

The *Drosophila funebris* Species Group in North America (Diptera: Drosophilidae)

DAVID A. GRIMALDI¹

ABSTRACT

Although the global human commensal *Drosophila funebris* (Fabricius) is well known and is the type species of the genus *Drosophila* Fallén, the four native North American species of the *funebris* group have been poorly defined morphologically. *D. macrospina limpiensis* Patterson and Wheeler is newly recognized as a species distinct from *D. macrospina*, with diagnostic morphological characters provided. The subspecies *D. macrospina ohioensis* Stalker is synonymized under *D. macrospina*. Species native to the Palearctic and to the Nearctic are morphologically distinct, each probably a monophyletic group. Detailed descriptions and redescriptions are provided for both sexes of *D. macrospina* Stalker and Spencer, *D. limpiensis* Patterson and Wheeler, *D. subfunebris* Stalker and Spencer, and *D. trispina* Wheeler, the latter two being very rare species from southern California. Neotypes are designated for *D. macrospina* and *D. subfunebris*. A key to the five Nearctic species of the *funebris* group is provided.

INTRODUCTION

The naming and description 234 years ago of the original species of *Drosophila*, *funebris* (originally within *Musca*), by Linneaus' great student Johann Christian Fabricius (1745–1808), is not merely coincidence. The species is a global human commensal fond of a wide array of human landscapes, including stables, farms, and all sorts of human refuse. Doubtless it was everywhere in Denmark where Fabricius was a professor. Another global commensal, *Drosophila melanogaster*—equally widespread and in even larger numbers, but preferring

¹ Division of Invertebrate Zoology, American Museum of Natural History.

decaying fruits—was not described by Johann Meigen until 43 years later, well before it became the darling of experimental biology in the early 20th century. If *melanogaster* had been described first, then the current taxonomic situation in *Drosophila* may have been very different.

The genus *Drosophila* as currently recognized is polyphyletic, the main subgenera, *Drosophila* and *Sophophora*, not particularly closely related (Throckmorton, 1975; Finet et al., 2021). If classifications should reflect phylogenetic relationships—which biologists generally agree should be the case—this presents a conundrum. Do we call just the subgenus *Drosophila* as the genus *Drosophila*, and *melanogaster* becomes *Sophophora melanogaster*? Or do we transfer the name and concept of what is currently the subgenus *Sophophora* to be the new, revised version of the genus *Drosophila*? Or do we just continue to use the genus name *Drosophila* for both of these subgenera, with an understanding that they are not sister taxa? Whatever the outcome, *Drosophila funebris* as a type species is consequential to any concept of a genus *Drosophila*. In this regard, an understanding of its close relatives in the *funebris* group is significant. This study clarifies several aspects of the native North American species of the group, two of which are very rare and hardly known.

METHODS AND MATERIALS

Preserved specimens in the AMNH were studied along with newly preserved material from cultures provided by the *Drosophila* Species Center (DSC), formerly at the University of California, San Diego (now at Cornell University, Ithaca, New York). Cultures were the following: “*macrospina limpiensis*,” culture no. 15120-1921.00, from Patagonia, Arizona; “*macrospina macrospina*,” 12120-1931.02, from Sonora, Mexico; and *funebris*, 15120-1911.01 from Mexico City, Mexico. Culture no. 15120-1931.03, from Austin, Texas, which was received from the DSC but was misidentified, being actually *Drosophila melanica*. AMNH material includes the collection of the late Marshall R. Wheeler who was at the University of Texas, Austin, the author’s collections, and those of others.

Point-mounted specimens were measured and photographed using a Nikon SMZ1500 stereoscope and Elements® software. Proportions of head and setation used standard measurements and ratios (e.g., Bächli et al., 2004). Male and female terminalia were macerated in 10% KOH, rinsed in water and dilute HAc, disarticulated in glycerine, and slide mounted in glycerin jelly for study at 100-400× using a Nikon Eclipse compound scope.

Repositories of type specimens and sources of cultures are cited under the species treatments, abbreviated as the following:

AMNH, American Museum of Natural History, New York, New York

DSC, *Drosophila* Species Center, Cornell University (formerly at the University of California, San Diego)

NMNH National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

THE *DROSOPHILA FUNEBRIS* SPECIES GROUP

Drosophila funebris group: Sturtevant, 1942: 31 (diagnosis, classification); Patterson and Stone, 1952; Bächli et al., 2004.

DIAGNOSIS: Species with dark brownish to red-brown thorax and head; abdominal coloration dimorphic (tergites in males with more extensive, darker pigmentation). Male: Epandrium and cerci completely lacking microtrichia; ventral epandrial lobe very small, bearing several small, stout setae (these short and thornlike in Old World species; slender, spinelike in New World species); male cerci with stout, heavy spines on ventral portion (most of the mesal margin in *funebris*).

IMMATURES AND BREEDING SITES: Eggs with four fine filaments (known for *limpiensis*, *macrospina*, *multispina*, *subfunebris*, and *trispina*). Larval stages and puparia described for *D. funebris* and *D. multispina* (Okada, 1968), and the puparia described for *D. macrospina* and *D. limpiensis* (Patterson, 1943). Species of the *funebris* group have been caught at decaying fruits and in vinegar traps, at sap fluxes, on macrofungi, usually in forested habitats (Werner et al., 2020a, 2020b; Miller et al., 2017; see individual species, below).

MATING BEHAVIOR: Studied by Spieth (1952) for five of the North American species (*Drosophila funebris*, *limpiensis*, *macrospina*, *subfunebris*, and *trispina*) and by Ewing (1979) for all of these except *trispina* but including the Old World species *multispina* Okada. Spieth (1952) stated that courtship and copulation among species “is relatively uniform and conforms to the basic pattern found in the subgenus *Drosophila*,” although courtship is “reminiscent” of the *quinaria* group and male aggressiveness to that in the *virilis* group. Ewing (1979) studied the male courtship songs (see below, under *limpiensis*).

SPECIES INCLUDED:

altukhovi Imasheva et al., 1994: Daghestan. Type locality (TL): Makhachkala, Republic of Daghestan.

funebris (Fabricius, 1787): worldwide (originally Palearctic). TL: Copenhagen, Denmark.

limpiensis Mainland, 1941: southwestern North America. TL: Limpia Canyon, Texas.

multispina Okada, 1956: China, Far East Russia, India, Japan. TL: Sapporo, Hokkaido, Japan.

macrospina Stalker and Spencer, 1939: eastern North America. Neotype locality: New Orleans, Louisiana.

pentaspina Parshad and Duggal, 1966: Jammu and Kashmir, India. TL: Srinigar, Kashmir Valley, India.

subfunebris Stalker and Spencer, 1939: California, United States. Neotype locality: Pasadena, California.

trispina Wheeler, 1949: California, United States. TL: near Earp, California.

It is interesting that half the species are poorly known, presumably localized species, while *Drosophila funebris* is a widespread invasive. *Drosophila macrospina*, *limpiensis*, and *multispina* have larger distributions than the four rare species that are known just from their type localities. *Drosophila trispina* and *subfunebris* are among the rarest drosophilids in North America.

Okada (1956) originally included *Drosophila maculinotata* in the *funnebris* group because of the spines on the cercus, but this species is certainly not within this group based on the structure of the spermathecae, female and male internal reproductive organs; deep cheeks, and various other features. Additional species in the group will probably be found in southern China and the Himalayan region; it is unlikely that new species will be found in North America.

The four species native to the Palearctic can morphologically be defined as a monophyletic group based on the short, thornlike setae on the ventral epandrial lobe in the male (Bächli et al., 2004; Imasheva et al., 1994; Okada, 1956; Parshad and Duggal, 1966). The native Nearctic species all have the derived features of serrate preapical lateral lobes on the aedeagus and a very distinctive pair of serrate apical lobes that articulate with the apex of the aedeagus, as described herein. Thus, there appears to be two lineages in the species group, one Palearctic and another Nearctic, each with four species.

RELATIONSHIPS WITHIN DROSOPHILA: Molecular and morphological evidence agrees that the *funnebris* group is within the *tripunctata* radiation sensu Throckmorton (1975), although Throckmorton indicated a relatively isolated position for *funnebris* within the subgenus *Drosophila*. Morphological features supporting placement in the “tripunctata radiation” are the following: Internally, male ejaculatory bulb with a pair of diverticula, vas deferens with a common stem; and female with ventral receptacle highly coiled (Okada, 1956; Throckmorton, 1962). Externally: anterior reclinate orbital seta between the proclinate and posterior reclinate orbital setae (vs. lateral to proclinate or nearly so); two strong pairs of vibrissae; microtrichia reduced to entirely lost on epandrium and cerci.

There is molecular disagreement as to whether the *funnebris* group is most closely related to the *testacea* group (Robe et al., 2005; Russo et al., 2013), or to the large Holarctic *quinaria* group (Robe et al., 2010; Morales-Hojas and Vierera, 2012). Finet et al.’s (2021) molecular analysis indicates that the *funnebris* group is closely related to a group comprised of *Drosophila testacea* + *macroptera* + *bizonata* + *histrio*, and this collectively is the sister group to the *quinaria* group. Morphological evidence agrees best with the molecular study by Izumitani et al. (2016), that the *funnebris* group is sister group to the rest of the *tripunctata* radiation after the *immigrans* species group. This is based on the plesiomorphic absence in the *funnebris* and *immigrans* groups of a scoop-shaped “dorsal arch” between and articulating with the two ends of the posterolateral arms of the hypandrium (a distinctive structure present in the *quinaria*, *testacea*, *tripunctata*, and most other groups of the radiation).

Drosophila funnebris (Fabricius)

Figure 9A

Musca funnebris Fabricius 1787: 345.

Drosophila funnebris (Fabricius): Type species of genus *Drosophila*. Patterson, 1943 (redescription, internal reproductive organs, immature stages, chromosomes, North America distribution); Bächli et al., 2004 (redescription, European distribution); Miller et al., 2017 (redescription, genitalia, eastern North America distribution); Werner et al., 2020a, 2020b (identification, biology).

DIAGNOSIS: Easily distinguished from other Nearctic species of the *funebis* group by the numerous spines, ~12, on the male cercus along the mesal margin (vs. 4–6 in native Nearctic species), and by the short, thornlike setae on the epandrial lobe (vs. slender, spinelike setae); female with oviscapt having dorsal knob (vs. without) (fig. 9A).

DESCRIPTION: A detailed description was provided by Bächli et al. (2004) and others (above).

