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Review of the native Hawaiian leafhopper genus *Nesophrosyne* (Hemiptera: Cicadellidae: Deltocephalinae) with description of eight new species associated with *Broussaisia arguta* (Hydrangeaceae)

GORDON M BENNETT[1] & PATRICK M O'GRADY
University of California, Berkeley. Department of Environmental Science, Policy and Management, 137 Mulford Hall #3114 Berkeley, CA 94720, USA.
[1] *Corresponding author. E-mail: gbennett@berkeley.edu*

Abstract

A review of the native Hawaiian leafhopper genus *Nesophrosyne* (Hemiptera: Cicadellidae: Deltocephalinae) is presented. Specimens were examined from across the entire Hawaiian Archipelago, *Nesophrosyne* is redescribed, and the subgenus *Nesoreias* is synonymized with *Nesophrosyne*. Eight new species associated with the widespread host plant species *Broussaisia arguta* are described: *N. heopoko* **sp. n.** from Kaua'i; *N. makaihe* **sp. n.** from O'ahu; *N. magnaccai* **sp. n.** from Moloka'i; *N. broussaisiai* **sp. n.**, *N. ogradyi* **sp. n.**, and *N. kaupoi* **sp. n.** from Maui; and, *N. aakokohaikea* **sp. n.** and *N. kanawao* **sp. n.** from Hawai'i Island. Morphological and molecular characters were employed to delineate new species. Populations associated with *B. arguta* on different islands, individual volcanic mountains, and discrete geographic areas represent reciprocally monophyletic species. A monophyletic complex of five sibling species, morphologically cryptic on individual islands, were identified from Maui and Hawai'i Island. The *kanawao* species group is erected for these species and is further subdivided into two species subgroups based on monophyly, island endemicity, and morphology: *broussaisiai* species subgroup containing *N. broussaisiai, N. ogradyi,* and *N. kaupoi* on Maui; and, *aakokohaikea* species subgroup containing *N. aakokohaikea* and *N. kanawao* on Hawai'i Island.

Key words: Hawaiian Islands, Sibling Species, Biogeography, Taxonomy, Phylogeny, Endemism

Introduction

The native Hawaiian leafhopper genus *Nesophrosyne* Kirkaldy (1907) (Cicadellidae: Deltocephalinae: Opsiini) is a diverse and ubiquitous, yet understudied, element of the Hawaiian entomofauna. The native group currently comprises sixty-two described species (Kirkaldy 1907, 1910; Osborn 1935; Zimmerman 1948), distributed across the high islands of the archipelago (*e.g.*, Kaua'i – Hawai'i). The Hawaiian species are single island endemics, occurring in almost all habitat types from coastal scrub to sub-alpine regions (2500–3100 meters above sea level). Nearly all species are host plant specific, utilizing approximately 25% of the native Hawaiian plant genera, and 75% of the most species rich and ecologically dominant genera (*e.g.*, genera of the lobelloid group, *Myrsine, Hedyotis, Coprosma*: Kirkaldy 1907, 1910; Osborn 1935; Zimmerman 1948; Wagner *et al*. 1999).

Kirkaldy (1907) first described *Nesophrosyne* based on the presence of a large median anteapical cell and a small outer anteapical cell on the forewing. He later expanded the description to include more detail on forewing cell number and size, venation, and the relative size of the pronotum, which resulted in splitting the genus into two subgenera, *Nesophrosyne* and *Nesoreias* (Kirkaldy 1910). The latter subgenus being separated by the complete absence of the outer anteapical cell (Fig. 1). The shape of the outer anteapical cell is extremely plastic in size and presence, negating the subgeneric taxonomic classification. Unfortunately, Kirkaldy's treatments further complicated taxonomy within *Nesophrosyne* by issuing cursory descriptions of forty-one species. These descriptions, sometimes limited to only a few sentences, highlighted color and other variable traits and are inconsistently based on either males or females, which can show dramatic sexual dimorphism. Kirkaldy (1910) also neglected to provide illustrations and a key to these species.

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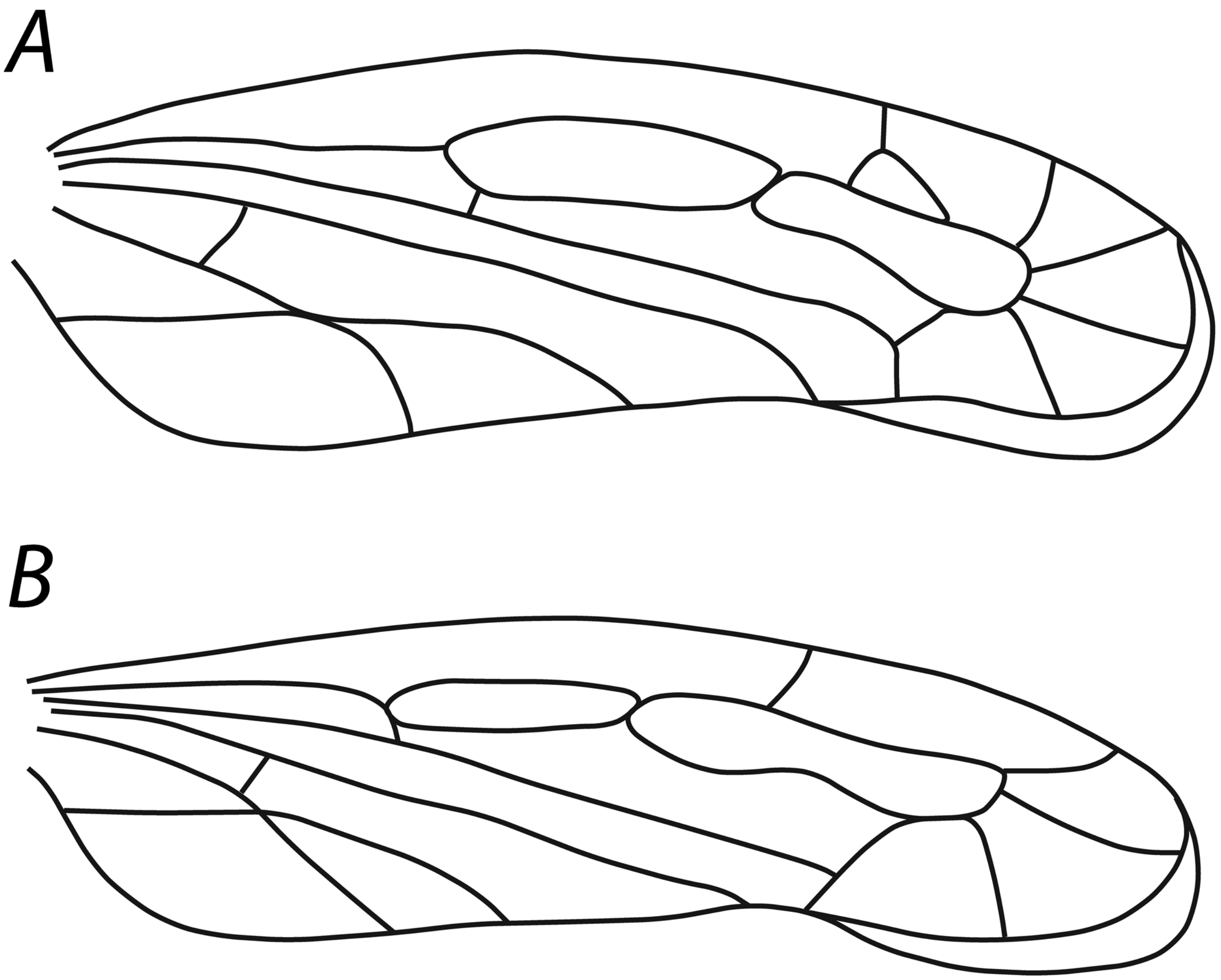

FIGURE 1. *Nesophrosyne* wing venation illustrating the variable outer anteapical cell. A) *Nesophrosyne (Nesophrosyne) perkinsi*, and B) *Nesophrosyne (Nesoreias) insularis*. Adapted from Kirkaldy (1948).

Osborn (1935) described twenty-one new species, and redescribed thirty-seven of the species originally proposed by Kirkaldy (1910). The redescriptions provide clarity to the taxonomic issues presented by the shortcomings of Kirkaldy's (1907, 1910) treatments. While Osborn's species descriptions are more comprehensive with excellent illustrations and discussion of phylogenetic relationships, their utility is somewhat limited. Osborn's (1935) descriptions were made from either females or males, focused on highly variable characters, failed to include internal genitalia, and did not provide a key to separate species (except for *Nesoreias*). Osborn's circuitous discussion on crown evolution and similarities in wing venation to *Scaphoideus*-like genera did not provide any further insight into morphological characters uniting species in *Nesophrosyne*.

Zimmerman (1948) synthesized previous work on *Nesophrosyne*, including for the first time, a short discussion of a bifurcate aedeagus with slender hooked apical processes and drawings of internal genitalic characters. Unfortunately, Zimmerman did not extend full descriptions of external or internal genitalia beyond the type species, offering only a single synonymy. He did provide an ambitious key to the *Nesophrosyne* species based largely on coloration and relative sizes, which is difficult to use in some cases. Cognizant of the challenges in treating *Nesophrosyne*, Zimmerman (1948) paused to presciently note of his key (and taxonomic state of the genus) that "*Nesophrosyne* [presents a] confusing natural complex of complexes I realize [the key is] difficult to use, and it may not work for all species or all specimens of a single species" Despite the difficulties, Zimmerman's (1948) treatment provides a good starting point for identifying Hawaiian *Nesophrosyne* and its species diversity.

Ghauri (1966), in a revision of the genus *Orosius* Distant, provided a more thorough genus level redescription of *Nesophrosyne*. He included a description of the internal genitalia in an attempt to resolve phylogenetic relationships between the genera and to establish their taxonomic status (see also Linnavuori 1960a, 1960b, 1975). However, Ghauri's (1966) redescription was restricted to the type species of the genus, and his treatment falls short of describing the morphological diversity found among *Nesophrosyne* species. For example, some characters used to delineate *Nesophrosyne* (*e.g.*, apical processes of the aedeagal arms) are variable or absent in some species, others are seemingly erroneous (*e.g.*, posterior processes of styles not hooked, and the convergence of gonoducts at base of aedeagus; see Figs. 4–6 & 8–9), and utilize antiquated terminology.

Other species outside of the Hawaiian Archipelago have been placed in the genus *Nesophrosyne* at various points. *Orosius ryukyuensis* Ishihara (1965) and *Orosius argentatus distans* Linnavuori (1960b) were described as members of *Nesophrosyne*. Linnavuori (1975) and Ghauri (1966) moved both species to *Orosius*, respectively. *Orosius filigranus* (Dlabola 1964) and *O. cellulosa* Lindberg (1958) were moved from *Thamnotettix* to *Nesophrosyne*, and were subsequently transferred to *Orosius* by Ghauri (1966). Linnavuori (1960a, 1960b) treated *Nesophrosyne*, synonymizing it with *Orosius* (even considering *Orosius* a subgenus of *Nesophrosyne*). However, Ghauri (1966) split the two genera back into their previous designations, which was later confirmed by Linnavouri (1975), removing all of the non-Hawaiian taxa from *Nesophrosyne*. Thus, the genus *Nesophrosyne* currently refers to the lineage endemic to the Hawaiian Archipelago.

Aside from Ghauri's (1966) generic level redescription, *Nesophrosyne* has remained untreated for over 60 years. Much remains to be understood, and previous work has left some taxonomic confusion that must be overcome in order to provide reliable species concepts and identification keys to species. *Nesophrosyne* needs to be more thoroughly circumscribed, with a complete description of the morphological variation present in the group with updated terminology. Species descriptions need to be made consistent. The mixed gender of Osborn's (1935) and Kirkaldy's (1910) descriptions and type specimens make positive identification of some species difficult. Described species need to be redescribed to include internal genitalia, which provide a more reliable suite of morphological characters for species determination. Moreover, *Nesophrosyne* is far more diverse than previous work suggests, with many species waiting description (Fig. 2: See Kaua'i, Maui, and Hawai'i). Once species have been more thoroughly treated, comprehensive, user-friendly keys need to be devised.

