

A Subgroup Structure for the Modified Mouthparts Species Group of Hawaiian *Drosophila*

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Abstract. Here we present the first complete subgroup-level classification of the *modified mouthparts* group of Hawaiian *Drosophila*. Previously, only three small groups had been proposed, accounting for only a third of the known species in this large group. The *modified mouthparts* group, as now defined, consists of fourteen subgroups: *adventitia* (1 described species), *bridwelli* (9), *ceratostoma* (2), *dissita* (14), *freycinetiae* (5), *fuscoamoeba* (8), *hirtitarsus* (1), *mimica* (20), *mitchelli* (5), *nanella* (1), *quadrisetae* (4), *scolostoma* (3), *semifuscata* (5), and *setiger* (4). One species, *D. tetraspilota*, is unknown in the male and remains unplaced. At least 40 undescribed species from all except the *mimica* and *scolostoma* subgroups are present in collections. Three new synonymies are recognized in the current paper: *Drosophila vicaria* Hardy, 1965 n. syn. is a junior synonym of *Drosophila amydrospilota* Hardy 1965, *Drosophila aethostoma* Hardy and Kaneshiro, 1968 n. syn. is a junior synonym of *Drosophila humeralis* Grimshaw, 1901, and *Drosophila odontostoma* Kam and Perreira, 2003 n. syn. is a junior synonym of *Drosophila chaetopeza* Hardy, 1965.

Key words: *Drosophila*, Diptera, modified mouthparts, taxonomy

Introduction

The remarkable diversity of the Hawaiian *Drosophila* has produced four main lineages, defined by both morphological and ecological characters: the fungus-breeding *haleakalae* group, the mainly leaf-breeding *antopocerus*–*modified tarsus*–*ciliated tarsus* clade, the bark-breeding *picture wing*–*nudidrosophila* clade, and the polyphagous *modified mouthparts* group (Bonacum 2001, Magnacca et al. in press). The last is the largest, with 86 described and at least 40 undescribed species (Nishida 2002, unpublished data). It is poorly studied, both taxonomically and ecologically, compared to the more famous *picture wing* group that has served as a model system for studying ecology and speciation (e.g., Montgomery 1975, Carson and Kaneshiro 1976, Carson and Templeton 1984, Carson 1992). Recently, attention has turned to the other groups of Hawaiian *Drosophila* and taxonomic progress is being made. Revisions of the *haleakalae* group (Hardy et al. 2001) and the *mimica* subgroup of the *modified mouthparts* group (O'Grady et al. 2003) have been done recently, and works on the *nudidrosophila* group and the smaller *modified mouthparts* subgroups are underway (Magnacca and O'Grady in prep.).

The *modified mouthparts* group is characterized by modifications of the labellum, consisting of enlarged spine-like setae and sometimes including sclerotized appendages. These occur only in the male and are used during courtship (Spieth 1966). Females can usually be placed in the group by gestalt and the shape of the ovipositor, which is short and broad but lacking prominent teeth as in the *modified tarsus* species. However, females usually cannot be placed into subgroup except for some (such as *setiger*) where coloration and other non-sexual characters are distinctive. The group was informally recognized by Hardy (1965),

but has never been formally defined. It is generally held to consist of all Hawaiian *Drosophila* with modifications of the mouthparts, though some members of the *adiastola* clade of the *picture wing* group (e.g., *D. ornata*; see Figure 8b in Hardy and Kaneshiro 1969) also possess modified mouthparts.

The monophyly of the group has never been fully tested. A recent phylogenetic study (Bonacum 2001) had *D. adventitia* strongly supported as a basal member of the *picture wing*–*nudidrosophila* lineage, while all other *modified mouthparts* species (members of the *ceratostoma*, *freycinetiae*, *mimica*, *mitchelli*, *quadrisetae*, and *setiger* subgroups were included) formed a single clade. Interestingly, the ovipositor of *D. adventitia* appears to have the long, narrow form of the *picture wing* and *nudidrosophila* groups rather than the broad, blunt form found in most *modified mouthparts* species. From this preliminary evidence, it appears possible that *D. adventitia* may not be evolutionarily a member of the *modified mouthparts* clade.

