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The placement of *Engiscaptomyza, Grimshawomyia,* and *Titanochaeta*, three clades of endemic Hawaiian Drosophilidae (Diptera)

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Abstract

Based on a combination of molecular and morphological characters, two endemic Hawaiian genera, *Titanochaeta* Knab and *Grimshawomyia* Hardy, are transferred to subgenera within the genus *Scaptomyza* Hardy as is the *Drosophila* subgenus *Engiscaptomyza* Kaneshiro. Replacement names for three preoccupied species, *Scaptomyza (Titanochaeta) neoevexa* O'Grady et al., **nom. nov.** (for *Titanochaeta evaza* Hardy), *S. (Titanochaeta) neokauaiensis* O'Grady et al., **nom. nov.** (for *Titanochaeta kauaiensis* Hardy), and *S. (Titanochaeta) neosilvicola* O'Grady et al., **nom. nov.** (for *Titanochaeta silvicola* Hardy), are proposed. This brings the total number of described species in the genus *Scaptomyza* to 272, of which 141 are endemic to the Hawaiian Archipelago. In comparison, the genus *Drosophila* contains 368 species endemic to the Hawaiian Islands. Keys for the identification of the Hawaiian subgenera of *Scaptomyza* and species of *Engiscaptomyza*, *Titanochaeta*, and *Grimshawomyia* are also included.

Key words: Drosophilidae, Hawaiian Islands, *Titanochaeta*, *Grimshawomyia*, *Scaptomyza*, *Engiscaptomyza*, Hawaiian *Drosophila*

Introduction

The Hawaiian Drosophilidae is an impressive radiation of an estimated 1,000 species (Kaneshiro 1997) which have traditionally been placed in a total of nine genera (Hardy 1965). Based on a variety of morphological characters, Throckmorton (1966) recognized two major lineages: "drosophiloids" and "scaptomyzoids." Each lineage was initially composed of a number of genera, subgenera, and species groups. For example, the drosophiloid lineage contained all members of the genus *Drosophila* Fallén, 1823 endemic to

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Hawai'i, as well as the endemic Hawaiian genera *Nudidrosophila* Hardy, 1965, *Antopocerus* Hardy, 1965, *Ateledrosophila* Hardy, 1965, and *Idiomyia* Grimshaw, 1901. Kaneshiro (1977) formally synonymized these four genera with *Drosophila* based on analysis of male genitalic characters. The scaptomyzoid lineage includes all the Hawaiian *Scaptomyza*, as well as those species placed in three genera, *Celidosoma* Hardy, 1965, *Grimshawomyia* Hardy, 1965, and *Titanochaeta* Knab, 1914. In addition to these two lineages, there were also a small number of intermediate taxa possessing the characteristics of both major groups of Hawaiian Drosophilidae. Kaneshiro (1969) erected a new subgenus, *Engiscaptomyza*, in the genus *Drosophila* for the six taxa thought to be intermediate between the drosophiloid and scaptomyzoid lineages (a seventh member of this group has since been added).

Molecular and morphological studies over the course of the past 40 years have shown that Throckmorton's (1966) drosophiloid and scaptomyzoid lineages were actually allied with one of two genera, *Drosophila* or *Scaptomyza*. This supports Kaneshiro's reclassification of the drosophiloid genera (Kaneshiro 1977) and prompts a similar reclassification of the poorly known scaptomyzoid lineage. Molecular phylogenetic analyses recover a monophyletic Hawaiian *Drosophila* (*i.e.*, drosophiloid) lineage and strongly support the placement of *Grimshawomyia*, *Titanochaeta* and the *Engiscaptomyza* within the genus *Scaptomyza* (Bonacum 2001). The male genitalic morphology of *Titanochaeta*, *Grimshawomyia*, *Scaptomyza*, and *Engiscaptomyza* are all characterized by having "prominent, well developed and exposed, male claspers" (Hardy 1965: 573), further supporting a synonymy of these taxa. Here we combine molecular systematic results and morphological data to synonymize two genera (*Titanochaeta* and *Grimshawomyia*) and move one subgenus (*Engiscaptomyza*) from the genus *Drosophila* to *Scaptomyza*.

Specimens examined in this study derive from the following institutions (responsible curator in parentheses): AMNH – American Museum of Natural History (Dr. P.M. O'Grady); BPBM – Bernice P. Bishop Museum (Dr. N.L. Evenhuis); UHM – University of Hawaii, Manoa (Dr. K.Y. Kaneshiro).

Systematics

Scaptomyza Hardy, 1850

(Figures 1—6)

Scaptomyza Hardy, 1850: 361. Type species: *Drosophila graminum* Fallén, 1823, by subsequent designation (Coquillett, 1910: 603).

Titanochaeta Knab, 1914: 167. Type species: *Titanochaeta ichneumon* Knab, 1914, by original designation. **Syn. nov.**

Scaptomyzella Hendel, 1928:290. Type species: *Drosophila flava* Fallén, 1823, by original designation.

