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TAXONOMIC AND MOLECULAR STUDIES IN CLERIDAE AND HEMIPTERA

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TAXONOMIC AND MOLECULAR STUDIES IN CLERIDAE AND HEMIPTERA

DISSERTATION

A dissertation submitted in partial fulfillment of the requirements
for degree of Doctor of Philosophy in the Department of Entomology,
College of Agriculture at the University of Kentucky

By
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ABSTRACT OF DISSERTATION

TAXONOMIC AND MOLECULAR STUDIES IN CLERIDAE AND HEMIPTERA

Taxonomic changes are made based on checkered beetle (Coleoptera: Cleridae) types of the Natural History Museum, London (BMNH). Lectotypes are designated (and holotypes and paralectotypes recognized) for 44 species of Hydnocerinae, including the type species for *Isolemidia*, *Parmius*, *Paupris*, *Allelidea*, *Blaesiopthalmus* and *Lemidia*, four species of *Enoclerus* (Clerinae), and 14 species of *Cymatodera* (Tillinae). Annotations include comments on additional type material, new type locality, previous (type series) locality, and questionable or missing types. *Phyllobaenus pallipes* (Gorham) and *P. rufithorax* (Gorham) are synonymized with *P. flavifemoratus* (Gorham), *P. chapini* (Wolcott) is synonymized under *P. lateralis* (Gorham), and *P. villosus* (Schenkling) is synonymized under *P. longus* (LeConte), new synonymies.

The first molecular phylogeny of the clerid lineage (Coleoptera: Cleridae, Thanerocleridae) is presented and compared with the two most recent phylogenetic hypotheses of the group. Phylogenetic relationships of checkered beetles wareere inferred from approximately 5,000 nucleotides amplified from four loci (28S, 16S, 12S, COI). A worldwide sample of ~70 genera is included and phylogenies are reconstructed using Bayesian Inference and Maximum Likelihood. The results are not entirely congruent with either of the current classification systems. Three major lineages are recognized. Tillinae are supported as the sister group to all other subfamilies, whereas Thaneroclerinae, Korynetinae *sensu latu* and a new subfamily formally described here, Epiclininae, new subfamily, form a sister group to Clerinae + Hydnocerinae.

To assess the phylogeny and evolution of Hemiptera, a comprehensive mitogenomic analysis integrating mitogenome-based molecular phylogenetics, fossil-calibrated divergence dating (using BEAST), and ancestral state reconstructions are presented. The 81 sampled mitogenomes represent the most extensive mitogenomic analyses of Hemiptera to date. The putatively primitive “Homoptera” was previously rendered paraphyletic by Heteroptera, whereas the presented results support each group as monophyletic. The results from both diet and habitat ancestral state reconstructions support that 1) Heteroptera (and Homoptera) evolved from a phytophagous ancestor, contrary to the popular hypothesis that the ancestor was predaceous; and 2) family-level radiation of Heteroptera is coincident with the apically-produced labium and the novel hemelytron. It is here proposed these morphological innovations facilitated multiple

independent shifts from phytophagy to predation and multiple independent colonizations of aquatic habitats.

KEYWORDS: Cleridae, molecular systematics, Hemiptera phylogeny, mitochondrial genome, evolution of true bugs

John Moeller Leavengood, Jr

Student's Signature

July 22, 2015

Date

TAXONOMIC AND MOLECULAR STUDIES IN CLERIDAE AND HEMIPTERA

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This dissertation is dedicated to my father, John Moeller Leavengood (Sr.), who has always supported me through my struggles to find my passion…which led me here.

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My academic career has seen more than its share of peaks and valleys. The support of many ushered me to change majors from accounting to entomology 14 years ago. Among them were Dr. Don Hall, Dr. John Strayer and Dr. Paul "Skip" Choate, Jr. But after completing to a Master's Degree at the University of Florida I found myself most disenfranchised with academia andsought greener pastures only to return years later to advance to my doctoral studies. Throughout that journey my father's support was unflagging. Without him, I wouldn't have made the leap of faith back into the arms of science.

I must also thank my advisor, Dr. Michael Sharkey. He managed to mold a persuasive writer from a persuasive speaker and remained forever patient by my wandering interests which unerringly pulled me away from my dissertation work. I was encouraged to pursue every opportunity and more often than not, I was successful. Dr. Eric Chapman, however, was a most unlikely ally in my graduate studies, and he became a close friend in the process. It seems that over the course of our five years spent down the hall, then across the hall and finally in the same lab, we continually challenged each other to question more, read more, analyze more, and write thoughtfully. I must also thank Stephanie Clutts (former lab technician) for teaching me techniques for PCR, stacking macrophotography and sequence assembly, Kacie Athey (former lab member; graduated) for holding my hand through all basic endeavors technological regarding my computer and software, and Erika Tucker (lab member) for teaching me useful tricks in PhotoShop and Micrsoft PowerPoint.

Many had a hand in pushing me along my journey—most of them going unnamed as there are far too many. But to them all, I am grateful.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: Introduction

Over the last hundred years, the approaches to taxonomy have broadened significantly. Descriptive taxonomy and museum work paved the way for systematic analysis, eventually utilizing both molecular and morphological data, increasingly advanced programs and genome-scale datasets. The dissertation herein includes classical museum work based on morphology and a family-wide multi-locus molecular phylogeny on checkered beetles (Coleoptera: Cleridae), as well as an order-wide mitogenomic phylogeny and diversification study examining the evolution of Hemiptera.

In the second chapter, taxonomic changes and notes based on the checkered beetle (Coleoptera: Cleridae) types of the Natural History Museum, London (BMNH). Lectotypes were designated (and holotypes and paralectotypes recognized) for 44 species of Hydnocerinae, including the type species for *Isolemidia, Parmius, Paupris, Allelidea, Blaesiopthalmus* and *Lemidia*, four species of *Enoclerus* (Clerinae), and 14 species of *Cymatodera* (Tillinae). Annotations include comments on additional type material, new type locality, previous (type series) locality, and questionable or mysterious types. *Phyllobaenus pallipes* (Gorham) and *P. rufithorax* (Gorham) are synonymized with *P. flavifemoratus* (Gorham), *P. chapini* (Wolcott) is synonymized under *P. lateralis* (Gorham), and *P. villosus* (Schenkling) is synonymized under *P. longus* (LeConte), **new synonymies**. *Phyllobaenus longus* (LeConte) is discovered in New Mexico, **new state record**.

This work was done in collaboration with Beulah H. Garner (Natural History Museum, Department of Entomology, London, United Kingdom). Garner provided information from the BMNH database and valuable correspondence after my departure from the BMNH.

The third chapter the first molecular phylogeny of the clerid lineage (Coleoptera: Cleridae, Thanerocleridae) within the superfamily Cleroidea is presented and compared with the two most recently proposed phylogenetic hypotheses of the group. Phylogenetic relationships of checkered beetles were inferred from approximately 5,000 nucleotides of both nuclear and mitochondrial rDNA (28S, 16S, and 12S) and the mitochondrial protein-coding gene COI. A worldwide sample of ~70 genera representing almost a quarter of

generic diversity of the clerid lineage was included and phylogenies were reconstructed using Bayesian and Maximum Likelihood. Results support the monophyly of many proposed subfamilies but were not entirely congruent with either of the current classification systems. The subfamilial relationships within the Cleridae are resolved with support for three main lineages. Tillinae are supported as the sister group to all other subfamilies within the Cleridae, while Thaneroclerinae, Korynetinae *sensu latu* and a new subfamily formally described here, Epiclininae, form a sister group to Clerinae + Hydnocerinae.

This work was done in collaboration with Nicole L. Gunter (CSIRO, Ecosystem Sciences, Canberra, ACT, Australia), Eric G. Chapman (Department of Entomology, University of Kentucky, Lexington, Kentucky, U.S.A.), Justin S. Bartlett (Queensland Primary Industries Insect Collection, Biosecurity Queensland, Brisbane, Queensland, Australia) and Stephen L. Cameron (Earth, Environment & Biological Sciences School, Queensland University of Technology, Brisbane, Queensland, Australia). Gunter and Cameron did all molecular work for the Australian taxa and shared the writing and analytical workload. I did the molecular work, sequence assembly and editing for the non-Australian taxa, and part of the analytical workload under the tutilege of Chapman, who also assisted with writing. Bartlett provided assistance with writing and assumed the primary role in the description of the new subfamily and identifying synapomorphies for major clades recovered in our analyses. The majority of all work was equally shared by Gunter and I.

In the fourth chapter, a mitogenomic analysis of Hemiptera reveals key innovations in the adaptive radiation of true bugs (Heteroptera). Hemiptera, the largest order among non-holometabolous insects, represents ~7% of metazoan diversity. With extraordinary life histories and highly specialized morphological adaptations, hemipterans have exploited a multitude of habitats and food sources through ~300 million years of evolution. To address outstanding questions regarding the phylogeny and evolution of Hemiptera, we carried out a comprehensive mitogenomic analysis integrating mitogenome-based molecular phylogenetics, fossil-calibrated divergence dating, and life history-mediated ancestral state reconstructions. The 26 newly sequenced and 55 published mitogenomes, covering all the suborders and infraorders, represent the

most extensive mitogenomic analyses of Hemiptera to date. The putatively primitive "Homoptera" (Sternorrhyncha, Auchenorrhyncha and Coleorrhyncha) was previously rendered paraphyletic by Heteroptera, whereas my results support each group as monophyletic. A BEAST analysis inferred that Homoptera is not primitive, suggesting that historical morphological hypotheses could have been misled by character reductions/losses which are consistent with sedentary feeding behaviors in the entirely terrestrial, plant-feeding Homoptera. The results from both diet and habitat ancestral state reconstructions support that 1) Heteroptera (and Homoptera) evolved from a phytophagous ancestor, contrary to the popular hypothesis that the ancestor was predaceous (based on the "basal infraorders"); and 2) family-level radiation of Heteroptera is coincident with two key morphological innovations; the apically-produced labium and the novel hemelytron (protective forewing). We propose that the success of heteropterans, with their diverse feeding behaviors and broad habitat colonization is not because of angiosperm coevolution, but rather key morphological innovations facilitating multiple independent shifts from phytophagy to predation and multiple independent colonizations of aquatic habitats.

This work was done in collaboration with Xuguo Zhou and Eric G. Chapman (Department of Entomology, University of Kentucky, Lexington, Kentucky, U.S.A.), Wanzhi Cai and Li Hu (Department of Entomology, China Agricultural University, Beijing, China). All DNA extraction, sequence assembly and preliminary analyses were done by Hu (in part for his dissertation; advisor Cai). Chapman and I conducted all presented analyses (along with alignment, editing, evolutionary model estimation). Chapman produced ancestral state recontronstrions and I assumed the primary role in writing the paper with assistance from Chapman and Hu.

CHAPTER 2: TAXONOMIC CHANGES AND NOTES BASED ON THE CHECKERED BEETLE (COLEOPTERA: CLERIDAE) TYPES OF THE NATURAL HISTORY MUSEUM, LONDON (BMNH)

2.1 Introduction

The subfamily Hydnocerinae has historically been in taxonomic disarray. Revisionary works are needed to establish generic limits and to serve as diagnostic tools for distinguishing species. Before this can be done, much type material must be identified and lectotypes designated. During a research trip to the Natural History Museum (London, BMNH) I reviewed the type material for Hydnocerinae, designated lectotypes and recognized paralectotypes for 44 species including the type species of *Isolemidia, Parmius, Paupris, Allelidea, Blaesiopthalmus* and *Lemidia*. All species for these genera were assessed, with the exception that for *Lemidia* only specimens of *L. nitens* (Newman) received a type designation. A subsequent visit to the Museum National d'Histoire Naturelle (Paris, MNHN) permitted the recognition of additional paralectotypes from Gorham's private collection. No type designations were made for syntypes of *Callimerus* species and allied Asian Callimerini (e.g., *Stenocallimerus*) because this group is currently under investigation by other researchers (Gerstmeier et al. 2012).

Most of the examined material comprised species of *Phyllobaenus* (including all species of *Hydnocera* that were not assigned to *Wolcottia* or *Isohydnocera*) and *Isolemidia* described by Gorham (1877; 1883-1886). Most species were from the organized labor Biologia Centrali-Americana (BCA), which includes the most significant contribution to our knowledge of Central American Cleridae to date. In BCA, Gorham (1883-1886) described many species and commented on previously described taxa as well. Of the BCA material, all 44 species of Hydnocerinae received type designations (either Lectotype designation or Holotype recognition), as well as four species of *Enoclerus* and all fourteen species of *Cymatodera* (upon request by a fellow cleridologist).

All members of *Hydnocera* (excluding species later assigned to *Wolcottia* or *Isohydnocera*) are recognized as *Phyllobaenus*. Wolcott (1944) explained the status of *Hydnocera* (a junior synonym, in part, of *Phyllobaenus*) in great detail. The incorrect

placement of various species created some confusion since *Phyllobaenus* has bifid tarsal ungues, whereas *Isohydnocera* has simple tarsal ungues; many species assigned to each genus based on habitus-based gestalt defy this rule (Leavengood et al. 2012). Despite its utilization in several faunal keys (Dillon and Dillon 1972; Downie and Arnett 1993; Knull 1951; Leavengood 2008), I consider tarsal ungal bifidity alone to be an ill-suited character for generic delimitation. Kolibáč (1998) synonymized *Cephaloclerus* under *Phyllobaenus* and *Isohydnocera* under *Wolcottia*. I consider that these changes were made in the absence of sufficient understanding of variation within these genera, and I therefore choose not to accept Kolibáč's reclassification. Recent molecular evidence (Gunter et al. 2013) substantiates the rejection of both of Kolibáč's synonymizations. However, I agree with Kolibáč's tribes of Hydnocerinae and no changes in higher classification will be made at this time.

Anecdotal evidence suggests that both A. B. Wolcott (Dybas 1951) and W. F. Barr (Westcott & Merickel 2011) shared the hope of revising *Phyllobaenus* (*in litt*., W. Opitz, J. Rifkind). Both designated numerous specimens as “future types” with manuscript names which never met publication. Despite this interest, the types of the genus had never been audited nor had the comprising series been accounted. The lack of such knowledge has limited taxonomic progress. Few have inventoried, designated and/or commented on the clerid types of any single taxon or museum. A notable exception is Ekis’ (1975) comprehensive assessment of the clerid types described by Massimiliano Spinola (1841, 1844) included the recognition of *nomina nuda*, lectotype designation, paralectotype recognition, photographs of species previously unillustrated or indistinguishable by present literature, and historical and taxonomic notes. Spinola’s understanding of intraspecific variation was limited, his descriptions were consequently brief, and not all species could be illustrated, making Ekis’ work a valuable contribution. Döbler (1982) summarized the label data of all clerid type series specimens of the Deutsches Entomologisches Institut and provided the reference for each original description.

Such works seem simple, but are critical. With passing years one curator after the next may have differing opinions on that which is or is not a primary type or syntype (in the absence of type designations) and sometimes, simply on the basis that it is in “their”

museum (as was the case for many BCA Gorham types), identify specimens as “types” with their own labels. Because even Gorham sometimes placed his own manuscript name labels on two specimens in a single type series, it is not always obvious which specimen is or should be the primary type. Other complications include card-mounted pairs of specimens indicated by Gorham (by manuscript name labels) as types (e.g., *Phyllobaenus subvittatus*; below) wherein two different species are present or when the recognition of a type is not possible by simply examining the specimen and label data (e.g., *P. nunnenmacheri*, *Isohydnocera aegra,* and *I. curtipennis*; below). Taxonomists and curators should restrict similar future work to comprehensive approaches as have Ekis, Döbler and the present authors. Such punctuated progress enables ensuing researchers to more easily continue the work of their retired peers.

2.2 Materials and Methods

I performed type designations and indicated with yellow paralectotype labels and red lectotype labels. To holotypes, a black-bordered red label was added. These new holotype labels contain "HOLOTYPE," the species name, and identify the senior author (and date) as the authority of specimen identity. As specimens were examined at the BMNH, the drawers including BCA Hydnocerinae were re-curated from cork and/or foam-slatted drawers into unit trays and subsequent curation of unit tray labelling and databasing using the Museums relational database KeEMu was carried out by Beulah Garner. These data are available online via the BMNH website.

In the text below, each species is presented by subfamily (concordant with Opitz 2010; species of each genus arranged alphabetically), recognized by its current combination in agreement with Corporaal (1950), then by its original combination. Label data for designated types, new type localities (based on lectotype designations) and “type series localities” are presented. Additional comments are presented regarding the type series, other (yet unrecognized) syntypes from other museums, and missing types and their probable whereabouts. When the precise number of specimens of a type series is known it is presented. Otherwise, one must assume the possibility of other syntypes awaiting paralectotype recognition. The majority of BCA syntypes were deposited in the

BMNH and MNHN. Gorham was known to divide large series among the MNHN, BMNH, MHNG (Geneva), and the personal collections of Champion, Schenkling, Corporaal and Sharp. As such, lectotypes were designated by recognizing the type labels and handwriting of the describing author in combination with specimen locality and original descriptions.

List of Abbreviations:

BCA	Biologia Centrali-Americana
BMNH	Natural History Museum (London, UK)
BYUC	Monte L. Bean Life Science Museum (Provo, Utah)
FSCA	Florida State Collection of Arthropods (Gainesville, FL)
ICZN	International Commission of Zoological Nomenclature
MHNG	Muséum d'Histoire Naturelle (Geneva, Switzerland)
MNHN	Museum National d'Histoire Naturelle (Paris, France)
NMNH	National Museum of Natural History (Washington, DC)
SDEI	Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany)
UNMA	University of New Mexico, Alburquerque (Alburquerque, New Mexico)

In Gorham's discussions (part of the original description) he often refers to a series of specimens. It is presumed that all BCA (Gorham 1882-1886) specimens that can be associated with the discussion by locality in combination with Gorham's comments on sex and variation and Gorham's determination labels constitute the type series (ICZN Article 72.4.1.1). Although Gorham does not identify a "type" in the text of the original publication, he does place a "type" label on a specimen of the type series. This specimen is not a holotype (ICZN Articles 73.1, 73.1.1). All BMNH BCA specimens have a determination label, but Gorham's "types" bears an additional label with the new species name. These specimens, having a determination label, nominal label, and a "type" label, are designated as lectotypes (ICZN Article 72.4.1.1). All other specimens of each type series are designated paralectotypes. Type series specimens described from the Fry Collection (Gorham 1877) were identified by similar means. Gorham's intended primary

types (not specified in the original publication) have a label with the species' name (written in Gorham's handwriting).

Type specimens of almost all species covered herein are imaged. Photographs were taken in the Sackler Biological Imaging Lab using a Zeiss camera, images were stacked in Helicon Focus v.5.2, and then modified using Adobe PhotoShop.

This work was done in collaboration with Beulah H. Garner (Natural History Museum, Department of Entomology, London, United Kingdom). Garner provided information from the BMNH database and valuable correspondence after my departure from the BMNH. I did all work with specimens, writing and research. This work was published (Leavengood and Garner 2014).

2.3 Results and Discussion

2.3.1 Subfamily HYDNOCERINAE

All types for species recognized as *Phyllobaenus, Isohydnocera, Parmius, Paupris, Allelidea, Blaesiophthalmus* and *Isolemidia* were assessed. Only the type-species of *Lemidia* (*L. nitens*) was assessed.

Tribe HYDNOCERINI

The number of hydnocerine genera was reduced considerably by Kolibáč (1998: 129). *Isohydnocera* Chapin was synonymized under *Wolcottia* Chapin and several Old World genera were synonymized under *Phyllobaenus* Dejean. However, in forming this conclusion, no type-specimens were examined. Additionally, recent evidence (Leavengood *in prep*) suggests that it is questionable as to whether the correct species was actually assessed when estimating the generic limits of *Isohydnocera*. However, such evidence will result in more generic shuffling, which is not the purpose of the present work. The generic epithets here recognized ignore Kolibáč's changes and are consistent with the majority of current literature (e.g., Downie & Arnett 1993; Opitz 2002;

Leavengood 2010, for world taxa; Opitz 2010, for world taxa; Leavengood et al. 2012). The changes herein reduce *Phyllobaenus* from 121 to 117 described species.

Phyllobaenus aeneicollis (Schenkling, 1907: 306) (Fig. 2.1)

Original Combination: *Hydnocera aeneicollis*

Types: The designated paralectotypes do not share the type locality. However, Schenkling stated that multiple specimens were placed in the BMNH (and only one has the type locality; here designated the lectotype). Many others were apparently collected from different localities during the same expedition by H. H. Smith. Döbler (1982) substantiated all specimens from these localities as syntypes except for the Omilteme specimen, which I believe Döbler overlooked. Additional syntypes exist in the SDEI (Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany).

Series Locality: Schenkling identified the type locality corresponding to the designated lectotype. The series spans Chilpancingo, Amula and Omilteme, all in Guerrero, Mexico.

Type Locality: Chilpancingo, Guerrero, Mexico, 4600' elevation.

LECTOTYPE (here designated): Type [round, red-bordered label], Chilpancingo, Guerrero, 4600 ft., [Schenkling's type label] (BMNH; 1).
PARALECTOTYPES: Xucumanatlan, Guerrero, 7000 ft, July, H. H. Smith, [Schenkling det label] (BMNH; 1); Amula, Guerrero, 6000 ft, Aug., H. H. Smith, [Schenkling det label] (BMNH; 1); Chilpancingo, Guerrero, 4600 ft, Aug., H. H. Smith, [Schenkling det label] (BMNH; 1); Omilteme, Guerrero, 8000 ft, Aug., H. H. Smith, [Schenkling det label] (BMNH; 1).

Phyllobaenus chalybeatus (Gorham, 1883: 170) (Fig. 2.2)

Original Combination: *Hydnocera chalybeata*

Types: Gorham referred to seven specimens in his description (which I consider to represent the complete type series). All have been accounted.

Series Locality: Calderas, San Gerónimo and Capetillo, Guatemala and Playa Vicente, Mexico.

Type Locality: Playa Vicente, Mexico.

LECTOTYPE (here designated): Type [round, red-bordered label]; Playa Vicente, Mexico, Hoege, *Hydnocera chalybeata* Gorham, Type, B. C. A. Col. III. (2). Hydnocera chalybeata Gorham (BMNH; 1). **PARALECTOTYPES**: Mexico, Salle Coll; B. C. A. Col. III. (2). Hydnocera chalybeata Gorham (BMNH; 2); Calderas, Guatemala, Champion, Hydnocera chalybeata Gorham, B. C. A. Col. III. (2). Hydnocera chalybeata Gorham (BMNH; 1); Calderas, Guatemala, Champion, *Hydnocera chalybeata* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); S. Geronimo, Guatemala, Champion, *Hydnocera chalybeata* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Capetillo, Guatemala, G. C. Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus clavatus (Gorham, 1883: 172) (Fig. 2.3)

Original Combination: *Hydnocera clavata*

Types: In 1971 W. F. Barr had placed a lectotype label on a specimen. I am now formally designating it and recognizing the paralectotype. These two specimens represent the complete type series.

Series/Type Locality: Juquila, Mexico.

LECTOTYPE (here designated): Juquila; Mexico, Salle Coll.; B. C. A. Col. III. (2). Hydnocera clavata Gorham; [Barr lectotype label] (BMNH; 1).
PARALECTOTYPE: Juquila; Mexico, Salle Coll.; Paralectotype [round label]; B. C. A. Col. III. (2). Hydnocera clavata Gorham (BMNH; 1).

Phyllobaenus corticinus (Gorham, 1883: 173)

Original Combination: *Hydnocera corticina*

Types: Gorham stated “seven specimens were collected at Las Mercedes, only one or two in each of the other localities.” Six of the seven syntypes from Las Mercedes have been accounted. From each of the other localities either one or no specimens, but at least one specimen from one of these localities, are in one or more other museums. The lectotype and four paralectotypes were previously designated (Leavengood et al. 2012). Four additional paralectotypes are here recognized.

Series Locality: El Tumbador, Las Mercedes, and Cerro Zunil, Guatemala, and Mexico.

Type Locality: Mexico.

PARALECTOTYPES: Las Mercedes, 3000 ft., Champion, *Hydnocera corticina* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Las Mercedes, 3000 ft., Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 3).

Phyllobaenus cyanipennis (Gorham, 1883: 175) (Fig. 2.7)

Original Combination: *Hydnocera cyanipennis*

Types: Gorham identified the complete type series to comprise eleven specimens, nine of which are from the type locality. Four from Calderas and the one specimen from the Quiche Mountains are in the BMNH, leaving five from Calderas and the one specimen from Capetillo in one or more other museums. Döbler (1982: 416) recognized two of the Calderas syntypes in the SDEI.

Series Locality: Calderas, Quiche Mountains and Capetillo, Guatemala.

Type Locality: Calderas, Guatemala.

LECTOTYPE/PARALECTOTYPE (here designated): Type [round, red-bordered label], Calderas, Guatemala, Champion, Type, B. C. A. Coll. III (2) Hydnocera cyanipennis Gorham, *Hydnocera cyanipennis* Gorham (BMNH; 2 sharing a card mount, "LT" is written below the lectotype, the other specimen is a paralectotype).
PARALECTOTYPES: Calderas, Guatemala, Champion, B. C. A. Coll. III (2) Hydnocera cyanipennis Gorham (BMNH; 2 sharing a card mount); Quiche Mts., 7-9000 ft., Champion, B. C. A. Coll. III (2) Hydnocera cyanipennis Gorham, *Hydnocera cyanipennis* Gorham (BMNH; 1).

Phyllobaenus cylindricollis (Gorham, 1886: 343) (Fig. 2.8)

Original Combination: *Hydnocera cylindricollis*

Types: Gorham vaguely referenced "about a dozen examples," six of which are in the BMNH and one in the MNHN. When Gorham (1883) discussed *Hydnocera*

bituberculata Chevrolat he had included both of these species. Two specimens originally considered to be *bituberculata* Chevrolat by Gorham (1883) were included in the type series for *cylindricollis*. There are several remaining unrecognized syntypes in other museums. Döbler (1982: 416) considered two SDEI specimens from Bugaba (collected by Champion; not necessarily making it part of the type series) and Teapa, Tabasco (collected by H. H. Smith in January) to be syntypes, the latter of which is most confusing considering Teapa was not included in Gorham's locality list. Until they can be examined, these two specimens are here excluded from the type series.

Series Locality: Chontales, Nicaragua, and Bugaba, David and Volcan de Chiriqui, Panama.

Type Locality: Bugaba, Panama.

LECTOTYPE (here designated): Type [round, red-bordered label], Bugaba, Panama, Champion, Sp. figured, *Hydnocera cylindricollis*, B. C. A. Col. III (2), *Hydnocera cylindricollis* Gorham (BMNH; 1). **PARALECTOTYPES**: Chontales, Nicaragua, Janson, B. C. A. Col. III (2), *Hydnocera cylindricollis* Gorham (BMNH; 1); David, Panama, Champion, B. C. A. Col. III (2), *Hydnocera cylindricollis* Gorham (BMNH 1); V. de Chiriqui, 800-1500 ft, Champion, B. C. A. Col. III (2), *Hydnocera cylindricollis* Gorham (BMNH; 1); Bugaba, Panama, Champion, Sharp Coll. 1905-313, *Hydnocera bituberculata* (BMNH; 2); Bugaba, 800-1500 ft, Champion, *H. cylindricollis*, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a single cardmount).

Phyllobaenus flavifemoratus (Gorham, 1877: 261) (Fig. 2.11)

Original Combination: *Hydnocera flavifemorata*

= *Phyllobaenus pallipes* (Gorham, 1877: 261) [*Hydnocera pallipes*], **new synonymy**

= *Phyllobaenus rufithorax* (Gorham, 1877: 262) [*Hydnocera rufithorax*], **new synonymy**

Comments: There are no structural differences in the specimens in these three type series. The characters described to distinguish *pallipes* (Fig. 2.12) from *flavifemoratus* fall within the range of variation observed in *flavifemoratus*. Regarding

color, *flavifemoratus* varies considerably (as do most hydnocerine species) with the legs commonly distinctly banded or faded and largely pale, and the elytral maculae of varying shape and size. The head, thorax and elytra are broadly black, with or without a bluish tinge, or varyingly mottled testaceous to brownish-orange, even reddish-orange as described in *rufithorax* (Fig. 2.13), the most extreme example yet examined. The elytral apex may be more rounded, evenly weakly serrate, or slightly truncated (less rounded) with an occasional gap in the serration at the apex, or of intermediate form. All three species (Figs. 2.11-2.13) were described in the same publication, so as the first reviser I fix the precedence of *flavifemoratus*, selecting it because it was described earliest in the article.

Types: Others syntypes may exist.

Series/Type Locality: Amazon.

LECTOTYPE (here designated): Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll. 1905.100., *H. flavifemorata* (BMNH; 1). **PARALECTOTYPES**: Type, Gorham Type [red label], Amazon, Bates, Fry Coll. 1905.100. (BMNH; 1); 25161 [*Hydnocera flavifemorata* Gorh. Type. Amazon. Pará. Bates.], Type, Amazon, Bates, Fry Coll. 1905.100. (BMNH; 1); Type, Amazon, Bates, Fry Coll. 1905.100. (BMNH; 1); Amazon, Bates, *H. flavifemorata*, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus furcatus (Gorham, 1886: 342) [= *P. discoideus* (LeConte)]

Original Combination: *Hydnocera furcata*

Types: Gorham refers to “ten or twelve” specimens. Five are deposited in the BMNH and Döbler (1980: 419) indicated that a syntype was deposited in the SDEI, making the whereabouts of at least half of the type series known.

Series/Type Locality: N. Sonora, Mexico.

LECTOTYPE: N. Sonora, Mexico, Morrison, Sp. figured, B. C. A. Col. III (2), Hydnocera furcata Gorham, *Hydnocera furcata* (BMNH; 1). **PARALECTOTYPES**: N. Sonora, Mexico, Morrison, B. C. A. Col. III (2), Hydnocera furcata Gorham, *H. furcata* [male] (BMNH; 1); N. Sonora, Mexico, Morrison, B. C. A. Col. III (2), Hydnocera furcata Gorham (BMNH; 3).

Phyllobaenus haematicus (Gorham, 1883: 172) (Fig. 2.4)

Original Combination: *Hydnocera haematica*

Types: Two BMNH specimens match the two forms described by Gorham and have the same respective sexes (marked with "?" on Gorham's determination labels) and locality data from the original description. Another two were discovered in the MNHN. There may be additional syntypes in other museums. The paralectotype from the BMNH (Fig. 2.5) is *P. gorhami* (Wolcott), which was described after *haematicus*. Referring to *gorhami* Wolcott (1910: 378) indicated: "This appears to be the same as the species placed doubtfully as the female of *haematicus* by Gorham."

Series/Type Locality: Puebla, Cuernavaca, Mexico. The paralectotype is from "Cuernavaca, Mexico."

LECTOTYPE (here designated): Syntype [round, blue-bordered label], type [round, red-bordered label], Puebla, Mexico, Salle Coll., B. C. A. Col. III (2), *Hydnocera haematica* Gorham [male] ? (BMNH; 1). **PARALECTOTYPES**: Syntype [round, blue-bordered label], Cuernavaca, Mexico, Salle Coll., B. C. A. Col. III (2), *Hydnocera haematica* Gorham [female] ? (BMNH; 1, now *P. gorhami*); Cuernavaca, Mexico, Salle Coll., *Hydnocera haematica* Gorh. [female], Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Cuernavaca, Mexico, Salle Coll., *Hydnocera haematica* Gorh. [male] ?, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus impressus (Gorham, 1883: 176) (Fig. 2.9)

Original Combination: *Hydnocera impressa*

Types: Gorham referred to ten specimens. One syntype from Volcan de Chiriqui and another from Cordova are in other museums.

Series Locality: Volcan de Chiriqui, Panama, and Cordova, Mexico.

Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE/PARALECTOTYPE (here designated): Syntype [round, blue-bordered label], Type [round, red-bordered label], V. de Chiriqui, 2-3000 ft, Champion, Sp. figured, B. C. A. Col. III (2), *Hydnocera impressa* Gorham, *Hydnocera impressa*

Gorham (BMNH; 2, sharing a card mount, “LT” is written below the lectotype, the other specimen [to the right] is a paralectotype). **PARALECTOTYPES**: Syntype [round, blue-bordered label], V. de Chiriqui, 2-3000 ft, Champion, B. C. A. Col. III (2), *Hydnocera impressa* Gorham (BMNH; 2); V. de Chiriqui, 2-3000 ft, Champion, *Hydnocera impressa* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a card mount); V. de Chiriqui, 2-3000 ft, Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2).

Phyllobaenus intricatus (Gorham, 1883: 174) (Fig. 2.10)

Original Combination: *Hydnocera intricata*

Types: Two specimens are in the BMNH. Gorham made no reference to the number of specimens examined.

Series/Type Locality: Sinanja Valley, [Baja] Verapaz, Guatemala.

LECTOTYPE/PARALECTOTYPE (here designated): Sinanja, Vera Paz, Champion; Type [round, red-bordered label]; Hydnocera intricata G., B. C. A. Col. III. (2). Hydnocera intricata Gorham, Hydnocera intricata Gorham (BMNH; 2, sharing a single card mount, “LT” is written below the lectotype, the other specimen is the paralectotype).

Phyllobaenus lateralis (Gorham, 1883: 169) (Fig. 2.17)

Original Combination: *Hydnocera lateralis*

= *Phyllobaenus chapini* (Wolcott, 1927: 81) [*Hydnocera chapini*], **new synonymy**

Comments: The elytral and pronotal shapes described to distinguish *lateralis* from *chapini* were produced from a limited sample of specimens which did not properly illustrate their variation. The eyes, proportions of the head and pronotum, and parallel to sinuate elytral forms vary within the species and include intermediate forms. The plasticity in elytral margins and apices is typical of other *Phyllobaenus* species with the same elytral form (e.g., *P. subulatus*).

Types: Gorham indicated eleven specimens. Seven are in the BMNH and three are in the MNHN. One syntype was deposited in another museum. While all are from the same locality, there are specimens bearing labels with different elevations from the type locality. The specimen marked "type" was collected at "2-3000 ft." For now, only BCA specimens from the type locality with this elevation (of which 10 have been located) are considered to be part of the type series.

Series/Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE/PARALECTOTYPE (here designated): Syntype 1+2/7 [round, blue-bordered label], Type [round, red-bordered label], V. de Chiriqui, 2-3000 ft, *Hydnocera lateralis* Gorham, Champion, B. C. A. Col. III (2), *Hydnocera lateralis* Gorham (BMNH; 2 specimens on a single card mount; the lectotype indicated by LT and the paralectotype indicated by PLT, written on the card mount). **PARALECTOTYPES**: Syntype 3+4/7 [round, blue-bordered label], V. de Chiriqui, 2-3000 ft, Champion, B. C. A. Col. III (2), *Hydnocera lateralis* Gorham (BMNH; 2 specimens on a single card mount); Syntype [round, blue-bordered label], V. de Chiriqui, 2-3000 ft, Champion, B. C. A. Col. III (2), *Hydnocera lateralis* Gorham (BMNH; 3, with 5/7, 6/7, and 7/7 on the Syntype labels); V. de Chiriqui, 2-3000 ft, Champion, *Hydnocera lateralis* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a card mount); V. de Chiriqui, 2-3000 ft, Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus longus (LeConte, 1884: 22) (Fig. 2.32)

Original Combination: *Hydnocera longa*

= *Phyllobaenus villosus* (Schenkling, 1908: 702) [*Hydnocera villosa*], **new synonymy**

Comments: I find no variation between *villosus* specimens from Mexico and *longus* specimens from the United States. The type locality of *villosus* is San Isidro, which expands the known distribution of *P. longus* from Texas and Arizona (LeConte 1884: 22) to Mexico. However, there are 18 Mexican states with a San Isidro. The only other specimens from Mexico I have examined are from Sonora [Mexico: Sonora, 5 miles

east of Cananea, 16-IX-1970, K. Stephan (FSCA; 5)]. This northern Mexican record better represents the species' distribution. Additional specimens have been examined (FSCA, BYUC, NMNH) from Eddy, Grant, Hidalgo, Lea and Union Counties in New Mexico, **new state record**.

Phyllobaenus nigroaeneus (Gorham, 1883: 174) (Fig. 2.6)

Original Combination: *Hydnocera nigro-aenea*

Types: Gorham referred to eight specimens, seven from Guanajuato and one from Puebla. Four from Guanajuato are in the BMNH, another in the MNHN, leaving two syntypes from Guanajuato and one from Puebla in other museums. Döbler (1982: 424) indicated that the Puebla specimen was deposited in the SDEI. The paralectotype with the upside down "582" label is actually a specimen of *Phyllobaenus sordidus* (Gorham) with a faded color pattern and notably different elytral structure.

Series Locality: Guanajuato and Puebla, Mexico.

Type Locality: Guanajuato, Mexico.

LECTOTYPE (here designated): Guanajuato, Type [round, red-bordered label], Mexico, Salle Coll., Type, B. C. A. Col. III (2), Hydnocera nigro-aenea Gorham, *Hydnocera nigro-aenea* Gorham (BMNH; 1 female). **PARALECTOTYPES**: Guanajuato, Mexico, Salle Coll., 582, B. C. A. Col. III (2), Hydnocera nigro-aenea Gorham (BMNH; 1 female, actually *P. sordidus*); Guanajuato, Mexico, Salle Coll., 579, B. C. A. Col. III (2), Hydnocera nigro-aenea Gorham (BMNH; 1 female); Guanajuato, Mexico, Salle Coll., 581, B. C. A. Col. III (2), Hydnocera nigro-aenea Gorham (BMNH; 1 female); Guanajuato, Mexico, Salle Coll., *Hydnocera nigro-aenea* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus obscurus (Gorham, 1883: 172) (Fig. 2.21)

Original Combination: *Hydnocera obscura*

Types: Gorham referred to ten specimens, seven being from the type locality. The BMNH and MNHN house eight. The two remaining syntypes are from Rio Maria Linda and San Gerónimo.

Series Locality: Paso Antonio, Rio Maria Linda and San Gerónimo, Guatemala, and David, Chiriqui, Panama.

Type Locality: San Gerónimo, Guatemala.

LECTOTYPE (here designated): Type [round label]; S. Geronimo, Guatemala, Champion; Type; B. C. A. Col. III. (2). Hydnocera obscura Gorham, Hydnocera obscura Gorham (BMNH; 1). **PARALECTOTYPES**: S. Geronimo, Guatemala, Champion; B. C. A. Col. III. (2). Hydnocera obscura Gorham (BMNH; 2); S. Geronimo, Guatemala, Champion; *Hydnocera obscura* Gorham; Museum Paris Coll Gorham 1914 [blue label]; Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a cardmount); S. Geronimo, Guatemala, Champion; Museum Paris Coll Gorham 1914 [blue label]; Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Paso Antonio, 400 ft, Champion; B. C. A. Col. III. (2). Hydnocera obscura Gorham (BMNH; 1); David, Chiriqui, Champion; B. C. A. Col. III. (2). Hydnocera obscura Gorham (BMNH; 1).

Phyllobaenus pallipes (Gorham, 1877: 261) (Fig. 2.12)

Original Combination: *Hydnocera pallipes*

Types: I have encountered three syntypes. More syntypes may exist.

Series/Type Locality: Amazon.

LECTOTYPE (here designated): Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll. 1905.100., *H. pallipes* (BMNH; 1). **PARALECTOTYPE**: Type, Amazon, Bates, Fry Coll. 1905.100. (BMNH; 1); Amazon, Bates, Gorham Type [red label], *H. pallipes*, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus pulchellus (Gorham, 1883: 171) (Figs. 2.14-2.15)

Original Combination: *Hydnocera pulchella*

Types: At least one syntype from San Gerónimo and perhaps others from Volcan de Chiriqui are in other museums. There is a MNHN specimen from Volcan de Chiriqui collected by Champion, but the label differs in that it was collected at 25-4000 ft. This specimen is not considered a paralectotype.

Series Locality: Volcan de Chiriqui, Panama, and San Gerónimo, Guatemala.

Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE (here designated): Type [round, red-bordered label], V. de Chiriqui, 2-3000 ft, Champion, B. C. A. Col. III (2) *Hydnocera pulchella* Gorham, *Hydnocera pulchella* Gorham (BMNH; 1). **PARALECTOTYPE**: V. de Chiriqui, 2-3000 ft, Champion, B. C. A. Col. III (2) *Hydnocera pulchella* Gorham, *Hydnocera pulchella* Gorham (BMNH; 1); V. de Chiriqui, 2-3000 ft, Champion, *Hydnocera pulchella* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus rudis (Gorham, 1886: 342) (Fig. 2.22)

Original Combination: *Hydnocera rudis*

Types: Gorham referred to two specimens. The lectotype was discovered separated from its point mount and in pieces. It was reassembled by the junior author.

Series/Type Locality: Northern Sonora, Mexico.

LECTOTYPE (here designated): Type [round, red-bordered label], Type, N. Sonora, Mexico, Morrison, *Hydnocera rudis* G., B. C. A. Col. III. (2). Hydnocera rudis Gorham (BMNH; 1). **PARALECTOTYPE**: N. Sonora, Mexico, Morrison, *Hydnocera rudis* G., Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus rufipes (Newman, 1840: 363) (Fig. 2.23)

Original Combination: *Hydnocera rufipes*

Types: In the BMNH there is a specimen with a type label (applied by a BMNH curator) and another specimen with nearly identical label data. The second specimen indicates the collector whereas the first does not. However, Newman's species descriptions from the Entomology Club were often based on specimens that lacked the locality and/or collector data cited in his original publications. Because only "a single specimen" was collected by Doubleday (Newman 1840), I here recognize the specimen with the locality data most perfectly matching the publication (i.e., "East Florida" with no additional information). The specimen from St. John's Bluff, East Florida is presumed to

have been collected after the description of *rufipes*. Nonetheless, a lectotype is designated herein as it is certain that this mystery will never meet any solution.

Series/Type Locality: East Florida.

HOLOTYPE (fixed by monotypy): Type [circular, red-bordered label], *Hydnocera rufipes*, Ent. Club 44-12, *Hydnocera rufipes* Newm., East Florida (BMNH; 1).

Phyllobaenus rufithorax (Gorham, 1877: 262) (Fig. 2.13)

Original Combination: *Hydnocera rufithorax*

Types: One specimen accounted; number not specified.

Series/Type Locality: Amazon.

LECTOTYPE (here designated): Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll. 1905.100., *H. rufithorax* (BMNH; 1).

Phyllobaenus scapularis (Gorham, 1883: 170) (Fig. 2.18)

Original Combination: *Hydnocera scapularis*

Types: Two specimens.

Series/Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE (here designated): Type [round, red-bordered label], V. de Chiriqui, 2-3000 ft, Champion, *Hydnocera scapularis* Gorh, B. C. A. Col. III (2), *Hydnocera scapularis* Gorham (BMNH; 1); **PARALECTOTYPE**: V. de Chiriqui, 2-3000 ft, Champion, [male], *scapularis* G., Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus serratus (Newman, 1838: 379), **new combination**

Original Combination: *Hydnocera serrata*

Types: The type series comprises two specimens collected by Foster at Mount Pleasant, Ohio (Newman 1838: 380). In the same publication Newman described *Hydnocera*, making *Hydnocera serratus* the type-species. *Phyllobaenus serratus* is a junior synonym of *Phyllobaenus pallipennis* (Say, 1825: 176; *Clerus pallipennis*).

Series/Type Locality: Mount Pleasant, Ohio.

LECTOTYPE (here designated): Type [circular red-bordered label], [one folded, blank label, dark on one side], *Hydnocera serrata* Newm., Ent. Club 44-12 (BMNH; 1). **PARALECTOTYPE**: Ent. Club 44-12, *Hydnocera serrata* Newm. Ent Mag. T. 3T9 Ohio.

Phyllobaenus sordidus (Gorham, 1883: 173) (Figs. 2.27-2.31)

Original Combination: *Hydnocera sordida*

Types: Gorham referred to seven specimens from the Salle collection, two of which remain undesignated. However, the number of specimens collected by Dugès was not identified.

Comments: This species clearly caused Gorham more confusion than any other. A rather infuscate (appearing entirely black) specimen of *sordidus* was included as a paralectotype of *P. nigroaeneus*. Another specimen (non-type) was identified by Gorham as *P. guatemalensis* (Gorham) while other specimens thought by Gorham to be *sordidus* were later identified as an undescribed species. Future diagnosticians or curators mistook several other species for *sordidus* or *sordidus* for other species. The reason for this confusion is the tremendous variation in color pattern and the apparent overlap with the color pattern expression ranges of its congeners. With few specimens at hand it is understandable that these very different color patterns (e.g., Figs. 2.27-2.28, Figs. 2.29-2.30, and Fig. 2.31) were suggestive of more than one species.

Series/Type Locality: Guanajuato, Mexico.

LECTOTYPE (here designated): Syntype [round, blue-bordered label], Type [round, red-bordered label], Guanajuato, Mexico, Salle Coll., 584, Type, B. C. A. Col. III (2), *Hydnocera sordida* Gorham (BMNH; 1). **PARALECTOTYPES**: Syntype [round, blue-bordered label], Guanajuato, Mexico, Salle Coll., B. C. A. Col. III (2), *Hydnocera sordida* Gorham (BMNH; 2); Guanajuato, Mexico, Salle Coll., *Hydnocera sordida* Gorham, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Guanajuato, Mexico, Salle Coll., Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Mexique, Guanajuato, E. Dugès, Museum Paris ex. Coll. R. Oberthur (MNHN; 10).

Phyllobaenus subulatus (Gorham, 1883: 169) (Fig. 2.20)

Original Combination: *Hydnocera subulata*

Types: The number of unrecognized syntypes in other museums is not known. There may be unrecognized paralectotypes from Senahu.

Comments: This species is strikingly similar to *P. subvittatus* (Fig. 2.19), which has pale, often transverse maculae on the elytra. While entirely dark bodied at first glance, one specimen from the type series of *P. subulatus* hints at pale discoloration at the elytral base. Both species also share the same general distribution from Guatemala to Panama. Until the species groups of *Phyllobaenus* are revised and morphology is carefully assessed I will not emend the status of either species.

Series Locality: Sabo, Senahu, and Sinanja Valley, Guatemala; Volcan de Chiriqui and
Bugaba, Panama.

Type Locality: Sabo, Vera Paz, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Sabo, Vera Paz, Champion, Type, Sp. figured, *Hydnocera subulata* Gorham, B. C. A. Col. III (2), *Hydnocera subulata* Gorham (BMNH; 1). **PARALECTOTYPES:** Senahu, Vera Paz, Champion, B. C. A. Col. III (2), *Hydnocera subulata* Gorham (BMNH; 1); V. de Chiriqui, 3-4000 ft, Champion, B. C. A. Col. III (2), *Hydnocera subulata* Gorham (BMNH; 1); V. de Chiriqui, 2-3000 ft, Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2); V. de Chiriqui, 25-4000 ft, Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Bugaba, 800-1500 ft, Champion, B. C. A. Col. III (2), *Hydnocera subulata* Gorham (BMNH; 1); Sinaja, Vera Paz, Champion, Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus subvittatus (Gorham, 1883: 170) (Fig. 2.19)

Original Combination: *Hydnocera subvittata*

Types: Gorham does not specify the number of types, but states “specimens occur both from this and all the other localities” implying at least one specimen per locality. If

this assumption is correct, then at least one syntype may remain from Tamaha and San Juan, and all specimens (assuming more than one) from Volcan de Chiriqui are as yet unaccounted.

Comments: Gorham considered this "a very indefinite species, varying a good deal in size and colour, and (if I am right in uniting them as one) in the length of the elytra." There are, in fact, two species present in the type series. Although not specified, it is assumed by the language of Gorham's original discussion that all specimens of the "other" likely undescribed species (with short elytra) were from Bugaba and, therefore, that all (if any) missing specimens from elsewhere are of *subvittatus*. Of the type series four specimens (including a card-mounted pair) truly represent *subvittatus*; two represent the other species with shorter elytra, and an additional pair of card-mounted specimens (one specimen representing each species on the same card!). While one "specimen" (the card-mounted pair representing both species) has a type label placed by Gorham (or a curator), it was never indicated which specimen on the card mount was the type. Pursuant to ICZN Article 72.4.7, this type designation is not valid. The present designation recognizes a specimen of the species with longer, apically truncate elytra as the lectotype of *subvittatus*.

Series Locality: Chiacam, San Juan, and Tamahu, Guatemala; Volcan de Chiriqui and Bugaba, Panama.

Type Locality: Tamahu, Vera Paz, Guatemala.

LECTOTYPE (here designated): Tamahu, Vera Paz, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 1). **PARALECTOTYPES**: Type [round, red-bordered label], Chiacam, Vera Paz, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 2, a card-mounted pair); San Juan, Vera Paz, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 1); Bugaba, Type, 800-1500 ft, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 1, this specimen shares a card-mount with the other species); **PARALECTOTYPES represented by the other species**: Bugaba, Type, 800-1500 ft, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 1, this specimen shares a card-mount with the other species); Bugaba, Panama, Champion, B. C. A. Col. III (2), *Hydnocera subvittata* Gorham (BMNH; 2).

Phyllobaenus testaceus (Gorham, 1883: 169) (Figs. 2.24-2.26)

Original Combination: *Hydnocera testacea*

Types: Of the type series localities Gorham indicated multiple specimens from Volcan de Chiriqui and Bugaba. There could also be multiple specimens from Cerro Zunil. He specified that there was only one specimen from Mexico. The number of remaining syntypes in other museums is unknown, however the Mexican specimen is accounted for here and there is at least one specimen from Cerro Zunil unaccounted. One syntype from Cerro Zunil is in the SDEI (Döbler 1980: 431).

Comments: The type series likely contains more than one species. The lectotype (Fig. 2.24) has two dorsolateral dark vittae while some paralectotypes (Figs. 2.25-2.26) have three, one central and two lateral. The elytral form of all three figured specimens appears quite different, so if the figured specimens truly are the same species, then there is considerable plasticity in elytral form.

Series Locality: Playa Vicente, Mexico; Cerro Zunil and Quiche Mountains, Guatemala; Volcan de Chiriqui and Bugaba, Panama.

Type Locality: Quiche Mountains, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Quiche Mts., 7-9000 ft, Champion, Type, *Hydnocera testacea* Gorham, B. C. A. Col. III (2), *Hydnocera testacea* Gorham (BMNH; 1). **PARALECTOTYPES**: *Hydnocera testacea* Gorham, Quiche Mts: Ch., Museum Paris Coll Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); Playa Vicente, Mexico, Hoge, B. C. A. Col. III (2), *Hydnocera testacea* Gorham (BMNH; 1); V. de Chiriqui, 8000 ft, Champion, *H. testacea* Gorh., Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a card mount); V. de Chiriqui, 8000 ft, Champion, Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); V. de Chiriqui, 8000 ft, Champion, B. C. A. Col. III (2), *Hydnocera testacea* Gorham (BMNH; 3, one label in cursive rather than typed); V. de Chiriqui, below 4000 ft, Champion, [incorrectly named], G. J. A., B. C. A. Col. III (2), *Hydnocera testacea* Gorham (BMNH; 1); Bugaba, Panama, Champion, [incorrectly named], G. J. A., B. C. A. Col. III (2),

Hydnocera testacea Gorham (BMNH; 1); Bugaba, 800-1500 ft, Champion, B. C. A. Col. III (2), *Hydnocera testacea* Gorham (BMNH; 1).

Phyllobaenus trichrous (Gorham, 1883: 171) (Fig. 2.16)

Original Combination: *Hydnocera trichroa*

Types: All three syntypes are here accounted.

Series Locality: Dueñas and San Gerónimo, Guatemala.

Type Locality: San Gerónimo, Guatemala.

LECTOTYPE (here designated): Syntype [circular, blue-bordered label]; Type [circular, red-bordered label]; S. Geronimo, Guatemala, Champion; Type [label]; Sp. figured [label]; B. C. A. Col. III. (2). Hydnocera trichroa Gorham (BMNH; 1). **PARALECTOTYPE**: Syntype [circular, blue-bordered label]; Duenas, Guatemala, G. C. Champion; B. C. A. Col. III. (2). Hydnocera trichroa Gorham (BMNH; 1); Duenas, Guatemala, G. C. Champion; *Hydnocera trichroa* Gorham; Gorham 1914 [blue label]; Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Phyllobaenus villosus (Schenkling, 1908: 702) (Fig. 2.32)

Original Combination: *Hydnocera villosa*

Types: Eight specimens in the BMNH. There are also two syntypes in the SDEI (Döbler 1980: 433). There may be additional syntypes elsewhere.

Comments: (see *Phyllobaenus longus*)

Series/Type Locality: San Isidro, Mexico.

LECTOTYPE (here designated): San Isidro, Mexico, Höge, 1907-156, Type [circular, red-bordered label], *Hydnocera villosa* n. sp. [folded label in cursive], [Schenkling type label] (BMNH; 1). **PARALECTOTYPES**: San Isidro, Mexico, Höge, 1907-156, [Schenkling type label] (BMNH; 7).

Phyllobaenus vitrinus (Gorham, 1886: 343) (Figs. 2.33-2.34)

Original Combination: *Hydnocera vitrina*

Types: There is one specimen each from Tuxtla and Bugaba, and an unknown number of specimens from Volcan de Chiriqui. Unrecognized syntypes may exist in other museums.

Series Locality: Tuxtla, Mexico; Bugaba and Volcan de Chiriqui, Panama.

Type Locality: Bugaba, Panama.

LECTOTYPE (here designated): Syntype [round, blue-bordered label], Type [round, red-bordered label], Type, Sp. figured, Bugaba, Panama, Champion, B. C. A. Col. III (2), *Hydnocera vitrina* Gorham (BMNH; 1). **PARALECTOTYPES**: Syntype [round, blue-bordered label], Tuxtla, Mexico, Salle, B. C. A. Col. III (2), *Hydnocera vitrina* Gorham (BMNH; 1); Syntype [round, blue-bordered label], V. de Chiriqui, 4000-6000 ft, Champion, B. C. A. Col. III (2), *Hydnocera vitrina* Gorham (BMNH; 1); *H. vitrina*, V. de Chiriqui, 3-4000 ft, Champion, Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); V. de Chiriqui, 25-4000 ft, Champion, Museum Paris Coll. Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 3); V. de Chiriqui, below 4000 ft, Champion, *H. vitrina*, Museum Paris Coll. Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1); V. de Chiriqui, below 4000 ft, Champion, Museum Paris Coll. Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 1).

Isohydnocera aegra (Newman, 1840: 364) (Fig. 2.37)

Original Combination: *Hydnocera aegra*

Types: A single specimen was collected by Doubleday (Newman, 1840: 364).

Comments: There is a BMNH specimen which reads "?Type", but lacks any other distinctive label information (e.g., collector or locality). Another label on this specimen reads "the largest very near *Evenus filiformis* Spinola t38 f2" indicating a misidentification as a result of the lack of a locality label. The final label reads "*Hemipeplus marginipennis* N. Amer. was on this card," suggesting that perhaps the locality label was allocated to the Mycterid specimen. Searching through the BMNH Mycteridae, I encountered many specimens—with simple, handwritten data such as "Florida" on a small round label or "Fla" typed on a tiny label—collected in the correct timeframe from Florida. However, none read "Ent. Club" or Doubleday, and none

appeared as if cut from a shared mount with the *aegra* specimen. Of course, the *Hemipeplus* may have been re-mounted, which, under the circumstances, would make matching this *aegra* to label data impossible. However, the handwritten labels ("aegra" and "Hydnocera aegra Newm.") are typical of Newman's type specimens. As such, the following specimen is here recognized as the holotype.

Series/Type Locality: East Florida.

HOLOTYPE (fixed by monotypy): *aegra*, *Hydnocera aegra* Newm, ?Type, the largest very near *Evenus filiformis* Spinola t38 f2 [blue label], *Hemipeplus marginipennis* N. Amer. was on this card [upside down] (BMNH; 1, the specimen is card mounted, with the abdomen on its own card mount below the specimen).

Isohydnocera cryptocerina (Gorham, 1883: 175) (Figs. 2.35-2.36)

Original Combination: *Hydnocera cryptocerina*

Types: Gorham did not indicate the number of specimens in the type series. No syntypes from Tumbador or El Reposo have yet been accounted.

Series Locality: Chacoj, Teleman, El Reposo, and El Tumbador, Guatemala.

Type Locality: Chacoj, Vera Paz, Guatemala.

LECTOTYPE/PARALECTOTYPE (here designated): T [on card mount], Type [round, red-bordered label], Chacoj, Vera Paz, Champion, Type, B. C. A. Col. III (2), *Hydnocera cryptocerina* Gorham (BMNH; 2, sharing a card mount, the "T" indicating the Lectotype, the other being a paralectotype). **PARALECTOTYPE**: Teleman, Vera Paz, Champion, B. C. A. Col. III (2), *Hydnocera cryptocerina* Gorham (BMNH; 1); Chacoj, Vera Paz, Champion, *Hydnocera cryptocerina* Gorham, Museum Paris Coll. Gorham 1914 [blue label], Museum Paris ex. Coll. R. Oberthur [blue label] (MNHN; 2, sharing a single card mount, one specimen is missing).

Isohydnocera curtipennis (Newman, 1840: 365) (Fig. 2.38)

Original Combination: *Hydnocera curtipennis*

Types: Two specimens collected by Doubleday (Newman, 1840: 364).

Series/Type Locality: East Florida.

LECTOTYPE/PARALECTOTYPE (here designated): New [on card mount], Syntype [round, blue-bordered label], Type [round, red-bordered label], *Hydnocera curtipennis*, Ent. Club 44-12 (BMNH; 2, sharing a card mount, the left specimen, when viewed such as to read "New" on the card mount, is the Lectotype).

Tribe LEMIDIINI

The number of lemidiine genera was reduced considerably by Kolibáč (1998: 185). All genera except for *Allelidea* Waterhouse and *Isolemidia* Gorham were synonymized under *Lemidia* Spinola. I do not believe that sufficient taxa were reviewed to support this conclusion and herein recognize these genera without such synonymizations and in a manner consistent with the majority of current literature (e.g., Leavengood 2010; Opitz 2010).

Parmius debilis Sharp, 1877: 272 (Figs. 2.39-2.40)

Original Combination: *Parmius debilis*

Types: Two.

Series Locality: Tairua and Christchurch, New Zealand.

Type Locality: Christchurch, New Zealand.

LECTOTYPE (here designated): *Parmius debilis*, Type, D. S., Christchurch, N. Z. [all written on card mount], Holotype [round, red-bordered label], Christchurch, New Zealand, Sharp Coll., 1905-313 (BMNH; 1). **PARALECTOTYPE**: Syntype [round, blue-bordered label], 32, *Parmius* n. sp., Tairua, Sharp Coll., 1905-313 (BMNH; 1).

Parmius longipes Sharp, 1877: 272

Original Combination: *Parmius longipes*

Types: Two.

Series/Type Locality: Tairua, New Zealand.

LECTOTYPE (here designated): *Parmius longipes*, Type, D. S., Tairua [all written on card mount], Type [round, red-bordered label], Sharp Coll., 1905-313

(BMNH; 1). **PARALECTOTYPE**: Syntype [round, blue-bordered label], Tairua [red, circular label], Sharp Coll., 1905-313 (BMNH; 1).

Paupris aptera Sharp, 1877: 271 (Fig. 2.41)

Original Combination: *Paupris aptera*

Types: Six.

Series/Type Locality: Auckland, New Zealand.

LECTOTYPE (here designated): *Paupris aptera* Type, D. S., N. Z., Auckland [written on card mount], Type [round, red-bordered label], Syntype [round, blue-bordered label], Auckland, New Zealand, Sharp Coll. 1905-313 (BMNH; 1).
PARALECTOTYPES: *Paupris aptera* 2nd. Type, D. S., N. Z., Auckland [written on card mount], Syntype [round, blue-bordered label], Auckland, New Zealand, Sharp Coll. 1905-313 (BMNH; 5).

Isolemidia apicalis Gorham, 1877: 259 (Fig. 2.42)

Original Combination: *Isolemidia apicalis*

Types: Two.

Series/Type Locality: Amazon.

LECTOTYPE (here designated): Syntype [round, blue-bordered label], Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll., 1905.100, *Isolemidia apicalis* Gorham (BMNH; 1). **PARALECTOTYPE**: 25167 [*Isolemidia apicalis*. Gorh. Type. Amazon. Ega. Bates], Syntype [round, blue-bordered label], Type, Amazon, Bates, Fry Coll., 1905.100 (BMNH; 1).

Isolemidia batesi Gorham 1877: 259 (Fig. 2.43)

Original Combination: *Isolemidia batesi*

Types: Two.

Comments: Despite the label indications of the "type," I have designated the notably less damaged specimen as the Lectotype.

Series/Type Locality: Amazon, village of Sao Paulo, Brazil.

LECTOTYPE (here designated): Syntype [round, blue-bordered label], Amazon, Bates, Fry Coll., 1905.100 Gorham (BMNH; 1). **PARALECTOTYPE**: 25166 [*Isolemidia batesi*. Gorh. Type. Amazon. S. Paulo. Bates.], Syntype [round, blue-bordered label], Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll., 1905.100, *Isolemidia batesi* Gorham (BMNH; 1).

Isolemidia pulchella Gorham, 1877: 258 (Fig. 2.44)

Original Combination: *Isolemidia pulchella*

Types: At least one. There are two BMNH specimens with the following label data: Ega [circular blue label] (BMNH; 2). The blue label indicates that a past curator considered these to be syntypes. The labels match other such specimens collected by Fry, but the data does not match the published locality.

Series/Type Locality: Amazon.

LECTOTYPE (here designated): 25165 [*Isolemidia pulchella*. Gorh. Clinging to slender dead twigs. Type. Amazon. Ega. Bates.], Syntype [round, blue-bordered label], Type [round, red-bordered label], Type, Gorham Type [red label], Amazon, Bates, Fry Coll., 1905.100, *Isolemidia pulchella* Gorham (BMNH; 1).

Isolemidia subtilis Gorham, 1877: 259 (Fig. 2.45)

Original Combination: *Isolemidia subtilis*

Types: One found; number not specified.

Series/Type Locality: Rio de Janeiro, Brazil.

LECTOTYPE (here designated): 1381, Syntype [round, blue-bordered label], Type [round, red-bordered label], Type, Fry, Rio Jan., Fry Coll., 1905.100, *Isolemidia subtilis* (BMNH; 1).

Isolemidia subviridis Gorham, 1883: 177 (Fig. 2.46)

Original Combination: *Isolemidia subviridis*

Types: There are two specimens in the type series.

Series/Type Locality: Volcan de Chiriqui, Panama

LECTOTYPE (here designated): Syntype 2/1 [round, blue-bordered label], Type [round, red-bordered label], V. de Chiriqui, 4000-6000 ft, Champion, B. C. A. Col. III (2), *Isolemidia subviridis* Gorham (BMNH; 1). **PARALECTOTYPE**: Syntype 2/2 [round, blue-bordered label], V. de Chiriqui, 4000-6000 ft, Champion, B. C. A. Col. III (2), *Isolemidia subviridis* Gorham (BMNH; 1).

Isolemidia virescens (Gorham, 1877: 262) (Fig. 2.47)

Original Combination: *Hydnocera virescens*

Types: Gorham did not indicate the number of types. Three have been found, but other unrecognized syntypes may exist.

Series Locality: Parana and Rio de Janeiro, Brazil.

Type Locality: Rio de Janeiro, Brazil.

LECTOTYPE (here designated): Type [round, red-bordered label], 20257 [*Hydnocera virescens*. Gorh. Type. Rio de Janeiro. January to March 1860.], Type, Gorham Type [red label], Fry, Rio Jan., Fry Coll. 1905.100., *virescens* (BMNH; 1). **PARALECTOTYPE**: Type, Fry, Rio Jan., Fry Coll. 1905.100. (BMNH; 1); Parana, Gorham Type [red label], *Hyd. virescens* Gorh., Museum Paris Coll. Gorham [blue label], Type [red label] (MNHN; 1).

Allelidea brevipennis Pascoe, 1862: 48 (Fig. 2.48)

Original Combination: *Allelidea brevipennis*

Types: One; total not specified.

Series/Type Locality: Melbourne, Australia.

LECTOTYPE (here designated): Melbourne, Type [round, red-bordered label], *Allelidea brevipennis* Type Pascoe (BMNH; 1).

Allelidea ctenostomoides Waterhouse, 1839: 194 (Fig. 2.49)

Original Combination: *Allelidea ctenostomoides*

Types: Four.

Series/Type Locality: Sydney, Australia.

LECTOTYPE (here designated): Syntype [round, blue-bordered label], Type [round, red-bordered label], Sydney, Australia, C. Darwin, *Allelidea ctenostomoides* Wat. Sydney (BMNH; 1). **PARALECTOTYPES**: Syntype [round, blue-bordered label], Sydney, Australia, C. Darwin, *Allelidea ctenostomoides* Wat. Sydney (BMNH; 3).

Allelidea viridis Blackburn, 1891: 302 (Fig. 2.50)

Original Combination: *Allelidea viridis*

Types: Blackburn referred to no fewer than three specimens in his description. Paralectotypes are deposited in the Australian Museum (2 specimens) and the South Australian Museum (1 specimen) (J. Bartlett, *in litt.*).

Series/Type Locality: Mordialloc, Victoria

LECTOTYPE (here designated): 3808 T Al. [?] [on card mount], Type [round, red-bordered label], Australia, Blackburn Coll., B. M. 1910-236, *Allelidea viridis* Blackb. (BMNH; 1).

Blaesiophthalmus accinctus (Newman, 1842: 364) (Fig. 2.51)

Original Combination: *Thanasimus accinctus*

Types: One found; number not specified.

Series/Type Locality: Port Philip, South Australia.

LECTOTYPE (here designated): Type [round, red-bordered label], *Thanasimus accinctus* Newm. Entomol 36[4] (BMNH; 1). The assumption of the “364” is because Newman's labels included the page number of the description in The Entomologist (J. Bartlett, *in litt.*).

Blaesiophthalmus variegatus **(**Blackburn, 1891: 304) (Fig. 2.52)

Original Combination: *Metabasis variegata*

Types: Blackburn referred to more than one specimen in his description. One Paralectotype is deposited in the Institut Royal des Sciences Naturelles de Belgique, two more are deposited in the South Australian Museum.

Series/Type Locality: Near Port Lincoln, South Australia.

LECTOTYPE (here designated): T. 898 [written on card mount], Type [round, red-bordered label], Australia, Blackburn Coll., B. M. 1910-236, *Metabasis variegata*, Blackb. (BMNH; 1).

Lemidia nitens (Newman, 1841: 36) (Fig. 2.53)

Original Combination: *Hydnocera nitens*

Types: Described from one specimen.

Series/Type Locality: Van Dieman's Land.

HOLOTYPE (fixed by monotypy): Type [round, red-bordered label]. *Hydnocera L. nitens* Newm. [cursive], Van Diem[en's] L[and] J. Walker, Ent. Club 44-12 (BMNH; 1).

(Diem = Diemen's, Ln = Land, as in Van Diemen's Land. Also, the L after Hydnocera must represent Lemidia).

2.3.2 Subfamily CLERINAE

The following species were selected for specific investigative interests. They do not represent all BCA species of *Enoclerus*. The specimens of *Enoclerus* in the MNHN are in disarray. It is possible that unrecognized syntypes (paralectotypes) went undiscovered during the senior author's visit to this museum.

Enoclerus cautus (Gorham, 1883: 152) (Fig. 2.54)

Original Combination: *Clerus cautus*

Types: Gorham did not specify the number of specimens in the type-series. Seventeen syntypes have been designated from the BMNH and MNHN. This series represents all localities indicated by Gorham. However, other syntypes may exist.

Series Locality: San Juan, Panzos, Teleman, Chiacam and Senahu, Guatemala.

Type Locality: Senahu, Vera Paz, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Senahu, Vera Paz, Champion, Type, *Clerus cautus* Gorh., B. C. A. Col. III (2) *Clerus cautus* Gorham (BMNH; 1). **PARALECTOTYPES**: Senahu, Vera Paz, Champion, B. C. A.

Col. III (2) *Clerus cautus* Gorham [and another, identical label upside down], *Clerus cautus* Gorham (BMNH; 2, sharing a single card mount); Senahu, Vera Paz, Champion, Museum Paris Coll. Gorham 1914 (MNHN; 2); Senahu, Vera Paz, Champion, Type Co., *Clerus cautus* Gorh., Museum Paris Coll. Gorham 1914 (MNHN; 2, sharing a single cardmount); Teleman, Vera Paz, Champion, B. C. A. Col. III (2) *Clerus cautus* Gorham (BMNH; 1); Panzos, Vera Paz, Champion, B. C. A. Col. III (2) *Clerus cautus* Gorham (BMNH; 1); San Juan, Vera Paz, Champion, B. C. A. Col. III (2) *Clerus cautus* Gorham (BMNH; 3, 2 of which share a card mount and have a second, upside down BCA label); Chiancaman, Vera Paz, Champion, B. C. A. Col. III (2) *Clerus cautus* Gorham (BMNH; 1); Chiancaman, Vera Paz, Champion, *Clerus cautus* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 2, sharing a single cardmount); Senahu, Vera Paz, Champion, Museum Paris Coll. Gorham 1914 (MNHN; 2).

Enoclerus hoegei (Gorham, 1883: 159) (Fig. 2.55)

Original Combination: *Clerus högei*

Types: This species was described from a single specimen.

Series/Type Locality: Cerro de Plumas, Mexico.

HOLOTYPE (fixed by monotypy): Type [round, red-bordered label], Cerro de Plumas, Mexico, Hoege, *Clerus hogei* Gorh., B. C. A. Col. III (2) *Clerus hogei* Gorham (BMNH; 1).

Enoclerus puellus (Gorham, 1886: 339) (Fig. 2.56)

Original Combination: *Clerus puellus*

Types: Gorham did not specify the number of specimens in the type series. Five syntypes have been found in the BMNH and MNHN. This series represents all localities indicated by Gorham.

Series Locality: San Gerónimo, San Joaquin, and Tocoy in Vera Paz, Guatemala.

Type Locality: San Gerónimo, Vera Paz, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], S. Geronimo, Guatemala, Champion, *Cl. puellus*, Type, Sp. figured, B. C. A. Col. III (2) *Clerus puellus* Gorham (BMNH; 1). **PARALECTOTYPES**: San Joaquin, Vera Paz,

Champion, *Cl. puellus*, B. C. A. Col. III (2) *Clerus puellus* Gorham (BMNH; 1); Tocoy, Vera Paz, Champion, B. C. A. Col. III (2) *Clerus puellus* Gorham (BMNH; 1); S. Geronimo, Guatemala, Champion, *C. puellus* Gorh., Museum Paris Coll. Gorham 1914 (MNHN; 1); S. Geronimo, Guatemala, Champion, Type Co., *C. puellus* G., Museum Paris Coll. Gorham 1914 (MNHN; 1).

Enoclerus x-album (Gorham, 1883: 169) (Fig. 2.57)

Original Combination: *Clerus x-album*

Types: Gorham did not specify the number of specimens in the type series. Sixteen syntypes have been found in the BMNH and MNHN. This series represents all localities indicated by Gorham except for Bugaba. Other syntypes may exist. Two specimens (on a single card mount) bear an "Ekis" determination label. It is believed that these specimens lost their Gorham label and/or was mis-sorted. As such they, too, are designated a paralectotype.

Series Locality: Zapote and El Reposo, Guatemala.; Rio Sarstoon, British Honduras (now Belize); Chontales, Nicaragua; Bugaba and David, Panama.

Type Locality: Zapote, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Zapote, Guatemala, G. C. Champion, Type. Sp. figured, *Clerus x-album* Gorham, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1). **PARALECTOTYPES**: Zapote, Guatemala, G. C. Champion, Museum Paris Coll. Gorham 1914 (MNHN; 1); *Clerus x-album* Gor., Type Co., Zapote, Guatemala, G. C. Champion, Museum Paris Coll. Gorham 1914 (MNHN; 2, sharing a single cardmount); Zapote, Guatemala, G. C. Champion, *Clerus x-album* Gorham, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1); Zapote, Guatemala, G. C. Champion, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 2); Zapote, Guatemala, G. C. Champion, *Clerus* [#] 5 n. sp., *Clerus x-album* Gorham, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1); Zapote, Guatemala, G. C. Champion, *Clerus* n. sp. A, [Ekis det label] (BMNH; 2, sharing a single card mount); Chontales, Nicaragua, Janson, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1); R. Sarstoon, B. Honduras, Blancaneau, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 2); R. Sarstoon, B. Honduras, Blancaneau, *Clerus x-album* Gor., Museum Paris

Coll. Gorham 1914 (MNHN; 1); David, Panama, Champion, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1); El Reposo, 800 ft, Champion, B. C. A. Col. III (2) *Clerus x-album* Gorham (BMNH; 1).

2.3.3 Subfamily TILLINAE

The following species represent all fourteen BCA species of *Cymatodera*, all of which are currently recognized by their original combination.

Cymatodera angulifera Gorham, 1882: 133 (Fig. 2.60)

Types: "A series of this species were taken at Dueñas" according to Gorham. Eleven have been accounted.

Series/Type Locality: Dueñas, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Duenas, Guatemala, G. C. Champion, *Cymatodera angulifera* Gorham, B. C. A. Col. III (2) *Cymatodera angulifera* Gorham (BMNH; 1). **PARALECTOTYPES**: Duenas, Guatemala, G. C. Champion, *Cymatodera angulifera* Gorham, B. C. A. Col. III (2) *Cymatodera angulifera* Gorham (BMNH; 6, two of which share a card mount and one of which has an additional "Cym. 7" label under the locality label); Duenas, Guatemala, G. C. Champion, *Cymatodera angulifera* Gorham [blue label], *Cymatodera* 5, Museum Paris Coll. Gorham 1914 (MNHN; 2, sharing a cardmount); Duenas, Guatemala, G. C. Champion, Museum Paris Coll. Gorham 1914 (MNHN; 2).

Cymatodera bipunctata Gorham, 1882: 135

Types: Described from two specimens. Both are accounted.

Series/Type Locality: Oaxaca, Mexico.

LECTOTYPE (here designated): Type [round, red-bordered label], Oaxaca, Mexico, Hoege, Type, Sp. figured, *Cymatodera bipunctata* Gorham, B. C. A. Col. III (2) *Cymatodera bipunctata* Gorham (BMNH; 1). **PARALECTOTYPE**: Oaxaca, Mexico, Hoege, Type, *Cymatodera bipunctata* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera championi Gorham, 1882: 131 (Fig. 2.58)

Types: Described from one male (lectotype) and one female (paralectotype). Some non-types were collected at Bugaba during the BCA expedition, but they were not included in the type series.

Series/Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE (here designated): Type [round, red-bordered label], V. de Chiriqui, 2-3000 ft, Champion, Sp. figured, Type, *Cymatodera championi* Gorham, B. C. A. Col. III (2) *Cymatodera championi* Gorham (BMNH; 1). **PARALECTOTYPE**: V. de Chiriqui, 2-3000 ft, Champion, *Cymatodera championi* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera flexuosa Gorham, 1882: 136 (Fig. 2.61)

Types: Described from a single specimen.

Series/Type Locality: Orizaba, Mexico.

HOLOTYPE (fixed by monotypy): Orizaba, Type [round, red-bordered label], Mexico, Salle Coll., Type, *Cymatodera flexuosa* Gorham, B. C. A. Col. III (2) *Cymatodera flexuosa* Gorham (BMNH; 1).

Cymatodera grandis Gorham, 1882: 130 (Fig. 2.66)

Types: Gorham referenced no fewer than four specimens. All localities and collectors/collections referenced by Gorham are accounted by the specimens listed below.

Series Locality: Mexico, Guanajuato, Puebla.

Type Locality: Puebla, Mexico.

LECTOTYPE (here designated): Puebla, Type [round, red-bordered label], Mexico, Salle Coll., 479, [male], *Cymatodera grandis* Gorham, B. C. A. Col. III (2) *Cymatodera grandis* Gorham (BMNH; 1). **PARALECTOTYPES**: Puebla, Mexico, Salle Coll., *Cymatodera discoidalis* Chev. [folded over], B. C. A. Col. III (2) *Cymatodera grandis* Gorham (BMNH; 1); Guanajuato, Mexico, Salle Coll., 484, B. C. A. Col. III (2) *Cymatodera grandis* Gorham (BMNH; 1); Guanajuato, Mexico, Salle Coll., 485 [label

upside down], *Cymatodera grandis* [(]Sturm) Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1); Mexico, Salle Coll., 474, Ex. Coll. J. Sturm, [female] ?, Mexico, *Notoxus grandis, Cymatodera grandis* Gorham, B. C. A. Col. III (2) *Cymatodera grandis* Gorham (BMNH; 1*, The micropin on this cork is bare. The specimen (i.e., pieces of it) is in a gel capsule which also has a paralectotype label (which is intentionally abbreviated).

Cymatodera grossa Gorham, 1882: 138 (Fig. 2.69)

Types: Described from two specimens.

Series/Type Locality: Jalapa, Mexico.

LECTOTYPE (here designated): Type [round, red-bordered label], Jalapa, Mexico, Hoege, Type, *Cymatodera grossa* Gorham, B. C. A. Col. III (2) *Cymatodera grossa* Gorham (BMNH; 1). **PARALECTOTYPE**: Jalapa, Mexico, Hoege, Type, *C. grossa* Gorham, B. C. A. Col. III (2) *Cymatodera grossa* Gorham (BMNH; 1).

Cymatodera hoegei Gorham, 1882: 135 (Fig. 2.65)

Types: Four specimens from each Mexican locality and one per Guatemalan locality. All but one Jalapa specimen of the type series have been accounted.

Series Locality: Jalapa and Trapiche, Mexico; San Gerónimo and Capetillo, Guatemala.

Type Locality: Trapiche, Mexico.

LECTOTYPE (here designated): Type [male] [round, red-bordered label], Type [male], Trapiche, Mexico, Hoege, *Cyamtodera hogei* Gorham, B. C. A. Col. III (2) *Cymatodera hogei* Gorham (BMNH; 1). **PARALECTOTYPES**: Type [female] [round, red-bordered label], Jalapa, Mexico, Hoege, Type [female], *Cyamtodera hogei* Gorham, B. C. A. Col. III (2) *Cymatodera hogei* Gorham (BMNH; 1); Jalapa, Mexico, Hoege, [male], B. C. A. Col. III (2) *Cymatodera hogei* Gorham (BMNH; 1); Jalapa, Mexico, Hoege, Museum Paris Coll. Gorham 1914 (MNHN; 1); [male], Trapiche, Mexico, Hoege, *Cymatodera* 1, Museum Paris Coll. Gorham 1914 (MNHN; 1); [female], Trapiche, Mexico, Hoege, Museum Paris Coll. Gorham 1914 (MNHN; 1); Trapiche, Mexico, Hoege, Museum Paris Coll. Gorham 1914 (MNHN; 1); Capetillo, Guatemala, G. C. Champion, [female], Museum Paris Coll. Gorham 1914 (MNHN; 1); S. Geronimo,

Guatemala, Champion, [female], *Cymatodera högei* Gorh., Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera liturata Gorham, 1882: 134 (Fig. 2.62)

Types: Described from two specimens.

Series/Type Locality: Cerro Zunil, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Cerro Zunil, 4-5000 ft, G. C. Champion, Type, *Cymatodera liturata* Gorham, B. C. A. Col. III (2) *Cymatodera liturata* Gorham (BMNH; 1). **PARALECTOTYPE**: Cerro Zunil [cursive], *Cymatodera liturata* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera lunulata Gorham, 1882: 133 (Figs. 2.63-2.64)

Types: Described from "a very considerable series of specimens." Twelve have been accounted.

Comments: The figured specimens demonstrate sexual dimorphism observed in apical antennomere length.

