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A SECOND FLIGHTLESS CRANE FLY FROM HAWAI'I (DIPTERA: TIPULIDAE)[1]

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Abstract. A second Hawaiian subapterous crane fly, *Limonia (Dicranomyia) hardyana,* from the island of O'ahu, is described and illustrated. Modifications of the thorax associated with flightlessness are discussed; these include loss of the transverse mesonotal suture and extreme reduction of the meron.

Extreme wing reduction is common in crane flies, particularly in females. It is ordinarily seen, however, in species of cold environments such as high mountains, arctic, subarctic, and subantarctic regions, or of temperate places during winter seasons (Byers 1969, Rentz & Gagné 1968). Only within recent years have tropical subapterous crane flies been discovered, and even these are montane (Byers 1982).

The species described here was first found by Dr Wayne Gagné of the Bishop Museum, Honolulu, in September 1973 (Gagné 1975). Dr D. Elmo Hardy of the University of Hawaii provided additional specimens, and more recently Mr S.L. Montgomery and Mr W.D. Perreira have made special efforts to collect further specimens, observe them alive, and note their habitat.

Limonia (Dicranomyia) hardyana Byers, **new species** Fig. 1–11

Description based on 4♂, 1♀ pinned, and 9♂ preserved in alcohol.

General appearance phalangid-like because of short body, extremely reduced wings, and long, slender legs. Body and legs contrastingly colored brown and yellowish brown, particularly abdominal segments darkened posteriorly and femora banded.

Head. Frons and vertex dark yellowish brown to brown, occiput darker brown in some specimens; ventral surface dark yellowish brown; setae sparse, blackish; shallow median groove from occiput to near middle of frons. Eyes separated at vertex by width of about 3 rows of ommatidia, ventrally by width of 7 or 8 rows. Width of compound eye, in lateral aspect, only about ¾ length of head behind eye. Rostrum, including labellar lobes, about as long as dorsoventral diameter of eye. Antennae dark grayish brown, with subcylindrical scape, ovoid pedicel and 12 flagellomeres; length in ♂ about 1.2 mm, ♀ about 1.24 mm.

Thorax. Dorsum light grayish brown, grading into darker brown laterally on entire pleuron of prothorax, anepisternum, anepimeron and entire postnotum of mesothorax (Fig. 11). Coxae pale yellowish, lower pleural surfaces light yellowish brown. Pronotum elongate, subequal in length to combined prescutum and scutum, divided into saddlelike antepronotum and much shorter postpronotum by infolding that deepens laterally and continues as pleural suture between prothoracic episternum and epimeron. Wings rudimentary (Fig. 4, 11), about 4× as

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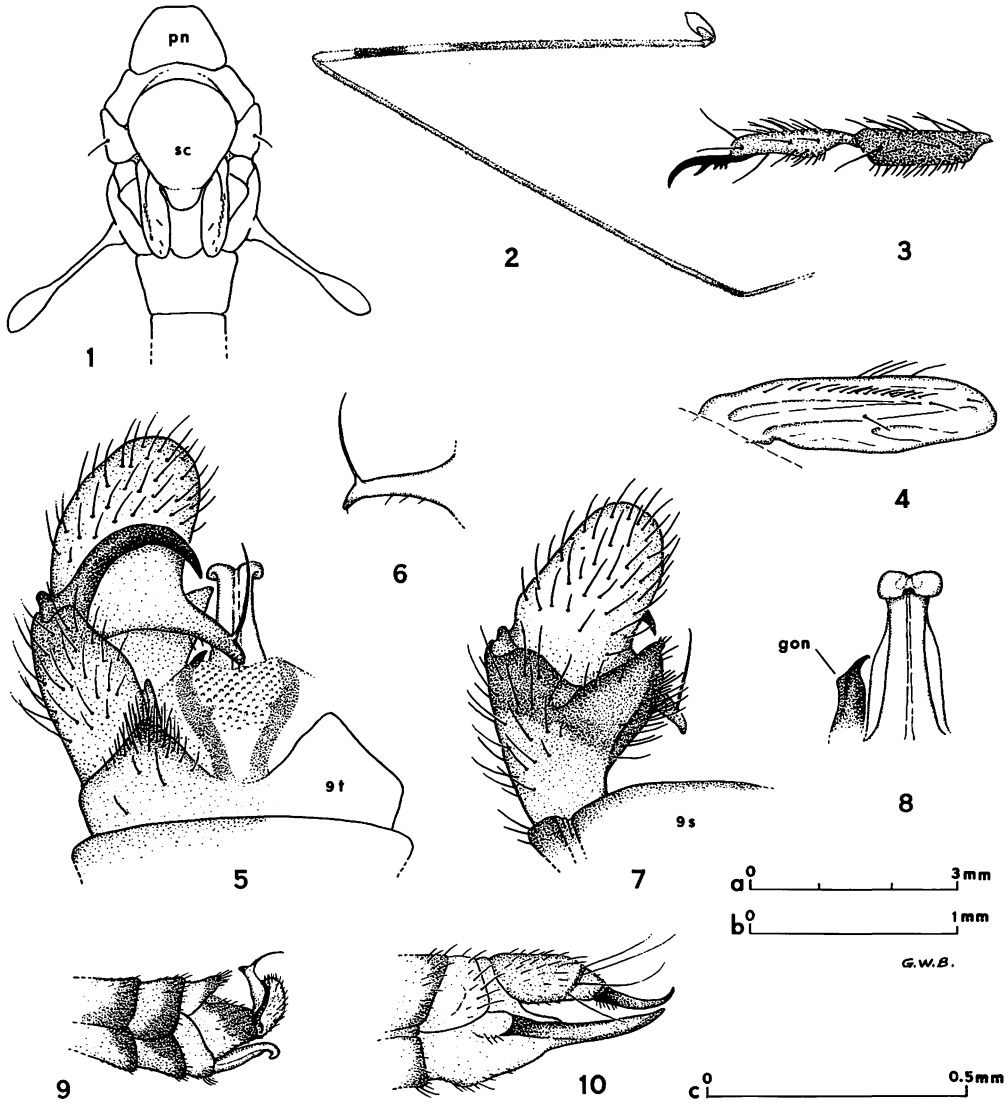

