DROSOPHILA MAYA, A NEW NEOTROPICAL MEMBER OF THE DROSOPHILA OBSCURA SPECIES GROUP (DIPTERA: DROSOPHILIDAE)

WILLIAM B. HEED¹ AND PATRICK M. O'GRADY²

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 (E-mail: wheed@u.arizona.edu)

²Department of Entomology, American Museum of Natural History, Central Park West @ 79th Street, New York, New York 10024 (E-mail: ogrady@amnh.org)

Abstract.—A new Neotropical member of the *Drosophila obscura* species group from El Salvador and Honduras, *Drosophila maya*, is described. This species belongs to the New World *pseudoobscura* subgroup and, based on a variety of internal and external morphological characters, is most closely related to *D. lowei*. This species is distinguished from other members of the *pseudoobscura* subgroup by the shape of the hypandrium and by having fewer teeth on the sex combs. Ecologically, *D. maya* inhabits cloud forests at elevations around 2,000 m in El Salvador and Honduras. A key to eight members of the *obscura* species group which have been recorded in and near the Neotropical region is presented.

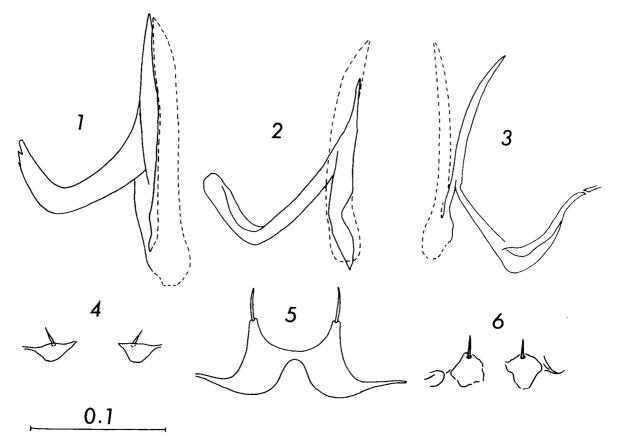
The obscura species group of the subgenus Sophophora has been the subject of many evolutionary studies (e.g., Dobzhansky and Powell, 1975; Powell, 1997). The obscura group is divided into five subgroups; affinis, microlabis, obscura, pseudoobscura, and subobscura. The obscura subgroup occurs in Europe and Asia (Lakovaara and Saura, 1982). Species in the subobscura subgroup are found in the western Palearctic as well as northern Africa (Lakovaara and Saura 1982). The microlabis subgroup is found only in the Afrotropical Region (Tsacas et al., 1985; Cairou et al., 1988). The affinis and pseudoobscura subgroups are found mainly in the New World temperate and tropical zones (Lakovaara and Saura, 1982), although two species from the Old World, D. helvetica and D. epiobscura, may belong to the affinis subgroup. Here we describe Drosophila maya, a new member of the pseudoobscura subgroup. Drosophila maya is known exclusively from the Neotropical montane forests of El Salvador and Honduras where it was collected in 1954 at elevations of about 2,000 m. The existence of D. maya in these two countries extends the distribution of the pseudoobscura subgroup beyond Guatemala in Central America. Drosophila maya is one of the 67 undescribed species in the genus Drosophila from El Salvador listed by Heed (1957).

Drosophila maya, new species

Figs. 3, 6, 7

Diagnosis. Drosophila maya can be distinguished from other members of the Drosophila pseudoobscura subgroup by the numbers of teeth on its proximal (3–5) and distal (2–4) sex combs and by the shape of the hypandrium (Figs. 1–6).

