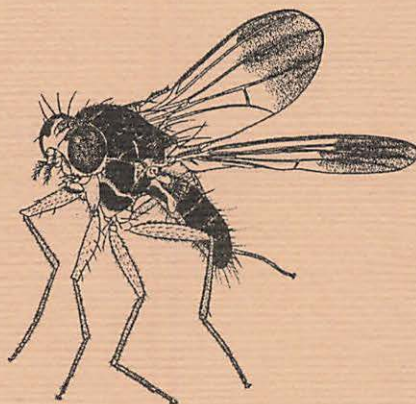


BISHOP MUSEUM BULLETINS IN ENTOMOLOGY

Review of the *haleakalae* Species Group
of Hawaiian *Drosophila*
(Diptera: Drosophilidae)

D. Elmo Hardy, K.Y. Kaneshiro, F.C. Val & P.M. O'Grady



Bishop Museum Bulletin in Entomology 9

Bishop Museum Press
Honolulu

Bishop Museum Press has been publishing scholarly books on the natural and cultural history of Hawai'i and the Pacific since 1892. The *Bernice P. Bishop Museum Bulletin* series (ISSN 0005-9439) was begun in 1922 as a series of monographs presenting the results of research in many scientific fields throughout the Pacific. In 1987, the *Bulletin* series was superseded by the Museum's four current monographic series, issued irregularly:

<i>Bishop Museum Bulletins in Anthropology</i>	(ISSN 0893-3111)
<i>Bishop Museum Bulletins in Botany</i>	(ISSN 0893-3138)
<i>Bishop Museum Bulletins in Entomology</i>	(ISSN 0893-3146)
<i>Bishop Museum Bulletins in Zoology</i>	(ISSN 0893-312X)

Bishop Museum Press also published *Bishop Museum Occasional Papers* (ISSN 0893-1348), a series of short papers describing original research in the natural and cultural sciences.

To subscribe to any of the above series or to purchase individual publications, please write to: Bishop Museum Press, 1525 Bernice Street, Honolulu, Hawai'i 96817-2704, USA. Phone: (808) 848-4135. Fax: (808) 841-8968.
E-mail: press@bishopmuseum.org

Institutional libraries interested in exchanging publications may write to: Library Exchanges, Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i 96817-2704, USA. Phone: (808) 848-4148. Fax: (808) 841-8968.
E-mail: libex@bishopmuseum.org

**Review of the *Drosophila haleakalae*
Species Group of Hawai‘i
(Diptera: Drosophilidae)**

D. Elmo Hardy, K.Y. Kaneshiro, F.C. Val & P.M. O’Grady

Bishop Museum Bulletin in Entomology 9



**Bishop Museum Press
Honolulu, 2001**

Cover illustration: *Drosophila longiperda* Kambysellis, drawn by F.C. Val.

Published by
Bishop Museum Press
1525 Bernice Street
Honolulu, Hawai'i 96817-2704, USA

Copyright ©2001 Bishop Museum
All Rights Reserved
Printed in the United States of America

ISBN 1-58178014-1
ISSN 0893-3146

TABLE OF CONTENTS

Acknowledgments	vii
Abstract	viii
Introduction	1
Materials and Methods	5
General Organization and Keys	5
Species Descriptions	5
Systematics	8
Key to subgroups and species complexes in the <i>Drosophila haleakalae</i> species group	8
I. The <i>anthrax</i> subgroup	8
II. The <i>cilifemorata</i> subgroup	18
IIa. The <i>cilifemorata</i> complex	20
IIa1. The <i>venusta</i> cluster	23
IIa2. The <i>cilifemorata</i> cluster	28
IIb. The <i>denotata</i> complex	29
IIc. The <i>insignita</i> complex	31
III. The <i>haleakalae</i> subgroup	46
IIIa. The <i>atrifacies</i> complex	47
IIIb. The <i>brunneicrus</i> complex	48
IIIc. The <i>fungiperda</i> complex	51
IIId. The <i>haleakalae</i> complex	55
IV. The <i>luteola</i> subgroup	58
IVa. The <i>fuscoapex</i> complex	58
IVb. The <i>luteola</i> complex	60
V. The <i>polita</i> subgroup	61
VI. The <i>scitula</i> subgroup	77
Literature Cited	86
Index	88

ACKNOWLEDGMENTS

The late Dr. Herman T. Spieth, Univ. of California at Davis, was especially responsible for this study. He devised the field collecting techniques that made it possible to do an adequate job of sampling this important group (Kaneshiro *et al.*, 1977). He spent a great deal of time working with these flies in the field and the laboratory; perfecting the mushroom bait collecting technique, gathering ecological data, and attempting to find ways to introduce these flies to laboratory culture. We are much appreciative of the close association he had with our project over the years, his intellectual input and scientific curiosity had a stimulating effect on all aspects of our evolutionary studies and his research contributions have been a most important building block in our gaining an understanding the processes of evolution in this remarkable fauna.

We also thank Rob DeSalle (ANMH) for his support of this project and Angela Klaus of the Interdepartmental Laboratories Facility at the American Museum of Natural History for assistance and advice with the SEM equipment.

ABSTRACT

This study is a review of the *haleakalae* species group. This clade, as currently defined, contains a total of 51 species, 18 of which are described here as new: *Drosophila atrifacies*, *D. brunneicrus*, *D. chicao*, *D. clara*, *D. cryptica*, *D. curtitarsis*, *D. dives*, *D. fascigera*, *D. fulgida*, *D. hemianthrax*, *D. lissodora*, *D. multiciliata*, *D. ochropleura*, *D. paraanthrax*, *D. quinquerosa*, *D. setositibia*, *D. subopaca*, and *D. tanytarsis*. Two species are proposed as new synonyms: *Drosophila reburra* is a junior synonym of *D. nigra*; *D. transfuga* is a junior synonym of *D. polita*. We propose 6 subgroups within the *haleakalae* species group: *anthrax*, *cilifemorata*, *haleakalae*, *luteola*, *polita* and *scitula*. Some subgroups, such as the *cilifemorata*, *haleakalae*, and *luteola*, are further divided into complexes and clusters. The relationships among the 6 subgroups, as well as within the *anthrax* and *polita* subgroups, remain unclear.

INTRODUCTION

This study deals with the *haleakalae* species group, a clade of *Drosophila* endemic to the Hawaiian Islands (Table 1). This group has previously been referred to as either the “white (or light) tip scutellum” (Spieth, 1966; Throckmorton, 1966; Heed, 1968) or the “rimmed labellum” species groups, based on morphological characters. However, several taxa in this clade lack either the white apical tip on the scutellum (*D. nigropolita* and *D. setositibia*), or the rimmed labellum (*D. fungiperda*, *D. nigella*, and *D. nigra*), although they are clearly members of this clade based on other morphological, genetic, and behavioral criteria. Furthermore, some members of the *picture wing* (*D. primaeva* & *D. attigua*), *modified mouthpart* (*D. semifuscata*), and *rustica* (“*D. curiosa*”, *D. praesutilis*, & *D. rustica*) species groups possess a sclerotized black rim on the margin of the labellum (O’Grady *et al.*, 2001a,b). Several authors have also referred to this clade as the *fungus feeder* group (e.g. Thomas & Hunt, 1993; Kambysellis & Craddock, 1997) based on the ecological niche that its members exploit. Although larvae of several species are fungivores and the adults can often be found feeding on or ovipositing in fleshy fungi (Table 2), the exact larval substrates of the majority of species in this group are still unknown.

Hardy (1965) first referred to this group as the “*haleakalae* complex” of species, defined as species “characterized by having the body shining black in ground color, the upper 2/3 of the front black and the lower third rufous, and the scutellum black with a yellow spot at the tip”. We are designating the species listed in Table 1 as members of the *haleakalae* species group based on Hardy’s (1965) definition and one of the oldest described members of this clade, *D. haleakalae* (Grimshaw, 1901) because of priority. Although this goes against the long standing tradition in Hawaiian *Drosophila* systematics of naming species groups after their major diagnostic character, we feel this is most appropriate, especially given the lack of diagnostic morphological characters and uncertainty of ecological niches in the majority of species in this group.

The *Drosophila haleakalae* species group is characterized by having slender, shiny black bodies and low body profile, a “gestalt” that is readily recognized in the field without the aid of magnification. Several synapomorphies that define this clade have been discussed previously, including: male genitalia lacking anal sclerite (Throckmorton, 1966); females with weakly sclerotized, non-telescoped, non-pigmented and non-functional spermathecae; sperm that are retained by females are found in the seminal receptacle (Throckmorton, 1966; Kambysellis & Craddock, 1991); short-filamented eggs (Throckmorton, 1966; Kambysellis, 1993) that are only partially inserted into their substrate (Kambysellis, 1993); and a relatively simple male mating behavior characterized by an apparent lack of preliminary courtship (Spieth, 1966).

The results of Throckmorton’s (1966) morphological studies (Fig. 1a), as well as recent molecular analyses (Kambysellis *et al.*, 1995; Baker & DeSalle, 1997; Remsen & DeSalle, 1998; Fig. 1b), suggested that the genus *Scaptomyza*, not other members of the genus *Drosophila*, is the sister clade of the Hawaiian *Drosophila*. This suggests that the genus *Drosophila*, as currently defined, may not be monophyletic. Based on this phylogeny, Throckmorton (1966) proposed that the family Drosophilidae have either colonized the Hawaiian Islands once or twice. In the single-colonization scenario, one ancestor gave rise to both the *Scaptomyza* and *Drosophila* lineages. These groups then diversified in Hawai’i. The fact that the genus *Scaptomyza* is not endemic to Hawai’i (i.e., some species are found elsewhere) suggests that (a) some *Scaptomyza* “escaped” from Hawai’i and diversified in other places, or (b) the original colonist was “*Scaptomyza*-like” and that genus had already begun to diversify at the time Hawai’i was colonized. The two-colonization scenario requires that the ancestors of the Hawaiian *Drosophila* and Hawaiian *Scaptomyza* were distinct sister taxa at the time they colonized the Hawaiian Archipelago. Grimaldi (1990) presented a very different view of

Table 1. Taxonomic relationships within the *Drosophila haleakalae* species group

Subgroup	Complex	Cluster	Species
I. <i>anthrax</i>			<i>anthrax</i> <i>demipolita</i> <i>fascigera</i> <i>fuscifrons</i> <i>hemianthrax</i> <i>melanoloma</i> <i>multiciliata</i> <i>nigropolita</i> <i>retrusa</i> <i>seorsa</i>
II. <i>ciliifemorata</i>	a. <i>ciliifemorata</i>	1. <i>venusta</i>	<i>inciliata</i> <i>longiperda</i> <i>tanytarsis</i> <i>venusta</i>
		2. <i>ciliifemorata</i>	<i>ciliifemorata</i> <i>dolichotarsis</i> <i>flaviceps</i> <i>iki</i> <i>nigra</i> <i>stenoptera</i> <i>swezeyi</i>
	b. <i>denotata</i>		<i>denotata</i> <i>sabroskyi</i>
	c. <i>insignita</i>		<i>chicae</i> <i>curtitarsis</i> <i>insignita</i>
III. <i>haleakalae</i>	a. <i>atrifacies</i>		<i>atrifacies</i>
	b. <i>brunneicrus</i>		<i>brunneicrus</i> <i>ochropleura</i>
	c. <i>fungiperda</i>		<i>fungiperda</i> <i>nigella</i>
	d. <i>haleakalae</i>		<i>clara</i> <i>cryptica</i> <i>haleakalae</i> <i>macrochaetae</i>
IV. <i>luteola</i>	a. <i>fuscoapex</i>		<i>fuscoapex</i> <i>tamashiroi</i>
	b. <i>luteola</i>		<i>luteola</i> <i>quinquaramosa</i>
V. <i>polita</i>			<i>bipolita</i> <i>canipolita</i> <i>dives</i> <i>flavistemum</i> <i>illusiopolita</i> <i>lissodora</i> <i>mecocnemia</i> <i>paraanthrax</i> <i>polita</i> <i>pretiosa</i>
VI. <i>scitula</i>			<i>fulgida</i> <i>melanosoma</i> <i>scitula</i> <i>setositibia</i> <i>subopaca</i>

Table 2. Rearing records from the *Drosophila haleakalae* species group

Species (subgroup)	Distribution	Substrate	Reference
<i>D. bipolita</i> (<i>polita</i>)	Hawai'i, Maui, Moloka'i, O'ahu	"gill fungi"	Heed (1968)
<i>D. chicae</i> (<i>ciliifemorata</i>)	Hawai'i	"fungi"	new record
<i>D. curtisarsis</i> (<i>ciliifemorata</i>)	Kaua'i	"mushrooms"	new record
<i>D. demipolita</i> (<i>polita</i>)	Hawai'i	"gill fungi"	Heed (1968)
<i>D. denotata</i> (<i>ciliifemorata</i>)	O'ahu	"fleshy fungi"	Hardy (1965)
<i>D. fungiperda</i> (<i>haleakalae</i>)	Hawai'i	<i>Polyporus sulphrea</i>	Spieth (1967)
<i>D. iki</i> (<i>ciliifemorata</i>)	Hawai'i, Maui	"gill fungi"	Heed (1968)
<i>D. illusiopolita</i> (<i>polita</i>)	Hawai'i	"gill fungi"	Heed (1968)
<i>D. luteola</i> (<i>luteola</i>)	O'ahu	"gill fungi"	Heed (1968)
<i>D. macrochaetae</i> (<i>haleakalae</i>)	Maui	"soft-shelf fungus"	Hardy (1965)
<i>D. melanoloma</i> (<i>anthrax</i>)	Lāna'i, Maui, Moloka'i	<i>Agaricus</i> sp.	Heed (1968)
<i>D. nigella</i> (<i>haleakalae</i>)	Maui	<i>Polyporus sulphrea</i>	Heed (1968)
<i>D. ochroleura</i> (<i>haleakalae</i>)	Hawai'i	"gill fungi"	new record
<i>D. polita</i> (<i>polita</i>)	Hawai'i, Lāna'i, Maui, Moloka'i	"gill fungi"	new record

Hawaiian drosophilid evolution in his morphological revision of the family Drosophilidae. Figure 1c indicates that *Scaptomyza* and Hawaiian *Drosophila* are not sister taxa. Therefore, if Grimaldi's (1990) hypotheses are correct, at least 2 colonizations of Hawai'i are required to explain the current distribution of species.

Throckmorton's (1966) phylogeny, as well as recent molecular studies (Kambysellis *et al.*, 1995; Baker & DeSalle, 1997), indicated that the *haleakalae* species group is the basal lineage within the Hawaiian *Drosophila* (Figs. 1a,b). Several characteristics of the *haleakalae* species group, including the short respiratory filaments on the eggs (Kambysellis, 1993) and the simple courtship behavior (Spieth, 1966), are reminiscent of the genus *Scaptomyza* and support this assertion. However, even though one *haleakalae* group species (*D. bipolita*) is basal in Grimaldi's (1990) phylogeny, none of the traditionally recognized Hawaiian species groups are monophyletic in his analysis (Fig. 1c). This indicates that the morphological characters used by Grimaldi (1990) to infer relationships within Drosophilidae are of little use in determining which species group is basal within the Hawaiian *Drosophila*.

Relationships within the *haleakalae* species group have traditionally been very difficult to define. Part of this difficulty stems from the fact that there is little character variation in this group; many species are small and dark with subhyaline wings and have no other defining characters. When characters do vary, they are either autapomorphic or highly variable and, therefore, not useful for cladistic analysis. However, there are some characters that are useful in defining subgroups within the *haleakalae* species group. The master key (see page 8) is intended to separate the species examined in this study into subgroups and complexes and is intended to be used for species that have either a rimmed labellum or lightened apical spot on the scutellum. Additional keys, included with the descriptions of each species subgroup or complex, can be used to further sort species.

We have proposed several lineages (species subgroups, complexes or clusters) within the *haleakalae* group (Table 1). These are based on a variety of internal and external morphological characters and will be further tested and refined in combined morphological and molecular phylogenetic analyses (O'Grady, in prep.).

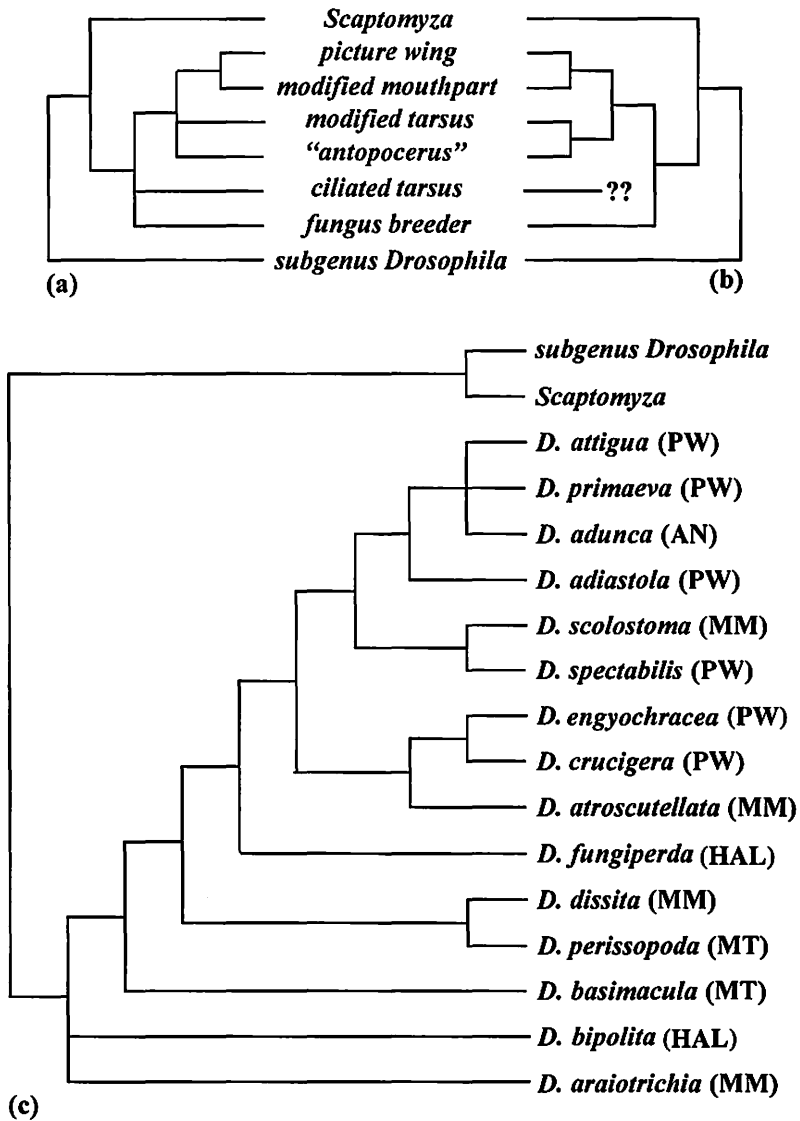


Figure 1. Proposed phylogenetic relationships within the *Drosophila haleakalae* species group. a. Morphological phylogeny of Throckmorton (1966); b. Composite molecular phylogeny based on the molecular characters of Kamysellis *et al.* (1995) and Baker & DeSalle (1997); c. Morphological phylogeny of Grimaldi (1990), redrawn after Baker & DeSalle (1997). Abbreviations: AN = "antopocerus" species group, HAL = *haleakalae* species group, MM = modified mouthpart species group, MT = modified tarsus species group, PW = picture wing species group.

MATERIALS AND METHODS

General Organization and Keys

This paper divides the *haleakalae* group into species subgroups, complexes, and clusters (Table 1). Descriptions of each species are found under the heading of the species complex to which it belongs. The first key serves as a “master key” to divide the *haleakalae* group into species subgroups and species complexes. The numbers following each species complex name refer to the couplet in that species complex section. This key is numbered consecutively throughout the paper.

Species Descriptions

Previously described species included in this revision list the original reference as well as any subsequent treatments. In many cases we have added characters to these descriptions, usually those that describe patterns of setation on the posterolateral region of the mesonotum or characters of the ovipositor.

DESCRIPTIONS: The general morphological terminology follows McAlpine (1981). For example, sternopleural setae are referred to as katepisternal setae in order to maintain clear homology statements between Drosophilidae and other dipteran groups. Those morphological terms specific to the family Drosophilidae follow Grimaldi (1987, 1990) and readers should consult those publications for excellent reviews of drosophilid morphology. Terminology specific to this publication is discussed below.

All *haleakalae* species possess between 2 and 18 well developed supernumerary setae in posterolateral region of the mesonotum, defined as the area bounded by the supra-alar, inner and outer postalar, and dorsocentral setae. These setae are a good synapomorphy for this clade as no other Hawaiian *Drosophila* studied to date possess such chaetotaxy. Some clades, like the *venusta* cluster, have many heavy setae in this area, making it impossible to differentiate the inner postalar from the supernumerary setae. For this reason we have labeled only the outer postalar, supra-alar, and posterior dorsocentral in the figures. The inner postalar is given a number, as are all the supernumerary setae. These numbers are not intended to signify homology; they are merely present for purposes of clarity. We have added this character to the original descriptions when we were able to examine these taxa. Although most species display identical patterns of setation between males and females, some taxa display sexual dimorphism in this character [*e.g.*, *D. denotata* (Figs. 51, 52) and *D. bipolita* (Figs. 110, 111)].

Patterns of setae and cilia found on the forelegs of some male *haleakalae* species are described as being either complete, extending the full length of the leg segment, or incomplete, extending only a portion of the leg segment. When incomplete, the fraction of the leg segment that the setae or cilia extend is stated. Wings are described using the terminology employed in Diptera (McAlpine, 1981) and applied to Drosophilidae by Wheeler (1981) and Stark *et al.* (1999).

More detailed characteristics of the ovipositor are also included here, both for species where the female was previously known and for those where this is the first description of the female. Drawings were made from prepared slide mounts. The presence of ovisensilla on the dorsolateral and ventral margins of the ovipositor are measured based on how far they extend down the ovipositor plate. The inner subapical ovisensilla refers to the long, setae-like ovisensilla present in the subapical position on the inner margin of the ovipositor plates. The length of these ovisensilla is measured as a percentage of the maximum width of the ovipositor.

FIGURE ABBREVIATIONS: The following abbreviations are used in the figures:

acrs - acrostichal seta	pvc - posteroventral cilia
as - anterior scutellar seta	pvs - posteroventral seta
avc - anteroventral cilia	sas - supra-alar cilia
dcs - dorsocentral seta	sc - scutellum
dr - dorsal ray of arista	vc - ventral cilia
oc - ocellus	vmc - ventral-medial cilia
ocs - ocellar seta	vr - ventral ray of arista
pas - post alar seta	wb - wing base
pocs - postocellar seta	

MEASUREMENTS: Several morphological structures from the holotype, allotype, and a maximum of 10 paratypes of each sex were measured (Sturtevant, 1942; Grimaldi, 1987). Abbreviations used in the measurements section include: (1) thorax length (TL), distance from anterior notal margin to the posterior apex of the scutellum, (2) wing length (WL), maximum distance from the humeral crossvein to the apex of the wing, (3) ratio of thorax length to wing length (TL/WL), (4) head width (HW), greatest distance between apical margins of the eyes, (5) ratio of head width to thorax length (HW/TL), (6) costal index (CI), length of costa from subcostal break to R_{2+3} / length of costa from R_{2+3} to R_{4+5} , (7) fourth vein index (4V), length of M_1 from crossvein dm-cu to apex/ length of M_1 from crossvein r-m to crossvein dm-cu, (8) length of CuA1 from crossvein dm-cu to apex/ length of crossvein dm-cu (5X), (9) length of costa from R_{2+3} to R_{4+5} / length of M_1 from crossvein r-m to crossvein dm-cu (4C), and (10) length of CuA1 from crossvein dm-cu to apex/ length of M_1 from crossvein r-m to crossvein dm-cu (M). Holotype and allotype measures, when obtained, appear individually in their respective sections and are also included in the means and ranges. The measurements section of each description includes mean value of each measurement for each gender. Numbers in parentheses are the range of values observed for each measurement.

MATERIAL: The following codens indicate the location of specimens examined in this study (after Samuelson *et al.*, 2001):

AMNH	= American Museum of Natural History, Pinned Collection, New York
AMNH-MC	= American Museum of Natural History, Monell Collection for Microbiology and Molecular Biology, New York
BPBM	= Bernice P. Bishop Museum, Honolulu
BMNH	= The Natural History Museum, London
UHM	= University of Hawai'i at Mānoa Entomology Collection, Honolulu
USNM	= National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Accession numbers accompany the Bishop Museum material. Further information on previously described species can be found in Evenhuis (1982). With the exception of *D. flaviceps*, which is designated *nomen oblitum*, all species in this study have been examined by one or more of the authors. Homotypes that have been designated are noted. The depository of all type material is stated in the "Types" section of each description. Holotypes of all new species described in this study are deposited in BPBM. Material present in the AMNH-MC collection is assigned a DNA accession number.

Some 50 collectors have contributed to the specimens covered by this manuscript. Collector abbreviations used in this report are as follows: ATO = Alan T. Ohta; CPH = C.P. Hoyt; CWS = Curtis W. Sabrosky; DEH = D. Elmo Hardy; DF = D. Futch; DG = D. Gubler; DHH = D.H. Habeck; DJP = David J. Preston; DS = D. Sargent; ECZ = E.C. Zimmerman; ED = E. Dresner; EHB = Edwin H. Bryan; EJF = E.J. Ford; EMC = Elysse M. Craddock; FCV = Francisca C. do Val; FEC = F.E. Clayton; FGH = Francis G. Howarth; FXW = Francis X. Williams; GBM = Gordon B. Mainland;

HLC = Hampton L. Carson; HT = H. Toba; HTS = Herman T. Spieth; Iw = Iwamoto; JAT = Joaquin A. Tenorio; JKF = Jack K. Fujii; JO = John Obata; JPM = John P. Murphy; JBS = Julian B. Stark; JWB = John W. Beardsley, Jr; KTK = Kevin T. Kaneshiro; KYK = Kenneth Y. Kaneshiro; LHT = Lynn H. Throckmorton; LW = L. Wheeler; MDD = Mercedes D. Delfinado; MPK = Michael P. Kambyzellis; MRW = Marshall R. Wheeler; MSA = Marian S. Adachi; MT = M. Tamashiro; NLHK = Noel L.H. Krauss; OB = O. Bryant; OHS = Otto H. Swezey; PHT = Philip H. Timberlake; PMO = Patrick M. O'Grady; RMB = R.M. Brown; RM = Ryoji Namba; SLM = Steven L. Montgomery; WBH = William B. Heed; WCM = Wallace C. Mitchell; WI = W. Ibara; WPM = William P. Mull; YK = Yoshio Kondo. Some specimens also have collection numbers associated with them: C-H refers to H.L. Carson's Hawaiian collections; OG refers to P.M. O'Grady collections. Full records for a given collection are available upon request.

MOLECULAR BIOLOGY: This section has been added to review the molecular data gathered for a given species at the time of this revision. Information on loci examined, Genbank Accession numbers for sequences generated, and the appropriate references are included here. Species undescribed at the time of some molecular publications are included here to serve as a link between those sequences and the name of the species. It is also intended to give information about DNA or frozen tissue that may be present for a given taxon. This material, like pinned specimens in a traditional museum collection, is accessible to the scientific community for research purposes.

SYSTEMATICS

KEY TO SUBGROUPS AND SPECIES COMPLEXES IN THE
DROSOPHILA HALEAKALAE SPECIES GROUP

- A. Wings of males with conspicuous dark brown maculations; markings may be (a) extensive, covering most of wing, (b) discretely restricted to apex of wing, (c) or distinct infuscations along long veins *cilifemorata* subgroup, **B** (p. 23)
 - . Wings of both sexes entirely hyaline, subhyaline, or when infuscated, usually lightly so; marks always diffuse, never prominently defined. Species small to medium in size **D**
- B. Maculations extensive, not restricted to apical portion of wing. Crossvein r-m infuscated *cilifemorata* complex, **10** (p. 25)
 - . Wing markings restricted to apical portion of wing. Crossvein r-m not distinctly infuscated **C**
- C. Markings on wings restricted to areas surrounding apical portions of veins R_{2+3} , R_{4+5} , and M_1 ... (O'ahu) *denotata* complex, **19** (p. 40)
 - . Markings restricted to apex of wing in males only, wing of female entirely hyaline ... (Hawai'i, Kaua'i, O'ahu) *insignita* complex, **20** (p. 41)
- D. Front basitarsus of males very short; less than 1/5 length of tibia ... (Kaua'i) *scitula* subgroup, **40** (p. 77)
 - . Front basitarsus of males greater than 1/5 length of femur **E**
- E. Inner margin of arista with numerous (6 or more) densely placed setae ... (Hawai'i, Maui, Moloka'i) *haleakalae* subgroup, **22** (p. 46)
 - . Inner margin of arista sparsely setose **F**
- F. Pleura unicolorous **G**
 - . Pleura dark above, lighter below ... (all islands) *polita* subgroup, **31** (p. 61)
- G. Pleura entirely yellow ... (O'ahu, Maui) *luteola* subgroup, **30** (p. 58)
 - . Pleura entirely dark brown to black ... (all islands) *anthrax* subgroup, **1** (p. 8)

I. The *anthrax* subgroup

The *anthrax* subgroup contains all those species with relatively small body size, dark bodies, and wings that are either subhyaline or lightly infuscated. The pleura of *anthrax* subgroup species are entirely dark brown to black. The monophyly of and relationships among these species are not well resolved. As such, no species complexes or clusters within this subgroup are proposed at this time.

Species of the *anthrax* subgroup are found on all the major high islands except O'ahu. Maui Nui is home to 6 species in this subgroup (Figs. 2a,c,e,f), 3 are from the Big Island (Fig. 2d), and a single species, *D. fascigera*, is found on Kaua'i (Fig. 2b). *Drosophila melanoloma*, which is found on all the islands of the Maui Nui cluster (Fig. 2e), has the widest distribution. It is unclear whether *D. fascigera* is basal within this subgroup and the extant species have dispersed from Kaua'i, the oldest high island, or if members of the *anthrax* subgroup evolved on some more recent island and have recently back-migrated to Kaua'i.

The ecology of this group is largely unknown. Heed (1968) reported rearing *D. melanoloma* from *Agaricus* sp. (Table 2), but the breeding substrates of the other nine species in this subgroup remain to be discovered.

KEY TO SPECIES IN THE *DROSOPHILA ANTHRAX* SUBGROUP

1. Scutellum unicolorous black, lacking lightened apical area. Costal fringe short, extending only 1/4 distance between veins R_{2+3} and R_{4+5} ... (Moloka'i) *nigropolita* Hardy
- . Scutellum with lightened area at apex. Otherwise not as above 2
2. Tibia and tarsi lacking conspicuous long cilia 3
- . Tibia, tarsi, or both ciliated 8
3. Males with dense cluster of black cilia on venter of front femur (Fig. 13) ... (Kaua'i) *fascigera* Hardy & Kaneshiro, n. sp.
- . Venter of forefemur lacking cilia 4
4. Frons of males entirely dark brown to black. Frons of female narrowly yellow ... (Maui) *fuscifrons* Hardy
- . Frons dark brown to black above, yellow below 5
5. Wings faintly fumose with very pale brown infuscations in upper apical portion and over r-m crossvein ... (Moloka'i) *melanoloma* Hardy
- . Wings lightly infuscated with brown but not as above..... 6
6. Palpi with 2–3 long black setae at apex and a series of long yellow setae on posterior margin (Fig. 4) ... (Moloka'i) *retrusa* Hardy
- . Palpi with single long apical seta 7
7. Thorax polished black, pleura tinged with rufous ... (Hawai'i) *demipolita* Hardy
- . Entire thorax dusted with gray ... (Maui) *seorsa* Hardy
8. Foretibia of males with ca. 5 posteroventral cilia, front basitarsus lacking cilia ... (Moloka'i) *anthrax* Hardy
- . Foretibia and foretarsi of males both ciliated 9
9. Forelegs heavily ciliated; front tibia with row of ventral and posteroventral cilia extending over apical 2/5, forebasitarsus with ca. 5 long black posteroventral cilia and 4 long anteroventral cilia extending full length (Fig. 15) ... (Hawai'i) *multiciliata* Hardy & Kaneshiro, n. sp.
- . Front tibia with 6 posteroventral cilia, which extend over apical 2/3–3/4 of segment; no ventral cilia present. Front basitarsus with 4 moderately long posteroventral cilia extending full length; no anteroventral cilia present (Fig. 14) ... (Hawai'i) *hemianthrax* Hardy & Kaneshiro, n. sp.

Drosophila anthrax Hardy

Figs. 2a, 5

Drosophila anthrax Hardy, 1965: 148.

DIAGNOSIS: *Drosophila anthrax* can be differentiated from closely related species in this clade by having the antennae and palpi brown, the face black, the front femora yellow and tinged faintly with brown, the mid and hind femora brown and tinged with rufous, and by lacking cilia on the front basitarsus.

DESCRIPTION: ♂ (♀ unknown). In addition to the description provided by Hardy (1965), we note several characters important to the taxonomic placement of this species. *Thorax*. About 10 setae, each ca. 1/4 length of postalar, present in posterolateral region of mesonotum (Fig. 5). *Legs*. Front basitarsus not ciliated, ca. 2/3 as long as tibia.

MEASUREMENTS: N = 2♂. TL = 1.4 mm (1.4–1.5); WL = 2.6 mm; TL/WL = 0.6 (0.5–0.6); HW = 1.1 mm (1.0–1.1); HW/TL = 0.7; CI = 4.4 (4.1–4.6); 4V = 1.3 (1.2–1.3); 5X = 1.5 (1.3–1.7); 4C = 0.5 (0.4–0.5); M = 0.4.

TYPES: MOLOKA'I: Holotype ♂ (BPBM 6,293), Manawainui Valley, vii.1952, DEH. TL = 1.5 mm; WL = 2.6 mm; TL/WL = 0.6; HW = 1.1 mm; HW/TL = 0.7; CI = 4.1; 4V = 1.2; 5X = 1.3; 4C = 0.5; M = 0.4. One paratype male, topotypic with the holotype, UHM.

DISTRIBUTION: Known only from the island of Moloka'i (Fig. 2a).

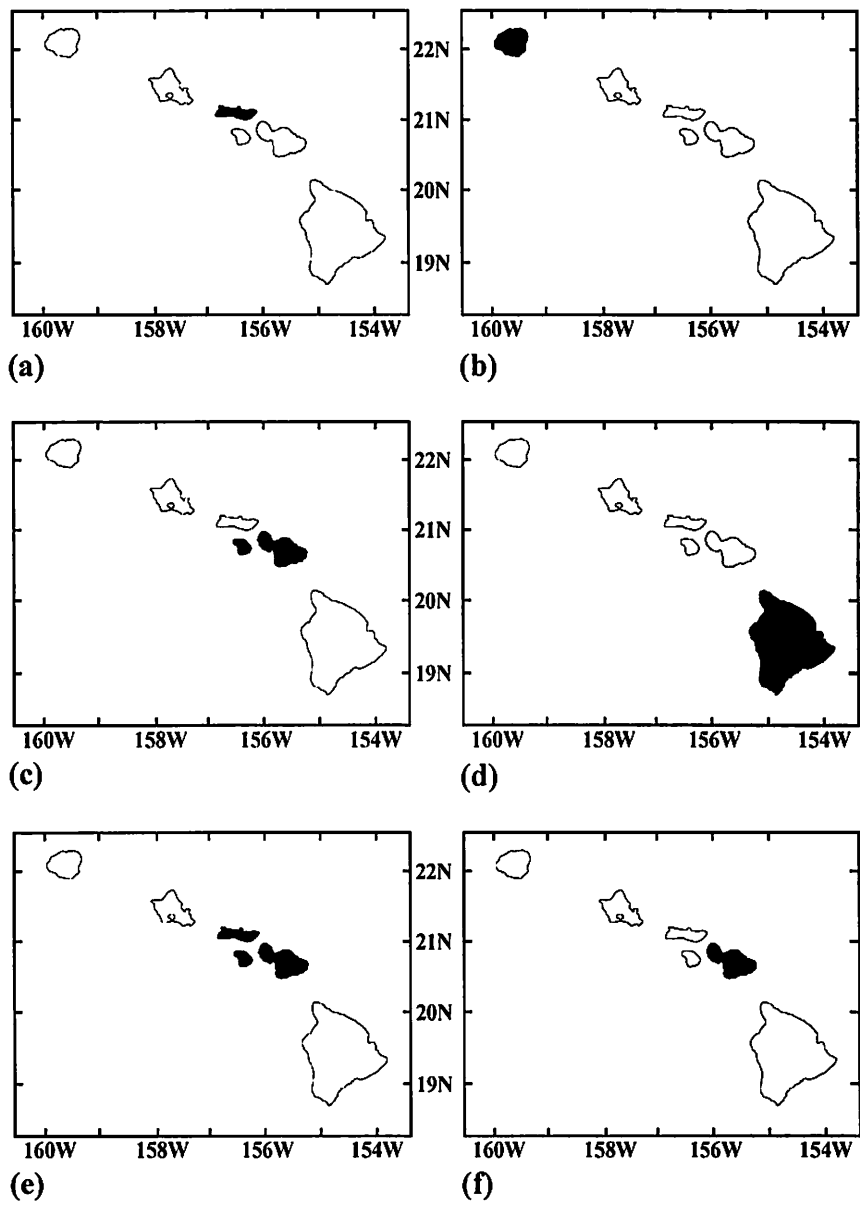


Figure 2. Distribution of species in the *Drosophila anthrax* subgroup. a. *D. anthrax*, *D. nigropolita*, and *D. retrusa*; b. *D. fascigera*; c. *D. fuscifrons*; d. *D. hemianthrax*, *D. multiciliata*, and *D. demipolita*; e. *D. melanoloma*; f. *D. seorsa*.

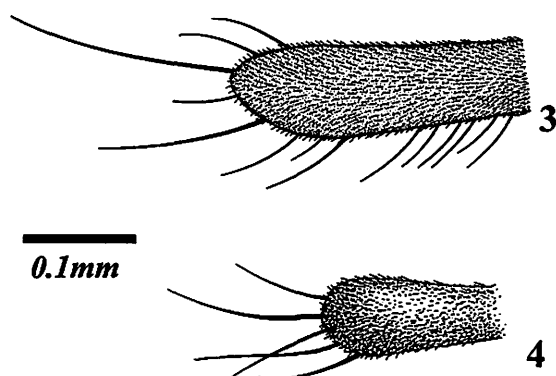
Review of the
Drosophila haleakalae
Species Group

D. ELMO HARDY is Emeritus Professor of Entomology at the University of Hawai'i at Mānoa and a Research Associate with the Department of Natural Sciences, Bishop Museum, Honolulu, Hawai'i

KENNETH Y. KANESHIRO is the director of the Center for Conservation Research and Training at the University of Hawai'i at Mānoa and a Research Associate with the Department of Natural Sciences, Bishop Museum, Honolulu, Hawai'i

FRANCISCA C. DO VAL is an entomologist with the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil

PATRICK M. O'GRADY is a curatorial associate with the American Museum of Natural History, New York



Figures 3–4. Palpi of some *Drosophila anthrax* subgroup species. 3. *D. multiciliata*, 4. *D. retrusa*.

Drosophila demipolita Hardy

Figs. 2d, 6, 16

Drosophila demipolita Hardy, 1965: 239.

DIAGNOSIS: *Drosophila demipolita* is easily distinguished from other members of this clade based on its brown third antennal segment, clypeus and palpi, entirely yellow legs, and each palp with 1 apical seta.

DESCRIPTION: ♂, ♀. Hardy (1965) described the external morphology of this species and the diagnosis above lists those characters critical to its identification. Here we describe some additional characters. *Thorax.* Posterolateral regions of mesonotum with ca. 11 setae (Fig. 6), ranging in size from minute (seta 1), to subequal to postalars. *Abdomen.* Ovipositor acute at apex (Fig. 16). Apex with 4 sharp, stout peg ovisensilla. Dorsolateral region with 3 peg ovisensilla. Ventral margin with 13 ovisensilla extending to 4/5 ovipositor length. Inner sub-apical ovisensilla ca. 1/2 ovipositor width (Fig. 16).

MEASUREMENTS: N = 1 ♂. TL = 1.0 mm; WL = 2.5 mm; TL/WL = 0.4; HW = 0.8 mm; HW/TL = 0.8; CI = 3.4; 4V = 1.3; 5X = 1.9; 4C = 0.6; M = 0.4. N = 1 ♀. TL = 1.2 mm; WL = 2.6 mm; TL/WL = 0.5; HW = 1.0 mm; HW/TL = 0.8; CI = 4.4; 4V = 1.4; 5X = 2.0; 4C = 0.5; M = 0.5.

TYPES: HAWAII: Holotype ♂ (BPBM 6,338), 5 mi southwest of Honoka'a, viii.1952, DEH, abdomen collapsed (Evenhuis, 1982). Not measured. Allotype in BPBM (6,338a). Three paratypes have been examined from the UHM. 2 ♂, 1 ♀, Southwest of Honoka'a, viii.1952, DEH.

MATERIAL EXAMINED: HAWAII: Thirty-nine other specimens, 26 males and 13 females, in the UHM were also studied. 1 ♂, S78, "*demipolita*", no date, location, or collector given; 2 ♂, Bird Park, Kīlauea, 5–6.xii.1963, MRW; 1 ♂, Bird Park, Kīlauea, 24.vi.1963, LHT; 1 ♂, Forest above Pa'auiilo, 19.iv.1964, LHT; 1 ♀, Mauloa Trail, Keanakolu, "on *Cheirodendron* leaves on ground", DEH; 1 ♂, Kīpuka Kī, 9.ix.1964, "ex: gill-type fungi", HTS; 1 ♂, 2 ♀, Forest above Pa'auiilo, 300 ft, 26.vii.1965, HLC; 1 ♂, Kīpuka Kī, 24.vii.1966, HTS; 1 ♂, 1 ♀, Pu'u 'O'o, Volcano Trail, 4,500 ft, 29.ix.1967; 3 ♀, Bird Park, Kīlauea, 3.vi.1974, HTS; 1 ♂, 1 ♀, Kīpuka Kī, 1,285m, 3.vi.1974, HTS; 2 ♂, Greenwell Ranch, Pauahi, 27.vi.1974, KYK; 3 ♂, 2 ♀, Kahuku Ranch Road, South Kona, 3,800 ft, 20.v.1975, KYK; 1 ♀, Bird Park, Kīlauea, 25.vii.1975, 1,220 m, HTS; 3 ♂, 1 ♀, Kīpuka Kī, 25.vii.1975, HTS; 1 ♂, Kahuku Ranch, 3,800 ft, 12.viii.1975, KYK; 3 ♂, Kahuku Ranch, 4,000 ft, 14.iv.1976, KYK; 1 ♂, Wright Road, Pole #44, Volcano, 10.iv.1978, HTS; 1 ♂, 1 ♀, Manukā, South Kona, 15.i.1979, DEH; 2 ♂, Manukā Forest Reserve, 5,200 ft, 13.x.1980, KYK.

DISTRIBUTION: This species is known only from the island of Hawai'i (Fig. 2d).

ECOLOGY: This species has been bred from gill fungus (Hardy, 1966).

DISCUSSION: Two females, which are identified as *D. demipolita*-like "Kaua'i", are present in the UHM. These are not conspecific with *D. demipolita* and may represent a new species.

Drosophila fascigera Hardy & Kaneshiro, new species

Figs. 2b, 7, 13

DIAGNOSIS: *Drosophila fascigera* is differentiated from all known Hawaiian *Drosophila* by having a dense clump of black cilia near the base of the venter of the front femur (Fig. 13) and by lacking cilia on the front tibiae and tarsi.

DESCRIPTION: ♂, (♀ unknown). *Head*. Front dark brown to black to level slightly below proclinate setae, rufous on lower portion. First 2 antennal segments yellow with faint tinge of brown on dorsum. Third segment entirely dark brown. Arista with 7 dorsal, 3 ventral rays in addition to apical fork. Face white to yellow-white through the central portion, yellowish down the orbits. Clypeus, palpi and mouthparts, except for black rim, pale yellow. Each palp with 1 apical, plus 1 subapical seta on posterior margin. Front and vertex entirely gray pollinose except for polished area on vertex along each side of ocellar triangle. Eyes sparsely short pilose. *Thorax*. Shining black, lightly dusted with gray pollen but with ground color shining through. Anterior katepisternal setae ca. 1/3 as long as posterior katepisternals. Posterolateral region of mesonotum with ca. 6 setae (Fig. 7). Only extreme apex of scutellum marked with yellow, when observed in dorsal view. *Legs*. Mostly yellow with slight tinge of brown on apical 1/2 of mid and hind femora. Front legs as mentioned above and in Fig. 13. *Wings*. Entirely subhyaline, costal fringe extending 1/2 distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Entirely dark brown to black, subshining, lightly gray-brown pollinose.

MEASUREMENTS: N = 5♂. TL = 1.0 mm (0.9–1.1); WL = 2.0 mm (1.9–2.3); TL/WL = 0.5; HW = 0.9 mm (0.9–1.0); HW/TL = 0.9; CI = 4.1; 4V = 1.7; 5X = 2; 4C = 0.6; M = 0.5.

TYPES: KAUA'I: Holotype ♂ (BPBM 16,354), Mahanaloa Valley, Koke'e, 1,950 ft, 23.iii.1973, KYK. TL = 1 mm; WL = 2.3 mm; TL/WL = 0.4; HW = 0.9 mm; HW/TL = 0.9; CI = 4.4; 4V = 1.6; 5X = 2; 4C = 0.6; M = 0.4. Four paratypes, all males. Mahanaloa Gulch, 19.vii.1974, SLM. Two paratypes are in UHM and 2 have been placed in the BPBM.

DISTRIBUTION: This species is known only from Kaua'i (Fig. 2b).

ETYMOLOGY: Latin, "bundle bearing". This species is named for the dense clump of setae males bear on the venter of the femur.

DISCUSSION: The female of this species is currently unknown. One female specimen on hand, from the same collection as the type, fits the general features of the male except that it lacks ciliation on the front legs and has a brown discoloration through median portion of the face. However, it is not possible to positively associate this female with the males of this species and it is not being designated as part of the type series.

