

Systematics and evolution of *Iolania* (Hemiptera: Fulgoromorpha: Cixiidae) from Hawai'i

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Abstract. Within the planthopper taxon Cixiidae, which is distributed worldwide, only two lineages have colonized the Hawaiian Islands: *Iolania* Kirkaldy, 1902, and *Oliarus* Stål, 1862, and subsequently given rise to endemic species. Neither radiation has been studied in depth hitherto. Here the degree of speciation within *Iolania* is assessed and a taxonomic revision including a key to the species based on the male genitalic characters is provided. Six endemic species are recognized: *I. perkinsi* Kirkaldy, *I. koolauensis* Giffard, *I. oahuensis* Giffard, *I. lanaiensis* Giffard, *I. mauiensis* Giffard and *I. kraussohana* sp.n. A lectotype is designated for the type-species *I. perkinsi* Kirkaldy, and *I. perkinsi notata* Kirkaldy is interpreted as an invalid name. Morphological arguments for the monophyly of *Iolania* and phylogenetic relationships among the species are discussed. A plausible scenario for the sequence of speciation events and history of colonization within the Hawaiian Islands is attempted. Combined information from taxon- and area-cladograms suggests progressive inter-island dispersal from older to younger islands in the Hawaiian chain as the major pattern of colonization and speciation.

Introduction

With more than 200 endemic species, the Fulgoromorpha, or planthoppers, are among the dominant elements in the native Hawaiian arthropod fauna. These phytophagous insects occur in nearly all Hawaiian ecosystems, and mostly are mono- or oligophagous on native Hawaiian plants (Asche, 1997). The endemic fauna involves two of the world's eighteen planthopper families, Delphacidae and Cixiidae. Most Hawaiian species were discovered and described in the first three decades of the twentieth century (Asche, 1997) but some groups of Delphacidae have been revised recently (Asche, 1998, 2000) and Hawaiian Cixiidae have not been re-examined in the light of modern systematics since Zimmerman (1948). All species of Hawaiian Cixiidae are endemic, and belong to two major lineages: *Oliarus* and *Iolania*. Whereas *Oliarus* has apparently undergone intensive radiation following a single colonization

(Asche, 1997), and now comprises more than eighty species and subspecies on all of the main islands and in a wide variety of habitats (Giffard, 1925), including cave-dwelling species in lava tubes (Howarth, 1972; Fennah, 1973; Hoch & Howarth, 1993, 1999), *Iolania* is much less speciose: five species have been described from all major islands except Moloka'i. Nearly no information exists on their biology, ecology or evolution. My own field studies and examination of new and previously unstudied material from various collections provides the basis for an attempt to assess the degree of speciation within this group, revise the taxonomy accordingly, analyse phylogenetic relationships, and hypothesize the sequence of speciation events and colonization history within the Hawaiian Islands.

Historical background

The genus *Iolania* was proposed by Kirkaldy (1902) for a taxon from Hawai'i (Hawai'i Island, O'ahu, Lana'i), which he considered 'allied to *Cixius* Latreille, but differing principally by the structure of the vertex' (Kirkaldy, 1902: 118). Kirkaldy recognized a single species, *I. perkinsi*, which he designated as the type species. In 1909, he distinguished as a

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variety of *Iolania perkinsi* the form *notata* (Kirkaldy, 1909: 75), which was regarded later as a subspecies by Zimmerman (1948). Giffard (1925) continued Kirkaldy's studies and found 'that body characters and venation of the tegmina present no variations of specific importance' (Giffard, 1925: 100); however, upon studying the male genitalia, Giffard discovered 'that the aedeagus is practically the only means of discriminating the species in this genus' (Giffard, 1925: 99–100). He recognized five distinct species: one each from Hawai'i (*I. perkinsi*), Lana'i (*I. lanaiensis* Giffard, 1925) and Maui (*I. mauiensis* Giffard, 1925), and two from O'ahu (*I. oahuensis* Giffard, 1925, and *I. koolauensis* Giffard, 1925). Kirkaldy and Giffard considered *Iolania* a close relative to the worldwide distributed genus *Cixius*. Giffard (1925: 99) hypothesized that extant *Iolania* species 'evidently [were] derived from one ancestor ... which is now extinct'. No *Iolania* specimens from Moloka'i or Kaua'i were available to him. Later, unidentified *Iolania* specimens were reported also from Moloka'i (Swezey & Bryan, 1929), and *I. perkinsi* from Kaua'i (Krauss, 1945). Two Cixiini species were described from Australia and assigned to *Iolania*, based on the absence of lateral hind tibial spines (Muir, 1931). In the only comprehensive treatment of Hawaiian planthoppers to date, Zimmerman (1948) questioned the taxonomic status of the Hawaiian *Iolania* species, indicated the existence of unidentified material from Kaua'i and Moloka'i, and doubted any phylogenetic relationship between *Iolania* species from Hawai'i and Australia. Zimmerman (1948: 132) 'failed to find external characters from which to assemble a key' and suggested that further studies be made. In his review of current knowledge on Hawaiian planthoppers, Asche (1997) agreed with Zimmerman's suspicions that neither Australian *Iolania* species is closely related to Hawaiian *Iolania*.

Materials and methods

All specimens mentioned are deposited in Bishop Museum, Honolulu, U.S.A. (BPBM) unless stated otherwise (abbreviations generally follow Evenhuis & Samuelson, 2004): AH, private collection of M. Asche and H. Hoch, Berlin, Germany; BMNH, The Natural History Museum, London, U.K.; CUIC, Cornell University Insect Collection, Ithaca, U.S.A.; HDOA, Hawai'i State Department of Agriculture, Honolulu, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. Specimens from the Giffard collection (at BPBM) and type material of all described *Iolania* species were re-examined.

All specimens were preserved dry. Genitalia were macerated in 10% KOH (24 h) at room temperature, washed in water, transferred to glycerine for storage, and to glycerine-jelly for drawings. Drawings were made using a Leitz stereomicroscope with camera lucida. For scanning electron microscopy, male genitalia were macerated, dehydrated in increasing ethanol concentrations (70–85%) and mounted on aluminium specimen stubs with adhesive pads.

The aedeagus was coated with gold–palladium and studied on a LEO 1450VP scanning electron microscope (running 32 V02.03 software) at 10 kV.

The phylogenetic analysis was carried out in a Hennigian way by 'hand and mind'. Based on outgroup comparison, the plesiomorphic/apomorphic states of thirty morphological characters were estimated (see Appendix). Information on the morphological configuration of outgroup representatives was obtained directly from specimens of the corresponding species, and extracted from the literature.

Results

Taxonomy

The material examined contained six morphologically distinguishable units. Based on the assumption that consistent morphological discontinuities between populations may point to interrupted gene flow and reproductive isolation (Remane, 1968), I interpret these morphological units as biological species, i.e. reproductively isolated entities. Discriminating characters between these taxa were found – as already pointed out by Giffard (1925) – in the structures of the male genitalia whereas the species are not easily recognizable by external characters, which are too conservative (e.g. carination of the head) among and/or too variable within populations (e.g. coloration of the tegmina). Five of the six taxa recognized here are consistent with the species described by Giffard. The taxon on Kaua'i was unknown previously and is described as a new species.

The degree of differentiation, or even speciation, may in fact be much higher: differentiation on the genetic or behavioural level may conceal cryptic species, e.g. *I. oahuensis* is reported here from four islands (O'ahu, Moloka'i, Lana'i, Maui) and *I. lanaiensis* from two islands (Lana'i and Moloka'i). Whether or not gene flow is maintained among these allopatric populations can be decided only on the basis of population genetics.

Iolania Kirkaldy, 1902: 118

Type species. Iolania perkinsi Kirkaldy, 1902: 119.

Diagnosis. Total length (tip of head to distal margin of tegmina): males 4.8–6.3 mm, females 6.2–7.1 mm. Moderately large cixiids of robust appearance (Fig. 1); tegmina more or less shallowly tectiform, exceeding tip of abdomen with *c.* one-third of total length. Tegmina and wings translucent to hyaline. Tegmina (Figs 2, 3) with colour pattern within populations variable, ranging from hyaline with little recognizable patterns to distinct dark brown spots or stripes, especially at tegmen base and in distal third. Granules on veins usually brownish. Body coloration inconspicuous, intraspecific variation ranging from yellowish brown to darker brown. Coloration of body and tegmina usually slightly darker in females.

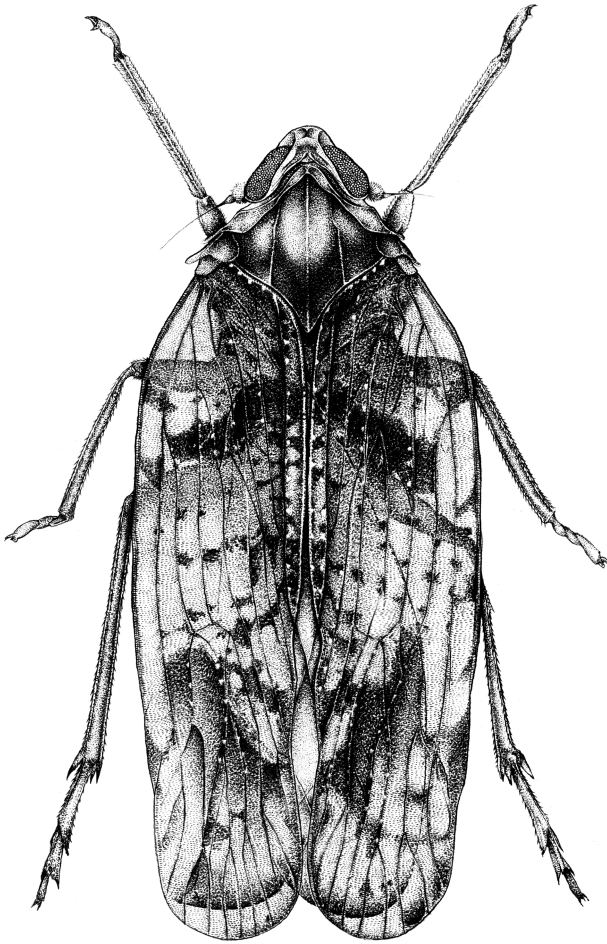


Fig. 1. *Iolania perkinsi* Kirkaldy. Habitus, female (specimen from Hawai'i Island: Hawai'i Volcanoes National Park, Ola'a forest).

Vertex short, mesonotum tricarinate, hind tibiae laterally with 3 minute spines. Easily distinguishable externally from other Hawaiian cixiid genus, *Oliarus*, by their tricarinate mesonotum (vs. pentecarinate in *Oliarus*). Distinguished from all other known Cixiini by the morphological configuration of the male copulatory organ, the aedeagus (shaft bilaterally symmetrical, smooth; flagellum rigid, short, not movable against shaft; phallotreme near base of flagellum, exposed dorsally).

Supplementary description. To complement the original description of the genus *Iolania*, characters of head, thorax and male and female genitalic structures are provided.

Head. Compound eyes large. Lateral ocelli present; median frontal ocellus absent. Width of head including compound eyes distinctly narrower than pronotum. Vertex concave, posterior margin deeply incised, lateral margins strongly ridged, gradually converging anteriorly, transverse carina forming subacute angle. Areolets (or 'fossette' *sensu* Giffard, 1925) distinctly divided medially

by short blunt carina. Frons narrow at apex, widening towards frontoclypeal suture, widest at base of antennae; apex separated from anterior margins of areolets by obtuse transverse carina. Longitudinal carinae of frons and clypeus sharply ridged. Frontoclypeal suture semicircular. Postclypeus slightly vaulted. First antennal segment short, ring-like; pedicel cylindrical, slightly longer than wide. Rostrum slightly exceeding posterior margin of hind coxae.

Thorax. Pronotum short; posteriorly deeply incised; with obtuse median and two sharply ridged lateral carinae. Mesonotum tricarinate; carinae distinctly ridged; lateral carinae slightly divergent posteriorly. Mesonotum in midlength *c.* 2× pronotum and vertex combined length; strongly vaulted. Tegmina with distal margins broadly rounded, in some specimens subtruncate (Figs 2,3); widest at level of pterostigma; pterostigma aligned with apex of clavus; veins distinctly granulate. Hind tibiae with 3 minute lateral spines and 6 apical teeth. Basitarsus elongate, about twice as long as tarsal segments II and III combined; with 6 apical teeth. Tarsomere 2 with 7 apical teeth; lateral outer apical teeth more strongly pronounced. First and second metatarsomere without supapical macrochaetae (platellae).

Male genitalia. Genitalic segment slightly taller than wide, dorsolateral margin rounded, mesoventral process simple, triangular, slightly variable among species. Parameres with medioventral margin distinctly ridged. Aedeagus with basal part (shaft) bilaterally symmetrical, without spinose processes; membranous distal part (flagellum) short, in repose bent straight dorsobasad; pair of spinose processes arising laterally at transition between shaft and flagellum; phallotreme at base of flagellum, dorsally exposed.