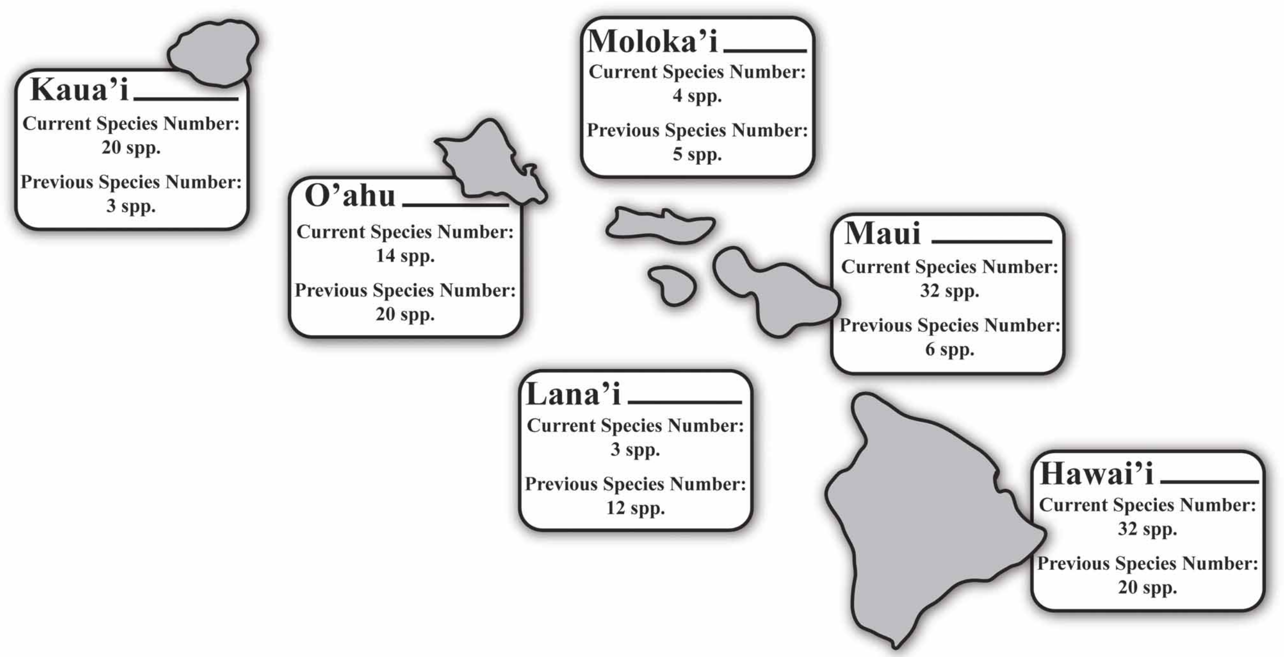

FIGURE 2. Hawaiian Islands. Boxes show per island estimates of the current number of species (*Current Species Number*) and the number of species previously described (*Previous Species Number*; Kirkaldy 1907, 1910; Osborn 1935; Zimmerman 1948).

Here, we provide a review of *Nesophrosyne* based on specimens collected from across the Hawaiian Islands. A redescription of the genus with updated terminology is included to encompass morphological variation in external and internal genitalic characters. We examined wing venation and molecular characters within *Nesophrosyne* and conclude that *N.* (*Nesoreias*) is a synonym of *N.* (*Nesophrosyne*). Finally, we use morphology, geography, and molecular tools to delineate and describe eight new species associated with the host plant *Broussaisia arguta*.

Material and methods

Taxonomy. Collection permits were obtained from the State of Hawai'i Department of Land and Natural resources, Division of Forestry and Wildlife for access to state lands and Natural Area Reserves; and from the National Park Service for access to Hawai'i Volcanoes National Park and Haleakala National Park. Permits were also obtained from the following private landowners: East Maui Irrigation, The Maui Land and Pineapple Company, and Parker Ranch.

Specimens were collected by sweep netting and placed directly into 95% ethanol. Specimens were field-sorted based on geographic collection locality and plant associations, and given a four-digit decimal collection barcode (*e.g.,* GB-006.7) for reference. Material was returned to U.C. Berkeley for identification, description, and molecular analyses (see below). Specimens were examined, photographed, and measured using Nikon SMZ1500 microscope with a DS-L1 imaging system. Wing venation was examined for all specimens collected from across the islands in an effort to assign species to a subgenus. Entire abdomens were removed, and a small cross section was saved in 95% ethanol for DNA extraction. Remaining abdominal segments were incubated overnight in 10% potassium hydroxide solution at room temperature. Cleared genitalia were placed in glycerin in plastic genitalia vials and pinned with specimens.

Species identities for fifty-two of the previously described species were determined. Thirty-two type specimens deposited in the Bernice P. Bishop Museum (BPBM), Honolulu, HI, were examined. The remaining types are in the British Museum. Twenty species, determined by Osborn, Zimmerman, Perkins, and other workers, were examined from the BPBM and U.H. Manoa Entomology Museum (UHM). The non-type material examined from the BPBM and UHM collections covers a majority of the type specimens deposited in the British Museum. In addition ~1500 specimens, including twenty-one described species and many undetermined species from D.A. Polhemus' personal collection were examined. The Polhemus material is on loan from the Smithsonian Institute, Washington D.C. The types of three species, *N. ignigena*, *N. nimbigena* and *N. insularis*, are missing (Osborn 1936; Zimmerman 1948) and were not examined, however specimens determined as these species by Perkins exist in the Bishop Museum and have been examined.

The *Nesophrosyne* type material has been treated twice (Osborn 1935; Zimmerman 1948), and the resultant published resources are adequate to determine specimens of newly collected material and to designate new species. Osborn's (1935) descriptions, redescriptions of Kirkaldy's types, and included drawings adequately treat the external morphology of all *Nesophrosyne* species, and are usable for species determinations. He failed to treat two type specimens in the British Museum, but Zimmerman (1948) reviewed them. Zimmerman (1948) later treated the Hawaiian *Nesophrosyne* and many of the type specimens, as well as synthesizing Kirklady's (1907, 1910) and Osborn's (1935) treatments. He accounted for each of the type specimens and their locations, and effectively redescribed them all by generating a workable master key and island-by-island keys to each of the species. Zimmerman (1948) also included photographs and drawings of nearly all of the described species and their types.

Collected specimens were identified to species using Zimmerman's (1948) key to the described species, and Osborn's (1935) comprehensive species treatments, with included redescriptions of nearly all of Kirkaldy's described species (1907, 1910). They were further compared against redescriptions and a key to the thirty-two species in the type collection at the BPBM (Bennett unpub). Species unable to be identified with these resources and representative of new ecological and host plant associations are considered to be new. Terminology for new species descriptions follows Dietrich (2005) based on Oman (1949), and Dietrich and Dmitriev (2007). Holotypes and a series of paratypes have been deposited in the BPBM, Honolulu, HI.

Molecular analyses. The molecular data and phylogenetic analyses presented here are preliminary results of a larger systematics research project, which will be published elsewhere. Molecular analyses are used to strictly reinforce morphological results and address the phylogenetic placement of species in the subgenus *Nesophrosyne* (*Nesoreias*), the polyphyly of species associated on *Broussaisia arguta*, and the cryptic nature and monophyly of the *kanawao* species group. Methodological details pertinent to the presented results are outlined below. Specific laboratory procedures and resultant data (*e.g.,* DNA extraction, PCR amplification, individual sequence data, etc.) will be published elsewhere.

Taxonomic sampling for molecular analyses include 107 *Nesophrosyne* terminals representing 75 endemic Hawaiian species, and three outgroups, *Nesophyla variata* Osborn, Nesophyla sp. and Deltocephalus sp., from the Marquesas Islands, French Polynesia. The island sampling distribution of Hawaiian *Nesophrosyne* is as follows: Kaua'i = 11 spp.; O'ahu = 19 spp.; Lana'i = 1 spp.; Moloka'i = 3 spp.; Maui = 24 spp.; Hawai'i = 17 spp.

Four genes, two mitochondrial (mtDNA: Cytochrome Oxidase II (COII) & 16S) and two nuclear (nucDNA: Histone 3 & Wingless), were used to reconstruct phylogenetic relationships in *Nesophrosyne*. Primer sequences were obtained from previous studies: COII, Takiya *et al*. 2006 ;16s, Dietrich *et al*. 1997; Histone 3, Ogden & Whiting 2003; and, Wingless, Cryan *et al*. 2004. The three protein-coding genes (COII, Histone 3, and Wingless) sequences were conceptually translated in MacClade (Maddison & Maddison 2003) and manually aligned against an annotated GenBank sequence. The 16S ribosomal dataset includes stems and loop regions that are non-trivial to align. To deal with this, we used Probalign v1.2. accessible through the CIPRES web portal (Miller *et al*. 2009), which optimizes pairwise posterior probabilities of sequence residues with a partition function approach (Roshan & Livesay 2005). Probalign was chosen based on its superior performance over other available alignment programs. Base pair positions for which statements of homology are questionable were removed from downstream analyses. The total concatenated data set was 1914 base pairs in length.

Uncorrected pair-wise distances for COII were estimated in PAUP* (Swofford 2002). COII was used as an alternative to the commonly used Cytochrome Oxidase I (COI) in assessing molecular divergence as further evidence for species hypotheses (Savolainen *et al*. 2005). Repeated attempts to sequence COI with previously published primer sequences (Simon *et al*. 1994) and multiple primer pairs designed for this study failed. Phylogenetic trees were constructed using Maximum Likelihood. Models of evolution were estimated in Modeltest 3.7 using the Akaike Information Criterion (Posada & Crandall 1998). Phylogenetic analyses were performed in RAxML-VI-HPC v7.2.5 on the Abe server accessible through Cipres Portal (Stamatakis 2006, 2008; Miller *et al*. 2009). Runs were performed with 100 bootstrap partitions under the GTR+I+Γ model of nucleotide substitution for two data partitions: mtDNA and nucDNA. Runs were restarted three times to confirm that searches converged on the same posterior optima.

Results and discussion

Nesophrosyne and *Nesoreias*

We examined wing venation in a total of 1085 specimens, in at least 107 distinct morphological species from across the Hawaiian Archipelago (See Appendix 1 for annotated list of species examined). The examined specimens confirm that wing venation is highly variable not only within the genus, but also within species and even single individuals. Presence of the outer anteapical cell is the most common state, however variation in the size, shape, and presence (in one or both wings) is common in large populations. In some rare instances, the cell is subdivided with individuals having up to four outer anteapical cells. The character's extreme variability demonstrates the lacking predictive, evolutionary functionality necessary to define a cohesive subgenera, or taxonomic grouping. Thus, the outer anteapical cell cannot be used to differentiate subgenera of *Nesophrosyne*.

Molecular phylogenetic analyses reveal *Nesoreias* as polyphyletic, falling out in at least three clades (data not shown). *Nesophrosyne eburneola* Osborn 1935 and *N. marginalis* Osborn 1935 are placed as sister species with high support, however *N. insularis* Kirkaldy 1910 and *N. sp.1* are nested well within two different clades with high support. The distribution of species with individuals without cells, with one cell, or with extreme size variation is random across the tree with high support for some groups. These molecular data, coupled with genus-wide morphological assessment, indicate that the subgenus *Nesoreias* is dubious and we synonymize it with *Nesophrosyne.*

Delimitation of new species associated with *Broussaisia arguta*

Broussaisiai arguta (Gaud. 1830) (Hydrangeaceae) belongs to a monotypic genus endemic to the Hawaiian Islands. It grows as a shrub predominately in wet forest habitats, ranging in elevation from 370m–2070m (Wagner *et al.* 1999). *Nesophrosyne* species are commonly found on *B. arguta* across the archipelago. Except for Hawai'i Island, no species have been documented or described exclusively from *B. arguta*. Zimmerman (1948) indicated a single collection of *Nesophrosyne pluvialis* Kirkaldy 1910 on *B. arguta* and two other hosts (*Coprosma sp*. and *Acacia koa*). *N. pluvialis* was redescribed as occurring on the genus *Coprosma* (Osborn 1935), and recent collections have found it only on *Coprosma sp.* from multiple collection localities and over several years (Bennett unpub). The collection record referred to by Zimmerman (1948) is likely a chance collection.

Nesophrosyne species collected from *B. arguta* do not match any described by Kirkaldy (1907, 1910) or Osborn (1935), are unable to be keyed (Zimmerman 1948; Bennett unpub), and are distinct from the type specimens redescribed by Osborn (1935) at the British Museum and Bennett (unpub) at the Bishop Museum. Examination of morphology combined with molecular results show eight unique species occurring on Kaua'i (1 sp.), O'ahu (1 sp.), Moloka'i (1 sp.), Maui (3 sp.), and Hawai'i (2 sp.). Species on Kaua'i, O'ahu, and Moloka'i are morphologically distinct from each other and from species on Maui and Hawai'i Island, indicating independent switches to *Broussaisiai arguta*. Species on Maui and Hawai'i Island show strong similarities for internal male genitalia (*e.g.,* the unique structure of the connective), supporting monophyly of this group. Populations occurring on different volcanic mountains on a single island (*e.g.,* Hawai'i Island: Kohala Range and Mauna Loa) are difficult to distinguish and morphologically cryptic, but do show subtle variation in external morphology, and in some cases in internal male genitalia (Maui: West Maui and East Maui Haleakalā leeward face). The species assemblages on Maui and Hawai'i are easily discernable from one another by external morphology and pigmentation (*e.g.*, Hawai'i Island species being darker). The species of the *broussaisiai* subgroup (Maui) can be separated by a combination of claval pigmentation and the reduced aedeagal processes in *N. kaupoi*. *Nesophrosyne broussaisiai* (West Maui) represents a darker form than *N. ogradyi* and *N. kaupoi* (East Maui). While there is some overlap in the species of the *aakokohaikea* species subgroup (Hawai'i Island), they can usually be separated by external claval pigmentation, as *N. kanawao* is generally paler than *N. aakokohaikea*.

Partitioned likelihood phylogenetic analyses (Fig. 3), combined with COII uncorrected pairwise distances (Table 1), provide strong support for species hypotheses. Results demonstrate that there are unique species on each island, with evidence for at least three switches to *B. arguta* as a host plant (see species descriptions for more detail). Species from Hawai'i Island and Maui represent a monophyletic lineage, with highly supported geographic sub-structuring (Fig. 3). Results confirm that geographically separated species co-occurring on single islands, although morphologically cryptic, are reciprocally monophyletic sister lineages. Uncorrected pairwise distances for COII (Table 1) demonstrate relatively high sequence divergence between these lineages: 4.2% – 11.24% (percent divergence within populations = 0.0% – 1.82%). These genetic breaks are separated according to volcano formation and unique geographic provenance (*e.g.,* Haleakalā leeward face, Maui), which conform to potential discontinuities in *B. arguta*, ecological, and climatological ranges.

