Studies in *Phlebia*. Six species with teeth

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Six species of *Phlebia* (Meruliaceae, Basidiomycotina) with toothed hymenophores are described and illustrated. The genus name *Mycoacia* is placed in synonymy under *Phlebia*. Four new combinations are proposed: *P. aurea*, *P. fuscoatra*, *P. nothofagi*, and *P. uda*. *Phlebia* gilbertsonii sp. nov. is described from Louisiana and Florida, U.S.A., and *P. albofibrillosa*, from Nepal and northern India, is redescribed.

Keywords: Basidiomycetes, Corticiaceae, Mycoacia, systematics.

*Phlebia* Fr. is a morphologically diverse genus of principally resupinate, wood decay fungi. The circumscription of the genus is still being determined, although until recently taxa with teeth were excluded. Taxa with *Phlebia*-like phenotypes but with toothed hymenophores were placed in *Mycoacia* Donk (Donk, 1931, 1957). Although this is an arbitrary distinction, it was recognized by many mycologists. Christiansen (1960) was the first to include toothed species in *Phlebia* after *Mycoacia* had been introduced in 1931, namely *P. queletii* (Bourdôt & Galzin) M. P. Christ. and *P. hydnoides* (Cooke & Masse) M. P. Christ. Subsequently, other hydnaceous species were placed in *Phlebia* (Hallenberg & Hjortstam, 1988; Nakasone, 1990; Wu, 1990).

In this paper, four taxa previously assigned to *Mycoacia* are transferred into *Phlebia*, a new species with teeth and encrusted cystidia from southeastern United States is described, and *P. albofibrillosa* is redescribed.

**Materials and methods**

Microscopic examination of basidiomata was made from free-hand sections mounted in 2% (w/v) aqueous potassium hydroxide and 1% (w/v) aqueous phloxine or in Melzer’s reagent (Hawksworth & al., 1983). Color names are from Kornerup & Wanscher (1978), and herbarium designation follow Holmgren & al. (1990). Drawings were
made with the aid of a drawing tube. Photomicrographs were taken on an Olympus BH2 microscope, with or without differential interference contrast, and a PM-10AD photosystem.

Description of taxa

*Phlebia albofibrillosa* Hjortstam & Ryvarden, Mycotaxon 20: 139. 1984. - Figs. 1, 5, 6, 11.


Basidiomata resupinate, appressed, beginning as small patches, coalescing, up to 2 x 4 cm, thin, up to 200 µm thick, brittle, spinose to odontoid with smooth or finely porose areas between teeth, up to 5 teeth per mm, soft, pale yellow (4A3) to light yellow (4A4); not reacting in KOH; often with fine cracks; context homogeneous, white, membranous; teeth up to 1.5 mm long, becoming smaller toward margins, terete or fused laterally, bristly from protruding cystidia, apices obtuse to acute, penicillate; margins gradually thinning out, up to 2 mm wide, closely appressed, concolorous or paler than hymenium, occasionally translucent, irregular in outline, sterile or appressed and silky, sometimes appressed with scattered raised tufts of mycelia, white to yellowish white (4A2), with fimbriate edges. - Hypal system monomitic. - Teeth consisting of a central core of subicular hyphae, tramal cystidia, and cystidium-like elements enclosed by thin subhymenial and hymenial layers; cystidium-like elements cylindrical to clavate, up to 150 µm long and up to 12 µm diam, with a basal clamp, often with secondary septa, walls hyaline, thin to slightly thickened, smooth or lightly encrusted with small hyaline crystals, difficult to separate, often observed at tooth apices, rarely embedded in hymenium. Subiculum between teeth up to 125 µm thick, consisting of hyphae and scattered encrusted cystidia arranged parallel to substrate to form a loose, nonagglutinated matrix, then hyphae and cystidia changing to a vertical orientation at subhymenial interface; hyphae 2–6 µm diam, nodose septate, moderately branched, often branching from clamps, walls hyaline, thin, distinct, smooth. - Subhymenium up to 30 µm thick, composed of short-celled, somewhat agglutinated subhymenial hyphae and encrusted cystidia; hyphae 2–3 µm diam, nodose septate, frequently branched, walls hyaline, thin, distinct, smooth. Hymenium composed of basidia, encrusted tramal and hymenial cystidia, and rare cystidium-like elements. - Cystidia of two types: (a) hymenial cystidia fusiform, conical, or clavate, 30–60 x 7–11 µm, tapering to 2–3 µm diam at base, with a basal clamp, embedded or protruding up to 30 µm, walls hyaline, up to 2 µm thick, distal end heavily
Figs. 5-10. - Photomicrographs of *Phlebia* species. - 5, 6. *P. albofibrillosa* (HSK 4205): squash mount of teeth showing tramal cystidia. Bar = 65 µm. - 7, 8. *P. nothofagi* (PRM 756721): freehand section through tooth showing embedded tramal and hymenial cystidia. In Fig. 7, bar = 70 µm, and in Fig. 8, bar = 34 µm. - 9, 10. *P. uda* (FP 102252): Bar = 31 µm. - In Fig. 9, squash mount of tooth surface in water shows undifferentiated hyphal tips encrusted with brownish yellow materials. Fig. 10 shows acerose crystals in tooth trama.
encrusted with hyaline crystals, originating in hymenium, best observed in well-squashed mounts; (b) tramal cystidia fusiform with a long stalk, \(72 - 130 \times 7 - 12 \, \mu m\), tapering to \(2.5 - 3 \, \mu m\) diam at base, clamped at base, often with secondary septa, linear and embedded in tooth trama and subiculum or curved and penetrating through subhymenium and hymenium, embedded in or protruding through hymenium, walls hyaline, up to \(2.5 \, \mu m\) thick, encrusted throughout or limited to apex with hyaline crystals, readily observed and abundant throughout teeth, originating in subiculum and tooth trama. - Basidia clavate, \(16 - 24 \times 4 - 5 \, \mu m\), tapering to \(2 - 2.5 \, \mu m\) diam at base, with a basal clamp, 4-sterigmata, walls hyaline, thin, smooth. - Basidiospores subglobose, \(4 - 5 \times 3 - 3.5 \, (-4) \mu m\), walls hyaline, slightly thickened, smooth, negative in Melzer’s reagent.

