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Autor: Singer, Rolf
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PHAEOLLYBIA IN THE OAK WOODS OF COSTA RICA, WITH NOTES ON EXTRALIMITAL TAXA.

Rolf Singer

Field Museum of Natural History
Chicago, Ill. USA

Summary: Three new species of oak woods inhabiting *Phaeocollybia* from Costa Rica are described. These belong to three different sections of the genus. An analysis of the species belonging to each section supports the assumption that the taxonomic position of the host is not decisive for that of the fungus and that phytogeography reflecting early migration routes of the fungi has a more meaningful correlation with the affinities of the *Phaeocollybia* species to each other. Observations on extralimital taxa include the description of three new Amazonian species and observations on a few other taxa from Europe, North America and Asia. Keys to the sections and to the neotropical species are provided.

Zusammenfassung: Drei neue Arten von Eichenwald-bewohnenden *Phaeocollybiae* aus Costa Rica werden beschrieben. Diese gehören in drei verschiedene Sektionen der Gattung. Eine Analyse der zu jeder Sektion gehörenden Spezies unterstützt die Annahme, dass die systematische Stellung des Wirtes nicht für die des Pilzes entscheidend ist und dass Phytogeographie als Ausdruck früher Migrationsrouten dieser Pilze eine bedeutsamere Beziehung zu den Affinitäten innerhalb der Gattung zeigt. Beobachtungen an *Phaeocollybia*-Arten von ausserhalb Costa Ricas schliessen die Beschreibung von vier neuen Arten aus Amazonien und Daten über einige Taxa aus Europa, Nord Amerika und Asien ein. Schlüssel zu den Sektionen und zu den neotropischen Arten von *Phaeocollybia* werden eingeschlossen.

Résumé: Trois nouvelles espèces de *Phaeocollybia* des chênaies du Costa Rica sont décrites. Elles appartiennent à trois sections différentes de ce genre. Une étude des espèces appartenant à chaque section étaye l'idée que la position systématique de l'hôte n'est pas déterminante pour celle du champignon; la phytogéographie témoignant d'anciennes voies migratoires des champignons montre une corrélation plus significative avec les affinités respectives des espèces de *Phaeocollybia* entre elles. Hors du Costa Rica, trois nouvelles espèces d'Amazonie sont décrites et d'autres observations concernent quelques taxa d'Europe, d'Amérique du Nord et d'Asie. Des clés sont proposées pour les sections et pour les espèces néotropicales de *Phaeocollybia*.

I. INTRODUCTION

The genus *Phaeocollybia* Heim has been reported in the tropics (SINGER 1970; HORAK 1974, 1977). While it is true that the northern species are found in coniferous forests as stated by SMITH (1957), this cannot be generalized for the genus since the neotropical species are all collected in forests without conifers. While SMITH (1957) and SMITH & TRAPPE (1972) considered it possible that some of the American *Phaeocollybiae* are mycorrhizal with conifers, REDHEAD & MALLOCH (1986) have shown that at least *P. christinae* (Fr.) Heim is apparently neither saprophytic nor mycorrhizal, but a root parasite. Since other tropical species have been found in fully anectotrophic forests, it is probable that the non-mycorrhizal (or at least non-ectomycorrhizal) status of *Phaeocollybia* can now be generalized. It is less certain that all species are parasitic since the pseudorrhiza of *P. amazonica* Sing. in one case seemed to end in rotten wood.

Most species thus far known from the lowland neotropics belong in section *Subattenuatae* Sing. It was therefore of interest to find the position of three new species discovered in the Querceta of Costa Rican tropical-montane vegetation between 2200 and 3200 m elevation. Since in my treatment of the genus (1986) some regrettable printing errors remain uncorrected (p. 665*), I use the opportunity to correct them here. For easier disposition of the species here discussed I shall now give the characters of the sections in form of a key:

1. Clamp connections present, sometimes scattered among simple septa (in *P. oligoporpa*), in the carpophores.
 2. Spores 7.5-11.3 μm long in 4-spored forms, even larger in 2-spored forms; cheilocystidia rather versiform. **Sect. *Subattenuatae*** Sing.
 - 2* Spores up to 7.3 μm long, mostly $\pm 6 \mu\text{m}$ long; cheilocystidia all or almost all capitate or subcapitate. **Sect. *Radicatae*** Sing.
- 1* Clamp connections absent (or quite exceptional) in the carpophores.
 3. Spore length 6.5 μm or more.
 4. Cheilocystidia attenuated to subacute above and often capitate at the apex. **Sect. *Versicolores*** A. H. Smith
 - 4* Cheilocystidia clavate, cylindrical or utriform. **Sect. *Phaeocollybia***
 - 3* Spore length up to 6.5 μm **Sect. *Microsporae*** Sing.

*) Line 20, read Corner & Horak in Horak instead Horak; line 14-15, omit *P. cidaris* ...; line 17 read > instead of <; line 22 read > instead of <; line 27 read laterarius instead of lateria

II. NEOTROPICAL OAK-ASSOCIATED SPECIES

Sect. *Subattenuatae* Sing., Flora Neotropica, Monograph 4: 4, 1970.

