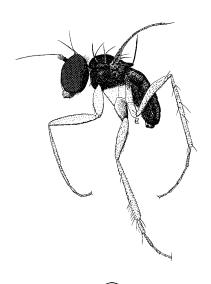
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REVIEW OF FLIGHTLESS
DOLICHOPODIDAE (DIPTERA)
IN THE HAWAIIAN ISLANDS

Neal L. Evenhuis





BISHOP MUSEUM PRESS HONOLULU Cover: *Emperoptera mirabilis* Grimshaw, from Tantalus, Oʻahu, Hawaiian Islands.

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REVIEW OF FLIGHTLESS DOLICHOPODIDAE (DIPTERA) IN THE HAWAIIAN ISLANDS¹

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Abstract. The flightless species of Dolichopodidae in the Hawaiian Islands are reviewed. The endemic Hawaiian genus *Emperoptera* Grimshaw is resurrected from synonymy and distinguished from the more generally distributed *Campsicnemus*. Three new species of *Emperoptera*, *E. montgomeryi*, **n. sp.** (O'ahu), *E. hardyi*, **n. sp.** (West Maui), and *E. zimmermani*, **n. sp.** (East Maui), are described and illustrated, raising the total number of flightless species in Hawaii to eight (5 in *Emperoptera*; 3 in *Campsicnemus*). *Emperoptera hawaiiensis* Hardy & Delfinado is a **new combination** (transferred from *Campsicnemus*). A **lectotype** is designated for *Emperoptera mirabilis*. Comparisons with other flightless Dolichopodidae found outside of the Hawaiian Archipelago are made. A key to the species of flightless *Campsicnemus* and *Emperoptera* found in Hawaii is given.

Flightless Dolichopodidae are relatively uncommon. Out of an estimated 5,000 named species of Dolichopodidae worldwide (Bickel & Dyte, 1989), only 9 flightless forms have been described previous to this study. An additional 3 species are described in this paper. It is interesting to note that of the 12 described flightless species of Dolichopodidae worldwide, 8 (= 75%) of these occur in the Hawaiian Islands (see Table 1).

Hardy and Delfinado (1974) gave the last review of flightlessness in Hawaiian Dolichopodidae, which arose out of a study made under the auspices of the International Biological Program's (IBP) Island Ecosystem Research (Hardy & Delfinado, 1973). In both papers, a table of the known flightless Dolichopodidae worldwide was presented with form of wing reduction, habitat, and locality given for each species. Of the 9 species of flightless Dolichopodidae known worldwide at that time, 5 of those were from Hawaii, all placed in the genus *Campsicnemus*. In the present study, *Emperoptera* is found to be generically distinct from *Campsicnemus* and 3 new species of *Emperoptera* from Hawai'i are described and illustrated. Flightless Dolichopodidae in Hawai'i are comprised of 2 forms: those with stenopterous (= narrow, strap-like), and those with micropterous (= extremely narrow, toothpick-like) wings.

MATERIALS AND METHODS

Descriptive morphological terminology and associated abbreviations used here follow Bickel (1991). Terminology for types of reduction or loss of wings follows Hackman (1964).

Specimens were examined in or loans requested from the following institutions and collections: Bishop Museum, Honolulu (BPBM), Canadian National Insect Collection, Agriculture Canada, Ottawa (CNC), The Natural History Museum, London (BMNH), the National Museum of Natural History, Washington, D.C. (USNM), Royal Museum of Scotland, Edinburgh (RMSE), and the University of Hawai'i at Mānoa, Honolulu (UHM).

Diagnoses and key characters in flightless Dolichopodidae, as with most Dolicho-

^{1.} Contribution No. 1997-010 to the Hawaii Biological Survey.

podidae in general, are based almost entirely on the male. Females within a genus are, for the most part, indistinguishable from each other and can only be accurately assigned to species on the basis of association with males. In only 2 cases in Hawai'i are there localities where flightless species occur sympatrically: 1) Mt. Ka'ala, on O'ahu and 2) the Upper Hāna Forest on East Maui. However, in both of these instances, one of the sympatric species is of the genus *Emperoptera* and the other is a species of *Campsicnemus*. Thus, assigning females of flightless Hawaiian dolichopodids to species when they are not associated with males can be accomplished with confidence on the basis of locality information alone.

Where known, museum type numbers are indicated. Known locality data not found on the labels of specimens are given in square brackets. Lectotype label data is given verbatim by the use of double quotes ("") to indicate beginning and ending of each label; and soliduses (/) to indicate end of lines on each label. Metric conversions assume that the elevational data given in feet on the labels are accurate.

Geographical localities in the Hawaiian Islands are given with Hawaiian diacritics and follow the orthography given in Pukui *et al.* (1974). The terms "West Maui" and "East Maui" refer to the former separate volcanic islands of Pu'u Kukui (West Maui) and Haleakalā (East Maui), which formed 0.8–1.3 mya and have since consolidated to form the current island of Maui. They are given separate terminology because of the distinctness of the fauna of each "island" and that many Hawaiian insects are endemic to one or the other. Though West Maui is currently geographically connected to East Maui and separated by the waters of the Pailolo Channel from Moloka'i, many cases are known where insect species found on West Maui are more closely related to species found on Moloka'i than to those found on East Maui (Howarth, 1990).

Abbreviations used:

I, II, III = fore, mid, and hind leg

 $egin{array}{lll} C & = \cos a \\ F & = femur \\ T & = tibia \\ \end{array}$

MSSC = male secondary sexual characters

= acrostichal setae ac= dorsocentral setae dc= postpronotal setae hm= notopleural setae np= ocellar setae oc= post alar setae pa ph= posthumeral setae = supra-alar setae sa = scutellar setae SC = tarsus t

t1-5 = tarsomeres 1 to 5 vt = vertical setae

SYSTEMATICS

Genus Emperoptera Grimshaw

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

The treatment of Emperoptera and composition of species within the genus has varied since its original description by Grimshaw in Grimshaw and Speiser (1902). Grimshaw described the genus for the Hawaiian E. mirabilis, at that time the only known flightless dolichopodid in the world. It was only logical then for Zimmerman (1938), when he discovered a second flightless Hawaiian species (from Maui) with characters similar to mirabilis, to place it in Emperoptera. Adachi (1954) subsequently described an additional flightless Hawaiian species from Moloka'i and also placed it in Emperoptera. However, when Hardy & Kohn (1964) described the new species aeptus from Pu'u Kukui, West Maui, they made Emperoptera a junior synonym of Campsicnemus (Hardy & Kohn 1964: 17). No explanation for this synonymization was given by Hardy & Kohn (1964), but Hardy & Delfinado (1974) realized the lapse and provided the first explanation for the synonymization, which was "because of the close resemblance (other than flight characters) and obvious relationship to normal, fully winged species." It is true that there are species of Emperoptera with similar appearances to species of Campsicnemus. However, some of the genera of Sympycninae worldwide are superficially similar in many respects including male genitalia, but this does not necessarily mean that these sympyonines are congeneric.

In the present study, it was found that *Emperoptera* is a monophyletic group within the subfamily Sympycninae separate from *Campsicnemus* defined by the following morphological synapomorphies: extreme reduction of the halteres, microptery in the wing, lack of a basicostal seta, absence of acrostichal setae on the mesoscutum, and the hemitergites of the female oviscapt possessing small acanthophorites that are less than half the length of the cerci. The origin of the *Emperoptera* clade and its relationships to other sympycnine genera is beyond the scope of this paper, but is part of a larger phylogenetic study in preparation on the classification of the genera of Hawaiian Dolichopodidae.

Zimmerman (1938) cautioned that, because of the poor condition of the type series of *E. mirabilis*, the halterless condition found in that species may have been due to the halter knobs having been broken off. After study of the material at hand, it is clear that the greatly reduced halteres in species of *Emperoptera* and in the type series of *E. mirabilis* are not artifacts. The micropterous wing (reduced to only a thin, sclerotized costal portion of the wing) is also characteristic of species of *Emperoptera*. Flightless forms of the genus *Campsicnemus* in contrast have the halteres fully developed and the wing is stenopterous (having at least the radial and sometimes the medial veins present).

In addition to morphological characters, a behavioral character may be also used to differentiate the 2 genera. In flightless forms of *Campsicnemus*, individuals hold their wings horizontally and perpendicular to the body while hopping or walking. In species of *Emperoptera*, the wings are held straight back while hopping or walking on substrata. However, both genera hold their wings back at rest.

Male. Length: 1.34–1.80 mm. Wing: 0.85–1.15 mm. *Head*. In lateral view higher than wide; in frontal view semi-triangular; eyes with interommatidial hairs most dense between lower facets; eyes constricted medially below antennae, holoptic or nearly holoptic just below antennae for short dis-

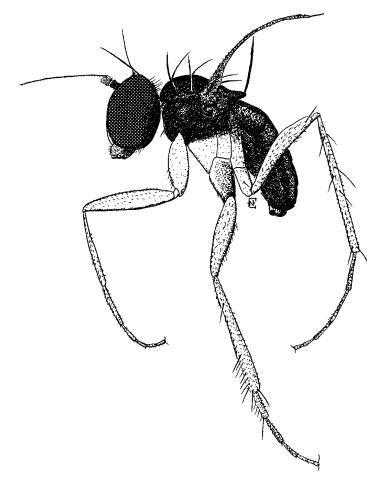


Fig. 1. Emperoptera mirabilis Grimshaw, habitus.

tance (eyes holoptic for distance equal to diameter of 1–4 ommatidia or slightly separated by diameter of 1–2 ommatidia); vertex not sunken lateral to ocellar tubercle, often with yellow to brown pollinosity laterally and posteriorly; oc and vt strong, black, comparatively larger and stouter than fully winged Campsicnemus species; palp minute, gray to brown with yellow to brown pollinosity and short black hairs apically; proboscis slightly protruding below eye level, not as well produced as in Sigmatineurum Parent and large species of Eurynogaster Van Duzee; antennal scape subcylindrical, slightly flared apically; pedicel subglobular with short apical neck, pedicel usually inserted into concave apex of scape, with minute hairs dorsally and laterally as ring at apex; flagellomere subtriangular, covered with pubescence, inserted onto neck of pedicel; arista inserted subbasally on dorsal surface of flagellomere, slightly pubescent.

