

A Review of the Systematics of Hawaiian Planthoppers (Hemiptera: Fulgoroidea)¹

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ABSTRACT: With 206 endemic species, the phytophagous Fulgoroidea, or planthoppers, are among the most important elements of the native Hawaiian fauna. These principally monophagous or oligophagous insects occur in nearly all Hawaiian terrestrial ecosystems. Species of two of the 18 planthopper families occurring worldwide have successfully colonized and subsequently radiated in Hawai'i. Based on collections made mainly by Perkins, Kirkaldy, Muir, Giffard, and Swezey, more than 95% of these species were described in the first three decades of this century. The systematics of the Hawaiian planthoppers has changed little in the past 60 yr and is not based on any phylogenetic analyses. This paper attempts a preliminary phylogenetic evaluation of the native Hawaiian planthoppers on the basis of comparative morphology to recognize monophyletic taxa and major evolutionary lines. The following taxa are each descendants of single colonizing species: in Cixiidae, the Hawaiian *Oliarus* and *Iolania* species; in Delphacidae, *Aloha* partim, *Dictyophorodelphax*, *Emoloana*, *Leialoha* + *Nesothoe*, *Nesodryas*, and at least four groups within *Nesosydne*. Polyphyletic taxa are the tribe "Alohini," *Aloha* s.l., *Nesorestias*, *Nesosydne* s.l., and *Nothorestias*. Non-Hawaiian species currently placed in *Iolania*, *Oliarus*, *Aloha*, *Leialoha*, and *Nesosydne* are not closely allied to the Hawaiian taxa. The origin of the Hawaiian planthoppers is obscure. The Hawaiian *Oliarus* appear to have affinities to (North) American taxa.

ALTHOUGH THE HAWAIIAN ISLANDS are the most isolated islands on earth, they house a remarkably rich flora and fauna. The more than 5000 recorded native insect species are predominant components of the Hawaiian biota (see Nishida 1994). This fauna is assumed to have derived from only 400 primary colonizing species (Howarth 1990). Several groups of Hawaiian insects have been studied in great detail (summarized in Wagner and Funk 1995), such as the Drosophilidae, which have been the focus of studies on genetics, evolutionary biology, molecular evolution, population ecology, and biogeography (e.g., Carson and Kaneshiro 1976, Kaneshiro 1976, Carson and Templeton 1984, Carson 1987, DeSalle and Hunt 1987).

Other groups of Hawaiian insects have received far less attention, although they are speciose and ecologically, as well as behaviorally, highly differentiated from each other. The Hawaiian planthoppers (Fulgoroidea) represent one such neglected group. Although initially recorded from the Hawaiian Islands more than 100 yr ago, little is known about their biology, ecology, and evolution.

Over 95% of the 206 currently recognized native Hawaiian planthopper species were described in the first three decades of this century. The first phase of planthopper research was based on the contributions of R. C. L. Perkins and G. W. Kirkaldy. In the beginning of this century, Perkins was the first to collect substantial numbers of planthoppers on all major Hawaiian islands. He also made valuable observations on their ecology and distribution, which were later published in *Fauna Hawaiiensis* (Kirkaldy 1902, 1910, Perkins 1913). Before his death in 1910, Kirkaldy had described 72 endemic

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Hawaiian planthopper species and established seven genera (for complete references see Zimmerman [1948]).

The second phase of Hawaiian planthopper research relied upon the important contributions of F. Muir and W. Giffard. Between 1916 and 1922, Muir described 82 new endemic species and one endemic genus of Delphacidae (e.g., Muir 1916; further references in Zimmerman [1948]). Soon after, Giffard revised the Hawaiian Cixiidae, describing 44 new species and subspecies (Giffard 1925). Zimmerman (1948) summarized these contributions in *Insects of Hawaii*. Only seven endemic Hawaiian delphacids (Swezey 1937, Zimmerman 1948, 1952, Beardsley 1956, 1960, Asche in press *a*) and two cixiids (Fennah 1973) have been described in the past 70 yr.

