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# A SYNOPSIS OF THE NORTH AMERICAN SPECIES OF *BYSSONECTRIA* (PEZIZALES) WITH COMMENTS ON THE ONTOGENY OF TWO SPECIES

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## ABSTRACT

*Byssonectria,* previously placed in the Hypocreales, is treated as a member of the Pezizales; *Pseudocollema* and *Inermisia* are considered synonyms. Four species are recognized from North America: *B. terrestris,* a new combination which provides the oldest traceable name for the common North American and European species; *B. cartilagineum,* also a new combination, is based on the type species of *Pseudocollema; B. fusispora*; and *B. seaveri,* a new species for a large-spored North American collection. The ascomata of *Byssonectria cartilagineum* and *B. terrestris* are initially cleistohymenial. They open during the mesohymenial phase. The ascogonium is a multicellular filament, one cell of which produces ascogenous hyphae. This filament becomes surrounded by vegetative hyphae which build up the body of the ascoma. Young cleistohymenial ascomata could be mistaken for perithecia; such a mistake seems to account for original placement of the type species of *Byssonectria* in the Hypocreales.

Key Words: *Byssonectria, Inermisia,* ontogeny, Pezizales, *Pseudocollema,* taxonomy

The genus *Byssonectria* P. A. Karsten was originally assigned to the Hypocreales and, subsequently, several pyrenomycete species were treated in it. Investigations by Rogerson and Korf (Korf, **1971**) showed that the type material of the type species, *B. obducens* P. A. Karst., was in fact an immature member of the Pezizales. They determined that *Byssonectria* provided an older name for *Inermisia* Rifai (**1968**). *Inermisia,* based on *Peziza fusispora* Berk., was introduced to accommodate specimens that were previously referred to *Octospora* Hedwig : Fr. and were characterized by their occurrence on nitrogen-rich substrates and by their excipular construction. Sivertsen (**1991**) suggested that *Pseudocollema* Kanouse & Smith (**1940**) was congeneric with *Byssonectria.* The purpose of this paper is to give a synopsis of the species known from North America and to elucidate the early stages in the development of ascomata of two of the species of *Byssonectria.* The ascomatal ontogeny sheds light on the reasons for Karsten's original interpretation of his material as perithecial.

The literature on *Byssonectria* is confused by its use in two orders of ascomycetous fungi; some investigators have urged that it not be used in the Discomycetes at all (Dennis, **1978**). Modern treatments of the Hypocreales (Rogerson, **1970**) have abandoned the genus *Byssonectria* and the species previously assigned to it have been removed to other genera of the Hypocreales. There seem to be no general objections to adopting the name as Rogerson and Korf (Korf, **1972**, **1973**) have done. *Pseudocollema* and *Inermisia,* here considered to be synonyms of *Byssonectria,* were published later and do not compete with *Byssonectria* by virtue of its priority.

Species concepts are difficult in *Byssonectria.* The tangle of possible synonyms is long, and I have attempted to settle on the oldest available epithets for the taxa recognized in order to stabilize the names as far as possible. Clearly, North American material needs to be sought and critically studied beyond that which has been possible with dried specimens. Synonymy is based on Rifai (**1968**) and other authors except where noted. In the literature, circumscriptions vary but the following should be consulted: Dennis and Itzerott (**1973**), under the name *Inermisia*; Eckblad (**1968**), under *Octospora*; Khare and Tewari (**1978**), under *Octospora* subgenus *Byssonectria*; Benkert (**1987**) and Korf (**1971**), under *Byssonectria.*

## MATERIALS AND METHODS

To study ascomatal development, single ascomata or groups of ascomata were removed from the subiculum using a flattened needle. They were rehydrated in water for 5–15 min after which they were sectioned using a freezing microtome. The sections, approximately 25 μm thick, were mounted in water. Microscopic observations and photographs were made with an Olympus BH 2 microscope with both bright field and Nomarski differential interference contrast optics. After measurements were taken, the specimens were mounted in Congo Red in ammonia (0.3% in commercial ammonia cleaner) to further stain and differentiate cells. Semipermanent mounts were made by replacing the Congo Red solution with undiluted glycerine.

Two species were studied, *Byssonectria cartilagineum* and *B. terrestris.* Herbarium specimens used in this study follow: the primary materials for *B. terrestris* were *Smith 74290* (MICH), and for *B. cartilagineum* were *Smith 29018* (MICH), WSU 25316 and TRTC 48816.

## A SYNOPSIS OF THE NORTH AMERICAN SPECIES OF *BYSSONECTRIA*

*Byssonectria* P. A. Karsten, Meddeland Soc. Fauna Fl. Fenn. 6: 6. 1881.

= *Pseudocollema* Kanouse & Smith, Mycologia 32: 756. 1940.
= *Inermisia* Rifai, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 57(3): 198. 1968.

*Ascomata* apothecial, cylindrical, turbinate, or obconical, initially cleistohymenial, opening prior to ascospore maturation, up to 5 mm broad, densely clustered on the substrate, often situated on a mycelial mat which may be extensive and up to 5 mm thick. *Hymenium* convex to plane, yellow to orange, with an irregular rim at the margins. *Excipulum* of globose and angular cells, outer surface and margins of pseudoparenchymatous tissue with the outermost layer of globose thin-walled cells; excipulum within of somewhat loosely interwoven angular-elongate cells. *Asci* cylindrical, J-, with a distinct terminal operculum. *Ascospores* narrowly elliptical to fusoid, biguttulate or, more rarely, uniguttulate, smooth, lateral walls thin, polar areas of the wall thickened, sometimes giving the spores an almost apiculate appearance. *Paraphyses* slender, only slightly enlarged above, straight, curved, or slightly intertwined.

*Habitat.* On nitrogen-rich substrates, i.e., plant debris where deer and elk urinate, rodent dung, porcupine dung, on burnt areas, and in association with cyanobacteria.

*Type species. Byssonectria obducens* P. A. Karsten.

Species distinctions in this genus rely on ecological features as well as morphological characters. Ascospore size is used but overlapping size ranges occur. Ascospores take on their characteristic shape early in development but mature in size and wall thickness relatively slowly. The question of ascospore size variation must be addressed by studying fresh material and discharged ascospores; this has not been possible in this study. Rifai (**1968**) largely discounted the use of ascospore size differences to distinguish species. He examined primarily type collections and proposed a broad species concept recognizing a single species *Inermisia fusispora* (Berk.) Rifai with a wide ascospore size range. The realization that there are ascospore size discrepancies is not new; Winter (**1881**) made specific reference to such differences in *Peziza fusispora* Berk.

