



## New species of Hawaiian picture wing *Drosophila* (Diptera: Drosophilidae), with a key to species

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### Abstract

The picture wing species group of Hawaiian *Drosophila* is the only one to be relatively well known taxonomically, but species continue to be discovered. Here seven new species are described: *Drosophila kikiko* **new species**, *Drosophila kinoole* **new species**, *Drosophila moli* **new species**, *Drosophila nukea* **new species**, *Drosophila opuhe* **new species**, *Drosophila pihulu* **new species**, and *Drosophila pilipa* **new species**. In addition, the male of *Drosophila oreas* Hardy is described for the first time, and *Drosophila virgulata* Hardy & Kaneshiro is reduced to a **new junior synonym** of *Drosophila lanaiensis* Grimshaw, and the status of the latter and *Drosophila ciliaticrus* Hardy is clarified. A complete key to all the picture wing species is provided.

**Key words:** Hawaii, Idiomyia, *Drosophila* taxonomy, endangered species

### Introduction

The Hawaiian picture wing *Drosophila*, numbering over 100 species, are unusual among the endemic insect fauna of the Hawaiian Islands for being both relatively charismatic and recognizable, and biologically well-studied. This is largely due to a concerted effort by a number of prominent researchers in the 1970's, including a series of taxonomic papers by D. Elmo Hardy and Kenneth Kaneshiro (1965–1978) which ended with 105 described species. Many other researchers contributed to the broader Hawaiian *Drosophila* Project, providing information on all aspects of their genetics, evolution, and behavior (e.g., Carson, 1992; Clayton, 1966; Heed, 1968; Kambysellis & Heed, 1971; Montgomery, 1975; Spieth, 1980). Despite continued interest in the group, only four species have been described since then, and it is notable that of these only one (*D. mulli*; Perreira & Kaneshiro, 1990) was first collected after 1978. In contrast, other groups of Hawaiian *Drosophila* continue to have significant numbers of species discovered (Hardy & Kaneshiro, 1979; Hardy, *et al.*, 2001; Magnacca & O'Grady, 2008b; 2009; O'Grady, *et al.*, 2003), and a large backlog of undescribed taxa exists in collections. The lack of additional species discoveries in the *picture wing* group may also be related to the general decline that has taken place in abundance since that time, particularly after the introduction of the western yellowjacket, *Vespa pensylvanica* (Carson, 1986). Twelve species are currently listed as endangered or threatened (U.S. Fish and Wildlife Service, 2006), and many more are at high risk of extinction.

This paper describes seven new species, three of which are newly-discovered from the island of Kaua'i. The other four have existed for some time in collections, but were never formally described, no doubt in part due to their rarity and similarity to named species. Only one species of the latter group has been collected since 1973, and two are known from single individuals. Three previously-described species, *D. ciliaticrus*, *D. lanaiensis*, and *D. oreas*, are redescribed; all are of conservation significance.

At least three additional species are known but remain undescribed. One female, listed as “species near *peniculipedis*” in Montgomery (1975), was reared from *Touchardia* bark on Hawai'i. This specimen cannot be located, and no additional specimens have been found despite rearing from *Touchardia* at other locations. Two females identical to *D. liophallus* were collected from Hawai'i island (Pu'u La'ala'au, Kohala Mts., 4000', 3–4.viii.1966,

H. L. Carson, UHIM). They almost certainly represent a separate species, since there are no picture wing species shared between Maui and Hawai‘i. However, no males have ever been found and there are no recent specimens of it, or of *D. liophallus*, for genetic testing. No other members of this subgroup are known from Hawai‘i, and the hostplant, *Pleomele hawaiiensis*, is now extremely rare in the wild, with less than 400 individuals (the majority in sites too dry for *Drosophila*) and little reproduction (U.S. Fish and Wildlife Service, 2003). Finally, while this paper was in review, a single female was collected on Maui (Waikapū Valley, 2300 ft., 16.x.2011, S. L. Montgomery). The wing pattern is very similar to *D. alsophila* from Hawai‘i, but it has a distinct dorsal stripe like *D. kinoole*, suggesting it is related to both.

The last complete key to Hawaiian *Drosophila* was published in 1965 (Hardy, 1965), when there were 232 species by the current circumscription (several species groups were separated as genera at the time, while some aberrant *Scaptomyza* were included with *Drosophila*). It is a synoptic key that often groups completely unrelated species based on peculiar convergent characters, such as the presence of elongate acrostichal setae. Since then, 184 species have been described, primarily in revisions of single species groups (Hardy, 1977a; Hardy & Kaneshiro, 1979; Hardy, *et al.*, 2001; Magnacca & O’Grady, 2008b; 2009; O’Grady, *et al.*, 2003; O’Grady, *et al.*, 2001). Below, a new key to separate the major species groups of Hawaiian Drosophilidae, as well as a comprehensive key for the *picture wing* group and related species, is provided to help researchers and resource managers identify the increasing number of species. While new species continued to be discovered across the radiation, only three major assemblages—the *bristle tarsus* and *ciliated tarsus* subgroups of the *modified tarsus* group, and the *dissita* subgroup of the *modified mouthparts* group—are not currently covered by revised keys into which new species can be readily placed. Each of these three contains about 20 named species, with at least an equal number undescribed.

## Material and methods

Material comes from historic pinned specimens and recent collections (2009–2011). Specimens were either caught on fermented banana and mushroom baits, or reared in the laboratory from wild-caught individuals or rotting host plant substrates. All historic material is from the University of Hawai‘i Insect Museum (UHIM), except type material which is at the B. P. Bishop Museum (BPBM). Holotypes and allotypes of new species have been deposited at the UHIM, and paratypes at B. P. Bishop Museum (BPBM) as noted. The UHIM collection was extensively used in constructing the key. Other specimens are currently held at the University of Hawai‘i–Hilo research collection (D. Price lab) for ongoing study and will ultimately be deposited at BPBM or UHIM; they are not designated as paratypes. See Figure 2B for definition of wing characters.

## Keys

The key to species groups is necessarily based on males, and relies heavily on secondary sexual characters. Mouthpart and leg characters in this key refer to males only unless otherwise specified. Citations for the most recent species-level keys to the groups are provided, where available. Females may be partially separated by the form of the ovipositor: in the majority of the *modified tarsus* group (*antopocerus*, *split tarsus*, *spoon tarsus*, and *bristle tarsus* subgroups), it is strongly sclerotized, toothed ventrally, and pointed and slightly beaked apically; in the *modified mouthparts* group, it is broadly triangular, not as strongly sclerotized, and rounded apically. The paraphyletic *ciliated tarsus* subgroup contains some species with both forms, but predominantly the latter. Species in the *picture wing* clade (including the *nudidrosophila* group) have an elongate, tubular, slightly curved ovipositor, except for the *adiastola* group, which resemble the *modified mouthparts* type. For a review of ovipositor shapes, see Craddock and Kambysellis (1997).

*Picture wing* species of both sexes are immediately recognizable due to their wing patterns. Thus, in making the key to them, we have attempted to utilize characters that are not sexually dimorphic as much as possible, in order to enable identification of females. However, it is important to note that certain wing markings (notably the median spots along the anterior margin and on R<sub>4+5</sub>) may be reduced or absent in aberrant or teneral individuals, which may then fail to key properly. Species with frequent variation, sexual dimorphism, or potentially confusing interpretation of color characters (*D. ciliaticrus*, *D. nigribasis*, *D. odontophallus*, *D. prostopalpis*, and *D. punalua*) are keyed out twice.

The key to the *picture wing* clade includes all species in the clade, with the exception of the *nudidrosophila/ateledrosophila* group. The latter are now recognized as being derived from within the *picture wing* clade (O’Grady, *et al.*, 2011), but are morphologically highly divergent and a key to the species is found in Magnacca & O’Grady (2008b). Due to convergence in many characters, the recognized species groups and subgroups (O’Grady, *et al.*, 2010) do not fully cluster in the key; they are only named when they do.

## Key to species groups

1. Usually with only one ventral ray on the arista in addition to the apical fork, or none. Mesonotum often with only 2–4 rows of acrostichal setulae between the dorsocentral setae. Males without modified setae on the legs or mouthparts (rarely with long setae on the femora). Male genitalia with surstyli conspicuously developed, visible without dissection; epandrium, cerci, or both with enlarged ventral lobes. Ovipositor usually either soft and fleshy, or strongly sclerotized, thin and lanceolate . . . . . *Scaptomyza* (Magnacca & O’Grady, 2008a)
- Arista almost always with at least two ventral rays in addition to the apical fork. Mesonotum always with 6 or more rows of acrostichal setulae. Males usually with conspicuous secondary sexual characters, including elongate or thickened setae on the front legs, elaborations of the front tarsi, modified frontal setae, and/or modified mouthparts. Surstyli small and quadrate, almost completely hidden in lateral view; rarely with lobes on either the epandrium or cerci, never both. Ovipositor moderately to strongly sclerotized, triangular to elongate tubular; not fleshy or needle-like. Hawaiian *Drosophila* . . . . . 2
- 2 (1). Thorax and abdomen predominantly black, except the pleura sometimes partly or entirely yellow. Scutellum usually yellow or white apically, labellum of male usually with a sclerotized black rim; always with at least one of these two characters . . . . . *haleakalae* group (Hardy, *et al.*, 2001)
- Coloration variable but never black with the scutellum apically pale. Labellum of male rarely with a sclerotized black rim, if so then the thorax is brown . . . . . 3
- 3 (2). Front basitarsus of male with a prominent dorsoapical lobe extending beyond insertion of second segment; front tarsus with only four segments . . . . . *split tarsus* group (Hardy & Kaneshiro, 1979)
- Front basitarsus of male sometimes expanded dorsally but never with an apical lobe (rarely the second segment is lobed); all tarsi with five segments. . . . . 4
- 4 (3). Front basitarsus of male with three or more (rarely only one) strong, usually spine-like setae at or near the apex; usually without long cilia along its length, if more than two present then the second tarsal segment is projected into a dorsal lobe (polyphyletic) . . . . . *bristle tarsus* group
- Front basitarsus of male without apical spine-like setae, either with multiple elongate cilia along the segment or unadorned; second tarsal segment not lobate except in *D. polliciforma* . . . . . 5
- 5 (4). Second tarsal segment of male shorter than the third, usually broad, concave on the anterior surface, spoon-like . . . . . *spoon tarsus* group (Lapoint, *et al.*, 2009)
- Second tarsal segment of male not as above, longer than third and cylindrical except in *D. atroscutellata*, *D. fastigata*, and *D. gubleri*, which have the basitarsus short and quadrate but not concave . . . . . 6
- 6 (5). Anterior surface of male front tibia flattened and bare, lacking any setae or fine setulae. First and second antennal segments of male elongate, second as long as third or nearly so; arista with dense hairs dorsally, bare on ventral surface . . . . . *antopocerus* group (Hardy, 1977b)
- Front tibia of male with fine setulae over entire surface and cylindrical; occasionally flattened antero-posteriorly or bare dorsally, but never both. First antennal segment very small and ring-like, second much smaller than third; arista with both dorsal and ventral branches . . . . . 7
- 7 (6). Male labellum modified with spinose setae or at least a conspicuous lateral sclerite fringed with hairs. Wings with markings only at the apex, crossveins, and/or basal margin except in the *fuscoamoeba* subgroup, in which veins R<sub>4+5</sub> or M are sinuate and/or the apex of R<sub>4+5</sub> is on the anterior wing margin; or anterior half of wing diffusely infuscated, but without discrete spots . . . . . 8
- Male labellum lacking modifications except in *D. ornata* and the *D. varipennis* complex, which do not have the veins modified as above. Wing markings variable, sometimes extensively marked with discrete spots . . . . . 11
- 8 (7). Male labellum with an articulated rod-like appendage dorsally, fleshy labellar lobes present. Ovipositor elongate, parallel-sided, similar to the *picture wing* clade. Kaua’i . . . . . *D. adventitia* Hardy, 1965
- Male labellum without an articulated appendage; if appearing to have a sclerotized appendage, it is formed from the labellar sclerite and the fleshy lobes are absent. Ovipositor triangular, relatively short . . . . . 9
- 9 (8). Male labellum without a sclerotized apical rim, but with at least some spinose setae except in the *hirtitarsus* subgroup. Body color variable, often dark brown to black. Most species with at least some elongate cilia on the front tibia, tarsus, or both . . . . . *modified mouthparts* group (Magnacca & O’Grady, 2009; O’Grady, *et al.*, 2003)
- Male labellum with a sclerotized black rim, similar to the *haleakalae* group; without spinose setae. Thorax rufous to yellow. Lacking elongate cilia on the front legs except in *D. rustica* . . . . . 10
- 10 (9). Smaller species, wing length 1.8-3.0 mm. Male labellum with two short, conical setae near the dorsal margin. . . . . *rustica* group (O’Grady, *et al.*, 2001)
- Larger species, wing length 4.9-6.2 mm. Male labellum without distinct conical setae. Kaua’i . . . . . *D. primaeva* Hardy & Kaneshiro, 1968 and *D. sharpi* Grimshaw, 1901

- 11 (7). Wings with markings well-defined, always with a subbasal mark in cell Sc and at least one mark at the wing apex, often with a mark on the mid anterior margin or more extensively infuscated; or markings diffuse and covering most of the wing, or along entire anterior margin . . . . . *picture wing* group  
 - Wing markings poorly defined and more restricted; if present, usually anteroapical, never with a subbasal mark . . . . . 12
- 12 (11). Preapical protuberance of aedeagus small and inconspicuous. Ovipositor tapering, usually toothed ventrally, held horizontally at rest . . . . . *ciliated tarsus* group  
 - Preapical protuberance of aedeagus prominent, hooked or triangular. Ovipositor elongate, parallel-sided, without teeth, usually held vertically at rest . . . . . *nudidrosophila/ateledrosophila* group (Magnacca & O'Grady, 2008b)

## Key to picture wing species

1. Wing with an extra crossvein between  $R_{4+5}$  and M. . . . . 2  
 - Wing with normal venation . . . . . 20
- 2 (1). Basal 2/3 of wing above  $CuA_1$  entirely dark brown. O'ahu . . . . . *D. nigribasis* Hardy, 1969 (males)  
 - Basal portion of wing with at least some hyaline areas . . . . . 3
- 3 (2). Wing mottled with numerous dark spots and hyaline areas . . . . . 4  
 - Wing predominantly hyaline, with marks on crossveins, apex, and anterior margin . . . . . 6
- 4 (3). Extra crossvein in cell  $R_3$  slightly basad of dm-cu crossvein; wing largely dark and highly mottled, five small hyaline spots in cell  $R_1$ . Setae of T6 normal. O'ahu. . . . . *D. neogrimshawi* Hardy & Kaneshiro, 1968  
 - Extra crossvein in cell  $R_3$  about halfway between r-m and dm-cu crossveins; wing marks larger, only one or two large hyaline areas in cell  $R_1$ . Setae of T6 clavate in male, flattened apically . . . . . 5
- 5 (4). Wing of male with a large quadrate brown mark extending from the middle of  $R_{4+5}$  to the costa. East Maui. . . . .  
 . . . . . *D. clavisetae* (Hardy, 1966)  
 - Wing of male without a large quadrate mark; cell  $R_3$  with narrow transverse brown marks near the middle, and cell  $R_1$  with an elongate mark near the costa. West Maui . . . . . *D. neoclavisetae* Perreira & Kaneshiro, 1990
- 6 (3). Head short and broad, front three times wider than long in male, two times longer than wide in female. Hawai'i . . . . .  
 . . . . . *D. heteroneura* (Perkins, 1910)  
 - Head normal, front about as long as wide . . . . . 7
- 7 (6). Anterior margin of wing almost entirely infuscated, about as strong as other wing marks. Basal edge of apical wing mark distinctly diagonal, mark on M shorter than that on  $R_{4+5}$ . At least posterior half of scutellum yellow . . . . . 8  
 - Anterior margin of wing not continuously infuscated, cell  $R_1$  sometimes with a diffuse smoky streak but always fainter than other wing marks and fading distally. Basal edge of apical wing mark more or less perpendicular to long axis of wing, apical marks of more or less equal length. Scutellum rufous to black. . . . . 9
- 8 (7). Extra crossvein placed even with or just basad of the dm-cu crossvein. Scutellum black on the anterior half. Front tibia and basitarsus of male with long cilia. O'ahu . . . . . *D. hemipeza* (Hardy, 1965)  
 - Extra crossvein well distad of the dm-cu crossvein. Scutellum almost entirely yellow. Male front leg without long cilia. O'ahu . . . . . *D. substenoptera* Hardy, 1969
- 9 (7). Arista with about five dorsal and two ventral rays in addition to apical fork; no medial rays. Posterior half of mesonotum predominantly black. Maui, Moloka'i . . . . . *D. neopicta* Hardy & Kaneshiro, 1968  
 - Arista with 9 or more dorsal and 3–4 ventral rays, and numerous short medial rays. Thorax variable. . . . . 10
- 10 (9). Extra crossvein situated basad of the dm-cu crossvein; costa of male always nearly straight, similar to female . . . . . 11  
 - Extra crossvein situated more or less in line with the dm-cu crossvein; costa of male often strongly arched just beyond the end of  $R_1$  . . . . . 13
- 11 (10). Palpi yellow. Legs entirely black. Posterior half of mesonotum black, anterior half variable. Hawai'i . . . . .  
 . . . . . *D. silvestris* (Perkins, 1910)  
 - Palpi black. Legs predominantly yellow, apices of middle and hind femora and tibiae brown to black. Mesonotum predominantly yellow with distinct black stripes . . . . . 12
- 12 (11). Face predominantly yellow. Moloka'i . . . . . *D. differens* Hardy & Kaneshiro, 1975  
 - Face black except along lower margin. Maui . . . . . *D. planitibia* (Hardy, 1966)
- 13 (10). Cell  $R_1$  with a round mark near the end of  $R_1$  in both sexes, near the arched costal section in the male. Head and appendages predominantly yellow except third segment of antenna. Legs yellow except apices of middle and hind femora and tibiae. O'ahu . . . . . *D. oahuensis* (Grimshaw, 1901)  
 - Wing sometimes with a streak of brown in cell  $R_1$  but never a distinct spot. Head and appendages predominantly black (females with the face yellow to rufous in some species). Legs variable . . . . . 14
- 14 (13). Legs mostly yellow to rufous . . . . . 15  
 - At least femora dark brown to black . . . . . 18
- 15 (14). O'ahu . . . . . *D. nigribasis* Hardy, 1969 (females)  
 - Maui Nui. . . . . 16
- 16 (15). Costa of male not arched. Mesonotum rufous. Basal cilia of front tibia relatively long, about twice as long as width of tibia. Abdomen predominantly yellow with brown markings medially. West Maui . . . . . *D. hanaulae* Hardy, 1969  
 - Costa of male strongly arched just beyond end of  $R_1$ . Mesonotum variable, predominantly rufous to entirely dark brown,

