The genus *Bombardioidea*

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The taxonomy and ecology of the fungal genus *Bombardioidea* (Ascomycotina, Lasiosphaeriaceae) are discussed. Descriptions and illustrations are provided for the four accepted species: ***Bombardioidea anartia*** n.sp., *Bombardioidea bombardioides*, *Bombardioidea serignanensis*, and *Bombardioidea stercoris*. Observations from axenic culture are provided for *B. bombardioides*, and an *Angulimaya* (*Phialophora*-like) anamorph is reported. The coriaceous and gelatinous aspects of the peridium are considered to be adaptations to xerophytic environments.

Key words: *Bombardioidea*, *Angulimaya*, *Phialophora*, coprophilous, ecology, taxonomy.

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Les auteurs discutent la taxonomie et l'écologie du genre fongique *Bombardioidea* (Ascomycotina, Lasiosphaeriaceae). Ils présentent les descriptions et les illustrations de quatre espèces acceptées : ***Bombardioidea anartia*** n.sp., *Bombardioidea bombardioides*, *Bombardioidea serignanensis* et *Bombardioidea stercoris*. On présente des observations en culture axénique du *B. bombardioides* ainsi que celles de son anamorphe *Angulimaya*, qui resemble à *Phialophora*. Les auteurs considèrent que les aspects coriaces et gélatineux du péridium constituent des adaptations à des milleux xériques.

Mots clés : *Bombardioidea*, *Angulimaya*, *Phialophora*, coprophile, écologie, taxonomie.

[Traduit par la rédaction]

Introduction

In recent years a considerable amount of attention has been placed on the Sordariaceae sensu lato. Lundqvist (1972) restricted the family to include those genera with asci that possess a distinct apical ring, lacking filiform paraphyses, with one- or two-celled ascospores with one or two germ pores and lacking gelatinous appendages. Other genera previously placed in the Sordariaceae were redisposed to the Lasiosphaeriaceae. Studies of taxa from both families in axenic culture appear to support this conclusion.

During studies of the Sordariaceae sensu lato, it became quite apparent that both *Podospora* Ces. and *Sordaria* Ces. & de Not. were still very heterogeneous. With the availability of additional information it became possible to segregate some of the unrelated elements into other genera. One of these was *Bombardioidea*, which Moreau (1953) erected based on *Sordaria bombardioides* Auersw. in Niessl, but as no Latin diagnosis was included, the genus was not validated until Lundqvist (1972) fulfilled the necessary requirements.

In erecting *Bombardioidea*, Moreau (1953) emphasized the "carbonaceous" nature[2] of the perithecia as well as the two polar germ pores in the ascospores. Lundqvist (1972) expanded the concept to include species with either one or two germ pores and several smaller pores that have no apparent function. He considered the ascocarps to be stromatic and that *Bombardioidea* was closely related to *Fimetariella* Lundq. (Lundqvist 1964), which along with *Periamphispora* Krug (Krug 1989) are the only other sordariaceous genera with the scattered smaller pores.

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[2]In the original text the ascomata are referred to as "... les périthèces carbonacés ..." Although "carbonacé" is not known from current French usage, we assume the author derived this term by transliterating directly from the Latin *carbonaceus* meaning dark brown in colour, hardened and brittle by fire. For clarity we are employing the term coriaceous, meaning having the colour and consistency of leather, which we feel remains consistent with Moreau's intent.

Materials and methods

All specimens cited as TRTC are deposited in the Cryptogamic Herbarium, Royal Ontario Museum, Toronto. Duplicates of a paratype collection of *Bombardioidea anartia* Krug & Scott, described herein, will be distributed in a new exsiccata on selected Canadian fungi.

Cultural studies were carried out on Czapek's Dox agar (CZA) (Malloch 1981), Czapek's yeast autolysate agar (CYA) (Pitt 1979), malt extract agar (MEA) (Malloch 1981), Weitzman–Silva-Hutner's agar (WSHA) (Weitzman and Silva-Hutner 1967), and modified Leonian's agar (Malloch 1981). All cultures were grown at room temperature under ambient lighting conditions. Microscopic mounts were made in lactophenol cotton blue and cross sections in lactofuchsin with Gurr's water mounting medium (Carmichael 1955). Histological observations were made from mounts in Gurr's medium, while for consistency, the illustration (Fig. 13) was prepared from a mount in lactophenol cotton blue. Colour descriptions cited correspond to the colour chart of Kornerup and Wanscher (1978).

Taxonomy

Bombardioidea Moreau in Lundq., Symb. Bot. Ups. 20: 274. 1972

Ascocarps saprobic, usually aggregated in small clusters or occasionally scattered, confluent at the base or single, superficial or rarely erumpent, nonstromatic, slightly roughened, bare, ovoid to oblong, red-brown to blackish brown, with an almost indistinguishable or indistinct, slightly depressed, dark brown to black ostiolar region at the apex; peridium coriaceous, consisting of three layers, an outer rind of pseudoparenchymatous, dark brown, thick-walled cells, a middle layer of noncellular gelatinous matrix interspersed with hyaline, thin-walled hyphae and an inner layer of pseudoparenchymatous, hyaline, thin-walled cells, the layer tapering and containing pigmented cells towards the perithecial base. Asci unitunicate, nonamyloid, 4- or 8-spored, cylindrical, with an elongated stipe and a thickened, usually distinct apical ring. Paraphyses filiform, septate, hyaline, longer than and mixed with the asci. Ascospores uniseriate or partially biseriate, one-celled, surrounded by a hyaline gelatinous sheath, ellipsoidal, ovoid or oblong-ellipsoidal, sometimes flattened on one side, dark

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brown, with two terminal germ pores and several smaller apparently nonfunctional pores. Anamorph *Angulimaya* (*Phialophora*-like), phialidic, producing dry conidia in chains.

TYPE SPECIES: *Bombardioidea bombardioides* (Auersw. in Niessl) C. Moreau in Lundq.

Key to the species

1. Asci 4-spored 2
1. Asci 8-spored 3

2. Ascospores ellipsoidal, 35–43 × 16–22 μm, with two distinct germ pores ..... *B. stercoris*
2. Ascospores ovoid, 25–31(–34) × 16–19(–20) μm, with a large apical germ pore and a less conspicuous basal pore ..... *B. serignanensis*

3. Ascospores uniseriate, ellipsoidal, symmetrical, 19–29 × 10–14 μm, on leporid dung ..... *B. bombardioides*
3. Ascospores frequently irregularly biseriate, oblong-ellipsoidal, asymmetrically flattened, (25–)26–35(–38) × 12–14(–15) μm, on cervid dung ..... *B. anartia*

Bombardioidea anartia Krug & Scott, sp.nov.