DISTRIBUTION: A worldwide species found in close association with humans and their domestic animals, and distinct from native North American species by its tolerance of cold; *funebis* is absent from hot, lowland tropics. The species is present in Iceland and Greenland, and is widespread in Scandinavia, occurring as far north as Longyearbyen, Spitzbergen Island, Norway, 66°19'9.8" N, no doubt surviving the coldest months within human dwellings (Bächli et al., 2004). It occurs throughout North America, including Texas and northern Mexico, but is more prevalent in cooler climates and higher altitudes (Patterson and Wagner, 1943). Northern limits of its distribution in North America are not well explored, especially the western portion, including Alaska. In the east *D. funebis* is recorded from southern Québec, Nova Scotia, eastern Newfoundland, and generally in southern Ontario to ~200 km SW of James Bay at about 52° N (Miller et al., 2017), although it probably occurs even farther north.

Drosophila macrospina Stalker and Spencer, 1939

Figures 1B, 2B, 3A–D, 4B, 5B, C; 6C, D, I; 7A, B, 8B–D, 9C

Drosophila macrospina Stalker and Spencer, 1939: 110. Subsequent refs: Mainland, 1942 (hybrid sterility); Patterson, 1943 (redescription, internal reproductive organs, immature stages, chromosomes); Patterson and Wagner, 1943 (distribution); Patterson and Stone, 1952 (distribution); Miller et al., 2017 (identification, eastern distribution); Werner et al., 2020a, 2020b (identification, biology);

Drosophila macrospina ohioensis Spencer, 1940: 304. NEW SYNONYM.

DIAGNOSIS: Very similar to *Drosophila limpiensis*. Postocellar setae slightly to strongly convergent to crossing; male with lateral lobes of distiphallus broader and more protruding than in *D. limpiensis* (especially at the apex); apical lobes with more lateral serrations; large gap between largest (dorsalmost) cercal spine (1) and next one (2) (gap is ~width of spine 2, vs. with barely any gap); ventral epandrial lobe with 4–5 small setae (vs. 2 thick ones in *limpiensis*). Female: oviscapt dark, sclerotized as in *limpiensis*. No distinction between the two species is apparent in the surstyli or female terminalia.

DESCRIPTION: Body size, ThL 1.12 mm (0.92–1.30); wing length, 2.25 mm (1.95–2.74). **HEAD:** significantly broader than deep HW/HD 1.39; frons short, FL/LFW 0.74 (0.69–0.82), UFW/LFW 1.39 (1.30–1.51). Eye dull, light red, with dense ommatrichia, proportions in lateral view ED/EW 1.26 (1.16–1.34). Frons, face, antennae dull, pollinose, light brown; frontal-orbital plates and ocellar triangle slightly shiny, FOPs (frontal-orbital plates) and carina lighter. Frons

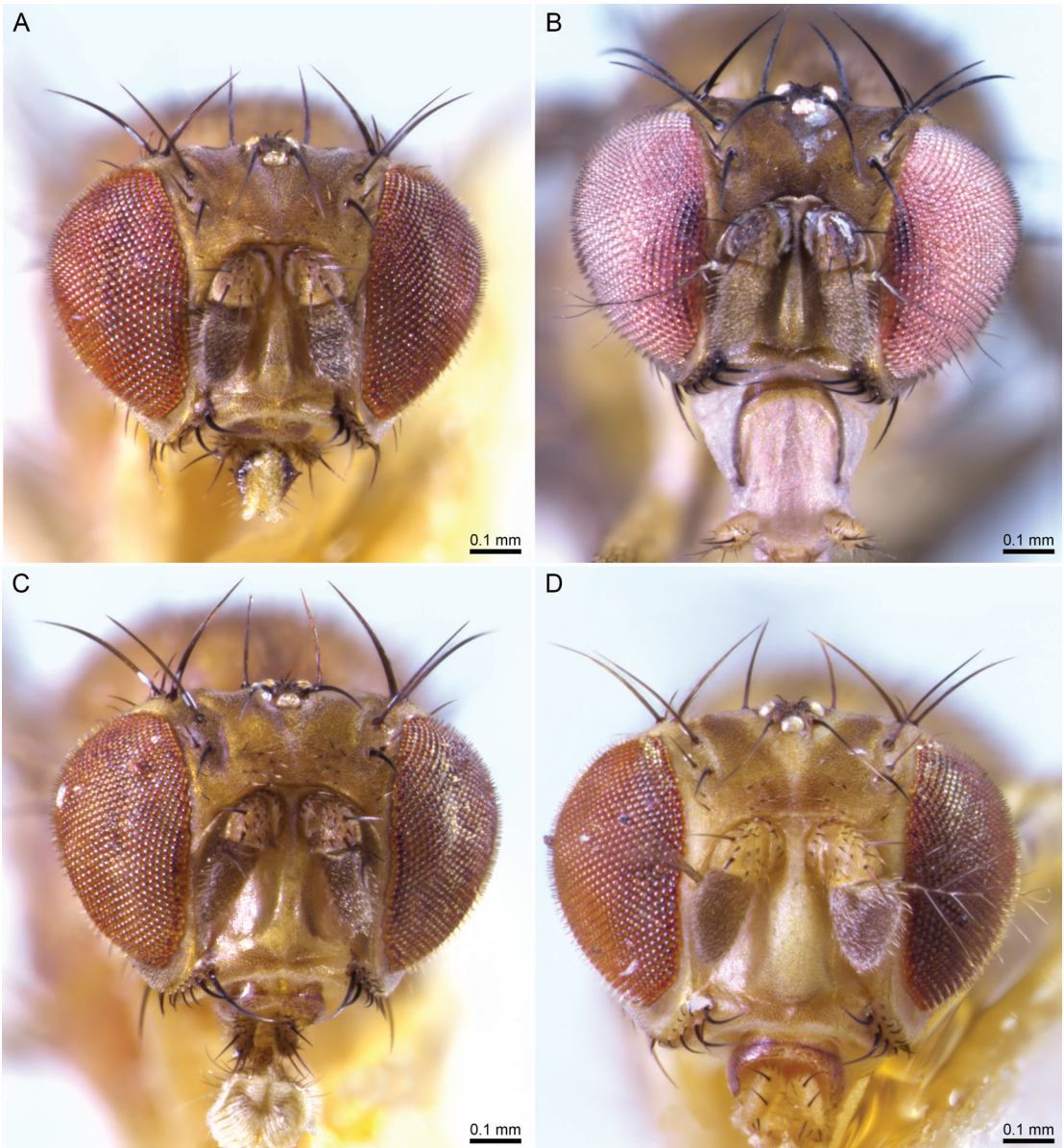


FIG. 1. Heads, frontal views, of native North American species of the *Drosophila funebris* group. **A.** *D. limpiensis* (ex: type locality: Limpia Canyon, Texas). **B.** *D. macrospina* (ex: Rochester, NY). **C.** *D. subfunebris* (ex: type series: Pasadena, CA). **D.** *D. trispina* (ex: type series: Earp, CA). To the same scale.

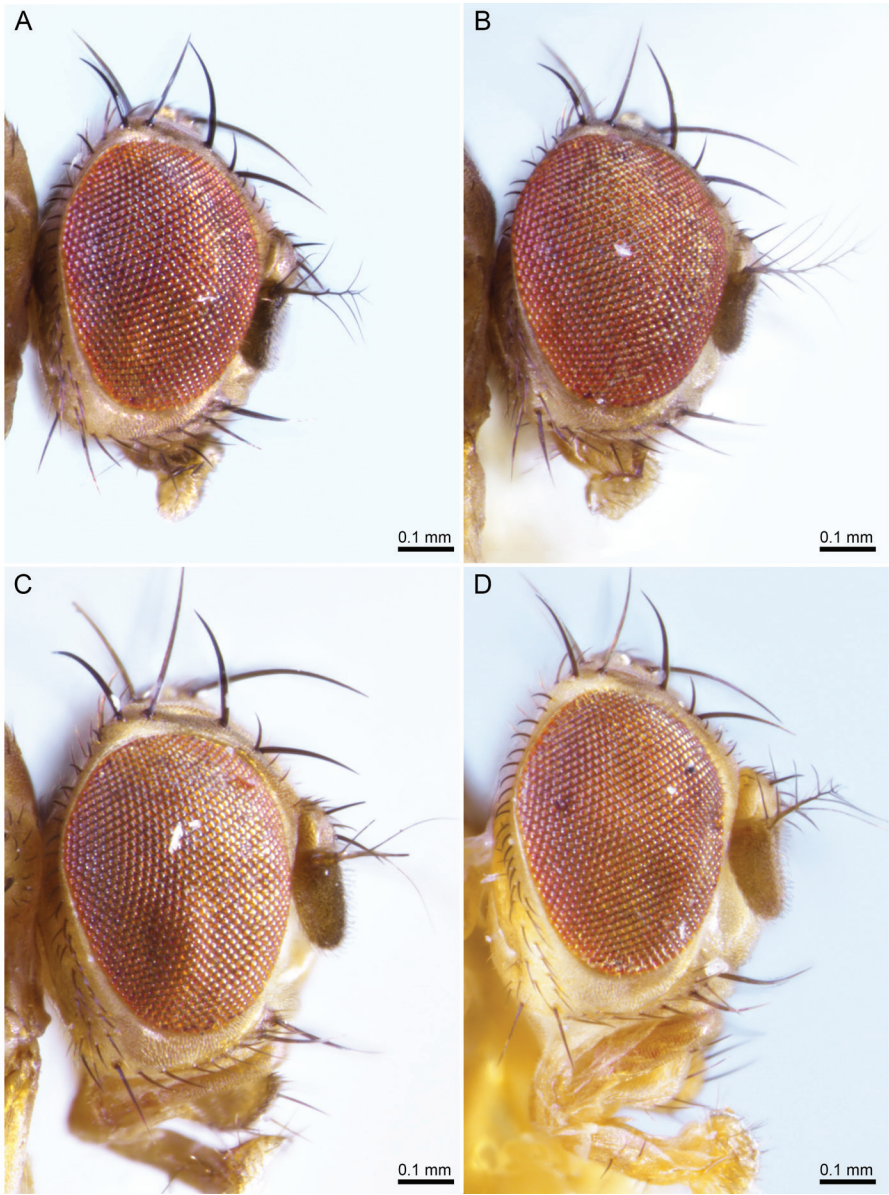


FIG. 2. Heads, lateral views, of native North American species of the *Drosophila funebris* group. **A.** *D. limpiensis* (ex: Limpia Canyon, TX). **B.** *D. macrospina* (ex: Piqua, OH). **C.** *D. subfunebris* (ex: Pasadena, CA). **D.** *D. trispina* (ex: Earp, CA). To the same scale.



