A REVISION OF

THE GENUS *CHIONOMUS* FENNAH

(HEMIPTERA: FULGOROIDEA: DELPHACIDAE):

CLEANING OUT *DELPHACODES* FIEBER

by

Kathryn M. Weglarz

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Entomology

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NOMENCLATURAL NOTE

This work is considered unpublished for the purposes of zoological nomenclature (Art. 8.3, ICZN 4th ed., 1999).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The original description of *Chionomus* Fennah, 1971 placed three Neotropical species from the problematic and polyphyletic genus *Delphacodes* Fieber, 1866 within the taxon. Morphological evidence and recent molecular analyses suggest that additional *Delphacodes* species are allied with *Chionomus*.

Here *Chionomus* is redescribed; the definition is broadened to include 10 new species, bringing the total number of valid species to 13. Eight species are moved from the genus *Delphacodes*, two new species are described, and an additional four species are synonymized. Phylogenetic analyses of morphological and molecular sequence data, from the mitochondrial gene *Cytochrome Oxidase I*, for 6 ingroup and 5 outgroup taxa in the Delphacini provide support for the monophyly of *Chionomus* as described here. Phylogenetic analyses were performed using 3 optimality criteria (Maximum Likelihood, Maximum Parsimony, and mixed model Bayesian). All analyses support paraphyly of the original definition of *Chionomus* and monophyly of the revised genus. The maximum likelihood and Bayesian analyses suggest the same ingroup branching pattern of *C. tenae* (*C. puellus* ((*C. haywardi* + *C. pacificus*) + (*C. havanae* + *C. balboae*)).

Chapter 1

GENERIC REVISION OF *CHIONOMUS* FENNAH 1971

1.1 Introduction

With over 2100 described species worldwide, the delphacid planthoppers (Hemiptera) compose the largest family in the infraorder Fulgoromorpha. These small insects, frequently 2-4 mm in length, include numerous crop pests of serious economic importance, such as the brown planthopper, *Nilaparvata lugens* (Stål), and the white-backed planthopper, *Sogatella furcifera* (Horváth) (Dyck and Thomas 1979, Wilson and O'Brien 1987). Most of this family's pestiferous members, a small subset of the taxon, are broadly known; however, most species remain poorly investigated. Many delphacid species are still unknown to science, and while most of these species are from the tropics, some can still be found in well-explored regions of the world (e.g., Weglarz and Bartlett 2011). These undecribed species may be essential to understanding relationships between species and providing insight on important morphological features. An in-depth understanding of this family relies on exploration of the relationships among species and this will allow more informed investigations of the ecology, genetics, and physiology of these insects.

1.1.1 A General Background of the Family Delphacidae

The Delphacidae is a clearly defined yet enigmatic taxon. It is basal within the Fulgoroidea and is most closely related to the Cixiidae, with which they may be paraphyletic (Asche 1985, Ceotto *et al*. 2008, Urban *et* al. 2010). Delphacids are

easily recognized by the autapomorphic calcar, or posttibial spur, found on the hind legs (Figure 1).

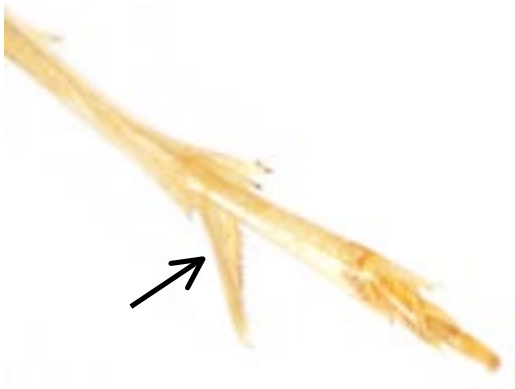

Figure 1. The calcar of *Delphacodes banosensis*.

This spur arises from one of the apical teeth on the hind tibiae between the 1st and 3rd larval instars (Emeljanov 1996). The structure of this spur can be informative at the higher taxonomic levels, especially subfamily. Currently, the family is divided into 6 subfamilies (Urban *et al.* 2010; Table 1); only one of these is not native to the New World.

Table 1. The subfamilies of Delphacidae including the number of genera and species in each, updated from Asche (1985). * Indicates the subfamily is found in the New World.

Subfamily	Number of Genera	Number of Species
Asiracinae*	25	180
Viscayinae	2	10
Plesiodelphacinae*	2	7
Kelisiinae*	2	54
Stenocraninae*	8	86
Delphacinae*	298	1,724
Total	**337**	**2,071**

Delphacids frequently live in wet or moist habitats, but can be found in all major biomes including deserts, grasslands, tundra, and rainforests (Wilson *et al.* 1994). Even though they originated prior to the Cretaceous period, and radiated with the flowering plants, these phloem-feeding insects are predominantly associated with monocots (Wilson *et al.* 1994). Their host constraints are most notably, but not singularly, contradicted on the oceanic islands (especially Hawaii) where delphacids are of widespread occurrence on dicots (Wilson *et al.* 1994). Additionally, a number of delphacids have made interesting host shifts, including one to the moss *Polytrichastrum alpinum* (Hedw.) G.L. Sm. (Wheeler 2003).

Of the 2,163 species of delphacids (Bartlett *pers. comm.*), 85 are considered serious crop pests (Wilson and O'Brien 1987, Wilson 2005). It has been suggested that delphacids may have had a role in the downfall of Mayan civilization (Brewbaker 1979) and are known to have caused serious rice famines in Japan and Korea throughout the ages (Dyck and Thomas 1979, Matsumura 2000, Otuka *et al.* 2007, Wantanabe *et al.* 2009). They remain a serious concern for rice farmers in Asia and migrations of these insects are often tracked by satellite in the region (Otuka *et al.* 2005). Feeding and oviposition account for much of the damage by planthoppers

(Urban *et al*. 2010). Planthoppers also serve as vectors for 36 plant pathogens and one phytoplasma (Wilson and O'Brien 1985, Wilson 2005, Arocha *et al.* 2005). Eight vector species are found in the continental US, of these 2 are introduced, highlighting the need to monitor for these insects at our ports (Meagher *et al.* 1991, Bartlett and Gonzon 2008). As serious crop pests, the ability to identify these insects correctly is vital. Unfortunately, lack of adequate keys to species and genera limits identification to specialists. This problem is exacerbated by the existence of large genera that are poorly defined, such as *Delphacodes*.

1.1.2 The Problematic Genus *Delphacodes*

Delphacodes Fieber, 1866, was originally established as a subgenus of *Delphax* Fabricius, 1798 (Delphacinae: Delphacini). Fieber (1866) erected this subgenus to separate 10 species based on features of the head, especially relating to the carinae of the frons and vertex. Kirkaldy (1904) raised *Delphacodes* to genus and designated the type species as *Delphacodes mulsanti* (Fieber, 1866) (Figure 2).

Figure 2. Lateral view of *D. mulsanti* from the Wagner collection.

Kirkaldy designated the lectotype of *Delphacodes mulsanti* in 1907. The specimen was a female in poor condition, and this designation exacerbated confusion over the definition of this genus. *Delphacodes* became interpreted very broadly, causing other genera to become subsumed under *Delphacodes*.

Once *Delphacodes mulsanti* was designated as the type species, the taxonomic composition and status of *Delphacodes* became more complicated. At various times this genus had been sunk under *Megamelus* Fieber, 1866 (Crawford 1914, Haupt 1935, Dlabola 1954) and *Calligypona* J. Sahlberg, 1871 (China 1954). Muir (1917), Metcalf (1943), Dlabola (1957), Linnavouri (1957), and Nast (1958) supported *Delphacodes* status as a valid genus, and treated it as a senior synonym of *Delphacissa* Kirkaldy, 1906; *Paraliburnia* Jensen-Haarup, 1917; and *Opiconsiva* Distant, 1917 (Metcalf 1943); but all of these genera are currently considered valid (Nast 1972, Asche 1985). Meanwhile, other workers described or moved new species into an increasingly dubious genus (e.g., Muir and Giffard 1924, Muir 1926, Beamer 1948a, b, c, Caldwell and Martorell 1951).

Delphacodes sensu stricto did not begin to take shape until Nast (1958) restricted its definition. Wagner (1963) and Asche and Remane (1983) upheld Nast's assertion that this genus was limited to the western Palearctic region. Throughout time 122 Nearctic species have been placed in *Delphacodes s.l.*, and currently there are 108 (Bartlett *pers. comm.*). Between Asche (1985) and after Metcalf (1943), the only attempts made to remove New World species from *Delphacodes* were by R.G. Fennah, who described a series of genera as *Delphacodes* segregates (e.g., Fennah 1963, 1965, 1971), including *Chionomus*. Recently, efforts to fix the *Delphacodes*

problem have been renewed (i.e., Gonzon and Bartlett 2007, Bartlett and Hamilton 2011).

1.1.3 The Genus *Chionomus*

Fennah (1971) moved 3 species from *Delphacodes* into the new genus *Chionomus*. He designated *Chionomus*' type species as *Delphacodes havanae* Muir and Giffard, 1924 (Figure 3b). He also included *D. balboae* Muir and Giffard, 1924 and *D. haywardi* Muir, 1929, a vector of Mal de Rio Cuarto virus (MRCV) (Velázquez *et al.* 2003). Since Fennah (1971), there has been no further taxonomic work on *Chionomus*; however, it has become evident that several taxa currently in *Delphacodes* belong in *Chionomus*. Some *Delphacodes* display a strong superficial resemblance to *Chionomus* (e.g., *C. havanae*, Figure 3b, and *D. puella*, Figure 3a), further corroborated by similarities in male genitalic features. Phylogenetic analyses using combined molecular data from 18S, 28S, *Wingless* (Wg) and *Cytochrome Oxidase I* (COI) plus morphology placed *Chionomus havanae* sister to *Delphacodes puella* (Urban *et al*. 2010), encouraging further taxonomic investigation of *Chionomus* and similar *Delphacodes*.

This project investigates the taxonomy and phylogenetics of the genus *Chionomus* and morphologically similar *Delphacodes.* It seeks to provide (1) an adequate morphological revision of *Chionomus* to include species previously excluded, (2) a key to species, (3) uniform descriptions and illustrations for all included species, and (4) phylogenetic analyses of the genus using data from morphology and the mitochondrial gene *Cytochrome Oxidase I* (*COI*). The taxonomic investigation will be presented in the first chapter and the phylogenetic analyses in the second.

1.2 Materials and Methods

The 3 species of *Chionomus* and 23 morphologically similar species of *Delphacodes* were examined for taxonomic revision (Table 2). In total, 634 specimens of *Chionomus* were examined for this study. Abbreviations for institutional collections are below (Table 3). Collection abbreviations follow Arnett *et al.* (1993) with the addition of the Vince Golia Collect (VGC) and the Central Missouri State University Collection (CMSU). Curation and specimen dissection techniques followed McPherson (1980), Bartlett and Deitz (2000), and Wilson (2005), but are briefly detailed as follows.

As with most small insects, specimens are glued to points on the right side of their thorax and then placed on insect pins. All specimens are labeled with collection locality, date, collector, and, when known, method of collection. In order to identify species examination of the male genitalia was generally necessary. This was done by removing the abdomen from the specimen and placing it in approximately 10% potassium hydroxide (KOH) solution at room temperature for 12-24 hours for clearing. The abdomen was then washed in water and moved to glycerin for examination. For long-term storage, all dissected material was placed in a microvial with a small amount of glycerin and pinned with the rest of the specimen.

Species distributions are compiled from literature records and material examined. Distribution summaries and material examined are given approximately north to south by country. US States are abbreviated according to the official US Postal Service abbreviations; Canadian provinces are abbreviated according to Canada Post. All specimens examined are listed in Material Examined for the species. Specimen data follows the format of the label, with added notes in square brackets; male "♂", and female "♀" symbols are used. 546 specimens were macropters (434

male, 112 female) and 88 specimens were brachypters (62 male, 26 female) (Table 4). For primary types, label information is quoted, with each line break indicated by "/" and each label separated by "//".

Table 2. Species considered for inclusion in *Chionomus* with description information and location of types.

Species	Author, Year	Type Location
Chionomus havanae	(Muir & Giffard, 1924)	BPBM
C. balboae	(Muir & Giffard, 1924)	BPBM
C. haywardi	(Muir, 1929)	INHS
Aethodelphax concavus	(Beamer, 1948)	SEMC
Delphacodes aculeata	Beamer, 1948	SEMC
D. arcuata	Beamer, 1948	SEMC
D. ardentis	Beamer, 1948	SEMC
D. banosensis	Muir, 1926	BPBM
D. bellicosa	Muir & Giffard, 1924	BPBM
D. dentis	Beamer, 1948	SEMC
D. gluciophila	Muir, 1926	BPBM
D. mesada	Caldwell, 1951	USNM
D. pacifica	(Crawford, 1914)	USNM
D. penepuella	Beamer, 1948	SEMC
D. puella	(Van Duzee, 1897)	USNM
D. quadridentis	Beamer, 1948	SEMC
D. quadrispinosa	Muir & Giffard, 1924	USNM
D. sagae	Beamer, 1946	SEMC
D. saxicola	Muir, 1926	BPBM
D. scocholoa	Cronin & Wilson, 2007	SEMC
D. securigera	Muir, 1926	BPBM
D. serrata	Beamer, 1948	SEMC
D. silvae	Beamer, 1946	SEMC
D. tenae	Muir, 1926	BPBM
D. vaccina	Caldwell, 1951	USNM
Syndelphax dissapatus	(Muir, 1926)	BPBM

All observations were made using a Wild-Herbrugg dissecting scope with 20x oculars and a 6-50x objective lens. All photographs and measurements were taken using a Nikon SMZ-1500 Digital Imaging Workstation with Nikon DS-U1 digital camera and NIS Elements Imaging software (version 3.0). All illustrations were made by tracing photographs with a scale bar in Adobe Illustrator. All measurements are reported in millimeters (mm) as averages with the number of specimens measured indicated ('n'). Total body length was measured from the anterior margin of the vertex to the end of segment X (i.e. excluding the anal tube and wings) in dorsal view. Body width was measured in dorsal view as the distance between the tegulae. Scale bar length is 0.2 mm for full body and frons views and 0.05 mm for genitalic images and illustrations unless otherwise noted.

All morphological terminology follows Asche (1985) with the exception of the parameres being referred to as having a proximal 'basal angle' and a distal 'inner angle' (*sensu* Metcalf 1949). The use of the heading 'genitalia' should be understood as male and include terminal segments. Segment I will reference the first segment of the antennae and segment II will reference the second. The number and arrangement of sensory pits of the antennae (rhinaria) will be described by listing the number found in each vertical row, beginning with the dorsal-most row (i.e., 3, 3-4, 2, 2). Diagnostic descriptions are included for all species in *Chionomus*. Features between species in the generic description that are invariant among the species are not repeated in species descriptions unless necessary for clarity. Species descriptions include known hosts, relevant literature since Metcalf (1943), consistent genitalic illustrations, and the sequence of a 540 base pair section of the mitochondrial gene *Cytochrome Oxidase I* (COI) (when available) with the GenBank number. A URL to a genus page on the

World Wide Web developed by the author has been provided; detailed species information will be provided here as soon as this work is published in accordance with the rules of the ICZN. All material examined is to be included on the American Museum of Natural History's Plant Bug Inventory Database (PBI). All reported host plants are compiled from literature and label data. Host plant nomenclature, including common names, follows the USDA online PLANTS database (USDA, NRCS 2011) or ITIS (Integrated Taxonomic Information System; ITIS 2011) if not available on PLANTS. Methods for extraction and amplification of *COI* are discussed in detail in the following chapter.

1.3 Results

Thirteen species are included in the new definition of *Chionomus.* Two new species were described and of 26 previously described species were considered, 11 are excluded and 4 are treated as junior synonyms.

1.4 Systematic Treatment: Taxon descriptions

1.4.1 Genus *Chionomus* Fennah

Chionomus Fennah, 1971: 323-324.

Type species: *Chionomus havanae* (Muir & Giffard, 1924), by original designation.

COLOR. General body color brunneous, legs paler, white to stramineous or light brown; with carinae of the head, paranota, posterior edge of pronotum, and scutellum pale. Pronotum with wide white band along posterior margin, (lacking in *C. banosensis, C. gluciophilus, C. quadrispinosus*), paranota paler along margins or more

broadly, pronotal carinae contrasting in color in some species (*C. bellicosus, C. dissipatus*). Wings clear with fuscous mark near apex of clavus.

STRUCTURE. Head narrower than pronotum, vertex quadrate, approximately as wide as long (except *C. herkos* n. sp.); carinae distinct, stem of Y-shaped carina weak, median carinae of vertex converging at fastigium. In lateral view, genal carinae angled anteroventrad to meet anterior margin of clypeus, fastigium rounded. Carinae of frons distinctly contrasting with darkened foveae, lateral margins of frons parallel to subparallel, widest point between midpoint of compound eyes to just below ventral edge; median carina distinct, forked at fastigium. Antennae short, reaching just posterior of tegulae, circular in cross-section, segment I just longer than wide, II longer than I, expanded apically, conical. Pronotal carinae weak, median carinae of pronotum always reaching posterior margin, lateral carinae curved, diverging posteriorly, not reaching hind margin. Mesonotum dark in color, *C. bellicosus* and *C. pacificus* with median vitta or carinae lightened, scutellum always white except in males of *C. dolonus,* mesonotal carinae weak in macropters, median carinae never reaching scutellum, lateral carinae diverging, reaching hind margins, carinae more pronounced in brachypters. Legs quadrate in cross-section, tibia carinate, hind tibiae just distal to joint with femur and one at midpoint, 5 teeth at apex of tibiae. Calcar foliaceous, about half length of basitarsus. Veins of macropter distinct, sparsely setaceous; R+Sc 3 branched, M 3 branched, CuA 3 branched, CuP unbranched, claval veins fusing midlength (Figure 4); tegmina of brachypter rounded apically.

Abdomen compressed dorsoventrally, tapering caudad to truncate apex in males. Male pygofer longer ventrally than dorsally, broad in lateral view; in caudal

view opening round or mildly dorsoventrally compressed; dorsolateral margins may be produced (i.e. *C. gluciophila, C. herkos*) but typically smooth, ventral margin smooth except in *C. dolonus* which has a caudally projecting tooth. Diaphragm strong, well-developed, dorsal margin concave leaving large inverted triangular or trapezoidal opening between diaphragm and segment X; armature distinctly projecting caudad (Figure 5), often bilobed or indented with aedeagus resting in space provided, lacking in *C. havanae* and *C. haywardi*, may be produced as a triangulate boss (*C. havanae*, *C. balboae, C. haywardi, C. herkos*), bifurcate processes (*C. banosensis, C. bellicosus, C. pacificus, C. puellus*), quadrate process (*C. dissipatus, C. gluciophilus*), U-shape projection (*C. quadrispinosus*), or projecting fold or shelf (*C. dolonus, C. tenae*). Aedeagus tubular, parallel sided, except *C. havanae, C. bellicosus, C. herkos*; slightly to distinctly curved dorsad, gonopore subapical and dorsal. Parameres flattened apically but inner angle may be slightly curved or caudally produced (*C. banosensis, C. dissipatus, C. herkos*), basal angle strong, widest in basal third (except *C. tenae*), lateral margins concave, widened apically. Segment X quadrate, bearing 0, 2, or 4 processes on caudal margin, ventrally directed; segment XI shorter than segment X.

Remarks.

Chionomus is a cryptic genus. The general coloration of these insects is helpful for identification but not unique to *Chionomus* alone. Both the dark spot at the apex of the clavus and the lightening of the pronotum can be found in other genera (e.g., *Javesella* Fennah, 1963 and *Falcotoya* Fennah, 1969). The combination of these traits and the caudally projecting armature of the diaphragm are unique to this genus. Externally, the members of this genus are very similar, male genitalia are necessary for clearly delineating species. *Chionomus* superficially resembles *Falcotoya*, but

Falcotoya lacks the produced armature of the diaphragm and *Chionomus* lacks the sickle shaped, strongly downcurved aedeagus of *Falcotoya*. The general coloration is shared by some members of *Javesella*, but these lack the dark spot on the clavus, and have a much broader opening of the pygofer with widely diverging parameres and processes on segment 10 always closely approximated. *Isodelphax* Fennah, 1963, also shares the same general appearance but this genus lacks the dark spot on the clavus and the parameres are strongly diverging apically with a strongly projected basal angle.

Chionomus species are commonly found and may be abundant in collections. Most taxa come readily to lights.

Etymology.

The original author did not indicate the gender or derivation of the name *Chionomus.* It appears to stem from the Greek noun *chionos*, meaning snow, possibly referencing the whitened posterior edge of the pronotum, with–*mus* added to make the name euphonious. The names of three species originally placed in *Chionomus* do not indicate gender, as they are Latinizations of proper nouns in the genitive. Following article 30.2.4 of the ICZN (4th ed., 1999) the name is treated as masculine (consistent with a -*us* Latin ending).

Genus Page URL.

http://ag.udel.edu/enwc/research/delphacid/species/Chionomus.htm

1.4.2 Key to Males of the Genus *Chionomus*

1. Armature of diaphragm distinctly bilobed (Figures 15d, 31d, 34d) – (2).

   Armature of diaphragm not distinctly bilobed, may be cordate, notched, or U-shaped (Figures 8d, 23d, 37d) – (5).

2. Armature of diaphragm hooked, lobes parallel; processes of segment X present but not particularly strong, specimens with carinae of the mesonotum lightened frequently forming a vitta (Figures 14-15, 29-31) – (3).

   Armature of diaphragm not hooked, lobes distinctly diverging; processes distinct and directed ventrad, carinae of mesonotum concolorous (Figures 12, 13, 32-34) – (4).

3. Armature of diaphragm hooked only in apical half, lobes only diverging in apical half; aedeagus with toothed flange on left side (Figures 12, 13) – *C. bellicosus.*

   Armature of diaphragm hooked along entire length, lobes diverging from point of origin; aedeagus without flange, with two rows of scattered teeth (Figures 30, 31) – *C. pacificus.*

4. Lobes of armature diaphragm small and closely approximated; processes of segment X parallel. Posterior edge of pronotum dark, only paranota white in color (Figures 12, 13) – *C. banosensis.*

   Lobes of armature of the diaphragm produced, diverging from point origin; processes of segment X diverging. Posterior edge of pronotum white, paranota also white (Figures 33, 34) – *C. puellus.*

5. Pygofer with prominent quadrate, dorsolateral process. Parameres not flattened at apex. (Figures 27, 28) – *C. herkos.*

   Pygofer without dorsolateral processes, if produced at dorsolateral margin, not quadrate. Paramere flattened at apex. (Figures 8, 19, 25) – (6).

6. Segment X with a total of 4 processes (Figures 19a, 21a, 23a, 37a) – (7).

   Segment X with only 2 processes or processes vestigial (Figures 8a, 11a, 25a, 40a) – (9).

7. Secondary processes of segment X small, spine-like. Armature of diaphragm shelf-like. Ventral margin of pygofer with caudally projecting median process (Figures 20, 21) – *C. dolonus.*

Secondary processes of segment X long, sinuate. Armature of diaphragm quadrate, quadrate and notched, or U-shaped. Ventral margin of pygofer lacking median process (Figures 19, 23, 37) – (8).

8. Armature of diaphragm quadrate or cordate/notched, toothed along vertical margins; aedeagus not distinctly enlarged at base (Figures 19c, d, 23c, d) – (9).

   Armature of diaphragm U-shaped, lacking teeth; aedeagus with distinctly enlarged, quadrate base (Figures 37c,d) – *C. quadrispinosus.*

9. Armature of diaphragm notched along ventral margin; aedeagus with slight enlargement apically. Parameres not produced opposite of basal angle. Posterior compartments of vertex and stem of Y-shaped carina dark (Figures 22, 23) – *C. gluciophilus.*

   Armature of diaphragm quadrate, notch along ventral margin not evident; aedeagus tapering along entire length, not enlarged apically. Parameres with rounded projection opposite of basal angle. Posterior compartment of vertex light but with fuscous markings, stem of Y-shaped carina light (Figures 17, 19) – *C. dissipatus.*

10. Aedeagus nearly straight, may have slight dorsal curve (Figures 8c, 11c, 25c) – (11).

    Aedeagus with distinct curve dorsad, nearly forming a right angle apical hook on left, small teeth along length. Segment X with two rounded processes, lobe-like, arising from the middle of segment. Specimens frequently large for *Chionomus*, with wings infuscate (Figures 38-40) – *C. tenae*.

11. Aedeagus with subapical and distinctly projecting flagellum, lacking teeth and hooks (Figure 8c) – *C. havanae.*

    Aedeagus without flagellum, with hooks and/or teeth (Figures 11c, 25c) – (12).

12. Aedeagus with large hooks on right side of aedeagus; apex of parameres anvil shaped (Figures 11b,c) – *C. balboae.*

    Aedeagus with small teeth in two scattered rows, lacking any sort of hook; apex of parameres quadrate (Figures 25b,c) – *C. haywardi.*

1.4.3 *Chionomus havanae* (Muir and Giffard, 1924)

(Figures 3b, 4, 5a, 6-8)

Delphacodes havanae Muir & Giffard, 1924: 37.

Chionomus havanae (Muir & Giffard), comb. by Fennah, 1971: 324.

Type Locality.

Cuba, Havana.

Diagnosis.

Body light to dark brown, with white to ivory markings. Vertex quadrate; foveae of frons and vertex dark. Carinae distinct, pale; antennae light brown. Pronotum dark anteriorly, shading to white posteriorly, paranota white. Armature of diaphragm forming smooth triangular boss, apex of parameres with outer angle strongly produced, rounded. Aedeagus sinuate, bearing a caudally projected process that extends past apex.

Description.

COLOR. *Macropter.* Body dark to light brown, bearing white or ivory markings. Carinae of head (including genal carinae) distinct, paler. Foveae of head fuscous. Antennae dark brown proximally, shading paler distally. Pronotum dark brown anteriorly, white posteriorly. Mesonotum dark shining brown, white posteriorly at termini of lateral carinae and scutellum. Legs yellow bearing light brown stripes on anterior face, apex of tarsi brown. Wings hyaline with dark marking near apex of clavus, some specimens with fuscous marking along claval fold and nodal line. Abdomen brown, caudal edge of terga and sterna often paler. Pygofer brown, segment X light brown. *Brachypter.* Similar, bearing white stripe at tegmina apex.

STRUCTURE. *Body*. Body length (in mm) macropters male (♂) 1.59±0.13 (n=22); ♂ brachypter 1.88±0.04 (n=3); width ♂ 0.74±0.08 (n=25). *Head*. Vertex length 0.18±0.03 (n=25); vertex width 0.17±0.02 (n=25); frons length 0.46±0.02 (n=25); frons width 0.21±0.02 (n=25). *Macropter*. Vertex approximately quadrate in dorsal view, barely wider than long; carinae distinct, stem of Y-shaped carina obsolete. In lateral view (Figure 6b,d), fastigium rounded; projecting in front of the eye about 1/6th eye length. Carinae of frons distinct (Figure 7a), subparallel, widest at ventral margin of compound eyes. Antennae with segment I subequal in length to second, segment II wider than segment I, sparsely setaceous; sensory pits of segment II arranged 4, 3-4, 2, 2, evenly spaced; surrounded by small black setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending before scutellum, lateral carinae diverging posteriorly, reaching hind margin. Tibiae carinate; sparsely setaceous, two rows of small black spines along ventral margin. Calcar bearing 22-26 small teeth (holotype with 24). *Brachypter*. Same as above, tegmina rounded apically, reaching to apex of 5 abdominal segments.

Abdomen. Macropter. Slightly dorsoventrally compressed, tapering caudad to truncate apex; long, fine setae surrounding each abdominal spiracle. *Brachypter.* Same as above.

Genitalia. Pygofer in lateral view (Figure 7c) nearly thrice as long ventrally as dorsad, ventral margin sinuate. In caudal view (Figure 7b, 8d), as tall as wide, globular; dorsolateral margins mildly produced. Opening to inner chamber triangular, pointed ventrad. Diaphragm strong, armature distinctly produced and projecting caudad, apex triangular to bilobed, smooth. Parameres flattened distally, widest in

basal third, basal angle strong, projecting, quadrate; dorsolaterally diverging to convexly curved apices, lateral margins concave, inner angles weak, acute; outer angles produced to rounded apices. Suspensorium inconspicuous. Aedeagus terete in cross-section, widest near base, irregularly tapering for most of length, abruptly tapering distally to blunt apex, weakly curved ventrad in apical quarter, keeled ventrally, gonopore apical; bearing conspicuous straight dorsal spine projecting beyond aedeagus apex. Segment X longer than tall, quadrate, not armed. Segment XI produced, about ½ length of segment X, projecting caudally.

Hosts.

Axonopus compressus (Sw.) P. Beauv. Common carpetgrass (Fennah, 1959).

Distribution.

USA: FL; Cuba; Cayman Islands (Grand Cayman); Puerto Rico; Jamaica, Trinidad; Mexico; Belize; Guatemala; Honduras; Costa Rica; Panama; Colombia; Venezuela; Guyana; Brazil; Peru; Bolivia.

COI Sequence.

5' –

GAAGTTTATATTTTAATTTTACCTGGATTTGGTTTAATTTCACATATTATTA
TGCAAGAAAGAGGTAAACGAGAAACCTTTGGATCAATTGGTATAATTTAT
GCAATGTTGGCTATTGGAGTTCTAGGATTTATTGTTTGAGCACACCATATA
TTCACTGTCGGAATAGATATTGATACACGAGCCTACTTTACTTCAGCAACC
ATAATTATTGCAGTTCCTACAGGAATTAAAATTTTTAGATGAATCGCCACA
ATTTATGGATCTAAAATTAACTTTTCCCCCCAAATAATCTGATCAATAGGG
TTTATTTTATTATTTACAATTGGTGGATTAACAGGAGTTATGCTTGCAAATT
CATCAATTGATATTGTTCTACACGATACCTATTATGTTGTTGCACACTTTCA

TTATGTATTATCAATAGGAGCTGTCTTTACAATTGTAGCCAGATTTATTCAT
TGATATCCACTTTTTACAGGTGTATTAATAAATAAAAAATGATTAAAAATT
CAATTTAATTCAATATTTATCG – 3’

Remarks.

C. havanae is common in collections. It is usually collected in association with *C. balboae*, particularly at lights. This species is easily differentiated by the sinuate shape of the parameres (basal angle strong, apices convexly curved) and the apical spine on the aedeagus. Males can frequently be identified without dissection if the parameres and apical spine of the aedeagus can be seen. This species may be most closely allied with *C. balboae* and *C. haywardi,* which have similarly a similarly triangular shaped armature of the diaphragm but lack the spine of the aedeagus.

Type Material Examined.

Holotype [BPBM]: Macropterous ♂, “Havana / Cuba.Baker // Megamelus / albopalliatus / Uhl. [Handwritten] // ♂ [Handwritten] // [Blue paper] // Holotype [Red paper, vertical orientation, affixed to following label] //Delphacodes / havanae / ♂ M.G // under / puella / Crawf Col / havana [Handwritten, last line vertical orientation]// Paratype [reverse side of previous label, yellow paper] // 1075 [Handwritten]”.

Other Material Examined.

United States: Florida. Broward Co, Ft. Lauderdale, 14-III-1975, NL Woodiel (UDCC, 1m♂); Collier Co., Fatahachee Strand St. Res., 18-V-1998, C.W. O’Brien (LBOB, 1m♂). **Mexico:** ca. 25mi N. C. Monte. Nacimiento del Rio Frio Tam, 31-VII-1970, C.W. O’Brien (LBOB, 1m♂); Jachitan 17mi E Oax, 8-VII-1953, University of Kansas (SEMC, 1m♂); Ver., 250’ Los Tuxtlas, Biol Sta. UNAM, 20-V-1983, C&L

O'Brien & G Marshall (LBOB, 3m♂); Campeche, Campeche, 4-VIII-1974, L.B. O'Brien (LBOB, 2m♂); Camp. Campeche, 9-VIII-1974, L.B. O'Brien (LBOB, 1b♂); Yuc., 15mi E Chichenltza, 7-VIII-1974, C.W.&L. O'Brien & Marshall (LBOB, 1m♂); Vera Cruz 3mi W Coatzacoalcos, 26-VI-1971, Ward & Brothers (LBOB, 10m♂). **Puerto Rico:** Guavanilla, IX-XI-1969, E. Murphy (USNM, 1m♂); Mayagüez, 3-4-VIII-1955, J.A. Ramos (LBOB, 2m♂). **Cayman Islands:** Cayman Brac. The Creek, 6-XII-1995, C.R. Dilbert (UDCC, 1m♂); The Creek, 27-XII-1995, C.R. Dilbert (UDCC, 2m♂); The Creek, 28-XII-1995, C.R. Dilbert (LBOB, 1m♂). **Belize:** Orange Walk Rio Bravo Res. Sta., 10-13-VI-1991, P.H. Freytag (LBOB, 7m♂); O.W. Dist. Rio Bravo Cons. Area Hdqrtrs, 8-VII-1996, L.B. O'Brien (LBOB, 1m♂); O.W. Dist. Rio Bravo Cons. Area Hdqrtrs, 13-VII-1996, L.B. O'Brien (LBOB, 3m♂); O.W. Dist. Rio Bravo Cons. Area Mahogeny Trail, 19-VII-1996, L.B. O'Brien (LBOB, 1m♂); Stann Creek Cockscomb Basin, 12-VI-1991, Tom Myers (LBOB, 10m♂); Toledo Dist. Blue Creek Village, 26-V-1999, J. Shuey (LBOB, 1m♂). **Honduras:** Zomorano, 3-IX-1964, G.A. Axtell (CSAC, 2m♂); Tela, 15-III-1936, John Deal (SEMC, 1m♂); Lancetilla, nr. Tela, 19-VI-1979, J.A. Chemsak, A.&M. Michelbacher, W.W. Middlekauff (UDCC, 1m♂, 2m♀); Cho. 14 mi NW Choluteca, 16-VI-1974, L.B. O'Brien (LBOB, 2m♂); Dept of Cortes, La Lima United Fruit Co., 3-VI-1964, F.S. Blanton, A.B. Broce, R.E. Woodruff (LBOB, 1m♂). **Costa Rica:** Heredia, nr Puerto Viejo, La Selva Biol. Sta., 19-VIII-2003, CR Bartlett (UDCC, 17m♂); Limon, Guayabo, 19km NE Turrialba, 11-IX-1998, C.W.&L.B. O'Brien (LBOB 1m♂); Car. Turrialba, 20-VI-1974, L.B. O'Brien (LBOB, 1m♂); Province of Cartago, Turrialba, 17-20-VIII-1969, R.E. Woodruff (LBOB, 1m♂). **Trinidad:** Curepe, Santa Margarita Circular Rd, 5-VII-1972, F.D. Bennett (LBOB, 1m♂). **Panama:** Fort Clayton, 8-15-

IX-1978, H.J. Harlan (LBOB, 2m♂); Barro Colorado Is., 7-VIII-1967, C.W. & L. O'Brien (LBOB, 1m♂); Coco Solo Hosp, C.Z., 29-V-1975, D. Engleman (LBOB, 1m♂); Gamboa Chagas R., 30-VI-1974, L.B. O'Brien (LBOB, 1m♂); Las Cumbres, 4-VII-1974, C.W.&L.B. O'Brien & Marshall (LBOB, 1m♂); Las Cumbres, 16-VII-1971, M Daykin (CSAC, 1m♂); Las Cumbres, 28-VII-1971, M Daykin (CSAC, 1m♂). **Colombia:** Dept. Valle Mun. Candelaria Finca San Luis, 3-5-III-1975, R. C. Wilkerson (LBOB, 2m♂). **Venezuela:** Apure, near San Fernando de Apure, 20-VI-2000, P.M. Freytag, M.A. Gaiani, Q. Arias (UDCC, 1m♂). **Brazil:** Rondonia. 62km SW Ariquemes, Fzda Rancho Grande, 3-15-XII-1996, JE Eger (LBOB, 4m♂); 62km SW Ariquemes, Fzda Rancho Grande, 4-16-XI-1997, JE Eger (LBOB, 1m♂); 62km SW Ariquemes, Fzda Rancho Grande, 19-21-XI-1997, U. Schmitz (LBOB, 1m♂); 62km SW Ariquemes, Fzda Rancho Grande, 8-20-XI-1994, JE Eger (LBOB, 1m♂); Sao Paulo. Piracocaba, 20-I-1966, CA Triplehorn (UDCC, 1m♂). **Peru:** Pasco Villa Rica, 21-X-2002, C.J. Dietrich (INHS, 3b♂); Loreto 3km Tournavista Rd., 34km W Pucallpa, XII-1971, R.T. & J.C. Schuh (UDCC, 2m♂, 1m♀). **Bolivia:** Santa Cruz Dept. 3.7km SSE Buena Vista, Hotel Flora y Fauna, 14-28-X-2000, MC Thomas (UDCC, 1m♂); S.C., 10mi W Portachuelo, 27-III-1978, C.W. O'Brien (LBOB, 1m♂); S. Cruz, Saavedra Res. Sta, 25-III-1978, C.Ward & CW. O'Brien (LBOB, 1m♂).

