Dictyophorodelphax zwaluwenburgi vicar, New Subspecies (Homoptera: Delphacidae): Proposed Example of Allopatric Speciation on the Island of Kauai¹

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The Hawaiian Archipelago has become a laboratory for studies of speciation (Kaneshiro 1983, Carson & Templeton 1984, Otte 1989). The most simplistic and accepted model of species formation in Hawaii is interisland altopatry. In this scenario, an island is colonized by founders from a species on a neighbor island and then, due to genetic, ecological or behavioral factors, the founders achieve distinction (Zimmerman 1948a, Yoon et al. 1975, Carson 1987).

Allopatry and isolation may also occur within islands or at least what are currently contiguous islands. Sister taxa of insects have been identified from the Waianae and Koolau ranges on Oahu (Sarona, Asquith 1995a; Nesiomiris, Gagné 1995; Tetragnatha, Gillespie & Croom 1995), East and West Maui (Plagithmysus, Gressitt 1978), and the different volcanoes on Hawaii (Plagithmysus, Gressitt 1978; Neseis, Usinger 1942). In numerous other groups of insects for which phylogenetic relationships have not been hypothesized, there are species recognized as endemic to the various volcanoes on Oahu, Maui, and Hawaii (Howarth 1990).

Kauai, Lanai, and Molokai on the other hand are usually considered single biogeographic units by entomologists, without internal areas of endemism (Howarth 1990). However, many genera of insects have several species occurring on these islands, which suggests either multiple colonizations from other islands as in *Drosophila* (Carson 1980) or the presence of historic or currently unrecognized geographic areas that precipitate divergence, as has been suggested for crickets (Otte 1989). Understanding the patterns of intraisland endemism is therefore tantamount to deciphering the evolutionary history of the fauna and a requisite to designing conservation strategies for many of Hawaii's highly provincial arthropod groups (Howarth 1990). In this paper, I describe a new subspecies of Delphacidae restricted to the Haupu mountain range on Kauai and discuss areas of endemism on Kauai.

Dictyophorodelphax zwaluwenburgi vicar Asquith, new subspecies Figs. 1-3

Diagnosis: Distinguished from D. z. zwaluwenburgi Beardsley by the less concave ventral surface and greater height (maximum with id sagittal plane) of the cephalic horn in males (Figs. 1-2), and the longer cephalic horn in females (Fig. 1). Dictyophorodelphax z. vicar also has the baso-ventral lobe of the male aedeagus rounded rather than angular, and devoid of denticles (Fig. 3).

Description: Very similar to D. z. zwaluvenburgi, differing primarily in the length and shape of the cephalic horn and the ornamentation of the male aedeagus. MALE: Length 4.57-4.89 mm. Cephalic horn with ventral margin weakly sinuous to weakly concave on distal third (Fig. 2); dorsal margin weakly concave on proximal third; vertical height of horn shortest at midpoint. Tegmina reaching apex of fifth visible abdominal segment; metathoracic wings completely absent. General coloration variable from yellow to brown, typically with dark areas of fuscous mottling. Head yellow to brown with cephalic born darkest along mid-ventrolateral surface; carinae pale yellow basal-

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ty with apices of ridges dark fuscous. Antenna yellow to brown; first segment with longitudinal black stripes on anterior surface. Metapleura always dark fuscous, often outlined in white, remaining pleurae yellowish brown to fuscous. Sternum yellowish white. Legs yellow, with longitudinal black stripes on tibiae and femora; coxae often translucent white; tarsi variably infuscated. Median carinae of nota always pale. Tegmina highly variable from translucent pale yellow to strongly infuscated, imparting an opaque, smoky appearance; an elongate, dark fuscous mark present along distal claval margin and another smaller mark at apex of costal vein; small fuscous marks present at apices of all costal cells; proximal half of posterior costal vein always paler than remainder; bases of all setae along veins fuscous. Abdomen yellow to brown, posterolateral area of each segment fuscous. FEMALE: Length 5.57-6.0 mm. Cephalic horn with ventral margin straight to weakly and evenly concave; dorsal margin weakly sinuous. Remainder of appearance as in male except for an orange to red coloration of abdominal dorsum.