FIG. 1–10. *Limonia* (*Dicranomyia*) *hardyana*, details of structure. **1**, dorsum of thorax, showing relative proportions of pronotum and mesonotum and absence of transverse mesonotal suture (cf. Fig. 11) [pn = pronotum (anterior part), sc = scutum]. **2**, left front leg (tarsus omitted), ♂ holotype, showing banding pattern. **3**, tarsomeres 4 and 5 and pretarsus, hind leg. **4**, right wing, dorsal aspect. **5**, terminal abdominal segments, ♂ paratype, dorsal aspect (most of left side omitted) (9t = 9th tergum). **6**, rostrum of left ventral dististyle, dorsal aspect. **7**, left basistyle and dististyles, ♂ paratype, ventral aspect (9s = 9th sternum). **8**, aedeagus and left gonapophysis (gon), ventral aspect. **9**, terminal abdominal segments, ♂ holotype, left lateral aspect. **10**, terminal abdominal segments, ♀ allotype, left lateral aspect. Scales: a, Fig. 2 only; b, Fig. 1, 9–10; c, Fig. 3–8.

long as wide, with black setae along costal border and on fold behind costa (possibly representing radius); wing about as long as prescutum-scutum, lacking any distinct venation. Prescutum and scutum merged, with no evidence of transverse mesonotal suture (Fig. 1). Pleural suture of mesonotum widened and deepened near midlength, forming pit similar to that of prothorax. All coxae large for subgenus, especially mesothoracic coxa much enlarged, adjacent meron correspondingly reduced (Fig. 11). Setose mesal protuberance near ventral apex of each mesothoracic and metathoracic coxa. Femora approximately 1.4× body length, slightly and gradually thickening toward apex; tibiae longer than femora, basitarsi almost 2× length of other tarsomeres combined. In a ♂ having total body length (excluding antennae) of 4.6 mm, measurements of leg segments (femur, tibia, basitarsus, tarsomeres 2–5) were as follows (in mm): front leg 6.3, 8.0, 4.5, 2.2; middle leg 6.3, 8.0, 3.9, 2.1; hind leg 6.5, 8.0, 3.4, 2.2. Proportions approximately same in ♀; body length 5.1 mm; front leg (in mm) 6.6, 9.0, 5.8. 2.8. Femora conspicuously banded, yellowish brown near base grading into brown through most of length, with short yellowish apical band and longer, more proximal yellowish brown band, separated by band of dark brown (Fig. 2). Tibiae light brown, narrowly darkened near tips; tarsi light brown except 4th tarsomere abruptly darker brown than others. Pretarsal claws (Fig. 3) with large ventral tooth near midlength and 3 smaller, more basal teeth.