Thorax. Mesoscutum much flatter than winged species of Campsicnemus; dc normal in size, lateral (np, pa, sa) and posterior (sc) setae very strong and long, much longer and stouter than winged species of Campsicnemus. Setation as follows: 2–3 dc; 2–2 +1 np; 1–1+2 ph; 1 pa; 1 sa; 1–1+1 sc; ac absent.

Legs. Shape of segments normal except for those associated with MSSC. MSSC primarily confined to segments on leg II (usually TII and IIt1). CI with 3–6 setae anteromedially at apex, 2–3 shorter setae posteriorly at apex, CII with brown hairs on medial surface, CIII with single black seta subapically on lateral surface. Femora without strong ventral setae, some hairs may be present, FII with or without and FIII with single strong black seta subapically on lateral surface. Tibia (Figs. 2–6) of varying shapes, usually slightly wider apically than basally, TII with MSSC, other tibiae not modified; TIII with strong black setae at various points along entire length. I- and IIIt1–5 normal, not modified; IIt1 (Figs. 2–6) usually shorter than IIt2, with MSSC; IIt2 inserted at apex of IIt1; IIt2-5 normal, not modified.

Wing. Micropterous, strongly reduced in venation and membrane; only costal vein evident; apex with or without strong seta; tegula with 1 seta; no other strong setae before costagial break; costa spinose along most of its length, spines gradually becoming fine hairs at and beyond apex to posterior margin of wing. Lower calypter not evident on thorax. Halter greatly reduced, vestigial, consisting of a small stub with very short hairs apically. Wing (see Fig. 11) with transverse line of weakness from costagial break to anal area in posterior margin of wing (this line of weakness allows the wing to fold and lie flat along the abdomen when at rest).

Abdomen. In males and females, abdomen generally dorsoventrally flattened, wider than high when viewed caudally, with small, fine hairs dorsally. Hypopygium small, recessed in abdominal tergites with usually only cerci partially exposed.

Female. Length: 1.44–1.53 mm. Wing: 0.65–1.15 mm. As in male except for MSSC. Abdominal coloration often darker in portions than male. Female oviscapt (Figs. 16–18) with hemitergites variously shaped, acanthophorites very short, peglike to medium-sized, always less than half length of cerci.

Emperoptera hardyi Evenhuis, new species

Figs. 2, 11

Diagnosis. Most similar in appearance to *Emperoptera hawaiiensis* (Hardy & Delfinado), but can be separated from it in males by the lack of a long ciliated patch on the anterior surface of FII (present in *hawaiiensis*). Also, both males and females lack a silvery pollinose clypeus (present in *hawaiiensis*).

Male. Body length: 1.34–1.44 mm. Wing length: 0.86–0.88 mm. *Head*. Face and clypeus yellowish brown, front and vertex dark brown to black, subshining; *oc* and *vt* strong, black, about two-thirds length of antennal arista; clypeus slightly yellowish pollinose; face constricted at middle, eyes holoptic below antennae for a distance equal to diameter of 4 ommatidia; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel yellow, flagellomere brown; arista length subequal to head height.

Thorax. Yellowish brown on mesoscutum except yellow posteriorly and posterolaterally, scutellum yellow; thoracic setae black, dc normal, ph, np, pa, sa, and sc strong: 3 dc; 1 + 1 np; 2 + 2 ph; 1 pa; 1 sc; ac absent.

Legs. Coxae and femora yellowish brown, CII brown laterally. Leg I unmodified, without MSSC; all femora without setae or hairs on ventral surface. TII (Fig. 2) with strong black setae as follows: 2 subbasally, 1 at point 2/3 from base to apex, 2 subapically; patch of strong black setae (1/2 length of longest setae) along apical half in two rows (MSSC); IIt1 (Fig. 2) short, 1/8 length of TII, with slightly curved black apical spur (MSSC); IIt2–5 unmodified. Leg III unmodified, without MSSC.

I-2.8;2.6;1.2/0.6/0.5/0.5/0.3 II-3.6;3.8;0.5/0.8/0.8/0.5/0.3

III-4.4;4.6;1.0/1.0/0.6/0.5/0.3

Wing (Fig. 11). Reduced to just costal vein, with black seta at apex; transverse line of weakness at humeral crossvein. Halter reduced to small stub, with short hairs apically.

Abdomen. Yellowish brown with short black hairs posteriorly on each tergite, shorter, paler hairs dorsally and laterally. Hypopygium yellowish brown, not dissected.

Female. Length: 1.44 mm; wing: 0.85 mm. Similar to male except lacking MSSC; otherwise as follows: FIII and TIII brownish; abdomen generally dark brown, yellowish only anteriorly on tergite II and III, darker yellow to brown medially on tergite III. Oviscapt not dissected.

Types. Holotype male (BPBM 15,603) allotype female and 7♂,11♀ paratypes from Hawaiian Islands: Maui (W): Pu'u Kukui Ridge, 4500 ft. [1371 m], 27.ix.1973, D.E. Hardy. Other paratypes: 50',3 Q, Pu'u Kukui Trail, 4300 ft. [1310 m], 27.ix.1973, K.Y. Kaneshiro; 3 Q, Pu'u Kukui Trail below Violet Lake, 4400 ft. [1341 m], 23.vii.1973, S.L. Montgomery. Holotype and allotype in BPBM; paratypes in BPBM, UHM, USNM, and BMNH.

Discussion. D.E. Hardy (pers. comm.) informed me that this species was serendipitously collected while waiting out a typical Pu'u Kukui downpour. Standing under a protective canopy that included some Freycinetia, he looked at the ground and noticed "small brown things" hopping around the leaf litter. At closer inspection, these proved to be flightless dolichopodids. Based on Perkins's label data for mirabilis and the collecting methods described by Zimmerman (1938), it was commonly thought that all flightless dolichopodids were arboreal or semi-arboreal, either in Freycinetia or in moss and lichen on tree trunks. Hardy said it had taken him some 20 years to finally learn how to collect flightless dolichopodids and the answer was at his feet the whole time!

Etymology. The species is named in honor of D. Elmo Hardy, who helped lay the foundation of research in Hawaiian dolichopodids with his monumental work with Marian Adachi Kohn in the Insects of Hawaii series. His convivial talks with me over the years and his superb knowledge of the Hawaiian Diptera fauna have had a significant impact on my work with this family in Hawaii.

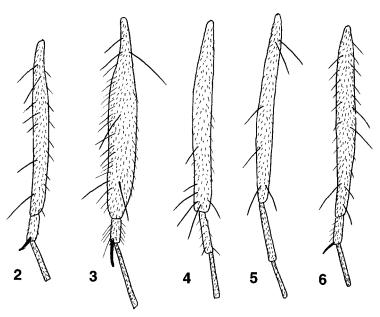
Emperoptera hawaiiensis (Hardy & Delfinado), new combination Figs. 3, 16; Map 1 Campsicnemus n. sp. A. Hardy & Delfinado, 1973: 6.

Campsicnemus hawaiiensis Hardy & Delfinado, 1974: 368. Nishida, 1992: 95; Nishida, 1994: 89. Evenhuis, 1995: 30. Evenhuis et al., 1996: 5.

Diagnosis. Most similar in appearance to Emperoptera hardy, n. sp., from West Maui, but can be separated from it in males by the long ciliated patch on the anterior surface of FII (not present in hardyi, n. sp.). Both males and females have silvery pollinosity on the clypeus (yellowish in hardy, n. sp.) and have only 2 dc (3 in all other Emperoptera).

Male. Body length: 1.53 mm. Wing length: 1.15 mm. Head. Face and clypeus blackish, front and vertex dark brown to black, subshining; oc and vt strong, black, about two-thirds length of antennal arista; clypeus bright silvery pollinose; face constricted at middle, eyes not holoptic, separated medially by diameter of 1-2 ommatidia; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel reddish yellow, flagellomere brown; arista about $1.5 \times$ head height.

Thorax. Yellowish brown throughout, subshining on mesoscutum; lateral and posterior thoracic setae strong, black, first dc small, weak, second dc long: 1+1 dc; 1 np; 2+2 ph; 1 pa; 1 sa; 1+1sc; ac absent. The sa seta is unusually close to the postalar callus.



Figs. 2–6. Emperoptera, tibiae and basistarsi. 2. E. hardy, n. sp.; 3. E. hawaiiensis (Hardy & Kohn); 4. E. mirabilis Grimshaw; 5. E. montgomeryi, n. sp.; 6. E. zimmermani, n. sp.

Legs. Coxae and femora yellowish to yellowish brown, CII brown laterally; Leg I unmodified, without MSSC; all femora without setae or hairs on ventral surface. FII with fine, long pale cilia on medial (inner) surface and ventrally (MSSC); TII (Fig. 3) slightly swollen medially, with strong black setae as follows: 2 subbasally, 1 at point 2/3 from base to apex, 2 subapically; patch of strong black setae (1/2 length of longest setae) on medial 2/3 (MSSC); IIt1 (Fig. 3) short, 1/7 length of TII, with slightly curved black apical spur (MSSC); IIt2–5 unmodified. Leg III unmodified, without MSSC.