The lack of scientific interest in the systematics and evolution of planthoppers is difficult to understand, particularly because these phytophagous, sap-feeding insects are ubiquitous in nearly all Hawaiian terrestrial ecosystems. Most native Hawaiian planthoppers have been reported as oligophagous or monophagous on native Hawaiian plant species, mostly on ferns and woody dicots (see, e.g., Giffard 1917, 1922, Zimmerman 1948, Swezey 1954). In the native Hawaiian flora, over 70 plant genera with several endemic species were reported as hosts of planthoppers, ranging from tree ferns (e.g., *Cibotium*, *Sadleria*), native grasses (e.g., *Eragrostis*, *Sporobolus*, *Vincentia*), and palms (*Pritchardia*) to herbs including the endangered silverswords, vines, shrubs, and trees (e.g., *Argyroxiphium*, *Dubautia*, *Freycinetia*, *Styphelia*, *Metrosideros*, *Acacia*) (e.g., Zimmerman 1948). Some of the introduced planthopper species are important pests of crops in Hawai'i, especially the Australasian delphacid *Perkinsiella saccharicida* Kirkaldy on sugarcane (see references in Zimmerman [1948]).

The current classification of Hawaiian planthoppers differs little from that employed by Zimmerman (1948), who largely followed Kirkaldy (1910), Muir (1915), and Giffard (1925). The supraspecific taxa (genera, tribes) are based on diagnostic characters mostly used in keys. In the following, I survey the current state of planthopper systematics and propose a preliminary phy-

logenetic analysis of the Hawaiian planthoppers. My review is an effort to reactivate systematic research on this group and suggest future research needs.

Review of the Hawaiian Planthoppers

Although the Fulgoroidea are diverse and speciose, with 18 families worldwide with over 15,000 species, only a small fraction reached Hawai'i and then successfully colonized and radiated there. Only the Cixiidae and the Delphacidae are present in the native Hawaiian fauna. The Hawaiian species represent only 1.5% of all planthopper species, but about 95% of these are endemic. The most comprehensive compilation of data on Hawaiian auchenorrhynchous Homoptera was published by Zimmerman (1948) in *Insects of Hawaii*, nearly 50 yr ago. The most recent listing is Nishida's (1994) Hawaiian terrestrial arthropod checklist, where the following numbers are given: 88 endemic taxa (63 species and 25 subspecies) of Cixiidae, 145 endemic taxa (143 species, 2 subspecies) of Delphacidae, and 13 mostly adventive nonendemic planthopper species (i.e., Delphacidae [9 species; see also Beardsley (1990)], Flatidae [2 species], and Derbidae [1 species]). Asche and Wilson (1989*a,b*) reported an additional immigrant delphacid species. In total, 219 planthopper species and 26 subspecies have been reported from Hawai'i. The thirteen adventive species are believed to have been introduced accidentally (e.g., Beardsley 1990); however, a few of them may actually be indigenous because they are widespread in the Pacific and on adjacent continents (e.g., the delphacids *Sogatella kolophon* (Kirkaldy), *Opiconsiva paludum* (Kirkaldy), and *Toya dryope* (Kirkaldy)).

The actual number of species of Hawaiian planthoppers is unknown, because of unsolved taxonomic problems and the lack of a modern survey. Most of the native species are known only from a few specimens from the type locality, and several are known from the holotype only.

Family CIXIIDAE

All 63 species and 25 subspecies of Hawaiian Cixiidae are endemic: *Oliarus* with 58 species

and 24 subspecies from all Islands, and *Iolania* with five species and one subspecies from all major Islands except Moloka'i (Table 1). Two *Oliarus* species are cavernicolous: both are troglolitic and were discovered by F. G. Howarth in lava tubes on Maui and Hawai'i Island (Fennah 1973). Hoch and Howarth (1993) mentioned at least four additional undescribed cave-dwelling *Oliarus* species, one from Moloka'i, two from Maui, and one from Hawai'i Island.

Genus *Oliarus*

The genus *Oliarus* must be regarded as polyphyletic because it is primarily based on the presence of five mesonotal carinae, a feature that is likely plesiomorphic and present in all members of the cixiid tribe Pentastirini. Despite the revisions of Van Stalle (e.g., 1986, 1987), the genus is still ill-defined. *Oliarus* s.l. species are known from all parts of the world: 133 species have been recorded from the Afrotropical Region (Van Stalle 1987), 51 species from North America (Mead and Kramer 1982), about 30 species from Central America and South America (e.g., Metcalf 1936), over 100 from the Oriental Region (e.g., Metcalf 1936), and nearly 30 from Australia (e.g., Metcalf 1936). Most palearctic species formerly assigned to *Oliarus* recently have been transferred to other genera (e.g., Emeljanov 1971). From oceanic islands in the Pacific (besides Hawai'i) 18 *Oliarus* species have been recorded from the Marquesas Islands, 2 species from the Society Islands, 1 species each from the Austral and Cook Islands (all Fennah [1958]), and 5 species from the Galápagos Islands (Fennah 1967).