Figs. 1, 2, 13, 15, 18

Perithecia dispersa, glabra, superficialia, pyriformia, circa 1100–1150 × 500–600 μm magna; perithecii pars ostiolo atribrunnea, indistincta; peridium atribrunneum vel olivaceibrunneum, coriaceum, e stratis tribus compositum. Asci octospori, cylindracei, 345–400 × 20–25 μm magni, apicem versus attenuati et truncati, basin versus in stipitem 135–240 μm longum attenuati; annulus apicalis parvus, saepius indistinctus. Paraphyses numerosae, filiformes, septatae, hyalinae. Ascosporae unicellulares, oblique irregulariter biseriales, vagina hyalina gelatinosa angusta circumdatae, oblongae vel ellipsoideae, in apice attenuatae, in latere uno applanatae, (25–)26–35(–38) × 12–14(–15) μm magnae, primum hyalinae vel fulvae, maturitate confirmata atribrunneae et opacae, foramen germinale circa 1.5–2 μm diametro crassum in utroque apice exhibentes.

HOLOTYPUS: In Alcis alcis fimo lectus est, apud flumen Little White vocatum, in Algoma comitatu, in Ontario provincia Canadensis regni, 14 Sept. 1956, *Cain*, TRTC 32361. In Museo Regi Ontarioensis Cryptogamarum herbario.

Perithecia scattered, superficial, bare, pyriform, ca. 1100–1150 × 500–600 μm, dark reddish brown, with an indistinct, dark brown ostiolar region with a small, indistinct ostiole; peridium dark brown to olivaceous brown by reflected light, coriaceous, appearing in surface view of indistinct cellular structure, consisting of three layers, a thin outer layer 2–4 cells thick, of angular to oblong, thick-walled, dark brown cells measuring 8–12 × 3–4 μm, a thick middle layer 80–140 μm thick, of noncellular, gelatinous matrix sparsely interspersed with branching, thin-walled, hyaline hyphae and an inner layer 6–8 cells thick, of elongated, thin-walled, hyaline to pallid cells measuring 10–16 × 1.5–2.5 μm, tapering towards the perithecial base about 200 μm long where this layer is composed of dark brown, thick-walled, angular cells measuring 7–10 × 4–5 μm. Asci 8-spored, cylindrical, 345–400 × 20–45 μm, narrowed and truncated at the apices, tapering into a long stipe measuring 135–240 μm; apical ring small, often indistinct. Paraphyses abundant, filiform, septate, hyaline, longer than and mixed with the asci. Ascospores one-celled, frequently obliquely irregularly biseriate, surrounded by a narrow hyaline gelatinous sheath, oblong-ellipsoidal, narrowed towards the ends, typically flattened on one side, (25–)26–35(–38) × 12–14(–15) μm, ranging from hyaline when young to yellow brown, finally dark brown and opaque at maturity, containing at each opposing end of the spore a germ pore measuring 1.5–2 μm in diameter.

HABITAT: On deer, moose and porcupine dung.

SPECIMENS EXAMINED: CANADA: ALBERTA: N of Beaver Mines, moose dung, 28.VII.1962, *Cain*, TRTC 38981; Miette Hot Springs, moose dung, 4.VIII.1962, *Luck-Allen*, TRTC 38860; Jasper National Park, Athabasca Falls, moose dung, 8.VIII.1962, *Cain*, TRTC 39024. BRITISH COLUMBIA: W of Yellowhead Pass, Ghita Creek, moose dung, 7.VIII.1962, *Cain* C2070a (TRTC), *Luck-Allen*, TRTC 39173, 39202. NEW BRUNSWICK: Fundy National Park, Alma, moose dung, 19.VIII.1963, *Cain*, TRTC 46319, Maple Grove Trail, 18.VIII.1963, *Cain*, TRTC 41918. ONTARIO: Algoma Dist.: Twp. 1B: Little White River, moose dung, 14.IX.1956, *Cain*, TRTC 32361, 32379a (IMI, TRTC), 32391 (S, TRTC), 33473; Shabatic River, moose dung, 20.VI.1961, *Cain*, TRTC 37547. Nipissing Dist.: Algonquin Prov. Park, Lake Opeongo, moose dung, 19.IX.1954, *Cain*, TRTC 32712. Thunder Bay Dist.: Nickel Twp.: Black River, moose dung, 17.VI.1963, *Cain*, TRTC 45431. Timiskaming Dist.: Holmes Twp.: 5.1 km SW of Rib Lake, moose dung in spruce woods, 3.IX.1981, *Malloch*, TRTC 51511. U.S.A.: ALASKA: Anchorage, moose dung, 23.V.1963, *Kempton* 5/23/63/9, as *Sordaria bombardioides*, ex NY (TRTC). CALIFORNIA: Siskiyou Co.: Mt. Shasta, Panther Creek Meadows, elev. 7500–8000 ft, deer dung, 1.VII.1951, *Cooke*, ex WSP 30081 (TRTC). IDAHO: Idaho Co.: Nez Perce National Forest, above Rakliff Creek Camp Ground, porcupine dung, 16.XI.1946, *Cooke* 18793, Mycobiot. North Amer. 244, as *Sordaria bombardioides* (TRTC). UTAH: Weber Co.: E of Ogden, Wasatch Mts., tributary of Ogden Canyon, Coldwater Canyon, moose dung as elk dung, 22.IX.1993, *Rogerson* UT 96-1, ex NY (TRTC). WYOMING: Teton Co.: Teton National Forest, Moran, moose dung, 30.VI.1955, *Cain*, TRTC 32051.

This species resembles *B. bombardioides*, in that both taxa possess 8-spored asci, but differs from that taxon by the typical biseriate spore arrangement and the larger, more oblong, asymmetrical ascospores. It can be separated from both *B. serignanensis* and *B. stercoris* by the 8-spored asci and the narrower, asymmetrical ascospores.

Ecologically *B. anartia* appears to be largely restricted to moose dung and is distributed in the boreal region of North America and possibly also in northern Europe although no such collections have been examined. The other species of *Bombardioidea* are confined primarily to leporid dung.

