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SPECIES OF *PHLEBIA* SECTION *LEPTOCYSTIDIOPHLEBIA*
(APHYLLOPHORALES, CORTICIACEAE) IN NORTH AMERICA

K. K. NAKASONE, H. H. BURDSALL, JR., AND LAURIE A. NOLL

Center for Forest Mycology Research
Forest Products Laboratory^{1/}
USDA, Forest Service
Madison, Wis. 53705

SUMMARY

Species limits of three North American species of *Phlebia* section *Leptocystidiophlebia* are clarified using cultural and morphological data. The species studied are *Phlebia ludoviciana*, proposed as a new combination, *P. subochracea*, and *P. subserialis*. *Phlebia brevispora*, a related species, is also discussed. *Phlebia phlebioides* is considered conspecific with *P. subserialis*. *Phlebia subochracea* is reported for the first time from North America. *Corticium granulatum*, *Phlebia danica*, and *P. ochraceo-fulva* are considered to be synonyms of *P. subochracea*. Basidiocarp descriptions are included for all species, and cultural descriptions are provided for three species.

INTRODUCTION

During the daily task of identifying wood-inhabiting Hymenomycetes in pure culture, the senior author encountered difficulty distinguishing species of the *Phlebia subserialis* (Bourd. et Calz.) Donk-*Peniophora ludoviciana* Burt complex. The fruiting bodies of these two species were examined microscopically to resolve the problem. As a result, a new taxon, *Phlebia brevispora* Nakas. (Nakasone and Eslyn, 1981), was described, and a species new to North America, *P. subochracea* (Bres.) Erikss. et Ryv., was identified. The authors present here the morphological and cultural differences among the species in this complex. Methods and materials are described in Burdsall and Nakasone (1981). However, capitalized color names are from Ridgway (1912). Asterisks (*) indicate specimens from which polysporous cultures were obtained and studied.

BASIDIOCARP AND CULTURE DESCRIPTIONS

Phlebia ludoviciana (Burt) Nakas. et Burds., comb. nov. Fig. 1
= *Peniophora ludoviciana* Burt, Ann. Missouri Bot. Gard. 12:244.
1926. (Basionym)

^{1/} Maintained at Madison, Wis., in cooperation with the University of Wisconsin.

