

Systematics, Morphology and Biogeography

A new Costa Rican species of *Drosophila* visiting inflorescences of the hemi-epiphytic climber *Monstera lantii* (Araceae)

Carlos R. Vilela^{a,*}, Danyi Prieto^b

^a Universidade de São Paulo, Instituto de Biociências, Departamento de Genética e Biologia Evolutiva, São Paulo, SP, Brazil

^b Universidad Nacional, Heredia, Costa Rica



ARTICLE INFO

Article history:

Received 7 March 2018

Accepted 8 June 2018

Available online 27 June 2018

Associate Editor: Sarah Oliveira

Keywords:

Aroid

Central America

Drosophilinae

Taxonomy

ABSTRACT

Drosophila monsterae sp. nov. is described from 11 males and 13 females collected from the inside of closed inflorescences of *Monstera lantii* (Araceae) at 1810 m altitude in the Forest Reserve of Cerro de La Carpintera, Canton La Unión, Province of Cartago, Costa Rica. Although flies have been seen wandering and copulating inside the floral chambers of closed inflorescences during the floral female phase, eggs or larvae have not yet been found either in the spathe or in the fleshy spadix. The new species is related to *Drosophila tristani* Sturtevant, 1921, from San José, Costa Rica, from which it differs mainly by having smaller slightly circular compound eyes, distinctly broader genae (cheek index ca. 2.4 vs 5 in *D. tristani*), and the inner capsule of spermathecae with an unusual folded duct at basal half of its very wide introvert. This is the eighth species to be included in the New World, essentially Neotropical, subgenus *Phloridosa*. Photomicrographs of male and female terminalia are also provided.

© 2018 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

According to Bächli (2018), seven species of *Drosophila* are currently included in the New World, essentially Neotropical, subgenus *Phloridosa* Sturtevant, 1942. Arranged alphabetically, they are as follows: *Drosophila alei* Brncic, 1962, *D. alfari* Sturtevant, 1921, *D. cuzcoica* Duda, 1927, *D. denieri* Blanchard, 1938, *D. lutzii* Sturtevant, 1916, *D. merzi* Vilela and Bächli, 2002b, and *D. tristani* Sturtevant, 1921. Apparently, these species depend on flowers of different plant families to complete their life cycle, as is implied by its subgenus name (*Phloridosa*). The subgenus *Phloridosa* was proposed in 1942 by Sturtevant, who creatively recombined the letters of the word *Drosophila* to obtain an anagram word sounding like *floris*, the genitive Latin case for the Latin noun *flos* (flower). In the above cited paper he diagnosed the subgenus as follows: “Shining black or brown species; bristles and branches of arista short; sterno-index .3 or less; anterior Malpighian tubes absent; posterior Malpighian tubes fused to form a loop around the gut; testes long, spirally coiled; eggs without filaments or remains of follicle cells; flower-feeding species”.

Brncic (1983) listed six species (including *D. floricola* Sturtevant, which later on was considered a junior synonym of *D. lutzii*) out of

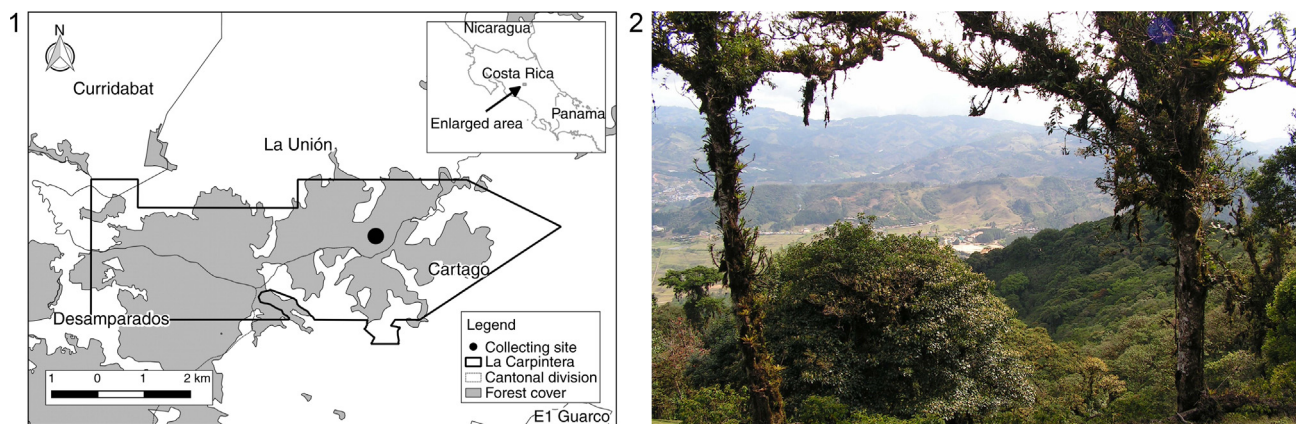
the seven species of the subgenus *Phloridosa* of *Drosophila* that have been bred from flowers belonging to the families Araceae, Boraginaceae, Convolvulaceae, Cucurbitaceae, Malvaceae and Solanaceae. Chassagnard and Tsacas (1992) added Apocynaceae to the plant families previously registered by Brncic (1983) which includes information and references on the breeding sites of the following species: *D. alei*, *D. alfari*, *D. denieri*, *D. floricola*, *D. lutzii* and *D. tristani*.