Review of molecular evidence, morphology, and geography indicate that there are at least eight new species associated with *B. arguta*, described below. Molecularly distinct populations on Maui and Hawai'i Island, represent morphologically cryptic sibling species deserving of individual species demarcation (Bickford *et al.* 2006; de Queiroz 2007). We recognize sibling species for their important information about the biotic diversity and endemicity of the Hawaiian entomo-fauna, and to avoid future taxonomic confusion presented by cryptic species (Bickford *et al.* 2006).

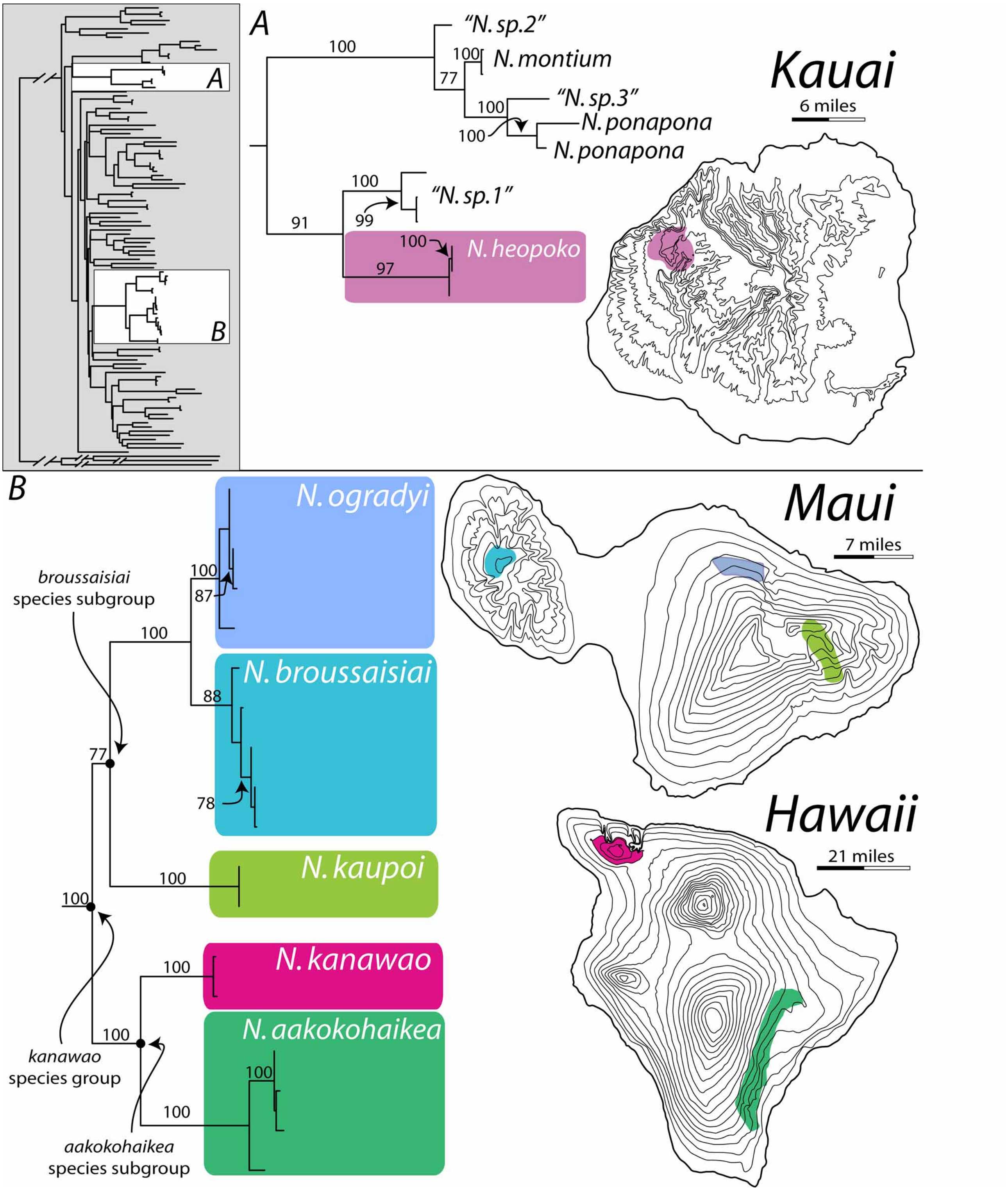

FIGURE 3. Partitioned Maximum Likelihood phylogeny of *Nesophrosyne* (Hemiptera: Cicadellidae) species reconstructed in RAxML-VI-HPC v7.2.5 under a GTR+I+Γ likelihood model with 100 bootstrap partitions. Gene partitions are according to the mitochondrial genome (COII, 16s) and nuclear genome (H3, Wingless). Subsections A & B highlight species relationships of newly described species occurring on the host plant *Broussaisia arguta*. A) Silhouette of full Maximum Likelihood phylogeny results. B) *Nesophrosyne heopoko's* associated with other species on Kaua'i. C) Relationships of the species within the *kanawao* species group on Maui and Hawai'i. The numbers above branches are bootstrap support values.

Taxonomy

Nesophrosyne Kirkaldy 1907: 160

Type species: *Euttetix perkinsi* Kirkaldy 1907: 160
Nesophrosyne (*Nesoreias*) Kirkaldy 1910: 573 **new synonymy**

Diagnosis. *Nesophrosyne* resembles other described genera in the tribe Opsiini, having a bifurcate aedeagus and two gonopores. The genus is most closely allied with *Orosius*, having two parallel aedeagal arms, curving posterodorsally; gonoducts arising independently from preatria at the base with gonopores usually subapical; styles with hooked posterior processes; the crown sometimes bluntly rounded, although often angularly produced and extended well beyond anterior edge of the eyes (*e.g.*, *N. anguilifera*); the outer anteapical cell in the forewing present and sometimes elongate relative to the central anteapical cell; and the forewing flecked in two species (*N. notatula* and *N. signatula*).

Nesophrosyne differs from *Orosius* and other opsiine genera in having the aedeagal arms with produced and hooked apical processes, varying from short-straight to long and recurving, but completely absent in some species; the body size larger (3.25mm – 5.5mm), with the smallest species overlapping with *Orosius* (2.63mm – 3.29mm); the frontoclypeus wide, but variable across species; the forewing often with extensive and distinct pale color patterning sometimes forming a solid saddle-like mark (*e.g.*, *N. pluvialis*); the pronotum and forewing without the brown stripes common in *Orosius*; the forewing with the outer anteapical cell reduced and sometimes absent, forming a small triangular structure with single R1 vein extending to the outer edge (some species with two); the subgenital plates tapering more gradually and remaining wider at the distal end, without an abrupt medial narrowing ledge and tube-like distal processes (*Orosius*); and the anal tube dorsally sclerotized and with lateral and ventral edges sclerotized.

Description. ***Dorsum*** (see Figs. 4–9): Small slight (3.25 mm) to large robust (5.5 mm) leafhoppers. Color and coloration patterns varying widely. Crown ranging from bluntly rounded to elongate and extremely produced. Ocelli visible in dorsal view, situated on margin of crown and face. Pronotum as wide as, or in some cases slightly wider than, head; anterior margin rounded, convex; posterior margin straight. Forewing with large central anteapical cell and smaller outer anteapical cell; central anteapical cell narrowed medially; outer anteapical cell variable in size and shape from nearly the length of the central anteapical cell to completely absent (varies within and between species). Clavus of many species with well-formed, conspicuous saddle mark (Fig. 7).

Venter: Frons and clypeus broad, width nearly 3/4 length; lateral margins not sinuate. Clypellus elongate, lateral margins subparallel.

Genitalia: Pygofer with 16 or fewer macrosete on posterior half of apical lobe, extending beyond posterior edge; fine stout microsete covering posterior half of apical lobes (Figs. 4–6b & 8–9b). Valve rounded, notched symmetrically on either side of posterior apex. Subgenital plate elongate, curved posterodorsad, tapering towards distal point; lateral edges hirsute from base to apex, with long filamentous and macrosete (usually 5) interspersed (not unique to this genus). Anal tube long, not fully membranous dorsally, with well sclerotized band; laterally and ventrally sclerotized. Aedeagus bifurcate with two aedeagal arms and gonopores; aedeagal arms curving posterodorsally, height of arms variable from sub-anal tube to terminating at the dorsal edge of pygofer; gonopore near apex, usually subapical, opening posteromesially; aedeagal arms with produced apical processes hooked anterolaterad, length from short-straight (~1/10 length of aedeagal arm) to long and recurving (~1/4–1/5 length of aedeagal arms), completely absent in some species; base of gonoducts not connected, forming two preatria; anterior base of aedeagus with apodeme pointed dorsad (Figs. 4–6c,f,g & 8–9c,f,g). Styles with well-developed posterior processes, curved posterolaterad; preapical lobe with fine microsete (Figs. 4–6e & 8–9e). Connective ‘Y’ shaped; body thinning medially, appearing hourglass shaped; anterior arms variably shaped and splayed (Figs. 4–6d & 8–9d).

Material examined. A total of 1085 specimens from at least 101 distinct morphological species were examined. Sampling from individual islands is as follows: Hawai’i Island, males = 232, females = 301, species = 32; Maui, males = 118, females = 93, species = 32; Lana’i, males = 1, females = 3, species = 3; Moloka’i, males = 18, females = 12, species = 4; O’ahu, males = 59, females = 37, species = 15; Kaua’i, males = 105, females = 106, species = 16.

Discussion. Despite intraspecifc variation in *Nesophrosyne*, color patterning offers useful characters for species identification (we refer readers to Zimmerman's (1948) well-illustrated review of *Nesophrosyne* for a photographic menagerie of the genus' external morphological diversity). However, external and internal genitalia provide a more reliable suite of morphological characters for species determination. These characters, combined with molecular data and species' geographic ranges, provide congruent lines of evidence for *Nesophrosyne* species and cryptic species groups. Results presented here provide evidence of cryptic sibling species, which may be common in other lineages associated with widespread host plants. Molecular characters may be necessary for identification of species within these groups.

Nesophrosyne's biogeographic origin and relationships to other Pacific cicadellid genera are currently unknown. Kirkaldy (1907, 1910) proposed a relationship to *Nephotettix*, but he did not explain the basis for this hypothesis. Osborn (1935) strongly argued for a *Scaphoideus*-like ancestor derived from either America or Asia, [colonizing] during the early history of life on the islands.

A plausible origin for the Hawaiian *Nesophrosyne* lineage is the genus *Orosius* found along the western Pacific Rim including Japan, Southeast Asia, and the Oceania region. Linnavuori (1960a, 1960b, 1975) first examined this relationship, and based on similarities in the bifurcate aedeagus, blunt crown and flecked forewing of some *Nesophrosyne* species, presence of an elongate outer anteapical cell, hollowing near the base of the antennae, and overlapping shape and size of the frontoclypeus of some species, he combined the genera with *Orosius* as a subgenus of *Nesophrosyne*. Ghauri (1966) later reexamined Linnavuori's conclusions, determining that morphological differences, including the anal tube structure, subgenital plate shape, divergence of frontoclypeus shape in some species, and hooking distal process found only in *Nesophrosyne* were sufficient to preserve *Nesophrosyne* and *Orosius* as separate genera. Linnavuori (1975) conceded, commenting that a thorough investigation of the biotic and morphological diversity of both genera is necessary to resolve the question. He further reiterated the opinion that *Nesophrosyne* originated from eastern Oceania. Both Ghauri (1965) and Linnavuori (1975) noted the presence of hooking apical processes on the aedeagal arms in *Nesophrosyne*, which are absent in *Orosius*. A more thorough investigation of *Nesophrosyne* genitalia reveals that the apical processes are absent in some species and the genitalic affinities between the two genera are stronger than previously thought. The relationship needs to be examined phylogenetically.

Key to *Nesophrosyne* species associated with *Broussaisia arguta* on the Hawaiian Archipelago

Note: In most cases knowledge of host plant and collection locality (island and volcanic mountain) alone will differentiate species associated with *Broussaisia arguta*.