Scaptomyzetta Hendel, 1928: 290 (incorrect original spelling of *Scaptomyzella*).

Grimshawomyia Hardy, 1965: 535. Type species: *Drosophila perkinsi* Grimshaw, 1901, by original designation. **Syn. nov.**

Engiscaptomyza Kaneshiro, 1969: 80 (as subgenus of *Drosophila*). Type species: *Drosophila crassifemur* Grimshaw, 1901, by original designation. **Syn. nov.**

Diagnosis. *Scaptomyza* is a cosmopolitan genus that currently contains about 15 subgenera (Wheeler 1981, 1986), some of which have been designated as separate genera at one time or another (Frey 1954; Hackman 1959, 1982; Malloch 1934). The traditional definition of *Scaptomyza* includes taxa with two to four rows of acrostichal setulae, two pairs of postsutural dorsocentral setae (and sometimes with a single set of presutural dorsocentrals as well), the third costal section 2.5 times longer than the fourth, and the head distinctly longer than high (Hardy 1965). However, a rather large radiation of about 150 described species present in the Hawaiian Archipelago, has broadened this definition somewhat, mainly because of atypical characters possessed by some of these taxa (Hackman 1959, 1962, 1982). For example, many members of the subgenus *Elmomyza* have six rows of acrostichal setulae, suggesting that this character may be quite variable within *Scaptomyza*. Therefore, having either two or four rows of acrostichals is not a good synapomorphy for the genus *Scaptomyza*, although it may be useful at delimiting some subgenera.

Perhaps the best character defining all *Scaptomyza* is the presence of well developed, exposed surstyli and enlarged lobes on either the epandrium (ninth tergite), cerci, or both. These morphologies are also characteristic of the genera *Grimshawomyia* and *Titanochaeta*, as well as the subgenus *Engiscaptomyza*. An additional character, found in females of most species, is a weakly developed, fleshy, non-dentate ovipositor. *Titanochaeta* is atypical in this character as females of this group have a slender, sharply pointed, stylet-like ovipositor, a character that may be an adaptation to a lifestyle as a spider egg sac predator.

Methods. We have examined the types, as well as large series of other material, from all species placed in *Titanochaeta*, *Engiscaptomyza*, and *Grimshawomyia* (Table 1). We also have examined material from most recognized subgenera of the genus *Scaptomyza*. Based on this work, we selected a number of taxa placed in the genus *Scaptomyza*, as well as representatives of *Drosophila* (*Engiscaptomyza*), *Grimshawomyia*, and *Titanochaeta* thought to be closely related to this genus, for use in the current molecular and morphological analyses. Over 3.3 kilobase pairs of nucleotide sequence from five genes (16S, *Adh*, COI, COII, *Gpdh*) were examined in about 120 drosophilid species using a variety of phylogenetic methods (Bonacum 2001). The phylogeny shown in figure 1 is the result of a maximum parsimony analysis (addition sequences = random, number of replicates = 100, branch swap = TBR). The search recovered four most parsimonious trees [length 33,181; CI = 0.31; RI = 0.53; see Bonacum (2001) for more detail]; figure 1 is from the strict consensus. Measures of support include bootstrap proportions (BP; Felsenstein 1985, 1988), and decay indices (DI; Bremer 1988). This phylogeny shown is part of a larger study treating phylogenetic relationships within the entire Hawaiian Drosophilidae (Bonacum 2001; Bonacum et al. in press) and includes several outgroups, as well as representatives of all major Hawaiian *Drosophila* lineages. Based on this taxon sampling, we feel confident in making statements concerning the relationships of the Hawaiian Drosophilidae and the genus *Scaptomyza*.

TABLE 1. Taxa examined in this study and summary of nomenclatural changes.