So far, the only species of the subgenus *Phloridosa* occurring in both Nearctic and Neotropical regions is *D. lutzii*, which seems to be an invasive species in USA (California, Arizona and Florida; under its junior synonym *D. floricola* Sturtevant, 1942) from where it had not been sampled until the 1940s. As suggested by Sturtevant (1942), the occurrence of this Neotropical flower-breeding species in the Nearctic region after the 1940s is most likely due to the cut flower trade. Forty years after the invasion of the Nearctic Region, *D. lutzii* (under the binomial *D. floricola*) was collected in IX–X.1980 in the Volcano National Park on Hawaii Island (Montagne and Kaneshiro, 1982) and, later on, in the islands of Oahu (Honolulu [Manoa] in II.1982; Hardy, 1982) and Maui (Haleakalā highway on 16.III.1999; O’Grady et al., 2002), all in the Hawaiian Archipelago.

The discovery of a new species of *Drosophila* belonging to the small subgenus *Phloridosa* and collected while visiting closed inflorescences of the aroid *Monstera lantii* Croat and Grayum (Grayum, 1997) (Araceae) in the mountains of the Costa Rican province of Cartago prompt this paper.

* Corresponding author.

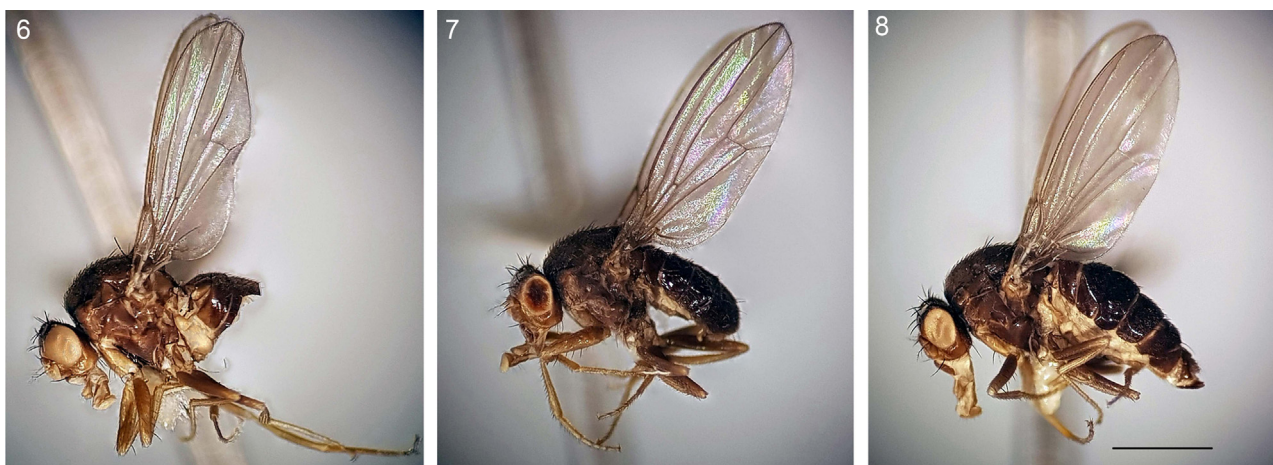
E-mail: cvilela@ib.usp.br (C.R. Vilela).



Figs. 1–2. Collecting site: 1. Map of Costa Rica and details of the collecting site; 2. photograph of a patch of the forest of La Carpintera and surrounding mountains.



Figs. 3–5. Close ups of three stages of inflorescence development of the aroid *Monstera lentii* in the study area: 3, closed inflorescence being manually opened, female phase; 4, just opened inflorescence with spadix in male phase (front), and inflorescence with ripening fruits after the spathe has fallen off (back); 5, opened inflorescence with darker spadix in male phase.