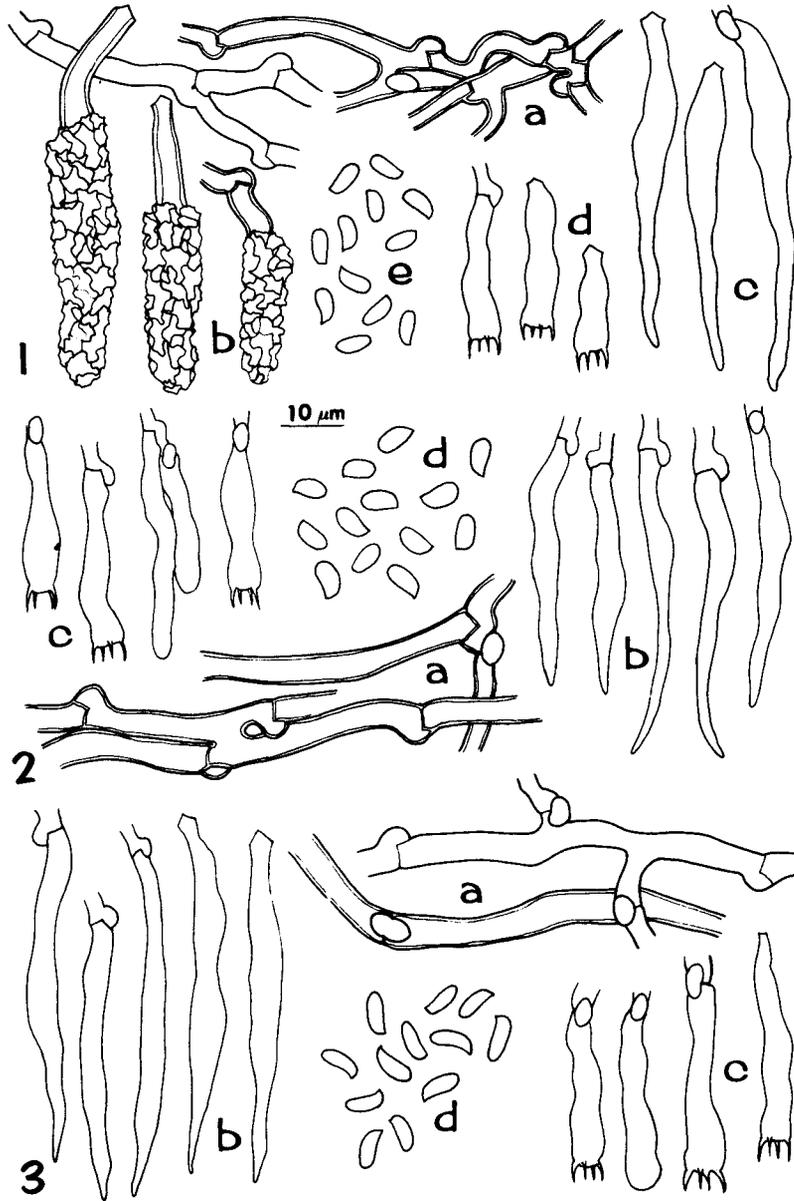


Fig. 1. Microscopic characters of *Phlebia ludoviciana* (HHB 9282): a. subicular hyphae; b. encrusted cystidia; c. smooth cystidia; d. basidia; e. basidiospores. **Fig. 2.** Microscopic characters of *Phlebia subochracea* (holotype): a. subicular hyphae; b. cystidia; c. basidia; d. basidiospores. **Fig. 3.** Microscopic characters of *Phlebia subserialis* (HHB 5796): a. subicular hyphae; b. cystidia; c. basidia; d. basidiospores.

=Hyphoderma ludovicianum (Burt) Martin et Gilbn., Mycotaxon 6:62. 1977.

Basidiocarp broadly effused or effused in small patches, up to 350 µm thick, phlebioid to membranous, fertile area Wax Yellow to Serpentine Yellow when fresh, drying to Cinnamon-Buff to Tawny-Olive or Isabella Color, smooth or with small warts; margin abrupt or fibrillose, concolorous or somewhat paler than fertile area.

Hyphal system monomitic; subiculum 100-200 µm thick; subicular hyphae more or less agglutinated, 3-4.5 µm diam, hyaline, nodose septate, with slight wall thickening, smooth to heavily encrusted with hyaline crystals near the substrate; subhymenium of agglutinated hyphae 2.5-3.5 µm diam, hyaline, nodose septate, thin walled, smooth or encrusted with hyaline crystals; cystidia of two types: (1) nearly cylindrical, 35-70 x 6-9 (-12) µm, with thickened walls, heavily encrusted with hyaline crystals, with basal clamp connection; (2) narrowly obclavate or ventricose, (35-) 45-70 x 5.5-7 µm, hyaline, thin walled, smooth with basal clamp; basidia clavate, 18-24 x 5.5-5 µm, thin walled, with basal clamp, 4-sterigmate, sterigmata up to 4 µm long; basidiospores ellipsoid, 5.5-6.5 x 2-2.5 µm, hyaline, thin walled, smooth, Melzer's -, acyanophilous.

Specimens examined: U.S.A.--FLORIDA: HHB 6564* on Liquidambar styraciflua L. (sweetgum), Alachua County, HHB 9659* and HHB 9437* on Quercus sp. (oak), and HHB 9640* on Acer rubrum L. (red maple), Leon County; ILLINOIS: HHB 9282 on Fraxinus sp. (ash), Johnson County; LOUISIANA: Langlois 1919, April 20, 1888, St. Martinsville, St. Martin County (holotype of Peniophora ludoviciana) (FH); WISCONSIN: HHB 10827 on Betula sp. (birch) and FP 101738* on Betula nigra L. (river birch), La Crosse County, HHB 8715* on Alnus sp. (alder), Fond du Lac County.