Series/Type Locality: San Gerónimo, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], S. Geronimo, Guatemala, Champion, Type, *Cymatodera lunulata* Gorham, B. C. A. Col. III (2) *Cymatodera lunulata* Gorham (BMNH; 1). **PARALECTOTYPES**: S. Geronimo, Guatemala, Champion, B. C. A. Col. III (2) *Cymatodera lunulata* Gorham (BMNH; 6, one of which has a [female] label above the locality label); S. Geronimo, Guatemala, Champion, *Cym. lunulata* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1); S. Geronimo, Guatemala, Champion, *Cymatodera* 4, Museum Paris Coll. Gorham 1914 (MNHN; 2, sharing a card mount); S. Geronimo, Guatemala, Champion, Museum Paris Coll. Gorham 1914 (MNHN; 2).

Cymatodera nitida Gorham, 1882: 134 (Fig. 2.67)

Types: Described from two specimens. The pin of the paralectotype (MNHN) is thin, delicate and quite bent. This specimen is also missing the head and prothorax.

Series Locality: Capulalpam, Mexico; Capetillo, Guatemala.

Type Locality: Capetillo, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], Capetillo, Guatemala, G. C. Champion, Type, *Cymatodera nitida* Gorham, B. C. A. Col. III (2) *Cymatodera nitida* Gorham (BMNH; 1). **PARALECTOTYPE**: Capulalpam, Mexico, Salle Coll., Type, *Cymatodera nitida* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera parallela Gorham, 1882: 132 (Fig. 2.68)

Types: Gorham indicated "a series of this species" from Cerro Zunil and one specimen from San Gerónimo. There may be additional syntypes.

Series Locality: Cerro Zunil and San Gerónimo, Guatemala.

Type Locality: Cerro Zunil, Guatemala.

LECTOTYPE (here designated): Type [round, red-bordered label], C. Zunil, *Cymatodera parallela* Gorham, B. C. A. Col. III (2) *Cymatodera parallela* Gorham (BMNH; 1). **PARALECTOTYPES**: Cerro Zunil, 4-5000 ft, Champion, B. C. A. Col. III (2) *Cymatodera parallela* Gorham (BMNH; 8, including three pairs of specimens sharing card mounts and a single specimen with an additional [male] label above the locality label); Cerro Zunil, 4000 ft, Champion, Museum Paris Coll. Gorham 1914 (MNHN; 3, one of which also has a "*C. parallela* Gorh." label); Cerro Zunil, 4000 ft, Champion, *Cym.* 13 sent to Chv, *C. parallela* G., Museum Paris Coll. Gorham 1914 (MNHN; 1, this specimen has another small beetle on the card mount).

Cymatodera saturata Gorham, 1886: 334 (Fig. 2.71)

Types: Described from two specimens. The BMNH has two specimens from the type locality however one of them was originally considered by Gorham as *C. parallela* and was not a part of that type series. Gahan later identified it as *saturata*.

Series/Type Locality: Volcan de Chiriqui, Panama.

LECTOTYPE (here designated): Type [round, red-bordered label], Type, Sp. figured, V. de Chiriqui, 4000-6000 ft, Champion, *C. saturata* Gorham, B. C. A. Col. III (2) *Cymatodera saturata* Gorham (BMNH; 1). **PARALECTOTYPE**: V. de Chiriqui,

4000-6000 ft, Champion, *C. saturata* Gorham, Museum Paris Coll. Gorham 1914 (MNHN; 1).

Cymatodera sericans Gorham, 1886: 333 (Fig. 2.59)

Types: Described from a single specimen.

Series/Type Locality: Volcan de Chiriqui, Panama.

HOLOTYPE (fixed by monotypy): Type [round, red-bordered label], V. de Chiriqui, 4000-6000 ft, Champion, [male], *Cymatodera sericans* G., B. C. A. Col. III (2) *Cymatodera sericans* Gorham (BMNH; 1).

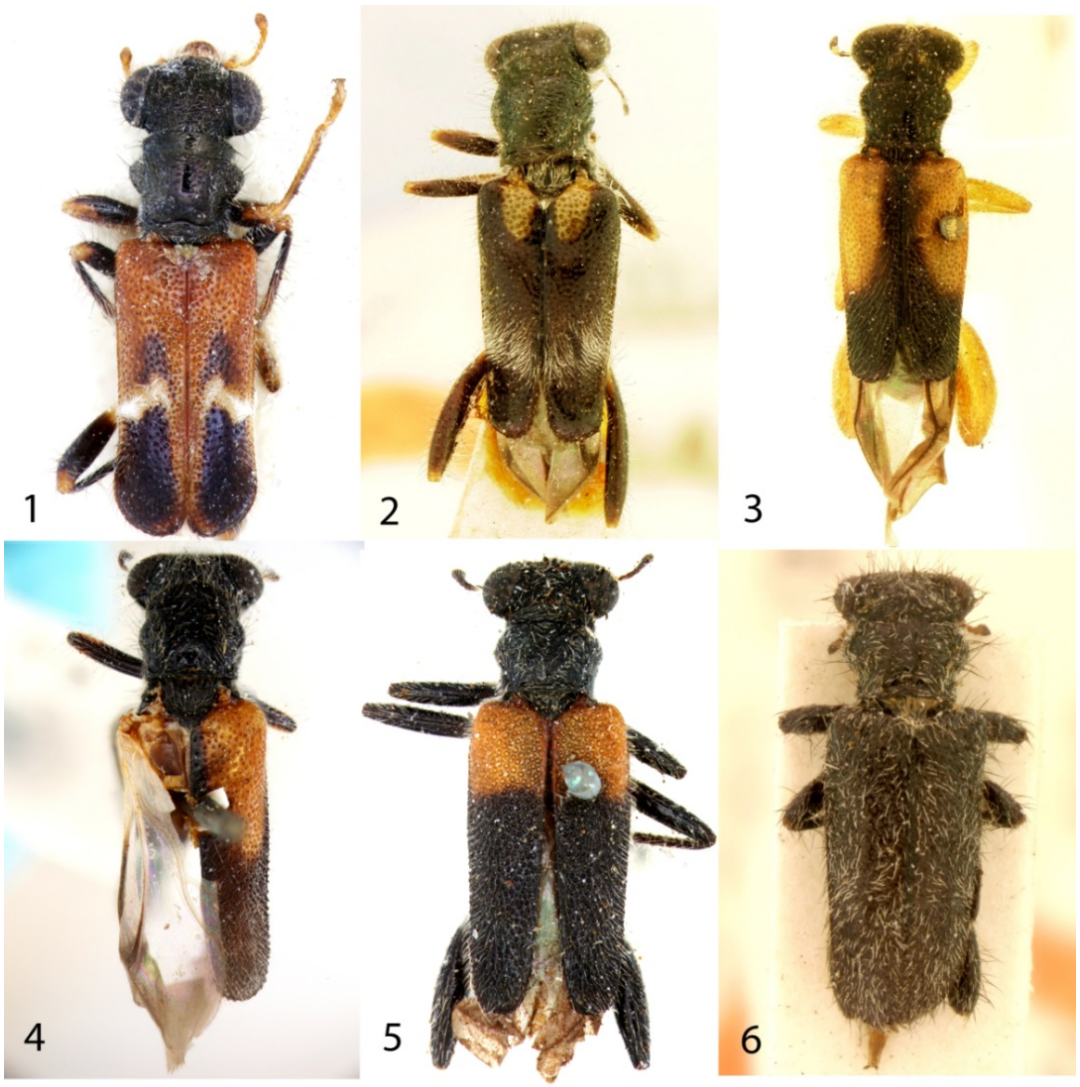
Cymatodera valida Gorham, 1883: 137 (Fig. 2.70)

Types: Gorham indicated that there was more than one specimen he considered female and at least one male. Seven specimens have been accounted.

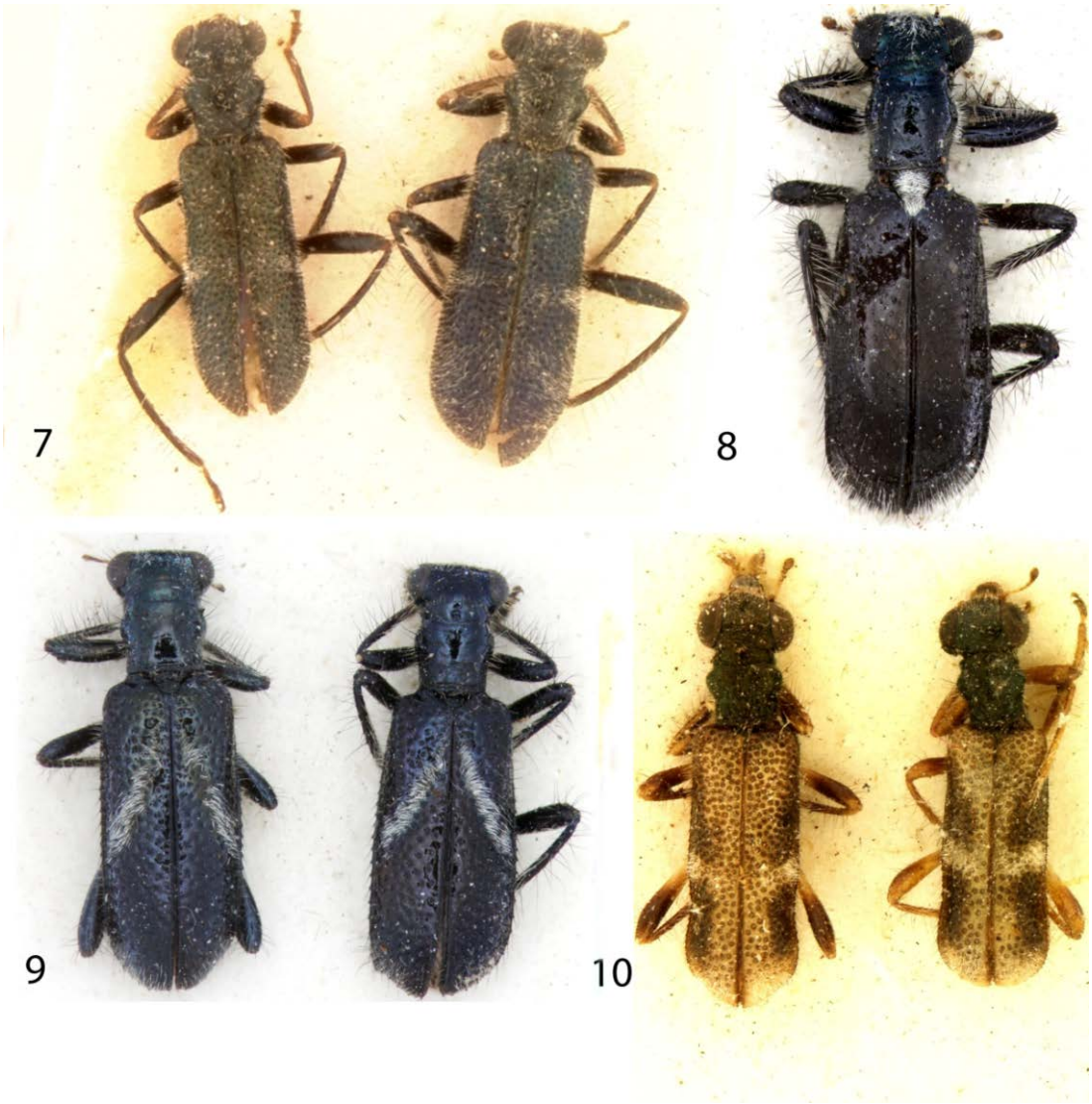
Series Locality: Dueñas and San Gerónimo, Guatemala.

Type Locality: San Gerónimo, Guatemala.

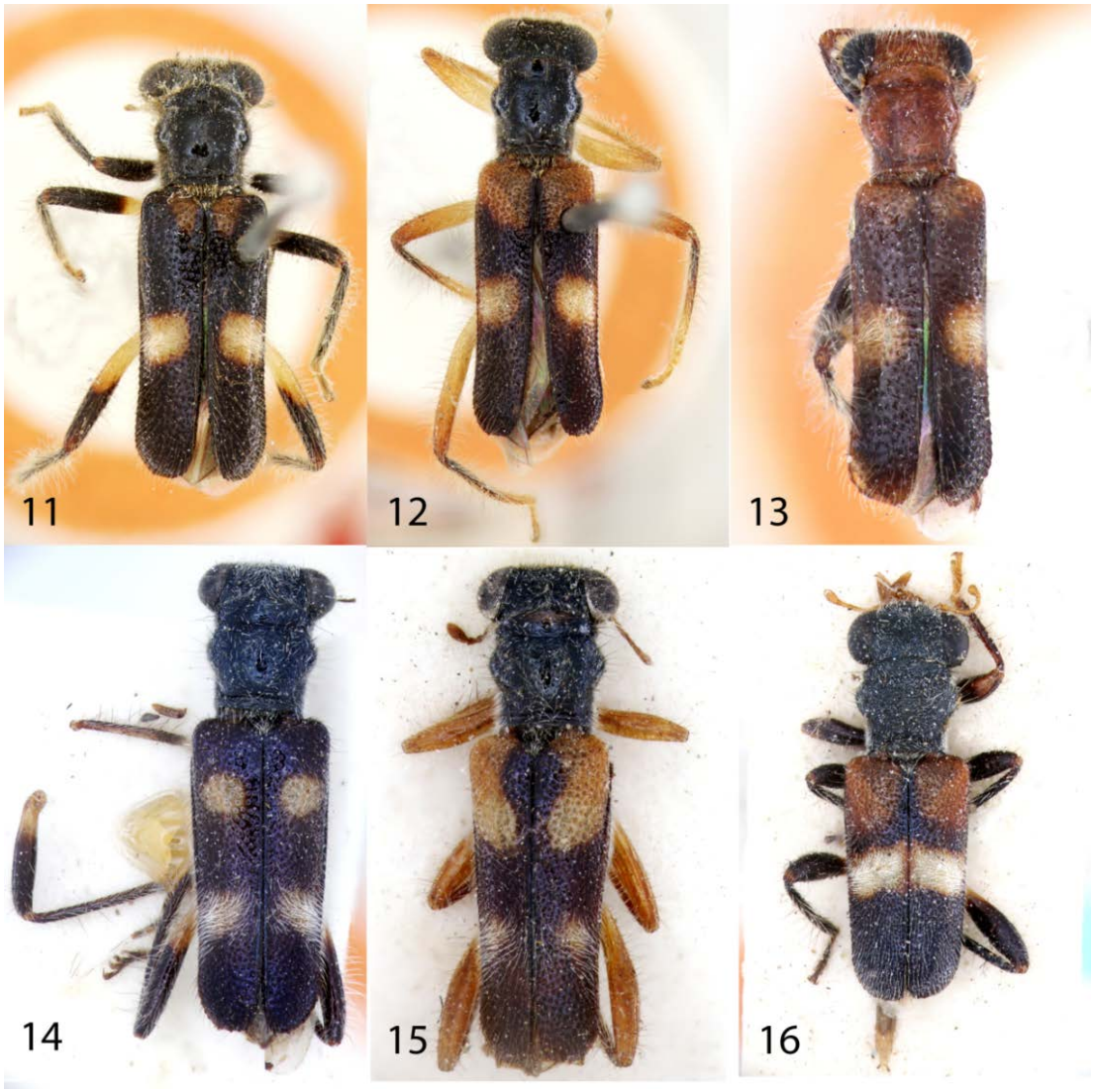
LECTOTYPE (here designated): [male], Type [round, red-bordered label], San Geronimo, Guatemala, Champion, Type, *Cymatodera valida* Gorham, B. C. A. Col. III (2) *Cymatodera valida* Gorham (BMNH; 1). **PARALECTOTYPE**: Duenas, Guatemala, G. C. Champion, B. C. A. Col. III (2) *Cymatodera valida* Gorham, *Cymatodera valida* Gorham (BMNH; 1); Duenas, Guatemala, G. C. Champion, Museum Paris Coll. Gorham 1914 (MNHN; 4, two of which share a card mount and a "*Cymatodera valida* Gorh." label); San Geronimo, Guatemala, Champion, Museum Paris Coll. Gorham 1914 (MNHN; 1).



Figures 2.1-2.6. Fig. 2.1) *Phyllobaenus aeneicollis* (Schenkling), Lectotype (BMNH); **Fig. 2.2)** *P. chalybeatus* (Gorham), Lectotype (BMNH); **Fig. 2.3)** *P. clavatus* (Gorham), Lectotype (BMNH); **Fig. 2.4)** *P. haematicus* (Gorham), Lectotype (BMNH); **Fig. 2.5)** *P. haematicus* (Gorham), Paralectotype (BMNH), actually *P. gorhami* (Wolcott); **Fig. 2.6)** *P. nigroaeneus* (Gorham), Lectotype (BMNH).



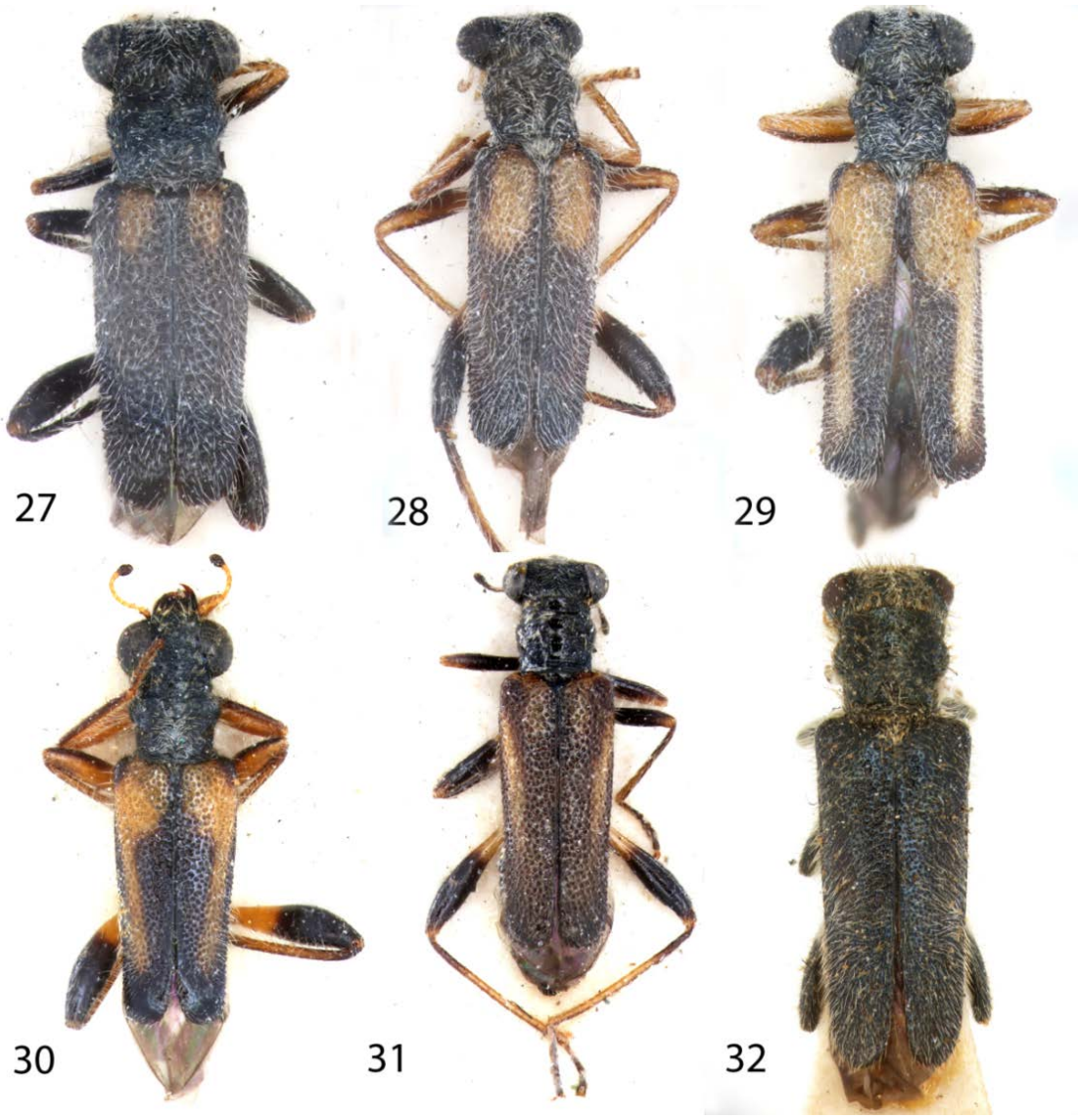
Figures 2.7-2.10. Fig. 2.7) *Phyllobaenus cyanipennis* (Gorham), Lectotype [left] and Paralectotype [right] (BMNH); **Fig. 2.8)** *P. cylindricollis* (Gorham), Lectotype (BMNH); **Fig. 2.9)** *P. impressus* (Gorham), Lectotype [left] and Paralectotype [right] (BMNH); **Fig. 2.10)** *P. intricatus* (Gorham), Lectotype [left] and Paralectotype [right] (BMNH).



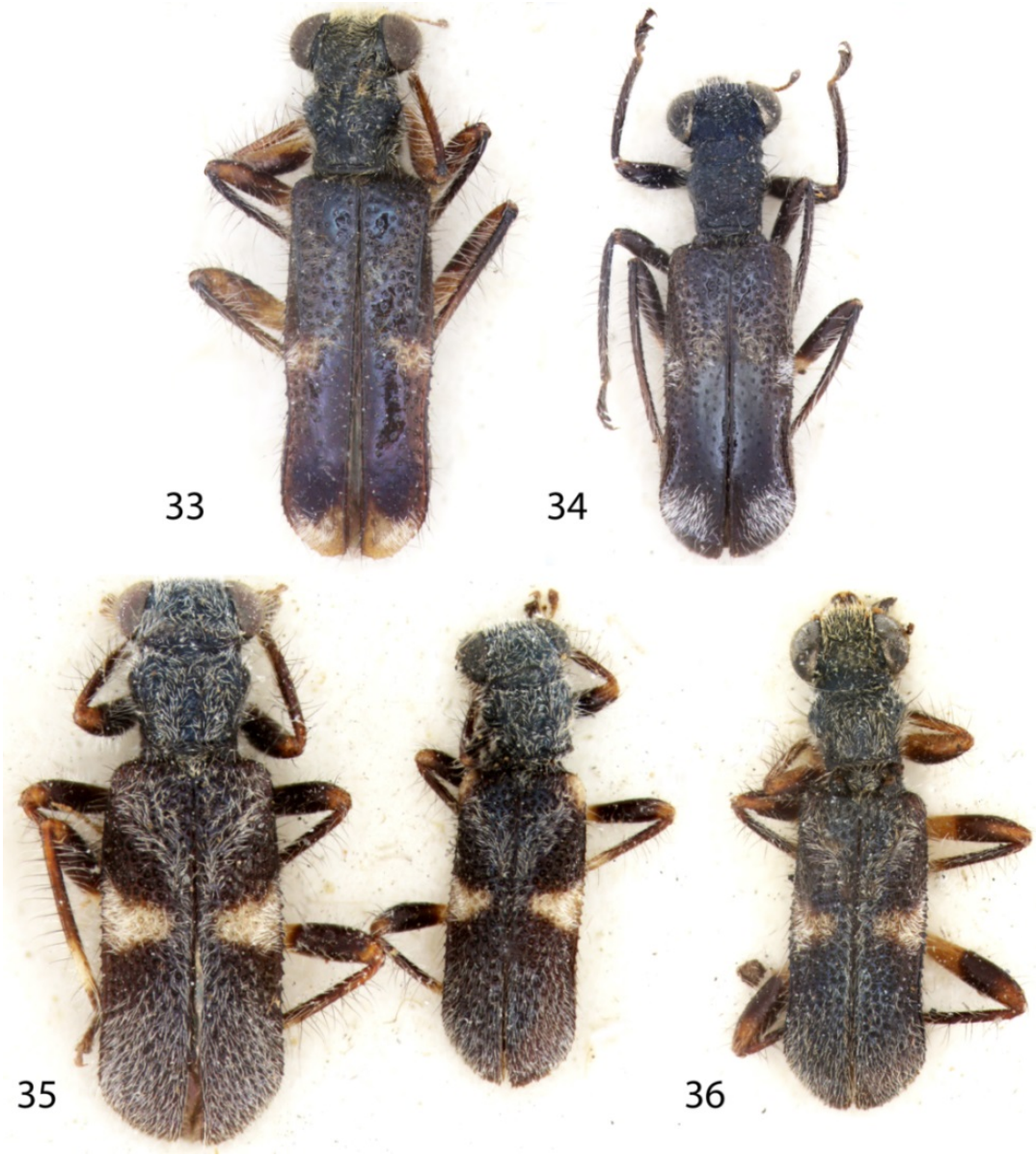
Figures 2.11-2.16. Fig. 2.11) *Phyllobaenus flavifemoratus* (Gorham), Lectotype (BMNH); **Fig. 2.12)** *P. pallipes* (Gorham), Lectotype (BMNH); **Fig. 2.13)** *P. rufithorax* (Gorham), Lectotype (BMNH); **Fig. 2.14)** *P. pulchellus* (Gorham), Lectotype (BMNH); **Fig. 2.15)** *P. pulchellus* (Gorham), Paralectotype (BMNH); **Fig. 2.16)** *P. trichrous* (Gorham), Lectotype (BMNH).

Figures 2.17-2.20. Fig. 2.17) *Phyllobaenus lateralis* (Gorham), Lectotype [right] and Paralectotype [right] (BMNH); **Fig. 2.18)** *P. scapularis* (Gorham), Lectotype (BMNH); **Fig. 2.19)** *P. subvittatus* (Gorham), two Paralectotypes (BMNH); **Fig. 2.20)** *P. subulatus* (Gorham); Lectotype (BMNH).

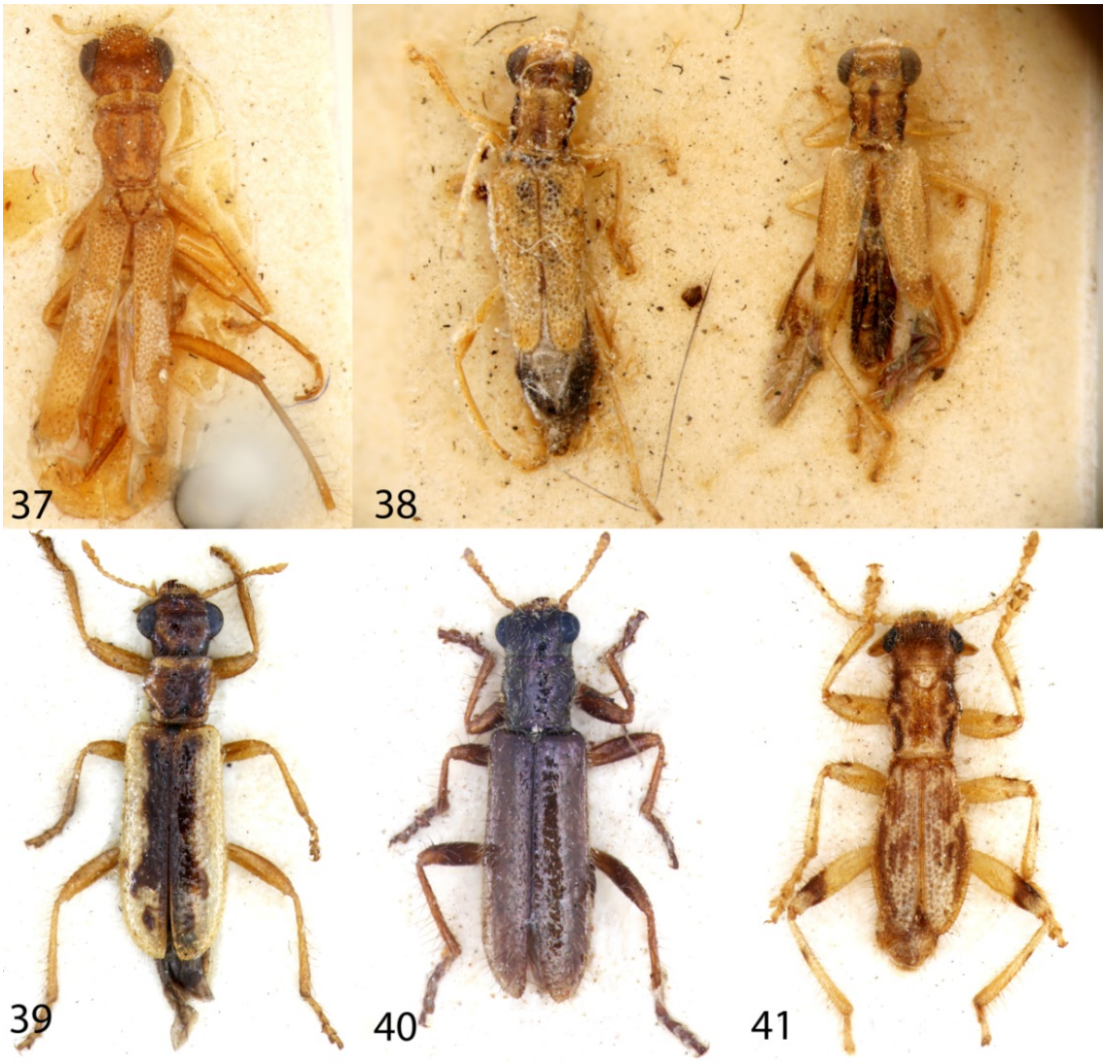
Figures 2.21-2.26. Fig. 2.21) *Phyllobaenus obscurus* (Gorham), Lectotype (BMNH); **Fig. 2.22)** *P. rudis* (Gorham), Lectotype (BMNH); **Fig. 2.23)** *P. rufipes* (Newman), Holotype (BMNH); **Fig. 2.24)** *P. testaceus* (Gorham), Lectotype (BMNH); **Fig. 2.25)** *P. testaceus* (Gorham), Paralectotype (BMNH); **Fig. 2.26)** *P. testaceus* (Gorham), Paralectotype (BMNH).



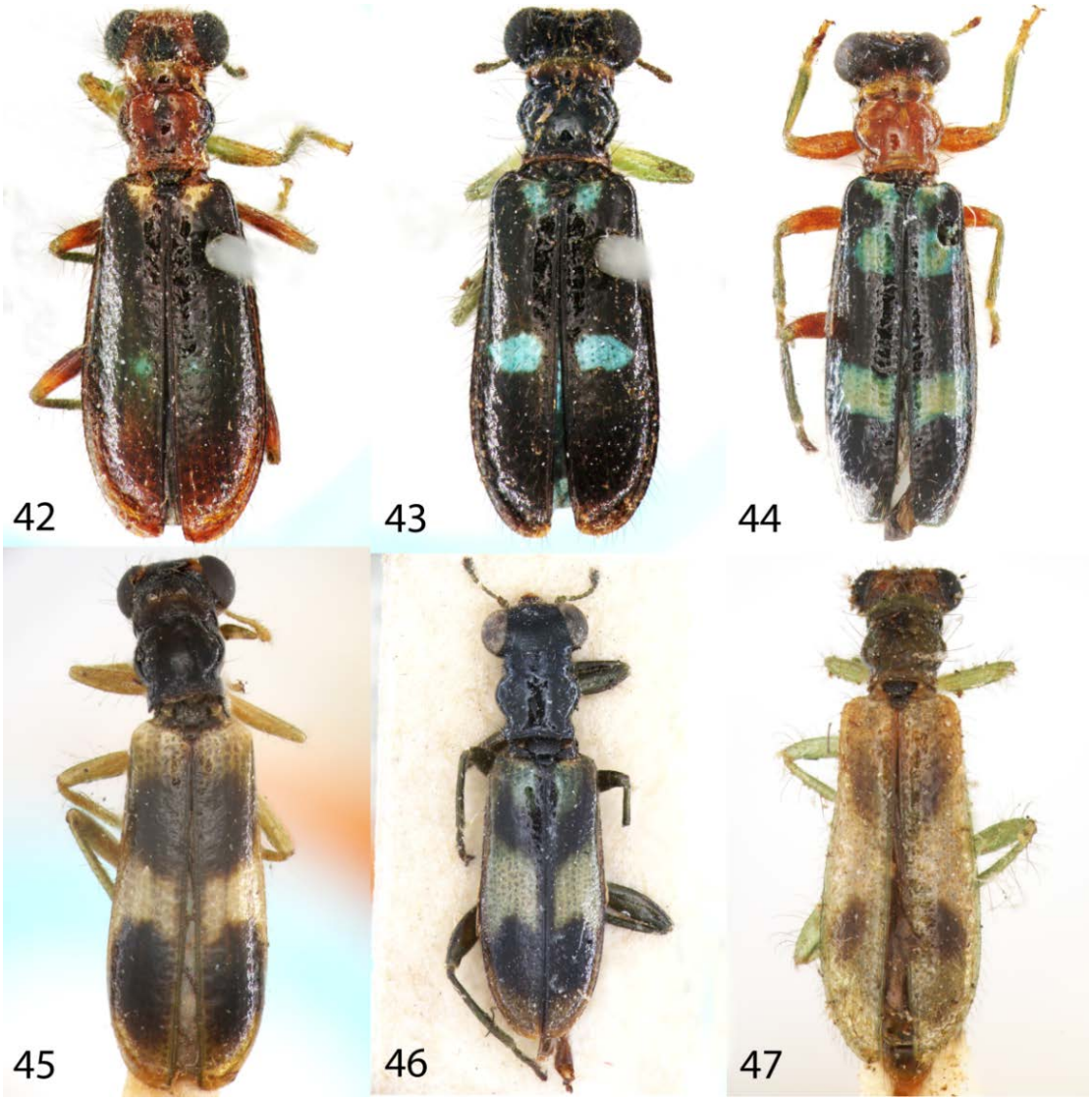
Figures 2.27-2.32. Figs. 27-31: *Phyllobaenus sordidus* (Gorham). **Fig. 2.27)** Paralectotype (BMNH); **Fig. 2.28)** Lectotype (BMNH); **Fig. 2.29)** Paralectotype (BMNH); **Fig. 2.30)** non-type; **Fig. 2.31)** non-type; **Fig. 2.32)** *P. villosus* (Schenkling), Paralectotype (BMNH).



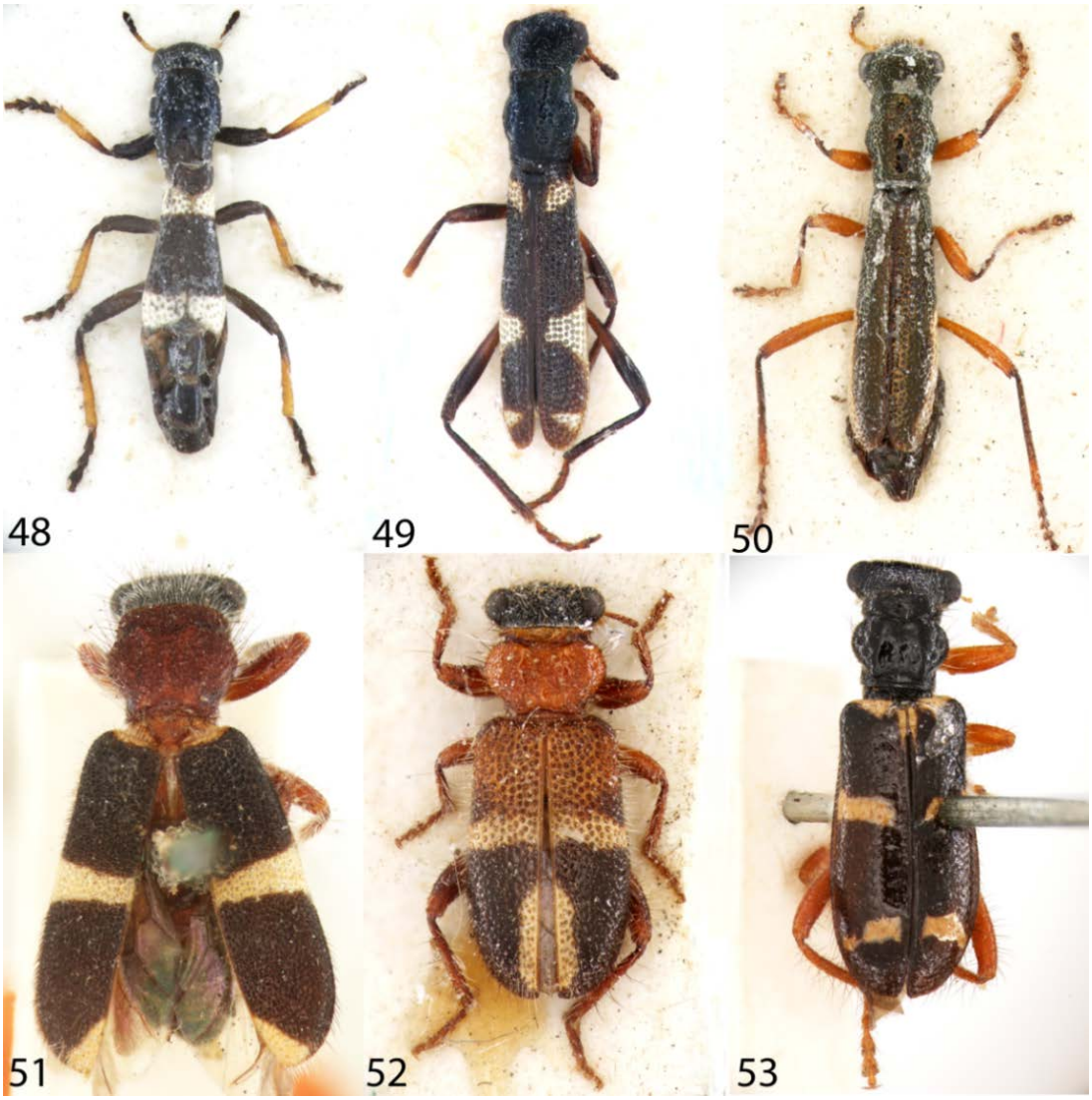
Figures 2.33-2.36. Fig. 2.33) *Phyllobaenus vitrinus* (Gorham), Lectotype (BMNH); **Fig. 2.34)** *P. vitrinus* (Gorham), Paralectotype (BMNH); **Fig. 2.35)** *Isohydnocera cryptocerina* (Gorham), Lectotype [left] and Paralectotype [right] (BMNH); **Fig. 2.36)** *I. cryptocerina* (Gorham), Paralectotype (BMNH).