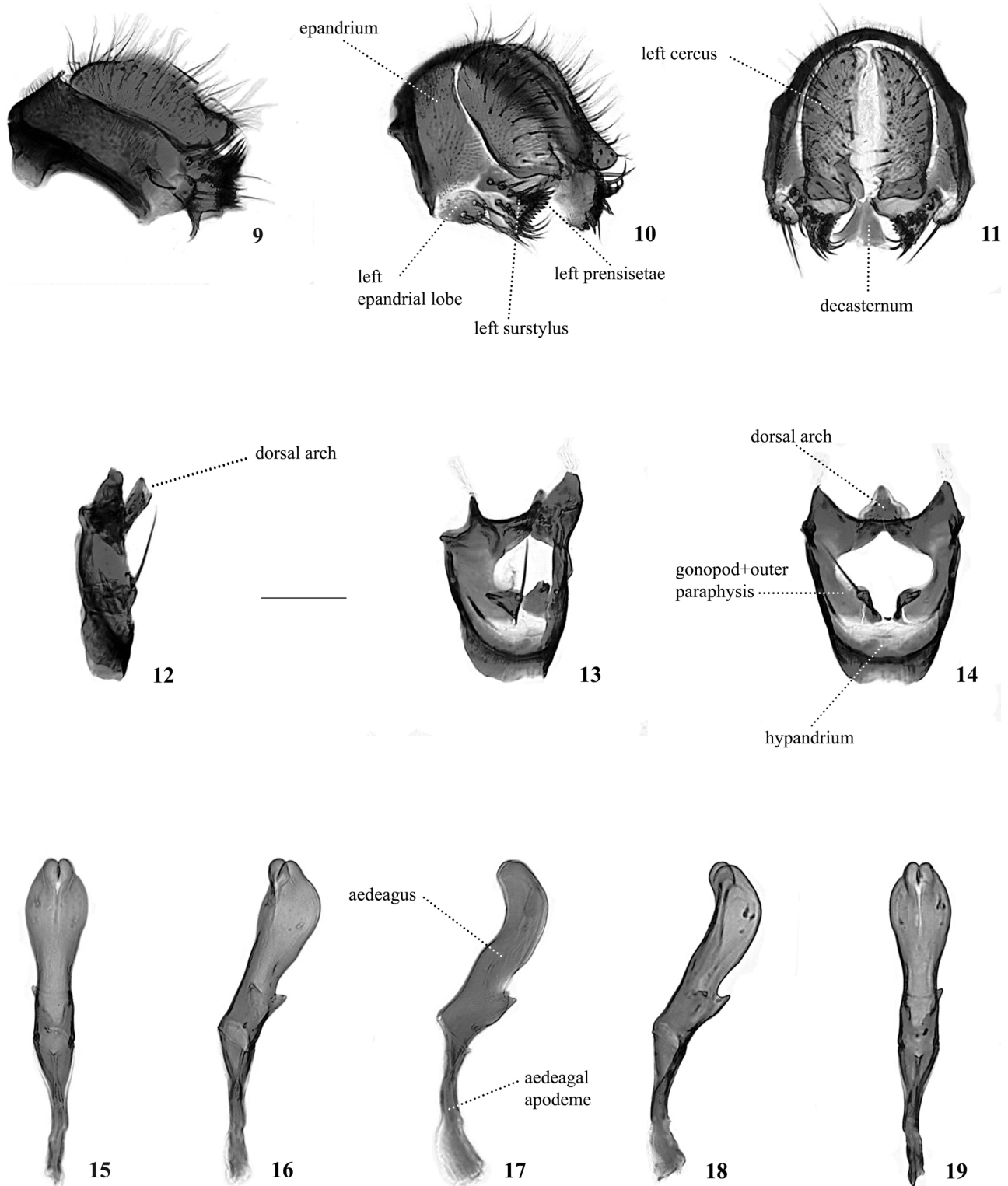
Figs. 6–8. *Drosophila monsterae*, sp. nov., habitus of three type specimens in left lateral view: 6, male holotype (terminalia removed); 7, male paratype; 8, female paratype. Scale bar, 1 mm.

Material and methods

Study site. As part of a study on the reproductive biology of *Monstera lentii* by Prieto and Cascante-Marín (2017) the flies were collected in a small mountainous conservation area in Costa Rica known as Cerros La Carpintera, Cartago province (9°53' N, 83°58' W; 1700–1850 m altitude; Figs. 1, 2). The forest is a mixture of

small primary forest remnants intermixed with old growth secondary forest (+75 y old), covering approximately 840 ha along the upper slopes, and surrounded by open pastures and tree pastures (Sánchez et al., 2008).

The area is characterized by a rainy season from May to November. The average annual rainfall varies between 1500 and 2500 mm, depending on altitude and location. Relative humidity ranges



Figs. 9–19. *Drosophila monsterae* sp. nov. male holotype, terminalia: 9, epandrium, cerci, surstyli and decasternum, left lateral view; 10, same, left posterior oblique view; 11, same, posterior view; 12, hypandrium and gonopods+paraphyses [fused], left lateral view; 13, same, left posterior oblique view; 14, same, posterior view; 15–19, aedeagus + aedeagal apodeme [fused] in several views from dorsal through ventral. Scale bar, 0.1 mm.

between 70% and 90%, and temperature between 15 and 23 °C (Ossenbach et al., 2003). According to the classification of Holdridge Life Zones, the area corresponds to the Lower Montane Wet Forest and Premontane Wet Forest (Bolaños and Watson, 1993).

Host plant. *Monstera lentii* (Figs. 3–5) is a secondary hemi-epiphyte of the understory (i.e. it germinates on the ground and

later loosely climbs onto the host tree by adventitious roots), reaching 3–4 m above the ground. It is endemic to Costa Rica and western Panama in montane wet, rain and cloud forests, from 1300 to 1700 m altitude (Grayum, 2003). *M. lentii* is distinguished by its protuberant conical or cylindrical style, with a capitate stigma. Leaf blades are ovate, more or less oblong (28–60 × 18–41 cm), with

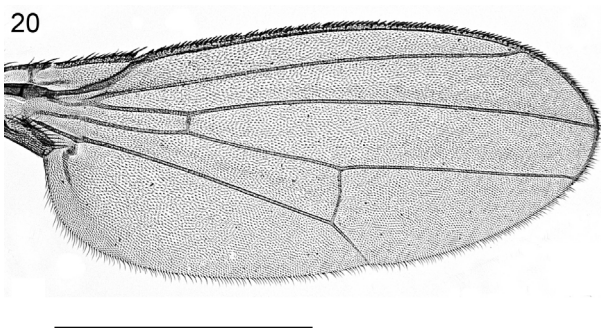


Fig. 20. *Drosophila monsterae* sp. nov. female paratype # 18, right wing, dorsal view. Scale bar, 1 mm.

the base cuneate to rounded or subcordate, often perforated, with about 14 primary lateral veins on each side and pinnatifid margins. The spadix is 5–16 cm long and the spathe is white or cream on the inside (Figs. 3–5; Grayum, 2003).