- but usually with brown stripes extending the full length. Tibial cilia variable. Abdomen entirely dark brown to black . 17
- 17 (16). Basal cilia of front tibia short, shorter than width of tibia, and sparse, not readily distinguished from setulae. Mesonotum variable, often predominantly rufous anteromedially with brown stripes. East Maui . . . . . *D. cyrtoloma* Hardy, 1969
- Front tibia of male with irregular rows of relatively long cilia at base, over twice as long as width of tibia, becoming progressively shorter apically. Mesonotum almost always entirely dark brown dorsally. Moloka'i . . . . .  
. . . . . *D. neoperkinsi* Hardy & Kaneshiro, 1968
- 18 (14). Costa of male not arched; both sexes lacking infuscation in cell  $R_1$ . Tibiae and tarsi yellowish. Maui . . . . .  
. . . . . *D. obscuripes* (Grimshaw, 1901)
- Costa of male distinctly arched beyond the end of  $R_1$ ; females usually with a smoky infuscation in cell  $R_1$ . Legs entirely dark brown to black . . . . . 19
- 19 (18). Front tibia of male with dorsal cilia at base in a single row; basitarsus with about four elongate anterodorsal cilia near the apex. East Maui . . . . . *D. melanocephala* (Hardy, 1966)
- Front tibia of male with dorsal cilia at base in several irregular rows; basitarsus lacking cilia. West Maui . . . . .  
. . . . . *D. ingens* Hardy & Kaneshiro, 1971
- 20 (1). Orbits with numerous, conspicuous short or long reclinate orbital setae; lacking the usual proclinate and reclinate setae in male, female with the posterior reclinate and a small proclinate present. . . . . 21
- Head chaetotaxy normal, with one proclinate and two reclinate setae (rarely reduced in size, but never with numerous orbital setulae) . . . . . 22
- 21 (20). Orbital setae very short in both sexes; proclinate seta of female much larger. Wing with a narrow transverse band across the middle and three spots at the apex; rounded apically, not particularly elongate. Hawai'i . . . . .  
. . . . . *D. setosifrons* Hardy & Kaneshiro, 1968
- Orbital setae long in male, nearly as long as the vertical setae anteriorly; those of female shorter, but about as long as the proclinate. Wing long and narrow, pointed apically; with a broad anteromedian mark, a broad anteroapical mark, and a mark on the dm-cu crossvein. Kaua'i. . . . . *D. pilipa* n. sp.
- 22 (20). Mesonotum pale beige in ground color with a distinctive dark brown anchor-shaped pattern and a transverse band above the anterior dorsocentral. Wing largely dark with small hyaline areas. Front and face entirely pale with strongly contrasting black antennae. Kaua'i . . . . . *D. picticornis* Grimshaw, 1901
- Never with a mesonotal pattern as described above; other characters variable . . . . . 23
- 23 (22). Wing truncate apically and short, about twice as long as wide or only slightly longer in male, three times in female; margin between  $R_{4+5}$  and M straight. Both sexes with cell C dark brown with a small circular white spot near the apex of  $R_1$  and a small dark spot anterior of the apex of M, usually with a spurious "dot vein" at the center; lacking apical marks, rest of wing evenly fumose in the female, male with dark streaks along  $R_{2+3}$  and  $CuA_1$ . Maui . . . . . *D. truncipenna* Hardy, 1965
- Wings rounded or slightly pointed, margin between  $R_{4+5}$  and M at least slightly curved; usually elongate, more than twice as long as wide except in the *D. hamifera* complex . . . . . 24
- 24 (23). Middle and hind tibiae yellow, banded with black apically; front tibia of male with a strong apical hook-like process. Wing with large contiguous dark areas and a few hyaline areas, or with diffuse smoky yellow-brown colorations (females with the wings much less marked than males); usually bent at the basal flexure in both living and mounted specimens. Apex of aedeagus dorsoventrally flattened, spatulate . . . . . 25
- Tibiae not colored or modified as above. Wings variable, sometimes predominantly dark but never with diffuse yellowish areas; not usually bent. Apex of aedeagus narrow, tapering, not flattened . . . . . 27
- 25 (24). Oral margin with a dense clump of elongate setae anteriorly. Anterior margin of wing more or less straight; wing almost entirely dark in male, with large hyaline areas along  $R_{2+3}$  and M in female. Maui . . . . . *D. varipennis* (Grimshaw, 1901)
- Only three oral vibrissae present. Anterior margin of male wing (and sometimes female) at least moderately arched, coloration variable. . . . . 26
- 26 (25). Front tibia of male with a row of short cilia along its entire length. Wing with distinct markings, including hyaline areas at the apex. East Maui . . . . . *D. hamifera* Hardy & Kaneshiro, 1968
- Front tibia of male with a row of four or five elongate cilia on the basal half. Wing largely yellow-brown, without hyaline areas at the apex. West Maui . . . . . *D. paenihamifera* Hardy & Kaneshiro, 1969
- 27 (24). Front basitarsus of male flattened laterally, with short erect setulae on the posterior surface but lacking elongate dorsal cilia except in *D. setosimentum*; front femur with an elongate posterior apical seta. Wing highly mottled, predominantly pigmented with irregular bands and hyaline spots, but usually not particularly dark or well-defined except in *D. spectabilis* (*adiastola* subgroup). . . . . 28
- Front basitarsus of male not flattened, femur without an elongate posterior seta; usually with elongate dorsal or anterodorsal cilia on the tibia, basitarsus, or both. Wing with a pattern of discrete spots or longitudinal stripes (sometimes large spots fused, in which case the wing is predominantly dark) . . . . . 36
- 28 (27). Cell  $R_1$  entirely brown except for a spot at the base near the end of  $R_1$ ; cell  $R_3$  with a series of evenly spaced, nearly circular hyaline spots. Entire body and legs almost entirely dark brown to black. Maui, Moloka'i, Lāna'i . . . . .  
. . . . . *D. spectabilis* Hardy, 1965
- Cell  $R_1$  with hyaline areas beyond the base; cell  $R_3$  with hyaline areas not regularly spaced or circular. At least face, palpi, and mouthparts yellow . . . . . 29
- 29 (28). Male labellum densely fringed with long brownish yellow setae. Kaua'i . . . . . *D. ornata* Hardy & Kaneshiro, 1969
- Male labellum not modified, with relatively few scattered, thin setae; younger islands . . . . . 30
- 30 (29). Antennae black. Face black at least along eye margins. Median brown stripe of mesonotum not extending forward beyond

	suture in male	31
-	Antennae predominantly yellow (sometimes tinged with brown in female). Face entirely yellow to white. Median brown stripe extending the full length of mesonotum except in males of <i>D. ochrobasis</i>	32
31 (30).	Face predominantly white, black only along the eye margins. Wing of male with a large hyaline area just past the end of $R_1$ . Hawai'i	<i>D. setosimentum</i> Hardy & Kaneshiro, 1968
-	Face entirely black. Wing of male without a large hyaline area, a brown spot present along the costa between $R_1$ and the large median mark. O'ahu	<i>D. touchardiae</i> Hardy & Kaneshiro, 1972
32 (30).	Mesonotum with a discrete narrow stripe down each dorsocentral row in addition to median and lateral stripes	33
-	Mesonotum lacking a discrete stripe down dorsocentral row; if the row is darkened, it is more or less continuous with the lateral stripe	34
33 (32).	Wing with apex of cell $R_1$ broadly hyaline; four hyaline spots in cell dm. Mentum setose only near the apex. Maui, Lāna'i	<i>D. adiaistola</i> Hardy, 1965
-	Wing with apex of cell $R_1$ infuscated (a small preapical hyaline spot present); only two hyaline spots in cell dm. Mentum setose to the base. Moloka'i	<i>D. cilifera</i> Hardy & Kaneshiro, 1968
34 (32).	Apical half of wing with two broad, solid, transverse bands in male; markings of basal half relatively faint. Hawai'i	<i>D. ochrobasis</i> Hardy & Kaneshiro, 1968
-	Wing with an irregular pattern of dark spots and hyaline areas in both sexes, without broad unbroken transverse bands as described above	35
35 (34).	Infuscations leading from second brown mark in cell $R_1$ (about halfway between end of vein $R_1$ and broad median mark) extend to the posterior margin in a nearly straight transverse brown band. Maui	<i>D. peniculipedis</i> Hardy, 1965
-	Infuscations leading from second brown mark in cell $R_1$ extend diagonally basad towards r-m crossvein, not aligning with mark in dm. Moloka'i	<i>D. toxochaeta</i> Perreira & Kaneshiro, 1990
36 (27).	Mesonotum with a median stripe (sometimes composed of two narrowly-separated stripes; sometimes faint in <i>D. digressa</i> ), always with lateral stripes or spots which are darkest in front of or just behind the suture; dark brown to black, strongly contrasting with the yellow ground color. Wings always with a median mark on the anterior margin, often with a continuous (not always straight) band or row of spots across the middle, or predominantly dark ( <i>lanaiensis</i> , <i>crucigera</i> , <i>aglaia</i> subgroups)	37
-	Mesonotum without a prominent median stripe: largely pale, largely dark, or with various forms of submedian and/or lateral stripes near the dorsocentral setae; if a faint brown median stripe is present ( <i>D. odontophallus</i> , <i>D. paucipuncta</i> , <i>D. uniseriata</i> ) it is not strongly contrasting with the rufous ground color, and presutural lateral stripes or spots are faint or absent. Wing markings various, sometimes with a continuous band across the middle but never predominantly brown, anterior median mark sometimes absent ( <i>orhnopeza</i> , <i>hawaiiensis</i> , <i>vesciseta</i> , <i>odontophallus</i> , <i>punalua</i> , <i>discreta</i> subgroups)	56
37 (36).	Wing lacking any marks on $R_{4+5}$ between the r-m crossvein and the apical mark; mark on dm-cu crossvein extending along $CuA_1$ in both directions and along M distally. Palp with a strong apical seta, about as long as the palpus. O'ahu	<i>D. kinoole</i> n. sp.
-	Wing with at least one median mark on $R_{4+5}$ (sometimes small or faint, rarely absent in some individuals); mark on dm-cu crossvein various, but never extended distally along M. Palpal seta variable, often either absent or inconspicuous, or very long and thin	38
38 (37).	Subbasal spot more or less round or quadrate, without a distal prolongation in cell br (sometimes faintly infuscated along $R_{4+5}$ ) and never extending posteriorly into cell $CuA_1$ . If the r-m crossvein is well beyond the apex of $R_1$ it is unmarked or has a separate brown spot	39
-	Basal radial cell (basad of the r-m crossvein) entirely infuscated, extending well distad of the anterior portion of the subbasal spot (rarely with the basal portion of cell br only faintly infuscated, thus r-m crossvein appearing to have an isolated spot); basal wing infuscation continued posteriorly in a band into cell $CuA_1$ ; r-m crossvein placed well beyond the apex of $R_1$ ( <i>crucigera</i> subgroup)	49
39 (38).	Vein M with a separate spot between the apical mark and dm-cu crossvein	40
-	Vein M without a separate spot between the apical mark and dm-cu crossvein	42
40 (39).	Wing without a large spot in cell $CuA_1$ or a distinct mark on the r-m crossvein; fourth costal section (between $R_{2+3}$ and $R_{4+5}$ ) about 1–1.5 times as long as fifth. Male with orbital setae present but small and inconspicuous, anterior reclinate about the same size as the small setulae and placed midway between proclinate and posterior reclinate. Male palpi elongate, narrow, and pointed, with a thick yellow apical seta. Kaua'i	<i>D. ocellata</i> Hardy & Kaneshiro, 1969
-	Wing with a large spot in cell $CuA_1$ and a separate mark on the r-m crossvein; fourth costal section (between $R_{2+3}$ and $R_{4+5}$ ) about twice as long as fifth. Orbital setae normal. Palpi not long and narrow, lacking strong apical setae	41
41 (40).	Anepisternum with a dark stripe along the upper margin. O'ahu	<i>D. aglaia</i> Hardy, 1965
-	Anepisternum entirely yellow. Kaua'i	<i>D. kikiko</i> n. sp.
42 (39).	Wing lacking a complete band across the middle, median spots on veins $R_{2+3}$ and $R_{4+5}$ fused and basad or distad of the dm-cu crossvein, both spots about equal in width ( $R_{2+3}$ smoky and without a distinct mark in <i>D. odontophallus</i> )	43
-	Wing with a complete pigmented band or row of spots across the middle, or at least with a spot on $R_{4+5}$ in line with the dm-cu crossvein; anterior mark on $R_{2+3}$ broad, $R_{4+5}$ mark narrow and circular except in males of <i>D. conspicua</i>	46
43 (42).	Apical wing marks confluent, edges nearly straight across basally; median mark on $R_{4+5}$ basad of dm-cu crossvein; r-m crossvein located far beyond end of $R_1$ , antepenultimate segment of M (measured from break) as long or longer than penultimate segment. Mesonotum lacking lateral stripes or faint	44

- Apical wing marks separate, mark on  $R_{4+5}$  much shorter than others; median marks on  $R_{2+3}$  and  $R_{4+5}$  distad of dm-cu crossvein; r-m crossvein located only slightly beyond end of  $R_1$ , antepenultimate segment of M much shorter than penultimate segment. Mesonotum with prominent lateral stripes . . . . . 45
- 44 (43).  $R_{2+3}$  with a distinct spot, fused with that on  $R_{4+5}$ ; mark on r-m crossvein small, not or scarcely extending into adjoining cells. Front basitarsus of male with only 3–4 cilia, tibia with none. O'ahu . . . . . *D. spaniothrix* Hardy & Kaneshiro, 1968
- Anterior median margin of wing with a smoky infuscation in cell  $R_1$  but lacking a distinct spot; mark on r-m crossvein large and conspicuous, extending into cell 1st M. Front tibia and tarsus of male with numerous elongate cilia in three rows. Maui, Moloka'i . . . . . *D. odontophallus* Hardy & Kaneshiro, 1968 (in part)
- 45 (43). Median wing mark large, square, reaching to the anterior margin and extending faintly basad almost to the r-m crossvein;  $R_{2+3}$  infuscated along the entire basal third, well beyond the subbasal mark; mark on dm-cu crossvein quadrate, extended basad along both M and  $CuA_1$ . Maui . . . . . *D. oreas* Hardy, 1965
- Median wing mark small, scarcely reaching between  $R_{2+3}$  and  $R_{4+5}$ ;  $R_{2+3}$  not infuscated between the quadrate subbasal and median marks; mark on dm-cu shaped like an inverted "T", extended along  $CuA_1$  but not M. Hawai'i . . . . .
- 46 (42). . . . . *D. macrothrix* Hardy & Kaneshiro, 1968
- R-m crossvein with a prominent isolated brown spot (may be faintly or narrowly connected to other marks, but not a broadly contiguous infuscation). Wing pattern sexually dimorphic: female with mark on  $R_{4+5}$  small and circular, those on M and  $CuA_1$  equal in length and about half as long as the anterior median mark; male with a broad band across middle of wing extending nearly to r-m crossvein, anterior mark only slightly longer than the others. Hawai'i . . . . .
- . . . . . *D. conspicua* Grimshaw, 1901
- No distinct mark on r-m crossvein (rarely faintly and narrowly infuscated around the vein). Wing pattern not sexually dimorphic (shape sometimes dimorphic), marks on  $R_{4+5}$ , M, and  $CuA_1$  always short, not much extended along veins except on  $CuA_1$  in *D. moli* . . . . . 47
- 47 (46). Mark on dm-cu crossvein L-shaped, extending basad along  $CuA_1$ . Wing of male elongate, about four times as long as wide; pointed apically, posteroapical margin slightly concave. Front tibia and tarsus with about 20 elongate cilia each, densely and evenly spaced. O'ahu . . . . . *D. moli* n. sp.
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- Median stripe of mesonotum and median anterior wing mark always dark. Apical seta of aedeagal paramere very short. Maui, Lāna'i . . . . . *D. lanaiensis* Grimshaw, 1901
- 49 (38). Cell M with a circular brown spot just distad of the dm-cu crossvein. Kaua'i and O'ahu . . . . . *D. crucigera* Grimshaw, 1902
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- . . . . . *D. balioptera* Hardy, 1965
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- 52 (51). East Maui . . . . . *D. disjuncta* Hardy, 1965
- West Maui . . . . . *D. affinisdisjuncta* Hardy, 1978
- 53 (51). Femora and katepisternum predominantly yellow. Anterodorsal cilia of male front tibia extending to base. Moloka'i . . . . .
- . . . . . *D. bostrycha* Hardy, 1965
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- 55 (54). Kaua'i and O'ahu . . . . . *D. craddockae* Kambysellis & Kaneshiro, 1999
- Maui, Moloka'i, and Lāna'i . . . . . *D. grimshawi* Oldenberg, 1914
- 56 (36). Wing with a median mark on  $R_{4+5}$  (median and apical marks sometimes fused into one long stripe in *D. hexachaetae* and *D. tarphytrichia*) . . . . . 57
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- 57 (56). Mesonotum entirely yellow to rufous, without distinct stripes. Infuscation along vein  $R_{4+5}$  often continuous between the level of the dm-cu crossvein and apex, sometimes fainter or interrupted in the middle; wing markings relatively faint overall, r-m crossvein unmarked . . . . . 58
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- 58 (57). Front tibia and basitarsus of male each with three widely spaced cilia. O'ahu (common) . . . . . *D. hexachaetae* Hardy, 1965
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- 59 (57). Median mark on  $R_{4+5}$  distinctly basad of dm-cu crossvein mark, separate or only narrowly connected. Anterior median mark in cell  $R_1$  absent or diffuse, never with a continuous band across the middle of the wing (*odontophallus* subgroup) .