FIG. 3. *Drosophila macrospina* thorax and abdomen (all ex: Rochester, NY). A. Head and thorax, dorsal. B. Thorax, lateral. C. Abdomen, male. D. Abdomen, female.

with small, scattered setulae on anterior half. Proclinate parallel, shorter than posterior reclinate. Ipsilateral proclinate, posterior reclinate, and inner vertical in line. Anterior reclinate posterolateral to proclinate, closer to proclinate than to posterior reclinate. Posterior reclinate slightly divergent. OR_1/OR_2 2.32 (1.8–2.8); OR_1/OR_3 0.69 (0.62–0.82). Inner verticals strongly inclinate, outer verticals strongly pointed posterolaterad; verticals nearly equal in length, VT-index 0.97 (0.92–1.07). Postocellars very strong, slightly convergent to strongly convergent and even cruciate for $\sim 0.5\times$ their length. Ocellar setae long, tips reaching slightly past ptilinal suture; setal sockets lie between anterior and posterior ocelli. Antennal pedicel with 2 larger setae (1 proclinate, 1 laterocline), plus ca. 12 smaller setulae; pedicel without long, fine setae on mesal surface; basal flagellomere with fine setulae short; arista with 4–5 dorsal and 3 ventral branches. Carina narrow, CL/CW 5.33 (3.6–6.5), edge slightly flattened, lying below level of flagellomere 1. Two pairs strong vibrissae present, vibrissa longer than subvibrissa, vibrissa-index 0.77 (0.65–0.88); 7–8 small setae on cheek, anterior margin of cheek darker; cheek shallow, ED/CD 8.90 (6.85–10.8). Clypeus U-shaped, shiny. Palp yellowish, asymmetrical, ventral margin convex, with 2–3 longer setae; dorsal margin flat. Mentum dark yellow, shiny, with ~ 10 long, fine setae. Labellum with 8–9 pseudotracheae. Occiput dark yellow and light brown.

THORAX: ThL males 1.06 mm (0.89–1.15 mm; $N = 9$), ThL females 1.29 mm (1.24–1.40 mm; $N = 4$). Scutum and scutellum light brown (centrally lighter for scutum), faintly pollinose, dull not shiny; pleura slightly lighter, especially katapisternum. Acrostichals in 8 rows between dorsocentrals; anterior to dorsocentral is row of 4–5 acrostichals slightly thicker and longer than others; transverse row of ~ 4 acrostichals $1.4\text{--}2.0\times$ length of others anterior to transverse suture. 2 postpronotal setae, lower one larger than upper, h-index 0.82 (0.76–1.0), thinner than notopleurals; 3 notopleural setae, 2 at ventral edge of notopleural suture, posterior seta short. Supraalar setae: 1 short, 1 long; 2 large katapisternal setae, anterior one significantly shorter than posterior dc, S-index 0.68 (0.62–0.75), with small seta between them and a vertical row of ~ 10 small setulae. Dorsocentral setae: large, well developed, anterior pair significantly shorter than posterior pair, DC-index 0.65 (0.51–0.70); scutellum with anterior pair of setae slightly shorter than posterior, Scut-index 0.91 (0.86–0.94), posterior scutellars slightly to strongly convergent. Legs yellow; fore femur with 3–4 long ventral setae, 1 fine, preapical dorsal seta; male fore tarsus without longer, erect, recurved setulae. Mid tibia with thick ventroapical seta, shorter preapical dorsal seta; hind tibia with 1 fine preapical dorsal seta. Wing: relative to body size, WL/ThL 2.00 (1.85–2.18); relatively broad, WL/WW 2.19 (2.11–2.23); C-index 2.98 (2.65–3.30); hb-index 1.96 (1.70–2.23); 4V-index 1.53 (1.41–1.62); distance of crossvein dm-cu from wing margin, 5-X-index 1.25 (1.08–1.42). Halter light.

ABDOMEN: Pigmentation sexually dimorphic; male tergites almost entirely dark blackish brown, shiny, with faint lighter areas in middle of tergites 1–3; epandrium and cerci lighter; sternites light. Female tergites with dark band on posterior half of each segment, anterior half light; dark band on tergites 2–4 with slightly median interruption, tergite 6 with middle of dark band enlarged; tergites 7, 8 light, yellowish, paraprocts slightly darker; oviscapt dark, especially at base.

MALE TERMINALIA: Epandrium lightly sclerotized, devoid of microtrichia, short and somewhat flattened (not capsulate); dorsolateral phragma well developed; ventral lobe small, closely pressed to surstylus, with 4–5 short, stout setae at apex. Cerci well developed, projecting well beyond margins of epandrium, lacking microtrichia, with many long setae; ventral margin with 3 heavily sclerotized spines, 3 smaller ones ventrally (sometimes 2), a large one apically (twice the size of other 2); no gaps between smaller spines; gap between smaller and large spine large, $\sim 1.5\times$ thickness of large spine. Surstylus well developed, with row of 9–10 peglike prenisetae, 8–14 thick setulae laterally. Hypandrium well developed, lightly sclerotized, anterior end narrowed to $\sim 0.60\times$ width of posterior end; gonopods (postgonites/paraphyses) with longer seta posteriorly, small seta ($\sim 0.5\times$ the length) mesally; inner lobe of gonopod more sclerotized; pair of narrow sclerites attached to posteromedial corners of hypandrium, not connected in middle. Aedeagus with slender neck of uniform thickness, moderately arched in lateral view; apex with medial lobe (roughly triangular in shape), pair of lateral, winglike lobes, and pair of serrate, apical lobes. Lateral lobes with fine scales/serrations on lateral margins and at base near neck; these lobes hardly sclerotized; “wingspread” $5.0\times$ (mean) thickness of aedeagal neck (range 4.3–6.0). Distal pair of lobes of aedeagus flattened, with irregular teeth/serrations on lateral, mesal and apical margins, ones on apex largest (generally 2–3 very large teeth). Aedeagal apodeme sclerotized, straight, slightly shorter than aedeagus. Ejaculatory apodeme small, bent at right angle, both arms approximately equal in length.

FEMALE TERMINALIA: Oviscapt heavily sclerotized (especially at base), with ~ 30 small, densely spaced marginal pegs, plus 3–4 discal ones; oviprovectator membrane with sparse, fine scales. Spermathecal capsule heavily sclerotized, no exterior microtexture, with introvert reaching almost to apex; inserted portion of spermathecal tube sclerotized.

TYPES: Neotype, male: United States: Louisiana: 0.5mi E Miss. River, New Orleans, VI/12/41, 1112.6, GB Mainland, MR Wheeler/M.R. Wheeler, W.K. Baker/Neotype, *Drosophila macrospina*, det. D. Grimaldi, 2022. Dissected by D.A.G., in AMNH. Stalker and Spencer (1939) mentioned that the original, type culture, established from a female collected on fungus and from which “type and gonotypes” were made, was from Austin, Texas. As for *D. subfunbris* (below), no types of *macrospina* occur in the AMNH, NMNH or other institutions, so a neotype is designated here. Specimens from the published type locality were not available.

SPECIMENS EXAMINED: All in AMNH. United States: Arkansas: Logan Co., Magazine Mtn., 2750 ft., D. Grimaldi, Collected on 9/VI/92 at 2200' with banana bait, 1M (dissected). Georgia: Crooked River State Park, VI/28–VI/29/53, WB Heed, MR Wheeler; Liberty Co., St. Catherine's Is. 11-20/IV/88, D. Grimaldi, 4M, F (1M dissected). Louisiana: .5mi E Miss. River, New Orleans, VI/12/41, 1112.6, GB Mainland, MR Wheeler/MR Wheeler, WK Baker. 7 M, F (1 M dissected). Mississippi: Claiborne Co., VI/5/50, H.D. Stalker, W.P. Spencer (1F). Missouri: Webster Groves, IX/50, H.D. Stalker, W.P. Spencer (1M, dissected). New York: Rochester, Highland Park, J. Jaenike, F₁ of isofemale culture coll. 16/VI/2016, 4M, 4F (1M dissected). Ohio: Piqua, July 1948, JT Patterson, 1035.3 (4M,F; 3 dissected). Oklahoma: 10 mi NE Tulsa, V/2/41, AB Blair, 996.3 (2F). South Carolina: 2 mi. SW Cross Anchor, VII/13–VII/4/53, W.B. Heed, M.R. Wheeler 2321.8b (1F).

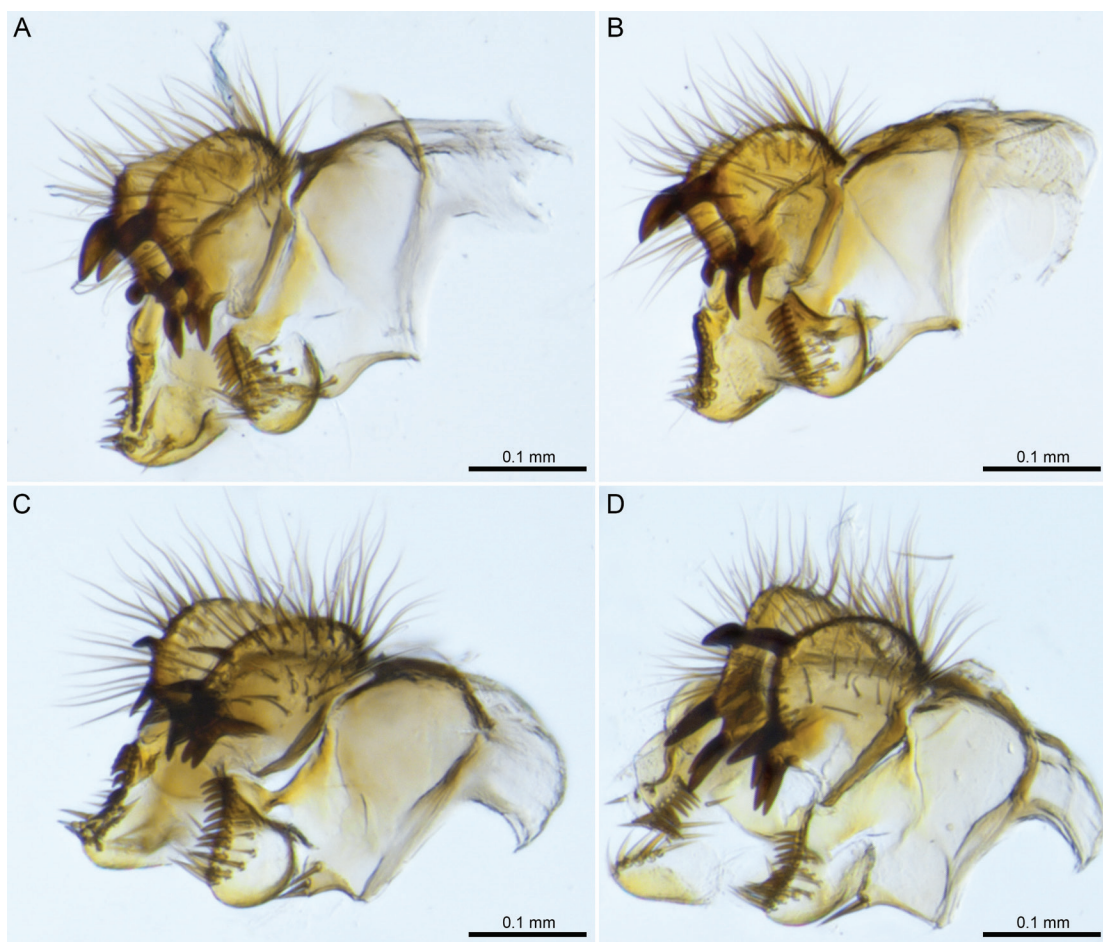


FIG. 4. Epandria (male) of native North American species of the *Drosophila funebris* group; posterolateral views (to same scale). **A.** *D. limpiensis* (ex: Limpia Canyon, TX). **B.** *D. macrospina* (ex: Magazine Mtn., AR). **C.** *D. subfunbris* (ex: Pasadena, CA). **D.** *D. trispina* (ex: Earp, CA).