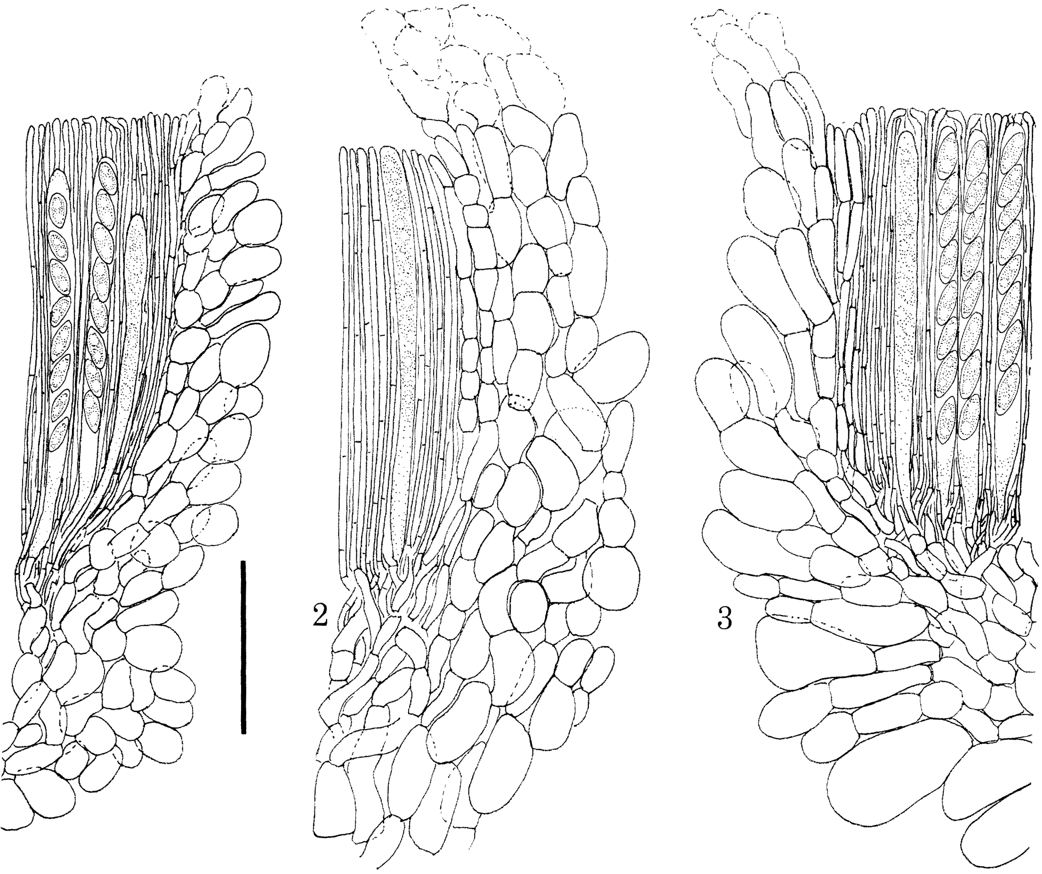
## KEY TO THE SPECIES

1. Ascomata gregarious on extensive mycelial mats. Associated with dung or urea ............... 2
1. Ascomata formed on mycelial tufts, subiculum scanty or lacking. Associated with burned areas or cyanobacteria on sandy soil ............. 3
    2. Subiculum 2–5 mm thick, covering and binding rodent dung under or associated with melting snow. Ascospores 20–24 × 8–9.6 μm .................. *B. cartilagineum*
    2. Subiculum less than 2 mm thick, arachnoid, covering and binding leaves, mosses, pine needles, and twigs and on soil in areas where animals have urinated; dung sometimes present. Ascospores 18.4–25.6 × 8–9.6(–10.4) μm ................. *B. terrestris*
3. Ascospores 29–36 × 8–10 μm, on sandy soil often associated with burned plant debris, paraphyses sometimes interwoven to form a thin epithecium .......................... *B. seaveri*
3. Ascospores 24–28.8 × 7.2–11 μm, on burned areas, paraphyses straight or curved, not interwoven ........................... *B. fusispora*

## ACCEPTED SPECIES

**Byssonectria terrestris** (Alb. & Schw.: Fr.) D. Pfister, *comb. nov.* FIGS. 1, 4, 7–13

≡ *Thelebolus terrestris* Alb. & Schw., Consp. Fung. Lusat. p. 71. 1805. Tab. II, fig. 4; Fries, Syst. Mycol. **2**: 307. 1822.
?= *Peziza mougeotii* Pers., Mycol. Eur. **1**: 289. 1822.
= *Peziza aggregata* Berk. & Br., Ann. Mag. Nat. Hist. III, **18**: 123. 1866.
≡ *Peziza fusispora* Berk. var. *aggregata* (Berk. & Br.) Cooke, Mycographia **1**: 20. 1875.
≡ *Humaria aggregata* (Berk. & Br.) Sacc., Syll. Fung. **8**: 133. 1889.



FIGS. 1–3. Cross sections of ascomata of three species of *Byssonectria*. 1. *B. terrestris*, drawn from the neotype, FH. 2. *B. cartilagineum*, drawn from Dublin 2115 in FH. 3. *B. seaveri*, drawn from Ravenel, *Fungi americani exsiccati*, no. 174 (holotype, FH). Scale = 100 μm.

