Records of the Hawaii Biological Survey for 2021. Edited by Neal L. Evenhuis. *Bishop Museum Occasional Papers* 142: 75–87. (2022)

lsid:zoobank.org:pub:38EA4820-865E-4FD0-9FA5-E4BFB39CE961

The *Scaptomyza cyrtandrae* species group, with the description of a new species (Diptera: Drosophilidae)

BEN BURGUNDER, AUGUSTO SANTOS RAMPASSO, AND PATRICK O'GRADY¹ Department of Entomology, Cornell University, 129 Garden Avenue, Comstock, Room 3140, Ithaca, New York 14853, USA

Abstract. The genus *Scaptomyza* includes over 270 species, about half of which are endemic to the Hawaiian Islands. These species show similar levels of host plant specificity and single island endemism as their sister group, the Hawaiian *Drosophila*, although they display less dimorphism in secondary sexual characters. Instead, *Scaptomyza* species possess diverse characters associated with the male terminalia, even between closely related species. Here we use dissections of male terminalia between two closely related taxa found living on the undersides of leaves of native *Cyrtandra* species to erect the *Scaptomyza cyrtandrae* group and describe one new species, *Scaptomyza neocyrtandrae* Burgunder, Rampasso, and O'Grady, from the island of Maui.

Key words: Elmomyza, Hawaiian Islands, description, Drosophilidae, taxonomy

INTRODUCTION

The genus *Scaptomyza* was erected by Hardy (1849) for *Scaptomyza graminum* and contains a total of 273 described species, 148 of which are endemic to the Hawaiian Islands (Rampasso & O'Grady 2022). Currently, twenty-one subgenera are placed within *Scaptomyza* (O'Grady *et al.* 2010), including several endemic Hawaiian groups formerly considered to be genera (*Grimshawomyia* and *Titanochaeta*) or subgenera (*Engiscaptomyza*) of *Drosophila*, but synonymized with *Scaptomyza* on the basis of male terminalia characters (O'Grady *et al.* 2003). In addition, Magnacca & O'Grady (2008) transferred eight *Drosophila* species to various subgenera of *Scaptomyza* on the basis of male terminal morphology. Nine *Scaptomyza* subgenera are either completely endemic to the Hawaiian archipelago (*Alloscaptomyza*, *Elmomyza*, *Engiscaptomyza*, *Exalloscaptomyza*, *Grimshawomyia*, *Tantalia*, and *Titanochaeta*) or contain species which are endemic to this island chain (*Bunostoma* and *Rosenwaldia*). The remaining 125 described species of *Scaptomyza* are placed in eleven subgenera and are found elsewhere in the world (O'Grady *et al.* 2010; Rampasso & O'Grady 2022; Wheeler 1981, 1986).

Throckmorton (1966) referred to all members of the genus *Scaptomyza* as "scaptoids" and considered the Hawaiian and mainland taxa to be monophyletic. O'Grady & DeSalle (2008) used a molecular phylogeny to examine the evolutionary and biogeographic history of this group. Their study supported all members of the genus *Scaptomyza* as the monophyletic sister group to the endemic Hawaiian *Drosophila*, which has been corroborated by several recent studies (Finet *et al.* 2021; Katoh *et al.* 2017; Lapoint *et al.* 2013; Russo *et al.* 2013; Suvorov *et al.* 2021; Yassin 2013) and reviewed in O'Grady & DeSalle (2018a, b). The mainland taxa were derived from a Hawaiian ancestor that left Hawaii and subsequently diversified within the past ~10 million years. The Hawaiian *Scaptomyza* have underdone significant radiation, particularly within the past 5 million

^{1.} Corresponding author: ogrady@cornell.edu

years, as more high islands with suitable rainforest habitat have emerged in the archipelago (Lapoint *et al.* 2013).