Unlike the *antopocerus*–*modified tarsus*–*ciliated tarsus* and *picture wing* groups, both of which contain a number of distinct subgroups and species clusters, the *modified mouthparts* group has not traditionally been split into smaller taxonomic units on the basis of obvious, identifiable, external morphological characters. The majority of phylogenetically informative differences in the *modified mouthparts* group are based on details of the labellar setae, structures that need to be examined under high magnification or dissected to describe, rather than the easily observable wing and foreleg characters used to separate subgroups in the remainder of the Hawaiian *Drosophila*. In most cases, the original descriptions of *modified mouthparts* taxa lack the detail necessary to diagnose species based on mouthpart characters and rely instead on more plastic characters that do not track the phylogenetic relationships of these species (Hardy 1965). Of the 86 described species in the *modified mouthparts* group, only 31 have been placed in three subgroups: *mimica* (Yoon et al. 1972, O'Grady et al. 2003), *mitchelli* (Hardy and Kaneshiro 1975), and *semifuscata* (Hardy and Kaneshiro 1968). This leaves nearly two-thirds of the described species (and nearly all of the known undescribed) in the “unassigned” category.

In order to facilitate future taxonomic studies on species in the *modified mouthparts* group, a more manageable classification system is sorely needed. The current study proposes a subgroup-level classification for all species placed in the *modified mouthparts* group. The establishment of this general framework is an important step that will lead to more rapid advances in the taxonomy, ecology, and evolutionary biology of the *modified mouthparts* group. The proposed taxonomic hierarchy also provides a framework that can be explicitly tested through more detailed study of morphology, DNA sequences and phylogenetic analyses.

Our classification is based primarily on the male mouthparts, although characters such as setation, coloration, and ecology are also useful (notably for the *fuscoamoeba*, *semifuscata*, and *setiger* subgroups). We believe mouthpart morphology to be one of the best characters for defining subgroups for several reasons. First, it is a sexually selected character. As a result, once a lineage has progressed in a certain direction it is difficult to lose the unique features that have developed (e.g., specialized spines and hairs) except by reverting to the ancestral, more or less unmodified condition. In contrast, ecological characters are highly subject to convergence in unrelated taxa that utilize a similar resource, while more neutral characters are subject to a high degree of homoplasy through both convergence and reversion to ancestral states. Second, it is highly plastic, leading to a high degree of diversity in the group; greater morphological complexity reduces the likelihood of convergence. While some of the subgroups described below have relatively unmodified mouthparts (e.g., *hirtitarsus* and *nanella*) and could potentially be paraphyletic, most are well-defined by unique synapomorphies.

Materials and Methods

Male specimens in the collections of the University of Hawaii–Manoa (UHIM) and the Bernice Pauahi Bishop Museum (BPBM) were examined, including holotypes (BPBM) or paratypes (UHIM) for all 86 described species. Specimens designated by D. E. Hardy as “homotypes” at the two museums were examined for species described by Grimshaw (1901), for which the types are at the Natural History Museum (London), with the exception of *D. humeralis* (no homotype designated). Undescribed species from the large unsorted collection at UHIM were also compared. Mouthparts are illustrated from intact pinned or alcohol-preserved specimens except *D. comatifemora*, which was drawn from a dissected and slide-mounted specimen.

Results

New synonyms: In the process of examining specimens it became apparent that *D. odontostoma* Kam and Perreira, 2003 is identical to *D. chaetopeza* Hardy, 1965, which was not previously recognized as a *mimica* subgroup species (O’Grady et al. 2003; compare their Figure 15e with Figure 60b of Hardy 1965). The former name is therefore reduced to a new junior synonym. Similarly, the only difference apparent between *D. aethostoma* Hardy and Kaneshiro, 1968 and *D. humeralis* Grimshaw, 1901 is a slight variation in wing and body coloration. The bizarre mouthparts are not mentioned in Hardy’s (1965) redescription of *D. humeralis*, but David Notton of the Natural History Museum (London) has confirmed that they are identical to those of *D. aethostoma*, and stated that the type of *D. humeralis* appears to be teneral. We therefore reduce *D. aethostoma* to a new junior synonym of *D. humeralis*. Finally, *D. vicaria* Hardy, 1965 was separated from *D. amydrospilota* Hardy 1965 only by the slightly larger wing mark of the latter; the tarsal cilia, labellar setae, broad flattened palpi, and genitalia are identical (compare Figure 28c and 208c of Hardy 1965). Wing infuscations were extensively used in the early taxonomy of Hawaiian *Drosophila*, but are often unreliable in non-*picture wing* species. The latter name is chosen as the valid name since the type is in better condition and nearly all later specimens have been identified as *D. amydrospilota*.

Subgroup designations: A total of 14 subgroups, diagnosed by the male labellum and other characters in the key and descriptions below, have been erected (Table 1). These include 82 of the 83 valid *modified mouthparts* species. One species, *D. tetraspilota*, appears to belong to the *modified mouthparts* group based on genetic evidence (unpublished data) and ovipositor morphology, but is known only from the female and cannot be placed at this time. It is readily distinguished from all other Hawaiian *Drosophila* by the bright yellow mesonotum with two short brown stripes, and distinct wing marks along the entire anterior margin and vein CuA_1 (=M₃₊₄). Based on these autapomorphies it does not appear related to the other known *modified mouthparts* species and likely forms its own subgroup, but this cannot be confirmed until the male is collected. Some undescribed species have very different mouthpart morphology and may represent separate subgroups, but these have not been fully studied.