≡ *Humaria fusispora* (Berk.) Sacc. var. *aggregata* (Berk. & Br.) Rehm in Rabenh. Kryptog.-Fl. I **3**: 957. 1894.
≡ *Humarina aggregata* (Berk. & Br.) Seaver, N. Amer. Cup-Fung., Operc. p. 136. 1928.
≡ *Inermisia aggregata* (Berk. & Br.) Svrček, Česká Mykol. **23**(2): 87. 1969.
≡ *Octospora aggregata* (Berk. & Br.) Eckblad, Nytt Mag. Bot. **15**: 44. 1968.
[≡ *Byssonectria aggregata* (Berk. & Br.) Rogerson & Korf in Korf, Phytologia **21**: 202. 1971, *non Byssonectria aggregata* Bres., Ann. Mycol. **9**: 275. 1911, a pyrenomycete]
= *Peziza thuemenii* P. A. Karsten in Thuem., Mycoth. Univ. no. 126. 1875.
≡ *Pyronema thuemenii* (P. A. Karst.) Sacc., Syll. Fung. **8**: 109. 1889.
≡ *Tapesia thuemenii* (P. A. Karst.) Quel., Bull. Soc. Amis Sci. Nat. Rouen, 9 suppl.: 31. 1880.
≡ *Humaria thuemenii* (P. A. Karst.) Quel., Echir. Fung. p. 288. 1886.
≡ *Octospora thuemenii* (P. A. Karst.) Khare & Tewari, Canad. J. Bot. **56**: 2118. 1978.
= *Peziza roumegueri* P. A. Karst., Grevillea **7**: 64. 1878.
≡ *Humaria roumegueri* (P. A. Karst.) Sacc., Syll. Fung. **8**: 132. 1889.
= *Peziza roumegueri* P. A. Karst. var. *carnosissima* Phill. in Phill. & Plow., Grevillea **10**: 67. 1881; Phillips, El. Brit. no. 158. 1881.
≡ *Humaria roumegueri* P. A. Karst. var. *carnosissima* (Phill. in Phill. & Plow.) Sacc., Syll. Fung. **8**: 132. 1889.
= *Byssonectria obducens* P. A. Karst., Meddeland. Soc. Fauna Fl. Fenn. **6**: 6. 1881.
= *Pyronema buchsii* P. Henn., Hedwigia **41**: 164. 1902.
≡ *Inermisia buchsii* (P. Henn.) Moravec, Česká Mykol. **23**: 223. 1969.
= *Orbilia crystallina* Rodway, Pap. & Proc. Roy. Soc. Tasmania **1919**: 114. 1920.
= *Humarina turbinata* Snyder, Univ. Wash. Publ. Biol. **8**(1): 26. 1938, *syn. nov.*

Rifai (**1968**) based his genus *Inermisia* on *Peziza fusispora* and, in his broad circumscription of *Inermisia fusispora,* he included a discussion of Seaver's (**1928**, **1942**) description of *Humarina fusispora.* Seaver's concept originated, in large part, from his study of Ravenel's *Fungi americani exsiccati* no. 174, a collection from South Carolina. Rifai rejected Seaver's circumscription of *H. fusispora* as "pure fantasy" because Rifai's study of the Kew specimen of Ravenel's exsiccatae did not show ascospores as large as Seaver had reported. I have verified that specimens of Ravenel's no. 174 at NY and FH have ascospores of the dimensions recorded by Seaver. In addition, the ecology of Ravenel's collection is quite different than that of *Byssonectria terrestris.* It occurs on sandy soil and burned areas, while the typical *B. terrestris* is on soil, leaves, and mosses where animals have urinated. Also, *Byssonectria terrestris* seems exclusively boreal or high montane, whereas other collections, including Ravenel's and those referred to *B. fusispora* in this treatment, occur most often in middle latitudes. Ravenel's collection is recognized here as a new species, and *B. fusispora* is recognized as a distinct species in agreement with Svrček (**1969**).

*Byssonectria terrestris* is found in early spring and is characterized by having ascospores in the range of 18.4–25.6 × 8–9.6 μm and by forming a thin, but prominent, white subiculum. It is this subiculum with associated turbinate to obconical ascomata that is clearly illustrated by Albertini and Schweinitz (**1805**) for their new species *Thelebolus terrestris.* Unfortunately no type material of *T. terrestris* has been located. Moreover, the name *T. terrestris* has been used in the past in the gasteromycete literature for an organism supposedly similar to *Sphaerobolus stellatus.* The perpetuation of this gasteromycetous interpretation seems to have been unimpeded by observations of the fungus itself for almost a century. Over this time the original illustration from Albertini and Schweinitz, was repeatedly reproduced [for two examples see Nees (**1817**) and Massee (**1889**)] and the epithet was combined in *Sphaerobolus* as *S. terrestris* (Alb. & Schw.) Smith. Hollós (**1904**), in revising the Hungarian gasteromycetes, identified the only Hungarian specimens labelled *T. terrestris* as *S. stellatus* Tode: Pers. To stablize the use of *B. terrestris,* a NEOTYPE is designated here: Liebenwalder Stadtwald, Schlesien, Deutschland, Kiefernhochwald auf Nadeln und Blättern neben Kaninchenkot, 14–19 April 1942, *M. Buchs* (ex Herbarium W. Kirschstein, FH).

*Byssonectria terrestris* is by far the most commonly collected species in the genus. It is circumboreal and is widely distributed. It is now known in the literature under the name *I. fusispora* (Dennis and Itzerott, **1973**; Rifai, **1968**), *I. aggregata* (Svrček, **1969**), *I. buchsii* (Moravec, **1969**), and *Byssonectria aggregata* (Korf, **1972**, **1973**), an invalid name because of the earlier homonym, *B. aggregata* Bres., which is a pyrenomycete. North American material was identified and filed as *Pyronema thuemenii* by W. G. Farlow (FH) based on his comparison of his collections with those issued in de Thümen's *Mycotheca universalis* no. 126. My study of the type material of *Humarina turbinata* Snyder clearly shows that this collection also should be placed in the synonymy of *B. terrestris.*

The operculate discomycete *Nannfeltiella aggregata* Eckblad is often found associated with *B. terrestris* both in Europe and North America. There are no reports of *N. aggregata* occurring with other species of *Byssonectria,* and diligent search of collections, most notably those of *B. cartilagineum,* has failed to demonstrate an association.