Drosophila fuscifrons Hardy

Figs. 2c, 8, 17

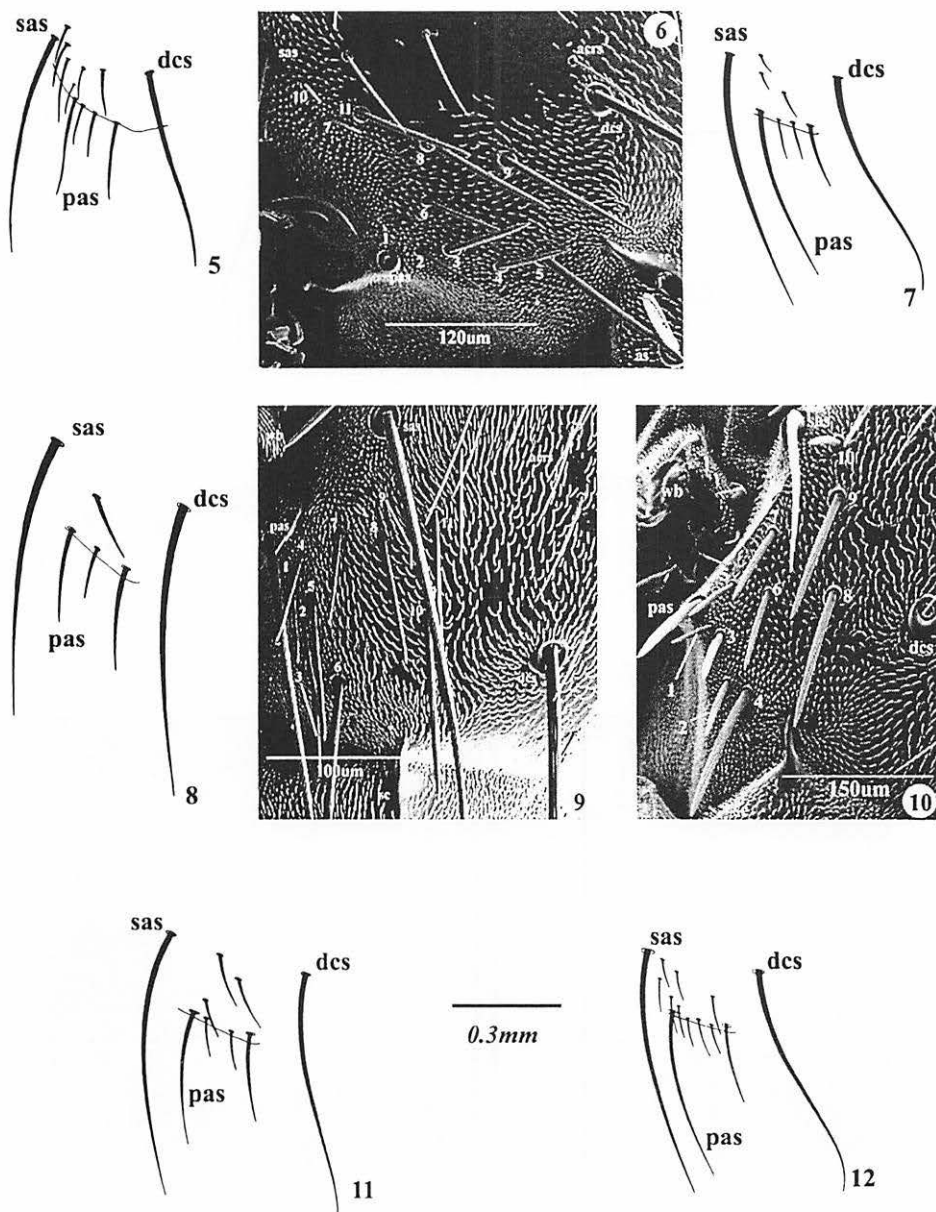
Drosophila fuscifrons Hardy, 1965: 287.

DIAGNOSIS: *Drosophila fuscifrons* males differ from other species in this clade by having the front entirely dark brown to black and dusted with gray pollen, face pale yellow to nearly white, clypeus mostly yellow with brown tinges, front basitarsus 1/2 as long as tibia, thorax mostly dark brown with rufous tinges in the ground color, and sternopleura yellow, tinged with brown. Females can be distinguished by having the lower front narrowly yellow, the face entirely yellow and the wings subhyaline with no markings at the apex or on r-m crossvein.

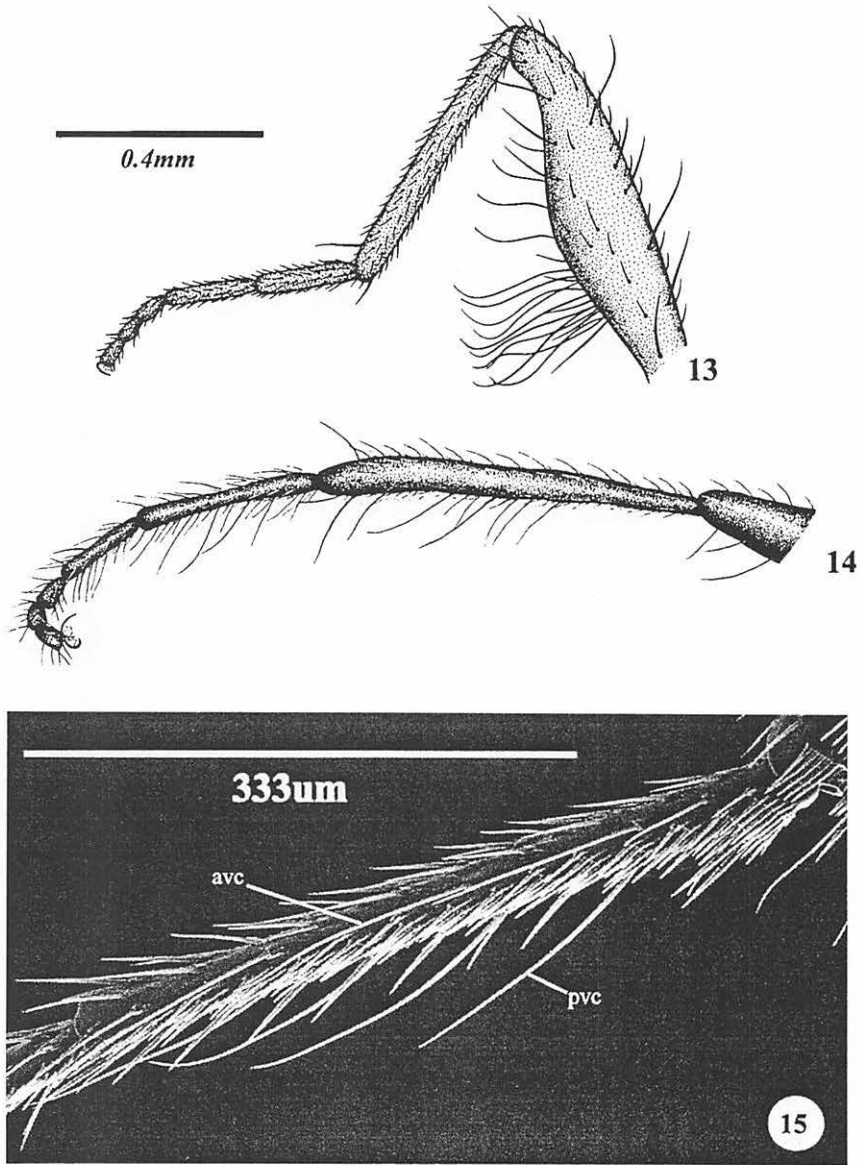
DESCRIPTION: ♂, ♀. Hardy (1965) provided a description of this species. Several characters are added to that description. *Thorax*. Posterolateral portion of mesonotum with 2–3 setae (Fig. 8). *Abdomen*. Ovipositor with rounded apex (Fig. 17). Ovisensilla short and pointed, extending along ventral margin to slightly more than 1/2 ovipositor length; dorsum with 1 peg ovisensilla, apex with dense cluster of ca. 4 peg ovisensilla; ventral margin with ca. 10 trichoid ovisensilla (Fig. 17). Length of inner subapical sensilla ca. 2/5 width of ovipositor.

MEASUREMENTS: N = 2♂. TL = 1.1 mm (0.9–1.2); WL = 2.3 mm (2.2–2.3); TL/WL = 0.5 (0.4–0.5); HW = 0.8 mm; HW/TL = 0.8 (0.7–0.8); CI = 4.4 (4.3–4.5); 4V = 1.3 (1.2–1.4); 5X = 1.8 (1.6–1.9); 4C = 0.5; M = 0.5 (0.4–0.5).

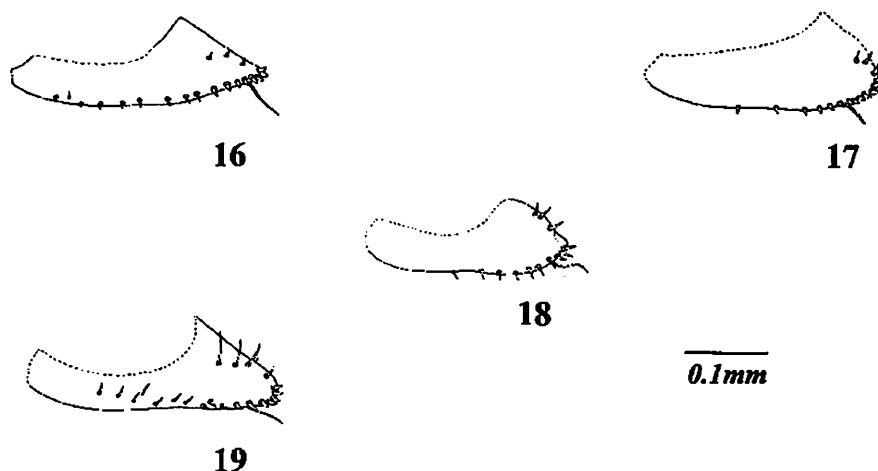
TYPES: MAUI: Holotype ♂ (BPBM 6,365), Kula Pipeline, 4,500 ft, 8.iv.1932, OB, right foreleg beyond first



Figures 5–12. Posterolateral region of the mesonotum of some *Drosophila anthrax* subgroup species; 5. *D. anthrax*; 6. *D. demipolita* (250×); 7. *D. fascigera*; 8. *D. fuscifrons*; 9. *D. melanoloma* (300×); 10. *D. multiciliata* (200×); 11. *D. nigropolita*; 12. *D. retrusa*.



Figures 13–15. Forelegs of some *Drosophila anthrax* subgroup males, 13. *D. fascigera*, 14. *D. hemianthrax*, 15. *D. multiciliata* (90 ×).



Figures 16–19. Ovipositors of some *Drosophila anthrax* subgroup females; 16. *D. demipolita*; 17. *D. fuscifrons*; 18. *D. melanotoma*; 19. *D. multiciliata*.

tarsomere, left foreleg beyond femur, both mid and hind legs beyond coxae, and abdomen beyond second segment missing, genitalia in microvial mounted beneath specimen (Evenhuis, 1982). Not measured. Allotype ♀ (BPBM 6,365a), same collection as holotype. Not measured. Two paratypes have been examined from the UHM. 1 ♂, 'Īao Valley, 8.viii.1918, OHS; 1 ♀, Ridge above Hā'ela'au, 3,000–3,200 ft, 21.xii.1928, EHB. LĀNA'I: One paratype has been examined from UHM. 1 ♂, Lāna'ihale, 3,200 ft, vi.1953, DEH.

MATERIAL EXAMINED: MAUI: Several other specimens in the UHM have also been studied. 1 ♂, Waikamoi Stream, Waikamoi, 2,900 ft, 13.x.1967, KYK; 3 ♀, Auwahi, 11.vii.1974, KYK; 40 ♀, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK; 3 ♀, Kaupō Gap, Haleakalā, 9.x.1975, KYK.

DISTRIBUTION: *Drosophila fuscifrons* is known from Maui and Lāna'i (Fig. 2c).

Drosophila hemianthrax Hardy & Kaneshiro new species

Figs. 2d, 14

DIAGNOSIS: *Drosophila hemianthrax* can be distinguished from other members of this clade by having yellow third antennal segments and palpi, a front basitarsus with 4 prominent posteroventral cilia extending along its full length, and a row of erect, closely placed, posteroventral setae on the basal 1/4 of the front tibia (Fig. 14).

DESCRIPTION: ♂, (♀ unknown). *Head.* Front subopaque dark brown to black over upper 2/3, pale yellow below. Face yellow, tinged with brown on extreme upper portion beneath antennae bases and blackish on lower 2/3. Antennae pale yellow except for tinge of brown over dorsal portion of second segment. Arista with 6 dorsal, 2 ventral rays in addition to apical fork. Inner margin of arista sparsely short haired. Sides of epistoma distinctly protruded with 2 strong vibrissae located on this prominence when viewed laterally. Genae of moderate width, ca. 1/12 width of eye. Palpi entirely yellow. Mentum subshining black. Mouthparts yellow except for narrow black sclerotized rim on labellum. *Thorax.* With the exception of the prominent yellow tip on scutellum, thorax entirely shining black in ground color, moderately dusted with gray-brown pollen over mesonotum. *Legs.* Predominantly yellow, front femur with streak of pale brown along posterodorsal surface, mid and hind femora

Table 3. *Drosophila haleakalae* species present on multiple islands

Species	Distribution of Types	Distribution of Other Populations	Notes
<i>D. bipolita</i>	Hawai'i, Maui	Moloka'i, O'ahu	-
<i>D. canipolita</i>	Hawai'i, Lāna'i, Maui, Moloka'i, O'ahu	Kaua'i	-
<i>D. cilifemorata</i>	Hawai'i, Maui, Moloka'i	-	-
<i>D. clara</i>	Hawai'i	Maui	-
<i>D. demipolita</i>	Hawai'i	Kaua'i	-
<i>D. fuscifrons</i>	Lāna'i, Maui	-	-
<i>D. haleakalae</i>	Maui	Hawai'i	-
<i>D. iki</i>	Hawai'i, Maui	-	-
<i>D. lissodora</i>	Hawai'i	Maui	-
<i>D. luteola</i>	O'ahu	Hawai'i, Kaua'i	dorsocentral number varies
<i>D. macrochaetae</i>	Maui	Hawai'i	-
<i>D. melanoloma</i>	Lāna'i, Maui, Moloka'i	Hawai'i	length of humeral setae varies
<i>D. multiciliata</i>	Hawai'i	Maui	-
<i>D. nigropolita</i>	Moloka'i	Maui, Hawai'i	-
<i>D. polita</i>	Lāna'i, Maui	Hawai'i, Moloka'i	-
<i>D. retrusa</i>	Moloka'i	Maui	-

tinged with brown apical 2/3. Front femur with complete row of ca. 8 posteroventral setae extending full length of segment and with row of 6 moderately long anteroventral cilia extending along basal 2/5 of segment. Front tibia with ca. 6 posteroventral cilia extending over apical 2/3–3/4 and with closely placed row of 5–6 erect posteroventral setae on basal 1/4–1/3 (Fig. 14). Basitarsus with 4 moderately long posteroventral cilia extending full length. Front basitarsus just slightly over 1/2 as long as tibia. *Wings*. Evenly infuscated, lacking markings. Costal fringe extending approximately 2/5 distance between apices of veins R_{2+3} and R_{4+5} . Last section of vein CuA1 ca. 1/2 length of M_1 between r-m and dm-cu crossveins. *Abdomen*. Entirely dark reddish brown to blackish. Male genitalia not dissected.

MEASUREMENTS: N = 3♂. TL = 1.2 mm (1.0–1.3); WL = 2.6 mm (2.3–2.9); TL/WL = 0.4; HW = 0.9 mm (0.7–1.0); HW/TL = 0.8; CI = 4.0; 4V = 1.4; 5X = 1.6; 4C = 0.5; M = 0.4.

TYPES: HAWAI'I: Holotype ♂ (BPBM 16,400), Kilauea Forest Reserve, 26.vii.1975, HTS. TL = 1.2 mm; WL = 2.9 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.2; 4V = 1.3; 5X = 1.5; 4C = 0.5; M = 0.4. Two paratypes, both male, are in UHM: 1♂, Forest above Pa'auilo, 3,000 ft, 26.vii.1965, HLC; 1♂, Halepiula Road, Kapu'a (land section), South Kona, 4,650 ft, vii.1977, DEH.

DISTRIBUTION: *Drosophila hemianthrax* is known only from the Big Island (Fig. 2d).

ETYMOLOGY: Greek, "half *anthrax*", referring to the smaller size of this species relative to *D. anthrax*.

Drosophila melanoloma Hardy

Figs. 2e, 9, 18

Drosophila melanoloma Hardy, 1965: 360.

DIAGNOSIS: *Drosophila melanoloma* has 2 humeral setae; pale brown marks on the apex and over the r-m crossvein of the wing; antennae, palpi, lower front, and all of face pale yellow; pleura entirely black and mesonotum rather densely gray pollinose. *Drosophila melanoloma* can be distinguished from other species in this clade by the distinct pattern of pale brown marks on the wings and by having the abdomen entirely black or dark reddish brown, the costal fringe short and the upper 2/5–1/2 of the front brown.

DESCRIPTION: ♂, ♀. Hardy (1965) provides a description of males and females. Additional characters include: *Thorax*. About 11 setae on posterolateral margin of mesonotum, arranged as in Fig. 9. *Wings*. Nearly

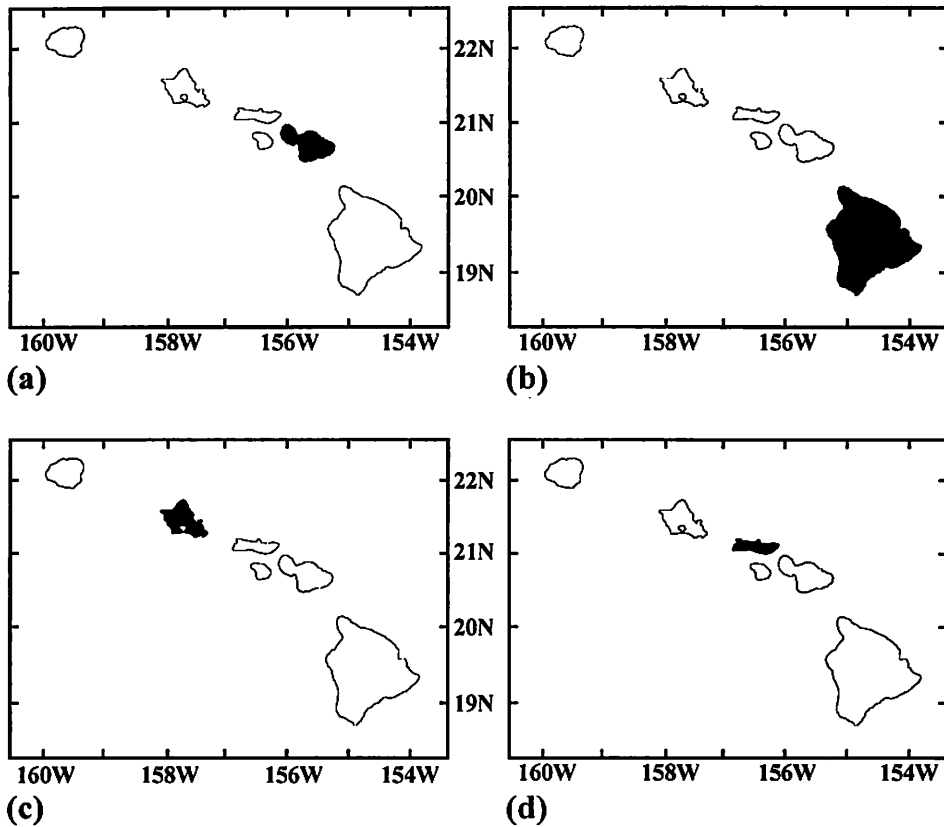
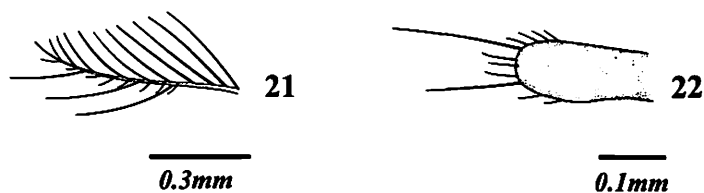


Figure 20. Distribution of species in the *Drosophila venusta* cluster (*cilifemorata* complex, *cilifemorata* subgroup); a. *D. inciliata*; b. *D. longiperda*; c. *D. tanytarsis*; d. *D. venusta*.

subhyaline in females, markings extremely faint or completely lacking. *Abdomen*. Ovipositor with long, pointed and peg-like ovisensilla (Fig. 18). Apex somewhat acute, with ca. 4 ovisensilla. Dorsal margin with 3 ovisensilla; ventral margin with ca. 6 ovisensilla, extending to slightly over 1/2 ovipositor length. Inner subapical sensilla long, ca. 4/5 width of ovipositor (Fig. 18).

MEASUREMENTS: N = 10♂. TL = 1.1 mm (0.8–1.3); WL = 2.5 mm (2.1–2.9); TL/WL = 0.4 (0.3–0.5); HW = 0.8 mm (0.7–0.9); HW/TL = 0.8 (0.7–0.8); CI = 3.7 (3.1–4.1); 4V = 1.5 (1.4–1.8); 5X = 2.1 (1.8–2.6); 4C = 0.6 (0.6–0.8); M = 0.5 (0.5–0.6). N = 5♀. TL = 1.4 mm (1.3–1.5); WL = 3.2 mm (3.1–3.5); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.9–1.1); HW/TL = 0.7; CI = 4.1 (3.7–5.2); 4V = 1.5 (1.3–1.7); 5X = 1.5 (1.3–1.8); 4C = 0.6 (0.5–0.7); M = 0.4 (0.4–0.5).

TYPES: MOLOKA'I: Holotype ♂ (BPBM 6,398), Pu'u Kolekole, 3,600 ft, vii.1953, DEH. Not measured. Allotype ♀ (BPBM 6,398a) same collection as holotype. Not measured. Sixteen paratypes, 15 males and 1 female, have been examined from the UHM. 6♂, Hanalilolilo, vii.1952, DEH; 2♂, Maunawainui Valley, vii.1952, DEH; 3♂, 1♀, Pu'u Kolekole, vii.1952, DEH; 4♂, Pu'u Kolekole, 3,600 ft, vii.1953, DEH. MAUI: Twenty-six paratypes in the UHM, 11 males and 15 females, have been examined. 5♂, 4♀, Kula Pipeline,



Figures 21–22. Head structures of some *Drosophila venusta* cluster species. 21. *D. inciliata*, arista; 22. *D. tanytarsis*, palp.

4.iv.1932, OB; 6♂, 11♀, Palikū, Haleakalā Crater, vi.1953, DEH.

MATERIAL EXAMINED: Additional material at UHM has also been examined. MAUI: 2♀, Palikū, Haleakalā Crater, 6,500 ft, vii.1958, DEH; 2♂, Pu'u Kukui Ridge, 4,500 ft, 4.viii.1964, HLC; 1♂, Palikū, Haleakalā, 21.vii.1965, KYK; 1♂, Waikamoi, 11.iii.1966, JPM; 1♂, Waikamoi, 29.iii.1966, JPM; 1♀, Waikamoi, 22.ii.1967, JPM; 1♂, Hana'ula, 4,000 ft, 7–8.v.1969, KYK; 3♂, Waikamoi 10.v.1974, HTS & KYK; 2♂, Auwahi, 11.vii.1974, KYK; 2♂, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK; 3♂, 7♀, Trail to Pu'u Kukui, 3,500 ft, 16–17.ix.1975, KYK; 2♀, Kaupō Gap, Haleakalā, 9.x.1975, KYK; 3♂, 2♀, Palikū, Haleakalā, 9.x.1975, HTS & KYK. MOLOKA'I: A large series of specimens at UHM has been examined. 1♂, Pu'u Kolekole, vii.1963, LHT; 3♂, Pu'u Kolekole, 3,600 ft, 24.vii.1964, HLC; 1♀, Hanalilolilo, 3,000 ft, 13.viii.1965, HLC; 49♂, 11♀, South of Hanalilolilo, 9.i.1975, ATO; 11♂, South of Hanalilolilo, 15.vii.1975, ATO; 17♂, 4♀, Waikolu Stream, South of Hanalilolilo, 5.v.1976, KYK. Eighteen individuals from AMNH have been studied. 9♂, 9♀, Nature Conservancy Cabin, Pu'u Kolekole, 19–21.iii.1999, OG58.6, PMO & JBS. LĀNA'I: Although no paratypes from Lāna'i were available, the following specimens of this species were examined from UHM. 48♂, 26♀, Lāna'ihale, 11.vii.1975, HTS; 3♂, 5♀, Kaiholena Gulch, 3,300 ft, 12.vii.1975, ATO.

DISTRIBUTION: The type series of this species includes specimens from Moloka'i, Maui, and Lāna'i (Fig. 2e).

ECOLOGY: *Drosophila melanoloma* has been reared from *Agaricus* fungus (Heed 1968).

MOLECULAR BIOLOGY: Representatives of this species (collection OG58.6) are present in the AMNH-MC.

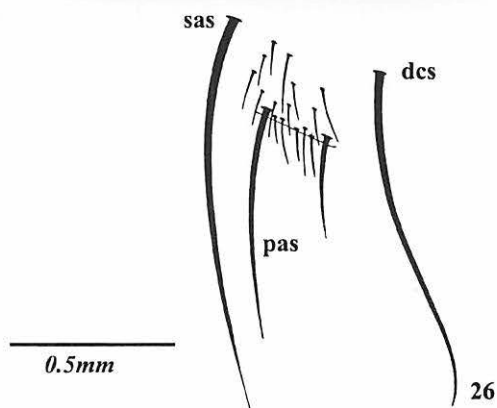
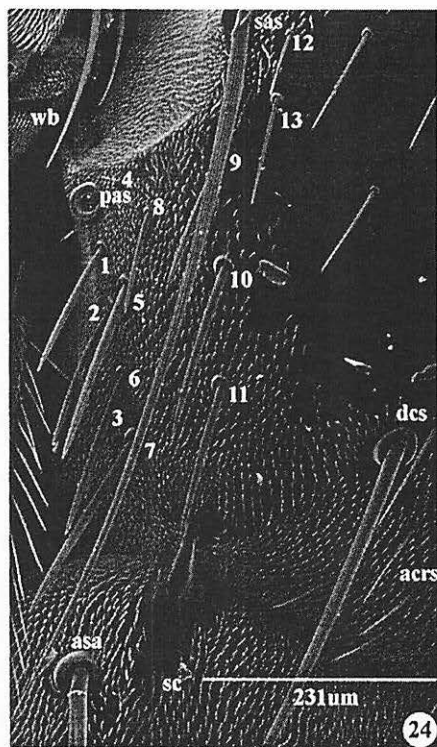
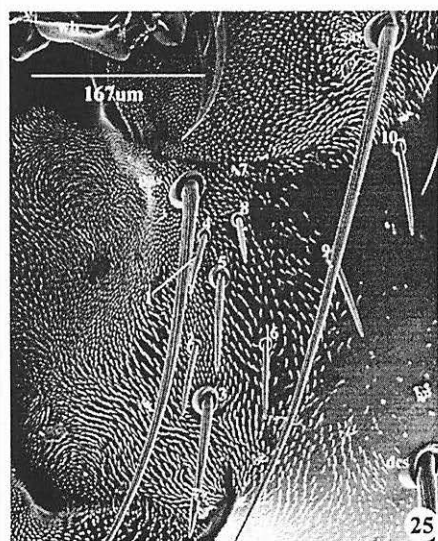
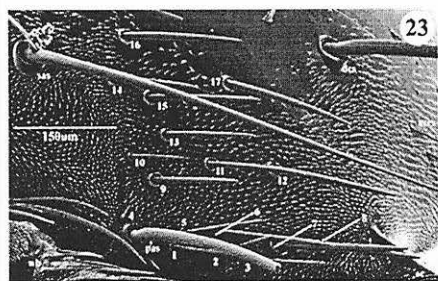
DISCUSSION: Approximately 140 specimens similar to *D. melanoloma* have been collected on the Big Island and are in the UHM (Table 3). These are nearly identical to the type series, except for variation in the size of the humeral setae. The lower humeral is well developed, between 2/3–3/4 as long as the upper seta in the type series from Moloka'i, and ranges from normal length to rudimentary to completely lacking in Hawai'i populations. Studies are currently underway to determine whether these different populations are representative of variation within *D. melanoloma* or if they represent a closely related sibling species (O'Grady & Val, in prep.).

Drosophila multiciliata Hardy & Kaneshiro, new species

Figs. 2d, 3, 10, 15, 19

DIAGNOSIS: *Drosophila multiciliata* is readily differentiated from the other species in this complex by a combination of leg and wing characters (see description).

DESCRIPTION: ♂, ♀. *Head.* Median portion of front yellow below level of anterior reclines, black above. Parafrontalia opaque black. Ocellar triangle mostly gray. Antennae, face, genae, and mouthparts, except for black rim, pale yellow in male. Third antennal segment, lower margin of face, and apices of palpi dark brown in female. Clypeus yellow, faintly tinged with brown in male, darker brown in female. Arista with 6 dorsal rays in addition to apical fork and between 3–5 scattered short hairs on inner margin. Palpi slender, with 2 prominent apical setae, the longer 2/3 length of shorter, and with a number of scattered black setae along both margins (Fig.



Figures 23–26. Posterolateral regions of the mesonotum of the *Drosophila venusta* cluster. 23. *D. inciliata* (200 ×), 24. *D. longiperda* (150 ×), 25. *D. tanytarsis* (180 ×), 26. *D. venusta*.

3). Genae narrow, area between vibrissal row and eye margins equal to ca. $1/7$ eye width. *Thorax*. Shining black with faint tinge of rufous in ground color, rather densely gray pollinose but not obscuring ground color on mesonotum. Apical portion of scutellum broadly yellow. Anterior katapisternal setae ca. $1/3$ length of posterior katapisternals. Posterolateral region of mesonotum rather densely setose, with series of ca. 10 thick setae (Fig. 10). *Legs*. Front legs predominantly black in male, front coxae yellow basally and along ventral margins, broadly brown to black apically. Tarsi of male yellow, tinged with brown. Front legs of female mostly yellow, brown on apical $1/3$ of front femora, otherwise as male. Front tibiae flattened laterally, with row of ventral and posteroventral cilia extending over apical $2/5$. Basitarsus slender, ca. $2/3$ length of tibia; with row of 5 long black, posteroventral cilia and 4 long anteroventral cilia extending full length (Fig. 15). Mid and hind legs mostly yellow with apical halves of femora broadly brown. Front basitarsus $2/3$ as long as tibia and ca. $2 \times$ as long as second tarsomere. *Wings*. Subhyaline, with faint tinge of brown in apical third and over r-m crossvein. Costal fringe extending ca. $1/2$ distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Entirely dark brown to black, gray-brown pollinose. External male genitalia dark brown to black. Ovipositor with rounded apex (Fig. 19). Dorsal margin with 3 long, pointed ovisensilla. Apex with cluster of ca. 7–8 short, pointed, peg ovisensilla. Ventral ovisensilla extend ca. $3/4$ length of ovipositor. Three apical-most ventral ovisensilla short and peg-like, remaining ventral ovisensilla long and pointed. Apical setae ca. $1/2$ ovipositor width (Fig. 19).

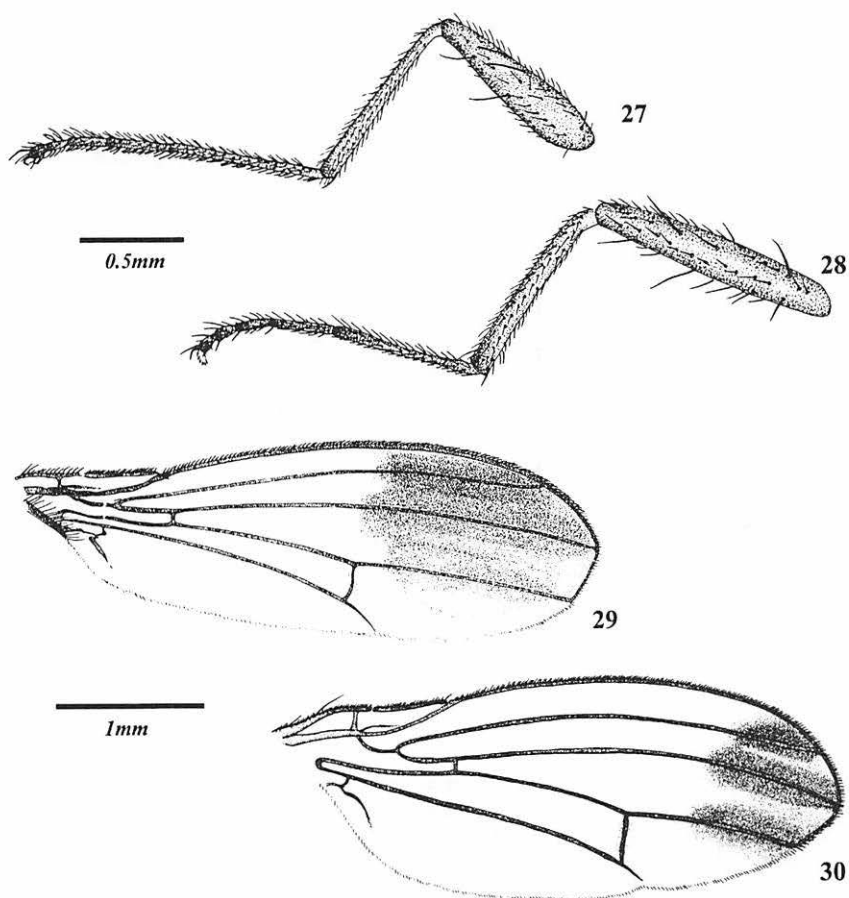
MEASUREMENTS: N = 11 ♂. TL = 1.3 mm (1.1–1.4); WL = 3.3 mm (3.0–3.6); TL/WL = 0.4 (0.3–0.4); HW = 1.0 mm (0.8–1.1); HW/TL = 0.7 (0.7–0.8); CI = 4.6 (4.3–5.2); 4V = 1.4 (1.3–1.5); 5X = 1.9 (1.7–2.0); 4C = 0.5 (0.5–0.6); M = 0.4 (0.4–0.5). N = 11 ♀. TL = 1.5 mm (1.4–1.6); WL = 3.6 mm (3.4–3.9); TL/WL = 0.4; HW = 1.1 mm (1.0–1.1); HW/TL = 0.7 (0.7–0.8); CI = 4.9 (4.5–5.4); 4V = 1.4 (1.3–1.6); 5X = 1.8 (1.6–2.0); 4C = 0.5 (0.4–0.6); M = 0.4.

TYPES: **HAWAII**: Holotype ♂ (BPBM 16,355), Kīpuka #9, Saddle Road, 5110 ft, 13.vii.1967, WBH. TL = 1.1 mm; WL = 3.2 mm; TL/WL = 0.3; HW = 0.8 mm; HW/TL = 0.8; CI = 5.0; 4V = 1.5; 5X = 1.8; 4C = 0.5; M = 0.5. Allotype ♀ (BPBM 16,355a), same collection as holotype. TL = 1.4 mm; WL = 3.4 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.7; CI = 4.5; 4V = 1.6; 5X = 1.7; 4C = 0.6; M = 0.5. Eighty-four paratypes, 50 males and 34 females, have been designated. 1 ♂, Kīpuka Kī, 18.vii.1964, LHT; 1 ♂, Pu'u Hualālai, 5,500 ft, 13.vi.1966, WBH; 3 ♂, Sinkhole, Hualālai, 13.vi.1966, KYK; 1 ♂, Pawaina, 2,500 ft, 7.vii.1967, DEH; 4 ♀, Kīpuka #1, Saddle Road, 5,560 ft, 9.vi.1967, WBH; 2 ♂, 4 ♀, Kīpuka #2, Saddle Road, 5,400 ft, 9.vii.1967, WBH; 1 ♂, Kīpuka #9, Saddle Road, 5,110 ft, 9.vii.1967, WBH; 2 ♀, Kīpuka #6, Saddle Road, 5,240 ft, 11.vii.1967, WBH; 5 ♂, 9 ♀, same information as holotype; 1 ♂, 3 ♀, Kīpuka #10, Saddle Road, 5,500 ft, 14.vii.1967, WBH; 1 ♂, Kīpuka #9, Saddle Road, 5,100 ft, 28–29.vii.1967, HLC; 1 ♂, 1 ♀, Kīpuka #2, Saddle Road, 5,400 ft, 10.viii.1967, WBH; 1 ♀, Kīpuka #11, Saddle Road, 5,600 ft, 10.viii.1967, WBH; 1 ♀, Kīpuka #9, Saddle Road, 5,400 ft, 13.ix.1967, HLC; 4 ♂, Keawewai Camp, 5,800 ft, 4.x.1967; 1 ♀, Kīpuka #10, Saddle Road, 5.x.1967, MPK; 1 ♂, Kīpuka #9, Saddle Road, 5,108 ft, 15–16.iv.1968, HLC; 1 ♂, 1 ♀, Hinakapoula, 5,800 ft, 19.vi.1968, HLC; 1 ♂, Kīpuka #9, Saddle Road, 5,100 ft, 4–5.x.1968, MPK; 1 ♂, 1 ♀, Kīpuka #10, 18.vii.1969, no collector given; 2 ♂, Pu'u Wa'awa'a, 19.xii.1969, SLM; 1 ♂, Pu'u Wa'awa'a, 4,300 ft, 22.xii.1969, KYK; 3 ♂, Moanuihuea, Hualālai, 3,400 ft, 23.xii.1969, KYK; 2 ♂, Kīpuka #14, Saddle Road, 15.i.1970, WBH; 2 ♀, Kīpuka #2, Saddle Road, 19.i.1970, WBH; 1 ♂, Kīpuka #10, Saddle Road, 19.i.1970, WBH; 1 ♀, Bird Park, Kīlauea, 1,220 m, 25.vii.1975, HTS; 1 ♂, Wright Road, Upper 'Ōla'a Forest Reserve, 25.vii.1975, HTS; 3 ♂, Kīlauea Forest Reserve, 26.vii.1975, HTS; 2 ♂, 'Ōla'a Forest, Volcano Experimental Station, 21.ii.1976, KYK; 10 ♂, 4 ♀, Halepiula Road, Kapu'a (land section), South Kona, 4,650 ft, vii.1977, DEH. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: *Drosophila multiciliata* is found only on the island of Hawai'i (Fig. 2d).

ETYMOLOGY. The name *multiciliata*, meaning "many cilia", refers to the distinctive cilia located on the front tibiae and tarsi of this species.

DISCUSSION: Specimens resembling *D. multiciliata* have also been collected on Maui (Table 3). We are currently studying these in order to determine if they are *D. multiciliata* or a similar species (O'Grady & Val, in prep.).



Figures 27–30. Thoracic structures of some *Drosophila venusta* cluster species. 27. *D. longiperda*, male foreleg. 28. *D. tanytarsis*, male foreleg. 29. *D. longiperda*, wing. 30. *D. tanytarsis*, wing.

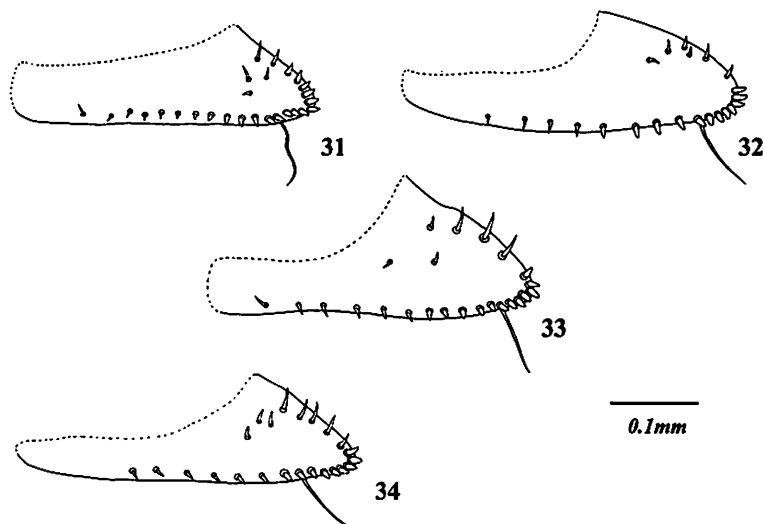
***Drosophila nigropolita* Hardy**

Figs. 2a, 11

Drosophila nigropolita Hardy, 1965: 394.

DIAGNOSIS: *Drosophila nigropolita* has 2 humeral setae, subhyaline wings, and entirely black pleura. It differs from most other members of the *haleakalae* group by having the scutellum entirely black, lacking the pale yellow apex. *Drosophila nigropolita* also has an extremely short costal fringe that extends just a short way beyond tip of vein R_{2+3} , $1/4$ the distance to R_{4+5} .

DESCRIPTION: ♂ (♀ unknown). Refer to Hardy (1965) for the original description. Additional characters



Figures 31-34. Ovipositors of the *Drosophila venusta* cluster. 31. *D. inciliata*. 32. *D. longiperda*. 33. *D. tanytarsis*. 34. *D. venusta*.

added here are: *Head*. Clypeus yellow with tinge of brown on dorsal portion. Front almost entirely golden pollinose. Pollinosity, which is best seen in direct light, extends over yellow portion below proclinate setae, over parafrontal areas, and on upper portion of front. Ocellar triangle dusted gray-brown. *Thorax*. Posterolateral region of mesonotum with ca. 6 setae (Fig. 11).

MEASUREMENTS: N = 5♂. TL = 1.0 mm (0.9–1.1); WL = 2.3 mm (2.1–2.7); TL/WL = 0.4 (0.4–0.5); HW = 0.9 mm (0.8–0.9); HW/TL = 0.9 (0.8–0.9); CI = 4.1 (3.5–4.5); 4V = 1.5 (1.4–1.5); 5X = 2.0 (1.6–2.4); 4C = 0.6 (0.5–0.6); M = 0.5 (0.4–0.5).

TYPES: MOLOKA'I: Holotype ♂ (BPBM 6,414), Pu'u Kolekole, 3,600 ft, vii.1953. DEH. Not measured. Allotype (BPBM 6,414a), same data as holotype. Seven paratypes, all males, have been examined from the UHM. 3♂, Pu'u Kolekole, vii.1952, MT; 2♂, Pu'u Kolekole, vii.1953, MT; 1♂, Pu'uoka'eha, 3,700 ft, vii.1953, DEH; 1♂, Pu'u Ali'i, 4,200 ft, vii.1953, DEH.

MATERIAL EXAMINED: MOLOKA'I: Other material on hand includes: 1♂, South of Hanalilolilo, 19.vii.1963, DEH; 2♂, Pu'u Kolekole, 3,600 ft, 10.vi.1964, LHT; 1♂, South of Hanalilolilo, 1.vii.1964, DG; 1♂, South of Hanalilolilo, 21.xii.1965, KYK.

DISTRIBUTION: This species is known only from Moloka'i (Fig. 2a).

DISCUSSION: Specimens from Auwahi in West Maui, Waikamoi Forest Preserve in East Maui and Alakahi Stream in South Kohala, Hawai'i are also in the collection (Table 3). It is possible that these represent a complex of closely related sibling species.

***Drosophila retrusa* Hardy**

Figs. 2a, 4, 12

Drosophila retrusa Hardy, 1965: 450.

DIAGNOSIS: This species has 2 humeral setae, subhyaline wings, and entirely black pleura. It is readily differentiated from other members of this clade by having the antennae, clypeus and palpi pale yellow, by having several long setae at or near the apex of the palpi (Fig. 4), and by having the mid and hind femora tinged with brown.

DESCRIPTION: Refer to Hardy (1965). Posterolateral region of mesonotum with ca. 10 short supernumerary setae, as in Fig. 12.

MEASUREMENTS: N = 1 ♂. TL = 1.2 mm; WL = 2.3 mm; TL/WL = 0.5; HW = 0.8 mm; HW/TL = 0.8; CI = 4.4; 4V = 1.3; 5X = 1.9; 4C = 0.5; M = 0.4.

TYPES: MOLOKA'I: Holotype ♂ (BPBM 6,437), Hanalilolilo, vii.1952, DEH; right hindleg beyond femur missing (Evenhuis, 1982). Not measured. One male paratype has been examined from the UHM: 1 ♂, Pu'u Kolehale, 3,600 ft, vi.1953, DEH.

MATERIAL EXAMINED: MOLOKA'I: Other material in the UHM includes: 3 ♂, Pu'u Kukui, 4,500 ft, iv.1954, MT; 1 ♂, Hanalilolilo, 9–11.i.1975, ATO.

DISTRIBUTION: This species is known only from Moloka'i (Fig. 2a).

DISCUSSION: One female from Hanalilolilo is in the UHM, but it cannot be definitely associated with the male. Three males that appear to be close to this species have also been collected from Pu'u Kukui, Maui (Table 3). This may represent a cluster of closely related species from several islands.

***Drosophila seorsa* Hardy**

Fig. 2f

Drosophila seorsa Hardy, 1965: 461.

DIAGNOSIS: *Drosophila seorsa* has 2 humeral setae, subhyaline wings, and the entirely dark brown to black pleura. It can be distinguished from closely related forms by having its entire thorax dusted with gray and the genae rather broad, ca. 1/3 the width of the eye.

DESCRIPTION: For further details refer to Hardy (1965).

TYPE: MAUI: Holotype ♂ (BPBM 6,442), Palikū, Haleakalā Crater, vi.1952, MT. TL = 1.1 mm; WL = 2.4 mm; TL/WL = 0.5; HW = 0.9 mm; CI = 4.5; 4V = 1.6; 5X = 1.8; 4C = 0.5; M = 0.5.

DISTRIBUTION: *Drosophila seorsa* is known only from a single male collected on Maui (Fig. 2f).

II. The *cilifemorata* subgroup

The *cilifemorata* subgroup consists of species which, when compared to other taxa in the *haleakalae* species group, are relatively large and showy, with conspicuous maculations on their wings. There are 3 distinct species complexes in this subgroup, *cilifemorata*, *denotata* and *insignita*. The *cilifemorata* complex, which is defined by its conspicuous wing maculations and large body size, consists of 11 species. One species in this complex, *D. nigra*, has lost the sclerotized black rim on its labellum, most likely in an independent evolutionary event from that giving rise to 2 members of the *haleakalae* complex, *D. nigella* and *D. fungiperda*, which also lack this character.

