



A review of *Erebomyia* (Diptera: Dolichopodidae), with descriptions of three new species

RICHARD L. HURLEY¹ & JUSTIN B. RUNYON^{2,3}

¹Deceased, formerly, Montana Entomology Collection, Montana State University, Room 50 Marsh Laboratory, Bozeman, Montana 59717, USA

²Rocky Mountain Research Station, USDA Forest Service, 1648 S. 7th Avenue, Bozeman, Montana 59717, USA

³Montana Entomology Collection, Montana State University, Room 50 Marsh Laboratory, Bozeman, Montana 59717, USA
E-mail: jrnyon@montana.edu

Abstract

The genus *Erebomyia* is reviewed and a key is provided for the four known species, three of which are described here: *Erebomyia aetheoptera* n. sp., *E. akidoptera* n. sp., and *E. ramseyensis* n. sp. The type species, *E. exalloptera* Runyon & Hurley, is redescribed and the male genitalia illustrated. *Erebomyia* is known from Arizona (3 spp.) and California (1 sp.), and males are notable for their modified wings, most exceptionally those of *E. exalloptera* whose left wing is of a different shape and size than the right wing. The occurrence of directional wing asymmetry in insects is reviewed to place the unique wings of *E. exalloptera* in context. Observations of *Erebomyia* courtship behavior are provided, and the potential adaptive significance of asymmetrical and modified wings of *Erebomyia* is discussed.

Key words: Nearctic, Sympycninae, wings, directed asymmetry, courtship display, long-legged flies, *Erebomyia*, Dolichopodidae

Introduction

During trips to southern Arizona in April 2001–2003 we collected three species belonging to a new genus of sympycnine dolichopodids from dark rock cavities in or near streams. Remarkably, we found that the wings in males of one species were directionally asymmetrical – the right wing was smaller and a different shape than the left wing (Fig. 1). The genus *Erebomyia* was erected for that species, *E. exalloptera*, and a courtship function for its asymmetrical wings was proposed (Runyon & Hurley 2004). The purpose of this paper is to describe three additional species of *Erebomyia* and to provide a more detailed description of *E. exalloptera*. The wings of the new species described here are symmetrical, but are variously modified in shape and adorned with hairs. The directed asymmetry displayed in wings of *E. exalloptera* is contrasted with such asymmetry reported in other insects. The courtship behavior of *E. exalloptera* and *E. ramseyensis* is described, and suggests a possible role for their wing modifications as sexual signals.

Materials and methods

Material from this work is housed in the following institutions: CAS = California Academy of Sciences, San Francisco; CNC = Canadian National Collection, Ottawa; FSCA = Florida State Collection of Arthropods, Gainesville; MTEC = Montana Entomology Collection, Montana State University, Bozeman; EMEC = University of California, Essig Museum of Entomology, Berkeley; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

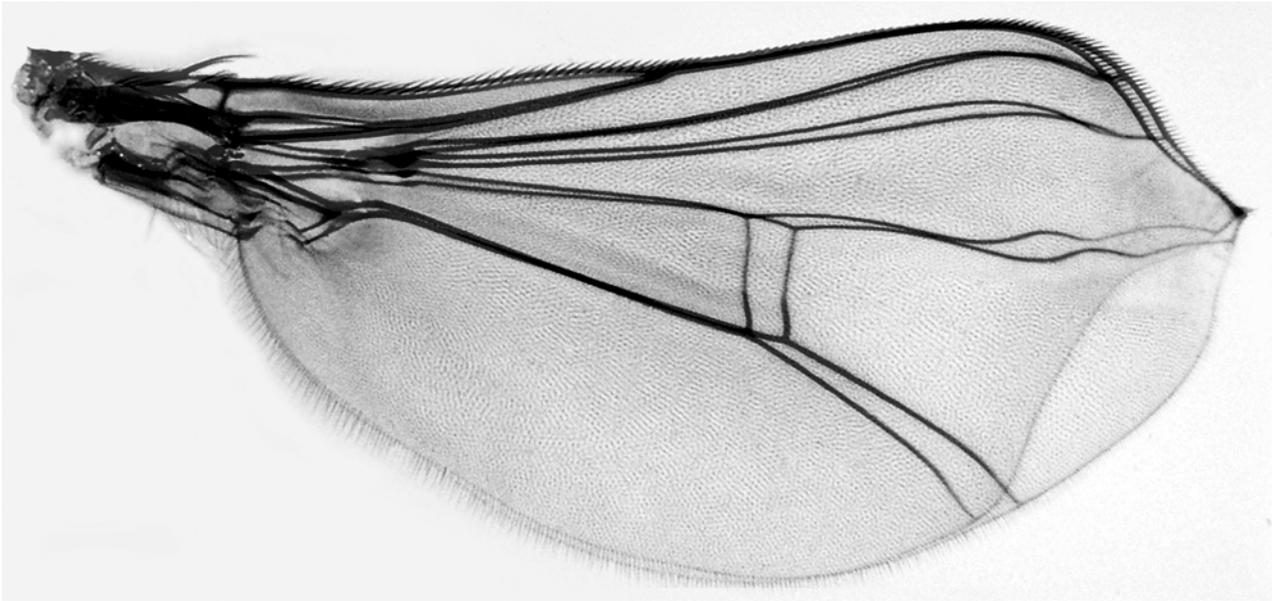


FIGURE 1. *Erebomyia exalloptera*, overlay of left (larger wing, on top) and right wings of male.

