

A REVISION OF THE LEAFHOPPER GENUS *XYPHON* (HEMIPTERA:
CICADELLIDAE)

A Thesis

by

THERESE A. CATANACH

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

August 2009

Major Subject: Entomology

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ABSTRACT

A Revision of the Leafhopper Genus *Xyphon* (Hemiptera: Cicadellidae).

(August 2009)

Therese A. Catanach, B.S., Texas A&M University

Chair of Advisory Committee: Dr. James B. Woolley

The leafhopper genus *Xyphon*, included in the sharpshooters, is a widely distributed group of insects whose species are vectors for various plant diseases. *Xyphon* has historically contained up to 9 species. These species have been poorly delimited in the past and their identification has been difficult using published keys. The genus is revised here based on a new species level phylogenetic assessment that incorporates both morphological and molecular data.

The genus *Xyphon* was erected to contain leafhoppers that possessed a reticulated forewing apex but lacked both a median sulcus on the crown and a carinate anterolateral crown-face margin both of which are present in the closely related genus *Draeculacephala*. Young (1977) revised most of the genera included in *Xyphon*'s containing subfamily. He did not attempt a revision of *Carneocephala* (the genus that formerly contained most *Xyphon* species), but noted the need for a revision of its species. This revision of the genus *Xyphon* is based on the examination of approximately 8,000 specimens and includes a phylogenetic analysis of the genus that includes data from one gene (NDI) and 47 morphological characters.

A generalized model of each preliminary taxonomic unit was used to test the monophyly of each species. These tests resulted in the synonymization of 4 former species: *Xyphon gillettei* to include *X. balli*; and *X. reticulatum* to include *X. diductum*, *X. dyeri*, and *X. sagittiferum*. Parsimony and Bayesian techniques were used to infer relationships among species. These analyses resulted in almost identical tree topologies. In all analyses *Xyphon* was monophyletic and *Draeculacephala* was its sister genus although clade support for the genus was generally low. The analyses found that *X. flaviceps* and *X. fulgidum* form a basal clade within *Xyphon*, above which *X. gillettei* and *X. n. sp. 1* (new species 1) form a clade that is sister to a third clade containing *X. triguttatum*, *X. nudum*, and *X. reticulatum*.

DEDICATION

I dedicate this thesis to my parents Bob and Rosie Catanach. As they always say, this is the science fair project that refuses to die.

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My family, especially Maria and Eddie (sorry mom and dad, you got the dedication) are endless fun. Whether we are solving the world's problems over Chinese, conversing in dinosaur-bird language, or taking steps to ensure that I don't accidentally blow myself up, y'all understand me better than anyone else. My entomology gang—Aubrey, Brad, Kira, and Mika— who are always there to argue species concepts while playing Worms (who says work and play don't mix). My wildlife friends— Andrea, Annaliese, Israel, Stephen, and Zach— reminded me that there is life outside of systematics (and got me out of the lab and into the deer blind). Rat Bob (sorry, you're permanently Rat Bob in my book) has been my friend and mentor since I arrived at Texas A&M University. You taught me about squirrels, but more importantly how to be a researcher and a professional. Ira Greenbaum was a voice of reason (and provider of food), activities that came in handy on more than one occasion. Jack Brady and Ron Ramsey watched my falcons while I traveled the world. Knowing that they were in your capable hands allowed me to enjoy these trips fully.

On a more professional note, many curators across the world made my work possible as without specimens coding is rather difficult. Mike Wilson has been especially helpful chasing down specimens and alerting me to interesting records. Jamie Zahniser, Suni Krishnankutty, Dani Takiya, Ana Clara Goncalves, and Jason Cryan were just an instant message away when I needed late night help. Markus Peterson showed

me that it's possible to combine a few different interests into a successful career (assuming of course, that I learn how to write).

Without my committee this thesis would not have been possible; my chair, Jim Woolley, resisted killing me on multiple occasions and used reams of paper while getting my thesis into a coherent form; John Oswald provided a research assistantship and very thorough thesis editing; Nova Silvy helped me keep my wildlife roots through teaching assistantships, keeping me on the Attwater's prairie chicken project, and serving as my major professor for a second master's degree. Finally, Chris Dietrich was there every step of the way— from suggesting a project on *Xyphon* to finding a spot in his lab for me to do molecular work. In addition, he cooked an awesome birthday steak (not to mention his daughter's amazing cake), all while introducing me to vegetables and ethnic foods.

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CHAPTER I

INTRODUCTION

The family Cicadellidae is a globally-distributed group of sap-feeding insects that contains ca. 22,000 described species (Dietrich 2004), many of which are vectors of plant pathogens. Among the most diverse and economically important groups of Cicadellidae are the xylem-feeding sharpshooters (subfamily Cicadellinae). The sharpshooter genus *Xyphon* is a small monophyletic group that is common throughout the New World from Argentina to Canada (Hamilton 1985), and has been introduced into parts of the Old World including Guam and western Africa. Three species, *X. triguttatum* (Nottingham), *X. fulgidum* (Nottingham), and *X. flaviceps* (Riley), are vectors of Pierce's disease, an important bacterial disease in grapes, and other crop plants (Nielson 1968).

Hamilton (1985) erected the genus *Xyphon* to hold selected members of *Carneocephala* Ball, 1927, after the latter became a junior synonym of *Draeculacephala* Ball, 1901 (when the type species of *Carneocephala* was placed in *Draeculacephala* by Hamilton). *Draeculacephala* was originally characterized by the presence of reticulate tegminal venation. Ball (1927) erected *Carneocephala* for

This thesis follows the style of *Zootaxa*.

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species of *Draeculacephala* that possessed an inflated head and a conically produced crown that lacked a definite lateral margin. Hamilton (1985) identified 2 putative synapomorphies supporting a *Draeculacephala-Xyphon* group: (1) the presence of reticulate anteapical venation in the forewing, and (2) an aedeagus that is thickest at the base (in lateral view) and bears lateroapical flanges. *Xyphon* was erected for species within this genus-group with a convex crown, no median sulcus on the crown, the proepisternum irregular apically, the appendix extending to the costal margin, and male pygofer and subgenital plates without setae. *Carneocephala floridana*, the type species of *Carneocephala*, lacked the characters of *Xyphon* and was placed back in *Draeculacephala*, making *Carneocephala* a junior synonym of *Draeculacephala*.

The most recent key to include *Xyphon* species is found in Nottingham's (1932) revision of *Carneocephala*. This key is based largely on color characteristics, and the species limits inferred from the key conflict with the species limits suggested by the figures of male genitalia provided by Nottingham (1932). For example, some specimens keyed out as *X. sagittiferum* do not have genitalia that match those attributed to this species in Nottingham's illustrations. Nottingham's key contained 9 species, 1 of which has since been removed from the genus. Due to disagreements between the key and the descriptions there is widespread agreement among specialists that a more reliable set of characters is needed (Young 1977). Additionally, Young (1997) and others have suggested that species concepts within the genus need to be re-examined. Some prior work has focused on crossing studies. Nielson and Toles (1970) crossed individuals of *X. triguttatum* and *X. nudum* in a laboratory setting. They found leafhoppers would mate but the male offspring were generally sterile.

Here, I use morphological and DNA-sequence data to infer the relative phylogenetic relationships among all *Xyphon* species and selected outgroups to: (1) determine if traditional morphological characters are adequate for delimiting species in this genus, (2) provide a revised classification of *Xyphon* and tools for species identification, and (3) revise the genus.

CHAPTER II

METHODOLOGY

Specimen Acquisition and Databasing

More than 8,000 *Xyphon* specimens were examined for my revision. Specimens from many institutions including Texas A&M University, University of Illinois Urbana-Champaign, National Museum of Natural History, The Ohio State University, University of California Riverside, University of Kentucky, Kansas State University, Snow Entomological Collection, Canadian National Collection, American Museum of Natural History, New York State Museum, Colorado State University, University of Colorado, University of Delaware, The British Museum of Natural History, and National Museum of Wales were received on loan. In addition to these dried and mounted specimens, ethanol-preserved specimens from throughout the New World were available through recent collecting efforts for molecular study.

Every specimen was labeled with a unique identification number and all label data (including prior determinations) recorded in an Excel spreadsheet. Additionally, each collecting event was stored in an Internet accessible relational database, 3I, developed by Dmitry Dmitriev (<http://ctap.inhs.uiuc.edu/dmitriev/index.asp>). My database can be accessed through http://ctap.inhs.uiuc.edu/dmitriev/3i_keys.asp. Approximately 90% of all localities were georeferenced using data found in the National Geospatial Agency's GEOnet Names Server (<http://earth-info.nga.mil/gns/html/index.html>).

Phylogenetic Assessment

Young (1977) suggested that *Xyphon* species exhibit minimal morphological divergence. Thus, the phylogenetic assessment made here includes both morphological and molecular (DNA) sequence data.

Morphological Data

Introduction– The morphological dataset includes traditional characters such as color pattern (especially of the dorsal head and thorax) and male genitalia (internal and external) along with new characters such as leg chaetotaxy. Many of these characters were used by Dietrich (1994) and Hamilton (1985) to distinguish species in the closely related genus *Draeculacephala*. High-quality images of morphological characters and their states are deposited in MorphBank (<http://www.morphbank.net>), an Internet archive for storing and sharing biological images. These images are not yet public but will be available in 2010.

Character Coding– Individual specimens were aggregated into morphospecies based on external characters and then sorted into geographic regions. After examining the range of color and morphological variation that occurred in each morphospecies, I selected specimens for coding. For species with fewer than 25 specimens every specimen was coded for morphological data (47 characters with up to 7 states); for species with more than 25 specimens a sample of approximately 25 specimens

encompassing the known range (both geographical and morphological) were selected for coding. These specimens were carefully picked to contain examples of all states found to occur in the morphospecies. Additionally, I included species from across the geographic and ecosystem range of the morphospecies. Based on this approach, I am confident the specimens coded included representatives encompassing the range of states exhibited. Males and females were typically included from the same collecting event, although in some cases only one sex was available for a particular location. By coding specimens from across the geographic range, the frequency of state occurrence could be calculated in cases where multiple states occurred in a single taxon. The full morphological matrix for 176 specimens can be viewed in Appendix 1.

Morphological Characters and States— Characters with asterisked numbers were taken from Dietrich (1994) with additional states added to describe characteristics of *Xyphon*. States shown in italics were used in Dietrich (1994), but are not used here. Asterisked figures note a figure that appears in a different publication. All multistate characters were treated as unordered in all analyses:

- 1*. Crown-face, anterolateral margin, lateral: (0) rounded (Fig. 7A), (1) carinate (Fig. 16H).
- 2*. Clypellus-frontoclypeus junction, lateral: (0) evenly convex, continuing contour of frontoclypeus (Fig. 11B); (1) distinctly angular (Fig. 12B).
- 3*. Frontoclypeus, color pattern: (0) mottled yellow and tan (*Hamilton 1985, Figs. 2, 3), (1) entirely yellow or yellow with brown muscle scars (Fig. 14B), (2) *tan*

with darker markings or mostly black (Dietrich 1994, Figs. 1–3), (3) uniformly tan (muscle scars appearing slightly darker) (*Dietrich 1994, Fig. 5), (4) cream with thin, broken lines (Fig. 12B), (5) *cream with thick, complete lines*, (6) mottled dark brown and yellow (Fig. 15B).

4. Face, white band along border with crown: (0) complete, well defined and not irregularly marked with face color (Fig. 9B), (1) poorly defined white band, splotched white and face color (Fig. 13B), (2) absent (Fig. 11B).
5. Crown, shape, dorsal view: (0) angular (Fig. 14A), (1) rounded (Fig. 11A).
6. Crown, median sulcus: (0) present, (1) absent (Fig. 8B).
- 7*. Crown, medioapical macula: (0) absent or poorly delimited (Fig. 12A), (1) entirely yellow or yellow with brown spot (Fig. 8E), (2) *tan with darker markings*, (3) uniformly tan (Fig. 11A), (4) dark brown (Fig. 15A).
8. Crown, median spot: (0) present, well defined (Fig. 14A), (1) present, without defined edges (fading into background color) or with patches of background color mixed in with median spot (Fig. 15A), (2) absent (Fig. 12A).
- 9*. Crown, pattern: (0) without dark lines or patterns (Fig. 12A), (1) with dark, vermiform lines (*Dietrich 1994, Figs. 8, 9), (2) with irregular brown spots (*Dietrich 1994, Figs. 11, 15), (3) brown background with light patches (Fig. 13A), (4) light brown lines (concentrated in middle of crown) (Fig. 11A), (5) with medioapical macula only (Fig. 14A).

10. Crown, dark markings other than median spot anteriorly: (0) without dark markings other than median spot anteriorly (Fig. 9A), (1) with dark markings other than median spot anteriorly (Fig. 13A).
11. Crown, orange pigment: (0) present (Fig. 12A), (1) absent (Fig. 13A).
12. Ocelli, distance from ocelli to lateral edge of head: (0) no more than twice ocellar width (Fig. 9A), (1) more than twice ocellar width (Fig. 10A).
13. Ocelli, distance between ocelli: (0) no more than 7.5 times ocellar width (Fig. 9A), (1) at least 7.5 times ocellar width (Fig. 10A).
14. Crown shape, lateral view: (0) convex (Fig. 7E), (1) concave (Figs. 7C, 11B), (2) flat (Fig. 7F).
- 15*. Postocellar maculae: (0) absent (12A), (1) large and well developed (Fig. 15A), (2) part of a broader pattern (Fig. 8E).
- 16*. Antenna, male flagellum: (0) not clavate (Fig. 11B), (1) *clavate*.
17. Antenna scape: (0) with posterior lobe, (1) without posterior lobe (Fig. 13B).
- 18*. Ventral preocular macula: (0) absent (Fig. 13B), (1) present (*Dietrich 1994, Fig. 16).
- 19*. Thoracic sterna, color, male: (0) yellow, (1) mesosternum with brown longitudinal macula, (2) thoracic sterna entirely brown.
20. Proepisternum, posterior edge: (0) irregularly shaped (Fig. 13B), (1) not irregularly shaped (Fig. 9B).
- 21*. Transpleural macula of thorax: (0) absent (Fig. 12B), (1) present but incomplete, poorly delimited (Fig. 13B), (2) present, concolorous with frontoclypeus and

ventral maculae (*Dietrich 1994, Figs. 1– 4), (3) present, distinctly darker than frontoclypeus (*Dietrich 1994, Figs. 5–7).

22. Pronotum, anterior edge, dark green/brown circular markings: (0) present (Fig. 13A), (1) absent (Fig. 10A).
23. Pronotum, anterior edge, circular indentations: (0) present (Fig. 15A), (1) absent (Fig. 10A).
- 24*. Pronotum and wings, color, blue pigment: (0) midline of pronotum and forewing veins white (Fig. 13C), (1) midline of pronotum and anal veins of forewing pale blue, (2) *pronotum with paired light blue lines and most forewing veins blue*, (3) midline of pronotum concolourous with pronotum, forewing veins white, (4) midline of pronotum white, anal veins of forewing pale blue (Fig. 15C), (5) midline of pronotum concolourous with pronotum, anal veins of forewing pale blue (Fig. 9C), (6) midline of pronotum white, anal veins of forewing green (Fig. 14C), (7) midline of pronotum concolorous with pronotum, anal veins of forewing green (Fig. 10C).
- 25*. Pronotum and forewing color (majority): (0) green (Figs. 8A, B, E, G), (1) tan, (2) gray, (3) nearly black/brown (Fig. 8F), (4) cream, (5) straw (Fig. 8C).
- 26*. Mesonotum, pattern on exposed part: (0) unmarked (Fig. 9C), (1) marked with pair of submedial spots, (2) marked with submedial spots and anterolateral triangles (Fig. 15C), (3) very lightly marked (Fig. 11C), (4) *marked with anterolateral triangles only*.
27. Forewings, green pigment: (0) present (Figs. 8A, B, E, G) (1) absent (Figs. 8C, F).

28. Forewing, crossveins at apex: (0) many crossveins, resembling a spiderweb especially at anterior edge of forewing (Fig. 16E), (1) more than 3 crossveins, but still with distinct rows of cells, large cells separated by thin veins (Fig. 16F), (2) only a 2 or 3 crossveins typically at the proximal portion of the apex (Fig. 16G).
29. Forewing, appendix, length: (0) extends to costal margin, (1) not extending to costal margin.
- 30*. Hind femur, macrosetal formula: (0) 2+1 (Fig. 16C), (1) 2+1+1, (2) 2+0 (Fig. 16A).
- 31*. Hind tarsomere, number of paleate setae on plantar surface: (0) 0, (1) 1–3, (2) 4–5 (Figs. 16B, 16D), (3) 6 or more.
- 32*. Abdominal sternum, color, male: (0) yellow, (1) brown, (2) red or orange.
- 33*. Pygofer: (0) approximately the same length as subgenital plate, (1) much longer than subgenital plate.
- 34*. Pygofer, erect basolateral setae: (0) absent, (1) present, scattered, (2) present, arranged in a definite band (*Dietrich 1994, Fig. 24).
- 35*. Subgenital plate, long fine dorsal setae: (0) absent, (1) present, numerous, distributed throughout dorsal margin, (2) *present, patch basally*.
- 36*. Subgenital plate, macrosetae: (0) absent, (1) present, small and scattered, (2) present, large, forming distinct band (*Hamilton 1985, Figs. 52–54).
37. Aedeagus, form, lateral view: (0) thickest at base (Fig. 15D), (1) not thickest at base.

- 38*. Aedeagal shaft, dorsal process, lateral view: (0) acute, compressed (Fig. 13D),
 (1) *absent*, (2) acute, not compressed (Fig. 11D), (3) *wave shaped* (Hamilton
 1985, Fig. 17), (4) *quadrate*, (5) *broadly arcuate* (Hamilton 1985, Figs. 16–19).
39. Aedeagus, dorsal process, shape laterally: (0) absent, (1) wider than tall (Fig. 11D),
 (2) taller than wide (Fig. 12D).
- 40*. Aedeagal shaft, ventral view: (0) narrowly ovoid (Fig. 12E), (1) broadly ovoid
 (Fig. 9E), (2) narrow with basolateral expansions (Fig. 14E), (3) *broad and
 quadrate* (Young and Davidson 1959, Fig. 2E), (4) with acute lateral processes
 at base of aedeagal shaft, (5) *distinctly bilobed*, (6) arrow shaped (Fig. 13E)
41. Aedeagus, ventral flange: (0) basolateral angles distinct (Fig. 14E), (1) not distinct
 (basal portion of aedeagus rounded) (Fig. 9E).
- 42*. Aedeagal shaft, dorsal margin: (0) compressed (*Young and Davidson 1959, Fig.
 2D), (1) not compressed.
43. Paraphyses, shape in ventral view: (0) forming a circle (Fig. 9E), (1) oval with
 basal side wider than apex (Fig. 14E), (2) forming a U (Fig. 15E).
- 44*. Paraphyses, ventral view: (0) short and stout, if reaching the shaft curved across
 shaft at or basad of midlength (*Dietrich 1994, Figs. 14, 18, 23), (1) long and
 narrow, curved across shaft distad of midlength, (2) *very long and narrow,
 apices surpassing shaft apex*.
- 45*. Paraphyses, lateral view: (0) sinuate (Fig. 15D), (1) *arcuate, curved caudally
 then dorsally* (*Hamilton 1985, Fig. 17).

