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Cover illustration: *Helicorthomorpha holstii* (Pocock) the flat-backed milliped, female, on O‘ahu. New state record. See p. 45 for more details. Photo: Frank G. Howarth.

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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 (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 poorly 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 unicula* Hardy, 1965: 495

***ciliated tarsus* subgroup**:

- *Drosophila brunneifrons* Hardy, 1965: 191
- *Drosophila caccabata* Hardy, 1965: 196
- *Drosophila carnosa* 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 nigritarsus* 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 cnecopleura 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 dasycnemia 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 choromosomal 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*, *hawaiiensis*, *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

***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 mulli 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 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 beardsleyi Hardy, 1965: 174
Drosophila brevissima Hardy, 1965: 186

Drosophila curvitibia 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 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 olaae 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 lelolua 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 umiumi” 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 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 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 *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 anomala Hardy, 1965: 591
Scaptomyza 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 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 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 affinicuspidata 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 multidenta 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 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 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 relicts 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. remota* (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*.

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 *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 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 santacruzi 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 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 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 gilvivirilia 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 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 prolixa (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
picture wing	adiastola	adiastola	12
		truncipenna	4
	anomalipes	–	2
	grimshawi	conspicua	9
		crucigera	8
		distingueda	3
		hawaiiensis	14
		orphnopeza	17
		pilimana	5
		punalua	8
		vesciseta	8
		unplaced	5
	planitibia	cyrtoloma	7
		neopicta	3
		planitibia	5
		picticornis	2
	primaeva	–	2
n/a	ateledrosophila	–	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**
Scaptomyza	*Alloscaptomyza*	8	Hawai‘i
	Boninoscaptomyza	1	Ogasarawa Is
	Bunostoma	15	Hawai‘i, Australia, Ogasarawa Is, Marquesas
	Celidosoma	1	Hawai‘i
	Dentiscaptomyza	5	Neotropics
	Elmomyza	86	Hawai‘i
	Engiscaptomyza	6	Hawai‘i
	Euscaptomyza	3	Africa
	Exalloscaptomyza	6	Hawai‘i
	Grimshawomyia	3	Hawai‘i
	Hemiscaptomyza	15	Nearctic, Neotropical, Palearctic
	Lauxanomyza	1	St. Helena I
	Macroscaptomyza	2	Tristan da Cunha
	Mesoscaptomyza	17	Neotropical
	Metascaptomyza	3	Africa
	Parascaptomyza	24	Tristan da Cunha, Hawai‘i, Azores, Marquesas, Neotropical, Nearctic, Taiwan, Cape Verde Is
	Rosenwaldia	7	Hawai‘i, Marquesas
	Scaptomyza	37	Palearctic, Neotropical, Azores, Canary Is Palearctic, Nearctic, St Helena I, Taiwan
	Tantalia	6	Hawai‘i
	Titanochaeta	12	Hawai‘i
	Trogloscaptomyza	1	Tristan da Cunha
	unplaced	11	

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Morphological and molecular evidence support the synonymy of *Emperoptera* Grimshaw with *Campsicnemus* Haliday (Diptera: Dolichopodidae)[1]

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Campsicnemus Haliday is a predominantly Holarctic and Polynesian genus of long-legged flies that is highly speciose in the Hawaiian Islands (over 160 species currently known from that island group; Evenhuis, 2007). *Emperoptera* Grimshaw was originally described (Grimshaw *in* Grimshaw & Speiser, 1902) for a single flightless species from O'ahu, *E. mirabilis*. Subsequently discovered new flightless species from the Hawaiian Islands were described in *Emperoptera* (Zimmerman, 1938; Adachi, 1954). However, in their revision of the Hawaiian *Campsicnemus*, Hardy & Kohn (1964) sunk *Emperoptera* under *Campsicnemus* without discussion, and an additional flightless species (*hawaiiensis*) was described in *Campsicnemus* by Hardy & Delfinado (1974). Evenhuis (1997) examined all available material of flightless Hawaiian dolichopodids proposed resurrecting *Emperoptera* based on characters of the wing and female ovipositor, described three new species in *Emperoptera* (*hardyi*, *montgomeryi*, *zimmermani*), placed two previously described *Campsicnemus* species in *Emperoptera* (*hawaiiensis*, *mirabilis*), and retained three other previously described species in *Campsicnemus (aeptus* Hardy & Kohn, *bryophilus* Adachi*, haleakalaae* Zimmerman*)*.

Recent molecular study of species of Hawaiian *Campsicnemus* and related genera as part of a larger NSF-funded study of biodiverse genera of Hawaiian Diptera shows *Emperoptera* to be nested well within other species of *Campsicnemus* (Fig. 1). This led to re-examination of material of *Emperoptera* and comparing to *Campsicnemus*, which resulted in the finding that the length of the spines of the ovipositor in *Emperoptera* (previously thought to be a good character in separating the two genera) are well within the range of lengths of these spines in *Campsicnemus*. We therefore propose reducing *Emperoptera* once again as a junior synonym of *Campsicnemus*.

Materials and Methods

Specimens from the following collections and institutions have been examined or are deposited there as vouchers in the course of this study: Natural History Museum, London (BMNH), Bishop Museum, Honolulu (BPBM), Canadian National Insect Collection (CNC), Hawaii State Department of Agriculture (HDOA), Royal Museum of Scotland, Edinburgh (RMSE), Essig Museum, University of California, Berkeley (UCB), University of Hawai'i Insect Museum, Honolulu (UHM), National Museum of Natural History, Washington, DC (USNM). Data on taxa used in this analysis are listed in the Appendix.

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[1] Contribution No. 2010-008 to the Hawaii Biological Survey.

Morphological terminology follows recent taxonomic studies in Evenhuis (1997, 2007, 2008, 2009). Molecular analyses were performed using five mitochondrial (12S, 16S, COI, COII, NADH2) and two nuclear (CAD, Ef1α) loci. Protein coding sequences were aligned using conceptual amino acid translations and were trivial to perform by eye. Ribosomal loci were aligned in Clustal W (Higgins *et al*. 1994) and then adjusted manually based on stem and loop regions. All noncoding regions (439 base pairs) were excluded, yielding a final matrix of 5,419 characters.

