

Revision of the ‘nudidrosophila’ and ‘ateledrosophila’ species groups of Hawaiian *Drosophila* (Diptera: Drosophilidae), with descriptions of twenty-two new species

KARL N. MAGNACCA and PATRICK M. O’GRADY

Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, U.S.A.

Abstract. The ‘nudidrosophila’ and ‘ateledrosophila’ species groups, formerly described as genera, are a relatively small and understudied part of the enormous Hawaiian *Drosophila* radiation. Only nine species were described previously. Here we revise the two groups, provide a key to males and females, and describe fully all species. The ‘ateledrosophila’ group now contains three species, *D. diamphidia* Hardy, *D. papala* sp.n., and *D. preapicula* Hardy. The 28 species of the ‘nudidrosophila’ group are separated into five subgroups: ‘hirtitibia’ (*D. hirtitibia* Hardy, *D. konaensis* sp.n., *D. mawaena* sp.n., and *D. papaalai* sp.n.); ‘kahania’ (*D. kahania* sp.n. and *D. longipalpus* sp.n.); ‘nudidrosophila’ (*D. aenicta* Hardy, *D. amita* Hardy, *D. canavalia* sp.n., *D. eximia* Hardy, *D. gemmula* Hardy, *D. kualapa* sp.n., *D. lepidobregma* Hardy, *D. mahui* sp.n., *D. malele* sp.n., *D. panoanoa* sp.n., and *D. poonia* sp.n.); ‘okala’ (*D. akoko* sp.n., *D. kuhao* sp.n., *D. makawao* sp.n., *D. okala* sp.n., and *D. panina* sp.n.); and ‘velata’ (*D. halapepe* sp.n., *D. kauaiensis* sp.n., *D. lauoho* sp.n., *D. milolii* sp.n., *D. pohaka* sp.n., and *D. velata* Hardy).

Introduction

One of the distinctive features of the Hawaiian *Drosophila* fauna is the diversity of secondary sexual characters that have evolved in the males. These range from simple cilia on the legs to modified spine-like setae on the mouthparts, sclerotization of the labellum, the addition of spoons, bristles and extensions to the front tarsi, changes in the size and number of head setae, and a wide range of wing pigmentation patterns. When Hardy (1965) reviewed the Drosophilidae of Hawaii, he erected the genera *Ateledrosophila* and *Nudidrosophila* based on the number, size, and position of the diagnostic head setae and arista, and the absence of the preapical dorsal setae on the front tibia. Initially, the former included only two species, *A. diamphidia* and *A. preapicula*, and the latter four, *N. amita*, *N. eximia*, *N. gemmula*, and *N. lepidobregma*. He consid-

ered them worthy of generic status because, despite females being indistinguishable from those of the genus *Drosophila*, *Ateledrosophila* males had no anterior reclinate or ocellar setae, and had the arista displaced toward the apex of the third antennal segment; *Nudidrosophila* males completely lacked reclinate, proclinate and ocellar setae, instead having the front covered with short, dense setulae. However, when Hardy (1966) added a fifth species, *N. aenicta*, to this group, he noted the similarities of both males and females to the sympatric *D. hirtitibia* and stated, ‘I believe it is evident that *Nudidrosophila* should not be retained as a genus but probably should be sunk as a direct synonym of *Drosophila*.’

Kaneshiro (1976) used characters of male genitalia, most notably the shape of the aedeagus, to evaluate the generic divisions of Hawaiian Drosophilidae. He demonstrated that *Nudidrosophila* was closely related to two species previously described by Hardy (1965), *D. hirtitibia* and *D. velata*, and that the shape of the aedeagus in *Ateledrosophila* was virtually identical to that of the ‘picture-wing’ group. Consequently, both genera were reduced to synonyms of *Drosophila*.

Correspondence: Karl N. Magnacca, Department of Environmental Science, Policy, and Management, University of California, 137 Mulford Hall, Berkeley, CA 94720, U.S.A. E-mail: magnack@tcd.ie

Throckmorton's (1966) morphological study suggested a close relationship between the 'nudidrosophila', 'ateledrosophila', and 'picture-wing' species. Recent molecular evidence (Bonacum, 2001) further suggests that 'nudidrosophila' forms a clade with the 'grimshawi' and 'planitibia' subgroups of the 'picture-wing' group, to the exclusion of the 'adiastola' subgroup ('ateledrosophila' was not represented). Although highly divergent in overall appearance, morphological characters uniting this clade include the presence of a prominent preapical protuberance on the aedeagus (Kaneshiro, 1976) and an elongate, parallel-sided, blunt-tipped ovipositor that is usually held vertically at rest, nearly touching the hypoproct (subanal plate) (Fig. 1A). The latter is presumably related to the shared ecological character of breeding almost exclusively in bark, stems, and sap flux (Magnacca *et al.*, in press). Both the male and female terminalia of the 'adiastola' subgroup are more similar to those of the 'modified-mouthparts' group: the preapical protuberance is an indistinct bump, and the ovipositor is broadly triangular, short, and points caudally at rest. Kaneshiro (1997) has suggested an association between the 'modified-mouthparts' group and the 'adiastola' subgroup because of the presence of mouthpart modifications in some species (e.g. *D. ornata*) in the latter clade.

It has been suggested that the Hawaiian *Drosophila* be separated as the genus *Idiomyia* (Grimaldi, 1990), a name originally proposed for the species now referred to as the 'planitibia' subgroup (Grimshaw, 1901; Kaneshiro, 1976). However, an expanded definition of *Idiomyia* has not been explicitly specified and evaluated, new combinations have not been published, and the usage has not been widely adopted. Additional reasons for retaining the standard definition of *Drosophila* are summarized in O'Grady (2002), along with formal redesignations of species assigned to *Idiomyia* by Grimaldi (1990). Grimaldi's (1990) results conflict strongly with those of other studies, which place *Scaptomyza* as sister to the Hawaiian *Drosophila* (Thomas & Hunt, 1993; Bonacum, 2001). In addition, reanalysis of the

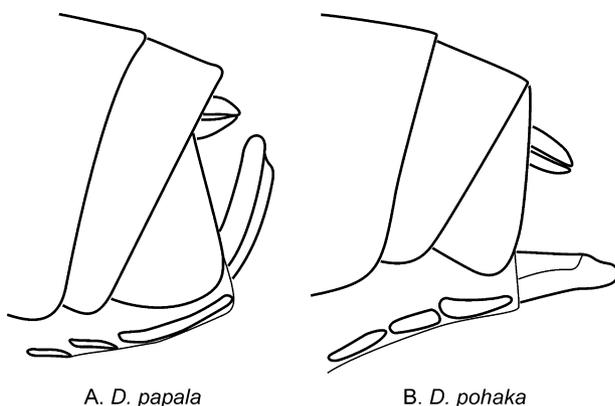


Fig. 1. Apex of female abdomen, showing the ovipositor in resting position. (A) *D. papala*, typical form for the 'ateledrosophila' and 'nudidrosophila' groups; (B) *D. pohaka*.

Grimaldi morphological data set with more modern methods produced thousands of equally parsimonious trees, which resulted in a consensus that was largely unresolved (Remsen & O'Grady, 2002). Although *Drosophila* is paraphyletic with respect to at least *Scaptomyza* and possibly several other genera, and the current broad definition makes it unwieldy and of limited utility (Remsen & O'Grady, 2002), it would require an enormous taxonomic effort to split it into multiple, clearly defined genera. Therefore, until a better generic classification scheme for Drosophilidae is established, we will continue to refer the Hawaiian species to *Drosophila*.

The ecological habits of these species are relatively well known, thanks in large part to their similarity to those of the well-studied 'grimshawi' subgroup of the 'picture wings' (Montgomery, 1975; Magnacca *et al.*, in press). Nearly two-thirds of the 31 'nudidrosophila' and 'ateledrosophila' species have at least one rearing record, and over one-third have multiple records. Although small sample sizes prevent definitive conclusions about hosts, it is clear that the 'nudidrosophila' group as a whole consists of specialists on bark and stems. The long ovipositors of females may be an adaptation to this. The fact that seven of the 11 species with multiple records have been reared from more than one host family suggests that they may be more general in their host requirements than the 'picture-wing' group (Magnacca *et al.*, in press). In general, 'nudidrosophila' are found in mesic habitats, and show strong associations with several genera of plants characteristic of mesic forests (Gagné & Cuddihy, 1990): *Charpentiera*, *Claoxylon*, *Pisonia*, *Pleomele*, *Sapindus*, and *Urera* (Table 1). Only a single species, *D. okala*, is known to breed in the typical wet forest *Drosophila* hosts, *Cheirodendron* and *Clermontia*, and it has been recorded from *Sapindus* as well.

The current study revises the 'nudidrosophila' and 'ateledrosophila' species groups, providing descriptions, collection records, and ecological information for all described taxa; it also includes a key to species and subgroups. The 'nudidrosophila' species group is defined by the hooked preapical protuberance of the aedeagus (Kaneshiro, 1976; Fig. 2B, C). It includes five distinct subgroups: 'hirtitibia', 'kahania', 'nudidrosophila', 'okala', and 'velata'. The 'ateledrosophila' group contains only three species. These divisions are relatively easily separated by the secondary sexual characters of the male head (Figs 4, 5) and front legs (Figs 8–14). Most females of both groups are easily separated from other Hawaiian *Drosophila* by the distinctive shape of the ovipositor (Fig. 1A; some species of the 'velata' subgroup have shorter ovipositors, as in Fig. 1B); their small size and lack of extensive wing markings distinguishes them from the 'picture-wing' group, which has a similar ovipositor. This revisionary work lays the groundwork for future studies on the ecology, biogeography, and phylogenetic relationships of species in the 'nudidrosophila' and 'ateledrosophila' species groups. Because many species show a marked preference for mesic forest habitats, this work also suggests that the present-day species diversity may be a remnant of a much more extensive fauna, and that

Table 1. Distribution and larval breeding host records of species in the 'ateledrosophila' and 'nudidrosophila' groups.

Species group	Subgroup	Species	Author	Distribution	Rearing Records	Hosts
ateledrosophila		<i>diaphidia</i>	(Hardy, 1965)	Hawai'i		
		<i>papala</i>	sp.n.	Hawai'i	5	<i>Charpentiera</i> , <i>Pisonia</i>
		<i>preapicula</i>	(Hardy, 1965)	O'ahu		
nudidrosophila		<i>hirtitibia</i>	Hardy, 1965	O'ahu	1	<i>Urera</i>
		<i>konaensis</i>	sp.n.	Hawai'i	3	<i>Charpentiera</i> , <i>Pisonia</i>
		<i>mawaena</i>	sp.n.	Moloka'i, Maui?, Lāna'i?	2	<i>Pisonia</i>
		<i>papaalai</i>	sp.n.	Kaua'i		
kahania		<i>kahania</i>	sp.n.	O'ahu	1	<i>Urera</i>
		<i>longipalpus</i>	sp.n.	Hawai'i		
nudidrosophila		<i>aenicta</i>	(Hardy, 1966)	O'ahu	2	<i>Chamaesyce</i> , <i>Urera</i>
		<i>amita</i>	(Hardy, 1965)	Hawai'i	2	<i>Charpentiera</i> , <i>Claoxylon</i>
		<i>canavalia</i>	sp.n.	Hawai'i	2	<i>Canavalia</i> , <i>Charpentiera</i>
		<i>eximia</i>	(Hardy, 1965)	Maui, Moloka'i, Lāna'i	3	<i>Freycinetia</i> , <i>Pisonia</i> , <i>Urera</i>
		<i>gemmula</i>	(Hardy, 1965)	O'ahu	3	<i>Urera</i>
		<i>kualapa</i>	sp.n.	Kaua'i		
		<i>lepidobregma</i>	(Hardy, 1965)	Hawai'i	1	<i>Sapindus</i>
		<i>mahui</i>	sp.n.	Hawai'i	1	<i>Claoxylon</i>
		<i>malele</i>	sp.n.	Kaua'i		
		<i>panoanoa</i>	sp.n.	Hawai'i		
		<i>poonia</i>	sp.n.	Kaua'i	1	<i>Charpentiera</i>
okala		<i>akoko</i>	sp.n.	O'ahu	1	<i>Chamaesyce</i>
		<i>kuhao</i>	sp.n.	O'ahu	1	<i>Hibiscus</i>
		<i>makawao</i>	sp.n.	Maui, Moloka'i		
		<i>okala</i>	sp.n.	Hawai'i	5	<i>Cheirodendron</i> , <i>Clermontia</i> , <i>Sapindus</i>
		<i>panina</i>	sp.n.	O'ahu		
velata		<i>halapepe</i>	sp.n.	Hawai'i	1	<i>Pleomele</i>
		<i>kauaiensis</i>	sp.n.	Kaua'i	2	<i>Pleomele</i>
		<i>lauoho</i>	sp.n.	Maui, Moloka'i	4	<i>Pleomele</i>
		<i>milolii</i>	sp.n.	Kaua'i	1	<i>Charpentiera</i>
		<i>pohaka</i>	sp.n.	Maui, Hawai'i		
		<i>velata</i>	Hardy, 1965	O'ahu		

extinction may have played a significant role in the history of this group.

Materials and methods

Material comes from recent collections (1997–2006, both pinned and in ethanol), older pinned specimens, and flies reared from hosts. Most specimens came from either sweeping of vegetation or rearing from hosts, as these species are not attracted to standard banana/mushroom baits. Unless otherwise noted, all historic material is from the University of Hawai'i Insect Museum (UHIM), except for holotypes and allotypes, which are from the Bernice

P. Bishop Museum (BPBM). Holotypes and allotypes of new species have been deposited at the BPBM, and paratypes at BPBM, UHIM, and the Hawai'i Volcanoes National Park Insect Collection (HVIC), as noted.

Measurements were taken with an eyepiece micrometer. Measurements are primarily those used by Hardy *et al.* (2001), and are defined as follows. TL: thorax length, distance from the anterior notal margin to the posterior apex of the scutellum. WL: wing length, maximum distance from the humeral crossvein to the apex of the wing. TL/WL: ratio of thorax length to wing length. HW: head width, greatest distance across the eyes. HW/FS: ratio of head width to width between the eyes above the frontal suture. HW/TL: ratio of head width to thorax length. CI: costal index,

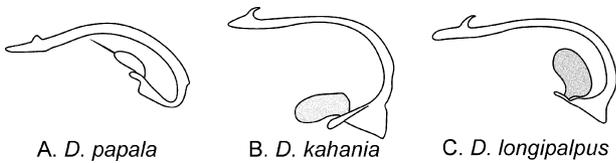


Fig. 2. Aedeagus of (A) *D. papala* ('ateledrosophila' group); and (B) *D. kahania* and (C) *D. longipalpus* ('nudidrosophila' group, 'kahania' subgroup).

length of costa from subcostal break to R_{2+3} /length of costa from R_{2+3} to R_{4+5} . 4V: fourth vein index, length of M from crossvein dm-cu to apex/length of M from crossvein r-m to crossvein dm-cu. 5X: length of CuA_1 from crossvein dm-cu to apex/length of crossvein dm-cu. 4C: length of costa from R_{2+3} to R_{4+5} /length of M from crossvein r-m to crossvein dm-cu. M: length of CuA_1 from crossvein dm-cu to apex/length of M from crossvein r-m to crossvein dm-cu.

Collectors are MSA (Marian S. Adachi Kohn), GMB (Gordon M. Bennett), HLC (Hampton L. Carson), WMG (William M. Giffard), DEH (D. Elmo Hardy), KH (Kirsten Heckmann), FMI (Faith M. Inman), KYK (Kenneth Y. Kaneshiro), MPK (Michael P. Kambyzellis), LL (Luc LeBlanc), GBM (Gordon B. Mainland), KNM (Karl

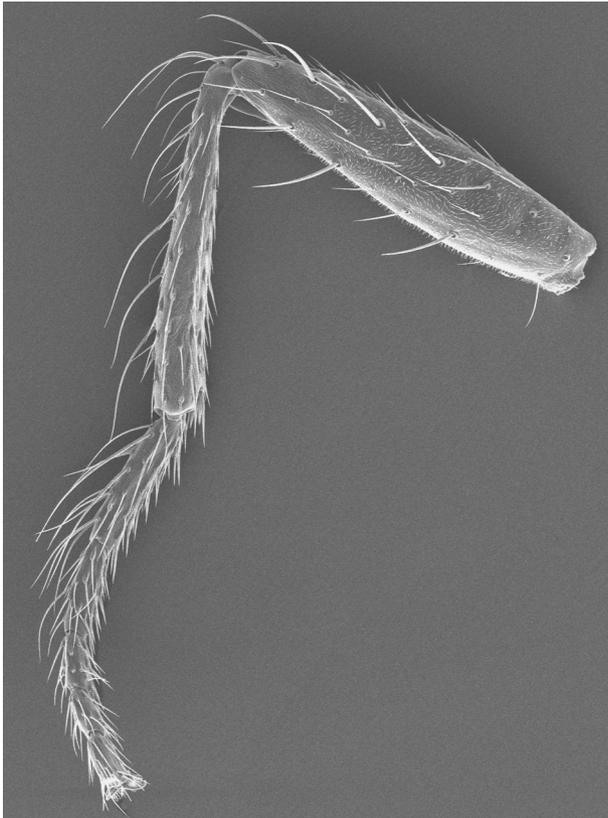


Fig. 3. Right front leg of *D. papalai*, anterior view.

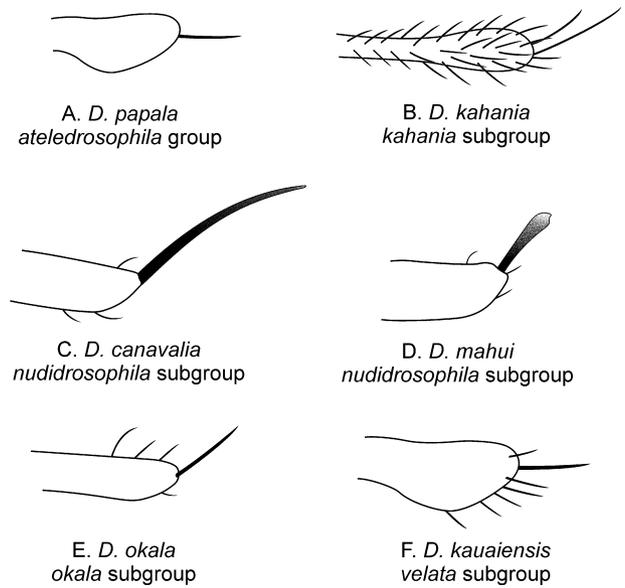


Fig. 4. Right palpi of males, dorsal view.

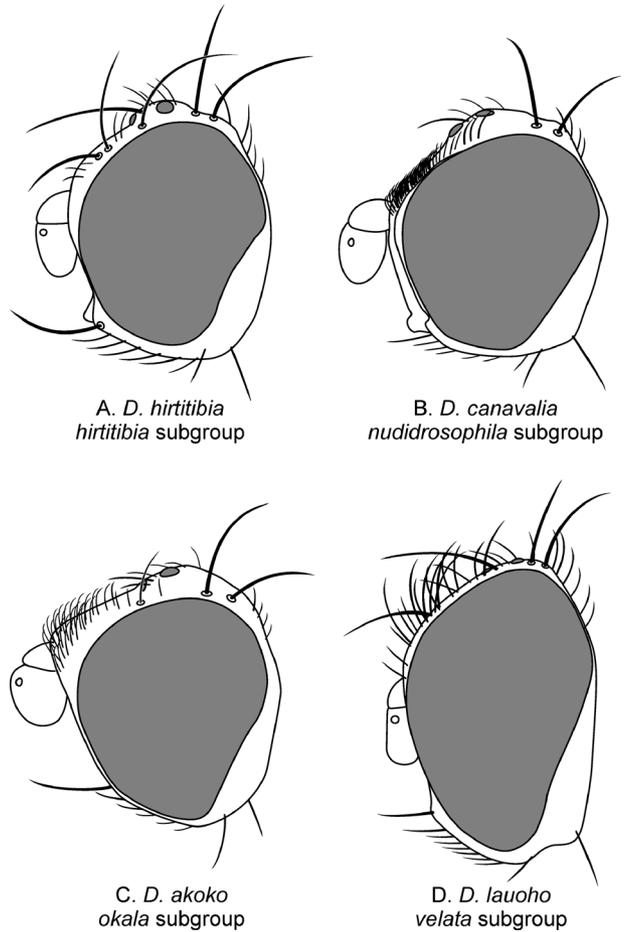


Fig. 5. Heads of males of the 'nudidrosophila' group (lateral view), showing variation in setation of the front.

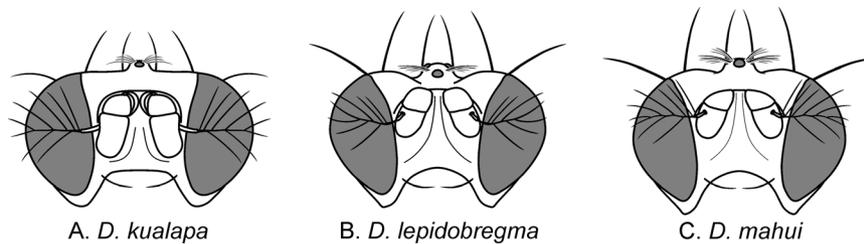


Fig. 6. Heads of (A) *D. kualapa*, (B) *D. lepidobregma*, and (C) *D. mahui* males, frontal view. Frontal setulae not shown.

N. Magnacca), SLM (Steven L. Montgomery), PMO (Patrick M. O'Grady), HTS (Herman T. Spieth), JBS (Julian B. Stark), OHS (Otto H. Swezey), MT (Minoru Tamashiro), MRW (Marshall R. Wheeler), and ECZ (Elwood C. Zimmerman).

Leg illustrations show only the modified cilia. The legs also contain a large number of setulae (see Fig. 3) that are not taxonomically useful. The latter are found on all legs of both sexes and are more or less prostrate, straight, and uniformly short. Cilia are found only on the front tibia and tarsus of males and are more erect, curved, and usually much longer, often of varying length. The cilia are often thinner relative to their length than setulae. The two types of setae are clearly distinct except in the 'okala' subgroup, in which, in addition to a row of elongate curved cilia, most species have a row of anterodorsal setulae that vary from erect but otherwise undifferentiated setulae (*D. akoko*) to distinct thin, elongate cilia (*D. okala*). Colouration is a useful character, but must be treated with caution. Most species are described from relatively old (>30 years) pinned specimens, which are often discoloured. This is especially the case for the legs, pleura, and abdomen, where the cuticle is thin. Light-coloured areas may appear darker than in life because the underlying musculature shows through, whereas areas that are nearly black usually fade to brown in pinned specimens. Specimens in alcohol preserve the colour of the cuticle better, but are subject to bleaching over time in storage. Thus, colouration characters that may be consistent in fresh specimens may not be suitable for the separation of older ones.

