

Taxonomic relationships within the endemic Hawaiian Drosophilidae (Insecta: Diptera)

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The Hawaiian Drosophilidae are an incredibly diverse group which currently consists of 559 described species and several hundred species that are known, yet await description (Kaneshiro, 1997; O'Grady, 2002). Early morphological studies identified two main groups of Hawaiian Drosophilidae, the “drosophiloids” and the “scaptomyzoids” (Throckmorton, 1966), all the members of which are now referred to as Hawaiian *Drosophila* and *Scaptomyza*, respectively. Although one morphological study suggests that these two lineages are not closely related (Grimaldi, 1990), all other analyses to date support the monophyly of the Hawaiian Drosophilidae (DeSalle, 1992; Thomas & Hunt, 1993; O'Grady, 1998; Remsen & DeSalle, 1998; Remsen & O'Grady, 2002). Furthermore, comprehensive sampling within *Scaptomyza* suggests that the continental members of this genus are derived from the Hawaiian taxa (O'Grady & DeSalle, 2008).

The Hawaiian *Drosophila* lineage was initially composed of members of the genus *Drosophila* endemic to Hawai'i, as well as several endemic Hawaiian genera including *Nudidrosophila*, *Antopocerus*, and *Ateledrosophila*. These three genera were subsequently synonymized with *Drosophila* and are now considered to be of species group rank within a larger clade of endemic Hawaiian *Drosophila* (Kaneshiro, 1976). The Hawaiian *Drosophila* are currently divided into the following species groups (Table 1), based on morphological characters: *antopocerus*, *ateledrosophila*, *haleakalae*, *picture wing*, *modified mouthpart*, *modified tarsus*, *nudidrosophila*, and *rustica*. Recent revisionary work has treated the *antopocerus* (Hardy, 1977), *haleakalae* (Hardy *et al.*, 2001), *nudidrosophila* (Magnacca & O'Grady, 2008a), *rustica* (O'Grady *et al.*, 2001), and parts of the *modified mouthpart* (Hardy & Kaneshiro, 1975a; O'Grady *et al.*, 2003b; Magnacca & O'Grady, 2009) and *modified tarsus* (Hardy & Kaneshiro, 1979; Lapoint *et al.*, 2009) species groups. Phylogenetic work has revised notions of higher-level relationships among species groups (Kambysellis *et al.*, 1995; Bonacum, 2001) and the phylogenetic relationships at the species group level (Carson *et al.*, 1995; O'Grady & Zilversmit, 2004; Bonacum *et al.*, 2005).

The genus *Scaptomyza* is divided into about 18 subgenera (Ashburner *et al.*, 2005; O'Grady *et al.*, 2003a), several of which are endemic to Hawai'i (Table 1). Grimaldi's (1990) cladistic analysis of morphological characters indicated that, while *Celidosoma* and *Grimshawomyia* are closely affiliated with *Scaptomyza*, *Titanochaeta* is not. Grimaldi's phylogeny placed this taxon at the base of the subfamily Drosophilinae, distinct from any other Hawaiian group, even though he stated that he is “skeptical that *Titanochaeta* is a primitive drosophiline” (Grimaldi, 1990). Instead, he “suspects” that *Titanochaeta* is related to the Hawaiian *Drosophila* lineage based on the length of interfrontal setulae (Grimaldi, 1990). Recent molecular work (Bonacum, 2001), however, suggests that *Titanochaeta*, *Scaptomyza*, *Grimshawomyia*, and the subgenus *Engiscaptomyza* (genus *Drosophila*) form a well supported clade. Based on these molecular characters, as well as examination of the male genitalia of these taxa, O'Grady *et al.* (2003a) placed these as subgenera within the genus *Scaptomyza*.

Workers studying both Hawaiian *Drosophila* and *Scaptomyza* have erected a number of lower level (below genus) taxonomic groups to organize the impressive species diversity. Some of these, such as the subgenera of *Scaptomyza*, are formal rankings. Others follow the informal classification system of “species groups” and “species subgroups” introduced by Sturtevant (1939). Furthermore, with the advent of phylogenetic approaches and more detailed examination of neglected taxa, several additional groups and subgroups have been recognized (Magnacca & O’Grady, 2006, 2008a, 2009). While these groups do not hold a formal taxonomic rank and are not recognized by I.C.Z.N. (1999), they are quite useful and often correlate with monophyletic groups when tested in a phylogenetic framework. Our goal in this paper is to summarize the valid species groups and subgroups of Hawaiian *Drosophila* and to discuss some that, while present in online databases (e.g., GenBank, TaxoDros), are not used by Hawaiian *Drosophila* workers. Below we list all valid species groups and subgroups and enumerate the species present in each.

Summary of Taxonomic Changes

The current catalog is an effort to move from a hierarchical framework of nested groups toward an evolutionary framework based on phylogenetic analyses. Several groups have been examined in an evolutionary context and will be designated as clades (monophyletic groups), indicating their unique phylogenetic history. However, the sheer size of the Hawaiian Drosophilidae precludes a comprehensive phylogenetic analysis at this time, meaning that several groups will retain formal or informal ranks. This section lists the newly proposed taxonomic changes and reorganizations supported by recent phylogenetic analyses.

***Idiomyia*.** This name has been applied variously to a number of different groups within the Hawaiian *Drosophila* (see below in *picture wing* clade section for a detailed history). O’Grady (2002) argued that this name should be considered a synonym of *Drosophila*. Several online databases (GenBank, Taxodros) maintain the use of *Idiomyia* for some, but not all, Hawaiian *Drosophila* species. Brake & Bächli (2008) resurrected this name in their catalog of world Drosophilidae and applied it to all Hawaiian *Drosophila* species. We feel that this is taxonomically confusing and ignores the phylogenetic work showing that the Hawaiian species to be nested within the larger genus *Drosophila*. Therefore we herein move all species of *Idiomyia* (*sensu* Brake & Bächli, 2008) back to the genus *Drosophila*.

***AMC Clade*.** This is a new grouping based on phylogenetic evidence that suggests the *antopocerus* and *modified tarsus* species groups form a clade. This was first suggested by Heed (1968) on the basis of ecological associations within this group.

***modified tarsus species group*.** We are expanding the definition of this group to include species previously placed in the *ciliated tarsus* species group. Recent analyses (e.g., Bonacum, 2001) show that these taxa are imbedded within the *modified tarsus* species group.

***picture wing clade*.** This clade refers to all members of the *grimshawi*, *planitibia*, and *adiastola* species groups (after Kaneshiro *et al.*, 1995). We add the *anomalipes*, and *primaeva* species groups.

***Scaptomyza Lineage*.** The genus *Scaptomyza* now includes several endemic Hawaiian groups previously considered as genera, such as *Celidosoma*, *Grimshawomyia*, and

Titanochaeta. Furthermore, the subgenus *Engiscaptomyza* of the genus *Drosophila* (Kaneshiro, 1969) was thought to be intermediate between the Hawaiian *Drosophila* and *Scaptomyza* because it shared characters with each. O'Grady *et al.* (2003a) placed *Grimshawomyia*, *Titanochaeta*, and the subgenus *Engiscaptomyza* as subgenera within *Scaptomyza*. The status of *Celidosoma* remains uncertain. Recently Magnacca & O'Grady (2008b) transferred eight unplaced *Drosophila* into the genus *Scaptomyza*.

Catalog

Hawaiian Drosophilidae Clade

This monophyletic group includes all members of the Hawaiian *Drosophila* clade and the *Scaptomyza* lineage, as discussed above and listed below. It is a well supported monophyletic group in multiple phylogenetic analyses (e.g., DeSalle, 1992; Russo *et al.*, 1995; O'Grady & DeSalle, 2008)

Hawaiian *Drosophila* Clade

The Hawaiian *Drosophila* is one of the most consistently supported groups across all phylogenetic analyses of higher level relationships within the family Drosophilidae (reviewed in Markow & O'Grady, 2006, see also O'Grady & DeSalle, 2008) and can safely be designated as a clade based on the wealth of evidence. While phylogenetic relationships within and among Hawaiian *Drosophila* are clear, the nomenclature of this group is somewhat confusing. Grimshaw (1901) erected the genus *Idiomyia* for a number of endemic Hawaiian taxa possessing a supernumerary crossvein. In his revision of the Hawaiian Drosophilidae, Hardy maintained the distinction between *Idiomyia* and *Drosophila*, although he considered *Idiomyia* "very close to *Drosophila*" with the only character separating the two being the extra crossvein in cell r5 (Hardy, 1965). The two genera existed in parallel until the late 1960s when Carson and colleagues (Carson *et al.*, 1967; Carson & Stalker, 1969), synonymized *Idiomyia* with *Drosophila* based on polytene chromosome banding patterns and the morphology of male genitalia.

When Grimaldi (1990) revised the Drosophilidae, he resurrected the name *Idiomyia* and applied it to all Hawaiian *Drosophila*. He considered *Idiomyia* to be distinct from *Drosophila* and nested within the *Hirtodrosophila* genus group, an assemblage of mycophagous taxa. This relationship is in conflict with all other phylogenetic studies (reviewed in Markow & O'Grady, 2006). Furthermore, reanalysis of Grimaldi's (1990) data demonstrates that his methodology was flawed and there is no distinction between Hawaiian *Drosophila* and the remainder of the genus *Drosophila* (Remsen & O'Grady, 2002). Based on these data, O'Grady (2002) transferred all species in the genus *Idiomyia* to the Hawaiian *Drosophila* clade. Recently, Brake & Bächli (2008) have, following Grimaldi (1990), applied the name *Idiomyia* to all endemic Hawaiian species of *Drosophila*. We disagree with this taxonomic change on the grounds that (1) it resurrects a name that is specifically linked to a homoplasious morphological character—the supernumerary crossvein has evolved and been lost multiple times in the Hawaiian species, (2) it includes no morphological synapomorphy or diagnosis for *Idiomyia*—no formal revision or examination of type material has been done to justify this placement, and (3) it disassociates the large literature on Hawaiian *Drosophila* from the species names. Therefore, we are placing all *Idiomyia* species (*sensu* Brake & Bächli, 2008) into the Hawaiian *Drosophila* clade.

AMC Clade

The AMC clade (Bonacum, 2001) consists of the *antopocerus*, *modified tarsus*, and *ciliated tarsus* species. Heed (1968) placed many of these species in the leaf breeder group based on rearing experiments that discovered these species utilize the leaves of various endemic Hawaiian plants as oviposition substrates. Subsequent ecological work (Magnacca *et al.*, 2008) has shown that some members of this group, particularly those in the *ciliated tarsus* subgroup, use stems and bark of a variety of native Hawaiian host plants as oviposition substrates. Furthermore, many *modified mouthpart* species also utilize leaves as oviposition substrates. Phylogenetic work (Kambyzellis *et al.*, 1995; Baker & DeSalle, 1997; Bonacum, 2001; O'Grady & DeSalle, 2008) supports the monophyly of this clade.

