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Systematics of Longhorned Beetles (Insecta: Coleoptera: Cerambycidae)

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SYSTEMATICS OF LONGHORNED BEETLES (INSECTA: COLEOPTERA: CERAMBYCIDAE)

by

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DISSERTATION

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DEDICATION

I dedicate this work to my parents, Joseph Eugene Nearns and Bruna Palanza Nearns: thank you for instilling within me the value of hard work and education.

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ABSTRACT

The longhorned wood boring beetles (Insecta: Coleoptera: Cerambycidae) are a diverse and economically important group of insects. With an estimated 4,000 genera and more than 35,000 described species, the Cerambycidae comprise one of the largest beetle families. Cerambycid beetles are found on all continents except Antarctica, from sea level to montane sites as high as 4000 m. Cerambycids are among the most serious wood boring pest species globally, affecting many agricultural crops, ornamental trees, and lumber products, causing millions of dollars in damage each year. Despite their economic importance and biological diversity, relatively little is known of cerambycid beetle ecology, behavior, or phylogenetic relationships. A better understanding of all of these factors would greatly contribute to conservation of endangered species, and in managing invasive species that could become pests in their new countries and habitats.

In Chapter 1, I present the phylogenetic relationships among the tribes and genera of longhorned beetle subfamilies Prioninae Latreille and Parandrinae Blanchard (Coleoptera: Cerambycidae) inferred from DNA sequence data. Four genes (12S rRNA, 28S rRNA, cytochrome oxidase I, and histone III) were sequenced for 60 taxa representing the outgroup cerambycoid family Disteniidae Thomson and four cerambycid subfamilies: Cerambycinae Latreille, Lamiinae Latreille, Lepturinae Latreille, and Spondylidinae Audinet-Serville. The monophyly of Prioninae was tested using parsimony and Bayesian analyses. Prioninae (including Parandrinae and the cerambycine genus *Plectogaster*) was recovered as a monophyletic group in the Bayesian analysis. In the parsimony analysis, Prioninae (including Parandrinae but excluding two prionine genera: *Aesa* and *Sarmydus*) was also recovered as a monophyletic group. Both analyses recovered the subfamilies Lamiinae, Lepturinae, and Spondylidinae as monophyletic groups, as well as the Parandrinae + Prioninae clade as sister to Cerambycinae. Relationships among prionine tribes had low support values in both analyses, likely due to missing sequence data for a majority of included taxa, as well as relatively sparse taxonomic coverage (23 of 200 described genera, 11 of 18 tribes included).

In Chapter 2, I present the first morphological study and phylogenetic analysis of the tribe Onciderini Thomson (Cerambycidae: Lamiinae). Members of this tribe are commonly referred to as the “twig girdlers” due to the peculiar behavior exhibited by adult females of at least four of 80 described genera. For the morphological study, specimens representing 74 of the 80 described genera of Onciderini were disarticulated and dissected. Twenty-three morphological characters were illustrated and studied,

including the head, mandible, ligula, pronotum, prosternum, mesonotum, metendosternite, hind wing, and aedeagus. Seventy-four ingroup taxa and three outgroup taxa were scored for 23 morphological characters. Results of both the cladistic and Bayesian analyses suggest that Onciderini is monophyletic with respect to the outgroup taxa chosen and supported by one unambiguous synapomorphy (pronotum transverse, from 1.2–1.5× as long). Relationships among the 74 species of Onciderini included were poorly resolved and not well supported.

Finally, six works published in partial fulfillment of this dissertation are listed as Appendices A–F. Included in these six works are four publications in which a total of 20 new cerambycid taxa are described, 58 new country records are recorded, and identification keys to the species of six genera are presented. The remaining two published works ("Oncid ID: Tool for diagnosing adult twig girdlers," and "Longicorn ID: Tool for diagnosing cerambycoid families, subfamilies, and tribes") are identification tools developed for port identifiers via competitive grant funding from the US Department of Agriculture - Animal and Plant Health Inspection Service (USDA-APHIS). Both tools contain interactive (Lucid) identification keys, extensive photographic galleries, and informational fact sheets to various groups of cerambycid beetles.

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INTRODUCTION

The longhorned wood boring beetles (Insecta: Coleoptera: Cerambycidae) are a diverse and economically important group of insects. With an estimated 4,000 genera and more than 35,000 described species, the Cerambycidae comprise one of the largest beetle families (Lawrence, 1991; Tavakilian & Chevillotte, 2012). Cerambycid beetles are found on all continents except Antarctica, from sea level to montane sites as high as 4000 m (Monné & Bezark, 2012). Nearly all are phytophagous or xylophagous as larvae, feeding within living, moribund, or decaying wood. Cerambycids are among the most serious wood boring pest species globally, affecting many agricultural crops, ornamental trees, and lumber products, and causing millions of dollars in damage each year (Solomon, 1995).