The flowering cycle of *M. lentii* is a process of 8–9 days. The cycle starts when the spathe around the spadix begins to slightly unfold to form a floral chamber. By the third or fourth day of the cycle, the stigmas begin to look wet and shiny, a slight bittersweet odor is produced, and a few (4–8) flies arrive in the floral chamber. For the next few days, an average of 28 (± 24 S.D.) individuals of *Drosophila* stay in the floral chamber, wander along the spadix and copulate, until the end of the floral cycle when they leave (Prieto and Cascante-Marín, 2017).

Flies, description and imaging. A total of 24 specimens, being 11 males (#1 to #11) and 13 females (#12 to #24) collected from the inside of closed inflorescences of *Monstera lentii* (Araceae) were used to describe the new species of *Drosophila*. The inflorescences were surveyed for the presence of potential pollinators by the junior author in a Forest Reserve (9°53'01"N, 83°58'22"W; 1810 m) of Cerro La Carpintera, Canton La Unión, Province of Cartago, Costa Rica, in September 2010.

The 24 specimens were initially preserved in 70% ethanol, and later dried, double-mounted to cardboard tips following Bächli et al. (2004: 3, alternative b), and measured under a STEMI DV4 Zeiss stereomicroscope (4 \times objective). Morphological terminology, measurements and indices used in the description follow Vilela (1983), Vilela and Bächli (1990) and Bächli et al. (2004); methods of preparing the terminalia follow Kaneshiro (1969) and Wheeler and Kambysellis (1966). The right wing of the female paratype # 18 was removed, kept in a solution of 70% ethanol plus 5% glycerin for 1 h (to get rid of air bubbles inside veins) on a microscope well slide placed inside a petri dish, followed by the addition of a drop of pure glycerin to the above solution. The wing was finally transferred to a drop of pure glycerin on a microscope slide and covered with a coverslip to be photomicrographed. The removed wing and the disarticulated terminalia were later placed in a glass microvial filled with glycerin and attached by the stopper to the pinned specimen. Photomicrographs of the wing and terminalia were taken under a 4 \times and 10 \times objectives, respectively, on an Olympus BX60 microscope equipped with an Olympus Q-color 5 digital camera and the images captured with Image-Pro Plus 5.1 software. For each view, a set of 21–99 photomicrographs was taken at different depths of focus and digitally stacked by two methods (simple stack and weighted average; at first separate, then combining the two outputs by weighted average method) to create an all-in-focus composite using the open-source software CombineZP (Hadley, 2010). Photomicrographs of imagoes were taken with a Samsung Galaxy S8 smartphone connected to a Leica stereomicroscope (SZ11) eyepiece through a magnetic adapter. To get a single all-in-focus final image of three imagoes, only a set of three images for each view was

taken at different depth of focus and digitally combined by “all methods” stacking algorithm using the cited software. Line drawing of the valve of oviscapt was made with pencil using a camera lucida (1.6 \times) attached to a Zeiss microscope (40 \times objective), later copied to transparent paper and scanned with Epson Perfection 4189 photo. The final images of both line drawing and photomicrographs were edited with Adobe Photoshop software. Whenever in the same plate, all photomicrographs were taken and enlarged to the same magnification.

Label data attached to the pin of the holotype are cited in full. A forward slash designates a label change. Clarifying notes are included in brackets. The type series will be deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP).

Drosophila (*Phloridosa*) *monsterae* sp. nov.

(Figs. 6–29)

Drosophila, subgenus *Phloridosa*, Prieto and Cascante-Marín, 2017: 61.