The term 'normal' is used in the descriptions to refer to the configuration of head setae found in the typical Hawaiian *Drosophila* species, character states that are ancestral to the species treated here. These are: one proclinate and two reclinate orbital setae, with the anterior reclinate inserted just posterior to the proclinate; fronto-orbital plate (orbit) nearly parallel-sided and ending just anterior of the proclinate seta; two long vertical setae, with the outer strongly directed laterally and the inner curving slightly medially; a pair of strong ocellar setae placed medial of the longest axis of the lateral ocelli and directed anterolaterally. Other characters that are consistent among the species treated here unless otherwise noted are: eyes only slightly higher than long and red-brown, with relatively long pile, about the length of two facets; antennal arista with four to six dorsal and two to three ventral rays

in addition to the apical fork (variable within species); ocellar tubercle (central portion of the ocellar triangle) gently or not at all raised; two humeral setae, the ventral two-thirds to three-quarters as long as the dorsal; and two pairs of dorsocentral setae on the thorax, the anterior shorter than the posterior.

Naturally, the keys presented here must be used with the caveat that more species undoubtedly remain to be described. For example, the key to females includes couplets relying solely on distributional information to separate species. When additional collections are made it may be found that specimens keying to such couplets include multiple sympatric species rather than only one. There are no females known for *D. diamphidia*, *D. longipalpus*, *D. panina*, and *D. panoanoa*; these are not included in the key.

Key to species of the 'nudidrosophila' and 'ateledrosophila' groups

Males

1. Orbits not extending far beyond the ocellar triangle and usually nearly parallel-sided (except in *D. panina*); margins usually distinct. Setulae of front dark, sparse (Fig. 5A) to moderately dense (Fig. 5C). Apical seta of palp normal, not enlarged (Fig. 4A, E, F), or absent (Fig. 4B). At least a strong posterior reclinate seta is present, although it may be obscured by long frontal setulae (as in Fig. 5D) 2
- Orbits expanded anteriorly, reaching the frontal suture and occupying at least half the width of the front, usually very densely covered with short scale-like setulae (Fig. 5B; hair-like and less dense in *D. canavalia*, *D. gemmula*, and *D. malele*); margins somewhat indistinct or obscured by setulae anteriorly. Apical seta of palp thickened (weakly so in *D. malele*), sometimes flattened and blunt-tipped (Fig. 4C, D). All orbital setae usually absent (sometimes a weak posterior reclinate present) ('nudidrosophila' subgroup) 6
- 2(1). Front legs with long cilia on the tibia, tarsus, or both. Palpi relatively short, less than three times as long as wide, not reaching the apex of the labellum (may be

- closer when labellum retracted, in which case the palpi are hidden); with sparse, inconspicuous setulae and usually one or two distinctly stronger apical or subapical seta (Fig. 4E, F) 3
- No cilia on front legs. Palpi long, about four times as long as wide, reaching the apex of the labellum; with many long pale setulae (those near the apex about half as long as the palp), but no distinctly stronger apical seta (Fig. 4B) ('kahania' subgroup) 16
- 3(2). Long curved cilia present at the extreme base of the tibia (Figs 9, 13) 4
- No long cilia at the extreme base of the tibia, basal one-quarter bare or with short cilia (Figs 8, 14) 5
- 4(2). All orbital setae present (Fig. 5A). Tarsus with long cilia (Fig. 9). Anteromedial portion of front with relatively few (about 20 or less) setulae, which are mainly inclinate to proclinate ('hirtitibia' subgroup) 17
- Proclinate and anterior reclinate setae absent (Fig. 5C). Tarsus without ciliation (Fig. 13). Anteromedial portion of front covered with dense to scattered erect, bristly, reclinate setulae, conspicuous in lateral view ('okala' subgroup) 20
- 5(3). Front tarsus bare or with only one to two thin cilia near the middle of the basitarsus; front tibia with a row of cilia along over the apical three-quarters (Fig. 8). Head more or less round, only slightly higher than long (as in Fig. 5A-C) ('ateledrosophila' group) 24
- Front tarsus with at least six cilia, including some on the second and third segments; tibia with cilia confined to the apical half, usually almost bare (Fig. 14). Head usually dorsoventrally elongate, distinctly higher than long in lateral view (Fig. 5D) ('velata' subgroup) 26
- 6(1). Ocellar tubercle (central part of ocellar triangle) strongly raised, sides steep in frontal view (Fig. 6) 7
- Ocellar tubercle weakly raised or not at all, sides gently sloping 9
- 7(6). Pleura entirely brown. Basitarsus with two to three cilia. Posterior portion of front depressed, creating a furrow between the ocellar triangle and the orbits, clear in frontal view (Fig. 6B). Anterior portion of front not unusually steep, much less so than the ocellar tubercle. Apical seta of palp entirely pale. Hawai'i *D. lepidobregma*
- Katepisternum largely yellow. Basitarsus usually with four or more cilia (rarely three). Front more or less flat around the ocellar tubercle (Fig. 6A, C). Anterior portion of front steep, slope continuous with ocellar tubercle. Apical seta of palp black at least at the base 8
- 8(7). Front tibia with 9-11 cilia in the anterodorsal row and a distinct clump of three to four dorsal cilia at the base. Hawai'i *D. mahui*
- Front tibia with seven to eight cilia in the anterodorsal row, only one long cilia at the base. Kaua'i *D. kualapa*
- 9(6). Tibia lacking elongate basal cilia (one short cilia in *D. gemmula*), those along the segment not much longer than the width of the tibia. Basitarsus with a row of elongate, hooked cilia (Fig. 11) 10
- Tibia with elongate cilia (more than twice the width of the tibia), longest at the base. Basitarsal cilia not hooked 11
- 10(9). Tibia with a complete row of short, straight cilia dorsally (Fig. 11A). Hawai'i *D. amita*
- Tibia nearly devoid of cilia, with only three inconspicuous cilia scattered along the segment and two at the apex (Fig. 11B). O'ahu *D. gemmula*
- 11(9). Basitarsus with a single row of at least five to six cilia (Fig. 12A, E) 12
- Basitarsus with a total of five or fewer cilia, sometimes present in more than one row but never with more than three in any one row (Fig. 10) 13
- 12(11). Katepisternum brown. Maui and Moloka'i *D. eximia*
- Katepisternum yellow. Hawai'i *D. panoanoa*
- 13(11). Basitarsus with one to two cilia, the remainder of the tarsus bare (Fig. 10B, C). Mid and hind femora distinctly tinged with brown on the dorsum. Pleura entirely brown 14
- Basitarsus with four to five cilia, second tarsal segment with two cilia (Fig. 10A, D). Legs and katepisternum yellow 15
- 14(13). Basitarsus with a single cilia and nearly twice as long as the second tarsal segment. Tibia with six anterodorsal and nine to ten anteroventral cilia (Fig. 10B). Hawai'i *D. canavalia*
- Basitarsus with a pair of cilia and hardly longer than the second segment. Tibia with seven anterodorsal and six anteroventral cilia (Fig. 10C). Kaua'i *D. malele*
- 15(13). Tibia with seven to eight pale brown anterodorsal cilia and five brown to black anteroventral cilia (Fig. 10A). O'ahu *D. aenicta*
- Tibia with 11 anterodorsal and seven anteroventral cilia (Fig. 10D). Kaua'i *D. poonia*
- 16(2). Pleura entirely brown. Hawai'i *D. longipalpus*
- Pleura entirely yellow. O'ahu *D. kahania*
- 17(4). Anterior reclinate seta about one-third longer than the proclinate seta (Fig. 5A). Front tibia with three rows of five to seven cilia each extending the entire length of the dorsal, anterodorsal, and anterior surfaces. Wing entirely hyaline. O'ahu *D. hirtitibia*
- Anterior reclinate much shorter than proclinate. Cilia of front tibia variable, often with one or more rows incomplete. Wing hyaline or with an anteroapical infuscation 18
- 18(17). Middle (anterodorsal) row of tibial cilia consisting of four to five cilia extending entire length of segment (Fig. 9D). Wing infuscated at apex. Kaua'i *D. papaalai*
- Middle row of tibial cilia consisting of only two cilia near apex (Fig. 9B, C). Wing variable 19

- 19(18). Dorsal row of cilia on front tibia with two on the apical half in addition to the long basal cilia, bare in the middle (Fig. 9C). Wing hyaline. Maui Nui *D. mawaena*
 – Front tibia with three dorsal cilia over the apical one-half–two-thirds (Fig. 9B). Wing usually with an anteroapical infuscation (lacking in some teneral specimens). Hawai'i *D. konaensis*
- 20(4). Front tibia with anteroventral cilia only on the basal half (Fig. 13B). Costa narrowly infuscated between the apices of R_{2+3} and R_{4+5} . O'ahu *D. kuhao*
 – Front tibia with anteroventral cilia extending nearly the entire length. Wing either hyaline or with a large anteroapical infuscation 21
- 21(20). Pleura bicoloured: dorsal half brown, katapisternum largely yellow. Front tibia with 9–11 strong but short anteroventral cilia, scarcely longer than the apical width of the tibia (Fig. 13E). O'ahu *D. panina*
 – Pleura unicoloured, nearly all yellow or all brown. Front tibia usually with nine or fewer anteroventral cilia, which are always much longer than the width of the tibia (Fig. 13A, C, D) 22
- 22(21). Wing with a large anteroapical infuscation, extending basally nearly to the level of the dm–cu crossvein. Hawai'i *D. okala*
 – Wing hyaline or faintly smoky anteroapically, but without a distinct mark 23
- 23(22). Pleura entirely yellow. O'ahu *D. akoko*
 – Pleura entirely brown. Maui, Moloka'i *D. makawao*
- 24(5). Tibia with two short basal cilia and a row of longer cilia along the apical two-thirds of segment (Fig. 8A). Tarsus without cilia. Hawai'i *D. diamphidia*
 – Tibia with a row of cilia that become longer towards the apex and then grow shorter, the longest at about one-third from the apex (Fig. 8B, C). Basitarsus with a single thin, erect cilia 25
- 25(24). Mid and hind femora and last two tarsal segments brown. Hawai'i *D. papala*
 – Legs all yellow except for a faint tinge of brown at the apices of the mid and hind femora. O'ahu *D. preapicula*
- 26(5). Ground setulae of front long, erect, reclinate; anterior reclinate seta not distinct (Fig. 5D). Ocellar setae nearly parallel 27
 – Frontal setulae prostrate to semi-erect, not unusually long, inclinate to proclinate; anterior reclinate seta usually distinct. Ocellar setae strongly diverging 29
- 27(26). Front tibia with long cilia over the apical third (Fig. 14B). Kaua'i *D. kauaiensis*
 – Front tibia without long cilia, with only a few inconspicuous, thin cilia near the apex 28
- 28(27). Femora, halteres, and cerci dark brown. Maui, Moloka'i *D. lauoho*
 – Femora, halteres, and cerci yellow. Hawai'i *D. halapepe*
- 29(26). Pleura mostly yellow. O'ahu *D. velata*
 – Pleura entirely brown 30
- 30(29). Hind tarsus dark brown. Wing with a small but distinct anteroapical mark, extending only slightly basal of the apex of R_{2+3} . Hawai'i *D. pohaka*
 – Hind tarsus yellow. Wing with an indistinct infuscation that extends along R_{2+3} and R_{4+5} to approximately the dm–cu crossvein. Kaua'i *D. milolii*

Females

1. Frontal setulae mostly inclinate or proclinate; if numerous reclinate setulae are present they are elongate, similar to the anterior reclinate seta 2
 – Nearly all frontal setulae reclinate (except one or two pairs at the frontal suture inclinate), short ('nudidrosophila' and 'okala' subgroups) 3
- 2(1). Head width (greatest width across the eyes) over $2.5\times$ the width of the front at the level of the frontal suture, ratio usually 2.6–2.8 ('velata' subgroup) 12
 – Head width less than $2.5\times$ that of the front at the frontal suture, ratio usually 1.8–2.3 ('hirtitibia', 'kahania', and 'ateledrosophila' subgroups) 14
- 3(1). Ocellar tubercle abruptly raised, prominent in anterior view, lateral slopes steep (as in Fig. 6) 4
 – Ocellar tubercle not or only slightly raised, not prominent in anterior view, sides gently sloping .. 5
- 4(3). Pleura entirely brown. Only three dorsal rays on the arista (rarely four). Hawai'i *D. lepidobregma*
 – Katapisternum largely yellow. Four or more dorsal rays on the arista, sometimes five or six *D. mahui* (Hawai'i), *D. kualapa* (Kaua'i)
- 5(3). Pleura entirely brown 6
 – At least the katapisternum largely yellow 9
- 6(5). Wing hyaline or with a small, faint anteroapical infuscation 7
 – Wing with a large infuscation, extending through cell r_{2+3} from the apex about halfway to the dm–cu crossvein. Hawai'i *D. okala*
- 7(6). Mid and hind femora tinged with brown, at least on the apical third 8
 – Femora all yellow. O'ahu *D. gemmula*
- 8(7). Mesonotum with only two strong setae in the dorso-central rows. Maui, Moloka'i *D. makawao*
 – Mesonotum with a prominent seta just ahead of the anterior dorsocentral and about half as long *D. canavalia* (Hawai'i), *D. eximia* (Maui Nui), *D. malele* (Kaua'i)
- 9(5). Pleura almost entirely yellow, strongly contrasting with the dark mesonotum; orbits mostly bare, with scattered setulae but never dense; orbits not expanded, front between the orbits almost parallel-sided anterior of the median ocellus 10
 – Dorsal half of pleura at least tinged with brown, not strongly contrasting with the mesonotum; orbits with short, dense setulae around the proclinate and anterior reclinate setae; orbits slightly expanded,

- front between the orbits slightly narrowing anterior of the median ocellus 11
- 10(9). Costa between R_{2+3} and R_{4+5} narrowly infuscated. O'ahu *D. kuhao*
 – Wing hyaline. O'ahu *D. akoko*
- 11(9). Dorsal half of pleura brown, similar to mesonotum; katepisternum brown above the posterior seta, yellow below *D. amita* (Hawai'i), *D. poonia* (Kaua'i)
 – Dorsal half of pleura tinged with brown but distinctly lighter than mesonotum; katepisternum entirely yellow. O'ahu *D. aenicta*
- 12(2). Front with all setulae inclinate. Mid and hind femora and halteres usually yellow (tinged with brown in some *D. pohaka*) *D. milolii* (Kaua'i), *D. pohaka* (Hawai'i), *D. velata* (O'ahu)
 – Front with erect, reclinate setulae. Mid and hind femora and halteres brown 13
- 13(12). Arista usually with six dorsal and three ventral rays. Hawai'i *D. halapepe*
 – Arista usually with five dorsal and two ventral rays
 *D. kauaiensis* (Kaua'i), *D. lauoho* (Maui Nui)
- 14(2). Pleura entirely dark brown. Hawai'i *D. papala*
 – At least the katepisternum largely yellow 15
- 15(14). Palpi yellow, long and cylindrical, about 3× as long as wide. O'ahu *D. kahania*
 – Palpi yellow to brown, relatively short and broadened in the middle, 2–2.5× as long as wide. Kaua'i 16
- 16(15). Dorsal half of pleura brown, similar to mesonotum; katepisternum brown above the posterior seta, yellow below. O'ahu *D. preapicula*
 – Dorsal half of pleura tinged with brown but distinctly lighter than mesonotum; katepisternum entirely yellow *D. hirtitibia* (O'ahu), *D. konaensis* (Hawai'i), *D. mawaena* (Maui Nui), *D. papaalai* (Kaua'i)

The 'ateledrosophila' group

Hardy (1965) initially described two species in the genus *Ateledrosophila*, *A. diamphidia* and *A. preapicula*, based primarily on the placement of the arista near the apex of the third antennal segment and the lack of anterior reclinate and ocellar setae. Kaneshiro (1976) later synonymized *Ateledrosophila* with *Drosophila* based on the similarity of the aedeagus with that of species in the 'picture-wing' group, and considered it a species group. Although the arista appears to be strongly displaced from its usual position at the base of the segment, close examination reveals that it is much less so than originally described. The base is elongate and directed downwards, making it appear to be attached further down than it actually is. Even in *D. preapicula*, which has the greatest displacement, it is just past the middle of the segment (Fig. 7; compare with Fig. 17A of Hardy, 1965 and Fig. 3 of Kaneshiro, 1976); in the other two species, it is shifted only

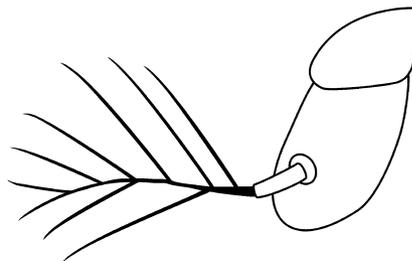


Fig. 7. Left antenna of male *D. preapicula*, lateral view.

slightly, about a third of the way down the third antennal segment.

The 'ateledrosophila' group appears to be most closely related to the 'nudidrosophila' group, on the basis of the elongate female ovipositor, abundant frontal setulae of the males, and the reduction in numbers of major head setae (orbitals and ocellars) in some taxa. However, the shape of the preapical protuberance on the aedeagus is triangular (as in the 'grimshawi' and 'planitibia' subgroups of the 'picture-wings') rather than hooked. As there is no apparent synapomorphy for the entire assemblage, 'nudidrosophila' and 'ateledrosophila' are retained as separate species groups.

Only two described species, *D. diamphidia* from Hawai'i and *D. preapicula* from O'ahu, are included here; we describe one new species, *D. papala* from Hawai'i, as well as the female of *D. preapicula*. These species are very rare in collections: *D. diamphidia* is still known only from the holotype, and *D. preapicula* from the holotype and six paratypes. However, 68 specimens of *D. papala* have been reared from *Charpentiera* bark (Magnacca *et al.*, in press), and it can be easily collected by sweeping around this plant. It is possible that these rare taxa represent a distinct lineage of Hawaiian *Drosophila*, and additional species may be found on Kaua'i and Maui Nui.

Drosophila diamphidia (Hardy)

(Fig. 8A)

Ateledrosophila diamphidia Hardy, 1965: 63.

Diagnosis. Differs from the other 'ateledrosophila' species by having the cilia of the front tibia irregular in length, lacking cilia on the basitarsus, and having an entirely yellow katepisternum.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits brown, pollinose; orbits normal, not expanded anteriorly. Front dull brown, pollinose, slightly paler than the orbits;

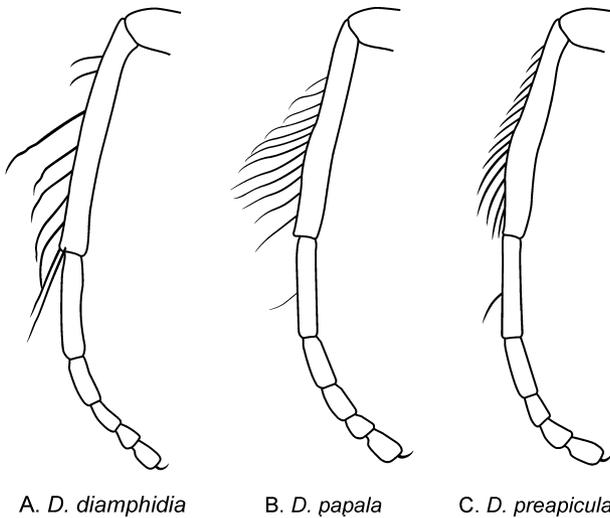


Fig. 8. Right front legs of males of the 'ateledrosophila' group, anteroventral view.

frontal setulae erect, dense, mostly reclinate but many inclinate or proclinate as well. Proclinate and posterior reclinate setae present, anterior reclinate not distinct from the frontal setulae. Ocellar setae highly reduced, only about as long as the frontal setulae. Eyes normal. Face brown, raised into a rounded carina medially. Antenna brown; arista attached just under halfway down the dorsal surface of the third segment, with moderately long medial rays, the longest about two-thirds the length of the terminal fork. One strong oral vibrissa, the other oral setae less than half its length. Gena yellow. Palp yellow, flattened, with a single moderately strong apical seta. *Thorax.* Mesonotum brown, pollinose. Pleura brown on dorsal half, katepisternum yellow. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; without any additional elongate setae in the dorsocentral row. *Legs.* Yellow. Front tibia with a row of six long, thin, anterodorsal cilia along the apical two-thirds, a single, thicker, anterior seta at the apex, and two short cilia on the basal one-quarter. Front tarsi lacking elongate cilia. *Wings.* Nearly hyaline, with a very faint yellowish tinge. Costal fringe extending about halfway between the apex of R_{2+3} and R_{4+5} . *Abdomen.* Broken off in holotype.

♀. Unknown.

Measurements. $n = 1♂$. TL = 1.16 mm; WL = 2.1 mm; TL/WL = 0.6; HW = 0.84 mm; HW/FS = 2.2; HW/TL = 0.7; CI = 3.5; 4V = 1.9; 5X = 1.9; 4C = 0.8; M = 0.6.

Material examined. HAWAII: Holotype ♂ (BPBM 6281), Kaiholena, Kohala Mountains, Ditch Trail, 2000 ft, vii.1958, DEH.

Distribution and ecology. Hawaii; known only from the holotype. Breeding hosts unknown.

Discussion. The type locality is not certain; Kaiholena is a hill above 1200 m, and nothing by that name can be found at lower elevations, suggesting that the locality name is incorrect or refers to a site not on current maps, or that the elevation is incorrect. There are relatively few *Drosophila* recorded from the Kohala mountains in general, and most are from very wet forest around 1200 m. At lower elevations, much of the area has been heavily impacted by pigs and invasive plants. If *D. diamphidia* is an inhabitant of mid-elevation forests, its range may be highly restricted.

Drosophila papala sp.n.

(Figs 1A; 2A; 4A; 8B)

Diagnosis. Differs from the other species in having the femora brown rather than yellow. The cilia of the front tibia are very similar to those of *D. preapicula*, but are somewhat longer and do not extend as far up the segment (compare Fig. 8B, C).