Remarks: Some specimens of P. ludoviciana have poorly developed or rare encrusted cystidia and are therefore easily confused with P. subochracea.

Phlebia ludoviciana has been placed most recently in the genus Hyphoderma (Martin and Gilbertson, 1977). However, because of the phlebioid aspect of the basidiocarp, as well as the simple septate hyphae of the advancing zone in culture, we feel that this species should be placed in the genus Phlebia.

Cultural Characters

Growth on malt extract agar (MEA) rapid, plates covered in 1 wk, mats white, appressed, thin, subfelty, with cottony-woolly mounds scattered over mat, developing large fruiting areas by 4 wk, Sulphine Yellow or Dark Olive Buff, smooth to grandinioid; margin even, appressed; odor none; agar usually bleached by 2 wk. Oxidase reactions at 1 wk on gallic acid agar (GAA) moderate, mat (trace-) 20-43 mm diam; on tannic acid agar (TAA) strong, mat 15-23 mm diam, or sometimes a stain and no growth. Optimum temperature 32C (Fig. 4).

Microscopic characters: Hyphae of advancing zone 3-6 µm diam, thin walled, simple septate, branched; hyphae of submerged mycelium 3-4 µm diam, thin walled, nodose septate, branched; hyphae of aerial mat similar to submerged hyphae except narrower, 2.5-3 µm diam, with slightly thickened walls at 2 wk, occasionally encrusted; chlamydo-spores observed once or twice in submerged mycelium, globose, 20-30 µm diam, thin walled, hyaline, terminal.

Key patterns: A-P-F-1-10; A-P-F-1-10-14. Species code: 2.4.7. 14.(34).36.40.41.42.48.54.59.

Monosporous cultures: Four monosporous isolates of HHB 8715 and six isolates of FP 101738 were studied with each mating type represented. They resembled the polysporous isolates except that they did not have clamp connections.

Incompatibility system: Biggs (1938) reported *P. ludoviciana* to possess a bipolar incompatibility system. Our pairings have confirmed her results: FP 101738 $A_1 = 1,2,9,10,11,12,14$, $A_2 = 3,4,5,7,13,15$;

HHB 8715 $A_3 = 1,3,8,9$, $A_4 = 2,5,6,10$.

Cultural descriptions: Hayashi (1974); Biggs (1938).

Remarks: Cultures of *P. ludoviciana* are fairly uniform but the growth rate on GAA at 1 wk may vary. The lack of asexual spores distinguishes this species from others in the complex.

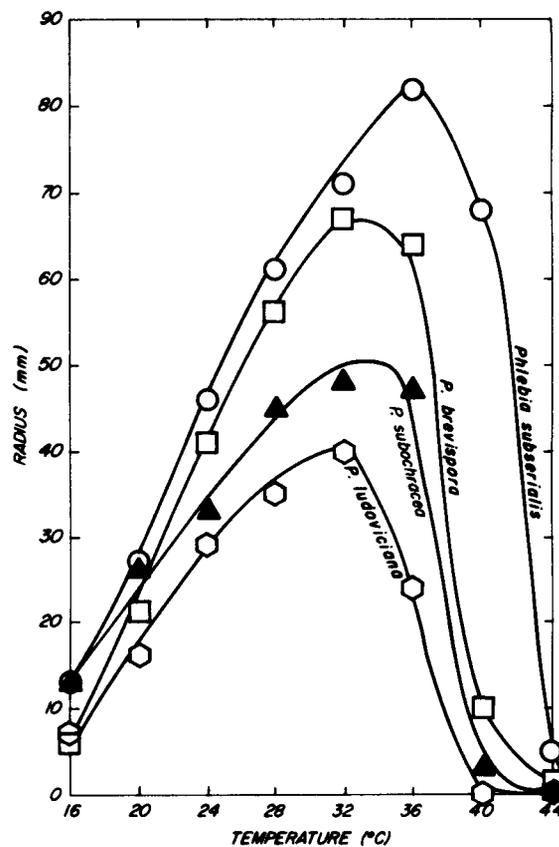


Fig. 4. Average radial growth of *Phlebia* species on MEA after 4 days at 8 temperatures.