Original Combination	New Combination
Drosophila (Engiscaptomyza) amplilobus Hardy	*Scaptomyza (Engiscaptomyza) ampliloba* (Hardy)
Drosophila (Engiscaptomyza) crassifemur Grimshaw	*Scaptomyza (Engiscaptomyza) crassifemur* (Grimshaw)
Drosophila (Engiscaptomyza) inflatus Kaneshiro	*Scaptomyza (Engiscaptomyza) inflatus* (Kaneshiro)
Drosophila (Engiscaptomyza) lonchoptera Hardy	*Scaptomyza (Engiscaptomyza) lonchoptera* (Hardy)
Drosophila (Engiscaptomyza) nasalis Grimshaw	*Scaptomyza (Engiscaptomyza) nasalis* (Grimshaw)
Drosophila (Engiscaptomyza) reducta Hardy	*Scaptomyza (Engiscaptomyza) reducta* (Hardy)
Drosophila (Engiscaptomyza) undulata Grimshaw	*Scaptomyza (Engiscaptomyza) undulata* (Grimshaw)
Grimshawomyia palata Hardy	*S. (Grimshawomyia) palata* (Hardy)
Grimshawomyia perkinsi Grimshaw	*S. (Grimshawomyia) perkinsi* (Grimshaw)
Titanochaeta bryani Wirth	*S. (Titanochaeta) bryani* (Wirth)
Titanochaeta chauliodon Hardy	*S. (Titanochaeta) chauliodon* (Hardy)
Titanochaeta contestata Hardy	*S. (Titanochaeta) contestata* (Hardy)
Titanochaeta evexa Hardy	*S. (Titanochaeta) neoevexa* O'Grady et al.
Titanochaeta glauca Hardy	*S. (Titanochaeta) glauca* (Hardy)
Titanochaeta ichneumon Knab	*S. (Titanochaeta) ichneumon* (Knab)
Titanochaeta kauaiensis Hardy	*S. (Titanochaeta) neokauaiensis* O'Grady et al.
Titanochaeta setosiscutellum Hardy	*S. (Titanochaeta) setosiscutellum* (Hardy)
Titanochaeta silvicola Hardy	*S. (Titanochaeta) neosilvicola* O'Grady et al.
Titanochaeta swezeyi Wirth	*S. (Titanochaeta) swezeyi* (Wirth)
Titanochaeta vittiger Hardy	*S. (Titanochaeta) vittigera* (Hardy)

Morphological analyses were done either using light or scanning electron microscopy. Specimens were prepared as follows: adult flies stored in 70% ETOH were completely dehydrated via sequential washes with 80%, 90%, 95% and 100% ETOH. These specimens were then critical point dried using standard protocols (Grimaldi 1987). Male genitalic structures were dissected from the abdomen and adhered to a specimen mount (Ted Pella, Inc.) using double coated, carbon conductive tabs (Ted Pella, Inc.). The material was sputter coated and visualized using a Hitachi S4700 Field Emission Scanning Electron Microscope. All image files were saved in .tif file format and edited in Adobe Photoshop 5.0 (Adobe Systems, Inc.). Image files are available upon request.

Figure 1.