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits brown, pollinose; orbits normal, not expanded anteriorly. Front dull velvety brown, pollinose, darker than orbits; frontal setulae semi-erect, dense, mixed reclinate, inclinate, and proclinate. Proclinate and posterior reclinate setae present; anterior reclinate usually not distinct from the frontal setulae, but sometimes slightly longer. Ocellar setae highly reduced, only about as long as the frontal setulae. Eyes normal. Face brown, raised into a rounded carina medially. Antenna evenly dark brown to black; arista attached about one-third of the way down the dorsal surface of the third segment, with moderately long medial rays, the longest about two-thirds as long as the terminal fork. One oral vibrissa is present, which is stronger but often only slightly longer than the other oral setae. Gena dark brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, with a single moderately strong apical seta. *Thorax.* Mesonotum dark brown to black, densely pollinose. Pleura entirely dark brown to black, densely pollinose. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about one-third the length of anterior dorsocentral and just anterior of it. *Legs.* Yellow except coxae and femora smoky brown (darker on mid and hind legs). Front tibia with a row of about 12 curved anterodorsal cilia along almost the entire length; the cilia start off relatively short and become longer, reaching maximum length at about one-third the length from the apex; the row is somewhat diagonal, starting almost anterior near the base and ending almost dorsal at the apex. Front basitarsus with one semi-erect, elongate, anterodorsal cilia at the middle, about twice as long as the prostrate setulae; some other setulae sometimes somewhat erect. *Wings.* Uniformly hyaline. Costal fringe extending about one-third the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen.* Solid brown, slightly lighter than the thorax. Cerci brown.

♀. Identical to the male with the following exceptions. *Head*. Frontal setulae prostrate, inclinate to proclinate. Orbital and ocellar setae normal. One strong oral vibrissa, a second seta also strong, up to half as long; the other oral setae smaller. *Legs*. Lacking long cilia. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 5♂$. TL = 1.01 (0.95–1.08) mm; WL = 2.04 (1.85–2.18) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.76 (0.65–0.81) mm; HW/FS = 2.3 (2.2–2.3); HW/TL = 0.7 (0.7–0.8); CI = 3.5 (3.3–3.7); 4V = 1.8 (1.7–1.8); 5X = 1.6 (1.6–1.9); 4C = 0.7 (0.7–0.8); M = 0.5 (0.5–0.6). $N = 5♀$. TL = 1.22 (1.18–1.28) mm; WL = 2.46 (2.28–2.66) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.84 (0.78–0.9) mm; HW/FS = 2.1 (2–2.2); HW/TL = 0.7 (0.7–0.7); CI = 3.7 (3.3–4); 4V = 1.7 (1.7–1.8); 5X = 1.6 (1.4–1.8); 4C = 0.7 (0.6–0.7); M = 0.5 (0.5–0.6).

Material examined. HAWAII: Holotype ♂ (BPBM 16683), Hawai'i Volcanoes National Park, 'Ōla'a, pole 44, reared ex *Charpentiera obovata* bark, 4.xii.2005, KNM & FMI. Allotype ♀ (BPBM 16683a), as holotype. 16♂ 10♀ paratypes, 'Ōla'a, ex *Charpentiera* stems, viii.1974, SLM (UHIM). 3♂ 7♀ paratypes, as holotype (HVIC). 2♀ paratypes, Kīpuka Kī, 4200 ft, sweeping vegetation and ground, 20.vi.2006, KNM (HVIC).

Distribution and ecology. HAWAII: known only from the 'Ōla'a–Kīlauea area. Reared from *Charpentiera obovata* (Amaranthaceae) and *Pisonia brunoniana* (Nyctaginaceae), in company with *D. amita* and *D. konaensis*.

Etymology. From the Hawaiian *pāpala*, the name for plants in the genus *Charpentiera*; *Pisonia* is also known as *pāpala kēpau*, or sticky *pāpala*.

Discussion. Unlike the other two species in this group, a relatively large number of specimens are known, primarily as a result of rearing from *Charpentiera*. In some specimens, one of the frontal setulae is longer than the others and may represent the anterior reclinate. However, the socket is distinctly smaller than that of the posterior reclinate.

Drosophila preapicula (Hardy)

(Figs 7; 8C)

Ateledrosophila preapicula Hardy, 1965: 64.

Diagnosis. Very similar to *D. papala*; see under that species.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits brown, pollinose; orbits normal, not expanded anteriorly. Front dull velvety brown, pollinose, darker than the orbits; frontal setulae erect, mostly reclinate but many inclinate or proclinate as well. Proclinate and posterior reclinate setae present, anterior reclinate not distinct from the frontal

setulae. Ocellar setae highly reduced, only about as long as the frontal setulae. Eyes normal. Face brown, raised into a rounded carina medially. Antenna brown, third segment slightly paler; arista inserted about one-half–two-thirds of the way down the third segment, with moderately long medial rays, the longest about as long as the terminal fork. One moderately strong oral vibrissa, other oral setae less than half its length. Gena brown, fading to yellow posteriorly. Palp yellow-brown, flattened, straight on the medial margin and convex on the lateral, with a single moderately strong subapical seta. *Thorax*. Mesonotum dark brown, pollinose. Pleura brown dorsally, yellow below the katepisternal setae. Dorsocentral setae normal, anterior about four times as long as acrostichals; without any additional elongate setae in the dorsocentral row. *Legs*. Yellow, mid and hind femora faintly tinged with brown on the apical one-third. Front tibia with a row of 13–14 curved anterodorsal cilia along almost the entire length; the cilia relatively short basally and becoming longer, reaching maximum length at about one-quarter the length from the apex; the row is somewhat diagonal, starting almost anterior near the base and ending almost dorsal at the apex; dorsal surface of tibia slightly bulging over apical half. Front basitarsus with one semi-erect, elongate cilia at the middle (one specimen with two cilia on one side). *Wings*. Subhyaline, faintly smoky anteroapically. Costal fringe extending about halfway between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Largely brown, sixth tergum pale posterolaterally. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Frontal setulae prostrate, inclinate to proclinate. Orbital and ocellar setae normal. Arista inserted slightly less than halfway down the third antennal segment. *Legs*. Lacking long cilia. Front tibia not swollen. *Abdomen*. Solid dark brown. Ovipositor yellow, long.

Measurements. $n = 4♂$. TL = 0.95 (0.88–1.03) mm; WL = 1.83 (1.73–1.98) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.75 (0.68–0.83) mm; HW/FS = 2.3 (2.2–2.4); HW/TL = 0.8 (0.7–0.8); CI = 3.7 (3.4–3.9); 4V = 1.8 (1.7–1.9); 5X = 1.7 (1.4–2); 4C = 0.7 (0.6–0.7); M = 0.6 (0.5–0.6). $n = 1♀$. TL = 1.7; WL = 3.48; TL/WL = 0.5; HW = 1.32; HW/FS = 2.4; HW/TL = 0.8; CI = 3.7; 4V = 2; 5X = 1.9; 4C = 0.7; M = 0.7.

Material examined. O'AHU: Holotype ♂ (BPBM 6282), Honolulu Mountains, 1800 ft (no date or collector). 1♂ paratype, Mt Tantalus, vi.1956, DEH. 1♂, 'Ōpae'ula, viii.1963, WBH. 2♂ 1♀, Mānoa Cliff Trail, sweeping *Pisonia*, 25.ii.2007, KNM.

Distribution and ecology. O'AHU: known from very few specimens. Breeding hosts unknown.

Discussion. One paratype is labelled 'Kil H', which was presumed by Hardy (1965) to be short for Kīlauea, Hawai'i. Although it appears to have yellow femora and the arista displaced as in *D. preapicula*, the specimen is in

poor shape, and it is possible that it might be mislabelled or a specimen of *D. papala*. This species was originally described by Hardy (1965) as having the thorax entirely dark, but recent specimens show that the pleura are actually yellow ventrally. Other species have shown similar discolouration in older pinned specimens, particularly in the pleura.

The 'nudidrosophila' group

'hirtitibia' subgroup

The 'hirtitibia' subgroup consists of four species, three of which are new. At present, only one species is known from each island. Hardy (1965) described *D. hirtitibia* from O'ahu; we are adding *D. konaensis* from Hawai'i, *D. mawaena* from Maui Nui, and *D. papaalai* from Kaua'i. The subgroup is distinguished from the 'nudidrosophila' and 'okala' subgroups by both males and females having a full set of strong orbital and ocellar bristles, with inclinate or proclinate setae on the medifrons. It is also united by the presence of long cilia on both the front tibia and tarsus of males, and all species have the pleura largely yellow, or at least significantly paler than the mesonotum. The dense ciliation on the legs can make the species difficult to distinguish, but at present only one species is known from each island.

These species appear to be ecologically similar to the 'nudidrosophila' subgroup, with rearing records from *Charpentiera*, *Pisonia*, and *Urera*.

Drosophila hirtitibia Hardy

(Figs 5A; 9A)

Drosophila hirtitibia Hardy, 1965: 306.

Diagnosis. *Drosophila hirtitibia* differs from related species by having the anterior reclinate longer than the proclinate, the front tibia with three complete rows of cilia, and the wings hyaline.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits normal, not expanded anteriorly. Front dull dark brown above, pollinose, orange-brown below the ocellar triangle; frontal setulae prostrate, mostly more or less medially directed. Orbital setae normal, anterior reclinate only slightly above the proclinate, slightly longer but distinctly thinner than proclinate. Ocellar setae normal, about as long as the posterior reclinate. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown, second segment paler dorsoapically; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow-brown, flattened, straight on the medial margin and convex on the lateral, with a single weak

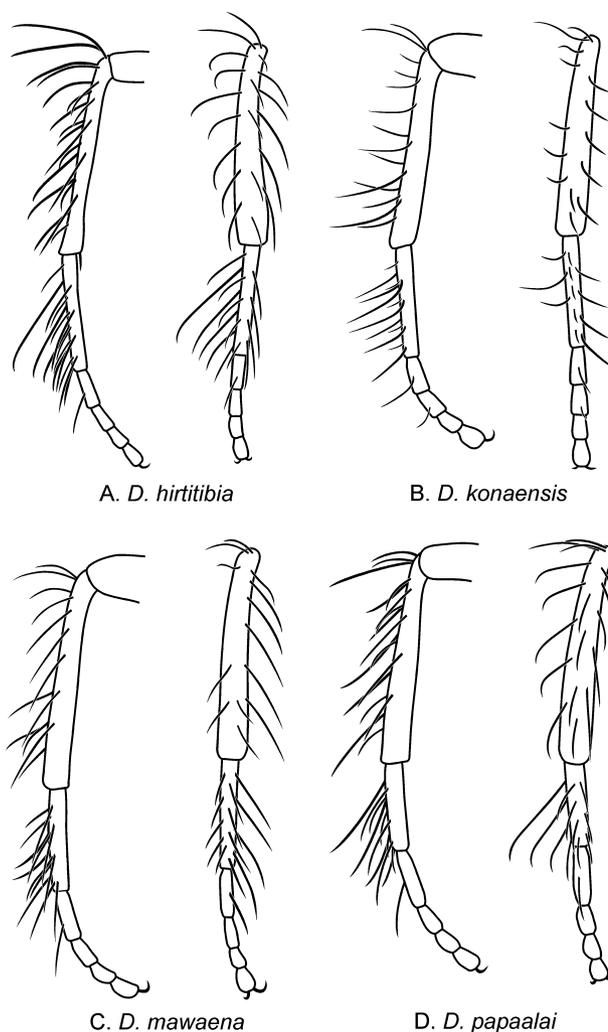


Fig. 9. Right front legs of males of the 'hirtitibia' subgroup, anterovenral (left) and anterodorsal (right) views.

apical seta. *Thorax.* Mesonotum brown, pollinose. Pleura yellow, upper half faintly tinged with brown. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals, without additional short setae. *Legs.* Yellow. Front tibia with an anterior row of five to six and a dorsal row of six to seven long, dark cilia along almost the entire length; an anterodorsal row of four to five shorter, thinner cilia between them; and two to three additional long dorsal cilia near the tibiofemoral joint. Front basitarsus with three rows of cilia, three to four anterior, four to six anterodorsal, and five dorsal; the last much longer at the base, becoming shorter towards the apex; second tarsal segment with a single anterior cilia. *Wings.* Uniformly hyaline. Costal fringe extending about halfway between R_{2+3} and R_{4+5} . *Abdomen.* Solid brown. Cerci pale.

♀. Identical to the male with the following exceptions. *Head.* Vertex, ocellar triangle, and orbits dull. Anterior

recline distinctly above the proclinate, about one-third the distance to the posterior reclinate. Apical seta of palp strong. *Thorax*. Dorsocentral row with an additional short seta, about one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Lacking long cilia. *Abdomen*. Ovipositor yellow, long.

Measurements. $n = 2\♂$. TL = 0.94 (0.89–0.99) mm; WL = 1.78 (1.68–1.88) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.65 (0.6–0.7) mm; HW/FS = 2.2 (2.1–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.9 (3.7–4.1); 4V = 1.7 (1.7–1.7); 5X = 1.5 (1.4–1.7); 4C = 0.6 (0.6–0.6); M = 0.5 (0.5–0.5). $n = 2\♀$. TL = 1.06 (1–1.13) mm; WL = 2.11 (1.88–2.35) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.73 (0.68–0.79) mm; HW/FS = 2.2 (2.2–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.9 (3.8–4); 4V = 1.6 (1.6–1.6); 5X = 1.5 (1.5–1.6); 4C = 0.6 (0.6–0.6); M = 0.5 (0.4–0.5).

Material examined. O'AHU: Holotype ♂ (BPBM 6372), Mt Ka'ala, v.1952, MT. Allotype ♀ (BPBM 6372a), as holotype. 2♂ paratypes, Mānoa Valley, 1947, no collector given. 2♂ 1♀ paratypes, Haleanau Valley, Mt Ka'ala, banana trap, 21.iv.1949, GBM. 10♂ 9♀ paratypes, Mt Ka'ala, v.1952, MT. 2♂ 1♀, Pōhākea Pass, iv.1959, DEH. 14♂ 2♂, Kawainui, 20.vi.1964. 3♂, Kūpaua Valley, 30.viii.1965, HLC. 1♂ 2♀, Pu'u Kāua, ex *Ureia* stem, 2.viii.1970, SLM. 4♂ 18♀, Wai'anae Mountains, swept in *Pisonia umbellifera* grove, 10.ii.2000, MPK, SLM, & PMO (PMO collection). 69♂ 77♀, Mākua Valley, swept in *Pisonia umbellifera* grove, 20.ii.2000, SLM, PMO, & JBS (PMO collection).

Distribution and ecology. O'ahu. Reared from *Ureia* sp. (Urticaceae) and *Pisonia umbellifera* (Nyctaginaceae).

Discussion. Here we are restricting the definition of *D. hirtitibia* to specimens from O'ahu with the tibial ciliation as described. Hardy's (1965) original description of *D. hirtitibia* included paratypes from Moloka'i and Maui. It states (p. 308) that 'One male specimen from Kahuaawi Gulch, Molokai, July, 1932 (D. E. Hardy) appears to be *hirtitibia* but has the anterior reclinate shorter than normal. It is not being designated as a paratype'. The paratype from Manawainui Valley (the only Maui Nui paratype found at UHIM; the remainder are presumably at the USNM and BMNH, which were not visited) also has the anterior reclinate short, but this was not noted by Hardy. The latter is here designated the holotype of *D. mawaena*; given the distribution of species in this subgroup, the others are almost certainly *D. mawaena* as well.

Drosophila konaensis sp.n. (Fig. 9B)

Diagnosis. Distinguished by having the front tibia with a complete row of dorsal cilia but only two small, incon-

spicuous cilia in the anterodorsal (middle) row. The anteroapical portion of the wing is usually infuscated, but this is lacking in some (possibly teneral) specimens. It is also one of the palest of the 'nudidrosophila' group, often with yellow extending onto the lateral and anterior portions of the mesonotum.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits normal, not expanded anteriorly. Front dull brown above, pollinose, grading to yellow at the frontal suture; frontal setulae prostrate, mostly more or less medially directed. Orbital setae normal, anterior reclinate slightly above the proclinate, and shorter and distinctly thinner than it. Ocellar setae normal, about as long as the posterior reclinate. Eyes normal. Face brown, raised into a rounded carina dorso-medially. Antenna brown, second segment paler dorsoapically; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow, slightly flattened, straight on the medial margin and convex on the lateral, with a few setulae near the tip but no distinct apical seta. *Thorax*. Mesonotum pale brown, pollinose, rufous to yellow anteriorly and laterally. Pleura yellow, tinged with brown on the dorsal half. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, one-half to one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with an anterior row of five to six long, dark cilia and a dorsal row of three thinner cilia along the apical two-thirds; two shorter cilia between these rows on the apical quarter; and three to four long dorsal cilia near the tibiofemoral joint. Front basitarsus with three rows of cilia, three to four anterior, four to five anterodorsal, and three dorsal; second tarsal segment with a single anteroventral cilia. *Wings*. Hyaline, infuscated between the apices of R_{2+3} and R_{4+5} , extending one-third–one-half the distance from the wingtip to the dm–cu crossvein. Costal fringe extending about one-third the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Brown dorsally, yellow laterally. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits pollinose. Anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. One strong oral vibrissa, sometimes with a second seta up to half its length; the other oral setae smaller. Palp with a single moderately strong apical seta. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. Costal fringe extending just under half the distance between R_{2+3} and R_{4+5} . *Abdomen*. Ovipositor yellow, long.

Measurements. $n = 4\♂$. TL = 1.06 (1–1.11) mm; WL = 2 (1.89–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.75 (0.65–0.8) mm; HW/FS = 2.3 (2.3–2.4); HW/TL = 0.7 (0.7–0.8); CI = 4.1 (3.8–4.6); 4V = 1.7 (1.5–1.9); 5X = 1.7 (1.6–1.9); 4C = 0.6 (0.5–0.6); M = 0.5 (0.5–0.6). $n = 5\♀$. TL = 1.2

(1.11–1.35) mm; WL = 2.36 (2.13–2.68) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.82 (0.75–0.95) mm; HW/FS = 2.2 (2.1–2.4); HW/TL = 0.7 (0.7–0.7); CI = 4.2 (4.1–4.3); 4V = 1.7 (1.7–1.8); 5X = 1.7 (1.7–1.9); 4C = 0.6 (0.6–0.6); M = 0.6 (0.5–0.6).

Material examined. HAWAII: Holotype ♂ (BPBM 16684), Pāpā, South Kona, 2200 ft, 4.vii.1998, UHIM #Z64ZA, PMO & SLM. Allotype ♀ (BPBM 16684a), Kahuku, Pu'u 'Akihi Gulch, 800 m, reared ex *Charpentiera obovata* bark, 31.i.2006, KNM. 2♂ paratypes, near Pāpā, Kapu'a, South Kona, Q10, "'Pisonia stem" (ex?)', 20.viii.1971, SLM (UHIM). 108♂ 39♀ paratypes, 'Kapu'a (land section), Ho'ōpūloa, (quadrant)', South Kona, 2650 ft, vii.1977, DEH (UHIM). 12♂ paratypes, as holotype (UHIM). 3♀ paratypes, as allotype (HVIC). 1♂ paratype, Kipuka Puau-lu, 4000 ft, sweeping vegetation and ground, 19.vi.2006, KNM (HVIC).

Distribution and ecology. Hawaii; known only from the southern half of the island (South Kona and Hawaii Volcanoes National Park). Reared from *Charpentiera obovata* (Amaranthaceae) and *Pisonia brunoniana* (Nyctaginaceae).

Etymology. Named for the Kona region of the Big Island, from which most specimens have come.

Drosophila mawaena sp.n. (Fig. 9C)

Diagnosis. Distinguished from related species by the combination of hyaline wings and interrupted dorsal and anterodorsal cilia rows on the front tibia of the male.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining brown, pollinose; orbits normal, not expanded anteriorly. Front dull brown, pollinose; frontal setulae prostrate, mostly more or less medially directed. Orbital setae normal, anterior reclinate only slightly above the proclinate and less than half as long, thinner. Ocellar setae normal, about as long as the posterior reclinate. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown, second segment paler medioapically; arista with long medial rays, the longest about two-thirds as long as the terminal fork. One strong oral vibrissa, the other oral setae less than half its length. Gena yellow. Palp yellow-brown, flattened, straight on the medial margin and convex on the lateral, broad apically, with a single weak apical seta. *Thorax.* Mesonotum brown, pollinose. Pleura yellow, upper half faintly tinged with brown. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs.* Yellow. Front tibia with an anterior row of six long, dark cilia almost the entire length; two similar cilia dorsally along the apical half; two shorter, paler cilia

between these rows on the apical quarter; and three long dorsal cilia near the tibiofemoral joint. Front basitarsus with three rows of four to five cilia each (anterior, anterodorsal, and dorsal) along the basitarsus; second tarsal segment with a single anterior cilia. *Wings.* Uniformly hyaline. Costal fringe extending about one-third the distance between R_{2+3} and R_{4+5} . *Abdomen.* Solid brown. Cerci apparently dark brown (may be discoloured).

♀. Identical to the male with the following exceptions. *Head.* Palp with a single moderately strong apical seta. *Thorax.* Pleura brown above, grading to yellow on the katepisternum. *Legs.* Lacking long cilia. *Abdomen.* Ovipositor brown, long.

Measurements. $n = 1♂$. TL = 0.96 mm; WL = 1.93 mm; TL/WL = 0.5; HW = 0.7 mm; HW/FS = 2.4; HW/TL = 0.7; CI = 3.7; 4V = 1.7; 5X = 1.6; 4C = 0.7; M = 0.5. $n = 3♀$. TL = 1.26 (1.19–1.3) mm; WL = 2.52 (2.33–2.65) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.88 (0.84–0.9) mm; HW/FS = 2.4 (2.3–2.4); HW/TL = 0.7 (0.7–0.7); CI = 4.1 (3.7–4.4); 4V = 1.5 (1.4–1.6); 5X = 1.4 (1.3–1.6); 4C = 0.6 (0.5–0.6); M = 0.5 (0.4–0.5).

Material examined. MOLOKA'I: Holotype ♂ (BPBM 16685), Maunawainui Vall. (= Manawainui Valley), vii.1952, DEH (originally designated a paratype of *D. hirtitibia*). Allotype ♀ (BPBM 16685a), Mākolēlau, reared ex *Pisonia* stem, 4.iii.1972, SLM. MAUI: 1♂ paratype, Kahanaikei Gulch, 2100 ft, sweeping *Pisonia*, 7.viii.2007, KNM. LĀNA'I: 5♀, Kaiholena Gulch, reared ex *Pisonia* stem, Q20, 8.xi.1971, SLM (UHIM).

Distribution and ecology. Maui and Moloka'i; probably Lāna'i as well (see *Discussion*). Reared from *Pisonia* sp. (Nyctaginaceae).

Etymology. From the Hawaiian *mawaena*, in between, for its similarity to both *D. hirtitibia* and *D. konaensis*, and its physical distribution between them.

