DEAD BUGS DO TELL TALES: IMPLICATIONS OF A NEW FOSSIL ASSASSIN BUG (HETEROPTERA: REDUVIIDAE) FOR THE EVOLUTIONARY HISTORY AND SYSTEMATICS OF AN EXTANT LINEAGE

BY

DANIEL R. SWANSON

THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology in the Graduate College of the University of Illinois at Urbana-Champaign, 2016

Urbana, Illinois

Master's Committee:

Doctor Sam W. Heads, Co-Chair, Co-Director of Research
Doctor Steven J. Taylor, Co-Chair, Co-Director of Research
Professor Andrew V. Suarez
ABSTRACT

The following thesis comprises three parts: (1) the description of a new fossil assassin bug, (2) the use of this newly described taxon to inform the phylogenetic history of the family, and (3) a survey of previously-described extinct taxa compiled into the first taxonomic catalog of fossil Reduvioida.

The first chapter presents a new Eocene (Ypresian) fossil assassin bug, *Aphelicophontes iuddorum* gen. et sp. nov. (Reduviidae: Harpactorinae), described from the Green River Formation of Colorado. The specimens informing this description are marked by an extraordinary level of preservation, particularly in external and internal structures of the adult male genitalia. Following the description, discussions of phylogenetic signal and the implications for the systematics and evolutionary history of the group are presented.

The second chapter uses *Aphelicophontes iuddorum* gen. et sp. nov. as a new calibration point in order to re-estimate the divergence dates of Reduvioida. This analysis also utilizes a new set of fossil calibrations from previous studies. Tree topology is inferred using MrBayes and RAxML, and divergence dates are inferred using BEAST2. Convergence was not reached in the BEAST analysis, resulting in divergence estimates with low levels of support in which the divergence of Reduvioida from Heteroptera was suggested to be 344 Ma. The potential problems with this and previous divergence estimates are discussed.

To supplement and better justify the description and placement of the new taxon, an annotated taxonomic catalog of the fossil Reduvioida was compiled; this composes the third chapter of the thesis. This catalog marks the first such compilation for the 47 extinct members of the group and documents additional information such as the taphonomy, age (with
references), and type repository for each fossil. Supplementing the catalog proper is a
discussion of the subfamilial distribution of fossil reduvioid taxa, with tables enumerating
undescribed fossil reduvioid material and fossil species originally but erroneously described in
Reduviidae.

The thesis concludes with a general discussion of potential future work involving fossil
Reduvoidea.
ACKNOWLEDGMENTS

First and foremost, I am grateful to Daniel Judd for the donation of the holotype described herein to the INHS Paleontology Collection. It is often through such generosity that scientific collections prosper, which, in turn, ultimately furthers our understanding of the natural world around us, both past and present. I have elsewhere made the case for the importance of fossils, and the significance and uniqueness of these specimens makes their contribution especially and highly valued. In this same vein, I am grateful to Yinan Wang, Arlington, Virginia, for donation of the paratype and additional material to the INHS Paleontology Collection.

I thank my advisors, Sam W. Heads and Steven J. Taylor, both INHS, for their guidance during the course of this project, both in the broad sculpting of the project and in the execution and technical minutiae. It also was no small portion of gentle encouragement that facilitated the completion of this thesis. To Sam, I am grateful for opening my eyes to the world of fossil insects. Let us hope that this is far from the last time that I work with fossil bugs, but no matter the outcome, this is an appreciation that I will carry for the rest of my career. To Steve, I am grateful for the creative and exuberant perspective that he lent to the project. Let us hope that I never forget to open a fresh eye in the course of future studies and to always bring his sense of curiosity and enthusiasm to a new scientific problem. I also owe many thanks to the third member of my Master's committee, Andy Suarez. It is no small burden to guide and shape the scientists of tomorrow (let alone comb over 100+ pages of thesis), and it was always a helpful, thoughtful, and purposed insight that he brought to my committee. To all three, my great appreciation; this project would not be what it is without them.
I owe a large debt of gratitude to my friend and colleague in the Taylor lab, Aron Katz. I cannot overestimate the help he has provided, not only in trouble-shooting my analysis all along the way, but also in making me more competent and confident in my dealings with phylogenetic software. I still have a lot to learn, but Aron is, in large part, responsible for what I currently know. He was always willing to help, always ready to commiserate over a newly-arisen problem, and always happy to repeat an explanation for umpteenth time. No doubt his involvement will benefit me for the rest of my scientific career. I only hope that some day I am able to return the favor.

I also thank my friend and colleague in the Heads lab, M. Jared Thomas, for his patient technical and photographical assistance. The fossil images presented in this treatment are as much a product of his training as my hand.

The preparation of a taxonomic catalog is no small endeavour, and I am extremely grateful for the curators and collections managers that tolerated/indulged my lengthy emails and lengthier requests regarding fossil type material around the world: Antonio Arillo & Rafa López (MCNA), Stephan Blank & Angelika Weirauch (DEI), Ingomar Fritz & Martin Gross (SLJG), Talia Karim (UCMC), Katarina Krizmanić (HPM), Andreas Müller (ETHZ), Claire Mellish (BMNH), Christian Neumann (ZMHB), Ricardo Perez-de la Fuente (NMNH), Torsten Wappler (GPIB), and Irene Zorn (GBA). Although not all of the information that they provided made it into this thesis, it has spawned a small contingency of fossil side projects that will keep me busy for longer. For loans of extant material and the permission to dissect specimens within that material, I thank the collection managers, Chris Grinter (INHS) and Mark O’Brien (UMMZ), for
these dissections had a profound influence on the hypothesized taxonomic relationships of the new fossil species.

My thanks to Christiane Weirauch, Michael Forthman, and Paul Masonick (all University of California, Riverside), as well as Guanyang Zhang (Arizona State University), all for various discussions involving reduviid systematics. I appreciate the efforts of the "BEAST Support Group" at UIUC, who devoted several sessions to my personal phylogenetic software problems. For taking his valuable time to provide generous help with a Chinese translation, I thank Jun-Jie Gu (College of Biological Science and Engineering, Beifang University of Nationalities, Yinchuan, China).

And finally, I wish to thank my fiancée, Christina Silliman. Whenever I was facing the depths of a phylogenetic software-induced slump, she always had a listening ear, encouraging words, or a loving hug to chase the haunting BEAST away.
# TABLE OF CONTENTS

**GENERAL INTRODUCTION** .................................................................................................................. 1

Literature Cited ................................................................................................................................. 3

**CHAPTER 1: A NEW REMARKABLY-PRESERVED FOSSIL ASSASSIN BUG (HETEROPTERA: REDUVIIDAE) FROM THE EOCENE GREEN RIVER FORMATION OF COLORADO** .................. 6

Introduction ......................................................................................................................................... 6

Geological Setting and Stratigraphy .................................................................................................. 7

Materials and Methods ....................................................................................................................... 8

Results .............................................................................................................................................. 10

Discussion ....................................................................................................................................... 19

Literature Cited ................................................................................................................................. 33

Figures and Tables ............................................................................................................................ 47

**CHAPTER 2: RE-EXAMINATION OF THE DIVERGENCE DATES OF REDUVIOIDEA (HETEROPTERA) IN LIGHT OF NEW FOSSIL DATA** .............................................................................. 62

Introduction ....................................................................................................................................... 62

Materials and Methods ....................................................................................................................... 63

Results .............................................................................................................................................. 68

Discussion ....................................................................................................................................... 70

Literature Cited ................................................................................................................................. 76

Figures and Tables ............................................................................................................................ 86

**CHAPTER 3: AN ANNOTATED TAXONOMIC CATALOG OF THE DESCRIBED FOSSILS OF REDUVIOIDEA (HETEROPTERA)** ....................................................................................... 93

Introduction ....................................................................................................................................... 93

Materials and Methods ....................................................................................................................... 95
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Results</td>
<td>98</td>
</tr>
<tr>
<td>Discussion</td>
<td>99</td>
</tr>
<tr>
<td>Annotated Catalog of Fossil Reduvoidea</td>
<td>105</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>140</td>
</tr>
<tr>
<td>Figures and Tables</td>
<td>160</td>
</tr>
<tr>
<td>Index to Annotated Catalog</td>
<td>167</td>
</tr>
<tr>
<td>EPILOGUE: PROMISING PROBLEMS; OR POTENTIAL FOR FUTURE WORK IN FOSSIL REDUVIOIDEA</td>
<td>176</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>178</td>
</tr>
<tr>
<td>APPENDIX A: LIST OF GENBANK SPECIMENS AND ACCESSION NUMBERS</td>
<td>179</td>
</tr>
<tr>
<td>APPENDIX B: RAXML CALL LINES AND MRBAYES BLOCK</td>
<td>190</td>
</tr>
</tbody>
</table>
GENERAL INTRODUCTION

Fossils are important (and often coveted) entities in the study of natural history and evolution. At their best, they provide definitive evidence for hypotheses (e.g., continental drift: Wegener 1912a, b, c; origin and dispersal of modern humans: Stringer & Andrews 1988). At their worst, they still permit a glimpse of exotic life that often has long since gone extinct. Functioning as windows into the biota of the past, they allow inference about the evolution of extant organisms (e.g., Norell & Novacek 1992a, Valentine et al. 1996, Zhou 2004). They also can be used in phylogenetic reconstruction (Donoghue et al. 1989) and to calibrate molecular clocks, thereby providing a more-testable chronological context for hypotheses (e.g., Forest 2009). Pointedly, each fossil is a unique and invaluable parcel of information unattainable and unknowable by any other means, such as the origin and evolution of ecological or behavioral interactions, character state combinations absent in extant taxa, polarization of sets of character states, and the existence of stem group lineages (e.g., Norell & Novacek 1992b, Raff 2007).

However, fossils too often tell a fragmentary tale. Despite the fact that fossils, on the whole, are fairly common, focusing on a particular group results in a completely different story. The probability that any given organism becomes fossilized is astronomically small, and geological processes, and the eons over which they act, are not hospitable to brittle organic tissues (Allison & Briggs 1991, Zherikin 2002). Even if a given organism does fossilize, various forms of upheaval and disturbance, both natural and anthropogenic, greatly impact whether a fossil even survives to make it into the hands of a paleontologist (Zherikin 2002).
Fortunately, certain areas, due to their paleoecology and geologic history, are more prone to be highly fossiliferous. These fossil-rich "hotbeds", or Lagerstätten (literally, German, *Lager* 'storage, lair' and *Stätte* 'place'), have yielded a large portion of the fossilized biota known to science. Broken into two main types, Lagerstätten are characterized as places featuring great numbers of fossils (concentration deposits, or Konzentrat-Lagerstätten) and places featuring exceptionally preserved fossils (conservation deposits, or Konservat-Lagerstätten) (Grimaldi & Engel 2005). Fortunately, Lagerstätten reach back through time, with at least one site representing every major prehistoric period since the Silurian (Rasnitsyn 2002, Figs. 3–5). Located throughout the world, many of these sites are now protected, as their value is well understood (e.g., Lipps 2009).

Not all fossils are equal. Even when a fossil is discovered, the level of completeness greatly influences which inferences can be made, and diagnostic characters necessary to classify a fossil or glean potentially useful phylogenetic information might not always be present. Additionally, the relationship of a fossil to already-described taxa, or lack thereof, can modulate the importance of a given fossilized specimen, such as with present-day disease vectors or with stem-group taxa with no apparent living counterpart. Certain groups of taxa are more prone to fossilization based on natural history, habitat, ecology, etc., making some taxa much more abundant in the fossil record (e.g., Raup 1979, Labandeira & Sepkoski 1993) and boosting the value (both scientifically and monetarily) of rare specimens. So when a rare fossil is encountered, it becomes a scientific duty, an intellectual imperative, to describe and study it.

The discovery of a remarkably preserved insect belonging to the family Reduviidae afforded a unique opportunity to explore the implications and utility of such a fossil. Besides
representing an undescribed genus and species with apparent affinities with an extant group, the specimen possesses remarkably well-preserved and discernible internal and external genitalia. The first chapter describes this new fossil, supplying a name so that the taxon can be studied and discussed by others. It also probes such questions as "What kind of phylogenetic signal, if any, exists in fossilized insect genitalia?" The second chapter takes this a step further in asking "Can this particular specimen be used to inform phylogenetic hypotheses?" and seeks to re-calibrate a previously-generated molecularly-inferred phylogenetic tree of Reduviidae (i.e., Hwang & Weirauch 2012). In considering the systematic position of this new species, it was necessary to familiarize myself with the entire gamut of previously described fossil taxa. One cannot know if a species is truly "new" without knowing what already is. This need precipitated the third chapter of this project, the first systematic catalog of the fossil Reduvioidea of the world. This chapter tries to answer questions such as "How many and what types of fossilized assassin bugs even exist?"

LITERATURE CITED


CHAPTER 1: A NEW REMARKABLY-PRESERVED FOSSIL ASSASSIN BUG (HETEROPTERA: REDUVIIDAE) FROM THE EOCENE GREEN RIVER FORMATION OF COLORADO

Keywords. Systematics, taxonomy, new species, Harpactorinae.

INTRODUCTION

Reduviidae, or the assassin bugs, are among the most successful families of predatory animals on the planet, containing over 7000 species (updated from Maldonado 1990). This globally-distributed monophyletic group is diverse in form and habit, and its members exhibit an array of fascinating biological phenomena: dietary specializations (most notably on highly eusocial groups like ants and termites) from a generalist ancestor (McMahan 1983, Weirauch & Cassis 2006, Hwang & Weirauch 2012), aposematism (Forthman 2015), parental care (Odhiambo 1958, Tallamy et al. 2004, Gilbert et al. 2010), vertebrate hematophagy & pathogen transmission (Lent & Wygodzinsky 1979), trans-oceanic convergence in phenotype and/or prey specialization (Hwang & Weirauch 2012, Zhang & Weirauch 2014, pers. obs.), mimicry (Villiers 1967, Schaefer & Ahmad 1987, Santiago-Blay & Maldonado 1988, Maldonado & Lozada Robles 1992), and phenotypic plasticity relating to external resource dependence (Punzalan et al. 2008a, b). Therefore, elucidating the evolutionary history and relationships of the Reduviidae is of great utility, as many potential model systems are accessible in this group.

With such a large and diverse group, it is easy to be optimistic about the level of reduviid representation in the fossil record. Indeed, approximately 50 fossil taxa of Reduviidae have been described (see Chapter 3), and many more undescribed forms exist (e.g., Koch & Wedmann 2012; see also Chapter 3: Table 3.3). However, problems, such as skewed subfamilial representation, changing taxonomic framework, misidentified taxa, and an overall
lack of attention, have limited the utility of the described species. Despite such obstacles, some taxa have been used in calibrating molecularly-inferred phylogenies (i.e., Hwang & Weirauch 2012). For a more detailed discussion of these issues, see Chapter 3 and the Epilogue.

Herein, I describe a new species of fossil assassin bug, *Aphelicophontes iuddorum* gen. et sp. nov., the holotype of which possesses extraordinarily well-preserved male genitalia. This high fidelity of preservation facilitates comparison with homologous morphologies of extant taxa and allows the species to be assigned confidently to a lineage within the reduviid phylogeny at great taxonomic resolution. The justification for this placement is discussed along with other implications for the evolutionary history of the group.

**GEOLOGICAL SETTINGS AND STRATIGRAPHY**

**Location.** The Green River Formation is a Lagerstätte in the present-day western United States (Colorado, Utah, and Wyoming) between 38 and 44°N and 106 and 112°W (Figs. 1.1–2). The fossils described herein were collected near Meeker in Rio Blanco County, Colorado.

**Formation.** The Green River Formation comprises a series of sedimentary deposits (Fig. 1.1) representing a complex of ancient lakes (Fig. 1.2), which at their peak around 52 Ma contained three large bodies of water: Fossil Lake, Lake Gosiute, and Lake Uinta (Grande 2013). The fossils treated herein came from the Parachute Creek Member of the Piceance Basin from former Lake Uinta. Portions of the longest-lived lake, Lake Uinta, stretched into Colorado, and its deposits consist of six members, of which the Parachute Creek Member is the youngest (Grande 2013).

**Lithology and Preservation.** Most of the fossilized fauna and flora found in this deposit are oil-shale compressions (Cole & Picard 1978). These resulted from the deposition of
mudstones on sheets of carbonate (Carroll et al. 2006). Many fossils coming from the Green River Formation are associated with alluvial or lacustrine deposits.

**Age/Dating.** The formation has been radiometrically dated to the Middle Eocene, from approximately 53.5–48.5 Ma (Smith et al. 2003, Smith et al. 2008). This places the fossil in the Ypresian or Lutetian Stage of the Eocene (Table 1.1).

**Paleoclimate.** In the Eocene, this region was much warmer and more humid than in the present and likely comprised swampy and/or riparian habitats as the lacustrine areas receded (Grande 2013). This interpretation is supported by the abundant fossilized fish found in the formation, as well as the abundance of plant fossils representing present-day moisture-adapted taxa (i.e., ferns, sycamore, cattails) and various fossilized turtles, snakes, and crocodiles (Grande 1984). Floral analyses (MacGinitie 1969, Wilf 2000) have sought to infer paleoclimate, based largely on phylogenetic association with extant species, e.g., presence of cold-intolerant plants like palms; these studies further suggested warm winters and a mean annual temperature of approximately 16°C.

**Faunal Studies.** Early work on the fauna of the Green River Formation was pioneered by Samuel S. Scudder (1878, 1890) and T. D. A. Cockerell (see Weber 2000). Wilson (1978) and Grande (1984, 2013) summarized the insect fauna described from the formation.

See Wappler et al. (2015) for further details and additional references.

**MATERIALS AND METHODS**

**Fossil Work.** Specimens were received in their current form by one of the co-advisors (SWH), sent from Mr. Dan Judd (holotype) and Mr. Yinan Wang (paratype). Specimens were photographed using a Canon EOS 5D SLR camera with a Canon MP-E 65mm macro lens and
Tiffen 58mm circular polarizer attached to a StackShot Automated Focus Stacking Macro Rail motorized carriage mounted to a Kaiser copy stand. Paired Neewer CN-216 LED video lights were used for additional lighting, and the fossils were gently covered with a thin layer of ethanol to improve contrast and bring out details. Each fossil was imaged in a grid-like fashion, photographing the full fossil in a complement of 12–20 sections. Unprocessed sections were focus-stacked using Helicon Focus version 5.3 (Helicon Soft Ltd., Ukraine). The mosaic was stitched together using the Photomerge function and the resulting composite was further processed in Adobe Photoshop CS5 (Adobe Systems Inc., San Jose, CA). Line drawings were made from photographs in Adobe Illustrator CC (Adobe Systems Inc., San Jose, CA). In the line drawings, complete lines indicate the margin of sclerites, whereas dashed lines indicate margins other than sclerite boundaries, i.e., incomplete or broken margins of tissue. Measurements were made from the digitized image.

All fossils herein described have been deposited in the Illinois Natural History Survey Paleontology Collection at the University of Illinois at Urbana-Champaign (INHS). All images and associated data have been accessioned into the National Science Foundation (NSF) funded Fossil Insect Collaborative digitization initiative (iDigBio 2016).

**Work with Extant Material.** In order to investigate the phylogenetic position of the fossil within the family, I dissected the pygophores of several extant genera of Harpactorini for comparison. Pygophores were removed after soaking the caudal end of the specimen in hot water for several minutes and then carefully extending and excising from the abdomen using forceps and occasionally iridectomy scissors. The pygophore then was placed into hot 10% potassium hydroxide (KOH) for approximately 8–15 minutes, depending on size. The
pygophore was subsequently removed from KOH to a watch glass filled with water and soft
tissue was gently teased away using fine forceps. After imaging, the pygophores were placed in
glycerin-filled vials and affixed to the pin via the rubber stopper-cap beneath the specimens’s
body.

Pygophores were photographed with Zeiss AxioCam HRc Rev. 3 digital camera mounted
to Zeiss SteREO Discovery V.20 stereomicroscope with PlanApo S 0.63x objective. As with the
fossils, pygophore images were focus-stacked with Helicon Focus and processed using Adobe
Photoshop CS5.

Morphological terminology, particularly that of reduviid genitalia, generally follows
Davis (1966).

RESULTS

Systematic Palaeontology

Order **Hemiptera** Linnaeus, 1758

Suborder **Heteroptera** Latreille, 1810

Family **Reduviidae** Latreille, 1807

Remarks. The specimen clearly is a cimicomorphan true bug. Taxa provided in parentheses
after each character are rejected by possessing a dissenting character state: fusiform structure
of the head (Enicocephalomorpha), length >8 mm (Dipsocoromorpha, Leptopodomorpha),
antennae long and conspicuous (Nepomorpha), and scape long with gradually narrowing
antennal segments (Pentatomomorpha) (Schuh & Slater 1995). Within Cimicomorpha, the
specimen is referrable to the superfamily Reduvioidea, again, by elimination: length >10 and/or
symmetrical male genitalia (Miridae, Cimicoidea), lack of areolate thorax and hemelytra
(Tingidae), form of pygophore (Nabidae), and body size/general habitus (Joppeicidae, Medocostidae, Microphysidae, Thaumastocoridae, Velocipedidae) (Schuh & Slater 1995). In Reduvioida, the absence of enlarged profemora will rule out Pachynomidae (Schuh & Slater 1995), and the length of the hemelytra and absence of a costal fracture excludes the extinct family Ceresopseidae (Shcherbakov 2007). Furthermore, although none of the diagnostic characters for Reduviidae appear to have been preserved in the fossil (i.e., three-segmented rostrum, midlongitudinal prosternal groove), the habitus clearly corroborates the placement of the specimen in this family.

**Subfamily Harpactorinae** Amyot & Audinet-Serville, 1843

**Remarks.** Similarly, few of the diagnostic characters for the Harpactorinae are visible in the fossil (i.e., basal quadrate cell in the hemelytra, pronotal sulcation). However, in the context of the New World, systematic exclusion allows several of the major lineages (i.e., Ectrichodiinae, Emesinae, Peiratinae, Phymatinae, Stenopodainae, Triatominae) and various minor subfamilies (i.e., Bactrodinae, Cetherinae, Chryxinae, Elasmodeminae, Holoptilinae, Microtominae, Phimophorinae, Physoderinae, Saicinae, Salyavatinae, Sphaeridopinae, Tribelocephalinae, Vesciinae) to be removed from consideration, using states of various morphologies (i.e., length and thickness of the legs, division of antennal segments, division of pronotum, shape of head, armature/pilosity of integument, and position of eyes) or a distinctive derived habitus. Reduviinae is the only subfamily that is not demonstrably excluded, although the generic affinities to Harpactorinae (see below), morphological trends (e.g., fossa spongiosa, length of scape, general armature of the thorax and legs in Reduviinae), and general habitus still support
the identity as a harpactorine. The fossil specimen also shows fewer affinities with the reduviine species present in North America today than with those belonging to Harpactorinae.

**Tribe** *Harpactorini* Amyot & Audinet-Serville, 1843

**Remarks.** The specimen is easily excluded from the Apiomerini by the scape being distinctly longer than the head and by the absence of "resin-gathering' morphology on the fore and mid legs. Other than the nominate tribe, none other occurs in the New World and the habitus agrees with members belonging to Harpactorini.

**Genus** *Aphelicophontes* Swanson, Heads & Taylor gen. nov.

**Type species.** *Aphelicophontes iuddorum* Swanson, Heads & Taylor sp. nov.

**Diagnosis.** The following enumeration describes a combination of characters that makes this taxon unique among the North American harpactorines. Genera provided in parentheses after each character possess a dissenting state for a character deemed of diagnostic value at the genus-level: scape distinctly longer than head (*Rhynocoris*); profemora and protibia unarmed (*Acholla, Sinea*); length smaller than 20 mm (*Arilus*); abdomen oval, not gradually widened posteriorly (*Heza, Rocconota*) or parallel (*Doldina*); metafemur longer than profemur (*Zelus*); humeral angles apparently unarmed (*Atrachelus*); hemelytra not greatly extended beyond abdomen (*Castolus, Repipta*); pygophore apex with broad triangular process (*Fitchia*); dark bands of connexiva and legs broad, with three dark bands on femora and tibiae (*Pselliopus*).

**Etymology.** The new generic name comes from the Greek ἀφήλικος, -ον, Latinized *aphelicos*, 'beyond youth, old', and the Greek -φόντης [from φονεύς], Latinized *phontes* [from
phoneus], 'slayer, murderer'. This references the old age of the specimen (as a fossil) and the predaceous aspect of reduviids. The genus is masculine. /əˈfɛlɪ·koʊ·ˈfɒ·tɪz/.

**Remarks.** The new taxon could not be adequately separated from the genera *Pselliopus*, *Cosmoclopius*, *Ecelonodalus*, or *Pyrrhosphodrus* using morphology. However, for reasons given in the discussion, a new genus was erected to receive this specimen.

*Aphelicophontes iuddorum* Swanson, Heads & Taylor sp. nov.  
(Figs. 1.3–9, 1.11, 1.12)

**Diagnosis.** As for genus by monotypy.

**Occurrence.** Middle Eocene: Ypresian–Lutetian, approximately 53.5–48.5 Ma (Smith et al. 2003).

**Etymology.** The new species is named for the collectors of the fossil, the Judd family, in honor of their gracious donation of the specimens to the Illinois Natural History Survey Paleontology Collection.

**Material.** *Holotype*: INHSP-2222-1; near complete adult male preserved in dorsoventral aspect as compression fossil. Composed of part and counterpart, cleaved in the coronal plane in more-or-less equal proportions. Locality: COLORADO: Rio Blanco Co., Bill Hawes Quarry, 39°43′45″N, 107°58′36″W, 2200 m, 34.5 km S of Meeker[,] Parachute Creek Member[,] Green River Formation (Eocene), 5 April 2006, D. & J. Judd. *Paratype*: INHSP-2221-1; near complete unsexed adult preserved in dorsoventral aspect as compression fossil. Locality: *idem*.

**Description.**

*Material Examined: Holotype (part & counterpart)* (Figs. 1.3–6, 1.11, 1.12)
Length at least 12.4 mm (part: 9.5 mm, counterpart: 12.4 mm) measured from apex of tylus [=clypeus] to apex of abdomen; at least 13.3 mm (part: 10.2 mm, counterpart: 13.3 mm) to apex of pygophore.

Head: Fusiform, length at least 2.3 mm (part: 1.5 mm, counterpart: 2.3 mm) measured from apex of tylus to posterior margin of collum. Eyes: incompletely preserved, interocular distance approximately 0.3 mm. Ocelli apparently present, incompletely preserved.

Antennae: incompletely preserved, at least portions of 4 individual segments visible in one antenna, inserted between anterior margin of eye and apex of tylus, length of scape at least 2.6 mm (part: 1.9 mm, counterpart: 2.6 mm), mostly dark with pale annulus approximately near midpoint, length of third segment at least 2.8 mm (part: 2.1 mm, counterpart: 2.8 mm), length of fourth segment at least 0.8 (part: 0.5 mm, counterpart: 0.8 mm).

Rostrum: not preserved.

Thorax: Pronotum: incompletely preserved, somewhat trapezoidal, apparently longer than wide, length at least 2.4 mm (part: 2.0 mm, counterpart: 2.4 mm), widest point at least 1.9 mm (part: 1.3 mm, counterpart: 1.9 mm), humeral angles not preserved. Scutellum: incompletely preserved, triangular, longer than wide, length at least 0.6 mm (part), width at least 0.4 mm at base (part).

Hemelytra: incompletely preserved, length at least 7.2 mm (part: 5.8 mm, counterpart: 7.2 mm), width at least 2.2 mm (part: 1.6 mm, counterpart: 2.2 mm).
Abdomen: mostly complete, intersegmental sutures not preserved, length at least 7.4 mm (part: 6.6 mm, counterpart: 7.4 mm), width at least 2.4 mm (part: 2.1 mm, counterpart: 2.4 mm) at widest point; connexiva banded with light and dark.

Legs: Forelegs: procoxae mostly contiguous; profemur at least 3.6 mm (part: 2.9 mm, counterpart: 3.6 mm), with discrete alternating light and dark bands, dark bands longer than light bands, apparently base of profemur light and apex dark with three of each band; protibia incompletely preserved, at least 3.4 mm (part: 2.9 mm, counterpart: 3.4 mm), with discrete alternating light and dark bands, dark bands longer than light bands, apparently base of protibia with small light band near junction with profemur, beyond with at least three dark bands and two light bands; protarsi not preserved.