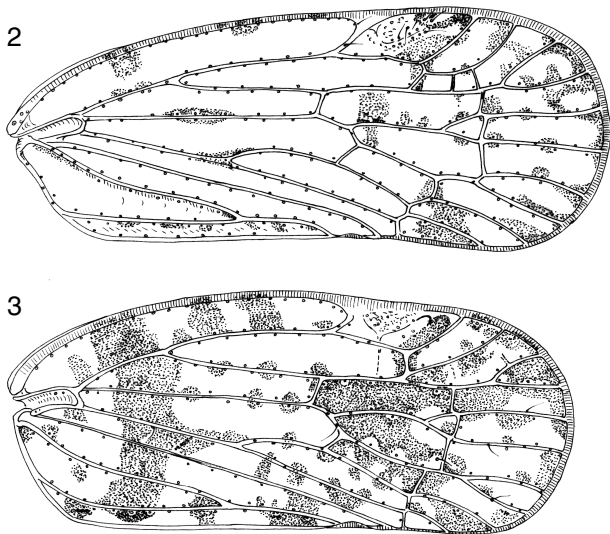
Female genitalia. Ovipositor elongate, ensiform, slightly surpassing anal segment. Tergite IX truncate, distally slightly concave; strongly rounded laterally; with wax-secreting area inconspicuous. Anal segment slender, subcylindrical, with ventrocaudal margin slightly produced. Genital chamber (vestibulum) strongly recurrent posteriorly; *ductus receptaculi* simple, without helix-twirled part (Remane & Asche, 1979), as in several other Cixiini (Holzinger *et al.*, 2002), but with bladder-like dilation distad of receptaculum seminis.

Distribution. Endemic to the Hawaiian Islands.

Remarks. *Iolania vittipennis* Muir, 1931, and *Iolania clypealis* Muir, 1931, from Australia are no longer regarded congeners (Asche, 1997; Emeljanov, 2000; see also Discussion).

***Iolania koolauensis* Giffard, 1925: 154** (Figs 4–10)

Diagnosis. Total length: males 5.6–6.1 mm, females 7.1 mm *I. koolauensis* can be distinguished from other *Iolania* species by the combination of the following male genitalic characteristics (Figs 4–10). Anal segment (Figs 6, 7)

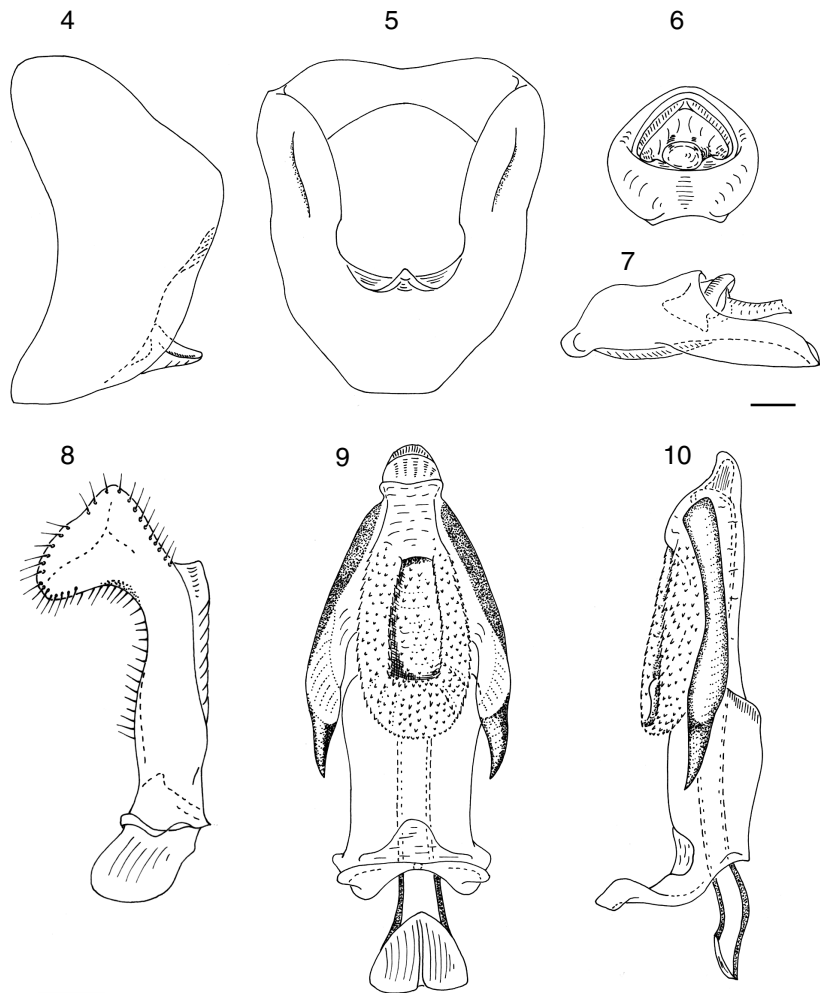


Figs 2, 3. *Iolania perkinsi* Kirkaldy, right tegmen. 2, male from Hawai'i Island: Volcano; 3, female from Hawai'i Island: Kohala. Scale bar = 0.5 mm.

in caudal view dorsally rounded, ventral margin slightly concave. Parameres (Fig. 8) proximally slender; ventrally ridged; distal portion dilated, dorsally produced; with caudal margin triangular. Aedeagus (Figs 9, 10) symmetrical, shaft base well sclerotized; in lateral aspect straight. Flagellum with distinctly sculptured surface; paired processes slender, proximally taeniform, distally terete with acute tips, in repose pointed straight basad. Dorsal surface of flagellum medially concave, with conspicuous groove distad of phallotrema. Gonoduct with conspicuous protuberance at apex of shaft; similar to *I. oahuensis* and *I. perkinsi*.

Distribution and ecology. Endemic to O'ahu: northern Koolau Mountains (type locality: Waiahole), at some localities syntopic with *I. oahuensis* (Punaluu, Poamoho). Host plants unknown. 600–830 m. Adults collected in January, June, July and October.

Material examined. Holotype ♂ (here re-examined): O'ahu, Waiahole, BPBM: type number 314; genitalia dissected by Giffard and embedded in caedax. – Additional material. 1♂, Kahuku Cabin, 2500 ft, 7.x.1978



Figs 4–10. *Iolania koolauensis* Giffard, male genitalia (O'ahu, Punaluu). 4, genital segment, left lateral aspect; 5, same, caudal aspect; 6, anal segment, caudal aspect; 7, same, left lateral aspect; 8, left paramere, left lateral aspect; 9, aedeagus, dorsal aspect; 10, same, left lateral aspect. Scale bars = 0.1 mm.

(Montgomery); 1♂, Poamoho Trail, 6.x.1965 (Beardsley); 2♂♂, 1♀, Poamoho Trail, 600 m, 13.i.1980, at light (Gagné); 1♂, Punaluu, 11.vi.1911 (Swezey), HDOA; 2♂♂, Opaepa, 19.vii.1925 (Swezey).

***Iolania kraussohana* sp.n.** (Figs 11–18)

Description

Total length. (tip of head to distal margin of tegmina): male 5.7–6.0 mm ($n = 3$).

Colour. Mostly light brown; lateral portions of pro- and mesonotum slightly darker; tegmen yellowish brown, translucent, with dark brown markings along longitudinal and crossveins, most strongly pronounced along exterior branch and common stem of Y-vein; pterostigma comparatively inconspicuous, light brown.

Head. Vertex short, *c.* 2.6× as wide at base as long in midline, anterior margin medially slightly pointed anteriorly. Areolets distinct, concave; anteriorly separated from frons by obtuse transversal carina. Frons slightly longer than maximum width; disc concave. Frons and clypeus with distinct longitudinal carina. Post- and anteclypeus together as long as frons. First antennal segment short, ringlike; pedicel subglobose, densely beset with sense organs.

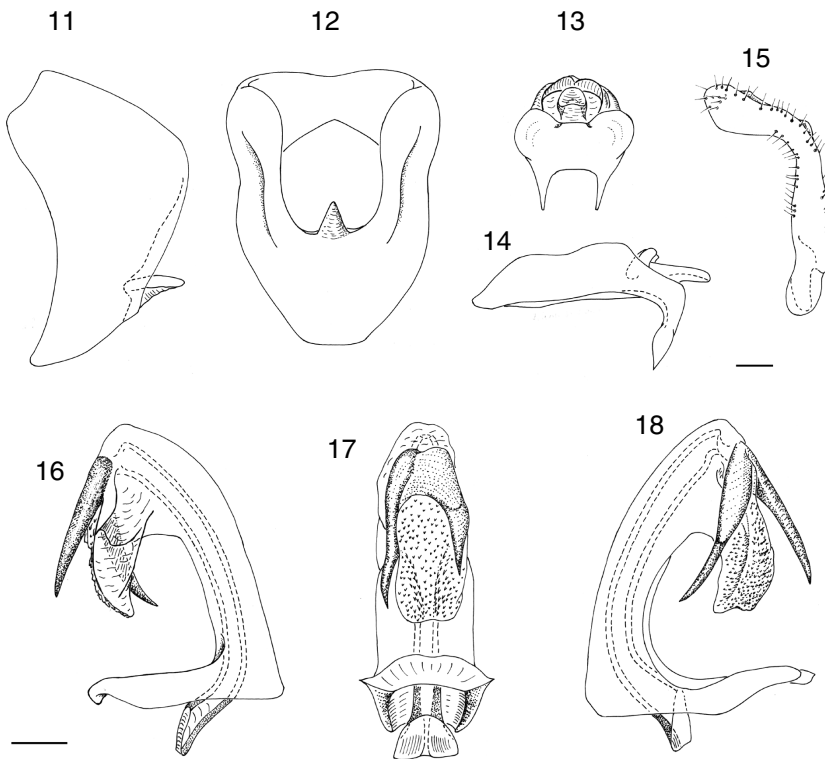
Thorax. Pronotum in midline about half as long as vertex, 1.4× as wide as maximum width of head, posterior

margin deeply incised. Mesonotum in midline *c.* 11× length of pronotum. Hindleg with basitarsus with 5–6 and tarsomere 2 with 6–7 apical teeth. Tegmen *c.* 2.45× as long as wide. Longitudinal veins densely but inconspicuously papillate.

Male genitalia. Genital segment (Figs 11, 12) in caudal aspect *c.* 1.5× taller than wide; in lateral aspect *c.* 3× as long as tall; caudal margin smooth; mesoventral process slender. Anal segment (Figs 13, 14) symmetrical, in dorsal aspect long, narrow, distally truncate; in lateral aspect distal portion bent ventrobasad and laterally produced into 2 distinct spinose processes. Parameres (Fig. 15) simple, slender, distally bent dorsad; distal part rounded. Aedeagus (Figs 16–18) basal part (shaft) slightly curved dorsad, without spinose processes; distal membranous part (flagellum) tongue-shaped, directed straight dorsobasad; with pair of asymmetrical lateral spines arising from near its base, left spine directed dorsobasad, right spine directed ventrobasad, in rest position.

Female unknown.

Etymology. The species is named after two Hawaiian legacies, entomologist Noel Krauss (1910–1996), and his sister, ethnobotanist Beatrice Krauss (1903–1998). Both have contributed in immeasurable ways to the knowledge of the natural and cultural history of Hawai'i Nei. The species is also dedicated to their family, who keep alive the true spirit of *aloha*.



Figs 11–18. *Iolania kraussohana* sp.n., male genitalia (paratype, Kaua'i: Kokee State Park). 11, genital segment, left lateral aspect; 12, same, ventrocaudal aspect; 13, anal segment, left lateral aspect; 14, same, caudal aspect; 15, left paramere, left lateral aspect; 16, aedeagus, dorsal aspect; 17, same, left lateral aspect; 18, same, right lateral aspect. Scale bars = 0.1 mm.

Distribution and ecology. Endemic to Kaua'i. Adults were collected from ferns belonging to genera *Cibotium* (Thyrsopteridaceae) and *Sadleria* (Blechnaceae), in January, February, and October. 300–1400 m.

Remarks. *I. kraussohana* sp.n. is clearly distinct from all other *Iolania* species by its anal tube with spinose processes and aedeagus with asymmetrical spines.

Material examined. Holotype ♂ Kaua'i, Kokee State Park, Alakai Trail, 17.x.1989 (Asche, Hoch, Pereira & Kaneshiro), BPBM (type # BP 16555). – *Paratypes:* 1♂, Kauai, Kokee State Park, Pihea Trail (near lookout), on ferns: *Cibotium* sp. and *Sadleria* sp., 19.ii.1998 (Asche & Hoch). 1♂, Kauai, Hanapunipuni, near Kapaia, 20.i.1944 (Krauss), HDOA.

