spore prints were lacking) on the apical stipitipellis. Basidiospores measured on the gills were found to be slightly smaller and/or highly variable whereas those measured on the pileus (particular in pilei with a high degree of gelification of the suprapellis) were often greatly enlarged and distorted. The dimensions cited in the technical descriptions in Chapter 6 are the mean and standard deviation (computed from the means of all individual collections examined) followed by parenthesized overall range data. A minimum of 20 spores per collection were measured, and collections with outlier means were carefully re-evaluated before calculating the collection mean. Basidiospores were all measured in KOH and many also checked in Melzer's and fresh in water.

Discussion of taxonomically significant characters

(See Chapter 5 and Appendix A regarding morphological characters used in phenetic analyses.)

Macrocharacters

Color -- Although numerous authors remark on the large number of Phaeocollybias characterized by orange- to red-brown pigments, there are a number of Pacific Northwest species that can be characterized by ochraceous yellow, bright orange, olive green, purplish drab or blackish brown pilei There is also variation in the color of the young lamellae, which may be characteristically white, cream-colored, yellowish, pinkish, orange, or violet before darkening beneath rusty-brown to cinnamon colored spores. Two of the most striking colors, however, tend to be mutable. Horak (1989), noting the ephemeral nature of the violet and green pigments found in

some species, stated that the "...taxonomic value of these pigments appears to be low or close to nil." *Phaeocollybia fallax* exemplifies the crux of the problem Horak addresses, for it characteristically produces basidiomes with green pilei and violet lamellae. Yet many collections of *P. fallax* have been made containing pilei variously bluish green, yellow green, reddish brown, or dark brown, with some individuals possessing two-toned pilei (*e. g.*, simultaneously rusty-brown and green. See also comments under *P. olivacea* and *P. pseudofestiva* in Chapter 6). However, it should be noted that although there may have been instances where *P. fallax* has been misidentified due to the absence of a diagnostic transitory pigment, this should not negate the taxonomic value of that pigment when present.

While every effort was made to observe and record subtle gradations in color and hue, for the most part fine color distinctions are rarely taxonomically significant. Even subtle color differences among the seemingly similar pilei of different species within the *P. kauffmanii* complex can be summarized used relatively few color terms (*i.e.*, orange, tawny brown, purplish-brown, ochraceous yellow, yellow brown). It is nonetheless extremely helpful to refer to some generally accepted color reference when making field notes, particularly in view of the innate subjectivity of color perception.

Many Phaeocollybias can be provisionally identified in the herbarium from the color of the dried pilei alone, often from the presence or absence of a metallic overlay on the dried cuticle surface. Several examples have been noted in Pacific Northwest species:

-- *Phaeocollybia fallax, P. olivacea,* and *P. pseudofestiva* all are characterized by green pilei but after complete dehydration the pilei of the first two are a pale metallic greenish gold while those in *P. pseudofestiva* are instead very dull dark reddish brown. (This is particularly helpful in view of the fact that *P. pseudofestiva* is frequently found among *P. fallax* and *P. olivacea* in the field and, subsequently, in the herbarium).

-- Similarly *P. dissiliens* and *P. sipei* -- which also fruit closely together and which produce very similar hollow-stiped basidiomes with orange to orange brown pilei -- can be differentiated after drying -- *P. dissiliens* having a metallic gold pileus and *P. sipei* a matte dull brown one.

-- The distinctive ochraceous yellow color associated with *P. luteosquamulosa* has been occasionally observed also in very young pilei of *P. ammiratii.* After drying, however, the pilei of *P. ammiratii* turn a rich yellow copper color while those of *P. luteosquamulosa* remain a matte dark yellow.

-- While the characteristically drab *P. gregaria* and brilliant orange to reddish orange *P. piceae* are clearly distinct in the field, microscopically they are almost identical. However the dried pilei are metallic bronze in *P. gregaria* and a deep wine dark red in *P. piceae.*

Although the characteristics of dried pilei can prove helpful, particularly in the herbarium, the characters are always predictable. For instance, pilei in *P. benzokauffmanii* and *P. rifflipes* consistently turn a dull charcoal black on the surface after being dried. Unfortunately, so do most other Phaeocollybias that are senescent when collected, 'baked' until dry or kept too long before drying become similarly blackened or caramelized.

Pileus -- In addition to color, the diameter of the mature pileus and presence of scales on the surface are probably the most important pileus features. While also helpful, the degree of visicidity and general shape of the pileus are less important features. It is true that while most Phaeocollybias produce basidiomes with viscid to glutinous pilei, there are others that are merely lubricous, and one (*P. luteosquamulosa*) that is almost dry. Determination of this character can be difficult in the field, however, for most Phaeocollybias appear glutinous in the rain or merely tacky during times of low humidity. (Fortunately, innate degree of viscidity can usually be determined from microscopical examination of the pileipellis). For the most part, degree of opacity and presence or absence of striations is of minor taxonomic importance. Shape is also generally believed to be a taxonomically useful character, (*e. g.*, the inrolled versus straight pileus edge, the narrowly versus broadly conic pileus, the acuteness of the umbo). Unfortunately the pileus shape -- some form of conic to campanulate for all Phaeocollybias -- is closely tied to the developmental stage of the basidiome. It is difficult at times to know whether a particular specimen with a conic-convex pileus with papillate umbo and slightly incurved edge represents a young or fully mature specimen.

Odor and taste -- The subjective perception of odor and taste has been frequently noted (*e. g.*, Smith, 1949; Arora, 1985) . Problems arise when the researcher cannot differentiate bitter from sweet (re 'odor' or 'taste' blind, *cf.* Smith, 1949), or when a specimen that has been collected and stored for a long time is sampled as it is beginning to decompose. Nonetheless, odor and taste, while not particularly reliable, can be extraordinarily helpful. Odors are best sampled from crushed tissues of the pileus and stipe both in the field at the time of collection and later after the basidiome has warmed to room temperature.

In Europe the single-most frequently cited odor and taste is 'raphanoid' (Horak, 1977; Gulden, 1983; Jakobsson & Stridvall, 1983). For Pacific Northwest Phaeocollybias, the four most informative character states are 'farinaceous', 'gebrenzlich/potato/pansy', 'not distinctive', and 'bitter'. 'Farinaceous', which refers to the odor of freshly ground meal, is commonly used to

describe the odor of certain tricholomas. In this study the term 'farinaceous' was used in the broad sense, incorporating both pleasant tones (i.e. 'sweetly farinaceous' in Chapter 6) or very slightly unpleasant and/or bitter tones similar to those found in raw bitter cucumbers or carrots. Preliminary studies being conducted at Humboldt State University suggest that farinaceous odors may be linked to anti-feedant chemicals that protect some basidiomes from herbivorous attack by insects or micro-arthropods (Wood, pers. comm., 1992; Largent, pers. comm., 1992, 1996). Uncommonly noted in European Phaeocollybias (Jacobsson & Stridvall, 1983), farinaceous odors are characteristic of five Pacific Northwest Phaeocollybias, including *P. ammiratii, P. kauffmanii, P. oregonensis, P. benzokauffmanii*, and *P. redheadii*. This may be an important diagnostic character since these species exhibit mild to strong Syringaldazine reactions (*q.v.*) and are rarely, if ever, attacked by insects. (It should be noted that in *P. ammiratii* -- characterized by only weakly positive Syringaldazine reactions -- farinaceous odors are detectable only when the flesh is crushed. Basidiomes in the other four species are both strongly farinaceous and strongly reactive in Syringaldazine.)

Other, more fragile basidiomes such as *P. fallax* or *P. scatesiae* are characterized by a subtle complex odor that if smelled once is readily recalled. Unfortunately the odor is -- like farinaceous -- equally difficult to describe: variously called 'grebrenzlich' (German for burnt hair) by Horak (1996, pers. comm.), 'musty raw potatoish' by Barron and Redhead (pers. comm., 1992), and 'slightly floral, like pansies' by Fox (pers. comm., 1992), Roger (pers. comm., 1994) and the present author. (Pacific Northwest Phaeocollybias with this distinctive odor -- *e. g., P. fallax, P. attenuata, P. sipei* -- are also Syringaldazine negative and frequently inhabited by insects. See also comments in Chapter 5.)

Lamellae -- Here the most important diagnostic character is the color of the young lamellae, particularly in the violet-gilled *P. fallax, P. lilacifolia* and *P. rifflipes*. The breadth of the mature lamellae (and possibly the length: width ratio) also appear to be taxonomically useful characters. While the dispersal of the lamellulae among the lamellae might have taxonomic potential, the interlocking wedge-shaped patterns appear to be too intricate to be efficiently accessible. Features that are influenced by the age of the basidiome (*e. g.*, lamellar closeness, gill shape) or too easily altered by outside influences (the mature gill edge) have not proved particularly useful.

Stipe -- The two most important characters of the stipe are the width at the apex and the presence or absence of stipitipith. The relative width of the cartilaginous cortex can also be diagnostic (*e. g., P. californica* and *P. scatesiae* with thick cartilaginous rinds versus the unusually thin rinds found in *P. rufotubulina*). Color is useful in young to maturing specimens that have not yet developed the overall ferruginous tones common throughout the genus. The retention of drab or

violaceous tones at the apex after the lamellae mature can aid in differentiating *P. fallax* and *P. lilacifolia* from *P. olivacea* and *P. pseudofestiva* in the field. Stipe length and shape have proved too variable within each species to be taxonomically useful.

(Rhizomorphic) pseudorhizae -- The recently discovered pseudorhizal growth patterns fully outlined and illustrated in Chapter 2 appear to be highly diagnostic. Their current taxonomic utility is considerably diminished by the fact that completely intact pseudorhizae are rarely collected due to the difficulty encountered in attempting to extricate them from rocky or root-filled soils. More research is still required before their full taxonomic potential can be analyzed.

Spore print -- The color of the spores in mass does follow species specific patterns (*e. g.*, the dark blackish red-brown of *P. attenuata* versus pinkish cinnamon of *P. fallax).* However, because most of the color differences are subtle and depend to a certain degree on the depth of deposit, dependence upon spore print color for species recognition is impractical.

Microcharacters

Cheilocystidia There are two distinct cheilocystidial forms represented in *Phaeocollybia*: thin-walled filamentous to more or less clavate elements (cf. *P. kauffmanii, Fig. 6.15* and *P. sipei, Fig. 6.44)* and refractive thick-walled lageniform to tibiiform elements (cf. *P. pseudofestiva, Fig. 6,31).* Smith (1957b) considered cheilocystidia with refractive thick-walled necks to represent the most recently derived form, noting their extreme rarity in other genera. However, given the similar morphology of these thick-walled tibiiform cheilocystidia to the generically significant tibiiform diverticula that are an integral part of the pellicular veil (see Chapter 2), it seems equally possible that the thick-walled cheilocystidia represent an ancestral form that has been lost in those species characterized by thin-walled clavate cheilocystidia. In this interpretation, the indeterminate thin-walled cheilocystidia would be considered modified extensions of the central hyphae of the lamellar trama which have evolved to assume the same protective and secretory functions as their thick-walled refractive antecedents. Phylogenetic analyses in the current study (Chapter 5) imply that seven out of eight Pacific Northwest Phaeocollybias characterized by tibiiform cheilocystidia form a very closely related clade also characterized by racemose pseudorhizae (with the exception of *P. spadicea*) . Species with thin-walled clavate cheilocystidia, on the other hand, are generally characterized by vertical monopodial pseudorhizae. See Chapter 5 for further observations.

Most Pacific Northwest species are characterized by having only one type of cheilocystidia. However, Smith (1957b) observed that some species with clavate cheilocystidia (*e. g., P. olivacea)* tended to develop what he referred to as 'forerunners' of the thick-walled elements. Examinations of the type of *P. olivacea* by this author shows that while most specimens produce

only clavate cheilocystidia, one specimen does possess highly heteromorphic cheilocystidia, with clavate elements intermixed with occasional elements topped with long thin extensions that even more occasionally appeared capitulate; very rarely, however, was any thickening of the cheilocystidial wall noted. More likely this specimen contains 'regenerating' cheilocystidia described in Chapter 2. As noted there, while the refractive thick-walled lageniform to tibiiform cheilocystidia appear to be determinate in length, most clavate cheilocystidia continue to grow apically, continually developing new septa and often producing long filamentous outgrowths. As the confusion surrounding the type of *P. olivacea* indicates, this "germination" tendency can complicate correct interpretation of the cheilocystidial morphology in a senescent or improperly stored specimen where such artifacts occur. The fact that some species with clavate cheilocystidia (notably *P. fallax)* rarely if ever form apical outgrowths has often proved helpful in microscopically differentiating species that do develop them (*i. e., P olivacea).*

Because lengths of thin-walled clavate cheilocystidia (indeterminate in nature) are highly developmentally dependent, widths appear to be taxonomically more informative. (Lengths of the tibiiform thick-walled cheilocystidia appear to be considerably less variable within a taxon.) The thin-walled cheilocystidia are usually categorized by the progression 'mucronate','filamentous', 'cylindrical',' irregularly cylindrical', 'narrowly clavate', 'broadly clavate', 'subcapitate', or 'subglobose'. A tendency for some of the broadly clavate thin-walled elements to become greatly enlarged in age has been observed in certain material.

Clamp Connections -- While an extremely useful character, true clamp connections are rare in Pacific Northwest Phaeocollybias, with only four taxa (*P. ammiratii, P. dissiliens, P. phaeogaleroides, P. radicata)* currently recognized as having clamp connections. The fact that all four species otherwise differ so greatly from one another in appearance and anatomy, however, suggests that the taxonomic utility of clamp connections is more helpful at a specific than at a subgeneric level. The dual hyphal system now recognized to occur in some tramal tissues in *Phaeocollybia* appears to have caused considerable historical confusion regarding the presence or absence of clamp connections in certain species (see Chapter 2), as have the branch initials that are found at the septa of the pellicular hyphae (no doubt prompting an exasperated Smith (1957b) to describe clamp connections as being absent "...for all practical purposes" in his description of *P. spadicea*). Basidiomes in the four species characterized by the presence of clamp connections (cited above), however, produce clamp connections that are relatively frequent and clearly visible within the narrow hyphae in the suprapellis and usually present on the bases of the cheilocystidia. In these species, clamp connections are also present at the basidial bases where, however, they are more difficult to detect. As noted in Chapter 2, use of Nomarsky optics (DIC) and oil immersion aid considerably in the correct interpretation of individual characters in highly gelatinous sarcodimitic tissues; it was by this means that the type of *P. oregonensis* (described by

Smith & Trappe (1972) as having 'very rare' clamp connections) was shown not to possess clamps but rather a highly developed dual hyphal system.

Basidiospores -- Smith (1957b) noted the taxonomic utility of size, degree of ornamentation, shape and color of basidiospores. Pacific Northwest Phaeocollybias produce basidiospores that range in length from ~5 µm (*P. radicata)* to 10.5 µm (*P. redheadii)* and in width from ~3 µm (*e.g., P. radicata)* to 6-6.5 µm (*e.g., P. luteosquamulosa, P. olivacea).* Mean (as in 'median') basidiospore dimensions have been found to be taxonomically informative and remain surprisingly constant throughout a species, even in view of the wide overall range of sizes encountered within a single specimen. (Use of means over averages also eliminates the unrealistically precise measurements resulting from the arithmetical averaging process.)

Basidiospore size is useful in differentiating taxa at the specific level. Observations of the unusually large limoniform basidiospores noticed in *P. redheadii* was one of the first indications of the existence of cryptospecies in *P. kauffmanii.* The small size of the limoniform spores found in *P. rifflipes,* a species first revealed by molecular analyses (see chapters 4, 5, & 6), are been used to differentiate the new species from *P. fallax.* Basidiospore size (and general morphology) is perhaps the singlemost helpful character that can be used to differentiate unusually large and brown basidiomes in *P. oregonensis* from similar appearing basidiomes of *P. kauffmanii.*

The general morphology of the basidiospore (which is usually described in the genus as 'subellipsoidal', 'ellipsoidal', 'amygdaliform' or 'limoniform') is also helpful in identifying species. Here use of the length:width ratio (*i.e.* 'Q') is not as informative as one might wish, since it is computed by the widest dimensions measured. More significant is how gradually or abruptly the spore widens (hence the introduction of 'limoniform-globose' or 'roundly limoniform' to describe the distinctive basidiospores in *P. attenuata* and *P. 'similis"* sensu Smith). Also useful is the absence or presence and degree of prominence of the apical callus (referred throughout as the 'apical beak') as well as its position on the spore in relation to the opposing apiculus.

The color of the spore when viewed under the microscope is closely linked to the thickness of the spore wall and degree of ornamentation. Thus there is a general continuum from extremely pale amber basidiospores with ornamentation scarcely discernible when mounted in KOH and viewed in oil immersion (*i. e., P. oregonensis)* and very dark amber basidiospores with coarsely rugulose-warty ornamentation clearly visible at low power (i.e. *P. attenuata).* The presence of a plage -- here an area of lowered or more subdued (but not smooth) ornamentation -- is not as taxonomically informative as in *Galerina,* although there are some species where the suprahilar area that do appear fully ornamented. These 'plages' can be detected with difficulty via optical

sectioning under oil; only rarely are they immediately apparent or sharply delimited from the more ornamented areas. Scanning electron micrographs clearly show that even the 'smoothest' *Phaeocollybia* spore is in fact ornamented *(cf. P. oregonensis, Fig. 6.24)* and the plage areas seen on more highly ornamented wider basidiospores of *P. ammiratii* and *P. kauffmanii*, (*Fig. 6.2* and *Fig. 6.17* respectively).

Pileipellis -- Little taxonomic use has been made of the pileipellis structure in *Phaeocollybia*, yet the existence of the unusually well delimited layers, the different degrees of gelification, hyphal separation, pigment reactivity and incrustation within the layers makes the pileipellis a useful taxonomic tool. The terms 'epicutis' and 'hypodermium' are somewhat confusing in this genus, particularly in view of the use of the morphological term 'cutis' to refer to the hyphal alignment (as opposed to 'trichoderm'). Despite problems that can arise from the fact that topographical terms do not necessarily reflect the origins of the tissues, the terms 'suprapellis', 'mediopellis' and 'subpellis' have been used to describe the pileipellis layers in this treatment (*cf.* also, Bas, 1969; Largent & Thiers, 1977; Largent & Baroni, 1988).

The number of clearly delineated layers is perhaps the most useful character. Most of the Phaeocollybias found in the Pacific Northwest are 'bilaminate' with a non-pigmented suprapellis overlying a pigmented subpellis. One species, *P. luteosquamulosa*, is 'trilaminate' with a highly pigmented suprapellis, colorless mediopellis, and pigmented subpellis. (This is one instance where reliance on topological terms causes difficulty, for the mediopellis in this instance is clearly homologous to the more typical suprapelli found elsewhere.) There is a small group of Phaeocollybias with subgelatinous bilaminate pileipelli in which both suprapellis and subpellis are pigmented (*e. g., P. attenuata*); in these species the two layers are recognized by differences in hyphal diameters with the narrow cylindrical hyphae of the suprapellis easily distinguished from the more inflated hyphae within the subpellis. (In most species, there can be confusion in distinguishing the subpellis from the pileitrama due to lack of integrity of the tramal hyphae or the different hyphal orientation . Thus the taxonomic usefulness of the pileitrama appears limited.)

The arrangement of hyphae within the suprapellis and the degree of gelification present are two other potentially useful characters. Most Pacific Northwest Phaeocollybias with glutinous pilei have an ixocutis with radially aligned long narrow branched hyphae. Many are characterized by a gelatinous matrix in which loosened or well separated hyphae are embedded. Smith (1957b), who usually described this type of a pellis as a 'collapsed ixotrichodermium', noted "...a careful study of [the] manner of origin [of the hyphae] has convinced me that in most species they arise as a turf, but because great elongation takes place, the elements soon become decumbent with the result that in sections of revived material they may appear as filaments radially appressed or somewhat interwoven.". Observations of a primordial series in *P. scatesiae* by this author

indicate that the long narrow hyaline hyphae originate as a cutis -- tightly packed and radially aligned beneath the pigmented pellicular veil of the primordium (see also Chapter 2). It thus appears that after pileal expansion and loss of pellicular veil, there is an increased tendency toward branching and elongation which when combined with continual gelification of the surrounding tissue produces the characteristic separated and slightly interwoven hyphae embedded within a gelatinous matrix described above. Gelification of the suprapellis appears to be consistent within species; one of the helpful characters delimiting *P. scatesiae* from *P. californica* is that in the former species gelification occurs to such a degree as to obscure hyphal walls.

In fresh material (and to some extent in dried material that has been rehydrated) the color of the subpellis in water mounts is highly useful. These pigments are reactive in KOH, however, so that many pigments (*e. g.*, green, brown) appear orange to orange brown when mounted in KOH. Additionally the intensity of the color varies with the thickness of the mount, thus complicating the interpretation of 'deepness' and 'paleness' of a color. More useful is pigment topology, in particular the presence of incrusting and diffuse pigments. Most Pacific Northwest Phaeocollybias contain (intra)parietal pigments that are not lost (although the color may change) when placed in KOH. The bright orange pigment in the subpellis of *P. piceae*, however, is plasmatic (or 'diffuse') and rapidly disappears in KOH, often leaving behind a completely non-pigmented tissue. Heavily encrusting pigments can be rare and are often more readily discerned in fresh material mounted in water; in dried specimens,the encrusting pigments in *P. kauffmanii* and *P. redheadii* are generally noted only under oil immersion. It is possible that the subpellis in *P. olivacea* contains parietal, plasmatic and incrusting pigments, but the tendency of the parietal pigments to coagulate within the hyphal walls in KOH mounts of dried material (and thus mimic a spottily distributed incrusting pigment) complicates determination of pigment topography. There are a number of species characterized by the presence of incrusting pigments within the suprapellis. The closely allied species *P. scatesiae, P. californica* and *P. rufotubulina* can be microscopically differentiated by the lack or presence of incrusting pigments, with none in the first, concentric hyaline to pale amber incrustations in the second, and concentric dark reddish-orange incrustations in the third. (This is most obvious in fresh material.)

Evaluation of the diagnostic potential of oleiferous hyphae within the pileipellis revealed that both presence or absence and content color of these cells are developmentally dependent and too variable within a given taxon to prove taxonomically helpful.

Basidia -- The taxonomic potential of certain basidial characters such as basidial width, sterigmatal height, ratios (*e. g.*, length : width, number of 4-spored : number of 2-spored) remains to be systematically explored. All Pacific Northwest species are 4-spored, although some species do appear to have a certain number (small) of 2-spored basidia intermixed; statistical comparisons of

the different proportions of 2-spored to 4-spored basidia proved inconclusive. As can be seen from the microdrawings (Chapter 6), there is a fair degree of variation among basidia from different species, but phenetic analyses of comparative data indicates that basidiospore measurements are far more useful.

Pleurocystidia -- True pleurocystidia (as opposed to cheilocystidial 'outliers') are very rare in the genus. However one new species (*P. pleurocystidiata*) has been found that was immediately recognized as distinct by its possession of abundant thick-walled tibiiform pleurocystidia (morphologically similar to the cheilocystidia). While it is possible that thin-walled clavate pleurocystidia might be mistaken for basidioles and young basidia, the existence of thin-walled pleurocystidia has been verified only in one Pacific Northwest species. The occasional to frequent narrow thin-walled pleurocystidia or paraphyses found in the newly recognized *P. rifflipes* are probably more properly termed 'hyphidia' (*Cf.* Singer, 1986.)

Tramal Tissues -- Although the generic significance of sarcodimitism in the genus is still under consideration, a dual hyphal system composed of [i] thin-walled narrow highly branched flexuous and [ii] thick-walled wide rigid cylindrical elements is definitely present in the tramal tissues of pseudorhizae in all Pacific Northwest *Phaeocollybia* species examined thus far (although admittedly rudimentary in species with more fragile basidiomes such as *P. phaeogaleroides).* At the specific level, there is no doubt that the differential retention and degree of development of sarcodimitism in the lamellar, pileal, and stipe tramas is taxonomically informative. In general, larger more robust basidiomes show a relatively high degree of sarcodimitism with a fully developed dual hyphal system extending well up into the pileal and lamellar tramas (*cf., P. benzokauffmanii* and *P. oregonensis).* As a rule, in species that develop hollow stipes, sarcodimitic tissues are generally restricted to the tissues of the pseudorhizal pith, which has been consistently present even in mature basidiomes for all species. (See also Chapter 2; Corner, 1966, 1991; Redhead, 1987; Norvell *et al.,* 1993b)

Tibiiform diverticula -- While clearly diagnostic at the generic level (See Chapter 2), more complete data are needed before their taxonomic utility can be fully demonstrated at the specific level. However, a fair amount of patience and expertise is required to detect them, as they are restricted to the remnants of the pellicular veil on the external cortex which is easily everted during mounting. More unfortunately, the parts of the organism on which they are universally present -- *i. e.,* the mycelia, primordia, and pseudorhizae -- are all too often left in the field, restricting their utility in differentiating herbarium specimens. Nonetheless distribution of the diverticula over the mature basidiome does occur in species specific patterns. In most species diverticula are restricted to the pseudorhiza and accompanying mycelium; in others they also occur on the apical stipitipellis

and/or pileipellis, thus indicating the differential retention of the pellicular veil. That the dimensions may vary in species specific patterns is indicated by the fact that while most diverticula are generally quite small, (5 -30 µm long) those found in *P. phaeogaleroides* are considerably larger (30 to >60 µm long).

Fluorescence and macrochemicals

Fluorescence -- Observation of Dr. Joe Ammirati using ultraviolet light to aid in the identifications of some *Cortinarius* specimens prompted a decision to investigate fluorescence in *Phaeocollybia* as well. While collections were not routinely tested, exposure of numerous fresh specimens indicated that most Phaeocollybias do appear to fluoresce to a certain degree under UV light. The most reactive part of the basidiome is generally the lamellae, which typically emit a white to dull orange light under ultraviolet (generally ranging from bright greenish white to brilliant whitish yellow in young expanded specimens, intense brilliant yellow in more mature specimens, or dull spotted yellow to orange in specimens with spore-covered lamellar surfaces). The context occasionally turns a dull orange in places and there are often deep brilliant purple areas on the pseudorhizal interior. Determination of whether the fluorescence patterns are generic, specific or developmental in nature will require further investigation. Ultraviolet exposure of dried specimens appears to produce similar (if somewhat muted) results; whether dried material consistently produces the same fluorescence patterns as are found in fresh material needs to be tested.

Chemical spot-tests Of the ten reagents spot-tested on fresh Phaeocollybias, five appeared to produce uniform results throughout the genus: alpha-Naphthol (purplish context, greenish lamellae), Guaiac (oxydase positive -- blackish malachite green), Guaiacol (oxydase positive -- intense cherry red), 10% NH_4OH (no color change), and PDAB (no color change). The few times L-Tyrosine was used, it produced a slightly pinkish reaction; however, its use was abandoned early in 1992 when the difficulty of using and storing it in the field was discovered.

Two other reagents produced variable results, although some differences in degree of intensity of the color change were noted. Para-Cresol typically turned tissue a strong reddish orange color although occasionally no color change was seen. FeSO4 turned samples a variably intense pale green, greenish gray, or a dull brownish green.

Two chemicals tested appear to have good taxonomic potential in the genus: KOH and Syringaldazine. Application of KOH on the pileus and lamellar tissues produced a range of reactions ranging from no color change to latent browning to immediate browning. Unfortunately only a 3-10% KOH aqueous solution (most often the 3-6% KOH mounting

medium) was used; a 15-20% KOH aqueous solution, which should produce more consistent and better results, is suggested for future testing.

Syringaldazine shows the greatest taxonomic potential of the chemicals tested. Its use was introduced by workers who found that the production of laccase by growing cultures could be identified by a positive (magenta) Syringaldazine response while L-Tyrosine and Para-Cresol both indicated the presence of tyrosinase (Marr *et al.* 1986). As a result of their research into the taxonomic potential of laccase/tyrosinase spot tests of basidiome tissues, Marr *et al.* (1986) sorted agarics into four reactivity groups (negative, tyrosinase dominant , laccase dominant, and equivalent). Representatives of the Cortinariaceae were mixed in their reactivity and *Cortinarius* species were represented in all but the laccase dominant groups. While Marr and his associates tested no *Phaeocollybia* species, representatives from almost all species have been consistently tested in the current study and have responded in surprisingly coherent species-specific patterns. Strongly positive Syringaldazine reactions were noted for *P. benzokauffmanii, P. kauffmanii, P. oregonensis, P. tibiikauffmanii, P. redheadii, P. spadicea* and *P. pseudofestiva.* Significantly the first six named are all characterized by large stature, viscid to glutinous pilei and massive fleshy stuffed stipes with vertical monopodial pseudorhizae. (The morphology of the ultimate origins of the smaller less robust basidiomes in *P. pseudofestiva* is still unresolved; stuffed stipes with vertical monopodial pseudorhizal origins were observed in several solitary collections of that species but some evidence of racemose pseudorhizae were noted in collections of gregarious basidiomes . See additional discussion under both species descriptions in Chapter 6). Weakly positive responses (with a mild magenta reaction observed after 15-30 minutes then generally confined to the pseudorhizal cortex) are characteristic of *P. ammiratii, P. olivacea, P. pleurocystidiata, P. rufotubulina, P. scatesiae* and *P. sipei. Phaeocollybia attenuata, P. dissiliens, P. fallax, P. luteosquamulosa, P. phaeogaleroides, P. picea, P. rifflipes* and *P. similis* characteristically display negative Syringaldazine reactions. (This character is discussed further in Chapter 5.)

CHAPTER 4. MOLECULAR CHARACTERS GENERATED FROM THE ITS1 + 5.8S + ITS2 RDNA REGION

Introduction

As stated previously, the primary goal of this research is to determine which *Phaeocollybia* species occur in the Pacific Northwest and to ascertain the taxonomic relationships among them. During identification and evaluation of previously described species from this region, discovery of undescribed taxa dictated the development of species hypotheses generated from new sets of potentially diagnostic characters. Morphological characters are treated in the previous and following chapters. This chapter introduces the second character set generated from restriction enzyme digestion of the ITS1 + 5.8S + ITS2 rDNA region (hereafter referred to simply as 'the ITS region' -- see *Figure 4.1).*

Recent innovative technological advances have placed molecular characters within easy reach of taxonomic researchers. Introduction of polymerase chain reaction (PCR) 'fingerprinting' techniques has enabled rapid and relatively economical identification of restriction endonuclease digestion phenotypes for homologous genes from a large number of individuals (Bowman *et al.* 1992; Foster et al., 1993; Kohn, 1990, 1992; Metzenberg, 1991; Rogers et al. 1990). Restriction fragment length polymorphisms (RFLPs) in nuclear and mitochondrial DNA have also been used in many different fungal taxonomic and phylogenetic studies (*e. g.* Anderson et al., 1987; Baura et al., 1992; Bruns et al., 1989, 1991,1992; Erland et al., 1994; Förster et al., 1993; Gardes et al., 1990, 1991a, 1991b; Hibbett & Vilgalys, 1991; Hintz et al., 1985; Rogers et al., 1989, 1990; Smith & Anderson, 1989; Taylor, Smolich & May, 1986; Vilgalys & Hester, 1990), and the ITS rDNA region has proved to be both easily isolated and phylogenetically informative due to the combination of the highly conserved 18S gene and more variable and less highly conserved internal transcribed spacers that prove more informative at lower taxonomic levels (*e.g.* Berbee & Taylor, 1992a, 1992b; Feibelman et al., 1994; Gardes et al. 1990; White et al. 1990).

Within the homobasidiomycetes, restriction enzymes have been used successfully to detect interspecific and infraspecific genetic variation within and among at least 20 genera including *Agaricus* (Hintz *et al.*, 1985, 1988, 1989; Kerrigan *et al.*, 1993), *Agrocybe* (Rehner & Ammirati, 1987; Rogers *et al.*, 1989), *Armillaria* (Anderson *et al.*, 1987, 1990; Smith & Anderson, 1989), *Cantharellus* (Feibelman *et al.*, 1994; Danell *et al.*, in preparation; Redhead *et al.*, 1996, 1997), *Coprinus* (Hopple & Vilgalys, 1994; May & Taylor, 1988; Wu *et al.*, 1983), *Dermocybe* (Rogers *et al.*, 1989; Liu *et al.*, 1995), *Ganoderma* (Park *et al.*, 1996), *Gauemannomyces* (Ward & Akrofi, 1994), *Hebeloma* (Marmeisse *et al.*, 1992), *Laccaria* (Gardes *et al.*, 1990, 1991, 1992), *Lentinula* (Hibbett, 1990; Kulkarni,1991; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992; Fukuda *et al.*, 1994), *Lentinus* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992),

Neolentinus (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), *Grifola* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), *Phialophora* (Ward & Akrofi, 1994), *Polyporus* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), *Pleurotus* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), *Mycena* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), *Collybia* (Hibbett, 1990; Hibbett & Vilgalys, 1991; Molina *et al.*, 1992), and *Tylospora* (Erland *et al.*, 1994).

There are problems inherent with using restriction enzymes to discriminate among species. Possible sources of error fall into two classes: [i] those associated with estimation of the 'true' gene tree and [ii] those associated with selection of the appropriate genomic region for differentiating taxa at the taxonomic level desired. With respect to [ii], the ITS region appears to have yielded highly consistent and informative data for discriminating taxa, particularly at the specific level, in the studies listed above. With respect to [i], however, RFLP analysis and restriction site mapping are both processes that may lead to erroneous conclusions.

RFLP analysis uses fragments or banding patterns as characters. Problems arise when, "...one tries to use the number of fragment differences to estimate the degree of difference or nucleotide divergence or [when] one treats the individual fragments as independent characters. The greatest problem is if length mutations are present and if multiple enzymes are surveyed..... In this case a single mutation will be counted as at least 2N differences where N equals the number of enzymes surveyed..... Furthermore, even without length differences, fragments are clearly not independent characters because single site or length changes always result in multiple fragment changes." (Bruns *et al.*, 1991) Preferable to RFLP analysis is restriction site mapping, in which the locations of restriction sites on the DNA region under analysis are deduced from the band lengths produced by enzyme digestion. If done well, mapping produces discrete characters that can be more reliably analyzed. Bruns *et al.* (1991) observe, however, that mapping can be "...a time consuming and relatively error-prone process... [complicated by] length mutations (*i.e.* insertions and deletions).... Restriction sites are prone to convergent loss and saturate quickly. For these reasons mapping to make phylogenetic comparisons among fungi is of limited value."

Nonetheless, the fact that restriction enzyme analysis has provided good diagnostic characters for discriminating species in numerous other studies (and the fact that it has until recently been far less expensive and time-consuming than DNA sequencing) outweigh the potential problems cited above. For this reason molecular characters have been generated from representatives of Pacific Northwest *Phaeocollybia* species through PCR amplification and single restriction enzyme digestion of the ITS region. The goal of this research has been to develop species hypotheses from analyses of these molecular characters and to determine whether these hypotheses are congruent with those developed from morphological characters.

Materials and Methods

Specimen selection and preparation: Beginning in 1993, specimens were selected from type collections of previously published species or well documented collections made by the investigator in 1991-1994. Individual species or putative species were represented by as many Pacific Northwest localities as possible, resulting in the selection of 191 Pacific Northwest *Phaeocollybia* collections. Additionally selected for comparative purposes were 18 collections representing seven extralimital *Phaeocollybia* species and six outgroup taxa (*Caulorhiza umbonata* (Peck) Lennox, *Cortinarius vanduzerensis* Smith & Trappe, *Galerina autumnalis* (Peck) Smith & Singer, *Gymnopilus spectabilis* (Fr.) A. H. Smith, *Stagnicola perplexa* (Orton) Redhead & Smith; *Xerula megalospora* (Clements) Redhead, Ginns & Shoemaker).

Dried mature basidiomes from target collections were first screened under a dissecting microscope for contaminants, moulds, insect larva, or damage, after which small portions of dried lamellae were removed from each pileus with clean forceps, placed into 1.5 mL Eppendorf tubes, capped, labeled and stored in desiccant until use. The pilei were placed into plastic zip-locks bags for later microscopical verification. All samples, vouchers and source collections were tagged with DNA identification codes on coded colored labels. (Appendix C-1).

DNA Extraction and Isolation: DNA was successfully extracted from 117 samples using a 'hot CTAB' procedure adapted from in Rogers & Bendich (1988, 1994), Bruns *et al.*, (1990), Doyle & Doyle (1990), and Rogers (1994). Small amounts of lamellar tissue were transferred from storage vials to 1.5 mL Eppendorf tubes where they were ground to a fine powder with Kontes minipestles after being plunged into liquid nitrogen. An equal volume of 24:1 Chloroform/IAA was added to equal amounts ground lamellae and 2x CTAB (cetyltrimethylammonium bromide) buffer heated to 65° C. The tube was capped, thoroughly shaken and then alternately plunged first into liquid N2 and then into a 65° C water bath two or three times before being briefly spun down in an Eppendorf bench microcentrifuge. The epiphase was transferred to a 0.5 mL Eppendorf tube, 2/3 volume isopropanol (chilled to -20° C) added, and the mixture chilled for 1-3 hours. After microfugation for 10 minutes, the contents were decanted, the supernatant discarded, and the pellet air dried for thirty minutes. 25-100 µL high salt TE was added to the pellet; the contents were heated to 65 °C and vortexed until the pellet dissolved. After addition of two volumes 95% ETOH and overnight precipitation at -20° C, the suspension was microfuged for 5-15 minutes, decanted, supernatant discarded, and pellet washed in 100-200 µL 80% ETOH. After microfugation and decantation, the open tube with the pellet was placed into vacuum desiccator for 30 minutes and completely air-dried. The pellet was then resuspended in 25-100 µL 0.1x TE and stored at -20° C until needed.

Direct Amplification -- DNA was successfully isolated from 82 samples by amplifying the target DNA region directly from basidiospores (without intervening extraction) in a procedure originally devised by Nakasone (pers. com., 1994) and modified as necessary during the current investigation. Basidiospores were obtained either from spore prints or gill flakes. Basidiospores obtained from spore prints were scraped with a glass cover slip and washed with 50 µL 1x TE into a 0.5 mL Eppendorf microfuge tube to which a small number of acid washed <106 µm diam glass microbeads had been added. The mixture was vortexed at full speed for two minutes, plunged first into liquid N_2 and then into a water bath heated to 65° C. Alternate chilling and heating was repeated as necessary to ensure spore wall fractionation, after which the mixture was microfuged, and the transferred epiphase stored overnight at -20° C before amplification. 1 µL of spore suspension was generally found to be sufficient for one 25 µL PCR-reaction.

The same protocol was followed for basidiospores contained on gill flakes except that first basidiospores were removed from the lamellar tissues. Gill flakes covered with 50-100 µL 1x TE were vortexed gently for 10-20 seconds to loosen the spores and then briefly microfuged to separate spore suspension and lamellar tissue. The spore-laden epiphase was transferred to another tube, microfuged for two minutes, decanted, and then prepared according to the protocol outlined above. Here also 1 µL of spore suspension was sufficient for one 25 µL PCR-reaction.

Spore suspensions obtained by either protocol variation were generally prepared a day ahead of a scheduled PCR amplification; suspensions not amplified within one week of preparation were discarded.

Quantification Procedures and Gel Electrophoresis -- The first 79 DNA templates obtained via CTAB extraction were quantified by comparing 2 µL newly extracted DNA to DNA standards (1-, 5-, 10-, 20-, 50-, and 100- and 200 ng/µL DNA) on spotplates containing 1% Agarose gels prestained with Et-Br. Each spot-plate was exposed to ultraviolet light and photographed. In instances where there appeared to be little correlation between amount of DNA quantified and amplification success, DNA templates were checked for DNA degradation via gel electrophoresis. Templates and molecular standards (BMB Mol 1114-19 bp, GibcoBRL 100 bp DNA ladder, or Gibco BRL 1 kb DNA ladder) were electrophoresed at 100V through a 1.2% Agarose gel (Sigma Ultrapure Grade Agarose in 0.5x TBE) on Hoefer HE33 'Minnie' horizontal submarine units. The minigels, stained with EtBr and washed in dH_2O (*q.v.*), were then visualized as above to determine whether the extracted DNA was long enough (> 800 bp) to permit amplification of the entire ITS region. After sufficient experience was gained in interpreting the degradation minigels, spot-plate quantification was discontinued.

PCR Amplification and Gel Electrophoresis -- Oligonucleotides derived from *Saccharomyces cerevisiae* (ITS4: 5'-TCC TCC GCT TAG TTA TAT GC-3' & ITS5:5'-GGA AGT AAA AGT

CGT AAC AAG G-3' -- originally donated by John Stiller and later ordered from Howard Hughes Medical Institute) and specific for the ITS region were used to prime amplification of segments of nuclear DNA according to procedures outlined in Bruns *et al.* (1990), Paäbo (1990), White *et al.* (1990), and Rogers (1994, pers. comm.). The most reliable PCR reaction mix was found to contain 10% 1x PCR buffer; 10% 0.2mM dNTP mix, 5% ITS4 primer, ITS5 primer, 4% DNA-0.1x TE suspension, 1% Bovine Serum Albumin; 0.5-1% Taq Polymerase; 64-64.5% sterile ddH_2O. Shortly before loading, all reagents except the Taq polymerase and DNA template were mixed into a master mix and kept chilled on ice; the Taq polymerase, kept at -20° C, was combined with the master mix, and this reaction mix was aliquotted into labeled 0.5 reaction tubes. Each suspended DNA template (generally ~1µL/25µL reaction) was dispensed into the appropriately labeled tube, which was briefly microfuged. After tubes were each topped by 1-2 drops of mineral oil, capped, and briefly microfuged, they were loaded immediately into a PTC-100 Thermal Programmer (MJ Research, Inc.). The biocycler was programmed in accordance with suggestions by J. Stiller (pers. comm. 1993), S. Rogers (1994), and Y. Liu (1995); the program included a 5 minute incubation at 95°C followed by a 30-35 cycle run (1 min. @ 95°C; 2 min. at 55°C; ramp to 72°C at the rate of 1°C/8sec.; 2 min at 72°C) and a final 10 min. incubation at 72°C. Amplifications, generally run in lots of 12-20, always included one control/reaction mix to which no DNA template had been added. Amplification success was judged by loading a 1.2% Agarose minigel with samples of the amplified product (2 µL loading buffer, 6 µL ddH_2O, and 2 µL PCR amplified product or control) and a molecular standard which was electrophoresed 100V for 45-60 minutes. After being stained in 150 mL dH_2O+ 10 µL EtBr, the minigels were destained for 30 minutes in H_2O, and then visualized under UV radiation.

Restriction Enzyme Digests -- Selected samples of amplified DNA were initially tested with 19 different restriction endonucleases (AluI, Ava2, BamHI, CfoI, DraI, EcoR1, EcoR5, HinD3, HinfI, KpnI, MspI, Nde2 (=MboI), PalI (=Hae3), PstI, Pvu2, RsaI, SalI, XbaI, XhoI obtained from BMB, GibcoBRL, NEB, and/or Pharmacia). Electrophoresis of the incubated PCR products in 2% Agarose (Sigma DNA Typing Grade in 0.5x TBE) exposed restriction fragment length polymorphisms (RFLP). The 9 enzymes producing the most informative RFLPs for *Phaeocollybia* (CfoI, EcoR1, HinfI, Nde2, PalI, Pvu2, RsaI, SalI and XhoI) were then incubated with each of the successfully amplified isolates in 10 µL lots using buffers provided by the suppliers of the endonucleases (see Appendix C). Generally 2 µL of amplified product was combined with 1 µL restriction nuclease, 1 µL RE buffer, and 6 µL ddH_2O and incubated for 2-3 hours at 37°C. If the PCR amplified product was very strong or very faint, more or less product was added to the incubation mix and the level of ddH_2O adjusted accordingly. Incubations were stopped with 2 µL of loading buffer (20% Ficoll, 50mM EDTA, 0.05% bromo-methyl-bromide in ddH_2O). Three additional enzymes (Ava2, MspI, XbaI) were also identified as potentially useful for delimiting the out-taxa from *Phaeocollybia*.

Electrophoresis and visualization -- The digested products were run on 2% Agarose (Sigma DNA Typing Grade in 0.5x TBE) medium- ('midi') or large-sized gels for two hours at 80-100V, first within groups representing identical taxa to determine infrataxonimc variation and then across taxa to access intertaxonomic variation. The banding patterns on the gels were photographed under ultraviolet illumination. During 1993-1994, all photographs of fluoresced gels were taken using a stationary Polaroid Land camera loaded with Type 557 Polaroid Film. In 1995, the addition of an IBM compatible computer-assisted visualization system greatly accelerated the visualization process. The ability to refine and sharpen bands before recording greatly facilitated estimation of band lengths.

Calculation of polymorphism lengths -- Band lengths resulting from incubations of individual enzymes with the diagnostic ITS region and gel electrophoresis were compared against the above cited molecular standards. Distances in mm were hand scored for each gel and then converted to base pairs (bp) via a natural log conversion formula. Fragments for each isolate were added together and the average and means of all sums from each reliable run were evaluated to determine the lengths of the uncut ITS regions and used to help determine representative band lengths for each isolate. (See Chapter 5 for discussion of anomalies among isolates within each operational taxonomic unit and Appendix C for estimated band lengths per taxon).

RFLP profiles -- Interspecific variation is summarized graphically in RFLP profiles (*Figures 4.2-4.6*). Because of the large number (169) of isolates incubated with (at least) 9 different enzymes, RFLPs were visually analyzed via summary 'profiles': these depict diagramatically the estimated band lengths produced by each enzyme per putative species rather than per isolate. Because of difficulties encountered in the graphing program (MS Excel), the RFLP bands are presented in linear-based patterns rather than the log-based patterns normally encountered on a gel. Nonetheless some idea of the arrangement of the polymorphisms on the gels can be gained. A list of the incubations of each individual isolate per each of the 9 key enzymes is given in Appendix C, as are the estimated band lengths per putative taxon.

Results and Discussion 1: Evaluation of Protocols and Procedures

Contamination -- Problems are occasionally encountered by amplification of DNA derived from contaminants within the donor specimen. Despite initial screening, evidence of the presence of a common basidiomycetous mould was later detected in some of the source collections. Fortunately, because most taxa were represented by three or more isolates, because most isolates were amplified more than once, and because most enzymes were tested at least twice per isolate wherever possible, the likelihood of misinterpreting polymorphisms derived from contaminants was considerably diminished. Possible contamination still remains a possible source of confusion in some specimens from which there was only one successful amplification, however.

Advantages and disadvantages of direct amplification -- Attempts to extract and amplify DNA from older herbarium specimens were only occasionally successful, and limitations of direct amplification were soon discovered. With one exception, no direct amplifications were successfully obtained from basidiospores derived from material older than five years. The two major advantages of direct amplification are the savings in time (DNA suspensions require only brief preparation the night before the amplification run) and preservation of integrity of type material particularly when spore prints have been collected. However, there are three main disadvantages that limit the utility of direct amplification:

-- DNA templates in spore suspensions cannot be held in reserve because they degrade rapidly when stored -20°C (probably somewhat more slowly at -80°C), necessitating preparation of spore suspensions shortly before each amplification;

-- Due to rapid degradation of the directly amplified product during storage, it must be used within one to two weeks before breakdown begins or stored at -20°C between each use; and

-- The process should only be used on recently collected basidiospores, limiting its utility for older materials. Rogers (pers. comm., 1994) indicates that as basidiospores age, the cytoplasm is gradually bound to the DNA to such an extent that eventually a detergent (*e. g.* CTAB) is needed to break loose the proteins.

Direct amplification, then, appears to be ideal for rapid testing and verification of recently collected material, but the resulting amplification product is not as pure or as stable as that obtained from amplification of previously isolated DNA.

DNA degradation and amplification success rate -- The most severe problem encountered (with respect to developing phylogenetic species hypotheses for comparison with traditional morphological species hypotheses) was that of DNA degradation in type specimens. During 1993-1994, most DNA to be tested was isolated from basidiomes selected from personal collections made the previous two or three years. Initial difficulties encountered in isolating and amplifying DNA from the ITS region were predictable, manageable and relatively easily remedied. The rate of successful amplifications from these recent collections was gratifyingly high (Table 4.1; see also Appendix C-2), bands of the PCR amplified products were clear and strong, and preliminary restriction digests of representatives of 20 species produced what appeared to be taxonomically useful polymorphisms from the outset (*q. v.*). After developing protocols for direct amplification of DNA from basidiospores, DNA from all collections made after 1990 were successfully amplified (65 isolates, in all).

DNA was not, however, successfully amplified for 10 (out of 26) types. Degradation gels of the ten unamplified type isolates revealed that the DNA had degraded to such an extent that it seemed

unlikely that amplification of the entire ITS region seemed unlikely. Attempts to amplify a shorter region (*i.e.* ITS1 or ITS2 alone) were somewhat successful for some species, but there was little to no success in *P. attenuata, P. fallax* or *P. kauffmanii.* Given the necessity for sampling as little type material as possible, it appears that sequencing is actually a more economical and reliable method for obtaining molecular information from older type specimens. It appears that DNA degradation in the types resulted from enzymatic activity initiated by the absorption of water vapor from the air by the desiccated tissues. To forestall such enzymatic degradation by ambient humidity in the future (and in view of the increased reliance on molecular taxonomic research, it would seem prudent for research institutions to store small portions of valuable collections in tubes which should be stored in desiccants..

Results and Discussion 2: Molecular characters generated from the ITS region

In general, good results were obtained for all taxa with the following exceptions:

[i] No DNA was isolated from the newly proposed species *P. phaeogaleroides* and *P. tibiikauffmanii,* which were not discovered until all molecular research had been completed.

[ii] Amplified DNA isolated from type material of *P. dissiliens* (collected in 1970) behaved erratically in most digests. Evaluation of the few digests that appeared informative indicated that they were in fact contaminants, and so *P. dissiliens* was not represented in the final analyses.

[iii] CTAB-isolated DNA was twice successfully amplified from from the types of *P. deceptiva* (collected in 1968) and *P. gregaria* (collected in 1970); the lengths of the PCR products were consistent in all cases. Nonetheless because of the erratic behavior in some enzymes digests, caution should be used in relying on the molecular data, particularly in view of the fact that no other representatives of the taxa were included in this study.

[iv] DNA from the holotype of *P. radicata* (collected in 1906) was not successfully extracted; only one other representative was tested in the study.

Length variations of the ITS region in Phaeocollybia

There is a fair amount of variability in the lengths of the ITS regions across Phaeocollybian taxa, with 9 different lengths estimated for 24 different putative species (*Table 4.1*; *Figure 4.2*). In general, lengths are consistent within putative taxa and appear to support morphologically based species hypotheses. In particular:

-- Within the *P. californica* complex, ITS length polymorphisms support separation of *P. rufotubulina* from *P. californica* and *P. scatesiae* (see Chapter 6).

-- ITS polymorphisms do not support the synonymy of *P. gregaria* with *P. piceae* as proposed by Horak (1977).

-- The 20 base pair difference between isolates of *P. attenuata* and *P. 'similis'* implies genetic separation despite the similarity of the morphological features.

-- While length mutations do not in and of themselves signify genetic isolation (particularly in the ITS region), it is interesting to note that two of the five outgroups tested -- *P. deceptiva* (645 bp) and *Stagnicola perplexa* (755 bp) -- have ITS regions well outside the 690-740 bp range of the *Phaeocollybia* isolates.

-- On the other hand the other outgroups -- *Caulorhiza umbonata, Cortinarius vanduzerensis, Gymnopilus spectabilis* -- have ITS regions (735-740) within the *Phaeocollybia* range.

Restriction Fragment Length Polymorphisms within Phaeocollybia occur in species specific patterns that proved to be taxonomically significant. The RFLPs for the *P. kauffmanii* complex will be fully analyzed in the next chapter, but a brief overview of the restriction sites for certain taxa is presented below (See also Chapter 6 and Appendix C).

Cfo1 (*Figure 4.2)* -- Although all isolates tested had at least one Cfo1 restriction site, differences among the banding patterns were at best subtle. However the fact that all eight *P. carmanahensis* and *P. oregonensis* isolates were the only isolates to have two Cfo1 restriction sites (with a 420-200-100 profile) supports synonymy of the two species as indicated by reevaluation of morphological and anatomical characters.

EcoR1 (*Figure 4.3)* --All isolates had one EcoR1 site, but differences among the banding patterns were exceedingly subtle. Nonetheless there were diagnostic polymorphisms produced by isolates of four taxa. In the *P. californica* complex, *P. rufotubulina* (365-325) was separated from *P. californica* and *P. scatesiae*, both of which produced two equal length bands (350-350). This pattern was shared by all eight *P. piceae* isolates.

Hinf1 (*Figure 4.3)* -- All isolates were also cut in Hinf1, which proved to be a fairly informative enzyme. Hinf1 restriction sites appeared linked, however, to the ITS length variations, as exemplified by the contrasting profiles produced by isolates in the following sets of putatively closely related taxa:

--*P. attenuata* (390-345) vs. *P. 'similis'* (390-255-70)
--*P. californica -P. scatesiae* (355-345) vs. *P. rufotubulina* (365-325)
--*P. fallax - P. lilacifolia* (380-325) vs. *P. rifflipes* (400-190-140)
-- *P. piceae* (360-195-145) vs. *P. gregaria* (400-340) isolates.

--Nonetheless, ten *P. luteosquamulosa* isolates (400-190-140) are clearly separated from six *P. redheadii* isolates (385-345), even though all sixteen isolates have the same 730 bp ITS region.

-- All twelve *P. spadicea* isolates (395-125-110-70) produced a banding pattern unique within the genus.

Nde2 (*Figure 4.4)* -- All isolates also had at least one Nde2 restriction site. (Because of the difficulties in estimating the length of the lower bands, only the top bands are included in the RFLP profiles). Again, most of the differences appear linked to the innate ITS length variation. The unusually low top bands (295 bps) produced by the *P. 'similis'* and *P. spadicea* isolates appear highly informative, however.

Pal1 (*Figure 4.4)* -- All isolates showed at least one Pal1 restriction site except for the two sets of isolates representing *P. piceae* and *P. 'similis'*. Fifteen sets of isolates had two sites, seven groups had three sites, and two (representing *P. kauffmanii* and *P. redheadii*) had four sites. Here also differences appeared linked to innate ITS length mutations as can be seen in:

-- the *P. kauffmanii* complex, in particular the closely related seven *P. kauffmanii* isolates (235-230-105-90-80), the five *P. benzokauffmanii* isolates (450-105-90-70) and the six *P. redheadii* isolates (220-220-110-90-90). More interesting here is the difference between the twelve *P. ammiratii* isolates (400-225-90) and the *P. benzokauffmanii* isolates as all seventeen isolates have an estimated 715 bp ITS region.

-- two *'attenuata'* isolates (460-95-95-86) vs. five *P. 'similis'* isolates (450-295).

-- eight *P. piceae* isolates (610-90) vs. two *P. gregaria*; isolates (450-165-125).

-- ten *P. fallax* and 5 *P. lilacifolia* isolates (470-120-115) vs. five *P. rifflipes* isolates (475-170-85).

-- the distinctive banding pattern produced by seven *P. spadicea* isolates (480-120-110) as compared to other representatives of Section *Versicolores.*

The single *P. carmanahensis* isolate and all six *P. oregonensis* isolates, which appear to have the same restriction sites in any enzyme tested (with the exception of an occasional extra band produced for two of the *P. oregonensis* isolates) also show no variation in Pal1.

All *P. olivacea* isolates have estimated 720 bp ITS regions but are divided into two groups based on their Pal1 banding patterns:

-- five isolates have two Pal1 restriction sites ('oli A': 450-180-90)

--six isolates have three Pal1 restriction sites ('oliB': 450-100-90-80).

It appears in this instance that the oliB isolates have an extra PalI restriction site in the 180bp band produced in the oliA isolates.

Pvu2 (*Figure 4.5*) -- Eight groups of isolates have no Pvu2 restriction sites. These include

-- six *P. ammiratii* and six *P. kauffmanii* isolates. The fact that six *P. kauffmanii* isolates were not cut while five *P. benzokauffmanii* isolates (625-90) and five *P. redheadii* isolates (640-90) have Pvu2 restriction sites supports to a certain degree delimitation of *P. kauffmanii* from *P. benzokauffmanii* and *P. redheadii.*

-- all twelve isolates from the *P. fallax* complex, including *P. fallax* (705 bps), *P. lilacifolia* (705 bps) and *P. rifflipes* (730 bps).

-- five 'oliA' isolates (720 bps). four 'oliB' isolates (630-90) were cut in Pvu2.

-- five *P. piceae* isolates. Both *P. gregaria* isolates (645-95) were cut.

-- both *P. sipei* isolates.

Informative banding patterns produced by the isolates with Pvu2 include:

-- five *'attenuata'* isolates (625-80-30) and five *P. 'similis'* isolates'(605-80-30); here there appears to be an insertion-deletion in the 605/625 band.

-- banding patterns generated by three *P. rufotubulina* (600-90), 2 *P. californica* isolates (610-90) and four *P. scatesiae* isolates (610-90) indicate an insertion-deletion in the 610/600 band.

-- six *P. oregonensis* and one *P. carmanahensis* isolates produce 640 and 80 bp bands.

-- Two groups of *P. pseudofestiva* isolates -- three PseA (640-60) and three PseB (605-95) -- imply a transposition in the 605/640 region. In addition to *P. pseudofestiva,* all isolates representing species that would be placed into Section *Versicolores* sensu Singer have Pvu2 restriction sites, *i. e.* seven P. spadicea (615-95) and all three 'pleurocystidiata' isolates (630-80-?30) in addition to the isolates representing *P. rufotubulina, P. californica, P. scatesiae* mentioned above. All *P. pleurocystidiata* isolates appear to have two Pvu2 restriction sites.

Rsa1 (*Figure 4.5*) -- Among all *Phaeocollybia* isolates, only the five *P. benzokauffmanii* isolates (630-85) have an Rsa1 site, which provides a degree of molecular support for the delimitation of *P. benzokauffmanii* from the closely related *P. kauffmanii* and *P. redheadii.* It should be noted, however, that all three groups of isolates have different ITS lengths.

Sal1 (*Figure 4.6*) -- Five groups of isolates possess Sal1 restriction sites, including

-- eight *P. luteosquamulosa* isolates (535-195). The fact that 25 isolates representing the other morphological species in the *P. kauffmanii* complex are not digested in Sal1 supports to a certain degree delimitation of *P. luteosquamulosa* from *P. ammiratii, P. benzokauffmanii, P. kauffmanii,* and *P. redheadii.* The fact that *P. luteosquamulosa* and *P. redheadii* have the same estimated 730 bp ITS 1-2 regions is highly informative.

-- five *P. 'similis'* isolates (565-150). The five ostensibly related *P. attenuata* isolates (with a longer 735 bp ITS 1-2 region) lack a Sal1 restriction site.

-- two *P. rifflipes* isolates(535-190). None of the twelve isolates representing the closely related *P. fallax* and *P. lilacifolia* appear to possess Sal1 restriction sites on their shorter ITS regions (705 bps).

-- eight *P. piceae* isolates (515-185). Neither of the two isolates (740 bps) representing the anatomically similar *P. gregaria* possess a Sal1 restriction site.

-- *P. spadicea* (520-190). All other members representing Section *Versicolores* sensu Singer lack Rsa1 restriction sites.

Xho1 (*Figure 4.6*) -- Within *Phaeocollybia,* only the six *P. rufotubulina* isolates (500-190) have Xho1 restriction sites in the ITS region. It is interesting to note that none of the nine *P. californica* and P. scatesiae isolates have their longer (700 bps) ITS regions cut in Xho1.

RFLP-derived characters and morphologically based species hypotheses

To this point, only RFLP based characters have been presented and discussed. As noted in the introduction to this chapter, relying on RFLPs alone can lead to misinterpretation. What preliminary conclusions can be made from comparisons of the RFLP data and species circumscribed from morphological characters? (Presentation of restriction site data and discussion of results of computer-assisted multivariate, phenetic, and cladistic analyses of both RFLPs and restriction site data will be included in Chapter 5).

Molecular support for morphologically based species hypotheses appears for the most part to be linked to insertion-deletions within ITS region. For that reason single-enzyme digests appear to be most useful for their ability to generate banding patterns ('fingerprints') that are consistent and more or less invariable at the specific level. The fact that many enzymes produce instantly diagnostic banding patterns that are easily interpreted without recourse to mathematical calculation makes them a useful taxonomic tool.

Molecular characters generated from single-enzyme digests provided variable support for *Phaeocollybia* morphological species hypotheses. For example:

-- Of significance was the molecular clarification of initial taxonomic confusions resulting from over-reliance on clamp connections and basidiospores morphology within the *P. kauffmanii* complex. Isolates from specimens originally identified as *P. luteosquamulosa* (kal5), *P. ammiratii* (kaa13, kab1, kab12) and *P. benzokauffmanii* (kab2) produced RFLP profiles that conformed to those produced by *P. kauffmanii*. The conflicting molecular profiles prompted a re-evaluation of microscopical characters that in turn uncovered the taxonomic utility of trilaminate pileipellis structure and inert reactivity in Syringaldazine in *P. luteosquamulosa*, and the misinterpretation of flexuous hyphae in sarcodimitic tissues as clamp connections in *P. kauffmanii*. (see also Chapters 2 and 3).

-- RFLPs also implied distributional separation not indicated by morphological or anatomical characters. The 700 bp ITS region of seven *P. pseudofestiva* isolates produces three different RFLP profiles. PseA isolates cut in Cfo1, EcoR1, Hinf1, Nde2, Pal1, and Pvu2 but not in Rsa1, Sal1 & Xho1. PseB isolates produce different banding patterns in all enzymes where PseA is cut (the most informative enzyme being Pvu2 with 640-60 for PseA and 605-95 for PseB) (*Fig. 4.2*). The single PseAB isolate produces a RFLP profile with double bands that appear combine the PseA and PseB profiles. While there appear to be no consistent morphological characters separating the three groups, there is a geographical one: PseA isolates are derived from southern specimens (California), PseAB from an Oregon collection, and PseB from northern material (British Columbia and Washington). Many more isolates need to be tested and evaluated before any formal conclusions can be drawn, however.

-- RFLPs support the suspected synonymy between two putative species, *P. carmanahensis* and *P. oregonensis*.

--RFLPs do not support the morphological differences noted between *P. californica* and *P. scatesiae* (both with estimated 700 bp ITS regions) and between *P. fallax* and *P. lilacifolia* (both with 705 bp regions).

The taxonomic utility of RFLPs at the supergeneric level

There are obvious differences in the banding patterns produced by the out-taxa isolates (see *Figs 4.2-6*). Nonetheless, except for *P. deceptiva* (with an unusually short ITS region) and *Stagnicola perplexa* (with a relatively long ITS region), few obvious differences in banding patterns could be seen between the out- and 'in-' taxa in Cfo1, EcoR1, Hinf1 and Nde2. The out-taxa *Stagnicola* and *Caulorhiza* isolates lack Pal1 restriction sites, but then so do the *P. sipei* isolates. No 'out' isolates have a Pvu2 restriction site, but 8 groups of isolates within *Phaeocollybia* also lacked Pvu2 restrictions sites. *Stagnicola* and *Caulorhiza* have Xho1 sites while within *Phaeocollybia*

only the *P. rufotubulina* isolates are uncut. *Stagnicola* and *Cortinarius vanduzerensis* have RsaI restriction sites; only the *P. benzokauffmanii* isolates have RsaI restriction sites in *Phaeocollybia.*

The taxonomic utility of RFLPs at the subgeneric level

During the study, three null hypotheses regarding subgeneric classification were developed for testing by molecular characteristics. These were:

[1] Sections *Phaeocollybia* and *Versicolores* sensu Smith are monophyletic and genetically separate.
[2] Sections *Phaeocollybia, Versicolores, Microsporae, Radicatae* and *Subattenuatae* sensu Singer are monophyletic and genetically separate, and
[3] Subgenera *Phaeocollybia* and *Fibulophaeocollybia* as proposed by Bandala and Montoya (1994) are monophyletic and genetically separate.

RFLP support of Phaeocollybia sections based on cheilocystidial morphology (Table 4.2)-- Smith (1957b) circumscribed Sections *Phaeocollybia* and *Versicolores* based on cheilocystidial morphology (see Chapter 1). Preliminary comparison of the DNA profiles for each putative species reveals that five out of seven species characterized by thick-walled cheilocystidia have ITS regions between 690-710 base pairs. The *P. radicata* and *P. pleurocystidiata* isolates (both with estimated 730 bp ITS regions), however, have lengths similar to isolates representing several species placed into Section *Phaeocollybia*. Comparison of RFLP patterns produced by each enzyme also proves inconclusive: Banding patterns for the representatives of species characterized by cheilocystidia with thick-walled narrow refractive necks versus thin-walled more or less clavate cheilocystidia per individual enzyme can be summed up as follows:

Cfo1 -- banding patterns equally variable in both cheilocystidia-based sections;
EcoR1 -- banding patterns variable except for *P. californica, P. scatesiae* and *P. pseudofestiva* (group A only) isolates -- all representing Section *Versicolores sensu* Smith.
Hinf1 -- banding patterns equally variable in both cheilocystidia-based sections;
Nde2 -- no obvious grouping patterns;
Pal1 -- no obvious grouping patterns;
Pvu2 -- all 'thick-walled cheilocystidia' isolates have a Pvu2 restriction site; 'thin-walled cheilocystidia' isolates are variably cut and uncut;
Rsa1 -- not informative, as only *P. benzokauffmanii* isolates have Rsa1 restriction sites;
Sal1 -- all 'thick-walled cheilocystidia' isolates (except for all P. spadicea isolates) lack Sal1 restriction sites; 4 out of 21 thin-walled isolate groups have Sal1 sites.
Xho1 -- not informative as only *P. rufotubulina* isolates have Xho1 restriction sites.

In summary, random fragment length polymorphisms of the ITS 1-2 region appear to provide little to no support for a sectional classification of *Phaeocollybia* based on cheilocystidial form.

RFLP support of Phaeocollybia sections based on basidiospore morphology + cheilocystidial morphology + presence or absence of clamp connections (Table 4.1; Figs 4.2-4.6) -- Singer (1970) circumscribed five sections (Section *Phaeocollybia*, Section *Versicolores*, Section *Subattenuatae*, Section *Radicatae*, Section *Microsporae*) based on the combination of the three above characters (see Chapter 1). Unfortunately isolates representing only one species for each of two sections (Section *Subattenuatae* and Section *Radicatae*) were tested. Because these isolates do not appear to differ greatly from representatives of the other three sections, no support for the existence of Sections *Subattenuatae* and *Radicatae* can be demonstrated within the confines of the current study. However, some generalizations might be made about Sections *Phaeocollybia*, *Microsporae*, and *Versicolores*, with isolates representing 13, 4, and 6 species respectively tested in this study.

With the exception of the three *P. pleurocystidiata* isolates (730 bps), all 'Section *Versicolores sensu* Singer' isolates have ITS regions between 690 to 710 base pairs in length except for those representing *P. pleurocystidiata*. The isolates representing Sections *Phaeocollybia* and *Microsporae*, appear to have longer ITS regions except for *P. piceae* (700 bps) in Section *Phaeocollybia*. Restriction sites are summarized below:

Cfo1 -- similar RFLP profiles across all sections (RFLP profile for *P. carmanahensis* and *P. oregonensis* (Section *Microsporae)* unique);

EcoR1 -- variable across sections;

Hinf1 -- variable across sections;

Nde2 -- variable across sections;

Pal1 -- variable across sections;

Pvu2 -- all 'Section *Versicolores* sensu Singer' isolates have one Pvu2 restriction site; otherwise restriction site distribution is variable across Sections *Phaeocollybia* and *Microsporae;*

Rsa1 --all isolates lack Rsa1 restriction sites except for those representing *P. benzokauffmanii* (Section *Phaeocollybia);*

Sal1 -- all Section *Microsporae* isolates lack Sal1 restriction sites as do all Section *Versicolores* sensu Singer, except for P. spadicea isolates; variable in Section *Phaeocollybia;*

Xho1 -- Only *P. rufotubulina* isolates have a Xho1 restriction site: no sectional support.

These observations indicate that either there is little molecular support for the five sections as proposed by Singer (1970), the region tested is not conservative enough to provide taxonomically

informative characters at the sectional level, or RFLPs should not be used for analyses at the sectional level.

Restriction enzyme support of Phaeocollybia subgenera based on the presence or absence of clamp connections (Table 4.2) -- Bandala & Montoya (1994) delimited two subgenera based on the presence or absence of clamp connections. Unfortunately, of the four known Pacific Northwest Phaeocollybias now known to possess clamp connections, only two -- *P. ammiratii* and *P. radicata* -- were tested. (*P. oregonensis*, previously reported to have clamp connections by Smith & Trappe (1972) has been discovered to lack true clamp connections. *q.v.*). Hence, there are too few taxa to test this hypothesis in the current study.

The diagnostic value of RFLPs in Phaeocollybia

There appear to be a suite of distinct RFLP profiles or 'fingerprints' exhibited by the isolates tested that suggest that RFLPs can be a valuable diagnostic tool. However, inferences of phylogenetic relationships in *Phaeocollybia* based on RFLPs are severely compromised by the existence of so many length mutations between seemingly closely related taxa. It is obvious that a phylogeny cannot be inferred from single-digest RFLPs of the ITS region alone, and it is equally obvious that restriction site mapping, sequencing, or probing another part of the genome would prove far more phylogenetically informative. The next chapter discusses results obtained from analyses both of RFLPs and of restriction site data generated from the partial mapping of seven enzymes. Although sequencing of the ITS region may eventually provide far more useful data, generation of a restriction-derived character set in this study has proved exceedingly helpful in circumscribing new taxa.

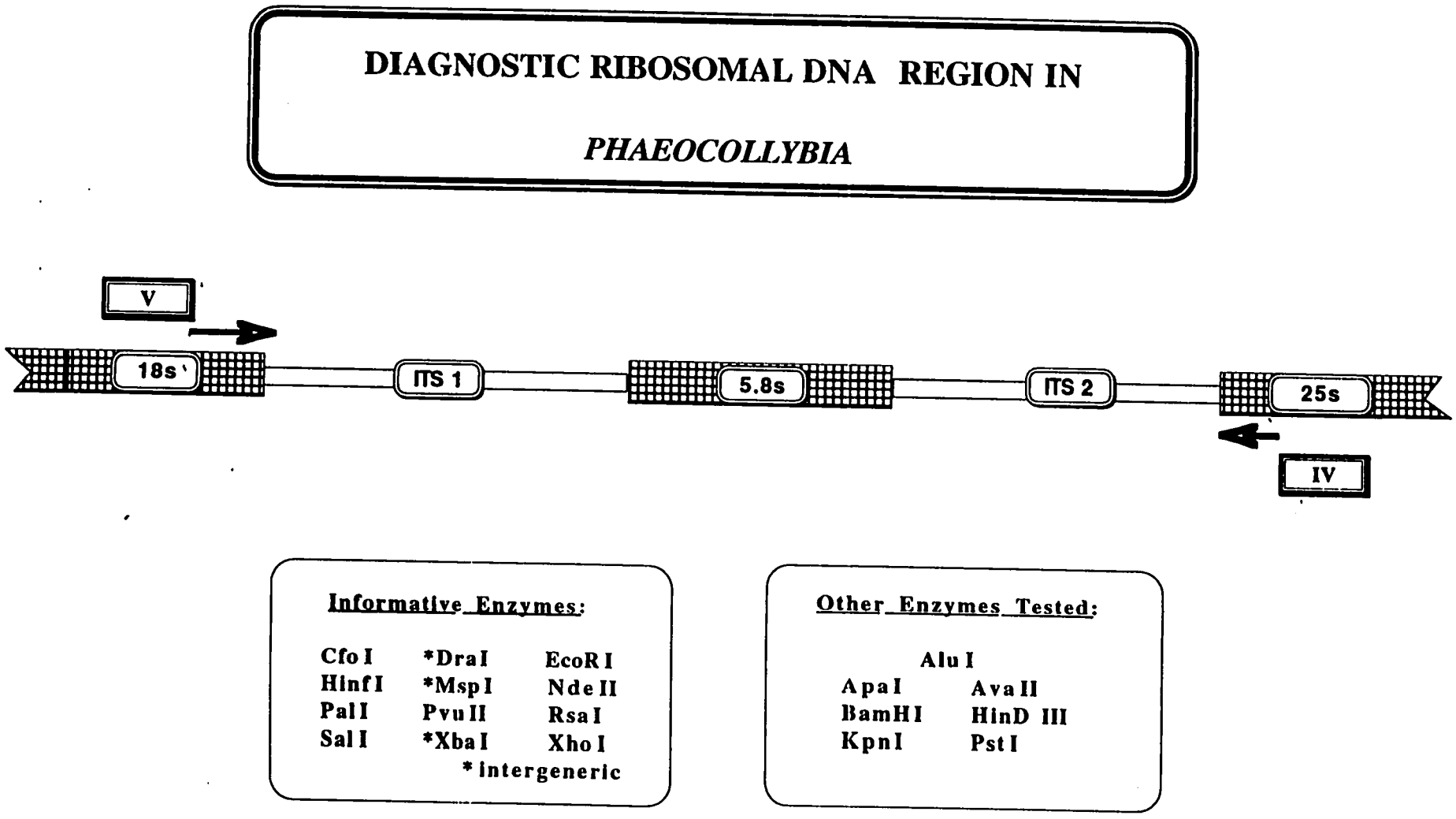


Figure 4.1 Diagram of the diagnostic ITS1 + 5.8S + ITS2 ribosomal DNA region used in restriction enzyme analyses in *Phaeocollybia*. Olignonucleotides (derived from *Saccharomyces cerevisiae*) used to prime amplifications are ITS4 (5'-TCC TCC GCT TAG TTA TAT GC-3') and ITS5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3'). Of the 19 enzymes tested nine proved to be taxonomically informative at the specific level.

Table 4.1 Amplification success of the ITS region.

(a) all specimens

	1994	1995	1994 + 1995
specimens successfully amplified	139	53	**176***
specimens not successfully amplified	29	23	**33***
% specimens successfully amplified	82.74%	69.74%	**84%***
number of amplifications attempted	420	133	**553**
number of successful amps	250	70	**320**
% of successful amplifications	59.52%	52.63%	**58.00%**

*%not additive (1994+1995) due to re-amplifications during 1995

(b) type specimens

SUCCESSFUL AMPLIFICATIONS		UNSUCCESSFUL AMPLIFICATIONS	
SPECIES	AGE OF SPECIMEN (in years)	SPECIES	AGE OF SPECIMEN (in years)
*P. ammiratii**	2	*P. attenuata*	59
*P. benzokauffmanii**	2	*P. fallax*	59
P. californica	2	*P. kauffmanii*	57
P. carmanahensis	3	*P. lilacifolia*	42
'P.' deceptiva	26	*P. oregonensis*	47
P. dissiliens	24	*P. piceae*	24
*P. rifflipes**	2	*P. pseudofestiva*	57
P. gregaria	24	*P. radicata*	88
*P. luteosquamulosa**	2	*P. similis*	42
P. olivacea	38	*P. spadicea*	59
*P. pleurocystidiata**	0.2		
*P. redheadii**	3		
*P. rufotubulina**	2		
P. scatesiae	24		
P. sipei	59		
average age	**13.44**	**average age**	**53.40**

*previously undescribed

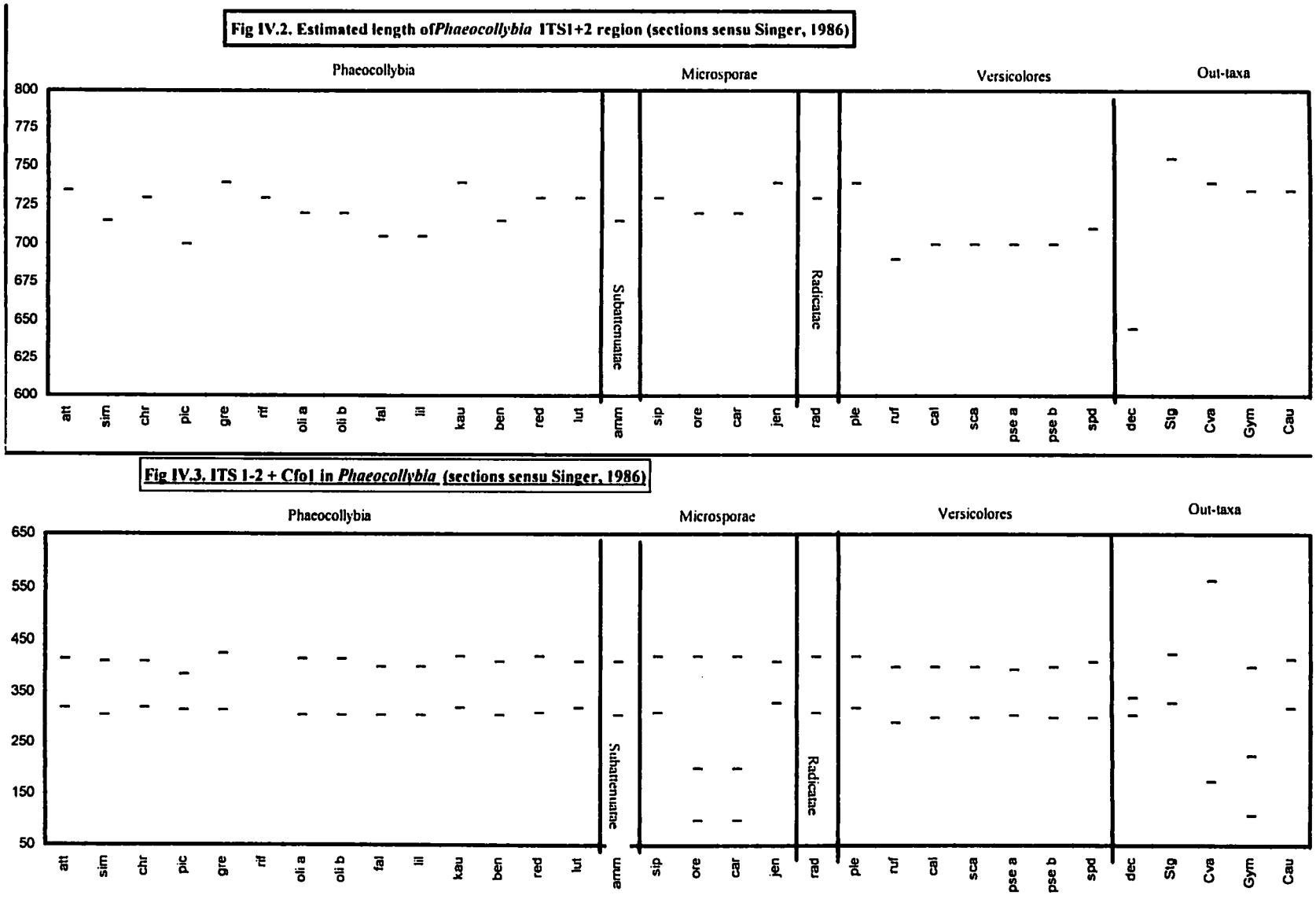
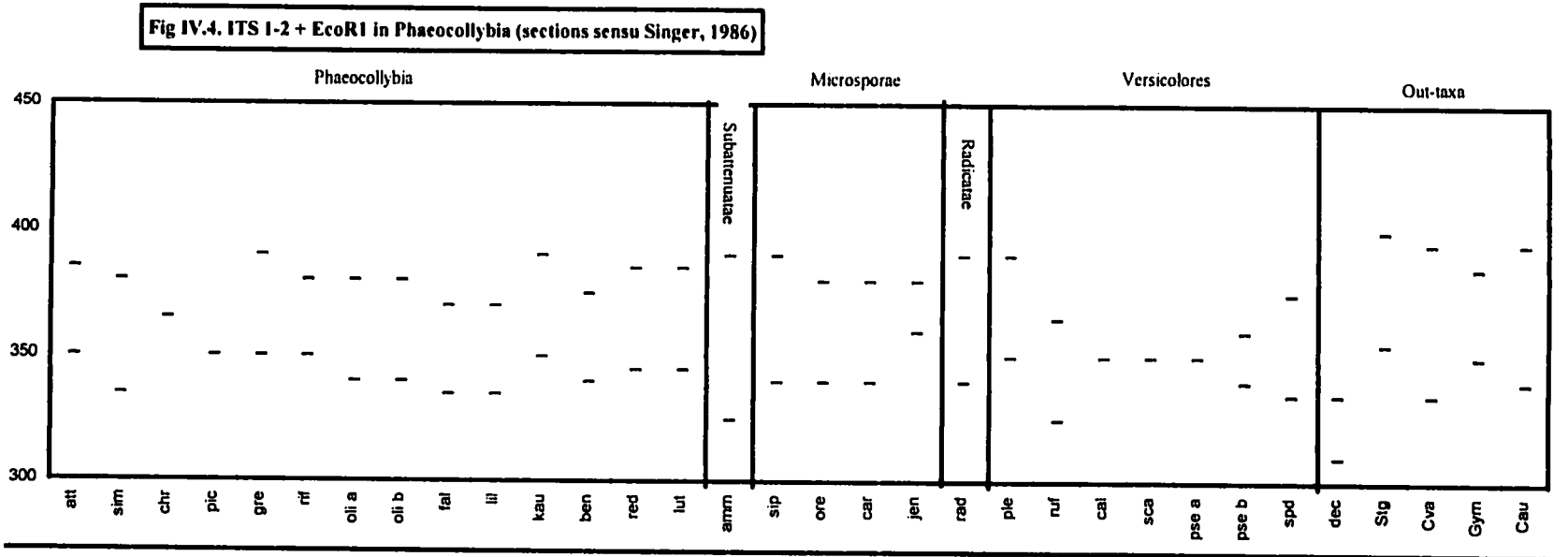


Figure 4.2 4.2 ITS length polymorphisms **(top)** and Cfo1 **(bottom)** RFLP profiles in *Phaeocollybia.* (A linear scale representation of the length and fragment banding patterns for 27 Phaeocollybias and five out-taxa).



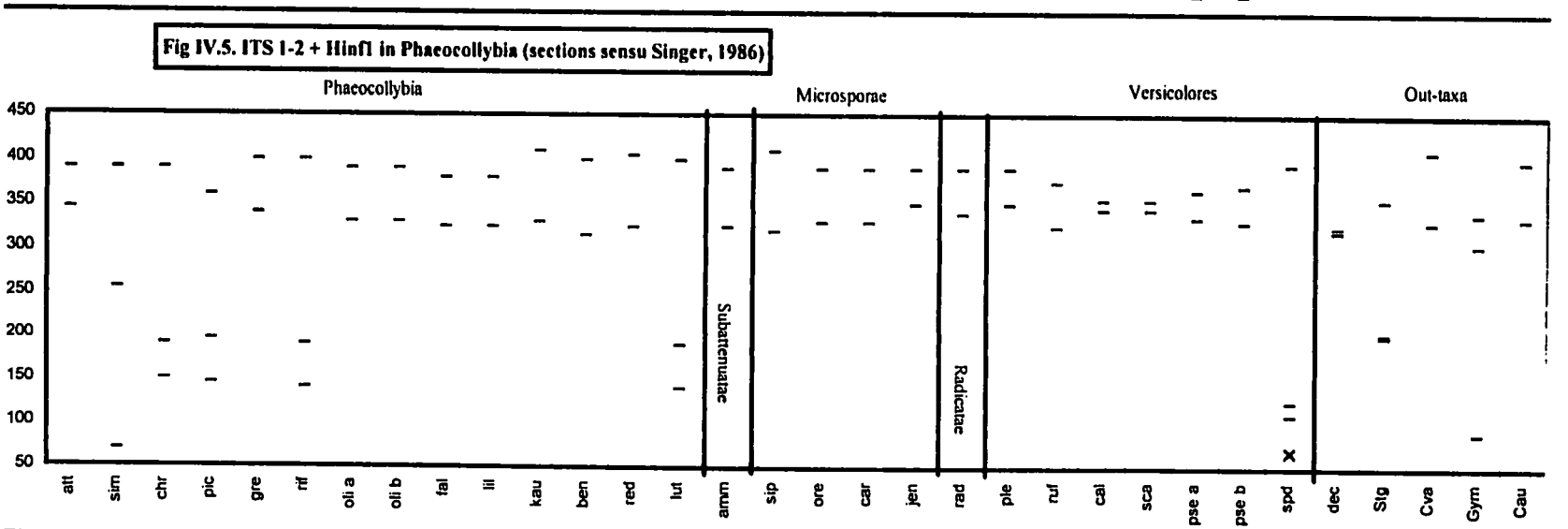


Figure 4.3 EcoR1and HinfI (**bottom**) RFLP profiles in *Phaeocollybia* (A linear scale representation of the length and fragment banding patterns for 27 Phaeocollybias and five out-taxa).

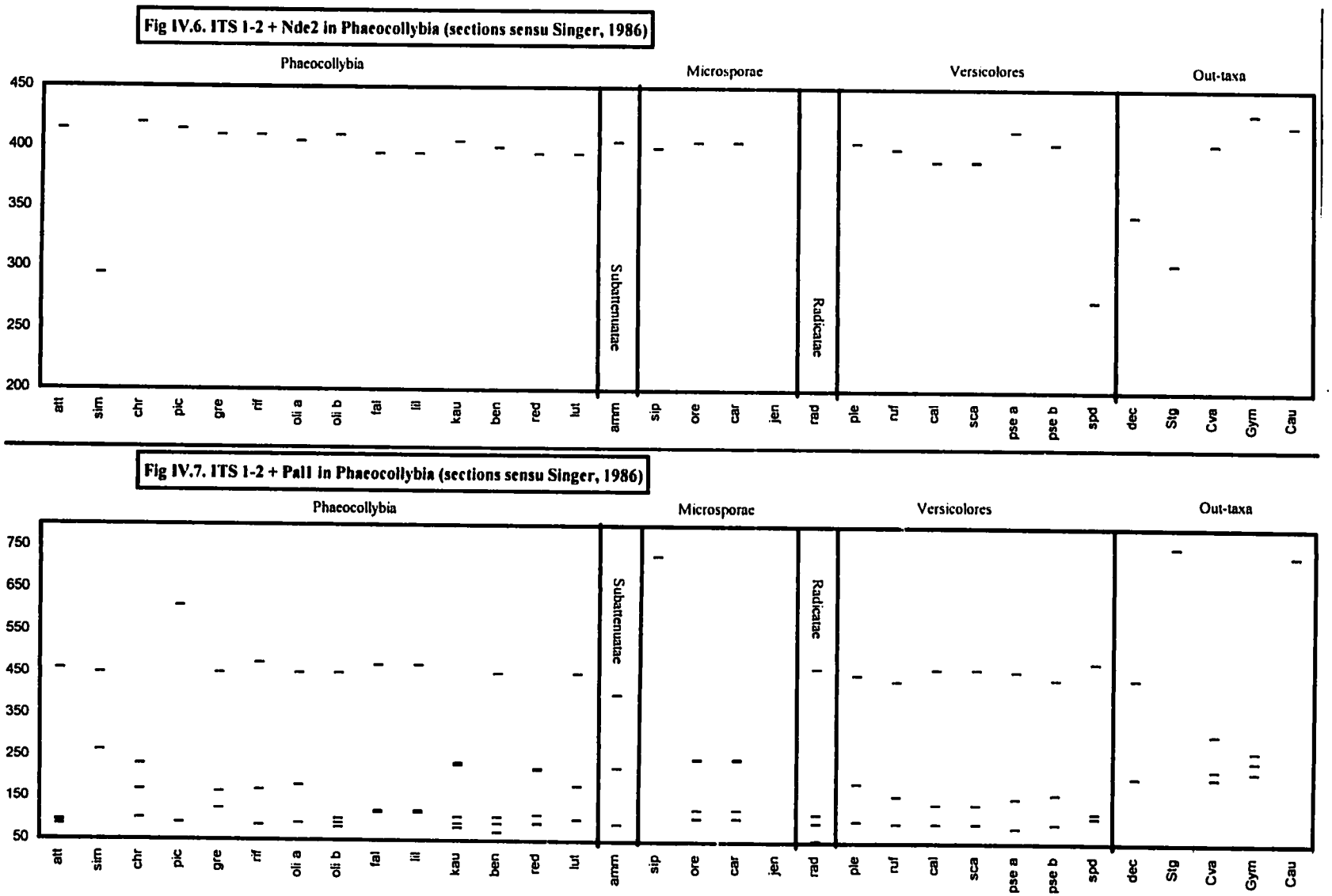


Figure 4.4 Nde2 and Pal1 **(bottom)** RFLP profiles in *Phaeocollybia* (A linear scale representation of the length and fragment banding patterns for 27 Phaeocollybias and five out-taxa).

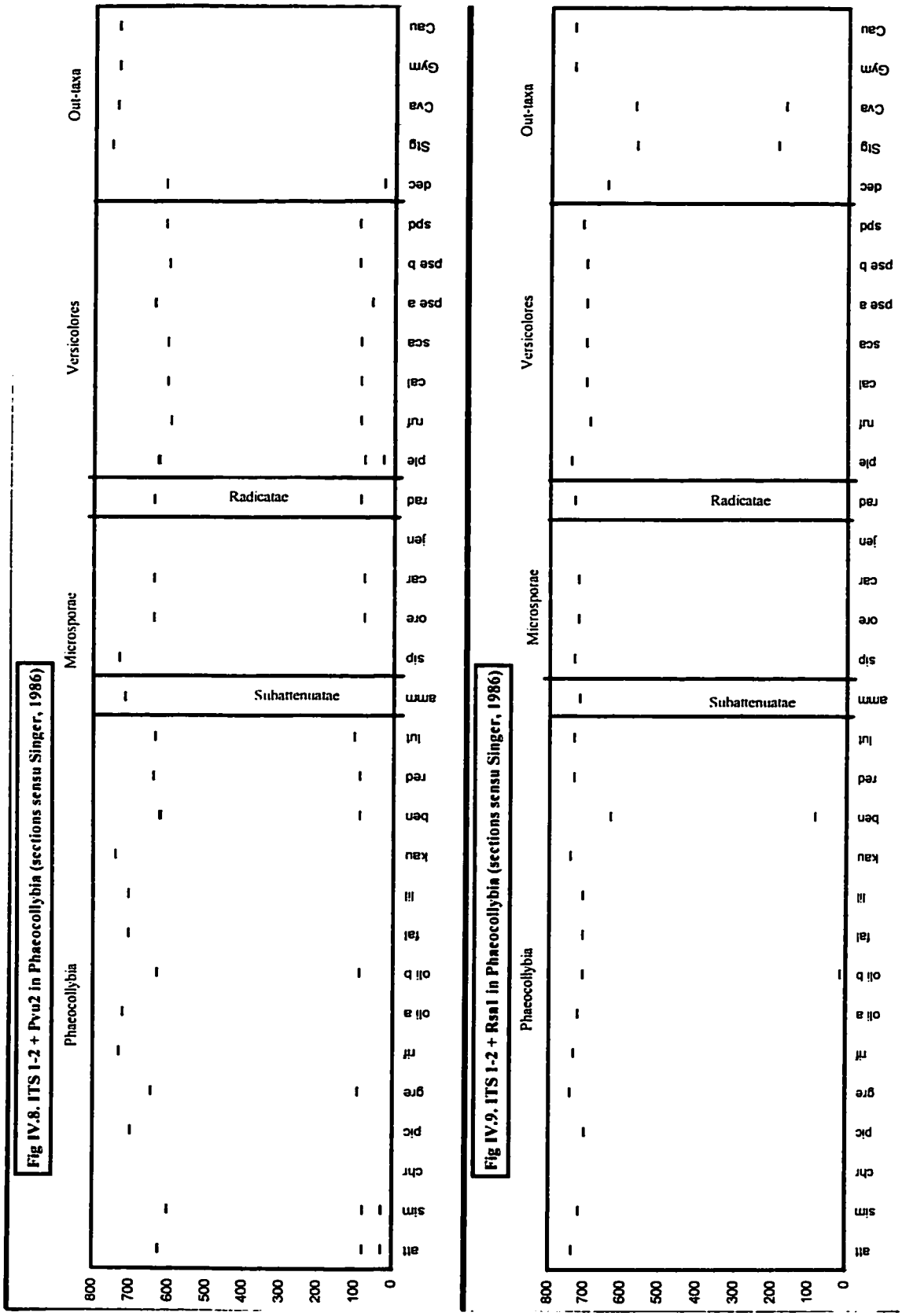


Figure 4.5 Pvu2 and Rsa1 (**bottom**) RFLP profiles in *Phaeocollybia* (A linear scale representation of the length and fragment banding patterns for 27 Phaecollybias and five out-taxa).

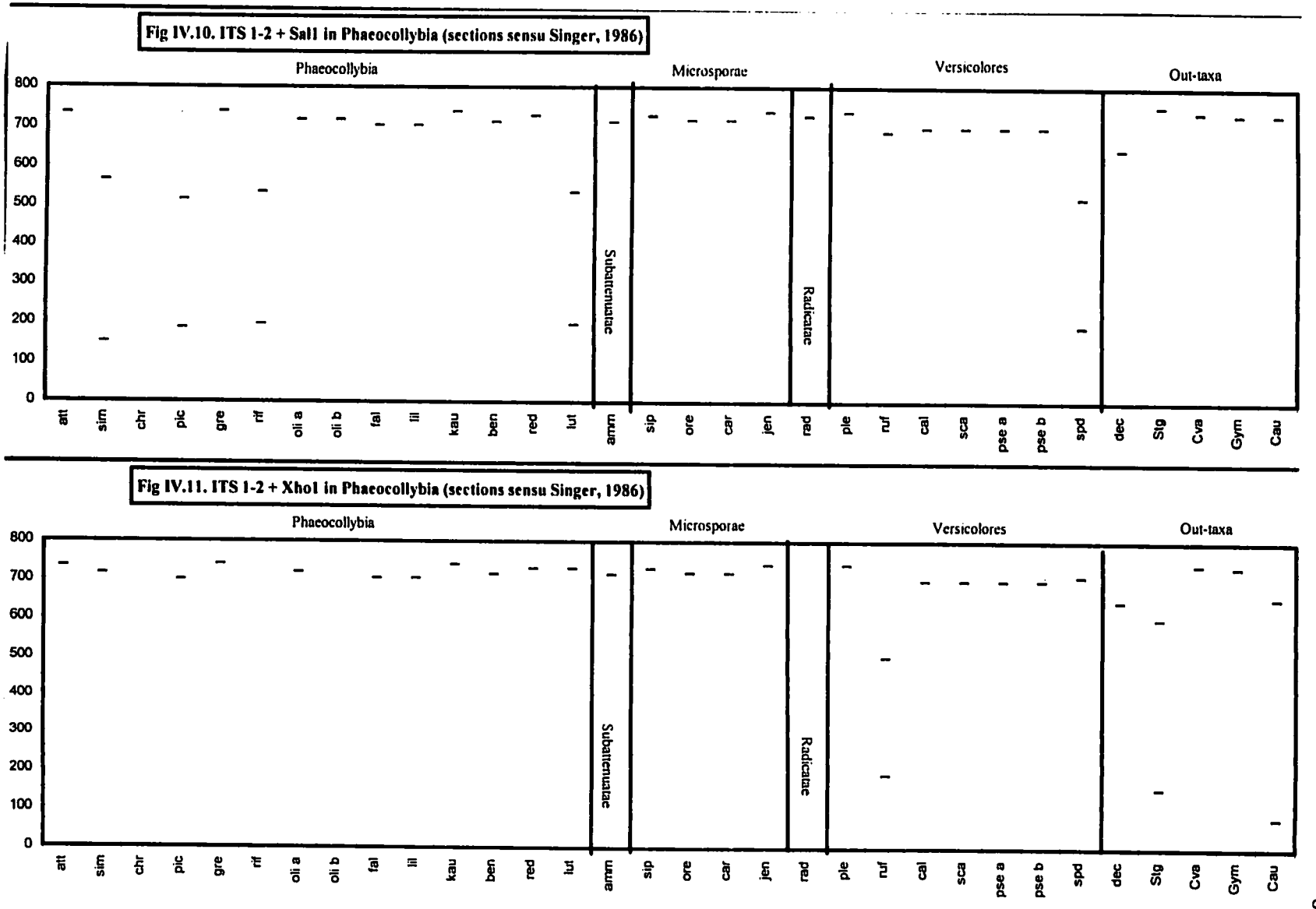


Figure 4.6 Sal1 and Xho1 **(bottom)** RFLP profiles in *Phaeocollybia* (A linear scale representation of the length and fragment banding patterns for 27 Phaeocollybias and five out-taxa).

Table 4.2 Estimated lengths (in base pairs) of the ITS region in Pacific Northwest *Phaeocollybia* species.

A. Comparison of length of ITS region in taxa organized according to cheilocystidial morphology

	645	690	700	705	710	715	720	730	735	740
clavate (thin-walled)	dec		pic	fal-lil		amm ben sim	car-ore oli	lut red rif sip	att	gre kau
tibiiform (thick-walled)		ruf	cal-sca pse,		spd			rad		ple

B. Comparison of length of ITS region in taxa organized according to occurrence of clamp connections

	645	690	700	705	710	715	720	730	735	740
absent		ruf	cal-sca pse pic	fal-lil	spd	ben sim	car-ore oli	lut red rif sip	att	gre kau ple
present	dec					amm		rad		

C. Comparison of length of ITS region in taxa organized according to basidiospore size

	645	690	700	705	710	715	720	730	735	740
large-spored (>6.5 µm)	dec	ruf	cal-sca pse pic	fal-lil	spd	amm ben sim	oli	lut red rif	att	gre kau ple
small spored (>6.5 µm)							car-ore	sip rad		

CHAPTER 5. Analyses of Morphological and Molecular Characters

Introduction -- Species Concepts

A continuing biological controversy revolves around the definition of a species, with the current *Dictionary of Fungi* (Hawksworth et al., 1995) listing no fewer than five different species concepts that have been used in mycology:

[i] *morphological* -- inferred from morphological characters, "... ideally by discontinuities in several such;"

[ii] *biological* -- inferred from "...actually or potentially interbreeding populations reproductively isolated from other such groups, whether or not they are distinguishable morphologically;"

[iii] *phylogenetic* -- inferred from "...measurable differences in biochemical, molecular or any other characters assessed by cladistic analysis;"

[iv] *ecological* --inferred from "...adaptation to particular niches rather than reproductive isolation;" and

[v] *polythetic* -- inferred from "...a combination of characters, not all of which are necessarily present in each individual."

The most useful of the five concepts to agaric taxonomists are the morphological, biological and phylogenetic. Morphologically based species have predominated since the time of Linnaeus and Fries and are still used by most field taxonomists. Early in this century, however, agaricologists began to recognize that a biological species concept might approximate a 'natural' (as opposed to 'artificial') taxon more closely than would a morphological species concept, and in his final revision of *The Agaricales in Modern Taxonomy* Singer observed "...lacking evidence to the contrary, it has been assumed since Vandendries' basic work [in the 1920s and 1930s] that in the Agaricales, the normal and typical species is not interfertile with other species...." (Singer, 1986) Although biological species concepts still predominate throughout mycology, phylogenetic species are beginning to emerge in importance as cladistic analyses of chemical and molecular characters reveal genetic relationships not implied by either morphological characters or mating studies. Hibbett & Donoghue (1996) point out the emphasis in the biological species concept on "...demonstration of mating ability in controlled laboratory crosses rather than on evidence of actual gene flow in nature" and note that a phylogenetic species concept encompasses "...independently evolving lineages, regardless of the retained plesiomorphic ability to interbreed or morphological similarities among lineages" (Hibbett & Donoghue, 1996). Additionally, in their study of *Lentinula edodes*, Hibbett et al. (1995) noted the "...strong correlation between the geographic origins of the isolates and the lineages supported."

In this study species hypotheses were initially developed from morphological characters. Nonetheless, testing of those species hypotheses by analyses of restriction site and ITS length data has enabled me to attempt to identify and describe taxa within a phylogenetic framework. The goal is to ensure that each existing or proposed species encompasses an independently evolving lineage descended from a common ancestor. As such, each taxon -- whether it be species, section, genus, or family -- should be considered to be monophyletic.

However one defines a species, delimitation of taxa based on only a few characters has been shown to vary considerably from taxa described from numerical analyses of all non-redundant characters (Høiland, 1983; Mueller, 1985; Sokal, 1986; Kuyper, 1986; Schumacher, 1990). Without analyzing many characters, species concepts tend to be based on the intuition of the author and tend not to address the continuum of variation present within taxa. For a species to be recognized, it must be both diagnosable and possess a suite of characters unique to it. Kuyper (1994), who recognizes morphological species, has adopted the position that "good" species differ in at least "...two interdependent morphological characters; if taxa differ in only one character, the difference should be considered 'infro'specific." Noting that "...single characters usually lead to artificial divisions..." Kuyper adds that because a taxonomic "...classification is a scientific hypothesis about natural order, it is of the utmost importance to choose the most relevant character." Thus with the addition of each new specimen, character or character set, one tests that hypothesis, so that when "...classification A is proved false, it must be replaced by classification B when B is more predictive than A...." (Kuyper, 1994). From this one can infer that taxonomy is the science of predictability, and as such must be rooted in statistical analyses as well as in logic.

The usefulness of a taxonomic revision lies in its ability to facilitate identification of the organisms under consideration. Agaricologists who define species within a phylogenetic context should not abandon morphological, biological or developmental features (although those characters may not necessarily reflect phylogenetic relationships), for these are the characters most readily available to those studying the organisms in their natural state. Historical reliance on morphology in *Phaeocollybia* by all previous workers dictates continued use of morphological characters. One of the objectives of this investigation was to obtain data from morphological, molecular and ecological sources for computer-assisted ordination and cluster analyses. While it was hoped that the results would support previous and current morphological species, the primary objectives were [i] to reveal phylogenetic species and [ii] to determine by which morphological or development characters they might be recognized. The ultimate goal was not necessarily circumscription of new species but the integration of morphological and molecular data in a complete taxonomic revision of Pacific Northwest species of *Phaeocollybia*. A secondary goal

was to infer phylogenetic relationships among species and to determine which morphological characters might prove diagnostic of species implied by cladistic analyses.

Although DNA from 160 different isolates representing 38 putative taxa has been amplified and tested, some isolates have not yet been fully statistically analyzed. For this reason, a sample of 44 individuals representing five putative species in the newly discovered *P. kauffmanii* complex has been selected to illustrate the analytical processes used in the current study. Additionally, phylogenetic inferences were made from cladistic analyses of ITS and restriction polymorphisms in OTUs selected to represent 28 different 'morpho' and/or 'molecular' species.

Materials and Analytical Methods

Choice of characters and character sets: Morphological and ecological characters -- Comprehensive character sets *(Appendix A.1)* were developed and possible character states determined from examinations of Pacific Northwest material, augmented by published descriptions of other *Phaeocollybia* species (*e.g.* Smith, 1957b; Smith & Trappe, 1972; Horak, 1977; Singer, 1986; Redhead & Malloch, 1986) and any potentially useful characters identified in phenetic (numerical) analyses of other genera (Høiland, 1983; Kuyper, 1986; Mueller, 1985; Schumacher, 1990; Lutzoni & Vilgalys, 1995; Lutzoni & Brodo, 1995). Character data were scaled (assigned numerical status on a suitable scale) before subjecting them to any subsequent numerical analyses, with discrete states coded wherever possible and quantitative characters coded at discontinuities in variation *(Appendix A.2)*. Initial screening of the large sample sets resulted in trimming obviously dependent (i.e. linked), invariable, or overly variable characters. Additional character (in)variability and linkages among characters and between characters and ecological or developmental factors were assessed by [1] plotting the coded character states against sample scores on WingZ or Microsoft Excel generated graphs and [2] ordination analyses using the multidimensional scaling (MDS), eigenvector and eigenvalue generating (EIGEN), orthogonal projection (PROJ), minimum spanning tree (MST), and three dimensional modeling (MOD3D) programs associated with NT-SYSpc 1.80 (Rohlf, 1993). These characters sets were further pruned of characters revealed by additional analyses to be linked, variable within a given individual, invariable throughout the sample individuals, associated with too many missing data, or characters for which no discrete character states could be found (*Table 5.1; cf.* also Lutzoni & Vilgalys, 1995).

Molecular characters -- Molecular character sets were developed from data generated by PCR-amplification of the rDNA ITS region and subsequent RFLPs generated by nine different enzymes (*Chapter 4, Appendix C; cf.* also Hibbett & Vilgalys, 1991; Lutzoni & Vilgalys, 1995; Lutzoni & Brodo, 1995). Restriction polymorphisms were initially scored on the presence or absence of co-migrating fragments produced by each enzyme. Cluster nodes in

phenograms generated for individual enzyme sets by the SAHN, NJOIN, and CONSEN programs associated with NT-SYSpc 1.80 (Rohlf, 1993) were then rescored with and without substituted hypothetical scores for missing data to generate a different RFLP-based character set. The final molecular-based character sets *(Tables 5.2-5.3)* were derived from partially mapped (inferred from single digests) restriction sites on the PCR-amplified ITS regions.

Evaluation and selection of algorithms and coefficients: RFLP-generated fragment patterns for a 20-individual sample set were analyzed [1] through scoring the presence or absence of co-migrating fragments between taxa and computing a similarity matrix for distance-based analyses *(Appendix C.5)* and [2] through scoring the presence or absence of restriction sites for 5 informative enzymes. Coded data were standardized and used to calculate pair-wise dissimilarity-similarity matrices using SIMQUAL (from discrete or qualitative character states) and SIMINT (for interval or quantitative character states) associated with the NTSYS-pc 1.80 computer analysis application (Rohlf, 1993). Similarity and dissimilarity matrices were generated from discrete data sets using Canberra, Taxonomic distance, Euclidian distance, Manhattan distance and Dice similarity and dissimilarity coefficients. Phenograms were generated using the Neighbor-Joining (NJOIN) and Sequential Agglomerative Hierarchical Non-overlapping (SAHN) methods associated with the NTSYS-pc 1.80 computer analysis program (Rohlf, 1993), and three different SAHN algorithms (i. e. Single-linkage, complete linkage & UPGMA) were tested. Consensus trees were computed for the resultant phenograms using the NT-SYS pc 1.80 consensus program (CONSEN; Rohlf, 1993). Robustness and fit of phenograms to input data were compared using the NT-SYS pc 1.80 cophenetic (COPH) and matrix comparison (MXCOMP) programs (Rohlf, 1993). Visual inspection and comparison of cophenetic values indicated that UPGMA produced the most consistently reliable phenograms. Coefficients for calculating similarity/dissimilarity matrices that produced phenograms with the consistently highest cophenetic correlation values from qualitative data were determined to be the Taxonomic distance (in UPGMA) and Euclidian distance (in NJOIN) coefficients. Matrices generated from quantitative data in SIMINT using the NTSYS-default simple matching (SM) coefficient were found to produce the most reliable results. (A complete discussion of the selection process is presented in *Appendix C.*)

Discovery of a putative complex and its diagnostic characters (*Fig. 5.1, Table 5.4;* see also *Chapters 4 & 6*): The existence of a complex of species resembling *P. kauffmanii* was first revealed by the discovery of specimens that appeared closely related to *P. kauffmanii* but which had unusually large basidiospores (Norvell & Redhead, 1992; Redhead & Norvell, 1993). Examination of herbarium material also revealed numerous other collections identified as *P. kauffmanii* but which (unlike *P. kauffmanii)* had clamp connections (Norvell &

Redhead, 1992). Later examination of fresh collections suggested that there were potentially two additional species that could also be characterized by a robust stature, orange-ochraceous to brown pilei, thick fleshy stipes that never became hollow, fleshy vertical monopodial pseudorhizae, large (>8 x 5 µm) verruculose to verrucose amygdaliform to limoniform basidiospores and thin-walled clavate cheilocystidia (Norvell & Ammirati, 1993). Evaluation of basidiospore measurements *(Fig. 5.1)* and recognition of several other striking to subtle differences among and between these putative *P. kauffmanii* collections *(Table 5.4)* soon led to the hypothesis that there were five morphologically distinct species: [i] one characterized by pinkish-brown coloration (*P. benzokauffmanii)*; [ii] one characterized by a scaly ochraceous pileus (*P. luteosquamulosa);* [iii] one characterized by a bright to brownish orange pilei when young and relatively small basidiospores (*P. kauffmanii)*; [iv] one with an ochraceous to orange brown pileus and clamp connections (*P. ammiratii)*; and [v] one characterized by a dull orange brown to dark brown pileus, relatively large basidiospores and subcapitate pedicellate cheilocystidia (*P. redheadii).* A total of 44 individuals thought to represent the five putative species were selected for restriction and phenetic analyses.

Phenetic analyses of morphological and molecular characters in the P. kauffmanii complex (Tables 5.1-5.3; Appendix C.5): All individuals were scored for 25 morphological, 8 restriction sites, and 37 co-migrating fragments. Dissimilarity-similarity matrices were computed from standardized coded data (via SIMQUAL and SIMINT); UPGMA and NJOIN generated phenograms were evaluated through visual inspection and cophenetic correlation coefficients (via COPH and MXCOMP), and consensus trees were generated using CONSEN. After phenetic and ordination analyses of individual and combined character sets implied the existence of five discrete taxa, type collections were provisionally selected for the new taxa from cluster centers inferred from cluster analyses produced by multidimensional scaling and minimum spanning tree ordination analyses (visualized in MOD3D).

Preliminary phylogenetic analyses of Pacific Northwest species of *Phaeocollybia*: One isolate was selected to represent each putative species implied through preliminary analyses of molecular characters (as described above for the *P. kauffmanii* complex). Restriction loci were determined for seven enzymes (Cfo2, Hin1, Pal1, Pvu2, Rsa1, Sal1 and Xho1) by partial mapping from single digests (*q. v.)* and similarity/dissimilarity matrices were generated from the discrete characters using SIMQUAL. OTUs representing the 25 putative *Phaeocollybia* species and three out-groups (*Stagnicola perplexa, 'Phaeocollybia' deceptiva,* and *Caulorhiza umbonata*) were analyzed phenetically and cladistically. Unrooted phylogenetic trees were generated from discrete molecular characters using the FITCH (Fitch-Margoliash), NEIGHBOR, and CONSENSE algorithms associated with Phylip 3.57 computer-assisted phylogenetic inferencing program (Felsenstein, 1995), and a preliminary

phylogeny was inferred for the genus. Diagnostic morphological characters were provisionally identified by imposition of morphological characters upon the cladograms generated from molecular data.

Results

Morphological and ecological characters

As noted above, previously described *Phaeocollybia* species have been circumscribed based on the presence or absence of certain morphological characters (*e.g.* pileus color, lamellar color, cheilocystidial form, clamp connections, basidiospore morphology, pileipellis structure, pigment topography). Ecological features such as geographic distribution or plant associations have occasionally been cited in support of a newly proposed species. At the beginning of this study, a list of potential characters drawn from a survey of all Phaeocollybias in personal collections and published descriptions of extralimital taxa contained 112 morphological (i.e. 59 macroscopical and 53 microscopical), 8 macrochemical, and 29 ecological characters *(Appendix A.1)*. These characters were scaled and coded *(Appendix A.2)*; in instances where character utility was suspect, the character was plotted against data from 15 personal collections representing five putative species (*P. ammiratii, P. fallax, P. kauffmanii, P. luteosquamulosa, P. pseudofestiva)* to evaluate its diagnostic potential *(Appendix A.5)*. Certain characters were also graphed against other characters or developmental stages to determine potential linkages *(Appendix A.6)*. After incorporating macrochemical characters into the morphological character set, trimmed ecological and morphological character subsets were submitted to ordinational (MDS+MST+PROJ+EIGEN) and phenetic (UPGMA, NJOIN, CONSEN) analyses.

Ecological characters *(Fig. 5.2)* -- Not unexpectedly, both ordination and phenetic analyses produced clusters considerably at odds with those generated from the other character sets *(Fig. 5.2a)*. In most instances, phenograms generated clusters that were linked clearly to collection site, and multidimensional scaling of 16 ecological characters revealed several obvious linkages (*e.g.* coastal distribution + high ambient humidity + canopy cover + *Picea*; clearcut + fire + thinning. *Fig. 5.2b*). Ordinational analyses of ecological characters show great potential for identifying preferred habitats among clearly different taxa. It appears, however, that the similar requirements exhibited by most Pacific Northwest Phaeocollybias limit the taxonomic utility of ecological characters, and they were not used in subsequent phenetic analyses.

Morphological characters -- Initially 120 morphological and macrochemical characters were identified as potentially diagnostic for recognition of *Phaeocollybia* species (Appendix A.1). Preliminary evaluation of documentation accompanying the sampled specimens revealed many characters that were either too variable within a single collection or putative taxon (*e.g.* pileus

diameter, pileus shape), invariable throughout the genus (*e.g.* presence of a pseudorhiza), difficult to quantify (spore print color), or likely to be missing (size of mature pileus, color of young lamellae, fluorescence reactions of fresh material). Graphs *(Appendix A.6)* and ordinational analyses eliminated additional characters by flagging characters as possibly linked to other characters (*e.g.*, colors of the stipe apex *vs.* those of the pileus; basidial width: spore length ratio *vs.* basidial length), or developmentally dependent (*e.g.* degree of incurving of the pileus edge). Inspection of three dimensional models revealed instances where sample individuals were unrealistically scattered as a result of the inadvertent weighting of color-associated characters resulting from assigning binary states to inherently multistate characters. The final trimmed morphological character set contained 44 characters, of which 25 were used in phenetic analyses of the *P. kauffmanii* complex.

Secondary diagnostic morphological characters (Table 5.4, Fig. 5.1) -- Important morphological characters that helped differentiate between putative species of the *P. kauffmanii* complex included

P. luteosquamulosa -- trilaminate pileipellis with a thin, heavily incrusted, highly pigmented suprapellis (unique among Pacific Northwest Phaeocollybias); a scaly dry to merely lubricous pileus (unique to rare among Pacific Northwest Phaeocollybias); negative reaction in Syringaldazine (unique within the *P. kauffmanii* complex, but common elsewhere in the genus).

P. ammiratii -- clamp connections (unique within the *P. kauffmanii* complex, shared with only three other known Pacific Northwest Phaeocollybias -- *P. dissiliens, P. phaeogaleroides,* and *P. radicata*); only weakly Syringaldazine positive on pseudorhizal pellis (unique in *P. kauffmanii* complex); suprapellis hyphae embedded in a thick gelatinous colorless matrix (shared with *P. kauffmanii* and *P. redheadii;* common elsewhere in the genus).

P. benzokauffmanii -- drab coloration of the pileus (unique within the *P. kauffmanii* complex, known elsewhere in the Pacific Northwest only in *P. oregonensis, P. gregaria.);* thin suprapellis lacking a well developed gelatinous matrix and/or incrusting pigments (distinguishes this from *P. ammiratii, P. kauffmanii* and *P. redheadii* in the *P. kauffmanii* complex, frequent elsewhere in the genus); strongly Syringaldazine positive (shared with *P. kauffmanii* and *P. redheadii* in the complex, and with *P. oregonensis, P. pseudofestiva* and *P. tibiikauffmanii* outside the complex).

P.redheadii -- larger (~10.5 x 6 µm) basidiospores (lower range slightly overlapping with upper range basidiospore size in *P. luteosquamulosa* and *P. benzokauffmanii;*

ornamentation and development of apical callus differentiates these spores from the larger ones found outside the complex); subcapitate long pedicellate thin-walled cheilocystidia with wide subglobose apices (unique within the complex, relatively rare elsewhere -- *P. olivacea, P. fallax)*; strongly Syringaldazine positive (see notes after *P. benzokauffmanii);* suprapellis hyphae embedded in a thick gelatinous colorless matrix (shared with *P. ammiratii* and *P. redheadii;* common elsewhere in the genus).

P. kauffmanii -- smaller (~8.5 x 5 µm) basidiospores (distinctive in the complex although the upper end of the range overlaps with those from *P. ammiratii* and the lower end of of the range for *P. benzokauffmanii*); strongly Syringaldazine positive (see notes after *P. benzokauffmanii);* suprapellis hyphae embedded in a thick gelatinous colorless matrix (shared with *P. ammiratii* and *P. redheadii;* common elsewhere in the genus).

Primary diagnostic (monophyletic) morphological characters -- Mapping of morphological characters on the phylogenetic trees (*q. v.)* indicated that seven characters show potential for diagnosing infrageneric clades. These include cheilocystidial form, pseudorhizal pattern, stipitipith presence or absence, basidiospore size and morphology, syringaldazine reactivity, farinaceous odor, and clamp connections. Incongruence between morphologically based trees generated solely from the three putative sectional diagnostic characters (*i.e.* clamp connections, basidiospore size, and cheilocystidial form) and DNA trees generated both from fragment and from restriction site data suggest that sections as proposed by Smith (1957b) and Singer (1970) are probably polyphyletic. There is some support, however, for using certain characters to recognize groups of phylogenetic species; these diagnostic characters supporting monophyletic superspecific taxa will be discussed in more detail below.

Molecular characters (Tables 5.2-5.3, 5.7; Appendix C.4-C.5): The procedure for generating and estimating the ITS length polymorphisms, RFLPs, and restriction site polymorphisms produced by nine enzymes (Cfo1, EcoR1, Hinf1, Nde2, Pal1, Pvu2, Rsa1, Sal1 and Xho1) has been outlined in the previous chapter . Estimated band lengths for OTUs representing 27 putative *Phaeocollybia* species plus 5 out-taxa and 43 individuals from the *P. kauffmanii* complex are presented in Appendix C.4 and C.5 respectively. Individuals and OTUs were analyzed phenetically and cladistically based on [i] presence or absence of co-migrating fragments (using the DICE similarity matrix coefficient; cf. Hibbett & Vilgalys, 1991) and [ii] restriction sites inferred from partial mapping.

Co-migrating fragments as molecular characters -- UPGMA and NJOIN analyses of individuals in the *P. kauffmanii* complex produced relatively cohesive clusters that supported the existence of five taxa. It is probable, however, that ITS length polymorphisms contributed significantly to cluster separation in consensus of the individual trees derived from co-migrating fragments

obtained in each enzyme. For example, a molecular difference between *P. redheadii* and *P. kauffmanii* isolates would be indicated by Rsa1, Sal1, and Xho1 (even though none of the individuals representing those two taxa possessed Rsa1, Sal1 or Xho1 restriction sites) because the ITS lengths themselves (740 bp for *P. kauffmanii*, 730 bp for *P. redheadii*) would be scored as a distinctive character three times. Phenograms generated from a combined character set containing all fragments produced by the digestion of all 43 ITS regions in all 9 enzymes also showed very strong support for five taxa, not surprising in view of the ITS length polymorphisms (~715-740 base pairs in the *P. kauffmanii* complex and ~690-740 base pairs in the genus). Logic would dictate that groups of individuals separated by length polymorphisms (which may well represent only a single mutation event) would exhibit consistent band length differences in all enzymes, as appeared to be the case. A single mutational event (insertion/deletion) can become magnified when analyzing co-migrating fragments produced by several different enzymes together. Interpretation of double bands found present in all enzymes for some isolates (*e.g.* lut1, lut3, lut6) that otherwise produced identical fragments with other closely related isolates was also problematical. While the existence of double bands may be meaningful, their taxonomic significance may be exaggerated by the analytical processes used in this study. (One advantage of analyzing fragments as opposed to restriction loci is that subtle shifts in band lengths noted in some individual may reveal genetic differences that become obscured by the process of inferring restriction loci from single digests. See *Figure 5.3*). In view of the potential for misinterpreting the results of analyses of fragment data, it would appear that characters generated from length and restriction polymorphisms might prove more informative.

Restriction sites as molecular characters -- Without the additional information provided by double digests, mapping restriction sites can be highly difficult, particularly when there are several loci present for one enzyme. Fortunately in this study there were relatively few and/or easily interpreted recognition sites per individual in five enzymes -- Cfo1 (1-2 loci), Pvu2 (0-1), Rsa1 (0-1), Sal1 (0-1), and Xho (0-1) *(See Table 5.2)*. No isolates were scored for EcoR1 where all individuals appeared to possess only one site (except for those that consistently produced double bands) and the variation in the banding patterns appeared to be greatly influenced by the length of the ITS region. Restriction loci were mapped for Hinf 1 (with 1-3 estimated loci per OTU) and Pal1 (with 0-4 estimated loci per OTU) *(Table 5.2)*. After finalizing restriction locus estimates, individuals and OTUs were analyzed from several different character sets (*q.v*), although most clusters remained fairly similar throughout the analyses of different sets. The full restriction site + ITS length polymorphism character set (the largest) contained 31 characters *(Table 5.3)*.

Phenetic analyses of the P. kauffmanii complex

Results from preliminary analyses of sample isolates and morphological or molecular characters all implied sharp separation of individuals corresponding to the proposed species hypotheses. In

one set of analyses, three-dimensional models and UPGMA, NJOIN and CONSEN generated trees consistently displayed 18 individuals representing *P. benzokauffmanii, P. kauffmanii, P. redheadii* and three unresolved taxa generally in three distinct species-specific clusters. (A summary of the trees generated from seven different character sets is presented in *Table 5.5*). R-values, which measure fitness of phenogram to input data ranged from excellent (r = 0.95) for trees generated from morphological characters to to fair (0.78) for trees generated from macromorphological data. (Loosely interpreted, r-values ≥ 9.00 indicate a very good fit, ≥ 8.00 a good fit; ≥ 7.00 a poor fit; and below 7.00 a very poor fit.) Separate analyses of 16 individuals representing *P. kauffmanii, P. ammiratii,* and *P. luteosquamulosa* produced similar results. In all preliminary analyses, separation of one or two individuals from their putative taxa was noted in trees generated from morphological characters but was rare in trees derived from molecular characters.