1.4.4 *Chionomus balboae* (Muir and Giffard, 1924)

(Figures 9-11)

Delphacodes balboae Muir & Giffard, 1924: 36.

Chionomus balboae (Muir & Giffard), comb. by Fennah, 1971: 324.

Type Locality.

Mexico, Veracruz, Jalapa [Xalapa].

Diagnosis.

Body dark brown and shining, with white to ivory markings. Vertex quadrate; foveae of frons and vertex dark. Carinae distinct, off-white in color; antennae light brown. Pronotum dark anteriorly with band of white along posterior edge, paranota paler at posterior edge. Armature of diaphragm forming triangular or cordate boss, apex of parameres anvil-shaped. Aedeagus tubular, right side bearing preapical hook with proximal flange on distal third opposite 2 preapical spines on the left.

Description.

COLOR. *Macropter*. Body dark, brunneous, shining, with white or ivory markings. Carinae of head (including genal carinae) distinct, ochraceous to off-white in color, usually with a small amount brown at apex of carinae; median carinae of vertex less evident. Antennae brown to light brown proximally, shading distally paler to yellow. Pronotum dark brown to brown anteriorly, posterior edge and ventral edge of paranota white to ivory. Mesonotum dark, median and lateral carinae light brown in some specimens. Legs light brown, with hind legs lighter, occasionally yellow. Forewings hyaline, sometimes with faint fuscous markings, dark spot just before apex of clavus. Abdomen brown, caudal edge of each segment lightened to yellow or white, lateral projections of sternites yellow to white. Pygofer and segment X brown. *Brachypter*. Similar to above, tegmina infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter 1.67±0.13 (n=25); ♂ brachypter 1.74 (n=1); width ♂ 0.71±0.09 (n=25). Head: Vertex length 0.17±0.03 (n=25); vertex width 0.17±0.03 (n=25); frons length 0.45±0.03 (n=25); frons width 0.20±0.02 (n=25). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina

faint. In lateral view (Figure 9b,d), fastigium rounded; projecting in front of the eye about 1/5th eye length. Carinae of frons and clypeus distinct (Figure 10a), frons subparallel, widest just below compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 4, 3-4, 2, 2, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with 2 rows setae on ventral margin of femora, mostly bare. Calcar bearing 22-26 small teeth (holotype with 22). *Brachypter*. Same as above but with lateral carinae mesonotum evident, diverging posteriorly; tegmina apically rounded, reaching to apex of 7th abdominal segment.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex; abdominal spiracles surrounded by fine setae. *Brachypter*. Same as above.

Genitalia. Pygofer in lateral view (Figure 10c) nearly 2/3rds as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figure 10b, 11d), as tall as wide, rounded; margins raised, weakly carinate. Opening to inner chamber triangular, pointed ventrad. Armature of diaphragm triangular to heart shaped, smooth, distinctly projecting caudad. Parameres, widest in basal third, basal angle strong, projecting, quadrate; dorsolaterally diverging to anvil-shaped apices, lateral margins concave, inner angles weak, acute; outer angles produced to rounded apices. Aedeagus circular in cross-section, slightly curved dorsad, widest near base, slightly tapering for most of length, with slight subapical expansion before pointed apex; Aedeagus bearing 1 to 2

teeth on left and large subapical flange on right bearing 2 hooks; distal hook large, directed caudoventrally; proximal hook smaller, directed anteriorly; gonopore dorsal, subapical. Segment X quadrate, processes vestigial. Segment XI produced, about 2/3rds length of segment X.

Hosts.

None reported.

Distribution.

USA: FL; Mexico; Dominican Republic; Jamaica; Puerto Rico; St. Lucia; Cayman Islands; Belize; Guatemala; Honduras; Costa Rica; Panama; Guyana; French Guiana; Venezuela; Brazil; Ecuador; Bolivia; Paraguay; Argentina.

COI Sequence.

5'-

GTTTAATTTCACATATTATTATGCAAGAAAGAGGTAAGCGAGAAACTTTCG
GATCAATTGGTATAATCTATGCAATACTGGCTATTGGAGTATTAGGATTTA
TCGTATGAGCTCATCATATATTTACTGTAGGTATAGATATTGATACGCGAG
CCTACTTCACTTCAGCAACTATAATTATTGCAGTCCCCACTGGAATTAAAA
TCTTTAGATGAATCGCCACAATCTATGGTTCTAAAATTAATTTTTCCCCCCA
AATAATTTGATCTATAGGATTCATTTTATTATTTACAATTGGTGGATTGACA
GGAGTAATACTTGCTAACTCATCAATTGATATTGTCCTACATGACACTTAC
TATGTTGTAGCCCACTTTCATTATGTTTTATCCATAGGAGCTGTATTTACAA
TTGTAGCCAGATTTATCCACTGATACCCCCTATTTACAGGAGTTTCATTAA
ATAAAAAA -3'

Remarks.

This species is very frequently found mixed with specimens of *C. havanae*. The combination of the anvil shape of the parameres and the frequent projection of the large hook on aedeagus make it easy to separate from *C. havanae*. The arrangement of teeth on the aedeagus makes this species difficult to place; however it may reasonably be placed close to *C. havanae* and *C. haywardi* because of the triangular shaped armature of the diaphragm. Both of these species lack similar arming of the aedeagus, *C. havanae* bares a dorsal spine while *C. haywardi* is armed with small scattered teeth.

Type Material Examined.

Holotype [BPBM]: Macropterous ♂, "Jalapa / Crawford // [Blue paper] // Holotype [Red paper, vertical orientation, affixed to following label] // Delphacodes / balboae / ♂ M.G. [Handwritten] // ♂ gen. Slide No 8 / Series II/ Liburnia pacifica Crawf. / det. Crawford. / Single ♂ / Jalapa, mex. / Crawf. Coll. [Handwritten] // 854 [Handwritten]".

Other Material Examined.

United States: Florida. Putnam Co 3mi E Melrose, K. Ordway Preserve, 16-VII-1998, C.W. O'Brien & P. Kovarik, (LBOB, 2m♂). **Mexico:** Campeche. 9-VIII-1974, L.B. O'Brien (LBOB, 17m♂); 4-VIII-1974, L.B. O'Brien (LBOB, 2m♂); Sinaloa. Los Mochis, 20-VII-1922, CT Dodis (CASC, 3m♂); Jalisco 20 mi W of Tecolotian, 15-IX-1938, L.J. Lipovsky (SEMC 2b♂); Veracruz 3 mi W Coatzacoalcos, 26-VI-1971, Ward & Brothers (LBOB, 6m♂). **Belize:** Cayo District. nr. Teakettle Bank, Pooks Hill, 5-VII-2003, CR Bartlett (UDCC, 1m♂); Western Highway Mile 66, VI-15-1968, C. & D. Hasse (LBOB, 1m♂); Orange Walk. Rio Bravo Res. Sta., 10-13-VI-1991, P.H. Freytag (LBOB, 1m♂); Rio Bravo Cons. Area,

Mahogany Trail, 10-VII-1996, C.W. & L.B. O'Brien (LBOB, 1m♂); Rio Bravo Cons. Area, Hdqrtrs, 11-VII-1996, L.B. O'Brien (LBOB, 1m♂); Stann Creek Cockscomb Basin, 12-VI-1991, Tom Myers (LBOB, 2m♂). Orange Walk Town, 16-VII-1968, W.L. Hasse (LBOB, 1m♂). **Guatemala:** Quetzaltenango, Fuentes Georginas, Volcan Zunil, 8km SE Zunil, 16-II-2007, ATGonzon & R Donovall (UDCC, 1b♂). **Honduras:** Dept. of Comayagua, Comayagua, 1-VIII-1966, J.M. Matta (LBOB, 1m♂). **Panama:** Nueva Gorgano, 16-IX-1952, FS Blanton (USNM, 1m♂); Coco Solo Hosp. C.Z., 29-V-1975, D. Engleman (LBOB, 1m♂). **French Guiana:** 8km W. Risquetout, 10-11-VI-2005, JE Eger (LBOB, 5m♂); 14km E of N2 on rd to Dégrad Corréze, 6-XII-2002, J.E. Eger (LBOB, 2m♂). **Venezuela:** Rancho Grande Girardot Aragua, 14-VII-1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin, R.I. Schuster (CSAC, 1m♂); Guanare, estado Portuguesa, 10-13-IX-1957, Borys Malkin (CASC, 2m♂); Apure, Hato El Frio, 26km W El Saman de Apure, 24-VII-1988, C. & L. O'Brien & G. Wibmer (LBOB, 1m♂). **Ecuador:** Napo Province, Limoncocha, on Tio Napo, 14-I-1974, Boyce A. Drummond, III (LBOB, 1m♂); S.A. Runtun Val., Tungurahua, 22-XI-1938, F.M. & H. H. Brown (SEMC, 6b♂). **Brazil:** Belem, Para, VII-1954, NLH Krauss (USNM, 1m♂); Santa Catarina Nova Tenonia, 13-XII-1949, F. Plaumann (SEMC, 1m♂); Rondonia. 62km SW Ariquemes, Fzda Rancho Grande, 5-17-X-1993, JE Eger (LBOB, 2m♂); Rondonia. 62km SW Ariquemes, Fzda Rancho Grande, 8-24-IX-1994, JE Eger (LBOB, 1m♂); Rondonia. 62km SW Ariquemes, Fzda Rancho Grande, 3-15-XII-1996, JE Eger (LBOB, 4m♂, 1b♂). **Bolivia:** Dept Santa Cruz, 38km S. Santa Cruz de la Sierra, Ingenio La Delgica, 19-I-1980, L.A. Stange (LBOB, 2m♂); Cbb., Pto. S. Francisco, 19mi NW Villa Tunari, 1-IV-1978, C.W. & L.B. O'Brien & G.B. Marshall (LBOB, 1m♂); S.C., 10 mi W Portachuelo, 11-IV-

1978, GB Marshall (LBOB, 1m♂); S.C., Saavedra Res. Sta., 23-III-1978, CW & LB O'Brien (LBOB, 1m♂); Santa Cruz Est. Exp. Saavedra, 9-VIII-1980, D Foster (UDCC, 1m♂); Sta. Cruz., 5km SSE Buena Vista Hotel Flora & Fauna, 17-II-2007, C.W. & L.B. O'Brien (LBOB, 1m♂). **Paraguay:** 3km E Ypacarai, 7-X-1968, C.W. & L. O'Brien (LBOB, 2m♂); D. Cordillera, 7km W Caacupe, 6-VII-1968, L. & C.W. O'Brien (LBOB, 1m♂); San Lorenzo, 6-VII-1968, C. & C.W. O'Brien (LBOB, 1m♂); B. Acerval, 12-X-1968, C.W. & L. O'Brien (LBOB, 1m♂); Col. Independencia Villarrica, X-1951, F.H. Shade (SEMC, 1m♂). **Argentina:** Santa Ge, Villa Guillermina, II-1946, Willink & Hayward (SEMC, 1m♂); Chaco P.N. Chaco, 10-I-2008, C.H. Dietrich (INHS, 2m♂); Misiones, Pto. Iguazú Viejo Amer. Campgd., 7-I-2008, C.H. Dietrich (INHS, 1m♂); Corrientes, P.N. Mburucuyá, 0.5km N campgd, 8-I-2008, C.H. Dietrich (INHS, 3m♂); Corrientes, P.N. Mburucuyá, 0.5km N campgd, 9-I-2008, C.H. Dietrich (INHS, 1m♂);Corrientes, P.N. Mburucuyá, 0.5km N campgd, 8-10-I-2008, Dietrich et al (INHS, 1m♂).

1.4.5 *Chionomus banosensis* (Muir, 1926), new combination

(Figures 12-13)

Delphacodes banosensis Muir, 1926: 31.

Type Locality.

Ecuador, Tungurahua Province, Banos.

Diagnosis.

Body brunneous, dark, shining, with stramineous markings. Vertex quadrate; foveae of frons and vertex very dark. Carinae of the head distinct, yellow in color except for genal carinae and median carina of the vertex; antennae light brown. Pronotum entirely dark, paranota ivory. Armature of diaphragm posteriorly

projecting, composed of two diverging but closely approximated lobes; parameres with apices Y-shaped, sinuate, with distinct secondary process on proximal edge at midpoint. Aedeagus tubular, enlarged at base, upwardly directed, with a row of scattered teeth on either side connecting at the aedeagal base; segment X with 2 processes.

Description.

COLOR. *Macropter*. Body shining, dark, brunneous, with stramineous markings. Carinae of head (excluding genal carinae and median carinae of vertex) distinct, ochraceous to off-white in color, usually with a small amount brown at apex of carinae; median carinae of vertex and genal carinae concolorous with foveae. Antennae yellow, infuscate at joint of two segments. Pronotum dark, concolorous with body, paranota distinctly ivory. Mesonotum dark, median and lateral carinae obscure. Legs yellow; forewings hyaline, dark spot at apex of clavus not evident in holotype.

STRUCTURE. *Body*. *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina obscure. In lateral view (Figure 12b), fastigium rounded. Carinae of frons and clypeus distinct (Figure 12c), frons subparallel, widest midway below compound eyes and frontoclypeal suture. Antennae with first segment subequal in length to second, segment II wider than segment I; 2nd segment with sparse setae surrounding sensory pits.

Thorax. *Macropter*. Carinae of mesonotum evident, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly and ending anterior to hind margin.

Abdomen. *Macropter*. Specimen has been dissected, abdomen was not observed.

Genitalia. Pygofer in caudal view (Figure 12d) nearly as wide as tall, rounded; dorsal margins raised, carinate. Opening to inner chamber trapezoidal, pointed ventrad. Armature of diaphragm triangular composed of 2 lobes, smooth, projecting caudad. Parameres, widest in basal third, basal angle strong, projecting, quadrate, dorsolaterally diverging; apices with inner and outer angles distinct, diverging, Y-shaped. Exterior lateral margin of parameres concave, interior margin convex with distinct median process. Aedeagus circular in cross-section, curved dorsad in distal 1/3rd, with distinct widened base, tapering at apical 1/4th; aedeagus bearing row of scattered teeth on both sides, beginning dorsally at proximal edge of gonopore and converging ventrally at base of aedeagus. Segment X quadrate, processes distinct, directed ventrad. Segment XI produced, about ½ length of segment X

Hosts.

None known.

Distribution.

Ecuador.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Remarks.

This species is only known from the holotype. It is distinctive in the shape of its parameres, with a median interior projection, and the closely approximated bilobed armature of the diaphragm. It is closely allied with *C. gluciophilus, C.*

quadrispinosus, and *D. dissipatus,* even though it bares only 2 processes on segment X, because of the similar coloration of pronotum and paranota.

Type Material Examined.

Holotype [BPBM]: Macropterous ♂, "Type 1148 [Handwritten, white card with hole punch containing genitalia embedded in balsam] // Banos, Or. / Ecuador / XII-28-1922 [Date Handwritten] // F.X. Williams / Collector // ♂ // Holotype [Red paper, vertically oriented, affixed to following label] // Delphacodes / banosensis / ♂ Type 1148 Muir [Handwritten, label with black border] // 855 [Handwritten]"

Other Material Examined.

None known.

1.4.6 *Chionomus bellicosus* (Muir and Giffard, 1924), new combination.

(Figures 14-16)

Delphacodes bellicosa Muir and Giffard, 1924: 34.

Type Locality.

USA, California, Tulare County, Three Rivers.

Diagnosis.

Body brown to light brown, with ivory to cream markings. Vertex quadrate; foveae of frons and vertex dark, posterior compartments of vertex light with fuscous markings. Carinae distinct, off-white in color; antennae light brown. Pronotum light, white to cream in color, infuscate directly behind eyes, paranota white. Mesonotum brown, lateral and median carinae cream; wing with faint fuscate mark at apex of clavus. Armature of diaphragm bifurcate, hooked at apex; parameres sinuate, outer angles enlarged. Aedeagus tubular, directed dorsoposteriorly, large flange with teeth on apical ½ of left side, 2 subapical teeth on right.

Description.

COLOR. *Macropter.* Body brown to light brown, matte, with cream or ivory markings. Carinae of head (including genal carinae) distinct, ochraceous to off-white in color; median carinae of vertex evident. Foveae of frons and vertex brown, posterior compartments of vertex light brown. Antennae cream to stramineous. Pronotum white to cream, fuscate markings directly posterior to eyes. Mesonotum dark brown to brown, median and lateral carinae light brown to cream. Legs stramineous to brown, with fuscous markings on anterior face of femora; apex of tarsi brown. Forewings hyaline, faint fuscous spot just before apex of clavus. Abdomen brown. *Brachypter*. Similar to above, tegmina infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) [All specimens previously dissected]; width ♂ macropter 0.82±0.09 (n=3); ♂ brachypter 0.75 (n=1). Head: Vertex length 0.19±0.02 (n=4); vertex width 0.19±0.01 (n=4); frons length 0.47±0.02 (n=4); frons width 0.26±0.02 (n=4). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina faint but evident. In lateral view (Figure 14b, d), fastigium rounded; projecting in front of the eye about 1/6th eye length. Carinae of frons and clypeus distinct (Figure 15a), frons bowed, widest just below compound eyes. Antennae segments subequal in length, segment II wider; 2nd segment sparsely setaceous, bearing sensory pits arranged 3, 4, 4, 2-1, evenly spaced around segment. Sensory pits surrounded by small setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum evident, median carina ending at scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with 2 rows of small setae on ventral margin of femora, mostly bare. Calcar bearing 17- 23

small teeth (holotype with 17). *Brachypter*. Same as above; tegmina apically rounded.

Abdomen. *Brachypter*. Compressed dorsoventrally, tapering caudad.

Genitalia. Pygofer in caudal view (Figures 15b, 16d), about as tall as wide, rounded; margins rounded. Opening to inner chamber triangular, pointed ventrad. Armature of diaphragm bifurcate, hooked apically, distinctly projecting caudad. Parameres, widest in basal half, basal angle strong, projecting, quadrate; dorsolaterally diverging to quadrate apices, lateral margins concave, inner angles weak, pointed; outer angles produced to rounded apices. Aedeagus circular in cross-section, slightly curved ventrad, directed dorsoposteriorly, widest near base, slightly tapering for most of length. Aedeagus bearing toothed flange on left distal half, to subapical teeth on right. Segment X quadrate; processes distinct, projected posteriorly. Segment XI produced, about 2/3rds length of segment X.

Hosts.

Paspalum distichum L. (PADI6), knotgrass (Wilson 1985).

Distribution.

USA: CA.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Remarks.

This species is rare in collections. It is closely allied with *C. pacificus* but can be distinguished by the shape of the aedeagus and the hook of the bifurcate armature of the diaphragm being only apical. This bifurcate armature is also mirrored in *C. puellus* but the processes are not hooked; additionally, the ventral edge of the

parameres is distinctly S-shaped in *C. puella* while they are nearly straight in *C. bellicosus.*

Type Material Examined.

Holotype [BPBM]: Brachypterous ♂, "Delphacodes / bellicosa / ♂ M.G. [Handwritten, white card with hole punch containing genitalia embedded in balsam] // Three Rivers / Cal. Clortson // Holotype [Red paper, vertically oriented, affixed to following label] // Delphacodes / bellicosa / M.G. / ♂ [Handwritten, label with black border] // 1074 [Handwritten]"

Other Material Examined.

United States: California: Butte Co, Chico, 20-V-1981, SW Wilson (UDCC, CMSU, USNM; 3m♂).

1.4.7 *Chionomus dissipatus* (Muir, 1926), new combination

(Figures 17-19)

Delphacodes dissipata Muir, 1926: 33.

Syndelphax dissipatus (Muir), comb. by Fennah, 1967: 76.

Delphacodes dentis Beamer, 1948: 102, **new synonymy**.

Delphacodes vaccina Caldwell and Martorell, 1951: 186, **new synonymy**.

Type Locality.

Ecuador, Tungurahua Province, Banos.

Diagnosis.

Body dark brown, with white markings. Vertex quadrate; foveae of frons and vertex dark, posterior compartments of vertex light with fuscous markings. Carinae distinct, off-white in color; antennae light brown. Pronotum dark anteriorly with white band along posterior edge, paranota white with dark marks just below eyes;

carinae distinctly white or ivory. Armature of diaphragm quadrate, lined with small teeth on vertical edges; inner and outer angles of parameres diverging, basal angle produced, rounded. Aedeagus tubular, tapering apically, with linear row of teeth on either side; segment X armed with 4 distinct processes.

Description.

COLOR. *Macropter*. Body dark, brunneous, with white or ivory markings. Carinae of head (including genal carinae) distinct, stramineous to off-white in color, usually with a small amount brown at apex of carinae; stem of Y-shaped carina less evident. Antennae light brown, fuscous at joint of the two segments. Pronotum dark brown, posterior edge (including ventral edge of paranota) white to ivory, carinae distinctly white to ivory. Mesonotum dark, median and lateral carinae light brown in some specimens, frequently females. Legs light brown to stramineous, proximal half of femora infuscate. Forewings hyaline, dark spot just before apex of clavus. Abdomen dark brown, lateral projections of sternites light brown; pygofer and segment X brown.

STRUCTURE. *Body*. Body length (in mm) macropter ♂ 1.70±0.16 (n=11); female (♀) macropter 1.95±0.13 (n=3); brachypter ♂1.66 (n=1); width ♂ 0.70±0.08 (n=19); ♀ 0.78±0.01 (n=3). Head: Vertex length 0.13±0.02 (n=25); vertex width 0.16±0.03 (n=25); frons length 0.31±0.05 (n=32); frons width 0.14±0.03 (n=32). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina faint. In lateral view (Figure 17b, d), fastigium rounded; projecting in front of the eye about 1/5th eye length. Carinae of frons and clypeus distinct (Figure 18a), frons subparallel, widest at ventral edge of compound eyes. Antennal segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged

3, 3, 2, 2, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter.* Same as above.

Thorax. *Macropter*. Carinae of mesonotum obscure, median carina ending anterior to scutellum, lateral carinae faint, reaching hind margin. Legs mostly bare; calcar bearing 18-20 small teeth. *Brachypter.* Same as above; tegmina rounded at apex.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex. *Brachypter.* Same as above.

Genitalia. Pygofer in lateral view (Figure 18c) nearly half as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figures 18b, 19d), 3/4ths as tall as wide, rounded; margins raised, dorsolateral margins produced, carinate. Opening to inner chamber trapezoidal, pointed ventrad. Armature of diaphragm quadrate, toothed on vertical edges, distinctly projecting caudad. Parameres, widest in basal third, basal angle strong, projecting, rounded, mirrored on exterior edge; dorsolaterally diverging, apices nearly flat, lateral margins concave, inner and outer angles approximately equally produced. Aedeagus oval in cross-section, slightly curved dorsad, widest near base, slightly tapering for most of length; aedeagus bearing row of equally spaced teeth on both sides, along ventral edge, sometimes with 2-4 extra teeth just proximal to gonopore; gonopore dorsal, subapical. Segment X quadrate, taller than wide; with 4 processes, first pair short broadly approximated, second pair long, closely approximated. Segment XI produced, about half length of segment X.

Hosts.

None reported.

Distribution.

Can: NT [Questionable record]; USA: TX, LA; FL; Puerto Rico; Mexico; Guatemala; Honduras; Panama; Cayman Is; St. Thomas; Ecuador; Galapagos Islands.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Remarks.

This species is identical to *D. vaccina* and *D. dentis* and has priority over these names. The type of *D. dissipata* was examined and an array of at least 10 paratypes (including topotypes) were examined for *D. vaccina* and *D. dentis.* *Chionomus dissipatus* is closely allied with *C. gluciophilus* and may be easily misidentified. It can be distinguished by white or ivory carinae of the pronotum, the non-bifurcating armature of the diaphragm, and the pattern of the teeth on the aedeagus. *Chionomus gluciophilus* shares the toothing along the armature of the diaphragm but bears a notch along the dorsal margin, is similar in the shape of the aedeagus but scattered rows of teeth as opposed to parallel evenly spaced rows, and lacks the expansion mirroring the basal angle found in *C. dissipatus.*

This species is also closely allied with *C. quadrispinosus* which both share 4 processes on segment X. *Chionomus quadrispinosus* has a similar tooth pattern on the aedeagus but has a quadrate expanded base and is more distinctly upwardly directed.

Type Material Examined.

Holotype *Delphacodes dissipata* [BPBM]: Brachypterous ♂, "Banos, Or. / Ecuador / XII-28-1922 [Date handwritten] // F.X. Williams / Collector // ♂ // Holotype [Red paper, vertically oriented, affixed to following label] // Delphacodes / dissipata / ♂ Muir/ Type No 1149. [Handwritten, label with black border]".

Topotype *Delphacodes dentis* [SEMC]: Macropterous ♀, "Brownsville, Tex. / Dec. 29, 1945 / R. H. Beamer / In Palm Forest // PARATYPE / Delphacodes / dentis / R. H. Beamer [Blue paper]".

Holotype *Delphacodes vaccina* [USNM]: Macropterous ♂, "P.R. Acc. No / Isabela, P.R. / 8-29-47 [Date Handwritten]// Delphacid [handwritten]/ HOLOTYPE / vaccina [Handwritten, Pink paper] // [Microvial containing genitalia] // JS Caldwell / Collection / 1959 // Delphacodes ♂ [Handwritten]/ vaccina [handwritten]/ det 49 Holotype [4 is handwritten crossed out 1, Holotype is handwritten]/ JS Caldwell".

Other Material Examined.

United States: Florida: Monroe, Co., Middle keys, US Rt 1, Marathon Holiday Inn, 10-Jan-2006, AT Gonzon (3 UDCC, CMSU, 4m♂). **Puerto Rico:** Lajas, Sep-Nov 1960, M. Beauchamp (USNM, 1m♂, 1m♀). **Cayman Islands:** Cayman Brac, The Creek, 8-XII-1995, CR Dilbert (LBOB, 4m♂). **Mexico:** Br. Tex., II-20-5 (USNM, 1m♂). **Honduras:** Lancetilla, Aug (NCSU, 2m♂). **Panama:** Patino, 19-VII-52, FSBlanton (USNM, 1m♂); Canal Zone, Fort Clayton, Sept 8-15, 1978, H.J. Harlan (LBOB, 2m♂). **Venezuela:** Cagua, 25-XI-1975, CK and GF Smith (NCSU, 1m♂); Merida Libertador VII 3 1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin, R.O. Schuster (CSAC, 1m♂); Amazonas, Aqua Linda R., 18-20.vi.2000, P.Freytag (UDCC, 1m♂). **Brazil:** Nova Tentonia, 8 Catarina, May, 18, 1945, Remett Piaomann (NCSU, 1m♂).

1.4.8 *Chionomus dolonus*, new species

(Figures 20-21)

Type Locality.

Argentina, Santiago del Estero, Rio Dulce Road 1km west of Route 9.

Diagnosis.

Body brown to dark brown, white and stramineous markings. Vertex quadrate, foveae infuscate. Carinae of frons distinct, noticeably contrasting with foveae, stramineous to cream in color. Antennae yellow. Pronotum dark brown between lateral carinae, light brown shadowing eye, thick white to cream colored band along posterior edge, paranota white. Mesonotum dark brown, shining, lacking white scutellum in males; wings with dark mark at apex of clavus, infuscate along nodal line. Armature of diaphragm shelf-like, produced caudad; apical edge of parameres sinuate. Aedeagus tubular, curved dorsad, subapical posteriorly directed spine on right; segment X with two strong ventrally directed processes, apices blunt.

Description.

COLOR. *Macropter*. ♂. Body dark, brunneous, white and stramineous markings. Carinae of head (excluding genal carinae) distinct, yellow in color, usually with a small amount brown at apex of carinae; median carinae of vertex evident. Foveae brown, posterior compartments of vertex tan, antennae stramineous. Pronotum white, anteriorly dark brown between lateral carinae, light brown shadowing eyes; paranota white. Mesonotum dark, median and lateral carinae concolorous. Legs yellow, apex of tarsi brown. Forewings hyaline, infuscate along nodal line, dark spot just before apex of clavus. Abdomen brown, caudal edge of each segment yellow, lateral projections of sternites yellow. Pygofer brown. ♀. Similar, mesonotum lighter, centrally light brown reminiscent of vitta, scutellum white.

STRUCTURE. *Body*. Body length (in mm) macropter 1.83 (n=1); female (♀) macropter 2.06±0.18 (n=3); width ♂ 0.8±0.01 (n=2); ♀ 0.87±0.03 (n=3). Head: Vertex length 0.20±0.03 (n=5); vertex width 0.22±0.02 (n=5); frons length 0.50±0.04

(n=5); frons width 0.24±0.01 (n=5). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina evident. In lateral view (Figure 20b), fastigium rounded; projecting in front of the eye about 1/4th eye length. Carinae of frons and clypeus distinct (Figure 20c), frons parallel ventrad of eyes, narrowing towards fastigium, widest at ventral margin of compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment setaceous, bearing sensory pits arranged 4, 3, 2, 2, evenly spaced around segment. Sensory pits surrounded by small brown setae.

Macropter. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with sparse rows light brown setae, mostly bare. Calcar bearing 21-25 small teeth (holotype with 24).

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex.

Genitalia. Pygofer in lateral view nearly half as long dorsally as ventrad, ventral margin sinuate, caudally projecting ventral process. In caudal view (Figure 20e), as taller than wide, rounded; lateral margins mildly raised. In ventral view (Figure 20f), caudal margin sinuate, prominent median projection, quadrate. Opening to inner chamber triangular, pointed ventrad, rounded dorsad. Armature of diaphragm shelf-like, smooth, curved dorsad to fit aedeagus. Parameres, widest in basal third, basal angle produced, rounded; dorsolaterally diverging to anvil-shaped apices, lateral margins concave, inner angles strong, acute; outer angles produced to rounded apices. Aedeagus circular in cross-section, curved dorsad, widest near base, slightly tapering for most of length, gonopore dorsal, apical. Segment X quadrate, 4 processes, 2 arising from apical margin of segment X, strong directed ventrad, hooked, secondary

processes small, spine-like, arising from midsection of segment X. Segment XI produced, about 1/3rd length of segment X.

Hosts.

None reported.

Distribution.

Argentina.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Etymology.

The specific epithet *dolonus* stems from the Greek noun, *dolon,* meaning dagger or stiletto. This name was chosen in reference to the shape of the process of the aedeagus. The noun is neuter and in the genitive plural. The ending *–us* is an arbitrary combination of letters added to make the epithet euphonious and for gender agreement.

Remarks.

Chionomus dolonus is unique to *Chionomus* in possessing a median ventral process of the pygofer and is thus easily distinguishable. This feature is uncommon among the higher Delphacini, it is notably shared in new world taxa with species of *Kosswigianella* Wagner (*sensu* Hamilton 2002) formerly in *Acanthodelphax* Le Quesne. *Kosswigianella analis* (Crawford) also shares similar coloration; however, the shape of the aedeagus and parameres of *C. dolonus* do not fit the description of this genus.

The shape of the parameres and armature of the diaphragm places this species close to *C. tenae;* however, the pygofer is much more constricted in this species. It

may also be allied with *C. balboae,* which shares the anvil shape of the apices of the parameres but has a triangular shaped armature of the diaphragm.

Type Material.

Holotype [INHS]: Macropterous ♂, "ARGENTINA: Stgo. del Estero / Rio Dulce Rd 1 km W rt 9 / S 27°37.589'W 64°37.126' / 450m, 21 Jan 2008 C.H.Dietrich / vacuum, AR32-1 // ♂ // INHS #2316 [Green paper] // HOLOTYPE / Chionomus herkos / KMWeglarz 2012 [Red Paper] ".

Paratypes: **Argentina**: Stgo. del Estero, rt 9 SE Termas del T. Hondo, km 1191, 450m, 21 Jan 2008, C.H.Dietrich, vacuum (1♂m, 1♀m); Stgo. del Estero, Staniago del Estero, 300m, 21 Jan 2008, C.H.Dietrich, vacuum (2♀m).

1.4.9 *Chionomus gluciophilus* (Muir, 1926), new combination

(Figures 22-23)

Delphacodes gluciophila Muir, 1926: 35.

Type Locality.

Ecuador, Tungurahua Province, Banos.

Diagnosis.

Body brunneous, dark, shining, with stramineous markings. Vertex quadrate; foveae of frons and vertex very dark. Carinae of the head distinct, yellow in color except for median carina of the vertex; antennae stramineous. Pronotum entirely dark, paranota ivory. Armature of diaphragm forming toothed cordate or dorsally notched boss; parameres with apices slightly concave, broadest in basal third. Aedeagus tubular, sinuate, with a row of scattered teeth on either side connecting at the aedeagal base; segment X with 4 processes.

Description.

