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

P.M. O’Grady, K.N. Magnacca & R.T. LaPoint (University of California, Berkeley, Department of Environmental Science, Policy & Management, 117 Hilgard Hall, Berkeley, California 94720, USA; email: ogrady@nature.berkeley.edu)

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 (Kane-shiro, 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 Ateleedrosophila. 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, atelederosophila, 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 setae (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 anomipes, 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 (Kambysellis 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 brunneneisetae* 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 quasieparsa* Hardy, 1965: 444
- *Drosophila reducita* Hardy, 1965: 446
- *Drosophila sechus* Hardy, 1965: 458
- *Drosophila spicula* Hardy, 1965: 472
- *Drosophila torula* Hardy, 1965: 484
- *Drosophila trichaeoteta* Hardy, 1965: 489
- *Drosophila unicula* Hardy, 1965: 495

**ciliated tarsus subgroup:**
- *Drosophila brunnenefrons* Hardy, 1965: 191
- *Drosophila caccabata* Hardy, 1965: 196
- *Drosophila carnea* Hardy, 1965: 204
- *Drosophila clavitiibia* Hardy, 1965: 213
- *Drosophila diffusa* Hardy, 1965: 242
- *Drosophila dorsociliata* Hardy, 1965: 256
- *Drosophila dumalis* Hardy, 1965: 260
- *Drosophila fisticula* Hardy, 1965: 292
- *Drosophila gilvilateralis* Hardy, 1965: 294
- *Drosophila imparsietae* Hardy, 1965: 315
- *Drosophila kraussi* Hardy, 1965: 336
- *Drosophila latigena* Hardy, 1965: 342
- *Drosophila mediais* Hardy, 1966: 244
- *Drosophila melanopeds* Hardy, 1965: 362
- *Drosophila nigrigaris* Hardy, 1965: 390
- *Drosophila orestes* Hardy, 1965: 400
- *Drosophila paucula* Hardy, 1965: 405
- *Drosophila setipalps* 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 chaetoccephala* Hardy & Kaneshiro, 1979: 76
Drosophila clavata Hardy, 1965: 211
Drosophila crenopleura 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 furcatarsus 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 systenopeza 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 dasycenemia Hardy, 1965: 236
Drosophila fastigata Hardy, 1965: 271
Drosophila incognita Hardy, 1965: 319
Drosophila kikalaeele 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 adiastola* Hardy, 1965: 134
*Drosophila cilifera* Hardy & Kaneshiro, 1968: 237
*Drosophila clavisetae* (Hardy), 1966: 219
*Drosophila neoclavisetae* Perreira & Kaneshiro, 1990: 81
*Drosophila neogrimshawi* 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 paenehamifera* 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 *punala* 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

**orphnopeza 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 nulli Perreira & Kaneshiro, 1990: 79
Drosophila murphyi Hardy & Kaneshiro, 1969: 46
Drosophila obtatai Hardy & Kaneshiro, 1972: 156
Drosophila ochracea Grimshaw, 1901: 61
Drosophila orphnopeza 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 punahua 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 ores 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 melanoccephala (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 curtitaris 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 brunnecirus 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 quinqueramus 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 meiocnemia* 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 (*nomendubium*)

**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 wikan* Magnacca & O’Grady, 2009: 42

**dissita subgroup**

*Drosophila amydrospilota* Hardy, 1965: 143  
*Drosophila artigena* Hardy, 1965: 161  
*Drosophila beardseyi* Hardy, 1965: 174  
*Drosophila brevissima* Hardy, 1965: 186
Drosophilacurvitibia Hardy, 1965: 234
Drosophiladissita Hardy, 1965: 248
Drosophiladracenaehardy, 1965: 258
Drosophilaeumecothrix Hardy, 1965: 264
Drosophilalaciniosa Hardy, 1965: 337
Drosophilalarifuga Hardy, 1965: 340
Drosophila polliciforma Hardy, 1965: 419
Drosophilapychnochaetae Hardy, 1965: 438
Drosophilataeniata Hardy, 1965: 476
Drosophilavelutifrons Hardy, 1965: 501

freycinetiae subgroup
“Drosophila anapuu Magnacca & O’Grady, 2009: 46
Drosophilasketostoma Hardy, 1965: 163
Drosophilacomatifemora Hardy, 1965: 218
Drosophiladentilabia Magnacca & O’Grady, 2009: 51
Drosophilafreycinetiae Hardy, 1965: 277
Drosophilahirticoxa Hardy, 1965: 302
Drosophilakualii Magnacca & O’Grady, 2009: 55
Drosophilanalomanono Magnacca & O’Grady, 2009: 57
Drosophilaprominens Hardy, 1965: 432

fuscoamoeba subgroup
Drosophilagitona Hardy, 1965: 138
Drosophilaaquila Hardy, 1965: 158
Drosophilaraotricha Hardy, 1965: 159
Drosophilabrevicilia Hardy, 1965: 185
Drosophilaclydonia Hardy, 1965: 214
Drosophilafurva Hardy, 1965: 284
Drosophilafuscoamoebabryan, 1934: 438
Drosophilamegasticta Hardy, 1965: 358

hirtitarsus subgroup
DrosophilagoureauhiHardy & Kaneshiro, 1972: 161
Drosophilahirtitarsushardy, 1965: 304