Descriptions of the structural terminology follow McAlpine (1981), except for genitalia which follow Cumming et al. (1995) and Sinclair & Cumming (2006). Illustrations of male genitalia are shown as they appear on the intact specimen (rotated approximately 180°), but in descriptions “dorsal” and “ventral” refer to the true morphological positions, with the top of the page ventral and the bottom of the page dorsal. Genitalia were cleared using KOH and mounted in glycerin for examination and illustration. Body length is measured from the base of antenna to tip of the abdomen. Wing length is measured from the humeral crossvein to the wing apex.

Density of pollen is characterized as follows: sparse, if pollen present, but not noticeably modifying integument color; moderately dense, if pollen lending its own color generally to the surface, but not completely obscuring integument beneath; dense, if integument completely hidden by pollen.

The following abbreviations and terms are used: *ad* = anterodorsal(ly); *av* = anteroventral(ly); *pd* = posterodorsal(ly); *ac* = acrostichal seta(e); *dc* = dorsocentral seta(e); T1, T2, etc. = abdominal tergum one, abdominal tergum two, etc.; S1, S2, etc. = abdominal sternum one, abdominal sternum two, etc. Legs are designated by roman numerals, tarsomeres by bracketed arabic numerals (e.g. Tarsus III(4) = 4th tarsomere of metathoracic leg).

Genus *Erebomyia* Runyon & Hurley

Erebomyia Runyon & Hurley, 2004: S114. Type species: *Erebomyia exalloptera* Runyon & Hurley, 2004, by monotypy.

Diagnosis. Body length 3.0–4.5 mm. Vertex of head not excavate. Antennal scape without dorsal setae; pedicel without medioapical thumb-like projection. Wing with costa continuous to tip of unbranched vein M; crossvein dm-cu shorter than last part of CuA₁. Thorax with postpronotal hairs (Fig. 2; see Remarks); 6 dc setae; posterior scutum not distinctly flattened; notopleuron with 2 setae; proepisternum with only a few hairs. Femur II and III with preapical seta. Hypopygium forming a cap to abdomen. Males: wings modified in shape, with hairs near apex (Figs. 1, 3–5). Left hypandrial arm large, hooked; right hypandrial arm short (Figs. 6–8).

Description. Males: Head: without lower postcranial hairs (beard) or gena. Face short, not reaching ventral margin of eyes; very narrow to obliterated near middle by encroaching eyes. Postocular setae white, with dorsal 5–7 usually yellow-brown to brown, becoming slightly longer and more slender ventrally. Ocellar

and outer vertical setae long. Scape and pedicel mostly yellow; first flagellomere triangular, brown. Arista basal, hispid; with somewhat thickened basal aristomere. *Thorax*: 6 long dc; ac in a single row. Postpronotal hairs present (Fig. 2; see Diagnosis of genus). Scutellum with one pair of long setae, without hairs. Proepimeron bare. Notopleuron with 2 long setae. Halter yellow. Calypter yellow, black at apex; with fan of long yellow setae. *Legs*: including coxa, long and slender, yellow, with distal tarsomeres often brownish. Anterior surface of coxa I with white hairs and yellow-brown to brown setae at apex. Coxa II and III with long, slender, dorsal seta near 1/2. Tibia I without distinct setae. Femur II and III with preapical anterior seta; with *av* seta near apex. *Wing*: male wings variously modified, but all with slender, very short to long marginal hairs near apex (Figs. 1, 3–5). *Abdomen*: cylindrical; dark brown, with some yellow near base. T1 with very long, slender setae along posterior edge, lateral setae longest and often yellowish, medial setae shorter and darker. Hypopygium (Figs. 6–8) small, mostly embedded; epandrium longer than wide, without distinct lobes. Surstylus with ventral lobe larger than dorsal lobe; dorsal lobe narrow, digitiform, with one lateral seta before apex; ventral lobe much broader, with 3–4 apical setae and subapical digitiform lobe bearing one seta at apex. Postgonites present as a pair of tubular sclerites, extending around base of phallus and looping ventrally then dorsally to weakly fuse with ventral surface of a small sclerite ventroapical of sperm pump, and branching laterally to fuse with base of bacilliform sclerites. Cerci short, narrow, pale brown with yellow setae and hairs, with 2–3 very long pale yellow setae at apex. Hypandrium (Fig. 6) asymmetrical, arrowhead-shaped ventrally, extending dorsally near base on each side, then arising as hooked arms extending apically which fuse basally with bacilliform sclerites; right apical hypandrial arm short; left hypandrial arm very large, hooked to the left, with microtrichia covering apex.



FIGURE 2. *Erebomyia exalloptera*, left lateral view. Arrow indicates left postpronotal hairs on anterior slope of scutum.

Females: Similar in appearance to *Sympycnus* and *Calyxochaetus*; can be recognized by postpronotal hairs. Similar to males but: face broader, only slightly narrowed below (width subequal to width of first flagellomere); palpus broader; first flagellomere short triangular, a little wider than long; scape and pedicel often with some brown dorsally; wings unmodified.

Remarks: *Erebomyia* belongs to the subfamily Sympycninae, a diverse cosmopolitan taxon containing many genera and species. Although its position within the subfamily is unclear, *Erebomyia* appears to be monophyletic based on the presence of postpronotal hairs (Fig. 2), development of the left hypandrial arm into a large hook, modified wings in males, and perhaps habitat specialization - occurring only on deeply shaded vertical or overhanging, bare rock. The paucity of specimens in collections (we have searched most of the major collections in North America) is surprising given their occurrence, often in large numbers, in well-collected areas, e.g., Madera Canyon and Cave Creek Canyon in Arizona. Increased attention to the microhabitats in which *Erebomyia* occur (dark rock cavities near streams) particularly in southwestern U.S.A. and Sonora Mexico, should provide additional species.

Postpronotal hairs, though sometimes difficult to see, appear to be a synapomorphy separating *Erebomyia* from other Nearctic Sympycninae and perhaps other Dolichopodidae in general. They are a cluster of very short, pale hairs found on the extreme anterior slope of the scutum in line with the dc setae (Fig 2).