Following these preliminary analyses, 44 individuals representing all five taxa and three as-yet unresolved out-taxa were submitted for final phenetic analyses. All minimum spanning trees, three dimensional models, UPGMA, NJOIN, and consensus trees generated from the 25 morphological character set *(Table 5.6)* strongly imply existence of five OTUs within the complex as predicted in the previous analyses. The consensus tree *(Fig. 5.4)* of the UPGMA and NJOIN phenograms also implies existence of five discrete taxa, with only one individual (the problematical 'amb4') separated from the other 12 putative representatives of *P. ammiratii*; cophenetic correlation between the UPGMA (r = 0.95) and NJOIN (r =).87) trees is high (r = 0.91).

Forty-two individuals were analyzed based on character sets derived from the presence/absence of co-migrating fragments from each of the five informative enzymes *(Appendix C.5)*. The HinfI, PalI, Pvu2, RsaI and SalI subsets produced UPGMA phenograms *(Fig. 5.5)* with high cophenetic correlation values (r-values = 0.98, 0.90, 0.98, 0.99 and 1 respectively). The HinfI, PalI, and Pvu2 derived phenograms all support distribution of 39 individuals into five clusters. The RsaI and SalI derived phenograms imply four main groups with no separation between the *P. redheadii vs. P. luteosquamulosa* and *P. ammiratii vs. P. benzokauffmanii* individuals respectively. (Individuals in each set have identical ITS lengths and lack restriction sites in RsaI and SalI) Analysis of the 39 individuals from characters scored for ITS length polymorphisms and restriction sites *(Table 5.7)* also imply five (or possibly six) taxa, but there are, however, shifting alliances implied by the analyses of different data sets: inclusion of the *P. kauffmanii* and *P. redheadii* isolates in one clade implied by analyses of restriction loci contradicts inclusion of the *P. kauffmanii* and *P. ammiratii* isolates within the same clade when ITS lengths are also analyzed. More problematical is the existence of two *P. luteosquamulosa* clusters implied from analyses for which 'redundant' bands present in the 'lutA' isolates in HinfI, PalI, and SalI are

scored. (Here the consistent scoring of both ITS 'alleles' magnifies the perceived genetic separation between the two groups of isolates).

Each of the two differently derived molecular character sets were separately combined with the trimmed morphological-character set and then submitted to ordinational and phenetic analyses. The 3-dimensional model generated by the multidimensional scaling of 40 individuals *(Fig. 5.6)* implies five discrete clusters. UPGMA, neighbor-joining and consensus trees *(Fig. 5.7)* for the morphological+fragment-based and the morphological+ITS-based character sets also imply five main groups, all supported by good to very good cophenetic correlation values (r-values ranging from 0.82 to 0.99). Except for one individual ('amb4') that remains linked with but only rarely nests within the *P. ammiratii* cluster, phenetic analyses support placement of all individuals consistently within the same clusters. Most phenograms suggest the greatest degree of genetic isolation for the *P. luteosquamulosa* clade, implying the same degree of separation between the two clusters within the *P. luteosquamulosa* clade as between and among the putative taxa within the '*P. ammiratii* + *benzokauffmanii* + *kauffmanii* + *redheadii*' clade.

Preliminary phylogenetic analyses of Pacific Northwest species of Phaeocollybia

Comparison of the putative species within the *P. kauffmanii* complex with other species was viewed as the best way to test both integrity of the complex and to illuminate relationships within the genus as a whole. Data obtained from isolates were used to build restriction data sets for 25 *Phaeocollybia* OTUs and 3 outgroups: *P. deceptiva* ('dec'), *Stagnicola perplexa* ('Stg') and *Caulorhiza umbonata* ('Cau'). *'Phaeocollybia' deceptiva,* now believed to represent a *Cortinarius* (*q. v. Chapter 6*), is characterized by large brown ornamented basidiospores and medallion clamp connections; it lacks the cheilocystidia, cartilaginous stipe cortex, and tibiiform diverticula characteristic of *Phaeocollybia* and has the shortest ITS region (645 bp) tested. *Stagnicola perplexa* was originally described in *Phaeocollybia* but lacks a pseudorhiza, tibiiform diverticula, ornamented basidiospores and gelatinized tramal tissues and was removed to its own monotypic genus within the Cortinariaceae by Redhead & Smith (1986). It is characterized by small smooth brown basidiospores, clamp connections, cheilocystidia and has the longest ITS region (755 bp) among the representatives tested. *Caulorhiza umbonata* is a member of the white-spored Xerulaceae. While it does possess both highly developed sarcodimitic tissues and a long pseudorhiza, it lacks a cartilaginous stipe cortex, gelatinized tissues, cheilocystidia, tibiiform diverticula and brown ornamented basidiospores; its ITS region (735 bp) is between that of *P. kauffmanii* on the one hand and *P. luteosquamulosa* and *P. redheadii* on the other.

Relationships among all OTUs were initially tested by two different character sets *(Table 5.8)* composed of [i] eight morphological binary characters used to delimit both the genus and the five sections proposed by Singer (1970) and [ii] seven ITS and restriction site multistate characters (*i.*

e. number of restriction sites per OTU per enzyme). Trees produced by phenetic analyses of the morphological characters clearly support sections as traditionally delimited through presence or absence of clamp connections, spore size, and cheilocystidial morphology *(Fig. 5.8a)* and imply separation of *P. ammiratii* (sole representative of Section *Subattenuatae* in the Pacific Northwest) from the other four complex OTUs (all of which would be placed in Singer's Section *Phaeocollybia*). This morphologically-based 'sectional' tree, however, is more or less incongruent with the 7-character DNA tree *(Fig 5.8b)*, although 5 out of 7 representatives of Section *Versicolores* are retained in one 'clade'.

Previous phenetic and ordinational analyses had been conducted with the express purpose of aiding in the circumscription of species and testing morphological species hypotheses. Revision of the molecular data set to incorporate 26-31 binary characters derived from restriction loci (with and without ITS length polymorphisms produced slightly different clusters which appeared to conform slightly better to the morphologically derived hypotheses. Now, however, the goal was to identify phylogenetic species using only well supported discrete molecular characters for phylogenetic inferences. Two restriction-derived character sets (with and without characters derived from the ITS polymorphisms) were submitted for analysis using the NEIGHBOR, FITCH (Fitch-Margoliash), and CONSENSE algorithms associated with Phylip 3.572c (Felsenstein, 1995). The DNA trees generated by all algorithms from both character sets imply a notable degree of separation of *P. ammiratii* and *P. luteosquamulosa* from the more closely associated *P. benzokauffmanii, P. kauffmanii* and *P. redheadii (Fig. 5.9)* as had been predicted by the multivariate and phenetic analyses of morphological and molecular characters. All analyses -- whether phenetic or phylogenetic -- imply the existence of five discrete taxa within the P. kauffmanii complex.

Comparison of morphological and phylogenetic hypotheses

More important than disposition of taxa within the *P. kauffmanii* complex are the existence of and the relationships among all known Pacific Northwest *Phaeocollybia* taxa implied by the phylogenetic analyses. Taxonomic quandaries revealed and/or resolved by phylogenetic analyses include support for several new taxa (*i.e. P. ammiratii, P. benzokauffmanii, P. luteosquamulosa, P. redheadii, P. rifflipes, P. rufotubulina, P. olivacea* 'A' & 'B', *P. pseudofestiva* 'A', 'B' & 'C'), implied synonymy of others (*P. oregonensis & P. carmanahensis, P. californica & P. scatesiae, P. fallax & P. lilacifolia*), and the polyphyletic nature of sections as they are currently defined.

Support for new species -- Molecular support of the existence of several new taxa belonging to the *P. kauffmanii* complex has already been discussed in detail. Four of the taxa supported by phylogenetic analyses are recognized here as new species -- *P. ammiratii, P. benzokauffmanii,*

P. luteosquamulosa and *P. redheadii*. The consensus tree of all tested Pacific Northwest taxa suggests that these do not appear to belong to the same subgeneric clades, although they share a large number of characters in common (*e.g.* possession of thin-walled clavate cheilocystidia, large limoniform basidiospores, pseudorhizae displaying vertical-monopodial patterns, stipes with abundant stipitipith and matte longitudinally line surfaces, generally large size, etc.; see *Figs 5.10-5.11*). Both phenetic and phylogenetic analyses of this loose 'complex' also imply the existence of a sixth taxon closely allied to *P. luteosquamulosa*. Analyses of the molecular sets strongly imply separation between the two *P. luteosquamulosa* clusters at the same level of separation as is now indicated for *P. kauffmanii* vs. *P. redheadii*. Unfortunately whereas *P. redheadii* and *P. kauffmanii* can be recognized using morphological criteria (tawny brown pileus coloration, very large basidiospores, subcapitate long pedicellate cheilocystidia in the former and orange pileus coloration, smaller basidiospores, and cylindrical to narrowly clavate cheilocystidia in the latter), at this time there appear to be no morphological, developmental, or geographic diagnostic characters that facilitate differentiation of *P. luteosquamulosa* 'A' from *P. luteosquamulosa* 'B'. The two taxa appear to differ only in the presence or absence of an 'allelic' double band produced in three enzymes, a difference that may not be taxonomically significant. Even if the difference is deemed sufficient to recognize a new taxon, recognition may not be warranted at the specific level. Therefore formal recognition of these taxa will be withheld until sequence data and/or morphological differences obtained from fresh material verify two discrete taxa at a useful level.

On the other hand, the existence of two new species, *P. rifflipes* and *P. rufotubulina*, initially revealed through their distinctive RFLP profiles and implied as phylogenetic species in analyses of restriction loci can be diagnosed using morphological characters. (*P. rufotubulina* is discriminated from the closely related *P. californica* by darkly pigmented concentrically incrusted hyphae in the suprapellis, a smaller stature, more vivid coloration, possession of a subviscid rather than viscid pileus, and the possession of an unusually thing stipe cortex. *P. rifflipes* differs from both *P. fallax* and *P. lilacifolia* (both also characterized from lilac to violaceous young lamellae) by its distinct small obscurely ornamented limoniform basidiospores, large inflated cheilocystidia, and tawny to black pileus color.) Thus both new taxa, first recognized through molecular data, are to be formally described and recognized at the specific level.

More problematical are the newly implied phylogenetic species associated with *P. olivacea* and *P. pseudofestiva*. In each case, analyses clearly support separation of taxa at the specific level, but there are, unfortunately, at this time no morphological criteria by which these phylogenetic species can be recognized. With respect to the three closely related *P. pseudofestiva* OTUs, DNA was not successfully amplified from either the type or topotypical material. Formal recognition of new taxa must be withheld at least until additional isolates from all geographic regions including

the type locality have been screened molecularly and/or more intensive comparisons of newly collected material can be made. (It should be noted here that the molecular differences may be less significant than they appear in analyses of restriction data and may only signify evolving taxa that are perhaps better recognized at the subspecific level.)

DNA was successfully amplified from the type of *P. olivacea* and despite erratic performance in some digests it appears to belong to the 'olivacea A' clade. Unfortunately documentation of certain potentially diagnostic morphological characters (*e.g.*, pseudorhizal pattern, Syringaldazine reactivity) for the isolates belonging to the two clades is inconsistent and at times contradictory. Here also a conservative approach will be followed with regard to formal circumscription of a new species until more field work and molecular screening is completed.

Differentiating between *P. attenuata* and *P. 'similis' sensu* A. H. Smith presents a slightly different problem. Again DNA was not successfully amplified from either type (of *P. attenuata)* or original reference collection (of Smith's *P. 'similis'*). However there are two different RFLP profiles produced by 9 different isolates (including topotypical material for each putative species) do doubt tied to a 20 bp insertion/deletion in the ITS region. Once more molecular data suggest the presence of two taxa while morphological support is vague to conjectural. In this instance, because there is historical precedence (albeit a misapplication of an earlier name) for keeping the two phylogenetic taxa separate at a specific level, existence of two taxa will continue to be recognized informally with a new name being proposed for *P. 'similis'* when and if there are sufficient diagnostic characters to justify recognition at either the varietal or the specific level.

Support for species synonymies -- There are also instances where morphological criteria imply more taxa than do phylogenetic analyses. *Phaeocollybia carmanahensis* was differentiated initially from *P. oregonensis* based on morphological differences which now appear to have been developmentally influenced (see Chapter 6 for a full discussion). DNA successfully amplified from the type of *P. carmanahensis* and topotypical material of *P. oregonensis* produced identical and unique RFLP banding patterns that strongly suggested that the later named species was in fact phylogenetically identical to *P. oregonensis.* Recognition of this molecular 'synonymy' led to re-evaluation of the morphological criteria on which *P. oregonensis* was based and confirmed that the two morphologically- derived species in fact represented the same phylogenetic and morphological taxon.

Support for synonymy of *P. fallax* and *P. lilacifolia* (as implied by analyses of the molecular data) is less convincing. On the one hand, there is recognition of two separate species by A. H. Smith; on the other there is a synonymy proposed by Horak (1977). No DNA (again) was successfully amplified from either type, and the collections provisionally identified as representing *P. lilacifolia* (including one from a paratype) are now believed after microscopical re-evaluation to represent *P.*

fallax. In the absence of good molecular evidence and until DNA from the types or topotypical material can be obtained, the two species are retained based on their original descriptions. (See Chapter 6 for further discussion).

The *P. californica* complex also presents an unresolved taxonomic quandary. Smith (1957b) described *P. californica* from northern California in 1956. Smith and Trappe (1972) later described *P. scatesiae* from coastal Oregon. Again Horak (1977) synonymized two species based on microscopical examination of the type specimens. Collections were made of *P. scatesiae* from Oregon and what was assumed to be *P. californica* from Mendocino County, California by the current author in 1992. However, comparison of RFLP profiles from the Mendocino collections with those obtained from the type specimens of both *P. californica* and *P. scatesiae* showed that the Mendocino collections produced distinctly different RFLP profiles that contrasted with those of the latter two species, which were identical to each other. The Mendocino collections, provisionally named *P. rufotubulina*, are also morphologically quite distinct from the *P. scatesiae* collections. Recent successful collections of *P. californica* from Oregon have revealed that *P. californica* is clearly morphologically much closer to *P. rufotubulina* and quite distinct from *P. scatesiae* despite the seeming molecular union with *P. scatesiae* (although possibility of contamination of the type always exists). For the moment three species are recognized based on morphological criteria although there is only firm phylogenetic support for two. This situation should be resolved when sequence data are obtained from all three types (See Chapter 6 for additional discussion).

Mapping morphological characters on DNA trees

(Figures 5.10, 5.11)

The current phylogenetic tree, derived as it is from restriction site polymorphisms inferred from fragments generated in single restriction digests, is perforce preliminary and should be expected to change as extra-limital taxa are added and more reliable molecular data are analyzed. Even so, the phylogenies implied in the current analyses do offer certain insights into the genus as a whole.

As noted above, the phylogenetic trees were for the most part incongruent with trees generated from characters currently used to diagnose sections in *Phaeocollybia*. Despite this incongruence, there do seem to be primary characters that show potential for diagnosing some subgeneric monophyletic clades.

The taxonomic utility of basidiospore size and presence/absence of clamp connections cannot be tested by the current DNA tree as only three and two (out of 25) taxa sampled are characterized (respectively) by small basidiospores and the presence of clamp connections. The third 'sectional' character, cheilocystidial morphology used by Alexander H. Smith (1957b) to divide

Phaeocollybia into two sections, does show strong taxonomic potential. The DNA tree derived from analyses of 25 different putative species implies that seven (out of eight possible) taxa characterized by thick-walled 'tibiiform' cheilocystidia occur within one coherent clade. Furthermore, no species characterized by thin-walled clavate cheilocystidia are included within the clade, although *P. gregaria* (characterized by slightly heteromorphic clavate thin-walled cheilocystidia) is basal to it. Furthermore, the fact that the outlying eighth species characterized by tibiiform cheilocystidia is unique among Pacific Northwest Phaeocollybias in its possession of abundant thick-walled tibiiform pleurocystidia and vernal phenology raises the possibility of genetic isolation..

Also interesting is that five of the six species for which pseudorhizal patterns are known can be characterized as racemose (*Chapter 2*). Elsewhere in the genus only *P. sipei* (and possibly *P. olivacea* 'A') are suspected of having racemose pseudorhizae, although no branching pseudorhizae have yet been recovered. Within the 'tibiiform' clade, possession of racemose pseudorhizae appears to be also accompanied by fibrillose pith which shrinks and soon disappears while the basidiome is very young. The existence of a diagnostic suite of characters is challenged, however, by the presence of *P. spadicea* within the clade. While this species is characterized by 'tibiiform' cheilocystidia, it is also characterized by having a vertical monopodial pseudorhiza and abundant stipe stipitipith.

The remaining Pacific Northwest Phaeocollybias (with the exception of *P. pleurocystidia* mentioned above) can be characterized by thin-walled 'clavate' cheilocystidia and monopodial pseudorhizae. The *P. kauffmanii* clade is also characterized by abundant stipitipith, vertical monopodial pseudorhizae, a farinaceous odor, and positive Syringaldazine reactivity *(Figs 5.10-5.11)*; these last characters appear to show superspecific diagnostic potential as well.

Conclusion

Results of phenetic and phylogenetic analyses of the individual and combined morphological and molecular individual and combined character sets show consistent support for five species previously thought to represent one taxon, *Phaeocollybia kauffmanii.* Computer-generated trees based on molecular character sets show the greatest resolution and are congruent with equally well supported trees generated from morphological character sets. Almost all analyses imply a very close relationship among *P. benzokauffmanii, P. kauffmanii sensu stricto,* and *P. redheadii* and imply separation of *P. ammiratii* and *P. luteosquamulosa* from the complex 'core'. Ordination analyses of both morphological and molecular characters imply clear separation among the five species.

Cladistic analyses of representatives of other Pacific Northwest species based on ITS length and restriction polymorphisms imply the existence of 22 taxa among the Pacific Northwest representatives analyzed.

Mapping of morphological characters on the phylogenetic trees indicate that some characters (particularly cheilocystidial morphology, stipe morphology, pseudorhizal patterns, and Syringaldazine reactivity) exhibit good potential for diagnosing higher level monophyletic taxa (at the subgeneric level) while other appear taxonomically informative only at the specific level.

An attempt has been made to circumscribe monophyletic phylogenetic species, although only species that can be recognized from morphological characters are treated in the following chapter. It is difficult to summarize species relationships definitively during the process of discovering and documenting newly discovered taxa with different sets of characters combined in previously unrecognized patterns. To infer a complete phylogeny on partial data sets (*i.e.* prior to documenting the existing variation) is admittedly premature. What has been accomplished in this study is the bringing together of as many elements as possible -- whether they be of morphological, ecological, biological, or molecular origin -- and the description of all taxa using the best characters at hand. At this point in time, the most reliable characters, unfortunately, are still morphologically derived. The best that can be done is to test species hypotheses with a molecular character set derived from restriction digests of only one small region of the genome. It is hoped that the work has been done sufficiently well so that the species documented in the following chapter represent monophyletic phylogenetic species. The end result -- newly circumscribed species described well enough that other workers can recognize them by morphological characters -- must first be tested with far more extensive molecular inquiries and generation of a phylogeny based on all representative species in the genus.

Table 5.1 Morphological and ecological characters selected for phenetic analyses of *Phaeocollybia* isolates. **(a)** Morphological characters.

Category	Character description	Character states	Coding procedure
	----------Field Characters----------		
Pileus	Mature pileus diameter	small, medium, large	quantitative, scaled
Pileus,Stipe	Mature pileus diameter / stipe apex	average ratio	quantitative; scaled
Pileus	Mature umbo	obtuse, acute, papillate	multistate, coded
Pileus	Mature pileus edge	inrolled, incurved, straight	multistate, coded
Pileus	Fibrillose patches	presence/absence	qualitative
Pileus	‡ Moisture	moist, viscid, glutinous	multistate, coded or qualitative
Pileus	‡ Desiccated cuticle color	black, metallic, matte, colors	multistate, coded
Pileus	‡ Young color	green, drab, ochre, orange	multistate, coded
Pileus	Context	thin, average, thick	quantitative, scaled
Pileus	*Farinaceous	farinaceous; gebrenzlich	qualitative
Lamellae	‡ Young color	violet, greenish, yellowish, drab, salmon	multistate, coded or qualitative
Lamellae	Young gill edge	finely serrulate;even	qualitative
Stipe	*Mature firm pith	Presence/absence	qualitative
Stipe	Cortex width	<1 mm; >3 mm	quantitative, scaled
Stipe	‡ Apex width	small, medium, large	quantitative, scaled
Stipe	‡ Fibril patches	presence/absence	qualitative
Stipe	‡ Stipe surface	matte, shiny, corneous	multistate, coded
Stipe	Stipe apex color	drab, greenish, orange, ochre	multistate, coded
Pseudorhiza	* Growth pattern	Monopodial; criniform	qualitative
Chemical	*Syringaldazine (Syr)	present/absent; strong,weak,negative	multistate, coded or qualitative
Chemical	‡KOH	dark brown = positive	qualitative
	----------Anatomical Characters----------		
Basidiome	(*)Clamps	present/absent	qualitative
Pileipellis	‡ Pellis layers	bi- vs. trilaminate	qualitative
Pileipellis	‡Supra height	< 20 µm, > 50 µm	quantitative
Pileipellis	Supra color	present/absent	qualitative
Pileipellis	‡ Supra diameter	<3 µm / > 4 µm	qualitative
Pileipellis	‡ Supra kinked	present/absent	qualitative
Pileipellis	‡ Incrusting pigs	present/absent	qualitative
Pileipellis	‡ Refractive septa	present/absent	qualitative
Pileipellis	‡ Supra gel matrix	present/absent	qualitative
Basidia	Length	short, med, long	quantitative, scaled
Basidia	Width	<6 / >8	quantitative, scaled
Basidiospore	(*) Length	>7 / < 7;	qualitative
Basidiospore	‡ Length	multistate range	quantitative, scaled
Basidiospore			
Basidiospore	‡ Spore width	multistate range	quantitative, scaled
Basidia/ Spore	‡ Basidium:Spore Q	ratio	quantitative, scaled
Basidiospore	‡ Ornamentation	punctate-rough / rugulose-warty	qualitative
Basidiospore	(*) Shape	ellispoidal vs.limoniform	qualitative
Basidiospore	‡ Apical beak	multistate range	quantitative, scaled
Cheilocystidia	* Morphology	thick-walled vs. thin-walled	qualitative
Cheilocystidia	‡ Morphology (thin-walled)	mucronate, cylindrical, broad clav,	multistate, coded
Pleurocystidia	(*)Occurrence	present/absent	qualitative
Tib diverticula	Location	psr only, stipe, pileus	multistate, coded
Tib diverticula	Size	> or < 30 µm	qualitative
Sarcodimitism	Location	psr only, stipe, lamellae, pileus	multistate, coded

* = primary diagnostic character ((*) denotes potentially a primary diagnostic character
‡ = secondary diagnostic character

Table 5.1 (continued) **(b)** Ecological characters .

Category	Character description	Character states	Coding procedure
Overstory	Forest Age	immature, mature, ancient	quantitative, scaled
Overstory	Management	fire, thin, clear cut, ancient	multistate, coded
Overstory	Canopy	closed completely / open	qualitative
Overstory	Dominant species	Abies, Picea, Pseudotsuga, Pinus, Sequoia,	multistate, coded ; also qualitative
Understory	Dominant shrub	Ericaceous, Gaultheria, Sword fern	multistate, coded; also qualitative
Ground cover	Mosses	present/ absent	qualitative
Ground cover	Vascular herbaceous	present/absent	qualitative
Substrate	Composition	clay, sand (rock), humic	multistate, coded; also qualitative
Ambient humidity	Summer	low, moderate, high	multistate, coded; also qualitative
Substrate	moisture content	well-drained, floodplain,	multistate, coded
Temperature pattern	Winter	Severe with snow, mild	qualitative
Phenology	Spring	present / absent	qualitative
Distribution	Latitude	North, Middle, South	multistate coded, also qualitative
Distribution	Longitude	Coastal, low inland, western slope	multistate coded, also qualitative
Distribution	Elevation	sea level, montane	qualitative
Manner of growth	Habit	solitary, scattered, closely gregarious	multistate-coded, also qualitative
Manner of growth	Sociability with other species	Consistent Rare	qualitative

Table 5.2 Estimated restriction loci (inferred from single restriction digests of the ITS region amplified from representatives of 25 putative *Phaeocollybia* species and *Stagnicola perplexa*.

OTU	ITS (bp)	Cfo1	Hinf1	Pal1	Pvu2	Rsa1	Sal1*	Xho1*
*amm	715	B	D	A,G	--	--	--	--
*ben	715	B	E	C,E,H	B	B	--	--
*kau	740	B	E	A,C,E,H	--	--	--	--
*lut	730	B	D,F	C,G	B	--	A	--
*red	730	B	D	A,C,E,H	B	--	--	--
att	735	B	A	C,E,H	A,C	--	--	--
cal	700	B	B	D,F	B	--	--	--
car	720	B,C	C,D	B,D,G	C	--	--	--
fal	705	B	D	D,G	--	--	--	--
gre	740	B	E	C,G	B	--	--	--
lil	705	B	D	D,G	--	--	--	--
olA	720	B	D	C,E,H	--	--	--	--
olB	720	B	D	C,E,G	B	--	--	--
ore	720	B,C	C,D	B,D,G	C	--	--	--
pic	700	A	A,F	G	--	--	A	--
ple	740	B	C	C,H	A,C	--	--	--
psA	700	B	C	D,F	D	--	--	--
psB	700	B	C	C,F	C	--	--	--
rad	730	B	C	D,F,H	B	--	--	no data
rif	730	no data	D,F	D,E	--	--	A	no data
ruf	690	B	C	C,F	B	--	--	A
sca	700	B	B	D,F	B	--	--	--
sim	715	B	A,G	C	A,C	--	B	--
sip	720	B	D	--	--	--	--	--
spd	710	B	C,F,G	D,F	B	--	A	--
Stg (out)	755	B	A,F	--	--	A	--	B

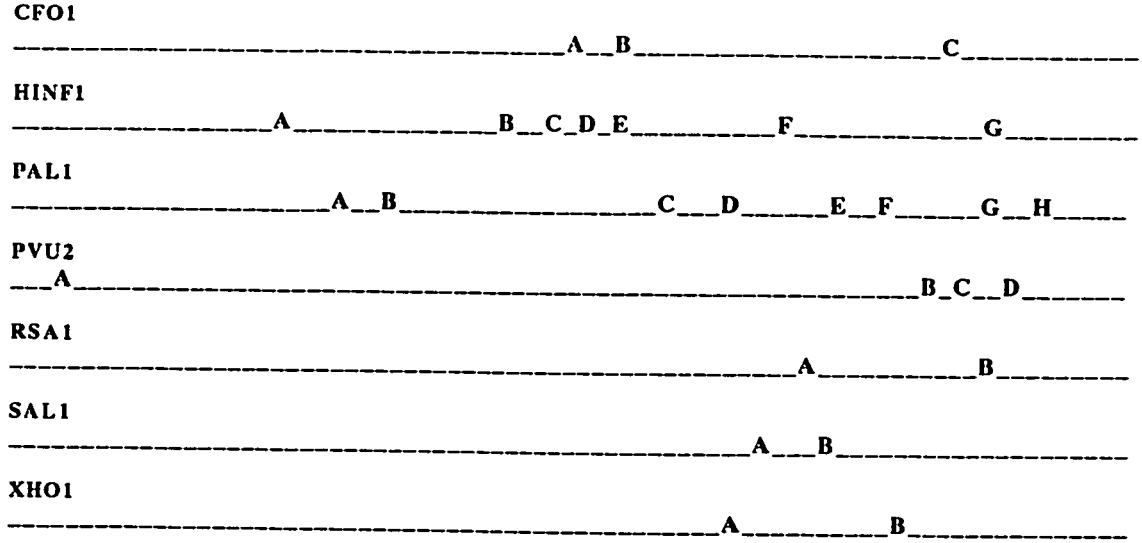


Table 5.3 Molecular character set derived from restriction loci and length polymorphisms of the ITS region for phylogenetic analyses of 25 putative *Phaeocollybia* species and *Stagnicola perplexa*. (a) *Stagnicola* (^), Section *Microsporae* (°), Section *Radicatae* (+), and Section *Versicolores*.

	Stg^	sip°	car°	ore°	rad+	cal	sca	ruf	psA	psB	ple	spd
Cfo1 A	0	0	0	0	0	0	0	0	0	0	0	0
Cfo1 B	0	0	0	0	0	0	0	0	0	0	0	0
Hinf1 A	1	0	0	0	0	0	0	0	0	0	0	0
Hinf1 C	0	0	0	0	1	0	0	1	1	1	1	1
Hinf1 D	0	1	1	1	0	0	0	0	0	0	0	0
Hinf1 E	0	0	0	0	0	0	0	0	0	0	0	0
Hinf1 F	1	0	0	0	0	0	0	0	0	0	0	1
Hinf1 G	0	0	0	0	0	0	0	0	0	0	0	1
Pal1 A	0	0	0	0	0	0	0	0	0	0	0	0
Pal1 B	0	0	1	1	0	0	0	0	0	0	0	0
Pal1 C	0	0	0	0	0	0	0	1	0	1	1	0
Pal1 D	0	0	1	1	1	1	1	0	1	0	0	1
Pal1 E	0	0	0	0	0	0	0	0	0	0	0	0
Pal1 G	0	0	1	1	0	0	0	0	0	0	0	0
Pal1 H	0	0	0	0	1	0	0	0	0	0	1	0
Pvu2 A	0	0	0	0	0	0	0	0	0	0	1	0
Pvu2 B	0	0	0	0	1	1	1	1	0	1	0	1
Pvu2 C	0	0	1	1	0	0	0	0	0	0	1	0
Pvu2 D	0	0	0	0	0	0	0	0	1	0	0	0
Rsa1 A	1	0	0	0	0	0	0	0	0	0	0	0
Rsa1 B	0	0	0	0	0	0	0	0	0	0	0	0
Sal1 A	0	0	0	0	0	0	0	0	0	0	0	1
Sal1 B	0	0	0	0	0	0	0	0	0	0	0	0
Xho1 A	0	0	0	0	X	0	0	1	0	0	0	0
Xho1 B	1	0	0	0	X	0	0	0	0	0	0	0
ITS 700	0	0	0	0	0	1	1	0	1	1	0	0
ITS 715	0	0	1	1	0	0	0	0	0	0	0	1
ITS 730	0	1	0	0	1	0	0	0	0	0	0	0
ITS 740	0	0	0	0	0	0	0	0	0	0	1	0
ITS 755	1	0	0	0	0	0	0	0	0	0	0	0

Table 5.3 (continued). **(b)** Section *Subattenuatae* (*), Section *Phaeocollybia.*

	am*	ben	kau	lut	red	gre	fal	lil	olA	olB	rif	att	'sim'	pic
Cfo1 A	0	0	0	0	0	0	0	0	0	0	X	0	0	1
Cfo1 B	0	0	0	0	0	0	0	0	0	0	X	0	0	0
Hinf1 A	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hinf1 C	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Hinf1 D	1	0	0	1	1	0	1	1	1	1	1	0	0	0
Hinf1 E	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Hinf1 F	0	0	0	1	0	0	0	0	0	0	1	0	0	1
Hinf1 G	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pal1 A	1	0	1	0	1	0	0	0	0	0	0	0	0	0
Pal1 B	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pal1 C	0	1	1	1	1	1	0	0	1	1	0	1	1	0
Pal1 D	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Pal1 E	0	1	1	0	1	0	0	0	1	1	1	1	0	0
Pal1 G	0	1	0	1	0	1	1	1	0	1	0	0	0	1
Pal1 H	1	0	1	0	1	0	0	0	1	0	0	1	0	0
Pvu2 A	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Pvu2 B	0	1	0	1	1	1	0	0	0	1	0	0	0	0
Pvu2 C	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Pvu2 D	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rsa1 A	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rsa1 B	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Sal1 A	0	0	0	0	1	0	0	0	0	0	1	0	0	1
Sal1 B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Xho1 A	0	0	0	0	0	0	0	0	0	0	X	0	0	0
Xho1 B	0	0	0	0	0	0	0	0	0	0	X	0	0	0
ITS 700	0	0	0	0	0	0	1	1	0	0	0	0	0	1
ITS 715	1	1	0	0	0	0	0	0	1	1	0	0	1	0
ITS 730	0	0	0	1	1	0	0	0	0	0	1	1	0	0
ITS 740	0	0	1	0	0	1	0	0	0	0	0	0	0	0
ITS 755	0	0	0	0	0	0	0	0	0	0	0	0	0	0

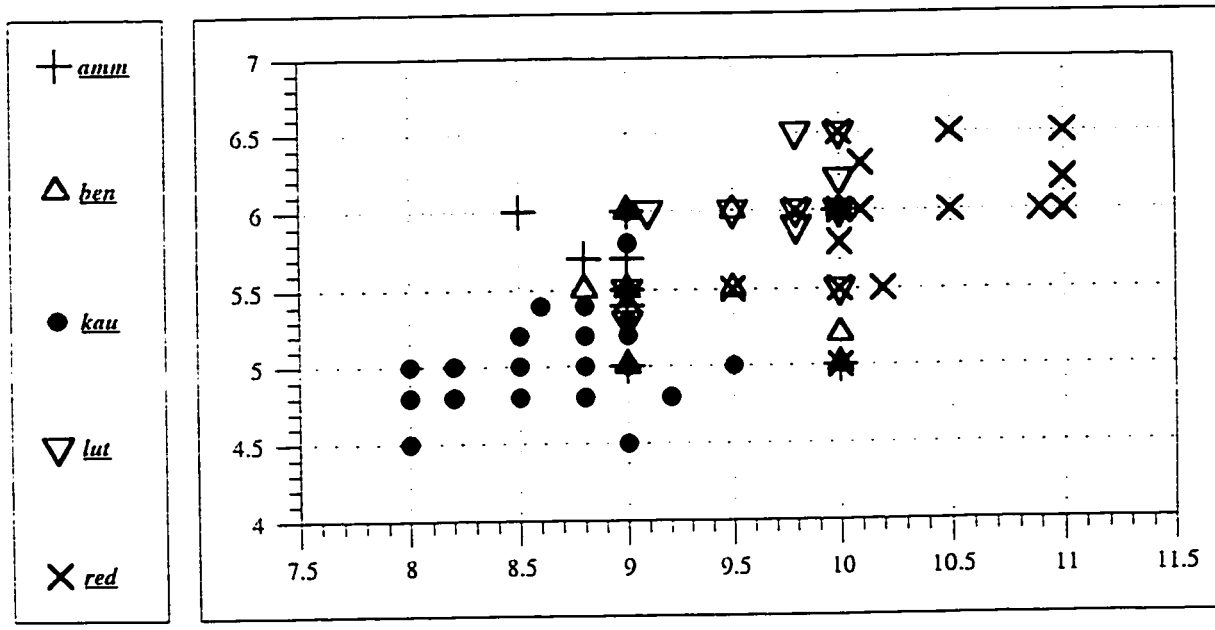


Figure 5.1 Basidiospore morphology in the *P. kauffmanii complex:* width versus length.

Table 5.4. Variable characters in the *Phaeocollybia kauffmanii* complex

	KAUFFMANII S.S.	*AMMIRATII*	*BENZOKAUFFMANII*	*LUTEOSQUAMULOSA*	*REDHEADII*
YOUNG PILEUS	foxy orange to orange brown, viscid, smooth	tawny yellow, viscid, smooth	**drab, viscid, smooth**	**ochre, moist to dry, appressed scaly**	pale tawny, viscid, smooth
SYR REACTION	intense magenta overall	*weak, +/- restricted to pseudorhiza*	intense magenta overall	**negative**	intense magenta overall
CLAMPS	very rare	**abundant**	absent	absent	very rare
PILEIPELLIS	bilaminate ixocutis; thick gelatinous matrix	bilaminate ixocutis; thick gelatinous matrix	*bilaminate ixocutis; mod. gelatinous matrix*	**trilaminate ixocutis; supra- bright orange-yellow**	bilaminate ixocutis; thick gelatinous matrix
SPORES (µM) MEAN	*8.5 x 5 (± 0.4 x 0.2)*	9 X 5.5 *(± 0.3 x 0.4)*	9 X 5.5 *(± 0.3)*	10 X 6 *(± 0.5 x 0.4)*	**10.5 x 6** *(± 0.4 x 0.3)*
CHEILO APICES	irregular outline, narr/med mix	*cylindrical to narrowly clavate*	irregular outline, narr/med mix	*inflated apices dominant*	**subcapitate pedicellate dominant**
DIAGNOSTIC ENZYMES	PalI, PvuII, RsaI, SalI	**PalI**	**RsaI**	**HinfI, PalI, SalI**	PalI, PvuII

Primary diagnostic characters in bold
Secondary diagnostic characters italicized

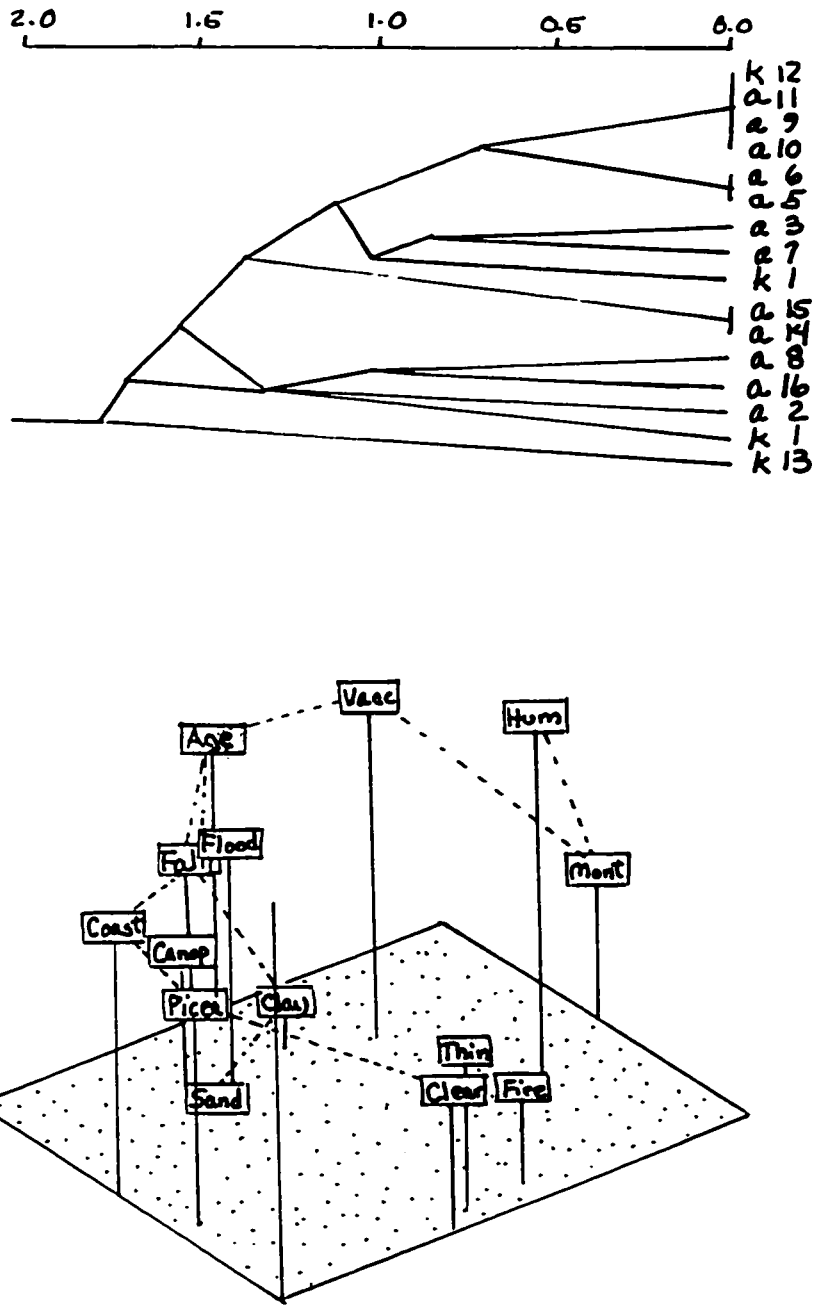


Figure 5.2 Evaluation of ecological characters. (**a**) UPGMA tree of 16 individuals (a= amm; k = kau; S = Site #: 1 = Seymour Watershed, City of Vancouver; 2 = Sol Duc, ONP; 3 = Rugged Ridge, ONP; 4 = Lake Quinault, ONP; 5 = Barlow Pass, BSNF; 6 = Ipsut Creek, MRNP; 7 = Wildcat Ridge, MHNF; 8 = Cascade Head EF; 9 = Big Lagoon SP; 10 = Jackson SF). (**b**) three-dimensional model generated from multivariate cluster analyses of 14 ecological characters (dotted line represents minimum spanning tree).

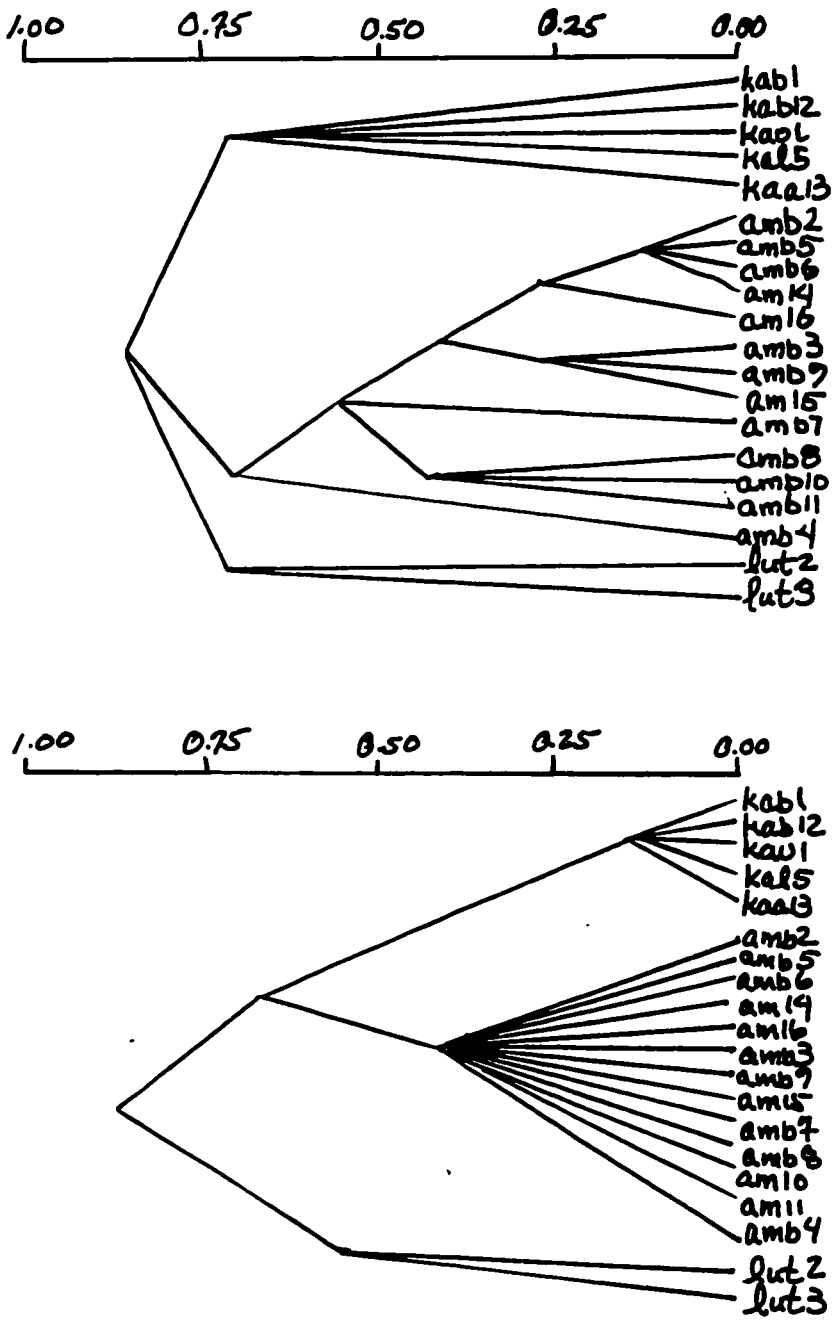


Figure 5.3 Comparison of consensus trees for 20 individuals generated from (**a**) RFLP-derived co-migrating fragments (r = 0.84) and (**b**) estimated restriction loci (r = 0.87) for 9 enzymes from the ITS region of 20 individuals . Lack of close resolution in (b) may result from underestimation of sites resulting from inferences of restriction loci from single-digests.

Table 5.5 Preliminary analyses: Summary of UPGMA trees of 17/18 individuals generated from different data sets.

Character Set	with *'benzo'* cluster	with *'red"* cluster	with *'kau'* cluster	unique
Pal1+Pvu2+Rsa1 RFLPs *(r = 0.95)*	ben1,ben3,bek3,ben4, ben5,**ouk7**	rec1,rec2,rek4,rek5, reo2	kau1,kab2,kau2,kau6, **ouu6**	ouk9
9 enzyme RFLPs; *(r = 0.95)*	ben1,ben3,bek3,ben4, ben5,**ouk7**	rec1,rec2,rek4,rek5, reo2,**ouu6**	kau1,kab2,kau2,kau6	ouk9
7 enzyme RE loci *(r = 0.95)*				
morph + mol *(r = 0.95)*	ben1,ben3,bek3,ben4, ben5,**ouk7**	rec1,rec2,rek4,rek5, reo2	kau1,kab2,kau2,kau6	ouk9,ouu6
anatomical *(r = 0.91)*	ben1,ben3,bek3,ben4, ben5	rec1,rec2,rek4,rek5, reo2	kau1,kab2,kau2, kau8 (type)	**kau6,** ouk7,ouk9,ouu6
morphological *(r = 0.89)*	ben1,ben3,bek3,ben4, ben5	rec1,rec2,rek4,rek5, reo2	kau1,kab2,kau2,kau6, kau8 (type)	ouk7,ouk9,ouu6
field (macro) *(r = 0.87)*	ben1,ben3,bek3,ben4	**kab2,** rec1,rec2,rek5,reo2	kau1,kau6, kau8(type),**rek4**	**bek3,kau2,** ouk7,ouk9,ouu6

'Misplaced' individuals in **bold-face**

ouk7, ouu6, ouk9 represent individuals with unresolved affinities (unknowns)

Table 5.6 Final *P. kauffmanii* complex analyses: Macro- and microcharacters selected for final phenetic analyses.

Individuals:

K8,K1,K2,B3,R4,R5,K6,O7,K8,O9,B1,K2,B3,B4,B5,R1,R2,O6,R2,L1,L2,L3,L4,KAL5,L6,L7,L8,L9,L10,K12,A11,A9,A10,A8, A4,A2,A3,A6,A7,A5,K13,A15,A14,A16,K1

Characters:

Pileus scales	0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,1,1,0,1,1,1,1,X,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Viscidity	1,1,1,1,1,1,1,1,1,1,1,1,1,X,1,1,1,1,0,0,0,0,0,0,X,0,X,1,1,1,1,1,1,1,1,1,1,1,1,1,0,1,1
Dry pileus black	0,0,0,1,0,1,1,0,0,1,0,1,1,1,1,1,1,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Dry pileus metallic	1,1,0,1,0,1,1,1,0,1,0,0,0,1,0,1,0,0,0,0,0,1,0,0,0,0,0,0,1,1,1,1,1,1,1,1,1,1,1,1,1,1,0
Pileus drab	0,0,0,1,0,0,0,0,1,0,1,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Pileus yellow	0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,1,1,0,1,1,1,1,1,0,1,0,1,0,0,0,0,0,0,0,0,0,0,0,0
Odor farinaceous	1,1,1,X,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,0,0,0,1,0,0,X,0,X,X,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
Taste bitter	0,0,0,X,0,0,0,0,0,1,0,1,0,1,1,0,0,0,1,X,X,1,0,1,1,X,1,X,X,0,0,1,0,0,0,1,0,1,1,0,1,1,1,0
Stipe apex diam	4,4,3,4,4,4,4,4,2,2,3,3,3,3,3,3,3,2,3,3,3,3,2,X,3,3,X,2,X,X,2,X,2,4,3,2,2,2,3,2,4,3,2,3,X
Stipe w fibrils	0,0,0,0,0,0,0,1,1,1,0,0,0,0,0,0,0,0,1,0,0,0,0,1,0,X,0,X,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0
Stipe Drab	0,0,0,1,0,0,X,1,0,1,0,1,1,0,0,0,0,X,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Syringaldazine	X,1,1,X,X,1,X,0,0,1,1,X,1,X,X,1,1,X,0,0,0,0,1,0,0,X,0,X,X,X,X,X,X,0,0,1,1,1,X,1,1,0,1,0,1
Clamps	0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,1,1,1,1,1,1,1,0,1,1,1,0
Pellis layers	1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,2,2,2,2,1,2,2,2,2,2,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
Supra arrangement	0,0,0,1,0,0,0,1,1,1,0,1,1,1,0,0,0,0,1,1,1,1,0,1,1,1,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Supra color	0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,00,0,1,1,1,1,0,1,1,1,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Incrusting pigmnts	1,1,1,0,1,1,1,0,0,0,1,0,0,0,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,0,0,0,0,0,0,0,0,0,1,0,0,0,1
Basidial widths	4,3,3,2,3,4,2,4,4,3,2,3,3,3,3,4,1,4,4,5,4,5,X,4,4,X,4,4,X,4,4,X,4,3,3,3,3,3,3,3,4,4,3,3
Spore length	5,5,5,5,7,7,6,5,4,5,5,5,6,5,7,7,5,7,6,6,6,6,X,6,6,X,6,6,X,5,5,X,5,6,5,5,5,5,6,5,5,5,5,5
Spore widths	3,3,3,3,4,4,3,3,3,3,3,3,4,3,4,4,4,4,3,3,4,3,4,X,4,4,X,4,4,X,3,3,X,3,5,5,3,3,3,4,3,3,4,4,3
Cheilos filamentous	1,1,1,0,0,0,1,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,1,1,1,1,1,1,1,1,1,1,1
Cheilos subcapitate	0,0,0,0,1,1,0,0,0,0,0,0,0,0,0,0,1,1,0,1,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
Cheilo apex diam	3,3,3,3,5,4,3,3,3,3,3,3,3,5,5,3,4,4,4,4,3,3,4,5,3,4,4,3,3,3,3,3,3,3,3,3,3,3,3,3,3,3,3
Tibi div location	1,1,1,1,1,1,1,2,2,2,1,1,1,1,1,1,X,1,4,1,1,4,1,1,2,2,1,2,1,1,1,1,1,4,1,1,1,1,1,1,1,1,1,1
Tibi div length	1,1,1,1,2,2,1,1,2,1,1,1,1,1,2,2,X,2,2,2,2,2,2,2,2,2,2,2,2,1,2,1,X,2,1,1,1,1,1,1,2,1,1,1

a = ammiratii; b = benzokauffmanii; k = kauffmanii; l = luteosquamulosa; r = redheadii; o = unknown/out-taxon

X = *missing data*

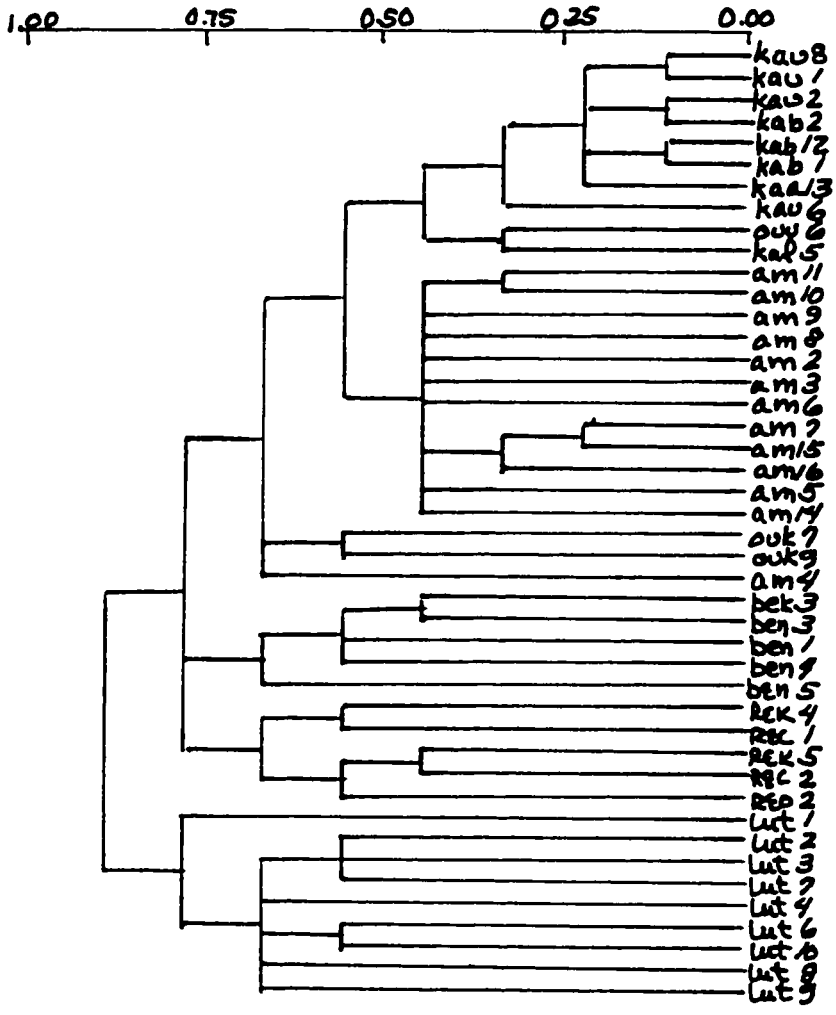


Figure 5.4 Final *P. kauffmanii* complex analyses: Consensus tree of UPGMA (r = 0.95) + NJOIN (r = 0.87) trees generated from morphological characters (r = 0.91).

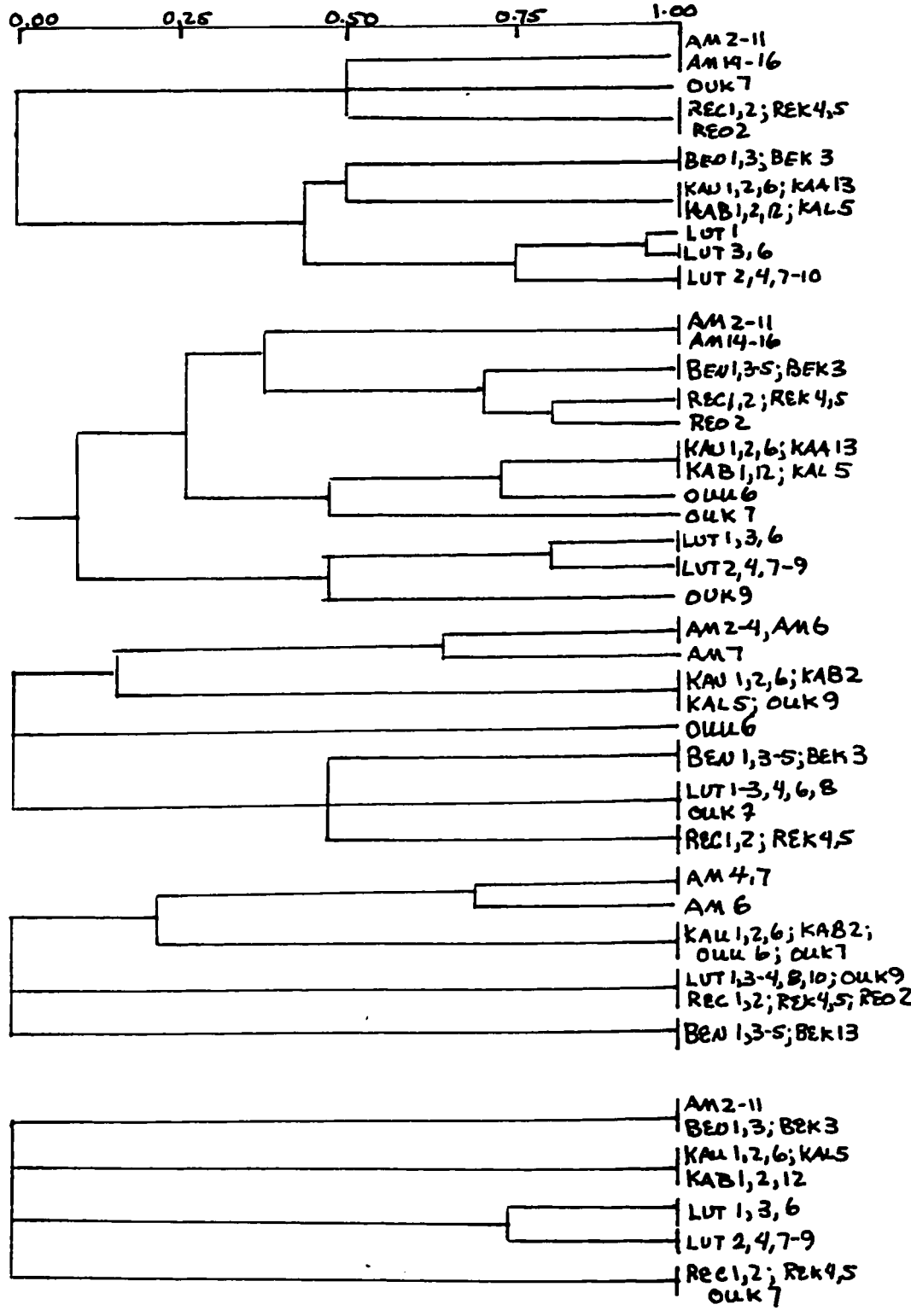


Figure 5.5 Final *P. kauffmanii* complex analyses: UPGMA/Dice trees generated from co-migrating fragments produced by individual enzyme digestions of rDNA ITS region. (a) Hinf1 (r = 0.98); (b) Pal1 (r = 0.90); (c) Pvu2 (r = 0.98); (d) Rsa1 (r = 0.99); (e) Sal1 (r= 1.00).

Table 5.7 Final *P. kauffmanii* complex analyses: Length and restriction polymorphisms of rDNA ITS region amplified from 39 individuals.

Individuals:

A11,A9,A10,A8, A4,A2,A3,A6,A7,A5,A15,A14,A16, B1,B3,B4,B5,B3, K1,K2,K6,K1,K2,K12,K5, L1,L2,L3,L4,L6,L7,L8,L9,L10, R1,R2,R2,R4,R5

Characters:

ITS 740 --	0,0,0,0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0, 1,1,1,1,1,1,1,1, 0,0,0,0,0,0,0,0,0, 0,0,0,0,0
ITS 730 --	0,0,0,0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 1,1,1,1,1,1,1,1,1,1, 1,1,1,1,1
ITS 715 --	1,1,1,1,1,1,1,1,1,1,1,1,1, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0
Hinf1 D --	1,1,1,1,1,1,1,1,1,1,1,1,1, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 1,1,1,1,1,1,1,1,1,1, 1,1,1,1,1,
Hinf1 E --	0,0,0,0,0,0,0,0,0,0,0,0,0, 1,1,1,1,1, 1,1,1,1,1,1,1,1, 0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0,
Hinf1 F --	0,0,0,0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 1,1,1,1,1,1,1,1,1,1, 0,0,0,0,0,
Hinf1 H --	0,0,0,0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 1,0,1,0,1,0,0,0,0, 0,0,0,0,0
Pall A --	1,1,1,1,1,1,1,1,1,1,1,1,1, 0,0,0,0,0, 1,1,1,1,1,1,1,1, 0,0,0,0,0,0,0,0,X, 1,1,1,1,1
Pall C--	0,0,0,0,0,0,0,0,0,0,0,0,0, 1,1,1,1,1, 1,1,1,1,1,1,1,1, 1,1,1,1,1,1,1,1,X, 1,1,1,1,1
Pall E --	0,0,0,0,0,0,0,0,0,0,0,0,0, 1,1,1,1,1, 1,1,1,1,1,1,1,1, 1,1,1,1,1,1,1,1,X, 1,1,1,1,1
Pall H --	1,1,1,1,1,1,1,1,1,1,1,1,1, 1,1,1,1,1 1,1,1,1,1,1,1,1, 0,0,0,0,0,0,0,0,X, 1,1,1,1,1
Pall I --	0,0,0,0,0,0,0,0,0,0,0,0,0, 0,0,0,0,0, 0,0,0,0,0,0,0,0, 1,0,1,0,1,0,0,0,X, 0,0,0,0,0
Pvu2B --	X,X,X,X,0,0,0,0,0,X,X,X,X, 1,1,1,1,1, 0,0,0,0,0,X,0, 1,1,1,1,1,X,1,1,X, 0,0,0,0,0
RsaIB --	X,X,X,X,X,0,X,X,0,0,X,X,X,X, 1,1,1,1,1, 0,0,0,X,0,0,0, 0,X,0,0,X,0,0,0,0, 0,0,0,0,0
Sal1 A --	X,X,X,X,0,0,0,0,0,0,X,X,X, 0,0,X,X,0, 0,0,0,0,0,0,0, 1,1,1,1,1,1,1,1,X, 0,0,0,0,X
Sal1C --	X,X,X,X,0,0,0,0,0,0,X,X,X, 0,0,X,X,0, 0,0,0,0,0,0,0, 1,0,1,0,1,0,0,0,X, 0,0,0,0,X

A = ammiratii; B = benzokauffmanii; K = kauffmanii; L= luteosquamulosa; R= redheadii

X = missing data

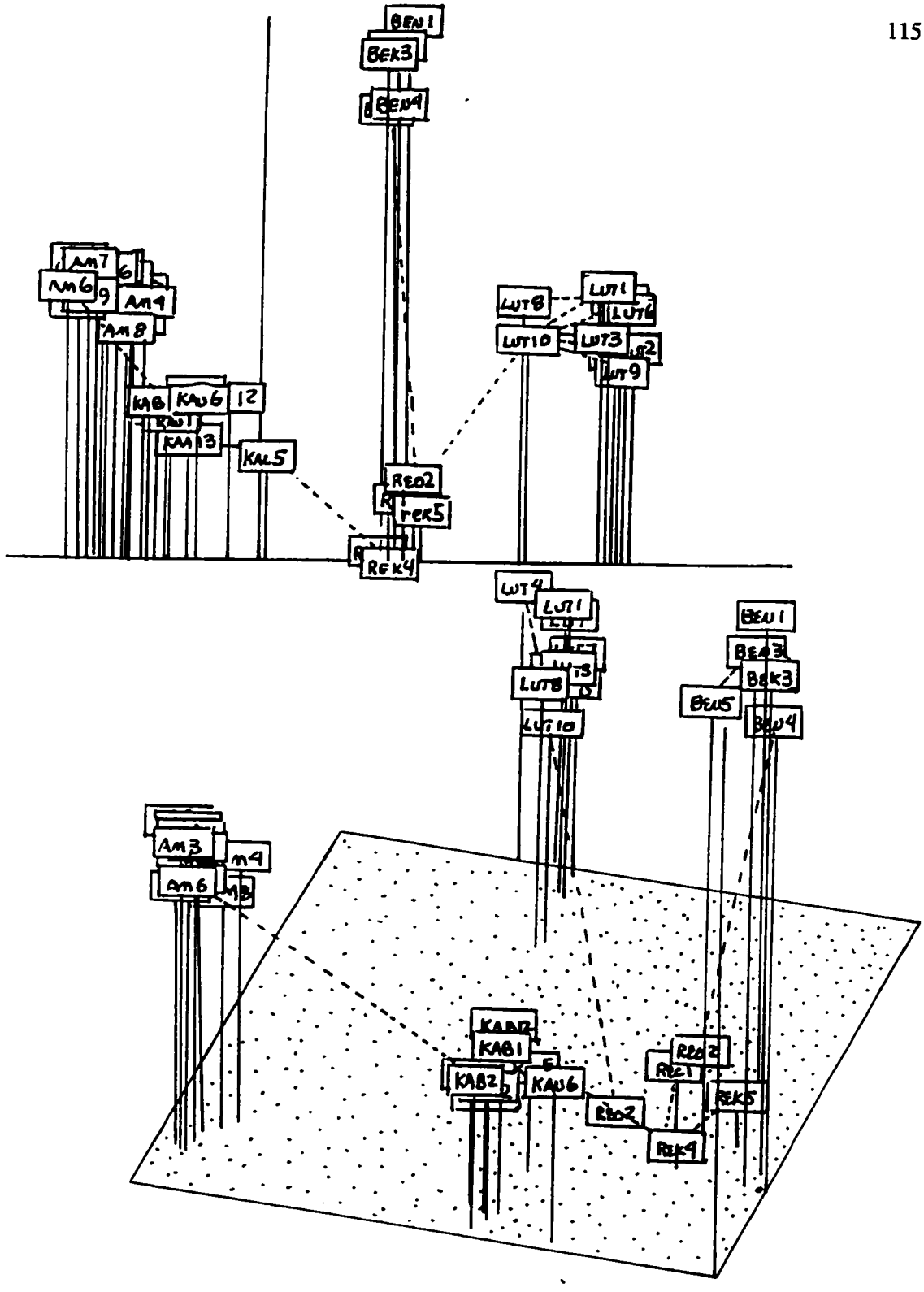


Figure 5.6 Final *P. kauffmanii* complex analyses: Three-dimensional model (two views) of 40 individuals generated by multivariate analyses of combined morphological + restriction site/ ITS length character set

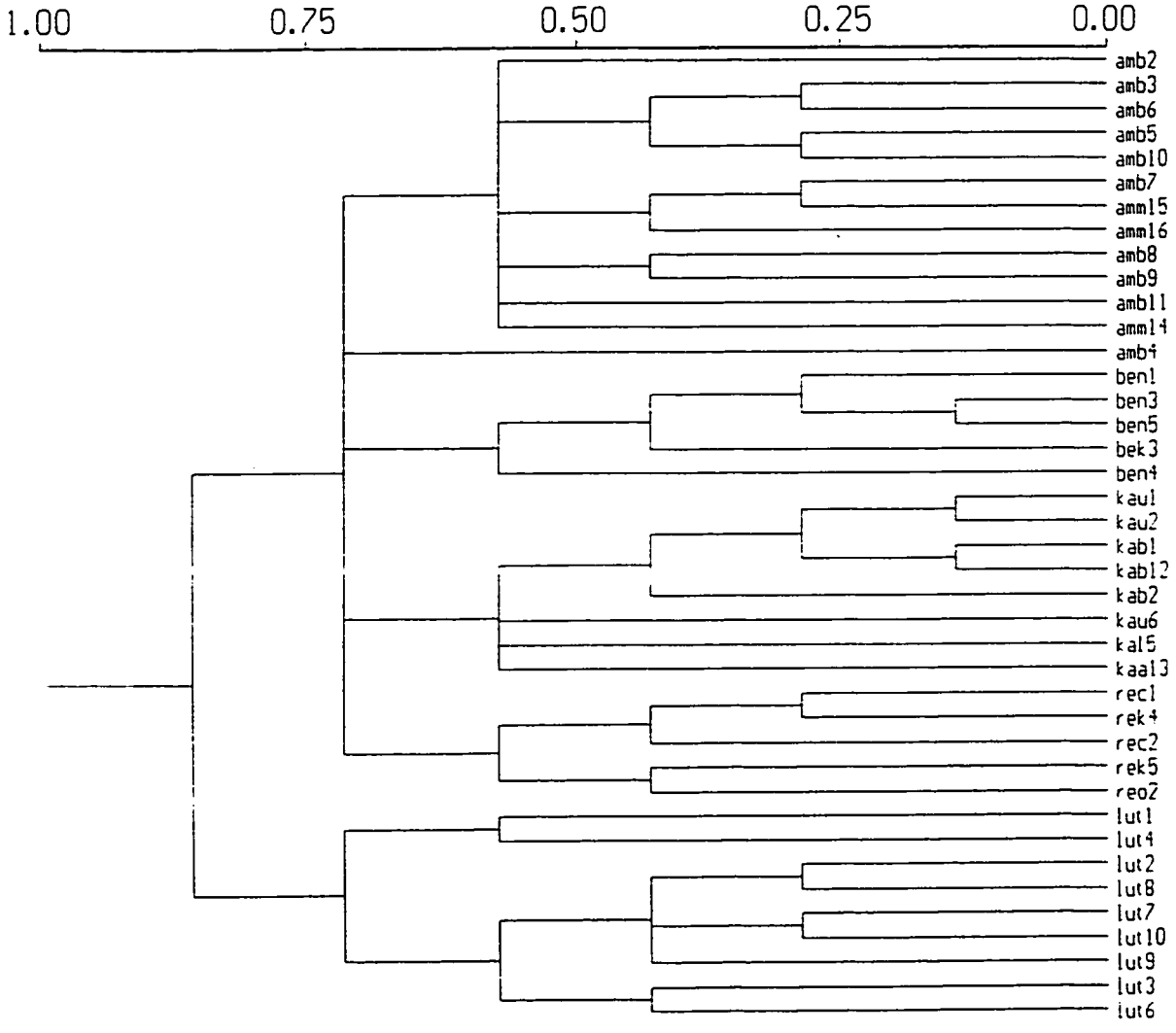


Figure 5.7 Final *P. kauffmanii* complex analyses: Consensus tree (r = 0.97) of UPGMA trees generated from UPGMA consensus trees derived from restriction site molecular + morphology character sets and and ITS molecular + morphological character sets..

Table 5.8 Microscopical and molecular characters used in preliminary sectional phenetic analyses.

OTUs --

Phaeocollybia --
amm, att, ben, cal, dis fal, gre, kau, lil, lut oli, ore, pic, ple pse rad, red, rif, ruf, sca sim, sip, spd,

Out-taxa --
Stg, Cau, dec

Character set (in above order) --

Morphologica

ChShp	**1**	1	**1**	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	1	0	1	1	1
Clamp	**0**	1	**1**	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
SpLng	**1**	1	**1**	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	0	0	1
TibDv	**1**	1	**1**	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
GelTs	**1**	1	**1**	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
SpCol	**1**	1	**1**	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Cheilo	**1**	1	**1**	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0

Molecular (number or restriction sites per enzyme)

ITS	3	4	**3**	2	X	2	4	**4**	2	**4**	3	3	2	4	2	4	4	4	2	2	3	4	3	5	4	1
Hinf1	**1**	1	**1**	1	X	1	1	**1**	1	**2**	1	1	2	1	1	1	1	2	1	1	2	1	3	2	1	1
Pal1	**2**	3	**3**	2	X	2	2	**4**	2	**2**	2	3	1	2	2	3	4	2	2	2	1	0	2	0	0	1
Pvu2	**0**	1	**1**	1	X	0	1	**0**	0	**1**	0	1	0	2	1	1	1	0	1	1	1	0	1	0	0	1
Rsa1	**0**	0	**1**	0	X	0	0	**0**	0	**0**	0	0	0	0	0	0	**0**	0	0	0	0	0	0	1	0	0
Sal1	**0**	0	**0**	0	X	0	0	**0**	0	**1**	0	0	1	0	0	0	**0**	1	0	0	1	0	1	0	0	0
Xho1	**0**	0	**0**	0	X	0	0	**0**	0	**0**	0	0	0	0	0	X	**0**	X	1	0	0	0	0	1	1	0

OTUs in *P. kauffmanii* complex in **bold-face**

X = missing data;

Microscopical character states:

Cheilocystidial Shape -- 0 = tibiiform with thickened walls; 1 = not tibiiform
Clamp connections -- 0 = present in hymenium/pileipellis; 1 = absent
Basidiospore length -- 0 = <6.5 µm; 1 = >6.5 µm
Tibiiform diverticula -- 0 = absent; 1 = present
Gelatinized tissues -- 0 = tramal tissues not gelatinized; 1 = gelatinized
Basidiospore color -- 0 = hyaline; 1 = amber
Cheilocystidia -- 0 = absent; 1 = present

Molecular character states:

ITS lengths -- <680 = 1; 690-705 = 2; 710-725 = 3; 730-745 = 4; >750 = 5

Hinf1 -- 1, 2, or 3 sites
Pal1 -- 1, 2, 3 or 4 sites
Pvu2 -- 0 = site absent; 1 = site present
Rsa1 -- 0 = site absent; 1 = site present
Sal1 -- 0 = site absent; 1 = site present
Xho1 -- 0 = site absent; 1 = site present

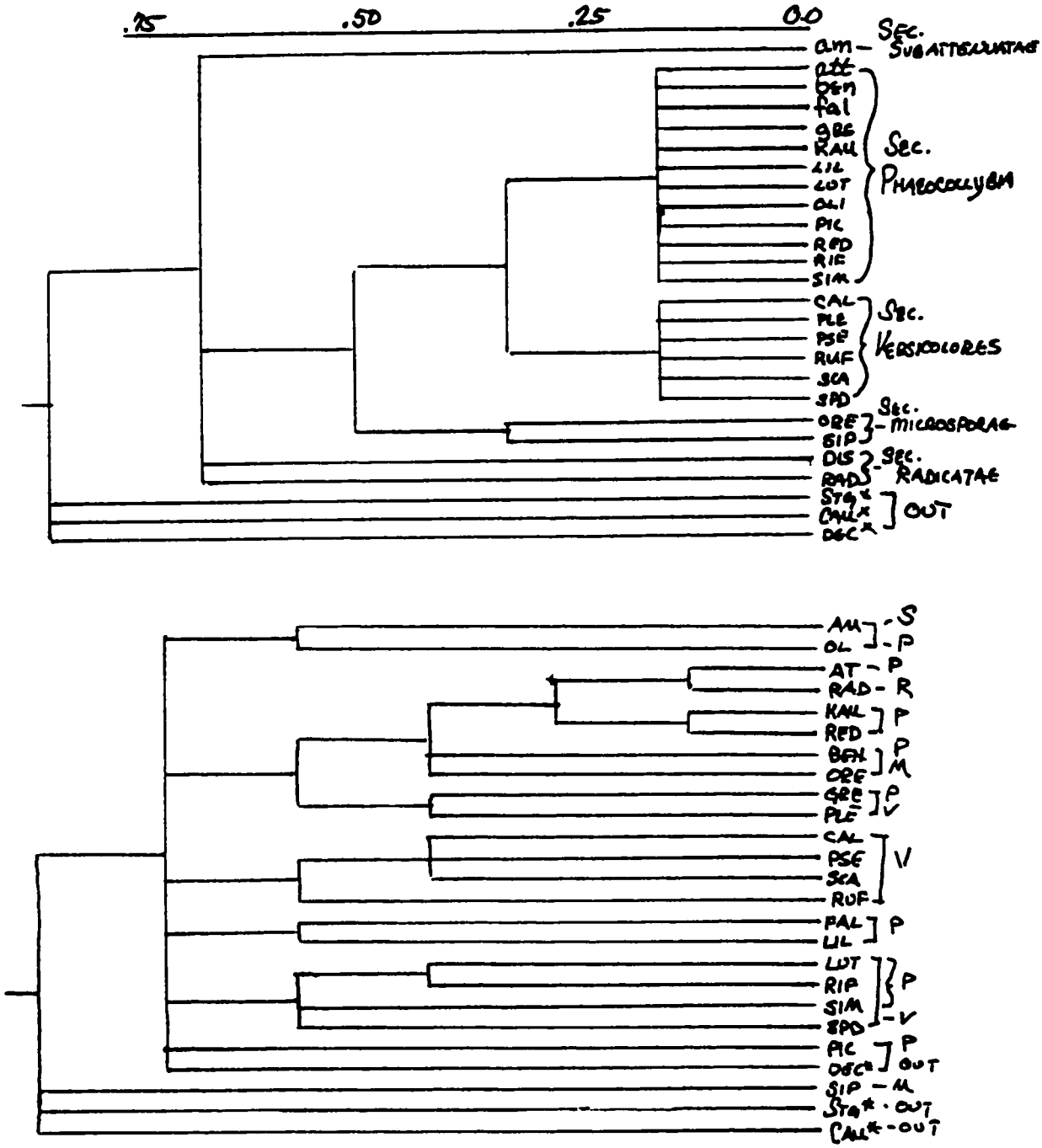


Figure 5.8 47 *Phaeocollybia* sections vs. out-taxa: Comparison of phenograms of Phaeocollybias and three out-taxa generated from (a) microscopical (r = 0.90) and (b) 7 molecular (r = 0.78) characters. The microscopical character set is based on generically and sectionally significant characters. The morphological and molecular trees are not congruent.

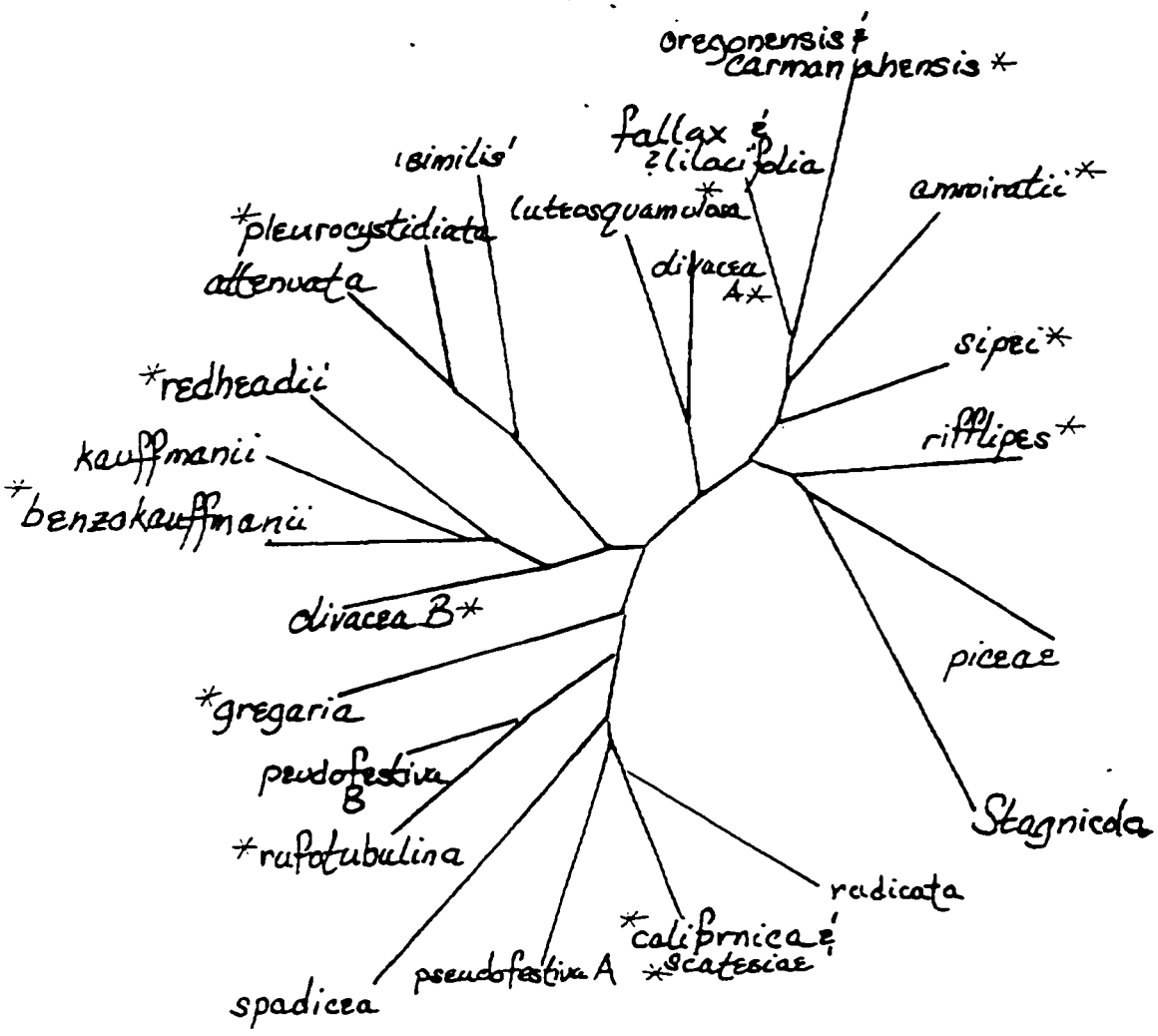
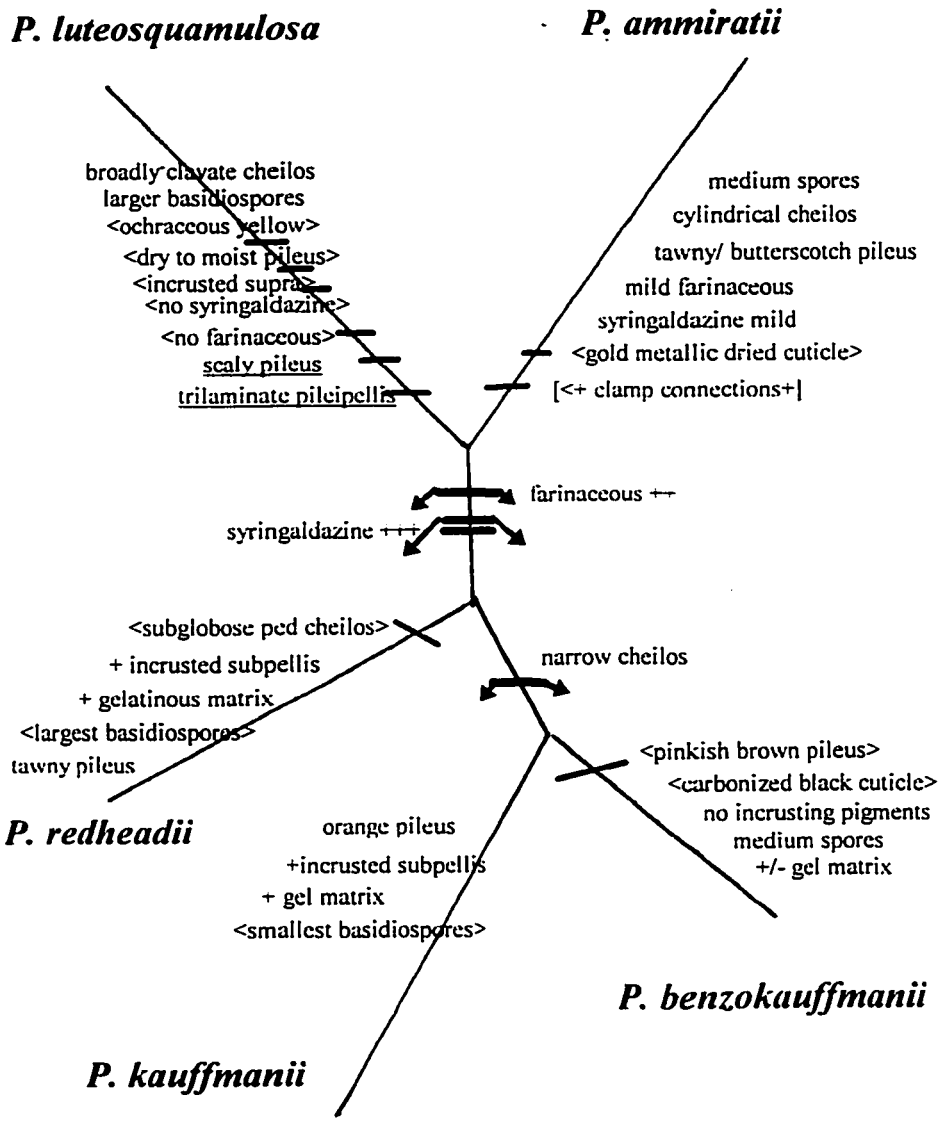


Figure 5.9 Phylogenetic relationships among representatives of 25 putative Pacific Northwest *Phaeocollybia* species and *Stagnicola perplexa* (out-group) -- Unrooted consensus tree of FITCH and NEIGHBOR trees (* = DNA successfully amplified from type material.).



KEY
[brackets]: [rare] in PNW
underlined: unique in PNW
<angled>: <unique> in complex

Figure 5.10 Potentially diagnostic morphological characters mapped upon consensus phylogenetic tree derived from restriction site data of species in the Pacific Northwest. All species are characterized by a large stature, stipe with matte surface and stuffed with mature pith in age, vertical monopodial pseudorhizae, thin-walled clavate cheilocystidia, large (> 8 x 5 µm) beaked moderately ornamented limoniform basidiospores.

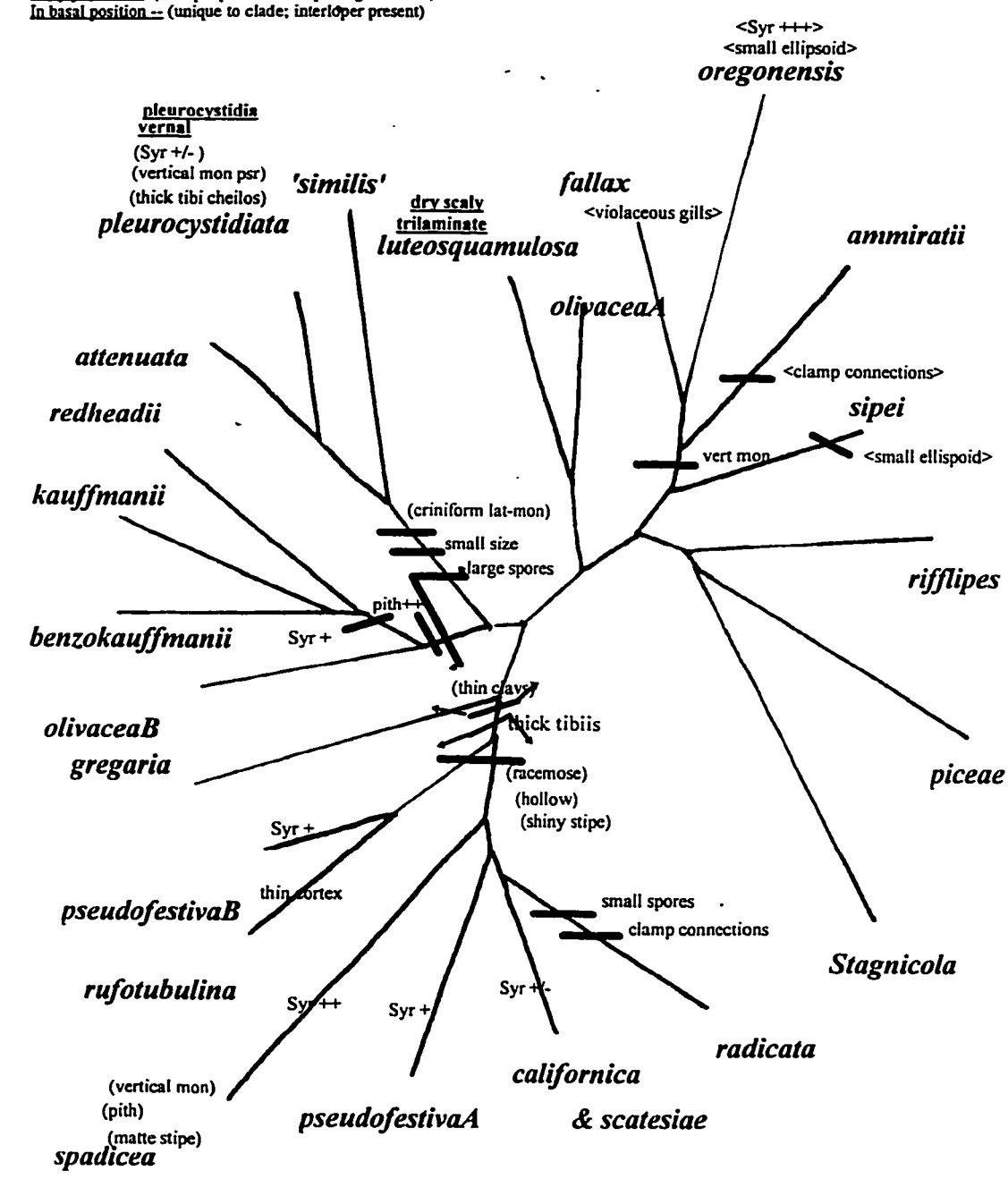


Figure 5.11 Diagnostic morphological characters mapped upon consensus phylogenetic tree of Pacific Northwest *Phaeocollybia* species.

CHAPTER 6. TAXONOMY OF PACIFIC NORTHWEST *PHAEOCOLLYBIA* SPECIES

Phaeocollybia Heim, Encyclopedie mycologique 1:70, 1931.

Emended

Pileus conic, obtusely conic or campanulate, finally expanding to plano-umbonate in some, margin long remaining inrolled; the surface virtually glabrous or sometimes bearing small squamulose remnants of the pellicular veil, typically glutinous to viscid to merely lubricous, rarely dry, variously colored but generally with a tendency toward ferruginous tones in age and 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 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 after spore formation but usually not distinctly marginate.

Stipe cartilaginous, in some smaller species becoming corneous, in others more flaccid,usually stiff and strict, glabrous and naked over most of the surface with short fibrillose patches often scattered over the superior portion, the surface either matte and closely longitudinally lined or naked and shining, developing ferruginous tones in age; the cortex often thick and distinct, the interior hollow or stuffed.

Pseudorhiza long, often thick sometimes thin or hairlike, either [i] ascending and giving rise to a single basidiome (vertical-monopodial) and then continuous with the stipe and gradually narrowing downwards to a somewhat blunt origin, [ii] extending laterally through the substrate before turning upwards (lateral-monopodial) and then a thin criniform wire differentiated from a fleshier stipe, [iii] racemose and tapering to a branched flexible thread or cord (sequential-racemose), or [iv] apically umbellately branched (fasciculate-racemose); frequently rhizomorphic in function.

Veil pellicular, scant and easily overlooked, sheathing the subterranean primordium but soon tearing and becoming inconspicuous, often evident as traces on the epigeous portion of mature basidiomes as irregularly to concentrically arrayed fibrillose patches on the aerial stipe, less frequently evident as short appressed fibrillose patches over the pileus surface, most frequently obliterated on emergent basidiomes.

Basidiospores in mass some shade of yellowish to pinkish cinnamon brown; shape ranging from subellipsoidal with rounded apex to amygdaliform or limoniform with the apical callus projecting as a distinct beak, rarely punctate-roughened, more frequently rugulose-warty ornamented,

always less ornamented to completely smooth apically; ornamentation often lower and less pronounced in the suprahilar area (as in a 'plage') but never completely smooth, color pale to dark amber in KOH, dextrinoid or non-dextrinoid in Melzer's reagent.

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

Cheilocystdia always present and usually falling into two basic categories: [i] either thin-walled filamentous to clavate (hyaline or very pale amber) or [ii] ventricose to equal below but with a narrow thick-walled highly refractive neck above and frequently with colored walls in KOH, the apex minutely capitate merely blunt or acute and usually secretory; in some species intermediate types of cystidia are frequent.

Pleurocystidia usually absent, but when present similar in morphology to the accompanying cheilocystidia or filamentous and more properly termed hyphidia (paraphyses).

Pileipellis typically a two layered ixocutis with suprapellis of subgelatinous to highly gelatinized narrow frequently hyaline hyphae above a pigmented subpellis of gelatinized wide often inflated hyphae or more rarely a three-layered ixocutis with remnants of the pellicular veil forming a suprapellis of narrow pigmented hyphae over a hyaline mediopellis and pigmented subpellis; top hyaline layer either with loosened ascending hyphae embedded in a gel matrix or tightly radially aligned; pigments typically intraparietal and/or plasmatic, occasionally slightly encrusting pigments also present; oleiferous hyphae often present.

Tramal tissues moderately to heavily gelatinized, but not forming a clear gel, but instead forming a compact cartilaginous tissue, occasionally homogeneously monomitic, more often sarcodimitic and composed of two hyphal types (long, wide, thick-walled fundamentals versus branched, narrow, and thin-walled generatives), with highest degree of sarcodimitism evident in the pseudorhizal trama, sarcodimitism also often present to lesser degrees in the stipititrama, pileitrama, and lamellar trama; pileitrama 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 either 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 an integral part of the superficial pellicular veil hyphae and always present on the mycelia and pseudorhizal pellis, often on the apical stipitipellis, and occasionally on the pileipellis, especially on patchy (scaly) veil remnants;

Development: (pileo)stipitocarpic monovelangiocarpy.

Habit- habitat, distribution: Solitary, scattered, gregarious, or cespitose, some in arcs where the carpophores may be clustered or gregarious in the line of the arc. In western North America typically found in moist mesic mature coniferous or coniferous-fagaceous forests. Mycorrhizal and/or possibly mildly parasitic.

Type species: *Agaricus lugubris* E. M. Fries: E. M. Fries, *Systema* p. 254. 1821. *Typus conserv.* Greuter *et al.* p. 157. 1994.

Phylogenetic considerations

Relationships with other genera -- Singer (1986) recognized *Phaeocollybia* as belonging to the tribe Cortinareae in the family Cortinariaceae, which is characterized by the possession of rusty-brown thick-walled ornamented basidiospores lacking a germination pore. Among the genera in this tribe, *Phaeocollybia* shares the closest affinities with *Cortinarius, Galerina, Gymnopilus* and *Pyrrhoglossum. Phaeocollybia* is morphologically differentiated from these genera by the presence of a stipe with a cartilaginous cortex originating from a long pseudorhiza and the diverticulate hyphae of the mycelium and pellicular veil.

Biologically it appears most closely related to the mycorrhizal genus *Cortinarius*, in particular the Subgenus *Myxacium* with which it also shares general aspect, thin-walled cheilocystidia, basidiospore color and morphology and relatively rare possession of clamp connections in the pileipellis. *Cortinarius,* however, is characterized by the presence of a persistent cortina, which *Phaeocollybia* lacks.

Those who have not recognized the mycorrhiza forming capabilities in *Phaeocollybia* consider the genus more closely related to the saprophytic genera *Gymnopilus, Galerina* and *Pyrrhoglossum,* all of which also characteristically produce deep yellow-brown to rusty brown basidiomes. *Gymnopilus* basidiomes share a similar stature, spore ornamentation and cheilocystidia with *Phaeocollybia* but can be distinguished by the presence of attached lamellae, ubiquitous clamp connections, bright brownish orange spore color, and pigments that are consistently soluble in KOH.

With the exception of producing similarly colored basidiomes with yellow- to rusty brown colored basidiomes, *Phaeocollybia* appears to share little in common with *Galerina,* a saprophytic genus characterized by small fragile basidiomes with smooth or ornamented basidiospres; most ornamented Galerinas possess a very well delimited smooth plage (unlike the ill-defined plage found on some Phaeocollybias); Galerinas that produce fully ornamented basidiospores consistently lack clamp connections.

Horak (1989) suggested that *Pyrrhoglossum*, which with *Phaeocollybia* also produces basidiomes with green or violet (in addition to the yellow to rusty brown) colors, is perhaps the most closely related genus to *Phaeocollybia*. Both genera produce pigments that are unstable in KOH and very similar basidiospores and cheilocystidia; the saprophytic and pleurotoid habit of *Pyrrhoglossum*, however, separates that genus from the pseudorhizal and mycorrhizal *Phaeocollybia*. Phylogenetic relationships among the genera in Tribe Cortinareae may eventually be resolved through molecular analyses.

Relationships among species -- Although the species hypotheses in this study were initially developed from morphological characters, restriction enzyme analyses have facilitated delimitation of taxa within a phylogenetic framework. It is hope that the species proposed here are monophyletic taxa that will be supported by cladistic analyses of additional molecular data. Recognition of higher taxa at the sectional or subgeneric level is being withheld until after genetic evaluation of the majority of the known species in *Phaeocollybia* and its allied genera.

Species descriptions

Expanded technical descriptions are based primarily on data taken from the type collections and molecularly tested specimens collected by the author, with dimensions and color references considerably augmented by data from other personal collections. Descriptions based solely on examinations of new type collections are currently on file with the type specimens at WTU. General non-standardized color names in lower case are accompanied by italicized color standard references by Ridgway (1912) in capitals and Munsell (1976) in alpha-numeric code. Microdescriptions are based on tissues from dried specimens rehydrated in 3-6 % aqueous KOH unless otherwise noted. Mean dimensions accompanied by standard deviations computed from all collections measured are followed by parenthesized overall range data. Collections examined are cited in Appendix C and listed according to locality followed by date, herbarium number, depositor name and number, collector (if different from the depositor) and (in brackets) the herbarium abbreviation (Holmgren et al., 1990) (Collections are deposited in the University of Washington Herbarium (WTU) unless otherwise noted). DNA-reference numbers (in bold subscript) are placed after collection numbers; Strategy 1 cited collections (USDA-DI, 1994; Norvell, 1995) of significance to forest management policy are marked with an asterisk (*). Norvell collection numbers start with initials, year, month, and day, *e.g.* LLN 94.11.06-18-amm16 = *November 6, 1994,* 18th collection, DNA ref. amm16. Longitudes and latitudes have been approximated either by converting Township-Range-Section data from U.S.D.A. Forest Service maps using TRS2LL (Wefauld, 1995) or by accessing the G.N.I.S. database at the Yale Peabody Museum of Natural History via GOPHER on the Internet.

Conspectus of Pacific Northwest Species of *Phaeocollybia*

Dichotomous Key to Pacific Northwest Species of *Phaeocollybia*

1a. Cheilocystidia thick-walled, fusiform, lageniform to capitulate tibiiform with narrow, distinctly refractive necks, with or without apical secretory droplets
.....2

1b. Cheilocystidia thin-walled, generally narrowly to broadly clavate, mucronate, or subcapitate, occasionally with filamentous apical secondary growth in senescent or improperly preserved specimens, but always lacking thickened refractive necks
.....9

2a. Basidiospores small (~5.8 x 3.2 µm), inequilaterally ellipsoidal and minutely punctate; clamp connections abundant. (Section *Radicatae*)
.....*P. radicata*

2b. Basidiospores larger (> 7 µm long), more or less limoniform with subdued to pronounced apical beaks; clamp connections absent (Section Versicolores)
.....3

3a. Pleurocystidia abundant, capitulate tibiiform; stipes < 5 mm in diameter; fruiting vernal
.....*P. pleurocystidiata*

3b. Pleurocystidia absent to extremely rare; stipe apices > 5 mm in diameter; fruiting autumnal
.....4

4a. Pilei with olive green coloration
.....*P. pseudofestiva*

4b. Pilei lacking green coloration
.....5

5a. Basidiomes robust and firm, with thick (≥ 10 mm wide) stipe apices; stipes stuffed with solid, compact pith; if decapitated when fresh the stipe cortex not recurving as described below; stipe base gradually narrowing to a vertical-monopodial pseudorhiza; basidiomes solitary, scattered, or clustered
.....6

5b. Basidiomes medium-sized with ± slender (≤ 10 mm wide) stipe apices; stipes soon becoming hollow and fistulose (retaining at most only fibrillose interior remnants at maturity); if decapitated when fresh, the stipe walls often splitting lengthwise and slowly recurving like a dandelion scape; stipe base adjoining a threadlike, vertical to lateral racemose pseudorhiza; basidiomes densely gregarious to cespitose
.....7

6a. Pileus bright orange to tawny; cheilocystidia heteromorphic, with refractive frequently bifurcating capitulate tibiiform elements intermixed with occasional thin-walled clavate elements; all tissues magenta in syringaldazine

.....*P. tibiikauffmanii*

6b. Pileus dark chestnut to date brown; cheilocystidia also heteromorphic with refractive capitulate and lageniform elements not bifurcating; only pseudorhizal pellis magenta in syringaldazine.

.....*P. spadicea*

7a. Mature stipes tubular with a large hollow cavity and a very thin (< 1 mm thick) cartilaginous cortex; reddish-orange pilei merely lubricous to subviscid; pseudorhizae sequential-racemose.

.....*P. rufotubulina*

7b. Mature stipes with a relatively smaller hollow cavity and a moderately thick (~2 mm) cartilaginous cortex; brownish orange, amber-brown or dark brown pilei (always duller than the previous species) viscid to heavily glutinous; pseudorhizae sequential- or fasciculate racemose.

.....8

8a. Basidiospores generally ~9 x 5 µm (range 8-10 x 5-6 µm) with coarse dark ornamentation easily seen in spore outline; pale amber suprapellis with pale orange concentrically incrusted hyphae; pilei viscid, amber-brown to brownish orange; basidiomes closely gregarious in loose bundles but rarely massed in large cespitose humps.

.....*P. californica*

8b. Basidiospores generally ~8.5 x 5 µm (range 7.2-9.5 - 4.5-5.6 µm), moderately coarse somewhat pale spore ornamentation slightly visible in spore outline; colorless suprapellis with hyaline hyphae lacking incrustations but with refractive septa; pilei heavily glutinous, amber brown when young, becoming blackish-brown in age; basidiomes densely cespitose, often erumpent in fascicles of 50 or more.

.....*P. scatesiae*

9a. Basidiospores ellipsoidal, lacking clearly differentiated apical beaks and with very subdued punctate-roughened ornamentation.

.....10

9b. Basidiospores limoniform to amygdaliform, with either subdued or pronounced apical beaks and verruculose to warty ornamentation

.....13

10a. Basidiospores large (~10 x 5.8 µm, range 9-12 x 5-6.2 µm); clamp connections abundant; basidiomes thin and fragile; stipe ≤ 4 mm; tibiiform diverticula generally large (20-50 x 1-2 µm).

.....*P. phaeogaleroides*

10b. Basidiospores much smaller (< 7 µm long); clamp connections present or absent; basidiomes moderately fleshy and robust; stipe ≥ 5 mm; tibiiform diverticula generally < 30 µm long (Section *Microsporae*).

.....11

11a. Pilei drab to grayish brown; stipes stuffed with firm pith, never becoming hollow; fresh cartilaginous rind generally 1-2 mm thick; clamp connections absent (pseudoclamps may be present).

.....*P. oregonensis*

11b. Pilei bright to reddish orange to dark orange rufous; stipes soon becoming hollow; fresh cartilaginous cortices unusually thick (2-3 mm); clamp connections present or absent.

.....12

12a. Clamp connections abundant on hyphae, cheilocystidia, and basidia; fresh pilei bright orange to brownish orange with thick gelatinous pellicle, dried pileus metallic gold (if handled properly); basidiospores ~6.2 x 4 µm (range 6-7.3 x 3.4-4.5 (5) µm).

.....*P. dissiliens*

12b. Clamp connections absent in all tissues; fresh pilei dark orange rufous, dried pileus dull matte apricot orange (if handled properly); basidiospores ~6.8 x 3.8 µm (range 5.8 - 7.5 x 3.3 - 4.5 µm).

.....*P. sipei*

13a. Basidiospores ≤ 7.5 x 4.5 µm; basidiomes moderately small with tawny to dark olive brown glutinous pilei, violet young lamellae.

.....*P. rifflipes*

13b. Basidiospores ≥ 7.5 x 4.5 µm; basidiomes small to large with variously colored (including tawny to dark olive brown), dry to glutinous pilei, variously colored young lamellae (including violet).

.....14

14a. Pileipellis an indistinct ixocutis predominantly composed of pigmented gel-incrusted hyphae; mature basidiomes usually small and generally "collybioid", with lubricous to subviscid pilei ≤ 40 mm, stipe corneous to cartilaginous, frequently soon dark reddish brown nearly to apex, apices rarely > 4 mm in diameter; pseudorhizae criniform.

.....15

14b. Pileipellis a distinct clear or layered ixocutis; mature basidiomes medium to large and generally "tricholomatoid", usually with dry to glutinous pilei >40 mm broad; stipes not corneous, variously pigmented but typically not soon dark reddish brown up to the apex, stipe apices > 5 mm in diameter; pseudorhizae pliant.

.....16

15a. Basidiomes often with acutely umbonate papillate pilei, pinkish to vinaceous drab or lilac-tinged young lamellae, 3-8 mm wide stipe apices, and inert in syringaldazine.

.....*P. attenuata*

15b. Basidiomes often with obtusely umbonate, rarely papillate pilei, yellowish to pinkish buff (rarely lilaceous) young lamellae, 1.5-3 mm wide stipe apices, and pseudorhizal pellis latently reactive in syringaldazine.

.....*P. 'similis'*

16a. Basidiomes large and robust; mature stipes ≥ 15 mm diam and stuffed with solid firm pith, mature pilei generally ≥ 60 mm broad

.....17

16b. Basidiomes medium-sized and less robust; mature stipes generally ≤ 12 mm diam and often hollow or with fibrillose pith, mature pilei usually ≤ 50 mm broad [with greenish or dark to dull brown coloration].

.....22

17a. Pilei predominantly olive green with or without brown tones, in age becoming more or less uniformly dark olive-brown; basidiospores more or less coarsely ornamented, distinctly limoniform in profile with dorsally eccentric abrupt conical apical beaks and apiculi with strongly convex curved abaxial surfaces; lower pseudorhizae frequently narrow and cord-like.

.....*P. olivacea*

17b. Pilei yellowish, orangish, pinkish, or red brown, but lacking olive tones, basidiospores moderately ornamented, amygdaliform to limoniform with subdued to only moderately developed beaks; pseudorhizae fleshy, never cord-like

.....18

18a. Pilei dry to moist (never glutinous), appressed-scaly, and ochraceous yellow; pileipellis trilaminate with narrow bright orange-yellow suprapellis (retained pellicular veil), relatively narrow (75-100 µm thick) colorless gelatinized mediopellis, and orange yellow subpellis; all tissues negative in syringaldazine

.....*P. luteosquamulosa*

18b. Pilei glabrous (never scaly), viscid to glutinous, and lacking ochraceous yellow tones in mature specimens; pileipellis bilaminate with highly gelatinized hyaline suprapellis and pigmented subpellis; at least some tissues immediately or tardily magenta in syringaldazine

.....19

19a. Clamp connections present throughout, notably on the suprapellicular hyphae, cheilocystidia, and basidial bases; pseudorhizal pellis weakly magenta after 30 minutes in syringaldazine (Section *Subattenuatae*)

.....*P. ammiratii*

19b. Clamp connections absent in suprapellicular hyphae, cheilocystidia, and basidial bases but sometimes present in stipitipellis; all tissues immediately magenta in syringaldazine.

.....20

20a. Pilei and stipe apices with drab (pinkish- to purplish-brown) colors (young pileus glabrous, viscid, drab; stipe apex pink to drab); clamp connections absent in all tissues; subpellis with dull brown diffuse pigments.

.....*P. benzokauffmanii*

20b. Pilei orange, pale tawny, brownish orange to orangish brown, lacking drab to pinkish-brown colors when young; clamp connections occasionally present in stipitipellis; subpellis with brownish-orange incrusting pigments.

.....21

21a. Basidiospores generally ~10.5 X 6 µm (overall range 8.5-12 x 5-7 µm); cheilocystidia generally pedicellate and subcapitate (sub-globose apices frequent); young pilei pale tawny, becoming red-brown to brown in age.

.....*P. redheadii*

21b. Basidiospores generally ~8.5 x 5 µm (overall range 7.5-10 x 4-6 µm); cheilocystidia irregularly cylindrical to narrowly clavate, rarely pedicellate or subcapitate; young pilei bright to dull orange, becoming brownish orange or tawny in age

.....*P. kauffmanii*

22a. Cheilocystidia narrowly irregularly clavate to occasionally mucronate, slightly to moderately gelatinized but not in a gelatinous band; basidiospores broadly limoniform, generally ≥ 9 x 5.5 µm.

.....23

22b. Cheilocystidia broadly clavate and frequently forming a dense gelatinous barrier (except in old or highly degraded specimens); basidiospores narrowly limoniform, ≤ 9 x 5.5 µm).

.....24

23a. Pilei apricot to orange rufous to orange red; cartilaginous stipes stuffed but often soon insect infested and thus hollow at ground level; taste bitter

.....*P. piceae*

23b. Pilei wood to dark brown, grayish buff when dried; stipes stuffed, soon becoming hollow; taste not distinctive

.....*P. gregaria*

24a. Basidiospores generally 9 x 5 µm (overall range 8-10 x 4-6 µm), medium amber, and verrucose-rugulose; subpellis orange in KOH; pilei long olive green, becoming orangish to dark brown due to age or weather conditions, underlying olive color sometimes obscured by dull orange or dark brown glutin; young lamellae bluish-violet, soon fading to drab or losing violaceous tones; basidiomes usually small and fragile with drab to greenish-tinted stipe apices rarely > 9 mm diam.

.....*P. fallax*

24b. Basidiospores generally 8 x 5 µm (overall range (7) 8-9 x 4.5-5.5 µm), pale medium amber, and verrculose-rugulose; subpellis dull orange-brown in KOH; pilei uniformly dark brown with no olive-greenish tones; young lamellae lilaceous, soon fading to drab or losing lilaceous tones; basidiomes medium sized and relatively robust with drab to brownish stipe apices frequently ≥ 10 mm.

.....*P. lilacifolia*

Synoptic Key to Pacific Northwest Species of *Phaeocollybia*

Note: ( ) indicates outlier or occasional occurrence

amm . *ammiratii...*
att .. *attenuata*
ben .. *benzokauffmanii*
cal .. *californica*
dis .. *dissiliens*
fal .. *fallax*
gre .. *gregaria*
kau . *kauffmanii*
lil ... *lilacifolia*
lut ... *luteosquamulosa*
oli ... *olivacea*
ore ... *oregonensis*
pha .. *phaeogaleroides*
pic ... *piceae*
ple ... *pleurocystidiata*
pse ... *pseudofestiva*
rad ... *radicata*
red... *redheadii*
rif ... *rifflipes*
ruf ... *rufotubulina*
sca ... *scatesiae*
sim .. *'similis'*
sip ... *sipei*
spd .. *spadicea*
tib ... *tibiikauffmanii*

Field Characters

Basidiome

Small (mature pileus < 30 mm) -- *att, dis, fal, pha, pic, ple, (pse), rad, rif, (ruf), sim*

Medium-sized (mature pileus 30 - 70 mm) -- *(amm), cal,dis, (fal), gre, lil, oli, ore, (pha), pic, pse, (rif), ruf, sca, sip, spd, tib*

Large (mature pileus > 80) -- *amm, ben, kau, lut, (ore), red, sip, spd*

Fleshy -- *amm, ben, kau, lut, (oli), ore, ple, red, (rif),spd, tib*

Slender and cartilaginous pliant -- *att, cal, fal, dis, gre, lil, (oli), pic, pse, rif, ruf, sca, sim, sip*

Fragile and brittle - *(dis), pha, rad, (sip)*

Odor farinaceous -- *amm, ben, kau, ore, (pic), (ple), red, (sip), (tib)*

Odor complex either floral (pansy-like) or burnt hair (gebrenzlich) or boiled potatoes -- *att, fal, oli, (rif), ruf, sca, (sim), (spd), (sip), (tib)*

Odor slightly pungent, like fava beans (raw) or corn-silk -- *cal, dis, lil*

Odor not distinctive -- *dis, gre, lut, pha, pic, (ple), pse, rad, rif, spd*

Pileus

Young pileus ochraceous yellow -- *(amm), lut, (pha), (ple), (sim), sip*

Young pileus orange to orange red -- *(cal), dis, kau, pic, ruf, tib*

Young pileus yellow-brown, orange-brown or reddish-brown -- *att, amm, cal, pha, ple, rad. red, rif, sca, sim, sip, tib*

Young pileus olive green -- *fal, oli, pse*

Young pileus drab (pinkish to purplish grey brown) -- *ben, gre, ore*

Young pileus blackish-brown -- *(fal), lil, (oli), (rif), sca. spd,*

Surface dry to very slightly lubricous -- *lut, (pha), (sim)*

Surface moist to lubricous -- *att, (lut), pic, ple, rad, ruf, sim, (sip)*

Surface subviscid to viscid -- dis, *pha, (pic), ple, rad, ruf, sip, tib*

Surface viscid to glutinous -- *amm, ben, cal, fal, gre, kau, lil, oli, ore, pse, red, rif, sca, spd*

Completely dried pileus with metallic sheen -- *amm, cal, dis, (fal), gre, (kau), oli, (ple), (pse), ruf, sca*

Completely dried pileus carbonized black -- *ben, rif*

Lamellae

Young gills pale pinkish cinnamon -- *att, (ben), kau, ple, red, sca, (spd),*

Young gills creamy yellow, pale orange, ochraceous -- *amm, cal, dis, lut, oli, pic, (pse), (?rad), ruf, sca, sim, sip, tib*

Young gills greenish -- *(oli), pse*

Young gills lilaceous, caesius, violaceous -- *(att), fal, lil, rif*

Young gills tan (pale yellow brown) -- *cal, (lut), pha, ple, rad, sim*

Young gills whitish to smoky grey -- *ben, gre, ore, (spd)*

Veil (stipe)

Appressed fibrillose patches on surface -- *lut*

Fibrillose patches on stipe apex -- *att, (ben), dis, fal, (kau), lil, oli, (ore), (ple), pse, (red), rif, sca, (sim), (sip), spd!, tib*

Isolated fibrils on stipe apex -- *pic, ruf*

Stipe

Young stipe apex creamy yellow to yellow buff -- *(amm), lut, red*

Young stipe apex orange buff -- *(cal), pic, ruf, sca, tib*

Young stipe apex greenish -- *fal, oli, pse*

Young stipe apex violaceous to drab -- *ben, fal, gre, lil, ore, rif, spd*

Young stipe apex pinkish to pinkish cinnamon -- *amm,dis, kau, ple, (pse), red, sca, sim, spd, (tib)*

Young stipe apex watery to brownish tan -- *att, cal, pha, sip*

Mature stipe apex < 5 mm diam -- *att, pha, ple, rad, (red), ruf, sca, sim*

Mature stipe apex 5 - 10 (12) mm diam -- *(amm), cal, fal, dis, (gre), (lil), (lut), (oli), (ore), pic, pse, rif, ruf, sca, sip, tib*

Mature stipe apex > 11 mm diam -- *amm, ben, (cal), gre, kau, lil, lut, oli, ore, red, (sip), spd, (tib)*

Mature stipe stuffed with firm compact pith -- *amm, ben, (fal), gre, kau, lut, (oli), ore, (pic), red, spd, (tib)*

Mature stipe stuffed with fibrillose pith -- *(amm), (att), (dis), (fal), (lil), oli, pha, ple, pse, rif, sim, (sip), (tib)*

Mature stipe hollow -- *att, cal, (dis), fal, lil, (pha), (pse), rad, (rif), ruf, sca, sim, (sip)*

Mature stipe corneous -- *att, sim*

Stipe surface smooth and shiny -- *(amm), att, cal, dis, fal, lil, oli, pha, (pic), (ple), pse, (rad), rif, sca, sim, sip*

Stipe surface matte with fine longitudinal lines -- *amm, ben, kau, lut, ore, pic, ple, red, ruf, spd, tib*

Cartilaginous rind ≤ 1 mm -- *(att), pha, ple, ruf, sim*

Cartilaginous rind 1-2 mm -- *att, fal, lil, oli, ore, pic, pse, rad, rif, tib*

Cartilaginous rind > 2 mm -- *amm, (att), ben, cal, dis, kau, lut, red, sca, sip, spd,*

Pseudorhiza (lower)

Criniform and wirelike -- *att, (?pha), sim, (?rad)*

Pliable and thread-like -- *cal, (?dis), (?oli), (pseA?), ruf, sca, (sip)*

Gradually tapering and continuous with aerial stipe -- *amm, ben, fal, (?gre), kau, (?lil), lut, oli, ore, pha, pic, ple, (?pseB), red, rif, (?sip), spd, tib*

Tissues in syringaldazine (untested: *cal, gre, lil, rad*)

Overall deep magenta -- *ben, kau, ore, red, tib*

Only stipe and pseudorhiza deep magenta -- *pse, spd*

Slowly pale to medium magenta (usually confined to pseudorhiza) -- *amm, (oli), ple, ruf, sca, (sim?), sip*

No magenta reaction -- *att, dis, fal, lut, oli, pha, pic, rif, sim*

Habit

Densely gregarious or fasciculate -- *ben, cal, dis, gre, oli, ore, (pseA), (red), ruf, sca, sim, sip*

Scattered to gregarious -- *amm, att, fal, dis, kau,(oli), ore, pic, ple, (pseB), red, (rif), (sim), spd*

Solitary to scattered -- *(att), (kau), lil, lut, pha, rad, rif, spd, tib*

Phenology

Vernal -- *(cal), ple, red*

Autumnal (early) -- *amm, att, ben, cal, gre, (kau), lil, lut, oli, (pic), pse, red, rif, ruf, sca, sim, sip, tib*

Autumnal (late) -- *att, cal, dis, fal, kau, ore, pha, (pic), pse, rad, sca, (sip), spd, (?tib)*

Anatomical Characters

Basidiospores

Ellipsoidal to bullet shaped, lacking apical beak -- *dis, ore, pha, rad, sip*

Limoniform or amygdaliform with apical beak -- *amm, ben, cal, fal, gre, kau, lil, lut, (oli), (pic), ple, pse, red, rif, ruf, sca, spd, tib*

Subglobose-limoniform with pronounced apical beak -- *att, oli, (ple), sim*

Mean length ≤ 7 µm -- *dis, ore, rad, rif, sip*

Mean length 7-8 µm -- *lil, (pse), spd, (tib)*

Mean length 8-9.5 µm -- *amm, att, ben, cal, fal, (gre), kau, lil, pic, ple, pse, ruf, sca, sim, tib*

Mean length ≥ 10 µm -- *gre, lut, oli, pha, red*

Color pale straw in KOH and appearing smooth under low power -- *dis, ore, pha, rad, sip*

Color amber to dark medium amber in KOH; ornamentation moderate and observable under low power -- *amm, ben, fal, gre, kau, lil, lut, pic, ple, red, rif, sca, spd, tib*

Color medium to dark amber in KOH; ornamentation heavy and extending beyond spore outline -- *att, cal, oli, pse, ruf, sim*

Cystidia

Cheilocystidia predominantly thick-walled and tibiiform to lageniform with refractive necks -- *cal, ple, pse, rad, ruf, sca, spd, (tib)*

Cheilocystidia predominantly thin-walled and more or less clavate -- *amm, att, ben, dis, gre, kau, lil, lut, oli, ore, pha, pic, red, rif, 'sim'*

Cheilocystidia a heteromorphic mix of thin- and thick-walled elements -- *ruf, (spd), tib*

Thin-walled cheilocystidia subcapitate -- *(ben), (dis), fal, (gre), (kau), (pha), (pic), red, sip*

Thin-walled cheilocystidia filamentous to narrowly clavate -- *amm, att, ben, dis, gre, kau, lil, pha, pic, rif, sim, sip*

Thin-walled cheilocystidia narrowly to broadly clavate -- *(fal), (kau), lil, lut, oli, ore*

Thin-walled cheilocystidia developing filamentous outgrowths in old or stored specimens -- *amm, ben,dis, gre, kau, lil, lut, oli, ore, red, sim*

Thin-walled cheilocystidia not seen with filamentous outgrowths -- *fal, ?pic, ?rif, sip*

Pleurocystidia abundant, tibiiform with refractive necks -- *ple*

Pleurocystidia occasional, filamentous with thin-walled (hyphidia) -- *(lut), rif*

Pleurocystidia absent -- *amm, att, ben, cal, dis, fal, gre, kau, lil,oli, ore, pha, pic, pse, rad, red, ruf, sca, sim, sip, spd, tib*

Pileipellis

Pileipellis two-layered -- *amm, att, ben, cal, dis, fal, gre, kau, lil, oli, ore, pha, pic, ple, pse, rad, red, rif, ruf, sca, sim, sip, spd, tib*

Pileipellis three-layered -- *lut*

Suprapellis very thin (< 20µm) -- *(att), lut, (pic), ple, sim*

Suprapellis thin, generally < 100 µm -- *att, cal, dis, lut, (pha), (pic), ple, rad, sim*

Suprapellis thick, generally > 100 µm -- *amm, ben, fal, gre, kau, lil, oli, ore, red, rif, ruf, spd, tib*

Suprapellis hyphae gel- or pigment-encrusted -- *att, cal, dis, lut, ple, ruf, sim*

Subpellis hyphae pigment-incrusted -- *cal, dis, kau, lut, ore, ple, pse, red, sim, tib*

Incrusting pigments absent from pileipellis -- *amm, (att), ben, fal, gre, lil, oli, pha, pic, rad, rif, sca, (sip), spd*

Suprapellis hyphae separated and embedded in a clear gelatinous matrix -- *amm, dis, fal, gre, kau, lil, (oli). ore, pse, red, rif,sca, sip*

Suprapellis hyphae compactly aligned and embedded in clear gelatinous matrix -- *ben, cal, (oli), ruf, spd, tib*

Suprapellis not forming a clear gelatinous matrix -- *att, lut, pha, ple, rad, sim, pic*

Clamp Connections

Abundant in pileipellis, on cheilocystidia and at basidial bases -- *amm, dis, pha, rad*

Absent from pileipellis, cheilocystidia, and basidia -- *att, ben, cal, fal, gre, kau, lil, lut, oli, ore, pic, ple, pse, red, rif, ruf, sca, sip, sim, spd, tib*

ITS Restriction Characters *-- (dis, pha, tib -- no data available)*

Cfo1 (number of restriction sites)

1 site -- *amm, ben, cal, fal, gre, kau, lil, lut, oli, pic, ple, pse, rad, red, rif, ruf, sca, sim, sip, spd*

2 sites -- *ore*

HinfI (number of restriction sites)

1 site -- *amm, att, ben, cal, fal, gre, kau, lil, oli, ore, ple, pse, rad, red, ruf, sip*

2 sites -- *lut, pic, rif, sim*

3 sites -- *spd*

PalI (number of restriction sites)

No sites -- *sip*

1 site -- *pic, sim*

2 sites -- *cal, fal, gre, lil, lut, oliA, ple, pse, rif, ruf, sca, spd*

3 sites -- *amm, att, ben, oliB, ore, rad*

4 sites -- *kau, red*

Pvu2 (number of restriction sites)

No sites -- *amm, fal, kau, (?lil), oliA, pic, rif, sip*

1 site -- *att, cal, gre, lut, oliB, ore, ple, pse, rad, red, ruf, sca, sim, spd*

Rsa1 (number of restriction sites)

No sites -- *amm, cal, fal, gre, kau, lil, lut, oli, ore, pic, ple, pse, rad, red, rif, ruf, sca, sim, sip, spd*

1 site -- *ben*

Sal1 (number of restriction sites)

No sites -- *amm, ben, cal, fal, gre, kau, (lil), oli, ore, ple, pse, rad, red, ruf, sca, sip*

1 site -- *lut, pic, rif, sim, spd*

Xho1 (number of restriction sites)

No sites -- *amm, ben, cal, fal, gre, kau, lil, lut, oli, ore, pic, ple, pse, rad, red, rif, sca, sim, sip, spd*

1 site -- *ruf*

Species Descriptions

Phaeocollybia ammiratii nom. prov.