	.....	60
-	Median mark on R <sub>4+5</sub> in line with or only slightly basad of dm-cu crossvein, usually broadly joined to crossvein mark and anterior mark in a continuous band; or if distinctly basad of crossvein, the mark on R <sub>2+3</sub> is as well. Anterior median wing mark strong, distinct ( <i>hawaiiensis</i> subgroup and others) .....	63
60 (59).	Thorax predominantly brown: mesonotum densely pollinose, all brown or with a broad median dark stripe and yellow laterally, but without contrasting lateral stripes; pleura striped above, katapisternum entirely dark brown. Palpi yellow ..	61
-	Thorax yellow in ground color, mesonotum with four prominent dark brown stripes; pleura almost entirely yellow. Palpi dark brown .....	62
61 (60).	Median area of cell R <sub>1</sub> smoky brown. Front tibia of male with only 5–6 cilia in anterodorsal and posterodorsal rows. Maui .....	<i>D. odontophallus</i> Hardy & Kaneshiro, 1968 (in part)
-	Cell R <sub>1</sub> entirely hyaline. Front tibia of male with about 9–15 cilia each in anterodorsal and posterodorsal rows. O'ahu .....	<i>D. psilophallus</i> Hardy & Kaneshiro, 1971
62 (61).	Antennae dark brown to black. Anepisternum with a brown stripe on the upper margin, extending caudad to about a level with the posterior notopleural seta. Maui, Hawai'i? .....	<i>D. liophallus</i> Hardy & Kaneshiro, 1968
-	Antennae yellow to rufous. Anepisternum with only a small brown spot on the upper margin, extending caudad to about a level with the anterior notopleural seta. O'ahu .....	<i>D. gymnophallus</i> Hardy & Kaneshiro, 1975
63 (59).	Vein CuA <sub>1</sub> with a long brown mark extending basad from the dm-cu crossvein to beyond a level with the r-m crossvein. Hawai'i .....	<i>D. prolaticilia</i> Hardy, 1965
-	Vein CuA <sub>1</sub> without such a mark .....	64
64 (63).	Crossvein r-m located near the middle of cell dm (measured from the subbasal break in M to dm-cu crossvein), penultimate and antepenultimate sections of M about equal; r-m with a prominent isolated brown spot .....	65
-	Crossvein r-m located well before the middle of cell dm, penultimate section of M distinctly longer than antepenultimate; r-m without a distinct isolated brown spot except in <i>D. heedi</i> .....	71
65 (64).	Femora and coxae dark brown to black; front tibia of male with a single row of long cilia on anterodorsal surface except in <i>D. hirtipalpus</i> .....	66
-	Legs mostly yellow to yellow-brown; front tibia of male with posterodorsal and anterodorsal rows of cilia. ....	68
66 (65).	Palpi yellow, tinged with brown; with dense setulae in the male. Front tibia of male with two rows of long cilia. Maui, Moloka'i .....	<i>D. hirtipalpus</i> Hardy & Kaneshiro, 1968
-	Palpi dark brown, without dense setulae. Front tibia of male with a single row of long cilia on anterodorsal surface ...	67.
67 (66).	Face entirely black. Front tibia of male with about 6–7 long anterodorsal cilia, bare at the base. Maui .....	<i>D. gymnobasis</i> Hardy & Kaneshiro, 1971
-	Upper half of face white, lower half black. Front tibia of male with about 14 cilia in the anterodorsal row and a cluster of longer cilia at the base. Hawai'i .....	<i>D. silvarentis</i> Hardy & Kaneshiro, 1968
68 (65).	Palpi of male densely covered with setulae; apical seta long, hairlike. Front tibia of male with cilia scattered irregularly over anterodorsal and dorsal surfaces, tarsus bare. Hawai'i .....	<i>D. psilotarsalis</i> Hardy & Kaneshiro, 1975
-	Palpi with relatively sparse, short setulae; apical seta relatively short and straight. Front tibia and tarsus of male with cilia in distinct anterodorsal and posterodorsal rows .....	69
69 (68).	Anterior median wing mark long, usually close to or contiguous with subbasal mark at end of R <sub>1</sub> . Maui .....	<i>D. lasiopoda</i> Hardy & Kaneshiro, 1975
-	Anterior median wing mark usually shorter, separated from subbasal mark by about the length of the dm-cu crossvein ..	70
70 (69).	Moloka'i .....	<i>D. villitibia</i> Hardy, 1965
-	Hawai'i .....	<i>D. formella</i> Hardy & Kaneshiro, 1972
71 (64).	Scutellum predominantly yellow .....	72
-	Scutellum dark brown except around the rim .....	74
72 (71).	Front tibia and basitarsus of male both with two rows of long cilia of more or less even length. Dark stripes of mesonotum usually extending to posterior margin. O'ahu .....	<i>D. turbata</i> Hardy & Kaneshiro, 1969
-	Front tibia of male lacking long cilia, basitarsal cilia in a single row, longest at the base and becoming shorter toward the apex. Dark stripes of mesonotum usually ending before posterior dorsocentral setae, posterior portion yellow .....	73
73 (72).	Cilia of male front basitarsus strongly graduated, about 1/3 as long at apex as at base. Mesonotum yellow medially between the dark stripes. O'ahu .....	<i>D. gradata</i> Hardy & Kaneshiro, 1968
-	Cilia of male front basitarsus weakly graduated, over half as long at apex as at base. Mesonotum entirely dark anteriorly, stripes indistinct from the ground color. Hawai'i .....	<i>D. hawaiiensis</i> Grimshaw, 1901
74 (71).	Median wing marks on R <sub>2+3</sub> and R <sub>4+5</sub> distinctly basad of dm-cu crossvein mark. Front tibia of male bent, dorsal margin concave in lateral view. O'ahu .....	<i>D. flexipes</i> Hardy & Kaneshiro, 1968
-	Median wing marks on R <sub>2+3</sub> and R <sub>4+5</sub> not distinctly basad of dm-cu crossvein mark. Front tibia of male normal .....	75
75 (74).	Crossvein r-m with a distinct brown spot. Face entirely black. Front tibia of male bare, basitarsus with cilia longest at the base, becoming progressively shorter toward the apex, the latter less than half as long as the basal cilia. Hawai'i .....	<i>D. heedi</i> Hardy & Kaneshiro, 1971
-	Crossvein r-m without a distinct spot, hyaline or touched by subbasal spot. Face usually yellow to white, at least medially. Cilia of front basitarsus not strongly graded, those at the base only slightly longer than those at the apex .....	76
76 (75).	Face pale yellow to white, dark only along the ventral margin. Median wing band broader at anterior margin, mark on R <sub>2+3</sub> twice as wide as that on R <sub>4+5</sub> .....	77



- Face predominantly brown, pale only on the median carina. Median wing band more or less parallel-sided, mark on  $R_{2+3}$  usually not or only slightly wider than that on  $R_{4+5}$  ..... 79
- 77 (76). Median wing band distinctly sinuate, mark on  $R_{4+5}$  basal of the adjoining marks and mark on dm-cu crossvein L-shaped, extending basally further along  $CuA_1$  than along M (see Fig. 144b in Hardy, 1965). Front tibia of male lacking long cilia. Kaua'i ..... *D. musaphilia* Hardy, 1965
- Median wing band with the spots more or less in line; mark on dm-cu crossvein hourglass-shaped, extending equally along  $CuA_1$  and M (see Fig. 5B). Ciliation variable. .... 78
- 78 (77). Thorax entirely dark brown. Front tibia of male lacking long cilia. Moloka'i. .... *D. nukea* n. sp.
- Lateral margins of mesonotum yellow, pleura usually blotchy brown and rufous. Front tibia of male with numerous long cilia down the entire length. Maui ..... *D. recticilia* Hardy & Kaneshiro, 1968
- 79 (76). Median wing band located distally, mark on  $R_{4+5}$  distinctly closer to apical mark than to r-m crossvein. Kaua'i ..... *D. villosipedis* Hardy, 1965
- Median wing band not shifted distally, mark on  $R_{4+5}$  about equidistant from apical mark and r-m crossvein. .... 80
- 80 (79). Front basitarsus of male with about six straight cilia in anterodorsal row, 2–6 cilia in posterodorsal row. Maui, Lāna'i, Moloka'i ..... *D. orthofascia* Hardy & Kaneshiro, 1968
- Front basitarsus of male with 15 or more cilia in three irregular rows. Hawai'i ..... *D. ciliaticrus* Hardy, 1965 (in part)
- 81 (56). Wing without a median anterior spot in cell  $R_1$  or on vein  $R_{2+3}$  ..... 82
- Wing with a median anterior spot in cell  $R_1$  (note: some weakly-pigmented individuals may be lacking this spot). .... 94
- 82 (81). Scutellum entirely yellow; mesonotum yellow to rufous, sometimes with a median brown stripe but lacking lateral stripes. Pleura largely or entirely yellow, sometimes tinged with brown but usually without strongly contrasting dark marks ... 83
- Scutellum dark brown; mesonotum yellow to brown, if pale then four distinct stripes are present. Pleura with strongly contrasting dark brown marks at least on the anepisternum, or mostly brown to dark brown. .... 86
- 83 (82). Apical wing marks large, conspicuous, discrete; subbasal mark relatively large, extending well into cells Sc and  $R_3$ , sometimes reaching r-m crossvein. Front leg of male without cilia or other modifications. Palp of male with two long yellow apical setae. Maui ..... *D. prostopalpis* Hardy & Kaneshiro, 1968 (in part)
- Apical wing marks small and inconspicuous, or confluent; subbasal mark very small, not or scarcely extending into cells Sc and  $R_3$ . Front leg of male with cilia on tibia or femur. Only one black apical palpal seta, not particularly long ..... 84
- 84 (83). Face white; antennae yellow. Front tibia and tarsus of male covered with long dorsal cilia, otherwise unmodified; femur without additional ventral setae. Hawai'i ..... *D. mulli* Perreira & Kaneshiro, 1990
- Face yellow; antennae brown to dark brown. Front tibia of male with a ventral knob-like process at the apex; lacking cilia on the tibia or tarsus, but with conspicuous ventral setae on the front femur. Kaua'i ..... 85
- 85 (84). Apex of wing with a large dark mark between  $R_{2+3}$  and M in male, female with a narrow infuscation along the margin or discrete spots at the ends of the veins. Antennae dark brown, palpi brown. Front femur of male with a ventral clump of short, thick setae over the basal half. Ovipositor brown. Kaua'i ..... *D. anomalipes* Grimshaw, 1901
- Wing infuscated only narrowly at the base and over dm-cu crossvein, apex without markings. Antennae brown, palpi rufous. Front femur of male with long, thin setae over the entire ventral surface. Ovipositor yellow. Kaua'i ..... *D. quasianomalipes* Hardy, 1965
- 86 (82). Apical wing spots separate. Mesonotum rufous to brown, usually without distinct stripes; if a faint darker median stripe is present then there are no lateral stripes. Small species, to 4.5 mm long ..... 87
- Apical wing spots fully confluent. Mesonotum yellow to brownish with four conspicuous dark stripes (median portion sometimes darkened). Mostly larger species ..... 89
- 87 (86). Apical wing spots small, at least spot on M usually inconspicuous. Subbasal spot very small, not or scarcely reaching into cells Sc and  $R_3$ . Front tibia of male with moderately long cilia down the basal 2/3 and a very long hair at the base; basitarsus bare. Kaua'i ..... *D. micromyia* Hardy & Kaneshiro, 1975
- Apical wing spots large and conspicuous, usually nearly touching. Subbasal spot moderately large, extending well into cells Sc and  $R_3$ . Ciliation of male front tibia different from above, basitarsus with cilia. .... 88
- 88 (87). Front tibia of male with an anterodorsal row of about seven long cilia. O'ahu ... *D. uniseriata* Hardy & Kaneshiro, 1968
- Front tibia of male with two short, inconspicuous cilia near the apex. Hawai'i ..... *D. paucipuncta* Grimshaw, 1901
- 89 (86). Mesonotum yellow to rufous with four distinct narrow stripes, one inside the dorsocentral row and one just outside on each side ..... 90
- Mesonotum more or less evenly brown, without distinct stripes; if two faint submedian stripes are present, there are none lateral of the dorsocentral setae ..... 92
- 90 (89). Mesonotal stripes evenly spaced, submedian stripes well separated from the dorsocentral setae, extending nearly to the posterior margin, the space between them sometimes darkened. A narrow brown mark sometimes present on the median portion of  $R_{2+3}$  (wing pattern sexually dimorphic, females with a prominent spot). Front tibia and basitarsus with long cilia down the entire length. O'ahu ..... *D. punalua* Bryan, 1934 (males)
- Submedian stripes of mesonotum very close to dorsocentral rows and lateral stripes, ending near the anterior dorsocentrals ..... 91
- 91 (90). Front tibia of male with elongate cilia down most of its length, absent on the basal fourth. Katepisternum entirely yellow. O'ahu (larger, rare) ..... *D. divaricata* Hardy & Kaneshiro, 1971
- Front tibia of male almost bare, with only two short cilia near the preapical dorsal seta. Katepisternum at least tinged with brown, often entirely dark. O'ahu (smaller, common) ..... *D. inedita* Hardy, 1965
- 92 (89). Mesonotum with faint submedian stripes, separated by only about two rows of acrostichal setulae. Front tibia of male with

	long cilia over the apical 2/3. O'ahu	<i>D. distinguenda</i> Hardy, 1965	
-	Mesonotum without any indication of markings. Front tibia of male with cilia only on the basal 1/3		93
93 (92).	Front tibia of male with about 10 cilia at the base. Hawai'i	<i>D. basisetae</i> Hardy & Kaneshiro, 1968	
-	Front tibia of male with about 7 cilia at the base. O'ahu	<i>D. paucicilia</i> Hardy & Kaneshiro, 1971	
94 (81).	Thorax almost entirely yellow to rufous dorsally, not distinctly pollinose (mesonotum rarely with a narrow brown streak laterad of the dorsocentral setae); scutellum always yellow, at most faintly tinged with brown		95
-	Mesonotum with four distinct brown stripes or entirely dark, often distinctly pollinose; scutellum usually with dark brown markings, rarely the scutellum appearing yellow ( <i>D. pilatsetae</i> ) and/or mesonotal stripes obscured by heavy pollinosity ( <i>D. obatai</i> and <i>D. sodomae</i> )		104
95 (94).	Crossvein r-m with an isolated brown spot. Hawai'i	<i>D. ochracea</i> Grimshaw, 1901	
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-	Anterior median portion of wing with a single brown mark across cells R <sub>1</sub> and R <sub>3</sub> , centered on vein R <sub>2+3</sub> . Subbasal wing spot smaller, not extending into dm and not or only narrowly touching r-m crossvein. Front tibia and tarsus of male with abundant long cilia. Palp of male not modified as above, broadened near the middle, with a short black apical seta. All small species		97
97 (96).	Mark on dm-cu crossvein extended apically along M. Front tibia of male with cilia only on the apical 2/3. Hawai'i	<i>D. alsophila</i> Hardy & Kaneshiro, 1971	
-	Mark on dm-cu crossvein hourglass-shaped, not extended along M. Front tibia of male with long cilia along the entire length ( <i>vesciseta</i> subgroup)		98
98 (97).	Palpi and labella brown to black. Front tibia of male with posterodorsal cilia absent or only a few on the apical half		99
-	Palpi and labella yellow. Front tibia of male with a row of 6–12 posterodorsal cilia over at least the basal 2/3		100
99 (98).	Palpi black. Front tibia of male with an anterodorsal and a posterodorsal row of cilia. Maui	<i>D. vesciseta</i> Hardy & Kaneshiro, 1968	
-	Palpi reddish brown. Front tibia of male with only one row of cilia along the anterodorsal surface. O'ahu	<i>D. ambochila</i> Hardy & Kaneshiro, 1971	
100 (98).	Third antennal segment and lower front clear yellow		101
-	Third antennal segment and lower front reddish brown		102
101 (100).	Anterior median wing mark about twice as long as wide. Anepisternum yellow with a distinct dark brown stripe along the dorsal edge. Front tibia of male with posterodorsal and anterodorsal cilia about equal in length. Maui, Moloka'i	<i>D. pihulu</i> n. sp.	
-	Anterior median wing mark about three times as long as wide. Anepisternum entirely yellow, without a dark dorsal stripe. Front tibia of male with posterodorsal cilia distinctly shorter than anterodorsal. Hawai'i	<i>D. assita</i> Hardy & Kaneshiro, 1969	
102 (100).	Anepisternum yellow with a distinct dark brown stripe along the dorsal edge. Mesonotum with a streak of brown just outside the dorsocentral setae. Front tibia of male with posterodorsal row of cilia only on the basal 2/3. O'ahu	<i>D. montgomeryi</i> Hardy & Kaneshiro, 1971	
-	Anepisternum yellow, smoky, or largely brown, but lacking a distinct dorsal stripe. Mesonotum without distinct dark marks. Front tibia of male with posterodorsal row of cilia extending the full length, though they may be short apically		103
103 (102).	Anepisternum yellow or faintly tinged with brown. Male cerci yellow to yellow-brown, semicircular, higher than long. Hawai'i	<i>D. pisonia</i> Hardy & Kaneshiro, 1971	
-	Anepisternum almost entirely brown. Male cerci dark brown, elongate, about 1.5 times as long as high. Kaua'i	<i>D. opuhe</i> n. sp.	
104 (94).	Fourth costal section (between R <sub>2+3</sub> and R <sub>4+5</sub> ) about twice as long as fifth. Subbasal wing spot large, extending well into dm and broadly touching r-m crossvein. Front tibia of male bare or with cilia extending to the base ( <i>discreta</i> subgroup)		105
-	Fourth costal section usually about 1.5 times as long as fifth; subbasal wing spot usually smaller, not extending into dm and not reaching r-m crossvein (in case of exceptions, both characters never occurring together). Front tibia of male variable, often with cilia over most of its length except at the extreme base ( <i>orphnopeza</i> subgroup, <i>D. pilimana</i> )		108
105 (104).	Propleura yellow, rest of pleura largely dark brown. Front tibia of male with long cilia over basal 2/3. Kaua'i	<i>D. glabriapex</i> Hardy & Kaneshiro, 1968	
-	At least central portion of anepisternum yellow, pleura sometimes largely yellow; propleura sometimes brownish. Front tibia of male not as above		106
106 (105).	Palpi and mouthparts pale, rufous to yellow. Front tibia of male with long cilia down entire length. Maui	<i>D. discreta</i> Hardy & Kaneshiro, 1968	
-	Palpi and mouthparts dark brown to black. Front tibia of male without long cilia		107
107 (106).	Apical wing spots partly confluent. Front basitarsus of male with a row of about six dorsal cilia. West Maui	<i>D. lineosetae</i> Hardy & Kaneshiro, 1968	
-	Apical wing spots fully discrete. Front basitarsus of male with a dense cluster of setae near the middle and a row of about 5 anterodorsal cilia. Moloka'i, East Maui	<i>D. fasciculisetae</i> Hardy, 1965	
108 (104).	Pleura predominantly yellow with only a few small brown spots; katapisternum largely or entirely yellow. Mesonotum not		