1. Head obliquely triangulate (Fig. 4a), with crown produced medially, bluntly pointed. Kaua'i. . . . . *N. heopoko* **sp. nov.**

\- Head not triangulate, crown weakly produced (Figs. 5–6a & 8–9a), rounded apically. 2

2. Gonopores subapical; aedeagus with apical processes produced distally, elongate 1/4–1/5 length of aedeagal arms (Figs. 4 & 5f). 3

\- Gonopores apical; apical processes of aedeagus extending from pore, short (~1/10 length of arm) or absent (Figs. 8 & 9f); Maui and Hawai'i.. . . . . *kanawao* species group, ...4

3. Dorsum with well-formed saddle mark, tapering to point anterad; posterior end subflat, appearing arrow-like pointing anterad; O'ahu (Fig. 5) . . . . *N. makaihe* **sp. nov.**

\- Species without any pale markings on clavus; forewing veins prominent, darkly pigmented; Moloka'i (Fig. 6). . . . . *N. magnaccai* **sp. nov.**

4. Dorsum with central pale saddle mark always present, usually with paired pale blotches anterad, appearing as three pale marks showing bilateral symmetry; palest forms with clavus entirely pale; Maui (Fig. 7 & 8).. . . . . *broussaisiai* species subgroup...5

\- Dorsum darker than above, usually without conspicuous saddle mark; claval veins discontinuously pale, extending short length from commissural line (appearing as two pale lines curving anterad) and with anterior intersection of claval veins pale, showing bilateral symmetry; palest forms with irregular, large pale blotches throughout clavus; Hawai'i Island (Fig. 7 & 9). . . . . *aakokohaikea* species subgroup, 7

Note: The following are a closely related assemblage of *Nesophrosyne* species most easily discerned by knowledge of collection locality:

5. West Maui; almost always with three pale marks (Fig. 7a); darkest forms with only central oval saddle mark; apical process present, short 1/10 length of aedeagal arm . . . . *N. broussaisiai* **sp. nov.**

\- East Maui; characters not as above 6

6. Claval coloration ranging from three mark forms to entirely pale; apical process present, short 1/10 length of aedeagal arm

(Fig. 7 & 8). . . . . *N. ogradyi* **sp. nov.**

\- East Maui, Haleakalā leeward face; species with claval coloration usually entirely pale; darker forms with dark bands across clavus, appearing disrupted; apical processes absent . . . . *N. kaupoi* **sp. nov.**

7\. Claval veins partially pale, extending from commissural line (appearing as two pale line curving anterad), with anterior intersection of claval veins pale, showing bilateral symmetry (Fig. 7 & 9). . . . .*N. aakokohaikea* **sp. nov.**

\- Clavus predominately pale, appearing irregularly shaped, connected with thin pale line across commissural line. . . . . *N. kanawao* **sp. nov.**

Nesophrosyne heopoko Bennett sp. nov.

(Fig. 4a–g)

Diagnosis. Length: male = 3.94mm, female = 5.03mm. Brown-copper colored species. Head obliquely triangulate with crown produced; posterior end conspicuously concave. Forewing venation dark except on clavus. Clavus without saddle mark, veins partially pale extending from commissural line. Pygofer rounded; posterior-dorsal edge convex. Aedeagus with preapical gonopore; apical processes short and straight. Style with depressed preapical lobe. Endemic to Kaua'i.

Description. ***Dorsum*:** Brownish-copper colored species (Fig. 4a). Head triangular with oblique vertices; crown produced and rounded with articulated dark markings, separating the anterior 1/3 into a pale triangular shape, two lateral dark dots at 2/3 distance from crown divided by coronal suture. Pronotum predominately pale; anterior margin infused with dark blotches; darkest forms showing faint 'V' form, extending to posterior margin. Mesonotum predominately pale; mesonotal triangles darkly colored and edged with orange. Scutellum pale. Forewing cells hyaline; veins darkly colored throughout; darkest forms with cells infused with dark pigmentation; outer anteapical cell present, triangular. Clavus without prominent saddle mark; veins partially pale extending from commissural line, curved anterad.

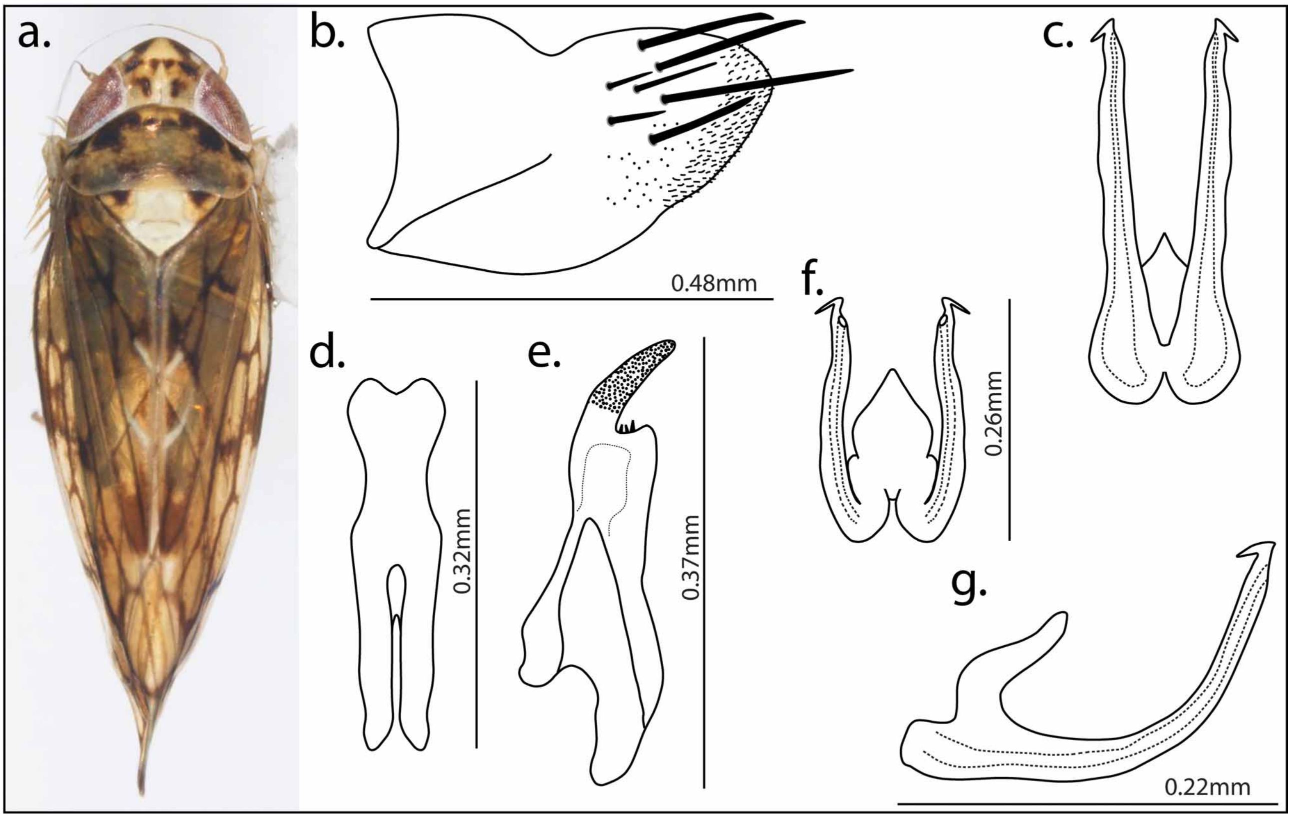

FIGURE 4. *Nesophrosyne heopoko* endemic to Kaua'i: a. dorsum; b. male pygofer; c. aedeagus ventral view; d. connective; e. style; f. aedeagus posterior view; and, g. aedeagus lateral view.

Venter: Face with clypeus pale, with dark coloration restricted to posterior lateral margins; clypellus varying between posterior half dark to completely dark; lorum edged in dark, with darkest forms being dark throughout; gena pale, with antennal ledges and margin along eye dark. Abdominal segments predominately dark, with thin pale line along each posterior margin; pleurites partially dark on anterior half. Legs mostly pale, with femora and tibiae partially dark; bases of macrosetae dark.

Genitalia: Pygofer (Fig. 4b) bluntly pointed at mid-length, appearing rounded; ventral lobe reduced and rounded, edge to apex slightly rounded at base then straightening; posterior-dorsal edge convexly rising from apex; dorsal edge flat; 7 macrosete. Aedeagus (Fig. 4c, f, g) with bifurcate aedeagal arms relatively close in width, rising conspicuously higher than central apodeme, arms slender; gonopore preapical; apical processes distad of gonopore, tapering and hooking at apex, short and straight (difficult to see without removing internal genitalia). Style (Fig. 4e) posterior processes curved, widening at base; preapical lobe, with microsete extending from depression and along dorsal groove. Connective (Fig. 4d) elongate, relatively close in length to styles; anterior edge slightly depressed; width between posterior arms narrowed.

Distribution. USA: Hawaiian Islands, Kaua'i, North West Kōke'e State Park, >1220m (Fig. 3).

Measurements. *Body length*: Male (n=6) = 3.94mm (3.80mm–4.10mm); Female (n=3) = 5.03mm (4.90mm–5.20mm). ***Genitalia*** (n=5): Pygofer = 0.48mm (0.47mm–0.50mm); Style = 0.37mm (0.36mm–0.39mm); Connective = 0.32mm (0.31mm–0.33mm); Aedeagus lateral length = 0.22mm (0.21mm–0.25mm); Aedeagus posterior height = 0.26mm (0.25mm–0.27mm).

Material examined. *Type material*: Holotype: 1 male, Hawaiian Islands, Kaua'i, Kōke'e State Park Road (State Highway 550), N22^{o} 07.125, W159^{o} 38.016, Elevation: 1270m, 17May2007. Host Plant: *Broussaisia arguta*, Coll. G.M. Bennett and K.M. Magnacca. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17301. ***Additional material***: 5 males, 3 females, same as holotype. Deposited in the BPBM, Honolulu, Hawai'i

Etymology. *Heopoko* is Hawaiian for short-tipped end of penis: *Poko* is the adjective for short, and *Heo* is the noun for the tip of the penis. The name was chosen to describe the short apical processes of the aedeagal arms.

Discussion. One species is described from Kaua'i occurring on *Broussaisia arguta*. Extensive sampling through topographically difficult areas would be required to test if there are other species occurring on this island. However, Kaua'i represents a relatively low, single volcanic mountain reducing the probability of other lineages. Phylogenetic results indicate that *N. heopoko* is unrelated to other species associated with *B. arguta*, representing an independent shift to the host plant. *Nesophrosyne heopoko* is morphologically similar and closely related to *N. sp.1* (Fig. 3; COII % divergence avg. = 15.01%), co-occurring in the same range on the host plant *Pipturus sp.*. They are easily distinguished from each other using head shape, length of aedeagal distal processes, and absence of the outer anteapical cell in *N.sp.1*.

Nesophrosyne makaihe Bennett sp. nov.

(Fig. 5a–g)

Diagnosis. Length: male = 3.74mm, female = 4.97mm. A dark species, with a prominent saddle mark resembling a spear point, pointed anterad. Crown produced and bluntly rounded. Pygofer with a pointed apex at 2/3 height from base. Aedeagus with long apical processes, recurving anterolaterally 1/4 length of aedeagal arms. Endemic to O'ahu, Wai'anae Mountain Range.

Description. *Dorsum*: Dark species with prominent pale-yellow markings, extending from clavus through mesonotum (Fig. 5a). Crown and pronotum dark; lighter forms with pale light brown blotches between ocelli. Mesonotum mesially pale; mesonotal triangles dark, extending to lateral margins. Scutellum pale. Forewing predominantly dark with cells and veins obfuscate in dark pigmentation; costal cells along posterior half clear, divided by a darkly pigmented R1 vein; outer anteapical cells present, triangular. Clavus with large conspicuous saddle mark, widest at base and tapering anteriorally, resembling a spear point.

Venter: Face with well-formed grill pattern on clypeus, divided by central dark latitudinal line, posterior half entirely dark; clypellus, lorum, and gena dark. Abdominal segments predominately dark with thin pale line along each posterior margin; pleurites partially dark on anterior half. Legs almost entirely pale; hind femora dark anteroventrad; hind tarsal segments dark at joints.

Genitalia: Pygofer (Fig. 5b) produced and pointed, rising at 2/3 height from base; ventral lobe produced with long flat edge, angled posteroventrad, giving rise sharply to apex; posterior-dorsal edge rising form apex rounded; posterior edge flat; 11 macrosete. Aedeagus (Fig. 5c,f,g) with aedeagal arms widely splayed, rising above central apodeme; gonopore preapical; apical processes long approximately 1/4 length of aedeagus, distad of gonopore, tapering before hooking anterolaterally. Style (Fig. 5e) large; posterior processes short; preapical lobe flat and angular with microsete. Connective (Fig. 5d) short; posterior edge notched; anterior appendages splayed widely.