Figures: 6.1-2

Selected descriptions and illustrations: Smith, 1949 (as *P. kauffmanii)* -- stereoscopic color transparency.

General Impression: moderately large, fleshy, farinaceous deeply rooting basidiomes with viscid brownish yellow to butterscotch-scotch colored convex (inrolled) to broadly campanulate (incurved) pilei, orange creamy young lamellae, vinaceous-tinged ventricose to equal stuffed stipes, vertical monopodial pseudorhizae, ~9 x 5.5 µm verrucose limoniform basidiospores with subdued beaks, thin-walled cylindrical cheilocystidia, bilaminate pileipellis with suprapellicular hyphae loosely embedded in a colorless gelatinous matrix above an orange subpellis, and clamp connections. Pseudorhizal rind slowly magenta in syringaldazine. Dried pileus metallic copper.

Pileus 40-80 (115) mm, convex with tightly inrolled edges expanding to broadly campanulate with low frequently papillate umbo and incurved to straight edges, glabrous, viscid to glutinous when wet, opaque, non-striate, when young overall dingy brownish yellow to pale butterscotch *(Antimony Yellow, Isabella Color, Ochraceous Tawny -- 10 YR 4-5/6-8)* or distinctly zonate with dark reddish brown disc *(Russet, Verona Brown -- 5 YR 3-4/4-8)*, paler outer margin *(Tawny, Sayal Brown, Amber Brown -- 5YR 4-5/7-9)*, and pale yellowish-brown edge *(Buckthorn Brown -- 10 YR 4-5/6-7)*, becoming ±

uniformly tawny to butterscotch-colored in maturity, dried pileus generally a distinctly metallic bright orange-brown copper; Context: 3-8 (12) mm thick at the disc, very pale pinkish to yellowish white *(Pale Pinkish Cinnamon -- 10 YR 7-8/2)*, when wet often developing a 1-3 mm wide dark brown band at the lamellar/pileus interface; **Context:** 3-8 (12) mm thick at the disc, very pale pinkish to yellowish white; **Odor** distinctly cucumber-farinaceous when cut or crushed; **Taste** somewhat unpleasant and often bitter, reminiscent of bitter cucumbers;

Lamellae ascending, free to narrowly attached, ventricose, thin with ± even young edges soon becoming serrulate, lamellulae in 3-7 irregularly intermixed tiers, narrow and crowded when young, broader (to 10 mm) and close in mature specimens (mean length : width ratio 3.3-6.3 with 11-30 L+l/cm at the edge and 9-20 L+ll at the midpoint), orangish cream *(Light Ochraceous Buff, Cream Buff, Cinnamon Buff, Pale Pinkish Buff -- 2.5 Y 6-8/2-6)* when young, orange tones later obscured by pinkish cinnamon brown spores;

Veil occasionally evident as fibrillose patches on aerial stipe or young pileus edges;

Stipe central to eccentric, usually 25-60 (105) mm above ground level with 6-15 (18) mm wide apex, overall length including pseudorhiza reaching 300 mm or above, swollen and ventricose when immature, ± equal to ground level when mature, appressed fibrillose under hand lens with occasional detached fibrils on the aerial portion, longitudinally lined, dry, apex generally concolorous with gills, pale creamy or pinkish white *(Vinaceous Cinnamon, Ochraceous Buff, Light Pinkish Cinnamon -- 7.5 YR 6-8/4-8)* when young, becoming more orange in age, below grading to tawny at ground level and characteristically with a dingy vinaceous tinge above and below insertion point *(Mikado Brown, Kaiser Brown, Fawn Color, Cinnamon Drab -- 5YR 4-6/1-6)*, stuffed with 2-4 mm thick cartilaginous rind surrounding firm pale creamy to pale pinkish white *(Pale Pinkish Cinnamon, Chamois -- 7.5YR 8/2)* stipitipith, dried stipes distinctly burgundy-colored;

Pseudorhiza vertical-monopodial, generally 2/3-5/6 of overall stipe length, gradually tapering to a fleshy narrow straight or loosely coiled blunt origin, vinaceous to tawny-colored over-all becoming pale buff to salmon at the origin.

Spore Print pale cinnamon brown *(Pinkish Cinnamon (7.5 YR 6/4-6)*.

Basidiospores 9 x 5.5 ± 0.3 x 0.4 µm (overall range 8.4-9.2 (10) X 5-6 (6.5) µm), terete or slightly compressed, amygdaliform to limoniform with subdued to pronounced apical beak in profile, fusoid-elliptical in face view, verruculose to verrucose except on 1-1.5 µm long mammiform beaked apex and eccentric apiculus, suprahilar plage an area of decreased ornamentation barely visible in oil immersion, more noticeable in SEMs, pale to

medium dark amber or orange-amber in KOH, paler in H_2O, weakly dextrinoid in Melzer's;

Cheilocystidia cylindrical to narrowly clavate, thin-walled, abundant, emanating from the lamellar trama and forming a distinct gelatinous barrier, 2-5 µm wide with apex usually only slightly swollen, lengths developmentally variable from very short to >45 µm long, with medallion-like clamp connections often visible, heavily gelatinized, usually hyaline (occasionally with pale yellowish oily contents), often developing long filamentous apical outgrowths in extreme age or after long storage;

Pleurocystidia absent;

Basidia usually 4- but sometimes also 2-spored, projecting up to 10 µm above developing hymenium, tight clusters of basidia and basidioles often obscuring basal clamp connections, 29-35 (40) X 7-8 µm, hyaline;

Pileipellis a bilaminate ixocutis with a 150-400 µm thick suprapellis composed of radially aligned cylindrical narrow (3-5 µm) hyaline hyphae with medallion-like clamp connections loosely embedded in a clear gelatinous matrix overlying a moderately thick (120-300 µm) orange subpellis of 5-12 µm wide inflated hyphae with intercellular and intraparietal pigments; **Stipitipellis** a 200 µm thick layer of parallel long branched cylindrical highly gelatinized thick-walled brownish hyphae; **Pseudorhizal pellis** similar to the stipitipellis with abundant tibiiform diverticula emergent from external hyphae;

Tramal tissues gelatinized, strongly sarcodimitic in the pseudorhiza and predominantly consisting of wide thick-walled rigid cylindrical hyphae surrounded by less conspicuous thin-walled branched flexuous hyaline hyphae that become gradually more numerous toward the stipe apex, the rigid elements becoming narrower and thinner-walled, with most hyphae in the pileus distorted and more or less thin-walled; Lamellar trama parallel, with 2-10 µm wide thick-walled hyphae in the central region narrowing to 2 µm at the edges to form a compact rudimentary hymenium (thin-walled narrow branched flexuous hyphae also occasionally present);

Tibiiform diverticula abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex, 4-20 x 0.5-1 µm, hyaline and highly refractive with no septum between base and hyphae, with or without slightly larger ligulate to subglobose capitellum and/or apical droplet;

Clamp Connections frequent to abundant, medallion-like and readily visible on suprapellicular hyphae and cheilocystidia, present but less visible at basidial bases; also present in tramal tissues and stipitipellis.

Macrochemical Reactions: syringaldazine -- generally only pseudorhizal cuticle weakly reactive (slightly magenta after 30 minutes); KOH -- no change to slightly browning; FeSO4 -- greenish.

Fluorescence: lamellae intense whitish yellow in young basidiomes, becoming less intense as spores obscure lamellar faces during maturation.

RFLP profile ITS region for 13 isolates including type = 715 bps. Pal1 (400-225-90) most informative enzyme. Also cut in Cfo1, EcoR1, Hinf1, and Nde2. Uncut in Pvu2, Rsa1, Sal1, and Xho1.

Ecology: Solitary to clustered in the early autumn in humid coastal and inland regions, usually in mixed coniferous (*Picea, Tsuga, Abies)* forests, occasionally in mixed deciduous-coniferous (*Pinus, Lithocarpus, Pseudotsuga*).

Range and distribution: Collected from 21 different sites from southern British Columbia, Washington, Oregon and northern California coastal and montane regions.

Type: LLN 94.10.28-10 (WTU) on October 28, 1994 by L.L. Norvell and J. Roger, Wildcat Mountain, Mt. Hood National Forest, Clackamas County, Oregon. Elevation 3100'.

Comments: *Phaeocollybia ammiratii* is similar to and has previously been confused with the more robust *P. kauffmanii* and can be with difficulty differentiated in the field by its slightly more fragile stature, straight to only slightly inrolled mature pileus edges, and characteristic purplish vinaceous 'bloom' over the lower aerial stipe. The pseudorhizal pellis is the only portion of the basidiome which appears mildly reactive to syringaldazine (developing subdued magenta tones after 30 minutes); this mild reaction distinguishes it *P. redheadii, P. benzokauffmanii,* and *P. kauffmanii* which produce basidiomes with tissues that turn brilliant magenta almost immediately. Young ochraceous yellow forms of *P. ammiratii* can also be confused in the field with *P. luteosquamulosa* (the fifth member of the *P. kauffmanii* complex) which is distinguished by a dry to barely moist appressed fibrillose pileus, lack of tawny brown tones in mature specimens, and negative syringaldazine response.

Phaeocollybia ammiratii is clearly separated from the rest of the complex microscopically by the presence of frequent to abundant clamp connections that are particularly noticeable on the irregularly cylindrical cheilocystidia and narrow hyaline hyphae in the suprapellis. The distinctive Pal1 RFLP pattern clearly separates *P. ammiratii* from all other tested *Phaeocollybia* species. The occurrence of clamp connections (first noted by Dr. Joe Ammirati in the early 1970s) fueled a growing suspicion that there was a complex of species hiding under the name *P. kauffmanii.* Six collections cited by Smith in his 1957 monograph as belonging to *P. kauffmanii* (Gruber-700, A.H. Smith 3727 *p.p.*, 17545, 19467, 20173, 49479 -- all MICH) are now assigned to *P. ammiratii,* which is only one of two species from Pacific Northwest North America characterized as having large spores and clamp connections.

Of the twenty-two other species characterized by clamp connections, thirteen produce smaller or differently shaped basidiospores, one is characterized by thick-walled tibiiform capitate cheilocystidia, and four produce very small fruiting bodies. One species characterized by clamp

connections, originally described as *P. deceptiva* (Smith & Trappe, 1972), lacks the characteristic tibiiform diverticula, gelatinized pileipellis, cartilaginous stipe cortex, and true cheilocystidia and more properly belongs in *Cortinarius*.

Two remaining species -- *P. amazonica* Singer (1961) and *P. oligoporpa* Singer (1987) -- share certain characters with *P. ammiratii*. However *P. amazonica* is described as having distinct striations over 1/4 of its pileus, a narrower hollow stipe that attentuates suddenly (not gradually) at the pseudorhiza, a non-gelatinized cutis, smaller (8.2 X 4.8 µm) and less ornamented basidiospores , and much shorter (17 µm) basidia (Singer 1961).

Examinations made of *Phaeocollybia oligoporpa* (the Costa Rican type and two Columbian collections, *cf.* Horak & Halling, 1991) reveal close similarities with *P. ammiratii*. The overall stature of the type of *P. oligaporpa* is quite similar to that of *P. ammiratii;* additional similarities include bitter taste, watermelon-like to farinaceous odor, pseudorhizal morphology, and cap color (*Cf.* Singer, 1987; Horak & Halling, 1991; Bandala & Montoya, 1994; Bandala, 1994). However the pilei dry blackish to dark purplish red (not metallic copper) and the spore print is a much darker brown (*Sayal Brown).* Association with *Quercus humboldtii,* the presence of a comparatively thin (100 µm) ixocutis and the absence of an embedding gelatinous matrix, presence of incrusting pigments in the pileipellis, larger (10 X 6 µm) and less highly ornamented spores, and more variably clavate cheilocystidia are more significant differences. Additionally in *P. oligoporpa* clamp connections are found in the suprapellis only rarely. The 'highly heteromorphic' cheilocystidia are not as variable as it would appear from reading Singer's description. Most of the variability appears to be a developmental artifact caused by extended storage of the basidiomes before drying. The two Colombian collections appear to differ slightly from the type of *P. oligoporpa* : in R.E. Halling 6165 clamp connections, apparently absent from the more uniformly shaped cheilocystidia and suprapellicular hyphae, are found only at basidial bases, while the variable cheilocystidia in R.E.Halling 6137 are similar to those of the type (in some instances appearing to break into arthrospores), but clamp connections are rare and the suprapellicular hyphae more cohesive.

This species is named in honor of Dr. J. F. Ammirati, who first noted the presence of a *P. kauffmanii*-like species with clamp connections in the Pacific Northwest.

Phaeocollybia attenuata (A. H. Smith) Singer, *Lilloa* 22: 567. 1951
= ***Naucoria attenuata*** A. H. Smith, *Mycologia* 29: 48. 1937.
Emended

Figures: 2.5, 6.3-4

Selected descriptions and illustrations: Smith, 1937 -- type description with black and white photograph; Smith, 1957 -- amended description with black and white photograph and anatomical drawings; Horak, 1977 -- anatomical drawings; Norvell, 1997 -- black & white photographs and line drawings; Phillips, 1991 -- color photograph as *P.similis;*

General impression: small cartilaginous scattered to gregarious rooting basidiomes with moist to subviscid orange-brown to tawny campanulate pilei, pale pinkish buff to caesius young lamellae, pale to dark brown slender cartilaginous (when young) to corneous shiny fibrillose-stuffed to hollow stipes, blackish lateral-monopodial criniform pseudorhizae, ~9 x 5.8 µm warty subglobose-limoniform basidiospores with pronounced apical beaks, narrowly clavate thin-walled cheilocystidia, a bilaminate pileipellis with a thin yellowish suprapellis containing gel-incrusted hyphae overlying a thicker gelatinized orange-brown subpellis, and no clamp connections. Negative in syringaldazine.

Pileus 15-50 mm broad, narrowly to broadly conic-campanulate with incurved outer margin and edge, often with acute papillate umbo when young, moist to lubricous, glabrous, hygrophanous, edge rarely striatulate; color either uniformly brownish orange (*Clay Color, Amber Brown, Ochraceous Tawny)* or zonate with slightly darker brown disc (*Warm Sepia, Tawny, Sayal Brown, Buckthorn Brown),* yellow- to orange-brown margin (*Antimony Yellow, Clay Color, Snuff Brown, Pinkish Buff)* and paler yellow brown edge *(Tawny Olive, Buckthorn Brown)*; **Context** 1-2 mm thick, cartilaginous pliant, at first pallid (*Cream Color, Straw Color),* becoming duller and darker with age *(Tawny Olive, Mustard Yellow)*; **Odor** variably strong to not distinctive, raphanoid, slightly fishy smelling, or strongly floral (like pansies) with complex undertones (similar to boiled potatoes or burnt hair *['gebrenzlich']*); **Taste** slightly to strongly disagreeable, often bitter;

Lamellae attached by decurrent tooth, nearly free in age, 2-4 mm broad, equal to ventricose, when young subdistant, becoming close to crowded in age, edges even to slightly uneven, lamellae polydymous with 3-7 lamellulae irregularly interspersed, color pinkish buff to lilac-colored when young (*Light Pinkish Cinnamon, Pale Pinkish Buff, Pale Vinaceous Drab, Light Pinkish Lilac),* becoming moderately pinkish brown during maturation *(Pinkish Buff, Cinnamon Buff, Vinaceous Cinnamon, Pale Vinaceous Fawn, Vinaceous Buff)* and finally dark orange brown in age *(Clay Color);*

Veil when seen frequently evident as sparsely distributed short fibrillose patches on the stipe apex;

Stipe central to slightly eccentric, 2-5 mm wide at the apex, up to 70 mm long above ground level, overall length (including pseudorhiza) up to 220 mm long, equal, polished, cartilaginous when young and palest, soon corneous after darkening, initially stuffed with densely compacted to loose fibrillose pith and becoming hollow in age, at first overall pale yellowish brown *(Ochraceous Buff, Cinnamon Brown, Pale Pinkish Cinnamon)* but gradually becoming ferruginous from ground upwards, with narrow deep orange brown

(Mikado Brown) band separating the pale yellowish brown apex from darker lower portion until entire stipe becomes dark reddish brown (*Liver Brown, Hay's Russet*);

Pseudorhiza lateral-monopodial, cartilaginous upper portion continuous with the reddish brown lower stipe and gradually tapering below to thin, brittle (criniform) brownish-black rhizomorphic pseudorhiza, wire-like portion frequently with lateral bend below cartilaginous portion;

Spore Print deep reddish brown (*Hay's Brown, Cameo Brown-- 10R 3/2).*

Basidiospores 9 x 5.75 ± 0.5 x 0.3 µm (range (7) 8-10 x 4.5-7 µm), broadly ovate to amygdaliform in face view, subglobose-limoniform to sublimoniform in profile with a short narrow eccentric apiculus and prominent central apical beak, the beak either abruptly delimited from the body and up to 2 µm wide and 2 µm long or gradually tapered and pointed; ornamentation rugulose-warty except over the smooth apiculus and beak, the suprahilar plage an ill-defined area of lowered ornamentation, perisporium often loosened in KOH, the dark brown rugulose ornamentation easily distinguished from tawny ground under low magnification in KOH;

Cheilocystidia frequent to occasional, filamentous to narrowly clavate, emanating from the lamellar trama and variable in length (usually 20-30 µm long), gradually expanding to 3-5 (6) µm above 2.5-3 µm wide septa, thin-walled, smooth, hyaline to pale yellowish in KOH, highly gelatinous individual elements easily separating in fresh mounts but forming a yellowish agglutinated barrier when revived in KOH, isolated thick-walled capitulate elements rarely intermixed;

Pleurocystidia absent;

Basidia 4-spored; 25-35 x 5-7 µm, hyaline;

Pileipellis a bilaminate ixocutis with a thin (25-50 µm) suprapellis composed of radially aligned long (40-60 µm) narrow (1-2 µm) gel-incrusted hyaline to pale orange-yellow hyphae overlying a much thicker (100-300 µm) pale to dark orange-brown subpellis of inflated (4-8 µm wide) subgelatinous hyphae with intraparietal pigments; **Stipitipellis & pseudorhizal pellis** composed of 5-9 µm highly gelatinized hyphae, pale orange brown near apex or 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 (up to 20 µm) thick-walled (up to 3 µm) rigid hyphae are surrounded with numerous less conspicuous thin-walled branched flexuous hyaline 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 µm wide) gelatinized hyphae with slightly thickened walls; Lamellar trama subparallel, with central 2.5-4 µm wide hyaline hyphae

continuous with cheilocystidia and two to three outermost 1-2.5 µm wide yellowish hyphae giving rise to a rudimentary subhymenium;

Tibiiform diverticula abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex; rarely present on pileipellis;

Clamp Connections absent.

Macrochemical reactions: Syringaldazine: negative; KOH: reactions not noted; FeSO4: pale to dark greenish gray;

Fluorescence: young lamellae -- intense whitish yellow;

RFLP profile: preliminary ITS region for 5 isolates = 735 bps (DNA from holotype too degraded for RFLP analysis); Distinctive runs HinfI 390-345 bp; PalI -- 460-95-95-86 bps; also cut in CfoI, EcoRI, Nde2, Pvu2; uncut in RsaI, SalI, and XhoI.

Habit and ecology scattered to closely gregarious from mid to late autumn in highly humic soils in moist coniferous *Picea sitchensis, Tsuga heterophylla, Abies)* or mixed deciduous-coniferous (*Sequoia, Tsuga, Lithocarpus*) forests;

Range and distribution restricted to low-lying low coastal regions in Washington, Oregon and California.

Type A. H. Smith 3343 (MICH) -- October 2, 1935, Quillayute River near La Push (Clallam County), Washington.

Comments: *P. attenuata* is easily distinguished from all except *P. similis* by its small size, moist tawny pileus, thin shiny tough brown cartilaginous to corneous stipe, dark brown brittle thin rhizomorphic-pseudorhiza, and large rough subglobose-limoniform basidiospores. In the field, its small size and tawny coloration separate it from all other Pacific Northwest Phaeocollybias except *P. radicata, P. pleurocystidiata,* and *P. 'similis' sensu* Smith. *P. radicata,* which can be distinguished with difficulty in the field by its dull yellowish young lamellae and slightly more fragile stipe with a narrow vertical-monopodial non-criniform pseudorhiza, produces very small, almost smooth ellipsoid basidiospores and thick-walled tibiiform capitulate cheilocystidia. *P. pleurocystidiata* is distinguished macroscopically by its ochraceous yellow conic-convex pileus, more fleshy and less corneous stipe, vertical monopodial non-criniform pseudorhiza, and vernal fruiting habit. It is microscopically easily distinguished by its abundant thick-walled capitulate pleurocystidia and cheilocystidia and narrower basidiospores.

Differentiation between *P. attenuata* from *P. 'similis' sensu* Smith is more difficult. Smith (1957) based his concept of *P. similis* in part on his collection from Mt. Rainier which had longer broader spores than *P. attenuata* and exhibited a greater tendency for the basidiomes to become ferruginous in age. Smith & Trappe (1972), in their revised key to North American Phaeocollybias, cited differences in stipe and spore widths. Current microscopical comparisons of

nine *P. attenuata* type specimens to the Mt. Rainier *P. 'similis'* specimens, however, reveal little discernible difference in basidiospore size and shape. More phylogenetically informative is a molecular difference between topotypical material representing *P. attenuata* and *P. similis*. Although DNA from either of the Smith collections was not successfully amplified, it was sampled from topotypical material. Comparison of the PCR-amplified products shows a 20-bp length mutation separating one group of 5 isolates (including topotypical material of *P. attenuata*) from a second group of 5 isolates (including topotypical' material of *P. 'similis' sensu* Smith).

Comparison of the types and DNA-tested specimens show that basidiomes identified as *P. attenuata* appear to be slightly large in size, often have a more acute to papillate pileus with incurved outer margin (versus a broadly campanulate pileus with straight margin and low broad umbo in *P. 'similis'*), lack ochraceous tones in young specimens, often produce caesious to lilaceous lamellae, appear restricted to low coastal regions, and are frequently associated with spruce. Microscopically, in *P. attenuata* the young subpellis is brownish orange and not orange-yellowish, and the clavate cheilocystidia appear to lack the dense amber colored contents characteristically found in the *P. 'similis"* vouchers. Although it is true that this length mutation may merely indicate populational or strain differences, in view of these admittedly subtle distinctions, the two taxa are provisionally recognized as separate. (See also Comments under *P. similis).*

Phaeocollybia benzokauffmanii nom. prov.

Figures: 2.3-2.4; 6.5-6

Selected descriptions and illustrations: Norvell, 1997 -- SEM micrograph, black & white photograph of primordium;

General impression: Large fleshy farinaceous closely gregarious deeply rooting basidiomes with glutinous pinkish- to purplish-brown convex deeply inrolled convex to campanulate pilei, dry pale pinkish or grayish-white young lamellae, pale pinkish to drab stuffed stipes, relatively thick blunted vertical monopodial pseudorhizae, ~9 X 5.5 µm verrucose limoniform basidiospores with moderate apical beaks, thin-walled filamentous to occasionally subcapitate cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae tightly compacted in a dense gelatinous matrix overlying a dull-orange-brown subpellis, no clamp connections. Immediately deep magenta in syringaldazine. Dried pileus usually carbonized matte black.

Pileus 40-145 mm wide, convex to plano-umbonate with broad umbo, incurved margin and strongly inrolled edge at all stages of development, glabrous, smooth, opaque, non-striate heavily glutinous, either overall a mixture of various shades of pinkish to purplish brown *(Benzo Brown, Cinnamon Drab, Wood Brown, Avellaneous, Fawn Color, Army Brown,*

Natal Brown -- 5YR 3-5/2-5), or zonate with differentiated disc *(Benzo Brown, Cinnamon Drab, Fawn Color -- 5YR 4-5/2-5)*, margin *(Benzo Brown, Cinnamon Drab, Light Brownish Drab, Verona Brown -- 5YR 3.7-5/2-4)*, and generally paler edge *(Army Brown, Cinnamon Drab, Dark Vinaceous Drab, Light Drab, Pale Brownish Drab -- 5YR 4-5/2-3.5; Light Drab -- 10YR 6/2)*, damaged spots and patches dark blackish brown to black, dried pileus generally overall matte charcoal black, or carbonized black at the disc with dull orange-brown margin; Context firm and confluent with stipe pith, up to 11 mm thick at the disc, purplish or pinkish white *(Light Drab, Light Cinnamon Drab, (Pale) Pinkish Buff, Cartridge Buff -- 5YR 6/4, 1.25Y 7-8/1-2)*, when water-soaked darker overall *(Drab, Light Vinaceous Cinnamon)* and often with a distinct 1-3 mm wide dark zone separating the pilear-lamellar interface; **Odor** slightly floral or sweetly farinaceous; **Taste** farinaceous or reminiscent of bitter cucumbers;

Lamellae ascendant, free or attached by a small narrow tooth, occasionally forking, ventricose with uneven edges, polydymous with lamellulae irregularly interspersed in 5-7 tiers, broad (up to 15 mm, with length:width ratio 1.9-6 [mean = 3.1]), crowded (edge: 17-28 L+ll/cm; midpoint: 7-14), white to pinkish or grayish white when very young *(Pale Pinkish Buff, Light Pinkish Buff, Tilleul Buff, Pale Drab Gray -- 10YR 7-8/1)*, developing smoky drab tones as maturing *(Vinaceous Buff, Avellaneous, Pinkish Buff, Light Drab, Drab -- 10YR 5-7/2-4)*, and dark yellowish gray in age *(Tawny Olive, Wood Brown, Isabella Color, Saccardo's Umber, Buckthorn Brown -- 10YR 4-5/4-7)*;

Veil occasionally evident as fibrillose patches on aerial stipe;

Stipe central to slightly eccentric, terete or slightly compressed, aerial portion usually 35-100 mm tall above ground level with 7-23 (30) mm wide apex, overall length including pseudorhiza up to 250 mm, either equal or slightly tapering downwards or ventricose and swelling to 28 (42) mm at ground level, appressed fibrillose under hand lens and occasionally covered with sparsely distributed darker purplish-brown fibrillose patches on the aerial portion, longitudinally lined, dry, apex pinkish- or purplish grey *(Buff Pink, Cinnamon Drab, Fawn Color, Light Cinnamon Drab, Light Vinaceous Fawn, Vinaceous Buff, Vinaceous Cinnamon, Vinaceous Fawn -- 5YR 5-6/3-5)* darkening below to deep purplish or reddish brown *(Army Brown, Benzo Brown, Bone Brown, Cinnamon Drab, Fawn, Hay's Brown, Hessian Brown, Liver Brown -- 5YR 3-5/2-4, 10R 2.5-3.5/3-5)*, stuffed with 2-3 mm thick cartilaginous rind occasionally splitting longitudinally revealing the proliferating firm whitish to pinkish white *(Light Pinkish Cinnamon, Cartridge Buff, Pinkish Buff, Pale Pinkish Buff -- 10YR 7-8/2-3)* pith that develops dark cartilaginous intrusions and stains dark brown to black where bruised (*Cinnamon , Verona Brown, Cinnamon Buff, Fuscous Black -- 7.5YR 5-6/6-7, 5YR 2-4/1-4);*

Pseudorhiza vertical-monopodial, generally 1/2-2/3 of overall stipe length, gradually tapering to a fleshy blunt or loosely curled origin, overall deep reddish brown *(Hazel,*

Hay's Brown, Liver Brown -- 10R 2-4/3-5) or paler *(Cinnamon Buff, Warm Buff -- 10YR 6-8/5-6)* at the origin;

Spore Print pale purplish to dull yellowish brown *(Drab to Buckthorn Brown -- 10YR 5/6).*

Basidiospores 9 X 5.5 ± 0.3 µm (overall range 8.2-10 X 5-6 µm), terete or slightly compressed in end view, fusoid-elliptical in face view, sub-limoniform in profile view, verruculose to verrucose except on 0.5 µm long beaked apex and distinct eccentric apiculus, medium amber in KOH, paler in H_2O, dextrinoid in Melzer's;

Cheilocystidia abundant, emanating from the lamellar trama in a dense highly gelatinous barrier forming an unpigmented gill edge visible to the naked eye, thin-walled, hyaline, lengths developmentally variable, thin-walled, pedicellate narrowly and broadly clavate elements intermixed, with apices ranging from predominantly 3 µm across (when young) to 5-7 µm (when fully mature) above long 2-3 µm wide pedicels, often with long filamentous apical outgrowths in extreme age or after long storage;

Pleurocystidia absent;

Basidia 4-spored, 27-38 X 6-7.5 µm, clavate above long 2 µm-wide pedicel, projecting up to 5 µm above basidioles and younger basidia, hyaline, granular when young, vacuolate when mature;

Pileipellis a bilaminate ixocutis with a thick (100-300 µm) suprapellis composed of radially aligned sparingly branched cylindrical narrow (3-5 (6) µm) highly gelatinized hyaline hyphae tightly compacted in a thick gelatinous matrix overlying a narrower (50-100 µm) dull orange brown subpellis of slightly thick-walled heavily gelatinized 5-8 µm wide hyphae with intracellular pigments; **Stipitipellis** a 70-150 µm thick layer of parallel highly gelatinized long sparingly branched thick-walled cylindrical narrow (2-3 µm) hyaline to dark brown hyphae with highly refractive septa; **Pseudorhizal pellis** similar to stipitipellis with outermost hyphae densely covered with tibiiform diverticula;

Tramal tissues highly gelatinized and colorless, strongly sarcodimitic in the pseudorhiza and stipe with long thick-walled (up to 2 µm) wide (up to 30 µm) cylindrical and slightly fusoid hyphae supported by less conspicuous highly branched thin-walled (0.5 µm) narrow (2-4 µm) flexuous hyphae that widen slightly (up to 6 µm) and become more numerous toward the stipe apex, with the rigid elements becoming slightly thinner-walled (to 1 µm) and not present in the pileus. Lamellar trama parallel, with long thin-walled gelatinized 2-3 (5) µm wide hyaline hyphae in the central region narrowing to 2-3 µm on the edges to give rise to a rudimentary subhymenium;

Tibiiform diverticula: abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex;

Clamp Connections absent in all tissues.

Macrochemical Reactions: syringaldazine -- immediately deep magenta overall; KOH -- dull brown.

Fluorescence: young lamellae -- intense pale yellow; pileus edges -- purple.

RFLP profile ITS region of 5 isolates (including type) = 715 bps. Unique in Rsa1 (630-85); Pal1 (450-105-90-70) and Pvu2 (625-90) other informative enzymes. Also cut in Cfo1, EcoR1, Hinf1, Nde2; uncut in Sal1 and Xho1.

Habit and ecology: gregarious, originating at the albic horizon in podzolic sandy or humic soils in ancient or mature second-growth mesic mixed closed canopy coniferous forests in early to mid-autumn.

Range and distribution: Uncommon to rare in coastal and inland regions; collected from 8 different sites from Washington, Oregon, and northern California coastal forests.

Type: LLN 92.11.20-1**ben1** (WTU) on November 20, 1992 by L. L. Norvell and S. A. Redhead, Van Damme State Park (123.7°W,39°N), Mendocino County, California.

Comments: Mistaken for *P. kauffmanii* by earlier collectors, the generally more massive basidiomes of *P. benzokauffmanii* are found in similar habitats and have equally narrow to moderately clavate cheilocystidia, large limoniform spores, and lack clamp connections. The distinctive massive convex glutinous pileus with its low broad umbo and whitish to pinkish grey young lamellae distinguish *P. benzokauffmanii* in the field from other members of the *P. kauffmanii* complex. (Basidiomes of *P. redheadii* can, however, develop similar purplish brown tones on the pileus when exposed to frost or drying or when under attack by moulds.) Microscopically very similar to *P. kauffmanii*, this newly named taxon has slightly longer and broader spores, slightly broader (often collapsing) more closely cohesive suprapellicular hyphae, and no incrusting pigments in the cutis. Within the *P. kauffmanii* complex, *P. benzokauffmanii* produces the only ITS region digested in Rsa1.

Only nine other published *Phaeocollybia* species have remotely similar coloration of pileus and gills, and of those only *P. gregaria* shares enough morphological and anatomical characters to be considered close. *Phaeocollybia gregaria* was first described from the Cascade Head Experimental Forest (Smith & Trappe, 1972) where *P. benzokauffmanii* has also been collected. *Phaeocollybia gregaria* basidiomes also are produced in tightly gregarious clusters, have moderately large (30-60 mm wide) pilei and 8-15 mm thick stipes) and similarly colored (*Wood Brown* "slimy" pilei with grayish pallid lamellae), produce similarly sized (9-11 X 5.5-6 µm) and shaped basidiospores, and lack clamp connections. However the older named taxon produces basidiomes with conic shaped pilei, contexts described as being "thin and cartilaginous pliant", a taste described as never bitter, and -- most importantly -- very distinctive long, irregular filamentous cheilocystidia (Cf. *Figure 6.12).* RFLP profiles differ completely. The dried type

specimens of *P. gregaria* appear more fragile than dried *P. benzokauffmanii* basidiomes and have acutely pointed, brassy-colored metallic pilei with longitudinally splitting stipes.

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

Figures: 6.7-8

Selected descriptions and illustrations: Smith, 1957 -- type description with black&white photograph and anatomical drawings; Arora, 1981 -- color photograph; Bandala, Guzmán & Montoya, 1989 -- habit and anatomical drawings; Bandala, 1994 -- habit and anatomical drawings with SEM micrographs; Horak, 1977 -- anatomical drawings.

General impression: Densely gregarious moderately sized, slightly pungent cartilaginous deeply rooting basidiomes with viscid yellowish brown to brownish orange expanded campanulate pilei, whitish to pale orange buff young lamellae, slender smooth watery tan to orange buff polished hollow stipes with relatively thick cartilaginous cortices, sequential-racemose thread-like pseudorhizae, ~9 x 5 µm warty-rugulose limoniform spores with pronounced apical beaks, thick-walled tibiiform cheilocystidia with refractive necks and secretory capituli, a bilaminate pileipellis with a moderately thin yellowish suprapellis containing narrow hyphae spirally incrusted with hyaline gel or very pale amber pigments overlying a thin dull brownish-orange subpellis, no clamp connections. Untested in syringaldazine. Dried pileus a metallic yellow copper.

Pileus (20) 30-80 mm, conic when young, soon campanulate with low broad umbo (occasionally also with minute acute papilla with down-turned inner margin and inrolled edge or outer margin strongly uplifted in age with slightly incurved edge), glabrous, viscid, hygrophanous, faintly striatulate, when young yellowish brown to pale brownish orange *(Amber Brown, Ochraceous Orange)*, in age becoming uniformly reddish brown *(Sayal Brown through Cinnamon Brown)*, brassy copper metallic when dried; **Context** whitish in central disc, cartilaginous and concolorous with cuticle elsewhere, staining reddish when bruised or cut; **Odor** slightly tart (similar to chlorine when old) or pungent (particularly in age); **Taste** not distinctive, slightly raphanoid, slightly bitter;

Lamellae ascending, nearly free to attached, ventricose, thin with even, uneven, or wavy edges, crowded, regularly to irregularly polydymous, narrow to broad, initially whitish to pale orange buff *(Orangish Buff, Cinnamon Buff)* becoming cinnamon-colored *(Cinnamon, 7.5 YR 5/6)* before turning rusty brown in age;

Veil evident as more or less sparse reddish fibrils (scattered or in fibrillose patches) on stipe apex;

Stipe ± central, usually 40-90 mm above ground level, overall length >200 mm, apex generally 6-10 (15) mm wide, ± equal, polished beneath fibrillose patches, apex watery tan to pale pinkish brown *(Pinkish Buff, Pale Ochraceous Salmon, Cinnamon)*, soon becoming ferruginous from base up, drying dark bay-brown, hollow with thick (2-3 mm) cartilaginous cortex surrounding central cavity lined with whitish long fibrils below solid pileus context;

Pseudorhiza ?racemose, of undetermined length, gradually tapering to a long narrow cord or thread, dark bay-brown to liver brown;

Spore Print Color reddish brown (close to *Sayal Brown*);

Basidiospores 9 x 5 ± 0.5 x 0.4 µm (overall range = 8-10 x 5-6 µm), limoniform (inequilateral) in profile with eccentric short apiculus and short beak, ovate with short apical beak in face view, rugulose-roughened to warty except over 0.5-1 µm long apical beak, suprahilar plage an ill-defined zone of lowered ornamentation; in KOH tawny to rusty-brown with ornamentation distinctly darker especially at low magnification, inamyloid and nondextrinoid in Melzer's;

Cheilocystidia 20-30 x 2-5 (base), 1.5-2 (neck), 2.5-3 (capitellum) µm, sparsely distributed lageniform to capitulate tibiiform elements with narrow, distinctly refractive necks frequently surrounded by apical secretory droplets, necks frequently bent over making elements difficult to locate, also frequently obscured by surrounding clavate elements (basidioles?), hyaline or with oily amber contents beneath the refractive neck walls;

Pleurocystidia absent;

Basidia 4-spored; 30-35 x 7-8 µm;

Pileipellis a bilaminate ixocutis with a relatively thin (50-100 µm) suprapellis composed of radially aligned narrow (1-4 µm) gelatinized hyaline cylindrical hyphae roughened by concentric hyaline to very pale brownish pigments overlying a dull orange to brown subpellis of inflated thick-walled hyphae with intraparietal pigments; **Stipitipellis** a 50-100 µm thick layer of parallel, highly gelatinized, narrow (2-4 µm), thick-walled cylindrical hyphae over increasingly wider hyphae;

Tramal tissues highly gelatinized, sarcodimitic in the pseudorhiza and lower stipe with wide (up to 30 µm) thick-walled (up to 3 µm) cylindrical rigid yellowish hyphae supported by less conspicuous branched thin-walled (below 0>5 µm) flexuous hyphae, with both hyphal types also present in the pileus but with the rigid hyphae with thinner (1 µm) walls narrowing to 5-10 µm diam; Lamellar parallel, composed of highly gelatinized 4-6 µm wide slightly thick-walled pale amber hyphae with refractive septa and intraparietal pigments giving rise to a 10 µm thick subhymenium (slightly more complex than most other Pacific Northwest Phaeocollybias);

Tibiiform diverticula: abundant on pseudorhizal pellis, occasional on fibrillose pellicular veil remnants on stipe apex;

Clamp Connections absent.

Macrochemical reactions untested.

RFLP profile Data from 2 isolates (including type) shows the 700 bp ITS region identical with that of *P. scatesiae;* Hinf1 (355,345) and EcoR1 (350,350) diagnostic enzymes. Also cut in Cfo1, Nde2, Pvu2; uncut in Rsa1, Sal1, and Xho1.

Habit and ecology *gregarious in arcs under conifers, late autumn, rare.* Four collections made in November,1995 (Benton County, Oregon) represent the only fresh specimens observed by this author. Two were collected from a mixed *Quercus-Tsuga-Pseudotsuga* Forest (Paul Dunn State Forest) and the other two in a 60(?) year old *Pseudotsuga* plantation (McDonald State Forest). *Vaccinium* present in both locations.

Range and distribution coastal to inland lowlands, western central Oregon south to extreme northern California.

Type A. H. Smith 55610 (MICH) -- November 23, 1956, Crescent City, Del Norte County, California.

Comments This species forms a complex with two closely related taxa, *P. scatesiae* (placed in synonymy with *P. californica* by Horak in 1977) and the newly described *P. rufotubulina. P. californica* and *P. scatesiae* are obviously very similar -- both [1] produce similarly sized, highly gregarious basidiomes with similarly-shaped rugulose-roughened basidiospores and morphologically similar cheilocystidia and [2] exhibit identical RFLP profiles. Striking macroscopical and subtle microscopical differences support separation between the two species, however: the densely fasciculate, highly glutinous *P. scatesiae* basidiomes erupt in mounds rather than 'gregarious arcs', the yellowish brown to dark blackish-brown pilei are broadly conic with sharply acute umbos, and the spore prints are a much less intense yellow brown. Microscopically, *P. californica* can be distinguished by its larger, more rounded, slightly darker basidiospores, less abundant cheilocystidia, and 'furred' suprapellicular hyphae (spirally hyaline to pale amber encrusted) with clearly visible, frequently refractive septa. (In *P. scatesiae* the smooth-walled hyphae of the suprapellis are usually so submerged within a thick gelatinous matrix that individual septa can be distinguished only with difficulty).

P. californica is also very closely related to *P. rufotubulina*, which when first collected was mistaken for a very intensely colored form of the earlier-named species. In addition to the brilliant orange to reddish orange coloration of the pileus, *P. rufotubulina* is slightly smaller, has a much thinner stipe cortex surrounding a completely hollow cavity, and slightly darker.

Separation of the two species is also supported by a length mutation in the ITS region that results in a completely different RFLP profile.

In the field more highly colored forms of *P. californica* may be confused with *P. sipei,* which is clearly distinguished microscopically by small nearly smooth ellipsoidal basidiospores and filamentous to subcapitate thin-walled cheilocystidia.

Smith (1957) originally likened *P. californica* to *P. laterarius* [sic] (now considered by some to be conspecific with *P. christinae),* which he noted lacked the yellow-brown coloration, pungent odor (particularly in revived material), size, gregarious habit, and tibiiform cheilocystidia of *P. californica*.

Phaeocollybia dissiliens A. H. Smith & Trappe, *Mycologia* 64: 1143-1144. 1972.
Emended

Figures: 2.9; 6.9-10

Selected descriptions and illustrations: Smith & Trappe, 1972 -- type description; Norvell -- black & white micrograph.

General impression: scattered to gregarious small to moderately-sized cartilaginous brittle deeply rooting basidiomes with viscid bright orange to brownish orange conic-campanulate pilei, pale orange yellowish young lamellae, pinkish buff to red-orange polished hollow stipes with thick longitudinally splitting cartilaginous rinds, ~6.2 x 4 µm ellipsoidal (bullet-shaped) punctate-roughened basidiospores with rounded to slightly pointed apices, thin-walled filamentous to slightly subcapitate cheilocystidia, a bilaminate pileipellis with narrow gel-encrusted hyphae embedded in a colorless gelatinous matrix overlying a relatively narrow orange subpellis with incrusting pigments, clamp connections. Negative in syringaldazine.Dried pileus pale metallic copper.

Pileus 20-80 mm, narrowly conic with incurved edge to broadly conic-campanulate with low pointed umbo, straight margin and incurved opaque to striatulate edge, subviscid to viscid, glabrous, when young bright orange to brownish orange *(Orange Cinnamon, 10YR 7/8 = Antimony Yellow)* with orange brown disc *(7.5YR 5/8 = Raw Sienna)* and yellowish brown edge *(10YR 5/6 = Buckthorn Brown),* developing cinnamon tones in age *(7.5YR 7/6 = Cinnamon, Pinkish Cinnamon),* hygrophanous with edge often paler than the disc, dried pileus pale metallic copper and finely radially-wrinkled; **Context** 2-4 mm thick, whitish at first *(10YR 9/3)* but soon cartilaginous, watery tan to concolorous with pileus cuticle; **Odor** not distinctive to slightly raphanoid or slightly pungent (reminiscent of *Oxalis*); **Taste** not distinctive or faintly raphanoid to slightly bitter nutty;

Lamellae narrowly attached to free, ventricose, close to crowded, polydymous with lamellulae irregularly interspersed, narrow (length:width ratio mean = 4), thin with uneven whitish edges (paler edges noticeable in dried material), pale orange yellowish when young *(10YR 8/2)*, later dulling to orangish cinnamon brown *(10YR 6/6 = Buckthorn Brown to Warm Buff)*;

Veil evident as brownish-orange fibrillose patches on aerial stipe (almost annulate in one collection);

Stipe central to slightly eccentric, usually 40-80 mm above ground level with 5-10 mm wide apex, overall length including pseudorhiza >180 mm, more or less equal, readily splitting lengthwise, dry to moist, with pale pinkish buff apex at first *(7.5YR 6-7/4 = Pale Pinkish Cinnamon, Light Pinkish Cinnamon)*, eventually becoming deep orange-red from ground upwards *(7.5YR 5/8 = Raw Sienna)*, hollow with 2-3 mm thick cartilaginous cortex surrounding central cavity lined with whitish pallid fibrillose pith;

Pseudorhiza possibly racemose toward origin (as indicated by 5-6 mm long threadlike remnants on two specimens), fragile, dark reddish to rusty brown at origin *(2.5YR 4/4-6 = Walnut Brown, Cacao Brown)*;.

Spore Print Color yellowish cinnamon *(10YR 5/6 = Buckthorn Brown)*.

Basidiospores 6.2 x 4 ± 0.3 x 0.2 µm (overall range 6-7.3 x 3.4-4.5 (5) µm), ovoid to subellipsoidal in face view, in profile subellipsoidal, ventrally rounded with small eccentric apiculus and rounded to obscurely pointed apex, finely punctate-roughened under oil immersion, pale medium amber in KOH, inamyloid, nondextrinoid in Melzer's;

Cheilocystidia emanating from the lamellar trama and variable in length (near 28-45 µm long), 3.5-4 µm wide, filamentous, cylindrical to slightly irregular in outline to slightly inflated and subcapitate or sometimes mucronate, thin-walled, hyaline to pale straw-colored, with frequent clamp connections

Pleurocystidia absent or possibly very scattered (see comments below);

Basidia 4-spored, 24-30 x 6 - 6.5 µm, hyaline to pale amber, with clamp connections at bases;

Pileipellis a two-layered ixocutis, with 70-100 µm thick suprapellis composed of a gelatinous matrix with hyaline, smooth to hyaline-encrusted, narrow (3.5-4 µm diam) occasionally clamped hyphae overlying relatively narrow (50-75 µm thick) orange to dark orange brown subpellis of 5-8 µm wide hyphae with incrusting and intraparietal pigments;

Tramal tissues highly gelatinized, sarcodimitic in the pseudorhizal thread with wide (up to 30 µm) thick-walled (up to 1 µm) rigid cylindrical hyphae supported by less conspicuous branched thin-walled (0.5 µm) flexuous hyphae; both hyphal types also present at the base of the stipe where rigid elements are slightly thicker walled (up to 3 µm) and wider (to 40 µm); Lamellar trama parallel, composed of long, cylindrical 4-8 µm wide highly

gelatinized slightly thick-walled hyaline hyphae giving rise to a rudimentary subhymenium;

Tibiiform diverticula abundant on pseudorhizal pellis;

Clamp Connections present and relatively common, readily visible on suprapellicular hyphae of the pileipellis and on cheilocystidia, present but less visible at basidial bases'

Macrochemical reactions Syringaldazine -- negative (slight dulling of tissues but no magenta reaction); KOH -- strongly positive (immediate dark brown); FeSO4 -- slightly greenish to dark dull green.

RFLP profile: fragmentary -- ITS region from type material amplified with contaminants.

Habit and ecology scattered to gregarious in saturated soils from mid to late autumn under *Picea sitchensis, Pseudotsuga menziesii,* and *Tsuga heterophylla* near flood plains or swampy areas.

Range and distribution at sea level to low elevations in northern Oregon coastal coniferous rainforests.

Type: A. H. Smith 79252_{dis3} (MICH) -- October 23, 1970; Cape Lookout State Park. Tillamook County, Oregon.

Comments: Key field characters include the somewhat fragile aspect of the small to medium sized basidiomes, pale bright orange to brownish orange fresh pilei, pale orange buff gills, hollow stipes with the relatively thick, longitudinally splitting cartilaginous rinds and pale orange brass or coppery, radially wrinkled dried pilei. Important microscopical features include filamentous to subcapitate cheilocystidia (rarely exceeding 4 µm at the apex), small punctate roughened bullet-shaped basidiospores (reminiscent of *P. sipei* and *P. oregonensis*), and frequent clamp connections found at basidial bases, and septa of cheilocystidia and cuticular hyphae. As neither Redhead (unpublished material, 1992) nor this author have been able to verify the presence of pleurocystidia reported by Smith & Trappe (1972), their presence is not considered diagnostic. In 1977 Horak, prior to examining the type material of *Naucoria radicata* , synonymized *P. dissiliens* with *P. radicata;* since his subsequent examination of authentic material, however, he no longer considers the two taxa to be conspecific (private communication 1995, 1996).

A very distinctive, pretty mushroom when young, the distinctive orange of the fragile pileus of *P. dissiliens* soon dulls and can be mistaken in the field for *P. sipei*, another small spored taxon. However *P. sipei* produces less brightly colored, more robust basidiomes that lack clamp connections and have wider cheilocystidia and slightly larger basidiospores. Preliminary and incomplete RFLP data also suggest a molecular separation between the two species.

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

Figures: 6.11-13

Selected descriptions and illustrations: Smith, 1957 -- type description with black & white photograph and anatomical drawings; Bandala, 1994 -- habit and anatomical drawings with SEM micrograph; Horak, 1977 -- anatomical drawings; Lincoff, 1981 -- description and color photograph; Phillips, 1991 -- color photograph; Smith, 1975 -- color photograph.

General Impression: scattered to gregarious small to medium-sized cartilaginous deeply rooting basidiomes with viscid to glutinous olive-green conic-campanulate pilei, violet young lamellae, slender shiny hollow to fibrillose stuffed stipes with drab or dull greenish apices orange to reddish bases, characteristically curled vertical monopodial pseudorhizae,~9 x 5 µm verruculose to verrucose elongated limoniform basidiospores with moderate apical beaks, thin-walled broadly subcapitate secretory cheilocystidia, a bilaminate pileipellis with kinked narrow hyaline hyphae loosely embedded in a thick gelatinous matrix overlying a thick greenish (in H2)) or orange (in KOH) subpellis, no clamp connections. Negative in syringaldazine. Dried pileus metallic gold to bronze.

Pileus (10) 20-65 mm broad, 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, glabrous, viscid to glutinous, usually some shade of light to dark olive-green *(Olive Buff, Citrine Drab)*, either uniform with different greenish tones in patches or zonate with darker disc *(Dark Olive, Citrine Drab,* or *Olive Buff)* and paler edge *(Buffy Brown)*, under certain conditions underlying olive-green ground color obscured by dark orange or brown glutin, hygrophanous with noticeably striate edge when moist, when dried either shiny mahogany brown with paler gold edge or metallic brownish bronze overall;

Context 1-5 mm over disc and quite thin in the margin, pale to dark olive buff to deep olive, often consumed by insects; **Odor** most often reminiscent of pansies, boiled potatoes or burnt wet hair ('gebrenzlich'), otherwise faintly raphanoid or not distinctive; **Taste** usually mild, occasionally raphanoid, glutin becoming bitter in older specimens;

Lamellae narrowly attached, thin, edges even when young, becoming uneven in age, polydymous with ≥ 6 tiers of truncate lamellulae irregularly interspersed among lamellae, close to subcrowded (16-33 L+l/cm at edge, 9-16 at mid-point), narrow (2-6 (9) mm), when young bluish violet (varying intensities of *Bluish Violet, Endive Blue, Quaker Drab, Vinaceous Drab, Grayish Lavender)*, later warming to drab *(Brownish Drab, Ecru Drab, Fawn Color, Avellaneous, Cinnamon Drab)*, eventually obscured by spores in age *(Wood Brown)*, in dried specimens often with noticeably ruffled whitish edges;

Veil usually evident as irregularly to concentrically arrayed short appressed orange *(Salmon Colored)* or dark brown *(Mikado Brown)* fibrillose patches on aerial stipe;

Stipe central to slightly eccentric, 30-60 (80) mm tall above the ground with 3-8 (12) mm wide apex, overall length including pseudorhiza 60-200 (275) mm long, usually slightly fusiform, occasionally equal or tapering, rarely ventricose, cartilaginous, viscid to moist, smooth and more or less polished beneath fibrillose patches, color at the apex grayish drab or dull olive buff *(Avellaneous, Fawn Color, Light Grayish Olive, Deep Olive Buff, Drab, Wood Brown)* above gradually more intense deep orange to orange-brown colors *(Mikado Brown, Tawny, Cinnamon, Pinkish Cinnamon)*, becoming overall orange to orangish/reddish brown in age, usually hollow (tubular and lined with thin fibrils) but occasionally stuffed with fibrillose to firm pith, with 1-2 mm thick cartilaginous cortex surrounding the interior portion in all instances;

Pseudorhiza vertical monopodial and gradually narrowing towards a curled or nippled origin, up to 3/4 of total stipe length, dark reddish or orangish brown *(Liver Brown, Kaiser Brown)* above a tawny to dark reddish brown *(Tawny, Liver Brown)* origin;

Spore Print *Pinkish Cinnamon.*

Basidiospores: 9 x 5 ± 0.5 x 0.2 µm (overall range 7-10 x 4-6 µm), in face view ovate with elongated apical beak, in profile limoniform-fusoid with eccentric apiculus and elongate central to slightly tilted tapered beak (to 1.5 µm), verrucose-rugulose except over smooth beak and apiculus, suprahilar plage an area of lowered ornamentation discernible in oil immersion, medium amber brown in KOH, dextrinoid in Melzer's;

Cheilocystidia: abundant, crowded together to form a dense gelatinous barrier with individual elements frequently surrounded by apical gelatinous secretions in KOH, broadly clavate 7-9 µm wide elements intermixed with subcapitate clavate 5-7 µm wide elements, thin-walled, yellowish or hyaline in KOH;

Pleurocystidia absent;

Basidia 4-spored, 30-42 x 7-9 µm, clavate, hyaline or yellowish in KOH;

Pileipellis a well-delimited bilaminate ixocutis with a very thick (200-500 µm) suprapellis composed of a 'tangled turf' of uplifted long branched narrow (2-4 µm wide) straight or curling hyaline hyphae embedded in a gelatinous matrix overlying a 300-400 thick orange subpellis (greenish-amber in H2O) containing long (to 100 µm) thick-walled inflated (up to 15 µm from 6-10 µm wide septa) hyphae with intraparietal orange pigments, bright orange oleifers frequent; **Stipitipellis** ~40 µm thick, composed of sparingly branched, long, narrow, highly gelatinized dull brownish hyphae beneath remnants of pellicular veil with greenish-brown incrusting pigments and abundant tibiiform diverticula;

Tramal Tissues highly gelatinized, strongly sarcodimitic in pseudorhiza, composed of long wide (to 20 µm) thick-walled (to 2 µm) pale brown rigid cylindrical hyphae supported by

less conspicuous thin-walled branched flexuous hyphae, both hyphal types also present in the stipe apex where the long rigid elements are slightly narrower (to 10 µm); Lamellar trama parallel, with long 3-5 µm wide gelatinized ochraceous to pallid hyphae in the ~50 µm wide central region narrowing to 2-3 µm on the edges to give rise to a rudimentary subhymenium;

Tibiiform diverticula abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex;

Clamp Connections absent.

Macrochemical reactions: Syringaldazine -- negative; KOH -- dark brown; FeSO4 -- dull greenish-brown.

Fluorescence: Lamellae -- intense yellowish white when young, becoming dull yellow as mature;

RFLP profile preliminary (DNA from the holotype possibly contaminated). 12 isolates indicate 705 bp ITS region cut in Cfo1 Hinf1, Nde2, and Pal1 and uncut in Pvu2, Rsa1, Sal1, and Xho1.

Habit and ecology scattered to gregarious on the ground during autumn and early winter in mixed coniferous rainforests associated with *Tsuga heterophylla, Picea sitchensis, Pseudotsuga menziesii, Abies spp. Polystichum munitum, Oxalis oregana, Vaccinium spp.* also frequently present.

Range and distribution: not uncommon in coastal, inland, and montane regions in British Columbia, Washington, Idaho, Oregon and California.

Type: A. H. Smith 3342 (MICH 00011609) on October 26, 1935, La Push, Clallam County, Washington, USA.

Comments Basidiomes with olive-green pilei and intense bluish violet lamellae are instantly identifiable as *P. fallax*, which is also characterized by a sharply conic-umbonate glutinous pileus, dull drab to greenish stipe apex above a hollow polished orange stipe, and a moderately small stature and fragile aspect. Unfortunately the diagnostic green and violet coloration is ephemeral. The distinctive violet young lamellae, so helpful in separating *P. fallax* from *P. olivacea* and *P. pseudofestiva* in the field, rapidly dull and darken as they mature. The olive-green cuticle also often darkens with age or exposure and can also be obscured by a bright orange-brown to dark brown glutin, thereby causing confusion with the brown pileate *P. lilacifolia* and newly named *P. rifflipes*, both of which also produce basidiomes with violet lamellae.

Phaeocollybia fallax shares much in common with *P. lilacifolia* and *P. rifflipes* beyond violaceous lamellae (including similar cheilocystidia, basidiospores, stature, and pigments). These three western species are in turn closely related to the European *P. festiva*. The type collection of *P. fallax* was originally reported as *Naucoria festiva* by Smith (1937); only after comparison with

the European material did Smith (1957) recognize his collections as representing a separate species characterized by narrower, violet-colored lamellae and more sharply conic-umbonate pilei (*Phaeocollybia festiva* is no longer recognized from western North America).

Character variations observed during the current study should be mentioned here. While Smith (1957) characterized *P. fallax* stipes as 'tubular-hollow', stipes stuffed with relatively firm (*i. e.* not fibrillose) pith have been observed in several specimens otherwise clearly identifiable as *P. fallax*. Likewise, while most specimens sampled did taste 'mild', several collections of older specimens, (including all those collected in 1992 from the Humboldt Redwoods State Park in California) were found to have pilei with bitter-tasting cuticles and/or glutin. Additionally, although a few specimens examined were found to produce the "basidia-like" cheilocystidia originally described and illustrated by Smith, a much greater number -- including those in the type collection -- have been found with these broadly clavate elements dominated by distinctly subcapitate cheilocystidia, which Smith considered more characteristic of *P. lilacifolia* (*q.v.*). In KOH *P. fallax* cheilocystidia characteristically exude a clear heavy gel that eventually spreads out into a dense gelatinous matrix; evidence of this matrix can also be seen in squash mounts in which the abundant cheilocystidia stick together in a dense agglutinated barrier, particularly in older or poorly preserved specimens. Finally, the fact that no apical outgrowths have yet been observed on the clavate cheilocystidia has been found to be taxonomically informative in separating the *P. fallax* complex from *P. olivacea*

It is possible that in the future two taxa might be differentiated on the basis of spore length. Most basidiomes examined produced spores measuring 9 x 5 µm; a smaller number (26 out of 122 collections examined) produced spores measuring 8 x 5 µm. However, because these differences do not appear to be consistently supported by other morphological, anatomical, or molecular characters, no variety is recognized at this time.

More problematical are seven collections from Wildcat Mountain (Mt. Hood National Forest, Clackamas County, Oregon). While macroscopically similar to *P. fallax*, their uniformly azonate dull dark olive pilei lack striations and have straight rather than inrolled to incurved edges, and their slightly narrower lamellae are less intensely violet. Except for slightly larger spores and absence of filamentous cheilocystidia and paraphyses, these collections are microscopically very close to *P. rifflipes*. For the time being, however, these collections are placed in *P. fallax* due to the presence of secretory cheilocystidia and green pigments not found in *P. rifflipes*.

P. fallax is most closely related to *P. lilacifolia* and *P. rifflipes* (with *P. festiva*), which are discussed in more detail below. Two other macroscopically similar taxa -- *P. olivacea* and *P. pseudofestiva* -- produce olive-green colored basidiomes. *Phaeocollybia olivacea* is differentiated by yellowish lamellae, consistently stuffed stipes, obtusely umbonate to plano-campanulate pilei, duller coloration, characteristically larger, rounder spores, and a tendency to develop apical outgrowths in older specimens. Basidiomes of *P. pseudofestiva*, which also lack violet lamellae,

are easily distinguished by the their refractive tibiiform cheilocystidia and shorter rounder basidiospores.

Phaeocollybia gregaria A. H. Smith & Trappe, *Mycologia* 64: 114. 1972.
(Observations below based on examination of type specimens)
(Italicized portion quoted directly from type description)

Figures: 6.14

Selected descriptions and illustrations: Smith & Trappe, 1972 -- type description.

General Impression: highly gregarious medium sized cartilaginous deeply rooting basidiomes with glutinous drab to grayish brown broadly conic pilei, grayish young lamellae, drab stuffed stipes, ~9.8 x 6 µm verruculose to verrucose amygdaliform basidiospores with subdued to prominent apical beaks, thin-walled filamentous to narrowly clavate cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae loosely embedded in a gelatinous matrix overlying a dull brownish subpellis, no clamp connections. Untested in syringaldazine. Dried pileus metallic yellow bronze.

Pileus *30-60 mm, conic, becoming radially rugulose in some, glabrous, glutinous, 'wood brown' (light grayish yellow brown), grayish buff when 'faded', opaque at all stages, hygrophanous*, yellowish bronze when dried; **Context** *thin and cartilaginous pliant,* **odor** *not distinctive* [faintly reminiscent of pansies in LLN 93.11.04-5,10]; **taste** *not distinctive*

Lamellae *ascending-adnate,(nearly free), crowded with even edges, narrow, initially grayish pallid, becoming dull cinnamon from the spores;*

Stipe *overall up to 180 mm* [aerial portion unknown]; *apex 8-15 mm wide, glabrous above, apex pinkish gray,* stuffed with pallid-whitish pith;

Pseudorhiza of unknown origin (probably vertical-monopodial), *tapering to a long pseudorhiza, rusty-red to moderate reddish brown.*

Basidiospores 9.8 x 6 ±0.4 µm (9-10.5 x 5-6 µm), amygdaliform in profile with eccentric apiculus and obscure to moderate apical beak, ovate-pointed in face view, verruculose to verrucose, pale to medium amber in KOH.

Cheilocystidia abundant, originating deep within the lamellar trama, lengths developmentally variable, 2-5 µm wide, filamentous to narrowly clavate with rounded, subcapitate or tapering apex, thin-walled, moderately gelatinized, hyaline, long filamentous apical extensions present in old or stored basidiomes;

Pleurocystidia absent;

Basidia 4-spored, 30-40 x 6-7 µm wide, frequently inflated above long, narrow (2-4 µm) pedicel, hyaline;

Pileipellis a bilaminate ixocutis with a thick (to 400 µm) suprapellis composed of uplifted narrow (1-2 µm) highly gelatinized hyaline cylindrical hyphae loosely embedded within a gelatinous matrix overlying a dull brownish to orangish subpellis of 4-7 µm wide gelatinized hyphae with intercellular pigments, 4-6 µm wide colorless oleiferous hyphae present in both layers, 2-3 µm wide oleiferous hyphae with dark orange amber contents present in subpellis;**Stipitipellis** a 20-40 µm thick layer of 1.5 µm longitudinally arrayed gelatinous hyaline (in KOH) hyphae overlying inflated (up to 10 µm) thick-walled hyaline hyphae that merge into stipititrama;

Tramal tissues moderately gelatinized, strongly sarcodimitic in the lower stipe and consisting of wide (up to 10 µm) thick-walled (1 µm) rigid fusoid hyaline hyphae supported by less conspicuous thin-walled branched narrow (1.5 µm) hyaline flexuous hyphae; lamellar trama parallel with 5-8 µm wide hyaline to sordid brownish gelatinous hyphae in the central region narrowing to 3 µm at the edges to give rise to a closely interwoven subhymenium;

Clamp Connections absent;

Tibiiform diverticula occasional on stipitipellis, abundant on pseudorhizal pellis, up to 20 x 1 µm, usually with 1.5-2 µm wide capituli, secretory.

Macrochemical Reaction: *KOH negative; FeSO4 negative.*

RFLP profile: ITS region of 2 isolates (including the type) = 740 bps. Cut in Cfo1, EcoR1, Hinf1, Nde2, Pal1 and Pvu2; uncut in Rsa1, Sal1, and Xho1.

Habit and ecology: densely gregarious in small areas in mid to late autumn under spruce (*Picea sitchensis)* and hemlock (*Tsuga heterophylla).*

Range and distribution: verified only from type locality in Cascade Head Experimental Forest, Otis, Oregon.

Type: A. H. Smith 79075 (MICH) -- October 16, 1970,Cascade Head Experimental Forest, Tillamook County, Oregon.

Comments *P. gregaria* produces medium-sized basidiomes with 'slimy' grayish brown pilei, smoky white lamellae, pinkish gray stipes, and a nondistinctive odor and taste. The only fresh collections made during the current study (LLN 93.11.04-5,10) contained overly mature specimens that were not identified to species until after being dried, thus contributing little to a 'field' sense of the species.

Horak (1972) synonymized *P. gregaria* with *P. piceae*, a bright orange mushroom with a bitter taste, based on his comparison of the type collections. Examination of the types confirms that in

addition to a striking similarity in color and general appearance of the dried material, basidial, basidiospore and cheilocystidial morphology are virtually identical. In fact, the only striking anatomical difference appears to be that in *P. gregaria* the extensive (up to 400 µm thick) suprapellis is composed of a gelatinous matrix containing narrow hyphae that readily separate when rehydrated whereas in *P. piceae* the thinner (between 30-100 µm thick) suprapellis contains slightly wider hyphae 'interwoven in the basal area' (*cf.* Smith & Trappe, 1972) that tend to retain their close parallel alignment in mountants. (At the macroscopic level, this variation is perceived as differences in degree of viscidity, with *P. gregaria* and *P. piceae* producing respectively viscid to glutinous and moist to merely thinly viscid pilei.) It is possible that such differences in pileipellis structure could be influenced by age or environmental factors.

While the microscopical differences between *P. gregaria* and *P. piceae* are subtle, the macroscopic and molecular differences are more obvious. Both type and paratype of *P. gregaria* produce ITS regions approximately 740 base pairs in length. Although DNA was not successfully amplified from the type of *P. piceae*, it was from recently collected basidiomes (including topotypical material). A 40 base pair deletion in the amplified ITS region of *P. piceae* results (not unexpectedly) in a strikingly different RFLP profile and supports the existence of two different species: (1) *P. piceae*, characterized by smaller, orange, bitter-tasting thinly viscid basidiomes with slightly narrower cheilocystidia and closely aligned, non-separating suprapellis, and (2) *P. gregaria*, characterized by larger, mild-tasting, glutinous, grayish-brown basidiomes with slightly more heteromorphic cheilocystidia and extensive suprapellis.

Smith and Trappe (1972) note that *P. gregaria* differs from *P. spadicea* in large spore size, absence of bitter taste, and paler pileus coloration. Their observation that there is 'some' difference in the cheilocystidia and mention in the technical description of *P. gregaria* that the cheilocystidia are 'intermediate in shape between sections *Phaeocollybia* and *Versicolores* deserve comment. Examination of the four known collections of *P. gregaria* reveal that in young, well preserved specimens the cheilocystidia are consistently thin-walled and clavate/filamentous and lack the characteristically refractive necks and small secretory capituli characteristic of *P. spadicea*. In older specimens, however, many cheilocystidia were observed with long hair-like apical extensions (see apical outgrowths under 'cheilocystidial development' in Chapters II and III) which could easily be misinterpreted as tibiiform cheilocystidia when viewed under lower magnification or in the absence of differential interference contrast. It appears that this species readily forms such artifacts, which are particularly abundant in the over-mature specimens of LLN 93.11.04-5.

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

-= *Naucoria kauffmanii* A. H. Smith, *Mycologia* 29: 52. 1937.

Emended

Figures: 2.7; 6.15-17

Selected descriptions and illustrations: Smith, 1937 -- type description and black & white photograph; Arora, 1981 -- black & white photograph; Bandala, 1994 -- habit and anatomical drawings with SEM micrograph; Bandala, Guzmán & Montoya, 1980 -- anatomical drawings; Bessette & Sundberg, 1987 -- color photograph; McKenny, Stuntz & Ammirati, 1987 -- color photograph; Norvell, 1997 -- line drawing; Redhead & Norvell, 1993 -- discussion of variation (drawings and photograph of *P. redheadii*); Smith, 1980 -- color photograph.

General Impression: solitary to gregarious very large fleshy farinaceous deeply rooting basidiomes with viscid to glutinous orange to tawny strongly inrolled convex-campanulate pilei, pale pinkish cream colored young lamellae, dry robust pinkish cinnamon dry stipes stuffed with dense solid whitish stipitipith, moderately large (~8.5 x 5 µm) verrucose limoniform basidiospores with prominent apical beaks, narrowly clavate cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae loosely embedded in a clear thick gelatinous matrix overlying a brownish orange subpellis with weakly encrusting pigments, no clamp connections. Mature basidiomes immediately deep magenta in syringaldazine. Dried pileus characteristically dark red copper with darker winy pointed disc.

Pileus (30) 45-150 (195) mm wide, conic-convex and usually with sharp minute papilla when young, expanding to broadly campanulate with broad low umbo and slightly decurved or occasionally upraised margin, extreme edge inrolled at all times, glabrous, smooth, viscid to heavily glutinous, opaque, non-striate, pristine basidiomes most often zonate with deep orange brown or bright brownish orange disc *(Tawny, Russet, Amber Brown, Mikado Brown, Mars Brown, Verona Brown -- 5YR 3-5/4-8; Kaiser Brown, Ochraceous Tawny, Sanford's Brown, Hazel -- 2.5YR 3-5/6-8),* pale to bright brownish orange margin *(Ochraceous Tawny, Ochraceous Buff, Ochraceous Orange, Tawny, Zinc Orange, Mars Yellow-- 6.25YR 5-7/7-10; Amber Brown, Chestnut, Cinnamon Buff, Orange Rufous),* and deep yellow to orange brown edge *(Buckthorn Brown, Dresden Brown, Antimony Yellow -- 10YR 4-5/5-7; Russet, Tawny, Amber Brown, Argus Brown, Cinnamon Brown, Ochraceous Tawny -- 5YR 3-5/4-8),* occasionally ± uniformly deep orange brown or bright brownish yellow orange over all, areas of damage blackish or deep brown, dried pileus generally reddish copper, frequently with darker winy or blackish pointed disc; **Context** firm and confluent with stipe pith, 3-10 mm thick at the disc, when young pale yellowish cream or smoky pink *(Pale Ochraceous Salmon, Pinkish*

Buff, Cartridge Buff. -- 2.5Y 8-9/1-4; Pale Pinkish Cinnamon, Pale Ochraceous Buff -- 7.5YR 8-9/2-4), when wet often developing a deep orange-brown 1-3 mm wide zone between context and lamellae or between otherwise confluent pilear and stipe contexts; **Odor** mildly to strongly farinaceous, occasionally not distinctive; **Taste** slightly to strongly farinaceous, occasionally slightly bitter;

Lamellae ascendant, free or sometimes attached by a small tooth, ventricose with end nearest stipe almost truncate, thin, usually uneven to slightly serrulate, eroded in age, occasionally forked, lamellulae in 5-7 tiers with 2-6 interspersed, narrow when young and very broad in mature specimens (to 20 mm) with mean length:width ratio 4 (young to mature range 1.3-9), crowded when young, becoming subcrowded in age (edge 13-38 L+l/cm, midpoint: 8-20), pinkish cream when very young *(Pinkish Buff, Pale Pinkish Buff, Cartridge Buff -- 2.5Y 6-8/1-4)* maturing to pale brownish yellow-orange *(Light Ochraceous Buff, Ochraceous Buff, Pale Ochraceous Buff, Pinkish Cinnamon -- 6.25YR 6-8/5-8); Pale Salmon Color),* and dull smoky golden brown in age *(Clay Color, Cinnamon Buff, Avellaneous, Buckthorn Brown, Cinnamon, Dresden Brown -- 10YR 5-7/5-7);*

Veil when evident present as scattered fibrils or scant fibrillose patches on the stipe apex;

Stipe central to slightly eccentric, terete, usually 40-60 (110) mm tall above ground with 9-25 mm wide apex, usually swelling to 10-37 mm above ground level before tapering downwards to the pseudorhiza, overall length including pseudorhiza up to 400 mm, smooth, appressed fibrillose under hand lens on the aerial portion, matte and finely longitudinally lined, moist, apex light yellowish brown or pale pinkish buff when young *(Light Pinkish Cinnamon, Pale Pinkish Cinnamon, Pinkish Cinnamon -- 7.5YR 6/6-8/2; Light Ochraceous Salmon, Light Vinaceous Cinnamon -- 5YR 7-8/2-6),* developing darker tones when mature *(Pinkish Buff, Cinnamon Buff--10YR 7-8/4-8; Cinnamon -- 7.5YR 4-6/5-7),* darkening below to deep orange brown *(Army Brown, Natal Brown -- 5YR 3-5/2-5),* staining orange then darkening when cut, stuffed with 1-3 mm thick cartilaginous rind surrounding firm pinkish or dull yellowish white pith becoming deep orange brown when crushed or cut, long narrow yellowish or orangish brown water-soaked lines occasionally visible in interior areas;

Pseudorhiza generally 2/3 to 5/6 of overall stipe length, gradually tapering to a blunt origin overall deep red or orange brown *(Liver Brown-- 7.5R 2-3/4-5; Kaiser Brown, Mars Brown, Tawny, Mikado Brown -- 5YR 3-5/4-8)* or paler brownish yellow-orange or golden brown *(Light Ochraceous Buff -- 6.25YR 5-7/6-8; Cinnamon Buff -- 10YR 5-6/5-6)* at the origin.

Spore Print Color cinnamon brown *(Cinnamon -- 7.5YR 5/6; Buckthorn Brown -- 10YR 5-6/4-6)*

Basidiospores 8.5 X 5 ± 0.4 x 0.2 µm (overall range 7.5-10 x 4-6), terete to slightly compressed, inequilaterally amygdaliform or strongly limoniform in profile view, fusoid-elliptical or almost naviculate in face view, verruculose to verrucose except on the 0.5-1.5 µm long mammiform beaked apex and eccentric prominent apiculus, suprahilar plage an area of slightly lower ornamentation visible in SEMs *(Fig. 6.17)* but not readily discernible under oil immersion, medium pale to dark amber in KOH, pale yellow amber in H2O, dextrinoid in Melzer's;

Cheilocystidia abundant, emanating from the lamellar trama to form a dense highly gelatinous barrier, sometimes multiply septate or catenate, lengths developmentally variable (approximately 15-50 µm long), irregularly cylindrical to narrowly clavate elements with 2-4 µm wide apices and 3-4 µm wide septa intermixed with broadly clavate to (very rarely) pedicellate subcapitate cells to 6 µm diam in mature basidiomes, thin-walled, highly gelatinized, hyaline or occasionally with oily pale amber or brownish contents in older basidiomes, often developing long filamentous apical outgrowths in very old or stored fresh specimens;

Pleurocystidia absent;

Basidia 4- (occasionally 2-) spored, 30 X 7 µm (30-38 X 6-7 [10] µm), clavate, hyaline;

Pileipellis a bilaminate ixocutis with a very thick (200-700 µm) composed of long branching narrow (2-4 µm) thin-walled easily collapsing highly gelatinized hyaline hyphae with refractive septa embedded in a thick colorless gelatinous matrix overlying a much thinner (60-180 µm) dull orange brown to yellow orange subpellis with inflated (up to 12 µm from 3-5 µm wide septa) hyphae with incrusting, intraparietal and intercellular pigments; **Stipitipellis** a narrow (100-150 µm) compact layer of parallel short-branched thick-walled narrow (2-4 µm) highly gelatinized hyaline hyphae slightly inflated at the septa and incrusted with dark brown gelatinous pigments; **Pseudorhizal pellis** ~300 µm thick and composed of melanized or dark brown hyphae with moderately coarse incrusting and coagulated brownish intraparietal pigments with the outermost hyphae densely covered with tibiiform diverticula, clamp and/or pseudo-clamp connections rarely to occasionally present in both stipitipellis and pseudorhizal pellis;

Tramal Tissues highly gelatinized, oleiferous hyphae present throughout, tissues strongly sarcodimitic in pseudorhiza with long parallel aligned rigid thick-walled (3 µm) wide (30 µm) hyaline cylindrical hyphae supported by similarly colored highly branched, thin-walled (up to 0.5 µm) narrow (2-3 µm) hyaline flexuous hyphae that widen to 3-4 µm towards the stipe apex where the rigid elements narrow (to 7-15 µm) and become thinner walled (1 µm), both hyphal types also present in the pileus and lamellar trama; Lamellar trama parallel with long highly gelatinized thick-walled hyphae 3-4 µm diam in 100-150 µm wide central region narrowing to 2-3 µm on the edges to form a compact rudimentary subhymenium composed of interlocking short 3 µm wide elements, narrow, highly

branched flexuous hyphae also occasionally present; oleiferous hyphae present in all tramal tissues

Tibiiform diverticula abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex, up to 15 (20) x 1 µm in size, hyaline to slightly straw-colored, highly refractive with no septum between base and hypha, with or without slightly larger ligulate to subglobose capitellum and/or apical droplet;

Clamp Connections occasionally observed in stipitipellis and pseudorhizal pellis, absent in all other tissues.

Macrochemical Reactions: syringaldazine -- immediately deep magenta overall (restricted to pseudorhiza or patchy when young); KOH -- orange pileus cuticle becoming brownish; FeSO4 -- greenish.

Fluorescence: Young basidiomes -- lamellae dull whitish to yellowish white; Mature basidiomes -- lamellae whitish yellow to intense yellow, pileal pith orange, apical pith purplish, pseudorhiza exterior dull whitish.

RFLP profile (DNA from A.H.Smith 3523 (Holotype) too degraded for RFLP analysis) -- ITS region of 8 isolates 740 bps. PaI1 (235-230-105-90-80) most informative enzyme. Also cut in Cfo1, EcoR1, Hinf1, Nde2; uncut in Pvu2, Rsa1, Sal1, and Xho1.

Habit and ecology solitary, scattered or gregarious, often in loamy soils with high humus content from early to late autumn in coastal and inland mesic closed-canopy mixed coniferous rainforests; less frequent in poor soils in open mixed coniferous-deciduous (*Pinus, Lithocarpus, Pseudotsuga)* forests.

Range and distribution Perhaps the most widely distributed and common *Phaeocollybia* found from southern British Columbia south to Mendocino County in northern California and east to Idaho.

Type: A. H. Smith 3523 (MICH) -- October 18, 1935 near Lake Tahknetich, Douglas Co. Oregon.

Comments: All species of the *P. kauffmanii* complex (also including *P. ammiratii, P. benzokauffmanii, P. luteosquamulosa,* and *P. redheadii*) produce very large fleshy basidiomes with solidly stuffed stipes, large amber-brown verruculose to verrucose basidiospores, and clavate cheilocystidia. *P. kauffmanii sensu stricto* can be differentiated in the field by its much brighter, almost orange, viscid glabrous pileus. Microscopically *P. kauffmanii* produces the smallest basidiospores in the complex, with means from 122 collections ranging from 8-9.5 X 4.8-5.5 (6) µm. Examinations of the type material show a preponderance of much more narrowly clavate cheilocystidia than those depicted by Smith in his 1957 monograph (the more bulbous cheilocystidia depicted are far more rarely encountered than one might infer from the illustration).

Although it appears that *P. kauffmanii* is the most widespread and common taxon in the complex, only five of the 16 collections (including the type and one paratype) cited in Smith's 1957 monograph remain identified as *P. kauffmanii.* In a draft of his 1957 monograph, Smith made a note under *P. kauffmanii* to "check all collections for clamps". Apparently he either forgot that note to himself or interpreted any clamp connections he did find as a result of the sarcodimitic tangle of two hyphal types, for six of the 16 collections cited in 1957 (listed below under *P. ammiratii)* do contain clamped basidiomes. Five other collections (including 3 paratypes) contain large-spored basidiomes now believed to belong to *P. redheadii.* (In 1957 Smith reassigned the two remaining paratypes to species well outside the kauffmanii complex: Kauffman XII.7.1925 was designated as a paratype of *P. californica* and AHS 3339 (with part relabeled as *P. lugubris,* UC# 55794) was made the type for *P. spadicea.).*

Phaeocollybia kauffmanii has also been reported from eastern North America (Bigelow & Barr 1966). Examinations of Bigelow #13570 from Vermont reveal that the clamp connections previously reported by Redhead & Norvell (1993) were in fact misinterpretations of sarcodimitic tissue. Until collections of mature basidiomes are made, however, specific identification of the material still remains tentative. *Phaeocollybia kauffmanii*is also reported as the most common *Phaeocollybia* in the *Pinus/Abies* forests in Mexico (Guzmán *et al.* 1987, Bandala-Muñoz *et al.* 1980, Bandala 1994).

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

Emended

(macroscopical portion reformatted but unchanged from Smith, 1957)

Figure 6.18

Selected descriptions and illustrations: Smith, 1957a -- Type description; Smith, 1957b -- anatomical drawings; Horak, 1973 -- anatomical drawings.

General Impression: Gregarious medium sized fleshy cartilaginous deeply rooting basidiomes with viscid dark brown obtusely conic pilei, lilac young lamellae, drab shiny hollow stipes, (probably) vertical monopodial pseudorhizae, moderately large (8 x 5 µm) verruculose plump limoniform basidiospores with moderate apical beaks, broadly clavate thin-walled cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae loosely embedded in a thick gelatinous matrix overlying a brown subpellis, no clamp connections. Negative in syringaldazine.

Pileus 30-50 (100) mm broad, obtusely conic with an inrolled margin, expanding to plano-umbonate, slimy-viscid, dark brown *(Cinnamon Brown to Rood's Brown),*

hygrophanous and fading to dingy pale vinaceous-tawny; **Context** cartilaginous, pallid; **Odor** of crushed flesh pungent; **Taste** somewhat disagreeable, but not farinaceous.

Lamellae free or narrowly attached at apex of the stipe, close to crowded, narrow, Lobelia Violet, slowly becoming dark rusty-brown;

Veil [no mention in macrodescription but evident on upper stipe in microscopic mounts];

Stipe 80-120 (150) mm long, 8-15 mm at the apex, tapered downward to a long pseudorhiza, hollow, cartilaginous, concolorous with the gills, lilac, gradually fading and then the surface concolorous overall, the base not appreciably darker;

Pseudorhiza [presumably vertical-monopodial];

Basidiospores 8 x 5 ± 0.4 x 0.0 µm ((7) 8-9 x 4.5-5.5 µm), in profile limoniform with a relatively prominent apiculus and tapered to small apical beak, ovate in face view with an abrupt small apical projection, the surface obscurely rugulose-verruculose except over the smooth apiculus and apical beak, suprahilar plage an area of lowered ornamentation discernable in oil, pale medium amber in KOH;

Cheilocystidia 5-6 µm wide thin-walled clavate elements intermixed among 3-5 µm wide narrowly clavate elements, emanating from the lamellar trama and variable in length (approximately 20-38 µm), gelatinized, hyaline to amber, gelatinous, occasional apical outgrowths noted in older specimens;

Pleurocystidia: absent;

Basidia 4-spored, 26-35 x 6-7 µm, clavate, hyaline to pale amber in KOH;

Pileipellis a bilaminate ixocutis with a 100-400 µm thick suprapellis composed of a colorless gelatinous matrix containing a 'dense turf' of long branched narrow (2-4 µm wide) gelatinous hyaline hyphae overlying a 'dark rusty brown' subpellis of compact radially arranged 6-10 µm wide inflated gelatinized hyphae with pigmented walls; **Stipitipellis:** composed of long 10 µm wide lightly gelatinized hyphae with brownish walls; numerous remnants of pellicular veil hyphae diverticulate and covered with greenish incrusting pigments;

Tramal tissues: Lamellar trama subparallel with gelatinized hyaline hyphae 3-5 µm wide in central region, narrowing to 2-3 µm on the edges to form a compact rudimentary subhymenium; Pileitrama pale brown to hyaline; Stipititrama composed of 8-12 µm wide thin-walled hyaline hyphae;

Tibiiform diverticula abundant on pellicular veil, apical stipitipellis and pseudorhizal pellis, approximately 10 x 0.5 µm, refractive, hyaline to slightly amber;

Clamp Connections absent.

Macrochemical Reactions FeSO4 and KOH listed as negative in Smith collection #79082 (MICH); no notations found on description accompanying type specimens.

RFLP profile preliminary and fragmentary (DNA from the holotype possibly contaminated). 4 possible isolates indicate 705 bp ITS region cut in Cfo1 Hinf1, Nde2, and Pal1 and uncut in Pvu2, Rsa1, Sal1, and Xho1.

Habit and ecology gregarious on the ground in early to late autumn under "...hemlock and other conifers including redwood..."

Range and distribution rare, from widely separated sites in Washington (montane), Oregon coastal and ?montane), and California (coastal).

Type: A. H. Smith 39976 (MICH Type 00011625) collected by MacIntyre and Smith on September 16, 1952, Ipsut Creek Trail near Carbon River, Mt. Rainier National Park, Washington.

Comments: The largest representative of the *P. festiva* complex in North America, *P. lilacifolia* is distinguished from *P. fallax* by its slightly broader dark brown pileus, thicker stipe, dark orange-brownish subpellis, consistently narrower cheilocystidia, and slightly disagreeable odor; it differs from *P. rifflipes* by its much larger size, darker pileus, hollow stipe, larger basidiospores, and narrower cheilocystidia. Although Horak (1977) synonymized *P. lilacifolia* with *P. fallax* without commenting on the pigmentation differences, he did address the mutability of both green and lilac pigments in *Pyrrhoglossum* and *Phaeocollybia*, genera which he considered to be closely allied (Horak, 1989; *cf.* also Chapter 3). Collection of numerous basidiomes of *P. fallax* with simultaneous green and brown coloration in the current study has also underscored the problem of relying solely on pileus pigmentation for species differentiation in this difficult group. It is interesting to note that in his illustration of basidiospores and cheilocystidia four years earlier, Horak (1973) showed clear differences between *P. fallax* and *P. lilacifolia* in basidiospore ornamentation, size and extent of plage. Bandala (1994) has recently rejected Horak's synonymy, noting the differences in pileus and lamellar colors and the basidiospore size. Unfortunately, molecular data are still too fragmentary and inconclusive to prove helpful in testing the two species hypotheses. In view of the stature difference noted by Smith in 1957 (with *P. lilacifolia* cited as being generally more robust) accompanying a consistent difference in mean spore size of the types (8 x 5 for *P. lilacifolia* versus 9 x 5 in *P. fallax).*the two taxa are being retained as separate pending further morphological and molecular analyses. (Nomenclatural note: It should be noted that in his 1957 monograph, Smith discussed *P. lilacifolia,* a species he had previously described in another paper published the same year (Smith, 1957a), before describing *P. fallax.* From this an argument can be made that the name *P. lilacifolia* has priority and should be used if the two species are to be considered synonymous. See additional comments after *P. fallax.).*

Conflicting observations of basidiospore size and cheilocystidial morphology in the type collections suggest that it may be mixed, Examination of the larger basidiome available on loan reveals basidiospores ranging from 7-8 x 5-5.5 µm in accordance with the dimensions published

originally by Smith and those found in other collections determined by him to belong to *P. lilacifolia*, whereas those found in the smaller type specimen average 9 x 5 µm (similar to the majority of the *P. fallax* collections examined). Furthermore, repeated searches of the the lamellar edges of the larger specimen failed to locate the broader cheilocystidia listed by Smith as being characteristic for the species: "cheilocystidia filamentous-subcapitate with the enlarged part 4-9 µm or clavate and the broadest part 6-9 µm". This mix of subcapitate and capitate elements appears to be more characteristic of *P. fallax* (described by Smith as having cheilocystidia resembling young basidia), with the more narrowly clavate elements characteristic of the other collections identified as *P. lilacifolia* by Smith. Unfortunately this author has collected only one specimen with large stature, brownish pileus, and lilac lamellae provisionally identified as *P. lilacifolia* and sampled for DNA analysis; the specimen differed from the type in slightly narrower spores, a greater number of broadly subcapitate cheilocystidia, and paler warmer pileus.

Phaeocollybia luteosquamulosa nom. prov.

Figures: 2.2, 2.9; 6.19-20.

Selected descriptions and illustrations: Norvell, 1997 -- black & white photographs.

General Impression: solitary to scattered large fleshy ochraceous to tawny yellow deeply rooting basidiomes with dry to merely lubricous scaly ochraceous yellow strongly inrolled convex to campanulate appressed pilei, yellowish young lamellae, dry robust ochraceous to salmon-colored stipes stuffed with dense solid whitish stipitipith, thick vertical monopodial pseudorhizae, relatively large (~10 X 6 µm) verruculose broadly amygdaliform to limoniform basidiospores, cylindrical to broadly clavate thin-walled cheilocystidia, a trilaminate pileipellis with a very thin suprapellis of heavily encrusted orange-yellow hyphae overlying a colorless mediopellis of highly gelatinized hyaline hyphae above a moderately thick (100 µm) bright orange subpellis, no clamps. Negative in syringaldazine. Dried pileus brown, often with a dull orange margin.

Pileus 25-95 mm diam when mature; convex when young, expanding to conico-umbonate or broadly campanulate with incurved margin and tightly inrolled edge; surface moist to dry, hygrophanous, ± nonstriate, sparsely silky with short appressed scales on outer margin and edge, overall some shade of ochre yellow *(Ochraceous Tawny, Ochraceous Buff, Antimony Yellow, Raw Sienna,Light Orange Yellow -- 8.75YR 5-8/7-9)* often with darker disc *(Russet, Dresden Brown, Antique Brown -- 8.75YR 4-5/5-7)*, brighter/paler outer margin *(Antimony Yellow, Amber Brown, Buckthorn Brown -- 10 YR 5-7/6-8)*, darker/brighter damaged areas *(Russet, Sudan Brown -- 5YR 4-5/6-7)*, and slightly darker/brighter scales *(Tawny, Ochráceous Orange -- 5YR 4.5-6/8-10)*, dried pileus matte dark reddish-/orangish brown, often with dull orange margin; **Context:** firm and

confluent with stipe pith, up to 11 mm at the disc, creamy white *(Cartridge Buff, Pale Ochraceous Salmon, Pale Ochraceous Buff -- 6.25YR 8/2-3)*; **Odor** not distinctive to faintly raphanoid when cut or crushed; **Taste** either not distinctive or more often bitter;

Lamellae ascendent, free to almost free, ± ventricose with slightly uneven edges, lamellulae in many irregular tiers, narrow when young, becoming broad (up to 11 mm) with mean length:width ratio 3.0 (range 2.3-8.7), crowded (edge: 25-27 L+l/cm; midpoint: 10-18), yellowish to orangish cream when young *(Cartridge Buff, Pale Ochraceous Salmon, Light Ochraceous Buff, Light Buff -- 10YR 8-9/2-3; 5YR 7-8/4-6)*, darkening to yellowish brown in age *(Cinnamon Buff, Ochraceous Buff -- 1.25Y 6-7/5-6, 7.25YR 6-7/7-8)*;

Veil evident as (a) fibrillose remnants of pellicular veil on unexpanded specimens running from pileal edge to stipe and (b) in mature basidiomes as sparsely scattered,small appressed pileal scales which become more conspicuous when dry and irregularly scattered fibrillose patches on the aerial stipe, yellow-orange brown *(Tawny, Ochraceous Orange -- 5YR 4.5-6/8-10)*;

Stipe ± central, terete or slightly compressed, usually 30-80 (100) mm tall above ground with 8-15 mm apex, equal or enlarging up to 20 mm wide slightly above ground level, overall length including pseudorhiza up to 400 mm, matte and finely longitudinally line, dry, appressed fibrillose under hand lens and apex occasionally covered with sparsely distributed orange brown fibrillose patches, apex some shade of buff *(Orange Buff, Ochraceous Buff, Light Ochraceous Buff, Warm Buff, Pinkish Buff -- 6.25YR 7-8/6-8, 10YR 7-8/4-6)*, below grading to pale orange brown *(Orange Cinnamon, Cinnamon Rufous -- 5YR 4-6/7-9)* at ground level and often staining orange *(Ochraceous Orange, Zinc Orange -- 5YR 5-6/10-12)* with 2-3 mm thick cartilaginous rind surrounding firm pale creamy pith;

Pseudorhiza generally 2/3-5/6 of overall stipe length, gradually tapering to a loosely coiled or straight blunt origin, dark reddish brown colored *(Kaiser Brown, Orange Cinnamon, Xanthine Orange, Carob Brown, Russet, Cinnamon Rufous -- 5YR 4-5/6-9.5, 2.5YR 3-5/5-8)* over all, either paler *(Ochraceous Buff, Light Ochraceous Salmon -- 5YR 6-7/7-8)* or dark *(Chestnut Brown, Ferruginous -- 2.5YR 3-4/5-8)* at the origin.

Spore Print pale cinnamon brown *(Light) Pinkish Cinnamon (7.5 YR 6-7/4-6);*

Basidiospores 10 X 6 ± 0.5 x 0.4 µm (9-11 x 5-6.8), terete in end view, broadly amygdaliform to broadly limoniform in profile, verruculose with exosporium irregularly projecting beyond outline except on 1-1.5 µm long mammiform apex and distinct eccentric apiculus, medium amber in KOH, paler in H_2O, inamyloid and nondextrinoid in Melzer's;

Cheilocystidia abundant, emanating from the lamellar trama and forming a distinct gelatinous barrier,, a mixture of long straight cylindrical 3 µm wide elements and inflated to slightly subcapitate clavate elements up to 9 µm wide above 3 µm wide septa, lengths

developmentally variable but generally from 24-37 µm long, thin-walled, gelatinized, usually hyaline, long filamentous apical outgrowths frequently present in very old or stored fresh specimens;

Pleurocystidia absent or present only as occasional filamentous 1-2 µm wide hyphidia;

Basidia 4-spored, 28-43 X 7-9 µm, projecting up to 10 µm above developing hymenium, occasionally intermixed with filamentous paraphyses in mature basidiomes, hyaline;

Pileipellis an trilaminate ixocutis with brilliant orange yellow oleiferous hyphae running throughout -- Suprapellis a remnant of the pellicular veil, composed of one to four radially aligned 5 µm wide slightly gelatinized brilliant yellow to yellow-orange very occasionally diverticulate hyphae with encrusting pigments that dissolve into pools in KOH and intraparietal pigments that frequently concentrate at the refractive septa; Mediopellis 75-110 µm thick and colorless, composed of unbranched cylindrical (2) 3-5 µm wide gelatinized hyaline hyphae; Subpellis 100 µm thick with a mix of intraparietal, diffuse, and incrusting orange pigments, composed of thin-walled gelatinized hyphae inflating to 15 µm wide from 5 µm wide septa; **Stipitipellis** a compact parallel layer composed of long, cylindrical, highly gelatinized thick-walled 4 µm wide orange pigmented hyphae with tiny orange-yellow surface crystals present when mounted in KOH; **Pseudorhizal pellis** similar to but darker than stipitipellis and with abundant tibiiform diverticula emergent from external hyphae;

Tramal tissues moderately gelatinized, strongly sarcodimitic in pseudorhiza with long rigid wide (up to 15 µm) thick-walled (up to 2 µm) hyaline hyphae supported by highly branched, thin-walled (~0.25 µm thick), 2-3 µm wide flexuous hyphae that widen slightly (up to 6 µm) in the stipe apex, where the rigid elements widen also (to 30 µm) and become thinner walled (to 1 µm); the pileus trama composed of gelatinized inflated orange hyphae and not noticeably sarcodimitic; Lamellar trama parallel with cylindrical thin-walled gelatinized hyaline hyphae 3-6 µm diam in 100-300 µm wide central region, narrowing to 2-3 µm wide on the edges to form a compact 2-4 stranded rudimentary subhymenium;

Tibiiform diverticula rare to occasional on pileal scales, frequent on stipe fibrillose patches, and prolific on the pseudorhizal pellis, up to 30 X 2 µm, aseptate, highly refractive, hyaline, with or without slightly larger ligulate to subglobose capitellum and/or apical droplet;

Clamp Connections absent in all tissues.

Macrochemical reactions: Syringaldazine -- no reaction; KOH -- no macroscopical reaction, but frequently producing 0.5 µm wide crystals in mounts of pellicular tissues; FeSO4 -- slightly greenish.

Fluorescence: young lamellae -- intense whitish yellow; pileus context -- dull yellow-orange; aerial stipitipith -- dull purple.

RFLP profile: ITS region of 9 isolates including type = 730 bps. Unique in Hinf1 (400-190-140) and Sal1 (535-195). Also cut in Cfo1. EcoR1, Nde2, Pal1, and Pvu2; uncut in Rsa1 and Xho1.

Habit and ecology solitary to clustered in humic podzolic soils at the onset of the autumnal mushroom fruiting season in of coastal and inland ancient or mature second growth mesic mixed closed canopy coniferous rainforests (*Tsuga heterophylla* and *Abies* spp.) or mixed coniferous-fagaceous forests (*Tsuga, Abies, Lithocarpus* and *Sequoia).*

Range and distribution Collected thus far from only four localities from northern Washington, Oregon, and northern California.

Type: S.A.Redhead 7481**lut3** (WTU; isotype at DAOM) on November 25, 1992 by S. A. Redhead and G. L. Barron in Jackson State Forest, Mendocino County, California (123.6°W, 39.4°N).

Comments *Phaeocollybia luteosquamulosa* can be easily recognized in the field by its squamulose, dry to moist, yellow ochre pileus. It is further easily distinguished from other members of the *P. kauffmanii* complex by its non-distinctive odor and often bitter taste, negative syringaldazine reaction, and trilaminate pileipellis with the patchy narrow brilliant yellow suprapellis. *P. luteosquamulosa* produces a unique RFLP profile in which banding patterns produced by digestion of the ITS region with Hinf1, Pal1, and Sal1 are distinct from the other four taxa. The proposed name is based on the ochraceous coloration and presence of appressed pileal scales (unusual in the genus).

No other known species shares the robustness, pigmentation, cuticular structure, and spore morphology of *Phaeocollybia luteosquamulosa.* Of the 14 published species described as having some sort of pileal scales, only two -- *P. coniuncta* Horak 1980 and *P. tentaculata* Horak 1977 -- have dry to moist pilei even vaguely similar in color. The Indian *P. coniuncta* is described as a small basidiome with a dirty yellowish-brown pileus, a slender hollow stipe, cylindrical cheilocystidia, and normally cespitose habit. The Australian *P. tentaculata* , also very small, is clearly different microscopically with small spores, clamp connections, and very distinctive tentaculate capitulate cheilocystidia. It has been reassigned to the genus *Melanomphalia* by Singer (1986, 1987).

One collection from Jedediah Smith State Park (J.F.Ammirati 6018) is very closely affiliated with *P. luteosquamulosa* with which it shares a moist to dry fibrillose pileus, similar stature, trilaminate pileipellis with a 2-hyphae thick brilliant yellow pigmented suprapellis, and similarly shaped clavate cheilocystidia. However the Chestnut Brown coloration of the young pilei, densely

gregarious habit, and considerably smaller basidiospores (8 x 4.5) are atypical. While these anomalies may eventually be included within the species circumscription at a varietal status, the collection is excluded from the species at the present time.

Phaeocollybia olivacea A. H. Smith, *Brittonia* 9: 204-205. 1957
Emended

Figures: 6.21-22

Selected descriptions and illustrations: Smith, 1957b -- Type description with black & white photographs and anatomical drawings; Arora, 1981 -- black & white photograph; Kibby, 1992 -- color watercolor; Smith, 1975 -- color photograph.

General Impression: gregarious moderately-sized fleshy-cartilaginous deeply rooting basidiomes with glutinous greenish to brownish olive convex to campanulate pilei, creamy yellow to greenish young lamellae, tall slender or clavate silky fibrillose-stuffed stipes with pale yellowish to olivaceous buff apices and reddish bases, long tapering to thread-like pseudorhizae, large (~10 x 6 µm) warty-rugulose plump limoniform basidiospores with conspicuous abrupt 1 µm long apical beaks, and thin-walled clavate cheilocystidia often observed with long apical outgrowths in older specimens, a bilaminate pileipellis with narrow frequently kinked suprapellicular hyphae embedded in a colorless gel matrix overlying a dark orange pellis with intraparietal pigments, no clamp connections. Negative to faintly magenta (pseudorhizal pellis only) in syringaldazine. Dried pileus metallic greenish yellow bronze.

Pileus 25-120 mm broad, obtuse to convex with inrolled margin becoming expanded umbonate, the surface glabrous, glutinous, hygrophanous, either over-all uniform to irregularly mottled some shade of yellowish to brownish olive (*Buffy Brown, Citrine Drab* to *Dark Citrine,. Deep Olive Buff, Deep to Dark Olive, Olive Brown -- 5Y 3-5/2-6)* or zonate with a more deeply colored disc *(Dark Olive Brown, Chaetura Drab, Clove Brown, Ivy Green -- 10Y 3/2, 5& 3/2)* and distinct edge *(Deep Olive Buff, Buffy Brown, Isabella Color, Buckthorn Brown -- 2.5Y 4/4)*, areas of damage usually darker brown or black, when dried often a metallic greenish yellow bronze; **Context** 3-6 mm high at disc, evenly tapering to pileus edge, cartilaginous, greenish yellow to olive *(Deep Olive Buff, Citrine Drab;* **Odor** fleeting, similar to raw cucumbers or potatoes; **Taste** mild and not distinctive with glutin sometimes bitter;

Lamellae free to deeply adnexed and barely attached to the apex of the stipe, broad (5-9 (20) mm) with wavy to eroded edges, close to crowded (L+ll/cm = ~24/11 in expanded specimens), initially pale yellowish cream-colored (*Tilleul Buff, Cartridge Buff, Chamois),* soon developing duller golden or greenish tones *(Buffy Brown, Isabella*

Color), maturing to darker greenish yellow brown *(Buckthorn Brown, Tawny Olive)*, and becoming rusty brown *(Clay Color)* in maturity;

Veil evident as dark olive to dull brown fibrillose patches on the superior stipe;

Stipe overall 75-220 mm in length (aerial portion 40-100 mm), 6-15 (20) mm across at the apex, equal or expanding downwards to 15-20 (35) mm, often narrowing abruptly below ground level to a thread-like pseudorhiza, moist to lubricous, smooth beneath fibrillose veil patches, apex pale green ('watery olivaceous' according to Smith, 1957) or golden *(Chamois, Cream Buff, Pale to Dark Olive Buff, Isabella Color, Honey Yellow -- 2.5Y 8-9/4-6, 10YR 6/4-6)* and initially distinguished from reddish to orangish red *(Mikado Brown, Kaiser Brown -- 2.5 YR 4/6)* base, reddish tones gradually extending upwards from base eventually turning entire aerial stipe reddish brown, often staining orange or brown where bruised *(Zinc Orange, Mikado Brown, Liver Brown)*, never hollow but with 1-2 mm thick cartilaginous rind surrounding initially firm and white pith that often stains orange- to reddish brown *(Mikado Brown, Liver Brown)* and that in age becomes silky fibrillose and yellowish *(Maize Yellow, Pale Cartridge Buff)*, greenish *(Pale Olive Buff)* or pale cinnamon *(Pale Pinkish Buff)* in color;

Pseudorhiza ?vertical-monopodial, long and narrow, originating from a (rarely collected) thread-like extension, generally liver brown overall except for paler *(Light Pinkish Cinnamon)* ultimate origin.

Spore Print light brown to rusty-brown *(Fawn Color, Mikado Brown, 5YR 4-5/4)*.

Basidiospores: 10 x 6 µm (range of means 9-10 x (5) 5.5-6 µm, overall range 8-11 x 5-7 µm), broadly ovate with an abrupt projecting snout in face view, broadly inequilateral in profile with a dorsally eccentric apiculus and abrupt conspicuous beak, surface rugulose-warty roughened except over the smooth 0.5-1.5 µm apical beak and with a distinct, less coarsely ornamented suprahilar plage, tawny to dark amber in KOH, inamyloid and non-dextrinoid in Melzer's;

Cheilocystidia abundant, emanating from the lamellar trama and of variable lengths, occasionally septate, 3-4 µm wide irregularly cylindrical elements intermixed with 5-7 µm wide clavate elements, gelatinous, in older specimens often observed with thin-walled filamentous (rarely capitulate) apical extensions, sometimes surrounded by a gelatinous matrix or collapsed in an agglutinated barrier, hyaline to yellowish in KOH;

Pleurocystidia: absent;

Basidia 4-spored, 25-40 x 7-9 µm, hyaline in KOH;

Pileipellis a bilaminate ixocutis with a 150-400 µm thick suprapellis composed of radially arrayed cylindrical hyaline hyphae that frequently swell from 1-2 µm near the septa to 3-4 µm with uppermost hyphae slightly separated and often slightly curled or kinked overlying a 200-400 µm thick subpellis composed of thin-walled inflated (5-10 µm)

hyphae with intraparietal pale to dark orange pigments (that can coagulate irregularly within the walls in older specimens) intermixed with oleiferous hyphae filled with oily amber to dark orange intracellular pigments; **Stipitipellis** a thick layer of 5-8 µm wide cylindrical gelatinized and gel-incrusted hyaline hyphae intermixed with oleiferous hyphae filled with pale greenish amber oily contents;

Tramal tissues with dark amber to deep orange oleiferous hyphae occasionally throughout, highly gelatinized, strongly sarcodimitic in pseudorhiza with occasionally thick-walled wide cylindrical hyaline hyphae intermixed with slightly thinner-walled narrow flexuous hyaline hyphae, both hyphal types become less distinct near the stipe apex with wall thicknesses for both types approaching (0.5 to 1 µm) and the wide rigid elements becoming less frequent, the pileal tissues more or less monomitic and greatly similar to those of the subpellis; Lamellar trama parallel, with 3-7 µm wide yellowish hyphae in the central region narrowing to 2 µm at the edges to form a compact rudimentary subhymenium ;

Tibiiform diverticula abundant on mycelia, primordial surfaces and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex, infrequently observed on pileipellis of mature basidiomes;

Clamp Connections absent in all tissues.

Macrochemical Reactions: Syringaldazine usually negative except for occasional pale magenta reactions on the pseudorhizal pellis; KOH soon darkening to a deep blackish brown; $FeSO_4$ soon darkening to a dark greenish brown;

Fluorescence no fresh specimens tested; pith of stipe apex appears deep bright orange under UV light in dried material.

RFLP profile: The 720-bp ITS region of 8 isolates (including type) is represented by two distinct profiles: the 'typical' group of 5 isolates is cut in Pal1 (450-180-190) as well as Cfo1, EcoR1, Hinf1 and Nde2 and uncut in Pvu2, Rsa1, Sal1 and Xho1. Three isolates are cut in Pvu2 (630-90), appear to be cut in Rsa1 (bands are estimated at 705 bp, and produce a different profile in Pal1 (450-100-90-80).

Habit and ecology closely gregarious to cespitose in arcs (occasionally solitary to scattered) on soil in early to late autumn, usually in mixed deciduous-coniferous forests (*Quercus-Pinus* or *Pseudotsuga/Abies/Tsuga-Lithocarpus*), infrequently found in 30 year old *Pseudotsuga* plantations.

Range and distribution at low coastal or higher inland regions in Oregon and California. (Previously reported Washington distributions are based on misidentified collections.)

Type: A. H. Smith 55767 (MICH #00011627), November 17, 1956 from Grants Pass, Josephine County, Oregon.

Comments Smith (1957), who described this species based on abundant material he collected near Grant's Pass Oregon, cited the large size, olive-colored pileus, pallid immature gills, 'silky' fibrillose stipitipith, and orange-reddish stipe in age as constant key field characters. In the field, however, *P. olivacea* can often only with difficulty be differentiated from *P. fallax* and *P. pseudofestiva*, two other endemic Pacific Northwest Phaeocollybias producing green pilei, which frequently grow closely intermingled with specimens of *P. olivacea*. (numerous personal and herbarium collections identified as *P. olivacea* on the basis of field characters were revealed after microscopical examination to contain either *P. fallax* or *P. pseudofestiva* specimens. See also Appendix C -- Specimens Examined).

Phaeocollybia pseudofestiva, which also produces large gregarious to cespitose clusters of similarly colored basidiomes, can be microscopically distinguished by its abundant thick-walled capitulate lageniform and tibiiform cheilocystidia. It tends to produce smaller basidiomes which occasionally develop hollow stipes in maturity (See additional comments under *P. pseudofestiva.*).

Basidiomes of *P. fallax*, which soon lose their diagnostic violet gill coloration and occasionally possess stipes filled with a silky fibrillose stipitipith -- are less easily microscopically differentiated from *P. olivacea* since both species are characterized by thin-walled clavate cheilocystidia. Smith (1957) selected the distinctive basidiospore morphology (stressing the conic apical beak and fairly large basidiospore size) as the key anatomical character of *P. olivacea*. The rotund basidiospores with abrupt beaks up to 1.5 µm long are, in fact, among the most prominently beaked of all North American Phaeocollybias and, according to Redhead (unpublished material, 1992) have a 'strongly convex abaxial surface' that '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.' The basidiospores of *P. fallax* tend to be narrower and the beaks, while often long, tend to be tapered rather than abruptly conic. Nonetheless, in the absence of reference material, a more helpful feature (when present) may be the presence of apical outgrowths found on the cheilocystidia of older *P. olivacea* specimens. While the normally subcapitate thin-walled cheilocystidia in *P. fallax* may expand in diameter with age or storage, they rarely (if ever) develop the thin filamentous apical extensions usually found in older specimens of *P. olivacea*.

It should be noted that proliferation of these apical outgrowths occurs to such an unusual degree in *P. olivacea* that they appear to have been misinterpreted as representing thick-walled capitulate cheilocystidia. Bandala (1994) and Bandala & Montoya (1994) erroneously placed *P. olivacea* into Section *Versicolores* based on Bandala's examination of the type; microscopical examination by the current author using oil immersion and differential interference contrast reveals that while numerous capitulate appendages are indeed present in one of the type specimens, they are thin-

walled and clearly represent developmental outgrowths on originally clavate cheilocystidia rather than the thick-walled capitulate cheilocystidia characteristic of Section *Versicolores* (see also Chapter 3 and Norvell, 1997). It appears that *P. olivacea* properly belongs in Section *Phaeocollybia* where originally placed by Smith (1957).

Despite the existence of two distinct molecular groups as indicated by the RFLP profiles above, the current author could not identify consistent morphological, anatomical, chemical or ecological differences that support two taxa. Better documentation of certain diagnostic characters in newly collected and RFLP tested material are necessary before circumscription of the newly implied taxon can be published formally.

Phaeocollybia oregonensis A. H. Smith & Trappe, *Mycologia* 64: 1145. 1972.
= *Phaeocollybia carmanahensis* Redhead & Norvell, *Mycotaxon* 46: 343-359. 1993
Emended

Figures: 6.23-24

Selected descriptions and illustrations: Horak, 1977 -- anatomical drawings; Redhead & Norvell, 1993 (type description of *P. carmanahensis)* -- black & white photograph with anatomical drawings.

General impression: gregarious medium to moderately-large fleshy farinaceous deeply rooting basidiomes with viscid drab to grayish-brown convex to broadly campanulate pilei, smoky white young lamellae, dry drab stipes stuffed with firm dense white pith, gradually attenuating fleshy vertical-monopodial pseudorhizae, relatively small (6.8 x 4 µm) punctate roughened ellipsoidal (bullet-shaped) basidiospores with rounded apices, long clavate thin-walled cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae embedded in a thick colorless gelatinous matrix above a dull brownish to brownish orange subpellis with incrusting and intraparietal pigments, and the absence of clamp connections. Immediately deep magenta in syringaldazine. Dried pileus reddish to orange brown.

Pileus (20) 30-80 (110) mm broad, conic convex when young with inrolled edges when young, expanding to broadly conic-campanulate with sharply conic subacute umbo, straight margins, and incurved to straight edges, subviscid to viscid or occasionally glutinous (under wet conditions), glabrous, opaque, color generally some shade of drab gray or purplish brown *(Light Drab, Drab, Benzo Brown, Fawn, Avellaneous, Wood Brown, Chaetura Drab)*, very rarely reddish brown, slightly hygrophanous, reddish- to orange-brown when dry; **Context** thick (up to 7 mm) and pallid in young unexpanded specimens, soon thin, cartilaginous, and concolorous with the cuticle; **Odor** farinaceous or cucumber-like, developing unpleasant pungent tones when dry; **Taste** usually farinaceous and bitter;

Lamellae narrowly attached to free, ventricose, narrow to broad (3-10 mm, with mean length-ratio 3.4, range 2-7), crowded, thin with edges even when young to serrulate or eroded in age, polydymous with 3-7 tiers of truncate lamellulae regularly to irregularly interspersed, smoky white when young *(Mouse Gray, Drab Gray)*, becoming yellowish buff before obscured by light yellowish brown spores;

Veil occasionally evident as scattered, short, drab fibrillose patches on aerial stipe;

Stipe central to slightly eccentric, usually 40-85 mm tall above ground level with (4) 7-16 (20) mm wide apex, overall length including pseudorhiza up to 210 mm, usually equal to narrowing downwards, rarely swollen from proliferating pith, longitudinally striate, dry, color generally grayish pink or drab (most frequently *Avellaneous* or *Vinaceous Buff*) at apex, turning to grayish reddish brown *(2.5 YR 3-6/2-4 = Cacao or Walnut Brown)* upwards from ground level, 1-2 mm thick cartilaginous cortex surrounding firm to fibrous whitish or pinkish buff stipitipith;

Pseudorhiza vertical-monopodial, up to 1/2 to 3/4 of overall length, gradually narrowing to blunt,nippled, or curled origin, grayish to dark reddish brown *(2.5 YR 4-5/4-6 = Cacao Brown to 10R 3/4 = Chestnut);*

Spore Print Color dull yellowish cinnamon *(10 YR 6/6* = yellower than *Cinnamon*, darker than *Isabella Color*).

Basidiospores 6.8 x 4 ±0.2 µm (range of means 6.3 - 7.2 x 3.6 - 4.1µm, overall range 5.4 - 7.5 x 3.5-5 µm), distinctly inequilateral in profile (adaxially nearly plane, abaxially convex with a somewhat rounded cone-shaped apex), elliptical to slightly obovate with a tapered bluntly rounded apex giving the spore a 'bullet' shape in face view, germ pore absent but small eccentric apiculus conspicuous, surface virtually smooth to punctate roughened (ornamentation not visibly projecting in profile), relatively thin-walled (compared to most Phaeocollybias), golden brown in KOH, young spores (with thinner exosporium) visibly dextrinoid in Melzer's;

Cheilocystidia generally narrowly clavate (filamentous), emanating from the lamellar trama 12-36 x 5-6 (8) µm on slightly narrower (2-4 µm) pedicels and with penultimate elements often swelling below terminal septa, thin-walled, smooth, hyaline; developmental filamentous apical extensions observed in old or stored basidiomes;

Pleurocystidia: absent;

Basidia 4-spored, 28-36 x 6-6.5 µm, narrowly clavate, hyaline to slightly brownish at the base in older specimens;

Pileipellis a bilaminate ixocutis, with a (30) 100-200 µm thick gelatinous suprapellis (diminishing in age or when affected by weather) composed of 2-5 µm wide repent hyaline hyphae with refractive septa embedded in a gelatinous matrix overlying a 50-200 µm thick dull brownish to brownish-orange (in KOH) subpellis composed of slightly

thicker walled, wider (6-10 µm) elements with incrusting and intraparietal pigments; **Stipitipellis** a thin layer of loose, filamentous, 1-3.5 µm wide hyaline hyphae over a compact layer of 2-4 µm wide hyphae sheathing a compact sordid rind of 5 µm wide hyphae;

Tramal tissues highly gelatinized, strongly sarcodimitic in pseudorhiza, stipe and pileus where long cylindrical wide (to 15 µm) thick-walled (to 2 µm in pseudorhiza and 1 µm in stipe) rigid hyaline hyphae are supported by less conspicuous thin-walled narrow (2-4) branched hyaline flexuous hyphae, both hyphal types also evident in lamellae and pileus; Lamellar parallel with gelatinized predominantly 3-8 µm wide hyaline hyphae in central region, narrowing to 2-3 µm on the edges to form a compact 2-3 stranded rudimentary subhymenium, narrow, highly branched flexuous hyphae also occasionally present;

Tibiiform diverticula abundant on pseudorhizal and primordial pelli, also frequent on vestiges of pellicular veil on stipe apex;, up to 20 µm long, 1.5-1.8 µm wide basally with necks less than 1 µm, with or without a small capitulum and/or apical droplet;

Clamp Connections absent from basidial bases, cheilocystidia and cuticular hyphae, pseudoclamps (see below) occasionally present in tramal tissues;

Macrochemical reactions: Syringaldazine strongly positive (immediately magenta) in all tissues; KOH browning; FeSO4 dull brownish green.

Fluorescence pseudorhizal pellis brilliant pale yellow, stipitipith pale violet; elsewhere dull orange.

RFLP profile: 720 bp ITS region (not successfully amplified from holotypical material of *P. oregonensis)* run for 8 isolates, including isotypic material of *P. carmanahensis* -- Cfo1 (420-200-100) and Pal1 (245-245-125-105) diagnostic enzymes; also cut in EcoR1, Hinf1, Nde2, Pvu2; uncut in Rsa1, Sal1, and Xho1.

Habit and ecology closely gregarious in moist locations in mid to late autumn under *Tsuga heterophylla* and *Abies procera* or *Abies amabilis*; also associated with *Vaccinium, Polystichum munitum,* and *Rhytidiadelphus loreus* or other dense mosses;

Range and distribution: rare, known only from four locations at higher elevations in Oregon (4000', Larch and Wildcat Mountains in Mt. Hood National Forest), USA and British Columbia (Upper Carmanah Valley (type locality for *P. carmanahensis*) and Mt. Seymour), Canada.

Type: A. H. Smith 28420 (MICH) -- October 20, 1947, Larch Mountain, Multnomah County, Mt Hood National Forest, Oregon.

Comments: Diagnostic characters of *P. oregonensis* include the distinctly drab-brown to grayish pileus, smoky white to dark yellowish brown lamellae, consistently stuffed stipe, tissues that become immediately deep magenta in syringaldazine, thin-walled clavate cheilocystidia that readily

develop apical outgrowths, and small, virtually smooth basidiospores. (The basidiospore ornamentation is finer than depicted by Horak in his 1977 review of *Phaeocollybia* types. Visible under the light microscope only under oil immersion, it does not visibly modify the outline of the spore under the light microscope. There is no germ pore.)

Although Smith and Trappe (1972) originally described *P. oregonensis* as having rare clamp connections, extensive examination of fresh and dried material reveals a total absence of any clamps on basidia, cheilocystidia, and cuticular hyphae. However, the tramal hyphae do appear to produce occasional to not infrequent 'pseudo-clamps' (small branchlets or balloon-like diverticula noted close to or well away from the septa) that could easily be misinterpreted as true clamp connections. These pseudo-clamps (far more noticeable in fresh material) are more easily identified as such when examined under oil immersion using Nomarsky optics (differential interference contrast). It is possible that Smith & Trappe misinterpreted these as true clamp connections. The ends of flexuous hyphae winding around the more rigid thick-walled elements within the tramal tissues could also be similarly misinterpreted (*Cf.* sarcodimitism, Chapter 3).

Redhead & Norvell (1993) separated *P. carmanahensis* from the microscopically similar *P. oregonensis* based in part on the lack of clamp connections, although they were aware of the unpredictable appearance of clamps in the older-named taxon. Other differentiating characters included a thinner 'glassy' suprapellis, absence of incrusting pigments, smaller stature, and drab coloration of pilei that contrasted with the 'dark reddish brown to dull liver brown' originally described for *P. oregonensis*. Subsequent collections (including topotypical material) of *P. oregonensis* from three different localities has provided a much better basis for comparison of the two species. The absence of true clamp connections in *P. oregonensis* has been noted. Seventeen recent collections indicate that *P. oregonensis* characteristically produces somewhat small to moderately large basidiomes identical in color to that described for *P. carmanahensis*. Examination of older specimens that have been exposed to freezing temperatures or hard precipitation suggests that the gelatinous matrix of the suprapellis can be washed off to some degree, with the thin remaining layer developing the glassy appearance and dissolution of incrusting pigments noted by Redhead and Norvell (1993) for *P. carmanahensis*. The differences in color might be explained by the fact that Smith and Trappe did not collect the type themselves but were handed material collected by another; and it could have been degraded. In view of the identical RFLP profiles and now recognized macroscopical and microscopical similarities, *P. carmanahensis* is now considered synonymous with *P. oregonensis*.