46*. Shank of style, dorsal view: (0) short, strongly curved mesad, (1) elongate, weakly curved.

47. Style, setae: (0) absent, (1) single setae per side, (2) pair of setae per side.

Test of Species Monophyly– After coding was completed and the percentages of each state occurrence were calculated, duplicate OTU's (where multiple specimens had identical character state suites) were removed from the matrices of individual species.

OTU's (operational taxonomic units) are the basic coded level in a taxonomic study.

In the tests of monophyly OTU's are individual specimens while in the species

phylogeny OTU's are the species themselves. In cases of missing data, the

questionable character was not included when searching for duplicates (so if a species was coded for 46 out of 47 characters, as long as the coded characters exactly matched another OTU it was considered a duplicate).

Once duplicates were removed, PAUP* was used to test the monophyly of each species. First, I attempted to analyze all OTU's together in a single analysis, but this resulted in a completely unresolved consensus tree. I created a generalized representative for each morphospecies by determining the state that most often occurred for each character. I tested the monophyly of each species by analyzing all male non-duplicate OTU's of each morphospecies against a data set consisting of calculated generalized morphospecies of all other taxa. Only data from male specimens were used because of the high number of morphological characters found only in males. The monophyly of non-duplicate state arrays of original morphospecies

was tested against the generalized morphospecies arrays and the suite of outgroups using parsimony in PAUP (1,000 random addition sequences, using TBR branch swapping). The process was repeated for each morphospecies to determine which ones formed monophyletic clades.

Molecular Data

DNA preparation– The majority of specimens for molecular phylogenetic analysis were preserved after collection in 95% ethanol and stored at -20° C. A few specimens were collected into 95% ethanol but dried and pinned prior to extraction and sequencing. Specimen preparation and sequence extraction was undertaken at the Illinois Natural History Survey using protocols detailed in Takiya et al. (2006). DNA was extracted from the head and thorax of specimens (abdomen removed for genitalic study) using the protocol detailed in the DNeasy Tissue Handbook for Isolation of Total DNA from Animal Tissue (DNeasy 2007). The only modifications to this protocol occurred in step 8, where 50µl of Buffer AE was used rather than 200µl and incubation occurred at room temperature for 5 minutes rather than 1 minute. The DNeasy tissue kit (QIAGEN Inc.) was used for all extractions.

PCR and Sequencing– Three genes, 2 mitochondrial and 1 nuclear were sequenced, although not all specimens were sequenced for each gene. Cytochrome oxidase subunit I (COI) sequences were amplified using the primers 3014 and COI, NADH dehydrogenase subunit I (NDI) using NDI +1/-1, and Histone (H3) using Hex 3F/R

(Table 1). Taq DNA polymerase (0.1 μ l) (Promega Corp.) was used for amplification. PCR was performed using the protocol shown in Table 2. After PCR was completed, products were held at 10° C until removed from the machine. Products were then checked for yield using a 1% agarose electrophoresis gel stained with Bromophenol Blue, then checked under UV light. After yield was confirmed products were purified using the QIAQuick PCR purification kit (QIAGEN Inc.). The ABI PRISM Big Dye terminator kit version 3 (PE Applied Biosystems) was then used to sequence both strands. Products were then submitted for high-throughput sequencing at the Biotechnology Center of the University of Illinois at Urbana-Champaign.

Alignment– Sequencher 4.2 (Gene Codes Corp.) was used to check chromatograms, reconcile complementary strands, and align protein coding genes sampled across taxa. Sequences were then aligned using ClustalX 1.83 with all parameters set at default, then manually aligned by eye.

Vouchers and Outgroups

Vouchers– Voucher specimens (actual DNA-sequenced specimens preserved in glycerin, and where possible, additional unsequenced specimens from the same collecting event) were deposited in the Texas A&M University Insect Collection (voucher numbers 674). All sequence data was deposited in GenBank (accession numbers GQ302960- GQ302971), and aligned data in Tree Base (numbers not yet available for this project).

Outgroups– Outgroups were selected from closely related genera to include 3 species of *Draeculacephala*, 1 species of *Syncharina*, 1 species of *Chlorogonalia* and 1 species of *Plesiommata* (Young 1977). *Draeculacephala* is widely considered to be the sister genus to *Xyphon* based on various synapomorphies, including the presence of reticulated crossveins in the apical region of the forewing. The other genera are thought to compose a clade with *Draeculacephala* + *Xyphon* (Young 1977).

Phylogenetic Analyses

Model Selection– Molecular data were analyzed in parsimony and Bayesian frameworks using PAUP* 4.0b10 (Swofford 2003), TNT (using new technologies) (Goloboff et al. 2008), and Mr. Bayes (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Each data partition (morphology and NDI) was analyzed separately, and then the 2 were combined to reveal hidden Bremer support. Modeltest (Posada & Crandall 1998) was used to pick the best model for the molecular dataset. I picked the model using the web implementation of FindModel using both PAUP and Weighbor to construct initial trees, then selected the model with the lowest AIC value.

Analyses– Results from 3 analyses are included here:

Analysis I was based on 47 morphological characters analyzed using parsimony and included all *Xyphon* species plus 6 outgroups. This analysis was conducted with PAUP* (1,000 random addition searches, TBR branch swapping, and all other options set on default) and TNT (all new technologies, all options on default). All multistate characters were treated as unordered.

Analysis II was a parsimony-based analysis of 47 morphological characters and 1,100 molecular characters and included all *Xyphon* species plus 6 outgroups. Included in the *Xyphon* species were representatives of 3 of the 4 species that are now synonymized with *X. reticulatum*. This analysis was completed using PAUP* (1,000 searches, TBR branch swapping) and TNT (all new technologies). Unambiguous state changes of morphological characters were mapped on the resulting tree (Fig. 4).

Analysis III was a Bayesian analysis of 47 morphological characters and 1,100 molecular characters and included 4 *Xyphon* species plus 4 outgroups (taxa lacking molecular data: *X. gillettei*, *X. fulgidum*, *X. n. sp. 1* and 2 outgroups were excluded), a Jukes-Cantor model was used for morphology and a General Time Reversal + Gamma for NDI. Two species: *X. flaviceps* and *X. reticulatum* have multiple representatives in both Analysis II and III. There are 4 representatives of *X. reticulatum* because sequencing occurred prior to synonymization of *X. sagittiferum*, *X. dyeri*, and *X. diductum*. There are 2 representatives of *X. flaviceps* because specimens from 2 different areas were submitted for sequencing. The analysis was completed with 500,000 generations and 4 chains. I judged stability to be reached by the standard deviation of split frequencies being less than 0.1 which indicates that the 2 runs are converging on a stationary distribution. A burnin of 250 generations was assumed and the plot of generations versus the log likelihood value showed no apparent trend after burnin. The Potential Scale Reduction Factor approached 1.0 at 500,000 generations, again indicating that the analysis was stationary.

CHAPTER III

RESULTS

Sequence Data

Sequences for COI and H3 appeared to lack enough divergence to be useful based on the number of parsimony informative characters, so NDI was the only gene used for phylogenetic study. The NDI sequences contained up to 1,096 base pairs, 577 of which were constant. Of the remaining 519 characters 238 bases were parsimony informative. There were 9 gaps of varying lengths. The sequences were AT rich with 50%T, 27%A, 14%G, and 9%C. The Ti/Tv ratio was 0.83. The COI sequence contained 790 characters, of which 360 were constant. Of the remaining characters, 278 were parsimony uninformative, and 152 parsimony-informative. There were up to 4 gaps, all of which were short (4 bases or less). The sequences were AT rich with 38%A, 34%T, 14%G, and 14%C. The Ti/Tv ratio was 1.11. The H3 sequences contained 289 base pairs, of which 157 were constant. Of the remaining characters, 88 were parsimony uninformative and 44 parsimony informative. The sequences generated for H3 have base frequencies of 34%C, 28%G, 22%A, and 16%T. The Ti/Tv ratio is 1.53.

Monophyly of Species

Based on the methodology explained above under Test of Species Monophyly, *Xyphon gillettei*, *X. nudum*, *X. triguttatum*, *X. flaviceps*, *X. fulgidum*, and *X. reticulatum*

were all interpreted to be monophyletic. *Xyphon balli* was synonymized with *X. gillettei* as characters distinguishing these species were not found. Knull (1940) described *X. balli* as resembling *X. gillettei* but smaller. My examination specimens to encompass a range of sizes with some leafhoppers of intermediate size.

Similarly, *Xyphon sagittiferum*, *X. dyeri*, and *X. diductum* were synonymized under *X. reticulatum* based on a lack of distinguishing characters. Further supporting the decision to bring *Xyphon sagittiferum*, *X. dyeri*, and *X. diductum* and *X. reticulatum* into synonymy, 2 series (1 from Guinea in western Africa and 1 from Guam in the Pacific) of approximately 20 *Xyphon* were available for examination. Each series consisted of a single collecting event and both were found to contain the full range of morphological character variation found among the synonymized taxa. Assuming each introduction event was a single species, the fact each series covers the range of phenotypes exhibited by the former species suggests that these phenotypes are intra-specific variation.

Analysis I: Parsimony Based Morphologic Analysis

Analysis I (Fig. 1) identified a clade made up of *X. gillettei* and *X. n. sp. 1* as the most basal group in *Xyphon*. Next, *X. fulgidum* is sister to *X. flaviceps* + *X. reticulatum* + *X. triguttatum* + *X. nudum*. *Xyphon flaviceps* is sister to *X. reticulatum* + *X. triguttatum* + *X. nudum*. This clade has *X. nudum* as the basal member. The principal difference between Analysis I and the Analyses II and III is the absence of a *X. fulgidum* + *X. reticulatum* clade in the former. In Analysis I, the monophyly of

Xyphon is weakly supported (bootstrap value of 64, Bremer support value of 1), and most of the interior nodes have bootstrap values of less than 50. Exceptions to this are the clade containing *X. gillettei* and *X. n. sp. 1* and a clade containing the rest of *Xyphon*; both of these clades have bootstrap values of 90.

Analysis II: Parsimony Based Morphology and Molecular Analysis

Tree topologies derived from PAUP* and TNT were identical (2 equally parsimonious trees each 1,036 steps long) so they are presented as one discussion. I used all “new technologies” in TNT which did not result in any shorter trees. A strict consensus tree of these 2 equally parsimonious trees resulted in a well-resolved parsimony trees for both PAUP* and TNT as shown in Figure 2. This tree placed *X. fulgidum* as sister to the 2 specimens of *X. flaviceps*, and this clade sister to the rest of *Xyphon*. *Xyphon gillettei* + *X. n. sp. 1* was placed as sister to a clade containing *X. triguttatum* (basal member), *X. nudum*, and *X. reticulatum*. *Xyphon nudum* was placed within a clade containing 4 representatives of *X. reticulatum* which will be discussed in depth in a later section. While *Xyphon* is monophyletic in this analysis, its bootstrap value is low at 65. The interior nodes of *Xyphon* are all supported with values ranging from 64 to 88 except one clade (which had a bootstrap value of less than 50) which contains all members of *Xyphon* except *X. flaviceps* and *X. fulgidum*.

Analysis III: Bayesian Based Morphologic and Molecular Analysis

Analysis III (Fig. 3) supported a monophyletic *Xyphon*, with a low posterior probability of 0.52, and placed *X. flaviceps* as the sister species to the rest of *Xyphon*. The internal branches of *Xyphon* (except that for the 2 specimens of *X. flaviceps*) were all well-supported, with posterior probability values of 1.00.

CHAPTER IV

DISCUSSION

Xyphon is monophyletic with respect to the selected outgroups in all analyses, although the support values for its monophyly are low. There are a number of morphological characters that appear to be synapomorphies for *Xyphon* (Fig. 4, unambiguous state changes; Fig. 5, minimum and maximum synapomorphy numbers for both morphological and molecular data). These include the absence of a median sulcus on the crown (Character 6), the presence of a rounded anterolateral margin between the crown and face (Character 1), and the presence of a single seta on the style (Character 47). *Xyphon* and *Draeculacephala* form a monophyletic clade in Analyses I and II. This relationship is supported (Fig. 4) by 3 synapomorphies including the presence of numerous reticulate crossveins on the apex of the forewing and an aedeagus that is widest at the base in lateral view (Character 37). In Analysis III the 2 *Draeculacephala* species form a clade with outgroups *Syncharina* and *Chlorogonalia* (in Analyses I and II these 2 *Draeculacephala* species are resolved sisters to *Xyphon*).

Character Evolution

All discussions in this section refer to Figure 4 unless otherwise stated. Only characters shown to have value in diagnosing clades or species are discussed here. Studying character evolution can help determine which characters are useful for phylogenetic study in related groups.

Head

Crown-face, anterolateral margin (Character 1): The anterolateral margin of the crown of most *Draeculacephala* (Dietrich 1994 lists all species except *D. angulifera*) is carinate (State 1), while all members of *Xyphon* have a rounded margin (State 0). This is a key characteristic that distinguishes *Draeculacephala* from *Xyphon*.

Frontoclypeus, color pattern (Character 3): This character was quite variable across *Xyphon*. Members of *X. reticulatum* tended to have a face that was mottled dark brown with yellowish areas (State 6). *X. nudum* and *X. flaviceps* tended to have a tan face (State 3) while *X. triguttatum*, *X. gillettei*, and *X. fulgidum* had a face that was mostly yellow with some brown areas (State 1). Outgroups also were variable.

Crown, shape, dorsal view (Character 5): Having an angular crown (State 0) in dorsal view united a *reticulatum* + *nudum* + *triguttatum* clade, while its sister species *X. gillettei* had a rounded crown (State 1) in dorsal view. Additionally *X. flaviceps* has a rounded crown while its sister species, *X. fulgidum* has a more angular crown in dorsal view.

Crown, median sulcus (Character 6): This character provides support for the genus *Xyphon*. All examined members of *Draeculacephala* (and those coded by Dietrich 1994) have a median sulcus on the head (State 0) while it is absent (State 1) in all *Xyphon*.

Crown, medioapical macula (Character 7): Most members of the genus lacked a consistent mesoapical spot on the crown (State 0). *X. triguttatum* is the only species

that always has a dark brown spot. A number of individual specimens of *reticulatum* had a dark brown spot (State 4) (which ranged from well to very poorly defined). Conversely a few species, *X. nudum*, *X. gillettei*, *X. flaviceps*, and *X. fulgidum* always lacked a mesoapical spot (although in the case of *X. gillettei* brown lines occurred down the center of the crown). All of the *Draeculacephala* examined had a yellow mesoapical spot (State 1).

Crown, median spot anterior third of crown (Character 8): This character is variable across *Xyphon*, although the complete absence (State 2) of a median spot serves to unite the *flaviceps* + *fulgidum* clade.

Crown, dark markings other than median spot on anterior third of crown (Character 10): Based on Analysis II, this character seems to have been present (State 1) in *Xyphon* but subsequently lost (State 0) in a few lineages such as the *flaviceps* + *fulgidum* clade, *X. triguttatum*, *X. nudum*, and in a few specimens of *X. reticulatum*. This conflicts with the analysis of exclusively morphological data which uses the absence of dark markings on the head to unite the clade containing *triguttatum*, *nudum*, *flaviceps*, *fulgidum* and *reticulatum* (although this character varies widely in *reticulatum*).

Crown, orange pigment (Character 11): The presence (State 0) of orange coloration on the head appears to be variable although it unites the *flaviceps* + *fulgidum* clade. It has subsequently reappeared in both *X. triguttatum* and *X. nudum*.

Ocelli, distance from ocelli to lateral edge of head (Character 12): This character was variable across *Xyphon*, although having a distance to edge of head less

than 2 times ocular width (State 0) united *reticulatum* + *nudum* + *triguttatum*. It was also the distinguishing character between *X. flaviceps*, which have a distance to edge of head less than 2 times ocular width, and *X. fulgidum*, having a distance to edge of head more than 2 times ocular width (State 1).

Ocelli, distance between ocelli (Character 13): This character was variable across *Xyphon*, although having the distance between ocelli be less than 7.5 times ocular width (State 0) united *reticulatum* + *nudum* + *triguttatum*. It was also the distinguishing character between *X. flaviceps*, which have the distance between ocelli less than 7.5 times ocular width, and *X. fulgidum*, have the distance between ocelli less than 7.5 times ocular width (State 1).

Ventral preocular macula, lateral view (Character 18): No *Xyphon* had a ventral preocular macula (State 0), a feature that was found in all *Draeculacephala* and many other outgroup genera (State 1).

Thorax

Thorax, transpleural macula (Character 21): All species of *Xyphon*, except some specimens of *X. reticulatum* (typically darker individuals which have a present but incomplete, poorly delimited transpleural macula (State 1)) lack a transpleural macula (State 0). However, many outgroups had a well defined transpleural macula (State 2).

Proepisternum, posterior edge (Character 20): This character was suggested by Hamilton (1985) as a distinguishing character of *Xyphon*. However, I found it to be

quite variable in all species coded and only 1, *X. triguttatum*, typically had an irregular apical edge of the proepisternum (State 0).

Pronotum, anterior edge, dark green/brown circular markings (Character 22): The presence of dark circular markings on the pronotum (State 0) is present in *reticulatum* but absent in other species (State 1), including *X. nudum* with which it forms a paraphyletic clade in Analyses II and III.

Pronotum and wings, color, blue pigment (Character 24): This character united a *reticulatum* + *nudum* clade in Analyses II and III. While this character is variable across *Xyphon*, this clade has a pronotum with a white midline and anal veins green to yellow (State 6).

Pronotum and forewing color (majority) (Character 25): In general all taxa sampled (both ingroup and outgroups) had a pronotum and forewings that were mainly green (State 0). The only exceptions to this were the clade of *X. gillettei* and *X. n. sp. 1* which is straw colored (State 5) and tropical representatives of *X. reticulatum* which can be so dark they are approaching black (State 3).

Mesonotum, pattern on exposed part (Character 26): Most specimens of *X. reticulatum* had a mesonotum that was marked rather darkly- typically with submedial spots and anterolateral triangles (State 2) of varying sizes. Other members of the genus (and outgroups in the genus *Draeculacephala*) typically had an unmarked mesonotum (State 0) although some species such as *X. gillettei* were pretty evenly split between unmarked and very lightly marked mesonotum (State 3).

Wings

Forewing, green pigment (Character 27): This character seems to have been present (State 0) in *Xyphon* but lost in the clade containing *X. gillettei* and *X. n. sp. 1* whose members lack green pigment (State 1). It also can be variable in *reticulatum*, as some specimens have wings that are black.

Forewing, crossveins at apex (Character 28): This is a character that unites a *Xyphon + Draeculacephala* clade as these 2 genera have few (State 1) or many (State 0) crossveins at the wing apex. This character also is useful at the species identification level as *X. flaviceps* and *X. fulgidum* have many crossveins at the apex of the forewing. Additionally, *X. n. sp. 1* can be recognized by the presence of at most 3 crossveins (State 2).

