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Biogeographical patterns in pyrenomycetous fungi and their taxonomy. 4. *Hypoxylon* and the southern United States

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Abstract — A biogeographic region with a peculiar species composition and located in the southern states of the United States is discussed. It is proposed that this region is a part of a possible Caribbean center of fungal biodiversity. *Hypoxylon confertisilvae*, *H. ilicinum*, *H. meridionale*, *H. minicroceum*, and *H. rolingii* are described as species new to science.

Key words — *Ascomycota*, distribution, *Xylariaceae*

Introduction

A group of the southern states of the United States (Arkansas, Alabama, Florida, Louisiana, Mississippi, Missouri, and Texas) represent a region of considerable interest with respect to the biogeography of pyrenomycetous fungi. First, one can observe typical species that are known only from southeastern North America, including such examples as *Biscogniauxia atropunctata* (Schwein.) Pouzar and *Diatrype atlantica* Lar.N. Vassiljeva on *Quercus* spp., *Diatrype tremellophora* Ellis on *Magnolia* spp., and *Diatrype virescens* (Schwein.) M.A. Curtis on *Fagus grandifolia*. Second, there are species that occur mainly in the southern states listed above, with one example being *Camillea signata* (S.C. Jong & C.R. Benj.) Læssøe et al. The same preference for this region is observed in *Biscogniauxia schweinitzii* Y.M. Ju & J.D. Rogers, *Rosellinia glandiformis* Ellis & Everh., and *R. langloisii* Ellis & Everh.

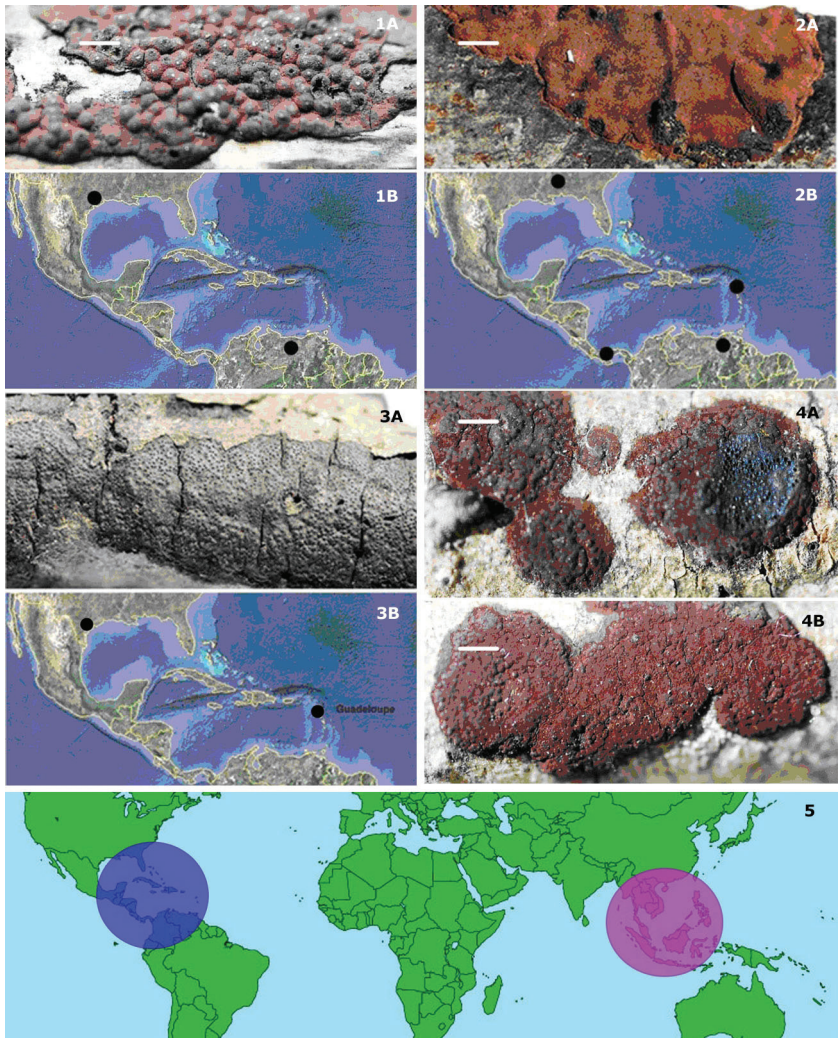
Over a period of several years (2006–11) surveys for pyrenomycetous fungi were carried out in a number of localities in this region, mostly in Arkansas (the Buffalo National River Park, the Ouachita Mountains Biological Station, and the Ozark National Science Center) and Texas (the Big Thicket National Preserve). The survey results combined with literature data suggest a very specific center of fungal biodiversity.