Although *P. oregonensis* might be confused with smaller, more slender specimens of *P. kauffmanii* or *P. benzokauffmanii* in the field, the latter are readily differentiated by their larger, limoniform-rostrate, clearly verrucose, darker basidiospores. Microscopically, it is clearly separated from *P. sipei* and *P. dissiliens*, two species with clearly different macroscopic

appearance but with very similar basidiospores, by differences in cheilocystidial morphology and pigmentation. (*Phaeocollybia dissiliens* is further differentiated by having clamp connections on the basidia, cheilocystidia, and cuticular hyphae.)

Phaeocollybia phaeogaleroides nom. prov.

Figures: 6.25-26

General Impression: solitary to widely scattered small fragile cartilaginous rooting basidiomes with subviscid pale to dark yellow brown thin-fleshed broadly campanulate pilei, pallid to buff young lamellae, thin cartilaginous slightly polished fibrillose-stuffed to hollow dark brown stipes, wire-like (criniform?) monopodial pseudorhizae, large (~10 X 5.8 µm) faintly verruculose-roughened ellipsoid basidiospores with rounded to very slightly pointed apices, cylindrical to slender subcapitate thin-walled cheilocystidia, an ill-defined bilaminate pileipellis with clamped narrow hyaline suprapellicular hyphae overlying a pale orange-yellow subpellis, clamp connections, and unusually long (up to 50 µm) tibiiform diverticula. Negative in syringaldazine.

Pileus 28-50 mm wide, convex-campanulate with prominent obtuse umbo when young, broadly campanulate with or without an acute umbo and uplifted margin with cuticle extending beyond lamellae when mature and sometimes radially rugose around the disc, glabrous, subviscid to viscid, hygrophanous, long pellucid striate when moist, when young uniformly honey brown (*Warm Buff, Yellow Ochre -- 10YR 6/6)* becoming darker and ferruginous (*Clay Color)* in age; **Context:** thin (2 mm thick at the disc), whitish to pale tan; **Odor** & **Taste** not distinctive;

Lamellae narrowly sinuate attached, ventricose, 4-8 mm broad (length:width ratio 3.8), thin with slightly serrulate edges, close, with 3-5 tiers of lamellulae more or less regularly interspersed, pallid to buff colored when young *(Warm Buff)* when young, pale rusty brown when mature;

Veil no remnants visible;

Stipe central, terete, overall length including pseudorhiza up to 180 mm, aerial portion 60 mm long, apex 2-4 mm diam, more or less equal above and gradually narrowing below to pseudorhiza, glabrous, dry, slightly polished, apex when young honey brown (*Warm Buff -- 10YR 7/6*), becoming dark reddish vinaceous brown from ground upwards in maturity, very thin (0.5 mm) cartilaginous rind surrounding fibrillose whitish pith when young, stipe fistulose in age;

Pseudorhiza (?lateral) monopodial, slightly >1/2 overall stipe length, gradually tapering to a wiry point where broken off, dark red brown *(2.5 YR 5/6)*;

Spore Print Color reddish brown *(Cacao Brown, 2.5YR 4/4-6)*.

Basidiospores 10 X 5.8 ± 0.6 x 0.4 µm (overall range 9-12 x 5-6.2 µm), terete or slightly compressed, ellipsoidal with eccentric apiculus and rounded to slightly pointed apex, very finely verruculose roughened, that ple an ill-defined area of lowered ornamentation faintly discernible in oil immersion, amber in KOH, yellowish in H2O, inamyloid and nondextrinoid in Melzer's;

Cheilocystidia cylindrical to subcapitate, emanating from the lamellar trama, 25- 50 x 2-4 µm, occasionally narrowing to form 2 µm non-refractive neck beneath 3-5 µm wide subcapitate apices, thin-walled, hyaline to pale orange yellow in KOH, more or less applutinated in revived material;

Pleurocystidia: absent;

Basidia 2- &4-spored, 28-32 X 8-10 µm, with basal clamp connections, hyaline;

Pileipellis an ixocutis with a 50-100 µm thick colorless subgelatinized suprapellis composed of cylindrical 2-4 µm thin-walled gelatinized hyaline hyphae with clamp connections and a 150-200 µm thick pale orange yellow subpellis composed of 4-8 µm wide gelatinized hyphae; **Stipitipellis** not well delimited and composed of a colorless layer of tightly packed 2-4 µm wide subgelatinized hyaline hyphae overlying a pale orange-yellow zone of heavily gelatinized 10-15 µm wide hyphae; **Pseudorhizal pellis** with a hyaline pellicular veil composed of 2-3 µm wide hyaline diverticulate hyphae overlying a pigmented zone of 5-10 µm wide rusty brown hyphae with 0.5 µm thick walls;

Tramal tissues gelatinized, with occasional oleiferous hyphae throughout, weakly sarcodimitic in the pseudorhiza and lower stipe with long (50-80 µm) wide (10-15 µm) hyaline hyphae with 0.5 µm thick walls intermixed with thinner-walled 2-4 µm wide gelatinized hyaline flexuous hyphae; elsewhere only one hyphal type found with the the pileitrama a 20-50 µm thick zone of gelatinized pale amber to hyaline hyphae similar in shape those found in the subpellis; Lamellar trama parallel and relatively narrow, composed of highly gelatinized thick-walled 3-7 µm wide pale orange yellow hyphae;

Tibiiform diverticula unusually long (15-50 µm) and wide (1-2 µm), present on stipitipellis and abundant on pseudorhizal pellis, hyaline and refractive, usually capitulate with 2-3 µm diam capitulum and/or apical droplet;

Clamp Connections present on suprapellicular hyphae and at basidial bases.

Macrochemical reactions: Syringaldazine -- negative; KOH -- slightly reddish brown; FeSO4 -- greenish;

Fluorescence: Fresh material not tested; young dried lamellae bright yellow orange;

RFLP profile: not tested

Habit and ecology: solitary to scattered in late autumn in moss in damp low lying areas in relatively open areas near or under young to mature mixed coniferous (*Picea sitchensis, Tsuga heterophylla)* forests.

Range and distribution Collected from four different sites in British Columbia and Oregon.

Reference collections: [1] G.Wright 2103 (MICH as *P. radicata)*; collected November 20, 1980, 15 miles north of Florence, Coos County, Oregon; [2] LLN 95.11.06-1 (WTU) collected by N.S. Weber at Drift Creek, Lincoln County, Oregon. [3] R) 109 by R. Outerbridge near Fairy Lake, Hwy 124, Vancouver Island, BC, [4] RO 298 by S. A. Redhead at U.K. M/L Hwy 95 #7, Vancouver Island, BC.

Comments: *Phaeocollybia phaeogaleroides* was first discovered in the Michigan herbarium by this author from a collection by Greg Wright. Many of its diagnostic characters -- small fragile aspect, solitary to scattered habit in moss near spruce, more or less uniform honey-brown coloration, and large ellipsoidal non-dextrinoid basidiospores recall the genus *Phaeogalera* for which it is named. In the field it might be mistaken for *P. attenuata* or *P. similis* which are discriminated microscopically by heavily ornamented subglobose-limoniform prominently beaked basidiospores and the absence of clamp connections. Other diagnostic characters include the unusually large tibiiform diverticula and the strangulated or subcapitate narrow thin-walled cheilocystidia. No molecular research has been performed on *P. phaeogaleroides* to date.

Under low power the basidiospores may appear smooth and to possess apical pores similar to those characterizing the genus *Phaeogalera*. Under oil immersion, however, the faintly verruculose-roughened ornamentation is visible and the 'pores' are seen to be small callus deposits that produce refractive rounded to slightly pointed apices. Large ellipsoidal punctate-roughened basidiospores, rarely found in the genus, also characterize *P. christinae*, which also has a small fragile stature and filamentous to subcapitate thin-walled cheilocystidia. *P. phaeogaleroides* differs in its possession of clamp connections in the pileipellis and at the basidial bases, slightly longer and wider basidiospores with more subdued ornamentation, much larger tibiiform diverticula, and a more subdued coloration.

Phaeocollybia piceae A. H. Smith & Trappe, *Mycologia* 64: 1145, 1972.

Emended

Figures: 2.4, 6.27-28

Selected descriptions and illustrations: Smith & Trappe, 1972 -- type description; Horak, 1977 -- anatomical drawings; Norvell, 1997 -- drawing.

General Impression: scattered to gregarious small to medium-sized fleshy deeply rooting basidiomes with moist to subviscid bright orange to reddish orange

convex to campanulate pilei, yellow buff young lamellae, orangish slender slightly swollen matter to polished stipes stuffed with frequently insect-eaten pith, gradually attenuating salmon-colored vertical-monopodial pseudorhizae, ~9.4 x 6 µm verruculose to verrucose broadly limoniform basidiospores with rounded apical beaks, cylindrical to slightly subcapitate narrow thin-walled cheilocystidia, a bilaminate pileipellis with a thin colorless suprapellis of narrow hyphae overlying an orange (in H20, soon disappearing in KOH) subpellis composed of thin inflated hyphae with intercellular pigments, no clamp connections. Frequently associated with spruce. Inert in syringaldazine. Dried pileus pale orange copper (from young specimens) to dark reddish brown (old).

Pileus 15-60 mm, obtusely conic-convex with tall umbo, incurved margin and inrolled edges expanding to broadly campanulate with low broad umbo, straight to down-turned margin and incurved edge, often with sinus on one side, moist to thinly viscid, glabrous, occasionally striate, color uniformly some shade of bright to dull orange *(Ochraceous Orange, Zinc Orange, Ochraceous Buff, Tawny, Ochraceous Tawny, Orange Rufous)* or zonate with darker/duller disc and paler/darker edges, hygrophanous, dried pileus a pale orange copper in young specimens, dark rufous brown matte in older; **Context** thin (2-3 (5) mm at disc), firm and creamy white *(Pale Pinkish Buff, Pale Ochraceous Salmon, Light Ochraceous Salmon)* when young but soon cartilaginous and concolorous with cuticle; **Odor** sometimes not distinctive but usually slightly raphanoid to sweetly farinaceous, pungent in very old specimens; **Taste** usually but not always bitter, occasionally mild or raphanoid/farinaceous;

Lamellae ascending-adnexed to almost free, initially crowded becoming merely subclose to almost distant in expanded specimens (L+ll/cm = 13-25 edge, 9-13 midpoint), narrow (3-4 (6) mm, mean L:W = 4.8), thin, edges even at first, then serrulate ruffled, color when young yellow buff *(Pale Ochraceous Salmon, Pale Ochraceous Buff, Ochraceous Buff, Pinkish Buff, Cinnamon Buff)*, darkening in age to cinnamon or rusty brown *(Cinnamon, Tawny, Clay Color)* when fully mature;

Veil infrequently evident as sparse appressed short reddish-brown fibrils on stipe apex;

Stipe ± central, usually 40-80 mm above ground level with 4-12 mm wide apex, overall length including pseudorhiza up to 225 mm long, equal or gradually narrowing except for characteristic slight swelling at ground level, dry to lubricous, glabrous and smooth (sometimes polished), inconspicuously longitudinally striate, dry to moist, moderate orange to pinkish buff apex *(Light Orange, Zinc Orange, Orange Cinnamon, Pinkish Cinnamon)* gradually deepening to deeper orange or orange red *(Xanthine Orange, Hay's Russet, Chestnut)* at ground level, staining bright orange *(Mars Yellow, Tawny)*, 1-2 mm

thick cartilaginous cortex surrounding firm to spongy pinkish-orange pith that characteristically is completely consumed by insects above and below substrate surface;

Pseudorhiza vertical-monopodial, 1/2 to 2/3 of overall length, narrowing to 2-3 mm wide generally curled-upwards origin, sometimes found attached to older pseudorhizae or pseudorhizal remnants from older specimens, dark reddish to orangish brown *(Hay's Russet, Hazel, Russet)*, staining bright orange *(Zinc Orange)*;

Spore Print dark reddish brown *(Munsell 5 YR/ 5/4-6 = Fawn Color)*.

Basidiospores 9.4 x 6 ± 0.4 x 0.2 µm (overall (8) 9-10.2 x (5) 5.3 - 6.3 µm), broadly amygdaliform with subdued apical snout in face view, broadly inequilateral (limoniform) in profile with rounded apical snout and distinct eccentric apiculus, ornamentation subdued to slightly more pronounced except over apex and apiculus, plage either indistinct or absent, pale medium to medium orange amber in KOH, paler in H20, dextrinoid in Melzer's;

Cheilocystidia abundant, filamentous with rounded to very slightly subcapitate apices, emanating from the lamellar trama, variable in length but up to 50 µm long, 2.3-3 µm wide, with apices swelling occasionally to 4 µm, thin-walled, hyaline in KOH and H20;

Pleurocystidia absent;

Basidia 4- (rarely 2-) spored, 30-45 x 6.5-8.5 µm, clavate, frequently on long 2-3 µm wide pedicels, hyaline;

Pileipellis a bilaminate ixocutis with a thin (20-50 µm) suprapellis composed of radially aligned 2-3 µm wide hyaline gelatinized hyphae overlying an orange (in H2O) subpellis of long (up to 85 µm), inflated (6-8 µm wide) thin-walled 'sausage-shaped' hyphae that narrow abruptly to highly refractive septa, pigment in subpellis orange and diffuse, visible in H20 but readily soluble in KOH where soon undetectable in young specimens except where (rarely) concentrated in brilliant orange pools, occasional orange oleiferous hyphae also present; **Stipitipellis** of parallel, 2-3 µm wide, heavily gel-incrusted hyphae (hyaline in KOH) over 6-8 (10) thick-walled hyphae; **Pseudorhizal pellis** of 1-2 µm wide orange-amber hyphae, septate tibiiform thin-walled (non-refractive) caulocystidia occasionally intermixed with tibiiform diverticula;

Tramal tissues subgelatinized, sarcodimitic in the pseudorhiza and weakly sarcodimitic in the stipe apex and pileus with long (~150 µm) wide (8-15 µm) rigid thick-walled (1 µm) hyaline elements considerably more abundant than inconspicuous thin-walled narrow (2-3 (4) µm) branched flexuous hyaline hyphae; Lamellar trama parallel with 2-4 µm wide thin-walled hyaline hyphae in the central region narrowing to 1-2 µm at the edges to form a rudimentary subhymenium;

Tibiiform diverticula abundant on pseudorhizal pellis, up to 20 µm x 1 µm, usually with 1.5-2 µm wide capituli, secretory;

Clamp Connections absent.

Macrochemical reactions: Syringaldazine -- negative; KOH -- gills immediately dark brown; FeSO4 -- gradually dull brownish green (all tissues).

Fluorescence: Lamellae intense pale yellow.

RFLP profile: ITS region of 8 isolates = 700 bps (type DNA not successfully amplified). Unique in EcoR1 (350-350), Hinf1 (360-195-145), Pal1 (610-90), and Sal1 (515-185). Also cut in Cfo1 and Nde2; uncut in Pvu2, Rsa1 and Xho1.

Habit and ecology Solitary to scattered in small groups on sandy to well-drained humic soils in mid to late autumn, characteristically under *Picea* + *Abies* or *Picea* + *Tsuga* (found in mixed coniferous forest under *Tsuga* + *Abies* 20 miles south of last established *Picea sitchensis* grove on the California coast).

Range and distribution generally at low elevations along the Pacific coast (to 80 miles inland) in British Columbia (Vancouver Island), Washington, Oregon, California (Mendocino County), (LLN 94.10.22-7 was collected at the 4000' elevation near Mt. Hood (Oregon)).

Type: A. H. Smith 79085 MICH -- October 16, 1970 Cascade Head Experimental Forest, Tillamook County, Oregon.

Comments: *Phaeocollybia piceae* apparently was collected only once by Smith & 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 Heaven's Grove (Lower Carmanah Valley), Vancouver Island at the northernmost limits of its known range, the species has proved considerably more elusive in Washington, Oregon, and California, although it was collected from the same spot from Oregon's Oswald West State Park during consecutive seasons from 1991-1994. Numerous recent collections indicate that only rarely are more than four basidiomes found close together and that a solitary to scattered distribution is fairly typical. Nonetheless observation of younger basidiomes arising from 'nurse' pseudorhizae of older specimens (See Chapter 2) verifies that a cespitose habit, reported as typical by Smith & Trappe (1972), also occurs.

Field characters for *P. piceae* include its small to medium size, bright orange to reddish orange moist pileus (described as being 'about the same color as *P. christinae*' by Smith & Trappe, 1972), often bitter taste, orange equal then basally swollen stuffed stipe, and frequent (although not obligate) association with spruce. The stipitipith in mature basidiomes is characteristically consumed by insects at ground level, causing otherwise fresh specimens to tip over when touched (unusual in Pacific Northwest Phaeocollybias); most lower stipes and pseudorhizae were therefore retrieved in pieces. Microscopically very similar to the far more robust *P. kauffmanii*, *P.*

piceae has larger basidiospores with less pronounced apical beaks, narrower cheilocystidia, a much thinner suprapellis lacking a gelatinous matrix, and diffuse orange pigments that dissolve in KOH.

There appears to be variation in basidiospore ornamentation and color -- from minutely warty, pale amber (in topotypical material) to more coarsely roughened, medium orange amber (in Californian and British Columbian material). Although the ITS region has not yet been successfully amplified from type specimens, it has been successfully obtained and tested from 1993 topotypical material along with 7 other isolates. All isolates display the same unique profile (see above), suggesting that the minor variations in basidiospore ornamentation and color are not taxonomically significant.

Phaeocollybia pleurocystidiata nom. prov.

Figures: 6.29-30

General impression: gregarious small pliant ochraceous-tawny faintly farinaceous deeply rooting basidiomes with subviscid tawny yellow to yellow brown convex-umbonate pilei, pale pinkish buff to tan young lamellae, pale orangish pink slender equal stipes stuffed with fibrillose pith, large (~9.25 x 6 µm) verrucose-rugulose limoniform basidiospores with rounded apical beaks, highly refractive tibiiform cheilocystidia and pleurocystidia, a bilaminate pileipellis with a thin suprapellis of narrow yellow encrusted hyphae overlying a moderately thick orange to orange-brown subpellis with incrusting and intraparietal pigments, no clamp connections. Negative to tardily magenta in syringaldazine. Vernal.

Pileus 10-30 mm diam, convex-umbonate with incurved margin and edge when young, expanding to conic campanulate with down-turned margin and slightly undulate edge, umbo often with small sharp papilla, surface glabrous except for occasional edge fibrils, moist to thinly viscid, slightly hygrophanous, nonstriate, when moist uniformly yellow brown overall *(Buckthorn Brown, Cinnamon, Sayal Brown)*, under dry conditions becoming zonate with foxy brown *(Tawny)* disc and papilla, ochraceous yellow *(Yellow Ochre, Ochraceous Buff)* margin, and yellow brown *(Buckthorn Brown)* edge; **Context** 2 mm thick at the disc, pale buff *((Pale) Pinkish Buff)*; **Odor** not distinctive to slightly farinaceous or raphanoid when crushed; **Taste** raphanoid or slightly farinaceous;

Lamellae free, ventricose, thin with ± even to sinuous pallid edges, both forked and reverse-forked lamellae present, polydymous with 3-7 lamellulae regularly interspersed, narrow (mean length:width ratio 5.5), subcrowded, faces pale buff *((Pale) Pinkish Buff)* when young, becoming rusty brown *(Clay Color)* in age;

Veil occasionally evident as isolated brownish *(Mikado Brown)* fibrils on pileal edge and stipe apex;

Stipe central to slightly eccentric, 2-4 mm wide at the apex, up to 50-80 mm long above ground level, overall length (including pseudorhiza) up to >130 mm long, terete and more or less equal, surface innately longitudinally lined and slightly polished, smooth except for irregularly distributed fibrillose and glutinous patches, lubricous, color at first over all pinkish brown *((Light) Pinkish Cinnamon)* but soon darkening from ground upwards to dark reddish-brown *(Liver Brown)*, occasionally with orange-brown *(Mikado Brown)* band between paler apex and darker lower portion, 1 mm thick cartilaginous rind surrounding compact fibrillose pale buff *((Pale) Pinkish Buff)* stipitipith in young insect-free specimens, stipitipith loosening and becoming stringy in older material;

Pseudorhiza vertical monopodial, slightly >1/2 overall stipe length, gradually tapering to slightly blunt origin, dark red brown;

Spore Print Color: not obtained; spores on mature gills close to dark reddish brown *(Hay's Brown).*

Basidiospores 9.25 x 6 ± 0.2 µm (overall range 8-11 x 5-7 µm); in profile broadly limoniform with a medium-sized eccentric apiculus and rounded to tapered ≤ 0.5 µm long beaked apex, in face view ovate to very slightly amygdaliform, verrucose to finely rugulose roughened except over apiculus and beak, suprahilar area an ill-defined plage with lowered ornamentation visible only under oil immersion, ornamentation noticeably darker under low magnification, but when viewed under oil immersion entire spore appearing more or less deep orange in KOH;

Cheilocystidia abundant and tightly packed, lageniform to tibiiform, 17-30 µm lengthwise, ventricose basal portion swelling above 2-3 µm wide septum to 4-5 (6) µm before sharply attenuating to highly refractive thick-walled narrow (1-1.5 µm) neck, some with a 1.5-2 µm diam capitulum with or without a surrounding secretory apical droplet, hyaline;

Pleurocystidia frequent, similar to lageniform and tibiiform cheilocystidia in form, secretory and often accompanied by apical droplets, refractive necks (dull medium amber in KOH) with ochraceous contents visible under a hand lens on fresh gill faces;

Basidia 4-spored, clavate to slightly irregularly saccate in revived material, 25 x 6-8 µm, hyaline to slightly yellowish in older material;

Pileipellis a bilaminate ixocutis with a thin (20-50 µm) rudimentary suprapellis composed of radially aligned 1-2 µm wide gelatinized pale yellowish spirally encrusted hyphae intergrading into a ~120 µm thick orange to orange-brown subpellis of 2-6 µm gelatinized hyphae with brownish encrusting and orange intraparietal pigments, occasional orange oleiferous hyphae present; **Stipitipellis** of 1-2 µm wide gelatinized hyphae with dull grayish orange encrusting and orange intraparietal pigments intermixed with wider occasional dark bright orange oleiferous hyphae;

Tramal Tissues moderately to highly gelatinized, strongly sarcodimitic in pseudorhiza with long (95-200 µm) wide (15-20 µm) thick-walled (up to 4 µm) hyaline rigid (*i. e.* 'vessel')

hyphae supported by inconspicuous branched narrow (4-6 µm) thin-walled (0.5 µm) hyaline 'flexuous' hyphae that become less numerous towards the stipe apex where the thick-walled (1 µm) wide (10-15 µm) vessel hyphae predominate, the glassy-appearing tissue in pileus consisting predominantly of interwoven moderately thick-walled elements; Lamellar trama subparallel, with 4-6 µm wide highly gelatinized thin-walled hyaline hyphae in the central region narrowing at to edges to 1-2 µm, giving rise to a rudimentary subhymenium;;

Tibiiform diverticula abundant on pseudorhizal pellis, 5-15 x 1-2 µm, refractive, hyaline, with or without apical secretory droplets;

Clamp connections: absent in all tissues.

Macrochemical reactions: Syringaldazine -- negative to latently positive (magenta after 45 minutes); KOH -- not tested; FeSO4 -- greenish;

Fluorescence: lamellae -- intense white when very young, developing brilliant yellow tones in older material and finally becoming dull mustard yellow in age;

RFLP profile: ITS region of 3 isolates (including type) = 740 bps. Pal I (450-190-10) most informative enzyme. Also cut in Cfo1, EcoR1, Hinf1, Nde2, and Pvu2. Uncut in Rsa1, Sal1, and Xho1.

Habit and ecology: Vernal fruiting (January through June), scattered to gregarious in loam in moist coastal mature to ancient mixed coniferous forests (*Tsuga, Picea, Abies)* amidst *Polystichum munitum, Blechnum spicant, Vaccinium, Hylocomium splendens.*

Range and distribution: Collected along from 6 different sites in Washington, Oregon, and California.

Type: LLN 94.03.30-1, (holotype at WTU; isotype at DAOM) -- collected by L. L. Norvell & S. A. Redhead along Bogachiel River trail, Olympic National Park, Clallam County, Washington.

Comments:*Phaeocollybia pleurocystidiata* was first discovered in the herbarium as a new species by Dr. S. A. Redhead, who noted the unusual presence of abundant pleurocystidia in a collection donated and previously identified as *P. attenuata* by Dr. H. D. Thiers. Its vernal fruiting habit, ochraceous yellow to tawny pileus, small stature, and large limoniform basidiospores are other defining features. In the field it could be mistaken for *P. radicata* (which has small ellipsoidal basidiospores, lacks pleurocystidia, has clamp connections, and fruits only in the autumn) and *P. attenuata* and *P. 'similis'* (both of which produce thin-walled clavate cheilocystidia, lack pleurocystidia, have criniform lateral-monopodial rhizomorphic pseudorhizae, and fruit in the autumn). According to Singer's (1986) sectional classification, *P. pleurocystidiata* would be placed into Section *Versicolores* with *P. californica, P. pseudofestiva, P. rufotubulina, P. scatesiae,*and *P. spadicea.* It is worth noting, however, that its unusually long ITS region

(740) distinguishes it molecularly from those species and gives it a unique RFLP profile. Preliminary phylogenetic analyses generated from restriction enzyme polymorphisms imply a close relationship with *P. attenuata* and *P. similis*.

Phaeocollybia pseudofestiva A. H. Smith, *Brittonia* 9: 213-214, 1957.
Emended

Figures: 6.31-32

Selected descriptions and illustrations: Smith, 1957 -- type description with anatomical drawings; Horak, 1997 -- anatomical drawings.

General impression: gregarious small to medium-sized cartilaginous deeply rooting basidiomes with viscid to glutinous dark olive green conic-campanulate pilei, pale dull yellow young lamellae, apically pale greenish slender fibrillose-stuffed to hollow stipes tapering below to long cord-like (?vertical-monopodial(pseudorhizae, medium-sized (~8 x 5 µm) verrucose to rugulose ornamented tapered limoniform basidiospores with prominent tapered apical beaks, abundant lageniform and tibiiform thick-walled refractive-necked cheilocystidia, a bilaminate pileipellis with curly to collapsed hyaline suprapellicular hyphae floating in a colorless gelatinous matrix overlying a greenish amber (in H2O) subpellis with slightly encrusting and intraparietal pigments, and no clamp connections. Magenta in syringaldazine. Dried pilei with dark red brown discs with or without slightly metallic orange brown margins.

Pileus (15) 25-75 (100) mm broad, acutely convex with incurved to slightly inrolled edge to conic-campanulate with slightly incurved to straight edge, glabrous, viscid to glutinous, hygrophanous and faintly striatulate, either over-all uniformly to mottled dark olive green *(Citrine Drab, Dark Olive -- Y5 4-6/2-4)* or more often zonate with darker-colored disc *(Dark to Deep Olive, Light Brownish Olive, Olive Black, Olive Brown -- Y5 2-4/1-2)* and brighter yellowish green margin *(Citrine Drab, Honey Yellow, Isabella Color, Dark Olive Buff -- Y5 4-6/2-4, Y2.5 4-6/4-6)* bordered by a greenish olive to greenish brown edge *(Dark to Deep Olive, Dark Olive Buff, Buffy Brown, (Light) Brownish Olive, Buffy Olive -- Y5 4-6/2-4)*, areas of damage dark brown *(Verona Brown, Kaiser Brown -- Y 2.5 4/6)*, when dried a dark reddish brown over the disc and slightly metallic orange brown over margin and edge; **Context** 2-5 (6) mm thick at disc and gradually thinning over the gills, cartilaginous, dull yellowish to very pale olive green *(Isabella Color, Buffy Olive, Pale Olive Buff -- Y5 8/1, Y2.5 4-6/6;* **Odor** mild (not distinctive) or very occasionally faintly sweet-nutty; **Taste** mild (not distinctive);

Lamellae free to deeply adnexed, medium broad (3-7 mm) with even to eroded edges, moderately close (L+l/cm 14-26 edge, 9-12 midpoint) with 4-5 tiers of lamellulae

irregularly interspersed, initially pale yellowish or greenish buff *(Ivory Yellow, Chamois, (Pale) Olive Buff, Light Ochraceous Buff,* rarely *Pinkish Buff -- Y1.25 6-8/4, Y5 6-8/1-2, Y7.5 8/2),* darkening in maturity *(Isabella Color, Deep Olive Buff, Cinnamon Buff -- Y2.5 4-6/4-6)* and in age becoming dark greenish brown *(Saccardo's Umber -- Y1.25 4/2-4)* beneath spores;

Veil evident as numerous short gold to greenish brown *(Dark Green, Deep Olive Buff, Dark Olive)* fibrillose patches (occasionally concentrically arrayed) on stipe apex;

Stipe central to slightly eccentric, usually 30-70 (100) mm tall above the ground (overall length including pseudorhiza up to 235 mm long, 4-13 mm across at the apex, equal, tapering or slightly broader at ground level, dry to moist, slightly polished beneath scattered short fibrillose patches, greenish to pinkish buff *(Deep Olive Buff, Ecru Olive, Tea Green, Light Cinnamon Buff -- Y5 4-8/2-4)* young apex darkening in age *(Olive Buff, Buffy Brown, Wood Brown, Cinnamon -- YR 7.5YR 5-6/6-8),* basal portion soon dark green or dark yellowish to reddish brown *(Buffy Brown, Hazel, Pecan Brown -- YR3.75 4/6, YR8.75 4/3),* often staining brown where bruised, 2 mm cartilaginous cortex usually surrounding firm to closely compacted (when young) or stringy (older) fibrillose pith, sometimes becoming hollow or insect-infested in very old or water-logged specimens, young stipitipith pale greenish to pinkish buff *(Pale Olive Buff, Buffy Olive, Pale Pinkish Buff, Cinnamon Buff -- Y5 8/1, YR7.5 8/2);*

Pseudorhiza either vertical-monopodial and tapering to a more or less blunt curled origin or possibly racemose (see comments below) tapering to a thin cord, dark orange to reddish brown *(Mikado Brown, Verona Brown, Liver Brown, Kaiser Brown -- YR 2.5-5 4/4-6, R8.75 2-4/4-6);*

Spore Print pale to deep pinkish cinnamon colored *([Light] Pinkish Cinnamon -- 7.5 YR 6-7/6).*

Basidiospores 8 x 5 ± 0.6 x 0.3 µm (overall range 7-9.5 (10) x 4.5-5.5 (6) µm), ovate with elongated narrow apical beak in face view, fusiform in profile with dorsally eccentric apiculus opposed to a central beak, surface verrucose to rugulose warty roughened except over 0.5-1.0 µm long apical beak, ornamentation also slightly subdued over indistinct plage area, pale to medium amber in KOH, inamyloid and non-dextrinoid in Melzer's;

Cheilocystidia abundant, lageniform to capitulate tibiiform, overall 25-79 µm long with a 3-7 µm wide hyaline base that narrows to a long (12-20 µm) 0.5-2 µm wide neck, acute or capitulate, capituli generally small but occasionally up to 2.5 µm wide and often obscured by apical secretory droplets, thickened highly refractive walls of neck pale greenish in H2O and ochraceous in KOH, elements sometimes gel-encrusted;

Pleurocystidia: absent;

Basidia 4-spored, 23-32 x 6-8 µm, hyaline to pale amber in KOH;

Pileipellis a bilaminate ixocutis with a 100-250 µm thick suprapellis composed of a clear gel matrix in which are embedded long slightly branching curly to collapsed 1-2 (3) µm wide gelatinous hyaline hyphae overlying a subpellis composed of much wider ('floccose', cf. Smith, 1957) hyphae with intraparietal and/or diffuse pale greenish amber pigments (faintly encrusting when fresh) that turn pale orangish amber when viewed in KOH intermixed with occasional hyaline to pale amber oleiferous hyphae; **Stipitipellis** a thick layer of sparingly branched long cylindrical 2-4 µm wide hyaline to pale greenish amber hyphae;

Tramal tissues gelatinized with amber to colorless oleiferous hyphae occasional present throughout; Lamellar trama parallel, ~50 µm wide, composed of long 2-3 µm wide hyaline hyphae of which the outermost two or three form a rudimentary subhymenium, hyaline to pale amber in KOH;

Tibiiform diverticula abundant on mycelia, primordia, vestiges of hyaline to brownish pellicular veil (stipe apex) and pseudorhizal pellis, tibiiform, 5-20 x 1 x 0.5 µm;

Clamp Connections absent.

Macrochemical Reactions: Syringaldazine magenta on stipe and pseudorhiza; KOH brown; FeSO4 greenish;

Fluorescence no fresh material tested; dried lamellae and upper pith bright yellow orange under UV;

RFLP profile: PseA: ITS region of 3 isolates = 700 bps (DNA from holotype too degraded for RFLP analysis). Cut in Cfo1, EcoR1, Hinf1, Nde2, Pal1, and Pvu2; uncut in Rsa1, Sal1 & Xho1. **PseB:** ITS region of 4 isolates = 700 bps, but with different banding patterns in all enzymes where PseA cut (most informative Pvu2 with 640-60 for PseA and 605-95 for PseB). **PseAB** ITS region (1 isolate) = 700 bps, RFLP profile a combination of PseA and PseB profiles.

Habit and ecology solitary to highly gregarious and cespitose under mixed conifers (*Picea, Abies, Tsuga* and *Pseudofestiva*), conifers accompanied by *Lithocarpus* in the southern part of the range.

Range and distribution Relatively rare in coastal to inland temperate rainforests from Vancouver Island (British Columbia) south through Washington and Oregon to Santa Cruz County (California).

Type: A. H. Smith 8274 (MICH 00011632) -- October 31, 1937, Crescent City, California.

Comments The greenish viscid conic pileus and dull to ochraceous yellow lamellae are key field characters for this species. In stature, pileus shape and pileus color, basidiomes of *P. pseudofestiva* greatly resemble those of *P. fallax;* young specimens of the two species can be differentiated in the field by the presence or absence of the violet coloration of the lamellae and

stipe apex (characteristic of *P. fallax).* In the field, *P. pseudofestiva* has been far more frequently mistaken for the larger, more robust *P. olivacea*, a frequent close associate throughout the southern part of its range (Oregon, California), due to the fact that both species have similarly colored pilei and lamellae. Microscopically *P. pseudofestiva,* with its abundant lageniform and tibiiform cheilocystidia, is clearly distinct from *P. fallax* and *P. olivacea,* both of which are characterized by thin-walled clavate cheilocystidia. The moderately large fusiform basidiospores with the prominent tapered beaks are also diagnostic.

In the type description, Smith (1957) described basidiomes of *P. pseudofestiva* as having 'hollow' stipes and a "fleetingly pungent" odor, emphasizing the former as diagnostic for differentiating basidiomes of *P. pseudofestiva* from those (consistently stuffed) of *P. olivacea.* However, only a minority of the *P. pseudofestiva* stipes examined in the current study proved to be hollow; stipitipith -- pale and firm in immature and young basidiomes or dark spongy to stringy in mature or waterlogged material -- was far more frequently documented. *P. pseudofestiva* basidiomes collected in this study had either a non-=distinctive or a mildly sweet nutty odor; the 'fleetingly pungent' odor of fresh specimens described by Smith was not encountered and is probably not diagnostic. A sugary sweet odor (vaguely reminiscent of maple syrup and not uncommon in dried Phaeocollybias) has been detected in herbarium specimens.

There is a fair amount of variability in various morphological features among the collections currently identified as *P. pseudofestiva.* While the relatively small size of the basidiomes tended to be fairly consistent and proved very helpful in separating *P. pseudofestiva* from *P. olivacea* in mixed herbarium collections, one outlier collection from Mendocino County did contain unusually large pilei (up to 100 mm across, *cf.* LLN 92.11.23-5). Likewise while most collections contained basidiomes with moderately narrow spores (4.5-6 µm), mean spore widths of 5.5 µm were observed in five collections. Variability in pseudorhizal morphology, habit, basidiome size and spore size also deserve additional comment. Numerous collections of solitary basidiomes identified as *P. pseudofestiva* in the northern part of the range do not conform to the gregarious/cespitose habit observed by Smith (1957) for the type collection. Observations of both blunted vertical-monopodial and cord-like pseudorhizae (the latter similar in basic form to the racemose pseudorhizae characteristic of *P. scatesiae* and *P. rufotubulina*) raise the possibility of two pseudorhizal types within what is currently recognized as a single species. It was further noted that collections of solitary specimens tended to be monopodial, while those made from cespitose or densely gregarious basidiomes originated from narrower cord-like pseudorhizae. Although only short severed unbranched lengths or cords were retrieved in the gregarious collections, it is possible that the pseudorhizae may have been ultimately racemose.

These morphological differences become important in the recognition of three different DNA profiles for seven isolates (with three pseA isolates extracted from Californian collections, three

pseB isolates extracted from Vancouver Island and Washington collections, and one 'hybrid' pseAB isolate extracted from an Oregon collection) implying the existence of three closely allied but geographically separated taxa. Currently, however, no consistent morphological, anatomical, or chemical characters have been found to support these molecular 'taxa'. Considering the relatively small number of isolates tested, it seems prudent at the present time to accommodate all green-pileate basidiomes producing lageniform to tibiiform cheilocystidia provisionally within a single species despite the wide but unresolved variation noted above. Comparison and analysis of additional collections (with close attention paid to pseudorhizal morphology, habit, size, presence or absence of stipitipith, and basidiospore morphology) and further molecular research (including sequencing the ITS and other genomic regions) may well provide better support for the existence of additional varieties or other taxa.

Phaeocollybia radicata (Murrill) Singer, *Lilloa* 22: 567. 1951.
= *Naucoria radicata* Murrill, *N. Amer. Flora* 10: 181. 1917.

Emended

(Macroscopical portion based on observations by Murrill, 1917, and Smith, 1957)

Figures: 6.33

Selected descriptions and illustrations: Murrill, 1917 -- very brief type description; Smith, 1957 -- black & white photograph and anatomical drawings

General Impression: solitary to scattered small fragile cartilaginous deeply rooting basidiomes with moist reddish brown to ochraceous tawny broadly convex to campanulate pilei, dull yellowish young lamellae, chestnut colored slender hollow brittle stipes with pseudorhizae of unknown origins, very small (~5.8 x 3.2 µm) punctate roughened ellipsoidal ('bullet-shaped') basidiospores with rounded apices, refractive tibiiform cheilocystidia, a bilaminate pileipellis with a thin suprapellis overlying a pale brown subpellis, and clamp connections. RARE.

Pileus 20-40 mm broad, convex to campanulate with an inconspicuous to prominent rounded umbo and incurved margin, smooth, glabrous, lubricous to subviscid, hygrophanous with slightly striatulate margin when wet, 'uniformly fulvous' [Murrill] or 'dark reddish brown on the disc with an ochraceous tawny margin fading very slowly to apricot buff' [Smith]; **Context** thick over disc and thin toward the margin, soft and fragile, concolorous with the surface; **Odor & Taste** [Smith] none;

Lamellae narrowly attached, polydymous, crowded, rather narrow [Murrill] to broad [Smith], edges 'slightly uneven' [Smith] or 'serrulate' [Murrill], 'whitish to pale isabelline initially, ferruginous when dried' [Murrill], near 'cinnamon rufous' at maturity [Smith];

Veil none mentioned by either Murrill or Smith;

Stipe up to 180 mm long; apex 2-5 mm wide, slightly fusiform, fistulose, cartilaginous, glabrous, very fragile, concolorous with or paler than the pileus above, chestnut below, especially in age;

Pseudorhiza long, tapering, chestnut;

Spore Print unknown.

Basidiospores: 5.8 x 3.2 ± 0.4 x 0.3 µm (4.7-6.2 x 2.8-4 µm), inequilaterally ellipsoidal in profile with eccentric apiculus and rounded to slightly pointed apex, ovate in face view, minutely punctate roughened in oil immersion; pale yellowish brown in H2O, pale amber in KOH, dextrinoid in Melzer's;

Cheilocystidia: abundant but inconspicuous, 18-35 x 2-4 µm, hairlike to most often lageniform with swollen ventricose bases and very thin, refractive long necks, with/without minute capituli (tibiiform) and/or apical secretory droplets, frequently collapsed or turned down and difficult to find when revived in KOH, hyaline to slightly amber tinged;

Pleurocystidia: absent;

Basidia 4-spored, 17-26 x 5-7 µm, hyaline in KOH;

Pileipellis a bilaminate ixocutis with a 25-50 µm thick suprapellis composed of radially aligned cylindrical 2-4 µm wide slightly gelatinized hyaline hyphae with clamp connections overlying a pale orange-brown subpellis composed of inflated gelatinized hyphae, occasional oleiferous hyphae also present;

Lamellar trama parallel to subparallel composed of 5-10 (12) µm wide gelatinized dingy ochraceous hyphae;

Tibiiform diverticula abundant on pseudorhizal pellis;

Clamp Connections occasional to frequent throughout the basidiome on basidial bases, cheilocystidia, and gelatinous suprapellicular hyphae.

Macrochemical reactions unknown.

RFLP profile based on fragmentary data produced by amplification of 730 bp ITS region from A.H. Smith #3763 [MICH] (DNA from the holotype not successfully amplified). Cut in Cfo1, Eco R1 Hinf1, Pal2, and Pvu2. Uncut in Rsa1 and Sal1.

Habit and ecology solitary to scattered in late autumn to early winter. According to Murrill the type was collected among dense primarily second-growth conifers mixed with occasional old oaks. Five other collections (made by Smith and Thiers from 1935-1967, *cf.* Appendix C:

Specimens Examined) from the same general vicinity in Humboldt County, California are cited as found scattered under either redwoods (Smith) or mixed conifers (Thiers).

Range and distribution rare, from coastal lowlands in southern Oregon and northern California coastal and inland regions.

Type: Murrill 775 (NY) as *Naucoria* -- November 7, 1911; Glen Brook, Oregon.

Comments This species appears to be truly rare, for despite numerous visits over six field seasons to the type locality and other known sites, no recently collected fresh specimens of *P. radicata* have been observed by this author. The above macrodescription is based on descriptions by Murrill (1917) and Smith (1957), while the microscopical description is based on examination of type material and five other verified collections. Among western Phaeocollybias, this species produces the smallest, least roughened basidiospores. Smith (1957) noted that although the spores almost smooth, when viewed under oil immersion, they are minutely "warty-rugulose". Smith (1957) compared *P. radicata* with the eastern North American *P. jennyae* from which it can be differentiated by the hyaline, clamped cuticular hyphae, the mild taste, and the more rusty-brown coloration of the older stipe. More importantly , the cheilocystidia in *P. jennyae* (placed in the Section *Microsporae* by Smith) lack the refractive necks and lageniform to tibiiform morphology common to *P. radicata*. In 1986, Singer erected the Section *Radicatae* based on *P. radicata*.

Phaeocollybia redheadii nom. prov.

Figures: 2.11-2.12; 6.34-35

Selected descriptions and illustrations: Redhead & Norvell, 1993 (as *P. kauffmanii)* -- black & white photograph with anatomical drawings; Norvell, 1997 -- black & white photographs.

General Impression: gregarious massive fleshy farinaceous deeply rooting basidiomes with viscid to glutinous orange-brown to dark brown strongly inrolled campanulate pilei, pinkish buff or yellowish cream-colored young lamellae, dry robust pinkish buff dry stipes stuffed with dense solid whitish stipitipith, gradually narrowing massive vertical-monopodial pseudorhizae, large (10.5 x 6 µm) verrucose elongate amygdaliform basidiospores with smooth eccentric prominent apical beaks, broadly clavate to subcapitate (with subglobose heads) long pedicellate cheilocystidia, a bilaminate pileipellis with narrow hyaline suprapellicular hyphae loosely embedded in a thick colorless gelatinous matrix overlying an orange brown subpellis with incrusting and intraparietal pigments,, no clamp connections in hymenia and pileipelli but occasional clamps or pseudoclamps observed in the stipitipellis. Immediately deep magenta in syringaldazine. Dried pileus with blackened umbo and brownish bronze to shiny mahogany margin.

Pileus (23) 45-140 mm wide, conic-convex when young with decurved margin expanding to broadly campanulate with broad low umbo, decurved margin, extreme edge inrolled at all

times, glabrous, smooth, viscid to heavily glutinous, opaque, non-striate, pristine basidiomes either generally warm orange-brown overall *(Verona Brown, Warm Sepia -- 5YR 3-5/3-5; Sayal Brown -- 7.5YR 4-5/5)* or zonate with deep orange brown to dark blackish brown disc *(Verona Brown,Warm Sepia, Bone Brown -- 5YR 3-5/3-5; Snuff Brown, Clove Brown -- 7.5YR 4/2-4)*, dark yellowish brown or brownish orange margin *(Sayal Brown, Snuff Brown, Cinnamon Brown -- 7.5YR 4-5/4-6; Tawny, Verona Brown, Mikado Brown, Russet -- 5YR 3-5/4-8)*, and dark brown edge *(Warm Sepia, Verona Brown, Mikado Brown, Snuff Brown -- 5YR 3-5/3-6)*, older basidiomes becoming blackish or purplish brown overall, mould-attacked or frost-bitten basidiomes frequently developing dull purplish or greenish brown tones *(Benzo Brown, Army Brown -- 5YR 4/2-4; Saccardo's Umbo, Isabella Color -- 2.5YR 3-5/3-5)*, areas of damage generally black or blackish brown, dried pileus with blackened umbo and brownish bronze metallic margin, or shiny deep orangish-brown mahogany over-all ; **Context** firm and confluent with stipe pith, up to 12 (15) mm thick at the disc, when young pale yellowish cream or pinkish white *(Pale Pinkish Buff, Pinkish Buff, Cartridge Buff -- 2.5Y 7-8/1-4)*, when old or waterlogged dark yellowish brown *(Snuff Brown, Sayal Brown -- 7.5YR 4-5/4-5)*, staining orangish or deep orange-brown when cut *(Xanthine Orange, Verona Brown -- 5YR 4-5/4-5 (9))*, when wet often developing a deep orange-brown to greenish brown 1-3 mm zone between lamellae and context; **Odor** strongly farinaceous, often with a floral component when cut or crushed; **Taste** strongly farinaceous or cucumber-like, gluten latently slightly to extremely bitter;

Lamellae ascendant, free or sometimes attached by a small tooth, greatly ventricose with broad central portion narrowing at either end, occasionally forked (most evident in primordia and very young specimens), lamellulae in (3) 5-7 irregular tiers with lamellulae distributed in wedge-shaped patterns, broad in mature specimens (up to 15 mm) with mean length:width ratio 4.6 (range 3.2 - 8.3, 14 for very young basidiome), crowded (edge 15-24 L+l/cm, midpoint: 8-14), pinkish white or pale to dull yellowish cream when very young *(Pale Pinkish Buff -- 10YR 9/2; Cartridge Buff -- 2.5Y 8/2; Ochraceous Buff, Tilleul Buff 7.5YR 8/1-2)*, maturing to brownish grayish yellow or darker yellowish brown *(Pinkish Buff, Cinnamon Buff -- 10YR 6-7/4-5; Cinnamon -- 7.5YR 4-7/4-7)*, and dark yellowish brown to deep brownish yellow in age *(Sayal Brown, Snuff Brown -- 7.5YR 3-5/4-5; Tawny Olive 1.25Y 4-5/4-5)*;

Veil occasionally evident as fibrillose patches on aerial stipe;

Stipe central to slightly eccentric, terete to slightly compressed, 40-100 mm tall above ground level with a wide (10-23 mm diam) apex, overall length including pseudorhiza up to 340 mm, aerial portion occasionally equal or tapering downward, but most often ventricose, swelling to 12-30 mm slightly above ground level before tapering downwards to the pseudorhiza, smooth or appressed fibrillose under hand lens on the aerial portion,

longitudinally lined, moist, apex pale to medium pinkish buff in young specimens *(Light Pinkish Cinnamon, Pinkish Cinnamon -- 7.5YR 6-8/4-6; Light Vinaceous Cinnamon, Orange Cinnamon -- 5YR 5-8/4-6)*, grayish orange- or yellow- brown in old or damaged specimens *(Vinaceous Cinnamon, Cinnamon Drab -- 5YR 5-6/3-6; Cinnamon, Avellaneous -- 7.5YR 5-6/4-7)*, darkening below to deep orange-brown *(Ferruginous, Kaiser Brown -- 2.5YR 4/4-8; Mikado Brown, Pale Orange Cinnamon, Verona Brown, Warm Sepia -- 5YR 3-6/3-5)*, staining deep red brown, 2-4 mm thick cartilaginous rind surrounding firm pith, pinkish to yellowish white in young specimens *(Pale Pinkish Buff, Cartridge Buff -- 2.5Y 8/0-2)* and light to dark yellowish brown in age *(Cinnamon, Pale Pinkish cinnamon -- 7.5YR 5/7, 8-9/2-4)*, pith frequently proliferating so abundantly as to split cortex;

Pseudorhiza vertical-monopodial, generally 2/3 to 5/6 of overall stipe length, gradually tapering to a blunt fleshy origin, overall deep red- to rusty- brown *(Liver Brown, Bay -- 7.5YR 2-3/4-5; Kaiser Brown, Pecan Brown -- 2.5YR 3-4/5-6)* or paler pinkish-orange *(Salmon Color)* at the origin;

Spore Print cinnamon brown *(Cinnamon -- 7.5YR 5/6)*.

Basidiospores 10.5 X 6 ± 0.4 x 0.3 µm (8.5-12 x 5-7 µm), terete to almost angular in end view, elongated inequilaterally amygdaliform in profile view, elongate-elliptical in face view, verrucose with obscurely banded rugosity present everywhere except on the 1 µm long mammiform beaked apex and eccentric prominent apiculus, suprahilar plage an area of slightly lower ornamentation visible in SEMs *(Fig.6.35)* but not readily discernible in oil immersion; orange to medium amber in KOH, paler in H20, dextrinoid in Melzer's;

Cheilocystidia abundant, emanating from the lamellar trama to form a dense highly gelatinous barrier, lengths developmentally variable (~20-35 µm), broadly clavate elements intermixed with subcapitate elements with 6-10 (15) µm-wide globose heads atop variably long (2) 3-4 µm wide pedicels, sometimes catenulate with swellings noted in ultimate and penultimate elements, thin-walled, highly gelatinized, hyaline, often developing long filamentous apical outgrowths in very old or stored fresh specimens;

Pleurocystidia absent;

Basidia 4- (occasionally 2-) spored, 29-50 X (6) 7-8 (10) µm, clavate to somewhat cylindrical with pedicel slightly tapered to the 1.5-3 µm-wide base, hyaline;

Pileipellis a bilaminate ixocutis with a 200-600 µm thick suprapellis composed of a gelatinous matrix in which are embedded branching cylindrical 2-6 µm wide thin-walled highly gelatinized hyaline hyphae overlying a 75-200 µm thick yellow orange to dull orange-brown subpellis composed of unbranched thick-walled 5-8 µm wide inflated (to 14 µm) encrusted, intraparietally and diffusely pigmented hyphae with refractive septa; oleiferous hyphae present throughout pileipellis; **Stipitipellis** a compact layer of parallel

hyphae gradually intergrading with the stipititrama, composed of 4-9 µm wide hyphae with thick hyaline to orangish brown walls, with a few scattered loose 2.5-4 µm wide hyphae encased in a broken gelatinous sheath, clamp and pseudoclamp connections occasionally present; **Pseudorhizal pellis** up to 200 µm thick, composed of 20 µm wide dark brown hyphae covered with moderately coarse incrustations and coagulated brownish contents, outermost hyphae densely covered with tibiiform diverticula, clamp and pseudo-clamp connections occasionally present;

Trama tissues highly gelatinized with occasional amber oleiferous hyphae present, strongly sarcodimitic in the pseudorhiza with parallel long rigid thick-walled (up to 4 µm) wide (up to 40 µm) hyaline hyphae supported by inconspicuous branched thin-walled (0.5 µm), flexuous narrow (2-3 µm) hyphae, both hyphal types with equally thick walls in the stipe and pileus tissues where the 'vessel' hyphae become narrower (to 20 µm); hyphae within the pileus are loosely radially arranged, slightly less thick-walled, and 15-20 µm wide; Lamellar trama parallel, with gelatinized relatively thick-walled (≤ 1.0 µm) hyaline hyphae 3-10 µm wide in 200-400 µm central region, narrowing to 2-3 µm on the edges to give rise to a compact rudimentary subhymenium, narrow, highly branched flexuous hyphae also occasionally present;

Tibiiform diverticula abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex, up to 25 x 1 (1.5) µm, hyaline to slightly straw-colored, highly refractive with no septum between base and hypha, with or without slightly larger ligulate to subglobose capitellum and/or apical droplet;

Clamp Connections sporadic and occasional in stipitipellis, absent in all other tissues.

Macrochemical Reactions: syringaldazine -- immediately deep magenta on lamellae and pseudorhizal pellis; KOH -- immediate positive reaction (blackish, dull greenish brown); FeSO4 -- dull green to dull grey brown.

Fluorescence: Primordia -- dull orange context; Very young basidiomes -- lamellae no fluorescence to violet whitish; Young mature basidiomes -- lamellae intense whitish yellow to mottled yellowish, pileal pith dull purple over dull orange ground, apical stipe pith blue; Fully mature basidiomes -- lamellae brilliant intense yellow under spores; Damaged or mouldy areas -- brilliant mustard yellow around stained pith or on mold, other molds brilliant white.

RFLP profile: ITS region of 6 isolates including type = 730 bps. PaI1 (220-220-110-90-90) and Pvu2 (640-90) most informative enzymes. Also cut in Cfo1, EcoR1, Hinf1, Nde2; uncut in Rsa1, Sal1, and Xho1.

Habit and ecology solitary to scattered or gregarious during early to late autumn, originating at the albic horizon in humic podzolic soils in coastal and inland ancient or mature second-growth mesic mixed closed canopy *Tsuga-Abies* forests.

Range and distribution Fairly common from southern British Columbia to Humboldt County in northern California.

Type LLN 91.10.24-2 (WTU; Isotype at DAOM) -- collected by S. A. Redhead & L. L. Norvell, October 24, 1991 along boardwalk to *Picea sitchensis* canopy research station, Upper Carmanah Valley, Vancouver Island, British Columbia, Canada.

Comments When *P. redheadii* was first reported from Canada as *P. kauffmanii*, the possibility was raised that this large-spored variant might be a new species in an uninvestigated complex (Norvell & Redhead, 1992; Redhead & Norvell, 1993). Subsequent microscopical comparisons support a division of the brownish orange to orange brownish members of the *P. kauffmanii* complex into three taxa -- *P. kauffmanii sensu stricto*, the clamped *P. ammiratii* and *P. redheadii*. Analyses of molecular data also support recognition of these three taxa (See chapters 4 and 5).

In the field *P. redheadii* -- named in honor of Dr. Scott Redhead who first suggested the existence of a large-spored taxon within the complex -- can be easily confused with *P. kauffmanii* and more robust specimens of *P. ammiratii*,. The generally less robust stature and vinaceous colored stipes of *P. ammiratii* have been noted above. The difference between the more brightly colored (near orange when young) *P. kauffmanii* and darker (apricot brown) *P. redheadii* is a subtle one, and the two taxa are not easily differentiated based on field criteria.

Microscopically *P. redheadii* is easily differentiated from *P. kauffmanii* by rarely overlapping basidiospore sizes (mean dimensions are 10.5 x 6 µm and 8.5 x 5 respectively). The generally narrowly clavate cheilocystidia of *P. kauffmanii* also differ from the distinctive pedicellate, subcapitate cheilocystidia with globular apices of *P. redheadii*, although narrowly clavate cheilocystidia are occasionally present in the latter taxon as well. While *P. redheadii* produces the largest basidiospores in the *P. kauffmanii* complex, its basidiospores do intergrade with those of *P. benzokauffmanii*, which occasionally also produces slightly less subcapitate, inflated cheilocystidia. This latter confusion is further compounded by the fact that *P. redheadii* occasionally produces basidiomes with purplish-brown pilei (usually when attacked by mould or under adverse weather conditions such as drought or frost).

Phaeocollybia redheadii is distinguished molecularly from all other members of the *P. kauffmanii* complex by the fact that its ITS region is cut in Pvu2 and uncut in Rsa1, Sal1, and Xho1.

Three of the four paratype collections cited by Smith in his original description of *Naucoria. kauffmanii* (C.H.Kauffman X.11.1925, Sm 2495, & Sm 3888) and two collections cited under *P. kauffmanii* in the 1957 monograph (Sm 3727 *p.p.* & Sm 56489) are now reassigned to *P. redheadii*.

Of the six previously described *Phaeocollybia* species with basidiospore means or averages ≥ 10 X 6 µm, three produce basidiomes with clamp connections, and the fourth produces tibiiform cheilocystidia. Of the two remaining taxa, *P. muscicolor* Horak (1977) produces small olive-colored basidiomes with hollow stipes and even larger basidiospores. *Phaeocollybia quercetorum* Singer (1987) is described as being similarly colored, but generally smaller in stature, with hollow stipes, with a phenolic odor, and associated with *Quercus*-dominated forests. Furthermore, while Singer describes the Costa Rican type as having basidiospores with a very wide range (9.5-14X5.5-6.5 µm), Horak and Halling (1991) report a much narrower spore width (8-10 X 4.5-5) for their Columbian collections.

Phaeocollybia rifflipes nom. prov.

Figures: 6.36-37

Selected descriptions and illustrations: Smith, 1957 -- reference to North American collections of *P. festiva* .

General Impression: scattered to gregarious small to medium sized deeply rooting basidiomes with glutinous orange brown to dark brown convex-campanulate pilei, pale violet gray to dull pinkish brown young lamellae, drab slender fibrillose-stuffed to hollow shiny stipes, vertical-monopodial pseudorhizae, relatively small (~7 x 4.5 µm) verruculose limoniform basidiospores with smooth subdued to moderate apical beaks, narrowly to broadly clavate cheilocystidia, a bilaminate pileipellis with a thick colorless gelatinous matrix overlying an orange subpellis with intercellular pigments, no clamp connections. Negative in syringaldazine. Dried pileus carbonized to dark blackish brown.

Pileus (10) 20-40 (55) mm, conic-convex with acute papillate umbo when very young, soon conic-campanulate with low broad umbo and incurved to downturned margin with long inrolled edge, viscid to heavily glutinous, glabrous, initially tawny, when young some shade of foxy orange to brown with a darker disc *(Verona Brown, Russet, Hazel)*, tawny to orange brown margins *(Hazel, Tawny, Chestnut Brown, Sayal Brown, Verona Brown)* and orange to yellow brown edge *(Buffy Brown, Army Brown, Chestnut Brown, Cinnamon Brown)* in age a more or less uniform deep yellowish brown *(Olive Brown)* with a dark greenish brown *(Dark Olive)* edge, dark blackish brown with noticeable striations when dried;

Context 1-4 mm over disc sharply thinner over gills, pale (pinkish buff) when young, dulling to brown or drab in age or after exposure, often consumed by insects; **Odor** not distinctive or slightly floral; **Taste** mild, occasionally faintly bitter;

Lamellae narrowly attached to free, thin, edges even at first, then uneven to eroded, polydymous with 3-5 tiers of lamellulae irregularly interspersed among lamellae,

subcrowded (15 L+l/cm at edge, 12 at mid-point), of medium breadth (3-5 mm), pale violet or bluish gray when young *(Dark Vinaceous Gray, Pale Vinaceous Drab)*, as spores mature developing warm tones *(Light Brownish Drab, Avellaneous, Drab, Wood Brown, Vinaceous Buff)* eventually obscured by dark brown spores *(Verona Brown)* in age;

Veil usually present as scattered short concolorous fibrillose patches on stipe apex or occasionally as fibrils overlying lamellae;

Stipe overall length (including pseudorhiza) up to 165 mm; aerial portion generally 30-50 mm when pileus fully expanded, stipe apex diameter 4-9 (12) mm either swelling gradually below apex to ground level or tapering evenly to pseudorhizal origin, smooth and shiny beneath relatively dense fibrillose patches, usually stuffed with firm to spongy pallid pith when young, but often becoming hollow from water saturation or insect damage, apical portion generally grayish or pinkish brown (*Deep Quaker Drab, Benzo Brown, Army Brown, Avellaneous, Cinnamon Drab, Natal Brown, Pecan Brown, Wood Brown*) and gradually darkening below to dark orangish or reddish brown (*Army Brown, Dusky Drab, Fawn Color, Liver Brown, Natal Brown, Rood's Brown, Sayal Brown, Tawny Olive)*;

Pseudorhiza vertical monopodial, dark reddish brown *(Cameo Brown, Hay's Brown, Liver Brown, Mikado Brown, Van Dyke Brown, Verona Brown)* above curled or nippled blunt dull pinkish gray-brown fleshy origin;

Spore Print color pinkish cinnamon colored *(7.5YR 6-7/4 = (Light) Pinkish Cinnamon).*

Basidiospores 7 x 4.5 ± 0.0 x 0.3 µm (overall range 7-7.5 x 4-4.5 µm), ovate with small projecting apiculus in face view, strongly limoniform with distinct small apiculus and subdued to moderate beak in profile, verruculose to verrucose, slight plage only rarely visible under oil immersion, pale to medium pale amber in KOH;

Cheilocystidia abundant and crowded together to form a dense gelatinous barrier, emanating from the lamellar trama and variable in length (15-45 µm), narrowly to broadly clavate, long 3-4 µm wide pedicels most frequently expanding to 5-7 µm apically but often intermixed with narrower (2-3 µm) cylindrical and/or wider (up to 10 µm) elements, thin-walled, hyaline or filled with oily brownish contents;

Pleurocystidia occasionally present as 2 µm wide filiform hyphidia amidst basidial clusters;

Basidia 4- (sometimes 2-) spored, 26-36 x 6-7.5 µm, clavate, hyaline to brownish in older specimens;

Pileipellis a well-delimited bilaminate ixocutis with an extensive 150-350 µm thick colorless suprapellis composed of a gelatinous matrix in which float long branched narrow (1-3 µm wide) straight or occasionally curling hyaline hyphae uplifted from a radially aligned base over an intensely deep amber orange subpellis containing thin-walled 3-5 µm wide hyphae

frequently inflating to 5-8 (10) µm in mid-portion, intraparietal pigments generally most noticeable at the septa;

Tramal tissues Lamellar trama subparallel, composed of 3-5 µm wide highly gelatinized hyaline hyphae; Pileitrama continuous with subpellis, unpigmented;

Tibiiform diverticula abundant, on remnants of the pellicular veil (on apical stipe, over lamellae) and on pseudorhizal pellis, 5-12 (20) x 2 x 0.5 µm with/without 1-1.5 µm wide capitulum, usually surrounded by an apical secretory droplet.

Clamp Connections: Absent.

Macrochemical reactions: Syringaldazine -- negative (LLN 92.10.31-2 with very slight pinkening on lamellae); KOH -- dulling to slight browning; FeSO4 -- dull greenish-brown.

Fluorescence: young lamellae -- intense whitish yellow, becoming duller as covered by spores; stipitipith -- dull orange.

RFLP profile: ITS region of 4 isolates including type = 730 bps. Unique in Hinf1 (400-190-140); Pal1 (475-170-85) and Sal1 (535-190) other diagnostic enzymes. Also cut in EcoR1 and Nde2; uncut in Pvu2, Rsa1, and Xho1.

Habit and ecology: solitary to scattered (rarely gregarious) during mid to late autumn in montane old growth coniferous (*Tsuga heterophylla)* forests (*Abies spp. Picea sitchensis*, and *Pseudotsuga menziesii* may also be present).

Known range and distribution: collected from four sites at higher elevations (2000-4000') from the coastal and cascade ranges in northwest Washington and Oregon.

Type L. L. Norvell 93.10.20-1 (WTU) -- October 20, 1993, Barlow Pass, Baker Snoqualmie National Forest, Snohomish County.

Comments: *Phaeocollybia rifflipes* is a member of a difficult complex of mushrooms centered around *P. festiva*. Species in this complex -- *P. festiva, P. fallax, P. lilacifolia,* and *P. rifflipes* -- produce small to moderately sized, relatively fragile, relatively odorless/tasteless basidiomes with conic-campanulate glutinous pilei, 7-9 (10) x 4-5 µm verruculose to verrucose limoniform spores, thin-walled somewhat broadly clavate cheilocystidia, and highly gelatinized tissues lacking clamp connections. Field identification is complicated by mutable pigments found in the pilei and lamellae. Pileus colors can be green, brown, orange or some shade in-between while the initial lamellar colors -- yellowish buff, tan, pink, drab, violet -- are soon obscured by the mature orangish- to pinkish-brown spores. Additionally, stipes within a given species may be either firmly stuffed, stuffed with fibrillose pith, or hollow. Differentiation of the species using a rather undistinguished assemblage of microscopical characters is problematical as well, for in some species (notably *P. festiva)* spore size is highly variable while in others the size range appears to

more restricted. Cheilocystidial morphology ranges from filamentous to cylindrical to narrowly to broadly clavate to subcapitate subglobose pedicellate. The cheilocystidia are generally quite abundant and often there is a mix of all forms within a single specimen.

Phaeocollybia festiva (with *P. christinae* and *P. lugubris)* is one of the three most frequently discussed Phaeocollybias in the literature (see annotated world conspectus, Appendix D). First placed within the tribe *Naucoria* in *Agaricus* by Fries in his Epicrisis (1838), *P. festiva* was described as having a greenish brown glutinous pileus that dried to a dirty gold (isabelline), pale olive colored lamellae, an apically compressed (neither equal nor ventricose) stipe often covered with dark fibrils, and a raphanoid odor. Later authors expanded the original description to accommodate observed variability. Thus Kühner & Romagnesi (1953) noted that while the pileus was generally olive to olive brown, it could also be chestnut to reddish-brown (*'aussi bai ou roux'*). Moser (1983, 1995, pers. com.), Gulden (1983), and Jacobsson & Stridvall (1983) all remark on the violet lamellae found in occasional specimens, and Gulden (1983, 1992) mentions the drab to violet gray coloration found on some stipe apices (otherwise characterized as being olive-colored). A wide range of spore lengths from 7-10 is listed, and examinations of Gulden 771/81 (O) from Bredehaugen, Norway show that this range can be found within a single specimen. Descriptions of the spore ornamentation range from subdued and marbled (Kühner & Romagnesi,1953; Reid,1972) through minutely warty (Horak, 1977) to strongly or heavily ornamented (Laber, 1982; Gulden, 1983; Jacobsson & Stridvall, 1983). Examination of Gulden 771/81 reveals marbled spores with very low indistinct warts stopping well below the apex. Also observed in the same collection is a suprahilar plage (noted by Bon, 1992 and Watling & Gregory, 1993, but said to be absent by Horak, 1977) The shape is variously described as being ovoid (Horak, 1977) to limoniform.

Although *P. rifflipes* lacks the olive-green coloration on the pileus, it clearly belongs to the *P. festiva* complex, with which it shares the greatest number of characters. Comparisons of material identified as *P. festiva* as well of recent collections made in the current study with Gulden 771/81 indicate that *P. festiva* does not appear to occur in western North America. The verruculose, subdued roughened ornamentation and lack of a distinct plage, the lack of a raphanoid odor, the consistently vinaceous grey lamellae, the absence of olive tones in the young pileus, and the consistently small limoniform spores separate *P. rifflipes* from *P. festiva* as it is currently interpreted by most authors.Smith (1937) originally reported *Naucoria festiva* from the Pacific Northwest but later (Smith, 1957b) reassigned his collections to *P. fallax.* Smith *et al.* (1979) reintroduced the species in their keys but there is no published documentation or correctly identified material from western North America. Hence *P. festiva* is considered strictly extralimital .

Phaeocollybia. rifflipes appears to be molecularly distinct from both *P. fallax* and *P lilacifolia.* The ITS region amplified from 17 specimens provisionally identified as either *P. fallax* or *P. lilacifolia* produced 5 different enzyme profiles. One isolate --vouchered as *fal 3* -- from Barlow Pass (Washington) produced such a different profile from the others that the ITS region was originally thought to have been amplified from a contaminant. However, three 'unknowns' from Larch Mountain (Oregon) -- *unk 8, unk 9, unk 10* -- produced identical profiles. Subsequent microscopical and macroscopical comparisons revealed that the four specimens represented the same species. *P. rifflipes* differs from *P. lilacifolia* in its smaller size, zonate pileus, paler pileus color, narrower, duller lamellae, lack of disagreeable odor, usually hollow stipes, smaller spores, possession of filamentous paraphyses, and brilliant orange subpellis. *Phaeocollybia fallax* is characterized by an olive green young pileus, intense violet lamellae, usually hollow stipes, larger spores, and gel-secreting subcapitate cheilocystidia. The name 'rifflipes' refers to the discovery of a cryptic species from a RFLP profile.

Phaeocollybia rufotubulina nom. prov.

Figures: 2.1,, 2.3, 2.5, 2.6-2.10; 6.38-39

Selected descriptions and illustrations: Norvell, 1997 -- black & white photographs, line drawings.

General impression: Densely gregarious small to medium orange to orange-red deeply rooting basidiomes with moist to subviscid orange to orange red convex-campanulate moist pilei, pale orange young lamellae, pale orange to deep purplish red matte to more or less polished strict tubular stipes with very thin cortices, sequential-racemose thread-like rhizomorphic pseudorhizae, large (~9 x 5 µm) elongated limoniform coarsely warty-rugulose dark orange amber basidiospores with smooth elongated apical beaks, slightly heteromorphic cheilocystidia with predominantly thick-walled refractive lageniform and tibiiform elements intermixed with thin-walled mucronate elements, a bilaminate pileipellis with a moderately thin yellowish suprapellis containing narrow hyphae spirally incrusted with orange to orange brown pigments overlying a thin dull brownish-orange subpellis, no clamp connections. Negative to very faintly pink (pseudorhizae only) in syringaldazine. Dried pileus copper to winy red bronze.

Pileus: 15-62 mm broad, convex-umbonate with acute umbo and incurved margin when young, expanding to broadly campanulate with acute to low broad umbo, incurved to straight margin, and incurved edge, glabrous, lubricous to subviscid, opaque, nonstriate, generally bright reddish to brownish orange *(Xanthine Orange, Ochraceous Orange,Mars Yellow, Ochraceous Buff, Apricot Orange)*, often with slightly darker disc and edge

(Sanford's Brown, Dark Orange Brown, Tawny), brownish streaks and damaged areas occasionally present, dried pileus metallic, usually copper or winy-reddish bronze; **Context** 3-6 mm thick at the disc, pale orangish cream *(Pale Ochraceous Salmon, Pinkish Buff)*; **Odor** faintly floral (reminiscent of cultivated *Viola*) or like cooked potatoes (similar to *Amanita citrina)*, occasionally sharply farinaceous after cold storage then developing a green corn odor on warming; **Taste** mild and not distinctive to slightly bitter (reminiscent of raw potatoes);

Lamellae: nearly free, emarginate with a short tooth, ventricose, polydymous with 1-3 (young) to 2-6 (mature) lamellulae irregularly interspersed, 2-5 mm broad with mean length:width ratio 3.5, subcrowded (L+l 19-23 on the edge and 10-12 at mid-pileus), at first pale orangish cream *(Apricot Buff, Ochraceous Buff)*, maturing to foxy brown *(Ochraceous Tawny, Tawny, Clay Color)* with bright rusty orange streaks;

Veil: present as connective fibrils between pileus and stipe (immature) or as occasional densely scattered fine dark reddish brown fibrils on mature stipe apex;

Stipe: central to slightly eccentric, overall up to 180 mm (aerial portion up to 140 mm) long, apex 4-12 mm wide, strict, terete, uniformly equal except for slight bulbous swelling at ground level above sharply attenuating cord-like pseudorhiza, glabrous and smooth or covered with fine short reddish-orange fibrils, dry to lubricous, apex slightly paler than reddish orange pileus when young *(Xanthine Orange, Light Ochraceous Buff, Cinnamon)*, gradually darkening upwards to a dark reddish to purplish brown in age *(Hay's Russet, Kaiser Brown, Liver Brown)*, hollow with 1-1.5 mm thick brittle cartilaginous cortex surrounding empty lumen from pileus to rhizomorphic pseudorhiza;

Pseudorhiza: sequential-racemose, rhizomorphic, 1.5-2 mm thick cord of undetermined length (strands up to 55 mm have been retrieved) with dark reddish brown *(Liver Brown, Clay Color)* cartilaginous rind surrounding dark orange-brown *(Clay Color)* medulla;

Spore Print Color dark yellow brown (slightly darker than *7.5YR 4/4* ['*Sayal Brown*']).

Basidiospores 9 x 5 ± 0.6 x 0.3 µm (overall range 8.2-10 x 4.5-6 µm), limoniform with a prominent straight to slightly tilted beak in profile, ovate with swollen portion in face view, exosporium thick-walled, coarsely rugulose roughened except over the apiculus and beak, with less ornamented plage (oil immersion), dark to deep orange-amber in KOH, inamyloid;

Cheilocystidia: heteromorphic, with thick-walled and thin-walled lageniform,tibiiform and clavate elements intermixed, occasional to frequent 17-30 µm long mucronate/tibiiform elements with 3 µm wide ventricose bases narrowing to 1-µm wide refractive necks (with/without 1.5 µm diam capituli) containing viscous pale to dark amber material intermixed with moderately inflated, broadly clavate, thin-walled heavily gelatinized hyaline elements that may develop long filamentous apical outgrowths in age or in storage;

Pleurocystidia absent;

Basidia 4-spored, 25 -30 X 5-6 µm, sterigmata long (up to 8-µm), hyaline to pale straw-colored;

Pileipellis a bilaminate ixocutis of a 120-200 µm thick suprapellis composed of a pale orange-yellow gelatinous matrix in which are embedded long, branched, 2-4 µm wide, highly gelatinized roughened hyphae with spirally incrusting and intraparietal yellowish-orange to orange brown pigments overlying a thick (300-450 µm) subpellis composed of thick-walled (5) 8-15 µm wide highly gelatinized hyphae with orange-yellow to deep orange walls (KOH); **Stipitipellis:** longitudinal ixocutis of narrow (2-4 µm), thick-walled, cylindrical, highly gelatinized, medium to dark orange-amber to orange-red incrusted hyphae;

Tramal tissues: moderately to highly gelatinized, strongly sarcodimitic in the pseudorhiza and lower stipe with long (95-200 µm long) wide (up to 20 µm) thick-walled (up to 3 µm) cylindrical rigid yellowish hyphae supported by less conspicuous shorter (~20 µm) narrower (4-6 µm wide) branched thin-walled (below 0.5 µm) flexuous hyphae, with both hyphal types also present in the pileus but vessel hyphae with thinner (1 µm) walls; Lamellar parallel, composed of highly gelatinized 4-6 µm wide slightly thick-walled pale amber hyphae with refractive septa and intraparietal pigments giving rise to a compact 2-6 µm thick subhymenium;

Tibiiform diverticula: abundant on mycelium, primordial surfaces, and pseudorhizal pellis, also frequent on vestiges of pellicular veil on stipe apex;

Clamp Connections: absent in all tissues of mature basidiomes; occasionally present in primordial pellis.

Macrochemical Reactions: Syringaldazine -- negative to very slightly positive (slight blackening observed after 15 minutes, slight magenta on pseudorhiza after 60 minutes); KOH -- pileus dark brown; FeSO4 -- all tissues becoming slightly greenish;.

RFLP profile: Extensive data for 6 isolates (including type) shows the 690 bp (± 730 bp second band) ITS profile unique in Xho1 (500-190) and diagnostic in EcoR1 (365-325); also cut in Cfo1, Hinf1, Nde2, Pal1, and Pvu2; uncut in Rsa1 and Sal1.

Habit and ecology: October through January, densely gregarious in loose bundles in sandy loam under needle duff from mature mixed conifers (*Lithocarpus densiflorus, Sequoia sempervirens, Pseudotsuga menziesii, Abies grandis*) with shrubby understory of *Rhododendron* & evergreen *Vaccinium* and *Polystichum munitum.*

Range and distribution: coastal lowlands from southern Oregon (coos County) south to Marin County along the north central California coast.

Type: LLN 92.11.16-1_{call} (WTU, Isotype DAOM). November 16, 1992, Jackson State Forest, Mendocino County, California, by L. L. Norvell, S. A. Redhead & G. L. Barron.

Comments: *Phaeocollybia rufotubulina* is easily recognized in the field by its striking reddish-orange color, dense gregarious habit, and strict, tubular stipe that curls back into a floret when sliced crosswise similar to a dandelion scape. Microscopically it is marked by its long narrow highly ornamented dark red-brown spores, moderately thick pileipellis with incrusting hyphae, and heteromorphic mix of abundant tibiiform and clavate cheilocystidia. It is molecularly distinct from 28 other *Phaeocollybia* species tested thus far in that its ITS region is the only one completely digested in Xho1. *P. rufotubulina* appears to be restricted to Humboldt, Mendocino, and Marin Counties in California. (For ontogeny and pseudorhizal anatomy, see Chapter 2.)
A cryptic species previously mistaken for *P. californica*, with which it shares a large number of morphological similarities, *P. rufotubulina* produces slightly more highly pigmented, more strongly ornamented basidiospores, dark orange-pigmented (not hyaline) incrustations over slightly wider suprapellicular hyphae, a thinner, darker stipitipellis and more abundant tibiiform cheilocystidia . *Phaeocollybia californica* produces slightly larger, less highly pigmented basidiomes with stipes that -- while soon hollow -- have much thicker cartilaginous cortices lined with long white fibrils (See additional comments under *P. californica). Phaeocollybia rufotubulina* forms a complex with *P. californica* and *P. scatesiae* based on anatomical similarities and the possession of racemose rhizomorphic pseudorhizae. It is separated molecularly from the two other taxa by a 10 base pair deletion in the ITS region.

Phaeocollybia scatesiae A. H. Smith & Trappe, *Mycologia* 64: 1146-1148. 1972.

Emended.

Figures: 2.5,2.7, 2.9; 6.40-41

Selected descriptions and illustrations: Smith & Trappe -- type description; Lincoff, 1981 -- color photograph; Norvell, 1997 -- black and white photographs; Smith, 1980 -- color photograph.

General impression: Densely fasciculate small to medium-sized heavily glutinous basidiomes with glutinous light yellow-brown to dark brown broadly conic pilei, dingy pale yellow young lamellae, orange to ferruginous polished hollow stipes with relatively thick cartilaginous stipes, salmon-colored fasciculate-racemose rhizomorphic pseudorhizae subtending 'starbursts' of differentially developed basidiomes, moderately large (~8.5 x 5 µm) verrucose-roughened limoniform basidiospores with smooth 1 µm long apical beaks, abundant refractive tibiiform cheilocystidia, a bilaminate pileipellis with an extensive colorless gelatinous matrix overlying a pale amber subpellis, no clamp connections. Pseudorhizae occasionally weakly positive in syringaldazine. Dried pilei grayish brown to yellowish copper.

Pileus 30-65 mm broad, acutely to obtusely conic with inrolled margin becoming broadly campanulate with straight, decurved margin, umbo often acute and occasionally sharply papillate, edge rarely straight, often irregularly sinuate, surface glabrous, viscid to heavily glutinous, striatulate at the margin, overall color when young yellowish brown *(Snuff Brown, Saccardo's Umber, Dresden Brown, Tawny Olive)*, soon darkening in age to deep reddish or blackish brown *(Chestnut Brown, Bone Brown, Bister, Prout's Brown)*, often darker at the disc*(Bone Brown, Prout's Brown, Snuff Brown, Saccardo's Brown)*, reddish to orange brown at the inner and outer margins *(Bay, Auburn)* and paler yellow brown at the edge *(Buckthorn Brown, Dresden Brown)*, hygrophanous and characteristically drying in radial furrows with dark brown spots over grayish brown, dried pileus a grayish smoky brown to yellowish copper with metallic glints; **Context** thin, cartilaginous interface between pileus and lamellae watery brownish, smoky gray or dull olive *(Saccardo's Umber, Mummy Brown, Light Grayish Olive, Black)* and often surrounding a 2-3 mm high triangular buff pith *(Pale Pinkish Buff, Pinkish Buff, Tilleul Buff)*; **Odor** mildly floral when very young, later generally not distinctive or raphanoid, sometimes very slightly farinaceous, rarely pungent; **Taste** faintly bitter when very young, later generally mild and not distinctive with slight raphanoid or farinaceous undertones;

Lamellae ascending, free to narrowly attached, ventricose to lacrimate, thin with even (when young) to uneven or eroded (in age) edges, crowded (L+ll = 22-35 edge, 10-20 mid), polydymous with 6-7 tiers of lamellulae regularly to irregularly interspersed, narrow (1.5-6 mm), initially pale dingy yellowish or pale pinkish white *(light Buff, (Pale) Pinkish Buff, Tilleul Buff)*, becoming more cinnamon to dull brownish-yellow (*Vinaceous Buff, Pinkish Cinnamon, Isabella Color*), in age dingy yellow brown (*Tawny Olive, Sayal Brown, Verona Brown*);

Veil present as short brownish fibrillose patches on stipe apex;

Stipe ± central to slightly eccentric, terete, overall greater than 250 mm (aerial portion generally 40-65 mm, up to 100 mm in unusually large specimens), apex 4-8 (12) mm wide; naked and shining, dry to lubricous (sometimes viscid from pileus), initially over all pale pinkish to orangish buff (*Pinkish Buff, Cinnamon Buff, Pale Ochraceous Salmon)* and staining orange *(Zinc Orange, Ochraceous Orange, Orange Red)*, gradually becoming orange-cinnamon to dark orange brown *(Mikado Brown, Kaiser Brown, Orange Cinnamon)* from ground upwards, hollow with thick (2-3 mm) cartilaginous cortex surrounding central cavity lined with whitish long fibrils below solid pileus context;

Pseudorhiza fasciculate-racemose, rhizomorphic, of undetermined length; often with great numbers of differentially-developed basidiomes erupting from one point above subtending rhizomorphic pseudorhizal strand (*cf.* 'fasciculate starburst', Chapter 3), generally pallid at stipe/pseudorhiza junction, 1-2 mm wide thready portion usually salmon colored.

Spore Print Color medium yellowish brown (yellower than *'Pinkish Cinnamon'*).

Basidiospores 8.5 x 5 ± 0.6 x 0.1 µm (overall range 7.2-9.5 - 4.5-5.6 µm), ovate with short to long straight apical beak in face view, limoniform in profile with eccentric apiculus and central apical beak, verrucose-roughened to warty except over 1 µm long apical beak; with ornamented plage, pale tawny to pale rusty-brown in KOH, inamyloid in Melzer's;

Cheilocystidia relatively abundant, >20 x 2-3 x 1.5-2 µm, lageniform to capitulate tibiiform with narrow, refractive necks, with or without apical secretory droplets, hyaline or with pale amber oily contents surrounded by thick refractive walls;

Pleurocystidia: absent;

Basidia 4-spored, 26-34 x 5-6.5 µm, hyaline (occasionally with orange-amber contents during spore formation);

Pileipellis a bilaminate ixocutis with a 100-300 µm thick suprapellis composed of radially aligned uplifted frequently 'curly' 1-2 (3) µm wide gelatinous smooth hyaline hyphae embedded in an extensive gelatinous matrix overlying a subpellis composed of increasingly wider (4-15 µm), thick-walled, gelatinized hyphae with brownish to brownish-orange walls in KOH; **Stipitipellis** composed of longitudinally arrayed, narrow (1-3 µm), thick-walled, cylindrical, highly gelatinized, hyaline to pale amber hyphae;

Tramal tissues Very highly gelatinized, strongly sarcodimitic in the rhizomorphic pseudorhiza dominated by rigid parallel colorless long (200 µm) wide (up to 14 µm) extremely thick-walled (3-9 µm) cylindrical to slightly fusoid 'vessel hyphae; surrounded only occasionally by thin-walled flexuous hyphae, the thick-walled vessel hyphae less prominent in the pseudorhizal junction between the rhizomorphic cord and stipe bases and with thinner (2 µm) walls and supported by much shorter thin-walled (0.5 µm) highly branched narrower (4-5 µm wide) flexuous hyphae; Lamellar parallel, composed of long cylindrical to slightly inflated 3-5 µm wide highly gelatinized hyaline hyphae with non-refractive septa in the central region that narrow toward the edges to 1-2 µm, giving rise to a compact subhymenium;

Tibiiform diverticula: abundant on primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex;

Clamp Connections absent.

Macrochemical reactions: Syringaldazine -- slowly magenta on pseudorhizal pellis, negative in stipitipith, pileus, and lamellae; KOH -- no color change noted; FeSO4 -- greenish;

RFLP profile: Extensive data for 10 isolates (including the type and isotype) shows the 700 bp ITS profile identical with *P. californica;* Hinf1 (355,345) and EcoR1 (350, 350) diagnostic enzymes; also cut in Cfo1, Nde2, Pvu2 and uncut in Rsa1, Sal1, and Xho1.

Habit and ecology: locally abundant in densely cespitose mounds in woody humus in coniferous forests, most frequently (but not exclusively) associated with *Picea sitchensis, Abies* and/or *Vaccinium* species.

Range and distribution: coastal (sea level) to inland to 4000'; Washington, Oregon, California.

Type: A. H. Smith 79286_{sca6} (MICH) -- October 24, 1970, Cascade Head Experimental Forest, Tillamook County, Oregon.

Comments: *P. scatesiae* can be readily identified in the field by its extremely densely fasciculate habit (often with scores of tightly clustered moderately-sized basidiomes emanating from single points on subtending rhizomorphic pseudorhizae), moderately-sized, highly glutinous, pale yellow brown to blackish brown pilei with pallid to pinkish buff lamellae and equal, smooth, thickly cartilaginous hollow stipes. In 1977 Horak synonymized *P. scatesiae* with the clearly microscopically similar *P. californica.* This synonymy is supported in the current study by the identical RFLP profiles of the ITS rDNA region. However, macroscopical and microscopical comparisons of numerous fresh and dried collections support the existence of two taxa. The cespitose 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, frequently orangish to orange-brown basidiomes arranged in close to crowded 'loose bundles'. *P. californica* pilei, while subviscid to viscid, are rarely glutinous. There are subtle but clear microscopical differences as well: *P. scatesiae* has slightly smaller, frequently narrower, less coarsely ornamented, paler basidiospores, more abundant cheilocystidia, and a much more extensive suprapellis in which smooth (never hyaline incrusted) slightly narrower hyphae are embedded. Additionally because *P. scatesiae* aerial stipes appear to retain a greater number of fibrillose pellicular veil remnants, tibiiform diverticula are generally abundant and easily located in dried material. *Phaeocollybia scatesiae* appears to have a wider distribution than *P. californica,* extending further south to Marin County (California), further north (Washington), and further inland at higher elevations. (See also comments under *P. californica* and the also closely related *P. rufotubulina.)*

In the field the dark form of *P. scatesiae* may be confused with smaller, unusually closely gregarious forms of *P. spadicea,* which generally produces scattered large, robust basidiomes. However *P. spadicea* stipes are never polished nor hollow -- characteristically stuffed with firm solid pith -- and have vertical-monopodial, not racemose, pseudorhizae. Microscopically *P. spadicea* differs in having larger tibiiform cheilocystidia and slightly smaller basidiospores.

***Phaeocollybia similis sensu* A. H. Smith** *Brittonia* 9:207. 1957.

Emended

Figures: 2.7, 2.10; 6.42-43

Selected descriptions and illustrations: Bresadola, 1930 -- type description of *P. similis sensu stricto;* Norvell, 1997 -- line drawings and black & white photomicrograph; Smith, 1957b -- description of Smith's concept based on one collection from Carbon River, Mt. Rainier National Park, Washington.

General Impression: Densely gregarious small cartilaginous rooting basidiomes with lubricous to subviscid ochraceous yellow to tawny broadly campanulate pilei, pale buff young lamellae, thin shiny corneous soon hollow stipes with a reddish-brown zone separating the pale pinkish brown apex and deep purplish brown lower portion, blackish criniform lateral-monopodial pseudorhizae, large (~9 x 6 µm) conspicuously warty-rugulose subglobose-limoniform basidiospores with abrupt and prominent apical beaks, filamentous to narrowly clavate thin-walled cheilocystidia, a bilaminate pileipellis with a thin suprapellis with amber gel-incrusted hyphae overlying a pale orange to brownish yellow subpellis with incrusting and intraparietal pigments, no clamp connections. Negative to weakly positive in syringaldazine.

Pileus 10-38 mm broad, broadly convex-campanulate with straight margin and slightly incurved to straight edge, with or without a low broad umbo, dry to lubricous, glabrous, hygrophanous, edge often slightly striate, color when young either uniformly brownish-yellow to pale yellow brown (*Amber Yellow, Antimony Yellow, Yellow Ochre, Tawny Olive, Ochraceous Tawny*) or zonate with rusty brown (*Clay Color)* disc and pale yellow brown *(Buckthorn Brown)* edge, in age more or less uniformly rusty brown (*Clay Color, Mikado Brown, Sayal Brown, Verona Brown, Snuff Brown),* areas of damage dark brownish red (*Russet)*; **Context** 1-3 mm thick at the disc, when young and pristine pale yellow to pinkish buff (*Cream Buff, Light Buff, Pale Ochraceous Buff)* becoming cartilaginous pliant and rusty brown (*Clay Color)* in age; **Odor** vaguely sweetly floral to distinctly raphanoid; **Taste** bitter to slightly nutty;

Lamellae narrowly attached to nearly free, 2-5 mm broad with even to slightly uneven edges, ventricose, subdistant to close (L+ll/cm 17-21 (29) at pileus edge, 9-12 (14) midway between edge and disc), lamellae generally three-tiered with 3-7 lamellulae more or less regularly interspersed, when young yellowish to orangish buff (*Light Buff, (Pale) Pinkish Buff, Pale Ochraceous Salmon),* turning dark yellowish brown *(Ochraceous Tawny)* and then rusty brown (*Clay Color, Sayal Brown)* in age;

Veil occasionally evident as sparsely distributed short pale yellow brown fibrillose patches on stipe apex;

Stipe central to slightly eccentric, 1-4 mm wide at the apex, up to 20-40 mm long above ground level, overall length (including pseudorhiza) up to 160 mm long, equal to tapering below, polished, cartilaginous when young, soon corneous, initially stuffed with fibrillose to stringy pith, becoming hollow in age, surface at first overall pale yellowish or pinkish brown *(Avellaneous, Light Ochraceous Salmon, Pinkish Buff, Cinnamon Buff)* but soon darkening from ground upwards to dark red-brown (*Liver Brown*), frequently with narrow deep orange- to red-brown *(Warm Sepia, Mikado Brown)* band between pale apex and deep reddish-brown lower portion;

Pseudorhiza lateral-monopodial, cartilaginous upper portion continuous with the reddish brown lower stipe and gradually tapering below to brownish-black criniform rhizomorphic pseudorhiza that frequently runs laterally within the top humus layer to the point of origin.

Spore Print deep reddish brown (*Hay's Brown, Cameo Brown-- 10R 3/2)*

Basidiospores 9 x 6 ± 0.5 µm (range 8.5-10 x 5-7 µm), broadly ovate to amygdaliform in face view, subglobose-limoniform to sublimoniform in profile with a short narrow eccentric apiculus and prominent central apical beak, the beak up to 2 µm wide and 2 µm long and most frequently abruptly delimited from the body, more rarely merely tapered; ornamentation heavy and often extending 0.5 µm above spore outline and appearing deep brownish amber under low magnification in KOH, rugulose-warty roughened except over the smooth apiculus and beak, the suprahilar plage an ill-defined area of lowered ornamentation, dark tawny amber in KOH;

Cheilocystidia abundant, filamentous to narrowly clavate, emanating from the lamellar trama and variable in length, usually 20-30 µm long with 4-7 µm wide apices tapering gradually downward to 3-4 µm wide septa, thin-walled, smooth, highly gelatinous, pale to medium pale yellowish amber with 'oily' contents often coagulated when revived in KOH, individual elements separable in fresh mounts but forming a dense yellowish agglutinated barrier when revived in KOH;

Pleurocystidia absent;

Basidia 4- (rarely 2-) spored, 30-40 x 7-9 µm, hyaline in KOH (yellow in sections of the hymenium);

Pileipellis a bilaminate ixocutis with a very thin (15-20 µm) suprapellis composed of radially aligned narrow (1-2 µm) gel-incrusted hyaline to pale yellow hyphae grading into a very pale orange-yellow (in young material) to brownish yellow (in older material) subpellis of 4-8 µm wide gel-encrusted hyphae with pale to dark orange intraparietal pigments; **Stipitipellis** of 4-6 µm wide gelatinized hyphae, hyaline near apex in very

young material, more often with incrusting and intraparietal bright yellow orange pigments, septa slightly refractive and highly pigmented;

Tramal tissues subgelatinized, zonate in rhizomorphic pseudorhizal thread with a subcortical layer of long rigid wide (up to 50 µm) melanized hyphae overlying thin-walled narrower (6-8 µm wide), strongly sarcodimitic in the junction between the criniform portion and the pseudorhiza with long (up to 200 µm) wide (up to 25 µm) thick-walled (up to 2 µm) vessel hyphae supported by branched narrow (3-5 µm) thin-walled (<0.5 µm) hyphae, the pseudorhiza proper complex with a mix of unbranched thin-walled 6-12 µm wide generative hyphae intermixed among highly branched 3 µm wide thin-walled flexuous hyphae and occasional 100-160 µm long wide thick elements, primarily pale yellow to hyaline generative elements present within the pileus; Lamellar trama parallel, with 3-9 µm wide generative hyphae in the central region narrowing to 1-2 µm at the edges to form a compact rudimentary hymenium; (thin-walled narrow branched flexuous hyphae also occasionally present);

Tibiiform diverticula: abundant on mycelia and primordial and pseudorhizal pelli, also frequent on vestiges of pellicular veil on stipe apex;

Clamp Connections absent.

Macrochemical Reactions: Syringaldazine -- negative except for faint magenta in one pseudorhizal pellis; KOH -- reactions not noted; FeSO4 -- dark green;

Fluorescence: young lamellae -- brilliant yellow; context -- brilliant yellow;

RFLP profile: ITS region of 5 isolates = 715 bps; unique in HinfI (390-255-70), Nde2 (top band 295), PalI (450-295), and SalI (565-150); also cut in CfoI, EcoR1, Pvu2; uncut in RsaI and XhoI.

Habit and ecology closely to densely gregarious (sometimes in erumpent clusters) in highly humic soils during early to mid-autumn in low lying to montane mature to ancient moist coniferous forests (*Tsuga, Abies, Picea,* and rarely *Pseudotsuga).*

Range and distribution verified from four localities in British Columbia, Washington and Oregon.

Reference Collections: A. H. Smith 39988 (MICH) -- September 16, 1952, Carbon River Entrance to Mt. Rainier National Park, Pierce County, Washington. **Topotypical collection** -- L.L.Norvell 93.09.24-2, Ipsut Creek above Carbon River, Mt. Rainier National Park, Pierce County, Washington.

Comments: Bresadola (1930) described *P. similis* from material collected from China. Smith (1957) applied that species name to a collection of basidiomes which resembled *P. attenuata* but which had "...longer, broader spores and more of a tendency for the carpophores to become

ferruginous in age." Unable to examine the *P. similis* type collection, Smith compared his material to Bresadola's description, noting that "...it checks with Bresadola's original description on all major points. The spores are up to 7 µm broad and conspicuously roughened, the tendency to become reddish was present on the fruiting body, and the cap was not truly viscid -- Bresadola wrote 'viscosus (?)'. The stipes in dried specimens are blackish. The distributional pattern may seem to some to be out of line, but actually this is not true. From information at hand at this time, it is evident that a number of so-called Asiatic species occur along the Pacific Coast in North America." (Smith, 1957b).

Both Singer (1987) and Horak (1977) felt that the material identified by Smith as *P. similis* was probably distinct from *P. attenuata* but that it also probably did not represent *P. similis sensu* Bresadola. Horak's suggested alternative, *P. piceae*, differs from Smith's collection in basidiome stature and size, pileus color, stipe morphology, pseudorhizal pattern, pileipellis structure, and cheilocystidial and basidiospore morphology. Singer, who apparently did not examine Smith's collection, refers Smith's material to *P. neosimilis* (Singer, 1986), previously named *P. attenuata ssp. mexicana* Singer, 1970). Comparison of Singer's type to *P. attenuata* and *P. 'similis' sensu* Smith shows it to be very closely related. However, *P. neosimilis* is characterized by a suprapellis of heavily pigmented dark orange-brown heavily incrusted hyphae. While incrusting pigments are found in both *P. attenuata* and *P. 'similis'*, they are subtle and noticeable only under oil immersion; those found in *P. neosimilis* are easily observed at 400x magnification. In consideration of differences in pigment topography, it appears that Smith's collections should not be assigned to *P. neosimilis* as Singer suggested.

As noted above, *P. 'similis'* is closely related to -- if not conspecific with -- *P. attenuata* from which it differs by producing slightly smaller basidiomes with pilei that change from brownish yellow to rusty brown in age, pilei that have lower broader umbos and straight rather than incurved margins, young lamellae that appear to lack caesius to lilaceous tones, distribution also at higher elevations, a slightly more highly pigmented suprapellis and less highly pigmented subpellis and cheilocystidia filled with oily appearing dense amber colored contents. If one accepts topotypical collections made by this author as representing *P. attenuata* and *P. 'similis'* then one can also add a 20 bp length mutation in the ITS region to the above differences. For the time being, *P. 'similis'* is presented as a distinct species. When and if subsequent research reveals it to be distinct from *P. attenuata*, it will be formally delimited as taxon in its own right. (See also Comments under *P. attenuata.)*

Phaeocollybia sipei A. H. Smith, *Brittonia* 9: 207. 1957.

Emended.

Figures: 6.44-45

Selected descriptions and illustrations: Smith, 1957 -- type description with anatomical drawings.

General Impression: Closely gregarious medium to large deeply rooting basidiomes with subviscid deep brownish-orange to orange brown broadly campanulate pilei, pale yellowish young lamellae, pale orange to brownish orange polished fibrillose lined to hollow stipes with very thick longitudinally splitting cartilaginous rinds, small (~6.5 x 3.8 µm) ellipsoidal ('bullet-shaped') punctate-roughened basidiospores, subcapitate thin-walled filamentous cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae embedded in a colorless gelatinous matrix overlying a yellow-=brown subpellis, no clamp connections. Very slightly positive (pale magenta) on pseudorhizal pelli in syringaldazine (negative elsewhere). Dried pilei finely concentric wrinkled matte ark orange brown.

Pileus 25-120 mm broad, acutely or obtusely umbonate with downcurved margin and inrolled edge expanding to broadly campanulate with down-turned outer margin and edge, surface glabrous and viscid with tough thick gelatinous cuticle often splitting radially in age and during drying forming concentric ridges resulting from separation of suprapellis from subpellis, color either uniformly orange brown *(Chestnut, Auburn, Orange Cinnamon, Russet --5YR 4/4, 2.5YR 4/6-8)* or zonate with foxy orange *(Burnt Sienna, Mikado Brown, Orange Cinnamon)* margins and darker auburn disk and edge, dried specimens a matte dark orange brown and usually finely concentrically wrinkled; **Context** 3-8 mm thick over the disc and rapidly thinning from margin to edge, disc area buff colored *(Pale Pinkish Buff, Pinkish Buff, Light Buff, 10YR 8/4)* , remainder cartilaginous and concolorous with the cuticle; **Odor** not distinctive or very faintly farinaceous or 'gebrenzlich'/pansy; **Taste** not distinctive or very faintly raphanoid/farinaceous;

Lamellae ascending, free to narrowly attached, close to crowded, narrow to broad (up to 10 mm in fully expanded basidiomes), thin with even to slightly notched uneven edges, polydymous with truncate lamellulae irregularly interspersed, pale yellowish buff *(Cartridge Buff, Ivory Yellow)* when young, becoming pinkish buff *(Pinkish Buff, Light Drab)* and eventually a very deep yellow brown *(Buckthorn Brown, 10YR 6/6)* in age;

Veil evident as scattered orangish or brownish appressed fibrillose patches on aerial stipe;

Stipe central to slightly eccentric, usually 40-80 mm above ground level with 5-13 mm wide apex, overall length including pseudorhiza up to 210 mm long, equal or gradually expanding only slightly before tapering below soil surface, smooth except for fibrillose patches, apex pale tan at first *(Cartridge Buff, Cream Buff, 10YR 6/4)* above a pale brownish orange to cinnamon *(Apricot Buff, Cinnamon, 5YR 5/4)*, darkening to deep orange-red to reddish brown *(Cacao Brown)* from base upwards, initially stuffed but soon hollow below pileus with thick (3 mm) cartilaginous cortex lined with pale orange fibrils;

Pseudorhiza vertical-monopodial, up to 4/5 of overall stipe length, gradually narrowing below to blunt or slightly curled origin or occasionally tapering very gradually to a narrow cord, usually dark red brown, walnut brown, or liver brown overall, occasionally with a paler tip at the origin.

Spore Print Color medium yellow brown (*Cinnamon brown ('Buckthorn Brown')*.

Basidiospores: 6.5 x 3.8 ± 0.3 x 0.2 µm (overall range 5.8 - 7.5 x 3.3 - 4.5 µm), ovoid to subellipsoidal in face view, in profile subellipsoidal, ventrally rounded (bullet-shaped) with small eccentric apiculus and rounded to obscurely pointed apex, finely punctate-roughened under oil immersion, pale medium amber in KOH, inamyloid, nondextrinoid in Melzer's

Cheilocystidia 30-40 x 2-3 x 7-9 µm, a mixture of 2-4 (5) µm wide, smooth, thin-walled, irregularly filamentous to narrowly clavate elements with rounded, slightly mucronate, or subcapitate (up to 8 µm wide) apices with subcapitate elements predominating in younger specimens, hyaline;

Pleurocystidia: absent;

Basidia 4-spored, 22-28 x 6-8 µm, hyaline;

Pileipellis a bilaminate ixocutis with a colorless suprapellis composed of interwoven narrow (2-3 µm) gelatinized hyaline hyphae embedded in a colorless gelatinous matrix overlying an ochraceous-brown subpellis with inflated 8-30 µm wide hyphae;

Lamellar trama parallel, gelatinized, hyaline to yellowish and slightly refractive in KOH;

Tibiiform diverticula abundant on primordial and pseudorhizal pellis;

Clamp Connections absent.

Macrochemical Reactions: Syringaldazine negative in pileus and stipe tissues, very slightly positive (pale magenta) on lower pseudorhizal pellis; KOH positive: slightly blackish brown to dark brown in young specimens; FeSO4 positive -- initially dull greenish, becoming dark greenish brown after 30 minutes.

RFLP profile: ITS region of two isolates (including type) = 730 bps; unique in PalI (uncut), also uncut in Pvu2, RsaI, SalI, and XhoI; cut in CfoI, EcoR1, HinfI, and Nde2.

Habit and ecology: closely gregarious under conifers (*Picea, Tsuga,* and *Pseudotsuga);* more ephemeral in nature than most Phaeocollybias, frequently deteriorating rapidly in the field.

Range and distribution: patchy and thus perceived as rare, often locally abundant in isolated pockets in the western Willamette Valley and along the central and northern Oregonian coast; one specimen also collected from the Hoh Valley, Olympic National Park, Washington.

Type: F. P. Sipe Oct, (date/day unknown) 1937 (MICH) -- Eugene Oregon.

Comments: There are striking similarities between *P. sipei* and *P. dissiliens*, which share similar stature, orange coloration, cheilocystidial form, and small, ellipsoidal, almost smooth basidiospores. Basidiomes of *P. dissiliens* can be differentiated by their slightly smaller stature and brighter orange coloration, the finely radially-wrinkled metallic pale orange copper dried pilei and the presence of numerous clamp connections on the cheilocystidia and basidia. The RFLP profiles produced by representatives of the two species also appear distinct, although this needs confirmation. Smith (1957b) likened *P. sipei* microscopically to *P. christinae* (which has much larger spores and less heteromorphic, more inflated clavate cheilocystidia) and in color and stature to *P. jennyae.* However, recent collections indicate that *P. sipei* basidiomes can become much larger than previously indicated (Smith described pilei as being 30-50 mm broad and stipes as being up to 120 mm long and 6 mm wide). Smith was never able to observe the species in the field; numerous collections made during the 1995 and 1996 field seasons indicate that when fully mature, *P. sipei* basidiomes are quite large and in no way resemble *P. jennyae.*

Horak (1977) considered *P. sipei* as possibly synonymous with *P. californica.* He has since indicated (personal communication, 1995, 1996) that the specimen sent him from the apparently mixed type collection apparently belonged to *P. scatesiae* (which he considers synonymous with *P. californica).* His confusion apparently was compounded by the fact that although Smith (1957) described the spores of *P. sipei* as being very faintly ornamented, he included an illustration showing heavily ornamented spores. Examination of the entire type collection at Michigan as well as of numerous recent collections indicate that the spores are, in fact, very finely ornamented (practically smooth unless viewed under high-power oil immersion), lack apical beaks, are generally ellipsoidal ('bullet-shaped') and greatly resemble those of *P. dissiliens,* and *P. oregonensis.* Both *P. scatesiae* and *P. californica* lack the intense orange coloration of *P. sipei* and have tibiiform cheilocystidia. Two other sympatric orange mushrooms include *P. piceae,* smaller and more fragile with a thinner stipe cortex, firmer, less evanescent stipitipith, and much larger, more heavily ornamented spores and *P. kauffmanii,* considerably more robust with a stipe that never becomes hollow and which has large limoniform basidiospores.

Phaeocollybia spadicea A. H. Smith, *Brittonia* 9: 215-216. 1957.

Emended

Figures: 2.2,2.4; 6.46-47

Selected descriptions and illustrations: Smith, 1957 -- type description with black & white photograph and anatomical drawings; Norvell, 1997 -- black & white photograph.

General Impression: Scattered to gregarious medium to large fleshy deeply rooting basidiomes with viscid to glutinous dark brown convex-campanulate pilei, pinkish buff young lamellae, drab cinnamon to dull yellow brown stuffed stipes covered with unusually dense apical cinnamon to orange brown fibrillose patches, gradually attenuating vertical-monopodial pseudorhizae, medium-sized (~8 x 5 µm) verruculose limoniform basidiospores with obscure apical beaks, abundant thick-walled refractive capitulate tibiiform, and numerous thin-walled lageniform to capitate cheilocystidia, a bilaminate pileipellis with suprapellicular hyphae embedded in a colorless gelatinous matrix overlying a rusty-brown subpellis, and no clamp connections. Pseudorhizal tissues magenta in syringaldazine.

Pileus 26-120 mm broad, convex-campanulate with a low broad umbo, straight margin and slightly incurved to straight edge, glabrous and smooth, viscid to glutinous, subhygrophanous, edge non-striate, color either uniformly some shade of dark brown to chestnut brown *(Chestnut Brown, Bone Brown, Clove Brown, Snuff Brown)* or with darker disc *(Fuscous, Bister, Bone Brown, Clove Brown, Chestnut Brown, Hair Brown, Natal Brown)*, brownish drab to dark yellow brown margin *(Wood Brown, Avellaneous, Drab, Buffy Brown, Clove Brown, Snuff Brown, Saccardo's Umbo)* and pale pinkish to yellow brown edge (*Sayal Brown, Cinnamon, Snuff Brown, Tawny Olive, Saccardo's Umber, Vinaceous Buff, Avellaneous, Natal Brown, Wood Brown)*; **Context** 3-8 mm thick at the disc, tapering evenly to the margin with a distinct cartilaginous layer near the surface, when young pale pinkish tan to pale drab *(Pale Pinkish Cinnamon, Tilleul Buff, Vinaceous Buff, Light Drab, Pale Smoke Gray, Pale Drab Gray)*, darkening with age to dull or rusty brown *(Hair Brown, Clay Color)*; **Odor** not distinctive to raphanoid or slightly unpleasant ('gebrenzlich'); **Taste** not distinctive or raphanoid, occasionally bitter;

Lamellae narrowly attached to nearly free, 7-11 mm broad with even to slightly serrulate edges, close to crowded (L+ll/cm = (11) 15-26 at pileus edge, 8-15 midway between edge and disc), lamellae generally polydymous with 3-7 lamellulae irregularly interspersed, color at first pale pinkish tan (*Pinkish Buff, Tilleul Buff, Avellaneous)*, soon dulling to pinkish or yellowish brown *(Vinaceous Buff, Avellaneous, Cinnamon Buff, Buffy Brown, Isabella Color)*, becoming dark yellowish brown (*Buckthorn Brown, Tawny Olive, Wood Brown)* when mature;

Veil usually evident as cinnamon or dark orange brown *(Pinkish Cinnamon, Mikado Brown)* fibrillose patches on stipe apex;

Stipe central to slightly eccentric, 6-20 mm wide at the apex, up to 50-90 (120) mm long above ground level, overall length (including pseudorhiza) up to 210 mm long, equal or tapering gradually beneath apex or expanding slightly to ground level before narrowing below, fleshy, surface dry to moist, matte, and innately longitudinally lined, at the apex pinkish brown to drab when young *(Pinkish Buff, Light Pinkish Cinnamon, Cinnamon Buff, Drab)* becoming dark yellowish brown *(Tawny Olive, Wood Brown, Cinnamon Color)* in age, grading into dark pinkish to reddish brown *(Fawn Color, Mikado Brown, Kaiser Brown, Saccardo's Umber)* at ground level, stuffed with firm pale buff *((Pale) Pinkish Buff, Tilleul Buff)* stipitipith that turns brownish orange to dark yellow brown *(Orange Cinnamon, Army Brown, Wood Brown)* when sliced or crushed;

Pseudorhiza vertical-monopodial, more or less continuous with stipe and tapering gradually downwards to a blunt or nippled origin, occasionally giving rise to primordia or younger basidiomes (See Chapter 2), dark reddish brown *(Liver Brown, Saccardo's Umber, Kaiser Brown);*

Spore Print dark yellow brown *(Cinnamon, Wood Brown -- 7.5 YR 4-5/4-6)*

Basidiospores ~8 x 5 ± 0.5 µm (overall range 6-9 x 4-5.5 µm), broadly ovate to amygdaliform in face view, limoniform in profile with a short slender eccentric apiculus and gradually tapered ≤ 0.5 µm long central apical beak, verruculose-roughened except over the smooth apiculus and beak and ill-defined punctate-roughened suprahilar plage, medium dark amber in KOH, pale amber in H2O, dextrinoid in Melzer's Reagent;

Cheilocystidia abundant thick-walled lageniform to tibiiform elements with narrow, hyaline to amber refractive necks and capituli often surrounded by amber apical secretory droplets (23-32 x 3-5 x 1-1.5 x 1.5-2 µm) intermixed with less numerous to occasional thin-walled lageniform to capitate hyaline elements with ochraceous non-refractive necks (26-40 x 4-8 x 2 x 2-3);

Pleurocystidia absent;

Basidia 4- spored, 33-40 x 6-9 µm, hyaline;

Pileipellis a bilaminate ixocutis with a 200-450 µm thick suprapellis composed of a gelatinous matrix in which are embedded more or less radially aligned long cylindrical sparingly branched 1-2 µm wide hyaline hyphae above a subpellis of more or less radially arrayed gelatinized 6-12 µm wide inflated hyphae with pale to dark rusty brown walls;

Tramal tissues: highly gelatinized, strongly sarcodimitic in the pseudorhiza with long rigid wide thick-walled gelatinized 'vessel' hyphae intermixed with less frequent narrow branched, thin-walled flexuous hyaline hyphae; both hyphal types frequently also present

in the stipe apex; Lamellar trama parallel, hyaline in KOH, oleiferous hyphae occasionally present,;

Tibiiform diverticula: abundant on mycelium, pseudorhizal pellis, stipitipellis, and fibrillose pellicular veil remnants on stipe;

Clamp Connections absent.

Macrochemical Reactions: Syringaldazine -- strongly magenta on pseudorhizal tissues, negative on pileus and lamellar tissues; KOH -- dark brown; FeSO4 -- medium to dark dull green;

Fluorescence: lamellae -- intense whitish-yellow when young, very dull yellow in older lamellae covered with spores;

RFLP profile: ITS region of 13 isolates (DNA from type specimen not successfully amplified) = 710 bps. Unique in Hinf1 (395-125-110-70), Nde2 (top band 275), and Sal1 (520-190). Also cut in Cfo1, EcoR1, Pal1, and Pvu2. Uncut in Rsa1 and Xho1.

Habit and ecology: solitary to closely gregarious to cespitose in moist old second growth and ancient coniferous *(Picea, Tsuga, Pseudotsuga, Pinus)* or mixed deciduous/coniferous *(Pinus, Pseudotsuga, Lithocarpus, Quercus)* forests;

Range and distribution: relatively uncommon but at times locally abundant in coastal and inland regions of Washington, Oregon, California

Type: A. H. Smith 3339 (MICH 00011634) -- October 26, 1935 near Mora on the Quillayute River, Clallam County, Washington

Comments Diagnostic characters for *P. spadicea* include the glutinous dark brown broadly umbonate pileus, dry matte fleshy dull cinnamon brown stipe covered with frequently conspicuous pinkish cinnamon fibrillose patches, and the long narrow thick-walled refractive capitulate tibiiform cheilocystidia. In the field, *P. spadicea* closely resembles *P. scatesiae, P. gregaria* and *P. redheadii.* While *P. scatesiae* shares many characters in common with *P. spadicea* (dark brown glutinous pileus, similar sized basidiospores, thick-walled refractive tibiiform cheilocystidia), the former taxon is easily identified by its viscid polished consistently hollow cartilaginous stipes and fasciculate--racemose rhizomorphic pseudorhizae. *Phaeocollybia gregaria* shares similar coloration and habit but can be differentiated by its more fragile aspect, fibrillose stipitipith, much larger basidiospores and narrow thin-walled filamentous to clavate cheilocystidia. Unusually large representatives of *P. spadicea* have been mistaken for *P. redheadii*, which can become dark brown in age. *Phaeocollybia redheadii* is, however, characterized by a generally more robust stature, tightly inrolled pileus edge, warmer brown tones in the pileus and stipe, much larger basidiospores, and thin-walled subcapitate pedicellate clavate cheilocystidia.

Smith, who reported *Naucoria lugubris* from Oregon (Smith, 1937), named *P. spadicea* as a new species when he recognized that his collection differed in color, basidiospore morphology, and absence of caulocystidia (Smith, 1957). Horak (1977) later synonymized *P. spadicea* with *P. lugubris* after comparing Smith's type to topotypical European material. In so doing, however, Horak did not address Smith's observation that the basidiospores in *P. spadicea* were beaked while those of *P. lugubris* were not. In 1992 Redhead also compared North American and European representatives and noted that basidiospores in *P. spadicea* 'vary from ovoid to somewhat beaked in mass mounts when viewed in Melzer's reagent (or Cotton Blue in Lactic Acid). In KOH, which causes spore swelling, the slight concave curvature helping to delimit the beak is converted to a convex curvature, thus obscuring the presence of a beak. In this regard *P. spadicea* differs from *P. lugubris* as represented by DAOM 24325 (from Uppsala, Sweden) which lacks any beaked spores regardless of mountant' (Redhead, unpublished material, 1992). These observations have also been confirmed by this author..

In separating *P. spadicea* from *P. lugubris*, Smith (1957b) also noted differences in the presence or absence of 'caulocystidia', relative basidiome size and pigmentation. Citing Kühner & Romagnesi's (1953) earlier observation of abundant caulocystidia in *P. lugubris*, Smith noted that "I failed to find caulocystidia ... on the stipes of *P. spadicea*.... ' (Smith, 1957). It should be noted, however, that both *P. spadicea* and *P. lugubris* do have abundant tibiiform diverticula on the fibrillose remnants of the pellicular veil usually found on the stipe apex, and it is quite likely that Kühner & Romagnesi interpreted these diverticula as caulocystidia. The tibiiform diverticula occur far less frequently on the stipitipellis proper, however, which might explain Smith's inability to find them. It is also true that in the Pacific Northwest, representatives of *P. spadicea* can become quite large and robust; nonetheless, in view of the large variation in size encountered within the species and in view of the large numbers of smaller *P. spadicea* basidiomes encountered, the size difference between the two taxa does not appear to be a diagnostic one. There do appear to be consistent color differences between *P. spadicea* and *P. lugubris*, however. *Phaeocollybia lugubris*, is typically described and illustrated (*cf.* Moser & Jülich, 1994) as having olivaceous tones and considerably paler than the dark chestnut brown found in North American material. Considering the disjunct geographic distribution and subtle macroscopical and microscopical differences, *P. spadicea* is recognized as an independent and distinct species, separate from *P. lugubris*..

One further observation should be made concerning infraspecific variability. Basidiome size has been discussed briefly above. More important is the variation in cheilocystidial morphology that has been encountered during this investigation. All previous sectional taxonomists (Smith, 1957b; Singer, 1970; Bandala & Montoya, 1994) have placed *P. spadicea* into Section *Versicolores* based on its production of large limoniform basidiospores, thick-walled refractive capitulate to lageniform cheilocystidia, and absence of clamp connections. This placement ignores the fact that

in addition to thick-walled refractive capitulate or lageniform cheilocystidia, heteromorphic thin-walled filamentous, mucronate, and capitate cheilocystidia also occur and can be, at times, abundant. While Smith fully described the morphology of the thick-walled cheilocystidia, he merely acknowledged that 'some filamentose-capitate cells [are] also present'. This resulted in a certain amount of confusion during the present study when numerous small, unusually fragile 'spadiceas' were found to possess more thin-walled cheilocystidia than thick-walled. Despite these morphological differences, however, restriction analyses or numerous representatives of *P. spadicea* showed them to have highly distinct and unique restriction profiles; additionally comparison of molecular data with those obtained from other representatives in Section *Versicolores* showed *P. spadicea* closely related (See Chapter 5).

Phaeocollybia tibiikauffmanii nom. prov.

Figures: 2.9, 6.48-49

Selected descriptions and illustrations: Norvell, 1997 -- black and white micrograph.

General Impression: Solitary moderately large slightly farinaceous deeply rooting basidiomes with viscid brownish orange broadly campanulate to reflexed pilei, pale orange buff young lamellae, pale pinkish cinnamon dry stuffed stipes with compact pith, vertical-monopodial pseudorhizae, medium-sized (8 x 4.5 µm) limoniform verruculose basidiospores with prominent smooth tapered apical beaks, thick-walled capitulate refractive tibiiform cheilocystidia intermixed with thin-walled lageniform elements, a bilaminate pileipellis with a medium thick colorless suprapellis overlying a brownish-orange subpellis with intraparietal and incrusting pigments, and no clamp connections. Immediately magenta in syringaldazine.

Pileus: 42-50 mm wide, broadly conic-campanulate with acute papillate umbo, upturned margin and down-turned straight edge, glabrous, viscid, opaque to slightly hygrophanous, nonstriate, overall brownish orange or foxy brown *(5YR 5/8 -- Tawny, Orange Cinnamon)* or with tawny disc and orange cinnamon edge zone; **Context** 6 mm at the disc and confluent with stipitipith, pale orangish white *(10YR 9/3);* **Odor** faintly floral with farinaceous overtones; **Taste** mild, not distinctive;

Lamellae: nearly free, ventricose, thin with ± even edges, polydymous with 3-7 irregularly interspersed tiers, narrow (4-5 mm with average length:width ratio 5.5), close (L+ll/cm = 19 edge, 10 midpoint), pale orangish buff *(10YR 6-8/6 = Warm Buff)* when young, dull pinkish brown *(5YR 5/6 = Fawn Color)*when mature;

Veil: evident as occasional darker fibrillose patches on stipe apex;

Stipe: slightly eccentric, terete, 70 mm above ground level, overall length including pseudorhiza up to 230 mm, apex 10-12 mm diam, ± equal above, gradually narrowing below toward pseudorhiza; glabrous except for darker fibrillose patches, dry, innately

longitudinally lined, apex pale to deep pinkish-orange *(7.5 YR 6/5-8 = Pinkish Cinnamon, Orange Cinnamon)* below grading to dull pinkish brown *(5YR 5/6 = Fawn Color)*, 2 mm thick cartilaginous rind surrounding compact fibrillose orangish white stipitipith;

Pseudorhizal form vertical-monopodial, slightly >2/3 overall stipe length, gradually tapering to dark brown *(2.5 YR 4/6 = Cacao Brown)* pointed origin, firm pith brown where water-soaked, otherwise concolorous with stipitipith;

Spore Print Color dull pinkish brown *(Fawn Color, 5YR 4-5/4-6).*

Basidiospores: 8 x 4.5 ± 0.3 µm (range 7.5-9 x 4-5.2 µm), limoniform with a protruding beaked apex in profile, fusoid-elliptical in face view, verruculose to punctate roughened except on 0.5-1 µm long beaked apex and eccentric apiculus, suprahilar plage an indistinctly bordered area of lowered ornamentation discernible under oil immersion, orange-amber in KOH, ochraceous in H2O, inamyloid (very young spores still attached to basidia faintly dextrinoid in Melzer's);

Cheilocystidia abundant, diverticulate lageniform and tibiiform elements with refractive necks intermixed with occasional thin-walled clavate elements, lageniform/tibiiform elements 17-32 (50) µm long, branched at or above ultimate and penultimate 2-3 µm diam septa, often swelling above septa to 3-5 µm before narrowing to 8-15 X 0.5-2 µm necks, necks either thick-walled and refractive or thin-walled, with or without 1.5-3 µm diam capituli, hyaline;

Pleurocystidia absent;

Basidia 4-spored, 27-32 x 7-8 µm, hyaline;

Pileipellis a bilaminate ixocutis with a 100-120 µm thick suprapellis composed of radially aligned 2-6 µm wide highly gelatinized hyaline hyphae (the top 50 µm portion composed of cylindrical 2 µm wide closely compacted collapsed hyphae above a an area of 2-6 µm wide thin-walled often inflated hyphae) overlying a 170-200 µm brownish-orange subpellis composed of occasional orange oleiferous hyphae intermixed among 2-8 µm thin-walled inflated hyphae with refractive septa and intraparietal and faintly incrusted pigments; **Stipitipellis** of subgelatinized thin-walled 2-6 µm wide pale brownish green hyphae (diffuse pigments soluble in KOH); **Pseudorhizal pellis** of gelatinized dark orange brown 2-4 µm wide hyphae;

Tramal Tissues gelatinous, with oleiferous hyphae throughout; slightly sarcodimitic in the pseudorhiza with very occasional long 10-20 µm wide slightly thick walled (to 0.5 µm thick) hyphae intermixed with 2-6 µm wide irregularly inflating thin-walled flexuous hyphae, monomitic in the stipe and pileus; Lamellar trama parallel, of 65-80x 3-6 µm thin-walled inflated subgelatinized hyaline hyphae narrowing toward the gill edges to 2-3 µm wide hyphae, giving rise to the subhymenial layer;

Tibiiform diverticula abundant on mycelium and pseudorhizal pellis, less frequent on the fibrillose remnants of the pellicular veil on the stipe apex, 4-20 x 0.5-1 µm, hyaline;
Clamp connections absent in all tissues.