DISTRIBUTION: Patterson and Wagner (1943) mapped 45 records of *macrospina* in North America, which was updated by Patterson and Stone (1952). Their westernmost records are from Del Rio, Texas; Moclova, Cuahuila, Mexico; north to the northwest corner of Nebraska and Fort Peck Dam in northern Montana. The record from Albuquerque, New Mexico, may be due to a higher latitude and altitude in that area or to a zone of overlap with *limpiensis*, but needs to be confirmed. Although it was not recorded from Florida on their maps, records from Georgia and Florida were mentioned, but, regrettably, very few of the specimens from most of their localities were saved. Miller et al. (2017) added eastern records farther north, in southern Québec, Canada, and Rochester, New York. The species is abundant in eastern Texas, the Mississippi valley, Ohio, Michigan, east to coastal Carolinas and New Jersey—essentially encompassing the eastern half of North America from $\sim 48^{\circ}$ N to $\sim 27^{\circ}$ N latitude.



FIG. 5. Male genitalia of native North American species of the *Drosophila funebris* group, ventral views (to same scale). **A.** *D. limpiensis* (ex: Limpia Canyon, TX). **B.** *D. macrospina* (ex: St. Catherine's Island, GA). **C.** *D. macrospina* (ex: Rochester, NY). **D.** *D. subfunnebris* (ex: Pasadena, CA). **E.** *D. trispina* (ex: Earp, CA).

Mainland (1942) used stocks of *macrospina* for his crossing experiments from the following localities, some series of which are in the AMNH collection (above): United States: Arkansas: Petit Jean St. Park [Conway] (35.1204°, -92.9379°); Florida: Tampa (~28.0886°, -82.3224°); Louisiana: New Orleans (30.3003°, -90.7120°); Mississippi: Columbus (33.5215°, -88.4060°); Ohio: Overton [Chester Township] (40.8662°, -82.0053°); Texas: Austin (~30.3109°, -97.8234°), Del Rio (29.3802°, -100.8930°).

COMMENTS: Spencer (1940) made the name *D. macrospina ohioensis* apparently available as a brief mention within a review article on *Drosophila* speciation, as an example of “interfer-

tile races/subspecies...” in which “these two subspecies [*m. macrospina* and *m. ohioensis*] cross readily and the hybrid offspring are quite fertile.” Types were not designated, though a diagnosis was given. His observations were based on a culture of two males and two females that he collected “6 mi. north of Overton, Ohio” (Overton is a small town ca. 7 mi NW of Wooster, Ohio: 40.8662°, -82.0053°). He distinguished between the two subspecies based on features now known to be quite intraspecifically variable in *Drosophila*, particularly coloration.

Mainland (1941) did not distinguish these subspecies because he found no sterility in crosses between *m. macrospina* and *m. ohioensis*; he reported soon afterward (Mainland, 1942) a slight reduction in fertility between them. Subsuming *D. macrospina ohioensis* under the species is based not only on the reports of complete hybridization, but also my observations in which no consistent morphological differentiation was found. Fortunately, several specimens of “*ohioensis*” are in the AMNH collection, from Piqua, Ohio (culture 1035.3, collected by J.T. Patterson), and there is no distinction between the aedeagus of these flies and *macrospina* from other localities (the apex of the hypandrium is slightly narrowed, but this is quite variable in *Drosophila*; also, the middle cercal spine is rather small). It would be ideal to compare mitochondrial DNA sequences of flies from these localities.

Stalker and Spencer (1939) mentioned that *D. macrospina* flies were “subject to ‘cataclyptic’ fits when the container is disturbed,” but I did not observe this in the cultures examined. *Drosophila macrospina* seems to never be particularly abundant in its primary habitat, which is forests; the natural hosts are unknown. It can easily be bred in the lab. Geographic variation in the genetics of *D. macrospina* and *limpiensis* would be very useful for examining any zones of overlap and introgression.

Drosophila limpiensis Mainland, 1941, new status

Figures 1A, 2A, 4A, 5A; 6A, B, H; 7C; 8A; 9B

Drosophila macrospina limpiensis Mainland, 1941: 160. Mainland, 1942 (hybrid sterility); Patterson and Wheeler, 1942 (redescription, immature stages, internal reproductive organs, chromosomes); Patterson and Stone, 1952 (distribution); Ewing, 1979 (mating behavior)

DIAGNOSIS: Very similar to *macrospina*, with differences as noted. Postocellar setae parallel to very slightly convergent (vs. usually strongly convergent to crossing in *macrospina*); male with lateral lobes of distiphallus in *D. limpiensis* thinner (especially at the apex), less protruding than in *macrospina*; apical lobes with fewer lateral serrations; gap between cercal spines 2 and 3 slightly less than width of spine 2 (gap is substantially larger than width of spine 2 in *macrospina*). Female: oviscapt dark, sclerotized as in *macrospina*. No distinction between the two species is apparent in the surstyli or female terminalia.

DESCRIPTION: A description was provided by Patterson and Wheeler (1942), to which the following details of the adults are added ($N = 4$ specimens measured, all from type locality [Limpia Canyon, TX]): Body size: ThL 1.38 mm (1.35–1.44); wing length, 2.21 mm (2.15–2.35). **HEAD:** proportions HW/HD 1.38 (1.35–1.44); frons short, FL/LFW 0.71 (0.69–0.75), broad-

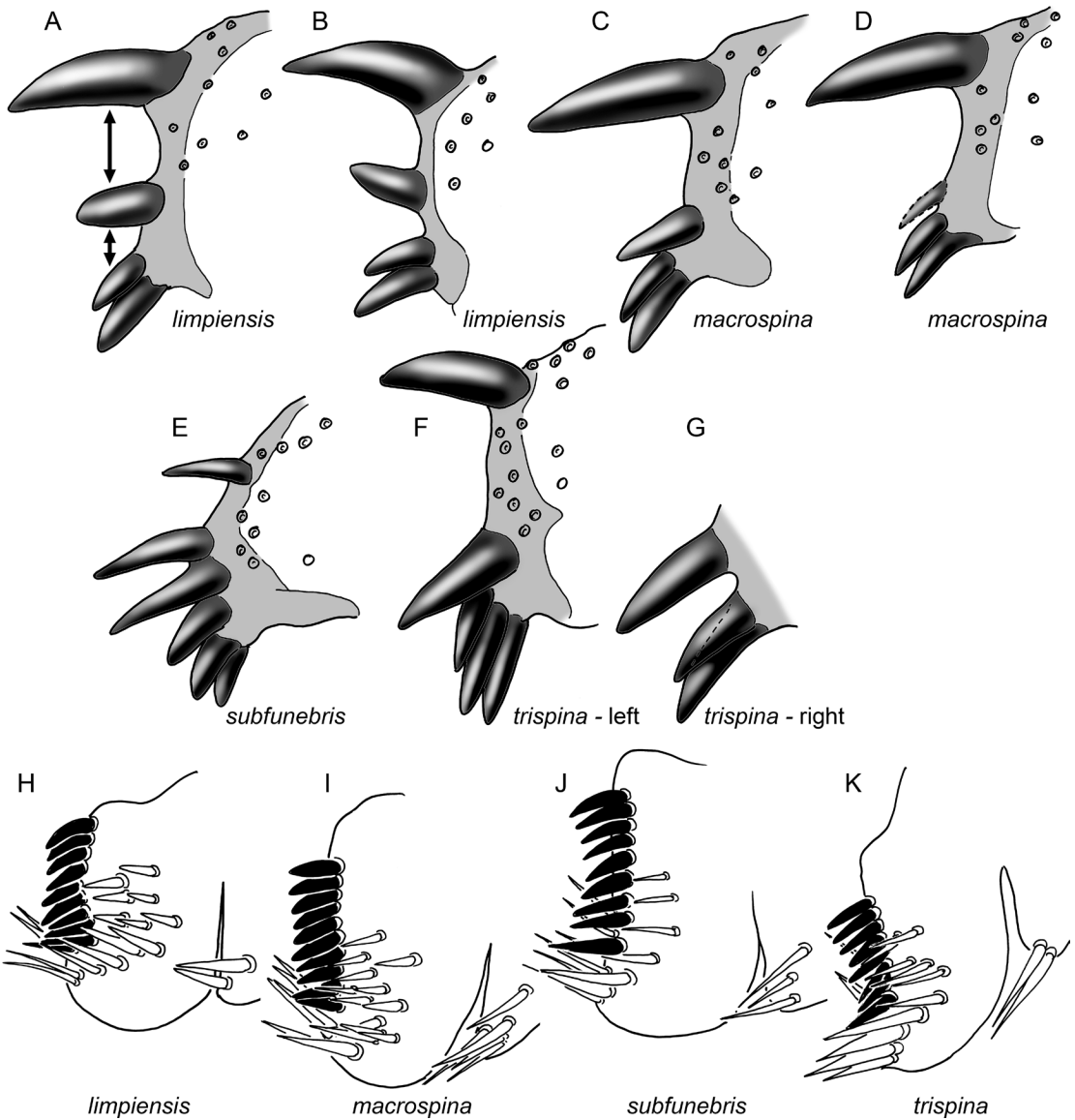


FIG. 6. External details of male terminalia, A–G: Cercal spines, right lateral views; H–K: Surstyli, lateral views. All to same scale. A. *D. limpiensis* (ex: Limpia Canyon, TX). B. *D. limpiensis* (ex: Patagonia, Arizona). C. *D. macrospina* (ex: New Orleans, LA). D. *D. macrospina* (ex: Piqua, OH), dashed line indicates spine sometimes missing. E. *D. subfunebris* ex: Pasadena, CA). F. G. *D. trispina* (ex: Earp, CA), G. showing right cercus with one less spine. H. *D. limpiensis* (ex: Limpia Canyon, TX). I. *D. macrospina* (ex: New Orleans, LA). J. *D. subfunebris* (ex: Pasadena, CA). K. *D. trispina* (ex: Earp, CA).