Discussion. The 'typical' colouration of this species is difficult to determine from the available specimens. The types from Moloka'i are rather dark, but are old pinned specimens that appear to be discoloured; the recent specimen from Maui has the anterior and lateral portions of the mesonotum, lateral areas of the abdomen, and halteres yellow (similar to *D. konaensis*), but the ptilinal suture appears to be unclosed and it may be teneral. The ciliation of the front legs and other structural details are identical. The Lāna'i specimens are presumably this species, as the islands of Maui Nui share many species, but are not being designated as paratypes because they cannot be distinguished from females of *D. hirtitibia* or *D. konaensis* and no males were collected with them. All specimens from Maui Nui formerly placed under *D. hirtitibia* are probably *D. mawaena* (see *Discussion* under the former species).

***Drosophila papaalai* sp.n.**

(Figs 3; 9D)

Diagnosis. The chaetotaxy of the male forelegs is very similar to that of *D. hirtitibia*; *D. papaalai* can be distinguished by having the anterior reclinate seta shorter than the proclinate, and possessing a distinct anteroapical mark on the wing.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits normal, not expanded anteriorly. Front dull brown, pollinose, paler below the ocellar triangle; frontal setulae prostrate, mostly more or less medially directed. Orbital setae normal, anterior reclinate slightly above the proclinate, and shorter and distinctly thinner than it. Ocellar setae normal, about as long as the posterior reclinate. Eyes normal. Face brown, weakly raised dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, sometimes with a second seta up to half its length; the other oral setae smaller. Gena yellow. Palp brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single moderately strong subapical seta. **Thorax.** Mesonotum shining brown, pollinose, slightly paler laterally. Pleura yellow, tinged with brown on the anepimeron. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, one-third the length of anterior dorsocentral and just anterior of it. **Legs.** Yellow. Front tibia with an anterior and a dorsal row of five long, dark cilia each; an anterodorsal row of four to five shorter, very fine cilia; and three long dorsal cilia near the tibiofemoral joint. Front basitarsus with three rows of basitarsal cilia: three to four anterior, five to six anterodorsal, and three to four dorsal, the last longer near the base; second tarsal segment with one or two anterodorsal cilia. **Wings.** Hyaline, infuscated between the apices of R_{2+3} and R_{4+5} , extending about one-third the distance from the wingtip to the dm-cu crossvein. Costal fringe extending one-quarter–one-third the distance between the apex of R_{2+3} and R_{4+5} . **Abdomen.** Brown, paler laterally. Cerci yellow.

♀. Identical to the male with the following exceptions. **Head.** Vertex, ocellar triangle, and orbits pollinose. Anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. **Thorax.** Pleura mostly yellow, brown along the dorsal margin. **Legs.** Lacking long cilia. **Wings.** Uniformly hyaline. **Abdomen.** Ovipositor brown, long.

Measurements. $n = 2♂$. TL = 1.05 (1.04–1.06) mm; WL = 2.01 (1.95–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.76 (0.75–0.78) mm; HW/FS = 2.3 (2.3–2.4); HW/TL = 0.7 (0.7–0.7); CI = 3.8 (3.7–3.8); 4V = 1.7 (1.7–1.8); 5X = 1.7 (1.7–1.7); 4C = 0.6 (0.6–0.7); M = 0.5 (0.5–0.5). $n = 2♀$. TL = 1.21 (1.15–1.28) mm; WL = 2.54 (2.43–2.66) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.83 (0.79–0.86) mm; HW/FS =

2.3 (2.3–2.3); HW/TL = 0.7 (0.7–0.7); CI = 4.1 (3.9–4.2); 4V = 1.6 (1.6–1.6); 5X = 1.7 (1.6–1.8); 4C = 0.6 (0.6–0.6); M = 0.5 (0.5–0.5).

Material examined. KAUA'I: Holotype ♂ (BPBM 16686), Papa'alai Ridge Road at Kōke'e Ditch, swept in *Pisonia* sp. grove, 24.ii.2000, PMO & JBS. Allotype ♀ (BPBM 16686a), as holotype. 2♂ 8♀ paratypes, as holotype (UHIM). 2♂ 3♀ paratypes, Mahanaloa-Ku'ia Valley junction, 1900 ft, on and under *Pisonia*, 20.v.2007, KNM (BPBM).

Distribution and ecology. Kaua'i. Breeding hosts unknown; probably associated with *Pisonia* (Nyctaginaceae).

Etymology. Named after the type locality, Papa'alai Ridge, in the Pu'u Ka Pele Forest Reserve.

'kahania' subgroup

Members of this subgroup are extremely rare: a total of only four specimens of the two species are known, and it is likely that additional species exist. They are distinctive largely in lacking the characters that distinguish the other subgroups: the frontal setae are all normal, and the front legs completely lack elongate cilia. They can be identified as members of the larger 'nudidrosophila' group by the hooked process on the aedeagus and the long, narrow ovipositor of the female. In addition to lacking ciliation on the front legs, the two known species are united by having elongate, setulose palpi, with some long setae but without a strong, black, apical seta in the males. The female palpi are similar to those of the male but possess a typical apical seta.

***Drosophila kahania* sp.n.**

(Figs 2B; 4B)

Diagnosis. Separated from *D. longipalpus* by having the lower half of the pleura yellow.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits brown, pollinose; orbits normal, not expanded anteriorly. Front dull brown above, pollinose, yellowish below the ocellar triangle; frontal setulae semi-erect, mostly more or less medially directed. Orbital setae normal; anterior reclinate about even with the proclinate. Ocellar setae normal. Eyes normal. Face brown, weakly raised into a rounded carina dorsomedially. Antenna brown, second segment paler apically; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, remaining oral setae about one-third its length. Gena yellow. Palp yellow, tinged with brown, flattened apically, elongate, extending beyond the apex of the labellum, with many elongate setulae, those near the apex about half as long as the palp but not stronger than the others. **Thorax.** Mesonotum brown, pollinose. Pleura yellow, upper half tinged with brown. Acrostichal setulae in six distinct rows.

Dorsocentral setae normal, anterior about four times as long as acrostichals; without any additional elongate setae in the dorsocentral row. *Legs*. Yellow. Front tibia and tarsi without elongate cilia or setae. *Wings*. Hyaline, faintly infuscated at the apex of R_{2+3} and R_{4+5} , extending about one-third the distance from the wingtip to the dm-cu crossvein. Costal fringe extending about halfway between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Frontal setulae prostrate to semi-erect. Palp about three times as long as wide, with a single strong apical seta. *Thorax*. Dorsocentral row with an additional short seta, about one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 1♂$. TL = 1.03 mm; WL = 2.08 mm; TL/WL = 0.5; HW = 0.75 mm; HW/FS = 2.3; HW/TL = 0.7; CI = 3.9; 4V = 1.8; 5X = 1.7; 4C = 0.6; M = 0.5. $n = 1♀$. TL = 1.13 mm; WL = 2.35 mm; TL/WL = 0.5; HW = 0.81 mm; HW/FS = 2.3; HW/TL = 0.7; CI = 3.9; 4V = 1.7; 5X = 1.6; 4C = 0.6; M = 0.5.

Material examined. O'AHU: Holotype ♂ (BPBM 16687), Ala'ihe'ihe Gulch, 11.vi.1970, ex *Urera* stem, P31, SLM. Allotype ♀ (BPBM 16687a), as holotype. 1♂, as holotype (UHIM).

Distribution and ecology. O'ahu; known only from the type collection in the Wai'anae mountains. Reared from *Urera* sp. (Urticaceae).

Etymology. From the Hawaiian *kahania*, smooth-shaven, referring to the lack of cilia on the front legs.

Discussion. The genitalia of the holotype was dissected and photographed (illustrated in Fig. 2B), but lost in preparation. Unfortunately, the only other male specimen is mouldy and in poor condition (it is not designated as a paratype).

***Drosophila longipalpus* sp.n.** (Fig. 2C)

Diagnosis. Pleura all brown, rather than part yellow as in *D. kahania*.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits brown, pollinose; orbits normal, not expanded anteriorly. Front dull brown above, pollinose, yellowish below the ocellar triangle; frontal setulae semi-erect, mostly more or less medially directed. Orbital setae normal; anterior reclinate only slightly above the proclinate. Ocellar setae normal, placed around the midline of the lateral ocelli and diverging. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown, second segment paler

apically (third segment missing in type). No distinct oral vibrissae (may be broken off). Gena yellow. Palp yellow, tinged with brown, flattened apically, elongate, extending beyond the apex of the labellum, with many elongate setulae, those near the apex about half as long as the palp but not stronger than the others. *Thorax*. Mesonotum brown, pollinose. Pleura brown, slightly paler ventrally. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; without any additional elongate setae in the dorsocentral row. *Legs*. Yellow. Front tibia and tarsi without elongate cilia or setae. *Wings*. Hyaline, faintly infuscated at the apex of R_{2+3} and R_{4+5} , extending about half the distance from the wingtip to the dm-cu crossvein. Costal fringe extending about two-fifths the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci brown.

♀. Unknown.

Measurements. $n = 1♂$. TL = 0.94 mm; WL = 1.9 mm; TL/WL = 0.5; HW = 0.71 mm; HW/FS = 2.2; HW/TL = 0.8; CI = 2.8; 4V = 2.1; 5X = 1.8; 4C = 0.9; M = 0.7.

Material examined. HAWAII: Holotype ♂ (BPBM 16688), Pu'u Wa'awa'a, 3800 ft, 1.viii.1971, swept under *Pisonia* grove, SLM. Genitalia dissected.

Distribution and ecology. Hawaii; known only from the holotype. Breeding hosts unknown.

Etymology. Refers to the unusually long palpi in this subgroup.

'nudidrosophila' subgroup

The 'nudidrosophila' subgroup is the largest, with 11 species. Five of these come from Hawaii, an unusual distribution. Hardy (1965, 1966) described five: *D. aenicta* and *D. gemmula* from O'ahu, *D. amita* and *D. lepidobregma* from Hawaii, and *D. eximia* from Maui, Moloka'i, and Lana'i. We describe four new species here: *D. canavalia*, *D. mahui*, and *D. panoanoa* from Hawaii, and *D. kualapa*, *D. malele*, and *D. poonia* from Kaua'i. The mesic habitats favoured by this group have been particularly poorly collected on Maui Nui, and, given the presence of multiple species on the other islands, it is highly likely that more species will be found there.

Morphologically, several synapomorphies unite the species in this subgroup. All males lack the proclinate and reclinate orbital setae, and have a thickened, spine-like seta on the palp. The orbits, normally narrow strips adjacent to the eyes that end just below the proclinate bristle, are greatly expanded to reach the frontal suture and occupy much of the front. The orbits have less distinct margins than normal, and are covered with dense reclinate setulae. In all species except *D. canavalia*, *D. gemmula*, and *D. malele*, these setulae are pale, flattened near the tip, and somewhat clavate. This is in contrast to the 'okala' subgroup, where

the frontal setulae are dark and hair-like, similar to those of other subgroups.

Three species complexes are suggested by the ciliation of the male front legs: *D. aenicta*, *D. canavalia*, *D. malele*, and *D. poonia* with the inner tibial row strongly directed ventrally and the basitarsus sparsely ciliate; *D. amita* and *D. gemmula* with short cilia on the tibia and a single row of hooked cilia on the basitarsus; and *D. eximia*, *D. kualapa*, *D. lepidobregma*, *D. mahui*, and *D. panoanoa* with two complete rows of long cilia on the tibia and one row of more or less straight cilia on the basitarsus.

The ecology of this subgroup is relatively well understood, with rearing data for eight of the 11 species. However, only three of these have more than one record, and none has more than three, so their full range of host plants and degree of host specificity are unknown. Those that have multiple records do not appear to be very host-specific. Targeting the plants known to be hosts – *Charpentiera*, *Claoxylon*, *Chamaesyce*, *Pisonia*, and *Urera* – as well as others in the same habitats will give a better picture of their breeding habits.

Drosophila aenicta (Hardy)

(Fig. 10A)

Nudidrosophila aenicta Hardy, 1966:227.

Diagnosis. Separated from most other species by having two rows of cilia on the front basitarsus. Differs from its sister species *D. poonia* by having fewer cilia on the front tibia and the pleura entirely yellow.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front brown, tinged

with yellow anteriorly. Orbital setae absent. Ocellar setae absent, with three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. No strong vibrissae, one seta about twice as long as other setae of the oral margin. Gena yellow, only about two facets wide. Palp yellow-brown, flattened, parallel-sided, tapering to a point on the medial margin, with a strong, long, black, thickened seta on the medioapical corner, tapering to a point. *Thorax.* Mesonotum brown, pollinose. Pleura entirely yellow. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs.* Yellow. Front tibia with a row of seven to eight thin anterodorsal and five to six longer, thicker anteroventral cilia, with two to three long dorsal cilia at the tibiofemoral joint. Front basitarsus with three anterior and two anteroventral cilia; one each on the second tarsal segment. *Wings.* Uniformly hyaline. Costal fringe extending halfway between R_{2+3} and R_{4+5} . *Abdomen.* Solid dark brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head.* Vertex, ocellar triangle, and orbits brown, with light pollen; orbits not expanded or reaching the frontal suture. Ocellar tubercle only slightly raised above the front. Front dull dark brown to black above, pollinose, orange-brown between the ocellar triangle and frontal suture, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. One very long and strong oral vibrissa, but not cruciate. Palp yellow-brown, flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Thorax.* Pleura yellow, tinged with brown at the dorsal and ventral margins of the anepisternum. *Legs.* Lacking long cilia. *Abdomen.* Ovipositor brown, long.

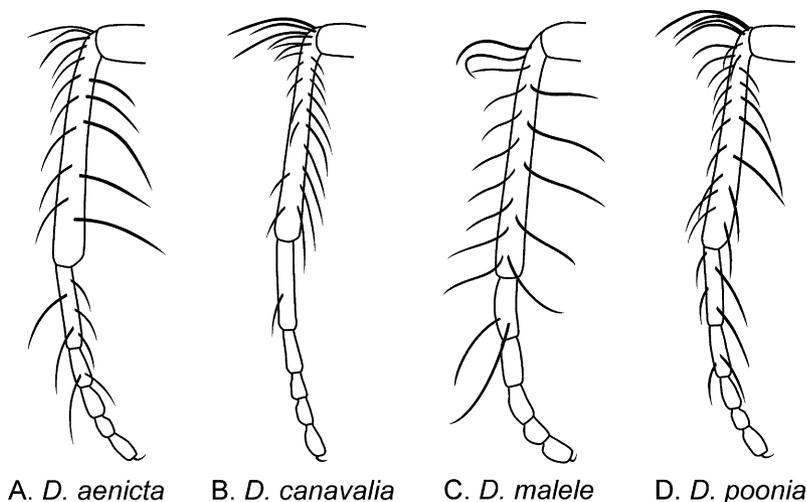


Fig. 10. Right front legs of males of the 'nudidrosophila' subgroup, 'aenicta' complex, anterior view.

Measurements. $n = 2\♂$. TL = 0.89 (0.83–0.96) mm; WL = 1.68 (1.58–1.78) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.66 (0.61–0.7) mm; HW/FS = 1.8 (1.8–1.8); HW/TL = 0.7 (0.7–0.7); CI = 3.2 (3–3.3); 4V = 1.8 (1.7–1.9); 5X = 1.8 (1.8–1.8); 4C = 0.8 (0.7–0.8); M = 0.6 (0.6–0.6). $n = 5\♀$. TL = 1.13 (0.85–1.25) mm; WL = 2.15 (1.7–2.35) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.79 (0.61–0.88) mm; HW/FS = 2.1 (2–2.2); HW/TL = 0.7 (0.7–0.7); CI = 3.6 (3.3–3.9); 4V = 1.8 (1.7–2); 5X = 1.9 (1.6–2.2); 4C = 0.7 (0.6–0.8); M = 0.6 (0.5–0.7).

Material examined. O'AHU: Holotype ♂ (BPBM 11268), Kawainui, 20.vi.1964, MRW. Allotype ♀ (BPBM 11268a), as holotype. 2♂ 3♀ paratypes, as holotype. 2♂ 1♀ paratypes, Drum Drive, 20.vi.1964, MRW. 3♂ 2♀, Mokulē'ia Jeep Rd., 1500 ft, 26–28.iii.1971, 'ex *Euphorbia* (= *Chamaesyce*) bark', SLM.

Distribution and ecology. O'ahu. Reared from bark of *Chamaesyce* sp. (Euphorbiaceae).

Discussion. A single male labelled as being from Hawai'i (Kohala Ditch Trail, 2045 ft, reared ex *Urera* stem, P29, 9–13.vi.1970, W. Gagné) cannot be distinguished from *D. aenicta*. However, the ciliation of the legs is not clearly visible, and it may be a separate species.

Drosophila amita (Hardy)

(Fig. 11A)

Nudidrosophila amita Hardy, 1965: 565.

Diagnosis. Separated from most species by having the cilia of the front tibia short, hardly longer than the width of the tibia, with no clump of long cilia at the base. Distin-

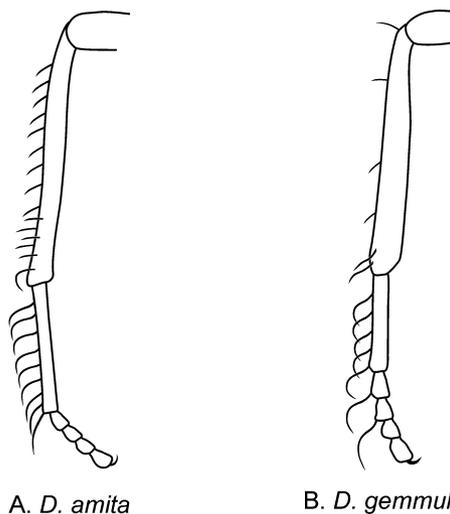


Fig. 11. Right front legs of males of the 'nudidrosophila' sub-group, 'amita' complex, anteroventral view.

guished from *D. gemmula* by possessing a row of cilia extending the full length of the segment, rather than scattered.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, with a yellow band above the frontal suture. Orbital setae absent, but some of the setulae in the area they would be in are slightly enlarged, about twice as long as those below. Ocellar setae absent, with three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow-brown, flattened, obliquely truncate, with a strong, long, black, thickened seta on the medioapical corner, tapering with a tiny, capitate, flattened tip. **Thorax.** Mesonotum brown, pollinose. Pleura brown on dorsal half, yellow on the katepisternum. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. **Legs.** Yellow. Front tibia with a complete row of 11 short, pale, dorsal cilia, hardly longer than the width of the tibia, and a row of four slightly longer anterodorsal cilia over the apical third; no long cilia at tibiofemoral joint. Front basitarsus with a row of eight to nine anterior cilia, the remaining segments without long hairs. **Wings.** Uniformly hyaline (sometimes faintly tinged at the apices of R_{2+3} and R_{4+5}). Costal fringe extending halfway between R_{2+3} and R_{4+5} . **Abdomen.** Solid dark brown.

♀. Identical to the male with the following exceptions. **Head.** Vertex, ocellar triangle, and orbits brown, with light pollen; orbits not expanded or reaching the frontal suture. Ocellar tubercle only slightly raised above the front. Front dull dark brown to black above, pollinose, orange-brown between the ocellar triangle and frontal suture, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. **Thorax.** Pleura mostly brown, yellow below the posterior katepisternal seta. **Legs.** Lacking long cilia. **Wings.** Uniformly hyaline. **Abdomen.** Ovipositor brown, long.

Measurements. $n = 3\♂$. TL = 1.03 (0.95–1.09) mm; WL = 1.93 (1.83–2.03) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.72 (0.7–0.76) mm; HW/FS = 2 (1.9–2.2); HW/TL = 0.7 (0.7–0.7); CI = 3.7 (3.5–4); 4V = 1.8 (1.7–1.8); 5X = 1.9 (1.7–2); 4C = 0.7 (0.6–0.7); M = 0.6 (0.6–0.6). $n = 5\♀$. TL = 1.14 (1.05–1.33) mm; WL = 2.24 (2.05–2.58) mm; TL/WL = 0.5

(0.5–0.5); HW = 0.79 (0.74–0.93) mm; HW/FS = 2.2 (2.1–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.7 (3.5–3.9); 4V = 1.9 (1.7–2.1); 5X = 1.8 (1.5–2.1); 4C = 0.7 (0.6–0.8); M = 0.6 (0.5–0.7).

Material examined. HAWAII: Holotype ♂ (BPBM 6480), Kīlauea, 27.vi.1917, OHS. Allotype ♀ (BPBM 6480a), as holotype. 1♂ 3♀ paratypes, as holotype. 1♂ paratype, Kīlauea, 4.viii.1946, ECZ. 2♀ paratypes, 'Kil. (Kīlauea) n. 03, sp. nr. plumosa', no other data. 1♂ 9♀, Kīpuka Kī, on underside of leaves, 10–11.ix.1964, HTS. 2♂ 9♀, Pu'u Wa'awa'a, 4000 ft, ex *Claoxylon* bark, 1.vii.1971, SLM. 1♂, Pu'u Wa'awa'a, 3800 ft, 1.viii.1971, swept under *Pisonia* grove, SLM (all above UHIM). 5♂ 1♀, 'Ōla'a Small Tract, reared ex *Charpentiera obovata*, 4.xii.2005, KNM (HVIC). 2♀, South Kona Forest Reserve, Kukuiope'e Unit, 3400 ft, sweeping vegetation and ground, 6.x.2006, KNM (BPBM).

Distribution and ecology. Hawaii; widely distributed. Reared from bark of *Charpentiera obovata* (Amaranthaceae) and *Claoxylon sandwicense* (Euphorbiaceae).

Discussion. One female paratype (Ka'ū, 4000 ft, no collector or other information) is actually a specimen of *D. lepidobregma*, with the distinctive raised ocellar tubercle.

***Drosophila canavalia* sp.n.**

(Figs 4C; 5B; 10B)

Diagnosis. Differs from all other species in the subgroup by having only a single cilia on the basitarsus. It also has the femora brown, a character shared only with *D. eximia* and *D. malele*.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front dull brown, tinged with yellow anteriorly. Orbital setae absent. Ocellar setae present but small, only slightly longer than the three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, relatively short and straight. Gena light brown. Palp yellow, slightly clavate, with a strong pale brown thickened seta, pointed at the apex, about as long as the palp. **Thorax.** Mesonotum brown, lightly pollinose. Pleura brown, tinged faintly with yellow in places. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about one-third the length of anterior dorsocentral and just anterior of it. **Legs.** Femora (especially mid and hind) brown, otherwise yellow. Front tibia with a row of nine to ten anteroventral cilia down the

entire length (pale at the base, becoming longer and darker towards the apex); four shorter anterodorsal cilia on the basal half and two on the apical third; and six to seven long, curved, erect cilia at the tibiofemoral joint. Front basitarsus with a single anterodorsal cilia. **Wings.** Uniformly hyaline except faintly smoky at the apex of R₂₊₃, extending down the vein about one-third the distance to the dm–cu cross-vein. Costal fringe extending halfway between R₂₊₃ and R₄₊₅. **Abdomen.** Solid brown. Cerci brown.