Analyses of individual and combined data matrices, using both maximum parsimony and Bayesian methods, were performed and were largely congruent with one another (data not shown). Here we present the results of parsimony analyses for the combined matrices containing all 63 taxa that have at least four of the seven loci sequenced (Fig. 1). We selected this analysis because it includes the most complete set of sequences that contain a representative of the genus *Emperoptera*. These results are comparable to analyses with fewer taxa but more complete character matrices and those with more species but more missing data (Table 1). Maximum parsimony analyses (PAUP*, ver 4.0; Swofford, 2002) were done using a heuristic algorithm with the following settings: number of replicates = 1000, addition sequence = random, branch swapping = TBR, non-coding regions = excluded. Support was assessed using 500 bootstrap replicates (Felsenstein, 1988) with the other settings as above.

Systematics

Genus ***Campsicnemus*** Haliday

Medeterus (*Camptosceles*) Haliday, 1832: 357. Suppressed by I.C.Z.N. (1958: 349) (Opinion 531).

Leptopezina Macquart, 1835: 554. Type species: *Diastata gracilis* Meigen, 1820, by monotypy. *Nomen oblitum*. [Article 23.9.2 of the I.C.Z.N. *Code* (1999) invoked by Evenhuis (2003) in treating this name as a *nomen oblitum*.]

Campsicnemus Haliday *in* Walker, 1851: 187. Type species: *Dolichopus scambus* Fallén, 1823, by validation of I.C.Z.N. (1958: 351) (Opinion 531). *Nomen protectum*. [Article 23.9.2 of the I.C.Z.N. *Code* (1999) invoked by Evenhuis (2003) in treating this name as a *nomen protectum*.]

Emperoptera Grimshaw *in* Grimshaw & Speiser, 1902: 81. Type species: *Emperoptera mirabilis* Grimshaw, 1902, by monotypy. **New synonymy**.

Camptoscelus Kertész, 1909: 306 (unjustified emendation of *Camptosceles* Haliday). Type species: *Dolichopus scambus* Fallén, 1823, automatic.

Because of the results of molecular analysis that shows *Emperoptera* to be nested well within species of Hawaiian *Campsicnemus* (see discussion below) as well as examination of the female ovipositor spines, the length of which are within the range of variation shown by other species of Hawaiian *Campsicnemus*, we return *Emperoptera* to junior synonymy under *Campsicnemus* as originally proposed by Hardy & Kohn (1964).

As a result of the new synonymy of *Emperoptera* under *Campsicnemus*, the following taxa are here transferred to *Campsicnemus*.

Campsicnemus elmoi Evenhuis, ***new replacement name***

Emperoptera hardyi Evenhuis, 1997: 5.

Campsicnemus hardyi (Evenhuis), **n. comb**. [Preoccupied by *Campsicnemus hardyi* Tenorio, 1969.

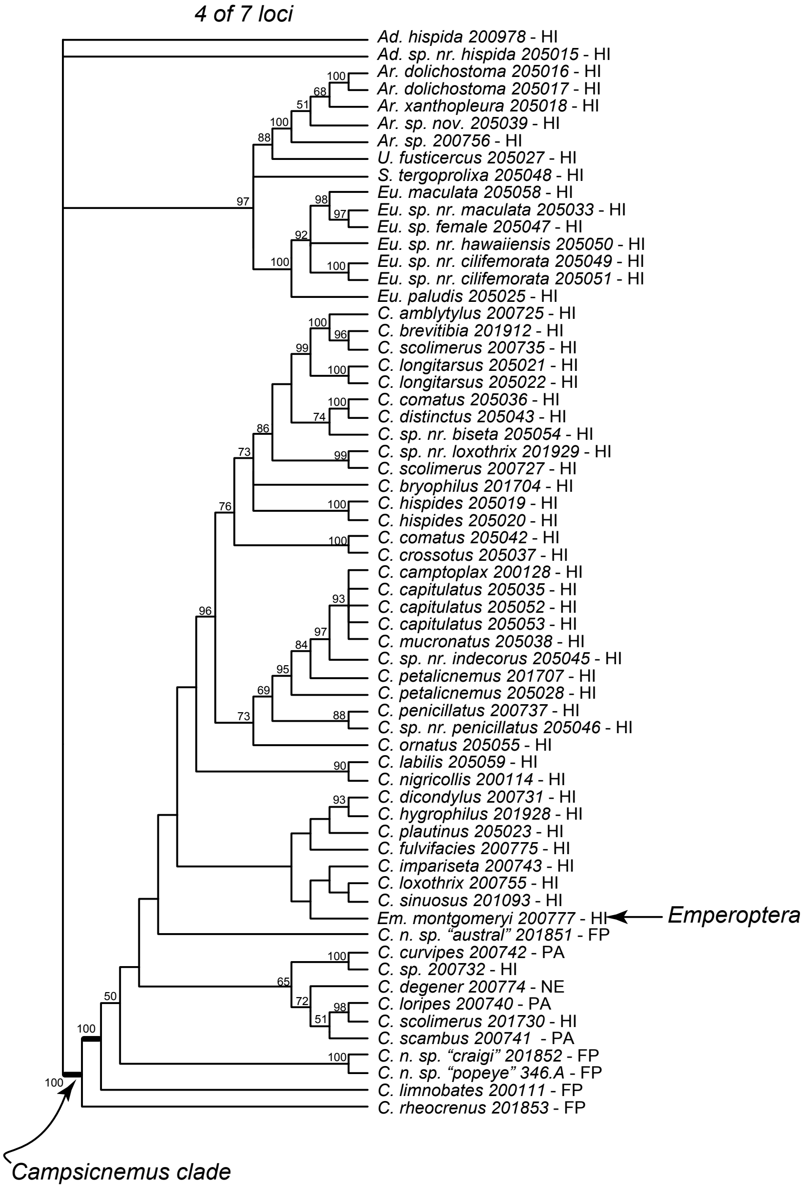

Figure 1. Phylogenetic placement of the genus *Emperoptera* relative to Hawaiian *Campsicnemus.* Geographical abbreviations: FP = French Polynesia; HI = Hawaiian Islands; NE = Nearctic; PA = Palaearctic. Taxonomic abbreviations: *Ad = Adachia; Ar = Arciellia; C = Campsicnemus; Em = Emperoptera; Eu = Eurynogaster; S = Swezeyella; U = Uropachys.*

Table 1. Results of Maximum Parsimony Analyses.