The southern United States as part of a possible Caribbean center of fungal biodiversity

Some species reported for Mexican border regions—*Biscogniauxia arima* F. San Martín et al., *Hypoxylon lividipigmentum* F. San Martín et al., and *Annulohypoxylon thouarsianum* var. *macrosporum* (F. San Martín et al.) Y.M. Ju et al. also have been found in Texas (Big Thicket National Preserve). Several species have distributions that extend from the southern United States to northern South America. Thus, *Hypoxylon venezuelense* Y.M. Ju & J.D. Rogers, described originally from Venezuela (Ju & Rogers 1996), also has been found in Texas (Fig. 1). *Hypoxylon rickii* Y.M. Ju & J.D. Rogers is known from French Guiana, Mexico, and St. John (U.S. Virgin Islands) as well as from Louisiana (Fig. 2). Other Caribbean islands seem to share species of pyrenomycetous fungi with adjacent continental areas, such as *Vivantia guadalupensis* J.D. Rogers et al., described originally from Guadeloupe (Rogers et al. 1996) and later found in Texas (Fig. 3).

There are additional data from some other biogeographic comparisons that support an independent Caribbean center of fungal biodiversity. We have previously discussed the "Asa Gray disjunction," a well-known distribution pattern that exists for many organisms, including fungi (Vasilyeva & Stephenson 2010). This pattern, which is characteristic of species occurring both in northeastern North America and northeastern Asia, is represented by 'sibling' species that replace each other in these two widely separated world regions.

Unexpectedly, a southern parallel to the "Asa Gray disjunction" was found to exist between southeastern Asia (tentatively consisting of the Indochina Peninsula, southern provinces of China, and the Malay Archipelago) and the region in and around the Caribbean Sea and the Gulf of Mexico (Fig. 5). When efforts are made to identify species collected in the Indo-Malayan center of biodiversity (Vasilyeva et al. 2012), the other species they most closely resemble often appear to be those reported from Mexico, the southern United States, or the Caribbean coast of South America. Sometimes, the morphological resemblance is so high that the species from the eastern and western hemispheres differ in only one or two features. (The same phenomenon is observed for the species involved in the northern "Asa Gray disjunction.") For example, *Biscogniauxia schweinitzii* from the southern United States and *B. lithocarpi* Lar.N. Vassiljeva et al. from northern Thailand have strikingly similar asci and ascospores but differ in their stromata. *Hypoxylon rubroargillaceum* Lar.N. Vassiljeva et al. is similar to *H. flavoargillaceum* J.H. Mill. (known from Colombia and Venezuela) but differs in ascal tips that do not turn blue in Melzer's reagent and the presence of granules immediately beneath the surface and among the perithecia that are not yellowish-brown but bright-red.



Figs. 1–5. 1. ***Hypoxylon venezuelense:*** A. Stroma (VLA P–2605), B. Collection localities; 2. ***Hypoxylon rickii:*** A. Stroma (VLA P–2607), B. Collection localities; 3. ***Vivantia guadalupensis:*** A. Stroma (VLA P–2448), B. Collection localities; 4A–B. Stromata of ***Hypoxylon subchlorinum*** (VLA P–2604); 5. Tentative location of the Caribbean and Indo-Malayan centers of fungal diversity. Scale bars: 1A = 1.5 mm; 2A = 9 mm; 3A = 4.5 mm; 4A–B = 2.5 mm. [The maps modified to show our data are taken from the web sites <http://www.biomedcentral.com> (Figs 1B, 2B, 3B) and <http://www.designus.com/vector-world-map> (Fig. 5).]