COLOR. *Macropter*. Body dark, brunneous, shining, with white or ivory markings. Carinae of head (including genal carinae) distinct, off-white to ivory in color; median carinae of vertex concolorous. Antennae stramineous, infuscate at joint of two segments. Pronotum dark brown, paranota white to ivory, fuscous marking directly below compound eyes. Mesonotum dark, median and lateral carinae obscure. Legs yellow, with fuscous striping on femora. Forewings hyaline, distinct dark spot just before apex of clavus. Abdomen dark brown, thin line along caudal edge of each segment yellow, lateral projections of sternites yellow. Pygofer and segment X concolorous with body. *Brachypter*. Similar to above. Tegmina infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) female (♀) macropter 2.45±0.11 (n=3), ♂ brachypter X.X±X (n=X); ♀ brachypter X.X±X (n=X); width ♂ 0.73±0.06 (n=7); ♀ 0.94±0.03 (n=3). Head: Vertex length 0.17±0.04 (n=10); vertex width 0.18±0.02 (n=10); frons length 0.51±0.04 (n=10); frons width 0.24±0.03 (n=10). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina faint. In lateral view (Figure 22b), fastigium rounded; projecting in front of the eye about 1/4th eye length. Carinae of frons and clypeus distinct (Figure 22c), frons parallel, widest at ventral third of compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 3, 3, 2, 2, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter*. Same as above except stem of Y-shaped carina evident.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with 2 rows setae on ventral margin of femora, mostly bare. Calcar bearing 23-

26 small teeth. *Brachypter*. Same as above but with lateral carinae mesonotum evident, diverging posteriorly; tegmina apically rounded, long.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex; abdominal spiracles with one or two fine setae.

Genitalia. . Pygofer in lateral view 3/5ths as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figure 22d), 4/5ths as tall as wide, rounded; margins raised, dorsolateral margins produced, carinate. Opening to inner chamber trapezoidal, pointed ventrad. Armature of diaphragm cordate, notched at dorsal margin, toothed on vertical edges, distinctly projecting caudad. Parameres, widest in basal third, basal angle strong, projecting, rounded; dorsolaterally diverging, apices slightly concave, lateral margins concave, inner and outer angles approximately equally produced. Aedeagus circular in cross-section, sinuate, widest near base, slightly tapering for most of length; aedeagus bearing row of scattered teeth on both sides, along ventral edge, sometimes with 2-4 extra teeth just proximal to gonopore; gonopore large, dorsal, subapical. Segment X quadrate, taller than wide; with 4 processes, first pair distinct, broadly approximated, second pair longer than first, closely approximated. Segment XI produced, about half length of segment X.

Hosts.

Phaseolus vulgaris L. (PHVU), kidney bean (label information).

Saccharum L. (SACCH), sugarcane (Muir, 1926).

Solanum tuberosum L. (SOTU), Irish potato (label information)

Distribution.

Guatemala; Costa Rica; Colombia; Ecuador.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Remarks.

Chionomus gluciophilus is closely allied with *C. dissipatus* and has an overlapping distribution. *Chionomus gluciophilus* can be distinguished by the dark carinae of the pronotum and posterior compartments of the vertex, the more scattered teeth on the aedeagus, the notch in the dorsal edge of the armature of the diaphragm, and the absence of a rounded projection on the basal exterior edge of the parameres. It is also similar to *C. quadrispinosus* but differs from it similarly to *C. dissipatus* (see remarks for that species).

Type Material Examined.

Holotype [BPBM]: Macropterous ♂, "Delphacodes / gluciophila / ♂ / Muir / Type 1152. [Handwritten, white card with hole punch containing genitalia embedded in balsam] // Banos, Or. / 6000 ft. / Ecuador / XII-26-1922 [Elevation and date Handwritten] // F.X. Williams / Collector // Sugarcane // Holotype [Red paper, vertically oriented, affixed to following label] // Delphacodes / gluciophila / ♂ Muir/ Type No 1152. [Handwritten, label with black border] // 865 [Handwritten]".

Other Material Examined.

Guatemala: Quetzaltenango, Fuentes Geoginas, Volcan Zunil, AT Gonzon R Donovall, 16.ii.2007 (UDCC, 1m♂). **Costa Rica:** San Pedro de Montes de Oca, 4-XII-1936, CH Ballou (USNM, 2m♂, 3m♀); S.J. 26 km N Sanlisidiro, III-V-1992, P. Hansons & C. Godoy (LBOB, 1m♂, 1b♂). **Colombia:** Sonson, Ant., 16-XI-1955, L. Pesada (USNM, 2m♂). **Ecuador:** Gualaceo, VII-30-1954, H.R.Yurst (USNM, 1m♂).

1.4.10 *Chionomus haywardi* (Muir, 1929)

(Figures 24-25)

Delphacodes haywardi Muir, 1929: 83.

Chionomus haywardi (Muir), comb. by Fennah, 1971: 324.

Type Locality.

Argentina, Villa Ana.

Diagnosis.

Body dark brown, with white and stramineous markings. Vertex quadrate; foveae of frons and vertex dark brown, posterior compartments of vertex brown. Carinae distinct, off-white in color; antennae stramineous with fuscous markings. Pronotum white with dark brown shadows directly posterior to eyes; paranota white. Armature of diaphragm forming inverted triangular boss, apex of parameres with inner angle mildly produced dorsally. Aedeagus tubular, 2 converging rows of scattered teeth surrounding apical half.

Description.

COLOR. *Macropter*. Body dark, brunneous, with white and stramineous markings. Carinae of head (including genal carinae) distinct, off-white in color, usually with a small amount brown at apex of carinae; median carinae of vertex evident. Antennae stramineous, infuscate at joint of the two segments. Pronotum white with dark brown shadows directly posterior to eyes; paranota white. Mesonotum dark to light brown, median and lateral carinae distinctly stramineous. Legs stramineous with brown striping, with hind legs lighter, tarsi brown. Forewings hyaline, distinct dark spot just before apex of clavus. Abdomen brown, some specimens with fine line of white on caudal edge of each segment, lateral projections of sternites yellow to white. Pygofer brown, segment X stramineous.

STRUCTURE. *Body*. Body length (in mm) macropter ♂1.94±0.09 (n=5); width 0.75±0.05 (n=15). Head: Vertex length 0.18±0.03 (n=15); vertex width 0.18±0.01 (n=15); frons length 0.47±0.04 (n=15); frons width 0.21±0.02 (n=15). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina evident. In lateral view (Figure 24b), fastigium rounded; projecting in front of the eye about 1/4th eye length. Carinae of frons and clypeus distinct (Figure 24c), frons nearly parallel, widest at ventral margin of compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 4, 4, 1, 2, evenly spaced around segment. Sensory pits surrounded by small black setae.

Thorax. *Macropter*. Carinae of mesonotum evident, median carina ending anterior to scutellum; lateral carinae diverging posteriorly to reach hind margin. Legs with a rows setae on anterior face margin of femora, mostly bare. Calcar bearing 24-25 small teeth.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex.

Genitalia. Pygofer in lateral view nearly half as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figure 24d), as tall as wide, globular; margins rounded, weakly raised at dorsolateral margins. Opening to inner chamber triangular, pointed ventrad. Armature of diaphragm triangular to cordate in shape, smooth or some specimens with toothing along vertical edges, distinctly projecting caudad. Parameres as wide in basal third as at apices, basal angle projecting, rounded; dorsolaterally diverging to flattened apices, lateral margins concave (inner margin more so than outer margin); inner angles acute, dorsally directed; outer angles

rounded. Aedeagus circular in cross-section, slightly curved dorsad, widest near base, slightly tapering for most of length, with two rows of scattered teeth surrounding apical; gonopore dorsal, apical. Segment X quadrate, bearing 2 processes; processes well developed, directed ventrad, slightly curved inward at apices. Segment XI produced, about 2/3rds length of segment X.

Hosts.

Oryza sativa L. (ORSA), rice (Velazquez *et al.* 2003).

Zea mays L. (ZEMA), corn (Teason and Lenicov 1989).

Triticum aestivum L. (TRAE), common wheat (Velazquez *et al*. 2003).

Avena sativa L. (Velazquez *et al.* 2003)

Hordeum vulgare L. (Velazquez *et al.* 2003)

Distribution.

Argentina.

COI Sequence.

5' –

GAAGTTTATATTTTAATTTTACCTGGATTTGGTTTAATTTCACATATTATTA
TGCAAGAAAGAGGTAAACGAGAAACCTTTGGATCAATTGGTATAATTTAT
GCAATGTTGGCTATTGGAGTTCTAGGATTTATTGTTTGAGCACACCATATA
TTCACTGTCGGAATAGATATTGATACACGAGCCTACTTTACTTCAGCAACC
ATAATTATTGCAGTTCCTACAGGAATTAAAATTTTTAGATGAATCGCCACA
ATTTATGGATCTAAAATTAACTTTTCCCCCCAAATAATCTGATCAATAGGG
TTTATTTTATTATTTACAATTGGTGGATTAACAGGAGTTATGCTTGCAAATT
CATCAATTGATATTGTTCTACACGATACCTATTATGTTGTTGCACACTTTCA
TTATGTATTATCAATAGGAGCTGTCTTTACAATTGTAGCCAGATTTATTCAT

TGATATCCACTTTTTACAGGTGTATTAATAAATAAAAAATGATTAAAAATT
CAATTTAATTCAATATTTATCG – 3’

Remarks.

This species is commonly associated with agriculture. It is similar in outward appearance to *C. pacificus* but is easily distinguished by range. This species closely allied with *C. havanae* and *C. balboae* (see remarks section on those species).

Type Material Examined.

Holotype [BMNH]: LOST (M. Webb, BMNH *pers. comm*.).

Other Material Examined.

Argentina: Entre Rios, Federación, Siriri Campgd, 4-I-2008, CHD (INHS, 3m♂); Entre Rios, rt 14 km 43, 24-I-2008, CHD (INHS, 2m♂); Buenos Aires, ca. Reserva Otamendi, 23-I-2008, CHD (INHS, 3m♂); Buenos Aires, ca. Reserva Otamendi, 24-I-2008, CHD (INHS, 1m♂); Buenos Aires, 2km N La Plata, 23-I-2008 (INHS, 1m♂); Buenos Aires, 3km N La Plata 27-I-2008, CHD (INHS, 1m♂);Buenos Aires, 3km N La Plata, 27-I-2008, CHD (INHS, 1m♂); Chaco, P.N. Chaco, 10-I-2008, CHD (INHS, 2m♂); Corr, 3km W SanCosme, 18-I-1989, C&L O’Brien & G.Wibmer (LBOB, 1m♂).

1.4.11 *Chionomus herkos*, new species

(Figures 26-28)

Type Locality.

USA, Louisiana, Baton Rouge.

Diagnosis.

Body brown to dark brown, white and stramineous markings. Vertex quadrate, longer than wide, foveae concolorous with body. Carinae of frons distinct, noticeably

contrasting with foveae, stramineous in color. Antennae yellow. Pronotum white, fuscous markings shadowing eyes, paranota dark, broad white band along margins. Mesonotum dark brown, shining; wings with dark mark at apex of clavus. Armature of diaphragm broad, rounded; apical edge of parameres sinuate. Pygofer with dorsolateral margins distinctly produced, quadrate. Aedeagus tubular, widest in base, flange with row of small teeth distal 2/3rd of left side, one to two subapical spines on right; segment X with two long processes, sinuate, directed ventrad, following margin of segment X, hooked just dorsal to aedeagus.

Description.

COLOR. *Macropter*. Body dark, brunneous, shining, with white or ivory markings. Carinae of head (sometimes including genal carinae) distinct, ochraceous to off-white in color, usually with a small amount brown at apex of carinae; median carinae of vertex obsolete. Foveae brown, antennae stramineous. Pronotum white, small amount of dark brown to brown anteriorly; paranota white to ivory, brown mark ventrad of eyes. Mesonotum dark, median and lateral carinae concolorous, inconspicuously lightened in some specimens. Legs yellow, apex of tarsi brown. Forewings hyaline, infuscate along anterior of clavus and nodal line, dark spot just before apex of clavus. Abdomen brown, caudal edge of each segment yellow or white, lateral projections of sternites yellow. Pygofer brown, dorsolateral projections and segment X stramineous in some specimens. *Brachypter*. Similar, tegmina darkly infuscate, hyaline along clavus, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter 1.65±0.12 (n=7); female (♀) macropter 1.96±0.18 (n=6), ♂ brachypter 1.59±0.17 (n=4); ♀ brachypter

1.79±0.16 (n=10); width ♂ 0.64±0.07 (n=13); ♀ 0.71±0.10 (n=11). Head: Vertex length 0.21±0.04 (n=27); vertex width 0.14±0.02 (n=29); frons length 0.48±0.04 (n=23); frons width 0.21±0.02 (n=23). *Macropter*. Carinae of vertex distinct, stem of Y-shaped obsolete. In lateral view (Figure 26b, d), fastigium rounded; projecting in front of the eye about 1/6th eye length. Carinae of frons and clypeus distinct (Figure 27a), frons converging apically, subparallel in basal half, widest in basal 1/4th. Antennae segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 3, 3, 2, 2, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with three rows of dark spines on femora (dorsal, ventral anterior face, ventral posterior face), evenly spaced. Calcar bearing 18-24 small teeth (holotype with 20). *Brachypter*. Same as above but with lateral carinae mesonotum evident, diverging posteriorly; tegmina apically rounded, reaching to apex of 7th abdominal segment.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex. *Brachypter*. Same as above.

Genitalia. Pygofer in lateral view (Figure 27c) nearly as long dorsally as ventrad, ventral margin sinuate; dorsolateral processes strongly produced caudad, quadrate. In caudal view (Figure 27b), just wider than tall, rounded; margins raised, produced dorsolaterally. Opening to inner chamber triangular, pointed ventrad. Armature of diaphragm broad, rounded, smooth, distinctly projecting caudad. Parameres widest in basal third, basal angle rounded; dorsolaterally diverging, lateral margins concave, dorsal margin sinuate, inner angles weak, acute; outer angles strong,

produced dorsad. Aedeagus circular in cross-section, sinuate, widest near base, slightly tapering for most of length, subapical flange on right bearing small teeth, one to two subapical spines on left. Gonopore dorsal, subapical. Segment X quadrate, taller than wide, armed with two processes; processes arising from midsection of segment, thin, directed ventrad, touching caudal face of segment X, hooked around aedeagus. Segment XI produced, about 2/3rds length of segment X.

Hosts.

None reported.

Distribution.

USA: FL, LA.

COI Sequence.

Material for molecular work was unavailable at the time of this study.

Etymology.

The specific epithet *herkos* is the Greek noun, meaning fence or wall. This name was chosen because the dorsolateral processes of the pygofer are reminiscent of a wall. The noun is in the genitive singular.

Remarks.

This species is easily distinguished from the rest of *Chionomus* by the dorsolateral projections of the pygofer. These projections combined with point of origin of the processes on segment X indicate that this species may be allied with *C. dissipatus, C. gluciophilus,* and *C. quadripinosus.* All three of these species have slight dorsolateral expansions of the pygofer however none are as prominently produced. Additionally, *C. herkos* differs from these species in having a rounded

armature of the diaphragm as opposed to having it toothed and quadrate (*C. dissipatus, C. gluciophilus*) or U-shaped (*C. quadrispinosus*).

Material Examined.

Holotype [USNM]: Macropterous ♂, "♂ // USA: LA: E. Baton Rouge Par. / BatonRouge,BluebonnetSwamp / 22-VII-03 CRBartlett, STDash / Beech-Magnolia-Cypress / 30 22.148N 91 06.304W // HOLOTYPE / Chionomus herkos / KMWeglarz 2012 [Red Paper]".

Paratypes: **United States**: Florida. Highlands Co., Sebring: Highlands Hammock S.P., Cypress Swamp Trail, 22.IX.2007, V. Golia, Sweeping (VGC, 4♂b, 4♀b); Baton Rouge, La. 7-4-72 (LSAM, 1♂b); Louisiana. same data as holotype (UDCC, 8♂m, 2♂b, 5♀m, 7♀b); LA, E. Baton Rouge Par., Baton Rouge, LSU Campus, Life Sciences Building, At lights, 23-May-2003, STDash (UDCC, 2♂m).

1.4.12 *Chionomus pacificus* (Crawford, 1914), new combination.

(Figures 29-31)

Megamelus pacificus Crawford, 1914: 626.

Liburnia pacifica (Crawford), comb. by Van Duzee, 1917:84.

Delphacodes pacifica (Crawford), comb. by Muir and Giffard, 1924: 34.

Type Locality.

California.

Diagnosis.

Body brown to light brown, with distinct median vitta and ivory to cream markings. Vertex quadrate, foveae infuscate. Foveae of frons dark; carinae distinct, noticeably contrasting with foveae, stramineous to cream in color. Antennae light cream colored to yellow. Pronotum light, white to cream in color, infuscate shadows

directly behind eyes, paranota white. Mesonotum brown with median white vitta; wings with dark mark at apex of clavus. Armature of diaphragm bifurcate, hooked along entirety; parameres sinuate, outer angles enlarged. Aedeagus tubular, with two rows of teeth along sides on distal 2/3rds.

Description.

COLOR. *Macropter*. Body brown to dark brown, matte, with cream or white markings. Carinae of head (including genal carinae) distinct, ochraceous to off-white in color; median carinae of vertex evident. Foveae of frons dark brown; vertex lighter than frons, foveae infuscate. Antennae cream to light brown, segment I dark brown in some specimens. Pronotum white to cream, fuscate markings directly posterior to eyes and between median and lateral carinae. Mesonotum dark brown to brown, median and lateral carinae cream to white, space between carinae also lightened. Legs white to light brown; apex of tarsi brown. Forewings hyaline, faint fuscous spot just before apex of clavus. Abdomen brown, fine line of white on caudal edge of each segment, lateral projections of sternites white. Pygofer brown. *Brachypter*. Similar to above, tegmina infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter ♂1.93±0.14 (n=31); ♀ macropter 2.21±0.12 (n=6); ♂ brachypter 1.85±0.05 (n=9); width ♂ 0.78±0.06 (n=50); ♀ 0.88±0.06 (n=6). Head: Vertex length 0.17±0.03 (n=50); vertex width 0.19±0.03 (n=50); frons length 0.50±0.03 (n=25); frons width 0.22±0.02 (n=25). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina evident. In lateral view (Figure 29b, c), fastigium rounded; projecting in front of the eye about 1/4th eye length. Carinae of frons and clypeus distinct (Figure 30a), frons subparallel, narrow at vertex,

widest at ventral edge of compound eyes. Antennae segments subequal in length, segment II wider; 2nd segment bearing sensory pits arranged 4, 4, 2, 1, evenly spaced around segment. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum evident, median carina ending at scutellum, lateral carinae distinct, parallel, reaching hind margin. Legs sparsely setaceous. Calcar bearing 22-25 small teeth. *Brachypter*. Same as above except lateral carinae of mesonotum diverging; tegmina apically rounded, reaching past pygofer.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex. *Brachypter.* Same as above.

Genitalia. Pygofer in lateral view (Figure 30c) nearly half as long dorsally as ventrad, ventral margin sinuate. Pygofer in caudal view (Figure 30b), about as tall as wide, rounded; margins rounded, slightly produced dorsolaterally. Opening to inner chamber triangular, pointed ventrad. Armature of diaphragm bifurcate, hooked along entirety, distinctly projecting caudad prior to dissection, apices of hooks pointed ventrad when fully dissected. Parameres, widest in basal half, basal angle mild, rounded; dorsolaterally diverging to expanded apices, lateral margins concave, inner angles weak, pointed; outer angles produced, rounded. Aedeagus circular in cross-section, slightly curved ventrad, directed dorsoposteriorly, widest near base, slightly tapering for most of length. Aedeagus with two rows of scattered teeth reaching from gonopore to ventral margin in apical 2/3rds; gonopore dorsally directed, apical. Segment X quadrate; bearing two weakly produced processes, projected posteriorly, hooked. Segment XI produced, about 1/2rds length of segment X.

Hosts.

Medicago sativa L. (MESA), alfalfa (label information).

Distribution.

USA: NC, SC, GA, FL, IL, LA, MS, TX, KS, CO, UT, AZ, NM, CA; Mexico; Guatemala; Panama; Venezuela; Colombia.

COI Sequence.

5'-

TTTAATTTTGCCTGGATTTGGTTTAATTTCCCACATTATCATGCAAGAAAGA
GGTAAACGAGAAACTTTTGGATCAATCGGTATAATCTATGCAATATTAGCT
ATTGGAGTTTTAGGCTTTATTGTATGAGCACATCATATATTTACTGTAGGA
ATAGATATTGATACACGAGCTTACTTTACTTCGGCAACGATAATTATTGCA
GTTCCCACAGGAATTAAAATTTTTAGATGAATTGCCACAATTTACGGATCT
AAAATTAACTTTTCCCCTCAAATAATCTGATCAATAGGATTTATTTTATTAT
TTACAATTGGGGGACTAACAGGAGTTATACTTGCCAATTCATCAATTGATA
TTGTTCTTCATGACACTTATTATGTTGTAGCACACTTTCATTATGTATTATC
AATAGGAGCTGTTTTCACAATTGTGGCCAGTTTTATTCACTGATATCCACTT
TTCACAGGTGTTTTAATAAATAAAAAATGACTCAAAATTCAATTTAACTCA
ATATTT – 3'

Remarks.

There is a large amount of variation in color for *C. pacificus*, some specimens are dark with the vitta faint and marking stramineous while others are light with almost perfectly white markings and distinct vittas. This species is closely allied with *C. bellicosus* and *C. puellus* (see the Remarks of *C. bellicosus)*.

Type Material Examined.

Holotype [USNM]: Macropterous ♂, under Megamelus pacificus, “Cala / 2351 [Handwritten]// Collection / CF Baker // Type / No. 15996 [Number handwritten] / U.S.N.M. [Red paper] // Megamelus / pacificus / D.G.C. Crawf [Handwritten, label with black border]”.

Other Material Examined.

United States: Kansas: Manhattan, 16-IV-1929, D.A. Wilbur (USNM, 1m♂). Utah: Hurricane, 18-VI-1935, G.F. Knowlton (USNM, 1m♂). North Carolina: Wake Co., Raleigh Marcom St, 19-VII-2000, CR Bartlett (UDCC, 1m♂); Haywood Co GSMNP Cataloochee ATBI Plot, (20-VIII)-(11-IX)-2001, (UDCC, 1m♂); Swain Co. GSMNP Clingman’s Dome Rd. Site #2, 30-VII-2003, CR Bartlett, D Nonne, A Gonzon (UDCC, 2m♂). South Carolina: Clemson, 14-X-1955, David Dunacan (USNM, 1m♂). Arkansas: Hot Springs Nat’l Park, 6-X-1963, BC Marshall (USNM, 1m♂); Hot Springs Nat’l Park, 11-X-1963, BC Marshall (USNM, 1m ♀). Texas: Brownwood, R.H. Painter (USNM, 1m♂); Del Rio, 25-V-1912, JD Mitchell (USNM, 1m♂); Harlingen, 12-III-1945, D.E. Hardy (USNM, 1m♂); Harlingen, 15-III-1945, D.E. Hardy (USNM, 1m♂); Robstown, (LSAM, 4m♂, 2m♀). NM: Las Cruces, 12-VI-1950, B.H. Beamer (SEMC, 1m♂). Arizona: Maricopa Co, Higley, 23-XI-2000, S.N. Johnson (BYU, 1m♂); Maricopa Co, Higley, 25-XI-2000, S.N. Johnson (BYU, 2m♂); Mesa, Maricopa Co, 12-19-VI-1959, M.W. Nielson (BYU, 1m♂); Patagonia, 7-IX-1929, E.D. Ball (USNM, 1m♂, 1m♀); Tucson, Pima Co 17-VII-1967, M.W. Nielson (BYU, 1m♂, 2m♀); Graham Mts, 15-VI-1914, E.G.Holt (USNM, 1m♂); Graham Mts, 25-VI-1914, E.G.Holt (USNM, 1m♂); Cochise Co., Huachuca Mts., Upper Garden Cyn Picnic Area, 21-VII-2009, C.W. O’Brien (UDCC, 1m♂); Cochise Co., Ash Creek, 28-VII-2003, AL Park (UDCC, 10m♂, 13m♀). CA: Cala, CF Baker

(USNM, 1m♂). GA: Peach Co, Ft. Valley, 9-VI-1945, Turner (USNM, 1m♂). Louisiana: St. Martin Par. JCT I-10 & PR 352, 1-X-1992, J.T. McBride (LSAM, 1m♂). Florida: Jefferson Co 2mi S Wacissa, 27-VI-2000, C.R. Bartlett (UDCC, 1m♂); Jefferson CO 4mi S Wacissa, 27-VII-2000, C.W. O'Brien (LBOB, 1m♂). **Mexico:** Jalisco 20mi W of Tecolotlan, 15-IX-1938, L.J. Lipovsky (SEMC, 23m♂, 10b♂); Manatlan, Jaliaco, 8-X-1980, D.M. DeLong (UKYC, 2m♂); Chihauhau 55mi SW C. Juarez, 25-XIII-1986, M.W. Nielson (BYU, 4m♂, 6m♀); Cuiteco Chih, 1-VIII-1969, TA Sears, RC Gardiner, CS Glaser (CDAE, 1m♂); Durango Rt. 45 31mi N Durango, 28-X, 1995, C.H. Dietrich (UDCC, 1m♂); Mexico City, 22-X-1945, D.M. DeLong (UKYC, 1m♂); Sonora Hermosillo, 14-IV-1982, Vasquez (UDCC, 1m♂); Paraiso, C.Z., X-1948, G.B. Fairchild (SEMC, 1m♂); Qro. 19mi SW Bernal, 27-VII-1982, C.W. & L. O'Brien & G. Wibmer (LBOB, 1m♂); Morelia, Mich., 4-IX-1938, L.J. Lipovsky (SEMC, 1m♂); Michoacán Rio Tuxpan K-185, 29-IX-1945, D.M. DeLong (UKYC, 1m♂). **Guatemala:** Quetzaltenango, Fuentes Georginas, Volcan Zunil 8km SE Zunil, 14-15-II-2007, AT Gonzon, R Donovall (UDCC, 2m♂); Antigua, 28-VIII-1952, R.H. Painter (USNM, 1m♂). **Venezuela:** Merida Libertador Merida, 3-VII-1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin, R.O. Schuster (CDAE, 1m♂). **Colombia:** Funza, Cun., 12-X-1955, L. Pesada (USNM, 1m♂); Duitama, Boy., 12-IV-1956, L. Pesada (USNM, 1m♂).

1.4.13 *Chionomus puellus* (Van Duzee, 1897), new combination

(Figures 32-34)

Liburnia puella Van Duzee, 1894: 191. [*nom. nud*.].

Liburnia puella Van Duzee, 1897: 151.

Delphax puella (Van Duzee), comb. by Kirkaldy, 1907: 161.

M[egamelus] puella (Van Duzee), comb. by Crawford, 1914: 622.

Megamelus puellis (Van Duzee), comb. and emendation by Crawford, 1914: 626.

Delphacodes puella (Van Duzee), comb. by Muir, 1917: 337; also Muir and Giffard, 1924: 32.

Delphacodes aculeata Beamer, 1948: 106, **new synonymy**.

Type Locality.

USA, Mississippi.

Diagnosis.

Body brown to dark brown, ivory to white markings. Vertex quadrate, foveae concolorous with body. Carinae of frons distinct, noticeably contrasting with foveae, stramineous to cream in color. Antennae shading from light brown to yellow. Pronotum dark anteriorly, thick white to cream colored band along posterior edge, paranota dark with white band. Mesonotum dark brown, shining; wings with dark mark at apex of clavus. Armature of diaphragm bifurcate, lobes diverging; apical edge of parameres sinuate. Aedeagus tubular, with scattered teeth on distal 2/3rds; segment X with two strong ventrally directed, diverging processes.

Description.

COLOR. *Macropter*. Body dark, brunneous, shining, with white or ivory markings. Carinae of head (including genal carinae) distinct, stramineous to off-white in color, usually with a small amount brown at apex of carinae; median carinae of vertex obscure. Antennae light brown proximally, shading distally to yellow. Pronotum dark brown to brown anteriorly, posterior edge and ventral edge of paranota white to ivory. Mesonotum dark, median and lateral carinae obscure. Legs light

stramineous, third tarsal segment infuscate. Forewings hyaline, sometimes with faint fuscous markings, dark spot just before apex of clavus. Abdomen brown, caudal edge of each segment lightened to yellow or white, lateral projections of sternites yellow. Pygofer and segment X brown, lightened at posterior margins. *Brachypter*. Similar to above, tegmina lightly infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter 1.63±0.13 (n=17); female (♀) macropter 1.98±0.18 (n=13), ♂ brachypter 1.50±0.07 (n=6); ♀ brachypter 1.81±0.23 (n=4); width ♂ 0.70±0.08 (n=18); ♀ 0.76±0.05 (n=11). Head: Vertex length 0.18±0.04 (n=23); vertex width 0.16±0.02 (n=25); frons length 0.50±0.05 (n=25); frons width 0.20±0.02 (n=25). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina not evident. In lateral view (Figure 32b), fastigium rounded; projecting in front of the eye about 1/6th eye length. Carinae of frons and clypeus distinct (Figure 33a), frons subparallel, widest at ventral margin of compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment setaceous, bearing sensory pits arranged 4, 3, 2, 1, evenly spaced around segment. Sensory pits surrounded by small brown setae. *Brachypter*. Similar to above but with stem of Y-shaped carinae faint but evident.

Thorax. *Macropter*. Carinae of mesonotum obscure, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly to reach hind margin. Legs with one row of setae on dorsal margin and two rows setae on ventral margin of femora. Calcar bearing 21-23 small teeth. *Brachypter*. Similar to above but carinae of mesonotum evident, median carina ending anterior of scutellum, lateral carinae

diverging reaching posterior margin; tegmina apically rounded, reaching to apex of pygofer.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex; abdominal spiracles surrounded by several long fine setae. *Brachypter*. Same as above.

Genitalia. Pygofer in lateral view (Figure 33c) nearly half as long dorsally as ventrad, ventral margin sinuate. Pygofer in caudal view (Figure 33b), slightly wider than tall, rounded; margins rounded, slightly produced dorsolaterally. Opening to inner chamber trapezoidal, pointed ventrad. Armature of diaphragm lobed, bifurcate, lobed strongly diverging from base, distinctly projecting caudad. Parameres, widest in basal third, basal produced, rounded; dorsolaterally diverging, lateral margins concave, inner angles pointed; outer angles produced, rounded, dorsal margin distinctly S-shaped. Aedeagus circular in cross-section, curved ventrad, widest near base, slightly tapering for entirety of length. Aedeagus with scattered teeth reaching from gonopore to ventral margin in apical 2/3rds; gonopore dorsally directed, apical. Segment X quadrate; bearing two strongly produced processes, projected ventrad, mildly curved, diverging. Segment XI produced, about 2/3rds length of segment X.

Distribution.

CAN: NS, ONT, QUE; USA: ME, VT, MA, CT, NY, NJ, PA, DE, MD, DC, NC, SC, GA, FL, OH, IN, IL, WV, TN, KY, AL, MS, LA, WI, MO, IA, AR, OK, NE, KS, TX, WA, OR, CA; Bermuda; Cuba; Jamaica; Puerto Rico; Mexico; Venezuela, Brazil.

COI Sequence.

5’-

AGTTTACATTTTAATTTTACCTGGATTTGGTTTAATTTCACATATTATCATG
CAAGAAAGAGGAAAGCGAGAAACTTTTGGATCAATCGGAATAATTTACGC
TATAATTGCTATTGGAATTTTAGGGTTTATTGTATGAGCACATCATATATTC
ACAGTTGGTATAGATATTGATACACGAGCCTACTTTACATCAGCAACTATA
ATCATTGCAGTCCCCACCGGAATTAAAATTTTCAGATGAATCGCCACAATT
TACGGGTCCAAAATTAAATTTTCACCCCAAATAATTTGATCAATAGGGTTC
ATTTTATTATTTACTATTGGTGGATTAACAGGAGTTATACTTGCTAATTCAT
CAATTGATATTGTACTTCATGATACATACTATGTAGTAGCCCATTTTCATTA
TGTTTTATCCATAGGAGCTGTATTTACAATTGTAGCTAGATTTATCCACTGA
TTTCCCCTATTCACAGGGGTTTCCATAAATAAAAAATGATTAAAAATTCAA
TTTTCATCAATATTTATTGGA – 3’

HM017484 (Urban *et al.* 2010).

Remarks.

The synonymy of *C. puellus* and *D. aculeata* is based on comparison of the primary type of *C. puellus* and X paratypes of *D. aculeate*, including topotypic specimens. Both the type specimen of *C. puellus* and paratype specimens of *D. aculeata* from the same collection event were examined (in addition to other paratypes). *Delphacodes aculeata* is a junior synonym of *D. puella*. *Chionomus puellus* is extremely common in collections, and may be one of the most commonly encountered eastern delphacid species (Gonzon *et al.* 2007). It can be easily identified using the diverging processes of segment X, the sinuate apical margins of the parameres, and the bifurcating armature of the diaphragm. This species is closely allied with *C. bellicosus* and *C. pacificus* (see the remarks section of *C. bellicosus*).

Type Material Examined.

Lectotype *Liburnia puella* [USNM]: Macropterous ♂ under Liburnia puella 1897, " Miss. // ♂ // Type // LECTOTYPE / Liburnia [Handwritten]/ puella [Handwritten]/ Van D. [Handwritten]/ Oman 1946 [Orange paper]".

Topotype *Delphacodes aculeata* [SEMC]

Other Material Examined.

