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THE GENUS GLOEODONTIA IN NORTH AMERICA

HAROLD H. BURDSALL, JR.

AND

FRANCES F. LOMBARD

Center for Forest Mycology Research, Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, Wisconsin 53705

The genus *Gloeodontia* was erected by Boidin (1966) to accommodate *Irpex discolor* Berk. & Curt. (=*Odontia eriozona* Bres.). He placed the genus in the family Auriscalpiaceae because basidiocarps of *G. discolor* (Berk. & Curt.) Boidin possess a dimitic hyphal system, gloeocystidia that become blue to black in sulfuric benzaldehyde, and amyloid minutely verrucose basidiospores. The family Hericiaceae was indicated to be an inappropriate family for *Gloeodontia* because the hyphal system in members of the Hericiaceae are monomitic and the gloeocystidia do not become blue or black in sulfuric benzaldehyde. Members of this family do, however, possess amyloid minutely verrucose basidiospores, and the family is considered closely related to the Auriscalpiaceae.

Gloeodontia has remained monotypic but Gilbertson (1971, p. 293) indicated doubt that a similar taxon found in the intermountain region of the western United States was actually conspecific with G. discolor. One of us (HHB) has also collected this taxon in Montana. Our studies of the basidiocarps, cultures, and mating system indicate that the taxon is an undescribed species in the genus Gloeodontia.

In this treatment, both species of the genus will be described and illustrated for basidiocarp, cultural, and genetic characters. Because of a departure from the published generic characters by the new species, the genus *Gloeodontia* is emended to include the characters of the new species.

METHODS

Microscopic characters of basidiocarps were studied from freeze-microtome sections and squashed tissue mounted in 2% KOH with 1% aqueous phloxine (Stevens 1974, p. 653), Melzer's reagent (Ainsworth et al. 1971, p. 362), and sulfuric benzaldehyde (Boidin 1958, p. 30).

The methods employed in studying the cultures, the arrangement of their descriptions, and the explanation of the "Key Pattern" are the same as used in previous studies (Davidson et al. 1942). Mat descriptions and growth rates were based on 7- and 14-day-old cultures incubated in 90 mm Petri dishes at 25°C on 1.5% malt extract agar (Davidson et al. 1942). Extra-cellular oxidase production was detected by the Bavendamm test described by Davidson et al. (1938), in which cultures are grown on malt agar containing 0.5% gallic and tannic acids, and by the gum guaiac test described by Nobles (1958), in which an alcoholic solution is applied to 3-week-old fungal mats grown on malt agar. For the constant temperature study, Petri dish cultures on malt agar were placed in incubators 24 hours after plating, and were measured at the end of 10 days incuba-

tion. Measurements of mat diameters represent averages of three replications of all of the individual isolates. Killing temperatures were determined by removing those cultures without observable growth from the high test temperatures and incubating them at 25° C for 3 weeks. Those that did not grow were presumed to have been killed at the test temperatures.

Microscopic structures were drawn with the aid of a camera lucida and a Zeiss drawing apparatus. Capitalized color names are from Ridgway (1912) and numerical color designations are from Kornerup and Wanscher (1967). Herbarium designations are those of Holmgren and Kueken (1974).

SPECIES DESCRIPTIONS

Gloeodontia columbiensis Burt ex Burdsall & Lombard, sp. nov.

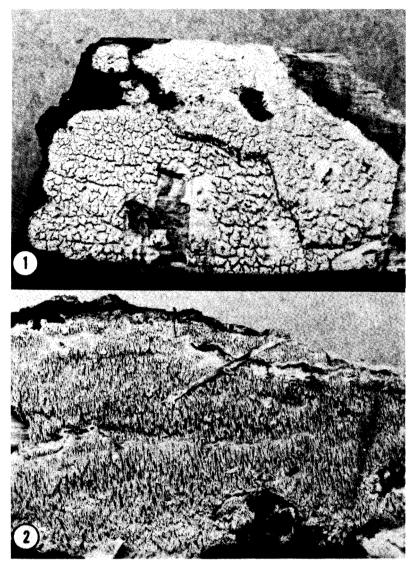
Figs. 1, 3–10, 19–21, 25–30. Specie differt a congeneribus diversa; hyphis systematis monomiticis; basidiis $20-28 \times 5-6\mu$ m; basidiosporis $5.5-6.5 \times 3.5-4$ (-4.5) μ m, ovoideis, complanatis adaxialibus.

- EтумоLOGY: From Columbia (ex British Columbia, western Canada) + ensis (L. suff. indicating origin) = columbiensis.
- HOLOTYPUS: HHB 7429, ad lignum mucidum Acer glabrum Torr., University of Montana Biological Station, Yellow Bay, Flathead Lake, Lake County, Montana, U.S.A., 11 IX 1973. In herbarium CFMR conservatum.

Basidiocarps (Fig. 1) broadly effused, crustaceous, often cracking into small angular blocks, hydnaceous, teeth up to 1 mm long, often fused into clumps at base, irregularly shaped, slightly fimbriate at apex, sometimes irregularly branched, pale yellow (3A3)¹ to near light yellow (4A4) with more orange, white at apex; margin sterile, very thin, finely pubescent, up to 1 mm broad, white.