KEY TO THE SPECIES KNOWN TO THE AUTHOR

1. Lamellae olive ("bistre green" Maerz & Paul) *P. elaeophylla* Sing., see part III
- 1* Lamellae not olive when young.
 2. Pileus with an ixocutis; spores (many or all) reaching more than 9 μm in length, with \pm rough circumference.
 3. Pileus diameter less than 30 μm ; spores 9.5-12.3 x 6-7 μm ; epicutis strongly gelatinized; hyphae of carpophore with numerous clamp connections. South American species growing in terra firme forest of the tropical lowlands.
 4. Basidia 2-spored; spores 11.7-12.3 x 6.5-7 μm .
P. megalospora var. *megalospora*, see part III
 - 4* Basidia (2-3-)4-spored; spores 9.5-11.5 x 6-7 μm
P. megalospora var. *tetraspora*, see part III
 - 3* Pileus diameter more than 30 μm ; spores (9)-9.5-11 x 5-6.5 μm ; epicutis weakly gelatinized and not very deep; many septa of the hyphae without clamp. Species of the montane Querceta in Central America.
 1. *P. oligoporpa* Sing.
(if small, from China, see *P. similis* (Bres.) Sing.)
 - 2* Pileus without an ixocutis; epicutis not or scarcely gelatinized.
 5. Spores over 9 μm long and over 5 μm broad. Species of the montane Querceta (see "3" above); species of the hylaea, cf. "8" below.
 - 5* Many or all spores less than 9 μm long. Species of the tropical lowlands.
 6. Stipe pallid, rusty dotted below; odor and taste raphanaceous; spores distinctly ornamented; cheilocystidia less than 30 μm long and less than 6 μm broad
P. subattenuata Sing.
 - 6* Stipe concolorous with pileus, or fulvous with the apex pinkish beige (between "rose beige" and "monkey skin" Maerz & Paul) or entirely "dorado" to "cinnamon" (Maerz & Paul); odor raphanaceous or none; spores as above or with indistinct, marbled to extremely finely punctulate ornamentation; cheilocystidia as above, or longer or broader.
 7. Odor distinctly raphanaceous; spore ornamentation very weak; edge of lamellae with some pseudoparaphysoid elements and cheilocystidia versiform, 33-47 x 6.8-8.2 μm *P. amazonica* Sing.

7* Odor none or very weak; ornamentation well visible; cheilocystidia as above or different.

8. Cheilocystidia all or mostly slightly subcapitate, thin neck and ventricose below, 25-32 x 6-6.5 μm ; spores 7.7-10.3 x 5.3-6.5 μm , with a callus-like mucro; basidia almost all 4-spored
P. brasiliensis Araujo ex Sing. var. *brasiliensis*

8* Cheilocystidia more variable; spores (7)-7.5-8.3 x 4.7-5.5 x 4.5-4.8 μm ; basidia mostly 4-spored, some 3-spored and 5-spored.
see *P. brasiliensis* var.

1. *Phaeocollybia oligoporpa* Sing. spec. nov. Pl. I, fig. 1.

Pileo latericio-brunneo vel aureobrunneo vel ochraceobrunneo, subviscidulo, conico vel conico-campanulato, umbonato vel papillato, 30-82 mm lato; lamellis brunneolis vel fuscis, ferruginascentibus e sporis; stipite 110-205 x 12-25 mm supra terram, pseudorrhiza attenuata, usque ad 245 mm longa, pileo subconcolori vel subaurantiaco et glabro apicem versus; odore debili. Sporis (9)-9.5-11 x 5-6.5 μm , verruculis 0.2 μm projicientibus et callo mucroneque 0.8-2.5 μm projiciente ornatis, circumferentia asperula; cheilocystidiis 15.5-37 x 4.5-10 μm , versiformibus, hyalinis, elementis hyphalibus filamentosis intermixtis. Hyphis defibulatis sed nonnullis septis fibulatis. Epicute tenui, ixocutiformi sed moderatim gelatinosa prope superficiem, ubi hyphae demum arthrosporas formant; hypodermio cutiformi, pigmento intraparietali et incrustante gaudentibus. Ad terram in quercetis costaricensibus montanis. Typus: Gomez 18196 (F).

Pileus lateritious-brown, gold-brown, or ochraceous brown when fresh, tending to become almost black when dried, evenly colored, with or without an innate radial lineate fibrilosity, only subviscid, glabrous, naked, smooth, dried \pm shiny, conic to campanulate, obtuse, more rarely subacute, umbonate, more rarely papillate or subumbonate, 30-82 mm broad, 23-70 mm high.

Lamellae at first varying from light brown to fuscous, with narrow pallid edge, becoming more rusty from the spores, ascendant, moderately to medium broad, later slightly ventricose, sometimes intervenose, close to almost crowded, subfree to adnexed.

Stipe orange-brownish with umber base or concolorous with the pileus, glabrous, dry, often shiny, smooth, subequal or slightly tapering upwards above ground, but with a long attenuated pseudorrhiza below ground, 110-205 x 12-25 mm (without the pseudorrhiza), pseudorrhiza up to 245 mm long. Veil none.

Context without distinctive or noticeable odor.

Spores (9)-9.5-11 x 5-6.5 μm , most frequently 9.5-10.5 x 6-6.3 μm , ellipsoid to more often pip-shaped, with a mostly low, more rarely projecting (1-2.5 μm) apical mucro and there with a callus (wall discontinuity hyaline), more rarely without it, in

lateral view asymmetrical but not lentiform, with a distinct but low, slightly contrasting by color, verruculose-punctate ornamentation about 0.2 μm high which in mature spores causes the outline to be somewhat rough, with rather indistinct perisporium, a plage absent, but plage-like small zones occasionally visible, rusty-ochraceous brownish with little contrasting warts and often hyaline or subhyaline mucro or callus region.