Macrochemical reactions: Syringaldazine -- positive (immediately magenta); KOH -- positive (immediately dark brown); FeSO4 -- greenish;.
Fluorescence fresh material not tested; dried lamellae dull yellow orange (one small area in one a brilliant orange yellow)
RFLP profile: not tested.

Habit and Ecology : November, solitary in humus under mature *Picea sitchensis* and *Tsuga heterophylla,* amidst *Polystichum munitum, Vaccinium,Oxalis oregana.*
Range and distribution: Known only from two sites along the coast in Lincoln County, Oregon..
Type: LLN 95.11.09-19 (WTU), Cascade Head Experimental Forest, Lincoln County, Oregon

Comments:

Diagnostic characters of *P. tibiikauffmanii* include its brownish orange viscid conic-campanulate pileus, moderately large size, stuffed tapering stipe, medium-sized punctate-roughened basidiospores, diverticulate thin- and thick-walled lageniform and tibiiform cheilocystidia and lack of clamp connections. It is macroscopically very similar to *P. kauffmanii* (for which it was mistaken by this author when first encountered in the field) and microscopically quite close to *P. pseudofestiva* and *P. spadicea. Phaeocollybia tibiikauffmanii* shares with *P. kauffmanii* a brownish orange viscid pileus, stature, tapering stuffed stipe, vertical-monopodial pseudorhiza, reactivity in syringaldazine and similar sized basidiospores, but the presence of thick-walled tibiiform cheilocystidia and the absence of heavily gelatinized, strongly sarcodimitic tissues, extensive gelatinous matrix in the suprapellis, pigment topography and sharply delimited stipitipellis and stipititrama clearly separates *P. tibiikauffmanii* from *P. kauffmanii.* In the field it may be differentiated by the lack of strongly inrolled pileus edge.

Phaeocollybia pseudofestiva shares general basidiospore and cheilocystidial morphology, syringaldazine reactivity, pileus shape, and odor and taste, but produces slightly smaller basidiomes with olive-green pilei, slightly wider more prominently beaked basidiospores, and non-diverticulate cheilocystidia. *P. spadicea* is also anatomically similar to *P. tibiikauffmanii* but can by differentiated by its dark blackish brown pileus, closely arrayed large fibrillose patches on the stipe apex, negative reactivity of the pileus and lamellar tissues to syringaldazine,

Although only two collections (both solitary specimens) have been found so far and this species has not yet been molecularly investigated, it is felt that this represents a unique morphological species.

Excluded Species:

Phaeocollybia deceptiva A.H. Smith & Trappe, *Mycologia* 64:1142-3, 1972.

Smith & Trappe (1972) named *P. deceptiva* based on a single collection from Northern Idaho. It is characterized by a tawny to yellowish brown moist conic-campanulate pileus, cinnamon lamellae, pallid solid stipe and pseudorhizae, large (8-10 x 4.5-6 µm) coarsely warty-rugulose ellipsoidal basidiospores, a poorly formed non-gelatinized suprapellis, and clamp connections. Smith & Trappe (1972), noting the lack of a viscid pellicle, ferruginous tones in the stipe, and the large, looping clamps, suggested the erection of an independent section to accommodate this species. Redhead (unpublished data, 1992) and this author also observed the absence of a cartilaginous stipe cortex, gelatinized tissues, cheilocystidia and pseudorhizal 'caulocystidia' that characterize *Phaeocollybia* and suggested that the collection might better belong in *Cortinarius*. Phaeocollybia spores are never ornamented more coarsely apically than elsewhere on their surfaces while the spores in *P. deceptiva* is ornamented on the apex. Subsequent microscopical evaluation by Ammirati (pers. comm., 1996) places this collection in *Cortinarius* subgenus *Telamonia*.

Figure 6.1 *Phaeocollybia ammiratii nom. prov.*(**top left**) Habit -- 3/4 actual size. LLN 95.10.18-10 (Holotype); also LLN 95.10.18-27 (both from Oregon); LLN 96.11.29-2 (California); (**top right**) Cheilocystidia with clamp connections; (**bottom**) Basidiospores and basidia.

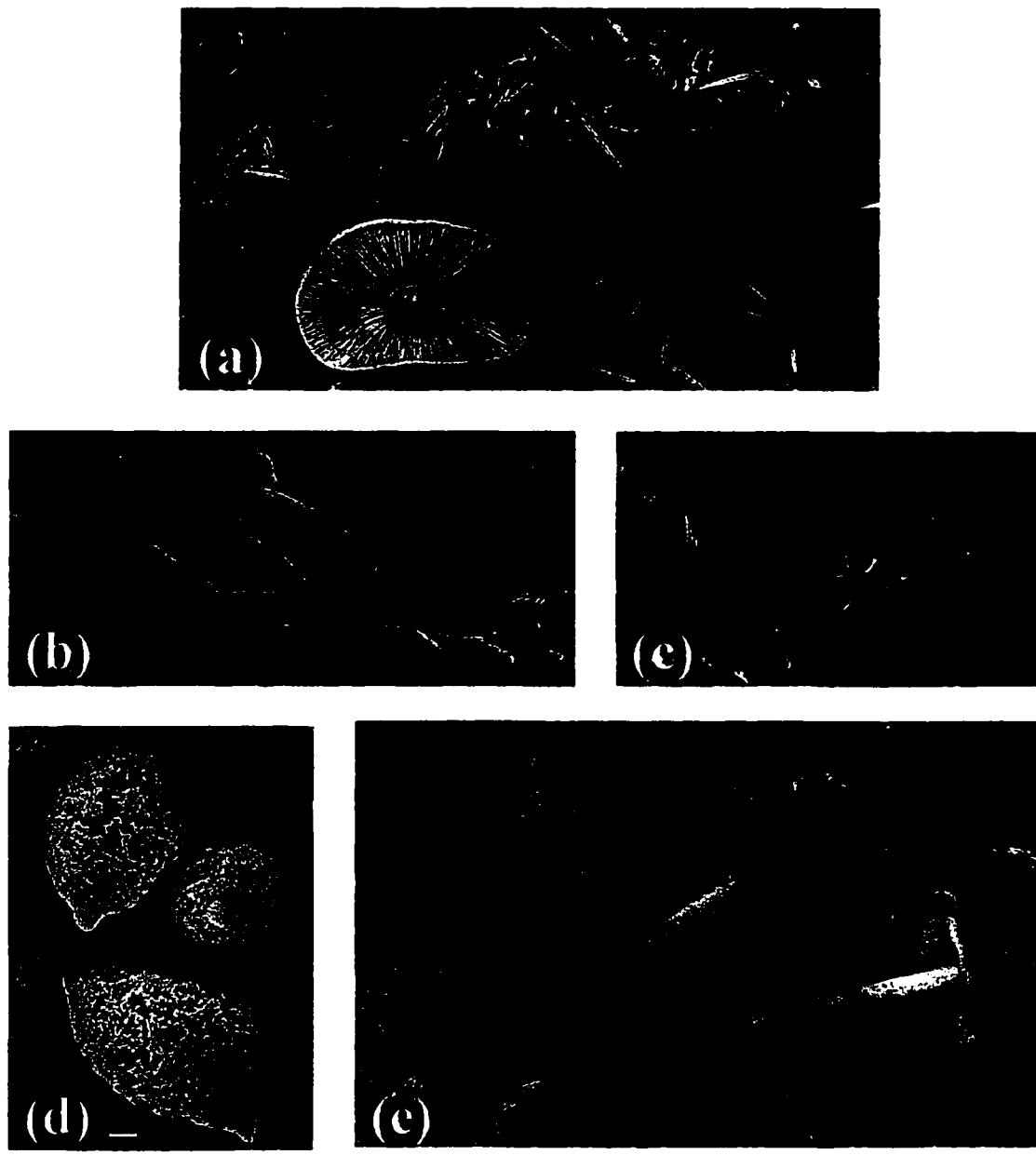


Figure 6.2 *Phaeocollybia ammiratii nom. prov.* **(a)** *In situ,* Barlow Pass (LLN 93.10.20-1). **(b)** Wildcat Mountain (LLN 94.10.28-9). **(c)** *In situ,* Wildcat Mountain (LLN 94.10.28-10). **(d)** Basidiospores (K.Scates 1167; SEM, Scale = 1 µm.). **(e)** Fragile basidiomes with characteristically vinaceous tones on stipe (LLN 95.10.18-27).

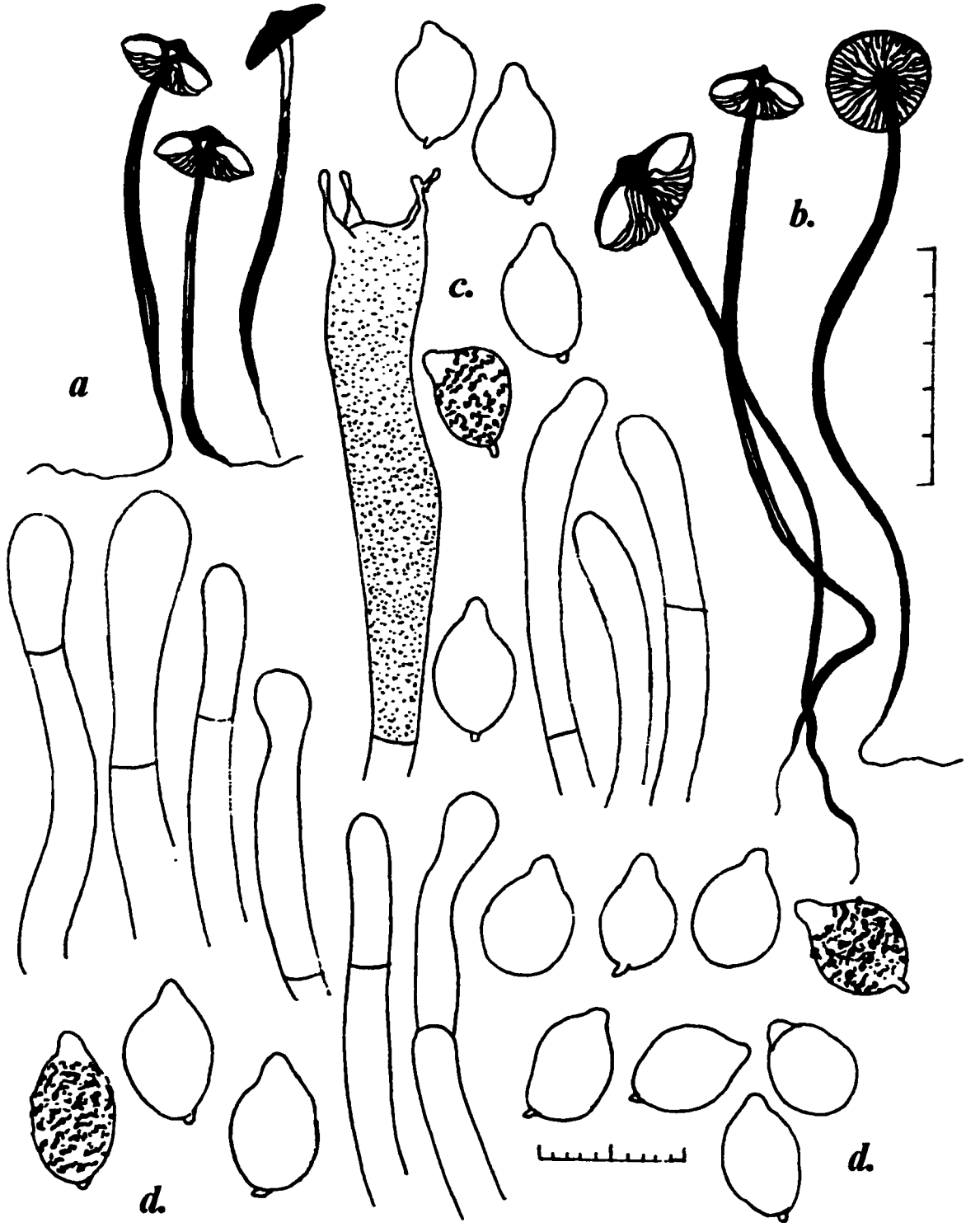


Figure 6.3 *Phaeocollybia attenuata.* .**a-b.** Habit -- 3/4 actual size **a.** (LLN 95.11.09-3,13 WTU). **b.** (LLN 95.11.17-13,21 WTU); **c.** Basidium, basidiospores, cheilocystidia (LLN 94.11.06-34$_{att13}$ WTU). **d.** Cheilocystidia, basidiospores (from three different specimens (Holotype A. H. Smith 3323, MICH).

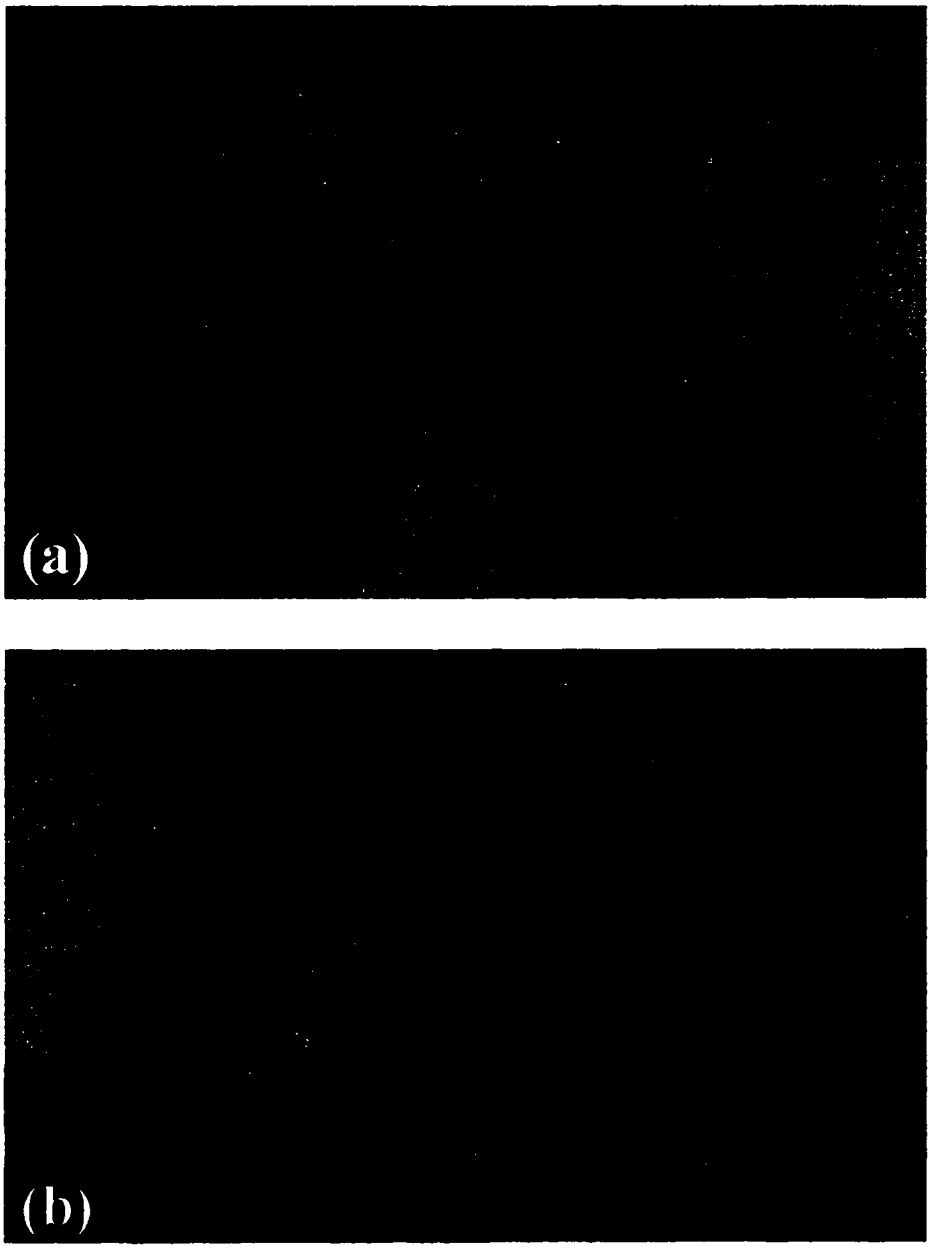


Figure 6.4 *Phaeocollybia attenuata.* **(a)** Collection from type locality (La Push, Wshington) showing characteristic criniform lateral-monopodial pseudorhizae (LLN 92.10.20-5). **(b)** Longitudinal section of specimens from Paul Dunn Forest, Oregon (LLN 95.11.17-9).

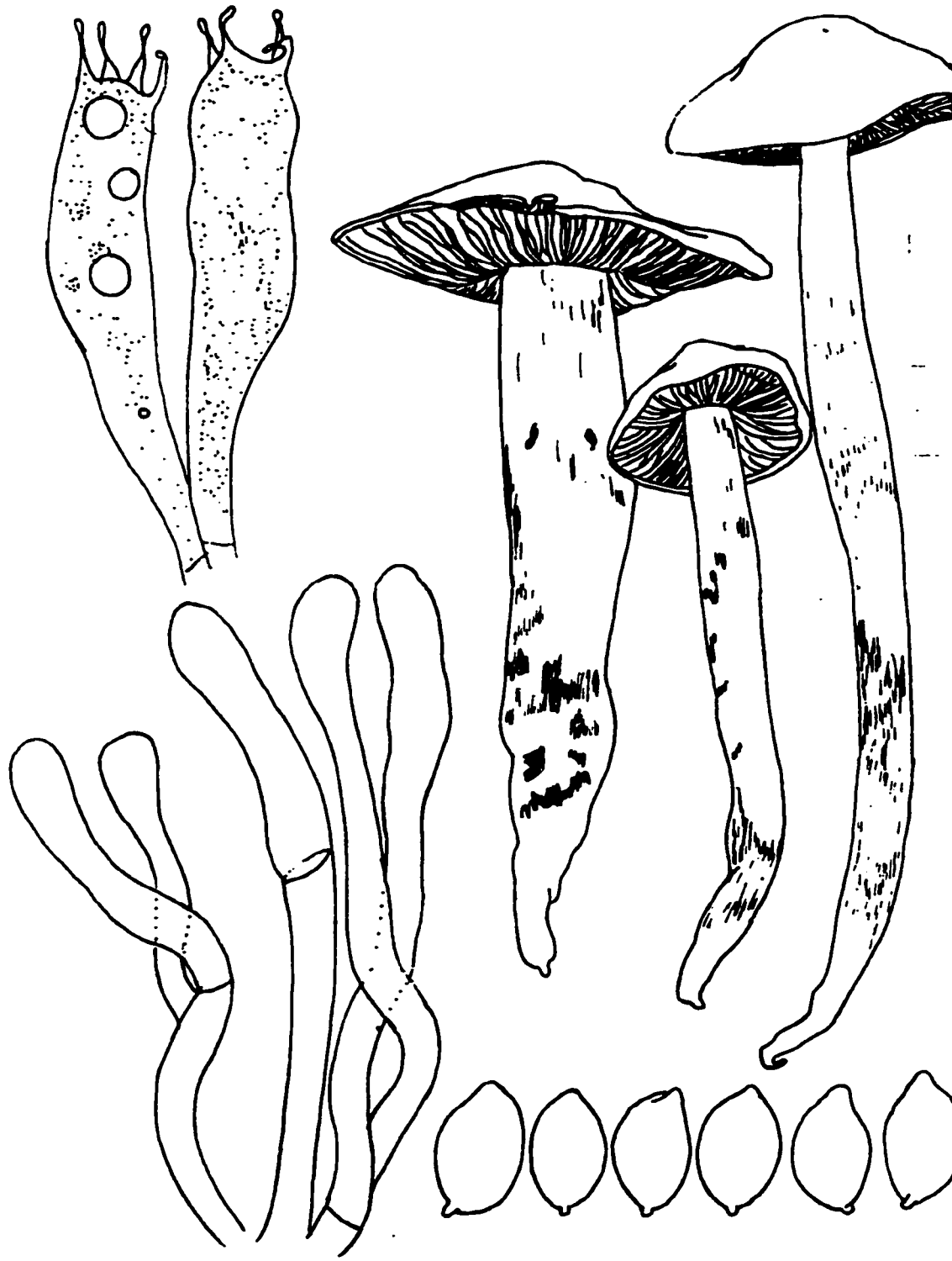


Figure 6.5 *Phaeocollybia benzokauffmanii nom. prov* (LLN 92.11.20-1 (WTU) Holotype).**a.** Habit -- 3/4 actual size. Robust form (Holotype) and slender form (LLN 92.10.23-5); **b.** Basidia, cheilocystidia, and basidiospores (Holotype);

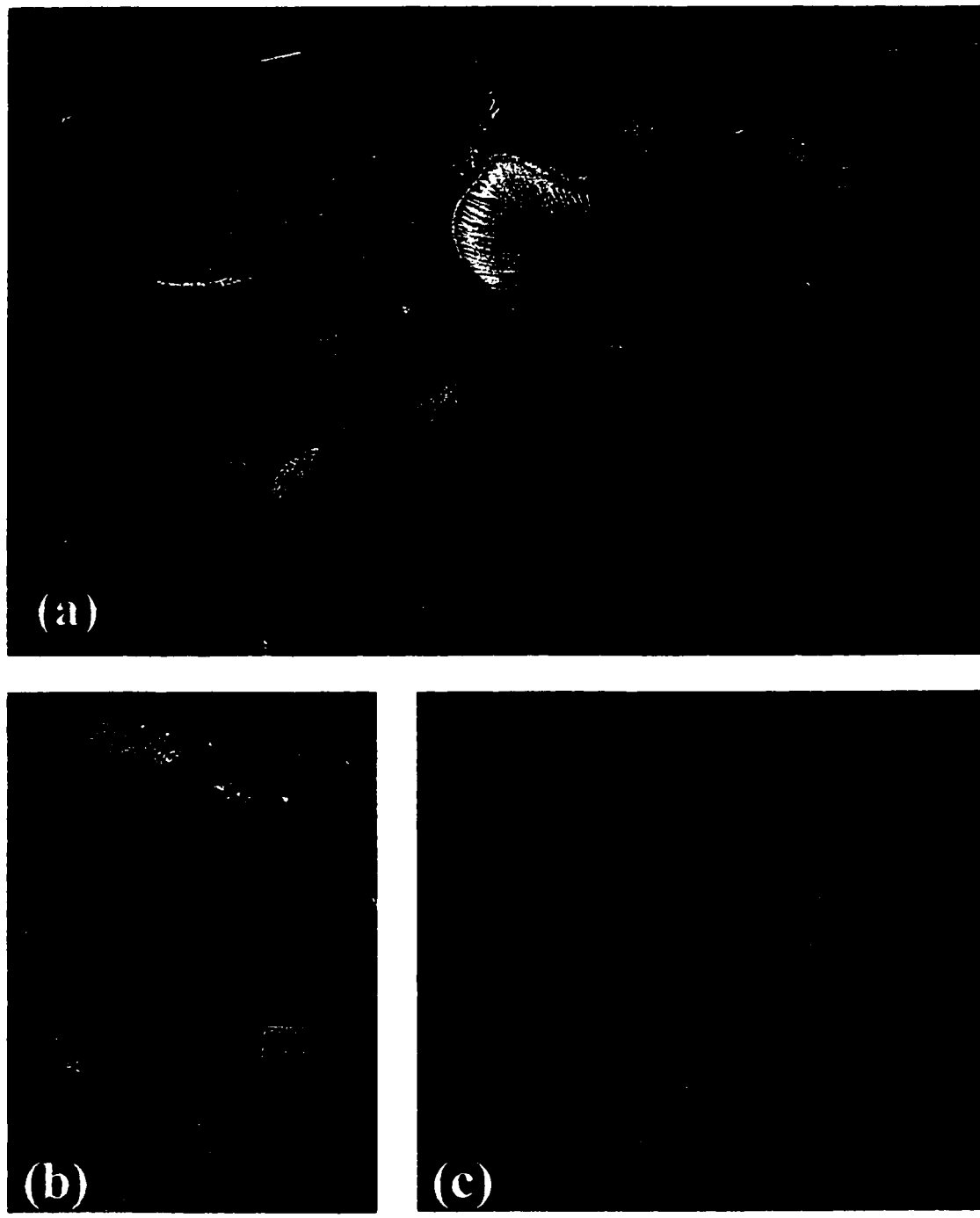


Figure 6.6 *Phaeocollybia benzokauffmanii nom. prov.* **(a)** Type specimens *in situ*, Jackson State Forest (LLN 92.11.20-5). **(b)** Excavation showing two mature basidiomes with one primordium, Olympic National Park (LLN 92.10.23-5). **(c).** Abundant tibiiform diverticula on fibrillose remnant of pellicular veil on stipe apex.

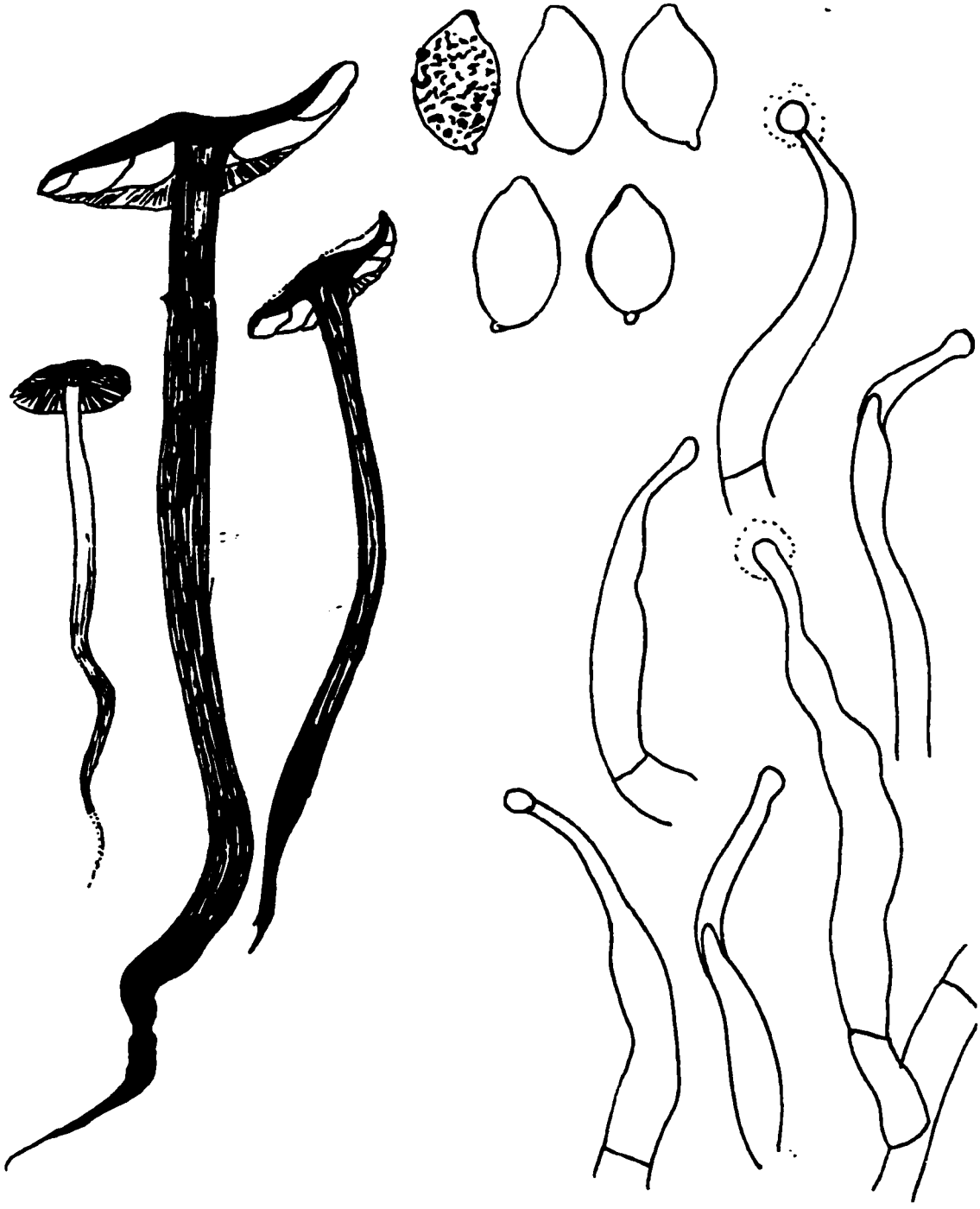


Figure 6.7 *Phaeocollybia californica.*(**left**) Habit -- 3/4 actual size.LLN 95.11.17-24,26; (**right**) Basidiospores, cheilocystidia, basidia.(A. H. Smith 55610 (MICH) -- Holotype)

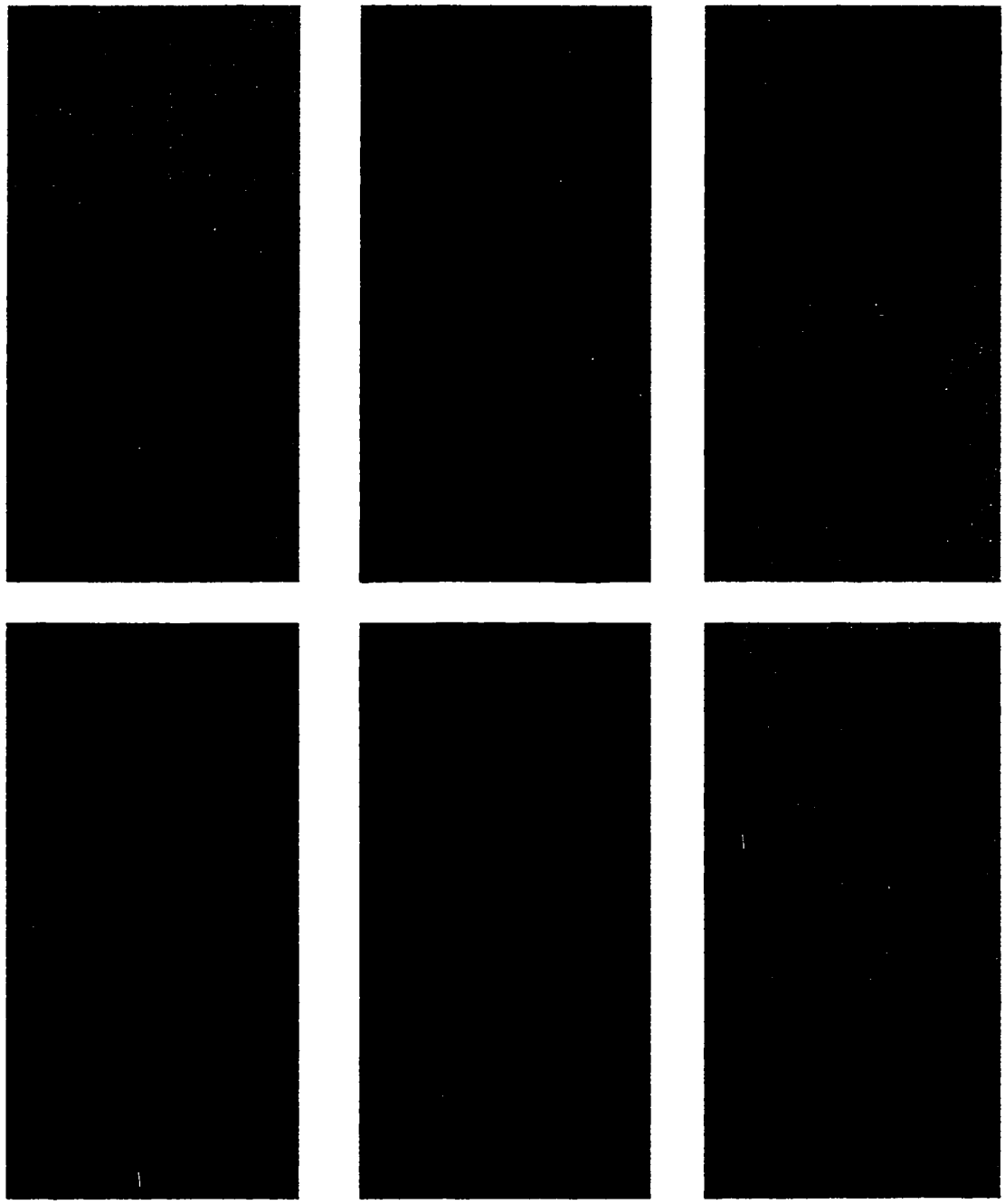


Figure 6.8 Comparison of **(top)** pileipellis structure (bright field, low dry) and **(bottom)** basidiospores on stipitipellis (DIC, oil immersion) from holotypes of (left to right) *P. scatesiae, P. californica* and *P. rufotubulina.*

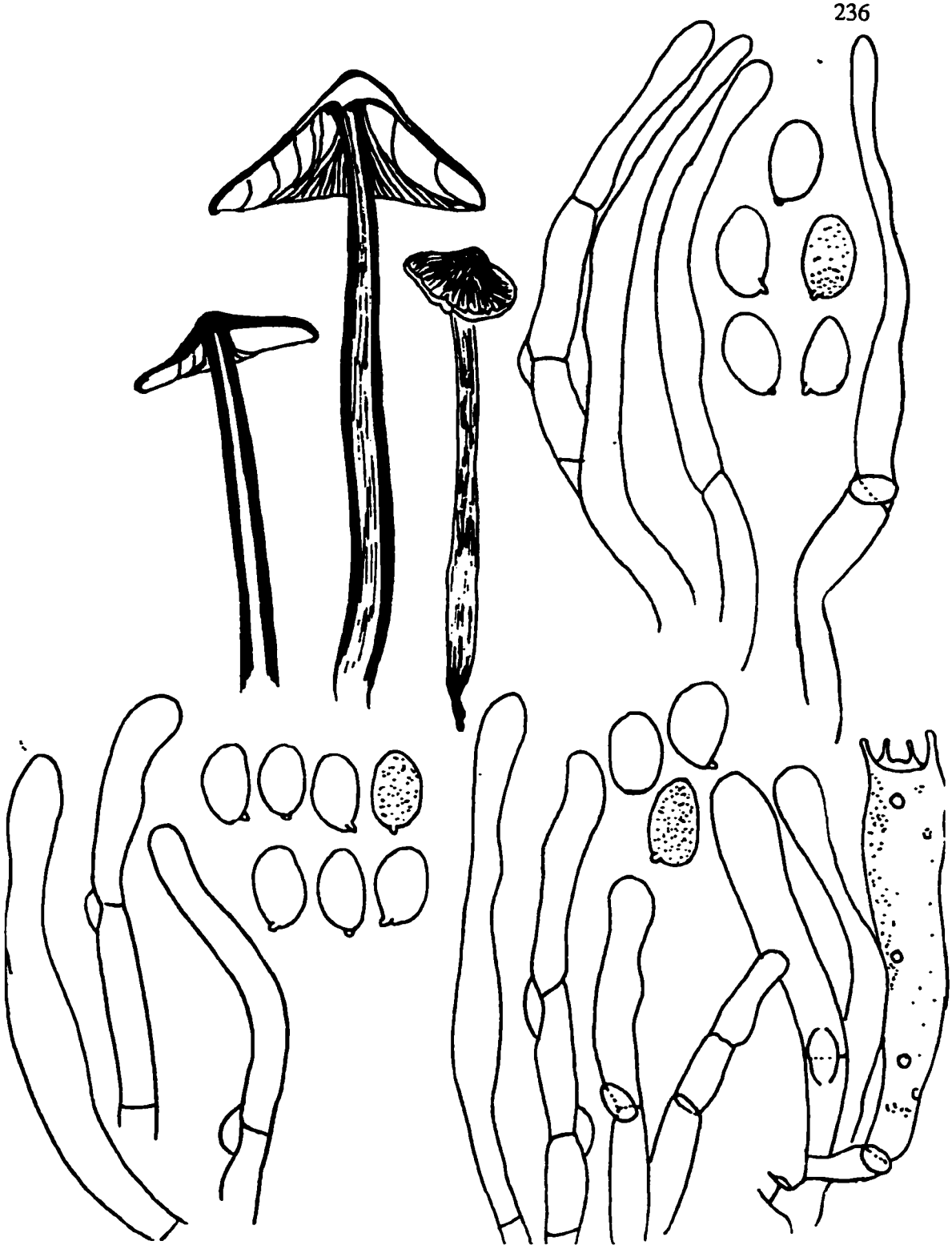


Figure: 6.9 *Phaeocollybia dissiliens*.(**top**) Habit (3/4 actual size), cheilocystidia, basidiospores.(LLN 95.11.09-1,16); (**lower right**) Basidium (LLN 95.11.09-1) (**lower left**) Cheilocystidia and basidiospores (A. H. Smith 79252 (MICH)--Holotype).

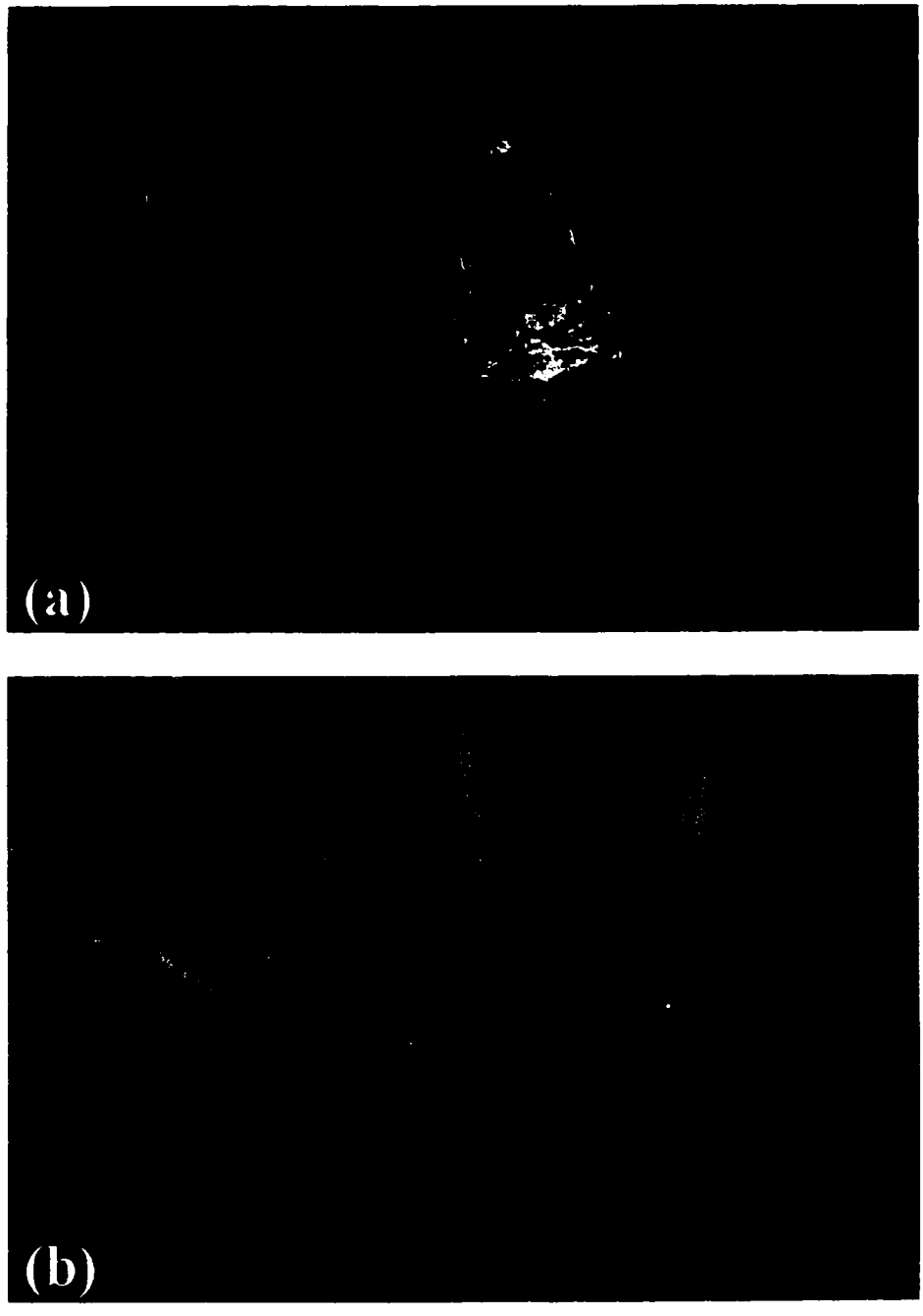


Figure 6.10 *Phaeocollybia dissiliens.* **(top)** *In situ,* Fogarty Creek State Park, Oregon (LLN 95.11.09-1). **(bottom)** Longitudinal section showing characteristically thick stipe cortex and hollow stipe (LLN 95.11.09-6).

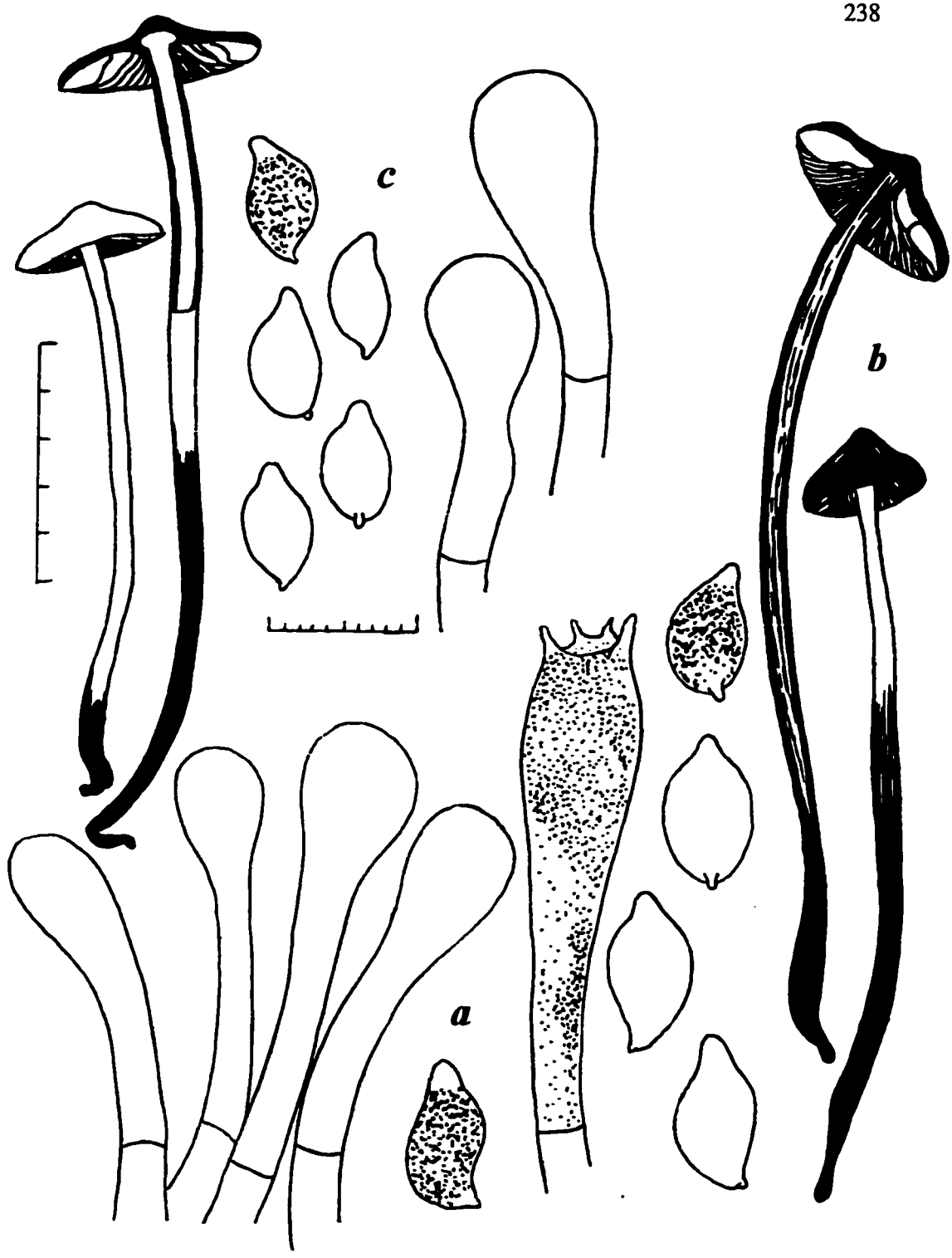


Figure: 6.11 a-b. *Phaeocollybia fallax* -- typical variant **a.** Cheilocystidia, basidium and basidiospores (Holotype: A.H.Smith 3342, MICH); **b.** Habit (3/4 actual size: LLN 95.10.22-1 WTU); **c.** *P. fallax* [small-spored variant]-- Habit, basidiospores, cheilocystidia (LLN 94.10.11-16, WTU).

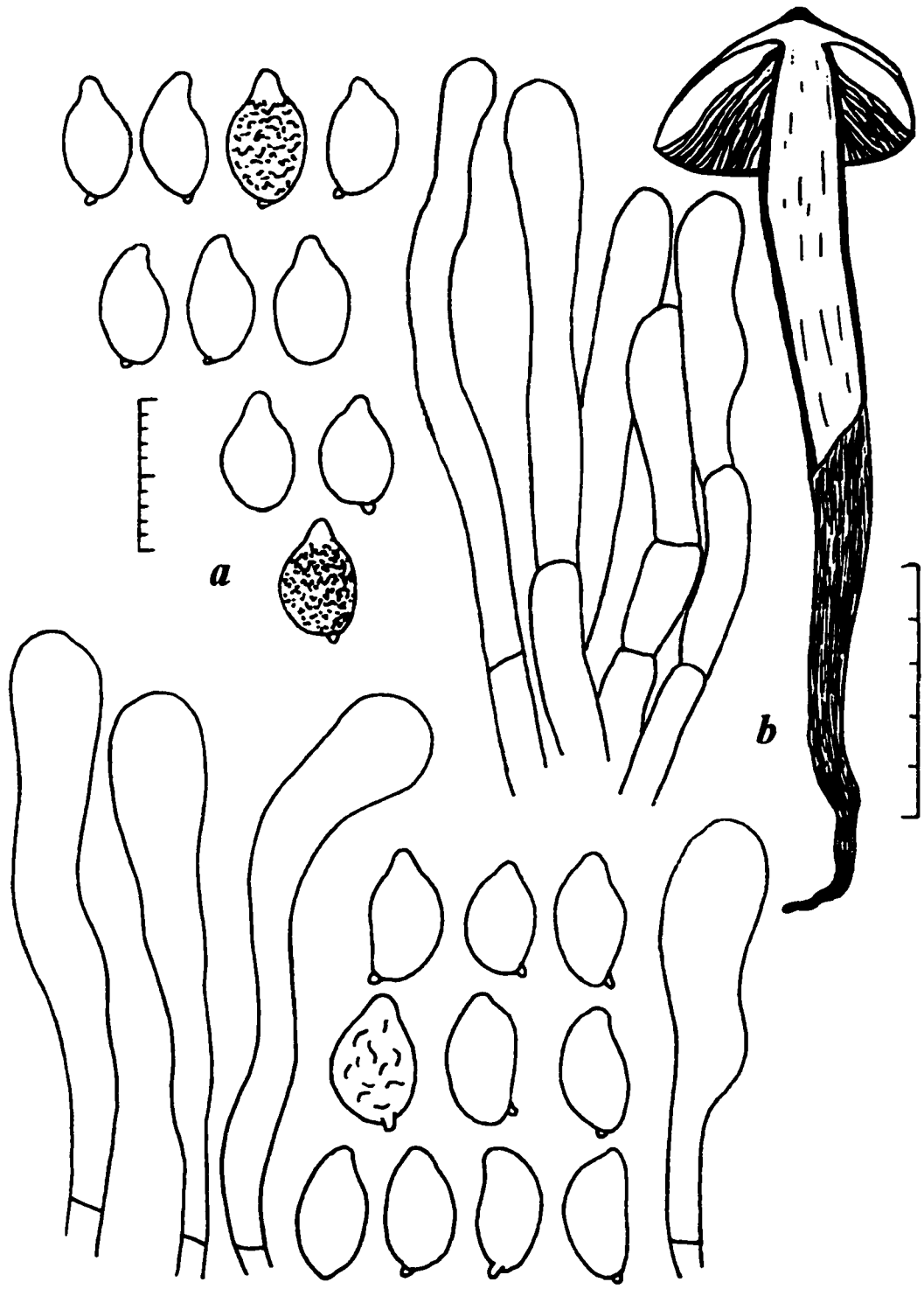


Figure: 6.12 a-b. *Phaeocollybia fallax* -- Wildcat variant (LLN 95.10.18-23a, WTU) **a.** Basidiospores and cheilocystidia; **b.** Habit (3/4 actual size); **c.** *Phaeocollybia festiva* -- Cheilocystidia and basidiospores (Gulden 771/81, O).

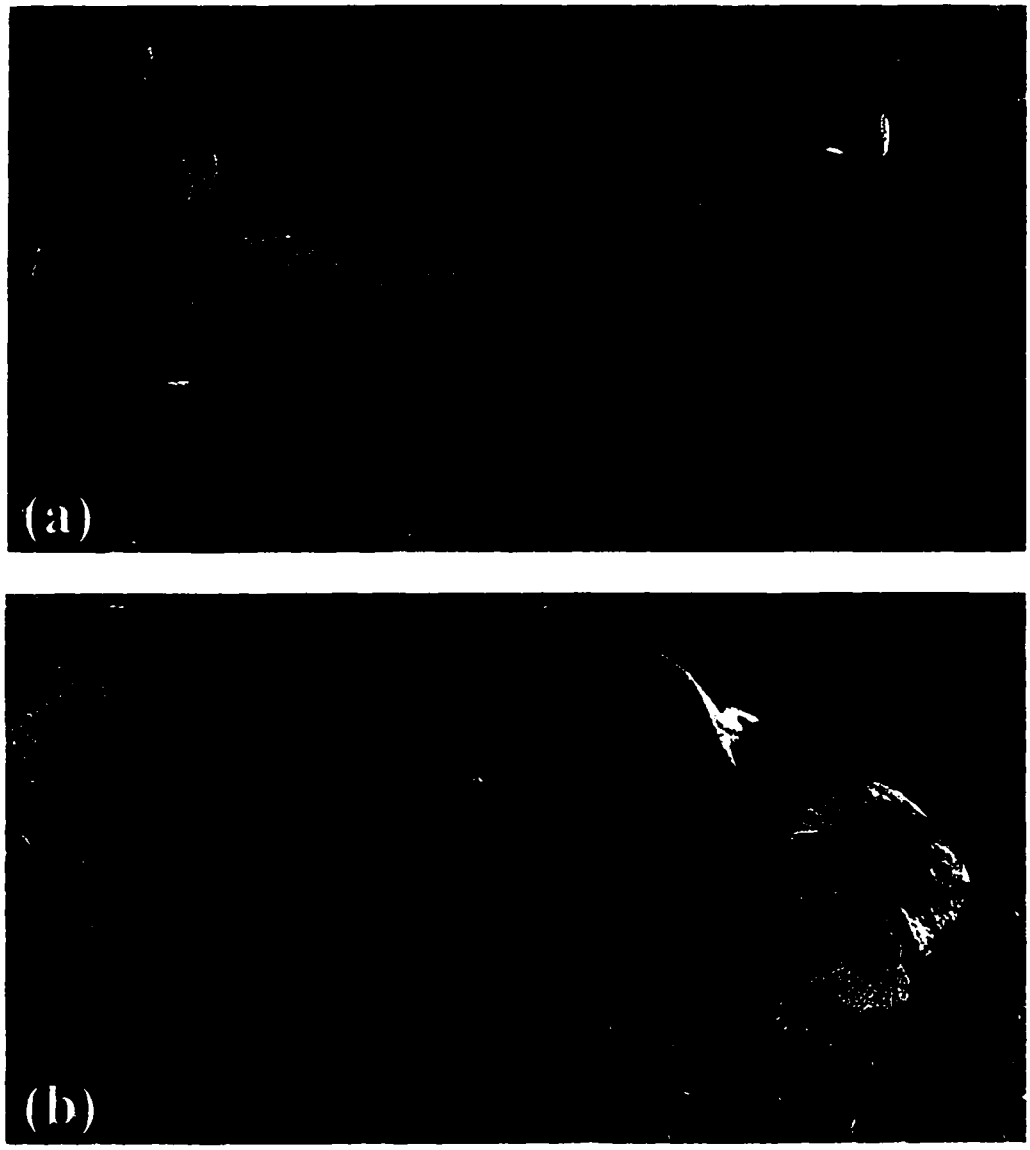


Figure 6.13 *Phaeocollybia fallax.* **(a)** Characteristic green pileus, intense lilac to violet lamellae and orange stipe in specimen from Upper Carmanah Valley, Vancouver Island (LLN 92.10.07-1). **(b)** Mature typical forms with hollow stipes (top) and young small-spored variant with firm stipitipith (LLN 95.10.28-2a,b).

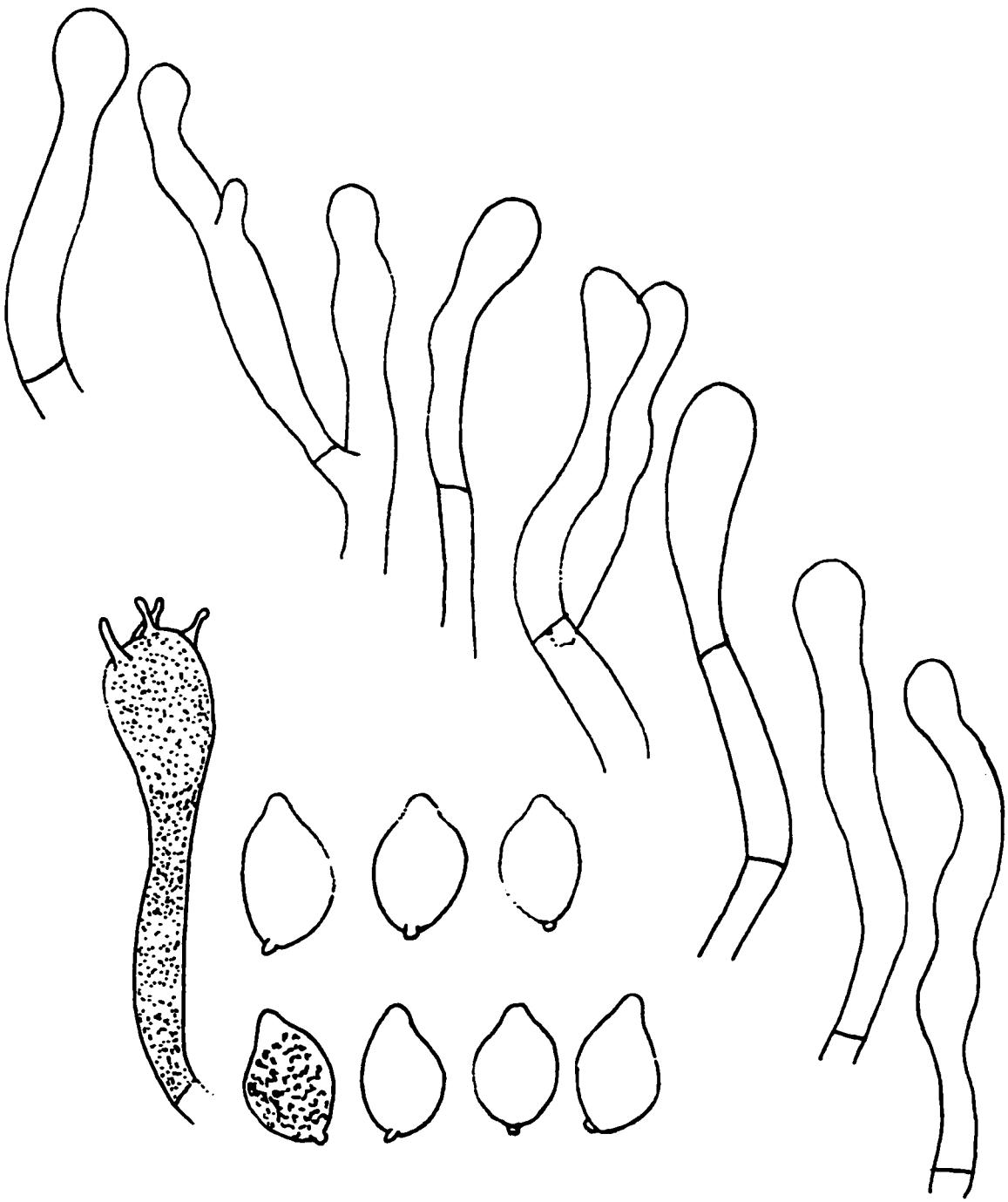


Figure 6.14 *Phaeocollybia gregaria* . Basidia , cheilocystidia and basidiospores (A. H. Smith 79075 (MICH) -- Holotype)

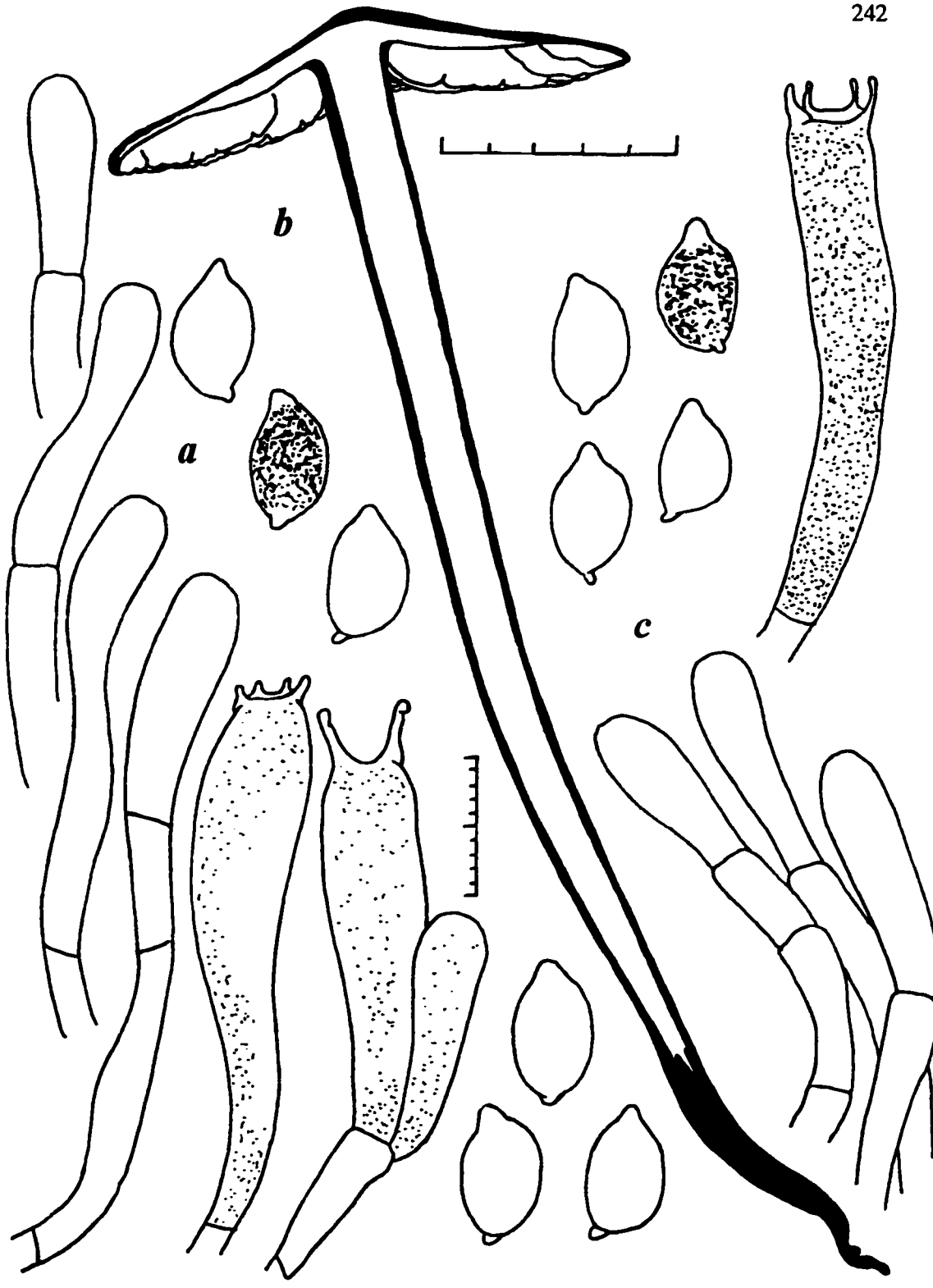


Figure 6.15 *Phaeocollybia kauffmanii*.. **a.** Cheilocystidia, basidia and basidiospores (Holotype A. H. Smith 3523, MICH); **b.** Habit (3/4 actual size -- LLN 94.10.22-4); **c.** Basidium, cheilocystidia and basidiospores (LLN 94.10.22-20).

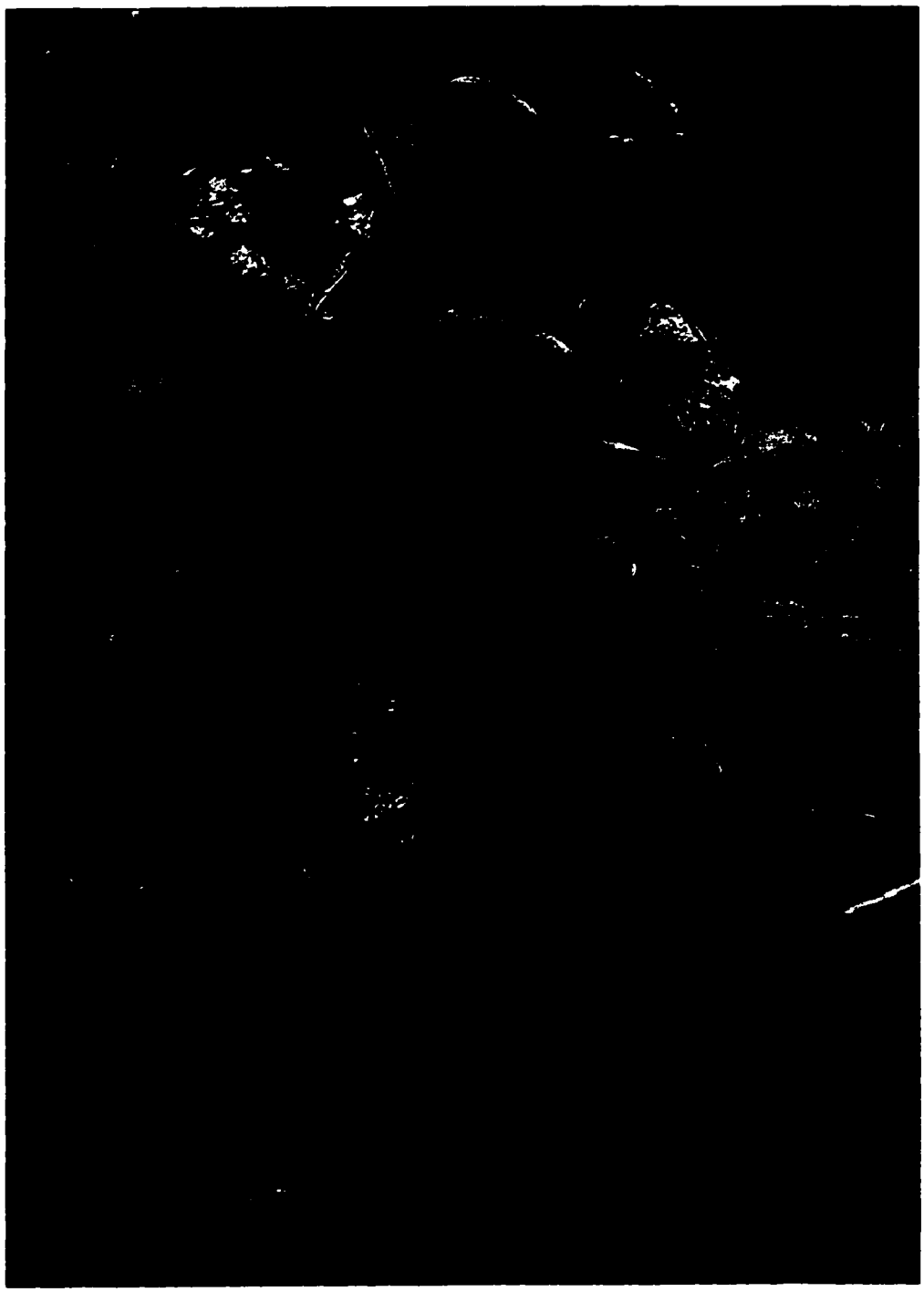


Figure 6.16 ***Phaeocollybia kauffmanii.*** Two mature specimens and primordium *in situ,* Jackson State Forest, Mendocino County, California (LLN 92.11.24-12)

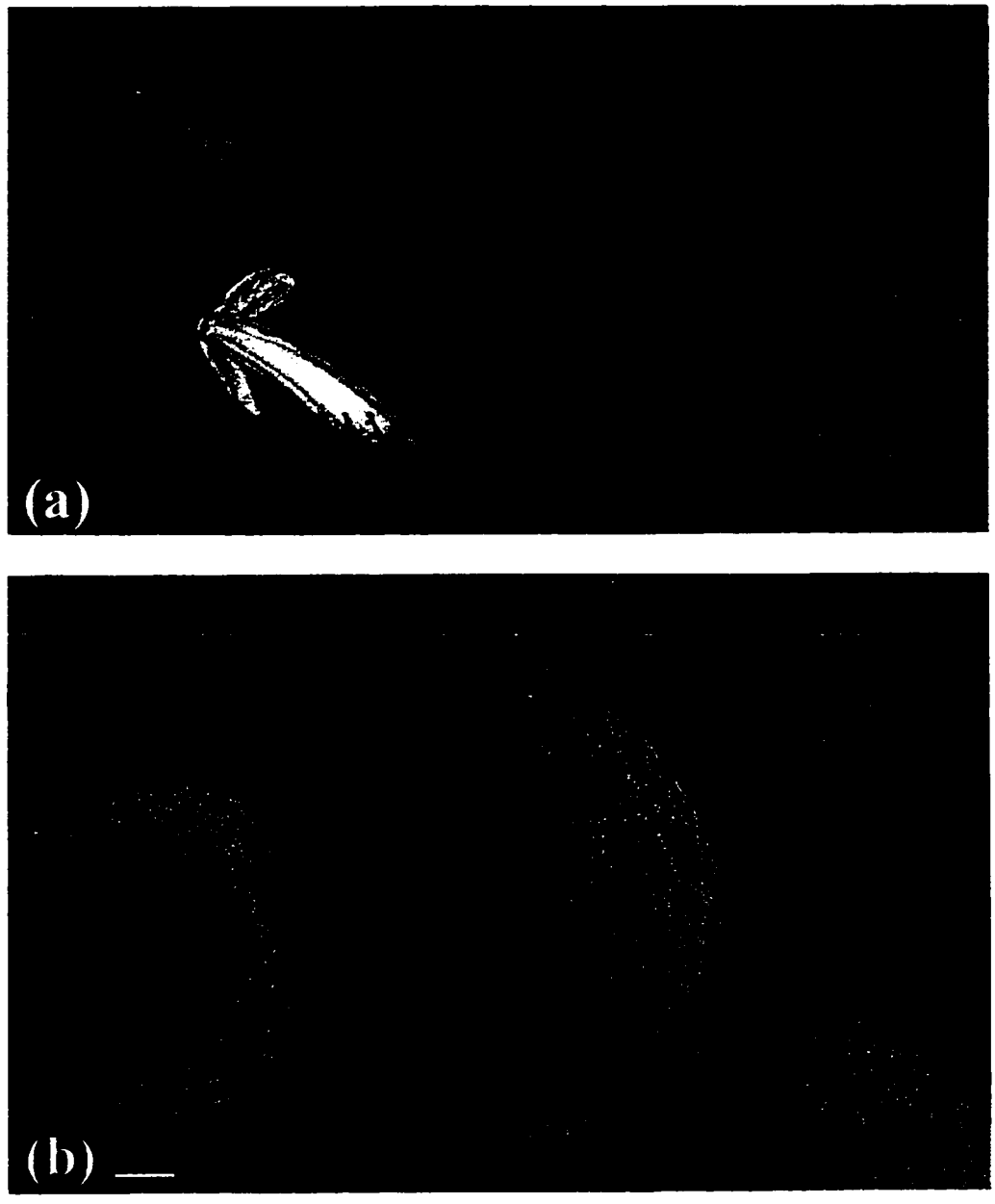


Figure 6.17 *Phaeocollybia kauffmanii.* **(a)** Longitudinal section showing firm stipitipith, thick stipe cortex, and characteristic orange coloration of young basidiome (LLN 95.11.09.28a, Cascade Head Experimental Forest). **(b)** Basidiospore from holotype (SEM, A.H.Smith 3523, MICH). Scale = 1 μm.

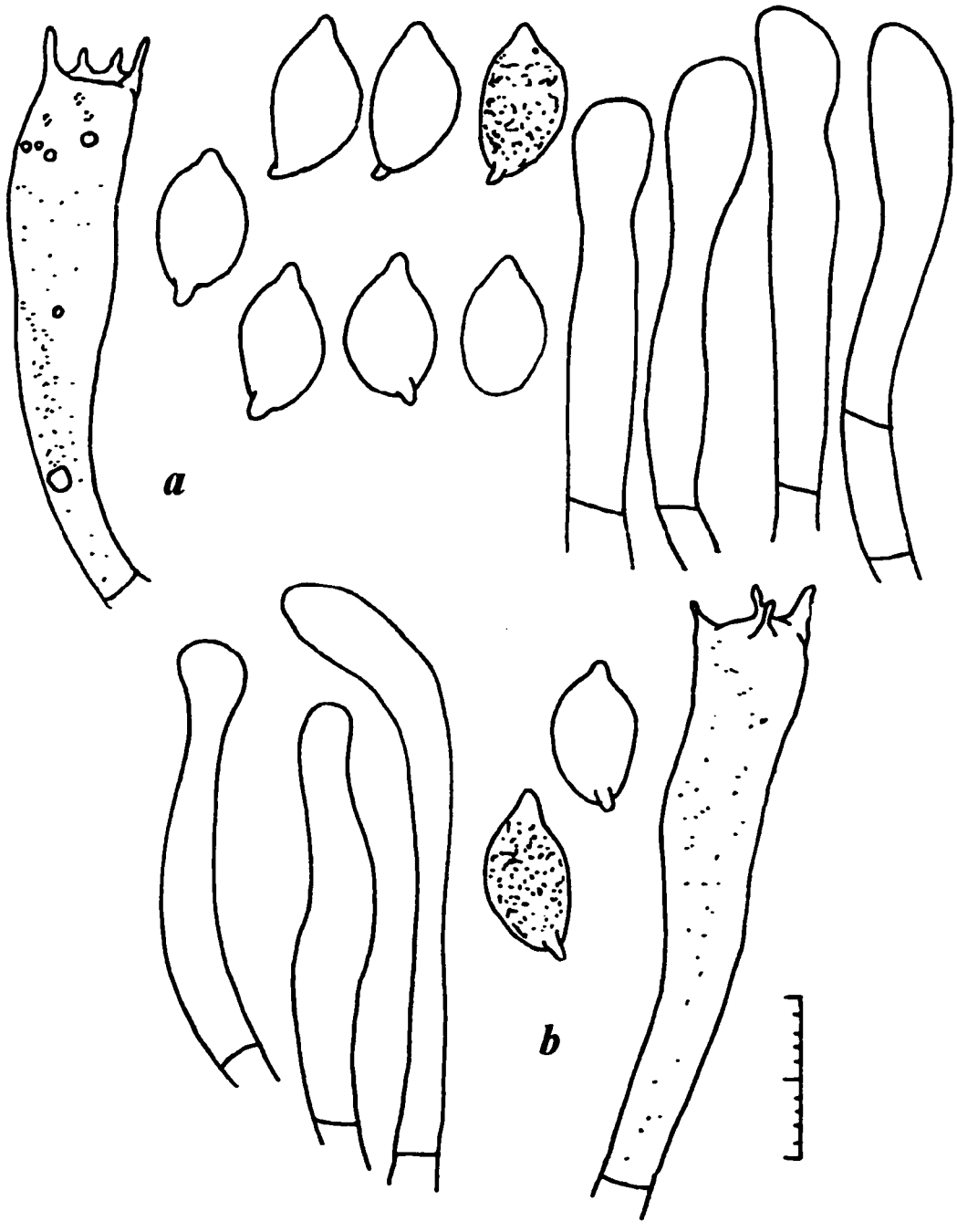


Figure 6.18 *Phaeocollybia lilacifolia.* (Holotype A. H. Smith 39976, MICH 00011625). **a.** Basidia basidiospores, and cheilocystidia (larger specimen); **b.** Cheilocystidia, basidiospores (smaller specimen)..

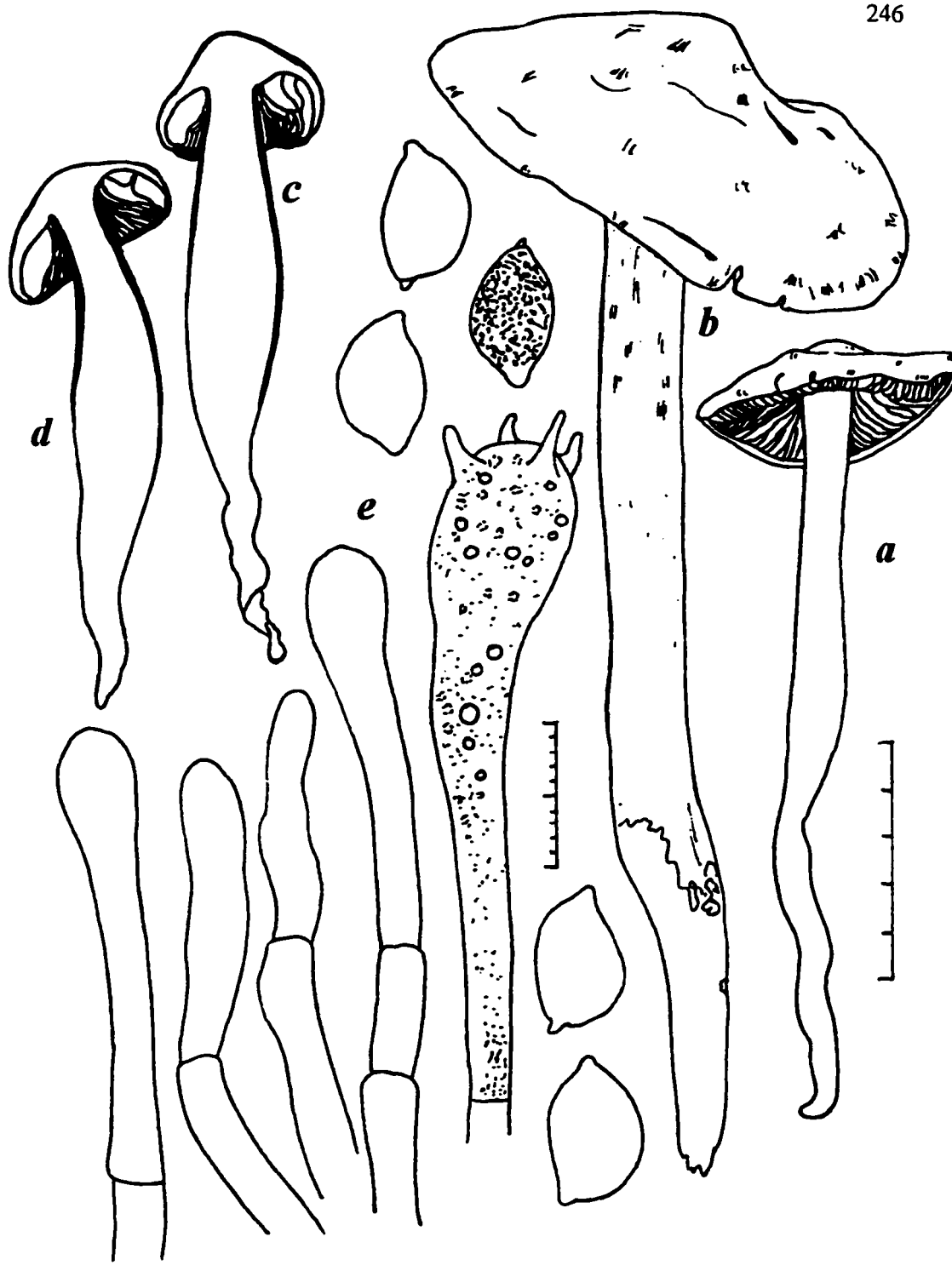


Figure 6.19 *Phaeocollybia luteosquamulosa nom. prov.* **a-d.** Habit (3/4 natural size) **a.** Holotype: SARedhead 7454 (WTU, isotype DAOM); **b.** LLN 92.11.24-1 (Paratype -- WTU); **c.** LLN 94.09.07-1 (WTU); **d.** LLN 93.11.05-9 (WTU); **e.** Basidiospores, basidia and cheilocystidia (LLN 93.10.24-10, WTU).

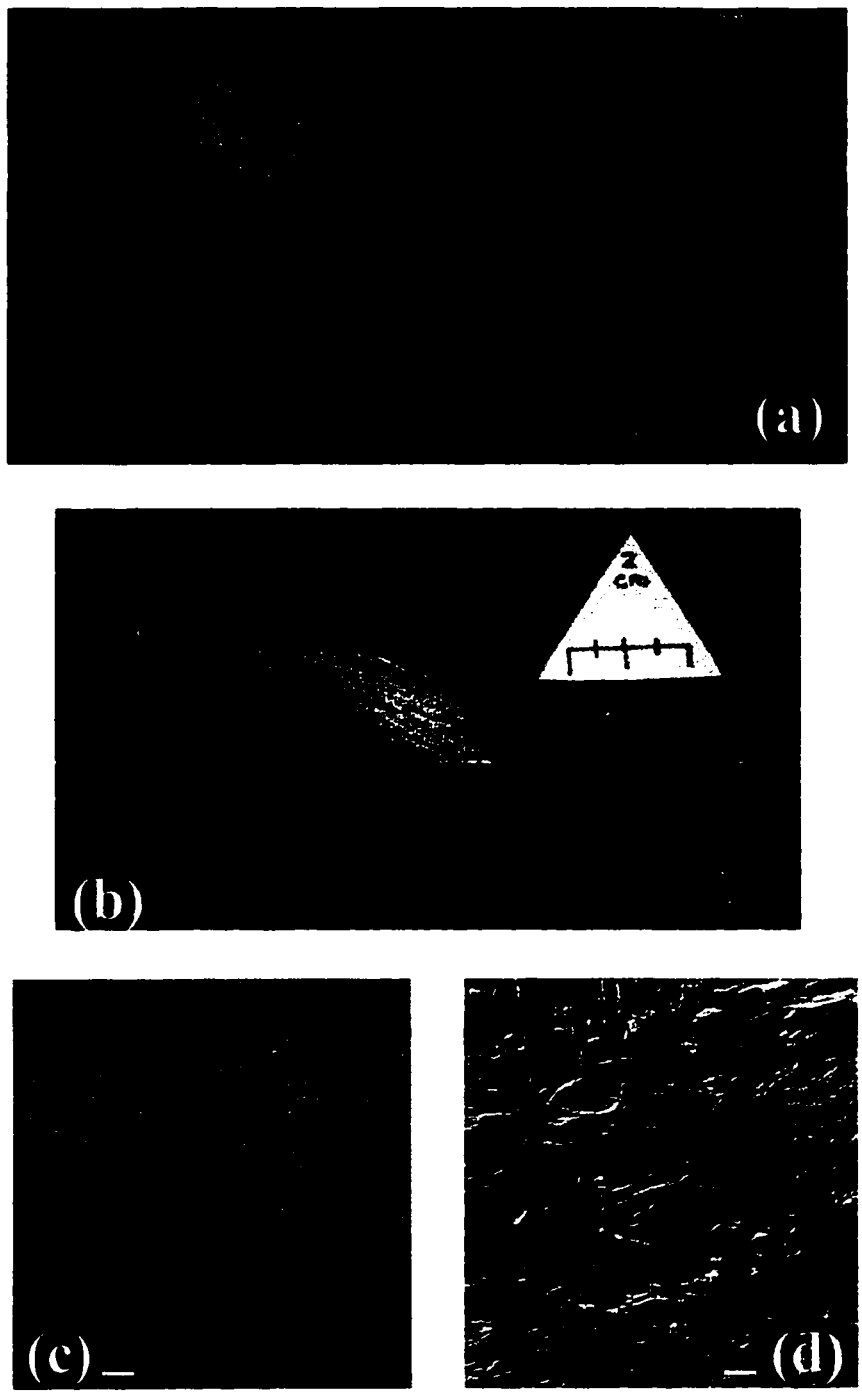


Figure 6.20 ***Phaeocollybia luteosquamulosa nom. prov.*** **(a)** Holotype *in situ*, Jackson State Forest, Mendocino County, California (S.A.Redhead 7454). **(b)** Specimen from Larch Mountain, Oregon (LLN 93.11.05-9). **(c)** Radial section of pileipellis showing trilaminate structure (Holotype). **(d)** Squash mount of scalp section of pileipellis showing broken pellicular veil (suprapellicular layer) (LLN 93.11.05-9) **(c & d)** Brightfield, scale = 10 μm).

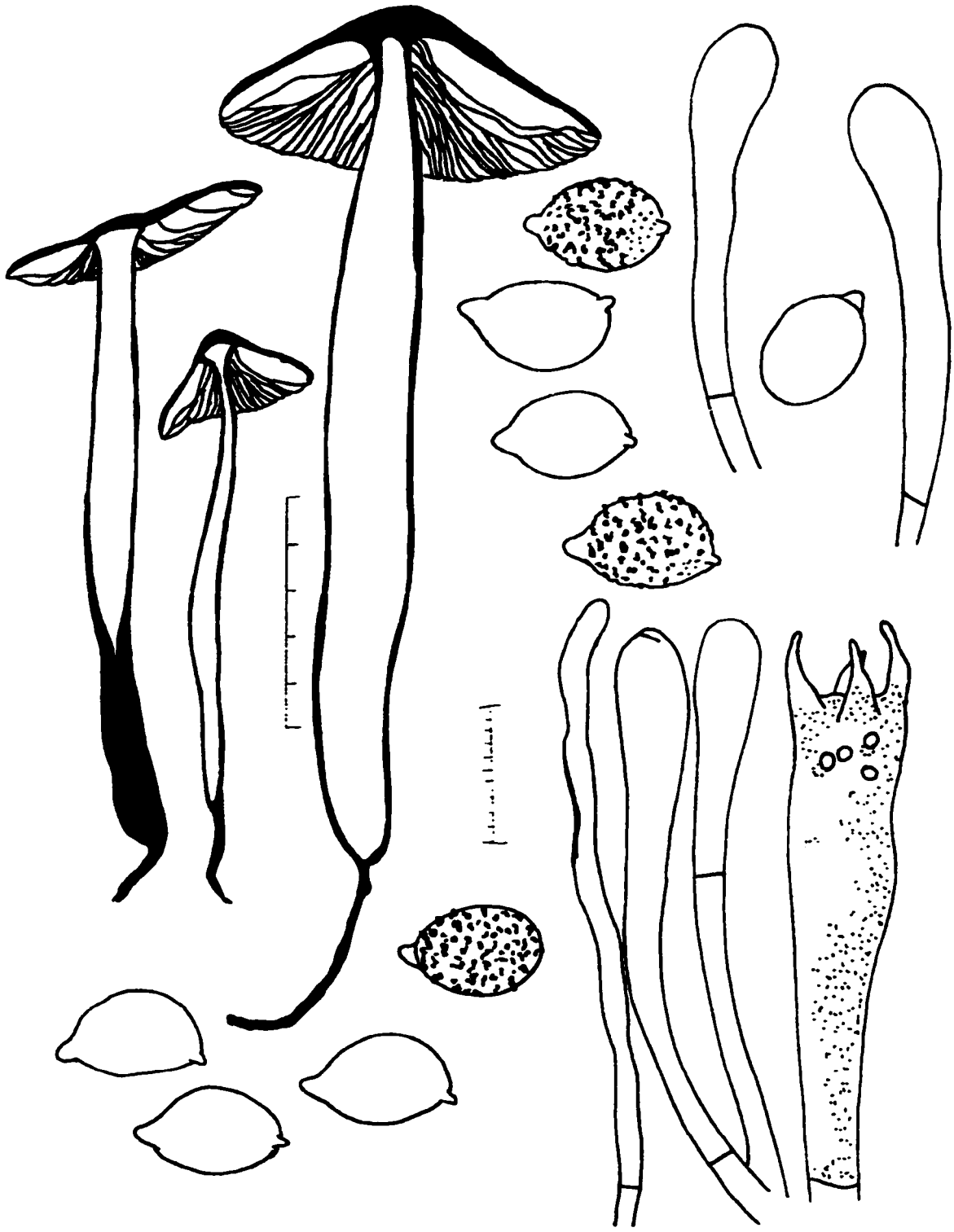


Figure 6.21 *Phaeocollybia olivacea*.. Habit (3/4 actual size) -- LLN 96.11.29-6 (left) and LLN 95.11.17-6 (right) **(upper right)** Cheilocystidia and basidiospores (A. H. Smith 55767 (MICH #00011627)-- Holotype) **(bottom)** Basidiospores, cheilocystidia, and basidium (LLN 94.11.28-1).

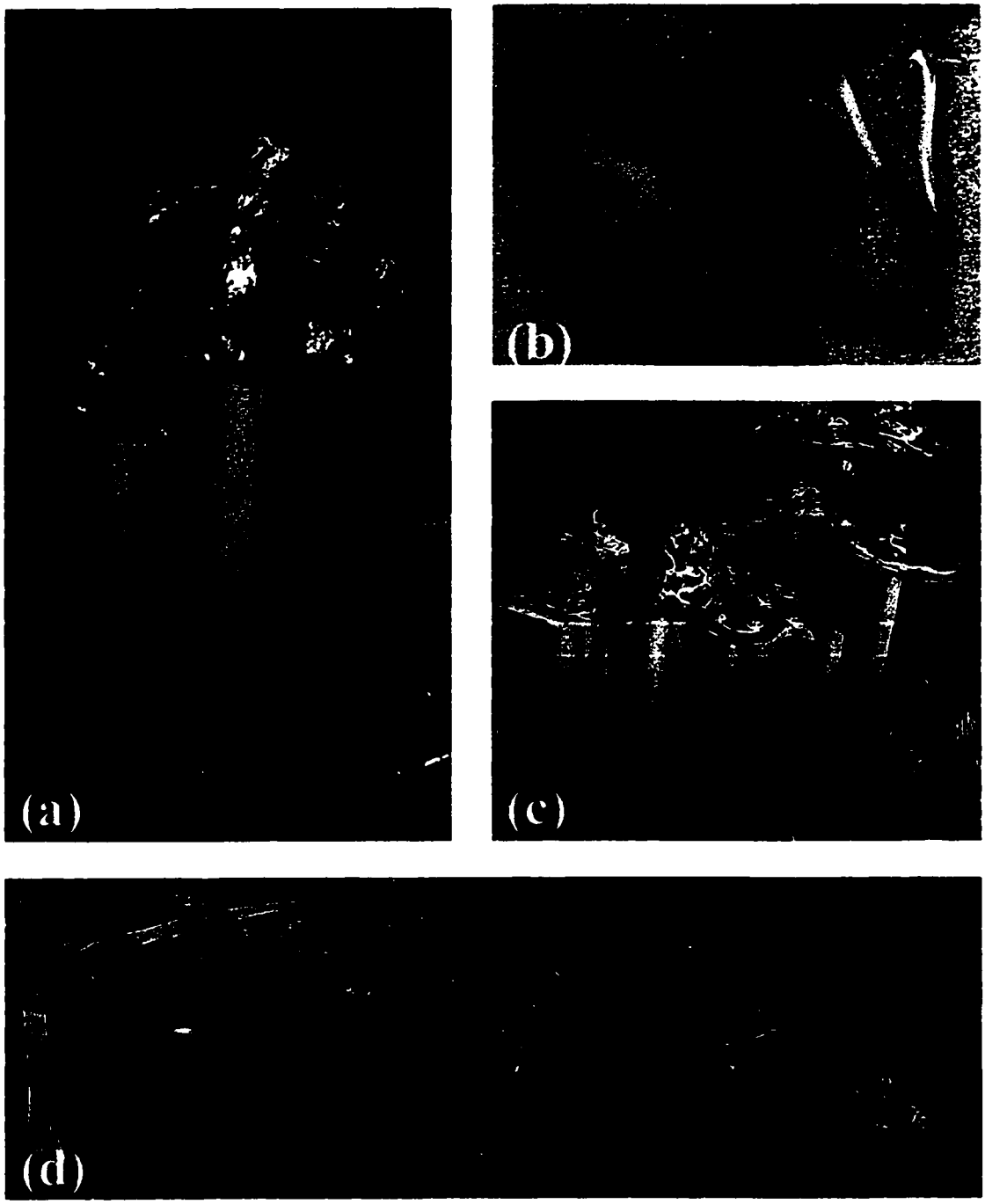


Figure 6.22 ***Phaeocollybia olivacea.*** **(a)** *In situ,* Mendocino County, California (LLN 92.11.16-4). **(b)** Specimens from Benton County, Oregon (LLN 95.11.17-6b). **(c)** *In situ,* Van Damme State Park, California (LLN 92.11.21-2). **(d)** Gregarious arc in duff under *Sequoia, Abies, Lithocarpus*, Van Damme State Park (LLN 92.11.23-4).

Figure 6.23 *Phaeocollybia oregonensis.* **(bottom)** Habit (3/4 actual size -- LLN 92.11.04-5; LLN 94.10.18-22); **(top)** Cheilocystidia, basidia, and basidiospores (A. H. Smith 28420 (MICH) -- Holotype).

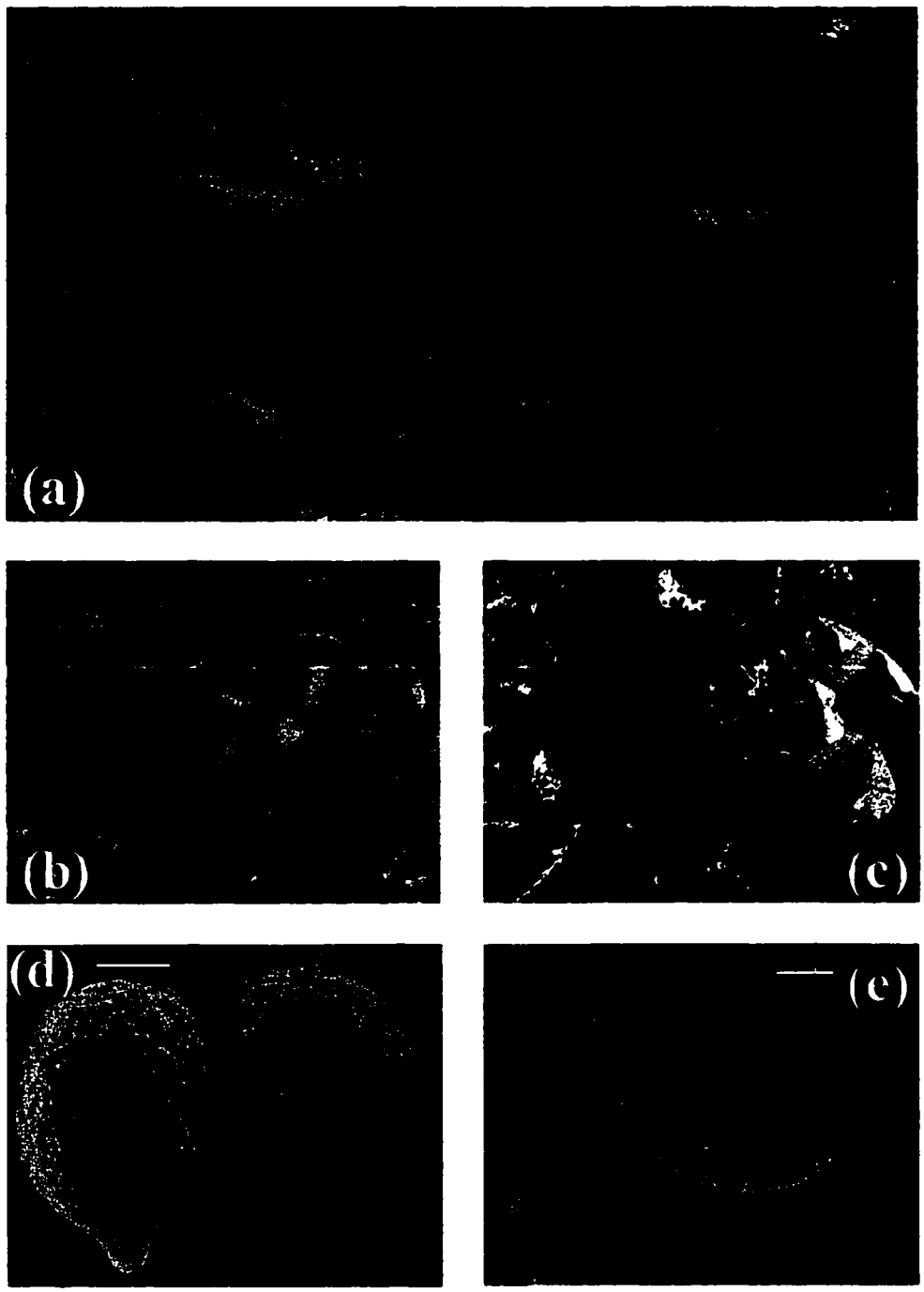


Figure 6.24 ***Phaeocollybia oregonensis.*** **(a)** Specimens from Larch Mountain, Oregon (LLN 92.11.04-6). **(b & c)** *In situ,* Wildcat Mountain, Mt. Hood National Forest, Oregon (LLN 95.10.18-4). **(d)** Basidiospores from holotype of *P. carmanahensis* (LLN 91.10.24-1, WTU). **(e)** Basidiospores from holotype of *P. oregonensis* (A.H.Smith 28240, MICH). **(d & e)** Scale = 1 μm.

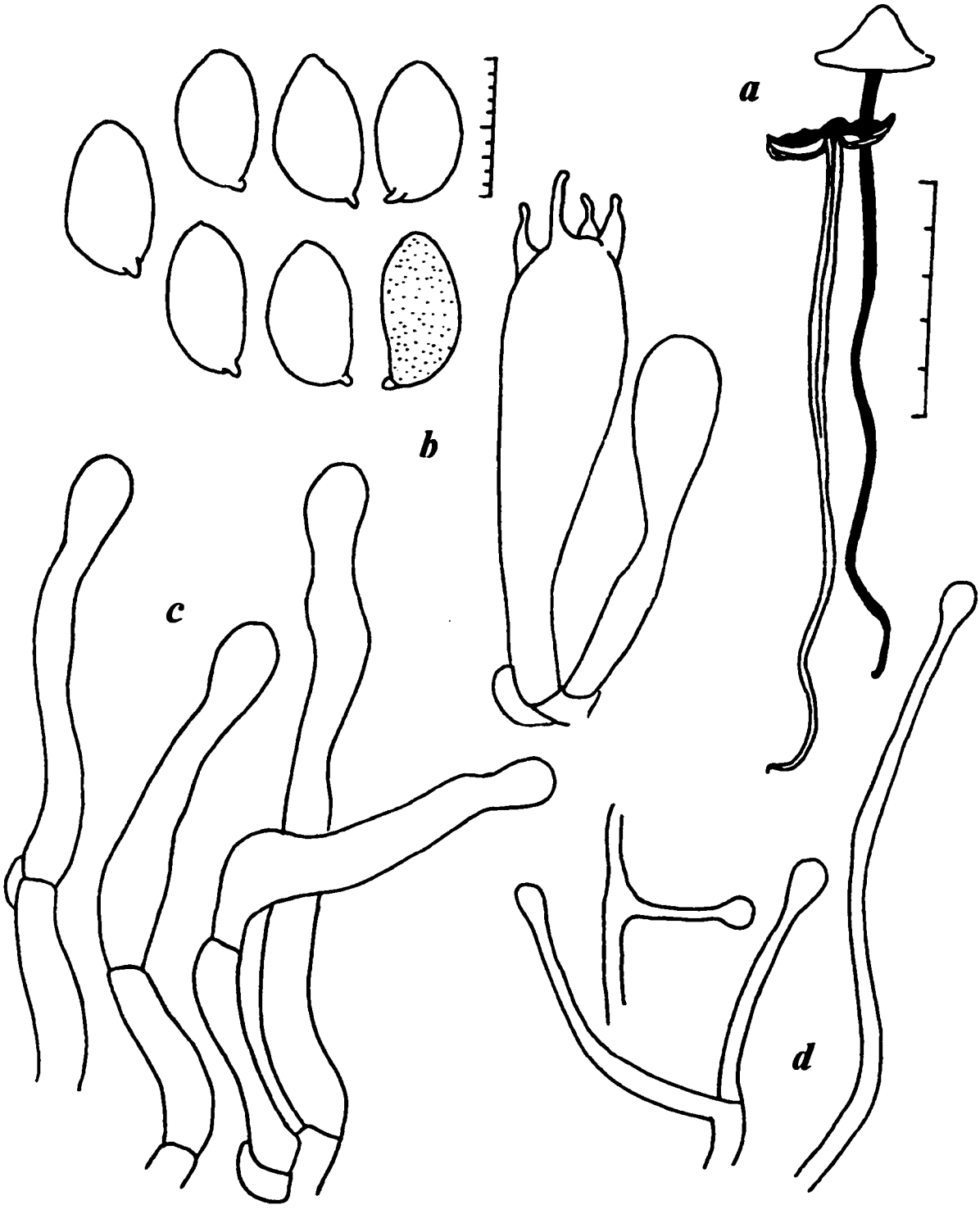


Figure 6.25 *Phaeocollybia phaeogaleroides nom. prov.* (LLN 95.11.06-1, WTU); **a.** Habit (3/4 actual size) ; **b.** Basidio spores and basidium; **c.** Cheilocystidia; **d.** Tibiiform diverticular from stipitipellis.

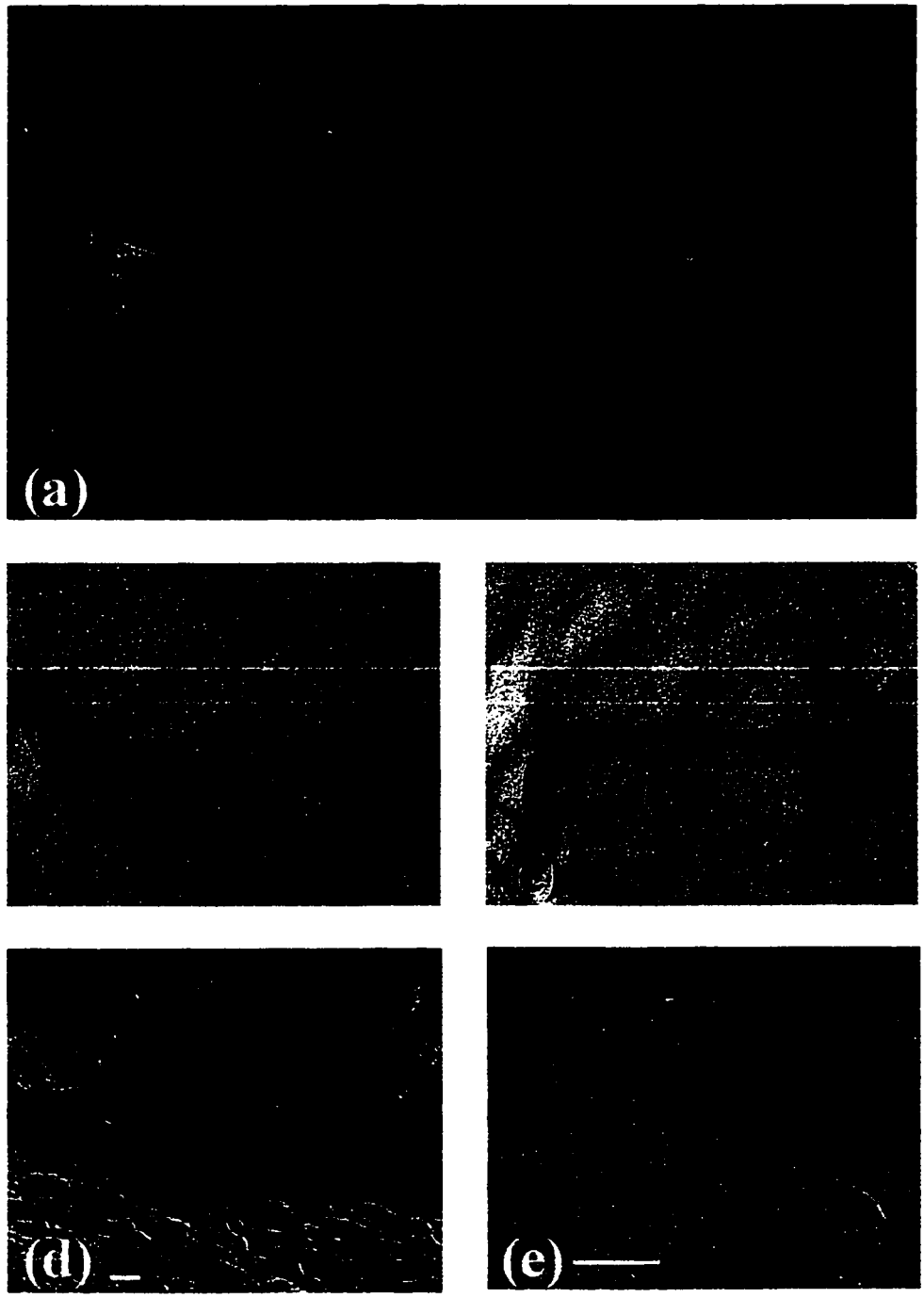


Figure 6.26 ***Phaeocollybia phaeogaleroides nom. prov.*** **(a)** Specimen from Drift Creek, Oregon (LLN 95.11.06-1). **(b, c)** Two views of specimen from Vancouver Island, BC (R. Outerbridge 298). **(d)** Suprapellis and subpellis (LLN 95.11.06-1, low dry, scale = 10 μm). **(e)** Clamp connections (arrows) on suprapellicular hyphae (LLN 95.11.06-1; oil immersion, DIC, scale = 10 μm).

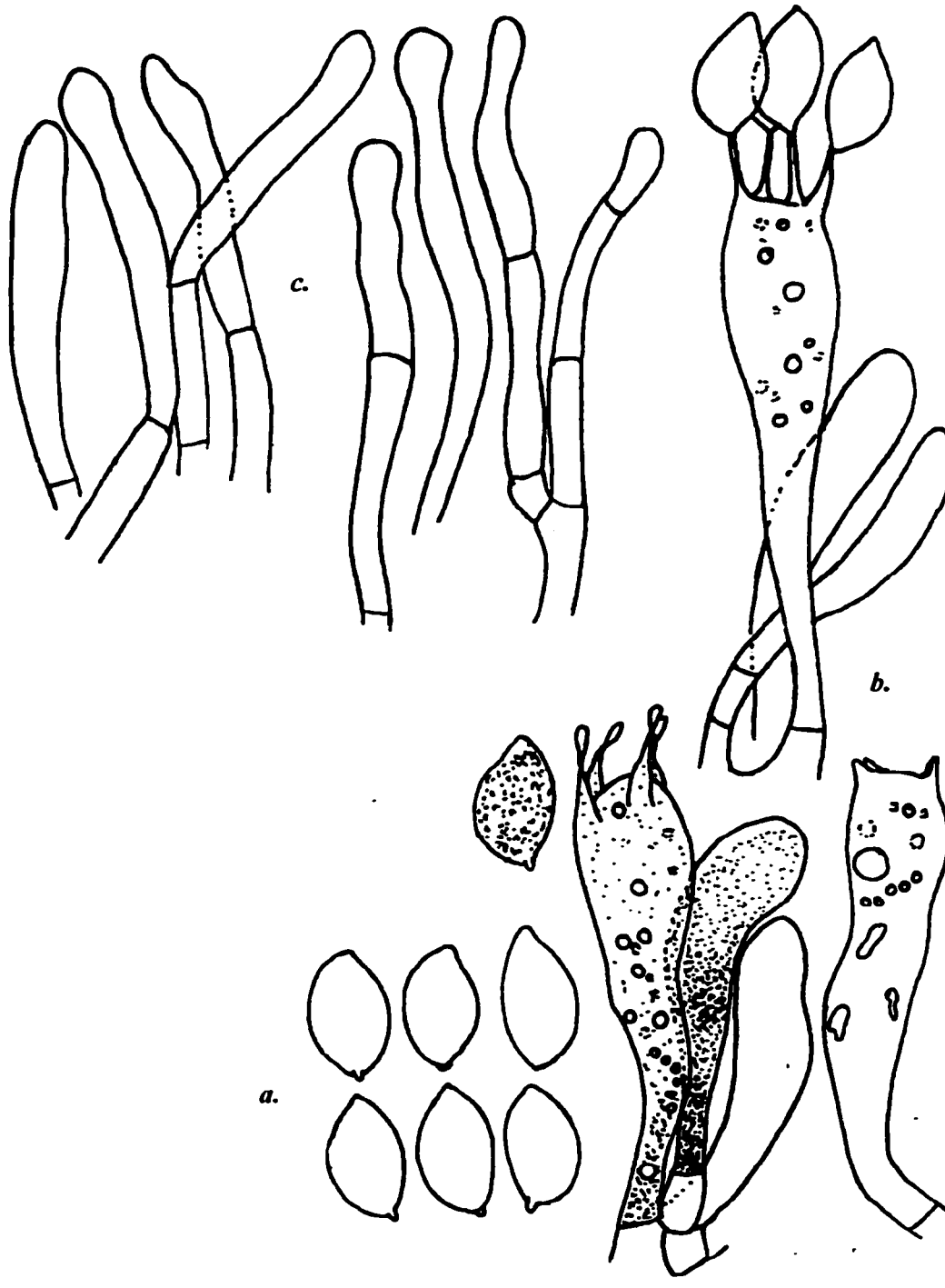


Figure 6.27 *Phaeocollybia piceae.* **a.** Basidiospores (A. H. Smith 79085 MICH -- Holotype); **b.** Basidia LLN 94.11.10-2 (topotypical material); c.Cheilocystidia (Holotype, LLN 94.10.22-4, LLN 94.11.10-2).

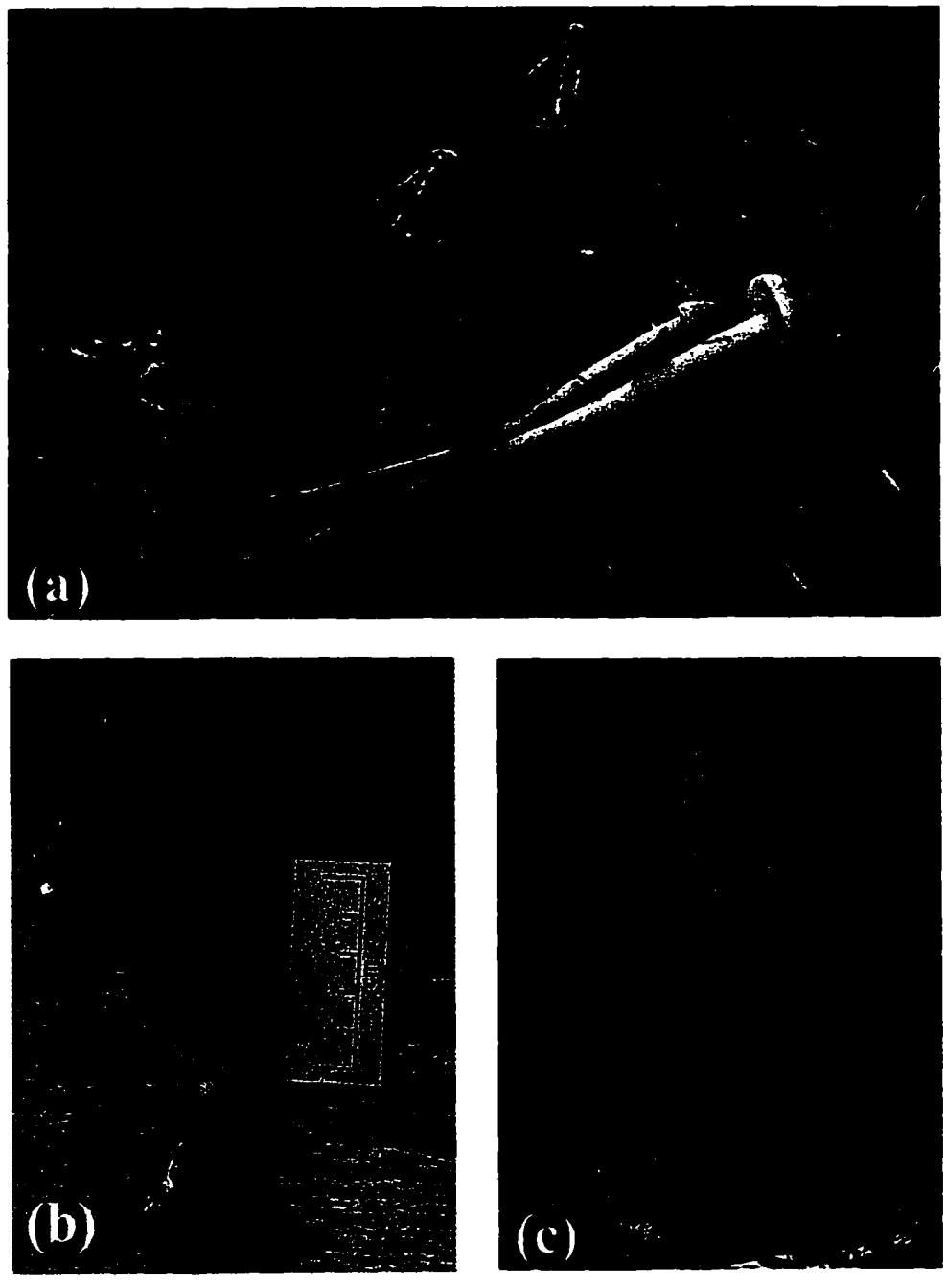


Figure 6.28 *Phaeocollybia piceae.* **(a)** *In situ* under *Picea* in type locality, Cascade Head Experimental Forest (LLN 94.11.06-1). **(b)** Insect infested stipe above curled vertical-monopodial pseudorhiza (LLN 92.10.09-22). **(c)** *In situ*, under ancient *Picea*, Lower Carmanah Valley, Vancouver Island (LLN 92.10.09-22).

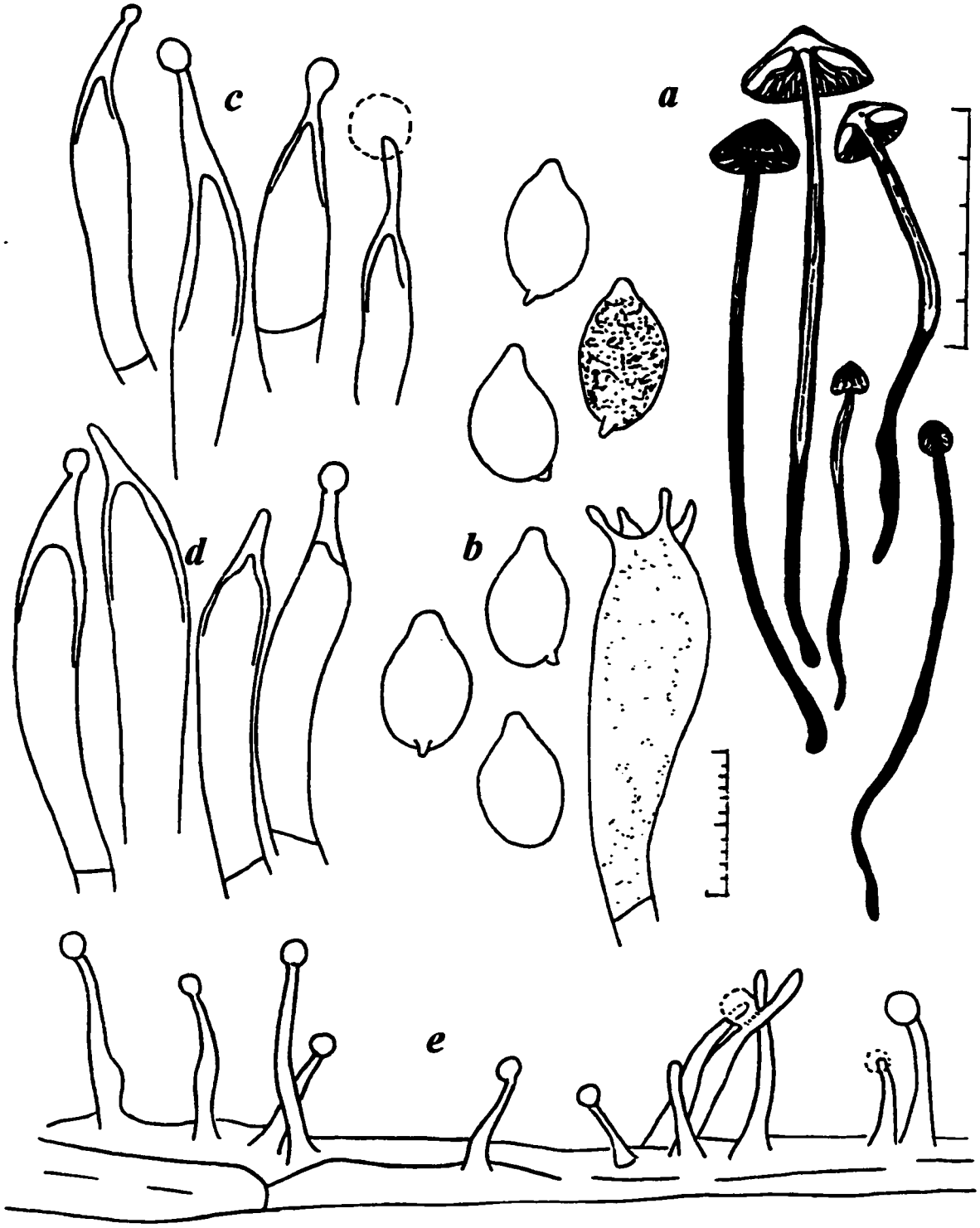


Figure 6.29 *Phaeocollybia pleurocystidiata nom. prov.* (Holotype and paratype: LLN 94.03.30-1,2 WTU) **a.** Habit (3/4 actual size); **b.**Basidia and basidiospores (holotype); **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Tibiiform diverticula on pseudorhizal pellis.

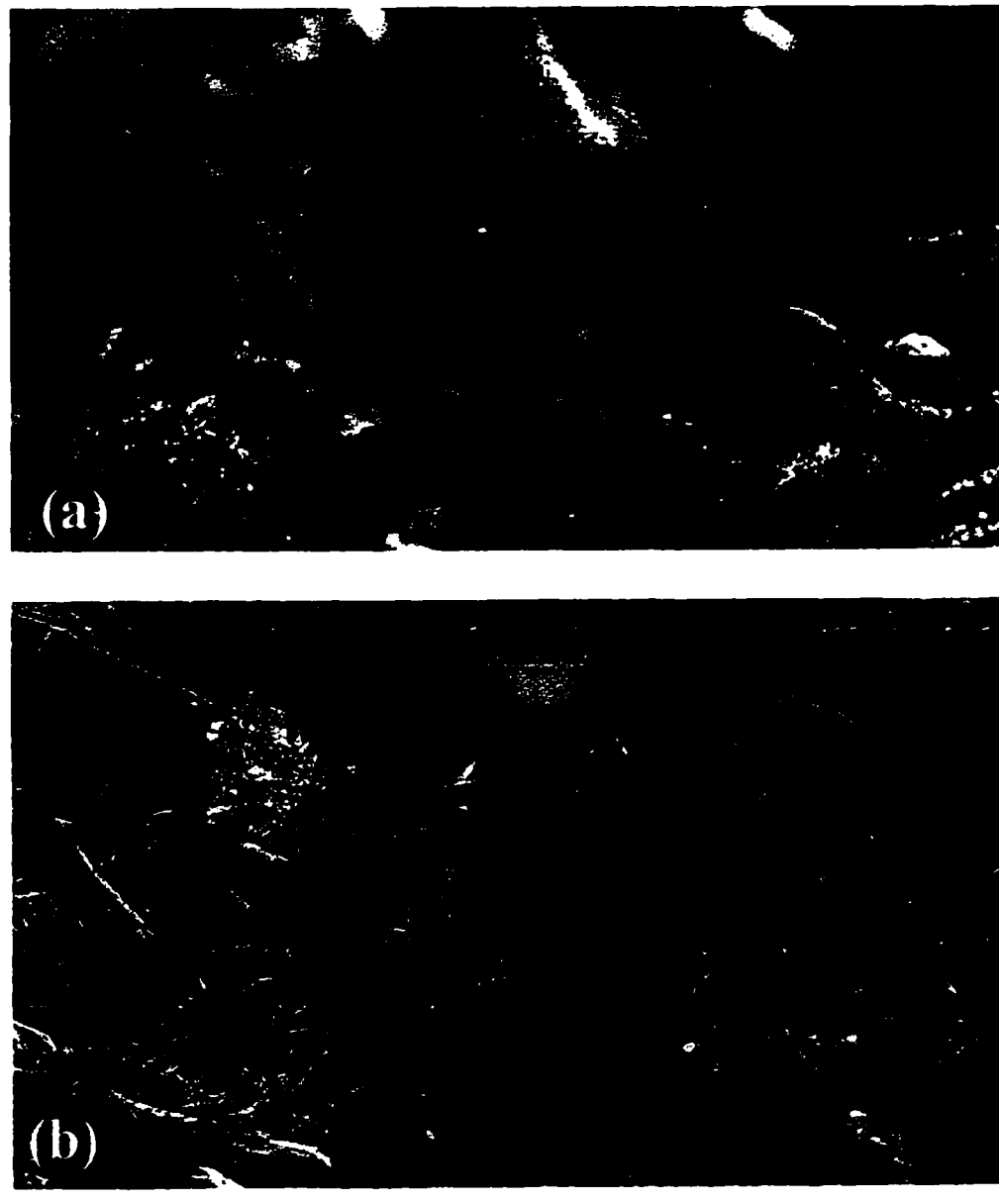


Figure 6.30 *Phaeocollybia pleurocystidiata nom. prov.* Type specimens *in situ*, Bogachiel Trail, Olympic National Park (LLN 94.03.30-1, holotype WTU; isotype, DAOM).