In section up to 30 μ m thick excluding teeth; hyphal system monomitic; subiculum a *textura intricata*, hyphae (Fig. 6) $2-3\mu$ m diam, hyaline to pale yellow, occasionally encrusted with elongate hyaline crystals, thin- to thick-walled (walls up to 1 µm thick), clamp connections present at all septa, branching frequent; tooth trama a *textura intricata-porrecta*, hyphae like those of subiculum, giving rise to two kinds of pseudocystidia, one kind (Figs. 3, 5, 7) cylindrical to subulate, sometimes with an apical bead (tramal gloeocystidia), up to $60 \times 6-10 \,\mu$ m, thinwalled, hyaline, smooth, with refractive to granular content that stains blueblack in sulfuric benzaldehyde, many bending and protruding through hymenium, other kind (Figs. 4, 10) cylindrical, of undetermined length, $7-10 \,\mu m$ diam, heavily encrusted with hvaline crystals, often in fascicles in axes of teeth. bending toward hymenium or protruding through apex, some protruding through hymenium, especially near tooth apex; hymenium of basidia and gloeocystidia, sometimes interrupted by encrusted pseudocystidia; gloeocystidia (Figs. 3, 5, 7) cylindrical to subulate with apical bead, hyaline, thin-walled, smooth, with refractive or granular content, $25-50 \times 5-7 \mu m$; basidia (Fig. 9) 20-27 \times 5–6 μ m, cylindrical to urniform, hyaline, thin-walled, 4-sterigmate, sterigmata up to 4.5 μ m long; basidiospores (Fig. 8) 5.5-6.5 × 3.5-4(-4.5) μ m, ovoid, adaxially flattened, with slight wall thickening, hyaline to pale yellow, surface minutely granulose, strongly amyloid in Melzer's reagent.

¹ Kornerup and Wanscher color notations indicate plate number, vertical column, and horizontal column, respectively.

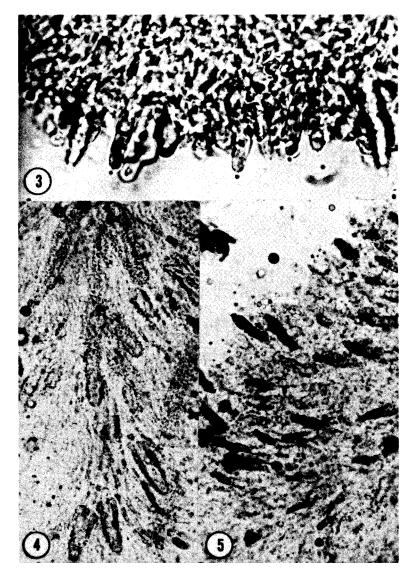


Figs. 1 & 2. Basidiocarps of *Gloeodontia* spp. 1. *G. columbiensis* \times 2. HHB 7422. 2. *G. discolor* \times 1. HHB 107.

HOLOTYPE: On dead wood of *Acer glabrum* Torr. (Rocky Mountain maple), University of Montana Biological Station, Yellow Bay, Flathead Lake, Lake County, Montana, 11 IX 1973. *H. H. Burdsall* 7429*². Conserved in herbarium CFMR.

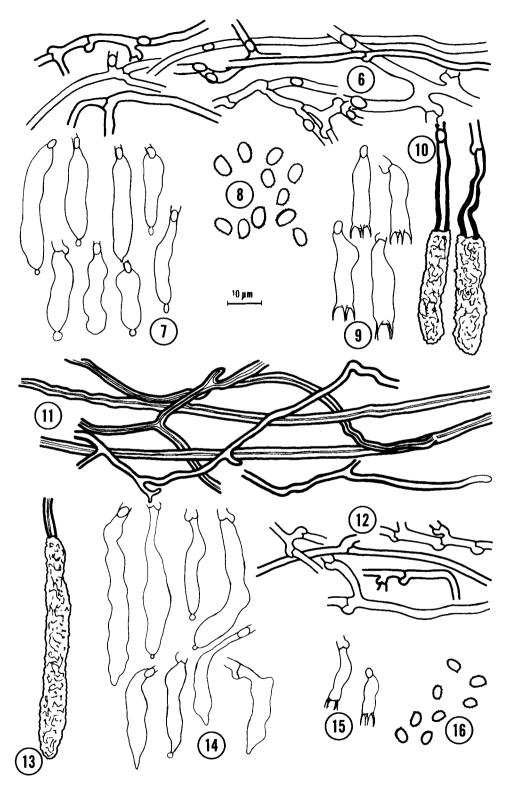
Other Specimens Examined. CANADA. Alberta: on Populus tremuloides Michx. (quaking aspen), MacKenzie Highway at Keg River, Bouchier & Baranya, DAOM 72402 (ARIZ); on Pinus sp. (pine), Mistayah River, Banff Natl. Park, R. L. Gilbertson 3475 (ARIZ); on pine, Saskatchewan River Crossing, Banff Natl. Park, R. L. Gilbertson 3538 (ARIZ). British Columbia: on Acer macrophyllum Pursh

^{2*} Specimens from which cultures were isolated and studied



Figs. 3–5. Photomicrographs of microscopic characters of *Gloeodontia columbiensis* HHB 7422.3. Gloeocystidia in 2% KOH-phloxine ×750. 4. Fascicle of encrusted pseudocystidia in sulfuric benzaldehyde ×750. 5. Gloeocystidia in sulfuric benzaldehyde ×400.