Habitat. - On wood and bark of angiosperms.

Distribution. - Nepal and northern India

Holotype specimen examined. - NEPAL: Gandaki Prov., Kuldi, Annapurna trek, 2400 m, 7. Nov. 1979, L. Ryvarden 18979 (O).


The encrusted cystidia, subglobose basidiospores, and restricted distribution distinguish P. albofibrillosa from similar species. Phlebia setulosa (Berk. & M. A. Curtis) Nakasone, P. nothofagi, and P. gilbertsonii also develop large encrusted cystidia; these taxa, however, have cylindrical or ellipsoid spores. Phlebia albofibrillosa is the same species that Rattan (1977) described as Metulodontia queletii (Bourdot & Galzin) Parmasto from northwestern Himalayas. Eight of the thirteen collections cited by Rattan (1977, p. 316) examined were conspecific with P. albofibrillosa. The generic placement of P. albofibrillosa is debatable. Based upon morphological data of the
Figs. 11–12. - Microscopic elements of *Phlebia* species. - 11. *P. albofibrillosa* (HSK 4198): (a) tramal cystidia, (b) subicular hyphae, (c) cystidium-like elements in teeth, (d) hymenial cystidia, (e) basidia, (f) basidiospores, (g) basidiospores, and (h) basidia (LR 18905, paratype). - 12. *P. aurea* (TAA 18601): (a) subicular hyphae, (b) basidia, (c) basidiospores, (d) basidiospores (FP 133219).
basidiomata, *P. albofibrillosa* appears to be best placed in *Phlebia* although it lacks a ceraceous texture and a well-developed thickening subhymenium. Hallenberg & Hjortstam (1988), however, transferred *P. albofibrillosa* to *Steccherinum* despite the fact that it lacks a dimitic hyphal system, which is one of the principal characters of the genus *Steccherinum*.

**Phlebia aurea** (Fr.) Nakasone, comb. nov. - Figs. 2, 3, 12.

- *Hydnum aureum* Fr., Elench. fung. 1, p. 137. 1828.
- *Acia aurea* (Fr.) P. Karst., Medd. Soc. Fauna Fl. Fenn. 5: 42. 1879 (nom. illegit.).

Basidiomata annual, closely adnate, widely effused, up to 13×4 cm, thin, up to 350 mm thick, denticulate to spinose, ceraceous throughout; not reacting with KOH; cracks absent or extensive and revealing white context; context bilayered, upper layer thin, up to 30 µm thick, concolorous with hymenium, ceraceous, lower layer next to substrate thicker, up to 300 µm thick, white or translucent, felty; hymenial surface spinose, 3–6 teeth per mm, with smooth areas between teeth, teeth terete, slender, typically single but occasionally fused at base or along entire length, gradually tapering toward apex, up to 2(–6)×0.4 mm, ceraceous, brittle, snapping off easily, apices acute and entire or blunt, white and tufted, often branched several times, color of teeth and fertile areas between teeth brown [6(DE)6–7, 7D7–8], brownish orange [66(6–7)], light orange (5A5), greyish orange (5B6), with younger areas greyish orange [5B4–5] or orange white (5A2), rarely light yellow (4A4) or yellowish white.
(4A2), gradually becoming paler toward apex, sometimes with a whitish cast; margins gradually thinning out, distinct, pulverulent and short odontoid, or 1–3(–8) mm wide, woolly to felty, with short ridges or teeth and short, stiff, appressed or slightly raised, radiating cordon at the edges, white, pale yellow (4A3), light yellow (4A4), light orange (5A4), or pale orange (5A3). - Hyphal system monomitic. - Teeth consisting of a central core of agglutinated, thin to slightly thick-walled, smooth subicular hyphae extending into apex, rarely encrusted with clusters of coarse, hyaline crystals, and enclosed by subhymenium and hymenium. - Subiculum 100–260 µm thick with a duplex structure, lower layer (40–200 µm thick) next to substrate a textura porrecta, composed of agglutinated hyphae arranged parallel to substrate, upper layer (30–100 µm thick) a textura intricata with hyphae vertically arranged in a loose, open texture with some hyphal segments heavily encrusted with particulate to small hyaline crystals; hyphae 2.2–5.5 µm diam, nodose septate, sparingly branched, walls hyaline, thin to slightly thick, occasionally up to 1 µm thick, smooth but occasionally hyphal segments coated with a thick, even layer of small, hyaline crystals. - Subhymenium thickening, up to 40 µm thick, composed of vertically arranged, compact, dense, indistinct, agglutinated hyphae; hyphae 2.2–3 µm diam, nodose septate, frequently branched, conglutinate, short-celled, walls hyaline, thin, smooth. - Hymenium a dense palisade of basidia and, rarely, cystidia. - Cystidia fusoid to cylindrical, 16–21 × 3–5 µm, tapering to 2–3 µm diam at base, with a basal clamp, walls hyaline, thin, smooth or distal end encrusted with a thin layer of crystalline materials, absent or rare. - Basidia clavate, 10.5–18 (–21) × 3.5–4(–5) µm, tapering to 2–3 µm diam at base, with a basal clamp, 4-sterigmate, walls hyaline, thin, smooth. - Basidiospores short allantoid to cylindrical, 3.5–4.5(–5.5) × 1.5–2(–2.2) µm, walls hyaline, slightly thickened, smooth, negative in Melzer’s reagent.

Habitat. - On wood and bark of angiosperms.