Middle legs: mesocoxae separated; mesofemur at least 3.1 mm (part: 2.6 mm, counterpart: 3.1 mm), banded as in profemur; mesotibia incompletely preserved, at least 2.6 mm (part: 2.0 mm, counterpart: 2.6 mm), banded as in protibia except third dark band apparent; mesotarsi not preserved.

Hind legs: metacoxae separated; metafemur incompletely preserved, at least 4.7 mm (part: 3.3 mm, counterpart: 4.7 mm), banded as in profemur; metatibia at least 5.6 mm (part: 4.3 mm, counterpart: 5.6 mm), banded as in protibia except three dark and light bands apparent; metatarsi approximately 0.9 mm, tarsal claw apparent (counterpart).

Male Genitalia: Pygophore: Length at least 2.4–3.1 mm (part: 2.1–2.2 mm, counterpart: 2.4–3.1 mm) (depending on inclusion of median process), width at least 1.2 (part: 1.0 mm, counterpart: 1.2 mm). Oval, anterior rim incompletely preserved. Apex of pygophore: broadly triangular, little longer than wide, length at least 0.8 mm (part: 0.4 mm, counterpart: 0.8 mm),...
width at least 0.4 mm (part: 0.3 mm, counterpart: 0.4 mm) at base. Parameres: not preserved. 
Articulatory apparatus triangular, symmetrical, basal plate arms apparently straight, ponticus 
basilaris straight, without ventral median projection or bend, pedicel biramous or incompletely 
preserved. Phallotheca incompletely preserved, with sclerotized margins.

Female: unknown.

Remarks. See the Discussion for an extended explanation regarding the generic placement of 
this new taxon, as well as the notes regarding the preservation of different 
morphologies.

Associated specimens. This fossil contains a single fossilized beetle, in addition to the assassin 
bug. Tentative identities of the beetle include a cliviniine carabid or a clerid. Although 
the vast majority of assassin bugs are thought to be generalist predators (see Hwang & 
Weirauch (2012) for a discussion of food specialization), there is no particular evidence 
that this coleopteran was prey of the reduviid.

Paratype (Figs. 1.7–8)

Length at least 9.6 mm measured from apex of tylus [=clypeus] to apex of abdomen.

Head: Obscured by profemur, length at least 1.7 mm. Eyes: incompletely preserved, 
length approximately 0.4 mm.

Antennae: incompletely preserved, at least portions of 3 individual segments visible in 
one antenna, insertion not preserved, length of scape at least 2.8 mm, alternating light and 
dark bands, length of pedicel at least 2.0 mm, length of third segment at least 2.8 mm.

Rostrum: not preserved.
Thorax: Pronotum: incompletely preserved, somewhat trapezoidal, length at least 2.2 mm, widest point at least 2.1 mm, humeral angles apparently rounded and inermous. Scutellum: obscured.

Hemelytra: incompletely preserved, length at least 4.8 mm, width at least 1.6 mm.

Abdomen: Length approximately 5.4 mm, width approximately 2.4 mm at widest point, vaguely elongate orbicular.

Legs: Forelegs: profemur approximately 2.8 mm, apparently with discrete alternating light and dark bands, dark bands longer than light bands; protibia incompletely preserved, at least 2.4 mm, apparently with at least one dark band; protarsi not preserved.

Middle legs: mesofemur approximately 3.1 mm, apparently with discrete alternating light and dark bands, dark bands longer than light bands, apparently base of profemur light and apex dark with three of each band; mesotibia incompletely preserved, at least 1.6 mm, dark bands longer than light bands, apparently base of protibia with small light band near junction with profemur, beyond with at least two of each band; mesotarsi not preserved.

Hind legs: metafemur incompletely preserved, at least 2.5 mm, apparently with at least one dark band; metatibia incompletely preserved, at least 2.6 mm, apparently with discrete alternating light and dark bands; metatarsi not preserved.

Sex: unknown.

Remarks. The slab containing the paratype of *A. iuddorum* is what is referred to as a "raft", which are thought to have formed by alluvial pooling and subsequent deposition of organic material into the substrate en masse. These types of fossils typically contain a wide assemblage of biota that amassed and fossilized in the same place at the same
time. Therefore, this piece is interesting in that it provides reliable interspecific and phenomenological data for an extinct ecosystem.

**Associated specimens.** Many other specimens are present in this slab. In the image provided (Fig. 1.7), several dipteran, or possibly hymenopteran, specimens are visible, as well as a cockroach. However, this is, by no means, a complete enumeration of the insects present in this raft, and further study likely will reveal many other interesting specimens in other taxonomic groups.

An additional poorly-preserved specimen is tentatively placed here, although it did not inform the above description:

*Aphelicophontes iuddorum*?

(Fig. 1.9)

**Occurrence.** As for holotype and paratype.

**Material.** INHSP-2220; unsexed adult preserved in dorsoventral aspect. Locality: as for holotype and paratype.

**Description.**

Length approximately 9.7 mm measured from apex of tylus [=clypeus] to apex of abdomen.

Head: Fusiform, length approximately 1.6 mm measured from apex of tylus to posterior margin of neck. Eyes: not preserved.

Antennae: incompletely preserved, segmentation not preserved, inserted behind apex of tylus, length of scape at least 1.6 mm, mostly dark with pale annulus approximately near midpoint, length of pedicel at least 2.3 mm.
Rostrum: not preserved.

Thorax: Pronotum: incompletely preserved, somewhat trapezoidal, apparently longer than wide, length at least 1.4 mm, widest point at least 1.6 mm, humeral angles obscured.

Scutellum: not preserved.

Hemelytra: incompletely preserved, length at least 5.0 mm, width at least 1.5 mm.

Abdomen: Length at least 5 mm, width at least 2.4 mm at widest point; connexiva obscured by surrounding matrix.

Legs: Forelegs: profemur at least 2.7 mm; protibia incompletely preserved, at least 2.7 mm, protarsi not preserved.

Middle legs: mesofemur incompletely preserved, at least 1.6 mm; mesotibia incompletely preserved, at least 1.8 mm, mesotarsi not preserved.

Hind legs: metafemur incompletely preserved, at least 3.2 mm; metatibia incompletely preserved, at least 2.5 mm, metatarsi not preserved.

Sex: unknown.

Remarks. Although greatly obscured by the surrounding matrix, this specimen appears to have a similar pattern of annuli as that described for A. iuddorum. This is most readily visible in the metafemora and metatibia.

Associated specimens. None.

DISCUSSION

Generic Identity of the Fossil. In order to adequately place the fossil, three scenarios required consideration, namely, that it belonged to: (1) an already-described extinct taxon; (2) an already-described extant taxon; and (3) an undescribed fossil taxon.
I. Already-described Extinct Taxon. In order to assess this, all reduviid fossils described from the central United States during the Cenozoic needed to be considered. It was at this point that the taxonomic catalog of fossil Reduviioidea first became integral (see Chapter 3). After its construction, it became apparent that, although many more undescribed specimens are available for study (Koch & Wedmann 2012), only two reduviid species have been described to date from this area: *Tagalodes inermis* Scudder, 1890 and *Poliosphageus psychrus* Kirkaldy, 1910. Note that the species described as *Reduvius? guttatus* Scudder, 1878 has since been considered to belong to Rhopalidae (Scudder 1890, 1891), and *Miocoris fagi* Cockerell, 1927 and *Eothes elegans* Scudder, 1890 are not reduviids (Swanson, in prep.). Although none of these fossils were physically examined, sufficient characters to eliminate conspecificity can be gleaned from each of the original descriptions. The length of the hind legs compared to the fore and middle legs, as well as the purported absence of ocelli, eliminates *T. inermis*. The presence of humeral spines, the shortened scape, and again, the length of the hind legs removes *P. psychrus* from consideration. Thanks to the kindness of T. Karim (University of Colorado, Boulder), I also was able to examine a high-resolution photograph of the holotype of *P. psychrus*. It is not a foregone conclusion that *P. psychrus* is an assassin bug, but if so, based on the terminal part of the abdomen, it is a female of another subfamily, most likely Reduviinae. Redescription of this species is in progress (Swanson, in prep.). Thus, it may be safely concluded that the new species erected herein is not a previously-described fossil taxon.

II. Already-described Extant Taxon. The age of the fossil (Eocene, 53.5–48.5 Ma) is sufficiently recent, such that, for the generic identity, extant taxa need be considered; this is known by the existence of many Eocene genus-level lineages still persisting today (e.g.,
Sinitshenkova 1999, Labandeira et al. 2001, Gǐška 2011, Vršansky et al. 2011). As previously indicated, the form justifiably represents a harpactorine assassin bug, even though all subfamilial diagnostic characters, i.e., basal quadrate cell in the hemelytra and pronotal sulcation, are not discernible. Furthermore, the identity can be further restricted to Harpactorini based on the length of the scape and the absence of the "resin-gathering" machinery of the Apiomerini (see Poinar 1992, Maldonado et al. 1993). Currently, there are about 54 genera of Harpactorini known from the New World (Putshkov & Putshkov 1985, 1988; Maldonado 1990; Swanson in prep.) and 13 of these genera are known from the present-day United States. Within the intersection of taxa in the Harpactorini and those living in the region today, 11 genera can easily be removed from consideration (see generic diagnosis of Aphelicophontes). However, the strong banding pattern is strikingly reminiscent of the genus Pselliopus Bergroth, 1905, although a similar banding pattern also is found in dark individuals of Castolus ferox (Banks, 1910) (Fig. 1.10). Thus, two extant North American genera require further consideration.

The similar banding pattern and geographic proximity of C. ferox bears further comment. In general, there is conspicuous sexual dimorphism in Castolus Stål, 1858: in males, the eyes are particularly salient and the third antennal segment is somewhat incrassated; both characteristics are present in C. ferox but absent in the fossil. Additionally, the hemelytra do not appear to project past the apex of the abdomen and thus are too short, as evidenced by the beginning of the apical curve in the counterpart. Further, the form of the lateral margins and posterior sublateral projections of the pygophore are different in Castolus (Maldonado 1976). Lastly, the banding pattern on the legs is too fine, if a strict interpretation based on C. ferox is
maintained. Even in dark-patterned *C. ferox*, the connexiva are not striped, as they appear to be in the fossil. Thus, *Castolus* may securely be removed from consideration.

As indicated in the generic diagnosis, the extant genus *Pselliopus* cannot be excluded by comparing diagnostic characters for the genus with characters present in the fossil. In particular, this results from the absence in preservation of either the rostrum or scutellum. However, a number of features make placement in the extant genus *Pselliopus* a dubious prospect. As the banding on legs, connexiva, and antennae provided the strongest evidence that *Pselliopus* is the closest extant taxon, more stringent scrutiny reveals that these bands appear too coarse to match any extant *Pselliopus*. There are two groups of banding patterns of the forelegs found in (at least) the North American species of *Pselliopus* (Barber 1924): the first involves five dark bands on the profemur, followed by 4–5 on the protibia. The second banding pattern involves 5–7 less discrete dark bands on each of the femora and tibiae, with intercalated speckles on the femora. Neither match the 3–4 thicker dark bands of the fossil specimen. Furthermore, presence of banding itself in fossil assassins preserved as compressions is known (i.e., *Harpactor chomeraciensis* Riou, 1999; *Harpactor maculipes* Heer, 1853; *Rhynocoris michalki* Statz in Statz & Wagner, 1950; *Reduvius diatomus* Zhang & Zhang, 1990), although the pattern admittedly is more extensive and definitive in *Aphelicophontes*. Other differences from *Pselliopus* include the inconspicuous connexiva and the lack of humped lateral margins and posterior sublateral projections on the pygophore. Thus, there are reasons to exclude *Pselliopus*, particularly when considering the configuration of the banding pattern.

Other New World genera should be considered, given the wildly different climate of the Eocene and the aerial dispersal capabilities of the taxa. The additional 41 genera of
Harpactorini found south of the United States (based on Swanson, in prep.) yield only three viable candidates: *Cosmoclopius* Stål, 1866; *Ecelonodalus* Elkins & Wygodzinsky, 1957; and *Pyrrhosphodrus* Stål, 1866 (Fig. 1.10). These three genera are hypothesized to be closely related to *Pselliopus*, coming out very near that species in two recent molecular phylogenies when included (i.e., Hwang & Weirauch 2012, Zhang & Weirauch 2014). Members of these genera also possess a similarly striped color pattern. Several of these taxa would benefit from re-diagnosis, and it would be an exercise in futility to place the fossil within these groups when adequate definitions do not necessarily exist. Fortunately, and perhaps not unexpectedly, all three share a similar banding pattern and thinness of bands as *Pselliopus*, making placement in any of these genera as unlikely as in *Pselliopus*.

A detailed discussion of the genitalia and its use in placing the taxon may be found below under the subheadings Preservation and Phylogenetic Signal.

**III. Undescribed Extinct Taxon.** Placing the fossil taxon in any of these four extant genera (hereafter, "banded" genera) makes a definitive statement about the evolution of the lineage, which is unjustified based on the evidence above. Thus, the fossil requires a new genus to be erected for its reception. Hence, *Aphelicophontes*.

**Preservation.** The specimen first and foremost represents a remarkable case of preservation. For one, it possesses a near fully-articulated external morphology, which is uncommon for a relatively delicate-bodied insect. Second, it is fortunate to have a specimen that was split through the coronal plane in essentially equal portions, affording comparison between two views of the same anatomical regions. Lastly, it is exceptional to have a clear, detailed view of the relatively delicate insect genitalia, given the prolonged and unrelenting
pressure inherent to fossilization by compression. Indeed, many genitalic structures, both external and internal, are not only present in the holotype but referable to those found in extant Reduviidae.

Of the external genitalia, a pygophore, or genital capsule, is clearly visible in the specimen. This allows the sex of the specimen to be identified as a male, and therefore, allows several somatic predictions to be made about A. iuddorum. First, it is likely that this specimen does not represent the upper size limit of this species, as females are typically bigger than males in extant harpactorines (pers. obs.). Second, a single abdominal band likely does not correspond to a single connexival segment. This is supported by three points. First, if this were the case, the pygophore would be reaching cephalad through at least the three rearmost pre-genitalic tergites, which is not the case for reduviids (Davis 1966). This is a useful proxy, because the connexival sutures were not preserved in the fossil. Second, there appear to be eight connexival segments on one side, whereas only six connexival segments should be present. In Reduviidae, the first tergite is subsumed by the metathorax, and the eighth and ninth tergites form part of the genitalia. Third, the connexival bands do not correspond with segments in extant genera such as Pselliopus (pers. obs.). The inner rim of the pygophore is visible in a few areas, particularly near the anterior margin. The shape of the median process of the pygophore also is clearly visible in the fossil. Typically a vertical or oblique structure in most reduviid genera, it is fortunate that the structure apparently remained virtually undistorted during its passage from the vertical to horizontal plane. This median process is frequently used in the alpha taxonomy of the family, making it potentially important for placing the fossil.
The parameres, if even present in *A. iuddorum*, are unpreserved, and this lack of parameres is surprising in some ways. On the one hand, the parameres are sclerotized structures, firmly anchored inside the pygophore and therefore, partly shielded. Yet, they articulate with the pygophore at the point of attachment, thereby providing a natural point of *detachment*, suggesting it would not be difficult for them to be lost, especially under harsh conditions. Furthermore, parameres generally are not particularly large or robust (examples in Fig. 1.13). However, it should be noted that some harpactorine genera have the parameres either reduced, i.e., *Ischnoclopius* Stål, 1868, or secondarily lost, i.e., *Atopozelus* Elkins, 1954, *Atrachelus* Amyot & Audinet-Serville, 1843, *Orbella* Maldonado, 1987; thus, it is not possible to conclude whether *Aphelicophontes* actually possessed parameres. Incidentally, the "banded" genera all possess the slender, slightly clavate parameres, typical of harpactorines.

The previous structures are external and sclerotized and thus could be expected to fossilize much in the same way as the thorax or abdomen; however, what really makes the preservation remarkable is the presence, and identifiable nature, of the internal genitalia. Two structures clearly anchor an interpretation of the preserved structures: the pedicel, a sclerotized often Y-shaped structure linking the articulatory apparatus with the anterior portion of the dorsal phallothecal sclerite, and the ponticus basilaris (=basal plate bridge), which links the two lateral arms of the articulatory apparatus (Davis 1966, Weirauch 2008). Once these two structures are accepted, other sclerotized portions of the phallotheca are more easily interpreted. The articulatory apparatus overlaps sclerotized areas that might be the anterior portions of the dorsal phallothecal sclerite. This sclerite extends caudad beyond the reach of the articulatory apparatus, which matches the general condition of reduviid internal genitalia.
as evidenced by figures presented by Davis (1966, 1969), Weirauch (2008), and Berniker et al. (2012). These internal genitalic structures also serve to orient the specimen: the part is the dorsal half of the specimen, whereas the counterpart representations the ventral portion. This is because the pedicel and basal plate are located dorsal within the genital capsule, and in the fossil, these two structures are more wholly preserved in the part. However, it is important to remember that the view afforded is from inside the insect, as it has been split through the coronal plane; thus, the part gives a ventral view of the dorsum and the counterpart gives a dorsal view of the venter. One assumption made is that non-sclerotized structures have not been preserved; therefore, the bulk of the phallosoma and endosoma would be expected to be absent.

The color pattern is equally well-preserved. *Aphelicophontes* possesses three thick dark bands per femoral and tibial segment, as well as alternating light and dark bands on the connexiva. The symmetry and consistency of the banding, particularly when comparing right and left limbs, suggests that this is no artifact of preservation but a real feature of the insect. Furthermore, preservation of a banded color pattern is known from other extinct Reduviidae (see Generic Identity of the Fossil: II. Already-described Extant Taxon above), and many extant species possess similar banding patterns, i.e., New World "banded" genera; some Old World taxa, including species of *Velinus* Stål, 1865, *Cosmolestes* Stål, 1866, *Sphedanolestes* Stål, 1866. Admittedly, there are dissimilarities between the banding configuration of these genera and *Aphelicophontes*, and these differences have been coopted as part of the defining characteristics of this new genus.
The preservation of the body and other somatic structures is helpful in some respects but deficient in others. In addition to the general habitus and the retention of most limbs and antennal segments (previously discussed), the proportions of the regions of the head, as well as the length of the femora, are useful, particularly in discriminating between various harpactorine genera. However, there are inadequacies among several preserved somatic characters. The internal view may be responsible for the obscurity of the rostrum. The outline of the thorax and scutellum is essentially obliterated in each of the specimens. Additionally, the wing venation is mostly obscured, although a few conspicuous veins for Reduviidae (as per Davis 1961) are presumed discernable, i.e., M, Cu or Pcu. There also appears to be either an unpreserved area or potential displacement between the posterior portion of the thorax and the anterior portion of the abdomen. Nevertheless, without the somatic details, the specimen likely could not have been assigned to so specific a lineage.

**Phylogenetic Signal.** The initial emphasis placed on the phylogenetic signal in color pattern requires further comment. Some cases have shown color pattern to be an important diagnostic character in the family, particularly at the species-level (e.g., Costa Lima 1940, Lent & Wygodzinsky 1979, Maldonado & Lozada Robles 1992, Melo 2007, Zhang & Weirauch 2011, van Doesburg & Forero 2012). Furthermore, the four "banded" genera of the New World are well-defined by the general banding pattern of the abdomen and limbs, and *Aphelicophontes* matches well this pattern in general scheme. Thus far, relationship between these extant genera have been supported molecularly (Hwang & Weirauch 2012, Zhang & Weirauch 2014), although this has not yet been deeply explored. However, color pattern is not always reliable as a diagnostic character, especially in Reduviidae (e.g., Ambrose & Livingstone 1987,
McPherson et al. 1991, Forero et al. 2010, Zhang & Weirauch 2011, Berniker & Weirauch 2012, Swanson 2015). Furthermore, similar "banded" patterns appear in some Old World harpactorines, such as members of Velinus, Cosmolestes, Sphedanolestes, genera that are neither closely related to the New World taxa, nor closely related to each other (Zhang & Weirauch 2014). This suggests that this type of pattern may evolve independently under particular ecological circumstances. Thus, it seems that the signal in color pattern alone varies in utility.

Yet, coupling color pattern with other characters seems to fortify the phylogenetic position of the fossil. Song & Bucheli (2010) already have presented a case for the strength of phylogenetic signal of male genitalia, as a composite of quickly evolving characters, and as mentioned throughout the original description of the new species and the Generic Identity section, several genitalic characters present in the fossil corroborate affinities initially based on color pattern. Within the external genitalia, the apex of the pygophore further supports a hypothesized relationship with Pselliopus and related genera: in Pselliopus, a similar triangular, possibly cleft, median process is found in several extant species, e.g., Pselliopus majestus Brailovsky & Barrera, 2004; Pselliopus mexicanus Champion, 1899; Pselliopus zebra (Stål, 1862), Pselliopus karlenae Hussey, 1954 (see Brailovsky & Barrera [2004]). Additionally, the shape of the arms of the basal plate differs markedly between the four "banded" genera, with the arms roundly and evenly diverging caudal in Pselliopus, straightly diverging (V-shaped) in Pyrrhosphodrus, and extending more-or-less parallel in Cosmoclopius. Ecelonodalus dysreutus Elkins & Wygodzinsky, 1957 appears somewhat intermediate between Pselliopus and Pyrrhosphodrus. Internally, the arms of the basal plate in Aphelicophontes (Figs. 1.11–12)
appear to be more similar to *Pselliopus* (Fig. 1.13). Unfortunately, the ponticus basilaris in the fossil specimen is somewhat poorly preserved, although the basic shape still most closely approaches *Pselliopus*. Hence, the hypothesized position of *Aphelicophontes* is basal to the genus *Pselliopus* (Fig. 1.14).

In some cases, the signal from these morphologies appears to be mixed or diluted, particularly at wider scopes. Members of *Castolus*, a genus not closely related to the "banded" genera, possess similar median triangular structures on the apical margin of the pygophore (compare Maldonado 1976, Brailovsky & Barrera 2004, Brailovsky et al. 2007). Furthermore, it is evident from figures presented by Forero & Weirauch (2012; Figs. 37–46) that morphological structure of the pygophore varies widely even within a single tribe. As examples, the median process or apex of the pygophore includes from bifurcate, convex, triangular, and truncate forms, and the length of the capsule itself, as well as the shape of the anterior and posterior openings varies between taxa. The basal plate is similarly mixed in its phylogenetic signal. In some ways, the condition of the basal plate of *Cosmoclopius* more closely resembles the unrelated *Castolus*, both in the basal plate arms and in the quadrate anterior rim of the pygophore. Additionally, the basal plate of the three species of *Ecelonodalus* exhibit the same triangular form reminiscent of the "banded" genera (excluding *Cosmoclopius*); yet, they vary intraspecifically as much as some intergeneric differences (e.g., *Ecelonodalus maderus* Elkins & Wygodzinsky, 1957 narrow as in *Cosmoclopius* & *Castolus* [Elkins & Wygodzinsky 1957, Figs. 17, 23, 29]). Conversely, Melo & Coscarón's (2004, p. 53, basal plate arms erroneously referred to as "phallus" in caption) survey of several species of *Cosmoclopius* revealed conserved parallel arms fit for generic diagnosis. Similarities between congeneres also are shown within *Pselliopus*,

29
Castolus, and Sinea Amyot & Audinet-Serville, 1843 in Fig. 1.13, again suggesting that the basal plate arms may be of phylogenetic utility. It seems telling that many of these characters, despite their use in the alpha taxonomy of the group, have not been used diagnostically at a supraspecific level. The existence of negative examples seems to dictate caution in relying on some of these characters to inform phylogenetic hypotheses, although utility of each may require assessment on an individual basis in a comparative framework.

The bright flashy (often orange) coloration of species of Pselliopus raises the question of potentially aposematic properties in the "banded" assassin bugs. However, there are several complications. The first is that there is no empirical evidence that species of Pselliopus are aposematic. To make this claim requires a working definition of aposematic and the bipartite one proposed by Harvey & Paxton (1981) is here adopted: an organism must be unpalatable and easily recognizable (usually via bright coloration) by predators. It is the former criterion for which evidence is lacking in regards to Pselliopus. Additionally, no study has been done to suggest that such a banding pattern would render the insect conspicuous in its natural habitat. This lack of data exists despite several studies on the biology of Pselliopus (i.e., Readio 1927, Swadener & Yonke 1975). Conversely, it is conceivable that such patterns could render the insect more cryptic, as several studies have suggested that apparent aposematic insects appear cryptic in specific situations (Rothschild 1964, Edmunds 1974, Papageorgis 1975, Endler 1978, Järvi et al. 1981, Fabricant & Herberstein 2015). Furthermore, the ringed pattern of Aphelicophontes, despite its similarity to the "banded" genera, does not guarantee similar integumental color. Even within the extant genera, the color palette can differ widely between congers: Pselliopus marmorosus Brailovsky, Mariño & Barrera, 2007 and P. zebra are
conspicuously blackish species, whereas many other species, notably *Pselliopus cinctus* (Fabricius, 1776) and *P. barberi*, are bright and/or pale in color. A similar dichotomy is present in *Cosmoclopius*, with the dark *Cosmoclopius poecilus* (Herrich-Schaeffer, 1846) strongly contrasting the palette of *Cosmoclopius pallidus* Berg, 1879; *Cosmoclopius nigroannulatus* (Stål, 1860); and *Cosmoclopius annulosus* Stål, 1872. Further work to test the aposematic potential of extant genera is certainly warranted, although extending this notion to *Aphelicophontes* seems unsupportable at this time.

**Biogeographic Implications.** The fossil species comes from the central United States. Of the four "banded" genera, only *Pselliopus* occurs in North America, being found from southern Canada south to northern South America (Putshkov & Putshkov 1988, Maldonado 1990, Swanson 2011). *Cosmoclopius*, *Ecelonodalus*, and *Pyrrhosphodrus*, on the other hand, are restricted to South America (Putshkov & Putshkov 1988, Maldonado 1990). The genitalic characters already suggest that *Aphelicophontes* is most closely related to *Pselliopus*, and the biogeography of the "banded" genera seems to support such a hypothesis. Incidentally, the southern South American species currently placed in *Pselliopus* belong to a different genus (Swanson, in prep.), giving *Pselliopus sensu stricto* a currently-hypothesized center of diversity in Mexico. However, this still leaves an interesting biogeographical question about the overall evolution of the "banded" genera. *Aphelicophontes* was present in North America, presumably isolated from the current South American genera, well before the closing of the Panamanian isthmus (ca. 3–20 Ma: Iturralde-Vinent & MacPhee 1999, Bacon et al. 2015). If they are indeed related, how did these relationships produce the distributional patterns seen today?
As discussed under Geological Settings and Stratigraphy, Eocene Colorado, from whence *Aphelicophontes* came, was likely a much moister environment. At least one extant species, *Pselliopus barberi* Davis, 1912 has been associated with American sycamore (*Platanus occidentalis* L.), a tree common in riparian areas. Therefore, it remains possible that insects of this lineage prefer wetlands and riparian environments. However, whether this affinity applies to other species of *Pselliopus* is poorly studied.

**Further Directions.** The level of phylogenetic signal and the ability to place this taxon within the phylogeny of the contemporary family allows this fossil to be integrated as a new fossil calibration point and inform a hypothesis for the divergence date of portions of the tree (see Chapter 2).

This study and the conclusions offered herein would greatly benefit from augmented sampling of extant taxa. Particularly salient, species of *Ecelonodalus* have not been included in any molecularly-inferred phylogenetic analyses, and a single species of *Pyrrhosphodrus* appears in only one (i.e., Zhang & Weirauch 2014). Inclusion of these taxa, in addition to other species of *Cosmoclopius* and *Pselliopus*, could strengthen the hypothesis of relatedness between these genera, thereby allowing more powerful inferences surrounding color and color pattern. Furthermore, genitalic differences discussed under Phylogenetic Signal are based mostly on one or two representatives per genus, and dissection of congeners is needed to more fully assess the strength of phylogenetic signal in these characters at genus-level. Greater intergeneric sampling within the subfamily also will aid this endeavor. This study highlights the potential for a novel system in the study of aposematism, which, if confirmed, could in turn have implications for *Aphelicophontes* and extant Reduviidae using such phylogenetic tools as
ancestral state reconstruction. Finally, for further areas of study involving fossil reduvioids, see the Epilogue.