Such morphological similarities shown by species associated with eastern and western centers of biodiversity is not surprising, given that molecular studies also pull together exactly such species from those areas. Thus, the most interesting and relevant xylariaceous phylogenetic tree (Hsieh et al. 2005) clusters together several species (*Hypoxylon crocopeplum* Berk. & M.A. Curtis, *H. dieckmannii* Theiss., *H. erythrostroma* J.H. Mill., *H. fendleri* Cooke, and *H. haematostroma* Mont.) from both Mexico (the Caribbean center) and Taiwan (the Indo-Malayan center). While this might support conspecificity of specimens from the western and eastern hemispheres, the specimens could just as easily be assigned to different species, as has been done for *Hypoxylon lividicolor* Y.M. Ju & J.D. Rogers from Taiwan and *H. lividipigmentum* from Mexico, two taxa that also cluster together with the same level of support (Hsieh et al. 2005) and which we have already (Vasilyeva & Stephenson 2010) suggested might represent a vicarious pair of species. The pantropical distribution of a number of species as well as the species concepts themselves might have to be reconsidered in the light of the existence of more restricted biogeographic centers of biodiversity.

Supporting data from non-pyrenomycetous fungi

The peculiar species composition of the fungal assemblages found in the southern United States and the occurrence of many species in only some portions of the Caribbean have been emphasized by basidiomycete specialists. For some of these, Wu & Mueller (1997) described a "Florida-Texas distribution pattern." The extensive literature on fleshy basidiomycetes described from Texas (Lewis & Ovrebo 2009) lists a number of species known only from Texas [e.g., *Boletus lewisii* (Both) Bessette et al., *Clitocybe texensis* H.E. Bigelow, *Cortinarius lewisii* O.K. Mill., *Megacollybia texensis* R.H. Petersen & D.P. Lewis, *Russula lewisii* Buyck, *R. texensis* Buyck et al.] or species more widely distributed in the southern United States bordering the Caribbean Sea. Thus, *Phylloporus boletinoides* A.H. Sm. & Thiers is known from Alabama, Florida, and Texas (Singer et al. 1990), whereas *Amanita westii* (Murrill) Murrill has been reported from Florida, Mississippi and Texas (Tulloss & Lewis 1994).

More recent information on basidiomycetes restricted to countries adjacent to the Caribbean Sea has been published. For example, *Ganoderma ravenelii* Steyaert is known from the southeastern states and Mexico (Torres-Torres & Guzmán-Dávalos 2008). Guzmán-Dávalos (2002) indicated that only 13% of Mexican *Gymnopilus* species are distributed worldwide, whereas the remaining 87% occur in only Mexico, in the United States and Mexico, in the United States, Mexico, and Cuba, or in Mexico and Central America. A number of agarics and boletes occur primarily in the montane oak forests of Costa Rica and Colombia (Halling & Mueller 2002). Lodge et al. (2002) note that "49 species of *Hygrocybe*,

Camarophyllopsis and *Cuphophyllus* are found in southeastern United States, excluding species in common with the Lesser Antilles, Trinidad and Venezuela" and that "58.8% (10/17) of the 38 southern Caribbean species would eventually be found in the Greater Antilles." Here the reference to "Caribbean species" surely indicates the existence of a special center of fungal biodiversity.

There are even some data on vicarious species in the Caribbean and Indo-Malayan centers of diversity. As such, *Trogia venenata* Zhu L. Yang et al. was described recently from southern China counterbalanced by a closely related Neotropical species [*Trogia buccinalis* (Mont.) Pat.], described originally from Guyana (Yang et al. 2012).

Possible resurrection of some species

At present, the names of some species reported from the southeastern United States have been reduced to synonyms, but their biogeographic distributional pattern suggests a separate taxonomic identity. For example, *Hypoxylon epiphaeum* Berk. & M.A. Curtis, which is restricted to *Magnolia* spp., was reported [as a variety of *H. investiens* (Schwein.) M.A. Curtis] for Alabama, Florida, Georgia, Louisiana, New Jersey, New York, North Carolina, South Carolina, and West Virginia (Miller 1961). The species also has been found twice in Texas (both on *Magnolia virginiana* L. from the David Lewis property near Bleakwood in Newton Co. and the Turkey Creek Unit of the Big Thicket National Preserve), but *H. epiphaeum* is treated by Ju & Rogers (1996) as a synonym of *H. monticulosum* Mont., a fungus commonly reported from the tropics and subtropics on different kinds of wood. Granted, the two species share some similarities (e.g., papillate ostioles, ascospore size, perispore dehiscent in 10% KOH). One Big Thicket specimen lacked KOH-extractable pigments and so resembled *H. monticulosum*, while another (seemingly younger) specimen displayed dark-livid to dark-vinaceous pigments. We differentiate *H. epiphaeum* from *H. monticulosum* by the possession of glomerate stromata with an underlying orange-red subiculum (Fig. 6) and purple pigments in the young stages and its association with *Magnolia* species in the southeastern United States. Unfortunately, the holotype of "*H. epiphaeum*" in Kew has stromata characteristic of *H. monticulosum,* leaving the fungus associated with *Magnolia* without a proper name so that a new name should be proposed for a common species.