Bombardioidea bombardioides (Auersw. in Niessl) C. Moreau in Lundq., Symb. Bot. Ups. 20: 277. 1972
Figs. 3, 4, 9–12, 14, 17

≡*Sordaria bombardioides* Auersw. in Niessl, Verh. Naturforsch. ver. Brünn, 10: 187. 1872. and Fungi europaei exsicc. 1527. 1872

≡*Sphaeria bombardioides* (Auersw. in Niessl) Phill., Grevillea, 5: 118. 1877

≡*Hypocopra bombardioides* (Auersw. in Niessl) Sacc., Syll. Fung. 1: 243. 1882

≡*Pleurage bombardioides* (Auersw. in Niessl) Kuntze, Rev. Gen. Plant. 3: 505. 1898

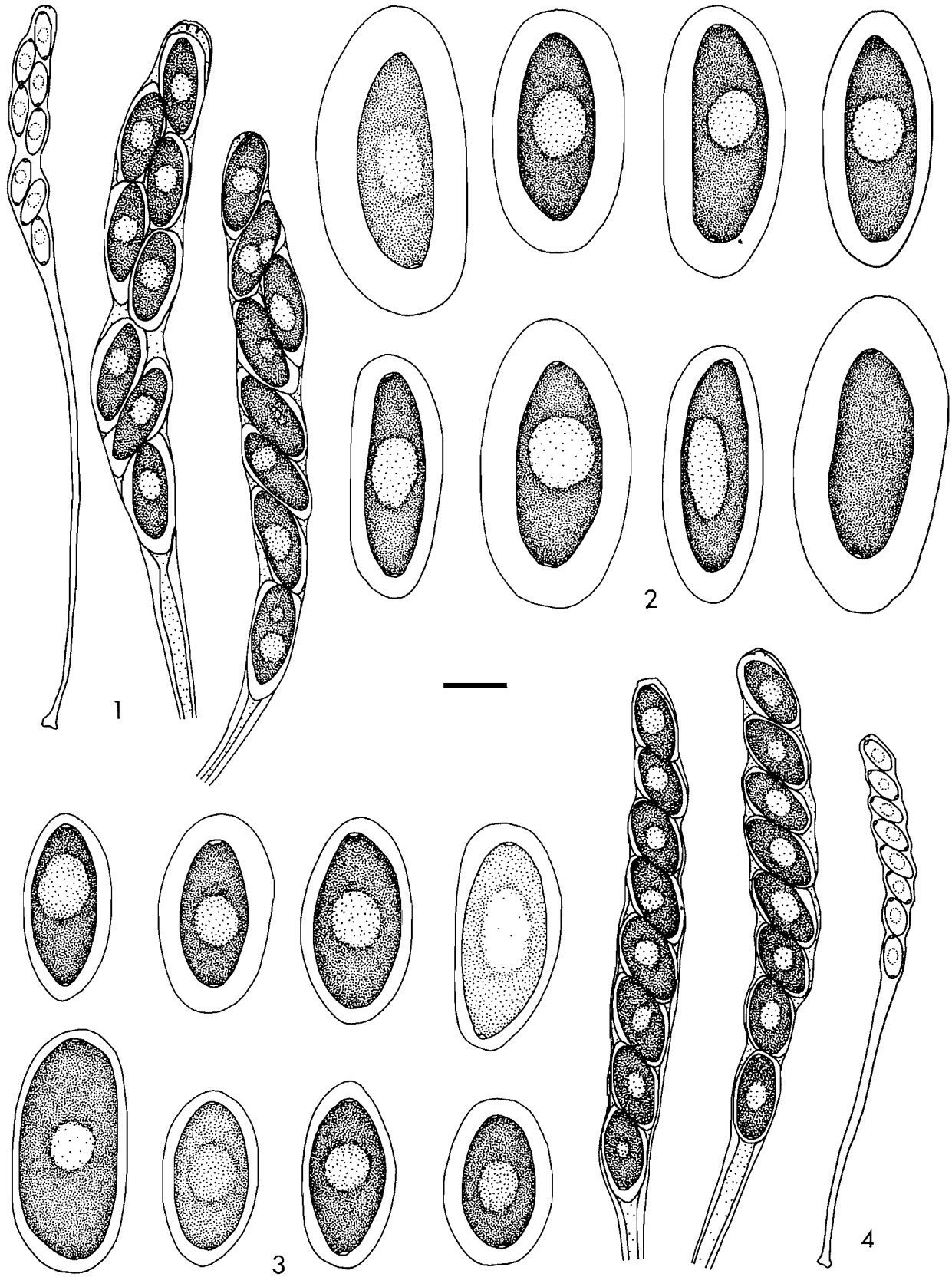
≡*Fimetaria bombardioides* (Auersw. in Niessl) Griff. & Seaver, N. Am. Flora, 3: 65. 1910

≡*Bombardioidea bombardioides* (Auersw. in Niessl) C. Moreau, Encycl. Mycol. 25: 317. 1953, nomen invalidum cui descriptio latina deest

