

THE TAXONOMIC STATUS OF *LOTOPHILA* LIOY,
WITH A REVIEW OF *L. ATRA* (MEIGEN)
(DIPTERA: SPHAEROCERIDAE)¹

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Abstract.—*Lotophila* Lioy, the senior objective synonym of *Olinea* Richards, is resurrected as a monotypic genus for *L. atra* (Meigen). A detailed redescription of *L. atra* is given and its phylogenetic relationship within the subfamily Copromyzinae is discussed. Information on its distribution and biology are compiled and a lectotype is designated.

Lotophila atra (Meigen) is a common coprophagous species in much of the Holarctic region. It is easily recognized from other Copromyzinae by the absence of an apical spur on the hind tibia and the presence of 4-5 pairs of stout marginal scutellar setae.

Originally described in the genus *Borborus* (Meigen, 1830), *L. atra* was confused for many years with the unrecognizable nominal species *Scatophora carolinensis* Rob.-Desv., *Olinea hirtipes* Rob.-Desv., and *Borborus geniculatus* Macquart. Duda (1923, 1938) and Richards (1930, 1961) largely clarified its taxonomic status, and Richards (1961) placed it in *Olinea* Richards, a monotypic subgenus of *Copromyza* Fallén (s. lat.). *Olinea*, however, is a junior synonym of *Lotophila* Lioy (1864), a genus proposed for *Borborus lugens* Meigen and a second, unrecognizable species, *B. punctipennis* Meigen. Richards (1930) designated *B. lugens* as the type species of *Lotophila*, however, Duda (1923) considered *B. lugens* a junior synonym of *B. ater* Meigen. After examining the type specimens of both nominal species we share this opinion, thus *B. ater* becomes the type of *Lotophila*, making *Lotophila* the senior objective synonym of *Olinea*.

Although recent workers have continued to treat *Olinea* as a subgenus of *Copromyza*, it is our opinion that *Lotophila* should be given generic rank in the tribe Copromyzini. *Lotophila* is the sister group of the genera *Gymnometopina* Hedicke, *Dudaia* Hedicke, and *Metaborborus* Vanschuytbroeck. All four taxa share three apomorphic characters of the male: 1) a triangular, convex sclerite, here termed the postphallic sclerite, present between the basiphallus and sternite 10; 2) the genital arch (fused epandrium and sternite 8) without lateral clefts; and, 3) clefts at least partially separating the cerci from the genital arch. *Gymnometopina*,

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Dudaia, and *Metaborborus* share several additional apomorphies: a narrow, posterior lobe on the median part of sternite 6 of the male; the male cerci completely separated from the genital arch; absence of the genal seta; and the arms of the male hypandrium narrow basally, not broad and triangular.

Here, we redescribe the genus *Lotophila* and *L. atra* and discuss its geographic distribution and infraspecific variation. We use the morphological terms of Kim and Cook (1966) and McAlpine (1981).

Genus *Lotophila* Lioy

(partim) *Borborus* auct.; Meigen, 1830: 198–209.

(nec) *Scatophora* Robineau-Desvoidy, 1830: 811 (fide Duda, 1938: 16).

(nec) *Olina* Robineau-Desvoidy, 1830: 812 (fide Duda, 1938: 15–16).

Lotophila Lioy, 1864: 1113 (Type-species: *Borborus lugens* Meigen, by designation of Richards, 1930: 264, = *B. ater* Meigen).

Borborus (*Olina*); Duda, 1923: 58, 99–101.

Scatophora; Spuler, 1925: 1–3.

Copromyza (*Olina*); Richards, 1930: 263–264, 315–316.

Borborus (*Borborus*); Duda, 1938: 35–36.

Copromyza (*Olinea*) Richards, 1961: 561–562 (Type-species: *Borborus ater* Meigen).