Relationships among taxa in the *cilifemorata* complex are largely unresolved, only the *venusta* cluster is clearly defined. The remaining species in the *cilifemorata* complex are placed in the *cilifemorata* cluster. The *venusta* cluster consists of 4 species, *D. inciliata*, *D. longiperda*, *D. tanytarsis*, and *D. venusta*. All species in this cluster have wing maculations, which cover the apical 1/3 of the wing, reduced shading over the posterior crossvein, shiny dark bodies, and very similar ovipositor shape and setation. The *venusta* cluster species are found on O'ahu, Moloka'i, Maui, and the

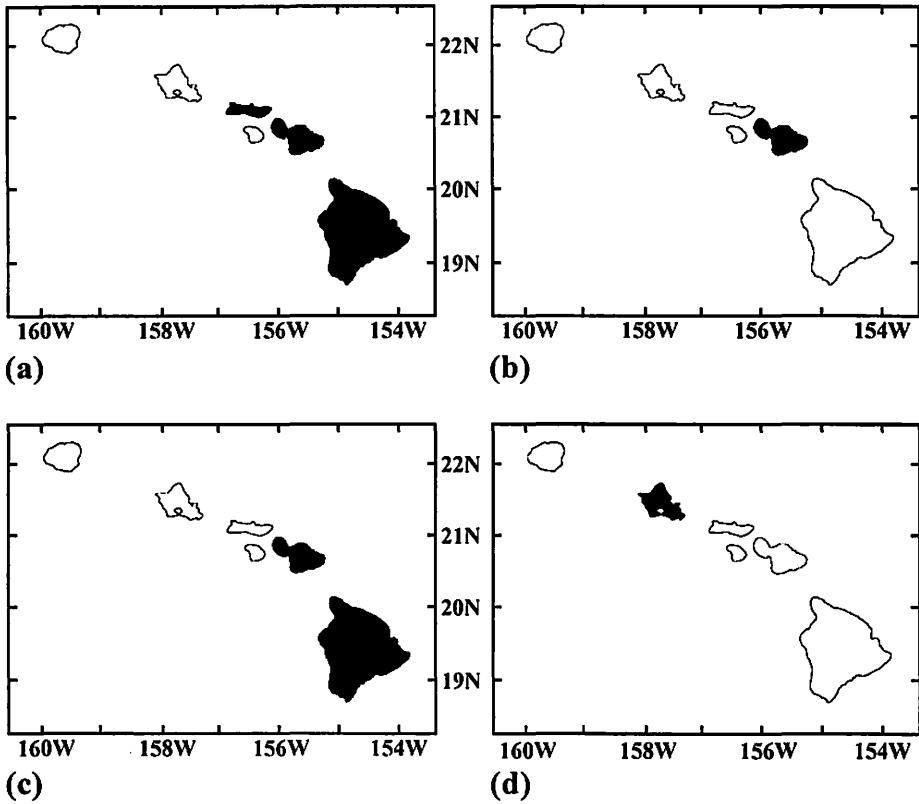


Figure 35. Distribution of species in the *Drosophila cilifemorata* cluster (*cilifemorata* complex, *cilifemorata* subgroup). a. *D. cilifemorata*, b. *D. dolichotarsis*, *D. nigra*, and *D. stenoptera*, c. *D. iki*, d. *D. swezeyi*.

Big Island (Fig. 20). The apparent absence of this subgroup on Kaua'i makes the maximum age of this complex between 2.6–3.7 million years (Carson & Clague, 1995). Based on their close morphological and molecular similarity, *D. inciliata* from Maui and *D. longiperda* from the Big Island are probably the most recently diverged species in this complex. The ecology of the *venusta* cluster is unknown. The *cilifemorata* cluster species (*D. cilifemorata*, *D. dolichotarsis*, *D. iki*, *D. nigra*, *D. stenoptera*, and *D. swezeyi*) are found on all the high islands except for Kaua'i and Lāna'i (Fig. 35). *Drosophila flaviceps* is being treated here as *nomen oblitum* (see below) and, therefore, it is not being considered in this discussion. The absence of this group on Lāna'i may be because of a lack of suitable ecological niches for these *Drosophila* on this island. The islands of Maui and Molokai together have 5 species in this lineage (Fig. 35a–c). Two species found on Maui Nui, *D. iki* and *D. cilifemorata*, have also been recorded from the Big Island. This suggests that the *cilifemorata* cluster may have radiated on Maui Nui with some species more recently colonizing other islands. Al-

though it unclear whether *D. swezeyi* from O'ahu is basal within this lineage, the biogeographic information suggests that the age of the *cilifemorata* cluster may be similar to that of the *venusta* cluster, approximately 3 million years. Heed (1968) reported that *D. iki* has been reared from "gill fungi" (Table 2).

The *denotata* complex contains 2 poorly known species from O'ahu (Fig. 50a). These species belong in the *cilifemorata* subgroup based on their wing patterns, ovipositors and the setation patterns on their mesonota. *Drosophila denotata* and *D. sabroskyi* are placed as sister taxa because of their wing patterns. *Drosophila denotata* has been reared from "fleshy" fungi (Heed, 1968), but no ecological information exists for *D. sabroskyi*. Further study is needed to determine the exact relationships and ecological habits of these species.

The *insignita* complex contains 3 small species, *D. chicae* from the Big Island (Fig. 50b), *D. curtitaris* from Kaua'i (Fig. 50c), and *D. insignita* from O'ahu (Fig. 50d). The wing maculations, which place them in the *cilifemorata* subgroup, are most apparent in the males; wings of female are less conspicuously marked. Two species in the *insignita* complex, *D. chicae* and *D. curtitaris*, have been reared from fungi by S.L. Montgomery and H.T. Spieth, respectively (from specimen labels).

IIa. The *cilifemorata* complex

KEY TO SPECIES IN THE *DROSOPHILA CILIFEMORATA* COMPLEX

10. ♂: Labellum lacking sclerotized black rim. Vibrissae heavily setose (Fig. 36). Forefemora heavily setose, foretibia and foretarsi heavily ciliated (Fig. 43). Wings subhyaline with large dark brown infuscations at apex and over crossvein dm-cu. Also with pale brown mark extending along basal portion of vein M₁. ♀: Wing maculations distinct, but more diffuse. Apical mark may diffuse into infuscation over crossvein dm-cu. Shading over crossvein dm-cu may extend beyond crossvein r-m in cells r₄+5 and dm. Ovipositor large, distinctive (Fig. 49) ... (Maui) *nigra* Grimshaw
- Labellum of ♂ with sclerotized black rim. Wing maculations of both sexes not as above 11
11. Two humeral setae present 12
- Only 1 humeral seta present 15
12. Tibia and tarsi of ♂ not ornate, lacking elongate cilia 13
- Male tibia ciliated on ventral surface; tarsi with both posterodorsal and posteroventral cilia 14
13. ♂: Forefemora not ciliated. Wings with distinct apical infuscation filling apical 1/4, extending ca. 2/3 of distance to crossvein dm-cu from wing margin. ♀: Wing markings less distinct, often divided into pale brown infuscations along apical portions of veins R₂₊₃, R₄₊₅, and M₁. Rarely, males have apical wing spot divided as in females, but maculations much darker ... (O'ahu) .
..... *tanytarsis* Hardy & Kaneshiro, n. sp.
- ♂: Forefemora ciliated on anteroventral surface. Wings with broad dark brown band, which extends through the middle of wing from costa at level of crossvein dm-cu. ♀: Lacking cilia on forefemora. Wings as in male ... (Maui, Moloka'i, Hawai'i) *cilifemorata* Hardy
14. ♂: Front tibia with long, erect ventral cilia on apical 2/5; front tarsi with erect setae on posteroventral and anteroventral surfaces. Wings with prominent brown markings over apical 1/4 and in region of crossvein dm-cu. Infuscation of dm-cu crossvein extends 1/2 distance to R₄₊₅. ♀: Lacking ornamentation on forelegs. Wing maculations as in male. Coxae and femora of both sexes dark brown to black; tibia, tarsi and trochanters yellow ... (Hawai'i, Maui)
..... *iki* Bryan

- δ : Front tibia with several moderately long erect cilia on apical 1/3 of posteroventral surface; front tarsi with conspicuous cilia on posteroventral and anteroventral surfaces. Wings with prominent markings over apical 1/4, extending slightly beyond M_1 , and crossvein dm-cu. Legs entirely yellow. $\varnothing$: not known ... (O'ahu) *swezeyi* Hardy
- 15. δ : Wings tinged with brown, straight sided and long, nearly 4 $\times$ longer than wide. Dark brown maculations present over apex of wing and in broad band extending over crossvein dm-cu into medial portion of cell r4+5. Wing base and crossvein r-m show slight infuscation. Front basitarsus subequal to tibia. $\varnothing$: Wings not so elongate, with same markings as male but more darkly fumose in ground color. Basitarsus distinctly shorter than tibia ... (Maui) *dolichotarsis* Hardy
- Wings and legs not as above 16
- 16. δ : Wings long, nearly 4 $\times$ longer than wide, but not straight sided. Broad brown transverse band across middle of wing. Apex of wing also infuscated. Front basitarsus 2/3 length of tibia ... (Maui) *stenoptera* Hardy
- Maculations restricted to apex and posterior crossvein, broad transverse band not evident ... 17
- 17. Apical maculation dark brown, covering 1/3 of wing, nearly extending to crossvein dm-cu. Spot over crossvein dm-cu diffusing along vein CuA1 ... (Moloka'i) *venusta* Hardy
- Wings markings not as extensive. Infuscation over dm-cu crossvein sometimes faint, inconspicuous 18
- 18. Femora of δ entirely yellow. Females with palpi and antennae mostly yellow, tinged with brown ... (Maui) *inciliata* Hardy & Kaneshiro
- Femora of δ with light brown preapical streak. Palpi and antennae of females entirely black ... (Hawai'i) *longiperda* Kambysellis

IIa1. The *venusta* cluster

Drosophila inciliata Hardy & Kaneshiro

Figs. 20a, 21, 23, 31

Drosophila inciliata Hardy & Kaneshiro, 1968: 251.

DIAGNOSIS: *Drosophila inciliata* is most closely related to *D. longiperda*. Males of *D. inciliata* can be differentiated from those of *D. longiperda* having femora entirely yellow, lacking a preapical streak of pale brown coloration on the posterior surface. Females can be distinguished by having the palpi yellow, tinged with brown at apex; the first antennal segment mostly yellow, the second mostly yellow, tinged with brown on the dorsum and third mostly brown.

DESCRIPTION: δ , $\varnothing$. In addition to those characters described in Hardy & Kaneshiro (1968), we add the following. *Head*. Arista with 6–8 supernumerary hairs (Fig. 21). *Thorax*. Coloration of sternopleuron shows some variation, either entirely black or dark reddish brown, tinged with black or dark rufous, tinged with brown. Posterolateral portions of mesonotum rather thickly covered with ca. 17 moderately long setae (Fig. 23). *Abdomen*. Ovipositor rounded at apex with ca. 11 peg ovisensilla (Fig. 31). Five long, pointed dorsolateral peg ovisensilla present. Ventral margin with row of ca. 11 peg ovisensilla extending to 3/4 ovipositor length (Fig. 31). Apical setae long, roughly equal to width of ovipositor.

Eggs/Developmental Biology. Kambysellis & Craddock (1991) have studied the ovarian development and insemination patterns of this species.

MEASUREMENTS: N = 4 δ . TL = 1.9 mm (1.7–2.0); WL = 4.1 mm (4.0–4.2); TL/WL = 0.5 (0.4–0.5); HW = 1.4 mm (1.2–1.5); HW/TL = 0.7; CI = 4.4 (4.0–4.8); 4V = 1.2 (1.2–1.3); 5X = 1.4 (1.2–1.7); 4C = 0.4 (0.4–0.5); M = 0.4 (0.3–0.4). N = 3 $\varnothing$. TL = 2.0 mm (1.8–2.1); WL = 4.3 mm (4.1–4.6); TL/WL = 0.5 (0.4–0.5); HW = 1.3 mm (1.2–1.4); HW/TL = 0.7 (0.6–0.7); CI = 5.1 (4.3–6.0); 4V = 1.3; 5X = 1.2 (1.1–1.3); 4C = 0.4 (0.4–0.5); M = 0.3.

TYPES: MAUI: Holotype δ (BPBM 8,927), Waikamoi, 4,000 ft, 23.vii.1965, DEH, axillary cell torn on left wing (Evenhuis, 1982). Not measured. Allotype: $\varnothing$ (BPBM 8,927a), same collection as type. Not measured.

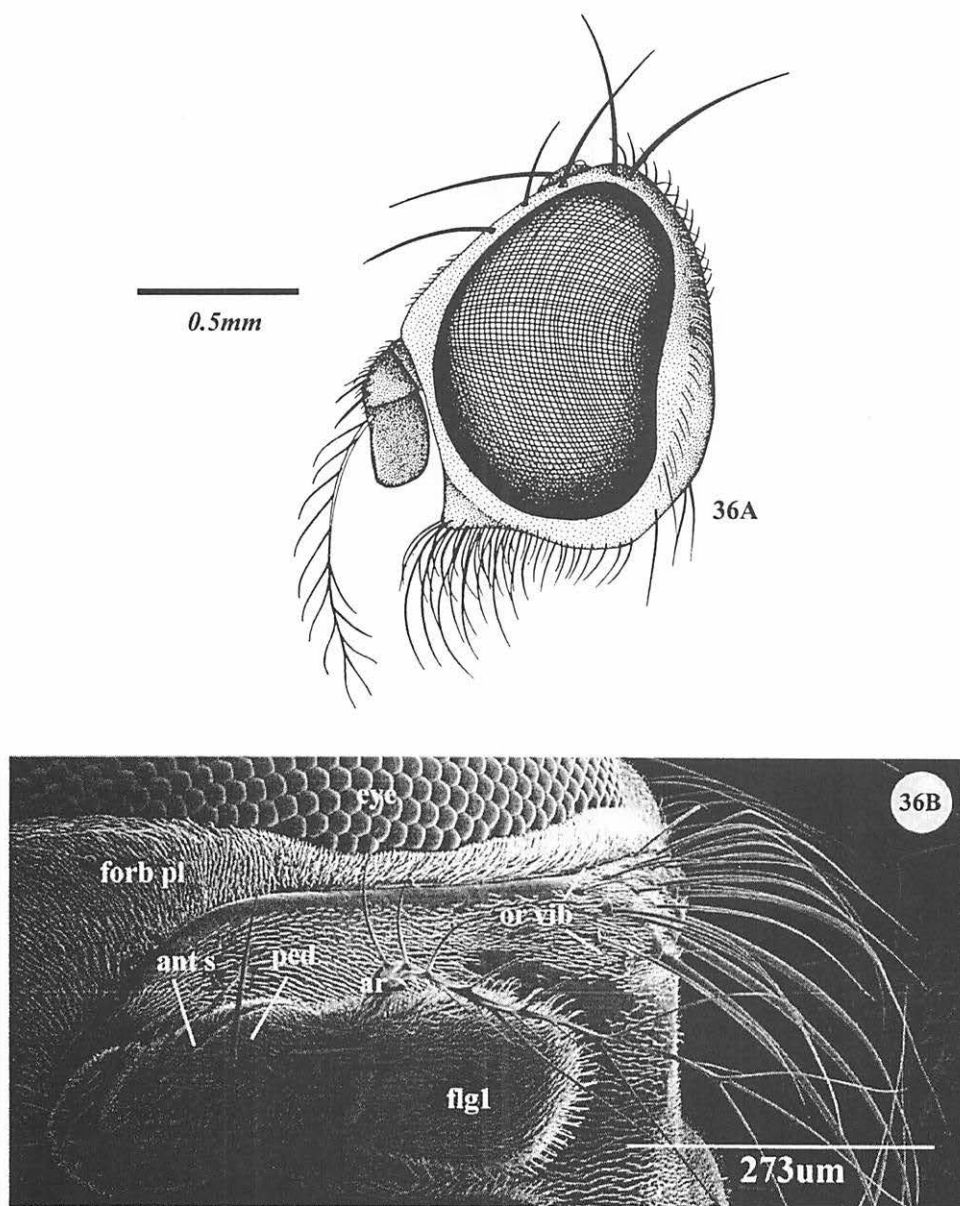


Figure 36. *Drosophila nigra*. a. Head, lateral. b. Facial chaetotaxy. Abbreviations: ant s = antennal suture, ar = arista, flg1 = first flagellomere, forb pl = fronto-orbital plate, or vib = oral vibrissae, ped = pedicel.

Eight paratypes, 4 males and 4 females, are in the UHM. All are from Waikamoi Forest Preserve. 1 ♀, 9–11.vi.1964, HLC; 1 ♂, 2.vii.1964, HLC; 1 ♀, 28.v.1965, DEH; 1 ♂, 1 ♀, 29.vi.1965, HLC & LHT; 1 ♂, 4,000 ft, 23.vii.1965, DEH; 1 ♂, 1 ♀, 15.x.1965, JPM.

MATERIAL EXAMINED: MAUI: Fifteen other specimens (not paratypes), 14 males and 1 female, were studied from the UHM. The majority of these collections were made in Waikamoi Forest Preserve. 1 ♂, 8.vii.1965, JPM; 1 ♂, 11.vii.1965, HTS; 1 ♂, 24.ix.1965, JPM; 1 ♂, 15.x.1965, JPM; 1 ♂, 24.xii.1965, JPM; 1 ♂, 14.vii.1966, JPM; 4 ♂, 7.ii.1967, JPM; Above dry forest, 4,600 ft, 12.x.1967, KYK; 3 ♂, 1 ♀, 10.v.1974, HTS. Other collections from Maui include: 1 ♂, Auwahi, 11.vii.1974, KYK. Specimens in the AMNH include: 1 ♂, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.K, PMO; 7 ♂, Hana'ula, 15–16.vi.1999, OG72.C, PMO, KYK, KTK, & YK.

DISTRIBUTION: This species is known only from Maui (Fig. 20a).

DISCUSSION: *Drosophila inciliata* and *D. longiperda* are very closely related, as the lack of morphological characters separating them suggests. Developmental data from the ovaries and insemination patterns, however, indicate that they are quite distinct (Kambyzellis & Craddock, 1991).

Drosophila longiperda Kambyzellis

Figs. 20b, 24, 27, 29, 32

Drosophila longiperda Kambyzellis, 1993: 425.

Drosophila longiperdis Kambyzellis, 1993: 422. *Incorrect original spelling.*

Drosophila longipedis Craddock & Kambyzellis, 1997: 479, 482, 484, 485. *Incorrect subsequent spelling.*

DIAGNOSIS: *Drosophila longiperda* males can be differentiated from other closely related species in this clade by having a pale brown preapical streak on the posterior surface of each femur. The females can be distinguished by having the palpi and antennae black, the antennal furrows dark brown, and a dark brown preapical streak on the posterior portion of each femur.

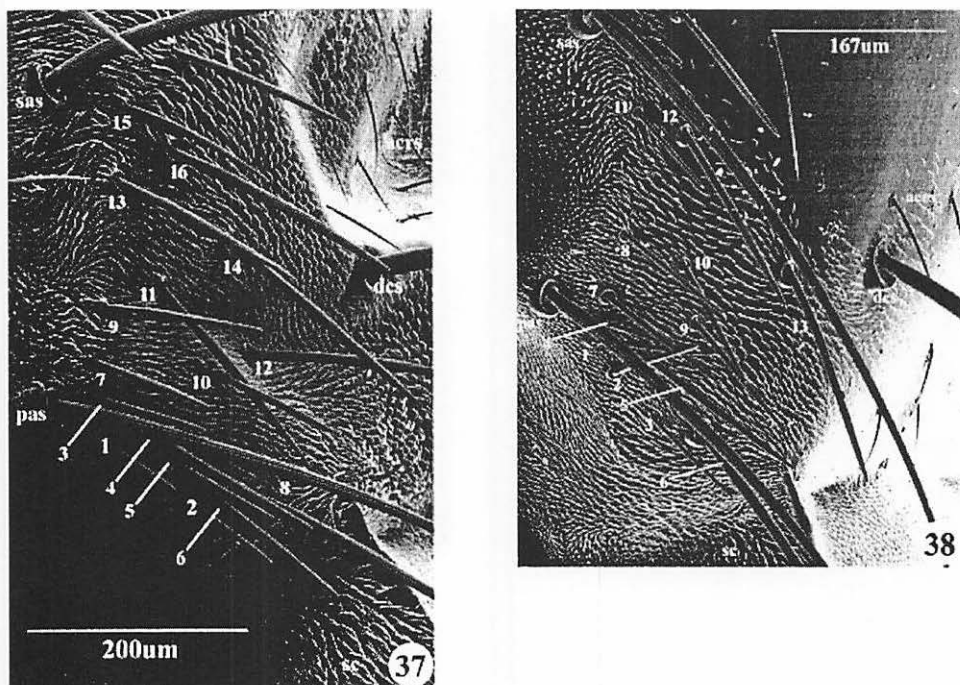
DESCRIPTION: ♂, ♀. This species closely fits the description of *D. inciliata*, except as noted above and discussed below. *Head.* Antennae and palpi entirely yellow in males. Antennae, palpi and clypeus of females mostly dark brown to blackish. Upper 1/2 of front black. Face of females discolored with brown. Females lack sclerotized black rim on labellum. *Thorax.* Pleura entirely black. Mesonotum polished black, bare of pollen except on margins. Roughly 13 setae arranged on posterolateral portions of mesonotum, as shown in Fig. 24. *Legs.* Front legs long and slender. Basitarsus subequal in length to tibia (Fig. 27). *Wings.* Crossvein dm-cu faintly infuscated. Apical infuscation extensive, extending ca. 1/3 wing length, nearly to level of dm-cu (Fig. 29). *Abdomen.* Ovipositor rounded at apex with cluster of 9–10 peg ovisensilla (Fig. 32). Four, pointed dorsolateral peg ovisensilla present. Ventral margin with row of ca. 8 peg ovisensilla extending to roughly 3/4 ovipositor length (Fig. 32). Apical setae long, roughly 4/5 ovipositor width.

Eggs/ Developmental Biology. Kambyzellis (1993) examined the ultrastructure of the egg chorion of this species.

MEASUREMENTS: N = 11 ♂. TL = 1.9 mm (1.6–2.3); WL = 4.5 mm (3.9–5.1); TL/WL = 0.4 (0.4–0.5); HW = 1.4 mm (1.1–1.6); HW/TL = 0.7 (0.6–0.8); CI = 4.7 (4.3–5.3); 4V = 1.2 (1.1–1.3); 5X = 1.5 (1.3–1.7); 4C = 0.5 (0.4–0.5); M = 0.3. N = 11 ♀. TL = 1.9 mm (1.6–2.2); WL = 4.1 mm (3.3–5.3); TL/WL = 0.5 (0.4–0.5); HW = 1.4 mm (1.1–1.5); HW/TL = 0.7; CI = 4.4 (4.0–4.8); 4V = 1.2 (1.1–1.3); 5X = 1.4 (1.1–1.8); 4C = 0.5 (0.4–0.6); M = 0.3 (0.3–0.4).

TYPES: Holotype ♀. The holotype of this species is the egg chorion described by Kambyzellis (1993). This specimen has been lost.

MATERIAL EXAMINED: HAWAII: 4 ♂, 3 ♀, 'Ōla'a, Volcano Experimental Station Forest, 21.ii.1976, KYK.. TL = 1.9 mm; WL = 4.6 mm; TL/WL = 0.4; HW = 1.4 mm; HW/TL = 0.7; CI = 4.9; 4V = 1.3; 5X = 1.7; 4C = 0.5; M = 0.3. TL = 2.2 mm; WL = 4.9 mm; TL/WL = 0.4; HW = 1.5 mm; HW/TL = 0.7; CI = 4.3; 4V = 1.2; 5X = 1.4; 4C = 0.5; M = 0.3. Thirty-six males and 85 females have been examined. 1 ♀, 'Ōla'a, Forest Reserve, 3,775 ft, 3.ix.1965, KYK; 1 ♂, Hōnaunau Forest Reserve, 8.ii.1966, KYK; 1 ♀, Pawaina, 3,100 ft, 18.vii.1966, HLC; 1 ♂, 2 ♀, Pu'u Lala'au, Kohala Mountains, 4,000 ft, 24–25.vi.1969, KYK; 1 ♂, 'Ōla'a Forest Reserve, Kilauea, 23.iv.1974, HTS; 1 ♂, Bird Park, Kilauea, 25.vii.1975, 1220 m, HTS; 1 ♀, Mauna Loa Strip Road, 1,380 m, 25.vii.1975, HTS; 2 ♀, Upper 'Ōla'a Forest Reserve, Wright Road, 25.vii.1975, HTS; 1 ♀, Kahuku Ranch,



Figures 37–38. Posterolateral regions of the mesonotum of some *Drosophila cilifemorata* complex species. 37. *D. cilifemorata*, 38. *D. dolichotarsis*.

3,800 ft, 12.viii.1975, KYK; 1♂, 1♀, Upper 'Ōla'a Forest, 19.vii.1976, HLC & KYK; 5♀, Halepuila Road, Kapu'a (land section), South Kona, 4,650 ft, vii.1977, DEH; 1♀, Kīpuka Kī, Mauna Loa Strip Road, 20–23.ix.1977, HTS; 1♂, 3♀, Bend in Wright Road, 'Ōla'a Tract, 23.vii.1977, KYK; 1♂, 1♀, Wright Road, Pole #44, 23.ix.1977, HTS; 17♂, 53♀, Waihaka Gulch, Ka'u Forest Reserve, 3,800–4,000 ft, 23–30.iii.1978, KYK; 2♂, 6♀, Kohala, 26.vii.1980, ATO; 3♂, 5♀, Maulua Forest Reserve, 5,200 ft, 13.x.1980, KYK; 3♂, Hakalau Forest National Wildlife Refuge, 6–7.ii.1999, OG48.3, PMO & SLM.

DISTRIBUTION: This species is known only from the island of Hawai'i (Fig. 20b).

ETYMOLOGY: Greek, "long foot", indicating the long and slender front legs of this species.

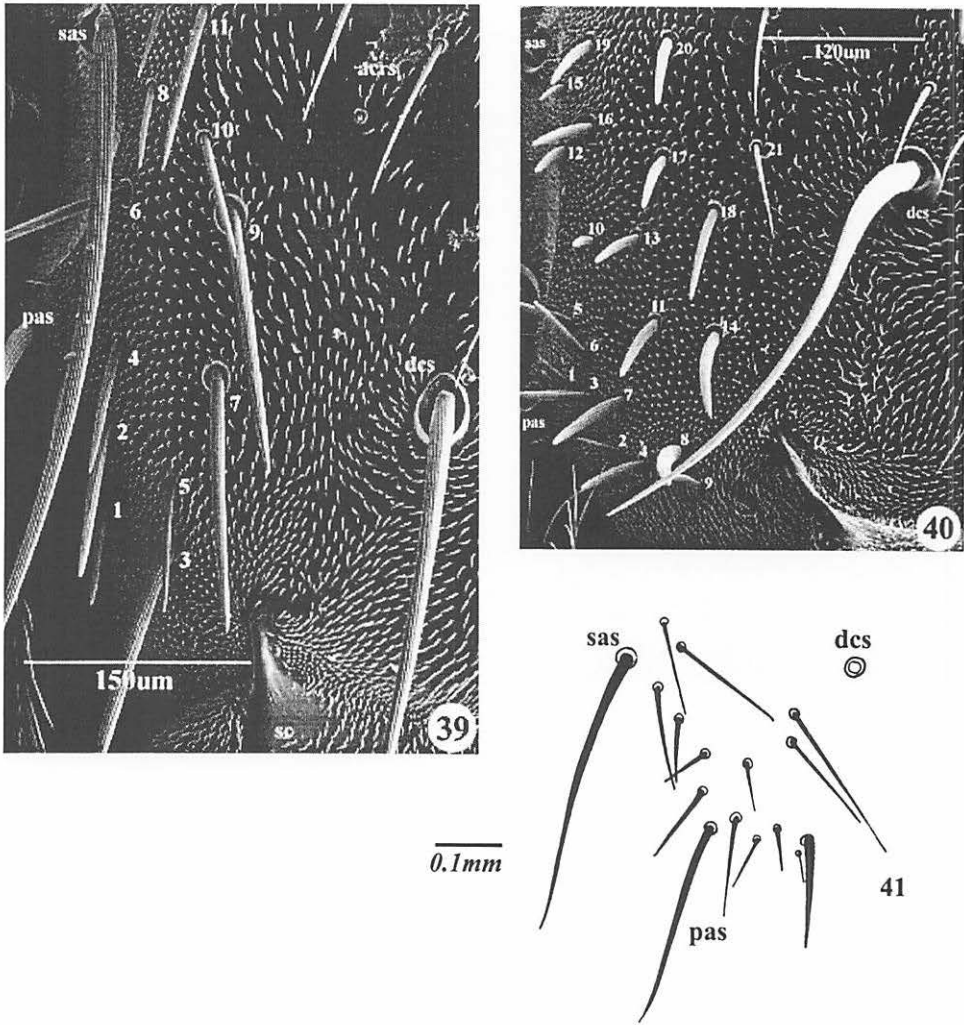
MOLECULAR BIOLOGY: Nucleotide sequences for the *hunchback* (U93010, U93011), *wingless* (U94567, U94568), *acetylcholinesterase* (U94274), *alcohol dehydrogenase* (U94200), *cytochrome oxidase III* (U94232), *16S* (U94246), *ND1* (U94259), and *cytochrome oxidase II* (U94216) have been determined for this species (Baker & DeSalle, 1997). This species is referred to as "*Drosophila* sp." in table 3 and WTS10n in many figures in Baker & DeSalle (1997).

DISCUSSION: This species has previously been treated as a population of *D. inciliata*-like from Hawai'i. More careful examination of developmental characteristics (Kambysellis & Craddock, 1991) indicated that *D. longiperda* and *D. inciliata* are distinct species.

***Drosophila tanytarsis* Hardy & Kaneshiro, new species**

Figs. 20c, 22, 25, 28, 30, 33

DIAGNOSIS: *Drosophila tanytarsis* differs from all other members of this complex by having 2



Figures 39-41. Posterolateral regions of the mesonotum of some *Drosophila cilifemorata* complex species. 39. *D. iki*, 40. *D. nigra*, 41. *D. stenoptera*.

strong, subequal, humeral setae. It also differs by having an relatively small apical wing spot that fills only ca. the apical 1/4 of the wing and extends ca. 2/3 the distance from wing margin to cross-vein dm-cu.

DESCRIPTION: ♂, ♀. *Head*: Eyes reddish brown with short inconspicuous pile. Head and appendages mostly yellow in males. Females with third antennal segment mostly brown, palpi tinged with brown on apical 1/2, and clypeus and lower portion of face tinged with brown laterally. Upper 1/2 of occiput, bounded by postocel-

lar setae, ocelli and ocellar triangle, black. Ocellar triangle polished reddish brown, devoid of pollen except in area bounded by ocelli. Orbits reddish brown to level with proclinate setae. Upper parafrontalia rufous with faint tinge of brown. Lower reclinate setae situated slightly above proclimates. Each arista with 7 dorsal, 3 ventral rays in addition to apical fork. Inner margin of arista with 5–6 short inconspicuous, well spaced hairs. Genae ca. 1/5 the width of eye. Each palp with 2 apical or subapical setae, plus numerous black setae around apex (Fig. 22). *Thorax*. Mostly polished black in ground color. Lower 1/2 of pleuron and the apical portion of scutellum yellow. Mesonotum completely bare of pollen except on margins. Anterior katepisternal setae well developed, ca. 2/3 length of posterior katepisternals, also with prominent black seta between katepisternals. Posterolateral region of mesonotum with ca. 9 setae, arranged as in Fig. 25. *Legs*. Entirely yellow. Front basitarsus ca. 4/5 as long as tibiae (Fig. 28). *Wings*. Markings of males as described above (Fig. 30). In some specimens brown apical mark may be divided into streaks along apices of the veins. In females, wing markings are less extensive; apical spot divided into pale brown marks along each apex of veins R_{2+3} , R_{4+5} and M_1 . The markings paler brown, not so dark and conspicuous as in the male. Crossvein dm-cu only weakly infuscated. *Abdomen*. Entirely polished black with gray pollen over first tergum, most of median portion of second, and extending onto median portion of third. Ovipositor rounded at apex, with 9 apical peg ovisensilla (Fig. 33) Dorsal margin with 4 long pointed peg ovisensilla. Ventral margin with ca. 8 peg ovisensilla extending to 3/4 ovipositor length. Apical setae ca. 1/2 ovipositor width (Fig. 33). Spermathecae small and weakly sclerotized.

MEASUREMENTS: N = 11 ♂. TL = 1.7 mm (1.3–2.0); WL = 3.4 mm (2.7–3.9); TL/WL = 0.5; HW = 1.1 mm (1.0–1.4); HW/TL = 0.8 (0.7–0.8); CI = 4.6 (4.0–5.4); 4V = 1.2 (1.1–1.3); 5X = 1.2 (1.0–1.7); 4C = 0.5 (0.4–0.5); M = 0.3 (0.2–0.3). N = 11 ♀. TL = 1.6 mm (1.4–1.8); WL = 3.2 mm (2.9–3.7); TL/WL = 0.5; HW = 1.2 mm (1.1–1.3); CI = 4.5 (4.0–5.0); 4V = 1.2 (1.1–1.3); 5X = 1.5 (1.2–1.7); M = 0.3 (0.3–0.4).

TYPES: O'AHU: Holotype ♂ (BPBM 16,357), Mt Ka'ala, 4,000 ft, 22.viii.1974, JO & SLM. TL = 1.7 mm; WL = 3.5 mm; TL/WL = 0.5; HW = 1.3 mm; HW/TL = 0.7; CI = 4.7; 4V = 1.1; 5X = 1.1; 4C = 0.5; M = 0.3. Allotype: ♀ (BPBM 16,357a), same information as type. TL = 1.8 mm; WL = 3.6 mm; TL/WL = 0.5; HW = 1.3 mm; HW/TL = 0.7; CI = 5.0; 4V = 1.1; 5X = 1.1; 4C = 0.4; M = 0.3. Thirty-one paratypes, 13 males and 18 females, are designated. 7 ♂, 7 ♀, same collection as type. 6 ♂, 11 ♀, Mt Ka'ala, 4,000 ft, 2.x.1975, HTS & KYK. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: *Drosophila tanytarsis* is known only from O'ahu (Fig. 20c).

ETYMOLOGY: Greek, "outstretched tarsus", indicative of the long tarsal segments this species.

Drosophila venusta Hardy

Figs. 20d, 26, 34

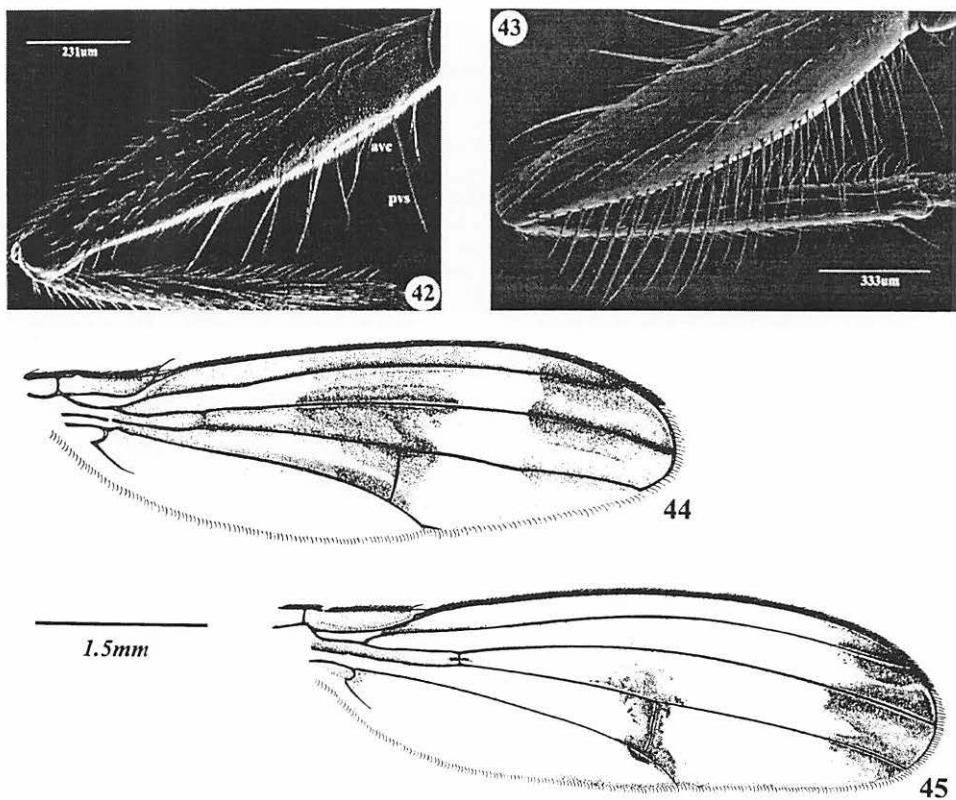
Drosophila venusta Hardy, 1965: 502.

DIAGNOSIS: *Drosophila venusta* differs from closely related species in this group by having the front mostly yellow with slight tinges of brown in the parafrontal areas and a black streak along each eye orbit extending almost to the proclinate setae, the apical wing mark extending almost to a level with crossvein dm-cu, the dark brown mark over crossvein dm-cu large and somewhat diffuse, and the sternopleuron completely yellow. Females can be differentiated by a combination of the above characters and by lacking a preapical brown streak on the posterior surface of the front femur.

DESCRIPTION: ♂, ♀. Hardy (1965) provides a description of the males. Here we add several male characters and describe the female of this species. *Head*. Parafrontal areas tinged darker brown, third antennal segment, clypeus and palpi brown in females. *Thorax*. Female sternopleuron rufous, tinged with brown. Posterolateral portions of mesonotum rather densely covered with ca. 16 strong setae (Fig. 26). Mesonotum polished black, devoid of pollen except on margins. *Abdomen*. Ovipositor rounded at apex with ca. 10 stout peg ovisensilla (Fig. 34). Dorsal and lateral margins with 7 longer pointed peg ovisensilla. Lateral margin with 7 peg ovisensilla that extend ca. 3/4 ovipositor length. Apical setae long, ca. 1/2 ovipositor width (Fig. 34).

MEASUREMENTS: N = 1 ♀. TL = 1.9 mm; WL = 4.2 mm; TL/WL = 0.5; HW = 1.4 mm; HW/TL = 0.7; CI = 2.3; 4V = 1.4; 5X = 1.5; 4C = 0.5; M = 0.4.

TYPES: MOLOKA'I: Holotype ♂ (BPBM 6,465), Pu'u Kolekole, 3,600 ft, vii.1952; MT, left midleg and right hindleg beyond coxae, and abdomen beyond 3rd segment missing, genitalia in microvial mounted below specimen (Evenhuis, 1982). Not measured.



Figures 42-45. Thoracic structures of some *Drosophila cilifemorata* cluster species. 42. *D. cilifemorata*, male foreleg (130 ×), 43. *D. nigra*, male foreleg (90 ×), 44. *D. cilifemorata*, wing, 45. *D. dolichotarsis*, wing.

MATERIAL EXAMINED: MOLOKA'I: Several specimens in the UHM were studied. 1 ♂, Kainalu Gulch, 9.v.1963, DEH; 1 ♂, Hanalilolilo, 9-11.i.1975, WI; 4 ♂, 18 ♀, South of Hanalilolilo, 9.i.1975, ATO; 12 ♂, 25 ♀, same information as allotype.

DISTRIBUTION: This species is known only from Moloka'i (Fig. 20d).

IIa2. The *cilifemorata* cluster*Drosophila cilifemorata* Hardy

Figures 35a, 37, 42, 44, 46

Drosophila cilifemorata Hardy, 1965: 209.

DIAGNOSIS: *Drosophila cilifemorata* can be distinguished from closely related members of this clade by having a broad dark brown band across the middle of the wing from costa at level with crossvein dm-cu (Fig. 44), antennae predominantly black, front coxae tinged with brown, and front femur with a row of moderately long pale cilia down anteroventral surface (Fig. 42).

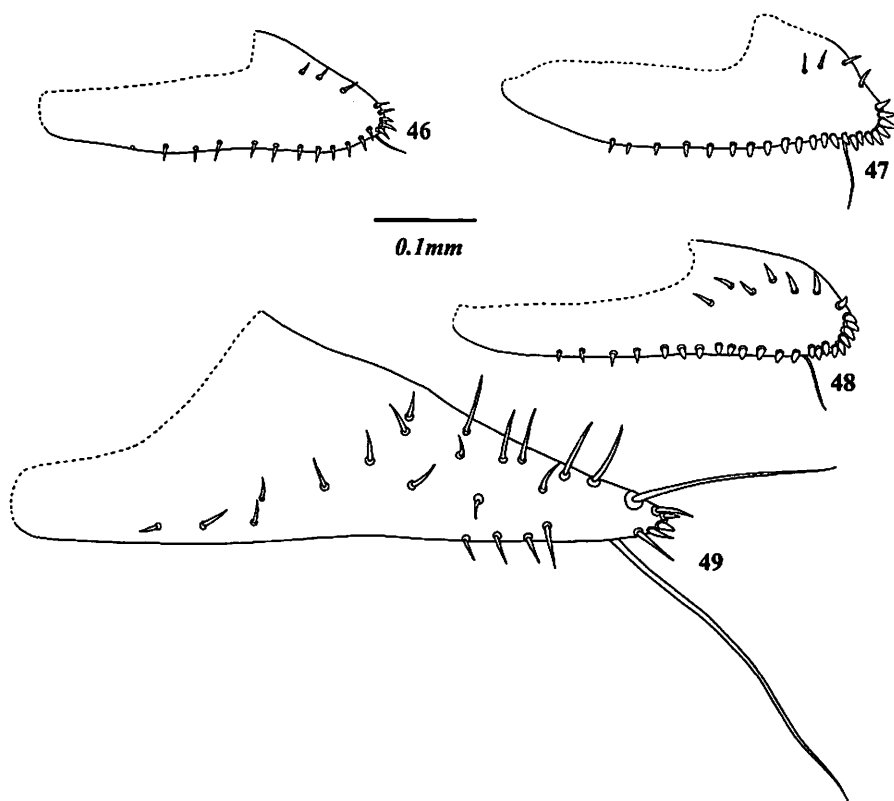
DESCRIPTION: ♂, ♀. The species is readily differentiated by the characters given in Hardy (1965), above, and as follows. *Thorax*. Posterolateral area of mesonotum rather thickly setose, with ca. 16 setae arranged as in Fig. 37. *Abdomen*. Ovipositor rounded at apex (Fig. 46). Ovisensilla relatively long and pointed. Dorsolateral region with 3 peg ovisensilla; apex with cluster of ca. 7 peg ovisensilla; ventral margin with row of ca. 9 peg ovisensilla that extend slightly over 1/2 length of ovipositor. Apical setae ca. 1/2 ovipositor width. *Internal Anatomy*. These are described based on Throckmorton (1966). Spermathecae subspherical to quadrate in shape, lacking an introvert, weakly sclerotized, and not pigmented.

TYPES: MAUI: Holotype ♂ (BPBM 6324), Pu'u Kukui, ca. 3,000–4,000 ft, vi.1953, DEH, apical portion of right arista broken off, abdomen beyond 4th segment missing, genitalia in microvial mounted below specimen, type label data cites altitude as "3000 – 4000 ft", published data is "circa. 4000 ft" (Evenhuis, 1982). Not measured. Allotype ♀ (BPBM 6324a), Waikamoi, 4,000 ft, vii.1956, DEH. Not measured. Four paratypes from the BPBM (18185–18188) have been examined. 3♂, Waikamoi, 11.ii.1966, JPM; 1♂, Upper 'Ōla'a Forest, 16.vi.1964, WBH.

MATERIAL EXAMINED: Additional specimens from Maui, Moloka'i and the Big Island were also studied. MAUI: One hundred thirty-five specimens, 121 males and 14 females, have been examined. Many collections have been made in Waikamoi Forest Preserve: 1♀, 4,000 ft, viii.1958, DEH; 1♂, 4,000 ft, 2.vii.1964, DEH; 1♂, 4,300 ft, 9.vii.1964, HLC; 2♂, 11.vii.1964, LHT; 1♀, 3.x.1964, HTS; 1♂, 21.x.1964, DEH; 2♂, 28.vi.1965, JPM; 3♂, 2.vii.1965, RMB; 1♂, Upper Road, 8.vii.1965, JKF; 2♂, 1♀, 11.vii.1965, HTS; 1♀, 4,000 ft, 23.vii.1965, DEH; 1♂, 30.viii.1965, KYK; 1♂, 9.ix.1965, KYK; 2♂, 1♀, 3.x.1965, HTS; 3♂, 1♀, 15.x.1965, DEH; 1♂, 7.i.1966, DS; 1♂, 26.i.1966, JPM; 7♂, 11.ii.1966, JPM; 1♂, 21.ii.1966, JPM; 9♂, 11.iii.1966, JPM; 2♂, 8.iv.1966, JPM; 3♂, 21.iv.1966, JPM; 3♂, 6.v.1966, JPM; 1♂, 20.v.1966, JPM; 2♂, 1.vii.1966, JPM; 2♂, 10–20.vii.1966, HTS; 1♂, 14.vii.1966, JPM; 1♂, 12.viii.1966, JPM; 1♂, 9.ix.1966, JPM; 2♂, 22.ix.1966, JPM; 1♂, 2.xi.1966, JPM; 2♂, 16.xi.1966, JPM; 5♂, 25.xi.1966, JPM; 1♂, 30.xi.1966, JPM; 3♂, 1♀, 14–16.xii.1966, JPM; 2♂, 27.xii.1966, JPM; 2♂, 27.i.1967, JPM; 4♂, 1♀, 7.ii.1967, JPM; 9♂, 1♀, 22.ii.1967, JPM; 7♂, 2♀, 8.iii.1967, JPM; 1♂, 4.iv.1967, JPM; 1♂, 19.iv.1967, JPM; 2♂, 17.v.1967, JPM; 2♂, 22.vi.1967, JPM; 3♂, 10.v.1974, HTS. Other Maui collections at UHM include: 1♀, Palikū, Haleakalā Crater, 6,500 ft, 23.vii.1963, DEH; 1♂, Pu'u Kukui Ridge, 4.viii.1964, HLC; 1♀, Hana'ula, 4,000 ft, 5.viii.1964, DEH; 1♂, 1♀, Palikū, Haleakalā Crater, 6,500 ft, 27.viii.1964, DG; 1♂, Hana'ula, 4,000 ft, 7–8.v.1968, JPM; 1♂, Pu'u Kukui Ridge, 4,000 ft, 20.vii.1971, DEH; 14♂, Pu'u Kukui Trail, 4,250 ft, 21.viii.1971, DEH; 1♂, Hanawī Ridge Trail, 6,500 ft, 3.viii.1973, SLM; 1♂, Trail to Pu'u Kukui, 3,500 ft, 17.ix.1975, KYK. Two individuals from the AMNH has been studied. 1♂, Heed Trail, Waikamoi Forest Preserve, 16–18.iii.1999, OG55.7, PMO & JBS; 1♀, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.9, PMO. MOLOKA'I: Six specimens, 4 males and 2 females were studied from the UHM. 1♂, Kawela, 14.xii.1956, JWB; 1♂, Pēpē'ōpae, 4,000 ft, 30.v.1959, DEH; 1♂, South of Hanalilolilo, 21.xii.1965, KYK; 1♂, 2♀, South of Hanalilolilo, 9.i.1975, ATO. One individual from the AMNH has also been examined. 1♀, Nature Conservancy Cabin, Pu'u Kolekole, 19–21.iii.1999, OG58.3, PMO & JBS. HAWAII: Fourteen specimens in the UHM, 12 males and 2 females, were examined. 1♂, Pauahi, viii.1952, DEH; 1♂, Upper 'Ōla'a Forest, 3.iv.1965, KYK; 3♂, Kahuku Ranch Road, South Kona, 3,800 ft, 20.v.1975, KYK; 1♂, 1♀, Kīlauea Forest Preserve, Volcano, 3.vi.1975, no collector given; 3♂, Kahuku Ranch Road, 3,800 ft, KYK; 2♂, Kahuku Ranch, Kahuku, 19–21.vii.1977, no collector given; 1♂, 1♀, Kohala, 26.viii.1980, ATO. One individual in the AMNH has been examined. 1♂, Stainback Road, Near Kulani Correctional Facility, 7–8.ii.1999, OG49.5, PMO & SLM.