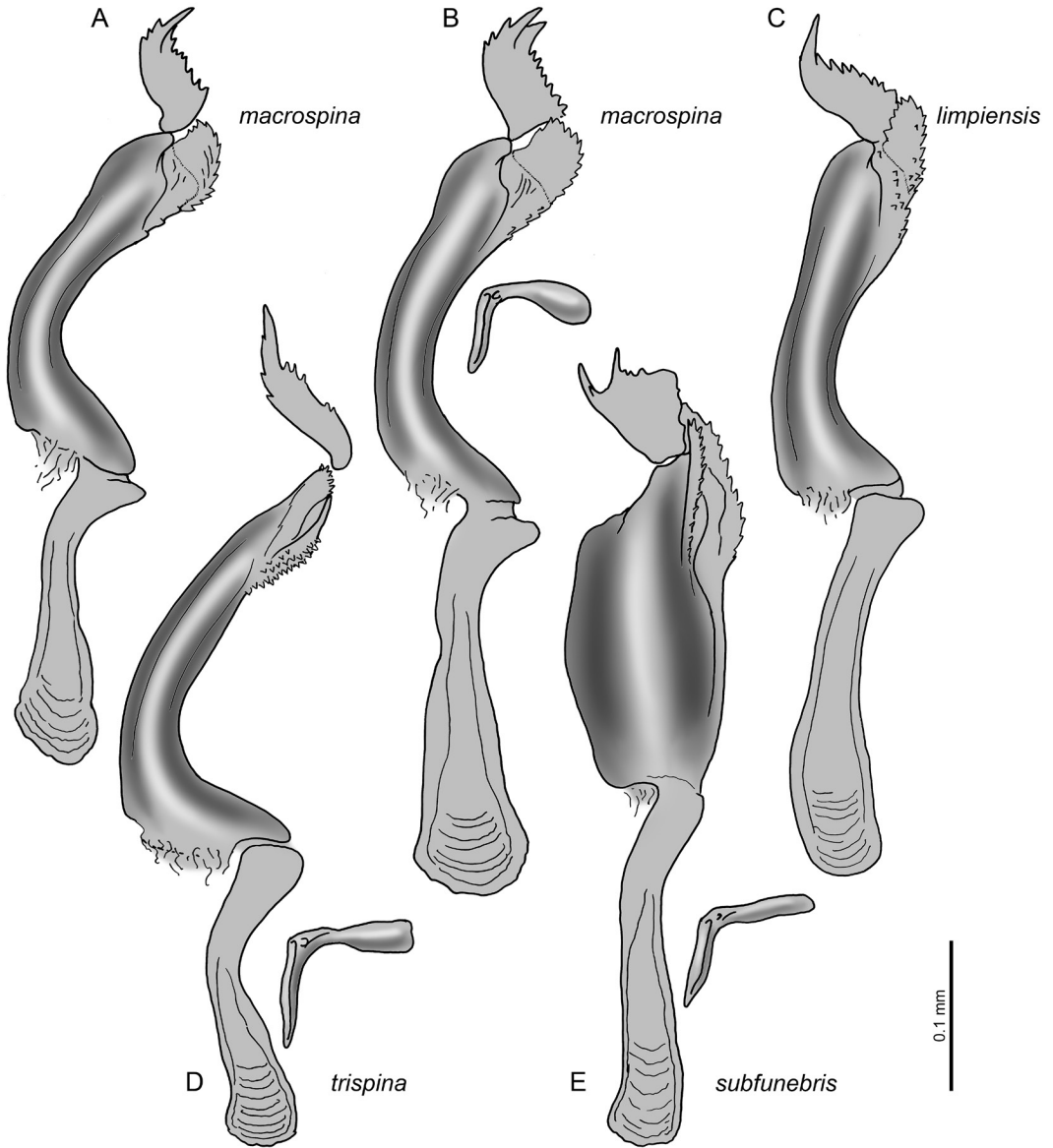


FIG. 7. Aedeagi with aedeagal apodemes, ejaculatory apodemes (B, D, E), lateral views (all to same scale). A. *D. macrospina* (ex: Magazine Mtn., AR). B. *D. macrospina* (ex: Rochester, NY). C. *D. limpiensis* (Limpia Canyon, TX). D. *D. trispina*. E. *D. subfunebris*.

ened dorsally, UFW/LFW 1.35 (1.30–1.38); vertical setae equal in size, VT-index 0.98 (0.96–1.03); vibrissa slightly larger than subvibrissa, vibrissa index 0.85 (0.65–1.05); ocellar setae significantly longer than postocellars. Eye shape ovoid, ED/EW 1.32 (1.28–1.37); cheek short, ED/CD 7.90 (7.1–8.3); proclinate seta twice the length of anteriorreclinate, OR_1/OR_2 2.09 (2.0–2.25), proclinate significantly shorter than posterior reclinate, OR_1/OR_3 0.68 (0.58–0.75); carina narrow, CL/CW 5.3 (4.6–5.8).

THORAX: Postpronotal setae very similar in size, h-index 0.89 (0.81–0.95); ant. dorsocentral seta shorter than post. dc, DC-index 0.68; post. katapisternal seta significantly larger than anterior one, S-index 0.59 (0.55–0.68); post. scutellar seta larger than ant. scutellar, Scut-index 0.85. WING of moderate length, WL/ThL 2.02 (1.94–2.09), relatively broad WL/WW 2.14 (2.01–2.21); C-index 2.82 (2.75–2.96); hb-index 1.93 (1.78–2.04); 4V-index 1.54 (1.51–1.60); dm-cu distant from wing margin, 5X-index 1.32 (1.08–1.42).

TYPES: Holotype, male (label typed): *D. macrospina/limpiensis* M/Limpia Canyon, Texas 1939/J.T. Patterson, col./Type. In AMNH.

SPECIMENS EXAMINED: MEXICO: Sonora, DSC stock no. 15120-1931.02 (4M, 4 F, 2 of each dissected) (no further locality data). United States: Arizona: Patagonia, ex DSC stock no. 15120-1921.00 (4M, 4F, 2 of each dissected); Texas: Ft. Davis/Limpia Canyon/MR Wheeler, WK Baker June 1947/1704.5 (3M, 3F; 1 dissected). Field notebooks from the former UT collection contain more detailed locality information for collection lot 1704.5, (recorded as *macrospina*): “Limpia Canyon, 10 mi W of junction of state highways #17 and #118 near Ft. Davis, Texas and 6.6 mi from Lot 1703. 4 traps.” Coordinates are 30.7775°, -103.7412°. All in AMNH.

DISTRIBUTION: Patterson and Wagner (1943) mapped 22 records of *limpiensis*, which was updated by Patterson and Stone (1952). They describe a distribution from northern Mexico (Sonora, central Chihuahua [Loredo]) north to western Texas (Davis Mountains) and portions of New Mexico, most of Arizona and the southwestern corner of Utah. There is a gap in central Texas and northward—in an area that the University of Texas lab sampled very well—where *limpiensis* ends and *macrospina* begins more eastward. Regrettably, most of the specimens from these localities were not saved.

Besides the specimens examined and Patterson records cited above, Mainland (1942) used stocks of *limpiensis* for his crossing experiments from the following localities: MEXICO: Sonora: Hermosillo (29.0745°, -110.9594°), Magdalena (30.6303°, -110.9699°), Punta del Agua (28.4258°, -110.4067°). United States: Arizona: Patagonia (31.5410°, -110.7531°); New Mexico: Silver City (32.7865°, -108.2652°), Radium Springs (32.4819°, -106.9072°); Texas: Limpia Canyon (30.7774°, -103.7412°); Utah: Zion National Park (~37.2550°, -112.9797°). This material was also the basis for the description by Patterson and Wheeler (1942).

COMMENTS: What were considered eastern and southwestern populations/subspecies of *macrospina* are now separated into two species, *macrospina* and *limpiensis*, respectively.

While the morphological evidence for separating *limpiensis* from *macrospina* is subtle, it is consistent as diagnosed above. Also, evidence from Mainland (1941, 1942) indicates substantial hybrid infertility between *Drosophila macrospina* and *D. limpiensis*. Flies of the two species readily mate but the F_1 hybrids of *limpiensis* female and *macrospina* male crosses were “sterile

to slightly fertile” (Mainland, 1942). Patterson and Stone (1952) mentioned an east-west gradient in hybrid sterility between *macrospina* X *limpiensis*, which may reflect the apparent geographical separation between these species in western Texas and Oklahoma. COII sequences of DSC stocks of *macrospina* and *limpiensis* in GenBank (National Center for Biotechnology Information, 2020) have 99% similarity based on BLAST analyses. Assuming the online sequences are correct, this is typically considered minimal identity for species separation (e.g., the sister species *Drosophila sechellia* and *D. simulans* have 97% similarity in the COI region). However, and for larger context, COII sequences between *D. macrospina* and *Zaprionus tuberculatus*, for example, and species in the *Drosophila cardini* group have 90% similarity. The close genetic similarity between *D. macrospina* and *limpiensis* no doubt reflects the subtle phenotypic differences between the species.

Spieth (1952: 434) mentioned that the mating behavior of *macrospina* and *limpiensis* is “identical in all respects,” but this was based on visual observation. He studied two cultures: no. 1897 from Alleghany State Park, New York (*macrospina*), and no. 1248.1b from San Bernardino, Arizona (*limpiensis*); specimens from the latter culture were morphologically studied here. Ewing (1979) reported significant differences in the male mating songs, based on two other cultures (numbers were not reported): one from Patagonia, Arizona (for *limpiensis*, presumably same material studied morphologically here), and one from Albuquerque, New Mexico (for *macrospina*, material not studied here). According to Ewing (1979) *Drosophila limpiensis* and *macrospina* differ in both the primary and secondary songs, *limpiensis* having longer interburst intervals, greater amplitude of sound pulses, and, in the secondary song, the pulses are more condensed.