Abdomen of ♂. Terga 1–7 yellowish brown medially with broad, uneven lateral and posterolateral borders; sterna yellowish brown narrowly darkened with brown along lateral and posterior margins, more broadly on posterolateral corners (Fig. 9). Sclerites only sparsely hairy. Pleural membrane dark grayish brown. Tergum 8 evenly brown. Tergum 9 (Fig. 5) bilobed with broad, U-shaped median emargination exposing papillose upper surface of tergum 10 (anal segment); narrowly rounded apex of each tergal lobe bearing numerous (25–30) setae, tergum otherwise mostly bare. Ventromesal lobe of basistyle (Fig. 7) about 1.5× as long as wide, apex pointed; setae most dense along mesal surface. Dorsal dististyle (Fig. 5) evenly curved, flattened, densely sclerotized throughout, blackened in apical ½. Ventral dististyle, excluding rostrum, about 2× as long as its greatest width; rostrum elongate, somewhat darkened along margins, with single, long, subterminal spine borne on basal tubercle. Aedeagus downcurved in apical ½, distinctly bilobed at apex. Gonapophyses (parameres) darkly sclerotized with narrowed tips turned upward and inward (Fig. 8). Tenth (anal) segment broad, with 2 darkened but lightly sclerotized bands diverging from notch in tergum 9 (Fig. 5); dorsum covered with tiny papillae aligned diagonally.

Abdomen of ♀. Generally darker brown than in ♂, with less contrast on terga between median pale areas and darker lateral and posterolateral borders. Terga 8 and 9 light brown, paler than either 7 or 10. Tergum 10 grayish brown with pitchy-black transverse band near midlength of posterior ½; long, pale setae arising from this band. Cerci (Fig. 10) amber-brown except densely sclerotized and blackened near bases, short, strongly upcurved, with sharp apices. Hypovalves similarly amber-brown generally but blackened basally; apices acute. Cerci somewhat separated at base, tips slightly divergent. Sternum 9 shriveled (specimen dried), largely concealed.

Body length, exclusive of antennae: ♂ holotype 3.6 mm, ♀ allotype 5.1 mm; ♂ paratypes 4.3 to 5.1 mm.

Types. Holotype ♂, HAWAII: Oahu I: Koolau Mts, Konahuanui (mountain peak), 3100 ft [954 m], 9.X.1983 (W.D. Perreira) (BPBM 13,098). Allotype ♀, Oahu I: Koolau Summit, above Kahuku, 2500 ft [769 m], 8.X.1978, "on leaf litter on windy ridge top" (S.L. Montgomery) (BPBM). Paratypes: HAWAII: Oahu I: 1♂, same data as holotype; 3♂, same data as allotype; 1♂,1♀, Honolulu, Bowman Trail, IX.1973 (W.C. Gagné); 1♂, Koolau Mts, summit, Kahuku, 2500 ft [769 m], 0.5 mi [0.8 km] SE of Puu Kainapuaa (mountain), "on ground litter on

windy ridge top" [no date] (Montgomery); 3♂, Konahuanui, 3100 ft [954 m], 27.VIII.1983 (W.D. Perreira); 1♂, same but 28.V.1983; 1♂, same but 13.I.1983, 2♂, Koolau Mts, summit, Laie Trail, 2200 ft [677 m], 10.II.1982, "on leaf litter in thicket" (Gagné & Montgomery). Holotype, allotype, and most paratypes deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii.[3] Two paratypes in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Habitat

Most individuals of *L. hardyana* were found along the summit of the Ko'olau Range, both at its northern end, overlooking Kahuku and Lā'ie, and near its southern end, only a few miles NE of Honolulu. This range is a basaltic ridge with steep slopes and precipitous cliffs along its northeastern side and somewhat less abrupt slopes to the SW. The descent from the type-locality, Kōnāhuanui, to Manoa Falls at the head of Manoa Valley in Honolulu, for example, is nearly 2000 feet [615 m] in 1 mile [1.6 km]. While the lower slopes are largely forested with a great diversity of native and introduced trees, the crests and upper, steeper, and less stable slopes support only small native trees, shrubs, herbaceous plants, ferns and bryophytes. Prevailing winds from the E and NE average only 14 to 16 km/h but are stronger at crests of ridges and through gaps in the mountains (for example, about 40 km/h at Nu'uanu Pali, between Honolulu and Kāne'ohe). Rainfall along the Ko'olau Range varies from about 375 to 750 cm/yr, and dense clouds form over the upper slopes almost daily.