Distribution. - United States, Canada, Costa Rica, Great Britain (Reid, 1958, as M. microcystidiatus), Norway, Sweden, Finland, Denmark, Switzerland (Breitenbach & Kranzlin, 1986), Germany, Austria, France, Spain, Czech Republic, Slovak Republic, Ukraine, Estonia, Lithuania, Russia, Armenia, Georgia, Turkey, Iran, Uzbekistan, Kenya and Tanzania (Hjortstam & Larsson, 1994), Nepal (Hjortstam & Ryvarden, 1984), India, Japan.

Type specimens examined. - [FRANCE(?), near Switzerland]: Chêne, entre l’écorce et le bois, Avril, 1822, leg. Chaillet, Herb. Persoon (HOLOTYPE of Hydnum membranaceum * stenodon: L 910.262–526). Herb. E. Fries, leg. Chaillet,

Phlebia aurea is characterized by slender teeth and abundant, small, allantoid or cylindrical basidiospores with slightly thickened walls. This species, however, displays macroscopic and microscopic morphological variability. For example, typically no cystidia are present although in a few specimens encrusted cystidia in the hymenium and tooth trama were observed. Basidiospore shape and width are also variable. The spores are distinctly curved in most specimens, but not all.

Fortunately, many type specimens were available for study. Hydnum aureum, however, lacks a type; a neotype is designated herein based on an authentic specimen collected and identified by Fries and discussed by Eriksson & Ryvarden (1976). The holotype of M. microcystidiatus was examined, and I agree with Parmasto (1967) and Eriksson & al. (1984, p. 1385) that it is conspecific with P. aurea. Similarly, I concur with Nikolajeva (1964) and Maas Geesteranus (1974) that M. mycophilus is conspecific with P. aurea. The holotype of Hericium fimbriatum has long teeth (6–8 mm) with rare fusiform cystidia protruding through the hymenium. Despite these unusual features, H. fimbriatum has basidiospores (4.3–5.5 × 1.5–2 µm) and other microscopic characters typical for P. aurea. Thus, H. fimbriatum is placed in synonymy under P. aurea. Gilbertson (1964), however, noted that H. fimbriatum displayed similarities with P. setulosa and Sarcodontia setosa (Pers.) Donk. Although Hydnum fascicularia Berk. & Curtis has been placed in synonymy under H. stenodon by Gilbertson (1965), Nakasone & Burdsall (1995) recognized H. fascicularia as a distinct species of Phlebia.

Basidioma descriptions, illustrations, and photographs are also available from Breitenbach & Kranzlin (1986), Eriksson & Ryvarden (1976), Maekawa (1993), and Rattan (1977). For cultural descriptions, see Boidin (1958) and Stalpers (1978). Boidin (1958) and Brown (1935) reported that P. aurea is homothallic.
Phlebia fuscoatra (Fr.: Fr.) Nakasone, comb. nov. - Figs. 4, 13.

Hydnum fuscoatra Fr.: Fr., Syst. mycol. 1, p. 416. 1821.
Hydnum castaneum Alb. & Schw. batrofuscum (Fr.) Pers., Mycol. eur. 2, p. 188. 1825.
Acia fuscoatra (Fr.: Fr.) P. Karst., Meddel. Soc. Fauna Fl. Fenn. 5: 42. 1879 (nom. illegit.).
Acia fuscoatra (Fr.: Fr.) Pat., Essai tax. Hyménomyc., p. 69. 1900 (nom. illegit.).
Steccherinum fuscoa trium (Fr.: Fr.) Gilb., Evol. higher basidiomycetes p. 294. 1971.
Hydnum weinmannii Fr., Elench. fung. 1, p. 198. 1838 (sec. Bresadola, 1897).

Basidiomata annual, resupinate, beginning as small circular patches, coalescing, becoming widely effused, up to 20 × 5 cm, thin, 70–325 μm thick, spinose to odontoid, teeth gradually becoming shorter and smaller toward margins, sometimes heavily coated with fine, soft, white crystalline materials; hymenium between teeth smooth to porose, ceraceous to crustaceous; often younger, light-colored basidiomata turning red or dark brown in KOH; cracks infrequent to numerous; context bilayered with a thin (up to 40 μm thick), ceraceous upper layer concolorous with hymenium and a thicker (up to 300 μm thick), buff-colored lower layer; hymenial surface spinose, 2–4 teeth per mm, occasionally with extensive smooth areas, teeth terete to compressed, single or fused at base, occasionally fused throughout length, gradually tapering toward apex, up to 2 × 0.4 mm, submembranous to ceraceous, with entire or fibrillose to penicillate apices, color variable, hymenium between teeth and bases of teeth greyish orange (5C6), brownish orange [5B6, 6C(6–8)], light brown [6D(5–6)] reddish brown (8D7), brown (7D8), light brown (6D6), or nearly black (6F6), becoming lighter toward apices, sometimes with a white pulveraceous covering over hymenium; margins typically distinct, closely appressed, adherent, abrupt or occasionally gradually thinning out, up to 1 mm wide, smooth to grandinioïd, orange white (5A2), light orange (5A5), pale orange (5A3), greyish orange (5B5), or white, edges closely attached, slightly raised, fimbriate to felty, white to pale yellow. - Hyphal system monomitic. - Teeth consisting of a core of parallel, vertically arranged, hyaline to yellowish brown subicular hyphae and brownish
yellow resinous materials enclosed by subhymenial and hymenial layers; subicular hyphae often glassy in appearance, developing numerous H-connections, frequently heavily encrusted with hyaline crystals and protruding through apex, occasionally developing aggregates of coarse, hyaline crystals, crystals up to 15×15 µm. - **Subiculum** in smooth areas between teeth 60–250 µm thick, a loose *textura intricata*, arranged parallel to substrate, agglutinated or not, coated with brownish yellow, resinous-like substances; subicular hyphae 2–4 µm diam, nodose septate, occasionally branched, with frequent H-connections, walls hyaline, thin to slightly thickened, smooth or coated with resinous materials. - **Subhymenum** slightly thickening, 20–40 µm thick, hyphae oriented perpendicular to substrate or long axis of teeth, forming a dense, compact layer; hyphae 1.5–3.5 µm diam, nodose septate, frequently branched, short-celled, walls hyaline, thin, smooth or covered with brownish yellow, resinous-like materials. - **Hymenum** a dense palisade of basidia and cystidia, often covered with brownish yellow, resinous-like materials, not agglutinated, usually not too difficult to separate individual elements. - **Cystidia** subulate, 22–36(-54)×3–4.5 µm, tapering to 2.5–3 µm diam at base, with a basal clamp, hyaline, walls hyaline, thin, smooth, arising from subhymenium and hymenium, protruding up to 25 µm beyond hymenium, scarce to numerous. - **Basidia** clavate, (14-)18-23-35)×4-5.5 µm, tapering to 2–3 µm diam at base, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. - **Basidiospores** short cylindrical, adaxial side straight, (4.5-)5-6 × 2-2.2(-2.5) µm, hyaline, walls hyaline, thin, smooth, negative in Melzer’s reagent.