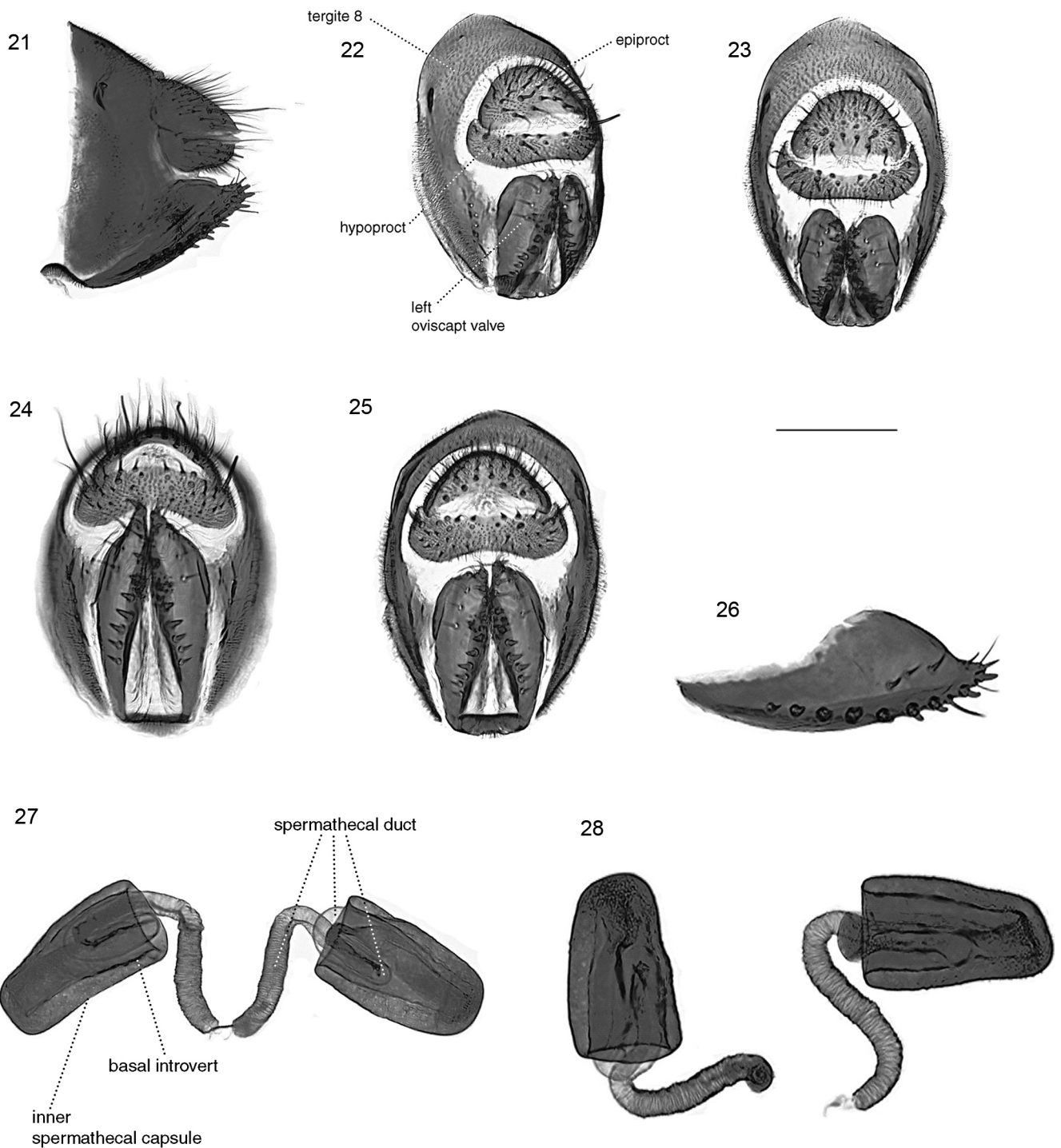
Drosophilid fly, Prieto and Cascante-Marín, 2017: 57, 60 (Fig. 3b), 61, 63.

Diagnosis. Shining black fly; branches of arista and most setae noticeably short, somewhat erect, black; small slightly circular compound eye; conspicuous broad gena; wing relatively long, hyaline; basal scutellars parallel or slightly convergent; gonopod not microtrichose; aedeagus sinuate in lateral view; inner spermathecal capsule with an unusual folded duct on basal half of introvert.

Material examined. Holotype male (dissected, Fig. 6), labeled: “Costa Rica, Cartago, La Unión, Cerro de La Carpintera, 9°53'1"N, 83°58'22"W, altitude 1810 m/collected in closed inflorescence of *Monstera lentii* (Araceae) IX.2010, D. Prieto coll./# 1/ σ *Drosophila monsterae* Vilela & Prieto/HOLOTYPE [red label]”. Paratypes (10 σ σ , 13 ♀ [2 dissected]); same data as holotype except for the last three labels = specimen number/sex/PARATYPE [red label].

Description. Male ($n=11$; Figs. 6, 7). Head. Frons black, dull, lighter anteriorly, frontal length = 0.33 (0.29–0.37) mm; frontal index = 0.83 (0.76–0.88), top to bottom width ratio = 1.43 (1.17–1.53). Frontal triangle distinct, apically narrow, pointed, about 79–100% of frontal length. Ocellar triangle about 33–46% of frontal length. Orbital plates subshiny, brown, lighter than adjacent frontal areas, apically broadened and slightly diverging from eye margin, about 80–100% of frontal length. Distance of or3 to or1 = 50–67% of or3 to vtm, or1/or3 ratio = 1.16 (1.00–1.25), or2/or1 ratio = 0.34 (0.33–0.40), postocellar setae = 42 (33–54)%, ocellar setae = 44 (38–50)% of frontal length; vt index = 1.29 (1.14–1.60); vibrissal index = 0.28 (0.18–0.50). Occiput black. Length-to-width ratio of flagellomere 1 = 1.55 (1.20–1.75). Arista with 4–6 short dorsal, 2–3 short ventral and 5–10 inner branches, plus small terminal fork. Face light brown. Carina distinctly broadened downwards, dorsally flat, noselike. Eye slightly circular, smaller than usual, index = 1.17 (1.07–1.33). Gena light brown, conspicuously broad. Cheek index = 2.43 (2.00–2.67). Vibrissa relatively long. Proboscis and palpus light brown; clypeus dark brown. Palpus with about two thin median-sized setae along lower margin.

Thorax dark coffee brown, subshiny, length = 1.13 (0.98–1.24) mm. 4–6 rows of acrostichal setulae. Postpronotum not so dark brown. h index = 0.95 (0.83–1.17). Transverse distance of dorso-central setae 118–150% of longitudinal distance; dc index = 0.61 (0.50–0.69). Scutellum apically roundish, distance between apical scutellar setae about 75–88% of that of the apical to the basal one; basal ones parallel or slightly convergent; distal ones relatively long and not cruciate or cruciate at the very tip; scut index = 0.73 (0.65–0.82). Sterno index = 0.48 (0.38–0.55), mid katepisternal seta about 33–75% of anterior one. Halteres light



Figs. 21–28. *Drosophila monsterae* sp. nov. female paratypes (21–25, 27, paratype # 12; 26, 28 paratype #18), terminalia: 21, tergite 8, epiproct, hypoproct and oviscapt valve, left lateral view; 22, same, left posterior oblique view; 23, same, dorso-posterior view; 24, same, ventral view; 25, anterior view; 26, left oviscapt valve, outer lateral view; 27, 28, pairs of inner spermathecal capsules. Scale bar, 0.1 mm.

brown. Legs proximally (coxa, trochanter and femur) brown, distally (tibia and tarsi) light brown. Tarsal claw distinctly long.

