



New combinations in Hawaiian *Drosophila* and *Scaptomyza* (Diptera: Drosophilidae)

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Abstract

The present paper transfers eight species from the genus *Drosophila* to the genus *Scaptomyza* based on characteristics of the male genitalia. One species, *Scaptomyza* (*Titanochaeta*) *canuta* (Hardy) **new combination**, fits within the concept of the subgenus *Titanochaeta*. The remaining seven taxa, *S. improcera* (Hardy) **new combination**, *S. magnipalpa* (Hardy) **new combination**, *S. parva* (Grimshawi) **new combination**, *S. prolixa* (Hardy) **new combination**, *S. taractica* (Hardy) **new combination**, *S. totonigra* (Hardy) **new combination**, and *S. vinnula* (Hardy) **new combination**, are included as unplaced species of *Scaptomyza*. An additional species, *Scaptomyza* (*Grimshawomyia*) *undulata* (Grimshaw) **new combination**, is transferred from the subgenus *Engiscaptomyza* to *Grimshawomyia* based on morphological and molecular characters. An expanded key to the subgenera of *Scaptomyza* that includes these unplaced taxa is presented. In addition, *Drosophila attigua* Hardy & Kaneshiro is reduced to a junior **new synonym** of *D. sharpi* Grimshaw.

Key words: Hawaii, *Drosophila attigua*, conservation, endangered species, *Scaptomyza*

Introduction

The endemic Hawaiian drosophilid fauna is composed of two genera, *Drosophila* Fallén and *Scaptomyza* Hardy. Phylogenetic analyses of molecular and morphological characters indicate that these groups are sister to one another (Remsen & O'Grady, 2002; Russo, *et al.*, 1995; Throckmorton, 1966). Expanded taxon sampling within the genus *Scaptomyza* suggests that this cosmopolitan genus originated and diversified in Hawaii, with some lineages escaping to give rise to cosmopolitan subgenera (O'Grady & DeSalle, 2008). In most parts of the world, *Drosophila* and *Scaptomyza* are morphologically distinct and can easily be distinguished by the presence of 6–10 rows of acrostichal setulae in the former and 2–4 rows in the latter. However, in the Hawaiian taxa, this character is less reliable for generic diagnosis, with members of several *Scaptomyza* subgenera (e.g., *Elmomyza*, *Engiscaptomyza*, *Titanochaeta*) possessing 6–8 rows of acrostichal setulae. To clarify the situation and provide diagnostic characters for the major lineages of Hawaiian Drosophilidae, O'Grady *et al.* (2003) redefined *Scaptomyza* to include species with “well developed, exposed surstyli and enlarged lobes on either the epandrium (ninth tergite), cerci, or both.” As a result, the genera *Grimshawomyia* Hardy and *Titanochaeta* Knab, and the *Drosophila* subgenus *Engiscaptomyza* Kaneshiro were transferred at that time to subgenera of *Scaptomyza*. Subsequently, as part of our ongoing phylogenetic studies of the Hawaiian Drosophilidae, we discovered several additional species that were originally placed in *Drosophila* but clearly fit in the revised concept of *Scaptomyza*, as well as a new synonym in *Drosophila*.

Material and methods

The type specimens of all species concerned were examined at the B. P. Bishop Museum (BPBM) and the Natural History Museum, London (BMNH). Additional alcohol-preserved specimens (*S. magnipalpa*, *S. parva*, and *S. undulata*) collected by the authors are stored in the O'Grady Lab collection, University of California–Berkeley (UCPO).