**Habitat.** - On wood and bark of angiosperm logs and branches; rarely on gymnosperms; associated with a white rot decay.

**Distribution.** - Canada, United States, Sweden, Finland, Germany, France, Portugal (Melo, 1994), Spain (Tellería, 1990), Czech Republic, Slovak Republic, Estonia, Lithuania, Russia, India (Rattan, 1977), Korea, Japan.


Figs. 13–14. - Microscopic elements of *Phlebia* species. - 13. *P. fuscoatra* (HHB 5666): (a) hypha from tooth trama, (b) basidiospores, (c) basidia, (d) cystidia. - 14. *P. gilbertsonii* (HHB 9649, holotype): (a) tramal cystidia, (b) subicular hypha, (c) hymenial cystidia, (d) basidiospores, (e) basidia; (from RLG 13319): (f) hymenial cystidia, and (g) basidiospores.


Phlebia fuscoatra is characterized by slender, subulate cystidia, cylindrical spores, encrusted hyphae in the tooth trama, and reddish brown basidiomata. Old or overmature specimens are ceraceous with abundant resinous materials that obscure the microscopic characters. In addition, the hymenia in old, dark-colored specimens often are degenerated, which complicates identification. The basidiospores of *P. fuscoatra* are narrower than those of the morphologically similar *P. uda* and *P. nothofagi*.

An attempt was made to examine all type specimens, but no specimens named *H. weinmannii* were found in Fries’ herbarium at UPS. Because *Hydnum fuscoatrum* lacks a type specimen, a neotype is designated. I agree with Miller (1934), Brown (1935), and Gilbertson (1962) that *H. carbonarium* is conspecific with *P. fuscoatra*. Also, I concur with Nikolajeva (1964) that *M. corneus* is conspecific with *P. fuscoatra*. However, the type specimen of *R. fuscescens* is clearly conspecific with *P. fuscoatra* and not to Sarcodontia (*Phlebia*) uda as reported by Nikolajeva (1964).

*Hydnum membranaceum* Bull. was not included in the synonymy above although it is often associated with *H. fuscoatrum*. *Hydnum membranaceum* was described and illustrated in 1791 by Bulliard. I have not seen the original publication but consulted the description (p. 302) and figure (plate 481, Fig. I) in a 1809 (Bulliard, 1809) reissue. Fries (1821) accepted *H. membranaceum* as a distinct species. Bresadola (1897, 1903) and Bourdot & Galzin (1928) followed Fries and noted its similarities to *H. fuscoatrum*. Miller (1934) and Lundell & Nannfeldt (Fungi exs. suecici no. 1410) went a step further and synonymized *H. membranaceum* under *H. fuscoatrum*. This is a logical conclusion since two of the three collections of *H. membranaceum* examined from Fries’s herbarium at UPS, from Sweden are conspecific with *P. fuscoatra*, and the specimen from Norway is a mixed collection of *P. rufa* (Pers.: Fr.) M.P. Christ. that includes one piece of *P. fuscoatra*. However, it is not clear what taxon Bulliard illustrated. Although some aspects of the description, especially the passages relating to basidioma color, appear to refer to *P. fuscoatra*, the illustrations depict a Steccherinum, Radulomyces or
Basidioradulum species. Bresadola (1897) suggested that H. membranaceum might be identical to Radulum molare Chaillet: Fr. (now Radulomyces molaris (Chaillet: Fr.) M. P. Christ.). Because of the uncertainty of what taxon the illustration represents (assuming that the 1809 illustration is similar to that in the original 1791 publication, which is the holotype), H. membranaceum is considered a nomen dubium.

Other basidioma descriptions, illustrations, and photographs are available in Breitenbach & Kränzlin (1986), Brown (1935), Eriksson & Ryvarden (1976), Maekawa (1993) and Melo (1994). The report of P. fuscoatra from India by Rattan (1977) requires confirmation because one of the two cited specimens, HSK 4269, is P. aurea. Cultures are described by Nakasone (1990) and Stalpers (1978).

Phlebia gilbertsonii Nakasone, sp. nov. - Figs. 14, 15.

Phlebiae nothofagi et P. setulosae affinis sed aculeis gracilibus, teretibus, cystidiis ventricosis-rostratis vel navicularibus, incrustatis, sed praesertim basidiosporis anguste cylindricis, hyalinis, laevibus, 4.5–6(–6.5) × 1.8–2 mm praedita.


Etymology. - Named for Robert L. Gilbertson in recognition of his numerous contributions to the systematics of wood decay basidiomycetes.