Description.—*Male*: Head—largely pruinose, length about equal to height; genal seta small; postocular setae in single row. Thorax—acrostichal setae in two complete rows; scutellum with four to five pairs of marginal macrosetae, all about equal in length except slightly larger apical pair (Fig. 5); katepisternum without macroseta on upper part. Legs—hind tibia without ventral apical spur or antero-ventral seta. Wing—cell dm elongate, crossvein dm-cu in apical third of wing; vein M reaching wing margin; vein Cu₁ ending short distance beyond dm-cu. Abdomen—sternite 8 and epandrium completely fused, no cleft in genital arch; hypandrial apodeme greatly reduced; cerci partly fused to genital arch; postphallic sclerite present between basiphallus and sternite 10; basiphallus with epiphallus greatly reduced. *Female*: Head, thorax, legs, and wing as in male. Abdomen—terminalia telescoped at rest; two spermathecae present, apodeme opposite duct opening small, its apex membranous.

Lotophila atra (Meigen)

Figs. 1–10

Borborus ater Meigen, 1830: 203.

Borborus modestus Meigen, 1830: 203 (fide Duda, 1923: 101).

Borborus lugens Meigen, 1830: 205.

(nec) *Scatophora carolinensis* Robineau-Desvoidy, 1830: 811 (fide Duda, 1938: 16).

(nec) *Olina hirtipes* Robineau-Desvoidy, 1830: 812 (fide Duda, 1938: 15–16).

(?) *Borborus geniculatus* Macquart, 1835: 567 (fide Richards, 1961: 562).

Lotophila lugens (Meigen); Lioy, 1864: 1113.

Olina ferruginea Becker, 1908b: 198 (fide Duda, 1938: 36).

Borborus (*Olina*) *geniculatus*; Duda, 1923: 99–101.

Scatophora carolinensis; Spuler, 1925: 1–3.

Copromyza (Olinea) hirtipes; Richards, 1930: 315–316.

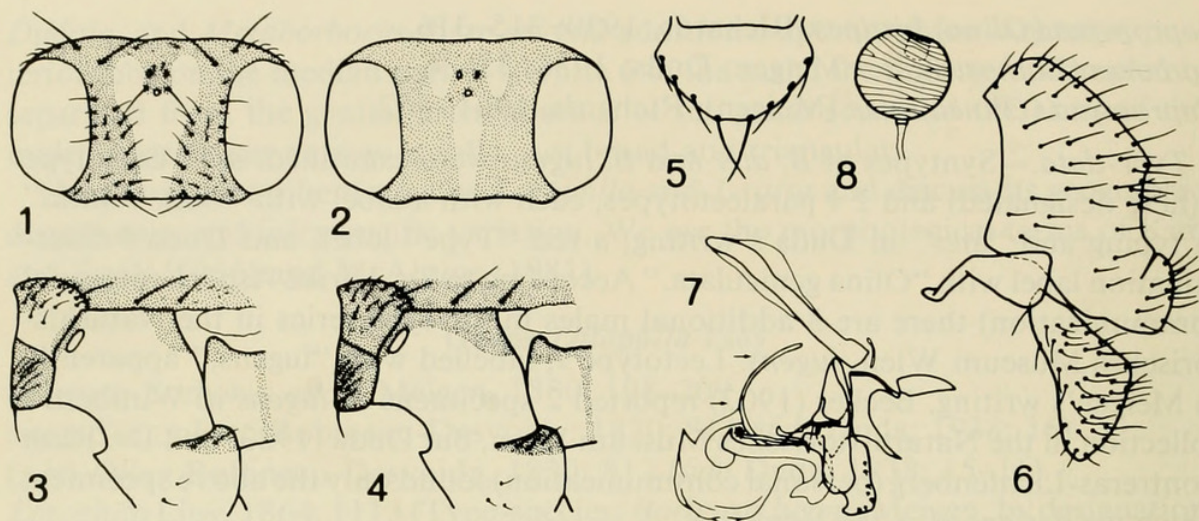
Borborus (Borborus) ater Meigen; Duda, 1938: 35–36.

Copromyza (Olinea) atra (Meigen); Richards, 1961: 562.

Type-data.—Syntypes of *B. ater* and *B. lugens* were examined. *ater*: Lectotype ♂ (here designated) and 2 ♀ paralectotypes, each with a label with “Coll. Winth.” in typing and “ater” in Duda’s writing, a red “Type” label, and Duda’s determination label with “*Olinea geniculata*.” According to Dr. Ulrike Aspöck (personal communication) there are 3 additional males in the type series in the Naturhistorisches Museum Wien. *lugens*: Lectotype ♀, labelled with “lugens,” apparently in Meigen’s writing. Becker (1902) reported 2 specimens of *lugens* in Winthem’s collection in the Naturhistorisches Museum Wien, but Duda (1923) and Dr. Ruth Contreras-Lichtenberg (personal communication) found only the above specimen, which we designate as the lectotype.