I-3.6;3.0;1.7/0.9/0.6/0.5/0.5

II-3.4;4.5;0.7/1.5/1.0/0.6/0.6

III-4.4;5.0;1.5/1.5/1.0/0.6/0.6

Wing (see Fig. 11). Reduced to just costal vein, with black seta at apex; transverse line of weakness at humeral crossvein. Halter reduced to small stub, with short hairs apically.

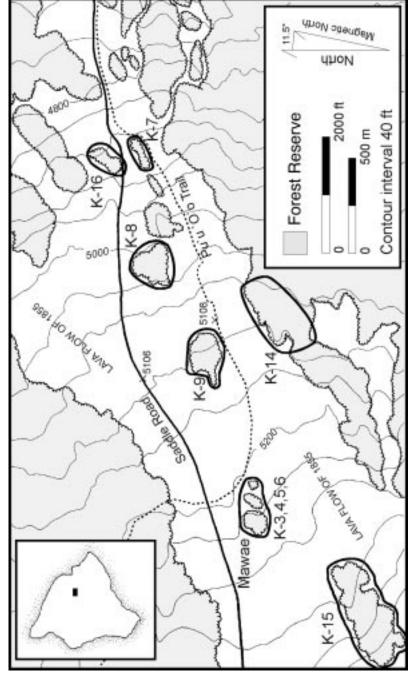
Abdomen. Yellowish brown with short black hairs posteriorly on each tergite, shorter, paler hairs dorsally and laterally. Hypopygium yellowish brown, not dissected.

Female. Length: 1.53 mm; wing: 1.15 mm. Similar to male except lacking MSSC; otherwise as follows: abdomen yellowish brown with black coloration restricted to posterior margin of tergites II–V as contrasting stripe. Oviscapt (Fig. 16) with hemitergites subquadrate, 2–3 small acanthophorites on mesoposterior half.

Types. Holotype \circ (BPBM 10,774) and $10\circ$ \circ paratypes from Hawaiian Islands: **Hawai'i**: $K\bar{\imath}puka$ 14, Saddle Road, 5100 ft. [1554 m], 25–27.ii.1972, M.D. Delfinado. Other paratypes: Hawaiian Islands: **Hawai'i**: $5\circ$ \circ \circ , $K\bar{\imath}puka$ 9, Saddle Road, 5100 ft. [1554 m], 25–27.ii.1972, M.D. Delfinado; $3\circ$ \circ , same locality, 18.ii.1973, sweeping, D. Fujii.

Specimens from the original type series were collected in 2 adjacent $k\bar{l}puka$ [a Hawaiian term referring to islands of vegetation in lava fields] (numbered 9 and 14)² in the

^{2.} The numbering system of the *kīpuka* in the Saddle area was devised by Dr. William Heed during the 1960s for the Hawaiian *Drosophila* project. The original number of *kīpuka* was 15. *Kīpuka* 16 was added during this study. Though the numbering system was originally intended for use only by *Drosophila* biologists, these *kīpuka* have since become internationally renowned as unique "island" laboratories of evolution and ecology for biologists of all disciplines and harbor many threatened, rare and/or unique organisms.



Map 1. Map of the Saddle area of the island of Hawai's showing numbered kipuka on the 1881 and 1855 Mauna Loa lava flows. Kipuka 9 and 14 are type localities for Emperopiera hawaiiensis (Hardy & Delfinado).

Saddle Road area of Hawai'i Island at 5100 ft. [1554 m] elevation (see Map 1). Hardy & Delfinado (1974) indicated that specimens of the type series were deposited in BPBM (7 specimens), UHM (9 specimens), and USNM (4 specimens). The entire type series including the holotype was examined in this study.

Other material examined: Hawaiian Islands: **Hawai'i**: 1♂, Kīpuka 14, Saddle Road, 5100 ft. [1554 m], 25.ii.1972, D.E. Hardy (UHM); 1♀, [Hawaii Volcanoes National Park]: Mauna Loa Truck Trail, IBP Site #9, 6600 ft. [2011 m], 18.viii.1972, M.D. Delfinado (BPBM).

Discussion. The label data of the holotype (though not specified in the original description) indicates it is from $k\bar{\imath}puka$ 14. A USGS Benchmark just outside $k\bar{\imath}puka$ 9 on an ancient Hawaiian footpath on the 1855 lava flow leading to $k\bar{\imath}puka$ 14 is labeled as 5107 feet. Specimens from the type series were reared from leaf litter samples each measuring 30 x 30 x 4 cm taken in each of the $k\bar{\imath}puka$. Hardy *et al.* (1981: 148) discussed in detail the methods used in rearing Diptera out of these samples, but did not mention this species in the textual discussion or in the list of species that were reared from the leaf litter.

No specimens have been collected of this species since the original collections in 1972 and 1973. Visits by me and colleagues to both $k\bar{\imath}puka$ 9 and 14, as well as $k\bar{\imath}puka$ 5, 6, 7, 8, and 16 (see Map 1), from 1993–1997 to specifically search for this species resulted in no collections. This, despite the use of numerous different trapping methods including the rearing of invertebrates out of leaf litter samples. Evenhuis (1995) implied that feral ungulates ($Sus\ scrofa$), which root in soft earth and disturb the forest floor leaf litter, may have had an adverse effect on the populations of $Emperoptera\ hawaiiensis$ in these $k\bar{\imath}puka$.

Emperoptera mirabilis Grimshaw

Figs. 1, 4, 7, 17

Emperoptera mirabilis Grimshaw in Grimshaw & Speiser, 1902: 81. Perkins, 1907: 49; Perkins, 1913: xlviii, clxxxiii; Bezzi, 1916: 171; Becker, 1922: 110; Van Duzee, 1933: 309; Bryan, 1934: 409, 448; Zimmerman, 1938: 145; Zimmerman, 1948: 153; Séguy, 1950: 331; Adachi, 1954: 294. Oldroyd, 1964: 279; Evenhuis, 1995: 30.

Campsicnemus mirabilis Grimshaw. Hardy & Kohn, 1964: 119; Takagi, 1972: 90; Hardy & Delfinado, 1973: 5; Hardy & Delfinado, 1974: 368; Gagné, 1974: 38; Opler, 1976: 33; Dyte, 1980: 224; Bickel & Dyte, 1989: 411; Nishida, 1992: 95; U.S. Department of Interior, Fish and Wildlife Service, 1994: 59019; Nishida, 1994: 89.

Diagnosis. This species is distinct from all others in the genus in 2 major respects: it has a generally polished dark brown to black mesoscutum and when viewed laterally has a striking dark brown/yellow demarcation in the pleural region (dark brown above, yellow below) (Fig. 1). Otherwise, it is similar to *montgomeryi*, n. sp. in the fact that it lacks an apical spur on IIt1 of the male. Instead of this spur on IIt1, the male FII has a dense patch of stronger and longer setae and hairs apically.

Male. Body length: 1.53–1.80 mm. Wing length: 0.86–1.00 mm. *Head*. Face and clypeus black, front and vertex dark brown to black, shining with a bluish green hue in some lights; *oc* and *vt* strong, black, about two-thirds length of antennal arista; clypeus densely silvery pollinose; face constricted at middle, eyes not holoptic, separated by diameter of 1 ommatidium; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel reddish brown to brown, flagellomere brown; arista slightly longer than head height.

Thorax. Dark brown to black, polished brown to black on mesoscutum; an episternum, metepimeron, and notopleural area dark brown to black above, yellow below; katepimeron yellow; lateral and posterior thoracic setae strong, black, dorsal setae weak: 3 dc; 2 np; 1+1 ph; 1 pa; 1 sa; 1 sc; ac absent.

Legs. Coxae and femora yellowish brown; FI unmodified, without MSSC; TI with single strong black seta on apical one-third (MSSC). FII with long, brown, wavy cilia on apical half (MSSC); TII (Fig. 4) with strong black setae as follows: 1 subbasally, 1 at point 2/3 from base to apex, 2 subapically; apical one-third with successively longer and denser setae on medial surface (MSSC); IIt1 with a few long hairs mesally; IIt2–5 unmodified. Leg III unmodified, without MSSC.

I-3.0;2.5;1.0/0.7/0.5/0.3/0.3

II-3.0;4.2;0.8/0.7/0.7/0.5/0.5

III-4.5:4.8:1.0/0.8/0.8/0.5/0.5

Wing (Fig. 1). Reduced to just costal vein, with black seta at apex; transverse line of weakness at humeral crossvein. Halter reduced to small stub, with short hairs apically.

Abdomen. Tergite I shining black dorsally with brown hairs dorsally; remainder of tergites shining dark brown with pale hairs dorsally and laterally. Hypopygium yellow, not dissected.

Female. Length: 1.44–1.53 mm; wing: 0.85 mm. Similar to male except lacking MSSC; otherwise as follows: abdomen dark brown throughout. Oviscapt (Fig. 17) with subelliptical hemitergites, with 2–3 small, peglike acanthophorites on each hemitergite, cerci with fine, medium-length hairs.

Types. The type series originally consisted of 9 specimens from the island of O'ahu (number of each sex not stated). All were found and examined in this study (3 syntypes in the BMNH; 3 syntypes in RMSE; and 3 syntypes in BPBM). Of these 9 specimens, a **lectotype male** (which is in the best condition of all the specimens) is here designated with the following labels: "Koolau Range / 12.1900 / on *Freycinetia*" in BMNH. The lectotype is on a card with 2 other specimens. The lectotype is the specimen in the middle of the 3 and was the one most likely depicted in the illustration in Grimshaw and Speiser (1902: 81). The other 2 paralectotypes on the card are females.