Key to *modified mouthparts* subgroups, based on males

1. Labellum with only a fringe of thin setae and without strong spine-like setae, distinct from non-*modified mouthparts* species only in being arranged in a row and attached to a weakly sclerotized plate (Figure 1a); lobes often folded together 2.
- Labellum distinctly modified, with at least one spine-like seta, a group of elongate setae, or an appendage 3.
2. (1) Wings with the entire anterior margin infuscated, often curving around to the dm-cu crossvein as well, but poorly defined *semifuscata* subgroup (in part)
- Wings usually unmarked (sometimes with the dm-cu crossvein faintly brown, but never the anterior margin) *hirtitarsus* subgroup
3. (1) Labellum bearing a sclerotized appendage from the dorsal margin, usually with black setae at the apex 4.
- Labellum without appendages (enlarged dorsoapical setae in the *larifuga* complex [Figure 4e] are superficially similar) 6.
4. (3) Appendage large, broad, divided before the apex, fleshy portion of labellum absent (Figure 1c–d) *ceratostoma* subgroup
- Appendage consisting of a single unbranched stalk, fleshy portion of labellum present 5.
5. (4) Body shining black, face usually white; appendage not much longer than the labellum, bare or bearing a clump of setae at the apex; labellum with about four strong but inconspicuous spines (Figure 1b); tarsus and/or tibia often with very long cilia (sometimes longer than the basitarsus) *setiger* subgroup
- Body brown pollinose; appendage twice as long as the labellum, with a few widely separated setae (Figure 1e); no spines on labellum; front leg with only a few moderately long cilia on the basitarsus *adventitia* subgroup
6. (3) Labellum with black spines or scales, sometimes prostrate, no elongate yellow spine-like setae; or if brown or yellow, they are dorsoventrally flattened, sclerotized, and not strongly curved (Figure 2a–d) 7.
- Labellum with enlarged yellow or brown setae, erect (at least some nearly at right angles to the rim of the labellum) and usually spine-like but not strongly sclerotized 8.
7. (6) Labellum with dorsoventrally flattened scale-like projections, usually black but sometimes orange-brown (Figure 2a–c) *freycinetiae* subgroup
- Labellum with sharp black spine-like projections (Figure 2d) ... *mitchelli* subgroup
8. (6) Labellum with a single short, thick spine near the middle and a fringe of yellow setae *nanella* subgroup
- Labellum with at least three long spines or strong setae 9.
9. (8) Labellum with one to five long, strong, closely-placed setae (often appressed and appearing as one) at the dorsal end, the remainder hair-like and rapidly becoming smaller (Figure 2e–f) 10.

- Labellum with a fringe of four or more spines or enlarged setae covering at least half the margin of the labellum, usually about the same length or becoming longer ventrally 11.
- 10. (8) Wings with marks at the apex and over the dm-cu crossvein, or unmarked; spines nearly straight or slightly curved; coloration variable, mesonotum often yellow-brown with dark marks on the pleura *bridwelli* subgroup
- Wings with the entire anterior margin infuscated, often curving around the apex to the dm-cu crossvein as well, poorly defined; spines strongly curved; dark brown *semifuscata* subgroup (in part)
- 11. (9) Labellum with about four very strong spines, the labellum lobed above their insertion (Figure 3a) *scolostoma* subgroup
- Labellum not lobed 12.
- 12. (11) Labellum with 4–5 spines and a few additional yellow hair-like setae (Figure 3b-d); wings usually with *picture wing*-like marks, of varying degree and sometimes faint but at least with a mark in the middle of the anterior margin and one between R_{4+5} and M, never with a solid mark across the tip of the wing; R_{2+3} sometimes bent anteriorly so that the fourth costal section is over twice as long as the fifth; R_{4+5} usually at least weakly sinuate beyond the dm-cu crossvein *fuscoamoeba* subgroup
- Labellum with more than 10 spine-like setae (Figure 4); wings never as described above, unmarked or with spots on the dm-cu crossvein and/or the apices of the veins, the latter sometimes confluent into a solid mark; R_{2+3} more or less straight, fourth costal section less than twice as long as the fifth; R_{4+5} not sinuate 13.
- 13. (12) At least three ventral setae flattened, blade-like, and conspicuously directed ventrally (Figure 4a) *quadrisetae* subgroup
- All setae slightly curved dorsally, sinuate, or nearly straight (*D. mimica* complex with one seta inconspicuously ventrally-directed) 14.
- 14. (13) A prominent gap present between the dorsal and middle setae (group I and II setae of O’Grady et al., 2003); first middle seta developed into a thickened, tusk-like spine distinct from the others (Figure 4b) *mimica* subgroup
- Dorsal and middle setae not separated by a distinct gap (sometimes the dorsal setae greatly enlarged and middle setae reduced, as in Figure 4e); no tusk-like setae, one or two middle setae sometimes longer and J-shaped but usually only slightly thicker than setae immediately behind (Figure 4c–f) *dissita* subgroup