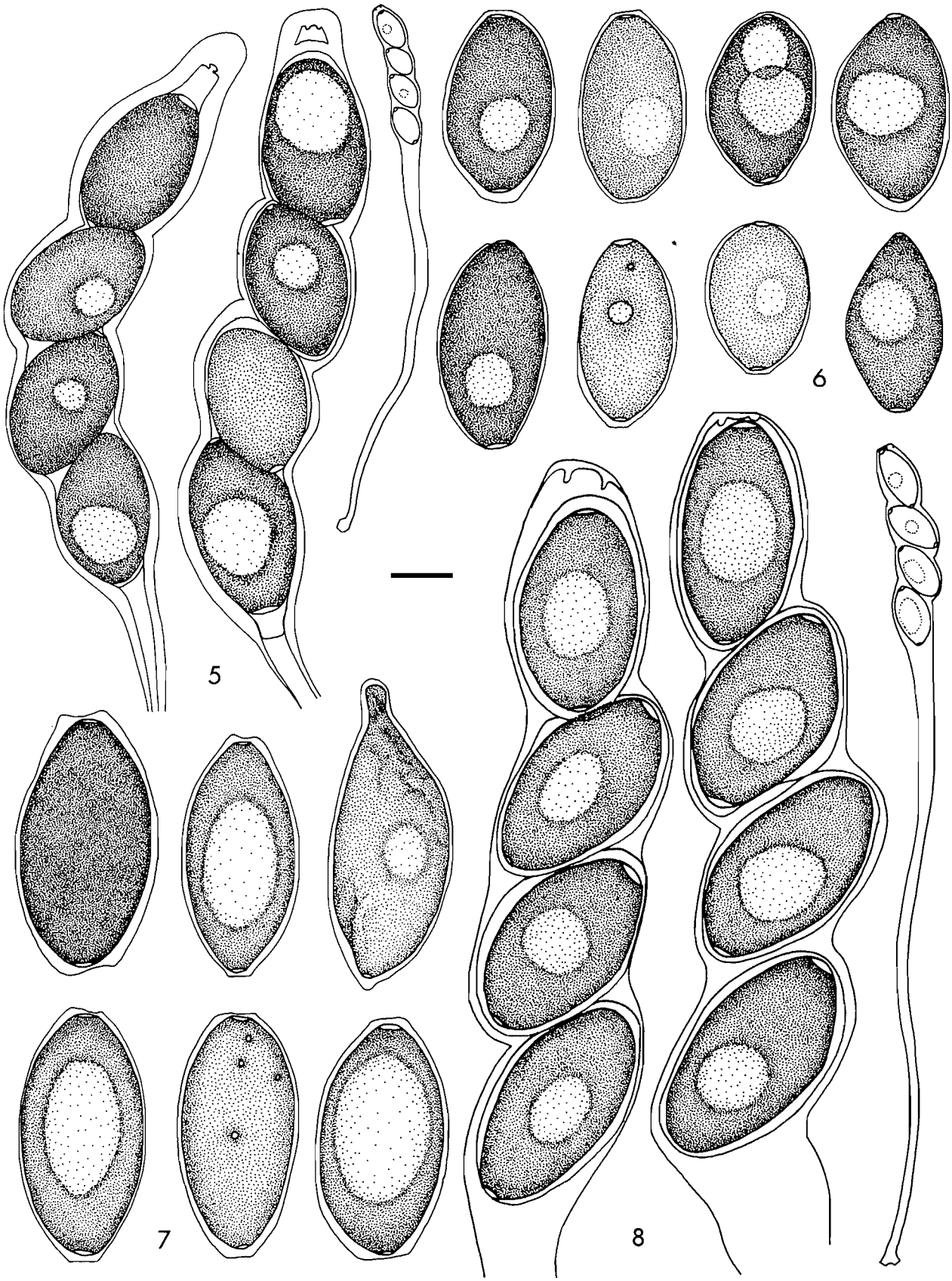
Perithecia aggregated in small clusters, confluent at the base or occasionally single, superficial, somewhat roughened, bare, ovoid to oblong or occasionally pyriform, 800–1500 × 500–800 μm, red-brown to blackish brown, with an indistinct, very dark brown ostiolar region with a small, very prominent ostiole at the apex; peridium dark brown by reflected light, thickened, very coriaceous, appearing in surface view of indistinct cellular structure, 125 μm thick, consisting of three layers, an outer layer 1–2 cells thick, of oblong, thick-walled, dark brown cells measuring 5–8 × 2–3 μm, a middle layer 80–100 μm thick, of noncellular gelatinous matrix sparsely interspersed with branching thin-walled, hyaline hyphae measuring 1.5–2 μm in diameter, and an inner layer 10–12 cells thick, of oblong to elongated, thin-walled, pale brownish cells measuring 8–15 × 2–3 μm, tapering towards the perithecial base where this layer is composed of angular, thick-walled, dark brown cells measuring 8–10 × 6–7 μm. Asci 8-spored, cylindrical, 240–350 × 15–20 μm, broadly rounded at the apices, tapering into a stipe measuring 90–200 μm long; apical ring indistinct. Paraphyses abundant, filiform, septate, hyaline, guttulate, longer than and mixed with the asci. Ascospores one-celled, obliquely uniseriate, surrounded by a hyaline gelatinous sheath reaching a width of 15 μm, ellipsoidal, rounded towards the ends, (17–)19–29 × 10–14 μm, ranging from hyaline when young to yellowish-brown, finally dark brown and opaque at maturity, containing at each opposing end of the spore a germ pore measuring 1.5–2 μm in diameter; apical pore often slightly smaller. Anamorph on WSHA at 4 weeks with conidiophores 2–2.5 μm in diameter, brown to dark brown, becoming hyaline towards apex, thick-walled, septate, branched or unbranched, with short, 1-, 2-, or 3-celled, swollen, 3–5 μm in diameter lateral metulae bearing clusters of 2–7 phialides. Phialides numerous, subhyaline to dark brown, subglobose to ampulliform, 4–5.5 × 2.5–3.5 μm, broadly attached to subtending cell, with a prominent, dark collarette 2–2.5(–3) μm in diameter; phialides produced terminally and laterally on metulae, singly or more commonly in irregular whorls of 3–7; clusters of phialides occurring at intervals of 10–30 μm along fertile hyphae, causing a nodal appearance. Conidia numerous, one-celled, thin-walled, hyaline to light brown, globose to subglobose, 2–3 μm in diameter, often with a distinct, truncated apiculus, produced in dry, readily disarticulating chains; conidia from aging colonies (> 12 weeks) thick-walled, 4–6.5 μm in diameter. Colonies reaching diameters of 7 mm on CZA, 75–80 mm on CYA, 60–70 mm on MEA and WSHA and 35–37 mm on MLA at 4 weeks; flat on all media tested. Aerial mycelium on CZA sparse or absent, pasty and white in appearance, subcompact at margin; on CYA and MEA cream coloured (4-5A1-2), closely appressed, closely concentrically zonate; on CYA velvety at centre becoming subfloccose and sparse towards margin; on MEA velvety at centre becoming minutely radially tufted and sparse towards margin; on MLA and WSHA, velvety, broadly concentrically zonate, reddish grey (12B2 to 12D3 to 12C4) at centre; on WSHA becoming pinkish (12A1-2) and sparse towards margin; on MLA becoming greyish yellow (4B3) in central zone, then pinkish (12A3) and finally cream coloured (4-5A1-2) at the margin. Margin regular on CZA, CYA, and WSHA, irregularly tufted on MEA, undulate on MLA. Reverse pigment indistinct on CZA, CYA and MEA, brown (6F6-6E6) at centre becoming greyish yellow (4B4) towards margin on WSHA and MLA. Fertile ascomata produced on WSHA after 12–16 weeks.

HABITAT: On hare and rabbit dung, occasionally recorded on cow, horse, sheep, moose, and porcupine dung.