The 3 paralectotypes in the BPBM collection consist of a male singly pinned and a card with 2 damaged specimens (1 female; the other specimen is too damaged to determine the sex). The single male has the label "back of Malukia", which is no doubt a misprint for "back of Maluhia". Maluhia [Hawaiian term meaning "peace"] was a cabin on Tantalus (Fig. 7) belonging to H.W. Schmidt, then the Swedish ambassador to Queen Lili'uokulani. This cabin could very well have served as a focal point of Perkins and may have been a place he visited while collecting in the area. Perkins (1913: clxxxiii) indicated that the label data "on *Freycinetia*", which Grimshaw had published as being associated with some specimens of the type series, were in error. The 3 syntypes in RMSE collection consist of 1 female pinned to an acetate card and 2 female specimens (with heads having become broken off) in alcohol. They are all without locality data; however, they all carry RMSE accession numbers, which correspond to a ledger entry with the words "back of Malukia, Dec. 1900."

The specimens were all collected from leaf litter in association with another flightless insect, the endemic Hawaiian hemipteran *Nesidiorchestes* Kirkaldy. Neither the dipteran nor the hemipteran are truly arboreal.

The type series is in deplorable condition. Almost all the specimens are damaged in some respect. The description above was made from examination of all the specimens and is not indicative of one specimen.

Discussion. It is very probable that this species is extinct. Perkins (1907) indicated that the specimens of *mirabilis* he had collected were "locally abundant" on Tantalus at that time, but collecting subsequent to the original in December 1900 had not revealed any further specimens. Various factors could be responsible for the possible demise of this species. Predatory ants of the genus *Pheidole* Westwood, which are a major factor in the loss of native fauna in many parts of the Hawaiian Islands, were already a problem at lower elevations in many places in the Hawaiian Islands during the time R.C.L. Perkins collected in the late 1890s. Additionally, Perkins remarked in his (1907) address concern-



Fig. 7. "Maluhia" cabin, Tantalus area, Oʻahu [misspelled in this photograph; other photographs of this cabin have the spelling corrected]. Photograph taken in September 1892. Note the upside down state flag signifying distress; perhaps in reference to the upcoming overthrow of the Hawaiian monarchy in January 1893 by U.S. businessmen. Photo courtesy of the Bishop Museum Archives.

ing the insects of Tantalus that much had changed in that area in the short amount of time that had elapsed since he had last collected there (December 1900). No doubt the impact of humans and invasive, non-indigenous, predatory species has had an irreversible effect on the populations of these flightless flies since their original collection. Continued monitoring of the original type locality as well as other suitable habitats in high elevations on Oʻahu should be coordinated with pitfall trapping, dark-colored pan trapping³ and lengthy visual observations (1–2 hours per site) in order to further assess the current status and possible extinction of this species.

Emperoptera montgomeryi Evenhuis, new species

Figs. 5, 8, 18; Pl. 1

[Unnamed species]. Imamori, 1994: 321.

Diagnosis. Most similar to *Emperoptera mirabilis* in lacking a spur on IIt1 in the male. It is easily separated from all other species of *Emperoptera* by the conspicuously long wing in the male (longer than the abdomen) and angled and foliate apex (the wing is essentially shaped much like a hockey stick) (Fig. 8). In other *Emperoptera* males, the wing is about half the length of the abdomen, is slightly curved throughout its length, and lacks any enlargement at the apex.

Male. Body length: 1.34-1.44 mm. Wing length: 1.06-1.15 mm (measured from base to bend). *Head*. Face and clypeus black, front and vertex dark brown to black, subshining; oc and vt strong,

^{3.} Based on the author's field experience with flightless Hawaiian dolichopodids, these small flies do not approach items that are yellow in color (leaves, water traps, etc.). They instead prefer to remain on dark colored objects (twigs, leaves, soil), which provide them with better camouflage.

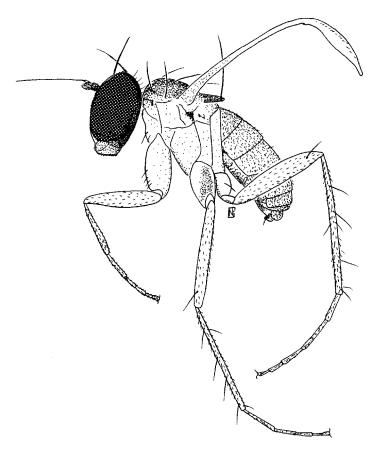
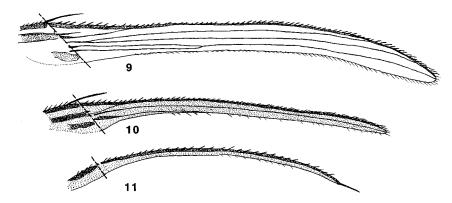


Fig. 8. Emperoptera montgomeryi, n. sp., habitus.

black, about two-thirds length of antennal arista; clypeus silvery pollinose; face constricted at middle, eyes holoptic below antennae for a distance equal to diameter of 3 ommatidia; palp minute, proboscis brown, extending only slightly below eye in lateral view; antennal scape, pedicel, and flagel-lomere brown; arista length about $1.3 \times$ head height.

Thorax. Mesoscutum subshining yellowish brown with 2 admedian longitudinal brown vittae following line of dc and coalescing in prescutellar area to form a brown rectangle, pleura yellowish; lateral and posterior thoracic setae strong, black, dorsal setae normal, not strong: 3 dc; 1+3 np; 1+2 ph; 1 pa; 1 sa; 1+1 sc; ac absent. First and third dc 1/2 length of second dc; sc almost as long as mesoscutum.

Legs. Coxae and femora yellowish brown, CII brown laterally; Leg I unmodified, without MSSC; all femora without setae or hairs on ventral surface. FII unmodified; TII (Fig. 5) with strong black setae as follows: 2 subbasally, 1 at point 2/3 from base to apex, 2 subapically; IIt1–5 unmodified. Leg III unmodified, without MSSC.



Figs. 9–11. Wings of flightless Hawaiian Dolichopodidae. 9. Campsicnemus bryophilus (Adachi); 10. Campsicnemus haleakalaae (Zimmerman); 11. Emperoptera hardyi, n. sp.. Dashed line marks line of weakness for folding (see text for discussion).

I-3.0;2.6;1.5/0.5/0.5/0.3/0.3

II-3.7;4.1;1.2/1.0/0.6/0.5/0.3

III-3.8;5.0;1.5/1.2/1.0/0.5/0.5

Wing (Fig. 8). Reduced to just costal vein, apical 1/3 angled and swollen into a foliate shape (MSSC), foliate portion with minute spicules along anterior margin; transverse line of weakness at humeral crossvein. Halter reduced to small stub, with minute hairs apically.

Abdomen. Light brown with short black hairs posteriorly on each tergite, shorter, paler hairs dorsally and laterally. Hypopygium yellowish, not dissected.

Female. Length: 1.44 mm; wing: 0.65 mm. Similar to male except lacking MSSC; otherwise as follows: abdomen generally dark brown to black, yellowish anteriorly and laterally on tergite II. Oviscapt with hemitergites (Fig. 17) semicircular, single pair of short acanthophorites on each hemitergite originating close to midline.

Types. Holotype \circlearrowleft (BPBM 15,604) from Hawaiian Islands: **Oʻahu**: Mt. Kaʻala, 4000 ft. [1220 m], summit bog, leaf litter, 3.viii.1994, N.L. Evenhuis. Allotype $\, \circlearrowleft \,$ topotypic, 4.vii.1994, leaf litter, N.L. Evenhuis. *Paratypes*: Hawaiian Islands: **Oʻahu**: 5 $\circlearrowleft \,$, 6 $\, \circlearrowleft \,$, topotypic, 19.i.1993, *Broussasia* leaf litter, 11.ix.1993, 6.vi.1994, 4.vii.1994, leaf litter, S.L. Montgomery, N.L. Evenhuis; 1 $\, \circlearrowleft \,$, same data except: 1200 m, 21.xi.1995, leaf litter, F.G. Howarth, S. Taiti (all in BPBM).

Discussion. This species is the only flightless dolichopodid known that exhibits distinct sexual dimorphism. Males have wings that extend over the abdomen with the lance-olate apical portion curved down past the apex of the abdomen when the wings are at rest. Female wings are much shorter (about one-half the length of the abdomen (and are the very narrow, toothpick-like wings typical of *Emperoptera* species. *Emperoptera montgomeryi* is the only species of flightless Hawaiian dolichopodid without MSSC on leg II. It is assumed that the exaggerated MSSC on the apex of the wing in this species has taken the place of MSSC anywhere on leg II.

With the knowledge that flightless dolichopodids may have become extinct on Mt. Tantalus due to predatory ant perturbations, suitable habitats have been searched over the years throughout high elevation localities on Oʻahu for possible new populations of *Emperoptera mirabilis* or other flightless dolichopodid species. After many years of fruitless

searches for flightless dolichopodids in and around the summit bog area of Mt. Kaʻala, the leaf-litter roaming species described above was discovered by Dr. Steven L. Montgomery in 2 populations in the summit bog. In one of the populations, this species occurs sympatrically with the sole Oʻahu population of the flightless fly *Campsicnemus bryophilus* (Adachi) (Evenhuis, 1995). Though *Emperoptera montgomeryi* occurs in at least 2 different but closely approximated populations on Mt. Kaʻala, it is still one of the rarest of the known species of *Emperoptera*. Concentrated collecting at the site by me has yielded about 1 specimen per hour. Recent human-induced damage to a portion of the fragile elfin cloud forest vegetation on Mt. Kaʻala may have had an adverse effect on the population numbers of this species. Collections previous to the damage at the site totaled more specimens per visit than collections after the damage took place and recent collecting efforts there in 1996 and 1997 has failed to locate further specimens.