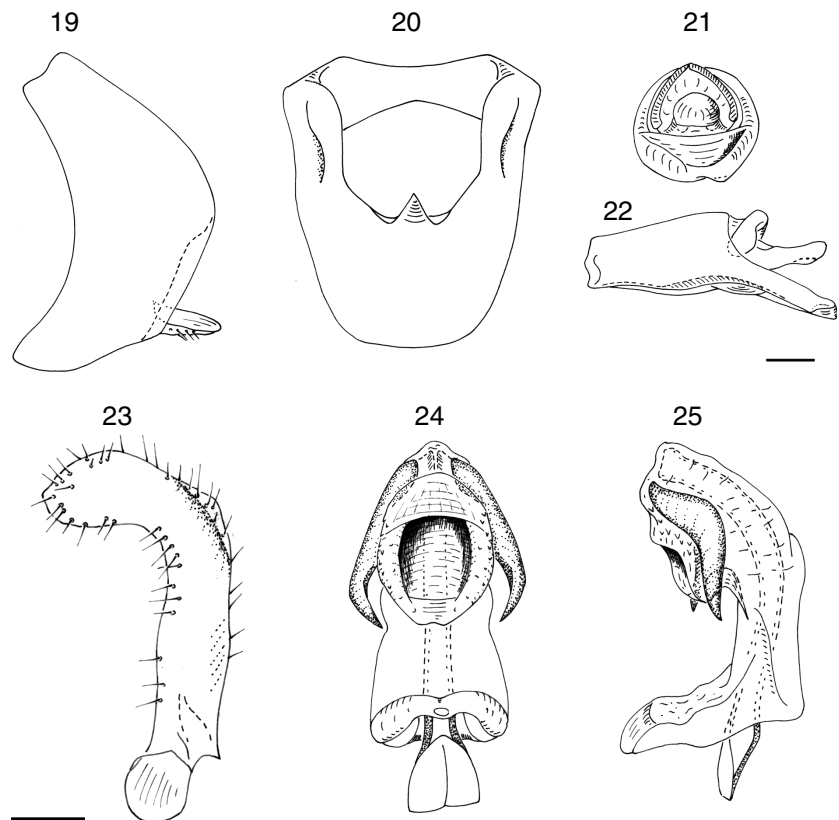
***Iolania lanaiensis* Giffard, 1925: 155** (Figs 19–25)

Diagnosis. Total length: males 5.1–6.3 mm, females 6.2–6.5 mm. *I. lanaiensis* can be distinguished from other *Iolania* species by the combination of the following male genitalic characteristics. Genital segment (Figs 19, 20) slightly taller than wide; dorsolateral margin rounded; mesoventral process triangular. Anal segment (Figs 21, 22) in caudal aspect rounded, ventral margin slightly asymmetrical. Parameres (Fig. 23) with distal portion

slightly dilated, dorsally produced; caudal margin rounded. Aedeagus (Figs 24, 25) symmetrical; shaft at midlength distinctly bent dorsad; flagellum short, dorsal surface strongly concave, with conspicuous groove distad of phallosoma; paired processes short, about as long as flagellum, in lateral view strongly bent dorsally on median portion, distally tapering, in dorsal view claw-like, curved mediad.

Distribution and ecology. Lana'i, type locality at 914 m, Moloka'i: various localities in the central and eastern part. Adults collected by beating vegetation or at light, from *Coprosma* (Rubiaceae) and *Freycinetia* (Pandanaeae) throughout the year. Approximately 1000–1400 m.

Material examined. Holotype ♂ (here re-examined): '3000 ft', BPBM: type number 316; genitalia dissected by Giffard and embedded in caedax. – Additional material. *Lana'i:* 2♂♂, Lanai, T.H., 28.xi.1935, *Coprosma* (Usinger); 1♂, Lanaihale, 3300 ft, 1.vii.1965 (Hardy); 3♂♂, 5♀♀, Mt Waiakeakua, Lanaihale, 3260 ft, 2.v.1993 (Polhemus); 1♂, Haalelepaakai, Munro Trail, 6.0 mi, 1025 m, 2.v.1993, beating vegetation (lot 02) (Liebherr), CUIC; 1♂, Waiakeakua, Munro Trail, 6.7 mi, 993 m, 2.v.1993, beating vegetation (lot 01) (Liebherr), CUIC. *Molokai:* 1♂, Kewela Gulch, 3500 ft, 19.iii.1966 (Beardsley); 1♂, Kawela Gulch, 1140 m, 4.i.1981, M.V. light trap (W.C. & B.H. Gagné). 1♂, Upper Kawela, 4000 ft, 26.vii.1979



Figs 19–25. *Iolania lanaiensis* Giffard, male genitalia (Lana'i: Mt. Waiakeakua, Lanaihale). 19, genital segment, left lateral aspect; 20, same, ventrocaudal aspect; 21, anal segment, caudal aspect; 22, same, left lateral aspect; 23, left paramere, left lateral aspect; 24, aedeagus, dorsal aspect; 25, same, left lateral aspect. Scale bars = 0.1 mm.

(Montgomery); 1♂, Wailau Val., 2000 ft, 27.vii.1936 (Gilbert); 2♂♂, Kanupa, 16.vii.1963 (Hardy); 3♂♂, Pepeopae, 4000 ft, 30.vii.1959 (Hardy); 1♂, above Waikolu V., 1400 m, 28.iv.1955 (Gressitt); 1♂, W end of Hanalilolilo Trail, 1070 m, 7.i.1981, M.V. light (Gagné); 1♂, 1♀, Kamakou Preserve (H98-19), 4000–4200 ft, 10.iii.1998 (Asche & Hoch), AH; 4♂♂, 2♀♀, Maunawainui Val., vii.1952 (Hardy); 2♂♂, ibid., viii.1953 (Hardy); 1♂, Kainalu, 2500 ft, 20.vii.1927 (Swezey); 1♂, ibid., 2000–2500 ft, 26.vii.1927, *Freycinetia* (i'e'i'e vine) (Bryan); 1♂, ibid., 29.vii.1927 (Bryan); 5♂♂, Puu Kolekole, vii.1952 (Tamashiro).

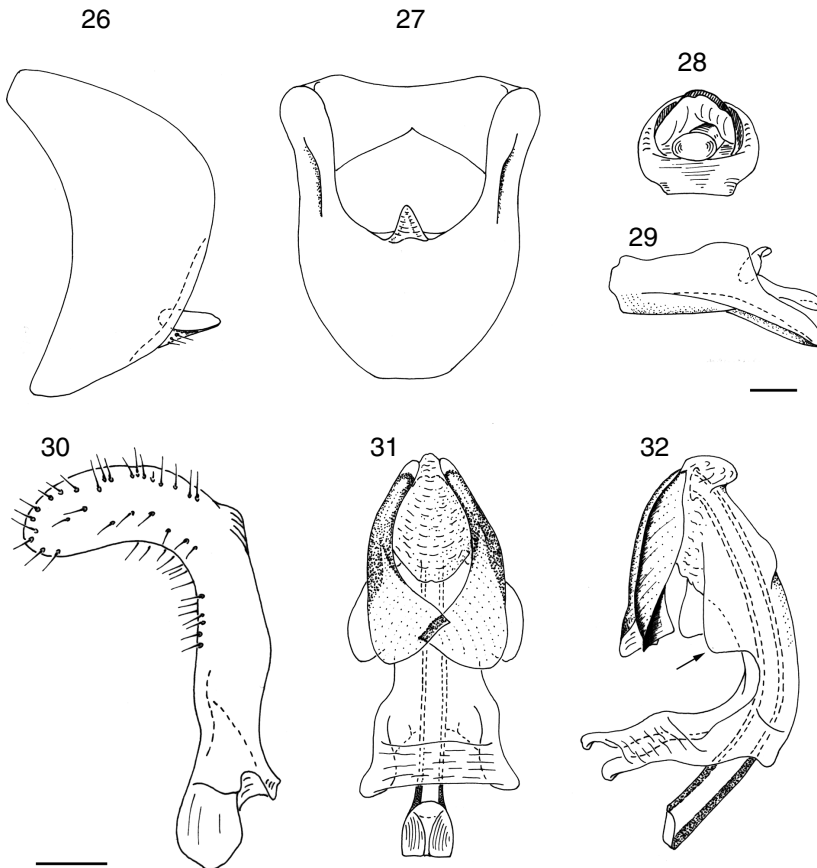
***Iolania mauiensis* Giffard, 1925: 155** (Figs 26–32)

Diagnosis. Total length: males 5.8–6.0 mm, females 6.5–7.0 mm. *I. mauiensis* can be distinguished from other *Iolania* species by the following combination of male genital characteristics. Genital segment (Figs 26, 27) slightly taller than wide, dorsolateral margin rounded, medioventral process triangular. Anal segment (Figs 28, 29) in caudal view dorsally rounded, ventrally truncate. Parameres (Fig. 30) with distal portion bent dorsad, only slightly dilated, finger-shaped. Aedeagus (Figs 31, 32) symmetrical, shaft in lateral aspect gently curved dorsad,

with two dorsolateral flanges (Fig. 32, arrow); flagellum reduced in length; paired processes distally foliately dilated, inserting near apex of the shaft; phallotreme not readily recognizable.

Distribution and ecology. Endemic to Maui (type locality: Waialuaiki): numerous localities in East and West Maui. Adults collected from (montane) rainforest understory, on *Broussaisia* (Hydrangeaceae), *Cibotium* (Thyrsopteridaceae), *Sadleria* (Blechnaceae), at light and in malaise traps, at 275–1730 m, throughout the year.

Material examined. Holotype ♂ (here re-examined): Maui, Waialuaiki, BPBM: type number 315; genitalia dissected by Giffard and embedded in caedax. – Additional material. *Maui*: 2♂♂, Waikamoi, 15.x.1965 (Hardy); 3♂♂, ibid., 16.vi.1965 (Hardy); 4♂♂, 2♀♀, ibid., 4000 ft, viii.1958 (Hardy); 1♂, 3♀♀, ibid., 16.vi.1965 (Beardsley); 4♂♂, 2♀♀, ibid., 4000 ft, 19.vii.1965 (Beardsley); 10♂♂, ibid., 24.viii.1965 (Beardsley); 1♂, 1♀, ibid., vs. 1967 (Krauss); 5♂♂, 2♀♀, Haleakala, along Waikamoi Flume, Koolau Forest Res., 1280 m, CL 8293; 20°48'32"N, 156°13'48"W, 26.v.1997 (Polhemus), USNM 2019096; 1♂, 1♀, Haleakala NP, Kipahulu Valley, 1525 m, 25.xi.1980; rain forest understory; sweeping (Gagné), Acc. no. 1980.545; 1♂,



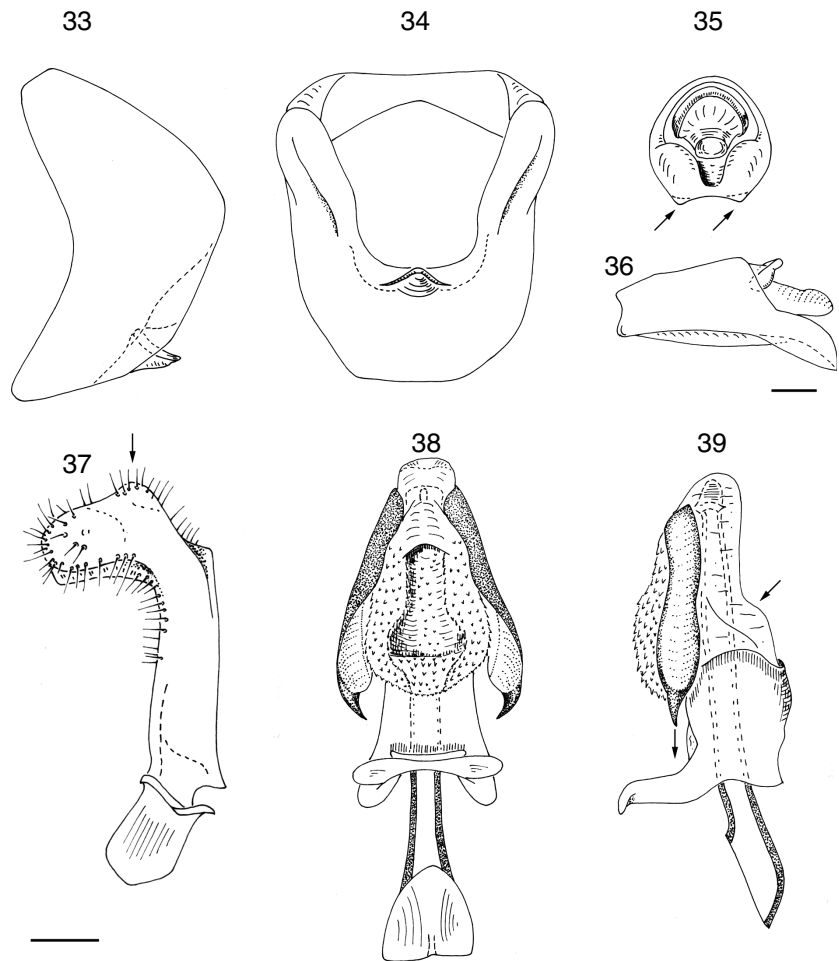
Figs 26–32. *Iolania mauiensis* Giffard, male genitalia (Maui: Waikamoi). 26, genital segment, left lateral aspect; 27, same, ventrocaudal aspect; 28, anal segment, caudal aspect; 29, same, left lateral aspect; 30, left paramere, left lateral aspect; 31, aedeagus, dorsal aspect; 32, same, left lateral aspect. Scale bars = 0.1 mm.

ibid., 915–1525 m, 26.xi.1980 (*Gagné*); 1♂, 1♀, Kipahulu Valley, Palikea Stream, 485 m, 5.vii.1980, M.V. light (*Gagné, Montgomery & Samuelson*), Lower Kipahulu Entomological Survey, Acc. no. 1980.322; 1♂, Kipahulu Valley, Camp 2, 1250 m, 18–20.viii.1967 (*Wilson*); 2♂♂, Kula Pipe Line, 4200 ft, vii.1956 (*Hardy*); 1♂, Haiku 'T.H.', 1.i.1931 (*Krauss*); 1♂, Auwahi, 3700 ft, 20.vii.1965 (*Yoshimoto*); 1♂, E. Hanawi Tr., 15.xi.1985, ex *Broussaisia* sp. (*Paulson*); 1♂, Keanae Valley, 19.vi.1967 (*Hardy*); 1♂ (paratype), 1♀, Wailua nui, 7.ii.1920 (*Bryan*); 2♂♂, Honakohau, 900 m, malaise trap, 26.ii.1972 (*Gressitt*); 1♂, 2♀♀, ibid., malaise trap, 29.i.1972 (*Gressitt*); 1♂, 1♀, Pu'u Kukui, Nakalalua Camp, H98-14, 4400 ft, 3.iii.1998, at night, on ferns: *Cibotium* and *Sadleria* spp. (*Asche & Hoch*), AH; 1♂, Pu'u Kukui, trail from Violet Lake to Nakalalua Camp, H98-13, 4500–5200 ft, 3.iii.1998 (*Asche & Hoch*), AH; 1♂, Pu'u Kukui, trail from Nakalalua Camp to Haela'au Cabin, H98-15, 2980–4400 ft, 4.iii.1998 (*Asche & Hoch*), AH; 2♂♂, 3♀♀, Puukukui [*sic*], 850 m, 31.x.–12.xi.1971, malaise trap (*Gressitt*); 3♂♂, ibid., 9–31.x.1971, malaise trap (*Gressitt*); 1♂, Kaukalewelewe: Pu'u Kukui Trail, 275–1035 m, 24–27.x.1966 (*Yoshimoto*); 3♂♂, 4♀♀, Ridge above Kaulalewelewe, 3000–4000 ft,

4.viii.1964 (*Hardy*); 1♂, 1♀, Puu Kukui Ridge, 4500 ft, 4.viii.1964 (*Hardy*); 1♂, 3♀♀, forest along Puu Kukui Trail above Kaulalewelewe Cabin, 1000 m, 14.v.1992 (*Polhemus*); 1♂, 1♀, montane rainforest nr. Violet Lake, 1480 m, 12.v.1992 (*Polhemus*); 1♂, valley and ridge S of Mt. Eke, 1310 m, 23–25.v.1997, CL 8291, 20°55'04"N, 156°34'22"W (*Polhemus*), USNM 2019096; 2♂♂, Mt. Lihau summit area, 4000 ft, 8–9.v.1993 (*Polhemus*); 1♂, Haleau, 7.ix.1932 (*Krauss*); 1♂, Honokawai Strm, 3000 ft, 26.viii.1965 (*Beardsley*); 1♂, Ridge above Haelaau, 3000–3300 ft, 21.xii.1928 (*Bryan*); 1♂, Haelaau, 17.xii.1928 (*Swezey*).