***antopocerus* species group**

This group was originally described as a genus (Hardy, 1965: 42) because of the highly unusual secondary sexual characteristics possessed by males. Perhaps the most notable character is the long, whip-like arista which is densely branched on the dorsal surface. Other male-specific characters are restricted to the highly specialized chaetotaxy of the forelegs. Kaneshiro demonstrated that these characters did not merit generic standing and sank this genus into the subgenus *Drosophila* as the *antopocerus* species group based on the morphology of male genitalia (Kaneshiro, 1976: 259). Hardy (1977: 83) cited Kaneshiro (1976) as being in press and states that "these characters found only in males are probably not more than species group importance" even though he concludes "for convenience sake, to treat *Antopocerus* as a subgenus" of *Drosophila*. As a result, *Antopocerus* was listed as a subgenus of the genus *Drosophila* in Wheeler's catalog (Wheeler, 1981, 1986), even though it should be considered a species group within the Hawaiian *Drosophila*. Hardy (1977) proposed three subgroups in this group, *adunca*, *diamphidiopoda*, and *villosa*.

***adunca* subgroup:**

- Drosophila adunca* (Hardy), 1965: 44
- Drosophila longiseta* Grimshaw, 1901: 68

***diamphidiopoda* subgroup:**

- Drosophila cognata* Grimshaw, 1901: 69
- Drosophila diamphidiopoda* (Hardy), 1965: 50
- Drosophila kaneshiroi* Hardy, 1977: 89
- Drosophila orthoptera* (Hardy), 1965: 56
- Drosophila tanythrix* (Hardy), 1965: 58
- Drosophila yooni* Hardy 1977: 89

***villosa* subgroup:**

- Drosophila apicalis* Hardy, 1977: 93
- Drosophila arcuata* (Hardy) 1965: 47
- Drosophila curvata* Hardy, 1977: 92
- Drosophila entrichocnema* (Hardy), 1965: 52
- Drosophila picea* Hardy, 1978a: 102
- Drosophila stigma* Hardy, 1977: 94
- Drosophila villosa* (Hardy), 1965: 61

***modified tarsus* species group**

Members of the *modified tarsus* species group possess spectacular modifications on the foretarsi of males. Four species subgroups, the *bristle tarsus*, *ciliated tarsus*, *split tarsus*, and *spoon tarsus*, have been erected based on the morphology of the tarsal modification. Hardy and Kaneshiro (1979) revised the *split tarsus* species group, but the other groups are poor-

ly known. The *ciliated tarsus* species are included as a subgroup here based on recent molecular work (Bonacum, 2001). Previously, these taxa had been considered basal in the Hawaiian *Drosophila* clade, closely related to the *haleakalae* species group, although this is clearly not the case.

***bristle tarsus* subgroup:**

- Drosophila apicisetae* Hardy, 1965: 152
- Drosophila apodasta* Hardy, 1965: 154
- Drosophila basimacula* Hardy, 1965: 170
- Drosophila bicondyla* Hardy, 1965: 176
- Drosophila brevitarsus* Hardy, 1965: 188
- Drosophila brunneisetae* Hardy, 1965: 193
- Drosophila expansa* Hardy, 1965: 268
- Drosophila lemniscata* Hardy, 1965: 343
- Drosophila perissopoda* Hardy, 1965: 412
- Drosophila petalopeza* Hardy, 1965: 532
- Drosophila prodita* Hardy, 1965: 427
- Drosophila quasiexpansa* Hardy, 1965: 444
- Drosophila redunca* Hardy, 1965: 446
- Drosophila seclusa* Hardy, 1965: 458
- Drosophila spicula* Hardy, 1965: 472
- Drosophila torula* Hardy, 1965: 484
- Drosophila trichaetosa* Hardy, 1965: 489
- Drosophila unricula* Hardy, 1965: 495

***ciliated tarsus* subgroup:**

- Drosophila brunneifrons* Hardy, 1965: 191
- Drosophila caccabata* Hardy, 1965: 196
- Drosophila carnosae* Hardy, 1965: 204
- Drosophila clavitibia* Hardy, 1965: 213
- Drosophila diffusa* Hardy, 1965: 242
- Drosophila dorsociliata* Hardy, 1965: 256
- Drosophila dumalis* Hardy, 1965: 260
- Drosophila fusticula* Hardy, 1965: 292
- Drosophila gilvilateralis* Hardy, 1965: 294
- Drosophila imparisetae* Hardy, 1965: 315
- Drosophila kraussi* Hardy, 1965: 336
- Drosophila latigena* Hardy, 1965: 342
- Drosophila medialis* Hardy, 1966: 244
- Drosophila melanopedis* Hardy, 1965: 362
- Drosophila nigratarsus* Hardy, 1965: 390
- Drosophila orestes* Hardy, 1965: 400
- Drosophila paucula* Hardy, 1965: 405
- Drosophila setipalpus* Hardy, 1965: 466
- Drosophila williamsi* Hardy, 1965: 512
- Drosophila xanthognoma* Hardy, 1965: 513
- Drosophila xanthosoma* Grimshaw, 1901: 68

***split tarsus* subgroup:**

- Drosophila ancyla* Hardy, 1965: 145
- Drosophila attenuata* Hardy, 1965: 165
- Drosophila basisetosa* Hardy, 1965: 173
- Drosophila capitata* Hardy, 1965: 202
- Drosophila chaetocephala* Hardy & Kaneshiro, 1979: 76

- Drosophila clavata* Hardy, 1965: 211
Drosophila cneocopleura Hardy, 1965: 216
Drosophila cornutitarsus Hardy & Kaneshiro, 1979: 78
Drosophila cracens Hardy, 1965: 227
Drosophila dicropeza Hardy & Kaneshiro, 1979: 79
Drosophila dorsigera Hardy, 1965: 254
Drosophila enoplotarsus Hardy, 1965: 262
Drosophila forficata Hardy, & Kaneshiro, 1979: 80
Drosophila fundita Hardy, 1965: 279
Drosophila furcatoris Hardy & Kaneshiro, 1979: 81
Drosophila kokeensis Hardy, 1966: 212
Drosophila paracracens Hardy & Kaneshiro, 1979: 82
Drosophila paucitarsus Hardy & Kaneshiro, 1979: 83
Drosophila pectinitarsus Hardy, 1965: 407
Drosophila proceriseta Hardy, 1965: 425
Drosophila propiofacies Hardy, 1965: 434
Drosophila spiethi Hardy, 1966: 217
Drosophila systemopeza Hardy & Kaneshiro, 1979: 85
Drosophila variabilis Hardy, 1965: 497

spoon tarsus subgroup:

- Drosophila atroscutellata* Hardy, 1966: 200
Drosophila conformis Hardy, 1965: 219
Drosophila contorta Hardy, 1965: 226
Drosophila dasyncnemia Hardy, 1965: 236
Drosophila fastigata Hardy, 1965: 271
Drosophila incognita Hardy, 1965: 319
Drosophila kikalaeleele Lapoint, Magnacca & O'Grady, 2009: 61
Drosophila mimiconformis Hardy, 1965: 367
Drosophila neutralis Hardy, 1965: 383
Drosophila percnosoma Hardy, 1965: 410
Drosophila sordidapex Grimshaw, 1901: 63
Drosophila waddingtoni Basden, 1976: 185

Unplaced modified-tarsus species:

- Drosophila gubleri* Hardy, 1966: 208

Picture wing clade

The *picture wing* species are undoubtedly the best-studied in the Hawaiian *Drosophila*. The monophyly and phylogenetic relationships have been tested with chromosomal (Carson *et al.*, 1967), morphological (Kaneshiro *et al.*, 1995), and molecular (Kambysellis *et al.*, 1995) characters. Several groups nested within the original *picture-wing* species group (*sensu*: Throckmorton, 1966) have, at various times, been referred to as species groups themselves (see Kaneshiro *et al.*, 1995). This has led to confusion about taxonomic ranks and nomenclature within this group. For this reason, as well as to reflect the wealth of phylogenetic information indicating monophyly of major groups within this clade, we follow Kaneshiro *et al.*, (1995) in referring to the larger assemblage as the *picture wing* clade and the major lineages as species groups.

While the bulk of the data currently support the monophyly of the *picture wings* as a whole, expanded taxonomic sampling in one recent study (Bonacum, 2001), suggests with modest support that the *nudidrosophila* (Bonacum, 2001) species group may be nested within a the picture wings. In lieu of additional phylogenetic work specifically addressed at testing the monophyly of the *picture wings* and the placement of *nudidrosophila* relative to this group, we designate the picture wings as a clade (*sensu* Kaneshiro *et al.* 1995).

***adiastola* species group**

The *adiastola* species group was first proposed by Hardy & Kaneshiro (1968: 236). The monophyly of this group is well supported in many studies. Kaneshiro *et al.* (1995) review the chromosomal and morphological studies which have, over more than thirty years, supported the *adiastola* clade. The behavior of flies in this clade also suggests monophyly (Spieth, 1968, 1982). Kambysellis *et al.* (1995) included five *adiastola* species in their molecular phylogeny and these taxa formed a well-supported monophyletic group. Two distinct lineages within the *adiastola* clade, the *adiastola* and *truncipenna* subgroups, are suggested by the morphological and chromosomal data (Kaneshiro *et al.*, 1995). The molecular data (Kambysellis *et al.*, 1995) suggests, albeit somewhat weakly, that the *adiastola* subgroup is paraphyletic with respect to the *truncipenna* subgroup.

***adiastola* subgroup**

- Drosophila adiaastola* Hardy, 1965: 134
- Drosophila cilifera* Hardy & Kaneshiro, 1968: 237
- Drosophila clavisetae* (Hardy), 1966: 219
- Drosophila neoclavisetae* Perreira & Kaneshiro, 1990: 81
- Drosophila neogramshawi* Hardy & Kaneshiro, 1968: 261
- Drosophila ochrobasis* Hardy & Kaneshiro, 1968: 240
- Drosophila ornata* Hardy & Kaneshiro, 1969: 49
- Drosophila peniculipedis* Hardy, 1965: 408
- Drosophila setosimentum* Hardy & Kaneshiro, 1968: 241
- Drosophila spectabilis* Hardy, 1965: 470
- Drosophila touchardiae* Hardy & Kaneshiro, 1972: 159
- Drosophila toxochaeta* Perreira & Kaneshiro, 1990: 84

***truncipenna* subgroup**

- Drosophila hamifera* Hardy & Kaneshiro, 1968: 254
- Drosophila paenhamifera* Hardy & Kaneshiro, 1969: 50
- Drosophila truncipenna* Hardy, 1965: 491
- Drosophila varipennis* (Grimshaw), 1901: 54

***anomalipes* species group**

This group consists of only two species, which appear to be close to the *primaeva* group as basal among the *picture wing* clade (Kaneshiro *et al.*, 1995). However, they have never been included in phylogenetic analyses to confirm this position.