DISTRIBUTION: This species is known from Maui, Moloka'i, and Hawai'i (Fig. 35a).

MOLECULAR BIOLOGY: Partial sequences of the *16S* and *ND1* genes (S45477) have been determined (DeSalle, 1992). One individual from OG49.5 is in the AMNH-MC collection.



Figures 46-49. Ovipositors of cilifemorata cluster females. 46. *D. cilifemorata*, 47. *D. dolichotarsis*, 48. *D. iki*, 49. *D. nigra*.

***Drosophila dolichotarsis* Hardy**

Drosophila dolichotarsis Hardy, 1966: 206.

Figs. 35b, 38, 45, 47

DIAGNOSIS: *Drosophila dolichotarsis* is the largest, most showy of the *haleakalae* group species. It is characterized by its large size, ornately pictured wings that are nearly straight sided and ca. 4 × longer than wide (Fig. 45), and long slender legs with front basitarsus subequal to tibia.

DESCRIPTION: ♂, ♀. Hardy (1966) provided a description of the males of this species. An additional characteristic not mentioned in the original description is the presence of ca. 13 dense setae on the posterolateral portion of the mesonotum (Fig. 38). A full description of female characters that differ from those of the male follows: *Head*. Third antennal segment, tips of palpi and clypeus brown. *Thorax*. Entirely black except for yellow spot at tip of scutellum. *Legs*. Normal in proportion; front basitarsus distinctly shorter than tibia. *Wings*. Normal in shape, not so conspicuously elongate. More dusky fumose than male, but with similar pattern of maculations. *Abdomen*. Apex of ovipositor somewhat acute, with dense cluster of ca. 9 long, pointed peg ovisensilla (Fig. 47). Two peg ovisensilla present on dorsal margin. A series of ca. 13 ovisensilla extend along ventral margin ca. 3/4

of length of ovipositor. Apical setae relatively long, approximately 3/4 ovipositor width.

Eggs/ Developmental Biology. Kambyssellis & Craddock (1991) and Kambyssellis (1993) have examined the ovarian development, insemination patterns, and ultrastructure of the egg chorion of this species. The species they refer to as *D. dolichotarsus* is *D. dolichotarsis*.

MEASUREMENTS: N = 2♂. TL = 2.3 mm (2.2–2.4); WL = 6.3 mm; TL/WL = 0.4 (0.3–0.4); HW = 1.6 mm (1.5–1.7); HW/TL = 0.7; CI = 6.0; 4V = 1.3 (1.2–1.3); 5X = 0.9 (0.7–1.0); 4C = 0.4; M = 0.2. N = 1♀. See allotype.

TYPES: MAUI: Holotype ♂ (BPBM 11.260), Waikamoi, 11–15.vii.1964, HLC. Not measured. Allotype ♀, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK, right 3rd antennal segment missing (Evenhuis, 1982). TL = 2.1 mm; WL = 4.9 mm; TL/WL = 0.4; HW = 1.4 mm; HW/TL = 0.7; CI = 7.4; 4V = 1.2; 5X = 0.9; 4C = 0.3; M = 0.3. Two paratypes in the UHM, both males, have been examined from Waikamoi Forest Preserve: 1♂, 8.vii.1964, LHT; 1♂, 11–15.vii.1964, HLC.

MATERIAL EXAMINED: MAUI: Twenty-four other specimens, 16 males and 8 females, have also been studied from the UHM. The majority of collections were made in Waikamoi Forest Preserve: 1♂, 11.vii.1965, HTS; 1♂, 3.viii.1965, KYK; 1♂, 15.x.1965, JPM; 1♂, 7.i.1966, JPM; 1♀, 29.iii.1966, JPM; 1♂, 8.iv.1966, JPM; 1♂, 21.iv.1966, JPM; 1♂, 1♀, 30.xi.1966, JPM; 1♂, 22.ii.1967, HTS; 2♂, 4.iv.1967, JPM; 3♂, 19.iv.1967, JPM; 1♀, 11.iv.1968, MPK; 2♂, 4♀, 10.v.1974, HTS. Other collections include: 1♂, Trail to Honomanū Valley, 5,300 ft, 24.vii.1965, KYK; 1♀, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK. Several specimens from the AMNH have also been examined. 5♂, Z68, MPK; 2♀, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.D, PMO.

DISTRIBUTION: This species is known from the island of Maui (Fig. 35b).

MOLECULAR BIOLOGY: Several accessions of this species are present in the AMNH-MC.

DISCUSSION: The females show rather striking dimorphism in several characters when compared to the males.

Drosophila flaviceps Grimshaw

Drosophila flaviceps Grimshaw, 1901: 63; Hardy, 1965: 275.

DISTRIBUTION: Hawai'i, Kona, 3,500 ft.

DISCUSSION: Hardy (1965) noted that the type of this species, which was originally deposited in the BMNH, has been lost. The label and pin are present, but the specimen and nadel are missing. It is impossible to place this species based on Grimshaw's (1901) meager description, and it should be treated as a *nomen dubium*.

Drosophila iki Bryan

Figs. 35c, 39, 48

Drosophila nigra var. *iki* Bryan, 1934: 439.

Drosophila iki Hardy, 1965: 310.

DIAGNOSIS: *Drosophila iki* is differentiated from other species in this subgroup by having 2 humeral setae, the front femur of the male not densely setose, femora brown to black, and the face yellow with brown to black tinges.

DESCRIPTION: ♂, ♀. Characters other than those previously published (Bryan, 1934; Hardy, 1965) include: *Thorax*. About 11 setae present on posterolateral portions of mesonotum, arranged as in Fig. 39. *Abdomen*. Ovipositor with rounded apex (Fig. 48). Eight long, pointed lateral peg ovisensilla extend from dorsal margin, across lateral surface, and to ca. 1/2 ovipositor length on ventral side (Fig. 48). Ten ventral ovisensilla ca. 1/2 length of laterals, extending to 2/3 ovipositor length. Apex with ca. 10 blunt peg ovisensilla, slightly longer than ventrals. Apical setae short, ca. 1/4 ovipositor width (Fig. 48).

Eggs/ Developmental Biology. Kambyssellis & Craddock (1991) have studied the ovarian development and

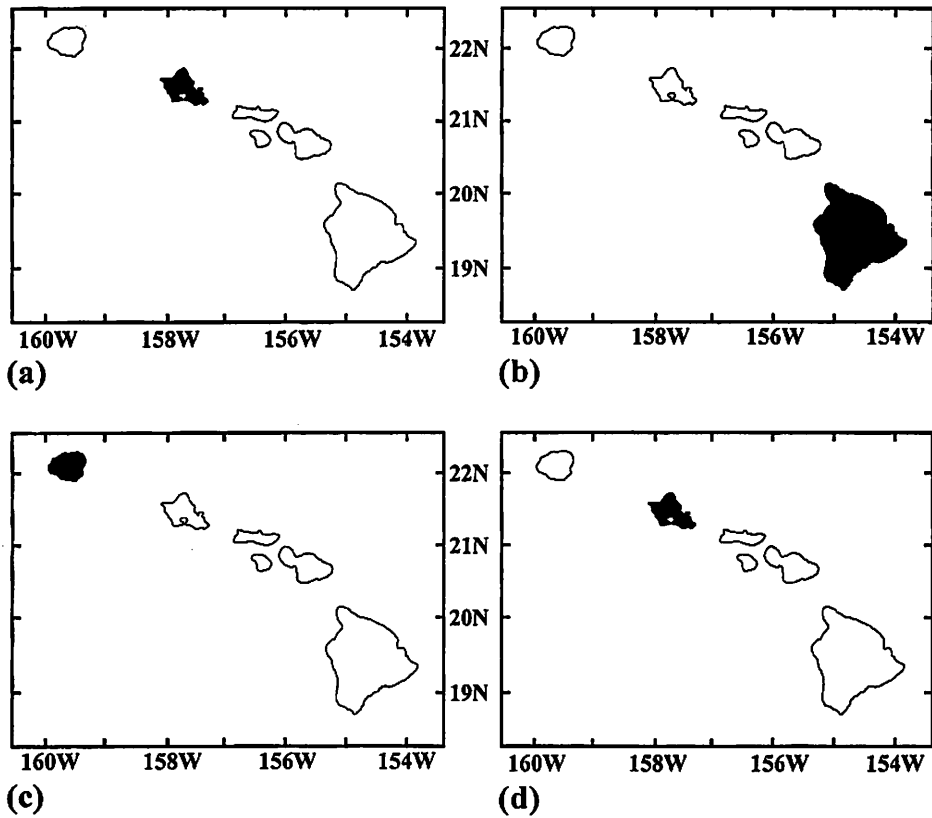


Figure 50. Distribution of species in the *Drosophila denotata* and *Drosophila insignita* complexes. a. *D. denotata* and *D. sabroskyi*, b. *D. chicao*, c. *D. curitarsis*, d. *D. insignita*.

insemination patterns of this species.

MEASUREMENTS: N = 1 ♂. TL = 1.7 mm; WL = 3.5 mm; TL/WL = 0.5; HW = 1.2 mm; HW/TL = 0.8; CI = 4.8; 4V = 1.4; 5X = 0.9; 4C = 0.5; M = 0.3. N = 2 ♀. TL = 1.8 mm (1.7–1.8); WL = 3.5 mm (3.3–3.7); TL/WL = 0.5; HW = 2.5 mm (2.3–2.6); HW/TL = 0.7; CI = 4.5 (4.3–4.7); 4V = 1.2; 5X = 1.0 (0.9–1.1); 4C = 0.5 (0.4–0.5); M = 0.3.

TYPES: HAWAII: Holotype ♂ (BPBM 814), Kilauea, vi.1908, W.M. Giffard. Not measured, apex of right wing torn off, sex of type not designated in original description (Evenhuis, 1982). Four homotypes in the UHM have been examined. 2 ♂, same information as holotype; 2 ♀, Pauahi, viii.1952, DEH.

MATERIAL EXAMINED: HAWAII: Forty-five other specimens, 17 males and 28 females, are available in the UHM. 1 ♂, Ka'u, 4,000 ft, no date or collector given; 1 ♂, Bird Park, Kilauea, 24.vi.1963; HLC; 1 ♂, 4 ♀, Kilauea 4,000 ft, 17.vii.1964, HTS; 1 ♀, Kipuka Ki, 9.ix.1964, HTS; 2 ♀, Hinakapoula, 5,200 ft, 14.vii.1965, HLC; 1 ♂, Kipuka Ki, 24.vii.1965, KYK; 1 ♀, Bird Park, Kilauea, 29.i.1969, MDD; 1 ♀, Pu'u Wa'awa'a, 4,200 ft, 22.xii.1969, KYK; 2 ♀, Kilauea Forest, Volcano, 3.vi.1974, HTS; 1 ♀, Kipuka Ki, 1,285 m., 3.vi.1974, HTS; 1 ♂, 1 ♀, Greenwell Ranch, Pauahi, 27.vi.1974, KYK; 5 ♀, Kipuka Ki, 25–26.vii.1975, HTS; 2 ♀, Greenwell Ranch, Pauahi, 24.x.1975, HTS; 1 ♂, Hualalai Ranch, 3,900 ft, 19.v.1976, HLC; 2 ♂, 1 ♀, Hualalai Ranch, 4,600 ft, 21.v.1976, KYK; 9 ♂, 7 ♀, Halepiula Road, Kapu'a, South Kona, 4,650 ft, vii.1977, DEH. MAUI: Thirty-two individuals in the UHM, 18 males and 14 females, were examined. Several collections were made in Waikamoi

Forest Preserve: 1♀, 29.vi.1964, HLC; 3♂, 3♀, 8.vii.1964, HLC; 1♂, 2♀, 4,300 ft, 9.vii.1964, HLC; 1♀, 29.vi.1965, HLC; 1♂, Pump Road, 5,800 ft, 29.vi.1965, HLC; 2♀, 11.vii.1965, HTS; 4♂, 31.vii.1965, HTS; 1♂, 9.ix.1965, KYK; 1♀, Pump House, 11.ii.1966, JPM; 1♂, Heed's Trail, 22.iv.1967, lw; 1♂, Above Dry Forest, 4,600 ft, 12.x.1967, KYK; 1♂, 11.iv.1968, MPK. Other collections include: 1♂, CH69.11; 2♂, Kula Pipeline, 11.vi.1927, OHS; 1♂, 'Āinahou Valley, 2,900–3,000 ft, 12.vii.1972, DEH; 3♀, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK; 1♂, 1♀, Kaupō Gap, 9.x.1975, KYK. Several individuals from the AMNH have been examined. 3♂, Upper Waikamoi Forest Preserve, Haleakalā National Park, 6.viii.1998, OG41.D, PMO & SLM; 1♀, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.K, PMO; 1♂, Hana'ula, 15–16.vi.1999, OG72.7, PMO, KYK, KTK, & YK.

DISTRIBUTION: This species is known from Hawai'i and Maui (Fig. 35c).

ECOLOGY: *Drosophila iki* breeds in gill fungi (Table 2; Heed, 1968).

MOLECULAR BIOLOGY: Nucleotide sequences for the *hunchback* (U93006, U93007), *wingless* (U94563, U94564), *acetylcholinesterase* (U94272), *alcohol dehydrogenase* (U94198), *cytochrome oxidase III* (U94230), *16S* (U94244), *ND1* (U94257), and *cytochrome oxidase II* (U94214) have been determined for this species (Baker & DeSalle, 1997).

Drosophila nigra Grimshaw

Figs. 35b, 36, 40, 43, 49

Drosophila nigra Grimshaw, 1901: 62; Hardy, 1965: 387.

Drosophila (*Hyphenomyia*) *reburra* Hardy, 1965: 522, new synonymy.

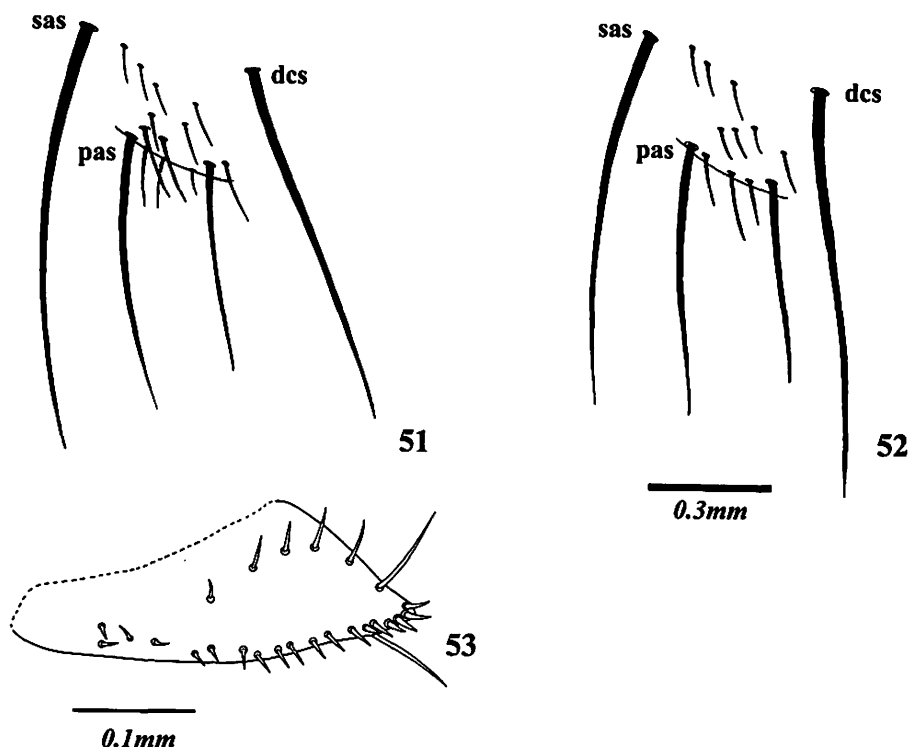
DIAGNOSIS: *Drosophila nigra* differs from other species in this group by having the front femur densely setose down the posteroventral surface (Fig. 43), front tibiae ciliated posteroventrally, vibrissae consisting of a dense clump of long black setae in 2 irregular rows (Fig. 36), and a distinctive ovipositor (Fig. 49). This species, like *D. nigella* and *D. fungiperda*, lacks a sclerotized rim on its labellum.

DESCRIPTION: ♂, ♀. Although descriptions of this species are provided by Grimshaw (1901) and Hardy (1965), we will repeat them here because of the potential for confusion (see DISCUSSION, below). *Head* Lower portion of front below proclinate setae yellow; face, genae, clypeus and palpi black or dark brown; antennae almost entirely dark brown to black. Palpi of males with numerous long, thin setae around apical margin. Vibrissae densely setose. Female palpi with only 1 long apical setae. Vibrissae of females not densely setose. *Thorax.* Entirely black, rather thickly gray pollinose with small apical yellow spot on scutellum between apical scutellar setae. About 21 thick, short setae arranged on posterolateral portions of mesonotum (Fig. 40). *Legs.* Front femur densely setose on posteroventral surface (Fig. 43). Front tibiae densely covered with erect setae down ventral surface. Coxae dark brown. Femora shining black. Remainder of legs yellow. *Wings.* Male wings subhyaline with the following markings; large brown spot occupying apex, another brown spot over crossvein dm-cu and pale brown diffuse infuscation extending along basal portion of vein M₁₊₂. Wings of female more diffusely infuscated; often apical mark will diffuse into mark over crossvein dm-cu which, in turn, extends basally, sometimes beyond crossvein r-m. *Abdomen.* Ovipositor very large, pointed at apex (Fig. 49). Two distinctive setae, 1 on dorsoapical surface and 1 on ventroapical surface, present. Dorsal seta ca. 1/2 ovipositor length; ventral ca. 3/4 ovipositor length. Peg ovisensilla on dorsal, lateral, apical and ventral surfaces long, sharply pointed. Apex with cluster of 5 ovisensilla. Dorsolateral region with ca. 15 ovisensilla that extend to ventral margin. Ventral margin with 4 ovisensilla clustered around 1/4 ovipositor length and 4 ovisensilla clustered around 3/4 ovipositor length.

Eggs/ Developmental Biology. Kambysellis & Craddock (1991) and Kambysellis (1993) examined the ovarian development, insemination patterns and ultrastructure of the egg chorion of this species.

TYPE: MAUI: Holotype (of *nigra*) ♀, Haleakalā, 5,000 ft, v.1896, not measured, in BMNH. Holotype (of *reburra*) ♂ (BPBM 6,473), Olinda, iii.1932, OB, not measured, head appears to be glued to thorax, left foreleg beyond coxa missing (Evenhuis, 1982).

MATERIAL EXAMINED: MAUI: Although none of the type series is available for examination, 40 other specimens, 24 males and 16 females, have been studied from the UHM. The following collections were made in Waikamoi Forest Preserve: 2♀, 8.vii.1964, HLC; 2♂, 11.vii.1964, LHT; 2♂, 16.iv.1965, JPM; 1♀, 28.v.1965,



Figures 51-53. Morphology of *Drosophila denotata*. 51. Posterolateral region of mesonotum, male, 52. Posterolateral region of mesonotum, female, 53. Ovipositor.

DEH; 1♀, 29.vi.1965, LHT; 1♀, 11.vii.1965, HTS; 1♂, 31.vii.1965, HTS; 1♂, 30.viii.1965, KYK; 1♀, 15.x.1965, JPM; 1♀, 7.i.1966, JPM; 1♂, 9.ix.1966, DEH; 1♂, 11.iv.1968, MPK; 13♂, 5♀, 10.v.1974, HTS&KYK. Other collections include: 1♂, Haleakalā, 5,000 ft, v.1898, no collector given; 1♀, Olinda, 4,500 ft, 15.iii.1932, OB; 1♀, Kula Pipeline, 4,500 ft, 8.iv.1932, OHS; 1♀, Palikū, Haleakalā Crater, 6,500 ft, 23.vii.1963, WBH; 2♂, Kaupō Gap, Haleakalā, 4,750 ft, 14.vi.1975, KYK; 1♀, Kaupō Gap, Haleakalā, 4,750 ft, 9.x.1975, KYK. Specimens present in the AMNH were also studied. 4♂, Z68, MPK; 1♂, Heed Trail, Waikamoi Forest Preserve, 16-18.iii.1999, OG55.9, PMO & JBS; 1♂, Pig Hunter's Trail, Upper Waikamoi Forest Preserve, 16-18.iii.1999, OG56.3, PMO & JBS; 22♂, 46♀, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.4, PMO.

DISTRIBUTION: This species is known only from Maui (Fig. 35b).

MOLECULAR BIOLOGY: The alcohol dehydrogenase gene sequence (M60793) has been determined for this species (Thomas & Hunt, 1991). Several accessions of this species are present in the AMNH-MC.

DISCUSSION: Grimshaw described the female of this species as *D. nigra* (types in BMNH). When Hardy (1965) described the drosophilid fauna of Hawai'i he added a description of the male to *D. nigra*. At the same time he also described the male of a new species, *D. reburra*, and placed types in the Bishop Museum. Hardy (1965) placed *D. reburra* in the subgenus *Hypenomyia* because

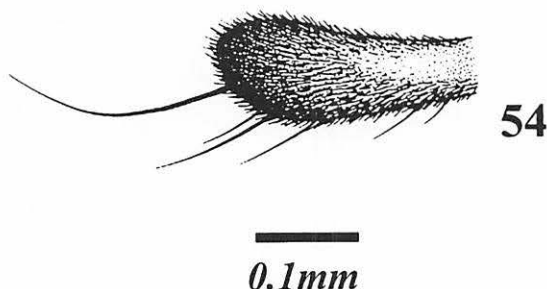


Figure 54. Palp of *Drosophila chicaoae*.

of the dense setation on its vibrissae. The vibrissal character has been found to be only of specific importance. *Hyponomyia* is considered a synonym of *Drosophila*. Furthermore, the specimen that Hardy (1965) described as *D. reburra* is clearly *D. nigra*. These species names are considered synonyms.

***Drosophila stenoptera* Hardy**

Figs. 35b, 41

Drosophila stenoptera Hardy, 1965: 473.

DIAGNOSIS: *Drosophila stenoptera* differs from other species in this clade by lacking long cilia on the anteroventral surface of the front femur and by having the antennae and front coxae yellow.

DESCRIPTION: Posterolateral margins of mesonotum as in Fig. 41. For further details refer to Hardy (1965).

TYPE: MAUI: Holotype ♂ (BPBM 6,447), Palikū, Haleakalā Crater, 6,500 ft, vi.1953, DEH. TL = 1.8 mm; WL = 5.1 mm; TL/WL = 0.4; HW = 1.3 mm; HW/TL = 0.7; CI = 4.6; 4V = 1.6; 5X = 1.7; 4C = 0.6; M = 0.4.

DISTRIBUTION: This species is known only from the type male and has only been collected on Maui (Fig. 35b).

***Drosophila swezeyi* Hardy**

Fig. 35d

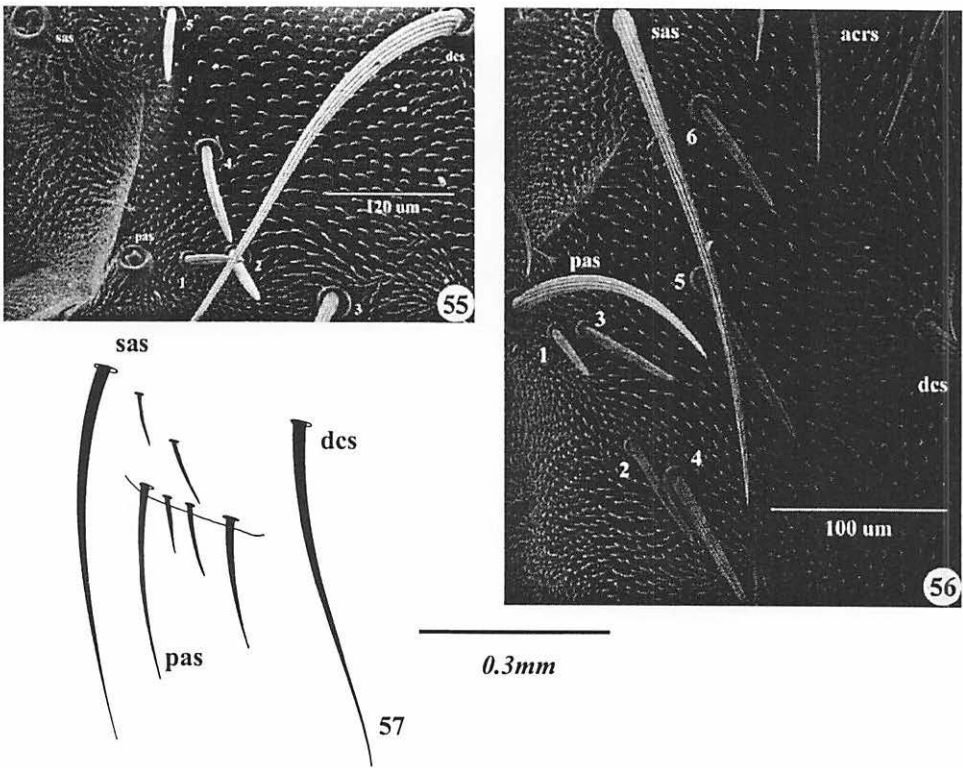
Drosophila swezeyi Hardy, 1965: 474.

DIAGNOSIS: *Drosophila swezeyi* differs from other species by having entirely yellow legs and a white face.

DESCRIPTION: For further descriptive information refer to Hardy (1965).

TYPE: O'AHU: Holotype ♂ (BPBM 6,448), Wai'anāe Mountains, 22.i.1924, OHS. TL = 1.3 mm; WL = 2.6 mm; TL/WL = 0.5; HW = 1.1 mm; HW/TL = 0.8; CI = 4.3; 4V = 1.4; 5X = 1.4; 4C = 0.5; M = 0.3.

DISTRIBUTION: This species has only been collected on O'ahu (Fig. 35d). It is known only from the type male and has not been collected since the original description.



Figures 55-57. Posterolateral regions of the mesonotum of the *Drosophila insignita* complex species. 55. *D. chicao*, 56. *D. curtitarsis*, 57. *D. insignita*.

Iib. The *denotata* complex

KEY TO SPECIES IN THE *DROSOPHILA DENOTATA* COMPLEX

19. Wings mostly hyaline with discrete maculations confined to regions surrounding apical portion of veins R_{2+3} , R_{4+5} , and M_1 ... (O'ahu) *denotata* Hardy
- . Wings mostly subhyaline, with distinctly brown infuscation covering apical 1/3. Longitudinal hyaline streaks extending through apices of cells c, r_{2+3} and r_{4+5} . Also with hyaline region in cell m1 ... (O'ahu) *sabroskyi* Hardy

Drosophila denotata Hardy

Drosophila denotata Hardy, 1965: 241.

Figs. 50a, 51–53

DIAGNOSIS: *Drosophila denotata* is differentiated from closely related species by having the mesonotum and scutellum dusted with gray to brownish pollen and the brown markings on wings

confined to veins R_{2+3} , R_{4+5} , and M_1 , with complete hyaline streaks between these veins. The female ovipositor is distinctive and differs from other known species by the presence of strong dorsal setae on the dorsoapical and ventroapical margins.

DESCRIPTION: ♂, ♀. The external morphology of this species was described by Hardy (1965). Additional characters are described here. *Thorax.* Lower 1/2 of pleura yellow. Arrangement of setae on sides of posterolateral portion of mesonotum dimorphic (Figs. 51 & 52). Males have ca. 13 setae in this area, females ca. 11. *Abdomen.* Apex of ovipositor somewhat acute (Fig. 53) with 4 long, sharply pointed peg ovisensilla. Two distinctive setae present, 1 on dorsoapical margin, another on ventroapical margin. Each setae roughly equal to 1/2 ovipositor width. Ventral margin with 15 sharp peg ovisensilla extending to 4/5 ovipositor length (Fig. 53). Dorsolateral region with 5 long peg ovisensilla extending to ca. 1/2 ovipositor width.

MEASUREMENTS: $N = 3\delta$. TL = 1.8 mm; WL = 3.8 mm (3.7–3.9); TL/WL = 0.5; HW = 2.7 mm (2.7–2.8); HW/TL = 0.7 (0.7–0.8); CI = 4.6 (4.5–4.7); 4V = 1.0 (1.0–1.1); 5X = 1.4 (1.1–1.7); 4C = 0.4 (0.4–0.5); M = 0.3 (0.2–0.3). $N = 4\eta$. TL = 1.8 mm (1.7–2.0); WL = 3.6 mm (3.3–3.9); TL/WL = 0.5; HW = 1.4 mm (1.2–1.5); HW/TL = 0.7; CI = 4.1 (4.0–4.3); 4V = 1.2 (1.1–1.2); 5X = 1.4 (1.1–1.5); 4C = 0.5; M = 0.3 (0.2–0.3). Five pupae were measured, length = 2.1 mm (2.0–2.2).

TYPES: O'AHU: Holotype ♂ (BPBM 6,339), Poamoho Trail, Ko'olau Mountains, "ex: fungi", x.1953, EJF. Allotype ♀ (BPBM 6,339a), same information as holotype. Ten paratypes, 3 males and 7 females, all from the same collection as the holotype, were examined. Seven pupae were also studied.

DISTRIBUTION: *Drosophila denotata* is known only from O'ahu (Fig. 50a).

ECOLOGY: This species has been bred from fleshy fungi (Table 2).

Drosophila sabroskyi Hardy

Fig. 50a

Drosophila sabroskyi Hardy, 1965: 453.

DIAGNOSIS: *Drosophila sabroskyi* is distinguished from other species in this group by the pattern of maculations on its wings and by having the mesonotum polished black, devoid of gray pollen.

DESCRIPTION: Refer to Hardy (1965) for more descriptive information.

TYPES: O'AHU: Holotype ♀, Poamoho Trail, Ko'olau Mountains, 27.vii.1961, CWS, holotype in USNM. Not measured.

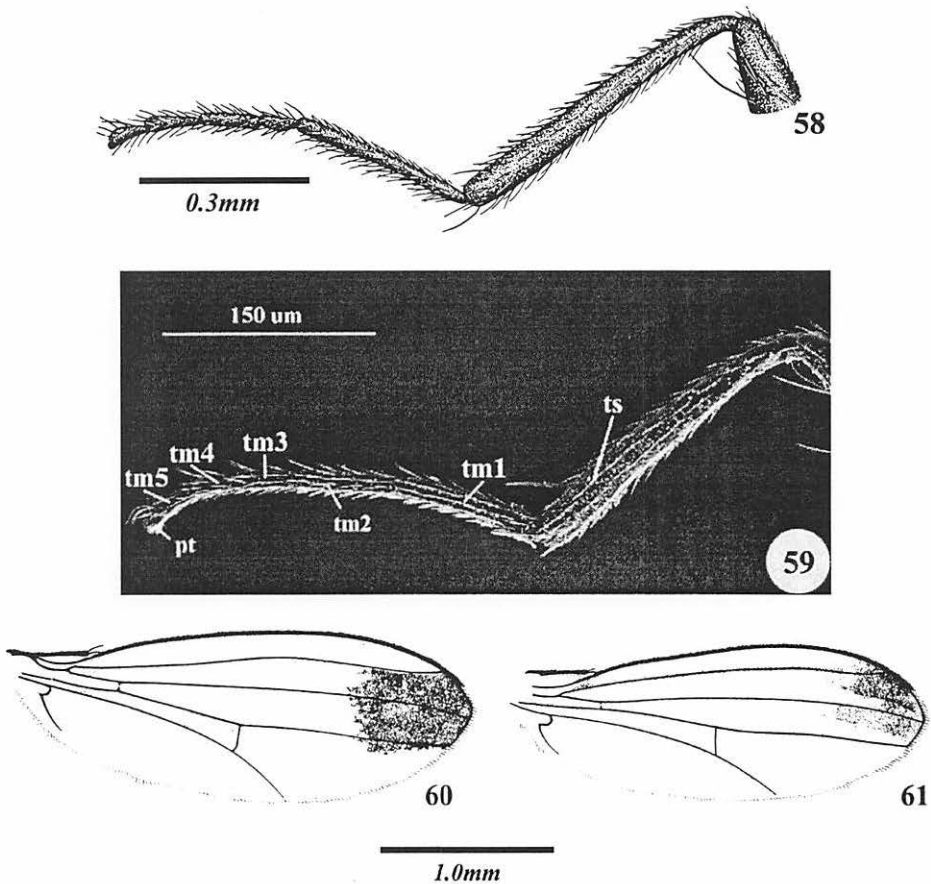
DISTRIBUTION: This species is known only from the type female, collected on O'ahu (Fig. 50a).

DISCUSSION: The male of this species has not been associated.

IIc. The *insignita* complex

KEY TO SPECIES IN THE *INSIGNITA* COMPLEX

20. Wings mostly hyaline; apical wing spot sharply defined, not diffuse. Bounded by vein R_{2+3} dorsally and extends only slightly beyond vein M_1 ventrally ... (Hawai'i) *chicae* Hardy & Kaneshiro, n. sp.
- . Apical infuscation extending beyond R_{2+3} into apical region of cell c 21
21. Apical infuscation slightly diffused, only extending into extreme apex of cell c. Infuscation does not extend to vein M_1 ... (Kaua'i) *curtitarsis* Hardy & Kaneshiro, n. sp.
- . Apical infuscation extends into lower apical margin of cell c and into upper portion of cell m1 ... (O'ahu) *insignita* Hardy



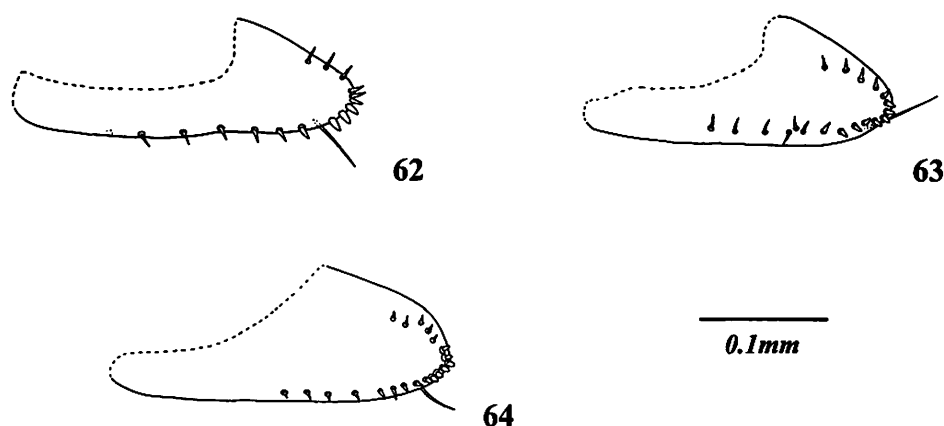
Figures 58–61. Thoracic structures of the *Drosophila insignita* complex species. 58. *D. chicae*, male foreleg, 59. *D. curtitarsis*, male foreleg, 60. *D. chicae*, wing (25 ×), 61. *D. curtitarsis*, wing (25 ×).

***Drosophila chicae* Hardy & Kaneshiro, new species**

Figs. 50b, 54, 55, 58, 60, 62

DIAGNOSIS: *Drosophila chicae* is differentiated from other species in this clade by having both the palpi and antennae brown, clypeus black, ocellar setae situated in line with median ocellus, the upper 1/2 of the pleura black, a front basitarsus that is ca. 2/3 as long as the tibia and twice as long as the second tarsomere (Fig. 58), and wings hyaline with a sharply defined infuscation not extending dorsally beyond vein R_{2+3} (Fig. 60).

DESCRIPTION: ♂, ♀. *Head.* Males with lower 1/2 of front, below level of lower reclinate setae, yellow; upper portion mostly black, tinged with rufous in ground color of parafrontal areas. Front of female entirely dark



Figures 62–64. Ovipositors of *Drosophila insignita* complex females. 62. *D. chicaoae*, 63. *D. curtisarsis*, 64. *D. insignita*.

brown to blackish, with slight rufous tinge in lower median portion. Mostly subopaque, lightly gray dusted, with vertex on each side of ocellar triangle polished black, area extending onto upper portion of front ca. 1/2 the length of ocellar triangle. First antennal segment pale yellow, 3rd segment dark brown to black. Arista with 4–5 dorsal rays, in addition to the apical fork and with ca. 5 short inconspicuous setae scattered along inner margin. Face yellow-white; genae and lower occiput pale yellow, except for faint tinge of brown along vibrissal row. Genae rather narrow, area between vibrissal row and eye margin scarcely equal to 1/10 eye width. Clypeus dark brown to black and palpi mostly brown to black, with several prominent setae around posteroapical margin (Fig. 54). *Thorax*. Mostly shining black, rather densely gray pollinose but not obscuring shining ground color. Apex of scutellum distinctly marked with yellow. Lower 1/2 of each pleuron pale yellow. Anterior katepisternal setae present but scarcely over 1/3 length of posterior katepisternals. About 5 setae present on posterolateral portions of mesonotum (Fig. 55). *Legs*. Entirely pale yellow, front basitarsus ca. 2/3 as long as tibia (Fig. 58). *Wings*. Mostly hyaline with very prominent apical maculation in males (Fig. 60). Wings of females entirely subhyaline. Costal fringe extends ca. 1/3 distance to apex of vein R_{4+5} . *Abdomen*. Entirely shining black, lightly gray pollinose. Ovipositor rounded at apex with cluster of 6 peg ovisensilla (Fig. 62). Dorsal margin with 3 thick, sharply pointed trichoid ovisensilla. Ventral margin with 6 trichoid ovisensilla that extend to ca. 3/5 ovipositor length. Apical setae ca. 1/2 ovipositor width (Fig. 62).

MEASUREMENTS: $N = 7\delta$. TL = 1.0 mm (0.9–1.1); WL = 2.6 mm (2.6–2.7); TL/WL = 0.3 (0.3–0.4); HW = 0.8 (0.7–0.9); HW/TL = 0.8 (0.8–0.9); CI = 6.8 (6.1–8.1); 4V = 1.7 (1.6–1.7); 5X = 2.6 (2.0–2.9); 4C = 0.4; M = 0.5 (0.5–0.6). $N = 6\eta$. TL = 1.1 mm (0.9–1.3); WL = 2.7 mm (2.3–2.9); TL/WL = 0.4; HW = 0.9 mm (0.7–1.0); HW/TL = 0.8; CI = 5.3 (4.6–5.6); 4V = 1.7 (1.5–1.9); 5X = 2.3 (2.0–2.6); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.6).

TYPES: HAWAII: Holotype δ (BPBM 16,358), Koko'olau Overlook, Kīlauea [= Hawaii Volcanoes] National Park, vi.1974, FCV. TL = 0.9 mm; WL = 2.6 mm; TL/WL = 0.3; HW = 0.8 mm; HW/TL = 0.8; CI = 6.7; 4V = 1.7; 5X = 2.9; 4C = 0.4; M = 0.6. Allotype η (BPBM 16,358a), Kīlauea Forest, Volcano Hawai'i, 3.vi.1974, HTS. TL = 0.9 mm; WL = 2.3 mm; TL/WL = 0.4; HW = 0.7 mm; HW/TL = 0.8; CI = 5.7; 4V = 1.6; 5X = 2.2; 4C = 0.5; M = 0.4. Seventeen paratypes, 9 males and 8 females, are designated. 1 δ , 1 η , same collection as allotype; 7 δ , 7 η , "reared ex: fungus", Manukā Forest Reserve, South Kona, 27.vi.1976, SLM; 1 δ , Kapu'a (land section), Ho'ōpūloa (quadrant), South Kona, vii.1977, DEH. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: *Drosophila chicaoae* is known only from the island of Hawai'i (Fig. 50b).

ETYMOLOGY: This species is named after Dr. Francisca "Chica" do Val, São Paulo, Brazil. In addition to extensive field work on Hawaiian drosophilids, Chica has made important contributions

to the evolutionary studies by working out techniques for measuring genetic differences between species using morphometric analysis of hybrids.

ECOLOGY: *Drosophila chicac* has been reared from fungi (Table 2). This species is sympatric with *D. polita*. Although the females of these 2 species closely resemble one another, *D. chicac* is differentiated by having only 1 humeral seta and the front nearly all dark colored.

***Drosophila curtisarsis* Hardy & Kaneshiro, new species**

Figs. 50c, 56, 59, 61, 63

DIAGNOSIS: *Drosophila curtisarsis* can be differentiated from other species in this clade by having yellow palpi, clypeus yellow with faint tinge of brown above. Front basitarsus 2/5 as long as the tibia and equal in length to second tarsomere (Fig. 59). Wings mostly subhyaline, with a slightly diffused apical wing spot in male that extends into the extreme apex of cell c (Fig. 61). Ocellar setae situated slightly above the median portion of the ocellus. The females are very similar to other females of this complex, but can be differentiated by having the ocellar setae situated above the median ocellus, as in the male.

DESCRIPTION: ♂, ♀. *Head.* In addition to the above, front black above proclinate setae, yellow to rufous below. Face, genae, palpi, mouthparts (except for sclerotized black rim), and first 2 antennal segments of male pale yellow to rufous. Third antennal segment of female entirely dark brown to blackish. Clypeus of female brown; palpi dark brown to blackish, except for narrow bases. Arista with 6–7 dorsal rays, in addition to apical fork and with a few scattered short hairs on inner margin. *Thorax.* Shining black, lightly dusted with gray pollen except on pale yellow lower 1/2 of each pleuron and yellow tip of scutellum. Anterior katepisternal setae distinct but only ca. 1/3 length of posterior katepisternals. Posterolateral portions of mesonotum sparsely setose, with ca. 6 setae (Fig. 56). *Legs.* Entirely pale yellow. Front femur with 5–6 brown posteroventral setae and 4 posterodorsal setae. Front tibia and tarsus as in Fig. 59. *Wings.* Male wings as in Fig. 61. Female wings lacking brown apical spot. *Abdomen.* Entirely shining black, terga 3–6 almost devoid of gray pollen. Ovipositor rounded at apex, with dense cluster of ca. 7 peg ovisensilla (Fig. 63). Dorsal margin with 4 peg ovisensilla extending to 1/4 ovipositor length; ventral margin with 8 ovisensilla extending to 3/5 ovipositor length. A single lateral ovisensilla opposite ventral margin at ca. 3/5 ovipositor length. Apical setae ca. 1/3 ovipositor length (Fig. 63).

MEASUREMENTS: N = 10♂. TL = 1.0 mm (1.0–1.1); WL = 2.4 mm (2.1–2.9); TL/WL = 0.4 (0.4–0.5); HW = 0.9 mm (0.8–1.0); HW/TL = 0.8 (0.8–0.9); CI = 5.2 (4.8–5.6); 4V = 1.6 (1.5–1.8); 5X = 3.3 (2.8–4.0); 4C = 0.5 (0.5–0.6); M = 0.6 (0.6–0.7). N = 7♀. TL = 1.2 mm (1.0–1.3); WL = 2.6 (2.1–2.9); TL/WL = 0.5 (0.4–0.5); HW = 0.9 mm (0.8–1.1); HW/TL = 0.8 (0.8–0.9); CI = 4.7 (4.5–4.9); 4V = 1.6 (1.5–2.1); 5X = 2.7 (2.3–3.0); 4C = 0.6 (0.5–0.7); M = 0.6 (0.5–0.8).

TYPES: KAUA'I: Holotype ♂ (BPBM 16,359), Berry Flat Trail, Koke'e, 18.iv.1974, "ex: mushrooms", HTS. TL = 1.0 mm; WL = 2.4 mm; TL/WL = 0.4; HW = 0.9 mm; HW/TL = 0.8; CI = 4.9; 4V = 1.6; 5X = 3.7; 4C = 0.5; M = 0.6. Allotype ♀ (16,359a), same collection as holotype. TL = 1.3 mm; WL = 2.9 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.6; 4V = 2.1; 5X = 3.0; 4C = 0.7; M = 0.8. Fifteen paratypes, 9 males and 6 females, have been designated. 1 ♀, Po'omau Valley, 3,000 ft, vii.1952, DEH; 1 ♂, Kawaikoi Stream, 3,700 ft, viii.1953, DEH; 1 ♀, Waipao Falls, viii.1953, DEH; 2 ♂, Halemanu Valley, 3,500 ft, 12.viii.1971, DEH; 1 ♂, 1 ♀, Mahanaloa Valley, Koke'e, 1,950 ft, 23.iii.1973, KYK; 4 ♂, 3 ♀, same data as holotype, HTS; 1 ♂, Koke'e, 19.iv.1974, HTS. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: This species is known only from Kaua'i (Fig. 50c).

ECOLOGY: This species has been reared from mushrooms (Table 2).

ETYMOLOGY: Latin, "short tarsus".

***Drosophila insignita* Hardy**

Figs. 50d, 57, 64

Drosophila insignita Hardy, 1965: 326.