My studies have shown that the Hawaiian *Oliarus* species are *not* closely related to other Pacific Cixiidae currently placed in *Oliarus*. This assumption is based on substantial morphological differences mainly of the male and female genitalia. Also, the Hawaiian species differ considerably in their morphology from the type species of *Oliarus*, *O. walkeri* Stål. According to the chaetotaxy of the posttarsi, the Hawaiian and most other Pacific taxa belong to the subtribe Pentastirina, whereas *O. walkeri* is in Oliarina.

The Hawaiian *Oliarus* species are most likely monophyletic. This is based on synapomorphies in external characters such as the configuration of the spines of the hind tarsi (first tarsal segment distally primarily with eight, second with seven rigid spines) and male genital characters (e.g., the special arrangement of primarily five spinose processes on the aedeagus; a short, stout, pointed process at the right dorsal apex of the perianthrium; a usually long and movable spinose process arising on the left side from the membranous transition between shaft and dorsally reflected distal part [= flagellum, phallus]; two rigid spines flanking the distal part at its middle; and a short rigid spine at the apex beneath the phallotreme). Other characters, such as carination of the vertex (fossette medially divided by carina versus nondivided), that were used by Giffard (1925) for separating five divisions within Hawaiian *Oliarus* are of limited value for phylogenetic reconstructions, because of inconsistencies even within the same species. It is likely that the ancestral colonizer had a clearly divided fossette, a common and likely plesiomorphic condition found in many non-Hawaiian Pentastirini. Many independent modi-

TABLE 1
NUMBER AND DISTRIBUTION OF CIXIIDAE IN HAWAII

CIXIIDAE	KAUA'I	O'AHU	MOLOKA'I	LĀNA'I	MAUI	HAWAII	TOTAL
<i>Iolania</i>	1 (0)	4 (2)	—	2 (0)	1 (1)	1 + 1* (0 + 1*)	5 + 1*
<i>Oliarus</i>	17 (15)	24 + 11* (17 + 10*)	13 + 3* (1 + 1*)	4 + 1* (0 + 0*)	14 + 5* (5 + 2*)	13 + 7* (6 + 6*)	58 + 24*
Σ total (Σ island endemics)	18 (15)	28 + 11* (19 + 10*)	13 + 3* (1 + 1*)	6 + 1* (0 + 0*)	15 + 5* (6 + 2*)	14 + 8* (6 + 6*)	63 + 25*

NOTE: In parentheses: number of species/subspecies endemic to the particular island; subspecies indicated by asterisk.

fications of this feature may have occurred in the Hawaiian taxa as well as in other lineages of *Oliarus*. This indicates that this character is not suitable for assessing the monophyly of the Hawaiian taxa.

The ancestor of the Hawaiian *Oliarus* could have reached Hawai'i from North America, as suggested for the mirid bugs of the genus *Sarona* (Heteroptera) (Asquith 1995). Similarities in the morphology of the female genitalia (the laterally dilated and flattened anal segment) suggest affinities with certain nearctic taxa (e.g., *Oliarus hesperius* Van Duzee). Support for this suggestion regarding the origin of the Hawaiian *Oliarus* will require a comprehensive phylogenetic evaluation of this genus and related cixiid taxa.

Genus *Iolania*

The genus *Iolania* belongs to the widely distributed tribe Cixiini. It contains five species and one subspecies from Hawai'i, and two species from Australia (Muir 1931, Zimmerman 1948). Examination of the two Australian *Iolania* species from Queensland has shown that neither is closely related to the Hawaiian *Iolania*, as noted by Zimmerman (1948). The Australian "*Iolania*" are also morphologically very different from each other and most likely represent two different evolutionary lines. Thus, *Iolania* is geographically confined to the Hawaiian Islands.

The relationship of *Iolania* to other cixiids is difficult to determine because most features appear to be plesiomorphic. The five species are so closely related to one another that they certainly originated from a single ancestral species; thus, as a group they can be considered "island-monophyletics."