Canada: Nova Scotia: At sea, 3-VII-1987, Uhler (USNM, 1m♂). **United States:** Vermont: Stowe, 22-VI-1927, CP Alexander (USNM, 2m♂). New Jersey: Salem Co., nr Salem 166 Maskell Mill Rd., 23-VIII-2003, CR Bartlett (UDCC, 24m♂, 1b♂, 27m♀, 2b♀). Pennsylvania: Chester County, Landenberg, 51 Morgan Hollow Way, 11-XI-2004, J.A. Wildonger (UDCC, 1m♀); Chester Co., nr. Avondale, 19-IX-1998, C. R. Bartlett (UDCC, 1m♂); Chester Co., Oxford, Old Rt 1, 2-VII-1999, RL Snyder (UDCC, 1b♀); Chester Co., Kennett Square, 17-IX-1999, Kathryn Musig (UDCC, 1m♀); Washington Co., Vestaburg 556 Vine St., VII-1997, R. Westich (UDCC, 1m♀). Delaware: New Castle County, 2 Miles W of Kirkwood N side of C & D Canal, 1-X-2004, J.A. Wildonger (2m♀); New Castle County, Vandyke, Peter's Tract Blackbird State Forest, 9-VI-2004, N.H. Nazdrowicz (UDCC, 1m♀); New Castle County, Newark, University of Delaware, Townsend Hall Habitat Trail, 3-IX-2004, C R Bartlett (UDCC, 2b♂); New Castle County, Newark, University of Delaware Woodlot, 26-IX-1996, C. Bartlett (UDCC, 1m♂); New Castle County, University of Delaware, Townsend Hall, 8-X-1996, David Hulburt (UDCC, 1m♂); New Castle County, Newark, Iron Hill, 13-IX-1997, WP Brown (UDCC, 2m♂); Kent, Clayton, Blackiston, 13-IX-1997, R. Mitchell (UDCC, 1m♂); Redden, Redden State Forest Headquarters Tract, 16-XIII-1994, T.A.R. (UDCC, 1m♀). Maryland: Fair Hill,

27-IX-1996, B. Galinskie (UDCC, 1m♂); Cecil Co., Fair Hill, Fair Hill NRA, 26-IX-2003, C R Bartlett (UDCC, 7m♂, 3m♀); Kent Co., nr. Fairlee Chesapeake Farms, 30-VI-1997, C.R. Bartlett (UDCC, 5m♂, 2b♂, 3m♀); Allegany Co., Little Orleans cmpgrnd, 5-VI-2003, CE Bartlett (UDCC, 1m♀). District of Columbia: Washington DC, 12-IX-1987, (USNM, 1m♂). Virginia: Arlington, 15-VII-1932, JW Scrivener (USNM, 1m♂). North Carolina: Swain Co., 3mi SW Newfound Gap, on Clingmans Dome Road, 1-VII-2001, S.M. Clark (BYU, 2m♂); Bladen Co., Nr. Bladen Lakes S.F., Bladen Lakes Sch. Rd., 17-IX-1994, C.R. Bartlett (UDCC, 8m♂, 13m♀); Bladen Co., White Lake, 16-IX-1995, C.R. Bartlett (UDCC, 1m♂); New Hanover Co., Nr. Wilmington, 17-V-1995, C.R. Bartlett (UDCC, 1b♀); Mecklenburg Co., Charlotte, (10-15)-IX-1974, J.F. Cornell (UDCC, 4m♂, 2m♀); Jackson Co., nr Balsam BR.P. "Wesner, Bald View", 31-VII-2003, C Bartlett, A Gonzon, D Nonne (UDCC, 2m♂). Louisiana: Baton Rouge, 1-X-1974, (LSAM, 1m♂); Baton Rouge, 10-XI-1975, (LSAM, 1m♂, 1b♂); Baton Rouge, 1973 (LSAM, 1b♂); Baton Rouge, XI-1975 (LSAM, 1b♂); E. Baton Rouge Par., 15-XI-1971, L.D.N. (LSAM, 1m♂); E Baton Rouge Par., 31-XII, 1971, (LSAM, 2b♂); E. Baton Rouge Par., 8-X-1992, A.L. Johnson (LSAM, 1m♂); E. Baton Rouge Par., 24-IX-1992, A.L. Johnson (LSAM, 1m♂). Florida: Highlands Co. nr Lake Placid Archbald Biol. Sta., 21-I-2002, CR Bartlett (UDCC, 2m♀, 1b♀); Jefferson Co. 3mi S Wacissa, 27-VII-2000, C.W. O'Brien (LBOB, 1m♂); LaBell, 16-VII-1939, Oman (USNM, 1b♂); Lamont, 7-III-1947, R.H. Beamer (UDCC, 2b♂, 5b♀); Yankeetown, 9-III-1947, R.H. Beamer (UDCC, 3b♂); Otter Creek, 9-III-1947, R.H. Beamer (UDCC, 3b♂, 2b ♀). TX: PR Uhler (USNM, 1m♂). **Mexico:** Veracruz Fortin' Flores micro. sta. 3-X-1982, J. Huber

(UDCC, 1m♂); VeraCruz 3mi W Coatzacoalcos 26-VI-1971, Ward&Brothers (LBOB, 1m♂). **Venezuela:** El Valle, 28-IX-1938, CH Ballou (USNM, 1m♂, 1m♀).

1.4.14 *Chionomus quadrispinosus* (Muir and Giffard, 1924), new combination

(Figures 35-37)

Delphacodes quadrispinosa Muir and Giffard, 1924: 37.

Type Locality.

Nicaragua, San Marcos.

Diagnosis.

Body dark brown to brown, with white markings. Vertex quadrate; foveae of frons and vertex concolorous with body. Carinae distinct, off-white in color; antennae light brown. Pronotum concolorous with mesonotum, paranota white along margins. Armature of diaphragm U-shaped; inner and outer angles of parameres diverging, basal angle produced, rounded. Aedeagus tubular, with two rows of teeth along venter, curved dorsad; base enlarged, quadrate. Segment X armed with 4 distinct processes, first processes closely approximated, second processes nearly touching.

Description.

COLOR. *Macropter*. Body dark, brunneous, shining, with white or ivory markings. Carinae of head (excluding genal carinae) distinct, off-white to ivory in color; median carinae of vertex concolorous with foveae. Antennae light brown, paler at apex. Pronotum concolorous with mesonotum, paranota white to ivory along margins. Mesonotum dark, median and lateral carinae obscure. Legs cream colored to yellow, apex of tarsi brown. Forewings hyaline, distinct dark spot just before apex of clavus. Abdomen dark brown, thin white line along caudal edge of each segment, lateral projections of sternites white. Pygofer and segment X brown. *Brachypter*.

Similar to above. Tegmina dark, infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter 1.60±0.02 (n=2); ♂ brachypter 1.46±0.12 (n=5); ♀ brachypter 1.69 ±0.09 (n=4); width ♂ 0.62±0.07 (n=16); ♀ 0.64±0.04 (n=4). Head: Vertex length 0.14±0.03 (n=16); vertex width 0.16±0.02 (n=13); frons length 0.41±0.06 (n=16); frons width 0.19±0.03 (n=16). *Macropter*. Carinae of vertex distinct, stem of Y-shaped obscure. In lateral view (Figure 35b, d), fastigium rounded; projecting in front of the eye about half the length of eye. Carinae of frons and clypeus distinct (Figure 36a), frons subparallel, widest just below ventral edge of compound eyes. Antennal segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 3, 3, 2, 2, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, diverging posteriorly, reaching hind margin. Forelegs with 2 rows setae on ventral margin of femora; legs mostly bare. Calcar bearing 18-22 small teeth. *Brachypter*. Same as above but with lateral carinae mesonotum evident; tegmina apically rounded, reaching to the midsection of the pygofer.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex; abdominal spiracles surrounded with one or two long, fine setae.

Genitalia. Pygofer in lateral view (Figure 36c) about as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figure 36b), 5/6ths as tall as wide, rounded; margins raised, dorsolateral margins produced, carinate. Opening to inner

chamber trapezoidal, pointed ventrad. Armature of diaphragm U-shaped, fitting aedeagus, smooth, distinctly projecting caudad. Parameres, widest in basal third, basal angle projecting, rounded; dorsolaterally diverging, apices concave, lateral margins concave, inner produced, quadrate, outer angles produced, rounded. Aedeagus oval in cross-section, curved ventrad, consistent in width excluding base, two rows of evenly spaced teeth along ventral margin; base wide, quadrate. Gonopore ventral, subapical. Segment X quadrate, wider than tall; with 4 processes, first pair distinct, closely approximated, second pair longer than first, more closely approximated, nearly touching. Segment XI produced, about 1/3rd length of segment X.

Hosts.

Phaseolus vulgaris L. (PHVU), kidney bean (Label information).

Distribution.

USA: FL, LA; Cuba; Guatemala; Honduras; Nicaragua; Costa Rica.

COI Sequence.

While material for molecular work was available, the author was unable to successfully amplify *COI* for this taxon.

Remarks.

Chionomus quadrispinosus is closely allied with *C. dissipatus* and *C. gluciophilus* and has an overlapping distribution (see Remarks of *C. dissipatus*). *Chionomus quadrispinosus* tends to be darker and can be distinguished by the armature of the diaphragm and shape of the aedeagus. This species is most frequently collected in brachypterous form.

The type specimen belonged in the Pomona Collection which was given to CASC. The specimen is not listed in the California Academy of Science's type

specimen database; a trip to the museum to look for the type failed to recover the material. Additionally, BPBM was checked because a number of holotypes were placed there. The type is believed lost.

Type Material Examined.

Holotype [Pomona Collection, transferred to CASC]: LOST.

Other Material Examined.

United States: Florida: Sanford, 29-V-1926, E.D. Ball (FSCA, 2b♂, 2b♀); Sanford, 11-III-1947, R.H.Beamer (FSCA, 1b♂, 1b♀); LaBelle, 16-VII-1939, Oman (FSCA, 3b♂). Louisiana: Baton Rouge, 10-XI-1975, (LSAM, 3b♂). **Dominican Republic:** La Vega: La Guardarraya, Mons. Nouel-Constanza Rd, J. Maldonado-Capriles (USNM, 1m♂). **Guatemala:** Quetzaltenango, Fuentes Georginas, Volcan Zunil, 8km SE Zunil, 14-15-II-2007, ATGonzon & R Donovall (UDCC, 1m♂). **Honduras:** Dept. Of Francisco Morazan, Zamorano, 23-IX-1961, J.M. Matta (LBOB, 1m♂). **Costa Rica:** San Pedro de Montes de Oca, 4-XII-1936, CH Ballou (USNM, 1m♂); 2km W. Empalme, I-1995, C. Godoy & P. Hanson (LBOB, 1m♂); Punt. S. Voco, Est. Biol. Las Alturas, X-1991, Hanson & Godoy (LBOB, 1m♂); Punt. S. Voco, Est. Biol. Las Alturas, II-1992, Hanson & Godoy (LBOB, 2m♂); Heredia nr Puerto Vieja La Selva Bio. Sta. , 24-II-2004, CR Bartlett, et al (UDCC, 1m♂, 1b♂); Heredia nr Puerto Vieja La Selva Biol. Sta. , (23-II)-(2-III)-2004, CR Bartlett, J Cryan, JUrban (UDCC, 1m♂); Heredia Estacion Biologica, La Selva, 12-I-1995, S.M. Clark (BYU, 1m♂);

1.4.15 *Chionomus tenae* (Muir, 1926), new combination

(Figures 5b, 38-40)

Delphacodes albinotata Muir and Giffard, 1924: 36 [nec. Crawford, 1914].

Delphacodes tenae Muir, 1926: 34.

Delphacodes arcuata Beamer, 1948: 105-106; replacement name for preoccupied *Delphacodes albinotata* Muir & Giffard [nec. Crawford], **new synonymy.**

Type Locality.

Ecuador, Napo, Tena.

Diagnosis.

Body dark brown, with white to cream colored markings. Vertex quadrate; foveae of frons and vertex dark. Carinae distinct, off-white in color; antennae light brown. Pronotum dark anteriorly with band of white along posterior edge, paranota pale along margins. Armature of diaphragm forming a triangular fold, apex of parameres avicephaliform. Aedeagus tubular, left side bearing preapical spine, posteriorly projected; segment X with processes produced as lobes.

Description.

COLOR. Body dark, brunneous, with white and stramineous markings. Carinae of head (including genal carinae) distinct, ochraceous in color, usually with a small amount brown at apex of carinae; median carinae of vertex evident. Antennae light brown, darkened at joint of the two segments. Pronotum white, dark brown shadows directly posterior to eyes, fuscous markings between lateral and median carinae; paranota dark with white border. Mesonotum dark, median and lateral carinae obscure. Legs light brown; forewings hyaline, infuscate, distinct dark spot just before apex of clavus. Abdomen dark brown, some specimens with fine line of white on caudal edge of each segment, lateral projections of sternites yellow to white.

Pygofer brown. *Brachypter*. Similar to above, lighter; tegmina infuscate, white stripe along apex, darkened spot near apex of clavus.

STRUCTURE. *Body*. Body length (in mm) macropter 1.88±0.14 (n=12); female (♀) macropter 2.2±0.2 (n=12), ♂ brachypter 1.72 (n=1); width ♂ 0.78±0.06 (n=24); ♀ 0.88±0.07 (n=14). Head: Vertex length 0.18±0.04 (n=38); vertex width 0.19±0.03 (n=38); frons length 0.50±0.05 (n=38); frons width 0.22±0.02 (n=38). *Macropter*. Carinae of vertex distinct, stem of Y-shaped carina faint. In lateral view (Figure 38b, d), fastigium rounded; projecting in front of the eye about 1/5th eye length. Carinae of frons and clypeus distinct (Figure 39a), frons subparallel, widest ventral 1/3rd of compound eyes. Antennae segments subequal in length, segment II wider than segment I; 2nd segment sparsely setaceous, bearing sensory pits arranged 3, 4, 2, 1, evenly spaced around segment. Sensory pits surrounded by small black setae. *Brachypter*. Same as above.

Thorax. *Macropter*. Carinae of mesonotum weak, median carina ending anterior to scutellum, lateral carinae faint, parallel posteriorly, reaching hind margin. Legs mostly bare. Calcar bearing 15-17 small teeth (holotype with 15). *Brachypter*. Same as above but with lateral carinae mesonotum evident, diverging posteriorly; tegmina apically rounded, reaching midsection of pygofer.

Abdomen. *Macropter*. Compressed dorsoventrally, tapering caudad to truncate apex; abdominal spiracles surrounded by long fine setae. *Brachypter*. Same as above.

Genitalia. Pygofer in lateral view (Figure 39c) nearly half as long dorsally as ventrad, ventral margin sinuate. In caudal view (Figure 39b), as tall as wide, globular; margins rounded, mildly produced dorsolaterally. Opening to inner chamber

triangular, pointed ventrad. Armature of diaphragm produced as a U-shaped fold, some specimens with center of fold dorsally produced, triangular, smooth, projecting caudad. Parameres, widest in basal third, basal angle weak; dorsolaterally diverging to avicephaliform apices, lateral margins concave, inner angles strong, acute; outer angles produced to rounded apices. Aedeagus circular in cross-section, strongly curved dorsad, wider near base, with slight subapical expansion before pointed apex; Aedeagus bearing 1 to 2 subapical spines on left, sometimes hooked, directed posteriorly; row of small teeth along either side in midsection; gonopore dorsal, subapical. Segment X quadrate, taller than long; processes produced from midsection, rounded, lobe like, surrounding aedeagus. Segment XI produced, about half length of segment X.

Hosts.

None reported.

Distribution.

Mexico; Cuba; Jamaica; Belize; Honduras; Costa Rica; French Guiana; Colombia; Venezuela; Brazil; Paraguay; Ecuador, Argentina.

COI Sequence.

While material for molecular work was available and the author was able to successfully amplify *COI* for this taxon, attempts at sequencing provided only unidirectional results. The sequence will not be submitted to GenBank until sequencing is successful.

Remarks.

The type specimen of *C. tenae* is not dissected and only paramere shape and general shape of the pygofer can be clearly determined. The distribution of confirmed

D. arcuata specimens, from every country surrounding Ecuador (type location of *C. tenae*), combined with the lack of positively identified specimens of *C. tenae,* and matching paramere shape of the two species has provided sufficient evidence that these two species are in fact synonyms.

This species may be allied with *C. dolonus* because of the folded shape of the armature of the diaphragm, although it is not nearly a posteriorly produced here. The pygofer is also not as laterally compressed in this species. It may also be allied with *C. balboae* because of the subapical spines of the aedeagus; however, this species has the aedeagus distinctly upturned (straight in *C. balboae*) and lacks the triangular boss on the armature of the diaphragm.

Type Material Examined.

Holotype *Delphacodes tenae* [BPBM]: Brachypterous ♂, "Tena, Ecuador / March 16, 1923 [Day handwritten] // F.X. Williams / Collector // ♂ // Holotype [Red paper, vertical orientation, affixed to following label] //Delphacodes / tenae / ♂ Muir / Type No.1153. [Handwritten]".

Topotype *Delphacodes arcuata*

Other Material Examined.

Mexico: 3mi W Gutierraz Zamora Vera Cruz, 25-VI-1953, University of Kansas (SEMC, 1m♂). **Cuba:** Jobabo, 19-I-1925, CF Stahl (UDCC, 1m♂). **Jamaica:** 5-7mi W Montego Bay, 4-VIII-1967, L&CW O'Brien (LBOB, 1b♂). **Belize: O**range Walk Rio Bravo Cons. Area, Mahogany Trail, 11-VII-1996, C.W. & L.B. O'Brien (LBOB, 1m♂); Cayo District nr Teakettle Bank, Pooks Hill, 8-VII-2003, CR Bartlett (UDCC, 1m♀); Rio Temas[h], VII-1937, A.J. White (NCSU, 2m♂, 1m♀); Rio Grande, VI-1932, J.J. White (NCSU, 4m♂, 11m♀). **Honduras:** Dept. of Cortes, La

Lima, United Fruit Co, 3-VI-1964, F.S. Blanton, A.B. Broce, R.E. Woodruff (LBOB, 1m♂). **Costa Rica:** Heredia nr Puerto Vieja La Selva Biol. Sta., 18-19-VIII-2003 CR Bartlett, J Cryan, JUrban (UDCC, 1m♂); Heredia nr Puerto Vieja La Selva Biol. Sta., 15-VIII-2003 CR Bartlett, J Cryan, JUrban (UDCC, 1m♂); Heredia nr Puerto Vieja La Selva Biol. Sta., 16-VIII-2003 CR Bartlett, J Cryan, JUrban (UDCC, 2m♂); Heredia nr Puerto Vieja La Selva Biol. Sta., 17-VIII-2003 CR Bartlett, J Cryan, JUrban (UDCC, 3m♂). **Colombia:** Cauca PNN Gorgona El Saman, 7-25-V-2001, R. Duque (UDCC, 1m♂). **French Guiana:** Entomotech Lodge 30km SE Roura on Kaw Rd, 1-12-XII-2002, J.E. Eger (LBOB, 1m♂). **Brazil:** S.P. Piracicaba, 24-II-1966, C.A. Triplehorn (UDCC, 1m♂, 2m♀). **Paraguay:** 3km E Ypacarai, 7-X-1968, C.W. & L. O'Brien (LBOB, 1m♂). **Argentina:** Chaco P.N. Chaco, 11-13-I-2008, Dietrich et al (INHS, 1m♂); Corrientes, P.N. Mburucuyá, 1.8km W campgd., 8-I-2008, C.H. Dietrich (INHS, 1m♂).

1.4.16 Species excluded from *Chionomus*

Eleven additional species were considered for inclusion in *Chionomus.* *Delphacodes penepuella* is most likely closely allied with *Ribautodelphax* because of the crossed processes on segment X; paratypes were examined. *Delphacodes sagae* lacks key features such as the light mark at the scutellum and dark spot at the apex of the clavus; the strongly downward curve of the aedeagus indicates it may be allied with *Falcotoya*. This genus may also be a good placement for *D. saxicola* which also has a downward curving aedeagus. *Delphacodes concava* was placed in *Aethodelphax* during the course this work (Bartlett and Hamilton 2011); the author agrees with this placement. *Delphacodes venusta* was moved to *Nothodelphax* in 2002; if this placement is correct the allied *D. serrata* should also be place there (Hamilton 2002).

Delphacodes silvae may be placed in *Toya* because of the t the shape of armature of the diaphragm. *Delphacodes securigera* and *D. ardentis* may be allied with *Tagosodes*. *Delphacodes mesada* and *D. scolochloa* have been considered but do not fit the description of *Chionomus*; at this point the author cannot make a recommendation for an alternative placement of these species.

1.5 Discussion

Ten species are moved into the genus *Chionomus* for a total of 13 valid species. Three of total species were placed in this taxon when it was originally described. Two species are newly described and 8 are moved into *Chionomus* from other genera. Additionally, four species are placed as junior synonyms – *D. dentis* Beamer and *D. vaccina* Caldwell are synonymized with *C. dissipatus* (Muir); *D. aculeata* Beamer with *C. puellus* (Van Duzee); and *D. arcuata* Beamer with *C. tenae* (Muir). The holotypes for *C. quadrispinosus* (Muir and Giffard) and *C. haywardi* (Muir) have been lost.

Members of *Chionomus* are most diverse in South America (Table 5). Ten of 13 species can be found in this area of the world, indicating this might be the point of origin of the genus. Eight of the 13 species, over half, are now known from more than one New World regions. The compilation of this work has greatly expanded the ranges for the majority of *Chionomus* species. It is now evident that majority of members of this taxon are widespread and seem to be well adapted for dispersion.

Host information for all *Chionomus* species are summarized in Table 6. While informative, most of these records need to be verified as feeding, rather than resting, records. Only 6 species of *Chionomus* have reported hosts, members of this genus

appear to be polyphagous, are frequently associated with crops, and are found predominantly on grasses.

This revision makes need for further work on *Chionomus* evident. While this genus is not large, it is frequently encountered when collections for delphacids are undertaken. A key to females of the genus is still lacking and while distributions can be inferred, more collecting is needed for confirmation. This knowledge will both further improve identification tools for this genus and provided the basis needed for future work in the ecology and evolution of these insects. The work presented here is merely the first step needed to spur further investigations of this genus.

Table 3. Collection name, codon, and number of *Chionomus* individuals from each institution that provided specimens.

Collection	Codon	No. of Specimens
Bernice P. Bishop Museum, Honolulu, HI	BPBM	7
Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT	BYU	18
California Academy of Sciences, San Francisco, CA	CASC	4
California State Collection of Arthropods, Sacramento, CA	CSCA	5
University of Central Missouri Insect Collection (in care of Stephen Wilson), Warrensburg, MO.	CSMU	1
Illinois Natural History Survey, University of Illinois Champaign, IL	INHS	31
Lois O'Brien Collection, Green Valley, AZ, *associated with CASC*	LBOB	161
Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, LA	LSAM	17
North Carolina State University Insect Collection, North Carolina State University, Raleigh, NC.	NCSU	18
Snow Entomological Museum, University of Kansas, Lawrence, KS	SEMC	50
University of Delaware Collection, University of Delaware, Newark, DE	UDCC	274
University of Kentucky Collection, University of Kentucky, Lexington, KY	UKYC	4
National Museum of Natural History, Smithsonian Institution, Washington, DC	USNM	36
Vince Golia Collection, FL	VGC	8

Table 4. Number of specimens observed for each species including the numbers of males, females, macropters, and brachypters.

Species	Males		Females	
	macropters	brachypters	macropters	brachypters
C. havanae	103	4	3	-
C. balboae	87	11	-	-
C. banosensis	1	-	-	-
C. bellicosus	3	1	-	-
C. dissipatus	17	1	-	-
C. dolonus	2	-	3	-
C. gluciophilus	8	1	3	
C. haywardi	15	-	-	-
C. herkos	11	6	5	11
C. pacificus	82	10	25	-
C. puellus	72	17	58	12
C. quadrispinosus	11	10	-	3
C. tenae	22	1	15	-
Total	**434**	**62**	**112**	**26**

Table 5. Number of *Chionomus* species found in each region of the new world.

Region	No. of Species
North America	7
Central America	8
Caribbean	3
South America	10

Table 6. Summary of recorded host plants for species of *Chionomus* and if the record is from the literature or label data.

Species	Host	Lit.	Label
C. havanae	*Axonopus compressus* (Sw.) P. Beauv.	X	
C. bellicosus	*Paspalum distichum* L.	X	
C. gluciophilus	*Saccharum* L.	X	
	Solanum tuberosum L.		X
	Phaseolus vulgaris L.		X
C. haywardi	*Oryza sativa* L.	X	
	Zea mays L.	X	
	Triticum aestivum L.	X	
	Avena sativa L.	X	
	Hordeum vulgare L.	X	
C. pacificus	*Medicago sativa* L.		X
C. quadrispinosus	*Phaseolus vulgaris* L.		X

Figure 3. Comparison of lateral habitus of *C. puellus* (a) and *C. havanae* (b).

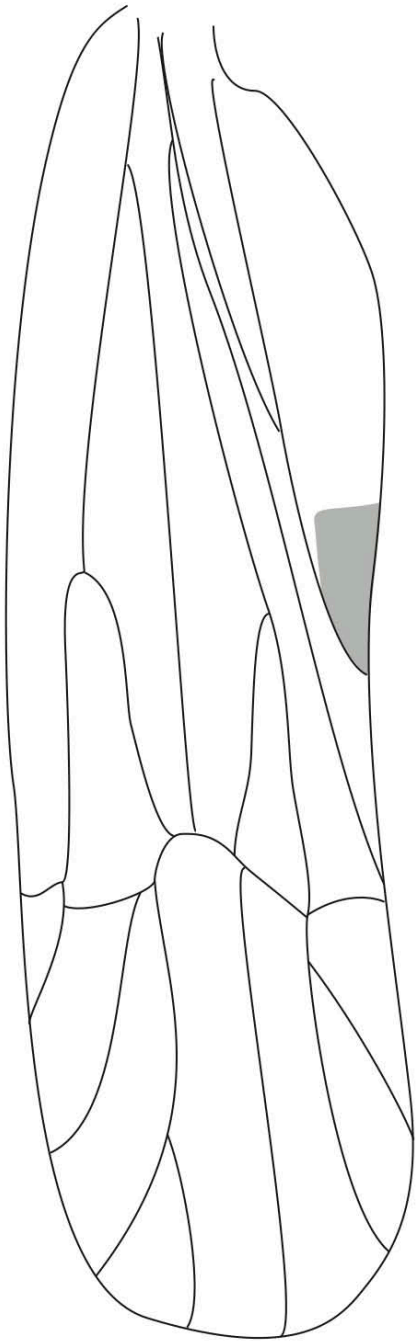

Figure 4. Macropterous wing venation of *C. havanae* (type species).

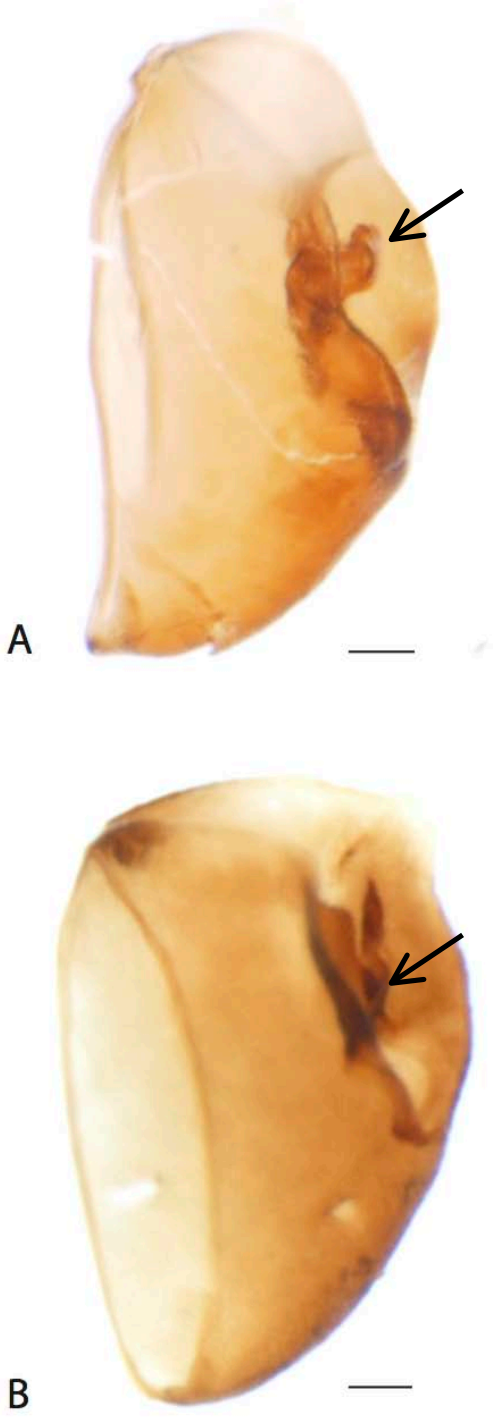

Figure 5. Lateral view of pygofer a. *C. havanae*, b. *C. tenae*.

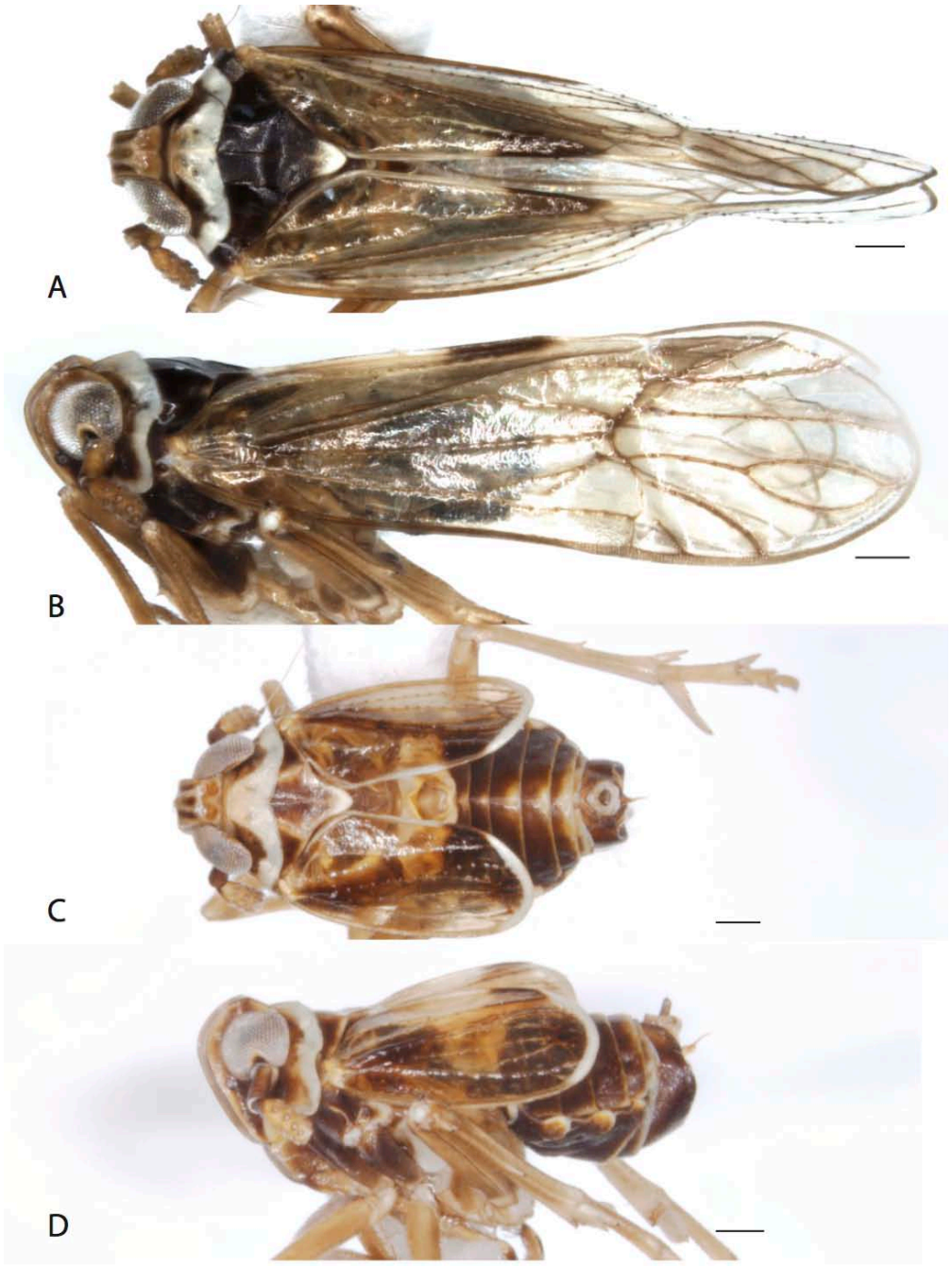

Figure 6. Images of *C. havanae* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

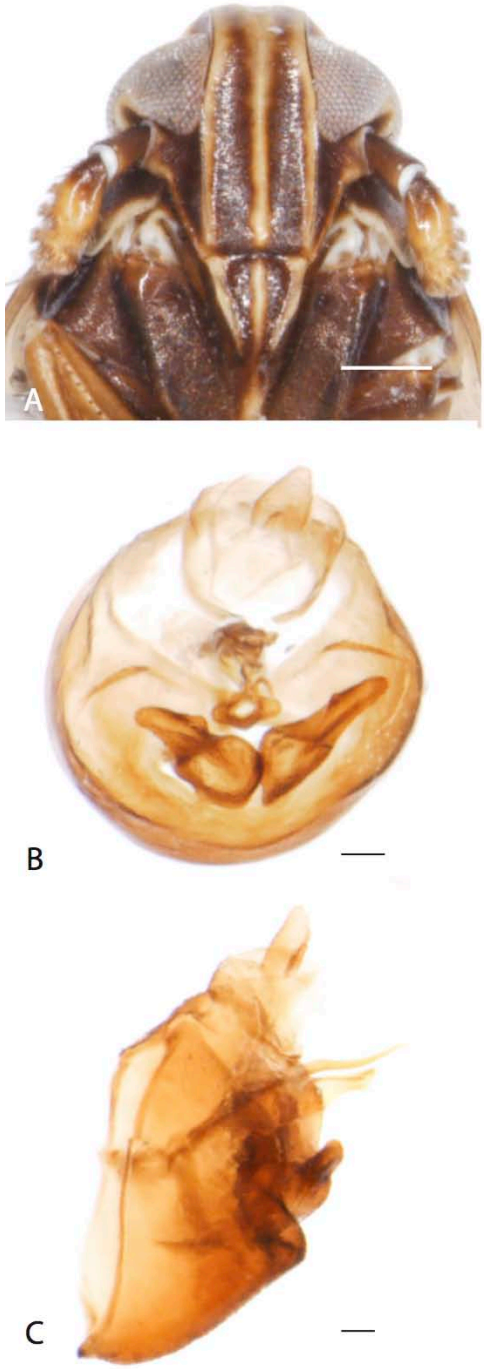

Figure 7. Images of *C. havanae* a. frons, b. pygofer, caudal view, c. pygofer, lateral view.