- Drosophila anomalipes* Grimshaw, 1901: 62
- Drosophila quasianomalipes* Hardy, 1965: 442

***grimshawi* species group**

The *grimshawi* group is supported as monophyletic by chromosomal (Carson & Yoon, 1982), morphological (Kaneshiro *et al.*, 1995), and molecular (Kambysellis *et al.*, 1995) characters. Although many species are placed in this group and not all have been sampled in every study, some clades within this group can be constructed. The *crucigera*, *hawaiensis*, *pilimana*, and *punalua* subgroups are well supported as clades by several studies. The *conspicua*, *distinguenda*, *orthnopeza*, and *vesciseta* subgroups are either not adequately sampled to test monophyly or have been shown to be non-monophyletic in at least one study.

***conspicua* subgroup**

- Drosophila aglaia* Hardy, 1965: 140
- Drosophila conspicua* Grimshaw, 1901: 59

- Drosophila gymnophallus* Hardy & Kaneshiro, 1975b: 58
Drosophila liophallus Hardy & Kaneshiro, 1968: 199
Drosophila macrothrix Hardy & Kaneshiro, 1968: 200
Drosophila odontophallus Hardy & Kaneshiro, 1968: 202
Drosophila psilophallus Hardy & Kaneshiro, 1971: 157
Drosophila spaniothrix Hardy & Kaneshiro, 1968: 223
Drosophila tarphytrichia Hardy, 1965: 479

crucigera subgroup

- Drosophila affinisdisjuncta* Hardy, 1978b: 350
Drosophila balioptera Hardy, 1965: 168
Drosophila bostrycha Hardy, 1965: 182
Drosophila craddockae Kaneshiro & Kambysellis, 1999: 209
Drosophila crucigera Grimshaw, 1901: 86
Drosophila disjuncta Hardy, 1965: 245
Drosophila grimshawi Oldenberg, 1914: 23
Drosophila pullipes Hardy & Kaneshiro, 1972: 157

distinguenda subgroup

- Drosophila distinguenda* Hardy, 1965: 252
Drosophila divaricata Hardy & Kaneshiro, 1971: 151
Drosophila inedita Hardy, 1965: 322

hawaiiensis subgroup

- Drosophila flexipes* Hardy & Kaneshiro, 1968: 186
Drosophila formella Hardy & Kaneshiro, 1972: 155
Drosophila gradata Hardy & Kaneshiro, 1968: 191
Drosophila gymnobasis Hardy & Kaneshiro, 1971: 153
Drosophila hawaiiensis Grimshaw, 1901: 60
Drosophila heedi Hardy & Kaneshiro, 1971: 155
Drosophila hirtipalpus Hardy & Kaneshiro, 1968: 192
Drosophila lasiopoda Hardy & Kaneshiro, 1975b: 58
Drosophila musaphilia Hardy, 1965: 375
Drosophila psilotarsalis Hardy & Kaneshiro, 1975b: 62
Drosophila recticilia Hardy & Kaneshiro, 1968: 212
Drosophila silvarentis Hardy & Kaneshiro, 1968: 219
Drosophila turbata Hardy & Kaneshiro, 1969: 52
Drosophila villitibia Hardy, 1965: 506

orphanopeza subgroup

- Drosophila atrimentum* Hardy & Kaneshiro, 1971: 158
Drosophila ciliaticrus Hardy, 1965: 207
Drosophila claytonae Hardy & Kaneshiro, 1969: 41
Drosophila engyochracea Hardy, 1965: 261
Drosophila limitata Hardy & Kaneshiro, 1968: 194
Drosophila mulli Perreira & Kaneshiro, 1990: 79
Drosophila murphyi Hardy & Kaneshiro, 1969: 46
Drosophila obtatai Hardy & Kaneshiro, 1972: 156
Drosophila ochracea Grimshaw, 1901: 61
Drosophila orphanopeza Hardy & Kaneshiro, 1968: 205
Drosophila orthofascia Hardy & Kaneshiro, 1968: 206
Drosophila reynoldsiae Hardy & Kaneshiro, 1972: 158
Drosophila sejuncta Hardy & Kaneshiro, 1968: 215
Drosophila sobrina Hardy & Kaneshiro, 1971: 159
Drosophila sodomae Hardy & Kaneshiro, 1968: 221
Drosophila sproati Hardy & Kaneshiro, 1968: 225
Drosophila villosipedis Hardy, 1965: 508

***pilimana* subgroup**

- Drosophila discreta* Hardy & Kaneshiro, 1968: 182
Drosophila fasciculisetae Hardy, 1965: 269
Drosophila glabriapex Hardy & Kaneshiro, 1968: 188
Drosophila lineosetae Hardy & Kaneshiro, 1968: 197
Drosophila pilimana Grimshaw, 1901: 61

***punalua* subgroup**

- Drosophila basisetae* Hardy & Kaneshiro, 1968: 178
Drosophila ocellata Hardy & Kaneshiro, 1969: 47
Drosophila paucicilia Hardy & Kaneshiro, 1971: 163
Drosophila paucipuncta Grimshaw, 1901: 62
Drosophila prolaticilia Hardy, 1965: 429
Drosophila prostopalpis Hardy & Kaneshiro, 1968: 210
Drosophila punalua Bryan, 1934: 438
Drosophila uniseriata Hardy & Kaneshiro, 1968: 229

***vesciseta* subgroup**

- Drosophila alsophila* Hardy & Kaneshiro, 1971: 165
Drosophila assita Hardy & Kaneshiro, 1969: 39
Drosophila digressa Hardy & Kaneshiro, 1968: 180
Drosophila hexachaetae Hardy, 1965: 300
Drosophila micromyia Hardy & Kaneshiro, 1975b: 60
Drosophila montgomeryi Hardy & Kaneshiro, 1971: 167
Drosophila vesciseta Hardy & Kaneshiro, 1968: 231
Drosophila virgulata Hardy & Kaneshiro, 1968: 234

Unplaced *grimshawi* species

- Drosophila ambochila* Hardy & Kaneshiro, 1971: 166
Drosophila lanaiensis Grimshaw, 1901: 60
Drosophila oreas Hardy, 1965: 400
Drosophila pilatisetae Hardy & Kaneshiro, 1968: 209
Drosophila pisonia Hardy & Kaneshiro, 1971: 168

***planitibia* species group**

The *planitibia* group was first used by Kaneshiro *et al.* (1995) and included the *cyrtoloma*, *picticornis*, and *planitibia* species subgroups. Several studies have supported the monophyly of this group, as well as all three groups within the *planitibia* clade. Recently, Bonacum *et al.* (2005) generated a phylogeny of the *planitibia* group and proposed the *neopicta* subgroup for three species. This phylogeny indicated that the *picticornis* subgroup is basal to the *planitibia*, *neopicta*, and *cyrtoloma* subgroups. The presence of a supernumerary crossvein in cell r5 has traditionally been used to define the *planitibia* group. In fact, this character led Grimshaw (1901) to describe the genus *Idiomyia*, a name that has since been abandoned (O'Grady, 2002). We argue that this crossvein is a poor character as members of the basal *picticornis* subgroup lack a supernumerary crossvein and some unrelated members of the *adiastola* subgroup possess a similar extra crossvein, indicating a high degree of homoplasy in this character.

***cyrtoloma* subgroup**

- Drosophila cyrtoloma* Hardy, 1969: 73
Drosophila hanaulae Hardy, 1969: 75
Drosophila ingens Hardy & Kaneshiro, 1971: 162
Drosophila melanocephala (Hardy), 1966: 222

Drosophila neoperkinsi Hardy & Kaneshiro, 1968: 261

Drosophila oahuensis (Grimshaw), 1901: 52

Drosophila obscuripes (Grimshaw), 1901: 52

neopicta subgroup

Drosophila neopicta Hardy & Kaneshiro, 1968: 261

Drosophila nigribasis Hardy, 1969: 76

Drosophila substenoptera Hardy, 1969: 72

planitibia subgroup

Drosophila differens Hardy & Kaneshiro, 1975b: 57

Drosophila hemipeza (Hardy), 1965: 545

Drosophila heteroneura (Perkins), 1910: 699

Drosophila planitibia (Hardy), 1966: 225

Drosophila silvestris (Perkins), 1910: 700

picticornis subgroup

Drosophila picticornis Grimshaw, 1901: 57

Drosophila setosifrons Hardy & Kaneshiro, 1968: 216

primaeva species group

Although lacking prominent wing marks, this group (consisting of two cryptic species separable only by details of the male genitalia) has long been considered the basal member of the *picture wing* lineage based on chromosome rearrangements (Carson & Stalker, 1969). This conclusion has been subsequently reinforced by phylogenetic analysis of DNA sequences (Bonacum, 2001).

Drosophila primaeva Hardy & Kaneshiro, 1968: 258

Drosophila sharpi Grimshaw, 1901: 65

ateledrosophila species group

This group was originally described as a genus on the basis of the preapically placed arista and lack of anterior reclinate or ocellar setae (Hardy, 1965: 62). However, later studies using male genitalic characters suggest that this group is synonymous with the subgenus *Drosophila* and is close to the picture wing clade (Kaneshiro, 1976: 259). The head chaetotaxy is similar to that of the *okala* subgroup of the *nudidrosophila* species group. No phylogenetic study to date has included any of the species placed in this group so their exact position relative to the remaining Hawaiian *Drosophila* remains enigmatic. Based on the form of the aedeagus and ovipositor, this group is likely to be either sister to the *nudidrosophila* group or separately derived from a lineage within the picture wing clade.