(bigleaf maple), Royal Oak, Victoria Island, W. G. Ziller, DAOM 72403 & DAOM 72404 (ARIZ); on dead Populus sp. (poplar), Sidney, J. Macoun 7, Missouri Bot. Gard. Herb. 55381 (BPI); on dead Salix sp. (willow), Sidney, J. Macoun 10, MBGH 55382; J. Macoun 11, MBGH 55380; J. Macoun 14, MBGH 55383; J. Macoun 29, MBGH 55384; J. Macoun 66, MBGH 55385; J. Macoun 86, MBGH 55387; J. Macoun 93, MBGH 55386; J. Macoun 96, MBGH 55388, (all ut Odontia columbiensis Burt ex BPI). U.S.A. Idaho: on Populus trichocarpa Torr. & Gray ex Hook. (black cottonwood), Coolin, Kaniksu Natl. Forest, Bonner County, J. R. Weir 10933 & 10942; on black cottonwood, Coolin, Kaniksu Natl. Forest, Bonner County, J. R.



Figs. 6–16. Line drawings of microscopic characters of *Gloeodontia* spp. Figs. 6–10, *G. columbiensis* Holotype HHB 7429: 6, subicular hyphae; 7, gloeocystidia; 8, basidiospores; 9, basidia; 10, encrusted pseudocystidia. Figs. 11 - 16, *G. discolor* JLL 12567: 11, skeletal hyphae; 12, generative hyphae; 13, encrusted skeletal hypha; 14, gloeocystidia; 15, basidia; 16, basidiospores.

ner County, J. R. Weir 10947, (all ut Odontia columbiensis Burt ex ARIZ). Minnesota: on quaking aspen, Lake Itasca State Park, Clearwater County, F. F. Lombard et al. FP³ 100754. Montana: on Alnus sp. (alder), University of Montana Biol. Sta., Yellow Bay, Lake County, R. L. Gilbertson 4851; on quaking aspen, Quartz Creek, Glacier Natl. Park, Flathead County, R. L. Gilbertson 6132 (both ut Odontia columbiensis ex ARIZ); on Rocky Mountain maple, University of Montana Biol. Sta., Yellow Bay, Lake County, H. H. Burdsall 7422* (ut Gloeodontia columbiensis ex CFMR, ARIZ, BPI). Oregon: on unidentified hardwood, Gold Beach, Curry County, J. L. Lowe 10555 (ARIZ, CFMR); on quaking aspen, Portland, Multnomah County, J. R. Weir 11 121 (ARIZ), (both ut Odontia columbiensis).

Remarks. Gloeodontia columbiensis is characterized macroscopically by its hydnaceous basidiocarps, often cracked into small blocks, the clusters of up to 12 teeth which are sometimes branched and have fimbriate apices. Microscopically, it is monomitic, with clamped hyphae, gloeocystidia in all tissues becoming blue to black in sulfuric benzaldehyde, and minutely granulose spores which are amyloid in Melzer's reagent. It differs from *G. discolor* as indicated in "Remarks" under that species.

According to Donk's (1967, p. 49) interpretation, the subicular and tramal gloeocystidia (pseudocystidia) should be considered part of a gloeoplerous (Donk 1967, p. 48–49) hyphal system, thus making basidiocarps of *G. columbiensis* dimitic despite the absence of skeletal hyphae. We feel that these pseudocystidia must be interpreted merely as specialized hyphal end cells. In most cases they apparently have been formed in the subhymenium, then imbedded by outward growth of the subhymenium. This leads us to interpret the hyphal system in basidiocarps of this species as monomitic.

Gloeodontia columbiensis is not a newly recognized taxon. Burt placed specimens of this species, collected by Macoun, in the fungus herbarium of the Missouri Botanical Gardens (now at BPI) under "*Odontia columbiensis* Burt." He had selected a specimen (Macoun 11) to be used as holotype, but never published the name or described the species as new. We have chosen, however, to use HHB 7429 as the holotype specimen since that collection demonstrates the characteristics of the species better than Macoun's No. 11. Also, the cultural and mating system studies were carried out on isolates from that specimen.

In contrast to G. *discolor*, this species is not restricted to hardwood substrates. Although it seems to prefer hardwoods, two specimens have been collected on pine in Alberta (RLG 3475 & 3538). With the exception of one record from north central Minnesota, it has been found only in the intermountain and Pacific coast regions of the western United States and Canada.

Hydnum pyramidatum Berk. & Curt. (from Cuba) is a species very similar to *G. columbiensis*. Studies of the holotype (K) and two isotypes (FH & FH-Curtis) reveal all three to be in poor condition with the hymenium degenerated or obliterated by mercury poison. This condition of the specimens has probably led to the differences in descriptions presented by Boidin (1966, p. 20), who says the hyphae are of one type, and Gilbertson (1965, p. 862), who describes thin-

³ Designation for CFMR herbarium accession numbers.

walled clamped hyphae and thick-walled, apparently aseptate hyphae. Our studies indicate the hyphal system to be monomitic. Both Gilbertson (1965) and Boidin (1966) report the absence of gloeocystidia, but we found rare gloeocystidium-like structures. The basidiospores of this species are minutely echinulate, amyloid, and $5-6 \times 4-5 \mu m$, more subglobose and broader than in *G. columbiensis*. The ornamentation of these spores also seems larger than those in *G. columbiensis*. These characters in conjunction with the longer spines (up to 3 mm long) and the subtropical distribution indicate to us that *H. pyramidatum* is a different species. It may well belong in the genus *Gloeodontia*, but the data on microscopic structures are too incomplete to make this decision.