The Hawaiian endemic subgenus *Elmomyza* is the largest group in *Scaptomyza*, with 85 described species (Bächli 2021; O'Grady *et al.* 2010; Rampasso & O'Grady 2022). Based on undescribed material present in the entomology collection at the Bernice Pauahi Bishop Museum, University of Hawai'i, Manoa, and in the Cornell University Insect Collection, the actual number of species in this subgenus may be nearly double the current number (O'Grady & Rampasso, pers. observ.). While additional taxonomic work focusing on the subgenus *Elmomyza* is necessary, this clade can be divided further into groups of closely related species on the basis of external morphology and ecological associations. For example, there are several clades distributed throughout the high islands that are associated with the same plant genera (Magnacca *et al.* 2008), suggesting the ancestor of these clades may have adapted to a host plant in the past and radiated on plants with similar chemistries, similar to the evolutionary pattern observed in the Hawaiian *Drosophila* (O'Grady *et al.* 2011).

Phylogenetic relationships within the genus *Scaptomyza* are poorly understood (reviewed in O'Grady & DeSalle 2018b). Lapoint *et al.* (2013) produced a phylogeny of 63 *Scaptomyza* species, representing 13 of the 21 established genera, using a dataset of ~5,000 molecular characters. Several Hawaiian subgenera (*Alloscaptomyza, Bunostoma, Engiscaptomyza, Grimshawomyia, Rosenwaldia, Tantalia, and Titanochaeta*) were recovered as monophyletic. Interestingly, the largest subgenus, *Elmomyza, was paraphyletic with respect to the subgenera Rosenwaldia and Tantalia.* Sampling within *Elmomyza included 25 described and 5 putative new species, accounting for about 30% of the known species diversity in this subgenus. The phylogeny sampled both <i>S. cyrtandrae* and *S. neocyrtandrae* and suggested that they were sister taxa with weak support (<50% bootstrap, 96% posterior probability). Clearly, additional taxon sampling and an expanded number of molecular characters will need to be analyzed before we have a more resolved understanding of evolutionary relationships within and between *Scaptomyza* subgenera.

Here we describe a new species of *Scaptomyza*, *S. neocyrtandrae* Burgunder *et al.*, and erect the *cyrtandrae* species group within subgenus *Elmomyza*, based on a combination of ecological associations, morphological characters, and phylogenetic relationships.

MATERIAL AND METHODS

Collections

Specimens were either aspirated directly from leaves of *Cyrtandra* spp. or swept from vegetation. This species is endemic to the island of Maui and has been collected in the Waikamoi Forest Preserve on East Maui, roughly at 4,000 ft. in elevation. Collection numbers are preceded with an O (O'Grady Collections), an L (Lapoint Collections) or an M (Magnacca Collections). Six-digit barcodes refer to O'Grady Lab Accession numbers. Museum abbreviations follow Evenhuis (2021).

Species Descriptions and Imaging

Hardy (1965) described *Scaptomyza cyrtandrae* based on individuals collected in the Napau Crater, Hawai'i, in July 1956. Through the following decades, additional collections of morphologically similar individuals from the hirsute leaves of *Cyrtandra* spp. (Gesneriaceae) were made on the Big Island of Hawai'i and on Maui. Upon examination of the male terminalia of specimens sampled on each island, it became evident that they were two distinct entities, and the population collected on Maui was an undescribed species.



Fig. 1: Habitus of *Scaptomyza cyrtandrae* Hardy, 1965 in left lateral (A) and dorsal (B) views. Scale bar = 1 mm. Photo: A.S. Rampasso.

All material was sorted to species and individuals within each of the two *cyrtandrae* group species were verified as conspecific prior to dissection and description. Measurements and indices follow Hardy *et al.* (2001), whereas all morphological characters follow recent nomenclatural revisions (Cumming & Wood 2009, 2017; Rampasso & O'Grady 2021; Rice *et al.* 2019). The holotype and allotype are housed in the Bernice Pauahi Bishop Museum. Paratypes are present in the Cornell University Insect Collection and the University of Hawai'i at Manoa Insect Museum.