DIAGNOSIS: *Drosophila insignita* can be differentiated from closely related forms in this clade by having the ocellar setae displaced, situated opposite the lower ocellars; the pleura predominantly yellow, an apical wing spot that diffuses into the lower apical margin of cell c and into the upper

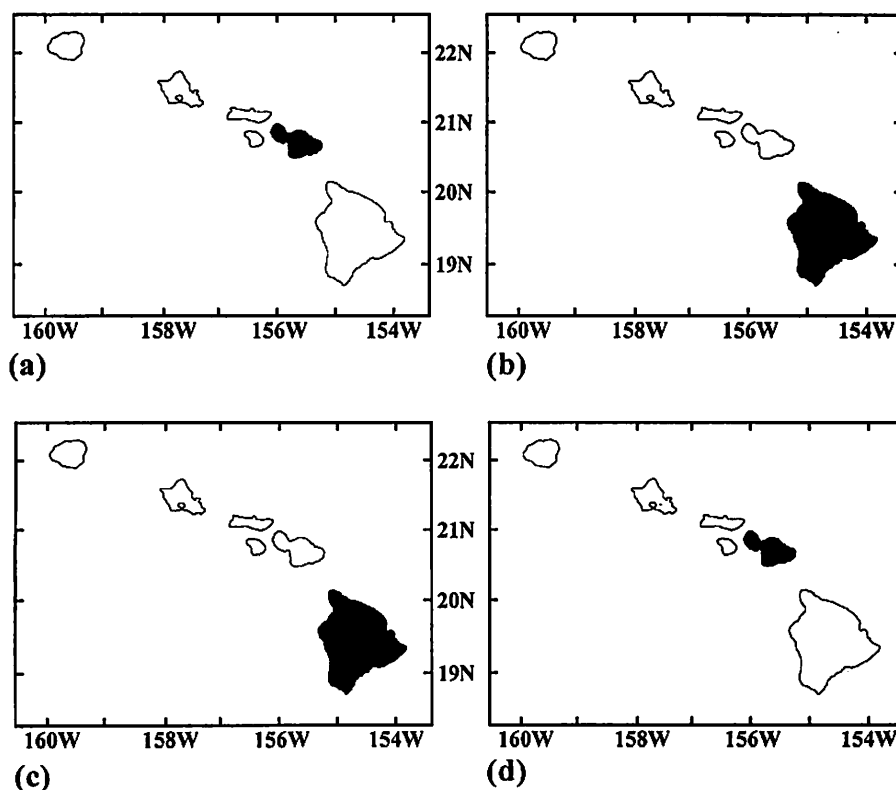


Figure 65. Distribution of species in the *Drosophila atrifacies*, *Drosophila brunneicrus*, and *Drosophila fungiperda* complexes. a. *D. atrifacies*, b. *D. brunneicrus* and *D. ochroleuca*, c. *D. fungiperda*, d. *D. nigella*.

portion of cell m1, palpi yellow, and antennae, which are yellow to rufous, except for the tinge of brown along the dorsal margin of the third segment.

DESCRIPTION: ♂, ♀. We add the following male characters and a description of the female to Hardy's (1965) description. Except as noted below, females fit description of males. *Head*. Palpi, clypeus, and third antennal segment of females brown. *Thorax*. Posterolateral portions of mesonotum sparsely setose, possessing 5 setae (Fig. 57). Upper 1/2 of pleura black in females. *Wings*. Entirely hyaline in females. *Abdomen*. Ovipositor rounded at apex, with 8 peg ovisensilla at tip (Fig. 64). Dorsal margin with 5 and ventral margin with 7 peg ovisensilla. Ovisensilla on ventral margin extend to ca. 1/2 ovipositor length. Apical setae ca. 1/3 ovipositor width (Fig. 64).

MEASUREMENTS: N = 1 ♂. TL = 0.7 mm; WL = 1.8 mm; TL/WL = 0.4; HW = 0.6 mm; CI = 5.8; 4V = 1.5; 5X = 2.4; 4C = 0.5; M = 0.5.

TYPES: O'AHU: Holotype ♂ (BPBM 6,380), Palikea, Wai'anae Mountains, 3,000 ft, 15.xi.1936, "on foliage", FXW, genitalia in microvial mounted below specimen is not from holotype (Evenhuis 1982). Not measured. One paratype male was studied. 1 ♂, Palikea, Wai'anae Mountains, 28.x.1911, FXW.

MATERIAL EXAMINED: O'AHU: Six males and 3 females from other collections were also examined from UHM. 2♂, Mt Tantalus, vi.1963, HLC; 2♂, Mt Tantalus, vi.1967, HLC; 1♂, Pahole Gulch, Mokuē'ia, 31.xii.1973, SLM; 1♂, 1♀, Makaha Valley, 2,300 ft, 16.iv.1975, SLM; 2♀, Palikea, 3,900 ft, 1977, DEH.

DISTRIBUTION: This species is known from both the Wai'anae and Ko'olau Mountains on O'ahu (Fig. 50d).

DISCUSSION: The number of humeral setae in this species seems to be variable. Some populations have only one, others have 2 and some are polymorphic for this character.

III. The *haleakalae* subgroup

This subgroup is defined by having the inner margin of the arista covered with numerous, densely placed hairs. The *haleakalae* subgroup is only known from the geologically more recent islands of Maui, Moloka'i, Lāna'i, and Hawai'i (Figs. 65, 83). No representatives of this clade have yet been collected on O'ahu or Kaua'i. This suggests that the maximum age of this subgroup is approximately 1.9 MY (Carson & Clague, 1995). Four species complexes, *atrifacies*, *brunneicrus*, *fungiperda*, and *haleakalae*, are designated within the *haleakalae* subgroup. The relationships among these species complexes is uncertain and the *haleakalae* subgroup may not be monophyletic (Bonacum, 2001).

The *atrifacies* complex contains a single species, *D. atrifacies*, from Maui (Fig. 65a). The *haleakalae* complex is comprised of 4 species: *D. clara* from Hawai'i (Fig. 83a), *D. cryptica* from Moloka'i (Fig. 83b), and *D. haleakalae* and *D. macrochaetae* from Maui (Fig. 83c). The host species of *D. clara*, *D. cryptica*, and *D. haleakalae* are unknown, but *D. macrochaetae* has been reared from a species of "soft-shell fungus" (Table 2).

The *brunneicrus* complex consists of 2 closely related species, *D. brunneicrus* and *D. ochropleura*, which are sympatric in some areas on the Big Island (Fig. 65b). Females in the *brunneicrus* cluster can only be differentiated by a tinge of brown on the mid and hind femora of *D. ochropleura* females. *Drosophila ochropleura* has been reared from a unknown species of "gill fungi" (Table 2).

The *fungiperda* complex consists of 2 species, *D. fungiperda* from Hawai'i (Fig. 65c) and *D. nigella* from Maui (Fig. 65d). These species in the *fungiperda* complex are united by a suite of morphological characters, most notably the lack of a sclerotized black rim on the labellum and by having long pointed peg ovisensilla, a characteristic not seen in any other *haleakalae* group species. *Drosophila fungiperda* and *D. nigella* also share the same host fungi, *Polyporus sulphrea* (Heed, 1968).

KEY TO SPECIES IN THE *DROSOPHILA HALEAKALAE* SUBGROUP

- 22. Sclerotized black rim on labellum absent 23
- . Sclerotized black rim on labellum present 24
- 23. Legs of male mostly yellow, with faint pale brown preapical streak on femora. Front femur of males not thickly setose. Wing infuscated at apex and over crossvein dm-cu. Females with brown streak before apex of posterior surface. Second antennal segment brown, 3rd segment mostly brown with some yellow markings at apex ... (Hawai'i) *fungiperda* Hardy
- . Femora mostly dark brown to black. Wings hyaline. Second antennal segment yellow, third antennal segment broadly yellow at base ... (Maui) *nigella* Hardy
- 24. Front femur with 7–8 extremely long, between 2/3 and 3/4 femur length, posteroventral setae ... (Maui) *macrochaetae* Hardy
- . Posteroventral setae on front femur not elongated 25

25. Pleura mostly yellow, with faint brown spot on metapleuron ... (Hawai'i) *ochropleura* Hardy & Kaneshiro, n. sp.
- Pleura entirely black 26
26. Legs entirely yellow 27
- Fore, mid or hind legs either partially or entirely brown 28
27. One humeral seta present. Wings entirely subhyaline. Male genitalia yellow ... (Hawai'i) *clara* Hardy & Kaneshiro, n. sp.
- Wings tinged with yellow. Apex and crossvein dm-cu lightly infuscated with brown. Abdomen polished brown to black ... (Maui) *haleakalae* Grimshaw
28. Palpi of males yellow, entirely brown in females. Palpi of both sexes rather slender, almost straight sided, each with 2 small setae at the apex in addition to setae around margin ... (Maui) *atrifacies* Hardy & Kaneshiro, n. sp.
- Coloration of palpi may be similar to above, but shape and setation are not 29
29. Forelegs entirely yellow. Palpi of males entirely yellow. Clypeus yellow, tinged with brown. Male genitalia black ... (Moloka'i) *cryptica* Hardy & Kaneshiro, n. sp.
- Forelegs with a slight tinge of brown. Palpi yellow, tinged with brown at apex. Clypeus black (Hawai'i) *brunneicrus* Hardy & Kaneshiro, n. sp.

IIIa. The *atrifacies* complex

Drosophila atrifacies Hardy & Kaneshiro, new species

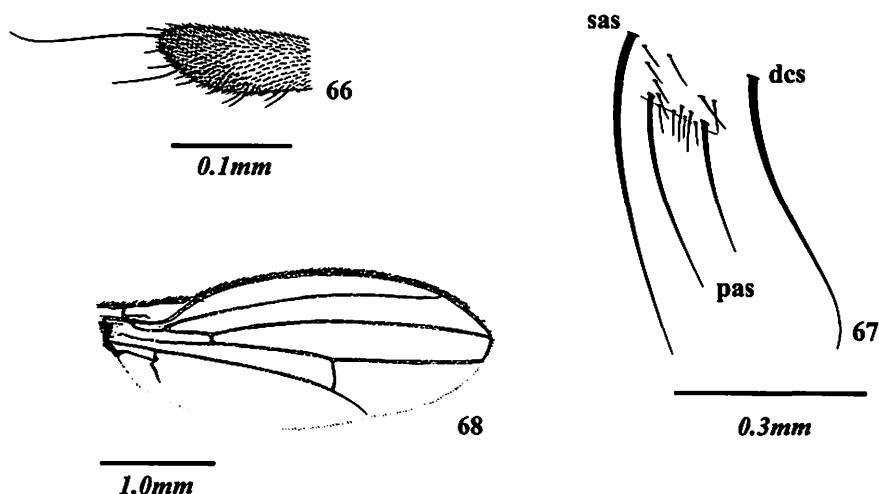
Figs. 65a, 66–68

DIAGNOSIS: *Drosophila atrifacies* is differentiated from other species in this clade by having the lower margin of the front clear yellow, face black except along sides, clypeus entirely black, front basitarsus ca. 3/4 as long as tibiae, and thorax entirely subshining black.

DESCRIPTION: ♂, ♀. *Head*. Front opaque black except for yellow lower margin. Face yellow-white down eye orbits, subopaque black in median portion, covered with gray pollen. First antennal segment of male yellow, second brown, tinged with rufous and third segment mostly yellow, tinged with brown along dorsal surface. Female antennae, as male, except that third segment is mostly dark brown. Two short dorsal setae present on second antennal segment. Arista with ca. 8 dorsal, 2 ventral rays, in addition to apical fork. About 6 short, well spaced hairs present on inner surface of each arista. Clypeus dark brown to black. Palp of male yellow, with faint tinge of brown on apical 1/2. Female palpi brown. Palpi of both sexes rather slender, almost straight sided (Fig. 66), with 2 small setae at apex in addition to setae around margin. Occiput entirely black except for extreme lower margin (Fig. 66). *Thorax*. Entirely shining black, dusted with gray pollen except for yellow apex of scutellum. Anterior katepisternal well developed, at least 1/2 as long as posterior. Setae on posterolateral portion of mesonotum arranged as in Fig. 67. *Legs*. Front coxae and femora mostly yellow with faint tinge of brown in males; entirely yellow in females. Mid and hind femora distinctly tinged with brown in males; mostly yellow and only faintly tinged with brown in females. Front basitarsus ca. 2/3 as long as tibia. Front femur with 3 moderately strong posteroventral setae on apical 1/2 and with a continuous row of short bristle-like setae extending toward base. One anterior seta situated at base of front femur and 3 posterodorsal setae widely spaced from just before base to apical 1/3. *Wings*. Mostly subhyaline, as seen in indirect light, with apex and crossvein dm-cu slightly brownish. Costal fringe extending ca. 1/2 distance to vein R₄₊₅ (Fig. 68). *Abdomen*. Entirely shining black, lightly dusted with gray pollen.

MEASUREMENTS: N = 6♂. TL = 1.7 mm (1.4–1.8); WL = 3.2 mm (2.8–3.5); TL/WL = 0.5; HW = 1.2 mm (1.1–1.3); HW/TL = 0.7 (0.7–0.8); CI = 4.7 (4.3–5.6); 4V = 1.2 (1.1–1.3); 5X = 1.4 (1.2–1.6); 4C = 0.4 (0.3–0.5); M = 0.4 (0.3–0.4). N = 1/ (see allotype).

TYPES: MAUI: Holotype ♂ (BPBM 16,360), Waikamoi, 10.v.1974, KYK. TL = 1.7 mm; WL = 3.5 mm; TL/WL = 0.5; HW = 1.2 mm; HW/TL = 0.7; CI = 4.8; 4V = 1.3; 5X = 1.6; 4C = 0.4; M = 0.4. Allotype ♀ (BPBM 16,360a), Trail to Pu'u Kukui, West Maui, 3,500 ft, 17.ix.1975, KYK. TL = 1.8 mm; WL = 3.8 mm; TL/WL = 0.5; HW = 1.3 mm; HW/TL = 0.7; CI = 4.5; 4V = 1.4; 5X = 1.5; 4C = 0.5; M = 0.4. Nine males, all designated



Figures 66–68. *Drosophila atrifacies*. 66. Palp, 67. Posterolateral region of the mesonotum, 68. Wing.

as paratypes. 1 ♂, Kula Pipe Line, 4,500 ft, iii.1932, OB. The other 8 paratypes were taken at same locality as the type in several collections, 1 ♂, 11.vii.1965, HTS; 2 ♂, 23.vii.1965, DEH; 1 ♂, 16.ix.1965; 1 ♂, 15.x.1965; 1 ♂, 29.vii.1966; 1 ♂, 22.vii.1967, JPM; 1 ♂, 10.v.1974, KYK. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: This species is known only from Maui (Fig. 65a).

ETYMOLOGY: Latin, "black face", referring to the entirely black face of this species.

IIIb. The *brunneicrus* complex

Drosophila brunneicrus Hardy & Kaneshiro, new species

Figs. 65b, 69, 71, 73, 75

DIAGNOSIS: *Drosophila brunneicrus* is differentiated from other members of this clade by having the mid and hind legs mostly brown, tinged with rufous and the front femora with a slight tinge of brown. Palpi brown at apices, clypeus black.

DESCRIPTION: ♂, ♀. This species closely fits the description of *D. haleakalae* except as discussed above and as follows. *Head*. Palpi with 1 strong apical seta and 2 moderately strong subapical seta on margin (Fig. 69). *Thorax*. Posterolateral regions of mesonotum with ca. 13 supernumerary setae, arranged as in Fig. 71. *Legs*. Basitarsus ca. 2/3 length of tibia (Fig. 73). Females with tinge of brown on mid and hind femora. *Wings*. Apical pale brown mark on wing extends ca. 1/2 distance to crossvein dm-cu, pale brown mark present on crossvein dm-cu. *Abdomen*. Ovipositor rounded at apex, with dense cluster of ca. 7 peg ovisensilla (Fig. 75). Dorsal margin with 2 peg ovisensilla extending to 1/8 ovipositor length; ventral margin with 8 ovisensilla extending to 3/4 ovipositor length. Inner subapical sensilla ca. 1/3 ovipositor width (Fig. 75).

MEASUREMENTS: N = 9 ♂. TL = 1.4 mm (1.3–1.7); WL = 3.2 mm (3.0–3.6); TL/WL = 0.5 (0.4–0.5); HW = 1.0 mm (0.9–1.2); HW/TL = 0.7; CI = 4.6 (3.9–5.2); 4V = 1.4 (1.3–1.6); 5X = 1.6 (1.4–1.8); 4C = 0.5 (0.4–0.6); M = 0.4 (0.3–0.4).

TYPES: HAWAII: Holotype ♂ (BPBM 16,361), Kilauea Forest Reserve, 26.vii.1975, HTS. TL = 1.6 mm;



Figures 69-70. Palpi of the *Drosophila brunneicrus* cluster. 69. *D. brunneicrus*, 70. *D. ochropleura*.

WL = 3.3 mm; TL/WL = 0.5; HW = 1.0 mm; HW/TL = 0.7; CI = 5.0; 4V = 1.3; 5X = 1.8; 4C = 0.5; M = 0.4. Eleven male paratypes have been designated. 1 ♂, Hualālai, 6.vii.1967, JAT; 1 ♂, Keawewai Camp, 5,800 ft, 4.x.1967, HLC; 6 ♂, Kilauea Forest Reserve, 3.vi.1974, HTS; 1 ♂, Kipuka Ki, 25.vii.1975, HTS; 2 ♂, Halepiula Road, Kapu'a Land Section, South Kona, 4,650 ft, vii.1977, DEH. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: *Drosophila brunneicrus* is known only from the island of Hawai'i (Fig. 65b).

ECOLOGY: This species lives in *Acacia koa* forests. It is known to be sympatric with *D. ochropleura* and *D. fungiperda*.

ETYMOLOGY: Medieval Latin, *brunne-*, for "brown" and Latin, *-crus*, for "leg", in reference to the diagnostic brown coloration on the mid, hind and forelegs of males.

Drosophila ochropleura Hardy & Kaneshiro, new species

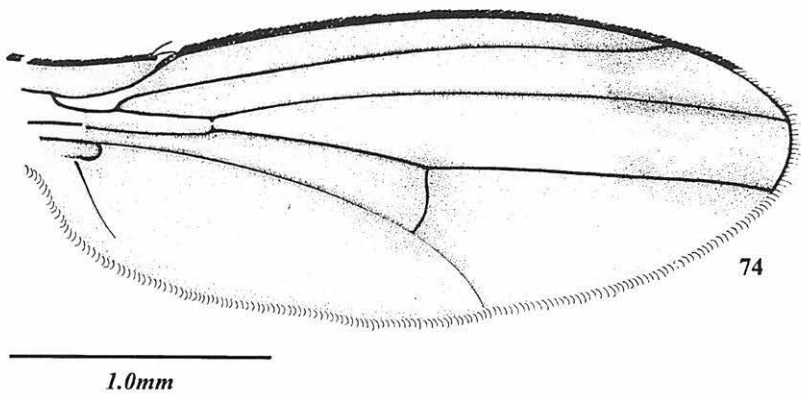
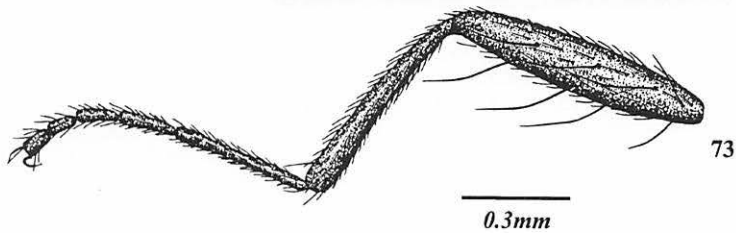
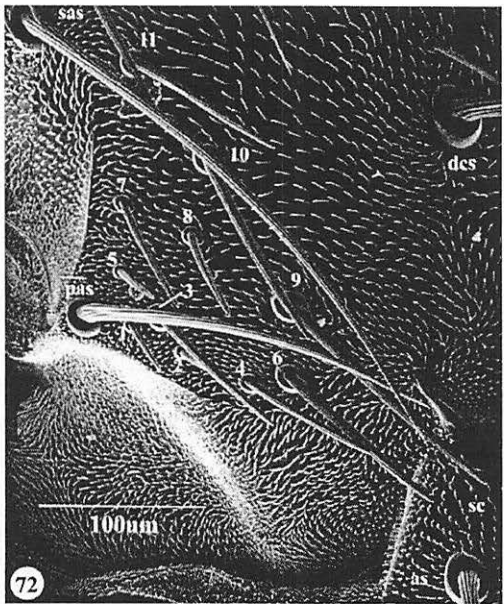
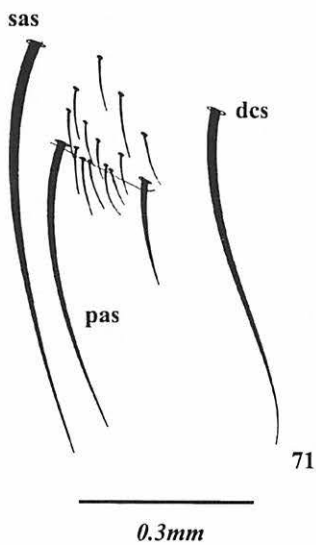
Figs. 65b, 70, 72, 74, 76

DIAGNOSIS: *Drosophila ochropleura* is differentiated from other species of this complex by having the pleura of the males entirely yellow except for a small spot of brown on the metapleuron.

DESCRIPTION: ♂, ♀. *Head.* Lower portion of front, below level with lower reclinate setae, all of face, clypeus, palpi, genae, lower 1/2 of occiput and mouthparts, with exception of black rim on labellum, pale yellow in males. Palpi dark brown at apices and clypeus entirely brown in females. Antennae mostly yellow in males with second antennal segment faintly tinged with brown on dorsum and third segment brown over dorsal 1/2. Female antennae mostly brown. Arista with ca. 12 closely placed, moderately long hairs along inner margin. Each palp with 1 moderately long plus 1 short apical seta (Fig. 70). *Thorax.* Mesonotum shining black, rather densely gray pollinose but not obscuring shining ground color. Scutellum dark brown to black on basal 3/5 with apical portion broadly yellow. Lower portion of each humerus, below main seta, yellow. Anterior katepisternal rather small, ca. 1/3 as long as posterior katepisternal. Metanotum brown with faint tinge of rufous in ground color, coloration extends over onto metapleuron. Pleura yellow in males, entirely black in females. Halteres yellow. About 11 setae present on posterolateral region of mesonotum (Fig. 72). *Legs.* Entirely pale yellow. Front basitarsus ca. 2/3 as long as tibia. *Wings.* Subhyaline with faint brownish tinge at apex of long veins R_{2+3} , R_{4+5} , and M_1 . Crossvein dm-cu also slightly infuscated. These markings lost when viewed in direct light (Fig. 74). Wing markings much more distinct in females. *Abdomen.* Mostly polished black, gray pollinose over first tergum and down median portions of terga 2 and 3. In some specimens pollinosity extends through median 1/2 of fourth tergum and along basal margins of fifth. Ovipositor rounded at apex, with dense cluster of ca. 9 peg ovisensilla (Fig. 76). Dorsal margin with 4 peg ovisensilla extending to 1/4 ovipositor length; ventral margin with 7 ovisensilla extending to 3/4 ovipositor length. Inner subapical sensilla ca. 1/3 ovipositor width (Fig. 76).

MEASUREMENTS: N = 11 ♂. TL = 1.3 mm (1.1–1.3); WL = 2.9 mm (2.6–3.1); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.9–1.1); HW/TL = 0.8 (0.7–0.8); CI = 4.2 (3.7–4.8); 4V = 1.6 (1.4–1.7); 5X = 2.1 (1.7–2.7); 4C = 0.6 (0.4–0.6); M = 0.5 (0.4–0.6). N = 11 ♀. TL = 1.4 mm (1.1–1.6); WL = 3.2 mm (2.8–3.6); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.8–1.2); HW/TL = 0.7 (0.7–0.8); CI = 4.4 (3.8–6.3); 4V = 1.5 (1.3–1.6); 5X = 2.0 (1.6–2.2); 4C = 0.5 (0.4–0.6); M = 0.5 (0.4–0.5).

TYPES: HAWAII: Holotype ♂, Kipuka Ki, 1285 m, 3.vi.1974, HTS, BPBM 16362. TL = 1.3 mm; WL = 3.1 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.7; CI = 4.2; 4V = 1.7; 5X = 1.9; 4C = 0.6; M = 0.5. Allotype



♀, Kilauea Forest, Volcano, 3.vi.1974, HTS, BPBM 16362a. TL = 1.5 mm; WL = 3.2 mm; TL/WL = 0.5; HW = 1.0 mm; HW/TL = 0.7; CI = 3.9; 4V = 1.5; 5X = 1.7; 4C = 0.6; M = 0.5. Two hundred seventy-three paratypes, 218 males and 55 females, are designated. 1♂, "C-H70.12", WBH; 1♂, "on ferns", Maulua Trail, Keanakolu, 5,200 ft, DEH; 2♂, Bird Park, 24.vi.1963, LHT; 1♂, Pohakuloa, 26.vi.1963, LHT; 5♂, Bird Park, 5–6.xii.1963, MRW; 2♂, 2♀, Bird Park, Kilauea, vii.1964, HTS; 1♂, Bird Park, Kilauea, 12.vii.1964, LHT; 3♂, Kipuka Ki, 17.vii.1964, LHT; 1♂, Keanakolu, 5,300 ft, 19.viii.1964, HLC; 1♂, "on pilo tree", Kipuka Ki, 9.ix.1964, HTS; 1♂, "ex: gill-type fungi", Kipuka Ki, 9.ix.1964, HTS; 1♂, 5♀, "on gill-type fungi", Kipuka Ki, 10.ix.1964, HTS; 1♂, Bird Park, 30.xii.1964, DG; 1♂, 1♀, Hinakapoula, 5,200 ft, 14.vii.1965, HLC; 11♂, Forest above Pa'auilo, 3,000 ft, 26.viii.1965, HLC; 1♂, Kipuka Ki, 29.vii.1966, HTS; 1♂, Sinkhole, Hualālai, Kona, 5,600 ft, 7.vii.1967, KYK; 1♂, Piha-Mauloa Boundary, Keanakolu Road, 6,500 ft, 12.vii.1967, WBH; 1♂, Humu'ula Saddle, 6,650 ft, 13.ix.1967, HLC; 1♀, Pu'u 'O'o Volcano Trail, 4,800 ft, 29.ix.1967, HLC; 6♂, Keawewai Camp, 6,200 ft, 30.ix.1967, HLC; 25♂, 5♀, Keawewai Camp, 5,800 ft, 4.x.1967, HLC; 2♂, Pu'u Wa'awa'a, 19.xii.1969, SLM; 1♂, Kipuka #2, Saddle Road, 19.i.1970, WBH; 3♂, Kilauea, 21–22.vi.1971, KYK; 4♂, 21♀, Bird Park, Volcano, 24.iv.1974, HTS; 1♂, 2♀, Kilauea Forest Volcano, 26.iv.1974, HTS; 2♂, Upper 'Ōla'a Forest, 26.iv.1974, HTS; 3♂, Bird Park, 3.vi.1974, HTS; 7♂, Kipuka Ki, 1,285 m, 3.vi.1974, HTS; 85♂, Kilauea Forest, Volcano, 3–5.vi.1974, HTS; 6♂, Greenwell Ranch, Pauahi, 27.vi.1974, KYK; 2♂, 5♀, Ahumoa Pōhakuloa, Saddle Road, 3.vii.1974, MPK; 26♂, 7♀, Kipuka Pahipa, Kahuku Ranch, 5,400 ft, 17.vii.1974, HLC; 2♂, 7♀, Kipuka 'Ākala, Kahuku Ranch, 5,000 ft, 18.vii.1974, WI; 2♂, Kahuku Ranch Road, South Kona, 3,800 ft, 20.v.1975, KYK; 3♂, Bird Park, Kilauea, 1,220 m, 25.vii.1975, HTS; 1♂, Kahuku Ranch, 3,800 ft, 12.viii.1975, KYK.

DISTRIBUTION: This species is known only from the island of Hawai'i (Fig. 65b).

ECOLOGY: This is one of the more common species found above 4,000 ft in elevation, typically in association with *Acacia koa*, on the island of Hawai'i. It occurs sympatrically with *D. fungiperda* and *D. brunneicrus*. *Drosophila ochroleuca* has been reared from gill fungi (Table 2).

ETYMOLOGY: Greek, "yellow pleura".

IIIc. The *fungiperda* complex

Drosophila fungiperda Hardy

Figs. 65c, 77, 79, 81

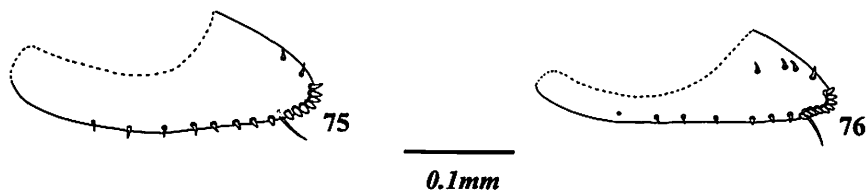
Drosophila fungicola Hardy, 1965: 282 (preoccupied).

Drosophila fungiperda Hardy, 1966: 244.

DIAGNOSIS: *Drosophila fungiperda* is one of 3 known species of *haleakalae* in which the male has no sclerotized rim on the labellum. It is readily differentiated by having the legs mostly yellow with a pale brown preapical streak on each posterior surface of the femora, wings infuscated with brown apically and on crossvein dm-cu, and posterior surface of front femur not thickly setose. The females are easily differentiated by having the front femur with a streak of brown before the apex of the posterior surface.

DESCRIPTION: ♂, ♀. Several characters are added to the original description (Hardy, 1965), including details of the female genitalia. *Head*. Each arista with 10 rather long, closely placed, conspicuous hairs along inner surface. *Thorax*. Area on each side of posterior portion of mesonotum rather thickly covered with ca. 17 prominent setae (Fig. 77). *Legs*. Femur with many dense setae on dorsal surface (Fig. 79). Remainder of leg more densely setose than typical *haleakalae* group species. *Abdomen*: Ovipositor rounded at apex (Fig. 81). Dorsal apical margin with 5 elongate peg ovisensilla. Dorsolateral region with ca. 7 irregularly arranged peg ovisensilla extending to roughly 3/5 ovipositor length. Ventroapical margin with cluster of 6 stout peg ovisen-

Figures 71–74. Posterolateral regions of the mesonotum and thoracic structures in the *Drosophila brunneicrus* complex. 71. *D. brunneicrus*, mesonotum, 72. *D. ochroleuca*, mesonotum, 73. *D. brunneicrus*, male foreleg, 74. *D. ochroleuca*, wing.



Figures 75–76. Ovipositors of *Drosophila brunneicrus* complex females. 75. *D. brunneicrus*, 76. *D. ochroleptura*.

silla. About 12 sharp peg ovisensilla extend to 4/5 ovipositor length. Inner subapical ovisensilla ca. 4/5 ovipositor width (Fig. 81).

Eggs/ Developmental Biology. Kambyssellis & Craddock (1991) and Kambyssellis (1993) have examined the ovarian development, insemination patterns and the ultrastructure of the egg chorion of this species.

MEASUREMENTS: N = 10♂. TL = 1.5 mm (1.4–1.7); WL = 3.6 mm (3.4–3.8); TL/WL = 0.4 (0.4–0.5); HW = 1.2 mm (1.1–1.2); HW/TL = 0.7 (0.7–0.8); CI = 4.1 (3.3–4.5); 4V = 1.3 (1.3–1.4); 5X = 2.1 (1.7–2.5); 4C = 0.5 (0.4–0.5); M = 0.4 (0.4–0.5). N = 10♀. TL = 1.6 mm (1.4–1.8); WL = 3.7 mm (3.5–4.1); TL/WL = 0.4 (0.4–0.5); HW = 1.2 mm (1.1–1.3); HW/TL = 0.7 (0.6–0.8); CI = 4.4 (3.8–5.0); 4V = 1.4 (1.3–1.6); 5X = 1.8 (1.7–2.3); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.6).

TYPES: HAWAII: Holotype ♂ (BPBM 6,362), Keanakolu, 5,200 ft, X.1952, DEH. Allotype (BPBM 6,362a), same collection as holotype. Forty-eight paratypes, 24 males and 24 females, have been examined from the UHM. 1♀, Hualālai, 6,000–6,500 ft, 20.iv.1944, NLHK; 4♂, Pauahi, 4,300 ft, viii.1952, DEH; 14♂, 1♀, Keanakolu, 5,200 ft, x.1952, DEH; 2♂, Bird Park, vii.1953, DEH; 19♀, North slope of Hualālai, 4,000–6,000 ft, vii.1953, “on bracket fungus”, DEH; 2♂, 2♀, Hawai’i National Park, 4,000 ft, iii.1954, RN; 1♂, Bird Park, vii.1956, DEH; 1♂, 1♀, Pauahi, 4,300 ft, viii.1956, DEH.

MATERIAL EXAMINED: HAWAII: Two hundred and twelve other specimens, 102 males and 110 females, were studied from the UHM. 2♂, C-H 68.29, “*fungicola*”, no date, collector or location given; 1♂, 2♀, Bird Park, vi.1963, LHT; 1♀, Pa’auilo, 2,900 ft, viii.1963, LHT; 3♂, 7♀, Hinakapoula, 5,200 ft, 14.vii.1964, HLC; 3♂, 3♀, Maulua Trail, Keanakolu, “on ferns”, 20.vii.1964, DEH; 9♂, Keanakolu, 5,300 ft, 19–20.viii.1964, HLC & DF; 25♂, 40♀, Kipuka Ki, “reared ex: bracket fungus”, 7–12.ix.1964, HTS; 1♂, Forest above Pa’auilo, 3,000 ft, 26.viii.1965, HLC; 2♂, 3♀, Volcano, Hawai’i Volcanoes National Park, ‘Ōla’a Tract, 3,800 ft, 12.xii.1976, WPM; 4♂, 10♀, Kipuka Ki, 20–23.ix.1977, HTS; 1♂, Wright Road, Pole #44, 23.ix.1977, HTS; 2♂, 3♀, 1 mi north of Hopuwai, Mauna Kea, 6,200 ft, 18.x.1977, HTS; 5♂, 16♀, Weather Station, Strip Road, Kīlauea, 5,400 ft, 20–23.x.1977, HTS; 41♂, 1♀, Waihaka Gulch, Ka’ū Forest Reserve, 3,800–4,000 ft, 28–30.iii.1978, KYK; 1♂, 21♀, Maulua Forest Reserve, 5,200 ft, 13.x.1980, KYK; 1♂, 3♀, Pihā Forest Reserve, 6,000 ft, 14.x.1980, KYK. Twenty-five individuals have also been studied from the AMNH. 5♂, 4♀, Kaloko Mauka, North Kona, 3.vii.1998, OG38.5, PMO & SLM; 8♂, 8♀, Bird Park, 4–5.v.1999, OG66.2, PMO & MPK.

DISTRIBUTION: This species is known only from the island of Hawai’i (Fig. 65c).

ECOLOGY: This species is common in *Acacia koa* forest between 4,000 and 6,000 ft. It has been reared from bracket fungi, especially *Polyporus sulphrea* (Spieth, 1966; Table 2).

MOLECULAR BIOLOGY: Frozen tissue samples (OG 38.5 & 66.2) are present in the AMNH-MC.

***Drosophila nigella* Hardy**

Figs. 65d, 78, 80, 82

Drosophila nigella Hardy, 1965: 385.

DIAGNOSIS: *Drosophila nigella* is one of the 3 members of the *haleakalae* species group that lacks the sclerotized black rim on the labellum of the male. It differs from closely related species by having the femora mostly dark brown to black, wings hyaline, second antennal segment yellow and third antennal segment broadly yellow at base.

DESCRIPTION: ♂, ♀. Hardy (1965) described the males and females of this species. We add to those descriptions the following characters: *Thorax.* Posterolateral portions of mesonotum covered with ca. 12 setae, arranged as in Fig. 78. *Legs.* In females, front femora entirely yellow with faint pale brown streak on posterior surface before apex; mid femora mostly brown and hind broadly tinged with brown on apical 1/2. Femur with dense seta on posterior surface (Fig. 80). *Abdomen.* Ovipositor rounded at apex (Fig. 82). About 6 peg ovisensilla present on dorsal margin, these are especially well-developed, elongate and spine-like. Dorsolateral region with ca. 6 irregularly placed peg ovisensilla extending to ca. 3/5 ovipositor length. Ventroapical margin with cluster of 5–6 peg ovisensilla. Ventral margin with 11 peg ovisensilla extending to ca. 3/4 ovipositor length. Inner subapical ovisensilla ca. 3/5 ovipositor width.

Eggs/ Developmental Biology. Kambysellis & Craddock (1991) have examined the ovarian development and insemination patterns of this species.

MEASUREMENTS: N = 2♂. TL = 1.6 mm; WL = 3.4 mm (3.2–3.5); TL/WL = 0.5; HW = 1.3 mm (1.2–1.3); HW/TL = 0.8; CI = 4.7; 4V = 1.3; 5X = 2.0 (1.9–2.1); 4C = 0.5 (0.4–0.5); M = 0.4. N = 3♀. TL = 1.8 mm (1.7–1.8); WL = 3.8 mm (3.7–3.8); TL/WL = 0.5 (0.4–0.5); HW = 1.3 mm (1.2–1.3); HW/TL = 0.7; CI = 4.4 (3.7–5.2); 4V = 1.4 (1.3–1.4); 5X = 1.6 (1.5–1.9); 4C = 0.5 (0.5–0.6); M = 0.4.

TYPES: MAUI: Holotype ♂ (BPBM 6,410), Pu'u Kukui, 4,500 ft, iv.1954, MT, abdomen beyond 3rd segment missing; genitalia in microvial mounted below specimen (Evenhuis, 1982). Allotype (BPBM 6,410a), same collection as holotype. Nine paratypes in the UHM, 4 males and 5 females, have been examined. 2♀, Ukulele, 13.vii.1919, PHT; 1♀, Kula Pipeline, 14.vi.1927, OHS; 1♂, Kula Pipeline, 4,500 ft, 15.iii.1932, OB; 2♂, 1♀, Kula Pipeline, 4,500 ft, 8.iv.1932, OB; 1♀, Pu'u Kukui, 4,500 ft, iv.1954, MT; 1♂, Waikamoi, 4,000 ft, vii.1956, DEH.

MATERIAL EXAMINED: MAUI: One hundred and fourteen individuals, 85 males and 29 females, have also been examined from the UHM. Many collections have been made in Waikamoi Forest Preserve. 4♀, 29.vi.1964, HLC; 2♂, 8.vii.1964, HLC; 1♂, 4,200 ft, 2.vii.1965, RMB; 8♀, 11.vii.1965, HTS; 1♂, 4,000 ft, 23.vii.1965, DEH; 1♂, 16.ix.1965, JPM; 17♂, 1.x.1965, KYK & JPM; 1♂, 11.ii.1966, JPM; 1♀, 25.ii.1966, JPM; 1♂, 29.iii.1966, JPM; 1♂, 1.vii.1966, JPM; 4♂, 9.ix.1966, JPM; 1♂, 22.ix.1966, JPM; 2♂, 2.xi.1966, JPM; 4♂, 14.xii.1966, JPM; 1♂, 19.iv.1967, JPM; 2♂, 3.v.1967, JPM; 1♂, 4,500 ft, 12.x.1967, HLC; 38♂, 3♀, 10.v.1974, HTS & KYK. Other collections were made at the following localities. 1♀, Palikū, Haleakalā Crater, 6,000 ft, 28.i.1965, DEH; 1♂, Trail to Honomanu Valley, 5,300 ft, 24.vii.1965, DEH; 5♂, 9♀, Camp One, Kipahulu Valley, 3,100 ft, 9.viii.1967, "ex: bracket fungus", KYK; 1♂, Kaualewelawe, 3,000 ft, 16.ix.1975, KYK; 3♀, Trail to Pu'u Kukui, 3,500 ft, 17.ix.1975, KYK. Several individuals in the AMNH have also been studied. 2♀, Heed Trail, Waikamoi Forest Preserve, 8.iii.1999, OG50.9, PMO, EMC, & MPK; 1♀, Pig Hunter's Trail, Upper Waikamoi Forest Preserve, 16–18.iii.1999, OG56.2, PMO & JBS; 32♂, 50♀, Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG77.B, PMO.

DISTRIBUTION: This species is known only from Maui (Fig. 65d).

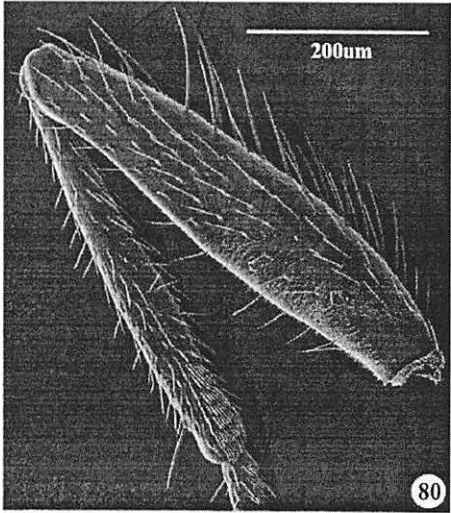
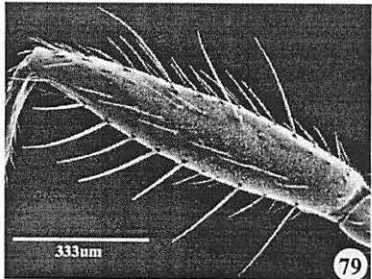
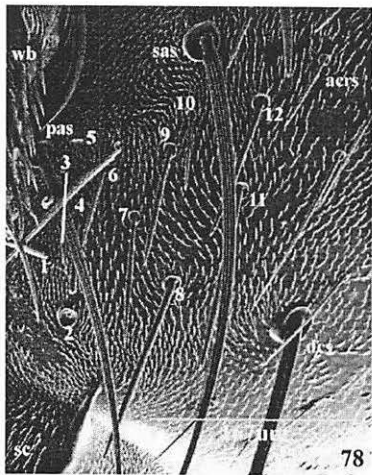
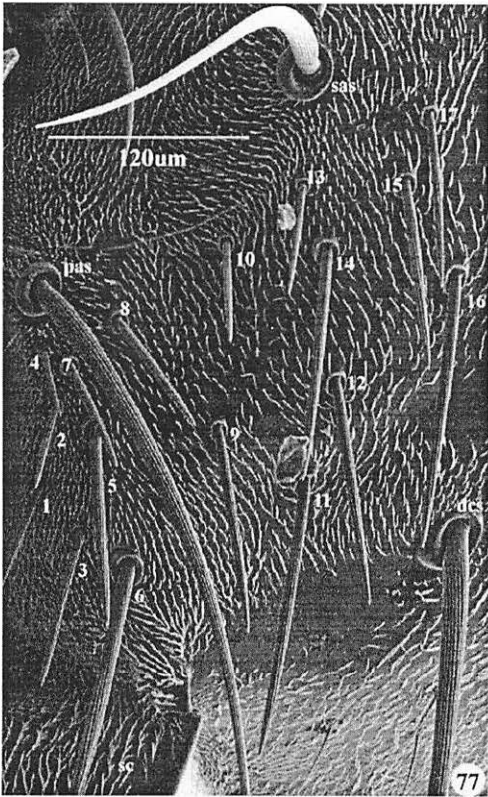
ECOLOGY: *Drosophila nigella* has been reared from the bracket fungi, *Polyporus sulphrea* (Heed 1968).

MOLECULAR BIOLOGY: Several collections have been accessioned into the AMNH-MC.

III.d. The *haleakalae* complex***Drosophila clara* Hardy & Kaneshiro, new species**

Figs. 83a, 84, 86, 88, 94

DIAGNOSIS: *Drosophila clara* differs from other closely related species by having only 1 humeral seta, a shining black mesonotum, which is lightly, but distinctly dusted with gray, yellow legs, wings that are entirely subhyaline, and yellow male genitalia.



DESCRIPTION: ♂, ♀. *Head*. Lower portion of front clear yellow to level almost with tip of ocellar triangle. Upper front opaque black in parafrontal areas, polished dark brown to black on ocellar triangle and black dusted with gray brown pollen in orbital areas to level with proclinate setae. Face, genae, palpi and mouthparts, except for black rim, pale yellow-white in male. Females similar to males except with palpi mostly brown. Palpi with 2 apical setae, shorter ca. 3/4 length of longer. Median surface of palpi with several long setae (Fig. 86). Clypeus with faint tinge of brown. First 2 antennal segments of male yellow, with slight tinge of brown on dorsum of second. Females with dorsal portion of second antennal segment distinctly dark brown. Third segment largely brown but extensively yellow on basal portion and on venter in both sexes. Arista with series of ca. 12 supernumerary hairs between dorsal and ventral rays (Fig. 84). Eyes thickly short yellow setose. Genae comparatively broad, at widest point equal to ca. 1/3 width of eye. *Thorax*. Entirely shining black except for yellow tip on scutellum, lightly dusted with gray pollen, not obscuring shining ground color. Anterior katepisternal seta well developed, at least 1/3 as long as posterior katepisternal seta. About 15 supernumerary seta present on posterolateral portions of mesonotum (Fig. 88). *Legs*. Entirely yellow. Front basitarsus ca. 2/3 as long as tibia and ca. 2 × longer than second tarsomere. *Wings*. Entirely subhyaline, costal fringe extending ca. 1/2 distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Tergites dark brown to black, subopaque, gray brown dusted on tergites 1, 2, and median portion of 3. Tergites 4–6 polished. Sterna yellow. External male genitalia yellow. Ovipositor rounded at apex with cluster of ca. 4–5 apical peg ovisensilla (Fig. 94). Dorsolateral region with 7 peg ovisensilla extending to 1/3 ovipositor length. Ventral margin with 8 peg and trichoid ovisensilla, extending to ca. 3/4 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width. Two moderately sclerotized, oval spermathecae present.

MEASUREMENTS: N = 11 ♂. TL = 1.3 mm (1.1–1.4); WL = 2.9 mm (2.8–3.3); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.8–1.1); HW/TL = 0.8 (0.7–0.8); CI = 4.3 (3.8–4.7); 4V = 1.4 (1.2–1.6); 5X = 1.9 (1.3–2.4); 4C = 0.6 (0.5–0.6); M = 0.4 (0.4–0.5). N = 7 ♀. TL = 1.4 mm (1.2–1.6); WL = 3.1 mm (2.8–3.4); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.9–1.1); HW/TL = 0.7 (0.7–0.8); CI = 4.4 (3.9–4.9); 4V = 1.4 (1.2–1.6); 5X = 2.1 (1.6–2.3); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.5).