Hymenium: Basidia 18-36 x 7-9.5 μm , 4-spored, with or without basal clamp. Cystidia none. Cheilocystidia making the edge of the lamellae heteromorphic (or almost so), 15.5-37 x 4.5-10 μm , mostly 24-33 x 6-8 μm , versiform, often flexuous, often mixed with filamentous hyphal elements \pm 2.5 μm broad, the cystidioid cells often long pedicellate, clavate, clavate-mucronate, cylindrical with basal or median swelling, ampullaceous, subulate, utriform, hyaline, later often ochraceous, thin-walled.

Hyphae: Hymenophoral trama regular, with hyphae broader in the central than in the outer layer, more septa without than with clamp connections both here and in the covering layers and the trama.

Covering layer: Epicutis of pileus a layer 30-50 μm deep, later becoming shallower since the hyphae disintegrate to form 1-3-celled arthrospores, the hyphae forming an ixocutis but only moderately gelatinized and eventually gelatinized only in the uppermost tier. Hypodermium - a cutis of brown, pigment-incrusted hyphae, 1-5 μm thick, i.e. broader than the filamentous hyphae (1-2.5 μm , very few to 5 μm) of the epicutis.

In *Quercus* dominated forest on the ground, under *Quercus* spec., in small groups, fruiting in the summer rainy season at elevations above 2400 m.

Material studied: Costa Rica: Cartago, along Panamerican highway km 55, La Chonta, 2500 m alt., 11 VII 1982, leg. GOMEZ 18196 (F), type. -- Cierro de la Muerte, 31 VII 1986, at 3200 m alt., SINGER B 14542 (F).

The scattered clamp connections may suggest affinity with section *Versicolores*, and, indeed, one of our oak-connected species belongs in that section. However, *P. columbiana*, a typically neotropical species growing in anectotrophic forest, is also placed in *Versicolores*, and a third species of the Querceta of Central America, obviously does not belong in either *Versicolores* or *Subattenuatae*. We must conclude therefore, that species of different affinities corresponding to migrations of different times and directions have contributed to the *Phaeocollybia* flora of the Querceta, a conclusion which is corroborated by the fact that similar situations are also assumed to reflect the history of the Central American flora in other classes. *P. viridis* Horak (New Guinea, under *Nothofagus*) as well as *P. similis* (see part III) also occur with Fagaceae.

Sect. *Radicatae* Sing., Flora Neotropica Monograph 4: 4. 1970.

Only one of the species from Costa Rica enters this section, and only one enters the neotropical lowlands.

KEY TO THE NEOTROPICAL SPECIES

1. Spores 6-7.3 x 4-4.5 μm , pip shaped; stipe deep chestnut. Species of the montane Quercetum 2. *P. subarduennensis* Sing.
- 1* Spores shorter, subglobose-ovoid; stipe yellow ("pond lilly" Maerz & Paul). Amazonian species *P. flava* Araujo ex Sing. (see part III)

2. *Phaeocollybia subarduennensis* Sing. spec. nov. Pl. II, fig. 2, CA, CH.

Pileo castaneo-brunneo, conico, subacuto, 8-12 mm lato; lamellis brunneolo-ochraceis, ascendentibus, adnexis; stipite 66-72 x 1-2 mm (cum pseudorrhiza), atrocastaneo, aequali sed pseudorrhiza longa attenuata; carne tenui, inodora, miti. Sporis 6-7.3 x 4.4-5 μm , punctatis; cheilocystidiis omnibus capitatis, 19-54 x 3.5-5 μm , capitulo (1.5)-2.5-4.5 μm diam.; hyphis fibulatis. Sub quercu in montanis costaricensibus. Typus: Gomez & Singer B 12583 (F).

Pileus chestnut brown, hygrophanous, glabrous, innately radially fibrillose-striate-lineate, smooth, naked, fading to ochraceous or rusty-ochraceous by dehydration, ochraceous brown when dried, not viscid, conical, subacute, often small papillate, 8-12 mm broad and high.

Lamellae brownish ochraceous, rather narrow, ascendant, close, with narrowly pallid edges, adnexed.

Stipe deep chestnut, glabrous, naked, equal or subequal above the long-attenuated pseudorrhiza, with pseudorrhiza 66-78 mm long, 1-2 mm broad above ground. Veil none.

Context paler than surfaces, thin, odor none, taste mild.

Spores 6-7.3 x 4.4-5 μm , pip-shaped, some subovate, not lentiform, with or without a suprahilar applanation, rusty ochraceous brown, inamyloid to slightly pseudoamyloid in accumulations, without a plage and without a distinct germ pore, but a callus-like, often indistinct apical discontinuity (hyaline) of the wall noticeable, ornamentation punctate and reaching 0.2 μm in height, apex neither truncate nor mucronate.

Hymenium: Basidia 22-25 x 5.5-6.2 μm , 4-spored, with exceptional 2-spored ones rarely encountered. Cystidia none. Cheilocystidia 19-54 x 3.5-5 μm , mostly with a basal ventricosity, more rarely with both a basal and a median ventricosity or without ventricosity and then filamentous, but always capitate at the apex (capitulum 1.5-4.5 μm diam.) and underneath the capitulum frequently constricted to (1)-1.4-2.5 μm , the capitulum sometimes double or triple, but mostly simple and

apex not forked, all hyaline and thin-walled, numerous and making the edge heteromorphic, often flexuous.

Hyphae with numerous clamp connections, inamyloid, not gelatinized, hymenophoral trama regular, pale stramineous to pale brownish stramineous, its hyphae 5-23 μm broad in the central stratum, towards hymenium narrower, without pigment incrustations.

Covering layers: Epicutis of pileus hyaline to subhyaline, not or very scarcely gelatinized, not or very slightly incrustated, consisting of thin-walled hyphae 1-1.5- (4.5) μm thick forming a cutis. Hypodermium ochraceous-ferruginous, consisting of somewhat interwoven, strongly deep-rusty incrustated hyphae, in an average broader than those of the epicutis, forming a cutis.