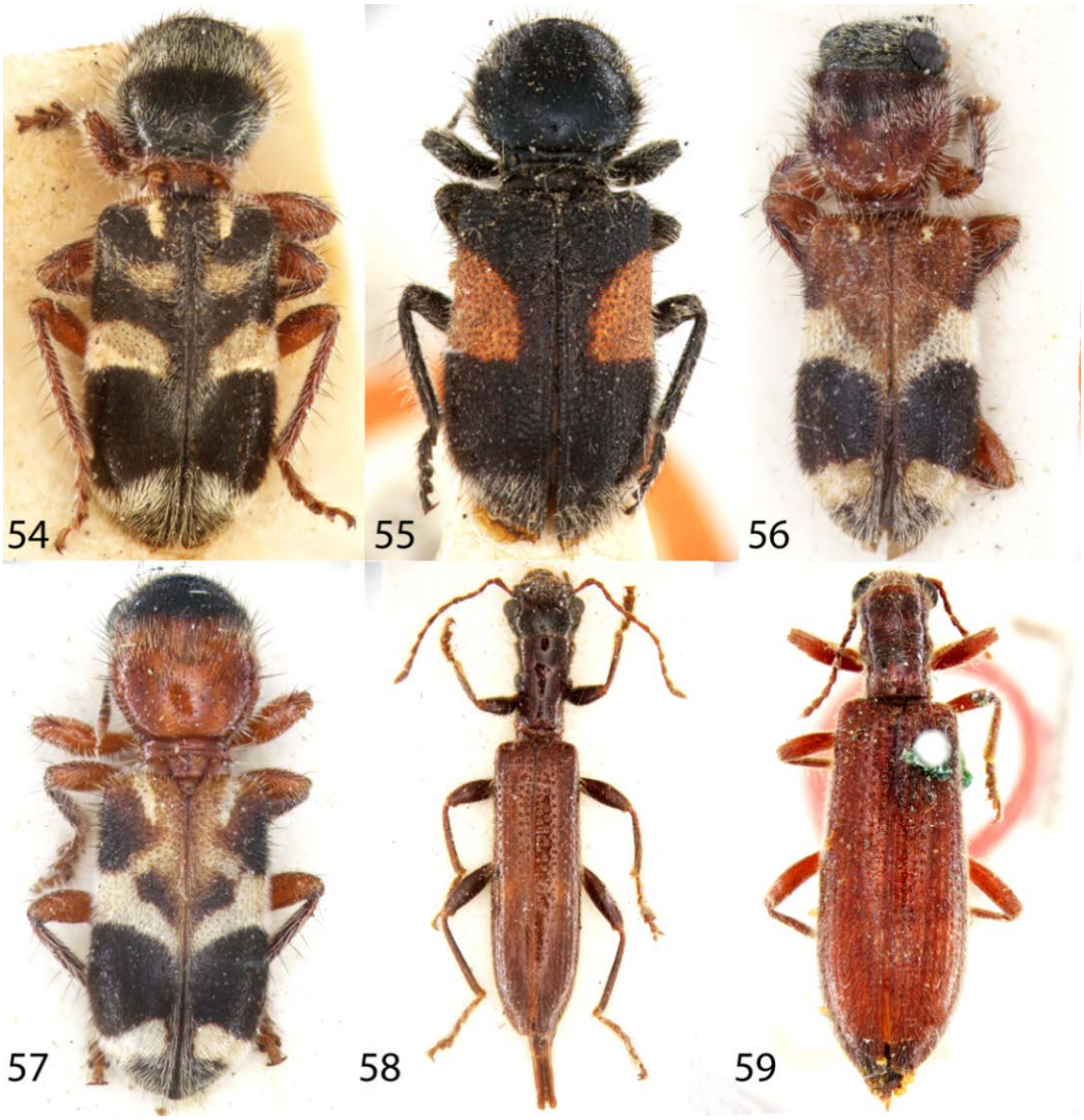
Figures 2.37-2.41. Fig. 2.37) *Isohydnocera aegra* (Newman), Holotype (BMNH); **Fig. 2.38)** *I. curtipennis* (Newman), Lectotype [left] and Paralectotype [right] (BMNH); **Fig. 2.39)** *Parmius debilis* Sharp, Lectotype (BMNH); **Fig. 2.40)** *P. debilis* Sharp, Paralectotype (BMNH); **Fig. 2.41)** *Paupris aptera* Sharp, Lectotype (BMNH).



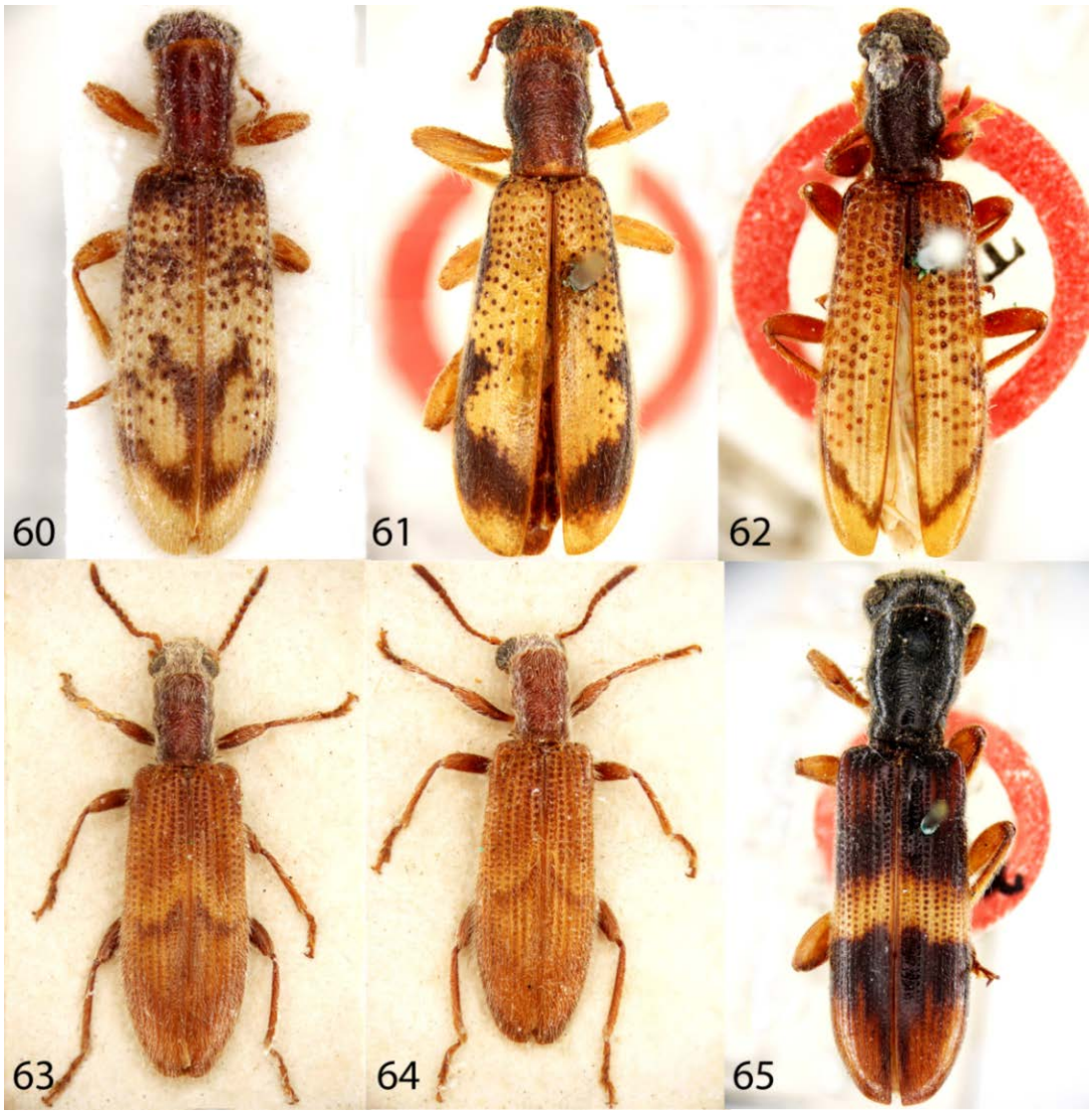
Figures 2.42-2.47. Fig. 2.42) *Isolemidia apicalis* (Gorham), Lectotype (BMNH); **Fig. 2.43)** *I. batesi* (Gorham), Lectotype (BMNH); **Fig. 2.44)** *I. pulchella* (Gorham), Lectotype (BMNH); **Fig. 2.45)** *I. subtilis* (Gorham), Lectotype (BMNH); **Fig. 2.46)** *I. subviridis* (Gorham), Lectotype (BMNH); **Fig. 2.47)** *I. virescens* (Gorham), Lectotype (BMNH).



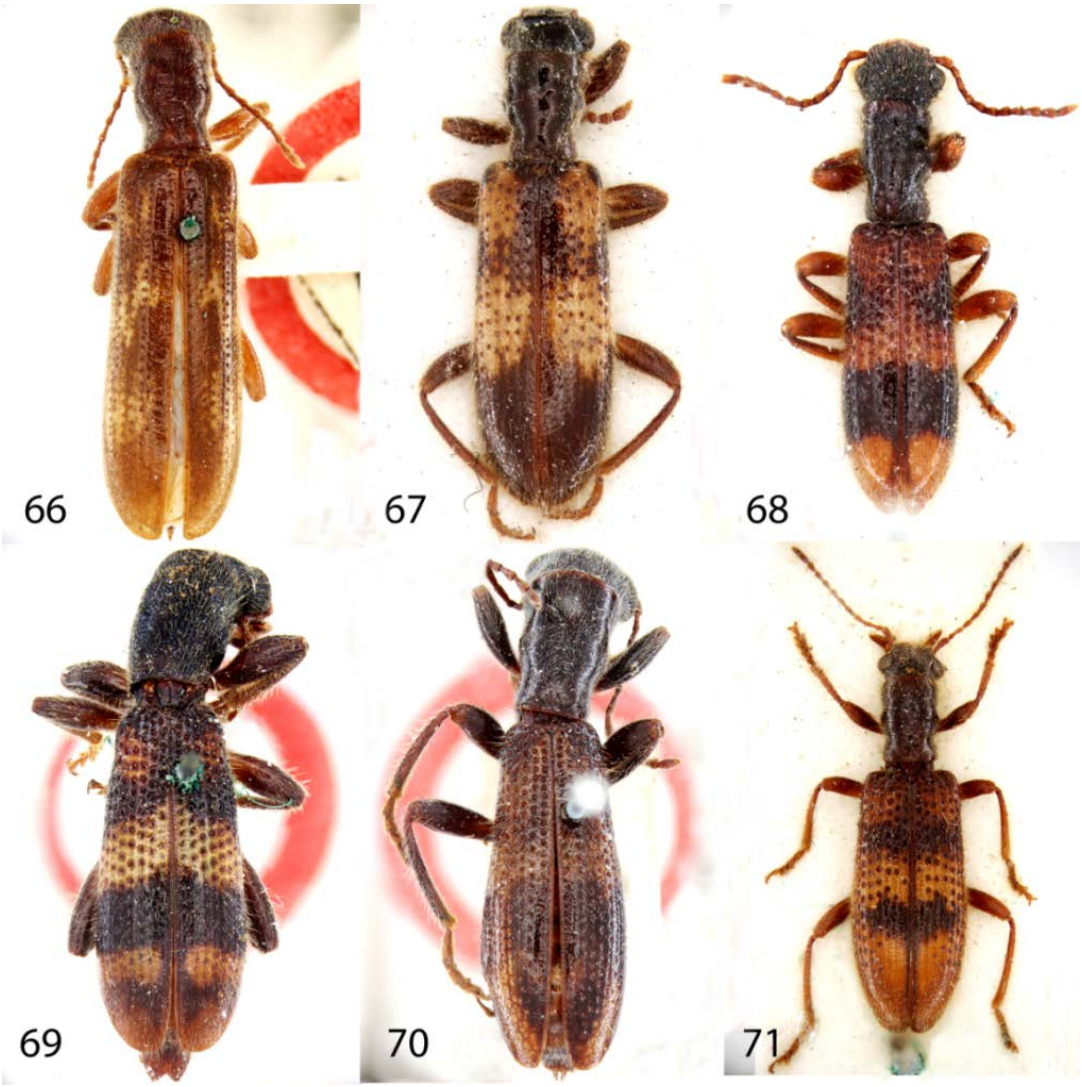
Figures 2.48-2.53. Fig. 2.48) *Allelidea brevipennis* Pascoe, Lectotype (BMNH); **Fig. 2.49)** *A. ctenostomoides* Waterhouse, Paralectotype (BMNH); **Fig. 2.50)** *A. viridis* Blackburn, Lectotype (BMNH); **Fig. 2.51)** *Blaesiophthalmus accinctus* (Newman), Lectotype (BMNH); **Fig. 2.52)** *B. variegatus* (Blackburn), Lectotype (BMNH); **Fig. 2.53)** *Lemidia nitens* (Newman), Holotype (BMNH).



Figures 2.54-2.59. Fig. 2.54) *Enoclerus cautus* (Gorham), Paralectotype (BMNH); **Fig. 2.55)** *E. hogei* (Gorham), Holotype (BMNH); **Fig. 2.56)** *E. puellus* (Gorham), Lectotype (BMNH); **Fig. 2.57)** *E. x-album* (Gorham), Paralectotype (BMNH); **Fig. 2.58)** *Cymatodera championi* (Gorham), Lectotype (BMNH); **Fig. 2.59)** *C. sericans* (Gorham), Holotype (BMNH).



Figures 2.60-2.65. Fig. 2.60) *Cymatodera angulifera* (Gorham), Paralectotype (BMNH); **Fig. 2.61)** *C. flexuosa* (Gorham), Holotype (BMNH); **Fig. 2.62)** *C. liturata* (Gorham), Lectotype (BMNH); **Fig. 2.63)** *C. lunulata* (Gorham), Paralectotype (BMNH); **Fig. 2.64)** *C. lunulata* (Gorham), Lectotype (BMNH); **Fig. 2.65)** *C. hogei* (Gorham), Lectotype (BMNH).



Figures 2.66-2.71. Fig. 2.66) *Cymatodera grandis* (Gorham), Lectotype (BMNH); **Fig. 2.67)** *C. nitida* (Gorham), Lectotype (BMNH); **Fig. 2.68)** *C. parallela* (Gorham), Paralectotype (BMNH); **Fig. 2.69)** *C. grossa* (Gorham), Lectotype (BMNH); **Fig. 2.70)** *C. valida* (Gorham), Lectotype (BMNH); **Fig. 2.71)** *C. saturata* (Gorham), Lectotype (BMNH).

CHAPTER 3: A MOLECULAR PHYLOGENY OF THE CHECKERED BEETLES AND A DESCRIPTION OF EPICLININAE *SUBFAM. NOV.* (COLEOPTERA: CLEROIDEA: CLERIDAE)

3.1 Introduction

The superfamily Cleroidea is a lineage of primarily predatory, though primitively fungivorous, beetles presently regarded as sister-group to Cucujoidea (Kolibáč 1997; Leschen 2010). The most recent treatment of Cleroidea lists 11 families containing 10,224 species and 573 genera (Leschen 2010). Bocakova et al. (2011) recognised three additional families (Malachiidae, Dasytidae and Rhadalidae) within a so-called 'melyrid lineage'; while Opitz (2010) rejected the family status of Thanerocleridae and Metaxinidae. Kolibáč (2004) assigned 15 families to four major cleroid lineages: melyrid, trogossitid, clerid and thaneroclerid. Phylogenies based on adult and/or larval morphology revealed the monophyly of a combined thaneroclerid (i.e. Thanerocleridae, Chaetosomatidae and Metaxinidae) + clerid (Cleridae) lineage with the former either sister to the latter (Beutel & Pollock 2000) or nested within it (Lawrence et al. 2011).

Cleridae is the second largest cleroid family (after Melyridae) with approximately 3,500 species and 300 genera (Gerstmeier 2000) whereas Thanerocleridae only comprises approximately 30 species in seven genera. Both Cleridae and Thanerocleridae are widespread in all non-Antarctic continents with highest diversity in the tropics. Most adult and larval checkered beetles are predatory: their larvae feed on xylophagous insects in their tunnels, immature Hymenoptera in nests or hives and a range of invertebrate eggs and pupae. Adults are agile hunters of beetles and other insects under bark, on felled timber and on foliage or flowers (Champlain 1920; Linsley and MacSwain 1943; Clancy 1946; Mamayev 1978; Mawdsley 2002; Bartlett 2009). Though numerous anthophilous clerids (mainly Clerinae) hunt other flower-visiting insects, adults of the Australian genus *Eleale* Newman, and southern South American genera, *Calendyma* Lacordaire and *Epiclines* Chevrolat, appear to be specialized pollen and nectar feeders (Crowson 1964; Opitz 2002; Solervicens 2007).

The history of Cleridae systematics can be traced primarily through the contributions of Spinola (1841, 1844), Lacordaire (1857), Gahan (1910), Chapin (1924), Böving and Craighead (1931), Crowson (1955, 1964), Winkler (1964, 1980), Kolibáč (1992, 1997, 1998, 2004) and Opitz (2009, 2010). Largely based on the classification of Chapin (1924), with the inclusion of Tarsosteninae, the eight subfamily system of Crowson (1964) has been, until recently, the most widely accepted hypothesis of clerid subfamilies. Crowson's system included Thaneroclerinae, Tillinae, Phyllobaeninae (junior synonym of the currently valid Hydnocerinae), Clerinae, Epiphloeinae, Enopliinae, Tarsosteninae and Corynetinae (a misspelling of Korynetinae). Three authors have worked on clerid systematics since Crowson. Winkler (1964, 1980, 1982) erected two new subfamilies and proposed a system of neutral terms as an interim measure to show relatedness among higher taxa, though none of his concepts were followed. The morphology-based classifications of Kolibáč (1992, 1997) and Opitz (1997, 2009, 2010) represent two recent, and opposing, subfamily hypotheses.

Employing Transformation Series Analysis methods (Mickevich 1982; Buckup & Dyer 1991), Kolibáč (1997) grouped all clerid taxa with a reduced fourth tarsomere under Korynetinae (synonymising with it Tarsosteninae, Enopliinae and Epiphloeinae) and assigned family-status to the clerid subfamily Thaneroclerinae (Kolibáč 1992). The resulting classification, consisting of Tillinae, Hydnocerinae, Clerinae and Korynetinae, was based on transformation series of pronotal shape, tarsus, antenna, tegmen and wing venation characters. Only Korynetinae was defined by an autapomophy (reduction in size of the fourth tarsomeres) while tentative synapomorphies were proposed for Hydnocerinae (larvae with endocarina absent and frontal arms U-shaped) (Kolibáč 1997). This classification is followed in the recent Handbook of Zoology, Coleoptera (Leschen, 2010).

Opitz (2009, 2010), erected an additional three subfamilies and attributed subfamily rank to the Isoclerini (of Thanerocleridae), recognised 12 subfamilies (Thaneroclerinae, Isoclerinae, Hydnocerinae, Anthicoclerinae, Tillinae, Clerinae, Epiphloeinae, Tarsosteninae, Peloniinae, Enopliinae, Neorthopleurinae, Korynetinae). Several subfamily-defining character-states, treated as synapomorphies in Opitz' (2010) data matrix, within the taxon descriptions, are qualified with statements such as "most

genera" and "almost always", for example, metacoxae with carina for Tillinae and furcal lamina [of metendosternite] absent in Epiphloeinae, while another, "pronotal commissure partially developed", is only revealed as synapomorphic because the states of the character "extent of development of pronotal commissure" are scored in a non-linear way, i.e.: 23(0) not developed, 23(1) partially developed; 24(0) not developed, 24(1) fully developed. Opitz' classification differs from Kolibáč's mainly in the following ways (see Fig 3.1): Thaneroclerinae (incl. Zenodosinae) and Isoclerinae = Thanerocleridae *sensu* Kolibáč 1992; Anthicoclerinae includes genera hitherto assigned to Clerinae; Epiphloeinae, Tarsosteninae, Peloniinae, Enopliinae, Neorthopleurinae and Korynetinae = Korynetinae *sensu stricto* (after Kolibáč).

Despite these differences in higher classification, the morphology-based phylogenies presented by Kolibáč (1992, 1997) and Opitz (2010) are relatively congruent, with the exception of the position of Anthicoclerinae (Fig. 3.1). However, these analyses are weighted towards the characters used as taxonomic discriminators between lineages and do not provide an unbiased assessment of the phylogenetic relationships. To date, no comprehensive molecular phylogeny of the clerid lineage has been attempted. Hunt et al. (2007) included 22 species of clerids and no thaneroclerids in the phylogeny of beetles and a sister group relationship is recovered between the Cleridae and Melyridae with Trogossitidae forming a grade at the base of the Cleroidea. Here we present the first molecular phylogeny of the checkered beetles to examine higher level systematics while attempting to resolve the relationships among subfamilies. This study complements the recent molecular phylogeny of the melyrid lineage (Bocakova et al. 2011).

3.2 Materials and Methods

This work was done in collaboration with Nicole L. Gunter (CSIRO, Ecosystem Sciences, Canberra, ACT, Australia), Eric G. Chapman (Department of Entomology, University of Kentucky, Lexington, Kentucky, U.S.A.), Justin S. Bartlett (Queensland Primary Industries Insect Collection, Biosecurity Queensland, Brisbane, Queensland, Australia) and Stephen L. Cameron (Earth, Environment & Biological Sciences School,

Queensland University of Technology, Brisbane, Queensland, Australia). Gunter and Cameron did all molecular work for the Australian taxa and shared the writing and analytical workload. I did the molecular work, sequence assembly and editing for the non-Australian taxa, and part of the analytical workload under the tutilege of Chapman, who also assisted with writing. Bartlett provided assistance with writing and assumed the primary role in the description of the new subfamily and identifying synapomorphies for major clades recovered in our analyses. The majority of all work was equally shared by Gunter and I.

In total, 148 species representing 70 genera of the clerid lineage were collected from all continents except Antarctica and preserved in 96% undenatured ethanol. Taxon sampling included species from all six subfamilies accepted by Kolibáč (1997) and 10 of 12 subfamilies accepted by Opitz 2010 (Table 1). Other members of Cleroidea were included as outgroups. The total data set included 193 taxa representing 11 of 13 cleroid families. A list of taxa, localities, code names, voucher location, and GenBank accession numbers is provided in Gunter et al. (2013; Table S1, S2).

3.2.1 ***DNA amplification and gene sequencing***. DNA was extracted from the head and thorax of specimens using a QIAGEN DNeasy tissue kit as per standard protocols. The mitochondrial genes, 16S rDNA, 12S rDNA and cytochrome *c* oxidase subunit I (COI), and the nuclear gene, 28S (LSU) rDNA, were amplified. A ~1,350 bp fragment spanning partial 16s, tRNA Val and 12S was amplified as a single fragment with the primers '16c' and '12sB' but in some cases was amplified in two smaller fragments using the primer pairs '16c' to '16z' and '16y' to '12sB'. Alternatively, a smaller partial 16s sequence was generated using the primers 'LR-N-13398' and 'LR-J-12887'. COI was amplified in 2 smaller fragments using the primer pairs 'LCO-1490' to 'HCO-700ME' and 'Jerry' and 'Pat' to produce a 1,500 bp fragment. Partial 28s sequences were also generated using 2 alternative primer pairs 'D1F' to 'D6R' and '28Sdd' to '28Sff', spanning ~1,300 and ~800 bp respectively to create a fragment spanning ~1,700 bp. Primer sequences and references are listed in Table 3.1.

Amplification and sequencing was carried out in two labs. Australian specimens were processed in the Australian National Insect Collection molecular systematics

laboratory (by Gunter) as follows: amplifications were carried out using 1U Taq polymerase (iStar HotStart Taq DNA Polymerase, Scientifix DNA Polymerase), 25 μM each dNTP, 0.1 μM each primer and 1 μL of template in 25 μL reaction volume. Typical PCR reactions (using the primers not specified below sequenced at the University of Kentucky; by me) were performed under the following conditions: 2 minutes at 94°C for initial denaturation, 1 minute at 94°C, 1 minute at 45°C, 1.5–2 minutes (depending on the length of the amplifying fragment) at 72°C for 40 cycles and 10 minutes at 72°C for final extension. PCR products were purified using EXOSAP-it (Affymetrix). Cycle sequencing reactions were performed using the BigDye Terminator v. 1.1 Cycle Sequencing Kit, the products of which were purified by alcohol precipitation and sent to JCSMR for sequencing. Sequences were edited by Gunter using Sequencher (v. 4.5; Gene Codes Corporation, Ann Arbor, MI, USA). All non-Australian specimens were amplified at the Advanced Genetic Technologies Center (AGTC), College of Agriculture, University of Kentucky as follows: amplifications were carried out using 0.25 μL TakaraEx Taq polymerase (Recombinant Taq DNA polymerase, Takara Bio Inc.), 2.5 μM of each dNTP, 0.1 μM of each primer, and 2 μL of template DNA in 50 μL reactions. PCR reactions were performed under the following conditions: 1 minute at 94°C for initial denaturation, 50 seconds at 94°C, 45 seconds at 40°C, 45 seconds at 72°C for 50 cycles for 16S (LR-N-13398 & LR-J-12887); 1 minute at 94°C for initial denaturation, 45 seconds at 94°C, 45 seconds at 60°C, 60 seconds at 72°C for 50 cycles for 28S (D1F & D6R); 1 minute at 94°C for initial denaturation, 45 seconds at 94°C, 45 seconds at 40°C, 45 seconds at 72°C for 50 cycles for COI (LCO-1490 & HCO-700ME). Amplification of PCR products were purified and sequenced by AGTC using the ABI Big-Dye Terminator mix v. 3.0. Bidirectional sequences were aligned to form contigs and edited using Geneious (v5.6; Drummond et al. 2012). All sequences were deposited in the publicly accessible database GenBank (Gunter et al. 2013; Table S2).

3.2.2 ***Multiple alignment and phylogenetic analysis***. Sequences of each of the four genes were aligned separately using default parameters of MUSCLE in Geneious (v. 5.6; Drummond et al. 2012). Each alignment was edited by eye before concatenation of the

dataset spanning ~5,000 nt. Only specimens with genetic data from at least two genes were included in the analyses.

The program PartitionFinder (Lanfear et al. 2012) was used to determine the best partitioning strategy and nucleotide substitution models for the analysis. The optimal partitioning scheme divided the data into six partitions, separating the genes but joining tRNA Val and 12S, and further subdividing the separate codon positions of COI. However, other partitioning strategies were also tested. Bayesian Inference was conducted using MrBayes 3.2.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Each analysis consisted of 30 million generations with a random starting tree, and two simultaneous runs with four Markov chains sampled every 1000 generations were conducted with unlinked partitions. Stationarity in MCM chains was determined in Tracer (Rambaut & Drummond 2007), and burn-in was set appropriately. A majority-rule consensus tree was obtained from the two combined runs to establish the posterior probabilities of clades. Maximum-likelihood (ML) analyses were performed using the RaxML blackbox cluster on the CIPRES portal and the same four partitioning strategies.

3.3 Results

3.3.1 ***DNA data and alignment.*** The lengths of the amplified fragments varied from 707 to 1503 bp for COI, 506 to 1616 bp for 16S (sometimes in combination with tRNA and 12S) and 564 to 1504 bp for 28S. The total length of the concatenated data set was 4958bp. Base frequencies were almost equal in the nuclear gene 28S (A = 23.1, C = 25.9, G = 31.7, T = 19.3), whereas the mitochondrial genes 16S (A = 42.5, C = 12.0, G = 6.0, T = 39.4), tRNA Val (A = 43.4, C = 9.8, G = 5.1, T = 41.8), 12S (A = 38.9, C = 15.0, G = 7.8, T = 38.3) and COI (A = 31.3, C = 15.9, G = 14.2, T = 38.6) showed a higher A-T bias. The full data set consisted of 70 genera with sequence data for at least two genes and comprised 157 16S sequences with 84 extending downstream to 12s, 175 28S sequences and 116 COI sequences. Included in this dataset were 185 taxa representing both families, Cleridae and Thanerocleridae *sensu* Kolibáč within the clerid lineage, all six subfamilies accepted by Kolibáč (1997) and 10 of 12 subfamilies accepted by Opitz

(2010). The remaining 34 taxa represented outgroups within the superfamily Cleroidea (Gunter et al. 2013; Table S1).

3.3.2 ***Phylogenetic inference.*** PartitionFinder selected six partitions (28S, 16S, tRNA Val + 12S, COI 1st codon, COI 2nd codon and COI 3rd codon positions) as the optimal partitioning scheme, with nucleotide substitution model GTR+I+G for all genes/codon positions. However, analyses using different partitioning strategies were also performed on the concatenated data sets (Table 3.2) to test if partitioning strategy had significant influence on topology.

The resulting topologies were nearly identical with well-supported family and subfamily level clades recovered in both Bayesian (Fig. 3.2) and Maximum Likelihood analyses. Tree topologies only varied with placement of early diverging taxa within several poorly supported clades and are indicated by a star in Fig. 3.2. For example, the position of *Tilloidea transversalis* (Charpentier) at the base of the Tillinae was moderately supported (PP 0.87) in the optimal partitioning scheme yet in all other partitions tested this relationship was not recovered. Although there was always strong support for the monophyly of Tillinae, a partially resolved polytomy was recovered which always supported *Monophllya terminata* (Say) + *Cylidrus centralis* Pascoe, and *Cladiscus obeliscus* Lewis + *Tillus elongatus* (Linnaeus) with varying relationships between other taxa. The weakly recovered relationship (PP 0.55) between *Tarsostenodes* Blackburn + *Blackburniella* Chapin and *Thriocerodes* Wolcott & Dybas in Fig. 3.2 was not recovered in all analyses. Instead a weakly supported relationship between *Tarsostenodes* + *Blackburniella* and *Apteropilo* Lea was recovered in the "by gene" partition, otherwise an unresolved polytomy consisting of *Tarsostenodes* + *Blackburniella, Thriocerodes* and *Apteropilo* was recovered. Occasionally weakly supported relationships were recovered between the clerine clades that include *Ctenoclerus* Solervicens + *Priocera* Kirby and *Natalis* Laporte, *Eunatalis* Schenkling + *Metademius* Schenkling; the phylogenetic position of *Dermestoides* Schaeffer was resolved at the base of the larger clade within the Korynetinae; or the position of *Neoscrobiger* Blackburn and *Enoclerus nigripes* (Say) was not resolved. Regardless of these minor differences, the resulting trees always supported the monophyly of the clerid

lineage as a whole. The Thanerocleridae was recovered as a monophyletic lineage within the paraphyletic Cleridae supporting the classification system of Opitz (2010) that "Thanerocleridae" represents a subfamily within the Cleridae. The Thaneroclerinae *sensu* Opitz was rendered paraphyletic by the inclusion of Isoclerinae *sensu* Opitz. In my analyses, the clerid lineage was divided into five main clades: (i) Tillinae, (ii) Thaneroclerinae, (iii) "Clerinae" taxa *Eleale* + *Epiclines* + *Cleromorpha* Gorham, (iv) Korynetinae *sensu* Kolibáč (1997), (v) remaining Clerinae + Hydnocerinae.

3.4 Discussion

Here we present the first multi-gene phylogeny of the clerid lineage to assess relationships between the major groupings and to address the current issues regarding higher classification. The monophyly of the clerid lineage was recovered in all analyses but interfamily relationships within the Cleroidea could not be fully resolved. The melyrid lineage consisting of the families Rhadalidae, Mauroniscidae, Prionoceridae, Melyridae, Dasytidae and Malachiidae was also recovered as monophyletic, consistent with the phylogeny of Bocakova (2011). However, Dasytidae was rendered paraphyletic by the inclusion of *Falsomelyris opaca* Schilsky, the only melyrid in the analyses. This result is likely to be an artefact of limited taxon sampling within the melyrid lineage as Bocakova (2011) recovered strongly supported monophyletic family level clades. The family Trogossitidae was never recovered as a monophyletic lineage which is congruent with previous morphological and molecular evidence (Beutel and Pollock 2000; Hunt et al. 2007).

The classification system of Kolibáč (1997) treated Thanerocleridae as a family containing two subfamilies (Thaneroclerinae and Zenodosinae) while Opitz (2010) proposed that Thaneroclerinae and Isoclerinae represented two distinct subfamilies within the Cleridae. Molecular data provided strong evidence in favour of Opitz' (2010) view that the thaneroclerids should be a subfamily within the Cleridae. Whether this lineage represents two distinct subfamilies remains debatable. Preliminary evidence based on sequences from only 3 of 7 genera (*Isoclerus* Lewis, *Thaneroclerus* Lefèbvre and *Zenodosus* Wolcott) provided some evidence for the division into Zenodosinae and

Thaneroclerinae proposed by Kolibáč (1997), whereas Opitz' (2010) conception of the Thaneroclerinae was rendered paraphyletic by the Isoclerinae. Further, Kolibáč (1992; before proposing subfamilies) believed that Zenodosini represented the basal lineage while Isoclerini and Thaneroclerini were derived sister lineages, which was supported by my molecular data.

Analyses recovered the Tillinae as sister to the remaining Cleridae, a relationship that has not previously been proposed. Previous morphology-based phylogenies recovered the Thaneroclerinae as sister to the remaining clerids whereas the Tillinae was a derived subfamily closely related to the Clerinae. Tillinae is the only clerid subfamily in which the procryptosternum is complete (Opitz 2010). Most members of other families within the Cleroidea (with the exception of the trogossitid subfamily Rentolininae) also have an incomplete procryptosternum (Escalona pers. comm.), so this feature could be considered apomorphic within Cleridae and, as suggested by Opitz (2010), a synapomorphy of Tillinae.

The remaining subfamilies were divided into two main lineages. The first clade contained three monophyletic lineages representing the Thaneroclerinae (including Zenodosinae and Isoclerinae), the Korynetinae *sensu* Kolibáč (1997) and a novel clade composed of the clerine genera *Eleale, Cleromorpha* and *Epiclines*. The second major lineage contained all hydnocerines and the remaining clerines, with neither subfamily recovered as a monophylum.

One of the most significant differences between the classification systems of Opitz (2010) and Kolibáč (1997) is the division by the former of the Korynetinae into multiple subfamilies. Under Kolibáč's system, the subfamilies Epiphloeinae, Tarsosteninae, Peloniinae, Enopliinae, Neorthopleurinae and Korynetinae would be classified as a single subfamily Korynetinae. DNA sequences are available for 21 genera in this lineage representing all subfamilies *sensu* Opitz except Enopliinae. The Korynetinae *sensu* Kolibáč was here recovered as monophyletic with strong support, and is also supported morphologically by the synapomorphic reduction of the fourth tarsomere. Of Opitz' (2010) "korynetine" subfamilies, only the Epiphloeinae was recovered here as monophyletic, while the Tarsosteninae, Peloniinae and Neorthopleurinae were recovered as para- or polyphyletic with Opitz' more restricted

Korynetinae represented by just two genera (*Necrobia* Olivier and *Opetiopalpus* Spinola). Taxon sampling within several of Opitz' (2010) subfamilies was limited relative to their overall diversity so it may be premature to reject this classification. However, our molecular results are currently more congruent with the higher classification system of Kolibáč (1997) wherein the korynetines represent a single subfamily.

Our results also suggest that neither Clerinae nor Hydnocerinae represent monophyletic lineages. Instead two clades containing hydnocerines are nested within a grade of clades containing most of the Clerinae (excluding *Eleale, Cleromorpha* and *Epiclines*). Historically, the Hydnocerinae has been divided into three tribes: Callimerini, Hydnocerini and Lemidiini (Kolibáč 1998). The tribes Callimerini and Hydnocerini were recovered as monophyletic lineages while Lemidiini was recovered as polyphyletic. Molecular evidence supported a close relationship between *Lemidia* Spinola (Lemidiini) and Hydnocerini while Callimerini + *Eurymetopum* Blanchard (Lemidiini) formed a closer relationship with the clerine species *Orthrius sepulcralis* (Westwood) and *Opilo whitei* Gorham.

Opitz' (2010) findings indicated that Hydnocerinae and Clerinae (plus Anthicoclerinae) both possess two secondary stomodaeal valve lobes (Tillinae and Thaneroclerinae have four, and Korynetinae *sensu lato* lack them entirely). In terms of the present results (Fig. 3.2), this distribution of secondary valves among higher taxa suggests that the ancestral character state is four lobes with independent reductions in the clerine/hydnocerine and korynetine lineages. The reduction from four to two secondary valves observed in the clade Clerinae + Hydnocerinae (see Opitz 2010) is therefore synapomorphic for this group (which would also include Anthicoclerinae if it were resurrected from synonymy with Clerinae – see Bouchard et al. 2011). Despite this, and as we are not yet able to formally recognise additional suprageneric groupings within Clerinae, we consider it premature to make any systematic change to the higher classification of this lineage until more comprehensive investigations (molecular or otherwise) into this clade are undertaken.

Preliminary investigations by Opitz (2003) into the phylogenetic significance of morphological traits associated with anthophyly (flower visiting) among clerine genera

suggested that those taxa possessing a mating-plug type of male spermatophore and antennae with peg sensilla (i.e., *Trichodes* Herbst, *Aulicus* Spinola, *Chilioclerus* Solervicens, *Opilo* Latreille, *Dieropsis* Gahan, *Phlogistus* Gorham, *Phlogistomorpha* Hintz, *Scrobiger* Spinola, *Trogodendron* Spinola, *Zenithicola* Spinola and *Balcus* Sharp) constitute a monophyletic group. Of these genera, molecular data from *Trichodes, Opilo, Phlogistus, Phlogistomorpha, Scrobiger, Trogodendron* and *Zenithicola* is included in the present study. Our results support the monophyly of such a grouping and indicate that *Odontophlogistus* Elston, *Olesterus* Spinola and *Neoscrobiger* also belong to that group. Along with the anthophylic genera examined by Opitz (2003), these three genera share with those studied by Opitz (2003) the following character states: tegmen with phallobasic struts fused to phallobasic apodeme, hind wing with closed wedge cell, terminal maxillary palpomeres securiform (if slender then not strictly digitiform) (JS Bartlett, pers obs.). We have not determined whether a mating-plug type of male spermatophore or antennal peg sensilla are present in *Odontophlogistus, Olesterus* and *Neoscrobiger* as the former character requires specially preserved specimens (in Pampel's fluid for example) while scanning electron microscopy is required to view the latter, but molecular results and the additional shared morphological features suggested a monophyletic flower-visiting clade within clerids.

Where possible we also tested the monophyly of clerid genera. Approximately one-quarter of described genera were included in this analysis with 23 represented by multiple species. Of these genera *Isoclerus, Eleale, Apopylus* Kolibáč, *Apteropilo, Omadius* Laporte, *Thriocerodes* and *Trichodes* each formed monophyletic clades containing at least three species. The monophyly of *Tenerus* Laporte, *Megaphloeus* Opitz, *Priocera, Neoscrobiger, Metademius, Trogodendron, Phlogistomorpha* and *Isohydnocera* Chapin was also supported however only two species of each were included. However, the specimen representing *Isohydnocera curtipennis* (Newman) is in fact a taxon wrongly synonymized under an unrelated species of *Phyllobaenus* Dejean and historically misidentified as the quite dissimilar *I. curtipennis* so the relationship observed here does not confirm the monophyly of *Isohydnocera*. *Eunatalis* and *Phlogistus* were rendered paraphyletic by the inclusion of *Metademius* and *Phlogistomorpha* respectively and the relationship between *Callimerus* Gorham and

Brachycallimerus Chapin remained unresolved. Six *Lemidia* species formed a strongly supported clade to the exclusion of *Lemidia hilaris* (Newman) which formed a weakly supported relationship with the genera of Hydnocerini. *Opilo whitei* formed a close relationship with *Orthrius sepulcralis* as sister group to the Callimerini + *Eurymetopum*, while *Opilo congruus* Newman and *Opilo* sp. 1 were closely related forming a strongly supported relationship with *Olesterus* and *Odontophlogistus*. *Enoclerus* Gahan, *Stigmatium* Gray and *Phyllobaenus* were paraphyletic. Three species of *Clerus* Geoffroy, the type genus of the family, were included in the analysis and a monophyletic lineage was not supported. Instead, *Clerus gilberti* (White), *C. mutillaecolor* (White) and *C. mutillarius* Fabricius (plus a single unidentified *Cardiostichus* sp.) are dispersed amongst a strongly supported clade containing 14 species of *Stigmatium*. Gerstmeier (2002) highlighted the similarity between *Clerus* and related genera while outlining his informal *Stigmatium*-, *Thanasimus*- and *Omadius*-groups, and transferred several *Stigmatium* species to *Clerus* (including *C. gilberti* and *C. mutillaecolor* of this study). Gorham (1894) was quick to criticise Kuwert's (1894) generic revision of the incredibly diverse, and taxonomically confounding, '*Stigmatium* complex'. It is clear that the genus-level taxonomy remains largely 'artificial' and that many lower level systematic boundaries require extensive investigation. Genetic data promises to provide *a posteriori* information to untangle the complexes of species/genera and provide a more natural classification.

The systematics of the Cleridae should be revised to reflect molecular data. Currently 113 genera are classified within the subfamily Clerinae, of which only 30 are included in the present phylogeny (Fig. 3.2). Certainly this molecular evidence suggests at least three genera do not belong within the Clerinae and that the lineage that contains the 'clerine' genera *Eleale*, *Cleromorpha* and *Epiclines* represents a new subfamily. The genus *Calendyma* has previously been considered closely related to *Epiclines* (Gahan 1910, Solervicens 2007) and to *Eleale* (Crowson 1964, Solervicens 2007). Most significantly, Solervicens' (2007) illustrations of the reproductive organs of *Calendyma, Epiclines* and *Eleale* demonstrated that these genera all have a particular form of tegmen in which the phallobasic apodeme is long and connected to the phallobase by a membrane, and the parameres are generally lobate and weakly sclerotized. In relation to this kind of tegmen, parallels may be found with the tegmina of *Tarsostenodes*

(Korynetinae) (regarding the lobate form of the parameres) or in those of *Eunatalis* and *Eurymetomorphon* Pic (Clerinae) (regarding the long apodeme). Kolibáč (1997) indicated that this "tegmen in two parts" was unique within Clerinae. Bartlett examined dissected tegmina of all four genera in question, confirming that all possess the abovementioned characteristics, although the membranous connection of apodeme to phallobase is transparent in *Eleale* and *Cleromorpha*, and pigmented in *Epiclines* and *Calendyma*. These genera also possess a spicular fork with an isolated longitudinal intra-spicular plate; a development known in all Korynetinae *sensu lato* (Opitz 2010) and in the tilline genus *Cylidrus* Latreille (JS Bartlett, pers. obs.). These morphological affinities provide further evidence that a new subfamily is warranted.