Males are easily identified to species using wing characters. Determination of females is difficult since, unfortunately, the distinct wing modifications of males are not reflected in females. Females of *E. ramseyensis* can be distinguished by the relatively short anterior preapical seta on femur III. Subtle differences appear to exist among the other species as noted in descriptions, but we cannot find reliable diagnostic features to allow confident identification of isolated females.

Key to males of *Erebomyia* Runyon & Hurley

1. Right wing excavate posterior to apex; left wing smoothly convex posterior to apex (Fig. 1) *exalloptera* Runyon & Hurley
- Right and left wings mirror images 2
2. Wing broadly acuminate at apex (Fig. 3)..... *akidoptera* Hurley & Runyon **n.sp.**
- Wing broadly rounded or rather truncate at apex, not pointed 3
3. Wing apex excavate between R_{4+5} and M_1 , with distinct broad lobe anterior and posterior to apex (Fig. 4) *aetheoptera* Hurley & Runyon **n.sp.**
- Wing broadly rounded at tip; costa with long clumped hairs between R_{4+5} and M_1 (Fig. 5) *ramseyensis* Hurley & Runyon **n.sp.**

Erebomyia aetheoptera Hurley & Runyon, n. sp.

(Fig. 4)

Description. Male: Body length: 4 mm; wing: 3.5 mm x 1.75 mm. *Head:* Face dense gray pollinose; middle third obliterated by encroachment of eyes, dorsal third and ventral third reduced to slender triangles. Vertex blue-green laterally, magenta medially, with moderate dense gray pollen. Ocellar setae long, subequal in size to dc setae. Outer vertical setae one-half length of ocellar setae. Palpus yellow-brown, elongate triangular; with rather long, light brown hairs. Scape cylindrical, rather long (subequal in length to first flagellomere), yellow. First flagellomere a little longer than wide. *Thorax:* Mesonotum dark brown with blue reflections; with sparse rusty-gray pollen. Pleura blue-green, with sparse gray pollen. Metepisternum and metepimeron yellow. Proepisternum with 2 short, slender white hairs on dorsal half and 2 similar hairs on ventral half. Thorax with 12 rather long, slender ac which are slightly longer than one-half length of dc. *Legs:* Coxa I with sparse anterior hairs. Coxa II narrowly darkened dorsally at base; with diffusely darkened stripe around insertion of brown *ad* seta; with moderately dense yellow hairs anteromedially. Coxa III with brown dorsal seta. Tibia II with *ad* setae near 1/5, 5/8; *pd* seta near 1/4. Tibia III with *ad* setae near 1/4, 5/8; with row of smaller dorsal setae on distal two-thirds; with about 5 short ventral setae. Tarsus III(2–5) brownish. Ratios of tibia:tarsomeres for leg I: 13-11-6-5-3-2; for leg II: 24-14-7-5-2-2; for leg III: 32-6-11-5-3-1.5. *Wing* (Fig. 4): rather broad, with distal margin bilobed because of shallow, wide indentation between tips of R_{4+5} and M_1 ,

which bears tuft of about 5 hooked cilia of increasing length (longest equal to distance between R_{4+5} and M_1 at apex). Costa with long seta just basal to humeral crossvein; with rather long, slender spines of gradually increasing length, becoming sparse near apex of R_{2+3} , then reappearing to apex of R_{4+5} ; with additional row of slender, hooked hairs before apex of R_{2+3} . Veins R_{2+3} and R_{4+5} gradually divergent; R_{4+5} and M_1 parallel beyond crossvein, both with gradual anterior bend. *Abdomen*: dark brown with poorly differentiated, yellowish areas on T2 and T3. T2 with long hairs laterally; T2-T5 with long, slender setae along posterior edge. S5 with moderately stout seta at each side preapically. Hypopygium (not dissected); cerci similar to *E. exalloptera* (Fig. 7), narrowed and darker on apical half, with 3 long (subequal to length of cercus), yellow setae at apex. Large, hooked left hypandrial arm visible in unprepared specimen.

Female: a single specimen collected with the holotype male appears to belong to this species. Body length: 4 mm; wing: 3.5 mm x 1.75 mm. The following combinations of characters should separate females of *E. aetheoptera*: femur III with preapical anterior seta equal to or longer than width of femur at insertion; wing broad (length approximately equal to 2 times width), bend in section of M_1 beyond crossvein dm-cu occurring at or just basal to termination of CuA_1 at wing margin.

Etymology: derived from Greek *aethes* (ἄηθης) = unusual, strange + *ptera* (πτέρων) = wing, in reference to the curiously modified wings of the male.

Holotype: ♂: ARIZONA: Cochise Co., Ramsey Canyon, Huachuca Mtns., 5500 feet, 23-IV-2002, R. Hurley & J. Runyon. Deposited: CAS.

Additional (non-type) material: ♀: same data as holotype.

Remarks: The male and female of *E. aetheoptera* were collected with *E. ramseyensis* along Ramsey Creek, Arizona, from a cavity created by several large boulders with some standing water underneath.