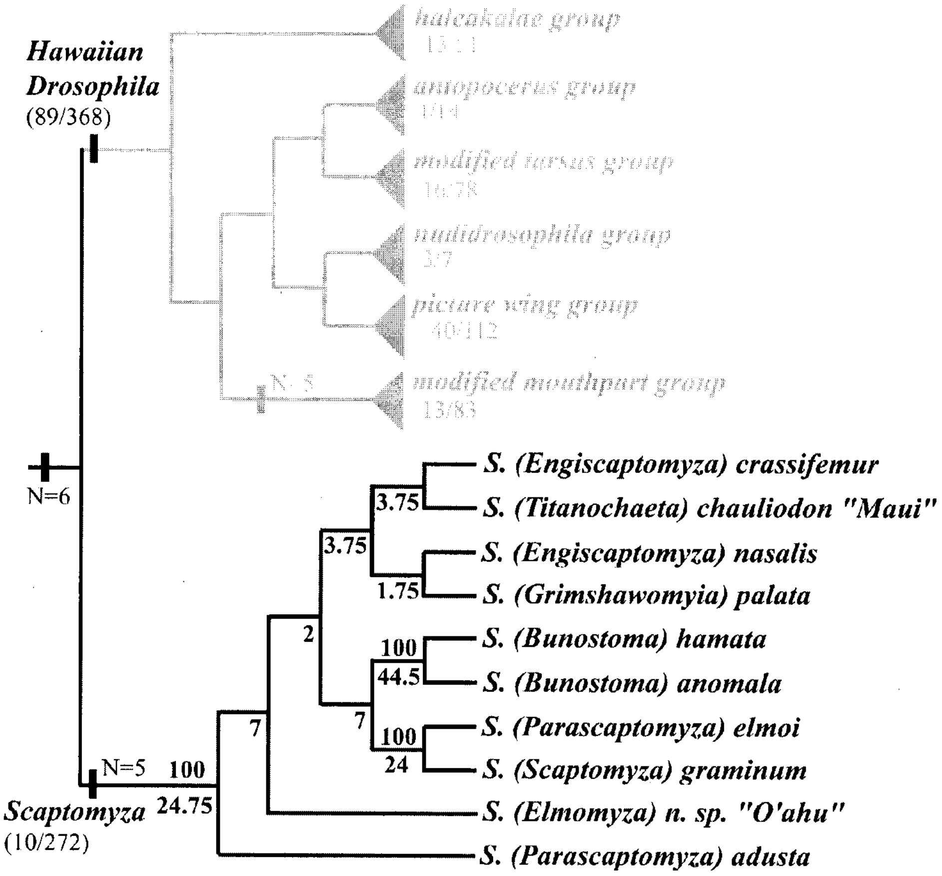


FIGURE 1. Phylogenetic relationships of the Hawaiian Drosophilidae (after Bonacum 2001), with particular emphasis on the genus *Scaptomyza* and associated groups (*Titanochaeta*, *Grimshawomyia*, and *Engiscaptomyza*). Numbers above the line at each node are bootstrap proportions, numbers below the line are decay indices (after Bonacum 2001; see text for details). Numbers of species sampled/total species described in a group is tabulated individually for the Hawaiian *Drosophila* lineages, as well as for the Hawaiian *Drosophila* and genus *Scaptomyza* as a whole (numbers are not additive due to species unplaced in described groups). Chromosome numbers for the ancestor of the Hawaiian Drosophilidae (N=6) and groups where two independent fusions are inferred (*modified mouthpart* group and genus *Scaptomyza*) are mapped on the tree, after (Clayton et al. 1972; Yoon et al. 1975).

Results and Discussion. The molecular and morphological data strongly support the notion that the genera *Titanochaeta* and *Grimshawomyia*, as well as the *Drosophila* subgenus *Engiscaptomyza*, actually belong within the genus *Scaptomyza*. The molecular phylogeny we present (Fig. 1) shows high support for a clade containing these three endemic Hawaiian groups with several subgenera of the genus *Scaptomyza* (BP = 100, DI = 24.75). Although support for the Hawaiian *Scaptomyza* lineage plus *Titanochaeta*, *Grimshawomyia* and the subgenus *Engiscaptomyza* is quite robust, relationships within this clade are not well supported. Only the monophyly of the subgenus *Bunostoma* (BP = 100, DI = 44.5) and the sister group relationship of *S. (Scaptomyza) graminum* and *S. (Parascaptomyza) elmoi* (BP = 100, DI = 24) are well supported (Fig. 1). The latter relationship, however, implies that the subgenus *Parascaptomyza* is not monophyletic. This phylogeny also calls into question the monophyly of *Engiscaptomyza*, placing *S. crassifemur* as the sister-taxon of *S. chauliodon* and *S. nasalis* as the sister of *S. palata* (Fig. 1). Clearly, the large *Scaptomyza* lineage will need to be surveyed more extensively and completely revised in order to resolve these issues..

Scanning electron microscopy was used to compare the morphology of the male genitalia of *Titanochaeta*, *Grimshawomyia*, and the *crassifemur* group with *Scaptomyza* and *Drosophila*. It is clear that, based on several characters, the three endemic Hawaiian groups are more closely related to *Scaptomyza* than they are to *Drosophila*. For example, the epandria and cerci of *Titanochaeta, Grimshawomyia, Scaptomyza*, and *Engiscaptomyza* are all highly modified, possessing expanded lateral lobes that often bear elongate setae (Figs. 2–6). Hardy (1965: 606) noticed these characters and cautioned against referring to them as secondary claspers because he preferred "to use this term only for those distinctly clasper-like lobes...which bear strong spines." In addition, the genitalia of *Scaptomyza, Titanochaeta, Grimshawomyia*, and *Engiscaptomyza* have a more "open" arrangement, where the surstyli and lateral lobes of the epandrium form a "cup" on the ventrodistal surface of the abdomen (Figs. 2-6). This is in contrast to the genus *Drosophila*, where the surstyli are closely oppressed on either side of the aedeagus and lateral lobes on the epandrium or anal plates are generally absent.

Chromosome studies also suggest a close affinity between *Scaptomyza*, *Engiscaptomyza* and *Titanochaeta* (Clayton et al. 1972; Yoon et al. 1975). The metaphase configurations (1 V-shaped, 3 rods, and 1 dot; N = 5) is shared between *Scaptomyza*, *Titanochaeta*, *Engiscaptomyza* and some species in the *modified mouthparts* species group (genus *Drosophila*). All other Hawaiian *Drosophila* species have the "ancestral" karyotype (5 rods and 1 dot; N = 6) for the genus *Drosophila*. It has been suggested that this reduction in chromosome number has taken place via centric fusion events (Patterson & Stone 1952). Our molecular phylogeny (Fig. 1) suggests that this has taken place at least twice – once in the *modified mouthpart* species and again in the *Scaptomyza* lineage (which contains *Titanochaeta*, *Engiscaptomyza*, and *Grimshawomyia*).

Based on the morphological, chromosomal, and molecular evidence, we propose placing the genera *Titanochaeta* and *Grimshawomyia* into the genus *Scaptomyza* as subgenera. We are also moving the subgenus *Engiscaptomyza* from the genus *Drosophila* to *Scapto-*

myza. This placement will broaden the morphological concept of the genus *Scaptomyza* which will, in turn facilitate further taxonomic studies on this poorly understood and complex group.