Description. (from pinned specimens) $\delta \circ Head$: Arista with 3 dorsal and 2 ventral branches in addition to terminal fork. From dull light brown, darker in ocellar tri-



Figs. 1-6. Male terminalia of three closely related species of the *Drosophila pseudoobscura* subgroup. Ventral view of posterior paraphyses (solid line) and aedeagus (dotted line). 1. *D. pseudoobscura*; 2. *D. lowei*; 3. *D. maya*. Ventral view of hypandrial setulae. 4. *D. pseudoobscura*; 5. *D. lowei*; 6. *D. maya*. Scale = 0.1 mm.

angle; ocelli brown. Proclinate orbital about ¾ length of anterior reclinate and ⅓ length of posterior reclinate. Distance from proclinate orbital to anterior reclinate one half that of distance from anterior reclinate to posterior reclinate. Face dull brown. Carina dull brown; narrow at the top; widening ventrally to three times the width at top. Palpus tan. Vibrissa strong. Subvibrissa thin and weak, about one half length of vibrissa. Proboscis dull tan. Cheek gray-brown, about ⅓ width of eye. Eye dull red.

Thorax. Acrostichal setulae in 6 rows; prescutellar setulae absent. Mesonotum unicolorous dark brown. Pleurae dark brown, subshining. Scutellum dark brown, but lighter at margin. Anterior scutellar setae slightly convergent; posterior scutellars cruciate. Halteres dull gray. Anterior katepisternal seta ½ length of posterior one. Mid katepisternal seta weak. Legs dull yellow with very faint light brown banding at joints. Proximal sex comb on basitarsus of front leg with 3–5 teeth; distal sex comb on second tarsomere with 2–4 teeth. Wings clear; veins dark brown; region between costa and second long vein slightly smoky in appearance.

Abdomen. Dark brown to black in males, shining dorsally, gray ventrally. Lower tip of cercus constricted and clustered with 8–10 setae. Surstylus (clasper) with 7–9 prensisetae (primary teeth) in a straight row and 2–3 secondary teeth outside prensisetae row. Posterior paraphyses same length as aedeagus (Fig. 3); anterior

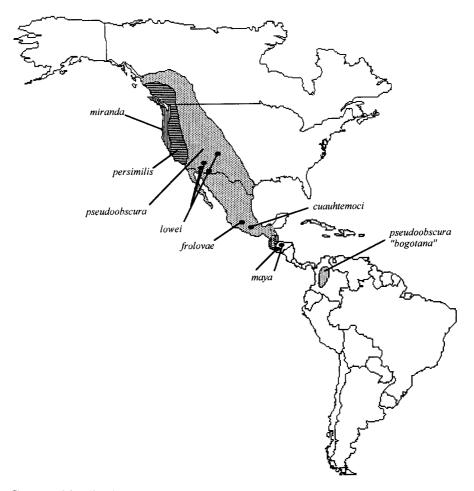


Fig. 7. Geographic distribution of seven species of the *Drosophila pseudoobscura* subgroup from North and South America. The three species *D. pseudoobscura*, *D. persimilis*, and *D. miranda* are sympatric in California, Oregon, Washington and British Columbia.

paraphyses slightly longer than aedeagus. Hypandrium with one pair of paramedian bristles, which extend ¹/₁₂ the distance to the tip of the aedeagus (Fig. 6). Penis index, the length of the penis divided by the width of penis' lamina, (Rizki, 1951) 10.5. Females dark brown and shining dorsally with posterior half of tergites 4 and 5 black, gray ventrally.

Measurements. N = 4 δ , 1 \circ . Thorax length, 0.8 mm δ (range: 0.6–0.95); 1.25 mm \circ . Wing length, 2.19 mm δ (range: 2.0–2.25); 3.0 mm \circ . Costal index, 2.5; 4th vein index, 2.0; 4c index, 0.85; 5x index, 2.0.

Type material. Holotype δ , EL SALVADOR, Cerro Monte Cristo, 2,100 m, 4-6.ii.1954, W.B. Heed (Collection Number H44.12). Paratypes: EL SALVADOR: 2 $\delta \delta$, 1 \circ , same data as holotype. HONDURAS: 1 δ , Monte Uyuca, 10 km northwest of Zamorano, 1,800 m, 22–25.iii.1954, W.B. Heed (Collection Number H49.22). The type material and genitalia preparations used in this study have been deposited in the collection of the Department of Entomology at the American Museum of Natural History.