- conspicuously pollinose, usually predominantly yellow with four distinct dark brown stripes (*D. sproati* often completely dark dorsally) . . . . . 109
- Pleura conspicuously marked with brown, at least with prominent dorsal and ventral stripes along the full length of the anepisternum; katepisternum with some dark markings, often all dark brown to black. Mesonotum predominantly dark, brown stripes broad and occupying most of dorsal surface (median area sometimes yellow), usually distinctly pollinose . . . . . 112
- 109 (108). Stripes of mesonotum evenly spaced, submedian stripes located well inside of dorsocentral row; space between submedian stripes sometimes darkened. Median wing mark on  $R_{2+3}$  longer than hyaline space between it and apical mark. O'ahu . . . . . *D. punalua* Bryan, 1934 (females)
- Submedian stripes of mesonotum widely separated, close to dorsocentral setae and only narrowly separated from lateral stripes; median portion of mesonotum never darkened. Median wing mark on  $R_{2+3}$  shorter than hyaline space between it and apical mark. . . . . 110
- 110 (109). Scutellum with two dark brown stripes, yellow medially. Mesonotum always clear yellow with brown stripes distinct. Front tibia and tarsus of male with short cilia down the entire length, shorter than width of tibia. Hawai'i . . . . . *D. engyochracea* Hardy, 1965
- Scutellum dark brown medially, yellow laterally. Coloration of mesonotum variable, often broadly brown medially, stripes not fully discernable. Front tibia of male with relatively long cilia, as long or longer than width of tibia; not covering full length of both tibia and tarsus . . . . . 111
- 111 (110). Median wing mark on  $R_{2+3}$  distinctly basad of the dm-cu crossvein mark. Front tibia of male with curled cilia along apical 3/4, continuing onto first three tarsomeres. Hawai'i . . . . . *D. sproati* Hardy & Kaneshiro, 1968
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- 112 (108). Apical wing spots confluent, mark on  $R_{4+5}$  about as long as that on M . . . . . 113
- Apical wing spots discrete or scarcely touching; mark on  $R_{4+5}$  small, about half the length of that on M . . . . . 116
- 113 (112). Face white. Scutellum yellow. Front tibia of male bare, basitarsus with a dorsal clump of long cilia on the apical half. Maui . . . . . *D. pilatisetae* Hardy & Kaneshiro, 1968
- Face yellow to black. Scutellum dark brown to black. Front tibia and basitarsus of male both with long cilia over most of their length . . . . . 114
- 114 (113). Median wing mark on  $R_{2+3}$  distinctly basad of the dm-cu crossvein mark. Basal margin of apical wing mark distinctly concave, stripes on each vein about the same length. Cilia of male front tibia shorter than preapical dorsal seta, the latter nearly twice as long as the apical ventral seta in both sexes. Maui, Moloka'i, Lāna'i . . . . . *D. limitata* Hardy & Kaneshiro, 1968
- Median wing mark on  $R_{2+3}$  in line with mark on dm-cu crossvein. Basal margin of apical wing mark nearly straight or only weakly concave, stripe on  $R_{2+3}$  distinctly shorter than that on  $R_{4+5}$ . Cilia of male front tibia longer than preapical dorsal seta, the latter only about as long as the apical ventral seta in both sexes . . . . . 115
- 115 (114). Pleura and sides of mesonotum with conspicuous yellow areas, legs almost entirely yellow. O'ahu . . . . . *D. sobrina* Hardy & Kaneshiro, 1971
- Thorax and femora usually almost entirely dark brown to black (some may approach the coloration of *D. sobrina*, but most of these have a median mark on  $R_{4+5}$  and will key to couplet 80). Hawai'i . . . . . *D. ciliaticrus* Hardy, 1965 (in part)
- 116 (114). Area between ocelli dark brown to black, contrasting with front; posterolateral portions of ocellar triangle beyond ocelli similar to front. Face white, palpi yellow, clypeus yellow medially, brown laterally. Mesonotum entirely brown dorsally, without yellow medially (sometimes stripes short, mesonotum entirely yellow anterior of suture). Front tibia and basitarsus of male with long straight cilia, tibia bare on basal and apical 1/4; basitarsus only about half as long as tibia. O'ahu . . . . . *D. pilimana* Grimshaw, 1901
- Area between ocelli usually slightly darker but not strongly contrasting with rest of front; entire ocellar triangle, including portions lateral of ocelli, concolorous. Face yellow to brown. Mesonotum often yellow at least between the submedian stripes. Front tibia and basitarsus of male with shorter curled cilia, tibia often bare at the base but cilia always extending to the apex; basitarsus about 2/3 as long as tibia . . . . . 117
- 117 (116). Mentum, labella, and clypeus dark brown to black . . . . . 118
- Mentum, labella, and clypeus yellow to rufous . . . . . 119
- 118 (117). Wings narrowed on apical half, apex distinctly pointed; fourth costal section (between  $R_{2+3}$  and  $R_{4+5}$ ) about 1.6 times as long as fifth, wing margin between M and  $CuA_1$  nearly straight. Front basitarsus of male with an anterodorsal row of 5–6 cilia along the apical 2/3 and three posterodorsal cilia on the apical 1/3. O'ahu . . . . . *D. reynoldsiae* Hardy & Kaneshiro, 1972
- Wing not unusually narrowed, apex rounded; fourth costal section (between  $R_{2+3}$  and  $R_{4+5}$ ) about 1.3 times as long as fifth, wing margin between M and  $CuA_1$  convex. Front basitarsus of male with two complete rows of cilia extending the full length. O'ahu . . . . . *D. atrimentum* Hardy & Kaneshiro, 1971
- 119 (117). Mark at apex of vein  $R_{2+3}$  short, about half as long as mark on M. Hind tarsus and sometimes tibia brown to black. Front basitarsus of male bare of cilia on basal 1/4. Palpi brown on basal half, yellow apically. Katepisternum entirely brown . . . . . 120
- Mark at apex of vein  $R_{2+3}$  elongate, nearly as long as mark on M (about 2/3 as long in *D. obatai*). Legs entirely yellow. Front basitarsus of male with cilia along the entire length or with only a small area near the basal joint bare. Palpi entirely yellow. Posteroventral portion of katepisternum predominantly yellow, though it may be marked with brown . . . . . 121
- 120 (119). Mesonotum entirely dark brown medially, or rarely with a very narrow yellow stripe, densely gray pollinose. Subbasal wing spot usually large, reaching r-m crossvein. Hind tibia variable, often dark brown to black. Hawai'i . . . . .

- ..... *D. murphyi* Hardy & Kaneshiro, 1969
- Mesonotum distinctly yellow medially, usually four brown stripes distinct. Subbasal wing spot small, not reaching r-m crossvein. Hind tibia never dark brown ..... *D. orphnopeza* Hardy & Kaneshiro, 1968
- 121 (119). Mesonotum not strongly pollinose, appearing brown. Front tibia of male with cilia not quite extending to the base, basal 1/10–1/6 bare. Wing mutations rare. Hawai'i ..... *D. claytonae* Hardy & Kaneshiro, 1969
- Mesonotum very densely pollinose in pinned specimens, appearing gray. Front tibia of male with cilia extending fully to the base. Wings often with spur veins developed in the marks on  $R_{2+3}$ . Older islands. .... 122
- 122 (121). Costal fringe long, extending at least 5/6 the distance between  $R_{2+3}$  and  $R_{4+5}$ , sometimes nearly reaching  $R_{4+5}$ . O'ahu ..... *D. obatai* Hardy & Kaneshiro, 1972
- Costal fringe extending about 2/3 the distance between  $R_{2+3}$  and  $R_{4+5}$ . Maui, Moloka'i ..... *D. sodomae* Hardy & Kaneshiro, 1968

## Species descriptions

### *Drosophila kikiko* Magnacca new species

Fig. 1

**Diagnosis.** This species is virtually identical to *D. aglaia* from O'ahu, differing only in lacking a stripe on the upper anepisternum and having slightly more cilia on the front basitarsus of the male (~40–45, compared to 30–35 for *D. aglaia*). The irregular wing pattern somewhat resembles some members of the *adiastola* species group at first glance, but is quite different when examined closely, with the typical markings of the *grimshawi* group augmented by an extra spot on M and connecting lines between the spots.

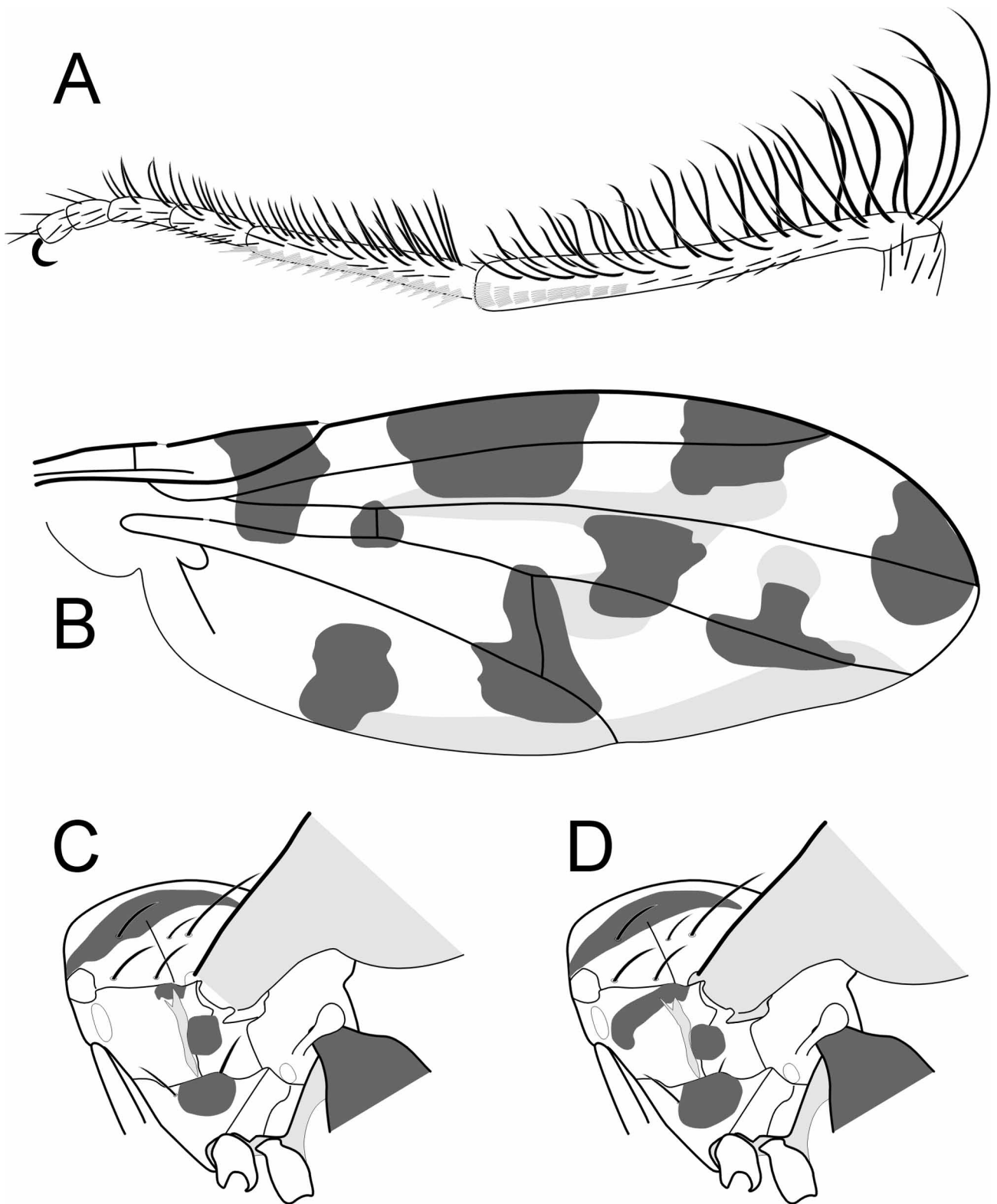
**Description.** Male. **Head.** Front pale, tinged with brown; ocellar triangle black. Fronto-orbital setae normal, anterior reclinate very small, about half as long as the proclinate and one-third as long as the posterior reclinate. Face and gena pale yellow except for a small black spot below the eye. Antenna with the second segment brown, third segment white; arista with about 11 dorsal and 4 ventral rays in addition to the apical fork, and numerous rather long median branches. One strong oral vibrissa, other oral setulae small and hairlike. Palp black, fading to pale yellow on the basal 1/4, paddle-shaped, broad and flattened, broadest near middle, rounded apically, lacking strong setae. Labellum and mentum dark brown to black. **Thorax.** Mesonotum largely yellow with three strongly contrasting black stripes, all tapering posteriorly; median stripe reaching the scutellum, lateral stripes ending near the posterior dorsocentral setae. Scutellum black medially for about 1/3 of its length, otherwise smoky. Pleura largely yellow, with three prominent dark marks—a small spot at the base of the wing; a square mark on the anterior margin of the anepimeron; and posterodorsally on the katepisternum, in the area bounded by the katepisternal setae. Two pairs of strong dorsocentral setae, the anterior about 2/3 as long as the posterior. **Legs.** All yellow except the mid and hind coxae marked with black and hind femur and tibia tinged with brown apically. Front tibia with regular anterodorsal and posterodorsal rows of 13–14 very long cilia along its entire length, longest at the base; about 18 shorter cilia between them dorsally in 1–2 irregular rows. Front tarsus densely covered with numerous irregularly placed dorsal cilia, about as long as those on the lower tibia but distinctly stronger, becoming shorter apically (largely absent from fifth segment); basitarsus with about 40–45 cilia. **Wings.** Extensively marked, rather irregular (see Fig. 1). Apical segment of M over twice as long as the penultimate segment (dm-cu crossvein nearly vertical), r-m crossvein located beyond the middle of cell dm (measured from the subbasal break), well beyond the end of  $R_1$ . Costal fringe extending about 3/4 the distance between apex of  $R_{2+3}$  and  $R_{4+5}$ . **Abdomen.** All segments with broad yellow areas dorsolaterally, dark brown medially, broadly laterally, and narrowly along the posterior margin. Cerci about as long as high or slightly longer, smoky yellow-brown. Genitalia not dissected.

Female. Identical to the male with the following exceptions. **Head.** Front noticeably brown. Third antennal segment tinged with brown. Palp with a moderately strong apical seta. **Legs.** Front legs without elongate cilia or setae. **Abdomen.** Ovipositor long, straight, yellow, pointed posteriorly at rest.

**Types.** **Kaua'i:** Holotype ♂, Kōke'e State Park, Nu'alolo Trail, 3800 ft., 22.132°N 159.660°W, on bait sponge, 23.i.2010, K. Magnacca (UHIM). Allotype ♀, Ku'ia Natural Area Reserve, Mahanaloa–Ku'ia Valley junction, 1900 ft., 22.137°N 159.701°W, on bait sponge, 23.vi.2009, K. Magnacca (UHIM); paratypes: 1 ♀, same locality as holotype, 25.vii.2010, D. Kapan (BPBM). 1 ♀, Kōke'e, 3600 ft., 22.vi.1964, H.L. Carson, C99.25 (UHIM).

**Distribution and ecology.** Kaua'i, in diverse mesic forest. Breeding hosts unknown (see Discussion below).

**Etymology.** From the Hawaiian *kikiko*, spotted or mottled, referring to the wing pattern.



**FIGURE 1.** *Drosophila kikiko*. A. Right front leg of male, anterior view. B. Wing. C. Thorax, lateral view. D. *Drosophila aglaia* thorax, lateral view.

**Discussion.** Like its O‘ahu relative, this species is extremely rare. Two captive females were offered vials with extracts from bark of *Charpentiera*, *Cheirodendron*, *Clermontia*, *Pisonia*, *Tetraplasandra*, *Touchardia*, *Urera*, and *Wikstroemia* over the course of three weeks, but did not lay any eggs. The most likely host is *Pleomele aurea*, because it is the only known potential host plant observed at both of the collection sites; unfortunately, none of this was available as an oviposition stimulus. Notably, Kaua‘i is the only island not yet known to have an oligophagous

picture wing species on either *Pleomele* or *Tetraplasandra* (Magnacca, *et al.*, 2008; the generalist species *D. crugigera* and *D. villosipedis* utilize both), despite both being much more abundant there than on other islands.

The closely-related *D. aglaia* is a federally listed endangered species (U.S. Fish and Wildlife Service, 2006). The host recorded in the literature is *Urera glabra* (Magnacca, *et al.*, 2008; Montgomery, 1975), but this was based on misidentification of *D. kinoole* (described below). Since *D. aglaia* has not been seen since 1997 and its host plant is now unknown, a thorough search for the host of *D. kikiko* may be informative for management of *D. aglaia*.

### ***Drosophila kinoole* Magnacca, new species**

Fig. 2

**Diagnosis.** Thoracic coloration and general habitus similar to *D. oreas* of Maui; differing by possessing a shorter, thicker apical seta on the palp (straight and about as long as the palp in *D. kinoole*, very thin, curved, and at least 1.5 times as long in *D. oreas*; compare Figs. 2C and 7D), and in wing markings by lacking the median mark on  $R_{4+5}$  and having the dm-cu crossvein mark extended apically along M. The wing marks are similar to *D. alsophila*, but the thoracic coloration and ciliation of the front leg will immediately separate it from that species, as well as from sympatric members of the *vesciseta* subgroup. The holotype was originally labelled as *D. aglaia*, with which it is sympatric; in addition to the very different wing marks, *D. aglaia* has the third antennal segment pale white to yellow in males (rather than brown as in *D. kinoole*; also brown apically in females of *D. aglaia*), lacks strong palpal setae, has elongate cilia on the distitarsus, the median mesonotal stripe narrows posteriorly rather than broadening, and has the r-m crossvein placed on the apical half of cell M rather than the basal half (compare Figs. 1B and 2B).

**Description.** Male. **Head.** Front pale, tinged with brown above; ocellar triangle and orbits darker brown. Fronto-orbital setae normal, anterior reclinate very small, about half as long as the proclinate and one-third as long as the posterior reclinate. Face and gena pale yellow except for a small brown spot below the eye. Antenna entirely brown; arista damaged on holotype, apparently with about 8–9 dorsal and 3–4 ventral rays in addition to the apical fork, and numerous moderately long median branches. One strong oral vibrissa, other oral setulae small and hair-like. Palp brown, fading to pale yellow on the basal 1/4, broad and flattened, broadest near middle, rounded apically, with a strong, nearly straight apical seta, about as long as the palp. Labellum and mentum dark brown to black. **Thorax.** Mesonotum largely yellow with three strongly contrasting dark stripes; median stripe reaching the scutellum and expanding posteriorly to fill the area between the dorsocentral setae, lateral stripes narrowing posteriorly and ending near the posterior dorsocentral setae. Disc of scutellum dark. Pleura largely yellow, with three prominent dark marks—a broad stripe along the dorsal margin of the anepisternum (narrower posteriorly); a square mark on the anterior margin of the anepimeron; and posterodorsally on the katepisternum, extending slightly ventrad of the posterior katepisternal seta. Two pairs of strong dorsocentral setae, the anterior about 3/4 as long as the posterior. **Legs.** All yellow except the mid and hind coxae marked with brown. Front tibia with anterodorsal and posterodorsal rows of 13–14 very long cilia along its entire length, longest at the base; dorsal surface with numerous irregularly placed shorter cilia. Front basitarsus about 3/5 as long as tibia, with about 15 irregularly placed dorsal cilia, longer than most of those on the tibia. Distitarsus lacking elongate cilia. **Wings.** Marks present at base, over ends of major veins, dm-cu crossvein, and medially on  $R_{2+3}$  (see Fig. 2). Basal mark small, extended narrowly along bases of veins to r-m crossvein. Apical segment of M slightly less than twice as long as the penultimate segment, r-m crossvein located at the basal 2/5 of cell dm (measured from the subbasal break), just beyond the end of  $R_1$ . Costal fringe extending about 2/3 the distance between apex of  $R_{2+3}$  and  $R_{4+5}$ . **Abdomen.** Entirely brown. Cerci slightly higher than long. Genitalia not dissected.

Female. Unknown.