Results and discussion

Eight species described as *Drosophila* were found to fall under the revised concept of *Scaptomyza*. Based on the characters used by O'Grady *et al.* (2003), *Scaptomyza canuta* (Hardy) is placed in the subgenus *Titanochaeta*: it has eight rows of acrostichal setulae, a high, short head, and prominent surstyli. It also has elongate inner vertical setae and densely pilose eyes, which are found in most *Titanochaeta* species. It is distinguished from all other species of the subgenus by having the surstyli fused to the epandrium (Hardy, 1965). Three of the species we are including as unplaced within *Scaptomyza*—*S. magnipalpa* (Hardy), *S. prolixa* (Hardy), *S. totonigra* (Hardy)—may be basal members of the *Titanochaeta* lineage on the basis of several morphological characters. All three species have elongate inner vertical setae, and all but *S. totonigra* have a trapezoidal epandrium with strongly dentate surstyli, similar to several *Titanochaeta* species. However, all have the head less compressed in lateral view and two or more ventral rays on the arista, and the known females (*S. prolixa*, *S. totonigra*) lack the narrow, sclerotized ovipositor characteristic of *Titanochaeta*, possessing instead the fleshy ovipositor found in most *Scaptomyza*. Therefore, until more detailed morphological and molecular studies are taken, we are designating them as unplaced within the genus *Scaptomyza*.

Scaptomyza taractica (Hardy) and *S. parva* (Grimshaw) share an affinity with one another and with the subgenus *Alloscaptomyza*, primarily based on the single ventral ray on the arista. *Scaptomyza taractica* was described by Hardy (1965) as being similar to *S. (Engiscaptomyza) reducta* (Hardy), but the genitalic morphology of this species is quite different from that of *Engiscaptomyza*. Wheeler's catalog of the family Drosophilidae (Wheeler, 1981) listed the species under *Scaptomyza* but did not place it within a subgenus; since then it has frequently been treated under that name. However, since *S. parva* was apparently never formally transferred to *Scaptomyza*, we are including it here. While most Hawaiian Drosophilidae are single island endemics (O'Grady 2002), *S. parva* is notable for being recorded from most of the major islands (Hardy, 1965). The close affinity of both *S. parva* and *S. taractica* to the subgenus *Alloscaptomyza* is supported by antennal and genitalic characters, but neither species possesses the broadened head that is diagnostic for *Alloscaptomyza*. Interestingly, a large number of undescribed species (unpubl. data) exist that have provisionally been placed in *Alloscaptomyza*. These taxa show a range of head widths, from those as broad as "typical" *Alloscaptomyza* to those as narrow as *S. parva* and *S. taractica*. It is possible that when *Alloscaptomyza* is revised and the concept of this subgenus is examined in the context of the new taxa, the diagnostic characters of this subgenus will need to be redefined.

Scaptomyza improcera (Hardy) and *S. vinnula* (Hardy) have very similar and distinctive genitalia, with prominent ventral lobes on the epandrium and broad, concave, setulose surstyli. On this basis they appear closely related to one another, but different from all other known species of *Scaptomyza*. In fact, given that they are both from O'ahu and appear to differ only in minor details of form and color based on old specimens, it is quite possible that they represent a single species. However, the genitalia of the *S. improcera* male holotype are missing (Evenhuis, 1982), and study of additional specimens will be required to delimit the range of color and genitalic variability before an official determination of synonymy can be made.

In addition to moving these eight species from *Drosophila* to *Scaptomyza*, we formally transfer *S. undulata* (Grimshaw) from the subgenus *Engiscaptomyza* to the subgenus *Grimshawomyia*. The original place-

ment of this unique species in *Engiscaptomyza* focused primarily on its difference from *S. nasalis* (Grimshaw), rather than synapomorphies that would group it with the other members of the subgenus {Kaneshiro, 1969}. However, it clearly belongs in the subgenus *Grimshawomyia* based on the pointed second antennal segment and the pattern of wing infuscation, which is very similar to the two described species of *Grimshawomyia*, *S. palata* (Hardy) and *S. perkinsi* (Grimshaw). Mitochondrial DNA sequences also show that *S. undulata* is much closer to *S. (Grimshawomyia) palata* than to *S. (Engiscaptomyza) crassifemur* (Grimshaw) (unpubl. data). It is rarely taken by normal *Drosophila* collecting methods (sweeping and baits), but is relatively common in pitfall traps in the ‘Ōla‘a area, suggesting that it and other *Grimshawomyia* species may be more abundant than realized.