♀. Identical to the male with the following exceptions. **Head.** Vertex, ocellar triangle, and orbits brown, with light pollen; orbits not expanded or reaching the frontal suture. Ocellar tubercle only slightly raised above the front. Front black, yellow near suture, with scattered inconspicuous, erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. One long and strong oral vibrissa, the tips usually cruciate. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a strong black seta, nearly as long as the male's but not unusually thickened. **Thorax.** Pleura entirely brown. **Legs.** Lacking long cilia. **Wings.** Uniformly hyaline. **Abdomen.** Ovipositor pale brown, long.

Measurements. $n = 2♂$. TL = 0.98 (0.94–1.01) mm; WL = 1.85 (1.8–1.9) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.72 (0.69–0.75) mm; HW/FS = 2.1 (2–2.1); HW/TL = 0.7 (0.7–0.7); CI = 3.3 (3.2–3.4); 4V = 1.8 (1.8–1.8); 5X = 1.7 (1.6–1.7); 4C = 0.8 (0.7–0.8); M = 0.6 (0.6–0.6). $n = 4♀$. TL = 1.1 (1.01–1.14) mm; WL = 2.18 (2.04–2.28) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.79 (0.75–0.84) mm; HW/FS = 2.1 (2.1–2.2); HW/TL = 0.7 (0.7–0.8); CI = 3.5 (3.1–4.1); 4V = 1.9 (1.7–2); 5X = 1.7 (1.6–1.9); 4C = 0.7 (0.6–0.8); M = 0.6 (0.5–0.7).

Material examined. HAWAII: Holotype ♂ (BPBM 16689), Honomalino, Ho'ōpūloa, South Kona, 3000 ft, reared ex *Canavalia* bark, 9.ix.1981, SLM. Allotype ♀ (BPBM 16689a), as holotype. 2♂ 3♀ paratypes, Manukā, reared ex *Charpentiera*, 4.vi.1976, SLM (UHIM). 2♀ paratypes, as holotype (UHIM). 3♂ 2♀ paratypes, Kahuku, Akihi Gulch, 800 m, reared ex *Charpentiera obovata*, 31.i.2006, KNM (HVIC).

Distribution and ecology. Hawaii. Known from South Kona and Ka'ū. Reared from bark of *Canavalia hawaiiensis* (Fabaceae) and *Charpentiera obovata* (Amaranthaceae).

Etymology. Named for the endemic plant *Canavalia* (Fabaceae), from which the holotype was reared.

Discussion. Aside from the highly polyphagous *D. crucigera*, this is the only species of Hawaiian Drosophilidae to be reared from the bark of a legume (Magnacca *et al.*, in press). Fabaceae in general is not a good host in Hawaii; although a number of *picture wing* species utilize sap fluxes on *Acacia koa*, the only other records from the family are

Canavalia flowers, *Erythrina* bark, *Sophora* leaves, and *Strongylodon* pods.

***Drosophila eximia* (Hardy)**
(Fig. 12A)

Nudidrosophila eximia Hardy, 1965: 567.

Diagnosis. Differs from most species in the long, dense ciliation of both the front tibia and basitarsus. Very similar to *D. panoanao*; most easily distinguished by having the pleura entirely brown.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, orange-brown between the ocellar triangle and frontal suture. Orbital setae absent. Ocellar setae present but small, only slightly longer than the three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow-brown, not flattened, blunt at the tip, with a strong, black, thickened seta at the apex, almost at a right angle to the palp and nearly as long, slightly flattened and drawn into a long thin apex, paler apically. *Thorax.* Mesonotum brown, pollinose. Pleura entirely brown. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs.* Yellow, tinged with brown on the femora. Front tibia with two rows of cilia down the entire length (eight anterior and nine anterodorsal, the latter thinner and shorter), and four long curved cilia at the tibiofemoral joint. Front basitarsus with a row of six to seven anterodorsal cilia, the remaining segments without long hairs. *Wings.* Uniformly hyaline. Costal fringe extending halfway between R_{2+3} and R_{4+5} . *Abdomen.* Solid dark brown.

♀. Identical to the male with the following exceptions. *Head.* Vertex, ocellar triangle, and orbits brown, with light pollen; orbits not expanded or reaching the frontal suture. Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, yellow between the ocellar triangle and frontal suture, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Legs.* Lacking long cilia. *Abdomen.* Ovipositor brown, long.

Measurements. $n = 2♂$. TL = 1.04 (1.01–1.08) mm; WL = 1.91 (1.9–1.93) mm; TL/WL = 0.5 (0.5–0.6); HW = 0.73 (0.7–0.76) mm; HW/FS = 2.1 (2.1–2.2); HW/TL = 0.7 (0.7–0.7); CI = 3.4 (3–3.7); 4V = 1.8 (1.7–1.9); 5X = 1.6 (1.6–1.6); 4C = 0.7 (0.7–0.8); M = 0.5 (0.5–0.5). $n = 3♀$. TL = 1.27 (1.16–1.39) mm; WL = 2.39 (2.2–2.63) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.87 (0.76–0.95) mm; HW/FS = 2.2 (2.1–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.6 (3.4–3.7); 4V = 1.8 (1.7–1.9); 5X = 1.5 (1.4–1.6); 4C = 0.7 (0.6–0.7); M = 0.5 (0.5–0.5).

Material examined. MAUI: Holotype ♂ (BPBM 6481), Makamakole Valley, vi.1953, DEH, 'left fore leg beyond tibia missing' (Evenhuis, 1982). Allotype ♀ (BPBM 6481a), Ke'anae, vii.1953, DEH, 'apex of abdomen in microvial mounted below specimen' (Evenhuis, 1982). 1♀ paratype, as holotype. 1♂ paratype, as allotype. MOLOKA'I: 1♂ paratype, Pu'u Kolekole, vii.1952, MT. 7♂, Mākolelau, ex *Pisonia* stem, 4.iii.1972, SLM. 1♂, Waiakuilani, SE Pu'u Kolekole, 3000 ft, reared ex *Freyinetia* stem, 25.i.1973, SLM. LĀNA'I: 4♂ 12♀, Kaiholena Gulch, reared ex *Urera* stem, Q20, 8.xi.1971, SLM.

Distribution and ecology. Maui, Moloka'i, and Lāna'i. Reared from bark and stems of *Freyinetia arborea* (Pandanaaceae), *Pisonia* sp. (Nyctaginaceae), and *Urera glabra* (Urticaceae).

***Drosophila gemmula* (Hardy)**
(Fig. 11B)

Nudidrosophila gemmula Hardy, 1965: 569.

Diagnosis. This species can be differentiated from other species in the 'nudidrosophila' subgroup by having slender, straight-sided palps that possess a single thick yellow seta, the tibia with only a few, short cilia, and the basitarsus with a row of four to five hooked anterodorsal cilia.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying almost the entire width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle (less dense and conspicuous than in related species). Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, paler below the ocellar triangle; nearly flat, ocellar triangle hardly raised above the remainder of the front. Orbital setae absent. Ocellar setae absent, lacking conspicuous lateral setulae as well. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. No strong vibrissae, one seta about twice as long as setae of oral margin. Gena yellow. Palp yellow, flattened, parallel-sided, tapering at the apex, with a strong, yellow-brown, thickened seta at the apex, almost at a right angle to the palp and nearly as long, slightly flattened and drawn into

a long thin apex. *Thorax*. Mesonotum brown, pollinose. Pleura entirely brown. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with a single posterodorsal cilia at the tibiofemoral joint, three short, thin, widely spaced anterodorsal cilia along the segment, and two longer anterior cilia at the apex. Front basitarsus with a row of five long, hooked cilia; one on each of the next two segments. *Wings*. Subhyaline along the anterior margin, hyaline in the remainder. Costal fringe extending halfway between R_{2+3} and R_{4+5} . *Abdomen*. Solid dark brown. Cerci pale brown.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits brown, with light pollen; orbits not expanded or reaching the frontal suture. Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, orange-brown between the ocellar triangle and frontal suture, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. One strong oral vibrissa, the other oral setae less than one-third its length. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 2♂$. TL = 1.04 (1.04–1.05) mm; WL = 1.89 (1.88–1.9) mm; TL/WL = 0.6 (0.6–0.6); HW = 0.76 (0.75–0.78) mm; HW/FS = 2.3 (2.3–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.3 (3–3.6); 4V = 1.9 (1.7–2); 5X = 1.7 (1.7–1.7); 4C = 0.7 (0.6–0.8); M = 0.6 (0.5–0.6). $n = 2♀$. TL = 1.12 (1.11–1.13) mm; WL = 2.28 (2.23–2.34) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.8 (0.8–0.8) mm; HW/FS = 2.2 (2.2–2.3); HW/TL = 0.7 (0.7–0.7); CI = 3.7 (3.4–3.9); 4V = 1.8 (1.8–1.8); 5X = 1.6 (1.5–1.7); 4C = 0.7 (0.6–0.7); M = 0.5 (0.5–0.6).

Material examined. O'AHU: Holotype ♂ (BPBM 6482), Tantalus, 1300 ft, 11.iii.1905, WMG, 'head and legs are in slightly greasy condition' (Evenhuis, 1982). 1♂, Nu'uauu, 16.iii.1915, no collector given. 1♂, Mt Ka'ala, iv.1949, GBM. 1♂, Pu'u Palikea, 3100 ft, 14.ix.1955, MSA. 1♀, Ka'ala Mountains, 9.vii.1916 (recorded on underside of label), '♀ not to be designated as allotype,' OHS. 1♂ 1♀, Ala'ihē'ihē Gulch, ex *Urera* stem, 2.vi.1970, SLM.

Distribution and ecology. O'ahu. Reared from bark of *Urera* sp. (Urticaceae).

Discussion. In the original description, Hardy (1965) states that 'A female specimen at hand (9.vii.1916) apparently belongs here', but explicitly states that it is not designated as the allotype, and the specimen bears a label to that effect. Comparison with the Ala'ihē'ihē Gulch

specimen (which was reared in company with a male) indicates that the earlier specimen is in fact *D. gemmula*.

Drosophila kualapa sp.n.

(Figs 6A; 12B)

Diagnosis. Very close to *D. mahui*; distinguished by the reduced ciliation of the front tibia and by having the abdomen pale apically. Also see the diagnosis of *D. lepidobregma*.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits brown, pollinose; orbits expanded anteriorly, reaching the frontal suture and occupying nearly two-thirds of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle relatively small but steeply raised above the level of the front and

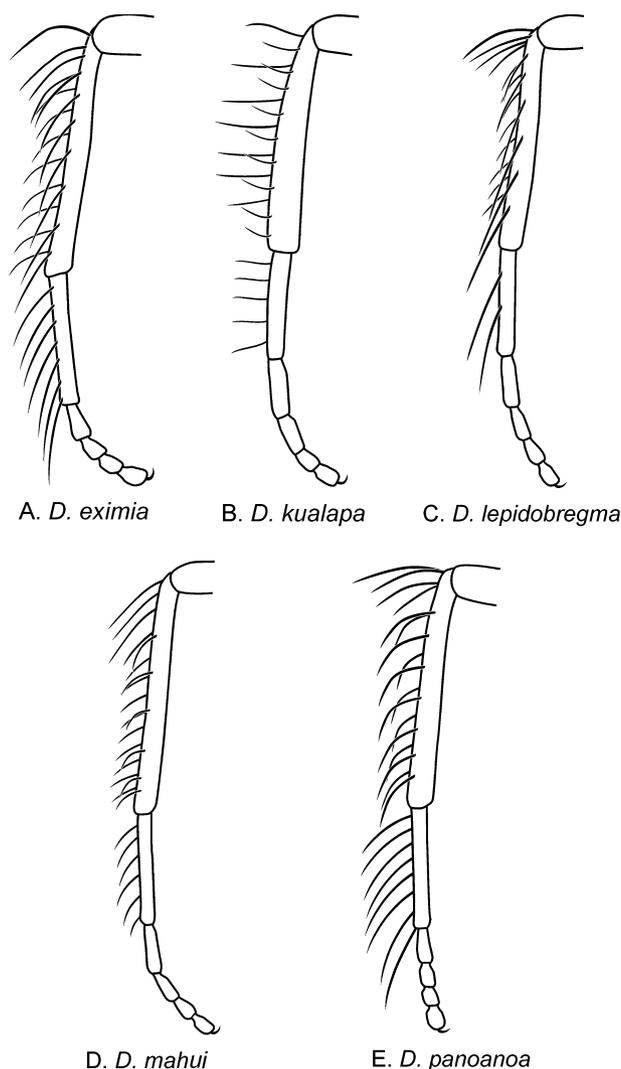


Fig. 12. Right front legs of males of the 'nudidrosophila' subgroup, 'eximia' complex, anteroventral view.

orbits, which are not swollen posteriorly. Front dull dark brown above, pollinose, paler below the ocellar tubercle; anterior half steep, slope continuous with the anterior margin of the ocellar tubercle. One reclinate orbital seta present, about twice as long and distinctly thicker than the longest orbital setulae. Ocellar setae absent, but with numerous laterally and dorsally directed setae on the ocellar tubercle. Eyes normal. Face brown, weakly raised dorso-medially. Antenna brown; arista with four to five dorsal rays and long medial rays, the longest the length of the terminal fork. One moderately strong oral vibrissa, the other oral setae less than half its length. Gena yellow, tinged with brown. Palp yellow, tinged with brown, tapering slightly toward the apex, with a strong, brown, thickened, apical seta, paler apically, flattened and blunt at the apex. *Thorax*. Mesonotum brown, pollinose. Pleura brown dorsally; katapisternum largely yellow, tinged with brown in the anterodorsal corner. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with two rows of elongate cilia (eight to nine anterior and six to seven longer, stronger anterodorsal), which are closely placed but the setae divergent; no additional cluster of cilia at the tibiofemoral joint. Front basitarsus with four to five (rarely six) anterodorsal cilia. *Wings*. Mostly hyaline, with a faint, diffuse infuscation anteroapically. Costal fringe extending nearly halfway between R_{2+3} and R_{4+5} . *Abdomen*. Mostly brown, apical segments pale laterally. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Orbits slightly wider anteriorly but not greatly expanded or reaching the frontal suture. Ocellar tubercle distinctly raised above the front, with steep sides, but not as high as in the male. Front covered with short reclinate setulae, not strongly sloping. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. Ocellar setae normal. One strong oral vibrissa (sometimes with a second strong seta present), the other oral setae less than half its length. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Thorax*. Katapisternum largely yellow, tinged with brown above the setae. *Legs*. Lacking long cilia. *Abdomen*. Solid dark brown. Ovipositor yellow-brown, long.

Measurements. $n = 5♂$. TL = 1.12 (1.06–1.19) mm; WL = 2.25 (2.13–2.35) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.87 (0.83–0.91) mm; HW/FS = 2 (1.7–2.1); HW/TL = 0.8 (0.8–0.8); CI = 3.9 (3.6–4.2); 4V = 1.9 (1.8–2); 5X = 1.6 (1.3–1.7); 4C = 0.7 (0.6–0.7); M = 0.5 (0.5–0.6). $n = 3♀$. TL = 1.15 (1.01–1.24) mm; WL = 2.5 (2.19–2.65) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.88 (0.79–0.95) mm; HW/FS = 2.1 (2–2.1); HW/TL = 0.8 (0.7–0.8); CI = 3.7 (3.7–3.8); 4V = 1.9 (1.9–1.9); 5X = 1.8 (1.7–1.9); 4C = 0.7 (0.7–0.7); M = 0.6 (0.6–0.6).

Material examined. KAUA'I: Holotype ♂ (BPBM 16722), 'Awa'awapuhi Trail, 3800 ft, 22.v.2007, sweeping vegetation

and ground, KNM. Allotype ♀ (BPBM 16722a), as holotype. 1♂ paratype, Pihea Trail, 3900 ft, sweeping vegetation and ground, 18.v.2007, KNM (BPBM). 1♂ 1♀ paratypes, Nu'alolo Trail, 3800 ft, 19.v.2007, KNM (BPBM). 1♂ paratype, as holotype (UHIM).

Distribution and ecology. Kaua'i; collected in wet forest in the Kōke'e area. Breeding hosts unknown.

Etymology. From the Hawaiian *kualapa*, ridge. Referring to the collection of all specimens of this species from ridgetop trails, whereas most 'nudidrosophila' are more common in valleys.

Discussion. The ocellar tubercle is less prominent in this species than in *D. lepidobregma* and *D. mahui*, particularly in the female, but is still distinct from the typical form. The cilia of the front legs are much more erect than those in the other species, but this may be an artifact of killing in alcohol.

Drosophila lepidobregma (Hardy)

(Figs 6B; 12C)

Nudidrosophila lepidobregma Hardy, 1965: 571.

Diagnosis. This species is distinguished from most others by the strongly raised ocellar tubercle, present in both males and females. In the male the front is somewhat depressed laterally, partially concealing the ocellar tubercle in direct lateral view and producing a distinct change in slope anteriorly between the mound and the front. It also appears consistently to have only three dorsal rays on the arista, and the pleura are entirely brown. The closely related *D. kualapa* and *D. mahui* have the ocellar tubercle similarly raised, but have the front more or less flat, the slope of the front continuous with the anterior face of the ocellar tubercle, the katapisternum yellow rather than brown, and the arista with four to five dorsal rays.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, with little pollen; orbits expanded anteriorly, reaching the frontal suture and occupying nearly two-thirds of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle strongly raised above the level of the front, forming grooves laterally between the ocelli and the orbits, which are also swollen. Front dull dark brown above, pollinose, orange-brown just above the frontal suture; anterior portion not unusually steep, break in slope present below the ocellar tubercle. One reclinate orbital seta present, only about one-half longer but distinctly thicker than the longest orbital setulae. Ocellar setae absent, but with numerous laterally and dorsally directed setae on the ocellar tubercle. Eyes normal. Face brown, raised into a broad, rounded carina dorsomedially. Antenna brown; arista with only three dorsal rays and long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than half its length. Gena yellow. Palp yellow, tapering at the apex, with a strong, pale brown to yellow, thickened seta, flattened and blunt at the apex. *Thorax*. Mesonotum brown, pollinose. Pleura entirely brown. Acrostichal setulae

in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with two rows of cilia down the entire length (six long, black anterior and eight thinner, paler anterodorsal), and five long curved cilia at the tibiofemoral joint. Front basitarsus with two to three anterodorsal cilia. *Wings*. Uniformly hyaline. Costal fringe extending halfway between R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits brown, with light pollen; orbits slightly wider anteriorly but not greatly expanded or reaching the frontal suture. Ocellar tubercle strongly raised above the front, with steep sides. Front dull dark brown to black above, pollinose, orange-brown between the ocellar triangle and frontal suture, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. Palp yellow, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Thorax*. Anterior dorsocentral about six times as long as acrostichals. *Legs*. Lacking long cilia. *Abdomen*. Ovipositor yellow-brown, long.

Measurements. $n = 3♂$. TL = 1.03 (0.98–1.06) mm; WL = 2.1 (2–2.23) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.75 (0.69–0.79) mm; HW/FS = 1.9 (1.9–1.9); HW/TL = 0.7 (0.7–0.8); CI = 3.8 (3.8–3.8); 4V = 1.9 (1.8–1.9); 5X = 1.9 (1.8–2); 4C = 0.7 (0.7–0.7); M = 0.6 (0.6–0.6). $n = 2♀$. TL = 1.18 (1.13–1.24) mm; WL = 2.49 (2.38–2.6) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.83 (0.78–0.89) mm; HW/FS = 2.1 (2.1–2.1); HW/TL = 0.7 (0.7–0.7); CI = 3.6 (3.4–3.9); 4V = 1.8 (1.7–1.9); 5X = 1.9 (1.7–2.1); 4C = 0.7 (0.6–0.7); M = 0.6 (0.5–0.6).

Material examined. HAWAII: Holotype ♂ (BPBM 6483), Kīlauea, 4.viii.1946, ECZ, 'posteroapical portion of left wing torn off' (Evenhuis, 1982). Allotype ♀ (BPBM 6483a), as holotype. 1♂ 1♀ paratypes, as holotype. 1♂, Upper 'Ōla'a Forest, 'C66.7', 14.vii.1963, HLC. 1♂, 'C-H 70.10', no other data. 3♂, Pu'u Wa'awa'a, 3800 ft, 'swept under *Pisonia* grove', 1.viii.1971, SLM. 2♂ 7♀, Kīpuka Kī, 'ex *Sapindus* bark', 27.ii.1972, SLM.

Distribution and ecology. Hawaii; collected primarily in the Kīlauea area, with one collection from Pu'u Wa'awa'a. Reared from bark of *Sapindus saponaria* (Sapindaceae).

Discussion. See Discussion under *D. mahui*.

***Drosophila mahui* sp.n.**
(Figs 4D; 6C; 12D)

Diagnosis. *Drosophila mahui* is differentiated from most other species except *D. kualapa* and *D. lepidobregma* by the strongly raised ocellar tubercle. See the diagnosis of the latter for characters to separate the three.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits brown, pollinose; orbits expanded anteriorly, reaching the frontal suture and occupying nearly two-thirds of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle strongly raised above the level of the front and orbits, which are not swollen. Front dull dark brown above, pollinose, orange below the ocellar tubercle; anterior half steep, slope continuous with the anterior margin of the ocellar tubercle. One reclinate orbital seta present, about twice as long and distinctly thicker than the longest orbital setulae. Ocellar setae absent, but with numerous laterally and dorsally directed setae on the ocellar tubercle. Eyes normal. Face brown, weakly raised dorsomedially. Antenna brown; arista with five (rarely four) dorsal rays and long medial rays, the longest the length of the terminal fork. One moderately strong oral vibrissa, the other oral setae less than half its length. Gena yellow. Palp yellow, broad, parallel-sided, with a strong, brown, thickened seta, paler apically, flattened and blunt at the apex. *Thorax*. Mesonotum brown, pollinose. Pleura brown dorsally, katapisternum yellow. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with two rows of elongate cilia (six to seven anterior and 9–11 anterodorsal), and three to four long curved cilia at the tibiofemoral joint. Front basitarsus with four to six (rarely three) anterodorsal cilia. *Wings*. Uniformly hyaline. Costal fringe extending halfway between R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits brown, with light pollen; orbits slightly wider anteriorly but not greatly expanded or reaching the frontal suture. Front dull brown, densely pollinose, obscuring the colour, with scattered erect, reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single strong apical seta. *Thorax*. Anterior dorsocentral about six times as long as acrostichals. *Legs*. Lacking long cilia. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 4♂$. TL = 1.12 (1.03–1.29) mm; WL = 2.18 (1.88–2.45) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.8 (0.7–0.9) mm; HW/FS = 1.8 (1.8–1.8); HW/TL = 0.7 (0.7–0.7); CI = 3.8 (3.6–4.1); 4V = 1.9 (1.8–2); 5X = 1.7 (1.5–1.8); 4C = 0.7 (0.6–0.7); M = 0.6 (0.5–0.6). $n = 4♀$. TL = 1.19 (1.09–1.48) mm; WL = 2.46 (2.25–2.95) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.83 (0.75–0.99) mm; HW/FS = 2 (1.9–2.1); HW/TL = 0.7 (0.7–0.7); CI = 3.6 (3.2–4); 4V = 1.9 (1.8–2); 5X = 1.9 (1.5–2.2); 4C = 0.7 (0.7–0.7); M = 0.6 (0.5–0.6).