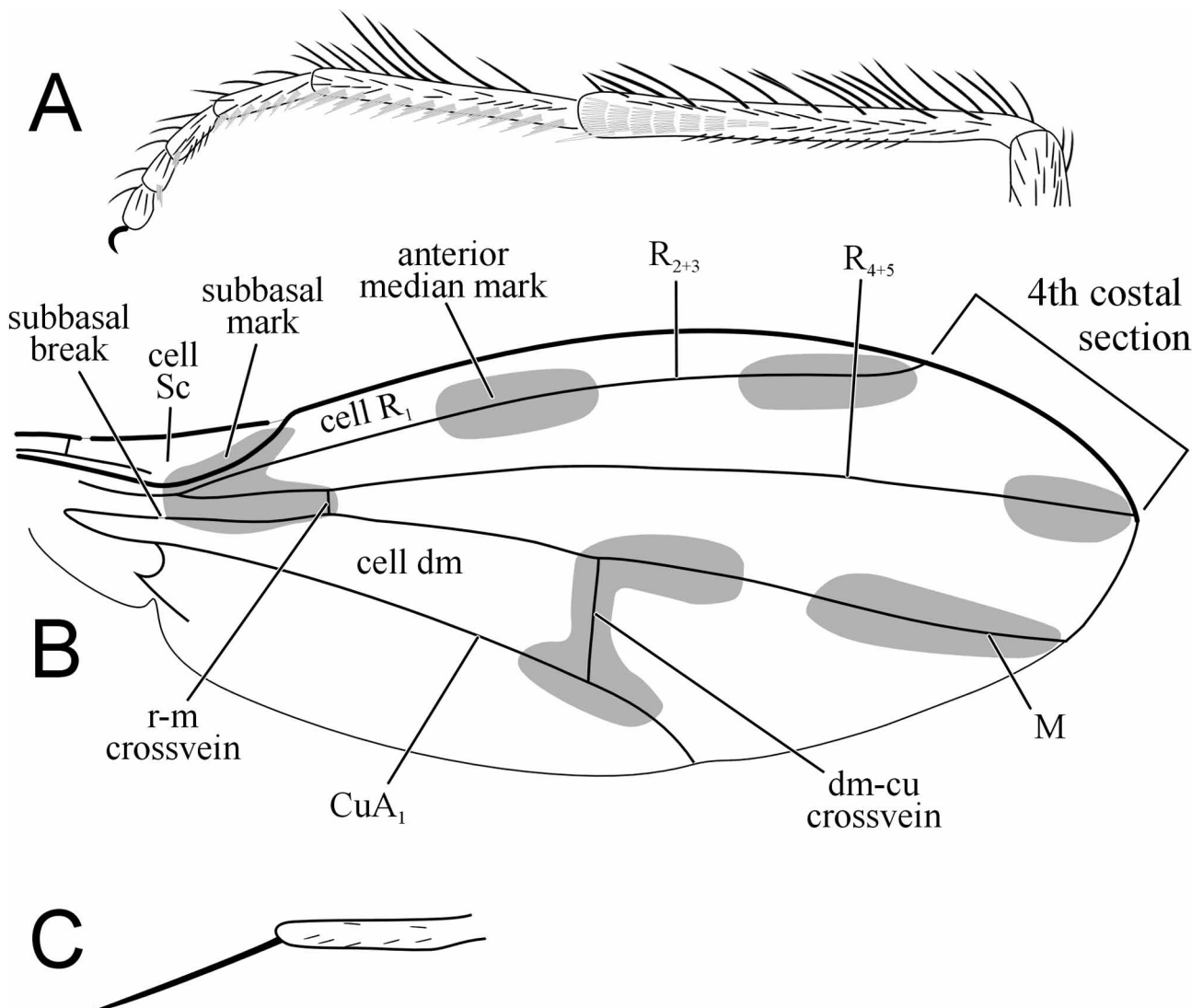
**Types.** O‘ahu: Holotype ♂, Kalua‘a Gulch, Pu‘u Hapapa area, 21.xi.1971, reared ex *Urera* bark, S.L. Montgomery (UHIM).

**Distribution and ecology.** O‘ahu, Wai‘anae range. Reared from bark of *Urera* sp. (‘ōpuhe, Urticaceae).

**Etymology.** From the Hawaiian *kino‘ole*, frail (literally, “without body”), referring to both the state of the holotype, which is largely hollowed out, and the status of the species as a whole, which has not been collected before or since.

**Discussion.** This is the specimen identified as *D. aglaia* in Montgomery (1975); consequently, the host for that species is now unknown (see Discussion under *D. kikiko*). Based on the thoracic and wing coloration it appears to

be most closely related to *D. alsophila* of Hawai'i. That species has a completely pale thorax like members of the *vesciseta* subgroup, but is the only other species with a similar dm-cu crossvein mark; its collection records are also consistent with being a *Urera* breeder. The pleural marks are strikingly similar to the sympatric *D. aglaia*, but the mesonotal stripes, palpi, and wing coloration and venation are distinctly different. These characters have been examined in all specimens of *D. aglaia* at UHIM (N = 8♂ 8♀) and show no significant variation. The legs of the *D. kinoole* type are abraded and the ciliation is impossible to fully characterize, although it is sufficiently visible to differentiate from *D. alsophila*. Elongate cilia may naturally be present at the base of the tibia, as in *D. oreas* and *D. aglaia*, but the specimen does not have them. The specimen also appears to be slightly teneral and the wing pattern may not be fully developed. However, the combination of characters that are evident clearly distinguish it from any other known species, and given the importance of recognizing it if it appears in the future (and the possibility that it may already be extinct), we feel justified in describing it from this specimen.



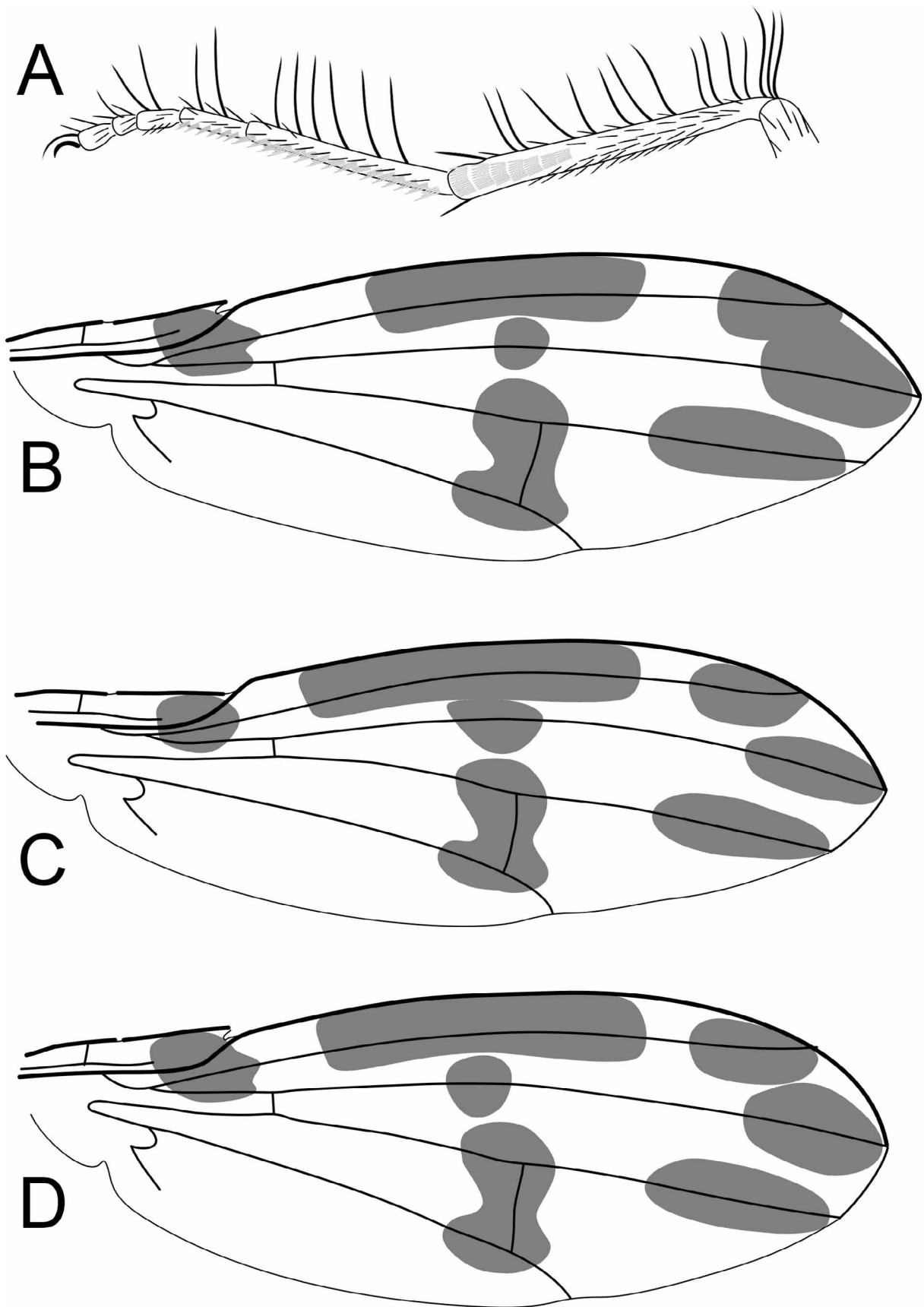
**FIGURE 2.** *Drosophila kinoole*. A. Right front leg of male, anterior view. B. Wing. C. Left palp of male, lateral (edge-on) view.

***Drosophila lanaiensis* Grimshaw, 1901**

Fig. 3

*Drosophila lanaiensis* Grimshaw, 1901:60. Type ♀, Lāna'i, 2,000 ft., xii.1893, R.C.L. Perkins, BMNH.

*Drosophila virgulata* Hardy and Kaneshiro, 1968:234–236 n. syn. Holotype ♂, Maui, Waikamoi, 22.ix.1966, J. P. Murphy. BPBM 8921.



**FIGURE 3.** *Drosophila lanaiensis*. A. Right front leg of Lāna'i male, anterior view. B. Male wing. C. Wing of type female (Lāna'i) in BMNH. D. Wing of recent female from 'Īao Valley, Maui.



**Diagnosis.** The wing and body coloration patterns resemble others in this species complex, including *D. digressa* of Hawai'i, to which it is closest, and *D. moli* of O'ahu. It is externally almost identical to the former except in the usually darker coloration of the anterior wing mark and median mesonotal stripe; the latter is distinguishable by the pointed wings and more extensive front leg setation of the male, and L-shaped mark on the dm-cu crossvein in both sexes (compare Figs. 3 and 4). See Discussion below.

**Description.** Male. **Head.** Front pale, faintly tinged with brown; ocellar triangle black. Fronto-orbital setae normal, anterior reclinate very small, about half as long as the proclinate and one-third as long as the posterior reclinate. Face and gena pale yellow except for a small black spot below the eye. Antenna with the second segment brown, third segment dirty yellow; arista with about 6–8 dorsal and 3 ventral rays in addition to the apical fork, and several rather long median branches. One strong oral vibrissa, followed posteriorly by several smaller setae, with numerous small setulae in between them. Palp largely yellow, slightly darker at the tip, nearly cylindrical; with a long, thin, yellow-brown apical seta. **Thorax.** Mesonotum largely yellow with three strongly contrasting dark brown to black stripes; lateral stripes dark, extending from the anterior margin of the humeri nearly to the scutellum; median stripe often fainter, broadening between the dorsocentral setae to fill the space between them, and extending onto the scutellum. Pleura almost entirely yellow except for a large dark mark on the posterior half of the anepisternum. Two pairs of strong dorsocentral setae, the anterior about 2/3 as long as the posterior. **Legs.** Entirely yellow, with faint tinges of brown at apices of femora and both ends of hind tibiae. Front tibia with anterodorsal and posterodorsal rows of 6–8 long cilia each along its entire length, slightly longer and more tightly clustered at the base; spacing irregular, often with large gaps. Front basitarsus with 7–11 dorsal cilia arranged in one or two irregular rows, similar to those of the tibia. Second and third tarsal segments also with 2–3 cilia. **Wings.** Shape normal, about three times as long as wide, rounded or only weakly pointed at apex. Subbasal wing spot small, scarcely reaching into cell R<sub>2</sub>. Anterior mark elongate, extending along about 1/3 the length of the wing; connected to the hourglass-shaped mark on the dm-cu crossvein via a small circular mark over R<sub>2+3</sub>. Apical marks confluent or nearly so. Costal fringe extending about 1/2 the distance between apex of R<sub>2+3</sub> and R<sub>4+5</sub>. **Abdomen.** Coloration variable, from each segment predominantly yellow with only a narrow posterior band dark brown, to predominantly brown with yellow anterolateral areas. Cerci yellow-brown. Parameres of aedeagus each with a very short apical setula.

Female. Identical to the male with the following exceptions. **Head.** Third antennal segment brown. Apical seta of palp shorter, stronger, black. **Thorax.** Median stripe of mesonotum broader on the anterior half and dark, similar to the lateral stripes. **Legs.** Front legs without elongate cilia or setae. **Abdomen.** Ovipositor long, straight, brown, pointed vertically at rest.

**Material examined.** Lāna'i: 2 syntype ♀, Lāna'i, 2,000 ft., xii.1893, R.C.L. Perkins (BMNH and BPBM). 1 ♂, ravine by Hi'i well, 20° 48.837'N 156° 52.772'W, A. & M. Hoikkala and S.L. Montgomery. Identified as *D. virgulata*: Maui: Holotype ♂ and allotype ♀, Waikamoi, 22.ix.1966, J.P. Murphy, J31C1. 1 ♂, 'Īao Valley, 20° 53.115'N 156° 32.637'W, 10.iii.2010, S.L. Montgomery. 1 ♀, Makawao Forest Reserve nr. reservoir, 2900 ft., 20.829°N 156.272°W, 11.iii.2010, D. Kapan. 2 ♂ 3 ♀, Waikapū Valley, 15.x.2011, KNM.

**Distribution and ecology.** Maui and Lāna'i; probably occurs on Moloka'i or formerly did. Breeds in *Charpentiera* (pāpala, Amaranthaceae).

**Discussion.** The recent collection of a male of this species from Lāna'i has finally allowed proper assignment of this name. The original description mentions a series of five females, but only one is present at the Natural History Museum (London). It is missing its head but otherwise in reasonably good condition. Another is at the Bishop Museum and is in good condition; I have examined both of these, the latter in person and the former in photographs, and they are identical. Hardy (1965) considered *D. lanaiensis* conspecific with specimens from O'ahu (described below as a new species, *D. moli*). Examination of the wing pattern shows that it instead matches *D. virgulata*, described from Maui; most obviously, the mark over the dm-cu crossvein is hourglass-shaped instead of L-shaped as in *D. moli*. The recent male specimen also matches *D. virgulata* in wing pattern, wing shape, and front leg setation. Therefore, *Drosophila virgulata* Hardy and Kaneshiro is reduced to a new junior synonym of *Drosophila lanaiensis* Grimshaw. While there are distinct differences in the wings and legs between the present species and *D. moli*, it is nearly identical to *D. digressa* of Hawai'i—in fact, the only consistent character separating them is the much longer seta of the aedeagal paramere (see Fig. 5 in Kaneshiro, 1969) of *D. digressa*. The latter typically has the anterior wing mark and median mesonotal stripe paler, but these are not consistent and dark individuals look externally almost identical to typical *D. lanaiensis*. However, they exhibit a high degree of mitochondrial gene

sequence divergence—*D. lanaiensis* is 5.9% (Lāna‘i) to 6.5% (Maui) different from *D. digressa* in the 5' cytochrome oxidase I (COI) region, while *D. lanaiensis* from Lāna‘i and Maui differ from each other by only 0.7% (unpubl. data)—indicating a long history of separation between Maui Nui and Hawai‘i populations, and exchange or recent vicariance between Maui and Lāna‘i. Thus, they are maintained as two species.

### *Drosophila moli* Magnacca, new species

Fig. 4

**Diagnosis.** The wing and body coloration patterns resemble others in this species complex, including *D. lanaiensis*, with which it was formerly grouped, and females of *D. conspicua*. Males can be immediately distinguished by the elongate, narrow wings, and both sexes have the mark over the dm-cu crossvein distinctly L-shaped.

**Description.** Male. **Head.** Front pale, faintly tinged with brown; ocellar triangle black. Fronto-orbital setae normal, anterior reclinate very small, about half as long as the proclinate and one-third as long as the posterior reclinate. Face and gena pale yellow except for a small black spot below the eye. Antenna with the second segment brown laterally, otherwise yellow; arista with about 9–10 dorsal and 4 ventral rays in addition to the apical fork, and several rather long median branches. One strong oral vibrissa, followed posteriorly by three progressively smaller setae, with numerous small setulae in between them. Palp largely yellow, slightly darker at the tip, nearly cylindrical; with a long, thin, yellow apical seta. **Thorax.** Mesonotum largely yellow with three strongly contrasting dark brown to black stripes; lateral stripes dark, extending from the anterior margin of the humeri nearly to the scutellum; median stripe fainter, broadening between the dorsocentral setae to fill the space between them, and extending onto the scutellum. Pleura almost entirely yellow except for a large dark mark on the posterior half of the anepisternum. Two pairs of strong dorsocentral setae, the anterior about 2/3 as long as the posterior. **Legs.** Entirely yellow. Front tibia with regular anterodorsal and posterodorsal rows of 10–12 long cilia along its entire length, slightly longer at the base, with a few scattered dorsal cilia in between. Front tarsus with about 20 dorsal cilia arranged in three irregular rows, similar to those of the tibia. Second and third tarsal segments also with sparse cilia. **Wings.** Extremely long and narrow, about four times as long as wide; apically pointed and slightly bent posteriorly, posterior margin between M and CuA<sub>1</sub> weakly concave. Subbasal wing spot small, scarcely reaching into cell R<sub>2</sub>. Anterior mark elongate, extending along about 1/3 the length of the wing; connected to the large L-shaped mark on the dm-cu crossvein via a small circular mark over R<sub>2+3</sub> (the latter rarely reduced or absent). Apical marks confluent or nearly so. Costal fringe extending about 1/2 the distance between apex of R<sub>2+3</sub> and R<sub>4+5</sub>. **Abdomen.** Coloration variable, from each segment predominantly yellow with only a narrow posterior band dark brown, to predominantly brown with yellow anterolateral areas. Cerci yellow-brown. Genitalia not dissected.

Female. Identical to the male with the following exceptions. **Head.** Third antennal segment tinged with brown. Apical seta of palp shorter, stronger, black. **Thorax.** Median stripe of mesonotum broader on the anterior half and dark, similar to the lateral stripes. **Legs.** Front legs without elongate cilia or setae. **Wings.** Not as long and narrow, about three times as long as wide; shape normal, posterior margin convex, apex only very weakly pointed. **Abdomen.** Ovipositor long, straight, yellow, pointed vertically at rest.

**Types.** O‘ahu: Holotype ♂ and allotype ♀, above Nu‘uanu Pali lookout, 1400 ft., 21.365°N 157.761°W, on bait sponge, 2.viii.2009, K. Magnacca (UHIM); paratype, ♂, same data (BPBM).