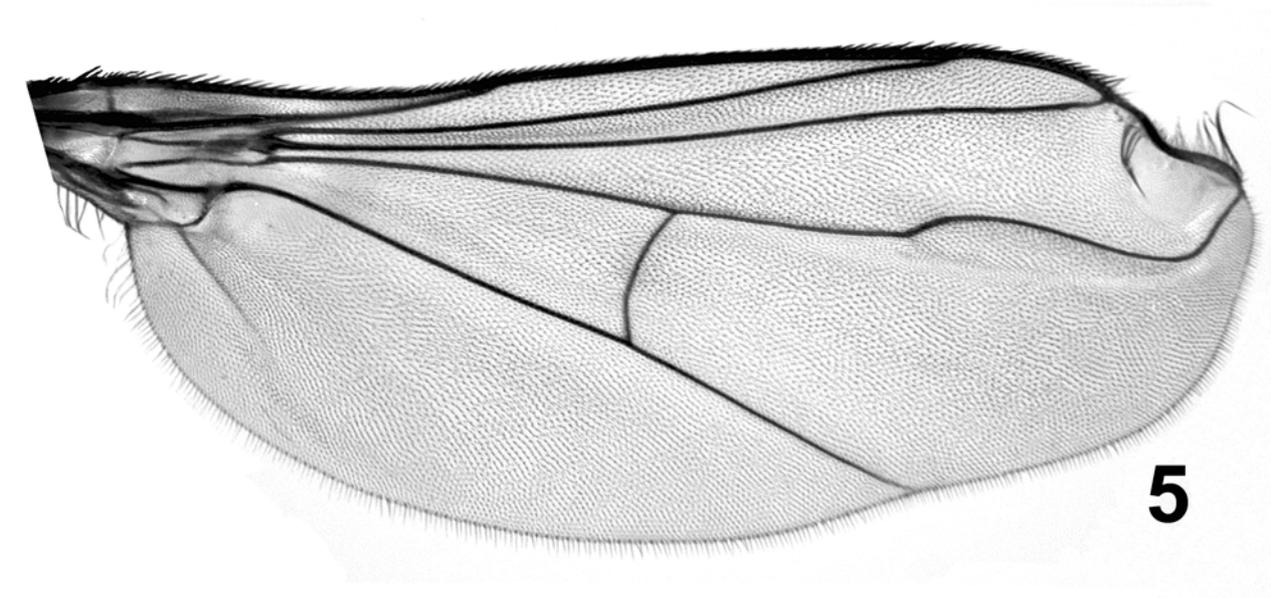
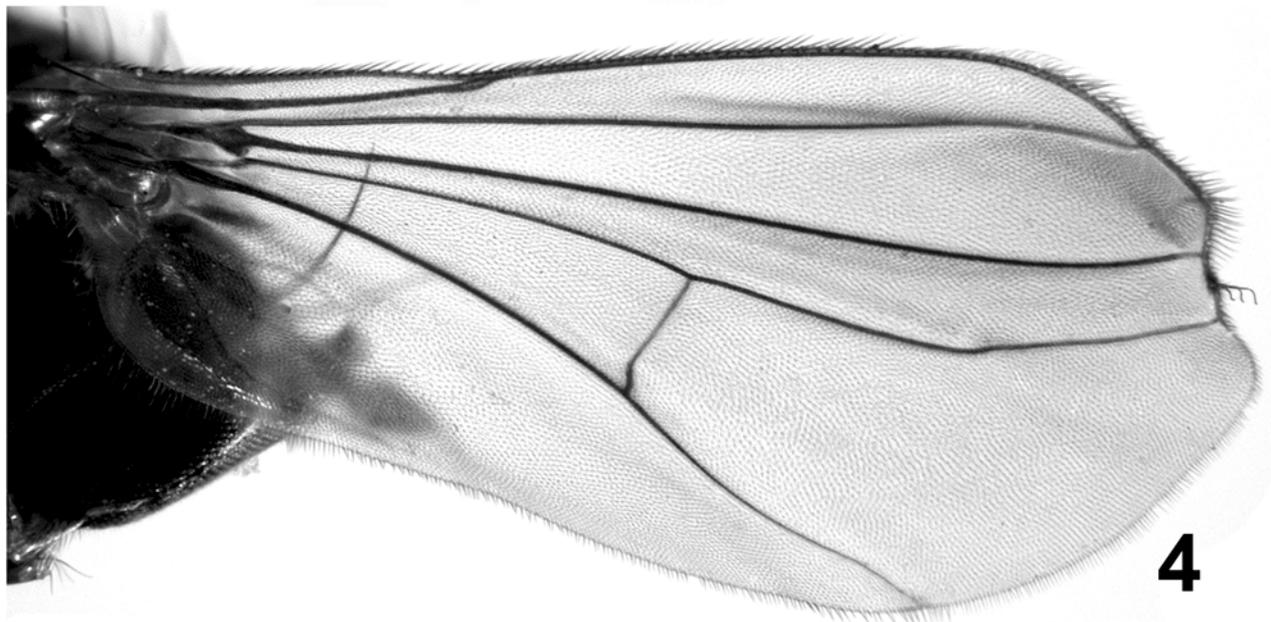
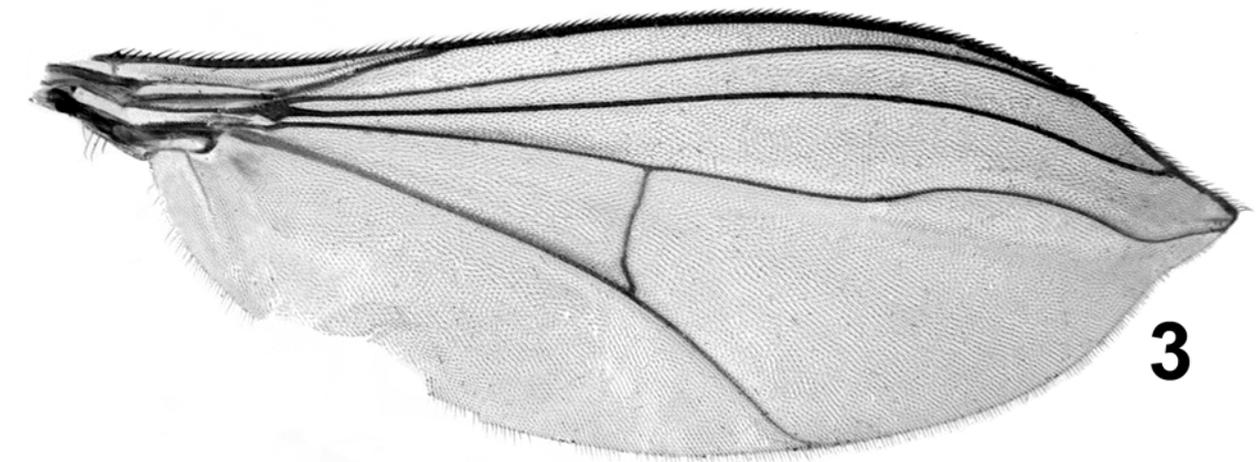
Erebomyia akidoptera Hurley & Runyon, n. sp.