3.4.1 Epiclininae, subfam. nov.

Type genus. *Epiclines* Chevrolat, 1838.

Differential diagnosis. Within Cleridae only the genera of Epiclininae can be defined by the following characters in combination: 2-2-2 tibial spur formula; 4-4-4 tarsal pulvillar formula; tarsal claw without basal denticle; eyes finely facetted and deeply emarginated; elytral punctation non-striate; male tegmen with long apodeme membranously connected to phallobase.

Description. ***Head***. Eyes finely facetted, emarginate; labium with terminal palpomeres securiform; maxillae with terminal palpomeres digitiform, lacinae longer (*Calendyma*) or shorter (*Epiclines, Eleale, Cleromorpha*) than palpi; frons slightly extended anteriorly (except *Cleromorpha*); clypeal anterior margin straight or weakly curved (not strongly concave); gular sutures convergent basally, sub-parallel anteriorly, gular process consisting of a pair of well-separated nodes; antennae 11-segmented, flagellum graduating in thickness from segment three or eight, terminal segments often forming a compact (*Eleale, Cleromorpha, Calendyma*) or loose (*Epiclines*) club. ***Thorax***. Prothorax subparallel or rounded laterally, without distinct lateral tubercles or baso-lateral pits; subapical depression indistinct medially; basal collar shallow or indistinct; procoxal cavities closed (*Eleale, Cleromorpha*) or open (*Calendyma, Epiclines*). Elytra punctate or not, when present punctations not striate; hindwing with wedge cell closed basally. Tibiae longitudinally carinate (*Eleale*) or not carinate

(*Cleromorpha*, *Epiclines*, *Calendyma*); tibial spur formula 2-2-2; tarsomere formula 5-5-5, fourth tarsomere not cylindrically diminished, meta-basitarsi long or short; tarsal pulvillar formula 4-4-4 (pulvilli of *Cleromorpha* less lobate); claw simple, without basal denticle. ***Abdomen***. Six visible sternites. Tegmen with long apodeme (at least half tegminal length), phallobasic struts not confluent with apodeme, parameres broad lobe-like (less so in *Cleromorpha*), membranous connection of phallobase to apodeme at least partly transparent (*Eleale*, *Cleromorpha*) or not transparent (*Calendyma, Epiclines*); spicular fork with long apodeme and isolated longitudinal intraspicular plate. Synapomorphies. Not known. The most obvious apomorphic morphological characteristics observed within the group (i.e., elongated lacinae, tegmen with transparent membrane connecting phallobase with apodeme) are not evident among all included taxa. Synapomorphous character-states may be revealed if the morphology of the group were thoroughly reviewed.

Included taxa. Seventy described species are currently recognized as valid. They are assigned to four genera: *Epiclines* Chevrolat, 1838 (7 spp.), *Calendyma* Lacordaire, 1857 (3 spp.), *Eleale* Newman, 1840 (59 spp.) and *Cleromorpha* Westwood, 1853 (1 sp.). Distribution. *Eleale* and *Cleromorpha* are endemic to Australia (*Cleromorpha* being absent from Tasmania) while *Epiclines* and *Calendyma* occur in Chile and Argentina (Corporaal 1950). The distribution of Epiclininae *subfam. nov.* implies a southern Gondwanan origin. Fossil representatives are not known (Opitz 2007).

Comments. The issue of authority of the newly proposed subfamily, Epiclininae, requires explanation. The name was first used by Crowson (1964: 311), who wrote "The Phyllobaeninae were until recently known as Hydnocerinae, while the name Epiclininae is now applied to what were called Phyllobaeninae". For the following reasons it is clear that Crowson's Epiclininae can be considered a **lapsus calami** and that he was actually referring to Epiphloeinae: 1) The taxon Epiphloeinae is currently applied to what was once referred to as Phyllobaeninae (Corporaal 1950: 2) there is no mention of Epiclininae in his key to subfamilies, but Epiphloeinae is included; 3) on page 312 he writes "the entirely American Epiclininae" - the only New World-restricted clerid higher taxon is Epiphloeinae; 4) Crowson does not formally propose Epiclininae as a new subfamily, or mention the genus *Epiclines* Chevrolat, in his paper. Regardless of Crowson's intention,

Epiclininae Crowson would be considered available if it qualified in accordance with the Code. Availability of a family-group name is dependent on whether the name of its type genus can be considered to have been valid in the new family-group taxon at the time of its formation (ICZN 2000). Article 11.7.1.1 states that, unless there is evidence to the contrary, the use of the stem Epiclin- alone is evidence that Crowson considered *Epiclines* to be valid within 'Epiclininae'. The fact that *Epiclines* Chevrolat was placed in Clerini by Lacordaire (1857), and has since been associated with only Clerinae (Gahan 1910, Corporaal 1950, Solervicens 1973), provides evidence to the contrary. Furthermore, Crowson could not have based Epiclininae on *Epiclines* **[**sensu**]** Spinola, which Wolcott (1944) listed as a synonym of *Eurycranium* Blanchard (now *Eurymetopum* Blanchard, see Solervicens 1986) of the subfamily Phyllobaeninae (now Hydnocerinae, not Epiphloeinae), as it is not an available name. I therefore deem Epiclininae Crowson, 1964 to be unavailable and hereby propose the new family-group name Epiclininae Gunter, Leavengood & Bartlett ***subfam. nov.***

3.5 Conclusion

The previous attempts to resolve the phylogeny of the checkered beetles were based exclusively on morphological characters. Unfortunately, given the nature of traditional classification systems based around morphology, these phylogenies tended to be weighted towards characters used to divide the subfamilies resulting in non-independent tests of relationships. This study represents the first assessment of clerid relationships based on molecular evidence. Taxon sampling at a generic level was relatively comprehensive with approximately one quarter of the described genera within the clerid lineage sampled with relatively even coverage proportional to the proposed subfamilies of both Kolibáč and Opitz. Gene selection was appropriate to recover deeper and shallow level divergence as almost all nodes were well supported when taxon sampling was sufficient. In the future, broader taxon sampling to incorporate more genera from the subfamilies Clerinae and Hydnocerinae may resolve the current paraphyly or confirm that they truly represent a single subfamily. Until such extensive sampling is available we propose to maintain these two subfamilies as distinct lineages for the ease of

classification. Our results indicate that Thaneroclerinae (including Isoclerinae or Zenodosinae) represents a single subfamily within the Cleridae and is congruent with the tribal division already existing. Until further taxon sampling of the Korynetinae and allies is conducted one cannot reject the classification of Opitz (2010), however, molecular results are congruent with the hypothesis of Kolibáč (1997) in that Korynetinae represents a single subfamily which includes Opitz' Epiphloeinae, Tarsosteninae, Peloniinae, Enopliinae and Neorthopleurinae. It is clear that the *Eleale, Cleromorpha* and *Epiclines* do not belong within the Clerinae and instead represent a new subfamily, Epiclininae *subfam. nov.* in which we also include *Calendyma*. Such insights into the systematics of the Cleridae may have remained unnoticed without the incorporation of molecular data. This preliminary phylogeny provides a solid framework for resolving other taxonomic issues within the Cleridae.

Table 3.1. Genes, primers and primer sequences used.

Gene	Primer	Sequence	Reference
COI	LCO-1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
	HCO-700ME	TCAGGGTGACCAAAAAATCA	Breton et al. 2006
	Jerry	CAACATTTATTTTGATTTTTTGG	Simon *et al*. 1994
	Pat	TCCATTGCACTAATCTGCCATATTA	Simon *et al*. 1994
28S rDNA	D1F	GGGACTACCCCCTGAATTTAAGCAT	Park & O'Foighil, 2000
	D6R	CCAGCTATCCTGAGGGAAACTTCG	Park & O'Foighil, 2000
	28Sff	TTACACACTCCTTAGCGGAT	Inward 2003
	28Sdd	GGGACCCGTCTTGAAACAC	Inward 2003
16S rDNA	LR-N-13398	CCGGTCTGAACTCAGATCACGT	Simon *et al*. 1994
	LR-J-12887	CGCCTGTTTACCAAAACAT	Simon *et al*. 1994
	16c	CGGTGTTATCCCTAAGGT	-
	16y	CCCTGATACCCAGGTAC	-
	16z	GTACCTGGGTATCAGGG	-
	12sB	AAACTAGGATTAGATACCC	Simon *et al*. 1994

Table 3.2. Partitions for Bayesian and maximum-likelihood analyses and log-likelihood scores for last 10 million generations of Bayesian analyses.

	Partitions (n)		**-lnL (BA)**
1	Unpartitioned (1)	unpartitioned	115304
2	16S, tRNA, 12S, 28S, COI (5)	by gene	112031
3	16S, tRNA, 12S, 28S, COI1, COI2, COI3 (7)	by codon	110627
4	16S, tRNA+ 12S, 28S, COI1, COI2, COI3 (6)	Partitionfinder	110573

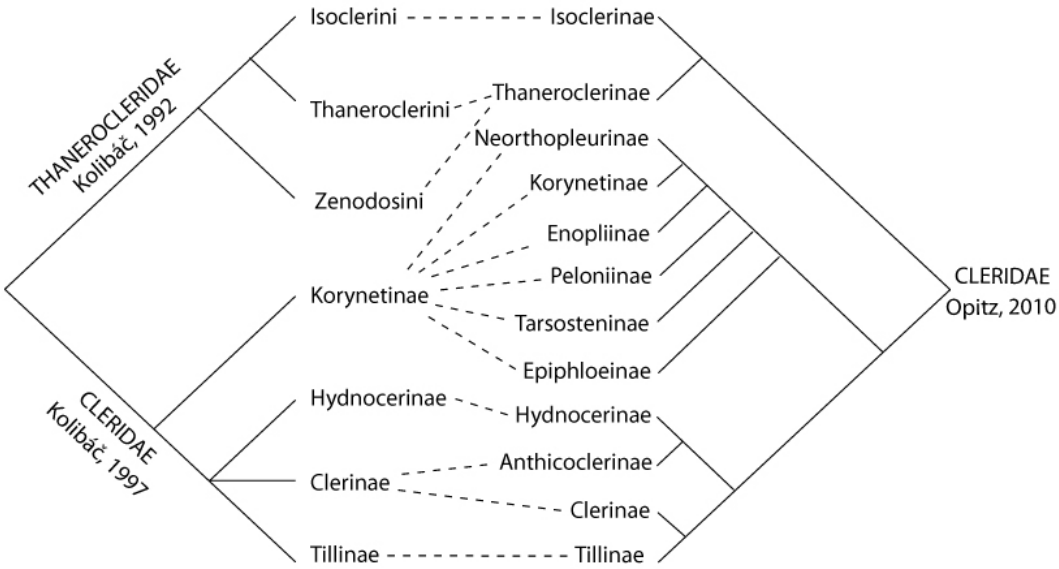
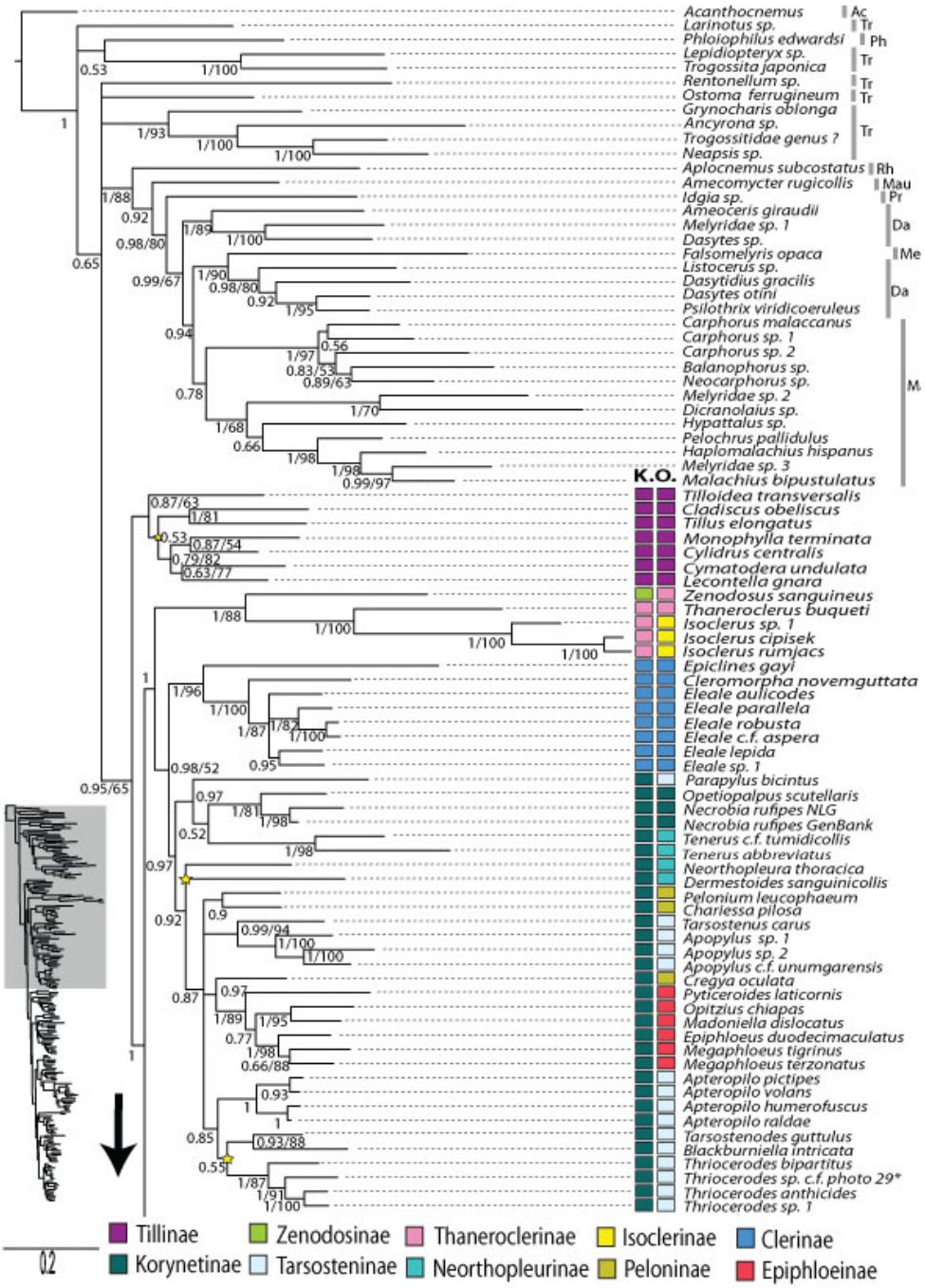


Figure 3.1. Comparision of morphology-based phylogenies and classification systems of Kolibáč and Opitz.



continued on next page

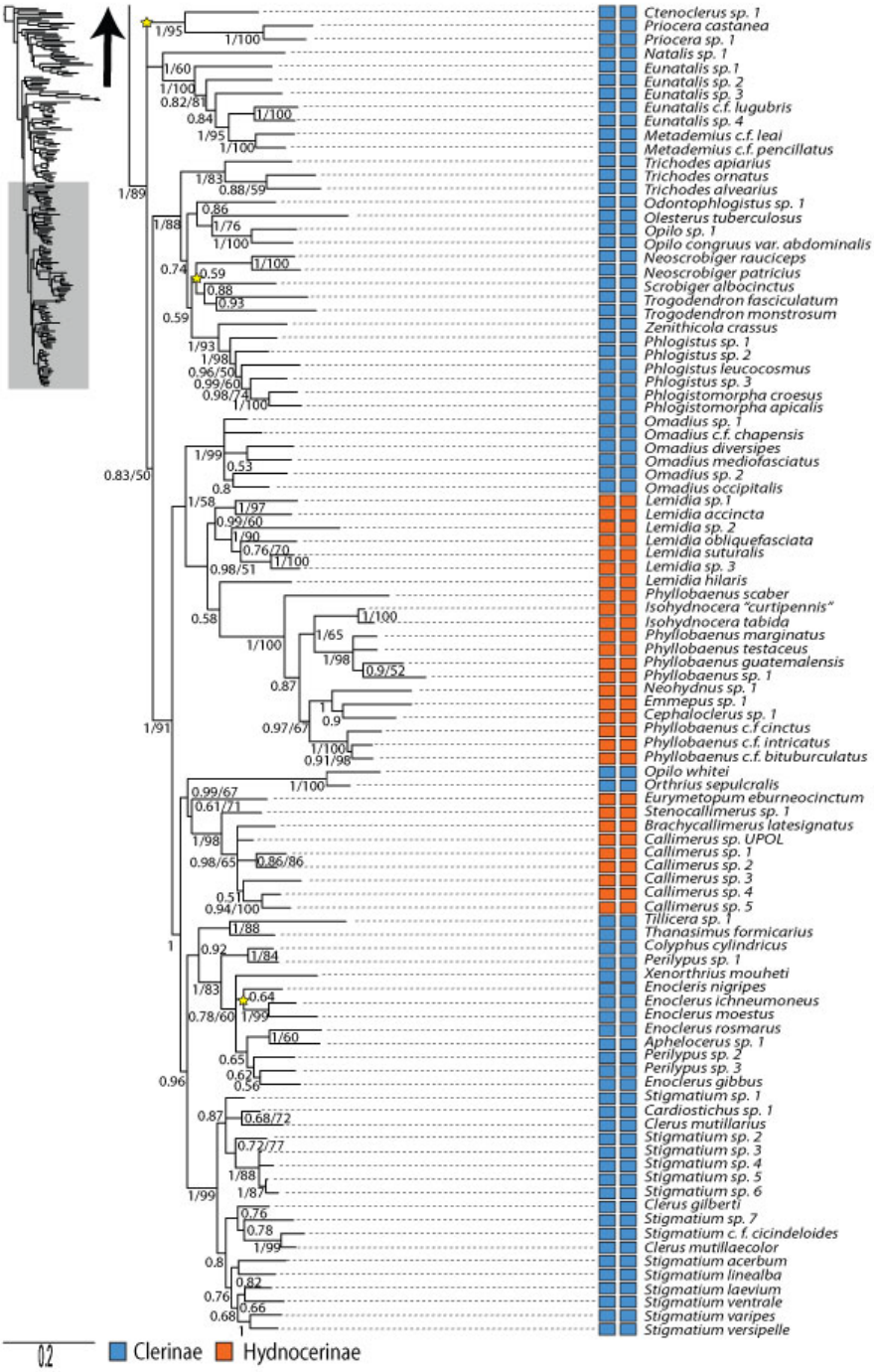


Figure 3.2. Consensus tree based on the Bayesian analysis of the optimal partitioning strategy predicted by PartitionFinder. Posterior probabilities are indicated at the nodes followed by ML bootstrap if supported. Subfamily classification is color-coded by the two main alternate classification systems K: *sensu* Kolibáč (1997) and O: *sensu* Opitz (2010). Stars represent nodal relationships that were not supported by all partitioning

strategies. Outgroup families are abbreviated as follows, Ac: Acanthocnemidae; Tr: Trogossitidae; Ph: Phloiophilidae; Rh: Rhadalidae; Mau: Mauroniscidae; Pr: Prionoceridae; Me: Melyridae; Da: Dasytidae and Ma: Malachiidae. Consensus tree based on the Bayesian analysis of the optimal partitioning strategy predicted by PartitionFinder. Posterior probabilities are indicated at the nodes followed by ML bootstrap if supported. Subfamily classification is color-coded by the two main alternate classification systems K: *sensu* Kolibáč (1997) and O: *sensu* Opitz (2010). Stars represent nodes relationships that were not supported by all partitioning strategies.

CHAPTER 4: MITOGENOMIC ANALYSIS OF HEMIPTERA REVEALS KEY INNOVATIONS IN THE ADAPTIVE RADIATION OF TRUE BUGS (HETEROPTERA)

4.1 Introduction

Ernst Mayr defined evolutionary novelty as "any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone" (Mayr 1963). Driven by adaptive modifications and the colonization of new ecospace, evolutionary radiations of animals and plants have long been recognized to drive today's biodiversity. Tracking the evolutionary origins of morphological novelty has fascinated biologists for over a century (Müller and Newman 2005). Even though stochastic factors lead to the development of new lineages, only a fraction of these have successfully diversified over time. Many of the largest Metazoan radiations, such as true flies (Wiegmann et al. 2011) and beetles (Hunt et al. 2007; Wang et al. 2014), have been well documented, but several mega-diverse invertebrate clades have not received the attention they deserve.

With an estimated 97,000 to 103,590 described and undescribed species (Catalogue of Life; Burckhardt et al. 2011; Weirauch and Schuh 2011; Zhang 2011a), Hemiptera represents ~7% of the metazoan diversity (Zhang 2011b). The biodiversity of Hemiptera includes, but is not limited to, plant-lice, cicadas, planthoppers, moss bugs and true bugs. Heteroptera (true bugs) has evolved diverse life histories and specialized morphological adaptations enabling them to colonize terrestrial and aquatic habitats, and to exploit various food sources ranging from plants, fungi, detritus to other arthropods, and vertebrate blood (Schuh and Slater 1995). Although its monophyly is well-supported (Hennig 1969; Carver et al. 1991), in particular by the synapomorphic segmented, piercing-sucking mouthparts with elaborate food and salivary pumps that permit fluid-feeding specializations (fig. 4.1A–D; Spangenberg et al. 2013), the higher-level classification of Hemiptera has been debated for over two and a half centuries (Linnaeus 1758; Myers and China 1929; Bourgoin and Campbell, 2002; Cryan and Urban 2012; Song et al. 2012; Cui et al. 2013). Based on the absence or presence of a gula, Hemiptera

has been traditionally categorized into Homoptera and Heteroptera (Myers and China 1929), although some consider that the two groups are of sufficient magnitude to warrant full ordinal status independently (e.g., Borror et al. 1981). Hemiptera has been subdivided into four major suborders, Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha and Heteroptera (Bourgoin and Campbell, 2002; Grimaldi and Engel 2005; Forero 2008; Cryan and Urban 2012).

Phylogenetic analysis of Hemiptera based on morphology has been challenging. The sedentary lifestyles consistent with plant fluid-feeding behaviors in some Auchenorrhyncha and especially Sternorrhyncha (fig. 4.1A-B; behaving as plant parasites) have spurred reductions, losses, neotenous females, extreme sexual dimorphism and convergently derived morphological characters otherwise useful in phylogenetic analyses (von Dohlen and Moran 1995; Gullan and Kosztarab 1997). The confusion of convergent character states with synapomorphies has contributed to the taxonomic reshufflings of superfamily composition within Homoptera (von Dohlen and Moran 1995). Due to a large number of morphological features unique to Hemiptera (e.g., the labium forming a sheath for the remaining mouthparts), important characters cannot be readily homologized with structures in more inclusive groups, resulting in ambiguous or even erroneous ancestral state reconstructions.

Historically, some hemipterists assumed that the ancestor of Homoptera was phytophagous (Sweet 1979), whereas the ancestor of Heteroptera was considered to be predaceous (Cobben 1978). The presumed diet of Homoptera was intuitive since all members of the order are plant-feeders. The predaceous ancestor of Heteroptera was inferred by the predatory behavior exhibited by the putatively “basal” infraorders, Enicocephalomorpha, Dipsocoromorpha and Gerromorpha (Cobben 1978). It is understood that after the Permian-Triassic extinction events, many previously exploited niches once again had become available for resource competition (Tanner et al. 2004). Although Heteroptera constitutes approximately 40% of the species of Hemiptera, it represents the vast majority of behavioral diversity in terms of diet and habitat, with the other three suborders being entirely terrestrial and predominantly phytophagous (Schuh and Slater 1995). Hypotheses of selective forces underlying the diversification of higher-

level hemipteran lineages have yet been substantiated outside of morphology and fossil-based extrapolation (Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005).

With the advent of the Genomics Era, recent analyses have increasingly embraced the use of molecular data to advance our understanding of the phylogeny of Hemiptera (Talavera and Vila 2011; Letsch et al. 2012; Song et al. 2012; Cui et al. 2013), nevertheless leaving several outstanding questions unsolved -- for example, the monophyly versus paraphyly of Auchenorrhyncha (Cryan and Urban 2012). With a huge influx of genomic resources, including the readily available mitogenomes, new phylogenetic hypotheses are emerging. Although representing only a subset of the genomic data (~ 12-17,000 nucleotides per mitogenome), recent comparative mitogenomic studies have made substantial contributions to resolve intraordinal relationships in many insects (Cameron 2014), including Isoptera (Cameron et al. 2012; Xiao et al. 2012), Orthoptera (Fenn et al. 2008; Leavitt et al. 2013), Lepidoptera (Kim et al. 2011; Wu et al. 2014), Hymenoptera (Castro and Dowton 2007; Dowton et al. 2009; Kaltenpoth et al. 2012), Diptera (Cameron et al. 2007; Wiegmann et al. 2011), Neuroptera (Cameron et al. 2009; Zhao et al. 2013), Coleoptera (Sheffield et al. 2009; Pons et al. 2010; Song et al. 2010; Timmermans et al. 2010; Timmermans and Vogler 2012; Gillett et al. 2014) and Hemiptera (Talavera and Vila 2011; Song et al. 2012; Cui et al. 2013).

Despite impressive taxonomic coverage, previous studies in Hemiptera did not sample all the suborders and infraorders, and had limited resolution due to the inadequate partitioning strategies, ambiguously aligned sequence data, and substitution saturation. Twenty-six newly sequenced mitogenomes complement the existing genomic data (55 hemipteran mitogenomes). This study represents the most robust mitogenomic analysis of Hemiptera to date and the first to include the mitogenomes from all four suborders and all seven infraorders, representing 88% of the superfamilies of Homoptera, the only superfamily of Coleorrhyncha, and 84% of superfamilies of Heteroptera. Furthermore, present analyses of 81 hemipteran mitogenomes represent a significant increase in OTUs over the previous most inclusive study (Cui et al. 2013; 49 OTUs). Using a fossil-calibrated divergence dating analysis, we carried out the first order-wide diversification study in Hemiptera to investigate the timing of major cladogenetic events. Equipped with

the most comprehensive mitogenomic analysis in Hemiptera and informed from the ancestral state reconstructions of habitat, morphological characters and feeding behaviors, we then address the following questions: **1)** What are the key morphological adaptations facilitated the habitat and feeding diversity of Heteroptera? **2)** Was the ancestor of Heteroptera a predator or a plant-feeder? **3)** What extinction and/or rapid radiation events coincide with the diversification of the major lineages of Hemiptera?

4.2 Materials and Methods

This work was done in collaboration with Xuguo Zhou and Eric G. Chapman (Department of Entomology, University of Kentucky, Lexington, Kentucky, U.S.A.), Wanzhi Cai and Li Hu (Department of Entomology, China Agricultural University, Beijing, China). All DNA extraction, sequence assembly and preliminary analyses were done by Hu (in part for his dissertation; advisor Cai). Chapman and I conducted all presented analyses (along with alignment, editing, evolutionary model estimation). Chapman produced ancestral state recontronstrions and I assumed the primary role in writing the paper with assistance from Chapman and Hu.

4.2.1 ***Taxon Sampling.*** Hemiptera's (n = 81) taxonomic diversity is thoroughly sampled to minimize long branches (Talavera and Vila 2011). Specimens were collected into 95–100% ethanol and stored at – 20°C in the Entomological Museum of China Agricultural University (Beijing, China). Previous studies recognized accelerated rates of gene rearrangement and nucleotide substitution in the mitogenomes of Phthiraptera (lice) and Thysanoptera (thrips) (Shao et al. 2001), and Aleyrodidae (whiteflies) (Thao et al. 2004). Talavera and Vila (2011) assessed mitochondrial phylogenetic signal limits in Paraneoptera and detected long-branch attraction artifacts among Phthiraptera, Thysanoptera and Sternorrhyncha. Thus, Phthiraptera and Thysanoptera were not included in the taxon sampling of outgroups. We included six outgroup species to represent other paraneopteran lineages as well as the putatively more ancient lineages Blattaria and Mantodea (table 4.6). Mitogenomic data for two outgroup taxa (Psocoptera) were generated from a previous study (Li et al. 2013); data for the remaining four

outgroup taxa were obtained from GenBank. 34 ingroup taxa were sequenced wholly or in part for this study (eight genomes from previous studies; see table 4.6). Complete or nearly complete mitogenomes were obtained from GenBank for 33 species of Heteroptera, seven Auchenorrhyncha and seven Sternorrhyncha. All 81 mitogenomes were aligned and represent each of the major hemipteran suborders (with coverage of extant taxa) as follows: Sternorrhyncha (seven species; 75% of recognized superfamilies); Coleorrhyncha (two species; 100% of recognized superfamilies); Heteroptera (60 species representing all seven major infraorders; 84% of recognized superfamilies); Auchenorrhyncha comprising Cicadomorpha (seven species; 100% of recognized superfamilies) and Fulgoromorpha (four species; 100% of recognized superfamilies) (table 4.6).

4.2.2 ***Complete Mitogenome Sequence Generation***. Genomic DNA was extracted from the thoracic muscle tissue of 26 specimens using the DNeasy blood and tissue kit (Qiagen) following the animal tissue protocol. Whole mitogenomes were generated by amplification, sequencing and assembly of overlapping PCR fragments employing general insect mitochondrial primers (table 4.7; Simon et al. 2006). Species-specific primers were designed based on the sequenced fragments to bridge gaps.

PCR reactions (total volume = 25 μL) consisted of 1X Qiagen PCR buffer, 0.2 mM of each dNTP, 0.5 μM of each primer, 1.25 U of Qiagen Taq and 1–4 μL of template DNA. Long PCR reactions (total volume = 25 μL) consisted of 1X LongAmp Taq reaction buffer, 0.3 mM of each dNTP, 0.5 μM of each primer, 2.5 U of NEB LongAmp Taq (New England BioLabs) and 1–4 μL of template DNA.

Short PCRs (< 1.5 kb) were carried out with the following cycling conditions: 5 min at 94 °C, followed by 35 cycles of 50 s at 94 °C, 50 s at 48–55 °C, 1–2 min at 72 °C depending on amplicon size, and a final elongation step at 72 °C for 10 min. Long PCRs (> 1.5 kb) were performed under the following cycling conditions: 30 s at 95 °C, followed by 40 cycles of 10 s at 95 °C, 50 s at 48–55 °C, 3–6 min at 68 °C depending on the size of amplicons, and the final elongation step at 68 °C for 10 min. The quality of PCR products was evaluated by spectrophotometry and agarose gel electrophoresis.

The PCR fragments were ligated into the pGEM-T Easy Vector (Promega) and resulting plasmid DNAs were isolated using the TIANprp Midi Plasmid Kit (Qiagen). All fragments were sequenced in both directions on an ABI 3730XL Genetic Analyzer, using the BigDye Terminator Sequencing Kit (Applied Biosystems) with two vector-specific primers and internal primers for primer walking.

4.2.3 ***Assembly, Annotation and Alignment.*** Sequences from each genome were assembled into contigs using SEQUENCER v. 5.1 (Gene Codes, Ann Arbor, MI). Protein-coding genes (PCGs) and rRNA genes were identified using BLAST searches (Karlin and Altschul 1990, 1993) of GenBank and alignment with homologous sequences. The tRNAs were identified with tRNAscan-SE v. 1.21 (Lowe and Eddy 1997). Sequences of each PCG (excluding stop codons) were aligned using MUSCLE (Edgar 2004), with alignment based on conservation of codon reading frame. Sequences of each RNA gene were aligned and ambiguous alignment positions were omitted using the default settings on the GUIDANCE server (Penn 2010) based on the GUIDANCE algorithm (Penn et al. 2010). Alignments of individual PCGs were concatenated and potential substitution saturation at each codon position was individually assessed, with transitions and transversions plotted against corrected genetic distance using DAMBE v. 5.3.20 (Xia and Xie 2001). Xia's saturation index (Xia et al. 2003) was used to determine whether there was significant substitution saturation in each protein-coding gene at any of the three codon positions and position 1+2 combined. Additionally, we tested these positions for the combined 13-gene partition for saturation.

Two data sets were concatenated for phylogenetic analysis: (1) The PCG123 matrix, including all three codon positions of the 13 PCGs, two rRNA genes, and 17 tRNA genes (total of 12,204 bp); (2) the PCG12 matrix, including the first and the second codon positions of the 13 PCGs, two rRNA genes, and 17 tRNA genes (total of 8,633 bp). Five tRNAs (Ala, Ile, Met, Gln, Ser) were not found in many nearly complete mitogenomes and therefore were excluded from my analyses.

4.2.4 ***Phylogenetic Analyses*****.** The PCG123 and PCG12 data sets were analyzed with Bayesian inference (BI) and maximum likelihood (ML) methods. Trees were rooted on

Reticulitermes (Blattaria, formerly Isoptera) with six total taxa from the orders Blattaria (cockroaches and termites), Mantodea (praying mantids) and Psocoptera (barklice) forming the outgroup. Appropriate models of nucleotide evolution for gene partitions were chosen using jModelTest v. 0.1.1 (Posada 2008), according to the Akaike Information Criterion (AIC; Akaike 1974) (table 4.8). We tested each PCG, each codon position of each PCG, the two rRNAs and the 17 tRNAs separately with jModelTest. The PCGs in the PCG123 and PCG12 data sets were either partitioned by gene or by codon position.

Partitioned ML and BI analyses were conducted with the molecular data from PCG123 and PCG12 matrix, using Garli v. 2.01 (Zwickl 2006) and MrBayes v. 3.2.2 (Ronquist and Huelsenbeck 2003). Individual partitions were created for each PCG (by codon position; 3 partitions per gene), 16S rRNA, 12S rRNA and all 17 tRNA genes. For the ML analyses, eight independent tree searches were performed to find the tree with the highest log-likelihood. The parameter estimates from the most likely tree were used as starting parameters in 200-replicate bootstrap analyses. For the BI analyses, two simultaneous runs were conducted which were terminated after the average standard deviation of split frequencies fell near or below 0.01.

Differences in phylogenetic analyses were based on how we treated the protein-coding genes, as tRNAs and rRNAs were always given separate partitions. Under Bayesian methods, we partitioned the PCGs (1) by gene (total of 32 partitions; figs. 4.6-4.9) and (2) by codon position (total of 58 partitions for PCG123, 45 for PCG12; figs. 4.14-4.17) under nucleotide models. We also analyzed the PCG123 data set with codon models (M3; Yang et al. 2000) assigned to the PCGs (figs. 4.18-4.19). To allow each partition to have its own set of parameter estimates, *revmat*, *tratio*, *statefreq*, *shape*, and *pinvar* were all unlinked during all analyses. To obtain the most accurate branch length estimates possible, the option *prset ratepr = variable* (assigns a separate branch length parameter for each partition) was employed as per the recommendations of Marshall et al. (2006), who found that BI analyses of partitioned data with a global branch length parameter resulted in significantly longer overall tree length. ML analyses were conducted on both data sets with PCGs partitioned by gene (figs. 4.10-4.13). Finally, we attempted to run eight ML tree searches with Garli assigning codon models to the PCGs.

A single replicate took 136 days on a 4-processor Mac with the last ~130 days spent optimizing the parameter estimates post-tree building. We abandoned the idea of bootstrapping this data set with codon models in the interest of time and present the single most likely tree produced from the lone replicate (fig. 4.20).

4.2.5 ***Topology Testing.*** We tested for significant differences in topologies between the best unconstrained tree and a topology produced by separate analyses constraining the following taxa to be monophyletic: (1) Auchenorrhyncha and (2) Cimicomorpha, because both were either para- or polyphyletic in all analyses. In each case, we used Garli to produce the site-likelihoods file (input file for Consel) from ML analyses of the PCG123 dataset with PCGs partitioned by gene. We used CONSEL (Shimodaira and Hasegawa 2001) to do the likelihood-based approximately unbiased (AU), Kishino-Hasegawa (KH), Shimodaira-Hasegawa (SH), weighted Kishino-Hasegawa (WKH), and weighted Shimodaira–Hasegawa (WSH) tests (Shimodaira and Hasegawa 1999; Shimodaira 2002).

4.2.6 ***Ancestral Character State Reconstruction.*** Ancestral states for feeding and living habits were reconstructed in Mesquite v. 2.75 (Maddison and Maddison 2010) with ML methods. We based ancestral state reconstruction on the BI analysis of the PCG123 data set with PCGs partitioned by codon position, using the tree of highest posterior probability from this analysis. For the ML optimizations, the 'Markov k-state 1 parameter model' (MK1 model in which 'forward' and 'backward' transition rates are equal; Lewis, 2001) was used. Sources of data for feeding type, living habits and mouthpart origin and presence of hemelytra are listed in table 4.9. To make decisions regarding the significance of ancestral character state reconstructions, we followed Pagel's (1999) recommendation (following Edwards 1972) that ancestral character state estimates with a log-likelihood two or more units lower than the best state estimate be rejected. For ease of interpretation, likelihoods of ancestral states are reported as proportional likelihoods (PL; scaled to add up to 1, thus expressed as a percent of total likelihood).

4.2.7 ***Divergence Time Estimation*****.** Divergence time estimates were calculated for ingroup-only combined data set with a Bayesian MCMC approach using the software

BEAST v. 1.8.0 (Drummond and Rambaut 2007; Drummond et al. 2012) in the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). BEAST uses the aligned sequence data to generate a tree in the MCMC (Markov chain Monte Carlo) process to infer divergence times. This analysis employed the models estimated with jModelTest for each partition with the PCGs partitioned by codon position. A relaxed molecular clock using the uncorrelated log-normal model was applied with a Yule process speciation prior for branching rates. The root of Hemiptera was limited at 296-303 Ma, corresponding to the approximate age of the earliest hemipteran fossil of the Carboniferous family Archescytinidae (Rasnitsyn and Quicke 2002). With the above exception, fossil ages were incorporated as taxon group priors with a log normal distribution with a hard-bound minimum age and a soft-bound maximum age that captures the date range within the 95% confidence interval (table 4.4). The final analysis was run for 40 million generations with parameters sampled every 1,000 generations to produce 40,000 trees. The initial 10,000 trees (25%) were discarded as burn-in using TreeAnnotator 1.8.0 (Drummond and Rambaut 2007). The remaining 30,000 trees were used to produce the maximum clade credibility tree and FigTree v. 1.3.1 (Rambaut 2010) was used to visualize the tree along with node ages and age deviations.

4.3 Results

4.3.1 ***Phylogenetic Analyses and Topology Tests*****.** Because both inadequate taxon sampling and nucleotide substitution saturation may cause long-branch attraction (Song et al. 2012), data was tested for substitution saturation in protein-coding genes (PCGs), a variety of partitioning strategies were implemented, and regions of ambiguous alignment within rRNA genes were assessed for confidence and/or omitted. The results of the saturation tests are presented in table 4.1. According to the results, strong evidence for saturation was found at the third codon position of every PCG plus the first positions of ATP6 and ND2. Weak evidence for saturation was found at every other codon position of each PCG. However, in spite of these results, model-based phylogenetic methods were able to compensate, as evidenced by the analyses including 3rd codon positions having

generally higher nodal support values across the trees than those omitting 3rd positions (Table 4.2).