**Distribution and ecology.** O‘ahu. Probably breeds in *Charpentiera*; females observed ovipositing in rotting trunk (not reared).

**Etymology.** From the Hawaiian *mōlī*, albatross, referring to the similarly long, narrow, pointed wings.

**Discussion.** Hardy (1965) considered this population from O‘ahu to be conspecific with *D. lanaiensis*, described from only females. However, it is now clear that the *D. lanaiensis* types are identical to recent specimens from Lāna‘i and those from Maui (previously known as *D. virgulata*), and different from the O‘ahu specimens (see Discussion under *D. lanaiensis* above). The drawing of the male wing in Hardy (1965) appears to be of an unusual specimen; all those I have seen possess a small but distinct spot in the middle of vein R<sub>4+5</sub>, as in *D. lanaiensis* and *D. digressa*, although it is missing on one wing of the *D. moli* allotype. This variation is occasionally seen in individuals of the other two species as well. None of the specimens examined by Hardy, or any other earlier ones, could be located in the BPBM or UHIM collections. Although it has not been reared from *Charpentiera*, it was observed ovipositing in a rotting tree, and *D. digressa* and *D. lanaiensis* have both been reared from it. This species is proba-

bly highly vulnerable due to habitat loss; although *Charpentiera* is still relatively common on O‘ahu, the restricted range suggests that *D. moli* requires large trees to breed in, and these are increasingly scarce. In recent years it has only been taken at the type locality. It has been reported from Hālawā Valley (S.L. Montgomery, pers. comm.), but the specimens could not be located. Other potential sites may exist in the middle and northern Ko‘olau range, but are difficult to access.

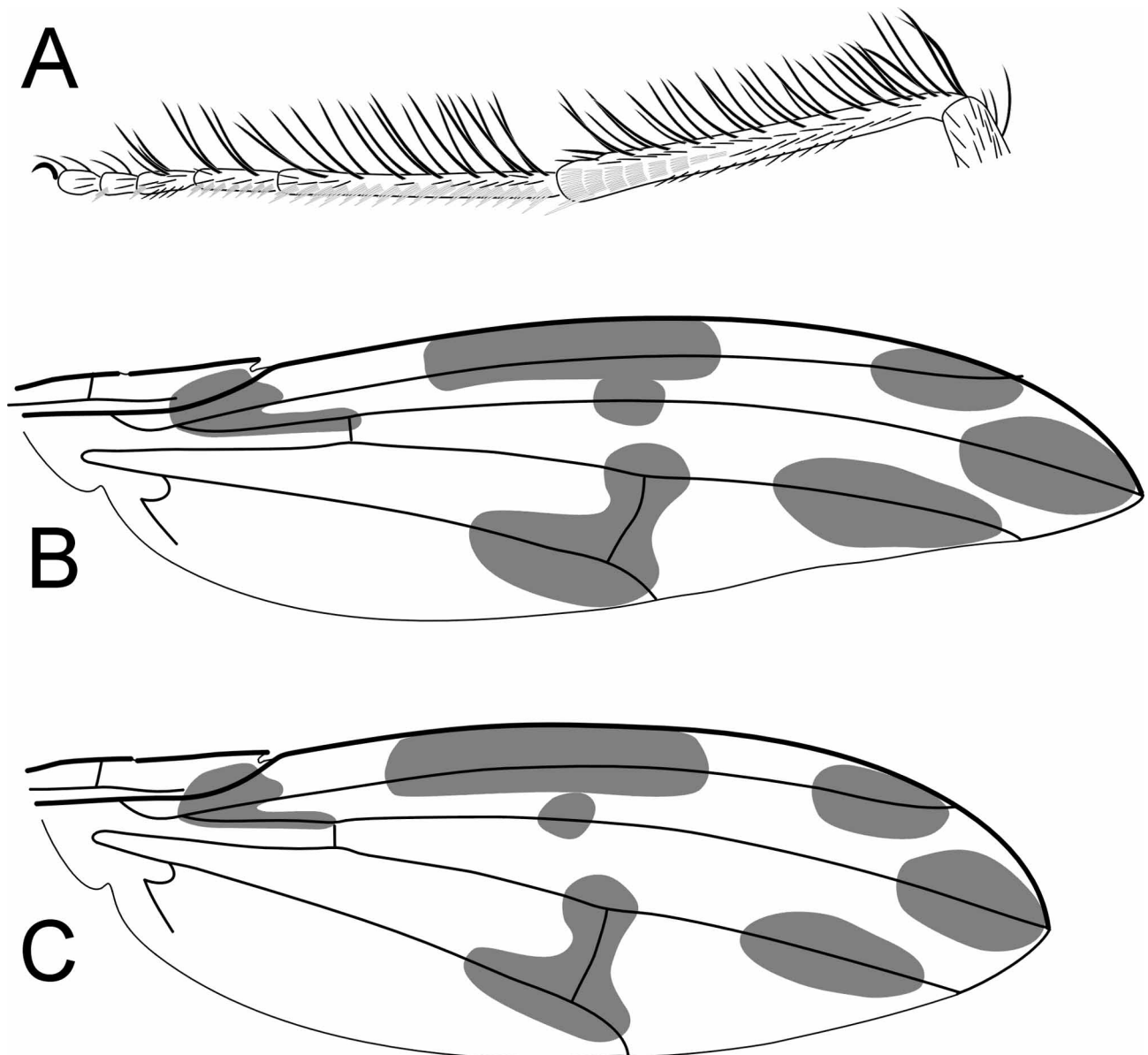


FIGURE 4. *Drosophila moli*. A. Right front leg of male, anterior view. B. Male wing. C. Female wing.

#### *Drosophila nukea* Magnacca, new species

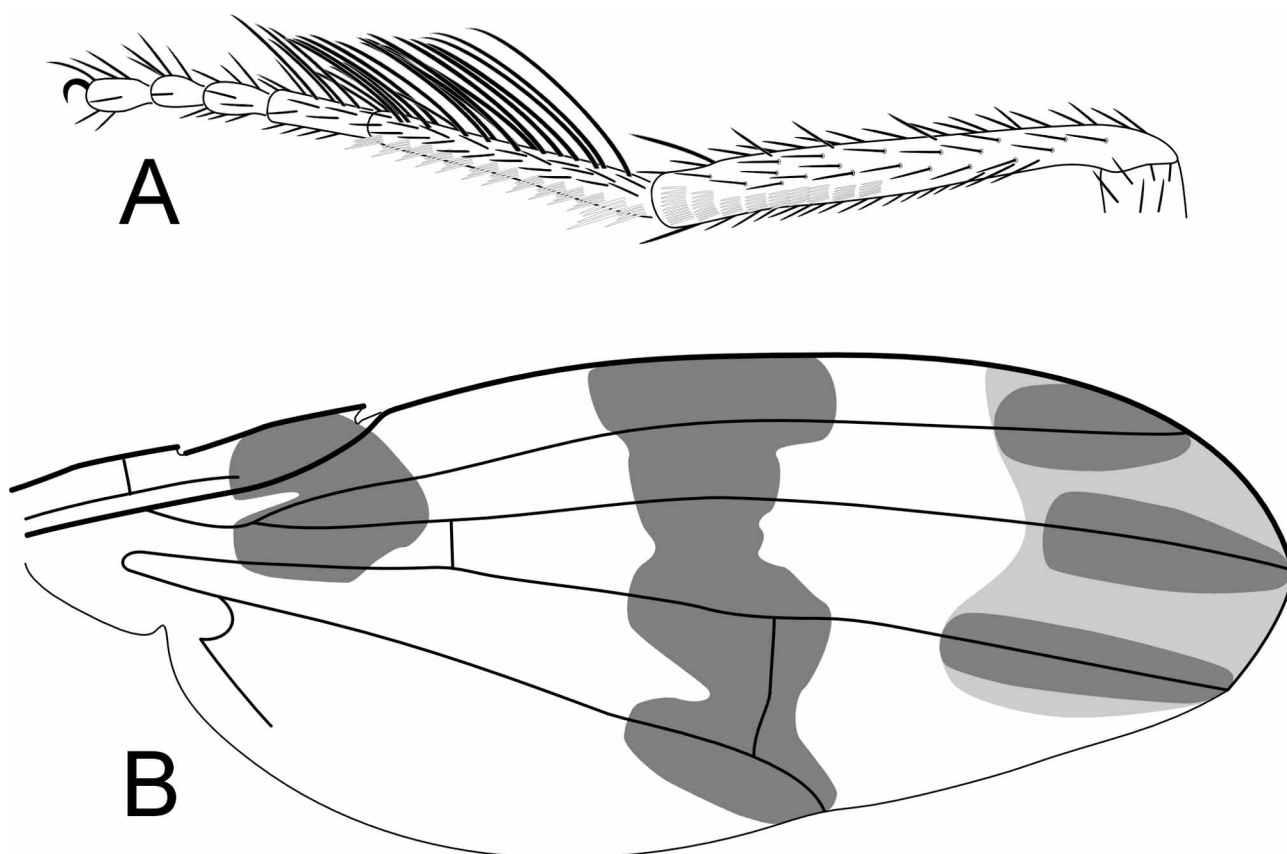
Fig. 5

**Diagnosis.** Among the *hawaiiensis* subgroup, this species is most similar to *D. gradata* of O‘ahu and *D. hawaiiensis* of Hawai‘i due to lacking cilia on the tibia. It is readily distinguished from both of those by the completely dark mesonotum and scutellum; at least the scutellum, and usually the posterior mesonotum, is pale brown in the other two species.

**Description.** Male. **Head.** Front brown, yellowish near the frontal suture; ocellar triangle and orbits dark brown pollinose. Fronto-orbital setae normal, anterior reclinate about half as long as the proclinate and posterior reclinate. Face bright white, gena pale yellow except for a small dark brown spot below the eye. Antenna dark

brown; arista with about 5–6 dorsal rays in addition to the apical fork (ventral rays mostly broken in holotype), and a few long median branches. Two strong oral vibrissae, other oral setulae smaller and hairlike. Palp brown, narrow and elongate, broadest near middle, rounded apically, with a single thin apical seta, slightly shorter than palp. Labellum and mentum brown. **Thorax.** Mesonotum and scutellum entirely brown, with conspicuous gray pollinose medially and along the dorsocentral row. Humeri yellow medially in a stripe between the humeral setae, brown above and below. Pleura entirely brown. Two pairs of strong dorsocentral setae, the anterior about 4/5 as long as the posterior. **Legs.** Predominantly yellow, tinged with brown on all coxae and apices of all femora. Front tibia lacking cilia, front basitarsus densely covered with about 20 long dorsal cilia in irregular rows, longest at the base, becoming slightly shorter apically; second segment with about five cilia, remaining segments bare. **Wings.** Subbasal spot relatively large, extending into cell  $R_5$ , but not reaching r-m crossvein. A continuous band present across middle of wing, nearly parallel-sided, slightly broadened at anterior margin. Marks at apices of  $R_{2+3}$ ,  $R_{4+5}$ , and M confluent. Costal fringe extending about 2/3 the distance between apex of  $R_{2+3}$  and  $R_{4+5}$ . **Abdomen.** Each segment with a pair of large yellow spots anterodorsally, remainder dark brown. Cerci slightly higher than long, yellow-brown. The genitalia have been dissected and appear to resemble *D. gradata* in having a depression beyond the preapical protuberance of the aedeagus and a distinct bend in the paramere near the apex, but they have dried in the vial and may be distorted.

Female. Unknown.



**FIGURE 5.** *Drosophila nukea*. A. Right front leg of male, anterior view. B. Wing.

**Types. Moloka'i:** Holotype ♂, So. Hanalilolilo, 3.iii.1966, J. P. Murphy (genitalia in a glass vial mounted on same pin) (UHIM)

**Distribution and ecology.** Moloka'i, in wet forests (but see Discussion). Host unknown; appears to be most closely related to species breeding in sap fluxes of *Acacia koa* (koa, Fabaceae), but this tree does not appear to live in the area where it was collected.

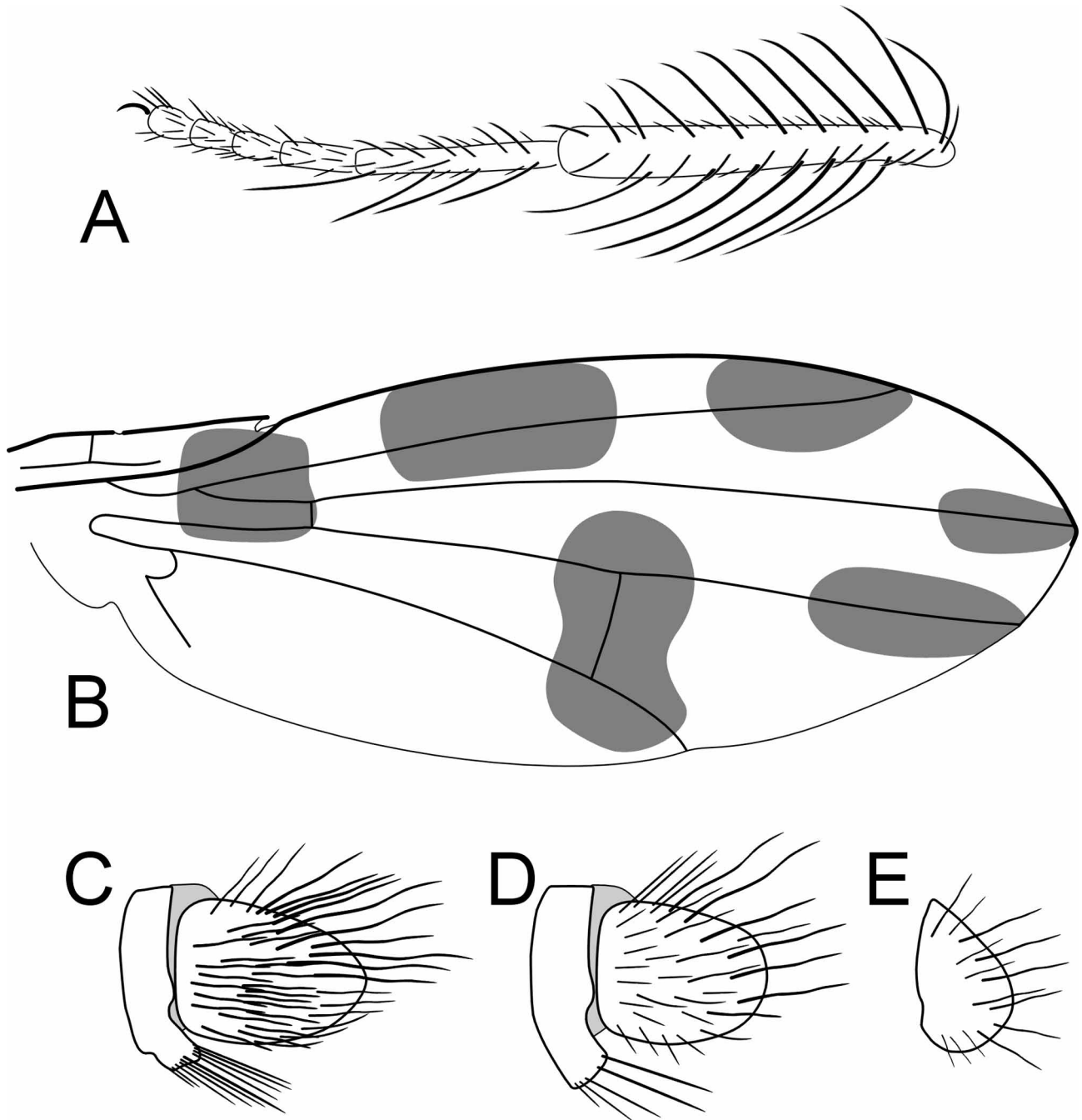
**Etymology.** From the Hawaiian *nūkea*, white-beaked or white-mouthed, a reference to the white face which contrasts against the dark coloration of the rest of the body.

**Discussion.** Given the relative abundance of *D. gradata* and *D. hawaiiensis* on O'ahu and Hawai'i respec-

tively, and the number of other species in this subgroup found on Maui, it is surprising that more specimens do not exist. However, koa is absent from the forest in the area where it was collected. The specimen may therefore be a vagrant from the drier, lower-elevation areas where koa occurs. Another species in this complex, *D. musaphilia* of Kaua'i, is also rare despite an abundance of koa.

***Drosophila opuhe* Magnacca, new species**

Fig. 6



**FIGURE 6.** *Drosophila opuhe*. A. Right front leg of male, dorsal view. B. Wing. C. Male epandrium and cercus, lateral view. D. *Drosophila montgomeryi* epandrium and cercus, lateral view. E. *Drosophila pisonia* cercus, lateral view.

**Diagnosis.** This species is nearly identical to *D. pisonia* of Hawai'i, differing only in the brown coloration of the anepisternum in both sexes (yellow in *D. pisonia*) and the unusual elongate dark cerci of the male. The latter is somewhat developed in *D. montgomeryi*, but to a lesser degree (compare Fig. 6C–E); *D. montgomeryi* also has

only a dorsal stripe on the anepisternum and two faint stripes on the mesonotum, and the posterodorsal cilia of the male front tibia only cover the basal 2/3. In *D. opuhe* the mesonotum lacks stripes and the posterodorsal cilia extend nearly to the apex of the tibia.

**Description.** Male. **Head.** Upper front, ocellar triangle, and orbits brown; lower front paler, yellowish. Fronto-orbital setae normal, anterior reclinate about 2/3 as long as the proclinate and 1/3 as long as the posterior reclinate. Face white, gena yellow except for a small brown spot below the eye. Second antennal segment brown, third segment rufous; arista with about 9 dorsal and 4 ventral rays in addition to the apical fork, and numerous long median branches. One strong oral vibrissae; following oral setulae progressively smaller. Palp yellow, broad and flattened, broadest near middle, rounded apically, with a prominent black apical seta, about half as long as the palp. Labellum and mentum yellow. **Thorax.** Mesonotum and scutellum entirely yellow to rufous, without dark markings. Pleura broadly brown across the upper half, anepisternum almost entirely brown. Katepisternum and lower third of anepimeron yellow. Two pairs of strong dorsocentral setae, the anterior about 3/4 as long as the posterior. **Legs.** Entirely yellow except all coxae tinged with brown. Front tibia with 2 very long curved basal cilia, and rows of about 7–9 anterodorsal and 8–10 posterodorsal cilia along its entire length, about equal in length (the two apical posterodorsals short, similar to the dorsal cilia); dorsal surface with a row of about 10 shorter cilia. Front basitarsus about 3/5 as long as tibia, with about 4–5 long anterodorsal and 6 shorter posterodorsal cilia. Distitarsus without elongate cilia. **Wings.** Marks present at base, over ends of major veins, dm-cu crossvein, and medially on  $R_{2+3}$ ; the last elongate, twice as long as high. Basal mark moderately large, reaching r-m crossvein. Costal fringe extending about 2/3 the distance between apex of  $R_{2+3}$  and  $R_{4+5}$ . **Abdomen.** Each segment with yellow spots anterolaterally, remainder dark brown. Cerci dark brown, about 1.5 times as long as high.