Type material. Holotype M, KAUAI: Haupu saddle road, 250 m, 13.111.93, ex. Chamaesyce sp., (A. Asquith), (BPBM 15532); 5M, 4F paratypes, same data as holotype (BPBM).

Other specimens examined, KAUAI: 4F, Hoary Head Mts, 24.VII.1970, Euphorbia (W.C. Gagné) (BPBM).

Distribution: Known only from the Haupu mountain range of southeast Kauai.

Kaua'i Subspecies of Dictyophorodelphax zwaluwenbergi

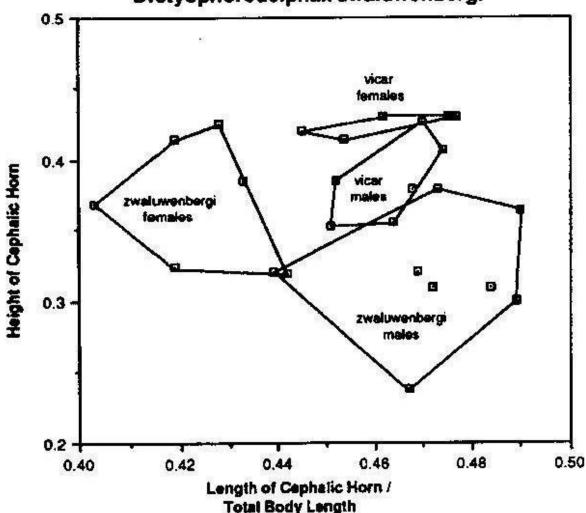


Fig. 1. Relationships between the height of the cephalic horn and cephalic horn/total body length ratio in sexes and subspecies of *Dictyophorodelphax zwalswenburgi*.

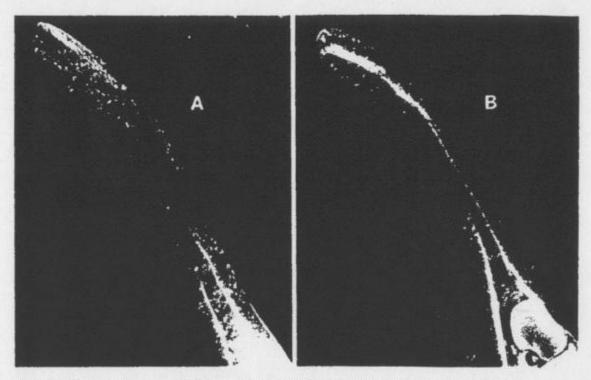


Fig. 2. Male cephalic homs of Dictyophorodelphax. a, D. zwaluwenburgi vicar. b, D. z. zwaluwenburgi.



Fig. 3. Male aedeagi of Dictyophorodelphax. a, D. zwaluwenburgi vicar. b, D. z. zwaluwenburgi.

Discussion

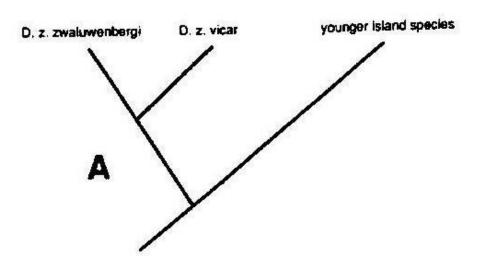
In addition to Dictyophorodelphax zwaluwenburgi, 4 other species of Dictyophorodelphax have been described: mirabilis Swezey and swezeyi Bridwell from Oahu, praedicta Bridwell from Maui, and usingeri Swezey from Lanai. All species differ significantly in length and shape of the cephalic horn (Zimmerman 1948b, Beardsley 1956) and in the structure of the male aedeagus (Bridwell 1918, 1919) (males of usingeri have not been examined). All species are restricted to Chamaesyce as a host and are found in similar habitats, thus there has been little ecological shift coincident with species formation.