*Specimens examined from North America.*—CANADA. ALBERTA: Consolation Valley, Banff National Park, 12 July 1950, *Imshaug 6814* (MICH). NEW BRUNSWICK: Campobello Island, July, 1901, *W. G. Farlow* (FH). MANITOBA: Vivian, under spruce, 11 May 1935, *G. R. Bisby* (NY). ONTARIO: Kenora District, Hwy no. 105, 18 mi. N of Vermilion Bay, on debris at base of Jack pine chewed by porcupines, 31 May 1956, *R. F. Cain* (TRTC 46986, FH, DAOM 158523); as above (TRTC 37837, collected 30 May 1956); Cedar Lake, 28 mi N. of Vermilion Bay, on decaying leaves, 5 June 1956, *R. F. Cain* (TRTC 38668); Red Lake Road, at Wabigoon R., Kenora District, on debris at base of Jack pine chewed by porcupine, 1 June 1956, *R. F. Cain* (TRTC 37851); Lake Timagami, Area 4, Nipissing District, on humus under conifer, 22 May 1960, *R. F. Cain* (TRTC 37246, 37830, 37836, 37848, 37849 = DAOM, 115249, 38644, 51180); Nipissing District, Algonquin Prov. Park, Lake Sasejewun, on porcupine dung and leaves, 14 May 1967, *R. F. Cain* (TRTC 48816); Thunder Bay D., Black Sturgeon Lake, Nonwatin Lake, on humus in woods, 2 Aug 1965, *R. F. Cain* (TRTC). QUEBEC: Gatineau Park, on litter on forest floor, needles of *Thuja, Pinus, Abies* etc. and seemingly on soil, *Eleanor and Harry Thomson* (DAOM 155491). USA. ALASKA: Near Montana Creek, growing on leaves and mosses, wet places in mixed woods, willow area, first noticed as a whitish, webby mycelial mat more than 20 cm diam which developed over forest litter, about time of snow melt, 1 June 1964, *Phyllis E. Kempton no. 2* (NY). MAINE: Rangely, Aug. 1904, *L. W. Riddle* (FH). MICHIGAN: Rifle River area, Lupton, Ogemaw Co., on debris, 9 May 1959, *A. H.*

*Smith 60814* (MICH); as above, 11 May 1962, *A. H. Smith 64860* (MICH); as above, 6 May 1967, *A. H. Smith 74289, 74290* (MICH); near dung, Reese's Bog, 11 May 1956, *N. J. and A. H. Smith 51306* (MICH); Antrim Co., *A. H. and H. V. Smith,* June 1979 (MICH). NEW HAMPSHIRE: N. Conway (Moat Mt.), ground under pines, 12 May 1918, *L. O. Overholts 5063* (NY). NEW YORK: Northwest of Cannon Corners, elev. ca 920 ft, on dung of porcupine, shaded cliffs of Potsdam Sandstone, 29 May 1971, *Stanley J. Smith 46238 and Harold H. Howard* (NY); Lake Placid, 1 Sept. 1914, C. H. Kauffman and E. B. Mains (MICH). TENNESSEE: Cades Cove, Great Smoky Mountains National Park, on soil under pine, 26 Feb. 1955, *T. H. Campbell* in *Korf, Discomycetes Exsiccati no. 53* (MICH). WASHINGTON: HOLOTYPE of *Humaria turbinata,* Ft. Lewis, on decaying moss and fir needles, 16 Feb. 1935, *Snyder* (WTU); on mosses and needles, near spruce, Oyhut, 1 Dec. 1957, *Ruby Egbert* (Stuntz 10664) (WTU). WISCONSIN: Madison, Jan. 1907, sent to Farlow by R. A. Harper (FH). WYOMING: Rim Summit Boundary, Teton Nat. Forest, Sublette Co., on decaying wood under snowbank, 5 June 1979, *Kent H. McKnight* (BPI 16239a).

*Extralimital specimens examined.*—FINLAND. NYLANDIA (U), SIPOO: Immersby, SE of Helgtrask, Forsskogbergen, alt 50 m, patches on open rock outcrops (six places observed), on mosses, lichens and dwarf shrubs, 15 May 1976, *Teuvo Ahti 31504 and George A. M. Scott* (TRTC); Mustiala, [on leaf litter and mosses], Sept. 1874, Karsten, ex herb. de Thümen (as *Pyronema thuemenii* Karst.) (FH); Tammela, Hieme, 1874, no. 126 in de Thümen, *Mycotheca universalis* (FH); Mustiala Synjele, 21 Sept. 1876, P. A. Karsten, (type specimen of *Byssonectria obducens* P. A Karst., slides and specimens at NY and FH in herb. von Höhnel and herb. Theissen). GERMANY. Liebenwalder Stadtwald, Schlesien, Kiefernhochwald auf Nadeln und Blättern neben Kaninchenkot, 14–19 April 1942, *M. Buchs* (ex herb. Kirschstein, FH). NORWAY. Trondheim, Hovringberget, 29 Apr. 1977, *Andres Gjervan* (TRTC, DAOM 174504). SWEDEN. UPPLAND: Ingvar Nordin, 21 Apr. 1963 (BPI), as above, 12 May 1963 (BPI). SWITZERLAND. Kt. Graubünden, Litzirüti, Pleassurbrücke, auf Rehlager, 11 June 1970, *Rahm* (TRTC).

**Byssonectria cartilagineum** (Kanouse et Smith) D. Pfister, *comb. nov.* FIGS. 2, 14–21

≡ *Pseudocollema cartilagineum* Kanouse & Smith, Mycologia **32**: 758. 1940.

As circumscribed here, *B. cartilagineum* is characterized by ascospores in the range of 20–24 × 8–9.6 $\mu$m and the ascomata are densely gregarious on a thick, tightly interwoven, white to tan subiculum which forms over rodent dung and associated debris which it binds into a firm mass. It is generally collected early in the season as the snow is retreating. All collections of this species examined have been made in the western mountains of the USA and Canada.

The narrow distributional range, thick subiculum and obligate association with dung leads me to disagree with Silvertsen's (**1991**) assertion that *P. cartilagineum* and *Byssonectria aggregata* (Berk. & Br.) Rogerson & Korf [= *P. terrestris*] are conspecific. *Byssonectria cartilagineum* has a limited distributional range, is a direct dung associate and has not been found in association with *Nannfeltiella aggregata.* On the other hand, *B. terrestris* is circumboreal in distribution, is only occasionally and incidentally associated with dung, and has been shown to be associated with *N. aggregata.* The simple morphology of the ascomata and somewhat variable ascospore size have surely contributed to confusion of the two species.