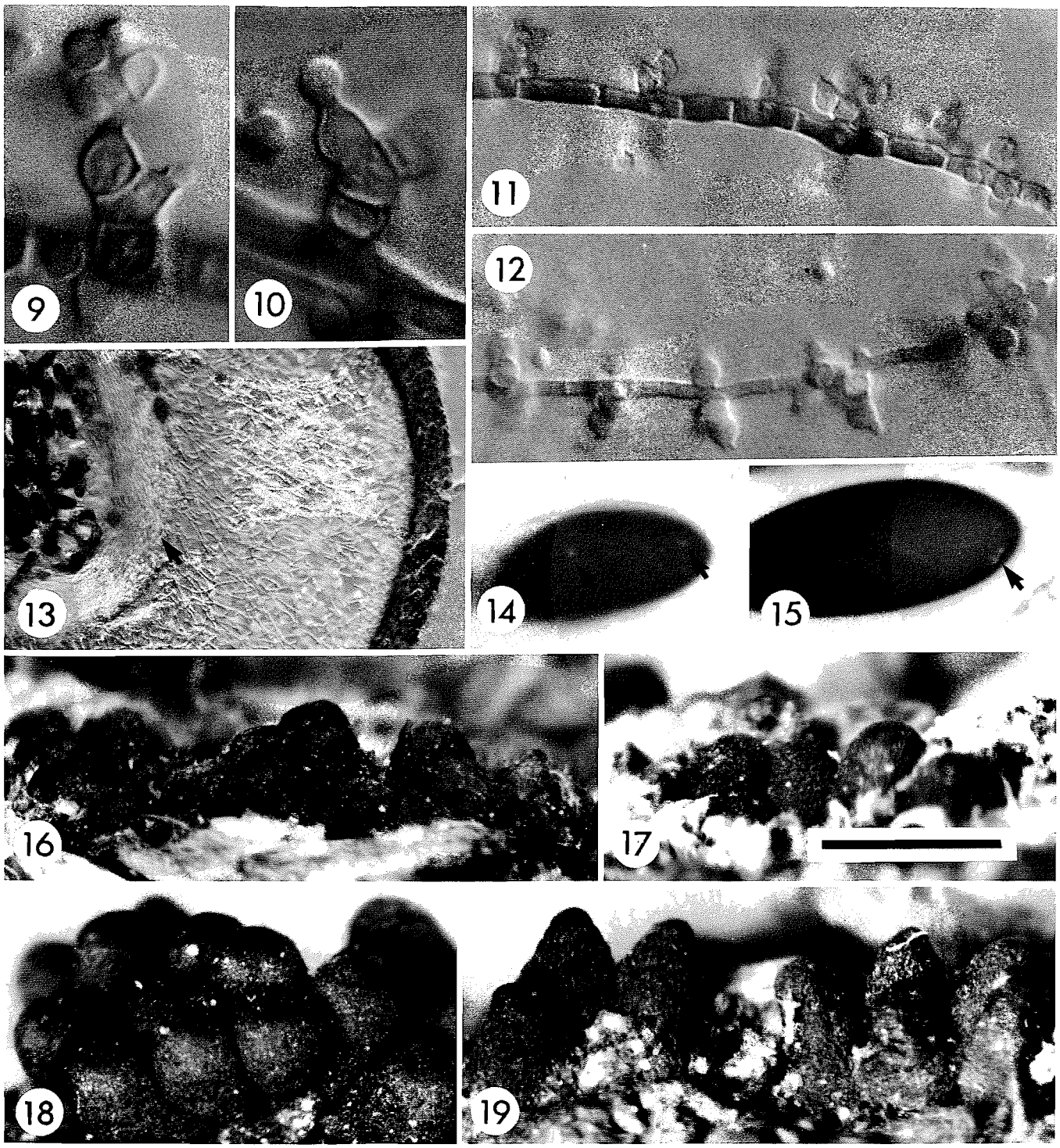
SPECIMENS EXAMINED: CANADA: ALBERTA: E of Jasper National Park, Hinton, moose dung, 3.VIII.1962, *Luck-Allen*, TRTC 40420. MANITOBA: Riding Mt. National Park, Clear Lake, porcupine dung, 16.VIII.1935, *Bisby*, TRTC 45441. NEW BRUNSWICK: McAdam Twp.: near McAdam, moose dung, 30.VIII.1991, *Scott*, TRTC 51510. ONTARIO: Algoma Dist.: Twp. 1B: Little White River, moose dung, 15.IX.1956, *Cain*, TRTC 32363a. Brant Co.: NW of Burford, rabbit dung, 29.IV.1939, *Cain*, TRTC 45454; N of Cathcart, N of Colles Pond, rabbit dung, 30.VIII.1942, *Cain*, TRTC 45443; 1 mi S of Hatchley, rabbit dung, 27.VIII.1934, *Cain*, TRTC 45438; 2 mi E of New Durham, rabbit dung, 22.V.1935, *Cain*, TRTC 45442. Bruce Co.: Lions Head, rabbit dung, 24.VII.1932, *Cain*, TRTC 45449; Millar Lake, rabbit dung, 11.VII.1930, *Cain*, TRTC 5130; Sauble Beach, rabbit dung, 11.VII.1930, *Cain*, TRTC 5101; Port Elgin, rabbit dung, 10.VII.1930, *Cain*, TRTC 45447. Grey Co.: Balaclava, rabbit dung, 14.VII.1931, *Cain*, TRTC 5102; Dornoch, rabbit dung, 7.VII.1930, *Cain*, TRTC 45446. Kenora Dist.: 28 mi N of Vermilion Bay, Cedar Lake, moose dung, 7.VI.1956, *Cain*, TRTC 35862. Manitoulin Dist.: Manitoulin Island, Sheguiandah, rabbit dung, 1.VIII.1933, *Cain*, TRTC 45448. Nipissing Dist.: Algonquin Provincial Park, Costello Lake, porcupine dung, 6.IX.1939, *Cain*, TRTC 45453; Lake Timagami, Bear Island, horse dung, 13.VIII.1936, *Cain*, TRTC 45452. Oxford Co.: 4 mi NW of Norwich, rabbit dung, 11.IX.1934, *Cain*, TRTC 45451. Thunder Bay Dist.: Lake Superior Provincial Forest, Black Sturgeon Lake, moose dung, 1.VIII.1965, *Cain*, TRTC 51509; W of Manitouwadge, moose dung, 18.VI.1963, *Cain*, TRTC 39923; 14 mi W of Manitouwadge, moose dung, 18.V.1963, *Cain*, TRTC 41980. Wellington Co.: Everton, rabbit dung, 26.VII.1932, *Cain*, TRTC 45444. QUEBEC: Montmorency Co.: Laurentide National Park, Lac Ste. Anne, moose dung, 22.VIII.1959, *Cain*, TRTC 45436. SASKATCHEWAN: Annaheim, snow-shoe rabbit dung, 21.VI.1934, *Russell*, TRTC 45440; E of Prince Albert National Park, Emma Lake, rabbit dung, 27.VIII.1934, *Russell*, TRTC 45450. CZECHOSLOVAKIA: MORAVIA: Brno, Schwaibwald, hare dung, spring, *Niessl*, Fungi europaei exsicc. 1527 (DAOM, G, M, S, UPS, ZT), 28.IV.1870 (M); Kohantowitz, hare dung, VIII.1876, *Niessl* (M); Kuřim, Čebínka hill, ca. 350 m, hare dung, 24.X.1942, *Smarda*, Musei Moraviensis Crypt. Čech. Exsicc. 7 (ZT); Ratschitz, hare and roe-deer dung, VIII.1886, *Niessl*