**Concluding Remarks.** This is not the first known instance of such remarkable preservation in Hemiptera. Shu et al. (2013) described a new species based on two procercopids preserved *in capulo* as compressions. In these specimens, several structures, including the pygofer and aedeagus, are each visible and shown where they functioned during mating. The authors also concluded that this mirrored how extant species mate today. This suggests a sort of evolutionary uniformitarianism, the idea that the same evolutionary forces that have shaped more contemporary taxa were at work during earlier geological periods, an idea not without critics (see overview by Erwin 2011). Regardless, *Aphelicophontes* remains the first of its kind for fossil Reduvioidea. It remains one of the oldest definitive reduviid fossils described (taking into account the wide age range placed on Baltic amber), being slightly younger than *Hymenopterites deperditus* Heer, 1870 (see discussion in Wappler et al. 2013). It also contributes strong evidence that the genitalia were similar in the group and likely under the same selective pressures discussed by Song & Bucheli (2010) for the past 50 million years.

**LITERATURE CITED**

Adobe Systems, Inc. 2014. Adobe Illustrator CC (version 2014.0.0) [software].

Adobe Systems, Inc. 1990–2011. Adobe Photoshop CS5 Extended (version 12.1 x64) [software].


Figure 1.1. Present-day geography of the Green River Formation. Modified from USGS-OSAT (2010).
Figure 1.2. General location and composition of the Green River Lake Complex in the Early Middle Eocene (ca. 52 Ma). Modified from Grande (2013).
Figure 1.3. Holotype (part) of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.4. Holotype (counterpart) of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.5. Diagrammatic sketch of holotype (part) of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.6. Diagrammatic sketch of holotype (counterpart) of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.7. Paratype of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.8. Diagrammatic sketch of paratype of *Aphelicophontes iuddorum* n. sp. Scale bar = 2.0 mm.
Figure 1.9. Tentatively-placed specimen of *Aphelicophontes iuddorum*?. Scale bar = 2.0 mm.
Figure 1.10. Examples of species within the complex of "banded" New World harpactorine genera. *Castolus ferox* is included for comparison, despite not belonging to this complex.
Figure 1.11. Genitalia of *Aphelicophontes iuddorum* n. sp. from holotype (part): (A) image; and (B) line drawing. Scale bar = 0.2 mm.
Figure 1.12. Genitalia of *Aphelicophontes iuddorum* n. sp. from holotype (counterpart): (A) image; and (B) line drawing. Scale bar = 0.2 mm.
Figure 1.13. Excised pygophores of various harpactorines.
Figure 1.14. Dissected pygophores of Fig. 1.13 arranged according to the most recently inferred relationships for Harpactorini (Zhang & Weirauch 2014).
Table 1.1. Generalized geologic time scale for *Aphelicophontes iuddorum* (highlighted).
Modified after the International Chronostratigraphic Chart from Stratigraphy.org (ICS 2015).

<table>
<thead>
<tr>
<th>Eon</th>
<th>Era</th>
<th>Period</th>
<th>Epoch</th>
<th>Stage</th>
<th>Onset (Ma)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phanerozoic</td>
<td>Cenozoic</td>
<td>Paleogene</td>
<td>Oligocene</td>
<td>Chattian</td>
<td>28.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Rupelian</td>
<td>33.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Priabonian</td>
<td>38.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Bartonian</td>
<td>41.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lutetian</td>
<td>47.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ypresian</td>
<td>56.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Thanetian</td>
<td>59.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Selandian</td>
<td>61.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Danian</td>
<td>66.0</td>
</tr>
</tbody>
</table>
CHAPTER 2: RE-EXAMINATION OF THE DIVERGENCE DATES OF REDUVIOIDEA (HETEROPTERA) IN LIGHT OF NEW FOSSIL DATA

Keywords. Systematics, taxonomy, calibration, phylogeny, assassin bug, Reduviidae.

INTRODUCTION

Reduciidae is a family of predaceous true bugs containing greater than 7000 described species (updated from Maldonado 1990). Being such a large and varied group, this family naturally has attracted attention regarding its inner relationships. Usinger (1943) and Carayon et al. (1958) conducted two of the earlier studies looking at intra-reduviid relationships, although having taken place well before the advent of genetic sequence data and computationally-powerful resources, the schemes proposed in those studies are largely obsolete. Weirauch (2008) inferred the first modern phylogeny, based on morphological dataset of 162 characters and 75 taxa. As a follow-up to that analysis, Weirauch & Munro (2009) provided the first molecularly-inferred phylogeny of the group, using four regions representing both mitochondrial and nuclear genes. Hwang & Weirauch (2012) built on that dataset and contributed the first estimation of divergence dates for the Reduviidae, wherein eleven fossil data points were used to calibrate a tree containing approximately 170 reduviid taxa (and eight heteropteran outgroups). Subsequent studies (Zhang & Weirauch 2014, Gordon & Weirauch 2016), improved taxon sampling, while maintaining a largely subfamily-specific focus (Harpactorinae, Salyavatinae, respectively). Zhang et al. (2016) integrated transcriptomic data in an effort to resolve the backbone of the tree, while exploring the multiple origins of raptorial forelegs within the family. Thus, the foundation has been laid for continued and improved phylogenetic study in Reduvioidea.
This study seeks to build on that foundation by integrating *Aphelicophontes iuddorum* gen. et sp. nov., the new taxon described in the previous chapter, as a new fossil calibration. It was hypothesized that the inclusion of this fossil would result in older estimates for the divergence times of several clades within the group and possibly for the whole of Reduviidae. This study also assessed those fossils used to calibrate previous studies (i.e., Hwang & Weirauch 2012), and explores potential problems associated with particular fossil taxa.

**MATERIALS AND METHODS**

**Sequences.** Sequences for each of five gene regions included in Hwang & Weirauch (2012) were downloaded from GenBank (Benson et al. 2013, NCBI 2015). These regions comprised four ribosomal gene regions (16S rDNA, 18S rDNA, 28S region D2 rDNA, 28S regions D3–D5 rDNA) and one nuclear protein-coding gene (wingless); hereafter, these regions will be referred to as 16S, 18S, 28SD2, 28SD3D5, and Wg, respectively. This dataset was chosen, because it represents one of the largest available, in terms of genes and taxa sampled, for the family; subsequent analyses (Zhang & Weirauch 2014, Gordon & Weirauch 2016, Zhang et al. 2016) had decreased taxon-sampling, i.e., focused on specific clades within the family, and inconsistent overlap in genes selected. A list of specimens and GenBank Accession Numbers are included in Appendix A. For information regarding specimens identification and vouchering, as well as extraction and sequencing of genetic material, see Hwang & Weirauch (2012).

**Alignment.** Sequences were aligned on-line using The GUIDANCE2 Server (Sela et al. 2015; http://guidance.tau.ac.il/ver2/), with the MAFFT alignment algorithm, 100 bootstrap repeats, 1000 iterations, and localpair (l-ins-i) pairwise alignment. All sequences, except for one in 28SD2, had a score above 0.6; this single sequence was removed and the gene region re-
aligned without it. Columns with < 0.930 confidence scores were discarded, except in the case of Wg, in which all column confidence scores were higher than 0.930; here, scores lower than the next highest confidence score (0.999) were discarded. The GUIDANCE alignment scores were as follows: 16S: 0.956950; 18S: 0.983692; 28SD2: 0.879951; 28SD3D5: 0.939811; and Wg: 0.999880. Sequences were concatenated in Mesquite version 3.04 (Madison & Madison 2009).

**Partitioning.** Fully concatenated sequences were loaded in PartitionFinder (Lanfear et al. 2012) in order to test the partitioning of the gene regions and to select an appropriate model of sequence evolution for each partition. The following settings were used: linked branchlengths, Bayesian Information Criteria (AIC), and greedy search scheme. Six iterations were performed, corresponding to each combination of RAxML, MrBayes, and BEAST with 4- and 5-partitioned schemes, viz. 28S combined or separated into 28SD2 and 28SD3D5. In the 5-partitioned scheme under models available to MrBayes and BEAST, PartitionFinder combined 28SD2 and 28SD3D5 into one partition. In the 5-partitioned scheme under models available to RAxML, PartitionFinder combined 18S and 28SD3D5 into one partition, although this approach was rejected by me because they represent different gene regions. In the 4-partitioned scheme, viz. 28S combined, PartitionFinder corroborated the partitions for each of the three model sets. Thus, all tree inferences involved the 4-partition set. For inferring a tree under the models available to RAxML, PartitionFinder selected GTR+I+G for all partitions; selection of GTR+I+G for all partitions parallels the analysis of Hwang & Weirauch (2012). For inferring a tree under the models available to MrBayes and BEAST, PartitionFinder selected GTR+I+G for 16S and Wg and selected SYM+I+G for 18S and 28S partitions.
Maximum Likelihood Analysis. A maximum-likelihood (ML) tree was inferred using RAxML v8.2.4 (Stamatakis 2014), after compiling the PTHREADS-AVX version. The analysis was run using for 1000 bootstrap replicates, using rapid bootstrapping, and a substitution model of GTR+I+G for all partitions. Three separate iterations were run, and each recovered largely congruent topologies for strongly-to-moderately supported nodes (bootstrap values ≥ 70). Strings used to call RAxML are included in Appendix B. Trees were viewed and further manipulated in FigTree v1.4.2 (Rambaut 2014).

Bayesian Analysis. A Bayesian tree was inferred using MrBayes v3.2.6 (Ronquist & Huelsenbeck 2003). This was run using MrBayes on XSEDE via the server on CIPRES Science Gateway v3.3 (Miller et al. 2010). Settings included: nruns=4, 100 million generations, sampling every 5000, savebrlens=yes, a substitution model of GTR+I+G for 16S and Wg, and a substitution model of SYM+I+G for 18S and 28S. MrBayes blocks of the Nexus file are included in Appendix B. The output was loaded into Tracer v1.6.0 (Rambaut et al. 2014), where convergence was visually assessed via the trace plot (all ESS values well over 200). A burn-in of 25% was removed, and the resulting trees were summarized in a majority-rules consensus (MRC) tree. The tree was viewed and further manipulated in FigTree v1.4.2 (Rambaut 2014).

BEAUi2. Parameters in BEAUi2 (part of BEAST2 package) were set as following:

Partitions tab: 4 partitions (as discussed above), unlinked site models, unlinked clock models.

Site Model tab: Substitution Rate: 1.0 (not estimated; default) Gamma Category Count: 4, Shape: 1.0 (estimated), Proportion Invariant: 0.1 (estimated), Substitution Model: RB. These settings were used for all partitions. Despite agreement between Hwang & Weirauch (2012)
and the output of PartitionFinder in implementing GTR+I+G (or SYM+I+G) for all partitions, the RBS package for BEAST2 was downloaded and the Reversible-jump Based (RB) substitution model (Green 1995) was used for all partitions. This was done because the RB model continually samples model space at no additional computational costs (Bouckaert et al. 2014), thereby lessening the chances of overparameterization.

**Clock Model tab:** Relaxed Clock Log Normal. This was used for all partitions.

**Priors tab:** Yule Model. See Table. 2.1 for settings of the fossil calibration priors. Uniform priors on the uclMean were replaced with a diffuse gamma prior (alpha = 0.001, gamma = 1000.0, offset = 0.0), according to recommendations by the developers of the software on public forums (Google Group: beast-users).

**MCMC tab:** Chain Length: 500000000, tracelog = 5000.

Other settings not mentioned were left in the default configuration. Tip dates were not used.

**BEAST2.** Divergence time estimates were carried out in BEAST2 v2.3.2 (Bouckaert et al. 2014), using Markov Chain Monte Carlo simulation. This was run using BEAST2 on XSEDE via the server on CIPRES Science Gateway v3.3 (Miller et al. 2010). As mentioned, the analysis was run for 500 million generations, sampling every 5000 generations. The output was loaded into Tracer v1.6.0 (Rambaut et al. 2014), where convergence was visually assessed via the trace plot (convergence was not achieved as several parameters had ESS values below 100). The output was loaded into TreeAnnontator v2.3.2, part of the BEAST2 package. The following settings were used: Burnin percentage: 25%, Target tree type: Maximum clade credibility (MCC) tree,
and Node heights: Mean heights. Posterior probability limit was left at 0.0, the default setting. Trees were viewed and further manipulated in FigTree v1.4.2 (Rambaut 2014).

Fasta files and Nexus files were variously manipulated throughout the study with TextWrangler v5.0 (Bare Bones Software, Inc.) and Mesquite v3.04 (Madison & Madison 2015).

**Use of Fossil Calibrations.** The use of fossil data is an integral part of calibrating trees, and many factors bear consideration. The specimen-based method was implemented (Parham et al. 2012), and the information associated with each fossil may be found in the annotated catalog (Chapter 3). The fossil taxa were used to calibrate nodes, rather than used as tip taxa (Arcila et al. 2015). Fossils were not placed on single taxon sets, i.e., *Neocentrocnemis* sp., *Emesaya* sp., *Empicoris* sp., although viable alternatives, e.g., consistently recovered sister-groups, were found in each of these cases. Each fossil has been considered for use in this study and the reasons for exclusion are summarized in Table 2.3.

**Figures.** The Bayesian tree was chosen as the presented tree, because (1) BEAST is a Bayesian inference program; (2) a Bayesian inference of topology was not performed in Hwang & Weirauch (2012), despite well-known biases in both ML and Bayesian methods (Alfaro et al. 2013); and (3) it was desired to highlight more strongly the areas of uncertainty, as available in a MRC tree. However, highly-supported branches have been annotated with bootstrap values from a ML analysis. Figures were manipulated in Adobe Illustrator CC and Adobe Photoshop CS5 (Adobe Systems Inc., San Jose, CA). The formatting of the trees was modeled after Hwang & Weirauch (2012) to facilitate comparison.

**Taxonomy.** I have purposefully used certain family-level names already in existence, in accordance with the Code (ICZN 1999, Art. 11.7), in response to various taxa previously shown
to be polyphyletic: Acanthaspidae Stål, 1874 (=Acanthaspida Stål, 1874, pp. 4, 63; =Acanthaspis clade sensu Hwang & Weirauch 2012) (stat. nov.), Lenaeninae Distant, 1904 (=Lenaemia Distant, 1904, p. 275; =Velitra clade sensu Hwang & Weirauch 2012) (stat. nov.), Psophidinae Distant, 1904 (=Psopharia Distant, 1904, p. 243; =clade containing Psophis Stål, 1863) (stat. nov.), in addition to resurrecting Eupheninae Miller, 1955. Many of these clades possess high support values, in addition to shared natural history, suggesting that they are real assemblages. Naturally, these taxa will require focused revision and updated diagnoses, but it is desirable to utilize names already in existence when discussing them. I have specifically avoided referring to Reduviinae sensu stricto in the Results and Discussion to prevent confusion while discussing the polyphyly of Reduviinae sensu lato, preferring to continue use of the Reduvius clade for the present time.

RESULTS

Inference of Tree in MrBayes and RAxML. The topology of the trees recovered from the Bayesian and ML analyses (Figs. 2.1, 2.2) were largely congruent with Hwang & Weirauch (2012); this makes sense as the results were generated from largely similar datasets. Among major divisions, Reduviidae was again recovered as monophyletic, as was a monophyletic "Phymatine Complex" sister to the rest of the family or "Higher Reduviidae".

Several major family-level divisions were recovered as monophyletic, i.e., Ectrichodiinae, Peiratinae, Phymatinae, Stenopodainae, as well as the tribes Apiomerini and Harpactorini. Most minor subfamilies also were recovered as monophyletic but were represented by two to three taxa: Holoptilinae, Microtominae (=Hammacerinae), Physoderinae,
Saicinae, Salyavatinae, Tribelocephalinae, and Visayanocorinae. Centrocnemidinae and Vesciinae each were represented by only a single taxon.

Many of the non-monophyletic subfamilies revealed in Hwang & Weirauch (2012) also were recovered. The polyphyletic nature of the dumping ground subfamily Reduviinae was recovered, and specific groups within each clade were largely identical to those found in Hwang & Weirauch (2012). The paraphyly of Triatominae with respect to *Opisthacidius* Berg, 1879 was identical. Lastly, the polyphyly of Cetherinae also was recovered, being split between the Old World taxa (=Cetherinae) and those in the New World (=Eupheninae).

Relationships between major subfamilies, particularly sister-groups, were similarly recovered. These include those within the "Phymatine Complex", Tribelocephalinae+Ectrichodiinae, and Stenopodainae+*Zelurus* clade. There were notable exceptions in Saicinae+Emesinae and separation of Visayanocorinae (all traditionally considered part of the "Emesine Complex") and the relative position of Ectrichodiinae+Tribelocephalinae within the Higher Reduviidae. There also were some minor differences in intergeneric relationships, although this was not the focus of the study and will not be discussed.

**Estimation of Divergence Dates in BEAST2.** The topology of the tree inferred by BEAST2 (Fig. 2.3) is largely similar to both Hwang & Weirauch's (2012: Fig. 4) and to the Bayesian and ML analyses of the present study. Perhaps the most conspicuous difference is the placement of Microtominae as sister to the rest of Reduviidae, rather than as part of the "Phymatine Complex".

However, the divergence estimates differ radically from those of the previous study. As expected, the new fossil pushed the divergence of *Pselliopus* back, here, to approximately 60
Ma. This, in turn, pushed the divergence of Harpactorini back to approximately 122 Ma, resulting in a vast increase in the age (approximately 50 Ma older than Hwang & Weirauch 2012) for the tribe. Similarly, nodes other than those separating terminal species-level taxa have been pushed backed substantially (see Table 2.2), including the divergence of Reduviidae from Heteroptera to around 344 Ma, which effectively doubles the age of the family. In line with these results is major expansion in the Higher Reduviidae around 250–210 Ma. However, it is essential to note that there are extremely large confidence intervals placed on these estimates, and there are problems in relying on the conclusions of this study (see Problems with Analysis below).

**DISCUSSION**

**Divergence Dating of the Reduvioidea.** Initially, it should be noted that differences in topology between the present study and Hwang & Weirauch (2012), e.g., paraphyly of Emesinae with respect to Saicinae, unresolved nature of (*Neostachyogenys, Reduvius sonoraensis*, Apiomerini, *Leogorrus+Reduvius* clade, Harpactorini), generally occur at nodes that received low support in both studies; thus, differences in topology are easily reconciled. These differences will not be discussed further in this study.

As mentioned, this study seems to support the idea that Reduviidae, as a whole, is much older than previously thought. To some extent, this is easily seen even without an analysis via BEAST2. In the chronogram of Hwang & Weirauch (2012: Fig. 4), the split between *Pyrrhosphodrus* and *Pselliopus* is ascertainable and dates to younger than 25 Ma. The taxonomic treatment of *Aphelicophontes* (see Chapter 1) equates it to a *Pselliopus* stem-group dated at approximately 50 Ma. Thus, if the systematic position of this fossil is accepted, it must
push this node back at least 25 Ma. The results of this study corroborate this logic, as the node for the split of *Pyrrhosphodrus* and *Pselliopus* occurs at 58.48 [95% HPD: 49.25, 72.39] Ma. This seems to support the original hypothesis of an older age for Reduviidae. Other studies, e.g., Patterson & Gaunt (2010), Wappler et al. (2013), have supported this idea.

Greater uncertainty rests in whether other branches would elongate similarly and if so, by how much. The results reported herein suggest that the divergence dates of other clades within the reduviid phylogeny would indeed get pushed back. However, mean differences for a select set of nodes give a difference in age ranging from 44–165 Ma (see Table 2.2). This range noticeably involves a clear bias: greater differences toward the base of the phylogeny, e.g., Reduviidae, Higher Reduviidae, Phymatinae; in other words, older nodes get older than younger nodes. Regardless, the magnitude of "push-back" makes it difficult to accept these conclusions.

**Problems with Analysis.** Difficulty comes in the incongruity of the projected reduvioid divergence dates with those previously estimated for higher taxa, e.g., Heteroptera, Insecta. Contemporary analysis (Misof et al. 2014) places the origin of Insecta in the Ordovician, approximately 465 Ma. This approximate date is backed by morphological fossil evidence, with the oldest insects dating to the Devonian, being approximately 400 Ma (Engel & Grimaldi 2004, Grimaldi & Engel 2005). While certainly not impossible, this makes a Carboniferous origin (ca. 360–300 Ma) of a single fairly-derived heteropteran family highly improbable, especially considering that Misof et al. (2014) dated the origin of Hemiptera+Thysanoptera (or more generally, orders within Paraneoptera) to this period. Both Li et al. (2012) and Misof et al. (2014: Fig. 2, Node 35) found a Triassic origin of approximately 245 Ma for Heteroptera based
on molecular evidence, although Grimaldi & Engel (2005) suggested a Permian origin for the suborder based on fossils. The former hypothesis may be slightly conservative given the presence of the reduvioid genus *Ceresopsis* from the Early Jurassic (Shcherbakov 2007), leaving only approximately 70 Ma for diversification of the infra- and supraordinal taxa before a basal reduvioid is known to have existed. Furthermore, the superfamily Reduviioidea belongs to the infraorder Cimicomorpha, a latter being a derived lineage far from the base of the heteropteran phylogeny (Wheeler et al. 1993, Weirauch & Schuh 2011).

Details from the analysis itself suggest caution in accepting this results. The effective sample size (ESS) during the MCMC tree search in BEAST2 obtained suboptimal levels (mostly under 50) for several important paramaters (as assessed in Tracer): posterior, prior, TreeHeight, YuleModel, birthRate, as well as the mean and variance for rate for each partition, and logP and mrcatime for 5 of 7 fossil calibrations. In other words, convergence was not achieved for this analysis, effectively rendering the results as unsupportable. It is difficult to know the reason for the failure in convergence, and many different iterations, i.e., removing genes, using different substitution models, supplying guide trees, were tried without success in an attempt to satisfy this criterion in the preliminary portion of this study. As a tree with high support values is achieved in MrBayes without any timing data, the source of the problem would appear to be either the fossil calibrations or the clock model, or likely some combination of both. However, low ESS values are recovered in the same parameters when fossils are systematically removed (two fossils used in minimum and both achieving high ESS values in logP and mrcatime). Thus, it seems there is some interaction between several of the parameters, as suggested by Andújar et al. (2012), that makes it difficult for the program to achieve convergence. No matter the
reason, divergence dates need to be re-inferred in an analysis that achieves convergence in order to have any confidence in its estimates.

**Improvements from Previous Study.** Despite the poorly-supported results, this study introduces several improvements from the previous divergence estimate for the group by Hwang & Weirauch (2012). First, it is imperative to have confidence in which node fossils calibrate on the tree, as this can have important implications for inference (Parham et al. 2012). An obvious example where such confidence breaks down is in reduviid fossils described by Heer, which have been virtually unstudied since their description in the mid 19th century. For example, *Peirates oeningensis* Heer, 1853 (Miocene, compression, Öhningen), used as a calibration point in the previous study, likely does not represent a peiratine and probably is conspecific with one of Heer's *Harpactor* spp. (pers. obs.). In this same vein, one calibration point, *Stenopoda oeningensis* Heer, 1861 (Miocene, compression, Öhningen), is not based on a described specimen; it is a *nomen nudum*. Furthermore, it does not belong in the New World genus *Stenopoda* Laporte, 1833, although it remains possible that it is correctly placed in the subfamily (pers. obs.), belonging to one of the three stenopodaine genera found in Europe, viz. *Pygolampis* Germar, 1817, *Sastrapada* Amyot & Serville, 1843, or *Oncocephalus* Klug, 1830. *Arilus faujasi* Riou, 1999 (Miocene: Tortonian, compression, Ardeche), similarly does not belong in *Arilus* Hahn, 1831, meaning the fossil is likely calibrating the wrong branch in Hwang & Weirauch (2012). In the most extreme case, *Koenigsbergia herczeki* Popov, 1993 (Eocene, Baltic amber, Yantarnyi), is not currently placed in the correct subfamily, instead belonging to Phimorphorinae (Swanson, unpublished), a taxon currently unrepresented by extant material in molecular analyses. Other choices of fossil calibrations, i.e., *Paleoploiariola venosa* Maldonado,
Santiago-Blay & Poinar, 1993 (Miocene: Burdigalian, Dominican amber, Dominican Republic), and Praecoris dominicanus Poinar, 1991 (Miocene: Burdigalian, Dominican amber, Dominican Republic) could be replaced with older fossils described at the time that calibrate the same node, i.e., Danzigia christelae Popov, 2003 (Eocene, Baltic amber, Yantarnyi) and Proptilocerus dolosus Wasmann, 1932 (Eocene, Baltic amber, Europe), respectively. It remains to be seen how strongly these incorrect calibrations affect the results, although the potential for serious modification is real (see discussion in Parham et al. 2012). Overall, this serves to highlight the importance of studying fossil material in a contemporary comparative framework.

Preliminary results of the present study strongly suggest that there may be other problems with the overall age estimation in the previous study. Hwang & Weirauch (2012) ran their Markov chain for 10 million generations, and it is generally accepted that this is too few generations for such an analysis. Furthermore, other iterations run by me, including one using the substitution model GTR+I+G, never fully converged in 500 million generations, even though it appeared to have reached convergence for a short time in the first 15 million generations. No information regarding the Trace file or ESS values was supplied in the previous study. Given the similarity of dataset between the present and the previous study, I suspect that the Hwang & Weirauch (2012) had not actually reached convergence in 10 million generations but had plateaued only briefly and would have failed had to converge had it run longer; thus, their divergence estimates are likely unreliable.

A forthcoming study (Zhang et al., in press) takes into account several of these issues, such as adding representatives of several extant lineages previously untested and removing a few problematic calibration points. However, there still remain problematic assumptions and
improper fossil calibrations, some of which have been discussed here in the context of the previous study. Furthermore, no new fossil calibrations are used, suggesting that *Aphelicophontes iuddorum* could still impact reduvioid divergence dates estimates.

**Conclusion.** Re-inferring trees in a Bayesian and ML framework in the present study corroborated topologies recovered by Hwang & Weirauch (2012). Furthermore, despite difficulties in achieving well-supported estimates in the present study, exploration of problematic assumptions by Hwang & Weirauch (2012) revealed easy steps for improving the power of divergence estimations for Reduviidae. It remains to be seen *how much* the divergence dates will change, although it still seems likely that at least portions of the family Reduviidae are older than previously thought.

**Further Directions.** There are several directions for improving the results of this study. In order to achieve an analysis with appropriate ESS values (>100, but more desirably >200), further modifications need to be considered. One possibility is to decrease the proportion of missing data by eliminating taxa or even genes (the majority of taxa in the present study have no sequence data for Wg). However, Zheng & Wiens (2015) have suggested that this might have little impact on divergence date estimations. On the other hand, other studies (e.g., Andújar et al. 2012, Duchêne et al. 2014) have suggested that clock model choice can have serious impacts on divergence dates; thus, it is possible that the random local clock model might prove successful for Reduvioidea. Indeed, this latter modification is already underway (Swanson, in prep.). Additionally, once a supportable set of divergence estimates is achieved, the data should be subjected to other tests of robustness: sampling from the prior, testing for...
saturation, and comparison of models via path sampling/stepping-stone procedures (Wilke et al. 2009).

In such a large and morphologically diverse family, greater gene- and taxon-sampling certainly would benefit future phylogenetic studies of Reduvioidae. Many extant lineages (e.g., Bactrodinae, Sphaeridopinae, Elasmodeminae, Phimophorinae) remain unrepresented at this time. Certainly, greater taxon sampling is needed throughout the polyphyletic nominate subfamily Reduviinae to better understand the placement of and constituents in each of the clades. Indeed, more recent molecular phylogenies (i.e., Zhang & Weirauch 2014, Gordon & Weirauch 2016) have augmented the representation of several lineages. Gene representation similarly should be augmented, given the heavy favor of ribosomal, rather than nuclear, genes in the previous and present study. Care in overlapping sampled genes with previous studies will be important, although use of transcriptomic data, such as that used by Zhang et al. (2016), should help to this end. Use of transcriptomic data by Zhang et al. (2016) also proved useful in strengthening the "backbone" of the tree, leading to more highly supported resolution in topology. The present study also highlights the need for contemporary treatment of fossil Reduvioidae, as fossils play an important role in studying the evolution of extant groups (e.g., Mitchell 2015; see also Chapter 3 and Epilogue). Nevertheless, phylogenetic study of Reduvioidae has a strong foundation on which to build and future studies should reveal much about the evolutionary history of this fascinating lineage of insects.