We used different individuals for the habitus and terminalia imaging. Although paratypes of *S. neocyrtandrae* were dissected, no holotypes were dissected. The habitus of two ethanol-preserved male individuals belonging to *Scaptomyza cyrtandrae* (Fig. 1) and two males of *Scaptomyza neocyrtandrae* sp. nov. (Fig. 2) were imaged. Material was held in position using white aquarium sand, then covered in ethanol prior to being imaged at different depths of focus in under a Nikon SMZ1500 stereomicroscope equipped with an Excelis HD Microscope Camera with an 11.6-in AU-600-HDS monitor. One male of each species was imaged in left lateral view, and the other, in dorsal view. Sets of 69–87 photos were taken with 15–20× magnification and the software CombineZP was used to stack the photos into all-in-focus composites, following Vilela & Prieto (2018)

One ethanol-preserved male specimen of *Scaptomyza cyrtandrae* (Figs. 3 and 4) and another of *Scaptomyza neocyrtandrae* sp. nov. (Fig. 5) were dissected and subsequently pointed. The technique of terminalia dissection is based on Wheeler & Kambysellis (1966), Kaneshiro (1969) and Bächli *et al.* (2004). The sclerites were disarticulated in depression slides filled with 70% ethanol, using a pair of entomological pins, and terminalia slides were prepared using Euparal as the mounting medium.

Slides were stored at room temperature and imaged under a Macroscopic Solutions Macropod Pro and Canon EOS 6D DSLR camera body using EF 70–200 mm zoom lens with $50 \times$ Mitutoyo objective lens in at least three positions (posterior, oblique posterior, and left lateral views). For each view, a set of 147–462 photos were taken in different depths of focus and stacked using Zerene Stacking Software Version 1.04 (Zerene Systems, LLC 2014). Since the male terminalia of *S. cyrtandrae* was heavily sclerotized and has multiple overlapping sclerites, initially the surstylus was disarticulated from the epandrium, and then the hypandrium and associated sclerites were disarticulated from the epandrium as well and imaged following the same methodology. The resulting all-infocus composites were edited on Adobe Photoshop 2021 to remove the background and correct color and white balance. The analyzed terminalia and the remaining of the abdomens were stored in microvials filled with glycerol and attached by the stopper to the pins of the dissected specimens.

Scaptomyza cyrtandrae Hardy, 1965

(Figs. 1, 3, 4)

Scaptomyza cyrtandrae Hardy, 1965: 673.

Diagnosis. *Scaptomyza cyrtandrae* is characterized by having four rows of acrostichal setae, a yellow body and two pairs of dorsocentral setae. It differs from its closest sibling species, *S. neocyrtandrae* Burgunder, Rampasso & O'Grady, by characters of the male terminalia (Fig. 3).

Distribution. Hawaiian Islands: Hawai'i.

Ecology. This species is associated with native *Cyrtandra* as both feeding and breeding sites (Hardy 1965).

Measurements. N=23: TL=0.6 mm (0.6); WL=1.5 mm (1.5); TL/WL=0.4 (0.4); CI=2.65 (2.6-2.7); 4V=1.75 (1.5-2.0); 5X=1.6 (1.4-1.8); 4C=0.9 (0.8-1.0); M=0.55 (0.5-0.6). N=19: TL =0.6 mm; WL=1.4 mm; TL/WL=0.4; CI=2.3; 4V=1.8; 5X=1.8; 4C=0.9; M=0.5.

Types. The holotype male and allotype female are deposited in the BPBM. **Hawai'i:** Napau Crater, 2,900 ft [884 m], Jul 1956, D.E. Hardy.

Material Examined. Hardy (1965) reported this species from a number of localities on the Big Island of Hawaii. Additional material, present in the BPBM, UHM, and CUIC collections has been examined. Hawaii: Crater Road, Kilauea, Hawaii, 3,300 ft [1,005 m], Jun 1918, W.M. Giffard; Upper Ola'a Forest, 4,000 ft [1219 m], Aug 1952, D.E. Hardy, W.C. Mitchell; Upper Ola'a Forest, 4,000 ft [1,219 m], Jul



Fig. 2: Habitus of *Scaptomyza neocyrtandrae* Burgunder, Rampasso and O'Grady, sp. nov. in left lateral (**A**) and dorsal (**B**) views. Scale bar = 1 mm. Photo: A.S. Rampasso.

