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

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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. Cortici um 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 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
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.

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 fimbriose, 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 32°C (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; chlamydospores 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. ludovicianus* 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. ludovicianus* 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.](image-url)

=Corticium ochraceo-fulvum

=Corticium ochraceo-fulvum
(Bourd. et Galz.) Donk. Fungus 27:12.

=Corticium granulatum

=Phlebia danica

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 6899* 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 Konigstein, October 1893, leg. W. Krieger (holotype of Grandinia subochracea) (S, isotype BPI). FRANCE–l’Aveyron: Bourdot 7790, Galzin 5531, sur chêne, 9 IV 1910, Bétrac (lectotype of Corticium ochraceo-fulvum); Bourdot 7791, Galzin 3164, sur aubépine, le Larzac TPC. – US.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; MISSISSIPPI: PP 106750 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); 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, subfetid, 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 32-36°C (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 A₁ = 3,11,12; A₂ = 4,9,10,13,14; RLG 4552 A₁ = 1,2,3,4,5,6,7; A₂ = 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.


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. (=P. menziesii (Mirb.) Franco),
TABLE 1. Results of interfertility tests between Phlebia subochracea and related species.

<table>
<thead>
<tr>
<th>Fungal species</th>
<th>Phlebia ludoviciana (FP 101738)</th>
<th>Phlebia subserialis (RLG 6074)</th>
<th>Phlebia subochracea (HHB 8494)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mating type</td>
<td>A1</td>
<td>A2</td>
<td>A3</td>
</tr>
<tr>
<td>Isolate number</td>
<td>1 2 4 6</td>
<td>14 25</td>
<td>3 11 4 9</td>
</tr>
<tr>
<td>Phlebia subochracea A1</td>
<td></td>
<td>-</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-</td>
<td>+ +</td>
</tr>
<tr>
<td>Phlebia subochracea A2</td>
<td>8</td>
<td>-</td>
<td>+ +</td>
</tr>
</tbody>
</table>

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, sublelty 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 am 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; chlamydomspores 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: A1 = 1,4,8,9,
A2 = 2,3,5,6,7,10,12,13,14; RLG 10693: A1 = 2,3,5,6,8,9,10,14,
A2 = 4,7,12,13,15.
Interfertility tests: The following cultures named P.
phlebioides were obtained from DAOM: 31797, 52313, WD 185817,
WD 198817, 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
Remarks: The thick walled hyphae, high optimum temperature, and
rapid growth at 40°C 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
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: HHH 7030 (holotype) on
Pinus elliottii 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

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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Substrate</th>
<th>Encrusted cystidia</th>
<th>Basidiospores (μm)</th>
<th>Bleached at 2 wk</th>
<th>Asexual spores</th>
<th>Growth rate1/ at 40°C (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. brevispora</em></td>
<td>Southeastern U.S.A.</td>
<td>Hardwoods and softwoods</td>
<td>None</td>
<td>4-4.5 x 2-2.5</td>
<td>Always</td>
<td>Blastocendia and chlamydocypores</td>
<td>10</td>
</tr>
<tr>
<td><em>P. ludoviciana</em></td>
<td>Throughout North America</td>
<td>Hardwoods</td>
<td>Well developed</td>
<td>5.5-6.5 x 2-2.5</td>
<td>Always</td>
<td>None</td>
<td>1-4</td>
</tr>
<tr>
<td><em>P. subochracea</em></td>
<td>Throughout North America</td>
<td>Hardwoods</td>
<td>Poorly developed</td>
<td>5-7(-8) x (2.5-)3-3.5</td>
<td>Sometimes</td>
<td>Arthroconidia and chlamydocypores</td>
<td>1-4</td>
</tr>
<tr>
<td><em>P. subserialis</em></td>
<td>Throughout North America</td>
<td>Softwoods rarely on hardwoods</td>
<td>None</td>
<td>5-7 x 1.5-2</td>
<td>Never</td>
<td>Chlamydocypores</td>
<td>64-90</td>
</tr>
</tbody>
</table>

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 GAAndtAA. The incompatibility system, where known for species of group 54, has been demonstrated to be bipolar. Many species in this group fruit readily in culture, produce numerous chlamydospores, and develop thick walled hyphae from the simple septate hyphae of the advancing zone.

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LITERATURE CITED