Gene Sampling	# Taxa	# PICs	# MPTs	Tree Length	*Campsicnemus* monophyletic?	*Emperoptera* present?	*Campicnemus* + *Emperoptera* clade?
all7	8	514	1	2105	Y	N	N
6of7	18	1111	1	3696	Y	N	N
5of7	42	1437	2	5404	Y	N	N
4of7	63	1537	42	6296	Y	Y	Y
3of7	79	1682	46	7618	Y	Y	Y
2of7	102	1791	13357	8780	N	Y	Y

The transfer of *Emperoptera hardyi* to *Campsicnemus* results in secondary homonymy with *Campsicnemus hardy* Tenorio. *Campsicnemus elmoi* is therefore proposed as a ***new replacement name*** and honors D. Elmo Hardy, the collector of the type specimens from Pu‘u Kukui, West Maui.

Campsicnemus montgomeryi (Evenhuis), **new combination**

Emperoptera montgomeryi Evenhuis, 1997: 11.
Campsicnemus montgomeryi (Evenhuis), **n. comb**.

This is apparently the only extant species of species formerly placed in *Emperoptera* and as such was the only material available for molecular analysis. Continued attempts to re-collect *C. hawaiiensis* in *kīpuka* along the Saddle Road of the Big Island of Hawai‘i as well as recent collecting (November 2009) on Pu‘u Kukui to recover *C. elmoi* have thus far been unsuccessful.

Campsicnemus zimmermani (Evenhuis), **new combination**

Emperoptera zimmermani Evenhuis, 1997: 14.
Campsicnemus zimmermani (Evenhuis), **n. comb**.

Molecular Analysis

Figure 1 shows the results of maximum parsimony analysis of 63 dolichopodid species, including 17 members of the endemic Hawaiian *Eurynogaster* complex, 45 *Campsicnemus* species from Hawai‘i, Europe, North America, and the Pacific, and a single representative of the genus *Emperoptera*, *E. montgomeryi*. This work is the result of an ongoing project, additional character and taxon sampling is currently underway and will expand our understanding of phylogeny within this complex group. Statistical support for many relationships within the *Eurynogaster* group and some clades of *Campsicnemus* is strong. While some basal nodes are not well supported, this analysis does strongly support the placement of *Emperoptera* within the genus *Campsicnemus* (bold lines, bootstrap proportion 100%), a placement that is unlikely to change with additional character and species sampling.

Acknowledgments

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Appendix. **Taxa used for analyses**

EURYNOGASTER COMPLEX	
Adachia hispida (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: HAWAI‘I: HAVO, Ola‘a Puu Unit, 13–14 Nov 2003, 4300', KN Magnacca; O'Grady Lab 200978
Adachia sp. nr. *hispida*	HAWAIIAN ISLANDS: KAUA‘I: Kawaikoi Stream, 3500', 18 May 2007, KN Magnacca 07-0447; O'Grady Lab 205015
Arciellia dolichostoma (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: KAUA‘I: Pu‘u O Kila Rd, 4080', 17 May 2007, KN Magnacca 07-0430; O'Grady Lab 205016
	HAWAIIAN ISLANDS: KAUA‘I: Pihea Trail, 3500', 18 May 2007, KN Magnacca 07-0449; O'Grady Lab 205017
Arciellia xanthopleura (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: KAUA‘I: Pihea Trail, 3600', 18 May 2007, KN Magnacca 07-0450; O'Grady Lab 205018
Arciellia sp. nov.	HAWAIIAN ISLANDS: MAUI: Kaupo Trail, 5000', 4 Aug 2007, KN Magnacca; O'Grady Lab 205039
Eurynogaster maculata Parent, 1940	HAWAIIAN ISLANDS: MAUI: Paliku, crater wall, 6600', 1 Aug 2007, KN Magnacca 07-0719; O'Grady Lab 205058
Eurynogaster paludis (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: KAUA‘I: Pihea Trail, 3600', 18 May 2007, KN Magnacca 07-0451; O'Grady Lab 205025
Eurynogaster sp. nr. *cilifemorata*	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0782; O'Grady Lab 205049
	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 31 Jul 2007, KN Magnacca 07-0702; O'Grady Lab 205051
Eurynogaster sp. nr. *hawaiiensis*	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0783; O'Grady Lab 205050
	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Carson Trail, 4200', 6 Aug 2007, KN Magnacca 07-0803; O'Grady Lab 205031
Eurynogaster sp. nr. *maculata*	HAWAIIAN ISLANDS: MAUI: Pu‘u Kukui Trail, 2900-3700', 8 Aug 2007, KN Magnacca 07-0825; O'Grady Lab 205033
Eurynogaster sp. female	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Kula Ppln. Rd, 4150', 31 Jul 2007, KN Magnacca 07-0705; O'Grady Lab 205047
Sweziella tergoprolixa (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0781; O'Grady Lab 205048

Uropachys fusticercus (Hardy & Kohn, 1964)	HAWAIIAN ISLANDS: MAUI: Pihea Trail, 3600', 18 May 2007, KN Magnacca 07-0452; O’Grady Lab 205027