Finally, in the process of examining types, *Drosophila sharpi* Grimshaw was also seen and found to be identical to *D. attigua* Hardy & Kaneshiro, and the latter is therefore reduced to a junior synonym. The synonymy of these two is notable: *D. sharpi* was considered an obscure species of uncertain affinities, while *D. attigua* is currently considered to be of high conservation significance and is proposed for listing as Endangered (U.S. Fish and Wildlife Service, 2005). Many of Grimshaw’s *Drosophila* types are in rather poor condition, but that of *D. sharpi* is extremely well-preserved. All important male characters are readily visible on the specimen, including the sclerotized labellar rim, elongate palpal seta, strong oral vibrissae, lack of cilia on the front legs, and elongate, glabrous aedeagus. The last is necessary to distinguish it from the closely related *D. primaeva* Hardy & Kaneshiro, which has the aedeagus apically setose. It is remarkable that this synonymy was not recognized earlier, as the species is quite distinctive; aside from *D. primaeva* there are no others it could be confused with. It should be noted that the wing coloration on the type male is much weaker and more diffuse than shown in Hardy’s (1965) illustration (Fig. 189c); there are faint stripes along the apical portions of veins R₂₊₃ and R₄₊₅, across the dm–cu crossvein, and at the apex of R₁, but none of these are particularly distinct and they probably vary in intensity among individuals.

TABLE 1. Summary of changes made in this paper.

New Combination	Previous Combinations
<i>Scaptomyza (Titanochaeta) canuta</i> (Hardy)	<i>Drosophila canuta</i> Hardy, 1965:200–202
<i>Scaptomyza improcera</i> (Hardy)	<i>Drosophila improcera</i> Hardy, 1965:317–319
<i>Scaptomyza magnipalpa</i> (Hardy)	<i>Drosophila magnipalpa</i> Hardy, 1965:352–354
<i>Scaptomyza parva</i> (Grimshaw)	<i>Drosophila parva</i> Grimshaw, 1901:65
<i>Scaptomyza prolixa</i> (Hardy)	<i>Drosophila prolixa</i> Hardy, 1965:430–432
<i>Scaptomyza taractica</i> (Hardy)	<i>Drosophila taractica</i> Hardy, 1965:479
<i>Scaptomyza totonigra</i> (Hardy)	<i>Drosophila totonigra</i> Hardy, 1965:486–487
<i>Scaptomyza vinnula</i> (Hardy)	<i>Drosophila vinnula</i> Hardy, 1965:510–512
<i>Scaptomyza (Grimshawomyia) undulata</i> (Grimshaw)	<i>Scaptomyza (Engiscaptomyza) undulata</i> O’Grady <i>et al.</i> , 2003:9 <i>Drosophila (Engiscaptomyza) undulata</i> Kaneshiro, 1969:83 <i>Drosophila undulata</i> Grimshaw, 1901:58
<i>Drosophila sharpi</i> Grimshaw	<i>Drosophila attigua</i> Hardy & Kaneshiro, 1969:41 (new junior synonym)

With the changes made here, nearly all of the “orphan” species of Hawaiian drosophilids are now placed within the species group classification structure. Five of the remaining species, *D. abjuncta* Hardy, *D. incompleta* Hardy, *D. joycei* Hardy, *D. molokaiensis* Grimshaw, *D. musae* Hardy, and *D. plumosa* Grimshaw clearly belong in the genus *Drosophila* but lack any characters that would allow them to be unambiguously placed in a species group. *Drosophila abjuncta* has a rather thick aedeagus that differs from that of other Hawaiian *Drosophila* but is still of the same general form, and does not have the enlarged surstyli that define *Scapto-*

myza. The holotype is in relatively poor condition, but new specimens that would allow fuller clarification of its status should be easily recognizable. The two Grimshaw species are known only from the type series and are unlikely to ever be identified with certainty. *Drosophila molokaiensis* is known only from the holotype; it bears some resemblance to members of the *haleakalae* group, but this cannot be confirmed as the type specimen is missing its head. The type series of *D. plumosa* consists of two females that differ in their head chaetotaxy; both lack any particularly distinctive characters that would allow them to be associated with a single male. Types of the last two unplaced species, *D. nigripalpus* Hardy and *D. varga* Hardy, have not yet been examined.

The changes made here are summarized in Table 1. A new key to the subgenera of *Scaptomyza* and species of the smaller subgenera, modified from O'Grady *et al.* (2003) to incorporate the unplaced species and other changes, is given below.