LITERATURE CITED

Adobe Systems, Inc. 2014. Adobe Illustrator CC (version 2014.0.0) [software].
Adobe Systems, Inc. 1990–2011. Adobe Photoshop CS5 Extended (version 12.1 x64) [software].


Bare Bones Software, Inc. 2015. TextWrangler (version 5.0) [software]. North Chelmsford, MA.


FIGURES AND TABLES

Figure 2.1. Top portion of Bayesian 50% MRC tree inferred in MrBayes. Branch support is given as posterior probabilities. All branches sharing similarly strong support in ML analysis have bootstrap values annotated near posterior probabilities.
Figure 2.2. Bottom portion of Bayesian 50% MRC tree inferred in MrBayes. Branch support is given as posterior probabilities. All branches sharing similarly strong support in ML analysis have bootstrap values annotated near posterior probabilities.
Figure 2.3. Bayesian MCC tree and divergence date estimates as inferred from BEAST2. Branch support is given as posterior probabilities.
Table 2.1. Fossil calibration points used in present study. M, S, and O in the final column refer to Mean, Standard Deviation, and Offset, respectively, of priors implemented in BEAST2.

<table>
<thead>
<tr>
<th>#</th>
<th>Family</th>
<th>Subfamily</th>
<th>Tribe</th>
<th>Genus</th>
<th>Species</th>
<th>Author</th>
<th>Year</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Ceresopseidae</td>
<td>–</td>
<td>–</td>
<td>Ceresopsis</td>
<td>costalis</td>
<td>Becker-Migdisova</td>
<td>1958</td>
<td>Dzhil Formation, Sogyuty, Kyrgyzstan</td>
</tr>
<tr>
<td>2</td>
<td>Reduviidae</td>
<td>Holoptilinae</td>
<td>Holoptilini</td>
<td>Proptilocerus</td>
<td>dolosus</td>
<td>Wasmann</td>
<td>1932</td>
<td>unknown</td>
</tr>
<tr>
<td>3</td>
<td>Reduviidae</td>
<td>Emesinae</td>
<td>Metapterini</td>
<td>Emesites</td>
<td>voigti</td>
<td>Popov &amp; Weitschat</td>
<td>2005</td>
<td>Merit-Pila coal mine, Sarawak, Borneo, Malaysia</td>
</tr>
<tr>
<td>4</td>
<td>Reduviidae</td>
<td>Emesinae</td>
<td>Collartidini</td>
<td>Collarhamphus</td>
<td>mixtus</td>
<td>Putshkov &amp; Popov</td>
<td>1995</td>
<td>unknown</td>
</tr>
<tr>
<td>5</td>
<td>Reduviidae</td>
<td>Triatominae</td>
<td>Triatomini</td>
<td>Panstrongylus</td>
<td>hispaniola</td>
<td>Poinar</td>
<td>2013</td>
<td>La Toca Mine, Cordillera Septentrional, Dominican Republic</td>
</tr>
<tr>
<td>6</td>
<td>Reduviidae</td>
<td>Harpactorinae</td>
<td>Apiomerini</td>
<td>Apicrenus</td>
<td>fossilis</td>
<td>Maldonado, Santiago -Blay &amp; Poinar</td>
<td>1993</td>
<td>La Toca Mine, Cordillera Septentrional, Dominican Republic</td>
</tr>
<tr>
<td>7</td>
<td>Reduviidae</td>
<td>Harpactorinae</td>
<td>Harpactorini</td>
<td>Aphelicophontes</td>
<td>iuddorum</td>
<td>Swanson, Heads &amp; Taylor</td>
<td>–</td>
<td>Green River Formation, Colorado, U.S.A.</td>
</tr>
<tr>
<td>#</td>
<td>Preservation</td>
<td>Geologic Timescale</td>
<td>Age (Ma)</td>
<td>Age Reference</td>
<td>Group Calibrated</td>
<td>Monophyly?</td>
<td>M, S, O</td>
<td></td>
</tr>
<tr>
<td>----</td>
<td>--------------</td>
<td>--------------------</td>
<td>-----------------</td>
<td>---------------</td>
<td>-----------------</td>
<td>------------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>compression</td>
<td>Mesozoic:</td>
<td>201.6–176 Ma</td>
<td>Shcherbakov 2007</td>
<td>ingroup</td>
<td>yes</td>
<td>178.0, 4.2, 176</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early Jurassic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Baltic amber</td>
<td>Cenozoic: Paleogene: Eocene</td>
<td>56–33.7 Ma</td>
<td>Perkovsky et al. 2007</td>
<td><em>Ptilocerus</em> sp., <em>Ptilocnemus</em> sp.</td>
<td>yes</td>
<td>35.0, 3.54, 33.7</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Baltic amber</td>
<td>Cenozoic: Paleogene: Eocene</td>
<td>56–33.7 Ma</td>
<td>Perkovsky et al. 2007</td>
<td><em>Empicoris</em> sp., <em>Ploiaria</em> sp. [sister to single <em>Mangabea</em> sp.]</td>
<td>yes</td>
<td>35.0, 3.54, 33.7</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Dominican amber</td>
<td>Cenozoic: Neogene: Miocene: Burdigalian</td>
<td>20–15 Ma</td>
<td>Iturralde-Vinent &amp; MacPhee 1996</td>
<td>3 spp. of <em>Panstrongylus</em></td>
<td>no</td>
<td>17.0, 3.9, 15.0</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Dominican amber</td>
<td>Cenozoic: Neogene: Miocene: Burdigalian</td>
<td>20–15 Ma</td>
<td>Iturralde-Vinent &amp; MacPhee 1996</td>
<td><em>Agriocoris</em> sp., 2 spp. of <em>Apiomerus</em>, <em>Heniartes</em> sp., <em>Micrauchenus</em> sp.</td>
<td>yes</td>
<td>17.0, 3.9, 15.0</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>shale compression</td>
<td>Cenozoic: Paleogene: Eocene</td>
<td>53.5–48.5 Ma</td>
<td>Smith et al. 2003</td>
<td>2 spp. of <em>Pselliopus</em></td>
<td>yes</td>
<td>49.0, 4.25, 48.5</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2. Select comparisons between divergence date estimations of Hwang & Weirauch (2012) and present study (age in millions of years [Ma]). Backslash (/) refers to split between two clades.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Hwang &amp; Weirauch (2012)</th>
<th>Present Study</th>
<th>Difference in Mean Age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Age</td>
<td>95% HPD</td>
<td>Age</td>
</tr>
<tr>
<td>Reduviidae</td>
<td>178.3</td>
<td>[176, 184.98]</td>
<td>344.2</td>
</tr>
<tr>
<td>Higher Reduviidae</td>
<td>160.3</td>
<td>[137.19, 179.59]</td>
<td>287.5</td>
</tr>
<tr>
<td>Phymatinae</td>
<td>113.7</td>
<td>[91.12, 140.1]</td>
<td>224.3</td>
</tr>
<tr>
<td>Centrocnemidinae/Holoptilinae</td>
<td>89.5</td>
<td>[66.63, 115.4]</td>
<td>162.6</td>
</tr>
<tr>
<td>Tribelocephalinae + Ectrichodiinae</td>
<td>83.6</td>
<td>[72.87, 95.55]</td>
<td>176.5</td>
</tr>
<tr>
<td>Ectrichodiinae/Tribelocephalinae</td>
<td>67.5</td>
<td>[57.03, 79.65]</td>
<td>150.1</td>
</tr>
<tr>
<td>Zelurus clade/Stenopodinae</td>
<td>52.9</td>
<td>[41.64, 64.56]</td>
<td>143.6</td>
</tr>
<tr>
<td>(Opisthacidius + Triatominae)/Zelurus</td>
<td>37.4</td>
<td>[29.74, 45.34]</td>
<td>105.7</td>
</tr>
<tr>
<td>Triatomini</td>
<td>31.3</td>
<td>[24.23, 38.17]</td>
<td>93.6</td>
</tr>
<tr>
<td>Rhodniini + Cavernicolini</td>
<td>27.5</td>
<td>[21.05, 33.49]</td>
<td>81.5</td>
</tr>
<tr>
<td>Rhodniini/Cavernicolini</td>
<td>22.2</td>
<td>[15.26, 27.97]</td>
<td>66.5</td>
</tr>
<tr>
<td>Salyavatinae</td>
<td>41.6</td>
<td>[31.35, 56.7]</td>
<td>106.4</td>
</tr>
<tr>
<td>Harpactorinae + Neostachyogenys</td>
<td>64.6</td>
<td>[54.6, 75.58]</td>
<td>154.6</td>
</tr>
<tr>
<td>Harpactorini</td>
<td>50.1</td>
<td>[40.05, 61.03]</td>
<td>122.8</td>
</tr>
</tbody>
</table>
Table 2.3. Fossils in Reduvioidea and their suitability as calibration points. Justification for exclusion: (1) unconfirmed/uncertain identity; (2) redundant—same age as used taxon; (3) younger than used confrrater; (4) extant taxon not sequenced.

<table>
<thead>
<tr>
<th>Fossil</th>
<th>Parent Taxon</th>
<th>Used?</th>
<th>Justification for Exclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ceresopsis</em> (3 spp.)</td>
<td>Reduvioidea: Ceresopseidae</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Redubinotus liedtkei</em></td>
<td>Centrocnemidinae</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Redubitus centrocnemarius</em></td>
<td>Centrocnemidinae</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Collarhamphus mixtus</em></td>
<td>Emesinae: Collartidini</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>&quot;Emesites&quot; voigti</em></td>
<td>Emesinae: Metapterini</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Alumeda</em> (4 spp.)</td>
<td>Emesinae: Ploiariolini</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Danzigia christelae</em></td>
<td>Emesinae: Ploiariolini</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Emesopsis</em> (2 spp.)</td>
<td>Emesinae: Ploiariolini</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Empicoris</em> (2 spp.)</td>
<td>Emesinae: Ploiariolini</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Empiploariola inermis</em></td>
<td>Emesinae: Ploiariolini</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Malacopus wygodzinskyi</em></td>
<td>Emesinae: Ploiariolini</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Apircerus fossilis</em></td>
<td>Harpactorinae: Apiomerini</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Amphibolus disponsi</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Aphelicophontes iuddorum</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Arilus faujasi</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Euagoras impressus</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Harpactor</em> (7 spp.)</td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Poliosphageus psychrus</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Rhynocoris michalki</em></td>
<td>Harpactorinae: Harpactorini(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Praecoris dominicanus</em></td>
<td>Holoptilinae</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Proptilocerus dolosus</em></td>
<td>Holoptilinae</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Proptilocnemus longispinis</em></td>
<td>Holoptilinae</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Peirates oeningensis</em></td>
<td>Peiratinae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Koenigsbergia herczeki</em></td>
<td>Phimophorinae</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td><em>Platymeris insignis</em></td>
<td>Reduviinae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Reduvius</em> (5 spp.)</td>
<td>Reduviinae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Hymenopterites deperditus</em></td>
<td>Saicinae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Tagalodes inermis</em></td>
<td>Saicinae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Oncocephalus astutus</em></td>
<td>Stenopodainae(?)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Panstrongylus hispaniolae</em></td>
<td>Triatominae: Triatomini</td>
<td>Y</td>
<td>–</td>
</tr>
<tr>
<td><em>Triatoma dominicana</em></td>
<td>Triatominae: Triatomini</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>
INTRODUCTION

It is difficult to describe new species in a responsible manner without first knowing what has already been named. To that end, taxonomic catalogs function as enumerations of already-described taxa and directories of historical literature. This kind of information is frequently sought by systematists, whereas the benefits to the general biologist are usually overlooked, despite being surprisingly numerous. Catalogs often reference keys for identification and updated range data, both important resources for biosurveyors, conservationists, biogeographers, and ecologists. Taxonomic catalogs serve as reliable sources for the authority (=author and year of publication) of a species, information that should be more frequently cited by non-systematists but, frustratingly, is not always readily accessible. Catalogs containing all relevant literature citations, although time-consuming to produce, can highlight the depth of work on a taxon and serve as an archive for non-systematic studies, be they ecological, genetic, physiological, etc. Clearly, taxonomic catalogs have much to offer the biological sciences as a source of information.

Reduviioidea is an evolutionarily-successful group of predatory true bugs found in every major ecozone. Among extant taxa, Reduviioidea comprises two families: the less speciose Pachynomidae (4 genera, 21 species, globally) and the hyperdiverse Reduviidae (ca. >900 genera, >7000 species, globally). Fortunately, there exists two independent, and nearly simultaneously-erected, world catalogs for the nominate family (i.e., Putshkov & Putshkov
1985, 1986, 1987, 1988a, 1988b; Maldonado 1990) and one forthcoming for the Pachynomidae (Swanson, in prep.) to help track this diversity. Understandably, these catalogs did not include fossil reduvioids, and until this point, no such catalog existed for the extinct taxa.

The literature on fossil Reduvioidae is much smaller than that of the extant species. Although fossil assassin bugs were mentioned as early as 1829 by Serres, the first valid fossil species were erected by the Swiss geologist Oswald Heer in 1853. Known for his pioneering work with fossil insects from Öhningen and Radoboj (Heer 1853), Heer described eight reduviid species in that work. A few species were added here and there by well-known paleoentomologists, such as Ernst Friedrich Germar and Samuel Hubbard Scudder. By 1900, 11 species had been described (along with *Hymenopterites deperditus* Heer, 1870, then thought to be a hymenopteran). Species described up to that point were catalogued by Scudder (1890, 1891) and Anton Handlirsch (1908, 1925). Seven more species were added in a piecemeal fashion through much of the 20th century, and it wasn’t until the 1980’s that the majority of the fossil species started to receive attention and description. In fact, 31 of the 49 species currently recognized as fossil reduvioids were described after 1979. Contemporary treatment has come mostly at the hand of heteropterist Yuri A. Popov, who has been involved in the description of 14 fossil taxa, approximately half those described in the last four decades. Other contemporary authors have tended to focus on particular fossil sites, like George O. Poinar, Jr. (Dominican amber) and Zhang Jun-feng and Zhang Xi-yu (Shanwang). Surprisingly, until quite recently, essentially no reduviologists have taken a particular interest in the fossil taxa, with a notable exception of J. Maldonado Capriles in the 1990s.
The work presented herein contains the first contemporary taxonomic catalog of the described extinct species of Reduvioidea. In a sense, the organization of this thesis is essentially reversed, because the previous chapters could not have commenced without aid of this newly compiled resource. In an effort to bring all of this information into one discrete location, I have supplemented this work with a discussion of the distribution of fossils within the family Reduviidae, as well as lists of undescribed fossil material and taxa originally misplaced in the family.

MATERIALS AND METHODS

The taxonomic entries in this catalog are modeled, in part, after Maldonado (1990). Taxa are arranged alphabetically, first by subfamily, next within by genus, and then by species. The taxonomy of the group generally follows the two world catalogs (i.e., Putshkov & Putshkov 1985, 1986, 1987, 1988a, 1988b; Maldonado 1990), with some modification. The list of fossil reduvioid taxa was cross-referenced with Fossilworks.org (Alroy 2016) and the EDNA Fossil Insect Database (Mitchell 2013). All information herein contained, other than type repository, has been gleaned from examination of the original descriptions of all taxa. Generic information, including authority and designation of type species, is included. For each species, I have endeavoured to include all references in the literature. Each literary citation in each species entry is annotated as to the type of information included, as is information on locality, taphonomy, age (period + numerical, with references), and type repository. In most cases, repository information for type material was confirmed by contacting curatorial staff at each institution, particularly for taxa described before 1990; however, label data for type material
has not been provided. Pertinent notes and annotations are included, where relevant. All taxon names are indexed at the end of this treatment.

No specimens were physically examined by me, other than the new taxon, *Aphelicophontes iuddorum* gen. et sp. nov., described in Chapter 1. Various taxa were examined via photographs provided by curators and collection managers of the respective repository; those individuals are thanked in the Acknowledgments section (p. iii). Codens for institutions or collections, following Arnett et al. (1993) in part, are listed below.

In general, I have tried to follow the principles of the Code (ICZN 1999) in dealing with taxa included in this catalog. In most cases of ambiguous or erroneous placement, I have retained the position of the most recent treatment, except in the face of overwhelming evidence. Several taxonomic changes enacted or noted in this catalog (i.e., homonyms; familial, subfamilial, generic re-assignments) will receive extended, focused treatment at a later date.

Maps were created using ArcGIS (Esri, Inc. 2013). Both tables and maps were further manipulated with Adobe Illustrator CC (Adobe Systems Inc., San Jose, CA).

*Repository Acronyms for Fossil Reduvioid Catalog*

American Museum of Natural History, New York, New York, U.S.A. .................................................AMNH

Natural History Museum, London, United Kingdom .............................................................................BMNH

Christel & Hans Werner Hoffeins private collection, Hamburg, Germany ...........................................CHC

Deutsches Entomologische Institut, Müncheberg, Germany ..............................................................DEI

Eidgenössische Technische Hochschule, Zürich, Switzerland ..........................................................ETHZ

F. Eichmann private collection, Hanover, Germany .............................................................................FEC

Geologische Bundesanstalt, Vienna, Austria ..........................................................................................GBA
Geological Museum of Shandong Province, Jinan, Shandong Province, China ................................. GMSP
Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Hamburg, Germany.......................................................... GPIH
Hans Liedtkei private collection, Hamburg, Germany................................................................. HLC
Hessisches Landesmuseum Darmstadt, Darmstadt, Germany..................................................... HLMD
Hrvatski Prirodoslovni Musej, Zagreb, Croatia ................................................................. HPM
Paleontology Collection, Illinois Natural History Survey, Champaign, Illinois, U.S.A............ INHS
Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A................. LACM
Museo de Ciencias Naturales de Álava, Vitoria, Spain ................................................................. MCNA
Musém national d'Histoire naturelle, Paris, France ................................................................. MNHN
Naturhistorisches Museum Wien, Vienna, Austria................................................................. NHMW
Smithsonian Institution, Washington, D.C., U.S.A............................................................... NMNH
Naturhistoriska Riksmuseet, Stockholm, Sweden ................................................................. NRM
Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, U.S.A. ....... OSAC
Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland ................................... PAS
Paleontological Institute, Russian Academy of Sciences, Moscow, Russia ............................ PIN
Steiermärkisches Landesmuseum Joanneum, Graz, Austria ...................................................... SLJG
Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany .................................. SMNKS
Staatliches Museum für Naturkunde, Stuttgart, Germany ..................................................... SMNS
Shanwang National Geology Park, Linqu, Shandong Province, China ................................... SNGL
Steinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Bonn, Germany................................................................................................................................... STIB
RESULTS

There are 47 described fossil species in 31 genera, and ten of the 25 currently-accepted reduviid subfamilies [or 40%) are represented (see Table 3.1). Of these, most major lineages (here, arbitrarily, subfamilies over 100 spp.) are exemplified (i.e., Emesinae, Harpactorinae, Peiratinae, Reduviinae, Saicinae, Stenopodainae, Triatominae), assuming accurate generic placements. Major gaps in subfamilial representation are found in the millipede assassins (Ectrichodiinae), the ambush bugs (Phymatinae), the termite assassins (Salyavatinae), and the triangle-headed bugs (Tribelocephalinae).

The specimens are preserved either as compressions [25 of 47; or 53%) or inclusions in fossilized resins [22 of 47; or 47%].

Fifteen different Lagerstätten are represented (Fig. 3.1), distributed among eleven different countries, in addition to a few unspecified sites. The type material of the described fossil species of Reduvioida are distributed among 21 different institutions (Fig. 3.2a), with major portions being held in Germany [17 of 47; or 36%) and the U.S.A. [10 of 47; or 21%] (Fig. 3.2b).

The main result of this study, the annotated catalog of fossil Reduvioida, follows the discussion.
DISCUSSION

In some ways, the level of taxonomic resolution among fossil Reduvioida is reasonably high. The large proportion of resin inclusions (47%), compared with other preservational modes, such as compressions, increases the likelihood of fidelity of diagnostic characters. Furthermore, diagnostic characters themselves, at a supraspecific level, remain somatic and usually are easy to score, again lending to higher resolution when associating fossil taxa with extant lineages. Continuous splitting, a well-known phenomenon in groups of greater diversity and/or older taxonomic provenance, similarly contributes to ease of obtaining a higher resolution, since each "little" difference begets a new division. As previously mentioned, close to half of the extant subfamilies are represented, spreading fossil representatives across the whole of the phylogenetic tree. In the contemporary practice of calibrating phylogenetic trees with extinct taxa, having 50 fossils from which to choose would be called a great luxury by many specialists of invertebrate groups. Thus, at this point, the knowledge of fossil Reduvioida is at a workable and comparatively fortunate state of inference. Furthermore, there are many specimens yet to be described (see below and Epilogue).

However, our picture of reduviid evolutionary history, in many ways, remains less clear. The sheer diversity of extant species (>7000 spp.) welcomes the supposition that only a small portion of the actual extinct diversity is represented and much remains unknown; yet, this is generally true for the whole of the fossil record (e.g., Zherikin 2002, Grimaldi & Engel 2005). This paradox of "more-is-less" suggests that, with such great diversity in the extant taxa, naturally, there are larger gaps due to extinct taxa both up and down and side-to-side on the phylogenetic tree. Admittedly, this presupposes that being speciose now correlates in previous
epochs of geologic history, i.e., extinct taxa also were speciose. However, this assumption may not necessarily be true and is difficult to test (e.g., Clapham et al. 2016). Mirroring previous points, whereas the high proportion of resin inclusions is a boon, the majority of the other half of reduvioid fossils, i.e., compressions, are an obstacle, with most specimens being poorly preserved, leaving extant affinities uncertain. Furthermore, representation is certainly greatly skewed, likely in several ways. Unsurprisingly, more speciose subfamilies (e.g., Emesinae, Harpactorinae, Reduviinae) tend to have greater representation, even though a few less speciose families are known from fossils (i.e., Centrocnemidinae, Phimophorinae). As with other fossilized insects (e.g., Labandeira & Sepkoski 1993, Zherikin 2002, Grimaldi & Engel 2005), only certain life styles or habitat preferences are conducive to fossilization; this certainly applies to Reduviidae, as many different life styles are represented within the family (see Hwang & Weirauch 2012: Fig. 3; also discussion below). An additional impediment is that many of the fossil taxa were described in the 19th century and have yet to be taxonomically revisited; during the last 150 years, the taxonomy of the group has changed extensively. Thus, a significant portion of the taxa is misplaced, resulting in lineages unknowingly or erroneously represented. Additionally, superficially and/or phylogenetically similar heteropteran taxa (Nabidae, in particular) require re-assessment. Thus, our picture is far from complete and far from error-free.

The representation of reduvioid taxa in the fossil record, on a taxonomic level, holds some interesting trends. Ten subfamilies represented by fossils (Table 3.1, Fig. 3.3); in decreasing numerical order by representation, they are: Harpactorinae (14), Emesinae (12), Reduviinae (6), Holoptilinae (3), Centrocnemidinae (2), Saicinae (2), Triatominae (2), Peiratinae
Based on sheer number of taxa, the first three most fossil-rich subfamilies make sense, as each represents a group with >950 spp. (the next subfamily represented by greatest number of fossils is Holoptilinae with 76 extant spp. and the next most extantly-speciose subfamily is Stenopodainae with 753 extant spp.). However, taxa placed in both Harpactorinae and Reduviinae in particular likely suffer from erroneous generic placement, because they possess a more general habitus among Reduviidae. Additionally, the single fossils currently placed in Peiratinae and Stenopodainae remain suspect. Conversely, members of some subfamilies (e.g., Emesinae, Holoptilinae) tend to be unmistakable and therefore more likely to be correctly placed. Thus, number of extant species correlates, to some degree, with the subfamilies represented, but this correlation may be less pronounced due to erroneous identifications.

The distribution of reduvioid fossils between fossilized resins and compressions also highlights some interesting trends. In particular, it would be predicted that the species composing the former category would have natural histories that associate them with resin. There are seven subfamilies preserved in fossilized resin and indeed, five of them, i.e., Centrocnemidinae, Emesinae, Harpactorinae, Holoptilinae, and to a less degree, Triatominae, have extant members that are arboreal or frequently taken on woody plants or vegetation. Fossilized resins also are much more likely to preserve delicate or slender specimens, which explains the high incidence of emesine fossils, and to a lesser extent ant bugs, preserved in resins. Compressions, on the other hand, form from the deposition of sediments around a dead specimen that subsequently undergo varying forms of mineralization and/or carbonization, as well as physical compression (Zherikin 2002). Deposition of fine sediments
occurs more commonly in aquatic environs, e.g., ponds, lakes, slow-moving rivers and creeks, deltas and other coastal marine environments. This also means that specimens more frequently found near aquatic environments will have a greater likelihood of being preserved as compressions. Among Reduviidae, this favors vegetation-associated groups, which might hunt among foliage overhanging or near to bodies of water. This makes sense for Harpactorinae and perhaps some Reduviinae and Stenopodainae. One particularly salient specimen is the paratypic specimen of *Aphelicophontes iuddorum* preserved in a "raft" of many other arthropods. Much as the leaves of plants are frequently preserved as compressions, owing to the minimal distortion that comes from their flattened shape, it can be predicted that similarly flattened portions of arthropods, i.e., wings, might be preserved, particularly more sclerotized portions like the elytra of beetles and the hemelytra of true bugs. This is found in the specimen of *Hymenopterites deperditus* (Saicinae). The representation of the remaining subfamilies in the fossil record either remains unchallenged, because not much is known about their life history (Phimophorinae or the extinct Ceresopseidae) or is legitimately surprising (Peiratinae as geodromic hunters). In some cases, as with the sole example of Peiratinae, re-examination is needed, particularly where a specimen is placed in a genus of old taxonomic provenance and is represented as a compression rather than in fossilized resin. Nevertheless, natural history of the extant lineage can certainly be invoked to help explain the preservational bias of reduvioid fossils.

Dearth of records is equally interesting. We would expect to see the African Diaspidiini and the southern Asian Ectinoderini, the Old World "resin bugs" (both tribes of Harpactorinae), in the same way that Apiomerini is represented in Dominican amber, although Lagerstätten are
lacking in these regions, particularly for the former (Rasnitsyn 2002: Figs. 3–5). Similarly, we might expect to see members of Microtominae and Elasmodeminae (both exclusively New World groups), in the fossil record given their association with tree bark, although they frequent subcorticolous, rather than epicorticolous, habitats. However, a purported specimen of Elasmodeminae exists from Messel (Koch & Wedmann 2012). All of these groups, as well as Bactrodinae, Cetherinae, Chryxinae, Manangocorinae, Pseudocetherinae, Sphaeridopinae, Vesiinae, Visayanocorinae, and the extant family Pachynomidae, contain relatively few species; thus, a lack of representation is more easily explained. Several groups missing from the fossil record can potentially be explained by such factors as a small and/or delicate body (e.g., Bactrodinae, Chryxinae, Visayanocorinae), suggesting low preservational potential. Conversely, it is surprising that no ectrichodiine fossils exist, given such factors as a generally robust body and sheer number of extant species; however, as cryptic, ground-dwelling millipede-hunters, their natural history might not result in a resting place conducive to fossilization. Similar attributes suggest that phymatines should be present in the fossil record, although a more terrestrially-biased habitat might limit this possibility. Admittedly, a fossil tentatively identified by Serres (1829) as a species of Syrtis (junior synonym of Phymata) needs examination. Of course, fossilization of a given organism is an extremely unlikely prospect, and while it is interesting to ask why we see what we do, there is no benefit in scouring world collections and "holding out" for a particular fossil of a given group.

Nevertheless, many fossil reduviid taxa remain to be described. There are a handful of fossil specimens already mentioned in the literature that are tentatively assigned to Reduvioida (Table 3.3). Furthermore, it can be difficult to assign even supra-familial
identifications, particularly to compression fossils, and there undoubtedly remains additional material among the unsorted Heteroptera in many of the fossil collections of the world. For further details, please refer to the discussion of future directions found in the Epilogue.
ANNOTATED CATALOG OF FOSSIL REDUVIOIDEA

Superfamily Reduvioidae

Latreille 1807, p. 126.


31 genera, 47 species.

Family Ceresopseidae


Ceresopseidae: Shcherbakov 2007, 16:408. As family in REDUVIOIDEA.


Taxa: 1 genus, 3 species.