- Phlebia subochracea* (Bres.) Erikss. et Ryv., Fig. 2
Cort. North Europe 4:873. 1976.
= *Grandinia subochracea* Bres., Hedwigia 33:206. 1894.
= *Corticium ochraceo-fulvum* Bourd. et Galz., Bull. Soc. Mycol.
France 27:257. 1911.
= *Phlebia ochraceo-fulva* (Bourd. et Galz.) Donk. Fungus 27:12.
1957.
= *Corticium granulatum* Burt, Ann. Missouri Bot. Gard. 13:236. 1926.
= *Peniophora danica* M. P. Chris., Friesia 5:207. 1956.
= *Phlebia danica* (M. P. Chris.) M. P. Chris., Dansk Bot. Archiv
19:167. 1960.

Basidiocarps broadly effused, up to 0.25 mm thick, phlebioid to membranous, fertile area Wax Yellow to Serpentine Green when fresh, Cinnamon-Buff to Warm Sepia on drying, smooth or slightly warted; margin abrupt to fibrillose, white to nearly concolorous with fertile area.

Hyphal system monomitic; subiculum 100-200 μm thick, with thick crystalline layer near substrate; subicular hyphae 3-5 μm diam, with irregular swellings, rarely up to 7 μm broad, hyaline, nodose septate, with slight wall thickening, usually heavily encrusted with hyaline crystals; cystidia of two types: (1) rare to abundant, narrowly obclavate, 35-65 x 5-7 μm , projecting up to 40 μm above basidia, hyaline, thin walled, smooth or rarely with scattered light granules, with basal clamp connection; (2) not always present, poorly differentiated pseudocystidia, imbedded, short cylindrical, 15-20 x 4-5 μm , lightly to heavily encrusted with hyaline crystals, thin walled, hyaline, with basal clamp connection; basidia clavate with slight constriction below apex, 24-27 x 5.5-6.5 μm , thin walled, with basal clamp connection, 4-sterigmate, sterigmata up to 4 μm long; basidiospores narrowly to broadly ellipsoid, 5-7 (-8) x (2.5-) 3-3.5 μm , hyaline, thin walled, smooth, Melzer's -, acyanophilous.

Specimens examined: CANADA--ONTARIO: RLG 6809* on *Betula papyrifera* Marsh. (paper birch), Frontenac County. DENMARK--MPC 259 on *Salix* sp., Sjaelland (holotype of *Peniophora danica*); MPC 4374 on *Alnus* sp., Fyn; MPC 4502 on *Salix* sp. (?), Lolland (C). EAST GERMANY--No. 71, an einem alten Stock von *Salix* auf einer Wiese bei Königstein, October 1893, leg. W. Krieger (holotype of *Grandinia subochracea*) (S, isotype BPI). FRANCE--l'Aveyron: Bourdot 7790, Galzin 5531, sur chêne, 9 IV 1910, Bétirac (lectotype of *Corticium ochraceo-fulvum*); Bourdot 7791, Galzin 3164, sur aubépine, le Larzac (PC). U.S.A.--ARIZONA: RLG 7030 on *Platanus wrightii* Wats. (Arizona sycamore), RLG 7362 on *Quercus* sp., and HHB 8494* on *Quercus arizonica* Sarg. (Arizona white oak), Santa Cruz County, JLL 9761* on Arizona sycamore and RLG 10313 on *Quercus hypoleucoides* A. Camus (silverleaf oak), Cochise County; ARKANSAS: FP 107000 on *Salix* sp. (willow), Desha County; IDAHO: J. R. Weir No. 33 on *Populus trichocarpa* Torr. et Gray (black cottonwood), Priest River (holotype of *Corticium granulatum*) (FH); MISSISSIPPI: FP 106750 on willow, Washington County; MONTANA: HHB 5668* on *Populus tremuloides* Michx. (quaking aspen) and RLG 4552* on *Populus* sp. (poplar), Lake County; NEW YORK: RLG 2651* on hardwood, Onondaga County.