Description.—Mostly blackish species, about 2.5–4.0 mm long; in general, macrosetae relatively short and stout. *Male*: Head—gena bare of pruinosity except along anterior and ventral margins, height about $\frac{3}{5}$ of long diameter of eye; parafacials yellow; frons with entire anterior margin yellow, the rest blackish, pruinosity usually as in Fig. 1; arista pubescence 0.01–0.02 mm long. Thorax—proepisternum pruinose; postpronotal lobe usually with most of lateral portion bare of pruinosity; scutum pruinose, density sometimes varying, producing faint pattern of longitudinal stripes; one pair of dorsocentral macrosetae (prescutellars); anepisternum largely bare, usually as in Fig. 3; katepisternum bare except for posterior half of dorsal margin and narrowly along sternal suture; anepimeron with anterior $\frac{3}{5}$ bare; scutellum pruinose. Legs—femora dark red-brown to black, except at extreme base and apex, posterior side largely bare of pruinosity; tibiae same color as femora, base and extreme apex yellowish; fore coxa usually with basal $\frac{1}{3}$ – $\frac{1}{2}$ brownish, the rest yellow; mid tibia with two small anterior macrosetae at about $\frac{2}{5}$ and $\frac{2}{3}$, small posteroventral at about $\frac{2}{3}$, dorsal at about $\frac{7}{8}$, and whorl of 7–8 preapicals at $\frac{9}{10}$; hind tibia with small dorsal preapical at $\frac{9}{10}$; fore and hind metatarsi without apical spurs. Wing—length subequal to body length; r-m at about $\frac{2}{5}$ – $\frac{1}{2}$ distance from bm-cu to dm-cu; crossveins unbanded. Abdomen—sternite 5 very irregularly shaped, anteriorly with broad internal projection, more developed on left side; sternite 6 with large posterior projection on right tip; cercus fused to genital arch, but with cleft from posterior corner to middle (Fig. 6); surstylus somewhat triangular in lateral view, relatively flat; basiphallus (Fig. 7) with very small epiphallus and sharply pointed pre-epiphallus arising at about its middle; distiphallus very complex, with numerous hooklike structures and long, thin, dorsal projection medially; paramere also complex, bilobed. *Female*: Head, thorax, legs, and wing as in male. Abdomen—tergite 5 narrow, about $\frac{3}{10}$ – $\frac{2}{5}$ as wide as syntergite; sternite 2 usually 1.5–2 times as wide as sternites 3 and 4; sternite 4 usually very weakly sclerotized; sternite 5 about $\frac{1}{4}$ – $\frac{1}{3}$ as wide as syntergite; tergites 6 and 7 and sternites 6 and 7 weakly sclerotized; intersegmental sections of terminalia with 3 lightly sclerotized longitudinal bands; spermatheca relatively small, surface sculptured with concentric rings, duct opening with small external collar (Fig. 8).

Biology.—Adults of *L. atra* have been found on dung of horses, cows, sheep, dogs, man, and pigs, as well as on carrion and decaying fungi (Howard, 1900;



Figs. 1-8. *Lotophila atra* (Meigen). 1,3,5,8, ♀, State College, Pennsylvania. 2,4, ♂, 10 mi. E. Toluca, Mexico. 6,7, ♂, Auburndale, Massachusetts. 1-2, Head dorsal view. 3-4, Anepisternum. 5, Scutellum. 6, Outer male genitalia, lateral view. 7, Inner male genitalia, lateral view. 8, Spermatheca.