Key to the Hawaiian Subgenera and Unplaced Species of *Scaptomyza*, and Species of Subgenera *Engiscaptomyza*, *Grimshawomyia*, and *Titanochaeta*

1. White longitudinal stripe present on scutellum, anteriorly reaching at least to posterior region of mesonotum, often extending along entire length of mesonotum; terminal fork of arista deep, each branch equal in length to dorsal rays of arista subgenus *Tantalia* Malloch
 - Scutellum and mesonotum may be striped 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* Hardy
 - 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 10
4. Eight rows of acrostichal setulae present; female ovipositor sclerotized, may be needle-like and pointed.. subgenus *Titanochaeta* Knab, 24
 - 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* Malloch
 - 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* Hackman
7. Two rows of acrostichal setulae present subgenus *Parascaptomyza* Duda
 - Number of acrostichal rows varies from four to six 8
8. Wings with marks over crossveins and at apices of R and M veins. Hawai'i, Moloka'i, O'ahu, Kaua'i *S. parva* (Grimshaw)
 - Wings completely hyaline 9
9. Head broader than thorax subgenus *Alloscaptomyza* Hackman
 - Head not broader than thorax. Hawai'i *S. taractica* (Hardy)
10. 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* Malloch
 - Mesonotum brown (black in *S. totonigra*), sometimes with longitudinal vittae; acrostichal setulae in six to

- eight rows; ocellar triangle not enlarged; hind trochanter lacking distinctive black setae 11
11. Second antennal segment sharply pointed apically, extending over base of third segment; wings distinctly infuscated around veins and margins, central portions of cells mostly hyaline subgenus *Grimshawomyia* Hardy, 22
- Second antennal segment not sharply pointed; wings hyaline or evenly smoky 12
12. Tibiae yellow with two narrow brown bands, fainter on front tibia subgenus *Engiscaptomyza* Kaneshiro, 17
- Tibiae all yellow, or brown with yellow apices 13
13. Palpi greatly enlarged, protruding beyond the oral margin. Kaua'i *S. magnipalpa* (Hardy)
- Palpi not enlarged, enclosed within the oral cavity when mouthparts retracted 14
14. Epandrium with a prominent anteroventral lobe, over half as high (dorsoventrally) as main portion of epandrium; surstyli long and broad, setulose over the concave medial surface (see Figs. 117c and 211c in Hardy, 1965) 15
- Epandrium lacking a prominent lobe; surstyli not broad and medially setulose; mesonotum brown to black; femora dark brown 16
15. Thorax entirely yellow; ventral lobe of epandrium broader at apex than at base. O'ahu *S. vinnula* (Hardy)
- Mesonotum and anepisternum rufous, tinged with brown; ventral lobe of epandrium nearly parallel-sided, about as wide at apex as at base. O'ahu *S. improcera* (Hardy)
16. Tibiae all yellow. Moloka'i *S. prolixa* (Hardy)
- Tibiae brown except narrow bases and apices. Moloka'i, O'ahu *S. totonigra* (Hardy)

Subgenus *Engiscaptomyza* Kaneshiro, 1969

17. Mesonotum vittate 18
- Mesonotum lacking vittae 21
18. Surstylus sharply concave, with distinct lobe at apex which forms a "C" shape; dorsal lobe of hypandrium narrowly pointed, with indistinct protrusion (see Fig. 1 in Kaneshiro, 1969). Kaua'i *S. (Engiscaptomyza) ampliloba* (Hardy)
- Surstylus less concave, straighter in profile 19
19. Protrusion on dorsal lobe of hypandrium somewhat short, indistinct. O'ahu *S. (Engiscaptomyza) inflata* (Kaneshiro)
- Protrusion on dorsal lobe of hypandrium elongate, finger-like 20
20. 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 *S. (Engiscaptomyza) 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 *S. (Engiscaptomyza) nasalis* (Grimshaw)
21. Legs entirely yellow, except for brown apex of tarsus; leg segments short and thick. Hawai'i *S. (Engiscaptomyza) reducta* (Hardy)
- Femora almost entirely brown, tinged faintly with black, narrowly yellow at 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 *S. (Engiscaptomyza) lonchoptera* (Hardy)