Remarks: *Phlebia subochracea* is difficult to distinguish from *P. ludoviciana*. Both species are bright yellow-olive when fresh but dry to tan or light brown. Microscopically, *P. subochracea* has broader spores and lacks the well-differentiated, encrusted cystidia found in *P. ludoviciana*.

Cultural Characters

Growth on MEA rapid, plates covered in 1 wk; mats white to pale yellow, azonate, appressed, thin, subvelvety, sometimes fruiting by 6 wk, developing Mustard Yellow to Pinard Yellow fruiting areas; margin even, appressed; odor none; agar bleached or unchanged. Oxidase reactions at 1 wk on GAA moderate, mat 45-70 (-90) mm diam; on TAA strong, mat 18-29 mm diam, but often staining with no growth. Optimum temperature 32-36C (Fig. 4).

Microscopic characters: Hyphae of advancing zone 6-8 μm diam, thin walled, simple septate, branched; hyphae of submerged mycelium 3-5 μm diam, thin to slightly thick walled, nodose septate, branched aerial mat absent; chlamydospores globose to limoniform, 8.5-14.5 (-21.5) μm diam, thin walled, terminal or intercalary, rare to abundant at 2 wk in submerged mycelium; arthroconidia cylindrical, 3-5 μm diam, of various lengths, developing from fragmented hyphae, rare at 2 wk, abundant at 6 wk in submerged mycelium.

Key patterns: A-P-F-1-2-10, A-P-F-1-10, B-P-F-1-2-5-6-10.

Species code: 2.4.7.(14).34.35.36.38.40.41.42.(48).54.59.

Monosporous cultures: Four monosporous cultures from HHB 8494 were examined. These cultures did not have clamp connections, produced arthroconidia in 1 wk, and occasionally developed thick walled hyphae; however, they resembled the polysporous cultures in all other growth and microscopic characters.

Incompatibility system: Eight monosporous cultures of HHB 8494 and RLC 4552 were paired in all combinations. In both cases two mating types were obtained: HHB 8494 $A_1 = 3,11,12$; $A_2 = 4,9,10,13,14$; RLG 4552 $A_3 = 1,2,3,4,5,6,7$; $A_4 = 8$. Thus, P. subochracea possesses a bipolar incompatibility system.

Interfertility tests: As the results of Table I indicate, P. subochracea is not conspecific with P. ludoviciana or P. subserialis.

Remarks: Cultures of P. subochracea are quite variable. They may or may not bleach MEA plates and may develop a strong reaction or only a weak stain on TAA. The microscopic characters, however, are stable. The development of chlamydospores and arthroconidia by P. subochracea distinguishes it from P. ludoviciana, which produces no asexual spores.

Phlebia subserialis (Bourd. et Galz.) Donk, Fig. 3

Fungus 27:12. 1957.

\equiv Corticium subseriale Bourd. et Calz., Hymén. France p. 219. 1928.

\equiv Peniophora phlebioides Jacks. et Deard., Can. J. Res., C, 27:150. 1949.

\equiv Phlebia phlebioides (Jacks. et Deard.) Donk, Fungus 27:12. 1957.

\equiv Jacksonomyces phlebioides (Jacks. et Deard.) Jülich, Persoonia 10:329. 1979.

Basidiocarps broadly effused, smooth, yellowish to pale buff, waxy. Hyphal system monomitic, subicular hyphae 3-6 μm diam, thin to slightly thick walled, nodose septate, gelatinized; cystidia cylindrical, tapering toward apex, 45-60 x 4-5 μm , thin walled, smooth; basidia clavate, 25-35 x 5-6 μm , 4-sterigmate; basidiospores allantoid, 5-7 x 1.5-2 μm , smooth, hyaline, Melzer's -, acyanophilous.