Under *Quercus* spec. and *Chusquea* spec. in a Quercetum of the tropical-montane zone, on the ground, in small groups.

Material studied: Costa Rica: Cartago, Cerro de la Muerte, at 3200 m alt., 2 VIII 1981, Gomez & Singer B 12583, (F), typus.

This species is close to two temperate-zone species, *P. arduennensis* Bon and *P. radicata* (Murr.) Sing., both connected with conifers. *P. arduennensis* Bon, Docum. Mycol. 9 (35): 42, 1979 differs in lower, campanulate to hemispheric-umbonate pileus, ventricose and less close lamellae (in *P. subarduennensis* there are about 40 through-lamellae), shorter stipe and somewhat smaller spores. *P. radicata* (Murr) Sing. has differently shaped cheilocystidia (although they are also capitate), and also narrower spores. Its carpophores are larger than those of both *P. arduennensis* and *P. subarduennensis*. The only neotropical species other than *P. subarduennensis* is *P. flava* Araujo ex Sing. which is much less closely related to the former because of the very short, pseudoamyloid spores, the colors of the carpophore and the habitat in an ectotrophic forest of the Amazonas region.

Section *Versicolores* A. H. Smith, Brittonia 9:109. 1957.

No oak-related and no Central American species have been found thus far. The only neotropical species, *P. columbiana* Sing., comes from the lowland rain forest of the Pacific coast near Buenaventura.

Section *Phaeocollybia*

KEY TO THE NEOTROPICAL SPECIES

1. Odor distinct, of phenol; epicutis in form of an ixocutis; spores more than 9.5 μm long; pileus glutinous; associated with *Quercus* 3. *P. quercetorum* Sing.

1* Odor distinct, raphanaceous; epicutis not or scarcely gelatinized; pileus not glutinous; spores less than 9.5 μm long; species associated with conifers (*Abies religiosa*) *P. neosimilis* Sing.

3. *Phaeocollybia quercetorum* Sing. spec. nov. Pl. II, fig. 3, CA, CH, SPQ.

Pileo atrobrunneo vel ferrugineo-brunneo, ad marginem pellucide striato, glutinoso, convexo, umbonato, 31-32 mm lato; lamellis cinnamomeo-argillaceo-brunneis, confertis; stipite (cum pseudorrhiza) 55-88 x 4-8 mm, sordide pallido ad apicem, vulpino ad basin, in zona intermedia brunneolo, aequali vel subtus ventricosus, sed pseudorrhiza longa attenuata praedito; carne pilei pallida; odore phenolico. Sporis 9.5-14 x 5.5-6.5 μm , amygdaliformibus et mucronatis, manifeste verruculoso-punctatis, laete brunneis. Cheilocystidiis versiformibus, vix capitatis. Epicute pilei ixocutiformi; hypodermio cutiformi sed cellulis multis brevibus et usque ad 30 μm latis, pigmento haud manifeste incrustante. Hyphis defibulatis. - Ad terram in quercetis sub quercubus in zona montana. Typus: Singer B 12399 (F).

Pileus rather deep brown to rusty brown, shining when dried, glutinous, transparently striate over 5-9 mm at the margin, smooth or somewhat uneven-rugose, glabrous and naked, conic-convex or convex, umbonate, 31-32 mm broad.

Lamellae cinnamon-brown or cinnamon-clay, then reddish umber, close, rather broad or medium broad, subfree.

Stipe dirty pallid at the apex, below apex brownish, at base fox red, smooth, glabrous, dry, either equal in upper part and ventricose in lower part, or entirely equal excepting the pseudorrhiza which is long and attenuated to the lower end, 55-88 mm long (with pseudorrhiza), the epigeous part 28-46 mm long and 4-8 mm thick.

Context of the pileus pallid; odor distinctly of phenol.

Spores 9.5-14 x 5.5-6.5 μm , those that are merely short mucronate at the apex measuring about 10-11 x 5.5-6 μm , those (fewer) that are apically long-beaked up to 14 x 6.5 μm , almond shaped or subfusoid-ellipsoid, distinctly verruculose-punctate, the mucro or beak often subhyaline and always smooth, the ornamentation projecting 0.2-0.3 μm , the circumference rugulose-uneven, the ornamentation weakly or almost not contrasting in color with the ground color, without plage, inamyloid.

Hymenium: Basidia 25-33 x 8-8.5 μm , 4-spored. Cystidia none. Cheilocystidia 17-41 μm long and versiform, making the edges almost or quite heteromorphic, of three basic types: (1) very narrowly clavate and mostly 6-6.5 μm broad; (2) clavate to subfilamentous and claviculate at the apex, 7-9.2 μm broad; (3) narrowly ventricose in the middle with a slight constriction underneath a subcapitate apex \pm 4 μm wide, venter about 7 μm in diameter (this type relatively uncommon).

Hyphae without clamp connections, inamyloid. Hymenophoral trama regular, not gelatinized.

Covering layer: Epicutis of pileus and ixocutis of hyaline, filamentous hyphae 1.5-3 μm broad, forming a deep layer. Hypodermium strongly cinnamon-brownish pigmented but without distinct incrustations, consisting of hyphae 15-30 μm broad and often short-celled and constricted at the septa, almost like a *Mycena*-structure, forming a cutis which is well differentiated from the epicutis.

In Quercetum of the tropical montane zone, under *Quercus* spec. on the ground (no conifers here), in small groups.

Material studied: Costa Rica: Cartago, El Empalme, at about 2300 m alt., 23 VII 1981, Singer B 12399 (F), typus.