Wing hyaline, veins yellow, relatively long (Figs. 6, 7), length=2.54 (2.34–2.66) mm, length to width ratio=2.58 (2.45–2.73). First costal section (between humeral and subcostal breaks) with setulae distinctly longer and more erect than those of second section. Indices: C=3.88 (3.68–4.41), ac=2.20

(2.00–2.43), hb=0.22 (0.21–0.26), 4C=0.67 (0.59–0.73), 4v=1.63 (1.50–1.74), 5x=1.16 (0.90–1.50), M=0.38 (0.34–0.44), prox. X=0.63 (0.57–0.70).

Abdomen shining (Figs. 6, 7), uniformly dark coffee brown except epandrium, cercus and pleura, light brown; length=1.27 (1.12–1.37) mm.

Terminalia (Figs. 9–19). Epandrium mostly microtrichose, devoid of setae; ventral lobe (Fig. 10) distally thumb-shaped,

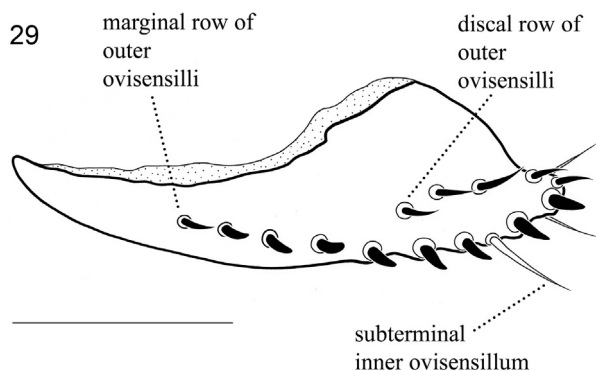


Fig. 29. *Drosophila monsterae* sp. nov. female paratype # 18, left oviscapt valve, outer lateral view. Scale bar, 0.1 mm.

microtrichose, anterodorsally membranous, bearing 2–3 longer setae and 0–1 shorter one. Cerci anteriorly linked to posterior margin of epandrium by membranous tissue, microtrichose (Figs. 10, 11) except lower 1/4; inner ventral tip double-walled, inner corner somewhat truncated; ventral margin concave in posterior view (Fig. 11); outer ventral tip projected outwards (Fig. 11). Surstylus not microtrichose; distal margin bearing a dorsoventral row of ca. 10 long, sharp-tipped, peg-shaped prenisetae, first dorsalmost and two ventralmost longer (Fig. 9); dorsal half strongly sclerotized, with a transverse, irregular row of ca. 6 outer, long, strong, curved setae; ventral half weak sclerotized, with ca. 5 outer, thinner, shorter setae; ca. 5 inner setae below lowermost prenisetae (Fig. 10). Decasternum as in Fig. 11. Hypandrium strongly sclerotized (Figs. 12–14), slightly shorter than epandrium, bearing a pair of sharp lateral projections pointed backwards as seen in the posterior view (Fig. 14); dorsal arch projected backwards in the lateral view (Fig. 12); anterior margin concave (Fig. 14); gonopod perpendicular and mostly fused to paraphysis, devoid of microtrichiae, bearing one long seta on anterior inner margin (Figs. 12–14). Aedeagus sinuate in lateral view (Fig. 17), subapically expanded laterally, rounded and slightly incised at tip (Figs. 15, 19) which is projected upwards; ventral margin subproximally bearing a curved spine projected apicalwards (Figs. 16–18); dorsal cleft at very anterior end (Figs. 15–17). Aedeagal apodeme shorter than aedeagus, bent; anterior region dorsoventrally expanded (Fig. 17). Ventral rod absent (Fig. 17). Paraphysis perpendicular and mostly fused to gonopod (Figs. 13, 14), devoid of setulae, linked to distal margin of aedeagal apodeme by membranous tissue.

Female ($n = 13$; Fig. 8). Difference to male: first costal section (between humeral and subcostal breaks; Fig. 20) with setulae just slightly longer than those of second costal section.

Measurements. Frontal length = 0.33 (0.29–0.37) mm; frontal index = 0.83 (0.75–0.93); top to bottom width ratio = 1.43 (1.28–1.53). Frontal triangle about 79–115% of frontal length.

Ocellar triangle about 29–38% of frontal length. Orbital plates about 80–100% of frontal length. Distance of or_3 to or_1 = 50–83% of or_3 to vtm , or_1/or_3 ratio = 1.07 (1.00–1.20), or_2/or_1 ratio = 0.38 (0.33–0.40), postocellar setae = 40 (36–46)%, ocellar setae = 45 (36–50)% of frontal length; vt index = 1.28 (1.17–1.40); vibrissal index = 0.27 (0.20–0.38). Length to width ratio of flagellomere 1 = 1.56 (1.40–1.75). Arista with 4–5 upper, 2 ventral and 6–10 inner branches, plus small terminal fork. Eye index = 1.16 (1.06–1.20). Cheek index = 2.55 (2.13–2.83).