Specimens examined: CANADA--BRITISHCOLUMBIA: ut Peniophora phlebioides OTB 11523 (holotype of P. phlebioides) and OTB 11546 on Pseudotsuga taxifolia (Lamb.) Britt. (\equiv P. menziesii (Mirb.) Franco),

TABLE 1. Results of interfertility tests between Phlebia subochracea and related species.

Fungal species	<u>Phlebia ludoviciana</u> (FP 101738)		<u>Phlebia subserialis</u> (RLG 6074)		<u>Phlebia subochracea</u> (HHB 8494)			
	Mating type	A ₁	A ₂	A ₁	A ₂	A ₃	A ₄	
		Isolate number	1 2	4 6	1 4	2 5	3 11	4 9
<u>Phlebia subochracea</u> (RLG 4552)	A ₁	2	- -	- -	- -	- -	+ +	+ +
	A ₂	8	- -	- -	- -	- -	+ +	+ +

Vancouver Island (DAOM). U.S.A.--ARIZONA: RLC 10693* on Pinus engelmannii Carr. (Apache pine), Cochise County, RLC 11639* on Abies concolor (Cord. et Glend.) Lindl. ex Hildebr. (white fir), Pima County; FLORIDA: HHB 9557 on oak and HHB 9842* on Pinus echinata Mill. (shortleaf pine), Leon County; MONTANA: HHB 5796* on Acer glabrum Torr. (Rocky Mountain maple) and RLG 6074* on Pinus contorta Dougl. ex Loud. (lodgepole pine), Flathead County.

Remarks: The narrow, allantoid spores of P. subserialis are distinctive in this complex. The short, slightly thick walled cystidia of P. phlebioides were used to distinguish it from P. subserialis. However, this character is not consistent; some cystidia in the type specimen of P. phlebioides were like those in P. subserialis. We consider the type specimen to be a somewhat unusual specimen of P. subserialis. Interfertility tests that follow support the morphological findings.

Cultural Characters

Growth on MEA rapid, plates covered in 1 wk; mats white to pale yellow, azonate, appressed, thin, subfely to downy, aerial mat often developing a reticulate pattern, firm to tough, usually developing Light Buff to Warm Buff fruiting patches in 2 to 4 wk; margin even, appressed; odor none; agar discoloration none. Oxidase reactions at 1 wk on GAA moderate, mat 63-90+ mm diam; on TAA strong, mat 12-20 mm diam, however, often a stain with no growth. Optimum temperature 36C (Fig. 4).

Microscopic characters: Hyphae of advancing zone 6-8 µm diam, thin walled, simple septate, branched, by 2 wk becoming thick walled, abundant, persisting; hyphae of submerged mycelium 2-3 µm diam, thin walled or with slight wall thickening, nodose septate, often with right angle branching; hyphae of aerial mat 1.5-3 µm diam, thin to slightly thick walled, nodose septate, branched, sometimes encrusted; chlamydospores globose, 13-21 µm diam, thin walled at first, walls up to 2 µm thick in age, terminal or intercalary, scattered, filled with yellow substances.

Key patterns: A-P-F-1-2-10-16; A-P-F-1-2-10-14; A-P-F-1-2-10; B-P-F-1-2-5-6-10. Species code: 2.4.(7).14.34.36.38.41.48.54.55.59.

Monosporous cultures: Five monosporous isolates of RLG 6074 and RLG 10693, with both mating types represented, were examined. These cultures did not have clamp connections; however, they resembled the polysporous cultures in all other growth and microscopic characters.

Incompatibility system: Boidin and Lanquetin (1965) reported *P. subserialis* to be heterothallic with a bipolar mating system. Our pairings have confirmed their results: RLG 6074: $A_1 = 1,4,8,9$,

$A_2 = 2,3,5,6,7,10,12,13,14$; RLG 10693: $A_3 = 2,3,5,6,8,9,10,14$,

$A_4 = 4,7,12,13,15$.