This species is close to *P. christinae* (Fr.) Heim which differs in rather obtuse umbo rather than a subacute papilla, more numerous and decidedly clavate cheilocystidia, and different odor and habitat. Also, the spores are narrower. It occurs in Europe and North America. Other similar American species are *P. gregaria* Smith & Trappe and *P. piceae* Smith & Trappe, both with much broader stipes, the former growing densely gregarious, the latter with somewhat different colors, both associated with *Picea sitchiensis*.

Other species belonging undoubtedly to section *Phaeocollybia* and associated with Fagaceae are apparently (according to published descriptions by HORAK 1977) *P. muscicolor* Horak, *P. procera* Horak, and *P. odorata* Horak, growing in *Nothofagus* forests (*P. procera*), *Nothofagus* forest mixed with *Lithocarpus* and *Castanopsis* (*P. muscicolor*), and *Lithocarpus* forests mixed with *Castanopsis* (*P. odorata*) in New Guinea. All these species grow in mountains near the Pacific as does *P. quercetorum*.

As for *P. neosimilis* Sing., see part III.

Sect. *Microspora* Sing., Flora Neotropica Monograph 4: 6. 1970

The type of this section is *P. christinae* Heim sensu Heim (i.e. *P. jennyi* (Karst.) Heim). While the type species and probably some others are associated with conifers, three species are apparently associated with Fagaceae: *P. corneri* Horak, *P. querqueti* Corner & Horak ap. Horak (*Quercus*) and *P. ratticauda* Horak (*Nothofagus*), but no neotropical species are known.

III. NOTES ON EXTRALIMITAL SPECIES

Phaeocollybia arduennensis Bon, Docum. Mycol. 9: 42. 1979. Pl. II, fig. 2, CAA, CHA.

Pileus blackish chestnut, not viscid, glabrous, subsmooth, conic-subpapillate but not acute, then campanulate with incurved margin, about 6 mm high and 8-10 mm broad.

Lamellae gold-brown, eventually more rusty, ascendant, close but not crowded,

subfree to slightly adnexed.

Stipe almost concolorous with the lamellae at apex, with the pileus below, smooth, subequal and about 28 x 2 mm above ground, with a pseudorrhiza about 17 mm long and attenuated downwards.

Context somewhat concolorous with surfaces; odor raphanaceous; taste submild.

Spores 5.5-7 x 4-4.7 μm (a few, from 2-spored basidia, 8-12 x 5-7.3 μm), ovate-ellipsoid to somewhat pip shaped, rusty-brown verruculose on rusty-pallid ground, the ornamentation about 0.2 μm high, neither distinctly pseudoamyloid nor cyanophilic, without mucro or beak, without plage, with a weak callus and not truncate.

Hymenium: Basidia 4-spored, very few 2-spored, 18-25.7 x (4)-5.3-6.5 μm . Cystidia none. Cheilocystidia making the edges heteromorphic, 26-43 x 3.6-7.5 μm , filamentous with capitate apex, or with basal ventricosity and also capitate, capitulum 2.8-4.7-(7.5) μm diam., mostly \pm constructed immediately below capitulum (there 1.5-2.8-(4.5) μm wide), wall thin, hyaline. Basal septa clamped.

Hyphae inamyloid, with clamp connections. Hymenophoral trama regular, non-gelatinized, with brown intraparietal pigment but scarce and very inconspicuous incrustation.

Covering layers: Epicutis of pileus not or scarcely gelatinized (and even that only in the uppermost tier where some of the filamentous hyphal ends are occasionally recurved, consisting of applicate 1.8-2 μm broad subhyaline, filamentous hyphae forming an up to 20 μm deep cutis. Hypodermium - a rather deep cutis - consisting of broader and strongly pigment-incrusted hyphae.

On mossy (*Leucobryum* and some other mosses) ground with some spruce needles, in a Piceetum (*Picea abies*) with a few pines (*Pinus silvestris*) mixed in. Small group.

The above description is given exclusively from the collection made in Austria, Nö, near Schrems, 15 IX 1979, SINGER C 9394 (WU). The species is new for Austria and is here described because a redescription appeared desirable for comparison with *P. subarduennensis* Sing.

P. arduennensis Bon may have been confused with the similar *P. hilaris* (Fr.) Romagnesi sensu Horak (= *P. cidaris* (Fr.) Romagnesi sensu Bresinsky) in Europe but this latter species - whatever the correct name to be applied (cf. Singer 1986, foot note) - has clampless hyphae and viscid pileus, differentiating it from *P. arduennensis* and *P. subarduennensis*. The specimens described above are undoubtedly conspecific with the type: they differ only in minor characteristics (darker colors of very slightly smaller carpophores with very slightly larger spores, presence of a raphanaceous odor).

Phaeocollybia brasiliensis Araujo ex Sing. spec. nov. (sect. *Subattenuatae*), Pl. III, fig. 6