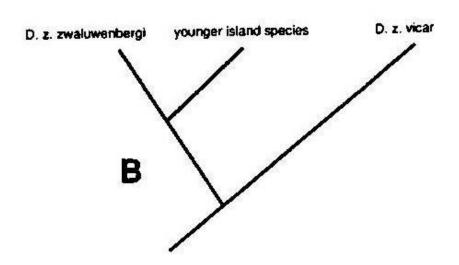
My interpretation of the Haupu populations as a subspecies rather than a full species is based on 1) the smaller degree of difference in the cephalic horn and aedeagus between the Alakai and Haupu populations when compared to differences among other species, 2) the distribution pattern fits the classical concept of a subspecies as a distinct geographic race (Mayr 1969), and 3) the proposed phylogenetic affinity between the Alakai and Haupu populations (Fig. 4A).

The hypothesis of the sister group relationship between the 2 subspecies (Fig. 4A), while likely, cannot be substantiated without a phylogenetic analysis of the genus. For example, the aedeagi of the 2 taxa are extremely similar, sharing the characters of 1) consistent width throughout the length, 2) strongly recurved shape, and 3) a single, contiguous patch of spines on the dorsal surface only. However, if the Kauai taxa are the most primitive (as in many Hawaiian groups), then these characters are probably plesiomorphic and cannot be used to argue for sister group status. It is possible therefore, that the founders of the species on Oahu and the younger islands (if that were the direction of colonization) originated from one of the 2 Kauai populations after they diverged from each other (Fig. 4B-C). Such a pattern could arise if the relative magnitude of the founder event (and genetic restructuring) involved in cladogenesis is more important in producing morphological apomorphies than just the sequence of cladogenesis. Thus, the lack of morphological synapomorphies may not preclude a sister-group relationship if apomorphies do not always arise at cladogenesis. Given the complex ecological, behavioral and geographic factors involved in the speciation of Hawaiian insects, this pattern should be considered in the phylogenetic studies of other taxa.

Dictyophorodelphax z. zwaluwenburgi is found in dry, open areas from 150-1100 m elevation and has been collected only on Chanaesyce celastroides (Boiss.) Croizat & Degener. It has been collected from the western ridges of Kokee such as Haeleele and Milolii, the east, north and west rims of Waimea Canyon, Kalalau Valley, and the Napali Coast Trail between Hanakapiai and Hanakoa Valleys. It probably also occurs in suitable areas on southern ridges such as those between Olokele and Hanapepe valleys. The type series of D. z. vicar was taken in a similar habitat consisting of a steep, dry, sunny slope at ca 250 m. Dictyophorodelphax was not found among the extensive growth of Chanaesyce celastroides along the summit of Nounou Ridge on eastern Kauai, also at 250 m.

No individual of any Dictyophorodelphax species I examined displays any development of the metathoracic flight wings. Even if some winged individuals are occasionally produced they must be rare, giving these insects very poor dispersal abilities. This trait means that the rare colonization of an isolated area or the vicariance of a once contiguous area would largely restrict gene flow of the separated populations, even if the distance is not great. Therefore, while the dry slopes of the Haupu Range are only 10–20 km from





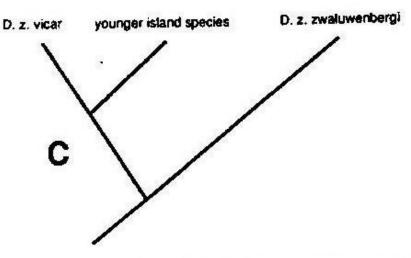


Fig. 4. Proposed (A) and alternative (B-C) relationships between Dictyophorodelphax z. zwalawenburgi, D. z. vicar, and species on younger Hawaiian islands.

similar habitats on the southern ridges of the Alakai massif, this distance could strongly limit the exchange of individuals between the two areas.