Etymology. This species is named in honor of Steven L. Montgomery, whose field pursuits of the incredible Hawaiian arthropod fauna have yielded as many important new species as he has found puzzles to confound and delight evolutionary biologists. His relentless collecting efforts for flightless dolichopodids, predatory geometrids and other endemic litter arthropods on Mt. Kaʻala over the years proved more successful than even he imagined. Upon his initial discovery of a population of flightless dolichopodids atop the mountain, he thought he had found only this species. But upon examination in the laboratory, it turned out to be 2 species (the other is the only known Oʻahu population of Campsicnemus bryophilus) living sympatrically with Emperoptera montgomeryi in a 10 m² patch of leaf litter!

Emperoptera zimmermani Evenhuis, new species

Fig. 6

Diagnosis. Similar to *Emperoptera hardyi*, n. sp. but can be distinguished in males by the presence of long, dense hairs on the basal half of TII (these hairs absent on the basal half in *hardyi*, n. sp.). Females of *zimmermani* can be distinguished from *hardyi*, n. sp. by the all brown abdomen (yellowish anteriorly on tergite II and III in *hardyi*, n. sp.).

Male. Body length: 1.53 mm. Wing length: 0.92 mm. *Head*. Face and clypeus yellowish brown, front and vertex dark brown to black, subshining; *oc* and *vt* strong, black, about 2/3 length of antennal arista; clypeus slightly yellowish pollinose; face constricted at middle, eyes holoptic below antennae for a distance equal to diameter of 4 ommatidia; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel yellow, flagellomere brown; arista length subequal to head height.

Thorax. Yellowish brown throughout, subshining on mesoscutum; lateral and posterior thoracic setae strong, black, dorsal setae normal in size: 3 dc; 1+2 np; 1 + 2 ph; 1 pa; 1 sa; 1+1 sc; ac absent.

Legs. Coxae and femora yellowish brown; Leg I unmodified, without MSSC; all femora without setae or hairs on ventral surface. FII unmodified; TII (Fig. 6) with strong black setae as follows: 2 subbasally, 1 at point 2/3 from base to apex, 2 subapically; long fine hairs on basal 1/2, patch of strong black setae (1/2 length of longest setae) along apical 1/2 (MSSC); IIt1 (Fig. 6) short, 1/8 length of TII, brown, with slightly curved black apical spur (MSSC); IIt2–5 unmodified. Leg III unmodified, without MSSC.

I-3.1;2.7;1.2/0.7/0.5/0.3/0.5

II-3.5:4.2:0.6/1.0/0.7/0.5/0.5

III—4.0;5.0;1.3/1.0/0.7/0.6/0.6

Wing (see Fig. 11). Reduced to just costal vein, with black seta at apex; transverse line of weakness at humeral crossvein. Halter reduced to small stub, with short hairs apically.

Abdomen. Yellowish brown with short black hairs posteriorly on each tergite, shorter, paler hairs dorsally and laterally. Hypopygium yellowish brown, not dissected.

Female. Length: 1.44 mm; wing: 0.85 mm. Similar to male except lacking MSSC; otherwise as follows: abdomen generally darker brown than in male. Oviscapt not dissected.

Types. Holotype male (BPBM 15,605), allotype female, and 10° , 10° paratypes from Hawaiian Islands: **Maui** (**E**): Upper Hāna Forest, near Wai'ele'ele, 6700 ft. [2042 m], 8.viii.1973, D.E. Hardy. *Other paratypes*: Hawaiian Islands: **Maui** (**E**): 30° , 30° , Upper Hāna Forest, 5680 ft. [1731 m], under *Lobelia*, 7.viii.1973, C.W. Whittle; 10° , same locality and collector, 5675 ft. [1730 m], 25.vii.1973; same locality and collector, 20° , 6800 ft. [2072 m], 8.viii.1973 (all BPBM). Holotype, allotype, and some paratypes in BPBM. Other paratypes in UHM.

Discussion. This species is known to occur sympatrically with Campsicnemus hale-akalaae in the Hāna rain forest area of East Maui.

Etymology. This species named in honor of Elwood C. Zimmerman, one of the great "renaissance" entomologists, whose seminal work on Hawaiian insects has given others the foundation from which to build a tremendous base of knowledge of one of the most biodiverse areas of the world in terms of native species per square kilometer.

Genus Campsicnemus Haliday

Camptosceles Haliday, 1832: 357 (as a subgenus of *Medetera* Fischer von Waldheim). Suppressed by I.C.Z.N., 1958: 349.

Campsicnemus Haliday in Walker, 1851: 187. Type species: Dolichopus scambus Fallén, 1823, by validation of I.C.Z.N., 1958: 351.

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

Species of the genus *Campsicnemus* are generally found in the Northern Hemisphere. Three areas of diversity below the equator are known: the Marquesas, Tahiti, and Rapa Island in the South Pacific (the last 2 localities are new distribution records for the genus and contain many undescribed species). No flightless forms have yet been found from these islands. However, there is no reason to believe that flightless forms of *Campsicnemus* do not exist in the higher elevations of the Marquesan and Tahitian islands. Concentrated collecting on the highest mountain tops on these islands using the techniques necessary to observe and collect these cryptic species may ultimately prove successful.

The flightless forms of this genus can be typified as follows:

Male. Length: 1.56–2.08 mm. Wing: 1.35–1.73 mm. Head. In lateral view higher than wide; in frontal view subtriangular; eyes with interommatidial hairs, most dense on lower facets; eyes constricted medially below antenna, holoptic or nearly holoptic just below antennae for short distance (eyes holoptic for distance equal to diameter of 1–4 ommatidia or slightly separated by diameter of 1–2 ommatidia); vertex not sunken lateral to ocellar tubercle, often with yellow to brown pollinosity laterally and posteriorly; oc and vt strong, black, larger and stouter than winged Campsicnemus species; palp minute, gray to brown with yellow to brown pollinosity and short black hairs apically; proboscis protruding below eye level more than Emperoptera, but not as well produced as in Signatineurum Parent and large species of Eurynogaster Van Duzee; antennal scape subcylindrical, slightly flared apically; pedicel subglobular in shape with short apical neck, pedicel usually inserted into concave apex of scape, with minute hairs dorsally and laterally as ring at apex; flagellomere subtriangular, covered with pubescence, inserted onto neck of pedicel; arista inserted subbasally on dorsal surface of flagellomere, more pubescent than in Emperoptera.

Thorax. Mesoscutum much flatter than winged species of Campsicnemus; thoracic setae very

strong and long, much longer and stouter than winged species of *Campsicnemus*. Propleuron with single seta. Setation as follows: 3–4 dc; 2+1 np; 2+1 ph; 1 pa; 1 sc; ac absent.

Legs. Shape of segments normal except for those associated with MSSC. MSSC primarily confined to segments on leg II (usually TII and IIt1). CI with 3–6 setae anteromedially at apex, 3–4 shorter setae posteriorly at apex, CII with brown hairs on medial surface, CIII with 1 black setae subapically on lateral surface. Femora with strong ventral setae (ventromedially in haleakalaae), additionally, some hairs may be present, FIII with single strong black seta subapically on medial surface. Tibia (Figs. 13–15) of varying shapes, usually wider apically than basally, TII with MSSC, other tibiae not modified; TIII with strong black setae at various points along entire length. I- and IIIt1–5 normal, not modified; IIt1 (Figs. 13–15) usually very much shorter than IIt2, with MSSC; IIt2 inserted subapically on IIt1 (aeptus and bryophilus) or inserted at apex of IIt1 (haleakalaae); IIt2-5 normal, not modified.

Wing. Stenopterous, reduced in venation and membrane; costal, radial, and sometimes medial veins evident; apex without strong seta; tegula with 1 seta; very strong, long black basicostal seta just before costagial break; costa spinose along most of its length, spines gradually becoming fine hairs at and beyond apex to posterior margin of wing. Lower calypter on thorax a small stub with short hairs at apex. Halter and knob normal, not reduced. Wing with transverse line of weakness from costagial break to anal area along posterior margin of wing (allowing the wing to fold and lie flat along the abdomen when at rest).

Abdomen. In males, abdomen generally flattened laterally, higher than wide when viewed caudally, with small, fine hairs dorsally; female abdomen as wide as high or flattened dorsoventrally and wider than high when viewed caudally. Hypopygium small, recessed in abdominal tergites with usually only cerci partially exposed.

Female. Length: 1.63–2.21 mm. Wing: 1.54–1.63 mm. As in male except for MSSC. Abdominal coloration often darker in portions than male. Oviscapt (Figs. 19–21) with hemitergite variable in shape, with acanthophorites as long as or slightly shorter than cerci, sometimes curved.

The genus *Campsicnemus* has undergone an incredible amount of speciation in the Hawaiian Islands as is evidenced by the 136 species currently described. There are more than 100 undescribed species known to me from Hawaii, making the genus one of the most diverse of the Hawaiian Diptera (outnumbered only by the genus *Drosophila*).

Flightless Hawaiian forms of *Campsicnemus* (all stenopterous) are known only from the islands of Maui, Moloka'i, and O'ahu.

Campsicnemus aeptus Hardy & Kohn

Fig. 13

Campsicnemus aeptus Hardy & Kohn, 1964: 41. Takagi, 1972: 90; Hardy & Delfinado, 1973: 5; Hardy & Delfinado, 1974: 368; Bickel & Dyte, 1989: 409; Nishida, 1992: 93; Nishida, 1994: 88.

Diagnosis. Most similar to *Campsicnemus bryophilus*, but is easily separated from it in the males by the strongly curved spur on IIt1 (this spur is straight with a basal zigzag in *bryophilus*) and different pattern of setae in the MSSC patch on TII.