Drosophila diamphidia (Hardy), 1965: 63

Drosophila papala Magnacca & O'Grady, 2008a: 403

Drosophila preapicula (Hardy), 1965: 64

haleakalae species group

The *haleakalae* species group, the subject of a recent revision (Hardy *et al.*, 2001) and phylogenetic study (O'Grady & Zilversmit, 2004) is an example of the nomenclatural confusion above the species level that continues to plague the Hawaiian Drosophilidae. This group has been referred to in the literature by a variety of names, including *white tip scutellum*, *light tip scutellum*, *rimmed labellum*, and *fungus feeder* based on either morphology or ecology (Throckmorton, 1966; Heed, 1968; Ashburner, 1989; Kambysellis, 1993). Hardy *et al.*

(2001) point out that, since not all species share the characteristics implied by these names, a less misleading name should be adopted. The *haleakalae* group derives its name from *Drosophila haleakalae* Grimshaw, one of the first described species in this group. This group is not well known, most likely because it is not possible to culture any *haleakalae* species in the laboratory. In addition to the subgroups listed below, Hardy *et al.* (2001) propose complexes and clusters within this group—but recent phylogenetic work, suggests that some may not be monophyletic (O’Grady & Zilversmit, 2004). Although taxon sampling was not extensive, the monophyly of the *haleakalae* species group is well supported in O’Grady & Zilversmit’s (2004) analyses.

anthrax subgroup

- Drosophila anthrax* Hardy, 1965: 148
- Drosophila demipolita* Hardy, 1965: 239; Hardy, 1966: 205
- Drosophila fascigera* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 12
- Drosophila fuscifrons* Hardy, 1965: 287
- Drosophila hemianthrax* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 15
- Drosophila melanoloma* Hardy, 1965: 360
- Drosophila multiciliata* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 18
- Drosophila nigropolita* Hardy, 1965: 394
- Drosophila retrusa* Hardy, 1965: 450
- Drosophila seorsa* Hardy, 1965: 461

cilifemorata subgroup

- Drosophila chicae* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 42
- Drosophila cilifemorata* Hardy, 1965: 209
- Drosophila curtitarsis* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 44
- Drosophila denotata* Hardy, 1965: 241
- Drosophila dolichotarsis* Hardy, 1966: 206
- Drosophila iki* Bryan, 1934: 439
- Drosophila inciliata* Hardy & Kaneshiro, 1968: 251
- Drosophila insignita* Hardy, 1965: 326
- Drosophila longiperda* Kambysellis, 1993: 425
- Drosophila nigra* Grimshaw, 1901: 62
- Drosophila sabroskyi* Hardy, 1965: 453
- Drosophila stenoptera* Hardy, 1965: 473
- Drosophila swezeyi* Hardy, 1965: 474
- Drosophila tanytarsis* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 30
- Drosophila venusta* Hardy, 1965: 502

haleakalae subgroup

- Drosophila atrifacies* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 47
- Drosophila brunneicrus* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 48
- Drosophila clara* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 53
- Drosophila cryptica* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 55
- Drosophila fungiperda* Hardy, 1966: 244
- Drosophila haleakalae* Grimshaw, 1901: 64
- Drosophila macrochaetae* Hardy, 1965: 348
- Drosophila nigella* Hardy, 1965: 385
- Drosophila ochropleura* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 49

luteola subgroup

- Drosophila fuscoapex* Hardy, 1965: 291
- Drosophila luteola* Hardy, 1965: 347
- Drosophila quinqueramosa* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 61
- Drosophila tamashiroi* Hardy, 1965: 477

polita subgroup

- Drosophila bipolita* Hardy, 1965: 177
Drosophila canipolita Hardy, 1965: 198
Drosophila dives Hardy & Kaneshiro, in Hardy *et al.*, 2001: 67
Drosophila flavisternum Hardy, 1965: 275
Drosophila illusiopolita Hardy, 1965: 311
Drosophila lissodora Hardy & Kaneshiro, in Hardy *et al.*, 2001: 69
Drosophila mecocnemia Hardy, 1965: 354
Drosophila paraanthrax Hardy & Kaneshiro, in Hardy *et al.*, 2001: 72
Drosophila polita Grimshaw, 1901: 71
Drosophila pretiosa Hardy, 1965: 423

scitula subgroup

- Drosophila fulgida* Hardy & Kaneshiro, in Hardy *et al.*, 2001: 77
Drosophila melanosoma Grimshaw, 1901: 68
Drosophila scitula Hardy, 1966: 213
Drosophila setositibia Hardy & Kaneshiro, in Hardy *et al.*, 2001: 83
Drosophila subopaca Hardy & Kaneshiro, in Hardy *et al.*, 2001: 85

unplaced haleakalae species

- Drosophila flaviceps* Grimshaw, 1901: 63 (*nomen dubium*)

modified mouthpart species group

The *modified mouthpart* species group is a large, diverse group of Hawaiian *Drosophila* whose monophyly and relationships have not been well tested. This is perhaps the largest species group of Hawaiian *Drosophila* and may contain close to 150 species when all known material has been described. *Modified mouthpart* species utilize nearly every ecological niche observed in the remaining groups of Hawaiian *Drosophila* (Heed, 1968; Magnacca *et al.*, 2008). These species are linked by modifications to their mouthparts, including additional thickened setae or, in some cases, appendages. Such characters, which are possessed only by males, are believed to be used during courtship and mating (Spieth, 1968).

Several subgroups within the *modified mouthpart* species group have been proposed. Hardy & Kaneshiro (1968) erected the *semifuscata* subgroup to contain those species with extensive patterns of infuscation on the wings. Hardy and Kaneshiro (1975a) proposed the *mitchelli* subgroup based on the setation patterns on the labellae of males. The *mimica* subgroup is defined by having a large, pointed curvate seta on the apicomedial margin of the labellum (O'Grady *et al.*, 2003b). The subgroups have been redefined to more accurately reflect characters of mouthpart morphology, and additional ones proposed to cover the full range of the group (Magnacca & O'Grady, 2006), but a number of unplaced species remain. At least one species, *D. adventitia*, appears to be more closely related to the *picture wing* clade than to the other *modified mouthpart* species (Bonacum, 2001).

ceratostoma subgroup

- Drosophila ceratostoma* Hardy, 1965: 203
Drosophila humeralis Grimshaw, 1901: 64
Drosophila orascopa Magnacca & O'Grady, 2009: 41
Drosophila wikani Magnacca & O'Grady, 2009: 42

dissita subgroup

- Drosophila amydrospilota* Hardy, 1965: 143
Drosophila artigena Hardy, 1965: 161
Drosophila beardleyi Hardy, 1965: 174
Drosophila brevissima Hardy, 1965: 186

Drosophila curvibtibia Hardy, 1965: 234
Drosophila dissita Hardy, 1965: 248
Drosophila dracaenae Hardy, 1965: 258
Drosophila eumecothrix Hardy, 1965: 264
Drosophila laciniosa Hardy, 1965: 337
Drosophila larifuga Hardy, 1965: 340
Drosophila polliciforma Hardy, 1965: 419
Drosophila pychnochaetae Hardy, 1965: 438
Drosophila taeniata Hardy, 1965: 476
Drosophila velutifrons Hardy, 1965: 501

***freycinetiae* subgroup**

“*Drosophila anapuu* Magnacca & O’Grady, 2009: 46
Drosophila asketostoma Hardy, 1965: 163
Drosophila comatifemora Hardy, 1965: 218
Drosophila dentilabia Magnacca & O’Grady, 2009: 51
Drosophila freycinetiae Hardy, 1965: 277
Drosophila hirticoxa Hardy, 1965: 302
Drosophila kualii Magnacca & O’Grady, 2009: 55
Drosophila nalomano Magnacca & O’Grady, 2009: 57
Drosophila prominens Hardy, 1965: 432

***fuscoamoeba* subgroup**

Drosophila agitona Hardy, 1965: 138
Drosophila aquila Hardy, 1965: 158
Drosophila araiotricha Hardy, 1965: 159
Drosophila brevicilia Hardy, 1965: 185
Drosophila clydonia Hardy, 1965: 214
Drosophila furva Hardy, 1965: 284
Drosophila fuscoamoeba Bryan, 1934: 438
Drosophila megasticta Hardy, 1965: 358

***hirtitarsus* subgroup**

Drosophila goureaui Hardy & Kaneshiro, 1972: 161
Drosophila hirtitarsus Hardy, 1965: 304

***mimica* subgroup**

Drosophila acanthos Kam & Perreira, in O’Grady *et al.*, 2003: 32
Drosophila antecedens Kam & Perreira, in O’Grady *et al.*, 2003: 35
Drosophila badia Hardy, 1965: 166
Drosophila chaetopeza Hardy, 1965: 206
Drosophila chimera Kam & Perreira, in O’Grady *et al.*, 2003: 22
Drosophila conjectura Hardy, 1965: 223
Drosophila echinostoma Kam & Perreira, in O’Grady *et al.*, 2003: 33
Drosophila flavibasis Hardy, 1965: 273
Drosophila gagne Kam & Perreira, in O’Grady *et al.*, 2003: 35
Drosophila inebria Kam & Perreira, in O’Grady *et al.*, 2003: 25
Drosophila infuscata Grimshaw, 1901: 63
Drosophila involuta Hardy, 1965: 330
Drosophila kambysellisi Hardy & Kaneshiro, 1969: 44
Drosophila kauluai Bryan, 1934: 439
Drosophila lobatopalpus Kam & Perreira, in O’Grady *et al.*, 2003: 36
Drosophila maemae Kam & Perreira, in O’Grady *et al.*, 2003: 31
Drosophila mimica Hardy, 1965: 365
Drosophila reschae Hardy & Kaneshiro, 1975b: 63
Drosophila soonae Takada & Yoon, 1989: 117
Drosophila xenophaga Kam & Perreira, in O’Grady *et al.*, 2003: 26

***mitchelli* subgroup**

- Drosophila biseriata* Hardy, 1965: 179
Drosophila furvifacies Hardy, 1965: 285
Drosophila hystriocosa Hardy & Kaneshiro, 1969: 42
Drosophila mitchelli Hardy, 1965: 370
Drosophila nigrocirrus Hardy, 1965: 392

***nanella* subgroup**

- Drosophila albifacies* Hardy, 1965: 141
Drosophila curticia Hardy, 1965: 232
Drosophila dolomata Hardy, 1965: 253
Drosophila nanella Hardy, 1965: 378

***quadrissetae* subgroup**

- Drosophila ischnotrix* Hardy, 1965: 331
Drosophila quadrissetae Hardy, 1965: 440
Drosophila residua Hardy, 1965: 448
Drosophila tendomentum Hardy, 1965: 481

***scolostoma* subgroup**

- Drosophila deltaneuron* Bryan, 1938: 40
Drosophila mediana Hardy, 1965: 356
Drosophila scolostoma Hardy, 1965: 456

***semifuscata* subgroup**

- Drosophila acanthostoma* Hardy & Kaneshiro, 1968: 244
Drosophila anoplostoma Hardy & Kaneshiro, 1968: 250
Drosophila apicipuncta Hardy, 1965: 150
Drosophila bridwelli Hardy, 1965: 189
Drosophila diminuens Hardy, 1965: 244
Drosophila magnimacula Hardy, 1965: 350
Drosophila mandibulata Magnacca & O'Grady, 2009: 74
Drosophila olae Grimshaw, 1901: 66
Drosophila peloristoma Magnacca & O'Grady, 2009: 77
Drosophila sadleria Bryan, 1938: 41
Drosophila semifuscata Hardy, 1965: 460
Drosophila wawae Magnacca & O'Grady, 2009: 82
Drosophila xuthoptera Hardy, 1965: 516
Drosophila z-notata Bryan, 1934: 437