Cultural Description

Key Pattern. A-P-M-1-10-16, (B-P-M-1-10-16 at 6 wks).

Growth Characteristics. Growth medium, forming a mat 24–31 mm in diam in 7 days and 64–73 mm in diam in 14 days (Fig. 19); mat white, the fragile, scant and appressed, azonate aerial growth thin short downy throughout the mat and radiating outward from the inoculum in very fine lines, with or without a cleared area around the inoculum in which the mycelium is more sparse and the substratum shows through; margin distinct, finely fimbriate, even; no reverse discoloration, bleaching malt agar in about 4 weeks; odorless; oxidase reactions positive, moderately strong with the Bavendamm test, no growth on gallic acid (Fig. 20) and 0 to a trace of growth with a moderately strong to very weak reaction on tannic acid (Fig. 21) agars in 7 days, and moderately strong with the gum guaiac test, in 3 min developing a color near Patent Blue. Mat on malt agar at 6 weeks appressed, thin downy with scattered, thickened and slightly raised woolly Cream Color patches.

Hyphal Characteristics. Hyphae staining in phloxine, with abundant simple clamp connections, (1.5-)2-3(-4)m in diam (Fig. 25); gloeoplerous hyphae with oily-appearing and coarsely granular contents that react with sulphuric benzal-dehyde, with clamps, with or without lateral papillae, $2.5-6\mu$ m in diam (Fig. 27); hyphae with homogeneous pale yellow contents, with thin hyaline walls and clamps, at first staining heavily but later not staining in phloxine, sparse at 4 weeks, abundant in the yellow patches on the mat at 6 weeks, $2.7-5\mu$ m in diam (Fig. 26); gloeocystidia not developing until after 4 weeks, then infrequent, with oily-appearing and coarsely granular contents that react with sulphuric benzaldehyde, with or without papillae, $17.5-30.8 \times 3-4.5\mu$ m (Figs. 28, 29); crystals heavily scattered over the mounts, mostly clumped aggregates of odd-shaped or needle-like pieces, rarely much-eroded small octahedrons (Fig. 30).

Temperature Relations. Optimum 24°C; killing 36°C in 10 days (Fig. 36).

Mating System. Heterothallic, bipolar, with the following distribution of mating types among a sample of 20 single basidiospore isolates from the dicaryotic isolate HHB 7429-Sp:

 $A_1:1,2,3,4,5,6,7,10,16.$

A₂: 8, 9, 11, 12, 14, 15, 17, 18, 19, 20, 21.

Cultures Studied. HHB 7422-Sp and HHB 7429-Sp (from the type specimen), both polysporous isolates.

Remarks. Cultures of *G. columbiensis* are characterized by the thin white mat that develops light yellow patches by 6 weeks, relatively low optimum and killing temperatures, bleaching of media in old cultures, positive oxidase reactions, bipolar mating system, and, microscopically, by the presence of clamp connections,

gloeoplerous hyphae, and gloeocystidia. The Species Code of Nobles (1965) based on 6-week-old dish cultures is 2.3.7.15.32.36.40.45.54.(55).59.

In addition to possessing morphological and cultural characters so similar to those of G. discolor, G. *columbiensis* also has in common the trait of bipolar heterothallism which is known in no other genera of the Auriscalpiaceae or Hericiaceae. This group of characters signifies a close relationship of the two species. Interspecific crosses between two haploid isolates (representing the two mating types) of *G. columbiensis* and 16 G. discolor haploids (representing the two mating types) were negative in every instance, thus furnishing substantial evidence that the two taxa are distinct despite their extremely close relationship.

Gloeodontia discolor (Berkeley & Curtis) Boidin, Cahiers Maboké 4: 22. 1966. Figs. 2, 11–18, 22–24, 31–35.

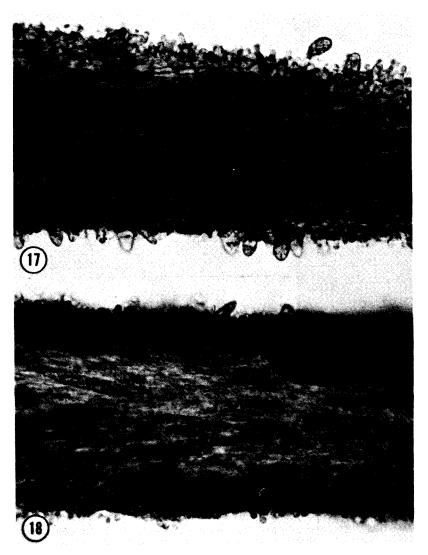
= Irpex discolor Berk. & Curt., Grevillea 1. 145 1873.

= Odontia eriozona Bres., Mycologia 17:71. 1925.