There appear to be no close relatives of *Iolania* in the faunas of the Pacific Islands, Australia, Asia, or North America and South America. *Iolania* has undergone little speciation compared with *Oliarus* on the Hawaiian Islands. Whether or not this fact suggests a relatively recent introduction, or whether it may indicate less potential for explosive speciation, cannot be decided.

Family DELPHACIDAE

Determining evolutionary lineages in the endemic Hawaiian Delphacidae is complicated

by the likelihood of multiple invasions of ancestral taxa that underwent subsequent radiation. A total of 153 species and 2 subspecies of delphacids has been found in Hawai'i; 143 species (93.5%) are endemic. These species have been included in 10 genera: *Aloha* with 9 species from all major islands including Ni'ihau; *Dictyophorodelphax* with 5 species from all islands except Moloka'i and Hawai'i; *Emoloana*, the former Hawaiian *Kelisia* species (Asche in press a), with 6 species and 1 subspecies from all islands; *Leialoha* with 12 species from all islands; *Nesodryas* with 2 species from O'ahu and Hawai'i; *Nesorestias* with 2 species from O'ahu; *Nesosydne* with 82 species and 1 subspecies from all islands; *Nesothoe* with 23 species from all islands; and *Nothorestias* with 2 species from O'ahu (Table 2). Ten immigrant delphacid species have been recorded from Hawai'i (Asche and Wilson 1989a,b, Beardsley 1990): the four pest species *Peregrinus maidis* (Ashmead) (the corn delphacid), *Perkinsiella saccharicida* (the sugarcane delphacid), *Tarophagus colocasiae* (Matsumura) and *Tarophagus proserpina* (Kirkaldy) (taro planthoppers), and, further, *Megamelus davisii* Van Duzee, *Opiconsiva paludum* (Kirkaldy), *Sardia rostrata pluto* (Kirkaldy), *Sogatella kolophon* (Kirkaldy), *Latistria eupompe* (Kirkaldy), and *Toya dryope* (Kirkaldy).

The Alohini Concept

All endemic Hawaiian Delphacidae, except for the six species of grass-feeding *Emoloana* (formerly *Kelisia*) species, have been placed in the tribe Alohini (Muir 1915). The diagnostic character used by Muir (1915) and subsequent workers (Zimmerman 1948, Fennah 1958) for this group is the shape of the posttibial spur, which is supposed to be solid, with both surfaces convex, and distinctly dentate along the posterior margin. Recent phylogenetic studies on Delphacidae (Asche 1985, 1990) have shown that the shape and dentation of the spur is quite variable, and is of little value as a feature for discriminating the higher delphacids. The spur of the "alohine" species is similar to that of many other delphacids and provides no obvious autapomorphy for the Alohini. It seems likely that in many delphacid taxa an "alohine" spur

TABLE 2
NUMBER AND DISTRIBUTION OF ENDEMIC AND IMMIGRANT DELPHACIDAE IN HAWAII

DELPHACIDAE	KAUA'I	O'AHU	MOLOKA'I	LĀNA'I	MAUI	HAWAII	TOTAL
Endemic							
<i>Aloha</i>	3 (0)	9 (6)	2 (0)	2 (0)	1 (0)	3 (0)	9
<i>Dictyophorodelphax</i>	1 (1)	2 (2)	—	1 (1)	1 (1)	—	5
<i>Emoloana</i>	2 (1)	4 (2)	1 (0)	1 (0)	2 (0)	3+1 (1+1)	6 + 1*
<i>Leiahola</i>	8 (4)	4 (0)	3 (0)	3 (1)	3 (0)	4 (1)	12
<i>Nesodryas</i>	—	1 (1)	—	—	—	1 (1)	2
<i>Nesorestias</i>	—	2 (2)	—	—	—	—	2
<i>Nesosydne</i>	9 (4)	29 + 1* (21 + 0*)	8 (3)	5 (4)	37 (26)	21 + 1* (10 + 0*)	82 + 1*
<i>Nesothoe</i>	9 (6)	10 (6)	1 (0)	7 (0)	3 (1)	7 (0)	23
<i>Nothorestias</i>	—	2 (2)	—	—	—	—	2
Σ total (Σ island endemics)	33 (16)	63 + 1* (42 + 0*)	15 (3)	15 (6)	47 (28)	38 + 2* (15 + 1*)	143 + 2*
Immigrant							
<i>Latistria</i>	1	1	—	—	—	1	1
<i>Megamelus</i>	—	1	—	—	—	—	1
<i>Opiconsiva</i>	—	1	1	—	—	1	1
<i>Peregrinus</i>	1	1	1	1	1	1	1
<i>Perkinsiella</i>	1	1	1	1	1	1	1
<i>Sardia</i>	1	1	—	—	—	1	1
<i>Sogatella</i>	1	1	1	1	1	1	1
<i>Tarophagus</i>	1	2	1	—	1	1	2
<i>Toya</i>	—	1	—	—	—	—	1
Σ total immigrant species per island	6	10	5	3	4	7	10