Ceresopsis Becker-Migdisova


Ceresopsis costalis Becker-Migdisova

1958 Ceresopsis costalis Becker-Migdisova, 2:66. Fig. 7. Based on hemelytra. In HOMOPTERA: MEMBRACIDAE. [original description].


2012 Ceresopsis costalis: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: Dzhil Formation, Sogyuty, Kyrgyzstan.

Preservation: compression.

Age: Mesozoic: Early Jurassic (201.6–176 Ma).


Extant Congeners: no

*Ceresopsis ornata* Becker-Migdisova

1962 *Ceresopsis ornata* Becker-Migdisova, 1962:94.  Fig. 7.  Based on hemelytra.  In HOMOPTERA: MEMBRACIDAE.  [original description].

2007 *Ceresopsis ornata*: Shcherbakov, 16:409.  Fig. 14.  [figured].

Locality: Dzhil Formation, Sogyuty, Kyrgyzstan.

Preservation: compression.

Age: Mesozoic: Early Jurassic (201.6–176 Ma).


Repository of type: Shcherbakov 2007, 16:403: holotype, unsexed, PIN [no. 358/487].

Extant Congeners: no

*Ceresopsis vitrea*

1962 *Ceresopsis vitrea* Becker-Migdisova, 1962:93.  Fig. 6.  Based on hemelytra.  In HOMOPTERA: MEMBRACIDAE.  [original description].

Locality: Dzhil Formation, Sogyuty, Kyrgyzstan.

Preservation: compression.

Age: Mesozoic: Early Jurassic (201.6–176 Ma).


Extant Congeners: no
Family Reduviidae

Latreille, 1807, p. 126.

Type genus: *Reduvius* Fabricius, 1775.

Fossil taxa: 30 genera, 44 species.

**Subfamily Centrocnemidinae**

*Redubinotus* Popov & Putshkov


*Redubinotus liedtkei* Popov & Putshkov


Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Repository of type: Popov & Putshkov 1998, 8–9:206: holotype, male, HLC.

Extant Congeners: no

*Redubitus* Putshkov & Popov

1993 *Redubitus* Putshkov & Popov, 75:222.

Redubitus centrocnemarius Putshkov & Popov

1993 Unnamed taxon: Popov & Herczek, 1:9. [undescribed fossil].

1993 Redubitus centrocnemarius Putshkov & Popov, 75:222. Figs. 1–9; Pl. 1, Figs. 1–2.
[original description].

2009 Redubitus centrocnemarius: Putshkov & Moulet, p. 111. [checklist].

Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Extant Congeners: no

Subfamily Emesinae, Tribe Collartidini

Collarhamphus Putshkov & Popov


Collarhamphus mixtus Putshkov & Popov

1995 Collarhamphus mixtus Putshkov & Popov, 78:181. Figs. 1–3; Pl. 1, Figs. 1–2.
[original description].

Locality: unknown.

Preservation: Baltic amber.
Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Extant Congeners: no

Subfamily Emesinae, Tribe Metapterini

"Emesites" Popov & Weitschat


"Emesites" voigti Popov & Weitschat

2005 "Emesites" voigti Popov & Weitschat, 89:177. Figs. 1–4. [original description].

Locality: Nyalau Formation, Merit-Pila coal mine, Sarawak, Borneo, Malaysia.

Preservation: Borneo (Sarawak) amber.

Age: Cenozoic: Neogene: Early to Middle Miocene (23–13 Ma).


Extant Congeners: no

Note: "The early nymphal stage (2nd stage) does not permit to determine exactly the systematic position of this reduviid bug and therefore this name is applicable only to the extinct specimen that has been formed by edding [sic] -ites (article 20 of ICZN
Subfamily Emesinae, Tribe Ploiariolini

*Alumeda* Popov

1989 *Alumeda* Popov, 150:3.


*Alumeda antilliana* Popov

1988 *Alumeda antilliana*: Spahr, 144:14. [catalog – "Im Druck"].


1999 *Alumeda antilliana*: Pérez-Gelabert, 1:40. [catalog].


Locality: Haiti, Hispaniola.

Preservation: Dominican amber.


Extant Congeners: no

*Alumeda dominicana* Popov

1988 *Alumeda dominicana*: Spahr, 144:14. [catalog – "Im Druck"].

1989 *Alumeda dominicana* Popov, 150:7. Figs. 9–16. [original description].

1999 *Alumeda dominicana*: Pérez-Gelabert, 1:40. [catalog].


Locality: Haiti, Hispaniola.

Preservation: Dominican amber.


Extant Congeners: no

*Alumeda nigricans* Popov

1988 *Alumeda nigricans*: Spahr, 144:14. [catalog – "Im Druck"].

1989 *Alumeda nigricans* Popov, 150:4. Figs. 1–8. [original description].

1999 *Alumeda nigricans*: Pérez-Gelabert, 1:40. [catalog].


Locality: Haiti, Hispaniola.

Preservation: Dominican amber.


Extant Congeners: no

*Danzigia* Popov

2003 *Danzigia* Popov, 87:165.
Type species: *Danzigia christelae* Popov, 2003, 87:165. By original designation.

*Danzigia christelae* Popov

2003 *Danzigia christelae* Popov, 87:165. Figs. 4–5, 8. [original description].

2012 *Danzigia christelae*: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: Yantarnyi, Kaliningrad Region, Samland Peninsula, Russia.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Repository of type: Popov 2003, 87:165: holotype, male, CHC [no. 1132].

Extant Congeners: no

*Emesopsis* Uhler

1893 *Emesopsis* Uhler, 1893:718.

Type species: *Emesopsis nubilus* Uhler, 1893, 1893:718. By monotypy.

1909 *Calphurnia* Distant, 3:502.


1914 *Hadrocranella* Horváth, 12:647.


*Emesopsis putshkovi* Popov & Chłond

2015 *Emesopsis putshkovi* Popov & Chłond, 4039:568. Figs. 1, 4, 6. [original description].
Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Repository of type: Popov & Chłond 2015, 4039:567: holotype, male, DEI [no. 1612-3].

Extant Congeners: yes

*Emesopsis similis* Popov & Chłond

2015 *Emesopsis similis* Popov & Chłond, 4039:568. Figs. 2, 3, 5. [original description].

Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Extant Congeners: yes

*Empicoris* Wolff


Type species: *Cimex vagabundus* Linnaeus, 1758, p. 450. By monotypy.

*Empicoris copal* Popov

1987b *Empicoris copal* Popov, 134:4. Figs. 1–6. [original description].

1999 *Empicoris copal*: Pérez-Gelabert, 1:40. [catalog].


Locality: Dominican Republic, Hispaniola.
Preservation: Dominican copal.

Age: Cenozoic: Quaternary: Holocene (280–0 ybp).


Extant Congeners: yes

**Empicoris electricus** Thomas

1992 *Empicoris electricus* Thomas, 100:535. Figs. 1–2. [original description].

Locality: Simojovel formation, Chiapas, Mexico.

Preservation: Chiapas amber.

Age: Cenozoic: Oligo-Miocene (23 Ma).


Repository of type: Thomas 1992, 100:537: holotype, male, AMNH [no. DT-055].

Extant Congeners: yes

**Empiploiariola** Popov

1993 *Empiploiariola* Popov, 35:436.


By original designation. Synonymized by Popov 2003, 87:160.

*Empiploiariola inermis* Popov

1993 *Empiploiariola inermis* Popov, 35:437. Figs. 1–10. [original description].

Dominican Republic. [original description]. Synonymized by Popov 2003a, 87:160.

1999 *Empiploiariola inermis*: Pérez-Gelabert, 1:40. [catalog].

1999 *Paleoploiariola venosa*: Pérez-Gelabert, 1:40. [catalog].

2005 *Empiploiariola inermes* [sic]: Arillo & Ortuño, 68:16. [catalog].


2012 *Paleoploiariola venosa*: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: La Toca Mine, Cordillera Septentrional, Dominican Republic.

Preservation: Dominican amber.


Extant Congeners: no

*Malacopus* Stål

1860 *Malacopus* Stål, 2:80.

*Malacopus wygodzinskyi* Popov

1987a *Malacopus wygodzinskyi* Popov, 130:11. Figs. 1–13. [original description].


1999 *Malacopus wygodzinskyi*: Pérez-Gelabert, 1:40. [catalog].


Locality: Dominican Republic, Hispaniola.

Preservation: Dominican amber.


Extant Congeners: yes

*Subfamily Harpactorinae, Tribe Apiomerini*

*Apicrenus* Maldonado, Santiago-Blay & Poinar


Type species: *Paleoploiariola venosa* Maldonado, Santiago-Blay & Poinar, 1993a, 24:140.

By original designation.

*Apicrenus fossilis* Maldonado, Santiago-Blay & Poinar

1993a *Apicrenus fossilis* Maldonado, Santiago-Blay & Poinar, 24:140. Figs. 1–3. [original description].
1999 *Apicrenus fossilis*: Poinar & Poinar, p. 124. Fig. 124. [ecological reconstruction].

1999 *Apicrenus fossilis*: Pérez-Gelabert, 1:40. [catalog].


2012 *Apicrenus fossilis*: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: La Toca Mine, Cordillera Septentrional, Dominican Republic.

Preservation: Dominican amber.


Extant Congeners: no

**Subfamily Harpactorinae, Tribe Harpactorini**

*Amphibolus* Klug

1830 *Amphibolus* Klug, [unpaginated].

Type species: *Reduvius (Amphibolus) venator* Klug, 1830, [unpaginated]. By monotypy.

*Amphibolus disponsi* Kinzelbach

1970 *Amphibolus disponsi* Kinzelbach, 98:16. Figs. 3–4; Pl. 2, Fig. 12. [original description].

Locality: Messel, Hesse, Germany.

Preservation: Messel oil shale compression.

Age: Palaeogene: Eocene: Lutetian (48–46.5 Ma).

Age Reference: Mertz & Renne 2005.


Extant Congeners: yes

Note: Does not belong in Amphibolus.

Aphelicophontes Swanson, Heads & Taylor

2016 Aphelicophontes Swanson, Heads & Taylor, p. 12 (Ch. 1, this thesis).

Type species: Aphelicophontes iuddorum Swanson, Heads & Taylor, 2016, p. 13 (Ch. 1, this thesis). By original designation.

Aphelicophontes iuddorum Swanson, Heads & Taylor

2016 Aphelicophontes iuddorum Swanson, Heads & Taylor, p. 13 (Ch. 1, this thesis).

Figs. 1.3–9 [habitus], 1.11–12 [genitalia]. [manuscript name].

Locality: Green River Formation, Colorado, U.S.A.

Preservation: shale compression.

Age: Cenozoic: Paleogene: Eocene (53.5–48.5 Ma).


Repository of type: Swanson, Heads & Taylor 2016, pp. 9, 13 (Ch. 1, this thesis): holotype, male, INHS [no. 2222-1].

Extant Congeners: no
Arilus Hahn

1831 *Arilus* Hahn, 1:33.


*Arilus faujasi* Riou

1984 Hyménoptère indét.: Mein, Méon, Romaggi & Samuel, 21:44. Pl. 1, Fig. 5.

[figured].

1999 *Arilus faujasi* Riou, 11–12:125. [original description].

2012 *Arilus faujasi*: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: Montagne d’Andance, Ardeche, France.

Preservation: compression.

Age: Cenozoic: Neogene: Miocene: Tortonian: Turolian (7.5–7.1 Ma).


Extant Congeners: yes

Notes: (1) The holotype was originally deposited in the Musée Paléontologique de la Voult-sur-Rhône (Riou 1999), which is now closed. Unfortunately, Riou's material is not present in MNHN (A. Nel, pers. comm. 2015), and the replacement repository is currently unknown. (2) Does not belong in *Arilus*; if a harpactorine, possibly in *Rhynocoris*.

Euagoras Burmeister

1835 *Euagoras* Burmeister, p. 226.

_Euagoras impressus_ Heer

1853 _Euagoras impressus_ Heer, p. 83. Pl. 5, Fig. 27; Pl. 10, Fig. 8. [original description].

1856 _Euagoras impressus_: Giebel, p. 368. [synopsis].

1891 _Euagoras impressus_: Scudder, 71:407. Tortonian. [catalog].

1908 (_Evagoras) impressus_: Handlirsch, p. 1038. [catalog].

Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Repository of type: Heer 1853, p. 83: holotype, unsexed, SMNK.

Extant Congeners: yes

_Harpactor_ Laporte

1833 _Harpactor_ Laporte, 1:8.


_Harpactor bruckmanni_ Heer

1853 _Harpactor bruckmanni_ Heer, p. 82. Pl. 5 Fig. 24. [original description].

1856 _Harpactor Bruckmanni_: Giebel, p. 367. [synopsis].

1891 _Harpactor bruckmanni_: Scudder, 71:409. Tortonian. [catalog].

1908 (_Harpactor) bruckmanni_: Handlirsch, p. 1038. [catalog].
Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Extant Congeners: yes

Notes: (1) The holotype is neither present in BMNH (C. Mellish, pers. comm. 2016), where much of Bruckmann's collection is deposited, nor in ETHZ (Müller, pers. comm. 2016), with the majority of Heer's species of Harpactor. (2) Does not belong in Harpactor; if a harpactorine, possibly in Rhynocoris.

Harpactor chomeraciensis Riou

1999 Harpactor chomeraciensis Riou, 11–12:125. Fig. 1. [original description].

Locality: Montagne d’Andance, Ardeche, France.

Preservation: compression.

Age: Cenozoic: Neogene: Micocene: Tortonian: Turolian (7.5–7.1 Ma).


Extant Congeners: no

Notes: (1) The holotype was originally deposited in the Musée Paléontologique de la Voultė-sur-Rhône (Riou 1999), which is now closed. Unfortunately, Riou's material is not present in MNHN (A. Nel, pers. comm. 2015), and the replacement repository is
currently unknown. (2) Does not belong in Harpactor; if a harpactorine, possibly in Rhynocoris.

Harpactor constrictus Heer

1853 Harpactor constrictus Heer, p. 80. Pl. 5 Fig. 22; Pl. 10, Fig. 5. [original description].

1856 Harpactor constrictus: Giebel, p. 366. [synopsis].

1891 Harpactor constrictus: Scudder, 71:409. Tortonian. [catalog].

1908 (Harpactor) constrictus: Handlirsch, p. 1038. [catalog].

Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Repository of type: Müller (pers. comm. 2016): holotype, unsexed, ETHZ (coll. Seyfried) [no. 3265].

Extant Congeners: yes

Note: Does not belong in Harpactor; if a harpactorine, possibly in Rhynocoris.

Harpactor gracilis Heer

1853 Harpactor gracilis Heer, p. 81. Pl. 5 Fig. 23; Pl. 10, Fig. 6. [original description].

1855 Harpactor gracilis: Heer, p. 201. [catalog].

1856 Harpactor gracilis: Giebel, p. 367. [synopsis].

1891 (Harpactor) cf. gracilis: Förster, 3:548. Brunstatt. [additional material?].

1891 Harpactor sp.: Scudder, 71:409. Brunstatt Alsatia, Middle Oligocene. [catalog].

1891 Harpactor gracilis: Scudder, 71:410. Mayencian. [catalog].
1908 (*Harpactor* gracilis): Handlirsch, p. 1038. [catalog].

1908 (*Harpactor* cf gracilis): Handlirsch, p. 1038. [catalog].

Locality: Radoboj, Croatia.

Preservation: compression.

Age: Cenozoic: Neogene: early to middle Miocene (20.4–11.1 Ma).

Age Reference: Bajraktarević 1984 [see discussion in Mlíkovský 1997, 98:145].

Repository of type: Zorn (pers. comm. 2016): holotype, unsexed, GBA (coll. Morlot) [no. 146].

Extant Congeners: yes

Notes: (1) The age references included support a Serravallian (=Sarmatian) date for this fossil; a Burdigalian date is often cited for Radoboj, although I have not been able to find any references with support from stratigraphical dating for this age. (2) After determining that the holotype was not present in the HPM (K. Krizmanić, pers. comm. 2016), NHMW (Ponomarenko & Schultz 1988a), or SLJG (M. Gross, pers. comm. 2016), it was located in GBA (I. Zorn, pers. comm. 2016). Additional, non-type material [nos. 3264, 3314], labelled as *Harpactor gracilis?*, is present in ETHZ (Müller, pers. comm. 2016). (3) Does not belong in *Harpactor*; if a harpactorine, possibly in *Rhynocoris*. (4) This name is the senior primary homonym of *Harpactor gracilis* Stål, 1855 (currently *Zamolxis gracilis*). I am petitioning the International Committee on Zoological Nomenclature (Swanson, in prep.) to rule on this issue.

*Harpactor longipes* Heer

1853 *Harpactor longipes* Heer, p. 78. Pl. 5, Fig. 20; Pl. 10, Fig. 3. [original description].
1856 *Harpactor longipes*: Giebel, p. 366. [synopsis].


1908 (*Harpactor*) *longipes*: Handlirsch, p. 1038. [catalog].

Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Repository of type: Müller (pers. comm. 2016): holotype, unsexed, ETHZ (coll. Lavaters) [no. 3260].

Extant Congeners: yes

Note: Does not belong in *Harpactor*; if a harpactorine, possibly in *Rhynocoris*.

*Harpactor maculipes* Heer

1853 *Harpactor maculipes* Heer, p. 79, 132. Pl. 5 Fig. 21; Pl. 10, Fig. 4. [original description].

1856 *Harpactor maculipes*: Giebel, p. 366. [synopsis].

1865 *Harpactor maculipes*: Heer, p. 391. Fig. 306. [figured].

1865 *Harpactor maculipes*: Lyell, p. 409. Fig. 193. [figured].

1891 *Harpactor maculipes*: Scudder, 71:410. Tortonian. [catalog].

1908 (*Harpactor*) *maculipes*: Handlirsch, p. 1038. [catalog].

Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).

Repository of type: Heer 1953, p. 79; Müller (pers. comm. 2016): holotype, unsexed, ETHZ [no. 3262].

Extant Congeners: yes

Notes: (1) The plate used in Heer 1865 was reproduced in Heer 1872, p. 479, Fig. 306; Heer 1876, p. 49, Fig. 306; and Heer 1879, p. 417, Fig. 348. The figure of *Harpactor maculipes* alone was reproduced in Scudder 1885, p. 784, Fig. 997; and Scudder 1887, p. 783, Fig. 1014. (2) Additional material [no. 3316] may be present in ETHZ (Müller, pers. comm. 2016). (3) Does not belong in *Harpactor*; if a harpactorine, possibly in *Rhynocoris*.

*Harpactor obsoletus* Heer

1853 *Harpactor obsoletus* Heer, p. 82. Pl. 5 Fig. 25. [original description].

1856 *Harpactor obsoletus*: Giebel, p. 367. [synopsis].

1891 *Harpactor obsoletus*: Scudder, 71:410. Tortonian. [catalog].

1908 (*Harpactor) obsoletus*: Handlirsch, p. 1038. [catalog].

Locality: Öhningen, Baden, Germany.

Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Repository of type: Heer 1953, p. 82; Müller (pers. comm. 2016): holotype, unsexed, ETHZ [no. 3315].

Extant Congeners: yes
Notes: (1) The specimen at ETHZ is marked with a "?"; therefore, it is possible that it is not the holotype (Müller, pers. comm. 2016). (2) Does not belong in Harpactor; if a harpactorine, possibly in Rhynocoris.

Poliosphageus Kirkaldy

1910 Poliosphageus Kirkaldy, 21:130.


Poliosphageus psychrus Kirkaldy


Locality: Station 13B, Florissant, Colorado, U.S.A.

Preservation: shale compression.

Age: Cenozoic: Palaeogene: Eocene: Priabonian (34.7–33.7 Ma).


Repository of type: Karim (pers. comm. 2015): holotype, unsexed, UCMC [ucm18621a, b].

Extant Congeners: no

Rhynocoris Hahn

1833 Rhynocoris Hahn, 2:20.

Type species: Reduvius cruentus Fabricius, 1787, p. 310. By subsequent designation:

Kirkaldy 1900, 33:242.
Rhynocoris michalki Statz

1950 *Rhynocoris michalki* Statz (in Statz & Wagner), 98:102. Pl. 21, Fig. 3; Pl. 22, Fig. 10 [hemelytron]; Pl. 23, Fig. 15–16. [original description].


Locality: Rott-am-Siebengebirge, Germany.

Preservation: slate compression.


Extant Congeners: yes

Notes: (1) Sphon 1973, 250:26 indicated that one "syntype" of *Rhynocoris michalki* should be in LACM but was missing. She also noted that there was another "syntype" in the Kastenholz collection. Petrulevičius, Wappler, Nel & Rust 2011, 130:69, reported that the Kastenholz collection was housed in STIB; however, Wappler (pers. comm. 2016) indicated that no such specimen seems to exist in that repository. Regardless, since Statz & Wagner 1950, 98:103, stated that the Fundstück came from the Kastenholz collection and the Gegenstück came from the Verfassers collection, it can be assumed that (a) the "syntype" missing from STIB corresponds to the part; and (b) the "syntype" missing from LACM corresponds to
the counterpart. (2) The plate used in Statz & Wagner 1950 was reproduced in Becker-Migdisova 1962, p. 218, Fig. 653 and Becker-Migdisova 1991, p. 305, Fig. 653.

Subfamily Holoptilinae

_Praecoris_ Poinar


_Praecoris dominicanus_ Poinar


1999 _Praecoris dominicana_: Poinar & Poinar, p. 110. Fig. 113. [ecological reconstruction].

1999 _Praecoris dominicana_: Pérez-Gelabert, 1:40. Erroneously in MIRIDAE. [catalog].

2005 _Praecoris dominicana_: Arillo & Ortuño, 68:17. [catalog].

2008 _Praecoris dominicana_: Pérez-Gelabert, 1831:188. [catalog].

2012 _Praecoris dominicana_: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: La Toca Mine, Cordillera Septentrional, Dominican Republic.

Preservation: Dominican amber.


Extant Congeners: no
Proptilocerus Wasmann

1932 Proptilocerus Wasmann, 3:2.

Type species: Proptilocerus dolosus Wasmann, 1932, 3:3. By monotypy.

Proptilocerus dolosus Wasmann

1932 Proptilocerus dolosus Wasmann, 3:3. Pl. 1, Fig. 4. [original description].


1951 Proptilocerus dolosus: Andrée, p. 62. [synopsis].

1949 Proptilocerus dolosus: Bachofen-Echt, p. 167. [synopsis].

1982 Proptilocerus dolosus: Keilbach, 29:226. [catalog].

1988 Proptilocerus dolosus: Spahr, 144:15. [catalog].

2009 Proptilocerus dolosus: Putshkov & Moulet, p. 111. [checklist].

2009 Proptilocerus dolosus: Heiss, 26:84. Ph. 1–8; Figs. 1–9. Baltic & Bitterfeld amber.

[additional material].

Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Repository of type: Heiss 2009, 26:84: holotype, nymph, GPIH.

Extant Congeners: no

Proptilocnemus Heiss

2009 Proptilocnemus Heiss, 26:89.

Type species: Proptilocnemus longispinis Heiss, 2009, 26:90. By monotypy.
Proptilocnemus longispinis Heiss

2009 Proptilocnemus longispinis Heiss, 26:90. Ph. 9–10; Figs. 10–12. [original description].

Locality: Bitterfeld, Sachsen-Anhalt, Germany.

Preservation: Baltic (Bitterfeld) amber.

Age: Cenozoic: Paleogene: Oligocene: Chattian (25.3–23.8 Ma).

Age Reference: Knuth, Koch, Rappsilber & Volland 2002 [see discussions in Standke 2008; Dunlop 2010, pp. 61–62].

Repository of type: Heiss 2009, 26:89: holotype, nymph, FEC [no. 8].

Extant Congeners: no

Subfamily Peiratinae

Peirates Serville


Type species: Reduvius stridulus Fabricius, 1787, p. 309. By subsequent designation:

Blanchard 1840, p. 106.

Peirates oeningensis Heer

1853 Pirates oeningensis Heer, p. 132. Pl. 15, Fig. 11. [original description].

1856 Pirates oeningensis: Giebel, p. 368. [synopsis].

1891 Pirates oeningensis: Scudder, 71:436. Tortonian. [catalog].

1908 (Pirates) oeningensis: Handlirsch, p. 1038. [catalog].


Locality: Öhningen, Baden, Germany.
Preservation: limestone compression.

Age: Cenozoic: Neogene: middle to late Miocene (12.7–5.3 Ma).


Repository of type: Müller (pers. comm. 2016): holotype, unsexed, ETHZ (coll. Seyfried) [no. 3268].

Extant Congeners: yes

Subfamily Phimophorinae

*Koenigsbergia* Popov


*Koenigsbergia herczeki* Popov

2003 *Koenigsbergia herczeki* Popov, 87:161. In PHYMATINAE: THEMONOCORINI. [original description].


Locality: Yantarnyi, Kaliningrad Region, Samland Peninsula, Russia.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Extant Congeners: no
Note: The subfamilial transfer of this species will be treated in greater detail in a subsequent work (in prep.).

Subfamily Reduviinae

*Platymeris* Laporte

1833 *Platymeris* Laporte, 1:80.


*Platymeris insignis* Germar & Berendt

1845 *Playtmeris* sp.: Berendt, p. 55. [undescribed fossil].

1856 *Platymeris insignis* Germar & Berendt, p. 21. Pl. 3, Fig. 12. [original description].

1891 *Platymeris* sp.: Scudder, 71:437.

1891 *Platymeris insignis*: Scudder, 71:437. Compared with *P. formicaria*, Brazil. Ligurian. [catalog].

1908 (*Platymeris*) insignis: Handlirshc, p. 1037. [catalog].

1925 ?*Platymeris insignis*: Handlirshc, p. 275. Fig. 232. Figure after Germar & Berendt 1856a. [catalog].

1982 *Plathymeris* [sic] *insignis*: Keilbach, 29:226. [catalog].

1988 *Platymeris insignis*: Spahr, 144:14. [catalog].

2009 *Reduvius* (?) *insignis*: Putshkov & Moulet, p. 111. [checklist].

Locality: unknown.

Preservation: Baltic amber.

Age: Cenozoic: Paleogene: Eocene (56–33.7 Ma).


Extant Congeners: yes

Notes: (1) The plate used in Handlirsch 1925a was reproduced in Müller 1963, p. 251, Fig. 357; Becker-Migdisova 1962, p. 218, Fig. 652; and Becker-Migdisova 1991, p. 305, Fig. 652. (2) Does not belong in Platymeris; if a reduviine, possibly in Reduvius.

Reduvius Fabricius

1775 Reduvius Fabricius, p. 729.

Type species: Cimex personatus Linnaeus, 1758, 10:446. By subsequent designation:

Latreille 1810, p. 433.

Reduvius diatomus Zhang & Zhang

1990 Reduvius diatomus Zhang & Zhang, 29:343, 347. Fig. 6; Pl. 2, Figs. 2–3. [original description].

1994 Reduvius diatomus: Zhang, Sun & Zhang, p. 77. Figs. 50–51; Pl. 9, Figs. 1–2. [synopsis; additional material].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.

Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.


Extant Congeners: yes
Note: Additional material recorded by Zhang, Sun & Zhang 1994 is housed in SNGL (see note in following entry).

*Reduvius immitus* Zhang, Sun & Zhang

1994 *Reduvius immitus* Zhang, Sun & Zhang, p. 80. Fig. 56; Pl. 10, Fig. 2. [original description].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.

Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.

Repository of type: Zhang, Sun & Zhang 1994, pp. 1, 81: holotype, unsexed, SNGL [no. SK000418].

Extant Congeners: yes

Note: Formally cited in Zhang, Sun & Zhang 1994 as Shanwang Management of Fossil Protection, Linqu County, Shandong Province, I have assumed that this corresponds to the national geopark cited above, in part because the Shanwang Fossil Museum (SFML) was listed as a separate institution with a different specimen code (i.e., nos. S _ _ _ _ _ _).

*Reduvius nicus* Zhang, Sun & Zhang

1994 *Reduvius nicus* Zhang, Sun & Zhang, p. 79. Fig. 54; Pl. 9, Fig. 4. [original description].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.
Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.


Extant Congeners: yes

Note: Formally cited in Zhang, Sun & Zhang 1994 as Shanwang Management of Fossil Protection, Linqu County, Shandong Province, I have assumed that this corresponds to the national geopark cited above, in part because the Shanwang Fossil Museum (SFML) was listed as a separate institution with a different specimen code (i.e., nos. S _ _ _ _ _ _).