Interfertility tests: The following cultures named *P. phlebioides* were obtained from DAOM: 31797, 52313, WD 188B17, WD 198C17, and WD 918A23 on *Pinus strobus* L. (eastern white pine), T23916B and T23924 on *Pinus banksiana* Lamb. (jack pine). All seven cultures were paired with four haploids of *P. subserialis* (RLG 6074, 4A₁ and 3A₂; RLG 10693, 2A₁ and 7A₂). After 10 days the haploids were checked for clamp connections. All pairings were successful. Two haploids of 52313 were paired with the same four haploids of *P. subserialis*. These pairings were also successful. These results support our morphological conclusion that *P. phlebioides* is conspecific with *P. subserialis*.

Cultural descriptions: Boidin (1958); Stalpers (1978); Hallaksela (1977).

Remarks: The thick walled hyphae, high optimum temperature, and rapid growth at 40C are distinctive characters of *P. subserialis* in pure culture. Our examination of cultures named *Peniophora phlebioides* isolated by Linzon during his study of sapwood decay in eastern white pine (Linzon, 1958) indicates that the deterioration should be attributed to *P. subserialis*.

phlebia brevispora Nakas., in Nakasone and Eslyn, Mycologia. (In press.) 1981.

Basidiocarps broadly effused, tuberculate, smooth near margin, when fresh Light Drab to Light Brownish Olive, darkening when dried; margin narrow, white.

Hyphal system monomitic; subicular hyphae difficult to observe in dried specimens, 5-10 μm diam, nodose septate, with thick, gelatinized walls; cystidia cylindrical, tapering toward apex, 65-75 x 5-6.5 μm , thin walled, smooth, protruding 40 μm ; basidia clavate, 16-23 x 4-5 μm , 4-sterigmate; basidiospores ellipsoid to short cylindrical, 4-4.5 x 2-2.5 μm , smooth, hyaline, Melzer's -, acyanophilous.

Specimens examined: U.S.A.--FLORIDA: HHB 7030 (holotype) on *Pinus elliotii* var. *densa* Little et Dorman (South Florida slash pine), Dade County.

Remarks: The distinguishing characteristics of *P. brevispora* are the short basidiospores and the production of blastoconidia in culture. For a more detailed description of basidiocarps and cultures see Nakasone and Eslyn (1981).

DISCUSSION

A summary of the characters which distinguish the species of the complex is presented in Table II.

TABLE II.--Summary of basidiocarp and cultural characters that differentiate species in the Phlebia subserialis - P. ludoviciana complex.

Species	Basidiocarp characters				Cultural characters on MEA		
	Distribution	Substrate	Encrusted cystidia	Basidiospores (μ m)	Bleached at 2 wk	Asexual spores	Growth rate ^{1/} at 40C (mm)
<u>P. brevispora</u>	Southeastern U.S.A.	Hardwoods and softwoods	None	4-4.5 x 2-2.5	Always	Blastoconidia and chlamydo spores	10
<u>P. ludoviciana</u>	Throughout North America	Hardwoods	Well developed	5.5-6.5 x 2-2.5	Always	None	1-4
<u>P. subochracea</u>	Throughout North America	Hardwoods	Poorly developed	5-7(-8) x (2.5-)3-3.5	Sometimes	Arthroconidia and chlamydo spores	1-4
<u>P. subserialis</u>	Throughout North America	Softwoods rarely on hardwoods	None	5-7 x 1.5-2	Never	Chlamydo spores	64-90

^{1/} Average radial growth on MEA after 4 days.

Phlebia subserialis and related species discussed here belong culturally to Nobles' (1958) group 54, although none are included among the 15 species treated in that work. However, Nobles includes three other Phlebia species: Phlebia albida Post ex Fr., Phlebia radiata Fr., and Phlebia rufa (Pers. per Fr.) H. P. Chris. The cultures of group 54 have a number of similarities. The most striking character is the broad, simple septate hyphae of the advancing zone that give rise to narrower hyphae with clamp connections. The cultures grow rapidly on MEA and develop strong, positive reactions on GAA and TAA. The incompatibility system, well known for species of group 54, has been demonstrated to be bipolar. Many species in this group fruit readily in culture, produce numerous chlamydo-spores, and develop thick walled hyphae from the simple septate hyphae of the advancing zone.

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