1953, D.E. Hardy, W.C. Mitchell; Upper Ola'a Forest, 4,000 ft [1,219 m], Jul 1956, D.E. Hardy, W.C. Mitchell; Hawaii Volcanoes National Park, Thurston Lava Tube, on leaves of Cyrtandra, Aug 1957, John W. Beardsley; Hawaii Volcanoes National Park, Thurston Lava Tube, on leaves of Cyrtandra, Apr 1962, H.A. Bess; Hawaii Volcanoes National Park, Thurston Lava Tube, on leaves of Cyrtandra, Dec 1962, John W. Beardsley; Stainback Highway, near Kulani Prison Camp, 25 mi [40.5 km] from Hilo, 7-8 Feb 1999, O49.C, 200341, P.M. O'Grady, S.L. Montgomery; Hawaii Volcanoes National Park, Kīpuka Kī, 9 Sep 2000, O99.8, 200177, P.M. O'Grady, D. Foote; Hawaii Volcanoes National Park, Ola'a Forest, 20 Oct 2000, O112.4, 200342, P.M. O'Grady; Hawaii Volcanoes National Park, Thurston Lava Tube, aspirated from Cvrtandra, 7 Jul 2004, O249.1, 201465, P.M. O'Grady, C.D. Specht, M. Gianullo; Hawaii Volcanoes National Park, Mauna Ulu, 11 Aug 2005, 313.I, 201201, P.M. O'Grady, G.M. Bennett; Stainback Highway, Tom's Trail, 3,200 ft [975 m], 1 Oct 2006, L3.6, 202313, R.T. Lapoint, G.M. Bennett, K.N. Magnacca; Stainback Highway, Kīpuka 3,600 ft [1,096 m], on Cyrtandra platyphylla, 1 Oct 2006, M06-1088, 202583, K.N. Magnacca; Tree Planting Road 4,100 ft [1,250 m], sweeping vegetation, 3 Oct 2006, M06-1109, 202586, K.N. Magnacca; Hawaii Volcanoes National Park, Ola'a Forest, Trail 1, 3,800 ft [1158 m], sweeping vegetation, 3 Oct 2006, M06-1115, 202588, K.N. Magnacca; Pu'u Huluhulu Crater 3,400 ft [1036 m], on Cyrtandra platyphylla, 4 Oct 2006, M06-1121, 202590, K.N.



Fig. 3. Male terminalia of *Scaptomyza cyrtandrae* Hardy, 1965 imaged in the present study in oblique posterior (**A**), posterior (**C**), and left lateral (**E**) views, in comparison to the drawings from the original species description in Hardy (1965) in posterior (**B**) and left lateral (**D**) views. Scale bar = 0.1 mm. Photo: A.S. Rampasso.

Magnacca; Hawaii Volcanoes National Park, Mauna Ulu, 9 Jan 2009, O512.2, P.M. O'Grady, G.M. Bennett, D. Crowser, E. Young, S. Bridgers; Hawaii Volcanoes National Park, Thurston Lava Tube, 9 Jan 2009, O513.1, P.M. O'Grady, G.M. Bennett, D. Crowser, E. Young, S. Bridgers.

Scaptomyza neocyrtandrae Burgunder, Rampasso & O'Grady, sp. nov.

(Figs. 2, 5)

lsid:zoobank.org:act:223B8B21-4381-4FA9-9A19-EC60107AD887

Diagnosis. This species fits in the complex characterized by having four rows of acrostichal setae, a yellow body and two pairs of dorsocentral setae. It differs from its closest sibling species, *S. cyrtandrae*, by having distinctly different male terminalia (Fig. 3).