***setiger* subgroup**

- Drosophila desallei* Magnacca & O'Grady, 2009: 87
Drosophila eurypeza Hardy, 1965: 266
Drosophila imitator Hardy, 1965: 312
Drosophila setiger Grimshaw, 1901: 64

Unplaced *modified mouthpart* group species

- Drosophila acrostichalis* Hardy, 1965: 132
Drosophila adventitia Hardy, 1965: 136
Drosophila apiki Magnacca & O'Grady, 2009: 16
Drosophila barbata Magnacca & O'Grady, 2009: 18
Drosophila gladius Magnacca & O'Grady, 2009: 20
Drosophila incongruens Magnacca & O'Grady, 2009: 22
Drosophila komohana Magnacca & O'Grady, 2009: 24
Drosophila lelohua Magnacca & O'Grady, 2009: 26
Drosophila omnivora Magnacca & O'Grady, 2009: 27
Drosophila tetraspilota Hardy, 1965: 483
Drosophila toxacantha Magnacca & O'Grady, 2009: 31
Drosophila uniumi Magnacca & O'Grady, 2009: 33

- Drosophila wahihuna* Magnacca & O'Grady, 2009: 34
Drosophila waikamoi Magnacca & O'Grady, 2009: 34
Drosophila wikstroemiae Magnacca & O'Grady, 2009: 36

***nudidrosophila* species group**

Hardy (1965) erected the genus *Nudidrosophila* based on the fact that, although females were not distinguishable from the genus *Drosophila*, males completely lacked reclinate, proclinate and ocellar setae. The absence of such taxonomically important structures was believed to warrant generic status. However, later Hardy (1966) stated that “*Nudidrosophila* should not be retained as a genus but probably should be sunk as a direct synonym of *Drosophila*.” Kaneshiro (1976) used characters of male genitalia, most notably the shape of the aedeagus, to show that *Nudidrosophila* was, in fact, congeneric with *Drosophila*. Interestingly, these genitalic characters also indicated that two species previously described by Hardy (1965), *D. hirtitibia* and *D. velata*, were closely related to the *nudidrosophila* species group. Recent taxonomic work has expanded the number of species in *nudidrosophila* to nearly 30 species and proposed five subgroups, *hirtitibia*, *kahania*, *nudidrosophila*, *okala*, and *velata* (Magnacca & O'Grady, 2008a).

***hirtitibia* subgroup**

- Drosophila hirtitibia* Hardy, 1965: 306
Drosophila konaensis Magnacca & O'Grady, 2008a: 406
Drosophila mawaena Magnacca & O'Grady, 2008a: 407
Drosophila papaalai Magnacca & O'Grady, 2008a: 408

***kahania* subgroup**

- Drosophila kahania* Magnacca & O'Grady, 2008a: 408
Drosophila longipalpus Magnacca & O'Grady, 2008a: 409

***nudidrosophila* subgroup**

- Drosophila aenicta* Hardy, 1966: 227
Drosophila amita Hardy, 1965: 565
Drosophila canavalia Magnacca & O'Grady, 2008a: 412
Drosophila eximia Hardy, 1965: 567
Drosophila gemmula Hardy, 1965: 569
Drosophila kualapa Magnacca & O'Grady, 2008a: 414
Drosophila lepidobregma Hardy, 1965: 571
Drosophila mahui Magnacca & O'Grady, 2008a: 416
Drosophila malele Magnacca & O'Grady, 2008a: 417
Drosophila panoanoa Magnacca & O'Grady, 2008a: 418
Drosophila poonia Magnacca & O'Grady, 2008a: 418

***okala* subgroup**

- Drosophila akoko* Magnacca & O'Grady, 2008a: 419
Drosophila kuhao Magnacca & O'Grady, 2008a: 420
Drosophila makawao Magnacca & O'Grady, 2008a: 421
Drosophila okala Magnacca & O'Grady, 2008a: 421
Drosophila panina Magnacca & O'Grady, 2008a: 422

***velata* subgroup**

- Drosophila halapepe* Magnacca & O'Grady, 2008a: 423
Drosophila kauaiensis Magnacca & O'Grady, 2008a: 424
Drosophila lauoho Magnacca & O'Grady, 2008a: 425
Drosophila milolii Magnacca & O'Grady, 2008a: 426
Drosophila pohaka Magnacca & O'Grady, 2008a: 426
Drosophila velata Hardy, 1965: 499

***rustica* species group**

This small group was proposed (O'Grady *et al.*, 2001) for three species that did not fit with the revised definition of the *haleakalae* group proposed by Hardy and colleagues (Hardy *et al.*, 2001). These taxa are seldom collected and, as a result, their placement is uncertain.

Drosophila curiosa Hardy & Kaneshiro, in O'Grady *et al.*, 2001: 257

Drosophila praesutulis Hardy, 1965: 422

Drosophila rustica Hardy, 1965: 452

Unplaced Hawaiian *Drosophila* species

Most of these species have the male genitalic characters of *Drosophila* rather than *Scaptomyza*, but lack the secondary sexual characters that define the species groups. All are rarely collected and their relationships are unknown. At least some, such as *D. achyla* and *D. confutata* are probably members of the AMC clade based on the form of the male aedeagus and female ovipositor.

Drosophila abjuncta Hardy, 1965: 130

Drosophila achyla Hardy, 1966: 195

Drosophila confutata Hardy, 1965: 221

Drosophila incompleta Hardy, 1965: 320

Drosophila joycei Hardy, 1965: 332

Drosophila mimiconfutata Hardy, 1965: 369

Drosophila molokaiensis Grimshaw, 1901: 67

Drosophila musae Hardy, 1965: 373

Drosophila nigripalpus Hardy, 1965: 389

Drosophila plumosa Grimshaw, 1901: 72

Drosophila varga Hardy, 1965: 496

Genus *Scaptomyza*

Scaptomyza is a very complex and poorly studied taxon. The placement and monophyly of this group is quite uncertain. Several morphological (Okada, 1973a; Throckmorton, 1966) and molecular studies (e.g., Remsen & DeSalle, 1998) have suggested that *Scaptomyza* is the sister taxon of the Hawaiian *Drosophila*. While the molecular studies, in particular, are poorly sampled, most of these support the monophyly of the genus *Scaptomyza*. Other studies (Hackman, 1959, 1982; Grimaldi, 1990) find that *Scaptomyza*, or part of *Scaptomyza*, is quite distinct from the Hawaiian *Drosophila* and forms a distinct lineage. Furthermore, these studies have called the monophyly of *Scaptomyza* into question (Hackman, 1982; Grimaldi, 1990). Relationships among and within most of the major lineages of *Scaptomyza* are not well understood. It is clear that further molecular and morphological studies need to be done to resolve these issues.

Twenty-one subgenera have been proposed within *Scaptomyza*, including several endemic Hawaiian groups formerly considered to be genera (*Celidosoma*, *Grimshawomyia*, *Titanochaeta*). These are all what Throckmorton (1966) referred to as "scaptoids." Ten of these groups, accounting for over 150 described species, are either completely endemic to the Hawaiian Archipelago (8) or contain species which are endemic to this island chain (*Bunostoma*, *Rosenwaldia*). The remaining 100 or so described species of *Scaptomyza* are placed in eleven groups and are found elsewhere. We discuss the biogeographic implications of this elsewhere (O'Grady & DeSalle, 2008) and are currently working to expand taxon sampling within *Scaptomyza* for a comprehensive phylogenetic analysis.

Subgenus *Alloscapteromyza*

This subgenus was erected by Hackman (1962) and includes eight species endemic to Hawai'i. Hackman considered this subgenus to be intermediate between *Elmomyza* (the Hawaiian species were placed in *Trogloscapteromyza* at the time, see below) and *Parascapteromyza*. While the branching patterns of the arista and the shape of the eye are similar in *Alloscapteromyza* and *Parascapteromyza*, the genitalia are quite distinct, the secondary clasper being reminiscent of *Elmomyza* (Hackman, 1962). Relationships among the described species of *Alloscapteromyza* are not well understood at present, and a number of species have been collected that resemble *Alloscapteromyza* but lack the broad head that defines the subgenus.

- Scapteromyza aberrans* Hardy, 1965: 578
Scapteromyza buccata Hackman, 1962: 39 [Type of subgenus]
Scapteromyza cerina Hardy, 1965: 581
Scapteromyza fuscifrons Hackman, 1962: 41
Scapteromyza longisetosa Hackman, 1959: 44
Scapteromyza mutica Hardy, 1965: 585
Scapteromyza semiflava Hardy, 1965: 587
Scapteromyza stramineifrons Hackman, 1962: 40

Subgenus *Boninoscapteromyza*

Boninoscapteromyza is a monotypic subgenus endemic to the Bonin Islands. Okada (1973a) proposed this new subgenus based on the presence of six acrostichal setulae. It is thought, based on the morphology of the male and female genitalia, to be most closely related to the subgenus *Parascapteromyza*, although this has not been studied in detail.

- Scapteromyza hexasticha* Okada, 1973: 86 [Type of subgenus]

Subgenus *Bunostoma*

Bunostoma is distributed on islands in the Pacific and on Australia (*australis*), with just over half found on islands in the Hawaiian Archipelago. This group was first described as a genus by Malloch (1932) and then sunk into the genus *Scapteromyza* by Hackman (1959). In a later study, Hackman (1982) pointed out that *Bunostoma* are “not typical *Scapteromyzas* in appearance” and were included in *Scapteromyza* because of a few “key characters,” suggesting that *Scapteromyza* may not be monophyletic. He argued that, because of genitalic characters and biogeography, *Bunostoma* probably did not originate on Hawai'i and likely represents a colonization of the Hawaiian Islands separate from the remaining endemic Hawaiian *Scapteromyza*. In contrast, Okada (1973a) proposed that *Bunostoma* forms a clade with the remaining Hawaiian *Scapteromyza*, excluding *Exalloscapteromyza*. Hackman (1982) proposed that *Bunostoma* is, instead, more closely related to the *Drosophila* subgenus *Lordiphosa*. Grimaldi's (1990) cladistic analysis of the family Drosophilidae also suggests an affiliation between *Lordiphosa* and *Scapteromyza*, although “not necessarily specifically with the subgenus *Bunostoma*.” Clearly, the placement of *Bunostoma* within the Drosophilidae has important implications for the origin and evolution of the endemic Hawaiian Drosophilidae. Additional work needs to be done in order to determine which groups, both within *Scapteromyza* and outside of this genus, are most closely related to *Bunostoma*.