*Specimens examined.*—CANADA. ALBERTA: Sunwapta Pass, Banff National Park, on old stump, 20 July 1964, *R. L. Gilbertson 4725* (NY); Highwood Pass, Kananakis Highway, on ground over dung of some small rodent under *Vaccinium,* etc., 19 July 1964, *R. L. Gilbertson 4684* (NY). USA. CALIFORNIA: Panther Creek Meadows, Butte Area, Mt. Shasta, Siskiyou Co., on coney dung, upper part of a subalpine talus slope, 20 July 1970, *W. B. and V. G. Cooke 42653* (WSU). UTAH: Summit Co., *McKnight 14835, 14836* (BPI and one collection FH); Duchesne Co., *McKnight 11922, 14120, 14121* (BPI); base of Murdock Mountain, Mirror Lake Basin, Wasatch National Forest, on rodent dung, 4 July 1974, *K. H. McKnight 14121* (BPI). WASHINGTON: Reflection Lake, on dung, 15 July 1948, *A. H. Smith 29018* (MICH); Deer Lake, Olympic Natl. Park, on mouse dung, 10 July 1939, *A. H. Smith 14992* (HOLOTYPE of *Pseudocollema cartilagineum,* MICH); Upper Eagle Lake, Okanogan Co., on coney manure, 20 July 1950, *C. G. Shaw* (WSU 25316). WYOMING: Medicine Bow Mts., University of Wyoming Science Camp, Aug. 1950, *G. Cronin* as *Smith 36245* (MICH); as above, *W. G. Solheim* as *Smith 34335* (MICH), another collection, 5 July 1950, *Smith 34474* (MICH); Headquarter's Park Area, Medicine Bow Mts., Carbon Co., on rodent dung, 3 July 1950, *W. G. Solheim 2841* (FH); Elk Park, on rodent dung under conifer log, 4 June 1965, *J. B. and K. B. McKnight 7676* (NY); Sublette Co., 5 June 1979, *McKnight* (BPI 16238a); Teton, 18 June 1979, *McKnight* (BPI 16366); Coal Creek, Teton Co., 18 June 1979, *K. H. McKnight (BPI).*

*Byssonectria fusispora* (Berk.) Rogerson & Korf in Korf, Phytologia **21**: 202. 1971.

≡ *Peziza fusispora* Berk., London J. Bot. **5**: 5. 1846.

≡ *Humaria fusispora (Berk.) Sacc., Syll. Fung.* **8**: 133. 1889.

≡ *Leucoloma fusispora* (Berk.) Rehm, Hedwigia **31**: 301. 1892.

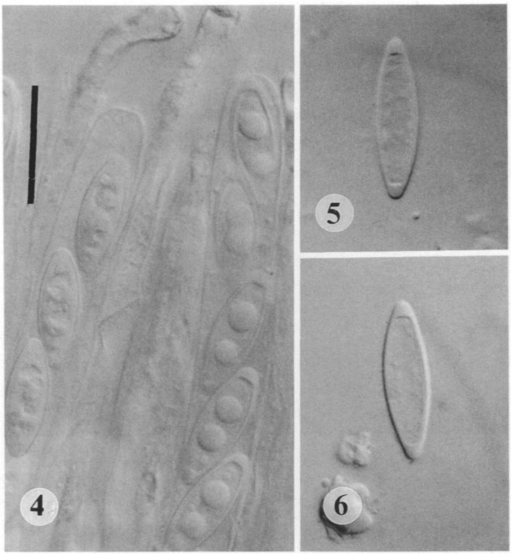
≡ *Humarina fusispora* (Berk.) Seaver, N. Amer. Cup-Fung., Operc. p.136. 1928.
≡ *Octospora fusispora* (Berk.) Brumm., Persoonia (Suppl.) **1**: 213. 1967.
≡ *Inermisia fusispora* (Berk.) Rifai, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. **57**(3): 198. 1968.
= *Peziza carbonigena* Berk. in Hook., Fl. Tasman. **2**: 274. 1860.
≡ *Humaria carbonigena* (Berk.) Sacc., Syll. Fung. **8**: 130. 1889.
≡ *Octospora carbonigena* (Berk.) Dennis, British Cup Fungi p.33. 1960.

I hesitate to use the species epithet *fusispora* in a way different than Rifai (**1968**). However, it does seem justifiable, and some review is necessary. Under *Inermisia fusispora,* Rifai delimited a taxon that is heterogeneous. I consider *B. fusispora* and *B. terrestris* to be distinct. *Byssonectria fusispora* has ascospores ranging from 23–28 μm, slightly larger than those of *B. terrestris* and the ascomata occur on mycelial tufts rather than well-developed subicula. Berkeley (**1846**), in the original description, said its ascomata were, "fixed to the soil by a little down." They seem to grow on soil particularly in which there is charred wood. In addition, the ascomata tend to be larger than those of the other species, ranging up to 6 mm diam. Several authors have recognized both taxa. Rogerson and Korf (Korf, **1971**) provided combinations in *Byssonectria* of *B. fusispora* and *B. aggregata* (= *B. terrestris*). Svrček (**1969**) recognized *Inermisia fusispora* also along the lines of the present treatment.

Seaver's (**1928, 1942**) treatment of the North American species is based on relatively few collections. Only one of them falls into *Byssonectria fusispora* as it is at present conceived. The collection with large spores, Ravenel's *Fungi americani exsiccati* no. 174, is the type specimen of a new species described below. There is no doubt that Seaver's concept of these species was muddled. For example, one of the specimens identified by him as *Humarina fusispora* is, in fact, *Rhodoscypha ovilla* (Peck) Dissing & Sivertsen. Gamundí's (**1975**) description also suggests that she had not this but another species.

Too few collections have been examined in this study to determine the development of *B. fusispora.*

*Specimens examined.*—CANADA. NORTHWEST TERRITORIES: N. E. Head of Good Friday Bay, Axel Heiberg Island, on sandy soil, 15 Aug. 1967, *M. Kuc* (DAOM 124704). GREAT BRITAIN. Menmur-Brechin, N. Britain, Rabenhorst, *Fungi europeaei* no. 1812 (ISOTYPE of *Peziza fusispora* var. *scotica,* FH). USA. INDIANA: Fair Oaks, grassy woods, on burnt soil, 22 March 1903, J. C. Arthur (MU, BPI, NY). FLORIDA: on the sand, thickly clustered, in an old grove wood, 17 Jan. 1881, Dr. Martin (NY, Ellis collection).