Richards, 1930; Coffey, 1966). Only cow dung has been reported as a suitable substrate for larval development (Laurence, 1954, 1955; Schumann, 1962; Coffey, 1966; Poorbaugh et al., 1968; Papp, 1971), although considering the distribution of *L. atra*, other materials may also be utilized. We collected numerous individuals on a deer carcass in Rothrock State Forest, Pennsylvania, several miles from the nearest farms. Nevertheless, although we were able to rear *L. atra* on cow dung, females failed to oviposit in rotting mushrooms, decaying meat, carrion from a dead groundhog, and CSMA medium (putrifying mixture of wheat bran and alfalfa meal). Laurence (1954, 1955) studied the ecology of cow dung communities and reported seasonal variation in the abundance and time of development of *L. atra*. Females appear to prefer fresh cow dung for oviposition, as they are found on it much less commonly once it has begun to crust. The eggs are usually laid in crevices or on the underside of the dung. Adults of both sexes commonly rest on nearby grassblades and other low vegetation, typically near the top. As with many sphaerocerids, when disturbed, they will often crawl down into the vegetation rather than fly away. We have observed mating pairs on the nearby vegetation and on the cow dung itself.

Lotophila atra is sometimes terricolous, occurring in mouse runs, rabbit holes (Richards, 1930), and rodent burrows (Hackman, 1963). It also has been taken in soil traps (Papp, 1976; Roháček, 1980). Richards (1930) recorded it throughout the year in Britain and it apparently is multivoltine in central Pennsylvania.

Lotophila atra may be dispersed by jet streams, as Glick (1960) collected it in an airplane trap at 500 ft. in Illinois. Dave Reling (personal communication) has also taken it in an airplane net at 500 ft. over State College, Pennsylvania.

Schumann (1961, 1962) described the egg and larval stages of *L. atra* and Laurence (1954) reported *Pentapleura pumilo* Nees (Braconidae) as a parasitoid in England. Phoretic mites are uncommon on *L. atra*, although numerous histiotomatid hypopi were present on two males and three females examined from California (CAS, CNC) and on a female from Washington (WSU).

Intraspecific variation.—A few examined specimens exhibited an interesting pattern of variation in several characters. The series from Mexico differs from

typical *L. atra* in the color of the fore coxa, which is almost completely brownish, and in pruinosity, with the bare area on the frons divided (Fig. 2), the postpronotal lobe completely pruinose, and the pruinose area on the anepisternum larger (Fig. 4). In the females, abdominal sternite 2 is no wider than sternite 3, and sternite 4 is as strongly sclerotized as the other sternites. In the males, the genitalia are almost identical to typical *L. atra*, but the marginal hooklike structures on the distiphallus are located at the base of the dorsal projection (same level as lower arrow, Fig. 7) and the posterior corner of the surstylus tends to be more acute in lateral view. Two males from Arizona appear to fit into a cline between the Mexican populations and typical *L. atra*. They resemble the Mexican specimens in all but anepisternal pruinosity, which is normal (Fig. 3). A male from Tibet also closely resembles the Mexican specimens except that the marginal hooks on the distiphallus are even higher on the dorsal projection (same level as upper arrow, Fig. 7) and the surstylus is not as acute posteriorly. Since similar variation apparently occurs independently in these widely separated populations, we regard them both as conspecific with typical *L. atra*.

Distribution.—*L. atra* occurs in most of the middle latitudes of the Holarctic region, extending further north in maritime areas, and further south at high elevations. Palearctic records include the Canary Islands (Becker, 1908a; Frey, 1958), the Madeira Islands (Becker, 1908b), the Azores (Hackman, 1960), the Faeroes, England, Scotland, Wales (Richards, 1930), Finland (Hackman, 1965), U.S.S.R.: Estonia and Latvia (Hackman, 1972), France (Séguy, 1934), Spain (Strobl, 1900), the Pyrenees, Corsica (Duda, 1923), the Balearic Islands (Papp, 1973b), Czechoslovakia (Roháček, 1978), Hungary (Papp, 1971), Rumania (Richards, 1930), Greece (Vanschuytbroeck, 1962), Afghanistan (Richards, 1962), U.S.S.R.: Tadzhikskaya (Papp, 1979), Mongolia (Papp, 1973a), and U.S.S.R.: maritime region near Vladivostok (Petrova, 1968). Among the Palearctic specimens examined, only the one from Tibet noticeably extends the known range. In the Nearctic region *L. atra* occurs from Newfoundland south to Florida, west through the midwest and Great Plains, and throughout the west from British Columbia to California. It seems rare in the southeastern United States, but probably occurs throughout the northern and central mountains of Mexico.