Pileo atrobrunneo, zona marginali hygrophana, estrio, haud viscido, \pm 35 mm lato; lamellis confertis, subliberis; stipite fusco, \pm 5 mm lato; carne subfusca, inodora. - Sporis 7.7-10.3 x 5.3-6.5 μ m, callo papillae apicali instructis, manifeste punctatis, perisporio levi vel subasperulo tectis, subcitriformibus; maturis plerumque leniter pseudoamyloideis cyanophilisque et pariete integra 0.5 μ m crassa praevisis; cheilocystidiis 25-32 x 6-7.5 μ m, plerumque anguste ventricosis, apice angusto (1.5 μ m diam.) et superne subcapitato (2.5-3 μ m diam.) instructis, hyalinis; basidiis \pm 26 x 8 μ m, plerumque tetrasporis, utrififormibus, rarius clavatis. Hyphis inamyloideis, fibulatis. Tramate hymenophorali regulari, ex hyphis subhyalinis efformato. Epicute pilei cutiformi, haud gelatinosa vel vix gelatinosa, ex hyphis hyalinis vel subhyalinis, 1.2-3 μ m crassis, parallelis, haud vel minime incrustatis efformata, sat tenui, dermatocystidiis 15-35 x 4-4.5 μ m, subampullaceis et cheilocystidiis similibus, sat sparsis; hypodermio cutiformi, in strato inferiore pigmento fortiter incrustato, cellulis usque ad 54 x 25 μ m. - Ad terram argillosam in silvis typi "terra firme". Typus: Singer B 11473, Brasilia: Amazonas, Reserva Ducke 7 I 1979, INPA 102712.

Phaeocollybia brasiliensis var: A form similar to *P. brasiliensis*, but differing in spores not reaching the maximal size indicated for the type and with some 3-spored and 5-spored basidia observed is mentioned here because its status cannot be determined as long as the type of *P. brasiliensis* has not been recollected so that its variability can be appreciated. In these forms near *P. brasiliensis* we find the cheilocystidia more variable, the colors of pileus, stipe and context lighter, some spores slightly lentiform, the lamellae somewhat broader than in the type of the species. Collections studied: Singer B 11056 and B 11058, both from the same place as var. *brasiliensis*, leg. Maria Alves & Izonete Araujo. 26 V 1978 (INPA).

Phaeocollybia elaeophylla Sing. spec. nov. (sect. *Subattenuatae*). Pl. III, fig. 7.

Pileo brunneo, hygrophano, siccando pallidiore atque olivaceo-flavo tincto, vix viscido, campanulato et papillato, dein convexo et umbonato, 20-40 mm lato; lamellis olivaceis ("bistre green"), siccando ochraceo-brunneis, mediocriter latis, confertissimis, rotundato-subliberis dente angustissimo subdecurrente stipite ad apicem cinnamomeo-pallido, ceterum fulvo, siccando atrocastaneo, glabro, fusoideo vel aequali, pseudorrhiza abrupte angustata, moderatim longa constanter praedito, 45-60 x 4-5 mm; carne sordide pallida; inodora, miti. - Pilei sicci margine fortiter castanescente KOH ope. - Sporis 8.5-10.3 x 4.5-6.5 μ m, ovatis vel ellipsoideo-fusififormibus et frequenter \pm rhomboideo-subangularibus (frontaliter visis), applanatione suprahilari saepe praeditis sed rarissime prominentia obtusa basali nota (lateraliter visis), laete ferrugineis, haud pseudoamyloideis sed endosporio inter-

dum pseudoamyloideo instructis, circumferentia laevigatis sed minutissime punctatis, poro germinativo angusto, interdum sat lato, interdum truncato munitis, zona levi suprahilari (plage) destitutis: basidiis 14.5-23.5 x 5.5-7 μm , 1-2-3-4-sporis. Cheilocystidiis ad aciem heteromorpham 17-49 x 3.5-5.5 μm , cylindraceutis vel anguste clavatis vel utriformibus vel subventricosis, plerumque (sed non omnibus) appendiculo longo (usque ad 20 μm) filiformi, saepe apicaliter furcato vel lateraliter semel vel bis ramoso, plerumque acuto vel subacuto raro apicaliter subcapitato praeditis, hyalinis, interdum aureo-melleis, interdum granulis minutis hyalinis incrustatis. Hyphis hyalinis, fibulatis, inamyloideis, nonnullis interdum lenissime pseudoamyloideis, haud gelatinosis, filamentosis, nonnullis leniter inflatis usque ad 7.5 μm ; tramate hymenophorali regulari, hyphis angustis, subparallelis. Epicute pilei subhyalina, cutiformi, saepe brunneolo incrustata pigmento, haud densa sed vix gelatinosa; hypodermio brunneo, fortiter incrustato pigmento, cutiformi. - Ad terram argillosam in silva typi "terra firme". Typus: Brasilia, Amazonas, Reserva Ducke, 26 V 1978, SINGER B 11063 (INPA).

Phaeocollybia flava Araujo ex Sing. spec. nov. (sect. *Subattenuatae*), Pl. II, fig. 3, CAF, DCF, CHF.

Pileo flavo-luteo ("amber y" vel "antique gold" in centro; "amber y" vel "lime y" ad marginem), glabro, subviscidulo, convexo dein applanato, centro papillato, \pm 28 mm lato; lamellis isabellino-subolivaceis (13 L 6), confertis, adnexis vel subliberis; stipite flavo ("pond lily"), glabro, (cum pseudorrhiza) \pm 64 x 3 mm; supra terram 30 mm longo et aequali; carne flavida vel flavido-pallida, inodora, miti. Sporis 5-5.5 x 4.5-5 μm , breviter subovatis, ferrugineo-ochraceis, asperis ex ornamentatione 0.2-0.3 μm alta, pseudoamyloideis; basidiis 22-23 x 5-6.5 μm , tetrasporis, utriformibus; cheilocystidiis, ampullaceis vel ventricosis, apice subcapitatis (capitulo 3.5-6.5 μm diam.), hyalinis vel flavis, numerosis; cystidiis perpaucis, cheilocystidiis similibus. Hyphis in NH₄OH, KOH exudantibus solutionem flavam pigmenti, fibulatis; tramate hymenophorali regulari. Epicute pilei cutiformi sed in strato tenuissimo externo subgelatinosa, subtus haud gelatinosa, hyalina, ex hyphis 1-4.5 μm latis, levibus efformata; hypodermio flavo et brunneolo, pigmento incrustato, ex hyphis eis epicutis latioribus, cutem formantibus consistente, in epicute nonnullis dermatocystidiis praesentibus, his 26-32 x 7-7.6 μm , ampullaceis vel utriformibus vel clavatis vel cylindraceuto-subcapitatis, plerumque flavidis. - Ad terram argillosam in silva typi "terra firme" solitario. Typus: Brasilia: Amazonas, 30 km a Manaus, in territorio EMBRAPA, 14 VI 1977, SINGER B 9976 (INPA).