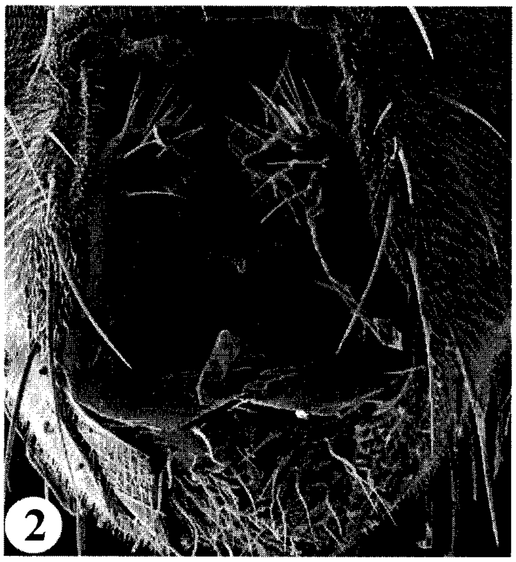


FIGURE 2. Male terminalia of *Scaptomyza* (*Tantalia*) *varipicta* Hardy.

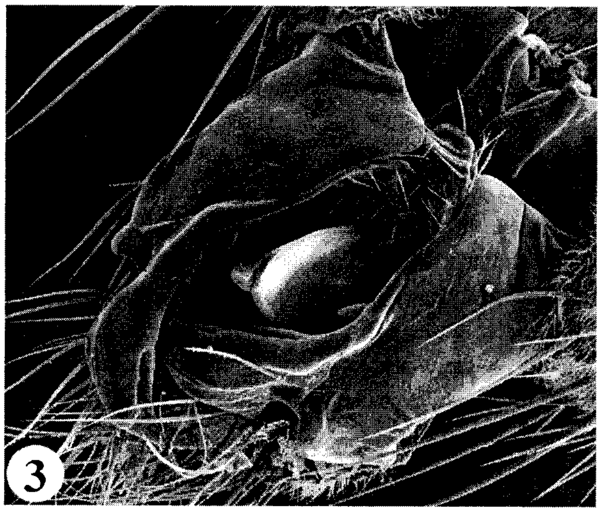


FIGURE 3. Male terminalia of *Scaptomyza* (*Titanochaeta*) *chauliodon* (Hardy).

Key to the Hawaiian Subgenera of *Scaptomyza*

(modified after Hardy 1965)

1. White longitudinal stripe present on scutellum and at least to posterior region of mesonotum, often extends along entire length of mesonotum; terminal fork of arista deep, each branch equal in length to dorsal rays of arista .... subgenus *Tantalia*
- Scutellum and mesonotum may be banded or unicolorous, but never with longitudinal white stripe described above; terminal fork of arista not deep, branches less than length of dorsal rays 2
2. Rays of arista short; chaetotaxy (e.g., katepisternal and dorsocentral setae) generally reduced; four rows of acrostichal setulae; two well-developed humeral setae .... subgenus *Exalloscaptomyza*
- Rays of arista elongate; combination of other characters not as above 3
3. Either zero or one ventral ray present on arista 4
- More than one ventral ray present on arista 8
4. Eight rows of acrostichal setulae present; female ovipositor sclerotized, may be needle-like and pointed .... subgenus *Titanochaeta*, 17
- Acrostichal setulae present in two to six rows; female ovipositor fleshy, non-sclerotized, non-dentate 5
5. Arista lacking ventral rays 6
- One ventral ray present on arista 7
6. Head flattened, longer than high; eyes strongly oblique; strong set of presutural dorsocentral setae present .... subgenus *Rosenwaldia*
- Head nearly square as seen in direct lateral view, lower margin approximately equal in length to the frontal margin; enlarged setulae may be present in presutural position, but not strong .... subgenus *Elmomyza*
7. Two rows of acrostichal setulae present; head not wider than thorax .... subgenus *Parascaptomyza*
- Number of acrostichal rows varies from four to six; head broader than thorax .... subgenus *Alloscaptomyza*
8. Shining black species, thorax and abdomen polished black; two or three ventral rays present on arista; ocellar triangle large, extending to level of proclinate setae; acrostichal setulae present in four rows; clump of black setae on hind trochanter .... subgenus *Bunostoma*
- Mesonotum brown, typically but not always with longitudinal vittae; acrostichal setulae in six to eight rows; ocellar triangle not enlarged; hind trochanter lacking distinctive black setae 9
9. Second antennal segment with a sharp point, extending over the base of the third segment; tibiae entirely yellow .... subgenus *Grimshawomyia*, 16
- Second antennal segment not sharply pointed; apices and bases of mid and hind tibiae with prominent brown bands .... subgenus *Engiscaptomyza*, 10

Scaptomyza (*Engiscaptomyza*)

Diagnosis. Mesonotum typically with five dark brown to black vittae extending the full length, the lateral vittae may be interrupted at the suture (Kaneshiro 1969). The male genitalia of the *Engiscaptomyza* species are also quite similar to those of the genus *Scaptomyza*, characterized by large lobes of the epandria and prominent surstyli (Fig. 4). Some species (i.e., *S. crassifemur*) also possess enlarged, swollen femora.