In addition to morphological, genetic, and behavioral distinctions, *Drosophila limpiensis* and *D. macrospina* also appear to be ecologically distinct, the former occurring in hot, dry areas in western Texas, New Mexico, Arizona, and northwestern Mexico. *Drosophila macrospina* is a resident of forested areas with humid climates from eastern Texas to Florida, north to New England; northernmost records are in Michigan; Rochester, New York; and southern Ontario, Canada (Miller et al., 2017).

Drosophila subfunnebris Stalker and Spencer, 1939

Figs. 1C, 2C, 4C, 5D; 6E, J; 7E, 8F, 9D

Drosophila subfunnebris Stalker and Spencer, 1939: 108. Subsequent refs: Patterson, 1943 (redescription, internal reproductive organs, chromosomes).

DIAGNOSIS: The most distinctive species of the group that is native to North America: anterior reclinate orbital seta lateral to proclinate or nearly so (vs. posterolateral to proclinate in other species). Male genitalia: aedeagus with broad, winglike lateral lobes; hypandrium distinctly constricted in middle; shaft of aedeagus thick in lateral view; male cercus with 6 (vs. 4–5) spines. Oviscapit lightly sclerotized, relatively thick in lateral view, with ca. 30 small marginal pegs.

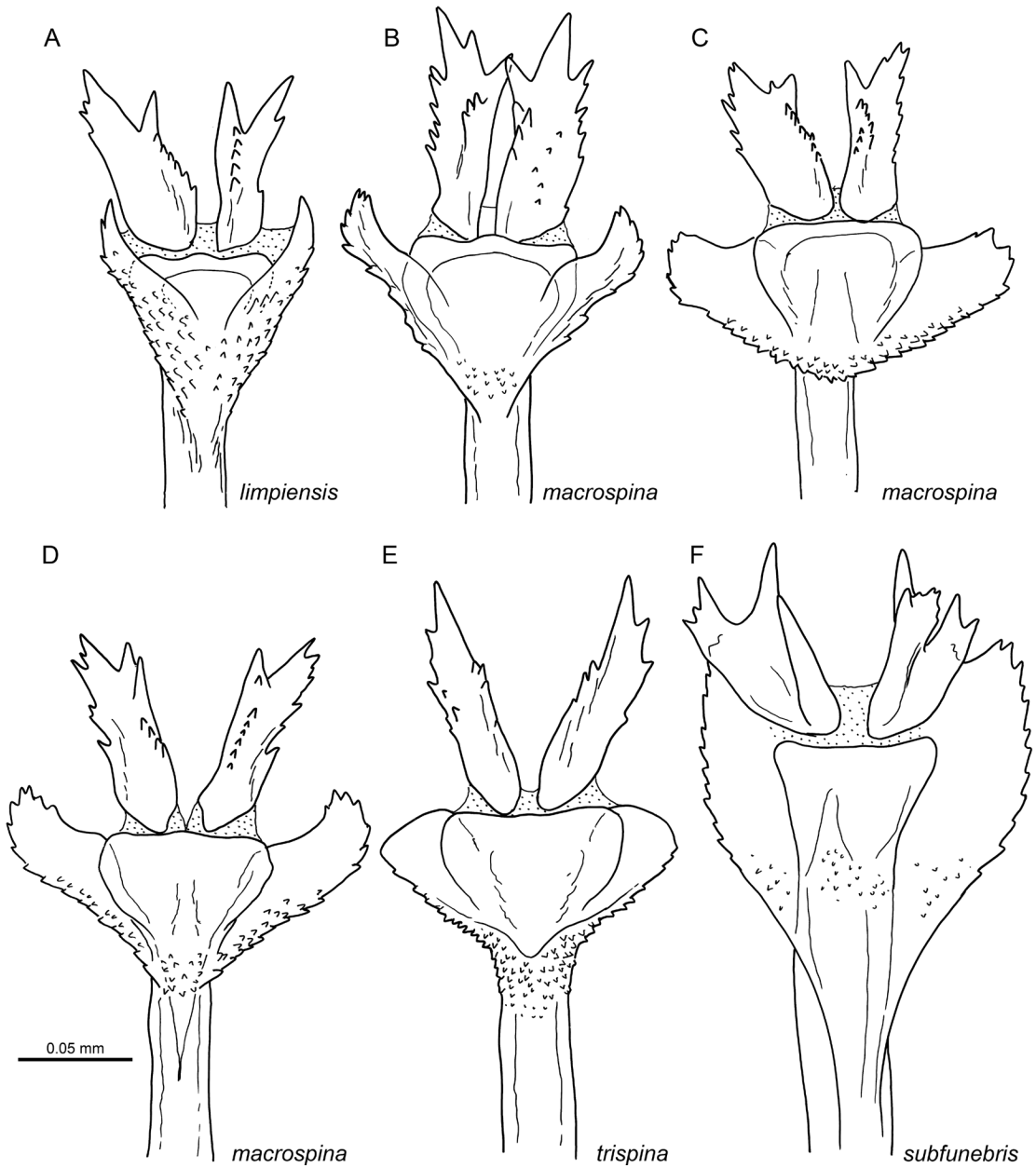


FIG. 8. Detail of apices of aedeagi (ventral views) of native North American species of the *D. funebris* group (all to the same scale). **A.** *D. limpiensis*. **B.** *D. macrospina* (ex: New Orleans, LA). **C.** *D. macrospina* (ex: Piqua, OH). **D.** *D. macrospina* (ex: Missouri). **E.** *D. trispina*. **F.** *D. subfunebris*.

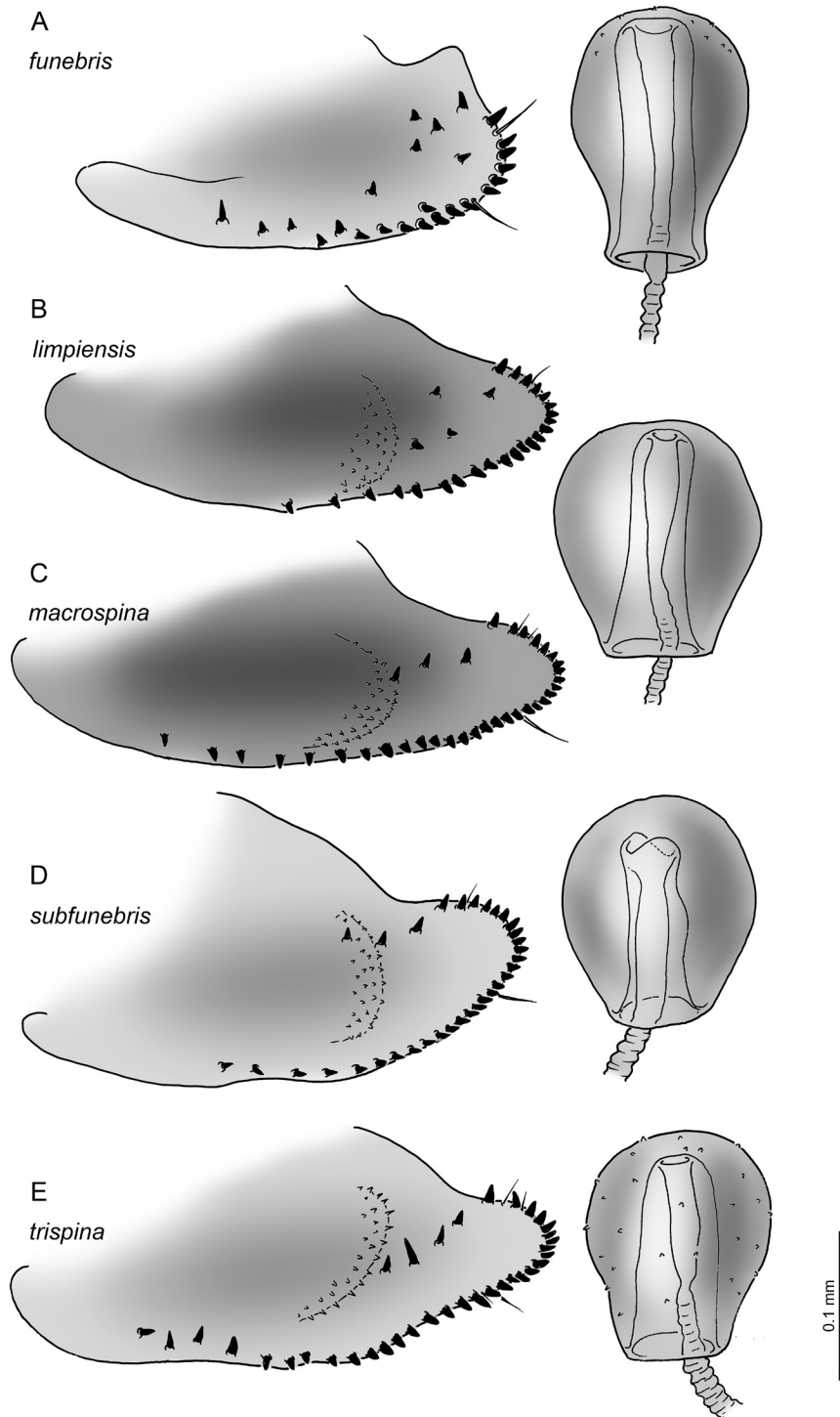


FIG. 9. Female terminalia (oviscapt, spermathecal capsules, and minutely scaled oviprovectro membrane [internal]) of North American species of the *D. funebris* group (all to same scale). **A.** *D. funebris* (introduced). **B.** *D. limpiensis*. **C.** *D. macrospina* (spermatheca of *limpiensis* and *macrospina* is identical). **D.** *D. subfunebris*. **E.** *D. trispina*.

DESCRIPTION: ($N = 4$ specimens, all measured from type series). Largest native *funebis*-group species, ThL 1.39 (1.25–1.48); wing length, 1.96 mm (1.90–2.03).

HEAD: significantly broader than deep, HW/HD 1.40 (1.38–1.44). Eye dull red, with dense ommatrichia, shape ovoid, ED/EW 1.27 (1.25–1.32). Frons short, FL/LFW 0.60 (0.58–0.63), wider dorsally, UFW/LFW 1.32 (1.27–1.36); frons and face dull, dark yellow, antennae very light brown; frontal-orbital plates and ocellar triangle slightly shiny. Proclinate orbital twice the length of anterior reclinate, OR_1/OR_2 2.1 (2.0–2.6), proclinate significantly shorter than posterior reclinate, OR_1/OR_3 0.61 (0.55–0.66); contralateral proclimates slightly divergent, posterior reclimates slightly divergent. Inner vertical slightly lateral to tangent running through ipsilateral proclinate and posterior reclinate. Anterior reclinate directly lateral to proclinate, distance of separation equal to diameter of socket. Vertical setae equal in size, VT-index 0.98 (0.96–1.00); inner vertical strongly inclinate, outer vertical almost directly posterior to inner vertical. Postocellars strong, convergent; ocellar setae significantly longer than postocellars, Ocellar S-Index 1.30 (1.24–1.36). Antennal pedicel with 2 strong setae (1 proclinate, 1 laterocline); arista [broken on all specimens]. Carina broader than in other species, CL/CW 4.39 (3.9–5.4), laterally declivous (not steep as in *macrospina* and *limpiensis*), more protruding. Vibrissa significantly longer than subvibrissa, vibrissa index 0.77 (0.71–0.84). Clypeus shiny, short, squared. Palp with apex brown, base yellow; dorsal margin flat, ventral margin convex with 3 strong setae. Labellum with 10 pseudotracheae. Cheek short, ED/CD 7.2 (6.1–8.4); occiput brown.