- Scapteromyza anomala* Hardy, 1965: 591
Scapteromyza australis Malloch, 1923: 618

- Scaptomyza bicolor* Malloch, 1934: 297
Scaptomyza boninensis Okada, 1973a: 85
Scaptomyza bryanti Hackman, 1959: 48
Scaptomyza cnecosoma Hardy, 1965: 594
Scaptomyza confusa Hardy, 1965: 597
Scaptomyza flavella Harrison, 1959: 284
Scaptomyza flavifacies (Malloch), 1932: 219 [Type of subgenus]
Scaptomyza fuscitarsis Harrison, 1959: 287
Scaptomyza hamata Hardy, 1965: 597
Scaptomyza palmae Hardy, 1965: 598
Scaptomyza philipensis Bock, 1986: 310
Scaptomyza varifrons (Grimshaw), 1901: 71
Scaptomyza xanthopleura Hardy, 1965: 602

Subgenus *Celidosoma*

Hardy (1965) described *Celidosoma* as a genus based on a single species, *C. nigrocincta*. Based on the morphology of the male terminalia, this group is probably best synonymized with *Scaptomyza*, although future phylogenetic work will be required to verify this placement.

- Scaptomyza nigrocincta* (Hardy), 1965: 67 [Type of subgenus]

Subgenus *Dentiscaptomyza*

Dentiscaptomyza is a small group first proposed by Takada (1966). These species are poorly known and are restricted to the South American continent. Grimaldi's (1990) cladistic study suggested that *Dentiscaptomyza* was paraphyletic, with one lineage being the sister group of the *Lauxanomyza-Alloscaptomyza-Rosenwaldia-Tantalia-Trogloscaptomyza* clade and the other being a member of a more inclusive clade with *Mesoscaptomyza*, *Scaptomyza*, *Parascaptomyza*, and *Bunostoma*. Additional phylogenetic work needs to be done to assess the monophyly of *Dentiscaptomyza* as well as its relationships to other clades within *Scaptomyza*.

- Scaptomyza budnikae* Brncic, 1983: 74
Scaptomyza denticauda Malloch, 1934: 449 [Type of subgenus]
Scaptomyza intermedia (Duda), 1927: 151
Scaptomyza melancholia (Duda), 1927: 153
Scaptomyza multispinosa Malloch, 1934: 450

Subgenus *Elmomyza*

The subgenus *Elmomyza*, with over eighty described species, is the largest subgenus in *Scaptomyza*. This group was proposed by Hackman (1982) to include all endemic Hawaiian species previously placed in the subgenus *Trogloscaptomyza*. This reorganization was not based on a phylogenetic analysis, but instead on a comparison of several morphological characters present in *Rosenwaldia*, a subgenus also endemic to Hawai'i, and *Trogloscaptomyza*. Hackman (1982) argued for the establishment of *Elmomyza* because *S. brevilamellata*, a species endemic to Tristan da Cunha and the only member of the subgenus *Trogloscaptomyza* not endemic to Hawai'i, occupied an "intermediate position" between the subgenus *Rosenwaldia* and the endemic Hawaiian species placed in *Trogloscaptomyza*. The character analysis and biogeography argued for splitting the subgenus *Trogloscaptomyza* in order to maintain it as monophyletic. Most species in *Scaptomyza*, with some exceptions (i.e., *Alloscaptomyza*) have either two or four rows of acrostichal setulae. *Elmomyza*, like many members of the genus *Drosophila*, has six.

- Scaptomyza acronastes* Hardy, 1965: 644
Scaptomyza adunca Hardy, 1965: 646
Scaptomyza affincuspudata Hardy, 1965: 646
Scaptomyza anechocerca Hardy, 1965: 648
Scaptomyza apicigutulla Hardy, 1965: 649
Scaptomyza apponopusilla Hardy, 1965: 651
Scaptomyza argentifrons Hardy, 1965: 653
Scaptomyza articulata Hardy, 1965: 654
Scaptomyza basiloba Hardy, 1965: 655
Scaptomyza bilobata Hardy, 1965: 657
Scaptomyza bipars Hardy, 1965: 659
Scaptomyza brachycerca Hardy, 1965: 660
Scaptomyza camptochaites Hardy, 1965: 662
Scaptomyza concinna Hardy, 1965: 663
Scaptomyza connata Hardy, 1965: 665
Scaptomyza cornuta Hardy, 1965: 666
Scaptomyza cryptoloba Hardy, 1965: 668
Scaptomyza ctenophora Hardy, 1965: 670
Scaptomyza cuspidata Hardy, 1965: 671
Scaptomyza cyrtandrae Hardy, 1965: 673
Scaptomyza decepta Hardy, 1965: 675
Scaptomyza dentata Hardy, 1965: 676
Scaptomyza devexa Hardy, 1965: 677
Scaptomyza diaphorocerca Hardy, 1965: 679
Scaptomyza domita Hardy, 1965: 681
Scaptomyza dubautiae Hardy, 1965: 682
Scaptomyza dubia Hardy, 1965: 683
Scaptomyza eurystylata Hardy, 1965: 685
Scaptomyza evexa Hardy, 1965: 686
Scaptomyza exigua (Grimshaw), 1901: 72 [**Type of subgenus**]
Scaptomyza fastigata Hardy, 1965: 690
Scaptomyza hackmani Hardy, 1965: 691
Scaptomyza hardyi Hackman, 1959: 39
Scaptomyza inaequalis (Grimshaw), 1901: 69
Scaptomyza inermis Hardy, 1965: 695
Scaptomyza infurcula Hardy, 1965: 697
Scaptomyza innotabilis Hardy, 1965: 698
Scaptomyza intricata Hardy, 1965: 700
Scaptomyza isopedon Hardy, 1965: 701
Scaptomyza kauaiensis Hackman, 1959: 40
Scaptomyza latitergum Hardy, 1965: 704
Scaptomyza levata Hardy, 1965: 706
Scaptomyza lobifera Hardy, 1965: 707
Scaptomyza longipecten Hackman, 1959: 37
Scaptomyza longipecten griseonigra Hardy, 1965: 710
Scaptomyza mecocerca Hardy, 1965: 711
Scaptomyza mediana Hardy, 1965: 712
Scaptomyza mimula Hardy, 1965: 714
Scaptomyza monticola (Grimshaw), 1901: 69
Scaptomyza multidentata Hardy, 1965: 716
Scaptomyza obscuricornis (Grimshaw), 1901: 71
Scaptomyza obscurifrons (Grimshaw), 1901: 72
Scaptomyza ochromata Hardy, 1965: 720

- Scaptomyza ostensa* Hardy, 1965: 722
Scaptomyza pallifrons Hackman, 1959: 38
Scaptomyza paralobae Hardy, 1965: 725
Scaptomyza penicula Hardy, 1965: 727
Scaptomyza photophilia Hardy, 1965: 728
Scaptomyza phryxothrix Hardy, 1965: 730
Scaptomyza platyrhina Hardy, 1966: 238
Scaptomyza protensa Hardy, 1965: 731
Scaptomyza punctivena Hardy, 1965: 733
Scaptomyza pusilla (Grimshaw), 1901: 70
Scaptomyza quadridentata Hardy, 1965: 737
Scaptomyza recava Hardy, 1965: 738
Scaptomyza recta Hardy, 1965: 740
Scaptomyza retusa Hardy, 1965: 742
Scaptomyza robusta Hardy, 1965: 742
Scaptomyza rostrata Hardy, 1965: 745
Scaptomyza rotundiloba Hardy, 1965: 746
Scaptomyza scoliops Hardy, 1965: 748
Scaptomyza scolopichas Hardy, 1965: 750
Scaptomyza setiger Hardy, 1965: 751
Scaptomyza setosiloba Hardy, 1965: 753
Scaptomyza silvicola Hardy, 1965: 754
Scaptomyza spilota Hardy, 1965: 756
Scaptomyza tenuata Hardy, 1965: 757
Scaptomyza trivittata Hardy, 1965: 759
Scaptomyza tumidula Hardy, 1965: 761
Scaptomyza uliginosa Hardy, 1965: 763
Scaptomyza umbrosa Hardy, 1965: 765
Scaptomyza univitta Hardy, 1965: 766
Scaptomyza vagabunda Hardy, 1965: 768
Scaptomyza varia Hardy, 1965: 769
Scaptomyza villosa Hardy, 1965: 770
Scaptomyza waialealeae Hardy, 1965: 772

Subgenus *Engiscaptomyza*

Hardy (1965) placed several members of this group within the genus *Drosophila* when he revised the Hawaiian *Drosophilidae*. This placement was based primarily on the external morphology of the males which seemed to fit the concept of *Drosophila*. However, later work on internal morphology (Throckmorton, 1966), behavior (Spieth, 1966) and metaphase chromosomes (Clayton, 1966; 1968) suggested that these species were most closely related to *Scaptomyza*. When Hardy (1966) described the new species, *amplilobus*, he suggested that this group should probably be placed in the genus *Scaptomyza*. Furthermore, he stated that within the Hawaiian *Drosophilidae* a "revision of the generic concepts is needed." Kaneshiro (1969) proposed removing this group of species from the subgenus *Drosophila* and erecting a new subgenus, *Engiscaptomyza*. This subgenus was considered to be placed in an intermediate position between *Drosophila* and *Scaptomyza* because of the conflicting characters found in each group. Subsequent phylogenetic work has suggested that the subgenus *Engiscaptomyza* is more closely related to *Scaptomyza* and, in fact, may actually be highly derived within it, rather than an intermediate between *Scaptomyza* and *Drosophila* (Kambysellis *et al.*, 1995; Baker & DeSalle, 1997; O'Grady, 1998; Remsen & DeSalle, 1998; Remsen & O'Grady, 2002; O'Grady & DeSalle, 2008). It

was formally merged with *Scaptomyza*, along with *Grimshawomyia* and *Titanochaeta*, by O'Grady *et al.* (2003a)

- Scaptomyza amplilobus* (Hardy), 1966: 197
Scaptomyza crassifemur (Grimshaw), 1901: 66 [Type of subgenus]
Scaptomyza inflatus (Kaneshiro), 1969: 80
Scaptomyza lonchoptera (Hardy), 1965: 345
Scaptomyza nasalis (Grimshaw), 1901: 66
Scaptomyza reducta (Hardy), 1965: 445

Subgenus *Euscaptomyza*

This African group was erected as a genus by Séguy (1938) and contains three species. Hackman (1955) considered this group to be “distinctly different from *Scaptomyza* s. lat.” Tsacas (1972), however, argued for including *Euscaptomyza* within the genus *Scaptomyza* because there was no “characteristic worthy of maintaining *Euscaptomyza* as a genus.” In contrast, Grimaldi's (1990) cladistic study suggested that *Euscaptomyza* was not a member of the genus *Scaptomyza*. Instead, he placed this taxon within a clade which included *Engiscaptomyza* and the genus *Marquesia*. The monophyly and relationships of *Euscaptomyza* clearly need to be examined with additional characters before a definitive decision can be made concerning the placement of this taxon.