Female. Identical to the male with the following exceptions. **Head.** Palp lacking a distinct apical seta. **Legs.** Front legs without elongate cilia or setae. **Abdomen.** Ovipositor long, nearly straight, brown, pointed vertically at rest.

**Types.** **Kaua'i:** Holotype ♂ and allotype ♀, 'Awa'awapuhi nr. road, 3600 ft., 2004, *Urera* stem reared, Z89, 22.144°N 159.648°W, S.L. Montgomery (UHIM).

**Distribution and ecology.** Kaua'i. Reared from rotting bark of *Urera glabra* ('ōpuhe, Urticaceae).

**Etymology.** From the Hawaiian name of its host plant.

**Discussion.** The elevation given on the label is incorrect; it was actually obtained from near 'Awa'awapuhi stream at almost 4000 ft. (P. O'Grady, pers. comm.; this is consistent with "nr. road," as 3600 ft. is about a mile downslope). *Urera* is uncommon in the Kōke'e area, and it is remarkable that this species persists there. Some lowland gulches of the Wailua River drainage have significant stands of *Urera*, but have not been extensively surveyed for *Drosophila*.

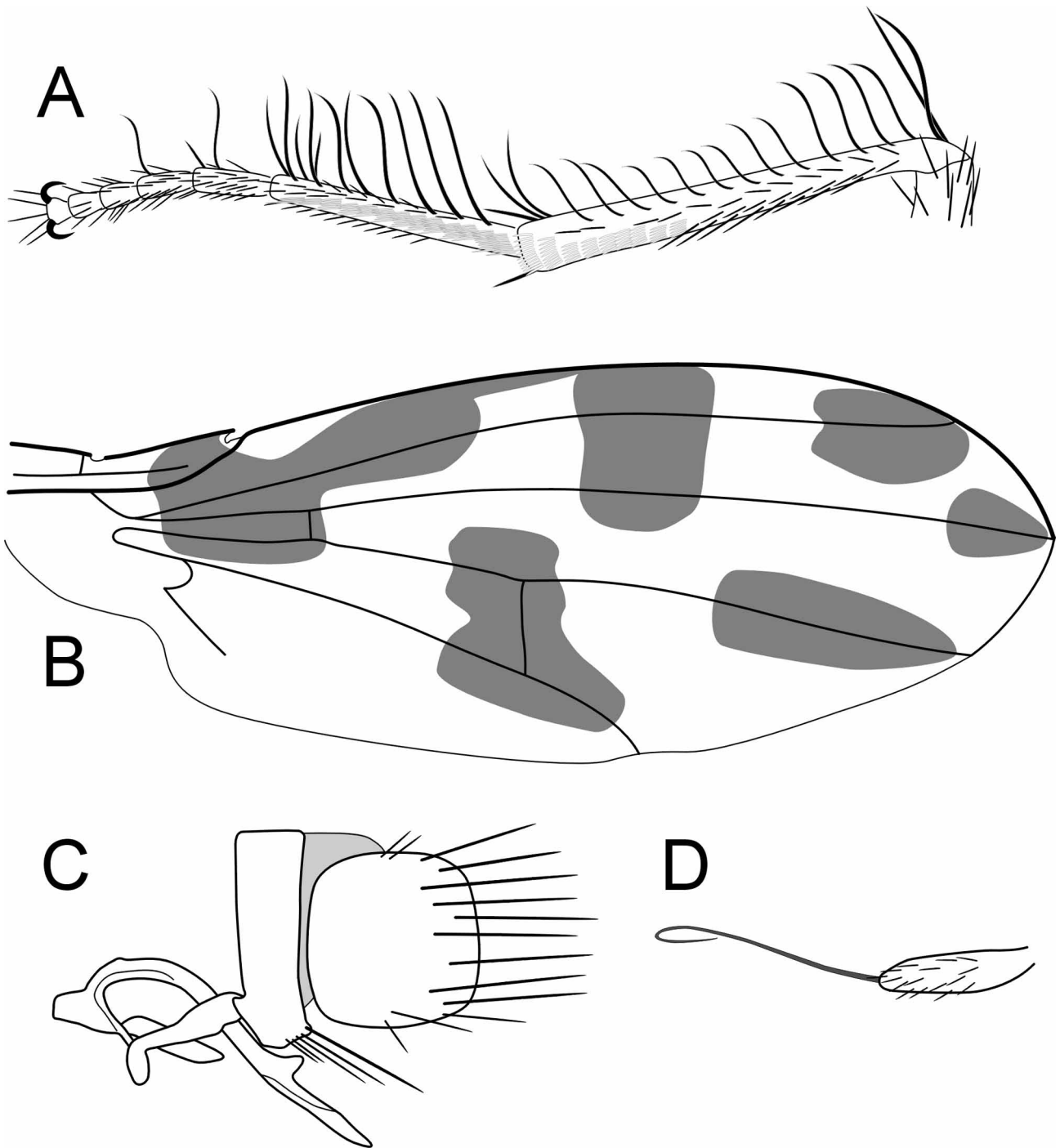
### *Drosophila oreas* Hardy, 1965

Fig. 7

*Drosophila oreas* Hardy, 1965:399. Type ♀, Haleakalā, 1,500 ft., no collector or date, BPBM 6415.

**Diagnosis.** The wing markings, with a quadrate anterior mark spanning  $R_{2+3}$  and  $R_{4+5}$  beyond the dm-cu crossvein, are distinctive enough to separate this species from all others. The male has not been previously described; the setation of the front legs is very similar to *D. macrothrix* of Hawai'i, to which it is most closely related.

**Description.** Male. **Head.** Front pale brown; area between ocelli slightly darker, remainder of ocellar triangle concolorous with front. Fronto-orbital setae normal, anterior reclinate small, about half as long as the proclinate and one-third as long as the posterior reclinate. Face and gena pale yellow except for a small black spot below the eye. Antenna with the second and third segments brown; arista with about 8–9 dorsal and 2 ventral rays in addition to the apical fork, and several median branches. One strong oral vibrissa, followed posteriorly by a row of smaller setae. Palp pale brown, elongate, narrow, slightly broadened near the middle; with a very long, thin, yellow-brown apical seta, curled at the apex, about 1.5 times as long as palp. Mentum brown. **Thorax.** Mesonotum largely yellow with three strongly contrasting dark brown to black stripes; lateral stripes dark, extending from the anterior margin of the humeri nearly to the scutellum; median stripe filling in most of the space between the acrostichal setulae, narrowing abruptly at posterior margin. Scutellum almost entirely dark brown to black except at lateral margins.



**FIGURE 7.** *Drosophila oreas*. A. Right front leg of male, anteroventral view. B. Wing. C. Male terminalia, lateral view. D. Left palp of male, dorsal view.

Pleura predominantly yellow, with a narrow dark stripe along the dorsal margin of the anepisternum; an irregular round mark on the anepimeron below the wing base; and the posterodorsal third of the katapisternum dark. Two pairs of strong dorsocentral setae, the anterior about 2/3 as long as the posterior. **Legs.** Almost entirely yellow, marked with brown on mid and hind coxae, all trochanters, and with faint tinges of brown at apices of femora and both ends of hind tibiae. Front tibia with an anterodorsal row of about 15 long curved cilia each along its entire length, slightly longer at the base, and a transverse row of 3 apical dorsal cilia; dorsal surface otherwise completely bare, lacking small setulae. Front basitarsus with a row of 7 anterodorsal cilia along the entire length, 3 posterodorsal cilia over the apical third, and a dorsal cilia at the apex. Second and third tarsal segments each with a single dorsal cilia. **Wings.** Shape normal, about three times as long as wide, rounded at apex. Subbasal wing spot large,

extending posteriorly into cell M, covering r-m crossvein, and with an anterior prolongation in cell R<sub>1</sub>. Anterior median mark quadrate, extending from costal margin posteriorly beyond R<sub>4+5</sub>. Apical marks discrete; mark at apex of R<sub>4+5</sub> small and nearly circular, mark on M elongate, reaching nearly halfway to dm-cu crossvein. Mark on dm-cu crossvein large and quadrate, extended distally on CuA<sub>1</sub>. Costal fringe extending about 1/2 the distance between apex of R<sub>2+3</sub> and R<sub>4+5</sub>. **Abdomen.** Each segment yellow on anterior half, brown posteriorly and medially. Cerci brown, quadrate, about as long as high. Parameres of aedeagus each with a very short, yellow apical setula. Preapical protuberance of aedeagus very strong, vertical on apical side.

Female. Identical to the male with the following exceptions. **Head.** Apical seta of palp shorter, stronger, black. **Legs.** Front legs without elongate cilia or setae. **Abdomen.** Ovipositor long, straight, brown, pointed vertically at rest.

**Material examined. Maui:** 1♂ 1♀, Pua'aka'a Stream, 1300 ft., 18.xii.2010, K. Magnacca. 2♂ 4♀, Waikapū Valley, 2000 ft., 15.x.2011, K. Magnacca.

**Distribution and ecology.** Maui; very rare. Breeds in *Pisonia umbellifera* (pāpala kēpau, Nyctaginaceae) (Montgomery, 1975).

**Discussion.** Nearly all specimens of this rare species previously came from a single site on East Maui, at Pua'aka'a. It had been collected only once on West Maui, at Pohakea Gulch, and no suitable habitat was found on a recent visit there. However, a sizable population was recently found in nearby Waikapū Valley, and other undiscovered sites may yet exist on both sides of the island. Its sister species, *D. macrothrix*, is likewise currently restricted to a single site on Hawai'i, though it was formerly more widespread. Together they are probably related to *D. spaniothrix*, which is only known from a few collections on O'ahu and has not been collected since 1971. At least *D. oreas* and *D. macrothrix* breed in *Pisonia*, but they may occupy a unique niche as the host is much more widespread than any of the species.

### *Drosophila pihulu* Magnacca, new species

Fig. 8

**Diagnosis.** This species is nearly identical to *D. assita* of Hawai'i and *D. montgomeryi* of O'ahu. It is readily separated from the sympatric *D. vesciseta* by the leg ciliation and yellow palpi, and from both it and the remaining members of the *vesciseta* subgroup except *D. montgomeryi* of O'ahu by possessing a distinct dark brown stripe along the upper edge of the anepisternum. In *D. pihulu* the posterodorsal cilia of the male front tibia extend the full length of the segment, while in *D. montgomeryi* they cover only the basal 2/3.

**Description.** Male. **Head.** Front yellow; ocellar triangle and orbits brown. Fronto-orbital setae normal, anterior reclinate nearly as long as the proclinate and about 2/5 as long as the posterior reclinate. Face and gena white to pale yellow except for a small brown spot below the eye. Antenna entirely pale yellow; arista with about 6–8 dorsal and 2–3 ventral rays in addition to the apical fork, and numerous long median branches. Two strong oral vibrissae, the upper one stronger; other oral setulae small and hairlike. Palp yellow, broad and flattened, broadest near middle, rounded apically, with a prominent black apical seta, about half as long as the palp. Labellum and mentum yellow. **Thorax.** Mesonotum and scutellum entirely yellow to rufous, without dark markings. Pleura largely yellow to rufous, with three prominent dark marks—a narrow stripe along the dorsal margin of the anepisternum; a square mark on the anterior margin of the anepimeron; and posterodorsally on the katepisternum, within the area bounded by the katepisternal seta. Anepisternum and lateral metanotum (above spiracle and haltere) usually tinged with brown to a greater or lesser degree, sometimes almost entirely brown. Two pairs of strong dorsocentral setae, the anterior about 3/4 as long as the posterior. **Legs.** Entirely yellow. Front tibia with a basal cluster of about 6–7 very long and 7–8 shorter curved cilia, and rows of about 10–12 anterodorsal and 12–15 posterodorsal cilia along its entire length, about equal in length; dorsal surface with about 20 shorter cilia in an irregular row. Front basitarsus about 3/5 as long as tibia, with about 6 long anterodorsal and 8 shorter posterodorsal cilia. Distitarsus usually lacking elongate cilia, sometimes with one pair on the second segment. **Wings.** Marks present at base, over ends of major veins, dm-cu crossvein, and medially on R<sub>2+3</sub>; the last elongate, twice as long as high. Basal mark moderately sized, but not reaching r-m crossvein. Costal fringe extending about 3/5 the distance between apex of R<sub>2+3</sub> and R<sub>4+5</sub>. **Abdomen.** Each segment with yellow spots anterolaterally, remainder dark brown. Cerci slightly longer than high. Genitalia not dissected.



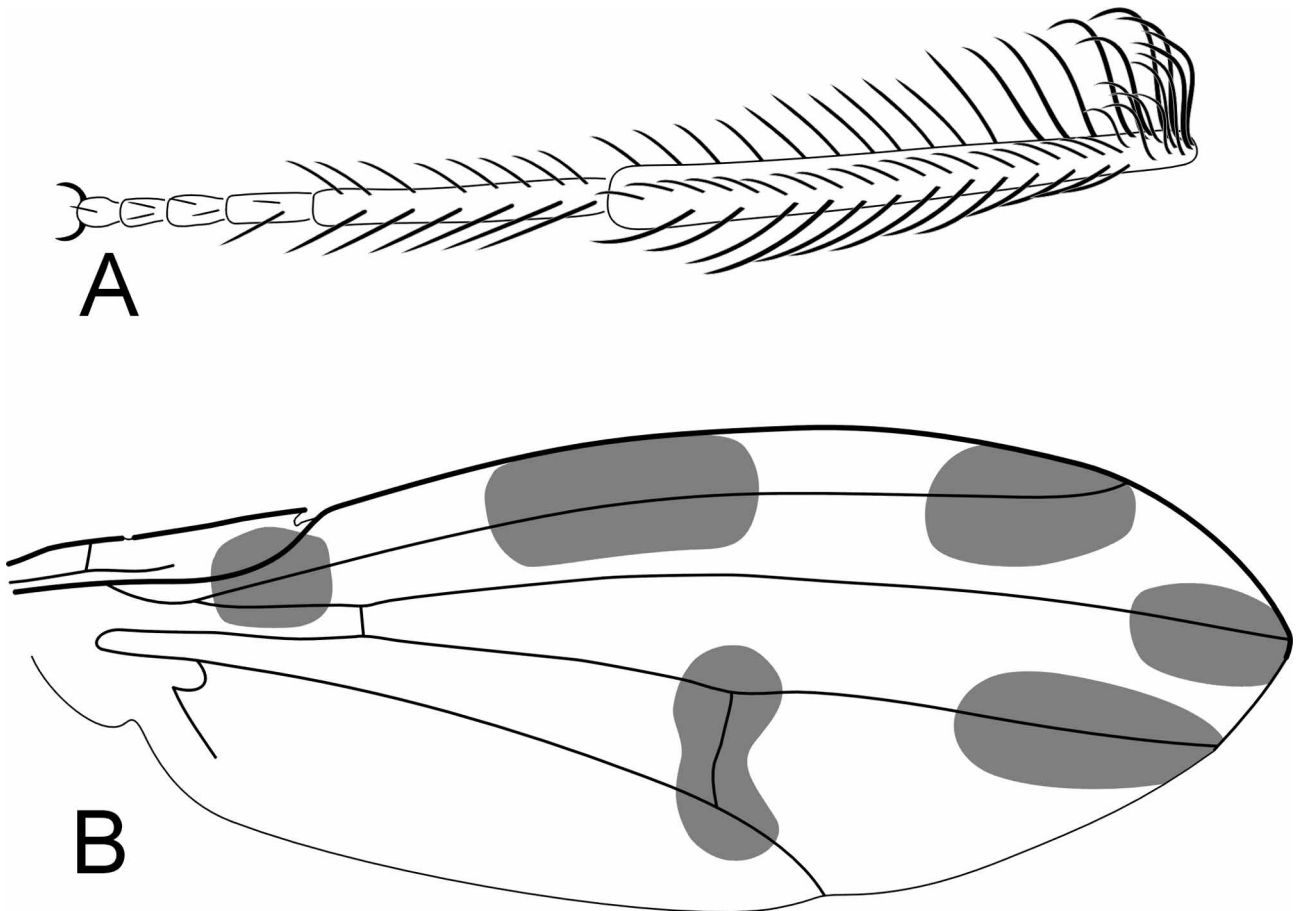


FIGURE 8. *Drosophila pihulu*. A. Right front leg of male, dorsal view. B. Wing.

Female. Unknown.

**Types.** **Maui:** Holotype ♂, Hana'ula, Pohakea, 3400 ft., 13.iv.1971, S.L. Montgomery (UHIM); paratypes: **Moloka'i:** 7♂, East 'Ōhi'a Gulch, 2000 ft., 24.i.1973, R84, S.L. Montgomery (UHIM).

**Distribution and ecology.** Maui and Moloka'i. Reared from rotting bark of *Urera glabra* ('ōpuhe, Urticaceae).

**Etymology.** From the Hawaiian *pihulu*, hairy or fuzzy, referring to the abundant ciliation of the legs.

**Discussion.** The type locality cannot be found precisely, and it is uncertain if the species still occurs there. Much of the mesic habitat around Hana'ula appears to have been lost since collections were made in the 1970's, but *Urera* may persist in wetter parts of gulches where native vegetation is still intact. All other members of the *vesciseta* subgroup (with the exception of *D. ambochila*) are now extremely rare.

### *Drosophila pilipa* Magnacca, new species

Fig. 9

**Diagnosis.** This unique species cannot be mistaken for any other. Although the wing pattern and body markings superficially resemble *D. hemipeza* and *D. substenoptera* of O'ahu, the elongate, pointed wings of the male (lacking an extra crossvein) and frontal setae (modified in both sexes, but elongate and conspicuous in the male) distinguish it immediately.

**Description.** **Male. Head.** Front yellow, with a narrow brown stripe extending through the ocellar triangle to the frontal suture. Orbits lacking the usual proclinate and reclinate setae, instead with about 18–20 long, erect setae on each side in 3 irregular rows; these are about as long as the ocellar setae (slightly shorter posteriorly) and straight for most of their length, the apical 1/5 abruptly bent back. Orbits nearly reaching the frontal suture but only slightly broadened; median frontal area almost bare, with only a few small proclinate setulae near the frontal

suture. Face yellow, gena broadly brown immediately below the eye. Antenna with the second segment brown, third segment yellow; arista with about 8 dorsal and 4 ventral rays in addition to the apical fork, and 6 rather long median branches. One moderately strong oral vibrissa present, other oral setulae weaker, about half as long. Clypeus expanded, about as long dorsoventrally as the width of the palps; brown laterally, pale anteriorly. Palp brown, broad, and short, not extending beyond the clypeus, broadest just before middle; one subapical seta slightly longer than the others. Labellum tinged with brown. **Thorax.** Predominantly yellow. Mesonotum on each side with a narrow stripe just inside of the dorsocentral setae, and a broader stripe just outside of the setae, extending the full length. Anepisternum with a dark brown stripe along the dorsal margin; anepimeron with a large brown spot posteroventrally; katapisternum tinged with brown above the posterior seta. Metanotum with two broad brown stripes, in line with the mesonotal stripes. Two pairs of strong dorsocentral setae, the anterior about 2/3 as long as the posterior. **Legs.** All yellow except the apex of the hind tibia and fifth tarsal segments tinged with brown. Front legs lacking elongate cilia or other modifications. **Wings.** Long and narrow, about 3.5 times as long as wide. Brown markings present at the apex of  $R_1$ , extending posterior to M; around the r-m and dm-cu crossveins; in an elongate mark on the mid anterior margin, occupying about 1/3 the wing length; and broadly at the apices of  $R_{2+3}$  and  $R_{4+5}$ . Otherwise more or less evenly fumose, the background color distinctly yellow in cell C and in cell  $R_3$  between the basal spot and the r-m crossvein. The r-m crossvein is well beyond the end of vein  $R_1$ ; penultimate and antepenultimate segments of M equal, about half as long as the last segment. Posterior wing margin between M and  $CuA_1$  straight or slightly concave. Dm-cu crossvein nearly perpendicular to long axis of wing. Costal fringe extending about half the distance between apex of  $R_{2+3}$  and  $R_{4+5}$ . **Abdomen.** Predominantly yellow, with a brown stripe extending along the lateral margins of all tergites and a medial brown stripe. Cerci semicircular, higher than long. Genitalia not dissected.