Reduvius piceus Zhang, Sun & Zhang

1994 *Reduvius piceus* Zhang, Sun & Zhang, p. 80. Fig. 55; Pl. 10, Fig. 1. [original description].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.

Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.


Extant Congeners: yes
*Reduvius shandongianus* Zhang & Zhang

1990 *Reduvius shandongianus* Zhang & Zhang, 29:344, 348. Figs. 7–8; Pl. 3, Figs. 1–4. [original description].

1994 *Reduvius shandongianus*: Zhang, Sun & Zhang, p. 78. Figs. 52–53; Pl. 9, Fig. 3. [synopsis].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.

Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.


Extant Congeners: yes

**Subfamily Saicinae**

*Hymenopterites* Heer

1870 *Hymenopterites* Heer, 8:78.

Type species: *Hymenopterites deperditus* Heer, 1870, 8:78. By monotypy.

*Hymenopterites deperditus* Heer

1870 *Hymenopterites deperditus* Heer, 8:78. Pl. 16, Figs. 44–45. [original description].


1908 *Hymenopterites deperditus*: Handlirsch, p. 893. In HYMENOPTERA incertae sedis. [catalog].
1977 *Hymenopterites deperditus*: Birket-Smith, 19:34. Fig. 21. As nomen relictum, a winged seed. [synopsis].


In SAICINAE. [redescription].

Locality: Grønfjorden NW (SE of Festningsodden), Spitsbergen, Norway.

Preservation: black shale compression.

Age: Cenozoic: Palaeogene: Paleocene (66.0–56.0 Ma).

Age Reference: Dallmann, Midbøe, Nøttvedt & Steel 1999 [see discussion in Wappler, Garrouste, Engel & Nel 2013, 58:883].

Repository of type: Wappler, Garrouste, Engel & Nel 2013, 58:884: holotype, [wing], NRM [Ar. 46].

Extant Congeners: no

*Tagalodes* Scudder

1890 *Tagalodes* Scudder, 13:356.

Type species: *Tagalodes inermis* Scudder, 1890, 13:356. By monotypy.

*Tagalodes inermis* Scudder

1890 *Tagalodes inermis* Scudder, 13:357. Pl. 26, Fig. 15. [original description].

1891 *Tagalodes inermis*: Scudder, 71:444. Oligocene. [catalog].

1908 *Tagalodes inermis*: Handlirsch, p. 1037. In CAPSIDAE. [catalog].

1909 *Tagalodes inermis*: Cockerell, 26:83. [catalog].

Locality: Florissant, Colorado, USA.

Preservation: shale compression.
Age: Cenozoic: Palaeogene: Eocene: Priabonian (34.7–33.7 Ma).


Repository of type: Perez de la Fuente (pers. comm. 2015): holotype, female, NMNH [no. 2696].

Extant Congeners: no

**Subfamily Stenopodainae**

*Oncocephalus* Klug

1830 *Oncocephalus* Klug, [unpaginated].

Type species: *Reduvius (Oncocephalus) notatus* Klug, 1830, [unpaginated]. By subsequent designation: Distant 1904, p. 227.

*Oncocephalus astutus* Zhang, Sun & Zhang

1994 *Oncocephalus astutus* Zhang, Sun & Zhang, p. 81. Fig. 57; Pl. 10, Fig. 3. [original description].

Locality: Shanwang Village, Linqu County, Shandong Province, China.

Preservation: shale compression.

Age: Cenozoic: Neogene: Miocene: Burdigalian (17 Ma).

Age Reference: Huaiyu, Chenglong, Yongxin, Tao, Zhaohua, Jimin & Rixiang 2011.

Repository of type: Zhang, Sun & Zhang 1994, pp. 1, 81: holotype, unsexed, SNGL [no. SK000631].

Extant Congeners: yes

Notes: (1) Formally cited in Zhang, Sun & Zhang 1994 as Shanwang Management of Fossil Protection, Linqu County, Shandong Province, I have assumed that this
corresponds to the national geopark cited above, in part because the Shanwang Fossil Museum (SFML) was listed as a separate institution with a different specimen code (i.e., nos. S _ _ _ _ _ _). (2) Does not belong in *Oncocephalus*; if a stenopodaine, possibly in *Pygolampis*.

Subfamily Triatominae

*Panstrongylus* Berg

1879 *Panstrongylus* Berg, 7:268.


*Panstrongylus hispaniolae* Poinar

2013 *Panstrongylus hispaniolae* Poinar, 6:4. Figs. 2–9. [original description].

Locality: La Toca Mine, Cordillera Septentrional, Dominican Republic.

Preservation: Dominican amber.


Repository of type: Poinar 2013, 6:4: holotype, male, OSAC (coll. Poinar) [no. HE-4-81].

Extant Congeners: yes

*Triatoma* Laporte

1833 *Triatoma* Laporte, 1:11.


*Triatoma dominicana* Poinar

2005 *Triatoma dominicana* Poinar, 5:76. Figs. 1–10. [original description].

2008 *Triatoma dominicana*: Pérez-Gelabert, 1831:188. [catalog].
2012 *Triatoma dominicana*: Hwang & Weirauch, 7:9, Tab. S4. [phylogeny calibration].

Locality: La Toca Mine, Cordillera Septentrional, Dominican Republic.

Preservation: Dominican amber.


Extant Congeners: yes

LITERATURE CITED

Adobe Systems, Inc. 2014. Adobe Illustrator CC (version 2014.0.0) [software].


FIGURES AND TABLES

Figure 3.1. Lagerstätten represented by fossil Reduvisoidea.

- Map of Lagerstätten
- Bar chart of number of Reduvioid fossils by Lagerstätte
Figure 3.2. Distributions of type material of fossil Reduvioida by repository and country.
Figure 3.3. Number of fossil species in Reduviidae by subfamily.
Table 3.1. Subfamilial representation of Reduviidae in the fossil record. In Totals, numbers outside of parentheses are the number of subfamilies represented and numbers inside of parentheses are number of taxa. Taxa are treated in a traditional sense: (1) tribal arrangement likely does not reflect true relationship in Harpactorinae, and (2) the known polyphyletic nature of Reduviinae is ignored.

<table>
<thead>
<tr>
<th>Extant Subfamily (25)</th>
<th>Represented by Described Fossils?</th>
<th>Preservation</th>
<th>Updated from Maldonado (1990)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Resin</td>
<td>Compression</td>
</tr>
<tr>
<td>Bactrodinae</td>
<td></td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Centrocnemidinae</td>
<td>Y (2)</td>
<td>✓</td>
<td>31</td>
</tr>
<tr>
<td>Cetherinae</td>
<td></td>
<td>22</td>
<td>6</td>
</tr>
<tr>
<td>Chryxinae</td>
<td></td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Ectrichodiinae</td>
<td></td>
<td>670</td>
<td>114</td>
</tr>
<tr>
<td>Elasmominae</td>
<td></td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Emesinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collartidini</td>
<td>Y (1)</td>
<td>✓</td>
<td>12</td>
</tr>
<tr>
<td>Deliastini</td>
<td></td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Emesini</td>
<td></td>
<td>211</td>
<td>20</td>
</tr>
<tr>
<td>Leistarchini</td>
<td></td>
<td>283</td>
<td>32</td>
</tr>
<tr>
<td>Metapterini</td>
<td>Y (1)</td>
<td>✓</td>
<td>276</td>
</tr>
<tr>
<td>Ploiariolini</td>
<td>Y (10)</td>
<td>✓</td>
<td>164</td>
</tr>
<tr>
<td>Harpactorinae¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apiomerini</td>
<td>Y (1)</td>
<td>✓</td>
<td>165</td>
</tr>
<tr>
<td>Diaspidiini</td>
<td></td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>Dicrotelini</td>
<td></td>
<td>22</td>
<td>7</td>
</tr>
<tr>
<td>Ectinoderini</td>
<td></td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>Harpactorini</td>
<td>Y (13)</td>
<td>✓</td>
<td>1994</td>
</tr>
<tr>
<td>Phonolibini</td>
<td></td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Rhaphidosomini</td>
<td></td>
<td>92</td>
<td>8</td>
</tr>
<tr>
<td>Tegeini</td>
<td></td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Holoptylinae</td>
<td>Y (3)</td>
<td>✓</td>
<td>76</td>
</tr>
<tr>
<td>Manangocorinae</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Microtominae</td>
<td></td>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td>Peiratinae</td>
<td>Y (1)</td>
<td>✓</td>
<td>330</td>
</tr>
<tr>
<td>Phimophorinae</td>
<td>Y (1)</td>
<td>✓</td>
<td>3</td>
</tr>
<tr>
<td>Phymatinae</td>
<td></td>
<td>291</td>
<td>26</td>
</tr>
<tr>
<td>Physoderinae</td>
<td></td>
<td>65</td>
<td>14</td>
</tr>
<tr>
<td>Pseudocetherinae</td>
<td></td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Reduviinae²</td>
<td>Y (6)</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Saicinae</td>
<td>Y (2)</td>
<td>✓</td>
<td>143</td>
</tr>
<tr>
<td>Salyatavinae</td>
<td></td>
<td>108</td>
<td>17</td>
</tr>
<tr>
<td>Sphaeridopinae</td>
<td></td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Stenopodinae</td>
<td>Y (1)</td>
<td>✓</td>
<td>753</td>
</tr>
<tr>
<td>Triatominae</td>
<td>Y (2)</td>
<td>✓</td>
<td>138</td>
</tr>
<tr>
<td>Tribelocephalinae</td>
<td></td>
<td>129</td>
<td>16</td>
</tr>
<tr>
<td>Vesciinae</td>
<td></td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Visayanocorinae</td>
<td></td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>10 (44)</strong></td>
<td><strong>7(22)</strong></td>
</tr>
</tbody>
</table>
Table 3.2. Fossil taxa originally but erroneously described in Reduviidae. (*) I am petitioning the International Committee on Zoological Nomenclature (Swanson, in prep.) to rule on this issue.

<table>
<thead>
<tr>
<th>Fossil</th>
<th>Author</th>
<th>Year</th>
<th>Citation</th>
<th>Locality</th>
<th>Preservation</th>
<th>Correct Placement</th>
<th>Reviser</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Eothes elegans</em></td>
<td>Scudder</td>
<td>1890</td>
<td>13:355</td>
<td>Florissant</td>
<td>compression</td>
<td>Heteroptera: Alydidae?</td>
<td>Swanson (in prep.)</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Liaoxia longa</em></td>
<td>Hong</td>
<td>1987</td>
<td>18:77</td>
<td>Yixan</td>
<td>compression</td>
<td>Heteroptera: Vetanthocoridae</td>
<td>Yao et al. (2006)</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Manevalia pachyformis</em></td>
<td>Piton</td>
<td>1940</td>
<td>p. 159</td>
<td>Menat</td>
<td>compression</td>
<td>Hymenoptera: Symphyta</td>
<td>Nel (1992)</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Miocoris fagi</em></td>
<td>Cockerell</td>
<td>1927</td>
<td>20:592</td>
<td>Florissant</td>
<td>compression</td>
<td>Heteroptera: Nabidae</td>
<td>Swanson (in prep.)</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Pygolampis gigantea</em></td>
<td>Germar</td>
<td>1839</td>
<td>19:207</td>
<td>Solnhofen</td>
<td>compression</td>
<td>Archaeorthoptera: Chresmodidae</td>
<td>Scudder (1891)?</td>
<td>junior synonym of <em>Chresmoda obscura</em> (Germar, 1839)</td>
</tr>
<tr>
<td><em>Propygolampis bronni</em></td>
<td>Weyenbergh</td>
<td>1874</td>
<td>1:84</td>
<td>Solnhofen</td>
<td>compression</td>
<td>Archaeorthoptera: Chresmodidae</td>
<td>Scudder (1891)?</td>
<td>junior synonym of <em>Chresmoda obscura</em> (Germar, 1839)</td>
</tr>
<tr>
<td><em>Reduvius? guttatus</em></td>
<td>Scudder</td>
<td>1878</td>
<td>4:771</td>
<td>Green River</td>
<td>compression</td>
<td>Heteroptera: Rhopalidae</td>
<td>Scudder (1890)</td>
<td>currently <em>Corizus guttatus</em>; junior primary homonym of <em>Reduvius guttatus</em> Walker, 1873*</td>
</tr>
</tbody>
</table>
Table 3.3. Sources mentioning undescribed reduvioid fossils.

<table>
<thead>
<tr>
<th>Author</th>
<th>Year</th>
<th>Page</th>
<th>Number</th>
<th>Repository of Fossil</th>
<th>Preservation</th>
<th>Taxon</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bachofen-Echt</td>
<td>1949</td>
<td>165,</td>
<td>unknown</td>
<td>[Baltic?] amber</td>
<td>Reduviidae, incl. Emesinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Handlirsch</td>
<td>1908</td>
<td>1039</td>
<td>1</td>
<td>Bosniaski coll.</td>
<td>Reduviidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heer</td>
<td>1853</td>
<td>203</td>
<td>1</td>
<td>ETHZ compression</td>
<td>Stenopoda gracilis [Stenopodinae] nomen nudum; no. 3261</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heer</td>
<td>1853</td>
<td>203</td>
<td>1</td>
<td>ETHZ compression</td>
<td>Stenopoda oeningensis [Stenopodinae] nomen nudum; no. 3272</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Koch &amp; Wedmann</td>
<td>2012</td>
<td>n/a</td>
<td>ca. 60</td>
<td>SMF</td>
<td>various, including Elasmodeminae; Harpactorinae: Apiomerini, Ectinodini, Harpactorini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Koch &amp; Wedmann</td>
<td>2012</td>
<td>n/a</td>
<td>ca. 25</td>
<td>NMNH</td>
<td>Reduviidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maldonado et al.</td>
<td>1993</td>
<td>141</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber, Apiomerini [Harpactorinae]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mellish (pers. comm.)</td>
<td>2016</td>
<td>n/a</td>
<td>1</td>
<td>BMNH compression</td>
<td>Reduviidae?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Müller (pers. comm.)</td>
<td>2016</td>
<td>n/a</td>
<td>3</td>
<td>ETHZ compression</td>
<td>Harpactor aemulus [Harpactorini?] manuscript name; nos. 3263, 3269, 3273</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Müller (pers. comm.)</td>
<td>2016</td>
<td>n/a</td>
<td>1</td>
<td>ETHZ compression</td>
<td>Reduviidae?  no. 3291</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poinar, Jr. &amp; Poinar</td>
<td>1999</td>
<td>203</td>
<td>?</td>
<td>unknown</td>
<td>Dominican amber, Apiomerus sp. [Apiomerini] same as Apiomerini in Maldonado et al.?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poinar, Jr. &amp; Poinar</td>
<td>1999</td>
<td>203</td>
<td>?</td>
<td>unknown</td>
<td>Rasohus sp. [Peiratinae]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Popov et al.</td>
<td>2011</td>
<td>714,</td>
<td>1</td>
<td>PAS amber</td>
<td>Redubitus sp. [Centrocnemidinae] no. 23989</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Popov et al.</td>
<td>2011</td>
<td>714</td>
<td>1</td>
<td>PAS amber</td>
<td>Emesinae; Ploiairolini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Putshkov &amp; Moulet</td>
<td>2009</td>
<td>110</td>
<td>?</td>
<td>unknown</td>
<td>unknown unknown Mongolian; Cretaceous(!)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Putshkov &amp; Moulet</td>
<td>2009</td>
<td>111</td>
<td>?</td>
<td>unknown</td>
<td>Baltic amber Oncerotrochelus sp. [Saicinae] &quot;à décrire&quot; but unknown to me</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Putshkov &amp; Moulet</td>
<td>2009</td>
<td>111</td>
<td>?</td>
<td>unknown</td>
<td>Baltic amber Rhynocoris or Sphedanolestes sp. [Harpactorinae]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schlee</td>
<td>1980</td>
<td>50</td>
<td>1</td>
<td>SMNS? amber</td>
<td>Emesinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serres</td>
<td>1829</td>
<td>228</td>
<td>1</td>
<td>unknown</td>
<td>Aix-en-Provence Ploiaia sp. [Emesinae]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serres</td>
<td>1829</td>
<td>226</td>
<td>1</td>
<td>unknown</td>
<td>Aix-en-Provence Phymata sp. [Phymatinae]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serres</td>
<td>1829</td>
<td>228</td>
<td>3</td>
<td>unknown</td>
<td>Aix-en-Provence Reduvis sp. [Reduviinae]</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.3 (cont.).

<table>
<thead>
<tr>
<th>Author</th>
<th>Year</th>
<th>ID</th>
<th>Type</th>
<th>Location</th>
<th>Genus and Family</th>
<th>Note</th>
<th>Catalogue Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shcherbakov</td>
<td>2007</td>
<td>409</td>
<td>1</td>
<td>PIN compression</td>
<td>Ceresopsis sp.</td>
<td>[Ceresopseidae] no. 457/43</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>156</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Triatominae? F-298</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>157</td>
<td>4</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Apiomerini [Harpactorinae] F-302, F-308, F-309, F-310; F-308–F-310 misidentified as &quot;Berytidae&quot;</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>157</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Triatominae? F-303</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>157</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Salyavatinae F-304, F-305, F-306</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>158</td>
<td>3</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Metapterini [Emesinae] F-311</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>163</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Phimophorinae F-337; misidentified as &quot;Hebridae?&quot;</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>163</td>
<td>1</td>
<td>unknown</td>
<td>Dominican amber</td>
<td>Saicinae? F-340</td>
<td></td>
</tr>
<tr>
<td>Wu</td>
<td>1996</td>
<td>163</td>
<td>1</td>
<td>unknown</td>
<td>Empicoris sp.</td>
<td>[Emesinae] F-341</td>
<td></td>
</tr>
<tr>
<td>Wygodzinsky</td>
<td>1966</td>
<td>73</td>
<td>1</td>
<td>UCMP</td>
<td>Chiapas amber</td>
<td>Empicoris sp. [Emesinae]</td>
<td></td>
</tr>
</tbody>
</table>
INDEX TO ANNOTATED CATALOG

Page numbers given for genera refer to the genus as a whole, viz. a generic name not followed by a specific epithet. Valid constituent species to which are referred in the text are then listed under a genus but pages numbers are only provided under the alphabetically-listed species epithets and will need to be looked up there. Species epithets are listed only once, with the current generic assignment first, followed by previous combinations in brackets. Genus- and species-level taxa mentioned in Tables 3.2 and 3.3 are included.

aemulus, Harpactor ........................................................................................................... 165

Alumeda ............................................................................................................................. 110

antilliana

dominicana

nigricans

solorzanokraemeris

Amphibolus ...................................................................................................................... 117

disponsi

antilliana, Alumeda .......................................................................................................... 110

Aphelicophontes ............................................................................................................... 118

iuddorum

Apicrenus ......................................................................................................................... 116

fossilis

Apiomerini ......................................................................................................................... 116
Apiomerus ................................................................................................................................... 165

Arilus ........................................................................................................................................ 119

*faujasi*

*astutus, Oncocephalus* ............................................................................................................. 138

*bronni, Propygolampis* ........................................................................................................... 164

*bruckmanni, Harpactor* ........................................................................................................... 120

*centrocnemarius, Redubitus* ................................................................................................... 108

Centrocnemidinae ....................................................................................................................... 107

Ceresopseidae ............................................................................................................................. 105

*Ceresopsis* ............................................................................................................................... 105, 166

*costalis*

*ornata*

*vitrea*

*chomeraciensis, Harpactor* ...................................................................................................... 121

*Chresmoda* ............................................................................................................................. 164

*obscura*

*christelae, Danzigia* ................................................................................................................ 112

*Collarhamphus* ....................................................................................................................... 108

*mixtus*

Collartidini ................................................................................................................................... 108

*constrictus, Harpactor* .......................................................................................................... 122

*copal, Empicoris* ...................................................................................................................... 113
Corizus ........................................................................................................................................ 164

guttatus
costalis, Ceresopsis .................................................................................................................. 105
Danzigia ...................................................................................................................................... 111

christelae
deperditus, Hymenopterites .................................................................................................. 136
diatomus, Reduvius ................................................................................................................ 133
disponsi, Amphibolus ............................................................................................................... 117
dolosus, Proptilocerus ............................................................................................................. 129
dominicana, Alumeda ............................................................................................................. 110
dominicana, Triatoma ............................................................................................................. 139
dominicanus, Praecoris .......................................................................................................... 128
electricus, Empicoris ............................................................................................................. 114
elegans, Eothes ....................................................................................................................... 164
Emesinae ................................................................................................................................. 108
Emesites .................................................................................................................................... 109

voigti
Emesopsis .................................................................................................................................. 112

putshkovi

similis
Empicoris .................................................................................................................................. 113, 166

copal

169
electricus

Empiploiaiola ............................................................................................................................. 114

inermis

Eothes ........................................................................................................................................... 164

elegans

Euagoras ........................................................................................................................................ 119

impressus

fagi, Miocoris .................................................................................................................................... 164

faujasi, Arilus.................................................................................................................................. 119

fossilis, Apicrenus .......................................................................................................................... 116

gigantea, Pygolampis ........................................................................................................................ 164

gracilis, Harpactor ........................................................................................................................... 122

gracilis, Stenopoda ............................................................................................................................ 165

guttatus, Corizus [Reduvius] ............................................................................................................. 164

Harpactor .......................................................................................................................................... 120

aemulus

bruckmanni

chomeraciensis

constrictus

gracilis

longipes

maculipes
obsoletus

Harpactorinae ............................................................................................................................. 116
Harpactorini ................................................................................................................................ 117
herczeki, Koenigsbergia .............................................................................................................. 131
hispaniolarae, Panstrongylus ......................................................................................................... 139
Holoptilinae ................................................................................................................................... 128
Hymenopterites ................................................................................................................................. 136
deperditus

immitus, Reduvius ............................................................................................................................. 134
impressus, Euagoras .......................................................................................................................... 120
inermis, Empiploiariola ..................................................................................................................... 114
inermis, Tagalodes .......................................................................................................................... 137
insignis, Platymeris ............................................................................................................................. 132
iuddorum, Aphelicophontes ........................................................................................................ 118
Koenigsbergia .................................................................................................................................. 131
herczeki

Liaoxia .................................................................................................................................................. 164

longa

liedtkei, Redubinotus .......................................................................................................................... 107
longa, Liaoxia ....................................................................................................................................... 164
longipes, Harpactor .......................................................................................................................... 123
longispinis, Proptilocnemus ........................................................................................................ 130
maculipes, Harpactor .................................................................................................................. 124
Malacopus ........................................................................................................................................ 115

	wygodzinskyi
Manevalia ........................................................................................................................................ 164

	

pachyliformis
Metapterini ......................................................................................................................................... 109
michalki, Rhynocoris ..................................................................................................................... 127
Miocoris ............................................................................................................................................... 164

	fagi
mixtus, Collarhamphus .................................................................................................................... 108

	nicus, Reduvius ................................................................................................................................ 134
nigricans, Alumeda .......................................................................................................................... 111
obscura, Chresmoda ........................................................................................................................ 164

	obsoletus, Harpactor ....................................................................................................................... 125

oeningensis, Peirates ........................................................................................................................ 130

oeningensis, Stenopoda .................................................................................................................... 165

Oncerotrachelus .................................................................................................................................. 165

Oncocephalus ..................................................................................................................................... 138

	astutus
ornata, Ceresopsis .......................................................................................................................... 106

pachyliformis, Manevalia ................................................................................................................ 164

Paleoploiariola ................................................................................................................................ 114
venosa

**Panstrongylus** ................................................................. 139

*hispaniolae*

Peirates ................................................................. 130

*oeningensis*

Peiratinae ...................................................................... 130

Phimorphinae .............................................................. 131

**Phymata** ...................................................................... 165

*piceus, Reduvius* .......................................................... 135

**Platymeris** ................................................................. 132

*insignis*

Ploia ................................................................. 165

Ploiarionli ................................................................. 110

**Poliosphageus** .......................................................... 126

*psychrus*

Praecoris ..................................................................... 128

*dominicanus*

Proptilocerus ............................................................... 129

*dolosus*

Proptilocnemus ............................................................ 129

*longispinis*

Propygolampis ............................................................ 164
bronni

psychrus, Poliosphageus ................................................................. 126

putshkovi, Emesopsis ................................................................. 112

Pygolampis ............................................................. 164

gigantea

Rasahus ................................................................. 165

Redubinotus ................................................................. 107

liedtkei

Redubitus .................................................. 107, 165

centricnemarius

Reduviidae ................................................................. 107

Reduviinae ................................................................. 132

Reduvius ................................................................. 133, 165

diatomus

guttatus

immitus

nicus

piceus

shandongianus

Rhynocoris ................................................................. 126, 165

michaliki

Saiicinae ................................................................. 136
shandongianus, Reduvius ............................................................................................................ 136

similis, Emesopsis ........................................................................................................................ 113

solorzanokraemeri, Alumeda ......................................................................................................... 165

Sphedanolestes ............................................................................................................................ 165

Stenopoda .................................................................................................................................... 165

    gracilis

    oeningensis

Stenopodainae ............................................................................................................................ 138

Tagalodes .................................................................................................................................... 137

    inermis

Triatoma .................................................................................................................................... 139

    dominicana

Triatominae ................................................................................................................................ 139

venosa, Paleoploiariola ............................................................................................................... 114

vitrea, Ceresopsis ....................................................................................................................... 106

voigtii, Emesites .......................................................................................................................... 109

wygodzinskyi, Malacopus ............................................................................................................ 116
EPILOGUE: PROMISING PROBLEMS; OR POTENTIAL FOR FUTURE WORK IN FOSSIL REDUVIOIDEA

The study of Reduvioidea, as with any speciose, evolutionarily-successful group, is an exciting one, full of interesting phenomena and potential model systems through which to study evolutionary questions. This is true even when limited to the tales (or tails?) of dead bugs. From the fossil perspective, there are three main objectives that require greater focus in order to augment our understanding of the evolutionary history of this group: 1) describing additional fossil species; 2) correcting the erroneous placement of already-described taxa; and 3) using these data (new species and revised placements) to re-calibrate molecularly-inferred phylogenetic trees.

There are many more fossil reduvioids that have yet to be described. A handful of scattered references, in fact, already exist in the literature (see Table 3.3). Koch & Wedmann (2012), in particular, noted large series of undescribed material from Messel (Germany) and the Green River Formation (U.S.A.), and some of these specimens appear to belong to reduviid lineages not yet represented in the fossil record (i.e., Elasmodeminae, Harpactorinae: Ectinoderini). If extant affinities can be sufficiently resolved, ages of both these sites are sufficiently old (ca. 50 Ma) to potentially affect the divergence dating of the group, as has been shown in this study with Aphelicophontes iuddorum. Undoubtedly, there is undescribed material not mentioned in the literature, and several fossil taxa are currently under description in China (C. Weirauch, pers. comm. 2015). Many of the species descriptions referenced in the systematic catalog are not reduviid-, or even heteropteran-, specific but focus on fossil insects or arthropods from a particular region or formation; thus, a specialist's eye might reveal
additional taxa glossed over by a more general previous treatment. Furthermore, only a fraction of the total Lagerstätten of the world (see lists of Eskov 2002 and Rasnitsyn & Zherikhin 2002) have yielded reduvioids; is this due to absence of reduviids or a bias in the study of particular fossil sites or taphonomies? The global distribution of extant Reduviidae suggests that it is not the former.

The re-examination and revision of already-described taxa is crucial, given that many of the fossil reduviid taxa are, to some degree, misplaced. This can happen for several different reasons. Most salient to the Reduvioidea, many taxa described in the mid-19th century have not been revisited since description. Concomitantly, the number of reduviid genera described at the time was much lower than it is today, resulting in taxa being dumped into "coarser" bins, i.e., genera of older provenance that today have drastically different or narrowed concepts (e.g., Euagoras, Harpactor, Peirates, Platymeris, Stenopoda). Preliminary evidence suggests that many of these fossils may not exhibit the diagnostic characters necessary to accurately associate them with an extant lineage, whereas other taxa may be conspecific with those bearing a different species name. Additionally, the scope should be widened to consider other superficially similar heteropteran taxa, such as damsel bugs (Nabidae). Some erroneous taxa have already been pruned (see Table 3.2), and other cases, highlighted elsewhere in this work, are currently in progress.