NOTE: In parentheses: number of species/subspecies endemic to the particular island (the single record of an *Aloha* species from Ni'ihau is not included); subspecies indicated by asterisk.

evolved independently, possibly to enhance walking on particular surfaces (e.g., on woody substrates).

In other morphological features, especially in male genital characters, "alohine" delphacids are remarkably diverse. None of these characters, however, could be interpreted as synapomorphic for the taxa summarized here. Thus, it has been hypothesized that the "Alohini" are polyphyletic (Asche 1985). All "alohine" taxa belong to the monophyletic tribe Delphacini (Asche 1985, 1990) and within this tribe to a highly derived monophyletic subgroup with specialized oviduct glands (for their morphology see Strübing 1956a,b). Accordingly, the "Alohini" do not form a distinct natural group of species *sensu* Muir (1915), but represent several lineages.

Monophyletic Groups

The endemic Hawaiian Delphacidae represent a rather heterogeneous array of morphologi-

cally different taxa. The eight "alohine" genera were separated from each other mainly by antennal proportions and carination of the frons. In fact, these genera were so broadly defined that several non-Hawaiian species from the Marquesas, Society, and Austral Islands, Rapa Island, the Galápagos, and the Seychelles Islands were placed in them (Fennah 1955, 1957, 1958, 1964, 1967). All non-Hawaiian species assigned to the Hawaiian genera *Aloha*, *Leialoha*, *Nesodryas*, and *Nesosydne* are *not* closely related to each other, nor to the Hawaiian taxa; thus they are not congeneric but represent quite different evolutionary lines.

No synapomorphy could be found to unite the Hawaiian "alohine" delphacid genera. The characters given by Zimmerman (1948) provide no clear means for constructing a phylogenetic classification. A similar variety of external characters found in many other modern Delphacidae most likely represent homoplasies. These characters have limited value for phylogenetic reconstruction; however, in combination with gen-

italic characters some of these external “diagnostic” characters may be of value.

The major evolutionary lines of the native Hawaiian Delphacidae are represented by the following monophyletic groups:

Emoloana. The species of *Emoloana* are the only grass-feeding native Hawaiian delphacids. Monophyly was based on features of the antennae in combination with genital characters (Asche, in press *a*).

Aloha PARTIM. The nine Hawaiian species of *Aloha* form three different morphological groups: the *A. artemisiae* group with four species, the *A. ipomoeae* group with four species, and *A. swezeyi* Muir. These groups differ in the shape of the aedeagus, especially in number and position of teeth or spines, and in the presence or absence of basal processes. The *A. artemisiae* group appears to be monophyletic on the basis of a specialized aedeagus with pointed tip. It is possible that *Nesorestias filicicola* Kirkaldy and *Nothorestias swezeyi* Muir also belong here. Although the *A. ipomoeae* group appears to have affinities to taxa of *Nesosydne* s.l. (e.g., *N. anceps* Muir), *A. swezeyi* also has similarities with certain species of *Nesosydne* s.l. (e.g., *N. naenae* Muir) and possibly with *Nesorestias nimbata* (Kirkaldy). Thus, the genus *Aloha* as previously defined is polyphyletic, and only part is monophyletic.

Dictyophorodelphax. This small group of five species appears to be homogeneous in their morphology and in their association with native *Chamaesyce* (*Euphorbia*) species. The male genitalia appear to be unique among the Hawaiian delphacids. It has been argued that *Dictyophorodelphax* might be a “local segregate of one of *Nesorestias*- or *Nesosydne*-like groups” (Zimmerman 1948) based on a tendency for head prolongation as in *Nesosydne leahi* (Kirkaldy). The genitalia of *N. leahi* are quite different from those of the *Dictyophorodelphax* species, and head prolongation apparently has arisen several times in various groups of Delphacidae. There appears to be no close relationship of *Dictyophorodelphax* to other Hawaiian taxa.