Separation Model

The main volcano of Kauai was active for roughly 2 million years from 5.5-3.5 million years ago (ma). The Haupu Range (up to 700 m) was formed as a side vent of the original volcano and therefore roughly the same age as the slopes of the Alakai massif (Stearns 1985). The present geography of eastern Kauai is probably not indicative of past habitat separations. For example, after the cessation of the main volcano, erosion created deep valleys on the east side of Kauai, including such areas as Weoweopilau or Knudsen's Gap, which separates the Haupu Range from Mt Kahili and the Wahiawa Range of the Alakai massif. From 1.4-0.6 ma, these eroded areas were repeatedly covered with lavas from the Koloa volcanic series. In addition, rainfall was greater during glacial periods in the last 0.5 million years causing dry and mesic adapted plants to become more restricted (Gavenda 1992), which probably also decreased the availability of dry ridge habitats for Dictyophorodelphax. Thus, once the soft lavas of the Na Pali formation began to erode and separate Haupu from the Alakai massif 2-3 ma, the intervening area was probably a significant barrier for nonvagile taxa such as Dictyophorodelphax. However, the present distribution of such allopatric taxa could have resulted from either true biological vicariance of a once contiguous population or by the colonization of one area by founders after the geographic vicariance of the areas.

Comparison with other taxa

Dictyophorodelphax z. vicar represents one of the few formally recognized arthropod taxa restricted to the Haupu Range, but several undescribed species of crickets and Rhyncogonus weevils may also be Haupu endemics (R. Rice, pers. comm.). Otte (1994) clearly documented Haupu as an area of endemism for crickets, with 4 species of Prognathogryllus and 2 species of Trigonidium found only in this mountain range. Haupu is also clearly an area of endemism for the nonvagile land mollusks. Carelia tenebrosa Cooke is known only from the Haupu Range, and Cooke (1931) hypothesized that C. tenebrosa is most closely related to C. olivacea, a species found predominantly in the Makaleha Mountains. Orobophana baldwini Ancey. Tornatellides productus Ancey. Hiona kipui Baker, and Godwinia haupuensis Cooke all appear to be Haupu endemics, with the caveat that the distribution of land mollusks on Kauai is even more poorly understood than that of arthropods (Cowie et al. 1995). Plants on the other hand, with their greater dispersal abilities, do not appear to have responded as strongly to the Haupu-Alakai vicariance, with only one taxon, Lipochaeta micrantha (Nutt.) A. Gray var. exigua (Degener & Sherff) Gardner restricted to the Haupu Range. Clearly, an intensive arthropod survey of the Haupu mountains, particularly of nonvolant groups in mesic forest habitats, should reveal additional endemics reflecting the Haupu-Alakai vicariance.

Additional areas of endemism on Kausi

Attempting to identify within-island areas of endemism for insects is difficult because of our limited knowledge of their distributions. While this is partly due to habi-

tat loss and extinctions, more importantly is a lack of adequate sampling for most groups. For example, the majority of the Kauai insect fauna was described in the Fauna Hawaitensis series (Sharp 1899-1913) and came from only a handful of localities, including: Makaweli (2000 ft), Halemanu, on Waialeale (3000 ft), mountains behind Waimea, and Kaholuamano (4000 ft). Virtually all these localities are at middle to high elevations on the western slopes of the Alakai massif. Later collectors, including O.H. Swezey, R.L. Usinger, and E.C. Zimmerman, also restricted their collecting to the western Alakai massif between 600-1200 m.

Some of the locality labels of Reverend Thomas Blackburn refer to "in mountains behind Lihue (3000 ft)," and apparently Otto Swezey did make some collections from Olokele Canyon in 1920. However, it has only been in the last 40 years that insects have been collected from a diversity of areas on Kauai. Several Collembola, for example, have been described from lowland areas on Kauai (e.g., Aethiopella kuolo Christiansen & Bellinger from the Hanalei River Valley) but these and many other insects have been so poorly collected that it impossible to generalize their distributions.

However, despite these limitations I have attempted to identify the distribution patterns of Kauai insects based on a review of the literature, specimens in the collections of the Bishop Museum and University of Hawaii, and extensive field collecting for 3 years. I have also compared plant (Wagner et al. 1990; D. Lorence & T. Flynn, pers. comm.) and land mollusk (Cowie et al. 1995 and references therein) distributions to search for congruent patterns.