This species, of all those belonging to *Phaeocollybia*, is the one closest to *Gymnopilus*. While in other species the spores are only vaguely pseudoamyloid in mature stage or not pseudoamyloid at all, here the spores are as definitely

pseudoamyloid as in any *Gymnopilus*. The glabrous stipe, partially subgelatinous epicutis and subviscidulous pileus, and the typically developed pseudorrhiza caused us to decide in favor of insertion in *Phaeocollybia*. The question of affinity to *Gymnopilus* seemed to make it desirable to have data on chemical reactions. We obtained the following: NH₄OH on dried pileus surface producing a slight rusty flush. - KOH on dried pileus: deep chestnut, eventually blackish chestnut; on spores on lamellar surfaces chestnut, but not becoming black.

Such reactions might fit some species of *Gymnopilus* as well as some of *Phaeocollybia*, and do not appear to be decisive inasmuch as the yellow stained medium of preparations can be observed in both genera and is not characteristic for all species of either of them.

Phaeocollybia megalospora Araujo ex Sing. spec. nov. (sect. *Subattenuatae*), Pl. III, fig. 5.

Var. *megalospora*.

Pileo brunneo, viscido, conico, acute papillato, 23 mm lato; lamellis coriicoloribus, sat latis, subliberis; stipite ceraceo-luteo, brunneo basin versus, glabro, subviscidulo, supra terram \pm 40 x 2-2.5 mm et aequali, radicante; carne inodora. - Sporis 11.7-12.3 x 6.5-7 μ m, fusoideis, in tertia parte inferiore latioribus, depressione suprahilari praeditis, fortiter verrucosis verrucis spadiceis supra fundum ochreum, ad apicem breviter rostratis vel rotundatis, pariete \pm 1 μ m crassa instructis, poro germinativo nullo. Basidiis 24-27 x 6.5-8.7 μ m, bisporis, clavatis; cheilocystidiis 25-35 x 5-6.2 μ m, ampullaceis vel subfilamentosis, rarius ad ipsum apicem dilatatis et tunc 4.2-5.2 μ m diam. Hyphis fibuligeris. Epicute pilei ex hyphis 1.7-2.3 μ m latis, nonnullis haud incrustatis, aliis incrustatione pigmenti flavi incrustatis, ixocutem profundam formantibus consistente. Hypodermio cutiformi, hyphis fortiter incrustatis pigmento atrobunneo, 3.3-9 μ m latis. - Ad terram argillosam in silva typi "terra firme", Brasilia: Amazonas, iter Manaus-Caracari, km 45, 11 VII 1977, leg. SINGER & ARAUJO, Singer B 10082 (INPA 102698).

Var. *tetraspora* Sing. var. nov.

Pileo convexo, papillato, ad marginem haud manifeste substriatulo, \pm 13 mm lato; lamellis latis, rotundato-adnexis; stipite vegeto et sicco pileo concolori, (cum pseudorrhiza) \pm 22 mm longo; sporis 9.5-11.2 x 6-7 μ m, callo instructis sed haud vel vix rostratis; basidiis 22-26 x 9.5-10.2 μ m, tetrasporis, utrififormibus vel clavatis; cheilocystidiis anguste cylindratis vel clavatis vel utrififormibus, obtusis, 40-50 x 3.8-6.5 μ m, hyalinis, paucis interne brunneolis; notis ceteris cum typo conformibus. - Ad terram argillosam in silva typi "terra firme" solitario. Typus: Brasilia: Amazonas, 30 km a Manaus septentrionem versus in territorio EMBRAPA, 14 VI 1977, SINGER B 9975 (INPA, 100937).

Phaeocollybia neosimilis Sing., Ag. mod. tax. 4th ed., p. 665. 1986 (sect. *Phaeocollybia*).

Basionym: *P. attenuata* ssp. *mexicana* Sing., Sydowia 11: 367. 1957.

For a complete description of this species see Flora Neotropica Monogr. 4:10. 1970. This differs from *P. piceae* Sm. & Trappe in not being viscid due to the lack of an ixocutis.

Phaeocollybia similis (Bres.) Sing., Lilloa 22: 567. 1949 (publ. 1951). Pl. III, fig. 4.

Naucoria similis Bres., Icon. Myc. 16, tab. 794. 1930.

This species clearly belongs in the section *Subattenuatae*. The type of this species from South China, collected "by native collectors", communicated by HANDEL-MAZZETTI, Iter Sinense nr. 12690 has been divided in Vienna into two parts, one at WU and one at W. Both contain the same fungus under the same collectors number. The WU material is mixed with some tricholomataceous material - *Mycena* or *Marasmius*, not studied by me - a fact also noticed by Horak (1977), and is therefore considered as an isotype, with the W material representing the holotype. The latter was studied by me, and compared with the isotype.