FIGURE 4. Male terminalia of *Scaptomyza* (*Engiscaptomyza*) *undulata* (Grimshaw).

Included Taxa. *Scaptomyza* (*Engiscaptomyza*) *ampliloba* (Hardy), **comb. nov.** from Kaua'i, *S.* (*Engiscaptomyza*) *crassifemur* (Grimshaw), **comb. nov.** from Maui and Moloka'i, *S.* (*Engiscaptomyza*) *inflata* (Kaneshiro), **comb. nov.** from O'ahu, *S.* (*Engiscaptomyza*) *lonchoptera* (Hardy), **comb. nov.** from Maui, *S.* (*Engiscaptomyza*) *nasalis* (Grimshaw), **comb. nov.** from Maui and Moloka'i, *S.* (*Engiscaptomyza*) *reducta* (Hardy), **comb. nov.** from Hawai'i, *S.* (*Engiscaptomyza*) *undulata* Grimshaw **comb. nov.** from Hawai'i (Nishida 2002)

Discussion. Kaneshiro (1969) recognized a single species group (*crassifemur*) containing two subgroups (*crassifemur* and *nasalis*) within this subgenus. We will leave all taxonomic ranks below the level of subgenus intact. The polytene chromosome of the subgenus *Engiscaptomyza*, unlike those of the remainder of the genus *Scaptomyza*, are large and easy to decipher. Yoon et al. (1975) examined the phylogenetic relationships between four species of the subgenus *Engiscaptomyza* using polytene chromosome banding patterns. Their work suggests that *S. reducta* (Hawai'i) and *S. crassifemur* (Maui Nui) are sister taxa. *Scaptomyza inflata* (O'ahu) is basal to this group and *S. ampliloba* (Kaua'i) is the most basal member of this subgenus.

KEY TO SPECIES OF THE SUBGENUS *Engiscaptomyza* Kaneshiro

10. Mesonotum vittate.. 11
- Mesonotum lacking vittae.. 15

11. Distinct infuscations along margin of wing, veins and crossveins, median portions of most cells are hyaline; front tarsi of male with numerous erect dorsal setae. Hawai'i.. *undulata* (Grimshaw)
- Wings faintly and evenly infuscated, no distinct markings 12

12. Surstylus sharply concave, with distinct lobe at apex which forms a "C" shape; dorsal lobe of hypandrium narrowly pointed, with indistinct protrusion (see Kaneshiro, 1969; Fig. 1) .... *ampliloba* (Hardy)
- Surstylus less concave, straighter in profile 13

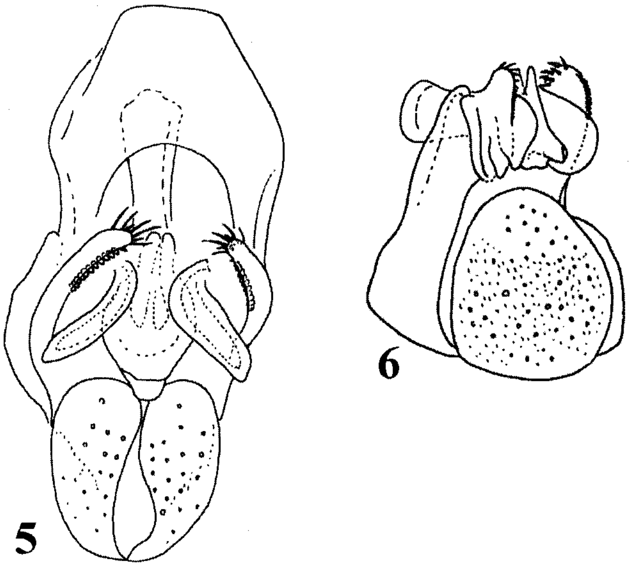
13. Protrusion on dorsal lobe of hypandrium somewhat short, indistinct.. *inflata* (Kaneshiro)
- Protrusion on dorsal lobe of hypandrium elongate, finger-like 14

14. Front femur swollen, rufous in color; scutellum with additional setulae inserted on margin between anterior and posterior scutellar setae; ovipositor blunt, with ca. 5 elongate setulae along margin. Maui, Moloka'i .... *crassifemur* (Grimshaw)
- Front femur swollen (not as distinctly as above), entirely black in color; scutellum only bears anterior and posterior scutellar setae; ovipositor blunt, with only a single elongate setula present at apex. Maui, Moloka'i .... *nasalis* (Grimshaw)

15. Legs entirely yellow, except for brown apex of tarsus; leg segments short and thick. Hawai'i *reducta* (Hardy)
- Femora almost entirely brown, tinged faintly with black and narrowly yellow at the bases and apices; tibia yellow with a broad brown band at apex and basal 1/3 of segment; tarsi yellow, tinged faintly with brown on apical segments. Maui .... *lonchoptera* (Hardy)