***Iolania oahuensis* Giffard, 1925: 154** (Figs 33–40)

Diagnosis. Total length: males 4.8–5.9 mm, females 6.6–7.1 mm. *I. oahuensis* can be distinguished from other *Iolania* species by the combination of the following male genitalic characteristics. Genital segment (Figs 33, 34) slightly taller than wide; dorsolateral margin rounded; mesoventral process triangular. Anal segment (Figs 35, 36) in caudal view dorsally rounded; with distinct



Figs 33–39. *Iolania oahuensis* Giffard, male genitalia (O'ahu: Mt. Kaala). 33, genital segment, left lateral aspect; 34, same, caudal aspect; 35, anal segment, caudal aspect; 36, same, left lateral aspect; 37, left paramere, left lateral aspect; 38, aedeagus, dorsal aspect; 39, same, left lateral aspect. Scale bars = 0.1 mm.

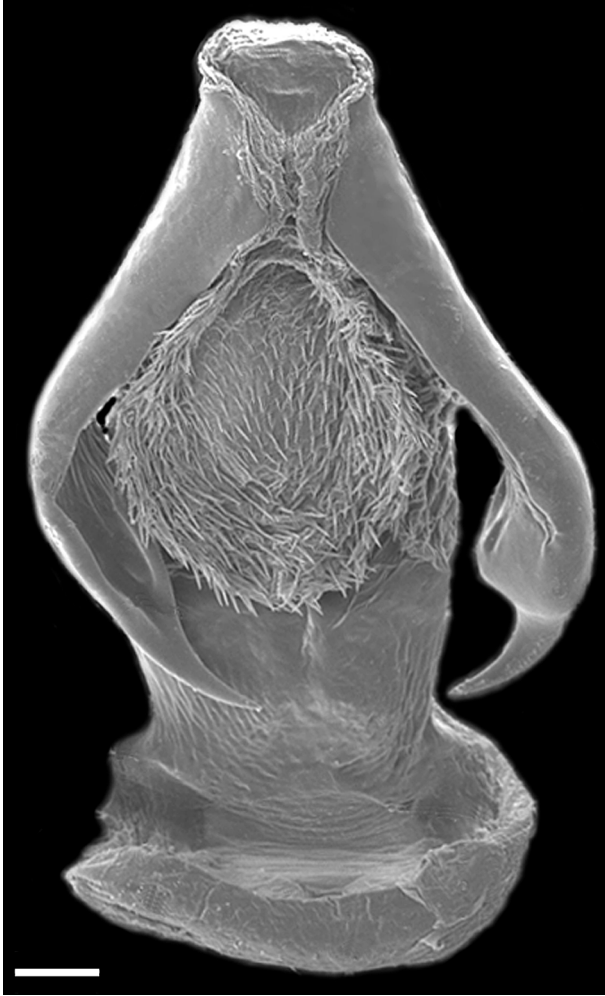


Fig. 40. *Iolania oahuensis* Giffard, male genitalia (O'ahu: 'Waianae Mts.'). Aedeagus (SEM), dorsal aspect. Scale bar = 0.1 mm.

lateroventral corners (Fig. 35, arrows). Parameres proximally slender; ventrally ridged; distal portion dilated, dorsally produced; caudal margin triangular (Fig. 37, arrow). Aedeagus (Figs 38–40) symmetrical; shaft at its base with enhanced sclerotization; ventral margin distinctly narrowed in apical half in lateral aspect (Fig. 39, arrow). Flagellum with distinctly sculptured surface (Fig. 40); paired processes arm-like, proximally taeniform, distally claw-like with acute tips, in repose pointed straight basad (Fig. 39, arrow); dorsal surface medially concave, with conspicuous groove distad of phallosoma. Gonoduct with conspicuous protuberance at apex of shaft, similar to *I. koolauensis* and *I. perkinsi*.

Distribution and ecology. Hawaiian Islands: O'ahu (widely distributed in the Koolau and Waianae Mountains, type locality: Palolo Valley; in the Koolau Mountains in part syntopic with *I. koolauensis*), Moloka'i (western and north-eastern Moloka'i, syntopic with

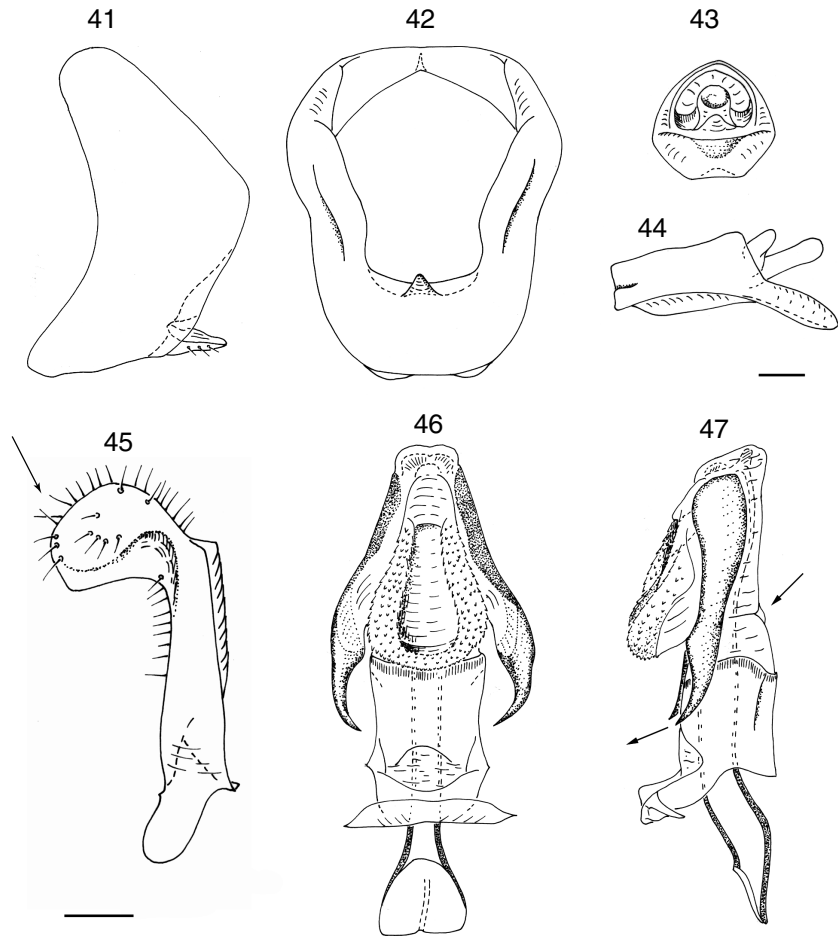
I. lanaiensis), Lana'i (1 specimen from Lanaihale, syntopic with *I. lanaiensis*), and Maui (various localities in West Maui, syntopic with *I. mauiensis*). Adults collected from shrubbery, on *Suttonia* [Myrsine] (Myrsinaceae), *Pipturus* (Urticaceae), *Melicope* (Rutaceae) and *Broussaia* (Hydrangeaceae), 760–1650 m, throughout the year.

Remarks. *Iolania oahuensis* is the most widely distributed species within *Iolania*. In the material studied, *I. oahuensis* specimens were represented from four islands (O'ahu, Lana'i, Moloka'i and West Maui). Although *Iolania* specimens documented in collections are undoubtedly not the result of a specific effort aimed at this taxon but rather of random collecting, it appears that O'ahu harbours a well-established population while there are fewer specimens represented from each of Lana'i, Moloka'i and West Maui.

Material examined. Holotype ♂ (here re-examined): Oahu, Palolo Valley, BPBM: type number 313; genitalia dissected by Giffard and embedded in caedax. – Additional material. **Oahu:** 1♂, Mt. Kaala, 25.vi.1937 (Anderson); 1♂, *ibid.*, iii.1954 (Ford); 1♂, Waianae Mts, vii.1955 (Ford); 1♂, Waianae Mts, Kamaileunu Ridge, N. Puu Kawiwi, 760 m, 31.v.1975, at light (Howarth & Montgomery); 1♂, Waianae, Puu Palikea, ix.1955 (Adachi); 1♂, 2♀, Konahuanui, 2600–3000 ft, 9.v.1943, beating shrubbery (Zimmerman); 1♂, 1♀, Pupukea Trail, 27.xii.1952 (Hoyt); 1♂, Manoa, 30.x.1932 (Krauss); 1♂, 3♀, Mt. Olympus, 20.ii.1937 (Zimmerman); 1♂, 1♀, Koolau Mts: Poamoho, 18.xii.1978 (Montgomery); 1♂, Puu Kalena, 19.iv.1931, *Suttonia* (Swezey), HDOA; 2♂♂, Castle Trail, 27.ix.1938, *Pipturus* (Bryan); 1♂, Punaluu, 11.vi.1911 (Swezey), HDOA; 1♂, Mt. Lanihuli summit area, 2500–2700 ft, 4–5.v.1996, on *Melicope* sp. (Rutaceae), beating vegetation (Polhemus, Asquith & Ewing), USNM 2019096; 1♂, 1♀, Schofield, Waikane Trail, 2000 ft, iii.1958 (Hardy); 1♂, Waimano Trail, iv.1953 (Ford); 2♂♂, 2♀♀, S. ridge Kipapa Gulch, 2200 ft, 4.vii.1932 (Hosaka); 1♂, 3♀♀, Wiliwilinui Rdg., 27.xi.1959 (Woolford); 4♂♂, 3♀♀, Puu Kanehoa, 10.viii.1959 (Beardsley). **Moloka'i:** 1♂, Olokui: Wailau, 3000 ft, 3.ix.1976 (Montgomery), Acc. no. 1983–353; 3♂♂, Kanupa, 16.vii.1963 (Hardy); 1♂, Kahuaawi Gul., vii.1952. **Lana'i:** 1♂, Lanaihale: Kaiholena, 762 m, at MV light, 21.v.1981 (Gagné). **Maui:** 1♂, Haelaau, 3000–5000 ft, *Broussaia*, 18.xii.1928 (Bryan). 1♂, Ridge above Haelaau, 3000–3600 ft, 19.xii.1928 (Bryan). 2♂♂, L. Ridge Iao Valley, ii.1928 (Williams); 2♂♂, 2♀♀, Honakohau, 900 m, 19.iii.1972, malaise trap (Gressitt).

***Iolania perkinsi* Kirkaldy, 1902: 119** (Figs 1–3, 41–2–47)

Diagnosis. Total length: males 5.5–5.9 mm, females 6.5–7.1 mm. *I. perkinsi* can be distinguished from other *Iolania* species by the following combination of male genitalic characteristics. Genital segment (Figs 41, 42)



Figs 41–47. *Iolania perkinsi* Kirkaldy, male genitalia (specimen from Hawai'i Island: Volcano). 41, genital segment, left lateral aspect; 42, same, caudal aspect; 43, anal segment, caudal aspect; 44, same, left lateral aspect; 45, left paramere, left lateral aspect; 46, aedeagus, dorsal aspect; 47, same, left lateral aspect. Scale bars = 0.1 mm.

slightly taller than wide; dorsolateral margin rounded; mesoventral process triangular. Anal segment (Figs 43, 44) in caudal view dorsally rounded; ventral margin straight. Parameres proximally slender; ventrally ridged; distal portion dilated, produced dorsally; caudal margin broadly rounded (Fig. 45, arrow). Aedeagus (Figs 46, 47) symmetrical; shaft in lateral aspect straight (Fig. 47, arrow), with enhanced sclerotization in basal third; flagellum with distinctly sculptured surface, dorsal surface medially concave, with conspicuous groove distad of phallotrema; paired processes arm-like, proximally taeniform, distally terete and tapering into acute tips, in repose pointed dorsad (Fig. 47, arrow). Gonoduct with conspicuous protuberance at apex of shaft, similar to *I. oahuensis* and *I. koolauensis*.