Subgenus *Grimshawomyia* Hardy, 1965

22. Last segment of vein M sinuate; wing infuscated along all veins, but centers of all cells hyaline except for r_1 and apical third of r_{2+3} . Hawai'i *S. (Grimshawomyia) undulata* (Grimshaw)
- Last segment of vein M not sinuate; veins lacking infuscation on basal half of wing; cell r_{2+3} almost completely infuscated beyond r-m crossvein and cell r_{4+5} infuscated directly anterior of dm-cu crossvein ..23
23. Clypeus and lower margin of 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 katapisternum yellow, surstyli longer than wide, each with a row of fine teeth on venter. Hawai'i *S. (Grimshawomyia) 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 *S. (Grimshawomyia) palata* (Hardy)

Subgenus *Titanochaeta* Knab, 1914

24. Arista with one ventral ray; male surstylus without a posterior spine; female ovipositor sometimes blunt25
- Arista without ventral rays, or if one present (rarely in *S. chauliodon*), the male surstylus bears a prominent black posterior spine; female ovipositor always pointed, needle-like26
25. Pleura and sometimes femora dark brown to black; surstyli fused to epandrium (female unknown). Hawai'i, Maui *S. (Titanochaeta) canuta* (Hardy)
- Pleura and femora entirely yellow; surstyli not fused to epandrium; female ovipositor blunt. O'ahu..... *S. (Titanochaeta) contestata* (Hardy)
26. Crossveins distinctly infuscated; M between crossveins dm-cu and r-m short, about 1/5 length of M measured from crossvein dm-cu to apex. Maui, O'ahu, Kaua'i *S. (Titanochaeta) swezeyi* (Wirth)
- Crossveins not infuscated; M between crossveins dm-cu and r-m greater than 1/5 the length of M between dm-cu and apex.....27
27. Sides of scutellum with conspicuous setae in addition to anterior and posterior scutellars; both katapisternal setae well developed, roughly subequal in length 28
- Scutellum lacking secondary setae; length of anterior katapisternal setae variable, ranging from short to subequal setae29
28. Mesonotum and scutellum entirely yellow, abdomen predominantly yellow. Southern O'ahu, Hawai'i, Maui, Moloka'i, Lāna'i *S. (Titanochaeta) bryani* (Wirth)
- Mesonotum mostly black in ground color, covered with gray pollen; scutellum black, abdomen mostly black. Moloka'i, Hawai'i..... *S. (Titanochaeta) setosiscutellum* (Hardy)
29. Anterior katapisternal strong, about equal in length to posterior katapisternal 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 *S. (Titanochaeta) chauliodon* (Hardy)
- Anterior katapisternal 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 bifid30
30. 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 *S. (Titanochaeta) vittigera* (Hardy)
- Predominantly black species, mesonotum and scutellum entirely black in ground color, lacking vittae. 31
 - 31. First two abdominal segments almost entirely yellow32
 - Abdomen almost entirely black, a narrow yellow band may be present at apex of second tergum34
 - 32. Tergites 3 and 4 shining black, 5 and 6 yellow; epandrium about 2 times longer than high, truncated ventrally; no projection along medial surface of surstylus visible in ventral view. Moloka'i
..... *S. (Titanochaeta) neoevexa* O'Grady *et al.*
 - Abdomen predominantly brown or black; epandrium about 2 times higher than long, tapered ventrally; moderate to strong projection on medial surface of surstyli in ventral view33
 - 33. Abdominal tergites 4 to 6 brownish yellow on lateral margins, darker on dorsum; male genitalia brownish yellow; pleura 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
..... *S. (Titanochaeta) ichneumon* (Knab)
 - Abdominal tergites 4 to 6, including genitalia, predominantly shining black; pleura 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
..... *S. (Titanochaeta) neokauaiensis* O'Grady *et al.*
 - 34. Abdomen shining black beyond second tergite; male genitalia yellow; anterior reclinate inserted near lower 1/3 of fronto-orbital plate. Maui *S. (Titanochaeta) glauca* (Hardy)
 - Abdomen black, dusted with gray; male genitalia black; anterior reclinate inserted near middle of fronto-orbital plate. Hawai'i *S. (Titanochaeta) neosilvicola* O'Grady *et al.*

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