The carpophores are typical for a rather small radicant *Phaeocollybia* and are well preserved, the pileus rust colored (now partly darkened), unshining, with some moss and earth particles still visible; lamellae rusty, subclose, rather broad, rounded-attached to rounded-subfree; spore print still bright rusty; the stipe now a rather deep brown, glabrous, hollow. Spores 8-10.8 x 5.7-6.8 μm , ellipsoid to short ellipsoid, with protracted callus sublimoniform, with strongly contrasting ornamentation which is irregularly warty and deep rusty-chestnut on yellowish ground and rough in circumference, without a plage and without a germ pore, apical mucro 1.4-1.9 μm projecting. Basidia 19.3-24 x 7-7.3 μm , (2)-4-spored. Cystidia none. Cheilocystidia 17-21.5 x 6-11.5 μm , versiform, basidiomorphous to utriform, or ampullaceous, fewer narrowly ventricose or broadly ventricose or subcylindrical, none capitate, all broadly rounded-obtuse at the apex, thin-walled, hyaline or brown inside. Hyphae with clamp connections. Hymenophoral trama regular, hyphae with subhyaline wall, not or indistinctly and scarcely incrustated by pigment, not gelatinized. Epicutis of pileus hyaline and non-incrustated, intermixed with some hyphae which are slightly yellow-incrustated, not gelatinized, the hyphae 1.2-4-(7.5) μm broad and forming a cutis. Hypodermium also in form of a cutis, its hyphae strongly rusty-incrustated, 4.5-11.5 μm broad and some hyphal cells rather short.

According to data available from the same general region, this fungus probably grows in fagaceous forests in the mountains.

Our data agree well with Bresadola's description except that the shiny surface of the pileus, also observed in some of the material seen by us, seems to be an artefact. It also agrees with HORAK's (1977) notes excepting the "gelatinized walls" of the

hyphae in the epicutis, the lack of clamp connections (it is true that some septa are clampless, but these seem to be secondary), and the presence of a plage on the spores (cf. my foot note on p. 664, 1986). SMITH (1957) described under the name *P. similis* (Bres.) Sing. a different species, found only once in Washington, U.S.A., which I suspect to be conspecific with *P. neosimilis* (see above).

IV. DISCUSSION

The fact that the three species occurring in the Querceta of Costa Rica belong to three different sections and are much more closely related to other species of their respective section than to each other confirms the conclusion that the identity of the host genus does not play a major role among the factors determining the characteristics of the major subdivisions of the genus. Indeed, we have a similar result if we consider the other two major ecological associations - aside from those with Fagaceae - viz the conifer-related group and the hylaea-group. While in the conifer-associated group, we have representatives in four of the five sections, and in the hylaea group in two of the five, Fagaceae-relation is observed in at least four out of five sections. This leaves out of consideration some species of uncertain position, particularly *P. perplexa* Orton which was transferred to a new genus, *Stagnicola* Redhead & Sm. (1986), *P. primulina* (Berk.) Horak which was transferred to *Gymnopilus* by Pegler (1965) and *P. tentaculata* Horak which, I believe, is a *Melanomphalia* rather than *Phaeocollybia*.

On the other hand, the fact that in the *Subattenuatae* we have five related species from Amazonia while the only neotropical hylaea species not belonging in this section belongs in section *Versicolores* tends to indicate that phytogeography reflects taxonomic arrangement, and the pantropical distribution of sect. *Subattenuatae* appears to confirm it. In this connection it is interesting to note that the genus *Laccaria*, in contrast to *Phaeocollybia*, seems to be entirely absent from Amazonia, but common and polymorphous in the Nothofagus region of South America where intensive search during several years has not produced a single specimen of a *Phaeocollybia*. Another group of related species of *Phaeocollybia* within section *Phaeocollybia* has been pointed out under *P. quercetorum* (no 3) where an area comparable to that of *Boletellus ananas* (Curt.) Murr. is involved. The *Subattenuatae* (with clamped hyphae, large spores), pan-tropical-subtropical, seems closest to the ancestral group from which *Phaeocollybia* originated.

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EXPLANATION OF FIGURES

PLATE I

Fig. 1: *Phaeocollybia oligoporpa* Sing.: CAE, epigeous part of carpophore. CAP, pseudorrhiza. SPI, small pileus. YPI, young pileus. OPI subumbonate pileus. CH, cheilocystidia.

PLATE II

Fig. 2: *Phaeocollybia subardennuensis* Sing.: CH, cheilocystidia. CA, carpophores. *Phaeocollybia arduennensis* Bon: CAA, carpophore. CHA, cheilocystidia.

Fig. 3: *Phaeocollybia quercetorum* Sing.: CA, carpophores. CH, cheilocystidia. SPQ, spores. HY, hyphae with normal, imperfect, and medallion clamps. *Phaeocollybia flava* Araujo ex Sing.: CAF, carpophore. CHF, cheilocystidia. DCF, dermatocystidia of pileus.

PLATE III

Fig. 4: *Phaeocollybia similis* (Bres.) Sing. CA, carpophore, dried. SP, spore. CH, cheilocystidia. All from holotype.

Fig. 5: *Phaeocollybia megalospora* Araujo ex Sing. CAE, carpophore of var. *megalospora*. BA, basidium of var. *megalospora*. CHM, cheilocystidia of var. *megalospora*. - CAT, carpophore of var. *tetraspora*. BT, basidium of var. *tetraspora*. CHT, cheilocystidia of var. *tetraspora*.

Fig. 6: *Phaeocollybia brasiliensis* Araujo ex Sing.: CAB, carpophore. DCB, Dermatocystidium of pileus. CHB, cheilocystidia.

Fig. 7: *Phaeocollybia elaeophylla* Sing.: CHE, cheilocystidia. CA, carpophores. CAY, young carpophore.