FIGS. 4–6. Asci and ascospores of *Byssonectria.* 4. *B. terrestris,* asci, ascospores and paraphyses (Smith 64860, MICH). 5, 6. Ascospores of *B. seaveri* (New Jersey, Ellis Herb. NY). Scale = 25 μm.

**Byssonectria seaveri** D. Pfister, *sp. nov.*
FIGS. 3, 5, 6

Apothecia gregaria, discoidea vel turbinata, 1–7 mm diam, margine distincto, fimbriata, disco aurantiaco. Excipulum e hyphis cylindraceis tenuiter tunicatus instructum. Ascosporae fusoidae, hyaline, 29–36 × 8–10 μm magnis. Habitat in terra arenaceo ustulato.

HOLOTYPUS: ad terram, Aiken, S. Carolina, H. W. Ravenel, *Fungi americani exsiccati,* no. 174 (FH), ISOTYPUS (NY).

The placement of large-spored collections of what is now known as *Byssonectria* has been confused. The confusion stems from the incorporation of apparently mistaken ascospore measurements in the literature and, in part, from the assumption by Rifai (**1968**) that Seaver was in error in reporting ascospores which ranged up to 33 μm in material named *Humarina fusispora* in Ravenel's *Fungi americani exsiccati* no. 174 at New York. My measurements and those of Clark Rogerson of the NY specimens, which were studied by Seaver, confirm Seaver's observations. Study of the Farlow Herbarium holdings of the Ravenel exsiccatae also show that the ascospores range from 29-36 × 8-10 μm. Whether the Kew material is immature or whether Rifai's measurements are in error is unclear but there is, in fact, a large-spored species, and it is named here in honor of F. J. Seaver.

*Byssonectria seaveri* is most like *B. fusispora* with which it shares a similar habitat, soil, and the production of ascomata on mycelial tufts rather than an extensive subiculum. It seems to have temperate rather than boreal affinities.

*Specimens examined.*—USA. SOUTH CAROLINA: Aiken, ad terram, H. W. Ravenel, *Fungi americani exsiccati* no . 174 (NY, FH, HOLOTYPE and ISOTYPE of *B. seaveri*). NEW JERSEY: Willow Grove, on barren sand (bits of charcoal are found in the sand), 14 Dec. 1898 (Ellis collection, NY).

## SOME EXCLUDED OR MISPLACED SPECIES

*Inermisia deformis* (P. A. Karst.) Dennis & Itzerott, Kew Bull. **28**: 21. 1973.

BASIONYM: *Peziza deformis* P. A. Karst., Fungi fennici ex. no. 628. 1867.

*Peziza deformis* is the type species of the genus *Kotlabaea* Svrček which is distinguished from *Byssonectria* by its eguttulate ascospores and general habitat.

*Inermisia gyalectoides* (Svrček & Kubicka) Dennis & Itzerott, Kew Bull. **28**: 22. 1973.

= *Octospora gyalectoides* Svrček & Kubicka, Česká Mykol. **17**:66. 1963.

*Inermisia lecithina* (Cooke) Dennis & Itzerott, Kew Bull. **28**: 22. 1973.

The monotypic genus *Miladina* Svrček is based on *Peziza lecithina* Cooke which is the basionym of the combination listed above. See Pfister and Korf (**1974**) for additional comments on *Miladina*, which genus has been widely accepted.

*Inermisia pilifera* (Cooke) Dennis & Itzerott, Kew Bull. **28**: 22. 1973.

None of the material that I have seen with this name has been referable to *Byssonectria*. Khare and Tewari (**1978**) included this in *Octospora* under the subgenus *Byssonectria*.

*Byssonectria tetraspora* (Fuckel) Korf & Rogerson, Phytologia **21**: 202. 1971.

This species has been treated in *Octospora*. The fusiform spores suggest those of *Byssonectria* but lack the polar thickening. In material I have examined, the construction of the excipulum is that of *Octospora* not *Byssonectria*.

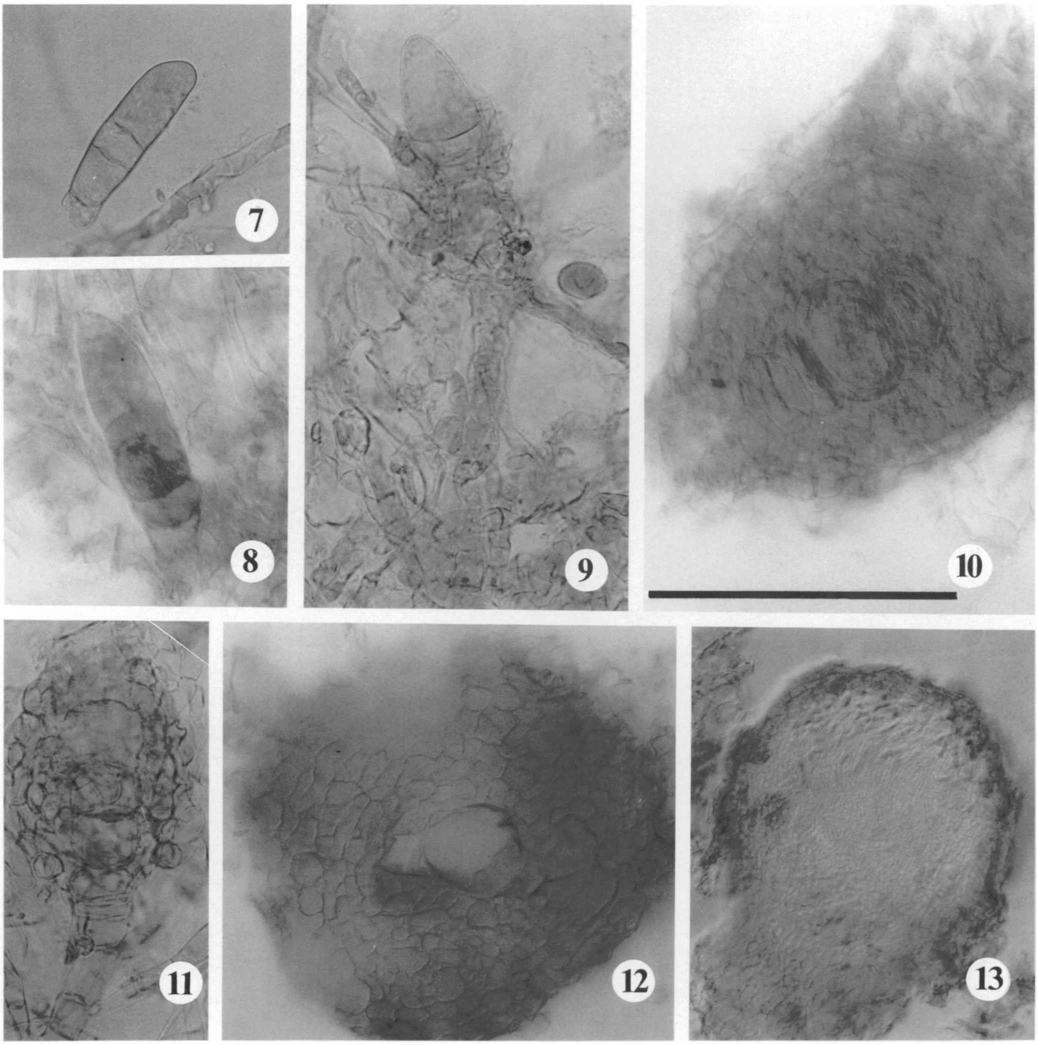
In addition to the species mentioned above, Khare and Tewari (**1978**) included three others in *Octospora* subgenus *Byssonectria*. None of them seems particularly well placed with the species treated here. They are *Octospora coccinea* (Cr.) Brumm., *O. convexula* (Pers.) L. Batra, and *O. cacaina* (Thind, Cash & Sethi) L. Batra.