Description. Male. Head. Pedicel and first flagellomere yellow-brown. Arista with two dorsal and no ventral branches in addition to terminal fork. Terminal fork deep, about 1/2-2/3 as long as basal segment of arista. Two small inner branches present at base of arista. Vertex, ocellar triangle and from brown. Anterior reclinate inserted posterolaterally to proclinate and short, about 1/4-1/5 length of proclinate. Proclinate orbital about 3/4 length of posterior reclinate. Ocellar and vertical setae strong, as least as long as posterior reclinate. Gena yellow to yellow-brown. Vibrissae strong. Subvibrissal setae minute, less than 1/5 length of vibrissae. Face, mouthparts and palps yellow to yellow-brown. Palps with three long subapical setae, longest on ventromedial surface, remaining palpal setae subequal, inserted on dorsolateral and dorsomedial surfaces. Shorter palpal setae 2/3 length of ventromedial seta. Thorax. Scutum with central yellow stripe roughly defined by medial pair of acrostichal setae. Remainder of scutum diffusely light brown; light brown coloration interrupted at transverse suture, on anterior margin of postpronotum, and along margin with pleurae. Scutellum is uniform light brown. Two pairs of dorsocentral setae present. Acrostichal setae in 4 regular rows when counted between anterior dorsocentral setae. Basal scutellar setae parallel; apical scutellar setae cruciate. Pleura light yellow. One postpronotal seta present. Anterior katepisternal seta approximately 3/4 length of posterior katepisternal seta. Legs. Pale yellow to white. Wings. Hyaline without distinct pattern. Abdomen. Light yellow, tinged with light brown on dorsal margin. Male terminalia. Epandrium microtrichose, with an anterodorsal phragma and neither posterior nor ventral lobes. Cercus rounded in lateral view, connected to epandrium by membranous tissue, setose in the dorsal and in the posteroventral regions. Surstylus strongly developed, with three posterior projections. The dorsal projection is digitate and bears a single surstylar tooth at the apex; the medial is broadened, whereas the ventral projection is apically narrowed in lateral view. Hypandrium shorter than epandrium. Phallus expanded and somewhat rectangular shaped in lateral view, with a narrowed projection on the posterodorsal region. Phallapodeme is about the same length as the phallus, laterally flattened and the anterior portion is expanded.

Female fits with the male in all characters except coloration. Frons light brown on anterior margin. Fronto-orbital plates, vertex, gena, and posterior margin of frons dark brown. Median yellow stripe and yellow areas on postpronotum, pleural margin and transverse suture reduced; remainder of scutum dark brown. Pleura with distinct yellow-brown tinges. Abdomen dark brown dorsally, with diffuse yellow white coloration on lateral margin. Measurements. N=1 \bigcirc , TL=0.53 mm; WL=1.66 mm; TL/WL=0.32; CI=2.43; 4V=1.73; 5X=1.60; 4C=0.93; M=0.53. N=1 \bigcirc , TL=0.56; WL=1.44; TL/WL=0.39; CI=2.25; 4V=1.50; 5X=2.0; 4C=1.0; M=0.50.

Distribution. Hawaiian Islands: Maui.



Fig. 4. Male terminalia of *Scaptomyza cyrtandrae* Hardy, 1965 in posterior view, with the left surstylus disarticulated (**A**), disarticulated left lateral surstylus in anterior view, and hypandrium and associated sclerites in posterior (**C**), oblique posterior (**D**), left lateral (**E**), oblique anterior (**F**), and anterior (**G**) views. Scale bar = 0.1 mm. Photo: A.S. Rampasso.



Fig. 5. Male terminalia of *Scaptomyza neocyrtandrae* Burgunder, Rampasso and O'Grady sp. nov. in left lateral (A), oblique posterior (B), and posterior (C) views. Scale bar = 0.1 mm. Photo: A.S. Rampasso.

Ecology. This species is associated with native *Cyrtandra* spp. as both feeding and breeding sites.

Types. The holotype male and allotype female are deposited in BPBM. **Maui:** Waikamoi Forest Reserve, Carson Trail, 3,600 ft [1097 m], 6 Aug 2005, O305.2, 205635, P.M. O'Grady, G.M. Bennett. **Material Examined.** The following paratypes are placed in the BPBM, UHM, and CUIC collections.

Maui: 23, 39, Waikamoi Forest Preserve, Heed Trail, 3,600 ft [1097 m], 4 Aug 2005, O301.G, 201368, P.M. O'Grady, G.M. Bennett, C. Hayashi, J.E. Gatesy; 53, 99, same collection as holotype and allotype; 23, 19, Waikamoi Forest Preserve, Heed Trail, 3,600 ft [1,097 m], 31 Jul 2007, O389, 200798, P.M. O'Grady, K. N. Magnacca, R.T. Lapoint, G.M. Bennett; 33, 19, Waikamoi Forest Reserve, Carson Trail, 3,600 ft [1,097 m], 6 Aug 2007, O406.8, P.M. O'Grady, K.N. Magnacca, R.T. Lapoint, G.M. Bennett; 13, Waikamoi Forest Reserve, Haiku Uka Flume Road, 31 Jul 2007, KNM07-0494, K.N. Magnacca.