Basidiomata annual (?), resupinate, effused, coalescing up to 9 × 3 cm, thin, up to 200 μm thick, subceraceous to ceraceous, closely adnate, hydnaceous, with distinct, smooth hymenium between teeth, greyish orange (5B3–4); not reacting to KOH; sometimes developing numerous small cracks that expose a homogenous or bilayered context; context with a thin, subceraceous upper layer which is concolorus with the hymenium and teeth, and a lower layer of thin, white, fibrillose to felty mycelium; teeth slender, terete, tapering gradually to apex, up to 2 mm long × 0.5 mm diam, single, sometimes fused, brittle, brownish orange (6C6) to light brown (6D5–6), becoming paler at tooth apices, apices acuminate, entire; margins indistinct, gradually thinning out, floccose to pruinose, closely adherent, smooth to papilllose, light orange to greyish orange [5(A–B)4].

Hyalosystem monomitic. - Teeth composed of a central core of trama hyphae and trama cystidia enclosed by subhymenium and hymenium; hyphae 2.2–4.5 μm diam, nodose septate, long-celled, rarely branched, with a few H-connections, rarely conglutinate, walls hyaline, thin to 1.5 μm thick, smooth. - Subiculum between teeth up to 80 μm thick, composed of agglutinated hyphae arranged
in a loose textura intricata with large open cavities next to substrate but becoming denser next to subhymenium; subicular hyphae 2–4.5 µm diam, nodose septate, moderately branched, agglutinated, walls hyaline, thin, smooth. - Subhymenium slightly thickening, up to 50 µm thick, composed of compact, agglutinated hyphae and embedded hymenial cystidia arranged perpendicular to substrate and tooth axis; hyphae 3–4 µm diam, nodose septate, short-celled, frequently branched, conglutinate, walls hyaline, thin to slightly thickened, smooth. - Hymenium a dense, compact, occasionally conglutinate, palisade of basidia, and hymenial and tramal cystidia.

- Cystidia of two types: (a) tramal cystidia cylindrical to clavate, up to 140 × 10 µm diam including encrustations, with a basal clamp, often with secondary septa, apex obtuse, walls hyaline, slightly thickened, smooth except upper part encrusted with hyaline crystals, originating in tooth trama, embedded or curving into subhymenium and protruding up to 30 µm through hymenium, best observed in very thin or well-squashed sections; (b) hymenial cystidia fusiform to ventricose-rostrate, 30–70 × 6–15 µm diam, tapering to 4 µm diam at base, hyaline, with a basal clamp, apex obtuse or beaked, walls hyaline, thin to thick, up to 1.5 µm thick, apex lightly to heavily encrusted with coarse, hyaline crystals, arising from subhymenium and hymenium between and on teeth. - Basidia clavate, 12–20 × 4–5 µm, tapering to 2 µm at base, with a basal clamp, 4-sterigmate, walls hyaline, thin, smooth. - Basidiospores narrowly cylindrical to allantoid, sides straight, 4.5–6(–6.5) × 1.8–2 µm, walls hyaline, distinct, thin to slightly thickened, smooth, negative in Melzer’s reagent.

Habitat. - On decorticate wood of angiosperms.

Distribution. - Florida and Louisiana.


*Phlebia gilbertsonii*, an uncommon species, is characterized by slender teeth, narrowly cylindrical basidiospores and encrusted, fusiform to ventricose-rostrate hymenial cystidia. Only the subhymenium and the subicum between the teeth are consistently agglutinated. The tooth trama is not agglutinated although the subhymenium developed in the teeth is somewhat agglutinated. This taxon is most similar to *Phlebia nothofagi* and *P. setulosa*, which also have encrusted tramal and hymenial cystidia. However, *P. nothofagi* and *P. setulosa* have larger basidia (20–40 × 4–6 µm) and wider basi-
diospores (2.2–2.9 µm and 3–3.5 µm diam, respectively) than *P. gilbertsonii*. Furthermore, *P. nothofagi* and *P. setulosa* are robust taxa with well-developed subicula whereas *P. gilbertsonii* has small, slender teeth with a very thin subiculum. Moreover, *Phlebia gilbertsonii* is known only from southeastern United States. In contrast, *P. nothofagi* has a world-wide distribution, and *P. setulosa* is widely distributed in eastern North America.
**Phlebia nothofagi** (G. Cunn.) Nakasone, comb. nov. –Figs.7,17,18,21.