TYPE: *Ravenel 1073*, underside of "carious" logs, Santee, South Carolina, U.S.A. Holotype in K?; isotypes in Curtis herbarium 2939 and Burt herbarium (both in FH).

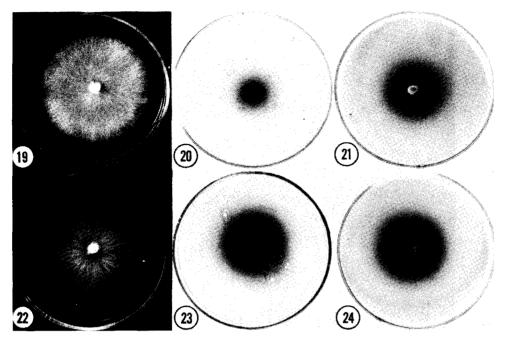
Basidiocarps (Fig. 2) broadly effused, extending to many mm long and wide, membranous to crustaceous, adnate, yellowish white (4A2) to greyish orange (5B3), hydnaceous, teeth 1-3 mm long, slender, pointed at apex; margin sterile, paler than fertile area, almost white.

In section 20-50 μ m thick excluding teeth; hyphal system dimitic; abhymenial surface not differentiated; subiculum a *textura intricata*; skeletal hyphae (Fig. 11) $2-4\mu$ m diam, thick-walled (walls up to 2μ m thick), pale yellow to rather strongly yellow, some encrusted with elongate hyaline crystals (Fig. 18), branching rare, septa rare, lacking clamps; generative hyphae (Fig. 12) $2-4\mu$ m diam, thinwalled, hyaline or yellow tinted, much branched, with clamp connections at all septa; gloeocystidia (Figs. 14,17) embedded and scattered throughout subiculum, $35-70 \times 6-10 \mu m$, cylindrical to subulate, often with apical bead, thin-walled, hyaline, variable in length and breadth, turning dark blue to black on application of sulfuric benzaldehyde; tooth trama a *textura porrecta*, skeletal hyphae like those of subiculum, generative hyphae like those of subiculum, at tooth apex becoming thin-walled and hyaline at protruding ends; gloeocystidia (Figs. 14, 17) like those in subiculum, numerous, often bending and protruding through hymenium, cylindrical to subulate, often with a small apical bead, thin-walled, hyaline, with clamp at basal septum, dark blue-black in sulfuric benzaldehyde (not reacting in some old specimens); other tramal cystidia (Figs. 13, 18) heavily encrusted with hyaline crystals up to $9 \,\mu m$ diam, sometimes subtended by a clamp connection, thick-walled, some turning and protruding up to 15 μ m through hymenium, sometimes forming fascicles in the axes of teeth and at tooth apex; hymenium of gloeocystidia and basidia; gloeocystidia (Figs. 14, 17) $25-65 \times 5-9$ μ m, cylindrical to subulate with apical bead, often swollen and/or curved at base, hyaline, thin-walled, subtended by clamp connection, protruding up to 25 μ m beyond hymenium, turning dark blue-black in sulfuric benzaldehyde except in some older specimens; basidia (Fig. 15) $12-20 \times 3.5-4\mu m$, cylindrical to urniform, hyaline, thin-walled, strongly tapered at base, with basal clamp connections, 4-sterigmate, sterigmata up to $4 \mu m$ long; basidiospores (Fig. 16) 3.5-4.5 $(-5.5) \times 2.5 - 3(-3.5)$ m, ovoid, adaxially flattened, with slight wall thickening, pale yellow, minutely granulose with inconspicuous apiculus, strongly amyloid in Melzer's reagent.



Figs. 17 & 18. Photomicrographs of microscopic characters of *Gloeodontia discolor* HHB 107. 17. Gloeocystidia in 2% KOH-phloxine ×500. 18. Encrusted skeletal hyphae in the tooth trama in 2% KOH-phloxine ×500.

Specimens Examined. USA. Alabama: on hardwood, Montgomery County, R. P. Burke 873, Weir 19579, LECTOTYPE of Odontia eriozona Bres. (BPI). Arizona: on Salix gooddingii Ball (Goodding willow), Nature Conservancy Reserve, Sonoita Creek, Santa Cruz County, R. L. Gilbertson 9964 (ARIZ). Florida: on Liquidambar styraciflua L. (sweetgum), Hogtown Creek Basin, Gainesville, Alachua County, H. H. Burdsall 6475* (CFMR); on Bursera simaruba (L.) Sarg. (gumbo-limbo), Gumbo-Limbo Trail, Everglades Natl. Park, Dade County, H. H. Burdsall 7004* (CFMR). Georgia: on Quercus sp. (oak), Bainbridge, Decatur County, R. W. Davidson et al, FP 90183* (CFMR); on oak, Bainbridge, Decatur County, R. W. Davidson et al. FP 105687* (CFMR); on hardwood, Bainbridge, Decatur County, R. W. Davidson et al. FP 105689* (CFMR). Mississippi: on sweet-



Figs. 19–24. Two-week-old cultures on malt agar and one-week-old cultures on gallic and tannic acid agars. 19 & 22, malt; 20 & 23, gallic acid; 21 & 24, tannic acid; 19–21, *Gloeodontia columbiensis*, HHB 7429-Sp; 22–24*G. discolor*, HHB 7004-Sp.

gum, Bluffs Exp. Forest, Vicksburg, Warren County, R. W. Davidson & E. R. Toole, FP 105031* (CFMR). South Carolina: Santee Canal, ISOTYPE of Irpex discolor Berk. & Curt., Ravenel 1073, Curtis 2939 (in Burt herb., Curtis herb., both in FH); on oak, Santee Exp. Forest, Francis Marion Natl. Forest, Berkeley County, J. L. Lowe 12567* (CFMR). Texas: on sweetgum, Big Thicket Scenic Area, San Jacinto County, H. H. Burdsall 107 & 131 (CFMR).