FIGS. 1 and 2. *Bombardioidea anartia* (TRTC 51511). Fig. 1. Asci and ascospores. Fig. 2. Ascospores typically oblong-ellipsoidal and flattened on one side, showing terminal germ pores and central globule. FIGS. 3 and 4. *Bombardioidea bombardioides* (Fungi europ. exsicc. 1527). Fig. 3. Ascospores typically ellipsoidal. Fig. 4. Asci and ascospores. Scale bar: 20 μm for large-scale asci in Figs. 1 and 4; 40 μm for small-scale asci in Figs. 1 and 4; 10 μm for Figs. 2 and 3.



FIGS. 5 and 6. *Bombardioidea serignanensis* (Lqt 2742a). Fig. 5. Asci and ascospores. Fig. 6. Ascospores showing two germ pores. FIGS. 7 and 8. *Bombardioidea stercoris* (Fungi europ. exsicc. 1340). Fig. 7. Ascospores showing large, distinct germ pores and one with smaller pores. Fig. 8. Asci and ascospores. Scale bar: 10 μm for large scale asci in Figs. 5 and 8; 40 μm for small scale asci in Figs. 5 and 8; 10 μm for Figs. 6 and 7.



FIGS. 9–12. *Bombardioidea bombardioides* (TRTC 51510). Fig. 9. Phialide and conidia. Fig. 10. Phialide and developing conidium. Fig. 11. Conidiophore and phialides. Fig. 12. Conidiophore showing whorled, nodal arrangement of phialides. FIG. 13. *Bombardioidea anartia* (TRTC 51511). Cross section of peridium showing outer rind, medial gelatinous matrix and inner layer (arrow). FIG. 14. *Bombardioidea bombardioides* (Fungi europ. exsicc. 1527). Ascospore showing scattered smaller pores (arrows). FIG. 15. *Bombardioidea anartia* (TRTC 51511). Ascospore showing smaller pores (arrow). FIG. 16. *Bombardioidea serignanensis* (Lqt 2742a). Perithecia. FIG. 17. *Bombardioidea bombardioides* (Fungi europ. exsicc. 1527). Perithecia. FIG. 18. *Bombardioidea anartia* (TRTC 51511). Perithecia. FIG. 19. *Bombardioidea stercoris* (Fungi europ. exsicc. 1340). Perithecia. Scale bar: 10 μm for Figs. 9 and 10; 25 μm for Figs. 11 and 12; 200 μm for Fig. 13; 17 μm for Figs. 14 and 15; 1 mm for Figs. 16–19.

(M). DENMARK: sine loco, hare dung, 5.IX.1875, *Hansen*, Fung. fimicolorum exempl. exsicc. p. 23(1) (C). GERMANY: BAVARIA: Bayerisch-Eisenstein, Steinhütte, hare dung, VII.1935, *Kirschstein* (B); Mittelfranken, Windsheim, hare and roe-deer dung, X.1873, *Rehm*, Ascomyceten 233 (B, M, NY, S) [Leipzig, hare dung, *Winter*, in G copy]; Munich, Grosshes-

sellob, rabbit dung, X.1904, *Rehm* (S); Niesnersberg, rabbit dung, VII.1907, *Buchs* (S). SAXONY: Sächsische Schweiz, Grosser Winterberg, rabbit dung, VIII.1892, *Wagner* (S); Schandau, hare dung, VI–VIII.1894–99/VII–VIII.1905, *Krieger*, Fungi saxonici 1948 (M, MICH, S, TRTC). THURINGIA: Arnstadt, hare dung, *Auerswald* (B, G, M). HUNGARY: SOMOGY: Kaposvár, Topanár Forest, rabbit dung, 1871, *Lojka*, Ascomycetes Hung. 168 (S). JAPAN: YAMANASHI PREF.: Minamikoma-gun: Kajikazawa-machi, Jukkoku, rabbit dung [published as hare dung by Furuya and Udagawa 1973], 4.XI.1966, *Udagawa*, NHL 2634. POLAND: SILESIA: Karlsbrunn, hare dung, VIII.1880, *Niessl* (M), VIII (ZT), VIII, Krypt. Exsicc. Museo Palatino Vind. 717 (G, M, NY, S, TRTC). U.S.A.: MICHIGAN: Ingham Co.: East Lansing, Michigan Agricultural College [now Michigan State University], horse dung, 27.IX.1893, *Hicks* (BPI, NY). NEW MEXICO: Colfax Co.: Ute Park, cow dung, 22.VIII.1916, *Standley* 13511 (NY). NEW YORK: Tompkins Co.: Ithaca, horse dung, *Kauffman*, MU 4754. WYOMING: Laramie Co.: Horse Creek, sheep dung, 2.IX.1963, *Luck-Allen*, TRTC 45437. YUGOSLAVIA: CROATIA: Velebit North: N of Karlobag: Mt. Mali Brizovac, NW of Cesaricka, elev. 900 m, cow dung, 7.V.1972, *Lundqvist* 7694 (UPS).

Isolates of the anamorph derived from TRTC 51510 will be deposited at UAMH.

This taxon is distinguished by the 8-spored asci and ascospore size. It differs from *B. anartia*, the only other species with 8-spored asci, in having uniseriately arranged, generally shorter and stouter, typically symmetrical ascospores. Both *B. serignanensis* and *B. stercoris* differ in possessing 4-spored asci and broader ascospores.

The anamorph of *B. bombardioides* is consistent with *Angulimaya* Subram. & Lodha, which was erected by Subramanian and Lodha (1964) based on a single species *A. sundara* Subram. & Lodha from cow dung. Subramanian and Lodha (1964) described this fungus as having "annellophores bearing many distinct annellations." Ellis (1971) noted the spore-bearing structures were phialides and that the interpretation of the former authors was incorrect. Our examinations of the anamorph of *B. bombardioides* show that this fungus is exclusively phialidic in young cultures, but with age (> 12 weeks) some phialides show progression of the conidiogenous locus beyond the collarette. This annellidic tendency is supported by the occasional presence of distinctly apiculate conidia. A similar anamorph also has been noted for *B. anartia* by G. White (personal communication).