Thorax length = 1.12 (0.98–1.24) mm. 4–6 rows of acrostichal setulae. h index = 0.92 (0.67–1.17). Transverse distance of dorso-central setae 120–200% of longitudinal distance; dc index = 0.59 (0.58–0.64). Distance between apical scutellar setae about 67–100% of that of the apical to the basal one; basal ones parallel or slightly convergent; $scut$ index = 0.71 (0.59–0.81). Sterno index = 0.52 (0.45–0.64), mid katepisternal seta about 29–50% of anterior one.

Wing (Fig. 20) length = 2.49 (2.20–2.85) mm, length to width ratio = 2.38 (2.29–2.49). Indices: $C = 3.74$ (3.48–4.12), $ac = 2.16$ (1.89–2.43), $hb = 0.22$ (0.16–0.30), $4C = 0.68$ (0.61–0.84), $4v = 1.61$ (1.40–1.88), $5x = 1.00$ (0.82–1.13), $M = 0.36$ (0.30–0.40), $prox. X = 0.63$ (0.57–0.74).

Abdomen length = 1.60 (1.34–1.88) mm.

Terminalia (Figs. 21–28). Tergite 8 dorsally microtrichose, bearing a curved row of 3–4 setulae adjacent to posterior/ventral margin (Fig. 22); epiproct and hypoproct microtrichose, setose, bearing a pair of setae longer than adjacent ones (Figs. 21, 24); valve of oviscapt (Figs. 24, 26, 29) apically narrowed, subapically expanded dorsad, ventrally convex at proximal half, sinuate at distal half, with ca. 4 discal, trichoid-like, and 10 marginal, peg-like, roundish-tipped (except the anterior most and the posterior most, sharp-tipped) outer ovisensilla; trichoid-like inner ovisensilla: 3 thin, unusually long, distally positioned (middle one probably accidentally missing as seen in Fig. 29), and 1 thick, longer, almost straight, subterminal; valves widely spaced at base (Figs. 24, 25). Inner capsule of spermatheca (Figs. 27, 28) finger cap-shaped, apically flattened, strongly sclerotized, devoid of basal furrows and apical introvert; basal introvert deeply invaginated, very wide at base, gradually narrowing toward apex; spermathecal duct unusually folded over itself at lower half of basal introvert.

Differences from consubgeneric species. *Drosophila (Phloridosa) monsterae* sp. nov. from Costa Rica differs from *D. alei*, *D. alfari*, *D. cuzcoica*, *D. denieri*, *D. lutzii*, *D. merzi* and *D. tristani* mainly regarding two structures of their heads as follows, respectively. Eye slightly circular vs. slightly elliptical; gena distinctly broad vs. not so broad. They also differ with respect to their terminalia: gonopod not microtrichose vs. distinctly microtrichose (males unknown for *D. cuzcoica* and *D. tristani*); aedeagus without a pair of subapical lateral expansions vs. presence of such structures (males unknown for *D. cuzcoica* and *D. tristani*); oviscapt valve with discal trichoid-like outer ovisensilla vs. discal peg-like outer ovisensilla (females

Table 1

Main differences in the terminalia among *Drosophila monsterae* sp. nov. and the remaining seven species of *Drosophila* belonging to the subgenus *Phloridosa*.

Species	Gonopods microtrichose	Pair of subapical lateral expansions in the aedeagus	Ventral rod	Epandrium seta(e) adjacent to base of surstylus	Discal outer ovisensilla of oviscapt valve	References
<i>D. monsterae</i>	No	Absent	Absent	Absent	Trichoid-like	1
<i>D. alei</i>	Yes	Present	Present	2	Peg-like	6
<i>D. alfari</i>	Yes	Present	Present	Absent	Unavailable data	2
<i>D. cuzcoica</i>	♂ unknown	♂ unknown	♂ unknown	♂ unknown	Peg-like	4
<i>D. denieri</i>	Yes	Present	Present	1–2	Peg-like	3
<i>D. lutzii</i>	Yes	Present	Present	1	Peg-like	2,5
<i>D. merzi</i>	Yes	Present	Present	1	♀ unknown	7
<i>D. tristani</i>	♂ unknown	♂ unknown	♂ unknown	♂ unknown	unavailable data	

References = 1, this paper; 2, Vilela (1984); 3, Vilela (1986); 4, Vilela and Bächli (1990); 5, Chassagnard and Tsacas (1992); 6, Vilela and Bächli (2002a); 7, Vilela and Bächli (2002b).

unknown for *D. merzi*; unavailable data for *D. alfari* and *D. tristani* (Table 1).

Conflicts of interest

The authors declare no conflicts of interest.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors

Acknowledgements

Paul Hanson (Universidad de Costa Rica) kindly made a first attempt to identify the flies. Campo Nacional Escuela Iztaarú (Guías y Scouts de Costa Rica) provided access to the study area and logistic support. Adrienne Wakabayashi helped with an early review of the manuscript. The Associate Editor (S. Oliveira) and two anonymous reviewers made corrections and suggestions for improvement.