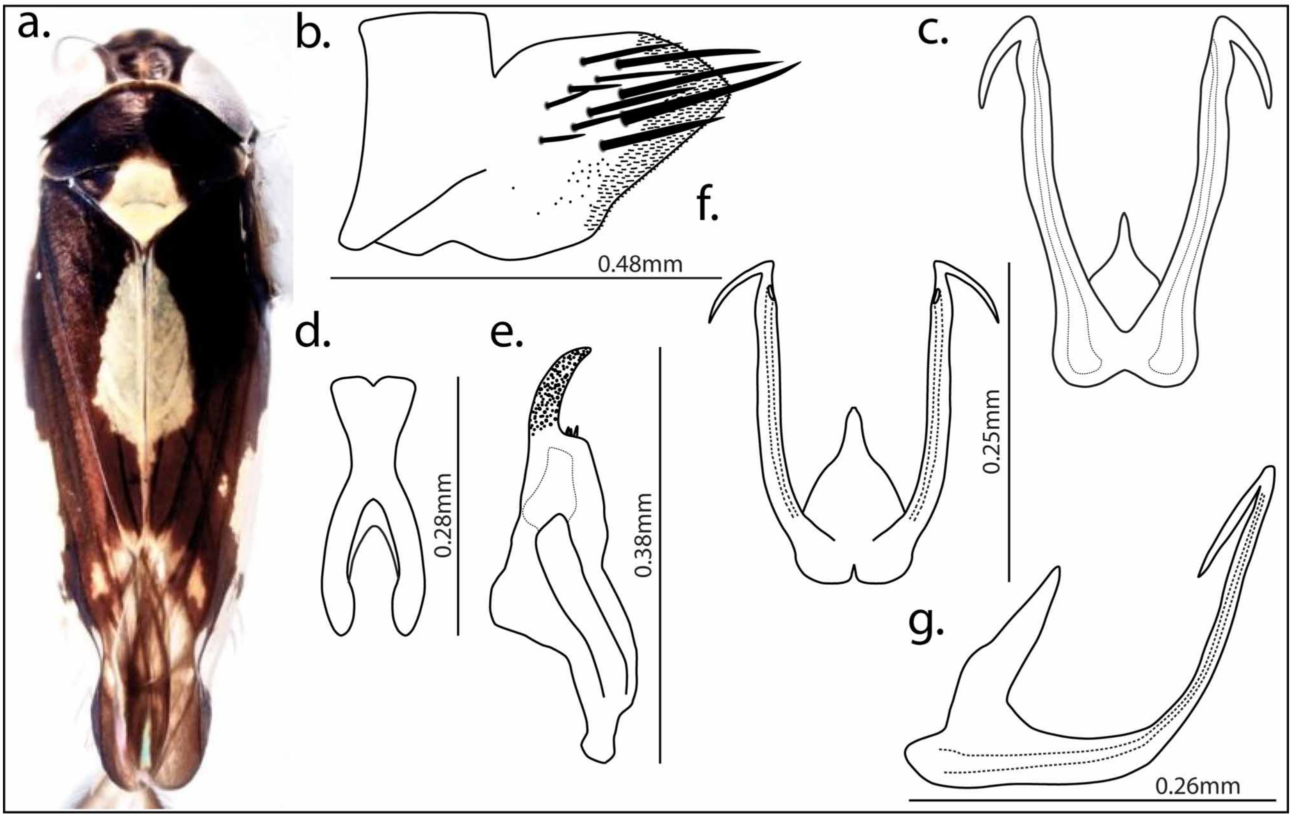

FIGURE 5. *Nesophrosyne makaihe* endemic to O'ahu, Wai'anae Range: a. dorsum; b. male pygofer; c. aedeagus ventral view; d. connective; e. style; f. aedeagus posterior view; and, g. aedeagus lateral view.

Distribution. USA: Hawaiian Islands, O'ahu, Western Wai'anae Mountain Range, ~1220m, wet forest

Measurements. ***Body length*** (n=8): Male (n=8) = 3.74mm (3.60mm–3.90mm); Female (n=10) = 4.97mm (4.80mm–5.10mm). ***Genitalia*** (n=6): Pygofer = 0.48mm (0.47mm–0.50mm); Style = 0.38mm (0.37mm–0.39mm); Connective = 0.28mm (0.27mm–0.29mm); Aedeagus lateral length = 0.26mm (0.24mm–0.27mm); Aedeagus posterior height = 0.25mm (0.23mm–0.27mm).

Material examined. ***Type material***: Holotype: 1 male, Hawaiian Islands, O'ahu, Wai'anae Mountains, Mt. Ka'ala, Summit Bog Boardwalk, N21º 30.504, W158º 08.865, Elevation: 1210m, 29Aug2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett, K. Magnacca, and D.A. Polhemus. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17302. ***Additional material***: 22 males, 12 females, Hawaiian Islands, O'ahu, Wai'anae Mountains, Mt. Ka'ala, Summit Bog Boardwalk, N21º 30.504, W158º 08.865, Elevation: 1210m, 26May2007, 27July2009, and 29Aug2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett, K. Magnacca, and D.A. Polhemus. Deposited in the BPBM, Honolulu, Hawai'i. 21 males, 7 females, Hawaiian Islands, O'ahu, Wai'anae Mountains, Mt. Ka'ala, Summit Bog Boardwalk, N21º 40'40" W158º 08'48", Elevation: 1220m, 6May2000. Host Plant: *Broussaisia arguta*. Coll. D.A. Polhemus. Deposited in D.A. Polhemus's personal collection at the Smithsonian, Washington D.C.

Etymology. *Makaihe* is a Hawaiian phrase for spear tip: *Maka* is the noun for point or tip of blade, and *Ihe* is the noun for spear. The name was chosen to describe the resemblance of the claval saddle mark to that of a spear point.

Discussion. A single species is described for the *Nesophrosyne* occurring on *Broussaisia arguta* on O'ahu. Three specimens of a morphologically similar population from the Ko'olau Range on East O'ahu were examined (provided by D. Polhemus). The male specimens are dorsally paler than the *N. makaihe* (West O'ahu); the genitalia were not examined due to limited sample size. Eastern O'ahu populations may represent a potential sibling species system as seen on Maui and Hawai'i (Fig. 3). Due to the difficulty of collecting species from *B. arguta* on the eastern side of O'ahu, we are unable to make an adequate comparison of the two populations here.

Phylogenetic evidence places *N. makaihe* in a clade with the *kanawao* species group, with low support. *Nesophrosyne makaihe* is placed sister to a clade associated with the host plant genus *Myrsine* (Myrsinaceae), containing two species found on East Maui and Hawai'i island (COII % divergence avg. = 16.03%). Both taxa occur in high elevation (~914.4m) rainforest.

Further gene and taxonomic sampling are required to resolve this relationship. *Nesophrosyne makaihe*'s internal genitalia is considerably different, further confusing inference of relationships to other species associated with *B. arguta*.

Nesophrosyne magnaccai Bennett **sp. nov.**

(Fig. 6a–g)

Diagnosis. Length: male = 4.7mm, female = 5.60mm. Brown species with conspicuous dark colored veins; without saddle mark or pale colored claval veins. Crown produced, bluntly rounded. Pygofer appearing triangular, with sharply produced apex rising at mid-length. Aedeagal arms widely splayed, appearing relatively compressed in ventral view; gonopore preapical, with apical processes recurving anterolaterad 1/5 length of aedeagal arms. Endemic to Moloka'i.

Description. ***Dorsum*** Brownish species with forewing veins conspicuous (Fig. 6a). Crown predominately dark with thin pale line extending along posterior margin, triangular pale region emerging at apex. Pronotum almost entirely dark except for lateral edges, which are marked with two lateral pale spots on margins. Mesonotum dark. Scutellum central region variably dark, lateral margins pale. Forewing veins dark and conspicuous, including clavus; cells clear tinged with brown; central anteapical cell infused with dark pigmentation at ends; discal cells dark; lacking any pale coloration common in *Nesophrosyne*; outer anteapical cell present, triangular.

Venter: Face with clypeus, clypellus, lorum dark; gena dark with lateral margins pale. Abdominal segments almost entirely dark with thin pale line along each posterior margin; pleurites dark with posterior edge variably pale. Forelegs pale, base of sete dark; middle femora and tibia dark at joints; hind femora and tibia mostly dark with pale macrosete.

Genitalia: Pygofer (Fig. 6b) triangular, sharply produced at mid-height from base; dorsal and ventral edges narrowing straight to apex; ventral lobe produced; 11 macrosete. Aedeagus (Fig. 6f,c,g) comparatively compressed in posterior view, rising nearly above of central apodeme; aedeagal arms splayed widely; gonopore preapical; apical processes extending just above gonopore, hooking approximately 1/5 the length of aedeagal arms. Style (Fig. 6e) preapical lobe sloping, forming an oblique angular edge, with microsete. Connective (Fig. 6d) with posterior edge notched and wider than anterior arms; anterior arms thick, moderately splayed.

Distribution. USA: Hawaiian Islands, Moloka'i Eastern Mountain Range, >1340m, wet forest.

Measurements. ***Body length*** (n=4): Male (n=4) = 4.70mm (4.46mm–4.80mm); Female (n=1) = 5.60mm. ***Genitalia*** (n=3): Pygofer = 0.60mm (0.59mm–0.62mm); Style = 0.46mm (0.45mm–0.47mm); Connective = 0.32mm (0.32mm–0.33mm); Aedeagus lateral length = 0.39mm (0.38mm–0.39mm); Aedeagus posterior height = 0.13mm (0.13mm–0.14mm).

Material examined. ***Type material***: Holotype: 1 male, Hawaiian Islands, Moloka'i, Kamakou Preserve, Pu'u Kolekole, N21° 06.436 W156° 54.141, Elevation: 1340m, 19Feb2007. Host Plant: *Broussaisia arguta*. Coll. K. Magnacca. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17303. ***Additional material***: 3 males, 1 female, same as holotype. Deposited in the BPBM, Honolulu, Hawai'i.

Etymology. This species is named after its collector Dr. Karl Magnacca (Hawaiian Entomologist, University of Hawai'i, Hilo) for his contributions to this project and for his extensive, and helpful guidance in the field.

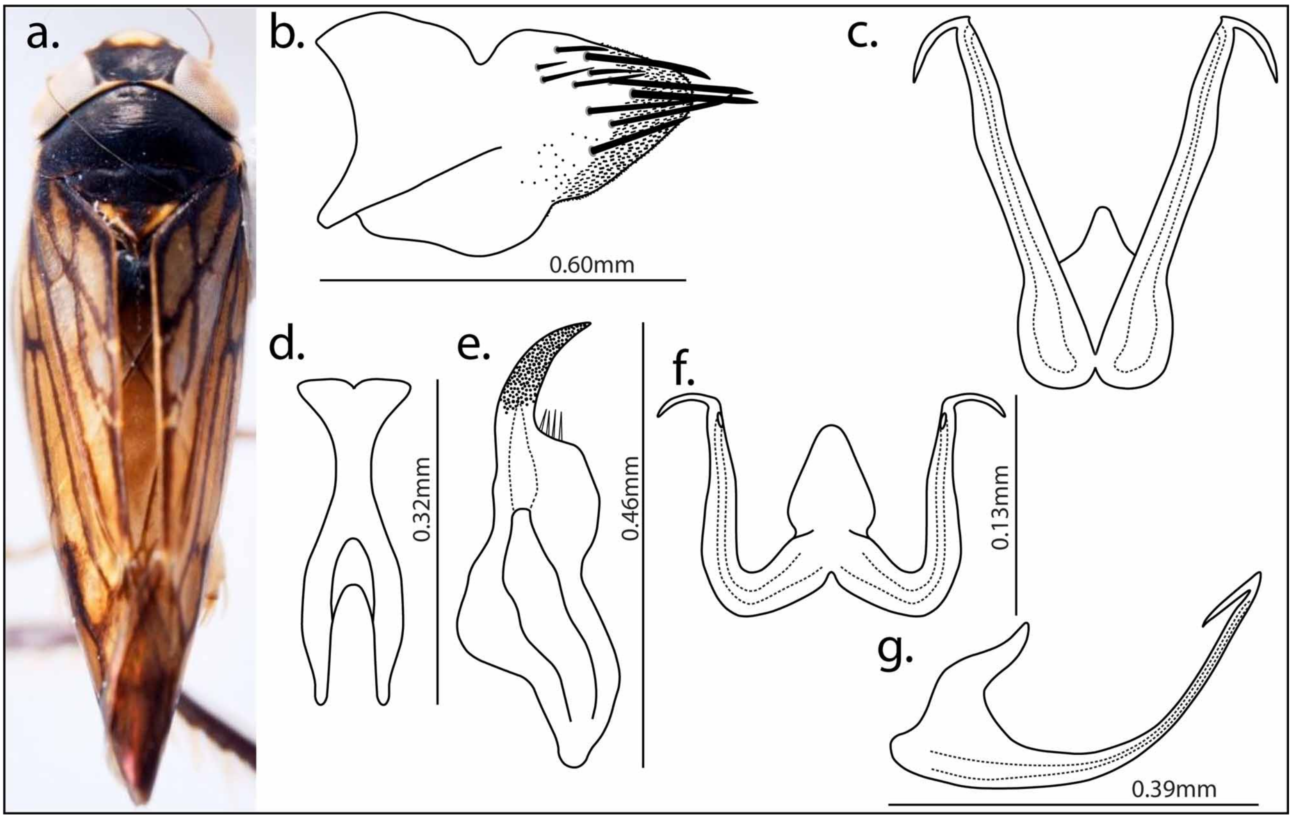

FIGURE 6. *Nesophrosyne magnaccai* endemic to Moloka'i: a. dorsum; b. male pygofer; c. aedeagus ventral view; d. connective; e. style; f. aedeagus posterior view; and, g. aedeagus lateral view.

Discussion. A single *Nesophrosyne* species associated with *Broussaisia arguta* is described from Moloka'i. Similarly to *N. heopoko*, the Moloka'i species is morphologically distinct from the other species described here. Current phylogenetic evidence provides weak support for an independent shift to *B. arguta*. *N. magnaccai* is placed sister to *N. sp.4* and *N. oblique* (data not shown), which are associated with the host plant genera *Lobelia* (Campanulaceae) and *Myrsine* (Myrsinaceae), respectively. Both sister taxa occur in on East Maui in high elevation (~914.4m) rainforest. COII percent divergence between *N. magnaccai* and *N. sp.4* avg. = 15.68%, and *N. magnaccai* and *N. obliqua* = 15.67%.

kanawao species group

(Figs. 7, 8a–g & 9a–g)

Diagnosis. Dark species with conspicuous, pale coloration on clavus. Aedeagus with arms short, rising just above central apodeme in ventral view; gonopore apical; apical processes short and straight, extending 1/10 the length of the aedeagal arm. Connective distinct with anterior arms large, thickening at mid-length, appearing as 90º angles along lateral edges. Endemic to Maui and Hawai'i Island.