Except for our cultural observations for *B. bombardioides*, reported herein, *B. stercoris* is the only other species for which cultural observations have been published. Moreau (1953) successfully cultured this species which he referred to as a 4-spored form of *Sordaria bombardioides*. He obtained on cornmeal agar a "dense growth of white, fibrous, superficial mycelium" but was unable to obtain mature ascomata.

Bombardioidea serignanensis (Fabre) Lundq., Symb. Bot. Ups. 20: 284. 1972 Figs. 5, 6, 16

≡ *Hypocopra serignanensis* Fabre, Ann. Sci. Nat. (Bot.) VI, 9: 77. 1878

≡ *Sordaria serignanensis* (Fabre) Cooke, Grevillea, 16: 55. 1887

≡ Pleurage serignanensis (Fabre) Kuntze, Rev. Gen. Plant. 3: 505. 1898

Perithecia clustered or occasionally slightly scattered, superficial, somewhat roughened, bare, ovoid to oblong, 800–1200 × 450–600(–750) μm, dark reddish brown to blackish brown, with an indistinct, slightly roughened, very dark brown, ostiolar region with a very small, indistinct ostiole; peridium very dark brown by reflected light, thickened, coriaceous, appearing in surface view of indistinct cellular structure, 125–150 μm thick, consisting of three layers, an outer layer 2–3 cells thick, of oblong, thick-walled, dark brown cells measuring 6–9 × 3–4 μm, a middle layer 75–100 μm thick, of noncellular, gelatinous matrix sparsely interspersed with branching, thin-walled, hyaline hyphae measuring 1–1.5 μm in diameter, and an inner layer 8–10 cells thick, of oblong to elongated, slightly thick-walled, pallid to brownish cells measuring 12–18 × 1–2 μm, tapering toward the perithecial base where this layer is composed of angular, thick-walled, dark brown cells measuring 6–9 × 4–5 μm. Asci 4-spored, cylindrical, 260–320 × 20–23 μm, narrowly rounded to somewhat truncated at the apices, tapering into a stipe measuring 80–170 μm long; apical ring very distinct, somewhat thickened. Paraphyses abundant, filiform, septate, hyaline, longer than and mixed with the asci. Ascospores one-celled, obliquely uniseriate, surrounded by a hyaline gelatinous sheath reaching a width of about 7 μm, ellipsoidal to ovoid, narrowed towards the ends (especially in ellipsoidal spores), (23–)25–31(–34) × 16–19(–20) μm, ranging from hyaline when young to yellow-brown, finally very dark brown and opaque at maturity, with each containing a large apical germ pore measuring 2–2.5(–3) μm in diameter and a somewhat less conspicuous, occasionally slightly smaller, basal pore, frequently orientated with the more distinct pore pointed downwards (especially in the lower spores).

HABITAT: On hare and rabbit dung.

SPECIMENS EXAMINED: SWEDEN: LAPPLAND: Torne Lappmark: 13 km NW of Abisko, Kopparåsen, hare dung, 9.IX.1960, *Lundqvist* 2742a (TRTC, UPS); Jukkasjärvi Parish: Abisko, hare dung, 17.VI.1970, *Gunnerbeck* 1962d (UPS), hare dung, 22–31.VII.1966, *Holm* s.n. (UPS). FINLAND: LAPPONIA INARENSIS: Utsjoki parish: Utsjoki, hare dung, 26.VII.1966, *Lundqvist* 4924a (UPS). U.S.A.: WYOMING: Niobrara Co.: N of Lusk, rabbit dung, 2.IX.1964, *Cain* C1924b (TRTC).

The only other species with 4-spored asci is *B. stercoris*, but this taxon can be distinguished by the larger ascospores, distinct apical and basal germ pores, and the rather indistinct apical ring. In the North American collection the asci appear to be somewhat smaller, measuring 180–235 × 20–25 μm, but otherwise, except for minor variations, the European and North American populations of *B. serignanensis* appear similar.

Lundqvist (1972) described the spores as possessing only a single germ pore and a number of smaller pores. An examination of a portion of the neotype (TRTC) revealed that the spores have two germ pores and often several scattered smaller pores. The apical pore is usually more distinct and occasionally larger while the basal pore is less conspicuous. Reverse orientation within the ascus appears to be frequent.

Bombardioidea stercoris (DC.: Fr.) Lundq., Symb. Bot. Ups. 20: 281. 1972 Figs. 7, 8, 19

≡ *Sphaeria stercoris* DC. in Lamarck & DC., Flore Française, ed. 3, 2: 294. 1805

≡ *Sphaeria stercoraria* Sow. β *stercoris* DC.:Fr., Syst. Mycol. 2: 456. 1823

≡ *Sphaeria stercoris* (DC.:Fr.) Fr., Elen. Fung. 2: 104. 1828

≡*Hormospora stercoris* (DC.:Fr.) Desm., Ann. Sci. Nat. 3 Ser. 16: 318. 1851

=*Sordaria maxima* Niessl in Rabenh., Hedwigia, 9: 137. 1870, and Fungi europaei exsicc. 1340. 1870

≡*Hypocopra maxima* (Niessl in Rabenh.) Sacc., Syll. Fung. 1: 245. 1882

≡*Pleurage maxima* (Niessl in Rabenh.) Kuntze, Rev. Gen. Plant. 3: 505. 1898

Perithecia aggregated in small clusters, confluent at the base or occasionally solitary, superficial or rarely erumpent, slightly roughened, bare, ovoid to oblong, 700−1200 × 500−625 μm, red-brown to black, with an indistinct, black ostiolar region with a small, prominent ostiole at the apex; peridium dark yellow-brown by reflected light, thickened, coriaceous, appearing in surface view of indistinct cellular structure, 100−125 μm thick, consisting of three layers, an outer layer 1−2 cells thick, of oblong, somewhat thick-walled, brownish cells measuring 6−10 × 2−3 μm, a middle layer 80−100 μm thick, of noncellular gelatinous matrix sparsely interspersed with branching, thin-walled, hyaline hyphae measuring 1−1.5 μm in diameter, and an inner layer 5−6 cells thick, of oblong, thin-walled, brownish cells measuring 8−12 × 1.5−2 μm. Asci 4-spored, cylindrical, 265−310 × 21−28 μm, broadly rounded at the apices, tapering into a very long stipe measuring 100−225 μm; apical ring small, indistinct. Paraphyses abundant, filiform, septate, hyaline, longer than and mixed with the asci. Ascospores one-celled, obliquely uniseriate, surrounded by a hyaline gelatinous sheath reaching a width of about 5 μm, ellipsoidal or rarely slightly flattened on one side, narrowed towards the ends, 35−43 × 16−22 μm, ranging from hyaline when young to yellowish brown and opaque at maturity, containing at each opposing end of the spore a germ pore measuring 2−5 μm in diameter.