Distribution and ecology. Widely distributed on Hawai'i Island (type locality Kilauea), and here reported from a single male specimen from north-eastern Maui (see Remarks). Adults collected from rainforest habitats, mossy and dried tree ferns, *Cibotium* (Thyrsopteridaceae), Uluhe (*Dicranopteris linearis*, Gleicheniaceae), *Metrosideros polymorpha* (Myrtaceae), *Cheirodendron trigynum* (Araliaceae), *Ilex anomala* (Aquifoliaceae), Guava (*Psidium*

guajava?, Myrtaceae) leaves, by pyrethrum fogging of mossy O'hia (*Metrosideros polymorpha*, Myrtaceae) and at light, at 730–1730 m, throughout the year.

Remarks. The designation of a lectotype for *I. perkinsi* (see below) is based on the finding of the single male specimen in the collection of the BMNH mentioned by Giffard (1925: 103) as Kirkaldy's type. According to Giffard it is labelled with the number 691, which refers to Perkins's collection and stands for 'Kilauea, Hawai'i, July 1895, Perkins coll.'. In Kirkaldy's description, however, there is no mention of any type material or type designation, no indication of the number of specimens, but only a list of various localities. Further material of Kirkaldy's original series could not be traced in any collections. The only specimen of the BMNH bears a label with Kirkaldy's handwriting ('*Iolania perkinsi* Type'). As surviving specimen from the original set of Perkins's collection it must be regarded as syntype, and is therefore designated as lectotype in accordance with the ICZN (article 74). It is worth mentioning that this specimen is not the one figured in Kirkaldy (1902: pl. 4, figs 3–3c) as the latter is a female; thus a label added to the specimen saying 'figured specimen' remains unclear.

A single male specimen from Maui mounted on a permanent slide carries the following labels (handwritten by Giffard) '*Iolania oahuensis?*', '*Iolania koolauensis*', 'will have to study more specimens like it'. According to aedeagal morphology this specimen most likely belongs to *I. perkinsi*. As the large amount of *Iolania* material from numerous localities examined from Maui otherwise did not contain any *I. perkinsi*, it is suspected that this single male *I. perkinsi* may be allochthonous, perhaps windblown to Maui from Hawai'i Island.

Kirkaldy (1909: 75) described under the taxon-name *Iolania perkinsi* (that time broadly defined and thought to be widespread on the Hawaiian Islands) the variety *notata* as 'a form with a large brown blotch at the base of the tegmina of the male', but neither indicated a specific locality, nor did he apparently designate a type for this form. Giffard (1925) found the coloration of the tegmina to be very variable in all localities from Hawai'i, Lana'i and O'ahu, and suggested that 'all these color forms, however, unless supported by structural characters, should not be considered of importance, as [...] each island would present at least two or more color varieties and eventually there would be no limit to such kind of discrimination' (Giffard, 1925: 100). Although Zimmerman (1948) formalized this variety to subspecific rank, *notata* must be regarded as an invalid name as it does not fulfil the requirements of the ICZN for a valid species group description (neither type designation, locality nor distinctive description).

Material examined. Lectotype ♂ (here designated), mounted with minute pin on cardboard, with white label '691', white label in Kirkaldy's handwriting '*Iolania perkinsi* Type' (underside crossed out by pencil: '*Nesocixius perkinsi* Type', unpublished name), orange label 'male', blackish label with imprint 'figured specimen', white label printed 'Sandwich Is., 1913–323', in BMNH. – Additional material. **Hawai'i Island:** 6♂♂, Kulani, 4000 ft, 17.vi.1964 (Hardy); 1♂, *ibid.*, 10.ii.1968 (Krauss); 10♂♂, 9♀♀, Waiakea For. Res., Stainback Hwy, 400 m, 10.xii.1976, at blacklight (Howarth), Acc. no. 1976.332; 2♂♂, Puu Makaala, 1200 m, 9–10.ii.1987, at MV light (Nishida); 1♂, same data except sweeping dried tree fern fronds at night; 2♂♂, 1♀, Volcano, Pu'u Maka'ala Nat. Area Res., 4.5 mi NNW, 1250 m, 27.iii.1991 (Liebherr), CUIIC; 1♂, Kau F.R., Mountain House Road, N19°09'19"–W155°36'51", 910–1080 m, 25.v.2001, lot 1, beat veg. (Liebherr), CUIIC; 1♂, Volcano, N19°27'03"–W155°12'16", 1160 m el., 23.v.2001, lot 01, beating *Ohia/Cibotium* at night (Liebherr), CUIIC; 1♂, Upper Waiakea F.R., N19°34'12"–W155°14'07", 1120 m, 26.v.2001, lot 01, pyr.fog mossy *Ohia* (Liebherr), CUIIC; 2♀♀, Saddle Road, 19°42'14"N, 155°14'05"W, 920 m, 21, 23.viii.1991, at UV light, Helco pole 397 (Nishida), voucher Humuula Saddle Project, Acc. no. 1991.358; 1♀, Kohala Mountains, Upper Hamakua Ditch, above Waimea, 1160 m, 6.vi.1997, CL 8095: 20°04'06"N, 155°40'13"W (Polhemus), USNM 2019096; 1♀, Kohala Mts, Haleaha Gulch, NE Puu Laelae, 1135 m, 11.x.1997, lot 01; beating *Cibotium* and *Uluhe* fern (Liebherr), CUIIC; 1♂, 1♀, N. Kohala, 22.ii.1969, ex forest (Kobayashi);

2♂♂, 1♀, Keanakolu, Maulua Trail, 5200 ft, 20.viii.1964 (Hardy); 1♂, Waikoekoe Forest, 2200 ft, 28.viii.1963 (Hardy); 1♂, Puu Pala, 3600 ft, 28.vii.1966 (Hardy); 1♀, Forest above Paauilo, 2800 ft, 19.vi.1964 (Hardy); 38♂♂, 60♀♀, Volcano Village, Mauna Loa Estates, 17.viii.–3.ix.1997, at light (Asche & Hoch), AH; 2♂♂, 4♀♀, Volcano Village, 9.ix.1989 (Asche & Hoch), AH; 1♂, Kilauea East Rift: Puna District, Keauohana Rd., 8.i.1987 (Asche & Hoch), AH; 3♀♀, Hawaii Volcanoes National Park: Ola'a forest, 11.viii.1989 (Asche & Hoch), AH; 1♂, 1♀, near Volcano, rainforest behind garbage dump, 14.i.1987 (Howarth, Asche & Hoch), AH; 1♀, Volcano Post Office, 9.i.1987 (Asche), AH; 2♂♂, S Hilo Distr. Stainback Hwy, 10.i.1987, at light (Howarth, Stone, Asche & Hoch), AH; 3♂♂, 1♀, Mud Lane, Hamakua Forest, 18.vi.1964 (Hardy); 1♂, Laupahoehoe, 4300 ft, 30.iv.1971 (Hardy); 1♀, Logging Road, Laupahoehoe Sec., 3000 ft, 3.x.1969 (Hardy); 1♂, Hilo Forest Reserve: Laupahoehoe; N. Hilo Dist., 1440 m, 25.ii.1971, *Cheirodendron trigynum* (Gagné); 2♂♂, 2♀♀, along Blair Road above Laupahoehoe, Laupahoehoe NAR, 1220 m, 3–4.vi.1997, CL 8298, 19°56'57"N, 155°16'56"W (Polhemus), USNM 2019096; 1♂, Near Pawaina, Kona, 3000 ft, 13.vii.1965 (Hardy); 2♂♂, 2♀♀, Kona, Greenwell Ranch, 3000 ft, 13.vii.1965 (Hardy); 2♂♂, 1♀, Mt. House Road above Naalehu, 3000 ft, 15.vii.1965 (Hardy); 2♀♀, Kau Forest Reserve, Mountain House Road, 3400–3650 ft, 22.i.2000; CL8348, 19°05'25"N, 155°37'29"W (Polhemus), USNM 2019096; 1♀, Pahala, 27.xii.1960 (Smith); 2♂♂, 1♀, Puna For. Res., 1600 ft, 7.v.1972 (Hardy); 2♂♂, Bishop Trust Road, Hualalai, 2200 ft, 14.vii.1965 (Hardy); 2♂♂, Hualalai, 2000 ft, 18.viii.1964 (Hardy); 1♀, Hualalai, Kaloko Dr., 1330 m, 17.x.1997, beating ferns & *Cibotium* (Liebherr), CUIIC; 1♂, Holualoa, 5.vii.1967 (Tenorio); 1♂, 3♀♀, Hawaii Volcanoes Nat. Park, nr. Park H.Q., 1219 m, 17.vi.1970, *Ilex anomala* (Drake); 1♂, Hawaii Nat. Park, 4000 ft, iii.1954 (Namba); 1♀, Kilauea, Haw. Nat. Park, 1200 m, 24.vi.1978 (Mills); 1♂, Napau Crater, Kilauea, vii.1955 (Hardy); 1♂, Hawaii Volcanoes Nat. Park, Puna, E.Rift, Boundary Puu, 730 m, 7.ix.1977, at light (Howarth); 2♂♂, 1♀, Kilauea, 29 mi, 24.viii.1958, light trap (Beardsley); 1♀, Wilderness Area, Haw. Nat. Park, ii.1968 (Krauss); 1♀, Volcano, Kilauea, State Rec. Area, 1150 m, 1.iv.1991, mossy tree ferns at night (Liebherr), CUIIC; 1♂, Kilauea For. Mauna Loa, 5300 ft 21.vi.1971, sweeping (Hardy); 2♀♀, Kilauea, 4000 ft, 28–29.i.1963 (Hardy); 4♂♂, 4♀♀, *ibid.*, 31.ix.1969 (Hardy); 4♂♂, 3♀♀, Hawaii Volcanoes Nat. Park, Kilauea Iki Trail, nr. Thurston Tube, 4000 ft, 11.v.1986 (Beardsley); 5♂♂, 1♀, Upper Olaa Forest, 4000 ft, vii.1956 (Hardy); 1♂, Glenwood, Kahau'alea NAR, 28.ii.1994, ex guava leaves at night (Asquith); 1♀, Keaau Orchard, 27.viii.1956, at light (Beardsley). – **Maui:** 1♂, Kanae Valley, 24.vi.1920 (Bryan & Giffard).

Key to males of *Iolania*

1. Aedeagus symmetrical; anal segment without spinose processes 2

- Aedeagus with asymmetrical paired spines; anal segment caudally bent ventrad, produced into two distinct ventrolateral spinose processes *I. kraussohana* sp.n.
- 2. Shaft of aedeagus in lateral aspect curved dorsad; flagellum without sculpturing; parameres not ventrally ridged 3
- Shaft of aedeagus straight; flagellum sculptured with numerous distinct tuberculous protuberances; parameres ventrally ridged 4
- 3. Paired spines of aedeagus foliately dilated
..... *I. mauiensis* Giffard
- Paired spines of aedeagus arm-like, curved dorsad at midlength *I. lanaiensis* Giffard
- 4. Parameres with caudal margin triangular; tips of aedeagal spines directed straight basad or basomedial 5
- Parameres with caudal margin rounded; tips of aedeagal spines directed dorsad *I. perkinsi* Kirkaldy
- 5. Anal segment distally with produced lateroventral corners; shaft of aedeagus in lateral aspect with ventral margin distinctly narrowed in apical half; tips of aedeagal spines curved mesally *I. oahuensis* Giffard
- Anal segment in caudal aspect ventrally rounded; shaft of aedeagus in lateral aspect same width throughout; tips of aedeagal spines directed straight basally
..... *I. koolauensis* Giffard

Phylogeny

Within the Cixiidae, the Hawaiian *Iolania* belongs to the world-wide tribe Cixiini (Holzinger *et al.*, 2002). Kirkaldy (1902) and Giffard (1925) assumed a relationship to *Cixius* Latreille. Although no synapomorphies for Hawaiian *Iolania* had been identified, Giffard (1925) recognized the species as closely related and Asche (1997) considered them as 'island monophyletics'. Here arguments supporting the monophyly of Hawaiian *Iolania* are provided and phylogenetic relationships among its species investigated. Relationships within the Cixiini, as for all Cixiidae, remain unclear. Although Emeljanov (2002) discussed the phylogenetic value of suprageneric characters in justifying tribal classification, monophyly of few taxa has been been substantiated (*Hyalesthes* Signoret: Hoch & Remane, 1985; *Solonaima* Kirkaldy: Hoch & Howarth, 1989, Soulier-Perkins, 2005; *Trirhacus* and related genera: Holzinger, 2002). A comprehensive global phylogenetic analysis of all higher taxa of the Cixiidae would be required to place *Iolania* and other Cixiini. Furthermore, incorrect selection of outgroup(s) will lead to zoogeographical conclusions (i.e. the origin of the ancestral species of Hawaiian *Iolania*), which may differ from the evolutionary history of this group. Nevertheless, for identification of the polarity of character states within *Iolania*, an outgroup comparison was mandatory. Outgroups selected were *Cixius nervosus* (Linné) (Cixiini) from Europe and North America, and *Pentastiridius leporinus* (Linné) (Pentastirini) from

Europe. *Iolania clypealis* Muir and *Iolania vittipennis* Muir from Australia were included in the analysis.