As more new descriptions and revisionary studies take place, better information becomes available to support phylogenetic hypotheses. The latter is particularly important, as misidentified fossils used in calibration can mislead phylogenetic inferences and estimates of divergence dates. Furthermore, phylogenetics programs and methods are rapidly improving,
necessitating that previous conclusions be re-examined and corroborated with new techniques. Additionally, the fossils discussed herein are not only useful for studying the Reduvioidea but also are of utility in groups for which Reduvioidea is a constituent: Heteroptera, Hemiptera, Insecta, and so on. Lastly, while I have emphasized the role that fossils play in this study, further phylogenetic study needs to augment sampling, both in extant taxa and in gathering more complete sequence data.

LITERATURE CITED


APPENDIX A: LIST OF GENBANK SPECIMENS AND ACCESSION NUMBERS

All sequences are previously published and have been downloaded from GenBank. Length is recorded in base pairs (bp). AN refers to the GenBank Accession Number. (–) denotes missing data.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Family-Level Rank</th>
<th>16S</th>
<th>18S</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Length</td>
<td>AN</td>
</tr>
<tr>
<td>Abedus breviceps</td>
<td>Outgroup: Belostomatidae</td>
<td>555</td>
<td>AY252676.1</td>
</tr>
<tr>
<td>Corixidae sp. CW-2009 voucher CW 385</td>
<td>Outgroup: Corixidae</td>
<td>553</td>
<td>FJ230383.1</td>
</tr>
<tr>
<td>Austrotechus rugosus</td>
<td>Outgroup: Pentatomidae</td>
<td>494</td>
<td>AY252745.1</td>
</tr>
<tr>
<td>Mezira sayi</td>
<td>Outgroup: Aradidae</td>
<td>495</td>
<td>EU683100.1</td>
</tr>
<tr>
<td>Nabis apicalis</td>
<td>Outgroup: Nabidae</td>
<td>524</td>
<td>EF487292.1</td>
</tr>
<tr>
<td>Corythucha sp. CW-2009 voucher CW 383</td>
<td>Outgroup: Tingidae</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Oligotylus carneatus</td>
<td>Outgroup: Miridae</td>
<td>508</td>
<td>AY252853.1</td>
</tr>
<tr>
<td>Phallospinophylus setosus voucher CW 382</td>
<td>Outgroup: Miridae</td>
<td>550</td>
<td>FJ230382.1</td>
</tr>
<tr>
<td>Neocentrocnemis stali strain 00001976</td>
<td>Centrocnemidinae</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Cethera musiva strain 00052215</td>
<td>Ceterinae</td>
<td>530</td>
<td>JQ897787.1</td>
</tr>
<tr>
<td>Cethera musiva strain 00052176</td>
<td>Ceterinae</td>
<td>525</td>
<td>JQ897788.1</td>
</tr>
<tr>
<td>Eupheno histrionicus strain 00014326</td>
<td>Ceterinae</td>
<td>479</td>
<td>JQ897795.1</td>
</tr>
<tr>
<td>Eupheno pallens strain 00052214</td>
<td>Ceterinae</td>
<td>521</td>
<td>JQ897796.1</td>
</tr>
<tr>
<td>Cleptria corallina voucher CW 014</td>
<td>Ectrichodiinae</td>
<td>562</td>
<td>FJ230388.1</td>
</tr>
<tr>
<td>Ectrichodia lucida voucher CW 013</td>
<td>Ectrichodiinae</td>
<td>551</td>
<td>FJ230387.1</td>
</tr>
<tr>
<td>Ectrychotes sp. 1 CW-2009 voucher CW 076</td>
<td>Ectrichodiinae</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Ectrychotes sp. 2 CW-2009 voucher CW 188</td>
<td>Ectrichodiinae</td>
<td>554</td>
<td>FJ230424.1</td>
</tr>
<tr>
<td>Maraenaspis sp. CW-2009 voucher CW 016</td>
<td>Ectrichodiinae</td>
<td>563</td>
<td>FJ230389.1</td>
</tr>
<tr>
<td>Racelda sp. CW-2009 voucher CW 041</td>
<td>Ectrichodiinae</td>
<td>548</td>
<td>FJ230398.1</td>
</tr>
<tr>
<td>Rhiginia sp. CW-2009 voucher CW 139</td>
<td>Ectrichodiinae</td>
<td>554</td>
<td>FJ230410.1</td>
</tr>
<tr>
<td>Mangabea barbiger voucher CW 288</td>
<td>Emesinae: Collartidini</td>
<td>551</td>
<td>FJ230441.1</td>
</tr>
<tr>
<td>Stenolemoides arizonensis voucher CW 304</td>
<td>Emesinae: Emesini</td>
<td>560</td>
<td>FJ230444.1</td>
</tr>
<tr>
<td>Stenolemus sp. CW-2009 voucher CW 147</td>
<td>Emesinae: Emesini</td>
<td>557</td>
<td>FJ230413.1</td>
</tr>
<tr>
<td>Emesaya incisa voucher CW 282</td>
<td>Emesinae: Metapterini</td>
<td>554</td>
<td>FJ230436.1</td>
</tr>
<tr>
<td>Empicoris sp. 1 CW-2009 voucher CW 109</td>
<td>Emesinae: Ploiariolini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ploiaria hirticornis voucher CW 054</td>
<td>Emesinae: Ploiariolini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ptilocerus sp. CW-2010 voucher UCR_ENT 00001974</td>
<td>Holoptilinae</td>
<td>470</td>
<td>GU188453.1</td>
</tr>
<tr>
<td>Species Name</td>
<td>Family</td>
<td>Genus</td>
<td>Voucher Code</td>
</tr>
<tr>
<td>--------------</td>
<td>--------</td>
<td>-------</td>
<td>--------------</td>
</tr>
<tr>
<td>Ptilocnemus femoralis</td>
<td>Holoptilinae</td>
<td>Ptilocnemus</td>
<td>CW 220</td>
</tr>
<tr>
<td>Harpactorinae sp. 1</td>
<td>Harpactorinae</td>
<td></td>
<td>CW 190</td>
</tr>
<tr>
<td>Agriocoris flavipes</td>
<td>Harpactorinae: Apiomerini</td>
<td></td>
<td>CW 132</td>
</tr>
<tr>
<td>Apiomerus lanipes</td>
<td>Harpactorinae: Apiomerini</td>
<td></td>
<td>CW 281</td>
</tr>
<tr>
<td>Apiomerus ochropterus</td>
<td>Harpactorinae: Apiomerini</td>
<td></td>
<td>CW 022</td>
</tr>
<tr>
<td>Heniartes putumayo</td>
<td>Harpactorinae: Apiomerini</td>
<td></td>
<td>CW 395</td>
</tr>
<tr>
<td>Micrauchenus lineola</td>
<td>Harpactorinae: Apiomerini</td>
<td></td>
<td>CW 035</td>
</tr>
<tr>
<td>Acanthischium sp.</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 391</td>
</tr>
<tr>
<td>Anilus cristatus</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 071</td>
</tr>
<tr>
<td>Castolus subinermis</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 347</td>
</tr>
<tr>
<td>Coranus callosus</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 244</td>
</tr>
<tr>
<td>Euagoras sp.</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 194</td>
</tr>
<tr>
<td>Poecilosphodrus gratiosus</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 214</td>
</tr>
<tr>
<td>Pselliopus spinicollis</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 284</td>
</tr>
<tr>
<td>Pselliopus zebra</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 280</td>
</tr>
<tr>
<td>Pyrrhosphodrus amazonus</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 031</td>
</tr>
<tr>
<td>Rhynocoris segmentarius</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 004</td>
</tr>
<tr>
<td>Ricolla quadrispinosa</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 396</td>
</tr>
<tr>
<td>Sinea diadema</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 108</td>
</tr>
<tr>
<td>Ulpius sp.</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 370</td>
</tr>
<tr>
<td>Velinus sp.</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 197</td>
</tr>
<tr>
<td>Vesbius purpureus</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 184</td>
</tr>
<tr>
<td>Zelus longipes</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 006</td>
</tr>
<tr>
<td>Zelus nr. renardii</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 090</td>
</tr>
<tr>
<td>Zelus renardii</td>
<td>Harpactorinae: Harpactorini</td>
<td></td>
<td>CW 403</td>
</tr>
<tr>
<td>Rhaphidosoma decorsei</td>
<td>Harpactorinae: Rhaphidosomini</td>
<td></td>
<td>CW 017</td>
</tr>
<tr>
<td>Microtomus cinctipes</td>
<td>Microtominae</td>
<td></td>
<td>CW 141</td>
</tr>
<tr>
<td>Microtomus sp.</td>
<td>Microtominae</td>
<td></td>
<td>CW 030</td>
</tr>
<tr>
<td>Specimen Name</td>
<td>Family</td>
<td>Genus</td>
<td>Accession Numbers</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>------------------</td>
<td>----------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Ectomocoris ornatus voucher CW 246</td>
<td>Peiratinae</td>
<td>—</td>
<td>879</td>
</tr>
<tr>
<td>Ectomocoris sp. CW-2009 voucher CW 363</td>
<td>Peiratinae</td>
<td>553</td>
<td>FJ230447.1</td>
</tr>
<tr>
<td>Peirates punctorius voucher CW 216</td>
<td>Peiratinae</td>
<td>552</td>
<td>FJ230430.1</td>
</tr>
<tr>
<td>Rasahus thoracicus voucher CW 313</td>
<td>Peiratinae</td>
<td>—</td>
<td>954</td>
</tr>
<tr>
<td>Lophoscutus sp. CW-2009 voucher CW 052</td>
<td>Phymatinae: Macrocephalini</td>
<td>553</td>
<td>FJ230400.1</td>
</tr>
<tr>
<td>Macrocephalus sp. 1 CW-2009 voucher CW 283</td>
<td>Phymatinae: Macrocephalini</td>
<td>549</td>
<td>FJ230437.1</td>
</tr>
<tr>
<td>Macrocephalus sp. CW-2009 voucher CW 128</td>
<td>Phymatinae: Macrocephalini</td>
<td>549</td>
<td>FJ230409.1</td>
</tr>
<tr>
<td>Phymata acutangula voucher CW 029</td>
<td>Phymatinae: Phymatini</td>
<td>552</td>
<td>FJ230394.1</td>
</tr>
<tr>
<td>Phymata forticata voucher CW 028</td>
<td>Phymatinae: Phymatini</td>
<td>—</td>
<td>955</td>
</tr>
<tr>
<td>Phymata pacifica voucher CW 070</td>
<td>Phymatinae: Phymatini</td>
<td>557</td>
<td>FJ230401.1</td>
</tr>
<tr>
<td>Phymata sp. 1 CW-2009 voucher CW 087</td>
<td>Phymatinae: Phymatini</td>
<td>556</td>
<td>FJ230407.1</td>
</tr>
<tr>
<td>Physoderes impexa strain 00052181</td>
<td>Physoderinae</td>
<td>458</td>
<td>JQ897830.1</td>
</tr>
<tr>
<td>Physoderes nr. vestita 00052186</td>
<td>Physoderinae</td>
<td>545</td>
<td>JQ897831.1</td>
</tr>
<tr>
<td>Physoderes sp. 00052221</td>
<td>Physoderinae</td>
<td>539</td>
<td>JQ897832.1</td>
</tr>
<tr>
<td>Acanthaspis bilineolata strain 00052224</td>
<td>Reduviinae</td>
<td>526</td>
<td>JQ897773.1</td>
</tr>
<tr>
<td>Acanthaspis nr. bimaculata 00052192</td>
<td>Reduviinae</td>
<td>530</td>
<td>JQ897777.1</td>
</tr>
<tr>
<td>Acanthaspis gulo strain 00052222</td>
<td>Reduviinae</td>
<td>527</td>
<td>JQ897774.1</td>
</tr>
<tr>
<td>Acanthaspis iracunda voucher CW 019</td>
<td>Reduviinae</td>
<td>555</td>
<td>FJ230392.1</td>
</tr>
<tr>
<td>Acanthaspis iracunda strain 00218775</td>
<td>Reduviinae</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Acanthaspis iracunda strain 00052190</td>
<td>Reduviinae</td>
<td>533</td>
<td>JQ897775.1</td>
</tr>
<tr>
<td>Acanthaspis laosensis strain 00052193</td>
<td>Reduviinae</td>
<td>528</td>
<td>JQ897776.1</td>
</tr>
<tr>
<td>Acanthaspis quadriannulata strain 00004575</td>
<td>Reduviinae</td>
<td>534</td>
<td>JQ897778.1</td>
</tr>
<tr>
<td>Acanthaspis sulcipes strain 00052174</td>
<td>Reduviinae</td>
<td>534</td>
<td>JQ897781.1</td>
</tr>
<tr>
<td>Acanthaspis westermannii strain 00052218</td>
<td>Reduviinae</td>
<td>529</td>
<td>JQ897782.1</td>
</tr>
<tr>
<td>Acanthaspis sp. 00052205</td>
<td>Reduviinae</td>
<td>534</td>
<td>JQ897779.1</td>
</tr>
<tr>
<td>Acanthaspis sp. 00218828</td>
<td>Reduviinae</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Acanthaspis sp. CW-2009 voucher CW 073</td>
<td>Reduviinae</td>
<td>548</td>
<td>FJ230403.1</td>
</tr>
<tr>
<td>Acanthaspis sp. 2 CW-2009 voucher CW 082</td>
<td>Reduviinae</td>
<td>553</td>
<td>FJ230406.1</td>
</tr>
<tr>
<td>Acanthaspis sp. 00052175</td>
<td>Reduviinae</td>
<td>384</td>
<td>JQ897780.1</td>
</tr>
<tr>
<td>Alloeocranum arboricolum strain 00052180</td>
<td>Reduviinae</td>
<td>532</td>
<td>JQ897783.1</td>
</tr>
<tr>
<td>Censorinus ferrugineus strain 00046577</td>
<td>Reduviinae</td>
<td>525</td>
<td>JQ897786.1</td>
</tr>
<tr>
<td>Durevius tuberculatus strain 00046578</td>
<td>Reduviinae</td>
<td>534</td>
<td>JQ897790.1</td>
</tr>
<tr>
<td>Durganda rubra strain 00052223</td>
<td>Reduviinae</td>
<td>526</td>
<td>JQ897791.1</td>
</tr>
<tr>
<td>Dyakocoris vulnerans strain 00052204</td>
<td>Reduviinae</td>
<td>537</td>
<td>JQ897792.1</td>
</tr>
<tr>
<td>Gerbelius nr. ornatus 00052225</td>
<td>Reduviinae</td>
<td>528</td>
<td>JQ897797.1</td>
</tr>
<tr>
<td>Common Name</td>
<td>Scientific Name</td>
<td>Genbank Accession Numbers</td>
<td>Species ID</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>------------------------</td>
<td>---------------------------</td>
<td>-----------</td>
</tr>
<tr>
<td>Gerbelius ornatus</td>
<td>Reduviinae</td>
<td>JQ897799.1, JQ897560.1</td>
<td>00052220</td>
</tr>
<tr>
<td>Gerbelius ornatus</td>
<td>Reduviinae</td>
<td>JQ897798.1, JQ897559.1</td>
<td>00052189</td>
</tr>
<tr>
<td>Gerbelius sp.</td>
<td>Reduviinae</td>
<td>JQ897800.1</td>
<td>00052219</td>
</tr>
<tr>
<td>Hermillus sp. CW-2009</td>
<td>Reduviinae</td>
<td>FJ230420.1, FJ230499.1</td>
<td>00052179</td>
</tr>
<tr>
<td>Inara alboguttata</td>
<td>Reduviinae</td>
<td>JQ897801.1, JQ897561.1</td>
<td>00002551</td>
</tr>
<tr>
<td>Inara flavopicta</td>
<td>Reduviinae</td>
<td>JQ897804.1, JQ897564.1</td>
<td>00052191</td>
</tr>
<tr>
<td>Inara flavopicta</td>
<td>Reduviinae</td>
<td>JQ897802.1, JQ897562.1</td>
<td>00052170</td>
</tr>
<tr>
<td>Kayanocoris wegeneri</td>
<td>Reduviinae</td>
<td>JQ897803.1, JQ897563.1</td>
<td>00052216</td>
</tr>
<tr>
<td>Leogorruus immaculatus</td>
<td>Reduviinae</td>
<td>JQ897804.1, JQ897564.1</td>
<td>00014323</td>
</tr>
<tr>
<td>Leogorruus litura</td>
<td>Reduviinae</td>
<td>FJ230386.1, FJ230459.1</td>
<td>000012955</td>
</tr>
<tr>
<td>Leogorruus longiceps</td>
<td>Reduviinae</td>
<td>JQ897806.1, JQ897566.1</td>
<td>00052197</td>
</tr>
<tr>
<td>Leogorruus sp. n.</td>
<td>Reduviinae</td>
<td>JQ897807.1, JQ897567.1</td>
<td>00052198</td>
</tr>
<tr>
<td>Microlestria nr. fuscinollis</td>
<td>Reduviinae</td>
<td>JQ897809.1, JQ897569.1</td>
<td>00052226</td>
</tr>
<tr>
<td>Microlestria nr. fuscinollis</td>
<td>Reduviinae</td>
<td>JQ897810.1, JQ897570.1</td>
<td>00052183</td>
</tr>
<tr>
<td>Microlestria fuscinollis</td>
<td>Reduviinae</td>
<td>JQ897808.1, JQ897568.1</td>
<td>00052185</td>
</tr>
<tr>
<td>Nalata setulosa</td>
<td>Reduviinae</td>
<td>JQ897813.1, JQ897573.1</td>
<td>00003121</td>
</tr>
<tr>
<td>Nalata nr. spinicollis</td>
<td>Reduviinae</td>
<td>JQ897812.1, JQ897572.1</td>
<td>00052188</td>
</tr>
<tr>
<td>Nalata squalida</td>
<td>Reduviinae</td>
<td>JQ897815.1, JQ897575.1</td>
<td>00002748</td>
</tr>
<tr>
<td>Nalata sp.</td>
<td>Reduviinae</td>
<td>JQ897814.1, JQ897574.1</td>
<td>00014328</td>
</tr>
<tr>
<td>Nanokerala browni</td>
<td>Reduviinae</td>
<td>JQ897816.1, JQ897576.1</td>
<td>00052179</td>
</tr>
<tr>
<td>Nanokerala nr. browni</td>
<td>Reduviinae</td>
<td>JQ897817.1, JQ897577.1</td>
<td>00052228</td>
</tr>
<tr>
<td>Neostachyogenys tristis</td>
<td>Reduviinae</td>
<td>JQ897818.1, JQ897579.1</td>
<td>00052184</td>
</tr>
<tr>
<td>Noualhierana furtiva</td>
<td>Reduviinae</td>
<td>FJ230432.1, FJ230510.1</td>
<td>000224</td>
</tr>
<tr>
<td>Opisthaciddius chinai</td>
<td>Reduviinae</td>
<td>JQ897819.1, JQ897580.1</td>
<td>00012957</td>
</tr>
<tr>
<td>Opisthaciddius nr. mexicanus</td>
<td>Reduviinae</td>
<td>JQ897820.1, JQ897581.1</td>
<td>00004576</td>
</tr>
<tr>
<td>Opisthaciddius sp.</td>
<td>Reduviinae</td>
<td>JQ897821.1, JQ897582.1</td>
<td>00052199</td>
</tr>
<tr>
<td>Paredocla chevalieri</td>
<td>Reduviinae</td>
<td>FJ230391.1, FJ230465.1</td>
<td>000218</td>
</tr>
<tr>
<td>Pasiropsis maculata</td>
<td>Reduviinae</td>
<td>JQ897825.1, JQ897586.1</td>
<td>00052227</td>
</tr>
<tr>
<td>Pasiropsis marginata</td>
<td>Reduviinae</td>
<td>JQ897826.1, JQ897587.1</td>
<td>00052177</td>
</tr>
<tr>
<td>Pasiropsis sp. n.</td>
<td>Reduviinae</td>
<td>JQ897827.1, JQ897588.1</td>
<td>00052178</td>
</tr>
<tr>
<td>Pasiropsis sp.</td>
<td>Reduviinae</td>
<td>JQ897829.1, JQ897590.1</td>
<td>00052217</td>
</tr>
<tr>
<td>Pasiropsis sp.</td>
<td>Reduviinae</td>
<td>JQ897828.1, JQ897589.1</td>
<td>00052195</td>
</tr>
<tr>
<td>Pasiropsis sp.</td>
<td>Reduviinae</td>
<td>JQ897833.1, JQ897594.1</td>
<td>00052196</td>
</tr>
<tr>
<td>Pasiropsis sp.</td>
<td>Reduviinae</td>
<td>JQ897834.1, JQ897595.1</td>
<td>00004573</td>
</tr>
<tr>
<td>Pasiropsis superbus</td>
<td>Reduviinae</td>
<td>JQ897835.1, JQ897596.1</td>
<td>00004571</td>
</tr>
<tr>
<td>Species</td>
<td>Subfamily</td>
<td>Collection</td>
<td>NCBI Accession</td>
</tr>
<tr>
<td>----------------------------------------------</td>
<td>---------------</td>
<td>------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Psophis sp. 00052230</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897836.1</td>
</tr>
<tr>
<td>Psophis sp. 00218947</td>
<td>Reduviinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduvius personatus strain 00004567</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897837.1</td>
</tr>
<tr>
<td>Reduvius sonoraensis strain 00004569</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897838.1</td>
</tr>
<tr>
<td>Staliastes rufus strain 00052172</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897842.1</td>
</tr>
<tr>
<td>Staliastes sp. 00052231</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897843.1</td>
</tr>
<tr>
<td>Tapeinus sp. 00052200</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897845.1</td>
</tr>
<tr>
<td>Tapeinus sp. CW-2009 voucher CW 183</td>
<td>Reduviinae</td>
<td></td>
<td>FJ230421.1</td>
</tr>
<tr>
<td>Tapeinus sp. 00218926</td>
<td>Reduviinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tiarodes versicolor strain 00052171</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897847.1</td>
</tr>
<tr>
<td>Tiarodes sp. 00052206</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897846.1</td>
</tr>
<tr>
<td>Varus flavoannulatus strain 00004574</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897852.1</td>
</tr>
<tr>
<td>Velitra rubropicta strain 00052173</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897853.1</td>
</tr>
<tr>
<td>Velitra sp. 00052201</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897854.1</td>
</tr>
<tr>
<td>Zelurus alcides strain 00014324</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897855.1</td>
</tr>
<tr>
<td>Zelurus petax voucher CW 167</td>
<td>Reduviinae</td>
<td></td>
<td>FJ230416.1</td>
</tr>
<tr>
<td>Zelurus pintoi strain 00011856</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897856.1</td>
</tr>
<tr>
<td>Zelurus sp. 00052209</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897857.1</td>
</tr>
<tr>
<td>Zelurus sp. 00052194</td>
<td>Reduviinae</td>
<td></td>
<td>JQ897858.1</td>
</tr>
<tr>
<td>Zelurus sp. CW-2009 voucher CW 146</td>
<td>Reduviinae</td>
<td></td>
<td>FJ230412.1</td>
</tr>
<tr>
<td>Kiskeyana palassaina voucher CW 010</td>
<td>Saicinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saica sp. CW-2009 voucher CW 042</td>
<td>Saicinae</td>
<td></td>
<td>FJ230399.1</td>
</tr>
<tr>
<td>Salyavatinae sp. 00052207</td>
<td>Salyavatinae</td>
<td></td>
<td>JQ897841.1</td>
</tr>
<tr>
<td>Lisarda sp. CW-2009 voucher CW 177</td>
<td>Salyavatinae</td>
<td></td>
<td>FJ230419.1</td>
</tr>
<tr>
<td>Lisarda sp. CW-2009 voucher CW 078</td>
<td>Salyavatinae</td>
<td></td>
<td>FJ230404.1</td>
</tr>
<tr>
<td>Stenopodainae sp. 00052212</td>
<td>Stenopodainae</td>
<td></td>
<td>JQ897844.1</td>
</tr>
<tr>
<td>Canthesancus sp. 00052211</td>
<td>Stenopodainae</td>
<td></td>
<td>JQ897784.1</td>
</tr>
<tr>
<td>Ctenotrachelus sp. CW-2009 voucher CW 166</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230415.1</td>
</tr>
<tr>
<td>Gageus micropterus voucher CW 309</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230445.1</td>
</tr>
<tr>
<td>Kodormus bruneosus voucher CW 402</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230452.1</td>
</tr>
<tr>
<td>Oncocephalus sp. CW-2009 voucher CW 079</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230405.1</td>
</tr>
<tr>
<td>Sastrapada sp. CW-2009 voucher CW 185</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230423.1</td>
</tr>
<tr>
<td>Stenopoda sp. CW-2009 voucher CW 154</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230414.1</td>
</tr>
<tr>
<td>Stenopodessa sp. CW-2009 voucher CW 398</td>
<td>Stenopodainae</td>
<td></td>
<td>FJ230451.1</td>
</tr>
<tr>
<td>Specimen</td>
<td>28SD2</td>
<td>28SD3DS</td>
<td>Wg</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>----------------</td>
<td>-----------------</td>
<td>------------</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>AN</td>
<td>Length</td>
</tr>
<tr>
<td>Abedus breviceps</td>
<td>—</td>
<td>388</td>
<td>AY252440.1</td>
</tr>
<tr>
<td>Corixidae sp. CW-2009 voucher CW 385</td>
<td>626</td>
<td>FJ230537.1</td>
<td>360,186</td>
</tr>
<tr>
<td>Austrotechus rugosus</td>
<td>—</td>
<td>531</td>
<td>AY252517.1</td>
</tr>
<tr>
<td>Mezira sayi</td>
<td>—</td>
<td>308</td>
<td>EF641177.1</td>
</tr>
<tr>
<td>Nabis apicalis</td>
<td>—</td>
<td>620</td>
<td>EF487339.1</td>
</tr>
<tr>
<td>Corythucha sp. CW-2009 voucher CW 383</td>
<td>710</td>
<td>FJ230536.1</td>
<td>381,194</td>
</tr>
<tr>
<td>Oligotylus carneatus</td>
<td>—</td>
<td>519</td>
<td>AY252596.1</td>
</tr>
<tr>
<td>Phallospinophylus setosus voucher CW 382</td>
<td>646</td>
<td>FJ230535.1</td>
<td>362,190</td>
</tr>
<tr>
<td>Neocentrocemis stali strain 00001976</td>
<td>593</td>
<td>GU188466.1</td>
<td>483</td>
</tr>
<tr>
<td>Cethera musiva strain 00052215</td>
<td>643</td>
<td>JQ897629.1</td>
<td>523</td>
</tr>
<tr>
<td>Cethera musiva strain 00052176</td>
<td>609</td>
<td>JQ897630.1</td>
<td>538</td>
</tr>
<tr>
<td>Eupheno histrionicus strain 00014326</td>
<td>311</td>
<td>JQ897636.1</td>
<td>535</td>
</tr>
<tr>
<td>Eupheno pallens strain 00052214</td>
<td>648</td>
<td>JQ897637.1</td>
<td>615</td>
</tr>
<tr>
<td>Cleptia corallina voucher CW 014</td>
<td>645</td>
<td>FJ230543.1</td>
<td>422,188</td>
</tr>
<tr>
<td>Species</td>
<td>Voucher</td>
<td>Accession</td>
<td>Informative 1</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------</td>
<td>-------------------</td>
<td>---------------</td>
</tr>
<tr>
<td>Ectrichodia lucida</td>
<td>CW 013</td>
<td>FJ230542.1</td>
<td>461, 188</td>
</tr>
<tr>
<td>Ectrichotes sp. 1 CW-2009</td>
<td>CW 076</td>
<td>FJ230560.1</td>
<td>415, 188</td>
</tr>
<tr>
<td>Ectrichotes sp. 2 CW-2009</td>
<td>CW 188</td>
<td>FJ230584.1</td>
<td>425, 188</td>
</tr>
<tr>
<td>Maraenaspis sp. CW-2009</td>
<td>CW 016</td>
<td>FJ230544.1</td>
<td></td>
</tr>
<tr>
<td>Racelda sp. CW-2009</td>
<td>CW 041</td>
<td>FJ230553.1</td>
<td>419, 187</td>
</tr>
<tr>
<td>Rhiginia sp. CW-2009</td>
<td>CW 139</td>
<td>FJ230571.1</td>
<td>398, 177</td>
</tr>
<tr>
<td>Mangabea barbiger</td>
<td>CW 288</td>
<td>FJ230602.1</td>
<td>407, 188</td>
</tr>
<tr>
<td>Stenolemoides arizonensis</td>
<td>CW 304</td>
<td>FJ230605.1</td>
<td>438, 188</td>
</tr>
<tr>
<td>Stenolemus sp. CW-2009</td>
<td>CW 147</td>
<td>FJ230573.1</td>
<td></td>
</tr>
<tr>
<td>Emesaya incisa</td>
<td>CW 282</td>
<td>FJ230598.1</td>
<td>421, 189</td>
</tr>
<tr>
<td>Empicoris sp. 1 CW-2009</td>
<td>CW 109</td>
<td>FJ230567.1</td>
<td></td>
</tr>
<tr>
<td>Ploia hirticornis vouch CW</td>
<td>CW 054</td>
<td>FJ230556.1</td>
<td>425, 188</td>
</tr>
<tr>
<td>Ptilocerus sp. CW-2010</td>
<td>UCR_ENT</td>
<td>GU188467.1</td>
<td>508</td>
</tr>
<tr>
<td>Ptilocnemos femoralis vouch CW</td>
<td>CW 220</td>
<td>FJ230591.1</td>
<td>364, 195</td>
</tr>
<tr>
<td>Harpactorinae sp. 1 CW-2009</td>
<td>CW 190</td>
<td>FJ230585.1</td>
<td>421, 187</td>
</tr>
<tr>
<td>Agriocoris flavipes vouch CW</td>
<td>CW 132</td>
<td>FJ230569.1</td>
<td>426, 170</td>
</tr>
<tr>
<td>Apiomerus lanipes vouch CW</td>
<td>CW 281</td>
<td>FJ230597.1</td>
<td>408, 169</td>
</tr>
<tr>
<td>Apiomerus ochropterus vouch CW</td>
<td>CW 022</td>
<td>FJ230548.1</td>
<td>429, 186</td>
</tr>
<tr>
<td>Heniartes putumayo vouch CW</td>
<td>CW 395</td>
<td>FJ230609.1</td>
<td>416</td>
</tr>
<tr>
<td>Micrauchenus lineola vouch CW</td>
<td>CW 035</td>
<td>FJ230552.1</td>
<td>428, 187</td>
</tr>
<tr>
<td>Acanthischium sp. CW-2009</td>
<td>CW 391</td>
<td>FJ230607.1</td>
<td>414, 180</td>
</tr>
<tr>
<td>Arilus cristatus vouch CW</td>
<td>CW 071</td>
<td>FJ230558.1</td>
<td>411, 184</td>
</tr>
<tr>
<td>Castolus subinermis vouch CW</td>
<td>CW 347</td>
<td>—</td>
<td>429, 187</td>
</tr>
<tr>
<td>Coranus callosus vouch CW</td>
<td>CW 244</td>
<td>FJ230594.1</td>
<td>407, 188</td>
</tr>
<tr>
<td>Euagoras sp. CW-2009</td>
<td>CW 194</td>
<td>FJ230587.1</td>
<td>415, 186</td>
</tr>
<tr>
<td>Poecilosphodrus gratiosus vouch</td>
<td>CW 214</td>
<td>FJ230589.1</td>
<td>423, 188</td>
</tr>
<tr>
<td>Pselliopus spinicollis vouch CW</td>
<td>CW 284</td>
<td>FJ230600.1</td>
<td></td>
</tr>
<tr>
<td>Pselliopus zebra vouch CW</td>
<td>CW 280</td>
<td>FJ230596.1</td>
<td>411, 188</td>
</tr>
<tr>
<td>Pyrrhosphodrus amazonus vouch CW</td>
<td>CW 031</td>
<td>FJ230551.1</td>
<td>416, 188</td>
</tr>
<tr>
<td>Species</td>
<td>Voucher Code</td>
<td>Accession Numbers</td>
<td>ND1</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>--------------</td>
<td>---------------------------------------------------</td>
<td>-----</td>
</tr>
<tr>
<td>Rhynocoris segmentarius</td>
<td>CW 004</td>
<td>FJ230538.1, FJ230616.1, FJ230695.1</td>
<td></td>
</tr>
<tr>
<td>Ricolla quadrispinosa</td>
<td>CW 396</td>
<td>FJ230610.1, FJ230687.1, FJ230766.1</td>
<td></td>
</tr>
<tr>
<td>Sinea diadema</td>
<td>CW 108</td>
<td>FJ230566.1, FJ230644.1, FJ230723.1</td>
<td></td>
</tr>
<tr>
<td>Ulpius sp. CW-2009</td>
<td>CW 370</td>
<td>405, 187, FJ230684.1, FJ230763.1</td>
<td></td>
</tr>
<tr>
<td>Velinus sp. CW-2009</td>
<td>CW 197</td>
<td>FJ230588.1, FJ230664.1, FJ230743.1</td>
<td></td>
</tr>
<tr>
<td>Vesbius purpureus</td>
<td>CW 184</td>
<td>FJ230582.1, FJ230659.1</td>
<td></td>
</tr>
<tr>
<td>Zelus longipes</td>
<td>CW 006</td>
<td>FJ230539.1, FJ230617.1, FJ230696.1</td>
<td></td>
</tr>
<tr>
<td>Zelus nr. renardii</td>
<td>CW 090</td>
<td>FJ230565.1, FJ230643.1, FJ230722.1</td>
<td></td>
</tr>
<tr>
<td>Zelus renardii</td>
<td>CW 403</td>
<td>417, 183, FJ230691.1, FJ230707.1</td>
<td></td>
</tr>
<tr>
<td>Rhaphidosoma decorsei</td>
<td>CW 017</td>
<td>FJ230545.1, FJ230622.1, FJ230701.1</td>
<td></td>
</tr>
<tr>
<td>Microtomus cinctipes</td>
<td>CW 141</td>
<td>FJ230539.1, FJ230649.1, FJ230728.1</td>
<td></td>
</tr>
<tr>
<td>Microtomus sp. CW-2009</td>
<td>CW 030</td>
<td>FJ230582.1, FJ230684.1, FJ230763.1</td>
<td></td>
</tr>
<tr>
<td>Ectomocoris ornatus</td>
<td>CW 246</td>
<td>FJ230595.1, FJ230633.1, FJ230712.1</td>
<td></td>
</tr>
<tr>
<td>Ectomocoris sp. CW-2009</td>
<td>CW 363</td>
<td>415, 187, FJ230682.1, FJ230761.1</td>
<td></td>
</tr>
<tr>
<td>Peirates punctorius</td>
<td>CW 216</td>
<td>FJ230590.1, FJ230666.1, FJ230745.1</td>
<td></td>
</tr>
<tr>
<td>Rasahus thoracicus</td>
<td>CW 313</td>
<td>425, 190, FJ230679.1, FJ230758.1</td>
<td></td>
</tr>
<tr>
<td>Lophoscutus sp. CW-2009</td>
<td>CW 052</td>
<td>FJ230555.1, FJ230633.1, FJ230712.1</td>
<td></td>
</tr>
<tr>
<td>Macrocephalus sp. 1</td>
<td>CW 283</td>
<td>FJ230599.1, FJ230673.1, FJ230752.1</td>
<td></td>
</tr>
<tr>
<td>Macrocephalus sp. CW-2009</td>
<td>CW 128</td>
<td>FJ230568.1, FJ230645.1, FJ230724.1</td>
<td></td>
</tr>
<tr>
<td>Phymata acutangula</td>
<td>CW 029</td>
<td>FJ230550.1, FJ230627.1, FJ230706.1</td>
<td></td>
</tr>
<tr>
<td>Phymata fortificata</td>
<td>CW 028</td>
<td>FJ230549.1, FJ230626.1, FJ230705.1</td>
<td></td>
</tr>
<tr>
<td>Phymata pacifica</td>
<td>CW 070</td>
<td>FJ230557.1, FJ230635.1, FJ230714.1</td>
<td></td>
</tr>
<tr>
<td>Phymata sp. 1 CW-2009</td>
<td>CW 087</td>
<td>FJ230564.1, FJ230642.1, FJ230721.1</td>
<td></td>
</tr>
<tr>
<td>Physoderes impexa</td>
<td>00052181</td>
<td>JQ897662.1, 581, JQ897748.1, 373, JQ897911.1</td>
<td></td>
</tr>
<tr>
<td>Physoderes nr. vestita</td>
<td>00052186</td>
<td>JQ897663.1, 571, JQ897749.1, 363, JQ897912.1</td>
<td></td>
</tr>
<tr>
<td>Physoderes sp. 00052221</td>
<td>565</td>
<td>JQ897664.1, 373, JQ897913.1</td>
<td></td>
</tr>
<tr>
<td>Acanthaspis bilineolata</td>
<td>00052224</td>
<td>617, JQ897690.1, 363, JQ897859.1</td>
<td></td>
</tr>
<tr>
<td>Acanthaspis nr. bimaculata</td>
<td>00052192</td>
<td>634, JQ897694.1, 373, JQ897863.1</td>
<td></td>
</tr>
<tr>
<td>Acanthaspis gulo</td>
<td>00052222</td>
<td>JQ897619.1, 603, JQ897691.1, 363, JQ897860.1</td>
<td></td>
</tr>
<tr>
<td>Acanthaspis iracunda</td>
<td>CW 019</td>
<td>FJ230547.1, 448, 187, FJ230624.1, FJ230703.1</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Accession Numbers</td>
<td>JQ897625</td>
<td>JQ897626</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------------------</td>
<td>----------</td>
<td>----------</td>
</tr>
<tr>
<td>Acanthaspis iracunda strain 00218775</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Acanthaspis iracunda strain 00052190</td>
<td>—</td>
<td>—</td>
<td>624</td>
</tr>
<tr>
<td>Acanthaspis lasensis strain 00052193</td>
<td>—</td>
<td>—</td>
<td>631</td>
</tr>
<tr>
<td>Acanthaspis quadriannulata strain 00004575</td>
<td>660</td>
<td>JQ897620.1</td>
<td>615</td>
</tr>
<tr>
<td>Acanthaspis sulcipes strain 00052174</td>
<td>—</td>
<td>—</td>
<td>616</td>
</tr>
<tr>
<td>Acanthaspis westermanni strain 00052118</td>
<td>—</td>
<td>—</td>
<td>614</td>
</tr>
<tr>
<td>Acanthaspis sp. 00052205</td>
<td>570</td>
<td>JQ897621.1</td>
<td>555</td>
</tr>
<tr>
<td>Acanthaspis sp. 00218828</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Acanthaspis sp. CW-2009 voucher CW 073</td>
<td>656</td>
<td>FJ230559.1</td>
<td>450, 187</td>
</tr>
<tr>
<td>Acanthaspis sp. 2 CW-2009 voucher CW 082</td>
<td>658</td>
<td>FJ230563.1</td>
<td>—</td>
</tr>
<tr>
<td>Acanthaspis sp. 00052175</td>
<td>650</td>
<td>JQ897622.1</td>
<td>590</td>
</tr>
<tr>
<td>Alloeocranum arboricolum strain 00052180</td>
<td>668</td>
<td>JQ897623.1</td>
<td>555</td>
</tr>
<tr>
<td>Censorinus ferrugineus strain 00046577</td>
<td>641</td>
<td>JQ897628.1</td>
<td>604</td>
</tr>
<tr>
<td>Durevius tuberculatus strain 00046578</td>
<td>656</td>
<td>JQ897631.1</td>
<td>601</td>
</tr>
<tr>
<td>Durganda rubra strain 00052223</td>
<td>641</td>
<td>JQ897632.1</td>
<td>—</td>
</tr>
<tr>
<td>Dyakocoris vulnerans strain 00052204</td>
<td>656</td>
<td>JQ897633.1</td>
<td>603</td>
</tr>
<tr>
<td>Gerbelius nr. ornatus 00052225</td>
<td>—</td>
<td>—</td>
<td>603</td>
</tr>
<tr>
<td>Gerbelius ornatus strain 00052220</td>
<td>—</td>
<td>—</td>
<td>593</td>
</tr>
<tr>
<td>Gerbelius ornatus strain 00052189</td>
<td>629</td>
<td>JQ897638.1</td>
<td>577</td>
</tr>
<tr>
<td>Gerbelius sp. 00052219</td>
<td>630</td>
<td>JQ897639.1</td>
<td>455</td>
</tr>
<tr>
<td>Hermillus sp. CW-2009 voucher CW 179</td>
<td>658</td>
<td>FJ230580.1</td>
<td>436, 189</td>
</tr>
<tr>
<td>Inara albiguttata strain 00002551</td>
<td>646</td>
<td>JQ897640.1</td>
<td>620</td>
</tr>
<tr>
<td>Inara flavopicta strain 00052191</td>
<td>—</td>
<td>—</td>
<td>636</td>
</tr>
<tr>
<td>Inara flavopicta strain 00052170</td>
<td>649</td>
<td>JQ897641.1</td>
<td>591</td>
</tr>
<tr>
<td>Kayanocoris wegneri strain 00052216</td>
<td>497</td>
<td>JQ897642.1</td>
<td>593</td>
</tr>
<tr>
<td>Leogorrus immaculatus strain 00014323</td>
<td>—</td>
<td>—</td>
<td>538</td>
</tr>
<tr>
<td>Leogorrus litura voucher CW 009</td>
<td>662</td>
<td>FJ230540.1</td>
<td>428, 189</td>
</tr>
<tr>
<td>Leogorrus litura strain 00012955</td>
<td>—</td>
<td>—</td>
<td>589</td>
</tr>
<tr>
<td>Leogorrus longiceps strain 00052197</td>
<td>—</td>
<td>—</td>
<td>600</td>
</tr>
<tr>
<td>Leogorrus sp. n. 00052198</td>
<td>—</td>
<td>—</td>
<td>599</td>
</tr>
<tr>
<td>Leogorrus sp. CW-2009 voucher CW 133</td>
<td>654</td>
<td>FJ230570.1</td>
<td>426, 188</td>
</tr>
<tr>
<td>Microlestria nr. fuscicollis 00052226</td>
<td>423</td>
<td>JQ897644.1</td>
<td>593</td>
</tr>
<tr>
<td>Microlestria nr. fuscicollis 00052183</td>
<td>—</td>
<td>—</td>
<td>596</td>
</tr>
<tr>
<td>Microlestria fuscicollis strain 00052185</td>
<td>626</td>
<td>JQ897643.1</td>
<td>592</td>
</tr>
<tr>
<td>Nalata setulosa strain 00003121</td>
<td>—</td>
<td>—</td>
<td>502</td>
</tr>
<tr>
<td>Nalata nr. spinicollis 00052188</td>
<td>636</td>
<td>JQ897646.1</td>
<td>476</td>
</tr>
<tr>
<td>Nalata squalida strain 00002748</td>
<td>336</td>
<td>JQ897648.1</td>
<td>574</td>
</tr>
<tr>
<td>Nalata sp. 00014325</td>
<td>621</td>
<td>JQ897647.1</td>
<td>375</td>
</tr>
<tr>
<td>Nanokerala browni strain 00052179</td>
<td>566</td>
<td>JQ897649.1</td>
<td>557</td>
</tr>
<tr>
<td>Species</td>
<td>Accession Numbers</td>
<td>Description</td>
<td>Accession Numbers</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>-------------------</td>
<td>----------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Nanokerala nr. browni 00052228</td>
<td>JQ897650.1</td>
<td></td>
<td>JQ897735.1</td>
</tr>
<tr>
<td>Neostachyogenys tristis strain 00052184</td>
<td>JQ897651.1</td>
<td></td>
<td>JQ897736.1</td>
</tr>
<tr>
<td>Noualhierana furtiva voucher CW 224</td>
<td>FJ230592.1</td>
<td>431, 187</td>
<td>FJ230668.1.</td>
</tr>
<tr>
<td>Opisthacidius chinai strain 00012957</td>
<td>JQ897652.1</td>
<td>537</td>
<td>JQ897737.1</td>
</tr>
<tr>
<td>Opisthacidius nr. mexicanus 00004576</td>
<td>JQ897653.1</td>
<td>555</td>
<td>JQ897738.1</td>
</tr>
<tr>
<td>Opisthacidius sp. 00052199</td>
<td>JQ897654.1</td>
<td>568</td>
<td>JQ897739.1</td>
</tr>
<tr>
<td>Paredocla chevalieri voucher CW 018</td>
<td>FJ230564.1</td>
<td>446, 186</td>
<td>FJ230623.1,</td>
</tr>
<tr>
<td>Pasiropsis maculata strain 00052227</td>
<td>JQ897658.1</td>
<td>590</td>
<td>JQ897743.1</td>
</tr>
<tr>
<td>Pasiropsis marginata strain 00052177</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pasiropsis n. 00052178</td>
<td>JQ897659.1</td>
<td>598</td>
<td>JQ897745.1</td>
</tr>
<tr>
<td>Pasiropsis sp. 00052217</td>
<td>JQ897661.1</td>
<td>480</td>
<td>JQ897747.1</td>
</tr>
<tr>
<td>Pasiropsis sp. 00052195</td>
<td>JQ897660.1</td>
<td>593</td>
<td>JQ897746.1</td>
</tr>
<tr>
<td>Platymeris biguttata voucher CW 175</td>
<td>FJ230578.1</td>
<td>434, 186</td>
<td>FJ230655.1,</td>
</tr>
<tr>
<td>Plynoides sp. 00052196</td>
<td>JQ897665.1</td>
<td>622</td>
<td>JQ897750.1</td>
</tr>
<tr>
<td>Pseudozelurus arizonicus strain 0004573</td>
<td>JQ897666.1</td>
<td>590</td>
<td>JQ897751.1</td>
</tr>
<tr>
<td>Pseudozelurus superbus strain 00004571</td>
<td>JQ897667.1</td>
<td>590</td>
<td>JQ897752.1</td>
</tr>
<tr>
<td>Psophis sp. 00052230</td>
<td>JQ897668.1</td>
<td>519</td>
<td>JQ897753.1</td>
</tr>
<tr>
<td>Psophis sp. 00218947</td>
<td>JQ897669.1</td>
<td>471</td>
<td>JQ897754.1</td>
</tr>
<tr>
<td>Reduvius personatus strain 00004567</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduvius sonoraensis strain 00004569</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Staliastes rufus strain 00052172</td>
<td>JQ897673.1</td>
<td>605</td>
<td>JQ897758.1</td>
</tr>
<tr>
<td>Staliastes sp. 00052231</td>
<td>JQ897674.1</td>
<td>525</td>
<td>JQ897759.1</td>
</tr>
<tr>
<td>Tapeinus sp. 00052200</td>
<td>JQ897676.1</td>
<td>567</td>
<td>JQ897761.1</td>
</tr>
<tr>
<td>Tapeinus sp. CW-2009 voucher CW 183</td>
<td>—</td>
<td>426, 188</td>
<td>FJ230658.1,</td>
</tr>
<tr>
<td>Tapeinus sp. 00218926</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tiarodes versicolor strain 00052171</td>
<td>JQ897678.1</td>
<td>590</td>
<td>JQ897763.1</td>
</tr>
<tr>
<td>Tiarodes sp. 00052206</td>
<td>JQ897677.1</td>
<td>602</td>
<td>JQ897762.1</td>
</tr>
<tr>
<td>Varus flavoanulatus strain 00004574</td>
<td>JQ897683.1</td>
<td>593</td>
<td>JQ897768.1</td>
</tr>
<tr>
<td>Velitra rubropicta strain 00052173</td>
<td>JQ897684.1</td>
<td>582</td>
<td>JQ897769.1</td>
</tr>
<tr>
<td>Velitra sp. 00052201</td>
<td>JQ897685.1</td>
<td>596</td>
<td>JQ897770.1</td>
</tr>
<tr>
<td>Zelurus alcides strain 00014324</td>
<td>JQ897686.1</td>
<td>583</td>
<td>JQ897771.1</td>
</tr>
<tr>
<td>Zelurus petax voucher CW 167</td>
<td>—</td>
<td>402, 189</td>
<td>FJ230653.1,</td>
</tr>
<tr>
<td>Zelurus pintoi strain 00011856</td>
<td>JQ897687.1</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Zelurus sp. 00052209</td>
<td>JQ897688.1</td>
<td>575</td>
<td>JQ897772.1</td>
</tr>
<tr>
<td>Zelurus sp. 00052194</td>
<td>JQ897689.1</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Zelurus sp. CW-2009 voucher CW 146</td>
<td>—</td>
<td>399, 188</td>
<td>FJ230650.1,</td>
</tr>
<tr>
<td>Kiskeyana palassaina voucher CW 010</td>
<td>FJ230541.1</td>
<td>431, 188</td>
<td>FJ230619.1,</td>
</tr>
<tr>
<td>Species</td>
<td>Accession Numbers</td>
<td>Details</td>
<td></td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>-------------------</td>
<td>---------</td>
<td></td>
</tr>
<tr>
<td>Saica sp. CW-2009 voucher CW 042</td>
<td>FJ230554.1</td>
<td>434, 190 FJ230632.1, FJ230711.1</td>
<td></td>
</tr>
<tr>
<td>Salyavatinae sp. 00052207</td>
<td>JQ897672.1</td>
<td>604 JQ897757.1</td>
<td></td>
</tr>
<tr>
<td>Lisarda sp. CW-2009 voucher CW 177</td>
<td>FJ230579.1</td>
<td>435, 188 FJ230656.1, FJ230735.1</td>
<td></td>
</tr>
<tr>
<td>Lisarda sp. CW-2009 voucher CW 078</td>
<td>FJ230561.1</td>
<td>429, 188 FJ230639.1, FJ230718.1</td>
<td></td>
</tr>
<tr>
<td>Stenopodainae sp. 00052212</td>
<td>JQ897675.1</td>
<td>430 JQ897760.1</td>
<td></td>
</tr>
<tr>
<td>Canthesancus sp. 00052211</td>
<td>JQ897624.1</td>
<td>569 JQ897701.1, JQ897870.1</td>
<td></td>
</tr>
<tr>
<td>Ctenotrachelus sp. CW-2009 voucher CW 166</td>
<td>FJ230575.1</td>
<td>391, 184 FJ230652.1, FJ230731.1</td>
<td></td>
</tr>
<tr>
<td>Gageus micropterus voucher CW 309</td>
<td>FJ230606.1</td>
<td>311, 100 FJ230678.1, FJ230757.1</td>
<td></td>
</tr>
<tr>
<td>Kodormus bruneosus voucher CW 402</td>
<td></td>
<td>397, 188 FJ230690.1, FJ230769.1</td>
<td></td>
</tr>
<tr>
<td>Oncocephalus sp. CW-2009 voucher CW 079</td>
<td>FJ230562.1</td>
<td>318, 159 FJ230640.1, FJ230719.1</td>
<td></td>
</tr>
<tr>
<td>Sastrapada sp. CW-2009 voucher CW 185</td>
<td></td>
<td>415, 188 FJ230660.1, FJ230739.1</td>
<td></td>
</tr>
<tr>
<td>Stenopoda sp. CW-2009 voucher CW 154</td>
<td></td>
<td>406, 188 FJ230651.1, FJ230730.1</td>
<td></td>
</tr>
<tr>
<td>Stenopodessa sp. CW-2009 voucher CW 398</td>
<td></td>
<td>411, 154 FJ230688.1, FJ230767.1</td>
<td></td>
</tr>
<tr>
<td>Thodelmus nigrispinosus voucher CW 369</td>
<td></td>
<td>398, 189 FJ230683.1, FJ230762.1</td>
<td></td>
</tr>
<tr>
<td>Cavernicola pilosa strain 00040130</td>
<td>JQ897627.1</td>
<td>519 JQ897704.1</td>
<td></td>
</tr>
<tr>
<td>Eratyrus mucronatus strain 00052168</td>
<td>JQ897635.1</td>
<td>566 JQ897711.1, JQ897882.1</td>
<td></td>
</tr>
<tr>
<td>Panstrongylus geniculatus strain 00052167</td>
<td>JQ897655.1</td>
<td>579 JQ897740.1, JQ897899.1</td>
<td></td>
</tr>
<tr>
<td>Panstrongylus nr. geniculatus 00052165</td>
<td>JQ897657.1</td>
<td>468 JQ897742.1, JQ897901.1</td>
<td></td>
</tr>
<tr>
<td>Panstrongylus lignarius strain 00052166</td>
<td>JQ897656.1</td>
<td>570 JQ897741.1, JQ897900.1</td>
<td></td>
</tr>
<tr>
<td>Paratriatoma hirsuta voucher CW 296</td>
<td>FJ230604.1</td>
<td>400, 187 FJ230676.1, FJ230755.1</td>
<td></td>
</tr>
<tr>
<td>Rhodnius neglectus strain 00052203</td>
<td>JQ897670.1</td>
<td>562 JQ897755.1, JQ897918.1</td>
<td></td>
</tr>
<tr>
<td>Rhodnius picipes strain 00052208</td>
<td>JQ897671.1</td>
<td>577 JQ897756.1, JQ897919.1</td>
<td></td>
</tr>
<tr>
<td>Triatoma dimidiata strain 00052169</td>
<td>JQ897679.1</td>
<td>532 JQ897764.1, JQ897928.1</td>
<td></td>
</tr>
<tr>
<td>Triatoma protracta voucher CW 294</td>
<td></td>
<td>398, 186 FJ230675.1, FJ230754.1, JQ897929.1</td>
<td></td>
</tr>
<tr>
<td>Triatoma recurva voucher CW 170</td>
<td>FJ230577.1</td>
<td>399, 188 FJ230654.1, FJ230733.1, JQ897930.1</td>
<td></td>
</tr>
<tr>
<td>Triatoma venosa strain 00052210</td>
<td>JQ897681.1</td>
<td>557 JQ897766.1, JQ897932.1</td>
<td></td>
</tr>
<tr>
<td>Triatoma sp. 00052202</td>
<td>JQ897680.1</td>
<td>581 JQ897765.1, JQ897931.1</td>
<td></td>
</tr>
<tr>
<td>Tribelocephala peyrierasi voucher CW 287</td>
<td>FJ230601.1</td>
<td>— —</td>
<td></td>
</tr>
<tr>
<td>Tribelocephalinae sp. 00052187</td>
<td>JQ897682.1</td>
<td>486 JQ897767.1</td>
<td></td>
</tr>
<tr>
<td>Mirambulus niger strain 00052182</td>
<td>JQ897645.1</td>
<td>509 JQ897729.1</td>
<td></td>
</tr>
<tr>
<td>Carayonia orientalis strain 00052232</td>
<td>JQ897626.1</td>
<td>538 JQ897703.1</td>
<td></td>
</tr>
<tr>
<td>Carayonia sp. n. 00003627</td>
<td>JQ897625.1</td>
<td>535 JQ897702.1</td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX B: RAXML CALL LINES AND MRBAYES BLOCK