Remarks. This species is similar, macroscopically, to *G. columbiensis* in color, in type of hymenophore, and in substrate preference. Both *G. discolor* and *G. columbiensis* are found most commonly on hardwood substrates but occasionally *G. columbiensis* has been collected on pine. Although both are hydnaceous, the spines in *G. discolor* are 1-3 mm long, usually separated, and not branched. The spines in *G. columbiensis*, conversely, are usually up to 0.5 mm long, often somewhat branched, have fimbriate apices, and often occur in clusters of up to 12 spines on a subiculum that is cracked into small angular blocks.

Microscopically, *G. discolor* specimens differ from those of *G. columbiensis* in possessing a dimitic hyphal system with pale yellow to yellow skeletal hyphae. *Gloeodontia columbiensis* is monomitic. The other major character for distinguishing the two species is basidiospore size:

G. discolor has small basidiospores, $3.5-4.5 (-5.5) \times 2.5-3 (-3.5) \mu$ m; *G. columbiensis*, large basidiospores, $5.5-6.5 \times 3.5-4 (-4.5) \mu$ m.

The isotype specimens (Curtis herb. and Burt herb., both in FH) are extremely similar to the other *G. discolor* specimens examined. An exception is the lack of a blue to black color forming on aplication of sulfuric benzaldehyde to the gloeocystidia. Earlier, Gilbertson (1965, p. 853) had indicated that the gloeocystidia in the isotype specimens reacted very weakly. Perhap in the addi-

tional 10 years the reacting material was altered further until the reaction was not distinguishable. Boidin (1966, p. 20) noted that 40 years after collection the reaction of gloeocystidia with sulfuric benzaldehyde does not occur. We have found, however, the the reaction is not noticeably affected by age in all collections. For example, our findings agree with Gilbertson's (1965, p. 853) that the sulfuric benzaldehyde reaction is still strong in the gloeocystidia of the lectotype specimen of *Odontia eriozona* collected in 192 1. The sulfuric benzaldehyde reaction itself is inconsistent and difficult to explain (Larsen & Burdsall, 1976); the cause of these inconsistencies is still unknown.

Gloeodontia discolor occurs throughout the southern United States, although it is not found commonly. The most northerly collections known to us are the type collection (Ravenel 1073) and another collection (J. L. Lowe 12567), both from east-central South Carolina. It appears from the localities of our collections that it is almost entirely restricted in distribution to the Coastal Plain regions of the United States. We have seen one collection from southern Arizona (RLG 9964).

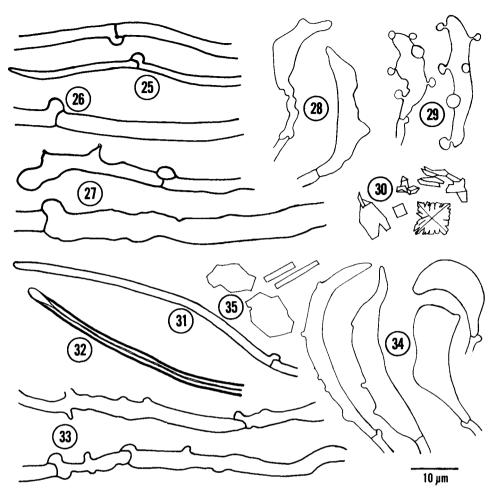
In our opinion, *G. discolor* also occurs in central Africa as indicated by Boidin (1966). He did not definitely identify the specimen he described, but referred to it as *Irpex* or *Gloeodontia* "cf" *discolor*. Boidin's description (1966) is so similar to that of G. *discolor* that the specimen to which he referred appears to us to be conspecific with *G. discolor*. The loose subiculum that he mentions is sometimes found in *G. discolor* and the spore size that he cites falls well within the range we have found for G. *discolor*. In addition, we found the mating system of this species to be heterothallic and bipolar just as he found for his collection.

Cultural Description

Key Patterns. A-P-M-1-10-16, B-P-M-1-10-16, (A-P-M-1-11-16 at 6 wks).

Growth Characteristics. Growth medium, forming a mat 24-37 mm in diam in 7 days and 64-90 mm in diam in 14 days (Fig. 22); mycelium white, but mat so thin that the discoloration in the medium (when present) shows through, giving the mat the appearance of having a Light Ochraceous-Salmon to Warm Buff central zone, the appressed and adherent, scant aerial growth fine downy throughout the mat, with very fine skeins radiating outward from the inoculum (these more distinct in some isolates than others) and becoming more finely branched and losing their distinctness near the margin, sometimes ending in sectors that give a scalloped effect to the margin, azonate or in some platings with faint, narrow zonations over most of the mat; margin finely fimbriate, distinct, even or rarely scalloped; reverse discoloration in some isolates at 14 days, developing in others later or failing to develop (individual isolates are inconsistent in this character, varying from one plating to another), usually under the inoculum and extending a short distance into the central zone area or rarely under the periphery of the mat, varying from Warm Buff to Yellow Ocher; odorless; oxidase reactions positive, strong with the Bavendamm test, no growth on gallic acid (Fig. 23) and 0-11 mm in diam on tannic acid (Fig. 24) agars in 7 days (in occasional platings the isolates failed to react on tannic acid agar, showing only a very slight stain), and strong with the gum guaiac test, quickly becoming Marine Blue.