Female. Identical to the male with the following exceptions. **Head.** Erect setae of orbits short and straight, only slightly longer than the prostrate setulae of the median frons. Proclinate and posterior reclinate setae present but both directed laterally; normally sized, the latter about twice as long as the former. **Wings.** Not as long and narrow, about three times as long as wide. Posterior wing margin between M and  $CuA_1$  convex. Segments of M in approximately the same proportions as in the male, but dm-cu crossvein distinctly angled basad anteriorly, and the mark over it obliquely angled relative to the vein. **Abdomen.** Ovipositor long and narrow, held vertically at rest. Eggs with four very short filaments, less than 1/3 as long as the egg.

**Types.** **Kaua'i:** Holotype ♂, F1 offspring of allotype ♀ coll. 24.vii.2010, 22.111°N 159.596°W, emerged 8.ix.2010 (UHIM). Allotype ♀, Alaka'i Wilderness Preserve, Mōhihi Trail, 3800 ft., 22.111°N 159.596°W, on bait sponge, 24.vii.2010, K. Magnacca (UHIM); paratypes: 1♂ 2♀, same data as holotype, emerged 18–23.ix.2010 (UHIM). 2♀ (BPBM), 1♀ (UHIM), same data as allotype.

**Other material.** **Kaua'i:** 1♂, Ku'ia Natural Area Reserve, Mahanaloa Valley enclosure, 2200 ft., 22.135°N 159.700°W, on bait sponge, 23.vi.2009, K. Magnacca.

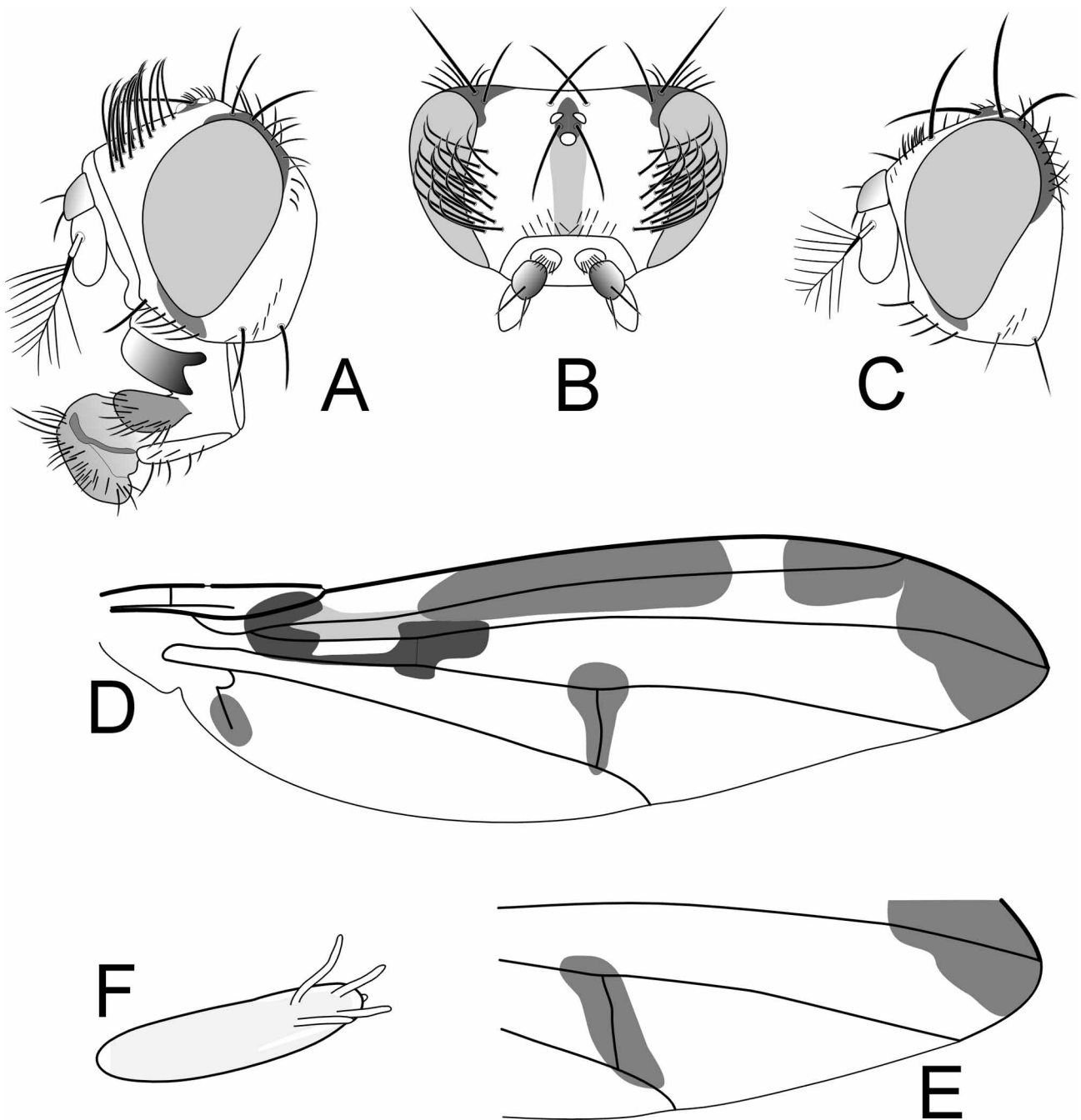
**Distribution and ecology.** **Kaua'i,** mesic forest. Probably breeds in *Charpentiera elliptica* (pāpala, Amaranthaceae). There are no records of rearing from field-collected material, but two wild-caught females presented with a variety of host extracts (*Charpentiera*, *Cheirodendron*, *Clermontia*, *Pisonia*, *Pleomele*, and *Wikstroemia*) laid eggs only on *Charpentiera*. This was also the only potential host shared between the two collection sites, though it was extremely rare at both.

**Etymology.** From the Hawaiian *pilipā*, hedge or fence, referring to the dense frontal setae.

**Discussion.** This striking species appears to be a morphological link between the basal *planitibia* group species, *D. hemipeza* and *D. substenoptera*, and other species that lack an extra crossvein in the wing. It closely resembles both of those species in the coloration pattern of the wing, thorax, and abdomen. However, phylogenetically it groups with *D. picticornis* and *D. setosifrons* as sister to the *nudidrosophila* group based on nuclear gene sequences (Magnacca and Price, in prep.). The frontal setae of *D. pilipa* are somewhat reminiscent of *D. setosifrons*, albeit much longer. That these three species form a monophyletic group but are genetically and morphologically distant, and have very different hosts (sap fluxes, araliad bark, and *Charpentiera* bark), suggests they may represent relictual members of a formerly larger lineage that has been displaced by the *grimshawi* group.

Eggs laid in laboratory vials were deposited on the surface of paper tissues soaked with extract, rather than inserted into the tissue as with most other species. Few eggs were laid, about 2–7 per week for the two females, suggesting a low reproductive rate. The filaments are much shorter than any of the species examined by Kambysellis and Heed (1971), which included *D. picticornis*. Only a few eggs were observed; oviposition vials were

changed every week and usually well-developed larvae were already present, indicating a very short period as an egg. The larvae developed on standard Wheeler-Clayton medium with no apparent mortality, but adult survivorship was low, apparently due to refusal to feed on the medium. Consequently the lab-reared adults did not survive to sexual maturity. Development was faster than in other species—total time from egg to adult was 33–35 days, with approximately 15 of those spent as a pupa.



**FIGURE 9.** *Drosophila pilipa*. A. Male head, lateral view (ptilinum protruding slightly). B. Male head, dorsal view. C. Female head, lateral view. D. Male wing. E. Female wing, posteroapical portion. F. Egg.

***Drosophila ciliaticrus* Hardy, 1965**

Fig. 10

*Drosophila ciliaticrus* Hardy, 1965:207–209. Holotype ♂, Hawai'i, Kaiholena Ridge [Ka'ū], 2300 ft., viii.1952, D.E. Hardy. BPBM 6323.

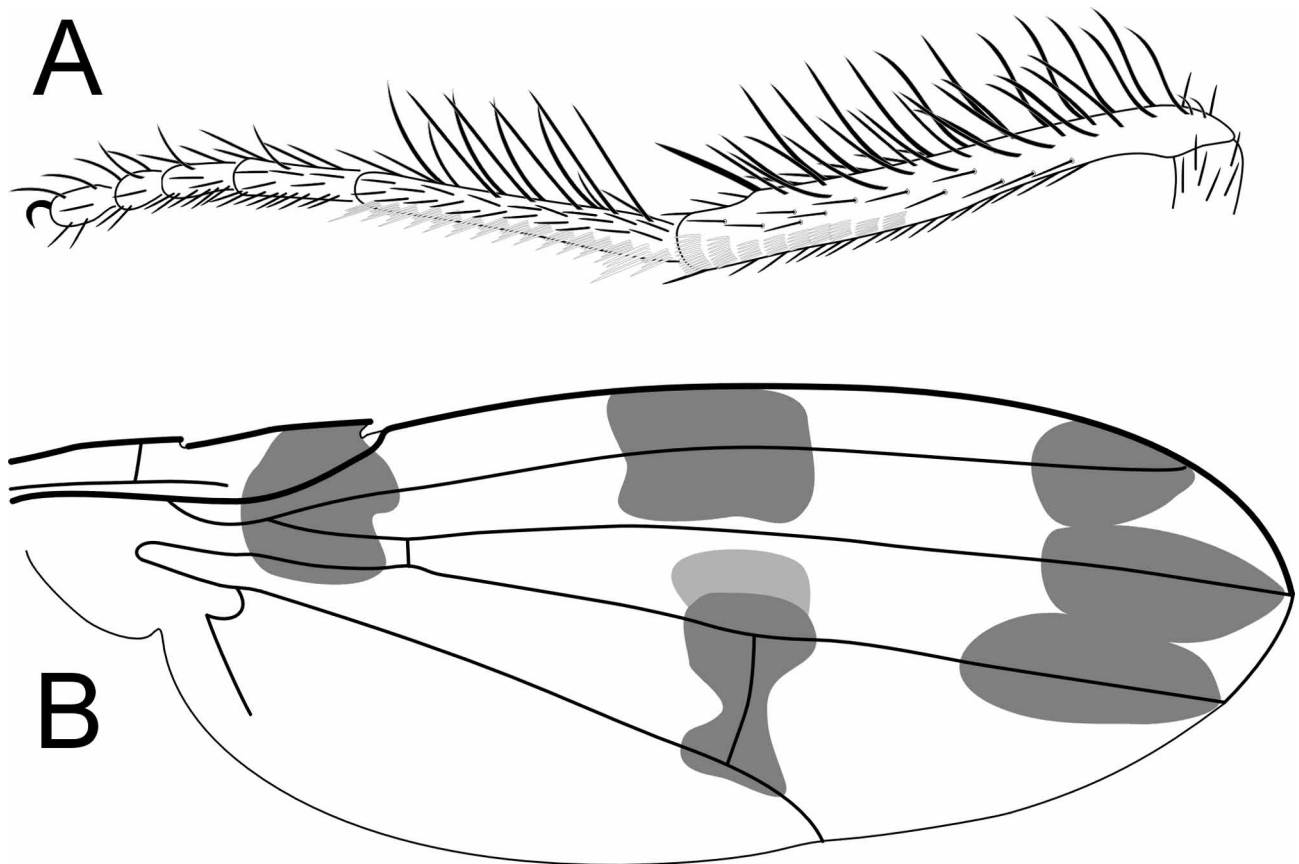


FIGURE 10. *Drosophila ciliaticrus*. A. Right front leg of male, anterior view. B. Wing.

**Material examined. Hawai'i:** Holotype ♂ and allotype ♀, Hawaii, T.H., Kaiholena Ridge 2300 ft. [Ka'ū], viii.1952, D.E. Hardy, BPBM. Specimens from UHIM: 2♂ paratypes, same data as holotype. 2♂ 4♀, Pu'u La'ala'au, Kohala Mts., 29.viii.1966, J29B11, K.Y. Kaneshiro. 3♂ 3♀, Pololū Valley trail, 1000 ft., 10.viii.1970, P50, reared ex rotten *Dracaena* [=Pleomele] stem, S.L. Montgomery. 3♂ 2♀, Pu'u Wa'awa'au, 3600 ft., 1.viii.1971, reared ex *Dracaena* [=Pleomele] stem, Q6, S.L. Montgomery. 4♀, Pu'u La'ala'au, N. Kohala Mts., 27–29.vi.1972, ex *Tetraplasandra* bark, P28, S.L. Montgomery. 1♂, Manukā Forest Reserve, 2300 ft., 21.viii.1976, U20, H.L. Carson. 1♀, Kapu'a (sect.), Ho'ōpūloa (quad.), S. Kona, 2650 ft., vii.1977, D.E. Hardy. 3♀, Manukā, S. Kona, 1000 ft. [sic.?], on fungus bait, 15.i.1979, D.E. Hardy. 1/2 mi. NW of Moanuaieha radio tower, Hualalai, 4.iv.1972, K.Y. Kaneshiro.

UHIM, labelled "*Drosophila tetraplasandrae*": Putative holotype ♂ and 2♂ 4♀ paratypes, Pololū Valley, N. Kohala, 1000 ft., 11.viii.1970, reared ex rotten flux of *Tetraplasandra hawaiiensis*, P50λ, S.L. Montgomery. Putative allotype ♀ and 1♂ paratype, Honokāne Nui Valley, 10.viii.1970, 1200 ft., reared ex *Tetraplasandra* bark-flux, P50α, S.L. Montgomery. 3♀, Pāpā, South Kona, 20.viii.1971, reared ex *Tetraplasandra* bark, Q10, S.L. Montgomery. 1♂, Kalapana, 100 ft., 28.ii.1972, reared ex *Reynoldsia* bark or flux, Q95, S.L. Montgomery. 1♂ 1♀, 'Ōla'a Forest Reserve behind Volcano Dump, 3200 ft., 4.vi.1978, reared ex *Tetraplasandra* sap, S.L. Montgomery & W.P. Mull. 9♂ 11♀, 'Ōla'a Forest Reserve, 3200 ft., at bait, 14.v–16.vi.1978, W.P. Mull.

Recent specimens at UHH: 1♂ 1♀, Stainback Highway, 3600 ft., 19.573°N 155.235°W, on bait sponge, 21.vii.2009, m0075-06, K. Magnacca. 1♀, Manukā, olopuia kipuka, 2300 ft., 19.118°N 155.813°W, on bait sponge, 7.viii.2009, m0100-02, K. Magnacca. 1♂ 1♀, 'Ōla'a Forest Reserve behind Volcano dump, 3200 ft., 19.45°N 155.206°W, 2.v.2010, on bait sponge, m0243-01, K. Magnacca. 1♂ 1♀, Stainback Highway, Tom's Trail upper forest, 3200 ft., 19.575°N 155.216°W, on bait sponge, 15.vi.2010, m0323-01, C. Yakym. 1♀, Leilani Estates, 600 ft., 19.455°N 154.912°W, collected as pupa on *Tetraplasandra hawaiiensis* bark-flux, 21.xi.2010, em. 4.xii.2011, m0331-01, K. Magnacca. 1♂ 2♀, F1 lab reared from ♀ collected at 'Ōla'a Forest Reserve behind Volcano dump, 3200 ft., 19.450°N 155.206°W, 1.iv.2011, m0382-01, K. Magnacca.

**Discussion.** This species exhibits significant morphological variation based on distribution, and may be in the process of speciation. Individuals from Kohala and North Kona typically have the legs entirely yellow; mesonotum brownish and densely pollinose; anepisternum with distinct longitudinal stripes; subbasal wing spot small, not extending into cell M and remote from r-m crossvein;  $R_{4+5}$  with a median spot in both sexes; and usually at least some cilia on the second tarsal segment in the male. Those from Waiākea, ‘Ōla‘a, and Puna have the legs entirely dark brown to black; mesonotum dark brown to black and less densely pollinose; anepisternum often entirely dark; subbasal wing spot larger, always extending into cell M and often touching the r-m crossvein;  $R_{4+5}$  often lacking a median spot in males, sometimes also in females; and apparently never with cilia on the second tarsal segment (Fig. 10). The former have been reared predominantly from *Pleomele hawaiiensis* (halapēpē, Asparagaceae), but a few come from *Tetraplasandra* spp. (‘ohe‘ohe and ‘ohe mauka, Araliaceae); the latter apparently breed exclusively in *Tetraplasandra* and *Reynoldsia* (*Pleomele* is very rare in Puna, typically in dry sites). Many specimens of the second, darker form are segregated in collections under the unpublished name “*Drosophila tetraplasandrae*”. These also include two series of dark *Tetraplasandra*-reared specimens from Kohala referred to as “sp. nr. *sobrina*” with collection codes P50 and Q10 in earlier publications (Magnacca, *et al.*, 2008; Montgomery, 1975). They were given holotype and paratype labels by D.E. Hardy (as noted above), but the name was never published. The few specimens available from South Kona appear to be intermediate, generally like the southeastern population but with yellow legs. However, specimens of the type series, from nearby Ka‘ū, are quite pale and resemble *Pleomele*-reared individuals from Kohala.

While extreme individuals superficially appear to be different species, in all populations many of the characters occur in various combinations. Leg color appears to be the only fixed character, and this is insufficient to separate species; *D. murphyi* shows a similar degree of variation in the legs, albeit without a geographic basis. DNA of a specimen from Manukā was sequenced and was over 6% different from four ‘Ōla‘a/Waiākea specimens in the COI gene—similar to the divergence found between sister species—but nearly identical at three nuclear loci (unpublished data). Even among individuals of the latter population, sequence variation is much higher than is observed in related sympatric species such as *D. sproati* and *D. murphyi*. No other recent collections from the Kona, Kaū, or Kohala populations are available to assess the full range of genetic variation. Therefore, we are retaining it as a single species across the island.

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