TYPES: HAWAII: Holotype ♂ (BPBM 16,363), Greenwell Ranch, Pauahi, Kona, 22.vi.1974, KYK. TL = 1.4 mm; WL = 3.2 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.6; 4V = 1.4; 5X = 1.8; 4C = 0.5; M = 0.4. Allotype ♀ (BPBM 16,363a), same collection as type. TL = 1.5 mm; WL = 3.3 mm; TL/WL = 0.5; HW = 1.1 mm; HW/TL = 0.7; CI = 4.8; 4V = 1.4; 5X = 1.6; 4C = 0.5; M = 0.4. Twenty-seven paratypes, 21 males and 6 females have been designated. 18 ♂, 5/ from the same collection as holotype; 1 ♂, Kīpuka #10, Saddle Road, 5,500 ft, 14.vii.1967, WBH; 1 ♀, Kīpuka Kī, Volcano, 29.vii.1966, HTS; 1 ♂, Kīpuka #10, Saddle Road, 19.i.1970, WBH; 1 ♂, Pu'u Wa'awa'a, 4,300 ft, 22.xii.1969, KYK. Paratypes have been split between BPBM and UHM.

DISTRIBUTION: This species is known only from the island of Hawai'i (Fig. 83a).

ETYMOLOGY: Latin, "clear", for the hyaline wings of this species.

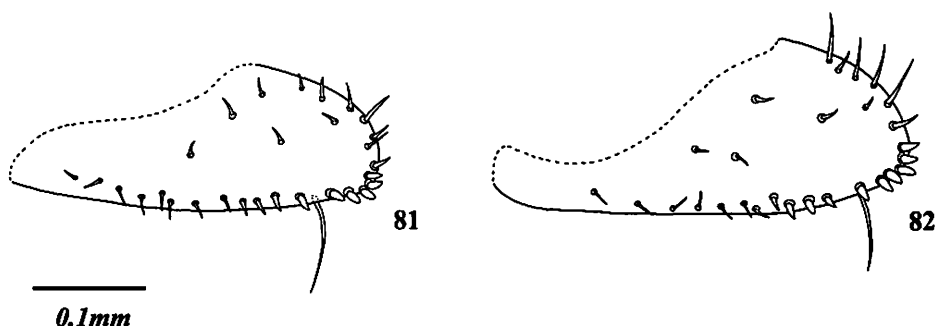
DISCUSSION: One male specimen in the UHM from Waikamoi, Maui, 10.v.1974, KYK fits exactly, but is not being designated as a paratype. Further collections, of both males and females, are required before the identity of the Maui specimen can be determined.

Drosophila cryptica Hardy & Kaneshiro, new species

Figs. 83b, 87, 89, 95

DIAGNOSIS: *Drosophila cryptica* is differentiated from other species in this clade by having the mid and hind femora tinged with brown; the wings slightly darker on the apices (as seen in dim or indirect light); the mesonotum polished black, nearly devoid of pollen and male genitalia that are black.

Figures 77–80. Posterolateral regions of the mesonotum and thoracic structures in the *Drosophila fungeperda* complex. 77. *D. fungeperda*, mesonotum. 78. *D. nigella*, mesonotum. 79. *D. fungeperda*, male foreleg. 80. *D. nigella*, male foreleg.



Figures 81–82. Ovipositors of *Drosophila fungiperda* complex females. 81. *D. fungiperda*, 82. *D. nigella*.

DESCRIPTION: ♂, ♀. This species fits the description of *D. clara*, except as noted above and as follows. *Head.* Each palp with several long apical setae in addition to elongate setae on medial surface (Fig. 87). *Thorax.* Posterolateral regions of mesonotum with ca. 12 supernumerary setae (Fig. 89). A rudimentary secondary seta on humerus present in some individuals, although this is scarcely larger than surrounding setae in most specimens. *Abdomen.* Ovipositor somewhat acute at apex (Fig. 95). Apex with 7–8 sharply pointed peg ovisensilla. Dorsolateral region with ca. 10 elongate peg ovisensilla, extending to ca. 2/5 ovipositor length. Ventral margin with 10 sharp peg ovisensilla, extending to 3/5 ovipositor length. Inner subapical ovisensilla ca. 1/4 ovipositor width.

MEASUREMENTS: N = 7 ♂. TL = 1.4 mm (1.2–1.5); WL = 3.0 mm (2.9–3.2); TL/WL = 0.5 (0.4–0.5); HW = 1.1 mm (1.0–1.2); HW/TL = 0.8 (0.7–0.8); CI = 4.5 (4.2–5.0); 4V = 1.3 (1.2–1.6); 5X = 1.7 (1.3–2.0); 4C = 0.5 (0.4–0.6); M = 0.4 (0.3–0.4). N = 2 ♀. TL = 1.6 mm (1.5–1.6); WL = 3.3 mm (3.1–3.5); TL/WL = 0.5; HW = 1.2 mm (1.1–1.2); HW/TL = 0.7; CI = 5.4 (5.0–5.8); 4V = 1.3; 5X = 1.7 (1.6–1.8); 4C = 0.5 (0.4–0.5); M = 0.4.

TYPES: MOLOKA'I: Holotype ♂ (BPBM 16,364), Hanalilolilo, 9.i.1975, ATO. TL = 1.4 mm; WL = 3.0 mm; TL/WL = 0.5; HW = 1.2 mm; HW/TL = 0.8; CI = 4.2; 4V = 1.3; 5X = 1.3; 4C = 0.6; M = 0.4. Allotype ♀ (BPBM 16,364a), same collection as holotype. TL = 1.6 mm; WL = 3.5 mm; TL/WL = 0.5; HW = 1.2 mm; HW/TL = 0.7; CI = 5.0; 4V = 1.3; 5X = 1.8; 4C = 0.5; M = 0.4. Eight paratypes, 7 males and 1 female, have been designated. 1 ♂, South of Hanalilolilo, 8.vii.1964, HLC; 2 ♂, Pu'u Kolekole, 3,000 ft, 20.vii.1964, HLC; 3 ♂, same collection as type, ATO&WI, 1 ♂, 1 ♀, Waikolu Stream, south of Hanalilolilo, 5.v.1976, KYK.

DISTRIBUTION: *Drosophila cryptica* is endemic to the island of Moloka'i (Fig. 83b).

ETYMOLOGY: Greek, "hidden", referring to the fact that this species is very closely related to *D. clara*.

***Drosophila haleakalae* Grimshaw**

Figs. 83c, 85, 90, 92, 96

Drosophila haleakalae Grimshaw, 1901: 64; Hardy, 1965: 297.

DIAGNOSIS: *Drosophila haleakalae* males are readily separated from closely related forms by having the legs and palpi yellow, and the clypeus yellow with faintly tinges of brown and by the presence of normal-length (not elongate) posteroventral setae on the front femora (Fig. 92). Females can be separated from closely related species by the presence of 2 humeral setae and a combination of characters listed below.

DESCRIPTION: ♂, ♀. Descriptions of the external morphology of this species have been published (Grimshaw, 1901; Hardy, 1965). Additional characters include: *Head.* Inner surface of arista with 10–12 erect moderately long hairs (Fig. 85). Palpi and clypeus of female dark brown. *Thorax.* Posterolateral portions of

mesonotum have ca. 15 strong setae, arranged as in Fig. 90. *Abdomen.* Ovipositor somewhat acute with strong, stout ovisensilla around ventral and apical margins (Fig. 96). Apex with 6 ovisensilla. Ventral margin with 12 ovisensilla, extending to ca. 4/5 ovipositor length. Dorsolateral region with 4 elongate, pointed ovisensilla that extend to ca. 1/4 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width.

MEASUREMENTS: N = 2♂. TL = 1.6 mm (1.5–1.6); WL = 3.4 mm; TL/WL = 0.5 (0.4–0.5); HW = 1.2 mm (1.1–1.2); HW/TL = 0.7; CI = 5.1 (5.0–5.2); 4V = 1.4 (1.3–1.4); 5X = 1.5 (1.4–1.6); 4C = 0.5 (0.4–0.5); M = 0.4. N = 1♀. TL = 1.9 mm; WL = 4.3 mm; TL/WL = 0.4; HW = 1.4 mm; HW/TL = 0.7; CI = 3.2; 4V = 1.3; 5X = 1.7; 4C = 0.7; M = 0.4.

TYPES: MAUI: Holotype ♂, Haleakalā, 6,000 ft, BMNH. Not measured. Four homotypes, 2 males and 2 females, were examined. 2♀, Palikū, Haleakalā Crater, vi.1952, DEH; 2♂, Palikū, Haleakalā Crater, 6,000 ft, vi.1953, DEH.

MATERIAL EXAMINED: MAUI: Three other specimens on hand, all males, include: 1♂, Palikū, Haleakalā Crater, 6,000 ft, vi.1953, DEH; 1♂, Waikamoi, 8.vii.1964, HLC 1♂, Palikū, Haleakalā Crater, 6,500 ft, 28.i.1965, DEH.

DISTRIBUTION: This species is known only from Haleakalā on the island of Maui (Fig. 83c).

DISCUSSION: Many specimens labeled as *D. haleakalae* and *D. haleakalae*-like from both Maui and Hawai'i have been collected (Table 3). Some of these specimens vary considerably in the size and development of the second humeral seta and may represent a sibling species present on both Maui and the Big Island. Alternatively, this may represent a recent expansion in the range of *D. haleakalae*. Further work on these species is currently underway (O'Grady & Val, in prep.).

Drosophila macrochaetae Hardy

Figs. 83c, 91, 93, 97

Drosophila macrochaetae Hardy, 1965: 348.

DIAGNOSIS: *Drosophila macrochaetae* differs from the other members of this complex by having only 1 humeral seta. Males are readily recognized from all other known species of Hawaiian *Drosophila* by having 7–8 extremely long, between 2/3–3/4 as long as the femur, posteroventral setae on the front femur (Fig. 93).

DESCRIPTION: ♂, ♀. Both sexes were originally described in Hardy (1965). Additional characters are discussed here. *Head.* Eyes with dense, short, yellow pile. Third antennal segment of female entirely dark brown to black. Second antennal segment extensively brown over dorsal portion in females. *Thorax.* Arrangement of 13 supernumerary setae on posterolateral portions of mesonotum as in Fig. 91. *Abdomen.* Ovipositor rounded at apex (Fig. 97), with cluster of ca. 9 stout peg ovisensilla present at apex. Three peg ovisensilla present on dorsolateral region. Ventral margin with ca. 9 peg ovisensilla that extend to 3/4 ovipositor length. Inner subapical ovisensilla ca. 1/4 ovipositor width.

MEASUREMENTS: N = 2♀. TL = 1.6 mm (1.4–1.8); WL = 3.5 mm (3.2–3.8); TL/WL = 0.4; HW = 1.1 mm (1.0–1.2); HW/TL = 0.7; CI = 4.0 (3.9–4.0); 4V = 1.7 (1.6–1.8); 5X = 2.0 (1.8–2.1); 4C = 0.8 (0.7–0.8); M = 0.6 (0.5–0.6).

TYPES: MAUI: Holotype ♂ (BPBM 6,392), Olinda, iii.1932, OB. Not measured. Allotype ♀ (BPBM 6,392a), same collection as holotype. Not measured. Four paratypes, 3 females and 1 male, have been examined. 1♀, Olinda, iii.1932, OB; 1♀, Olinda, 28.iii.1932, OB; 1♂, 1♀, Kula Pipeline, 4,500 ft, 8.iv.1932, OB.

MATERIAL EXAMINED: MAUI: Five other specimens, all females, have also been examined. 1♀, Haleakalā, 17.vii.1919; FXW; 2♀, Palikū, Haleakalā Crater, vii.1952, DEH & MT; 1♀, Palikū, Haleakalā Crater, vii.1953, DEH; 1♀, Palikū, Haleakalā Crater, viii.1953, WCM.

DISTRIBUTION: The type series of this species is known only from Haleakalā, Maui (Fig. 83c).

ECOLOGY: *Drosophila macrochaetae* has been collected on "soft shelf fungus" (Table 2).

DISCUSSION: Additional collections indicate that populations from the Island of Hawai'i, 4,000–6,000 ft cannot be morphologically differentiated from *D. macrochaetae* (Table 3). Work is currently underway to address this issue (O'Grady & Val, in prep.).

IV. The *luteola* subgroup

The *luteola* subgroup consists of the *fuscoapex* and *luteola* complexes. These are both small, poorly known groups that need further study to determine their exact placement within the *haleakalae* species group. The *fuscoapex* complex consists of 2 species, *D. fuscoapex* from Kaua'i (Fig. 98a) and *D. tamashiroi* from O'ahu (Fig. 98a). These 2 species are known only from a single male specimen and are not included in the key because of their rarity. The *luteola* complex is only slightly better known. *Drosophila luteola* was described from material collected on O'ahu (Fig. 98c). *Drosophila quinqueramosa*, which is known from Maui (Fig. 98d) is also a member of this complex.

KEY TO SPECIES IN THE *DROSOPHILA LUTEOLA* SUBGROUP

30. Basitarsus slightly less than 1/2 length of tibia. Sixth tergite yellow. Fifth tergite sometimes yellow ... (O'ahu)..... *luteola* Hardy
 —. Three pairs of dorsocentral setae. Anterior-most pair of dorsocentrals located at transverse suture; ca. 2 × length of ground setulae. Otherwise not as above ... (Maui) *quinqueramosa* Hardy & Kaneshiro, n. sp.

IVa. The *fuscoapex* complex*Drosophila fuscoapex* Hardy

Figs. 98a, 99

Drosophila fuscoapex Hardy, 1965, 291.

DIAGNOSIS: This species is differentiated by having a short front basitarsus, ca. 1/4–1/3 the length of the tibia and a brown infuscation covering the apical 1/3 of the wing.

DESCRIPTION: ♂. Hardy (1965) described this species from a single male; it has not been collected since. We have examined the holotype and add some setation characters of the mesonotum to the original description (Fig. 99).

TYPES: KAUA'I: Holotype ♂, Alaka'i Swamp, 3,800 ft, vii.1952, DEH, BPBM 6366. TL = 0.8 mm; WL = 1.9 mm; TL/WL = 0.4; HW = 0.6 mm; HW/TL = 0.7; CI = 3.7; 4V = 1.4; 5X = 2.4; 4C = 0.6; M = 0.4.

DISTRIBUTION: This species is known only from Kaua'i (Fig. 98a).

Drosophila tamashiroi Hardy

Figs. 98b, 100

Drosophila tamashiroi Hardy 1965, 477.

DIAGNOSIS: *Drosophila tamashiroi* is differentiated from other species in the *luteola* subgroup by having a front basitarsus 3/5 as long as the tibia and the apical infuscations on its wings roughly restricted to the area between veins R₂₊₃ and M₁.

DESCRIPTION: ♂. This species, like *D. fuscoapex*, is poorly known. We add characters of the mesonotum to the original description (Fig. 100).

TYPES: O'AHU: Holotype ♂ (BPBM 6,450), Makaleha Valley, "in stream bed", v.1951, MT. TL = 0.7 mm; WL = 1.9 mm; TL/WL = 0.4; HW = 0.7 mm; HW/TL = 0.9; CI = 7.0; 4V = 1.1; 5X = 3.2; 4C = 0.3; M = 0.4.

MATERIAL EXAMINED: The following material is present in the BPBM, after Evenhuis (1997). Wai'anae Mountains, Lualualei Naval Magazine, Halona Valley, Pohakea Spring, 475 m, 14.iii.1996, Malaise trap, DJP; same locality, 24.iv–16.v.1996, Malaise trap, DJP & FGH. Material determined by Keith Arakaki & Neal Evenhuis.

DISTRIBUTION: *Drosophila tamashiroi* is known only from O'ahu (Fig. 98b).

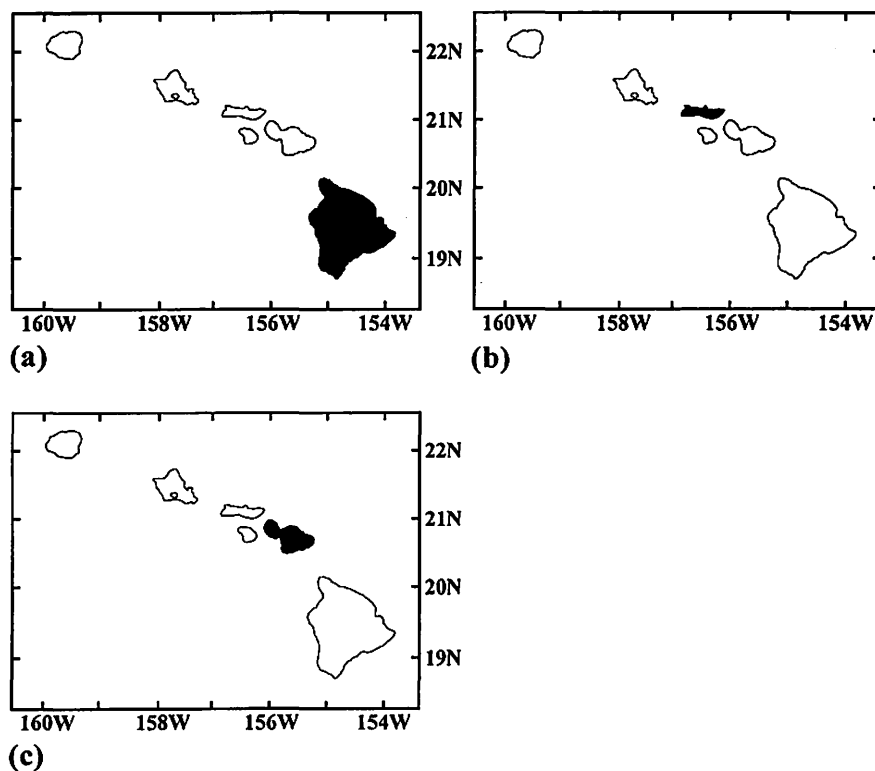


Figure 83. Distribution of species in the *Drosophila haleakalae* cluster. a. *D. clara*, b. *D. cryptica*, c. *D. haleakalae* and *D. macrochaetae*.

DISCUSSION: Arakaki & Evenhuis (*in* Evenhuis, 1997) synonymized *D. tamashiroi* and *D. insignita*. We find, based on the coloration of the pleura and wings and the number of setae on the posterolateral regions of the mesonotum that these are, in fact, distinct species.

IVb. The *luteola* complex

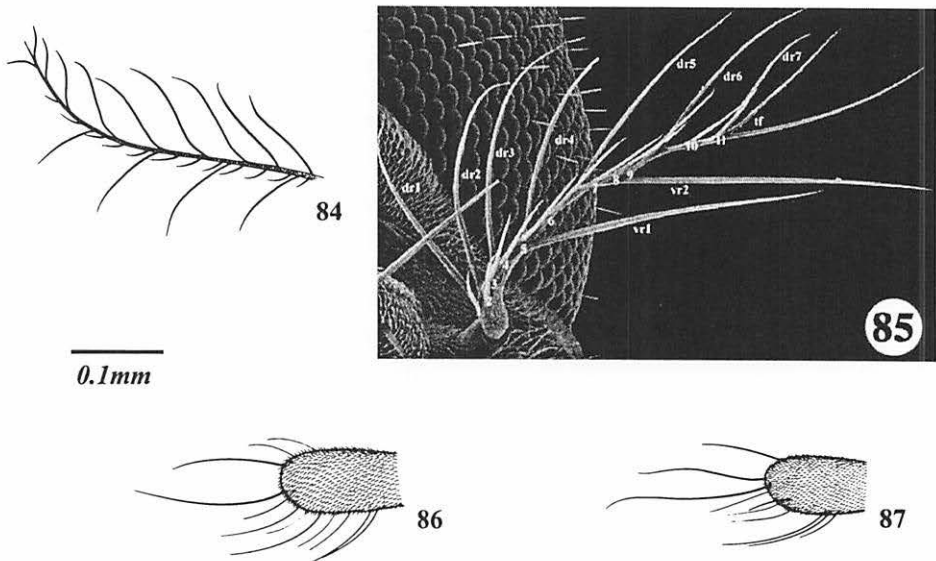
Drosophila luteola Hardy

Figs. 98c, 101, 103

Drosophila luteola Hardy, 1965: 347.

DIAGNOSIS: *Drosophila luteola* differs from other species in this clade by having the front basitarsus slightly less than 1/2 as long as tibia; the 6th, and usually the 5th, terga yellow and the arista with 6 dorsal and 3 ventral rays, in addition to the apical fork.

DESCRIPTION: ♂, ♀. The original description of this species is found in Hardy (1965). Additional male characters and a description of the female are presented here. Females fit description of males, except as noted. *Head*. Third antennal segment of female entirely dark brown to black. Area of front above proclinate setae black in females. *Thorax*. Posterolateral portions of mesonotum sparsely setose, with ca. 6 setae (Fig. 101). *Abdomen*: Abdomen of females entirely shining black. Ovipositor rounded at apex (Fig. 103). Apex with dense cluster of



Figures 84-87. Head structures of the *Drosophila haleakalae* cluster species, 84. *D. clara*, arista, 85. *D. haleakalae*, arista (400 ×), 86. *D. clara*, palp, 87. *D. cryptica*, palp.

8 stout peg ovisensilla. Dorsolateral region with 3 sharply pointed peg ovisensilla. Ventral margin with ca. 10 peg ovisensilla extending to 4/5 ovipositor length (Fig. 103).

MEASUREMENTS: N = 1 ♂. TL = 1.2 mm; WL = 2.3 mm; TL/WL = 0.5; HW = 0.9 mm; HW/TL = 0.7; CI = 4.2; 4V = 1.3; 5X = 1.5; 4C = 0.5; M = 0.3.

TYPES: O'AHU: Holotype ♂ (BPBM 6,391), Mt Ka'ala, v.1952, DEH, left foreleg beyond coxa missing (Evenhuis, 1982). Not measured. Two male paratypes have been examined. 1 ♂, Halawa Valley, Wai'anae Mts, 12.iii.1933, "on *Osmanthus*", OHS; 1 ♂, Mt Ka'ala, iv.1949, GBM.

MATERIAL EXAMINED: O'AHU: Fourteen other individuals, 9 males and 5 females, were examined from the UHM. 1 ♂, 1 ♀, C53.39, no locality or date, HLC; 1 ♀, Pūpūkea, viii.1963, WBH; 8 ♂, 1 ♀, Mt Tantalus, 20.xi.1963, "reared ex: mushrooms", MRW; 1 ♀, Kawaiinui, 16.vi.1964, MRW; 1 ♀, Tantalus, viii.1964, C109.15", HLC.

DISTRIBUTION: This species occurs in both the Ko'olau and Wai'anae Mountain Ranges on O'ahu (Fig. 98c).

ECOLOGY: *Drosophila luteola* has been reared from gill fungi (Heed, 1968; Table 2).

DISCUSSION: Populations of *D. luteola*-like from Hawai'i, Maui, and Kaua'i cannot be differentiated from the O'ahu type series (Table 3). The *D. luteola*-like specimen examined in Kambyse & Craddock (1991) is from the Big Island. We are currently studying these populations to determine if they represent separate species or simply extend the distribution of *D. luteola* beyond O'ahu (O'Grady & Val, in prep).

Drosophila quinquerosa Hardy & Kaneshiro, new species

Figs. 98d, 102

DIAGNOSIS: *Drosophila quinquerosa* is differentiated from other closely related species by having a third pair of dorsocentrals, ca. 2 × longer and stronger than the surrounding setae, present at the suture and by the combination of characters described below.

DESCRIPTION: ♂, (♀ unknown). *Head.* Front below level of proclinate setae pale yellow. Parafrontal areas dark brown to black. Antennae, face, palpi, and clypeus entirely yellow. Arista with 5 dorsal, 2 ventral rays in addition to apical fork. Genae, measured from vibrissal row to eye margin are ca. equal to 1/4 eye width. *Thorax.* Mesonotum shining black with tinge of reddish brown in ground color at margins and covered with light gray pollen. About 8 setae present on posterolateral portions of mesonotum (Fig. 102). Pleura all yellow. Scutellum with broad yellow apex. Anterior katepisternal seta at least 1/3 length of posterior katepisternal. *Legs.* Entirely yellow. Front basitarsus 2/3 tibia length. *Wings.* Costal fringe short, extending scarcely over 2/5 distance between apices of R_{2+3} and R_{4+5} . *Abdomen:* Polished reddish-brown to blackish, lightly pollinose over median portion.

MEASUREMENTS: N = 11 ♂. TL = 1.1 mm (0.9–1.1); WL = 2.4 mm (2.2–2.7); TL/WL = 0.4 (0.4–0.5); HW = 0.9 mm (0.7–0.9); HW/TL = 0.8; CI = 4.3 (3.7–4.9); 4V = 1.5 (1.4–1.6); 5X = 2.1 (1.7–2.3); 4C = 0.6 (0.5–0.6); M = 0.5 (0.3–0.6).

TYPES: MAUI: Holotype ♂ (BPBM 16,365), Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK. TL = 1.1 mm; WL = 2.3 mm; TL/WL = 0.5; HW = 0.9 mm; HW/TL = 0.8; CI = 4.2; 4V = 1.6; 5X = 1.7; 4C = 0.6; M = 0.3. Sixty paratypes, all males, have been designated. 1 ♂, Auwahi, 17.vi.1965, "on *Osmanthus* foliage", JWB; 22 ♂, Auwahi, 11.vii.1974, KYK; 24 ♂, same collection as holotype; 13 ♂, Auwahi, 29.iv.1976, KYK. The type and a series of paratypes have been placed in the BPBM. The paratypes have been divided among the collections of the BPBM and UHM.

DISTRIBUTION: *Drosophila quinquerosa* is known only from Maui (Fig. 98d).

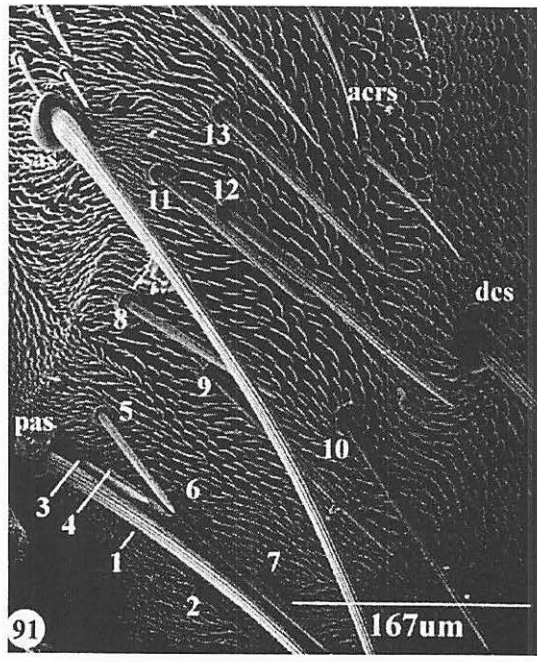
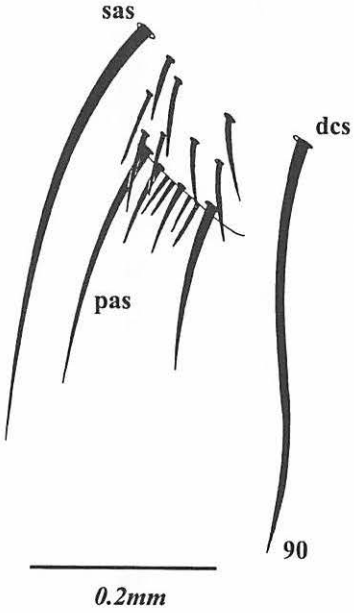
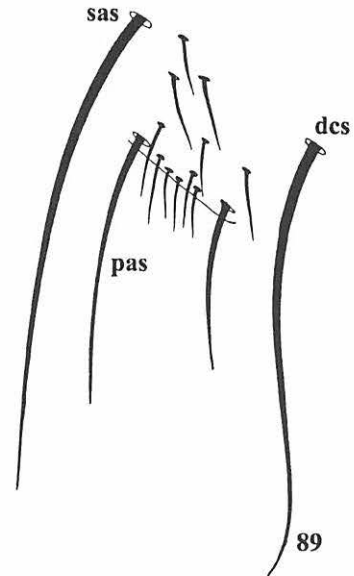
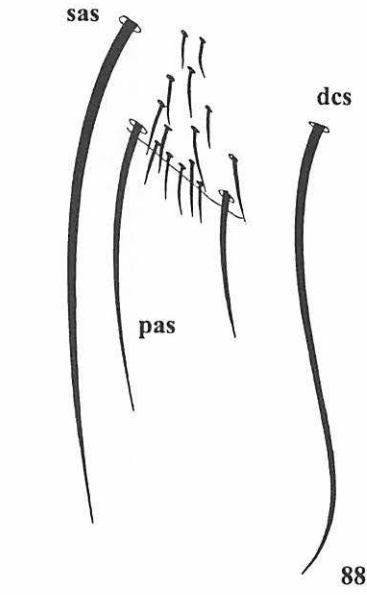
ETYMOLOGY: Latin, "5 branches". *Drosophila quinquerosa* is differentiated from *D. luteola* by having only 5 dorsal branches on the arista.

DISCUSSION: Specimens closely resembling *D. luteola* have been collected on the Big Island and Kaua'i (Table 3). We are currently examining these to determine whether they are distinct species or, instead, simply represent different populations of *D. luteola* (O'Grady & Val, in prep.). It should be noted that *D. luteola*-like populations from the island of Hawai'i also have the third pair of rudimentary dorsocentral setae present, suggesting a close relationship these forms and *D. quinquerosa*.

V. The *polita* subgroup

The *polita* subgroup contains all species with pleura that are dark above and light below. Relationships within the *polita* subgroup, as well as the relationships of some members of this subgroup to other subgroups of *haleakalae* species group, are poorly understood. We are not proposing species complexes and clusters within this clade because of lack of morphological characters and uncertainty about the monophyly of this subgroup (Bonacum, 2001). It is possible that future molecular work will clarify relationships within the *polita* subgroup.

The *polita* subgroup is found on all the high islands (Fig. 104). Three of the 10 species, *D. bipolita* (Fig. 104a), *D. canipolita* (Fig. 104b), and *D. polita* (Fig. 104f), are found on several islands, suggesting that they may be members of a morphocryptic species complex (O'Grady & Val, in prep.). All members of the *polita* subgroup for which host substrate information is available are found to use various "gill fungi" (Table 2). This may be an example of the clade-specific host use observed in other Hawaiian group (Heed, 1968; 1971; Montgomery, 1975; Kambysellis *et al.*, 1995).



KEY TO SPECIES IN THE *DROSOPHILA POLITA* SUBGROUP

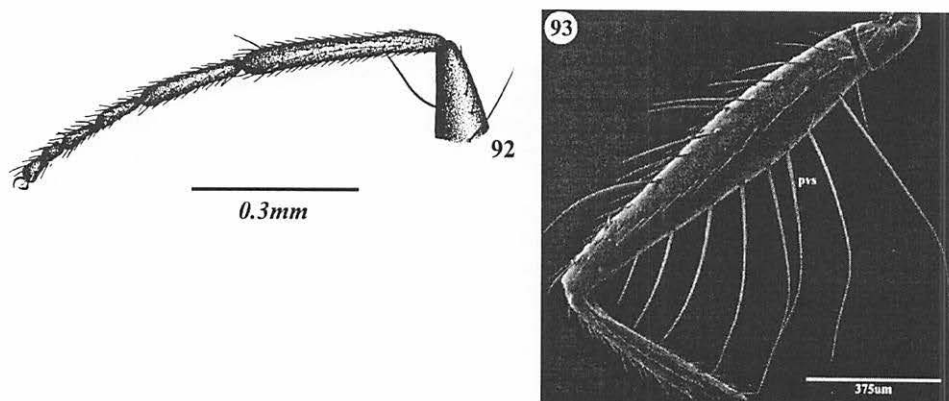
- 31. Setae present on posteroventral and anteroventral surfaces of male femora 32
- No posteroventral or anteroventral setae on femora of males 33
- 32. Front femur of males with complete row of black posteroventral setae and row of rather long anteroventral setae. Foretarsus rather thickly covered with short erect setae ... (Hawai'i) *dives* Hardy & Kaneshiro, n. sp.
- Legs heavily ciliated. Front femur with row of ca. 4 long posteroventral seta. Femur with long cilia arranged sub-basally along ventral margin from posteroventral to anteroventral surfaces. Front tibia with ca. 4 ventral and 4 posteroventral cilia arranged along apical 1/2 of segment. Front tarsus with number of moderately long, erect setae along posteroventral surface ... (Kaua'i) *paraanthrax* Hardy & Kaneshiro, n. sp.
- 33. Front entirely dark colored in both sexes; black above and brown tinged with rufous below ... (Hawai'i) *illusiopolita* Hardy
- Front dark above, light below 34
- 34. Fifth and sixth terga entirely yellow ... (Moloka'i, Maui, Lāna'i, O'ahu, Hawai'i) *canipolita* Hardy
- Sixth tergite entirely yellow or tinged with yellow, fifth tergite may be tinged with yellow. Both are never entirely yellow 35
- 35. Ocellars displaced, located anterior to ocellar triangle approximately even with proclinales ... (Lāna'i, Maui, Moloka'i, Hawai'i) *polita* Grimshaw
- Ocellars not displaced 36
- 36. Posteroventral surface of male foretarsi with ca. 3 elongate cilia ... (O'ahu) *flavisternum* Hardy
- Foretarsi lacking ornamentation 37
- 37. Anterior katapisternal completely absent. Clasper teeth short, not visible laterally. Wing lightly infuscated on apical 1/3 ... (O'ahu) *mecocnemia* Hardy
- Anterior katapisternal present. Other characters not as above 38
- 38. Face brown to black. Clypeus black ... (Hawai'i) *lissodora* Hardy & Kaneshiro, n. sp.
- Face yellow. Clypeus mostly yellow, sometimes tinged with brown 39
- 39. First antennal segment yellow, second and third segments brown. Thorax lightly dusted with gray pollen. Sixth tergite yellow. Claspers with conspicuous long teeth at apices ... (O'ahu, Maui, Moloka'i, Hawai'i) *bipolita* Hardy
- Antennae entirely yellow. Thorax shining black tinged faintly with brown on dorsum. Sixth tergite with some yellow on apex. Inner margins of claspers not setose ... (O'ahu) *pretiosa* Hardy

Drosophila bipolita Hardy

Figs. 104a, 110, 111, 125

Drosophila bipolita Hardy, 1965: 177.

DIAGNOSIS: *Drosophila bipolita* males differ from other species in this clade by having a lightly gray-dusted thorax, face and palpi yellow, clypeus yellow with not more than a faint tinge of brown above, and sixth abdominal tergum yellow. Females of *D. bipolita* can be distinguished from



Figures 92–93. Male forelegs of some *Drosophila huleakalae* cluster species. 92. *D. huleakalae*, 93. *D. macrochaetae* (80 ×).

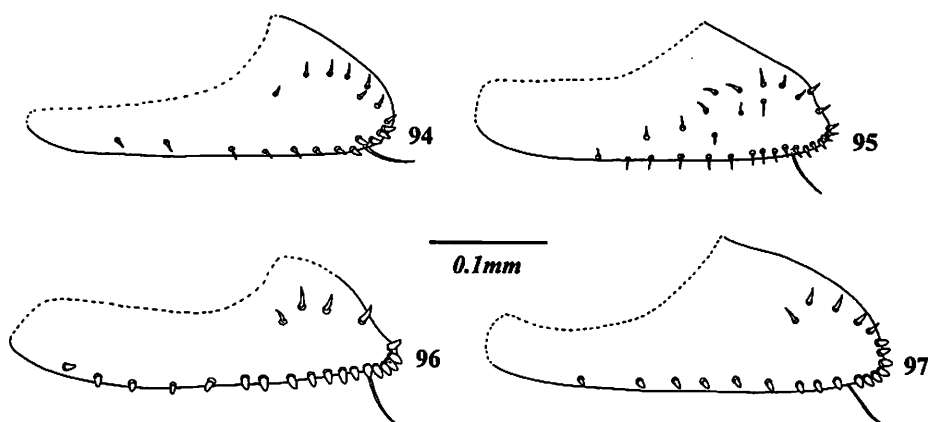
females of other species by having the lower 1/3 of front yellow and ocellar triangle polished black, and by the size and arrangement of the blunt, peg oviposensilla on the ovipositor.

DESCRIPTION: ♂, ♀. In addition to the description of Hardy (1965), several additional characters are described here. *Thorax.* Males and females differ in configuration of setae on each posterolateral area of mesonotum. Males have 3 seta in this area (Fig. 110); females possess ca. 8 (Fig. 111). *Abdomen.* Ovipositor rounded at apex with cluster of 7 stout apical peg oviposensilla (Fig. 125). Dorsal margin noticeably rounded and distended. About 7 short peg oviposensilla present in dorsolateral region, extending to ca. 1/2 ovipositor length. About 11 ventral oviposensilla, which are short and nearly trichoid extend to 3/4 ovipositor length. Inner subapical oviposensilla short, less than 1/4 ovipositor width.

MEASUREMENTS: N = 3♂. TL = 1.0 mm (0.8–1.1); WL = 2.0 mm (1.7–2.2); TL/WL = 0.5; HW = 0.8 mm (0.7–0.9); HW/TL = 0.8 (0.8–0.9); CI = 4.8 (4.7–5.0); 4V = 1.5 (1.4–1.6); 5X = 1.9 (1.6–2.1); 4C = 0.5; M = 0.4 (0.4–0.5). N = 6♀. TL = 1.2 mm (1.0–1.3); WL = 2.6 mm (2.2–3.3); TL/WL = 0.5 (0.4–0.5); HW = 1.0 mm (0.8–1.1); HW/TL = 0.8 (0.7–0.8); CI = 4.7 (3.7–5.2); 4V = 1.5 (1.4–1.5); 5X = 2.1 (1.5–2.7); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.6).

TYPES: O'AHU: Holotype ♂ (BPBM 6,309), Mt Ka'ala, v.1952, MT. Not measured. Allotype (BPBM 6,309a). Eight paratypes, 2 males and 6 females have been examined from the UHM. 2♀, Kahana, 7.ix.1924; 1♀, Palikea, Wai'anae Mts, 2,800 ft, 8.xi.1936, FXW; 1♂, 1♀, Mt Ka'ala, iv.1949, GBM; 1♀, Mt Ka'ala, iv.1952, MSA; 1♂, Makaleha, iv.1952, ED; 1♀, Pūpūkea, xii.1952, DEH. MAUI: One male paratype in the UHM has been examined. 1♂, Pu'u Kukui, 3,000 ft, vi.1953, DEH.

MATERIAL EXAMINED: O'AHU: Nine other specimens in the UHM, 6 males and 3 females, from O'ahu were also examined. 1♂, Pūpūkea, iv.1952, DEH; 2♂, Mt Ka'ala, 3.iv.1953, CPH; 1♀, Mt Tantalus, C53.31, vi.1963, HLC; 2♂, 1♀, Pūpūkea, viii.1963, DEH; 1♂, Pūpūkea, 9.v.1964, no collector given; 1♀, Mokule'ia, 28.vi.1971, SLM. MAUI: Seven other specimens, all females, from Maui are in the UHM. 2♀, Makamaka'ole Valley, vi.1953, DEH; 1♀, Waikamoi, 10.v.1974, HTS; 4♀, Kaupō Gap, 4,750 ft, 19.iv.1975, KYK. MOLOKA'I: One female in the UHM was examined. 1♀, Waikolu Stream, South of Hanalilolilo, 5.v.1976, KYK. HAWAII: Fifty-three other specimens, all females from the UHM, were examined. 2♀, Hawai'i National Park, 4,000 ft, iii.1954; 4♀, Bird Park, Kīlauea, 5.xii.1963, MRW; 1♀, Bird Park, 16.i.1964, MRW; 1♀, Kīpuka Kī, 9.ix.1964, "bred ex: gill-type fungi", HTS; 2♀, Kīpuka #1, Saddle Road, 5,560 ft, WBH; 2♀, Bird Park, Kīlauea, 3.vi.1974, HTS; 1♀, Kīlauea Forest, Volcano, 3.vi.1974, HTS; 1♀, Kīpuka Kī, 1,285 m, 3.vi.74, HTS; 1♀, Greenwell Ranch, Pauahi, 27.vi.1974; 5♀, Ahumoa Pōhakuloa, Saddle Road, 3.vii.1974, MPK; 6♀, Honokane Nui Valley, viii.1974, KYK; 1♀, Bird Park, Kīlauea, 25.vii.1975, HTS; 22♀, Kīpuka Kī, 25.vii.1975, HTS; 4♀, Manukā, South Kona, "on fungus bait", 15.i.1979, DEH.



Figures 94-97. Ovipositors of the *Drosophila haleakalae* cluster. 94. *D. clara*, 95. *D. cryptica*, 96. *D. haleakalae*, 97. *D. macrochaetae*.

DISTRIBUTION: This species is found on the islands of O'ahu, Maui, Moloka'i and Hawai'i (Fig. 104a).

ECOLOGY: *Drosophila bipolita* has been reared from "gill fungi mushrooms" (Heed, 1968).

DISCUSSION: Two females from Kaua'i also key to *D. bipolita*. It is possible that this species is actually a complex of closely related forms that have radiated on several islands. Morphometric and molecular analyses, aimed at studying populations on different islands, is currently underway (O'Grady & Val, in prep).

Drosophila canipolita Hardy

Figs. 104b, 112, 126

Drosophila canipolita Hardy, 1965: 198.

DIAGNOSIS: *Drosophila canipolita* differs from closely related forms because the dorsum of the thorax in both sexes is rather densely gray pollinose, obscuring the shining, brown to blackish, rufous-tinged ground color of the mesonotum. Further distinguishing characters are: ocellar setae normal in position, antennae yellow, and 5th tergum of males yellow.

DESCRIPTION: ♂, ♀. In addition to the description in Hardy (1965) and the distinguishing characters discussed above, we add additional characters and a description of some female characters. *Head.* Upper 1/2 of front tinged brown to blackish. *Thorax.* Scutellum and upper 1/2 of pleura brownish red or blackish with distinct tinge of rufous. Anterior katapisternal represented by single tiny pale seta. Posterolateral region of mesonotum not densely setose, both males and females possess only 4 setae in this area (Fig. 112). *Legs.* Forefemur lacking complete row of posteroventral black setae or row of anteroventral pale setae. *Abdomen.* Ovipositor somewhat acute at apex (Fig. 126). Apical margin with ca. 8 sharply pointed peg ovisensilla. Dorsolateral region with 2 peg ovisensilla. Ventral margin with 8 long thin ovisensilla. Inner subapical ovisensilla ca. 1/2 ovipositor width.

MEASUREMENTS: N = 10♂. TL = 0.9 mm (0.8-1.0); WL = 2.0 mm (1.9-2.2); TL/WL = 0.5 (0.4-0.5); HW = 0.8 mm (0.7-0.9); HW/TL = 0.9 (0.8-1.0); CI = 4.1 (3.6-4.6); 4V = 1.6 (1.5-1.9); 5X = 1.9 (1.6-2.1); 4C = 0.6 (0.5-0.7); M = 0.5 (0.4-0.6). N = 10♀. TL = 1.1 mm (1.0-1.2); WL = 2.4 mm (2.2-2.5); TL/WL = 0.5 (0.4-0.5); HW = 0.9 mm (0.8-1.0); HW/TL = 0.8 (0.8-0.9); CI = 4.4 (4.0-4.9); 4V = 1.5 (1.2-1.7); 5X = 1.8 (1.6-2.3); 4C = 0.5 (0.4-0.6); 0.5 (0.4-0.6).

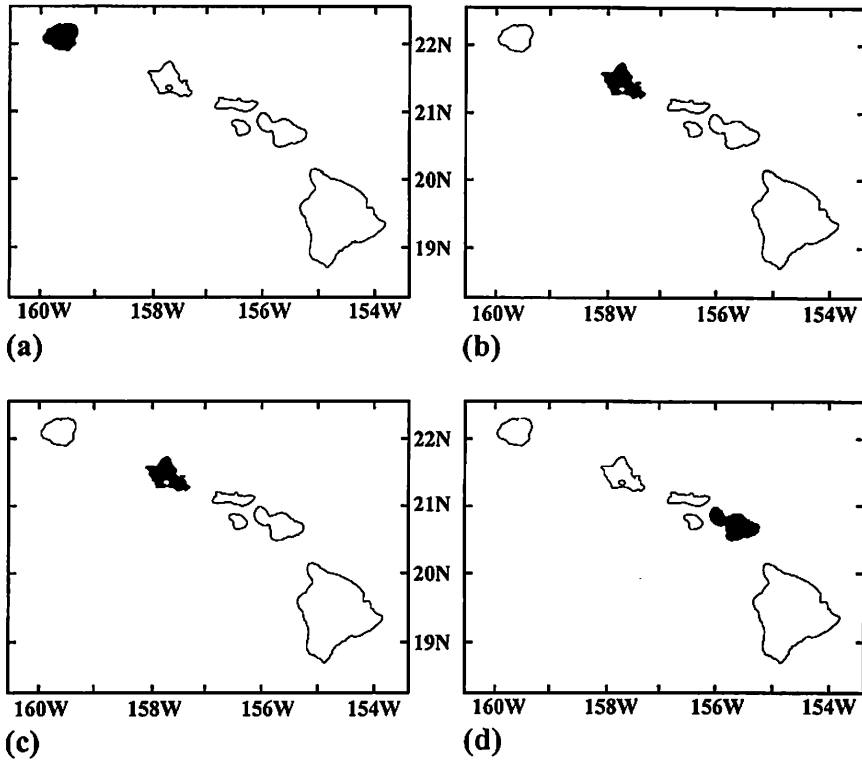
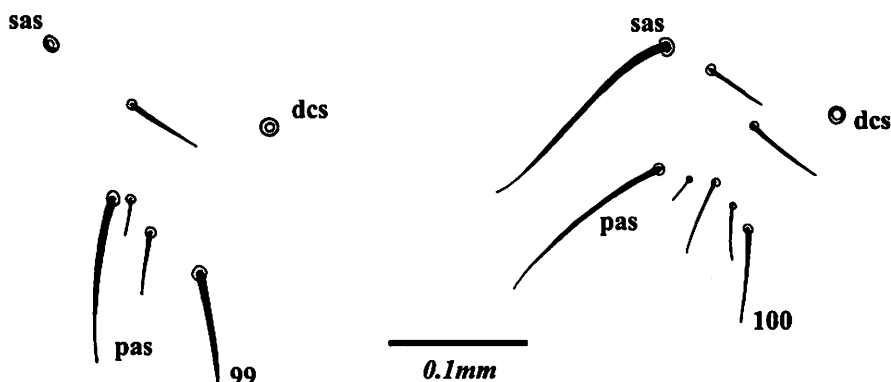


Figure 98. Distribution of species in the *Drosophila luteola* subgroup. a. *D. fuscouplex*, b. *D. tamashiroi*, c. *D. luteola*, d. *D. quinqueramosa*.