It appears that the distributions of most insects on Kauai are defined by host plant or habitat rather than geography per se, and many are, or were, widespread. In fact, the perception of precinctiveness in many Hawaiian insects (Howarth 1990, Howarth & Ramsay 1991) is probably derived from our limited knowledge rather than their limited ranges. Idiomyia crucigera (Grimshaw) and Drosophila villosipedis Hardy, for example, can be found breeding in the rotting bark of both native and introduced plants from Kokee to Alexander Dam, Kilohana Crater, Nounou Ridge, and Hanakapiai Valley at sea level (Carson et al. 1970, Montgomery 1975, A. Asquith, unpubl. data). Scaptomyta (Bunostoma) anomala Hardy occurs in wet forest at 1200 m to the dry windrows of macadamia nut orchards at 160 m (Asquith 1995b). Several species of Oliarus leafhoppers were described from "Lihue, lower forest zone, 800 feet elevation," but have also been collected in Kokee (Giffard 1925).

Elevation, rather than horizontal geography seems to have more strongly structured insect distributions. Certain aquatic stream or riparian insects are restricted to the low to mid elevation reaches of streams (Asquith & Messing 1993) and several species of Odynerus wasps (Perkins 1913), Omiodes (formerly Hedylepta) moths (Zimmerman 1958), and Nysius seed bugs (Usinger 1942) are or were exclusively lowland inhabitants. At least I species of native Psocoptera (Ptycta aaroni Thomton) is exclusively a lowland inhabitant on Oahu and Maui; and Kauai probably had an equivalent species (Thornton 1984). Other species of Ptycta exhibit elevational zonation on Kauai (Thomton 1984). Entire plant communities restricted to low elevation are detailed in Wagner et al. (1990), and 2 of the larger Kauai land snail genera Carelia and Orobophana were exclusively or predominantly lowland taxa (Cowic et al. 1995).

Likewise, many insects are restricted to wet forest habitats at middle to higher elevations. This is true for both phytophagous species dependent on certain host plants, and scavengers or predators that have particular substrate, humidity or temperature requirements. However, many phytophagous species may have more restricted distributions than their host plants [most *Metrosideros polymorpha* specialists for example (Gagné 1979)) or alternatively may feed on several related species so their distribution is greater than any one of their individual hosts (many of the orsilline Lygaeidae (Usinger 1942)].

Therefore, only a small portion of the Kauai insect fauna displays well delimited endemism, and many areas of endemism are as much ecologically as geographically defined. For example, the northeast Kauai-southern Kauai parapatry is a common pattern in plants, often with the sister taxa sympatric in the Wahiawa Mountains but occurring at different elevations (Wagner et al. 1990). In these cases, the different areas probably represent ecological conditions to which the endemic plant taxa have adapted (higher vs. lower rainfall), but there are no examples of this pattern in insects. In contrast, Dictyophorodelphax in Haupu and Nesiomiris plants bugs in the Makaleha Mountains are groups in which the ecology of the sister taxa are identical, and they likely diverged through geographic segregation only. However, with perhaps one exception, plants do not display this pattern. This suggests that the origins of many species in plants and insects on Kauai have been fundamentally different.

Waislesle Summit

This is a unique Metrosideros/Dubautia/Oreobolus bog at the summit region of Mt Waialeale (Gagné & Cuddihy 1990).

Plants: Lysimachia venosa (Wawra) St. John, Dubautia waialealae Rock, Cheiro-dendron dominii Kraj., and Dubautia imbricata St. John & G. Carr subsp. acronaea G. Carr.

I can find no example of any insect restricted to the summit of Waialeale because this area has unfortunately not received any insect collection efforts. However, several species are known only from the open boggy areas of the Alakai Swamp including *Drosophila apodasta* Hardy, *D. capitata* Hardy, *D. fuscoapex* Hardy, *Mestolobes quadrifascia* (Swezey), *Nysius hardyi* Ashlock, and *Limonia sabroskyana* Byers.