HABITAT: On hare and rabbit dung.

SPECIMENS EXAMINED: AUSTRALIA: VICTORIA: Glenburn, rabbit dung, VII.1966, *Dade* V532g (TRTC). CANADA: QUEBEC: NW Ungava: Payne Bay Post, ca. 60°N, 70°1′W, arctic hare dung, 15.VIII.1948, *Rousseau* 1393 (TRTC). CZECHOSLOVAKIA: MORAVIA: Brno, hare dung, autumn 1870, *Niessl*, Fungi europaei exsicc. 1340, as *Sordaria maxima* (FH, G, M, NY, S, TRTC, UPS, ZT), hare dung, 8.IX.1883, Rehm, Ascomyceten 744, as *Sordaria maxima* (FH, G, M, NY); Ratschitz, hare dung, VIII.1866, *Niessl*, as *Sordaria maxima* (M). SLOVAKIA: Prencow, Balov Kùt, hare dung, 21.IX.1897, *Kmet*, Fungi Schemnitzienses, under *Sordaria appendiculata* (BPI). FRANCE: SEINE-ET-MARNE: Fontainebleau, hare dung [as deer dung], *De Candolle*, as *Sphaeria stercoris* (G). GERMANY: BRANDENBURG: Berlin, Stolpe an der Nordbahn, hare dung, IX.1918, *Kirschstein*, as *Sordaria maxima* (B). POMERANIA: Rügen Is., Sellin, hare dung, VIII.1912, *Kirschstein*, as *Sordaria bombardioides* (B, TRTC), VII.1914 (B), 29.VII.1909 (B), 29.VII.1909 as *Hypocopra merdaria* (B). POLAND: SILESIA: Karlsbrunn, hare dung, *Niessl*, as *Sordaria fimiseda* and *Sordaria maxima*, but only the latter is present (M).

The diagnostic features of this species are the relatively large ascospores, the two distinct functional germ pores and the 4-spored asci. The only other species possessing 4-spored asci is *B. serignanensis*, which has much smaller ascospores with a prominent apical and less obvious basal germ pore.

In the type specimen of *Sphaeria stercoris*, the spores are largely immature. Fortunately, Lundqvist (1972) was able to find one mature ascocarp in which the ascospores compared favourably with those in the type of *Sordaria maxima*. Regrettably the slide, on which this observation was based, is no longer available at Geneva (G). Nevertheless, it is apparent from the appearance of the ascocarp and the young asci, which are obviously 4-spored, that *Sphaeria stercoris* is an older name for the organism previously known commonly as *Sordaria maxima*.

Among the collections cited above, the Canadian record, which was previously reported by Cain (1957) as *Sordaria maxima*, must be considered as dubious. In this collection, the ascocarps are similar to those in the type of *Sphaeria stercoris*, but the spores are all immature and smaller than in typical mature spores of the taxon. However, these immature spores compare favourably with young spores in other collections, including the type. Since the present record is the only one known from North America, we hesitate to report the species from this region. Nevertheless, we expect the organism to be circumpolar in distribution. In addition to the Australian record, this taxon also has been reported from the antipodes (New Zealand: Bell 1983; Chile: Muroi and Udagawa 1984; Argentina: Lorenzo 1992).

Discussion

We consider that morphologically the peridium consists of three continuous layers (Fig. 13). The outer melanized rind together with the partially gelatinous, hyphal-interspersed central layer are responsible for the coriaceous nature of the peridium. It is the opinion of Lundqvist (1972) that these two layers constitute stromatic tissue while only the innermost region of compact, thin-walled hyphae represents the true peridium. In addition he suggested that this morphology represented an archaic feature. On the contrary, we feel that hyphal continuity throughout all three peridial layers clearly shows that they constitute a single tissue. Although this tissue appears to be specialized, we believe that it is of common ontogenetic origin and thus nonstromatic. As Wehmeyer (1926) points out, a stroma is an aggregation of vegetative mycelium not resulting from sexual stimulus. In discussing stromata he states that the term should be applied in a broad sense to distinguish a type of mycelial differentiation rather than any particular morphological structure. He goes on to say that the definition excludes tissues arising as the result of sexual stimulus, such as the wall of the perithecium. This appears to exclude Lundqvist's (1972) interpretation that these outer layers of the peridium can be considered stromatic. A number of authors (Bell 1983; Muroi and Udagawa 1984; Lorenzo 1992) have followed Lundqvist's interpretation, which may not be supportable in the absence of developmental evidence.

In discussing the evolution of the Xylariaceae, Rogers (1979) emphasized that upright stromata appear to be adaptations to minimize desiccation of perithecia while providing for more efficient spore dispersal. Similarly, the elevated, thick-walled ascomata of *Bombardioidea* function in the same way by enhancing spore discharge and slowing ascomatal desiccation.

Lundqvist (1972) suggested that the carbonaceous, functionally stromatic, three-layered peridium represents an archaic feature. Whether this structural morphology is derived as in the Xylariaceae or archaic, we conclude that it is correlated to the superficial growth habit of these taxa as an adaptation to xerophytic environments. The coriaceous outer rind and the hygroscopic middle layer of the peridium function together to retain moisture and provide a buffer to desiccation while concomitantly affording a physical and possibly chemical deter-

rent to insect grazing. We have observed in dung cultures of *Bombardioidea* that ascospore liberation occurs primarily upon desiccation of the ascomata rather than upon hydration. Additionally, the asci of species of *Bombardioidea* are characterized by staggered maturation. Since *Bombardioidea* is a late successional stage dung-inhabiting fungus, most prevalent on very old, dry dung, ascospore ripening and discharge is likely accomplished by repeated cycles of hydration and drying as in many Xylariaceae (Rogers 1979). Similar observations have been made for other lignicolous pyrenomycetes inhabiting old, exposed, decorticated wood (W.A. Untereiner, personal communication).

Spore dispersal in *Bombardioidea* is likely accomplished through gut passage. This hypothesis is supported by the fact that these taxa have darkly pigmented, forcibly discharged ascospores with sticky gelatinous sheaths. Furthermore, the genus is not known to occur on decaying wood.

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