Basidio mata annual, resupinate, beginning as small, coalescing, circular patches that become widely effused, up to 15 × 7 cm, moderately thick, up to 1 mm thick, spinose, subceraceous with a soft, membranous context; light colored specimens turning pinkish red to dark brown in KOH; cracks infrequent, exposing a white, fibrous context; context of teeth and smooth areas between teeth distinctly bilayered, upper layer thin (up to 100 mm thick), concolorous with hymenium, ceraceous, lower layer thicker (up to 530 mm thick), white, soft, fibrous, felty; hymenial surface spinose, 1–2 teeth per mm, occasionally smooth with scattered teeth, teeth terete to flattened, single, fused at base or laterally throughout length, gradually tapering toward apex, 1–6(–10) mm long × 1 mm wide at base, soft, brittle, with an overall glaucous and velutinous appearance from protruding cystidia, apices acuminate, entire or blunt and tufted, color variable, typically darker between and at base of teeth, brown [6(E–F)(4–6)], then becoming brownish orange (6C6), light brown (6D6), greyish brown (5D3), light orange (5A4), greyish orange (5B4), or yellowish brown [5D(4–5)] toward apex, at apex pale orange (5A3) to yellowish white (4A2), sometimes brownish orange (6C8) or brown [6(E–F)(4–7)] throughout; margins typically distinct, ropy, abrupt, closely appressed, adherent, 2–4 mm wide, sterile, lighter in color than hymenium, pale yellow (4A3) light yellow (4A4), pale orange (5A3), light orange (5A4) to greyish orange (5B4, 6B5), odontoid to warded or with ridges, edges deeply lacinate and incised or sometimes indistinct, thinning out. - Hyp ha l s y s t e m monomitic. - Teeth consisting of a central core of vertically arranged, parallel, subicular hyphae that may be smooth or encrusted, and smooth or encrusted cystidia enclosed by subhymenium and hymenium, sometimes with elongate clusters of acerose or flattened, hyaline crystals and resinous materials, often with cystidia protruding at apex and through hymenium. - Sub i c u l u m of smooth areas between teeth up to 900 µm thick, sometimes stratose, with a very thin, yellow-orange basal layer, up to 50 µm thick, of agglutinated hyphae arranged parallel to substrate and a thicker layer of non-agglutinated hyphae, first arranged more or less parallel to substrate in a loose, open textura intricata that develops into a dense vertical palisade.
near subhymenial interface; hyphae 2.5–5.5 mm diam, rarely orange, nodose septate, sparingly to moderately branched, often branching from clamps and forming H-connections, walls hyaline, thin to slightly thickened, smooth. - Subhymenium thickening, 25–80 µm thick between teeth and near tooth apices, up to 300 µm thick at base of teeth, hyphae oriented perpendicular to substrate or to long axis of teeth, dense, compact, agglutinated, often indistinct and collapsed; hyphae 2–3.5 µm diam, nodose septate, frequently branched, conglutinate, short-celled, walls hyaline, thin, smooth. - Hymenium a dense palisade of basidia and cystidia, not agglutinated but difficult to separate individual elements, occasionally interspersed with clumps of reddish brown, resinous materials. - Cystidia of two types: (a) tramal cystidia fusiform, rarely cylindrical, with a long stalk, up to 180 µm long, 3.5–8(–14) µm wide including crystals, tapering to 3.5–4 µm diam at base, clamped at base, often with secondary septa, apex acute to rounded, walls hyaline to yellowish brown, thin throughout but sometimes slightly thickened at distal end, smooth or lightly to moderately encrusted at apex with hyaline, loosely adherent, coarse, crystalline materials, originating in subiculum or tooth trama, often curving into subhymenium and hymenium, becoming embedded or protruding up to 55 µm beyond hymenium, also extending into tooth apex, numerous in tooth trama; (b) hymenial cystidia fusiform, 35–90 × 5–7 µm, tapering to 1.5–2.5 µm diam at base, with a basal clamp, walls hyaline, slightly thickened, up to 1 mm thick, but often thinning at base, basal part smooth, distal part lightly to moderately encrusted with closely adherent, hyaline crystalline materials, embedded or protruding up to 45 µm, arising from subhymenium, numerous in subhymenium and hymenium. - Basidia clavate, 20–32(–36) × 4–6 µm, tapering to 2–2.5 µm diam at base, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. - Basidiospores ellipsoid, adaxial side straight or slightly concave, (4.5–)5–5.5(–6) × 2.2–2.5(–2.9) µm, walls hyaline, thin, distinct, smooth, negative in Melzer’s reagent.

Habitat. - On bark and wood of angiosperms.

Distribution. - Canada, United States, Great Britain, France, Spain, Portugal (Melo, 1985), Germany, Czech Republic, Slovak Republic, Switzerland, Romania (Hallenberg & Toma, 1989), Russia, Georgia, Azerbaijan, Thailand (Hjortstam & Ryvarden, 1982; Phanichapol, 1986), New Zealand, Australia.

Figs. 21–22. - Microscopic elements of *Phlebia* species. - 21. *P. nothofagi* (HBB 4273): (a) tramal cystidia, (13) subicular hyphae, (c) hymenial cystidia, (d) basidia, (e) basidiospores. - 22. *P. uda* (KHL 4711): (a) basidia, (b) cystidia, (c) basidiospores.

This is a variable species in form and color but shows little variation in microscopic characters. *Phlebia nothofagi* is distinguished by soft, brittle teeth and abundant, thick-walled, encrusted cystidia. Only the subhymenium and basal layer of the subiculum are agglutinated. A distinctive sharp but sweet odor is present in cultures as well as in fresh and recently dried specimens. Some specimens examined from New Zealand and Europe are particularly robust with long (up to 10 mm) and well-developed teeth whereas most of the specimens from North America have shorter teeth (2 mm long). Basidiospores are also variable in length. Reid (1963) recognized the variety *australiensis* on the basis of shorter and wider spores (3.8–4.3 × 2.2–2.5 µm); however, I observed basidiospores in the holotype and paratype specimens to be slightly larger (4.3–5.1× 2.2–2.9 µm) and well within the limits of the species.

Surprisingly, *P. nothofagi*, a distinctive and widely distributed species, was not described before 1959 probably because of its morphological similarity to *P. fuscoatra*. Some mycologists, however, did recognize *P. nothofagi* as a distinct species but used a variety of names. The earliest confirmed name for *P. nothofagi* appears to be by Pilát & Lindtner who described *M. fuscoater f. carnicolor* in 1938. A review of the literature disclosed the name *Hydnum castaneum* Alb. & Schwein., which may be the earliest name for *P. nothofagi*. Although this species is usually interpreted to be a variety of *H. fuscoatra* (Fries, 1821; Cejp, 1930), many aspects of the original description of *H. castaneum* by Albertini & Schweinitz (1805) appear to refer to a taxon similar to *P. nothofagi*. Unfortunately, this theory cannot be tested because there are no specimens of *H. castaneum* at PH, UPS or L; *H. castaneum* is considered a *nomen dubium*. In addition, a number of collections of *P. nothofagi* at PRM are filed as *Mycoacia odoratissima*, a herbarium name used by A. Pilát that was never published. *Phlebia nothofagi* was reported from North America under the name *Phlebia queletii* (Bourdot & Galzin) M. P. Christ. (Nakasone, 1990).