Male. Body length: 1.73-1.92 mm. Wing length: 1.63-1.73 mm. *Head*. Face and clypeus yellowish brown, front and vertex brown pollinose, subshining in some portions; oc and vt strong, black, about two-thirds length of antennal arista; clypeus slightly yellowish pollinose; face constricted at middle, eyes holoptic below antennae for a distance equal to diameter of 1-2 ommatidia; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel reddish brown, flagellomere brown; arista subequal to head height.

Thorax. Brown throughout, subshining bronze on anterior portion of mesoscutum, coppery pollinose admedially and along scutellar suture; pleura yellowish brown, propleuron dark brown; thoracic setae strong, black: $3-4\ dc$; $1+1\ np$; $2+1\ ph$; $1\ pa$; $1\ sc$; ac absent.

Legs. Coxae and femora yellowish brown, CII with brown laterally. Tibiae and tarsi brown. Leg I unmodified, without MSSC. FII with 7 strong black hairs and 4 shorter black hairs along ventral surface; TII (Fig. 13) slightly wider apically than basally, with 2 strong black setae subapically; patch of strong black setae (1/2 length of longest setae) along apical one-third (MSSC); IIt1 (Fig. 13) very short, 1/8 length of IIt2, with strongly curved black apical spur (MSSC); IIt2–5 unmodified. FIII with 3 black setae apicoventrally, remainder of leg III unmodified, without MSSC.

I-3.2;2.9;1.8/1.0/1.0/0.6/0.6

II-4.3:4.1:0.3/2.2/1.6/0.8/0.6

III-5.5;6.5;1.5/2.0/1.2/0.8/0.6

Wing (see Fig. 9). Stenopterous, most of medial field and all of anal field of wing absent; veins R_{2+3} and R_{4+5} and M_1 complete to wing margin. Vein M_1 ends slightly beyond apex of wing. Halter and knob normal, not reduced.

Abdomen. Dark brown with short black hairs dorsally on each tergite, a few longer hairs laterally. Hypopygium brown, not dissected.

Female. Unknown.

Type. Holotype male (BPBM 4084) from Hawaiian Islands: **Maui** (**W**): Pu'u Kukui, June 1953, C.R. Joyce.

Other material examined: Hawaiian Islands: Maui (W): 30', Pu'u Kukui, 5800 ft. [1767 m], 1.ii.1973, S.L. Montgomery (all in BPBM).

Discussion. Hardy & Kohn (1964) gave the elevation of the holotype as "4,000–4,500 ft." This may be likely incorrect. The labels with the holotype do not contain any elevational data and the only 3 specimens of this species subsequently discovered were collected on Pu'u Kukui at 5800 ft. [1767 m]. The only specimens of flightless dolichopodids from the 4000–4500 ft. [1219–1371 m] elevation on Pu'u Kukui seen during this study all belong to *Emperoptera hardyi*, n. sp.

Campsicnemus bryophilus (Adachi)

Figs. 9, 14, 19

Emperoptera bryophila Adachi, 1954: 294.

Campsicnemus bryophilus (Adachi). Hardy & Kohn, 1964: 51; Takagi, 1972: 90; Hardy & Delfinado, 1973: 5; Hardy & Delfinado, 1974: 368; Bickel & Dyte, 1989: 410. Nishida, 1992: 94; Nishida, 1994: 88.

"Campsicnemus bryophila". Evenhuis, 1995: 30.

Diagnosis. Most similar to *Campsicnemus aeptus*, but can be separated from that species by the straight spur on IIt1 (strongly curved in *aeptus*) and different MSSC patch of setae on TII.

Male. Body length: 1.56–1.96 mm. Wing length: 1.35–1.54 mm. *Head*. Face and clypeus yellowish brown, front and vertex brown pollinose, subshining in some portions; *oc* and *vt* strong, black, about two-thirds length of antennal arista; clypeus slightly yellowish pollinose; face constricted at middle, eyes not holoptic, slightly separated below antennae by diameter of 1 ommatidium; palp minute, proboscis yellowish brown, extending only slightly below eye in lateral view; antennal scape and pedicel yellow, flagellomere brown; arista length subequal to head height.

Thorax. Brown dorsally, pleura brown above, yellowish below, subshining bronze on anterior portion of mesoscutum, light brown pollinose medially in prescutellar area; thoracic setae strong, black: 3-4 dc; 1 + 1 np; 2 + 1 ph; 1 pa; 1 sa; 1 sc; ac absent.

Legs. Coxae and femora yellowish, CII brown laterally. Leg I unmodified, without MSSC. FII with 4 strong black hairs and 6 shorter black hairs along ventral surface; TII (Fig. 15) wider apically than basally, with 2 strong black setae subapically; small patch of strong black setae (at most 1/4 length of longest setae, some spatulate in shape) at subapical one-fourth (MSSC); IIt1 (Fig. 15) very short, 1/4 length of IIt2, with straight black apical spur (MSSC); IIt2 inserted subapically on IIt1;

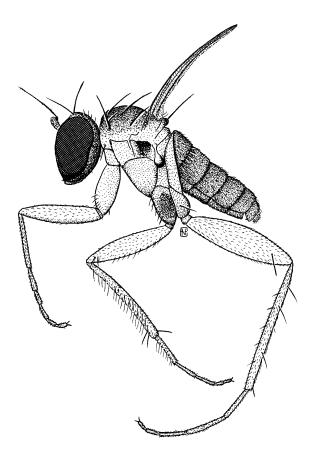


Fig. 12. Campsicnemus haleakalaae (Zimmerman), habitus.

IIt2-5 unmodified. Leg III unmodified, without MSSC.

 $I\!\!-\!\!3.7;\!3.0;\!2.0/1.0/0.8/0.5/0.5$

II-3.7;4.0;0.5/2.1/1.4/0.8/0.7

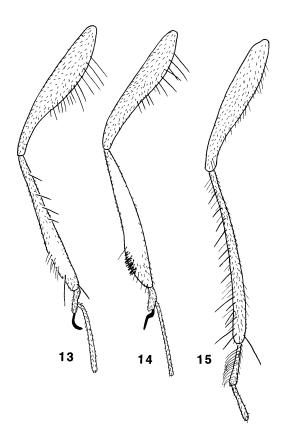
III—5.2;6.0;1.7/2.0/1.4/0.8/0.7

Wing (Fig. 9). Stenopterous, most of medial field and all of anal field of wing absent; veins R_{2+3} and R_{4+5} and M_1 complete to wing margin. Vein M_1 ends at apex of wing. Halter and knob normal, not reduced, yellow to white in color.

 $\label{lem:Abdomen.} Abdomen. \ Dark \ brown \ with \ short \ black \ hairs \ dorsally \ on each tergite, \ a \ few \ longer \ hairs \ laterally. \ Hypopygium \ brown, \ not \ dissected.$

Female. Length: 1.63–2.21 mm; wing: 1.54–1.63 mm. Similar to male except lacking MSSC. Oviscapt (Fig. 19) with hemitergites subrectangular, with pair of long, dark acanthophorites on mesoposterior 1/2 and long dark strong setae on lateral 1/2 of each hemitergite.

Types. The original series consisted of a holotype male (USNM), allotype female (USNM) and

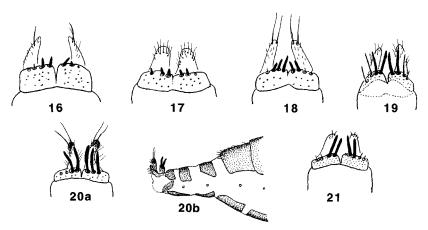


Figs. 13–15. Flightless Hawaiian *Campsicnemus* femora, tibiae, and tarsomeres 1–2. 13. *C. aeptus* Hardy & Kohn; 14. *C. bryophilus* (Adachi); 15. *C. haleakalaae* (Zimmerman).

103 paratypes from Hawaiian Islands: **Moloka'i**: Pu'uoke'aha, 3700 ft. [1140 m], July 1953, D.E. Hardy & M. Tamashiro. Seventy-nine specimens from the type series were examined in this study.

Other material examined: Hawaiian Islands: Moloka'i: 59 σ ,67 $^\circ$, Pu'u Kolekole, 3600 ft. [1097 m], 10.vi.1964. D.E. Hardy (UHM); 1 σ ,1 $^\circ$,1 $^\circ$, same locality, vii.1959, D.E. Hardy (UHM); 1 σ , Pēpē'opae, 4000 ft. [1219 m], 25.viii.1969, D.E. Hardy (UHM); 9 σ ,6 $^\circ$, Hanalilolilo, 20,24.iv.1973, C.W. Whittle (UHM); 2 σ ,2 $^\circ$, rim of Waikolu Valley, Hanalilolilo Trail, 3800 ft [1158 m], 4.v.1993, D.A. Polhemus; 4 σ ,10 $^\circ$, Transect 7 Trail above Kolekole Cabin, Kamakou TNCH Preserve, 1200 m, 15.v.1992, swept from ferns in understory, D.A. Polhemus; 3 σ ,1 $^\circ$, Kawela Gulch, 1068–1144 m, 18, 21.iii.1966, C.M. Yoshimoto; 1 σ ,2 $^\circ$, same locality, 1140 m, 8–10.vii.1968, 4–5.i.1981, W.C. Gagné (all BPBM); 7 $^\circ$, Oloku'i, Wailau, 3000 ft. [914 m], 4.x.1976, S.L. Montgomery & R. Villegas (UHM); 1 $^\circ$, Pu'u Kolekole, 9.v.1971, L. Uyenishi (BPBM). O'ahu: 2 σ ,4 $^\circ$, Mt. Ka'ala, west slope, 4000 ft. [1219 m], *Broussasia* leaf litter, 19.i.1993, S.L. Montgomery (BPBM).