Wahiawa and Alakai Swamps

This area represents the split distribution of several species that are found only in the bogs and surrounding wet forests of both Wahiawa and Alakai swamps.

Plants: Myrsine helleri (Degener & I. Degener) St. John, Lysimachia daphnoides (A. Gray) Hillehr., Melicope feddei (H. Lév.) T. Hartley & B. Stone, Melicope waialealae (Wawra) T. Hartley & B. Stone, Lobelia kauaensis (A. Gray) A. Heller.

The only documented insect that displays this pattern is the damselfly Megalagrion paludicola Maciolek & Howarth. This species breeds in small pools of water in the swampy ohia forest around the Wahiawa and Alakai swamps (Maciolek & Howarth 1979).

West-Southwest mesic forest

This is an area of mesic forest extending roughly from the southern rim of Kalalau Valley to Haeleele Ridge.

Plants: Psychotria hobdyi Sohmer, Hibiscus kokio Hillebr. & Wawta subsp. saintjohnianus (M. Roe) D. Bates, Hibiscus waimeae A. Keller subsp. waimeae. Kokia

kauaiensis (Rock) Degener & Duvel, Canavalia kauaiensis I. Sauer, Schiedea membranacea St. John, Delissea rhytidosperma H. Mann, Labordia helleri Sherff, Nothocestrum peliatum Skotish.

This region has been extensively collected entomologically in the last several decades and numerous new species have been described from this area. Both the delphacid leafhopper Nesothoe magnacarnis Beardsley (Beardsley 1960) and the plant bug Sarona laka Asquith (Asquith 1994) breed only on Claoxylon sandwicense Muell.-Arg. Both of these species have been collected only from the western mesic forest, although I have searched on Claoxylon extensively in other areas. The psyllid Hemischizocranium aloha (Caldwell) develops only on Zanthoxylum dipetalum H. Mann and has also been collected only from western ridges (Uchida & Beardsley 1992). Many other species have been described from collections along Awaawapuhi or Nualolo trails which also probably represent this distribution, such as Prognathogryllus hypomacron Otte (Otte 1994).

Na Pali Coast

An area consisting of coastal cliffs and valley floors from Hanakapiai to the Mana Plain.

Plants: Panicum lineale St. John, Pritchardia napaliensis St. John, Pittosporum napaliense Sherff, Hedyotis st-johnii B. Stone & Lane, Charpentiera densiflora Sohmer, Canavalia napaliensis St. John, Schiedea apokremnos St. John.

One species of dolichopodid fly (Sigmatineurum napali Evenhuis) is restricted to water drainages in this area (Evenhuis & Polhemus 1994). Additional research may show other Dolichopodidae that are restricted to the Na Pali valleys or even display individual valley endemism as apparently do some varieties of snails such as Hiona exaequata (Gould) (Cowie et al. 1995).

East-Northeast Kauai

This is the area extending from the Wahiawa Mountains to Wainiha Valley. The northwestern limit of this area is variable, as a few taxa are also found in the mesic valleys further west including Limahuli, Hanakapiai and Waiahuakua. Many of the species restricted to this area are apparently extinct or known only from the original collections. Thus, it is difficult to assess the original extent of the distribution of many of the representative taxa or if some actually had more restricted distributions.

Plants: Pisonia wagneriana Fosh., Pritchardia hardyi Rock, Pritchardia viscosa Rock, Pritchardia waialealeana Read, Psychotria wawrae Sohmer, Myrsine fernseei (Mez) Hosaka, Cyrtandra limahuliensis St. John, Cyrtandra pickeringii A. Gray, Cyanea asarifolia St. John, Cyanea fissa (H. Mann) Hillebr. subsp. fissa, Cyanea recta (Wawta) Hillebr., Cheirodendron forbesii (Sherff) Lowry, Bidens forbesii Sherff subsp. forbseil (excluding the Wahiawa drainage). Wikstroemia hanalei Wawra and Hibiscus clayi Degener & I. Degener, Labordia lydgatei C. Forbes, Hesperomannia lydgatei C. Forbes, Cyanea linearifolia Rock.