Appendix, length (Character 29): This character was suggested by Hamilton (1985) as a distinguishing character of *Xyphon*. However, I found the appendix extended to the costal margin of the wing (State 0) in some members of *Draeculacephala*.

Legs:

Hind femur, macrosetal formula (Character 30): This character does not vary widely (rarely specimens may have an abnormal macrosetal formula but this typically only occurs on 1 leg) across *Xyphon*, which typically have a macrosetal formula of 2+1 (State 0) with the exception of *X. gillettei* which has a macrosetal formula of 2+0 (State 2).

Hind tarsomere, number of paleate setae on plantar surface (Character 31):

There are 4 or 5 paleate setae (State 2) on the plantar surface of the hind tarsomere of all *Xyphon*, except *X. flaviceps*, which has between 1 and 3 (State 1), while all outgroups had none (State 0) or more than 6 (State 3).

External Genitalia

Abdominal sternum, color, male (Character 32): While *Xyphon* typically has yellow abdominal sternites (State 0), 1 species, *X. gillettei*, has abdominal sternites that are red or orange (State 2).

Pygofer, erect basolateral setae (Character 34): This character was variable across *Xyphon*, although the presence of scattered setae on the pygofer (State 1) united a *flaviceps* + *fulgidum* clade.

Subgenital plate, macrosetae (Character 36): This character was variable across *Xyphon*, although the presence of scattered setae on the subgenital plate united a *flaviceps* + *fulgidum* clade (State 1).

Internal Genitalia

Aedeagus, form (Character 37): Having an aedeagus that is thickest at the base (State 0) when viewed laterally unites *Xyphon* and *Draeculacephala*.

Aedeagal shaft, dorsal process, lateral view (Character 38): This presence of an acute, compressed dorsal process (State 0) on the aedeagal shaft united a *reticulatum* +

nudum + *triguttatum* clade. The presence of an acute but not compressed (State 2) on the aedeagal shaft united the *flaviceps* + *fulgidum* clade.

Dorsal process, shape in lateral view (Character 39): The presence of a dorsal process on the aedeagus that is wider than tall (State 1) unites *flaviceps* + *fulgidum*.

The presence of a dorsal process that is taller than wide (State 2) unites *reticulatum* + *nudum* + *triguttatum*.

Aedeagal shaft, ventral view (Character 40): The presence of an aedeagal shaft that was broadly ovoid (State 1) in ventral view united a *flaviceps* + *fulgidum* clade.

This shaft being arrow shaped (State 6) united the *triguttatum* + *reticulatum* + *nudum* clade, although in *nudum* the shaft has been modified to be narrowly ovoid (State 0).

Aedeagus, ventral flange (Character 41): Having indistinct basolateral angles (State 1) on the ventral phalange of the aedeagus unites *flaviceps* and *fulgidum*. The presence of distinct angles (State 0) unites the *gillettei* + n. sp. 1 + *triguttatum* + *reticulatum* + *nudum* clade, although in *nudum* this feature has reverted back to an indistinct state.

Paraphrases, shape in ventral view (Character 43): While there is some variability in specimens, in general all members of *Xyphon* have paraphrases that form an oval (State 1) in ventral view. The only exception is *X. gillettei* where they often form a U (State 2).

Style, setae, presence/absence (Character 47): The presence of a single seta (State 1) or rarely a pair of setae (State 2) on the style unites *Xyphon* as all sampled outgroups are lack setae (State 0).

NADH dehydrogease subunit I (NDI)

Trees derived from analyses of data from this gene only (not shown here) are largely congruent with morphological data, suggesting that it evolves at a rate useful for species-level phylogenetic analysis in the Cicadellinae. Additionally, other leafhopper studies on different subfamilies have used this gene for generating species level phylogenies (Dietrich et al. 1997). A saturation plot for NDI (Fig. 6) that predicted the number of changes in the sequence data for this gene is only slightly higher than the uncorrected p -values, verifying this gene is not saturated and is appropriate for use in phylogenetic inference.

Differences Among Data Analyses

Comparisons of parsimony and Bayesian-based analyses revealed few differences in the resulting trees. The primary difference between the 2 analytical techniques was that I could include taxa in the parsimony analysis that were missing NDI data with little loss of resolution in the resulting tree (Fig. 2) while Bayesian analysis of the same data resulted in an analysis which never reached stability. The tree resulting from parsimony analysis of NDI data only (not shown) was topologically identical to the tree resulting from Analysis III (Fig. 3). There were differences between trees from Analysis II, and the morphology tree (Analysis I). The most important difference is the presence of a clade containing *reticulatum* and *nudum* in Analyses II and III where these 2 species are paraphyletic. This contrasts with Analysis I in which these 2 species are not sisters.

In Analyses II and III (Figs. 2 and 3) the 4 specimens of *reticulatum* formed a clade with *nudum*. Removal of *nudum* from this clade would render *reticulatum* paraphyletic. However, I am hesitant to synonymize *nudum* which is morphologically distinct with many unifying characters. However, it is interesting that *reticulatum* becomes lighter with greater distance from the equator. Tropical specimens often have black wings, dark heads, and large dark markings on the mesonotum. Specimens collected from the southeastern United States have green wings and have much lighter markings on the head and mesonotum. It is conceivable that a desert dwelling race equivalent to the concept of *nudum* would be completely lacking dark markings on the head or mesonotum.

Other differences between the results of Analysis I and Analyses II and III include a paraphyletic *Draeculacephala* (Analysis I), the placement of *X. triguttatum* as sister a clade of *X. nudum* + *X. reticulatum* (Analyses II and III) or as sister to *X. reticulatum* only (Analysis I), and the grouping of *X. flaviceps* and *X. fulgidum* (Analysis II). The paraphyly of *Draeculacephala* in Analysis I was unexpected, and may be due to the limited selection of *Draeculacephala* outgroups in the analysis. The 3 *Draeculacephala* species used as outgroups include 2 closely related species and 1 species that is divergent from the other 2. The monophyly of *Draeculacephala* was well supported by Dietrich (1994), but he included representatives of all *Draeculacephala* species.

Xyphon triguttatum was sister to the *reticulatum* + *nudum* clade in Analyses II and III, but sister to *reticulatum* only in the morphological analysis. In Analyses II

(Fig. 2), *flaviceps* and *fulgidum* form a distinct clade that is well supported by bootstrap values and posterior probability values. However in the morphology analysis (Analysis I, Fig. 1) they do not form a clade. These species are differentiated by only a few morphological characters, so the fact that they did not group together was unexpected.

CHAPTER V

REVISION OF *XYPHON*, A SUMMARY OF THE GENUS**Xyphon Hamilton 1985***Xyphon* Hamilton 1985*Carneocephala* Ball 1927

Diagnosis: Medium-sized leafhoppers; typically green overall, rarely straw, brown, or black; similar to its sister genus *Draeculacephala* in having reticulate crossveins at apex of forewing (Character 28) and aedeagus thickest at base (Character 37); differing from *Draeculacephala* in lacking medial sulcus on crown (Character 6), having anterolateral margin of crown rounded not carinate (Character 2), and having appendix extending to costal margin (Character 29).

Genus description (synapomorphies italicized)

Head: Median sulcus of head absent. Anterolateral margin of the crown rounded to face. Head patterned or not, face usually with muscle scars.

Thorax: Pronotum patterning variable, with or without patterns, dark circles, or indentations; midline of pronotum concolorous with pronotum or blue or white; darker individuals sometimes with brown longitudinal stripes on mesosternum.

Legs: Usually 4 paleate setae on hind leg, species/individuals vary; all species (except *gillettei* whose macrosetal formula is 2+0) have 2+1 hind leg macrosetal formula.

Wings: *Appendix* extends to the costal margin; apex of forewing with many crossveins, typically densely reticulate; forewings green, rarely black, brown, or straw colored; anal veins of forewing typically white, blue, or green.

Male external genitalia: Seta on pygofer and/or subgenital plate although placement is variable; pygofer approximately same length as subgenital plate.

Male internal genitalia: Aedeagal shaft not compressed in dorsal view; in lateral view thickest at the base. Additionally paraphyses short and stout in ventral view, curving across shaft at or basad of midlength; appearing sinuate in lateral view. Shank of style is short, strongly curving mesad; single setae on each side of style.

Type species: *Diedrocephala flaviceps* Riley 1880, by original designation

Gender: Neuter, as indicated in original description, so it is fixed under Article 30.2.

Geographic range: *Xyphon* is native to most of the New World, although rarely collected in the northeast United States. Collection localities range from Canada to

Argentina, and include several Caribbean islands. One species, *X. reticulatum*, has been introduced into western Africa and several Pacific islands.

Temporal distribution: *Xyphon* can be collected year-round in the milder parts of its range. In areas with more seasonal variation *Xyphon* is most commonly collected from the late spring through early fall.

Biology: *Xyphon* species have been collected on a number of plant species including cotton (*Gossypium hirsutum*), cucumber (*Cucumis sativus*), alfalfa (*Medicago* sp.), sideoats grama (*Bouteloua curtipendula*), silverleaf nightshade (*Solanum elaeagnifolium*), beebalm (*Monarda* sp.), prickly Russian thistle (*Salsola tragus*), bermudagrass (*Cynodon dactylon*), vinegarweed (*Trichostema lanceolatum*), and saltgrass (*Distichlis spicata*). These data were acquired from label data so is by no means an exhaustive list. Based on this list, however, *Xyphon* would be expected to be quite generalized in its food plants.

Etymology: random combination of letters.

Key to the species of *Xyphon* using adult males and females

1. Forewing apex densely reticulate, forming a spider web of cells (Fig. 16E).....2

- 1a. Forewing apex not densely reticulate, with few crossveins creating regular cells (Fig. 16F).....3
- 2 (1). Distance between ocelli more than 7.5 times width of ocellus in dorsal view (Fig. 10A); distance from ocellus to margin of head more than 2 times width of ocellus (Fig. 10A); known distribution: California.....*Xyphon fulgidum*
- 2a. Distance between ocelli less than 7.5 times width of ocellus in dorsal view (Fig. 9A); distance from ocellus to margin of head less than 2 times width of ocellus (Fig. 9A); known distribution: United States east of Rocky Mountains, Mexico.....*Xyphon flaviceps*
- 3 (1a). Crown and pronotum without dark markings (Fig. 12A); known distribution: southwestern United States, Mexico.....*Xyphon nudum*
- 3a. Crown and pronotum with one or more dark spot (Figs.11A, 13A, 14A, 15A).....4
- 4 (3a). Head concave in lateral view (Fig. 7C).....5
- 4a. Head convex or flat in lateral view (Fig. 7A).....6

- 5 (4). Hind femur 2+0 macrosetal formula (Fig. 16A);
 known distribution: Colorado and Arizona.....*Xyphon gillettei*
- 5a. Hind femur 2+ 1 macrosetal formula (Fig. 16C);
 known distribution: Mexico.....*Xyphon n. sp. 1*
- 6 (4a). Head with a single black spot near anterior margin
 of crown (Fig. 14A); lacking other dark markings
 on head (Figs. 14A); clypellus in profile evenly
 convex, continuing contour of frontoclypeus (Fig. 14B);
 known distribution: western United States.....*Xyphon triguttatum*
- 6a. Head typically with more dark areas than single spot
 near anterior margin of crown (Fig. 8F);
 clypellus in profile not following angle of
 frontoclypeus (Fig. 12B); known distribution: southern
 United States south through Brazil, Caribbean islands,
 introduced into western Africa, and various Pacific islands
 including Hawaii, Guam, Taiwan, and Japan.....*Xyphon reticulatum*

Notes on Conventions Found in Species Re-descriptions

Various conventions are followed in the species re-descriptions below. First, in cases with a number of specimens coded (all species except *X. n. sp. 1*, percentages of each character state found in the given specimen were calculated as detailed in the

character coding section. In cases where all coded individuals possessed the same state no percentage was given.

Host plant data is based on specimen labels and is not meant to be an exhaustive list.

I examined all primary type specimens unless otherwise noted. Additionally, I recorded verbatim locality label data from all primary types. I used a “/” to denote a line break on the same label and a “//” to denote lines on a different label.

Xyphon flaviceps (Riley 1880)

(Figs.: 7A, 8A, 9)

Diedrocephala flaviceps Riley 1880

Tettigonia flaviceps (Riley 1880): Johnson and Fox 1892

Carneocephala flaviceps (Riley 1880): Nottingham 1932

Xyphon flaviceps (Riley 1880): Hamilton 1985

Diagnosis: This is a relatively large species (female 5.0–6.3 mm; male 4.5–5.0 mm).

The crown lacks dark marking and forewings have densely reticulate crossveins at the apex. Distinguishable from *Xyphon fulgidum* by the presence of larger ocelli which are separated by a distance of less than 7 times the ocellar width and located on the head less than 2 times the ocellar width from the edge of the crown.

Head: Clypellus-frontoclypeus junction, lateral view evenly convex (57%) or distinctly angular (43%); frontoclypeus mottled yellow and tan; crown rounded (96%)

or angular (4%); with white band typically present, but usually broken by face color (65%), less commonly absent (22%) or complete (13%), crown, median spot, absent, dark markings (other than median spot) on crown also absent, crown lacking dark line; medioapical macula of crown absent or poorly delimited; crown, orange pigment present; postocellar maculae absent or weak; crown concave (17%) or flat (83%). Distance from ocelli to lateral edge of head no more than 2 times ocellar width and distance between ocelli no more than 7.5 times ocellar width.

Thorax: Pronotum lacking dark green to brown circular markings at anterior margin; circular indentations on pronotum absent; midline of pronotum concolorous with lateral parts of pronotum (83%) or white (17%). Color of mesonotum green. Visible part of mesonotum unmarked; proepisternum, posterior edge, not irregular.

Forewings: Green pigment on wings; wings mostly green (78%) or gray (22%); anal veins green (96%) or pale blue (4%). Apex with many crossveins.

Legs: Hind femur, macrosetal formula 2+1 (96%) or 2+1+1 (4%). Plantar surface of hind tarsosome, paleate setae variable most commonly 1–3 (65%) but less commonly 4–5 (17%) or 0 (9%).

Abdomen: Abdominal sterna of male mostly yellow.

Male Genitalia

External: Pygofer, basolateral setae, scattered. Subgenital plate, macrosetae, small and scattered; subgenital plate without long, fine setae dorsally. Pygofers and subgenital plates, setae present.

Internal: Aedeagal shaft, lateral view, dorsal process acute and compressed or not. Dorsal process, wider than tall or taller than wide. Shaft, in ventral view ovoid, narrow or broad. Shaft, dorsal view not compressed. Aedeagus, ventral phalange, not distinct. Paraphyses, dorsal view, oval or forming “U”. Style, 1 setae per side.

Material Examined: I coded 14 males and 9 females. Approximately 1,000 additional specimens were examined.

Host plants: Collected from cotton (*Gossypium hirsutum*), cucumber (*Cucumis sativus*), alfalfa (*Medicago* sp.), beebalm (*Monarda* sp.), prickly Russian thistle (*Salsola tragus*), miscellaneous flowers, weeds, and pasture.

Distribution: Eastern and Central United States from Gulf Coast as far north as Wisconsin. Also, found in Mexico (Fig. 9F).

Primary types: Cotypes located in the USNM. I am designating one of these specimens to be the lectotype. Type is a male in good condition, appears to have been removed from a series of *X. flaviceps* all mounted on single pin. Verbatim label data: Feb, 9/76 / Texas// injuring wheat + oats / Texas Jan 1 76

Other notes: This species was at one time incorrectly synonymized by Ball with *X. reticulatum*, so it is common to see determination labels reflecting this.

Xyphon fulgidum (Nottingham 1932)

(Figs.: 7B, 8B, 10)

Carneocephala fulgida Nottingham 1932

Xyphon fulgida (Nottingham 1932): Hamilton 1985

Diagnosis: A large leafhopper (female 5.5–6.0 mm; male 4.5–5.0 mm) lacking dark markings on the head. The wings are similar to *X. flaviceps* from which it can be distinguished by the comparatively smaller ocelli (distance between ocelli greater than 7 times ocular width and ocelli located more than 2 times ocular width from edge of crown).

Head: Clypellus-frontoclypeus junction, lateral view, distinctly angular (90%) or evenly convex, (10%); frontoclypeus entirely yellow (possibly with brown muscle scars). Crown, medioapical macula absent or poorly delimited. Crown, anterior margin, angular; white band along boundary with the face either complete (43%), present but broken by face color (43%), or absent (14%); median spot absent (100%). Crown lacking dark markings or lines; crown, orange pigment, absent. Postocellar maculae absent or weak. Crown, lateral view, concave. Distance from ocelli to lateral edge of head more than 2 times ocelli width and distance between ocelli is at least 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular markings absent; circular indentations absent (90%) or present (10%); midline of pronotum concolorous with lateral areas of pronotum. Mesonotum, green. Mesonotum, visible areas, unmarked. Proepisternum, posterior edge, not irregular (62%) or irregular (38%).

Forewings: Green pigment present; wing mainly green; anal veins green. Apex with many crossveins.

Legs: Hind femur, macrosetal formula 2+1. Plantar surface of hind tarsomere, paleate setae, 4–5.

Abdomen: Sterna of male mostly yellow (100%).

Male Genitalia

External: Pygofer basolateral setae, scattered and erect; subgenital plate, macrosetae and long fine dorsal setae absent; pygofers and subgenital plates, setae, present.

Internal: Aedeagal shaft, lateral view, dorsal process acute, not compressed, wider than tall; ventral view broadly ovoid; shaft, dorsal view not compressed. Ventral phalange not distinct. Paraphyses, dorsal view, form “U”. Style, single setae per side.

Material Examined: I coded 11 males and 10 females. Additionally, approximately 100 specimens were examined.

Host plants: Collected from vinegarweed (*Trichostema lanceolatum*)

Distribution: Known only from California (Fig. 10F).

Type: holotype (and 85 paratypes) deposited in the Snow Entomological Collection, University of Kansas. Holotype is a male in good condition. Verbatim label on holotype: Lemon Grove / Calif. 7-24-29 / B. H. Beamer.

Xyphon gillettei (Ball 1901)

(Figs.: 7C, 8C, 11)

Draeculacephala gillettei Ball 1901

Carneocephala gillettei (Ball 1901): (Ball 1927)

Carneocephala balli Knull 1940 – NEW SYNONYM

Xyphon gillettei (Ball 1901): Hamilton 1985

Xyphon balli (Knull 1940): Hamilton 1985

Diagnosis: A robust leafhopper typically with brown markings on crown. Macrosetal formula of hind femur 2+0. Aedeagus with dorsal process not compressed (much wider than tall).

Head: Clypellus-frontoclypeus junction, lateral view, convex; frontoclypeus entirely yellow (possibly with brown muscle scars) (96%) or mottled yellow and tan (4%).