The phylogenetic analysis presented here is based on morphology of the adult head, thorax and genitalia of both sexes. Twenty-nine characters were examined and compared with the outgroups in order to polarize character states (see Appendix). The characters used and their hypothesized polarities are listed below, where the hypothesized states are (0) for the plesiomorphic and (1) for the apomorphic state. The main trends of evolution of characters and their polarities are discussed in the following part.

Head

1. *Vertex*: (0) long and narrow, (1) short and wide.

A long and narrow vertex is present also in other basal Fulgoromorpha, e.g. the Delphacidae, and is considered plesiomorphic within the Cixiidae. This configuration is found in *Pentastiridius* and *Iolania vittipennis*; however, in the latter this might be a secondary prolongation of the vertex, thus representing a convergence. *Cixius*, the Australian and the Hawaiian *Iolania* share the apomorphic configuration (a short, wide vertex). Although convergence cannot be excluded, it is more parsimonious to assume that for this clade it is an autapomorphy, i.e. a symplelesiomorphy for the ingroup taxa.

2. *Median carina of vertex*: (0) distinctly present, (1) faint or absent.

The presence of a median carina of the vertex is widespread within Cixiidae and other Fulgoromorpha, and thus is considered plesiomorphic. This configuration is found in *Cixius* and the Australian *Iolania*. *Pentastiridius* and the ingroup display the apomorphic configuration (median carina absent). As a reduction apomorphy there is possibility for convergence; thus, this configuration has possibly independently evolved in *Pentastiridius* and the ingroup. For the ingroup taxa it is considered a synapomorphy.

3. *Areolets*: (0) medially divided by a carina, (1) medially not divided.

In most Cixiidae the areolets are divided by a distinct median carina, thus here considered as plesiomorphy. The apomorphic configuration of medially not divided areolets is found in the Australian *Iolania* species, and probably is an autapomorphy of this group. For the ingroup taxa this character is a symplelesiomorphy.

4. *Frontal carina*: (0) not forked towards areolets, (1) forked towards areolets.

In Cixiidae a simple, apically unforked median frontal carina is widespread, and here considered plesiomorphic. A forked median frontal carina is present in *Pentastiridius* representing the apomorphic configuration. The ingroup taxa are symplelesiomorphic in this character.

5. *Frontoclypeal suture*: (0) shallowly arched, (1) highly arched.

A shallowly arched frontoclypeal suture is present in nearly all Cixiidae and regarded as plesiomorphic. Among the out- and ingroup taxa studied a highly arched suture is found only in *Iolania clypealis*, an autapomorphy for this species. The ingroup taxa are symplesiomorphic concerning this character.

6. *Median frontal ocellus*: (0) present, (1) absent.

The presence of the full set of ocelli (2 lateral and 1 frontal) is considered the plesiomorphic configuration in Cixiidae and all other Fulgoromorpha. This is also the case in *Pentastiridius* and *Cixius*. The absence of the frontal ocellus is apomorphic, although a reduction might have occurred independently several times. The frontal ocellus is absent in the Australian and the Hawaiian *Iolania* species; currently it is uncertain whether the absence can be regarded as synapomorphy of the Australian and the Hawaiian *Iolania* species.

Thorax

7. *Mesonotum*: (0) tricarinate, (1) pentecarinate.

Within the Cixiidae a tricarinate mesonotum is regarded as plesiomorphic as this configuration is observed in all taxa which have a complete, i.e. plesiomorphic, ovipositor (see below). Among the taxa concerned here, a pentecarinate mesonotum, consequently the apomorphic configuration, is only found in *Pentastiridius*. Thus, a tricarinate mesonotum must be regarded a symplesiomorphy for the ingroup taxa.

8. *1st metatarsus*: (0) distally without macrochaetae (platellae), (1) distally with macrochaetae (platellae).

9. *2nd metatarsus*: (0) distally without macrochaetae (platellae), (1) distally with macrochaetae (platellae).

Within the Cixiidae, the absence of macrochaetae or platellae on the first and second metatarsi is considered plesiomorphic. The development of macrochaetae by the enhancement of bristles beneath the spines on the distal margin of the corresponding metatarsi is considered apomorphic and has occurred repeatedly in various unrelated taxa. Among the species compared here, the apomorphic configuration is present only in *Pentastiridius*. Thus, the absence of platellae in the ingroup taxa must be regarded as a symplesiomorphy.

Male genital complex

10. *Flagellum of aedeagus*: (0) movable against shaft. (1) rigid.

11. *Flagellum*: (0) long, in repose nearly attaining base of shaft; (1) short, reaching to mid of shaft.

12. *Flagellum*: (0) distally bent dorsolaterad, (1) bent straight dorsad.

13. *Shaft of aedeagus*: (0) bilaterally asymmetrical, (1) bilaterally symmetrical.

14. *Shaft*: (0) with rigid spinose processes or teeth, (1) smooth, without any rigid spinose processes or teeth.

15. *Phallosome*: (0) terminally, near apex of flagellum; (1) near base of flagellum, dorsally exposed.

The plesiomorphic configuration of characters 10–15 is widespread within the Cixiidae and other Fulgoromorpha (Delphacidae: Ugyopinae, Asiracinae). Only the taxa of the ingroup display the apomorphic configuration of each character, by this constituting a unique aedeagus structure within the Cixiidae. Each of these characters is regarded as an autapomorphy for the ingroup. As they all pertain to the male copulatory organ, it is conceivable that the corresponding structures functionally interact during copulation and may have co-evolved.

16. *Spinose processes at base of flagellum*: (0) on both sides unequal in length and shape, (1) equal in length and shape.

The presence of spinose processes at the base of the flagellum is common in Cixiidae. In most species, however, these are unequal in length and shape. Thus, this configuration is regarded as plesiomorphic and occurs in all outgroup taxa and in *Iolania kraussohana*. By contrast, spinose processes inserting at the flagellum base that are equal in length and shape are regarded apomorphic. This configuration is found only within all ingroup taxa except *I. kraussohana* and regarded an autapomorphy for this group.

17. *Aedeagus shaft*: (0) more or less straight, (1) bent dorsad at midlength.

18. *Flagellum spines*: (0) slender, only slightly curved; (1) arm-shaped, bent in a nearly right angle basodorsad.

19. *Flagellum spines*: (0) distally not dilated, (1) distally foliately dilated.

The plesiomorphic configuration of characters 17–19 is distributed widely among the Cixiidae, including all outgroup taxa, and the ingroup taxa *I. kraussohana*, *I. oahuensis*, *I. koolauensis* and *I. perkinsi*. The apomorphic configuration of character 17, the aedeagus shaft being bent dorsad at midlength, is observed exclusively in *I. lanaiensis* and *I. mauiensis*, and is therefore considered a synapomorphy. Flagellum spines which either are arm-shaped and bent in a nearly right angle basodorsad or distally foliately dilated (apomorphic configuration of characters 18 and 19) are autapomorphies for *I. lanaiensis* and *I. mauiensis*, respectively.

20. *Aedeagus shaft*: (0) distally without any protuberances, (1) distally with protuberance.

21. *Surface of flagellum membrane*: (0) rugose, (1) distinctly villiform (Fig. 38).

The plesiomorphic configuration of characters 20–21 is widespread among the Cixiidae, including all outgroup taxa and the ingroup taxa *I. kraussohana*, *I. lanaiensis* and *I. mauiensis*. The presence of a distal aedeagus shaft protuberance and a distinctly villiform flagellum membrane surface are considered the apomorphic configuration of characters 20 and 21. These are observed exclusively in the ingroup taxa *I. koolauensis*, *I. oahuensis* and *I. perkinsi* and thus are considered autapomorphies for this clade.

22. *Parameres*: (0) medioventral margin smooth, (1) medioventral margin distinctly ridged.

In nearly all groups of Cixiidae, parameres display a more or less slender base with a smooth medioventral margin. This configuration is assumed to be plesiomorphic.

It is found in all outgroup taxa. Parameres with a distinctly ridged medioventral margin are considered apomorphic, and are found exclusively in the ingroup and regarded as an autapomorphy for the Hawaiian *Iolania*.

23. *Parameres*: (0) distal portion spoon-shaped, rounded; (1) distal portion triangularly dilated.

A rounded, spoon-shaped distal part of the parameres is widespread in the Cixiidae and considered plesiomorphic, while a triangularly dilated distal part is regarded here as apomorphic. The apomorphic configuration is observed only in the ingroup taxa *I. koolauensis*, *I. oahuensis* and *I. perkinsi*, and is considered an autapomorphy for this clade.

24. Ventrocaudal margin of anal segment: (0) without spinose processes, (1) with paired spinose processes.

Within the Cixiidae, the anal segment usually is hood-shaped, ventrally concave and – in some taxa – furnished with lobe-like projections of the ventrocaudal margin, and is considered a plesiomorphy. The presence of paired spinose processes on the ventrocaudal margin is regarded an autapomorphy for *I. kraussohana*.

Female genitalia

25. *Ovipositor*: (0) elongate, ensiform, orthopteroid; (1) short and stout.

An orthopteroid ovipositor is a groundplan character of the Fulgoromorpha (O'Brien & Wilson, 1985) and therefore considered a plesiomorphy for Cixiidae. It is widely distributed within the Cixiidae and present in the ingroup and all outgroup taxa except for *Pentastiridius* that have a short and stout ovipositor, which is most certainly a (reductive) apomorphy. Thus, the morphological display of this character in the ingroup is a symplesiomorphy.

26. *9th tergite*: (0) caudally with a median furrow, (1) caudally truncate and more or less concave.

27. *Ovipositor*: (0) nearly adapt to the shape of the 9th tergite, (1) nearly rectangularly exposed from 9th tergite.

28. *Wax pores on 9th tergite*: (0) not arranged in distinct plate(s), (1) organized in distinct plate(s).

Within Cixiidae, the 9th tergite and the ovipositor form a functional unit for the oviposition. As in other basal Fulgoromorpha taxa, e.g. Delphacidae, a complete ovipositor which in repose is embedded in a median furrow of the (otherwise convex) 9th tergite without distinctly limited wax-plates is considered plesiomorphic. In the taxa compared here, this configuration is found in the ingroup, and considered a symplesiomorphy.

In several cixiid lineages, however, modifications of this pattern have occurred, resulting in configurations that are regarded as apomorphic: the 9th tergite becoming caudally truncate and more or less concave and bearing distinctly limited wax-plates. This re-organization may be directly related to the ovipositor becoming rectangularly exposed. The apomorphic configuration of characters 26–28, although present in two of the outgroup taxa included here, *Pentastiridius* and *Cixius*, but also in other Cixiidae is therefore considered to have convergently evolved in the two

outgroup taxa. For *Iolania clypealis* and *Iolania vittipennis* the configuration of the female genitalia is unknown.

29. *Ductus receptaculi*: (0) tubular or bulbous, not heliciform; (1) elongate and heliciform.

Few cixiid taxa have been analysed regarding the internal ectodermal structures of the female genitalia, but a simple, tubular or bulbous ductus receptaculi (as in other basal Fulgoromorpha taxa, e.g. Delphacidae) constitutes the plesiomorphic configuration. This is present in all ingroup taxa and in *Pentastiridius*, but no information is available for the Australian '*Iolania*'. An elongate and heliciform ductus receptaculi is regarded as apomorphic, as is observed in the outgroup species *Cixius nervosus* (and in several related taxa: Holzinger *et al.*, 2002).

Monophyly of the Hawaiian *Iolania* and relationships to other Cixiidae

As already stated by Asche (1997) the Hawaiian *Iolania* species had been grouped on the basis of several symplesiomorphies. Outgroup comparison indeed revealed the plesiomorphic configuration in the following characters of the head (areolets medially divided by a carina, frons with median carina present and forked towards areolets, frontoclypeal suture shallowly arched), the thorax (mesonotum tricarinate), the legs (1st and 2nd metatarsus without platellae), the female genitalia (ovipositor elongate, orthopteroid, adapt to the shape of the 9th tergite, 9th tergite with median furrow and not truncate, wax pores not arranged in distinct plates, ductus receptaculi not heliciform) and one character of the male genital complex (anal segment symmetrical).

The following characters, all pertaining to the male genital complex, are here regarded as autapomorphies of Hawaiian *Iolania*: flagellum of aedeagus rigid, not movable against shaft, flagellum short, reaching to mid-shaft, flagellum bent straight dorsad (not dorsolaterad), shaft bilaterally symmetrical, smooth, without any rigid spinose processes or teeth, phallosome near base of flagellum, dorsally exposed, parameres with medioventral margin distinctly ridged. Comparison of Hawaiian *Iolania* species to the outgroups revealed no similarities in the male genitalia, especially in the aedeagus, between the Hawaiian *Iolania* species and any other cixiid taxon that could be interpreted as synapomorphies.

None of the autapomorphies of the Hawaiian *Iolania* is recognized in the Australian *I. clypealis* and *I. vittipennis*. Instead, both species differ from all Hawaiian *Iolania* species by the configuration of the vertex. In addition, *I. clypealis* differs from *I. vittipennis* and the Hawaiian *Iolania* species in characters of the frons (frontoclypeal suture highly arched). The absence of the median ocellus, although a (reductive) apomorphy, is unlikely to be a synapomorphy shared by *Iolania* species from Hawai'i and Australia. As the reduction of the median frontal ocellus has occurred repeatedly within the Cixiidae (e.g. Hoch & Howarth, 1989), it appears more parsimonious to assume a homoplasy. Thus, there is no reason to assume that these two species belong to the Hawaiian clade, and I suggest

them to be regarded for the time being as *incertae sedis*. In fact, Muir's decision to place the two taxa from Australia into *Iolania* was based on the (erroneous) observation that the hind tibiae in Hawaiian *Iolania* were laterally unarmed (Muir, 1931). Although minute, lateral hind tibial spines are present (see diagnosis for the genus), they apparently were overlooked previously.