TYPES: **MOLOKA'I:** Holotype ♂ (BPBM 6,318), Pu'u Kolekole, vii.1953, DEH, right wing missing (Evenhuis, 1982). Not measured. Allotype (BPBM 6,318a). Eleven paratypes, 6 males and 5 females, from the UHM have been examined. 1 ♂, Manawainui Valley, vii.1952, DEH; 1 ♀, Pu'u Kolekole, vii.1952, MT; 1 ♂, 1 ♀, Pu'u Ali'i, 4,200 ft, vii.1953, DEH; 4 ♂, 3 ♀, Pu'u Kolekole, 3,600 ft, vii.1953, DEH. **O'AHU:** Sixteen paratypes, 10 males and 6 females, from the UHM have been examined. 1 ♀, Makiki, 29.iii.1918, OHS; 2 ♂, Mt Ka'ala, iv.1949, GBM; 3 ♂, 1 ♀, Mt Ka'ala, iv.1952, DEH; 2 ♂, 2 ♀, Pūpūkea, iv.1952, DEH; 1 ♀, Mt Ka'ala, v.1952, MT; 2 ♀, Pūpūkea, xii.1952, DEH; 1 ♂, Mt Ka'ala, 3.iv.1953, CPH; 1 ♂, Mt Ka'ala, 4,000 ft, iv.1953, MSA; 1 ♂, Poamoho Trail, 1,700 ft, v.1953, MSA. **HAWAII:** Twelve paratypes, 11 males and 1 female, are at UHM. 1 ♂, Glenwood, 2.iii.1919, OHS; 3 ♂, South Kona, 8.viii.1919, OHS; 1 ♂, Upper 'Ōla'a Forest, 4,000 ft, vii.1956, DEH; 1 ♂, 1 ♀, Kaiholena Ditch, Kohala Mts, 2,000 ft, vii.1958, "in banana thicket", DEH; 4 ♂, Kulani Road, ECZ; 1 ♂, Kīlauea, viii.1958, JWB. **MAUI:** Three paratypes, 2 males and 1 female, are in the UHM. 1 ♂, 1 ♀, Makamaka'ole Valley, vi.1953, DEH; 1 ♂, Waikamoi, 4,000 ft, vii.1956, DEH.

DISTRIBUTION: Hardy (1965) recorded the type series of this species from Moloka'i, Maui, Lāna'i, O'ahu and Hawai'i (Fig. 104b).

DISCUSSION: In addition to the paratypes listed above, over 200 specimens, variously labeled as *D. canipolita*, *D. canipolita*-like, or *canipolita* complex are in the UHM. These have been collect-



Figures 99-100. Posterolateral regions of the mesonotum of the *Drosophila fuscoapex* complex species. 99. *D. fuscoapex*, 100. *D. tamashiroi*.

ed on Hawai'i, Lāna'i, Maui, Moloka'i, and O'ahu (Table 3). In some cases, it appears that there are more than a single form close to the "typical" *D. canipolita* on a single island. Although it is clear that further work is needed to clarify the status of this species, we are restricting the current investigation to the type series of this species defined in Hardy (1965) and will present the results of the inter-island studies in a future publication (O'Grady & Val, in prep.).

Drosophila dives Hardy & Kaneshiro, new species

Figs. 104c, 107, 113, 121, 123

DIAGNOSIS: *Drosophila dives* can be distinguished from other members of this subgroup by having a complete row of black posteroventral setae and a row of long anteroventral setae on the forefemur of males (Fig. 121).

DESCRIPTION: ♂, ♀. *Head.* Arista with 6 dorsal, 3 ventral rays in addition to apical fork, inner margin sparsely short haired. Third antennal segment of females brown. Clypeus tinged with brown. Palpi entirely yellow in males, tinged with brown at apices in females; slender, with 1 apical plus 1 subapical black seta on posterior margins (Fig. 107). Front mostly rufous, with thin line of brownish red on each parafrontalia extending to ca. level with proclinate setae. *Thorax.* Scutellum and upper 1/2 of pleuron black, covered with moderate gray pollen. Mesonotum of female more thinly gray pollinose. Anterior katapisternal black, thick, and well developed; ca. 1/2 size of posterior katapisternal. About 8 strong setae present on posterolateral region of mesonotum (Fig. 113). *Legs.* Forefemur with complete row of black posteroventral setae and row of rather long anteroventral setae (Fig. 121). Front basitarsus ca. 1/2 as long as tibia, tarsus rather thickly covered with short erect setae (Fig. 121). *Wings.* Display slight, but even, infuscation; very faintly darkened apically when seen in dim or indirect light (Fig. 123). *Abdomen.* Abdominal tergites of males mostly black in ground color, with dense gray pollen. Fifth tergum also mostly black, but with slight tinge of rufous. Sixth tergum predominately yellow to rufous, tinged with brown. Abdominal tergites of females entirely reddish brown; sterna yellow-white with faint tinge of brown. External male genitalia yellow with slight tinge of brown. Ovipositor yellow-white with faint tinge of brown, not dissected.

MEASUREMENTS: N = 5♂. TL = 1.3 mm (1.2–1.3); WL = 2.9 mm (2.7–3.1); TL/WL = 0.4; HW = 1.0 mm (0.9–1.1); HW/TL = 0.8; CI = 4.3 (4.1–4.8); 4V = 1.6 mm (1.4–1.8); 5X = 1.9 (1.6–2.3); 4C = 0.6 (0.5–0.6); M

= 0.5 (0.4–0.6). N = 1 ♀. See allotype measurements.

TYPES: HAWAII: Holotype ♂ (BPBM 16,366), Kīlauea, Volcanoes National Park, 29.i.1969, MDD. TL = 1.2 mm; WL = 2.8 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.1; 4V = 1.4; 5X = 1.6; 4C = 0.5; M = 0.4. Allotype ♀ (BPBM 16,366a), same collection as holotype. TL = 1.3 mm; WL = 2.8 mm; TL/WL = 0.5; HW = 0.9 mm; HW/TL = 0.7; CI = 3.8; 4V = 1.5; 5X = 1.8; 4C = 0.6; M = 0.4. Paratypes at UHM: 1 ♂ from same locality as holotype and allotype, 3–5.vi.1974, HTS; 4 ♂, Bird Park, Kīlauea, 3–5.vi.1974, HTS.

DISTRIBUTION: This species is known only from the Big Island (Fig. 104c).

ETYMOLOGY: Latin, “rich”, referring to the dark black ground color of this species.

***Drosophila flavisternum* Hardy**

Figs. 104d, 114, 127

Drosophila flavisternum Hardy, 1965: 275.

DIAGNOSIS: *Drosophila flavisternum* differs from other species in this clade by having the sternopleura, hypopleura and lower 1/2 of humerus yellow; front tibia with between 1 and 3 rather inconspicuous cilia on posteroventral surface, no cilia on front basitarsus and front femur lacking a row of anteroventral setae.

DESCRIPTION: ♂, ♀. Several characters are added to the original description (Hardy 1965). *Thorax.* Approximately 7 setae present on posterolateral region of mesonotum, as in Fig. 114. *Abdomen.* Ovipositor rounded at apex with stout peg ovisensilla. Apex with ca. 6 peg ovisensilla. Dorsolateral region with 7 pointed, slightly elongate peg ovisensilla. Ventral margin with series of 11 peg ovisensilla extending to 3/5 ovipositor length (Fig. 127). Inner subapical ovisensilla ca. 1/2 ovipositor length.

MEASUREMENTS: N = 1 ♂. TL = 1.3 mm; WL = 2.7 mm; TL/WL = 0.5; HW = 1.0 mm; HW/TL = 0.8; CI = 3.7; 4V = 1.6; 5X = 2.1; 4C = 0.7; M = 0.5.

TYPES: O'AHU: Holotype ♂ (BPBM 6,359), Pūpūkea, xii.1952, DEH. Not measured. Allotype ♀ (BPBM 6359a), same collection as holotype. Not measured. One male paratype has been examined from the UHM. 1 ♂, Mt Ka'ala, 3.iv.1953, CPH.

MATERIAL EXAMINED: Three other specimens are present in the UHM. O'AHU: 1 ♂ (no head), 1 ♀, Pūpūkea, viii.1963, DG; 1 ♂, Pūpūkea, 4.ii.1964, DG.

DISTRIBUTION: This species is known only from the island of O'ahu (Fig. 104d).

***Drosophila illusiopolita* Hardy**

Figs. 104c, 115, 128

Drosophila illusiopolita Hardy, 1965: 311.

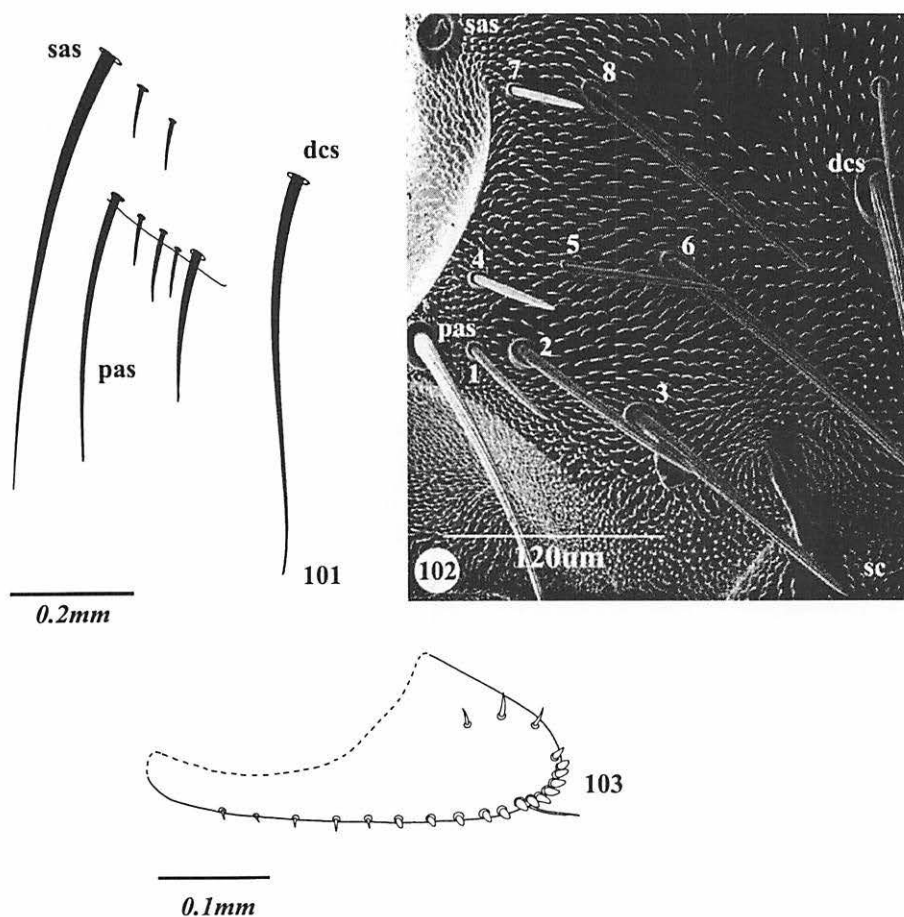
DIAGNOSIS: *Drosophila illusiopolita* differs from closely related forms by having the front all dark colored in both sexes; blackish above and brown tinged with rufous below and the palpi mostly brown.

DESCRIPTION: ♂, ♀. The following characters are added to the original description (Hardy 1965): *Thorax.* About 6 supernumerary setae present on posterolateral portions of mesonotum (Fig. 115). *Abdomen.* Ovipositor rounded at apex. Cluster of ca. 8 apical peg ovisensilla present on ovipositor, dorsoapical ovisensilla noticeably longer than ventroapical ones. Three peg ovisensilla present on dorsolateral region to ca. 1/4 ovipositor length. Ventral margin has series of 12 ovisensilla, extending to ca. 3/4 ovipositor length. Ventroapical ovisensilla much stouter than ventrodistal ones. Inner subapical ovisensillum ca. 1/3 ovipositor length (Fig. 128).

MEASUREMENTS: N = 1 ♂. TL = 1.0 mm; WL = 2.3 mm; TL/WL = 0.4; HW = 0.8 mm; HW/TL = 0.8; CI = 4.7; 4V = 1.4; 5X = 2.0; 4C = 0.5; M = 0.5.

TYPES: HAWAII: Holotype ♂ (BPBM 6,373), Kaiholena, Kohala Mountains, Ditch Trail, 2,000 ft, vii.1958, DEH. Not measured. Allotype ♀ (BPBM 6,373a), same collection as holotype. Not measured. One male paratype at UHM has been examined. 1 ♂, Upper 'Ōla'a Forest, vii.1953, DEH.

MATERIAL EXAMINED: Specimens examined from UHM include: 4 ♀, Bird Park, Kīlauea, 29.i.1969, MDD; 1 ♀, Pololu Valley, Kohala, 21.vii.1969, KYK; 1 ♂, Upper 'Ōla'a Forest, vii.1953, DEH. Other material in the UHM includes: 1 ♂, 1 ♀, Upper 'Ōla'a Forest, 26.iv.1974, HTS; 1 ♂, 3 ♀, Upper 'Ōla'a Forest, 25.vii.1975, HTS.



Figures 101–103. The *Drosophila luteola* complex. 101. *D. luteola*, mesonotum, 102. *D. quinquerosa*, mesonotum, 103. *D. luteola*, ovipositor.

DISTRIBUTION: This species is known from several locations on the Big Island (Fig. 104c).

ECOLOGY: This species has been bred from gill fungi (Table 2).

***Drosophila lissodora* Hardy & Kaneshiro, new species**

Figs. 104c, 108, 116, 129

DIAGNOSIS: *Drosophila lissodora* differs from other members of this clade by having the face brown to blackish, the palpi brown and the clypeus black.

DESCRIPTION: ♂, ♀. This species fits the description of *D. bipolita* (Hardy 1965) except as follows. *Head.* Face of female distinctly blacker than male, palpi dark brown to black. Parafrontal areas silvery white pollinose, as seen in dim light, almost obscuring black ground color of upper portion of front. Second antennal segment

distinctly tinged with brown over dorsal portion and third segment entirely dark brown to blackish. Palpi with 1 apical and 1 subapical seta, in addition to several long setae on margin (Fig. 108). Subapical palpal seta 1/2 length of apical seta. Palpi are more extensively dark brown to black in female. *Thorax*. Upper 1/2 of each pleuron is shining black. Female sternopleuron tinged with brown on upper portions. Eight supernumerary setae located on posterolateral portions of mesonotum (Fig. 116). *Abdomen*. External male genitalia entirely yellow. Ovipositor somewhat acute at apex, with cluster of ca. 7 apical, pointed peg ovisensilla. Dorsolateral region bears 3 peg ovisensilla. Ventral margin with 7 peg ovisensilla extending to ca. 3/4 ovipositor length. Inner subapical ovisensilla short, ca. 1/3 ovipositor width (Fig. 129).

MEASUREMENTS: N = 10♂. TL = 1.1 mm (1.0–1.3); WL = 2.5 mm (2.3–2.7); TL/WL = 0.5 (0.4–0.5); HW = 0.9 mm (0.8–1.1); HW/TL = 0.8 (0.8–0.9); CI = 4.6 (4.2–4.7); 4V = 1.4 (1.3–1.6); 5X = 2.2 (1.6–3.0); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.6).

TYPES: HAWAII: Holotype ♂ (BPBM 16,367), Above Manukā, Kapu'a (land section), Ho'opuloa (quadrant), South Kona, 2,650 ft, vii.1977, DEH. Not measured. Allotype ♀ (BPBM 16,367a), collected with holotype. Sixty-seven paratypes, 21 males and 46 females, are in UHM. 16♂, 33♀, from the same collection as the holotype and allotype; 2♂, 13♀, Halepiula Road, Kapu'a (land section), South Kona, 4,650 ft, vii.1977, DEH; 3♂, Manukā, South Kona, 1,000 ft, 15.i.1979, DEH. Four other individuals on hand, which are not being designated as paratypes, include: 1♂, Forest above Pa'auilo, 19.vi.1964, LHT; 1♀, Keanakolu, 20.viii.1964, DF; 1♀, Kipuka 'Ākala, Kahuku Ranch, 5,000 ft, 18.vii.1974, WI; 1♀, Honokane Nui Valley, viii.1974, KYK. The paratypes have been divided among the collections of the BPBM and UHM.

DISTRIBUTION: This species is known only from the island of Hawai'i (Fig. 104c).

ETYMOLOGY: Greek, "smooth hide", referring to the smooth-appearing shining black upper pleura.

DISCUSSION: Specimens that key to *D. lissodora* are also known from Maui and Moloka'i (Table 3). They are not being designated as paratypes.

Drosophila mecocnemia Hardy

Figs. 104d, 117, 124, 130

Drosophila mecocnemia Hardy, 1965: 354.

DIAGNOSIS: *Drosophila mecocnemia* differs from closely related forms by its yellow to rufous front; by lacking an anterior katepisternal seta and having the front basitarsus 2/3 as long as tibia.

DESCRIPTION: ♂, ♀. Refer to Hardy (1965) for descriptive information not discussed here. *Thorax*. Setae present on posterolateral portions of mesonotum more dense than closely related forms, ca. 10 setae present (Fig. 117). *Wing*. Evenly infuscated (cf. Fig. 124). *Abdomen*. Ovipositor rounded at apex (Fig. 130). Apex with cluster of 5 peg ovisensilla. Dorsolateral region with 3 long, pointed peg ovisensilla. Ventral margin with series of 6 peg ovisensilla extending to 1/2 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width.

MEASUREMENTS: N = 2♂. TL = 1.2 mm; WL = 3.1 mm (3.0–3.2); TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.5 (4.1–4.9); 4V = 1.6 (1.5–1.6); 5X = 2.0 (1.9–2.1); 4C = 0.6 (0.5–0.6); M = 0.5 (0.4–0.5).

TYPES: O'AHU: Holotype ♂ (BPBM 6,395), Pupukea, vii.1958, DEH. Not measured, small portion of axillary cell of left wing and posteroapical portion of right wing are torn off, abdomen beyond fourth segment missing, genitalia in microvial mounted below specimen (Evenhuis, 1982). Allotype ♀ (BPBM 6,395a). Paratypes in UHM include: 1♂, Pupukea, XII/52, DEH; 1♂, Lulumahu Valley, 18.iv.1937, genitalia slide #4, FXW.

MATERIAL EXAMINED: Other material in UHM includes: 2♂, 2♀, 'Ōpae'ula, vii.1964, HLC; 4♀, Manana Trail, Ko'olau Mountains, 26.v.1976, HTS.

DISTRIBUTION: *Drosophila mecocnemia* is known only from the Ko'olau Mountains of O'ahu (Fig. 104d).

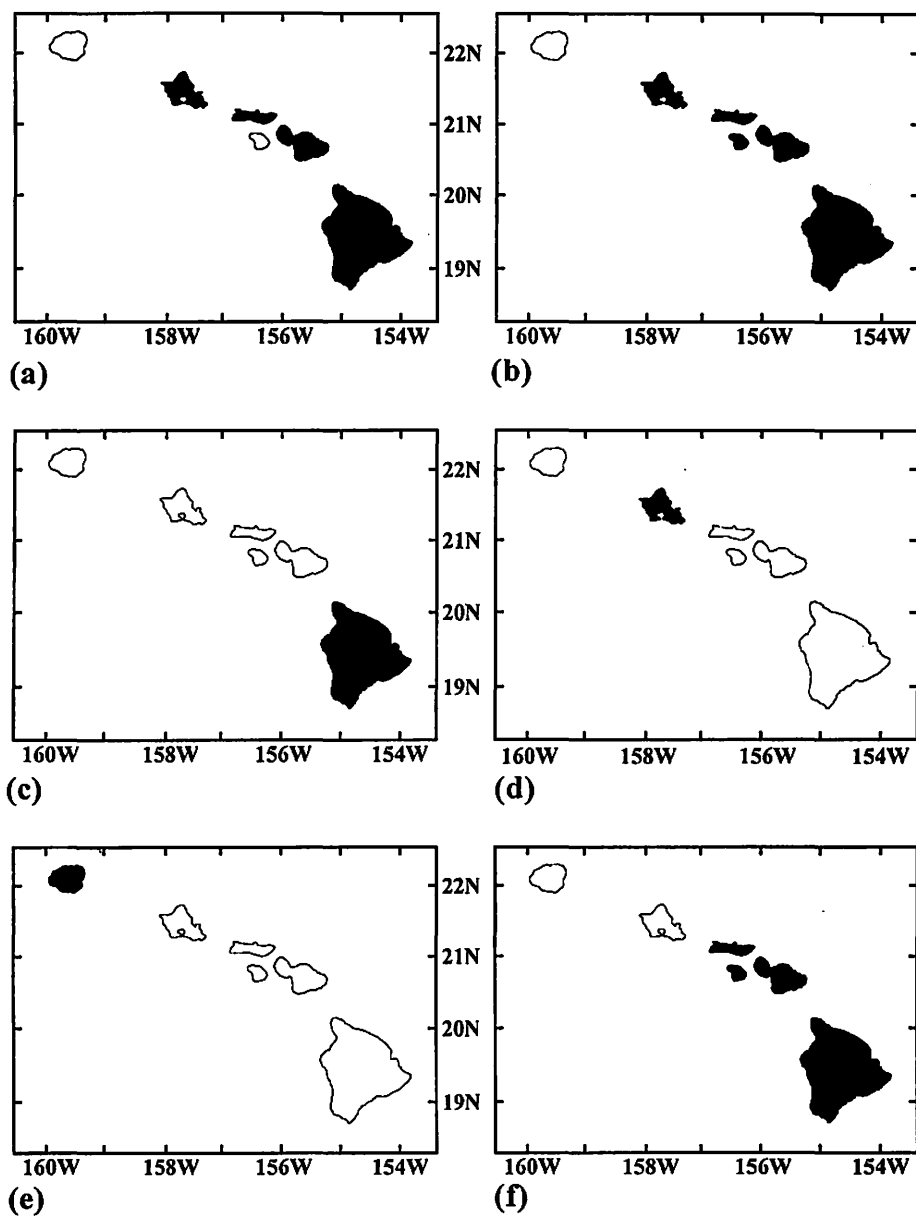
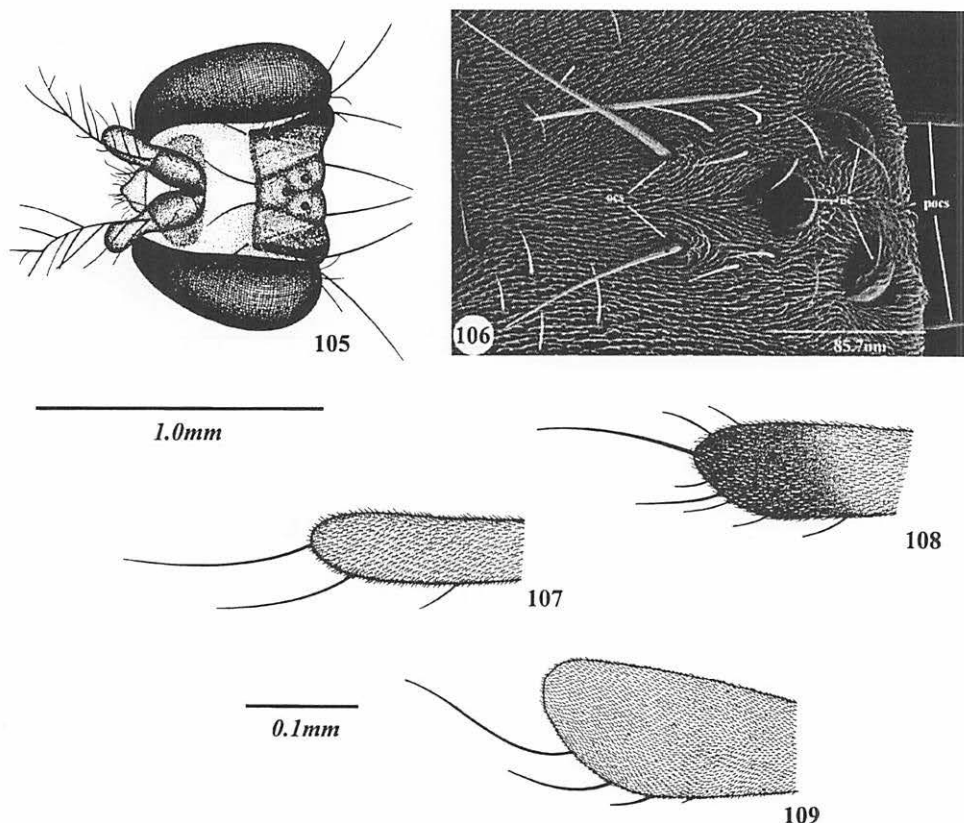


Figure 104. Distribution of species in the *Drosophila polita* subgroup. a. *D. bipolita*, b. *D. canipolita*, c. *D. dives*, *D. illusiopolita*, and *D. lissodora*, d. *D. flavisternum*, *D. mecocnemia*, and *D. pretiosa*, e. *D. paraanthrax*, f. *D. polita*.



Figures 105–109. Head structures of the *Drosophila polita* subgroup. 105. *D. polita*, head, 106. *D. polita* head, detail of front and ocelli, 107. *D. dives*, palp, 108. *D. lissodora*, palp, 109. *D. polita*, palp.

Drosophila paraanthrax Hardy & Kaneshiro, new species

Figs. 104e, 118, 122, 131

DIAGNOSIS: *Drosophila paraanthrax* is differentiated from closely related species in this clade by the patterns of setae and cilia on the legs of males (Fig. 122) and as described below.

DESCRIPTION: ♂, ♀. *Head*. Front of male yellow below proclinate setae, upper portion mostly black covered with grayish pollen. Face, antennae, and palpi of males entirely yellow. In females, antennae and apices of palpi brown, upper 1/2 of face tinged with brown. Genae rather narrow, at narrowest portion measured from vibrissal row to eye margin ca. 2 rows of eye facets. Clypeus brown. *Thorax*. Dark brown to blackish with faint tinge of rufous in ground color and rather densely gray pollinose but not obscuring shining ground color. Upper 1/2–2/3 of each sternopleuron and hypopleuron brown, tinged with rufous, lower portion yellow. Humerus dark brown to black. Anterior katepisternal well developed, nearly 1/2 as long as posterior katepisternal. Posterolateral portions of mesonotum with ca. 8 supernumerary setae (Fig. 118). *Legs*. Entirely yellow in males, lacking brown markings on mid and hind femora that characterize females. Front femur with row of 4 rather long posteroventral setae and with several long thick cilia arranged along ventral margin from posteroventral to

anteroventral surfaces (Fig. 122). Front tibia with ca. 4 ventral and posteroventral cilia arranged along apical 1/2 of segment and front tarsus with number of moderately long, erects setae along posterior surface. Front basitarsus approximately 1/2 tibia length. *Wings*. Entirely subhyaline. Costal fringe comparatively short, extending just slightly more than 1/3 distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Entirely dark brown to black in ground color, rather densely covered with gray pollen. Ovipositor somewhat acute at apex (Fig. 131). Apex with ca. 5 pointed peg ovisensilla. Dorsolateral region with 4 long, pointed ovisensilla that extend to ca. 2/5 ovipositor length. Ventral margin with 7 peg ovisensilla that extend to ca. 3/5 ovipositor length. Inner subapical ovisensilla ca. 1/4 ovipositor width (Fig. 131).

MEASUREMENTS: N = 11 ♂. TL = 1.1 mm (0.9–1.2); WL = 2.5 mm; (2.0–2.7); TL/WL = 0.4 (0.4–0.5); HW = 0.9 mm (0.7–1.0); HW/TL = 0.8; CI = 4.2 (3.9–4.6); 4V = 1.5 (1.4–1.7); 5X = 1.8 (1.5–2.1); 4C = 0.6 (0.5–0.7); M = 0.5 (0.4–0.5). N = 4 ♀. TL = 1.2 mm (1.2–1.3); WL = 2.9 mm (2.6–3.0); TL/WL = 0.4 (0.4–0.5); HW = 0.9 mm (0.8–1.0); HW/TL = 0.8 (0.7–0.8); CI = 4.5 (3.0–4.9); 4V = 1.5 (1.4–1.5); 5X = 2.0 (1.8–2.1); 4C = 0.5 (0.5–0.6); M = 0.5 (0.4–0.5).

TYPES: KAUA'I: Holotype ♂ (BPBM 16,368), Mōhihi Stream, Koke'e, 25.vi.1965, KYK. TL = 1.2 mm; WL = 2.7 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.5; 4V = 1.4; 5X = 1.8; 4C = 0.5; M = 0.5. Allotype: ♀ (BPBM 16,368a), Mōhihi Stream, Koke'e, 30.vii.1963, DEH. TL = 1.2 mm; WL = 2.6 mm; TL/WL = 0.5; HW = 0.8 mm; HW/TL = 0.7; CI = 4.9; 4V = 1.5; 5X = 2.0; 4C = 0.5; M = 0.5. Forty-one paratypes at UHM, 34 males and 7 females, are designated. 1 ♀, Waiaka'oli Valley, 3,700 ft, vii.1959, DEH; 1 ♂, 1 ♀, Mōhihi Stream, Koke'e, vii.1963, MRW; 1 ♀, Koke'e, 3,600 ft, vii.1963, LHT; 1 ♂, 1 ♀, Kumuwela Trail, i.iv.1964, DG; 2 ♂, Koke'e, 3,600 ft, 5.iii.1964, MRW; 1 ♂, Mōhihi Stream, Koke'e, 24.vi.1964, LHT; 1 ♂, Halemanu Valley, 4,000 ft, 25.vi.1964, LHT; 2 ♂, Mōhihi Stream, Koke'e, 3,700 ft, 26.vi.1964; 1 ♂, Near Waiaka'oli Stream, 3,700 ft, 26.vi.1964, DEH; 1 ♂, Mōhihi Stream, Koke'e, 26.viii.1964, DG; 1 ♂, Mōhihi Stream, Koke'e, 26.viii.1964, HTS; 1 ♂, Mōhihi Stream, Koke'e, 28.viii.1964, HTS; 6 ♂, 2 ♀, State Park, Mōhihi Stream, Koke'e, 23.vi.1965, LHT; 2 ♂, same collection as holotype; 6 ♂, Mōhihi Stream, Koke'e, 29.xii.1965, KYK; 1 ♂, Alaka'i Swamp, 4,000 ft, 23.vi.1966, DEH; 1 ♂, Mōhihi Stream, Koke'e, 18.vii.1966, WBH; 1 ♂, Mōhihi Stream, Koke'e, 21.vi.1967, JPM; 1 ♀, Kane'oele Swamp, 2,500 ft, 19–20.iii.1968, HLC; 1 ♂, Berry Flat Trail, Koke'e, 18.iv.1974, HTS; 4 ♂, Berry Flat Trail, Koke'e, 17.iv.1975, KYK. The paratypes have been divided among the collections of the BPBM and UHM.

DISTRIBUTION: *Drosophila paraanthrax* is endemic to Kaua'i (Fig. 104e).

ETYMOLOGY: Greek, "near *anthrax*", indicating the close morphological affinity of some characters between these 2 species.

Drosophila polita Grimshaw

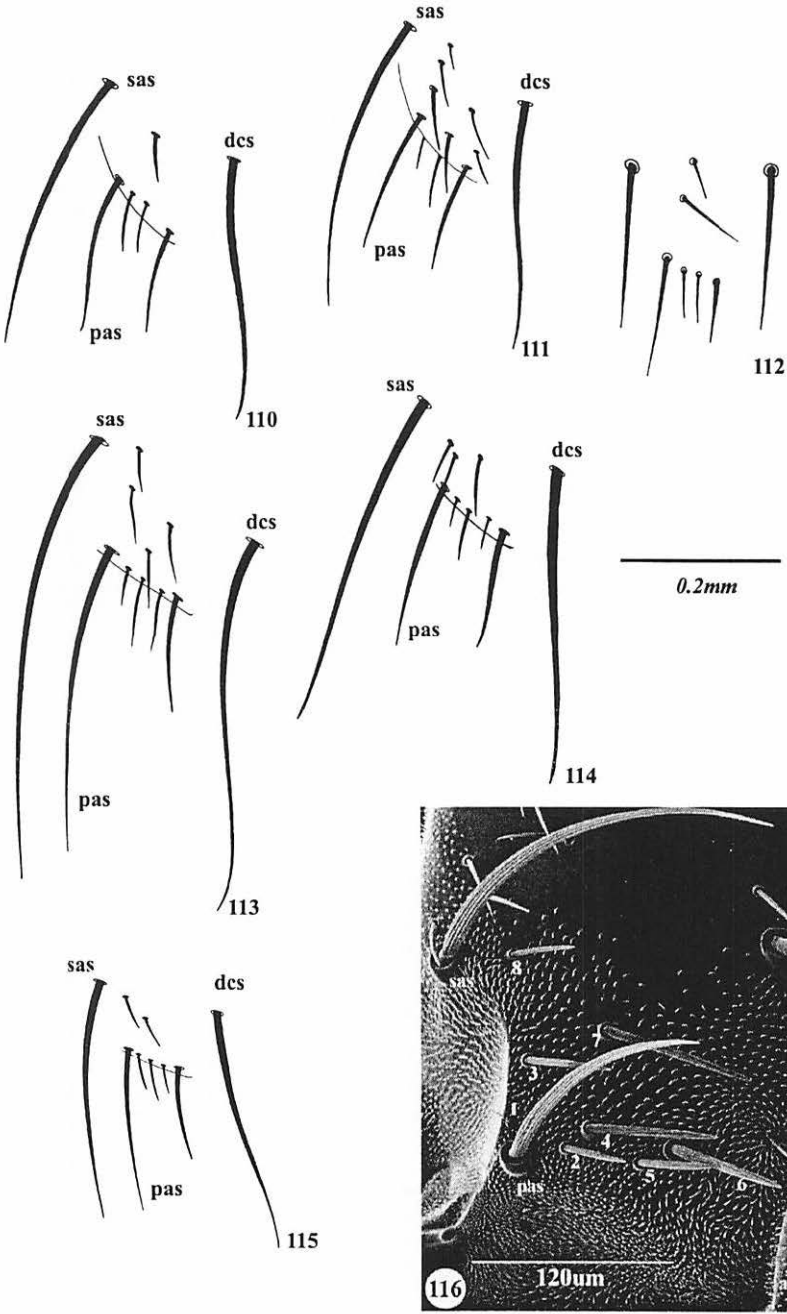
Figs. 104f, 105, 106, 109, 119, 132

Drosophila polita Grimshaw, 1901: 71.

Drosophila transfuga Hardy, 1965: 487, new synonymy.

DIAGNOSIS: *Drosophila polita* males have ocellars that are situated near the middle of the front, opposite the proclinate frontal setae (Figs. 105, 106). In the female they are situated just in front of the median ocellus on the lateral margins of the ocellar triangle. The densely silvery gray pollinose mesonotum of the male is also a characteristic feature; the pollen completely obscures the ground color.

DESCRIPTION: ♂, ♀. Although this species has been described elsewhere (Grimshaw, 1901; Hardy, 1965), we repeat that information here because of the synonymy of *D. polita* and *D. transfuga*. In addition to characters in the diagnosis: *Head*. Front of male below proclinate setae pale yellow with upper 1/2 densely gray pollinose, almost completely obscuring yellow to brownish ground color and covering ocellar triangle. Upper portion of front shining in females, with ocellar triangle polished dark brown to black. Antennae, face, genae, palpi, clypeus and mouthparts, except for black rim, entirely pale yellow to yellow-white in males. Third antennal segment and palpi brown in females. Palpi broad, expanded portion is scarcely longer than wide and has 2 prominent setae on outer edge (Fig. 109). *Thorax*. Mostly shining black in males, polished black and rather lightly gray pollinose in females. Lower halves of pleura pale yellow. About 11 supernumerary setae present on posterolateral region of mesonotum (Fig. 119). Apical portion of scutellum broadly pale yellow. Halteres are faintly tinged



with brown at apices. Anterior katapisternal seta moderately developed. *Wings*. Entirely subhyaline in females, tinged faintly brownish on apical third in males. *Abdomen*. Ovipositor rounded at apex with series of 5 short apical ovisensilla (Fig. 132). Dorsolateral region has ca. 6 short peg ovisensilla. Ventral margin with 7 short peg ovisensilla. Inner subapical ovisensilla short, ca. 1/5 ovipositor width (Fig. 132).

MEASUREMENTS: N = 8 ♀. TL = 1.4 mm (1.2–1.6); WL = 3.1 mm (2.7–3.3); TL/WL = 0.4 (0.4–0.5); HW = 1.0 mm (0.9–1.1); HW/TL = 0.8 (0.8–0.9); CI = 4.5 (4.0–5.5); 4V = 1.4 (1.3–1.5); 5X = 1.9 (1.7–2.2); 4C = 0.6 (0.4–0.6); M = 0.5 (0.4–0.5).

TYPES: *Lāna'i*: Holotype (of *polita*) ♀, no locality given, 2,000 ft, xii.1893, BMNH, excellent condition (Hardy, 1965). Not measured. Six homotype females have also been examined 6 ♀, *Lāna'ihale*, 11.vii.1975, KYK. *MAUI*: Holotype (of *transfuga*) ♂ (BPBM 6,457), 'Īao Valley, vi.1952, MT, right foreleg beyond coxae, left foreleg beyond tibia, and abdomen beyond fourth segment missing; genitalia in microvial mounted below specimen (Evenhuis, 1982). One homotype at UHM was studied. 1 ♀, Auwahi, 11.vii.1974, KYK. *HAWAII*: One homotype in UHM studied. 1 ♀, Keanakolu, 5,200 ft, x.1952, DEH. *MOLOKA'I*: One homotype from UHM was examined. 1 ♀, South of Hanalei, 19.vii.1963, DEH.

MATERIAL EXAMINED: We have examined representatives of this species from all islands *D. polita* is known from. All material is deposited in the UHM. *HAWAII*: A large series of specimens are on hand from the Big Island. 1 ♂, Kamuela, vi.1963, LHT; 2 ♂, Bird Park, Kilauea, 5.xii.1963, MRW; 5 ♂, Greenwell Ranch, Pauahi, 27.v.1974, KYK; 24 ♂, Hualālai Ranch, 4,600 ft, 20.v.1976, KYK; 16 ♂, 29 ♀, Manukā Forest Reserve, South Kona, 27.vi.1976, "reared ex: fungus", SLM; 20 ♂, 55 ♀, Kapu'a (land section), Ho'opuloa (quadrant), South Kona, 2,650 ft, vii.1977, DEH; 2 ♂, 2 ♀, Pu'u Wa'awa'a, 5,000–6,000 ft, 8.viii.1978, SLM. *LĀNA'I*: A series of specimens at UHM from *Lāna'i* have been studied. 2 ♂, Kaiholena Gulch, 2,150 ft, LW; 1 ♂, 1 ♀, *Lāna'ihale*, 11.vii.1975, KYK; 1 ♀, Kaiholena Gulch, 11.vii.1975, ATO. *MAUI*: Other material from UHM studied includes: 1 ♂, Pu'u Kukui, iv.1954, MT; 28 ♂, 13 ♀, Auwahi, 11.vii.1974, KYK; 21 ♀, Manawainui Gulch, 10.iv.1975, KYK; 1 ♂, Kaupō Gap, Haleakalā, 4,750 ft, 19.vi.1975, KYK.

DISTRIBUTION: This species is known from *Lāna'i*, *Maui*, *Moloka'i* and *Hawai'i* (Fig. 104f).

ECOLOGY: *Drosophila polita* has been reared from fungus (Table 2).

DISCUSSION: *Drosophila polita* was first described based on a single female from *Lāna'i* (Grimshaw, 1901). Hardy (1965) described the male of this species as *D. transfuga*, but was unable to associate it with the female at that time. We have examined the types of *D. transfuga* and *D. polita*, as well as a more recent series of collections, and find these taxa to be synonymous.

Drosophila pretiosa Hardy

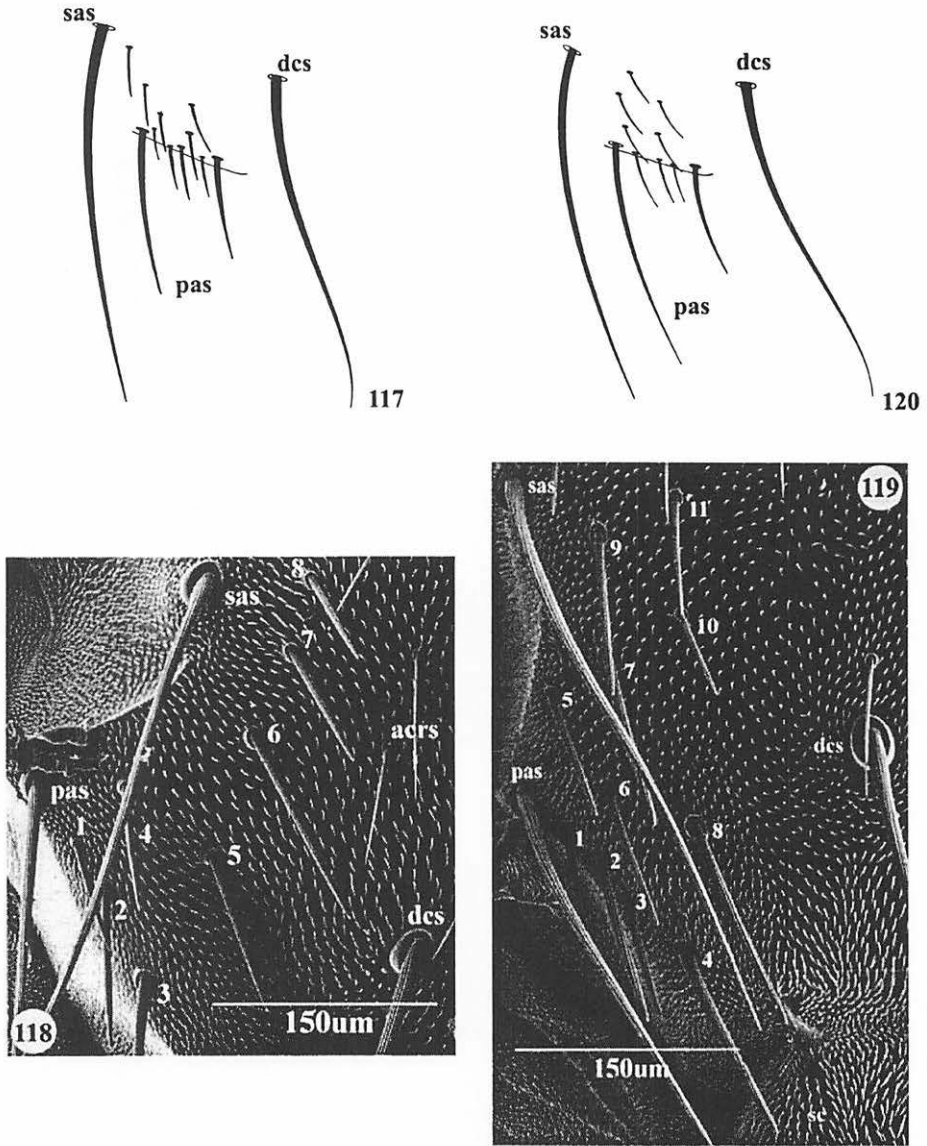
Drosophila pretiosa Hardy, 1965: 423.

Figs. 104d, 120, 133

DIAGNOSIS: *Drosophila pretiosa* males can be distinguished from other closely related species by having the upper 2/3 of the front, except for the eye orbits, dark brown to black, anterior katapisternal well developed and black, 2/3–2/5 as large as posterior katapisternal, the front basitarsus short, ca. 1/2 as long as tibia. This species has no posteroventral cilia on the front tibiae of males. Females can be differentiated by having a faint brown mark over the m crossvein, a yellow-brown sternopleura, mid and hind femora tinged with brown and lower 1/2 of the face white, tinged with blackish above.

DESCRIPTION: ♂, ♀. Refer to Hardy (1965) for a full description of the male. We add a description of the female here. Females fit the description of males, except as follows: *Head*. Third antennal segment and palp of female brown. *Thorax*. Female sternopleuron brown, tinged with yellow. About 9 supernumerary setae present on posterolateral portions of mesonotum in both sexes (Fig. 120). *Legs*. Mid and hind femora faintly tinged with

Figures 110–116. Posterolateral regions of the mesonotum of the *Drosophila polita* subgroup. 110. *D. bipolita*, male, 111. *D. bipolita*, female, 112. *D. canipolita*, 113. *D. dives*, 114. *D. flavisternum*, 115. *D. illustropolita*, 116. *D. lissodora*.



Figures 117-120. Posterolateral regions of the mesonotum of the *Drosophila polita* subgroup. 117. *D. meconemia*, 118. *D. paraanthrax*, 119. *D. polita*, 120. *D. pretiosa*.

brown on apical 1/2 in females. *Abdomen*. Ovipositor rounded at apex with only 2 pointed peg ovisensilla on apical margin. Two sharp peg ovisensilla occupy the dorsolateral region. Ventral margin bears 8 peg ovisensilla that extend to ca. 3/4 ovipositor length (Fig. 133).

MEASUREMENTS: N = 2♂. TL = 1.1 mm (1.0–1.1); WL = 2.1 mm (2.0–2.1); TL/WL = 0.5; HW = 0.8 (0.8–0.9); HW/TL = 0.8; CI = 3.9 (3.8–3.9); 4V = 1.4 (1.3–1.4); 5X = 1.9 (1.8–2.0); 4C = 0.6; M = 0.5. N = 1♀. TL = 1.3 mm; WL = 2.9 mm; TL/WL = 0.4; HW = 1.1 mm; HW/TL = 0.8; CI = 5.5; 4V = 1.3; 5X = 1.6; 4C = 0.4; M = 0.4.

TYPES: O'AHU: Holotype ♂ (BPBM 6,423), Pūpūkea, vii.1958, HT. Allotype (BPBM 6,423a). Paratypes studied at UHM include: 1♀, Mt Ka'ala, 17.ix.1946, GBM; 1♂, Pūpūkea, iv.1952, DEH; 1♂, Mt Ka'ala, 3.iv.1953, CPH.