THORAX: Scutum and scutellum dark yellowish to very light brown, slightly shiny. Acrostichals in 8 rows. Short row of 2–3 acrostichals anterior to anterior dorsocentral are faintly larger than others (similar for acrostichals anterior to transverse suture). Two long postprontal setae, lower seta slightly larger than upper one, h-index 0.88 (0.77–0.93). Three large notopleurals, 2 anterior ones longest. Anterior supraalar seta short, posterior one very long. Two large katepisternal setae, posterior one significantly longer than anterior, S-index 0.60 (0.57–0.63). Dorsocentral setae well developed, anterior seta significantly shorter than post. dc, DC-index 0.61. Scutellar setae nearly equal in length, Scut-index 0.93 (0.91–0.95); anterior scutellars parallel, posterior pair crossing for 0.25 to 0.5 $\times$ their length. Legs light yellow. Fore femur with 3–4 long, fine ventral setae, 2 lateral ones; male protarsus without longer, curved setulae. Midtibia with long, thick ventroapical seta, smaller dorsal-preapical seta; hind tibia with 1 fine, preapical-dorsal seta.

Wing entirely hyaline, of moderate length relative to body size WL/ThL 1.96 (1.90–2.03), relatively broad WL/WW 2.18 (2.10–2.24); C-index 2.91 (2.80–3.01); hb-index 1.94 (1.78–2.15); 4V-index 1.37; distance of crossvein dm-cu from wing margin nearly equal to length of xvein, 5X-index 1.10 (1.06–1.20).

ABDOMEN: Pigmentation with moderate sexual dimorphism. Male: tergites 3–6 entirely dark, shiny brown; tergites 1 and 2 with dark yellow medially; tergite 7 light brown, epandrium dark yellowish. Female: tergites 3–4 with dark yellow bands on anterior margin, tergite 5 with paramedian yellow areas; tergites 6 and 7 dark brown; tergite 8, paraprocts and oviscapt dark yellow.

MALE TERMINALIA: Epandrium short, lightly sclerotized, devoid of microtrichia and setae (except 3 short, stiff setae on ventral lobe), dorsolateral phragma very well developed. Cerci project-

ing, without microtrichia; setae abundant and long (lengths greater than cercal width), posteroventral margin with 6 heavily sclerotized spines: narrow one dorsally, separated by gap from others about $2\times$ width of spine; 5 ventralmost spines adjacent (no spaces between bases), 3 most ventral spines short and stout. Surstylus broadly rounded ventrally, with 9 prensisetae pegs, ~ 11 thick setae; no microtrichia on surstylus. Hypandrium lightly sclerotized, slightly longer than aedeagal apodeme, with lateral constrictions. Gonopods lightly sclerotized, each with one larger and one very fine seta. Aedeagus with shaft short, very broad in lateral view; preapically with pair of broad, winglike lobes having finely serrate lateral margins; distal lobes with coarse, spinelike teeth on apical margin and row of fine serrations on mesal margin. Aedeagal apodeme well sclerotized, slightly shorter than aedeagus. Ejaculatory apodeme relatively small, bent at right angle.

FEMALE TERMINALIA: Oviscapt not heavily sclerotized; short, broad in lateral view (depth $0.3\times$ the length), apex rounded, not pointed. Oviscapt with ~ 30 small pegs along margin, plus 3 pegs on dorsolateral portion of valve. Spermatheca faintly pear shaped (narrower at base), sclerotized; introvert long, $\sim 0.8\times$ length of capsule, apex of introvert with pair of small lobes.

TYPES: Neotype (designated herein), male (dissected): United States: California/ Pasadena, 1949/Neotype *Drosophila subfunnebris* det. D. Grimaldi, 2022. In AMNH.

SPECIMENS EXAMINED: United States: California: Pasadena, 1949 [no further information]. 5M, 3F (1 of each sex dissected), in AMNH.

DISTRIBUTION: Known only from the type series.

COMMENTS: Stalker and Spencer (1939) mentioned isofemale cultures of *D. subfunnebris* that were maintained for over a year, originally collected in Pasadena, California (V/1937, and XI/19-28/1936)—from which the “type and gonotypes” were taken—and at “Camp Rincon, San Gabriel Mountains, California (IV/24/1937)” ($\sim 34.4114^\circ$, -117.9206°). The Pasadena culture whose behavior was studied by Spieth (1952) and Ewing (1979) presumably was one of those made by Spencer. None of these existed by 2016 in the NDSC when it was at Univ. California, San Diego. The only specimens of this species of which I am aware is a small series of five males and three females in the AMNH from the Pasadena location, from which I am designating the neotype. A thorough search for type holdings of Spencer was made (AMNH, NMNH), including inquiries to the College of Wooster, Ohio, where Spencer was a professor. Typical for species described by Spencer, there are no designated types or other archived specimens. I collected in the San Gabriel Mountains in June 2017 at Wrightwood, California (34.4037° , -117.7243°) but did not find this species.

Drosophila trispina Wheeler, 1949

Figures 1D, 2D, 4D, 5E, 6F, G, 6K, 7D, 8E, 9E

Drosophila trispina Wheeler, 1949: 180.

DIAGNOSIS: Facial carina broad, bulbous, noselike. Aedeagus: lateral lobes short and broadly rounded, not curved posteriad; apical lobe longer and more slender than in other species of group, without large inner spine at apex; distiphallus more slender in lateral view. Male cercus with large gap between spine 1 and 2, with 4–5 spines total. Oviscapt lightly sclerotized,

ventral margin with slight emargination; with about 32 marginal pegs; spermathecal capsule with fine papillae.

DESCRIPTION: ($N = 4$, all measured specimens from type series), body size, ThL 1.10 mm (0.98–1.17); wing length, 2.11 mm (1.91–2.27)

HEAD: Significantly broader than deep, HW/HD 1.39 (1.32–1.48). Eye dull red, with dense ommatrichia; ovoid, ED/EW 1.31 (1.29–1.43). Frons, face dull, dark yellow (carina lighter), antenna slightly darker (flagellomere 1 with fine, whitish microtrichia); frontal-orbital plates and ocellar triangle slightly shiny. Frons short, FL/LFW 0.72 (0.71–0.74), broadened posteriorly, UFW/LFW 1.32 (1.28–1.38), with fine setulae near ptilinal suture. Proclinate slightly divergent, length more than $2\times$ that of anterior reclinate, OR_1/OR_2 2.42 (2.21–2.62), proclinate shorter than posterior reclinate, OR_1/OR_3 0.74 (0.70–0.80). Anterior reclinate posterolateral to proclinate, separated by distance slightly larger than diameter of socket. Posterior reclinate slightly divergent. Inner vertical in line with tangent running through ipsilateral proclinate and posterior reclinate. Verticals nearly equal in size, VT-index 0.96 (0.91–1.04); inner vertical strongly inclinate, outer vertical laterocline and almost directly posterior to inner one. Postocellar setae strong, convergent; ocellar setae significantly longer than postocellars, Ocellar S-Index 1.39. Antennal pedicel with 2 strong setae (1 proclinate, 1 laterocline); arista with 4–5 dorsal, 3 ventral branches. Carina relatively broad, CL/CW 3.9 (3.2–4.6), protruding, bulbous and noselike. Vibrissa slightly larger than subvibrissa, vibrissa index 0.94 (0.93–0.95). Cheek short, ED/CD 7.5 (6.6–8.6). Palp entirely yellow, asymmetrical, dorsal margin flat and ventral margin convex with 3 strong setae. Labellum with ~ 10 pseudotracheae; occiput brown.

THORAX: Scutum and scutellum dark yellowish to faint brownish, dark tan; slightly shiny. Acrostichals in 8 rows; short row of 3 acrostichals anterior to anterior dorsocentral slightly thicker and longer than others (same for transverse row of 4 acrostichals in front of transverse suture). Two long postpronotal seta, lower seta larger than upper, h-index 0.81 (0.80–0.84). Three notopleural setae, longest ones are 2 anterior setae; 1 short, anterior supraalar seta, 1 long posterior supraalar. Posterior katapisternal seta significantly longer than anterior, S-index 0.59 (0.55–0.65). Posterior dorsocentral significantly longer than anterior, DC-index 0.62. Posterior scutellar setae slightly longer than anterior, Scut-index 0.86 (0.83–0.92), anterior pair parallel, posterior pair crossing $\sim 0.3\times$ their length. Legs light yellow; fore femur with 3 fine ventral setae, 2 lateral ones. Male protarsus without longer, curved setulae; midtibia with long, thick ventroapical seta, smaller dorsal-preapical seta; hind tibia with 1 fine, preapical-dorsal seta.

WING: Entirely hyaline, of moderate length relative to body size WL/ThL 1.91 (1.89–1.94), wing relatively broad WL/WW 2.12 (2.07–2.18); C-index 2.47 (2.38–2.55); hb-index 1.78 (1.67–1.88); 4-V index 1.28 (1.25–1.31); crossvein dm-cu distant from wing margin, 5X-index 1.27 (1.20–1.38). Halter light.

ABDOMEN: Pigmentation sexually dimorphic. Male: Tergites 1–3 with most of central area dark yellow; tergites 4–7 entirely dark, shiny brown; epandrium dark yellowish. Female: Tergites more yellow than brown, tergites 1 and 2 all yellow; tergites 3–5 with brown band on posterior margins, each with median gap of yellow; tergites 6 and 7 dark brown, with yellow anterior band; tergite 8, paraprocts, oviscapt light yellow.