Etymology. Named for its close relationship with *S. cyrtandrae*.

DISCUSSION

Scaptomyza cyrtandrae and *S. neocyrtandrae* are associated with the plant genus *Cyrtandra,* a member of the African violet family (Gesneriaceae). This is a large, complex plant group endemic to the Hawaiian Islands, leading Wagner *et al.* (1999) to describe it as being characterized by "kaleidoscopic polymorphism" within a single small geographic area and rampant hybridization among species. Species numbers in the group have ranged from around 30 in the early revisions (Clarke 1883; Rock 1917, 1918, 1919a,b) to over 250 in St. John's work (*e.g.,* St. John & Takeuchi 1988). Wagner *et al.* (1999) recognized a total of 53 endemic species in six sections, and proposed 4-6 independent colonization events for the Hawaiian flora. However, recent phylogenetic studies (Clark *et al.* 2009; Cronk *et al.* 2005; Kleinkopf *et al.* 2019) suggest that the Hawaiian taxa are the sister clade to the rest of the Pacific species, and was the result of a single ancestral colonization event. Some recent work on endemic *Cyrtandra* suggest that the island of Hawaii was colonized multiple times and that *C. platyphylla* populations on the islands of Hawaii and Maui are quite distinct (Johnson *et al.* 2019).

The two species treated here are pale yellow and can be found on the hirsute undersides of *Cyrtandra* leaves as adults, larvae and pupae. Hardy (1965) reported the larvae of *S. cyrtandrae* were "rather sluggish and apparently feed on exudate from the hairs on the undersides of the leaves. The larvae appress their mouthparts closely to the hairs of the leaf and remain in one position for long periods of time." Both *S. cyrtandrae* and *S. neocyrtandrae* have been recorded from *C. platyphylla* (section *Crotonocalyces*) from Hawai'i and Maui, respectively. Additional research will be necessary to determine whether other *Scaptomyza* species are present, either within the section *Crotonocalyces*, or across the genus as a whole.

ACKNOWLEDGEMENTS

We thank Dr. Jason Dombroskie for allowing access to the Cornell University Insect Collection imaging equipment and Loren Donovan Jones for setting up the camera. We also thank Dr. Neal Evenhuis and an anonymous reviewer for their helpful comments on this manuscript. This paper was supported by NSF Grant 2030129 to PMO.

REFERENCES

- Bächli, G. 2021. Taxodros: The database of *Drosophila* taxonomy. Available from: https://www.taxodros.uzh.ch/ (Accessed 1 May 2022)
- Clark, J.R., Wagner, W.L. & Roalson, E.H. 2009. Patterns of diversification and ancestral range reconstruction in the southeast asian-pacific angiosperm lineage *Cyrtandra* (Gesneriaceae). *Molecular Phylogenetics and Evolution* **53**: 982–994. https://doi.org/10.1016/j.ympev.2009.092