Description. ***Dorsum***: Dark species with conspicuous pale coloration on clavus (Fig. 7). Mesonotum dark. Scutellum pale. Forewing veins obfuscate; costal cells hyaline, divided by dark pigmentation along R1; outer anteapical cell present, small and triangular. Clavus with extensive pale coloration, variable between species.

Venter: Clypeus with well formed grill mark on anterior half, posterior half forming dark basal triangle from which grill emerges; clypellus and lorum dark; gena dark with outer margins pale. Central abdominal segments dark with pale band expanding in anterior segments.

Genitalia: Aedeagus with relatively short arms rising just above central apodeme in ventral view; gonopore apical; apical processes short, extending anterolaterally 1/10 length of aedeagal arm (Figs. 8 & 9f,c,g); apical processes absent in *N. kaupoi*. Connective distinct with flat posterior edge, wider than waist; anterior arms thickening at mid-length, forming nearly 90º angles along lateral edges; anterior ends curving slightly, hooked laterad (Figs. 8 & 9d).

Distribution. USA: Hawaiian Islands, Hawai'i Island and Maui, 910–2080m, wet forest (Fig. 3).

Etymology. The *kanawao* species group is named after the Hawaiian word for *Broussaisia arguta* for the association of its constituent species with this plant species.

Discussion. The *kanawao* species group is a monophyletic assemblage of species associated with *Broussaisia arguta* on Maui and Hawai'i Island (Fig. 3). We describe five species, further subdividing them into two species subgroups: *broussaisiai* species subgroup (endemic to Maui) and *aakokohaikea* species subgroup (endemic to Hawai'i Island). These delineations conform to species' morphological similarities, islands of endemicity, and monophyly (Fig. 3). Phylogenetically, the species subgroups are sister (COII % divergence avg. = 11.52%; Table 1), showing retention of the *B. arguta* host plant association through colonization of a novel island. Polarity of this biogeographic pattern requires more sampling to resolve.

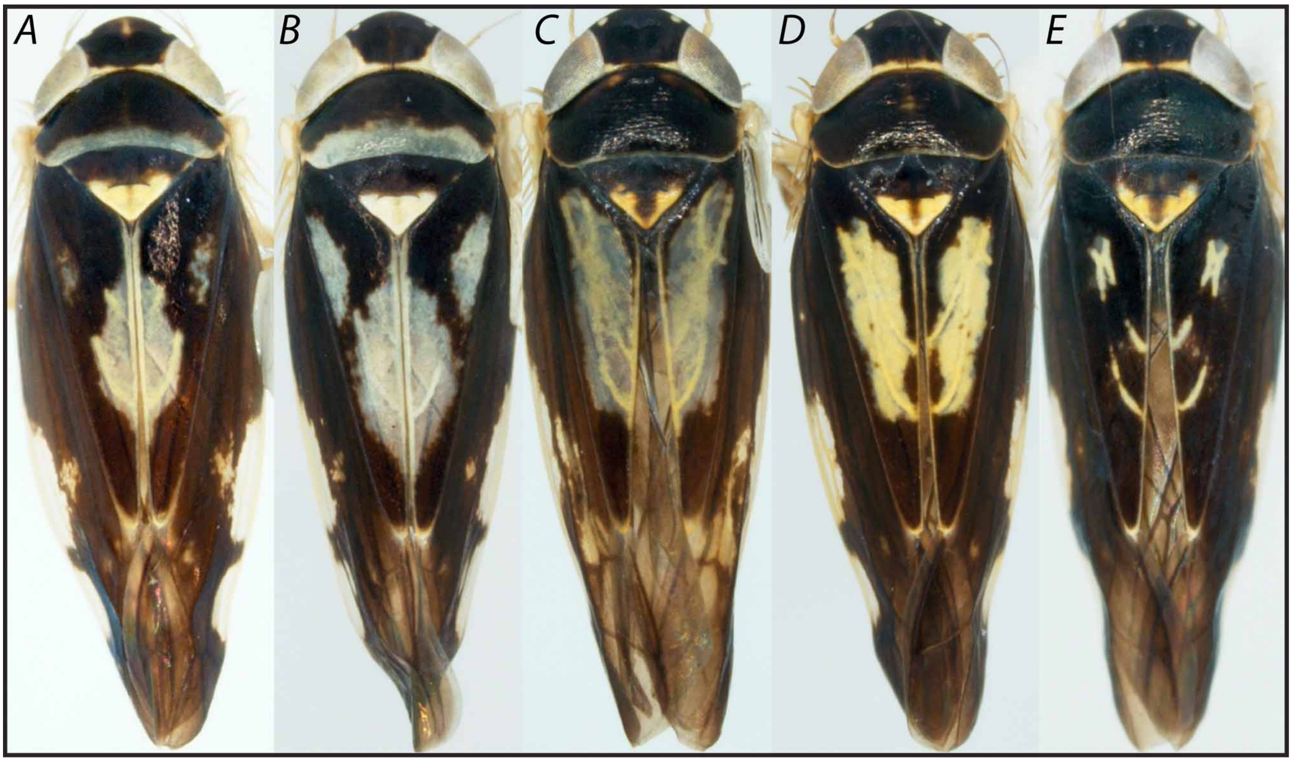

FIGURE 7. Dorsal habitus of the species comprising the *kanawao* species group: A. *N. broussaisiai*, B. *N. ogradyi*, C. *N. kaupoi*, D. *N. kanawao*, and E. *N. aakokohaikea*.

Internal genitalia in the *broussaisiai* and *aakokohaikea* species subgroups show similarity in the placement and length of the apical processes, and the unique shape of the connective. External morphology easily distinguishes the subgroups (*e.g.*, *aakokohaikea* species subgroup comprises darker species). Within subgroups, species are difficult to identify without knowledge of collection locality and subtle morphological differences, as there can be considerable overlap in external color patterning.

broussaisiai species subgroup

(Figs. 7a–c & 8a–g)

Diagnosis. Dark species with conspicuous, highly variable pale coloration on clavus, ranging from entirely pale to a central oval saddle mark anteriorly flanked by pale blotches. Pronotum with posterior half pale. Pygofer with apex at 3/4 height from base; without basal lobe; dorsal edge depressed. Aedeagus with arms widening at mid length, showing an angular bend; apical processes absent in *N. kaupoi*. Endemic to Maui.

Description. ***Dorsum***: Dark species with conspicuous and variable pale coloration on clavus. Crown predominately black with variable central pale mark at apex and a thin pale line along posterior margin. Pronotum dark with posterior pale band up to 1/2 width. Mesonotum dark. Scutellum pale. Clavus with saddle mark ranging in pale pigmentation; darkest forms with only a central round saddle mark, usually anteriorally flanked by lateral pale marks variable in size and color; palest forms with clavus appearing entirely pale with posterior angles dark.

Venter: Pleurites largely pale with variable central dark patches. Legs almost entirely pale; hind tibiae dark along anteroventral edge.

Genitalia: Pygofer apex bluntly rounded and turned slightly dorsad, rising 3/4 height from base; without basal lobe; posterior-dorsal edge depressed from slight to completely concave; dorsal edge flat, tapering towards anterior end; 13–15 macrosete. Aedeagus with arms widening at mid-length, showing an angular bend in ventral view; apical processes absent in *N. kaupoi*. Style large; posterior hooks comparatively thick; preapical lobe, sloping towards anterior end, rest of medial lobe rounded; posterior arm towards connective curving mesad, 's' like. Connective anterior ends or arms curving, slightly hooked laterad.

Distribution. USA: Hawaiian Islands, Maui, 910m–2080m, wet forest (Fig. 3)

Etymology. This species subgroup is named after the *Broussaisia* host plant genus.

Discussion. We describe three sibling species from Maui occurring on *Broussaisia arguta*. Genetic evidence demonstrates unique, reciprocally monophyletic evolutionary lineages with relatively high sequence divergence occurring on West Maui, East Maui Haleakalā windward face, and East Maui Haleakalā leeward face (Kaupo Gap). COII percent sequence divergence for these geographic ranges are as follows (Table 1): Haleakalā windward face – Haleakalā leeward face = 11.24%; Haleakalā windward face – West Maui = 4.22%; and, Haleakalā leeward – West Maui = 10.57%.

Morphologically, these species can be difficult to distinguish, but some external characteristics combined with geographic information are adequate to separate them. In general, West Maui represents a darker form than the both East Maui species, overlapping with *N. ogradyi* variants. *N. kaupoi* overlaps in color with the paler variants of *N. ogradyi*. *Nesophrosyne kaupoi* occurs at higher elevation (~2080m) than the other described species (910m – 1220m), which corresponds to the upper elevation of *B. arguta*.

The geographic structuring of these species provides unique insight into the potential evolutionary mechanisms that may contribute to the diversification of the genus. Haleakalā leeward, due to its inhospitable geographic divide across Haleakalā crater, high elevation, or differences in precipitation (or a confluence of all), may contribute to the genetic isolation and speciation of *Nesophrosyne* in this range. The distance, precipitation change and elevation change going from West Maui to East Maui are sufficient to maintain isolation between these species.

Nesophrosyne broussaisiai Bennett sp. nov.

(Fig. 7a)

Diagnosis. Length: male = 4.22mm, female = 5.21mm. A dark species, with three conspicuous pale spots on clavus. Clavus with a central round pale saddle mark, anteriorally flanked by lateral symmetrical pale marks, sometimes showing as clear patches along clavus (see Fig. 7a); darkest forms with only a central saddle mark. Crown and pronotum with posterior pale bands. Genitalia matching species group description (see Fig. 8b–g). Endemic to West Maui.

Distribution. USA: Hawaiian Islands, Maui, West Mauna Kahalawai, Pu'u Kukui, ~1220m, wet forest (Fig. 3).

Measurements. ***Body length*** (n=5): Male (n=5) = 4.22mm (4.15mm–4.30mm); Female (n=8) = 5.21mm (5.10mm–5.40mm). ***Genitalia*** (n=5): Pygofer = 0.57mm (0.55mm–0.59mm); Style = 0.47mm (0.46mm–0.48mm); Connective = 0.28mm (0.27mm–0.29mm); Aedeagus lateral length = 0.35mm (0.34mm–0.37mm); Aedeagus posterior height = 0.15mm (0.14mm–0.16mm).

Material examined. *Type Material*: Holotype: 1 male, Hawaiian Islands, West Maui, Mauna Kahalawai, Pu'u Kukui, Boardwalk Trail, N20º 56.078 W156º 36.985, Elevation: 1220m, 23Nov2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett, K. Magnacca, P.M. O'Grady. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17304. *Additional Material*: 12 males, 11 females, Hawaiian Islands, West Maui, Mauna Kahalawai, Pu'u Kukui, Boardwalk Trail, N20º 56.078 W156º 36.985, Elevation: 1220m, Elevation: 940m, 23Nov2009, 7Aug2007, Coll. G.M. Bennett, K. Magnacca, P.M. O'Grady. Deposited in the BPBM, Honolulu, Hawai'i. 1 female, Hawaiian Islands, West Maui, Wet Forest below Nakalalua, Pu'u Kukuii Trail, 1220m, 26May2004. N20º 54'58" W156º 35'37", Coll: DA Polhemus. Deposited in D.A. Polhemus's personal collection at the Smithsonian, Washington D.C.

Etymology. The name chosen for this species refers to the host plant genus name it occurs on, *Broussaisia*.

Discussion. This species is nearly indistinguishable from the East Maui sibling species. Morphologically, the only character that distinguishes *N. broussaisiai* is the variable color pattern on the clavus, which is generally darker.

Nesophrosyne ogradyi Bennett sp. nov.

(Fig. 8a–g)

Diagnosis. Length: male = 4.17mm, female = 5.65mm. A paler species than *N. broussaisiai*. Clavus entirely pale or with three spots, with a central round saddle mark flanked by lateral pale marks (Fig. 8a). Pronotum posterior 1/2 pale. Genitalia matching species group description (Fig. 8b–g). Endemic to East Maui, Haleakalā windward face.

Distribution. USA: Hawaiian Islands, Maui, Haleakalā windward face, >910m, wet forest (Fig. 3)

Measurements. ***Body length***: Male (n=10) = 4.17mm (4.00mm–4.30mm); Female (n=10) = 5.65mm (5.50mm–5.80mm). ***Genitalia*** (n=5): Pygofer = 0.57mm (0.56mm–0.58mm); Style = 0.47mm (0.46mm–0.48mm); Connective = 0.27mm (0.26mm–0.28mm); Aedeagus lateral length = 0.31mm (0.30mm–0.33mm); Aedeagus posterior height = 0.16mm (0.15mm–0.17mm).