Leialoha + *Nesothoe*. These two genera include 35 species found on all major islands. These genera differ in having either one (*Nesothoe*) or two (*Leialoha*) median frontal carinae. Monophyly of these two genera is based on the

elongate aedeagus bearing one to three terminal spinose processes or teeth and the distally constricted tegmina. It is likely that the Hawaiian Islands were colonized by a single ancestral species and that separation subsequently occurred. Presence of a single median frontal carina is plesiomorphic in adult Delphacini. Delphacid nymphs have two median frontal carinae that apparently are retained in the adults of some genera (e.g., *Achorotile* Fieber and *Pseudaraeopus* Kirkaldy [Muir 1915, Asche 1985]). If the paired frontal median carinae of *Leialoha* arose through paedomorphosis, then it is more likely that a species ancestral to *Nesothoe* colonized the Hawaiian Islands. This conclusion contradicts Zimmerman’s statement that *Nesothoe* “is derived from *Leialoha*” (Zimmerman 1948: 146). If *Leialoha* is considered monophyletic based on paired frontal carinae as autapomorphic, then *Nesothoe* becomes paraphyletic unless there is a sister-group relationship between these taxa.

Nesodryas. This genus includes two species confined to Hawai‘i: *N. freycinetiae* Kirkaldy (type species) from O‘ahu and *N. swezeyi* Zimmerman from Hawai‘i Island (Asche in press *b*). Synapomorphic characters supporting monophyly include carination of the head, configuration of the posttibial spines, structures of the male genitalia, and a specialized anal style in females (Asche in press *b*). They represent a separate evolutionary line resulting from an independent primary invasion. The origin of the ancestral species is unclear.

Nesosydne PARTIM. This genus of 82 species and 1 subspecies is represented on all islands and comprises a morphologically heterogeneous array of taxa. Not a single character was found that could be interpreted as synapomorphic for all Hawaiian *Nesosydne* species. Thus, *Nesosydne* must be treated as polyphyletic. It is likely that the Hawaiian *Nesosydne* are descendants of several colonizing species. *Nesosydne* s.l. contains at least six morphological groups, each of which may be monophyletic; four of these groups could have been derived from independent colonizing species. The following morphological groups are based on genital characters:

(1) *Nesosydne koae* group. This group consists of four species that feed on *Acacia koa*: *N. koae* Kirkaldy (type species of *Nesosydne*), *N.*

koaephyllodii Muir, *N. pseudorubescens* Muir, and *N. rubescens rubescens* Kirkaldy (*N. r. rubescens* and *N. r. pele* (Kirkaldy)). Synapomorphic characters are found in structures of the aedeagus, styles, and the diaphragm.

(2) *Nesosydne gunnerae* group. This group includes *N. gunnerae* Muir, *N. amaumau* (Muir), *N. nesogunnerae* Muir, *N. painiu* (Muir), *N. perkinsi* Muir, and possibly *N. ahinahina* (Muir). A synapomorphy within these species is the strongly bent aedeagus. The *N. gunnerae* group is not closely related to the *N. koea* group, and vice versa, because of differences in the male genitalia (anal segment, the shape and direction of the aedeagus, and location of the phallosome).

(3) *Nesosydne cyathodis* group. This group consists of five species: *N. cyathodis* Kirkaldy, *N. eeke* (Muir), *N. fullawayi* (Muir), *N. lanaiensis* (Muir), and *N. nigrinervis* (Muir). The latter four were originally described as subspecies of *N. cyathodes* (Muir 1917, 1919). The short, dorsally bent aedeagus without obvious teethlike structures serves as a uniting synapomorphy. Apparently, the species of this group underwent reduction of aedeagal processes. Although monophyletic, it is likely that it is derived from other Hawaiian *Nesosydne* and not from a separate primary colonizer.

(4) *Nesosydne asteliae* group. This group includes *N. asteliae* Muir, *N. rocki* Muir, and *N. timberlakei* Muir. Synapomorphies uniting this group are the ventrally curved aedeagus and the arrangement of aedeagal teeth.