References

- Bächli, G., 2018. TaxoDros: the database on taxonomy of Drosophilidae. Available at: <http://taxodros.unizh.ch/> (accessed 4 February 2018).
- Bächli, G., Vilela, C.R., Escher, A.S., Saura, A., 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica, 39. Brill, Leiden, pp. 362.
- Blanchard, E.E., 1938. Descripciones y anotaciones de dipteros argentinos. Anales de la Sociedad Científica Argentina 126, 345–386.
- Bolaños, R., Watson, V., 1993. Mapa ecológico de Costa Rica, según el sistema de clasificación de Zonas de Vida del mundo de L. R. Holdridge. 1:200 000. Centro Científico Tropical, San José, Costa Rica.
- Brcncic, D., 1983. Ecology of flower-breeding *Drosophila*. In: Ashburner, M., Carson, H.L., Thompson Jr., J.N. (Eds.), The Genetics and Biology of *Drosophila* v. 3d. Academic Press, London, pp. 333–382.
- Brcncic, D., 1962. New Chilean species of the genus *Drosophila*. Biologica 33, 3–6.
- Chassagnard, M.T., Tsacas, L., 1992. *Drosophila (Phloridosa) lutzii* Sturtevant (Diptera: Drosophilidae), especie antófila de México. Folia Entomológica Mexicana 85, 95–105.
- Duda, O., 1927. Die südamerikanischen Drosophiliden (Dipteren) unter Berücksichtigung auch der anderen neotropischen sowie der nearktischen Arten. Wiegmann's Archiv für Naturgeschichte, 1–229 (1925) (A) 91 (11/12).
- Grayum, M.H., 1997. Nomenclatural and taxonomic notes on Costa Rican Araceae. Phytologia 82, 30–57.
- Grayum, M.H., 2003. Araceae. In: Hammel, B.E., Grayum, M.H., Herrera, C., Zamora, N. (Eds.), Manual de plantas de Costa Rica, Volumen II. Gimnospermas y monocotiledóneas (Agavaceae–Musaceae). Missouri Botanical Garden Press, Missouri, pp. 59–200.
- Hadley, A., 2010. Combine ZP, <http://www.hadleyweb.pwp.blueyonder.co.uk/>.
- Hardy, H.D., 1982. *Drosophila (Phloridosa) floricola* Sturtevant. Proceedings of the Hawaiian Entomological Society 24, 7–8.
- Kaneshiro, K.Y., 1969. A study of the relationships of Hawaiian *Drosophila* species based on external male genitalia, 6918. University of Texas Publications, pp. 55–70.
- Montagne, J.R., Kaneshiro, K.Y., 1982. Flower-breeding Species of Hawaiian Drosophilids in an Early Stage of Sympatry. Pacific Insects 24, 209–213.
- O'Grady, P.M., Beardsley, J.W., Perreira, W.D., 2002. New records for introduced Drosophilidae (Diptera) in Hawai'i. Bishop Museum Occasional Papers 69, 34.
- Ossenbach, C., Ossenbach, M., Pupulin, F., 2003. Catálogo preliminar de las Orchidaceae de la Zona Protectora Cerros de la Carpintera, 7. Lankesteriana, Costa Rica, pp. 127–132.
- Prieto, D., Cascante-Marín, A., 2017. Pollination by nitidulid beetles in the hemiepiphytic aroid *Monstera lentii* (Araceae: Monsteroideae). Flora 231, 57–64.
- Sánchez, J., Durán, F., Vega, G., 2008. Diversidad de plantas, mamíferos y mariposas en los cerros de La Carpintera, Costa Rica. Informe Interno de Proyecto. Departamento de Historia Natural, Museo Nacional de Costa Rica. Ministerio de Cultura y Juventud, San José, Costa Rica.
- Sturtevant, A., 1916. Notes on North American Drosophilidae with descriptions of twenty-three new species. Annals of the Entomological Society of America 9, 323–343.
- Sturtevant, A., 1921. The North American species of *Drosophila*. Publications of the Carnegie Institute of Washington 301, IV + 150 pp. 3 pls.
- Sturtevant, A., 1942. The classification of the genus *Drosophila*, with descriptions of nine new species, 4213. The University of Texas Publication, pp. 5–51.
- Vilela, C.R., 1983. A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae). Revista Brasileira de Entomologia 27, 1–114.
- Vilela, C.R., 1984. Notes on the holotypes of four Neotropical species of the genus *Drosophila* (Diptera, Drosophilidae) described by A.H. Sturtevant. Revista Brasileira de Entomologia 28, 245–256.
- Vilela, C.R., 1986. The type-series of *Drosophila denieri* Blanchard (Diptera, Drosophilidae). Revista Brasileira de Entomologia 30, 223–226.
- Vilela, C.R., Bächli, G., 1990. Taxonomic studies on Neotropical species of seven genera of Drosophilidae (Diptera). Mitteilungen der schweizerischen Entomologischen Gesellschaft 63(suppl.), 1–332.
- Vilela, C.R., Bächli, G., 2002a. On the identity of four poorly known species of Neotropical Drosophilidae (Diptera). Mitteilungen der schweizerischen Entomologischen Gesellschaft 75, 197–210.
- Vilela, C.R., Bächli, G., 2002b. Two new North American *Drosophila* species (Diptera: Drosophilidae). Mitteilungen der schweizerischen Entomologischen Gesellschaft 75, 211–221.
- Wheeler, M.R., Kambysellis, M.P., 1966. Notes on the Drosophilidae (Diptera) of Samoa, 6615. University of Texas Publications, pp. 533–565.