## RESULTS

The pattern of ascomatal development is identical in the two species studied, *Byssonectria cartilagineum* and *B. terrestris*. Ascomatal initiation begins with the production of a multicellular ascogonial filament (FIGS. 7, 8). At first, these are cylindrical hyphae that are broader than the vegetative hyphae. The filament is composed of up to eight cells which, as the cells enlarge, become globose. Each cell becomes progressively larger toward the distal end of the filament. No male elements were seen and distinct trichogynes were not observed. Once formed, ascogonial filaments are surrounded by hyphae which originate from the neighboring vegetative hyphae and/or the basal cells of the filament (FIGS. 9, 10, 11). These hyphae eventually completely enclose the ascogonial filament (FIG. 12). The enclasping hyphae elongate and ramify to form a knot of tissue around the ascogonial filament and become, through expansion and mutual constriction, pseudoparenchymatous (FIGS. 13, 14).

Following the formation of pseudoparenchymatous tissue, one of the cells near the tip of the ascogonial filament enlarges and its cell wall becomes thickened and refractive (FIG. 15). This ascogonial cell becomes roughened, and decidedly papillate (FIG. 16). The papillae are incipient ascogenous hyphae. The ascogenous hyphae have thicker walls than the surrounding vegetative hyphae. They are closely septate and they branch irregularly (Figs. 17, 18, 19). The hyphae are constricted at the point at which they emerge from the ascogonial cell and the inner surface of the ascogonial cell is roughened (FIG. 19).

At about the time ascogenous hyphae emerge, a palisade layer of paraphyses develops within the pseudoparenchymatous tissue (FIG. 20). The formation of paraphyses displaces some of the

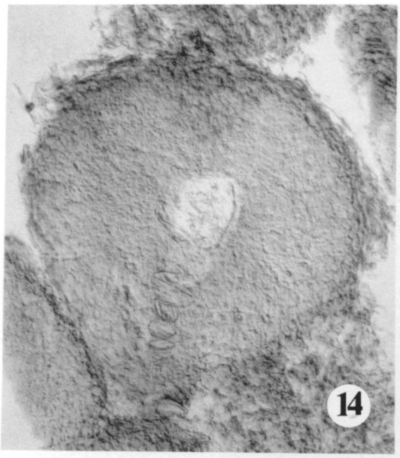


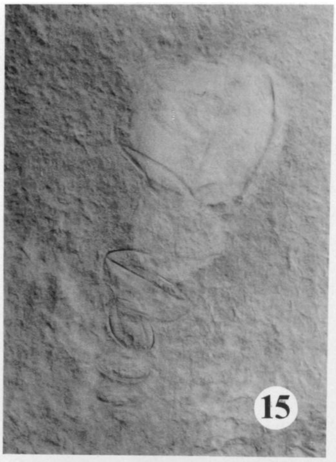
FIGS. 7–13. *Byssonectria terrestris*. 7. Ascogonial filament. 8. As above with a slightly more well-developed ascogenous cell. 9. Ascogonial filament with vegetative hyphae beginning to encircle it. 10. Further development of vegetative hyphae surrounding the ascogonial filament. 11. An ascogenous filament completely surrounded by vegetative hyphae. 12. An ascogenous filament with expanded cells surrounded by pseudoparenchymatous hyphae. 13. Young ascomata with hymenium beginning to form. All illustrated from Smith 74290 (MICH). Scale = 120 μm in FIGS. 7–12; scale = 240 μm in FIG. 13.

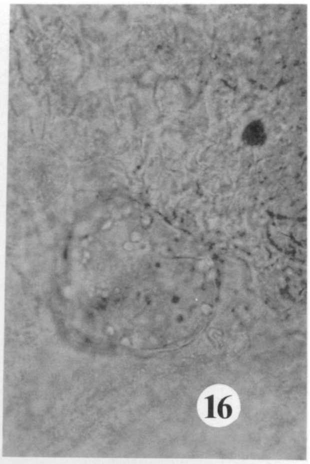
pseudoparenchymatous tissue but the paraphyses remain covered by a layer of tissue until asci begin to form causing the disc to expand. The ascomata increase in size by the enlargement of cells; the outer, least constricted, cells attain a more or less globose form (FIG. 21). The covering tissue splits to expose the hymenium and is carried back attached to the margins of the ascomata. This gives the margins a somewhat fringed or rimmed appearance.