(Fig. 3)

Description. Male: Body length: 3.2 mm; wing: 3.0 mm x 1.25 mm. *Head*: Face dense gray pollinose; narrowed to diameter of about 4 ommatidia at 1/2, becoming slightly broader below. Vertex blue-green, with moderately dense, rusty-gray pollen which is most dense medially. Ocellar setae long, subequal in size to dc setae. Outer vertical setae three-quarters length of ocellars. Palpus yellow-brown, triangular; with rather long, yellow-brown hairs. Scape cylindrical, shorter than first flagellomere. First flagellomere elongate triangular, twice as long as wide. *Thorax*: Mesonotum greenish-brown with moderately dense rusty-gray pollen. Pleura blue-green, with moderately dense gray pollen. Metepisternum mostly blue-green; ventral half of metepimeron yellow, dorsal half blue-green. Proepisternum with 2–3 short, white hairs on dorsal half and 2 longer, white setae on ventral half. Thorax with about 11 slender ac, about one-half length of dc. Postpronotals very short. *Legs*: Coxa I with short, sparse anterior hairs. Coxa II narrowly and diffusely darkened dorsally at base, with long, yellow-brown seta at 1/2; with yellow hairs anteromedially. Tibia II with *ad* setae near 1/4, 5/8; *pd* seta near 1/3. Tibia III with *ad* setae near 1/3, 1/2; with row of 5–7 short ventral setae; row of short setae dorsally on apical two-thirds. Ratios of tibia:tarsomeres for leg I: 13-10-6-4-3-2; for leg II: 18-13-6-4-3-2; for leg III: 26-6-9-4-2-1. *Wing* (Fig. 3): rather narrow with apex broadly acuminate; costa with tuft of 5–7 very short, slightly hooked hairs at apex. M_1 undulating beyond posterior crossvein. *Abdomen*: dark brown, with most of T2 and part of T3 diffusely yellow. T2 laterally with long, slender yellow to brown hairs. Hypopygium (not dissected); cerci relatively short, nearly parallel sided, rounded with 2–3 long yellow setae at apex. Large, hooked left hypandrial arm visible in both unprepared male specimens.

Female: Body length: 3.5 mm; wing: 3.5 mm x 1.75 mm. This is the only species in which the bend in section of M_1 beyond crossvein dm-cu occurs distinctly distal to termination of CuA_1 at wing margin.

Etymology: Specific name derives from the Greek ακιδος (*akidos*) = point and πτέρων (*ptera*) = wing, and refers to the pointed apex of the wing in males.



FIGURES 3–5. *Erebomyia*, male wings. **3.** *E. akidoptera*; **4.** *E. aetheoptera*; **5.** *E. ramseyensis*. Note: in wing of *E. aetheoptera*, the anterodistal and posterobasal margins are slightly bent forward (toward reader).

Holotype: ♂, CALIFORNIA, labeled: “U.S. Hwy 101 and Ash Cr., So. Mendocino Co Cal., VI-29-1951, W.C. Bentinck Collector”. Deposited: EMEC.

Paratypes: ♀, same data as holotype; ♂, CALIFORNIA: Sequoia National Park, VIII-6-1940, D.E. Hardy. Deposited: FSCA (♂), EMEC (♀).

Remarks: *E. akidoptera* appears to be rather widely distributed in California; it is known from the Coast Range north of San Francisco and Sequoia National Park in the southern Sierra Nevada. The type locality is not Mendocino County as on the label, but actually in northern Sonoma County.

Erebomyia exalloptera Runyon & Hurley

(Figs. 1–2, 6–7)