For other descriptions and illustrations of *P. nothofagi*, see Reid (1963), Hjortstam & al. (1981), Boidin & David (1981), Grosse-Brauckmann (1987), and Martini (1988). Boidin & David (1981) and Nakasone (1990, as *Phlebia queletii*) described cultures of *P. nothofagi* and reported that it has an unifactorial incompatibility system. In addition, dikaryotic and monokaryotic cultures of *P. nothofagi* from France (LY 5781 and LY 6552–Mirande, Gers, on dead wood, 6. Oct. 1970, A. David) were obtained from Dr. P. Lanquetin. Monokaryons of LY 5781 and LY 6552 were completely incompatible with monokaryons from North America (HHB 15422, British Columbia; HHB 4273, Tennessee).
**Phlebia uda** (Fr.) Nakasone, comb. nov. - Figs. 9, 10, 19, 20, 22.

- *Hydnum udum* Fr., Syst. mycol. 1, p. 422. 1821.
- *Acia uda* (Fr.) P. Karst., Medd. Soc. Fauna Fl. Fenn. 5: 42. 1879 (nom. illegit.).
- *Acia uda* (Fr.) Bourdot & Galzin, Bull. Trimest. Soc. Mycol. Fr. 30: 255. 1914 (nom. illegit.).
- *Acia uda* (Fr.) Bourdot & Galzin var. grisea (Pers.) Bourdot & Galzin, Hyménonomy. de France p. 414. 1928 (nom. illegit.).

Basidiomata annual, resupinate, small circular patches coalescing into widely effused structures, up to 22 × 5 cm, thin to moderately thin, 100–400 µm thick between teeth, hydnumaceous to verrucose, occasionally with smooth areas, generally subceraceous to ceraceous with a membranous context; turning dark purple, red to dark brown in KOH; cracks rare to frequent; context typically bilayered with a thin, ceraceous upper layer, up to 50 µm thick, concolorous with hymenium, ceraceous, and a thicker lower layer, up to 400 µm thick, soft, white to pale cream, fibrous; hymenial surface denticulate to spinose, 2–6 teeth per mm, up to 3 mm long × 0.5 mm diam, teeth conical to cylindrical, gradually or abruptly tapering toward apex, becoming smaller and more slender near margins, single or joined at the base, ceraceous, brittle when dried, with entire, acuminate or blunt, penicillate apices, color variable, dried hymenial surface between and at bases of teeth, pale yellow (4A3), light yellow [4A(4–5)], greyish yellow [3B4, 4(B–C)6], light orange (5A4), greyish orange [5B(4–5)], brownish orange (5C6), yellowish brown [5D(4–5)], or brown (6D8, 7D7), occasionally dark brown (6F8), becoming paler toward tooth apices, mature areas often darker than margins; margins of two types, on bark 1–3 mm wide, thin, closely appressed, adherent, silky, white, pale yellow, pale orange (5A3), light orange (5A4), occasionally translucent and yellowish brown [5D(4–5)], sterile, edges fimbriate, white; on wood often abrupt, sometimes thinning out then flocculose, rarely silky-cordonic, appressed, concolorous with or paler than hymenium, fertile, often with teeth or warts. –Hyphal system monomitic. –Teeth consisting of a central core of vertically arranged, parallel subicular hyphae, typically associated with loose acerose (up to 7.5 × 1 µm) or coarse (up to 10 × 10 µm) hyaline crystals, sometimes encrustations closely appressed, and undifferentiated hyphal tips encrusted with brownish yellow, resinous materials enclosed by subhymenium and hymenium; apices entire, sterile, composed of protruding subicular hyphae cov-
ered with hyaline, acerose crystals. - **Subiculum** between teeth stratose, 45–120 µm thick, composed of a very thin, basal layer, up to 10 µm thick, of agglutinated hyphae next to substrate topped by a thicker layer, 25–70 µm thick, of non-agglutinated hyphae, first arranged in a loose, open **textura intricata** that develops into a dense vertical palisade at subhymenial interface; hyphae 1.5–5 µm diam, nodose septate, sparingly to frequently branched, walls hyaline, thin or up to 1.5 µm thick, smooth or coated with brownish yellow, resinous materials. - **Subhymenium** in smooth areas between and in teeth slightly thickening, 15–30 µm thick, hyphae oriented perpendicular to substrate and to long axis of teeth, dense and agglutinated; hyphae 1.5–2.2 µm diam, nodose septate, frequently branched, conglutinate, short-celled, walls hyaline, thin, smooth. - **Hymenium** up to 25 µm thick, a dense palisade of basidia, cystidia and resinous coated undifferentiated hyphal tips, not agglutinated but difficult to separate individual elements. - **Cystidia** abundant to scarce, fusiform, with acute to rounded apices, 12–25 × 2–4 µm, tapering to 2–3 µm diam at base, clamped at base, enclosed in hymenium, walls hyaline, thin, smooth. - **Undifferentiated hyphal tips** cylindrical, up to 25 × 8 µm, covered with brownish yellow resinous materials, in hymenium or embedded in subicum and subhymenium, dissolving in 2% KOH, easily destroyed in squash mounts. - **Basidia** clavate, (16-)20–28(3–5) × 4–5 µm, tapering to 2–2.5 µm diam at base, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. - **Basidiospores** cylindrical to ellipsoid, (4.5–)5–6 (–6.5) × 2.5–3 µm, walls hyaline, distinct, slightly thickened, smooth, negative in Melzer’s reagent.

**Habitat.** - On bark and wood of angiosperms, especially branches, rarely on gymnosperms; associated with a white rot decay.

**Distribution.** - United States, Canada, Sweden, Denmark, Netherlands, Germany, France, Portugal (Melo, 1994), Spain (Tellieria, 1990), Italy, Czech Republic, Austria, Estonia, Russia, Georgia, Armenia, Azerbaijan, Turkmenistan, Turkey (Hallenberg, 1991), Iran (Hallenberg, 1981), Ethiopia (Hjortstam & Larsson, 1994), Morocco (Malençon, 1957).