Crown, anterior margin, rounded; white band absent; median spot present, but poorly defined (56%) or present and well defined (44%); crown, medioapical macula, brown but poorly delimited (84%) or dark brown and well defined (16%) which is almost always surrounded by cream. Dark markings (other than median spot) on crown

present; crown patterned variably, with light brown lines concentrated medially, crown, orange pigment, absent; postocellar maculae absent or weak (96%) or large and well developed (4%). Crown, lateral view, concave. Distance from ocelli to lateral edge of head more than 2 times ocelli width and distance between ocelli at least 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular markings absent; circular indentations present; midline variably white (72%), or concolorous with lateral areas of pronotum (28%). Mesonotum, straw colored, visible parts unmarked (72%), very lightly marked (12%), with submedial spots and anterolateral triangles (8%), or anterolateral triangles only (8%); proepisternum, posterior edge, not irregular (92%) or irregular (8%).

Forewings: Green pigment typically absent (96%) but rarely present (4%); wing majority colored straw (96%) or less commonly green (4%), anal veins white (52%) or forewing pale blue (48%). Apex, with few crossveins at apex (but more than 3).

Legs: Hind femur, macrosetal formula 2+0. Plantar surface of hind tarsomere, paleate setae numbering 1–3 (4%) or 4–5 (96%).

Abdomen: Sterna of male mostly red/orange (83%) or mostly yellow (17%).

Male Genitalia

External: Pygofer, basolateral setae, scattered and erect (75%) or absent (25%).

Subgenital plate, macrosetae, large, forming a distinct band (82%) or small and

scattered (18%); long fine dorsal setae absent. Pygofer and subgenital plates, setae, present.

Internal: Aedeagal shaft, lateral view, dorsal process, acute, not compressed (so wider than tall). Shaft in ventral view, narrow, basolateral expansions distinct. Shaft, dorsal view, not compressed. Paraphyses, dorsal view, forming a circle, an oval; or forming a “U”. Style, single setae on each side.

Material Examined: I coded 12 males, 11 females, and 1 unknown. Additionally, 5 additional specimens were made available for examination at the completion of this project.

Host Plants: *Salicornia* sp. and *Suaeda* sp.

Distribution: Known from Colorado and Arizona (Fig. 11 F).

Types: Lectotype at the USNM. Verbatim label for *Draeculacephala gillettei*: N. Colo / 3 20 '98. Lectotype is a male in good condition. Label under specimen notes designated by P. W. Oman (1946), but this paper has not been located, so I am designating this specimen the lectotype. In case a paper is later found identifying the lectotype, I have chosen to use the same specimen.

Verbatim label for *Carneocephala balli*: Holbrook, Ar. / VII- 28-38 // D.J. and J. N. Knull Collrs. Male in good condition, genitalia cleared and stored in glycerin under specimen.

Reasons for synonymy: I determined *balli* was a junior synonym of *Xyphon gillettei* due to there being little morphological difference between the 2 species. The original description notes that *balli* resembles *gillettei* but is smaller. The original description did not include any genitalia examination; in fact the holotype was not dissected. Dissection revealed genitalia identical to *gillettei*. While members of *balli* tend to be bit smaller this could easily be due to natural events such as temperature. Additionally, there are specimens of intermediate size adding further evidence to synonymy. Based on study of the types and series of specimens for each species, I could not find any reason to justify 2 separate species.

Xyphon nudum (Nottingham 1932)

(Figs.: 7D, 8D, 12)

Carneocephala nuda Nottingham 1932

Xyphon nuda (Nottingham 1932): Hamilton 1985

Diagnosis: This species is smaller (female 4.5 mm; male 4.0 mm) with head narrower than the pronotum. *Xyphon nudum* is easily recognizable due to its completely unpatterned crown (which is often orange), pronotum, and mesonotum. The wings are dark green with yellowish-green veins.

Head: Clypellus-frontoclypeus junction, lateral view, evenly convex (14%), or distinctly angular (76%); frontoclypeus, color pattern, mottled yellow and tan (69%) or entirely yellow (possibly with brown muscle scars) (21%) or uniformly tan (muscle

scars appearing slightly darker) (10%). Crown, angular (79%) or rounded (21%); white band present and complete (55%) or present but broken by face color (41%), rarely absent (3%); median spot absent; medioapical macula, absent or poorly delimited (72%) or entirely yellow or yellow with brown spot (28%). Dark markings (other than median spot) on crown absent; dark lines absent; crown, orange pigment, present (93%) or absent (7%). Postocellar maculae, absent or weak. Crown, lateral view, flat. Distance from ocelli to lateral edge of head no more than 2 times ocelli width and distance between ocelli no more than 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular markings, absent; circular indentations absent; midline of pronotum white (93%) or concolourous with lateral areas of pronotum (7%). Mesonotum, green (90%) or tan (10%), visible part unmarked (90%) or with pair of submedial spots (10%); proepisternum, posterior edge, not irregular (72%) or irregular (28%).

Forewings: Green pigment, present; wings, mainly green (90%) or tan (10%), anal veins white. Apex, with few crossveins.

Legs: Hind femur, macrosetal formula 2+1. Plantar surface of hind tarsomere, paleate setae numbering 1–3 (3%) or 4–5 (97%).

Abdomen: Abdominal sterna of male mostly yellow.

Male Genitalia

External: Pygofer, basolateral setae, scattered, erect. Subgenital plate, macrosetae, small, scattered; long fine dorsal setae absent.

Internal: Aedeagal shaft, lateral view, dorsal process, acute and compressed, taller than wide; ventral view, narrowly ovoid (without distinct angles); dorsal view, shaft not compressed. Paraphyses, dorsal view, forming a circle, oval, or U shape. Style, 1, rarely 2 setae per side.

Host Plants: No data available.

Material Examined: I coded 14 males, 15 females, and examined approximately 200 specimens.

Distribution: Southwestern United States and Mexico (Fig. 12F).

Primary Types: Holotype, Snow Entomological Collection. Holotype is a male in good condition. Verbatim locality label on holotype: Pima Co. Ariz / July 27, 1927 / P.A.

Radio

Xyphon reticulatum (Signoret 1854)

(Figs.: 7E, 8E, 8F, 13)

Tettigonia reticulata Signoret 1854

Tettigonia (Diedrocephala) sagittifera Uhler 1895 – NEW SYNONYM

Tettigonia diducta Fowler 1900 - NEW SYNONYM

Draeculacephala reticulata (Signoret 1854): Ball 1901

Draeculacephala sagittifera (Uhler 1895): Olsen 1918

Tettigonia dyeri Gibson 1919 – NEW SYNONYM

Carneocephala sagittifera (Uhler 1895): Ball 1927

Carneocephala dyeri (Gibson 1919): Nottingham 1932

Carneocephala diducta (Fowler 1900): Young 1977

Xyphon diducta (Fowler 1900): Hamilton 1985

Xyphon dyeri (Gibson 1919): Hamilton 1985

Xyphon reticulata (Signoret 1854): Hamilton 1985

Xyphon sagittifera (Uhler 1895): Hamilton 1985

Diagnoses: This species has a highly variable coloration with wings ranging from green to almost black. The head and crown can be solid colored (often tan) or marked with dark brown on a creamy background.

Head: Clypellus-frontoclypeus junction, lateral view, distinctly angular; color pattern of frontoclypeus mottled yellow and tan (16%) or mottled dark brown and yellow (84%). Crown, anterior margin, angular (97%) or rounded (3%); white band along edge of face complete (49%), splotched white and face color (46%), or absent (5%); crown, median spot, well defined (51%), poorly defined (24%), or absent (24%); medioapical macula, absent or poorly delimited (35%), entirely yellow or yellow with brown spot (5%), tan with darker markings (or uniformly tan (5%) or dark brown (54%); medial spot, completely surrounded by cream pigment (53%), lacking medial

spot (26%), or not surrounded by cream pigment (21%); dark markings (other than median spot) on crown absent (68%) or present (32%); dark lines, mostly brown with light patches (43%), absent (24%), irregular brown spots (22%), medioapical macula only (8%), or light brown lines (concentrated in middle of the crown) (3%), crown, orange pigment absent (95%) or present (5%). Postocellar maculae, absent or weak (59%) or part of a broader pattern (41%). Crown, lateral view, convex. Ocelli relatively large: from ocelli to lateral edge of head no more than 2 times ocelli width and distance between ocelli no more than 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular marking present (78%) or absent (22%) circular indentations absent (95%) or present (5%); midline white (92%) or concolorous with lateral areas of pronotum (7%). Mesonotum green, visible parts with submedial spots and anterolateral triangles (53%), very lightly marked (42%), unmarked (3%), or with pair of submedial spots (3%). Transpleural macula, incomplete and poorly delimited (84%) or absent (16%). Proepisternum, posterior edge, not irregular (89%) or irregular (11%). Thoracic sterna of male yellow (80%) or meosternum with brown longitudinal macula (20%).

Forewings: Green pigment, absent (89%) or present (11%). Wing overall color, black/brown (47%), gray (39%), green (11%), or straw (5%). Anal veins green (92%), or white (8%). Apex with few crossveins.

Legs: Hind femur, macrosetal formula, 2+1. Plantar surface of hind tarsomere, paleate setae, number 0 (3%) or 4–5 (97%).

Abdomen. Abdominal sterna of male mostly yellow.

Male Genitalia

External: Pygofer, erect basolateral setae, scattered (97%) or absent (3%). Subgenital plate, macrosetae, scattered (91%) or in a distinct band (9%); lacking long, fine dorsal setae.

Internal: Aedeagal shaft, lateral view, dorsal process, acute, compressed; taller than wide (96%) or wider than tall (4%). Shaft, ventral view, arrow-shaped dorsal view not compressed. Paraphyses, dorsal view, form oval (61%), “U” (26%), or circle (13%). Style, 1 (97%) or 2 (3%) setae per side.

Material Examined: I coded 36 males and 6 females. Additionally, I examined approximately 5,000 specimens.

Host Data: Collected from bermudagrass (*Cynodon dactylon*).

Distribution: This species is widespread ranging from the southern tier of states in the US south through Central America to Brazil. It also is found in the Caribbean. This species has been accidentally introduced in a number of countries including Guam and other Pacific Islands and western Africa (Fig. 13F).

Type: A holotype (which was not available for this revision) is located at the Naturhistorisches Museum Wien (Austria) according to Nottingham (1927).

Cotypes of *Tettigonia (Diedrocephala) sagittifera* at the USNM. Verbatim locality label: St. Vincent / W.I / H.H. Smith / 17 // Co-Type/ No. 10212/ U.S.N.M. I am designating one of these specimens as the lectotype.

Cotypes of *Tettigonia diducta* at the USNM. I am designating one of these the lectotype. Verbatim locality label: Amula / Guerreio 6000 ft / Aug. H. H. Smith // *Biol. Centr. Am., Homop.*

Holotype of *Tettigonia dyeri* verbatim locality label: Honduras / Tegucigulpa // June / 29 78 // FJDyer / Coll // 71612 / 42620 // Type number: 22114

Reasons for synonymy: Based on a morphological study of specimens from North and South America in addition to Guam and western Africa, I determined that there was no reliable way to differentiate between the species. Additionally, upon examination of insects introduced to areas outside their natural range the variation exhibited was similar to the variation across the 4 species. Since all the forms appeared to integrate into each other, I synonymized the species. Additional support was found in phylogenetic Analysis II and III where specimens from 3 of the 4 included species are OTUs. In these analyses, representatives form a clade. Lastly, a parsimony analysis including multiple specimens from all 4 former species was run in TNT. This analysis showed all members of the group formed a distinct clade but representatives of the various species did not group with other members of their former species.

Xyphon triguttatum (Nottingham 1932)

(Figs.: 7F, 8G, 8H, 14)

Carneocephala triguttata Nottingham 1932

Xyphon triguttata (Nottingham 1932): Hamilton 1985

Diagnosis: This is a large (female 5.4 mm; male 4.2 mm) leafhopper. The crown is lightly colored with a conspicuous dark brown to black spot on the crown.

Head: Clypellus-frontoclypeus junction, lateral view, evenly convex; color pattern of frontoclypeus entirely yellow (possibly with brown muscle scars) (55%) or mottled yellow and tan (45%). Crown, anterior margin, angular (90%) or rounded (10%); white band present but broken by face color (41%), absent (41%), or complete (17%); median spot present and well defined (93%) or present, but poorly defined (7%); medioapical macula of dark brown and surrounded by light pigment. Dark markings (other than median spot) on crown absent; medioapical macula present; crown, orange pigment, present (93%) or absent (3%); postocellar maculae, absent or weak. Crown, lateral view, flat (97%) or rarely concave (3%). Distance from ocelli to lateral edge of head no more than 2 times ocelli width and distance between ocelli no more than 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular markings, absent; circular indentations, absent (97%) or present (3%); midline of pronotum, white (76%) or concolorous with lateral areas of pronotum (24%). Mesonotum, green; visible parts unmarked; proepisternum, posterior edge, irregular (52%) or not irregular (48%).

Forewings: Green pigments present (97%) or absent (3%); main color green (86%) or gray (7%) or black/brown (7%). Apex with few crossveins. Anal veins white (69%) or pale blue (31%).

Legs: Hind femur, macrosetal formula 2+1 (93%) or rarely 2+0 (3%). Plantar surface of hind tarsomere, paleate setae numbering 1–3 (46%) or 4–5 (54%).

Abdomen: Abdominal sterna of male mostly yellow.

Male Genitalia

External: Pygofer, erect basolateral setae, absent (71%) or small and scattered (21%).

Subgenital plate, macrosetae, absent (36%) or small and scattered (64%); long fine dorsal setae absent.

Internal: Aedeagal shaft, lateral view, dorsal process, acute, compressed, taller than wide. Shaft, ventral view, arrow shaped, basolateral angles distinct. Shaft, dorsal view, not compressed. Paraphrases, lateral view, almost forming a circle, an oval, or forming a U. Style, single setae per side.

Material Examined: I coded 17 males, 12 females and examined approximately 300 specimens.

Host Data: alfalfa (*Medicago* sp.), sideoats grama (*Bouteloua curtipendula*), prickly Russian thistle (*Salsola tragus*), bermudagrass (*Cynodon dactylon*), desert pepperweed (*Lepidium fremontii*), sickle saltbush (*Atriplex falcata*) and saltgrass (*Distichlis spicata*)

Distribution: Western United States (Fig. 14F.).

Primary Types: Holotype and 32 paratypes, Snow Entomological Collection. Holotype is a male in good condition. Verbatim locality label: Coachella Calif / 7-15-30 / David G. Hall.

Xyphon n. sp. 1

(Figs.: 7G, 8I, 15)

Diagnosis: A robust leafhopper typically with brown markings on the crown similar to *X. gillettei*, but with wider markings on head and at most 2 crossveins on apex of wing. Macrosetal formula of hind femur 2+1. Aedeagus with dorsal process not compressed (much wider than tall).

Head: Clypellus-frontoclypeus junction, lateral view, evenly convex; frontoclypeus entirely yellow (possibly with brown muscle scars). Crown, anterior margin, rounded; white band, complete or absent; median spot, present and well defined; medioapical macula, dark brown and well defined; almost always surrounded by cream. Dark markings (other than median spot) on crown, present; with irregular brown spots or a brown background with light patches; crown, orange pigment absent; postocellar maculae, absent or well developed. Crown, lateral view, concave. Distance from ocelli to lateral edge of head more than 2 times ocelli width and distance between ocelli at least 7.5 times ocelli width.

Thorax: Pronotum, dark green to brown circular markings, present; circular indentations, present; midline of pronotum, white. Mesonotum, straw visible part with

submedial spots and anterolateral triangles or very lightly marked; proepisternum, posterior edge, irregular.

Forewings: Green pigment, absent; wing mostly straw, anal veins pale blue. Apex with 2 crossveins.

Legs: Hind femur, macrosetal formula 2+1. Plantar surface of hind tarsomere, paleate setae numbering 4–5.

Abdomen: Sterna of male mostly yellow.

Male Genitalia

External: Pygofer, erect basolateral setae, scattered. Subgenital plate, macrosetae, forming a distinct band; long fine dorsal setae absent. Pygofers and subgenital plates, setae, present.

Internal: Aedeagal shaft, lateral view, dorsal process, acute, not compressed; wider than tall; shaft, ventral view, narrow, basolateral expansions distinct; shaft, dorsal view, not compressed. Paraphyses, dorsal view, forming an oval. Style, single setae per side.

Material Examined: I coded 2 males. An additional male was available, but it appeared to be parasitized and lacked normal genitalia. A total of 5 specimens were available for this species.

Host Plants: No data available.

Distribution: Known from Mexico (Fig. 15F). Holotype verbatim label: Mexico: Zac: rt23 31km / S Fresnillo, 2300m / N22.90645 W102.93929 / 23-x-2005, C.H.Dietrich / MX05-3303 sweeping". 4 paratypes, 3 at Illinois Natural History Survey: 2 with identical label as above; 1 with MEXICO: Jalisco, rt.80 / km#149 NE Lagos de Moreno / 1875m,21°22'N101°53'E / 18 Oct 2001,G. Moya-Raygoza / sweeping this is collecting event MX 01-17 GMR,. 1 at the Canadian National Collection: San Juan Del Rio / 10 Mi. E. Quere Taro / Mex. 30- VII-1954 / J. G. Chillcott (Fig 15F)

Types: Holotypes and all paratypes except the one from San Juan Del Rio are deposited at the Illinois Natural History Survey, the remaining type deposited at CNC. The holotype is a cleared male in good condition with genitalia in vial under specimen.

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APPENDIX 1.

CODED MORPHOLOGICAL DATA FOR ALL SPECIMENS USED IN
PHYLOGENETIC STUDY.

Specimen numbers refer to individual number affixed by me to each specimen. For characters that could not be coded because the structure was absent, I used a “?” to denote this.

Taxa	Sex	Specimen Number	1	10	11	20	21	30	31	40	41	47
Chlorogonalia	M		00??014001	?1120011?1	?11??1?200	0?02021100	1110010					
D. angulifera	M		0112001211	1112000101	0111000101	3011020104	0001010					
D.clypeata	M		1162001221	1111000121	2014000110	0102020216	1100000					
D. soluta	M		1130001221	1001000111	3116000100	0002020220	1110000					
Plesiommata	M		0042114021	1100001001	2018431101	0001011101	1100010					
Syncharina	M		0012114121	0002101021	3018020201	0002021101	1110010					
flaviceps	F	3732	0001110200	00020010?1	0117000000	1?????????	?????????					
flaviceps	F	517	0101110200	00010010?1	0117000000	1?????????	?????????					
flaviceps	F	2394	0001110200	00010?10?1	0117000000	0?????????	?????????					
flaviceps	F	105	0101110200	00010?10?1	0116000000	0?????????	?????????					
flaviceps	F	3568	0001110200	00020?10?1	0114000000	1?????????	?????????					
flaviceps	F	4369	0001110200	00020?10?1	0117000000	1?????????	?????????					
flaviceps	F	2593	0102110200	00020?10?1	0116000000	1?????????	?????????					
flaviceps	F	14	0101110200	00020?10?1	0117000000	???????????	?????????					
flaviceps	F	2529	0000110200	00020?10?1	0117000001	1?????????	?????????					
flaviceps	M	3735	0112010200	0001001000	0107000000	1001010020	1110001					
flaviceps	M	4408	0012010200	0001001000	0107000000	1001010210	1110001					
flaviceps	M	1540	0012010200	0001001000	0107000000	1001010211	1100001					
flaviceps	M	45	0012010200	0001001000	0107000000	1001010211	1100001					
flaviceps	M	3569	0012010200	0001001000	0107000000	1001010211	1100001					
flaviceps	M	15	0112010200	0001001000	0107000000	1001010211	1100001					
flaviceps	M	710	0112010200	0001001000	0107000000	1001010211	1100001					
flaviceps	M	2595	0112010200	0001001000	0107000000	1001010211	1110001					
flaviceps	M	3623	0112010200	0001001000	0107000000	1001010211	1110001					
flaviceps	M	3612	0012010200	0001001000	0107000000	2001010211	1100001					
flaviceps	M	3727	0012010200	0001001000	0107000000	2001010211	1110001					
flaviceps	M	75	0012010200	0001001000	0107000000	2001010211	1100001					
flaviceps	M	3438	0100010200	0002001001	0117000000	20?????????	?????????					
flaviceps	M	2524	0001110200	0002001001	0117000000	???????????	?????????					
fulgidum	F	3262	0110010200	01110010?0	0117000000	2?????????	?????????					
fulgidum	F	556	0110010200	01110010?1	0117000000	2?????????	?????????					
fulgidum	F	2344	0010010200	01110?10?1	0117000000	2?????????	?????????					
fulgidum	F	1531	0111010200	01110?10?1	0117000000	2?????????	?????????					