Table 4.2 lists the nodal support values for the higher taxa in all iterations of the analyses. The monophyly of Hemiptera was strongly supported in all analyses (BI PP = 1; ML BSP = 100). All analyses recovered Heteroptera (BI PP = 1; ML BSP = 100) and Homoptera (including Coleorrhyncha; BI PP = 1; ML BSP = 64–70) as monophyletic. All infraorders were recovered as monophyletic with high support values (Table 4.2) with the exceptions of Cimicomorpha which was either para- or polyphyletic in the analyses and Auchenorrhyncha which was polyphyletic in all analyses. Four long-recognized clades were recovered within Homoptera: (Cicadomorpha + (Coleorrhyncha + (Fulgoromorpha + Sternorrhyncha))) (fig. 4.2). However, Auchenorrhyncha (i.e., Cicadomorpha + Fulgoromorpha) was recovered as polyphyletic, with Cicadomorpha (BI PP = 1.0, ML BSP ≥ 98) forming the sister group to all remaining Homoptera (BI PP = 1.0, ML BSP ≥ 79) and Fulgoromorpha (BI PP = 1.0, ML BSP = 100) forming the sister group to the Sternorrhyncha (BI PP = 1.0, ML BSP ≥ 96) (figs. 4.3, 4.6-4.20). When subjected to topology testing, the tree with Auchenorrhyncha constrained to monophyly was significantly worse (significantly lower log-likelihood) than the unconstrained tree under all topology-testing algorithms (table 4.3).

Within Heteroptera, Cimicomorpha is paraphyletic at the base of a clade that included all other non-pentatomomorphan infraorders in the ML, MAP (maximum *a posteriori*) and BEAST trees of most analyses. This paraphyletic Cimicomorpha was sister to (Leptopodomorpha + ((Gerromorpha + (Enicocephalomorpha + Dipsocoromorpha)) + (Nepomorpha))) (figs. 4.3, 3.6-4.21). However, when subjected to topology testing, the tree with Cimicomorpha constrained to be monophyletic was not found to have a significantly lower log-likelihood, i.e., we could not reject the monophyly of Cimicomorpha with the present data set (table 4.3).

4.3.2 ***Ancestral State Reconstructions.*** All proportional likelihoods (PL) presented below (with a single exception as noted) indicate that the character state being discussed is significantly more likely than all other possible states as judged by likelihood methods (see explanation in Methods section).

Feeding habit optimization indicates that the common ancestors of Hemiptera, Homoptera and Heteroptera were all phytophagous (PL > 99.99% in all cases; figs. 4.5, 4.22). There were two independent transitions from phytophagy to predation in Heteroptera with the potential of no fewer than two additional independent transitions if predatory Pentatomidae and Miridae had been included. There was a reversal (in part) from predation to omnivory within Nepomorpha (Corixidae). Miridae also includes omnivorous species not represented in this study. Fungivory in adults arose once from a phytophagous ancestor in Aradidae (PL = 89.16%) (and in nymphs of some Auchenorrhyncha). Hematophagy (blood feeding) arose twice independently from predatory ancestors in extant Heteroptera (Reduviidae and Cimicidae).

The common ancestors to Hemiptera, Homoptera and Heteroptera were all terrestrial (PL > 99.99% in all cases; figs. 4.5, 4.23). In Heteroptera, there were two independent transitions to shoreline habitat, one from a terrestrial ancestor (PL = 99.56%) and one from an aquatic ancestor within Nepomorpha (PL = 99.92%), and one transition to surface skimmers from a terrestrial ancestor (PL = 99.50%). There was a single transition from terrestrial to aquatic habitat (Nepomorpha; PL = 99.78%).

The optimization of mouthpart origin is ambiguous regarding the character state of the common ancestor to all Hemiptera (orthognathous (mid-placement) [fig. 4.1C]: PL = 80.54%, prognathous (apical) [fig. 4.1D]: PL = 19.37%; hypognathous (sternal) [fig. 4.1A-B]: PL = 0.09%, with the latter significantly less likely than the former two; figs. 4.5, 4.24). The ancestor to Homoptera had orthognathous mouthparts (PL = 99.90%) and the ancestor of Heteroptera had prognathous mouthparts (PL > 99.99%). Hypognathous mouthparts (Sternorrhyncha) arose from an ancestor with orthognathous mouthparts (PL = 94.99%).

The presence of hemelytra (fig. 4.1E) arose a single time in the common ancestor to all Heteroptera (PL = 99.99%; figs. 4.5, 4.25). This character state was lost in the common ancestor to Gerromorpha + (Enicocephalomorpha + Dipsocoromorpha) (PL = 99.44%).

4.3.3 ***Divergence Time Estimation.*** To calibrate divergence time estimates, the root of Hemiptera was limited at 296–303 Ma, corresponding to the approximate age of the

earliest hemipteran fossil of the Carboniferous family Archescytinidae (Rasnitsyn and Quicke 2002). With the above exception, we used minimum clade ages for calibration points in these analyses (table 4.4).

According to analyses, the separation of Homoptera and Heteroptera occurred in the late Carboniferous (300 Ma; fig. 4.4). The time-calibrated molecular phylogeny reveals periods of higher-level hemipteran radiations (figs. 4.4, 4.21; table 4.5): 1) From a Carboniferous-Permian boundary origin, early lineages of Homoptera rapidly diversified in the Permian (290–263 Ma) and formed four major lineages: Cicadomorpha (266 Ma), Coleorrhyncha (152 Ma), Fulgoromorpha (199 Ma) and Sternorrhyncha (240 Ma); 2) infraorders of Heteroptera radiated in the Triassic (270–178 Ma), and diversified into seven major lineages: Enicocephalomorpha (n/a; one OTU), Dipsocoromorpha (136 Ma), Gerromorpha (158 Ma), Leptopodomorpha (191 Ma), Nepomorpha (224 Ma), Cimicomorpha (218 and 234 Ma; two clades) and Pentatomomorpha (258 Ma), and the further diversification at superfamily or family level continued from middle Triassic to late Cretaceous (fig. 4.4). The origin of Heteroptera (~270 Ma) coincided with the evolution of the apically-produced labium (fig. 4.1D; i.e., a gula permitting a prognathous rostrum position), predatory behavior, and the novel protective forewing (fig. 4.1E; the hemelytron, which would later be lost in Gerromorpha, Dipsocoromorpha and Enicocephalomorpha).

4.4 Discussion

4.4.1 Phylogeny of Hemiptera

The presented phylogeny corroborates Latreille's (1810) notion that "Hemiptera" was, in fact, two distinct groups worthy of ordinal status: Heteroptera and Homoptera. In accordance with the molecular findings of Lin and Danforth (2004) and Talavera and Vila (2011), and heeding Bourgoin and Campell's (2002) warnings of the morphologically-driven "autapomorphic trap," I analyzed an ideal data set to resolve intraordinal relationships while accounting for substitution saturation-induced homoplasy and sampling taxa more thoroughly than any before us to infer the phylogeny of Hemiptera and all major constituent lineages.

Results corroborate Song et al. (2012), who also recovered both Homoptera and Heteroptera as monophyletic, and indicate that at least based on the current mitogenomic data the homopteran paraphyly is not a fact. We recovered monophyletic groups for each suborder and infraorder with the exception of Cimicomorpha (Heteroptera) and the long-doubted, and as such not surprisingly, Auchenorrhyncha (Homoptera) (fig. 4.2-4.3). Topology tests rejected the monophyly of Auchenorrhyncha but failed to reject the monophyly of Cimicomorpha (table 4.3). Whereas this study aimed to answer questions about Hemiptera *sensu lato*, we suggest further analysis focusing on Heteroptera's diversity to resolve the most curious placement of the families Tingidae (the lace bugs) and Miridae (the plant bugs), resulting in the paraphyly of Cimicomorpha.

Additional work is also needed to further test the monophyly of Homoptera with more extensive taxon sampling from Cicadomorpha, Fulgoromorpha, and Sternorrhyncha.

4.4.2 Diversification of Major Lineages

According to my analyses, Hemiptera shared a common ancestor with the remaining Paraneoptera about 342 Ma, and subsequently diversified into Homoptera and Heteroptera 300 Ma (fig. 4.4), at the end of the seed plant radiation 385–299 Ma (Sims 2012). This result supports Heslop-Harrison's (1956) hypothesis that Hemiptera *sensu lato* evolved from protohemipterous ancestors in the late Devonian. Results suggests that a Permian diversification of the homopteran suborders immediately followed by a Triassic diversification of the heteropteran infraorders (fig. 4.4).

From a Carboniferous-Permian boundary origin (300 Ma), early terrestrial lineages of Homoptera (290 Ma) radiated soon after the hypothesized origin of gymnosperms (Smith et al. 2010), and formed Cicadomorpha, Coleorrhyncha, Fulgoromorpha and Sternorrhyncha in the Permian (266–152 Ma; fig. 4.4). With the exception of some mycophagous nymphs, Homoptera is entirely phytophagous, feeding on fluids of phloem, xylem or cambium, with some inducing galls (some Psylloidea, Aphidoidea, and Coccoidea) (Rasnitsyn and Quicke 2002; Forero 2008). Extinct hemipteran taxa forming the ancestral stock of today's major lineages were consistently linked to gymnosperms. Shcherbakov (2002) inferred "such short-legged

[Archescytinidae] either lived in confined spaces of gymnosperm reproductive organs or clung tightly to the plant surface." Small, usually dorsoventrally depressed hoppers and their flattened cryptic nymphs (a body form possibly adapted to living between cone scales; Evans 1962) likely fed on phloem of thick gymnosperm stems (Rasnitsyn and Quicke 2002). The Clypeata (Cicadomorpha: Hylicelloidea) were the first xylem-feeding Hemiptera and existed during the gymnosperm-dominated Permian and Triassic forests (Rasnitsyn and Quicke 2002) and the large and clumsily-built early Permian boreoscytids possibly fed on large gymnosperm ovules (Rasnitsyn and Quicke 2002). Furthermore, fossils representing early members of Sternorrhyncha (Boreoscytidae), Cicadomorpha (Prosboloidea: Ingruidae and Prosbolopseidae) and Fulgoromorpha (Coleoscytoidea) were recovered from the same Kungurian (275–270 Ma) beds coincident with gymnosperm dominance (Rasnitsyn and Quicke 2002).

Analyses support that the diversification of the major lineages of Homoptera (Auchenorrhyncha-Cicadomorpha, 266 Ma; Sternorrhyncha, 240 Ma; Auchenorrhyncha-Fulgoromorpha, 199 Ma; Coleorrhyncha, 152 Ma) coincided with the diversification of gymnosperms. This was also the case with most family-level diversification events, the major exception being the families of Fulgoromorpha, whose diversification seems to coincide with the angiosperm radiation (150–60 Ma). However, the present analysis includes only four of the 21 families of Fulgoromorpha and one of the eight families of Psylloidea. Subsequent intrafamilial diversification occurred during the angiosperm radiations as indicated in the analysis with Aleyrodidae and Ortiz-Rivas et al. (2004) likewise linked angiosperm and aphid tribe diversification, producing angiosperm-feeding taxa. Since all extant superfamilies of Sternorrhyncha (scales, aphids, whiteflies) feed on angiosperms and gymnosperms yet evolved from gymnosperm feeders (Gullan and Kosztarab 1997; Shcherbakov 2000; Ortiz-Rivas et al. 2004; Drohojowska and Szwedo 2014), it is difficult to deduce the finer mechanisms behind their evolution. This notion is especially complicated considering that well after the era of gymnosperm replacement with angiosperms (beginning 150 Ma) there was an increase in gymnosperm diversification rates persisting over the last 100 Ma (Burleigh et al. 2012).

The infraorders of Heteroptera diversified in the Late Permian and Triassic (270–178 Ma), largely overlapping with the diversification of Homoptera's families. We

propose that the diversification of potential prey species following the Permian-Triassic extinction (252 Ma; Chen and Benton 2012) may have paved the way for the diversification of the arthropod-feeding heteropteran lineages. Basal cimicomorphan predators (assassin bugs, some plant bugs) and plant-feeders (plant and lace bugs) evolved from gymnospermous forest-inhabiting ancestors, but radiated afterwards during the rise of angiosperm dominance. The plant bugs (Miridae; 53 Ma) appear to have originated late. However, only the highly derived Mirini were sampled for this analysis. Jung and Lee (2012) inferred intrafamilial radiation of plant bugs during angiosperm radiations, with subfamily-level diversification occurring 275–150 Ma. Including more basal tribes with the present data set may yield an appropriately older clade age (i.e., >60 Ma).

All aquatic, shoreline and litter-dwelling true bugs were recovered as a monophyletic group. The aquatic (submerged) families of Nepomorpha diversified 219–162 Ma and the shore bugs (Leptopodomorpha; 191 Ma), largely pre-date the rise of angiosperm domination. The water surface skimmers (Gerromorpha; 158 Ma) originated near the beginning of the angiosperm radiation, followed by the litter-dwelling Dipsocoromorpha (136 Ma).

The true bug superfamilies of Pyrrhocoroidea (147 Ma), Coreoidea (136–89 Ma) and Pentatomoidea (123–83 Ma) all diversified during the rapid radiation of angiosperms, with some intrafamilial diversification occurring after 60 Ma. These families are all phytophagous except for some stink bugs (Pentatomidae). The diversification of Pentatomomorpha is clearly coincident with that of angiosperms. However, the mycophagous flat bugs (Aradidae; 208 Ma) pre-date angiosperm dominance and the speciose milkweed and seed bugs (Lygaeidae and Rhyparochromidae) were not sampled. The diversification of the sampled Lygaeoidea (201–139 Ma) span both gymnosperm and angiosperm-dominated periods.

Future studies sampling more members per family focusing on individual lineages (e.g., Sternorrhyncha or Pentatomomorpha) may prove informative in discerning differences in diversification trends between “within family” taxa as well as deeper relationships.

4.4.3 Ancestral State Reconstructions

Whereas ancestral mouthpart placement was ambiguous for Hemiptera, ancestral state reconstruction indicates that phytophagy (figs. 4.5, 4.22) was the ancestral feeding behavior of Homoptera + Heteroptera. The hypognathous (intercoxal) emergence of the labium (fig. 4.1A-B) in Sternorrhyncha occurred 240 Ma and is associated with the most extreme sedentary phytophagous feeding behavior in Homoptera (e.g., scale insects, some of which remain affixed to a single feeding site for much of their lives). Based on outgroup comparison (with non parasitic Psocodea) we postulate that the evolution of a gula with prognathy is synapomorphic for Heteroptera and hypognathy for Sternorrhyncha, respectively, leaving orthognathy plesiomorphic. This suggests an ancestral state of orthognathy.

Ancestral character state reconstruction of feeding habits suggests that the ancestor of Heteroptera was phytophagous (figs. 4.5, 4.22) and originated in the middle Permian (~270 Ma; fig. 4.4). Heteroptera was recovered as two large groups, with Pentatomomorpha sister to all of other infraorders (with the omnivorous Miridae + phytophagous Tingidae at its base). Wheeler (2001) considered zoophagy to be the ancestral state of Miridae (plant bugs) with multiple shifts to phytophagy, the opposite of the results. However, Jung and Lee (2012) deduced a phytophagous ancestral state for the omnivorous Miridae as we did. Most extant heteropterans are either predaceous or phytophagous, but three families (Cimicidae, Reduviidae, and Polyctenidae) contain blood-feeding species (Schaefer and Panizzi 2000; Schuh and Slater 1995). Most recently, Yao et al. (2014) reported a new family of true bugs including two new genera from ~125 Ma in northeastern China, representing the earliest evidence of blood feeding true bugs in the early Cretaceous. Results were consistent with those fossil records that hematophagous habits evolved twice independently from predatory ancestors in Heteroptera (Polyctenidae not included) and originated in the early Cretaceous (~145 Ma in Cimicidae and ~109 Ma in Reduviidae).

In Heteroptera, there were two independent transitions to shoreline habitat (one from terrestrial aquatic ancestors; Nepomorpha), one transition to surface skimming from a terrestrial ancestor and a single transition from terrestrial to aquatic habitat (Nepomorpha) (fig. 4.5, 4.23). Chapman et al. (2012) hypothesized that “any lineage that

(1) occurs in aquatic and terrestrial habitats, (2) respires the same way in aquatic and moist shoreline habitats (e.g., cuticular respiration or open tracheal system) and (3) has the same type of food available in both habitats (e.g., pulmonate snails) could show a similar pattern of multiple independent habitat transitions coincident with changes in behavioral and morphological traits." The results of the present study are suggestive that some lineages within these groups also show multiple convergences on aquatic or terrestrial habits when examined with modern phylogenetic comparative methods. Concurrent with Chapman et al.'s (2012) predictions, the aquatic and subaquatic infraorders of true bugs exhibit this pattern.

4.4.4 Key innovations in the adaptive radiation of true bugs

Whereas Homoptera was formerly considered "primitive", the morphology behind such hypotheses was adaptively obscured by sedentary feeding specialization on nutrient poor gymnosperms. The major lineages (infraorders) of Heteroptera diversified well before the advent of angiosperm dominance as well. The evolution and diversification of seed plants (385–299 Ma) gave rise to vast ecological niche space (Sims 2012). The evolution of the seed fueled not only the evolutionary success of plants for nearly 400 Ma, but probably also initiated and facilitated the subsequent success of Homoptera and Heteroptera as well. Most curious is that, despite the disparity in habitat and behavioral diversity, both Heteroptera and Homoptera have similar biodiversity, 42,000 and 55,000 species, respectively favoring Homoptera. Could Homoptera's greater species be a result of an historical taxonomic bias due to the gregarious and/or sedentary behavior of Homoptera making them easier to discover? The ancestral lineages of both groups hardly differ in age and both underwent major lineage diversification during a gymnosperm-dominated era. All infraorders of Heteroptera originated after the Permian-Triassic crisis. If the varied behavior of Heteroptera facilitated more microhabitat colonization, it apparently did not result in higher rates of diversification (of extant lineages). Perhaps many microhabitats less utilized by Homoptera haven't yet been sufficiently sampled to account for the greater behavioral diversity in true bugs.

Two key adaptations facilitated the rapid family-level radiation of Heteroptera coinciding with the shift from gymnosperm- to angiosperm-dominance. The evolution of

the apically-produced labium (prognathy, i.e., mouthparts emerging from the anterior tip of the head; figs. 4.1D, 4.24) and the novel hemelytron (the largely sclerotized, protective forewing; figs. 4.1E, 4.25), the adaptation behind the order's etymology (*hetero* + *ptera*, or different winged), likely facilitated multiple independent evolutions of predaceous behavior from a phytophagous ancestor (including two independent evolutions of haematophagy) and, perhaps as a consequence of having more varied feeding behaviors, multiple transitions to aquatic and semi-aquatic habitats. The prognathous placement of the labium clearly facilitates a more versatile suite of feeding behaviors including predation, blood-feeding, and mycophagy, none of which occur in the entirely phytophagous and terrestrial Homoptera (excepting some funigvorous nymphs). This behavioral diversity may explain how Heteroptera comprises more families (~90 vs. 75) that are "younger" (e.g., Pentatomoidea, Coreoidea) and less frequently contested, but fewer species.

A subsequent loss of the hemelytron (in Enicocephalomorpha, Dipsocoromorpha and Gerromorpha; the families of which originated 158–70 Ma; figs. 4.5, 4.25) likely occurred as a result of the radiation of angiosperms (150–60 Ma) producing a diverse understory flora with more readily decomposable litter habitats (Berendse and Scheffer 2009) in which the partially hardened forewing conferred less protective benefit. This suite of niches was filled by predaceous litter dwellers (Enicocephalomorpha and Dipsocoromorpha) likely exploiting the increased diversity of litter grazers. Predaceous water surface dwellers (Gerromorpha), submerged swimmers (Nepomorpha), and even shoreline inhabitants (Leptopodomorpha) would also benefit from increased litter turnover (and therefore, increased litter-feeding prey) as it would accumulate floating on the water surface, in detritus-rich beds, and along banks. The family diversification of hemelytrous Nepomorpha pre-dated the angiospermous litter increase, with their foraging advantaged by the three-dimensional space less affected by climate (e.g., drought, wind, rainfall) and also compromised by higher visibility by their vertebrate predators often away from the cover of surface or bed litter (hence the need for the protective wing). Interestingly, all aquatic, semiaquatic and litter-dwelling infraorders (incidentally all predators except the omnivorous Corixidae (Nepomorpha)) were recovered as a monophyletic group with the previously considered "basal infraorders" in a more derived

position than the plant bugs and lace bugs (mostly and entirely phytophagous, respectively). These “basal infraorders” supported the notion that Heteroptera had a predaceous ancestor, whereas the phylogeny (fig. 4.3) and ancestral state reconstructions (fig. 4.5) indicate a phytophagous ancestor for all Heteroptera, sharply contrasting hypotheses of their relictual status. Apparently a predaceous ancestor gave rise to all predaceous litter-dwelling and aquatic taxa in Heteroptera, but was itself derived from a phytophagous ancestor.

Angiosperm coevolution was often the default explanation for major radiations. The family diversification of Pentatomomorpha (especially Pentatomoidea and Coreoidea) coincided, in large part, with the consequent decline of gymnosperms (i.e., shift to angiosperm dominance; 125–100 Ma) (Berendse and Scheffer 2009). However, at the family-level there is little clear association to be made between hemipteran radiation and angiosperms even if proposed subsequent intrafamilial radiations in Homoptera coincided with angiosperm radiation. Whereas angiosperms may have driven much intrafamilial diversity in many groups, the diversity of habitat and feeding behavior observed in Heteroptera can almost entirely be linked to diversification events coincident with an era of angiosperm suppression before 150 Ma. Of course, hypothesizing explanations for such ancient events remains challenging. Future studies focusing on thoroughly sampling each suborder/infraorder must be conducted to elucidate finer intrafamilial radiation stories (perhaps for interfamilial relationships as well).

Similarly, Hunt et al. (2007) failed to directly link the “superradiation” of beetles (which account for 25% of all Metazoa) 285 Ma to angiosperm coevolution. Crowson (1981) instead suggested that it was, perhaps, the development of the elytron – the strongly sclerotized, sheath-like front wings typical of the order Coleoptera (beetles), which serve as a protective measure while preserving hindwing-propelled flight. Like beetles, true bugs exhibit immense versatility with diverse habitat colonization, varied feeding habits and modified forewings that confer protection and even facilitate plastron (air bubble) retention for aquatic respiration. The modified, protective forewings of beetles and true bugs may account for the rapid lineage diversification and likely facilitated the versatile feeding and habitat colonization (including multiple independent

shifts to predation and aquatic habitats; Hunt et al. 2007; figs. 4.4-4.5, 4.22-4.25) that birthed the biodiversity before us today.

Table 4.1 Test of substitution saturation of protein-coding genes.

Dataset	NumOTU	Iss	Iss.cSym[a]	P_{sym}[b]	Iss.cAsym[c]	P_{Asym}[d]	Evidence for selection
1st codon of PCGs	4	0.444	0.85	0	0.839	0	weak
	8	0.458	0.843	0	0.762	0	
	16	0.48	0.828	0	0.673	0	
	32	0.504	0.809	0	0.558	0.0002	
2nd codon of PCGs	4	0.322	0.85	0	0.839	0	weak
	8	0.335	0.843	0	0.762	0	
	16	0.359	0.828	0	0.673	0	
	32	0.382	0.809	0	0.558	0	
3rd codon of PCGs	4	0.717	0.85	0	0.839	0	strong
	8	0.734	0.843	0	0.762	0.0047	
	16	0.753	0.828	0	0.673	0	
	32	0.772	0.809	0.0027	0.558	0	
1st and 2nd codon of PCGs	4	0.385	0.855	0	0.845	0	weak
	8	0.4	0.846	0	0.765	0	
	16	0.414	0.844	0	0.679	0	
	32	0.439	0.815	0	0.571	0	
1st codon of ATP6	4	0.488	0.777	0	0.762	0	strong
	8	0.509	0.732	0	0.631	0.0064	
	16	0.519	0.653	0.0071	0.458	0.2155	
	32	0.537	0.685	0.0072	0.364	0.0019	
2nd codon of ATP6	4	0.327	0.777	0	0.762	0	weak
	8	0.335	0.732	0	0.631	0	
	16	0.35	0.653	0	0.458	0.0314	
	32	0.374	0.685	0	0.364	0.8706	
3rd codon of ATP6	4	0.829	0.777	0.1432	0.762	0.0626	strong
	8	0.841	0.732	0.0036	0.631	0	
	16	0.865	0.653	0	0.458	0	
	32	0.878	0.685	0	0.364	0	
1st and 2nd codon of ATP6	4	0.397	0.792	0	0.759	0	weak
	8	0.4	0.747	0	0.635	0	
	16	0.421	0.711	0	0.502	0.025	
	32	0.443	0.696	0	0.369	0.0644	
1st codon of ATP8	4	0.688	0.955	0.0027	1.115	0	weak
	8	0.726	1.058	0.0005	1.129	0	
	16	0.738	0.56	0.0697	0.711	0.7758	
	32	0.763	1.245	0	1.346	0	
2nd codon of ATP8	4	0.649	0.955	0.0011	1.115	0	weak
	8	0.677	1.058	0.0003	1.129	0	
	16	0.7	0.56	0.1901	0.711	0.9163	
	32	0.713	1.245	0	1.346	0	
3rd codon of ATP8	4	0.924	0.955	0.6785	1.115	0.0137	strong
	8	0.949	1.058	0.1576	1.129	0.0224	
	16	0.961	0.56	0	0.711	0.0042	
	32	0.987	1.245	0.0084	1.346	0.0004	
1st and 2nd codon of ATP8	4	0.654	0.816	0.0101	0.871	0.0007	strong

	8	0.668	0.817	0.0276	0.777	0.1078	
	16	0.7	0.581	0.1	0.5	0.0066	
	32	0.722	0.84	0.1415	0.648	0.3551	
1st codon of COX1	4	0.226	0.795	0	0.761	0	weak
	8	0.231	0.751	0	0.639	0	
	16	0.239	0.719	0	0.51	0	
	32	0.245	0.701	0	0.376	0	
2nd codon of COX1	4	0.107	0.795	0	0.761	0	weak
	8	0.111	0.751	0	0.639	0	
	16	0.114	0.719	0	0.51	0	
	32	0.118	0.702	0	0.377	0	
3rd codon of COX1	4	0.684	0.795	0	0.761	0.0008	strong
	8	0.711	0.751	0.0606	0.639	0.0008	
	16	0.711	0.719	0.6955	0.51	0	
	32	0.714	0.701	0.4766	0.376	0	
1st and 2nd codon of COX1	4	0.166	0.82	0	0.788	0	weak
	8	0.168	0.787	0	0.681	0	
	16	0.18	0.77	0	0.572	0	
	32	0.177	0.747	0	0.44	0	
1st codon of COX2	4	0.32	0.777	0	0.768	0	
	8	0.327	0.735	0	0.638	0	weak
	16	0.334	0.641	0	0.454	0.0039	
	32	0.341	0.692	0	0.378	0.3663	
2nd codon of COX2	4	0.186	0.777	0	0.768	0	weak
	8	0.186	0.735	0	0.638	0	
	16	0.189	0.641	0	0.454	0	
	32	0.195	0.692	0	0.378	0	
3rd codon of COX2	4	0.743	0.777	0.3576	0.768	0.4847	strong
	8	0.745	0.735	0.7676	0.638	0.0019	
	16	0.75	0.641	0.0006	0.454	0	
	32	0.762	0.692	0.0165	0.378	0	
1st and 2nd codon of COX2	4	0.249	0.788	0	0.757	0	weak
	8	0.256	0.741	0	0.63	0	
	16	0.254	0.7	0	0.491	0	
	32	0.265	0.69	0	0.361	0.0006	
1st codon of COX3	4	0.338	0.778	0	0.759	0	weak
	8	0.345	0.732	0	0.628	0	
	16	0.343	0.663	0	0.463	0.0005	
	32	0.361	0.683	0	0.357	0.9045	
2nd codon of COX3	4	0.205	0.778	0	0.759	0	weak
	8	0.209	0.732	0	0.628	0	
	16	0.223	0.663	0	0.463	0	
	32	0.233	0.683	0	0.357	0.0001	
3rd codon of COX3	4	0.697	0.778	0.0119	0.759	0.0538	strong
	8	0.732	0.732	0.9984	0.628	0.0005	
	16	0.731	0.663	0.0117	0.463	0	
	32	0.743	0.683	0.0145	0.357	0	
1st and 2nd codon of COX3	4	0.254	0.796	0	0.762	0	weak
	8	0.275	0.752	0	0.64	0	

	16	0.285	0.721	0	0.512	0	
	32	0.297	0.703	0	0.378	0.001	
1st codon of CytB	4	0.31	0.784	0	0.755	0	weak
	8	0.312	0.737	0	0.627	0	
	16	0.324	0.689	0	0.481	0	
	32	0.331	0.685	0	0.355	0.444	
2nd codon of CytB	4	0.162	0.784	0	0.755	0	weak
	8	0.158	0.737	0	0.627	0	
	16	0.167	0.689	0	0.481	0	
	32	0.174	0.685	0	0.355	0	
3rd codon of CytB	4	0.701	0.784	0.0029	0.755	0.0492	strong
	8	0.729	0.737	0.7442	0.627	0.0001	
	16	0.737	0.688	0.0277	0.481	0	
	32	0.745	0.685	0.003	0.355	0	
1st and 2nd codon of CytB	4	0.229	0.806	0	0.775	0	weak
	8	0.236	0.767	0	0.658	0	
	16	0.238	0.747	0	0.538	0	
	32	0.249	0.721	0	0.395	0	
1st codon of ND1	4	0.401	0.779	0	0.757	0	weak
	8	0.407	0.733	0	0.626	0	
	16	0.411	0.672	0	0.468	0.0978	
	32	0.415	0.682	0	0.354	0.076	
2nd codon of ND1	4	0.235	0.779	0	0.757	0	weak
	8	0.232	0.733	0	0.626	0	
	16	0.236	0.672	0	0.468	0	
	32	0.249	0.682	0	0.354	0.0002	
3rd codon of ND1	4	0.728	0.779	0.1038	0.757	0.3652	strong
	8	0.749	0.733	0.5759	0.626	0	
	16	0.757	0.672	0.0016	0.468	0	
	32	0.764	0.682	0.001	0.354	0	
1st and 2nd codon of ND1	4	0.297	0.799	0	0.767	0	weak
	8	0.315	0.757	0	0.646	0	
	16	0.323	0.731	0	0.52	0	
	32	0.332	0.708	0	0.38	0.0375	
1st codon of ND2	4	0.603	0.778	0	0.758	0	strong
	8	0.614	0.732	0.0008	0.627	0.711	
	16	0.623	0.664	0.2144	0.463	0	
	32	0.634	0.683	0.1323	0.357	0	
2nd codon of ND2	4	0.395	0.778	0	0.758	0	weak
	8	0.411	0.732	0	0.627	0	
	16	0.406	0.664	0	0.463	0.1135	
	32	0.417	0.683	0	0.357	0.0902	
3rd codon of ND2	4	0.855	0.778	0.015	0.758	0.0024	strong
	8	0.856	0.732	0	0.627	0	
	16	0.868	0.664	0	0.463	0	
	32	0.873	0.683	0	0.357	0	
1st and 2nd codon of ND2	4	0.486	0.796	0	0.762	0	weak
	8	0.482	0.752	0	0.641	0	
	16	0.495	0.722	0	0.513	0.472	

	32	0.503	0.703	0	0.378	0	
1st codon of ND3	4	0.485	0.801	0	0.839	0	weak
	8	0.478	0.789	0	0.732	0	
	16	0.481	0.591	0.0444	0.479	0.9765	
	32	0.492	0.791	0	0.561	0.1979	
2nd codon of ND3	4	0.326	0.801	0	0.839	0	weak
	8	0.33	0.789	0	0.732	0	
	16	0.34	0.591	0	0.479	0.0122	
	32	0.35	0.791	0	0.561	0.0002	
3rd codon of ND3	4	0.779	0.801	0.6507	0.839	0.2203	strong
	8	0.786	0.789	0.9506	0.732	0.2281	
	16	0.799	0.591	0	0.479	0	
	32	0.81	0.791	0.5772	0.561	0	
1st and 2nd codon of ND3	4	0.382	0.776	0	0.766	0	weak
	8	0.396	0.734	0	0.635	0	
	16	0.406	0.646	0	0.456	0.2113	
	32	0.411	0.689	0	0.372	0.3185	
1st codon of ND4	4	0.496	0.786	0	0.756	0	weak
	8	0.504	0.739	0	0.629	0	
	16	0.511	0.695	0	0.486	0.4163	
	32	0.52	0.688	0	0.358	0	
2nd codon of ND4	4	0.315	0.786	0	0.756	0	weak
	8	0.329	0.739	0	0.629	0	
	16	0.329	0.695	0	0.486	0	
	32	0.334	0.688	0	0.358	0.4316	
3rd codon of ND4	4	0.785	0.786	0.9682	0.756	0.287	strong
	8	0.8	0.739	0.0138	0.629	0	
	16	0.813	0.695	0	0.486	0	
	32	0.809	0.688	0	0.358	0	
1st and 2nd codon of ND4	4	0.413	0.809	0	0.778	0	weak
	8	0.408	0.771	0	0.663	0	
	16	0.416	0.752	0	0.545	0	
	32	0.43	0.726	0	0.404	0.2411	
1st codon of ND4L	4	0.558	0.852	0	0.939	0	weak
	8	0.56	0.882	0	0.874	0	
	16	0.572	0.567	0.9366	0.553	0.751	
	32	0.58	0.949	0	0.839	0	
2nd codon of ND4L	4	0.438	0.852	0	0.939	0	weak
	8	0.422	0.882	0	0.874	0	
	16	0.433	0.567	0.0574	0.553	0.0891	
	32	0.442	0.949	0	0.839	0	
3rd codon of ND4L	4	0.813	0.852	0.5348	0.939	0.0473	strong
	8	0.836	0.882	0.4172	0.874	0.506	
	16	0.839	0.567	0	0.553	0	
	32	0.848	0.949	0.0183	0.839	0.8382	
1st and 2nd codon of ND4L	4	0.493	0.784	0	0.799	0	weak
	8	0.503	0.755	0	0.677	0.0005	
	16	0.512	0.611	0.0426	0.458	0.2695	
	32	0.512	0.731	0	0.453	0.224	

1st codon of ND5	4	0.497	0.793	0	0.76	0	weak
	8	0.487	0.749	0	0.637	0	
	16	0.506	0.715	0	0.506	0.9944	
	32	0.516	0.699	0	0.372	0	
2nd codon of ND5	4	0.334	0.793	0	0.76	0	weak
	8	0.337	0.749	0	0.637	0	
	16	0.328	0.715	0	0.506	0	
	32	0.338	0.699	0	0.372	0.211	
3rd codon of ND5	4	0.787	0.793	0.7907	0.76	0.2585	strong
	8	0.804	0.749	0.012	0.637	0	
	16	0.805	0.715	0	0.506	0	
	32	0.811	0.699	0	0.373	0	
1st and 2nd codon of ND5	4	0.394	0.818	0	0.786	0	weak
	8	0.401	0.784	0	0.678	0	
	16	0.415	0.767	0	0.567	0	
	32	0.421	0.743	0	0.433	0.5488	
1st codon of ND6	4	0.59	0.839	0.0001	0.914	0	weak
	8	0.602	0.858	0.0001	0.838	0.0003	
	16	0.615	0.571	0.4544	0.533	0.162	
	32	0.617	0.909	0	0.769	0.0075	
2nd codon of ND6	4	0.379	0.839	0	0.914	0	weak
	8	0.377	0.858	0	0.838	0	
	16	0.379	0.571	0.0017	0.533	0.0108	
	32	0.392	0.909	0	0.769	0	
3rd codon of ND6	4	0.837	0.839	0.9827	0.914	0.1813	strong
	8	0.868	0.858	0.8471	0.838	0.553	
	16	0.872	0.571	0	0.533	0	
	32	0.872	0.909	0.3279	0.769	0.0072	
1st and 2nd codon of ND6	4	0.467	0.781	0	0.789	0	weak
	8	0.449	0.748	0	0.665	0	
	16	0.456	0.618	0.0004	0.455	0.9859	
	32	0.467	0.718	0	0.43	0.3996	

a Index of substitution saturation assuming a symmetrical true tree.
b Probability of significant difference between Iss and Iss.cSym (two-tailed test).
c Index of substitution saturation assuming an asymmetrical true tree.
d Probability of significant difference between Iss and Iss.cAsym (two-tailed test).

Table 4.2 Nodal support values for the higher taxa of Hemiptera. Analysis methods are Bayesian inference (BI) and maximum likelihood (ML) and data sets with PCGs (1) excluding (No 3rd) and including (All codon) third codon positions, (2) partitioned by gene (GP) and by codon (CP) position and (3) employing nucleotide and codon (M3) models.

Taxon	No 3rd (BI-GP)	No 3rd (BI-CP)	No 3rd (ML-GP)	All Codon (BI-GP)	All Codon (BI-CP)	All Codon (ML-GP)	All codon (BI-M3)
Hemiptera	1	1	100	1	1	100	1
Homoptera	1	1	64	1	1	70	1
Auchenorrhyncha	Polyphyly	Polyphyly	Polyphyly	Polyphyly	Polyphyly	Polyphyly	Polyphyly
Cicadomorpha	1	1	98	1	1	100	1
Fulgoromorpha	1	1	100	1	1	100	1
Coleorrhyncha	1	1	100	1	1	100	1
Sternorrhyncha	1	1	96	1	1	98	1
Heteroptera	1	1	100	1	1	100	1
Enicocephalomorpha[1]	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Dipsocoromorpha	1	1	100	1	1	100	1
Gerromorpha	1	1	100	1	1	100	1
Leptopodomorpha	1	1	100	1	1	100	1
Nepomorpha	1	1	87	1	1	66	1
Cimicomorpha	Paraphyly	Paraphyly	Paraphyly[2]	Paraphyly	Paraphyly	Paraphyly[2]	Polyphyly
Pentatomomorpha	1	1	98	1	1	94	0.87

[1] Only one terminal, so monophyly/clade support not determined

[2] Unresolved in majority rule consensus tree, but paraphyletic in best ML tree

Table 4.3. Results of the likelihood-based approximately unbiased (AU), Shimodiara-Hasegawa (SH), weighted Kishino-Hasegawa (WKH), and weighted Shimodiara-Hasegawa (WSH) tests calculated using CONSEL. Bold highlights statistical significance. Trees compared were the best topology from unconstrained analyses versus an analysis where Auchenorrhyncha and Cimicomorpha were constrained to be monophyletic.

			Test			
Constraint	**-ln L**	**Difference**	**AU**	**SH**	**WKH**	**WSH**
Unconstrained	-590892.43	(Best)				
Auchenorrhyncha	-590987.20	94.77	**p = 0.003**	**p = 0.008**	**p = 0.003**	**p = 0.006**
Cimicomorpha	-590940.27	47.84	p = 0.102	p = 0.159	p = 0.094	p = 0.153

Table 4.4 Fossil calibration with fossil taxonomic information, fossil age and references.

Fossil	Node assigned	Age (Ma)	References
Archescytinidae	Hemiptera	303-296	1
Elasmocelidium, Tetragonidium	Delphacidae+Fulgoridae+Flatidae+Issidae	205.7-197	2
Mesococcus asiaticus	Cicadellidae+ Aetalionidae+ Membracidae	248.2-205.7	3
Saldonia rasnitsyni	Leptopodomorpha	205.7-142	4
Proprecoris maculatus	Ochteroidea	295.7-197	5
Lethonectes naucoroides	Nepoidea	201.9-195.5	1, 6
Cretogerris albianus	Veliidae+Gerridae	105.3-99.7	7
Leipolygaeus similis	Lygaeoidea	205.7-180.1	8
Cydnavites, Orienicydnus	Pentatomoidea	142-121	1, 9, 10
Asopus puncticollis	Pentatomidae	65-54.8	11

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Table 4.5 Age estimates of selected hemipteran clades with mean ages and 95% highest probability density intervals.