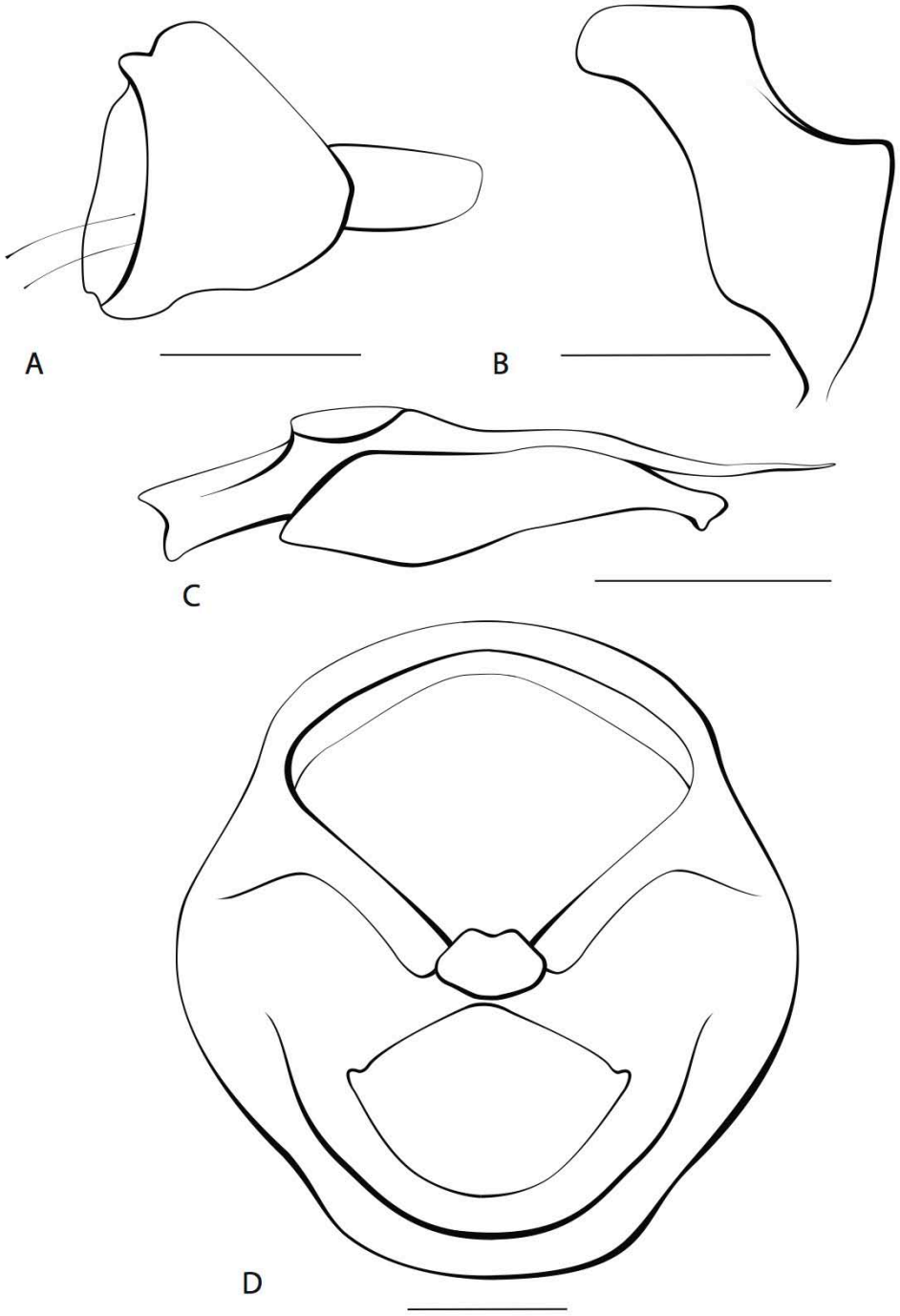

Figure 8. Illustration of the genitalia *C. havanae,* a. segment X, left lateral view, b. left paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

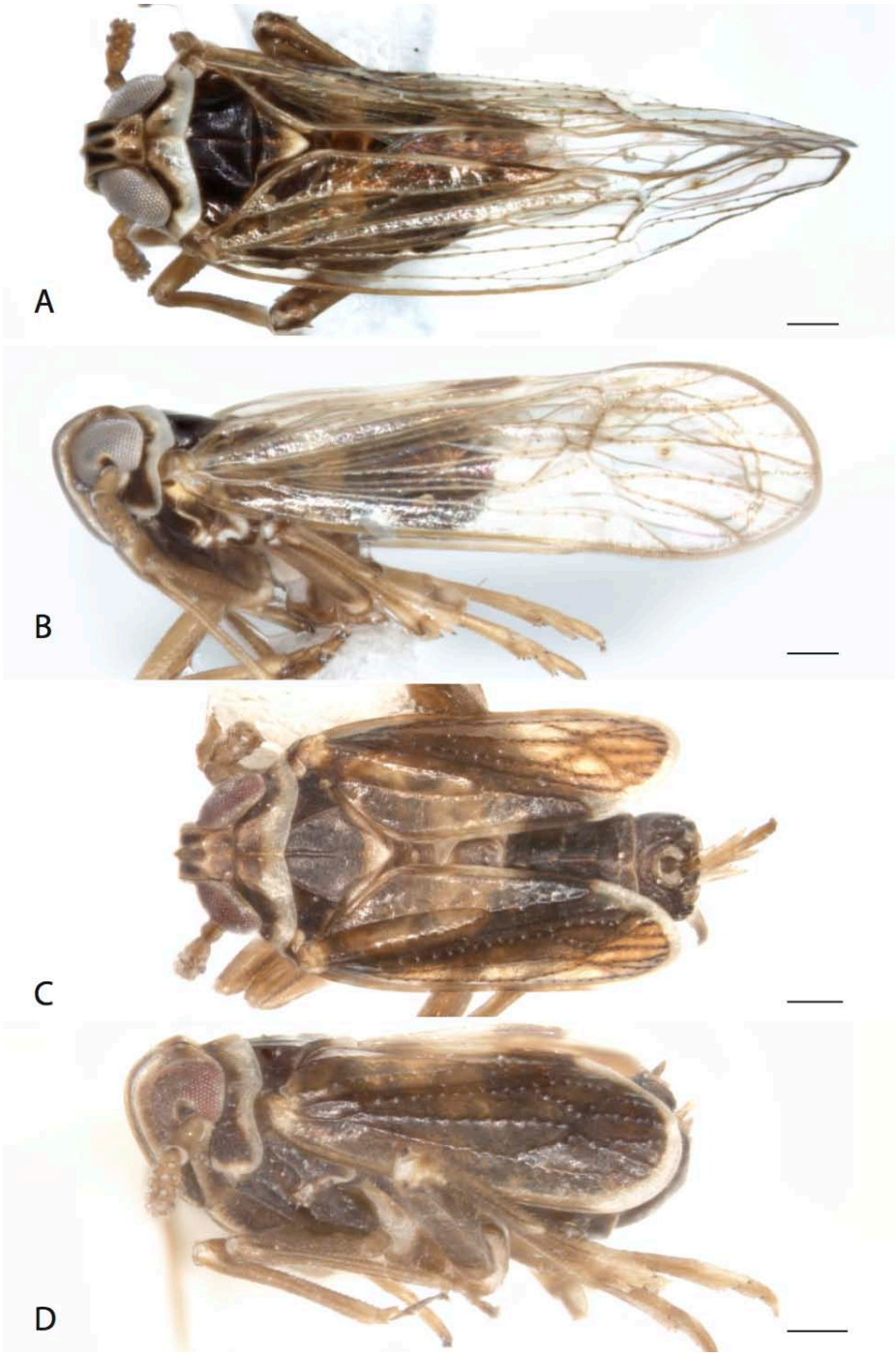

Figure 9. Images of *C. balboae* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

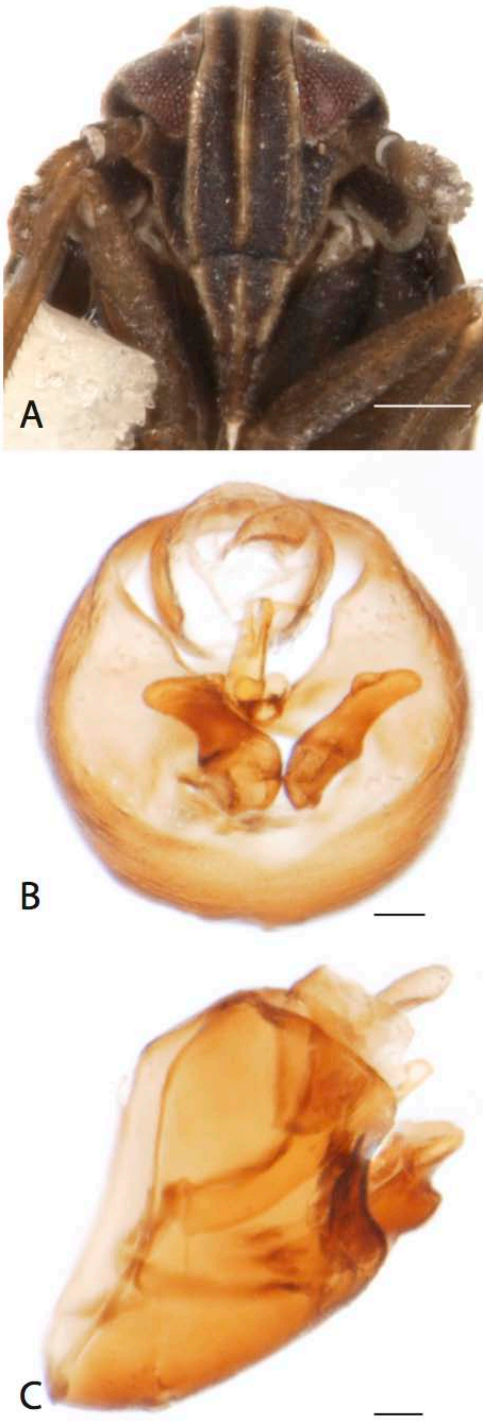

Figure 10. Images of *C. balboae* a. frons, b. pygofer, caudal view, c. pygofer, lateral view.

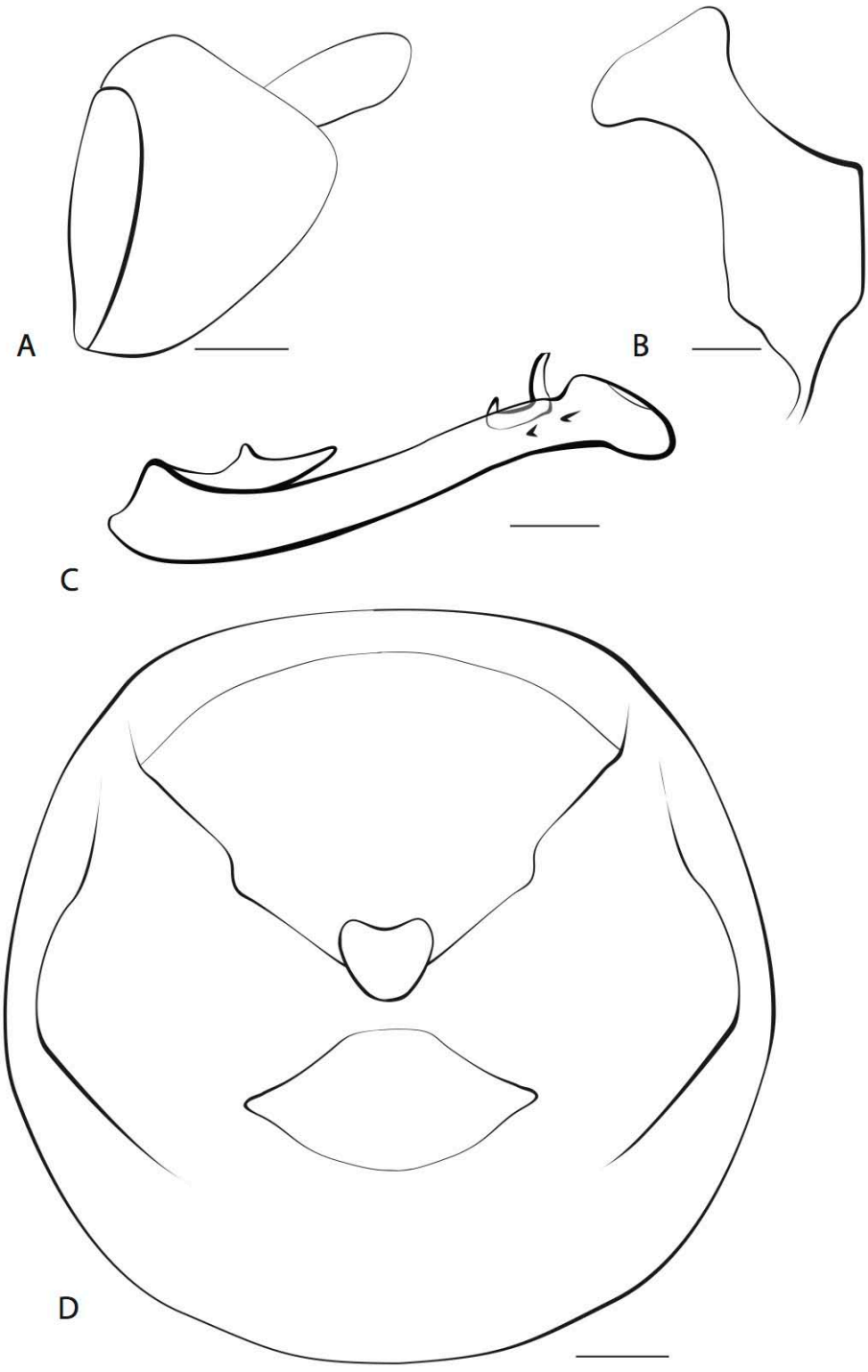

Figure 11. Illustration of the genitalia C. balboae, a. segment X, left lateral view, b. left paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

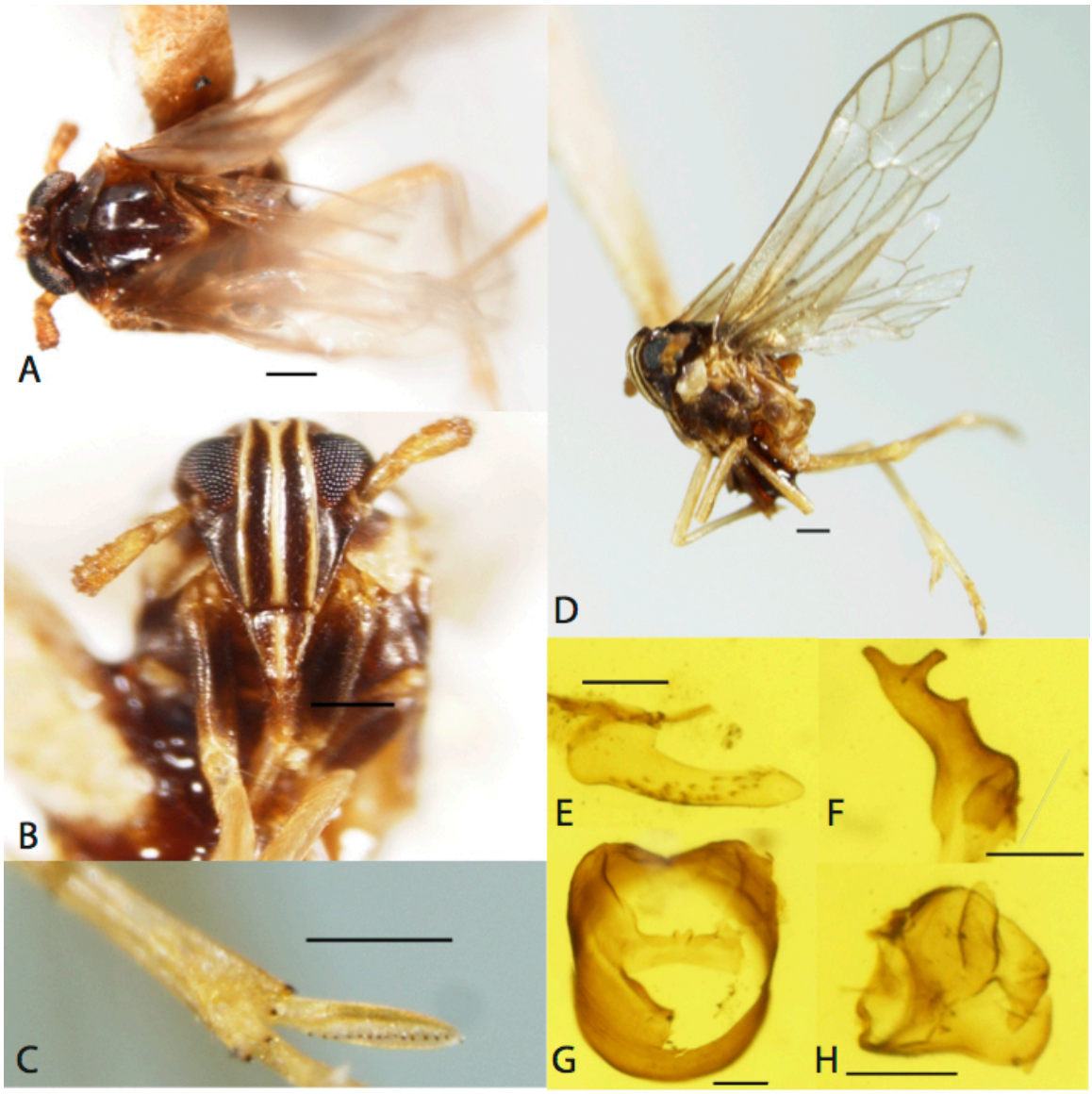

Figure 12. Images of *C. banosensis* holotype (scale bars 0.2 mm), a. dorsal habitus, b. frons, c. calcar, d. lateral habitus, e. aedeagus, left lateral view, f. left paramere, widest view, g. pygofer, caudal view, h. segment X, left lateral view.

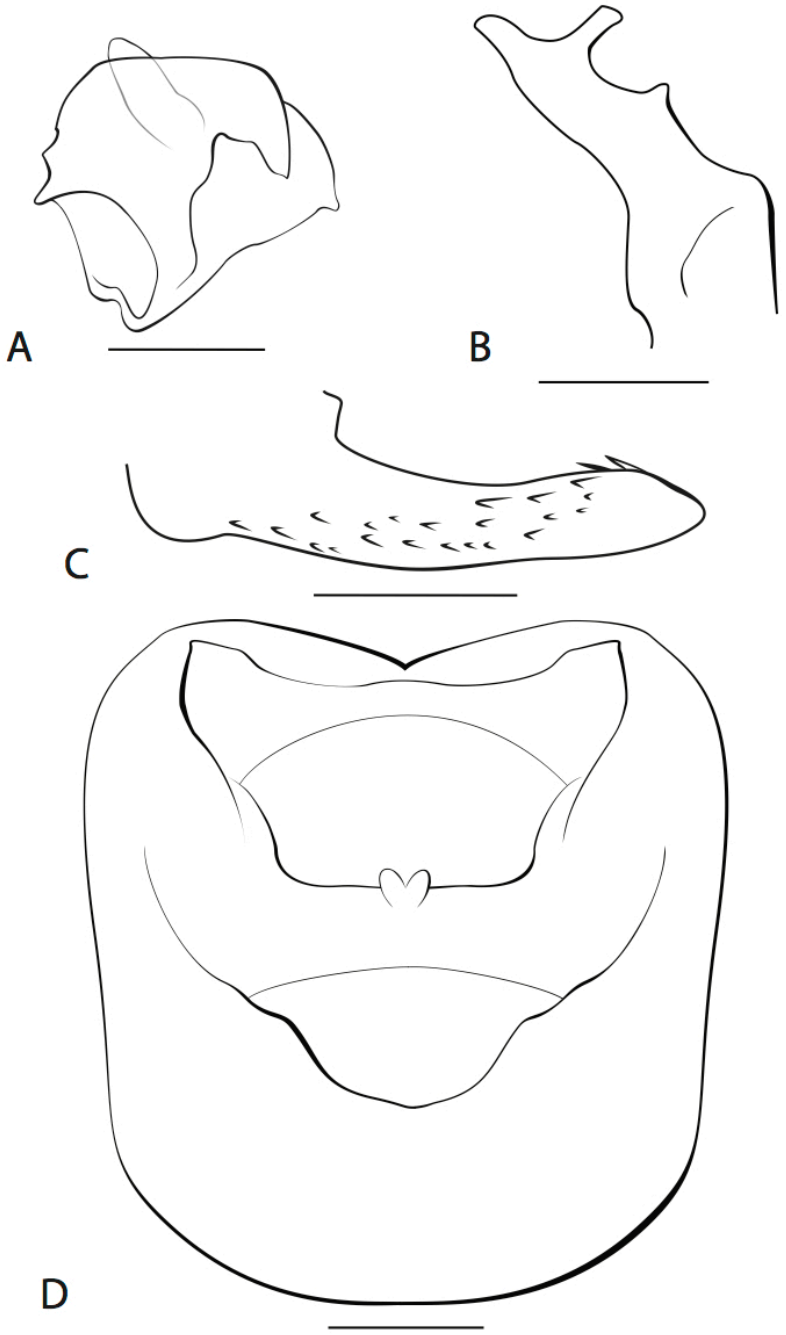

Figure 13. Illustration of the genitalia *C. banosensis* (scale bars = 0.2mm), a. segment X, left lateral view, b. left paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

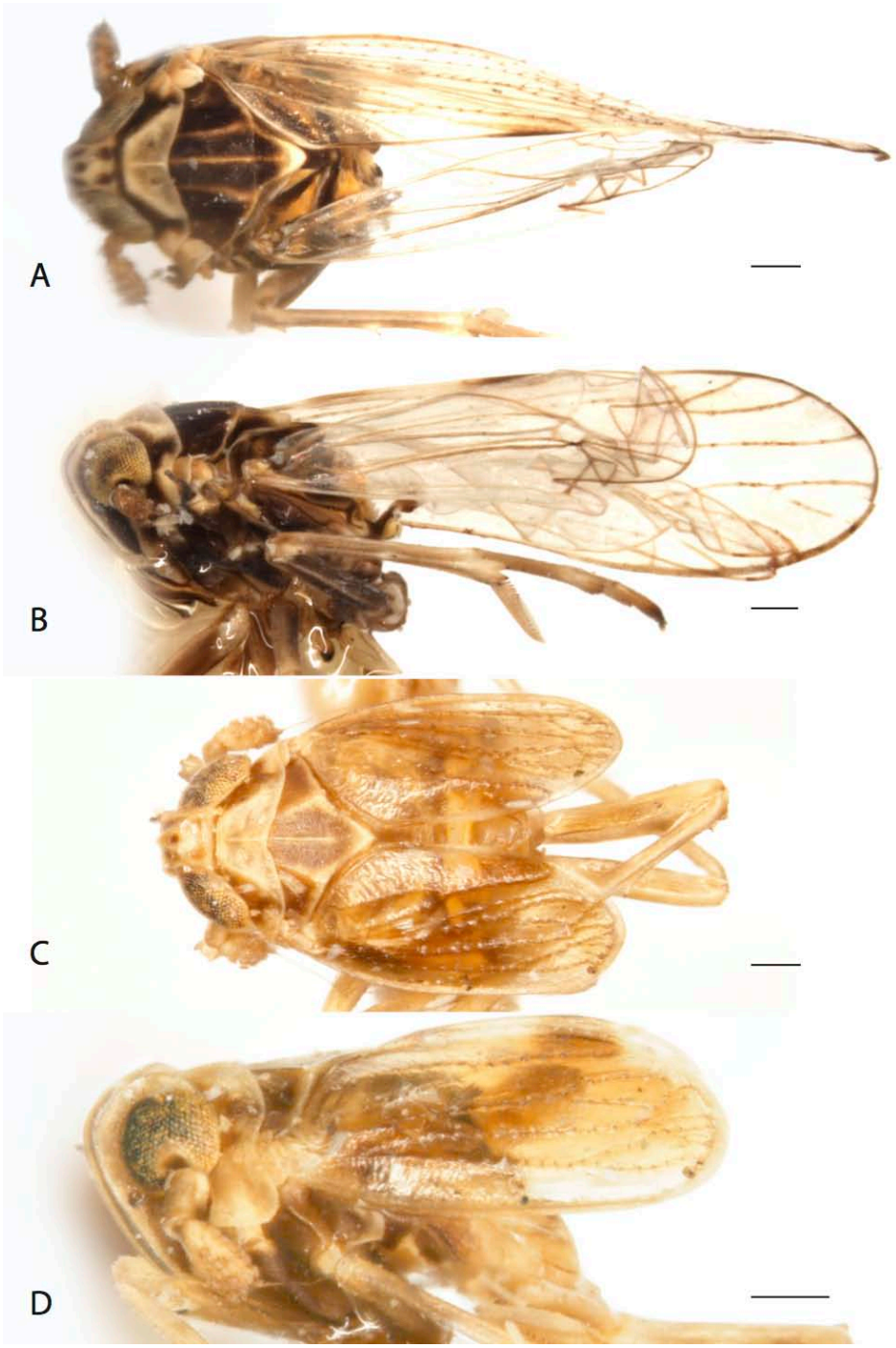

Figure 14. Images of *C. bellicosus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter),

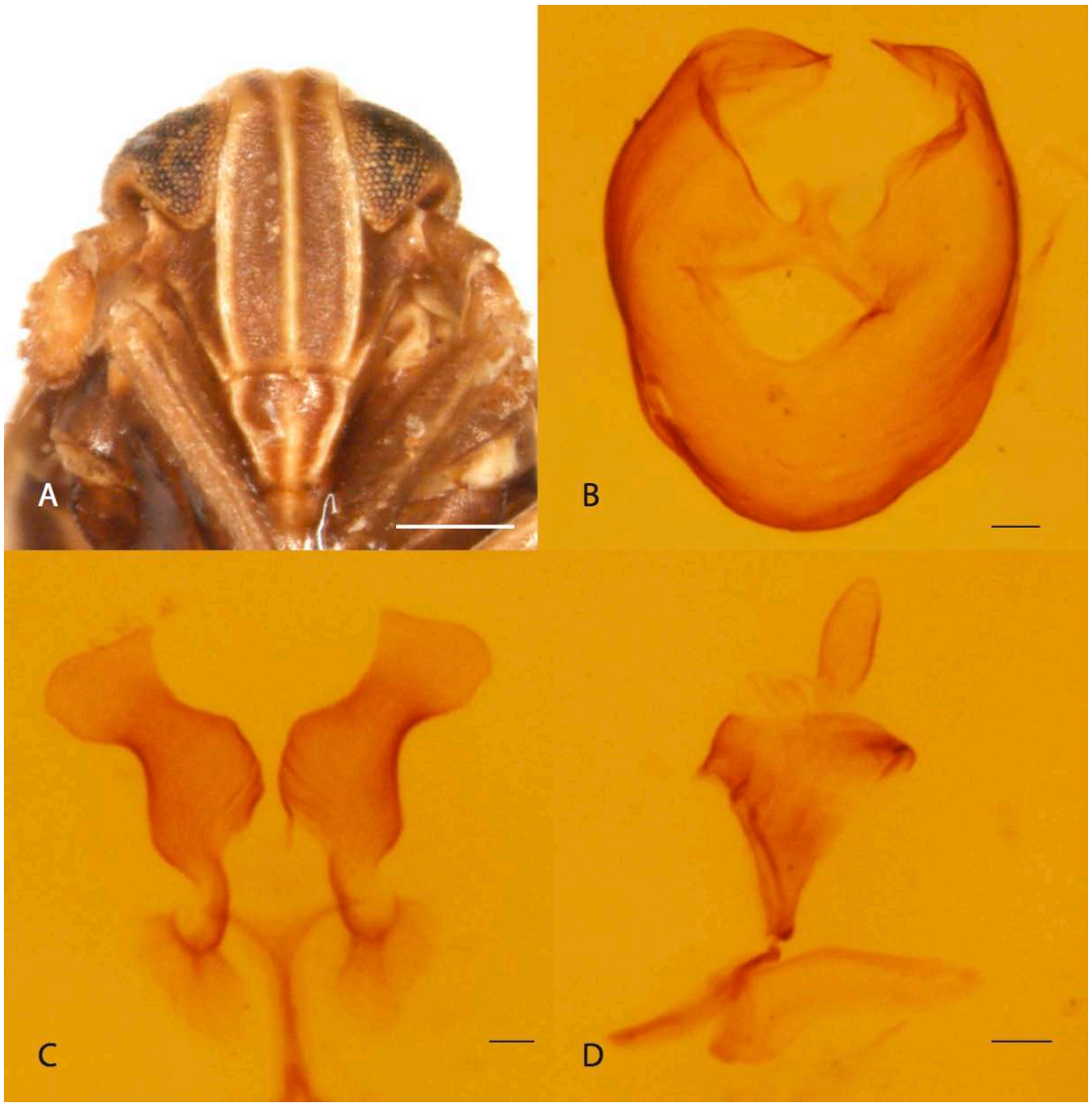

Figure 15. Images of *C. bellicosus*, a. frons [holotype], b. caudal view of pygofer [holotype], c. parameres, widest view [holotype], d. aedeagus and segment X, left lateral view [holotype].

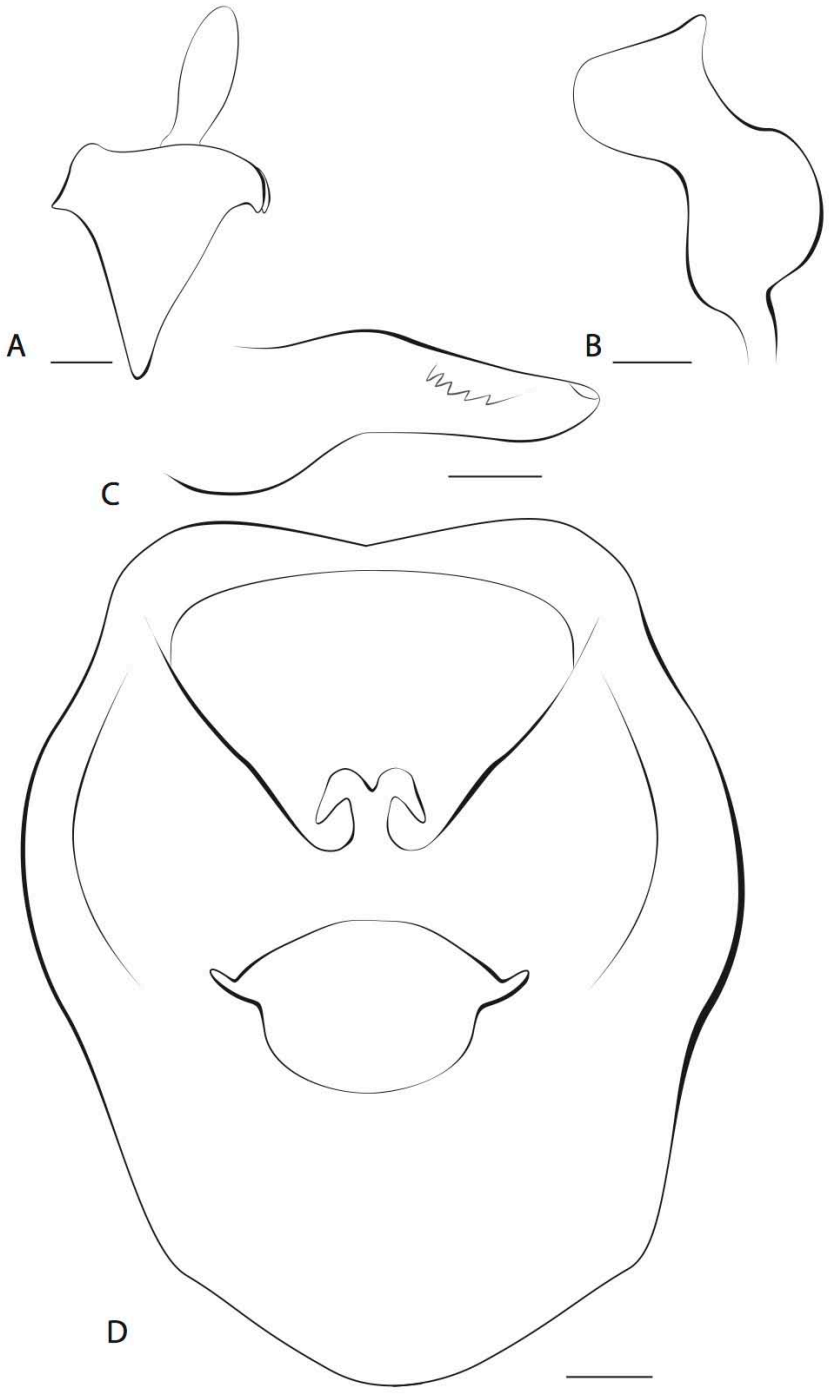

Figure 16. Illustration of the genitalia C. bellicosus, a. segment X, left lateral view, b. left paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

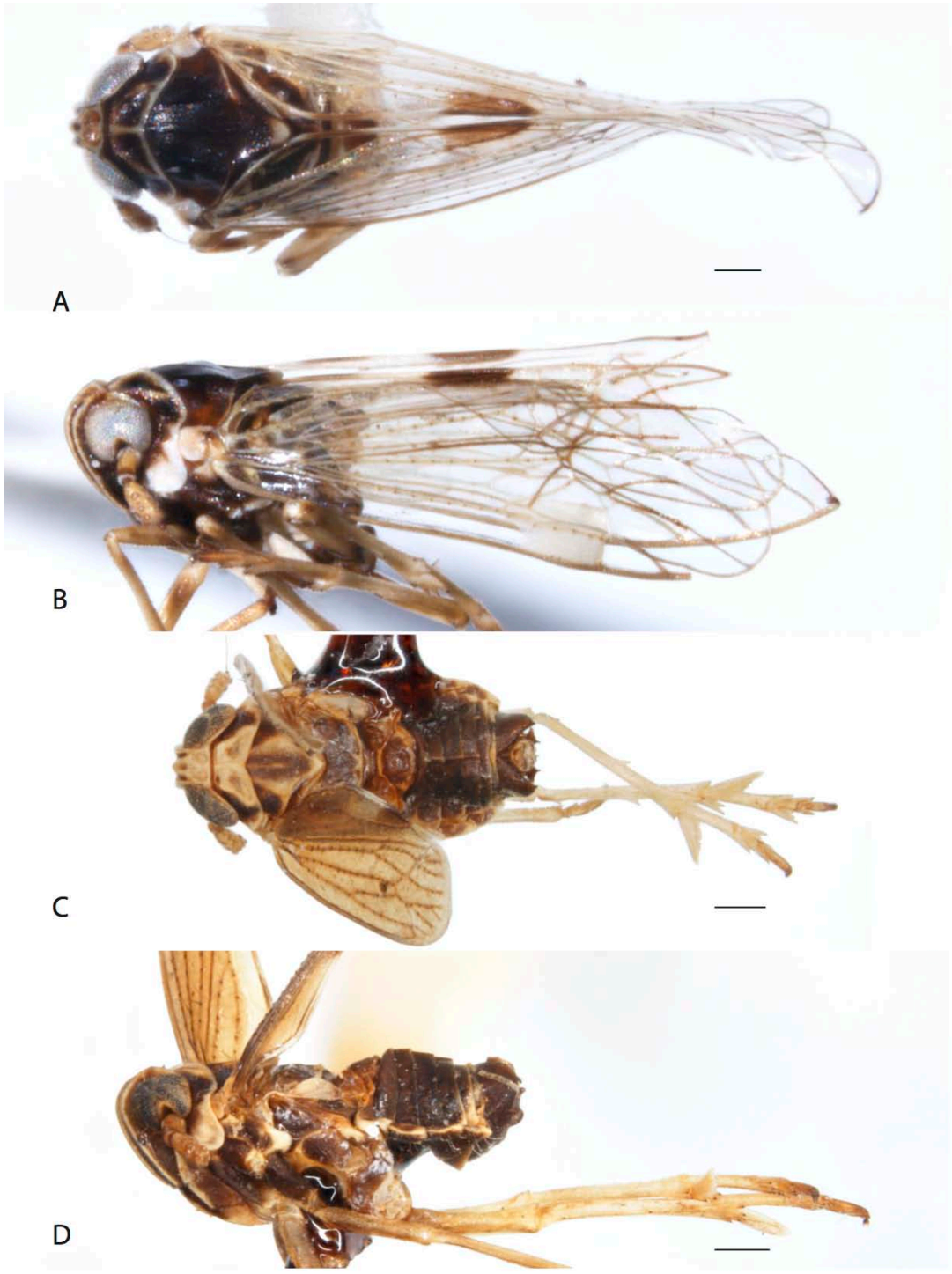

Figure 17. Images of *C. dissipatus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter) [holotype], d. lateral habitus (brachypter) [holotype].