Taxa	Sex	Specimen Number	1	10	11	20	21	30	31	40	41	47
fulgidum	F	1534	0110010200	01110?10?0	0117000000	2?????????	????????					
fulgidum	F	1537	0110010200	01110?10?1	0117000000	2?????????	????????					
fulgidum	F	1575	0110010200	01110?10?0	0107000000	2?????????	????????					
fulgidum	F	2310	0111010200	01110?10?1	0117000000	2?????????	????????					
fulgidum	F	2348	0112010200	01110?10?0	0117000000	2?????????	????????					
fulgidum	F	3261	0111010200	01110?10?1	0117000000	2?????????	????????					
fulgidum	M	2323	0112010200	0111001000	0107000000	2001010211	1110001					
fulgidum	M	291	0112010200	0111001000	0107000000	2001010211	1110001					
fulgidum	M	1524	0012010200	0111001000	0107000000	2001110211	1110001					
fulgidum	M	1527	0112010200	0111001000	0107000000	2001110211	1110002					
fulgidum	M	1573	0112010200	0111001000	0107000000	2001110211	1110001					
fulgidum	M	2332	0112010200	0111001000	0107000000	2001110211	1110001					
fulgidum	M	2334	0112010200	0111001000	0107000000	2001110211	1110001					
fulgidum	M	1626	0112010200	0111001000	0107000000	2001110211	1110001					
fulgidum	M	1533	01????????	?11??0????	??????????0	??0111????	????????					
fulgidum	M	2360	0111010200	0111001001	0117000000	2?????????	????????					
fulgidum	M	1760	0110010200	0111001001	0117000000	2?????????	????????					
gillettei	F	2351	0012110141	11110?10?1	0103501102	2?????????	????????					
gillettei	F	2361	0012110141	11110?10?1	0103501102	2?????????	????????					
gillettei	F	4520	0012110141	11110?10?1	0103531102	2?????????	????????					
gillettei	F	4515	0012110141	11110?10?1	0103000102	2?????????	????????					
gillettei	F	2355_3	0012110141	11110?10?1	0104531102	2?????????	????????					
gillettei	F	2355_4	0012114041	11110?10?1	0100531102	2?????????	????????					
gillettei	F	2358_3	0012110141	11110?10?1	0104501102	2?????????	????????					
gillettei	F	2358_4	0012110141	11110?10?1	0104501102	2?????????	????????					
gillettei	F	2359_2	0012110141	11110?10?1	0100501102	2?????????	????????					
gillettei	F	4521	0012110041	11110?10?1	0103501102	???????????	????????					
gillettei	F	2356_3	0012110041	11110?10?1	0104501102	???????????	????????					
gillettei	M	2355_1	0012110141	1111001001	0104501102	2200020212	0120001					
gillettei	M	2355_2	0012110141	1111001001	0104501102	2200020212	0120001					
gillettei	M	2356_2	0012114041	1111001001	0100531102	2201020212	0110001					
gillettei	M	4581	0012110141	1111001001	0103501102	2001020212	0100001					
gillettei	M	2358_1	0012110141	1111001001	0100501102	220101????	????????					
gillettei	M	2358_2	0012110141	1111001001	0104501102	220101????	????????					
gillettei	M	2356_1	0012110041	1111001001	0100501102	200102????	??20001					
gillettei	M	2359_1	0012110041	1111001000	0100501102	220102????	????????					
gillettei	M	2357_1	0012110041	1111001001	0104501102	220102????	????????					
gillettei	M	2357_2	0012110041	1111001001	0104531102	220102????	????????					
gillettei	M	2360	0002110141	1111001001	0104531102	220102????	????????					
gillettei	M	2352	??12110141	1??10?1001	010450110?	?2?????0212	0120001					
gillettei	U	4514	0012114041	11110?10?1	0103531102	2?????????	????????					
n.sp.1	M	4513	0010114021	1111001000	0004331202	2?01010212	0110001					
n.sp.1	M	3397	0012114031	1111101001	0004331202	22?????????	????????					
nudum	F	2754	0100010200	00020010?0	0116000100	2?????????	????????					
nudum	F	1510	0100010200	00020?10?1	0116000100	1?????????	????????					
nudum	F	3235_1	0100011200	00020?10?1	0116000100	2?????????	????????					
nudum	F	3235_2	0100010200	00020?10?1	0116000100	2?????????	????????					
nudum	F	3413	0100010200	00020?1001	0116000100	20?????????	????????					
nudum	F	3414	0101010200	00020?10?1	0110000100	2?????????	????????					
nudum	F	298	0110010200	00020?10?1	0116000100	2?????????	????????					

Taxa	Sex	Specimen Number	1	10	11	20	21	30	31	40	41	47
nudum	F	341	0100010200	00020?10?0	0116000100	2?????????	????????					
nudum	F	3480	0101011200	00020?10?1	0116000100	2?????????	????????					
nudum	F	377	0111110200	00020?10?0	0116000100	2?????????	????????					
nudum	F	3401	0110011200	00020?10?1	0116031100	2?????????	????????					
nudum	F	3632	0130011200	00020?10?1	0110101100	2?????????	????????					
nudum	F	3487	0?30010200	10020?10?0	0113131100	2?????????	????????					
nudum	F	365	0101110200	00020?10?1	0116000100	3?????????	????????					
nudum	F	3411	0101010200	00020?10?1	011600010?	?????????	????????					
nudum	M	3235_3	0000011200	0002001001	0116000100	2001010020	1100001					
nudum	M	3410	0000011200	0002001001	0116000100	2001010020	1100001					
nudum	M	3420	0000011200	0002001001	0116000100	2001010020	1100001					
nudum	M	1512	0100011200	0002001001	0116000100	2001010020	1120001					
nudum	M	300	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	350	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	294	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	368	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	369	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	373	0100011200	0002001001	0116000100	2001010020	1110001					
nudum	M	3235_4	0?00011200	0002001001	0116000100	2001010020	1110000					
nudum	M	3413	0100011200	00020?1001	0116000100	2001010020	1100001					
nudum	M	1632	0?00011200	00020?1001	0116000100	2001010020	1100001					
nudum	M	3626	0000011200	0002001001	0116000100	20????0020	1110001					
reticulatum	F	2586	0101014030	1000201001	0016020100	???????????	????????					
reticulatum	F	335	0160010230	10000?10?1	1016221100	2?????????	????????					
reticulatum	F	4446	0100010200	10000?10?1	1016221100	2?????????	????????					
reticulatum	F	2692	0161011030	10000?10?1	1006311100	2?????????	????????					
reticulatum	F	1396	0160011130	10000?10?0	0006231100	2?????????	????????					
reticulatum	F	2260	0161014030	10000?10?1	1016321100	2?????????	????????					
reticulatum	M	4434	0161010230	1000001001	1016321100	2001020020	1100002					
reticulatum	M	337	0160010200	1000001001	1116331100	2001010026	1110001					
reticulatum	M	371	0160010200	1000001001	1116331100	2001010026	1110001					
reticulatum	M	3244	0160010100	1000001001	1116331100	2001010026	1110001					
reticulatum	M	1395	0160010200	1000001001	1116331100	2001010026	1110001					
reticulatum	M	3189	0160010200	1000001001	1116331100	2001010026	1110001					
reticulatum	M	2719	0160010100	1000001001	1116331100	2001010026	1110001					
reticulatum	M	469	0160014031	1000201000	1017220100	2001010026	1110001					
reticulatum	M	3193	0100114150	0000001001	1016231100	2001010026	1110001					
reticulatum	M	3129	0161014031	1000201011	0010231100	2001010026	1110001					
reticulatum	M	1282	0161013150	1000001001	0016221100	2001010026	1110001					
reticulatum	M	1692	0160014031	1000201000	1016230100	2001010026	1110001					
reticulatum	M	1964	0161014031	1000201001	1016321100	2001010026	1120001					
reticulatum	M	2239	0100014021	1000001011	0016231100	2001010026	1120001					
reticulatum	M	2169	0161014031	1000201001	1016231100	2001010026	1120001					
reticulatum	M	2461	0161014030	1000201001	1013521100	?001010026	1110001					
reticulatum	M	1374	0161014030	1000201001	1017321100	?001010026	1100001					
reticulatum	M	3256	0161014031	1000201011	1016321100	?001010026	1120001					
reticulatum	M	1346	0?????????	?????????0?	???6221100	2001010026	1120001					
reticulatum	M	3772	0160010100	1000001001	1116331100	2001020026	1110001					
reticulatum	M	1640	0160010100	1000001001	1116331100	2001020026	1120001					
reticulatum	M	2110	0161014031	1000201010	1016231100	2001010116	1110001					

Taxa	Sex	Specimen Number	1	10	11	20	21	30	31	40	41	47
reticulatum	M	3628	0162010230	1000001001	1016321100	200101????	????????					
reticulatum	M	2796	0160010230	1000001001	1016321100	200101????	????????					
reticulatum	M	3199	0161014130	1000001001	1016321100	200101????	????????					
reticulatum	M	2276	0162014030	1000001001	1016321100	200101????	????????					
reticulatum	M	3135	0101014040	1000201000	1016221100	200101????	????????					
reticulatum	M	3192	0100013150	0000001001	1016221100	200101????	????????					
reticulatum	M	3127	0101014021	1000201001	1010231100	200101????	????????					
reticulatum	M	549	0161014031	1000201011	0016010100	2001110026	1100001					
reticulatum	M	2748	0160014031	1000201011	0165211000	????????	????????					
reticulatum	M	486	0161014031	1000201011	1016021100	20????????	????????					
triguttatum	F	3434	0011014050	00020?10?1	0110000100	1????????	????????					
triguttatum	F	1376	0012014050	00020?10?0	0100000100	1????????	????????					
triguttatum	F	1261	0002014050	00020?1000	0110000100	10????????	????????					
triguttatum	F	1220	0001114050	00020?10?0	0110000100	1????????	????????					
triguttatum	F	1226	0011014050	00020?10?1	0110000100	1????????	????????					
triguttatum	F	1246	0012014050	00020?10?1	0110000100	1????????	????????					
triguttatum	F	1090	0002014050	00020?10?1	0114000100	1????????	????????					
triguttatum	F	2996	0012014050	10010?10?0	0110000100	2????????	????????					
triguttatum	F	2954	0011014050	00020?10?1	0113000100	2????????	????????					
triguttatum	F	2769_4	0010114050	10020?10?1	0110000100	2????????	????????					
triguttatum	F	1082	0011014050	00020?10?0	0114000100	2????????	????????					
triguttatum	F	2350	0012114050	00020?10?0	0110000100	2????????	????????					
triguttatum	M	1232	0001014050	00020010?0	0114000100	1?00000026	0110001					
triguttatum	M	2998	0012014050	0002001001	0115000100	2000000026	0110001					
triguttatum	M	1093	0001014050	00020?10?0	0114000100	1?00000026	0110001					
triguttatum	M	1230	0002014050	0002001000	0110000100	1000010026	0110001					
triguttatum	M	3435	0011014150	00020010?1	0113000100	2?00010026	0110001					
triguttatum	M	1258	0002014050	0002001000	0110000100	2000010026	0110001					
triguttatum	M	1074	0002014050	0002001000	0110000100	2000010026	0110001					
triguttatum	M	1084	0012014050	0002001001	01100011?0	2000010026	0120001					
triguttatum	M	2936	0002014050	0002001001	0113000100	1001000026	0100002					
triguttatum	M	3433	0000014050	0002001000	0113000100	2001000026	0120001					
triguttatum	M	1379	0000014050	0002001000	011300010?	2?01000026	0120001					
triguttatum	M	2769_1	0011014150	00020010?1	0113000100	1?01010026	0110001					
triguttatum	M	1257	0002014050	0002001000	0110000100	2001010026	0110001					
triguttatum	M	1248	0002014050	0002001000	0110000102	2001010026	0110001					
triguttatum	M	3430	0002014050	00020?1000	0110000100	?001010026	0100001					
triguttatum	M	2769_2	0011014050	0002001000	0110000100	100001????	????????					
triguttatum	M	2769_3	0011014150	0002001001	0113000100	200001????	????????					

TABLE 1. Sequences of primers used for molecular analysis.

Locus	Primer	Sequence 5' → 3'	Citation
COI	COI	TTG ATT TTT TGG TCA TCC AGA AGT	Simon et al. (1994)
COI	3014	TCC AAT GCA CTA ATC TGC CAT ATT A	Simon et al. (1994)
Histone 3	HEX AF	ATG GCT CGT ACC AAG CAG ACG GC	Ogden and Whiting (2003)
Histone 3	HEX AR	ATA TCC TTG GGC ATG ATG GTG AC	Ogden and Whiting (2003)
NDI	NDI +1	ACA TGA ATT GGA GCT CGA CCA GT	Dietrich et al. (1997)
NDI	NDI -1	GAG TTC AAA CCG GCG TAA GCC AGG T	Dietrich et al. (1997)

TABLE 2. Cycling protocol used for PCR.

Step	Temperature	NDI and Histone	COI
1	94°C	3 minutes	3 minutes
2	94°C	1 minute	45 seconds
3	55°C	1 minute	90 seconds
4	72°C	2 minutes	2 minutes
		Repeat steps 2–4 27 times	Repeat steps 2–4 39 times
5	72°C	7 minutes	7 minutes

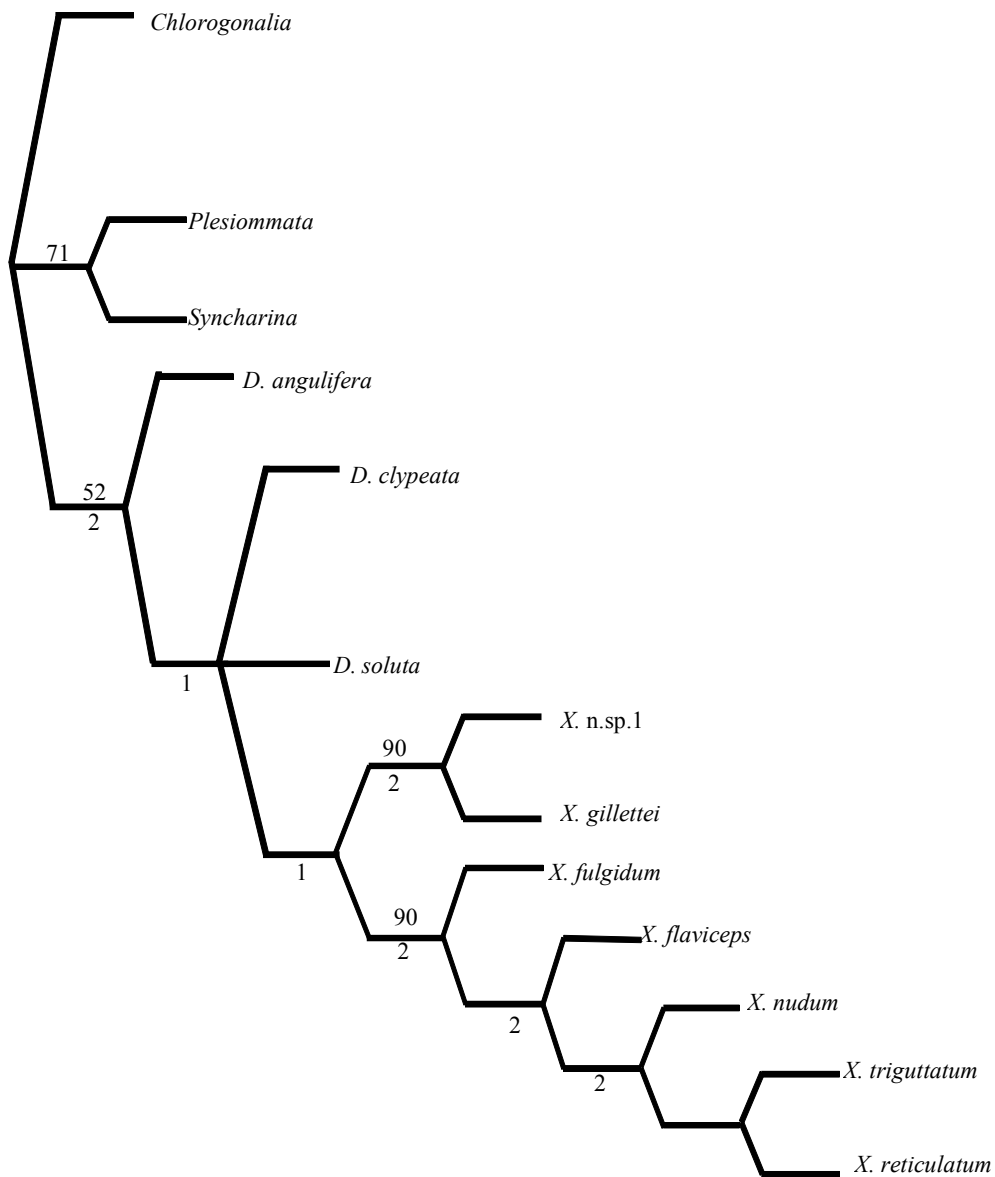


Figure 1: Strict consensus tree based on 2 equally parsimonious trees for 47 morphological characters (Analysis I). All characters unweighted and unordered. Tree Length: 146, CI: 0.57 and RI: 0.54. Boot strap values above 50 are shown above nodes, Bremer support values below nodes.