Etymology. The name *D. maya* refers to the group of American Indian peoples inhabiting the Yucatan Peninsula, Honduras, Guatemala, and El Salvador.

Distribution and ecology. Drosophila maya is known from two collections in Cen-

tral America (Fig. 7). The first collection was made between 4–6 February, 1954, on Cerro Monte Cristo, El Salvador, close to the northwest borders with Guatemala and Honduras. Temperatures ranged from 5 °C at night to 16 °C during the midafternoon. Fourteen individuals were netted over banana bait placed in a *Quercus-Podocarpus* cloud forest at an elevation of approximately 2,100 m. Carson (1951) and Heed et al. (1976) have shown that oak trees serve as breeding sites for some Nearctic members of the *pseudoobscura* subgroup. Therefore, the presence of *Quercus* may also have significance as a breeding site for *D. maya* in the Neotropics. The second collection was made between 22 and 25 March, 1954, on Monte Uyuca, Honduras, 10 km to the northwest of the city of Zamorano. A total of twenty individuals were netted over grapefruit bait in a cloud forest at an elevation between 1,300 and 1,800 m. Based on these collections, the habitat of *D. maya* seems to be restricted to higher elevations with mixed temperate and tropical vegetation.

Behavior. Drosophila maya is extremely sensitive to ether. Nearly all flies exposed died very rapidly after exposure and a culture of live flies could not be established. Relationship. Drosophila maya is a member of the pseudoobscura subgroup of the Drosophila obscura species group, subgenus Sophophora. This species is closely related to D. lowei, a species found on several mountain "islands" in southern Arizona and on the Colorado plateau in Arizona and Colorado (Heed et al., 1969). Drosophila maya resembles D. lowei in its smaller size compared to D. pseudoobscura. Drosophila maya and D. lowei also have fewer teeth on the proximal sex comb (3–5 vs. 4–6, respectively) and the distal sex comb (2–4 vs. 3–5, respectively) when compared to D. pseudoobscura, which has 6–8 teeth on the proximal and 4–6 teeth on the distal sex combs.

The male genitalia of all three species are compared in Figs. 1–6. The hypandrium process, the basal portion of the paramedian spines, is extremely protruded in *D. lowei* (Fig. 5), slightly swollen in *D. maya* (Fig. 6), and nearly flattened in *D. pseudoobscura* (Fig. 4). The number of prensisetae on the surstylus is also higher in *D. maya* and *D. lowei* (7–9 and 9–11, respectively) than in *D. pseudoobscura* (6–7). These characters indicate that *D. maya* and *D. lowei* are morphologically more similar to one another than either are to *D. pseudoobscura*. However, the penis indices (Rizki, 1951) of *D. pseudoobscura* (8.6) and *D. lowei* (8.5) are the same (Heed et al., 1969), while this measurement in *D. maya* (10.5) is quite different.

Remarks. The *obscura* species group presently contains approximately six dozen described species (Gleason et al., 1997; Watabe et al., 1996; Watabe and Sperlich, 1997) and is placed in the subgenus *Sophophora* as the sister group of the *melanogaster* species group. The common ancestor of the *melanogaster* and *obscura* groups is thought to have evolved from a "protomelanogaster" lineage in the Asian tropical region (Throckmorton, 1975). The *melanogaster* species group has diversified mostly in the Old World tropics (Lachaise et al., 1988). The *obscura* group, on the other hand, probably originated in the Old World, diversified in the Palearctic, and colonized the Nearctic via the Bering Land Bridge, probably prior to the mid-Miocene (Throckmorton, 1975).