(5) *Nesosydne* spp. incertae sedis. Additional morphological groups may be recognized. A group of 18 species has comparatively similar genital features to those of the species of the *N. koea* group and may belong there. If so, the *N. koea* group would comprise 25% of all Hawaiian *Nesosydne*. Another group of about 15 species around *N. aku* (Muir) has a straight aedeagus with distal spines or teeth. It is possible that part of *Aloha* (*A. artemisiae* and *A. ipomoeae* morphological groups) is related to these species. Another group of about six species around *N. imbricola* Kirkaldy has a short aedeagus flanked by two short, oblique rows of teeth. *N. sola* Muir and *N. gouldiae* Kirkaldy have an anal segment devoid of spines, but other structures are so different from each other that close rela-

tionships appear to be unlikely. The position of the remaining *Nesosydne* s.l. species is yet uncertain.

At the current stage of our knowledge, the Hawaiian *Nesosydne* s.l. cannot be linked to any morphologically similar forms in the Pacific or adjacent continental areas. The origin of the Hawaiian *Nesosydne* s.l. remains obscure. The male genitalia of most species are relatively simple and do correspond with the general morphological configuration of several other taxa of Delphacini such as some of the New World species of *Delphacodes* s.l. This suggests that, as in *Oliarus*, ancestors of the Delphacidae of the Hawaiian Islands originated from some American taxa. Unfortunately, the New World delphacid fauna requires a thorough revision before any phylogenetic conclusions can be made.

Polyphyletic Groups

In addition to *Nesosydne* s.l. and *Aloha* s.l., the genera *Nesorestias* and *Nothorestias* from O'ahu are not monophyletic. Synapomorphic features uniting the two species of *Nesorestias* and two species of *Nothorestias* could not be found; thus, these taxa are probably descendants of different groups within *Aloha* s.l. and *Nesosydne* s.l. and do not represent primary evolutionary lines. The monophyly of *Nothorestias* was doubted by Zimmerman (1948:166), who remarked that "each of its species has been derived from a different species group." Muir (1922) stated that *Nothorestias swezeyi* "comes nearer to *Nesorestias filicicola* Kirk. than it does to *Nothorestias badia* Muir, showing that the condition of the median frontal carina is not a good phylogenetic character." Although *Nesorestias nimbata* apparently has affinities to *Aloha swezeyi* (and species of *Nesosydne* s.l.), *Nesorestias filicicola* may have affinities to *Nothorestias swezeyi* Muir, and both to the *Aloha artemisiae* group. The position of *Nothorestias badia* Muir is still unclear.

Family FLATIDAE

Two immigrant species have been recorded from Hawai'i. *Siphanta acuta* (Walker), native

to Australia, was introduced to Hawai'i in the last century. A polyphagous species, it is now widespread in Australia, Tasmania, New Zealand, and on all major Hawaiian islands (e.g., Zimmerman 1948, Fletcher 1985, Nishida 1994).

Melormenis basalis Caldwell & Martorell, originally described from Puerto Rico (Caldwell and Martorell 1951), represents a fairly recent introduction to Hawai'i, where it has spread to all major islands except Lāna'i (Nishida 1994).

Family DERBIDAE

The only species of this family in Hawai'i is the adventive *Lamenia caliginea* (Stål), described from Tahiti and widespread on South Pacific islands. It is not mentioned in Zimmerman (1948) but is listed from Kaua'i in the Hawaiian terrestrial arthropod checklist (Nishida (1994).

DISCUSSION AND PERSPECTIVES

Our current knowledge on the biological diversity and systematics of the Hawaiian planthoppers can be summarized as follows.

In total, 219 planthopper species and 26 subspecies representing 4 families and 23 genera have been recorded from Hawai'i. Thirteen species are believed to have been accidentally introduced: 10 delphacid species with one species each in the genera *Perkinsiella* Kirkaldy, *Peregrinus* Kirkaldy, *Megamelus* Fieber, *Opiconsiva* Distant, *Sardia* Melichar, *Sogatella* Fennah, *Latistria* Huang & Ding, and *Toya* Distant, and two species in the genus *Tarophagus* Zimmerman; two flatid species in the genera *Siphanta* Stål and *Melormenis* Metcalf; one derbid species in the genus *Lamenia* Stål.