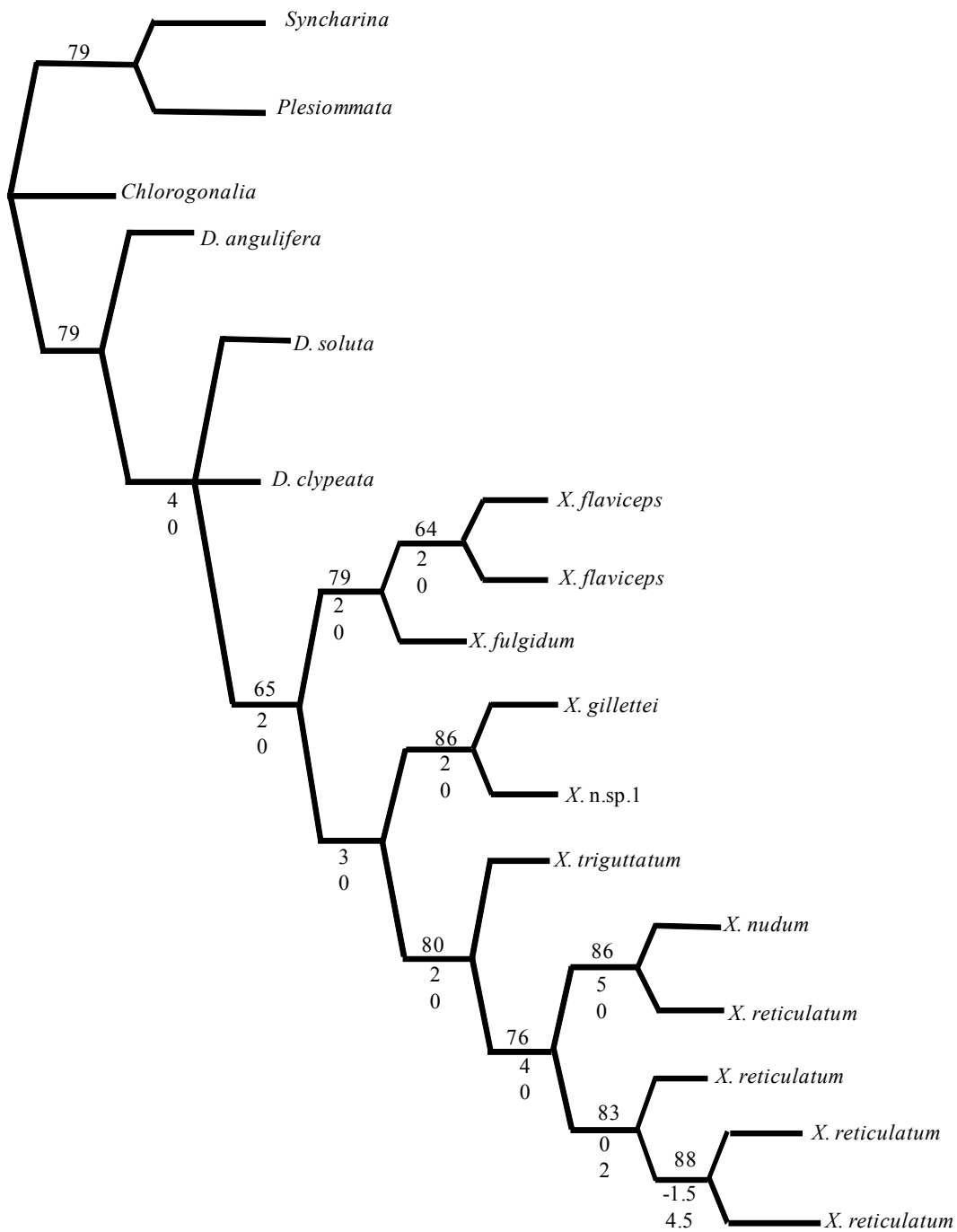


Figure 2. Strict consensus of 2 equally most parsimonious tree using combined morphology and NADH (Analysis II). Top numbers are bootstrap values (when over 50), bottom numbers are partitioned Bremer support values (upper number is morphology, lower number molecular). Tree length: 1044 CI: 0.727 RI: 0.559.

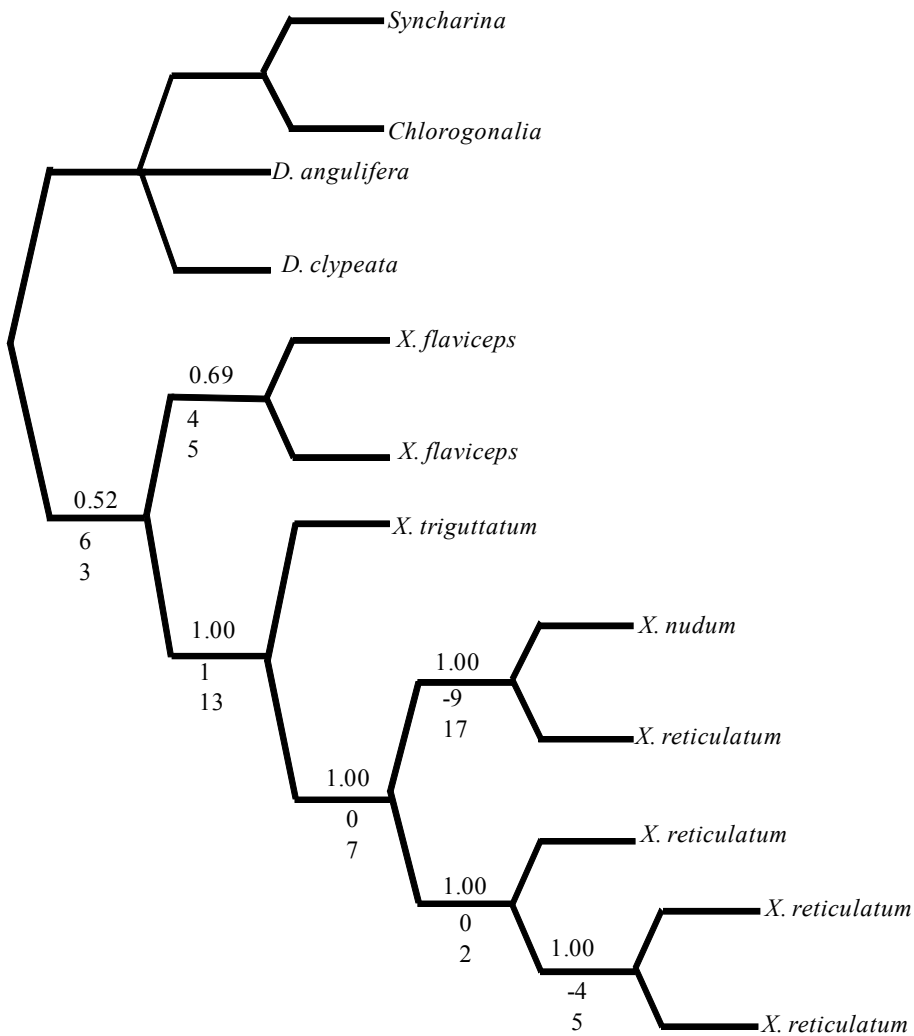


Figure 3: Results of a Bayesian analysis using 500,000 generations (Analysis III). Upper numbers are posterior probabilities; lower numbers are partitioned Bremer support (upper number morphology, lower number molecular). For settings see text.

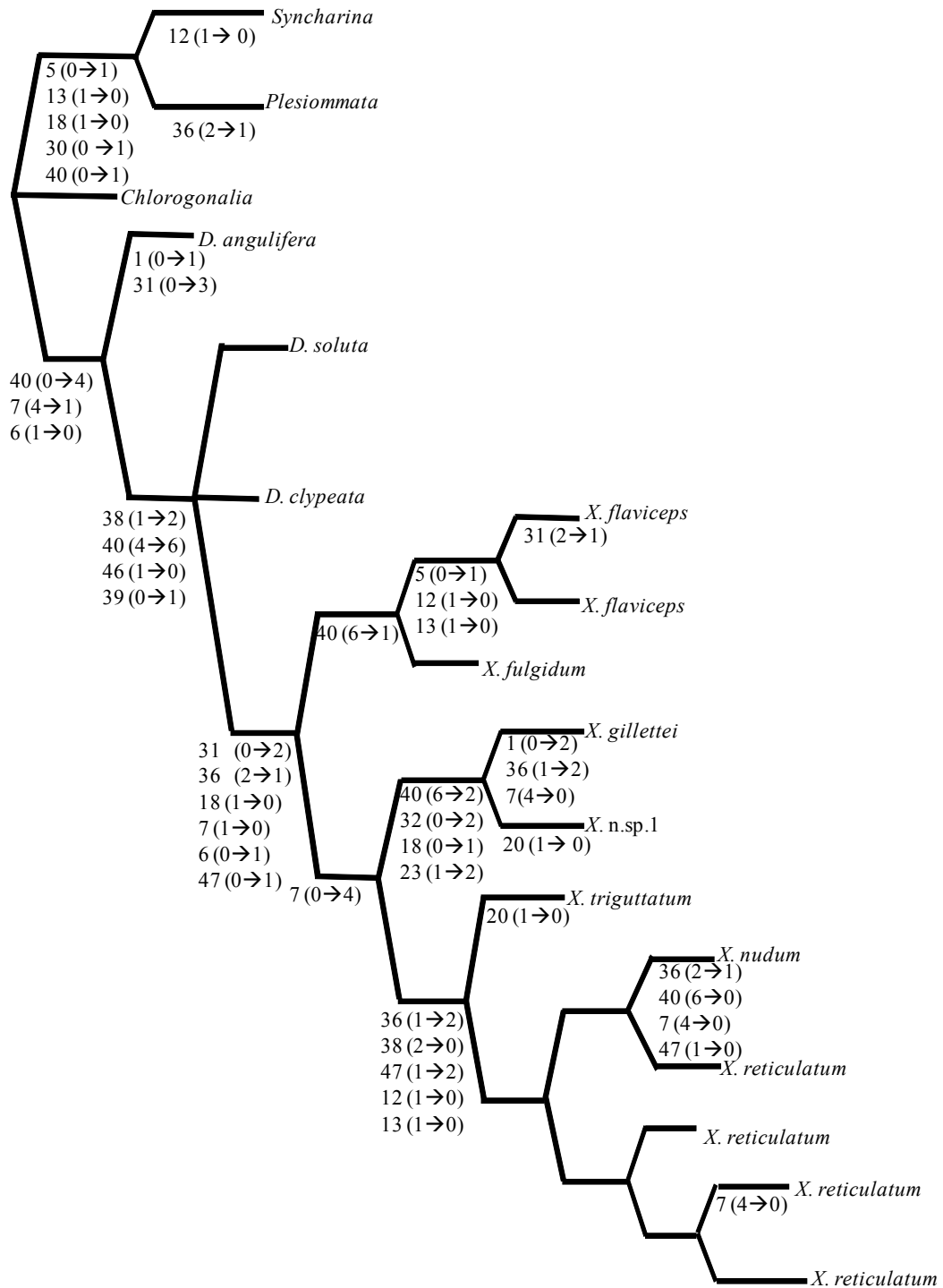


Figure 4. Map of unambiguous state changes plotted on tree from Analysis II.

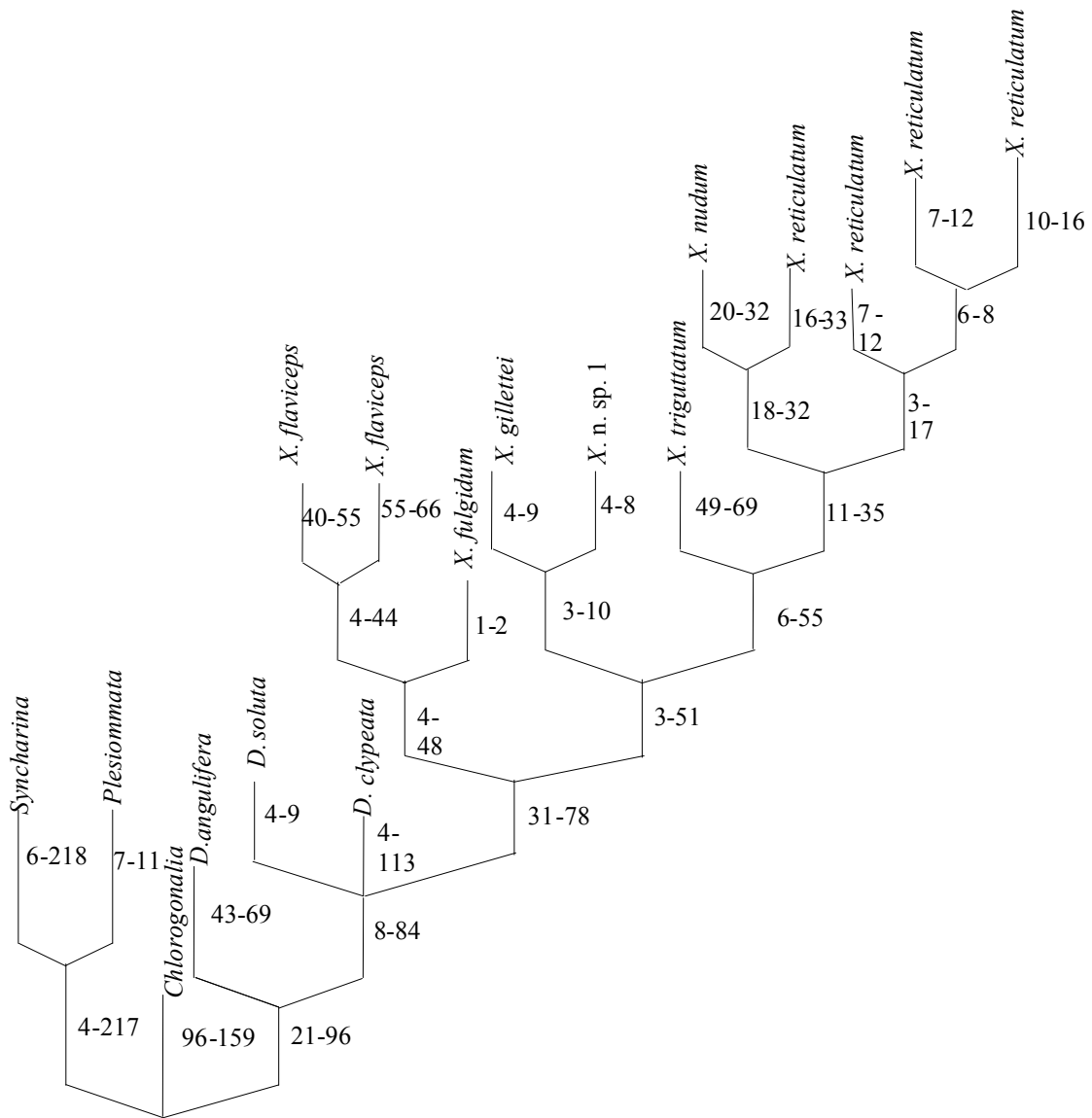


Figure 5. Maximum and minimum number of synapomorphies at each node based on all morphological and molecular characters.

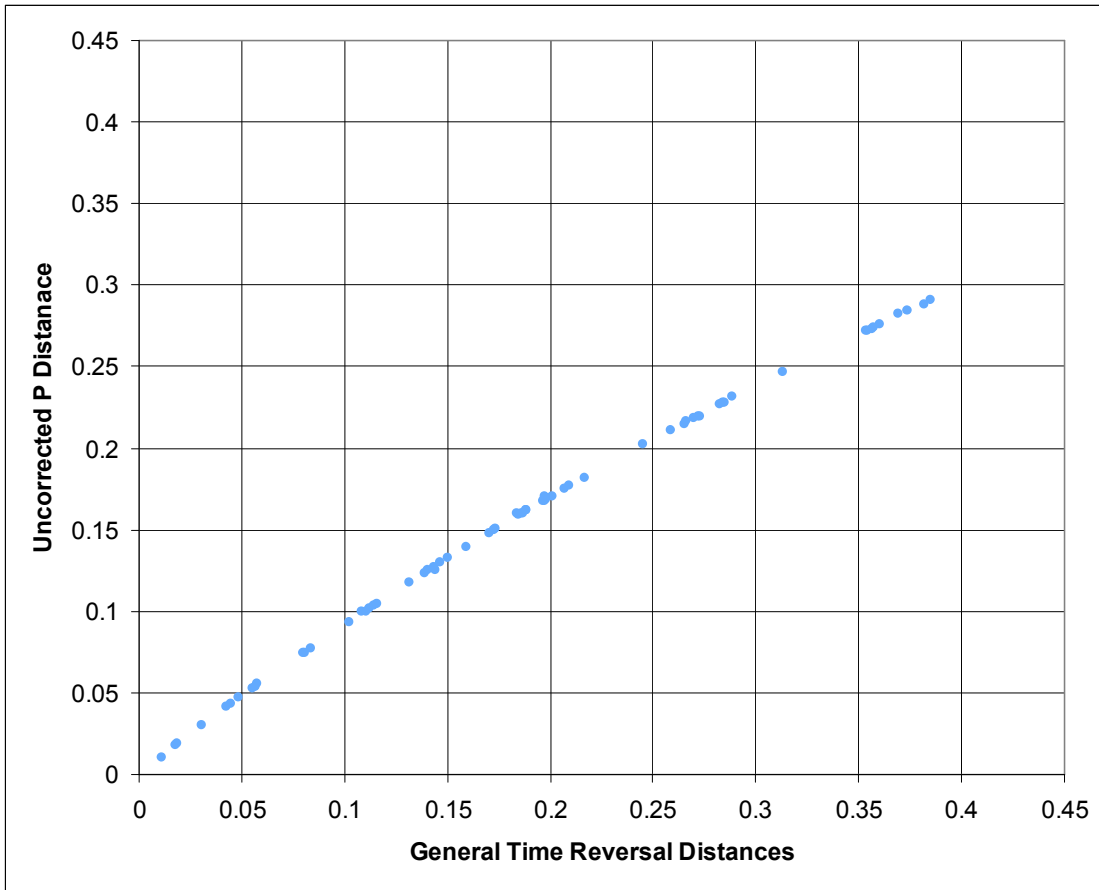


Figure 6. Saturation plot of NDI.