Description. See Runyon & Hurley (2004) for habitus photo. **Male:** Body length: 4.0–4.5 mm; Wing 3.5–4.0 mm x 1.75–2.0 mm. **Head:** Face dense gray pollinose; narrowed to width of 1 ommatidium or less just above midpoint, wider above and below. Vertex blue-green, to brownish-green, with some magenta reflections; with moderately dense gray pollen. Ocellar setae long, subequal in length to dc setae. Outer vertical setae two-thirds length of ocellars. Palpus yellow-brown, somewhat elongate, rounded apically; with long, slender, yellow-brown setae. Scape cylindrical, slightly longer than first flagellomere; mostly yellow, often partly brownish. Pedicel mostly yellow, often slightly brown. First flagellomere (Fig. 2) short triangular, a little longer than wide; somewhat rounded apically. **Thorax:** Mesonotum dark brown, with green/blue reflections; with moderately dense gray to brownish-gray pollen. Pleura blue-green with sparse gray pollen. Metepisternum and metepimeron largely yellow. Proepisternum with 2–3 short, white hairs on upper half, and 2 long white setae on lower half. Thorax with 8–12 slender ac, length about one-third of dc. Postpronotal hairs well developed, relatively long. **Legs:** Coxa I with moderately dense, yellow anterior hairs. Coxa II with blue-green color of pleura continued onto extreme base dorsally, and diffusely along *ad* edge. Tibia II with *ad* setae at 1/3, 2/3; with *pd* seta near 1/3. Tibia III with *ad* seta near 1/3, sometimes also at 2/3; with row of 5–7 short ventral setae; row of short setae dorsally on apical two-thirds. Ratios of tibia:tarsomeres for leg I: 24-17-8-5-4-2; for leg II: 30-21-9-6-3-2; for leg III: 42-9-14-7-4-2. **Wings** (Fig. 1): asymmetrical; both broad with apex mucronate; with branches of R_{2+3} and R_{4+5} crowded towards anterior edge; with R_{4+5} ending well before apex; M_1 undulating beyond posterior crossvein. Right wing excavate posterior to apex, left larger and wing smoothly convex; crossvein dm-cu occurring more distal in left wing. Costa with short, stiff spines, especially between R_{2+3} and M_1 ; with cluster of 3–5 minute hairs at apex. **Abdomen:** dark brown, with extensive yellow on T2, usually T3, and sometimes on T4. T2 with long, slender setae over entire surface (longest laterally). Hypopygium (Figs. 6–7); cerci broad at base, narrowed on apical two-thirds, with 2–3 long yellow setae at apex.

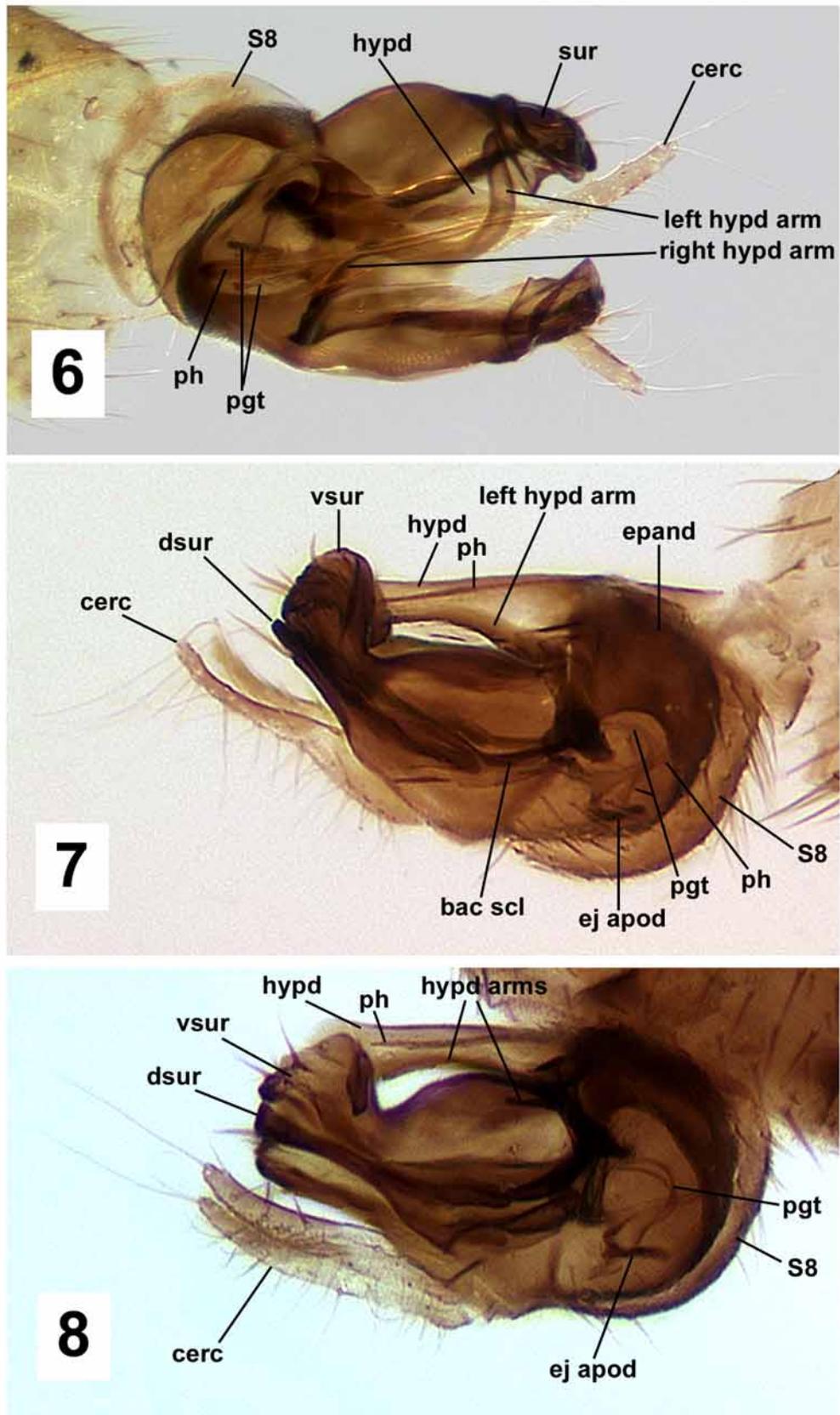
Female: Body length: 3.75–4.5 mm; wing: 3.5–4.25 mm x 1.5–2.0 mm. The following characters should separate females of this species: femur III with preapical anterior seta greater than or equal to width of femur at insertion; wing rather narrow (length distinctly greater than 2 times width); bend in section of M_1 beyond crossvein dm-cu occurring at or just basal to termination of CuA_1 at wing margin.

Remarks: *E. exalloptera* is known from two sites in southeastern Arizona: Madera Canyon in the Santa Rita Mountains and Wet Canyon in the Pinaleno Mountains (see Discussion).