Material examined. HAWAII: Holotype ♂ (BPBM 16690), Pu'u Wa'awa'a, 4000 ft, 1.vii.1971, ex bark of *Claoxylon*, SLM. Allotype ♀ (BPBM 16690a), as holotype. 1♂ 2♀

paratypes, as holotype (UHIM). 3♂ 1♀ paratypes, Pu'u Wa'awa'a, 3800 ft, 1.viii.1971, swept under *Pisonia* grove, SLM (UHIM).

Distribution and ecology. Hawai'i; only collected in the Pu'u Wa'awa'a area. Reared from bark of *Claoxylon sandwicense* (Euphorbiaceae).

Etymology. From the Hawaiian *māhu'i*, imitating. Referring to the similarity of this species to *D. kualapa* and *D. lepidobregma*.

Discussion. This species appears to be somewhat variable in the setation of the front basitarsus. Some specimens with only three cilia may be mistaken for *D. lepidobregma*, but the characters given in the diagnosis of that species are consistent and will separate them. Overall it is closer to *D. kualapa* from Kaua'i, differing by having a greater number of cilia on the front tibia and having the abdomen completely dark. The three species are probably very recently diverged.

Drosophila malele sp.n.

(Fig. 10C)

Diagnosis. Differs from most species in the 'nudidrosophila' subgroup by the bristly setae of the front and weakly enlarged palpal seta. Closest to *D. canavalia* from Hawai'i, distinguished by the presence of a pair of elongate cilia on the basitarsus rather than only one.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits shining dark brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at the level of the upper margin of the suture, narrowing somewhat anterior of this point; covered with hair-like reclinate setulae below the ocellar triangle. Ocellar tubercle nearly flat. Front dull dark brown. One reclinate orbital seta present, about twice as long as the longest orbital setulae but not stronger. Ocellar setae present but small, about as long as the reclinate orbital seta. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna dark brown, third segment slightly lighter; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than half its length; sometimes an intermediate-length seta also present. Gena brown. Palp yellow-brown, flattened, small, almost parallel-sided, with a strong brown apical seta, thicker than normal but less so than in other members of the 'nudidrosophila' subgroup, pointed and paler at the apex, about as long as the palp. *Thorax.* Mesonotum dark brown, lightly pollinose. Pleura brown, sometimes slightly paler ventrally. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs.* Mid and hind femora brown on the apical one-third, otherwise yellow. Basitarsus unusually short, about as long as the second tarsal segment and only about one-quarter as long as the

tibia. Front tibia with a row of eight to nine thin anterodorsal and five longer, stronger anteroventral cilia, with two to three long dorsal cilia at the tibiofemoral joint. Front basitarsus with a pair of long dorsal cilia on the apical half. *Wings.* Largely hyaline, indistinctly infuscated anteroapically. Costal fringe extending about two-fifths the distance between R_{2+3} and R_{4+5} . *Abdomen.* Solid dark brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head.* Orbits not expanded nor reaching the frontal suture. Front covered with short reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a strong black subapical seta. *Legs.* Lacking long cilia. *Abdomen.* Ovipositor yellowish brown, long.

Measurements. $n = 4♂$. TL = 0.98 (0.88–1.05) mm; WL = 1.93 (1.83–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.77 (0.7–0.83) mm; HW/FS = 2.2 (2.1–2.4); HW/TL = 0.8 (0.8–0.8); CI = 3.5 (3.3–3.7); 4V = 1.9 (1.8–2); 5X = 1.8 (1.7–1.9); 4C = 0.7 (0.7–0.8); M = 0.6 (0.5–0.7). $n = 5♀$. TL = 1.09 (0.95–1.3) mm; WL = 2.33 (2.1–2.76) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.81 (0.71–0.96) mm; HW/FS = 2.2 (2–2.3); HW/TL = 0.7 (0.7–0.8); CI = 3.4 (2.9–3.7); 4V = 1.9 (1.8–2); 5X = 1.6 (1.3–1.9); 4C = 0.7 (0.7–0.8); M = 0.5 (0.5–0.6).

Material examined. KAUA'I: Holotype ♂ (BPBM 16723) Kaluapuhi Trail, 4100 ft, sweeping vegetation and ground, 23.v.2007, KNM. Allotype ♀ (BPBM 16723a), as holotype. 1♂ 3♀ paratypes, Kumuwela Trail, 3500 ft, on and under *Corynocarpus*, 17.v.2007, KNM (UHIM). 1♂ 1♀ paratypes, Nu'alolo Trail, 3800 ft, sweeping vegetation and ground, 19.v.2007, KNM (BPBM). 1♂ 1♀ paratypes, Mahanaloa-Ku'ia Valley junction, 1900 ft, on and under *Pisonia*, 20.v.2007, KNM (BPBM). 1♀ paratype, 'Awa'awapuhi Trail, 3800 ft, sweeping vegetation and ground, 22.v.2007, KNM (BPBM). 1♂ paratype, as holotype (BPBM).

Distribution and ecology. Kaua'i; collected in wet to mesic forest in the Kōke'e area. Breeding hosts unknown.

Etymology. From the Hawaiian *malele*, scattered here and there. Referring to the collection of this species from a wide variety of sites and habitats.

Discussion. This species is somewhat intermediate between the 'nudidrosophila' and 'okala' subgroups; it has the hair-like frontal setulae and small palpi of the latter, and the expanded fronto-orbital plates and enlarged palpal seta of the former. Because the orbits and palpal seta are the defining characters of the 'nudidrosophila' subgroup, we are placing it in the latter, although these characters are less developed in *D. malele* than in other members of the subgroup.

***Drosophila panoanoa* sp.n.**

(Fig. 12E)

Diagnosis. Differentiated from closely related forms by the chaetotaxy of the male forelegs and colouration of the pleura. Sister species *D. eximia* has the katepisternum brown rather than yellow; the sympatric *D. amita* has the dorsal row of cilia short and pale and anterodorsal cilia only on the apical half, rather than two full rows of long cilia.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits expanded anteriorly, reaching the frontal suture and occupying about half of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front dull dark brown above, pollinose, orange-brown just above the frontal suture. Orbital setae absent. Ocellar setae present but small, only slightly longer than the three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a strong, long, black, thickened seta on the medioapical corner, tapering to a point. **Thorax.** Mesonotum brown, pollinose. Pleura brown on dorsal half, yellow on the katepisternum. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. **Legs.** Yellow. Front tibia with two rows of cilia down the entire length (seven long, black anterior and six thinner, paler anterodorsal), and four long curved cilia at the tibiofemoral joint. Front basitarsus with a row of eight anterodorsal cilia, the remaining segments without long hairs. **Wings.** Uniformly hyaline. Costal fringe extending nearly two-thirds the distance between R_{2+3} and R_{4+5} . **Abdomen.** Solid dark brown. Cerci yellow.

♀. Unknown.

Measurements. $n = 1♂$. TL = 1.19 mm; WL = 2.23 mm; TL/WL = 0.5; HW = 0.86 mm; HW/FS = 2.2; HW/TL = 0.7; CI = 3.8; 4V = 1.8; 5X = 1.9; 4C = 0.7; M = 0.6.

Material examined. HAWAII: Holotype ♂ (BPBM 16691), Pu'u Wa'awa'a, 5000 ft, 9.viii.1978, SLM.

Distribution and ecology. Hawaii; known only from the type. Breeding hosts unknown.

Etymology. From the Hawaiian *pānoanoa*, very rare, referring to the scarcity of this species.

Discussion. Although Pu'u Wa'awa'a is a productive area for the 'nudidrosophila' group, with six species recorded

there, *D. panoanoa* was collected at a higher elevation than all the others. It is possible that the lack of specimens is the result of a shift to a different host from those used by the other species. The female is unknown, but may also be mistaken for *D. amita*.

***Drosophila poonia* sp.n.**

(Fig. 10D)

Diagnosis. The ciliation of the male forelegs is similar to that of *D. aenicta*, but with more cilia in both rows on the tibia.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, yellow anteriorly, with little pollen, margins very distinct; orbits expanded anteriorly, reaching the frontal suture and occupying nearly two-thirds of the width between the eyes at this point, covered with dense reclinate setulae below the ocellar triangle. Ocellar tubercle only slightly raised above the front. Front dull brown, pollinose, slightly paler anteriorly. Orbital setae absent. Ocellar setae present but small, only slightly longer than the three to four laterally directed setae on each side between the anterior and lateral ocelli. Eyes normal. Face brown, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. No strong vibrissae, other oral setae inconspicuous. Gena yellow posteriorly, grading to brown near the vibrissal angle. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a strong, long, brown, thickened seta on the medioapical corner, tapering to a point. **Thorax.** Mesonotum dark brown, lightly pollinose. Pleura brown on dorsal half, yellow below the katepisternal setae. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. **Legs.** Yellow. Front tibia with two rows of cilia down the entire length (seven long, black anteroventral and 11 thinner, paler anterodorsal), two at the base between the rows, and four long curved cilia at the tibiofemoral joint. Front basitarsus with two anteroventral and two anterodorsal cilia; one of each on the second tarsal segment. **Wings.** Uniformly hyaline, sometimes faintly infuscated anteroapically. Costal fringe extending halfway between R_{2+3} and R_{4+5} . **Abdomen.** Dark brown dorsally, pale yellow-brown laterally. Cerci yellow.

♀. Identical to the male with the following exceptions. **Head.** Orbits not laterally expanded, but elongate, nearly reaching the frontal suture. Front covered with short reclinate setulae. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal. One strong oral vibrissa, the other oral setae less than half its length. Palp larger than in the male but similarly shaped and coloured, with a strong black subapical seta. **Legs.** Lacking long cilia. **Abdomen.** Solid dark brown. Ovipositor yellow-brown, long.

Measurements. $n = 2♂$. TL = 0.98 (0.95–1.01) mm; WL = 1.81 (1.75–1.88) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.74

(0.73–0.76) mm; HW/FS = 1.8 (1.7–1.9); HW/TL = 0.8 (0.8–0.8); CI = 3.2 (3.1–3.3); 4V = 1.9 (1.8–1.9); 5X = 1.8 (1.7–1.9); 4C = 0.7 (0.7–0.8); M = 0.6 (0.6–0.6). $n = 2\text{♀}$. TL = 1.18 (1.1–1.26) mm; WL = 2.3 (2.2–2.4) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.89 (0.83–0.95) mm; HW/FS = 2.1 (2.1–2.2); HW/TL = 0.8 (0.8–0.8); CI = 3.9 (3.7–4); 4V = 1.9 (1.9–1.9); 5X = 4.8 (1.7–7.9); 4C = 0.7 (0.6–0.7); M = 1.6 (0.6–2.6).

Material examined. KAUA'I: Holotype ♂ (BPBM 16692), Mahanaloa-Ku'ia Valley junction, 1900 ft, on and under *Pisonia*, 20.v.2007, KNM. Allotype ♀ (BPBM 16692a), as holotype. 5♂ paratypes, Miloli'i Valley, Kaua'i, P54, 'reared ex *Charpentiera* stem', 22.viii.1970, SLM (UHIM). 2♂ 7♀ paratypes, as holotype, KNM & GMB (BPBM).

Distribution and ecology. Kaua'i. Reared from stems of *Charpentiera* sp. (Amaranthaceae); commonly found in association with *Pisonia*, and probably breeds in it as well.

Etymology. From the Hawaiian *po'o nia*, meaning bald head. Named in reference to the seta-less front of the 'nudidrosophila' subgroup males.

'okala' subgroup

The 'okala' subgroup consists of five new species: *D. akoko*, *D. kuhao*, and *D. panina* from O'ahu, *D. makawao* from Maui and Moloka'i, and *D. okala* from Hawai'i. They are distinguished from the 'nudidrosophila' subgroup by having a normal-sized orbital area (except in *D. panina*, in which it is somewhat expanded), the posterior reclinate seta present, and cilia on the front tibia but not the tarsus. The front is covered with erect reclinate setulae, but these are less dense and usually longer than in species of the 'nudidrosophila' subgroup, similar to normal frontal setulae. Close inspection reveals that a small proclinate orbital hair is present in *D. makawao* and *D. okala*, but it is small, inconspicuous, and only distinguishable from the other frontal setulae by its direction and larger socket.

Ecologically this subgroup is somewhat distinct from the rest of the 'nudidrosophila' group, with records from the unusual hosts *Chamaesyce* (Euphorbiaceae) and *Hibiscus* (Malvaceae), and the only records in the entire group for the common *Drosophila* hosts *Cheirodendron* and *Clermontia*. It is likely that *D. makawao* is at least capable of breeding in the latter two as well, as it was collected in areas where there are few of the typical mesic host plants. However, few records exist for any of the species in this subgroup, and it remains to be seen if these are preferred or incidental hosts, or if the species are polyphagous.

Drosophila akoko sp.n.

(Figs 5C; 13A)

Diagnosis. Differs from other species in the subgroup by the combination of having the wing completely hyaline and the pleura entirely yellow.

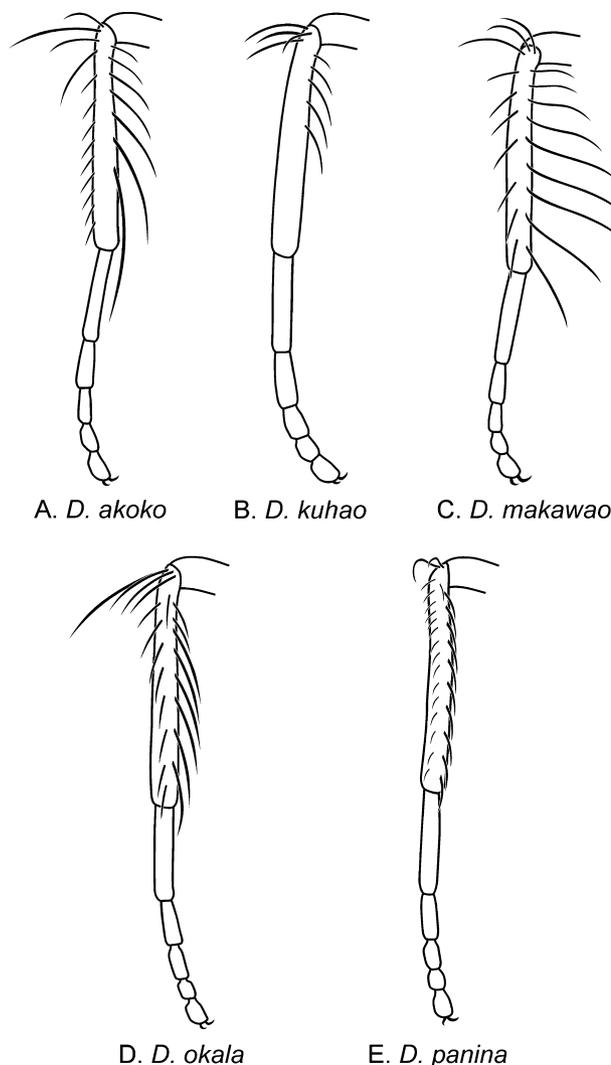


Fig. 13. Right front legs of males of the 'okala' subgroup, anterodorsal view.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits normal, not expanded anteriorly. Front dull dark brown above, pollinose, orange-brown below the ocellar triangle; evenly covered with erect reclinate setulae below the reclinate seta; about half as long as the reclinate, distinctly longer anteriorly. Only the posterior reclinate seta present. Ocellar setae present but moderately small, shorter than the reclinate seta. Eyes normal. Face brown, weakly raised dorsomedially. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow, small, more or less cylindrical, with a single small apical seta present. **Thorax.** Mesonotum brown, pollinose. Pleura entirely yellow. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals, without additional short

setae. *Legs*. Yellow. Front tibia with one anteroventral row of seven to eight cilia along the basal three-fifths, short, pale, and erect at the base, becoming long, strong, and prostrate below, and about five long dorsal cilia present near the tibiofemoral joint; a row of about ten short, straight, setulae in line with the basal cilia are conspicuously erect, but are not differentiated from the other setulae of the leg. Front tarsus lacking cilia. *Wings*. Uniformly hyaline except faintly infuscated at the very tip of R_{2+3} . Costal fringe extending just under half the distance between R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci brown.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits dull brown, pollinose. Frontal setulae shorter than in the male, only about one-quarter as long as the anterior reclinate. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal, about as long as the posterior reclinate. Face yellow-brown, raised into a rounded carina dorsomedially. Palp yellow-brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single moderately strong apical seta. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 3♂$. TL = 0.88 (0.86–0.91) mm; WL = 1.74 (1.73–1.75) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.64 (0.63–0.65) mm; HW/FS = 2 (1.9–2.1); HW/TL = 0.7 (0.7–0.7); CI = 3.5 (3.4–3.5); 4V = 1.8 (1.7–1.9); 5X = 2.1 (2–2.3); 4C = 0.7 (0.7–0.7); M = 0.6 (0.6–0.7). $n = 4♀$. TL = 1.14 (1.09–1.18) mm; WL = 2.27 (2.13–2.38) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.81 (0.78–0.84) mm; HW/FS = 2.1 (2–2.1); HW/TL = 0.7 (0.7–0.7); CI = 3.5 (3.3–3.8); 4V = 1.7 (1.6–1.8); 5X = 1.7 (1.7–1.8); 4C = 0.7 (0.6–0.7); M = 0.5 (0.5–0.6).

Material examined. O'AHU: Holotype ♂ (BPBM 16693), Mokulē'ia Jeep Rd, 1500 ft, 26–28.iii.1971, reared ex *Euphorbia* (= *Chamaesyce*) bark, P77, SLM. Allotype ♀ (BPBM 16693a), as holotype. 22♂ 26♀ paratypes, as holotype (UHIM).

Distribution and ecology. O'ahu; known only from the Wai'anae range. Reared from *Chamaesyce* sp. (Euphorbiaceae).

Etymology. From the Hawaiian 'akoko, the Hawaiian word for the only known host plant, *Chamaesyce*. The Hawaiian species of this genus were formerly placed in *Euphorbia*.

***Drosophila kuhao* sp.n.**
(Fig. 13B)

Diagnosis. This is the only species in the subgroup to lack long cilia on the apical half of the tibia. It also has a narrow anteroapical mark on the wing, compared with a much larger mark in *D. okala* and none in the other species.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, with light pollen; orbits normal, not expanded anteriorly. Front dull dark brown above, pollinose, orange-brown below the ocellar triangle; evenly but not densely covered with erect reclinate setulae below the reclinate seta except below the ocellar triangle, about half as long as the reclinate, of even length. Only the posterior reclinate seta present; short, scarcely distinguishable from the other frontal setulae. Ocellar setae present but small, shorter than the reclinate seta. Eyes normal. Face brown, nearly flat. Antenna brown; arista with long medial rays, the longest the length of the terminal fork. One small oral vibrissa, scarcely larger than the other oral setae. Gena yellow. Palp yellow, small, more or less cylindrical, with a single small apical seta present. *Thorax*. Mesonotum brown, pollinose. Pleura entirely yellow, tinged with brown on the anepimeron. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals, without additional short setae. *Legs*. Yellow. Front tibia with an anteroventral row of five thin, moderately long cilia along the basal half, none on the apical half; about four long dorsal cilia are present near the tibiofemoral joint. Front tarsus lacking cilia. *Wings*. A brown infuscation present at the apex of R_{2+3} and R_{4+5} , extending about one-third the distance from the wingtip to the dm-cu crossvein; also a basal spot between the humeral crossvein, apex of R_1 , and base of M, otherwise hyaline. Costal fringe extending just under half the distance between the veins. *Abdomen*. Brown dorsally, yellow laterally. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Vertex, ocellar triangle, and orbits dull brown, pollinose. Frontal setulae shorter than in the male, less than one-quarter as long as the anterior reclinate. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate. Ocellar setae normal, nearly as long as the posterior reclinate. Face brown below, yellow and raised into a rounded carina dorsomedially. Palp yellow, slightly flattened, straight on the medial margin and convex on the lateral, with a single moderately strong apical seta. *Thorax*. Dorsocentral row with an additional short seta, one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Lacking long cilia. *Wings*. Narrowly infuscated along the costa between the apices of R_{2+3} and R_{4+5} , otherwise hyaline. *Abdomen*. Solid dark brown; sixth tergum yellow. Ovipositor yellow, long.

Measurements. $n = 1♂$. TL = 0.91 mm; WL = 1.85 mm; TL/WL = 0.5; HW = 0.74 mm; HW/FS = 2.2; HW/TL = 0.8; CI = 3.4; 4V = 1.8; 5X = 1.6; 4C = 0.7; M = 0.5. $n = 1♀$. TL = 1.08 mm; WL = 2.3 mm; TL/WL = 0.5; HW = 0.81 mm; HW/FS = 2.2; HW/TL = 0.8; CI = 3.9; 4V = 1.8; 5X = 1.7; 4C = 0.7; M = 0.5.

Material examined. O'AHU: Holotype ♂ (BPBM 16695), Makaha Valley, ex *Hibiscus* bark, 28.v.1970, SLM. Allotype ♀ (BPBM 16695a), as holotype. 1♂ paratype, Wai'anae–Ka'ala Trail, ridgetop sweeping, 5.iii.2006, KNM (UHIM).

Distribution and ecology. O'ahu, Wai'anae mountains. Reared from bark of *Hibiscus* sp. (Malvaceae). This is an unusual host for Hawaiian *Drosophila*; the only other records are for *D. ischnotrix*, a member of the *modified mouthparts* group, and the highly polyphagous *picture-wing* species *D. crucigera*.

Etymology. From the Hawaiian *kūha'o*, standing alone or independent. Refers to the distinctness of the 'okala' subgroup from the other, previously recognized subgroups.

Discussion. The holotype has many of the setae broken off, and the description is partly based on the paratype.