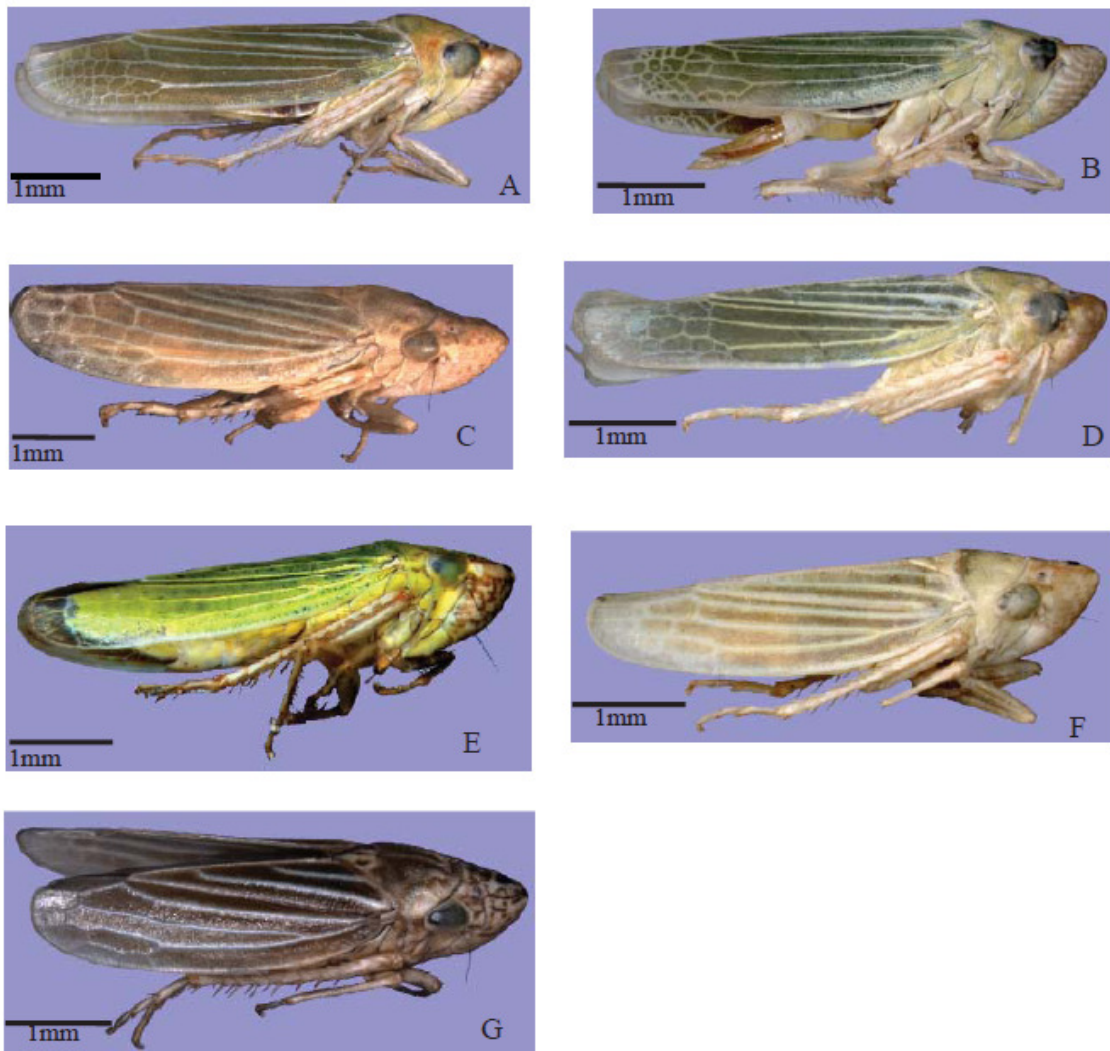


Figure 7: *Xyphon* species, lateral views.
A, *X. flaviceps*; B, *X. fulgidum*; C, *X. gillettei*; D, *X. nudum*; E, *X. reticulatum*; F, *X. triguttatum*; G, *X. n. sp. 1*.

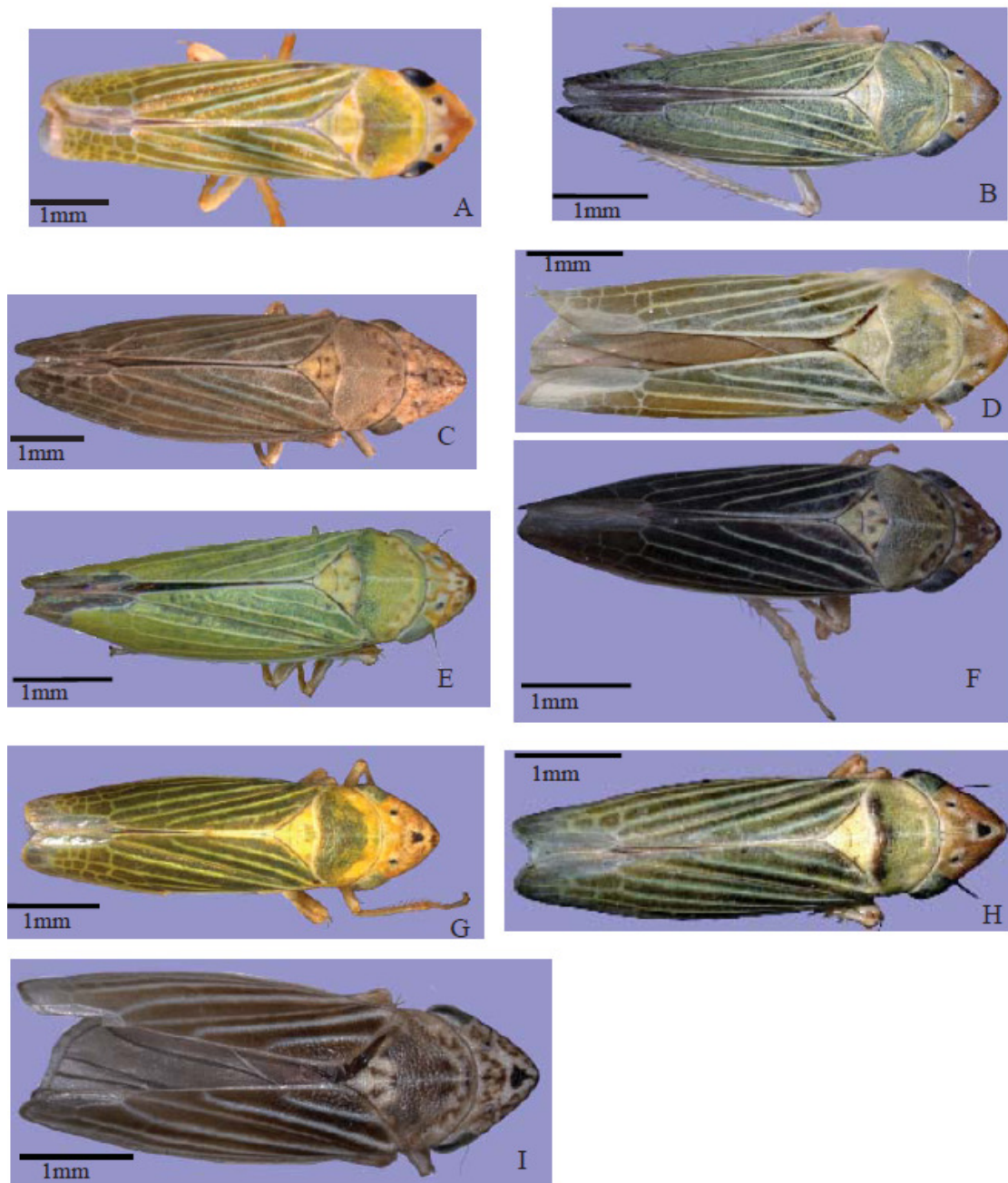


Figure 8: *Xyphon* species, dorsal views.

A, *X. flaviceps*; B, *X. fulgidum*; C, *X. gillettei*; D, *X. nudum*; E, *X. reticulatum*; F, *X. reticulatum*; G, *X. triguttatum*; H, *X. triguttatum*; I, *X. n. sp. 1*.

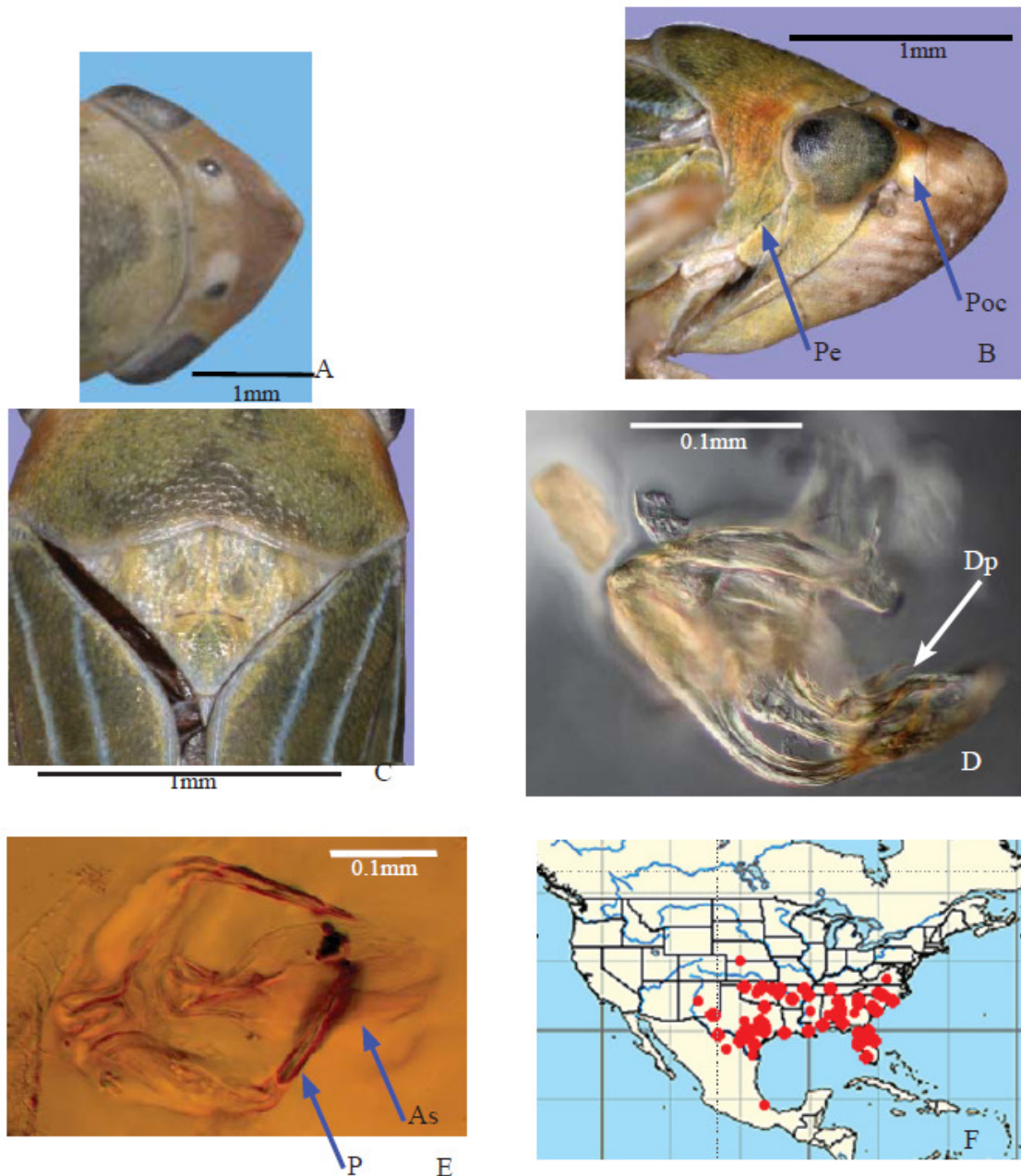


Figure 9: Photographs of characters used to distinguish *Xyphon flaviceps* with distribution map of specimens examined. A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal; D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P), preocular macula (Poc), proepisternum (Pe).

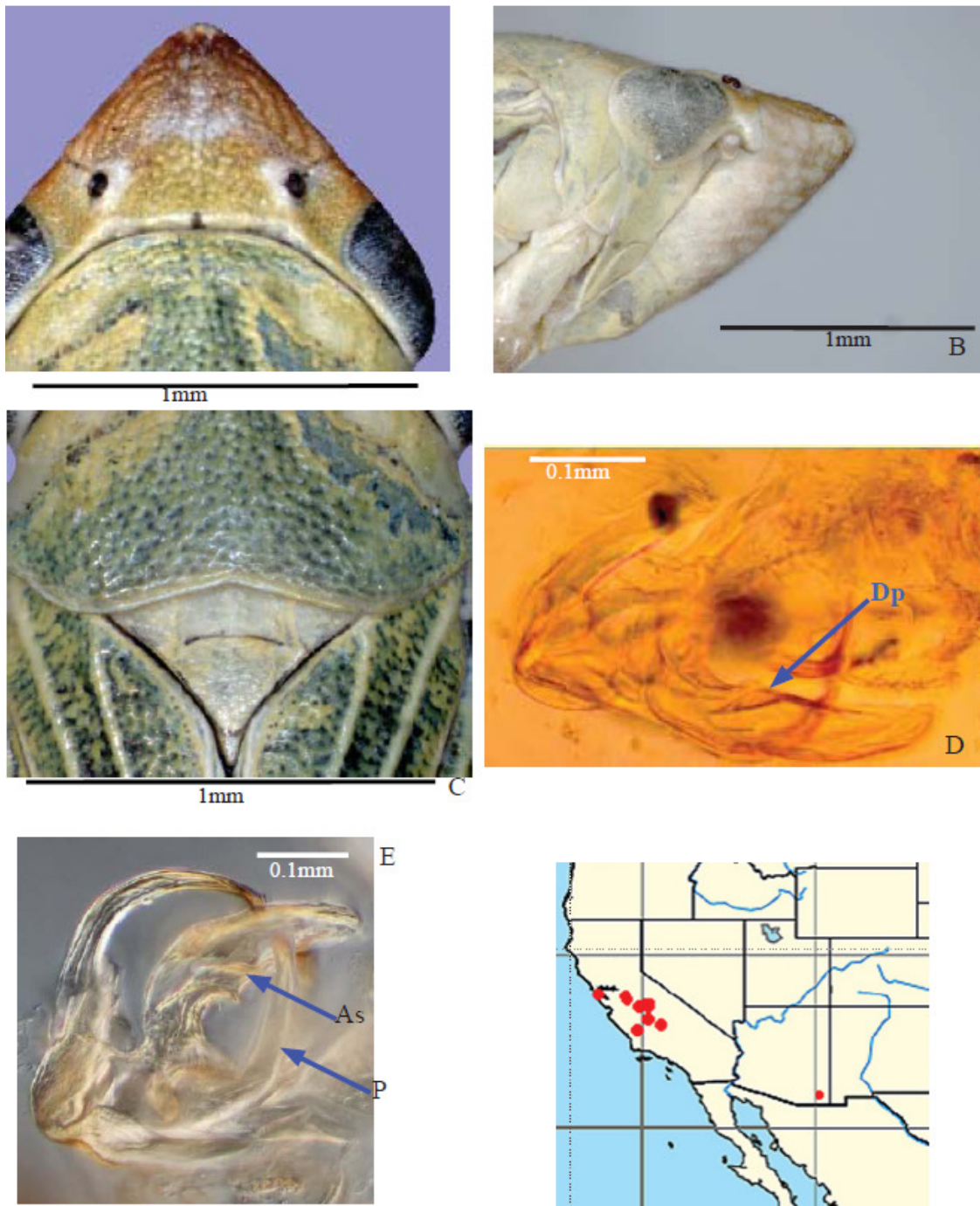


Figure 10: Photographs of characters used to distinguish *Xyphon fulgidum* with distribution map of specimens examined.
 A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal;
 D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P).

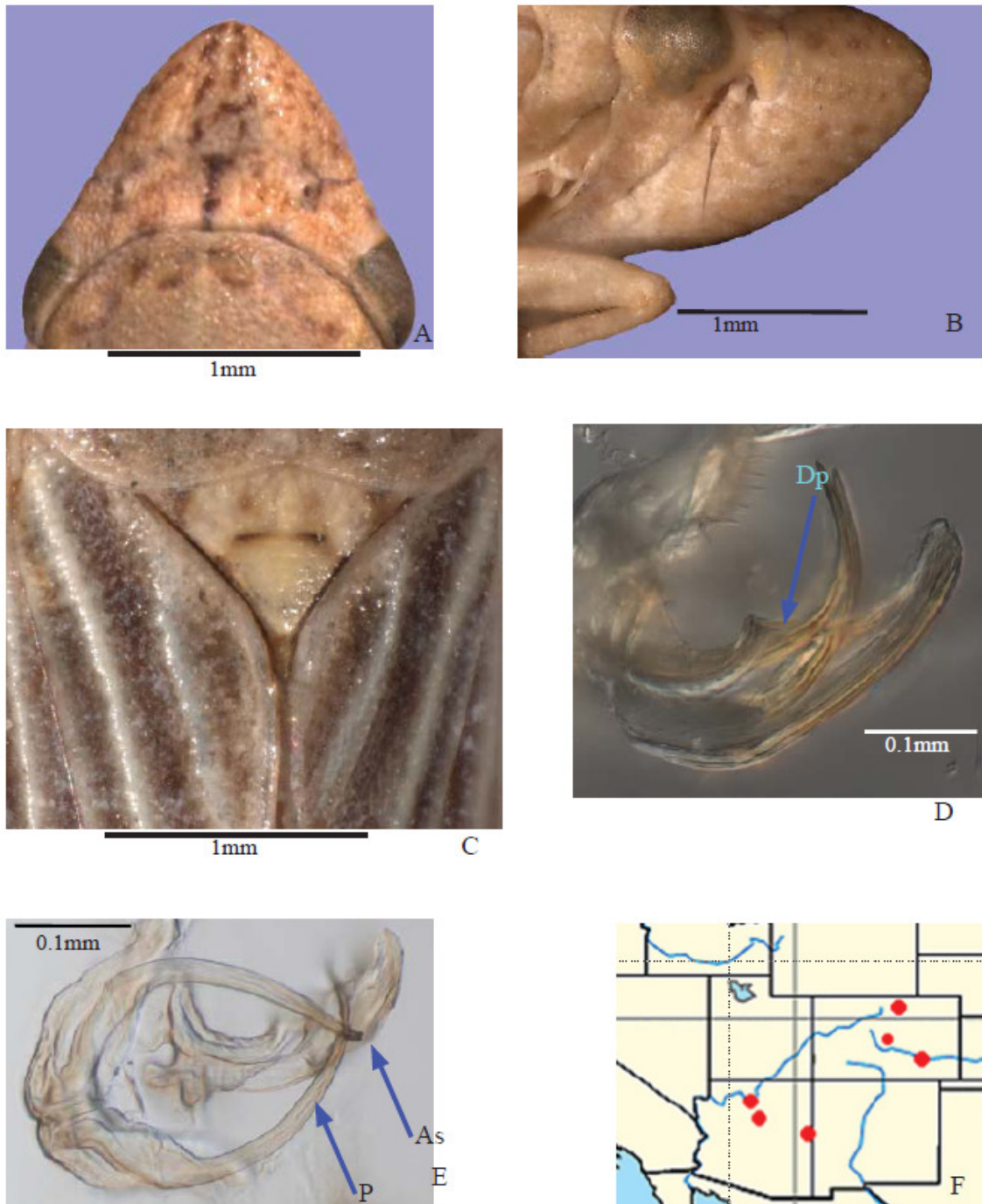


Figure 11: Photographs of characters used to distinguish *Xyphon gillettei* with distribution map of specimens examined.
 A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal;
 D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P) .