Discussion

hirtitarsus subgroup (Figure 1a)

Defined by the lack of spinose setae on the labellum, with only an even fringe of relatively thin setae. They can easily be mistaken for *ciliated tarsus* species, which usually have setae on the labellum, but members of the *hirtitarsus* subgroup have them only in an even row along the lightly sclerotized rim rather than scattered over the lobes. Some members of

the *semifuscata* subgroup have similar mouthparts, but have distinctive infuscations on the anterior half of the wing. Specimens of this group appear to die with the labellum lobes tightly folded together more often than other species, leading Hardy (1965:304) to describe it as having "a dark brown to black heavily sclerotized apical development on each labellum." Close inspection reveals that the lobes are actually folded together on all the paratypes, and the description and illustrations of "aberrations or possibly new species" from Hawaii in Hardy (1966) are more accurate for the original description. Currently *D. hirtitarsus* is the only described species in this subgroup, but the Hawaii island specimens and others present in collections likely represent additional species.

setiger subgroup (Figure 1b)

This small subgroup is very distinct based on general appearance: all species have the body and front shining dark brown to black, with a dull white face, and most have extremely long cilia on the front tibia. All other *modified mouthparts* species have pollinose bodies, usually brown to yellow, and nearly all lack cilia on the tibia. The labellum has an appendage from the dorsal end, in the form of a thin stalk usually with a clump of setae at the end. Strong spines are also present along the rim of the labellum, but they are curved under the labellum behind the appendage, and are usually inconspicuous. These suggest a possible relationship with the *scolostoma* and/or *fuscoamoeba* subgroups.

ceratostoma subgroup (Figure 1c–d)

This is the most divergent of the *modified mouthparts* subgroups, with a broad, sclerotized appendage and no fleshy labellum. Only two species, *D. ceratostoma* and *D. humeralis*, are placed here; the former has the appendage divided into three branches, while the latter has only two. Hardy's (1968) original description of *D. aethostoma* (now considered a synonym of *D. humeralis*; see Results) was as a member of the *semifuscata* subgroup based on the wing infuscation. However, members of that subgroup for which data exist are all sap flux breeders in mesic to even dry forest, while *D. humeralis* has been reared only from stems and fruit of *Clermontia* (Magnacca et al. in press). In addition, *D. ceratostoma* is clearly close to *D. humeralis* based on the bizarre mouthparts, but lacks the anterior wing infuscation.

adventitia subgroup (Figure 1e)

The members of this subgroup possess a sclerotized appendage like that of the *setiger* subgroup. However, the mouthparts differ in the details (appendage movable with respect to the labellum rather than fixed, labellar rim lacking spines), and they lack the other unusual synapomorphies of the *setiger* subgroup (shining black body, white face, and extremely long cilia on the leg). The placement of the *adventitia* subgroup with the other *modified mouthparts* species is uncertain (see above under "Subgroup designations").

freycinetiae subgroup (Figure 2a–c)

This subgroup consists of species with highly modified, flattened, scale-like spines. These can be more or less prostrate against the rim of the labellum and pointing dorsally (Figure 2a–b), or erect and blunt (Figure 2c). Although *D. comatiformora* has orange or brown spines rather than black, their form is similar to that of *D. prominens*; there is also an undescribed species with erect brown spines similar to those of *D.* "29.vi.1987". *Drosophila asketostoma* was formerly placed in the *mitchelli* subgroup; although it differs from other *freycinetiae* subgroup species in having most of the spines directed ventrally, they are of similar form. Some of the *mitchelli* species with shorter spines somewhat resemble those of the *freycinetiae* subgroup, and if other intermediates are found the two subgroups may need to be merged in

the future. They are apparently different ecologically, since *mitchelli* species are relatively common at standard banana/mushroom bait sponges (Carson 1986) and *freycinetiae* species are extremely rare, and for now they are maintained. In addition to the five described species, at least seven are undescribed; most of the latter have been collected only by rearing.

***mitchelli* subgroup** (Figure 2d)

This subgroup possesses strongly sclerotized black spines on the labellum, flattened at the base but drawn into a sharp point. It was established and reviewed by Hardy and Kaneshiro (1975). These were the only *modified mouthparts* species to regularly visit bait sponges in Olaa forest (K. Magnacca, unpublished data). See discussion above under the *freycinetiae* group.