- Scaptomyza chylizosoma* (Séguy), 1938: 347 [Type of subgenus]
Scaptomyza deemingi Tsacas, 1972: 348
Scaptomyza kilembea Tsacas, 1972: 351

Subgenus *Exalloscaptomyza*

Exalloscaptomyza is a small group endemic to the Hawaiian Islands. This subgenus was proposed by Hardy (1965). The relationships within *Exalloscaptomyza* and the phylogenetic placement of this subgenus within *Scaptomyza* remain enigmatic. Hackman (1982) considered this subgenus to be “a strongly differentiated off-shoot of the *Scaptomyzoid* branch.” Okada's (1973a) phenetic tree suggests that these flies are more closely related to a clade of Neotropical subgenera than they are to the other Hawaiian *Scaptomyza*. Hackman explained that this morphological similarity to *Hemiscaptomyza* is “probably due to parallelism,” owing to the unusual ecological niche occupied by these flies. In Hawai'i, *Exalloscaptomyza* utilizes the tubular flowers of a variety of species in the genus *Ipomaea*, morning glory plants (Heed, 1968). These flies are dark in color with shortened bristles on the body and short rays on the arista (Hardy, 1966). This phenotype is similar to species which utilize similar habitats in the neotropics, namely the subgenus *Phloridosa* (genus *Drosophila*) and the subgenus *Hemiscaptomyza*.

- Scaptomyza caliginosa* Hardy, 1966: 233
Scaptomyza deludens Hardy, 1966: 234
Scaptomyza mauiensis (Grimshaw), 1901: 67 [Type of subgenus]
Scaptomyza molokaiensis Hardy, 1966: 236
Scaptomyza oahuensis Hardy, 1966: 236
Scaptomyza throckmortoni Hardy, 1966: 237

Subgenus *Grimshawomyia*

Hardy (1965) named the genus *Grimshawomyia* after P.H. Grimshaw, an early entomologist studying Hawaiian Diptera. This genus is based on a variety of autapomorphic characters,

most specifically the highly unusual male genitalia. Throckmorton (1966) and Grimaldi (1990) both suggested that *Grimshawomyia* is actually part of the *Scaptomyza* lineage. Further morphological and molecular systematic work needs to be done on this group before its relationships can be determined.

- Scaptomyza palata* (Hardy), 1965: 536
Scaptomyza perkinsi (Grimshaw), 1901: 59 [Type of subgenus]
Scaptomyza undulata (Grimshaw), 1901: 58

Subgenus *Hemiscaptomyza*

Hemiscaptomyza is a widespread subgenus, with species in the Nearctic, Neotropical, and Palearctic Regions. Hackman (1959) erected this subgenus to contain those species with spotted wings placed in the *terminalis* species group by Wheeler (1952). Okada (1973a) considered these species as part of a basal branch in the genus *Scaptomyza*, closely related to the subgenus *Scaptomyza*. Grimaldi (1990) also placed them basally within *Scaptomyza*, although in his analysis they are the sister group to most of the remaining subgenera in the genus *Scaptomyza*.

- Scaptomyza apicata* (Thomson), 1869: 597
Scaptomyza apicipuncta Malloch, 1934: 451
Scaptomyza bipunctipennis Wheeler, 1952: 206
Scaptomyza carinata Okada, 1973b: 274
Scaptomyza hennigi Hackman, 1959: 60
Scaptomyza hirsuta Wheeler, 1949: 166
Scaptomyza hsui Hackman, 1955: 88
Scaptomyza longipennis Séguy, 1938: 349
Scaptomyza maculifera Becker, 1920: 210
Scaptomyza malada Wheeler & Takada, 1966: 60
Scaptomyza okadai Hackman, 1959: 58
Scaptomyza taigensis Sidorenko & Toda, in Toda *et al.*, 1996: 460
Scaptomyza terminalis (Loew), 1863a: 32
Scaptomyza trochanterata Collin, 1953: 150
Scaptomyza unipunctum (Zetterstedt), 1847: 2533 [Type of subgenus]

Subgenus *Lauxanomyza*

This monotypic subgenus was proposed by Tsacas & Cogan (1976). The placement of *horaeoptera* is enigmatic but based on wing patterns and internal morphology Hackman (1982) suggests that both *Euscaptomyza* and *Lauxanomyza* are “possibly relicts of an old branch of *Scaptomyza*.”

- Scaptomyza horaeoptera* Tsacas & Cogan, 1976: 91 [Type of subgenus]

Subgenus *Macrosaptomyza*

The two species in this subgenus are endemic to the island of Tristan da Cunha. Frey (1954) described two species in this subgenus, *S. helvola* and *S. altissima*, as being in the genus *Parascaptomyza*. The latter species has since been determined to be a synonym of *S. remota* (Walker) (Vilela & Bächli, 1991). Okada (1973a) considered them to be sister taxa in his phenetic study. Grimaldi (1990), however, suggested that *Macrosaptomyza* was the sister taxon of *Scaptomyza parva*, an unplaced Hawaiian species. These taxa were collectively the sister group of a clade including *Bunostoma*, *Parascaptomyza*, and *Scaptomyza*.

Scaptomyza helvola (Frey), 1954: 30

Scaptomyza remota (Walker) 1849: 1111 [Type of subgenus]

Subgenus *Mesoscaptomyza*

Mesoscaptomyza is a relatively large subgenus distributed almost exclusively in the Neotropical Region. Okada (1973a) was unable to determine the sister group of this subgenus. Instead, he placed *Mesoscaptomyza* within a large clade consisting of the majority of groups within *Scaptomyza*. Grimaldi (1990) placed this taxon as a relatively basal member of the genus *Scaptomyza*.

Scaptomyza bogotae Wheeler & Takada, 1966: 64

Scaptomyza coquilletti Wheeler & Takada, 1966: 64

Scaptomyza dankoi Wheeler & Takada, 1966: 66

Scaptomyza fuscinervis Malloch, 1924: 11

Scaptomyza nigricosta Wheeler & Takada, 1966: 68

Scaptomyza nigripalpis Malloch, 1924: 10

Scaptomyza paravittata Wheeler, 1952: 200

Scaptomyza personata Wheeler & Takada, 1966: 68

Scaptomyza pleurolineata Wheeler & Takada, 1966: 70

Scaptomyza pseudovittata Brncic, 1955: 246

Scaptomyza salvadorae Wheeler & Takada, 1966: 70

Scaptomyza samurai Wheeler & Takada, 1966: 71

Scaptomyza setosa Wheeler & Takada, 1966: 72

Scaptomyza striaticeps Wheeler & Takada, 1966: 72

Scaptomyza subvittata Hackman, 1959: 50

Scaptomyza vittata (Coquillett), in Johnson & Coquillett, 1895: 318

Scaptomyza wheeleri Hackman, 1959: 49 [Type of subgenus]

Subgenus *Metascaptomyza*

Metascaptomyza is a small African subgenus containing only three described species. Okada (1973a) considered this group to be closely related to the subgenera *Scaptomyza* and *Parascaptomyza*.

Scaptomyza cochleata Burla, 1957: 45 [Type of subgenus]

Scaptomyza dorsalis Séguy, 1938: 348

Scaptomyza pygaea Tsacas, 1990: 147

Subgenus *Parascaptomyza*

Parascaptomyza is a relatively large, widespread group with species found on most of the world's major land masses. When Duda (1924) erected this group he considered *Parascaptomyza* (as well as *Scaptomyza*) a subgenus of *Drosophila*. Frey (1954) described two *Parascaptomyza* species and placed them in different subgenera, which indicates some of the confusion concerning the placement and relationships of *Parascaptomyza* species. Phenetic analysis suggests that *Parascaptomyza* is the sister taxon of *Macrosaptomyza* and is nested in a clade of species from Africa and Tristan da Cunha. Grimaldi (1990), however, placed this group as the sister to the subgenus *Scaptomyza*. The sister group relationships of *Parascaptomyza* remain to be determined.

Scaptomyza adusta (Loew), 1862: 231

Scaptomyza angustipennis (Frey), 1954: 26

- Scaptomyza clavifera* Wheeler & Takada, 1966: 74
Scaptomyza elmoi Takada, 1970: 144
Scaptomyza exilis McEvey, 1990: 59
Scaptomyza freyi Hackman, 1959: 43
Scaptomyza frustulifera (Frey), 1954: 31
Scaptomyza himalayana Takada, 1970: 146
Scaptomyza horrida (Frey), 1954: 22
Scaptomyza impunctata (Frey), 1945: 70
Scaptomyza incerta (Frey), 1954: 25
Scaptomyza latifrons Malloch, 1932: 221
Scaptomyza macroptera Wheeler & Takada, 1966: 75
Scaptomyza mumfordi Malloch, 1933: 22
Scaptomyza oxyphallus Tsacas 1990: 148
Scaptomyza pallida (Zetterstedt), 1847: 2571 [Type of subgenus]
Scaptomyza paradusta Wheeler, 1952: 198
Scaptomyza pectinifera (Frey), 1954: 24
Scaptomyza picifemorata Hackman, 1959: 45
Scaptomyza quadriseriata Malloch, 1934: 194
Scaptomyza santacruzii Val, in Carson *et al.* 1983: 243
Scaptomyza spinipalpis Séguy, 1934: 11
Scaptomyza substrigata de Meijere, 1914: 268
Scaptomyza taiwanica Lin & Ting, 1971: 22

Subgenus *Rosenwaldia*

With the exception of *S. kaavae* from the Marquesas, all members of this small subgenus are endemic to the Hawaiian Archipelago. It was erected as a genus by Malloch (1934) and subsequently reduced to a subgenus of *Scaptomyza* by Hackman (1962). Both phenetic (Okada, 1973a) and cladistic (Grimaldi, 1990) studies suggest that this subgenus is closely related to *Alloscaptomyza* and *Elmomyza*, indicating that at least some of the endemic Hawaiian subgenera form a clade.