Taxa clade	Divergence time (Ma)	
	Mean age	**95% HPD**
Psocoptera+ Hemiptera	345.6	312.5-400.8
Hemiptera	300.7	296.2-304.8
Homoptera	291.6	280.8-300.5
Coleorrhyncha+Fulgoromorpha+Sternorrhyncha	275.5	253.6-291.9
Fulgoromorpha+Sternorrhyncha	261.3	237.1-279.1
Cicadomorpha	271.1	250.1-287.6
Fulgoromorpha	201.4	196.0-206.6
Coleorrhyncha	156.0	85.3-232.2
Sternorrhyncha	237.2	210.8-264.8
Heteroptera	271.7	251.2-291.9
Enicocephalomorpha+Dipsocoromorpha+Gerromorpha	206.2	163.3-239.5
Enicocephalomorpha+Dipsocoromorpha	168.1	46.8-213.5
Dipsocoromorpha	130.9	32.0-185.4
Gerromorpha	146.2	99.1-181.3
Nepomorpha	228.9	216.6-241.8
Leptopodomorpha	168.5	136.6-199.2
Cimicomorpha [a]	238.0	198.4-261.0
Cimicomorpha (Miridae+Tingidae)	228.9	187.4-256.1
Pentatomomorpha	249.2	219.6-270.5
Aradidae	183.6	101.4-242.2
Pentatomoidea	138.9	128.1-150.3
Pyrrochoroidea	124.5	24.9-189.1
Coreoidea	124.3	49.8-163.6
Lygaeoidea	184.7	160.2-198.8

[a] excluding Tingidae and Miridae.

Table 4.6. Taxa used in this study.

Order	Family	Species	Accession number	Reference
outgroups				
Isoptera	Rhinotermitidae	*Reticulitermes virginicus*	NC_009500	1
Blattodea	Ectobiidae	*Blattella germanica*	NC_012901	2
Mantodea	Mantidae	*Tamolanica tamolana*	NC_007702	3
Psocoptera	Lepidopsocidae	Lepidopsocid sp.	NC_004816	4
	Psocidae	*Psococerastis albimaculata*	JQ910989	5
		Longivalvus hyalospilus	JQ910986	5
ingroups				
Hemiptera				
Sternorrhyncha	Psyllidae	*Pachypsylla venusta*	NC_006157	6
	Aphididae	*Acyrthosiphon pisum*	NC_011594	Moran et al., unpublished
		Schizaphis graminum	NC_006158	6
	Aleyrodidae	*Aleurochiton aceris*	NC_006160	6
		Aleurodicus dugesii	NC_005939	6
		Bemisia tabaci	NC_006279	6
		Trialeurodes vaporariorum	NC_006280	6
Auchenorrhyncha	Flatidae	*Geisha distinctissima*	NC_012617	7
	Fulgoridae	*Lycorma delicatula*	NC_012835	8
	Issidae	*Sivaloka damnosa*	NC_014286	9
	Aphrophoridae	*Philaenus spumarius*	NC_005944	10
	Cercopidae	*Abidama producta*	NC_015799	Liu J, unpublished
	Cicadellidae		NC_006899	Baumann L, Baumann,P, unpublished
		Homalodisca vitripennis		
	Delphacidae	*Laodelphax striatellus*	NC_013706	11
	Cicadidae	*Oncotympana maculaticollis*	JQ910987	present study
		Cryptotympana atrata	JQ910980	present study
	Membracidae	*Leptobelus* sp.	JQ910984	present study
	Aetalionidae	*Darthura hardwicki*	JQ910982	present study
Coleorrhyncha	Peloridiidae	*Peloridora minuta*	JQ739183	present study
		Peloridium hammoniorum	JQ739182	present study
Heteroptera				
Enicocephalomorpha	Enicocephalidae	*Stenopirates* sp.	NC_016017	12
Dipsocoromorpha	Schizopteridae	*Hypselosoma matsumurae*	JQ739177	present study
	Ceratocombidae	*Ceratocombus japonicus*	JQ739175	present study
		Ceratocombus sp.	JQ739176	present study
Gerromorpha	Hydrometridae	*Hydrometra* sp.	NC_012842	8
	Gerridae	*Aquarius paludum*	NC_012841	8
	Veliidae	*Perittopus* sp.	JQ910988	present study

Order	Family	Species	Accession number	Reference
Nepomorpha	Notonectidae	*Enithares tibialis*	NC_012819	8
	Pleidae	*Paraplea frontalis*	NC_012822	8
	Gelastocoridae	*Nerthra* sp.	NC_012838	8
	Ochteridae	*Ochterus marginatus*	NC_012820	8
	Naucoridae	*Ilyocoris cimicoides*	NC_012845	8
	Nepidae	*Laccotrephes robustus*	NC_012817	8
	Belostomatidae	*Diplonychus rusticus*	FJ456940	8
		Kirkaldyia deyrolli	JQ910985	present study
	Aphelocheiridae	*Aphelocheirus ellipsoideus*	FJ456939	8
	Corixidae	*Sigara septemlineata*	FJ456941	8
Leptopodomorpha	Saldidae	*Saldula arsenjevi*	NC_012463	13
	Leptopodidae	*Leptopus* sp.	FJ456946	8
Cimicomorpha	Anthocoridae	*Orius niger*	NC_012429	13
	Reduviidae	*Triatoma dimidiata*	NC_002609	14
		Valentia hoffmanni	NC_012823	13
		Agriosphodrus dohrni	NC_015842	15
	Cimicidae	*Cimex lectularius*	JQ739180	present study
	Velocipedidae	*Scotomedes* sp.	JQ743677	present study
	Tingidae	*Stephanitis mendica*	JQ739184	present study
		Ammianus toi	JQ739178	present study
	Miridae	*Lygus lineolaris*	NC_021975	16
		Apolygus lucorum	NC_023083	17
	Nabidae	*Alloeorhynchus bakeri*	NC_016432	18
Pentatomomorpha	Aradidae	*Neuroctenus parus*	NC_012459	13
		Aradacanthia heissi	HQ441233	19
	Cydnidae	*Macroscytus subaeneus*	NC_012457	13
	Pentatomidae	*Nezara viridula*	NC_011755	13
		Halyomorpha halys	NC_013272	20
		Erthesina fullo	JQ743673	present study
		Dolycoris baccarum	JQ743672	present study
	Plataspidae	*Coptosoma bifaria*	NC_012449	13
		Megacopta cribraria	NC_015342	Eaton and Jenkins, unpublished
	Scutelleridae	*Eucorysses grandis*	JQ743671	present study
		Lamprocoris roylii	JQ743674	present study
		Poecilocoris nepalensis	JQ743675	present study
	Acanthosomatidae	*Acanthosoma labiduroides*	JQ743670	present study
		Sastragala edessoides	JQ743676	present study
	Tessaratomidae	*Eusthenes cupreus*	NC_022449	21
		Dalcantha dilatata	JQ910981	present study
	Urostylidae	*Urochela quadrinotata*	NC_020144	22

Order	Family	Species	Accession number	Reference
		Urochela sp.	JQ743679	present study
	Dinidoridae	*Coridius chinensis*	JQ739179	23
		Megymenum brevicorne	JQ739181	present study
	Berytidae	*Yemmalysus parallelus*	NC_012464	13
	Colobathristidae	*Phaenacantha marcida*	NC_012460	13
	Stenocephalidae	*Dicranocephalus femoralis*	JQ910990	present study
	Malcidae	*Malcus inconspicuus*	NC_012458	13
	Geocoridae	*Geocoris pallidipennis*	NC_012424	13
	Pyrrhocoridae	*Dysdercus cingulatus*	NC_012421	13
	Largidae	*Physopelta gutta*	NC_012432	13
	Coreidae	*Hydaropsis longirostris*	NC_012456	13
	Alydidae	*Riptortus pedestris*	NC_012462	13
	Rhopalidae	*Stictopleurus subviridis*	NC_012888	13
		Aeschyntelus notatus	NC_012446	13

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Table 4.7 Primer sequences used in this study.

No. fragment	Primer ID	Nucleotide sequence (5'-3')
1	TI-J34	GCCTGATAAAAAGGRTTAYYTTGATA
	C1-N1738	TTTATTCGTGGRAATGCYATRTC
2	TM-J210	AATTAAGCTACTAGGTTCATACCC
	TW-N1284	ACARCTTTGAAGGYTAWTAGTTT
3	C1-J1709	AATTGGWGGWTTYGGAAAYTG
	C1- N2776	GGTAATCAGAGTATCGWCGNGG
4	C1-J2756	ACATTTTTTCCTCAACATTT
	C2-N3665	CCACAAATTTCTGAACACTG
5	C2-J3399	TCTATTGGTCATCAATGGTACTG
	A8-N4061	GAAAATAAATTTGTTATCATTTTCA
6	TK-J3790	CATTAAGTGACTGAAAGCAAGTA
	A6-N4552	ATGACCTGCAATTATATTAGC
7	A6- J4463	TTTGCCCATCTWGTWCCNCAAGG
	C3-N5460	TCAACAAAATGTCARTAYCA
8	C3-J4792	GTTGATTATAGACCWTGRCC
	N3-N5731	TTAGGGTCAAATCCRCAYTC
9	C3-J5470	GCAGCTGCYTGATAYTGRCA
	TN-N6160	TCAATTTTRTCATTAACAGTGA
10	TN-J6155	TTTAATTGAARCCAAAAAGAGG
	N5-N7211	TTAAGGCTTTAYTATTTATRTGYGC
11	N5-J7077	TTAAATCCTTTGAGTAAAATCC
	N5-N7793	TTAGGTTGAGATGGTTTAGG
12	N5-J7572	AAAGGGAATTTGAGCTCTTTTWGT
	N4-N8727	AAATCTTTRATTGCTTATTCWTC
13	N4-J8641	CCAGAAGAACATAANCCRTG
	N4L-N9629	GTTTGTGAGGGWGYTTTRGG
14	N4-J9172	CGCTCAGGYTGRTACCCYCA
	CB-N10608	CCAAGTARTGAWCCAAARTTTCA
15	N4L-J9648	TCCCAACACACCTTCACAAAC
	CB- N11010	TATCAACAGCAAATCCTCCTCA
16	CB-J10621	CTCATACTGATGAAATTTTGGTTC
	CB-N11526	TTCTACTGGTCGTGCTCCAATTCA
17	CB-J11335	CATATTCAACCAGAATGATA
	N1-N12067	AATCGTTCTCCATTTGATTTTGC
18	N1-J11876	CGAGGTAAAGTMCCWCGAACYCA
	N1-N12595	GTWGCTTTTTTAACTTTATTRGARCG
19	N1-J12261	TACCTCATAAGAAATAGTTTGAGC
	LR-N13000	TTACCTTAGGGATAACAGCGTAA
20	LR-J12888	CCGGTTTGAACTCARATCATGTAA
	LR-N13889	ATTTATTGTACCTTKTGTATCAG
21	SR-J13342	CCTTCGCACRGTCAAAATACYGC

	SR-N14220	ATATGYACAYATCGCCCGTC
22	LR-J14197	GTAAAYCTACTTTGTTACGACTT
	SR-N14745	GTGCCAGCAAYCGCGGTTATAC
23	SR- J14610	ATAATAGGGTATCTAATCCTAGT
	TM- N200	ACCTTTATAARTGGGGTATGARCC

Table 4.8 Appropriate models of nucleotide evolution for gene and codon partitions according to the AIC in jModelTest.

Gene and codon partitions	**Model selection**
ATP6	GTR+I+G
1st and 2nd codon position of ATP6	GTR+I+G
1st codon position of ATP6	GTR+I+G
2nd codon position of ATP6	GTR+I+G
3rd codon position of ATP6	GTR+G
ATP8	GTR+I+G
1st and 2nd codon position of ATP8	GTR+I+G
1st codon position of ATP8	F81+I+G
2nd codon position of ATP8	GTR+I+G
3rd codon position of ATP8	GTR+I+G
COX1	GTR+I+G
1st and 2nd codon position of COX1	GTR+I+G
1st codon position of COX1	GTR+I+G
2nd codon position of COX1	GTR+I+G
3rd codon position of COX1	GTR+G
COX2	GTR+I+G
1st and 2nd codon position of COX2	GTR+I+G
1st codon position of COX2	GTR+G
2nd codon position of COX2	GTR+I+G
3rd codon position of COX2	GTR+G
COX3	GTR+G
1st and 2nd codon position of COX3	GTR+I+G
1st codon position of COX3	GTR+I+G
2nd codon position of COX3	GTR+I+G
3rd codon position of COX3	GTR+I+G
CytB	GTR+I+G
1st and 2nd codon position of CytB	GTR+I+G
1st codon position of CytB	GTR+I+G
2nd codon position of CytB	GTR+I+G
3rd codon position of CytB	GTR+G
ND1	GTR+I+G
1st and 2nd codon position of ND1	GTR+I+G
1st codon position of ND1	GTR+I+G
2nd codon position of ND1	GTR+I+G
3rd codon position of ND1	GTR+G
ND2	GTR+I+G
1st and 2nd codon position of ND2	GTR+I+G
1st codon position of ND2	GTR+I+G

2nd codon position of ND2	GTR+I+G
3rd codon position of ND2	GTR+G
ND3	GTR+G
1st and 2nd codon position of ND3	GTR+I+G
1st codon position of ND3	GTR+I+G
2nd codon position of ND3	GTR+I+G
3rd codon position of ND3	HKY+I+G
ND4	GTR+I+G
1st and 2nd codon position of ND4	GTR+I+G
1st codon position of ND4	GTR+I+G
2nd codon position of ND4	GTR+I+G
3rd codon position of ND4	GTR+I+G
ND4L	GTR+I+G
1st and 2nd codon position of ND4L	GTR+I+G
1st codon position of ND4L	GTR+I+G
2nd codon position of ND4L	GTR+I+G
3rd codon position of ND4L	GTR+G
ND5	GTR+I+G
1st and 2nd codon position of ND5	GTR+I+G
1st codon position of ND5	GTR+I+G
2nd codon position of ND5	GTR+I+G
3rd codon position of ND5	GTR+I+G
ND6	GTR+I+G
1st and 2nd codon position of ND6	GTR+I+G
1st codon position of ND6	HKY+I+G
2nd codon position of ND6	GTR+I+G
3rd codon position of ND6	GTR+G
tRNA-Arg	HKY+G
tRNA-Asn	HKY+G
tRNA-Asp	SYM+G
tRNA-Cys	HKY+G
tRNA-Glu	HKY+G
tRNA-Gly	GTR+G
tRNA-His	HKY+I+G
tRNA-Leu1	HKY+G
tRNA-Leu2	HKY+G
tRNA-Lys	HKY+G
tRNA-Phe	HKY+G
tRNA-Pro	HKY+G
tRNA-Ser	K80+G
tRNA-Thr	HKY+G
tRNA-Trp	HKY+G
tRNA-Tyr	GTR+G

tRNA-Val	GTR+G
12S rRNA	GTR+I+G
16S rRNA	GTR+I+G

Table 4.9 Sources of data for ancestral character state reconstruction.

Family	Species	Habitat	Feeding habits	Mouthpart origin	Presence of hemelytra
Rhinotermitidae	*Reticulitermes virginicus*	Terrestrial	Phytophagous	?	Absent
Ectobiidae	*Blattella germanica*	Terrestrial	Phytophagous	?	Absent
Mantidae	*Tamolanica tamolana*	Terrestrial	Predaceous	?	Absent
Lepidopsocidae	Lepidopsocid sp.	Terrestrial	Phytophagous	?	Absent
Psocidae	*Psococerastis albimaculata*	Terrestrial	Phytophagous	?	Absent
	Longivalvus hyalospilus	Terrestrial	Phytophagous	?	Absent
Psyllidae	*Pachypsylla venusta*	Terrestrial	Phytophagous	Sternal	Absent
Aphididae	*Acyrthosiphon pisum*	Terrestrial	Phytophagous	Sternal	Absent
	Schizaphis graminum	Terrestrial	Phytophagous	Sternal	Absent
Aleyrodidae	*Aleurochiton aceris*	Terrestrial	Phytophagous	Sternal	Absent
	Aleurodicus dugesii	Terrestrial	Phytophagous	Sternal	Absent
	Bemisia tabaci	Terrestrial	Phytophagous	Sternal	Absent
	Trialeurodes vaporariorum	Terrestrial	Phytophagous	Sternal	Absent
Flatidae	*Geisha distinctissima*	Terrestrial	Phytophagous	Middle	Absent
Fulgoridae	*Lycorma delicatula*	Terrestrial	Phytophagous	Middle	Absent
Issidae	*Sivaloka damnosa*	Terrestrial	Phytophagous	Middle	Absent
Aphrophoridae	*Philaenus spumarius*	Terrestrial	Phytophagous	Middle	Absent
Cercopidae	*Abidama producta*	Terrestrial	Phytophagous	Middle	Absent
Cicadellidae	*Homalodisca vitripennis*	Terrestrial	Phytophagous	Middle	Absent
Delphacidae	*Laodelphax striatellus*	Terrestrial	Phytophagous	Middle	Absent
Cicadidae	*Oncotympana maculaticollis*	Terrestrial	Phytophagous	Middle	Absent
	Cryptotympana atrata	Terrestrial	Phytophagous	Middle	Absent
Membracidae	*Leptobelus* sp.	Terrestrial	Phytophagous	Middle	Absent
Aetalionidae	*Darthura hardwicki*	Terrestrial	Phytophagous	Middle	Absent
Peloridiidae	*Peloridora minuta*	Terrestrial	Phytophagous	Middle	Absent
	Peloridium hammoniorum	Terrestrial	Phytophagous	Middle	Absent
Enicocephalidae	*Stenopirates* sp.	Terrestrial	Predaceous	Apical	Absent
Schizopteridae	*Hypselosoma matsumurae*	Terrestrial	Predaceous	Apical	Absent
Ceratocombidae	*Ceratocombus japonicus*	Terrestrial	Predaceous	Apical	Absent
	Ceratocombus sp.	Terrestrial	Predaceous	Apical	Absent
Hydrometridae	*Hydrometra* sp.	Surface Skimmer	Predaceous	Apical	Absent
Gerridae	*Aquarius paludum*	Surface Skimmer	Predaceous	Apical	Absent
Veliidae	*Perittopus* sp.	Surface Skimmer	Predaceous	Apical	Absent
Notonectidae	*Enithares tibialis*	Aquatic	Predaceous	Apical	Present
Pleidae	*Paraplea frontalis*	Aquatic	Predaceous	Apical	Present
Gelastocoridae	*Nerthra* sp.	Shoreline	Predaceous	Apical	Present
Ochteridae	*Ochterus marginatus*	Shoreline	Predaceous	Apical	Present
Naucoridae	*Ilyocoris cimicoides*	Aquatic	Predaceous	Apical	Present
Nepidae	*Laccotrephes robustus*	Aquatic	Predaceous	Apical	Present

Family	Species	Habitat	Feeding habits	Mouthpart origin	Presence of hemelytra
Belostomatidae	*Diplonychus rusticus*	Aquatic	Predaceous	Apical	Present
	Kirkaldyia deyrolli	Aquatic	Predaceous	Apical	Present
Aphelocheiridae	*Aphelocheirus ellipsoideus*	Aquatic	Predaceous	Apical	Present
Corixidae	*Sigara septemlineata*	Aquatic	Omnivorous	Apical	Present
Saldidae	*Saldula arsenjevi*	Shoreline	Predaceous	Apical	Present
Leptopodidae	*Leptopus* sp.	Shoreline	Predaceous	Apical	Present
Anthocoridae	*Orius niger*	Terrestrial	Predaceous	Apical	Present
Reduviidae	*Triatoma dimidiata*	Terrestrial	Hematophagous	Apical	Present
	Valentia hoffmanni	Terrestrial	Predaceous	Apical	Present
	Agriosphodrus dohrni	Terrestrial	Predaceous	Apical	Present
Cimicidae	*Cimex lectularius*	Terrestrial	Hematophagous	Apical	Present
Velocipedidae	*Scotomedes* sp.	Terrestrial	Predaceous	Apical	Present
Tingidae	*Stephanitis mendica*	Terrestrial	Phytophagous	Apical	Present
	Ammianus toi	Terrestrial	Phytophagous	Apical	Present
Miridae	*Lygus lineolaris*	Terrestrial	Phytophagous	Apical	Present
	Apolygus lucorum	Terrestrial	Phytophagous	Apical	Present
Nabidae	*Alloeorhynchus bakeri*	Terrestrial	Predaceous	Apical	Present
Aradidae	*Neuroctenus parus*	Terrestrial	Fungivorous	Apical	Present
	Aradacanthia heissi	Terrestrial	Fungivorous	Apical	Present
Cydnidae	*Macroscytus subaeneus*	Terrestrial	Phytophagous	Apical	Present
Pentatomidae	*Nezara viridula*	Terrestrial	Phytophagous	Apical	Present
	Halyomorpha halys	Terrestrial	Phytophagous	Apical	Present
	Erthesina fullo	Terrestrial	Phytophagous	Apical	Present
	Dolycoris baccarum	Terrestrial	Phytophagous	Apical	Present
Plataspidae	*Coptosoma bifaria*	Terrestrial	Phytophagous	Apical	Present
	Megacopta cribraria	Terrestrial	Phytophagous	Apical	Present
Scutelleridae	*Eucorysses grandis*	Terrestrial	Phytophagous	Apical	Present
	Lamprocoris roylii	Terrestrial	Phytophagous	Apical	Present
	Poecilocoris nepalensis	Terrestrial	Phytophagous	Apical	Present
Acanthosomatidae	*Acanthosoma labiduroides*	Terrestrial	Phytophagous	Apical	Present
	Sastragala edessoides	Terrestrial	Phytophagous	Apical	Present
Tessaratomidae	*Eusthenes cupreus*	Terrestrial	Phytophagous	Apical	Present
	Dalcantha dilatata	Terrestrial	Phytophagous	Apical	Present
Urostylidae	*Urochela quadrinotata*	Terrestrial	Phytophagous	Apical	Present
	Urochela sp.	Terrestrial	Phytophagous	Apical	Present
Dinidoridae	*Coridius chinensis*	Terrestrial	Phytophagous	Apical	Present
	Megymenum brevicorne	Terrestrial	Phytophagous	Apical	Present
Berytidae	*Yemmalysus parallelus*	Terrestrial	Phytophagous	Apical	Present
Colobathristidae	*Phaenacantha marcida*	Terrestrial	Phytophagous	Apical	Present
Stenocephalidae	*Dicranocephalus femoralis*	Terrestrial	Phytophagous	Apical	Present
Malcidae	*Malcus inconspicuus*	Terrestrial	Phytophagous	Apical	Present

Family	Species	Habitat	Feeding habits	Mouthpart origin	Presence of hemelytra
Geocoridae	*Geocoris pallidipennis*	Terrestrial	Predaceous	Apical	Present
Pyrrhocoridae	*Dysdercus cingulatus*	Terrestrial	Phytophagous	Apical	Present
Largidae	*Physopelta gutta*	Terrestrial	Phytophagous	Apical	Present
Coreidae	*Hydaropsis longirostris*	Terrestrial	Phytophagous	Apical	Present
Alydidae	*Riptortus pedestris*	Terrestrial	Phytophagous	Apical	Present
Rhopalidae	*Stictopleurus subviridis*	Terrestrial	Phytophagous	Apical	Present
	Aeschyntelus notatus	Terrestrial	Phytophagous	Apical	Present

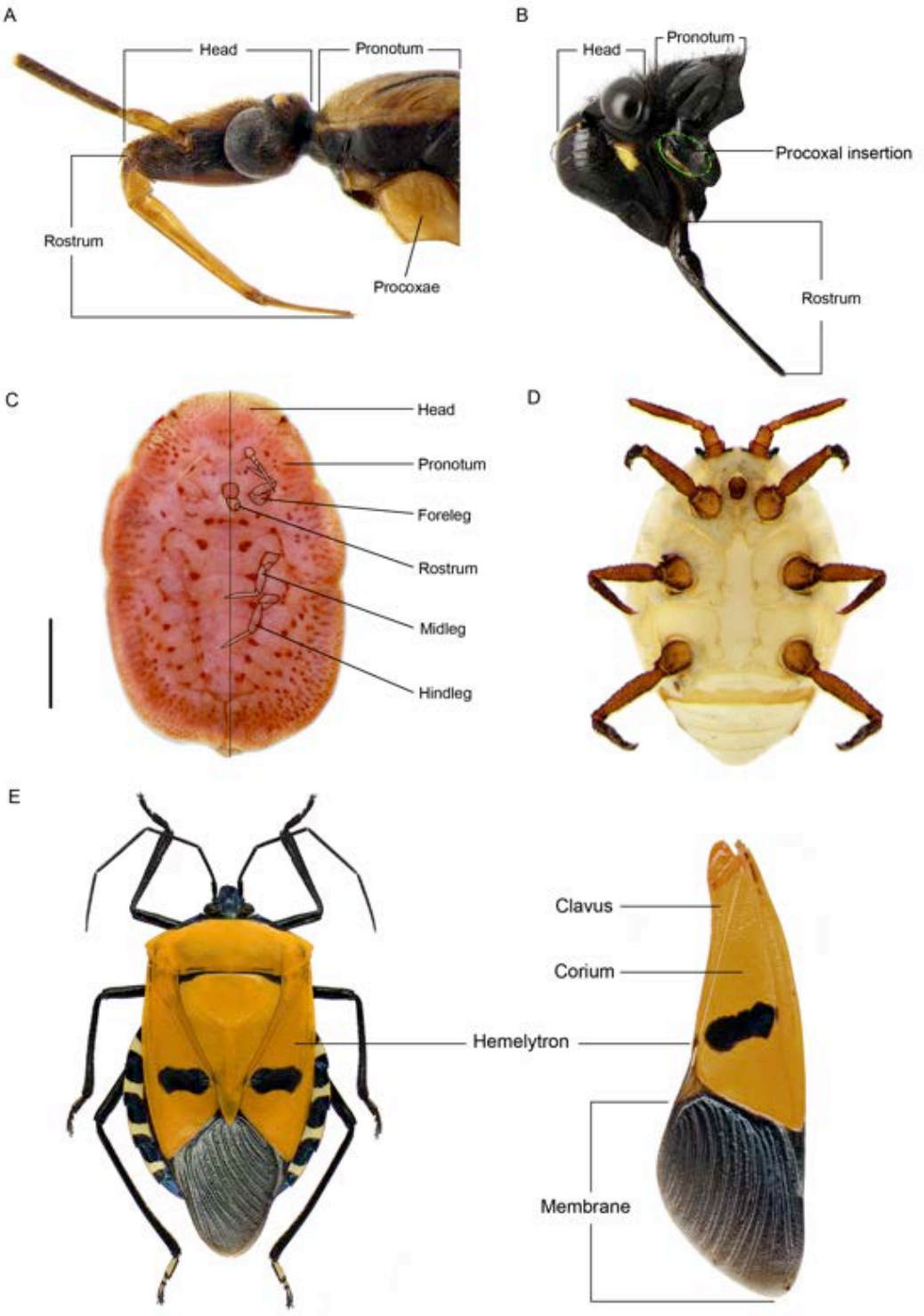

Figure 4.1. Mouthpart origin and hemelytra of hemipteran insects. **A**, apical mouthpart position (assassin bug, *Sirthenea flavipes*); **B**, middle mouthpart position (cicada, *Gaeana maculate*); **C**, sternal mouthpart position (wax scale insect, *Ceroplastes* sp.); **D**, scale insect, *Orthezia* sp.; **E**, tessaratomid bug, *Catacanthus incarnates* showing hemelytron structure. Scale: for A, 1.81 mm; for B, 3.84 mm; for C, 0.40 mm; for D, 0.65 mm; for E, 6.71 mm (for body of tessaratomid bug) and 4.73 mm (for hemelytron).

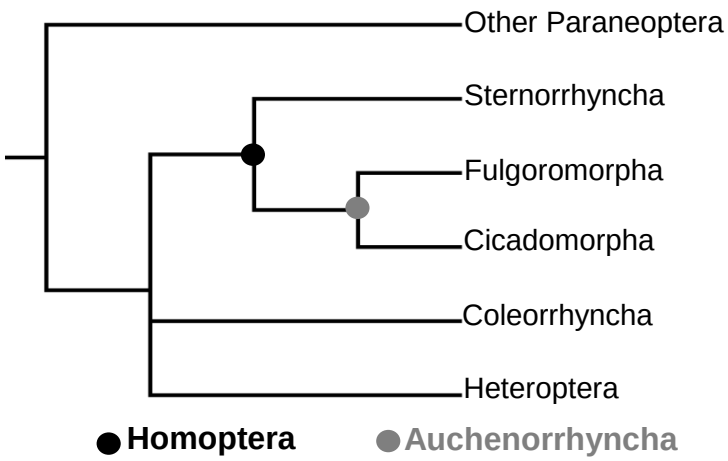

Figure 4.2. Traditional hypotheses on higher-level relationships of Hemiptera.

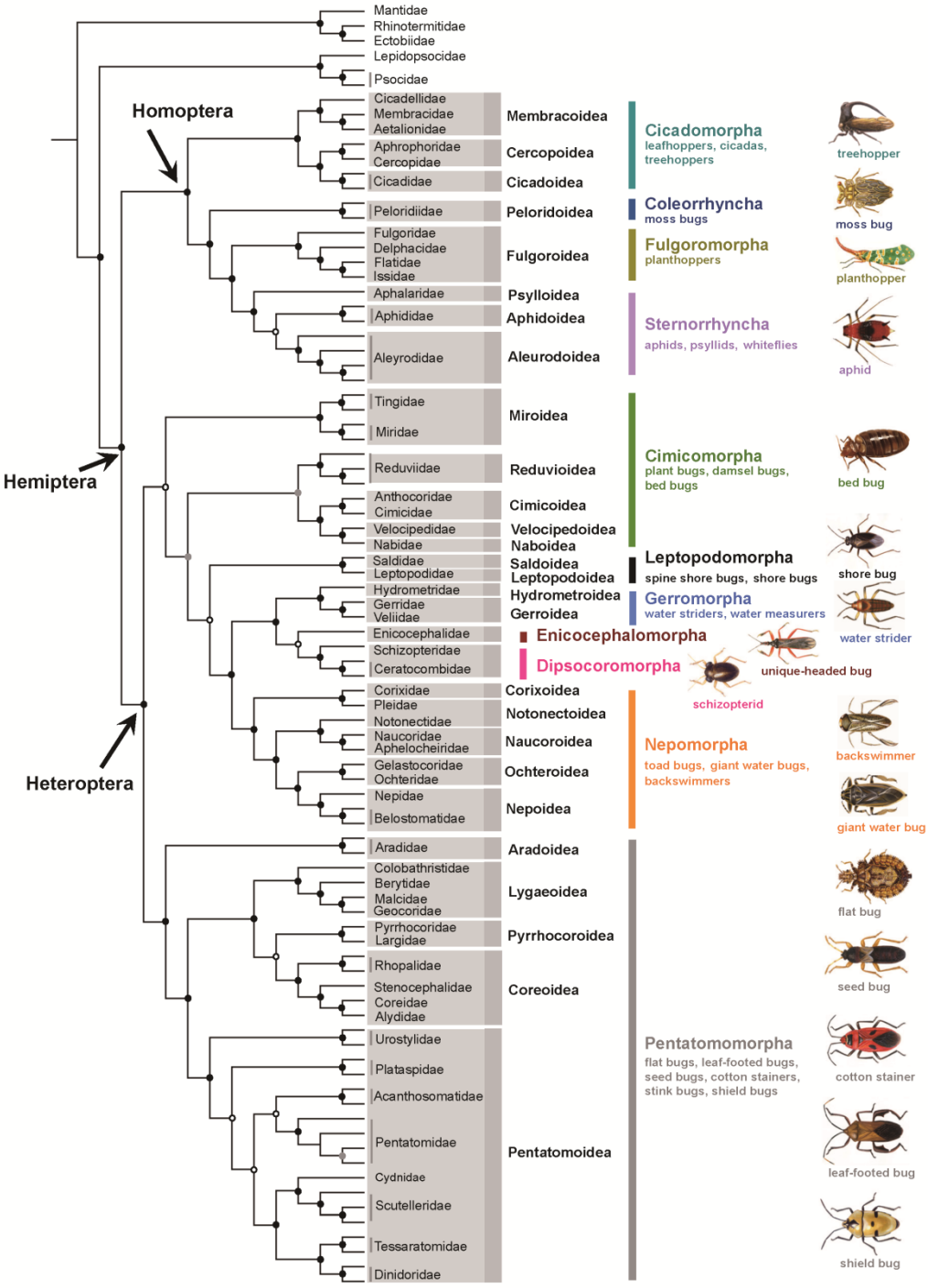

Figure 4.3. Phylogeny of Hemiptera produced from BI analysis of the PCG123 data set with PCGs partitioned by gene. Circles indicate Bayesian posterior probability clade support values >0.8 (black/PP=1.0, white/PP=0.90-0.99, and grey/PP=0.80-0.89).

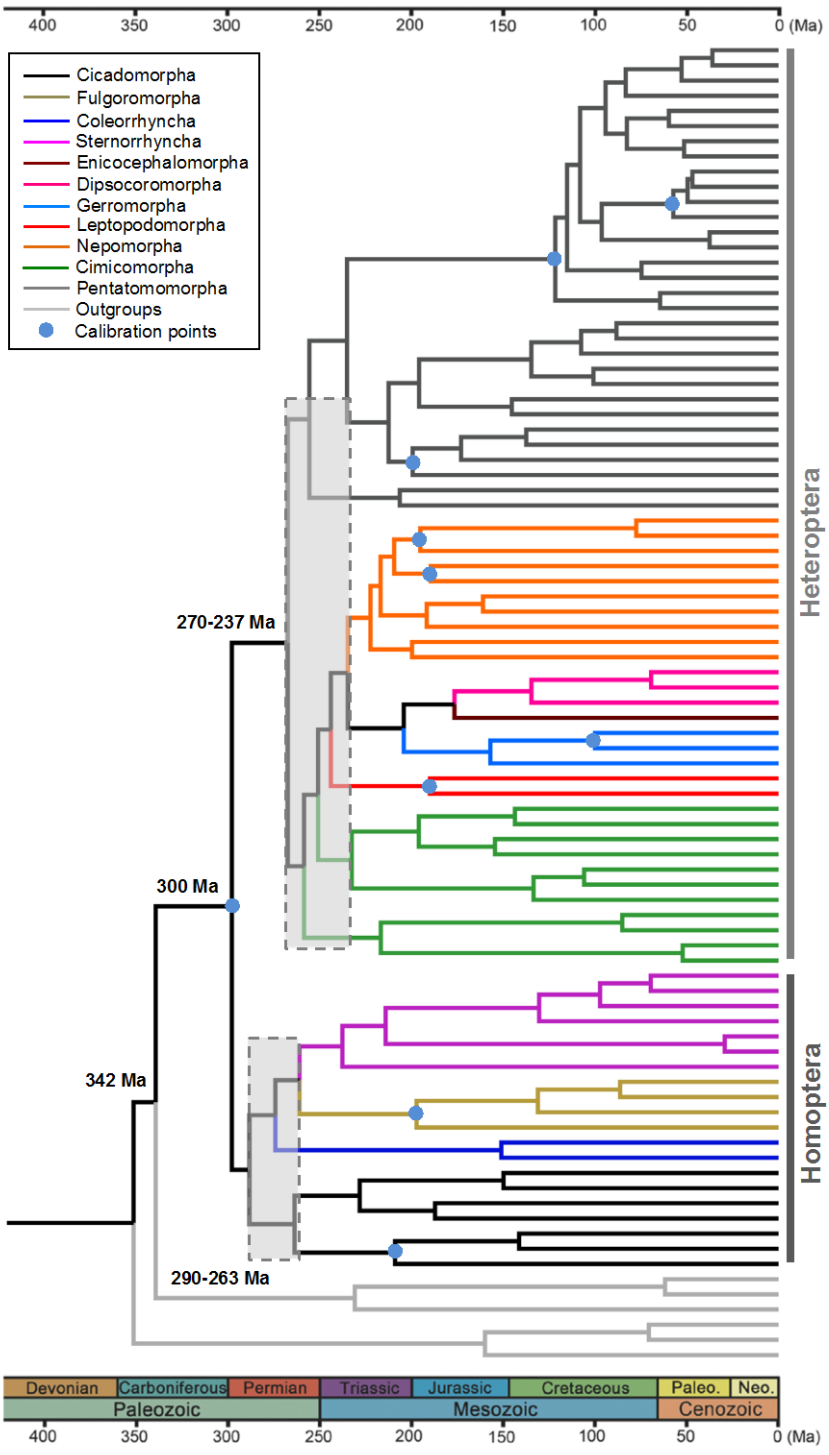

Figure 4.4. Chronogram depicting hemipteran phylogeny and divergence time estimates produced by a 60 million generation BEAST analysis of the PCG123 data set partitioned by codon position. A geological time scale is shown at the bottom. Dashed boxes correspond to major periods of rapid radiation in Hemiptera.

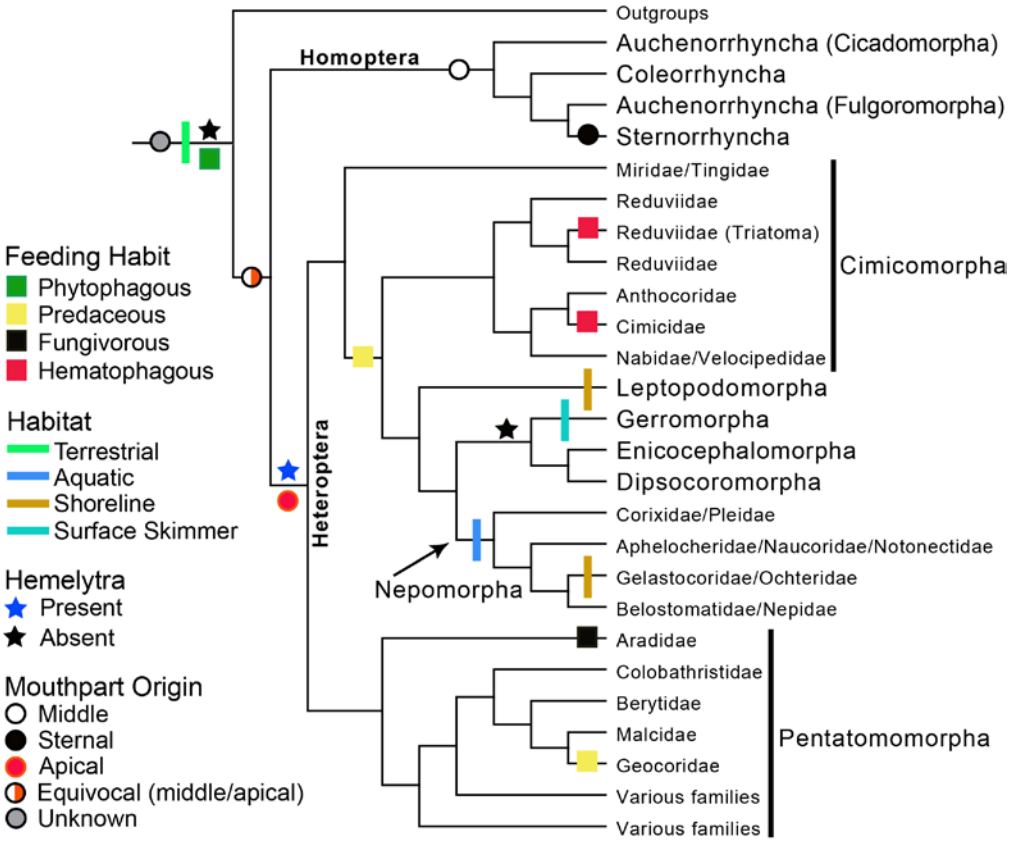

Figure 4.5. Summary of character state transitions for four characters (see **Figures 4.22-4.25** for full optimizations). All character state transitions are judged to be significant by ML methods except where otherwise noted (equivocal or unknown).