CAMPSICNEMUS – Hawaiian

Campsicnemus amblytylus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I, HVNP, Ola‘a Forest, Pole 48 (left side of road), 6–7 Jul 2004, PM O’Grady, M. Giannullo & CD Specht, 247.8; O’Grady Lab 200725
Campsicnemus biseta Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Kaupo Trail, 5500’, 4 Aug 2007, KN Magnacca 07-0752; O’Grady Lab 205040
Campsicnemus brevitibia Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I: Saddle Road, Kipuka Mosaic, 6 Apr 2004, DJ Preston & MKK McShane; O’Grady Lab 201912
Campsicnemus bryophilus (Adachi, 1954)	HAWAIIAN ISLANDS: MOLOKA‘I, Pu‘u Kolekole, 3854', 28–30 Jul 2004, PM O’Grady & CD Specht, 283.3; O’Grady Lab 201704
Campsicnemus camptoplax Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Waikamoi Forest Preserve, Pig Hunter’s Trail, 16 Dec 2003, PM O’Grady, 241.H; O’Grady Lab 200128
Campsicnemus capitulatus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Carson Trail, 4200', 6 Aug 2007, KN Magnacca 07-0801; O’Grady Lab 205035
	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 31 Jul 2007, KN Magnacca 07-0701; O’Grady Lab 205052
	HAWAIIAN ISLANDS: MAUI: Makawao Forest Reserve, 4500', 31 Jul 2007, KN Magnacca 07-0708; O’Grady Lab 205053
Campsicnemus comatus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Carson Trail, 4200', 6 Aug 2007, KN Magnacca 07-0802; O’Grady Lab 205036
	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0778; O’Grady Lab 205042
Campsicnemus crossotus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Pu‘u Kukui Trail, 2900–3700', 8 Aug 2007, KN Magnacca 07-0824; O’Grady Lab 205037
Campsicnemus dicondylus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I: Pu‘u Maka‘ala Trailhead, off Stainback Hwy, 11 Jul 2004, PM O’Grady & M Giannullo, 257.7a; O’Grady Lab 200731
Campsicnemus distinctus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0780; O’Grady Lab 205043
Campsicnemus fulvifacies Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MOLOKA‘I: Pu‘u Kolekole, 3854', 28–30 Jul 2005, PM O’Grady & CD Specht; O’Grady Lab 200775
Campsicnemus hispidipes Hardy & Kohn, 1964	HAWAIIAN ISLANDS: KAUA‘I: Pu‘u O Kila Road, 4080', 17 May 2007, KN Magnacca 07-0431; O’Grady Lab 205019
	HAWAIIAN ISLANDS: KAUA‘I: Pihea Trail, 3900’, 18 May 2007, KN Magnacca 07-0460; O’Grady Lab 205020
Campsicnemus hygrophilus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I: Saddle Road, Kipuka 9, 13–15 Aug 2008, NL Evenhuis & M. Nicholson; O’Grady Lab 201928

Campsicnemus impariseta Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I, Pu‘u Maka‘ala Trailhead, off Stainback Hwy, 11 Aug 2004, PM O’Grady & M Giannullo, 257.8b; O’Grady Lab 200743
Campsicnemus labilis Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: stream E of Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0795; O’Grady Lab 205059
Campsicnemus longitarsus Tenorio, 1969	HAWAIIAN ISLANDS: KAUA‘I: Kumuwela Trail, 3500', 17 May 2007, KN Magnacca 07-0417; O’Grady Lab 205021 HAWAIIAN ISLANDS: KAUA‘I: Pihea Trail, 3500', 18 May 2007, KN Magnacca 07-0443; O’Grady Lab 205022
Campsicnemus loxothrix Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I: HVNP, Upper Ola‘a Forest, end of Wright Rd, 8 Jul 2004, PM O’Grady, M Giannullo, D. Foote, 251.7; O’Grady Lab 200755
Campsicnemus mucronatus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Hanawi Stream, 2000', 12 Nov 1992, DA Polhemus; O’Grady Lab 200115 HAWAIIAN ISLANDS: MAUI: Makawao Forest Reserve, 4500', 6 Aug 2007, KN Magnacca 07-0809; O’Grady Lab 205038 HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0777; O’Grady Lab 205044
Campsicnemus nigricollis Van Duzee, 1933	HAWAIIAN ISLANDS: KAUA‘I, Lumahai River, 9 Nov 1994, DA Polhemus; O’Grady Lab 200114 HAWAIIAN ISLANDS: KAUA‘I: Namdokam Mtn, 4200', 22 May 2005, DA Polhemus; O’Grady Lab 201913
Campsicnemus ornatus Van Duzee, 1933	HAWAIIAN ISLANDS: O‘AHU: abv. Nu‘uanu Pali lookout, 1500', 29 Jul 2007, KN Magnacca 07-0686; O’Grady Lab 205055
Campsicnemus penicillatus Parent, 1933	HAWAIIAN ISLANDS: HAWAI‘I: Saddle Rd, Kipuka 9, 2004, NL Evenhuis; O’Grady Lab 200737
Campsicnemus perplexus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MAUI: Pu‘u Kukui Trail, 2900–3700', 8 Aug 2007, KN Magnacca 07-0822; O’Grady Lab 205029 HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Carson Trail, 4200', 6 Aug 2007, KN Magnacca 07-0800; O’Grady Lab 205032 HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 31 Jul 2007, KN Magnacca 07-0700; O’Grady Lab 205056 HAWAIIAN ISLANDS: MAUI: Haiku Uka, Heed Trail, 4200', 6.viii.2007, KN Magnacca 07-0775; O’Grady Lab 205057
Campsicnemus petalicnemus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: MOLOKA‘I, Pu‘u Kolekole, 3854', 28–30 Jul 2004, PM O’Grady & CD Specht, 283.6; O’Grady Lab 201707 HAWAIIAN ISLANDS: MAUI: Pu‘u Kukui Trail, 2900–3700', 8 Aug 2007, KN Magnacca 07-0823; O’Grady Lab 205028
Campsicnemus plautinus Adachi, 1953	HAWAIIAN ISLANDS: KAUA‘I: Pu‘u O Kila Road, 4100', 17 May 2007, KN Magnacca 07-0439; O’Grady Lab 205023