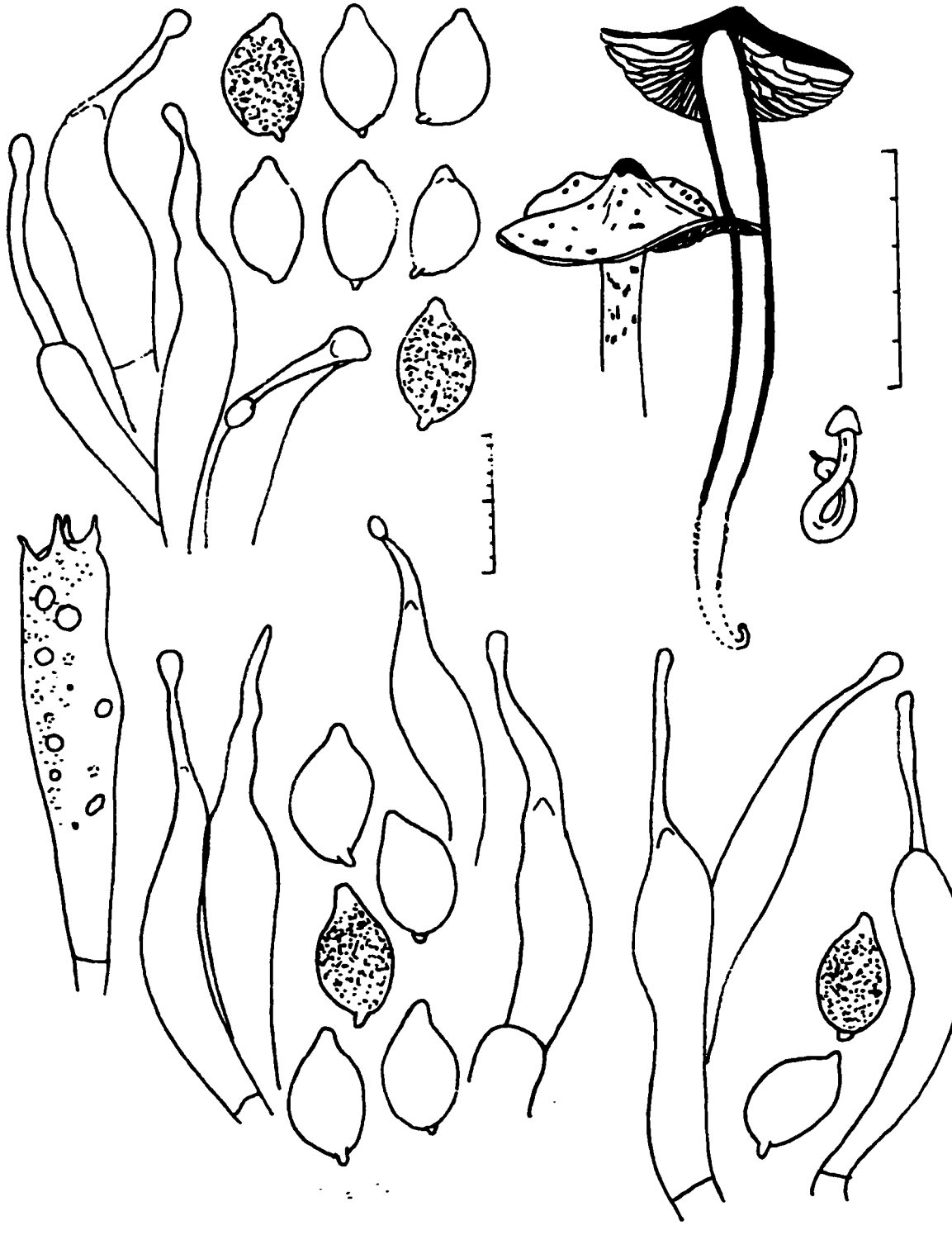


Figure 6.31 *Phaeocollybia pseudofestiva.* Habit (3/4 actual size) -- LLN 92.11.16-2 (left), LLN 95.10.18-11 (middle), LLN 92.11.21-1 (primordium); **(upper left)** Basidiospores and cheilocystidia (LLN 92.10.07-6 psB2); **(lower left)** Cheilocuystidia, basidiospores, basidium (LLN 92.10.23-28); **(lower right)** Cheilocystidia, basidiospores (A. H. Smith 8274 (MICH 00011632) -- Holotype).

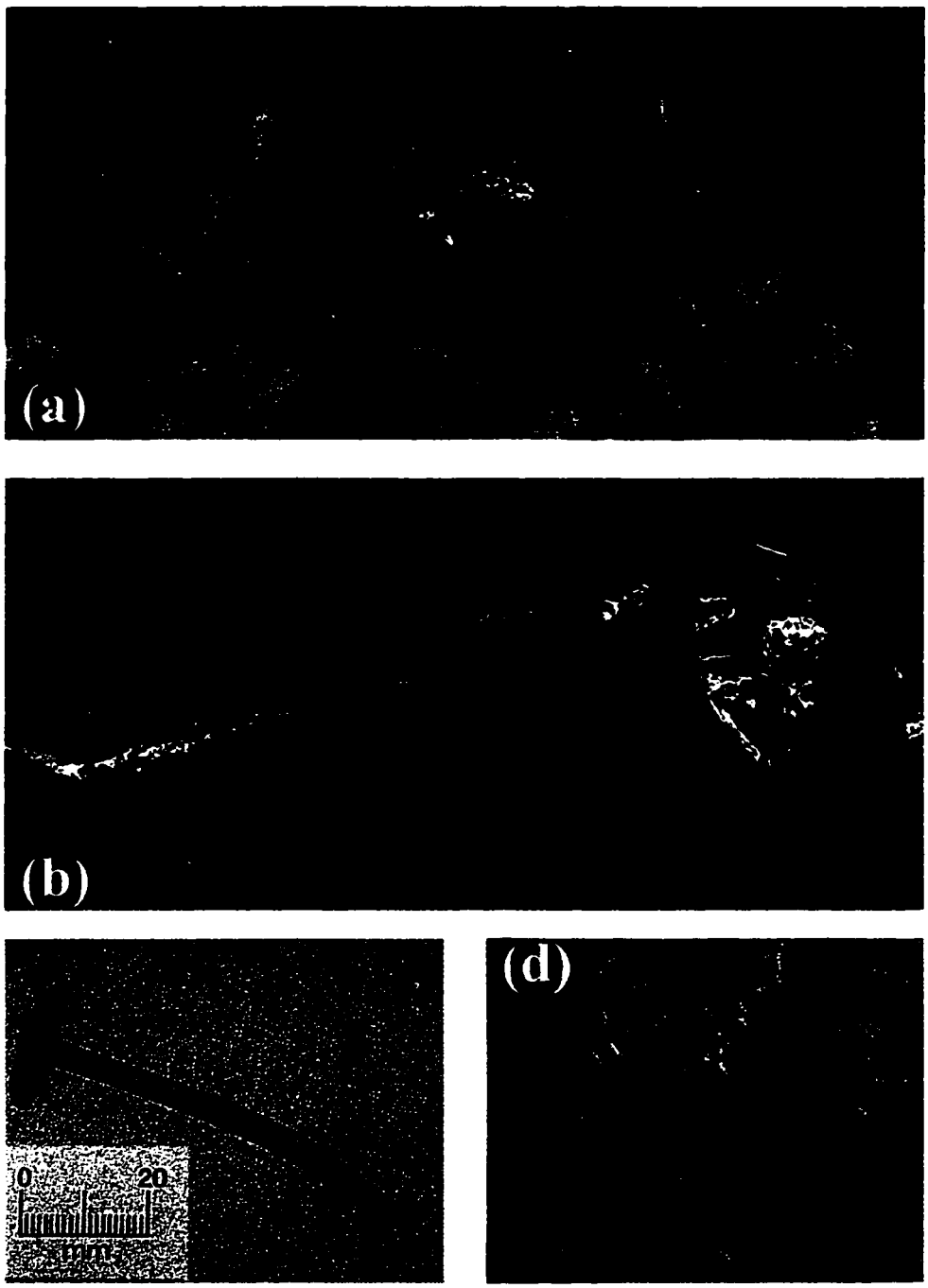


Figure 6.32 *Phaeocollybia pseudofestiva.* **(a)** *In situ* with *P. ammiratii* amongst *Rhytidiadelphus loreus* under *Abies procera,* Mt. Hood National Forest (LLN 95.10.18-11). **(b)** Two specimens from Van Damme State Park, California (LLN 92.11.23-8). **(c)** Greenish stipe apex and ochraceous gills in specimen from Upper Carmanah Valley, Vancouver Island (92.10.07-6). **(d)** Hartig net in root tip surrounded by tibiiform diverticula and attached to pseudorhiza (LLN 92.11.21-1).

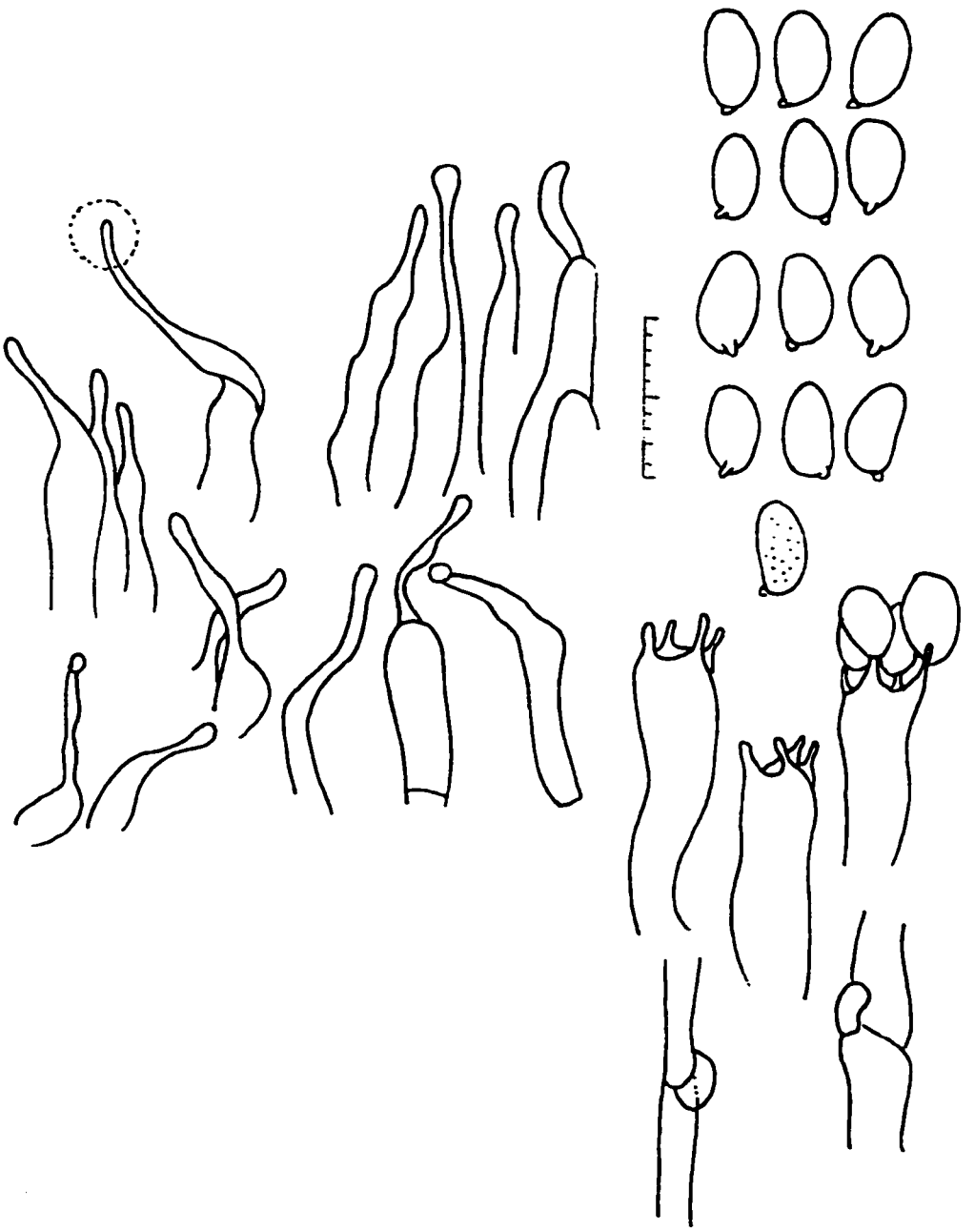


Figure 6.33 *Phaeocollybia radicata.* . **a.** Basidia and cheilocystidia (A. H. Smith (MICH) **b.** Basidiospores and cheilocystidia (Murrill 775 (NY)-- Holotype)

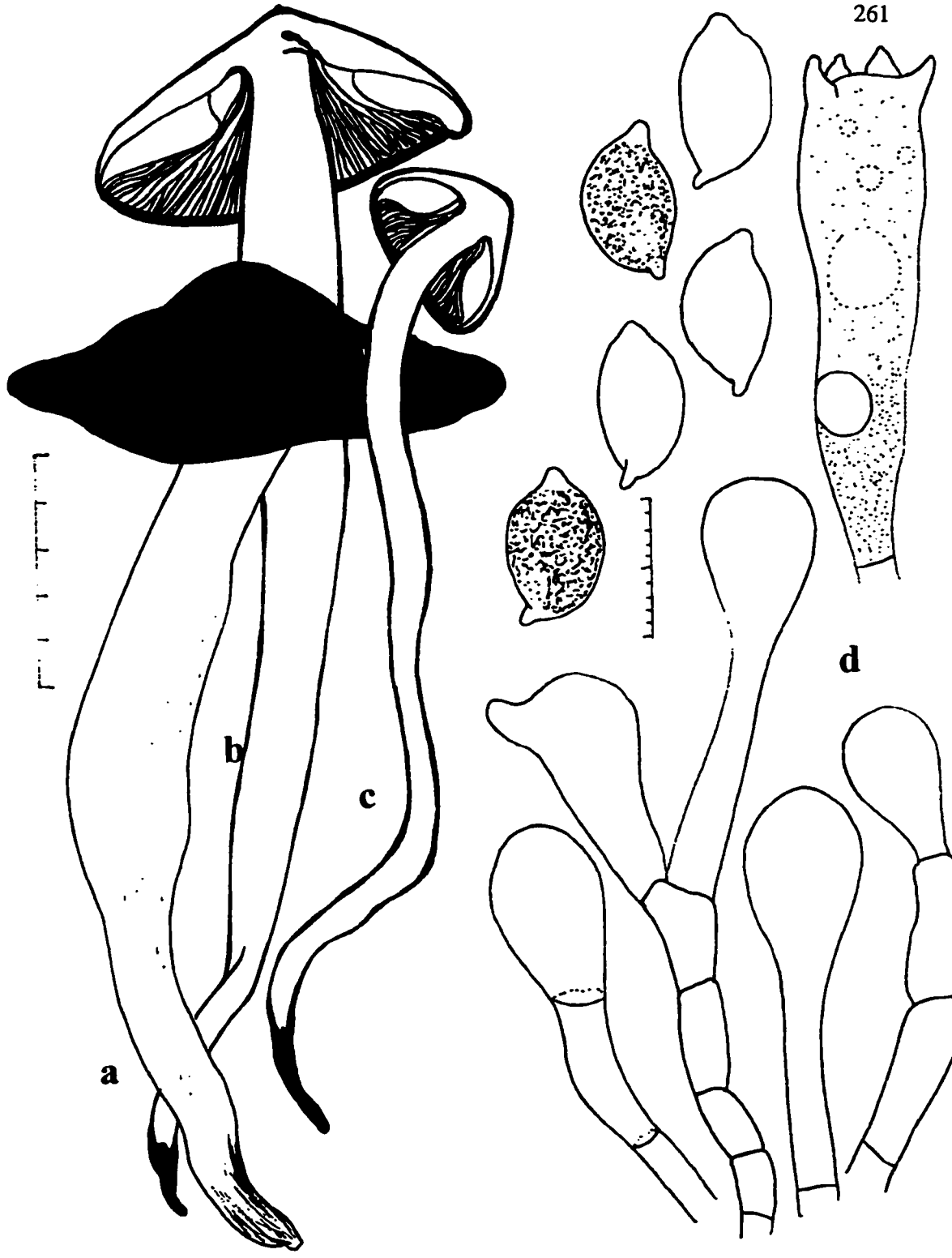


Figure 6.34 *Phaeocollybia redheadii nom. prov.*.**a-c.** Habit (3/4 actual size). Young form (LLN 91.10.24-2 -- Holotype), Mature form (LLN 92.10.09-?); **d.** Basidia, basidiospores, and cheilocystidia. (a = LLN 93.10.24-16; b = LLN 93.11.05-12; c = LLN 95.10.18-18. d = LLN 91.10.24-2, Holotype, WTU; Isotype, DAOM).

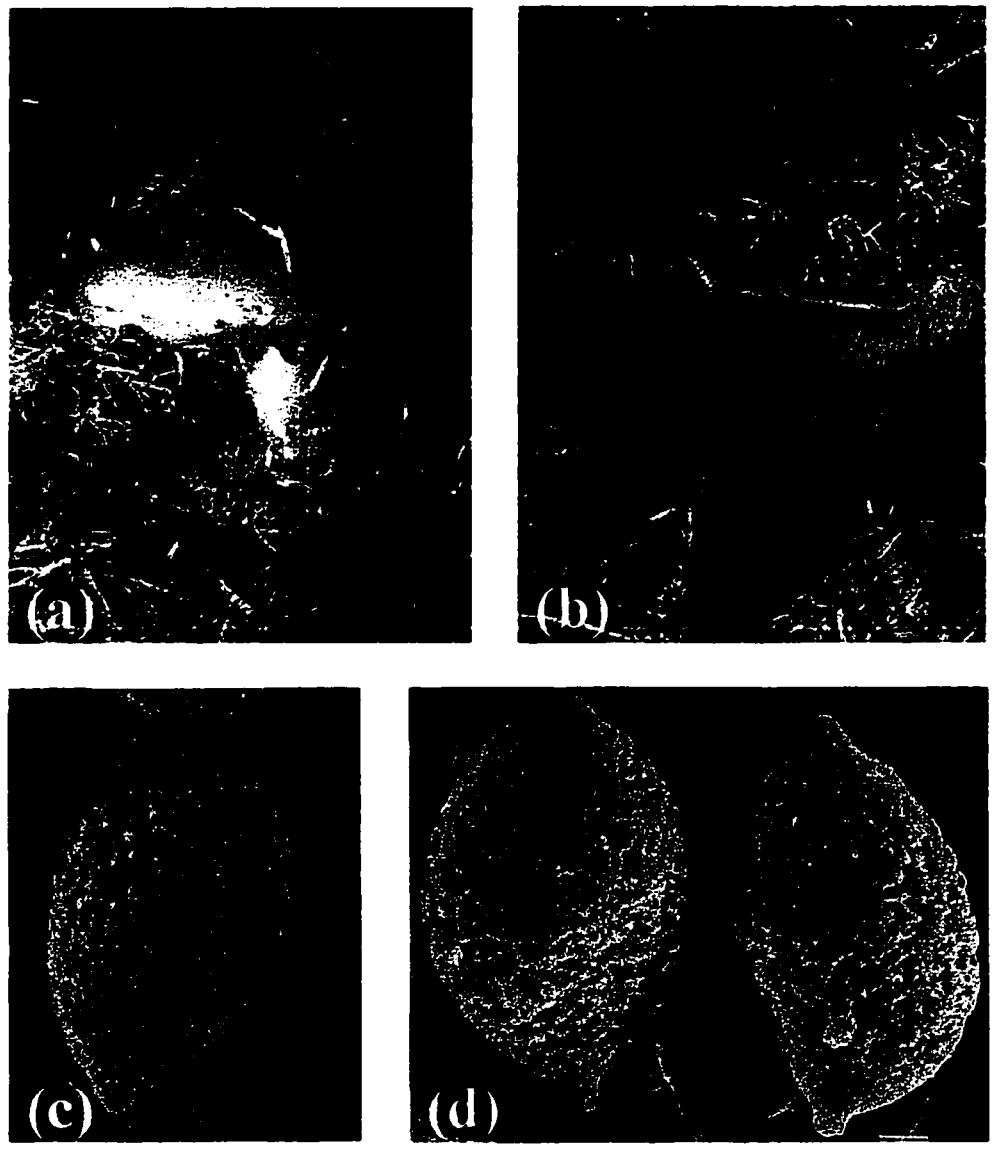


Figure 6.35 *Phaeocollybia redheadii nom. prov.* **(a)** Holotype *in situ*, Upper Carmanah Valley (LLN 91.10.24-2, WTU; Isotype at DAOM). **(b)** *In situ* under giant *Tsuga heterophylla*, Lower Carmanah Valley (LLN 92.10.09-20). **(c)** Basidiospore (SEM, LLN 91.10.24-1). **(d)** Basidiospores (SEM, Holotype).

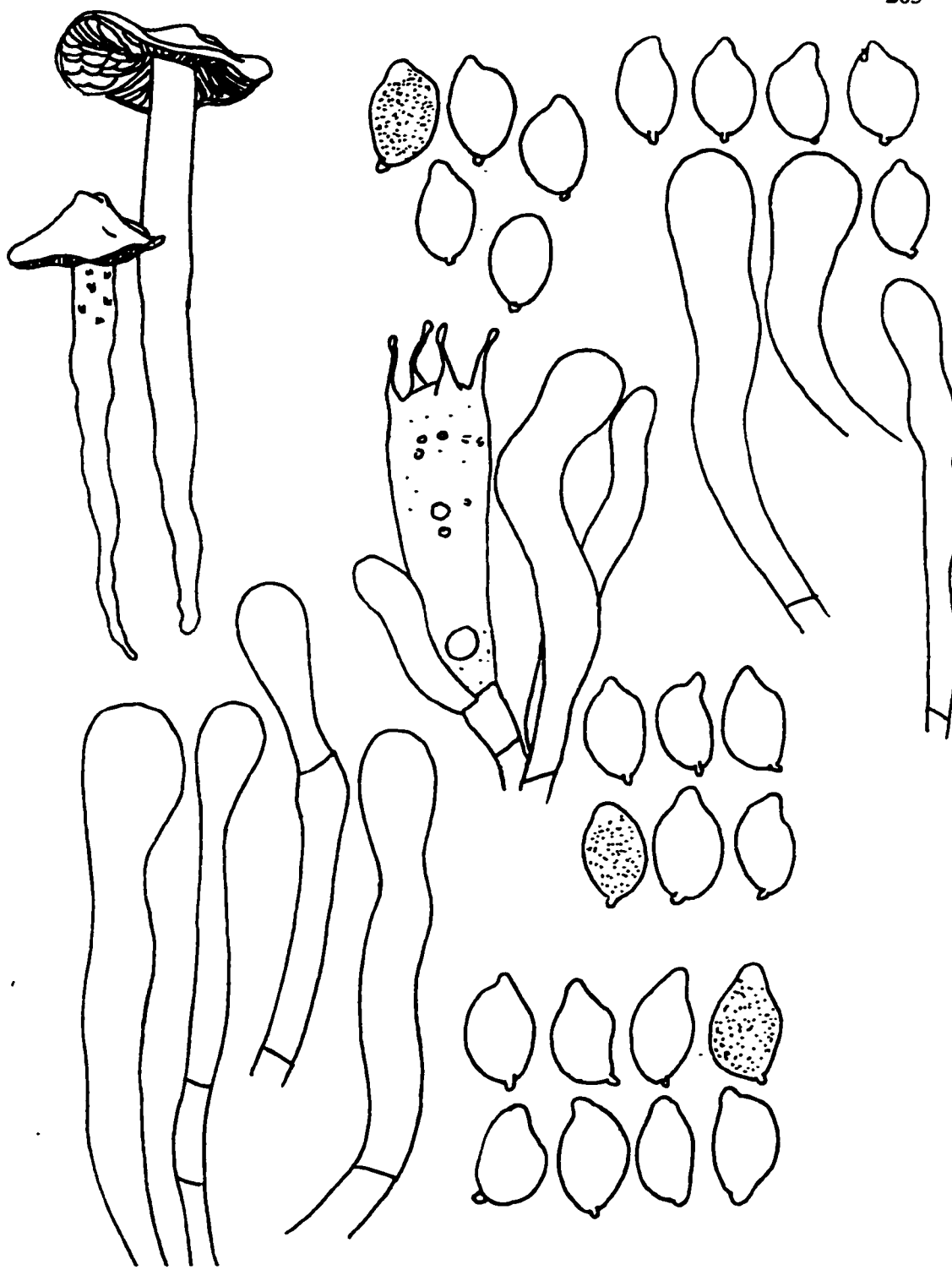


Figure 6.36 *Phaeocollybia rifflipes nom. prov.* Habit (3/4 actual size). Holotype (LLN 93.10.20-1); large form (LLN 92.10.23-8); **(upper right)** Basidiospores, cheilocystidia (Holotype -- LLN 93.10.20-1); **(middle right)** Basidia, hyphidia ('paraphyses'), basidiospores (LLN 92.10.23-8); **(lower left)** Cheilocystidia and basidiospores (LLN 92.11.04-5).

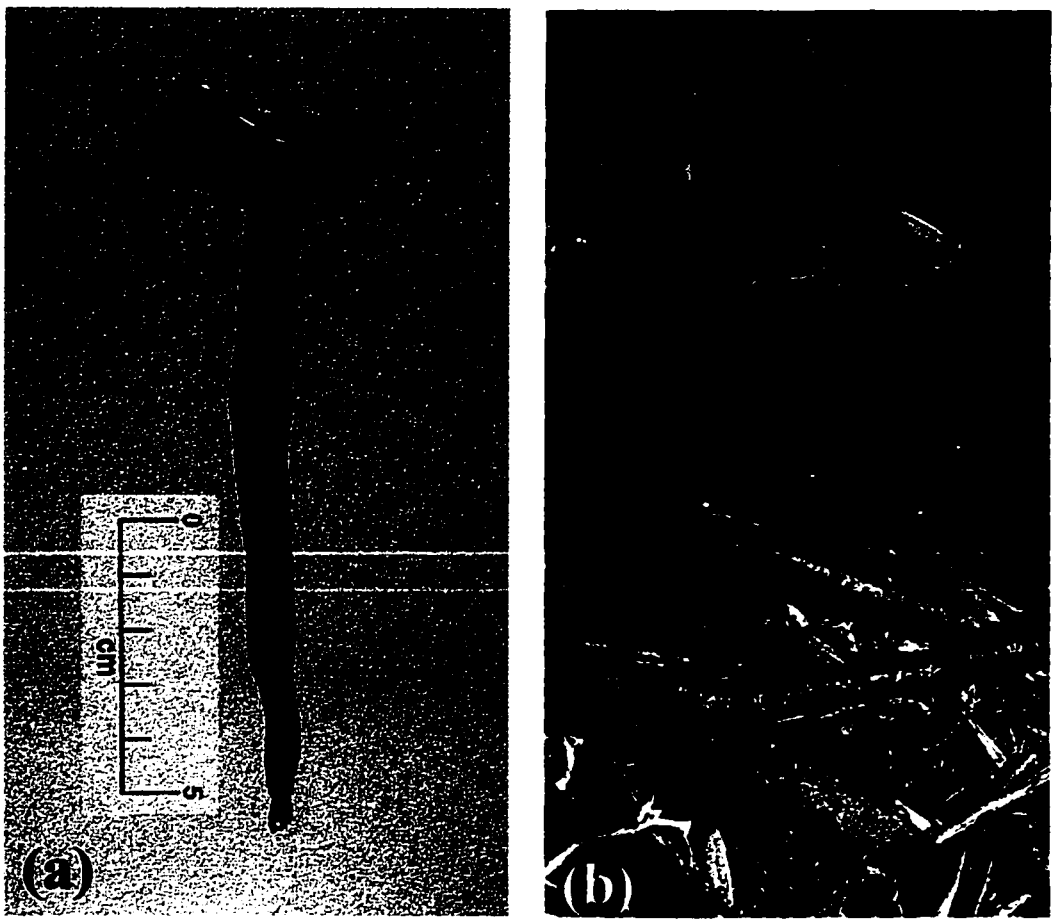


Figure 6.37 *Phaeocollybia rifflipes nom. prov.* **(a)** Young specimen from Rugged Ridge Trail, Olympic National Park (LLN 92.10.23-8). **(b)** Holotype *in situ*, Barlow Pass, Mt. Baker-Snoqualmie National Forest (LLN 93.10.20-1).

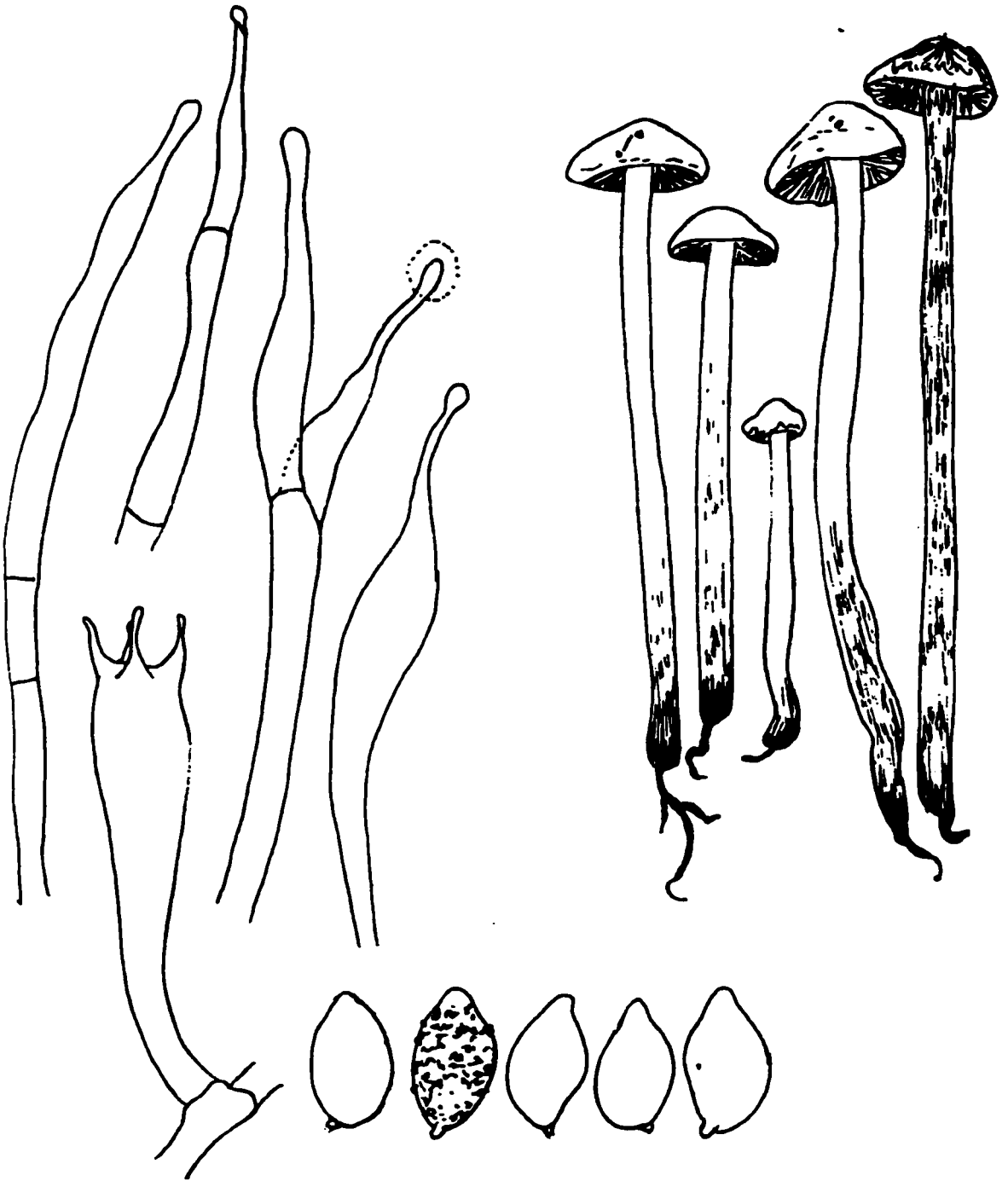


Figure 6.38 *Phaeocollybia rufotubulina* . (LLN 92.10.16-1 (WTU) -- Holotype) Habit (3/4 actual size), Cheilocystidia, basidium, and basidiospores.

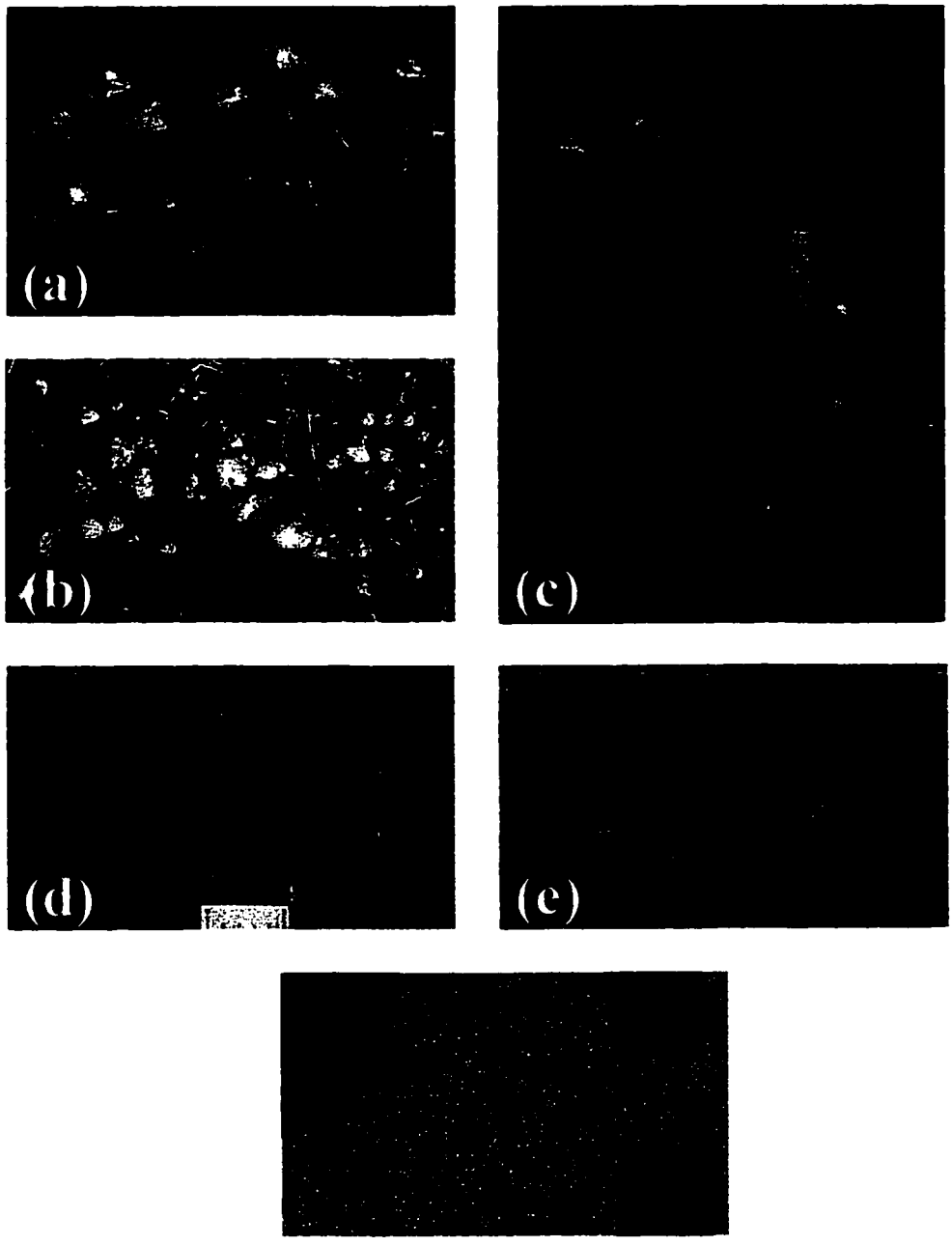


Figure 6.39 *Phaeocollybia rufotubulina nom. prov.* **(a-c)** Holotype *in situ* in characteristic loose phalanxes, Jackson State Forest, Mendocino County, California (LLN 92.11.16-1 WTU; Isotype DAOM). **(d)** Individual specimens from holotype collection. **(e)** Malformed specimens growing in bank, Russian Gulch State Park (SAR 7450). **(f)** Detail from dried holotypical material illustrating hollow interior and thin stipe cortex.

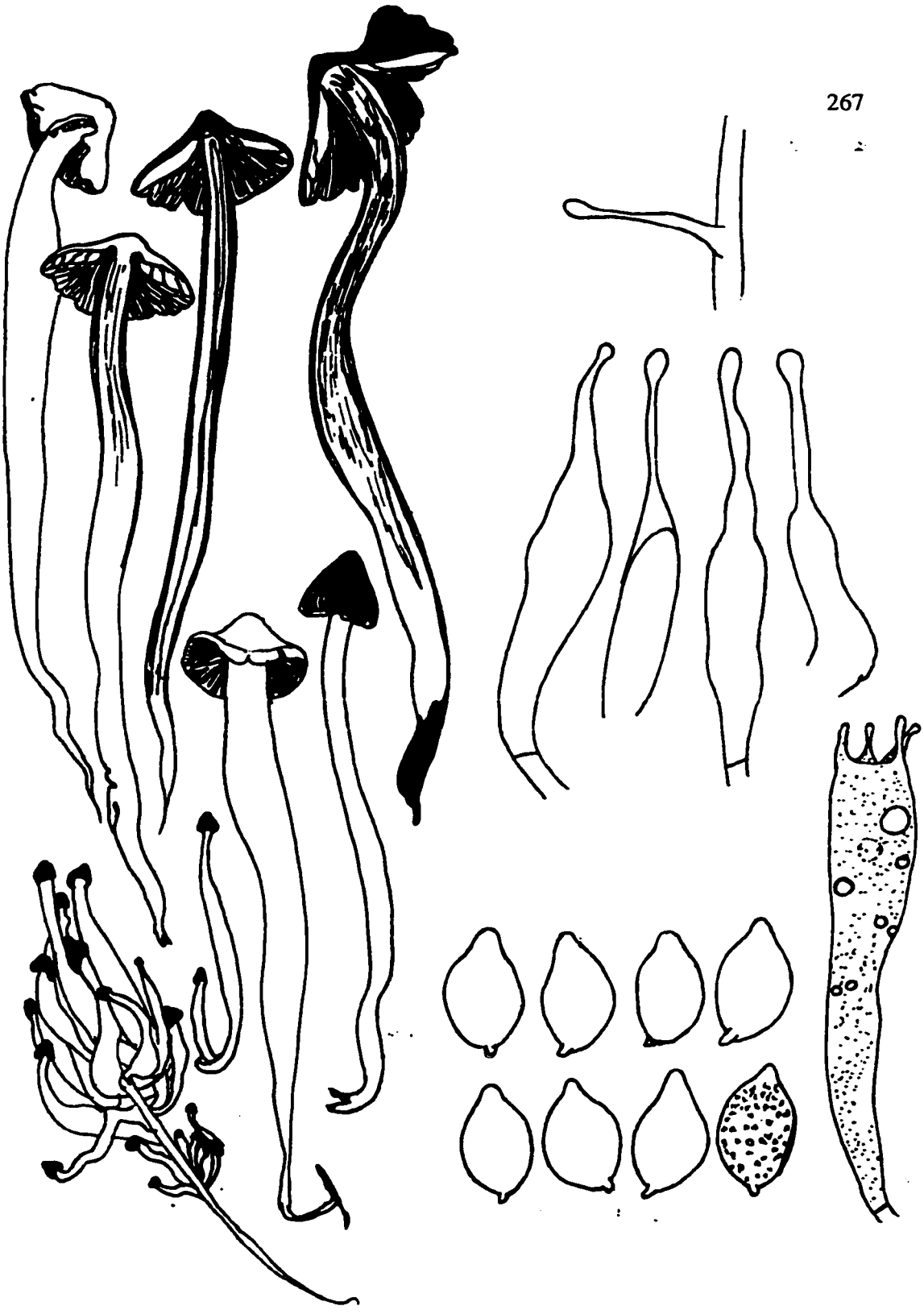


Figure 6.40 *Phaeocollybia scatesiae.* **a.** Habit (3/4 actual size). Fascicle of smaller basidiomes on rhizomorphic pseudorhiza (LLN 94.10.19-4); larger specimens from cluster of 93 (LLN 95.11.09-27); **b.** Cheilocystidia and basidiospores (Holotype -- A. H. Smith 79286_{sca6}); **c.** Basidium (LLN 95.10.18-2); **d.** Tibiiform diverticulum on pellicular veil hypha (LLN 95.11.09-25).

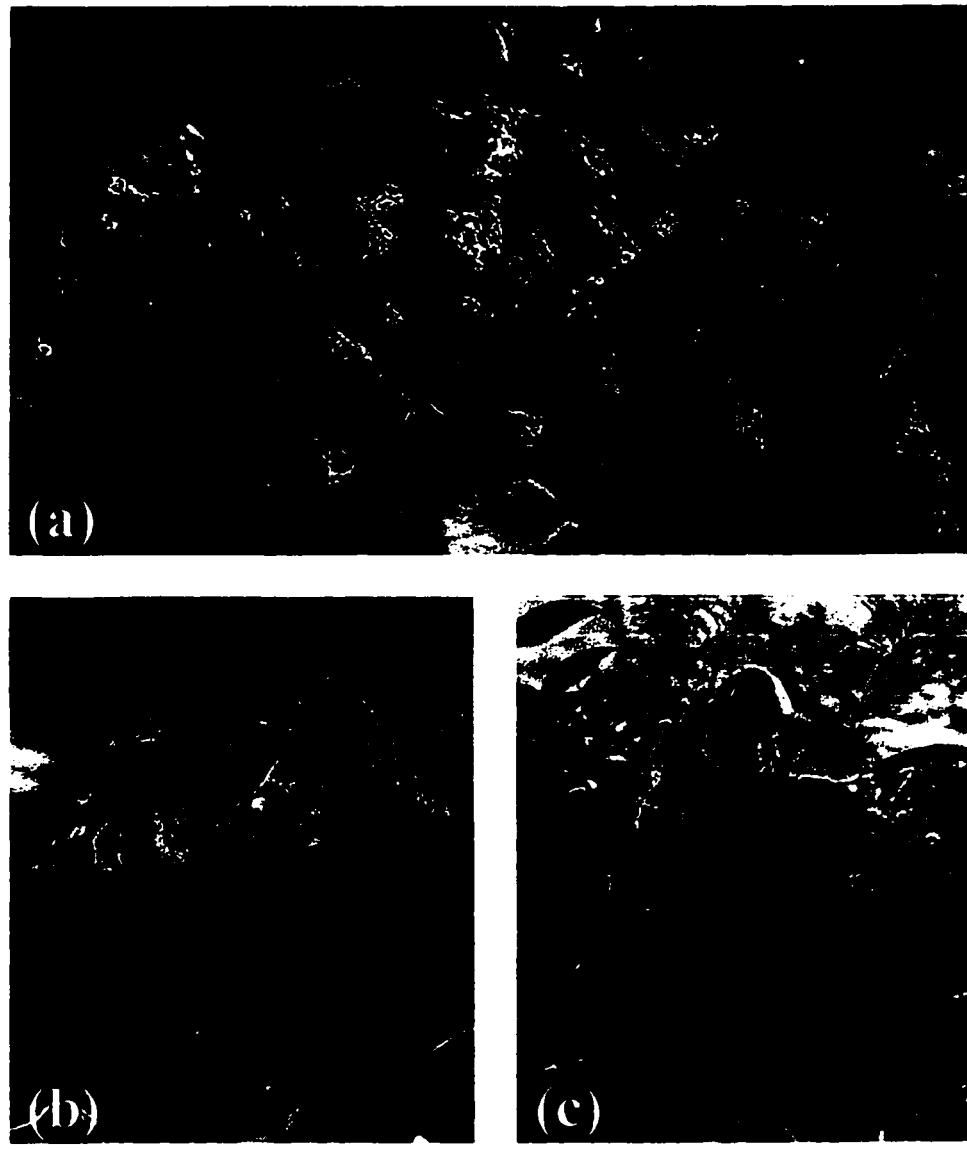


Figure 6.41 *Phaeocollybia scatesiae.* **(a)** Fasciculate masses in coarse woody debris in heavily thinned *Abies-Tsuga-Pseudotsuga* forest on Wildcat Mountain near Mt. Hood, Oregon (LLN 95.10.18-1). **(b)** Young specimens *in situ* under *Picea* and evergreen *Vaccinium* (LLN 93.11.04-2). **(c)** Pale form, *in situ,* Van Duzer Wayside, Lincoln County, Oregon (LLN 93.11.04-9).

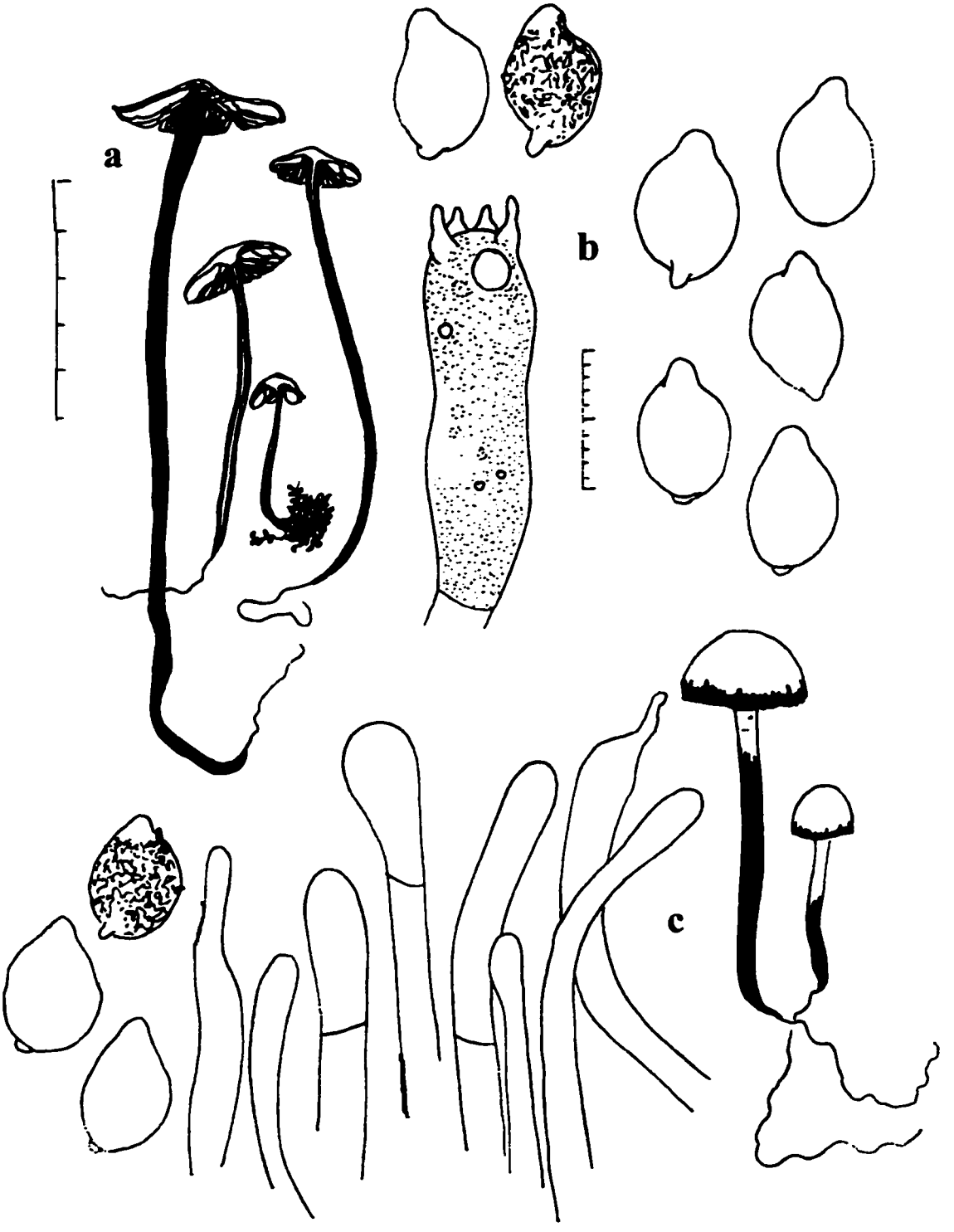


Figure 6.42 *Phaeocollybia 'similis' sensu* Smith 1957. **a.** Habit (3/4 actual size). (LLN 93.10.30-1 (a) & LLN 93.09.24-2 (c)); **b.** Cheilocystidia and basidiospores (A. H. Smith 39988 (MICH); **c.** Basidiospores (LLN 93.09.24-2).

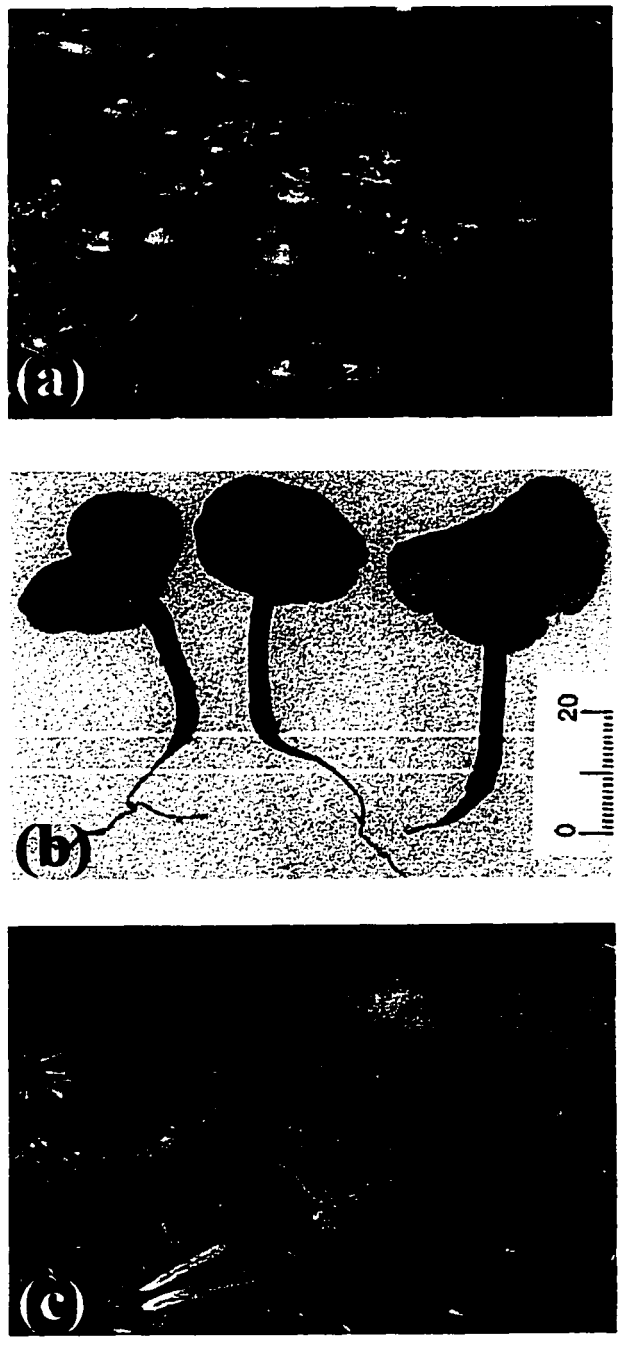


Figure 6.43 *Phaeocollybia similis sensu* A. H. Smith. **(a)** Gregarious masses *in situ* in ancient *Picea-Abies* forest, Upper Carmanah Valley, Vancouver Island (LLN 93.10.30-25). **(b)** Specimens with criniform vertical monopodial pseudorhizae from ancient *Picea* forest, Lower Carmanah Valley (LLN 92.10.09-18). **(c)** Specimens *in situ* in Ipsut Creek, Mt. Rainier National Park, Washington (LLN 93.09.24-2).

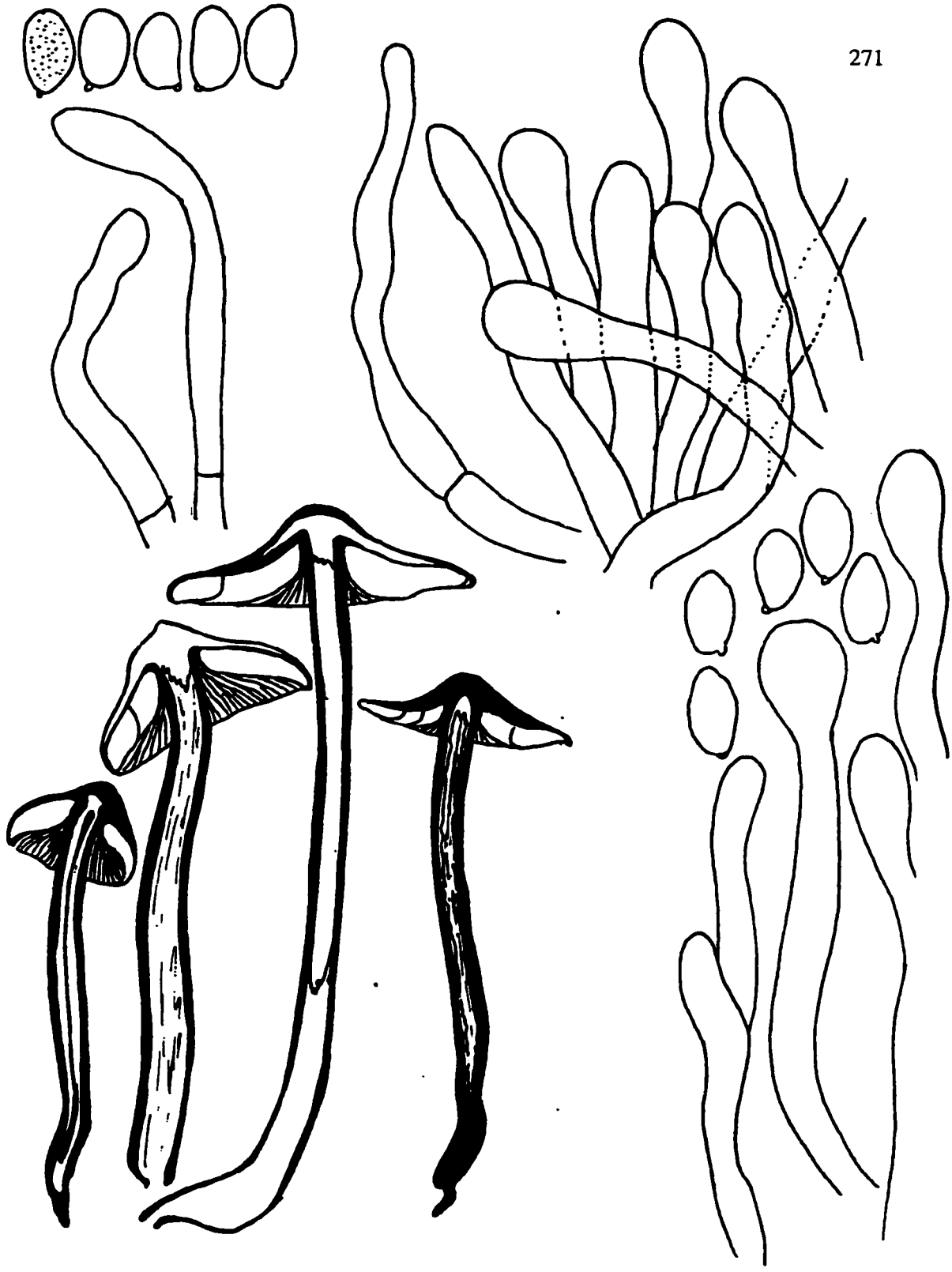


Figure 6.44 *Phaeocollybia sipei*. **a.** Habit (3/4 actual size). (LLN 95.11.09-5 (left), -7 (center two), 6 (right); **b.** Cheilocystidia and basidiospores (F. P. Sipe Oct. 1937 (MICH) -- Holotype); **c.** Cheilocystidia (LLN 95.11.09-5); **d.** Cheilocystidia and basidiospores (LLN 95.11.09-6).

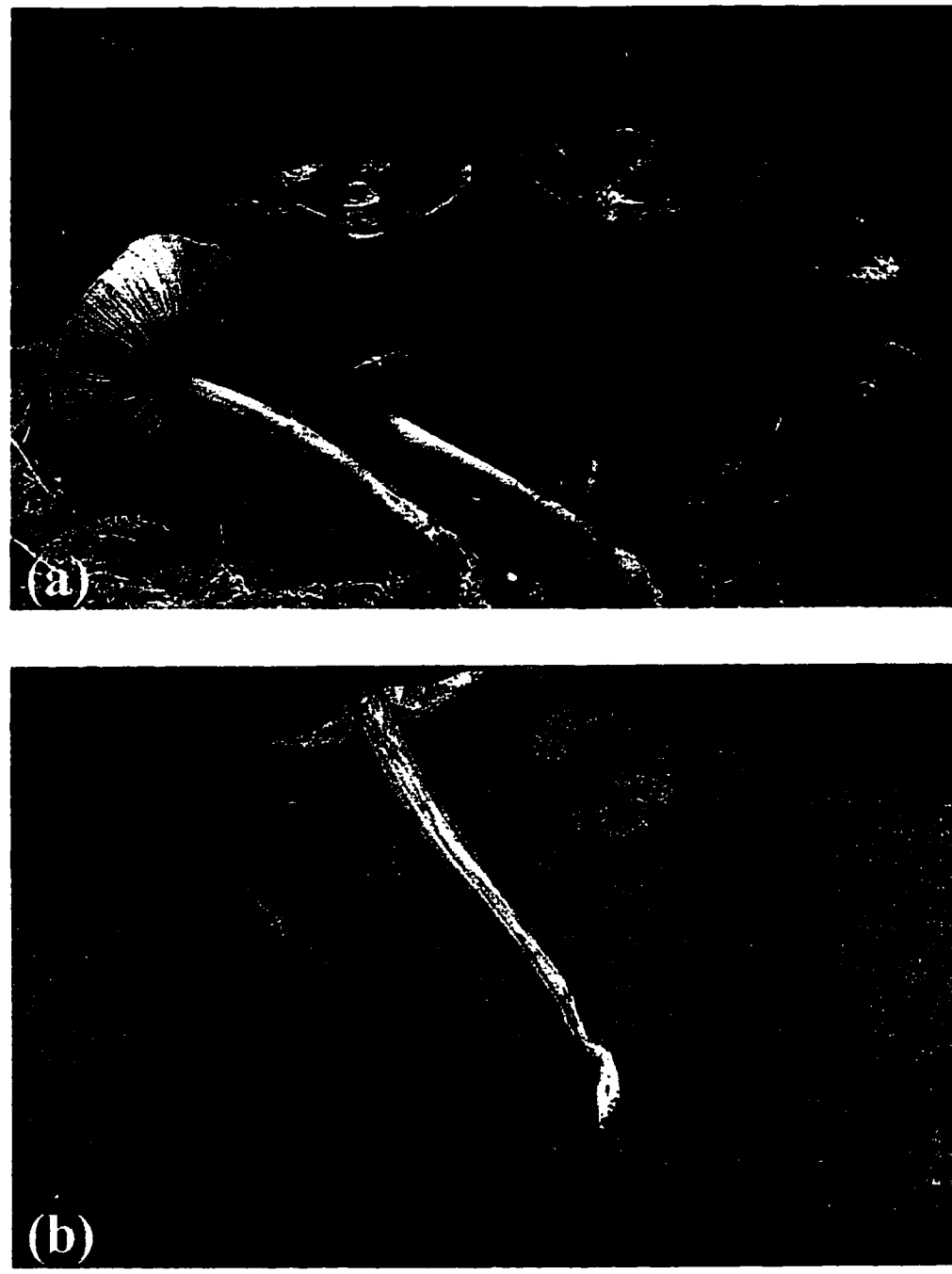


Figure 6.45 *Phaeocollybia sipei.* **(a)** Specimens *in situ*, Fogarty Creek State Park, Lincoln County, Oregon (LLN 95.11.09-2). **(b)** Longitudinal section illustrating cartilaginous pileus context, thick stipe cortex and fibrillose pith (LLN 95.11.09-6).

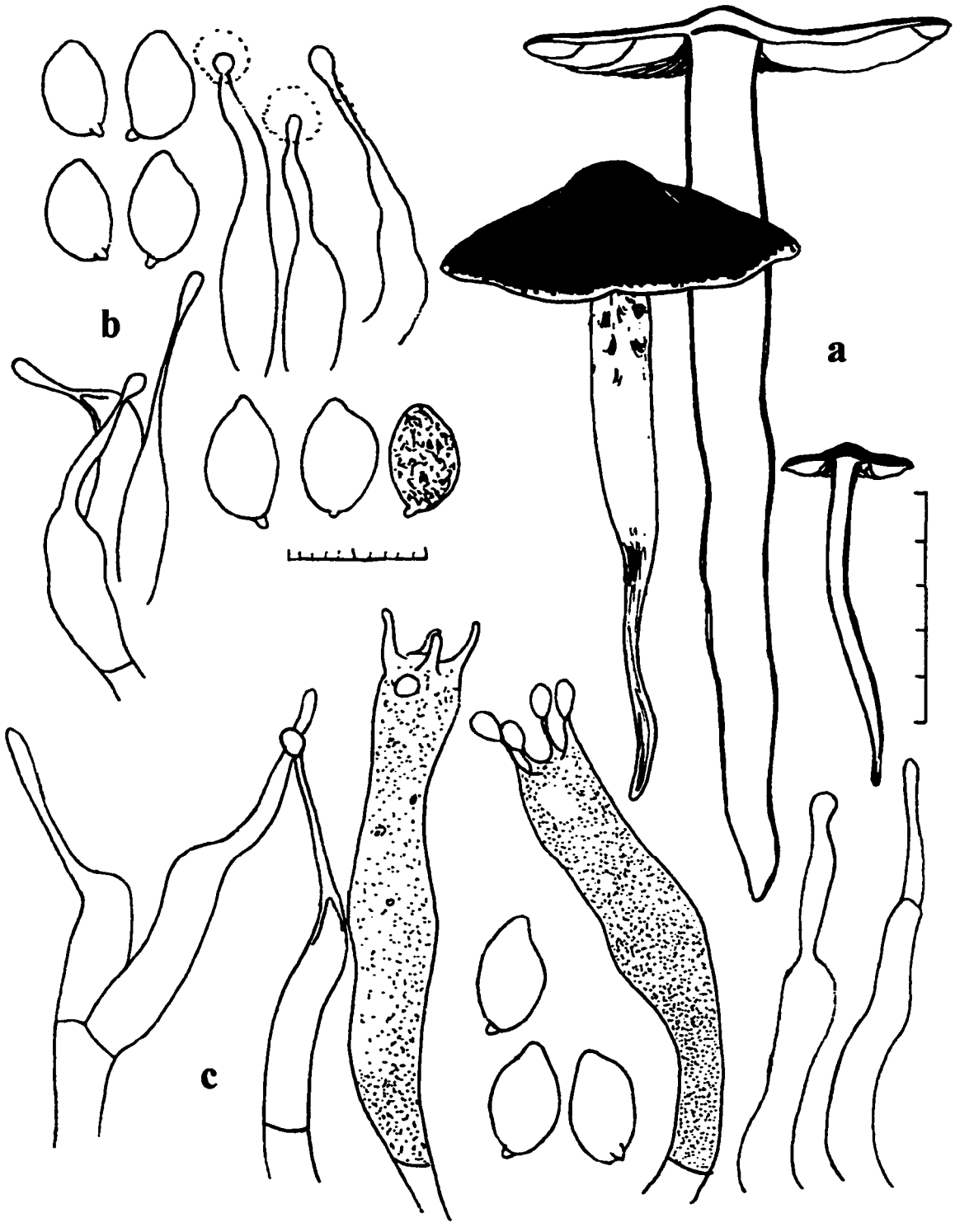


Figure 6.46 *Phaeocollybia spadicea* **a.** Habit (3/4 actual size). (LLN 93.11.14-6,7; LLN 95.11.09-20); **b.** Cheilocystidia and basidiospores (A. H. Smith 3339 (MICH 00011634) -- Holotype); **c.** Basidia, cheilocystidia and basidiospores (LLN 93.11.06.28a).

Figure 6.47 *Phaeocollybia spadicea.* **(a)** Gregarious specimens *in situ,* Hoh Rainforest, Olympic National Park (LLN 92.10.15-10). **(b)** Specimen with characteristic dingy ochraceous lamellae, firm fibrillose pith, and cartilaginous pileus from Cascade Head Experimental Forest (LLN 95.11.09-24). **(c)** Specimen from Oswald West State Park (LLN 93.10.23-6) with dense patches of pellicular veil remnants on stipe.

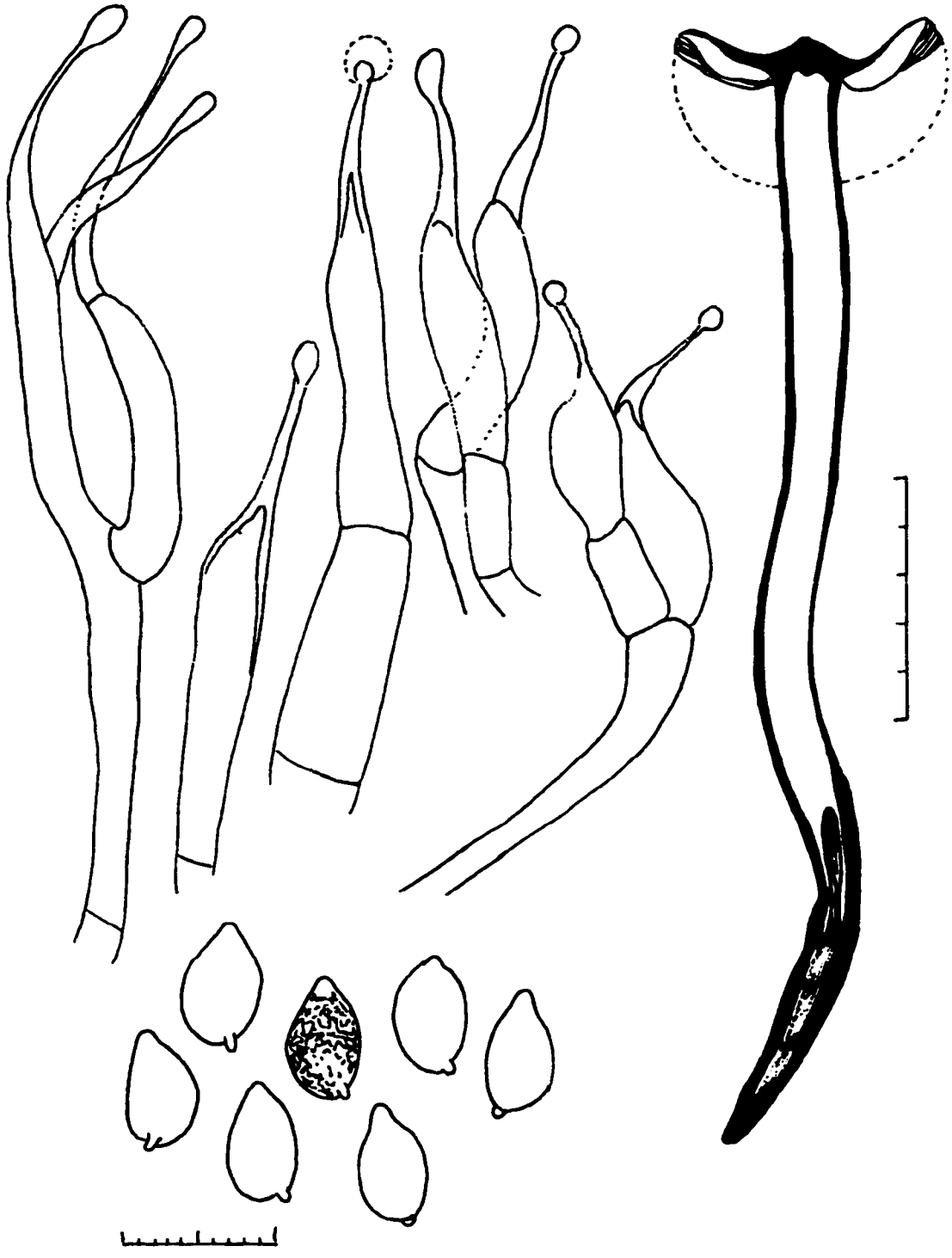


Figure 6.48 *Phaeocollybia tibiikauffmanii nom. prov.*(LLN 95.11.09-19 (WTU)-- Holotype) Habit (3/4 actual size); Basidia, cheilocystidia and basidiospores.

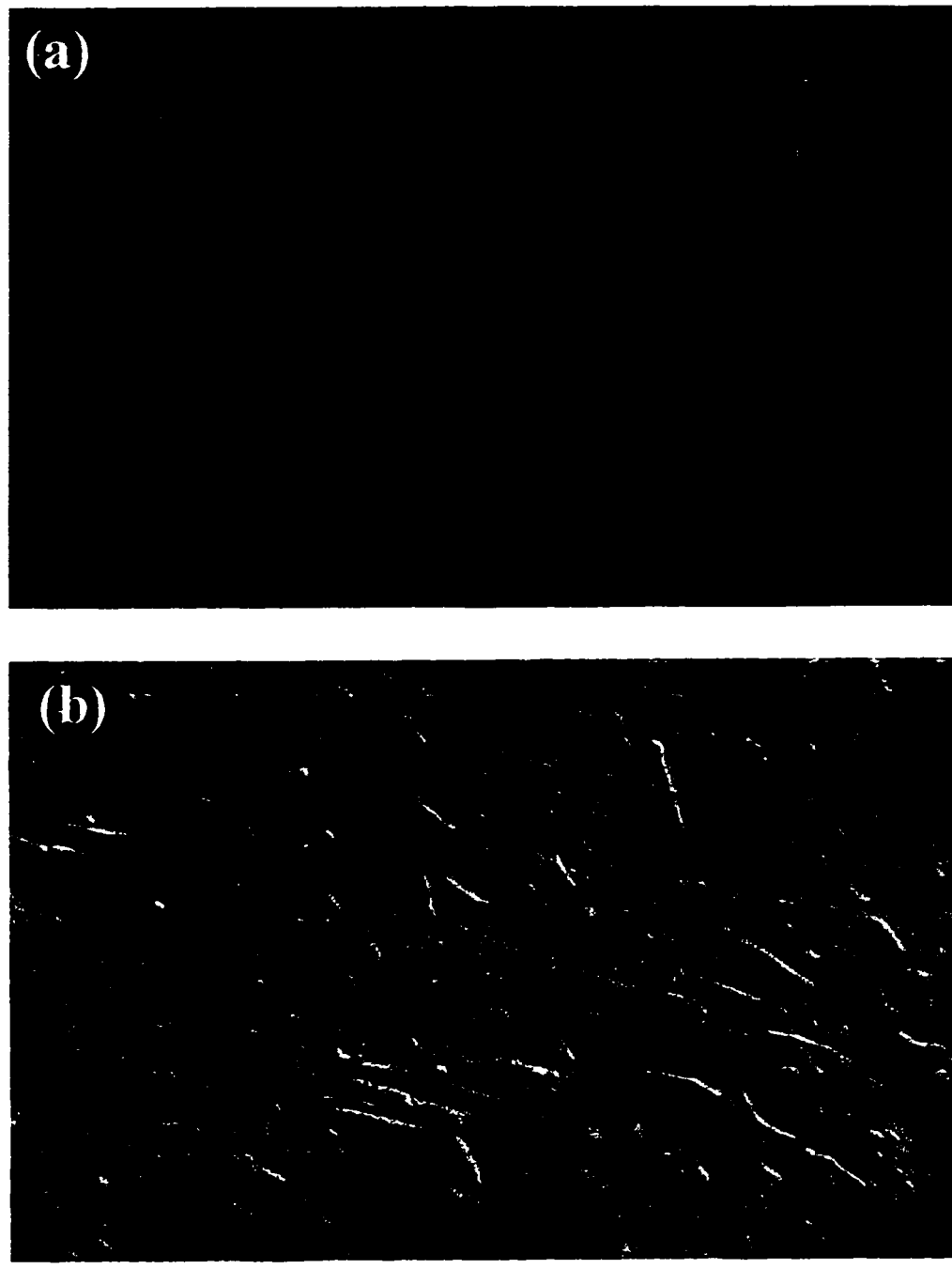


Figure 6.49 *Phaeocollybia tibiikauffmanii nom. prov.* **(a)** Holotype, from Cascade Head Experimental Forest, Lincoln County, Oregon (LLN 95.11.09-19, Holotype, WTU). **(b)** Basidiospores and tibiiform diverticula on remnant of the pellicular veil found on stipe apex (holotype).

CHAPTER 7. SUMMARY

Biology -- *Phaeocollybia* was investigated by examination of mycelia, primordia and basidiomes procured from field excavations within mature and ancient coniferous forests in British Columbia, Washington, Oregon and California. Objectives of the biological portion of the research were four-fold: (i) to uncover evidence supporting a biological strategy (trophic status) for the genus and to determine substrate soil horizons supporting the basidiomes, (ii) to ascertain a developmental sequence from primordium to senescent basidiome for representative Pacific Northwest species and thus infer an ontogeny for the entire genus, (iii) to determine which potentially diagnostic morphological characters might be developmentally dependent, and (iv) to investigate the mating compatibility between and among representatives of species identified during the study. Investigation of mating compatibility was forestalled at the outset by an inability to culture representatives of any *Phaeocollybia* species; because neither basidiospore germinations nor tissue cultures were successful, any biological insights into the genus were perforce gained through observation and examination of fresh or preserved specimens.

Sufficient new information was gained from primordia and intact pseudorhizae to answer biological questions that had been either insufficiently investigated by previous workers (*e. g.*, trophic status) or ignored by them (*e. g.*, ontogeny). Excavations and examination of substrates associated with representatives of *P. benzokauffmanii, P. kauffmanii, P. pseudofestiva, P. redheadii,* and *P. spadicea* offer extensive circumstantial evidence for ectomycorrhizae in *Phaeocollybia,* including association of pseudorhizae, primordia and characteristic diverticulate mycelia with senescent or viable rootlets with intact vascular steles and mantle-sheathed ectomycorrhizal tips possessing Hartig nets. This evidence also supports inclusion of *Phaeocollybia* with other demonstrably mycorrhizal genera within the Cortinariaceae (supported by most agaricologists) and contradicts inclusion of the genus within the saprophytic Strophariaceae as proposed by Kühner (1980).

The generically significant discovery of (pileo)stipitocarpic monovelangiocarpy in sixteen species (*P. ammiratii, P. attenuata, P. benzokauffmanii, P. fallax, P. kauffmanii, P. luteosquamulosa, P. olivacea, P. oregonensis, P. pseudofestiva. P. redheadii, P. rifflipes, P. rufotubulina, P. scatesiae, P. 'similis', P. sipei,* and *P. spadicea)* contradicts a gymnocarpic ontogeny previously assumed for *Phaeocollybia* by most workers. Discovery of a primordial pellicular sheath not only provides additional support for classifying *Phaeocollybia, Cortinarius, Hebeloma,* and *Inocybe* together in the Tribe Cortinareae but also unleashes a suite of new characters, some useful for discriminating taxa at specific and interspecific levels (*e.g.*, differential retention of the pellicular sheath in mature basidiomes) and others that are generically significant (*e.g.*, the characteristic tibiiform diverticula that are an integral part of Phaeocollybian mycelium and pellicular veil). The

secretory nature of the tibiiform diverticula and their ubiquitous presence on consistently intact pseudorhizae suggest that these microscopical processes are glandular in function and serve in a protective anti-feedant capacity.

Four different types of pseudorhizae are now recognized: (i) vertical-monopodial (observed in *P. ammiratii, P. benzokauffmanii, P. fallax, P. kauffmanii, P. lilacifolia, P. luteosquamulosa, P. olivacea pro parte, P. oregonensis, P. piceae, P. pleurocystdiata, P. redheadii, P. rifflipes, P. spadicea,* and *P. tibiikauffmanii)*; (ii) lateral-monopodial (*P. attenuata, P. phaeogaleroides,* and *P. 'similis'),* (iii) sequential-racemose (observed in *P. rufotubulina* and suspected in *P. californica, P. olivacea pro parte, P. pseudofestiva pro parte* and *P. sipei)* and (iv) fasciculate-racemose (*P. scatesiae).* Evaluation of these pseudorhizal growth patterns suggests that the Phaeocollybian pseudorhiza exhibits a previously unsuspected meristemoidal potential, with all pseudorhizal types possessing the ability to give rise to secondary basidiomes. Additionally, the ultimate origins (lower pseudorhizae) of lateral-monopodial, sequential-racemose and fasciculate-racemose pseudorhizae appear to serve a rhizomorphic function of some sort and are more properly termed rhizomorphic-pseudorhizae. A sarcodimitic dual hyphal system composed of rigid wide thick-walled fusoid to cylindrical vessel hyphae and narrow branched thin-walled flexuous hyphae appears to exist to some degree in all pseudorhizae examined. These newly discovered sarcodimitic tissues are generally most highly developed in primordia and at junctions between stipe and upper pseudorhiza (or upper pseudorhiza and rhizomorphic-pseudorhiza) in mature basidiomes. Highly developed sarcodimitism is also noted in the tramal tissues of the pileus, lamellae and stipe apex of long-lived fleshy basidiomes such as *P. benzokauffmanii, P. kauffmanii,* and *P. spadicea.* Smaller more fragile basidiomes such as *P. phaeogaleroides* appear to have a much less well-developed dual hyphal system confined to the pseudorhiza.

Comparison of immature, mature and senescent tissues reveals the developmental dependence of many diagnostic characters used in traditional taxonomy, such as pileus shape, lamellar spacing, pseudorhizal dimensions, and cheilocystidial lengths. Although capitulate refractive thick-walled cheilocystidia appear to exhibit determinate growth (*i.e.,* the distance between the terminal septum and the top of the capitulum remains fairly constant in mature specimens and is thus potentially taxonomically informative), the variable indeterminate nature of most thin-walled cheilocystidia precludes using their lengths in phenetic analyses. Additionally, flexuous filamentous extensions or outgrowths observed emerging from the apices of thin-walled cheilocystidia in many different species have been demonstrated to represent continued cheilocystidial growth in senescent or stored fresh basidiomes; the highly polymorphic cheilocystidial morphologies observed in many specimens (including one *P. olivacea* type specimen) are now recognized as developmental artifacts and not as diagnostic characters.

Taxonomy -- The taxonomy of Pacific Northwest species was investigated by combining phenetic and cladistic analyses of morphology and restriction site variation in ribosomal DNA (rDNA). The primary goal was to produce a regional monograph containing full technical descriptions of all Pacific Northwest *Phaeocollybia* species accompanied by a complete set of anatomical drawings, color photographs and taxonomic keys. Secondary objectives were five-fold: (i) to identify potentially diagnostic morphological, developmental and ecological characters from a survey of all Pacific Northwest Phaeocollybias for use in computer-assisted multivariate and phenetic cluster analyses; (ii) to generate restriction fragment length polymorphisms and restriction site data through isolation and amplification of the ITS1 + 5.8S + ITS2 rDNA region of the genome; (iii) to infer phylogenetic species relationships by using molecular characters in computer-assisted cladistic analyses; (iv) to infer subgeneric divisions using molecular characters; and (v) to determine the most reliable morphological characters for diagnosing species implied by phylogenetic analyses of restriction site data.

Multivariate and phenetic analyses of morphological, developmental and ecological characters suggest that at the present time ecological character sets are not taxonomically informative. Out of 120 morphological (and developmental) characters used in technical descriptions of *Phaeocollybia* species, sixty-six have been found useful in phenetic analyses. New diagnostic characters discovered include syringaldazine reactivity, differential retention of the pellicular sheath on the mature basidiome (*e.g.*, fibrillose patches on pileus and stipe), the existence of a trilaminate pileipellis in one species, and the differing pseudorhizal morphologies outlined above.

DNA has been successfully amplified from 160 specimens representing twenty-four putative Pacific Northwest Phaeocollybias (including fifteen types), two extralimital Phaeocollybias *(P. christinae, P. jennyae)* and seven out-taxa *('Phaeocollybia" deceptiva, Stagnicola perplexa, Cortinarius vanduzerensis, Gymnopilus spectabilis, Galerina autumnalis, Caulorhiza umbonata, Xerula megalospora).* A protocol developed for direct amplification of DNA from spores without previous isolation has proved useful for rapid testing of recently collected specimens. Nineteen restriction enzymes have been tested, of which nine (Cfo1, EcoR1, Hinf1, Nde2, Pal1, Pvu2, Rsa1, Sal1 and Xho1) produce taxonomically informative restriction fragment length polymorphisms (RFLPs) and seven (all but EcoR1 and Nde2) produce phylogenetically informative restriction site data used in cladistic analyses. Pacific Northwest individuals representing *P. ammiratii, P. attenuata, P. benzokauffmanii, P. fallax, P. gregaria, P. kauffmanii, P. luteosquamulosa, P. olivacea 'A' & 'B', P. piceae, P. pseudofestiva 'A' & 'B' & 'C', P. radicata, P. redheadii, P. rifflipes, P. rufotubulina, P. similis, P. sipei* and *P. spadicea* produce species-consistent RFLP profiles although seven *(P. attenuata, P. 'similis', P. olivacea 'A', 'B'; P. pseudofestiva 'A', 'B', 'C')* require further morphological evaluation. Profiles from the two extralimital representatives and seven out-taxa are also distinct. Representatives from two species

thought to be conspecific based on morphological criteria (*P. carmanahensis* and *P. oregonensis)* produce identical RFLP profiles, as do *P. californica* and *P. scatesiae* which represent two clearly morphologically distinct groups. The PCR-amplified product obtained from a type specimen of *P. dissiliens* has produced inconsistent results that were not used in final phylogenetic analyses. Further restriction data are also needed from three other species: microscopical re-evaluation of the *P. lilacifolia* -labled isolates suggests that they probably represent *P. fallax,* and no representatives of *P. phaeogaleroides* or *P. tibiikauffmanii* have been tested. Nine different ITS length polymorphisms prohibit reliable phylogenetic inferences being gained from fragment polymorphisms, although the ITS lengths (estimated at 690, 700, 705, 710, 715, 720, 730, 735 and 740 base pairs) appear consistent within taxa.

Multivariate, phenetic and cladistic analyses of morphology and restriction sites from forty individuals belonging to a morphological species complex closely related to *P. kauffmanii* imply three distinct but phylogenetically closely related species (*P. kauffmanii, P. benzokauffmanii, P. redheadii)* well separated from two other species (*P. ammiratii, P. luteosquamulosa*). Cladistic analyses of restriction sites from twenty-five putative *Phaeocollybia* species and three outgroups *(Stagnicola perplexa, "Phaeocollybia" deceptiva, Caulorhiza umbonata)* imply the existence of twenty-three different Pacific Northwest Phaeocollybias. Although there have been some contradictions resulting from analyses of restriction site data, there is for the most part excellent support for previously formed morphological species hypotheses. Congruence of the morphological and DNA trees produced by computer-assisted phenetic and phylogenetic analyses suggests that the species described herein are, for the most part, phylogenetically well-founded.

While obviously informative at a specific taxonomic level, restriction analyses of the ITS region are less informative at the sectional and subgeneric levels. Preliminary analyses imply a fair degree of support for a sectional classification based on cheilocystidial morphology as proposed by Smith (1957b) but little or no support for the generally accepted five-section classification first proposed by Singer in 1970. Singer's classification could not be well tested within the confines of the current study, however, for only one representative of Section *Subattenuatae* (*P. ammiratii*) and one representative of Section *Radicatae* (*P. radicata)* could be analyzed. Cladistic analyses of twenty-five Pacific Northwest Phaeocollybias suggest that there is probably a monophyletic section in *Phaeocollybia* that can be diagnosed using basidiospore, cheilocystidial and pseudorhizal characters. Mapping of morphological characters on a DNA gene tree generated from restriction site polymorphisms implies inclusion of species characterized by both thick-walled tibiiform cheilocystidia and racemose rhizomorphic-pseudorhizae within the same phylogenetic clade. Inclusion of the small-spored clamped *P. radicata* among otherwise large-spored unclamped representatives and the characteristically fleshy stuffed vertical monopodial *P. spadicea* among hollow-stiped racemose representatives within that same clade is problematical.

The most sectionally significant diagnostic characters appear to be stipe, pseudorhizal, cheilocystidial and basidiospore morphologies, the existence of clamp connections, syringaldazine reactivity, and pileipellis structure.

Suggestions for future research -- Several aspects of the biology and taxonomy of *Phaeocollybia* warrant further study. While there is good circumstantial evidence for ectomycorrhizal associations in five species, trophic strategies need to be investigated in other Phaeocollybias as well, particularly in view of the evidence for mild parasitism in *P. christinae* provided by Redhead and Malloch (1986). Additional information might be obtained using molecular or enzymatic probes of tree rootlets, and more sophisticated cultivation procedures using several different culture media and temperature regimes should be explored.

The degree of endemism for the genus needs to be researched: the current opinion held by this author that all Pacific Northwest Phaeocollybias are endemic to this region should be challenged by a rigorous morphological and molecular comparison with extralimital species. Additional material of *P. gregaria, P. lilacifolia, P. phaeogaleroides, P. radicata,* and *P. tibiikauffmanii* should be collected and analyzed, and more Phaeocollybias should be sought in outlying regions of the Pacific Northwest such as the spruce forests of the northern British Columbian and Alaskan coast, the inland coniferous forests of northern Idaho, and the inland coniferous-fagaceous forests of southern Oregon and northern California.

Newly discovered characters also warrant re-evaluation. Distribution of sarcodimitic tissues throughout mature basidiomes and their occurrence throughout the genus require additional documentation. Fluorescence should be systematically noted for all species and the possible generic significance of lamellar fluorescence investigated. Although the taxonomic utility of syringaldazine reactivity has been clearly demonstrated, some species are still to be tested and the consistency and intensity of responses reported here should be double-checked. The taxonomic utility of KOH also needs to be explored.

Species complexes centered around *P. californica, P. attenuata, P. olivacea,* and *P. pseudofestiva* implied by phenetic and phylogenetic analyses in this study should be statistically analyzed and evaluated much as the *P. kauffmanii* complex has been. Resolution of most unanswered taxonomic questions can be made only after sampling many extralimital Phaeocollybias using DNA sequence data from at least two regions of the genome so as to infer a reliable phylogeny for the entire genus. Further phylogenetic insights will be gained when *Phaeocollybia* representatives are also analyzed with numerous representatives from other Cortinariaceous genera. Only then will a phylogeny be produced that will realistically reflect the systematic relationships of taxa at all levels.

Conclusion -- Currently twenty-five species are recognized from British Columbia, Washington, Idaho, Oregon and California. Dichotomous and synoptic keys to the species and photographs and line drawings accompany full descriptions that integrate morphological, ecological, developmental, macrochemical and molecular information. Generation of molecular (here restriction site) data has proved to be the best method for inferring phylogenetic relationships among Phaeocollybian taxa while simultaneously testing morphologically engendered species hypotheses. Despite the numerous ITS length polymorphisms present among the individuals sampled, the fragment patterns produced in this study appear so predictive within and among taxa that inclusion of RFLP profiles within the technical species descriptions has been deemed useful. It is quite possible that such profiles will become as useful to working taxonomists as mat morphology is now to those investigating 'culturable' fungi; the fact that sequencing or more sophisticated molecular techniques may provide more phylogenetically reliable information does not negate the taxonomic value of RFLPs.

Integration of morphological, developmental, and molecular characters has resulted in a treatise that addresses all aspects of the organism. Developmental and biological research has not only resolved older controversies but also generated new characters that are taxonomically informative, both at the specific and generic levels. Consideration of all aspects of the basidiome and integration of morphological and molecular characters have resulted in an understanding of individual organisms and revealed the monophyletic integrity of the genus as a whole. This dissertation represents one of the most thorough Pacific Northwest agaric monographs to date.

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APPENDIX A. Morphological Features Utilized in Phenetic Analysis

Table A-1. Morphological, anatomical, chemical and ecological characters typically used in *Phaeocollybia* species descriptions

A-1a. Morphological [59 possible for *Phaeocollybia]*

CHARACTER	*LINKED*	*VARIABILITY*	*MISSING DATA*	*DEFINABILITY*
Pileus mean diam	dev; weather	sl too variable	likely when solitary	coll dependent
Pileus max diam	dev; weather	sl too variable	occ when solitary	good
Pileus diam/hgt	dev; weather	extreme	frequent	not informative
Pileus shape	dev; weather	extreme	infrequent	difficult, no ref
Pileus /stipe apex diam	dev; weather	sl too variable	infrequent	excellent
Pileus mature umbo	dev; weather	acceptable	occasional	sl difficult
Pileus mature edge	dev; weather	acceptable	frequent	rel easy
Pileus scales	dev; weather	good	frequent	somewhat difficult
Pileus moisture	dev; weather	good	infrequent	straightforward
Pileus zonation	dev; weather	sl too variable	rare to frequent	fair
Pileus striation	dev; weather	unknown	frequent	good
Pileus dry color dull	prep	good	none	good
Pileus dry color metallic	preparation	good	none	good
Pileus dry color -- diff	preparation	good	none	?
Pileus disc color	dev	good	occasional	overlapping
Pileus edge color	dev; weather	good	occasional	overlapping
Pileus overall orange	dev; weather	good	no	straightforward
Pileus overall green	dev; weather	good	no	straightforward
Pileus overall brown	dev; weather	good	no	straightforward
Pileus overall ochre	dev; weather	good	no	straightforward
Pileus overall drab	dev; weather	good	no	straightforward
Context height	dev; weather	good	occasional	straightforward
Context farinaceous	dev; weather	good	occasional	subjective
Context gebrenzlich	dev;weather	good	occasional	subjective
Context odor dry	dev; weather	good	occasional	subjective
Context taste bitter	dev; weather	good	occasional	subjective
Young gills violet	dev; weather	good	no	straightforward
Young gills green	dev; weather	good	no	straightforward
Young gills drab white	dev; weather	good	no	straightforward
Young gills ochraceous	dev; weather	good	no	straightforward
Young gill edges	dev; weather	unknown	frequent	sl difficult
Mature gill breadth	dev, prep; weather	fair	frequent	measurement
Mature gill length/width	dev; weather	fair	frequent	measurement
Gill proximity verbal	dev; weather	fair	frequent	measurement
Gill proximity edge	dev; weather	fair	+frequent	measurement
Gill proximity mid	dev; weather	fair	+frequent	measurement
Gill proximity edge/mid	dev; weather	fair	frequent	measurement
Spore print date brown	no	good	rare to frequent	fair
Spore print or-brown	no	good	rare to frequent	fair
Stipitipith insect infested	dev; weather	too variable	frequent	good
Stipitipith	dev	excellent	rare	good
Stipe cortex width	dev	good	frequent	measurement
Stipe |x| aerial length	dev; weather	too variable	frequent	too variable to use
Stipe max total length	dev; weather	too variable	frequent	too variable to use
Stipe apex diam	dev; weather	good	rare	measurement
Stipe apex/max	dev; weather	good	rare	measurement
Stipe aerial/apex	dev; weather	too variable	frequent	too variable to use

Table A-1 (continued). (A-1a concluded)

Stipe surface with flecks	dev; weather	good	occasional	good
Stipe surface polished	dev; weather	good	occasional	good
Stipe moisture	dev; weather	too variable	frequent	difficult
Stipe apexgreenish	dev; weather	good	no	straightforward
Stipe apex drab	dev; weather	good	no	straightforward
Stipe apex ochraceous	dev; weather	good	no	straightforward
Stipe serial color	dev; weather	poor	no	straightforward
Stipe aerial trizonate	dev; weather	fair	occasional	too dev dependent
Pseudorhizal color	dev; weather	poor	frequent	straightforward
Pseudorhiza max length	dev; weather	poor	very frequent	straightforward
Origin color	dev; weather	poor	very frequent	straightforward
Origin morphology	--	good	frequent	straightforward

A-1b. Anatomical characters [53 possible for Phaeocollybia]

CHARACTER	*LINKS*	*VARIABILITY*	*MISSING DATA*	*DEFINABILITY*
Clamps	?	acceptable	none	excellent
Pellis layers	?	acceptable	rare	excellent
Pellis structure	?	acceptable	none	excellent
Suprapellis gel	viscidity	acceptable	none	difficult
Suprapellis color	pileus color	acceptable	none	acceptable
Suprapellis diam	?	acceptable	none	excellent
Suprapellis clamps	other clamps	acceptable	no	excellent
Suprapellis septa	weather	infra problem	no	acceptable
Suprapellis incrust	dev, pres	acceptable	possible	good
Suprapellis height	weather, preservation	acceptable	rare	excellent
Suprapellis tibis	no	acceptable	possible	acceptable
Subpellis H2O color	pileus color	acceptable	frequent	fair
Subpellis hyph diam	development	acceptable	frequent	diff
Subpellis clamps	other clamps	acceptable	no	oft obscured
Pileal trama sarcodi	dev	acceptable	none	acceptable
Lamellar trama	?	invariable	no	excellent
Tramal diam	?, weather	unknown	no	excellent
Basidia lxl length	spore size; dev	good	occasional	excellent
Basidia lxl wid	spore size; dev	good	occasional	excellent
Basidia Q	bas & spore size; dev	good	occasional	excellent
Basidia projecting	dev, weather	unknown	no	good
Basidia clamp	other clamps	good	none	difficult
Basidia sterigmata	dev, spec prep	present	occasional	excellent
Spore lxl length	bas size; dev, prep	good	occasional	excellent
Spore lxl wid	bas size; dev, prep	good	occasional	excellent
Spore Q	bas size; dev, prep	good	occasional	excellent
Basidium/spore Q	dev,prep	good	occasional	excellent
Spore ornamentation	dev, prep	good	occasional	excellent
Spore ellipsoid	no	good	occasional	excellent
Spore amygdaliform	no	good	occasional	excellent
Spore beak	dev,prep	good	occasional	excellent
Spore color	dev,prep	good	occasional	diff, no ref
Cheilo tibii only	?	excellent	occasional	excellent
Cheilo fili only	?	excellent	occasional	excellent
Cheilo clavate only	?	excellent	occasional	excellent
Cheilo apex diam	dev, env	unknown	no	excellent
Cheilo neck diam	dev. env	unknown	no	excellent
Cheilo septa diam	dev,env	unknown	no	excellent
Cheilo length	dev, env	too variable	no	excellent
Cheilo origin	dev?	unknown	likely	diff
Cheilo gel barrier	?	acceptable	none	acceptable
Cheilo wall thickness	dev, env	unknown	likely	difficult
Cheilo color	dev, prep	poor	no	difficult
Pleurocystidia?	unknown	excellent	no	excellent
Stipitipellis diam	?	unknown	no	excellent
Stipitipellis gel	dev, prep, weather	likely variable	no	sl difficult
St-pellis diverticula	no	acceptable	occasional	acceptable
St-trama sarcodi	dev	acceptable	none	acceptable
Tib-div site	no	acceptable	occasional	acceptable
Pseudorhizal sarcodi	dev	acceptable	none	acceptable

Table A-1 (continued).

A1-c. Possible macrochemical characters [8 possible]

CHARACTER	LINKED	VARIABILITY	MISSING DATA	DEFINABILITY
Syringaldazine	dev?	excellent	frequent	acceptable
Pellis KOH color	?	acceptable	occasional	acceptable
Pith KOH color	poss dev	acceptable	frequent	acceptable
Fluorescence	unknown	unknown	over frequent	acceptable
Spore amyloidy	unknown	unknown	none	acceptable
FeSO4	unknown	invariable	over frequent	acceptable
Paracresol	unknown	invariable	over frequent	acceptable
Guaiacol	unknown	invariable	over frequent	acceptable

A1-d. Possible ecocharacters [29 possible]

CHARACTER	LINKAGE	VARIABILITY	MISSING DATA	DEFINABILITY
Forest age	management	acceptable	occasional	good
Management fire	?	acceptable	frequent	difficult
Management clear-cut	?	good	occasional	good
Management high-grade	?	unknown	frequent	difficult
Canopy cover	forest age	may be extreme	frequent	sl difficult
Picea present	?	unknown	occasional	excellent
Abies / Tsuga	?	unknown	occasional	excellent
Pinus/Quercus/ Lithocarpus	?	unknown	occasional	excellent
Sequoia + mix	?	unknown	occasional	excellent
Pseudotsuga total	?	unknown	occasional	excellent
Vaccinium/Rhododendron	overstory	unknown	frequent	excellent
Gaultheria	overstory	unknown	frequent	excellent
Polystichum	overstory	unknown	++frequent	excellent
Sphagnum	overstory	unknown	++frequent	excellent
Mosses (Non-Sphagnum)	overstory	unknown	++frequent	excellent
Saxifrage	overstory	unknown	++frequent	excellent
Linnaea	overstory	unknown	++frequent	excellent
Substrate clay	overstory	unknown	++frequent	difficult
Substrate sand/gravel	overstory	unknown	++frequent	difficult
Substrate heavy humus	overstory	unknown	++frequent	difficult
Floodplain	no	unknown	frequent	good
Humidity	no	unknown	rare	sl difficult
Habit	dev	may be extreme	occ to frequent	collector dependent
Sociability	other species	unknown	very frequent	collector dependent
Phenology: vernal	dev, dist,climate	unknown	no	care in coding
Phenology: late summer				
Phenology: late autumn				
Coastal	no	good	no	(first mtn range)
Montane	no	good	no	good
Endemic (for sectional analysis only]	no	unknown	extreme	very poor

Appendix A-2. Result of preliminary evaluation of character sets.

MORPHOLOGY	ELIMINATED FROM PHENETIC ANALYSES	RETAINED FOR FURTHER EVALUATION
Pileus dimensions	-- *mean diameter:* most collections lack representative cross section of basidiomes; maximum diameters deemed potentially more informative; size highly developmentally dependent. -- *diameter/height ratio:* developmentally dependent, with taller young pilei and lower mature pilei noted.	--*pileus : stipe apex diameter ratio*:potentially informative when immature specimens excluded (multistate, ordered). --*maximum diameter:* care in coding; probably developmentally dependent
Pileus shape	*overall:* a developmental progression of convex to conic to campanulate noted	--*mature umbo morphology*: possibly important in species differentiation. --*mature edge morphology*: highly taxonomically informative; care advised: developmentally dependent.
Pileus surface	--*striation*: linked to context thickness; may not be appropriate for phenetic analysis (binary only).	--*scale presence*: important; probably linked to presence of trilaminate pileipellis. --*moisture*: use care in coding.
Pileus color	--*disc & edge colors* -- linked to overall color and zonation (monochromatic color zones common in PNW Phaeocollybias).	--*overall color*: important; do not discriminate states too finely; analyze complexes first using binary 'cascade' (e.g. ochraceous vs. not ochraceous, brilliant orange vs. not brilliant orange). --*dried cap color:* possibly linked to specimen age and/or preparation; binary state (*i.e.* metallic/not metallic or black/not black);
Context	--*insect infested*: linked to specimen age& ecological circumstances and possibly to presence/absence of farinaceous odors. -- *dried odor*: sweet maple syrup smell probably tied to herbarium box; not detectable in poorly prepared dried material or naphthalene-stored specimens.	--*farinaceous odor*: possibly ephemeral; assume if TASTE is farinaceous, odor is likewise; binary? --gebrenzlich*(potato/pansy) odor*: distinctive; ephemeral; binary? --*taste bitter*: not linked to odor; binary. --*maximum PC height:* multistate ordered.
Lamellar dimensions	--*lamellar length:* developmentally dependent; -- *lamellar breadth:* developmentally dependent; -- *lamellar width*: developmentally linked; width of lamellar trama may be more informative.	-- *mature length/breadth* ration: may be developmentally linked; code carefully.
Lamellar proximity (closeness)	-- *unmeasured proximity estimate*: too vague --*proximity measure at edge*: -- many missing data anticipated; -- *proximity measure at midpoint*: many missing data anticipated	-- *proximity measurement edge/mid:* -- better estimate, but many missing data present
Lamellar color	--*mature color* -- too similar to be useful;	-- *young color*: very significant; missing data possible; binary series -- examine choices carefully (all zeros = pale pinkish cinnamon) ochre, olive, violet, gray white most important
Other Lamellar traits	-- *number of tiers* -- too many missing data; possibly developmentally dependent.	-- *young edges*: may be significant, but also dev linked; many missing data probable; code carefully if use.
Spore color in mass	--color interpretation difficult due to depth of print variation; too many missing data.	

Table A-2 (continued).

(MORPHOLOGY)	(ELIMINATED FROM PHENETIC ANALYSES)	(RETAINED FOR FURTHER EVALUATION)
Veil	*--fibrillose patches on stipe apex*: influenced by environment and developmental stage.	
Stipe dimensions	*--mean aerial length*: variable; developmentally dependent. *--maximum total length:* extremely variable; missing data. *--maximum pseudorhizal length:* extremely variable; too many missing data *--aerial/apex diameter ratio* length component too variable	*--stipe apex diameter:* Important -- best gauge of robust stature; multistate ordered
Stipe shape	*-- shape (apex/to ground level diameter ratio)*: overly variable within single collections	
Stipe surface	*-- degree of viscidity:* too easily misinterpreted;	*-- surface:* significant character; code carefully
Stipe color	*-- aerial color*: developmentally dependent *-- upper pseudorhizal color:* invariable; missing data. *--pseudorhizal origin color:* missing data. *--trizonate stipe:* helpful in one species complex, but developmentally dependent.	*--young apex color:* Significant; missing data possible; binary series (all zeros indicate pale pinkish cinnamon); ochre, olive, violet, gray white most important
Stipe context		*--stipitipith*: Important; multistate, ordered. *--rind thickness*: multistate, ordered.
Chemical / UV	*-- Fluorescence*: too many missing data	*-- KOH reactivity*: many missing data; *-- Syringaldazine:* Important; binary or multistate ordered.
ANATOMY	ELIMINATED FROM PHENETIC ANALYSES	RETAINED FOR FURTHER EVALUATION
Clamp connections	*--stipitipellis clamps*: missing data *--tramal clamps*: 'pseudo'/ sarcodimitic tissues a problem	*--in pileipellis, at cheilocystidial septa, and/or at basidial bases:* binary (present/absent)
Tibiiform diverticula	*--location:* important; sometimes inaccessible	*-dimensions:* multistate ordered or binary
Sarcodimitism	*--location:* possibly developmentally linked	*--presence in stipititrama:* binary;
Basidiospore dimensions	*--mean spore Q*: (per Parmasto, Qs not good in phenetic analyses)	*--mean spore length*: important; multistate range; linked to width?; *--mean spore width*: important; multistate range;
Basidiospore morphology	*-spore color/wall*: color dependent on wall thickness and ornamentation; subjective.	*-- shape* definition complicated: use only binary ellipsoidal/non-ellipsoidal; *--apical beak*: binary or multistate ordered; (degree developmentally dependent; linked to spore shape?) *-amyloidy*: binary. *--ornamentation*: multistate range.

Table A-2 (continued).

(ANATOMY)	(ELIMINATED FROM PHENETIC ANALYSES)	(RETAINED FOR FURTHER EVALUATION)
Basidia	--*mean width:* somewhat invariable, but also species restricted; length linked? --*mean length:* variable, but range may be species restricted; --*colors/contents*: developmentally dependent. --*distance above hymenium*: developmentally dependent	-- *% basidia with different # spores* (adjust): 3 100% 4-spored; 2 30% 4/ 70% 2-; 1 intermixed; 0= intermixed; 999 immature; --*length/width ratio*: preferable to length or width alone; multistate ordered or binary;
Cheilocystidia dimensions	--*abundance*: too vague; --*neck or minimum width:* linked to cheilocystidial morphology;	--*length*: good for 'tibiiform' (developmentally variable for clavate elements); --*septum width*: multistate ordered;
Cheilocystidial morphology	--*apical outgrowths*: developmentally dependent (NOTE: Presence/absence good for species). --*color:* possibly linked to developmental stage or preservation method.	--*neck wall thickness*: binary (thin vs. thick) --*capitate*: binary cascade? --*mean apex width*: may be difficult to measure in heteromorphic lamellae;
Pleurocystidia		--*presence/absence:* (absent or occasional to be coded the same).
Pileipellis composition	--*degree of gelatinization:* difficult to define. --cutis / *collapsed trichodermium*: dependent on specimen preparation or developmental stage.	--*suprapellis a gelatinous matrix:* possibly developmentally dependent; binary --*# of cuticular layers above subpellis:* multistate range, ordered;
Pileipellis dimensions	--*subpellis hyphal diameter*: often difficult to determine accurately due to tissue breakdown	--*suprapellis height:* may be dependent on preparation, development, or environment; -*suprapellis hyphal diameter;* multistate range;
Pileipellis pigment topography	--*diffuse*: default -- eliminated by intraparietal, incrusting analyses	--*intraparietal:* binary --*incrusting in suprapellis:* binary. --*incrusting in subpellis:* binary
Pileipellis colors	--*in H20:* linked to pileus color (but good when missing field notes);	--*suprapellis with refractive septa*: binary --*suprapellis colored:* binary. --*pellis color in KOH*: binary or multistate.
Stipitipellis	-*hyphal widths*: possibly informative, -*color:* developmentally dependent?	--*pigment topography:* potentially useful (incrusting pigments present/absent)
Tramal tissues	--*alignment lamellar trama:* invariable. --*hyphal width (lamellae):* linked to width of cheilocystidial septa; --*thickness in pileus:* developmental. --*hyphal width (pileus, stipe)*: developmentally dependent; influenced by sarcodimitism.	

Table A-2 (continued).

ECOLOGY	ELIMINATED FROM PHENETIC ANALYSES:	RETAINED FOR FURTHER EVALUATION:
Habit	--*solitary vs. abundant:* sampling dependent, phenology. --*sociability*: sampling dependent, phenology will skew perception;	--*phenology:* informative, but search dependent; multistate ordered (spring, early fall, late-fall to winter) or binary (spring vs. autumn)
Distribution	--*endemism*: possibly informative; sampling dependent	--*coastal/inland*: informative, binary --*montane:* informative; note connection of elevation and latitude; binary
Forest Management	--*Fire:* missing data probable --*High-graded/thinned vs. clear-cut:* missing data probable --*Clear-cut/ not clear cut:* missing data probable	--*Ancient vs. Second Growth* --*Immature vs. Mature* --*Canopy Cover*: useful only in personal collections; multistate ordered
Overstory	--*Picea present:* most forests mixed --*Abies present:* most forests mixed --*Lithocarpus present:* most forests mixed --*Sequoia present:* most forests mixed --*Quercus present* most forests mixed --*Tsuga present:* most forests mixed	--*Pseudotsuga plantation:* binary -- *coniferous* vs. *deciduous:* binary --*mixed coniferous and fagaceous:* binary
Understory	--*Vaccinium:* frequently mixed with *Rhododendron* --*Rhododendron:* frequently mixed with *Vaccinium*	--*Ericaceous shrubs present in understory:* present vs. absent ---*Gaultheria:* present vs. absent --*Understory:* present vs. absent
Ground Cover	*Kindbergia;* missing data --*Hylacomium;* missing data --*Rhytidiadelphus robusta;* missing data	--*Polystichum/Blechnum:* binary --*Sphagnum:* binary --*Saxifrage herbs:* binary. --*True mosses;* binary. --*Ground cover;* binary.
Substrate		--*Clay:* binary. --*Sand:* binary. --*Heavy humus:* binary. --*Floodplain:* binary.
Climate	*Annual precipitation:* too general to be useful	--*High ambient humidity:* may be too subjective to be useful; binary.

Table A-3. *Phaeocollybia* codes: characters and character states (revised after analyses)

A-3a. Ecological character states

CHARACTER	0	1	2	3	4	5	6	7
Forest Age (years)	no forest	<60	61-120	121-200	>200			
Management: Fire	no fire	fire						
Management: Clear-cut	no	yes						
Management: Thinning	no	yes						
Canopy	open	partial	closed					
Picea, Abies, Tsuga	no	yes						
Tsuga, Abies	no	yes						
Pseudotsuga plantation	no	yes						
Sequoia 'mix'	no	yes						
Pinus/fagaceous-	no	yes						
Pseudotsuga/fagaceous	no	yes						
Fagaceous	no	yes						
Vaccinium/Rhododendron	no	yes						
Gaultheria	no	yes						
Polystichum	no	yes						
Sphagnum	no	yes						
Moss	no	yes						
Linnaea	no	yes						
Saxifrages	no	yes						
Clay	no	yes						
Sand/gravel	no	yes						
Humic	no.	yes						
Floodplain	no	yes						
Fogbelt	no	yes						
Habit	solitary	scattered	greg.	clustered	fascic.			
Sociability (with Phaeo spp)	alone	w l	w >l					
Vernal	no	yes						
Late summer	no	yes						
Late autumn	no	yes						
Coastal	no	yes						
Montane	no	yes						

Table A-3 (continued).

A-3b. Macrochemical and anatomical character states

CHARACTER	0	1	2	3	4	5	6	7
SYR+	no	mild	strong					
KOH+	no	yes						
Clamps	no	yes						
Pileipellis	mono	bi	tri-					
Suprapellis height	<10	20	50	100	>200			
Suprapellis a gel matrix	no	yes						
Suprapellis colored	no	yes						
Suprapellis w incrust pigs	no	yes						
Suprapellis + intrapar- pigs	no	yes						
Suprapellis hyphal width	<1.9	203.9	4-5.4	>5.5				
Suprapellis + refractive septa	no	yes						
Subpellis +incrust pigs	no	yes						
Subpellis +intrapar- pigs	no	yes						
Basidial lxl length		<22.5	23-26.5	27-30.5	31-36	>36		
Basidial lxl width		<5.75	5.8-6.5	7-8	>8.5			
# sterigmata / basidium	immature	100% 2-	70% 2-	30% 2-	0% 2-	intermixed		
Spore lxl length		<4.2	4.4-6	6.25-7	7.2-8.25	8.5-9	9.2-10	>10.25
Spore lxl width		<3.3	3.4-4.1	4.2-5.75	5.8-6.25	6.5-7	>7.1	
Basidium length/Spore Q		<2.5	2.6-3.5	3.6-4.2	>4.3			
Spore ornamentation	none	punct (low)	low mod	mod rough	rough			
Spores ellipsoidal	no	yes						
Spores amygdaliform	no	yes						
Spore beaks	none	low to mod	extreme					
Cheilos thick-walled (tibi-)	no	yes						
Cheilos fili to cylindrical	no	yes						
Cheilos subcapitate	no	yes						
Cheilos forked	no	yes						
Cheilo apex diam	absent	<1.5	1.5-2.4	2.5-5	5.1-8	>8		
Cheilo septum diam	absent	<2	2.1-3.2	3.3-5.1	5.2-6	>6.1		
Pleurocystidia	no	hyphidia	abundant					
Tibi diverticula location	none	psr	psr+stpe	psr+cap	ubiq			
Tibi diverticula lxl length	none	<10	10-30	>30				
Sarcodimitism	absent	psr	stipe	lamella				

Table A-3 (continued).

A-3c. Macromorphological (field)character states

CHARACTER	0	1	2	3	4	5	6	7
Pileus max diam		<15	16-42	43-70	71-110	>110		
Pileus / apex ratio		<3.49	3.5-5.49	5.5-7.49	7.5-9	>9		
Mature umbo	none	low brd	acute	papillate				
Mature edge	straight	inrolled						
Scales	no	yes						
Moisture	dry	moist	viscid	glutin				
Dry metallic	no	yes						
Dry black	no	yes						
Pileus green	no	yes						
Pileus ochre	no	yes						
Pileus drab	no	yes						
Pileus orange	no	yes						
Max PC height		<3	3.1-6	6.1-9	9.1-12	>12.1		
Farinaceous	no	yes						
Gebrenzlich	no	yes						
Bitter	no	yes						
Lamellae violet	no	yes						
Lamellae greenish	no	yes						
Lamellae white	no	yes						
Lamellae serrulate	no	yes						
Pith	hollow	fibrillose	solid					
Cortex corneous	no	yes						
Cortex lxl width	none	<0.9	1-2	2.1-3.5	>3.6			
Stipe apex lxl width	none	<5	5.1-8	8.1-12	12.1-15.5	15.6-16.9	17-21.9	>22
Apex / insert+	none	<0.5	0.6-0.85	0.86-0.99	1-1.1	>1.2		
Stipe 'flecked'	no	yes						
Stipe shiny	no	yes						
Stipe orange	no	yes						
Stipe ochre	no	yes						
Stipe green	no	yes						
Stipe drab	no	yes						
Psr racemose	no	yes						
Psr criniform	no	yes						

APPENDIX B: Specimens Examined

P. ammiratii nom. prov.

BRITISH COLUMBIA: Vancouver Isl. Port Renfrew -- *X.7.1995* PK1796, PK1810 P.Kroeger (UBC); **Mainland,** Seymour Watershed -- LLN 93.10.06-1**bar3** coll. S.Gamiet 31-100693-5; LLN 93.10.20-5 coll. S.Gamiet 52-127; LLN 93.10.24-18 coll. S.Gamiet 31-102493-4; **WASHINGTON: Clallam Co.** Mt. Angeles 1235 W 480 N -- *X.4.1941* A.H.Smith 17545*(MICH) as *P. kauffmanii*; Sol Duc 1239W480N -- LLN 92.10.31-1**bar8** coll. G.L.Barron; LLN 93.10.11-2**bar7** coll. S.Trudell; **Grays Harbor Co.** Wishkah R 1238 W 470 N -- *XI.1.1970* Stz 16428* as *P. kauffmanii* coll. B.Woo; **Jefferson Co.** Twin Creek DNR Hoh River Valley 1240W479N -- LLN 93.10.15-5; **King Co.** Asahiel Curtis SP, Denny Creek 1214W474 N -- LLN 93.10.08-1**bar6** coll. S.Clark; **Pierce Co.** Greenwater 121°6W472N -- *X.29.1967* #30131* coll. R.H.Petersen (TENN); Mt. Rainier NP --Lower Tahoma Crk., 1219W 467 N -- *IX.23.1948* A.H.Smith 31664* (MICH) as *P. kauffmanii*; *X.21.1962* W.Isaacs 1960*; **Snohomish Co.** Baker-Snoqualmie NF, Barlow Pass 1214W480N -- *IX.7.1992* JFA 10697**barl1** coll. G.R.Walker; LLN 92.09.13-6**bar9** ,-8**barl0** coll. G.R.Walker; LLN 93.10.20-3**bar5** colls. with S.A.Redhead&G.L.Barron; **Thurston Co.** Capitold Foest near Fall Creek Campground -- *19.XI.1995* LLN 96.12.03-4 by R.W.Gaines; LLN 95.12.08-6,7,9 R.V.Gaines; **OREGON: Clackamas Co.** E Fork Salmon R. 121.7W453N -- *X.6.1944* A.H.Smith 19467* colls. W. B. Gruber & A.H.Smith (MICH) as *P. kauffmanii*; Rhododendron 1219W 453 N -- *X.24.1944* A.H.Smith 20173* w D.E.Stuntz, W.Gruber (MICH as *P. kauffmanii*); Wildcat Mtn FSR 2609 1221W453N -- LLN 94.10.28-1,-3,-9, -10**amm15** (HOLOTYPE),-11, -12, -14**amm14**,-15, -21 with J.Roger; LLN 95.10.18-5,10, 21, 27, 29 with J.Roger; **Lane Co.** Cape Mtn 124°8W 44°7 N -- *X.1994* LLN 96.02.21-mrl coll. M.Peeters; **Multnomah Co.** Larch Mtn summit 1221W455N -- *X.21.1945* WBGruber 700* (MICH as *P. kauffmanii*); LLN 91.11.27-01b by PSU students; LLN 92.11.04-8**bar4** w S.A.Redhead, G.T.Norvell, P.W.Trimm; LLN 93.11.05-2 coll. S.A.Redhead; **Tillamook Co.** Cascade Head Experimental Forest FR 1861 1239W450N -- LLN 94.11.06-18-**amm16** with G.T.Norvell; LLN 95.11.09-15, 29, 30; LLN 96.11.02-4; Nestucca, BLM property 5 mi S Cooper Mtns -- *25.X.1996* LLN 96.12.03-2 by J.Lindgren; **CALIFORNIA: Humboldt Co.** Big Lagoon State Park 1229W 412 N -- *XI.3.1984* #11201* coll. R.Watson 16 (HSC as *P. kauffmanii*); *X.18.1986* R.Watson 74* coll. DLLargent (HSC #11216 as *P. kauffmanii*); LLN 92.11.19-1**bar2** colls. L.L.Norvell, S.A.Redhead, DLLargent; Orick 1241W413N -- *XI.28.1991 coll.* R.E.Halling 6737* (NY as *P. kauffmanii*)); Patrick's Point St. Park 1242W411N -- *XI.4.1957* C.A.White* (MICH as *P. kauffmanii*)); *XII.4.1957* C.A.White 392* (Mich as *P. kauffmanii*), *XI.2.1965* H.D.Thiers 13942* (SFSU as *P. kauffmanii*)) **Shasta Co.** Castella -- LLN 96.11.29-1,2,3,4b,5 by J.F.Ammirati; **Sonoma Co.** Camp Meeker 1230W384N -- *XI.27.1960* Peters 192* coll. DLLargent (MICH as *P. kauffmanii*));

P. attenuata (A. H. Smith) Singer 1940

WASHINGTON: Clallam Co. La Push -- LLN 93.10.15-7**attl1** by P.Kroeger; Quillayute River near La Push -- *2.X.1935* A.H.Smith 3343**att9** (MICH -- *Holotype* 00011569); **OREGON: Tillamook Co.** Cascade Head Experimental Forest FR 1861 1239W450N -- LLN 94.11.06-34**attl3** w G.T.Norvell; Oswald West SP -- LLN 93.10.23-3**attl2** w G.T.Norvell; Van Duzer SWayside -- LLN 92.11.10-31**att7** w G.L.Barron & S.A.Redhead; **CALIFORNIA: Mendocino Co.** Van Damme SP -- LLN 92.11.20-8**att4** w S.A.Redhead.

Probably also: **WASHINGTON: Clallam Co.** La Push -- LLN 92.10.24-1 by E.Fox & S.A.Redhead; LLN 93.10.15-9; **Jefferson Co.** Olympic National Park, Twin Creek RNA, Hoh River Valley -- LLN 92.10.15-1, LLN 92.10.15-4,-6,-7 w S.A.Redhead, LLN 92.10.15-13 by G.L.Barron, LLN 92.10.15-21 by C.McClenaghan, LLN 92.10.15-31,35,36, LLN 92.10.17-13 by P.W.Trimm; **OREGON: Benton Co.** Bunker Hill -- J.F.Ammirati 5878 (MICH); Dinner Creek -- *no date* Hunt & Fogel (OSC 56450); McDonald Forest -- LLN 95.11.17-4, 5, 9, 15, 21 w F. Camacho, T. Lebel & N.S. Weber; **Lincoln Co.** Fogarty Creek SP-- LLN 95.11.06-6 w M.Moser, J.F.Ammirati; LLN 95.11.09-3, 13; LLN 96.11.02-2; **Tillamook Co.** Cascade Head Experimental Forest FR 1861 1239W450N -- *19.XI.1972* E.Tylutki 4449 (MICH -- as *P. radicata*),

P. attenuata (concluded)

LLN 94.11.06-5, 6, 7, 29, 30, 31, 32,33, 35 w G.T. Norvell; LLN 94.11.10-3b by M.T.Seidl; Van Duzer SWayside -- LLN 92.11.10-23,-25,-28 w G.L.Barron, LLN 92.11.10-26, LLN 92.11.10-27 w S.A.Redhead & G.L.Barron; Van Duzer Corridor -- J.F.Ammirati 6088 (MICH); **CALIFORNIA: Del Norte Co.** J.Smith SP: Rugg Grove -- *8.XI.1986* H.D.Thiers 50777 (SFSU); J.Smith SP: Stout Grove -- *5.XII.1937* A.H.Smith 9414 (MICH), *18.X.1969* HSC 2669 (HSC), D.L.Largent 4053 (OSC); **Humboldt Co.** Oric -- *7.XII.1935* (UC 629330); **Marin Co.** Audubon Canyon Ranch -- *8.XII.1984* C. Calhoun (SFSU); **Mendocino Co.** Jackson SF -- *11.XI.1961* H.D.Thiers 8814 (SFSU); *2.XII.1961* H.D.Thiers 9007 (SFSU);*13.XII.1966* H.D.Thiers 24510 (SFSU); *1.XII.1974* H.D.Thiers 33148 (SFSU); *24.XI.1979* H.D.Thiers 40469 (SFSU); *23.XI.1980* Sweet 480 (HSC 5943); *25.XI.1982* H.D.Thiers 45529; Jackson SF near Simpson Lane -- *2.XII.1961* Peters 730 (SFSU); *14.XI.1967* H.D.Thiers 21534 (NY); *11.XI.1969* H.D.Thiers 24208 (SFSU); Russian Gulch SP -- *30.XI.1991* H.D.Thiers 53908 (NY); Van Damme SP -- LLN 92.11.20-14, -16, -17 w S.A.Redhead; **Marin Co.** Bolinas Ridge Train -- *26.XI.1981* D.E.Desjardin 899 (SFSU); **San Mateo Co.** Huddart Park -- *23.XII.1964* W.Sundberg 195 (SFSU).

P. benzokauffmanii nom. prov.

WASHINGTON: Clallam Co. Olympic NP, Rugged Ridge Trail 124.2W,47.9N --; LLN 93.10.15-10$_{\textbf{ben5}}$; LLN 92.10.23-05$_{\textbf{ben4}}$,-06 w S.A.Redhead, G.L.Barron; **Grays Harbor Co.,** Sylvia Lake SP 123.6W,47N -- *XI.7.1964*, 2677 DLLargent 1066* (HSC as *P. kauffmanii*)); **Pierce Co.,** Mt Rainier NP, Ipsut Cr Trail 121.8W,47N -- LLN 93.09.24-01$_{\textbf{ben3}}$. **OREGON: Clackamas Co.,** Roger property outside Estacada,122.3W,45.2N -- LLN 92.10.17-1jr* coll J.Roger; Wildcat Mtn 122W 453N -- LLN 94.10.22-05* coll J.Roger; **Tillamook Co.** Cascade Head Experimental Forest -- LLN 94.11.06-02*; **CALIFORNIA: Mendocino Co.,** Jackson SF 123.6W,39.4N --*XII.6.1994*, H.D.Thiers 11863 (SFSU as *P. kauffmanii*)); *XII.4.1971*, H.E.Bigelow 16979 (NY as *P. kauffmanii*)); XII.12.1974, H.D.Thiers 33306 (NY as *P. kauffmanii*)); Jackson SF, 123.6W,39.4N, "Aleuria Glen", Hwy 409 1/2 m. W of 408 & 409 Jnctn. -- *XII.10.1988*, R.Zebell* (NY); Van Damme SP near Pygmy Forest 123.7W,39N -- LLN 92.11.20-01$_{\textbf{ben1}}$(HOLOTYPE),-04*,-05*,-06*,-07,-09, w S.A.Redhead & G.L.Barron; LLN 92.11.22-02 coll. T.Horton; LLN 92.11.22-03$_{\textbf{kau3}}$.