Discussion. This is one of the most common flightless species found in the Hawaiian



Figs. 16–21. Female oviscapt and hemitergites, dorsal view unless otherwise indicated. 16. Emperoptera hawaiiensis Hardy & Delfinado. 17. E. mirabilis Grimshaw. 18. E. montgomeryi, n. sp.; 19. Campsicnemus bryophilus (Adachi). 20a. C. haleakalaae (Zimmerman). 20b. C. haleakalaae postabdomen showing oviscapt in lateral view. 21. C. modicus Hardy & Kohn (a fully winged female Campsicnemus shown for comparison with oviscapts of flightless Campsicnemus).

Islands. It typically occurs in leaf litter and surrounding low-growing vegetation and moss. Its seems to be broadly distributed in the mountainous region of eastern Moloka'i from Pu'u Ka'eo southeast to Kamakou and north to Oloku'i. It is also the only known flightless species with a disjunct population on Mt. Ka'ala, O'ahu. All other flightless species of Hawaiian dolichopodids are endemic to a single island.

Based on the evidence of the geological past of the islands of Oʻahu and Molokaʻi, it is possible that the 2 current population were once contiguous. There was a short period of time geologically (~1.5 mya) when the volcanic islands of Oʻahu and Molokaʻi were once a single island (Carson & Clague, 1995). It is postulated here that during this period of the geological history of the Hawaiian Islands, *C. bryophilus*, which probably originated on Oʻahu, was able to expand its range to East Molokaʻi via West Molokaʻi, the latter which had a maximum height of 1600 meters [5250 feet] in its geologic past (Carson & Clague, 1995: 20). This altitude (which corresponds well to current elevations at which *Campsicnemus* has been collected) means that equitable climes and vegetational conditions could have existed continuously from Oʻahu to Molokaʻi allowing a terrestrial dispersal by this flightless fly from one volcanic "island" to the other. The subsequent separation of the 2 islands by the Kaiwi Channel (at about 1.0 mya) and subsequent subsidence and erosion of the Waiʻanae and Koʻolau volcanoes eventually led to the relict population on Mt. Kaʻala on Oʻahu.

Campsicnemus bryophilus occurs sympatrically with Emperoptera montgomeryi on Mt. Kaʻala, Oʻahu. This is an interesting association because of the small numbers of specimens known from each population on the mountain and the fact that they are both predatory in the same small (10 m²) patch of leaf litter in which they were observed. In order to maintain a surviving number of individuals of each population, successful

resource partitioning (at least among the immature stages) may be taking place.

This species is most likely one of the 2 flightless *Campsicnemus* collected and observed by R.C.L. Perkins in the Moloka'i mountains while he was making collections of insects, birds, snails, and other animals for the *Fauna Hawaiiensis* project (see below for further details on Perkins's collecting notes concerning flightless dolichopodids).

Campsicnemus haleakalaae (Zimmerman)

Figs. 10, 12, 15, 20; Pl. 2

Emperoptera haleakalaae Zimmerman, 1938: 146. Adachi, 1954: 294.

Campsicnemus haleakalaae (Zimmerman). Hardy & Kohn, 1964: 98; Takagi, 1972: 90; Hardy & Delfinado, 1973: 6; Hardy & Delfinado, 1974: 368; Bickel & Dyte, 1989: 411; Howarth & Mull, 1992: 144; Nishida, 1992: 95; Nishida, 1994: 89.

Campsicnemus sp. Peterson, 1976: 28; Villegas, 1976: 240, 246.

Diagnosis. This species is easily distinguished from the other 2 known flightless Hawaiian *Campsicnemus* species by the more stenopterous condition of the wing (medial vein not evident at apex of wing), and (in males) the lack of an apical spur on IIt1 (a strong apical spur is present in *aeptus* and *bryophilus*), and the densely hairy TII along its entire length (setae restricted to patches in apical portion of TII in *aeptus* and *bryophilus*).

Male. Body length: 1.53–2.08 mm. Wing length: 1.40–1.67 mm. *Head*. Face and clypeus yellowish brown, front and vertex grayish to black, brown pollinose, subshining bluish green in some portions; *oc* and *vt* strong, black, about 2/3 length of antennal arista; clypeus pale yellowish pollinose; face constricted at middle, eyes holoptic below antennae for a distance equal to diameter of 2 ommatidia; palp minute, proboscis brown, extending slightly below eye in lateral view; antennal scape and pedicel yellow, flagellomere brown; arista subequal to head height.

Thorax. Brownish throughout, subshining bronze on anterior portion of mesoscutum, pale brown pollinose laterally, posteromedially, and on scutellum; an epimeron yellowish at wing base; katepimeron with yellow spot medially; thoracic setae strong, black: 3-4 dc; 2+1 np; 2+1 ph; 1 pa; 1 sc; ac absent.

Legs. Coxae and femora yellowish, tibiae and tarsi brown, CII brown laterally. Leg I unmodified, without MSSC. FII with 4 strong brownish setae and 3 finer brown hairs along ventromedial surface; TII (Fig. 15) with strong black setae along entire length mixed with dense fine hairs (MSSC); IIt1 (Fig. 15) 1.5 × length of IIt2, with dense long hairs on medial surface (MSSC); IIt2–5 unmodified. FIII with 1 black setae apicoventrally, remainder of leg III unmodified, without MSSC.

I—3.7:2.9:2.2/1.0/0.5/0.4/0.3

II-4.0;4.6;1.5/1.0/1.0/0.7/0.6

III—6.1;6.3;1.7/1.7/1.5/1.0/0.7

Wing (Fig. 10). Stenopterous, most of medial field and all of anal field of wing absent; veins R_{2+3} and R_{4+5} and complete to wing margin; trace of vein M_1 present along posterior margin of wing in some specimens. Halter and knob normal, not reduced, yellowish in color.

Abdomen. Dark brown with short black hairs dorsally on each tergite, a few longer hairs laterally. Hypopygium yellowish brown, not dissected.

Female. Length: 2.02–2.12 mm; wing: 1.54–1.63 mm. Similar to male except lacking MSSC. Oviscapt (Fig. 20a) with hemitergites subrectangular, 2 dark, curved acanthophorites on each hemitergite, as long as cerci.

Types. Holotype male (BPBM 1,147) allotype female and 21 paratypes from Hawaiian Islands: **Maui** (**E**): northwest slope of Haleakalā, 6000–6500 ft. [1828–1981 m], 18.viii.1937, E.C. Zimmerman. One additional paratype from Hawaiian Islands: **Maui** (**E**): Kula Pipe Line in the forest near Olinda, 4000 ft. [1219 m], 20.viii.1937, E.C. Zimmerman. Twenty-one specimens of the type series including the holotype were examined during this study.

Other material examined. Hawaiian Islands: Maui (E): 10', Haleakalā N[ational] P[ark], west

rim, 6500 ft. [1981 m], 24.vi.1975, R. Burkhardt; $2\,$ Q, Maunawainui, above valley, plot 7 (Healani transect), 6500 ft. [1981 m], 22.vi.1976, R. Villegas, project staff; $1\,$ Q, same data except, Healani Camp, 6300 ft. [1920 m], R. Villegas; $1\sigma'$, same data except plot 6 (Hihia transect), 5190 ft. [1582 m], 19.vii.1976, project staff; $1\,$ Q, Koʻolau Forest Reserve, 6500 ft. [1981 m], sweeping, 13.iii.1974, W.C. Gagné; $3\sigma'$, $1\,$ Q, Upper Hāna Forest, 5675 ft. [1729 m], 6700 ft. [2042 m], 6800 ft. [2072 m], 26.vi.1973, 8.vii.1973, C.W. Whittle, D.E. Hardy; $2\sigma'$, $2\,$ Q, riparian site between Paliku cabins [1950 m], pitfall trap, vii.1985, S.M. Gon III (all BPBM).

Discussion. This is apparently a well distributed species on the summit of Haleakalā on East Maui. It was originally collected at 2 sites on the northwest slope of the mountain and has been since collected at other localities on the eastern and southern slopes of the mountain. In one case, it was found existing sympatrically with *Emperoptera zimmermani*, n. sp. at the 6800 ft [2072 m] level on the eastern slope of Haleakalā in wet forest. Most of the collections of this species were made either by beating moss and lichen onto sheets or by general sweeping of leaf litter. In one case, 4 specimens were collected in a pitfall trap. In addition, 3 specimens of this species were collected during the Maunawainui Research Project, which took place from April–November 1976 (Peterson, 1976; Villegas, 1976).