Material examined. ***Type Material***: Holotype: 1 male, Hawaiian Islands, East Maui, Waikamoi Forest Reserve, Heed Trail, N20º 48.638 W156º 14.509, Elevation: 1310m, 31July2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett, P.M. O'Grady, K.M. Magnacca. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17305. ***Additional Material***: 13 males, 17 females, Hawaiian Islands, East Maui, Makawao Forest Preserve, N20º 48.638 W156º 14.509, Elevation: 1310m, 31July2007, 6Aug2007, 6June2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. Deposited in the BPBM, Honolulu, Hawai'i. 2 males, 2 females, Hawaiian, Islands, East Maui, Waikamoi Forest Reserve, N20º 48.397 W156º 15.295, Elevation: 1300m, 1June2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. P.M. O'Grady, K.M. Magnacca. Deposited in the BPBM, Honolulu, Hawai'i. 5 males, Hawaiian Islands, Maui, Haleakalā, Pu'u O Kakai, TNCH, Waikamoi Preserve, N20º 48'00" W156º 14'44", Elevation: 1500m, 16May2003. Host Plant: *Broussaisia arguta*. Coll: D.A. Polhemus. Deposited in D.A. Polhemus's personal collection at the Smithsonian, Washington D.C.

Etymology. This species is named after Dr. Patrick O'Grady (Hawaiian Dipterologist) for his invaluable contributions to this project and for his positive scientific mentorship of G.M. Bennett.

Discussion. *Nesophrosyne ogradyi* represents a lighter form than *N. broussaisiai*. External morphology is nearly identical to *N. kaupoi*. *Nesophrosyne kaupoi* is distinguishable from *N. ogradyi* by its absent apical processes.

Nesophrosyne kaupoi Bennett sp. nov.

(Fig. 7c)

Diagnosis. Length: male = 4.18mm, female = 5.75mm. Paler species, matching palest forms of *N. ogradyi*. Crown with pale blotches. Clavus entirely pale except for posterior 1/4, which forms anterior dark triangles. Aedeagus without apical processes. Endemic to Maui, Haleakalā leeward face, Kaupo Gap.

Measurements. ***Body length***: Male (n=3) = 4.18mm (4.10mm–4.25mm); Female (n=4) = 5.75mm (5.70mm–5.80mm). ***Genitalia*** (n=2): Pygofer = 0.58mm (0.57mm–0.59mm); Style = 0.48mm (0.47mm–0.48mm); Connective = 0.29mm (0.28mm–0.29mm); Aedeagus lateral length = 0.33mm (0.32mm–0.34mm); Aedeagus posterior height = 0.15mm (0.13mm–0.16mm).

Material examined. ***Type Material***: Holotype: 1 male Hawaiian Islands, East Maui, Haleakalā, Paliku, Ridge Trail, N20º 43.074 W156º 08.470, Elevation: 2070m, 1Aug2007. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett, P.M. O'Grady, R. Lapoint, K.M. Magnacca. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17306. ***Additional Material***: 2 males, 1 female, same as holotype. Deposited in the BPBM, Honolulu, Hawai'i. 2 males, 3 females, Hawai'i Islands, East Maui, Paliku Seep, N20º 43.074, W156º 08.470, Elevation: 2070m, 1Sept2007. Host Plant *Broussaisia arguta*. Coll: K Magnacca. Deposited in the BPBM, Honolulu, Hawai'i.

Etymology. This species is named after its collection locality and area of endemicity.

Discussion. *Nesophrosyne kaupoi* occurs at a significantly higher elevation than the other *broussaisiai* subgroup species. It is the only species in the species group missing the apical processes on the aedeagal arms.

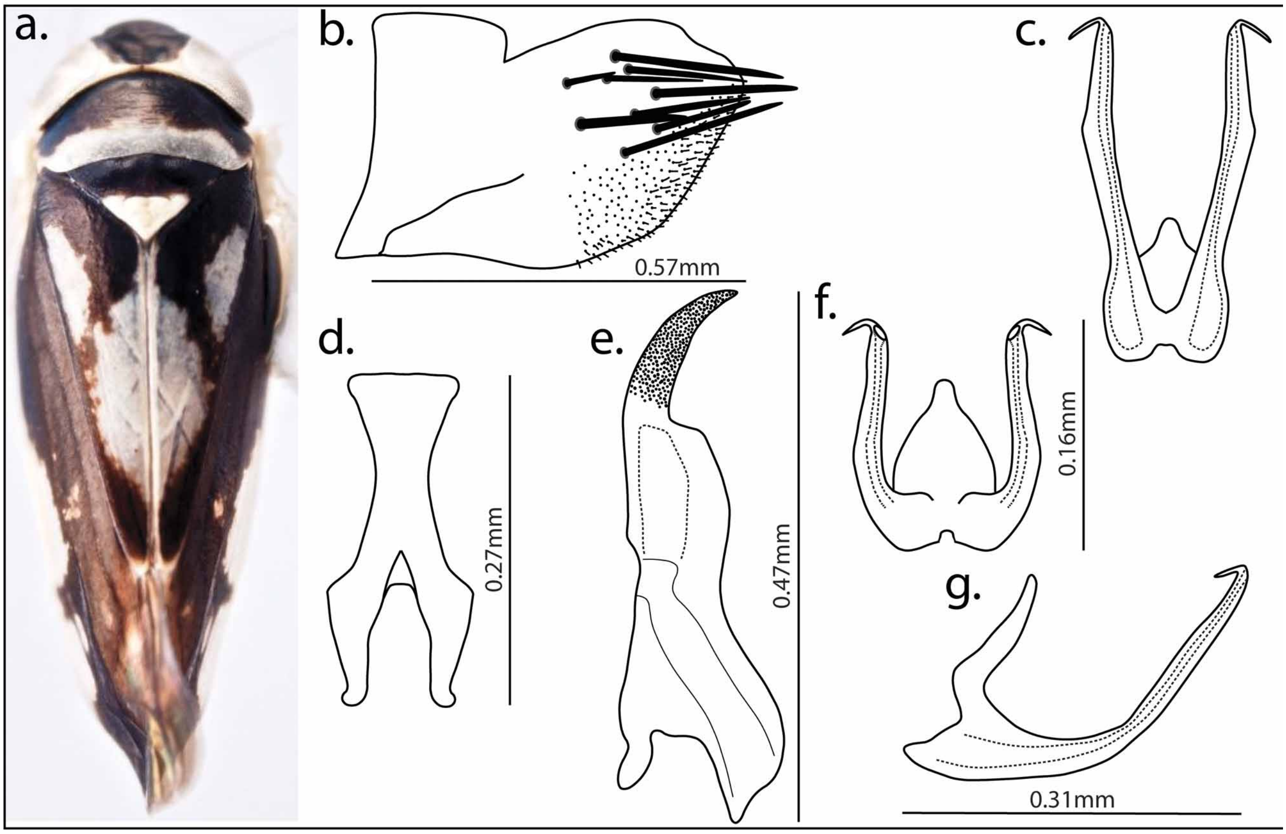

FIGURE 8. *Nesophrosyne ogradyi* endemic to Maui, Haleakalā windward face: a. dorsum; b. male pygofer; c. aedeagus ventral view; d. connective; e. style; f. aedeagus posterior view; and, g. aedeagus lateral view.

aakokohaikea species subgroup

(Figs. 7d–e & 9)

Diagnosis. Dark species, with pale coloration restricted to claval veins, scutellum, and posterior edge of crown. Pygofer apex bluntly pointed, rising at 1/3 height from base; basal lobe present, reduced. Aedeagal arms without thickening angular bend. Style with elongate, hooked thin posterior processes; preapical lobe flat. Endemic to Hawai'i Island.

Description. ***Dorsum***: Dark species, appearing almost entirely black except for articulated pale pigmentation along claval veins. Crown dark, with thin pale line along length of posterior margin (see Figs. 7d–e & 9a). Pronotum and mesonotum dark. Scutellum pale, usually with longitudinal dark line extending to posterior apex. Forewings predominately dark, with veins and cells mostly obfuscate. Clavus with veins irregularly pale, often with disjunct pigmentation at anterior intersection of claval veins; darkest forms with pale veins extending form commissural line as two thin lines curved anterad; palest species with pale pigmentation bleeding throughout clavus from center, appearing predominately pale.

Venter: Hind femora and base of tarsal segments dark, rest pale.

Genitalia**:** Pygofer (Fig. 9b) bluntly pointed at 1/3 height from base; ventral lobe reduced, edge flat and angled posteroventrad; dorsal edge flat; 12 macrosete. Aedeagus (Fig. 9c,f,g) with apodeme appearing pointed; aedeagal arms splayed widely. Style (Fig. 9e) with thin posterior hook approximately 1/3 length of style; preapical lobe flat with microsete, slightly slanted; medial lobe with nearly straight edge extending towards posterior processes; microsete present. Connective (Fig. 9d) anterior ends of arms straight and pointed.

Distribution. USA: Hawaiian Islands, Hawai'i, ~820m–1520m, wet forest (see Fig. 3).

Etymology. The name chosen for this species subgroup is adopted from one of its constituent species.

Discussion. The *aakokohaikea* species subgroup is closely related to the *broussaisiai* species subgroup endemic to Maui (Fig. 3), showing genetic sub-structuring according to volcanic mountains similar to the Maui species (COII % divergence avg. = 9.23%; Table 1). The Hawai'i Island sibling species are difficult to discern morphologically, as no consistent characters differentiate the lineages, except for subtle color variation on the clavus. Sampling for this study is limited to two geographic ranges or volcanic mountains: Kohala Range and Mauna Loa. Further investigation of other mountain ranges (*e.g.*, Mauna Kea and Hualālai) would undoubtedly reveal other sibling species to be placed in the *aakokohaikea* species subgroup.

Nesophrosyne aakokohaikea Bennett sp. nov.

(Fig. 9a–g)

Diagnosis. Length: male = 4.06mm, female = 5.51mm. Dark species with claval veins variably pale; darkest forms show predominately pale veins with pigmentation infused throughout the surrounding area; palest forms small length of claval veins pale extending from commissural line (Fig. 9a). Endemic to Hawai'i Island, Mauna Loa South Slope.

Distribution. USA: Hawaiian Islands, Hawai'i, South Eastern Slope of Mauna Loa, ~820m–1160m, wet forest (Fig. 3).

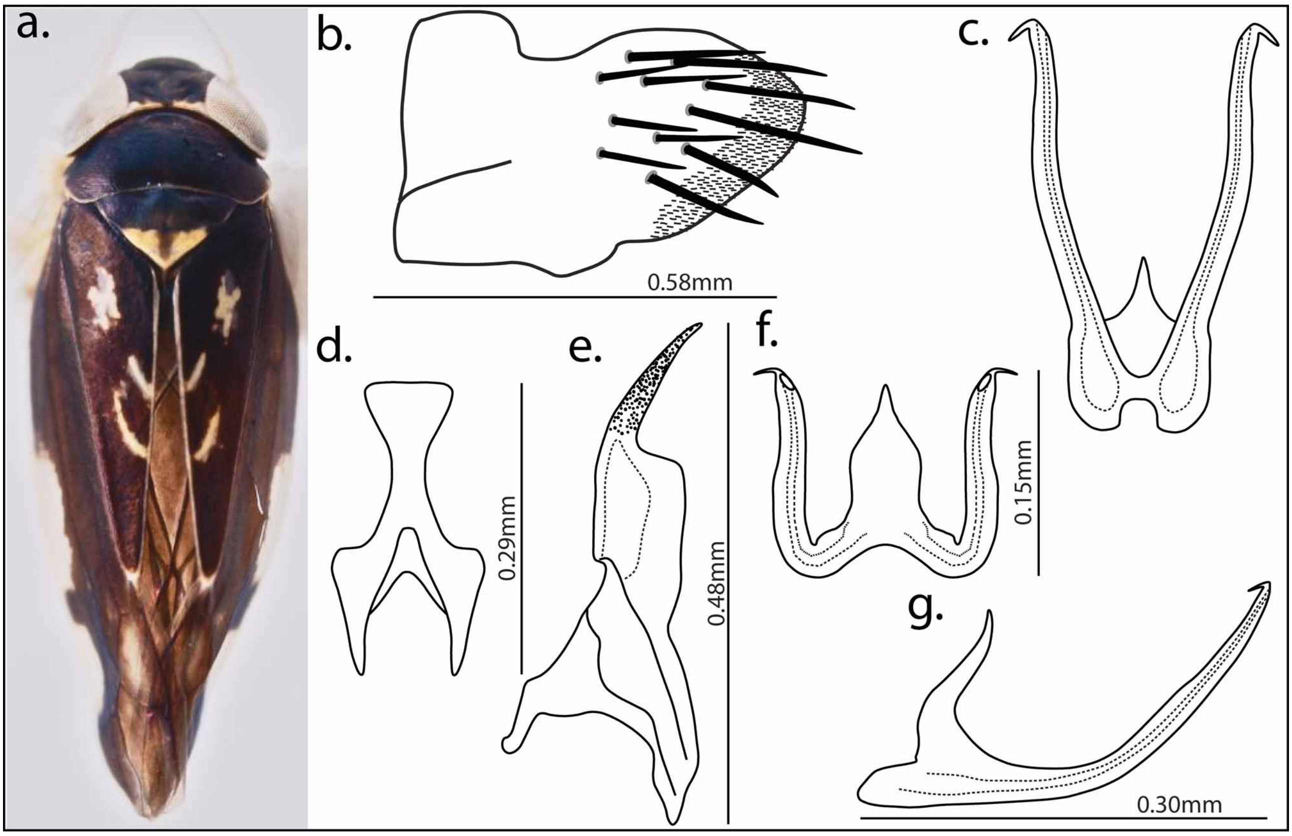

FIGURE 9. *Nesophrosyne aakokohaikea* endemic to Hawai'i Island, Mauna Loa South Slope: a. dorsum; b. male pygofer; c. aedeagus ventral view; d. connective; e. style; f. aedeagus posterior view; and, g. aedeagus lateral view.