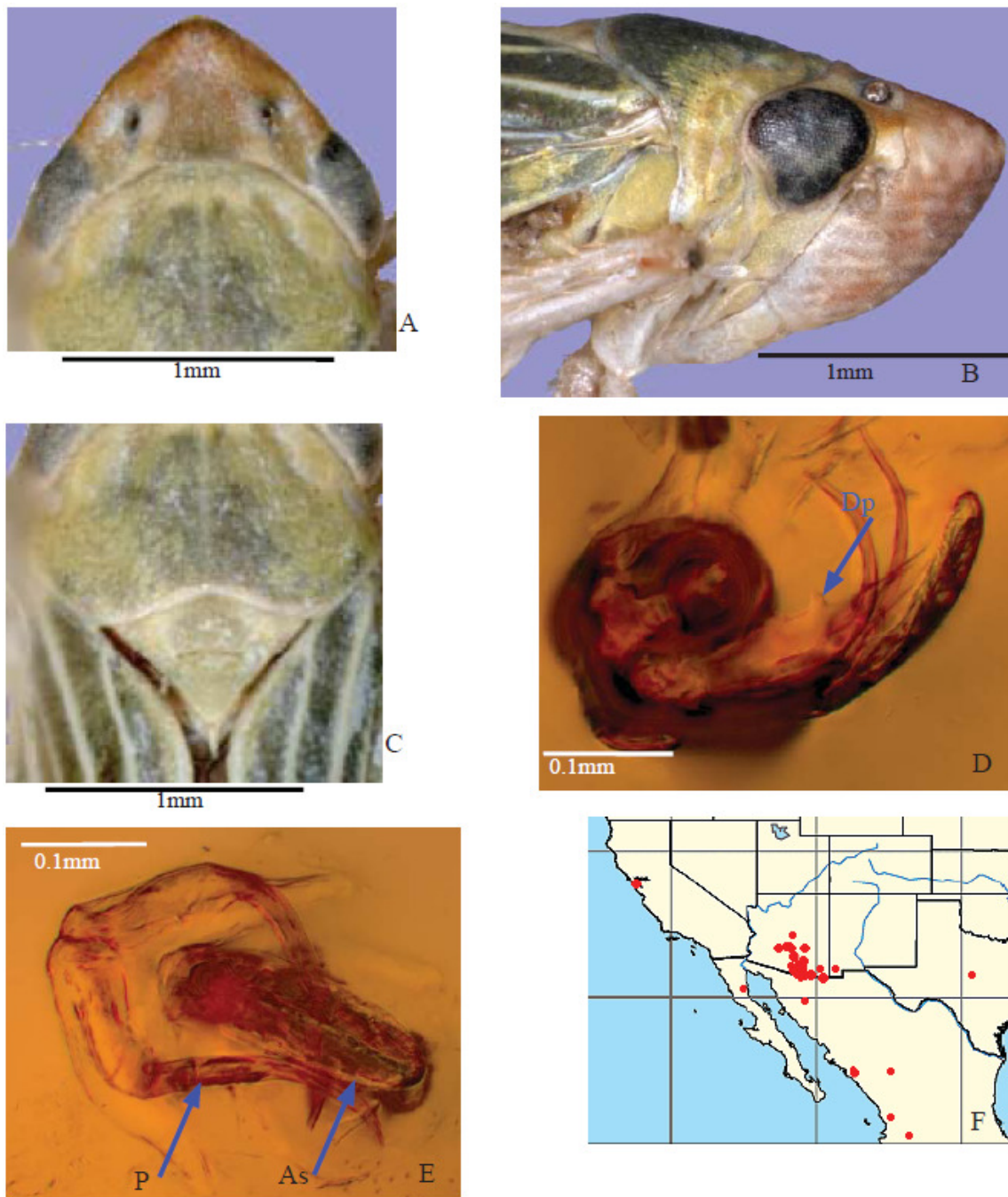


Figure 12: Photographs of characters used to distinguish *Xyphon nudum* with distribution map of specimens examined.

A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal;
 D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P) .

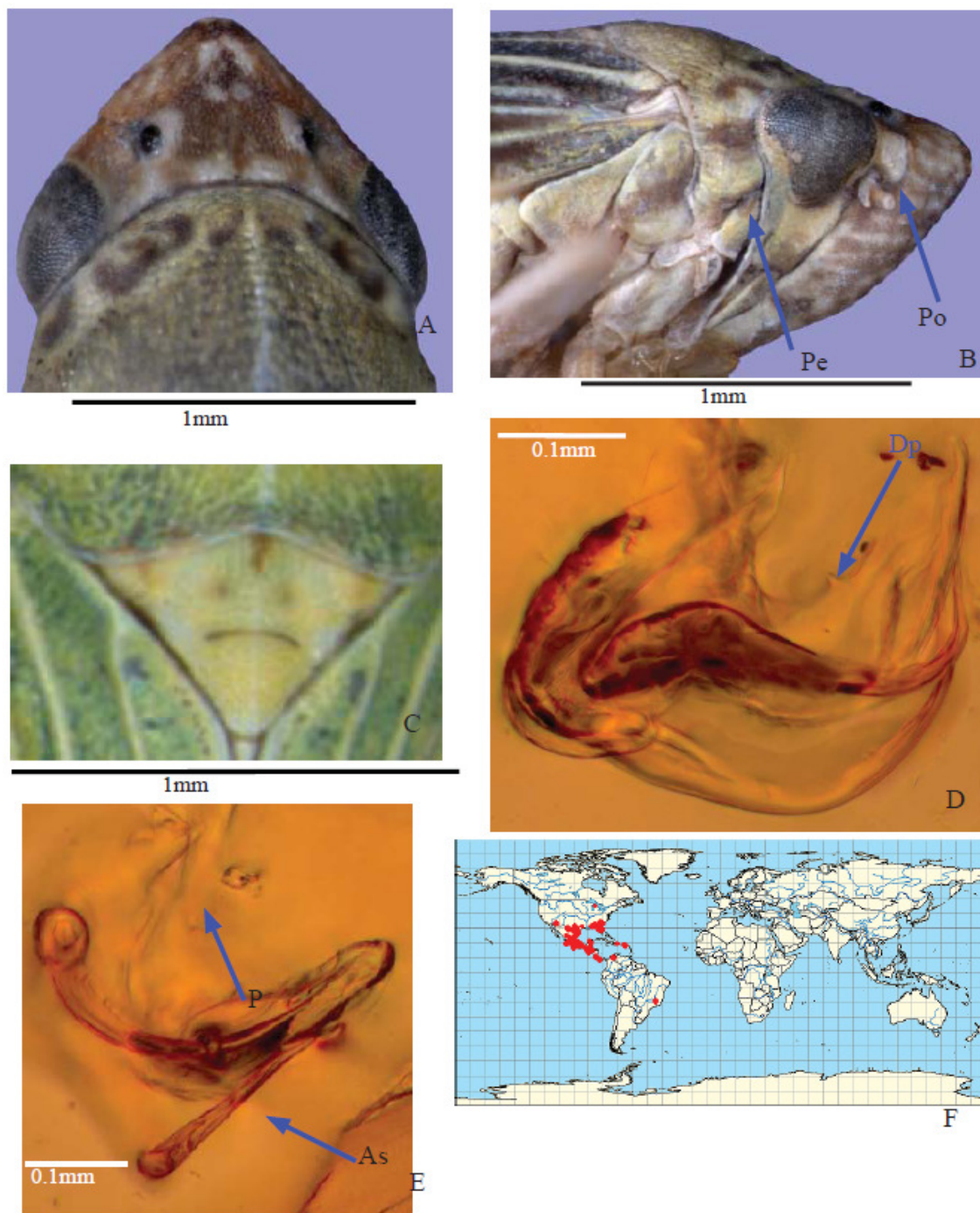


Figure 13: Photographs of characters used to distinguish *Xyphon reticulatum* with distribution map of specimens examined.
 A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal;
 D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P), preocular macula (Po), proepisternum (Pe).

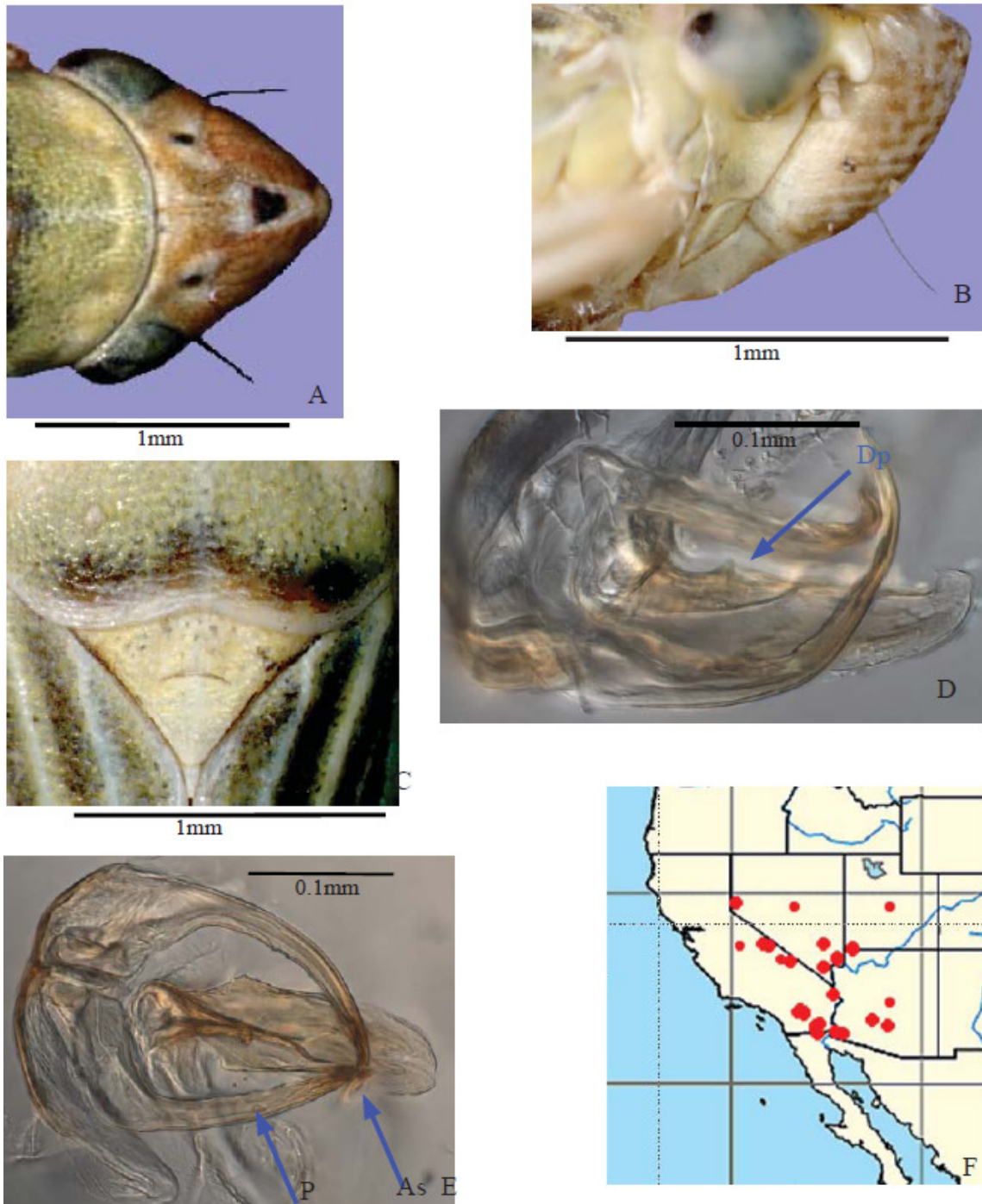


Figure 14: Photographs of characters used to distinguish *Xyphon triguttatum* with distribution map of specimens examined.

A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal; D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P) .

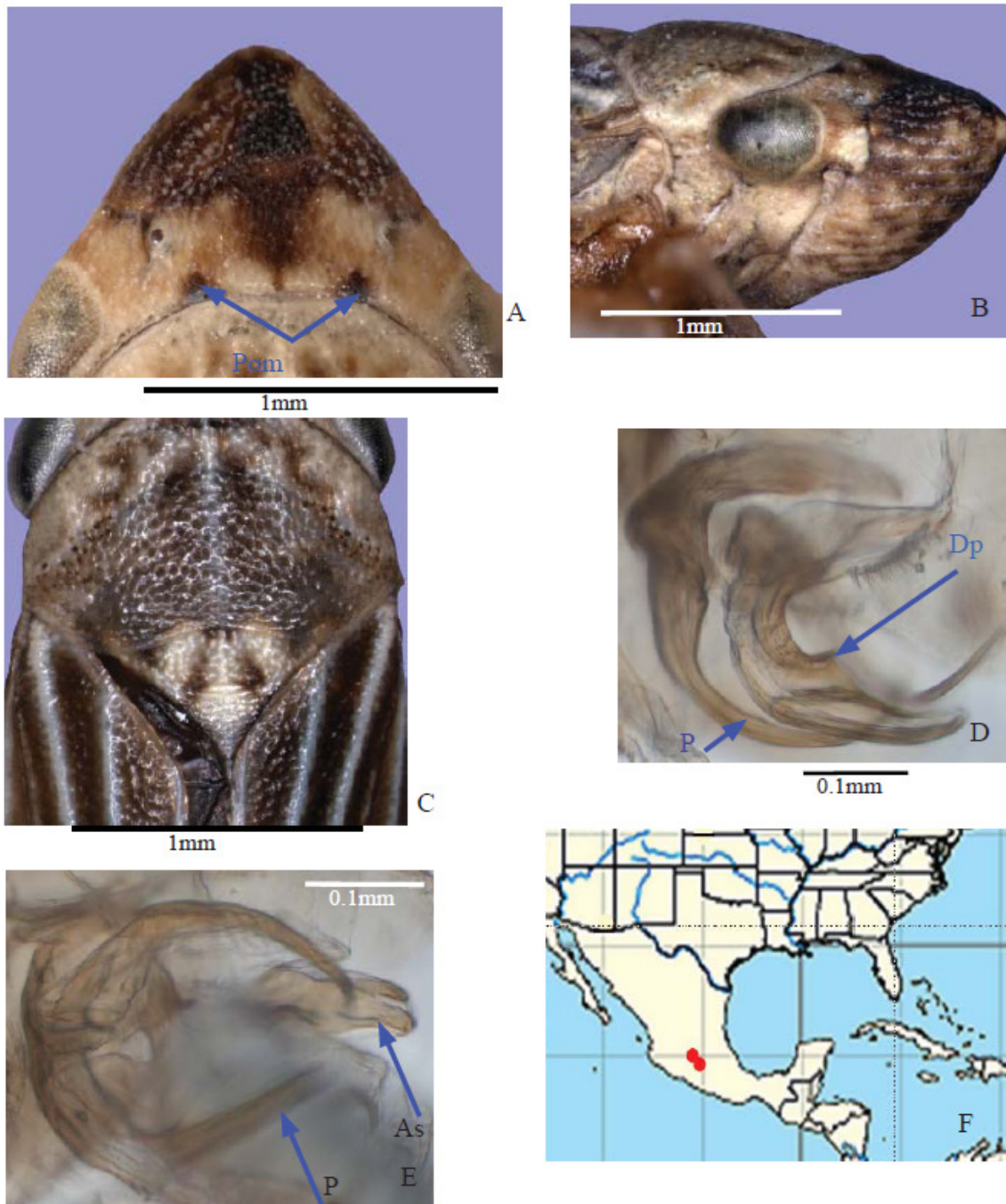


Figure 15: Photographs of characters used to distinguish *Xyphon* n. sp. 1 with distribution map of specimens examined.

A, Head and pronotum, dorsal; B, Head and thorax, lateral; C, Thorax, dorsal; D, Aedeagus, lateral; E, Aedeagus, dorsal; F, distribution map. Annotations: aedeagal shaft (As), dorsal process (Dp), paraphrases (P), postocellar maculae (Pom).

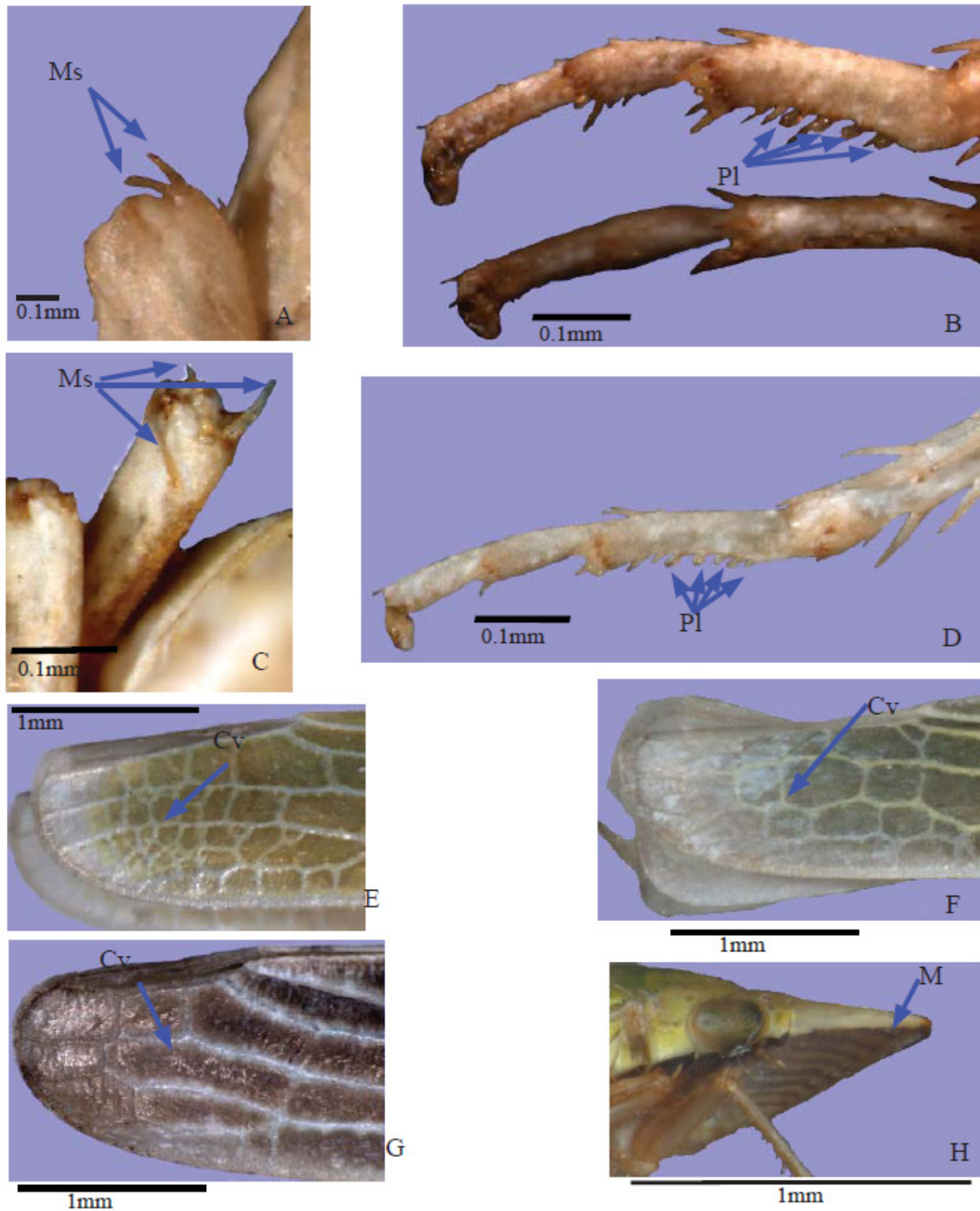


Figure 16: Additional characters useful for *Xyphon* identification.

A, Hind femur B, Hind tarsomere; C, Hind femur; D, Hind tarsomere; E, Forewing, apex; F, Forewing, apex; G, Forewing, apex (Cv); H, Head, lateral view (*Draeculacephala*). Annotations: crossvein (Cv), margin (M), macrosetal formula of hind femur (Ms), paleate setae (Pl).

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