Campsicnemus scolimerus Hardy & Kohn, 1964	HAWAIIAN ISLANDS: HAWAI‘I: HVNP, Olaa Forest, Pole 48 (left side of road), 6–7 Jul 2004, PM O’Grady, M. Giannullo & CD Specht, 247.8a; O’Grady Lab 200727 HAWAIIAN ISLANDS: HAWAI‘I: Tree Planting Rd, off Stainback Hwy, 11 Jul 2004, PM O’Grady & M Giannullo, 256.3c; O’Grady Lab 201730 HAWAIIAN ISLANDS: HAWAI‘I: Volcano, 20 Jul 2004, NL Evenhuis; O’Grady Lab 200735
Campsicnemus sinuosus Evenhuis, 2007	HAWAIIAN ISLANDS: HAWAI‘I: Saddle Rd, Kipuka 9, 13–15 Aug 2008, NL Evenhuis & M. Nicholson O’Grady Lab 201930
Campsicnemus sp.	HAWAIIAN ISLANDS: HAWAI‘I: Tree Planting Rd, off Stainback Hwy, 11 Jul 2004, PM O’Grady & M Giannullo, 256.3a; O’Grady Lab 200728
Campsicnemus sp.	HAWAIIAN ISLANDS: HAWAI‘I: Pu‘u Maka‘ala Trailhead, off Stainback Hwy, 11 Jul 2004, PM O’Grady & M Giannullo, 257.7b; O’Grady Lab 200732 HAWAIIAN ISLANDS: HAWAI‘I: HVNP, Upper Ola‘a Forest, end of Wright Rd, 8 Jul 2004, PM O’Grady & M Giannullo, D. Foote; O’Grady Lab 200756
Campsicnemus sp. nr. biseta	HAWAIIAN ISLANDS: MAUI: Kaupo Trail, 5500', 4 Aug 2007, KN Magnacca, 07-0753; O’Grady Lab 205054
Campsicnemus sp. nr. indecorus	HAWAIIAN ISLANDS: MAUI: Ha‘ikū Uka, Heed Trail, 4200', 6 Aug 2007, KN Magnacca 07-0779; O’Grady Lab 205045
Campsicnemus sp. nr. loxothrix	HAWAIIAN ISLANDS: HAWAI‘I: Saddle Road, Kipuka 9, 13–15 Aug 2008, NL Evenhuis & M. Nicholson; O’Grady Lab 201929
Campsicnemus sp. nr. penicillatus	HAWAIIAN ISLANDS: MAUI: Kaupo Trail, 5500', 4 Aug 2007, KN Magnacca 07-0751; O’Grady Lab 205046

CAMPSICNEMUS – Pacific

Campsicnemus n. sp. “*austral”*	FRENCH POLYNESIA: AUSTRAL ISLANDS: RAPA ISLAND: Mt. Perau, 1700-2000', 3 Mar 2002, KR Wood; O’Grady Lab 201851
Campsicnemus n. sp. “*craigi”*	FRENCH POLYNESIA: TAHITI: Mt. Mauru, Faatautia, 720 m, 19 Jul 2006, PM O’Grady; O’Grady Lab 201852
Campsicnemus limnobates Evenhuis, 2000	FRENCH POLYNESIA: MARQUESAS: UA HUKA I: Vaihonu Cascade, 1 Nov 1999, DA Polhemus; O’Grady Lab 200111
Campsicnemus n. sp. “*popeye”*	FRENCH POLYNESIA: TAHITI: Mt. Mauru, 14 Jul 2006, PM O’Grady, NL Evenhuis, DH Hembry, E Claridge, 346.a
Campsicnemus rheocrenus Evenhuis, 2008	FRENCH POLYNESIA, TAHITI: Punaru‘u River, 140–160 m, 20 Jul 2006, NL Evenhuis & PM O’Grady; O’Grady Lab 201853

CAMPSICNEMUS – European and North American

Campsicnemus curvipes (Fallén, 1823)	GENBANK ACCESSION: Bernasconi *et al*. (2007) **[COI**: **DQ456892**; **12S**: **DQ464828]** BELGIUM: Ghent-Osse meersen, 1993, M Pollet; O’Grady Lab 200742

Campsicnemus degener Wheeler, 1899	CANADA: NEW BRUNSWICK: Pokeshaw, 4 Sep 2001, SE Brooks & C. Chenard; O’Grady Lab 200774
Campsicnemus loripes (Halliday, 1832)	M Pollet; O’Grady Lab 200740
Campsicnemus scambus (Fallén, 1823)	M. Pollet; O’Grady Lab 200741

OTHER HAWAIIAN GENERA

Emperoptera montgomeryi Evenhuis, 1997	HAWAIIAN ISLANDS: O‘AHU, Mt. Ka‘ala, NL Evenhuis; O’Grady Lab 200777

Gene sequences generated in this study will be deposited in Genbank when sampling of Hawaiian and Pacific *Campsicnemus* and related dolichopodids has been completed.

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The Asian polydesmidan milliped, *Helicorthomorpha holstii* (Pocock) (Paradoxosomatidae), established in Hawai‘i

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In their review of the milliped family Paradoxosomatidae in Hawai‘i, Shelley *et al.* (1998) provided distinguishing features and occurrences for three Asian species inhabiting the archipelago: *Oxidus gracilis* (C.L. Koch, 1847), *Asiomorpha coarctata* (Saussure, 1860), and *Akamptogonus novarae* (Humbert and Saussure, 1869); all are widely introduced globally, particularly on islands. They deleted three species from the state's fauna that had been intercepted in quarantines but were not known to occur on the islands *per se*; however, they predicted that these and other widely introduced millipeds might eventually become established. We report here the establishment of one deleted species, *Helicorthomorpha holstii* (Pocock, 1895), on O‘ahu; it is indigenous to east Asia. Voucher specimens are deposited in the Bishop Museum (BPBM) and the North Carolina State Museum of Natural Sciences (NCSM).