***Drosophila makawao* sp.n.**

(Fig. 13C)

Diagnosis. Distinguished from other species in the subgroup by the all-brown pleura and lack of wing markings.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits brown, pollinose, weakly shining; orbits slightly expanded, but occupying less than half the width of the front and not reaching the frontal suture. Front dull dark brown above, pollinose, orange-brown below the ocellar triangle; with scattered semi-erect reclinate setulae below the reclinate seta, about one-third as long as the reclinate. Only the posterior reclinate seta is distinct; a small, pale, proclinate setula is also present, but it is about the size of the other frontal setulae. Ocellar setae present but small, less than half as long as the reclinate seta, and laterally directed. Eyes normal. Face brown, raised into a rounded carina dorso-medially. Antenna brown; arista with long medial rays, the longest longer than the terminal fork. One or two strong oral vibrissae, the other oral setae less than one-third their length. Gena dark brown. Palp light brown, small, more or less cylindrical, with moderately long setulae (about as long as width of palp) along the medial margin and a single apical seta present. *Thorax.* Mesonotum dark brown to black, pollinose. Pleura entirely dark brown. Dorsocentral setae with the anterior about three times as long as acrostichals; without additional short setae. *Legs.* Yellow, sometimes tinged with brown at the apices of mid and hind femora. Front tibia with an anteroventral row of eight to nine long, dark cilia and an anterodorsal row of seven to eight shorter, paler cilia along the entire length; three to four long dorsal cilia are present near the tibiofemoral joint. Front tarsus lacking cilia. Wings. Almost uniformly hyaline, faintly tinged with brown anteroapically. Costal fringe extending about one-third the distance between R_{2+3} and R_{4+5} . *Abdomen.* Brown dorsally, fading to yellow on lateral portions of terga; T6 often almost entirely yellow. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head.* Frontal setulae shorter than in the male, less than half as long as the anterior reclinate. Orbital setae normal, anterior reclinate even with or only slightly above the

proclinate. Ocellar setae normal, about as long as the posterior reclinate. Palp light brown, slightly flattened, straight on the medial margin and convex on the lateral, with a single moderately strong apical seta but with only the normal short setulae along the medial margin. *Legs.* Lacking long cilia. Mid and hind femora dark brown except narrowly at the base and apex. *Abdomen.* Entirely dark brown. Ovipositor brown, long.

Measurements. $n = 3♂$. TL = 0.88 (0.88–0.88) mm; WL = 1.84 (1.80–1.90) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.67 (0.65–0.69) mm; HW/FS = 2.2 (2.2–2.4); HW/TL = 0.8 (0.7–0.8); CI = 3.5 (3.2–3.8); 4V = 1.9 (1.8–1.9); 5X = 1.7 (1.6–1.8); 4C = 0.7 (0.7–0.8); M = 0.6 (0.6–0.6). $n = 2♀$. TL = 1.16 (1.09–1.24) mm; WL = 2.33 (2.28–2.38) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.78 (0.75–0.80) mm; HW/FS = 2.1 (2.1–2.1); HW/TL = 0.7 (0.6–0.7); CI = 3.8 (3.7–3.9); 4V = 1.7 (1.7–1.8); 5X = 1.7 (1.6–1.7); 4C = 0.6 (0.6–0.6); M = 0.5 (0.5–0.5).

Material examined. MAUI: Holotype ♂ (BPBM 16696), Waikamoi Preserve, Maile Trail in mesic forest, 4580 ft, BioLure trap 837, LL. Allotype ♀ (BPBM 16696a), Makawao Forest Reserve, Maile Trail in ecotone forest, 4380 ft, BioLure trap 845, LL. 5♂ paratypes, as holotype (UHIM). 2♀ paratypes, as allotype (UHIM). MOLOKA'I: 1♂ paratype, Kamakou Preserve, East Kawela Gulch, 3700 ft, 20.ii.2007, KNM (UHIM).

Distribution and ecology. Maui and Moloka'i, in wet forest. Breeding hosts unknown.

Etymology. Named for the type locality, the Makawao region of Haleakalā.

Discussion. Many additional specimens have been collected by LL in his studies on the attractiveness of tephritid lures to non-target insects. Most come from a wet to mesic forest area with abundant *Clermontia*, suggesting that it may breed on that plant like *D. okala*.

***Drosophila okala* sp.n.**

(Figs 4E; 13D)

Diagnosis. Differs from all other species in the subgroup by having a large anteroapical wing mark, extending nearly to the dm-cu crossvein in the male and about halfway in the female.

Description. ♂. *Head.* Vertex, ocellar triangle, and orbits brown, pollinose, weakly shining; orbits normal, not expanded anteriorly. Front dull dark brown above, pollinose, orange-brown below the ocellar triangle; with scattered semi-erect reclinate setulae below the reclinate seta, about one-third as long as the reclinate. Only the posterior reclinate seta is distinct; a small proclinate setula is also present, but it is slightly shorter and weaker than the other frontal setulae.

Ocellar setae present but moderately small, only about twice as long as the frontal setulae. Eyes normal. Face brown, convex. Antenna brown on second segment, yellow on third; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow. Palp yellow, small, more or less cylindrical, with a single small apical seta present. *Thorax*. Mesonotum brown, pollinose. Pleura entirely brown. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals, without additional short setae. *Legs*. Yellow. Front tibia with an anteroventral row of seven to eight long, dark cilia and an anterodorsal row of eight to nine shorter, paler cilia along the entire length; an additional cilia between them at the base of the anteroventral row; and about four long dorsal cilia near the tibiofemoral joint. A row of about ten short, straight, dorsal setulae are semi-erect and sometimes conspicuous. Front tarsus lacking cilia. *Wings*. Hyaline, with an anteroapical infuscation in cells r_1 and r_{2+3} , extending basally to about the level of the $dm-cu$ crossvein. Costal fringe extending about one-third the distance between R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci pale.

♀. Identical to the male with the following exceptions. *Head*. Frontal setulae shorter than in the male, less than half as long as the anterior reclinate. Orbital setae normal, anterior reclinate only slightly above the proclinate, about one-sixth the distance to the posterior reclinate. Ocellar setae normal, about as long as the posterior reclinate. Palp yellow, slightly flattened, straight on the medial margin and convex on the lateral, with a single moderately strong apical seta. *Legs*. Lacking long cilia. Femora tinged with brown. *Wings*. Anteroapical infuscation extending only about halfway to the $dm-cu$ crossvein. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 5♂$. TL = 1.03 (0.94–1.1) mm; WL = 2.02 (1.9–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.77 (0.69–0.79) mm; HW/FS = 2.1 (2–2.3); HW/TL = 0.7 (0.7–0.8); CI = 3.7 (3.4–4.2); 4V = 1.7 (1.6–1.9); 5X = 1.7 (1–2); 4C = 0.6 (0.6–0.8); M = 0.5 (0.3–0.7). $n = 5♀$. TL = 1.24 (1.19–1.29) mm; WL = 2.48 (2.38–2.55) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.88 (0.85–0.93) mm; HW/FS = 2.2 (2.1–2.2); HW/TL = 0.7 (0.7–0.7); CI = 4 (3.6–4.1); 4V = 1.7 (1.6–1.7); 5X = 1.6 (1.6–1.7); 4C = 0.6 (0.6–0.7); M = 0.5 (0.5–0.5).

Material examined. HAWAII: Holotype ♂ (BPBM 16697), Pauahi, 4500 ft, ex *Clermontia* stem, 3.iv.1972, KYK. Allotype ♀ (BPBM 16697a), as holotype. 1♂ 5♀ paratypes, Kīpuka Kī, ex *Sapindus saponaria* bark, 27.ii.1972, SLM (UHIM). 9♂ 7♀ paratypes, as holotype (UHIM). 1♂ paratype, Laupāhoehoe Forest Reserve, plot N4, reared ex *Cheirodendron trigynum* bark, 5.iii.1999, KH (HVIC). 2♂ paratypes, 'Ōla'a Small Tract transect 1, reared ex *Cheirodendron trigynum* bark, 28.iv.1999, KH (HVIC).

Distribution and ecology. Hawai'i, rare but widespread. Reared from bark of *Cheirodendron trigynum* (Araliaceae),

Clermontia sp. (Campanulaceae), and *Sapindus saponaria* (Sapindaceae).

Etymology. From the Hawaiian 'ōkala, bristling or erect hair, referring to the frontal setulae of the male.

Discussion. This is the only species in the 'nudidrosophila' group to be reared from *Cheirodendron* and *Clermontia*, the two most common *Drosophila* host plants of wet forest. This is probably the species referred to as 'n. sp. marked wings' from collection K14 in Heed (1968), but that specimen could not be found.

Drosophila panina sp.n.

(Fig. 13E)

Diagnosis. The short, prostrate cilia of the male front tibia will distinguish this species from others in the subgroup. It is also the only one with the pleura bicoloured.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits brown; orbits expanded anteriorly with indistinct margins. Front dull dark brown above, pollinose, paler below the ocellar triangle; evenly and relatively densely covered with erect reclinate setulae. A larger socket indicates that a posterior reclinate seta is probably present, but is broken off in all specimens. Ocellar setae absent, but with five or more laterally directed setulae. Eyes normal. Face yellowish brown, darker along the ventral margin, raised into a rounded carina dorsomedially. Antenna brown; arista with long medial rays, the longest nearly twice the length of the terminal fork. One strong oral vibrissa, the other oral setae less than one-third its length. Gena yellow-brown. Palp yellow, flattened, more or less parallel-sided, with a single small subapical seta present, stronger but scarcely longer than the rather dense setulae along the ventrolateral margin. *Thorax*. Mesonotum brown, pollinose. Pleura brown dorsally, katapisternum yellow, tinged with brown along the dorsal margin. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about half the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with an anterior row of 9–11 strong but short, prostrate cilia; two long dorsal cilia are present near the tibiofemoral joint. A row of about 15 short, straight, anterodorsal setulae are erect and sometimes conspicuous. Front tarsus lacking cilia. *Wings*. Hyaline, faintly smoky anteroapically but without a distinct mark. Costal fringe extending about halfway between R_{2+3} and R_{4+5} . *Abdomen*. Solid grey-brown. Cerci yellow.

♀. Unknown.

Measurements. $n = 3♂$. TL = 1.09 (1.09–1.09) mm; WL = 2.03 (2.03–2.05) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.79 (0.78–0.80) mm; HW/FS = 2.1 (2.0–2.2); HW/TL = 0.7 (0.7–0.7); CI = 3.7 (3.4–4.1); 4V = 1.9 (1.8–1.9); 5X = 1.8 (1.8–1.9); 4C = 0.7 (0.6–0.7); M = 0.6 (0.6–0.7).

Material examined. O'AHU: Holotype ♂ (BPBM 16698), Kalua'a Gulch, sweeping *Urera glabra*, 24.ii.2007, KNM. 2♂ paratypes, as holotype (UHIM).

Distribution and ecology. O'ahu; known only from the Wai'anae range. Breeding hosts unknown.

Etymology. From the Hawaiian *panina*, ending or conclusion. Refers to the collection of this species as the manuscript was nearly complete.

Discussion. This species shares some characters with the 'nudidrosophila' subgroup: diffuse margins on the orbits, lacking ocellar setae but with a series of laterally-directed setulae on the ocellar triangle, and possessing a small seta anterior to the anterior dorsoventral. It is placed in the 'okala' subgroup owing to the lack of an enlarged palpal seta and tarsal cilia. It also appears to have a posterior reclinate seta, although it is broken off and only the socket is visible in all available specimens. It may represent an intermediate between the 'nudidrosophila' and 'okala' subgroups, but more specimens are needed to confirm its placement.

'velata' subgroup

The 'velata' subgroup consists of six species, namely *D. velata* from O'ahu and five new species: *D. halapepe* from Hawai'i, *D. pohaka* from Maui and Hawai'i, *D. lauoho* from Maui and Moloka'i, and *D. kauaiensis* and *D. milolii* from Kaua'i. The 'velata' subgroup is distinguished from the 'hirtitibia' subgroup by the lack of long cilia on the basal half of the male foretibia, including the long dorsal cilia at the tibiofemoral joint that are unique to the 'nudidrosophila' group and a few 'picture-wing' species. They tend to be more shiny than other 'nudidrosophila' species, largely because the pollinose microtrichia are erect rather than prostrate and hence do not obscure the cuticle, and they have the head distinctly elongated dorsoventrally compared with most other *Drosophila* species (Fig. 5D). In the latter respect they superficially resemble certain undescribed 'modified mouthparts' species associated with *Pleomele*. The head width/front width (HW/FS) ratio is diagnostic in both males and females: it is 2.5–3 in the 'velata' subgroup, but 1.7–2.4 in other species. In *D. pohaka* and *D. velata*, the ovipositor is shorter than normal and points caudally at rest (Fig. 1B), like those of 'modified mouthparts' species, rather than being curved, parallel-sided, and pointing dorsally as in other members of the 'nudidrosophila' group (Fig. 1A).

This subgroup can be divided into two species complexes. One, with *D. halapepe*, *D. kauaiensis* and *D. lauoho*, consists of species that possess long reclinate setulae on the front (in both sexes; Fig. 5D); ocellar setae arising lateral of the lateral ocelli and nearly parallel; two thin cilia at the apex of the tarsus but no distinct preapical dorsal seta; and mostly gently curved cilia on the tarsus, with more than one row on

the basitarsus. The other, with *D. milolii*, *D. pohaka* and *D. velata*, has the front normal, with the setulae short, prostrate, and proclinate to inclinate; ocellar setae normal, placed medial of the lateral ocelli and diverging; the apex of the tibia with a short, straight, preapical dorsal seta; and two long, hooked cilia on each of the first three tarsal segments, and a nearly straight, prostrate cilia at the apex of the basitarsus. Most of these characters are restricted to the males, but the frontal setulae can be used to separate the females. The two complexes appear to be ecologically different as well. In the former, all have been reared only from *Pleomele* stems; of the latter group only *D. milolii* has been reared, from *Charpentiera*. Rearing flies from *Charpentiera* may well turn up the other two. It is likely that additional collecting will also discover a species from the first group from O'ahu.

Drosophila halapepe sp.n.

(Fig. 14A)

Diagnosis. Differentiated from most species by the chaetotaxy of the front legs, and from the related *D. lauoho* by having the femora yellow rather than brown in the male.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, not conspicuously pollinose; orbits normal, not expanded anteriorly. Front dark brown above, grading to yellow at the frontal suture; weakly shining, lacking pollen; with 8–12 erect, reclinate frontal setulae, about as long as the proclinate seta. Proclinate and posterior reclinate setae normal, anterior reclinate not distinct from the long frontal setulae. Ocellar setae widely separated, placed just lateral of the midline of the lateral ocelli, and parallel; long and relatively thin, similar to frontal setulae. Eyes much higher than long in lateral view. Face brown, raised into a narrow carina dorsomedially. Antenna brown, paler on the medial surface; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, sometimes with a second seta up to two-thirds its length; the other oral setae smaller. Gena pale yellow-brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, with a single moderately strong subapical seta. **Thorax.** Mesonotum shining brown, inconspicuously pollinose. Pleura entirely brown, similar to mesonotum. Acrostichal setulae in six distinct rows. Dorsoventral setae normal but anterior somewhat reduced, about 2.5–3× as long as acrostichals and half as long as the posterior; no distinct additional setae. **Legs.** Yellow. Front tibia with a dorsal and an anterodorsal cilia near the apex; lacking a typical short, straight preapical dorsal seta. Front basitarsus with one or two dorsal cilia near the middle, and three longer dorsal cilia and two long, strong anterior cilia near the apex; a pair of dorsal cilia near the apex of the next two segments. **Wings.** Hyaline with a faint spot at the apex of R₂₊₃ and R₄₊₅, extending about one-third the distance from the wingtip to the dm–cu crossvein. Costal fringe extending

less than one-quarter the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Solid brown, slightly paler apically. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Front with scattered erect, reclinate frontal setulae, shorter than in the male (about half as long as the anterior reclinate seta), as well as inclinate setulae near the frontal suture. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. Ocellar setae normal, about as long as the posterior reclinate. Face raised into a broad, rounded carina medially. Two strong oral vibrissae, the lower about three-quarters as long as the upper. *Thorax*. Strongly shining brown, not noticeably pollinose except on the supraalar area. Acrostichal setulae in six to eight irregular rows. Anterior dorsocentral normal, about three to four times as long as acrostichals. *Legs*. Lacking long cilia. Mid

and hind coxae and femora brown except narrowly at the base and apex, front femur and coxa pale brown; tibiae and tarsi yellow, sometimes tinged with brown. *Wings*. Uniformly hyaline. Costal fringe extending about one-third the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Ovipositor brown, long.

Measurements. $n = 3♂$. TL = 1.03 (0.98–1.09) mm; WL = 2.01 (1.93–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.83 (0.81–0.84) mm; HW/FS = 2.8 (2.6–2.9); HW/TL = 0.8 (0.8–0.8); CI = 3.6 (3.5–3.8); 4V = 1.6 (1.4–1.7); 5X = 1.4 (1.3–1.5); 4C = 0.6 (0.6–0.7); M = 0.4 (0.4–0.4). $n = 3♀$. TL = 1.35 (1.28–1.44) mm; WL = 2.46 (2.36–2.54) mm; TL/WL = 0.5 (0.5–0.6); HW = 1.02 (0.98–1.08) mm; HW/FS = 2.7 (2.6–2.7); HW/TL = 0.8 (0.7–0.8); CI = 3.9 (3.7–4.2); 4V = 1.4 (1.3–1.6); 5X = 1.1 (1.1–1.1); 4C = 0.6 (0.5–0.6); M = 0.4 (0.3–0.4).

Material examined. HAWAII: Holotype ♂ (BPBM 16699), Pu'u Wa'awa'a, 3600 ft, reared ex *Dracaena* (= *Pleomele*) stem, Q6, 1.viii.1971, SLM. Allotype ♀ (BPBM 16699a), as holotype except from 3500 ft. 2♂ paratypes, as holotype (UHIM). 4♀ paratypes, as allotype (UHIM).

Distribution and ecology. Hawaii'i; known only from Pu'u Wa'awa'a. Reared from *Pleomele hawaiiensis* (Agavaceae).

Etymology. From the Hawaiian *halapepe*, the name for plants in the genus *Pleomele*.

Drosophila kauaiensis sp.n.

(Figs 4F; 14B)

Diagnosis. Distinguished from all other members of the *velata* subgroup by having a row of long cilia along the apical half of the male front tibia.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, not conspicuously pollinose; orbits normal, not expanded anteriorly. Front dark brown above, paler below the orbits; weakly shining, lacking pollen; with 8–12 erect, reclinate frontal setulae, about as long as the posterior reclinate seta. Proclinate and posterior reclinate setae normal, anterior reclinate not distinct from the long frontal setulae. Ocellar setae widely separated, placed just lateral of the midline of the lateral ocelli, and parallel; long and relatively thin, similar to frontal setulae. Eyes distinctly higher than long in lateral view, although less so than for some other species in the subgroup. Face brown, raised into a narrow carina dorsomedially. Antenna brown, paler on the medial surface; arista with long medial rays, the longest about two-thirds as long as the terminal fork. No distinct oral vibrissae, only short oral setae present. Gena pale yellow-brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, with a single moderately strong subapical seta. *Thorax*. Mesonotum shining brown, lightly pollinose. Pleura entirely brown,

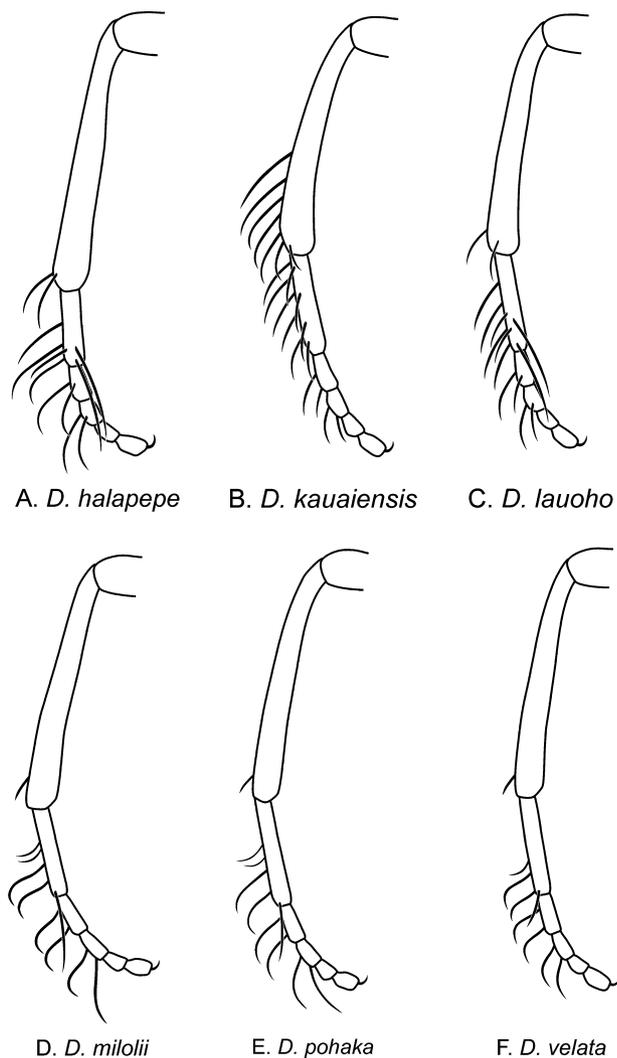


Fig. 14. Right front legs of males of the 'velata' subgroup, anterior view.

similar to mesonotum. Acrostichal setulae in six distinct rows. Dorsocentral setae normal but anterior somewhat reduced, about 2.5–3× as long as acrostichals and half as long as the posterior; no distinct additional setae. *Legs*. Yellow. Front tibia with a row of six to seven anterodorsal cilia along the apical half; no distinct preapical dorsal seta. Front tarsus with a row of long, semi-erect dorsal cilia (five on the basitarsus and two on each of the next two segments); basitarsus with a row of four to five shorter cilia just anterior of it. *Wings*. Uniformly hyaline. Costal fringe unusually variable, extending one-quarter–one-half the distance between the apex of R₂₊₃ and R₄₊₅. *Abdomen*. Solid brown. Cerci pale brown.