Hyphal Characteristics. Hyphae staining in phloxine, with abundant simple clamp connections, $(1-)2-3(-5)\mu$ m in diam (Fig. 31), some lightly encrusted with crystalline material; non-staining fiber hyphae with thick hyaline refractive walls and narrow lumina, branching rarely, aseptate, $1-2 \mu$ m in diam (Fig. 32),



Figs. 25–35. Line drawings of microscopic structures from cultures. Figs. 25–30, *Gloeodontia columbiensis*, HHB 7429-Sp: 25, staining hyphae from marginal growth; 26, thin-walled hypha with yellow contents; 27, gloeoplerous hyphae; 28, gloeocystidia from 3-wk-old culture; 29, gloeocystidia from 6-mo-old culture; 30, crystals. Figs. 31–35, G. discolor, HHB 6475-Sp: 31, staining hypha from marginal growth; 32, fiber hypha; 33, gloeoplerous hyphae; 34, gloeocystidia; 35, crystals.

not present at 14 days but develop by about 21 days; gloeoplerous hyphae with oily-appearing and coarsely granular contents that react with sulfuric benzaldehyde, thin-walled, with clamps, with or without lateral papillae, $1-2.5 \,\mu$ m in diam (Fig. 33); gloeocystidia abundant, usually asymmetrical, frequently curved, with or without papillae, with oily-appearing and coarsely granular contents that react with sulfuric benzaldehyde, $12-22 \times 4.5-13 \,\mu$ m (Fig. 34); crystals thin, eroded irregular plates and needles (Fig. 35).

Temperature Relations. Optimum 30°C; killing 44°C in 10 days (Fig. 36).

Mating System. Heterothallic, bipolar, with the following distribution of mating types among a sample of 20 single basidiospore isolates from the dicaryotic isolate L 12567-Sp:

 $\begin{array}{l} A_i: \ 1,2,5,6,8,10,12,14,16,17,18,20.\\ A_2: \ 3,4,7,9,11,13,15,19. \end{array}$

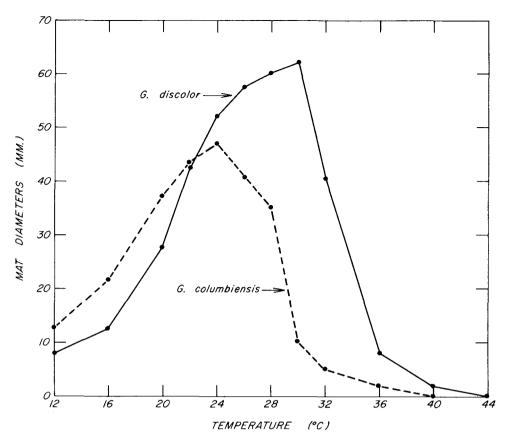


Fig. 36. Average mat diameters of *Gloeodontia columbiensis* (2 isolates) and G. discolor (8 isolates) on malt agar after 10 days incubation at 12 constant temperatures.

Cultures Studied. HHB 6475-Sp, HHB 7004-Sp, L 12567-Sp, FP 90183-Sp, FP 105031-Sp, FP 105687-Sp, and FP 105689-Sp, all polysporous isolates.

Remarks. Cultures of *G. discolor* are characterized by the white appressed mat, relatively high optimum and killing temperatures, reverse discoloration (Warm Buff to Yellow Ocher) on malt agar, positive oxidase reactions, bipolar mating system, and, microscopically, by the presence of thick-walled skeletal (fiber) hyphae (in old cultures), gloeoplerous hyphae, and gloeocystidia. The Species Code of Nobles (1965) based on 6-week-old cultures is 2.3.8.15.32.36.38. -39.45.54.59.

Three cultural characters distinguish the two species of *Gloeodontia*. The optimum and the killing temperatures for *G. discolor* are 30°C and 44°C, respectively, and for *G. columbiensis*, 24°C and 36°C, respectively. Malt agar is frequently discolored Warm Buff to Yellow Ocher by isolates of *G. discolor*, whereas isolates of *G. columbiensis* bleach malt agar after about 4 weeks incubation. Isolates of *G. columbiensis* lack the skeletal (fiber) hyphae found in *G. discolor* cultures.

Boidin (1966) described the cultural characters of dicaryotic and monosporous isolates of a fungus he referred to as "*Gloeodontia* cf. *discolor*." His cultural description is similar to ours, and the fungus possessed bipolar heterothallism as does ours.