Paradoxosomatidae

Helicorthomorpha holstii (Pocock, 1895) **New state record**

Diagnosis. Distinguished from the 3 other Hawaiian paradoxosomatids by the color pattern and configuration of the gonopods in males. Color (Fig. 1; Shelley & Lehtinen 1998:90, fig. 22; Chen & Chang 2004: figs. 15.1–15.8): dark brown with broad longitudinal stripe extending from collum to segment 19; stripe narrow on prozona but expanded and somewhat "egg shaped" on metazona, orange to bright red in life fading to whitish in alcohol. Paranota greatly reduced, represented by rounded peritremal swellings, similarly colored as stripe; legs orange. Body surface smooth, subcylindrical, sides nearly parallel, narrowing slightly caudad, more so near epiproct; approximately 20 mm in length. Gonopod (Fig. 2; Shelley & Lehtinen 1998:90, figs. 23–24; Chen & Chang 2004: figs. 42.1–42.4): telopodite elongate, narrow, branches intertwined into helical configuration, with 3 apical terminations.

Distribution. Ryukyu Islands, Taiwan, China, and Viet Nam; introduced into Florida, USA (Shelley & Lehtinen, 1998, Shelley & Edwards, 2001).

Occurrence in Hawai‘i. Known only from Honolulu and vicinity, O‘ahu.

Figure 1. *Helicorthomorpha holstii*, female dorsal color pattern. Photo: F.G. Howarth.

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1. Contribution No. 2010-009 to the Hawaii Biological Survey.

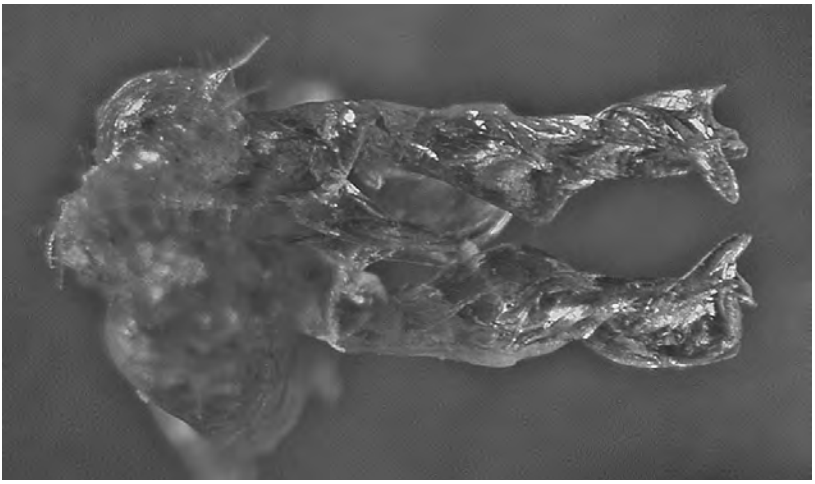

Figure 2. *Helicorthomorpha holstii,* distal portion of telepodites, ventral view. Photo F.G. Howarth.

Material examined. **O'AHU:** Honolulu, Kalihi, 120 m, N21°20.6', W157°52.61', 15–17 Feb 2008, in leaflitter and invading house, FG Howarth, 10♂, 10♀ (NCSM), 20♂, 25♀ (BPBM); same data except 12 May 2008, in house, FG Howarth, 2♂, 5♀ (BPBM); Tripler Army Medical Center, near unnamed stream, N21.361°, W157.893°, 26 Jul 2008, under rocks, DJ Preston & K Arakaki, 3♀ (BPBM).

Remarks. *Helicorthomorpha holstii* was first recorded from Hawai'i by Chamberlin (1923). He described it as *Chinosoma hodites* n. gen., n. sp. based on one male and three juveniles that had been intercepted in quarantine at Honolulu and were found in soil with a cactus plant from China. Jeekel (1980) subsequently synonomized *Chinosoma* with *Helicorthomorpha* and *C. hodites* with *H. holstii.* As no further Hawaiian specimens were known, Shelley *et al*. (1998) concluded that the species was not an inhabitant and deleted it from the state's fauna; we suspect that the present Honolulu population represents a separate and recent introduction. In 2000, a heavy infestation of *H. holstii* was discovered in a plant nursery greenhouse in Orange County, Florida (Shelley & Edwards, 2001). The greenhouse contained orchids imported from Taiwan, and the authors speculated that the millipeds had been introduced as eggs with the plants.

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The free-living soil nematode *Caenorhabditis briggsae* isolated from Kurtistown, Hawai'i

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The nematodes *Caenorhabditis elegans* and *Caenorhabditis briggsae* are of great interest to geneticists, cell and molecular biologists, and ecologists. Both *C. elegans* and *C. briggsae* have completely sequenced genomes and are used as model organisms for basic and applied biomedical research ranging from development to rational drug design. Species of the *Caenorhabditis* genus are cosmopolitan and noted to be highly anthropogenic (Barrière & Félix, 2005; Teotonio *et al*, 2006) thus we suspected their presence on former sugar cane farmlands. Previously identified strains isolated from unknown locales in Hawai'i at the *Caenorhabditis* Genetics Center, University of Minnesota but unreported in the Hawaii Biological Survey, include *C. elegans* CB4856 and *C. briggsae* VT847.

Peloderinae

Caenorhabditis briggsae UH1 (HI806-1) **New state record**

Isolated by Baermann funnel extraction (Barrière & Félix, 2006) and maintained on agar nematode growth medium plates with an *Escherichia coli* OP50 bacterial lawn. It is identified morphologically under Normarski optics by its smooth cuticle and a buccal opening characteristic of Rhabditiae (Barrière & Félix, 2006). It has an elegant sinusoidal swim and a pointy tail, symmetrical brownish gut granule coloration, wide cytoplasmic rachis, a didelphic gonad, and a short rectum characteristic of *Caenorhabditis*. It reproduces hermaphroditically. Also like other *Caenorhabditis*, it has a two-bulb pharynx featuring a buccal cavity, procorpus, metacorpus, isthmus, and terminal bulb (Yochem, 2006). It prefers to grow at temperatures between 18 and 20 °C, is sterile at 30 °C and is lethal at 36 °C. Males can be induced by standard temperature-dependent methods (Hope, 1999). Molecular barcode identification used the *glp-1* gene (Barrière & Félix, 2005) and sequence from the gene encoding the 18S subunit of the ribosome (Floyd *et al*., 2002). Biological speciation is determined by crossing males of this isolate with hermaphrodites of *C. elegans* N2 and CB4856 strains, and *C. briggsae* AF16 and VT847 strains, and vice versa.