Material examined.—726 specimens including 367 ♂ and 359 ♀. We list only those specimens of distributional or ecological significance; a complete list is available from the authors upon request. Lectotype, 2 paralectotypes of *ater*; lectotype of *lugens*; NORWAY: Bergen, 11.v.1922, 1 ♂ (UTA); SWEDEN: Pr. Jemtland, Aare, 16.vii.1929, 1 ♂ (USNM); SPAIN: Calicia Pontevedia, 23.viii.1979, 1 ♂ (USNM); SOVIET UNION: Zlatoust, Ufa, 27.viii.1927, 2 ♂ (USNM); CHINA: Yu-Long-Gong, Tibet border, 14,000 ft., 14.viii.1930, 1 ♂ (USNM); CANADA: BRITISH COLUMBIA: Bowser, 22.vi.1955, 1 ♀ (CNC); ONTARIO: Ottawa, Rockcliffe, "at bleeding maple," 20.iv.1955, 1 ♂ (CNC); NEWFOUNDLAND: Port Saunders, 6.viii, 1 ♂ 5 ♀ (AMNH); U.S.A.: WASHINGTON: Blue Mts., 8–11 mi. S. of Cloverland "reared from cow excrement," 30.vi.1956, 4 ♂ 6 ♀ (WSU); Colfax, "on pig excrement," 12.vii.1956, 1 ♂ (WSU); Pullman, "on pig excrement," 17.viii.1955, 1 ♀ (WSU); CALIFORNIA: Inyo Co., White Mts., 3100 m, 26.v.1973, 1 ♂ (CAS); Madera Co., Green Mt., 7600 ft., 20.viii.1971, 1 ♀ (CAS); Marin Co., Mill Valley, 25.ix.1965, 1 ♂ (CAS); San Diego Co., Rincon, 24.v.1937, 2 ♂ 1 ♀ (CAS); ARIZONA: White Mts., Coulter Ranch, 28.vi.1947, 1 ♂ (USNM); Alpine,

23.vi.1947, 1 ♂ (USNM); COLORADO: Electra Lake, 8400 ft., 29.vi.1919, 1 ♂ (USNM); MINNESOTA: Itasca St. Pk., 25.vi.1960, 3 ♂ (FEM); INDIANA: Lafayette, "on human excrement," v.1918, 1 ♂ (USNM); NEW HAMPSHIRE: Mt. Washington, 4800 ft., 14.vii.1958, 3 ♂ 1 ♀ (CNC); NEW YORK: Cold Spring Harbor, 2.vii.1931, 1 ♂ (ANSP); PENNSYLVANIA: Centre Co., "reared ex. cow dung," 15.v.1982, 7 ♂ 12 ♀ (FEM); State College, "airplane net at 500 ft.," 4.ix.1981, 1 ♂ (FEM); Mifflin Co., Rothrock St. Forest, "on deer carcass," 28.iv.1982, 4 ♂ 7 ♀ (FEM); WASHINGTON, D.C.: "on human feces," 16.v.1899, 1 ♂ 1 ♀ (USNM); NORTH CAROLINA: Swain Co., Mt. Collins, 5900 ft., "carrion," 17.v.1972, 1 ♂ 4 ♀ (SMC); TENNESSEE: Sevier Co., Gatlinburg, "carrion," 17.v.1972, 3 ♂ 2 ♀ (SMC); ARKANSAS: Washington Co., 26.iv.1969, 1 ♀ (UAF); GEORGIA: Black Rock Mt. St. Pk., 4.vii.1953, 1 ♀ (UTA); FLORIDA: Citrus Co., "cave," 25.vii.1895, 1 ♀ (USNM); MEXICO: Hidalgo, 10 mi. W. of Huachinango, 6650 ft., 22.viii.1962, 1 ♀ (KSU); Popocateptl, 12,000 ft., 11.viii.1936, 1 ? (USNM); Mexico, 10 mi. E. of Toluca, 8900 ft., 31.vii.1954, 6 ♂ 4 ♀ (CNC).

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