Another example is *Hypoxylon subchlorinum* Ellis & Calk. (Fig. 4), described originally from Florida and also found in Georgia and Texas. Ju & Rogers (1996, p. 124) cite the name *H. subchlorinum* under *H. fuscum* (Pers.) Fr., although they admit, "additional study might further subdivide this species." They accept a rather wide ascospore length range (8-20 µm) for *H. fuscum,* whereas northern temperate specimens usually have ascospores 12–15 µm long

(Miller 1961). *Hypoxylon subchlorinum* has smaller ascospores and differently shaped stromata. There is also a discrepancy between the original description of *H. subchlorinum* and its type specimens. Ellis & Everhart (1888) described the stromata as yellow and the ascospores as 7–8 µm long. However, the ascospores are 8–10.5 µm long in both holotype and one isotype of *H. subchlorinum* (both parts of exsiccate North American Fungi 2115: Florida, Jacksonville, 1886, Calkins, W.W., corticated wood). A piece of the same exsiccate studied in Herbarium of Michigan University was characterized by the flattened and rounded stromata also observed in the material from the Big Thicket. The Texas material was primarily from *Carpinus virginiana* Mill., but very similar stromata were found in a specimen of *H. subchlorinum* on *Celtis* from Louisiana (Farlow Herbarium: St. Martinville, 28 Jan 1889, A.B. Langlois). This species, which seems to be a characteristic representative of Florida, Louisiana, and Texas should be segregated from the "*H. fuscum*" complex.

A third candidate in need of resurrection is *Hypoxylon mulleri* J.H. Mill., described originally from Puerto Rico (Miller 1933) and later found in Florida (Miller 1961) and Texas (Big Thicket National Preserve). Its name has been suggested as synonymous with *H. placentiforme* Berk. & M.A. Curtis, but based on material collected in Texas, the shiny black stromata with conspicuous perithecial mounds of *H. mulleri* differ from the brown vinaceous and very smooth stromata of *H. placentiforme.* The *H. placentiforme* concept of Ju & Rogers (1996), which accepts 8.5–18.5 µm long ascospores, seems rather broad; such a range is very unusual, given the nature of repetitive variability within the *Hypoxylon* (cf. Vasilyeva & Stephenson 2010: Table 2). It would appear that the range has been 'synthesized' from several different taxonomic entities, and indeed, the synonyms cited under *H. placentiforme* have been applied to taxa with narrower ascospore ranges (Miller 1961, Whalley & Taligoola 1978). Prominent examples are *H. sclerophaeum* var. *macrosporum* (ascospores 14–20 µm long) and *H. sclerophaeum* var. *microsporum* (ascospores 7.5–12 µm long), whereas the lectotype of *H. placentiforme* [K(M)125651] from Cuba has ascospores 11–15 µm long.

Taxonomy

Hypoxylon confertisilvae Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.** Fig. 6C

MycoBank MB 808385

Differs from *Hypoxylon fuscum* by its finely papillate stromatal surface and KOH-extractable pigments between cinnamon and umber.

Type—USA, Texas, Big Thicket National Preserve, Turkey Creek Unit, Kirby Nature Trail, on bark of *Acer* sp., 4 Apr 2011, L. Vasilyeva (VLA P-2601).

Etymology—refers to the "thick forest" implying the place of collection (Big Thicket National Preserve)

Fig. 6. Stromata: A–B. "***Hypoxylon epiphaeum***" (VLA P-2454); C. ***Hypoxylon confertisilvae;*** D. ***Hypoxylon ilicinum;*** E. ***Hypoxylon meridionale;*** F. ***Hypoxylon croceum*** from the Great Smoky Mountains National Park (VLA P–1617); G. ***Hypoxylon minicroceum;*** H. ***Hypoxylon rolingii.*** Scale bars: A–B = 1.5 mm; C = 1.7 mm; D = 2.4 mm; E = 4.5 mm; F = 1 mm; G = 1.7 mm; H = 2.4 mm.