mimica subgroup
Drosophilacaanthos Kam & Perreira, in O’Grady et al., 2003: 32
Drosophilaantecedens Kam & Perreira, in O’Grady et al., 2003: 35
Drosophilabadia Hardy, 1965: 166
Drosophilachaeopeza Hardy, 1965: 206
Drosophila chimerakam & Perreira, in O’Grady et al., 2003: 22
Drosophilaconjectura Hardy, 1965: 223
Drosophilaechinostomakam & Perreira, in O’Grady et al., 2003: 33
Drosophilaflavibasis Hardy, 1965: 273
Drosophilagagnekam & Perreira, in O’Grady et al., 2003: 35
Drosophilainebria Kam & Perreira, in O’Grady et al., 2003: 25
Drosophilainsuscata Grimson, 1901: 63
Drosophilainvoltahardy, 1965: 330
Drosophilakambysellisi Hardy & Kaneshiro, 1969: 44
Drosophilakauwai Bryan, 1934: 439
Drosophilalobatopalpus kam & Perreira, in O’Grady et al., 2003: 36
Drosophilamaemae Kam & Perreira, in O’Grady et al., 2003: 31
Drosophilamimica Hardy, 1965: 365
Drosophilareschae Hardy & Kaneshiro, 1975b: 63
Drosophilasoonaetakada & Yoon, 1989: 117
Drosophilaxenophagakam & Perreira, in O’Grady et al., 2003: 26
mitchelli subgroup
Drosophila biseriata Hardy, 1965: 179
Drosophila furvifacies Hardy, 1965: 285
Drosophila hystricosa Hardy & Kaneshiro, 1969: 42
Drosophila mitchelli Hardy, 1965: 370
Drosophila nigrocirrus Hardy, 1965: 392

nanella subgroup
Drosophila albifacies Hardy, 1965: 141
Drosophila curticilia Hardy, 1965: 232
Drosophila dolomata Hardy, 1965: 253
Drosophila nanella Hardy, 1965: 378

quadrisetae subgroup
Drosophila ischnotrix Hardy, 1965: 331
Drosophila quadrisetae 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 oalae 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 leolua Magnacca & O’Grady, 2009: 26
Drosophila omnivora Magnacca & O’Grady, 2009: 27
Drosophila tetrasiplota Hardy, 1965: 483
Drosophila toxacantha Magnacca & O’Grady, 2009: 31
Drosophila umiumi” Magnacca & O’Grady, 2009: 33
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, procline 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 praesutilis* 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 aedegus 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 Alloscaptomyza**

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 *Trogloscaptomyza* at the time, see below) and *Parascaptomyza*. While the branching patterns of the arista and the shape of the eye are similar in *Alloscaptomyza* and *Parascaptomyza*, the genitalia are quite distinct, the secondary clasper being reminiscent of *Elmomyza* (Hackman, 1962). Relationships among the described species of *Alloscaptomyza* are not well understood at present, and a number of species have been collected that resemble *Alloscaptomyza* but lack the broad head that defines the subgenus.

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

**Subgenus Boninoscaptomyza**

*Boninoscaptomyza* 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 *Parascaptomyza*, although this has not been studied in detail.

*Scaptomyza 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 *Scaptomyza* by Hackman (1959). In a later study, Hackman (1982) pointed out that *Bunostoma* are “not typical Scaptomyzas in appearance” and were included in *Scaptomyza* because of a few “key characters,” suggesting that *Scaptomyza* 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 *Scaptomyza*. In contrast, Okada (1973a) proposed that *Bunostoma* forms a clade with the remaining Hawaiian *Scaptomyza*, excluding *Exalloscaptomyza*. 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 *Scaptomyza*, 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 *Scaptomyza* and outside of this genus, are most closely related to *Bunostoma*.

*Scaptomyza anomalala* Hardy, 1965: 591
*Scaptomyza australis* Malloch, 1923: 618
Scaptomyza bicolor Malloch, 1934: 297
Scaptomyza boninensis Okada, 1973a: 85
Scaptomyza bryanti Hackman, 1959: 48
Scaptomyza cneosoma 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 (Grimalshaw), 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 Lauanomyza-Alloscaptomyza-Rosenwaldia-Tantalia-Troglascaptomyza 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 it’s 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 melanochlia (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. brevillamellata, 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 aduncu Hardy, 1965: 646
Scaptomyza affinicuspidata Hardy, 1965: 646
Scaptomyza anechoerca Hardy, 1965: 648
Scaptomyza apiciguttula 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 etenophora 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 euryystylata 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 meccocerca Hardy, 1965: 711
Scaptomyza mediana Hardy, 1965: 712
Scaptomyza mimula Hardy, 1965: 714
Scaptomyza monticola (Grimshaw), 1901: 69
Scaptomyza multitenda 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 scoloplichas 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 lonicoptera* (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 *Engismaptomyza* 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 *Ipomoea*, 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 Palaearctic 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 relics of an old branch of *Scaptomyza*.”

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

**Subgenus Macroscaptomyza**

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. remonta* (Walker) (Vilela & Bächli, 1991). Okada (1973a) considered them to be sister taxa in his phenetic study. Grimaldi (1990), however, suggested that *Macroscaptomyza* 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*. 
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*.

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*.

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 *Macroscaptomyza* 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 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 munfordi Malloch, 1933: 22
Scaptomyza oxyphallus Tsacas 1990: 148
Scaptomyza pallida (Zetterstedt), 1847: 2571 [Type of subgenus]
Scaptomyza paradusta Wheeler, 1952: 198
Scaptomyza pectinisfera (Frey), 1954: 24
Scaptomyza picifemorata Hackman, 1959: 45
Scaptomyza quadriserata Malloch, 1934: 194
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 Hemi-scaptomyza. 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, 1973a: 435
Scaptomyza consimilis Hackman, 1955: 82
Scaptomyza flavia (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 nigrata 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 quadruangulata 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 subkiana 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.
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 sweyzei* (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 proliza* (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
Literature Cited


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

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