In lower geographic latitudes the *obscura* group is restricted to high elevation habitats with cool climates, e.g., the *microlabis* subgroup in the Afrotropical Region (Tsacas et al., 1985; Cariou et al., 1988), the *obscura* subgroup in southern China (Watabe et al., 1996; Watabe and Sperlich, 1997), and the recent colonization of the

Neotropical Region by a member of the *subobscura* subgroup, namely, *D. subobscura* (Brncic and Budnik, 1980; Val et al., 1986). Similarly, several members of the *pseudoobscura* subgroup are found in the highlands of the Neotropical Region (Fig. 2). Two uncommon species, *D. frolovae* and *D. cuauhtemoci*, are found in small numbers in Central Mexico, possibly restricted to single mountain ranges (Wheeler, 1949; Felix et al., 1976). *Drosophila pseudoobscura*, a widespread species, is sympatric with these two forms and further extends into the highlands of southern Mexico and Guatemala. A disjunct subspecies, *D. pseudoobscura bogotana*, is found in the highlands of Colombia (Prakash, 1972). *Drosophila maya* and *D. lowei* also inhabit higher elevations that are widely disjunct. The former is found in the highlands of Central America, the latter in the southern Rocky Mountains of Colorado and the mountains of the Basin and Range Province in southern Arizona.

Lakovaara and Saura (1982) have categorized *D. lowei*, *D. frolovae*, *D. cuauhtemoci*, and *D. maya* (known, but undescribed at that time) as the less known southern forms of the *pseudoobscura* subgroup. They considered these species to be relictual and proposed two hypotheses to explain the current distributions. One hypothesis states that these species could be the result of an earlier colonization of the New World from Asia. The other hypothesis proposes that these species represent forms close to the ancestors of *D. pseudoobscura* and its relations. Phylogenetic analysis of the nucleotide sequences indicates that *D. lowei* is basal to the other members of the *pseudoobscura* subgroup (Beckenbach et al., 1993; O'Grady, 1999), a result which supports the second hypothesis. Additional phylogenetic data will be required to resolve these two hypotheses.

KEY TO THE NEOTROPICAL DROSOPHILA OBSCURA GROUP SPECIES

This key is intended to identify the members of the *Drosophila obscura* species group that have been reported from Mexico, Central America, the West Indies, and South America. This key can be substituted for couplets 30–32 in Patterson and Mainland's (1944) key. It necessarily relies heavily on the characteristics of male morphology, as the females of some species are practically indistinguishable. Key characteristics of species we have not examined directly were obtained from Sturtevant and Dobzhansky (1936), Patterson (1943), Patterson and Mainland (1944), Hsu (1949), Wheeler (1949), Sulerud and Miller (1966), Shorrocks (1972), and Felix et al. (1976).

4.	Proximal and distal segments of sex combs with 9 or more teeth
	Proximal and distal segments each with fewer than 9 teeth
5.	Slightly enlarged setulae in prescutellar position; proximal sex comb with usually be-
	tween 14-16 teeth; distal sex comb with about 10-11 teeth. Michoacan, Mexico
	D. frolovae Wheeler
	Prescutellar setulae short, not as above; proximal sex comb with 10-15 teeth; distal
	sex comb with 9-13 teeth; external process of epandrium rounded and bulging at base
	and drawn out into a thin projection; surstylus large and cup shaped, laterally com-
	pressed and containing a very short and square looking comb with 6-8 teeth. Chile
	D. subobscura Collin
6.	Proximal sex comb with 6–8 teeth; distal sex comb with 5–6 teeth; surstylus with 6–7
	prensisetae. British Colombia to Guatemala, Bogota, Colombia
	D. pseudoobscura Frolova
-	Proximal sex comb with less than six teeth; distal sex comb with four or fewer teeth
	7
7.	Tibiae of the middle legs broadened, with rows of long bristles on either side. Mi-
	choacan and Hidalgo, Mexico D. cuahtemoci Felix and Dobzhansky
_	Tibiae of middle legs normal in width, not broadened; no elongate seta present on
	middle tibiae
8.	Mesonotum blackish, with a bronze-like sheen. Hypandrial setae highly elevated (Fig.
	5). Mountain habitats in Colorado, southeastern Arizona and probably southward into
	Mexico along the Sierra Madre Occidental
	Mesonotum unicolorous dark brown. Hypandrial setae only slightly elevated (Fig. 6).
	El Salvador, Honduras

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