Two hundred six species have been recorded as endemic in Hawai'i and were placed in the following taxa: of a total of 63 species and 25 subspecies in Cixiidae, 5 species and 1 subspecies were assigned to *Iolania* Kirkaldy, and 58 species and 24 subspecies to *Oliarus* Stål; of a total of 143 species and 2 subspecies in Delphacidae, 9 species were placed in *Aloha* Kirkaldy, 5 species in *Dictyophorodelphax* Swezey, 6 spe-

cies and 1 subspecies in *Emoloana* Asche (in press a), 12 species in *Leialoha* Kirkaldy, 2 species in *Nesodryas* Kirkaldy, 2 species in *Nesorestias* Kirkaldy, 82 species and 1 subspecies in *Nesosydne* Kirkaldy, 23 species in *Nesothoe* Kirkaldy, and 2 species in *Nothorestias* Muir.

This study has revealed that the native Hawaiian planthoppers comprise the following well-supported monophyletic taxa:

1. Cixiidae: *Iolania* and *Oliarus*; the species of both genera are likely to be descendants of a single ancestral colonizer each. Although *Iolania* is isolated with no close relationships to the Australian "*Iolania*," affinities of the Hawaiian *Oliarus* to (North) American taxa appear likely.

2. Delphacidae: at least nine monophyletic groups (*Emoloana*, *Aloha* partim [the *A. artemisiae* group], *Dictyophorodelphax*, *Leialoha* plus *Nesothoe*, *Nesodryas*, *Nesosydne* partim [the *N. koae* group, the *N. gunnerae* group, the *N. cyathodes* group, and the *N. asteliae* group]). The species that could not be assigned to one of these monophyletic groups (*Aloha swezeyi*, *Aloha ipomoeae*, and a set of similar species; several morphologically unique species within the rest of *Nesosydne* [e.g., *N. sola* and *N. gouldiae*]) remain problematic. Clearly polyphyletic are the Alohini as a group, *Aloha* s.l., *Nesosydne* s.l., *Nesorestias*, and *Nothorestias*. Close phylogenetic relationships of Hawaiian delphacids to any other Pacific taxa could not be found; however, similarities in genitalic features suggest affinities to some (North) American *Delphacodes* s.l.

The biological information available for the Hawaiian planthoppers is limited to host-plant associations. The studies of Perkins (1913), Giffard (1917, 1922), and Swezey (1954) provided information on host-plant affiliations, but many of them require confirmation. Over 70 plant genera with several species have been listed as hosts of planthoppers, but very few of them have been observed as breeding plants. For many planthoppers, the host plant is unknown (Zimmerman 1948). Almost nothing is known about behavior, life cycles, the number of generations per year, parasites, parasitoids, predators, and their ecology in the broadest sense. Although Pipunculidae, Dryinidae, Strepsiptera, and Mymaridae have been observed to attack delphacid nymphs, adults, and eggs (Zimmerman 1948), specific

data on the effects of parasitism (especially of purposely introduced biological agents to control immigrant pest species such as *Perkinsiella saccharicida*) on native Hawaiian planthoppers are scarce or not available.

Some biological information was provided by a recent biosystematic and behavioral study on cavernicolous *Oliarus*: the seemingly widespread species *Oliarus polyphemus* from several lava tubes all over Hawai'i Island was found to be a complicated complex of several morphologically similar but behaviorally (in terms of their vibrational courtship signals) clearly different populations that seem to be reproductively isolated and thus could be considered as biological species. About eight such potential "acousto-species" have been found (Hoch and Howarth 1993).

Future research on Hawaiian planthoppers should address the following goals: first, a new survey of the Hawaiian planthoppers to determine the number of species present, their geographic distribution, host-plant associations, and their ecology; second, a phylogenetic analysis of the Hawaiian planthoppers and their relatives as basis for a new systematics, and for future evolutionary and biogeographical evaluation. The study should employ data from morphology, biosystematics, ecology, host-plant associations, behavior, population genetics, and molecular systematics.

This scientific work needs to be done as soon as possible because of the high vulnerability of the Hawaiian Island ecosystems. Most native Hawaiian planthoppers are stenoecious, apparently monophagous, and many seem to have very restricted population sizes. Many are limited in distribution because they are brachypterous and have poor dispersal abilities. These species will not survive if their natural habitat is disturbed or destroyed. Currently, the Hawaiian Islands face the highest extinction rate in the world. Many of the native Hawaiian planthoppers are probably in danger of extinction if measures for the protection of their habitats are not taken. Systematic studies on planthoppers are essential to describe their current diversity and their role in the Hawaiian biota. The results of these studies will lead to a better understanding of the various Hawaiian ecosystems and contrib-

ute substantially to developing strategies for their conservation.

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