- Scaptomyza abrupta* Hackman, 1959: 37
Scaptomyza aloha Hackman, 1959: 35
Scaptomyza finitima Hardy, 1965: 612
Scaptomyza kaavae (Malloch), 1934: 195 [Type of subgenus]
Scaptomyza mediopallens Hackman, 1959: 35
Scaptomyza mitchelli Hackman, 1959: 36
Scaptomyza striatifrons Hackman, 1959: 36

Subgenus *Scaptomyza*

The placement and taxonomic rank of *Scaptomyza* has been a contentious point in drosophilid taxonomy. Duda (1934) considered this group, along with *Parascaptomyza*, a subgenus of *Drosophila*. Wheeler (1981), however, considered *Scaptomyza* a genus and proposed a series of species groups within this taxon. The current taxonomy recognizes the genus *Scaptomyza* and a series of subgenera within the concept of this larger taxon. Okada (1973a) suggested that the subgenus *Scaptomyza* is the sister group of the subgenus *Hemiscaptomyza*. A much different result was proposed by Grimaldi (1990). His analyses indicate that *Scaptomyza* is paraphyletic, with one lineage being closely related to the subgenus *Parascaptomyza* and another that is the sister group of most of the remaining species in the genus *Scaptomyza*.

- Scaptomyza acuta* Nishiharu, 1979: 41
Scaptomyza amplialata Takada, Beppu, & Toda, 1979: 115
Scaptomyza andiana Wheeler & Takada, 1966: 43
Scaptomyza atahulapa Hackman, 1959: 59
Scaptomyza atlantica Hackman, 1955: 89
Scaptomyza baechlii Sidorenko, 1993: 462
Scaptomyza choi Kang, Lee, & Bahng, 1965: 51
Scaptomyza clavata Okada, 1973c: 435
Scaptomyza consimilis Hackman, 1955: 82
Scaptomyza flava (Fallén), 1823: 7
Scaptomyza flaviventris Hackman, 1959: 63
Scaptomyza grahmi Hackman, 1959: 64
Scaptomyza graminum (Fallén), 1823: 8 [**Type of subgenus**]
Scaptomyza griseola (Zetterstedt), 1847: 2562
Scaptomyza heedi Wheeler & Takada, 1966: 46
Scaptomyza mateolata McEvey, 1990: 53
Scaptomyza melanissima Okada, 1966: 62
Scaptomyza merina McEvey, 1990: 56
Scaptomyza mimitantalia Tsacas & Cogan, 1976: 89
Scaptomyza montana Wheeler, 1949: 166
Scaptomyza neoandina Wheeler & Takada, 1966: 48
Scaptomyza nigrita Wheeler, 1952: 205
Scaptomyza nigrocella Wheeler, 1949: 167
Scaptomyza noei Brncic, 1955: 245
Scaptomyza parandina Wheeler & Takada, 1966: 50
Scaptomyza parasplendens Okada, 1966: 59
Scaptomyza polygonia Okada, 1956: 74
Scaptomyza quadrangulata Singh & Dash, 1993: 138
Scaptomyza santahelenica Tsacas & Cogan, 1976: 86
Scaptomyza sichuanica Sidorenko, 1995: 2
Scaptomyza silvata Okada, 1966: 63
Scaptomyza sinica Lin & Ting, 1971: 24
Scaptomyza sub&iana Wheeler & Takada, 1966: 50
Scaptomyza subsplendens (Duda), 1934: 70
Scaptomyza teinoptera Hackman, 1955: 82
Scaptomyza tistai Kumar & Gupta, 1992: 48
Scaptomyza yakutica Sidorenko & Toda *in* Toda *et al.*, 1996: 462

Subgenus *Tantalia*

Tantalia is an endemic Hawaiian group characterized by the presence of distinctive white stripe on the mesonotum. This group was named after Mt. Tantalus, O'ahu by Malloch (1938) and was initially given generic rank. Hackman (1959) sank it into *Scaptomyza* based on the similarity of these species to the subgenus *Elmomyza*. Okada (1973a) placed *Tantalia* in a clade of endemic Hawaiian *Scaptomyza*. Grimaldi (1990) placed this species close to *Elmomyza* in a clade of Hawaiian subgenera.

- Scaptomyza albovittata* (Malloch), 1938: 53 [**Type of subgenus**]
Scaptomyza brunnimaculata Hardy, 1965: 620
Scaptomyza flavida Hardy, 1965: 622
Scaptomyza gilvivilia Hardy, 1965: 624
Scaptomyza nigrosignata Hardy, 1965: 625
Scaptomyza varipicta Hardy, 1965: 627

Subgenus *Titanochaeta*

All species in *Titanochaeta* are larval predators on spider eggs. This bizarre ecology, coupled with some unique morphological changes, led Knab (1914) to propose this group as an endemic Hawaiian genus. Subsequent work (Bonacum, 2001) suggests that this group is actually derived from within the genus *Scaptomyza* and should be considered as a clade within this larger group (O'Grady *et al.*, 2003a).

- Scaptomyza bryani* (Wirth), 1952: 417
Scaptomyza canuta (Hardy), 1965: 200
Scaptomyza chauliodon (Hardy), 1965: 778
Scaptomyza contestata (Hardy), 1966: 240
Scaptomyza glauca (Hardy), 1965: 782
Scaptomyza ichneumon (Knab), 1914: 168 [Type of subgenus]
Scaptomyza neoevexa O'Grady, Bonacum, DeSalle, & Val, 2003: 12
Scaptomyza neokauaiensis O'Grady, Bonacum, DeSalle, & Val, 2003: 12
Scaptomyza neosilvicola O'Grady, Bonacum, DeSalle, & Val, 2003: 12
Scaptomyza setosiscutellum (Hardy), 1965: 788
Scaptomyza swezeyi (Wirth), 1952: 415
Scaptomyza vittiger (Hardy), 1965: 793

Subgenus *Trogloscaptomyza*

Trogloscaptomyza previously contained a number of Hawaiian species (Hardy, 1965) and the type species, *S. brevilamellata*, from Tristan da Cunha. Frey (1954) initially placed this group as a subgenus of the genus *Parascaptomyza*. When *Parascaptomyza* was merged with *Tristanomyza* and *Scaptomyza* to form the genus *Scaptomyza*, Hackman (1959) proposed keeping the subgeneric classifications of Frey (1954) and maintained *Trogloscaptomyza* as a subgenus of *Scaptomyza*. Later, Hackman (1982) removed the Hawaiian species from this group to the subgenus *Elmomyza* in order to preserve the monophyly of *Trogloscaptomyza*. This subgenus now contains a single species from Tristan da Cunha.

- Scaptomyza brevilamellata* (Frey), 1954: 21 [Type of subgenus]

Unplaced *Scaptomyza* species

Magnacca and O'Grady (2008) moved several of the species below from unplaced in Hawaiian *Drosophila* clade to unplaced in the *Scaptomyza* lineage based on the morphology of the male genitalia.

- Scaptomyza biseta* Malloch, 1932: 222
Scaptomyza gracilis (Walker), 1853: 239
Scaptomyza improcera (Hardy), 1965: 317
Scaptomyza magnipalpa (Hardy), 1965: 352
Scaptomyza parva (Grimshaw), 1901: 65
Scaptomyza proluxa (Hardy), 1965: 430
Scaptomyza ruficornis Meigen, 1838: 375
Scaptomyza spiculipennis Takada & Momma, 1975: 33
Scaptomyza taractica (Hardy), 1965: 479
Scaptomyza totonigra (Hardy), 1965: 486
Scaptomyza vinnula (Hardy), 1965: 510

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Table 1. Phylogenetic classification of the Hawaiian *Drosophila* clade

Clade	Species Group	Species Subgroup	No. Spp.	
AMC	antopocerus	adunca	2	
		diamphidiopoda	6	
		villosa	7	
	modified tarsus	bristle tarsus	18	
		ciliated tarsus	21	
		split tarsus	24	
		spoon tarsus	12	
		unplaced	1	
		adiastola	12	
	picture wing	adiastola	truncipenna	4
			—	2
		anomalipes grimshawi	conspicua	9
crucigera			8	
distingueda			3	
hawaiiensis			14	
orphanopeza			17	
pilimana			5	
punalua			8	
vesciseta			8	
unplaced			5	
planitibia			cyrtoloma	7
	neopicta	3		
	planitibia	5		
	picticornis	2		
n/a	primaeva ateledrosophila	—	2	
		—	3	
n/a	haleakalae	anthrax	10	
		cilifemorata	15	
		haleakalae	9	
		luteola	4	
		polita	10	
		scitula	5	
		unplaced	1	

Table 1. (continued) ...

Clade	Species Group	Species Subgroup	No. Spp.		
n/a	modified mouthpart	ceratostoma	4		
		dissita	14		
		freycinetiae	9		
		fuscoamoeba	8		
		hirtitarsus	2		
		mimica	20		
		mitchelli	5		
		nanella	4		
		quadrisetae	4		
		scolostoma	3		
		semifuscata	14		
		setiger	4		
		unplaced	15		
		n/a	nudidrosophila	hirtitibia	4
				kahania	2
nudidrosophila	11				
okala	5				
velata	6				
n/a	rustica	–	3		
unplaced	–	–	11		

Table 2. Phylogenetic classification and geographic distribution of the genus *Scaptomyza*

Genus	Subgenus	No. Spp.	Distribution
<i>Scaptomyza</i>	<i>Alloscaptomyza</i>	8	Hawai'i
	<i>Boninoscaptomyza</i>	1	Ogasarawa Is
	<i>Bunostoma</i>	15	Hawai'i, Australia, Ogasarawa Is, Marquesas
	<i>Celidosoma</i>	1	Hawai'i
	<i>Dentiscaptomyza</i>	5	Neotropics
	<i>Elmomyza</i>	86	Hawai'i
	<i>Engiscaptomyza</i>	6	Hawai'i
	<i>Euscaptomyza</i>	3	Africa
	<i>Exalloscaptomyza</i>	6	Hawai'i
	<i>Grimshawomyia</i>	3	Hawai'i
	<i>Hemiscaptomyza</i>	15	Nearctic, Neotropical, Palearctic
	<i>Lauxanomyza</i>	1	St. Helena I
	<i>Macrosaptomyza</i>	2	Tristan da Cunha
	<i>Mesoscaptomyza</i>	17	Neotropical
	<i>Metascaptomyza</i>	3	Africa
	<i>Parascaptomyza</i>	24	Tristan da Cunha, Hawai'i, Azores, Marquesas, Neotropical, Nearctic, Taiwan, Cape Verde Is
	<i>Rosenwaldia</i>	7	Hawai'i, Marquesas
	<i>Scaptomyza</i>	37	Palearctic, Neotropical, Azores, Canary Is
	<i>Tantalia</i>	6	Hawai'i
<i>Titanochaeta</i>	12	Hawai'i	
<i>Trogloscaptomyza</i>	1	Tristan da Cunha	
unplaced	11		