As indicated by label data under *Types,* above, S.L. Montgomery found the flies chiefly in leaf litter on the ground in the "elfin forest" along the Ko'olau summit. W.D. Perreira, in contrast, found them on the undersides of moss-matted adventitious roots of *Cheirodendron* trees 10–25 cm above ground level. He summarized the weather conditions at various times of collection as "very wet, windy, cloudy and cool," but added that at times there was only a light breeze and that occasionally the wind-exposed ridges became quite dry.

Relationships

Among the Hawaiian species of *Limonia, L.* (*D.*) *hardyana* most closely resembles *L.* (*D.*) *grimshawi* (Alexander) in the structure of the dististyles of the male (particularly the elongate rostrum of the ventral dististyle), the ventromesal lobes of the basistyles, and the shape of the 9th abdominal tergum, but the 2 species differ in nearly every structural detail of genitalia (cf. Hardy 1960: 50–51, Fig. 6a, b). The contrasting colors of *hardyana* also somewhat resemble those of *grimshawi,* although the pattern differs in detail. Greatly reduced wings occur also in *L.* (*D.*) *sabroskyana* Byers, from the mountains of Kaua'i; however, that species and *L.* (*D.*) *hardyana* appear, on the

3. At the suggestion of D.E. Hardy and S.L. Montgomery, the holotype (BPBM 13,097), allotype, and 1♂ paratype of *Limonia* (*D.*) *sabroskyana* Byers, 1982, have been transferred to the Bishop Museum from the University of Hawaii.

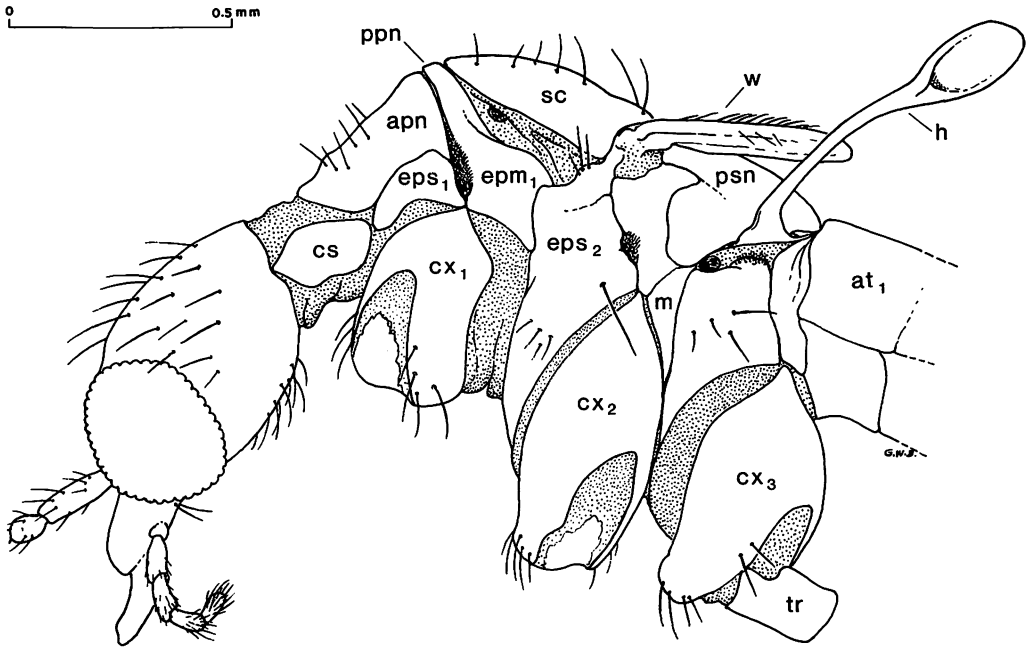

FIG. 11. Thorax and head of *Limonia* (*Dicranomyia*) *hardyana* (most of legs omitted). apn = antepronotum, at = abdominal tergum, cs = cervical sclerite, cx = coxa, epm = epimeron, eps = episternum, h = haltere, m = fused meron and katepimeron of mesothorax, ppn = postpronotum, psn = postnotum of mesothorax, sc = scutum and prescutum, tr = trochanter, w = wing.

basis of male genital characteristics, not to have any particularly close relationship within the subgenus. Rather, *sabroskyana* is most like *L. kauaiensis* (Grimshaw), which is endemic to Kaua'i, while *hardyana* most nearly resembles *grimshawi,* which is found on most of the major islands of Hawai'i. The single long rostral spine of the ventral dististyle is rare in the genus *Limonia* and unknown in any other Hawaiian species, 2 spines being the usual number, particularly in subgenus *Dicranomyia.* In the Pacific area, *L.* (*D.*) *guamicola* Alexander from Guam also has a single elongate rostral spine on each ventral dististyle.