♀. Identical to the male with the following exceptions. *Head*. Front with scattered erect, reclinate frontal setulae, shorter than in the male (about half as long as the anterior reclinate seta), as well as inclinate setulae near the frontal suture. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. Ocellar setae normal, placed directly anterior of the lateral ocelli and slightly diverging, about as long as the posterior reclinate. Face raised into a broad, rounded carina medially. *Thorax*. Strongly shining brown, not noticeably pollinose except on the supraalar area. Anterior dorsocentral normal, about three to four times as long as acrostichals. *Legs*. Lacking long cilia. Mid and hind coxae and femora brown except narrowly at the base and apex, tibiae and tarsi yellow. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 5♂$. TL = 0.97 (0.94–1) mm; WL = 1.8 (1.74–1.83) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.81 (0.79–0.83) mm; HW/FS = 2.8 (2.7–3); HW/TL = 0.8 (0.8–0.9); CI = 3.3 (3.1–3.7); 4V = 1.7 (1.5–1.8); 5X = 1.5 (1.4–1.8); 4C = 0.7 (0.6–0.7); M = 0.5 (0.4–0.5). $n = 5♀$. TL = 1.17 (1.1–1.23) mm; WL = 2.17 (2.05–2.29) mm; TL/WL = 0.5 (0.5–0.6); HW = 0.87 (0.75–1.03) mm; HW/FS = 2.6 (2.5–2.8); HW/TL = 0.7 (0.7–0.8); CI = 3.6 (3.4–3.9); 4V = 1.7 (1.6–1.7); 5X = 1.5 (1.3–1.6); 4C = 0.6 (0.6–0.7); M = 0.5 (0.4–0.5).

Material examined. KAUA'I: Holotype ♂ (BPBM 16700), Miloli'i Valley, 2000 ft, reared ex rotten *Dracaena* (= *Pleomele*) stem, 22.viii.1970, SLM. Allotype ♀ (BPBM 16700a), as holotype. 8♂ 8♀ paratypes, as holotype (UHM).

Distribution and ecology. Kaua'i; known only from the type collection. Reared from stems of *Pleomele halapepe* (Agavaceae).

Etymology. From the island of Kaua'i, where the species is found.

***Drosophila lauoho* sp.n.**
(Figs 5D; 14C)

Diagnosis. Similar to *D. halapepe*, but femora brown in both sexes rather than only in the female.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, not conspicuously pollinose; orbits normal, not expanded anteriorly. Front dark brown above, orange to yellow near the frontal suture; weakly shining, lacking pollen; with 8–12 erect, reclinate frontal setulae, slightly shorter than the proclinate seta. Proclinate and posterior reclinate setae normal, anterior reclinate not distinct from the long frontal setulae. Ocellar setae widely separated, placed just lateral of the midline of the lateral ocelli, and parallel; longer than the proclinate seta and relatively thin, similar to frontal setulae. Eyes distinctly higher than long in lateral view. Face brown, raised into a narrow carina dorsomedially. Antenna brown, paler on the medial surface of the second segment; arista with long medial rays, the longest the length of the terminal fork. One strong oral vibrissa, one or two setae below sometimes strong, up to one-half–two-thirds its length; remaining oral setae smaller. Gena pale yellow-brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, with a single moderately strong subapical seta; some of the lateral setulae are relatively long. *Thorax*. Mesonotum shining brown, inconspicuously pollinose. Pleura entirely brown, similar to mesonotum. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals and two-thirds as long as the posterior; with an inconspicuous seta, 2/5 the length of the anterior dorsocentral and just anterior of it. *Legs*. Mid and hind coxae and femora brown except narrowly at the base and apex, front femur and coxa pale brown; tibiae and tarsi yellow, sometimes tinged with brown. Front tibia with a dorsal and an anterodorsal cilia near the apex; lacking a typical short, straight preapical dorsal seta. Front basitarsus with three to four dorsal and one to two anterodorsal cilia in irregular rows, and two long, strong anterior cilia near the apex; a pair of dorsal cilia near the apex of the next two tarsal segments. *Wings*. Uniformly hyaline, sometimes with a faint anteroapical infuscation. Costal fringe extending one-quarter–one-third the distance between the apex of R₂₊₃ and R₄₊₅. *Abdomen*. Solid brown, slightly paler apically. Cerci brown.

♀. Identical to the male with the following exceptions. *Head*. Front with scattered erect, reclinate frontal setulae, shorter than in the male (about half as long as the anterior reclinate seta), as well as inclinate setulae near the frontal suture. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-quarter the distance to the posterior reclinate. Ocellar setae normal, about as long as the posterior reclinate. Face raised into a broad, rounded carina medially. *Thorax*. Strongly shining brown, not noticeably pollinose except on the supraalar area. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. *Abdomen*. Ovipositor brown, long.

Measurements. $n = 5♂$. TL = 1.14 (1.09–1.24) mm; WL = 2.04 (1.95–2.25) mm; TL/WL = 0.6 (0.5–0.6); HW = 0.89 (0.83–0.96) mm; HW/FS = 2.8 (2.6–3); HW/TL = 0.8 (0.8–0.8); CI = 3.6 (3.4–3.8); 4V = 1.5 (1.4–1.6); 5X = 1.4 (1.1–1.5); 4C = 0.6 (0.6–0.7); M = 0.4 (0.3–0.5). $n = 4♀$. TL = 1.38 (1.2–1.48) mm; WL = 2.54 (2.28–2.71) mm; TL/WL = 0.5

(0.5–0.6); HW = 1.02 (0.91–1.09) mm; HW/FS = 2.6 (2.6–2.6); HW/TL = 0.7 (0.7–0.8); CI = 3.7 (3.4–3.9); 4V = 1.4 (1.3–1.6); 5X = 1.2 (1.1–1.4); 4C = 0.6 (0.6–0.7); M = 0.4 (0.3–0.4).

Material examined. MOLOKA'I: Holotype ♂ (BPBM 16701), Kawela Gulch, 2900 ft, 11.ii.1972, ex *Dracaena* (= *Pleomele*) stem, SLM. Allotype ♀ (BPBM 16701a), as holotype. 2♂ 10♀ paratypes, Kawela Gulch, 2900 ft, 11.ii.1972, ex *Dracaena* stem, SLM. 3♂ 2♀ paratypes, Makakupa'ia Gulch, 12.ii.1972, ex *Dracaena* stem, SLM. MAUI: 1♂ paratype, Auwahi, 5–7.viii.1969, KYK. 1♂ paratype, Manawainui Gulch (West Maui), 2800 ft, 12.iv.1971, ex *Dracaena* stem, SLM. 1♂ 1♀ paratypes, 'Ulupalakua Gulch, 2000 ft, 17.iv.1971, ex *Dracaena* stem, SLM. 1♀ paratype, Manawainui Gulch (West Maui), 29.iv.1972, KYK. 3♂ paratypes, Auwahi, 2.vii.1974, KYK. 1♂ 11♀ paratypes, Auwahi, T99, 29.iv.1976, KYK (all at UHIM).

Distribution and ecology. Maui and Moloka'i. Reared from stems of *Pleomele auwahiensis* (Agavaceae).

Etymology. From the Hawaiian *lauoho*, head hair. Named in reference to the elongate setae on the front.

***Drosophila milolii* sp.n.**
(Fig. 14D)

Diagnosis. This species and the following two can be separated by the characters given in the key: *D. milolii* with a large diffuse wing mark; *D. pohaka* with a small, distinct wing mark; and *D. velata* with the wings hyaline and pleura largely yellow.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits shining brown, not conspicuously pollinose; orbits normal, not expanded anteriorly. Front dull brown, pollinose, paler below the ocellar triangle; frontal setulae short, semi-erect, inclinate to proclinate. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate; two weaker setulae are present medial of and slightly over half as long as the anterior reclinate. Ocellar setae normal, about three-quarters as long as the posterior reclinate. Eyes distinctly higher than long in lateral view. Face brown, raised into a narrow carina dorsomedially. Antenna brown, paler on the medial surface; arista with long medial rays, the longest about as long as the terminal fork. One strong oral vibrissa, the other oral setae less than half its length. Gena yellow-brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, broadly rounded at the apex, with a single moderately strong subapical seta. **Thorax.** Mesonotum shining brown, lightly pollinose. Pleura entirely brown, conspicuously pollinose. Acrostichal setulae in six to eight irregular rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an inconspicuous short seta, about one-third the length of anterior dorsocentral and just

anterior of it. **Legs.** Yellow. Front tibia with only a preapical dorsal seta, not ciliated. Front tarsus with a long, strong, prostrate but curved cilia at the apex of the basitarsus; two short, erect cilia near the middle of the basitarsus; and a row of erect, hooked dorsal cilia (two on the apical half of the basitarsus and two each on the next two segments). **Wings.** Anterior half smoky, darker towards the apex, fading to nearly hyaline beyond the dm-cu crossvein; posterior half hyaline. Costal fringe extending about one-third the distance between the apex of R₂₊₃ and R₄₊₅. **Abdomen.** Solid brown. Cerci brown.

♀. Identical to the male with the following exceptions. **Head.** Two strong oral vibrissae, the lower about three-quarters as long as the upper. **Legs.** Lacking long cilia. **Wings.** Uniformly hyaline. Costal fringe extending nearly half the distance between the apex of R₂₊₃ and R₄₊₅. **Abdomen.** Ovipositor hidden in allotype.

Measurements. n = 2♂. TL = 1.11 (1.08–1.14) mm; WL = 2.05 (2.03–2.08) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.89 (0.89–0.9) mm; HW/FS = 2.9 (2.8–3); HW/TL = 0.8 (0.8–0.8); CI = 3.6 (3.5–3.7); 4V = 1.5 (1.5–1.6); 5X = 1.3 (1.2–1.4); 4C = 0.6 (0.6–0.6); M = 0.4 (0.4–0.4). n = 1♀. TL = 1.39 mm; WL = 2.6 mm; TL/WL = 0.5; HW = 1.04 mm; HW/FS = 2.8; HW/TL = 0.7; CI = 3.6; 4V = 1.5; 5X = 1.1; 4C = 0.6; M = 0.3.

Material examined. KAUA'I: Holotype ♂ (BPBM 16702), Miloli'i Valley, 22.viii.1970, reared ex *Charpentiera* stem, SLM. Allotype ♀ (BPBM 16702a), as holotype. 1♂ paratype, as holotype (UHIM).

Distribution and ecology. Kaua'i; known only from the type collection. Reared from stems of *Charpentiera* sp. (Amaranthaceae).

Etymology. Named after the type locality, Miloli'i Valley, Kaua'i.

***Drosophila pohaka* sp.n.**
(Figs 1B; 14E)

Diagnosis. See *D. milolii*.

Description. ♂. **Head.** Vertex, ocellar triangle, and orbits brown, pollinose, weakly shining; orbits normal, not expanded anteriorly. Front dull brown, pollinose, paler below the ocellar triangle; frontal setulae short, semi-erect, inclinate to proclinate. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate; one to two weaker setulae are present medial of and slightly over half as long as the anterior reclinate. Ocellar setae normal, about three-quarters as long as the posterior reclinate. Eyes distinctly higher than long in lateral view, ratio about 1.4. Face brown, raised into a rounded carina dorsomedially. Antenna brown, paler on the medial surface; arista with long medial rays, the

longest about two-thirds as long as the terminal fork. One strong oral vibrissa, sometimes with a second seta up to the same length; the other oral setae smaller. Gena yellow-brown. Palp brown, flattened, straight on the medial margin and convex on the lateral, broadly rounded at the apex, with a single moderately strong subapical seta (sometimes also with an apical seta on one side). *Thorax*. Mesonotum shining dark brown but relatively densely pollinose, appearing 'frosted' in oblique view. Pleura brown, densely pollinose, paler than mesonotum, lower half of katepisternum yellow. Acrostichal setulae in six distinct rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an inconspicuous short seta, about one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow, hind tarsi brown. Front tibia with only a preapical dorsal seta, lacking cilia. Front tarsus with a long, strong, prostrate cilia at the apex of the basitarsus; two short, erect cilia near the middle of the basitarsus; and a row of erect, hooked dorsal cilia (two on the apical half of the basitarsus and two each on the next two segments). *Wings*. A distinct dark spot at the apex of R_{2+3} and R_{4+5} , hardly extending basal of the tip of R_{2+3} . Costal fringe extending about one-third the distance between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Solid brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Thorax*. Pleura almost entirely brown, similar to mesonotum except lower half of katepisternum tinged with yellow. *Legs*. Lacking long cilia. Maui specimens coloured as in the male; mid and hind femora tinged with brown in specimens from Hawai'i (see *Discussion*). *Wings*. Almost entirely hyaline; narrowly and faintly infuscated along the margin between the apex of R_{2+3} and R_{4+5} . Costal fringe extending about halfway between the apex of R_{2+3} and R_{4+5} . *Abdomen*. Ovipositor brown, relatively short, pointing apically at rest.

Measurements. $n = 5♂$. TL = 1.06 (0.96–1.13) mm; WL = 1.93 (1.83–2.10) mm; TL/WL = 0.5 (0.5–0.6); HW = 0.79 (0.71–0.85) mm; HW/FS = 2.9 (2.7–3.0); HW/TL = 0.7 (0.7–0.8); CI = 4.3 (4.0–4.5); 4V = 1.6 (1.6–1.6); 5X = 1.6 (1.3–1.8); 4C = 0.6 (0.5–0.6); M = 0.5 (0.4–0.5). $n = 5♀$. TL = 1.17 (1.06–1.26) mm; WL = 2.16 (2.03–2.28) mm; TL/WL = 0.5 (0.5–0.6); HW = 0.83 (0.80–0.88) mm; HW/FS = 2.6 (2.5–2.7); HW/TL = 0.7 (0.7–0.8); CI = 4.2 (4.1–4.5); 4V = 1.6 (1.6–1.8); 5X = 1.4 (1.3–1.7); 4C = 0.6 (0.6–0.6); M = 0.5 (0.4–0.6).

Material examined. MAUI: Holotype ♂ (BPBM 16703), Kahanaiki Gulch, 2100 ft, in BioLure trap, 7.viii.2007, KNM. Allotype ♀ (BPBM 16703a), as holotype. 3♂ 3♀ paratypes, same data as holotype (UHIM). HAWAII: 3♂ 4♀ paratypes, Stainback Highway, Tree Planting Road Forest, 2950 ft, 2–4.viii.2005, LL (UHIM). 4♂ 1♀, Greenwell Ranch, Pauahi, 27.vi.1974, KYK (UHIM). 20♂ 9♀, Kapu'a (land section), Ho'ōpūloa (quadrant), South Kona, 2650 ft, viii.1977, DEH (UHIM).

Distribution and ecology. Maui and Hawai'i; widespread but known only from a few collections. Breeding hosts unknown.

Etymology. From the Hawaiian *pōhaka*, spot or dot, referring to the small wing infuscation.

Discussion. This species is strongly and rapidly attracted to ammonium acetate and trimethylamine, components of the BioLure tephritid fruit fly lure. It is closely related to *D. velata*, as evidenced by the densely pollinose thorax, partly pale pleura, and short ovipositor. These are also the only two species in the 'nudidrosophila' group to sometimes have two strong setae on the palp. This last character is variable, and some specimens have one seta on one side and two on the other. Females collected with the Kona males have the femora dark brown and all tarsi yellow; Maui females have the leg colouration similar to that of males, whereas those from Stainback Highway are somewhat intermediate, with dark hind tarsi and all femora tinged with brown. The Kona females appear also to belong to the non-*Pleomele* breeding species complex of this subgroup, but it is possible that they are incorrectly associated; they are not included as paratypes.

Drosophila velata Hardy

(Fig. 14F)

Drosophila velata Hardy, 1965: 499.

Diagnosis. See Diagnosis of *D. milolii*.

Description. ♂. *Head*. Vertex, ocellar triangle, and orbits shining brown, pollinose; orbits normal, not expanded anteriorly. Front dull brown, pollinose, paler below the ocellar triangle; frontal setulae short, semi-erect, inclinate to proclinate. Orbital setae normal, anterior reclinate distinctly above the proclinate, about one-third the distance to the posterior reclinate; two weaker setulae are present medial of, and slightly over half as long as, the anterior reclinate. Ocellar setae normal, about three-quarters as long as the posterior reclinate or about equal. Eyes distinctly higher than long in lateral view. Face brown, raised into a narrow carina dorsomedially. Antenna brown, paler on the medial surface; arista with relatively short medial rays, the longest about one-third as long as the terminal fork. One strong oral vibrissa, the other oral setae less than half its length. Gena yellow. Palp brown, flattened, straight on the medial margin and convex on the lateral, broadly rounded at the apex, with a single moderately strong subapical seta (sometimes also with an apical seta on one side). *Thorax*. Mesonotum shining brown but relatively densely pollinose, appearing 'frosted' in oblique view. Pleura mostly yellow, tinged with brown on dorsal half, densely pollinose. Acrostichal setulae in six irregular rows. Dorsocentral setae normal, anterior about four times as long as acrostichals; with an additional short seta, about one-third the length of anterior dorsocentral and just anterior of it. *Legs*. Yellow. Front tibia with only a preapical dorsal seta, not ciliated. Front tarsus with a prostrate anterior cilia at the apex of the basitarsus (shorter and weaker than in the other species); a short,

erect, dorsal cilia near the middle of the basitarsus; and a row of erect, hooked dorsal cilia (two on the apical half of the basitarsus and two each on the next two segments). *Wings*. Hyaline (indistinctly smoky near the apex of R₂₊₃). Costal fringe extending about one-half the distance between the apex of R₂₊₃ and R₄₊₅. *Abdomen*. Solid brown. Cerci yellow.

♀. Identical to the male with the following exceptions. *Head*. Two strong oral vibrissae, the second about two-thirds as long as the first; the other oral setae smaller. Ocellar setae placed medial of the midline of the lateral ocelli but only weakly diverging, strong, about as long as the posterior reclinate. *Thorax*. Lightly pollinose. Pleura brown on dorsal half, katepisternum yellow tinged with brown, pollinose. *Legs*. Lacking long cilia. *Wings*. Uniformly hyaline. *Abdomen*. Ovipositor brown, relatively short, pointing apically at rest.

Measurements. $n = 4♂$. TL = 1.11 (0.95–1.28) mm; WL = 2.09 (1.85–2.33) mm; TL/WL = 0.5 (0.5–0.5); HW = 0.83 (0.73–0.93) mm; HW/FS = 2.6 (2.6–2.8); HW/TL = 0.8 (0.7–0.8); CI = 3.5 (3.3–3.6); 4V = 1.6 (1.6–1.7); 5X = 1.2 (1.1–1.3); 4C = 0.7 (0.7–0.7); M = 0.4 (0.4–0.5). $n = 1♀$. TL = 1.1 mm; WL = 2.06 mm; TL/WL = 0.5; HW = 0.88 mm; HW/FS = 2.8; HW/TL = 0.8; CI = 3.7; 4V = 1.5; 5X = 1.3; 4C = 0.6; M = 0.4.

Material examined. O'AHU: Holotype ♂ (BPBM 6463) Mt Ka'ala, v.1952, MT. Allotype ♀ (BPBM 6463a), as holotype. 5♂ 1♀ paratypes, as holotype. 1♂, Mānoa Valley, 1947, GBM.

Distribution and ecology. O'ahu. Breeding hosts unknown.

Discussion. At least one of the females mentioned by Hardy (1965) from the Mānoa collection is not *D. velata*, and is probably *D. hirtitibia* (the other could not be found).

Acknowledgements

Thanks to Betsy Gagné of the Hawai'i State Division of Forestry and Wildlife, Ed Misaki and Stefanie Loo of The Nature Conservancy of Hawai'i, and Tim Tunison and Rhonda Loh of Hawai'i Volcanoes National Park for their assistance with collecting permits; Dan Rubinoff, Will Haines, and Luc LeBlanc of the University of Hawai'i-Mānoa and Keith Arakaki and Shepherd Myers of the Bishop Museum for their support with examining and borrowing specimens from the UHIM and BPBM collections respectively; David Foote of USGS Kīlauea Field Station and Luc LeBlanc of the University of Hawai'i-Mānoa for allowing us to include their specimens in this revision; and

Steve Montgomery for his tireless collecting, without which many of these species would remain unknown.

References

- Bonacum, J. (2001) *Molecular systematics of the Hawaiian Drosophilidae*. PhD Thesis, Yale University, New Haven.
- Evenhuis, N.L. (1982) Catalog of entomological types in the Bishop Museum. Diptera: Drosophilidae. *Pacific Insects*, **24**, 318–367.
- Gagné, W.C. & Cuddihy, L.W. (1990) Vegetation. *Manual of the Flowering Plants of Hawaii* (ed. by W.L. Wagner, D.R. Herbst and S.H. Somer), pp. 45–114. University of Hawaii Press, Honolulu.
- Grimaldi, D.A. (1990) A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bulletin of the American Museum of Natural History*, **197**, 1–139.
- Grimshaw, P.H. (1901) Diptera. *Fauna Hawaiiensis*, **3**, 1–77.
- Hardy, D.E. (1965) *Insects of Hawaii Vol. 12. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypterae I. Family Drosophilidae*. University of Hawaii Press, Honolulu.
- Hardy, D.E. (1966) Descriptions and notes on Hawaiian Drosophilidae (Diptera). *University of Texas Publications*, **6615**, 195–244.
- Hardy, D.E., Kaneshiro, K.Y., Val, F.C. & O'Grady, P.M. (2001) Review of the *haleakalae* species group of Hawaiian *Drosophila* (Diptera: Drosophilidae). *Bishop Museum Bulletin in Entomology*, **9**, 1–88.
- Heed, W.B. (1968) Ecology of the Hawaiian Drosophilidae. *University of Texas Publications*, **6816**, 387–419.
- Kaneshiro, K.Y. (1976) A revision of the generic concepts in the biosystematics of Hawaiian Drosophilidae. *Proceedings of the Hawaiian Entomological Society*, **22**, 255–278.
- Kaneshiro, K.Y. (1997) R.C.L. Perkins' legacy to evolutionary research on Hawaiian Drosophilidae (Diptera). *Pacific Science*, **51**, 450–461.
- Magnacca, K.N., Foote, D. & O'Grady, P.M. (in press) A review of the endemic Hawaiian Drosophilidae and their host plants. *Zootaxa*, in press.
- Montgomery, S.L. (1975) Comparative breeding site ecology and the adaptive radiation of picture-winged *Drosophila* (Diptera: Drosophilidae) in Hawaii. *Proceedings of the Hawaiian Entomological Society*, **22**, 65–103.
- O'Grady, P.M. (2002) Notes on the nomenclature of the endemic Hawaiian Drosophilidae. *Bishop Museum Occasional Papers*, **69**, 36–40.
- Remsen, J. & O'Grady, P.M. (2002) Phylogeny of Drosophilidae (Diptera), with comments on combined analysis and character support. *Molecular Phylogenetics and Evolution*, **24**, 248–263.
- Thomas, R.H. & Hunt, J.A. (1993) Phylogenetic relationships in *Drosophila*: a conflict between molecular and morphological data. *Molecular Biology and Evolution*, **10**, 362.
- Throckmorton, L.H. (1966) The relationships of the endemic Hawaiian Drosophilidae. *University of Texas Publications*, **6615**, 335–396.

Accepted 22 June 2007

First published online 4 February 2008