***nanella* subgroup**

This consists of a single species, *D. nanella*, which has a single strong spine on the labellum. It is similar to the two enlarged middle setae of the *quadrisetae* subgroup (Figure 4a), or the tusk-like seta of the *mimica* subgroup (Figure 4b). There appear to be undescribed species that fit here, but these have not been closely studied.

***bridwelli* subgroup** (Figure 2e)

Defined by a clump of 1–5 long spines, often appressed and appearing as one, at the dorsal end of the labellum. Sometimes the next few setae are somewhat elongate and spine-like, but they rapidly become shorter and most are thin and hair-like, similar to the *hirtitarsus* subgroup. It has a moderate number of species (eight), but they are relatively rare in collections. An undescribed species from Hawaii in which all the labellar setae are hair-like, but the dorsal group are black and the remainder pale, may be a basal member of this subgroup. One of the paratypes of *D. bridwelli* (Oahu, Mt. Kaala, *Gunnera* sp., 3600 ft., 22.i.1939, F. X. Williams) lacks the dorsal spines and has different tarsal setae, and is probably a new species of the *hirtitarsus* subgroup.

***semifuscata* subgroup** (Figure 2f)

This subgroup is united by having the anterior margin of the wing infuscated, a character that also occurs in *D. humeralis*. Some species have labellar spines very similar to the *bridwelli* subgroup, but others lack spines altogether and are more similar to the *hirtitarsus* subgroup. The *semifuscata* subgroup's more uniform morphology and specialized ecology (all that are known are sap flux breeders, apparently favoring *Nestegis*) suggests it is derived from the *bridwelli* group rather than the other way around. The absence of spines in some species is surprising; evolutionary loss of a specialized courtship structure has not been documented in Hawaiian *Drosophila*.

***scolostoma* subgroup** (Figure 3a)

Only three species are included in this subgroup, and they are clearly very closely related. All possess a labellum with about 4 very strong, curved spines on each side. They are distinguished by having the sclerotized rim of the labellum lobed to create a deeper divide between the spines. They may be related to the *fuscoamoeba* subgroup, some of which have similar strong spines (Figure 3b). They are relatively rare in collections, possibly due to their ecology; the single rearing record (for *D. deltaneuron*) comes from *Pritchardia* fruit, a unique host.

***fuscoamoeba* subgroup** (Figure 3b–d)

This subgroup contains a number of species with striking patterns on the wings, and

several superficially resemble *picture wing* species. A strong gradient in intensity and complexity of wing infuscation is apparent, but all species have a mark near the center of the anterior margin of the wing and one spanning the tips of R_{4+5} and $M (=M_{1+2})$. At one end, *D. fuscoamoeba* and its close relatives have abundant, striking marks covering most of the wings; at the other, those of *D. aquila* are much smaller and barely visible. Most species also have contrasting coloration on the body, with a dark median stripe on the mesonotum and a pale ocellar triangle; very short tarsal cilia or none; and a sinuate vein R_{4+5} . Mouthpart ornamentation consists of 4–6 curved yellow spines along with hair-like setae. The former appear to be variable within species, with the one or two of the ventral spines sometimes reduced and hair-like; spines may also be more or less widely spaced (compare Figures 3b and 3c). Further study is needed to determine if this is the result of intraspecific variation, or cryptic or incipient species. At least two undescribed species from UHIM have mouthparts that are nearly identical to *D. fuscoamoeba*, as well as short cilia on the tarsi, but lack wing markings and a sinuate R_{4+5} .

***quadrisetae* subgroup** (Figure 4a)

A distinct group, separated by having the ventral spines of the labellum strongly directed ventrally rather than all straight or bent dorsally as in the *dissita* and *mimica* subgroups. Species in the *mimica* complex of the *mimica* subgroup have the last middle (group II) seta broad and pointing somewhat ventrally (see O'Grady et al. 2003, Figure 17), but it is inconspicuous and clearly not a group swept back in unison as in the *quadrisetae* subgroup. Only four described species are placed here, but at least five undescribed species have been collected.

***mimica* subgroup** (Figure 4b)

These last two subgroups are by far the largest, and can be somewhat difficult to distinguish. In general, *mimica* species have seta II-1 (O'Grady et al. 2003) enlarged into a tusk-like spine, wider in the middle, with a nearly right-angle bend and distinctly broader than the other group II (middle) setae. This forms a somewhat pincer-like shape with the ventrally-directed group I (dorsal) setae. In the *dissita* group, the largest spine is usually only slightly broader and longer than the other middle setae, and is never broadened into a tusk-like shape near the middle, and the dorsal setae are straight or more or less dorsally-directed. Despite the size of the group, mouthpart morphology in the *mimica* subgroup is quite homogeneous, with variation mainly in the strength of the setae rather than their arrangement.