Furthermore, no arguments in support of a closer relationship of *Iolania* to the taxon *Cixius*, as was stated casually by Kirkaldy (1902) and repeated subsequently by Giffard (1925), could be found: similarities between *Iolania* and *Cixius* are based exclusively on characters here regarded as plesiomorphies (e.g. ensiform ovipositor, tricarinate mesonotum). The only apomorphic character found in *Cixius*, the Australian and the Hawaiian *Iolania* is a short and wide vertex, which may be an autapomorphy on a more inclusive level, i.e. the Cixiini as a whole, and thus a symplesiomorphy for the ingroup.

Thus, Asche's statement ('there appear to be no close relatives of *Iolania* in the faunas of the Pacific Islands, Australia, Asia, or North America and South America', Asche, 1997: 369) cannot (yet) be rejected – the phylogenetic relationships of Hawaiian *Iolania* to other Cixiidae outside Hawai'i remain unresolved. It is clear, however, that the Hawaiian *Iolania* species are descendants of a single ancestral species.

Monophyletic groups and sister taxa relationships within *Iolania* (Fig. 48)

I. kraussohana

This species is morphologically rather isolated from the other *Iolania* species. It displays a special configuration of the male anal segment, which possesses conspicuous paired ventrocaudal spines (Figs 13, 14). This configuration is present in no other outgroup representative nor in any other ingroup taxa, and thus is regarded an autapomorphy for *I. kraussohana*. As all other *Iolania* species display the plesiomorphic state, an anal segment that essentially is hood-shaped and without such spinose processes, the assumption of a secondary reduction in those taxa (either once or several times independently) is less parsimonious. *Iolania kraussohana* is the only *Iolania* species in which the flagellum of the aedeagus is furnished with two spinose processes, which are unequal in length and shape. Because the presence of unequal flagellum spines is observed commonly in outgroup representatives (e.g. Kramer, 1981, 1983), this character state is regarded here as plesiomorphic.

All other *Iolania* species

All other five *Iolania* species display two flagellum spines that are equal in length and shape, a configuration that is not present in any outgroup taxon (nor any other

known cixiid) and is therefore regarded as an autapomorphy.

I. lanaiensis + *I. mauiensis*

This group is characterized by the configuration of the aedeagus shaft: in both species, the shaft is bent dorsad at midlength, whereas in all other *Iolania* species (and all outgroup taxa) it is straight. A straight shaft is considered to be plesiomorphic; thus, a shaft bent dorsad is considered apomorphic for this clade. The specific configuration of the (equal) flagellum spines (arm-shaped and in repose directed basodorsad at *c.* 90 °) is regarded an autapomorphy for *I. lanaiensis*, whereas distally foliately dilated flagellum spines are presumed an autapomorphy for *I. mauiensis*.

I. koolauensis + *I. oahuensis* + *I. perkinsi*

Members of this clade are characterized by displaying the following synapomorphic characters: aedeagus shaft distally with a distinct protuberance (plesiomorphic: shaft without protuberance as in the other *Iolania* species), surface of flagellum membrane distinctly villiform (Fig. 40) (plesiomorphic: rugose as in the other *Iolania*), and parameres slender at base, apically strongly dilated (plesiomorphic: parameres being slender throughout as in other *Iolania* species). The three species differ only slightly but consistently (see diagnoses for species) and appear to be very closely related. The phylogenetic relationships between these three species, however, cannot be resolved satisfactorily on the basis of morphological characters. Clues on the sequence of speciation events in this clade may be deducible from biogeographical information (see below).

Biogeography and colonization history

Endemism

The degree of endemism is high in *Iolania* species. Four of the six extant species are single-island endemics: *I. kraussohana* on Kaua'i, *I. koolauensis* on O'ahu, *I. mauiensis* on (East and West) Maui, and *I. perkinsi* on Hawai'i Island (the single male specimen from East Maui is considered allochthonous, see 'Remarks' under *I. perkinsi*). Only two species have a wider distribution: *I. lanaiensis* occurs on Lana'i and Moloka'i, and *I. oahuensis* on O'ahu, Moloka'i, Lana'i and West Maui.

Sequence of colonization events

To determine predominant patterns of dispersal (inter-island colonization) and to provide a plausible hypothesis for the sequence of colonization and speciation events, the taxon cladogram was used as the basis for a

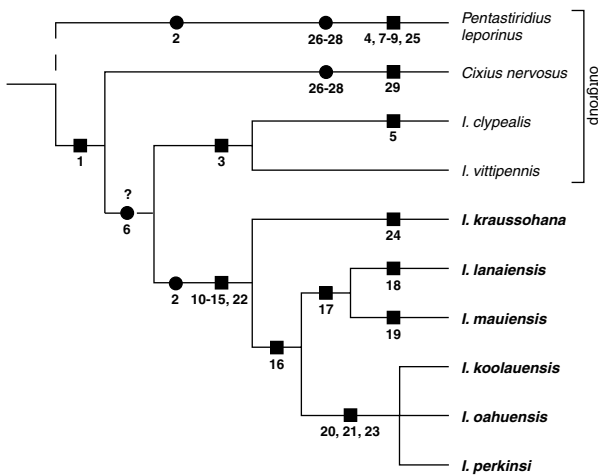


Fig. 48. Cladogram representing presumed phylogeny of extant Hawaiian *Iolania* species. Apomorphic character states are denoted by black squares, convergence denoted by black circles. The number of character states are those in the matrix. Uncertain phylogenetic relationships are indicated by a broken line.

biogeographical analysis. For this, terminal taxa in the cladogram (Fig. 48) were replaced by their respective distribution (e.g. Funk, 1995; Liebherr, 1997). The resulting area cladogram (Fig. 49) recognizes the principal pattern of dispersal within *Iolania* as a progressive colonization from Kaua'i, the oldest island in the Hawaiian chain, to the younger islands (Fig. 50). [For ages of islands see Clague & Dalrymple (1987).] The current distribution of extant taxa suggests that, originating from Kaua'i, two lineages have colonized (a) O'ahu (the ancestral species of the *oahuensis*–*koolauensis*–*perkinsi* clade) and (b) islands that formerly were part of the superisland Maui Nui (Maui, Moloka'i and Lana'i), bypassing O'ahu. The Maui Nui clade diverged subsequently, eventually giving rise to the two extant species *I. lanaiensis* (today present on Lana'i and Moloka'i) and *I. mauiensis* (endemic to Maui). Descendants of the O'ahu clade are endemic on O'ahu (*I. koolauensis*) and subsequently colonized Maui Nui (*I. oahuensis*, occurring on O'ahu, Lana'i, Moloka'i and W.Maui) and Hawai'i Island, giving rise to *I. perkinsi*. The occurrence of *I. perkinsi* on East Maui, although documented by a single specimen only, may point to a single back-colonization event. Although plausible, this scenario remains vague, as the phylogenetic relationships between the terminal taxa of the *oahuensis*–*koolauensis*–*perkinsi* clade are insufficiently resolved. However, the pattern of progressive colonization from older to younger islands appears to be common in Hawaiian terrestrial organisms, especially arthropods (e.g. insects, Diptera: *Drosophila*, DeSalle, 1995; spiders: *Tetragnatha*, Gillespie & Croom, 1995) and corresponds to the geodynamics of the archipelago: newly emerging islands are being colonized from source populations on older islands. This pattern often is superimposed by intra-island (adaptive) radiation, back-colonization and extinction (Funk & Wagner, 1995).

Patterns of speciation

The high degree of single-island endemics and the progressive colonization pattern suggest that in *Iolania*, speciation patterns predominantly are allopatric. Most speciation apparently has occurred with colonization of a new island. In *Iolania*, there appears to be no habitat shifts in or between islands – all species display similar habitat preferences. The habitat can be characterized most simply as *Metrosideros*/*Cheirodendron* cloud forest in mid elevations between c. 300/400 and 1800 m. Co-dominant species in the corresponding plant communities are *Metrosideros polymorpha* (Myrtaceae), or 'Ohia', and *Cheirodendron trigynum* (Araliaceae), or 'Olapa'. This community is found on all the main islands (except Niihau and Kahoolawe), and is confined to the cloud zone, especially on windward slopes, ridge crests and clifftops facing the tradewinds. Characteristics include a well-developed shrub layer, epiphytic mosses and hepatics, ferns, and vascular plants, and low temperatures and acid soils as abiotic parameters (Wagner *et al.*, 1999). The community comprises all plant species from which adult *Iolania* specimens have been collected. Whether (any of) these are also the host-plants of *Iolania* species cannot yet be determined: nymphs of *Iolania* are hitherto unknown – they most likely live (like the nymphs of all cixiids) close to or inside the soil, and are not documented in collections.

In many Hawaiian organisms inter-island dispersal may be important in promoting speciation, with isolation facilitating genetic change without habitat shifts (Funk & Wagner, 1995). The underlying reason may be genetic destabilization accompanying founder dispersal (Carson, 1987) and subsequent rearrangement of co-adapted gene complexes. In addition to this pattern, at least one speciation event may be attributable to the breakup of the Maui Nui complex: the current distribution of *I. lanaiensis* and *I. mauiensis* suggests that their common ancestor occurred throughout Maui Nui. According to recent findings (Price & Elliott-Fisk, 2004) the initial separation of the Maui Nui complex into several land masses occurred around 0.6 mya, and is here hypothesized as the maximum age of the divergence within the Maui Nui clade. The sequence of speciation events in the *oahuensis*–*koolauensis*–*perkinsi* clade is more problematic to rationalize. Although *I. oahuensis* is known from numerous localities in the Wai'anae and in the Koolau Mountains, *I. koolauensis* appears to be restricted to the Northern Koolaus. Liebherr & Zimmerman (2000: 153–164) report of a parallel in the *Blackburnia optata* and *B. hikia* species pair (Coleoptera: Carabidae), with *B. hikia* a northern Koolau endemic, and with the adelphotaxon to these two species, *B. micans*, being widespread on both Wai'anae and Koolau mountains. Both mountain ranges are remnants of ancient volcanoes, their maximum age being 3.7 Ma (Wai'anae's) and 2.6 Ma (Koolaus) (Clague & Dalrymple, 1987). Both volcanoes were greatly reduced while in their post-shield stage by large landslides, named the 'Wai'anae slump' (Wai'anae Mts) and the

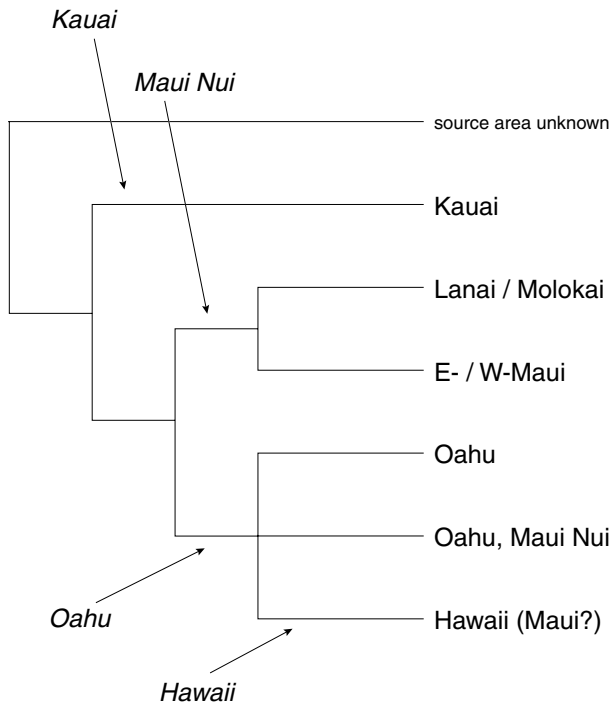


Fig. 49. Area cladogram as derived from the taxon cladogram. Arrows indicate colonization events by hypothesized ancestral species. See text for further explanation.

Nu'uauu landslide (Koolau Mts), and erosion which left the current mountain ranges as remnants of once far large crater rims (Clague, 1998). It is conceivable that the ancestral taxon of the lineage colonizing O'ahu from Kaua'i also followed a progressive colonization pattern, giving rise to *I. oahuensis* on Wai'anae volcano and to *I. koolauensis* on Koolau in allopatry. Loss of landmass and the resulting reduction of habitat suitable for *Iolania* (possibly simply by diminishing available square dimension) might have led to range fluctuation of (any of) the species on O'ahu. Thus, the present-day distribution of *I. koolauensis* (which is apparently restricted to the northern Koolaus) might be relictual. The northern Koolaus may represent a remnant windward area of endemism, greatly reduced in extent by the Nu'uauu landslip (J. K. Liebherr, personal communication). It would thus be parsimonious to assume that the present-day syntopic occurrence of *I. koolauensis* and *I. oahuensis* is secondary.

Hawai'i Island has been available for colonization for less than 0.6 my (Price & Elliott-Fisk, 2004), which is hypothesized here to be the maximum age for the colonization by a representative of the *oahuensis*–*koolauensis*–*perkinsi* clade.

The current state of knowledge of *Iolania* does not allow any conclusions on (a) the geographical origin of the ancestral species that initially colonized the Hawaiian Islands, or (b) on the island of its arrival. It is conceivable that initial colonization did not occur on Kaua'i (available for

colonization since *c.* 5 Ma), but on one of the (once high) islands in the north-western Hawaiian chain of which the oldest, Kure, formed about 29 mya (Carson & Clague, 1995). These islands have since been reduced to low atolls by erosion and subsidence, and any habitat suitable for sustaining *Iolania* no longer exists.