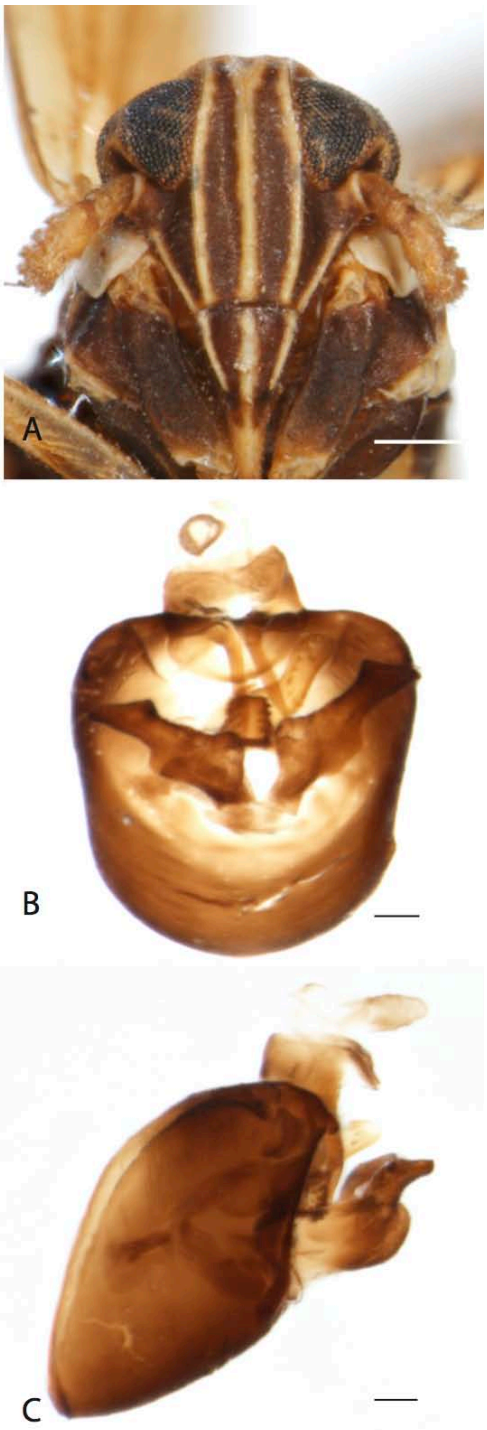

Figure 18. Images of *C. dissipatus* a. frons [holotype], b. pygofer caudal view, c. pygofer lateral view.

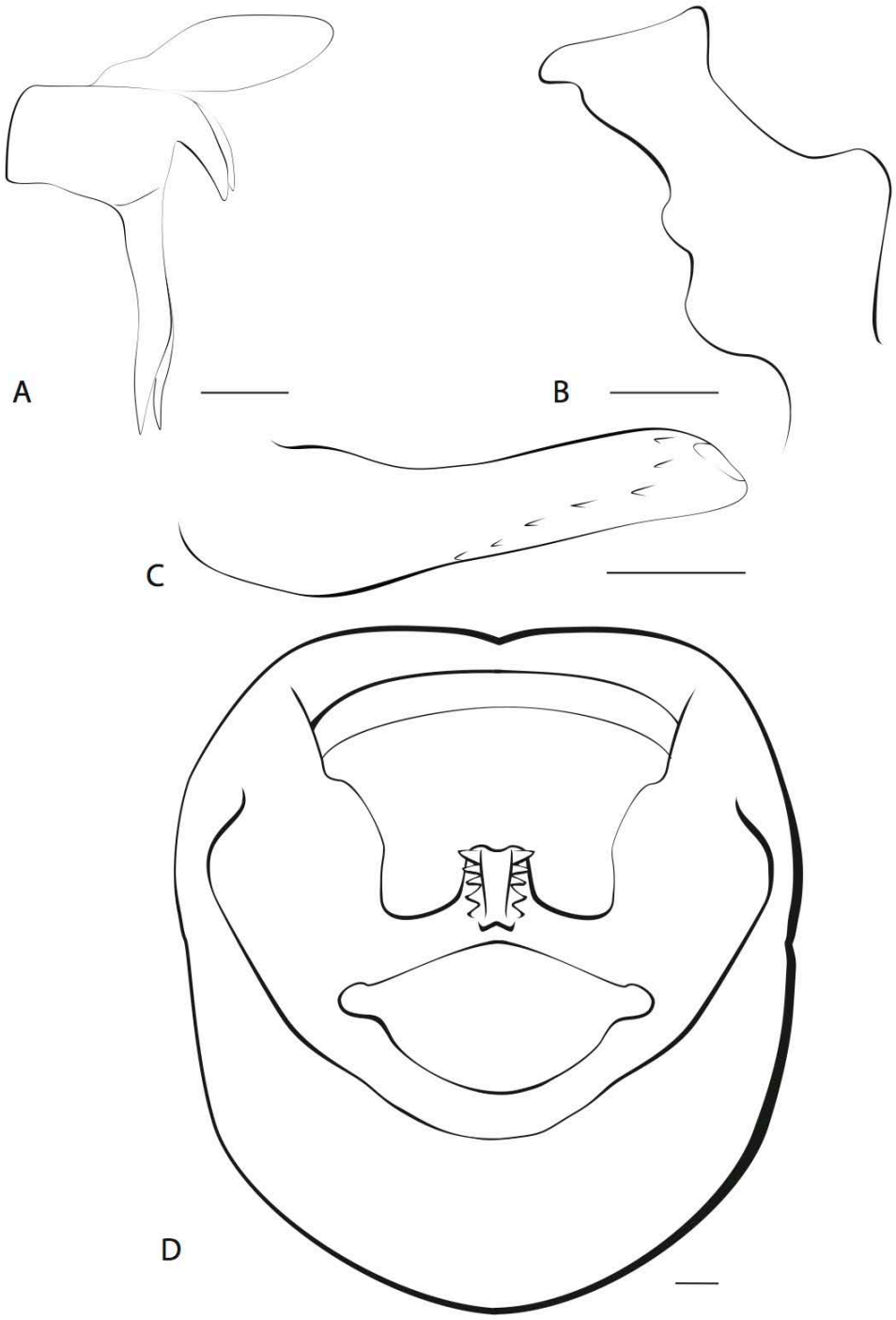

Figure 19. Illustration of the genitalia *C. dissipatus* a. segment X, left lateral view, b. paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

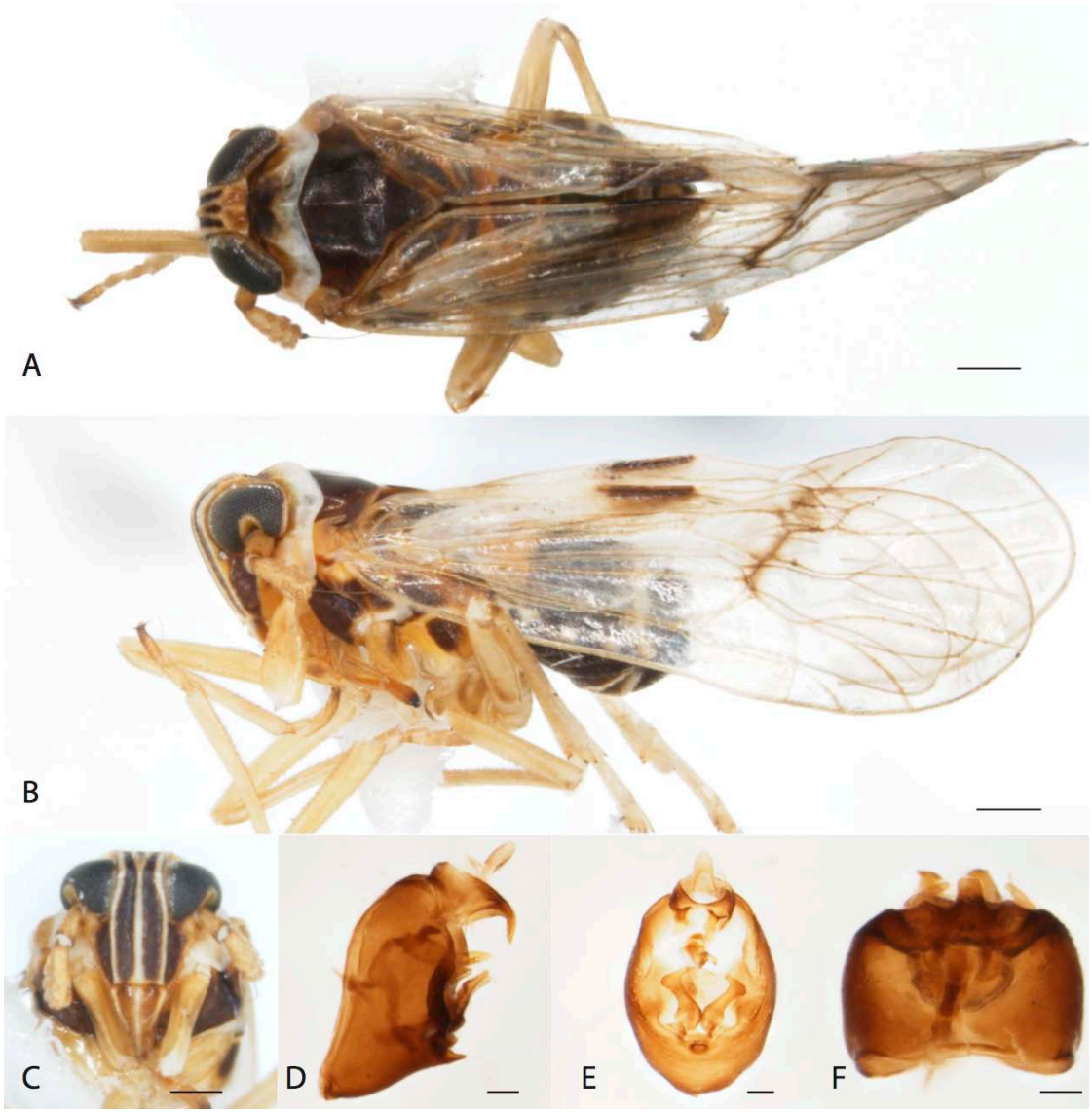

Figure 20. Images of *C. dolonus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. frons, d. pygofer, lateral view, e. pygofer, caudal view, f. pygofer, ventral view.

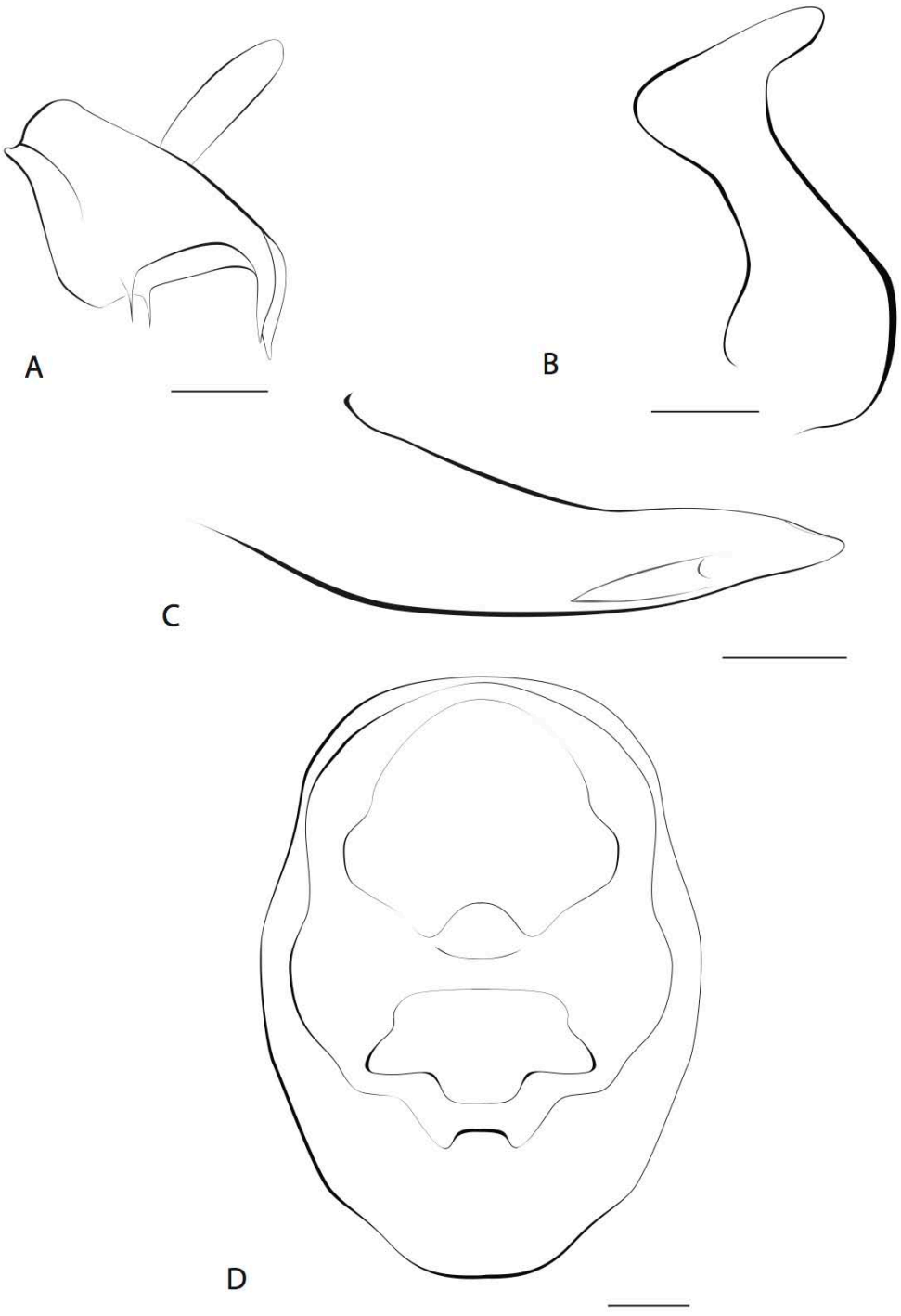

Figure 21. Illustration of the genitalia *C. dolonus* a. segment X, left lateral view b. paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

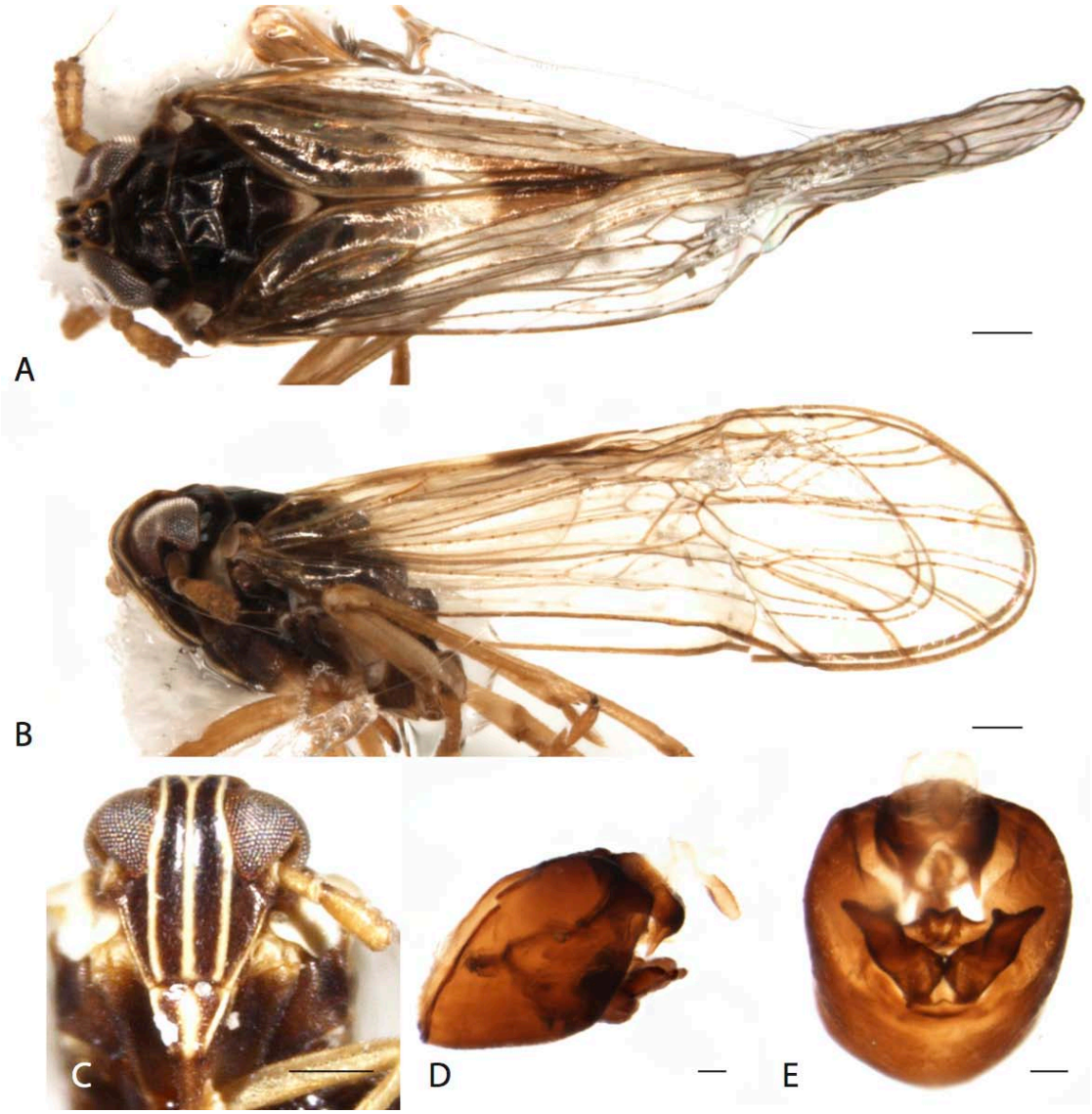

Figure 22. Images of *C. gluciophilus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. frons, d. pygofer, lateral view, e. pygofer, caudal view.

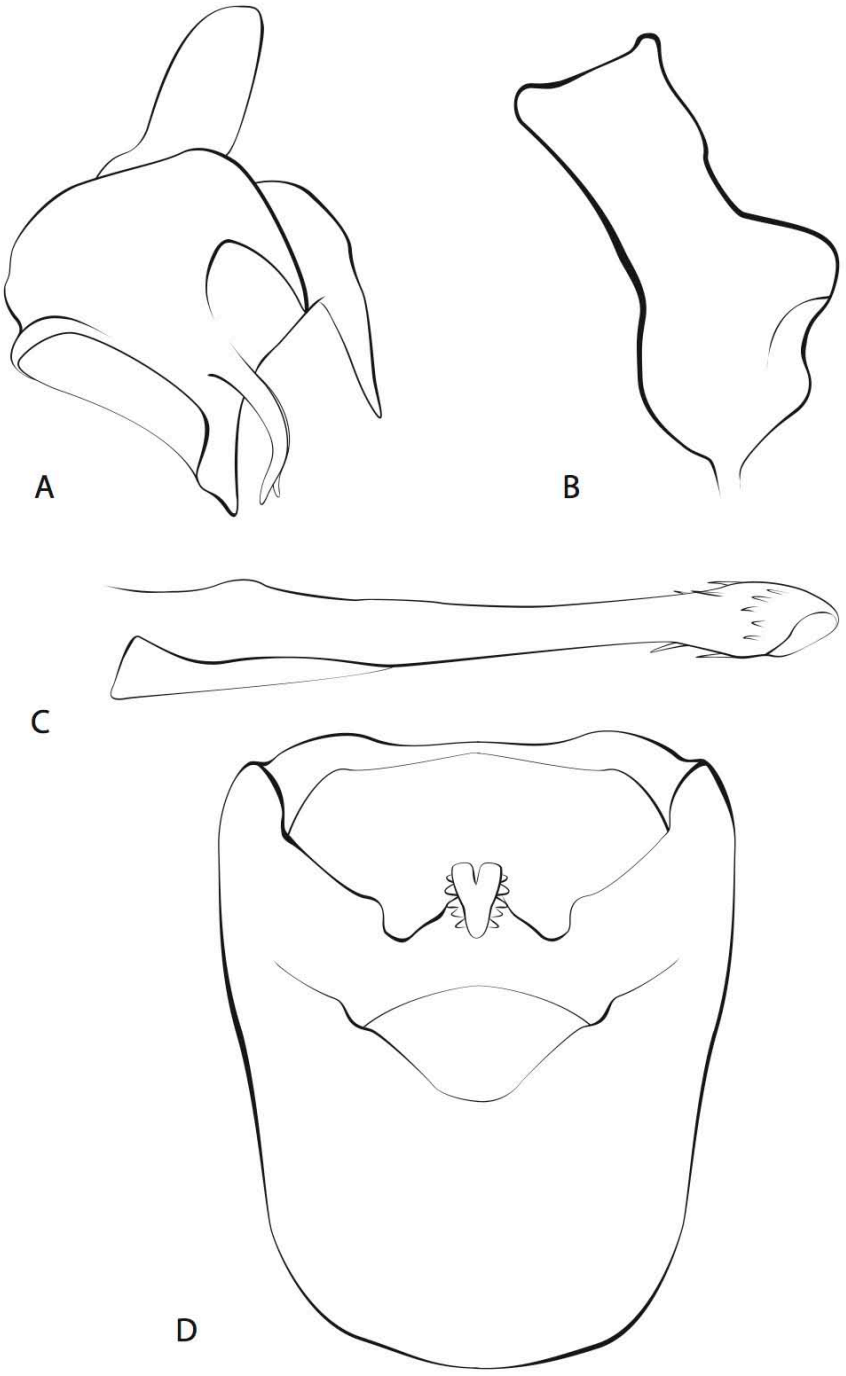

Figure 23. Illustration of the genitalia *C. gluciophilus* a. segment X, left lateral view b. parameres, widest view c. aedeagus, left lateral view d. pygofer, caudal view.

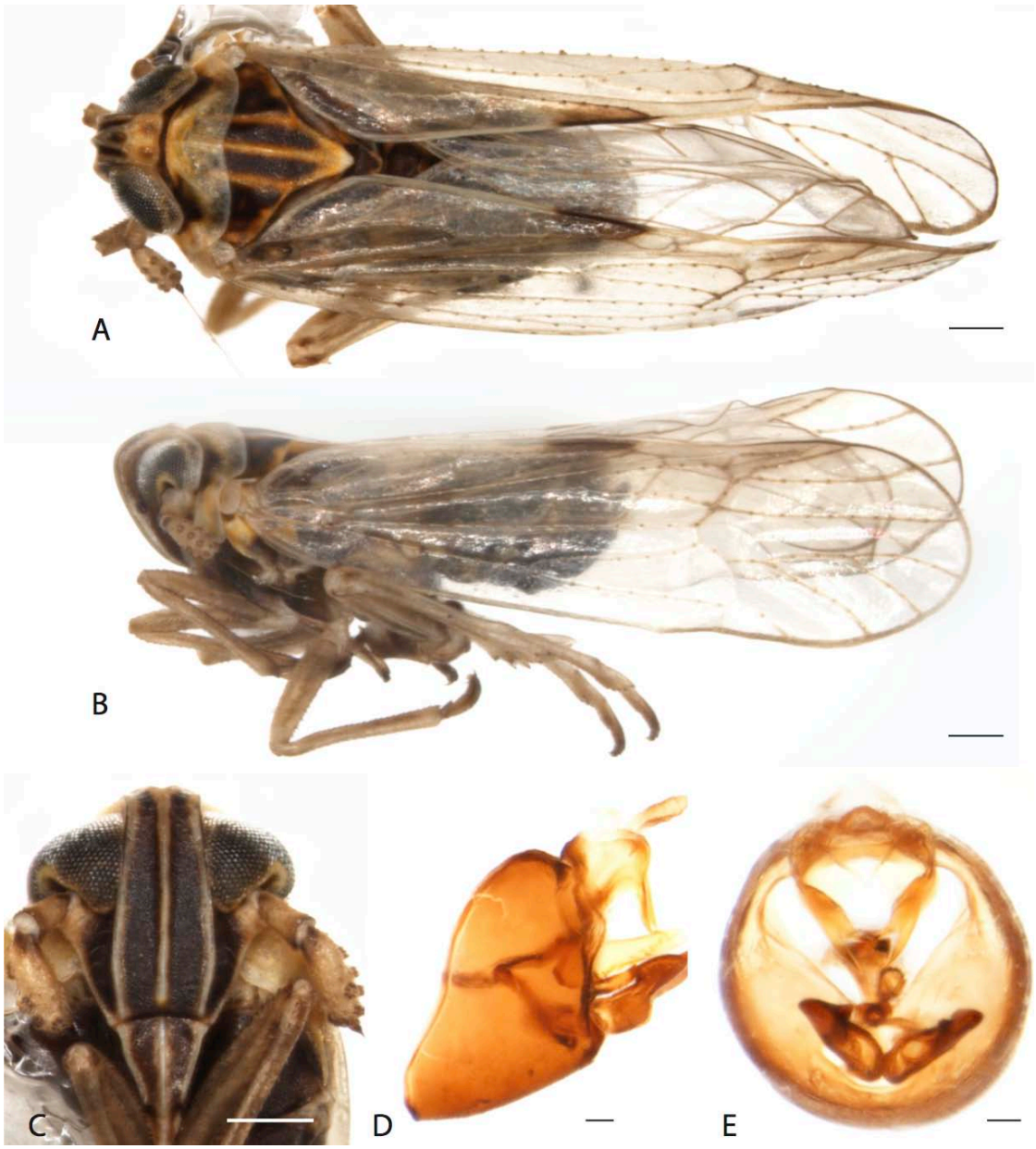

Figure 24. Images of *C. haywardi* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. frons, d. pygofer, lateral view, e. pygofer, caudal view.

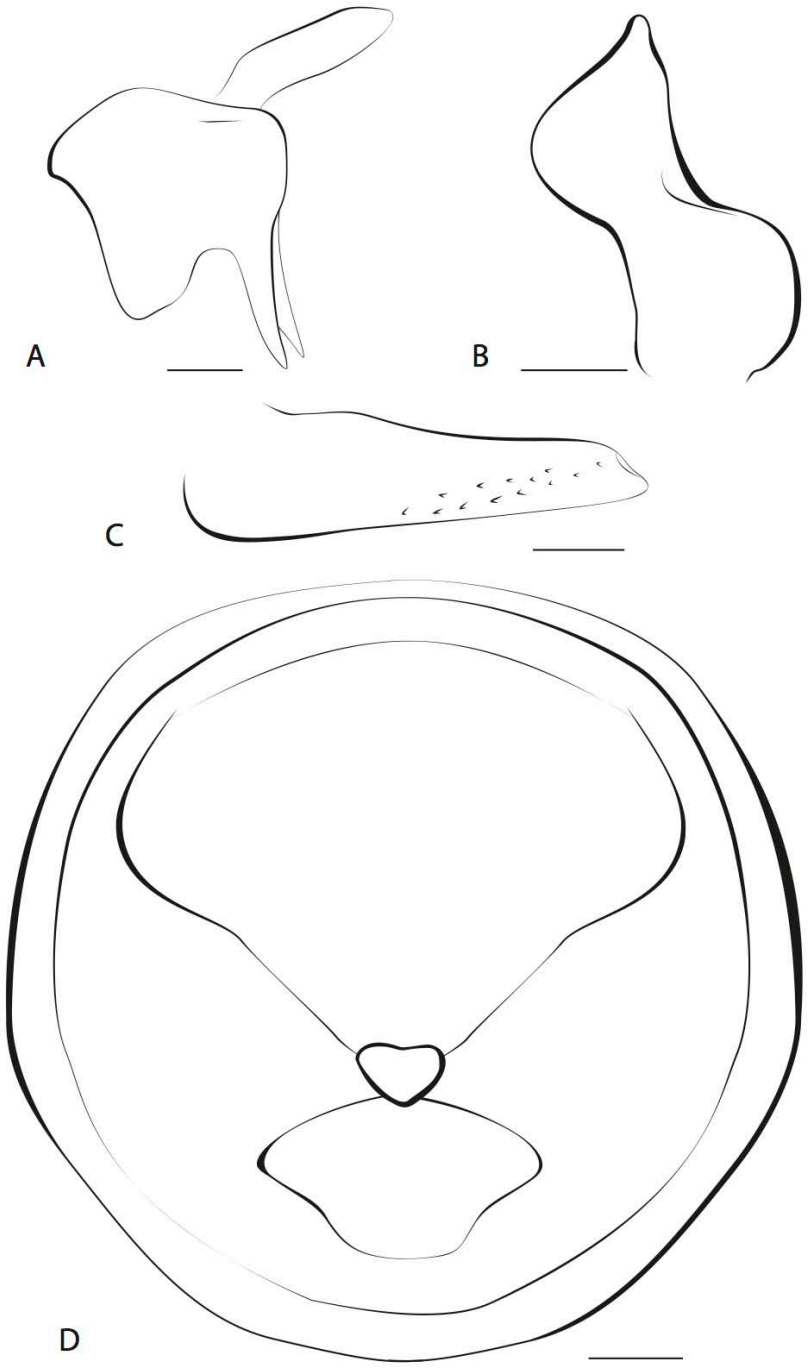

Figure 25. Illustration of the genitalia *C. haywardi* a. segment X, left lateral view b. paramere, widest view c. aedeagus, left lateral view, d. pygofer, caudal view.

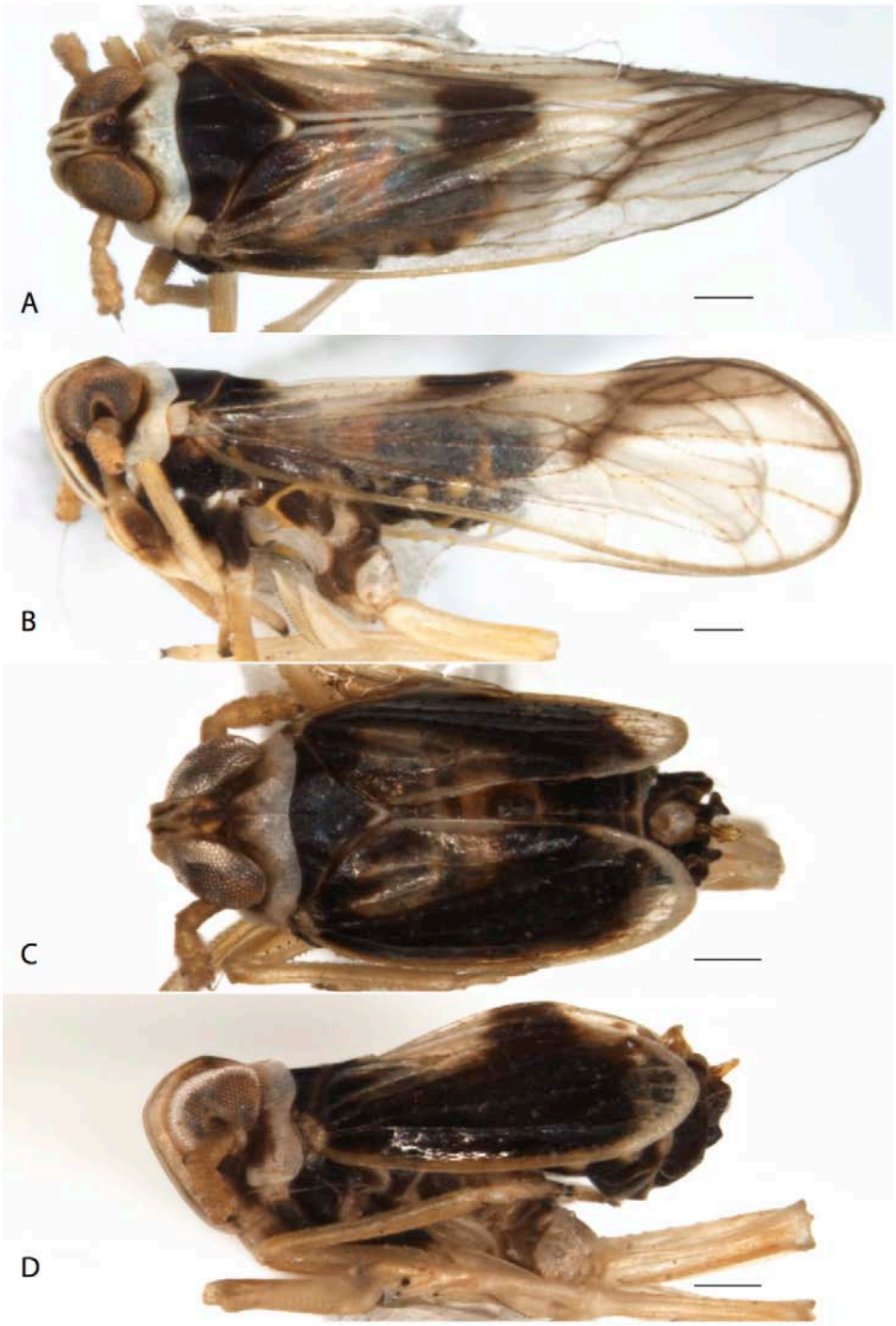

Figure 26. Images of *C. herkos* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

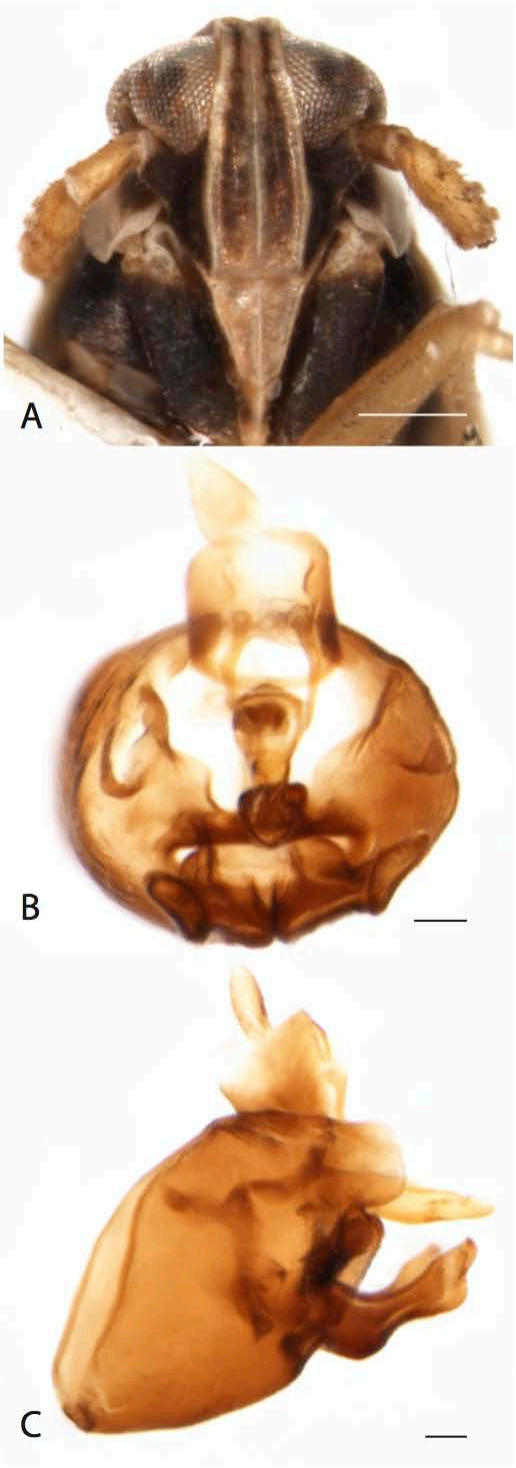

Figure 27. Images of *C. herkos,* a. frons, f. pygofer, caudal view, g. pygofer, lateral view.