- Clarke, C.B. 1883. Cyrtandreae (Gesnaracearum tribus). *Monographiae Phanerogamarum* 5: 1–303.
- Cronk, Q.C.B., Kiehn, M., Wagner, W.L. & Smith, J.F. 2005. Evolution of Cyrtandra (Gesneriaceae) in the Pacific Ocean: The origin of a supertramp clade. American Journal of Botany 92: 1017–1024. https://doi.org/10.3732/ajb.92.6.1017
- Cumming, J.M. & Wood, D.M. 2009. Chapter 2. Adult morphology and terminology, pp. 9–50. *In*: Brown, B.V., Borkent, B.V., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*. Volume 1. NRC Research Press, Ottawa, Ontario, Canada.
- Cumming, J.M. & Wood, D.M. 2017. Adult morphology and terminology, pp. 89–113. *In*: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4. South African National Biodiversity Institute, Pretoria.
- **Evenhuis, N.L.** 2021. The insect and spider collections of the world website. Available from: http://hbs.bishopmuseum.org/codens/ (Accessed 21 September 2021)
- Finet, C., Kassner, V.A., Carvalho, A.B., Chung, H., Day, J.P., Day, S., Delaney, E.K., De Ré, F.C., Dufour, H.D., Dupim, E., Izumitani, H.F., Gautério, T.B., Justen, J., Katoh, T., Kopp, A., Koshikawa, S., Longdon, B., Loreto, E.L., Nunes, M.D.S., Raja, K.K.B., Rebeiz, M., Ritchie, M.G., Saakyan, G., Sneddon, T., Teramoto, M., Tyukmaeva, V., Vanderlinde, T., Wey, E.E., Werner, T., Williams, T.M., Robe, L.J., Toda, M.J. & Marlétaz, F. 2021 DrosoPhyla: Resources for drosophilid phylogeny and systematics. *Genome Biology and Evolution* 13. https://doi.org/10.1093/gbe/evab179
- Hardy, D.E. 1965. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypteratae I. Family Drosophilidae. Insects of Hawaii. Hardy, D.E. (Ed.). University of Hawaii Press, Honolulu. 814 pp.
- Hardy, D.E., Kaneshiro, K.Y., Val, F.C. & O'Grady, P.M. 2001. Review of the *halea-kalae* species group of Hawaiian *Drosophila* (Diptera: Drosophilidae). *Bishop Museum Bulletin in Entomology* 9, viii + 88 pp.
- Hardy, J. 1849. Note on remedies for the turnip-fly amongst the ancients, and on the turnip-fly of New Holland, with notice of a new genus and species of Diptera. *History of the Berwickshire Naturalist's Club* 2: 359–362.
- Katoh, T., Izumitani, H.F., Yamashita, S. & Watada, M. 2017. Multiple origins of Hawaiian drosophilids: phylogeography of *Scaptomyza* Hardy (Diptera: Drosophilidae). *Entomological Science* 20: 33–44. https://doi.org/https://doi.org/10.1111/ens.12222
- Kleinkopf, J.A., Roberts, W.R., Wagner, W.L. & Roalson, E.H. 2019. Diversification of Hawaiian *Cyrtandra* (Gesneriaceae) under the influence of incomplete lineage sorting and hybridization. *Journal of Systematics and Evolution* 57: 561–578. https://doi.org/10.1111/jse.12519
- Lapoint, R.T., O'Grady, P.M. & Whiteman, N.K. 2013. Diversification and dispersal of the Hawaiian Drosophilidae: the evolution of *Scaptomyza*. *Molecular Phylogenetics and Evolution* 69: 95–108.
- Magnacca, K.N., Foote, D. & O'Grady, P.M. 2008. A review of the endemic Hawaiian Drosophilidae and their host plants. *Zootaxa* 1728: 1–58.

- Magnacca, K.N. & O'Grady, P.M. 2008. New combinations in Hawaiian Drosophila and Scaptomyza (Diptera: Drosophilidae). Zootaxa 1926: 53–60. https://www.mapress.com/zootaxa/2008/f/z01926p060f.pdf
- O'Grady, P., Bonacum, J., DeSalle, R. & Val, F. do 2003. The placement of *Engiscaptomyza*, *Grimshawomyia*, and *Titanochaeta*, three clades of endemic Hawaiian Drosophilidae (Diptera). *Zootaxa* **159**: 1–16.
- O'Grady, P.M. & DeSalle, R. 2008. Out of Hawaii: The origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biology Letters* 4(2). https://doi.org/10.1098/rsbl.2007.0575
- O'Grady, P. & DeSalle, R. 2018a. Hawaiian *Drosophila* as an evolutionary model clade: days of future past. *Bioessays* 40: 1700246. https://doi.org/ 10.1002/bies.201700246
- O'Grady, P.M. & DeSalle, R. 2018b. Phylogeny of the Genus *Drosophila*. *Genetics* 209: 1–25.