***dissita* subgroup** (Figure 4c–f)

This is the largest *modified mouthparts* subgroup. Fourteen species are currently described, but at least 18 more are known in collections (Magnacca et al. in press, unpublished data). It is also the most diverse in mouthpart morphology, and further study may find that it is not a monophyletic grouping. The basic form is of a fringe of long, yellow, thickened setae, either of similar length or becoming gradually longer ventrally, across the entire margin of the labellum (Figure 4c). Several species or species complexes have modified this form in various ways. One (referred to in Magnacca et al. in press as "*D. sp. 25*") has the middle setae shifted to create a pair of gaps in the fringe (Figure 4d). In *D. brevissima*, *D. larifuga*, and a complex of related, undescribed species, some of the dorsal setae are elongated and all others reduced (Figure 4e). This gives the appearance of an appendage like that of the *setiger* species complex. However, two undescribed species with both the elongate dorsal setae and a full fringe appear to represent the transition between these species and *D. dissita*. Another odd species, *D. polliciforma*, clearly fits here (Figure 4f) but an

undescribed sibling species from Kauai has the labellar setae pointing at different angles, with one enlarged. Tarsal cilia vary from long and moderately dense to nearly absent; *D. dissita* and related species have a characteristic arrangement of a row of short, erect setulae along the segment with 1–3 long, prostrate, black cilia near the apex. A somewhat similar arrangement is found in the *velata* subgroup of the *nudidrosophila* group.

Conclusion

Establishing this baseline classification for the *modified mouthparts* group is only a first step in the study of this remarkable group. It is our hope that breaking the taxonomic workload into smaller pieces will help facilitate the description of the dozens of undescribed species, some of which will undoubtedly result in adjustments of the subgroups. But even before taxonomic work is done, a subgroup classification will increase the power and usefulness of other studies such as ecological and phylogenetic work, and in biological surveys where numerous undescribed species are found. Many of the subgroups are rare (or at least, are rarely collected) or restricted to certain habitats or breeding hosts, an important piece of conservation information that is lost when species in a survey report are listed as “*Drosophila* spp.,” or “non-picture-wings.”

To quote Mark Twain, the secret of getting started is breaking your complex overwhelming tasks into small manageable tasks. We hope that this paper will provide such a starting point for greater study of this seemingly overwhelming, yet fascinating group.

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Table 1. Assignment of *modified mouthparts* species to subgroups. H = Hawaii, Ma = Maui, Mo = Molokai, L = Lanai, O = Oahu, K = Kauai.