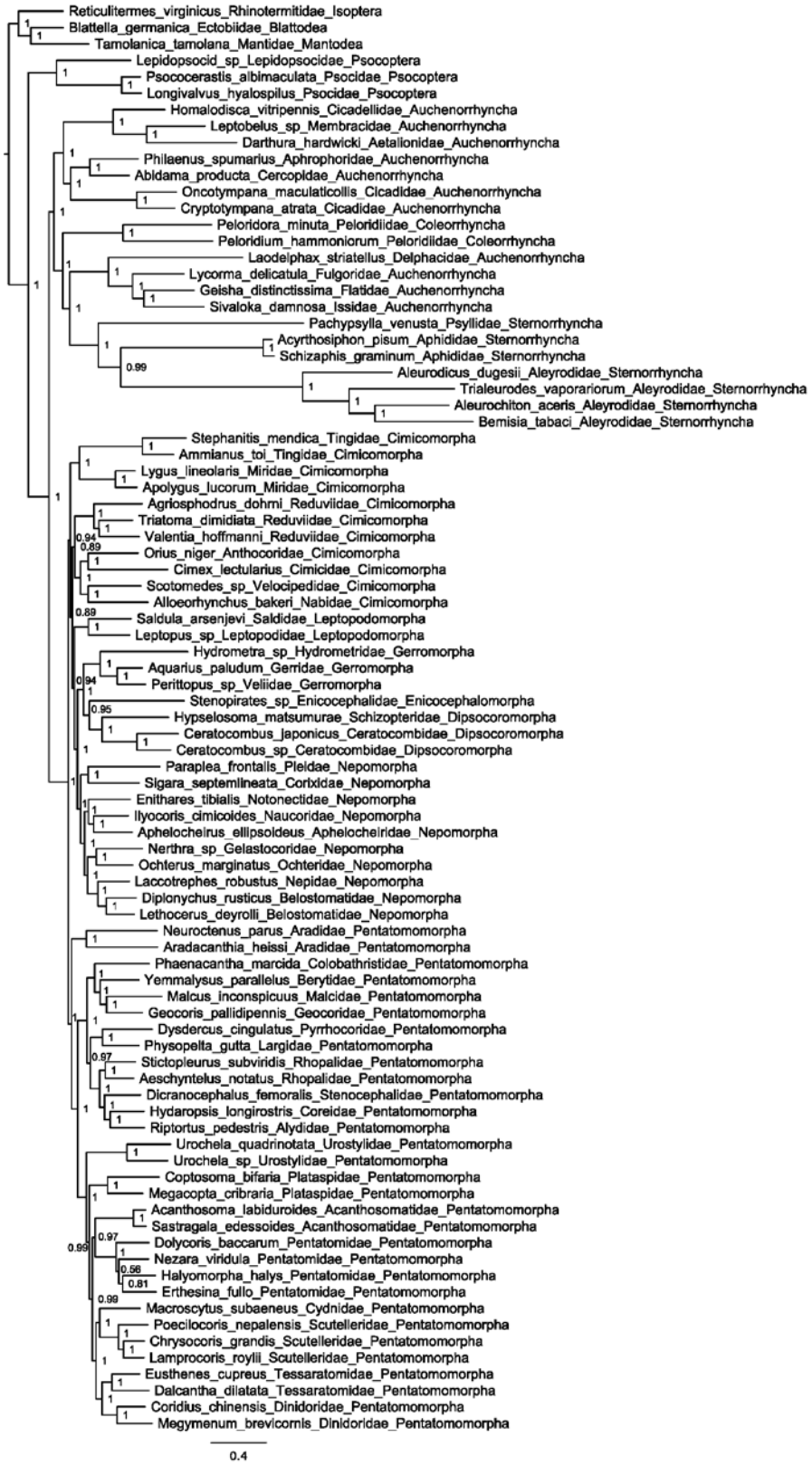

Figure 4.6. Consensus tree produced from BI analysis of the PCG123 data set with PCGs partitioned by gene.

Figure 4.7. MAP tree produced from BI analysis of the PCG123 data set with PCGs partitioned by gene.

Figure 4.8. Consensus tree produced from BI analysis of the PCG12 data set with PCGs partitioned by gene.

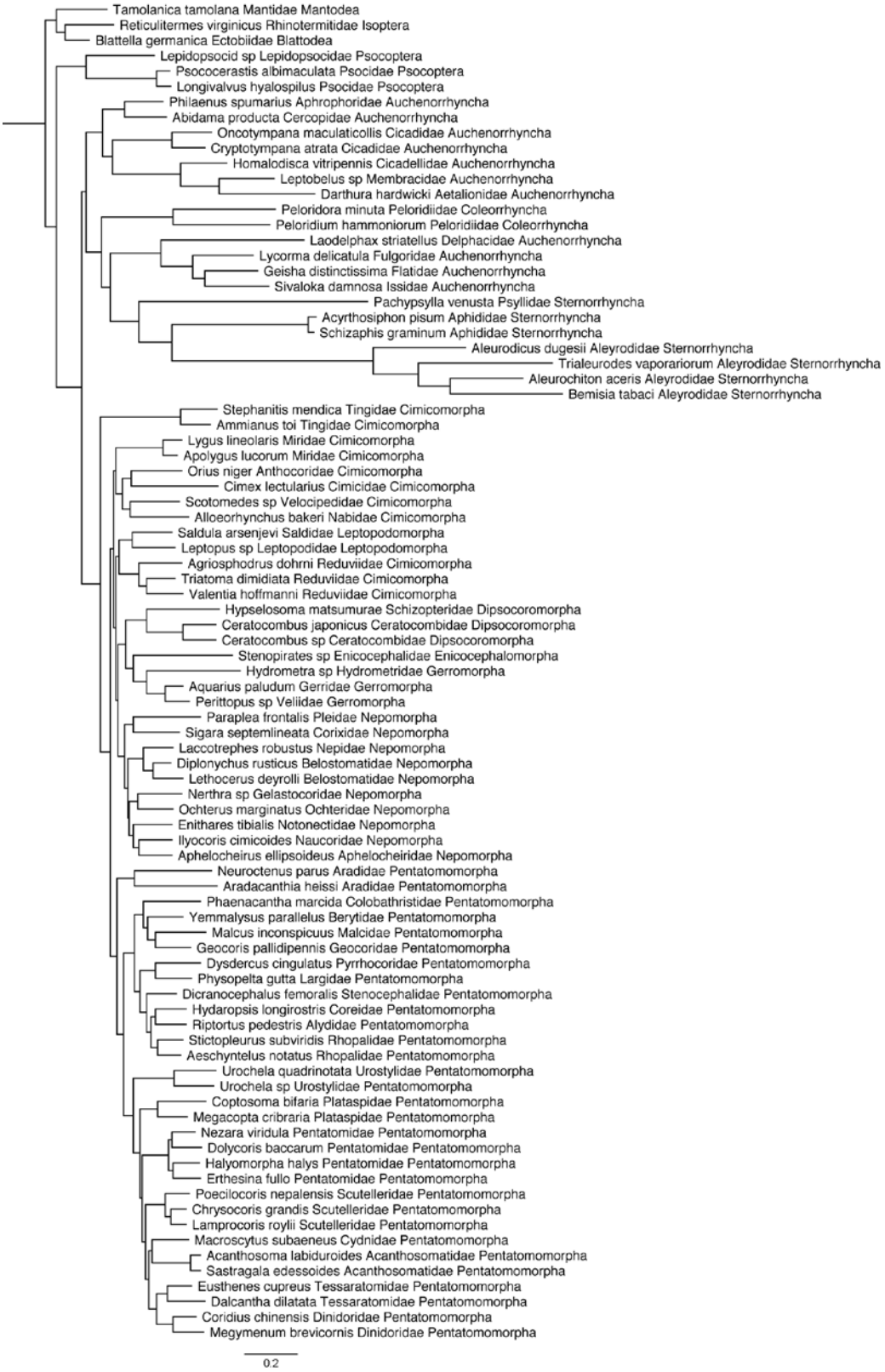

Figure 4.9. MAP tree produced from BI analysis of the PCG12 data set with PCGs partitioned by gene.

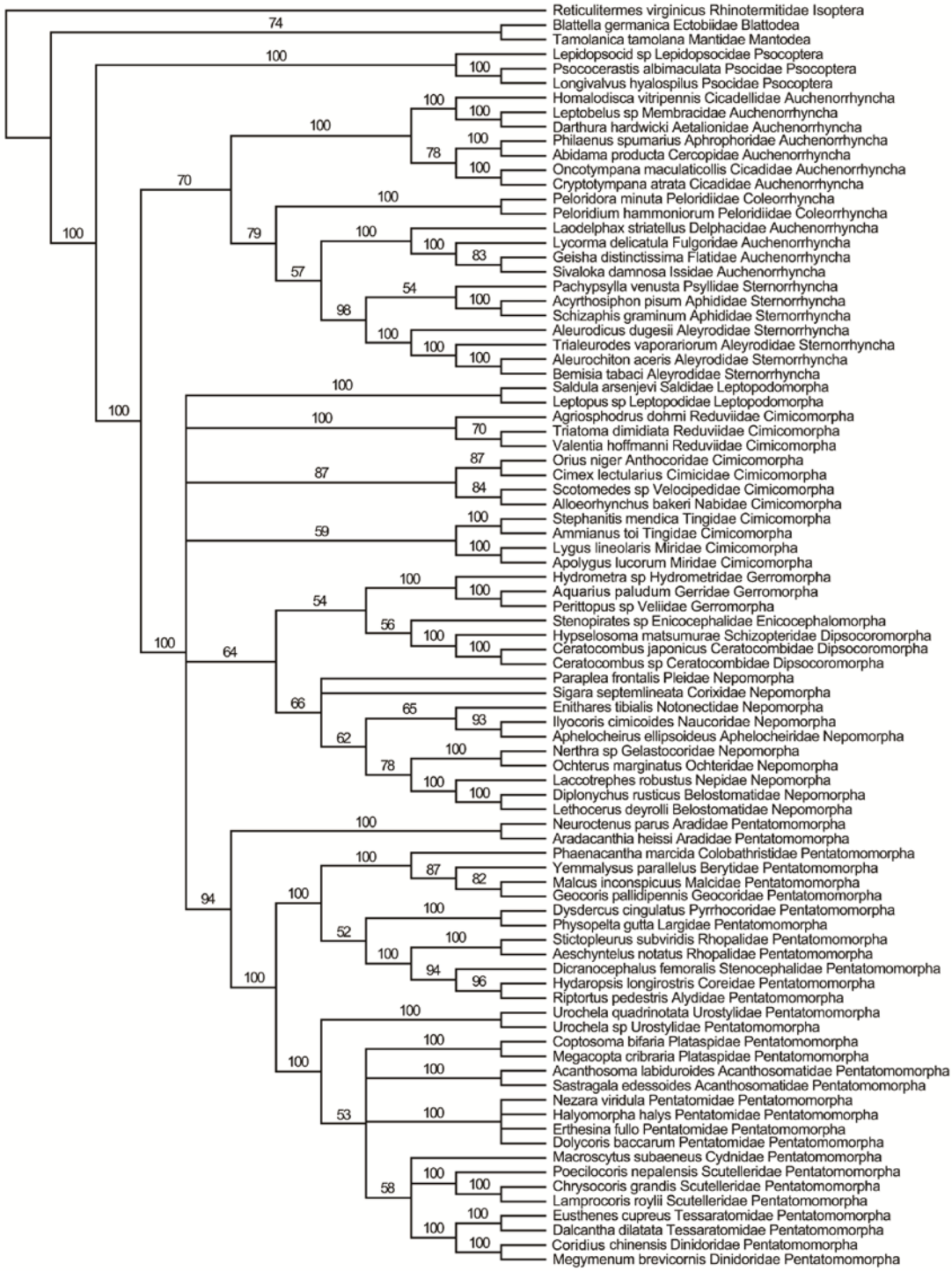

Figure 4.10. Bootstrap analysis (200 reps) produced from ML analysis of the PCG123 data set with PCGs partitioned by gene.

Figure 4.11. Best tree from an eight-replicate ML analyses of the PCG123 data set with PCGs partitioned by gene.

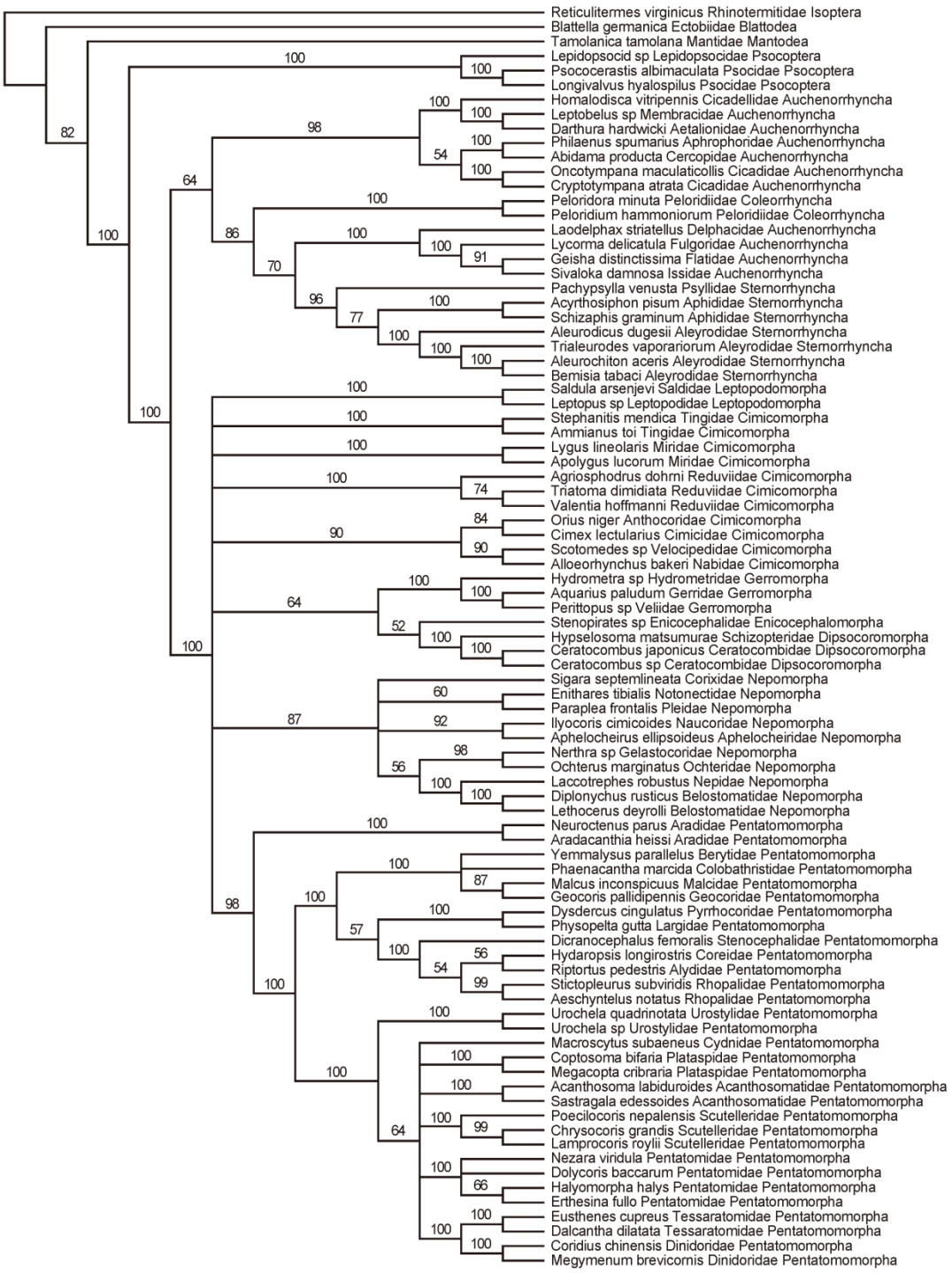

Figure 4.12. Majority rule consensus tree produced from a 200 replicate bootstrap analysis of the PCG12 data set partitioned by gene.

Figure 4.13. Best tree from an eight-replicate ML analysis of the PCG12 data set with PCGs partitioned by gene.

Figure 4.14. Consensus tree produced from BI analysis of the PCG123 data set with PCGs partitioned by codon position.

Figure 4.15. MAP tree produced from BI analysis of the PCG123 data set with PCGs partitioned by codon position.

Figure 4.16. Consensus tree produced from BI analysis of the PCG12 data set with PCGs partitioned by codon position.

Figure 4.17. MAP tree produced from BI analysis of the PCG12 data set with PCGs partitioned by codon position.

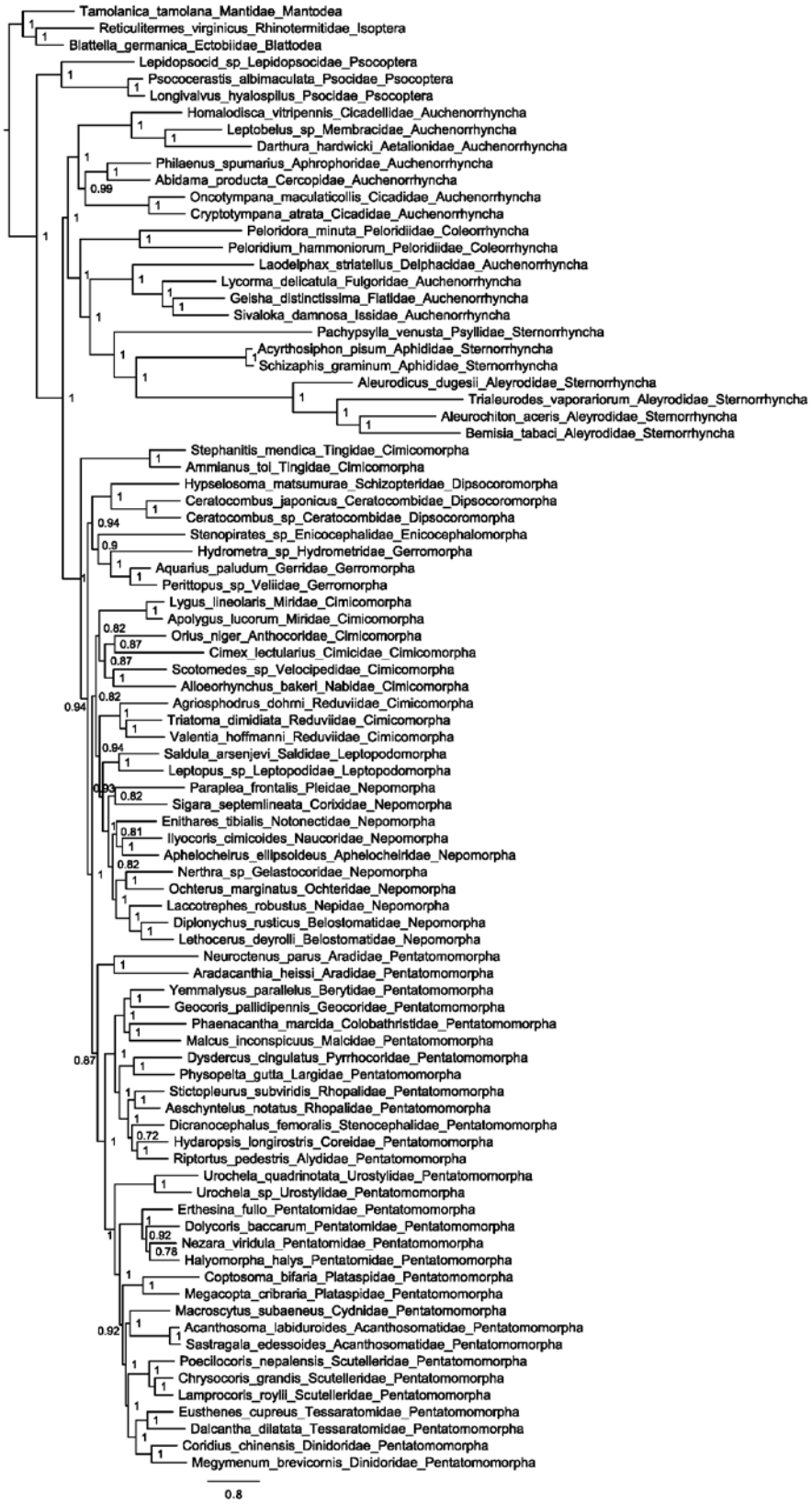

Figure 4.18. Consensus tree produced from BI analysis of the PCG123 data set with codon models (M3) assigned to each PCG.

Figure 4.19. MAP tree produced from BI analysis of the PCG123 data set with codon models (M3) assigned to PCGs.

Figure 4.20. The single tree produced from a ML search with M3 codon models assigned to the PCGs in the PCG123 data set. The search took 3275 hours (~136 days) and further analyses were aborted.

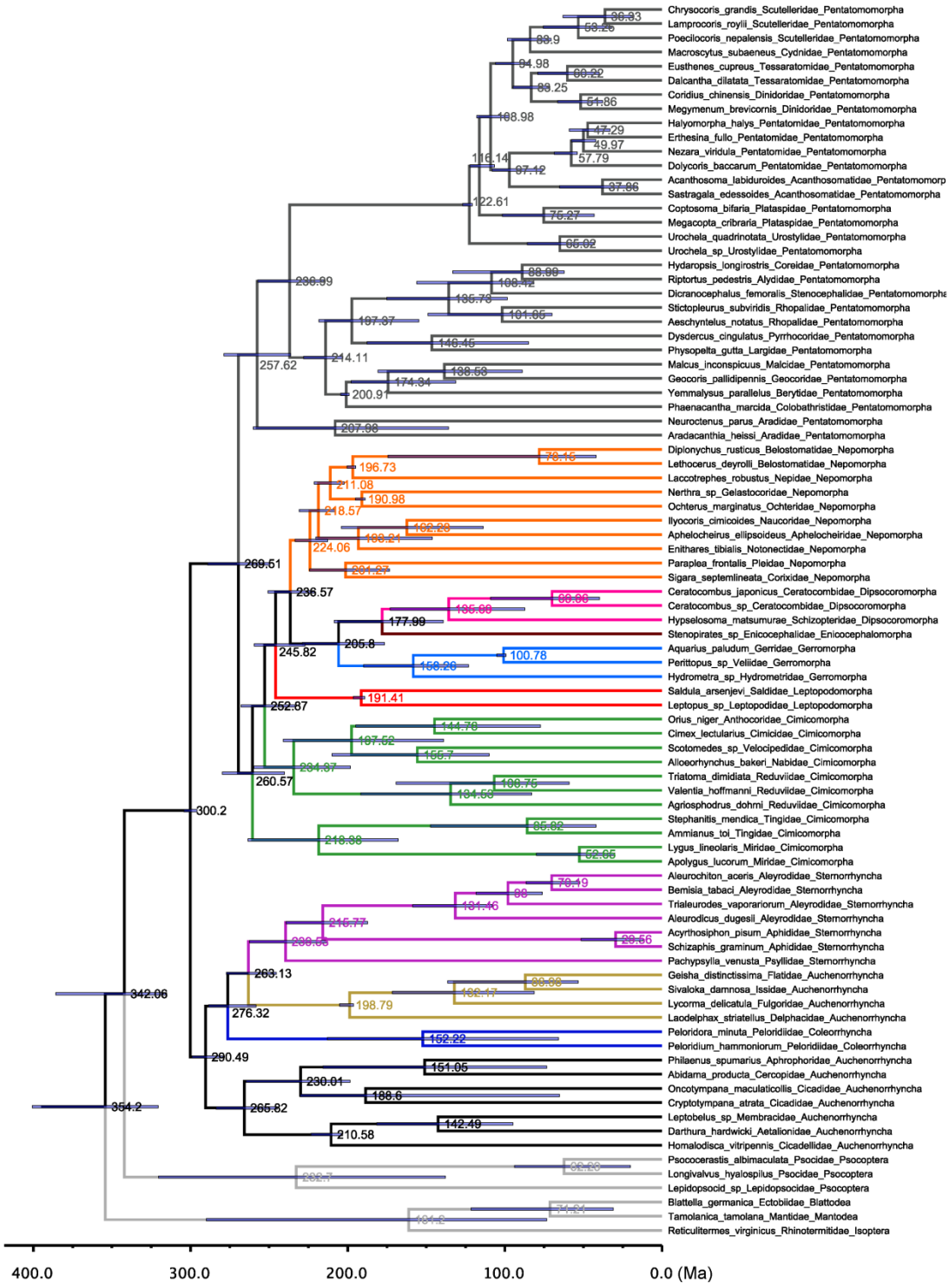

Figure 4.21. Divergence time estimates based on BEAST analysis of the PCG123 data set with PCGs partitioned by codon position. Shaded bars at the nodes indicate 95% highest posterior density (HPD) credibility intervals.

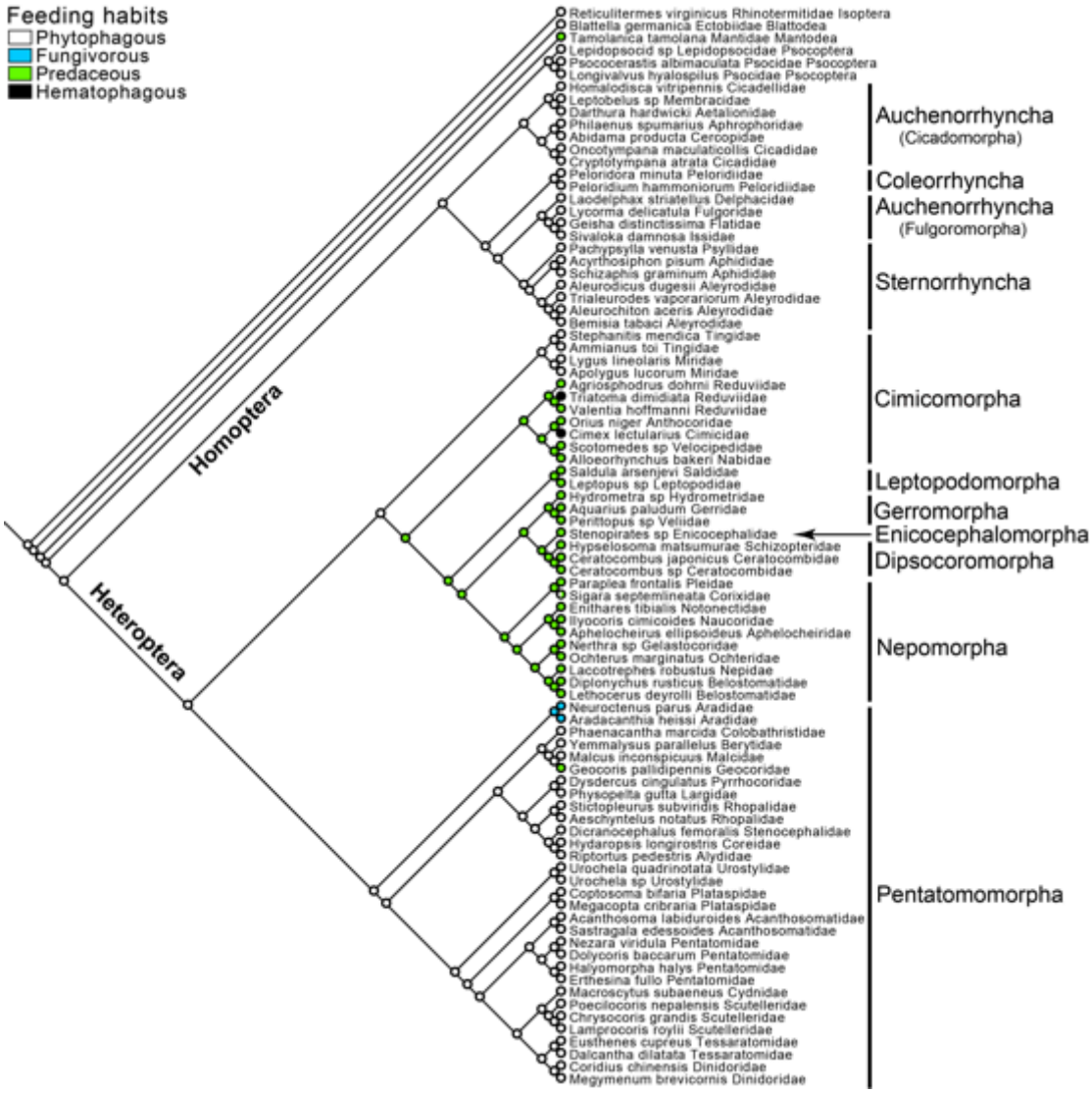

Figure 4.22. ML optimization of feeding habits conducted with Mesquite under the MK1 model of character evolution. All ancestral nodes are significant for the character state shown. Input tree is the MAP tree from the BI analysis of the PCG123 data set with PCGs partitioned by codon position. Note: Mesquite ML character optimizations do not allow terminals to be multistate. In this figure, *Sigara septemlineata* (Corixidae) is coded as predatory/phytophagous, but it was optimized both ways and neither coding made a significant change to any ancestral node shown on the current figure.

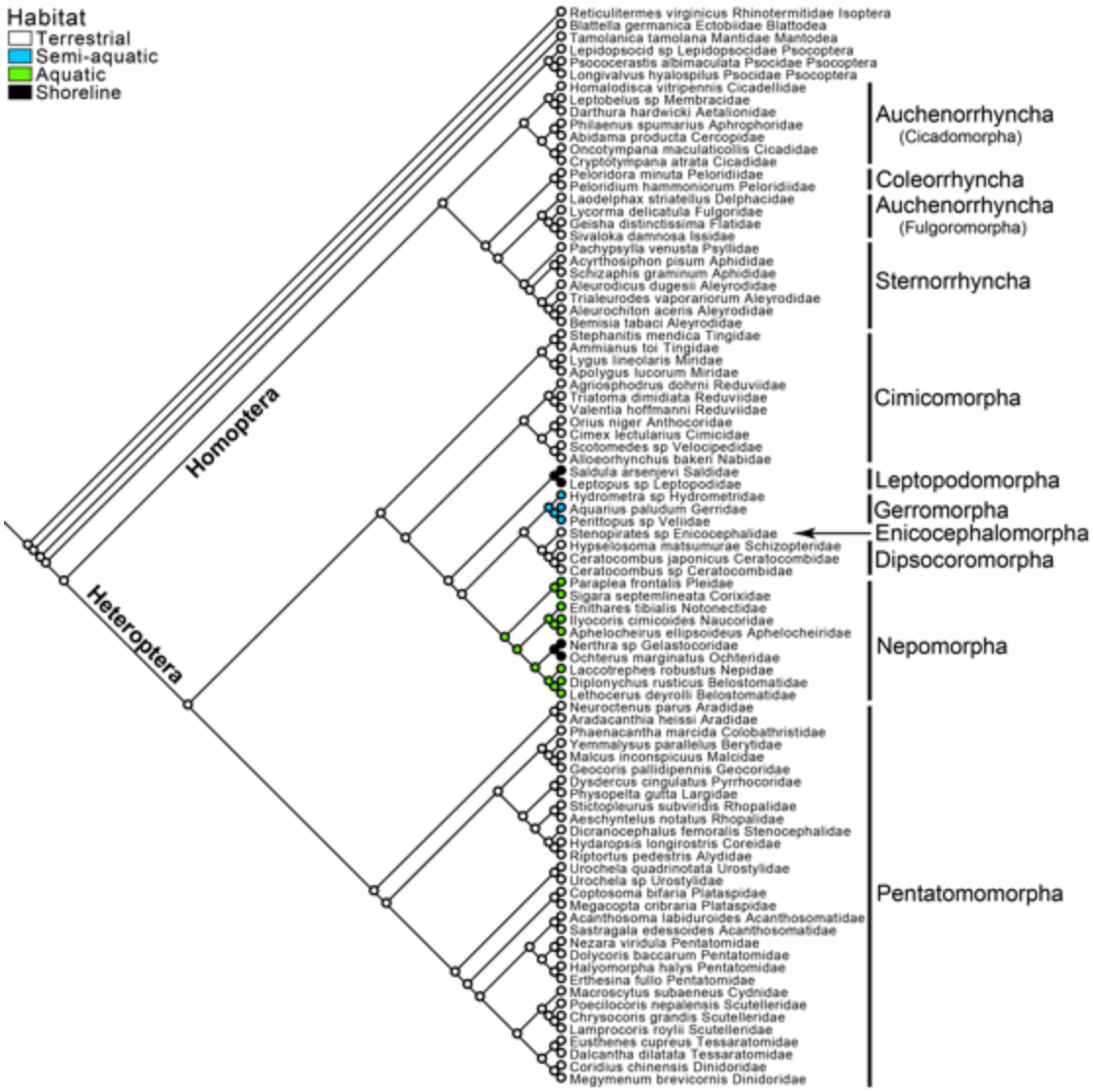

Figure 4.23. ML optimization of habitat conducted with Mesquite under the MK1 model of character evolution. All ancestral nodes are significant for the character state shown. Input tree is the MAP tree from the BI analysis of the PCG123 data set with PCGs partitioned by codon position.

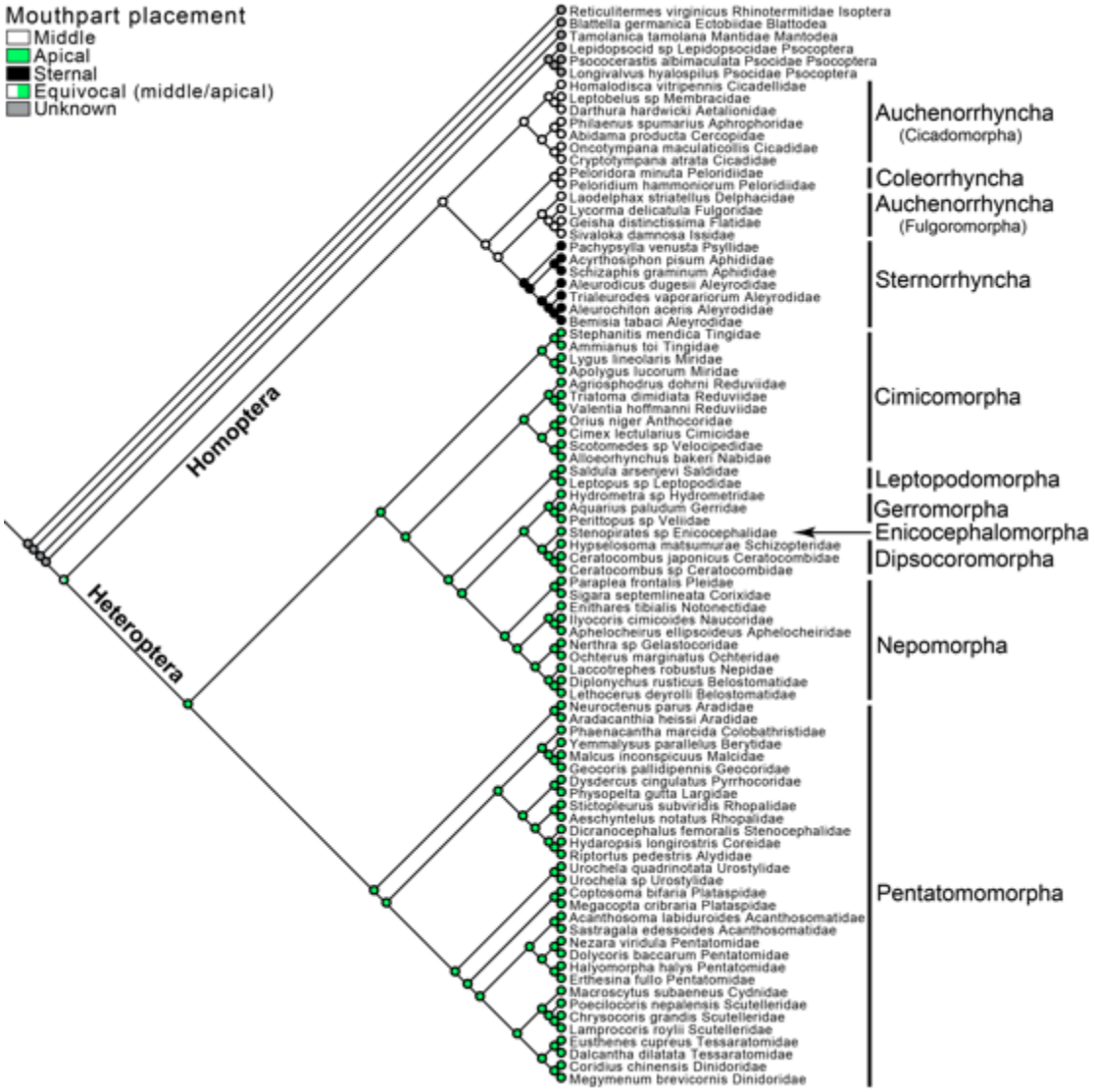

Figure 4.24. ML optimization of mouthpart origin conducted with Mesquite under the MK1 model of character evolution. All ancestral nodes are significant for the character state shown, except for the root of Hemiptera which is ambiguous between apical and middle, and the nodes leading to the outgroups for which mouthpart placement is unknown. Input tree is the MAP tree from the BI analysis of the PCG123 data set with PCGs partitioned by codon position.

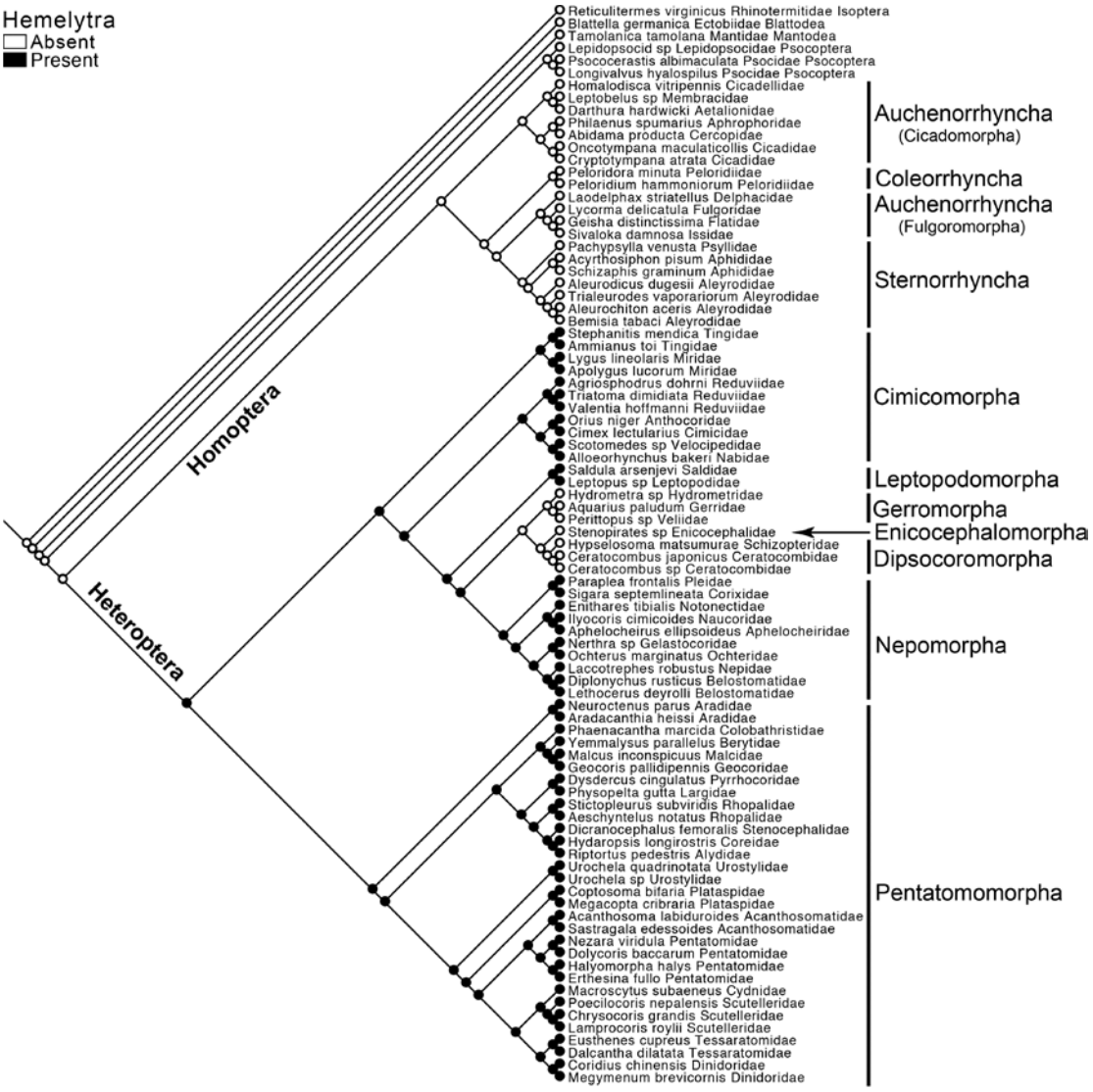

Figure 4.25. ML optimization of the presence of hemelytra conducted with Mesquite under the MK1 model of character evolution. All ancestral nodes are significant for the character state shown. Input tree is the MAP tree from the BI analysis of the PCG123 data set with PCGs partitioned by codon position.

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