Crickets probably provide the best example of this pattern among insects, with 3 species of Prognathogryllus, 7 species of Trigonidium, and at least 1 species of Laupala displaying this distribution (Otte 1994). Megatrioza kauaiensis Uchida & Beardsley is known only from Pritchardia hardyi along the Powerline trail (Uchida & Beardsley 1988). In what is probably the best example available of geographic endemism on Kauai, Gagné (1995) identified 2 species of *Nesiomiris* plant bugs endemic to the Makaleha Mountains, each with its respective sister taxon in the main Alakai massif. *Eurynogaster mediocris* Tenorio was also described and is known only from Waipahee, a stream draining the Makaleha range (Tenorio 1969). As discussed earlier, this Makaleha endemism for insects undoubtedly represents a different process than that giving rise to the general Northeast Kauai pattern in plants, even though some of the plant species are also found in the Makaleha Mountains.

The snail genus *Georissa* Blanchard is also known only from collections along the Powerline trail (Cowie et al. 1995). Many other snail species are known only from eastern or northeastern Kauai (e.g. *Endodonta laminata* (Pease) occurs from Kalihiwai to Haena), but in general they have very restricted distributions and do not display the same pattern of endemism as do the plants and insects.

South Kausi

This area extends from the Wahiawa mountains to Waimea Canyon, often including the Haupu range. It is the most poorly documented area of endemism on Kauai, largely because the land from the Wahiawa Mountains to Kapukapaia Ridge is inaccessible private property.

Plants: Myrsine mezii Hosaka, Cyanea fissa (H. Mann) Hillebr. subsp. gayana (Rock) Lammers, Lipochaeta micrantha (Nutt.) A. Gray var. micrantha, Schiedea sper-

gulina A. Gray var. spergulina.

Some insects described from early collections at Kaholuamano and Makaweli might represent species restricted to the southern ridges or valleys, but this will remain obscure until better collections are available. Even *Dictyophorodelphax z. zwaluwenburgi* has not been collected south or east of Waimea Canyon, and it is not known whether there is an endemic insect fauna of the southern slopes of Alakai massif that also occurs in the Haupu Range, as is the pattern for several plants.

Wahiawa Mountains

The area of the Wahiawa Mountains includes both the bog and the surrounding ridges. It is an area of exceedingly high floristic endemism with at least 12 species and several newly discovered undescribed taxa (Lorence & Flynn 1991).

Plants: Melicope paniculata (St. John) T. Hartley & B. Stone, Melicope quadrangularis (St. John) T. Hartley & B. Stone, Dubautia pauciflorula St. John & G. Carr, Dubautia imbricata St. John & G. Carr subsp. imbricata, Cyrtandra olona C. Forbes, Labordia tinifolia var. wahiawaensis St. John, Cyanea undulata C. Forbes, Cyanea spathulata (Hillebr.) A. Heller subsp. longipetiolata Lammers, Chamaesyce sparsiflora (A. Heller) Koutnik, Bidens forbesii Sherff subsp. kahiliensis Ganders & Nagata, Viola helenae C. Forbes & Lydgate, Viola kauaensis A. Gray var. wahiawaensis C. Forbes.

Hiona wahiawae Baker is the only mollusk recognized as endemic to this region (Cowie et al. 1995).

This area was apparently not accessed by early entomological collectors and even in recent years has received little attention. Here again crickets represent the best example of Wahiawa endemism, with 3 species of *Prognathogryllus*, Laupala kanaele Otte and Laupala pseudonoe Otte all restricted to this area (Otte 1994). The few other species that have been described from this area are also found elsewhere on Kauai. For example, Drosophila ornata Hardy & Kaneshiro was described from Wahiawa Bog but is now also

known from Pouli Stream in Hanalci, the Hono O Na Pali NARS area at 1050 m and the Kokee region. Given the botanic and physiographic uniqueness of this area (the only lowland bog in Hawaii), it would be surprising if the Wahiawa drainage does not harbor additional endemic arthropods.

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