MATERIAL EXAMINED: O'AHU: Forty-one other specimens, 37 males and 4 females, have been studied from the UHM. 1♂, Waiwa, 13.viii.1916, OHS; 1♂, Mt Ka'ala Trail, 2,500 ft, 20.v.1956, no collector; 1♂, Mt Tantalus, 18.vi.1963, no collector; 1♂, Pūpūkea, 9.v.1964, no collector; 1♂, Kawainui, 16.vi.1964, HLC; 3♂, 'Ōpae'ula, viii.1964, WBH; 1♀, Pūpūkea, 1,400 ft, 6.viii.1975, HTS; 29♂, 3♀, Manana Trail, Ko'olau Mountains, 26.v.1976, HTS.

DISTRIBUTION: This species has been collected in both the Wai'anae and Ko'olau Mountains of O'ahu (Fig. 104d).

ECOLOGY: *Drosophila pretiosa* occurs sympatrically with *D. mecocnemia* and *D. flavisternum* (Fig. 104d).

VI. The *scitula* subgroup

The *scitula* subgroup contains 5 species, all of which are found only on Kaua'i. This subgroup is characterized by males having a short front basitarsus, approximately 1/5 the length of the tibia. Examination of ovipositor morphology indicates that *D. scitula* is very different from the other species in this subgroup. This could represent a shift to a different oviposition substrate, although its ecology remains unknown. We are not designating species complexes and clusters in this subgroup at this time. Further morphological and molecular work will be needed in order to further divide this subgroup.

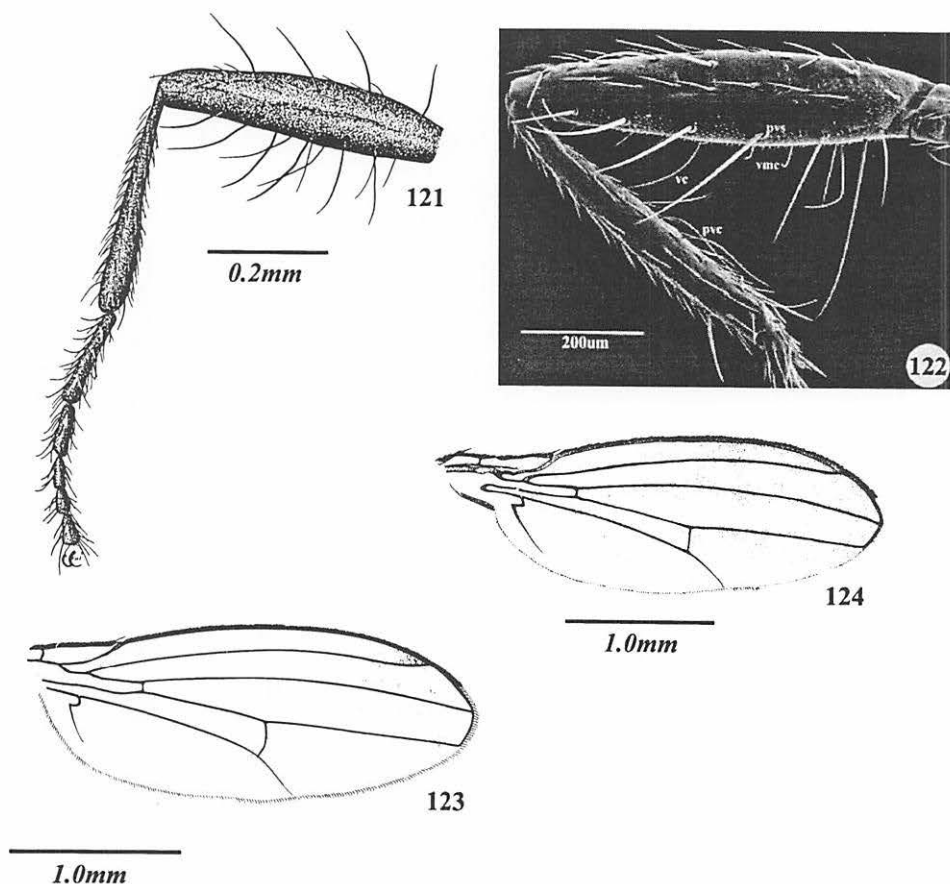
KEY TO SPECIES IN THE *DROSOPHILA SCITULA* COMPLEX

- 40. Scutellum entirely black, without lightened area at apex ... *setositibia* Hardy & Kaneshiro, n. sp.
- Scutellum with lightened area at apex 41
- 41. Tergites 5 and 6 of males entirely light tan *scitula* Hardy
- Tergites 5 and 6 of males dark brown to black 42
- 42. Ocellar triangle shining polished black, lacking pollen *fulgida* Hardy & Kaneshiro, n. sp.
- Ocellar triangle dull pollinose 43
- 43. Face white. Antennae, palpi and clypeus pale yellow *melanosoma* Grimshaw
- Face brown, with tinge of yellow; lower margin above clypeus dark brown to black. First 2 antennal segments yellow, 3rd segment brown. Palpi broadly brown apically. Clypeus dark brown to black *subopaca* Hardy & Kaneshiro, n. sp.

Drosophila fulgida Hardy & Kaneshiro, new species

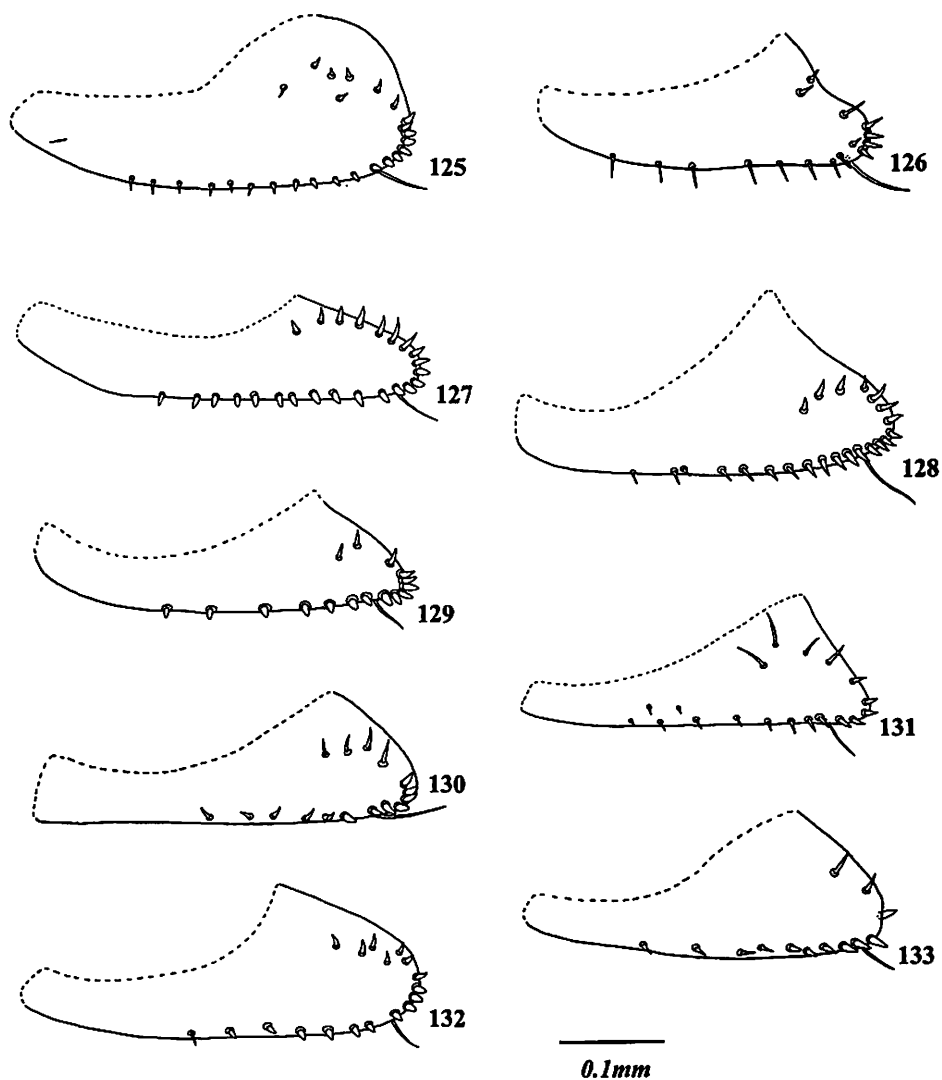
Figs. 134, 135, 137, 142, 147

DIAGNOSIS: *Drosophila fulgida* differs from other species in this clade by having the ocellar triangle, except for the area bordered by the ocelli, and the mesonotum polished black and bare of pollen, a well developed anterior katepisternal seta, the upper 1/2 of each pleuron brown to black, and the abdomen all brown to black.



Figures 121-124. Thoracic structures of some *Drosophila polita* subgroup species. 121. *D. dives*, male foreleg, 122. *D. paraan-thrax*, male foreleg (150 $\times$), 123. *D. dives*, wing, 124. *D. meconemia*, wing.

DESCRIPTION: ♂, ♀. *Head*. Front yellow below proclinate setae, upper portion brown to black, ocellar triangle polished and parafrontal areas subopaque. First 2 antennal segments yellow to rufous, third dark brown to blackish. Face of males moderately discolored brown to blackish through median portion. Face of females much more blackish in coloration. Clypeus and apices of palpi brown. Each palp with 1 rather small apical seta plus 1 small seta before apex on posterior margin (Fig. 135). The anterior reclinate setae are situated distinctly above proclimates. *Thorax*. Polished black to dark reddish brown over mesonotum, devoid of pollen except on margins. Scutellum black except for broadly yellow apex. Males with upper 1/2 of each pleuron dark reddish brown to black, lower portion clear yellow. Pleura of females entirely dark colored. Anterior katepisternal seta well developed, at least 1/3 as long as posterior katepisternal. Eight setae present on posterolateral portions of mesonotum (Fig. 137). *Legs*. Entirely yellow, with very short front basitarsus, as in Fig. 142. *Wings*. Entirely subhyaline with no dark markings. Costal fringe extending ca. 1/2 distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Mostly shining to polished black with tinge of rufous in ground color of first 2 terga and with these terga large-



Figures 125-134. Ovipositors of the *Drosophila polita* subgroup. 125. *D. bipolita*, 126. *D. canipolita*, 127. *D. flavisternum*, 128. *D. illusiopolita*, 129. *D. lissodora*, 130. *D. mecocnemia*, 131. *D. paraanthrax*, 132. *D. polita*, 133. *D. pretiosa*.

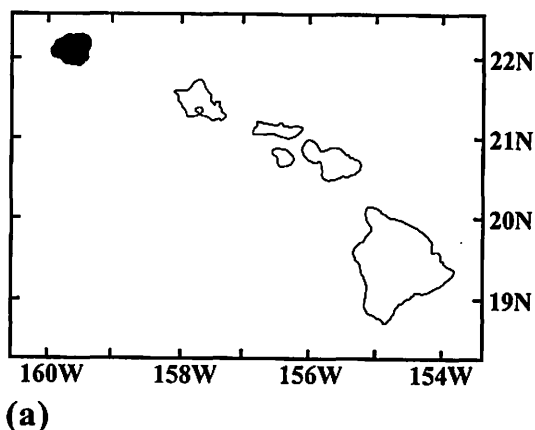


Figure 134. Distribution of the *Drosophila scitula* subgroup.

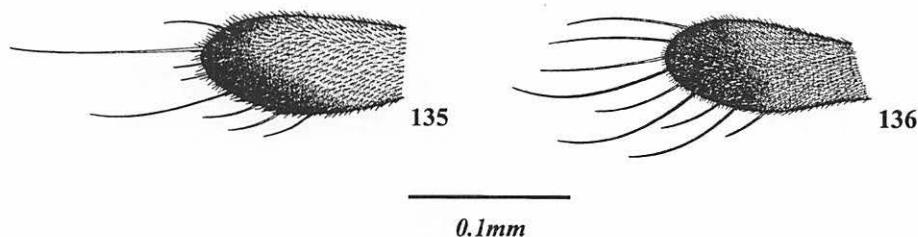
ly covered with gray pollen, third tergum with scattering of gray pollen over median portion. Ovipositor rounded at apex. Cluster of 7 stout peg ovisensilla present at apex. Dorsolateral region with 4 sharp peg ovisensilla extending to 1/3 ovipositor length. Ventral margin with series of 7 ovisensilla that extend to ca. 3/4 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width (Fig. 147).

MEASUREMENTS: N = 11 ♂. TL = 1.2 mm; WL = 2.6 mm (2.4–2.6); TL/WL = 0.5; HW = 1.0 mm (0.9–1.0); HW/TL = 0.8; CI = 4.2 (3.7–4.7); 4V = 1.5 (1.4–1.6); 5X = 2.2 (1.8–2.5); 4C = 0.6 (0.5–0.6); M = 0.5 (0.4–0.6). N = 11 ♀. TL = 1.4 mm (1.2–1.6); WL = 2.9 (2.6–3.1); TL/WL = 0.5 (0.4–0.5); HW = 1.1 mm (0.9–1.2); HW/TL = 0.8 (0.7–0.8); CI = 4.5 (3.8–5.8); 4V = 1.4 (1.3–1.5); 5X = 2.1 (1.7–2.5); 4C = 0.5 (0.4–0.6); M = 0.5 (0.4–0.6).

TYPES: KAUA'I: Holotype ♂ (BPBM 16,369), Mōhihi Stream, Koke'e, 2,700 ft, 30.vii.1963, DEH. TL = 1.2 mm; WL = 2.4 mm; TL/WL = 0.5; HW = 0.9 mm; HW/TL = 0.8; CI = 4.3; 4V = 1.5; 5X = 2.0; 4C = 0.6; M = 0.5. Allotype ♀ (BPBM 16,369a), same information as holotype. TL = 1.5 mm; WL = 2.9 mm; TL/WL = 0.5; HW = 1.1 mm; HW/TL = 0.7; CI = 4.1; 4V = 1.4; 5X = 1.9; 4C = 0.6; M = 0.5. One hundred twenty-five paratypes, 45 males and 80 females, from UHM are designated. 1 ♂, 2 ♀, Nualolo Valley, 3,400 ft, vii.1952, DEH; 1 ♂, Kainamanu, 3,800 ft, Kaua'i, vii.1952, DEH; 1 ♀, Kalalau Lookout, 4,000 ft, viii.1953, DEH; 1 ♀, Koke'e, 3,600 ft, Kaua'i, vii.1963, HLC; 1 ♂, Mōhihi Stream, Koke'e, Kaua'i, vii.1963, HLC; 1 ♂, Mōhihi Stream, Koke'e, Kaua'i, 27.vii.1963, DEH; 1 ♂, Mōhihi Stream, Koke'e, Kaua'i, 7.xi.1963, MRW; 1 ♀, Koke'e, 3,600 ft, Kaua'i, 8.xi.1963, MRW; 1 ♀, Koke'e, 3,600 ft, Kaua'i, 5.iii.1964, MRW; 1 ♂, Koke'e, 3,600 ft, Kaua'i, 22.vi.1964, HLC; 1 ♂, 3 ♀, Halemanu Valley, 4,000 ft, Kaua'i, 25.vi.1964, LHT; 2 ♂, 2 ♀, Kumuwela, Kaua'i, 27.vi.1964, LHT; 1 ♂, Mōhihi Stream, Koke'e, Kaua'i, viii.1964, HTS; 1 ♂, Halemanu Valley, 4,000 ft, Kaua'i, 25.v.1966, KYK; 1 ♀, Mōhihi Stream, Koke'e, Kaua'i, 18.viii.1966, WBH; 1 ♂, Halemanu Valley, 3,500 ft, 12.viii.1971, DEH; 2 ♂, 4 ♀, Koke'e, 27.iii.1975, DEH; 4 ♂, 25 ♀, Berry Flat Trail, Koke'e, Kaua'i, 18.iv.1974, HTS; 1 ♂, 1 ♀, Halemanu Valley, 4,000 ft, Kaua'i, 19.iv.1974, HTS; 17 ♂, 9 ♀, Berry Flat Trail, Koke'e, Kaua'i, 17.iv.1975, KYK; 9 ♂, 6 ♀, Berry Flat Trail, Koke'e, 8.iv.1976, HTS; 1 ♀, Nualolo Trail, 3,600 ft, Kaua'i, 3.xii.1976, DEH; 11 ♀, Berry Flat Trail, Koke'e, 28–30.xi.1978, HTS; 11 ♀, Pihea, Kaunūhū Ridge, 4,260 ft, 23.v.1979, DEH. The holotype, allotype and a series of paratypes have been placed in the BPBM.

DISTRIBUTION: *Drosophila fulgida* is endemic to Kaua'i (Fig. 134).

ETYMOLOGY: Latin, "shining". In reference to the polished black mesonotum of this species.



Figures 135–136. Palpi of the *Drosophila scitula* subgroup. 135. *D. fulgida*, 136. *D. setositibia*.

Drosophila melanosoma Grimshaw

Figs. 134, 138, 143, 145, 148

Drosophila melanosoma Grimshaw, 1901: 68, Hardy, 1965: 363.

DIAGNOSIS: *Drosophila melanosoma* differs from any of the species in this complex by having the antennae, palpi and clypeus pale yellow; the face white; and the upper 2/3 of front and the ocellar triangle rather densely silvery white pollinose, as seen in indirect light.

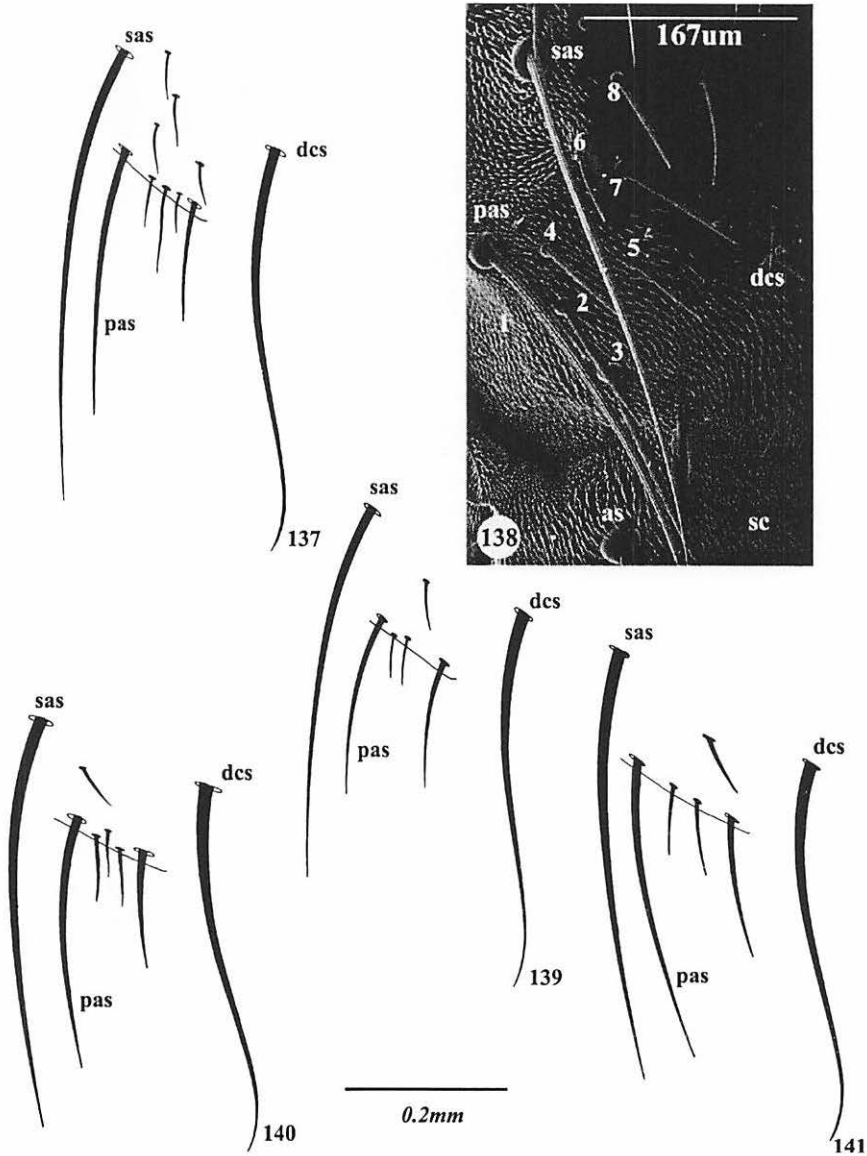
DESCRIPTION: ♂, ♀. We add the following characters to those described by Grimshaw (1901) and Hardy (1965): *Head.* Antennae of females mostly brown. Palpi with faint tinge of brown in females. *Thorax.* Eight supernumerary setae found on posterolateral portions of mesonotum (Fig. 138). *Legs.* Basitarsus short, ca. 1/5 length of tibia (Fig. 143). *Wings.* Light, diffuse infuscation on apical 1/3 of wing, nearly to level of crossvein dm-cu (Fig. 145). *Abdomen.* Ovipositor rounded at apex with dense cluster of 6 peg ovisensilla on ventroapical margin. Dorsolateral region with ca. 6 sharply pointed peg ovisensilla that extend to nearly 1/2 ovipositor length. About 10 ovisensilla on ventral margin extend to ca. 3/5 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width (Fig. 148).

MEASUREMENTS: N = 3 ♂. TL = 1.3 mm (1.3–1.4); WL = 2.9 mm (2.8–2.9); TL/WL = 0.5 (0.4–0.5); HW = 1.1 mm (1.0–1.1); HW/TL = 0.8; CI = 4.3 (3.7–4.8); 4V = 1.3 (1.2–1.4); 5X = 1.6 (1.5–1.8); 4C = 0.5 (0.5–0.6); M = 0.4 (0.3–0.4). N = 5 ♀. TL = 1.5 mm (1.4–1.7); WL = 3.1 (3.0–3.3); TL/WL = 0.5; HW = 1.1 mm (1.1–1.2); HW/TL = 0.7 (0.7–0.8); CI = 4.5 (4.2–5.0); 4V = 1.3 (1.2–1.4); 5X = 1.4 (1.3–1.5); 4C = 0.5 (0.4–0.5); M = 0.4 (0.3–0.4).

TYPES: KAUA'I: Holotype ♂, Mt Waimea, BMNH. Not measured. Eight homotypes, 3 males and 5 females, from the UHM have been examined. 1 ♂, 1 ♀, Nualolo Valley, vii.1952, 3,400 ft, DEH; 1 ♀, Kainamanu, 3,800 ft, vii.1952, DEH; 1 ♂, 3 ♀, Halemanu Swamp, viii.1953, DEH; 1 ♂, Wai'ala Stream, 3,600 ft, viii.1953, DEH.

MATERIAL EXAMINED: KAUA'I: Seventy-five other specimens, 54 males and 21 females, are at UHM. 4 ♂, 1 ♀, Pu'u Kapele, 14.viii.1915, OHS; 1 ♀, Kumuwela, "on *Osmanthus*", 27.vi.1932, OHS; 1 ♂, Koke'e, 3,600 ft, vii.1952, DEH; 7 ♂, 1 ♀, Halemanu Swamp, viii.1953, DEH; 1 ♀, Mt Wai'ala Trail, 4,500 ft, viii.1953, DEH; 21 ♂, 12 ♀, Nualolo Valley, 3,400 ft, viii.1953, DEH; 4 ♂, Wai'ala Stream, 3,600 ft, viii.1953, DEH; 1 ♂, Mōhihi Stream, Koke'e, 7.x.1963, MRW; 1 ♂, Koke'e, 3,600 ft, 5.iii.1964, MRW; 1 ♀, Halemanu swamp, 6.iii.1964, MRW & FEC; 2 ♂, Koke'e, 3,600 ft, 22.vi.1964, HLC; 1 ♂, 2 ♀, Halemanu Valley, 4,000 ft, 25.vi.1964, LHT; 3 ♂, Mōhihi, Koke'e, 18.vii.1966, WBH & KYK; 1 ♂, Mōhihi Stream, Koke'e, 21.vi.1967, JPM; 1 ♂, North Fork, Wailua River, 1,200 ft, 12.iii.1968, HLC; 1 ♂, Pouli Stream, Hanalei, 1,500 ft, 13.iii.1968, HLC; 2 ♂, Koke'e, 2–3.iv.1970, KYK; 1 ♂, Halemanu Valley, 3,500 ft, 12.viii.1971, DEH; 1 ♀, Berry Flat Trail, Koke'e, 18.iv.1974, HTS; 1 ♂, Nualolo Valley, 17.viii.1974, SLM; 2 ♂, 1 ♀, Berry Flat Trail, Koke'e, 17.iv.1975, KYK.

DISTRIBUTION: *Drosophila melanosoma* is endemic to Kaua'i (Fig. 134). This species is very common at higher elevations.



Figures 137–141. Posterolateral regions of the mesonotum of the *Drosophila* *scitula* subgroup. 137. *D. fulgida*, 138. *D. melanosoma*, 139. *D. scitula*, 140. *D. setositibia*, 141. *D. subopaca*.

Drosophila scitula Hardy

Figs. 134, 139, 146, 149

Drosophila scitula Hardy, 1966: 213.

DIAGNOSIS: *Drosophila scitula* differs from other species in this complex by having the anterior katepisternal seta absent; pleura mostly pale yellow, sometimes with a faint discoloration of brown on the mesopleuron, wings brown beyond the level of the m crossvein, and the first, fifth and sixth abdominal terga yellow.

DESCRIPTION: ♂, ♀. Refer to Hardy (1966) for a description of this species. Additional characters include: *Head.* Antennae, face, clypeus, genae, palpi and mouthparts, except for black rim, of male entirely pale yellow. Females with third antennal segment, clypeus and palpi dark brown; median portion of face mostly blackish. *Thorax.* Posterolateral areas of mesonotum sparsely setose, with 3–4 setae (Fig. 139). Upper 1/2 of pleuron dark brown to black in females. *Wings.* Males with distinct maculation covering apical 1/2 of wing, extending to crossvein dm-cu (Fig. 146). Females lack brown marking, wings entirely subhyaline. *Abdomen.* Entirely shining dark brown to black in females. Ovipositor somewhat pointed at apex (Fig. 149). About 6 long, sharply pointed ovisensilla distributed on apical margin. Four trichoid ovisensilla, extending to 3/5 ovipositor length, on ventral margin. Inner subapical ovisensilla long, ca. 1.25 × ovipositor width.

MEASUREMENTS: N = 4♂. TL = 1.2 mm (1.2–1.3); WL = 2.5 mm (2.3–2.7); TL/WL = 0.5; HW = 0.8 mm (0.7–0.9); HW/TL = 0.9; CI = 3.5 (3.4–3.7); 4V = 1.4 (1.3–1.5); 5X = 1.7 (1.6–1.8); 4C = 0.6 (0.6–0.7); M = 0.4 (0.3–0.4).

TYPES: KAUA'I: Holotype ♂, Mōhihi Stream, Koke'e, Kaua'i, 3,700 ft, vii.1963, LHT, BPBM 11263. Four paratype males have been examined from the UHM. 1♂, Mōhihi Stream, Koke'e, 30.vii.1963, DEH; 1♂, Koke'e, 3,600 ft, 8.xi.1963, MRW; 1♂, Halemanu Valley, 4,000 ft, 25.vi.1964, LHT; 1♂, Mōhihi Stream, Koke'e, 3,700 ft, 26.vi.1964, DEH. One paratype male from the AMNH has also been examined. 1♂, Halemanu Valley, 25.vi.1964, LHT.

MATERIAL EXAMINED: KAUA'I: Eighty-six specimens, 47 males and 39 females, are in the UHM. 1♀, Halemanu Swamp, viii.1953, DEH; 1♀, Alaka'i Swamp, 4,000 ft, 28.viii.1953, DEH; 1♂, Wahiawa Swamp, 27.xii.1965, KYK; 1♀, North Fork, Wailua River, 1,200 ft, 12.iii.1968, KYK; 1♀, Koke'e, 2–3.iv.1970, KYK; 1♂, Mahanuloa Valley, Koke'e, 1450 ft, 23.iii.1973, KYK; 1♂, Nualolo Valley, 17.viii.1974, SLM; 2♀, Berry Flat Trail, Koke'e, 17.iv.1975, KYK; 5♂, 4♀, Powerline Road, 1150 ft, "in *Pisonia* grove", vi.1977, DEH; 23♂, 2♀, Uhauliole Stream, Powerline Road, Kapa'a, 1,200 ft, 2.vi.1977, KYK; 16♂, 26♀, Powerline Road, Kapa'a, 1,400 ft, 12.vi.1977, KYK; 1♀, Berry Flat Trail, Koke'e, 28–30.xi.1978, HTS.

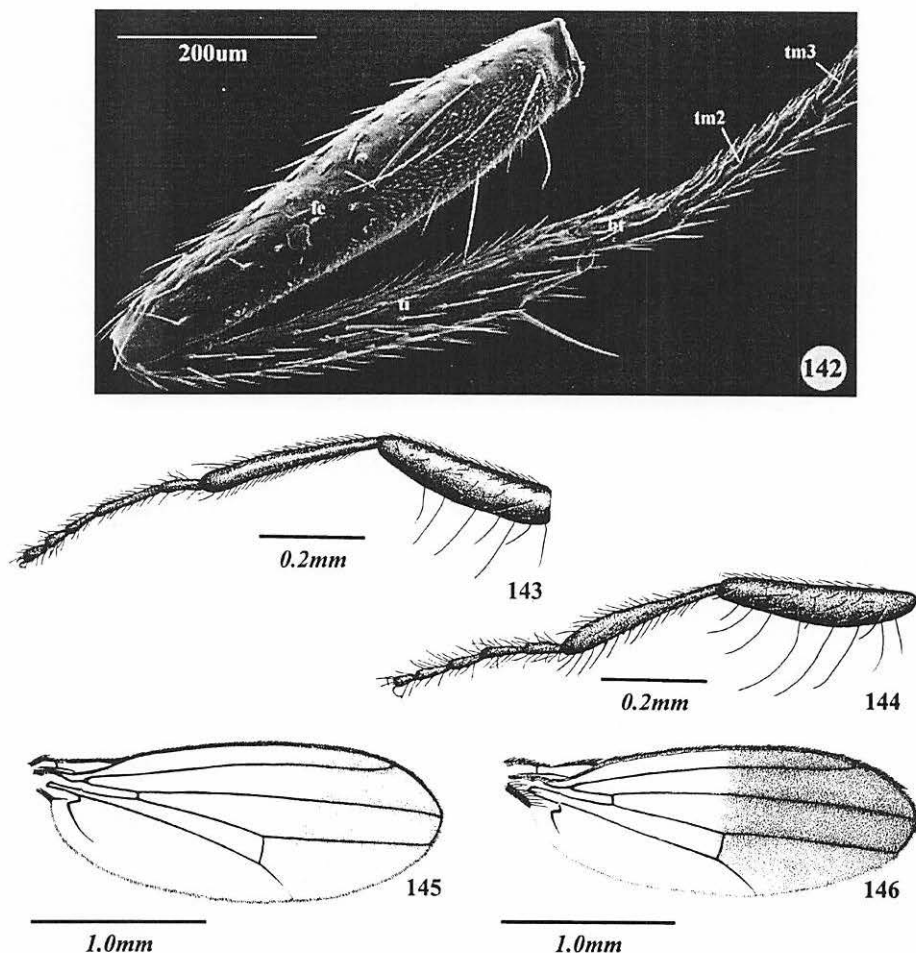
DISTRIBUTION: *Drosophila scitula* is common in the Koke'e, Alaka'i Swamp area of Kaua'i (Fig. 134).

Drosophila setositibia Hardy & Kaneshiro, new species

Figs. 134, 136, 140, 144, 150

DIAGNOSIS: *Drosophila setositibia* is differentiated by having the scutellum all black in both sexes, the upper portion of the sternopleuron brown to blackish tinged, front tibia of male with abundant erect setae over the posteroventral surface (Fig. 144) and the ocellar triangle mostly pollinose.

DESCRIPTION: ♂, ♀. *Head.* Lower reclinate setae situated distinctly above proclimates. Arista with 6–7 dorsal, 3 ventral rays, in addition to apical fork. Genae narrow, ca. equal in width to 2 rows of eye facets. Palpi are mostly yellow with apices broadly brown, rather densely covered with long setae around apices (Fig. 136). *Thorax.* Mostly polished black over mesonotum, thinly gray pollinose around margins with tinge of brown to black in upper portion of each sternopleuron and hypopleuron. Anterior katepisternal seta well developed, over 1/2 as long as posterior katepisternal. Scutellum entirely black with only very faint tinge of pale coloration in ground color when seen from direct end view. Posterolateral areas of mesonotum almost bare, with only 4–5 supernumerary setae (Fig. 140). *Legs.* Entirely yellow in males. Mid and hind femora of females extensively tinged with brown. Front femur with complete row of black setae along posteroventral and posterodorsal surfaces. Front tibia with numerous erect posteroventral setae extending over apical 3/5 in male (Fig. 144). Preapical dorsal seta large, at least 1/2 again as long as basitarsus. *Wings.* Entirely subhyaline, costal fringe extending slightly beyond middle of distance between apices of veins R₂₊₃ and R₄₊₅. *Abdomen:* Entirely shin-

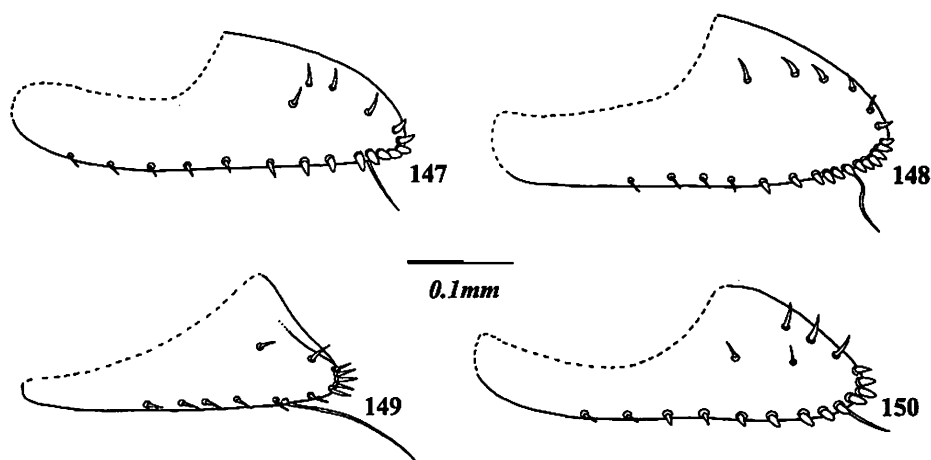


Figures 142–146. Thoracic structures of some species in the *Drosophila scitula* subgroup. 142. *D. fulgida*, male foreleg, 143. *D. melanosoma*, male foreleg, 144. *D. setositibia*, male foreleg, 145. *D. melanosoma*, wing, 146. *D. scitula*, wing.

ing dark brown to black except for gray pollinosity over first tergum and over median portion of second. Ovipositor rounded at apex (Fig. 150). Five sharp, slightly elongate peg ovisensilla present at apex. Dorsal margin with 3 long sharply pointed peg ovisensilla. Ventral margin with 8 peg ovisensilla that extend to 3/4 ovipositor length. Inner subapical ovisensilla ca. 1/3 ovipositor width.

MEASUREMENTS: N = 3♂. TL = 1.2 mm (1.2–1.3); WL = 2.5 mm; TL/WL = 0.5; HW = 1.0 mm (0.9–1.1); HW/TL = 0.8; CI = 4.4 (3.5–5.2); 4V = 1.4 (1.3–1.4); 5X = 1.8 (1.7–2.0); 4C = 0.5 (0.4–0.6); M = 0.4 (0.4–0.5). N = 1♀. See allotype.

TYPES: KAUA'I: Holotype ♂ (BPBM 16,370), Power Line Road, "in *Pisonia* grove", 1,150 ft, vi.1977, DEH. TL = 1.2 mm; WL = 2.3 mm; TL/WL = 0.5; HW = 0.9 mm; HW/TL = 0.8; CI = 3.5; 4V = 1.4; 5X = 1.7; 4C = 0.6; M = 0.4. Allotype ♀ (BPBM 16,370a), same collection as type. TL = 1.4 mm; WL = 3.0 mm; TL/WL



Figures 147–150. Ovipositors of the *Drosophila scitula* subgroup. 147. *D. fulgida*, 148. *D. melanosoma*, 149. *D. scitula*, 150. *D. setositibia*.

= 0.5; HW = 1.1 mm; HW/TL = 0.8; CI = 4.5; 4V = 1.3; 5X = 1.5; 4C = 0.5; M = 0.4. Two paratypes, 1 male and 1 female, are at UHM. 1 ♂, Mōhihi Stream, Koke'e, 27.vi.1964, FEC; 1 ♀, same collection as type.

DISTRIBUTION: *Drosophila setositibia* is known from Kaua'i (Fig. 134).

ETYMOLOGY: This species is named with reference to the setose foretibia in males.

Drosophila subopaca Hardy & Kaneshiro, new species

Figs. 134, 141

DIAGNOSIS: *Drosophila subopaca* can be distinguished from other species in this group by having the ocellar triangle and mesonotum subopaque and dusted with gray pollen.

DESCRIPTION: ♂, ♀ (unknown). *Head*. Front above proclinate setae opaque black, covered with gray pollen, lower portion yellow. First 2 antennal segments yellow with tinge of brown on dorsal portion of second. Third antennal segment brown except for narrow yellow base. Face brown with tinge of yellow, lower margin above clypeus dark brown to black. Clypeus dark brown to black, palpi broadly brown over apical portions, yellow on bases. Genae narrow, ca. equal in width to 2 rows of eye facets. *Thorax*. Dark shining brown to black in ground color, covered with gray pollen but with shining ground color not completely obscured. Lower 1/2 of each pleuron and extreme apex of scutellum is yellow. Area on each side of mesonotum sparsely setose, with only 3–4 setae, as in Fig. 141. *Legs*. With a very short basitarsus, as in other members of this complex. *Wings*. Subhyaline with a very faint tinge of brown on apical portions. Costal fringe extends to approximately middle of distance between apices of veins R_{2+3} and R_{4+5} . *Abdomen*. Entirely dark brown to black, lightly gray pollinose over terga.

TYPE: KAUA'I: Holotype ♂ (BPBM 16,371), Halemanu Valley, Koke'e, 4,000 ft, 25.vi.1964, LHT, TL = 1.2 mm; WL = 2.7 mm; TL/WL = 0.4; HW = 1.0 mm; HW/TL = 0.8; CI = 4.0; 4V = 1.3; 5X = 1.8; 4C = 0.5; M = 0.4.

DISTRIBUTION: This species is known only from the holotype male from Kaua'i (Fig. 134).

ETYMOLOGY: Latin, "less than obscure", in reference to the heavy dusting of pollen on the mesonotum.

DISCUSSION: A female has not yet been definitely associated with the male. Three female specimens on hand, which are not designated as part of the type series, appear to belong here. They differ from the male by having the upper portion of each sternopleuron extensively dark brown.

LITERATURE CITED

- Baker, R.H. & R. DeSalle. 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. *Syst. Biol.* 46: 654–73.
- Bonacum, J. 2001. Molecular systematics of the Hawaiian Drosophilidae. Ph.D. Dissertation, Yale University.
- Bryan, E.H. 1934. A review of the Hawaiian Diptera, with descriptions of new species. *Proc. Hawaii. Entomol. Soc.* 8: 434–40, 456–57.
- Carson, H.L. & D.A. Clague. 1995. Geology and biogeography of the Hawaiian Islands, p. 14–29. In: Wagner, W. L. V.A. & Funk, eds., *Hawaiian biogeography*. Smithsonian Institution Press, Washington and London.
- Craddock, E.M. & M.P. Kambyseilis. 1997. Adaptive radiation in the Hawaiian *Drosophila* (Diptera: Drosophilidae): ecological and reproductive character analyses. *Pac. Sci.* 51: 475–89.
- DeSalle, R. 1992. The origin and possible time of divergence of the Hawaiian Drosophilidae: evidence from DNA sequences. *Mol. Biol. Evol.* 9: 905–16.
- Evenhuis, N.L. 1982. Catalog of entomological types in the Bishop Museum. Diptera: Drosophilidae. *Pac. Insects* 24: 318–67.
- . 1997. New records, synonymies, and range extensions of two-winged flies (Diptera) from the Hawaiian Islands. *Bishop Mus. Occas. Pap.* 49: 29–32.
- Grimaldi, D.A. 1987. Phylogenetics and taxonomy of *Zygothrica* (Diptera: Drosophilidae). *Bull. Am. Mus. Nat. Hist.* 186: 103–268.
- . 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bull. Am. Mus. Nat. Hist.* 197: 1–139.
- Grimshaw, P.H. 1901. Diptera, p. 1–77. In: *Fauna Hawaiiensis*. Volume 3(1). Cambridge University Press, London.
- Hardy, D.E. 1965. *Insects of Hawai'i*. Vol. 12. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypterae I, Family Drosophilidae. University of Hawai'i Press. 814 p.
- . 1966. Descriptions and notes on Hawaiian Drosophilidae (Diptera). *Univ. Texas Publ.* 6615: 195–244.
- . & K.Y. Kaneshiro. 1968. New picture-winged *Drosophila* from Hawaii. *Univ. Texas. Publ.* 6816: 171–262.
- Heed, W.B. 1968. Ecology of the Hawaiian Drosophilidae. *Univ. Texas. Publ.* 6818: 388–419.
- Kambyseilis, M.P. 1993. Ultrastructural diversity in the egg chorion of Hawaiian *Drosophila* and *Scaptomyza*: ecological and phylogenetic considerations. *J. Insect Morphol. & Embryol.* 22: 417–46.
- . & E.M. Craddock. 1991. Insemination patterns in Hawaiian *Drosophila* species (Diptera: Drosophilidae) correlate with ovarian development. *J. Insect Behav.* 4: 83–100.
- . & E.M. Craddock. 1997. Ecological and reproductive shifts in the diversification of the endemic Hawaiian *Drosophila*. In: Givnish, T. J., & K.J. Systma, eds., *Molecular evolution and adaptive radiation*. Cambridge University Press, New York.
- , K.-F. Ho, E.M. Craddock, F. Piano, M. Parisi, & J. Cohen. 1995. Pattern of ecological shifts in the diversification of Hawaiian *Drosophila* inferred from a molecular phylogeny. *Curr. Biol.* 5: 1129–1139.
- Kaneshiro, K. Y., A.T. Ohta & H.T. Spieth. 1977. Research Note. *Dros. Inform. Serv.* 52: 85.
- McAlpine, J.F. 1981. Morphology and terminology — adults, p. 1011–1018. In: McAlpine, J.F. et al., coordinators, *Manual of Nearctic Diptera*. Vol. 1. Minister Supply and Services Canada and Research Branch Agriculture Canada, Monograph 28, Ottawa.

- Montgomery, S.L. 1975. Comparative breeding site ecology and the adaptive radiation of picture-winged *Drosophila* (Diptera: Drosophilidae) in Hawaii. *Proc. Hawaii. Entomol. Soc.* **22**: 65–103.
- Remsen, J. & R. DeSalle. 1998. Character congruence of multiple data partitions and the origin of the Hawaiian Drosophilidae. *Mol. Phylogen. Evol.* **9**: 225–35.
- Samuelson, G.A., G.M. Nishida & N.L. Evenhuis. 2001. The Insect and Spider Collections of the World. Web Version. <http://www.bishopmuseum.org/bishop/ento/codens-r-us.html> (revised 4 February 2001; accessed 1 March 2001).
- Spieth, H.T. 1966. Courtship behavior of endemic Hawaiian *Drosophila*. *Univ. Texas Publ.* **6615**: 245–313.
- Stark, J., J. Bonacum, J. Remsen, & R. DeSalle. 1999. The evolution and development of dipteran wing veins: A systematic approach. *Ann. Rev. Ecol. Syst.* **44**: 97–129.
- Sturtevant, A.H. 1942. The classification of the genus *Drosophila*, with descriptions of nine new species. *Univ. Texas Publ.* **4213**: 6–51.
- Thomas, R.H. & J.A. Hunt. 1991. The molecular evolution of the alcohol dehydrogenase locus and the phylogeny of Hawaiian *Drosophila*. *Mol. Biol. Evol.* **8**: 687–702.
- . & J.A. Hunt. 1993. Phylogenetic relationships in *Drosophila*: A conflict between molecular and morphological data. *Mol. Biol. Evol.* **10**: 362–74.
- Throckmorton, L.H. 1962. The problem of phylogeny in the genus *Drosophila*. *Univ. Texas. Publ.* **6205**: 207–343.
- . 1966. The relationships of the endemic Hawaiian Drosophilidae. *Univ. Tex. Publ.* **6615**: 335–96.
- . 1975. The phylogeny, ecology and geography of *Drosophila*, p. 421–469. In: King, R.C., ed, *Handbook of genetics: invertebrates of genetic interest*. Plenum Publ. Co., New York.
- Wheeler, M.R. 1981. The Drosophilidae: a taxonomic overview, p. 1–97. In: Ashburner, M., H.L. Carson & J.N. Thompson Jr., eds., *The genetics and biology of Drosophila*. Vol. 3a. Academic Press, New York.

INDEX

(new species names in **boldface**)

- anthrax, 9
atrifacies, 47
bipolita, 63
brunneicrus, 48
canipolita, 65
chicae, 42
clara, 53
cilifemorata, 33
cryptica, 55
curtitarsis, 44
demipolita, 11
denotata, 40
dives, 67
dolichotarsis, 34
fascigera, 12
flaviceps, 35
flavisternum, 68
fulgida, 77
fungicola, 51
fungiperda, 51
fuscifrons, 12
fuscoapex, 58
haleakalae, 56
hemianthrax, 15
iki, 35
illusiopolita, 68
inciliata, 26
insignita, 44
lissodora, 69
longipedis, 28
longiperda, 28
longiperdis, 28
luteola, 59
macrochaetae, 57
mecocnemia, 70
melanoloma, 16
melanosoma, 81
multiciliata, 18
nigella, 53
nigra, 37
nigropolita, 21
ochropleura, 49
paraanthrax, 72
polita, 23
pretiosa, 75
quiqueramosa, 61
reburra, 37
retrusa, 23
sabroskyi, 41
scitula, 83
seorsa, 23
setositibia, 83
stenoptera, 39
subopaca, 85
swezeyi, 39
tamashiroi, 58
tanytarsis, 30
transfuga, 73
venusta, 31