P. californica A. H. Smith 1957

CALIFORNIA: Del Norte Co.: Crescent City-- *X.23.1956* 00011607 A.H.Smith 55610*$_{\textbf{cal2}}$ (HOLTOTYPE), 55611*, 55612*$_{\textbf{cal14}}$,55613* (MICH); Jedediah Smith SP -- *XI.17.1961* B.Isaacs 1478*; **Shasta Co.:** Castle Crags SP -- *XI.23.1967* H.D.Thiers 21704* (SFSU); **OREGON: Benton Co.** Finley Wildlife Ref. -- *28.III.1983* C.Goetz 77*$_{\textbf{cal11}}$*pro parte* S.Morgan (MICH); McDonald Forrest -- LLN 95.11.17-13,14; Paul Dunn F -- LLN 95.11.17-24,26; **Josephine Co.:** Grants Pass -- *XI.17.1956* B.Isaacs 478*; Takilma *XII.7.1925* C.H.Kauffman 12/7/25* (MICH); **Lane Co.** Bunker Hill -- *X.12.1971* J.F.Ammirati 5881* (MICH); Cedar Creek -- *X.15.1937* 1343262 M.Doty* (F); Elmira -- *XI.1941* Sipe184*$_{\textbf{cal13}}$ (MICH); Siltcoos -- *XI.20.1982* K.Scates 6881*; **Tillamook Co.** Cape Meares *III.28.1983V.19.1982* C.Goetz 72* (MICH).

P. carmanahensis Redhead & Norvell 1993

See *P. oregonensis*.

P. christinae(Fr.) Heim 1931

CANADA: Quebec: Parc Laurentide, Rte Principal, close to exist for Dubergerre -- *15.VIII.1981* by S.A.Redhead (DAOM 180854); **FRANCE: Vosges:** St. Dié -- Bois d'Etival -- *5.IX.1965* R.L.Shaffer 4806 (MICH); **USA: WISCONSIN:** *23.IX.1993* R.G.Thorn 930923/03 (loan from collector)

P. deceptiva A. H. Smith & Trappe 1972

IDAHO: Bonner Co.: Priest Lake -- *X. 7.1968* A.H.Smith 77000 (HOLTOTYPE --MICH).

P.dissiliens A.H.Smith & Trappe 1972

OREGON: Benton Co. McDonald SF LLN 95.11.17-18; **Lane Co.** Bunker Hill N44.22• W122.8• -- *X.12.1971* J.F.Ammirati 5880* (MICH); **Lincoln Co.** Fogarty Creek SP -- LLN 95.11.06-2 N.S.Weber; LLN 95.11.09-1,8,16,18; LLN 96.11.02-3; **Tillamook Co.** Cape Lookout SP -- *XI.04.1970* A.H.Smith 79540*$_{dis2}$ (MICH); Cascade Head Exp.F N45.04• N123.92* -- *XI.1975* C.Goetz 18*,19*,20*,21*; Oswald West -- *XI.1975* C.Goetz , 18(7)*(as *P. radicata)*, 53*; Pacific City N45.20• W123.96• -- *XI.14.1972*A.H.Smith 83733* Sipe (MICH), *XI.15.1972* A.H.Smith 83820* (MICH), *XI.1975* C.Goetz 22*; Point Lookout SP -- *X.23.1970* A.H.Smith 79252*$_{dis3}$ (MICH 00011608 -- HOLOTYPE);

P. fallax A. H. Smith 1957

BRITISH COLUMBIA: Mainland: Mt. Seymour Watershed, Vancouver -- LLN 93.11.08-1 by S.Gamiet 31-110893-7; **Vancouver Island:** Upper Carmanah Valley -- 92.10.07-1**$_{fal2}$** w S.A.Redhead; **WASHINGTON: Clallam Co.:** near LaPush, along the Quillayute River -- *25.X.1935* A.H.Smith 3326 (MICH as *P. olivacea*); *26.X.1935* A.H.Smith 3342 (MICH)-*HOLOTYPE);* Olympic NF, Klahanie Cmpgrd. LLN 92.10.18-1 S.Trudell (#ST291-92-04) coll; Olympic N.P., Bogachiel River -- *X.1992* R.Petersen 6648 (TENN); Olympic N.P., Rugged Ridge Trail -- LLN 92.10.23-3 **$_{fal4}$**,-29,-30,-33 w G.L.Barron, E. Fox, S.A.Redhead;; **Jefferson Co.** Olympic NP, Queet's River Ranger Stn. -- LLN 92.10.17-2,-4,-5,-6,-7 S.A.Redhead; LLN 92.10.19-1,-**2**,-3 S.A.Redhead; Olympic NP, Twin Creek RNA -- LLN 92.10.15-3**fap10**, -8, -9, -11**fal1**, -20, -25, -27, -29, -30, -32, -34 w E.Fox & S.A.Redhead; LLN 92.10.17-8,-9,-12 w G.T.Norvell, O.L.Norvell, P. W. Trimm; Olympic NP, Hoh River Valley OG Transcect #10593, Ho Plot #16 LLN 93.10.27-1 by G.R.Walker & M.B.Puccio; **Snohomish Co.** Barlow Pass -- *9.IX.1989* M.Moser 89/451 w J.F.Ammirati (IB); LLN 92.10.16-2 J.F.Ammirati, coll.; *11.X.1993* M.T.Seidl 3787 byPSMS; **?IDAHO: Kootenai Co.** Coeur d'Alene, Elsie Coulter's woods -- *24.X.1974* A.H.Smith 83185**$_{fal11}$** (MICH); **OREGON: ?? Co.** Camp Clark *16.XI.1974* C.Goetz 1,2,3; **Benton Co.** McDonald Forest -- LLN 95.11.17-1,-20 w F.Camacho, T.Lebel, N.S.Weber; Paul Dunn Forest -- LLN 95.11.17-22 w F. Camacho, T. Lebel, N.S.Weber; **Clackamas Co.** Estacada -- LLN 91.12.30-3 w J.Roger; Mt. Hood NF, near Estacada 122° 16' W, 45°8'N -- J.Roger 92.10.1-2; Mt Hood NF, Wildcat Mtn -- LLN 95.10.14-3 by J.Roger; LLN 94.10.28-18; **Lincoln Co.** -- A.H.Smith 79353 by OMS (MICH); Cascade Head Experimental Forest -- *13.X.1970*, A.H.Smith 2294 (OSC 29,406); *26.X.70* A.H.Smith 79334 (MICH); *XI.1975* C.Goetz 9,13; LLN 93.11.04-7; Van Duzer Wayside SP -- LLN 92.11.10-7,-8,-9,-10,-11,-12**$_{fal7}$**, -14,-15,-16,-19,-20,-21 w G.L.Barron & S.A.Redhead; **Multnomah Co.** Mt. Hood N.F., Larch Mtn. summit -- LLN 91.11.27-2 by B.E.Lippert; LLN 92.11.04-3**x** by S.A.Redhead; LLN 93.11.05-14; LLN 94.10.11-5; Mt. Hood NF, Larch Mtn Road 5 miles from summit -- LLN 92.11.11-3,-7 w O.L.Norvell & P.W.Trimm; **Tillamook Co.** Cascade Head Exp. F. -- *12.X.70* A.H.Smith 78989 (MICH), (N FR 1861 W of Hwy 12) -- LLN 93.11.14-8**$_{fal6}$**; Neskowin Creek -- *21,X,70* A.H.Smith 79212 (MICH); Oswald West S.P. -- LLN 92.11.02-1**$_{fal\ 5}$**,-5,-6,-7,-13 w G.L.Barron & S.A.Redhead; LLN 93.10.23-4, -5 w G.T.Norvell; Pacific City -- *7.XI.1972*, A.H.Smith 83507**$_{III2}$** (MICH--as *P. lilacifolia*); *11-14.XI.72* A.H.Smith 83732 (MICH); **CALIFORNIA: Del Norte Co.** Crescent City -- *23..XI.1956* A.H.Smith 55627 (MICH) **Humboldt Co.**-- *22.XI.1986* OKMiller 22796 w Wiedler & Largent (VTMH - 1592); Arcata, College of the Redwoods, T 3N, R 1W, S4/5-- *16,XI.1972* Baroni 773; Freshwater Forest, College Forestry -- *25.XI.1972* T.Baroni 924 (HSC 2670); Humboldt Redwood SP, Davidson Rd. -- *28.XI.1991* H.D.Thiers 53886 (SFSU); LLN 92.11.07-3**$_{fal8}$** by G.L.Barron, -4 by T.R.Horton, -7**$_{fap5}$**,-8,-9,-10,-11,-12,-13 w G.L.Barron & S.A.Redhead; LLN 92.11.14-1 by G.L.Barron; Humboldt Redwood SP, Skunk Cabbage Trail -- LLN 92.11.07-6 by F.Garzas; Murray Rd near McKinleyville -- *7.XI.1986* H.Saylor 3708 (SFSU); Patrick's Point SP -- *9.XI.1957* C.A. White (MICH); *20.XI.1957* C.A.White 356 (MICH), *31.X.1986* (20 yd W Indian Rock) D.DeShazu 244 (HSC 10137); Trinidad -- *27.XI.1935*

P. fallax (concluded)

A.H.Smith 3634 (MICH); *3..XII.1956* A.H.Smith 56193 (MICH); *4..XII.1956* A.H.Smith 56283 (MICH); *7..XII.1956* A.H.Smith 56404 (MICH); *11.XII.1956* A.H.Smith 56570 (MICH); **Marin Co.** Audubon Canyon Ranch, gulch above Volunteer Canyon -- *8.XI1.1984* C.Calhoun 84-3927 (SFSU); **Mendocino Co.** Jackson SF -- *2.XII.1961* H.D.Thiers 9006 (SFSU); *9.XII.1961* H.D.Thiers 9051 (SFSU)); *6.XII.1964* J.F.Ammirati *s. n.* (SFSU as *P. olivacea); 20.XII.1966* H.D.Thiers 18108 (SFSU as *P. olivacea); 8.I.1967* H.D.Thiers 18418 (SFSU as *P. olivacrea); 16.I.1967* H.D.Thiers (SFSU as *P. olivacea); 9.XII.1967* H.D.Thiers 21405 (SFSU); *6.XII.1969* H.D.Thiers 24412 *pro parte* (SFSU as *P. olivacea); .XII.1979* H.D.Thiers 40602 (SFSU--as *P. festiva*); *2.XII.1979* JCurlin 378 (SFSU--as *P. festiva*); *11-22.XI.1980* DLLargent 5941 (HSC 5941); Jackson SF, Hwy 409 *13.XII.1990* D.E.Desjardin 5031 *pro parte* (SFSU as *P. olivacea);* Jackson SF, 'Aleuria Glen' -- LLN 92.11.24-11 w G.L.Barron; Jackson SF, 'Mushroom Corners' -- *2.XII.1979,* R.Ower *s.n.* (SFSU--as *P. festiva*); *25.X.1986,* HSaylor 3594 (SFSU--as *P. festiva*); Mendocino -- *18.XI.1989* Mycology class (UC 1575403 as *P. festiva*); LLN 92.11.16-7; LLN 92.11.17-6; LLN 92.11.18-2 by G.L.Barron; Van Damme SP, Fern Canyon Trail -- LLN 92.11.23-2$_{fal9}$,-3,-7, -10,-12,-16 w S.A.Redhead; Van Damme SP, Pygmy Forest -- LLN 92.11.20-15 w S.A.Redhead; **Santa Cruz Co.** Boulder Creek -- *6.XII.1970* H.D. Thiers 26973 *pro parte* (SFSU as *P. olivacea).*

'Wildcat' variant **OREGON: Clackamas Co** Mt. Hood NF, Wildcat Mtn. -- LLN 94.10.22-6 by J.Roger; LLN 94.10.28-4 ,-5, 8,-17; LLN 95.10.18--12, -23;

Questionable (immature) **OREGON: Benton Co.** Mary's Peak Summit -- *22.IX.1976* 4712 JTrappe (OSC 36,152); **Clackamas Co.** Mt. Hood NF, Wildcat Mtn. -- LLN 95.10.18-30; **Tillamook Co.** Cascade Head ExpF (at Lincoln Co line(-- *1.XI.1971* J.F.Ammirati 6063 (MICH); Oswald West S.P. -- LLN 92.11.02-12 w G.L.Barron & S.A.Redhead.

P. festiva (Fries) Heim

NORWAY: Oppland: Lunner: Öståsen, Bredehaugen -- *3.IX.1981* G. Gulden 771/81 (O).

P. gregaria A. H. Smith & Trappe 1972

OREGON: Benton Co.; Lincoln Co. ; Tillamook Co. Cascade Head Experimental Forest -- *X.16.1970* AH Smith 79075*$_{gre1}$ (MICH 00011626 -- HOLOTYPE), AH Smith 79087* $_{gre3}$, (MICH), LLN -5$_{unk2}$, 10*.

P. kauffmanii (A. H. Smith) Singer 1940

BRITISH COLUMBIA: Vancouver Isl. *X.7.1995*, P.Kroeger 1795 coll.L.Poapst (UBC); Lower Carmanah Valley -- LLN 93.10.30-23, coll. S.Berch&H.Massicott; Port Renfrew -- *X.7.1995*, P.Kroeger 1798 (UBC), P.Kroeger 1794, coll. R.Outerbridge (UBC); Upper Carmanah Valley -- LLN 93.10.30-26. **WASHINGTON: Clallam Co.** La Push 124.6W,47.7N -- 93.10.15-04*, coll PKroeger, BMcAdoo; La Push, 3rd Beach 124.6W,48.4N -- 10-15-92, R.J.Petersen 6647* (TENN); Olympic NP, Rugged Ridge Trail 124.2W,47.9N -- LLN 92.10.23-01$_{ben2}$,-09$_{kau6}$; LLN 93.10.11-03; **Grays Harbor Co.** 5 mi E Copalis 124.1W,47.1N -- *X.23.1969*, J.W.Lennox 440*; *X.25.1971*, J.F.Ammirati 8436; McCleary 123.3W,47.1N -- *XI.1970*, F.V.D.Bogart 672*; Sylvia Lake SP 123.6W,47N -- *X.28.1967*, 2676* DLLargent 3290 (HSC); Olympic NP, Lake Quinault, Colonel Bob's Trail 123.9N,47.5N -- 94.10.02-01, W.Steglich; **Jefferson Co.** Olympic NP, Hoh Valley 123.7W,47.9N -- *X.7.1935*, A.H.Smith 3024* (MICH); Olympic NP, Hoh Valley Twin Creek RNA 124.0W 47.9 N -- LLN 92.10.15-23; LLN 92.10.17-20; **Pierce Co.** 5 mi E of Grayland, 46.8N,124.1W -- *X.19.1969*, D.E.Stuntz 15651* by PSMS; Mt. Rainier NP, Carbon R. 121.9W,47N -- *X.6.1952*, A.H.Smith 40667* (MICH); **Snohomish Co.** Baker-Snoqualmie NF, Barlow Pass 121.4W 48.0N -- LLN 92.09.13-01,-03,-05 by G.R.Walker; LLN 92.09.13-04,-07 by PSMS member; LLN 92.09.21-01$_{bar1}$,-02,-03,-05,-06,-08; LLN 92.10.16-01,-03* by J.F.Ammirati; LLN 93.10.25-01 by PSMS crew; LLN 94.09.28-01 by W.Steglich;

P. kauffmanii (concluded)

IX.7.1992, J.F.Ammirati 10698, 10699 & 10696$_{bar12}$; *X.5.1992*, J.F.Ammirati 10781* coll. PSMS members; **Thurston Co.** Capitol Forest, Fall Creek -- *20.X.1995*, LLN 96.12.03-8 by R.W.Gaines; **Whatcom Co.,** Silver Fir Camp 121.7W,48.9N -- *XI.8.1987*, J.F.Ammirati 9662*. **IDAHO:** X.1966, R.H.Petersen T23245 (TENN). **OREGON: Benton Co.** Camp Tapawingo -- LLN 96.10.28-2 by OMS Foray; Mary's Peak, Chintimini Cr.123.5W,44.53N -- *X.6.1982*, 48,621, M.Castellano 7000* (OSU); **Clackamas Co.**-- Wildcat Mtn 122IW 453 N -- LLN 94.10.28-02*-11 w J.Roger; LLN 95.10.14-06 J.Roger; LLN 95.10.18-15,-17,-20,-22,-24 w J.Roger; **Coos Co.,** Winchester Forest 122.1W,42.8N -- *X.30.1989*, C.Ardrey 1494*; **Curry Co.,** Siskiyou NF 123.9W,42.1N -- *XI.6.1937*, A.H.Smith 8480* (MICH); **Douglas Co.,** Lake Tahkenitch 124.2NW,43.8N -- *XI.18.1935*, A.H.Smith 3523* (MICH-Holotype); **Lincoln Co,** near Otis, Van Duzer Corr 123.9W,45N -- *X.2.1970*, A.H.Smith 78766* (MICH); **Multnomah Co.** Larch Mtn summit 122IW455N -- LLN 91.11.27-1a by PSU students; LLN 93.10.24-01,-02,-04,-07,-09$_{lut5}$,&-15 w G.T.Norvell; LLN 94.10.11-04,-06,-07b,-09,-13,-20a,&-23; **Tillamook Co.** Cascade Head Experimental Forest FR 1861 123I W 45IN -- *X.27.1979*, C.Goetz 47*; LLN 93.11.14-01$_{kau2}$,-04* w G.T.Norvell; LLN 94.11.06-20*,-22; LLN 95.11.06-04; LLN 95.11.09-21,-28; Oswald West SP 124W,45.8N -- C.Ardrey 864*. **CALIFORNIA: Del Norte Co.** Crescent City 124.2W,41.4N -- *XI.23.1956*, A.H.Smith 55616 (MICH); Jedediah, Smith SP, Stout Grove 124.1W,41.8N -- *X.28.1971*, H.D.Thiers 28457* (SFSU); *X.25.1975*, 4741, unk. coll. #13* (HSC); **Humboldt Co.** Prairie Creek Redwood SP, 124W,41.4N; Murray Rd -- *X.26.1977*, 5866, D.L.Largent 7557 (HSC); *XI.13.1985*, 11140, R.Watson 46, (HSC); **Mendocino Co.,** Jackson SF 123.6W,39.4N -- *XI.19.1960*, H.D.Thiers 8322* (SFSU); *XI.25.1960*, H.D.Thiers 8476* (SFSU); *XI.4.1961*, J.Motta 111* (NY); *XI.17.1962*, H.D.Thiers 9885 (NY); *XI.5.1967*, H.D.Thiers 21399* (SFSU); *XI.14.1967*, H.D.Thiers 21640* (SFSU); *XII.6.1969*. H.D.Thiers 24411* (SFSU); *XII.19.1969*, H.D.Thiers 14637* (SFSU); *X.31.1972*, H.D.Thiers 30398* (SFSU);; *XI.5.1972*, H.D.Thiers 30479* (SFSU); *X.29.1977*, H.D.Thiers 38396* (SFSU); *XII.2.1979*, H.D.Thiers 40586* (SFSU); *X.25.1986*, K.S.Giles (NY); *XI.19.1988*, 5697216*Myc class (UC); *XII.13.1990*, D.E.Desjardin 5029 (SFSU); LLN 92.11.21-07,-10, coll. K,Shanks, -09, coll. USC/SFSU students, LLN 92.11.22-6 w SA Redhead; Jackson SF, 123.6W,39.4N, "Aleuria Glen", Hwy 409 1/2 m. W of 408 & 409 Jnctn. -- *XII.10.1988*, Zebell* (NY); LLN 92.11.24-12$_{kau1}$ by S.A.Redhead & G.L.Barron, -13*, -14* coll. R.E.Halling,H.D.Thiers, -15* w R.E.Halling, -16* w G.L.Barron,& -18* w R.E.Halling, H.D.Thiers; LLN 95.11.22-01 w G.T.Norvell; Jackson SF, 123.6W,39.4N, Little Lake Road -- *XI.19.1988*, 1569721 by Myc class (UC); *XI.18.1989*, 1572416 by Myc class (UC); Jackson SF, "Mushroom Corners", Hwy 408 & 409 Jnctn. 123.7W,39.3N -- *XI.11.1965*, W.Sundberg 400* (SFSU); *XI.20.1965*, G.Breckon 279 (SFSU); *X.25.1986*,1572625 M.T.Seidl 2106 (UC); *IX.19.1988*, Ingmire 11-1988*, Kelly 75* (NY); 92.11.21-08 by USC/SFSU students; 95.11.23-01 w G.T.Norvell; Russian Gulch SP 123.8W,39.4N -- *XI.30.1991*, R.E.Halling 6763* (NY); **Shasta Co.** Castella -- LLN 96.11.29-4a by J.F.Ammirati; **Sonoma Co.** Camp Meeker 123OW 38 4N -- *I.13.1968*, 2672 D.L.Largent 3589* (HSC).

EXTRALIMITAL (QUESTIONABLE): VERMONT: Lamoille Co, Bingham Falls -- *VIII.20.1964*, H.E.Bigelow 13570 (NY);

EXCLUDED: UNITED STATES: **TENNESSEE:**Great Smoky NP, Hesler 17217 (TENN); MEXICO: Popocatepetl *VII.19.1962*, G.Guzman 3118 (BPI).

P. lilacifolia A. H. Smith 1957

WASHINGTON: Pierce Co. Carbon River area, Mt Rainier NP -- *16.IX.1952* A.H.Smith 39976$_{lll1}$ (MICH 00011625 -- *HOLOTYPE*); **OREGON: Tillamook Co.** Cascade Head Exp. F. -- *16.X.1970* A.H.Smith 79082 (MICH), *20.X.1970* A.H.Smith 79182 (MICH), *25.X.1970* A.H.Smith 79298 (MICH-); **CALIFORNIA: Humboldt Co.** Prairie Creek St P -- *23.XI.1937* A.H.Smith 9012$_{lll4}$ (MICH);

P. lilacifolia (concluded)

Possibly also **OREGON: Clackamas Co.** Estacada -- Mt. Hood NF, Wildcat Mtn -- LLN 94.10.22-4$_{lll9}$; **Multnomah Co.** Mt. Hood N.F., Larch Mtn. summit -- *25.X.1954* A.H.Smith 49470$_{lll3}$ (MICH);

P. luteosquamulosa nom. prov.

WASHINGTON: Snohomish Co. Barlow Pass 121.4 W 48.0 N-*IX.7.1992*, J.F.Ammirati 10700$_{lut8}$; S.A.Trudell 250-92-04$_{lut10}$. **OREGON: Multnomah Co.** Larch Mtn summit 122.1W 45.5 N -- LLN 93.10.24-06$_{lut4}$,-08,-10a$_{lut2}$ w G.T.Norvell; LLN 93.11.05-09$_{lut6}$ w S.A.Redhead; LLN 94.09.07-01; LLN 94.10.06-03,-07&-11$_{lut7}$; LLN 94.10.11-01,-03,-11,-14,-18$_{lut9}$,-19,-20b&-21. **CALIFORNIA: Del Norte Co.,** Jedediah Smith SP, Stout Grove ,124.1W,41.8N -- *XII.5.1937*, A.H.Smith 9426 *pro parte* (MICH as *P. kauffmanii*); **Mendocino Co.,** Jackson SF 123.6W,39.4N -- *XI.23.1962* H.D.Thiers 9484 (SFSU as *P. kauffmanii*)); *XII.20.1962*, 272579* H.D.Thiers 9817 (UC as *P. kauffmanii*)); Jackson SF, 123.6W.39.4N, "Aleuria Glen", Hwy 409 1/2 m. W of 408 & 409 Jnctn. -- LLN 92.11.24-1$_{lut1}$ coll. R.Halling & H.D.Thiers; *XI.25.1992* S.A.Redhead 7481$_{lut3}$ *(Holotype)* w G.L.Barron.

EXCLUDED: CALIFORNIA: Del Norte Co., Jedediah Smith SP, Stout Grove ,124.1W,41.8N -- *X.28.1971*, J.F.Ammirati 6018 coll. J.Trappe (MICH).

P. neosimilis Singer, 1986.

MEXICO: Dist. Federal: Between San Pedro Nexapa & Paso de Cortés -- *24.VII.1971*, R. Singer M-1586 (MICH -- *Holotype* of *P. attenuata ssp. mexicana* 00011606).

P. oligoporpa Singer 1987

COLOMBIA: Dept. Nariño: Municipio Pasto 11 km E of Chachagüí, "Bosque el Común" *XI.22.1988* R.E. Halling 6137 with E. Horak (NY); **Dept. Antioquia:** Municipio Guarne, Centro. Exp. Piedras Blancas, 14 E Medellin *XI.28.1988* R.E. Halling 6165 with E. Horak (NY); **COSTA RICA: Cartago:** Chonta, KM 55, Route 1: -- *VII.11.1982* #1052230 coll. Gomez 18196 [HOLOTYPE - F].

P. olivacea A. H. Smith 1957

OREGON: Benton Co. BLM property R13S, R6W S33NWNW -- LLN 96.11.22-4 by R.Exeter; Corvallis -- *5.XI.1970* AH.Smith 79588 (MICH); McDonald Forest -- LLN 95.11.17-2,-3,-6,-8 w F.Camacho, T.Lebel, N.S.Weber; Paul Dunn Forest -- *30.X.1985* W.Denison (OSC 45974 as *P. fallax*), LLN 95.11.17-23,-25 w F.Camacho; **Clackamas Co.** Estacada, Roger property on Horner Rd -- LLN 91.12.30-1$_{oli6}$,-2 w J.Roger; J.Roger 92.10.21-3jr; LLN 94.11.28-1$_{oli8}$ by J. Roger; **Josephine Co.** Grant's Pass -- *17.XI.1956* A.H.Smith 55767 (MICH *Holotype* #00011627); *18.XI.1956* A.H. Smith 55827 (MICH); *19.XI.1956* A.H.Smith 55855 (MICH); *20.XI.1956* A.H.Smith 55890 (MICH), A.H.Smith 55898 *pro parte* (MICH as *P. pseudofestiva);* **Tillamook Co.** Cascade Head Exp. For. -- *XI.1975* C. Goetz 8, C.Goetz 14; C.Goetz 15; CX.Goetz 16; Pacific City -- *XI.1975* C. Goetz 17. **CALIFORNIA: Del Norte Co.** Crescent City -- *23.XI.1956* A.H.Smith 55614 (MICH); **Humboldt Co.** N.fork Mad River -- *9.XII.1935* A.H.Smith 3901 (MICH); Klamath Mountains, 3 mi. on Haypress Road -- *7.XI.1972* C.McLauchlin 465 (HSC 7734); Redwood NP, Davison Rd -- LLN 92.11.07-7B w S.A.Redhead; **Marin Co.** Audubon Canyon Ranch, gulch above Volunteer Canyon -- *25.XI.1984* Calhoun 84-3856 *pro parte* (SFSU), *8.XII.1984* C.Calhoun 84-3928 *pro parte* (SFSU); 9.6 mi E Fairfax on Bolinas Rd -- *26.XI.1981* D.E.Desjardin 898 (SFSU); **Mendocino Co.** Jackson SF near Mendocino -- *12.XI.1960* H.D.Thiers 8231 (UC 272538); *23.XI.1962* H.D.Thiers 9502 (SFSU); *20.XII.1962* H.D.Thiers 9818 (SFSU); *19.XII.1965* H.D.Thiers 14639 (SFSU); *14.XI.1967* H.D.Thiers 21655 (SFSU); *9.XII.1967* D.L.Laregent 3454 (HSC 2679);

P. olivacea (concluded)

8.XI.1969 H.D.Thiers 24182 (SFSU); *11.XI.1969* H.D.Thiers 24259 (SFSU); *27.XI.1972* M.Concannon 296 (DAOM 215233); *12.XII.1974* R.Halling 261 (DAOM 180698); *30.X.1977* H.D.Thiers 38391 (SFSU); *9.XI.1988* UC 1569695 by Mycology Class (UC); Jackson SF, Hwy 408 2 mi E of Hwy 500 -- LLN 92.11.22-4oli12; Jackson SF, 'Aleuria Glen' -- Hwy 409 -- *6.XII.1967* D.Ripley 913 (SFSU); *13.XII.1990* D.E.Desjardin 5031 *pro parte* (SFSU); LLN 92.11.16-8; LLN 92.11.24-17 by R.E.Halling, -19, 20 w R.E.Halling, -21, -22, -23, -25oli5 & 26 w R.E.Halling, H.D.Thiers; Jackson SF, 'Mushroom Corners; Intersctn Hwys 408 & 409 -- *11.XI.1965* W.H.Sundberg (SFSU); *20.XI.1965* G.Breckon 280 (SFSU); LLN 92.11.16-4oli3 w G.L.Barron, S.A.Redhead, LLN 92.11.17-5, -7 w S.A.Redhead; Van Damme SP -- *23.XI.1985* M.T.Seidl 717; Van Damme SP, lower Pygmy Forest -- LLN 92.11.20-10 w S.A.Redhead; LLN 92.11.20-11,-12oli11 w S.A.Redhead; Van Damme SP, Fern Canyon Trail -- LLN 92.11.23-4,-9,-13,-14 &-5 w S.A.Redhead; **San Mateo Co.** Huddart Roadside Park -- *4.XII.1963* H.D.Thiers 10990 (SFSU); *23.XII.1964* W.J.Sundberg 189 (SFSU); **Santa Cruz Co.** Big Basin, HWY 236 -- *6.XII.1975* R.E.Halling 1187 (SFSU); Boulder Creek -- *6.XII.1970* H.D.Thiers 26973 *pro parte* (SFSU); *30.XII.1970* H.D.Thiers 27062 (SFSU); **Shasta Co.** Castella, Ammirati property -- LLN 96.11.29-6& -7 by J.F.Ammirati; Castle Crags SP -- *17.XI.1967* H.D.Thiers 21603 (SFSU); *23.XI.1967* H.D.Thiers 21706 (SFSU); *24.XI.1967* H.D.Thiers 21713 (SFSU); **Sonoma Co.** Kruze Rhododendron St. Reserve -- *24.XI.1985* H.Saylor 4004 (SFSU); **Yuba Co.** Bullard's Bar Rec Area -- *27.XI.1981* H.D.Thiers 44092.

P. oregonensis A. H. Smith & Trappe 1972

BRITISH COLUMBIA: Mt. Seymour Seymour Watershed -- *X.13.1993* S.Gamiet 53-101393 (LLN # 93.10.13-1_{ore2}); **Vancouver Isl.** Upper Carmanah Valley -- *X.24.1991* DAOM 215607 SA Redhead & LL Norvell (HOLOTYPE of *P. carmanahensis*, ISOTYPE LLN 93.10.24-3_{car1} at WTU); **OREGON: Clackamas Co.** Mt. Hood NF, Wildcat Mtn, T22IW R453N -- LLN 94.10.22-3^{*}_{ore6} S Spencer; LLN 94.10.28-6^{*}_{ore7},13* w J Roger; LLN 95.10.14-1, 2a,2b J Roger; LLN 95.10.18-4, 6, 7, 9, 13; **Multnomah Co.** Mt. Hood NF, Larch Mtn, T22IW R55N -- *X.30.1947* AH Smith 28420^{*}_{ore3} w WB Gruber (HOLOTYPE 00011628 -- MICH), LLN 92.11.04-1^{*}_{ore5}, 6^{*}_{ore8}, 7_{ore4}, 19^{*}_{ore1} w GT Norvell, SA Redhead & PW Trimm.

P. phaeogaleroides nom. prov.

BRITISH COLUMBIA: Vancouver Isl. Plot U.K. Fd 98-8 *21.VII.1997* R. Outerbridge 109; Plot #2 *20.X.1997* R.Outerbridge 298 w S.A.Redhead; **OREGON: Lane Co.** 15 mi N Florence -- *20.XI.1980* G.Wright 21-3 (MICH); **Lincoln Co.** Drift Creek -- LLN 95.11.06-1 by N.S.Weber (HOLOTYPE).

P. piceae A. H. Smith & Trappe 1972

BRITISH COLUMBIA: Vancouver Isl. Lower Carmanah Vall. -- LLN 92.10.09-2, -3, $-7_{pic\ 1}$, 8, 9, 10, $11_{pic\ 3}$, 12, 14, 15, 16, 17, 22, 24, 30 w GL Barron, EFox, SA Redhead; **WASHINGTON: Clallam Co.** La Push -- LLN 93.10.06-$2^{*}_{pic\ 8}$ G.Lundren, LLN 93.10.15-6* -8* by P Kroeger; Rugged Ridge -- LLN 92.10.23-$27^{*}_{pic\ 4}$ w GL Barron, EFox, SA Redhead; **Jefferson Co.** Olympic NP, Hoh Valley, Twin Creek DNR -- LLN 92.10.15-14^{*}_{pic7},w GL Barron, EFox, SA Redhead, 18* by C McClenaghan; **OREGON:** Unknown locality -- *XI.25.1974* C Goetz 6 by OMS member; **Clackamas Co.**, Mt Hood NF, Wildcat Mtn -- LLN 94.10.22-$7_{pic\ 9}$; Mt Hood NF, Unknown locality -- *X.1981* CGoetz 82; **Lane Co.** Bunker Hill -- *X.12.1971* JF Ammirati 5879* (MICH); **Lincoln Co.** Unknown locality -- *X.27.1979* C Goetz 72; **Tillamook Co.** Cascade Head Experimental Forest -- *X.16.1970* AH Smith 79085*pic 2 (MICH 00011629-- HOLOTYPE), LLN 94.11.06-$1_{pic\ 10}$ w GT Norvell; Oswald West SP -- LLN 91.11.23-4 w GT Norvell, LLN 92.11.02-$9^{*}_{pic\ 5}$, 11* w GL Barron, SA Redhead, LLN 93.10.23-2* w GT Norvell, LLN 94.11.10-2 & 3a MSeidl; **CALIFORNIA: Humboldt Co.** Trinidad -- *XI.12.1937* -- AH Smith 8671* (MICH as *P. californica*); **Mendocino Co.** Jackson SF -- LLN92.11.22-$5^{*}_{pic\ 6}$, 7* w SA Redhead;

P. pleurocystidiata nom. prov.

WASHINGTON: Clallam Co. Olympic NP, Bogachiel R. trail -- LLN 94.03.30-1 (HOLOTYPE), 2**ple1** w S.A.Redhead; Olympic NF, Bogachiel R. trail -- LLN 94.03.30-3 w S.A.Redhead; **OREGON: Benton Co.** Finley Wildlife Refuge (10 mi. S Corvallis) -- *28.III.1983* C.Goetz 77 *pro parte* by S.Morgan (MICH as *P. californica);* **Linn Co.**7 mi E Sweet Home along S. Santiam R-- LLN 93.05.16-1**ple2** by L. & M. Bailey; **Tillamook Co.** Cape Meares -- *13.V.1982* C. Goetz 74 (as *P. jennyae)*; **CALIFORNIA: Mendocino Co.** Jackson SF -- *20.I.1965* H.D.Thiers 1211**ple4** (DAOM 128270); **San Mateo Co.** Wunderlich Park, Skyline trail -- *III.06.1986* M.T. Seidl 914**ple3** (SFSU as *P. attenuata*).

P. pseudofestiva A. H. Smith 1957

BRITISH COLUMBIA: Lower Carmanah Valley -- LLN 92.10.07-6$_{\mathbf{psB2}}$ w S.A.Redhead; Upper Carmanah Valley -- LLN 92.10.09-1$_{\mathbf{pse3}}$ by S.A.Redhead (WTU & DAOM); **WASHINGTON: Clallam Co.**Olympic NP, Rugged Ridge Trail 124.2W,47.9N -- LLN 92.10.23-28 &-32 w E.Fox; LLN 92.10.21-6,-12$_{\mathbf{psB4}}$; **Grays Harbor Co.** Sylvia Lake SP 123.6W,47N -- *21.X.1966* D.L.Largenyt 1886 (HSC 2687); **Jefferson Co.** Kalaloch -- 29.VII.1939 A.H.Smith 12097 (MICH as *P. olivacea);* Olympic NP, Queet's River Ranger Stn -- LLN 92.10.17-3 by S.A.Redhead; **OREGON: Josephine Co.** Grant's Pass -- *17.XI.1956* A.H.Smith 55768 (MICH); *20.XI.1956* A.H.Smith 55898 *pro parte* (MICH); **Lincoln Co.** Van Duzer Wayside -- LLN 92.11.10-17 w G.L.Barron; **Multnomah Co.** Mt. Hood NF, Larch Mtn, Summit -- LLN 92.11.04-10 w G.T.Norvell, S.A.Redhead, P.W.Trimm; Mt Hood NF, Wildcat Mtn. -- LLN 95.10.18-11; **Tillamook Co.** Cascade Head Exp.F. -- *17.XI.1970* A. H. Smith (MICH); Oswald West SP -- LLN 91.11.23-2$_{\mathbf{psAB8}}$,-3 w G.T.Norvell; **CALIFORNIA: Del Norte Co.** Crescent City -- *31.X.1937* A.H.Smith 8272 (MICH -- *Holotype* 00011632); **Humboldt Co.** Trinidad -- *6.XII.1935* A.H. Smith 3840 (MICH as *P. olivacea)*; *6.XII.1956* A.H.Smsith 56383 (MICH); **Marin Co.** Audubon Canyon Ranch, gulch above Volunteer Canyon -- *8.XII.1984* C.Calhoun 84-3928 *pro parte* (SFSU as *P. olivacea*); **Mendocino Co.** 5 mi S of Camp Wailaki -- *7.XII.1969* D.L.Largent 4255 (HSC); Jackson SF near Mendocino -- *19.XI.1960* Peters 142 (SFSU as *P. olivacea); 7.XII.1963* H.D.Thiers 11050 (DAOM 12878); *6.XII.1964* Ammirati *s.n. pro parte* (SFSU as *P. olivacea); 11.XI.1969* H.D.Thiers 24274 (SFSU as *P. fallax); 6.XII.1969* H.D.Thiers 24412 *pro parte (*SFSU as *P. olivacea*); Jackson SF, Mushroom Corners, Intersection Hwys 408 & 409 -- LLN 92.11.16-2$_{\mathbf{psA1}}$ by G.L.Barron; Van Damme SP, Fern Canryon Trail turn-around -- LLN 92.11.21-1 $_{\mathbf{psA6}}$ & -2a by S.A.Redhead; LLN 92.11.23-5,-8$_{\mathbf{psA11}}$ w S.A.Redhead; **Santa Cruz Co.** Big Basin SP *26.XII.1969* H.D.Thiers 24573 (SFSU); Felton -- *19.I.1967* H.D.Thiers 18544 by J.F.Ammirati (SFSU as *P. olivacea).*

P. radicata (Murrill) Singer 1940

OREGON: Benton Co.: Glen Brook -- *XI.07.1911*W.A. Murrill 775 (HOLTOTYPE as *Naucoria* --NY). **CALIFORNIA: Humboldt Co.** Prairie Creek State Park -- *23.XI.1937* A. H. Smith 9026 (MICH), *20.XI.1965* H.D.Thiers 14421 (SFSU); Oric -- *3..XII.1935* A.H.Smith 3746 (MICH), *4..XII.1935* A.H.Smith 3763 (MICH), *5.XII.1935* A.H.Smith 3788 (MICH), *7.XII.1935* A. H. Smith 3875 (MICH).

P. redheadii nom. prov.

BRITISH COLUMBIA: Lower Carmanah Valley -- LLN 92.10.09-20 w S.A.Redhead; Port Renfrew -- *X.7.1995*, P.Kroeger 1797, *s.n.* (UBC); Upper Carmanah Valley -- LLN 91.10.24-01,-02$_{\mathbf{cry1}}$ S.A.Redhead w LLN (HOLOTYPE); LLN 92.10.07-04,-05; LLN 92.10.07-08 by G.L.Barron. LLN 93.09.30-01,-05,-06; **WASHINGTON: Clallam Co.** LLN 93.10.08-03 coll G.Lungren; Cape Flattery 124.4W,48.4N -- *IX.18.1935*, A.H.Smith 2495* (MICH -- paratype of *P. kauffmanii*); near Moro LLN 93.10.11-01 coll. C.Leuthy*; Olympic NP, Rugged Ridge Trail 124.2W,47.9N -- LLN 92.10.23-34*; Olympic NP, Sol Duc Valley, Lover's Lane 123.9W,48N *X.19.1991*, S. Gamiet OP 0519-91 (UBC as *P. kauffmanii*); **Grays Harbor Co.** Copalis Crossing 124.1W,47.1N -- *X.27.1976*, K.Scates 4189*; *XI.16.1979*, K.Scates 5689b*; Olympic NP, Lake Quinault 123.9N,47.5N -- *X.11.1925*, C.H.Kauffman* (MICH -- paratype of *P.*

P. redheadii (concluded)

kauffmanii); Sylvia Lake SP 123.6W,47N -- *X.21.1966*, 2674 D.L.Largent 1876 (HSC); **Jefferson Co.** Olympic NP, Hoh River Road 124W,47.9N -- *X.7.1981*, J.Trappe 6443* (OSU as *P. kauffmanii*); Olympic NP, Hoh Valley 123.7W,47.9N --LLN 93.09.30-02 G.R.Walker; Olympic NP, Twin Creek RNA 1240 W 479 N -- LLN 92.10.17-21*$_{kau4}$; LLN 93.10.12-02* w S.A.Redhead,P.Krueger; LLN 93.10.15-03 T.Volk; **Mason Co,** Shafer SP 123.46W, 47.1N -- *X.29.1967*, D.E.Stuntz 14417* PSMS member as *P. kauffmanii*; **Snohomish Co.** Baker-Snoqualmie NF, Barlow Pass 1214 W 480 N -- LLN 92.09.13-02 PSMS member; LLN 92.09.21-04*$_{cry2}$,07*$_{oli2}$; LLN 95.09.22-02 J.F.Ammirati. **Thurston Co.** Capitol Forest near Fall Creek Cmpgrnd -- *20.X.1995* LLN 96.12.03-5 by R.V.Gaines; *2.XI.1995* LLN 96.12.03-10,11,12 by R.V.Gaines; **OREGON: Benton Co.,** Mary's Peak 123.6W,44.5N -- *IX.29.1966*, J.M.Trappe 934* (BPI,NY, OSU as 41245, SFSU all as *P. kauffmanii*); **Clackamas Co.,** Wildcat Mtn 122IW 453 N --- LLN 95.10.18-18 w J.Roger; **Lincoln Co,** Cascade Head Experimental Forest 123.9W,45N -- *X.14.1970*, A.H.Smith 2360* (OSU as *P. kauffmanii*); **Multnomah Co.** Larch Mtn summit 122IW455N -- *X.25.1954*, A.H.Smith 49479 (MICH as *P. kauffmanii*); LLN 92.11.04-13,-16,-17,-18,-20*,-23*,-24*&-25 w G.T.Norvell, S.A.Redhead & P.W.Trimm; LLN 93.10.24-03*$_{kau5}$,-12,-13,-14&-16 w G.T.Norvell; LLN 93.11.05-01,-03,-05,-06,-07,-08,-10,-11,-12,-13 w S.A.Redhead; LLN 93.11.13-01,-04,-05,-06,-07&-08 w O.L.Norvell; LLN 94.10.06-02a,-05,-10&-12; LLN 94.10.11-02*,-10,-15,-16,-17&-22; **Tillamook Co.** Cascade Head Experimental Forest FR 1861 1239 W 450N -- *X.12.1970*, A.H.Smith 78988 (MICH as *P. kauffmanii*); *X.15.1970*, A.H.Smith 79056 (MICH as *P. kauffmanii*); *X.23.1970*, K.Scates 1127* as *P. kauffmanii*; *X.6.1971*, J.F.Ammirati 10-06-71*(MICH); *X.7.1971*, J.F.Ammiratii 5828*,5829* (MICH); *XI.1975*, C.Goetz 17*; *X.28.1986*, 42,447 J.Trappe 9022* (OSU as *P. kauffmanii*); LLN 94.10.09-01 w G.T.Norvell; LLN 94.11.06-03*,-19*,-21*&-22b; LLN 94.11.10-04 coll MSeidl; LLN 95.11.09-26; LLN 96.11.02-5; **CALIFORNIA: Del Norte Co.** Jedediah Smith SP, Stout Grove ,124.1W,41.8N -- *X.5.1937*, A.H.Smith 9426* *pro parte* (MICH as *P. kauffmanii*)); *X.18.1969*, 2878 D.L.Largent 4052* (HSC as *P. kauffmanii*); **Humboldt Co.** Eureka, N fork Mad R 124W,40N -- *XII.9.1935*A.H.Smith 3888* (MICH-paratype of *P. kauffmanii;* split with UC as 629340); Orick, Prairie Creek SP 1241 W 413 N -- *XII.3.1935*, A.H.Smith 3727**pro parte* (MICH as *P. kauffmanii*); *XII.9.1956*, A.H.Smith 56489* (MICH as *P. kauffmanii*); Patrick's Point SP 124ZW,41IN -- *XI.11.1986*, 10,148 DeShazu 203* (HSC as *P. kauffmanii*).

P. rifflipes nom. prov.

WASHINGTON: Clallam Co.: Olympic NP, Rugged Ridge Trail 124.2W,47.9N -- LLN 92.10.23-8 w S.A.Redhead, E.Fox; **Snohomish Co:** Baker-Snoqualmie NF: Barlow Pass -- LLN 93.10.20-1$_{rif3}$ w S.A. Redhead & G. L. Barron (photo); **OREGON: Clackamas Co.** Mt. Hood NF, near Estacada 122° 16' W, 45°8'N -- J.Roger 92.10.1-2 ; **Multnomah Co.:** Mt. Hood NF, Larch Mtn summit -- LLN 92.11.04-2$_{riu10}$ with G. T. Norvell & P.W.Trimm, -3$_{riu9}$& -5$_{riu8}$ w S.A.Redhead; LLN 93.10.24-5* w G.T.Norvell (cited as immature *P. kauffmanii* in FEMAT); Mt. Hood NF, Larch Mtn Road 5 miles from summit -- LLN 92.11.11-2,5,6 w O.L.Norvell & P.W.Trimm.

P. rufotubulina nom. prov.

OREGON: Lane Co. near Florence *25.X.1997* LLN 97.10.31-1 by ?F.Rowe via D.Arora; **CALIFORNIA: Humboldt Co.** Murray Road, McKinleyville -- *26.X.1977* 5607* D.L.Largent (75540) (HSC as *P. californica*); **Marin Co.** Audubon Canyon Ranch -- *5.I.1984* Calhoun 84-3737* (SFSU as *P. californica*); Bolinas Ridge Trail -- *26,XII.1981* D.E.Desjardin 900* (SFSU as *P. californica*), *17.I.1992* H.D.Thiers 54067* (SFSU as *P. californica*); **Mendocino Co.** Caspar, Simpson Lane -- *22.XI.1982* A.S. Methven 2149* (NY as *P. radicata*); Jackson SF, near intersection of Hwys 408 & 409 ("Mushroom Corners")-- *22.XI.1980* 5930* M. Eichelberger (HSC as *P. scatesiae*), 5940* unk. coll. (HSC as *P. dissiliens*); LLN 11.92.16-1$_{ruc1}$ w S.A.Redhead, G. L. Barron (HOLOTYPE-WTU, ISOTYPE-DAOM), LLN 92.11.16-8, 92.11.17-8$_{ruc8}$ w S.A.Redhead, LLN 92.11.21-6$_{ruc9}$ by H.D.Thiers, R.Halling;

P. rufotubulina (concluded)

Jackson SF, Hwy 409, 1/2 mi E Hwy 408 ("Aleuria Glen") -- *X.1986* 25.M.T.Seidl 2114* (SFSU as *P. californica*), *13.XII.1990* D.E. Desjardin 5030* (SFSU as *P. californica*); LLN 92.11.24-2*$_{ruc3}$,-7* w S.A.Redhead & G.L.Barron, -3,-6,-10,-24 by LLN, -4&5 w H.D.Thiers & R.E. Halling. -8$_{ruc6}$ by R.E.Halling, -9 by H.D.Thiers & R.E.Halling; Jackson SF -- *25.XI1.1960* H.D.Thiers 8477* (SFSU as *P. attenuata*), *11.X11.1965* H.D.Thiers 14607* (SFSU as *P. californica*), *20.XII.1966* H.D.Thiers 18156* (SFSU as *P. californica*), *5.XI.1967* H.D.Thiers 21404* (SFSU as *P. attenuata*), *7.XII.1969* H.D.Thiers 24452* (SFSU as *P. californica*), *3.XII.1971* J.F.Ammirati 6222* (MICH), *31.X.1972* H.D.Thiers 30427* (SFSU as *P. californica*), *25.XI.1972* H.D.Thiers 30756* (SFSU as *P. californica*), *7.XII.1974* H.D.Thiers 33175* (SFSU as *P. californica*), *2.XI.1975* H.D.Thiers 35261* (SFSU), *8.XI.1986* H.Saylor 3681* (SFSU as *P. radicata*); Russian Gulch SP -- *25.XI.1992* S.A.Redhead 7454, 7500 [DAOM].

P. scatesiae A. H. Smith & Trappe 1972
(* collections previously (1995) designated as *P. californica*)

WASHINGTON: Grays Harbor Co. Copalis *X.20.1982* K.Scates 6790* (as *P. californica*); **Jefferson Co.** Olympic National Park, Hoh River Valley, Twin Creek DNR -- LLN 92.10.15-16*scc5 G.L.Barron, S.A. Redhead, -19*sca5 R.H.Petersen; **OREGON: Benton Co.** Dinner Creek, Alsea Summit -- *10.X.1977* F46058* by Hunt & Fogel (OSC), *24.X.1977* F46060* by Hunt & Fogel (OSC); **Clackamas Co.** Wildcat Mtn. -- LLN 95.10.14-4 J.Roger, -5M.Rogers; LLN 95.10.18-1,2,3,14 all w JRoger; **Coos Co.** Cape Mtn. -- *XI.13.1994* LLN 96.02.21-mr2,mr3 M.Peeters; **Lane Co.** Bunker Hill -- *X.12.1971* J. F. Ammirati 5882* (MICH); **Multnomah Co.,** Mt. Hood NF, Larch Mtn. summit -- LLN 92.11.04-14*,15***sca3** w G.T.Norvell, P.W.Trimm; **Lincoln Co.** Fogarty Creek SP -- LLN 96.11.02-1; Van Duzer Wayside -- LLN 92.11.10-3,4*, LLN 93.11.04-2*sca7, -9***sca1** w S.A.Redhead; **Tillamook Co.** Cascade Head Exp. F. -- *X.24.1970* 00011630 A.H.Smith 79286***sca2** (HOLTOTYPE -- MICH), K.Scates 1136***sca6** (ISOTYPE -- WTU), S.A.Rehner 11.10.82-1***scl4** , LLN 95.11.09-25,27; Coral Mtn. *X.30.1977* C.Goetz 33***sca9**, 34*; Longfibre Tree Farm -- *X.15.1971* J.F.Ammirati 5937*, 5938* (MICH), Nestucca *X.25.1996* LLN 96.12.03-1 by J.Lindgren; **CALIFORNIA: Del Norte Co.** Crescent City -- *XI.12.1937* A.H.Smith 8650* (MICH): **Mendocino Co.** Van Damme State Park -- LLN 92.11.23-1***sca4**,6 w S.A.Redhead.

P. 'similis' sensu A. H. Smith 1957 *(Incomplete -- complete allocation of loans to be made)*

BRITISH COLUMBIA: Vancouver Island, Lower Carmanah Valley -- LLN 92.10.09-13**sia2** w S.A.Redhead; Upper Carmanah Valley above Hummingbird at Phoenix Fld. Stn. -- 93.10.30-25**sia1** w S.A.Redhead; **WASHINGTON: Clallam Co.** Olympic NP, Rugged Ridge Trail -- LLN 92.10.23-17**sia3** w S.A.Redhead; **Pierce Co.** Mt. Rainier NP, Carbon R. entrance -- *16.IX.1952* A.H.Smith 39988**sia9** (MICH); Mt. Rainier NP, Ipsut Cr. above Carbon R. -- LLN 93.09.24-2**sia5** w S.A.Redhead; **OREGON: Tillamook Co.,** Cascade Head Exp.F. N FR 1861, app. 2 km W Hwy 12 -- LLN 93.11.14-12**sia6** w G.T.Norvell.

Possibly also: **BRITISH COLUMBIA: Vancouver Island,** Lower Carmanah Valley --LLN 92.10.09-27&29, LLN 92.10.09-5, 6, 13, 21 & 26 w G.L.Barron, LLN 92.10.09-18, 25 & 28 w S.A.Redhead, LLN 92.10.09-19 w G.L.Barron & S.A.Redhead; **WASHINGTON: Clallam Co.** Olympic NF, Klahanie Cmpgrd. -- LLN 92.10.18-2 by S.Trudell; Olympic NP, Rugged Ridge Trail -- LLN 92.10.23-2, 10, 12 & 13, LLN 92.10.23-11, 15, 16, 21, 22 & 31 w S.A.Redhead, LLN 92.10.23-14 & 20 w E. Fox & S.A.Redhead, LLN 92.10.23-25 w G. L. Barron, LLN 92.10.23-26 by G. L. Barron, LLN 92.10.31-8,13,14,16,17&18, LLN 92.10.31-15 w S.A.Redhead; **OREGON: Lincoln Co.** Cascade Head Exp. F. 20m E Hwy12, 30m S Tillamook Co. line -- LLN 93.11.04-11, LLN 93.11.04-8 w S.A.Redhead; LLN 93.11.14-15 w G.T.Norvell; **Tillamook Co.,** Cascade Head Exp.F. N FR 1861, app. 2 km W Hwy 12 -- LLN 93.11.14-5&11 w G.T.Norvell;

P. sipei A. H. Smith 1957

OREGON: Benton Co. BLM forest T 13S, R 6W, S 33N1/2, NW 1/4 -- LLN 96.11.22-2,7 R. Exeter; Dinner Creek, Alsea Summit -- 46245*, 46357*, 46437* (no dates), Hunt & Fogel (OSC); Mary's Peak -- *X.20,1971*, Ammirati 5990* (MICH); McDonald Forest -- LLN 95.11.17-12,17 w F. Camacho, T. Lebel, N.S. Weber; **Lane Co.** Eugene-- F. P. Sipe Oct. 1937* (*Holotype* - MICH); **Lincoln Co.** Fogarty Creek State Park -- LLN 95.11.09-2 (w M.Moser, J. Ammirati),4,6,7,9,10,12,14,17; **Tillamook Co.** Cascade Head EF -- LLN 93.11.04-1* w S.A.Redhead; Oswald West SP -- LLN 91.11.23-5,6*.

Probably also **WASHINGTON: Jefferson Co.** Twin Creek DNR in Hoh Valley -- LLN 92.10.15-33

P. spadicea A. H. Smith 1957 *(Incomplete -- complete allocation of loans to be made)*

WASHINGTON: Clallam Co.: Quillayute R. near Mora -- *X.26.1935* 00011634 A.H.Smith 3339 (HOLTOTYPE -- MICH); Olympic NP, Rugged Ridge Trail -- LLN 92.10.31-3spd4 w S.A. Redhead; **Jefferson Co.:** Olympic NP, Hoh River Valley, Alder Creek (2 mi fr Hwy 101 -- LLN 92.10.18-3 by S. Trudell; Olympic NP, Hoh River Valley, Twin Creek DNR -- LLN 92.10.15-10spsD1,26spd3 w S.A.Redhead; LLN 92.10.17-19 w G.T.Norvell & P.W.Trimm; **OREGON: Lincoln Co.** Cascade Head Exp. F, E of Hwy 12 100' S Tillamook Co. line -- LLN 93.11.04-3spsD4, 4spu1,6spsD5 w S.A.Redhead, LLN 93.11.14-7spd6,13spd8 w G.T.Norvell; LLN 95.11.09-20; **Tillamook Co.:** Oswald West SP -- LLN 92.11.02-3spd1 w S.A.Redhead, LLN 93.10.23-6spd2 w G.T.Norvell; Van Duzer Wayside -- LLN 92.11.10-22spd5 w G.L.Barron; **CALIFORNIA: Mendocino Co.:** Van Damme SP -- LLN 92.11.20-2 w S.A.Redhead.

P. tibiikauffmanii nom. prov. (Incomplete -- complete allocation of loans to be made)

OREGON: Lincoln Co. Cascade Head Exp. F, W Hwy 12, S Tillamook Co. line -- LLN 95.11.09-19 (HOLOTYPE); Fogarty Creek SP, trail to water tanks -- LLN 95.11.09-22.

APPENDIX C. Molecular characters

Table C-1 DNA Source Materials

DNA alpha-numeric codes are listed for each voucher collection containing the specimen selected for molecular testing. Collections with two DNA alpha-numeric codes were recoded after preliminary analysis of morphological and molecular data indicated field misidentification (original codes in parentheses). Type collections are listed in **bold-face**; starred (*) codes indicate collections from which ITS1+5.8S+ITS2 rDNA could not be successfully amplifed. 1993/1994 extraction and amplifications dates are in plain font; 1995 dates are underlined. Dates preceded by $ represent direct amplification from spores without previous extraction Dates following starred codes denote unsuccessful amplification and/or extraction attempts. Collection data (identification number and herbarium when different from WTU, collection year, state/province and location) are also cited.

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
Phaeocollybia ammiratii nom. prov.						
amb 2 (bar 2)	LLN 92.11.19-1	1992	CA	Big Lagoon	3/15	3/16, 3/31, 9/24
amb 3 (bar 3)	LLN 93.10.06-1	1993	BC	Mt. Seymour Watershed	3/27	3/31, 4/4, 9/24
amb 4 (bar 4)	LLN 92.11.04-8	1992	OR	Larch Mtn, Mt. Hood NF	3/27	3/31, 4/4, 9/24
amb 5 (bar 5)	LLN 93.10.20-2	1993	WA	Barlow Pass, Baker-Sno NF	3/27	3/31, 9/24
amb 6 (bar 6)	LLN 93.10.08-1	1993	WA	Denny Creek	3/27	3/31, 8/3, 29
amb 7 (bar 7)	LLN 93.10.11-2	1993	WA	Sol Duc	3/27	(2-banded) 3/31, 4/4
amb 8 (bar 8)	LLN 92.10.31-1	1992	WA	Rugged Ridge, Olympic NP	3/27	3/31, 9/24
amb 9 (bar 9)	LLN 92.09.13-6	1992	WA	Barlow Pass, Baker-Sno. NF	3/22	3/23, 9/24
amb 10 (bar10)	LLN 92.09.13-8	1992	WA	Barlow Pass, Baker-Sno NF	3/22	3/23, 9/24
amb 11 (bar11)	JFAmmirati 10697	1992	WA	Barlow Pass, Baker-Sno NF	3/27	3/31
amm 14	LLN 94.10.28-14	1994	OR	Wildcat Mtn., Mt. Hood NF	7/21	7/25, 9/24
amm 15-T	LLN 94.10.28-1	1994	OR	Wildcat Mtn., Mt. Hood NF	7/21	9/24
amm 16	LLN 94.11.06-18	1994	OR	Cascade Head Exp. Forest	7/21	9/24
Phaeocollybia attenuata (Smith) Singer 1951						
att 4	LLN 92.11.20-8	1992	CA	Van Damme SP		$4/28, $6/22
att 7	LLN 92.11.10-31	1992	OR	Van Duzer Wayside SP		$5/7, $6/22
***att 8-T**	AHSmith 3343 (MICH)	1935	WA	La Push	5/30	5/31,6/2,7/13,17
*att 10	KScates 7116	1985	OR	Cape Meares SP		$9/27
att 11	LLN 93.10.15-7	1993	WA	La Push		$9/27
att 12	LLN 93.10.23-3	1993	OR	Oswald West SP		$9/27
att 13	LLN 94.11.06-34	1994	OR	Cascade Head Exp. Forest		$9/27
Phaeocollybia benzokauffmanii nom. prov.						
bek 3 (kau 3)	LLN 92.11.22-3	1992	CA	Van Damme SP		$5/10, $7/16
ben 1-T	LLN 92.11.20-1	1992	CA	Van Damme SP	12/20	[.4 4/4 7/14 8/29
ben 3	LLN 93.09.24-1	1993	WA	Ipsut Creek, Mt. Rainier NP	5/25	5/25 7/14
ben 4-T	LLN 92.10.23-5	1992	WA	Rugged Ridge, Olympic NP		$9/25 $10/3
ben 5	LLN 93.10.15-10	1993	WA	Rugged Ridge, Olympic NP		$9/25 $10/3
*ben 7	LLN 94.10.11-2	1994	OR	Cascade Head Exp. F.		$9/25,26,27
Phaeocollybia californica A. H. Smith 1957						
cal 2-T	AHSmith 55610 (MICH)	1956	CA	Crescent City	4/13 7/21	4/8, 4/22, 28; 7/25
cal 10-pT	AHSmith 8650 (MICH)	1937	CA	Crescent City	4/21	4/22
*cal 12-pT	AHSmith 8671 (MICH)	1937	CA	Trinidad	4/21 7/21	4/22,28; 6/15, 7/18, 9/25
*cal 13-pT	FSipe 184 (MICH)	1941	OR	Eugene	4/21	4/22,28; 6/15, 7/18
*cal 14-pT	AHSmith 55611 (MICH)	1951	CA	Crescent City	4/21 7/21	4/22,28; 6/15, 7/18, 9/25
Phaeocollybia carmanahensis Redhead & Norvell 1993						
car 1-T	LLN 91.10.24-3	1991	BC	Upp.Carmanah, Vancouver Isl.	3/8	3/9, 7/16, 8/31

Table C-1 (continued).

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
Phaeocollybia christinae (Fr.) Heim 1931						
chr 1	AHSmith ###	1975	QUE		6/15	6/15
chr 2	RGThorn 930923/03	1993	WI		$5/31	
Phaeocollybia deceptiva A. H. Smith & Trappe 1972 = *Cortinarius phaeodeceptivus* Norvell, Ammirati & Redhead						
dec 1-T	AHSmith 77000 (MICH)	1968	ID	Macabee Falls	5/25	5/25, 7/21
Phaeocollybia dissiliens A. H. Smith & Trappe 1972						
*dis 2	AHSmith 79540 (MICH)	1970	OR	Cape Lookout SP	6/1	6/2, 6/11
dis 3-T	AHSmith 79252 (MICH)	1970	OR	Cape Lookout SP	6/1	6/10, $9/26,
Phaeocollybia fallax A. H. Smith 1957						
fal 1.	LLN 92.10.15-11	1992	WA	Hoh Valley, Olympic NP	2/28	3/2, 6/20
fal 2	LLN 92.10.07-1	1992	BC,	Upp.Carmanah, Vancouver Isl.	6/15	6/29, 9/9, $9/25
fal 6	LLN 93.11.14-8	1993	OR	Cascade Head Exp. Forest		$5/13, $9/26
fal 8	LLN 92.11.07-3	1992	CA	Humboldt Redwoods SP		$5/13, $9/25
fal 9	LLN 92.11.23-2	1992	CA	Van Damme SP		$5/13, $9/25
fal 10	LLN 91.12.31-3	1991	OR	Estacada		$5/13
*fal 11	AHSmith 83185 (MICH)	1972	ID	Coeur d'Alene	6/1	6/2, 3; 6/11 7/1
*fal 12-T	AHSmith 3342 (MICH)	1935	WA	La Push	6/1	6/2, 15; 7/1,13; $9/25, 26,
fal 13	LLN 93.11.05-14	1993	OR	Larch Mtn, Mt. Hood NF		$9/25
fal 14	LLN 94.10.28-18	1994	OR	Wildcat Mtn., Mt. Hood NF		$9/25
fal 4	LLN 92.10.23-3	1992	WA	Rugged Ridge, Olympic NP		$5/12
fal 5	LLN 92.11.02-1	1992	OR	Oswald West SP		$5/13
fap 5 (pse 5)	LLN 92.11.07-7	1992	CA	Humboldt Redwood SP		$5/10
fap 9 (pse 9)	LLN 92.10.17-2	1992	WA	Queet's River, Olympic NP		$9/27
fas2 (sps 2)	92.10.17-1	1992	WA	Queet's River, Olympic NP		$5/10 $9/25
*fll 2 (lil 2-pT)	AHSmith 83507 (MICH)	19???	OR	Pacific City	6/1	5/25, 31; 6/3,7/1
Phaeocollybia gregaria A. H. Smith & Trappe 1972						
gre 1-T	AHSmith 79075	1970	OR	Cascade Head Exp. Forest	6/1	6/10
gre 3-pT	AHSmith 79087	1970	OR	Cascade Head Exp. Forest	6/1	6/2,27, 29
Phaeocollybia hilaris (Fr.) Heim????						
*hil 1	F1018688 Sg (F)	1974	EUR	Slovakia	4/21	4/28, 6/15
Phaeocollybia jennyae (Karst.) Heim 1931						
*jen 1	AHSmith# (MICH)	1951	MI	Tahquamenon Falls SP.	4/21	4/22,28; 7/18, 7/25
*jen 2 (=ple)	CG 74	1982	OR	Cape Meares SP	5/30, 7/21	5/25,31;6/2,3; 9/18, 7/25, 9/25
jen 3.	AHSmith 61823 (MICH)	1959	QUE	St. Urbain	4/21	4/22

Table C-1 (continued).

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
Phaeocollybia kauffmanii A. H. Smith 1957						
kaa 13 (amm13)	LLN 94.10.02-1	1994	WA	Lake Quinault	7/21	7/25, 9/24, $9/27
kab 1 (bar 1)	LLN 92.09.21-1	1992	WA	Barlow Pass, Baker-Sno NF	12/20	(2-banded) I.4, 3/31, 7/21 9/24
kab 2 (ben 2)	LLN 92.10.23-1	1992	WA	Rugged Ridge, Olympic NP	3/15	3/16, 7/14, 7/16
kab 12 (bar 12)	JFAmmirati 10696	1992	WA	Barlow Pass, Baker-Sno NF	3/27	3/31
kal 5 (lut 5)	LLN 93.10.24-9	1993	OR	Larch Mtn, Mt. Hood NF	3/22, 4/13	3/23, 4/22, 9/9
kau 1	LLN 92.11.24-12	1992	CA	Jackson State Forest	12/20	I.4, 2/14, 3/9
kau 2	LLN 93.11.14-4	1993	OR	Cascade Head Exp. Forest	4/13	4/22, 7/14
kau 6	LLN 92.10.23-9	1992	WA	Rugged Ridge, Olympic NP		$5/12, $7/18
***kau 8-T**	AHSmith 3523 (MICH)	1937	OR	Lake Tahkenitch	5/30, 6/24	5/25, 31; 6/2,3, 28; 7/13
Phaeocollybia lateraria A. H. Smith 1957						
***lat 1-T**	AHSmith 38033 (MICH)	1951	MI	Tahquamenon Falls SP	6/1	6/2, 6/11
Phaeocollybia lilacifolia A. H. Smith 1957						
***lil 1-T**	AHSmith 39976 (MICH)	1952	WA	Ipsut Creek, Mt. Rainier NP	6/1	6/2,10,15; 7/1,13 (contam?)
*lil 3-pT	AHSmith 49470 (MICH)	1954	OR	Larch Mtn, Mt. Hood NF	6/1	5/25, 31; 6/3,7/1
*lil 4-pT	AHSmith 9012 (MICH)	1937	CA	Humboldt Redwoods	6/1	6/3, 6/11, 7/1
lil 5	LLN 92.11.07-2	1992	CA	Humboldt Redwoods SP		$5/13
lil 6	LLN 92.10.31-10	1992	WA	Rugged Ridge, Olympic NP	6/1	6/3
lil 9	LLN 94.10.22-4	1994	OR	Wildcat Mtn., Mt. Hood NF		$9/26
Phaeocollybia lugubris (Fr.) Heim 1931						
*lug 1	Bresadola (MICH)	1901	Italy		6/15	
Phaeocollybia luteosquamulosa nom. prov.						
lut 1	LLN 92.11.24-1	1992	CA	Jackson SF	12/20	I.5, 3/16, 9/9, $9/25
lut 2	LLN 93.10.24-10a	1993	OR	Larch Mtn, Mt. Hood NF	2/28	3/2, 3/16, 31, 7/21
lut 3-T	SARedhead 7481	1992	CA	Jackson SF	3/22	3/23, 7/26, 8/29, $9/25
lut 4	LLN 93.10.24-6	1993	OR	Larch Mtn, Mt. Hood NF	3/22	3/23, $9/25
lut 6	LLN 93.11.05-9	1993	OR	Larch Mtn, Mt. Hood NF	3/22	3/23
lut 7	LLN 94.10.06-11	1994	OR	Larch Mtn, Mt. Hood NF	7/21	$9/25
lut 8	JFAmmirati 10700	1992	WA	Barlow Pass, Baker-Sno NF	3/22	3/23, 4/4, 9/9, $9/25
lut 9.	LLN 94.10.11-18	1994	OR	Larch Mtn, Mt. Hood NF	7/21	7/24
lut 10	STrudell 250-92-04	1992	WA	Barlow Pass, Baker-Sno NF	7/21	7/25, 9/24, $9/25
Phaeocollybia olivacea A. H. Smith 1957						
oliA = uncut in Pvu2						
oli 1	LLN 92.11.23-4	1992	CA	Van Damme SP	2/28	3/2, 4/4, 7/1,21; 8/29, 9/26, $10/3
oli 6.	LLN 91.12.30-1	1991	WA	Estacada	6/2	6/3, 7/16
oli 7-T	AHSmith 55767 (MICH)	1956	OR	Grant's Pass	6/2	6/10, 7/16
oli 11	LLN 92.11.20-12	1992	CA	Van Damme SP		$9/25,26
oli 12	LLN 92.11.22-4	1992	CA	Jackson SF		$9/26

Table C-1 (continued).

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
oliB = cut in Pvu2						
oliB 3 (oli 3)	LLN 92.11.16-4	1992	CA	Jackson SF		$5/13, $7/16
oliB 5 (oli 5)	LLN 92.11.24-25	1992	CA	Jackson SF		$5/13, $7/16
oliB 7 (kau 7)	LLN 92.11.16-5	1992	CA	Jackson SF		$5/12, $7/18
oliB 8 (lil 8)	LLN 94.10.11-8	1994	OR	Larch Mtn, Mt. Hood NF		$9/26
oliB 8 (oli 8)	LLN 94.11.28-1	1994	OR	Estacada		$9/26
oliB 9 (oli 9)	LLN 92.11.10-20	1992	OR	Van Duzer		$9/26
oliB 10 (oli 10)	LLN 92.10.15-3	1992	WA	Hoh Valley, Olympic NP		$9/26
Phaeocollybia oregonensis A. H. Smith & Trappe 1972						
ore 1	LLN 92.11.04-19	1992	OR	Larch Mtn, Mt. Hood NF	3/8	3/9, 4/14, 7/21
ore 2	SG 53-101393-1	1993	BC	Mt. Seymour Watershed		$5/10
***ore 3-T.**	AHSmith 28420 (MICH)	1947	OR	Larch Mtn, Mt. Hood NF	6/3	5/25,31; 6/2, 3, 28; 7/13
ore 4	LLN 92.11.04-7	1992	OR	Larch Mtn, Mt. Hood NF	6/15	6/27
ore 5	LLN 92.11.04-1	1992	OR	Larch Mtn, Mt. Hood NF	6/15	6/27
ore 6	LLN 94.10.22-3	1994	OR	Wildcat Mtn., Mt. Hood NF		$9/25, 26
Phaeocollybia oregonensis (continued)						
ore 7	LLN 94.10.28-7	1994	OR	Wildcat Mtn., Mt. Hood NF		$9/25, 26
ore 8	LLN 92.11.04-6	1992	OR	Larch Mtn, Mt. Hood NF	4/12	4/14, 22; 7/1
Phaeocollybia piceae A. H. Smith & Trappe 1972						
pic 1	LLN 92.10.09-7	1992	BC	Low. Carmanah, Vancouver Isl.	3/8	3/9 4/14 7/21
***pic 2-T**	AHSmith 79085 (MICH)	1970	OR	Cascade Head Exp. Forest	6/2	6/3,11; 7/1 8/28
pic 3	LLN 92.10.09-11	1992	BC	Low.Carmanah, Vancouver Isl.		$5/7 $7/16
pic 4	LLN 92.10.23-27	1992	WA	Rugged Ridge, Olympic NP		$5/7 $7/16
pic 5	LLN 92.11.02-9	1992	OR	Oswald West SP		$5/7 $7/16
pic 6	LLN 92.11.22.5	1992	CA	Jackson SF		$5/7
pic 7	LLN 92.10.15-14	1992	WA	Hoh Valley, Olympic NP		$9/25 (faint), $10/3
*pic 8	LLN 93.10.08-2	1993	WA	Clallam Co.Olympic NP		$9/25, 26,27
pic 9	LLN 94.10.22-7	1994	OR	Wildcat Mtn., Mt. Hood NF		$9/25 $10/3
pic 10	LLN 94.11.06-1	1994	OR	Cascade Head Exp. Forest		$9/25,26 $10/3
Phaeocollybia pleurocystidiata nom. prov.						
ple 1-T	LLN 94.03.30-2	1994	WA	Bogachiel River, Olympic NP	7/21	$4/28 $5/9
ple 2	LLN 93.05.16-1	1993	OR	Sweet Home	7/21	$5/9 $6/22 $9/25
ple 3	MTSeidl 914	1986	CA	Wunderlich SP	5/30, 7/21	5/31 6/22 $9/25
*ple 4	DAOM 128270 (HDThiers coll)	1965	CA	Jackson SF	5/30, 7/21	5/25,31; 6/3,11; 7/25 9/25
Phaeocollybia pseudofestiva A. H. Smith 1957						
***pse 7-T.**	AHSmith 8274 (MICH)	1937	CA	Crescent City	6/2	6/3 6/11,29 $9/26,27
*pse 10	LLN 92.11.04-10	1992	OR	Larch Mtn, Mt Hood NF		$9/27
pseB(north)						
psa 1 (pse 1)	LLN 92.11.16-2	1992	CA	Jackson SF	2/28	3/2 7/21,26; 8/31 $9/26
psa 6 (pse 6)	LLN 92.11.21-1	1992	CA	Van Damme SP		$5/10
psa 11 (pse 11)	LLN 92.11.23-8	1992	CA	Van Damme SP		$9/27 $10/3
pseAB (central)						
psab (pse 8)	LLN 91.11.23-2	1991	OR	Oswald West SP		$5/13
pseA (south)						
psb 2 (pse 2)	LLN 92.10.07-6	1992	BC,	Upp.Carmanah, Vancouver Isl.		$5/10 $9/25
psb 3 (pse 3)	LLN 92.10.09-1	1992	BC	Low.Carmanah, Vancouver Isl.		$5/10 $9/25
psb 4 (pse 4)	LLN 92.10.31-12	1992	WA	Rugged Ridge, Olympic NP		$5/10

Table C-1 (continued).

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
Phaeocollybia radicata (Murrill) Singer 1940						
***rad 1-T**	Murrill (NY)	1906	OR	Glen Brook	6/15	7/18
rad 2	AHSmith 3763 (MICH)	1935	CA	Orick		$5/16
rad 3 (cal?)	ETylutki 4449 (MICH)	1972	OR	Cascade Head Exp. Forest	6/2	7/1,18
Phaeocollybia redheadii nom. prov.						
rec 1-T (cry 1)	LLN 91.10.24-2	1991	BC,	Upp.Carmanah, Vancouver Isl.	I.3	6/15 9/22
rec 2 (cry 2)	LLN 92.09.21-4	1992	WA	Barlow Pass, Baker-Sno NF	3/15	3/16 7/16 7/21
*rec 3 (cry 3)	LLN 92.10.09-20	1992	BC	Low.Carmanah, Vancouver Isl.		$9/25 $9/26
rec 5 (cry 5)	LLN 94.11.06-4	1994	OR	Cascade Head NP		$10/3
rec 6 (cry 6)	LLN 94.10.28-7	1994	OR	Wildcat Mtn, Mt. Hood NF		$10/3
*rec 7 (cry 7)	LLN 93.11.05-1	1993	OR	Larch Mtn, Mt Hood NF		$9/25..26..27
rek 4 (kau 4)	LLN 92.10.17-21	1992	WA	Hoh Valley Olympic NP	5/25	5/26 7/18 7/16
rek 5 (kau 5)	LLN 93.10.24-3	1993	OR	Larch Mtn, Mt. Hood NF	5/25	5/26 7/14 9/9
reo 2 (oli 2)	LLN 92.09.21-7	1992	WA	Barlow Pass, Baker-Sno NF		$5/13
Phaeocollybia rifflipes nom. prov.						
rif 3 (fal 3)	LLN 93.10.20-1	1993	WA	Barlow Pass, Baker-Sno NF		$5/12, $6/27
rif 4 (oli 4)	LLN 92.10.31-7	1992	WA	Rugged Ridge, Olympic NP		$5/13, $7/16
rif 8 (unk 8)	LLN 92.11.04-5	1992	OR	Larch Mtn, Mt. Hood NF		$5/10, $7/18
rif 9 (unk 9)	LLN 92.11.04-3	1992	OR	Larch Mtn, Mt. Hood NF		$5/10
rif 10 (unk 10)	LLN 92.11.04-2	1992	OR	Larch Mtn, Mt. Hood NF		$5/10
Phaeocollybia rufipes Bigelow 1963						
***ruf 1-T**	HEBigelow (NY)	1962	Maine		6/15	7/26
Phaeocollybia rufotubulina nom. prov.						
ruc 1 (cal 1)-T	LLN 92.11.16-1	1992	CA	Jackson SF	2/28	3/2 4/4,22 8/29 7/24
ruc 3 (cal 3)	LLN 92.11.24-2	1992	CA	Jackson SF	4/7	4/18,28
ruc 6 (cal 6)	LLN 92.11.24-8	1992	CA	Jackson SF	4/13	4/14,28
ruc 7 (cal 7)	SARedhead 7500	1992	CA	Russian Gulch	4/13	4/14
ruc 8 (cal 8)	LLN 92.11.17-8	1992	CA	Jackson SF	4/13	4/15
ruc 9 (cal 9)	LLN 92.11.21-6	1992	CA	Jackson SF	4/13	(2-banded) 4/15
Phaeocollybia scatesiae A. H. Smith & Trappe 1972						
sca 1	LLN 93.11.04-9	1993	OR	Van Duzer Wayside	2/28	3/2 4/4,22 7/18
sca 2-T	AHSmith 79286 (MICH)	1970	OR	Cascade Head Exp. Forest	4/13	4/22
sca 3	LLN 92.11.04-14	1992	OR	Larch Mtn, Mt. Hood NF	4/7	4/8
sca 4	LLN 92.11.23-1	1992	CA	Van Damme SP	4/7	4/8
sca 5	LLN 92.10.15-19	1992	WA	Hoh Valley, Olympic NP	4/7	4/8
sca 6.-1T	KScates 1136	1970	OR	Cascade Head Exp. Forest	4/13 7/21	4/22, 7/25
sca 7	LLN 93.11.04-2	1993	OR	Van Duzer Wayside	4/13	4/14
sca 9	CG 33	1977	OR	Coral Mtn		
scl 4 (cal 4)	SARehner 11.10.82-1	1982	OR	Cascade Head Exp F	4/7	4/11
scl 5 (cal 5)	LLN 92.10.15-16	1992	WA	Hoh Valley, Olympic NP	4/7	4/8
Phaeocollybia similis' sensu A. H. Smith 1957b						
sia 1(att 1)	LLN 93.10.30-25	1993	BC	Upp.Carmanah, Vancouver Isl.	I.31 3/8	3/9 4/4 9/19
sia 2 (att 2)	LLN 92.10.09-23	1992	BC	Low.Carmanah, Vancouver Isl.		$4/28 $6/22
sia 3 (att 3)	LLN 92.10.23-17	1992	WA	Rugged Ridge, Olympic NP		$4/28 $6/22
sia 5 (att 5)	LLN 93.09.24-2	1993	WA	Ipsut Creek, Mt. Rainier NP		$5/7, $6/22
sia 6 (att 6)	LLN 93.11.14-12	1993	OR	Cascade Head Exp. Forest		$5/7 $6/22
*sia 9 (att 9)	AHSmith 39988 (MICH)	1952	WA	Ipsut Creek, Mt. Rainier NP	5/30	5/31 6/2 7/13,17

Table C-1 (continued).

DNA #	COLLECTION	YEAR	STATE	SITE	CTAB	AMPLIFICATION
Phaeocollybia sipei A. H. Smith 1957						
sid 1 (dis 1)	LLN 93.11.04-1	1993	OR	Cascade Head Exp. Forest	3/8	3/9 5/12 7/21 $9/25,26.
sip 1-T	Sipe10.37 (MICH)	1937	OR	Eugene	4/21	7/1 (too faint for use)
sip 2	LLN 91.11.23-6	1991	OR	Oswald West SP	4/13	4/22 7/18 8/31
*sip 3	LLN 92.10.15-33	1992	WA	Twin Creek, Olympic NP		$9/25,27
Phaeocollybia spadicea A. H. Smith 1957						
spd 1	LLN 92.11.02-3	1992	OR	Oswald West SP	12/20	L5, 7/21 8/31
spd 2	LLN 93.10.23-6	1993	OR	Oswald West SP	12/20	L5
spd 3	LLN 92.10.15-26	1992	WA	Hoh Valley, Olympic NP		$5/10
spd 4	LLN 92.10.31-3	1992	WA	Rugged Ridge, Olympic NP		$5/10
spd 5	LLN 92.11.10-22	1992	OR	Van Duzer Wayside SP		$5/10
spd 6	LLN 93.11.14-7	1993	OR	Cascade Head Exp. Forest		$5/10
***spd 7-T**	AHS 3339 (MICH)	1935	WA	Quillayute	6/2	6/3 6/29,11
spd 8	LLN 94.11.19-1	1994	CA	Humboldt Redwood SP		$9/26
spds 1 (sps 1)	LLN 92.10.15-10	1992	WA	Hoh Valley, Olympic NP		$5/10
spds 4 (sps 4)	LLN 93.11.04-3	1993	OR	Cascade Head Exp. Forest		$5/10
spds 5 (sps 5)	LLN 93.11.04-6	1993	OR	Cascade Head Exp. Forest		$5/10
spds 6 (sps 6)	LLN 92.11.20-2	1992	CA	Van Damme SP		$5/10 $9/26 $10/3
spds 7 (sps 7)	LLN 94.11.06-28	1994	OR	Cascade Head Exp. Forest		$9/26, $10/3
spdu 1 (unk 1)	LLN 93.11.04-4	1993	OR	Cascade Head Exp. Forest		$5/10 $7/16
Phaeocollybia spoliata Horak 1974						
*spo-1	Guzman (NY)	1985		Mexico	6/15	6/29,7/18
Unresolved phaeocollybias						
unc 4 (cry 4)	LLN 93.10.15-2	1993	WA	Sol Duc, Olympic NP		$9/25,26,27 $10/3
uncal 11(cal11)	CGoetz 77	1983	OR	Corvallis	4/21	4/22, 9/25
unfal 7 (fal 7)	LLN 92.11.10-12	1992	OR	Van Duzer Wayside		$5/13
ungre 4 (gre 4)	LLN 94.11.06-24	1994	OR	Cascade Head Exp. Forest		$9/25 $10/3
unk 2	LLN 93.11.04-5	1993	OR	Cascade Head Exp. Forest		$5/10, $7/16
unk 3	LLN 93.10.15-1	1993	WA	La Push		$5/10, $7/16
*unk 4	LLN 93.11.14-15	1993	OR	Cascade Head Exp. Forest	6/1	
unk 5	LLN 93.11.05-4	1993	OR	Larch Mtn, Mt. Hood NF		$5/10
unk 6	LLN 93.11.13-2	1993	OR	Larch Mtn, Mt. Hood NF		$5/10
unk 7 (lut??)	LLN 92.11.04-9	1992	OR	Larch Mtn, Mt. Hood NF		$5/10
unkau 9 (kau 9)	LLN 92.11.21-3	1992	CA	Van Damme SP		$9/25,26
unlil 7 (lil 7)	LLN 92.11.04-4	1992	OR	Larch Mtn, Mt. Hood NF		$5/13, $7/26
unsps (sps 3)	LLN 92.10.18-4	1992	WA	Klahanie Cmpgd., Olympic NF		$5/9 $9/26
Out-taxa						
Caulorhiza umbonata (Peck) Lennox						
Cau 1	JWLennox 611(b)	1969	CA	50 mi N San Francisco	6/1	6/2 (very faint)
Cau (Cau 2)	LLN 92.11.15-1	1992	CA	Humboldt Redwood SP		$5/16, $5/31
Cortinarius vanduzerensis A. H. Smith & Trappe 1972						
Cva (Cva 1)	Ammirati 10234	1978	CA	Humboldt	3/8	3/9 4/14 8/31
Galerina autumnalis (Peck) Smith & Singer						
Gal 1	Ammirati 7947	1977	CAN	Ontario	3/15	3/16 (very faint)
Gymnopilus spectabilis (Fr.) A. H. Smith						
Gym (Gym 1)	CArdrey 1472	1989	OR	Coos Co	3/15	3/16, 4/14, 8/31
Stagnicola perplexa (Orton) Redhead & Smith 1986 (removed from *Phaeocollybia* in 1986)						
Stg (Stg 1)	LLN 93.09.24-4	1993	WA	Ipsut Creek, Mt. Rainier NP		$5/10, 13 $8/31
Xerula megalospora (Clements) Redhead, Ginns & Schumacher						
Xme	Halton 7	1990	ONT			$5/12,31 $6/10

Table C-2 Success of PCR-amplification of ITS region in *Phaeocollybia*

C-2a. 1994 PCR-amplification summary

TAXON	# CTAB AMP GOOD	# SP AMP GOOD	# FAIL	% ISOLATE SUCCESS	# SUCC. AMPS	# AMPS FAILED	# AMPS TRIED	% SUCCESS ALL AMPS
att	1	6	2	77.78	14	10	24	58.33
bar /amm	12	0	0	100.00	20	1	21	95.24
ben	3	0	0	100.00	9	2	11	81.82
cal	11	0	3	78.57	18	11	29	62.07
car	1	0	0	100.00	4	0	4	100.00
chr	1	1	0	100.00	2	1	3	66.67
cry	2	0	0	100.00	6	2	8	75.00
dec	1	0	0	100.00	2	3	5	40.00
dis	2	0	1	66.67	4	8	12	33.33
fal	2	8	2	83.33	13	0	13	100.00
fes	0	0	0	0.00	0	0	0	0.00
gre	2	0	0	100.00	4	7	11	36.36
hil	0	0	1	0.00	0	2	2	0.00
jen	1	0	2	33.33	1	12	13	7.69
kau	4	3	1	87.50	16	12	28	57.14
lat	0	0	1	0.00	0	2	2	0.00
lil	1	2	4	42.86	4	17	21	19.05
lug	0	0	1	0.00	0	0	0	0.00
lut	7	0	0	100.00	18	2	20	90.00
oli	3	4	0	100.00	15	9	24	62.50
ore	4	1	1	83.33	9	9	18	50.00
pic	1	4	1	83.33	10	11	21	47.62
ple	1	2	1	75.00	6	9	15	40.00
pse	1	6	1	87.50	13	4	17	76.47
rad	1	1	1	66.67	3	7	10	30.00
ruf	0	0	1	0.00	0	1	1	0.00
sca	7	0	0	100.00	10	1	11	90.91
sip	2	0	0	100.00	4	5	9	44.44
spd	2	4	1	85.71	8	3	11	72.73
spo	0	0	1	0.00	0	2	2	0.00
sps	0	6	0	100.00	6	3	9	66.67
unk	0	9	1	90.00	13	5	18	72.22
Cva	1	0	0	100.00	3	1	4	75.00
Cau	1	1	0	100.00	3	1	4	75.00
Pcg	1	0	0	100.00	1	2	3	33.33
Gal	2	0	1	66.67	2	3	5	40.00
Gym	1	0	0	100.00	3	0	3	100.00
Stg	0	1	0	100.00	3	0	3	100.00
Xme	0	1	0	100.00	3	0	3	100.00
Xra	0	0	1	0.00	0	2	2	0.00
totals	**79**	**60**	**29**	**82.73**	**250**	**170**	**420**	**59.52**

Table C-2 (continued)

C-2b. 1995 PCR-amplification summary

att	1	3	2	66.67	4	2	6	66.67
bar/amm	4	–	-0	100.00	2	2	4	50.00
ben	–	2	1	66.67	4	3	7	57.14
cry	1	3	2	66.67	7	10	17	41.18
dis	–	2	0	100.00	3	2	5	60.00
fal	1	5	1	85.71	6	13	19	31.58
gre	–	1	0	100.00	2		2	100.00
jen	0		2	0.00		2	2	0.00
kau	1		0	100.00	2		2	100.00
lil	–	2	2	50.00	2	4	6	33.33
lut	4	2	2	75.00	6	2	8	75.00
oli	1	5	0	100.00	8	1	9	88.89
ore	–	2	1	66.67	4	2	6	66.67
pic	–	3	1	75.00	7	2	9	77.78
ple	–	2	1	66.67	2	1	3	66.67
pse	1	2	4	42.86	4	6	10	40.00
sca	–	0	1	0.00		1	1	0.00
sip	0	–	2	0.00		5	5	0.00
spd	0	1	1	50.00	1	1	2	50.00
sps	1	3	0	100.00	6	4	10	60.00
totals	**15**	**38**	**23**	**69.74**	**70**	**63**	**133**	**52.63**

Table C-2 (continued)

C-2c 1994 PCR-amplifications: success quotients according to specimen age

COLLECTION YEAR	#CTAB AMPS	SP AMPS	NO SUCCESS	SUCCESS RATE	AGE OF SPECIMEN IN YEARS
1993	18	14	0	1.00	1
1992	38	39	0	1.00	2
1991	4	2	0	1.00	3
1990		2		1.00	4
1989	1			1.00	5
1987	2			1.00	7
1986	1			1.00	8
1985			1	0	9
1983	1			1.00	11
1982	1		1	0.50	12
1980			1	0	14
1978	1			1.00	16
1977	2			1.00	17
1976			1	0	18
1974			1	0	20
1972	1		2	0.33	22
1970	5		2	0.71	24
1969	1			1.00	25
1968	1			1.00	26
1965			1	0	29
1962			1	0	32
1959	1			1.00	35
1956	2			1.00	38
1954			1	0	40
1952			2	0	42
1951			2	0	43
1947			1	0	47
1941			1	0	53
1937			3	0	57
1935	1		3	0.25	59
1911			1	0	83
1906			1	0	88
totals	**81**	**57**	**25**	**0.85**	---

C-2d 1995 PCR-amplifications: success quotients according to specimen age

COLLECTION DATE	#CTAB AMPS	SP AMPS	NO SUCCESS	SUCCESS RATE	SPECIMEN AGE
1994	6	12	1	0.95	1.00
1993	3	7	5	0.67	2.00
1992	9	17	11	0.70	3.00
1991	1		2	0.33	4.00
1986		1		1.00	9.00
1983	1			1.00	12.00
1982			1	0.00	13.00
1970	1		1	0.50	25.00
1965			1	0	30.00
1952	1			1	43.00
1951			2	0	44.00
1947			1	0	48.00
1937			1	0	58.00
1935			1	0.00	60.00
totals	**16**	**25**	**26**	**0.61**	---

Table C-3 Restriction Digest Record

Dates are provided for successful digests of amplified isolates with enzymes Cfo1, EcoR1, Hinf1, Nde2, Pal1, Pvu2, Rsa1, Sal1 and Xho1 used in analyses. Other less informative enzymes are listed without dates. Digests run in 1994 (not underlined) and 1995 (underlined).

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
amb 2	3/25 7/24 10/3	4/6	3/24 7/24 9/26	9/25 10/2	3/24 4/5 7/24 9/26	4/6		4/5 ,6	4/6	Hind3 Msp1
amb 3	7/24	4/6 9/21	7/24 7/26 9/26	9/25	4/5 7/24	4/6		4/5 ,6 7/26	4/6	
amb 4	5/19 7/24	4/6 5/19	7/24	9/25	4/5 7/24	4/6 5/19	5/19	4/5 ,6	4/6	
amb 5	7/24	9/21	7/24	4/9 9/24	4/5 7/24 7/26			3/26 4/5		
amb 6	7/24	7/27 9/21	7/24	9/25	4/5 7/28 7/24	8/27	8/31	4/5		
amb 7	5/19 7/24	5/19 9/21	7/24	9/25	4/5 7/24	5/19	5/19	4/5		
amb 8	7/24	9/21 9/25	7/24	9/25	4/5 7/24			4/5		
amb 9	3/25 7/24	9/25	3/24 7/24	9/25	3/24 7/24	7/26		3/25		Hind3 Msp1
amb 10	3/25	9/25	3/24 7/24	9/25	3/24 7/24			3/25		Hind3 Msp1
amb 11	7/24	9/21	7/24		4/5 7/24			4/5		
amm 14		9/25	9/26	9/25						
amm 15		9/25	9/26	9/25	9/26					
amm 16		9/25	9/26	9/25	9/26					
att 4	6/17	6/21 9/29	6/17 9/29	6/21	6/21	9/29	6/21	6/17 9/29	6/17	
att 7	6/17 10/4	6/21 7/27	6/17 8/25	6/21 10/2	6/21 7/28	8/27	6/21 8/31	6/17 8/26	6/17 9/1	
att 11		9/29	9/29			9/29		9/29		
att 12		9/29	9/29			9/29		9/29		
att 13		9/29	9/29			9/29		9/29		
bek 3	7/11	5/17	7/11	7/11	7/11	5/17 7/12	5/17 7/12	7/12	7/12	Xba1 Msp1
ben 1	7/11 10/3 ,4	5/17 7/27 9/27	7/11 8/25	7/11 10/2	7/11,28 9/27 10/4 ,5	5/17 7/12 8/27 9/27	5/17 7/12 8/31 9/28 10/4	7/12 8/26	7/12 9/1	Dra EcoRV Kpn Pst Xba Alu Msp
ben 3	10/4		7/11	7/11	7/11 10/4	7/12	7/12 10/4	7/12	7/12	Alu Msp
ben 4	10/4	9/27			9/27 10/4	9/27	9/28 10/4			
ben 5	10/4	9/27			9/27 10/4	9/27	9/28 10/4			

Table C-3 (continued)

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
cal 2-T	10/4	4/25 7/24	4/25 8/5 7/24	4/25 10/3	4/25 8/25	4/27	4/27	4/25	4/8,25 8/5 7/23 7/26	Ava2 DraI XbaI
cal 10		7/24	7/24	10/2		10/2			7/23 10/2	
car 1	5/19 6/30 10/4	5/19 7/27 9/28	5/16 6/30 8/25	5/16 6/30 9/28 10/2	5/16 6/30 7/28 9/29	5/19 8/27 9/29	5/19 8/31	5/16 8/26	9/1 9/13 10/1	Alu2 EcoR5 MspI
Cau	5/26 10/3	7/27	5/25 8/25	10/2	5/25 7/27	8/27	5/26 8/31	5/26 8/26	5/26 9/1	Ava2 KpnI
chr 2	10/3	8/29		10/2	8/29					
Cva	4/12 ,25 5/26 10/3	3/16 7/27	4/25 8/25	4/13 10/2	5/25 7/27	4/12 8/27	4/12 5/26 8/31	4/26 5/26 8/26	4/26 5/26 9/1	Ava2 DraI KpnI MspI PstI XbaI
dec 1	5/26 10/3	7/27	8/25	10/2	7/27	8/27	5/26 8/31	8/26	5/26 9/1	
dis 3	7/1 7/17		7/1 7/17	7/1			7/17	7/1		
fal 1	6/22 10/3	6/22 7/27 9/14,29	6/22 8/25	6/22 10/3	6/27 7/15 7/28	8/27 9/29	8/31	6/27 7/15 8/26	9/1	Alu2 EcoR5 MspI
fal 2	7/1	9/14	6/1	6/29	7/1			7/1		
fal 4	6/22	6/22 9/14,29	6/22	6/22	6/27	9/29		6/27		
fal 5	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
fal 6	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
fal 8	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
fal 9	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
fal 10	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
fal 12	6/22	6/22	6/22	6/22	6/27			6/27		
fal 13		9/29				9/29				
fal 14		9/29				9/29				
fap 5	6/28	6/29 8/29	6/28 8/29	6/29	7/15 8/29	7/15	7/16	7/15	9/19	
fap 9		10/1	10/1	10/1						
fas 2	6/28 10/3	6/29 7/27	6/28 8/25 10/1	6/29 10/1 10/2	7/28	8/27 10/1		8/26		
Gal	4/12	3/16		4/13		4/12				DraI MspI PstI XbaI
Gym	4/12 5/26 10/3	3/16 7/27	5/25 8/25	4/13 10/2	5/25 7/27	4/ 12 8/27	5/26 8/31	5/26 8/26	5/26 9/1	Ava2 DraI KpnI MspI PstI XbaI

Table C-3 (continued)

DNA #	CFO1	ECORI	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
gre 1	6/30		6/30	6/30	7/28 7/14	8/27 7/14	7/14	6/30 8/26	7/14	
gre 3	6/30 10/4	9/30	6/30 9/30	6/30 10/3	10/4	7/14	8/31 7/14 6/30	9/11		
jen 3	6/17		6/17	6/21	8/29			6/17	6/17	
kaa 13		9/25		9/25						
kab 2	7/11 10/4	5/17 9/27	7/11	7/11	7/11 9/27 10/4	5/17 7/12 9/27	5/17 7/12 10/4	7/12	7/12	Xba Alu Msp
kab 12	7/24		7/24		4/5 7/24			4/5		
kab1	3/25 7/24	4/6 9/21 9/25	3/24 7/24 9/26	4/9 9/25	3/24 7/24 9/26	4/6		3/25 4/16	4/6	Alu2 BamH HinD3 Kpn1 Msp1
kal 5	3/24		3/24 7/24	9/29	3/24 7/26	7/26		7/26		HinD3 Msp
kau 1	7/11 10/3 10/4	5/17 7/27 9/27	7/11 8/25 7/24	7/11 10/2	7/11 7/28 7/26 9/27 10/4	5/17 7/12 7/27 7/26 9/27	4/12 5/17 8/31 10/4	7/12 8/26	7/12 9/12	Dra1, EcoR5 Kpn1 Msp1 Pst1 Xba1
kau 2	7/11	5/17	7/11	7/11	7/11	5/17 7/12	5/17 7/12	7/12	7/12	Xba1 Alu1 Msp1
kau 6	7/11	5/17	7/11	7/11	7/11	5/17 7/12	5/17	7/12		Xba1
lil 1			6/22	6/22	6/22			6/27		
lil 5	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
lil 6	6/22	6/22 9/14,29	6/22	6/22	6/27	9/29	6/27			
lil 9		9/29				9/29				
lut 1	3/24	9/26 9/29	3/24 7/26 9/28	9/26 9/29 10/2	3/24 7/26	7/26 9/29	9/28			Alu 2 HinD3 Msp1
lut 2	3/24,26 7/25	4/6	3/24,26 7/26		3/24,26 4/5 7/25 7/26	4/6 7/26		3/26 4/5,6	4/6	HinD3 Msp1
lut 3	3/24 ,26 10/3	4/6,17 7/27 9/26	3/24,26 8/25 7/26	4/17 9/26	3/24,26 7/25 7/26	4/6 ,17 8/27 7/26	8/13	3/26 4/6 8/26	4/6,17 9/1	HinD3 Msp1
lut 4	3/24	4/6 9/26 9/29	3/24 7/26 9/28	9/26 10/2	3/24 7/26	4/6 7/26 9/29	9/28	4/6	4/6	Alu2 HinD3 Msp1
lut 6	3/24,26	4/17 9/29 10/2	3/24,26 10/2	4/17 9/29	3/24,26 7/26	4/6 ,17 9/29 10/2		3/26 4/6	4/17	Alu2 HinD3 Msp1
lut 7	9/26	7/26	9/28		9/26		9/28	7/26		
lut 8	3/24,26 10/3	4/6 9/26 10/2	3/24,26 7/26 9/28 10/2	9/26	3/24 ,26 4/5 7/26	4/6 7/26 10/2	9/28	3/26 4/5 ,6 7/26	4/6	HinD3 Msp1
lut 9		9/26	7/26	9/26	7/26	7/26		7/26		
lut 10		9/26	7/26 9/28	9/26		9/28				
luu 7	7/11	10/2	7/11 10/2	7/11	7/11	7/12 10/2	7/12	7/12	7/12	

Table C-3 (continued)

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
oli A1		7/27 9/18 9/30a b	7/1 8/25 9/30	9/18 10/3	7/1 7/15 28 10/1	8/27 9/30	7/15 8/27 9/18.19	7/1 8/27 9/30	3/9	Alu2 BamH Dra1 Msp1 Pst1 Xba1
oliA 6		9/18. 9/30a.b	7/1	9/18	7/1 10/1	7/15 9/30	9/19	7/1		
olIA 7		9/18	7/1	9/18	7/15	7/15	7/15			
oli A11		9/30a.b	9/30		10/4	9/30		9/30		
oliA12	10/3	9/30a.b	9/30		10/4	9/30				
oliB3		9/18	7/1	9/18	7/1	7/15	7/15	7/1		
oliB 5		9/18. 9/30a.b	7/1	9/18	7/1	7/15 9/30	7/15b 9/19	7/1		
oliB 7	7/11 10/3 10/4	5/17 9/27 10/5	7/11	7/11 10/2	7/11 7/28 10/4	5/17 7/12 8/27 9/27	7/12 9/28 10/4	7/12	7/12	Msp1 Xba1
olIB 8	10/3	9/29		10/3		9/29				
oliB 8	10/3	9/30a.b	9/30	10/3	7/28 10/4	8/27 9/30				
oliB 9		9/30a.b	9/30		10/4	9/30		9/30		
oliB10		9/30a.b	9/30		10/4	9/30		9/30		
olk 9	10/4	9/27			10/4	9/27	9/28 10/4			
ore 1	5/19 6/30	5/19 7/27 9/28	5/16 6/30 8/25	5/16 6/30 9/28	5/16 6/30 7/28 9/29	5/19 8/27 9/29	5/19	5/16 8/26		Alu1 EcoR5
ore 2	5/19 6/30	5/19 9/28	5/16 6/30	5/16 6/30 9/28	5/16 6/30 9/29	5/19 9/29	5/19	5/16	10/1	Alu1 EcoR5
ore 4	6/30	9/28	6/30	6/30 9/28	6/30 9/29	9/29	8/31		9/1	Alu1 EcoR5
ore 5	6/30	9/28	6/30	6/30 9/28	6/30 9/29	9/29				Alu1 EcoR5
ore 6		9/25 10/5		9/28	9/29	9/29		10/1		
ore 7		9/25 10/5		9/28						
ore 8	5/19 6/30 10/4	5/19 7/27 9/28	5/16 6/30	5/16 6/30 9/28 10/2	5/16 6/30 7/28	5/19 9/29 10/5	5/19	5/16	10/1	Alu1 Ava2 Dra1 EcoR5 Xba1

Table C-3 (continued)

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
pic 1	6/30 10/4	7/27 9/30	6/30 8/25 9/30	6/30 10/3	7/28 7/14 10/4	8/27 7/14	8/31 7/14	6/30 8/26 10/4	7/14 10/1	
pic 3	6/30 10/4	9/30	6/30 9/30	6/30 10/3	7/14 10/4	7/14	7/14	6/30 10/4	7/14	
pic 4	6/30 10/4	9/30	6/30 9/30	6/30	7/14 10/4	7/14	7/14	6/30 10/4	7/14	
pic 5	6/30 10/4	9/30	6/30 9/30	6/30	7/14 10/4	7/14	7/14	6/30 10/4	7/14	
pic 6	6/30 10/4	9/30	6/30 9/30	6/30	7/14	7/14		6/30	7/14	
pic 7		9/30	9/30		10/4			10/4		
pic 9		9/30	9/30		10/4			10/4		
pic 10		9/30	9/30		10/4			10/4		
ple 1	6/17	6/21 7/27	6/17 8/25	6/21	6/21 7/28	8/27 7/26	6/21	6/17 8/26	9/1	
ple 2	6/17	6/21	6/17	6/21 10/2	6/21 7/26	7/26	6/21	6/17	6/17	
ple 3	6/17	6/21	6/17	6/21	6/21 7/26	7/26	6/21	6/17	6/17	
psa 6	6/28	6/29	6/28	6/29	7/15	7/15	7/16	7/15	9/19	
psa 11		10/1	10/1	10/1						
psa1	6/28 10/4	7/27 10/1	6/28 8/25 10/1	10/1 10/2	7/15 7/28	7/15 7/27 10/1	7/16 8/31	7/15 8/26	9/1 9/19	
psab 8	6/28	6/29 10/1	6/28 10/1	6/29 10/1	7/15	7/15	7/16 9/19	7/15	9/19	
psb 2	6/28	6/29	6/28	6/29	7/15	7/15	7/16	7/15	9/19	
psb 3	6/28 10/4	6/29	6/28	6/29 10/2	7/15	7/15	7/16	7/15	9/19	
psb 4	6/28	6/29	6/28	6/29	7/15	7/15	7/16	7/15	9/19	
rad 2	7/1,17	8/29	7/1 7/17		8/29			7/1		
rad 3	7/17		7/17		7/26	7/26				
rec 1	7/11 10/3 10/4	5/17 7/27 9/27	7/11	7/11 10/2	7/11 9/27 10/4 10/5	5/17 7/12 8/27 9/27	5/17 7/12 9/28 10/4	7/12	7/12	Alu1 Dra1 EcoR5 Kpn1 Pst1 Msp1 Xba1
rec 2	7/11 10/4	5/17 7/27	7/11 8/25	7/11	7/11 7/28 10/4	5/17 7/12 8/27	5/17 7/12 8/31 10/4	8/26	9/1	Alu1
rek 4	7/11	7/11	7/11	7/11	7/12	9/28 10/4	7/12	7/12	7/12	Alu1 Msp1
rek 5	7/11		7/11	7/11	7/11	7/12	7/12	7/12	7/12	Msp1
reo2		9/18	7/1	9/18	7/1	7/15	7/15	7/1		
reu 6	6/30 10/4		6/30	6/30	6/30 10/4		10/4			

Table C-3 (continued)

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
rif 3	6/22	6/22 8/.29	6/22 8/.29	6/22	6/27 7/15			6/27 7/15		
rif 4		8/.29	7/1 8/.29	9/18	7/1,15 8/.29 10/1	7/15	7/15a,b 9/19	7/1		
rif 8	5/19 7/17	5/19	7/17 10/2		10/2b	5/19	5/19			
rif 9	5/19 7/17	5/19	7/17 10/2		10/2b	5/19				
rif 10	5/19	5/19	10/2		10/2b	5/19	5/19			
ruc 1	4/18 10/4	4/8 &25 7/27 7/24	4/17 & 25 8/.5 & 25 7/24	4/18 4/25 10/2, 10/3	4/17 4/25 7/28 8/.25	4/27 8/.27 10/2	4/27 8/.31	4/25 8/.26	4/8,18, 25; 8/5 9/1,7/2 6 10/2	Ava2 BamH Alu2 Dra1 Kpn1 Xba1
ruc 3	4/18	4/18 7/24	4/17 7/24	4/18	4/17	4/27	4/27		4/18 7/23, 26	Ava2
ruc 6	4/18	4/18 4/25 7/24	4/17 7/24	4/18	4/17			4/25	4/18 7/23	Dra1 Xba1
ruc 7	4/18	4/18 7/24	4/17 7/24	4/18	4/17				4/18 7/23	
ruc 8	4/18	4/18 7/24	4/17 7/24	4/18 10/2	4/17	10/2			4/18 7/23 10/2	
ruc 9	4/18	4/18	4/17 7/24	4/18	4/17				4/18 7/23	
sca 1	4/18 10/4	4/18 4/25 7/24	4/17 4/25 7/24	4/18 10/2 103	4/17 4/25	4/27 10/2	4/27	4/25	4/8,18, 25 7/23, 26 10/2	Ava2 Dra1 Xba1
sca 2		7/27	4/25 8/.25	4/25	7/28	8/.27	8/.31	8/.26	4/25 9/1 7/23	
sca 3	4/18	4/18 7/24	4/17 7/24	4/18	4/17			4/8 7/23		
sca 4	4/18	4/18	4/17		4/17				4/8,18 7/23	
sca 5	4/18	4/18	4/17		4/17				4/8 ,18 7/23	
sca 6		4/25	4/25 8/.5	4/25	4/25 8/.5	4/27	4/27	4/25	4/25 8/.5	Ava Dra Xba
sca 7	4/18	4/18 7/24	4/17 7/24	4/25	4/17				4/18 7/23	
scl 4	4/18	4/18	4/17	4/18	4/17			4/8 4/18 7/23		
scl 5	4/18	4/18	4/17 7/24	4/18	4/17				4/8 4/18	
sia 1	10/4 6/17	9/29 7/27 6/21	9/29 8/.25 6/17	6/21 10/2	6/21 7/28 7/26	8/.27 7/26 9/29	6/21 8/.31	6/27 8/.26 9/29	6/17 9/1	Alu2 Dra1 EcoR5 Msp1 Pst1 Xba1
sia 2	6/17	6/21	6/17	6/21	6/21	9/29	6/21	6/17	6/17	
sia 3	6/17	6/21	6/17	6/21	6/21	9/29	6/21	6/17	6/17	
sia 5	6/17	6/21	6/17	6/21	6/21	9/29	6/21	6/17	6/17	
sia 6	6/17	6/21	6/17	6/21	6/21	9/29	6/21	6/17	6/17	

Table C-3 (continued)

DNA #	CFO	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1	OTHER ENZYMES
sid 1	7/1,17 10/4	5/17 7/27	7/1,17 8/.25 10/2	7/1,28	10/2a ,2b	5/17 8/.27	5/17 7/17 8/.31	7/1 8/26	9/1	Xba
sip 2	7/17	5/17 7/27	5/17 8/25	7/28	10/2b	5/17 8/27	5/17 7/17 8/31	8/26	9/1	Xba
spd 1	6/28 10/3	6/29 7/27 10/1	6/28 8/25 10/1	6/29 10/1 ,2	7/28 9/20	8/27 9/20 10/1	8/31	3/11 8/26 9/21	9/1	DraI BamH EcoR5 PstI Xba I
spd 2	6/28	6/29	6/28	6/29					3/9	
spd 3	6/28	6/29	6/28 10/1	6/29 10/1	9/20	9/20		9/21		
spd 4	6/28	6/29	6/28	6/29	9/20					
spd 5	6/28	6/29	6/28	6/29	9/20			9/21		
spd 6	6/28	6/29 10/1	10/1	10/1		10/1				
spd 8		10/1	10/1	10/1		10/1				
spds 1	6/28	6/29	6/28	6/29	9/20	9/20		9/21		
spds 4	6/28	6/29	6/28	6/29		9/20		9/21		
spds 5	6/28	6/29	6/28	6/29	9/20	9/20		9/21		
spds 6	6/28 10/3	6/29	6/28	6/29	9/20	9/20		9/21		
spdu 1	6/30	10/1	6/30 10/1	6/30 10/1	6/30	10/1				
Stg	5/26 10/3	7/27	5/25 8/25	10/2	5/25 7/27	8/27	5/26 8/31	5/26 8/26	5/26 9/1	Ava2 Kpn1
uncal 11		4/25	4/25	4/25 10/2	4/25	4/27 10/2	4/23	4/25	4/25 10/2	Ava2 Dra1 Xba1
unfal 7	6/22	6/22 9/14	6/22	6/22	6/27			6/27		
ungre 4		9/30	9/30		10/4					
unk 2		8/29 9/30	8/29		8/29 7/14	7/14	7/14	7/14 10/4	7/14	
unk 3	6/30		6/30	6/30	6/30	7/12	7/12	7/12	7/12	
unk 5	5/19	5/19 10/1	10/1	10/1		5/19 10/1	3/9			
unlil 7	6/22	6/22 9/14 9/29	6/22	6/22	6/27		6/27			
unsps 3	6/28	6/29	6/28	6/29		9/20	8/31		9/1	
unred 4	10/4	9/27			9/27 10/4	9/27	10/4a ,4b			
Xme	5/26		5/25		5/25		5/26	5/26	5/26	Ava2 Kpn1

Table C-4 Preliminary RFLP Summary

Band lengths resulting from incubations of individual enzymes with the diagnostic ITS1-ITS2 rDNA region and gel electrophoresis were compared against a molecular standard (i. e. BMB ladder -- 1114, 900, 692, 501, 489, 404, 320, 242, 190, 147, 124, 110, 57, and 34 bps; Gibco BRL kb ladder -- 1018, 517, 506, 396, 344, 298, 220, 201, 154, 134 and 75 bps; Gibco 100 bp ladder). Distances were hand scored for each gel and then converted to base pairs via a natural log conversion formula. Fragments for each isolate were added together and the average and means of all sums from each reliable run were evaluated to determine the lengths of the uncut ITS1-ITS2 regions and used to help determine representative band lengths for each isolate. (See Chapter V for discussion of anomalies among isolates within each operational taxonomic unit. The band lengths below represent a summary of all isolates within each morphological and/or molecular taxon; slight variations among isolates are not cited nor are extra or partially cut bands shown. Italicized numbers preceding band lengths indicate number of isolates per taxon represented.

Diagnostic runs (within a group of morphologically similar species) are in bold-face; * designates a rare to unique run within a given enzyme. Results are grouped according to generic sections as emended or proposed by Singer (1986) Because many small fragments produced by digestion with Nde2 were not consistently present on the gels, only top band lengths are included. A full discussion of the results can be found in Chapters 4 & 5

DNA #	ITS1-2	CFo1	EcoR1	HinF1	NdE2	PaL1	PvU2	RsA1	SaL1	XhO1
SECTION *PHAEOCOLLYBIA*										
CHR	*1*	*1*	**1*	**1*	*1*	*1* 230	--	--	--	--
	730	410	365	390	420	230				
		320	365	190		170				
				150		100				
SIM	*5*	*5*	*5*	**5*	**5*	*5* **450**	**5*	*5*	**5*	*5*
	715	410	380	**390**	**295**	**265**	605 80	715	**565**	715
		305	335	**255**			30		**150**	
				70						
ATT	*5*	*2*	*5*	*5*	*2*	*2*	**5*	*2*	*5*	*2*
	735	415	385	390	415	460 95	625	735	735	735
		320	350	345		95 84	80 30			
PIC	*8*	*5*	**8*	**8*	*5*	**8*	*5*	*4*	**8*	*5*
	700	385	350	**360**	415	610 90	700	700	515	700
		315	350	**195**					185	
				145						
GRE	*2*	*2*	*1*	*2*	*2*	*2* 450	*2*	*2*	*2*	*1*
	740	425	390	400	410	165	645	740	740	740
		315	350	340		125	95			
RIF	*5*	*4* ---	*5*	**5*	*2*	*5*	*4*	*3*	*1*	---
	730		380	**400**	410	**475**	730	730	**535**	
			350	**190**		**170**			**190**	
				140		**85**				
FAL	*9*	*7*	*9*	*7*	*7*	*7* 470	*3*	*1*	*7*	*1*
	705	400	370	380	395	120	705	705	705	705
		305	335	325		115				
LIL	*6*	*4*	*5*	*5*	*5*	*5* 470	*3*	*1*	*4*	*1*
	705	400	370	380	395	120	705	705	705	705
		305	335	325		115				
OLIA	*5*	*1*	*5*	*5*	*3*	*5* 450	*5*	*3*	*3*	*1*
	720	415	380	390	405	180 90	720	720	720	720
		305	340	330						
OLIB	*7*	*4*	*7*	*6*	*5*	*6* **450**	*7*	**3*	*5*	*1*
	720	415	380	390	410	**100**	**630**	**705**	720	720
		305	340	330		**90 80**	**90**	**?15**		

DNA #	ITS1-2	CFo1	EcoR1	HinF1	NdE2	PaL1	PvU2	RsA1	SaL1	XhO1

Table C-4 (continued)

DNA #	ITS1-2	CFO1	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1
SECTION *PHAEOCOLLYBI* (continued)										
KAU	*8* 740	*7* 420 320	*6* 390 350	*7* 410 330	*7* 405	*8* 235 230 105 90 80	*7* 740	*5* 740	*7* 740	*4* 740
BEN	*5* 715	*5* 410 305	*4* 375 340	*3* 400 315	*3* 400	*5* 450 105 90 70	*5* 625 90	**5* 630 85	*3* 715	*3* 715
RED	*6* 730	*5* 420 310	*4* 385 345	*6* 405 325	*6* 395	*6* 220 220 110 90 90	*5* 640 90	*6* 730	*5* 730	*4* 730
LUT	*10* 730	*8* 410 320	*10* 385 345	**10* 400 190 140	*9* 395	*10* 450 180 100	*10* 635 105	*6* 730	**8* 535 195	*6* 730
SECTION *SUBATTENUATAE*										
AMM	*13.....* 715	*10.....* 410 305	**13* 390 325	*13* 390 325	*12* 405	*12* 400 225 90	*6* 715	*3* 715	*10* 715	*3* 715
SECTION MICROSPORAE										
CAR	*1* 720	**1* 420 200 100	*1* 380 340	*1* 390 330	*1* 405	*1* 245 245 125 105	*1* 640 80	*1* 720	*1* 720	*1* 720
ORE	*7* 720	**5* 420 200 100	*7* 380 340	*5* 390 330	*7* 405	*6* 245 245 125 105	*6* 640 80	*4* 720	*4* 720	*3* 720
SIP	*2* 730	*2* 420 310	*2* 390 340	*2* 410 320	*2* 400	**2* 730	*2* 730	*2* 730	*2* 730	*2* 730
JEN	*1* 740	*1* 410 330	*1* 380 360	*1* 390 350	---	---	---	---	*1* 740	*1* 740
SECTION RADICATAE										
RAD	*2* 730	*2* 420 310	*1* 390 340	*2* 390 340	---	*2* 465 115 95 55	*1* 640 90	*1* 730?? ?	*1* 730	---
DNA #	ITS1-2	CFO1	ECOR1	HINF1	NDE2	PAL1	PVU2	RSA1	SAL1	XHO1

Table C-4 (continued)

DNA #	ITS1-2	CfoI	EcoR I	HinfI	NdeI	PalI	PvuII	RsaI	SalI	XhoI
SECTION VERSICOLORES										
RUP	*6* 690	*6* 400 290	*6* **370** **320**	*6* 365 325	*6* 400	*6* 435 160 95	*3* 600 90	*2* 690	*2* 690	**6* **500** **190**
CAL	*2* 700	*1* 400 300	**2* 350 350	*2* 355 345	*2* 390	*1* 465 140 95	*2* 610 90	*1* 700	*1* 700	*2* 700
SCA	*9* 700	*7* 400 300	**9* 350 350	*9* 355 345	*7* 390	*9* 465 140 95	*3* 610 90	*3* 700	*5* 700	*8* 700
PSEA	*4* 700	*3* 395 305	**4* 350 350	*4* 365 335	*4* 415	*3* 460 155 85	*4* 640 60	*4* 700	*4* 700	*4* 700
PSEB	*4* 700	*3* 400 300	*4* 360 340	*4* 370 330	*4* 405	*3* 440 165 (95)	*3* **605** **95**	*3* 700	*3* 700	*3* 700
SPD	*12* 710	*11* 410 300	*12* 375 335	**12* **395** **125** **110** **70**	**12* **275**	*8* 480 120 110	*9* 615 95	*1* 710	**9* **520** **190**	*2* 710
PLE	*3* 740	*3* 420 320	*3* 390 350	*3* 390 350	*3* 405	*3* **450** **190** **100**	**3* **630** **80** **30**	*3* 740	*3* 740	*3* 740
OUT-TAXA										
DEC	*1* **645**	*1* 340 305	*1* 335 310	*1* 320 325	*1* 345	*1* 440 205	*1* 615 30	*1* 645	*1* 645	*1* 645
STG	*1* **755**	*1* 425 330	*1* 400 355	*1* 355 200 200	*1* 305	*1* 755	*1* 755	*1* 565 190	*1* 755	*1* 600 155
CVA	*1* 740	*1* 565 175	*1* 395 355	*1* 410 330	*1* 405	*1* 310 225 205	*1* 740	*1* 570 170	*1* 740	*1* 740
GYM	*1* 735	*1* 400 225 110	*1* 385 350	*1* 340 305 90	*1* 430	*1* 270 245 220	*1* 735	*1* 735	*1* 735	*1* 735
CAU	*1* 735	*1* 415 320	*1* 395 349	*1* 400 335	*1* 420	*1* 735	*1* 735	*1* 735	*1* 735	*1* 655 80

| DNA # | ITS1-2 | CfoI | EcoR1 | HinfI | NdeI | PalI | PvuII | RsaI | SalI | XhoI |

Appendix C-5 Evaluation of (dis)similarity coefficients and clustering methods

(P. 'ammiratii' vs. P. kauffmanii vs. P. 'luteosquamulosa')

In view of the differing opinions regarding which type of resemblance coefficients and which clustering methods would generate the most reliable and informative phenograms (and considering the almost universal agreement among biostatisticians that no single method produces the most informative results all the time (Sokal & Sneath, 1973; McKelvey, 1982; Abbott et al., 1985; Hibbett & Vilgalys, 1991; Rohlf, 1993; Lutzoni & Vilgalys, 1995; Parmasto, pers. comm., 1996), it was decided to use several different methods initially to test two or three different types of molecular character sets and thus deduce best protocol for testing species hypotheses in *Phaeocollybia*. At this time four new individuals were added to the sample set), of which two represented a third putative species *(P. luteosquamulosa* -- 'lut') within the *P. kauffmanii* complex. Thus it was also possible to test separation of the 'amm' and 'kau' clusters implied during the familiarization process with the numerical analytical programs associated with NT-SYS pc1.80 (Rohlf, 1993).