Scaptomyza (Grimshawomyia)

Diagnosis. The genus *Grimshawomyia* was described by Hardy (1965) and contains two species, *G. palata* and *G. perkinsi*, the latter of which was initially described as a member of the genus *Drosophila* by Grimshaw (1901). The unique male genitalia, which feature surstyli that are exposed and an epandrium which is developed into a pair of moderately large lateral lobes, extending beyond the apices of the surstyli (Figs. 5-6), suggest that these taxa actually form a clade within the genus *Scaptomyza*. This clade is also characterized by having the second antennal segment sharply pointed at the apex, extending over the base of the third segment; the vertical and ocellar setae inserted into the somewhat swollen sides of the vertex; a long costal fringe, which extends nearly to vein R_{4+5}, and the distinctive wing markings.



FIGURES 5-6. **5**, Male terminalia of *Scaptomyza* (*Grimshawomyia*) *perkinsi* (Grimshaw); **6**, Male terminalia of *Scaptomyza* (*Grimshawomyia*) *palata* (Hardy).

Included Taxa. *Scaptomyza* (*Grimshawomyia*) *palata* (Hardy), **comb. nov.** from Maui and O'ahu, and *S.* (*Grimshawomyia*) *perkinsi* (Grimshaw), **comb. nov.** from Maui, O'ahu and Hawai'i (Nishida, 2002).

KEY TO SPECIES OF THE SUBGENUS *Grimshawomyia* Hardy

16. Clypeus and lower margin of the face yellow; wing with distinct pattern, apex lightly infuscated; two reclinate orbital setae present on frons; coxae predominantly yellow; foretarsi brown to black; third costal section shorter, roughly 2.5 times longer than fourth; each pleuron with a broad, transverse yellow vitta, lower 1/2 of katepisternum yellow, surstyli longer than wide, each with a row of fine teeth on venter. Hawai'i .... *perkinsi* (Grimshaw)

- Clypeus pale brown; lower margin of the face predominantly brown, with a thin band of yellow; wing pattern similar to above, but with hyaline area at apex; three distinct reclinate orbital setae present on frons; coxae brown; foretarsi yellow; third costal section longer, about 3.5 times longer than fourth; pleura almost entirely brown, lacking distinct vittae; surstyli plainly visible, evenly rounded on ventral surface, lacking conspicuous teeth. O'ahu, Maui .... *palata* (Hardy)

Scaptomyza (*Titanochaeta*)

Diagnosis. *Titanochaeta* was erected by Knab (1914) as a genus of endemic Hawaiian Drosophilidae. Hardy (1965) suggested that this genus actually should be considered a subgenus of *Scaptomyza* based on a variety of morphological characters including conspicuous surstyli which project well beyond the margins of the ninth tergite (Fig. 3), lack of ventral rays on the arista, and a short head which is approximately two times higher than long. We are placing the eleven known species of *Titanochaeta*, all of which are parasitic on spider egg sacs, in a subgenus of *Scaptomyza*. Chaetotaxy is an important synapomorphy of the subgenus *Titanochaeta*. These species have eight rows of acrostichal setulae, a character not seen in the other species of *Scaptomyza*. Furthermore, the setae on the head and thorax are very strong, the vertical setae are often longer than the head is wide. The shape of the head is also characteristic. It is equal to or narrower than the thorax in width, with a distinctly oblique, slanted front which is often more than two times longer than the lower margin of the head. The genae are straight sided and indented along the anterior eye margin. Finally, the ovipositor of most taxa is long and needle-like, probably due to the parasitic lifestyle of these taxa.

Discussion. The new subgeneric status of *Titanochaeta* in *Scaptomyza* requires that we propose new replacement names for *T. evexa*, *T. kauaiensis*, and *T. silvicola* because those specific epithets are preoccupied in the genus *Scaptomyza*. We propose: *Scaptomyza neoevexa* O'Grady et al., **new replacement name** for *Titanochaeta evexa* (Hardy, 1965) (preoccupied by *Scaptomyza evexa* Hardy, 1965), *Scaptomyza neokauaiensis* O'Grady et al., **new replacement name**, for *Titanochaeta kauaiensis* (Hardy, 1965) (preoccupied by *Scaptomyza kauaiensis* Hackman, 1959), and *Scaptomyza neosilvicola* O'Grady et al., **new replacement name**, for *Titanochaeta silvicola* (Hardy, 1965) (preoccupied by *Scaptomyza silvicola* Hardy, 1965).