Conclusions and perspectives

In *Iolania*, dispersal and speciation patterns appear to be closely linked to the life cycle of the volcanoes (with well-defined stages: Moore & Clague, 1992) that make up the Hawaiian Island chain: from older islands, basic clades colonized the newly emerging islands (in the shield-building stage) by progressive inter-island dispersal (from Kaua'i to Maui Nui and O'ahu, respectively, and from O'ahu to Hawai'i Island) (see also Fig. 50), while divergence events leading to terminal taxa may be attributable to geological events at a later stage of the volcanic island growth cycle (late-stage volcanism characterized by erosion and landslides, and subsidence stage), e.g. the breaking up of the Maui Nui complex in the case of *I. lanaiensis* and *I. mauiensis*, and perhaps the collapse of large parts of the Wai'anae and Koolau volcanoes on O'ahu in the case of *I. koolauensis* and *I. oahuensis*.

One of the most intriguing questions raised here is why *Iolania* – as compared with the other cixiid lineage that has successfully colonized the Hawaiian Islands, *Oliarus* – is so species-poor. Similar differences in speciation patterns are observed in other Hawaiian arthropod taxa (Howarth & Mull, 1992), and have been called 'great mysteries' of Hawaiian evolutionary biology by H. L. Carson (personal communication).

On the phenotypic level, factors like host specificity and dispersal ability may at least in part account for the observed differences between *Iolania* and *Oliarus*. In *Iolania*, host restriction is low (see above), and dispersal ability is high (adults, especially females, are flight-active: on moist, rainy

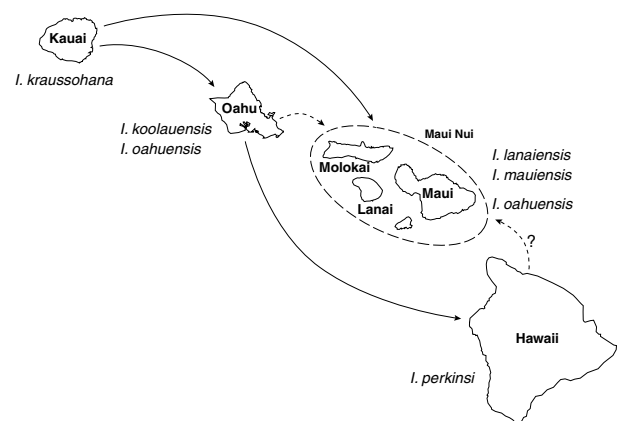


Fig. 50. Dispersal pathways of *Iolania* taxa as derived from taxon and area cladograms (Figs 48, 49). Bold arrows indicate dispersal of major lineages, and dotted-line arrows dispersal of terminal taxa (see text for further explanation).

nights they are attracted to light traps in great numbers; my personal observation). Both factors may have facilitated the maintenance of gene flow between populations and thus counteracted ecological specialization and, eventually, speciation. By contrast, Hawaiian *Oliarus* species are ecologically far more diverse (see Introduction) and are not frequently attracted to light (my personal observation), which is indicative of low dispersal ability. An answer to the question of why *Iolania* is so species-poor, however, can only be obtained through a comparative analysis of the two lineages on the genetic level as 'a detailed understanding of the genetic system of two such groups or organisms may indeed hold the keys to an understanding of why such variations in evolutionary pattern occur' (Carson, 1986: 809).

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References

- Asche, M. (1997) A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pacific Science*, **51**, 366–376.
- Asche, M. (1998) A review of the planthopper genus *Nesodryas* Kirkaldy and related taxa (Homoptera: Fulgoroidea: Delphacidae). *Proceedings of the Hawaiian Entomological Society*, **33**, 89–124.
- Asche, M. (2000) *Emoloana*, a new genus for the endemic grass-feeding Hawaiian Delphacidae (Homoptera: Fulgoroidea). *Proceedings of the Hawaiian Entomological Society*, **34**, 71–113.
- Carson, H.L. (1986) Patterns of inheritance. *American Zoologist*, **26**, 797–809.
- Carson, H.L. (1987) Colonization and speciation. *Colonization, Succession, and Stability* (ed. by A. J. Gray, M. J. Crawley and P. J. Edwards), pp. 187–206. Blackwell, Oxford.
- Carson, H.L. & Clague, D.A. (1995) Geology and biogeography of the Hawaiian Islands. *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago* (ed. by W. L. Wagner and V. A. Funk), pp. 14–29. Smithsonian Institution, Washington, DC.
- Clague, D.A. (1998) Geology. *Atlas of Hawai'i*, 3rd edition (ed. by S. P. Juvik and J. O. Juvik), pp. 37–46. University of Hawai'i Press, Honolulu, Hawai'i.
- Clague, D.A. & Dalrymple, G.B. (1987) The Hawaiian Emperor volcanic chain. Part I. Geologic evolution. *Volcanism in Hawai'i* (ed. by R. W. Decker, T. L. Wright and P. H. Stauffer), USGS Professional Paper 1350. US Gov. Printing Office, Washington, DC.
- DeSalle, R. (1995) Molecular approaches to biogeographic analysis of Hawaiian Drosophilidae. *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago* (ed. by W. L. Wagner and V. A. Funk), pp. 72–89. Smithsonian Institution, Washington, DC.
- Emeljanov, A.F. (2000) New genera of the family Cixiidae (Homoptera, Fulgoroidea) from Australia and neighbouring territories. *Entomological Review*, **80**, 251–270.
- Emeljanov, A.F. (2002) Contribution to classification and phylogeny of the family Cixiidae (Hemiptera, Fulgoromorpha). *Zikaden. Leafhoppers, Planthoppers and Cixiidae (Insecta: Hemiptera: Auchenorrhyncha)* (ed. by W. Holzinger and F. Gusenleitner), pp. 103–112. *Denisia* 4, zugleich Kataloge des OÖ. Landesmuseums Neue Folge 176, Linz, Austria.
- Evenhuis, N.L. & Samuelson, G.A. (2004) The Insect and Spider Collections of the World website (updated 10 June 2004). <http://hbs.bishopmuseum.org/codens/codens-r-us.html>.
- Fennah, R.G. (1973) The cavernicolous fauna of Hawaiian lava tubes. 4. Two new blind *Oliarus* (Fulgoroidea Cixiidae). *Pacific Insects*, **15**, 181–184.
- Funk, V.A. (1995) Cladistic methods. *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago* (ed. by W. L. Wagner and V. A. Funk), pp. 30–38. Smithsonian Institution, Washington, DC.
- Funk, V.A. & Wagner, W.L. (1995) Biogeographic patterns in the Hawaiian Islands. *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago* (ed. by W. L. Wagner and V. A. Funk), pp. 379–419. Smithsonian Institution, Washington, DC.
- Giffard, W.M. (1925) A review of the Hawaiian Cixiidae, with descriptions of species (Homoptera). *Proceedings of the Hawaiian Entomological Society*, **6**, 1–121.
- Gillespie, R.G. & Croom, H.B. (1995) Comparison of speciation mechanisms in web-building and non-web-building groups within a lineage of spiders. *Hawaiian Biogeography. Evolution*

on a Hot Spot Archipelago (ed. by W. L. Wagner and V. A. Funk), pp. 121–146. Smithsonian Institution, Washington, DC.

Hoch, H. & Howarth, F.G. (1989) Six new cavernicolous cixiid planthoppers in the genus *Solonaima* from Australia (Homoptera Fulgoroidea). *Systematic Entomology*, **14**, 377–402.

Hoch, H. & Howarth, F.G. (1993) Evolutionary dynamics of behavioral divergence among populations of the Hawaiian cave-dwelling planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae). *Pacific Science*, **47**, 303–318.

Hoch, H. & Howarth, F.G. (1999) Multiple cave invasion by the species of the cixiid planthopper *Oliarus* in Hawaii. *Zoological Journal of the Linnean Society*, **127**, 453–475.

Hoch, H. & Remane, R. (1985) Evolution und Speziation der Zikaden-Gattung *Hyalesthes* Signoret, 1865 (Homoptera Auchenorrhyncha Fulgoroidea Cixiidae). *Marburger Entomologische Publikationen*, **2**, 1–427.

Holzinger, W.E. (2002) A review of the European planthopper genus *Trirhacus* and related taxa, with a key to the genera of European Cixiidae (Hemiptera: Fulgoromorpha). *European Journal of Entomology*, **99**, 373–398.

Holzinger, W.E., Emeljanov, A.F. & Kammerlander, I. (2002) The family Cixiidae Spinola 1839 (Hemiptera: Fulgoromorpha) – a review. *Zikaden. Leafhoppers, Planthoppers and Ciadas (Insecta: Hemiptera: Auchenorrhyncha)* (ed. by W. Holzinger and F. Gusenleitner), pp. 113–138. Denisia 4, zugleich Kataloge des OÖ. Landesmuseums Neue Folge, 176. Linz, Austria.

Howarth, F.G. (1972) Cavernicoles in lava tubes on the island of Hawaii. *Science*, **175**, 325–326.

Howarth, F.G. & Mull, W.P. (1992) *Hawaiian Insects and Their Kin*. University of Hawai'i Press, Honolulu, Hawai'i.

Kirkaldy, G.W. (1902) Hemiptera. *Fauna Hawaiiensis* (ed. by D. Sharp), Vol. III, 2, pp. 93–174, pls 4–5. Cambridge University Press, Cambridge.

Kirkaldy, G.W. (1909) A conspectus of the Fulgoridae of the Hawaiian Hemiptera. *Proceedings of the Hawaiian Entomological Society*, **2**, 75–81.

Kramer, J.P. (1981) Taxonomic study of the planthopper genus *Cixius* in the United States and Mexico (Homoptera: Fulgoroidea: Cixiidae). *Transactions of the American Entomological Society*, **107**, 1–68.

Kramer, J.P. (1983) Taxonomic study of the planthopper family Cixiidae in the United States (Homoptera: Fulgoroidea). *Transactions of the American Entomological Society*, **109**, 1–58.

Krauss, N.L.H. (1945) Notes on some Hawaiian insects. *Proceedings of the Hawaiian Entomological Society*, **12**, 309–317.

Liebherr, J.K. (1997) Dispersal and vicariance in Hawaiian platynine Carabid beetles (Coleoptera). *Pacific Science*, **51**, 424–439.

Liebherr, J.K. & Zimmerman, E.C. (2000) *Insects of Hawaii*, Vol. 16. *Hawaiian Carabidae (Coleoptera), Part 1: Introduction and Tribe Platynini*. University of Hawai'i Press, Honolulu, Hawai'i.

Moore, J.G. & Clague, D.A. (1992) Volcano growth and the evolution of the island of Hawai'i. *Geological Society of America Bulletin*, **104**, 1471–1484.

Muir, F.A.G. (1931) Descriptions and record of Fulgoroidea from Australia and the South Pacific Islands, 1. *Records of the Australian Museum*, **18**, 63–83.

O'Brien, L.B. & Wilson, S.W. (1985) Planthopper systematics and external morphology. *The Leafhoppers and Planthoppers* (ed. by L. R. Nault and J. G. Rodriguez), pp. 61–102. John Wiley & Sons, Inc., Chichester.

Price, J.P. & Elliott-Fisk, D. (2004) Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. *Pacific Science*, **58**, 27–45.

Remane, R. (1968) Ergänzungen und kritische Anmerkungen zu der Heteropteren- und Cicadinen-Fauna der Makaronesischen Inseln. *Bocagiana, Funchal*, **16**, 1–14.

Remane, R. & Asche, M. (1979) Evolution und Speziation der Gattung *Cixius* Latreille 1804 (Homoptera Auchenorrhyncha Fulgoromorpha Cixiidae) auf den Azorischen Inseln. *Marburger Entomologische Publikationen*, **1**, 1–264.

Soulier-Perkins, A. (2005) Phylogenetic evidence for multiple invasions and speciation in caves: the Australian planthopper genus *Solonaima* (Hemiptera: Fulgoromorpha: Cixiidae). *Systematic Entomology*, **30**, 281–288.

Swezey, O.H. & Bryan, E.H. Jr (1929) Further notes on the forest insects of Molokai (Hawaii). *Proceedings of the Hawaiian Entomological Society*, **7**, 293–314.

Wagner, W.L., Herbst, D.R. & Sohmer, S.H. (1999) *Manual of the Flowering Plants of Hawai'i (Revised Edition)*, Vol. 1 and 2. Bishop Museum Special Publication 97. University of Hawai'i Press, Bishop Museum Press, Honolulu, Hawai'i.

Zimmerman, E.C. (1948) *Insects of Hawaii*. Vol. 4. *Homoptera: Auchenorrhyncha*. University of Hawai'i Press, Honolulu, Hawai'i.

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Appendix 1. Character matrix for *Iolania* species and selected outgroup taxa. Character states 0 and 1 polarized relative to outgroup; state ? is unknown.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>Pentastiridius leporinus</i>	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
<i>Cixius nervosus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Iolania clypealis</i>	1	0	1	0	1	1	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?
<i>Iolania vittipennis</i>	0	0	1	0	0	1	0	?	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?
<i>Iolania kraussohana</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>Iolania mauiensis</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0
<i>Iolania lanaiensis</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0
<i>Iolania koolauensis</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0
<i>Iolania oahuensis</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0
<i>Iolania perkinsi</i>	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0