Modifications of the thorax

Correlated with the flightless condition of *L.* (*D.*) *hardyana* (and *L. sabroskyana* from Kaua'i) are several interesting structural modifications of the thorax. Extensive development of the pronotum is not unusual in *Limonia*; however, the pronotum is usually much shorter than the combined prescutum and scutum. In these flightless Hawaiian dicranomyias, the mesonotal prescutum and scutum are greatly reduced. Moreover, the transverse suture (characteristically V-shaped in Tipulidae) is altogether absent in these flies. This suture, separating prescutum from scutum according to Alexander (e.g., 1966: 199) but subdividing the scutum in the view of most mor-

phologists, influences the buckling of the scutum on the down-stroke of the wings. Accordingly, it would serve no particular function in a flightless crane fly.

A second conspicuous modification concerns the meron (m, Fig. 11). Derived from the mesothoracic coxa, the meron in many Tipulidae is a large mesopleural sclerite between the middle and hind coxae. Originally serving as the insertion of coxal muscles, it typically becomes the origin of vertical indirect flight muscles in flies. Since it cannot have this function in *L. hardyana,* it is reduced and indistinguishably fused with the katepimeron, which itself is small.

All the coxae are greatly enlarged compared to those of a fully winged *Dicranomyia* species of similar overall size. This seems to be characteristic of pedestrian flies (cf. *Chionea*; Byers 1983: 69, 85, Fig. 6, 34) to accommodate enlarged muscles within the coxa for movement of the trochanter, which is immovably joined to the femur. Muscles within the coxae thus are those primarily involved in raising and lowering the body and supporting the weight of the insect. I have not dissected the thorax of *L. hardyana* to determine whether some of the muscles of the trochanter pass through the coxa and have broader surfaces of origin elsewhere within the thorax, as is the case in *Chionea.*

Length of the legs in flightless crane flies has probably undergone selection as a result of various environmental factors as yet unstudied. One such factor might be the nature of vegetation or other substrate over or through which the insect must move. At any rate, the legs of the tropical, flightless *L. hardyana* and *L. sabroskyana* are strikingly longer than those of extremely brachypterous species of comparable body size and of the same subgenus but from colder environments, for example, *L. (D.) lindrothi* Tjeder from Nome, Alaska (Tjeder 1963: 230). For comparison, in *L. lindrothi* the femur of the fore leg is about equal to overall body length of the fly (ratio 1.0:1.0), and the tibia is shorter, only 0.82 of body length. In *L. hardyana,* in contrast, the fore femur is 1.36× body length, and the tibia 1.71× body length. One is tempted to invoke Allen's rule, which, however, makes more sense for warm-blooded vertebrates than for crane flies.

The significance of a narrowed scutum is not clear. In fully winged crane flies, the thorax, in dorsal aspect, is ordinarily widest across the posterior scutum, at the level of wing attachment. In *L. hardyana,* in contrast, this part of the scutum is greatly narrowed (sc, Fig. 1), and the wing bases have shifted to a nearly dorsal position, with the laterotergites of the mesonotal postnotum projecting from beneath the costal wing margins.

Acknowledgments. This species is named for my friend and colleague Dr D. Elmo Hardy of the University of Hawaii. Dr Hardy is widely known for his numerous contributions to our knowledge of Diptera of the Pacific Region (including the Diptera volumes of "Insects of Hawaii") and for his many publications on Bibionidae, Pipunculidae, Tephritidae, etc., of all parts of the world. I am particularly indebted to him for providing me working space in his laboratory, for showing me good crane-fly habitats on O'ahu, and for numerous other favors during my stay in Hawai'i in 1963. I also acknowledge with many thanks the cooperation of William D. Perreira, Steven L. Montgomery, and Wayne C. Gagné, who collected the

specimens of *L. hardyana*. My studies of Tipulidae have been generously supported by the National Science Foundation, currently by grant no. DEB-8200862 (which grant, however, has nothing to do with Hawaiian crane flies); this help is much appreciated. Comments of an anonymous reviewer were particularly helpful.

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