Erebomyia ramseyensis Hurley & Runyon, n. sp.

(Figs. 5, 8)

Description. Male: Body length: 3.0–3.5 mm; Wing 2.5–3.0 mm x 1.25–1.50 mm. **Head:** Face dense dark gray pollinose; obliterated broadly near midpoint by encroaching eyes; narrow, recessed on lower one-fifth. Vertex blue-green, with moderately dense gray pollen. Ocellar setae long, subequal in size to dc setae. Outer



FIGURES 6–8. *Erebomyia* genitalia. **6.** *E. exalloptera*, ventral view; **7.** *E. exalloptera*, left lateral view; **8.** *E. ramseyensis*, left lateral view. Abbreviations: bac scl—bacilliform sclerite, cerc—cercus, dsur—dorsal lobe of surstylus, ej apod—ejaculatory apodeme, epand—epandrium, hypd—hypandrium, hypd arm—hypandrial arm, pgt—postgonite, ph—phallus, S8—sternite 8, vsur—ventral lobe of surstylus.

verticals one-half to two-thirds length of ocellar setae. Palpus small, yellow-brown, triangular, with dark hairs. Scape cylindrical, long (length equal to length of first flagellomere), yellow to yellow-brown. Pedicel yellow to yellow-brown. First flagellomere elongate triangular (length 2 times width), with apex rather rounded. *Thorax*: Mesonotum dark brown, with blue and/or green reflections; with sparse rusty-gray pollen. Pleura blue-green with moderately dense gray pollen. Dorsal metepisternum often brown; metepimeron blue-green dorsally. Postpronotal hairs relatively short. Proepisternum with 2–3 short, pale, hairs on upper half, 2 similar-sized hairs on lower half. Thorax with 6–10 slender ac, about one-half length of dc setae. *Legs*: Coxa I anteriorly with sparse, very short yellow hairs. Tibia II with long *ad* setae at 1/3 and 2/3; with long *pd* seta near 1/3. Tibia III with all setae short (less than or equal to width of tibia III); with 0–2 *ad* setae; row of 4–6 dorsal setae; with 4–6 very short ventral setae. Tarsomere I(2–4) slightly flattened ventrally. Ratios of tibia:tarsomeres for leg I: 16-12-5-3-3-2; for leg II: 20-14-6-4-3-2; for leg III: 27-6-10-5-3-2. *Wing* (Fig. 5): veins R₂₊₃ and R₄₊₅ slightly divergent, crowded anteriorly and ending well before wing tip; M₁ undulating beyond posterior crossvein, with sharp anterior bend near apex. Costa irregularly thickened beyond R₄₊₅; with short, erect hairs and long, hooked cilia between tips of R₄₊₅ and M₁ (longest equal to length of posterior crossvein); these cilia more or less fused apically into various hooked clumps, most notably at two places: just beyond R₄₊₅ with resulting compound, hooked “seta” projecting dorsally, and just before M₁ which projects anteriorly. *Abdomen*: dark brown with extensive paler areas on T2, T3, sometimes T4. T2 laterally with long, slender yellow to brown setae. Hypopygium (Fig. 8); cerci very slightly narrowed apically, with 1 long seta at apex and 1–2 long setae just before apex.

Female: Body length: 3.25–3.5 mm; wing: 3.5–3.75 mm x 1.50–1.75 mm. Can be distinguished from all other species by the short preapical anterior seta on femur III which is less than width of femur at insertion.

Etymology: *Erebomyia ramseyensis* is named for Ramsey Canyon in southeastern Arizona, the type locality. The Nature Conservancy graciously permitted us to collect in their Ramsey Canyon preserve, and the majority of specimens were taken there.

Holotype: ♂: ARIZONA: Cochise Co., Ramsey Canyon, Huachuca Mtns., 5500 feet, 16-IV-2003, J. Runyon & R. Hurley. Deposited: CAS.

Paratypes: 32 ♂, 9 ♀, same data as holotype; 12 ♂, 4 ♀, same data as holotype except 23-IV-2002; ARIZONA: Cochise Co.: 18 ♂, 5 ♀, South Fork Cave Creek, Chiricahua Mtns., 17-IV-2003, 5235 feet, J. Runyon & R. Hurley; Santa Cruz Co.: 14 ♂, 9 ♀, Madera Canyon, 5100 feet, 14-IV-2003, J. Runyon & R. Hurley; 1 ♂, same except 25-IV-2001; 3 ♂, Madera Canyon, 14-IV-1962, Paul A. Rude; 1 ♂, Santa Rita Mtns., Coronado Nat. Forest, Madera Canyon, 3-VI-1991, ex. bog spring, 6000 feet, B.J. Sinclair; Cochise Co.: 1 ♂, Cave Creek, 5785 feet, 7 mi. SW Portal, Chiricahua Mtns., 24-IV-2002, R. Hurley & J. Runyon; 1 ♂, 2 ♀, Miller Canyon, Huachuca Mtns., 5700 feet, 16-IV-2003, J. Runyon & R. Hurley; Pima Co.: 1 ♂, 4 ♀, Bear Creek, 5200 feet, 14 mi. NE Tucson, 26-IV-2001, R. Hurley & J. Runyon; Graham Co.: 7 ♂, 13 ♀, Wet Canyon, Jacobson Creek, 5900 feet, Pinaleno Mtns., 25-IV-2002, R. Hurley & J. Runyon; 1 ♂, 1 ♀, same except 26-IV-2001.

Paratypes (♂ and ♀) to be deposited: CAS, CNC, FSCA, EMEC, USNM; remainder in MTEC.

Remarks: *Erebomyia ramseyensis* is locally abundant and widely distributed in the ‘sky island’ mountains of southeastern Arizona (Chiricahua, Huachuca, Pinaleno, Santa Catalina, and Santa Rita mountains).