KEY TO SPECIES OF FLIGHTLESS DOLICHOPODIDAE IN HAWAII (based upon males)

1.	Halteres well developed, knob present; wing showing 2 or more longitudinal veins, wing membrane present; basicostal seta present (Campsicnemus Haliday) 2	
	Halteres vestigial; if evident, reduced to a small stub; wing micropterous, reduced to	
	thin, sclerotized costa, wing membrane not evident; basicostal seta absent (Em-	
	peroptera Grimshaw)	
2.	IIt1 short (one-third to one-fourth length of IIt2), with strongly sclerotized apical	
	spur 3	
	IIt1 approximately one-half length of IIt2, without strongly sclerotized apical spur	
	(E Maui) haleakalaae (Zimmerman)	
3.	Apical spur on IIt1 strongly curved (W Maui) aeptus Hardy & Kohn	
	Spur on IIt1 straight, not curved (Moloka'i, O'ahu) bryophilus (Adachi)	
4.	IIt1 short (one-third to one-fourth length of IIt2), with sclerotized apical spur \dots 5	
	IIt1 approximately one-half length of IIt2, without strongly sclerotized apical spur	
	7	
5.	FII with distinct patch of long fine cilia on anteroventral surface (Hawai'i Island)	
	hawaiiensis (Hardy & Delfinado)	
	FII without distinct patch of fine cilia anteroventrally; if cilia present, they are sparse	
	and mostly confined to ventral surface	
6.	FII without fine cilia (W Maui) hardyi Evenhuis, n. sp.	
	FII with sparse fine cilia ventrally (E Maui) zimmermani Evenhuis, n. sp.	
7.	Wing without apical seta; wing of male angled and foliate apically; upper pleura yel-	
	lowish brown to yellow, not contrasting with color of lower pleura (Mt. Ka'ala,	
	Oʻahu) montgomeryi Evenhuis, n . sp.	
	Wing with apical seta; wing of male not foliate apically; upper pleura dark brown to	
	black, contrasting with yellow lower pleura (Mt. Tantalus, Oʻahu)	
	mirabilis Grimshaw	

Table 1. World list of known flightless Dolichopodidae

Taxon	Location	Type of wing reduction
Apterachalcus Bickel, 1991		
borboroides Oldroyd, 1955	Campbell I	aptery
?new genus near Apterachalcus ¹		
new species ¹	Stewart I	stenoptery
Campsicnemus Haliday, 1855		1 ,
aeptus Hardy & Kohn, 1964	Hawaiian Is.	stenoptery
bryophilus (Adachi, 1954)	Hawaiian Is.	stenoptery
haleakalaae (Zimmerman, 1938)	Hawaiian Is.	stenoptery
n. sp.	eastern Canada	brachyptery
Emperoptera Grimshaw, 1902		
hardy n. sp.	Hawaiian Is.	microptery
hawaiiensis (Hardy & Delfinado, 1974)	Hawaiian Is.	microptery
mirabilis Grimshaw, 1902	Hawaiian Is.	microptery
montgomeryi n. sp.	Hawaiian Is.	microptery
zimmermani n. sp.	Hawaiian Is.	microptery
Hydrophorus Fallén, 1823		
celestialis Takagi, 1972	Nepal	brachyptery
Medetera Fischer von Waldheim, 1822		
aequalis Van Duzee	California, USA	brachyptery
Schoenophilus ²		
campbellensis Harrison, 1964	Campbell I	microptery
pedestris Lamb, 1909	Macquarie I	microptery

D.J. Bickel (pers. comm.)

FLIGHTLESSNESS IN DOLICHOPODIDAE

Morphology

There are 4 forms of flightlessness that exist in species of Dolichopodidae [definitions modified from Hackman (1964)]:

- brachyptery—wing distinctly reduced in length; not permitting flight. Wing broad and more or less blunt, usually shorter than abdomen.
- stenoptery—wing reduced in width, often very narrow; not permitting flight. Various gradations of this condition exist, but at least a radial vein is still distinct.
- microptery—wing a small appendage of varying shape, not permitting flight. Wing broad or narrow; at most, only traces of radial vein present.
- aptery—wing represented by only a small stub bearing bristles or hairs, or wing totally absent.

The most common forms of wing reduction encountered in flightless dolichopodids involves a narrowing of the wing to various degrees (Table 1). The Hawaiian species are either stenopterous (most flightless Campsicnemus), or micropterous (Emperoptera). A single Campsicnemus species (undescribed) exhibiting brachyptery is known from east-

The 2 species listed here probably belong in a genus other than Schoenophilus (Bickel, 1991)

ern Canada. Subantarctic and New Zealand forms have species that are micropterous and one that is apterous. Another brachypterous form (with a broad, but short wing) was described by Takagi (1972) for a Himalayan species of *Hydrophorus* from Nepal. Takagi labeled this type of reduction as micropterous, but in keeping with the definitions given above, it is really an extreme condition of brachyptery.

In examining the flightless species of Dolichopodidae at hand, it is apparent that certain morphological modifications or changes have occurred in concert with reduction of wings. In almost all the micropterous forms in which halteres were reduced to vestigial stubs, there was a strong seta located at the apex of the wing. This character has apparently evolved independently in 2 unrelated groups: *Emperoptera* (in the Sympycninae) and specimens tentatively identified as *Schoenophilus* Mik (in the Hydrophorinae), thus is apparently not as significant phylogenetically as other characters might be.

Among the flightless Hawaiian dolichopodids, thoracic setation is more developed than in fully winged forms. This is especially evident in the sc and ph setae (e.g., the sc are normally converging in flighted forms, but are so long in flightless forms as to become cruciate), but this phenomenon can also be seen in other mesoscutal setae such as dc, sa, pa, and np. Another characteristic typical of flightless Hawaiian dolichopodids is that the oc and vt are much longer and stouter than in fully winged taxa.

Habitat

Hardy & Kohn (1964) noted essentially 3 different color forms for *Campsicnemus* species in Hawaii, each corresponding to different adult habitat preferences: yellowish (on vegetation), brownish (on the ground or leaf litter), and dark brown to black (water skaters). This color differentiation appears to hold for the flightless forms of *Emperoptera* and *Campsicnemus* as well as the fully winged species; however, despite its polished dark brown to black coloration, *Emperoptera mirabilis* was not collected in pools or other types of water, but on leaf litter.

Climatic, vegetational, and altitudinal factors appear to play an important part in restricting the populations of flightless Hawaiian dolichopodids. All species of *Emperoptera* and flightless forms of *Campsicnemus* occur at altitudes above 4,000 feet [1220 m] (the sole exception being the enigmatic *Emperoptera mirabilis*, which was collected at 1,000 ft [305 m] in the hills behind Honolulu). In addition, the range of all the flightless species appears to coincide with habitats that possess a constant high humidity (upwards of 80 %) and constant cool temperatures (below 20 °C). All recent collections of *Emperoptera* species are at the uppermost limits of the 'ōhia/olapa (Metrosideros polymorpha/Cheirodendron trigynum) moist rain forest. Specimens of *Emperoptera* were also collected underneath *Broussasia arguta* in these rain forests. However, my observations of leaf litter preferences on Mt. Ka'ala showed that individuals of *E. montgomeryi* appear to prefer perching on brown leaves of *Cheirodendron* rather than those of *Brousassia*.

R.C.L. PERKINS AND FLIGHTLESS HAWAIIAN DOLICHOPODIDAE

The proposal here for treating flightless Hawaiian dolichopodids in two separate genera is not a novel concept. Perkins (1913), in relating his notes on his collections of Diptera in Hawaii, indicated he had collected flightless Dolichopodidae in both the genera *Emperoptera* and *Campsicnemus*. However, those forms in the latter genus remained

undescribed at that time; only the single species of *Emperoptera* was described. Though Perkins (1913: clxxxiii) mentioned "several species that frequent moss have the wings reduced to filaments", it is not known to what flightless forms of *Campsicnemus* Perkins was referring, and no *Fauna Hawaiiensis* material consisting of flightless *Campsicnemus* has yet been found, though some specimens may exist. However, an educated guess can at least be made as to what one of the species was that Perkins alluded to in his (1913) synthesis of his collection notes.

In Perkins's unpublished field notes (original transcribed copies in the Bishop Museum Archives), I have been able to find an entry dated 12 September 1893 [transcribed and annotated in 1936 (Manning, 1986)] that mentions flightless dolichopodids. The area of collection is the Makakupa'ia area upslope of Kaunakakai, Moloka'i, in the high forest [an elevation of 4500 ft. is mentioned in the previous entry of 11 September]. The 12 September entry is as follows:

"One of the Dolichopodids has rudimentary wings and can jump but is unable to fly (These flightless flies of which I collected 2 species are not described by Grimshaw in F[auna] H[awaiiensis]; possibly they looked as if the wings had been stuck together by being wet. They were quite different from the Emperoptera Grimsh. and both different habits)."

One of the "2 species" Perkins collected on Moloka'i most assuredly is *Campsicnemus bryophilus*. It is unfortunate that specimens thought to be in poor condition (wet wings) had caused it to remain unnamed for over 60 years. However, unlike *Emperoptera mirabilis*, *C. bryophilus* still exists and occurs in relative abundance the area that Perkins originally collected the undescribed specimens in 1893. It is one of the most common of the flightless species of Dolichopodidae in Hawai'i and is represented in material at hand by over 100 individuals.

However, no entry in Perkins's field notes for the second flightless *Campsicnemus* species to which Perkins's 12 September 1893 note refers could be found. Nor were any entries found for the collection of *Emperoptera mirabilis*. Unfortunately, most of Perkins's diaries were disposed of by him as he wrote the introduction to *Fauna Hawaiiensis* (especially those notes made between 1897–1901), some because they were illegibly written (Manning, 1986).

That Perkins was able to see the generic differences among the flightless forms that exist here and place some of them in the genus *Campsicnemus* is yet another example of the amazing acuity Perkins had in knowing and identifying the Hawaiian fauna. He collected barefoot in Hawaii's forests and was able to identify an incredible number of zoological species (birds, snails, insects of all orders) and plants. His surviving transcribed diaries (mainly from 1892–1895) offer a bounty of information on the fauna and flora of Hawai'i as it existed before the turn of the century. Each detailed entry paints a picture of the native Hawaiian forest as it existed in a relatively unspoiled condition and with a marvelous composition of faunal elements, some of which do not exist today. It is a shame that many of his diaries were destroyed. They not only would have helped us with accurate locality information and habitat, but would have given us a clearer picture of what Hawai'i looked like 100 years ago.

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Plate 1. Emperoptera montgomeryi Evenhuis, new species. Photo Mitsuhiko Imamori/Nature Production.



Plate 2. Campsicnemus haleakalaae (Zimmerman). Photo courtesy William .P. Mull.

slide #1 -- fpo center within box don't print keylines

Plate 1. Ischnura luta Asquith & Miller, n. sp., male

slide #2 -- fpo center within box don't print keylines

Plate 2. Ischnura luta A squith & Miller, n. sp., female