Included Taxa. *Scaptomyza* (*Titanochaeta*) *bryani* (Wirth), **comb. nov.** from Hawai'i, O'ahu, and Maui Nui, *S.* (*Titanochaeta*) *chauliodon* (Hardy), **comb. nov.** from Maui and O'ahu, *S.* (*Titanochaeta*) *contestata* (Hardy), **comb. nov.** from O'ahu, *S.* (*Titanochaeta*) *glauca* (Hardy), **comb. nov.** from Maui, *S.* (*Titanochaeta*) *ichneumon* (Knab), **comb. nov.** from Hawai'i, *S.* (*Titanochaeta*) *neoevexa* O'Grady et al., from Moloka'i, *S.* (*Titanochaeta*) *neokauaiensis* O'Grady et al., from Kaua'i, *S.* (*Titanochaeta*) *setosiscutellum* (Hardy), **comb. nov.** from Hawai'i and Moloka'i, *S.* (*Titanochaeta*) *neosilvicola* O'Grady et al., from Hawai‘i, *S.* (*Titanochaeta*) *sweyzei* (Wirth), **comb. nov.** from Kaua‘i, Maui, and O‘ahu, and *S.* (*Titanochaeta*) *vittigera* (Hardy), **comb. nov.** from Kaua‘i (Nishida, 2002).

Discussion. The species in this group are infrequently collected and poorly understood taxonomically. The fact that a number of species in the subgenus *Titanochaeta* are present on multiple, non-adjacent islands suggests that they are either better at dispersing or have a lower rate of speciation than other endemic Hawaiian groups. It also might indicate that there are additional cryptic species remaining to be described in this group.

KEY TO SPECIES OF THE SUBGENUS *Titanochaeta* Knab

17. Female ovipositor blunt, rounded at apex .... *contestata* (Hardy)
\- Ovipositor pointed, needle-like 18
18. Crossveins distinctly infuscated; M1 between crossveins dm-cu and r-m short, about 1/5 length of M1 measured from crossvein dm-cu to apex. Maui, O‘ahu, Kaua‘i .... *swezeyi* (Wirth)
\- Crossveins not infuscated; M1 between crossveins dm-cu and r-m greater than 1/5 the length of M1 between dm-cu and apex 19
19. Sides of scutellum with conspicuous setae in addition to anterior and posterior scutellars; both katepisternal setae well developed, roughly subequal in length 20
\- Scutellum lacking secondary setae; length of anterior katepisternal setae variable, ranging from short to subequal setae 21
20. Mesonotum and scutellum entirely yellow, abdomen predominantly yellow Southern O‘ahu, Hawai‘i, Maui, Moloka‘i, Lana‘i .... *bryani* (Wirth)
\- Mesonotum mostly black in ground color, covered with gray pollen; scutellum black, abdomen mostly black. Moloka‘i, Hawai‘i .... *setosiscutellum* (Hardy)
21. Anterior katepisternal strong, about equal in length to posterior katepisternal setae; surstyli bear a strong black spine at the apex of a prominent posterior projection; apical fork of arista long or bifid, giving the appearance of a ventral ray . Maui, O‘ahu ... . *chauliodon* (Hardy)
\- Anterior katepisternal not over 1/2 length of posterior, usually small and hair-like; male genitalia not as above; arista with short terminal fork, never long or bifid........ 22
22. Mesonotum predominantly yellow with three narrow brown vittae extending the full length; incomplete brown vittae present on the pleurae; scutellum with a brown spot extending over basal 1/2; abdomen dark brown, distinctly marked with yellow. Kaua‘i .... *vittigera* (Hardy)
\- Predominantly black species, mesonotum and scutellum entirely black in ground color, lacking vittae 23
23. First two abdominal segments almost entirely yellow 24
\- Abdomen almost entirely black, a narrow yellow band may be present at the apex of second tergum 26

24. Tergites three and four shining black, five and six yellow; epandrium about two times longer than high, truncated ventrally; no projection along medial surface of surstylus observed in ventral view. Moloka'i .... *neoevexa* O'Grady et al.

- Abdomen predominantly brown or black; epandrium about two times higher than long, tapered ventrally; moderate to strong projection on medial surface of surstyli when observed in ventral view 25

25. Abdominal tergites four to six brownish yellow on lateral margins, darker on dorsum; male genitalia brownish yellow; pleurae largely brown; surstyli, when observed in lateral view, with sharply pointed projection on mediolateral surface and sharply pointed spine-like process on posterior margin. Hawai'i .... *ichneumon* (Knab)

- Abdominal tergites four to six, including genitalia, predominantly shining black; pleurae entirely yellow; surstyli, when observed in lateral view, lacking sharply pointed projection on mediolateral surface, process on posterodorsal surface of surstyli broad, not spine-like and pointed. Kaua'i .... *neokauaiensis* O'Grady et al.

26. Abdomen shining black beyond second tergite; male genitalia yellow; anterior reclinate inserted near lower 1/3 of fronto-orbital plate. Maui .... *glauca* (Hardy)

- Abdomen black, dusted with gray; male genitalia black; anterior reclinate inserted near middle of fronto orbital plate. Hawai'i .... *neosilvicola* O'Grady et al.

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