MALE TERMINALIA: Epandrium lightly sclerotized, devoid of microtrichia, short, flattened (not capsulate); dorsolateral phragma well developed; ventral lobe very small, with 2 short, thick, stiff setae at apex. Cerci protruding, lobelike, lacking microtrichia, setae dense and long (lengths ~equal to thickness of cerci). Cercus with 4–5 heavily sclerotized spines; one large, dorsal spine far separated from others (~3× thickness of spine), group of 3–4 straighter spines ventrally (in one specimen left cercus was missing one of spines in ventral group). Surstylus most distinctive in group of *N.* American species: ventral margin not broadly rounded, apex of surstylus narrow; with 8 slender prenisetae on inner margin, 10 thick other setae. Hypandrium lightly sclerotized, lateral margins narrowed in middle; posterior width ca. 2× the anterior width; gonopod with 1 long, fine seta and one minute one. Aedeagus with shaft of uniform thickness, apex of aedeagus not as bulbous in lateral view as *macrospina* and *limpiensis*; apex with pair of lobes spreading 3.5× width of shaft; lobes short, rounded, partly serrate on margin and neck; distal lobes with coarse serrations, lacking large medial tooth seen in other species. Aedeagal apodeme sclerotized, relatively short, 0.7× length of main part of aedeagus (without apical lobes). Ejaculatory apodeme small, bent at right angle, both portions approximately equal in length.

FEMALE TERMINALIA: Oviscapt not heavily sclerotized, with slight depressions along dorsal and ventral margins in lateral view; apex narrowed; 30–32 pegs along margin, plus 4 slightly longer ones on dorsolateral portion of valve. Spermatheca slightly bulb shaped, sclerotized, introvert long, ~0.85× length of capsule, with fine papillae on surface of capsule.

TYPES: Holotype, male: United States: California, Earp/MR Wheeler, June 1948/ [lot]1858.5. In NMNH, not examined. Wheeler (1949) mentioned that the holotype was taken from the same isofemale culture that yielded the paratypes (below).

SPECIMENS EXAMINED: Paratypes, 4M, 2F (1 of each dissected), in AMNH: USA: California, Earp/MR Wheeler, June 1948/ [lot]1858.5. Field notebooks from former UT collection contains more detailed locality for this lot: “Traps set in brushy, woody grove along Colorado River, at Kinders’ Camp, at 4 mi [6.4 km] NW Earp, Calif., Coll. 6-14-48” (~34.2777°, -114.2326°).

DISTRIBUTION: Known only from the type series.

COMMENTS: Wheeler (1949: 181–182) mentioned that *D. trispina* can hybridize with *D. limpiensis*, but they produce sterile male offspring; when the female parent is *trispina* this yields offspring with reduced viability or that are inviable. The type locality of this species along the Colorado River, separating Arizona and California, is low, hot desert of approximately 120–150 m elevation.

KEY TO NEARCTIC SPECIES OF THE *DROSOPHILA FUNEBRIS* GROUP

- 1a. Male with ~12 spines on each cercus; thornlike setae on ventral epandrial lobe; oviscapt (female) with tubercle on dorsal margin, base of spermatheca with neck (fig. 9A) (introduced species) . . .
 *funebnis*
- 1b. Male with 4–6 spines on each cercus (fig. 4); ventral epandrial lobe with 2–5 thick setae (none thornlike); oviscapt without tubercle on dorsal margin, spermatheca without neck (fig. 9B–E) (native species) 2

- 2a. Male generally with 5–6 spines on cercus (fig. 6E–G), oviscapt not sclerotized (fig. 9D, E) (California)3
- 2b. Male with 4 cercal spines (fig. 6A–D); oviscapt noticeably sclerotized and dark (fig. 9B, C) (south-western US, northern Mexico, eastern North America)4
- 3a. Carina not bulbous, noselike (fig. 1C); aedeagus (male) with large, flangelike lateral lobes (figs. 5D, 8F), cercus with 6 spines (fig. 6E); oviscapt with slight emargination on dorsal margin (fig. 9D) *subfunebri*
- 3b. Carina bulbous, noselike (fig. 1D); aedeagus with much smaller lateral lobes (figs. 5E, 8E), cercus with 4–5 spines (fig. 6F); oviscapt dorsally and ventrally slightly emarginate (fig. 9E) *trispina*
- 4a. Aedeagus with broader lateral lobes (“wingspread” ~5× the thickness of aedeagal neck) (figs. 5B, C; 8B–D); gap between largest cercal spine and closest small one ~1.5× thickness of largest spine (fig. 6C, D) (eastern North America) *macrospina*
- 4b. Aedeagus with lateral lobes narrow, ~3.5–3.7× thickness of neck (figs. 5A, 8A); gap between largest cercal spine and closest small one <= to width of thickest spine (fig. 6A, B) (western Texas, Arizona, New Mexico, northern Mexico) *limpiensis*

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the help of John Jaenike, who provided a culture of *Drosophila macrospina* from Rochester, New York; the *Drosophila* Species Center for providing several cultures of *funebri*-group species; to Steve Thurston (AMNH) for help with the graphics; and to Shane McEvey (Australian Museum) and an anonymous reviewer for their careful reviews.

REFERENCES

Bächli, G., C.R. Vilela, A. Escher, and A. Saura. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 39: 1–362. Leiden: Brill.

Ewing, A.W. 1979. Complex courtship songs in the *Drosophila funebri* species group: escape from an evolutionary bottleneck. Animal Behaviour 27: 343–349.

Fabricius, J.C. 1787. Mantissa insectorum sistens species nuper detectas adiectis synonymis, observationibus, descriptionibus, emendationibus. Vol. 2: 1–381. Hafniae [Copenhagen]: Proft.

Finet, C., V.A. Kassner, and 31 coauthors. 2021. DrosoPhyla: Resources for drosophilid phylogeny and systematics. Genome Biology and Evolution 13(8). [doi:10.1093/gbe/evab179]

Imasheva, A.G., O.E. Lazebny, M.L. Cariou, J.R. David, and L. Tsacas. 1994. Drosophilids from Daghestan (Russia) with description of a new species (Diptera). Annales de la Société Entomologique de France 30 (2): 209–216.

Izumitani, H.F., Y. Kusaka, S. Koshikawa, M.J. Toda, and T. Katoh. 2016. Phylogeography of the subgenus *Drosophila* (Diptera: Drosophilidae): evolutionary history of faunal divergence between Old and New Worlds. PLoS One 11 (7): e0160051.

Mainland, G.B. 1941. Studies in *Drosophila* speciation, III. The *Drosophila macrospina* group. Genetics 26: 160–161.

Mainland, G.B. 1942. Studies in the genetics of *Drosophila*. VI. Genetic relationships in the *Drosophila funebri* group. University of Texas Publications 4228: 74–112.

- Miller, M.E., S.A. Marshall, and D.A. Grimaldi. 2017. A review of the species of *Drosophila* (Diptera: Drosophilidae) and genera of Drosophilidae of northeastern North America. *Canadian Journal of Arthropod Identification* 31: 1–282.
- Morales-Hojas, R., and J. Vieira. 2012. Phylogenetic patterns of geographical and ecological diversification in the subgenus *Drosophila* PLoS ONE 7 (11): e49552.
- National Center for Biotechnology Information. 2020. GenBank. Online resource (<https://www.ncbi.nlm.nih.gov>), accessed 15 November 2020.
- Okada, T. 1956. Systematic study of Drosophilidae and allied families of Japan. Tokyo: Gihodo Co.
- Okada, T. 1968. Systematic study of the early stages of Drosophilidae. Tokyo: Bunka Zugsisha Co.
- Parshad, R., and K.K. Duggal. 1966. Drosophilid survey of India. III. The Drosophilidae of Kashmir Valley. *Research Bulletin of the Panjab University* 17 (3-4): 277–290.
- Patterson, J.T. 1943 (“1942”). Studies in the genetics of *Drosophila* III. The Drosophilidae of the Southwest. University of Texas Publications 4313: 7–216.
- Patterson, J.T., and W.S. Stone. 1952. Evolution in the genus *Drosophila*. New York: MacMillan, 610 pp.
- Patterson, J.T., and R.P. Wagner. 1943. Geographical distribution of species of the genus *Drosophila* in the United States and Mexico. University of Texas Publications 4313: 217–281.
- Patterson, J.T., and M.R. Wheeler. 1942. Description of new species of the subgenera *Hirtodrosophila* and *Drosophila*. University of Texas Publications 4213: 67–109.
- Robe, L.J., V.L.S. Valente, M. Budnik, and E.L.S. Loreto. 2005. Molecular phylogeny of the subgenus *Drosophila* (Diptera, Drosophilidae) with an emphasis on Neotropical species and groups: a nuclear versus mitochondrial gene approach. *Molecular Phylogenetics and Evolution* 36: 623–640.
- Robe, L.J., E.L.S. Loreto, and V.L.S. Valente. 2010. Radiation of the *Drosophila* subgenus (Drosophilidae, Diptera) in the Neotropics. *Journal of Zoological Systematics and Evolution Research* 48 (4): 310–321.
- Russo, C.A.M., B. Mello, A. Frazão, and C.M. Voloch. 2013. Phylogenetic analysis and a time tree for a large drosophilid data set (Diptera: Drosophilidae). *Zoological Journal of the Linnean Society* 169: 765–775.
- Spencer, W.T. 1940. Levels of divergence in *Drosophila* speciation. *American Naturalist* 74: 299–311.
- Spiehl, H.T. 1952. Mating behavior within the genus *Drosophila* (Diptera). *Bulletin of the American Museum of Natural History* 99 (7): 399–474.
- Stalker, H.D., and W.P. Spencer. 1939. Four new species of *Drosophila*, with notes on the *funnebris* group. *Annals of the Entomological Society of America* 32: 105–112.
- Sturtevant, A.H. 1942. The classification of the genus *Drosophila*, with descriptions of nine new species. University of Texas Publications 4213: 5–51.
- Throckmorton, L.H. 1962. The problem of phylogeny in the genus *Drosophila*. University of Texas Publications 6205: 207–343.
- Throckmorton, L.H. 1975. The phylogeny, ecology, and geography of *Drosophila*. In R. King (editor), *Handbook of Genetics*: 421–469. New York: Plenum.
- Werner, T., T. Steenwinkel, and J. Jaenike. 2020a. The Encyclopedia of North American Drosophilids, vol. 1. Drosophilids of the Midwest and Northeast. Online resource (<https://digitalcommons.mtu.edu/oabooks/1/>).
- Werner, T., T. Steenwinkel, and J. Jaenike. 2020b. The encyclopedia of North American drosophilids: vol. 2. Drosophilids of the Midwest and Northeast. Online resource (<https://digitalcommons.mtu.edu/oabooks/1/>).
- Wheeler, M.R. 1949. Taxonomic studies on the Drosophilidae. University of Texas Publications 4920: 157–195.

All issues of *Novitates* and *Bulletin* are available on the web (<https://digitallibrary.amnh.org/handle/2246/5>). Order printed copies on the web from:
<https://shop.amnh.org/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

∞ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).