https://doi.org/10.1534/genetics.117.300583

- O'Grady, P.M., Lapoint, R.T., Bonacum, J., Lasola, J., Owen, E., Wu, Y. & DeSalle, R. 2011. Phylogenetic and ecological relationships of the Hawaiian *Drosophila* inferred by mitochondrial DNA analysis. *Molecular Phylogenetics and Evolution* 58. https://doi.org/10.1016/j.ympev.2010.11.022
- O'Grady, P.M., Magnacca, K.N. & Lapoint, R.T. 2010. Taxonomic relationships within the endemic Hawaiian Drosophilidae (Insecta : Diptera). *Bishop Museum Occasional Papers* **34**: 1–34.
- Rampasso, A.S. & O'Grady, P.M. 2022. Distribution and taxonomy of endemic and introduced Drosophilidae in Hawaii. *Zootaxa* 5106: 1–80.
- Rampasso, A.S. & O'Grady, P.M. 2022. Standardized terminology and visual atlas of the external morphology and terminalia for the genus *Scaptomyza* (Diptera: Drosophilidae). *Fly* 16: 37-61.

https://doi.org/10.1080/19336934.2021.1969220

- Rice, G., David, J.R., Kamimura, Y., Masly, J.P., Mcgregor, A.P., Nagy, O., Noselli, S., Nunes, M.D.S., O'Grady, P., Sánchez-Herrero, E., Siegal, M.L., Toda, M.J., Rebeiz, M., Courtier-Orgogozo, V. & Yassin, A. 2019. A standardized nomenclature and atlas of the male terminalia of *Drosophila melanogaster*. *Fly* 13: 51–64. https://doi.org/10.1080/19336934.2019.1653733
- Rock, J.F. 1917. Revision of the Hawaiian species of the genus *Cyrtandra*, section Cylindrocalyces Hillebr. *American Journal of Botany* **4**: 229–239.
- Rock, J.F. 1918. Cyrtandreae Hawaiiensis, section Crotonocalyces Hillebr. *American Journal of Botany* 5: 259–277.
- Rock, J.F. 1919a. Cyrtandreae Hawaiiensis, sections Microcalyces Hillebr. *American Journal of Botany* 6: 203–213.
- Rock, J.F. 1919b. Cyrtandreae Hawaiiensis, sections Schizocalyces Hillebr. and Chaetocalyces Hillebr. *American Journal of Botany* 6: 1–22.
- Russo, C.A.M., Mello, B., Frazão, A. & Voloch, C.M. 2013. Phylogenetic analysis and a time tree for a large drosophilid data set (Diptera: Drosophilidae). *Zoological Journal of the Linnean Society* 169: 765–775. https://doi.org/10.1111/zoj12062

- St. John, H. & Takeuchi, W. 1988. Enlargement of Oahu Cyrtandra (Gesneriaceae). Phytologia 65: 207–215.
- Suvorov, A., Kim, B.Y., Wang, J., Armstrong, E.E., Peede, D., D'Agostino, E.R.R., Price, D.K., Wadell, P., Lang, M., Courtier-Orgogozo, V., David, J.R., Petrov, D., Matute, D.R., Schrider, D.R. & Comeault, A.A. 2021. Widespread introgression across a phylogeny of 155 *Drosophila* genomes. *bioRxiv*, 2020.12.14.422758. https://doi.org/10.1101/2020.12.14.422758
- **Throckmorton, L.H.** 1966. The relationships of the endemic Hawaiian Drosophilidae. *University of Texas Publications* 6615, 335–396.
- Vilela, C.R. & Prieto, D. 2018. A new Costa Rican species of *Drosophila* visiting inflorescences of the hemi-epiphytic climber *Monstera lentii* (Araceae). *Revista Brasileira de Entomologia* 62: 225–231.
- Wagner, W.L., Herbst, D.R. & Sohmer, S.H. 1999. Manual of the flowering plants of Hawai'i. Vols. 1 and 2. Revised edition. University of Hawai'i Press and Bishop Museum Press, Honolulu.
- Wheeler, M.R. 1981. The Drosophilidae: a taxonomic overview. *The Genetics and Biology of Drosophila* **3a**: 1–97.
- Wheeler, M.R. 1986 Additions to the catalog of the world's Drosophilidae. *The Genetics and Biology of Drosophila* **3e**: 395–409.
- Yassin, A. 2013. Phylogenetic classification of the Drosophilidae Rondani (Diptera): the role of morphology in the postgenomic era. *Systematic Entomology* 38: 349–364. https://doi.org/10.1111/j.1365-3113.2012.00665.x