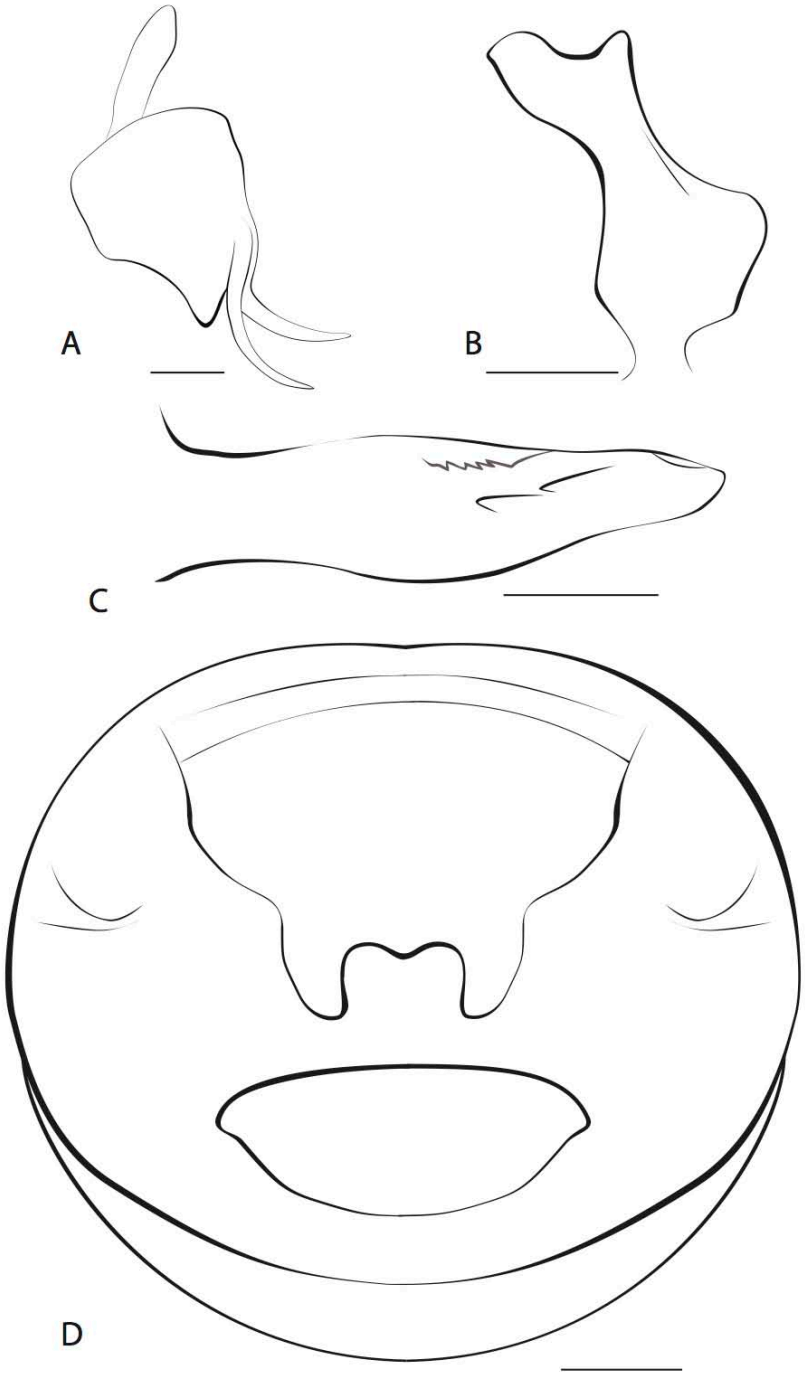

Figure 28. Illustration of the genitalia *C. herkos* a. segment X, left lateral view b. parameres, widest view c. aedeagus, left lateral view d. pygofer, caudal view.

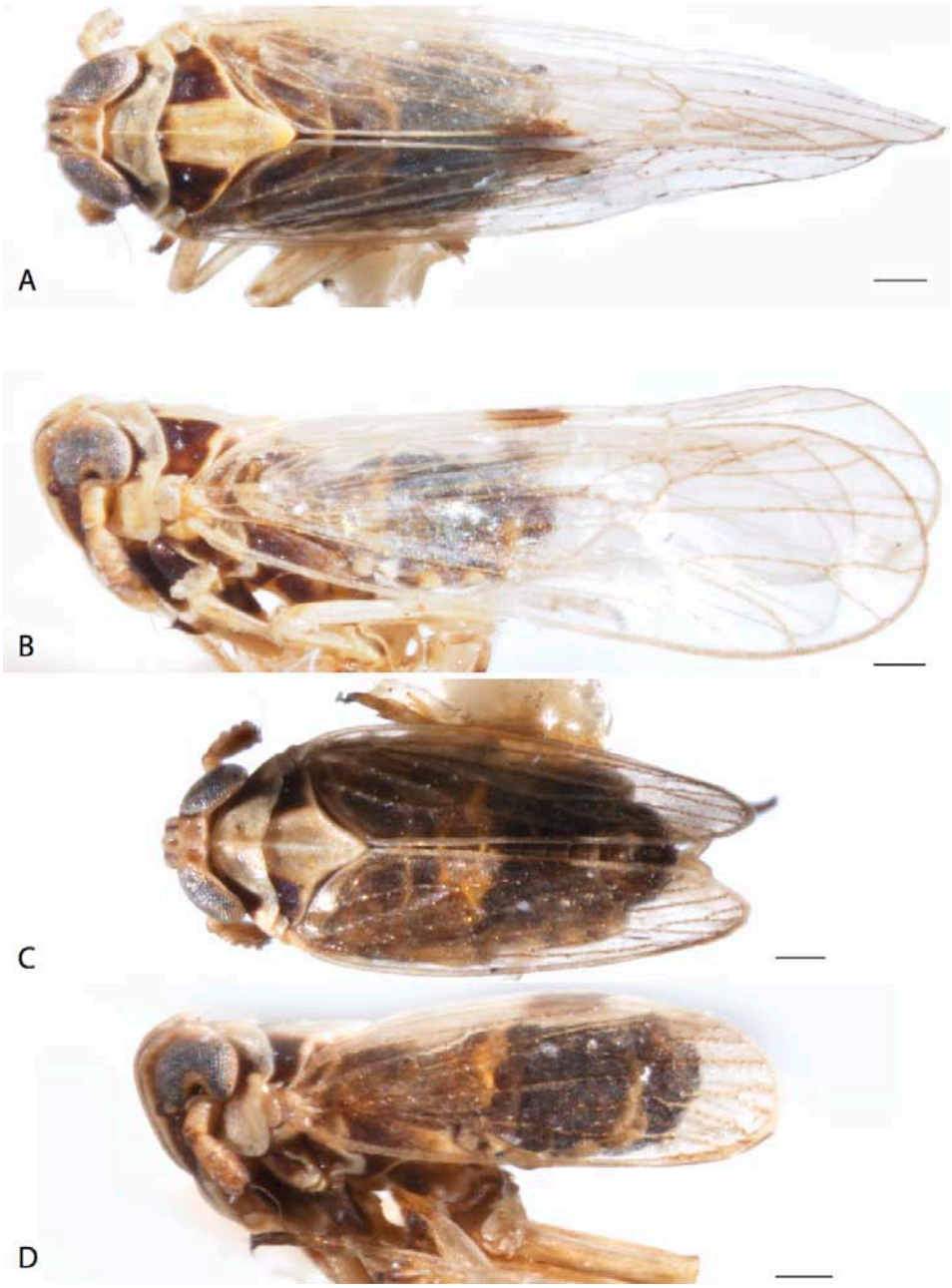

Figure 29. Images of *C. pacificus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

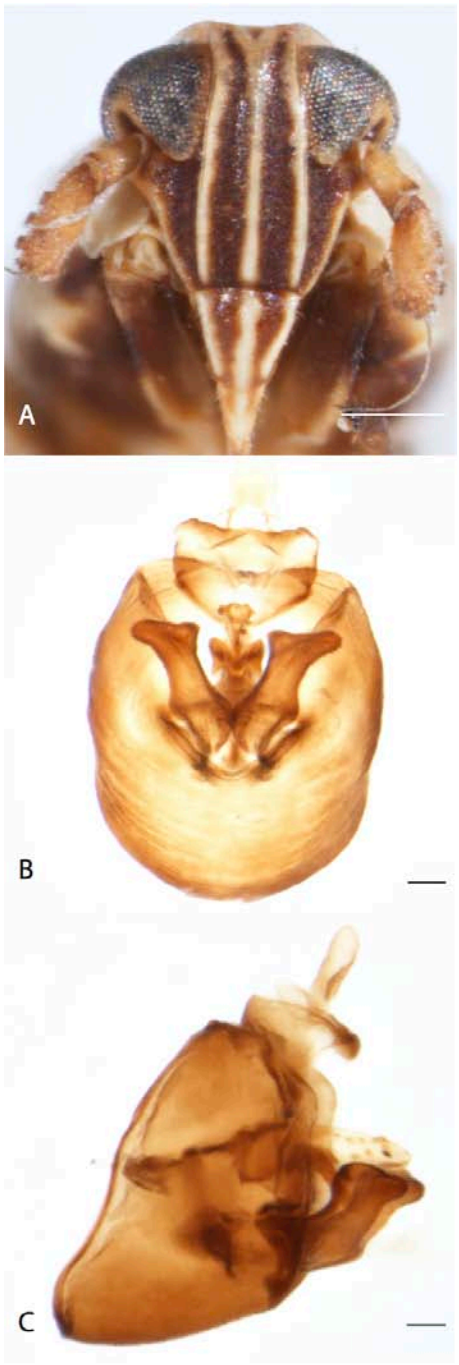

Figure 30. Images of *C. pacificus* a. frons, f. pygofer, caudal view, g. pygofer lateral view.

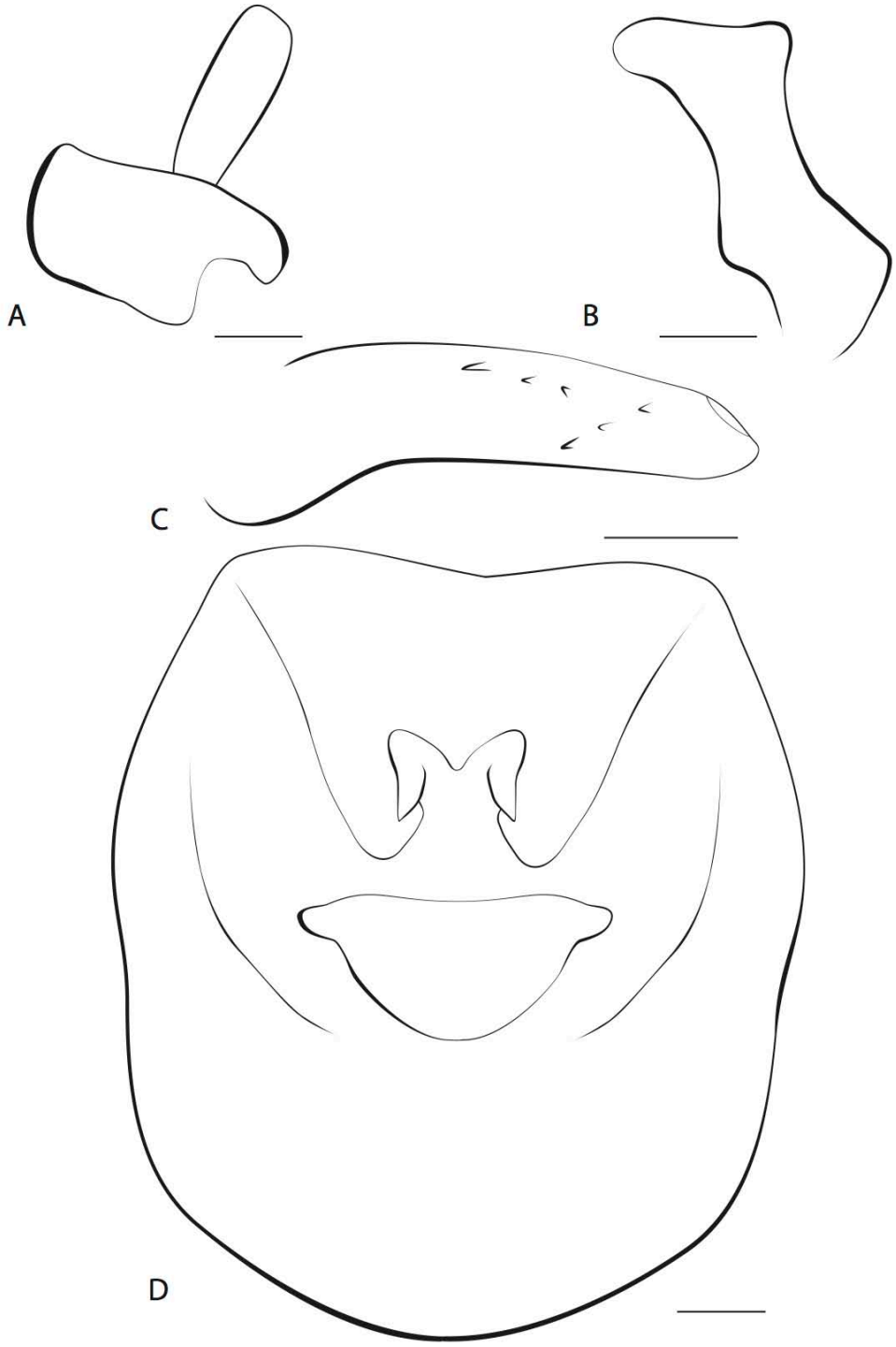

Figure 31. Illustration of the genitalia *C. pacificus* a. segment X, left lateral view b. parameres, widest view c. aedeagus, left lateral view, d. pygofer, caudal view.

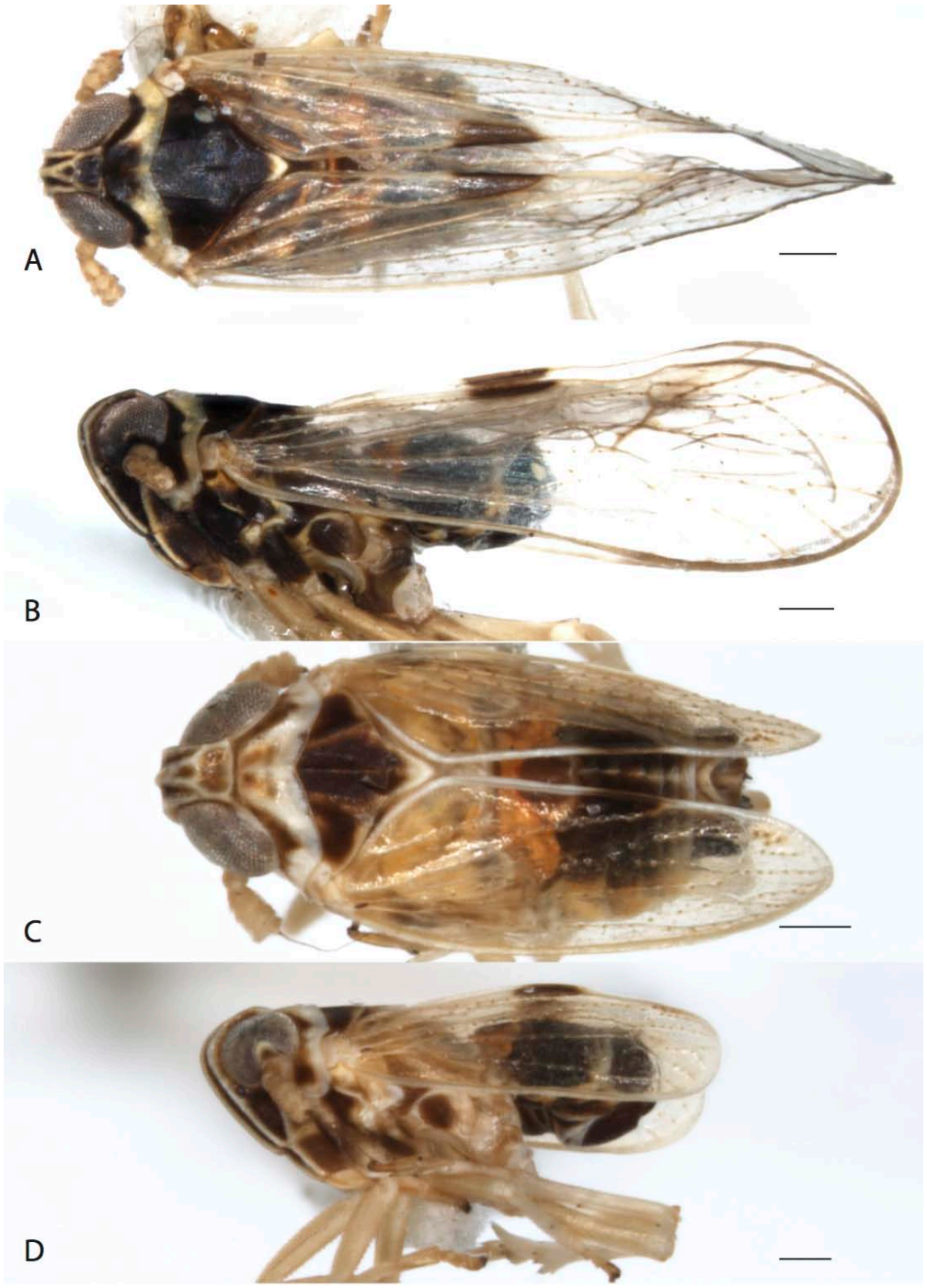

Figure 32. Images of *C. puellus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

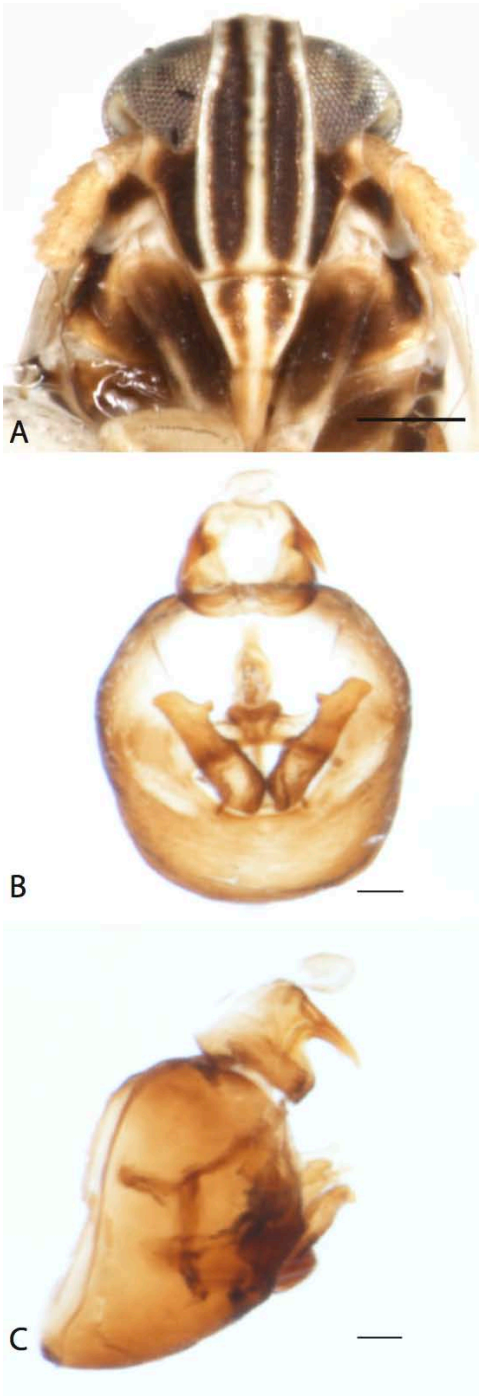

Figure 33. Images of *C. puellus,* a. frons, b. pygofer, caudal view, c. pygofer, lateral view.

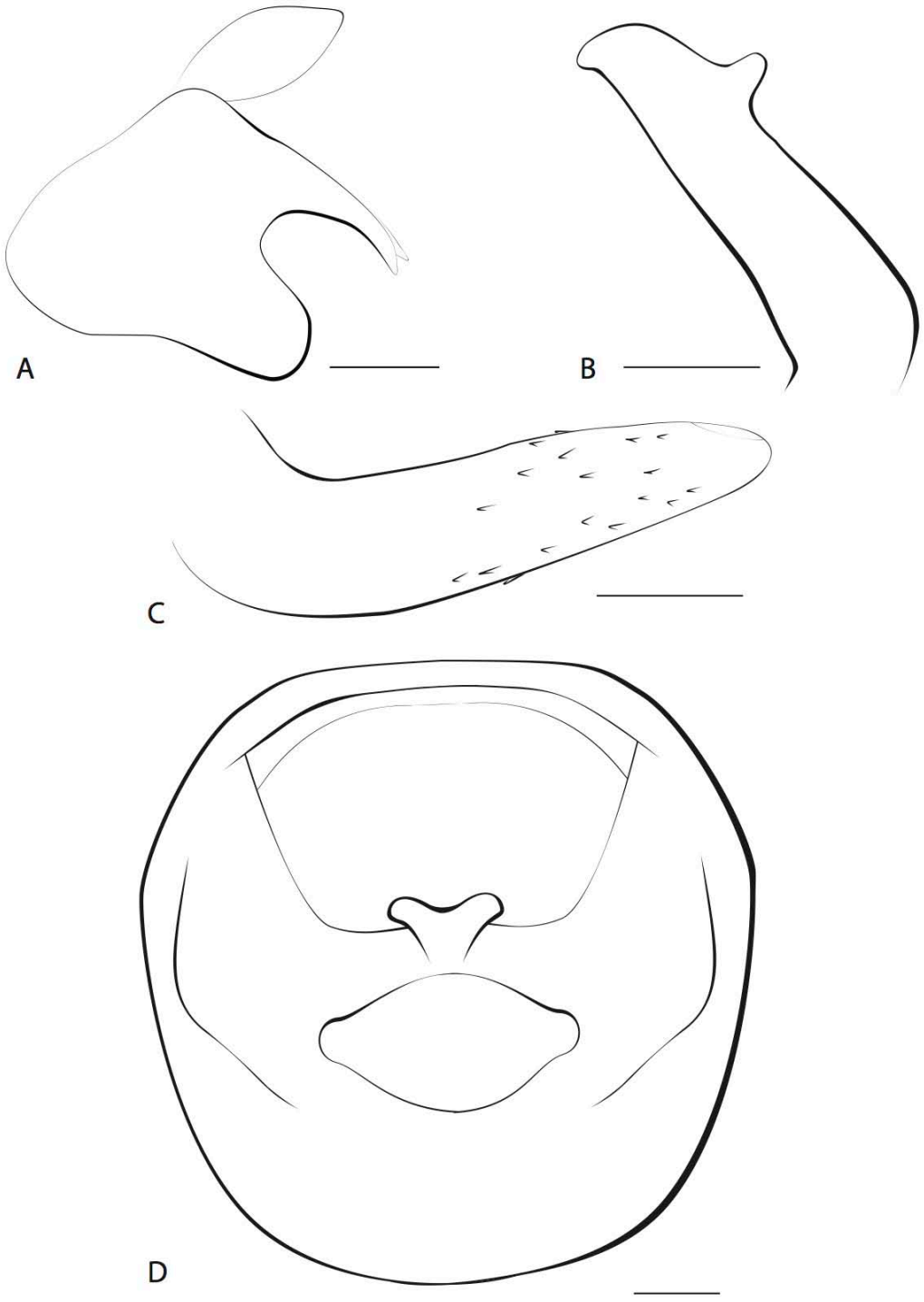

Figure 34. Illustration of the genitalia *C. puellus* a. segment X, left lateral view b. parameres, widest view c. aedeagus, left lateral view d. pygofer, caudal view.

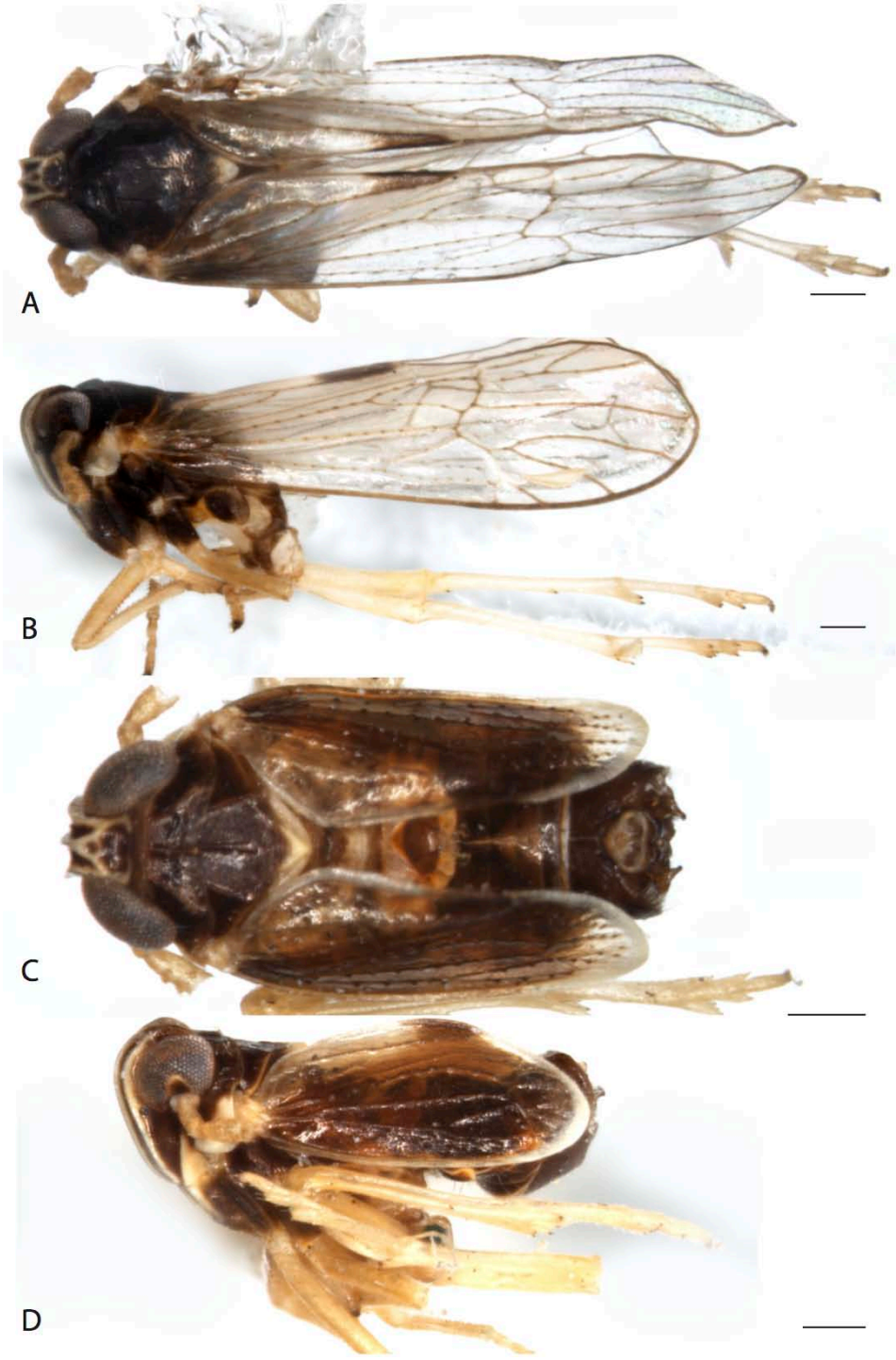

Figure 35. Images of *C. quadrispinosus* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter), d. lateral habitus (brachypter).

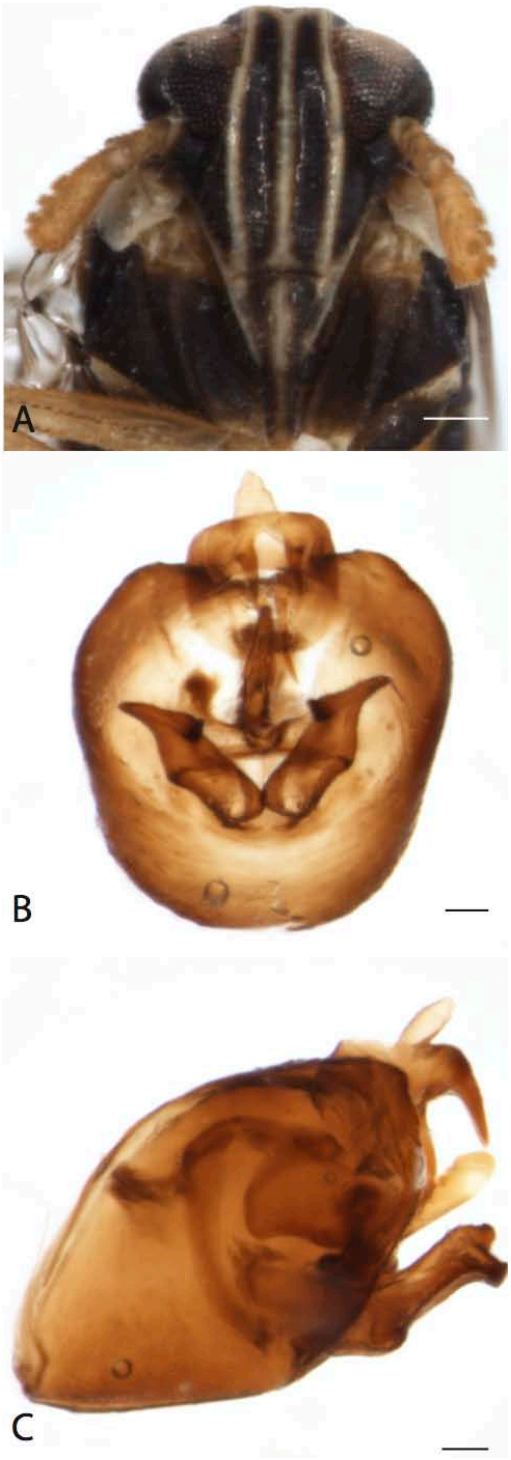

Figure 36. Images of *C. quadrispinosus,* a. frons, b. pygofer, caudal view, g. pygofer, lateral view.

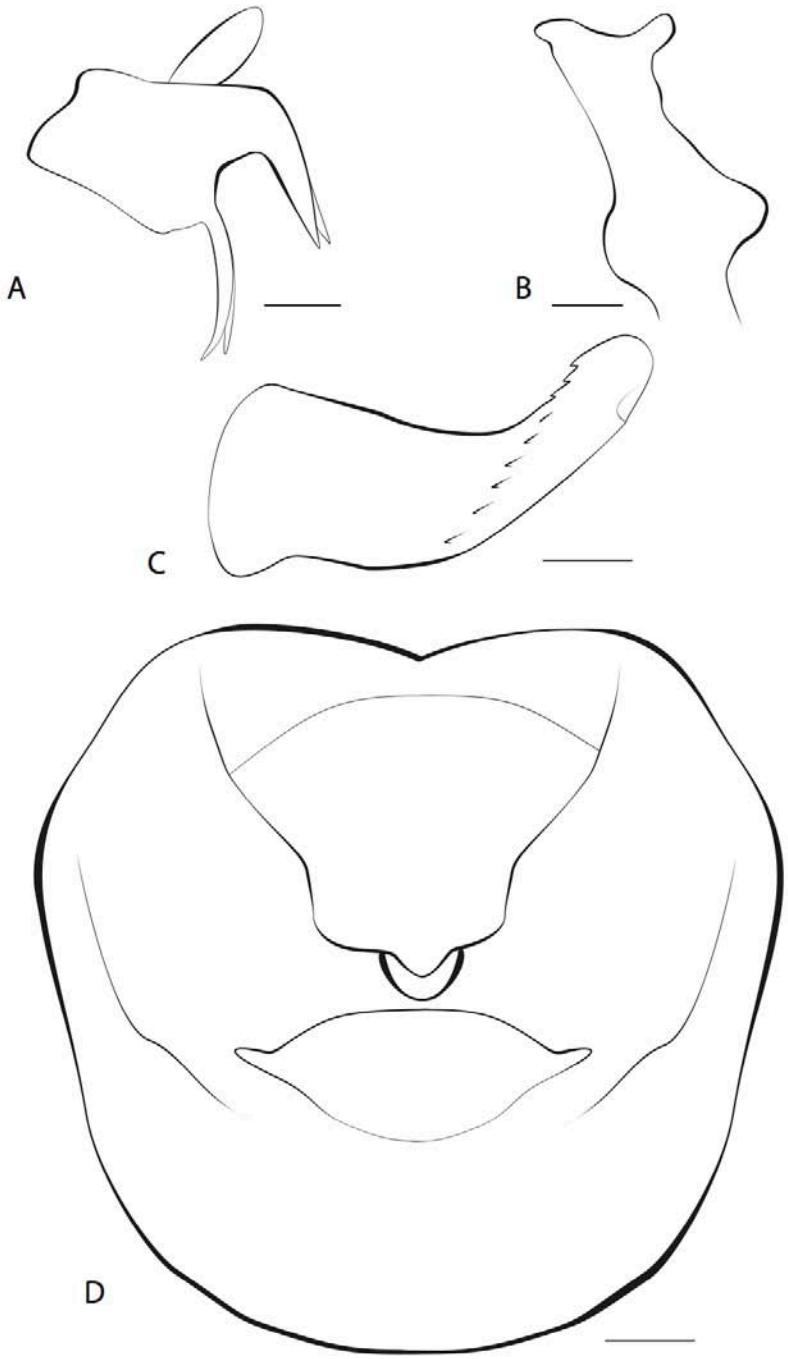

Figure 37. Illustration of the genitalia *C. quadrispinosus* a. segment X, left lateral view, b. paramere, widest view, c. aedeagus, left lateral view, d. pygofer, caudal view.