Discussion

Directional Asymmetry in Insect Wings: E. exalloptera is unique

Subtle biased asymmetry between the left and right wings appears to be widespread among insects. In a recent synthesis of directional asymmetry (DA) in wing size, Pélabon & Hansen (2008) found numerical evidence for such asymmetry in 47 insect species across seven orders. Although widespread, the extent of wing DA was small – only 0.7% of the wing size on average, and never greater than 2%. The wings of *E.*

exalloptera, therefore, are outstanding in that the left wing is about 6% larger than the right wing (Fig. 1), a degree of wing DA unknown for any other insect.

The potential adaptive significance of DA in holometabolous insects has been questioned since attempts to select for DA have failed, indicating lack of genetic variation and perhaps absence of a left-right body axis altogether (Maynard Smith & Sordhi 1960; Coyne 1987; Tuinstra et al. 1990; Monedero et al. 1997). In their review, Pélabon & Hansen (2008) found expression of wing DA to be extremely imprecise and conclude that it cannot have any major adaptive value: the small amounts of DA found would simply be overwhelmed by individual variation and developmental instability. However, the DA exhibited in *E. exalloptera* must result from distinct left-right sides, seems to be very precise, and is certainly not swamped by intrinsic developmental variation. Examination of the 28 known male specimens of *E. exalloptera* (collected at two sites about 150 km apart) reveals no discernable variation in size and shape between the left and right wings. The striking degree and apparent accuracy of DA, its occurrence solely in males, and observations of courtship behaviors suggest that wing asymmetry in *E. exalloptera* does have adaptive value (see below). This agrees with recent findings suggesting that DA in wing size and shape of *Drosophila* could evolve (Pélabon et al. 2006; Rego et al. 2006).

The Wing Modifications of Erebomyia Likely Function in Courtship

The possession of modified wings by only males of *Erebomyia* suggests they may serve a signaling function in courtship (Zimmer et al. 2003). A role for male wings as signals to females is further supported by the mating behavior of *E. exalloptera* and *E. ramseyensis* (observations of *E. exalloptera* were made in Arizona: Graham Co., Pinaleno Mts., Wet Canyon on 25-IV-2002 and 17-IV-2003; *E. ramseyensis* in Arizona: Cochise Co., Huachuca Mts., Ramsey Canyon on 23-IV-2002 and 16-IV-2003). The behaviors of *E. exalloptera* and *E. ramseyensis* are similar. Males and females occur in large numbers (estimated up to 20 per m²) on near vertical to overhanging, bare, dry rock within dark cavities. Males hover rather slowly close to rock face and quickly, but gently, tap any small dark spot on the rock. Resting males, when tapped, either fly or fan their wings in short bursts. When females are tapped they typically walk forward several millimeters. Males land directly behind females and approach to within 2 mm and will very quickly tap them, usually twice in rapid succession (both taps take about 1 second), by lurching forward without raising his legs. The tapped female sometimes flies away or walks forward several centimeters. If the female walks forward, the male pursues, repositions himself, and taps the female again. After several taps, the male extends his wings horizontally and fans them in a series of short bursts lasting 1–2 seconds, with 1–2 seconds separating bursts. If the female does not fly or walk away, the male will position himself above her abdomen and attempt to copulate while continually fanning his wings. Interestingly, females appear to be very choosy since males were almost always rejected and potentially successful copulations (female did not immediately fly away when male mounted) occurred in only two of the more than 50 events observed.

The dark habitat in which *Erebomyia* occur and their presence on rock seems to preclude any major role for visual or substrate vibration cues during courtship. However, males of other fly species exhibit wing-fanning behaviors similar to *Erebomyia* (Burk 1981; Tauber & Eberl 2003) which produce airborne sounds that can be used by females to judge and select mates (Sivinski et al. 1984; Hoikkala et al. 1998) or to recognize species (Saarikettu et al. 2005). If male *Erebomyia* communicate with females via wing-fanning, the species-specific shapes and hairs of male wings could produce distinct sounds and might have evolved via sexual selection. For example, it is known that the sound produced during flight changes with wing shape and length (Wülker 1985; Wekesa et al. 1998).

The asymmetrical wings of *E. exalloptera* seem to require further explanation. Because such pronounced wing asymmetry is clearly likely to adversely affect flying ability (McLachlan 1997) and predator avoidance (Møller 1996), we previously proposed the ‘handicap principle’ as an explanation (Runyon & Hurley 2004). Females prefer males with asymmetrical wings because they are costly to possess and maintain, and so are a reliable measure of quality. Wing asymmetry could be assessed using the sounds produced during wing-fanning. Males of *E. exalloptera* are able to compensate for differences in lift and thrust created by each wing

since observations show that they fly normally and can hover. However, why similar wing asymmetry has not evolved in other groups with similar behaviors (e.g. more than 100 species of *Drosophila* are known to produce courtship songs; Tauber & Eberl 2003) or elsewhere in the animal kingdom remains an enigma. Further research is needed to better understand the circumstances and selective pressures behind the origin and maintenance of wing asymmetry in *E. exalloptera* – findings that should be of interest and have broad implications in a variety of fields, including development, flight, communication, and natural selection.

Acknowledgments

We thank Mike Ivie (MTEC) for allowing us to use his Syncroscopy AutoMontagePro® system to create digital images, and Katie Hopp (MTEC) for help operating this system. Thanks go to Gary Steck (FSCA), Jeff Cumming (CNC), and Sherly Barr (EMEC) for loan of specimens, and the staff of other institutions that permitted us to visit and search for specimens. Thoughtful comments from Marc Pollet improved this manuscript.

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