RAxML call lines:

#RAxML_FossilBest_Run1
./raxmlHPC-PTHREADS-AVX -f a -m GTRGAMMA -p 32523523 -x 234235235 -q simpleDNApartition.txt -# 1000 -s FossilBest_RAxML.phy -n FossilBest_RAxML.phy_out -T 4

#RAxML_FossilBest_Run2
./raxmlHPC-PTHREADS-AVX -f a -m GTRGAMMA -p 12345678 -x 23456789 -q simpleDNApartition.txt -# 1000 -s FossilBest_RAxML.phy -n FossilBest_RAxML.phy_out -T 4

#RAxML_FossilBest_Run3
./raxmlHPC-PTHREADS-AVX -f a -m GTRGAMMA -p 22445566 -x 66554422 -q simpleDNApartition.txt -# 1000 -s FossilBest_RAxML.phy -n FossilBest_RAxML.phy_out -T 4

Partition file for RAxML (simpleDNApartition.txt):

DNA, 16S = 1-512
DNA, 18S = 513-2334
DNA, 28S = 2335-3429
DNA, Wg = 3430-3811

MrBayes Block:

BEGIN MRBAYES;
charset 16S = 1-512;
charset 18S = 513-2334;
charset 28S = 2335-3429;
charset Wg = 3430-3811;
partition combo = 4: 16S, 18S, 28S, Wg;
set partition = combo;
unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all);
lset applyto = (1) Nst=6 Rates=invgamma;
lset applyto = (2) Nst=6 Rates=invgamma;
lset applyto = (3) Nst=6 Rates=invgamma;
lset applyto = (4) Nst=6 Rates=invgamma;
prset applyto = (2,3) statefreqpr = fixed(equal);
prset applyto = (all) ratepr=variable;
mcmc ngen=1000000000 samplefreq=5000 printfreq=5000 nruns=4 savebrlens=yes;
end;