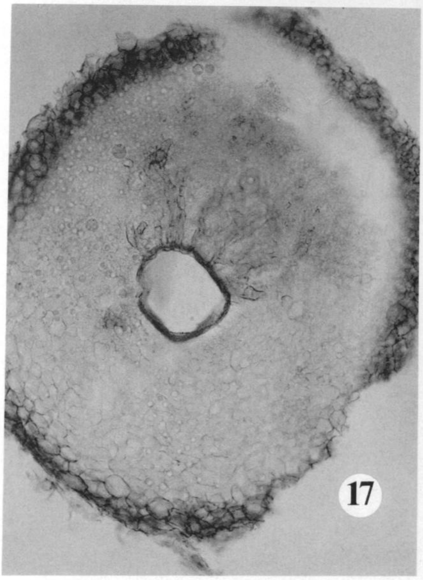
## DISCUSSION

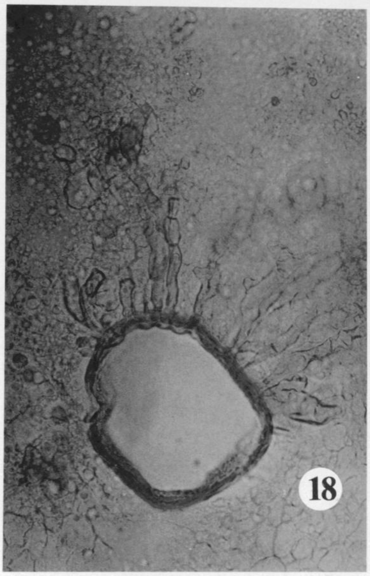
The events of the ascomatal development closely parallel those given for *Humaria granulata* Quel. (= *Coprobia granulata* (Bull.) Boud.) by Gwynne-Vaughan and Williamson (**1930**). In most respects the pattern follows that given for *Ascobolus magnificus* Dodge (= *A. leiocarpus* Berk. & Br.) by Dodge (**1920**). It differs from *Pyronema* Carus, as summarized by Moore

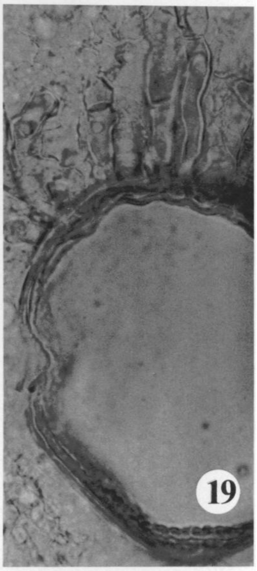


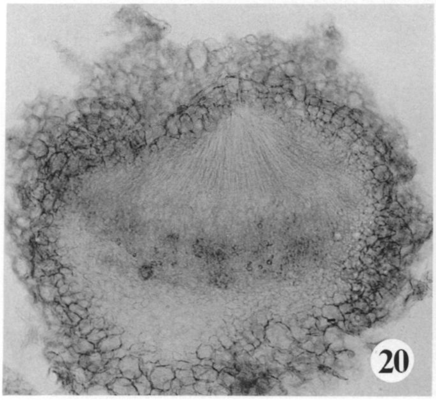


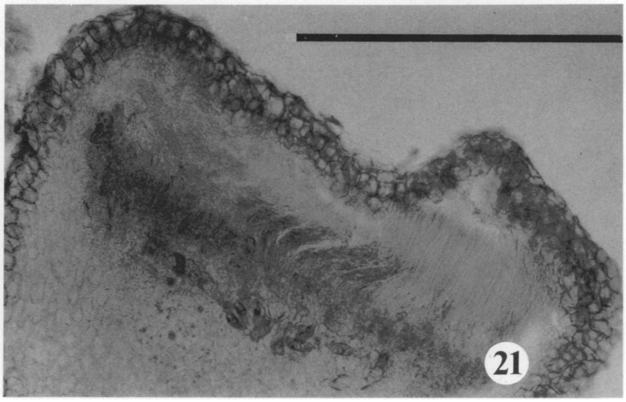












FIGS. 14–21. *Byssonectria cartilagineum*. 14. Ascogonial complex surrounded by vegetative hyphae. Smith 29018 (MICH). 15. Closer view of the above. 16. Ascogenous cell with ascogenous hyphal initials. TRTC 48816. 17. Ascogenous hyphae developing within the cleistohymenial ascomata. WSU 25316. 18. Enlarged view of FIG. 17. 19. Enlarged view of FIG. 17. 20. Ascomata, unopened with paraphyses beginning to form a hymenial

**(1963)**, and *Lasiobolus ciliatus* (Schm.: Fr.) Boud. (Conway, **1975**). In both of these cases multiple ascogonia are formed, unlike those found in *Byssonectria.* In addition, distinct trichogynes are formed in *Ascobolus* and *Pyronema. Cleistoiodophanus* Bezerra & Kimbrough **(1976)** is somewhat similar developmentally but differs from *Byssonectria* in details of ascogonial configuration and morphology. In *Byssonectria* there is no ascogonial coil and there is a single "privileged" cell that produces ascogenous hyphae, unlike the several privileged cells in *Cleistoiodophanus.* Other earlier developmental studies (Brown, **1911**; Fraser, **1907**, **1913**) also indicate that, in large part, the type of development observed here is similar in other carotenoid-containing members of the Pyronemataceae *sensu* Korf **(1972, 1973)**. Gwynne-Vaughan and Williamson **(1930)** noted that in *C. granulata,* a species they considered to be heterothallic, there were no antheridia or spermatia. They found that fusion occurred between undifferentiated hyphae prior to the formation of the ascogonial filament.

Development in these species of *Byssonectria* is cleistohymenial as defined by Brummelen **(1967)**, and the hymenium is exposed during the mesohymenial phase. This mode of development is not unlike *Acervus flavidus* (Berk. & Curt. in Berk.) Pfister as reported by Pfister **(1975)**. In that species a flap of tissue, attached to the margin of the ascoma, is thrown to one side of the ascoma as it expands. Rodway **(1920)** described these events for *Orbilia crystallina,* which was treated as a synonym of *Inermisia fusispora* by Rifai **(1968)**. He wrote that the hymenium was, "at first covered with a crystalline membrane; as the hymenium expands, the membrane bursts in the middle and remains as a toothed margin." The present study confirms the macroscopic observations made by Rodway.

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layer and ascogenous hyphae. WSU 25316. 21. Hymenium with paraphyses and young asci showing cellular hymenial covering. WSU 25316. Scale = 480 μm in FIGS. 14, 17, 20, 21; scale = 240 μm in FIGS. 15 and 18; scale = 120 μm in FIGS. 16, 19.

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