Measurements. ***Body length***: Male (n=6) = 4.06mm (3.92mm – 4.12mm); Female (n=10) = 5.51mm (5.3mm–5.8mm). ***Genitalia*** (n=6): Pygofer = 0.56mm (.54mm–0.57mm); Style = 0.45mm (0.44mm–0.47mm); Connective = 0.26mm (0.24mm–0.27mm); Aedeagus lateral length = 0.33mm (0.32mm–0.35mm); Aedeagus posterior height = 0.14mm (0.13mm–0.16mm).

Material examined. ***Type Material***: Holotype: 1 male, Hawaiian Islands, Hawai'i, Ka'u Forest Reserve, Kuahiwi Ranch, N19º 05.111 W155º 35.830, Elevation: 820m, 15Jan2009. Host Plant: *Broussaisia arguta*. Coll. G.M.

Bennett. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17308. ***Additional Material***: 1male, Hawaiian Islands, Hawai'i, Hawai'i Volcanoes National Park, Ōla'a Forest, N19º 27.725 W155º 14.875, Elevation: 1170m, 7January2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. Deposited in the BPBM, Honolulu, Hawai'i. 4 males, 1 female, Hawaiian Islands, Hawai'i, Hawai'i Volcanoes National Park, Ka'u, Kahuku Ranch, N19º 06.0654 W155º 40.582, Elevation: 1070m, 13Jan2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. Deposited in the BPBM, Honolulu, Hawai'i. 3 males, 1 female, Hawaiian Islands, Hawai'i, Ka'u Forest Reserve, Kuahiwi Ranch, N19º 05.111 W155º 35.830, Elevation: 840m, 15Jan2009. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. Deposited in the BPBM, Honolulu, Hawai'i. 21 males, 10 female, Hawaiian Islands, Hawai'i', Ka'u District, Mountain House Road, N19º 09'34" W155º 37'10", Elevation: 3494m, 24May2001. Host Plant: *Broussaisia arguta*. Coll: DA Polhemus. Deposited in D.A. Polhemus's personal collection at the Smithsonian, Washington D.C. 3 male, Hawaiian Islands, Hawai'i, Kiluea "29 miles", 1220m, 29Sept1917. Host Plant: Unknown. Coll: WM. Giffard. Deposited in D.A. Polhemus's personal collection at the Smithsonian, Washington D.C.

Etymology. The name chosen for this species is Hawaiian for pale vein: *Aakoko* is the noun for vein, and *Haikea* is the adjective for pale. The name was chosen for the pale coloration along the claval veins.

Discussion. *Nesophrosyne aakokohaikea* is difficult, and in some cases cannot be, morphologically separated from *N. kanawao* despite relatively high sequence divergence (Table 1). Knowledge of collection locality is necessary to differentiate the species without genetic information. Percent COII sequence divergence between species from Ka'u (western edge of range) and Ōla'a (eastern edge of range) is approximately 2%. This suggests that there may be some limitation of dispersal across this range.

Nesophrosyne kanawao Bennett sp. nov.

(Fig. 7d)

Diagnosis. Length: male = 4.19mm, female = 5.45mm. Dark species. Clavus predominately and irregularly pale, pigmentation bleeding throughout clavus from claval veins; costal cells and proximal cells partly hyaline (Fig. 7d). Endemic to Kohala Mountain Range, Hawai'i Island.

Distribution. USA: Hawaiian Islands, Hawai'i, North West Kohala Mountain Range, 1520m, wet forest (Fig. 3).

Measurements. ***Body length*** (n=4): Male (n=4) = 4.19mm (4.17mm – 4.21mm); Female (n= 4) = 5.45mm (5.3mm–5.6mm). ***Genitalia*** (n=4): Pygofer = 0.56mm (0.55mm–0.57mm); Style = 0.48mm (0.48mm–0.49mm); Connective = 0.27mm (0.26mm–0.28mm); Aedeagus lateral length = 0.36mm (0.34mm–0.37mm); Aedeagus posterior height = 0.22mm (0.21mm–0.23mm).

Material examined. ***Type Material***: Holotype: 1 male, Hawaiian Islands, Hawai'i, Kohala Mountains, Kawaihae Oka, Pu'u O Umi Natural Area Reserve, Elevation: 1520m, N20º 04.947 W155º 45.128, 5October2006. Host Plant: *Broussaisia arguta*. Coll. G.M. Bennett. Deposited in the BPBM, Honolulu, Hawai'i. Type #: 17307. ***Additional Material***: 5 males, 4 females, same as holotype. Deposited in the BPBM, Honolulu, Hawai'i.

Etymology. The *kanawao* species group is named after the Hawaiian word for *Broussaisia arguta* for the association of its constituent species with this plant species.

Discussion. There is considerable overlap in the external coloration between *N. kanawao* and *N. aakokohaikea*, despite relatively large COII percent divergence (COII % divergence avg. = 9.23%). *Nesophrosyne kanawao* occurs in the Kohala Range, which is higher in elevation than the described *N. aakokohaikea*. Similar to species in the *broussaisiai* species subgroup, it is unknown if adaptation to elevational gradients or geographic limits to dispersal contribute to speciation in this subgroup. Sampling from across Hawai'i Island on different volcanoes and at varying elevations would help elucidate this question.

Table 1. Cytochrome Oxidase II uncorrected pairwise distances for newly described *Nesophrosyne* species associated with *Broussaisia arguta*.

		Hawai’i		Maui			Moloka’i	O’ahu	Kaua’i
		Kohala Mtns. *N. kanawao*	Mauna Loa South Slope. *N. aakokohaikea*	West Maui. *N. broussaisiai*	Haleakalā Crater, E. Maui. *N. kaupoi*	Haleakalā North Slope, E. Maui. *N. ogradyi*	Pu’u, Kolekole. *N. magnaccai*	Wai’anae Mtns. *N. makaihe*	Kōke’e State Park. *N. heopoko*
Hawai’i	Kohala Mtns. *N. kanawao*	0.0014							
	Mauna Loa South Slope. *N. aakokohaikea*	0.0923	0.0182						
Maui	West Maui. *N. broussaisiai*	0.1067	0.1152	0.0077					
	Haleakalā Crater, E. Maui. *N. kaupoi*	0.0990	0.1282	0.1057	0				
	Haleakalā North Slope, E. Maui. *N. ogradyi*	0.1153	0.1269	0.0422	0.1124	0.0049			
Moloka’i	Pu’u, Kolekole. *N. magnaccai*	0.1521	0.1569	0.1360	0.1569	0.1416	0		
O’ahu	Wai’anae Mtns. *N. makaihe*	0.1573	0.1631	0.1324	0.1594	0.1450	0.1400	0	
Kaua’i	Kōke’e State Park. *N. heopoko*	0.1780	0.1862	0.1748	0.7872	0.1800	0.1774	0.1734	0

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APPENDIX 1. Species list of material examined for subgeneric classification and examination of outer anteapical cell character state distribution. Undescribed species are given provisional names. Undetermined species are given collection identification numbers.

Subgenus	Species	Island	Notes on outer anteapical cell
Nesoreias			
	N. eburneola	Hawai'i	Absent
	N. insularis	Hawai'i	Absent
	N. marginalis	Hawai'i	Absent
Nesophrosyne			
	N. umbratilis	Kaua'i	Present
	N. heopoko	Kaua'i	Present
	N. monticola	O'ahu	Present
	N. pelea	O'ahu	Present
	N. maritima	O'ahu	Present, extremely variable in shape and size. Inner anteapical cell sometimes subdivided
	N. makaihe	O'ahu	Present
	N. bobea	O'ahu	Present
	N. ponapona	O'ahu	Completely absent in some individuals
	N. procellaris	Moloka'i	Present. Additional cells adjacent to inner anteapical cell
	N. magnaccai	Moloka'i	Present
	N. lineata	Lana'i	Present, large
	N neuneu	Maui	Sometimes absent. Variable in presence, shape and size
	N. haleakala	Maui	Present, subdivided in some individuals
	N. obliqua	Maui	Present
	N. ogradyi	Maui	Present, reduced and absent in one wing for some individuals
	N. broussaisiai	Maui	Present, variable in size
	N. kaupoi	Maui	Present
	N. anguilifera	Maui	Present
	N. craterigena	Hawai'i	Sometimes absent. Variable in presence, shape and size
	N. caelicola	Hawai'i	Present
	N. cinera	Hawai'i	Present, large and variable in shape
	N. giffardi	Hawai'i	Present, small
	N. pele	Hawai'i	Present
	N. pluvialis	Hawai'i	Sometimes absent. Variable in presence, shape and size
	N. kanawao	Hawai'i	Present
	N. mabae	Hawai'i	Present
	N. giffardi interrupta	Hawai'i	Present
	N. aakokohaikea	Hawai'i	Present
Undescribed[1]			
	N. sp.1	Kaua'i	Absent in all individuals
	N. sp.21	Kaua'i	Sometimes absent from one wing.
	N. sp23	Kaua'i	Present, extremely large
	N. sp.25	Kaua'i	Present
	N. sp.31	Kaua'i	Present, variable in size
	N. sp.29	Kaua'i	Missing entirely of in one wing

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APPENDIX 1. (continued)

Subgenus	Species	Island	Notes on outer anteapical cell
	N. sp.2	Kaua'i	Present
	N. sp.54	Kaua'i	Present
	N. sp.36	O'ahu	Present
	N. sp.89	O'ahu	Present
	N. sp.86	O'ahu	Present
	N. sp.17.1	Moloka'i	Present
	N. sp.16	Moloka'i	Absent in most individuals
	N. sp37.B	Maui	Present, variable in size
	N. sp.56	Maui	Present
	N. sp.60	Maui	Sometimes absent. Variable in presence, shape and size
	N. sp.99	Maui	Sometimes absent. Variable in presence, shape and size
	N. sp.34.D	Maui	Present
	N. sp.57	Maui	Present
	N. sp.389	Maui	Present, large
	N. sp.66	Maui	Present
	N. sp.141	Maui	Absent in one wing for some individuals
	N. sp.62	Maui	Sometimes absent. Variable in presence, shape and size between wings
	N. sp.39.1	Maui	Present
	N. sp.35.6	Maui	Present
	N. sp.67	Maui	Present
	N. sp.35.A	Maui	Present, subdivided in some individuals.
	N. sp.34.E	Maui	Present
	N. sp.4	Maui	Present, variable in shape between wings.
	N. sp.128	Maui	Present
	N. sp.10	Maui	Present
	N. sp.6	Maui	Present, elongate and subdivided in some individuals
	N. sp.36.2	Maui	Absent in one wing in most individuals
	N. sp.75	Hawai'i	Present
	N. sp.12.2	Hawai'i	Present
	N. sp.10.6	Hawai'i	Present
	N. sp.12.3	Hawai'i	Present
	N. sp.11.6	Hawai'i	Present, variable in size and shape
	N. sp.12.3	Hawai'i	Present, extremely reduced
	N. sp.10.D	Hawai'i	Present
Undetermined			
	N. sp. (GB-021.1)	Kaua'i	Sometimes absent. Variable in presence, shape and size
	N. sp. (GB-022.4)	Kaua'i	Present, reduced
	N. sp. (GB-024.6)	Kaua'i	Present, extremely large, fusing with wing margin
	N. sp. (GB-029.2)	Kaua'i	Sometimes absent from one wing
	N. sp. (GB-029.1)	Kaua'i	Present but variable in size in all individuals
	N. sp. (km03)	Kaua'i	Missing in one wing for some individuals

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APPENDIX 1. (continued)

Subgenus	Species	Island	Notes on outer anteapical cell
	N. sp. (GB-030.5)	O’ahu	Present in all individuals
	N. sp. (GB-030.9)	O’ahu	Sometimes absent. Variable in presence, shape and size
	N. sp. (GB-031.7)	O’ahu	Present
	N. sp. (km32)	O’ahu	Present
	N. sp. (km33)	O’ahu	Present
	N. sp. (km34)	O’ahu	Sometimes completely absent, or missing in one wing
	N. sp. (GB-033.1)	Lana’i	Present, sometimes subdivided
	N. sp. (GB-033.4)	Lana’i	Present
	N. sp. (GB-034.1)	Maui	Present
	N. sp. (GB-034.A)	Maui	Present
	N. sp. (GB-035.6)	Maui	Present
	N. sp. (GB-035.8)	Maui	Present
	N. sp. (37)	Hawai’i	Present
	N. sp. (GB-001.C)	Hawai’i	Present
	N. sp. (GB-002.1)	Hawai’i	Present, variable in size between wings
	N. sp. (GB-002.7)	Hawai’i	Present, reduced nearly absent
	N. sp. (GB-004.1)	Hawai’i	Present
	N. sp. (GB-005.1)	Hawai’i	Present, reduced
	N. sp. (GB-010.1)	Hawai’i	Sometimes absent. Variable in presence, shape and size
	N. sp. (GB-011.2)	Hawai’i	Present
	N. sp. (GB-016.1)	Hawai’i	Present
	N. sp. (GB-016.3)	Hawai’i	Present, elongate. Inner anteapical cell sometimes subdivided
	N. sp. (GB-011.5)	Hawai’i	Present
	N. sp. (GB-010.A)	Hawai’i	Present