Stromata hemispherical to pulvinate, discrete 2–4 mm diam., with finely conspicuous perithecial mounds; surface dark-vinaceous; tissue black immediately beneath surface and among the perithecia, with KOH-extractable pigments between cinnamon (62) and umber (9). Perithecia 100–150 µm diam., ostioles black and finely papillate. Asci in spore-bearing part 85–90 × 6–7 µm, stalks 30–40 µm, with apical ring bluing in Melzer's iodine reagent, discoid, 0.3–0.5 µm high, 2.5–3 µm broad. Ascospores light brown, unicellular, elongated-ellipsoid, almost equilateral, 12–15 × 4.5–5 µm, germ slit not observed, perispore indehiscent in 10% KOH.

Comments—This species is similar to *Hypoxylon fuscum* in stromatal shape and color but differs with respect to the stromatal surface and KOH-extractable pigments. It also is similar to *H. minicroceum* (see below) in ascospore shape and color and the KOH-extractable pigments but differs in the stromatal shape and the larger ascospores.

Hypoxylon ilicinum Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.** Fig. 6D

MycoBank MB 808386

Differs from *Hypoxylon fuscum* by its smaller ascospores and luteous KOH-extractable pigments.

Type—USA, Texas, Big Thicket National Preserve, Jack Gore Baygall Unit, Blue Hole Trail, on branches of *Ilex* sp., 11 Apr 2011, L. Vasilyeva (VLA P-2593).

Etymology—refers to the association with branches of *Ilex* sp.

Stromata hemispherical to pulvinate, discrete 2–4 mm diam. or confluent, with inconspicuous or slightly conspicuous perithecial mounds; surface livid-vinaceous to dark-vinaceous; light brownish granules immediately beneath surface and among the perithecia, with KOH-extractable pigments luteous. Perithecia spherical, 200–300 µm diam., ostioles umbilicate. Asci in the spore-bearing part 75–80 × 6–7 µm, stalks 35–40 µm, with an apical ring bluing in Melzer's iodine reagent, discoid, 0.3–0.5 µm high, 2.5–3 µm broad. Ascospores brown, unicellular, ellipsoid-inequilateral, 8–12.5 × 4.5–5.5 µm, with a straight germ slit extending the length of the spore on the concave side; perispore dehiscent in 10% KOH.

Comments—This species resembles *H. fuscum* in shape and color of the stromata but differs in having smaller ascospores and KOH-extractable pigments. It also is similar to *H. porphyreum* Granmo in general appearance (Granmo 1999: Fig. 31) and ascospore size, but pigments of *H. porphyreum* are said to be "brown with a greenish tone" in 10% KOH. Moreover, *H. porphyreum* is found only on *Quercus* in Norway and Sweden. Another similar species is *H. vinosopulvinatum* Y.M. Ju et al. from Taiwan (Ju et al. 2004), which has pulvinate stromata of the same color, similar KOH-extractable pigments, comparably sized ascospores, and a perispore dehiscent in 10% KOH. However, H. *vinosopulvinatum* has rather conspicuous perithecial mounds and a germ slit on the convex side of the ascospore. The two species—*H. ilicinum* and *H. vinosopulvinatum*—could be considered vicarious, replacing each other in the Caribbean and Indo-Malayan centers of fungal biodiversity.

Hypoxylon meridionale Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.** Fig. 6E

MycoBank MB 808387

Differs from *Hypoxylon dieckmannii* by its larger and darker, as well as strongly inequilateral, ascospores.

Type—USA, Texas, Big Thicket National Preserve, Big Sandy Creek Unit, Woodlands Trail, on wood, 3 Apr 2011, L. Vasilyeva (VLA P-2602).

Etymology—refers to the south (of the United States).

Stromata widely effused, with slightly conspicuous perithecial mounds, surface brown vinaceous; cream-whitish granules immediately beneath surface, with grayish sepia (108) pigments. Perithecia spherical, 200–300 µm

diam., ostioles umbilicate. Asci not observed. Ascospores brown, ellipsoid-inequilateral, 8–12(12.5) × 4–4.5 µm, with a slightly oblique germ slit less than the length of the spore, perispore indehiscent in 10% KOH.