<i>adventitia</i> subgroup		<i>D. hirticoxa</i>	Ma	<i>mitchelli</i> subgroup	
<i>D. adventitia</i>	K	<i>D. prominens</i>	K	<i>D. biseriata</i>	O
				<i>D. furvifacies</i>	K
<i>bridwelli</i> subgroup		<i>fuscamoeba</i> subgroup		<i>D. hystricosa</i>	Ma
<i>D. albifacies</i>	H	<i>D. agitona</i>	K	<i>D. mitchelli</i>	H
<i>D. apicipuncta</i>	H	<i>D. aquila</i>	H	<i>D. nigrocirrus</i>	H
<i>D. bridwelli</i>	O	<i>D. araiotrichia</i>	Ma Mo		
<i>D. curticilia</i>	Ma	<i>D. brevicilia</i>	H	<i>nanella</i> subgroup	
<i>D. diminuens</i>	H	<i>D. clydonia</i>	Ma Mo	<i>D. nanella</i>	K
<i>D. dolomata</i>	O	<i>D. furva</i>	Ma		
<i>D. magnimacula</i>	O	<i>D. fuscamoeba</i>	O	<i>quadrisetae</i> subgroup	
<i>D. olaae</i>	H	<i>D. megasticta</i>	H	<i>D. ischnotrix</i>	O
<i>D. xuthoptera</i>	Ma Mo			<i>D. quadrisetae</i>	K
		<i>hirtitarsus</i> subgroup		<i>D. residua</i>	H
<i>ceratostoma</i> subgroup		<i>D. hirtitarsus</i>	Ma Mo	<i>D. tendomentum</i>	H
<i>D. ceratostoma</i>	H				
<i>D. humeralis</i>	K	<i>mimica</i> subgroup		<i>scolostoma</i> subgroup	
		<i>D. acanthos</i>	H	<i>D. deltaneuron</i>	O
<i>dissita</i> subgroup		<i>D. antecedens</i>	K	<i>D. mediana</i>	Ma
<i>D. amydrospilota</i>	Ma	<i>D. badia</i>	Ma	<i>D. scolostoma</i>	Ma
<i>D. artigena</i>	Ma	<i>D. chaetopeza</i>	H		
<i>D. beardleyi</i>	K	<i>D. chimera</i>	O	<i>semifuscata</i> subgroup	
<i>D. brevissima</i>	Mo	<i>D. conjectura</i>	Mo L	<i>D. acanthostoma</i>	H
<i>D. curvitibia</i>	Ma	<i>D. echinostoma</i>	Ma	<i>D. acrostichalis</i>	Ma
<i>D. dissita</i>	H	<i>D. flavibasis</i>	K	<i>D. anoplostoma</i>	Ma
<i>D. dracaenae</i>	K	<i>D. gagne</i>	O	<i>D. semifuscata</i>	Ma
<i>D. eumecothrix</i>	Mo	<i>D. inebria</i>	O	<i>D. z-notata</i>	O
<i>D. laciniosa</i>	Mo	<i>D. infuscata</i>	H		
<i>D. larifuga</i>	O	<i>D. involuta</i>	H	<i>setiger</i> subgroup	
<i>D. polliciforma</i>	H	<i>D. kambysellisi</i>	H	<i>D. apoxyloma</i>	Mo
<i>D. pychnochaetae</i>	O	<i>D. kauluai</i>	O	<i>D. eurypeza</i>	K
<i>D. taeniata</i>	Ma	<i>D. lobatopalpus</i>	O	<i>D. imitator</i>	O
<i>D. velutinifrons</i>	Mo	<i>D. maemae</i>	Ma	<i>D. setiger</i>	Mo
		<i>D. mimica</i>	H		
<i>freycinetiae</i> subgroup		<i>D. reschae</i>	O	unplaced	
<i>D. asketostoma</i>	Ma	<i>D. soonae</i>	H	<i>D. tetraspilota</i>	H
<i>D. comatifemora</i>	Ma	<i>D. xenophaga</i>	H		
<i>D. freycinetiae</i>	O				

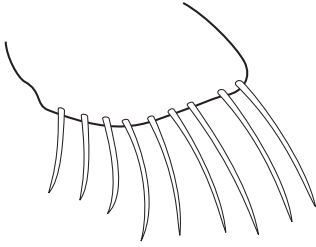
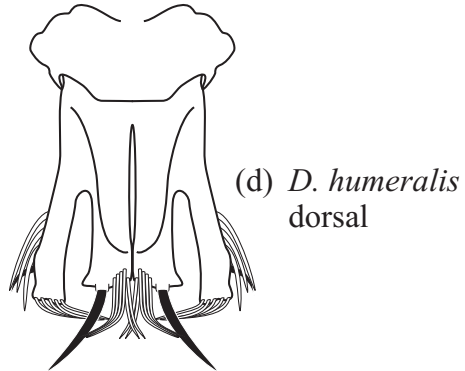
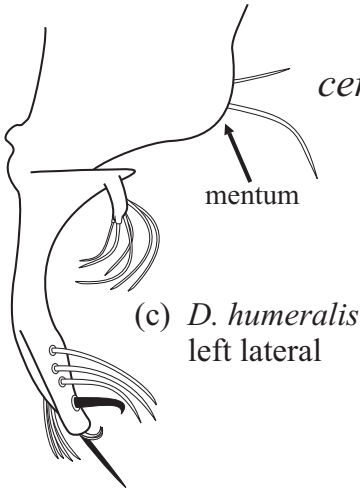
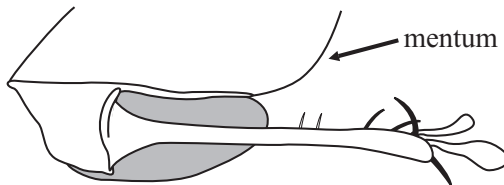
hirtitarsus subgroup(a) *D.* “sp. 26”*setiger* subgroup(b) *D. imitator**ceratostoma* subgroup*adventitia* subgroup(e) *D. adventitia*

Figure 1. Mouthparts of the *hirtitarsus* (a), *setiger* (b), *ceratostoma* (c-d), and *adventitia* (e) subgroups. All drawings are lateral views of the left lobe of the labellum, with “dorsal” to the left, except (d), which is a dorsal view of the entire labellum. The fleshy portion of the labellum (shaded) is only shown in (e).

freycinetiae subgroup

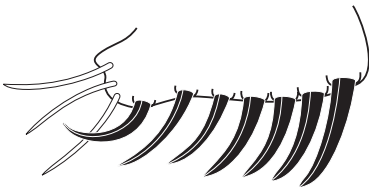
(a) *D. prominens*



(b) *D. comatifemora*



(c) *D.* "29.vi.1987"