In NT-SYS, resemblance matrices are generated using one of two algorithms. SIMINT, which computes resemblance indices for continuous data, offers a choice of many different resemblance coefficients of which four were selected for testing:

[i] Average Taxonomic Distance (DIST: NTSYS default coefficient)

$$d_{ij} = \sqrt{1/n \, \Sigma_k (x_{ki} + x_{kj})^2}$$

which has the advantage of being able to handle mixed data composed of both binary and continuous scores. McKelvey (1982) and other authors suggest standardizing input data before using this dissimilarity coefficient for forming matrices;

[ii] Canberra Metric (CANBERRA)

$$d_{ij} = \frac{1/n \; \Sigma_k \; | x_{ki} - x_{kj} |}{\Sigma_k \; (x_{ki} + x_{kj})}$$

suggested by Parmasto (pers. comm. 1996) as producing the most informative trees for corticioid fungi in single-linkage clustering. This coefficient adds a denominator to damp the more straightforward distance computation; its primary disadvantage is its lack of differentiation between instances in which a particular character is missing for two OTUs and instances wherein the character state is the same for two individuals (The CANBERRA coefficient is not appropriate for use in data sets with missing data.)

[iii] Euclidian Distances (EUCLID)

$$E_{ij,} = \sqrt{\Sigma_k (x_{ki} + x_{kj})^2}$$

which, according to Abbott et al. (1985) offers the advantage of being simply extensible to three or more dimensions;

[iv] Average Manhattan Distances (MANHAT)

$$M_{ij,} = 1/n \; \Sigma_k \; | x_{ki} - x_{kj} |$$

which is a 'simple summation of the absolute differences between two objects on each of the variables taken in turn.

Two different coefficients were selected for use with SIMQUAL, which computes resemblance indices for interval (i.e. discrete) data:

[i] Simple matching coefficient (SM; NTSYS default coefficient)

$$SM = m/n$$

for multistate data, and

[ii] Dice (1945) Coefficient (DICE)

$$DICE = 2a / (2a+b+c)$$

for molecular two-state data (i.e. presence or absence) as suggested in Hibbett & Vilgalys (1991).

(Dis)similarity matrices generated using one the above coefficients were then analyzed by three different clustering programs associated with NTSYS pc1.80 (Rohlf, 1993).

[i] Three different SAHN (Sequential, Agglomerative, Hierarchical, and Nested) programs were selected following Rohlf's recommendations that if UPGMA (his default algorithm for the SAHN program) was used, single- and complete linkage algorithms should also be tried since 'if the results are very similar, then the clusters must be rather distinct.' He goes on to observe 'clusters which are identical in both analyses are called 'ball-clusters' (in these clusters the most dissimilar objects within the cluster are more similar to each other than any object within the cluster is to any object outside the cluster). They can be found most easily by computing the strict consensus tree of the single and complete link trees.' (Rohlf, 1993). The three SAHN cluster algorithms selected included

[a] Single-linkage -- also known as 'nearest neighbor linkage'. This method pairs the most similar pairs separated by the smallest distance, and increases the odds that at each subsequent linkage 'OTUs will join an existing cluster rather than form a new one'. (McKelvey, 1982).

[b] Complete-linkage -- Complete linkage (once also termed 'farthest-neighbor linkage) pairs the initial two OTUs as in single linkage, but the next OTU selected is determined by the distance between the 'prospective joiner and the member of an extant cluster farthest away from it' (McKelvey, 1982). Complete linkage tends to form several small tightly knit clusters that stay together. Abbott et al.(1985) note that the algorithm has been sometimes perceived as space-dilating.

[c] UPGMA -- Unweighted Pair-Group Method Arithmetic Average (used in the analyses of the 16 OTU sample set during character selection and evaluation) is considered a compromise between the single-linkage and complete-linkage clustering algorithms. McKelvey (1982) notes that UPGMA generally produces the highest cophenetic correlation values (hence its default status in NTSYS). Sneath & Sokal's (1973) observation that complete-linkage and UPGMA results are closer to each other than either is to single-linkage results was borne out in the current study.

[ii] NJOIN (Neighbor-Joining) -- according to Rohlf, this program computes Saitou & Nei's (1987) neighbor-joining trees as estimated phylogenetic trees and is somewhat similar to agglomerative clustering in that the 'algorithm starts with a matrix of distances among the *t* OTUs and a completely unresolved phylogenetic tree. The closest pair of OTUs is found, merged into a new HTU (hypothetical taxonomic unit) and the original pair of OTUs is deleted until the matrix is reduced to a single HTU and the tree is fully resolved.' Here trees are constructed 'by linking together the two OTUs or HTUs that are the closest mutual "neighbors"'. Rohlf and his co-workers found the Neighbor-joining method to generate 'more accurate trees than either UPGMA or parsimony in most of the models they investigated' Rohlf (1993).

[iii] CONSEN (consensus tree building) -- Rohlf (1993) notes that this consensus tree building program both '...produces a consensus tree and computes the consensus indices from two or more rooted labeled trees.' The program can construct consensus trees by three different methods: 'strict', 'Stinebrickener' and 'majority rule' consensus.These indices indicate the degree to which the consensus tree is fully resolved (i.e. fully bifurcating). In this study consensus trees were evaluated by two consensus indices: [i] $\underline{CI_C}$ (= N set divided by the maximum possible value (i.e. n-2, which for 20 = 18 OTUs) for fully resolved trees. Also known as *consensus fork* or *Colless'* index.) and [ii] $\underline{N\ set}$ =

numerical total of subsets in the consensus tree, excluding the total set and the subsets with a cardinality of '1' (expectations: 2 for OTUs including unified outgroup and unified in-group).

The resulting phenograms generated by each of the above algorithms were then evaluated both by visual inspection and by the COPH (cophenetic value matrix) and MXCOMP (which compares a cophenetic value matrix with a dissimilarity matrix) programs. McKelvey (1982) noted that visual inspection is usually not sufficient to evaluate phenograms since any clustering method will 'invariably produce some kind of cluster dendrogram even when there is no cluster structure in the data.' He further noted that testing the 'internal validity of a numerical solution is best conceived as the ability of a clustering solution or dendrogram to reproduce the original similarity matrix' (McKelvey, 1982). The primary cophenetic correlation fitness measure consulted during the analytical method evaluations was the r-value. This 'computed product-moment correlation' can be loosely interpreted to indicate the following degrees of fitness: ≥ 9.00 = very good fit; ≥ 8.00 good fit; = $\geq$ = poor fit; and ≤ 7.00 = very poor fit (Rohlf, 1993). The r-values also could be used to approximate consensus tree fitness as well. According to Rohlf (1993), in analyses of more than 12 OTUs a correlation of 0.50 is considered statistically significant at the 1% level for comparing two matrices that correspond to two independently derived cladograms, two phenograms, or a phenogram and a cladogram.

SAHN+DICE analyses of individual enzyme subsets -- All SAHN generated phenograms of individual enzyme co-migrating fragments produced three relatively cohesive clusters that supported the three species hypotheses (*i.e. P. ammiratii, P. kauffmanii,* and *P. luteosquamulosa.)*. This outcome was anticipated, as here also insertion-deletions separated the ITS regions of the three OTU groups. These innate length differences were maintained in RsaI and XhoI (where no individual possessed any restriction sites) and could easily explain the length polymorphisms among individuals in CfoI and EcoRI where the estimated band lengths shifted only slightly. More informative phenograms were generated from the presence/absence of comigrating fragments in HinfI, PalI, Pvu2 and SalI. The individuals displayed group-specific and unique banding patterns in PalI that can not necessarily be explained by the ITS insertion/deletion. Additionally, where the 'amm' and 'kau' groups produced similar banding patterns in HinfI and lacked restriction sites in Pvu2 and RsaI, the two 'lut' individuals possessed restriction sites in the latter two enzymes as well as an extra site in HinfI, implying a separation displayed in the phenograms.

For the most part, visual comparison of the different trees produced by different SAHN methods for each enzyme showed little variation. The phenograms produced by all three methods were identical for PalI (all ITS regions cut) and Pvu2 (Only 'lut 2' and 'lut 3' regions cut). The SalI derived phenograms differ in degree of separation displayed among the three groups, with single-linkage characteristically exhibiting a lower degree of separation and complete-linkage a higher. Less easily interpreted are the differences among the three HinfI based phenograms. (The shifting of 'amb 4' to different nodes throughout the analyses is caused primarily by a top band separated by an estimated five base pairs from those of the other 'amm' representatives.) The UPGMA tree places all 'amm' representatives more or less equidistant from the 'kau' and 'lut' clusters (this tree both has the highest r-value and most resembles trees produced by analyses of other character sets). With juxtaposition of all but one 'amm' individual between the 'kau' and 'lut' individuals, the single-linkage method implies a greater degree of separation between the latter two clusters (while the single-linkage derived tree has the lowest r-value, it still has a very good fit of tree to input matrix). The complete-linkage method, on the other hand, not only interposes the 'lut' individuals between the 'amm' and 'kau' clusters, but interposes the 'lut' cluster between 'amb4' and the other 12 'amm' individuals.

NJOIN+EUCLID analyses of individual enzyme subsets -- The phenograms produced by the neighbor-joining algorithm (NJOIN) from Euclidian-distance generated dissimilarity matrices displayed cophenetic correlations that ranged from fair to good and which were consistently lower than the cophenetic correlation values associated with the SAHN+DICE generated trees. There were greater separations depicted among the terminal clusters (this is in part inherent in the neighbor-joining display selected by Rohlf), but in general the results, paralleling those generated by the SAHN algorithms, clearly supported separation of three main OTUs. The SalI derived NJOIN tree corresponds to those generated by the UPGMA and Single-linkage methods, while the HinfI NJOIN tree parallels the UPGMA+DICE generated tree.

Comparison of UPGMA, Single-Link, Complete-Link, and Neighbor-Joining algorithms -- All algorithms produced separation of the 20 individuals into their hypothesized representative OTUs (here assigned at the specific level as *P. ammiratii, P. kauffmanii,* and *P. luteosquamulosa).* Comparison of the r-values revealed that generally [i] the UPGMA algorithm appears to produce higher cophenetic values most of the time, and [ii] while the NJOIN algorithm generally produces the lowest correlation values, it generates trees similar in appearance to those generated by the UPGMA method. It was decided that probably a combination of UPGMA with NJOIN methods would produce the most reliable results throughout the remaining study.

Evaluation of (dis)similarity coefficients for use with UPGMA and NJOIN analytical algorithms Three different molecular character sets were composed for evaluating the coefficients' performances in the UPGMA and NJOIN programs. One combined character set was derived from the presence/absence of all fragments produced by the digestion of all 20 ITS regions in all 9 enzymes. A second character set consisted of one character per enzyme with multistate unordered states derived from placement in previously generated phenograms above. A third character set consisted of the second set, but with 'hypothetical' (i. e. anticipated) values substituted for missing data. (The second two character sets were devised in an effort to avoid the reinforcement of the ITS length variations; however, as noted above, they also would magnify any error during the previous generation of the single-enzyme trees and are no longer deemed reliable. It is far better to evaluate only those enzymes producing clearly dissimilar results and scoring the actual restriction sites rather than the comigrating fragments. While the phenograms generated from the last two methods will not be shown, the results of the coefficient comparisons will be summarized briefly below).

The combined enzyme character set was analyzed by UPGMA with Taxonomic Distance, Dice, and Manhattan coefficients) and NJOIN (with Canberra and Euclidian distance coefficients). Four of the five resulting phenograms implied separation of the 20 individuals into the same three OTUs The taxonomic distance and manhattan distance coefficients generated very similar UPGMA phenograms, with the manhattan-derived trees implying a closer relationship between the doubled-banded and single-banded individuals than the distance-derived trees . The Dice coefficient, which generated a strikingly different phenogram with an exceedingly poor r-value of 0.216, obviously should not be used with this type of combined set as the ITS differences appeared to have been magnified exponentially.

The Euclidian- and Canberra coefficients generated very similar Neighbor-joining trees and, with some minor node shifting within primary clusters, continued to support three main OTUs. The manhattan-derived tree showed a 'good' and the Canberra-derived tree a 'fair' to 'poor' cophenetic correlation.

Identical consensus trees were produced between the Euclidian-derived NJOIN generated trees and the [1] taxonomic distance-derived and [2] manhattan-derived UPGMA generated trees. The cophenetic correlation fitness measures were consistently higher for the NJOIN+taxonomic distance-derived UPGMA tree, however.

Various combinations of coefficients and clustering algorithms were tested. Unfortunately the bulk of these analyses were based on the two somewhat unreliable character sets derived from rescored individual enzyme phenograms. In all instances, the generated trees produced three distinct OTU clusters. Cophenetic correlation value comparisons of phenograms derived from all four coefficients via three different SAHN algorithms awarded UPGMA+distance based phenograms consistently higher R-values than any other combination (this is also the NT-SYS default setting). At the same time comparisons of phenograms derived from all four coefficients via the NJOIN algorithm showed that those derived from the Euclidean coefficient receives generally higher R-values. Additionally, comparison of the NJOIN-generated trees and their r-values suggested that unconstrained trees (those for which no outgroup was designated) were less misleading than constrained trees.

Conclusions: Cophenetic correlation indices obtained from numerous tests of different data sets indicate that the UPGMA and Complete-Linkage algorithms produce fairly similar results. Because the NTSYS default algorithm -- UPGMA -- had also received slightly higher r-values over than those computed for the Complete- or Single-linkage algorithm through the testing phase, it was decided that it would be more efficient to use UPGMA in SAHN-derived phenetic analyses. Similarly the generally high r-values associated with phenograms derived from the default 'distance' resemblance (dissimilarity) coefficients dictated its subsequent use in UPGMA clustering. Euclidian- or 'Distance' derived Neighbor-joining cladograms appeared to be equally well statistically supported and appeared to produce better resolved trees than did Manhattan or Canberra. Considering that more information might be gained by comparing trees derived from at least two different coefficients, it was decided to use the 'taxonomic distance' coefficient with UPGMA and 'euclidian distance' coefficients with NJOIN.

APPENDIX D. Annotated world conspectus of described *Phaeocollybia* species

** = habit illustrations or photographs; + = anatomical drawings*

(...) = distributional citation only; no discussion

Below are listed all species that have been described in *Phaeocollybia*. Diagnostic characters have been briefly summarized, and distribution, sectional classification (*sensu* Singer) and similar species noted. Nomenclatural discussions and observations by other authors are included with a list of complete references for each species.

1. *Phaeocollybia amazonica* Singer in *Sydowia* 15: 77, 1961.

CHARACTERS: small raphanoid deeply rooting basidiomes with brown striate hygrophanous convex-umbonate pilei, yellow-brown young lamellae, slightly swollen yellow-cinnamon hollow stipes, long sharply attenuated pseudorhizae, medium (8.2 x 4.8 µm) marbled-cloudy fusoid beaked basidiospores, variously shaped thin-walled clavate cheilocystidia intermixed with 'pseudoparaphysoid elements' with brown granular contents, non-gelatinized pileipelli, and clamp connections.

DISTRIBUTION: South America (Bolivia) on humus or soil in tropical rain forest

COMMENTS: Section *Subattenuatae* (Singer, 1970*+). *Phaeocollybia amazonica* is similar to *P. ammiratii* (which differs in its well developed ixocutis and stuffed stipe) and *P. oligoporpa* (which produces larger, more robust basidiomes). Horak's (1977) synonymy of *P. amazonica* with the macroscopically similar *P. subattenuata* is rejected by Bandala & Montoya (1994), who note the absence of apical callus on the basidiospores in *P. subattenuata*. Other differences exhibited by *P. subattenuata* include short abrupt pseudorhizae, punctate-roughened basidiospores, narrower cheilocystidia, and slightly gelatinized hyphae in the pileipellis.

2. *Phaeocollybia ambigua* Horak & Halling in *Mycologia* 83: 464, 1991

CHARACTERS: medium-sized raphanoid, bitter-tasting, deeply rooting basidiomes with date-brown viscid conic-campanulate pilei, pallid young lamellae, brownish-orange stipe apices, gradually tapering pseudorhizae, small (~6.5 x 4 µm) ellipsoidal minutely warted basidiospores, subclavate to clavate frequently septate thin-walled cheilocystidia, and no clamp connections.

DISTRIBUTION: South America (Colombia) & Central America (Costa Rica).

(P.ambigua continued)

COMMENTS: Section *Phaeocollybia* (Bandala & Montoya, 1994). Horak and Halling note the similarities of *P. ambigua* to *P. hilaris ss. auct. mex.*, a species associated with *Pinus* that is characterized by smaller basidiospores and very long thin-walled cylindrical subcapitate cheilocystidia. (Bandala & Montoya (1994*), who examined the type specimens, report considerably longer (to 8 µm) basidiospores and more uniformly narrow (only to 4.8 µm) cheilocystidia than reported in the type description.) Horak and Halling (1991) also suggest an affinity with *P. subarduennensis*, which differs in having clamp connections and thick-walled refractive capitulate cheilocystidia.

ADDITIONAL REFERENCE: Bandala, 1994*+; Halling, 1997*.

3. ***Phaeocollybia ammiratii nom. prov.***

CHARACTERS: See Chapter 6 for a complete technical description. Diagnostic characters include relatively large stature, viscid butterscotch colored pilei, vinaceous tinged relatively slender stuffed stipes, moderately large verrucose beaked limoniform basidiospores, well-developed bilaminate ixocutis, thin-walled cylindrical cheilocystidia, medallion-like clamp connections and mild Syringaldazine reactivity.

DISTRIBUTION: North America (British Columbia, Washington, Oregon, California).

COMMENTS: The only representative of Section *Subattenuatae* in the Pacific Northwest. In size, and general basidiospore and cheilocystidial morphology *P. ammiratii* resembles other members of the *P. kauffmanii* complex -- *P. benzokauffmanii, P. kauffmanii, P. luteosquamulosa,* and *P. redheadii* -- all of which lack clamp connections. *Phaeocollybia ammiratii* is also similar to *P. amazonica* (which lacks a well-developed ixocutis and has a hollow stipe) and *P. oligoporpa* (which lacks a well-developed gelatinous matrix in the suprapellis and incrusting pigments in the subpellis).

ADDITIONAL REFERENCES: Norvell, 1998; Smith, 1949* (as *P. kauffmanii).*

4. ***Phaeocollybia amygdalospora*** Bandala & Horak in Bandala, Montoya, Guzmán & Horak, *Mycological Research* 100: 239, 1996+.

CHARACTERS: Small slender rooting basidiomes with yellowish-brown violet tinged subviscid hygrophanous subconic-expanded pilei, pale violaceous young lamellae, apically violaceous fragile subcartilaginous stipes, medium-sized (6.5-9 x 4-5 µm) warty-verrucose amygdaliform basidiospores, thin-walled clavate cheilocystidia, pileipelli composed of gelatinized suprapelli with yellow-brown plasmatic pigments over subpelli with yellowish-brown incrusting pigments, no clamp connections.

DISTRIBUTION: North America (Mexico); solitary under *Pinus.*

(P. amygdalospora continued)

COMMENTS: Section *Phaeocollybia*. Considered closely related to *P. singeri* (with slender, pip-shaped spores and wider cheilocystidia) and *Phaeocollybia procera* (with more apically rounded basidiospores), both associated with angiosperms.

5. *Phaeocollybia arduennensis* Bon in *Documents Mycologique* 9: 42, 1979.

CHARACTERS: Very small dark fragile basidiomes with dark reddish to purplish brown lubricous fibrillose-silky striate convex-umbonate pilei, pale buff young lamellae, tough rooting stipes, small (5-6 x 3-4.5 µm) minutely verruculose ellipsoidal basidiospores, 4-7 µm wide capitate cylindrical thin-walled cheilocystidia, non-gelatinized pileipelli with incrusting pigments, and clamp connections.

DISTRIBUTION: Europe (Austria, France, Germany, Great Britain, Norway, Sweden); associated with *Picea* and *Abies*.

COMMENTS: Section *Radicatae* (Singer, 1986, 1987; Bandala & Montoya, 1994). Bon (1979) found that this species shared clamp connections, small basidiospores, and capitulate refractive cheilocystidia with *P. radicata*, which, however, lacked the purplish tones, small stature, non-viscid pileus, wider spores, and low degree of gelatinization in the pileipellis characteristic of *P. arduennensis*. Watling & Gregory (1993) noted similarities between *P. arduennensis* and *P. jennyae*, which has narrower, non-capitate thin-walled filamentous cheilocystidia. Singer (1987) noted the similarity of *P. arduennensis* to *P. subarduennensis*, which has a taller narrower pileus, closer lamellae, longer stipes, and slightly larger spores. The Mexican collections cited as *P. arduennensis* by Bandala, Guzmán & Montoya (1989) were later assigned to *P. subarduennensis* by Bandala & Montoya (1994+).

ADDITIONAL REFERENCES: Bandala, 1994, Bon, 1992; Gulden, 1983, 1992; Jacobsson & Stridvall, 1983; Krieglsteiner 1991; Laber 1982, 1991.

6. *Phaeocollybia attenuata* (Smith) Singer in *Lilloa* 22: 567, 1951.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the subviscid tawny yellow brown broadly campanulate pilei, shiny slender hollow corneous stipes, criniform pseudorhizae, large warty-rugulose subglobose-limoniform basidiospores, a bilaminate pileipellis with incrusting and intraparietal pigments, thin-walled clavate cheilocystidia, no clamp connections, and negative Syringaldazine reaction.

DISTRIBUTION: North America (British Columbia, Washington, Oregon, California).

COMMENTS: Section *Phaeocollybia* (Smith, 1957b; Singer 1970, Bandala & Montoya, 1994). Closely related to *P. neosimilis*, *P. similis*, *P. 'similis' sensu* Smith. There are some

(P. attenuata, continued)

confusing misidentifications in Phillips' (1991) Mushrooms of North America by Phillips: the plate labeled as *P. attenuata* in fact depicts *P. piceae* whereas the plate said to represent *P. similis* (*sensu* A. H. Smith) depicts *P. attenuata.*

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; (Goward, Redhead & Ryan, 1993); Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987; Horak, 1977+; Norvell, 1998*; (Redhead, 1997); Singer 1975, 1986, 1987; Smith, 1937*, 1957b*+; Smith, Smith & Weber, 1979; Smith & Trappe, 1972.

7. *Phaeocoilybia australiensis* Rees & Wood in *Mycotaxon* 52: 101, 1996*+.

CHARACTERS: Large basidiomes with dry buff-colored smooth convex to plano-reflexed pilei, pale mauve young lamellae, stuffed mauve stipes, vertical-monopodial pseudorhizae, large (9 - 12 x 5 - 6.5 µm) very faintly punctate elongated limoniform basidiospores, fusoid to ventricose-rostrate capitate refractive cheilocystidia, and no clamp connections.

DISTRIBUTION: Australia (New South Wales) singly on the ground in *Eucalyptus*-dominated dry sclerophyllous forest.

COMMENTS: Section *Versicolores.* The somewhat similar *P. singularis* has a smaller, darker pileus and smaller, less ornamented spores.

ADDITIONAL REFERENCE: (May & Wood, 1997).

8. *Phaeocollybia benzokauffmanii nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the massive fleshy stature, the pinkish brown-drab coloration, large verrucose limoniform basidiospores, thin-walled narrowly clavate cheilocystidia, well-developed ixocutis with no incrusting pigments, no clamp connections, and strongly positive Syringaldazine reaction.

DISTRIBUTION: North America (Washington, Oregon, California)

COMMENTS: Section *Phaeocollybia. Phaeocollybia benzokauffmanii* is anatomically closest to *P. kauffmanii* (which lacks the drab to pinkish-brown coloration and has incrusting pigments within the subpellis), *P. redheadii* (which has a tawny pileus, larger basidiospores and has incrusting pigments within the subpellis) and *P. gregaria* (which has a generally smaller stature and lacks the proliferating pith in the stipe interior).

ADDITIONAL REFERENCES: Norvell, 1998*.

9. *Phaeocollybia bicolor* Horak in *Sydowia*, Ser. II. 29: 64, 1977.

CHARACTERS: Small unpleasant smelling, non-pseudorhizal basidiomes with dry drab and light brown innately fibrillose inrolled conical pilei, violaceous young lamellae (with conspicuous blue edges when mature), bulbous stipes, small (3.4-4.5 x 2.5-3) oval asperulate basidiospores, filiform thin-walled cheilocystidia, and numerous clamp connections.

DISTRIBUTION: Australasia (New Guinea) in *Nothofagus* forests.

COMMENTS: Assigned to Section *Radicatae* by Bandala & Montoya (1994). The absence of a pseudorhiza and gelatinized hyphae suggests that this species may not belong in *Phaeocollybia*.

ADDITIONAL REFERENCES: (Garrido, 1988).

10. *Phaeocollybia brasiliensis* Araujo ex Singer in *Mycologia Helvetica* 2: 257, 1987.

CHARACTERS: Small mild-smelling basidiomes with dry blackish brown hygrophanous striate pilei, blackish slender stipes, large (7.7-10.3 x 5.3-6.5) punctate-roughened beaked limoniform basidiospores, ?thick-walled refractive capitulate lageniform cheilocystidia, pileipellis with a non-gelatinized to slightly gelatinized suprapellis and subpellis with strongly incrusting pigments, 'dermatocystidia' [?= tibiiform diverticula?] similar to the cheilocystidia, and clamp connections.

DISTRIBUTION: South America (Brazil).

COMMENTS: Section *Subattenuatae* (Singer 1986, 1987; Bandala & Montoya, 1994). The macroscopical characters listed in the Latin type description are minimal, and no mention is made of lamellar colors, stipe length, or the existence of a pseudorhiza. The accompanying and somewhat confusing sketch neither gives information on stipe/pseudorhizal length nor depicts any clamp connections.

11. *Phaeocollybia californica* Smith in *Brittonia*, 9: 216, 1957b*+.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include viscid orange brown campanulate pilei, hollow stipes with thick cartilaginous cortices, racemose pseudorhizae, large verrucose-roughened prominently beaked sublimoniform basidiospores, bilaminate pileipellis with incrusting pigments, thick-walled refractive capitulate fusoid cheilocystidia, no clamp connections (untested in Syringaldazine).

DISTRIBUTION: North America (California, Mexico, Oregon).

(P. californica, continued)

COMMENTS: Section *Versicolores* (Singer, 1986; Bandala & Montoya 1994). Very closely related to *P. rufotubulina* (with moist to lubricous bright reddish orange pilei and tubular strict stipes) and *P. scatesiae* (with pale yellow brown to dark brown glutinous pilei and densely cespitose habit).

ADDITIONAL REFERENCES: Arora, 1981*; Bandala, 1994*+; Bandala, Guzmán & Montoya, 1989*+; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987; Horak, 1977+; Lincoff, 1981; Norvell, 1995a, 1998; Norvell & Ammirati, 1993, 1995; Smith, 1980; Smith & Trappe, 1972

12. *Phaeocollybia carmanahensis* Redhead & Norvell, *Mycotaxon* 46: 346, 1993*+.

CHARACTERS: (Synonym of *P. oregonensis.)* Small to medium sized deeply rooting basidiomes with viscid drab brown conical pilei, smoky drab young lamellae,slender stuffed stipes, vertical-monopodial pseudorhizae, small minutely roughened ellipsoidal ('bullet-shaped') basidiospores, thin-walled clavate cheilocystidia, an ixocutis with a highly gelatinized suprapellis, no clamp connections.

DISTRIBUTION: Holotype from Vancouver Island, British Columbia, Canada in ancient mixed coniferous *(Tsuga, Picea, Abies)* temperate rainforest.

COMMENTS: Section *Microsporae.* See *P. oregonensis* in Chapter 6 for complete technical description.

ADDITIONAL REFERENCES: (Goward, Redhead & Ryan, 1993); Norvell, 1995a, 1998; Redhead, 1997.

13. *Phaeocollybia caudata* Horak & Halling in *Mycologia* 83: 466, 1991

CHARACTERS: Large raphanoid deeply rooting basidiomes with subviscid argillaceous to pale orange brown minutely squamulose convex-campanulate pilei, pale argillaceous young lamellae, concolorous brittle hollow stipes abruptly tapering to dark brown thread-like pseudorhizae, small (5-6 x 3-4 µm) minutely verruculose ellipsoidal (pruniform to pip-shaped) basidiospores, capitate tibiiform refractive cheilocystidia, no clamp connections.

DISTRIBUTION: South America (Colombia), Central America (Costa Rica); in *Quercus* forests.

COMMENTS: Section *Microsporae* (Bandala & Montoya, 1994). Halling (1997*+) mentions that the minutely squamulose pileus surface was originally overlooked in the original description. The most distinct field character is the abruptly tapering pseudorhiza just below the stipe base; microscopically it is noted for its small ovoid to pip-shaped basidiospores. *Phaeocollybia caudata* is similar to *P. querqueti* (which has less tapered pseudorhizae and a soapy odor) and *P. ratticauda* (Rees & Wood, 1996).

14. *Phaeocollybia christinae* (Fr.) Heim, *Encyclopédie Mycologique* 1: 71. 1931.

Basionym: *Agaricus christinae* Fries in *Epicrisis*. p. 192. 1833-1838.

= *Phaeocollybia laterarius* A. H. Smith in *Brittonia*. 9: 205. 1957.

= *Phaeocollybia hilaris sensu* Romagnesi

? = *Phaeocollybia rufipes* Bigelow in Bigelow & Barr, *Rhodora* 65: 297. 1963.

non Phaeocollybia christinae Heim sensu Heim (= *Phaeocollybia jennyae* (Karst.) Heim)

CHARACTERS: Small almond-smelling deeply rooting basidiomes with viscid brick red to brownish orange viscid campanulate pilei with sharply peaked umbos, yellowish ochre young lamellae, reddish thin hollow stipes, pseudorhizae, large (9-11 x 4.5-6 µm) punctate roughened long ellipsoidal basidiospores, thin-walled clavate cheilocystidia, no clamp connections.

DISTRIBUTION: Northern temperate -- Europe, Asia (China, Japan, Russia), and North America (eastern Canada and United States, Mexico); on soil under *Picea and Abies*.

COMMENTS: The sectional placement of *P. christinae* is as confusing as the historically shifting concepts surrounding its name. Initially Singer (1970) typified his new Section *Microsporae* with *P. christinae*, not realizing that Heim had confused *P. christinae* (now recognized to have large spores and thin-walled clavate cheilocystidia) and *P. jennyae* (recognized as having small spores and capitulate cheilocystidia with thick-walled refractive necks) when he described his new genus. Later recognizing the confusion, Singer (1986, 1987) corrected the name of the type of Section *Microsporae* to *P. jennyae*, moving *P. christinae* back to Section *Phaeocollybia* where it had originally been placed by Smith (1957b) (and where Bandala & Montoya (1994) retain it).

The character information above is based on illustrations and descriptions by Fries (1836-38, 1857, 1884), Gulden (1983, 1992), and Moser (1983). Fries, who named the mushroom after his wife, noted that in stature it resembled *Hygrophorus conicus*.

Although Horak (1977) has placed both *P. laterarius* and *P. rufipes* in synonymy with *P. christinae*, he is recently re-evaluating the status of *P. rufipes*, which he considers may represent an independent species (Horak pers. comm., 1997). It may well be that eventually North American material will be more properly represented by that name. Excellent descriptions of North American material can be found in Smith (1957b), Redhead & Malloch (1986), and Bandala (1994).

ADDITIONAL REFERENCES: Arora, 1981; Bandala, Guzmán & Montoya, 1989+; Bon, 1992; Bresadola, 1930*; Bresinsky, 1960; Farlow & Burt, 1929*; Farr & Farr, 1976; Goetz, 1975; Goetz, 1979; Goetz, Barnhart & Barnhart, 1987; Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987; Heim, 1930*; Imai, 1938; Imazeki & Hongo, 1969; Jacobsson & Stridvall, 1983; Karpenko, 1988; Karsten, 1879; Keissler & Lohwag, 1937; Konrad &

(P. christinae, continued)

Maublanc, 1948; Krieglsteiner 1991; Kühner 1980; Kühner & Romagnesi, 1953; Laber 1982, 1991; Lange & Hora, 1963*; Minot, 1989; (66); Moser & Jülich 1994; Murrill, 1917; Nezdoiminogo 1986, 1990; Norvell, 1998; Phillips, 1991*; Poelt & Jahn, 1963*; Ricken, 1920; (Romagnesi, 1942); Saccardo, 1916; Smith, 1952; Smith & Trappe, 1972; Teng, 1996; (Velenovsky, 1921); Zang, 1996.

15. *Phaeocollybia cidaris* (Fr.) Heim in *Encyclopédie mycologique* 1: 71, 1931.
Basionym: *Agaricus cidaris* Fries. *Epicrisis.* p. 192. 1836-38.

CHARACTERS: Very small mild-smelling rooting basidiomes with reddish smooth papillate conic-campanulate pilei, amber-colored young gills, apically reddish slender slightly compressed hollow stipes, long brownish thin pseudorhizae, moderately large amygdaliform apically conspicuously attenuated basidiospores, refractive capitulate cheilocystidia, and no clamp connections.

DISTRIBUTION: Europe (Austria, Finland, France, Germany, ?Norway, Sweden), Asia (eastern Siberia).

COMMENTS: *Phaeocollybia cidaris* is placed into Section *Versicolores* by Singer (1986) and Bandala & Montoya (1994). (In the 1986 publication Singer also included the line '*P. cidaris* (Fr.) Romagnesi (sensu Karst., Horak) under Section *Radicatae*, which he subsequently (1987) requested be eliminated). Horak (1977*+), who agreed with Karsten's (1879) concept of this species, noted that Ricken's (1915) and Kühner & Romagnesi's (1957) concepts of *P. cidaris* represented *P. jennyae.* Bandala et al. (1996*+) suggest that material cited as representing *P. cidaris* by Gulden (1983) is very close to their newly described *P. pseudolugubris.*

It should be noted that *Agaricus cidaris* var. *minor* is felt to represent an independent non-pseudorhizal species (Laber & Marklund, 1992) and is now considered a synonym of *Stagnicola perplexa (q. v.)*

The character information above is drawn from descriptions by Fries (1836-38, 1857), Karsten (1879) and Bandala et al. (1996).

ADDITIONAL REFERENCES: Bandala, 1994*; Bon, 1992; Bresinsky, 1960; Gulden, 1992; Jacobsson & Stridvall, 1983; Konrad & Maublanc, 1948; Laber, 1991; Moser 1983; Nezdoiminogo 1986; Poelt & Jahn, 1963*; Ricken, 1920; (Romagnesi, 1942); Singer, 1986.

16. ***Phaeocollybia columbiana*** Singer in *Flora Neotropica* 4: 6, 1970*+.

CHARACTERS: Small deeply rooting basidiomes with rusty 'spadiceous' dry to moist transparent-striate slightly hygrophanous marginally crenate papillate conic pilei, ochraceous brown lamellae, apically ochraceous equal hollow ('canaliculate') stipes, long thin pseudorhizae, very large (10-11 x 6.5-8 µm) punctate roughened variably mucronate ellipsoidal basidiospores, [refractive] capitulate fusoid-ventricose cheilocystidia, subpelli with brownish incrusting and parietal pigments, no clamp connections.

DISTRIBUTION: South America (Colombia)

COMMENTS: Section Versicolores (Singer 1970, 1986; Bandala & Montoya, 1994). Singer considered *P. columbiana* to be very close to *P. californica* (which has slightly shorter but much narrower basidiospores).

ADDITIONAL REFERENCES: (Bandala, 1994); Horak, 1977.

17. ***Phaeocollybia coniuncta*** Horak in *Sydowia* 33: 106. 1980*+.

CHARACTERS: Small raphanoid rooting fasciculate basidiomes with subviscid "...dirty (slightly yellowish) brown" minutely fibrillose acutely conic striatulate pilei, whitish to yellowish young lamellae, pallid to reddish brown cartilaginous hollow stipes, large (9-10 x 5-6.5 µm) verrucose limoniform basidiospores, 'inconspicuous' thin-walled cylindrical cheilocystidia, subpelli with encrusting yellowish-brown pigments, and no clamp connections.

DISTRIBUTION: India, Asia (China) at high elevations in coniferous (*Abies)* forests..

COMMENTS: Neither Singer (1986) nor Bandala & Montoya (1994) treat *P. coniuncta,* although it appears to belong to Section *Phaeocollybia* based on the type description. Horak (1980) noted the similarity of *P. coniuncta* to another Indian species, *P. spoliata* (which is characterized by distinctly capitate to subcapitate cheilocystidia) and to *P. similis* and *P. piceae.* Abraham (1992*+) refers a collection from Kashmir to this species; the specimens described, however, obviously belong elsewhere as they have much smaller basidiospores, ventricose-capitate cheilocystidia, and possess clamp connections.

ADDITIONAL REFERENCE: Zang, 1996*.

18. ***Phaeocollybia corneri*** Horak in *Sydowia,* Ser. II. 29: 65, 1977.

CHARACTERS: Large radish-tasting deeply-rooting basidiomes with subviscid reddish brown smooth to apically squamulose estriate convex to plano-papillate campanulate pilei, pale tawny young lamellae, hollow cartilaginous fusoid ferruginous stipes, small (4.5-5.5 x 3-3.5 µm) ovoid asperulate basidiospores, filiform to cylindrical cheilocystidia, subgelatinized

(P. corneri, continued)

pileipelli with yellow-brown incrusting pigments, and no clamps.

DISTRIBUTION: Australasia (Borneo, Singapore).

COMMENTS: Section *Microsporae* (Singer 1986, 1987; Bandala, 1994*+, Bandala & Montoya, 1994). Bandala et al. (1996*+) consider *P. herrerae* (with subellipsoid spores and more irregularly slightly broader cylindrical to filamentous cheilocystidia) closely related to *P. corneri.*

19. *Phaeocollybia deceptiva* Smith & Trappe in *Mycologia* 64: 1142, 1972.

CHARACTERS: Large deeply rooting basidiomes with moist tawny to yellowish brown hygrophanous conic to plano-umbonate pilei, cinnamon lamellae, pallid fleshy non-cartilaginous stipes, pallid pseudorhizae, large (8-10 x 4.5-6 µm) coarsely warty-rugulose elliptical basidiospores lacking apical beaks, no true cheilocystidia (if present then indistinguishable from basidioles), and poorly formed non-gelatinized suprapellis with large looping clamp connections. Tibiiform diverticula absent.

DISTRIBUTION: Only one known collection from North America (Idaho).

COMMENTS: Excluded species lacking a cartilaginous stipe cortex, gelatinized tissues, and tibiiform diverticula that more properly belongs in *Cortinarius* (See Chapter 6). Bandala & Montoya (1994) placed *P. deceptiva* into Section *Subattenuatae* based on the type description.

ADDITIONAL REFERENCES: Arora, 1981; (Bandala, 1994); Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Horak, 1977.

20. *Phaeocollybia dissiliens* Smith & Trappe in *Mycologia* 64: 1143. 1972.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the viscid bright orange pileus, hollow stipes with unusually thick cartilaginous rinds, small punctate-roughened ellipsoidal basidiospores, well developed bilaminate ixocutis with incrusting pigments, thin-walled cylindrical cheilocystidia, clamp connections, negative Syringaldazine reaction.

DISTRIBUTION: North America (Oregon); uncommon in lowland coastal *Picea* forests.

COMMENTS: Section *Radicatae.* Placed into synonymy with *P. radicata* by Horak (1977) which, however, has less brightly colored, smaller and more fragile basidiomes and refractive capitulate tibiiform cheilocystidia. Microscopically very close to *P. sipei*, which lacks clamp connections.

ADDITIONAL REFERENCES: Arora, 1981; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Norvell, 1995a, 1997+.

21. ***Phaeocollybia elaeophylla*** Singer in *Mycologica Helvetica.* 2: 257. 1987.

CHARACTERS: medium-sized deeply rooting basidiomes with viscid brown hygrophanous papillate-campanulate pilei, olivaceous young lamellae, apically pallid cinnamon equal to fusoid stipes, abruptly tapering pseudorhizae, large (8.5-10.3 x 4.5-6.5 µm) punctate-roughened beaked inequilaterally ellipsoid-fusoid basidiospores with plage and germ pore, thin-walled clavate cheilocystidia *[q.v.]*, pileipellis with incrusting pigments in both layers, and clamp connections.

DISTRIBUTION: South America (Brazil)

COMMENTS: Section *Subattenuatae* (Singer 1986, 1987; Bandala & Montoya 1994). The highly branched unusual cheilocystidia depicted by Singer greatly resemble the apical outgrowths previously observed on numerous old or improperly stored Phaeocollybias and may have no taxonomic significance.

22. ***Phaeocollybia fallax*** Smith in *Brittonia*, 9: 202, 1957*+

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include the viscid to glutinous olive green pileus, brilliant violet young lamellae, moderately large verruculose-verrucose sublimoniform basidiospores, well-developed bilaminate ixocutis with diffuse pigments, secretory thin-walled clavate cheilocystidia, no clamp connections, and negative Syringaldazine reaction.

DISTRIBUTION: North America (British Columbia, California, Idaho, Mexico, Oregon, Washington); reported also from Europe

COMMENTS: Section *Phaeocollybia* (Singer 1986; Bandala & Montoya, 1994). One of the most colorful of all Phaeocollybias, this species forms a closely related microscopical complex with *P. festiva, P. lilacifolia, (P. longipes),* and *P. rifflipes.*

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994*+; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Horak, 1977+; Lincoff, 1981*; Norvell, 1998; Phillips, 1991*; (Redhead, 1997); Smith, 1975*; Smith & Trappe, 1972; Smith, Smith & Weber, 1979

23. ***Phaeocollybia festiva*** (Fr.) Heim in *Encyclopédie mycologique* 1: 70, 1931.

CHARACTERS: See discussion under *P. rifflipes* in Chapter 6. Key characters include the viscid olive-green to olive brown pileus, buff to violet young lamellae, moderately large marbled-roughened beaked limoniform basidiospores, well-developed bilaminate pileipellis with diffuse pigments, thin-walled narrowly clavate cheilocystidia, no clamp connections.

(P. festiva, continued)

DISTRIBUTION: Under *Picea* in Europe, Asia (Japan, Siberia) and ?eastern North America; under *Nothofagus* in New Zealand (as *P. longipes*),.

COMMENTS: *Phaeocollybia festiva*, the type species of Section *Phaeocollybia* (Smith 1957b; Singer 1970, 1986; Bandala et al. 1994), is part of a complex of closely related species including *P. fallax*, *P. lilacifolia*, *P. longipes* and *P. rifflipes*. Horak (1977) suggested that *P. festiva* and *P. longipes* are conspecific.

Note: line drawings depicting the 'marginal cystidia' by Watling & Gregory (1993) are properly illustrated in Fig. 132, not Fig. 135 as is cited in the legend.

ADDITIONAL REFERENCES: Arora, 1981; (Bandala, 1994); Bon, 1992; Bresadola, 1930*; Bresinsky, 1960; Dennis, Orton &Hora, 1960; Fries, 1836-38, 1857; Garrido, 1988; Goetz, 1979; Gulden, 1983, 1992; Imai, 1938*; Jacobsson & Stridvall, 1983; Karsten, 1879; Konrad & Maublanc, 1948; Krieglsteiner 1991; Kühner 1980; Kühner & Romagnesi, 1953, 1957; Laber 1982*; Laber, 1991; (66); Moser 1983; Moser & Jülich 1994; Nezdoiminogo 1986, 1990; Poelt & Jahn, 1963*; Reid, 1972*; Ricken, 1920; (Romagnesi, 1942); Saccardo, 1916; Singer, 1951b; Smith, 1937, 1949, 1957b; Smith & Trappe, 1972; Smith, Smith & Weber, 1979.

24. *Phaeocollybia flava* Araujo ex Singer in *Mycologia Helvetica* 2: 258, 1987.

CHARACTERS: Small rooting basidiomes with subviscid amber yellow centrally papillate convex pilei, greenish yellow lamellae, yellow equal stipes, pseudorhizae, small (5-5.5 x 4.5-5) subovoid asperulate basidiospores, ampullaceous or ventricose subcapitate cheilocystidia, subgelatinous pileipelli with incrusting brownish and yellow pigments in the subpellis, clamp connections.

DISTRIBUTION: South America (Brazil); solitary in argillaceous soil in mixed tropical forest.

COMMENTS: Although Singer (1987) introduces *P. flava* with *P. subarduennensis* in the key to species within Section *Radicatae* (p. 252), he brackets (Section Subattenuatae) after the species name in the type description (p. 257). Given the small size of the spores, the former assignment is obviously correct. The status of the species is not clear in Singer's own mind, and he notes a close affinity with *Gymnopilus*, particularly in view of the strong dextrinoid reaction observed in mature spores. Singer justifies placement in *Phaeocollybia* with the presence of a glabrous stipe, subgelatinous pileipellis and subviscid pileus, and the characteristic pseudorhiza. Macrochemical reactions on dried material (a slight rusty flush noted with NH4OH; and then a chestnut darkening to blackish chestnut after application of KOH) appear to have been inconclusive with respect to generic placement.

25. *Phaeocollybia gregaria* Smith & Trappe, *Mycologia* 5: 1143, 1972.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the dull wood brown color of the basidiomes, large verruculose amygdaliform basidiospores, and narrowly clavate cheilocystidia.

DISTRIBUTION: North America (Oregon) in coastal *Picea* rainforests.

COMMENTS: Section *Phaeocollybia* (Singer 1987). Horak (1977) placed *P. gregaria* in synonymy with the microscopically very similar *P. piceae.* In view of the smaller stature, frequently bitter taste, bright orange pigments, and more abundant subcapitate thin-walled cheilocystidia found in the latter species, however, I choose to retain *P. gregaria* as an independent species.

ADDITIONAL REFERENCES: Arora, 1981; Goetz, 1975, 1979; Norvell, 1995a, 1997.

26. *Phaeocollybia guzmanii* Bandala & Montoya, *Mycotaxon* 52(2): 411. 1994+.

CHARACTERS: Small shallowly rooting basidiomes with viscid brownish to brownish orange striatulate convex-umbonate pilei, yellow brown young lamellae, narrow thin stipes, small (4.8-6.4 x 3.2-4 µm) ovoid to ellipsoid asperulate to minutely punctate basidiospores, thin-walled cylindrical to subcapitate clavate cheilocystidia, and an absence of clamp connections.

DISTRIBUTION: North America (Mexico), gregarious under conifers.

COMMENTS: Section *Microsporae.* This was first reported as *P. hilaris* by Bandala, Guzmán & Montoya, 1989*+; as is noted below, however, the taxonomy of *P. hilaris* is highly confused. Bandala and Montoya (1994) also note similarities of *P. guzmanii* to *P. jennyae* (which differs in its subglobose basidiospores and narrow filamentous cheilocystidia) and *P. rancida* (which differs in its rancid odor, young lilac lamellae and stipe context, and ventricose-fusoid cheilocystidia.

ADDITIONAL REFERENCE: Bandala, 1994*+.

27. *Phaeocollybia hamadryas* (Fr.) Heim, *Encyclopédie mycologique* 1:71, 1931.

COMMENTS: Included by Fries (1857) in a group of species that was later to form the core of the genus, this species is not generally included in modern monographic treatments of *Phaeocollybia.* After Heim (1931) included the species in his new genus, Romagnesi (1942) listed *P. hamadryas sensu* Cooke as a possible *Phaeocollybia.* Singer (1940) dismissed *Naucoria hamadryas sensu* Smith as a synonym of *Alnicola bohemica*, but did include *P. hamadryas sensu* Cooke in *Phaeocollybia* in his first edition of the *Agaricales in Modern Taxonomy* (Singer, 1951b). The epithet 'hamadryas' is not found in the fourth

(P. hamadryas, continued)

edition of the *Agaricales* (Singer, 1986) and appears to have been abandoned by modern workers.

28. *Phaeocollybia herrerae* Bandala & Montoya in Bandala, Montoya, Guzmán & Horak, *Mycological Research* 100: 240, 1996+.

CHARACTERS: Small deeply rooting basidiomes with viscid reddish-tinged yellowish brown to cinnamon brown translucent-striate subacute conic to subconvex-umbonate pilei, pale yellow young lamellae, pale brown to orange subcylindrical hollow subcartilaginous stipes, long pseudorhizae, very small (5-5.5 x 2.5-3 µm) subellipsoid to subovoid verrucose basidiospores, filamentous to cylindrical thin-walled cheilocystidia, gelatinized pileipelli with incrusting yellowish-brown pigments, and no clamp connections.

DISTRIBUTION: North America (Mexico)

COMMENTS: Placed into Section *Microsporae* by its authors, this species is closely related to *P. corneri* (which differs in its ovoid basidiospores and uniformly cylindrical cheilocystidia).

ADDITIONAL REFERENCES: Bandala, 1994*+.

29. *Phaeocollybia hilaris* (Fr.) Heim, *Encyclopédie mycologique* 1:71, 1931.

CHARACTERS: Small gregarious to cespitose basidiomes with pale reddish-brown campanulate, yellowish lamellae, equal yellowish equal stipes

DISTRIBUTION: Europe (on the ground under conifers.

COMMENTS: The description above is based on Fries (1821, 1836-38, 1857). Unfortunately the modern species concept is highly confused. Singer (1986) notes: "It is difficult to decide whether the original... corresponds to *Naucoria hilaris* sensu Ricken (1915, 1920) or to *P. hilaris* sensu Horak. Neither is based on authentic or topotypical material, but they are different from each other. Ricken's is certainly the first identifiable interpretation but Horak's is here preferred since Ricken's interpretation keys out with *P. christinae* ... of Horak's key which is based among other materials on Swedish collections. It is improbable that Fries used the same species to be named twice..." Horak (1977), who considers *P. cidaris sensu* Bresinsky (1960) conspecific, depicts the species with subcapitate filamentous thin-walled cheilocystidia and small ellipsoidal verruculose (punctate-roughened) basidiospores with apical callus or germ pore.

A collection previously identified as *P. hilaris* from Mexico (Bandala, Guzmán & Montoya, 1989) has been determined to represent instead a new species, *P. guzmanii* (see above). While researching that species, Bandala and Montoya (1994) found that the

(P. hilaris, continued)

collections on which Horak (1977) had based his concept of *P. hilaris* were in fact conspecific with *P. arduennensis* and that the collections reported as *P. hilaris* by Jakobsson and Stridvall (1982) were determined to belong to another genus by Laber (1982, 1991) and Gulden (1983). Bandala & Montoya conclude rightly that there appears to be no satisfactory concept of *Agaricus hilaris* Fr.

ADDITIONAL REFERENCES: Bon, 1992; Karsten, 1879; Konrad & Maublanc, 1948; Kühner 1980; Kühner & Romagnesi, 1957; Nezdoiminogo 1986; (Romagnesi, 1942); (Velenovsky, 1921).

30. *Phaeocollybia intermedia* Horak & Corner in Horak, *Sydowia,* Ser II 29:57, 1977.

CHARACTERS: Large, deeply rooting basidiomes with dry pinkish to rusty brown subsquamulose convex to plano-umbonate pilei, pale fawn colored young lamellae, fusiform slender tough horny hollow stipes, medium (6-8 x 4-5 µm) ovoid asperulate basidiospores, cylindrical to subcapitate thin-walled cheilocystidia, non-gelatinized pileipelli with incrusting brownish pigments, no clamp connections.

DISTRIBUTION: Australasia (Borneo, Malaya); Asia (China -- Yunnan); on soil in montane forests.

31. *Phaeocollybia jennyae* (Karsten) Heim in *Encyclopédie mycologique* 1: 70, 1931.
Basionym: *Naucoria jennyae* Karsten in Hedwigia 12: 178. 1881.

CHARACTERS: Small to medium-sized bitter-tasting deeply rooting basidiomes with dark reddish brown dry to lubricous conical to cuspidate-campanulate pilei, ochraceous crowded young lamellae, dark reddish brown slender tapering stipes, small (4.5-5 x 3-4 µm) slightly verruculose ovoid basidiospores without germ pores or plages, thin-walled filamentous cheilocystidia, and no clamp connections.

DISTRIBUTION: Europe (Austria, Finland, France, Germany, Great Britain, Norway, Sweden), North America (eastern Canada and United States), Asia (Siberia)

COMMENTS: The description above was based on Gulden (1983, 1992) and Moser (1983). Horak (1977+) lists *Naucoria cidaris sensu* Ricken 1915, *P. cidaris sensu* Kühner & Romagnesi (1957), and *P. christinae sensu* Heim (1930) as synonyms. This last has caused considerable confusion for Singer initially based his Section *Microsporae* (Singer, 1970) on *P. christinae sensu* Heim (1930). The confusion was clarified somewhat later when Singer (1986, 1987) noted that the name *P. christinae* more properly represented larger-spored species (Section *Phaeocollybia)* and listed *P. jennyae* (Karst.) Heim as the correct name for the type of Section *Microsporae.*

(P. jennyae, continued)

Redhead & Malloch (1986) provide an excellent description of North American material. They spell the species epithet 'jennyae' rather than 'jennyi'. This correction, which reflects the 'appropriate sex' of Karsten's wife, is in keeping with the International Code of Botanical Nomenclature (Greuter *et al.*, 1994: Art. 60.11) and is followed here.

ADDITIONAL REFERENCES: Arora, 1981; Bandala, & Montoya, 1994; Bigelow & Barr, 1963; Bon, 1992; Dennis, Orton &Hora, 1960; Goetz, 1979; Jacobsson & Stridvall, 1983; Karsten 1881; Konrad & Maublanc, 1948; Krieglsteiner 1991; Laber 1982+, 1991+; Moser, 1949+, 1950+, 1983; Moser & Jülich, 1994; Nezdoiminogo 1986, 1990; Pomerleau, 1980; (Romagnesi, 1942); Smith, 1952, 1957b; Smith & Trappe, 1972.

32. *Phaeocollybia kauffmanii* (Smith) Singer, *Revue de Mycologie* 5: 11, 1940.

Basionym: Naucoria kauffmanii A. H. Smith, *Mycologia* 29: 52, 1937.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include a viscid orange to orange-brown inrolled convex-campanulate pileus with tightly inrolled edges, robust solidly stuffed stipe, vertical monopodial pseudorhiza,moderately large beaked sublimoniform basidiospores, well-developed bilaminate ixocutis with incrusting and intraparietal pigments, thin-walled filamentous to narrowly clavate cheilocystidia, no clamp connections, and strongly positive Syringaldazine reaction.

DISTRIBUTION: North America (British Columbia, California, Idaho, Mexico, Oregon, ?Vermont, Washington)

COMMENTS: Section *Phaeocollybia* (Smith 1957b; Singer 1986; Bandala & Montoya 1994). Among the largest of all known Phaeocollybias, *P. kauffmanii* forms a complex with *P. ammiratii, P. benzokauffmanii, P. redheadii* and *P. luteosquamulosa* -- all of which are more or less equally robust and large, have stuff stipes originating from vertical monopodial pseudorhizae, large limoniform beaked basidiospores, and thin-walled clavate cheilocystidia. Basidiomes of *P. piceae*, also with orange pilei, and similar spores, and cheilocystidia, can be distinguished by their much less robust stature and bright orange diffuse, non-incrusting pigments in the pileipellis.

ADDITIONAL REFERENCES: Arora, 1981*, Bandala, 1994*+; Bandala, Guzmán & Montoya, 1989+; Bessette & Sundberg, 1987*; Bigelow & Barr, 1966; (Farr & Farr, 1976); Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987 (as *spoliata)*; Hesler, 1949; Horak, 1977; McKenny & Stuntz (Ammirati), 1987*; Minot, 1989; Norvell, 1995a, 1997*; Norvell & Ammirati, 1995; Norvell & Redhead, 1992; Phillips, 1991*; Pomerleau, 1980; Redhead, 1997; Redhead & Norvell, 1993; Singer, 1951; Smith, 1937, 1949; Smith, 1980*; Smith & Trappe, 1972; Smith, Smith & Weber, 1979; Watling & Gregory, 1993.

33. ***Phaeocollybia laterarius*** A. H. Smith, *Brittonia* 9: 205, 1957

CHARACTERS: small, deeply rooting basidiomes with viscid yellowish orange to brown sharply umbonate narrowly to broadly conic pilei, concolorous slender hollow cartilaginous stipes, large (9-11 x 4.5-5.5 µm) non-beaked subellipsoid roughened basidiospores, scattered filamentous to narrowly clavate thin-walled cheilocystidia, gelatinized pileipelli yellowish in KOH, and no clamp connections.

DISTRIBUTION: North America (Massachusetts, Michigan).

COMMENTS: Considered synonymous to *P. christinae* [in Section *Phaeocollybia*] by Horak (1977) and Redhead & Malloch (1986).

ADDITIONAL REFERENCES: Arora, 1981; Bon, 1975; Bresinsky, 1960; Farr & Farr, 1976; Goetz, 1979; 86*; Minot, 1989; Smith & Trappe, 1972

34. ***Phaeocollybia latispora*** Bandala, Guzmán & Montoya, *Mycotaxon* 35:128-129 1989+.

CHARACTERS: Small, shallowly rooting basidiomes with dry to moist reddish-brown to orange-brown conic to convex umbonate pilei, pale orange young lamellae, vinaceous-tinged orange brown fusoid fibrous stipes, very large coarsely verrucose broadly limoniform basidiospores, abundant thin-walled clavate cheilocystidia, incrusted suprapellicular and subpellicular hyphae, and rare to absent clamp connections.

DISTRIBUTION: North America (Mexico) in coniferous forests.

COMMENTS: Bandala, Guzmán and Montoya (1989) note the similarity of *P. latispora* with *P. similis*, which differs in the absence of a gelatinized cuticle and cheilocystidial dimensions. Both they and Bandala & Montoya (1994) place this species in Section *Subattenuatae*, but the former authors note "...it is also close to Section *Phaeocollybia* if we consider the clamps as rare or absent. It is probable that *P. latispora* together with *P. similis* belongs to another section."

ADDITIONAL REFERENCES: Bandala, 1994*+

35. ***Phaeocollybia lilacifolia*** Smith in *Sydowia*, ser. II. Beih. 1: 59, 1957.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the glutinous dark brown broadly conic-campanulate pilei, lilac lamellae, moderately large verruculose roughened limoniform basidiospores, well developed bilaminate ixocutis with intracellular pigments, broadly clavate cheilocystidia, and absence of clamp connections.

DISTRIBUTION: North America (Washington; Oregon, ?California) in old to mature *Picea* forests.

(P. lilacifolia, continued)

COMMENTS: Section *Phaeocollybia* (Smith 1957b; Singer 1986). Placed in synonymy with *P. fallax* by Horak (1977) on the basis of very close microscopical similarities, *P. lilacifolia* lacks the green pileus pigmentation and has a larger more robust stature, slightly smaller basidiospores, subtly different cheilocystidia, and a dull brownish subpellis in KOH. For those reasons it is retained here as an independent species. *Phaeocollybia lilacifolia* forms a close microscopical complex with *P. fallax, P. festiva, (P. longipes)* and *P. rifflipes.*

ADDITIONAL REFERENCES: Arora, 1981; Goetz, 1975, 1979; Horak, 1973+; Norvell, 1998+; Smith, Smith & Weber, 1979; Smith & Trappe, 1972.

36. *Phaeocollybia lilacina* *nom. prov.* Halling & Mueller in Halling*, (See comments below)

CHARACTERS: Small fragile farinaceous deeply rooting basidiomes with lilac-pink tinged pilei and young lamellae, apically lilaceous slender fragile stipes, medium-sized (>6.5 µm long) ovoid punctate roughened basidiospores, refractive (?) capitulate ventricose cheilocystidia, and no clamp connections.

COMMENTS: Section *Versicolores.* A photograph and description of this species were downloaded on June 4, 1997 from a NSF-sponsored web site [address: http//:www.nybg.org/bsci/res/hall/phlilac.html*] and has not yet been formally published. The general spore size was provided by Halling (personal communication, 1997).

DISTRIBUTION: Central America (Costa Rica).

37. *Phaeocollybia longipes* Horak in Beih. *Nova Hedwigia* 43: 188, 1973.

CHARACTERS: Medium-sized basidiomes with an odor similar to burnt hair, olive brown viscid hygrophanous, conic to broadly conico-umbonate pilei, pinkish crenulate young lamellae, brownish slender tapering fibrillose-stuffed stipes, gradually narrowing pseudorhizae, moderately large (8-9 x 5-5.5 µm) verrucose bluntly beaked elongate limoniform basidiospores with pronounced apiculi, thin-walled usually subcapitate narrowly clavate cheilocystidia, pileipelli a cutis of repent cylindric slightly gelatinized hyphae encrusted with brownish pigments, and no clamp connections.

DISTRIBUTION: Australasia (New Zealand).

COMMENTS: Presumably in Section *Phaeocollybia.* Horak (1977) suggests that *P. longipes* may be synonymous with *P. festiva,* which differs in the structure and degree of gelatinization of the pileipellis.

ADDITIONAL REFERENCES: (Garrido, 1988).

38. *Phaeocollybia lugubris* (Fr.) Heim, *Encyclopédie mycologique* 1: 71, 1931

CHARACTERS: Relatively large fleshy farinaceous bitter-tasting deeply rooting basidiomes with viscid grayish olive tinged buff long inrolled conico-convex to obtusely umbonate pilei, pallid to olivaceous buff young lamellae, pallid to honey colored smooth thick stuffed stipes, long tapering pseudorhizae, moderately large (7.5-9 x 4.5-5.5 µm) verrucose-roughened limoniform basidiospores, refractive capitulate occasionally forking tibiiform cheilocystidia, pileipelli with a gelatinized colorless suprapellis and amber-colored subpellis, and no clamp connections.

DISTRIBUTION: North temperate -- Europe (Sweden; Austria, Czechoslovakia, Finland, France, Great Britain, Germany, Italy, Norway); North America (?eastern United States and Canada, Mexico), Asia (China, Siberia).

COMMENTS: Type species of the Section *Versicolores* (Smith 1957b; Singer 1970, 1986; Bandala & Montoya, 1994). In 1977 Horak synonymized the North American *P. spadicea* with *P. lugubris*. While the two taxa are admittedly microscopically very close, that synonymy is not accepted here. Important differences (also noted by Smith,1957b; Smith, Smith & Weber, 1979; and Bandala, 1994*+) include the presence of a pronounced apical beak on the basidiospores and the absence of any olivaceous pigments on the uniformly dark brown pilei in the Pacific Northwest species. The above description is based on observations by Gulden (1983, 1992) and Watling & Gregory (1993).

ADDITIONAL REFERENCES: Bandala et al., 1996*+; Bon, 1992; Bresadola, 1930*; Bresinsky, 1960; Cetto, 1976*; Dennis, Orton &Hora, 1960; Fries, 1821, (1836-38), 1857, 1884*; Goetz, 1979; Goetz, Barnhart & Barnhart, 1987; Guzmán, Bandala-Muñoz & Montoya-Bello, 1987; Heim, 1930*; 1957; Horak, 1968 ; Jacobsson & Stridvall, 1983; Karsten, 1879; Konrad & Maublanc, 1948; Krieglsteiner 1991; Kühner 1980; Kühner & Romagnesi, 1953, 1957; Laber 1982, 1991; Mann, 1991; Minot, 1989; (66); Moser 1983; Moser & Jülich 1994; Nezdoiminogo 1986, 1990; Pazmany & Laszlo, 1987; Poelt & Jahn, 1963; Ricken, 1915; Ricken, 1920; (Romagnesi, 1942); Saccardo, 1916; Singer, 1951b; Smith, 1937, 1949; Smith & Trappe, 1972; Vesely, Kotlaba, & Pouzar, 1972; Zang, 1996.

39. *Phaeocollybia luteosquamulosa nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include its robust stature and moderately large size, dry to moist ochraceous yellow appressed fibrillose inrolled convex to broadly conic pilei, large verrucose amygdaliform basidiospores, trilaminate pileipellis with a thin suprapellis containing bright golden incrusting and plasmatic pigments above a relatively narrow gelatinized colorless

(P. luteosquamulosa, continued)

mediopellis, no clamp connections and negative Syringaldazine reaction.

DISTRIBUTION: North America (Washington, Oregon, California)

COMMENTS: Section Phaeocollybia. A member of the *P. kauffmanii* complex, easily differentiated from the others by its dry to moist frequently appressed fibrillose brownish ochre pileus and its three-layered pileipellis.

ADDITIONAL REFERENCES: Norvell, 1998*.

40. ***Phaeocollybia martinicensis*** Guzmán, Montoya & Bandala in Bandala, Guzmán & Montoya. *Mycotaxon* 35: 121, 1989+.

CHARACTERS: A single small basidiome with a viscid ochraceous to yellowish-brown slightly inrolled acutely umbonate plano-convex pileus, light yellowish brown lamellae with whitish edges, a thin subcartilaginous stipe, moderately large (7.2-8.8 x 4-4.8 µm) minutely verrucose to nearly verrucose-punctate amygdaliform basidiospores, subcylindric or subcylindric-mucronate thin-walled cheilocystidia, a gelatinized colorless suprapellis above a subpellis with incrusting yellowish-orange pigments, and no clamp connections.

DISTRIBUTION: North America (Vera Cruz, Mexico); solitary in humus in a mesophytic forest..

COMMENTS: Section *Versicolores* (Bandala, 1994; Bandala & Montoya, 1994). This species was described from a single dried specimen in poor condition and lacking the full stipe. No other specimens have been found by Bandala (1994*+). More material is needed to complete the species concept.

ADDITIONAL REFERENCE: Bandala, Montoya, Guzmán & Horak, 1996+

41. ***Phaeocollybia megalospora*** Araujo ex Singer, *Mycologia Helvetica* 2: 259, 1987.

CHARACTERS: Small rooting basidiomes with brown viscid acutely papillate-conic pilei, concolorous lamellae, waxy yellow subviscid equal stipes, pseudorhizae, very large (11.7-12.3 x 6.5-7) strongly warty fusoid rostrate basidiospores, thin-walled ampullaceous to moderately clavate cheilocystidia, highly gelified pileipellis with yellow incrusting pigments in the suprapellis and dark-brown strongly incrusting pigments in the subpellis, and clamp connections.

DISTRIBUTION: South America (Brazil); in argillaceous soil in mixed tropical rainforest.

COMMENTS: Section *Subattenuatae* (Singer 1986, 1987; Bandala, 1994; Bandala & Montoya 1994).

42. ***Phaeocollybia mexicana*** Corner & Horak in Horak, *Sydowia*, Ser. II 29: 40, 1977.

CHARACTERS: Small rooting basidiomes with mixed tawny and dark-brown viscid convex-campanulate pilei, fawn colored young lamellae, ferruginous stuffed cylindrical stipes, large (8.5-10 x 5-5.5 µm) verrucose strongly beaked sublimoniform basidiospores, refractive capitulate cheilocystidia, highly gelatinized pileipelli with incrusting brown pigments, no clamp connections.

DISTRIBUTION: North America (Mexico); solitary to scattered on soil under *Pinus* at high elevations.

COMMENTS: Section *Versicolores* (Singer 1970, 1986). Bandala (1994*+) notes similarities with *P. californica*, which is larger and has orange pigments, a pungent odor and narrower spores.

ADDITIONAL REFERENCES: Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987; Singer, 1970, 1986.

43. ***Phaeocollybia minuta*** Horak, *Beiheft Nova Hedwigia* 43: 187, 1973.

CHARACTERS: Very small raphanaceous ?rooting basidiomes with dry honey-colored to date brown striatulate conic to campanulate pilei, pale yellowish young lamellae, concolorous thin tough hollow fusoid rooting stipes lacking pseudorhizae, medium-sized (6-7 x 3.5-4 µm) rugulose roughened elongated limoniform to ellipsoid basidiospores, scattered filamentous thin-walled cheilocystidia, non-gelatinized pileipelli with incrusting brown pigments, and numerous clamp connections on cuticular hyphae and on basidial and cheilocystidial bases.

DISTRIBUTION: Australasia (New Zealand); on soil amongst mosses in *Nothofagus* forests.

COMMENTS: Section *Phaeocollybia?* (Bandala & Montoya, 1994). Outstanding characters noted by Horak (1973) are the very small (<15 mm wide) pilei (making *P. minuta* 'by far' the smallest known *Phaeocollybia)* and the clamp connections found on all septa of the cuticular hyphae. The absence of a pseudorhiza is not addressed.

ADDITIONAL REFERENCES: (Garrido, 1988); Horak, 1977

44. ***Phaeocollybia moseri*** Bandala & Guzmán in Bandala, Montoya, Guzmán & Horak, *Mycological Research* 100: 241, 1996*+.

CHARACTERS: Very small slightly farinaceous rooting basidiomes with viscid pale brown to orange brown broadly campanulate pilei, pale yellowish brown lamellae, yellowish orange brown cylindrical subcartilaginous stipes, gradually attenuating straight pseudorhizae, smallish (6.5 - 7.5 X 3.5 - 4.5 µm) ovoid to amygdaliform verruculose basidiospores,

(P. moseri, continued)

refractive capitulate fusoid to sublageniform occasionally forked cheilocystidia, gelatinized pileipelli with yellowish (brown) incrusting pigments, numerous clamp connections.

DISTRIBUTION: North America (Mexico) under *Pinus*.

COMMENTS: Section *Versicolores*. The authors cite as significant the brownish color, medium sized ovoid basidiospores, clampless hyphae and refractive capitate cheilocystidia and note macroscopical similarities with *P. pseudolugubris* and *P. martinicensis*, (both of which have different basidiospores and ecology) and microscopical similarities with *P. primulina* (now thought to belong in *Gymnopilus)*.

ADDITIONAL REFERENCES: Bandala, 1994*+.

45. *Phaeocollybia muscicolor* Horak, *Sydowia*, Ser II 29:41, 1977.

CHARACTERS: Small raphanaceous deeply rooting basidiomes with glutinous deep olive green radially innately fibrillose conic-campanulate pilei, olive-beige young lamellae, olivaceous hollow fusoid stipes, long pseudorhizae, very large (10.5-12.5 x 6-6.5 µm) warted amygdaliform basidiospores, broadly clavate thin-walled cheilocystidia, gelatinized pileipelli with incrusting brownish pigments, no clamp connections.

DISTRIBUTION: Australasia (New Guinea) on soil in *Nothofagus (*with *Castanopsis* and *Lithocarpus)* forests.

COMMENTS: Section *Phaeocollybia* (Singer 1986, 1987; Bandala & Montoya, 1994). Horak (1977) notes that *P. viridis*, another large-spored species from New Guinea, differs in odor, taste, basidiospore ornamentation, cuticular structure, and clamp connections.

ADDITIONAL REFERENCES: Bandala, 1994; (Garrido, 1988).

46. *Phaeocollybia neosimilis* Singer, *Agaricales in modern taxonomy*, 4th ed, p. 665. 1986.

= *Phaeocollybia attenuata* ssp. *mexicana* Singer in Sydowia 11: 367, 1957.

CHARACTERS: Small raphanaceous deeply rooting basidiomes with moist deep chestnut brown hygrophanous conic-umbonate pilei, 'rusty-brown' lamellae, deep chestnut brown smooth hollow stipes, very long thin pseudorhizae, large (8.2-9.4 x 4-5.8 µm) warty beaked ovoid basidiospores lacking either germ pore or plage, thin-walled broadly clavate cheilocystidia, slightly gelatinized pileipelli with cinnamon brown incrusting pigments (absent in the subpellis), no clamp connections.

DISTRIBUTION: North America (Mexico); at high elevations under *Pinus* and *Abies*.

COMMENTS: Section *Phaeocollybia* (Singer 1970, 1986, 1987; Bandala 1994*+; Bandala & Montoya, 1994). Originally described as a subspecies of *P. attenuata, P. neosimilis* was

(P. neosimilis, continued)

said to differ only in its darker pileus color and slightly larger basidiospores. Bandala and Montoya (1994) note that *P. similis, neosimilis,* and *P. attenuata* are the only species assigned to Section *Phaeocollybia* with limoniform-globose mucronate strongly ornamented basidiospores. The spores of *P. neosimilis* (given by Bandala and Montoya as 8.8-9.6 x 5.6-6.4) are larger than those of *P. attenuata* and smaller than those of the more coarsely ornamented *P. similis.*

47. *Phaeocollybia odorata* Horak, *Sydowia*, Ser. II 29: 52, 1977.

CHARACTERS: Small unpleasant smelling non-rooting basidiomes with subviscid brownish olive striate acutely papillate conic to plane uplifted pilei, olive argillaceous young lamellae, greenish slender cartilaginous hollow stipes, no pseudorhizae, moderately large (8.5-9.5 x 5-8 µm) amygdaliform to pip-shaped minutely warted to cloudy marbled basidiospores lacking plage or mucros, subcapitate fusoid thin-walled cheilocystidia, slightly gelatinized pileipelli with incrusting brownish pigments and subcellular subpelli, no clamp connections.

COMMENTS: Although Singer (1986) suggested placement of this non-pseudorhizal species into *Galerina*, he later (Singer, 1987) placed it into Section *Phaeocollybia*, where it is also retained by Bandala & Montoya, 1994..

DISTRIBUTION: Australasia (New Guinea)

ADDITIONAL REFERENCES: Bandala, 1994; Garrido, 1988.

48. *Phaeocollybia oligoporpa* Singer, *Mycologia Helvetica* 2: 250, 1987.

CHARACTERS: Large fleshy mild-tasting deeply rooting basidiomes with subviscid ochraceous to golden brown tall conic to broadly campanulate pilei, light brown young lamellae, orange-brown wide more or less equal stipes, very long attenuating pseudorhizae, very large (9.5-10.5 x 6-6.3 µm) coarsely warted beaked amygdaliform basidiospores, variably clavate, utriform or mucronate thin-walled cheilocystidia, moderately gelatinized pileipellis with brown incrusting pigments, and scattered medallion-like clamp connections.

DISTRIBUTION: South America (Colombia); Central America (Costa Rica); North America (Mexico) under *Quercus.*

COMMENTS: Section *Subattenuatae* (Horak & Halling, 1991; Singer 1986, 1987; Bandala, 1994*+; Bandala & Montoya, 1994). Horak and Halling (1991) consider the coarsely warted, strongly beaked amygdaliform to sublimoniform basidiospores and the medallion-like clamps at the basidia bases important characters and note very close similarities with *P. latispora*, which differs in its association with conifers. Bandala and Montoya (1994) note that their recent collections from Costa Rica have a strong farinaceous odor (Horak and

(P. oligoporpa, continued)

Halling note a similar 'watermelon-like odor') as opposed to the not distinctive odor described by Singer (See additional comments under *P. ammiratii.*).

ADDITIONAL REFERENCES: Bandala, Guzmán & Montoya, 1989+; Bandala, & Montoya,. 1994*+; Halling, 1997.

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

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the viscid to glutinous olive-green pileus, yellowish to olivaceous lamellae, stuffed stipes, large (10 x 6 µm) coarsely ornamented prominently beaked limoniform basidiospores, clavate thin-walled cheilocystidia, a well-developed bilaminate ixocutis with parietal pigments (greenish in H20 and orangish in KOH), no clamp connections. Negative in Syringaldazine except for occasional pale magenta on pseudorhizal pellis.

DISTRIBUTION: North America (Oregon; California).

COMMENTS: Section *Phaeocollybia* (Smith, 1957b, Singer 1986). Bandala & Montoya place this species in Section *Versicolores*. Bandala's examination notes enclosed in the type collection and examination of the same specimens by this author indicate that apparently the relatively abundant non-refractive apical outgrowths (developmental artifacts) found in one specimen were misinterpreted as indicating characteristically lageniform cheilocystidia. This species properly belongs in Section *Phaeocollybia.*

ADDITIONAL REFERENCES: Arora, 1981*; Bandala, 1994; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Horak, 1977; Kibby, 1992*; Norvell, 1998; Singer, 1986; Smith, 1975*; Smith & Trappe, 1972; Smith, Smith & Weber, 1979

50. *Phaeocollybia oregonensis* A. H. Smith & Trappe, *Mycologia,* 64: 1154, 1972.
= *Phaeocollybia carmanahensis* Redhead & Norvell in *Mycotaxon* 46: 343-359. 1993.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include a fairly robust stature, viscid drab-colored pilei, smoky whitish lamellae, thick stuffed stipes, small punctate roughened ellipsoidal (bullet-shaped) basidiospores, well-developed bilaminate ixocutis lacking incrusting pigments, broadly clavate thin-walled cheilocystidia, no clamp connections, and strongly positive Syringaldazine reaction.

DISTRIBUTION: North America (Oregon; British Columbia) in mature temperate coniferous rainforests.

COMMENTS: *Phaeocollybia oregonensis* was described by Smith & Trappe has having clamp connections. Examinations of the types of both *P. oregonensis* and *P. carmanahensis* and

(P. oregonensis, continued)

newly collected topotypical and other materials using Nomarsky optics have revealed no clamp connections. It is possible that the strongly sarcodimitic tramal tissues and the differential development of the basidia have contributed to the confusion. Bandala & Montoya (1994) placed *P. oregonensis* into Section *Radicatae* on the belief that clamp connections were present. The species properly belongs in Section *Microsporae.*

ADDITIONAL REFERENCES: Arora, 1981. Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Horak, 1977; Norvell, 1995a, 1998; Redhead, 1997 (as *P. carmanahensis).*

51. *Phaeocollybia parvispora* Corner & Horak in Horak, *Sydowia* Ser. II 29: 60, 1977

CHARACTERS: Moderately large radish-smelling deeply-rooting basidiomes with umber-brown marginally lilaceous dry appressed fibrillose-squamulose conico-convex to campanulate pilei, violaceous young lamellae, lilaceous to pale umber appressed-fibrillose cartilaginous easily separable subcylindrical hollow stipes, very small (3.5-4.5 x 2.5-3) asperulate ovate basidiospores, refractive fusoid-capitulate cheilocystidia, partly gelatinized pileipelli with incrusting brown pigments, no clamp connections.

DISTRIBUTION: Australasia (Singapore; Malaysia).

COMMENTS: Section *Microsporae* (Bandala & Montoya, 1994). The easily separable stipe and extremely small ovate basidiospores are unusual for the genus.

52. *Phaeocollybia perplexa* Orton, *Kew Bulletin* 31: 709-721, 1976.

CHARACTERS: Small bitter-tasting non-rooting saprophytic basidiomes with yellowish brown moist to lubricous translucent-striate silky conic to campanulate pilei, greenish -gray to amber colored young lamellae, corneous fibrous stipes with basal tomentum and no pseudorhizae, small (5-6 x 3-4 µm) smooth ellipsoid basidiospores lacking apical callus and and germ pores, thin-walled cylindrical to narrowly fusoid occasionally forking cheilocystidia, gelatinous pileipellis with golden brown parietal pigments, clamp connections, no tibiiform diverticula.

DISTRIBUTION: North temperate -- Europe (Scotland); North America (British Columbia, Idaho, Michigan, Newfoundland, Ontario, Oregon, Washington).

COMMENTS: Excluded species. Horak (1977) commented upon the doubtful placement of this species in *Phaeocollybia.* Redhead and Smith (1986), noting the absence of pseudorhizae, spore ornamentation, and tibiiform diverticula, erected the monotypic genus *Stagnicola* to accommodate *P. perplexa.* This disposition is now generally accepted (Singer, 1987; Laber & Marklund, 1992; Watling & Gregory, 1993; Hawksworth et al. 1995). Redhead and Smith note that Fries (1877 - 1884) treated the species as *Agaricus*

(P. perplexa, continued)

cidaris var. *minor*, differentiating that variety from the typical form based on the absence of a radicating stipe.

53. *Phaeocollybia phaeogaleroides nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include the fragile uniformly yellow brown to orange-brown basidiomes, moist thin-fleshed pilei, corneous stipes, large verruculose ellipsoidal basidiospores with very slight beaks, ill-defined bilaminate pileipellis, cylindrical to slightly clavate thin-walled cheilocystidia, clamp connections in the pileipellis and tramal tissues, unusually long tibiiform diverticula, negative Syringaldazine reaction.

DISTRIBUTION: North America (Oregon) in low depressed mossy areas.

COMMENTS: ?Section *Subattenuatae*.

REFERENCES: (Norvell, 1998).

54. *Phaeocollybia piceae* Smith & Trappe, *Mycologia* 64: 1145, 1972.

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include the bright orange coloration and small to medium-sized stature of the basidiomes, bitter taste, subviscid to viscid orange to orange-red pilei, frequently insect-consumed stipitipith, large verruculose amygdaliform beaked basidiospores, cylindrical to subcapitate thin-walled cheilocystidia, rapidly disappearing diffuse orange pigments in KOH mounts of the pileipellis, no clamp connections, and negative Syringaldazine reaction.

DISTRIBUTION: North America (Oregon; British Columbia, California, Washington) in coniferous forests (usually associated with *Picea).*

COMMENTS: Section *Phaeocollybia* (Singer, 1987; Bandala, 1994; Bandala & Montoya, 1994). Lack of incrusting pigments in the pileipellis discriminates *P. piceae* from the otherwise anatomically very close *P. kauffmanii.* Horak (1977+) synonymized the larger dull grayish brown mild-tasting *P. gregaria* with *P. piceae* based on microscopical characters; admittedly there is very little anatomical difference between the two species, they are clearly discriminated on the basis of morphological characters.

ADDITIONAL REFERENCES: Arora, 1981; Bon, 1992 (in Europe); Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Norvell, 1995a, 1998*; (Redhead, 1997).

55. *Phaeocollybia pleurocystidiata nom prov.*

CHARACTERS: See Chapter 6 for complete technical description and discussion. Key characters include vernal fruiting habit, small stature, subviscid tawny yellow to yellow

(P. pleurocystidiata, continued)

brown conic-convex pilei, abundant refractive capitulate thick-walled cheilocystidia and pleurocystidia, moderately large verrucose beaked sublimoniform basidiospores, bilaminate pileipellis with incrusting pigments, no clamp connections, and negative to latently mild Syringaldazine reaction.

DISTRIBUTION: North America (Washington; California) in mature coniferous forests.

COMMENTS: Section *Versicolores*. The only other species known to possess abundant refractive capitulate pleurocystidia, rare in the genus, are *P. ratticauda* and *P. tasmanica*, which produce completely different colored and sized basidiomes and much smaller basidiospores.

ADDITIONAL REFERENCES: Norvell, 1998.

56. *Phaeocollybia primulina* (Berkeley) Horak, *Sydowia*, Ser II 29: 49, 1977+

CHARACTERS: See Comments.

DISTRIBUTION: Australasia (New South Wales)

COMMENTS: Excluded species. Originally described by Berkeley (1878) as a *Marasmius*, this species was later transferred to *Gymnopilus* by Pegler (1965) before being placed into *Phaeocollybia* by Horak. Singer (1986), who initially indicated it might more properly belong in *Galerina*, seemed to reconsider its placement in *Gymnopilus* (Singer, 1987). Rees & Wood (1996), acknowledging the poor condition of the immature type specimens and noting the attachment of the basidiomes to a small twig, the presence of basal mycelium, and the now irretrievable cystidia described by previous researchers as being refractive and lecythiform, suggest retention in *Gymnopilus* until new material is collected.

ADDITIONAL REFERENCE: May & Wood, 1997.

57. *Phaeocollybia procera* Horak in *Sydowia*, Ser II 29: 56, 1977.

CHARACTERS: Moderately large deeply rooting basidiomes with uniformly brown dry innately fibrillose inrolled conic to campanulate pilei, yellowish young lamellae, brownish dry equal to fusoid hollow stipes, gradually attenuating long pseudorhizae, moderately-large (8-9.5 x 4.5-5) distinctly beaked amygdaliform basidiospores ornamented with cloudy-marbled warts, clavate thing-walled cheilocystidia, gelatinized pileipelli with brownish encrusting pigments, and no clamp connections.

DISTRIBUTION: Australasia (New Guinea); on soil under *Nothofagus*.

COMMENTS: Section *Phaeocollybia* (Singer 1987; Bandala 1994+; Bandala & Montoya, 1994). Horak (1977) notes that the shape, size and color of its basidiomes makes *P. procera* an "...outstanding exception to the otherwise monotonous fungal flora found in the

(P. procera, continued)

Nothofagus forests of New Guinea".

ADDITIONAL REFERENCE: (Garrido 1988).

58. *Phaeocollybia pseudofestiva* A. H. Smith, *Brittonia* 9: 213, 1957+

CHARACTERS: See Chapter 6 for full technical description and discussion. Key characters include the glutinous olive green conic-campanulate pileus, yellowish young lamellae, refractive capitulate cheilocystidia, medium-sized prominently beaked verrucose-rugulose limoniform basidiospores, well-developed bilaminate ixocutis with slightly incrusting and intraparietal pigments, no clamp connections. Stipe and pseudorhiza deep magenta in Syringaldazine.

DISTRIBUTION: North America (Washington; British Columbia, Oregon, California); on the ground in mature coniferous forests; uncommon.

COMMENTS: Section *Versicolores* (Smith, 1957b; Bandala & Montoya, 1994).

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Bandala et al. 1996; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Goward, Redhead & Ryan, 1993; Norvell, 1998; (Redhead, 1997); Smith & Trappe, 1972.

59. *Naucoria pseudohilaris* Velenovsky in *Ceské houby*: 524, 1921.

COMMENTS: This species is included here only for reference purposes. Velenovsky (1921), who observed that *N. pseudohilaris* appears closely related to *N. hilaris* Fr., made no mention of the presence of a pseudorhiza in his original description of this small amber viscid basidiome with moderately large (6-9 µm long) ovoid-amygdaliform spores and filamentous cheilocystidia. A Latin translation of the original Czech description can be found in Pilat (1948).

60. *Phaeocollybia pseudolugubris* Bandala & Horak in Bandala, Montoya, Guzmán & Horak, *Mycological Research* 100: 242. 1996+.

CHARACTERS: Small cucumber-tasting deeply rooting basidiomes with viscid initially dark violaceous later light brown to yellowish orange brown glabrous conical to umbonate-applanate pilei, pale violet young lamellae, apically violaceous tinted yellowish orange brown slender tapering subcartilaginous stipes, large (8-9 x 4-5 µm) subellipsoid verruculose-verrucose basidiospores, refractive capitulate long-necked subcylindrical to subfusoid occasionally forking cheilocystidia, gelatinized pileipelli with incrusting yellowing pigments, no clamp connections.

DISTRIBUTION: North America (Mexico); scattered in *Abies/Pinus* forests.

(P. pseudolugubris, continued)

COMMENTS: Section *Versicolores.* The authors consider this species microscopically close to *P. lugubris* but easily distinguished in the field by its smaller size and more fragile aspect, violaceous coloration and lack of olive brown tones. They consider the spores similar to those found in *P. martinicensis* and *P. cidaris.* Some collections identified by Gulden (1983) as *P. cidaris* are considered by Bandala *et al.* to represent instead a different species very closely related to *P. pseudolugubris.*

ADDITIONAL REFERENCES: Bandala, 1994*+.

61. *Phaeocollybia quercetorum* Singer, *Mycologia Helvetica* 2: 254, 1987.

CHARACTERS: Small phenolic smelling deeply rooting basidiomes with glutinous deep brown transparent-striate conic-convex pilei, cinnamon-brown (young?) lamellae, apically dirty pallid more or less equal stipes, very long (9.5-14 x 5.5-6.5 µm) coarsely ornamented, apically beaked amygdaliform spores, polymorphic narrowly clavate to subfilamentous or narrowly ventricose thin-walled cheilocystidia, highly gelatinized pileipelli with cinnamon-brown non-incrusting pigments and no clamp connections.

DISTRIBUTION: South America (Colombia) & Central America (Costa Rica) under *Quercus.*

COMMENTS: Section *Phaeocollybia* (Singer 1986, 1987; Bandala & Montoya, 1994). . Singer (1987) noted the anatomical similarity between *P. quercetorum* and *P. christinae* (which differs in its odor, habitat, more obtuse umbos, more abundant decidedly clavate cheilocystidia and narrower basidiospores) and between *P. quercetorum* and *P. gregaria* and *P. piceae* (both with much broader stipes and associated with *Picea).* Horak and Halling (1991*+) observed that *P. quercetorum* is easily recognized by its coarsely warted amygdaliform beaked spores and polymorphic clavate to subcapitate clampless cheilocystidia and greatly resembles *P. martinicensis* and *P. singeri* (also associated with angiosperms). They also cited the absence of phenolic odors in their collections and resemblance to the coniferous associated species, *P. kauffmanii* and *P. piceae*

ADDITIONAL REFERENCES: Bandala, 1994*+; Guzmán, Bandala-Muñoz,& Montoya-Bello, 1987.

62. *Phaeocollybia querqueti* Corner & Horak in Horak, *Sydowia*, Ser II 29: 61, 1977.

CHARACTERS: Medium-sized soapy-tasting rooting basidiomes with viscid pale brown opaque conical to acutely umbonate plano-convex pilei, pale brownish young lamellae, pale fawn slender smooth hollow cartilaginous stipes, tapering pseudorhizae, small (4.5-5.5 x 3-3.5 µm) asperulate ovoid basidiospores, refractive capitulate fusoid cheilocystidia, gelatinized pileipellis with incrusting brown pigments, and no clamp connections.

(P. querqueti, continued)

DISTRIBUTION: Australasia (Borneo) with *Quercus*.

COMMENTS: Section *Microsporae* (Singer 1987, Bandala & Montoya, 1994). Rees & Wood (1996) mention the similarity of this species with *P. rancida* and *P. ratticauda* (which has larger basidiospores, a sharply attenuating pseudorhiza, and smells like Thai fish sauce or burnt hairs).

ADDITIONAL REFERENCES: Bandala, 1991; Horak & Halling, 1991.

63. *Phaeocollybia radicata* (Murrill) Singer in *Lilloa* 22: 567, 1951.

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include its small, fragile stature, moist tawny to red brown pilei, very small and nearly smooth ellipsoidal basidiospores, bilaminate pileipellis with a thin colorless suprapellis, refractive capitulate fusoid to lageniform thick-walled cheilocystidia, and clamp connections.

DISTRIBUTION: North America (Oregon; California), rare in coastal coniferous rainforests.

COMMENTS: Singer (1970) based the Section *Radicatae* on this species. *Phaeocollybia dissiliens*, considered synonymous with *P. radicata* by Horak (1977), produces much larger, more robust basidiomes and stipes with very thick cartilaginous cortices. Singer (1987) noted the similarity of *P. radicata* with *P. arduennensis* and *P. subarduennensis*, both producing smaller basidiomes with slightly differently shaped cheilocystidia. *Phaeocollybia subarduennensis* also has broader basidiospores.

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Bandala & Montoya, 1994; Goetz, 1975; Goetz, 1979; Goetz, Barnhart & Barnhart, 1987; Murrill, 1917; Norvell, 1998; Smith, 1937, 1957b; Smith, Smith & Weber, 1979; Smith & Trappe, 1972.

64. *Phaeocollybia rancida* Horak in *Acta Botanic Indica* 2(1):70. 1974*+.

CHARACTERS: Small rancid-smelling rooted basidiomes with glutinous ochraceous to tawny clay radially rugulose conic-campanulate pilei, lilac-violet lamellae, lilac-tinged to amber brown minutely innately fibrillose hollow stipes, small (5-6 x 3-3.5 µm) ovoid minutely warted basidiospores, fusoid subcapitate cheilocystidia, no clamp connections.

DISTRIBUTION: India (Himalayas) at high elevations in coniferous forests.

COMMENTS: Section *Microsporae* (Horak, 1974; Singer, 1986). Horak notes similarities with *P. ratticauda (*associated with *Nothofagus* in Australasia and with a differently shaped pileus, abruptly attenuating pseudorhiza, wider basidiospores, and capitate cheilocystidia), as well as with the lilac gilled *P. lilacifolia* and *P. fallax* (both with larger and more heavily ornamented basidiospores).

ADDITIONAL REFERENCES: Bandala, 1994; Horak, 1977+.

65. *Phaeocollybia ratticauda* Horak, *Beiheft Nova Hedwigia* 43: 184, 1973.

CHARACTERS: Small deeply rooting basidiomes with an odor of burnt hair, lubricous to subviscid tan appressed fibrillose conic-convex to plano-reflexed pilei, dull cream to purplish young lamellae, violaceous to tan equal cartilaginous hollow stipes, abruptly tapering pseudorhizae, small (~5.3 x 4 µm) verruculose pip-shaped basidiospores, refractive capitulate tibiiform cheilocystidia, abundant pleurocystidia, slightly gelatinized pileipellis with incrusting light rusty pigments, no clamp connections.

DISTRIBUTION: Australasia (New Guinea; New Zealand, New South Wales) on soil under *Nothofagus.*

COMMENTS: Section *Microsporae* (Singer 1986, 1987; Bandala & Montoya, 1994). Horak (1977) and Rees & Wood (1996*+) draw attention to the macroscopical similarity of this species to *P. rancida* (with a less abruptly tapering pseudorhizae and smaller spores) and microscopical similarity to *P. caudata* (with a differently shaped and differently colored pileus) and *P. querqueti* (with smaller basidiospores, a more gradually tapering pseudorhiza, and soapy taste and odor). The photograph identified as *P. ratticauda* in Fuhrer & Robinson (1992) represents a different species, *P. tasmanica* (Rees & Wood, 1996).

ADDITIONAL REFERENCES: (Garrido, 1988); Horak, 1977+, 1983; May & Wood, 1997.

66. *Phaeocollybia redheadii nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include its massive stature, large viscid tawny to dark orange brown pileus, very large eccentrically beaked long limoniform basidiospores, well-developed ixocutis with incrusting and intraparietal pigments, thin-walled subglobose-capitate long-pedicellate cheilocystidia, no clamp connections and strongly positive Syringaldazine reaction.

DISTRIBUTION: North America (British Columbia; Oregon, Washington); in woody humus in ancient and old growth coniferous forests (probably mycorrhizal with *Tsuga* and/or *Abies* species).

COMMENTS: Section *Phaeocollybia.* The large basidiospores and cheilocystidial morphology separate this species from the macroscopically similar *P. kauffmanii, P. benzokauffmanii, P. luteosquamulosa* and *P. ammiratii.*

ADDITIONAL REFERENCES: Norvell, 1992* (as *P. kauffmanii)*; Norvell, 1998; Redhead & Norvell, 1993 (as *P. kauffmanii).*

67. *Phaeocollybia rifflipes nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include the small stature, glutinous tawny to dark brown fragile campanulate pilei, violet young lamellae, small verruculose limoniform basidiospores, well developed bilaminate ixocutis with intracellular pigments, non-secreting thin-walled clavate cheilocystidia, no clamp connections, and negative Syringaldazine reactivity.

DISTRIBUTION: North America (Washington; Oregon, California)

COMMENTS: ?Section *Phaeocollybia*. This species can be differentiated from other species in the *P. festiva* complex by its consistently smaller (~7 X 4.5 µm) basidiospores.

ADDITIONAL REFERENCES: (Norvell, 1998).

68. *Phaeocollybia rufipes* Bigelow, in Bigelow & Barr, *Rhodora* 65: 297, 1963.

CHARACTERS: Small raphanaceous to slightly farinaceous deeply rooting basidiomes with brownish orange viscid convex-umbonate pilei, pinkish buff young lamellae, pinkish buff cartilaginous stuffed to hollow stipes that become reddish from base upwards, medium-sized (7-8.5 x 4-5 µm) basidiospores, thin-walled filamentous to subcapitate cheilocystidia, subpellicular hyphae "...finely encrusted with pigment or sinuous-thickened", and absent clamp connections.

DISTRIBUTION: Eastern North America.

COMMENTS: (Section *Phaeocollybia*). *Phaeocollybia rufipes* was synonymized with *P. christinae* by Horak (1977), who now suspects that *P. rufipes* may well represent an independent species (Horak pers. comm., 1997). Redhead & Malloch (1986) noted that all their collections of *P. 'christinae'* matched the type of *P. rufipes*, and it is possible that eastern North American material currently identified as *P. christinae* would belong here. Until additional research is done, the status of this species remains uncertain.

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Farr & Farr, 1976; Minot, 1989; Pomerleau, 1980; Smith & Trappe, 1972.

69. *Phaeocollybia rufotubulina nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the moist to lubricous reddish-orange convex-campanulate pilei, tubular strict stipes with unusually thin cortices, sequential-racemose thready pseudorhizae, large warty-verrucose prominently beaked sublimoniform basidiospores, a bilaminate pileipellis with incrusting pigments, abundant refractive capitulate fusoid thick-walled cheilocystidia, no clamp connections, and negative to mild latent Syringaldazine reaction.

(P. rufotubulina, continued)

DISTRIBUTION: North America (California) in sandy soil in mixed coniferous and *Lithocarpus* forest.

COMMENTS: Section *Versicolores.* Easily differentiated in the field from the microscopically very closely related *P. californica* and *P. scatesiae* by its much brighter orange to orange red coloration and unusually thin stipe cortex.

ADDITIONAL REFERENCES: Norvell, 1998*.

70. *Phaeocollybia scatesiae* A. H. Smith & Trappe, *Mycologia* 64: 1146-1148, 1972.

CHARACTERS:See Chapter 6 for a complete technical description. Key characters include the densely cespitose habit, glutinous pale to dark brown broadly conic pilei, viscid smooth hollow stipes, fasciculate-racemose rhizomorphic-pseudorhizae, moderately large verrucose prominently beaked limoniform basidiospores, well-developed bilaminate ixocutis with no incrusting pigments, abundant refractive capitulate fusoid thick-walled cheilocystidia, no clamp connections and negative to mild latent Syringaldazine reaction..

DISTRIBUTION: North America (Oregon; California, Washington); in compacted clays or heavy humus in coniferous forests mixed with *Vaccinium* spp.

COMMENTS: Section *Versicolores.* Microscopically very similar to *P. californica* (with which it was synonymized by Horak, 1977) and *P. rufotubulina*; differentiated macroscopically by the dense fasciculate habit, extremely glutinous pilei, and lack of orange colors in the pileus.

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Goetz, 1975, 1979; Lincoff, 1981*; Norvell, 1995a, 1997*; Norvell, Ammirati & Redhead, 1994; Norvell & Ammirati, 1993, 1995; Smith, 1980*.

71. *Phaeocollybia similis* (Bresadola) Singer, *Lilloa* 22: 567, 1951.
Basionym: Naucoria similis Bresadola, *Icon. Mycologica.* 16 tab. 794, 1930.

CHARACTERS: Very small deeply rooting basidiomes with viscid (?) reddish orange convex-campanulate pilei, reddish-brown equal thin fistulose stipes, large (9-11 x 6-7 µm) coarsely warted, prominently beaked limoniform-globose basidiospores, subcylindric to clavate thin-walled cheilocystidia, suprapelli with a mix of non-encrusting and yellowish incrusting pigments, subpelli with strongly incrusting rusty pigments, and (no?) clamp connections (*q. v.*).

DISTRIBUTION: Asia (China).

COMMENTS: This species was placed in Section *Subattenuatae* by Singer (1987) based on the presence of clamp connections and large basidiospores in the material he examined. Bandala and Montoya (1994) later examined the same material and, finding no clamp

(P. similis, continued)

connections, assigned this species to the Section *Phaeocollybia*. Microscopical observations on the type specimens given by Horak (1977), Singer (1987), and Bandala & Montoya (1994) seem to agree except for the presence of gelatinized hyphae in the suprapellis and of a plage on the basidiospores (both features noted only by Horak) and the presence of clamp connections (observed only by Singer, 1987, who noted "...it is true that some septa are clampless, but these seem to be secondary.")

Smith (1957b), who was unable to examine the type collection, reported *P. similis* from Washington state based on Bresadola's type description. Disposition of that collection is discussed below. It should be noted here that the photograph published by Phillips (1991) as *P. similis* represents North American material (probably *P. attenuata*).

ADDITIONAL REFERENCES: Arora, 1981; Goetz, 1975, 1979; Keissler & Lohwag, 1937; Singer, 1986; Smith & Trappe, 1972; Teng, 1996; Zang, 1996.

72. *Phaeocollybia 'similis' sensu* A. H. Smith (1957b+).

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the small aspect, gregarious habit, moist ochraceous tawny thin pilei, criniform lateral-monopodial rhizomorphic-pseudorhizae, large coarsely ornamented prominently beaked limoniform-globose basidiospores, bilaminate pileipellis with incrusting and intraparietal pigments, thin-walled clavate cheilocystidia, no clamp connections, and negative Syringaldazine reaction.

DISTRIBUTION: North America (British Columbia; Washington, Oregon)

COMMENTS: Section *Phaeocollybia*. Closely related to *P. attenuata*, *P. neosimilis*, and *P. similis*,. Originally treated by Smith (1957b) as *P. similis* based on the description by Bresadola (1930). Horak (1977), who had access to the type, felt that the American material was distinct, and suggested that it might better be considered as *P. piceae* (a much more robust species with much different basidiospores). Singer (1970), who also examined *P. similis*, indicated that *P. similis* sensu Smith was very similar to his *P. attenuata* ssp. *mexicana* (later named by him as *P. neosimilis).*

ADDITIONAL REFERENCES: Norvell, 1998*.

73. *Phaeocollybia singeri* Bandala, Guzmán & Montoya, *Mycotaxon* 35(1): 134-136. 1989+.

CHARACTERS: Medium-sized deeply rooting basidiomes with lubricous light yellowish brown smooth conic-campanulate pilei, grayish brown lamellae, orange-brown elastic stipes that become vinaceous brown to nearly black at the base, moderately large (8 - 9 X 4 - 5 µm)

(P. singeri, continued)

verrucose punctate amygdaliform basidiospores, heteromorphic thin-walled clavate to clavate subglobose to lageniform cheilocystidia, and no clamp connections.

DISTRIBUTION: North America (Mexico); *Quercus* associated.

COMMENTS: Section *Phaeocollybia* (Bandala, 1994; Bandala & Montoya, 1994). Bandala et al. (1996+) note the similarity of this species with *P. amygdalospora*, which differs in its coniferous associations, warty verrucose amygdaliform basidiospores, and narrower cheilocystidia.

74. *Phaeocollybia singularis* Horak & Halling, *Mycologia* 83: 470, 1991.

CHARACTERS: Small radish-tasting deeply rooting basidiomes with lavender-tinted black lubricous smooth to apically appressed-squamulose conic to conico-convex pilei, lilaceous young lamellae, violaceous twisted silky hollow subfusoid stipes, moderately large (8-9.5 x 4.5-5 µm) prominently beaked sublimoniform verrucose-rugose ornamented basidiospores, refractive capitulate fusoid cheilocystidia, strongly gelatinized pileipelli with yellowish brown incrustations, oleifers, and no clamp connections.

DISTRIBUTION: South America (Colombia); North America (Mexico); under *Quercus*.

COMMENTS: Horak and Halling, who placed *P. singularis* into Section *Versicolores*, cited it as the first species to combine lilac colors, sublimoniform spores, typically refractive capitulate fusoid cheilocystidia, and association with *Quercus*. Bandala (1994*+) notes similarity of this species with the conifer-associated *P. mexicana*.

75. *Phaeocollybia sipei* A. H. Smith, *Brittonia*, 9: 207, 1957.

CHARACTERS: See Chapter 6 for full a complete description and discussion. Key characters include the subviscid orange to dark orange brown broadly campanulate subviscid pilei, fibrillose lined to hollow stipes with thick cartilaginous cortices, small punctate roughened basidiospores, well-developed bilaminate ixocutis, filamentous subcapitate thin-walled cheilocystidia, no clamp connections and mild latent Syringaldazine reaction.

DISTRIBUTION: North America (Oregon): in lowland coniferous rainforests.

COMMENTS: Section *Microsporae* (Singer 1986). This species is microscopically very similar to the smaller and slightly more fragile *P. dissiliens*. The latter species, however, is characterized by clamp connections. *Phaeocollybia sipei* was erroneously placed in synonymy with *P. californica* (Section *Versicolores*) by Horak (1977).

ADDITIONAL REFERENCES: Arora, 1981; Goetz, 1975, 1979; Norvell, 1995a, 1997; Smith & Trappe, 1972

76. *Phaeocollybia smithii* Bandala, & Montoya *Mycotaxon* 52(2):406-407. 1994*+

CHARACTERS: Small bitter-tasting rooting basidiomes with viscid chestnut brown conic-campanulate pilei, dingy ochraceous young lamellae, pallid tan stipe that becomes purplish brown from the base upwards, small (5.2-5-3.2-3.6 µm) subglobose finely verrucose basidiospores, thin-walled clavate cheilocystidia, and abundant clamp connections.

DISTRIBUTION: Eastern North America (Michigan) under conifers among *Pteridium* rhizomes.

COMMENTS: This was originally reported as *P. jennyi [sic]* by Smith (1957b), who noted that his specimens possessed clamp connections while the type of *P. jennyae* did not. Bandala and Montoya also examined both, and concluded that the North American specimens are separate and "...belong to an independent taxon which is distinguished by spore size, clamped hyphae and cheilocystidia form. It must be considered as an isolated new species in Section *Radicatae.*" The authors also compare *P. smithii* to *P. radicata* (which differs in having thick-walled capitate cheilocystidia) and *P. oregonensis* (which they note has bigger subellipsoid spores). While Bandala & Montoya mention that most of the septa are clamped, they do not illustrate the cheilocystidia with clamp connections.

77. *Phaeocollybia spadicea* Smith in *Brittonia*, 9: 215, 1957.

CHARACTERS: See Chapter 6 for a complete technical description and discussion. Key characters include the glutinous dark brown broadly campanulate pileus, stuffed drab colored stipe with cinnamon-colored fibrillose patches, medium-sized verrucose beaked limoniform basidiospores, well-developed bilaminate ixocutis, heteromorphic cheilocystidia with refractive capitulate to lageniform thick-walled cheilocystidia intermixed with occasional to frequent thin-walled clavate elements, absent clamp connections, strong Syringaldazine reaction on stipe and pseudorhiza.

DISTRIBUTION: North America (Washington; Oregon, California); coastal lowlands on the ground in ancient to mature *Picea* forests.

COMMENTS: Section *Versicolores.* Horak (1977) synonymized *P. spadicea* with the closely related *P. lugubris,* which has a distinctly olivaceous cast to its paler-colored pileus and and basidiospores that lack a developed apical callus.

ADDITIONAL REFERENCES: Arora, 1981; Bandala, 1994; Goetz, 1975, 1979; Goetz, Barnhart & Barnhart, 1987; Norvell, 1998*; Smith, Smith & Weber, 1989; Smith & Trappe, 1972.

78. *Phaeocollybia sparsilamellae* Liu, *Mycotaxon* 56: 98-99, 1995*+.

CHARACTERS: Moderately small rooting basidiomes with dry brown sparsely striate convex to acutely papillate reflexed pilei, very distant brown lamellae, brown to dark brown slender

(P. sparsilamellae, continued)

hollow swollen stipes, pseudorhizae covered by white tomentum, large (8.2 x 5.3 µm) verrucose ellipsoidal basidiospores, cylindrical to clavate thin-walled cheilocystidia, slightly gelatinized, encrusted cutis, and clamp connections in pileipellis and on cheilocystidia.

DISTRIBUTION: Asia (Yunnan, China)

COMMENTS: The combination of several characters -- the widely separated lamellae, low degree of gelatinization of the pileipellis, presence of a white tomentum on the pseudorhizae (drawn as being quite shaggy), and shape and sparse striation of the pileus -- suggest that this species may not belong in *Phaeocollybia*. Liu makes no mention as to the presence or absence of tibiiform diverticula anywhere on the basidiomes.

79. *Phaeocollybia spoliata* Horak, *Acta Botanica Indica* 2: 72, 1974.

CHARACTERS: Small reddish orange-brown unpleasantly raphanaceous deeply rooting basidiomes with subviscid minutely striate pointed conical pilei, dry innately fibrillose hollow stipes with pale brownish salmon apices and dark purple-red brown pseudorhizae, large (9.5-10 x 5-5.5 µm) warted amygdaliform basidiospores, slightly fusoid subcapitate cheilocystidia, subpellicular hyphae encrusted with brown pigments, and conjectural clamp connections *(q. v.)*.

DISTRIBUTION: India on soil in *Pinus-Abies* forests.

COMMENTS: As described, this species would belong to Section *Versicolores*, where placed by Singer (1986). However Bandala & Montoya (1994) discovered scattered clamp connections in their examinations of the type and have placed it into Section *Subattenuatae*. The report of *P. spoliata* from Mexico by Guzmán, Bandala-Muñoz,& Montoya-Bello (1987) appears to have been an error; re-evaluation of the specimens by Bandala (1994) reveals them to belong to *P. kauffmanii*.

ADDITIONAL REFERENCE: Horak, 1977+.

80. *Phaeocollybia subarduennensis* Singer, *Mycologia Helvetica* 2: 252,m 1987.

CHARACTERS: Very small fragile deeply rooting basidiomes with dry chestnut brown (papillate) subacutely conical pilei, brown ochraceous young lamellae, narrow deep chestnut naked equal stipes, medium-sized (6-7,3 x 4-4.5 µm) punctate-roughened pip-shaped basidiospores, refractive capitate ventricose lageniform tibiiform cheilocystidia, slightly gelatinized pileipelli with deep rusty incrusting pigments in the subpellis, and clamp connections.

DISTRIBUTION: Central America, North America (Mexico), montane under *Quercus*.

(P. subarduennensis, continued)

COMMENTS: Section *Radicatae* (Singer, 1987; Bandala & Montoya, 1994). *Phaeocollybia subarduennensis* is very close to *P. arduennensis* and *P. radicata* (both conifer-associates). Phaeocollybia *arduennensis* differs in its lower broader pilei, more distant lamellae, shorter stipes, and slightly smaller spores. *Phaeocollybia radicata* has differently shaped cheilocystidia, narrower spores, and larger basidiomes. Bandala (1994) has re-evaluated the collections from Mexico previously identified as *P. arduennensis* (Bandala, Guzmán & Montoya, 1989) and determined that they in fact represent *P. subarduennensis.*

81. *Phaeocollybia subattenuata* Singer in *Sydowia* 15: 78, 1961.

CHARACTERS: Small raphanaceous shallowly rooting basidiomes with reddish brown lubricous to subviscid translucent-striate conic-campanulate pilei, ochraceous brown young lamellae, pallid slender hollow stipes, short abrupt pseudorhizae, medium-sized (7.5-8 x ~5 µm) punctate-roughened subellipsoidal to subamygdaliform basidiospores, highly variable thin-walled clavate cheilocystidia, slightly gelatinized pileipellis, and clamp connections.

DISTRIBUTION: South America (Bolivia) and Central America (Costa Rica) in *Quercus* forests.

COMMENTS: Section *Subattenuatae* (Singer, 1970*+, 1986; Bandala, 1994+; Bandala, & Montoya,.1994*+). *Phaeocollybia subattenuata* is similar to *P. amazonica* (considered conspecific by Horak, 1977) which differs in having a long sharply attenuating pseudorhiza, basidiospores with a prominent apical callus and marbled ornamentation, polymorphic slightly wider cheilocystidia, and a completely non-gelatinized pileipellis.

ADDITIONAL REFERENCE: Horak, 1977+.

82. *Phaeocollybia tasmanica* Rees & Wood, *Mycotaxon* 57: 110, 1996*+;

CHARACTERS: Medium-sized deeply rooting basidiomes with moist chestnut brown broadly convex pilei, lilaceous young lamellae, brown hollow bulbous stipes, long thread-like pseudorhizae, small (6.2 x 4 µm) verruculose elliptical to pip-shaped basidiospores, asymmetrical to bifurcating refractive tibiiform cheilocystidia and (numerous) pleurocystidia, and no clamp connections.

DISTRIBUTION: Australasia (Tasmania)

COMMENTS: Probably Section *Microsporae.* Similar to *P. ratticauda,* which has more sharply tapered pseudorhizae beneath swollen stipe areas, paler, shorter and wider basidiospores, and shorter cheilocystidia. The photograph identified as *P. ratticauda* in Fuhrer & Robinson (1992) represents *P. tasmanica.*

ADDITIONAL REFERENCE: (May & Wood, 1997.)

83. *Phaeocollybia tentaculata* Horak, *Sydowia*, Series II 29: 48-49.

CHARACTERS: Small fragile farinaceous non-rooting basidiomes with amber-dark brown dry innately fibrillose conic-convex pilei, argillaceous young lamellae, dry fibrillose hollow equal stipes, small (5.5- 7 x 3.5-4 µm) ovoid asperulate brown basidiospores, frequently furcating refractive capitulate cheilocystidia, non-gelatinized pileipelli with incrusting brown pigments, numerous clamp connections.

DISTRIBUTION: Australasia (New Guinea); at high elevations on soil or rotten wood in *Nothofagus* forests.

COMMENTS: Excluded species. The absence of a pseudorhiza and lack of gelatinized hyphae in the pileipellis suggests that this species may not belong in *Phaeocollybia*. Singer (1986) placed this species into *Melanomphalia* based in part on the lack of pseudorhiza. Horak considered the most conspicuous characters to be the bi- to tri-furcate refractive capitulate cheilocystidia. Similar cystidia can be found in *P. lugubris* and *P. tibiikauffmanii*. Bandala & Montoya (1994) apparently accept the species as a true *Phaeocollybia*, placing it into Section *Radicatae*.

ADDITIONAL REFERENCE: (Garrido, 1988).

84. *Phaeocollybia tibiikauffmanii nom. prov.*

CHARACTERS: See Chapter 6 for a complete technical description. Key characters include the viscid orange campanulate pileus, firm stuffed stipe, vertical monopodial pseudorhiza, moderately large rugulose roughened beaked sublimoniform basidiospores, moderately well-developed bilaminate ixocutis with incrusting and intraparietal pigments, heteromorphic cheilocystidia with abundant frequently forking refractive capitulate fusoid elements intermixed with thin-walled clavate elements, no clamp connections, strongly positive Syringaldazine reaction.

DISTRIBUTION: North America (Oregon) associated with *Picea*.

COMMENTS: This species, which would be placed into Singer's Section *Versicolores*, could be mistaken in the field for the slightly more robust *P. kauffmanii* or much smaller *P. piceae*, both of which, however, produce only thin-walled clavate cheilocystidia.

ADDITIONAL REFERENCE: Norvell, 1998+.

85. *Phaeocollybia viridis* Horak, *Sydowia* Ser. II 29: 44, 1977.

CHARACTERS: Small greenish rooting basidiomes with olive-green dry wrinkled convex to campanulate rugulose pilei, ?chocolate-brown lamellae, olive-green slender hollow stipes, long slender pseudorhizae, very large (9-11 x 5.5-6.5 µm) verrucose amygdaliform to

(P. viridis, continued)

limoniform basidiospores, polymorphic clavate thin-walled cheilocystidia, non-gelatinized pileipellis with incrusting brown pigments, and numerous clamp connections.

DISTRIBUTION: Australasia (New Guinea); on ground under *Nothofagus.*

COMMENTS: Section *Subattenuatae* (Bandala & Montoya, 1994). Horak (1977) emphasizes as key characters the wrinkled olive pileus, very slender pseudorhizae, clamp connections, and conspicuous plage on the large basidiospores.

ADDITIONAL REFERENCE: (Garrido, 1988).

APPENDIX E: Taxonomic index

Phaeocollybias

* = Pacific Northwest species
Bold = primary discussion
Bold italic = illustration
(...) = DNA abbreviation(s)

Appendix E (continued): Taxonomic index

Other fungi

Plants

Appendix E (continued): Taxonomic index

APPENDIX F: Photographic Credits

Elizabeth Fox (all photographs used with permission of Agriculture & Agri-foods Canada)

P. attenuata -- *Fig.* 2.5a; *Fig.* 6.4 (a)
P. benzokauffmanii -- *Fig.* 2.4(c); *Fig.* 6.6 (b)
P. fallax -- *Fig.* 6.13 (a)
P. piceae -- *Fig.* 6.28 (b,c)
P. pseudofestiva -- *Fig.* 6.32 (c)
P. redheadii -- *Fig.* 6.35 (b)
P. rifflipes -- *Fig.* 6.37 (a)
P. 'similis' -- *Fig.* 6.43 (b)
P. spadicea -- *Fig.* 6.47 (a)

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P. ammiratii -- *Fig.* 6.2 (b,c,d,e); *Fig.* 6.32 (a)
P. attenuata -- *Fig.* 6.4 (b)
P. benzokauffmanii -- *Fig.* 2.3 (b); 6.6 (c)
P. californica -- *Fig.* 6.8 (b,e)
P. carmanahensis -- *Fig.* 6.24 (d)
P. dissiliens -- *Fig.* 2.9 (a); *Fig.* 6.10 (a,b)
P. fallax -- *Fig.* 6.13 (b)
P. kauffmanii -- *Fig.* 6.17 (a,b)
P. luteosquamulosa -- *Fig.* 2.2 (a, b); *Fig.* 2.9 (b, c); *Fig.* 6.20 (b, c, d)
P. olivacea -- *Fig.* 6,22 (b)
P. oregonensis -- *Fig.* 6.24 (a,b,c,e)
P. phaeogaleroides -- *Fig.* 6.26 (a, d,e)
P. piceae -- *Fig.* 6.28 (a)
P. pseudofestiva -- *Fig.* 6.32 (a, d)
P. redheadii -- *Fig.* 2.11 (b); *Fig.* 2.12 (a, b, c, d); *Fig.* 6.35 (c,d)
P. rufotubulina -- *Fig.* 2.1 (a,b); *Fig.* 2.3 (a); *Fig.* 2.6(b); *Fig.* 2.8 (a,b); *Fig.* 2.9 (e); *Fig.* 2.10 (b); *Fig.* 6.8 (c,f); 6.39 (d,f)
P. scatesiae -- *Fig.* 2.5 (c, d); *fig.* 2.6 (c); *Fig.* 2.10 (c); *Fig.* 6.8 (a,d); *Fig.* 6.41 (a,b,c)
P. 'similis' -- *Fig.* 2.10 (a)
P. sipei -- *Fig.* 2.6(a); *Fig.* 6.45 (a,b)
P. spadicea -- *Fig.* 2.2 (c); *Fig.* 6.47 (b,c)
P. tibiikauffmanii -- *Fig.* 2.9 (d); *Fig.* 6.49 (a,b)

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P. ammiratii -- *Fig.* 6.2 (a)
P. benzokauffmanii -- *Fig.* 6.6 (a)
P. kauffmanii -- *Fig.* 6.16
P. luteosquamulosa -- *Fig.* 6.20 (a)
P. olivacea -- *Fig.* 6.22 (a,c,d)
P. phaeogaleroides -- *Fig.* 6.24 (b,c)
P. pleurocystidiata -- *Fig.* 6.30 (a,b)
P. pseudofestiva -- *Fig.* 6.32 (b)
P. redheadii -- *Fig.* 2.11 (a); *Fig.* 6.35 (a)
P. rifflipes -- *Fig.* 6.37 (b)
P. rufotubullina -- *Fig.* 6.39 (a,b,c,e)
P. 'similis' -- *Fig.* 6.43 (a,c)
P. spadicea -- *Fig.* 2.4 (a)

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Selected scientific publications:

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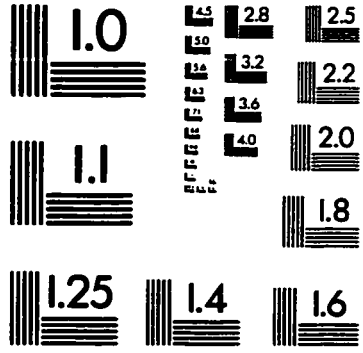
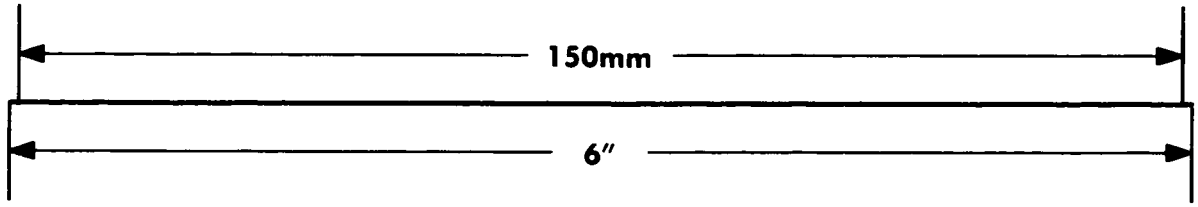
TEST TARGET (QA-3)





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