Comments—The species is similar to *H. dieckmannii*, which can also possess brown vinaceous stromata with grayish sepia KOH-extractable pigments, 6.5–10(11) µm long ascospores, and a perispore indehiscent in 10% KOH. *Hypoxylon dieckmannii* has been reported from Brazil, French Guiana, Mexico, and Louisiana (New Orleans) in the United States, so its occurrence in Texas could be expected. However, the specimen from the Big Sandy Creek Unit—with a similar stromatal surface, pigments, and indehiscent perispore—has longer (although overlapping) ascospores (10–12 µm) that do not fall into the characteristic ascospore range for *H. dieckmannii.* In addition, Miller (1961: 33, Fig. 48) described *H. dieckmannii* as having 6–8 µm long ascospores and illustrated these as small and light brown; their shape (almost equilateral and ellipsoid) also differs from the ascospores of Texas specimens, which are darker and strongly inequilateral. It also should be noted that the fresh stromata produced an olivaceous pigment in NaOH, a feature that suggests *H. anthochroum* Berk. & Broome, but *H. meridionale* differs from *H. anthochroum* in having an indehiscent perispore.

Hypoxylon minicroceum Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.** Fig. 6G

MycoBank MB 808388

Differs from *Hypoxylon croceum* by its smaller stromata and KOH-extractable pigments.

Type—USA, Texas, Big Thicket National Preserve, Jack Gore Baygall Unit, Blue Hole Trail, rotten wood, 11 Apr 2011, L. Vasilyeva (VLA P-2591).

Etymology—refers to the similarity with *Hypoxylon croceum*.

Stromata glomerate to effuse-pulvinate, with conspicuous to almost naked perithecial mounds; surface fuscous; dark brown woody tissue immediately beneath surface and among the perithecia, with KOH-extractable pigments between umber (9) and cinnamon (62). Perithecia spherical, (100–)120–150 µm diam., ostioles papillate. Asci in spore-bearing part 80–95 × 4.5–5 µm, stalks 17–20 µm, with apical ring bluing in Melzer's iodine reagent, discoid, 0.5–0.7 µm high, 1.5–2 µm broad. Ascospores light brown, unicellular, narrow-ellipsoid, almost equilateral, 10–12.5 × 4–4.5 µm, with a straight germ slit the length of the spore; perispore indehiscent in 10% KOH.

Comments—The stromata of *H. minicroceum* resemble those of *H. croceum* J.H. Mill. (Fig. 6F) but are much smaller. Both species have comparable ascospore size and a perispore indehiscent in 10% KOH, but they differ in their KOH-extractable pigments. *Hypoxylon croceum* has been reported from a restricted area in the southeastern United States (Georgia, North

Carolina, Ohio, and Tennessee) and also has been reported from Venezuela (Ju & Rogers 1996). When the perithecial mounds are not very prominent, *H. minicroceum* is similar to *H. submonticulosum* Y.M. Ju & J.D. Rogers but differs in the cinnamon KOH-extractable pigments and ascospore shape. With respect to its small and inconspicuous stromata, *H. minicroceum* is similar to *H. inconspicuum* J.D. Rogers & Y.M. Ju, described originally from Costa Rica (Ju et al. 2005), which differs in a number of features (smaller ascospores, dark vinaceous KOH-extractable pigments and umbilicate ostioles).

Hypoxylon rolingii Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.** Fig. 6H

MycoBank MB 808389

Differs from *Hypoxylon crocopeplum* by its very thin stromata of a different color and the KOH-extractable pigments.

Type—USA, Texas, Big Thicket National Preserve, large palmetto area along Little Pine Island Bayou, on dead branches, 8 Apr 2011, L. Vasilyeva (VLA P-2590).

Etymology—after the volunteer Paul Roling, who provided assistance to researchers in the Big Thicket National Preserve.

Stromata effused-pulvinate, with conspicuous perithecial mounds, very thin (about 0.15–0.2 mm); surface bay (6) or dark-vinaceous (82), with dark tissue immediately beneath surface and among perithecia, with fresh KOH-extractable pigments chestnut (40) or sepia (63), but umber (9) or cinnamon (62) after the slides dry up. Perithecia spherical, 150–200 µm diam., ostioles black and very faintly papillate. Asci in the spore-bearing part 70–75 × 5–6 µm, stalks 25–30 µm long, with an apical ring bluing in Melzer's iodine reagent, discoid, 0.5–0.7 µm high, 1.5–2 µm broad. Ascospores light brown, unicellular, ellipsoid, almost equilateral, 10–13.5 × 4–5 µm, with a straight germ slit extending the length of the spore; perispore indehiscent in 10% KOH.

Comments—The stromata are very thin but are somewhat reminiscent of those in *H. crocopeplum* in having rather conspicuous perithecia mounds. In many other respects (e.g., color of surface and KOH-extractable pigments, indehiscent perispore), *H. rolingii* differs from *H. crocopeplum*.

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