Material examined: **HAWAI'I**: Kurtistown, Hwy 11 at 11 mi marker, in decomposing vegetative sample from pumpkin garden, hermaphrodite (*Caenorhabditis* Genetics Center, University of Minnesota).

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Helminth records for the Madagascan giant day gecko, *Phelsuma grandis* (Gekkonidae) from Hawai‘i[1]

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The Madagascan giant day gecko, *Phelsuma grandis* Gray is native to Madagascar (Henkel & Schmidt, 2000). This species was first collected in Hawai‘i in December 1996 in Mānoa Valley, O’ahu where it was intentionally established (Kraus, 2002, as "*P. madagascariensis*").

Between 1996 and 2008, 60 *P. grandis* were collected on O‘ahu, (mean snout-vent length, SVL = 87 mm ± 26.7 SD, range = 34–118 mm), fixed in 10% formalin then transferred to 70% ethanol for storage in the herpetology collection of the Bishop Museum (BPBM), Honolulu, Hawai‘i. The following specimens of *P. grandis* were loaned to SRG and examined at Whittier College, Whittier, California: BPBM 13285, 14089, 14092, 14756, 18226, 18227, 20990, 20999, 21000, 21138-21140, 21142, 21143, 21150, 21151, 23521, 23597, 23601-23603, 23917, 23918, 23975, 24106, 24107, 24110, 24112, 24123, 24217, 24710-24712, 24718, 25360, 25589, 27297, 28353-28357, 28361-28364, 28654-28663, 28665-28667, 31551. The gastrointestinal tract and lungs were removed and searched for helminths. Nematodes and pentastomes were placed in glycerol on glass slides, allowed to clear and examined under a light microscope. Voucher helminths were placed in vials of alcohol and deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland and the Bishop Museum, Honolulu (BPBM). The following species were found and are recorded below as new host records.

Cestoda: Linstowiidae

Oochoristica javaensis Kennedy, Killick & Beverley-Burton **New host record**

Oochoristica javaensis was originally described from the small intestines of geckos, *Gehyra mutilata, Hemidactylus platyurus,* and *H. frenatus* from Java, Indonesia (Kennedy *et al.,* 1982), and there is one report from Hawai’i (*H. frenatus*; Goldberg & Bursey, 2000a). It is a wide-ranging species currently known only from lizards: a second report in *H. platyurus* from Indonesia (Matsuo & Oku, 2002); additional reports in *Gehyra mutilata* from Guam, Indonesia, and the Philippine Islands (Kugi, 1993; Goldberg *et al.,* 1998; Matsuo & Oku, 2002; Goldberg *et al.,* 2005); *Gehyra oceanica* from Guam and Oceania (Goldberg *et al.,* 1998; Goldberg & Bursey, 2002); additional reports in *H. frenatus* from Oceania, Philippines and Thailand (Hanley *et al.,* 1998; Goldberg & Bursey, 2001a, 2002); *Lepidodactylus paurolepis* from the Marshall Islands (Goldberg & Bursey, 2002); *Mabuya carinata* from Bangladesh (Yesmin *et al.,* 2006) and *Sphenomorphus jobiensis* from Papua New Guinea (Bursey *et al.,* 2005). Criscione & Font (2001) reported *O. javaensis* in nonnative *Hemidactylus turcicus* collected in the southern United States and they experimentally infected nonnative *Hemi*-

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[1] Contribution No. 2010-009 to the Hawaii Biological Survey.

dactylus garnotii and native *Sceloporus undulatus*. Prevalence (number infected hosts/ number hosts examined): 1/60 (2%); mean intensity (mean number parasites per infected host): 1.0, infection site, small intestine.

Material examined: **O'AHU** (BPBM F328).

Nematoda: **Seuratidae**

Skrjabinelazia machidai Hasegawa **New host record**

Skrjabinelazia machidai was originally described from the intestine of the gekko, *Gekko japonicus* from Okinawa Island, Japan by Hasegawa (1984). In Hawai'i, it was first found in *Lepidodactylus lugubris* by Goldberg & Bursey (1997) and subsequently reported in *L. lugubris* and *Hemidactylus frenatus* by Hanley *et al.* (1998) and Goldberg & Bursey (2000a). It has also been reported from Australia in the gecko *Diplodactylus ciliaris* (Goldberg & Bursey, 2001b), as well as *Gehyra mutilata, Hemidactylus garnotii*, *Lepidodactylus moestus* from Oceania (Goldberg & Bursey, 2002), and *Leptodactylus aureolineatus* from the Philippines (Goldberg & Bursey, 2001a). There is one additional report for *Hemidactylus frenatus* from Guam (Goldberg *et al.,* 1998). Prevalence: 2/60 (3%): mean intensity: 2.0 ± 1.4: range 1–3; infection site, small intestine.

Material examined: **O'AHU** (BPBM H408; USNPC 101876).

Nematoda: **Pharyngodonidae**

Spauligodon hemidactylus Bursey & Goldberg **New host record**

Spauligodon hemidactylus was originally described from the large intestine of the gecko *Hemidactylus frenatus* from American Samoa by Bursey & Goldberg (1996), who also reported it from *H. frenatus* collected in Hawai'i, Fiji, Guam, Marshall Islands, Palau, Philippines, Samoa, Solomon Islands, Society Islands, Vanuatu, and Thailand. It was also reported in *H. frenatus* from Hawai'i by Hanley *et al.* (1998) and Goldberg & Bursey (2000a). It is currently known only from lizards. Other hosts include *Hemidactylus platyurus, Gehyra mutilata, H. garnotii, Hemiphyllodactylus typus* and *Lepidodactyus lugubris* (Goldberg *et al,* 1998, 2005; Goldberg & Bursey, 2001a, 2002; Matsuo & Oku, 2002) Prevalence: 2/60 (3%); mean intensity: 1.0, infection site large intestine.