AN EMENDED CONCEPT OF THE GENUS GLOEODONTIA

Specimens of G. *columbiensis* do not agree completely with the generic description of *Gloeodontia* (Boidin 1966) because they possess a monomitic rather than a dimitic hyphal system. Neither the imbedded gloeocystidia nor the encrusted pseudocystidia should, in our opinion, be interpreted as differentiated hyphal systems. They are merely specialized hyphal end cells subtended by clamp connections, just as are the hymenial elements. Studies of specimens of G. *discolor* indicate that, although the skeletal hyphae in that species may be encrusted, at least some of the encrusted pseudocystidia (some embedded) have basal clamp connections, indicating that they also are only specialized hyphal end cells. They are analogous to those in G. *columbiensis*.

Except for the difference in hyphal system, the characters of G. *columbiensis* agree with the generic characters of *Gloeodontia*, and the species apparently is very closely related to *G. discolor*. The similarity of the two species in culture and the fact that both possess a bipolar heterothallic mating system reinforces our opinion that they are congeneric.

Considering the extreme similarity of these two species, other than the hyphal system, it appears that the character of the monomitic vs. the dimitic hyphal system is not important as a generic character for *Gloeodontia*. Therefore, we are emending the description of *Gloeodontia* to include the characters of G. *columbiensis*.

Gloeodontia Boidin, Cahiers Maboké 4: 22. 1966. emend.

Basidiocarps effused, adherent, hydnaceous, subiculum well developed; teeth cylindrical to conic, often fimbriate at apex. Hyphal system monomitic or dimitic; generative hyphae much branched, clamped, thin-walled or with slight wall thickening; skeletal hyphae rarely branched, aseptate or septa rare, lacking clamps, thick-walled; pseudocystidia arising in tooth trama, cylindrical, heavily encrusted with hyaline crystals; gloeocystidia scattered in tooth trama, frequent in hymenium, blue to blue-black in sulfuric benzaldehyde; holobasidia present; basidiospores white in mass, hyaline to pale yellow under the microscope, wall noticeably thickened, surface granulose, amyloid.

DISCUSSION

Further studies of *Gloeodontia* species and the related genus *Gloiodon* Karst. may lead to the consolidation of the two genera. *Gloiodon*, the older name, would then include species having basidiocarps with monomitic or dimitic hyphal systems. The bipolar mating system in *Gloeodontia columbiensis* and G. *discolor* as opposed to the tetrapolarity found in *Gloiodon strigosus* (Schw. ex Fr.) Karst. (Fries 1941) and the different growth habit of the members of the two genera cause us to maintain them as separate genera at this time.

The genus *Dentipellis* Donk also seems closely related to *Gloeodontia*. The type species, *D. fragilis* (Pers. per Fr.) Donk, is based on basidiocarps having a monomitic hyphal system, but the gloeocystidia do not react with sulfuric benzaldehyde turning the contents blue to black. Consequently, this genus is placed in the Hericiaceae. This genus seems no further removed from *Gloeodontia* on one end of the spectrum than *Gloiodon* does on the other. We know of no mating system evidence to indicate closer or more distant relationship. However, *Dentipellis* is segregated on characters (reaction of gloeocystidia in sulfuric benzaldehyde and type of hyphal system) that are just as uncertain as those on which *Gloeodontia* and *Gloiodon* are based.

The questionable characters used to separate these genera are the same ones used to delimit the families Auriscalpiaceae and Hericiaceae. Maas Geesteranus (1963) cast doubt on using a dimitic hyphal system as a worthy character when he included *Gloiodon* in the Auriscalpiaceae. He (1963, pp. 433–434) said of the skeletal hyphae in *G. strigosus*, "it is clear that the definition originally given by Corner is not applicable to the present genus", and refers to the "generative trend of the skeletal-like hyphae." Despite the lack of true skeletal hyphae in basidiocarps of *Gloiodon*, Maas Geesteranus (1963) believed the relationship to be sufficiently close to other members of the Auriscalpiaceae to place it in that family.

The type of hyphal system does not seem to be a consistent character within the Auriscalpiaceae. The only consistent character for its separation from the Hericiaceae would seem to be the reaction of gloeocystidia with sulfuric benzaldehyde turning the contents blue to black. However, Larsen and Burdsall (1976) show this reaction to be inconsistent and apparently in need of only small chemical change to affect the reaction. In our opinion the Auriscalpiaceae and Hericiaceae at this particular time are separated on very tenuous grounds. Studies on members of these two families should be undertaken to find more consistent characters for this separation or additional reasons for their consolidation.

SUMMARY

Studies of a species very closely related to *Gloeodontia discolor* indicated that the previous concept of *Gloeodontia*, containing only species with basidiocarps composed of dimitic hyphal systems, was too narrow. *Gloeodontia columbiensis*, a new species having basidiocarps with a monomitic hyphal system, agrees in all other respects with the characters of the genus *Gloeodontia*. The generic description of the genus is, therefore, emended to include species with basidiocarps possessing either a monomitic or a dimitic hyphal system.

Gloeodontia discolor and G. columbiensis are described and illustrated, and a possibility of a need to include Hydnum pyramidatum in the genus is indicated.

The questionable taxonomic value of the dimitic vs. the monomitic hyphal system and the reaction of gloeocystidium content with sulfuric benzaldehyde for the separation of genera in the Auriscalpiaceae is discussed, as is the value of these characters for separating the Auriscalpiaceae and the Hericiaceae.

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