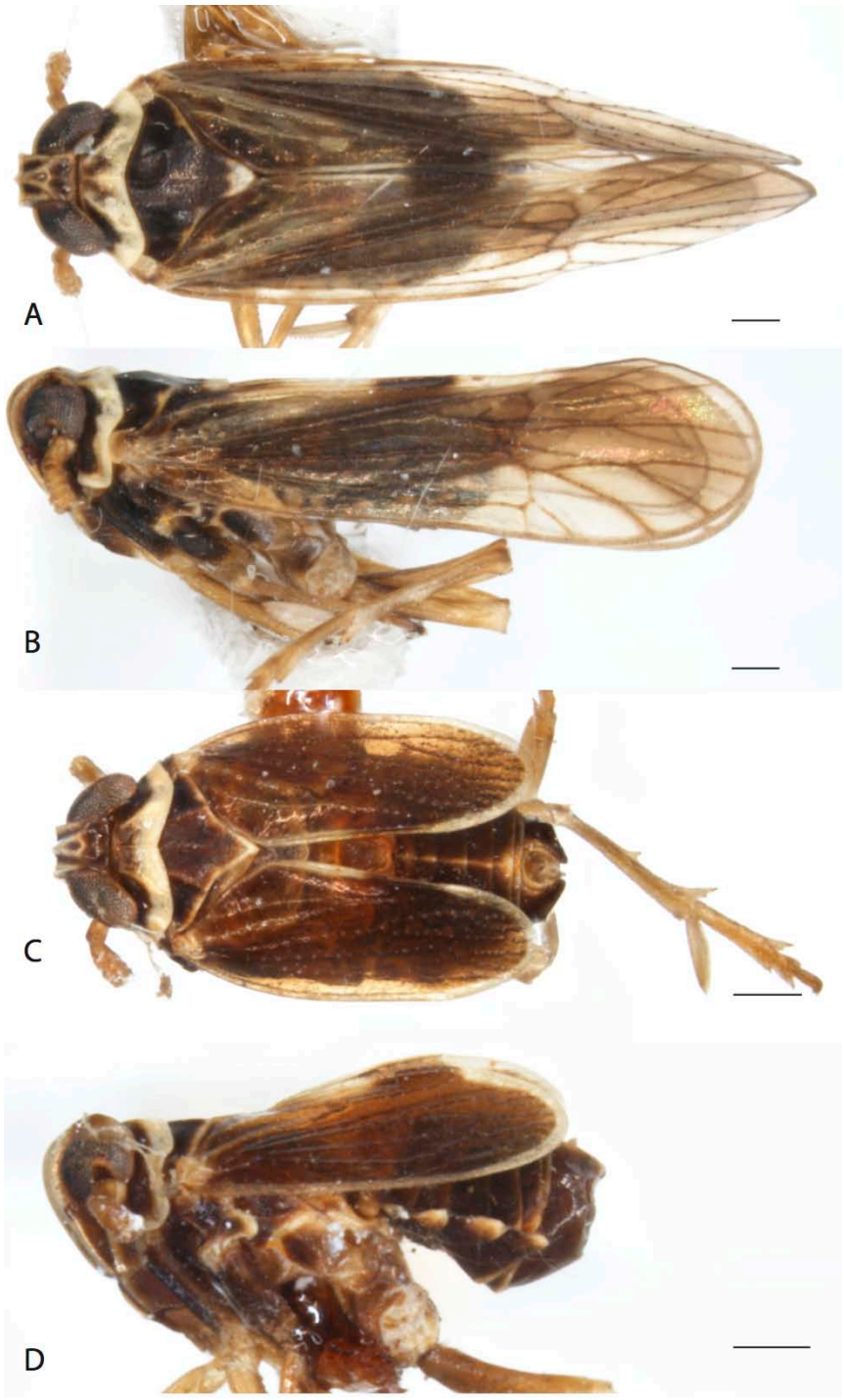

Figure 38. Images of *C. tenae* a. dorsal habitus (macropter), b. lateral habitus (macropter), c. dorsal habitus (brachypter) [holotype], d. lateral habitus (brachypter) [holotype].

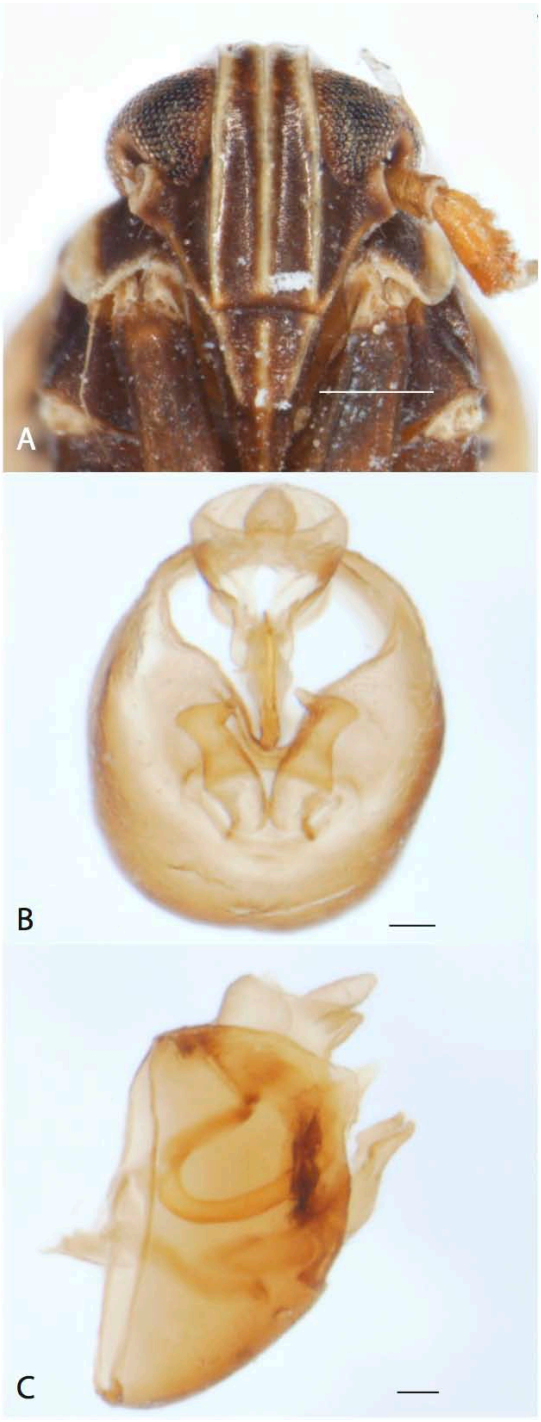

Figure 39. Images of *C. tenae* a. frons [holotype], b. pygofer, caudal view, c. pygofer, left lateral view.

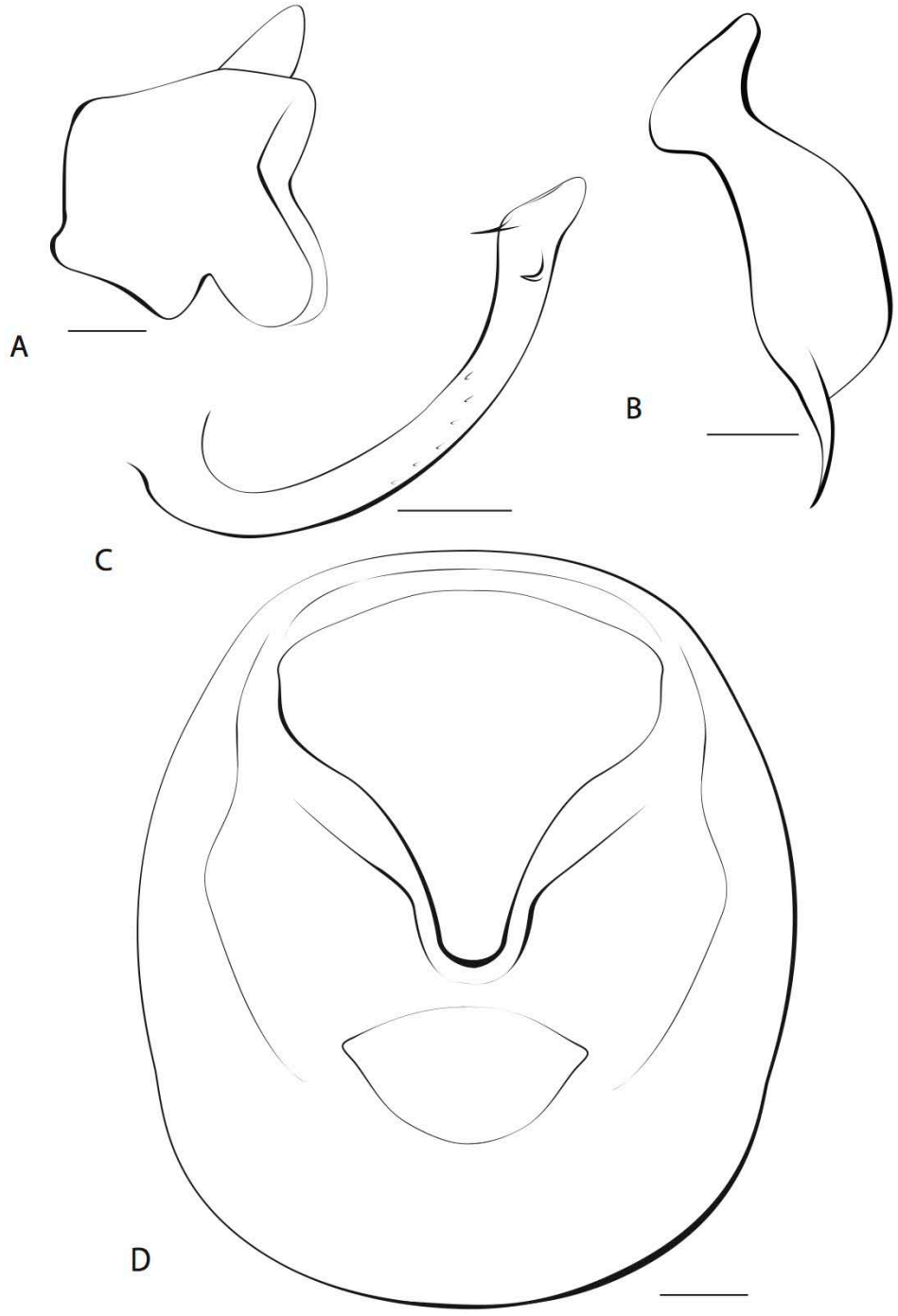

Figure 40. Illustration of the genitalia *C. tenae* a. segment X, left lateral view b. parameres, widest view, c. aedeagus, left lateral view d. pygofer, caudal view.

Chapter 2

PHYLOGENETIC ANALYSIS OF THE GENUS *CHIONOMUS*

2.1 Introduction

The phylogenetic relationships within the Delphacidae are not fully resolved, particularly among the higher Delphacini. Early attempts at providing a phylogeny lacked a quantitative basis (Muir 1915, Haupt 1929, Muir 1930, Metcalf 1943). In 1963, Wagner provided the first quantitative analysis of the family recognizing 9 subfamilies: Asiracinae, Kelisiinae, Jassidaeinae, Stirominae, Achorotilinae, Delphacinae, Chlorioinae, Stenocraninae, and Megamelinae. However, Wagner's (1963) phylogeny is widely regarded as methodologically flawed (e.g., Asche 1985). Asche (1985, 1990) produced the first cladistic treatment of the family based on morphology. He divided the family into 7 clades at that time (Table 1), with Asiracinae paraphyletic, divided into two tribes (Asiracini and Ugyopini) of uncertain relationship. In 1996, Emeljanov proposed a phylogeny utilizing traits of immature forms. The branching pattern of this tree is consistent with Asche's work, although he raised Asche's (1995) Asiracini and Ugyopini to subfamily and described a series of new tribes within each. Hamilton (2006) advocated subsuming Kelisiini under Stenocranini and Saccharosydnini under Tropidocephalini as subtribes, but offered no quantitative evidence for his suggestions. Asche's (1985, 1990) phylogeny has been supported by the recent molecular work of Urban and colleagues (2010), although they subsumed the Asiracinae and Ugyopinae into a single subfamily. The most advanced delphacid tribe, the Delphacini, has been left relatively untouched; both *Chionomus* and *Delphacodes* are consistently placed within this taxon. The most notable

emendation to this tribe came in 1985, when Asche sunk many of Wagner's higher groups into the Delphacini. The tribe contains nearly 75% of all delphacid species and yet it's the phylogeny remains underinvestigated. Urban *et al.* (2010) included 45 genera and 89 species from this taxon in their analyses, providing some framework for understanding the tribe.

Recent molecular and mixed model analyses have shed some light on relationships within the Delphacini. Work by Dijkstra *et al*. (2003, 2006) was moderately successfully in elucidating relationships among genera, suggesting that *COI* is informative for generic relationships, although his sampling was limited. Urban and colleagues (2010) undertook the first large-scale analysis of the family. The resultant Bayesian tree was well supported but lacked definition in the higher Delphacini. Short branch lengths in the higher Delphacini, despite data from four genes, suggest a rapid radiation of the advanced members of this tribe. This study clearly demonstrated that the genus *Delphacodes s.l.* is polyphyletic (previously an assertion based on morphology, e.g., Asche & Remane 1983), highlighting the need for further investigations in this area of the tree. There work also showed that *Chionomus* is derived within the Delphacini.

Here I address the phylogeny of the genus *Chionomus.* Unlike *Delphacodes,* this genus is not polyphyletic but rather paraphyletic. In the Urban *et al.* study, *C. havanae* was sister to *D. puella* with strong nodal support in the Bayesian analysis. A broader definition of *Chionomus* will be tested for monophyly utilizing both molecular and morphological data, helping to ensure that traits chosen for revision are informative.

2.2 Materials and Methods

2.2.1 Taxon Sampling

All specimens available for molecular work (Table 7) were collected and stored in 95 – 100% ethanol at −80◦ C at the New York State Museum's Genome Bank or as part of the NYSM Genome Bank at the University of Delaware. Specimens representing 6 of the in-group species were available for this study. Five out-group species were chosen based on topology from Urban *et al.* (2010) and included in the analysis (Table 7).

2.2.2 Morphological Data

Forty multistate morphological characters were coded and compiled (Tables 8 and 9) using Mesquite v 2.75 (Maddison and Maddison 2011).

2.2.3 Molecular Data

A 555 base pair section of sequence data was generated for the mitochondrial gene *COI* for all available ingroup taxa (6 species) and the outgroup taxa (Table 7). DNA Extractions were made from thoracic or hind leg tissue using Qiagen DNEasy Kits (Qiagen, Inc. Valencia, CA). Polymerase chain reactions (PCRs) were run in 25 µl volumes using Qiagen Taq core PCR kits (Qiagen, Inc. Valencia, CA) with the following cycling protocol: 35-40 cycles of 60 seconds at 94°C, 60 seconds at 41-45°C, and 60 – 75 seconds at 72°C, followed by 10 minutes incubating at 72°C. Oligonucleotide primers used were COI-RLR (Simon *et al.* 1994) and Calvin (Lin and Wood 2002), the primer Ron (Simon *et al.* 1994) was evaluated but failed to produce amplification; all primers were synthesized by Integrated DNA Technologies (Coralville, IA). The primer Calvin consistently failed for a number of individuals,

two internal primers (KATF and KATR) were developed to attempt a primer redesign however sequencing results never produced sufficient data.

Amplified DNA was visualized using electrophoresis on a 1–2% agarose gel with ethidium bromide staining. Qiagen MinElute DNA kits (Qiagen, Inc. Valencia, CA) were used to purify PCR products or products were extracted directly from gels using Qiagen Qiaquick gel extraction kits (Qiagen, Inc. Valencia, CA). Sequences were obtained using an ABI Prism 3130XL Genetic Analyzer at the University of Delaware's Delaware Biotechnology Institute. Complimentary strands were edited and inspected using 4Peaks version 1.7 (Griekspoor and Groothuis 2005) and assembled using CAP3 (Huang and Madan 1999). Due to poor sequencing results with the primer Calvin, the unidirectional sequences produced using COI-RLR was used for *D. tenae*. Additional delphacid *COI* sequences from Urban and colleagues (2010) were added to the data set (Table 7) and aligned using MUSCLE (Edgar 2004). The resulting *COI* sequence data, derived from single specimens, is provided with species descriptions and generated sequence data was submitted to GenBank.

2.2.4 Phylogenetic Analyses

2.2.4.1 Maximum Parsimony Analysis

Phylogenetic analyses using the maximum parsimony (MP) criterion based on the *COI* sequence data for the 7 in-group taxa and 5 out-group taxa was performed using PAUP* 4.0b10 (Swofford 2001) to assess the monophyly and phylogeny of the redefined *Chionomus*. One thousand random-addition search replicates were used for heuristic tree searches with the tree bisection and reconnection (TBR) heuristic

algorithm. Bootstrap support values, with 100 standard replicates, were estimated for nodal support.

2.2.4.2 Maximum Likelihood Analysis of Molecular Data

Maximum likelihood (ML) analysis using *COI* was conducted on the same dataset as MP. TIM2+I+G was best fitting model for the aligned sequences determined using JModelTest (Posada 2008) under the Akaike information criterion corrected for small sample size (AICc; Hurvich and Tsai 1989). ML analysis was run using GARLI v2.0 (Zwickl 2006). Twenty independent search replicates, each with 1,000,000 generations, were performed consistent with methods used by Urban and colleagues (2010). Bootstrap support values were generated by 100 bootstrap replicates for 100,000 generations in GARLI. A bootstrap consensus tree was calculated using PAUP* 4.0b10 (Swofford 2003).

2.2.4.3 Bayesian Analysis of Combined Molecular and Morphological Data

Bayesian analysis of the combined *COI* and morphological data matrix was conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Since MrBayes does not accept the TIM2+I+G model a GTR+I+G model was used for the molecular data. This was second best scoring model for the data determined using JModelTest (Posada 2008) under the Akaike information criterion corrected for small sample size (AICc; Hurvich and Tsai 1989). For the morphological data, a Markov model + G was implemented (Lewis 2001).

The analysis was run for one million generations, model parameters were estimated independently across the two partitions. A total of two independent runs with four chains each were performed. Three of the chains were heated and one was

cold. Uninformative priors and trees were sampled every 100 generations. The first 25% (2,500) of the sampled trees were discarded as burnin. The 50% majority rule consensus tree was constructed from the remaining trees. The sump command was used to generate the harmonic mean of likelihoods for the remaining trees.

2.3 Results

2.3.1 MP analysis

MP analysis produced a single tree with poorly resolved topology (Figure 41). The tree has a score of 450 steps. The analysis recovered the redefined *Chionomus* as monophyletic with strong bootstrap support (96). The topology was particularly poorly resolved within *Chionomus* except for a strong support of *C. haywardi* and *C. pacificus* as sister groups.

2.3.2 ML analysis

The topology of best scoring tree (Figure 42), out of the 20 runs, was very similar to of the all trees that were produced in this analysis. The –ln L scores ranged from 2549.0538 to 2549.0543. This analysis recovered *Chionomus* in its original definition as paraphyletic and a monophyletic redefined *Chionomus*. The bootstrap support value for this clade was high (95). Within *Chionomus*, *C. tenae* was basal followed by *C. puellus,* then the pairs *C. haywardi* + *C. pacificus* and *C. havanae* + *C. balboae* were recovered.

2.3.3 Bayesian analysis

The two independent runs produced two (identical) 50% consensus trees (Figure 43). The combined harmonic mean of these trees was –ln=2805. This well

supported tree produced the same branching pattern, for the in-group, as the ML analysis. *Chionomus tenae* is basal in the lineage with strong posterior probability. Additionally, the broad definition of *Chionomus* is supported as monophyletic, while the original definition is paraphyletic.

2.4 Discussion

Of the three resultant trees from the analyses, the Bayesian and ML trees are similar in their branching patterns and contrast with the topology of the MP tree. The consensus of the ML and Bayesian tree indicate that they may represent the relationships within the dataset more definitively than the MP tree. MP analyses do not account for variable evolutionary rates, making MP subject to analytical artifacts such as 'long-branch attraction' (Whitfield and Kjer 2008). Molecular evolutionary rates are known to vary among planthopper lineages (Urban and Cryan 2009), which implies that analytical techniques less vulnerable to molecular rate variation should be preferred. Also, MP's frequent failure to resolve rapidly radiating groups may be specifically problematic in the delphacids; their diversity is noted as a rapid radiation (Urban *et al.* 2010). This knowledge, combined with the conflicting branching pattern, indicates less reliance should be placed on the MP tree.

One branch within the in-group was consistent across all three trees; *C. haywardi* and *C. pacificus* resulted as sister to one another with strong branch support. This may indicate that the pale median vitta both these species possess is a potential revolving trait; it seems to be diagnostic within *Chionomus* however it arises sporadically throughout the Delphacini. The presence of this feature among many Stenocraninae and Kelisiinae suggests that it may be a plesiomorphic trait.

The Bayesian and ML trees provide further insight into the relationships between members of *Chionomus*. Both recover *C. havanae* and *C. balboae* as sisters; however, this branch is not as well supported as the *C. haywardi* + *C. pacificus* branch. *Chionomus tenae* is consistently placed as basal in the group. Morphological features of the species further support this placement, specifically consistent coloration and a posteriorly projecting but poorly produced armature of the diaphragm.

Most importantly all three topologies (ML, MP, and Bayesian) support the monophyly of *Chionomus* as defined here. Additionally, the topologies show original three species in *Chionomus* are in-fact paraphyletic. Further work will be necessary to increase clarity of the relationships between individual members of *Chionomus*. Taxon sampling needs to be more extensive, ideally all members of *Chionomus* will be sampled, and additional genes, such as EF-1a and ND1, should be included to provide further resolution within the genus. However, the results of this work validate the proposed broader definition of *Chionomus,* supporting the morphological interpretations used to define the genus.

Table 7. Taxa included in molecular analyses, with specimen locality information.

Species	Locality	In/Out group	From Urban *et al.* 2010
Isodelphax basivitta	USA: Pennsylvania	Out	X
Prokelisia marginata	USA: Delaware	Out	X
Prokelisia dolus	USA: Delaware	Out	X
Javesella pellucida	USA: Pennsylvania	Out	X
Muirodelphax arvensis	USA: Pennsylvania	Out	X
C. puellus	USA: Pennsylvania	In	X
C. havanae	Nicaragua	In	
C. balboae	Argentina	In	
C. haywardi	Argentina	In	
C. pacificus	USA: Louisiana	In	
C. tenae	Argentina	In	

Table 8. Morphological characters and states.

Body

1. Median vitta: 0 absent, 1 present

Head

2. Width of head compared to pronotum: 0 narrower, 1 equal
3. Color of carinae of frons: 0 concolorous with frons, 1 contrasting
4. Color of Vertex: 0 concolorous, 1 anterolateral compartments dark, anterior and posterior compartments and all carinae pale, 2 all compartments dark, 3 all compartments dark with carinae pale, 4 just posterior compartments pale, carinae pale
5. Submedian length of vertex: 0 shorter than pronotum, 1 about equal to pronotum, 2 longer than pronotum
6. Y-shaped carinae of vertex: 0 weak/absent, 1 strong
7. Stem of Y-shaped carinae: 0 weak/absent, 1 strong
8. L:W ratio of basal compartments of vertex: 0 shorter, 1 equal, 2 longer
9. Ratio of length of anterior and basal compartments of vertex: 0 anterior shorter, 1 equal, 2 anterior longer
10. Ratio of vertex width at apex and base: 0 apex narrow, 1 equal, 2 apex wider
11. Head projected in front of eye: 0 not, 1 less than 1/2 width of eye, 2 greatly
12. Vertex rounding onto frons: 0 rounded, 1 angulate, 2 carinate
13. Color of frons: 0 concolorous, dark, carinae pale, 2 pale, dark margins, carinae pale, 3 bicolored

14. Sides of frons: 0 parallel to subparallel, 1 bowed outward, 2 diverging
15. Color of post clypeus: 0 concolorous, 1 dark with pale carinae, 2 pale, dark margins, pale carinae

Thorax

16. Pronotum color: 0 Concolorous but different from vertex and mesonotum: 1 concolorous, concolorous with body: 2 median vitta
17. Paranota: 0 all dark, 1 dark with white apical band, 2 all white/light
18. Lateral carinae of pronotum: 0 reaching hind margin, 1 terminating prior to margin, not curved, 2 curving to follow contour of eye, not reaching hind margin
19. Mesonotum color: 0 concolorous, 1 pale median stripe
20. Scutellum color: 0 concolorous, 1 paler
21. Mesonotum lateral carinae (macropter): 0 Reaching hind margin, 1 not reaching hind margin
22. Apical spines on midtibiae: 0 4, 1 5, 2 6, 3 7+
23. Size of calcar teeth: 0 small, 1 midsized, 2 large
24. Number of teeth on calcar: 0 none, 1 less than 11, 2 11-15, 3 16-20, 4 21-25, 5 26-30, 6 31+
25. Apical tooth of calcar: 0 larger than other teeth, 1 similar sized to other teeth, 2 smaller than other teeth, 3 absent
26. Macropterous wing color: 0 patterned, 1 not patterned, with dark spot at apex of clavus, 2 not patterned, lacking dark spot
27. Dark spot at wing-coupling mechanism: 0 absent, 1 present
28. Claval fold on brachypters: 0 absent, 1 present

Genitalia

29. Dorsocaudal angles of pygofer: 0 normal, 1 strongly produced, 2 slightly produced
30. Ventrocaudal margin of pygofer: 0 with process, 1 strongly excavated, 2 shallow U or V excavation, 3 continuous with margin
31. Armature of diaphragm: 0 absent, 1 present
32. Direction of armature: 0 not projecting, 1 dorsocaudally projecting, 2 caudally projecting
33. Shape of armature of diaphragm: 0 boss, 1 fold/shelf, 2 U, 3 bifurcate
34. Aedeagus: 0 narrow, elongate, 1 stout
35. teeth on aedeagus: 0 present, 1 absent
36. Parameres: 0 Not flattened apically, 1 Flattened apically
37. Basal angle of parameres: 0 absent, 1 mildly produced, 2 strongly produced
38. Processes on segment 10: 0 present, 1 absent
39. Processes on segment 10: 0 1 pair closely approximated: 1 1 pair widely separated, 2 1 pair, lobes, 3 2 pair of spines, 4 absent
40. Processes on segment 10: 0 straight, 1 hooked

Table 9. Character states for morphological analysis.

Species	Character States
I. basivitta	00131 00011 10101 10100 01131 20002 11110 02010
P. dolus	00010 11100 21220 12000 00220 20102 12010 111--
P. marginata	00010 11100 21220 12000 00220 20102 12010 111--
M. arvensis	01001 11011 10000 02210 11131 20003 02101 101--
J. pellucida	01131 00011 10101 01201 01132 10002 10210 000-0
C. havanae	00131 00011 10101 01201 11141 11002 12001 111--
C. balboae	00131 00011 10101 01201 11141 11002 12000 111--
C. haywardi	10141 00011 10101 02211 11141 11002 12000 11001
C. pacificus	10111 00011 10101 02211 11141 11002 12300 11000
C. puellus	00131 00011 10101 01201 11141 11002 12300 11011
C. tenae	00131 00011 10101 01201 11131 11002 12100 1102-

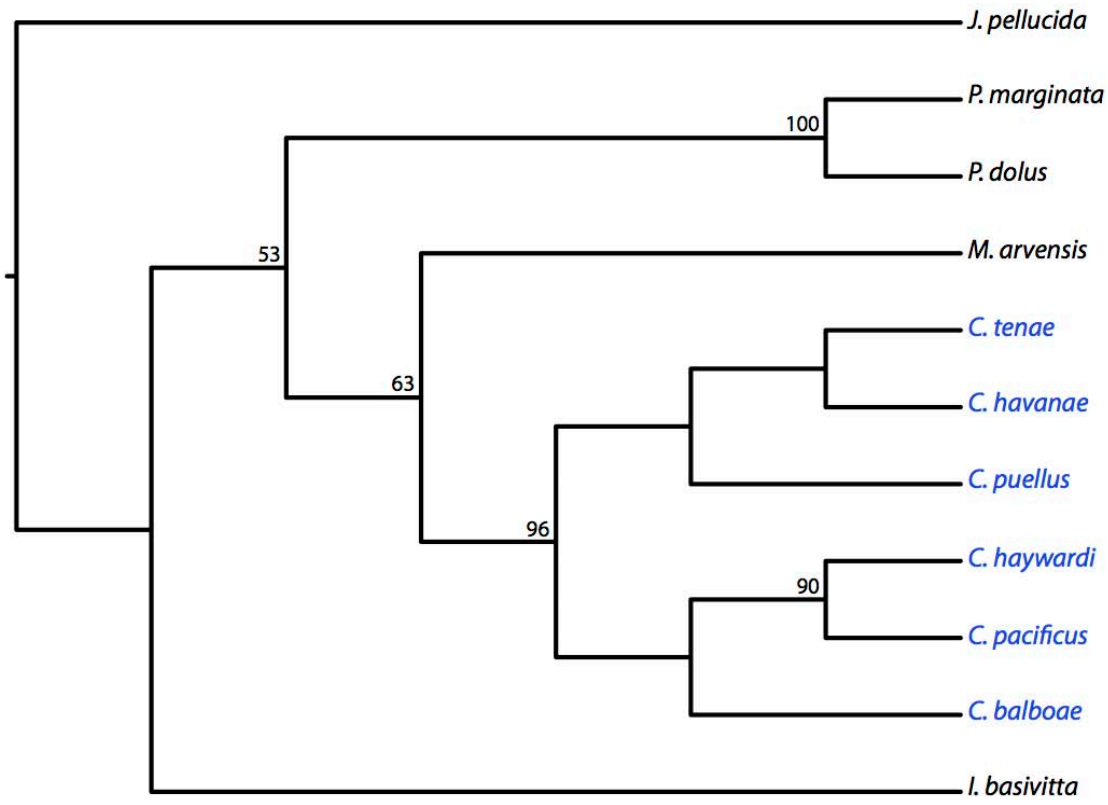

Figure 41. The best scoring MP tree (length=450 steps). Bootstrap support values are given above the branch.

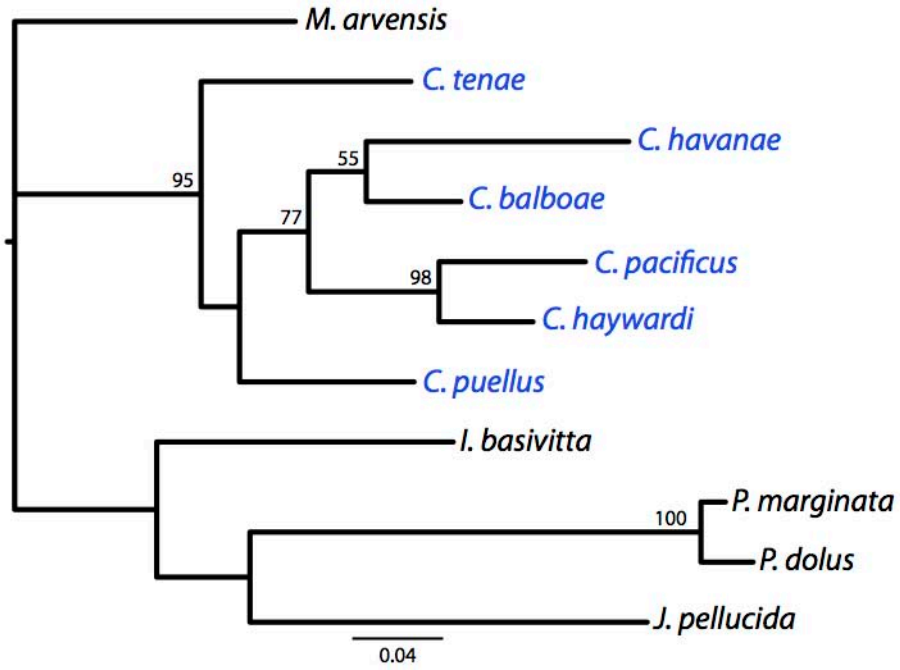

Figure 42. Best scoring ML tree (likelihood, -2549.0538) resulting from 20 independent GARLI search replicates of the *COI* data; bootstrap support values above 50% are shown above branches. The scale bar is equivalent to 0.04 substitutions per site.

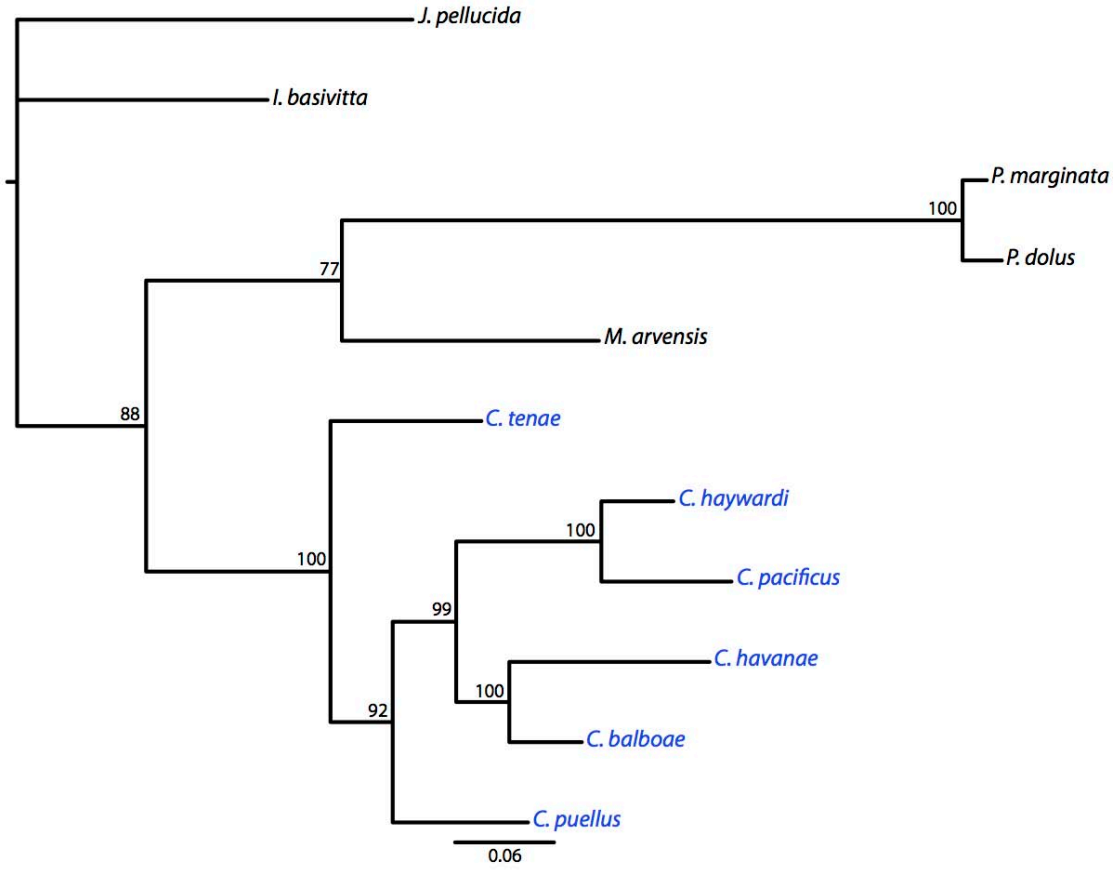

Figure 43. The tree topology (harmonic mean of –ln = 2805.42) resultant from a mixed model Bayesian analysis of combined morphological and *COI* data. Posterior probabilities are indicated at the nodes; the scale bar is equivalent to 0.06 changes per site.

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