Material examined: **O'AHU** (USNPC 101877).

Nematoda: **Spirocercidae**

Physocephalus sp. (larvae) **New host record**

Adults of *Physocephalus* have been found in the stomachs of swine, horses, cattle, and rabbits: infective larvae have been recovered from dung beetles and are found in terrestrial vertebrates which have ingested infected beetles (Anderson, 2000). Larvae of *Physocephalus* sp. were first reported from Hawai'i in *Hemidactylus frenatus, H garnotii,* and *Lepidodactyus lugubris* by Brown *et al.* (1995). Hanley *et al.* (1998) provided a second report for *H. frenatus* and there is a third report for this host (Goldberg & Bursey 2000a). Other lizards from Hawaii harboring this species include *Anolis carolinensis, Gehyra mutilata,* and *Lampropholis delicata* (Goldberg *et al.,* 2004). Prevalence: 21/60 (35%); mean intensity: 12.6 ± 10.8 SD: range 1–32, infection site, stomach wall.

Material examined: **O'AHU** (BPBM H409; USNPC 101878).

Pentastomida: **Cephalobaenidae**

Raillietiella frenatus Ali, Riley & Self **New host record**

Raillietiella frenatus was originally described from the lungs of *Hemidactylus frenatus* collected in Malaysia by Ali *et al.* (1981), who reported it from the same host from the Philippine Islands, South Vietnam, Taiwan, and Thailand. *Raillietiella frenatus* was first reported in *H. frenatus* and *Lepidodactylus lugubris* from Hawai'i by Brown *et al*. (1995). Goldberg & Bursey (1997) provided a second report for *L. lugubris*. It was subsequently reported in both hosts by Hanley *et al.* (1998). Goldberg & Bursey (2000a) provided a third report for *H. frenatus* and a first report for *Anolis sagrei* (Goldberg & Bursey, 2000b). It is known only from lizard hosts, which include *Hemidactylus platyurus, Gehyra mutilata, Gekko monarchus, Japalura swinhonis,* and *Mabuya longicaudata* from Indonesia and Taiwan (Ali *et al*., 1981; Matsuo & Oku, 2002). Prevalence: 19/60 (32%); mean intensity: 3.7 ± 3.5 SD: range 1–14, infection site: lung.

Material examined: **O'AHU** (BPBM H410; USNPC 101879).

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Land snail records for Mokapu Islet, Moloka‘i, Hawaiian Islands

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Mokapu is an offshore islet of 110 m (360 ft) elevation with an estimated area of 60,000 m^2 (14.8 acres), and is located around 2.4 km (1.5 mi) east of Kalaupapa peninsula, Moloka‘i (N21°10'59", W156°55'26" at summit). The islet is managed by the Hawaii Department of Land and Natural Resources (DLNR), Division of Forestry and Wildlife (DOFAW) as a State Seabird Sanctuary. Botanically, Mokapu represents a *Chamaesyce celastroides* var. *amplectens*-*Chenopodium oahuense* coastal dry shrubland with regions dominated by relictual *Diospyros sandwicensis* forest and its total flora is composed of ca 47 vascular plant taxa, 17 of which are endemic, 14 indigenous, 15 non-native naturalized, and one Polynesian introduction (Wood & LeGrande, 2002, 2003). Mokapu islet is characterized by a long narrow summit ridge with very steep slopes and is one of two last remaining sites where the native loulu palm *Pritchardia hillebrandii* (Arecaceae) occurs. Rats (i.e., *Rattus exulans*) were eradicated from Mokapu in February 2008 making this islet ideal for the reintroduction of coastal native species. The land snail fauna of Mokapu has never been reported. Here we report on collections of two species, both introduced to the Hawaiian Islands.

Specimens were collected on 15 October 2008 by collecting surface soil at the base of large basalt boulders along the central summit ridge of the islet and sifting the material back at camp. Shrubs of *Chamaesyce celastroides* var. *amplectens* and *Chenopodium oahuense* composed the dominant vegetation at the collection site. Associated plants included *Sida fallax*, *Plumbago zeylanica*, *Artemisia australis*, *Portulaca lutea*, *Lepidium bidentatum* var. *o-waihiense*, *Cyperus phleoides*, *Eragrostis variabilis*, *Cassytha filiformis*, and *Doryopteris decipiens*. Non-native invasive plant taxa in the immediate vicinity included *Lantana camara*, *Pluchea carolinensis*, and *Portulaca oleracea*.

The collected material is deposited in the Bishop Museum (BPBM) Malacology Collection. Catalog numbers are BPBM Malacology Collection numbers. Latitude and longitude coordinates were recorded by GPS using the WGS 84 map datum.

Subulinidae

Paropeas achatinaceum (Pfeiffer)

This species is widespread and abundant on many Pacific islands (Cowie, 2001) and is one of the most widespread and abundant land snails in the Hawaiian Islands (Cowie *et al*., 2008). First recorded in the Islands in 1904, it has previously been recorded from Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, Maui, and Hawai‘i (Cowie, 1997; Hayes *et al*., 2007).

Material examined: **MOLOKA‘I**: MOKAPU: surface soil at the base of large basalt boulders along the central summit ridge, (N21°10'59.6", W156°55'26.4"), K.R. Wood, 15 Oct 2008 (270274, 18 dead shells).

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Vertiginidae

Gastrocopta servilis (Gould)

This species had been previously recorded from Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, Maui, and Hawai‘i, as well as from Midway, Pearl and Hermes, and Laysan, and has been present in the Hawaiian Islands since at least 1892 (Cowie, 1997; Hayes *et al*., 2007).

Material examined: **MOLOKA‘I**: MOKAPU: surface soil at the base of large basalt boulders along the central summit ridge, (N21°10'59.6", W156°55'26.4"), K.R. Wood, 15 Oct 2008 (270273, 17 dead shells).

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