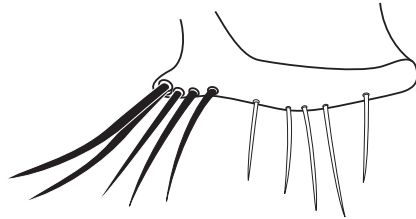
mitchelli subgroup

(d) *D. hystricosa*



bridwelli subgroup

(e) *D. apicipuncta*



semifuscata subgroup

(f) *D. acanthostoma*

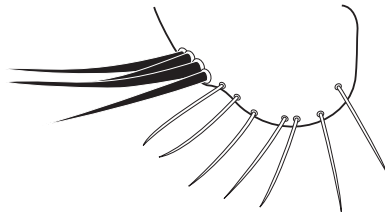


Figure 2. Mouthparts of the *freycinetiae* (a-c), *mitchelli* (d), *bridwelli* (e), and *semifuscata* (f) subgroups. Views as in Figure 1.

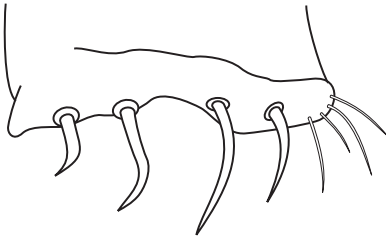
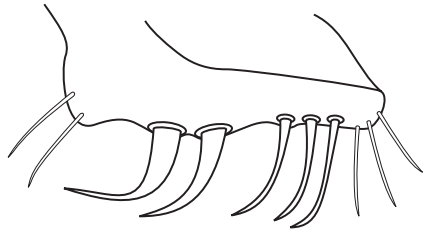
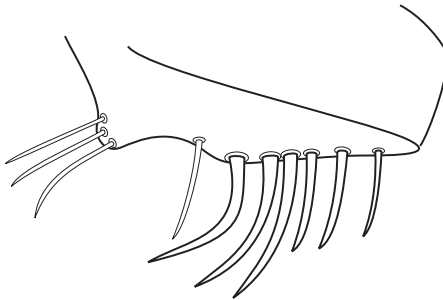
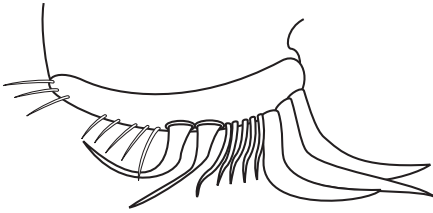
scolostoma subgroup(a) *D. deltaneuron**fuscoamoeba* subgroup(b) *D. aquila*, Olaa(c) *D. aquila*, Saddle Rd.(d) *D. fuscoamoeba*

Figure 3. Mouthparts of the *scolostoma* (a) and *fuscoamoeba* (b-d) subgroups. Views as in Figure 1.

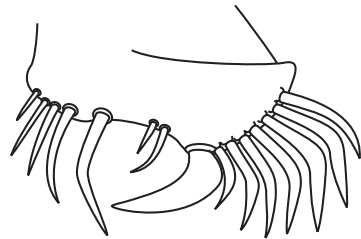
quadrisetae subgroup

(a) *D. ischnotrix*



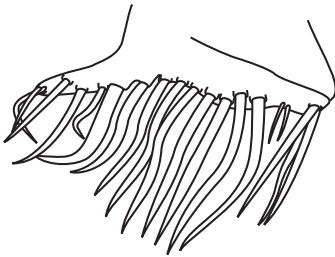
mimica subgroup

(b) *D. xenophaga*



dissita subgroup

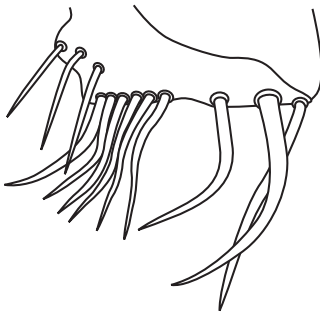
(c) *D. dissita*



(e) *D. larifuga*



(d) *D. "sp. 25"*



(f) *D. polliciforma*

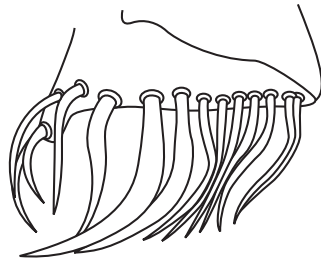


Figure 4. Mouthparts of the *quadrisetae* (a), *mimica* (b), and *dissita* (c-f) subgroups. Views as in Figure 1. Ventral setae not shown in (b), (e), and (f).