**Type specimen examined.** - No country, no date, #910.270-471 (NEOTYPE of *Sistotrema griseurn*: L).


Phlebia uda is distinguished by basidiomata that turn purple, red or brown in KOH, resinous covered hyphal-end cells in the teeth, short, fusiform cystidia, and ellipsoid basidiospores. The cystidia are distinctive but often inconspicuous and difficult to observe. The variable color of the basidiomata results in different reactions to KOH. Yellow specimens typically turn bright red in KOH, while tan or brown specimens turn dark brown. Although sometimes confused with P. fuscoatra, P. uda can be distinguished by its lighter colored basidioma, resinous covered hyphal end-cells, shorter cystidia, and wider basidiospores.

Although Bresadola (1897) considered S. griseum to be conspecific with H. fuscoatra, Bourdot & Galzin (1928) and Nikolajeva (1964) reduced S. griseum to a variety of H. uda. Because S. griseum lacks a type specimen, a neotype is designated (L #910.270–471). This specimen is from Persoon’s herbarium and is labeled in Persoon’s hand. In addition, there is a label attached to the specimen sheet by M. A. Donk that has “original” on it. This neotype material is in fair condition. Although many of the teeth had broken off at the base, a few basidiospores (4.7–5.4× 2.5–2.7 µm) and golden brown resinous masses capping undifferentiated hyphal tips in the teeth were observed. The hymenium is dark brown and did not change color as expected with KOH; nevertheless, I agree with Bourdot & Galzin and Nikolajeva that S. griseum is conspecific with H. uda and not with H. fuscoatra. A type specimen of H. udum apparently does not exist and a neotype needs to be designated.

For other descriptions, illustrations, and photographs, see Breitenbach & Kranzlin (1986), Brown (1935), Eriksson & Ryvarden (1976), and Welden (1960). The basidiospore width (2–2.5 µm) reported by Eriksson & Ryvarden (1976) is in error, since the widths of the basidiospores in the accompanying drawing are 2.5–3 µm. For culture information, see Boidin (1958), Nakasone (1990), and Stalpers (1978). Paired single-spore and polyspore cultures of P. uda from Canada, Norway, Sweden, Spain and Turkey were all inter-compatible (Hallenberg 1985; 1991).

**Discussion**

Phlebia aurea, P. fuscoatra, and P. uda are widely distributed and well-known taxa, Phlebia nothofagi is also widely distributed but has been reported under a variety of names. Phlebia aurea is a cosmopolitan species reported from 29 countries. A total of 72 specimens, representing 24 countries, were examined. Phlebia aurea
appears to be rather common in Europe but quite rare in North America as only seven specimens have been seen. Although reported from only 16 countries, *P. fuscoatra* is the most common and abundant species of the taxa discussed herein. Approximately 210 specimens of *P. fuscoatra* were examined from thirteen countries. It is widely distributed throughout Europe and North America, with a few records from Asia. *Phlebia nothofagi* is known from 17 countries including New Zealand and Australia. Forty-four specimens, representing 14 countries, have been studied. Although not common, *P. nothofagi* is widely distributed in Europe and the United States. Similarly, *Phlebia uda* is common and widely distributed in Europe and North America. It is reported from 22 countries; 17 countries were represented among the 135 specimens examined.

*Phlebia albofibrillosa* and *P. gilbertsonii*, in contrast, are quite limited in distribution. *Phlebia albofibrillosa* is known only from Nepal and northern India. Represented by 14 specimens, this species appears to be locally abundant. *Phlebia gilbertsonii* is rare, with only four known specimens from Louisiana and Florida in the southeastern United States.

*Phlebia* was originally characterized by resupinate basidiomata with conspicuously veined or wrinkled hymenia (Fries, 1821). Donk (1931; 1957) greatly expanded the genus concept to include taxa with smooth and tuberculate hymenial configurations, waxy, gelatinous or mucous texture, and thickening hymenia. However, to accommodate species microscopically similar to *Phlebia* but with toothed hymenophores, Donk (1931) introduced the genus *Mycoacia*. Subsequent researchers (Boidin, 1964; Parmasto, 1968; Eriksson & Ryvarden, 1976; Kropp & Nakasone, 1985; Wu, 1990; Wu & Chen, 1992) also recognized the close relationship between *Phlebia* and *Mycoacia*.


Besides morphological evidence, cultural, genetic and molecular data support a close relationship between *Phlebia* and *Mycoacia*. Boidin (1964) noted that *M. uda*, *M. setosa* (Pers.) Donk, and several *Phlebia* species display astatocoenocytic nuclear behavior and possess bipolar or unifactorial incompatibility systems. In addition, some species of *Phlebia* and *Mycoacia*, as well as *Merulius*, *Sarco-
*odontia* and *Cystidiophorus*, produce simple septate hyphae in the margin and extracellular phenoloxidase enzymes (Stalpers, 1978). Nakasone (1990) recognized numerous cultural similarities between *M. uda* and *M. fuscoatra* and *Phlebia* species. Moreover, preliminary sequence data from the internal transcribed spacer region of the nuclear ribosomal RNA indicate that *Mycoacia* is a paraphyletic genus that is embedded in *Phlebia* (Nakasone, 1991).

The evidence is overwhelming that *Mycoacia* should be synonymized under *Phlebia*. Thus, three of the original taxa in *Mycoacia*, namely, *M. fuscoatra*, *M. stenodon* and *M. uda*, are transferred to *Phlebia* based on morphological, cultural, and molecular data. With the transfer of *M. fuscoatra*, the generic type, *Mycoacia* is effectively placed in synonymy under *Phlebia*. The final disposition of other taxa presently in *Mycoacia* must await further studies.

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**References**


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