One of the most notorious cerambycids is the Asian Longhorned Beetle (*Anoplophora glabripennis*, or ALB). In 1996, this invasive species was discovered in New York City and later in Chicago. Native to China and the Korean peninsula, ALB was accidentally imported into the US via wooden shipping materials (Lingafelter & Hoebeke, 2002). By 1998, ALB infestations resulted in the destruction of nearly 7,000 trees. Recently, the USDA estimated that, if left uncontrolled, ALB and other Chinese wood boring beetles could cause more than $100 billion in damage to the US economy (Meyer, 2010). Accidental introductions continue, and as recently as 2011 a population of ALB was detected in southwest Ohio (USDA-APHIS, 2011).

The family Cerambycidae is a charismatic group that has been popular with insect collectors for centuries. Cerambycid beetles exhibit a remarkable diversity of biology

and morphology, and range in size from a few mm to over 17 cm. Many species are nocturnal and cryptically colored; others are diurnal and exhibit spectacular mimicry of hymenopteran forms (e.g., bees, wasps, and ants) and behavior (e.g., Silberglied & Aiello, 1976). Cerambycid beetles have been associated with a wide variety of plant hosts, including grasses, bamboo, conifers, hardwoods, and cacti. In addition, cerambycid beetle larvae are known to utilize nearly all parts of a host tree, including the roots, trunk, branches, leaves, and seeds. Despite their economic importance and biological diversity, relatively little is known of cerambycid beetle ecology, behavior, or phylogenetic relationships. A better understanding of all of these factors would greatly contribute to conservation of endangered species, and in managing invasive species that could become pests in their new countries and habitats.

There is a need for systematic expertise within Cerambycidae in order to resolve higher-level classification and provide a robust phylogenetic framework within which to explore and answer evolutionary questions regarding their diversity, ecology, conservation, and pest management. My dissertation incorporates several aspects of systematic entomology: field work, new species discovery, morphological study, molecular analysis, scientific illustration, macro photography, ecology, and the development of interactive identification tools.

In Chapter 1, I present the phylogenetic relationships among the tribes and genera of longhorned beetle subfamilies Prioninae Latreille and Parandrinae Blanchard (Coleoptera: Cerambycidae) inferred from DNA sequence data. Four genes (12S rRNA, 28S rRNA, cytochrome oxidase I, and histone III) were sequenced for 60 taxa representing the outgroup cerambycoid family Disteniidae Thomson and four cerambycid

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In Chapter 2, I present the first morphological study and phylogenetic analysis of the tribe Onciderini Thomson (Cerambycidae: Lamiinae). Members of this tribe are commonly referred to as the "twig girdlers" due to the peculiar behavior exhibited by adult females of at least four of 80 described genera. For the morphological study, specimens representing 74 of the 80 described genera of Onciderini were disarticulated and dissected. Twenty-three morphological characters were illustrated and studied, including the head, mandible, ligula, pronotum, prosternum, mesonotum, metendosternite, hind wing, and aedeagus. Seventy-four ingroup taxa and three outgroup taxa were scored for 23 morphological characters. Results of both the cladistic and Bayesian analyses suggest that Onciderini is monophyletic with respect to the outgroup taxa chosen and supported by one unambiguous synapomorphy (pronotum transverse,

from 1.2–1.5× as long). Relationships among the 74 species of Onciderini included were poorly resolved and not well supported.

In addition to the two chapters previously mentioned, six works previously published in partial fulfillment of this dissertation are included as Appendices A–F. Appendix A, titled "A new species of *Plectromerus* Haldeman from Central America and description of the female of *Plectromerus dezayasi* Nearns and Branham, 2008 (Coleoptera: Cerambycidae: Cerambycinae: Plectromerini)" was published in the peer-reviewed open-access journal *ZooKeys* by Nearns & Miller in October 2009. In this work we described a new species of longhorned beetle in the genus *Plectromerus*, as well as the previously unknown female of a congener. Appendix B, titled "Oncid ID: Tool for diagnosing adult twig girdlers (Cerambycidae: Lamiinae: Onciderini)" was published simultaneously as a CD-ROM and open-access website by Nearns *et al*. in May 2011. Funded by a grant from USDA-APHIS, Oncid ID is a fully illustrated identification tool to the longhorned beetle tribe Onciderini, featuring an interactive Lucid key, gallery of habitus images of representatives of each of the 80 genera, as well as head illustrations for each genus. Appendix C, titled "New taxa and combinations in Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae)" was published in the peer-reviewed open-access journal *Insecta Mundi* by Nearns & Swift in September 2011. In this work we described a new genus and six new species of longhorned beetle in the tribe Onciderini, proposed three synonymies, transferred two taxa, and added 37 new country records. Appendix D, titled "Longicorn ID: Tool for diagnosing cerambycoid families, subfamilies, and tribes" was published as an open-access website by Nearns *et al*. in August 2012. Funded by a grant from USDA-APHIS, Longicorn ID is a fully illustrated

identification tool to the cerambycoid beetles of the world, featuring five interactive Lucid keys, as well as a gallery of habitus images of representatives of each of four families, 11 subfamilies, and 49 tribes currently included within the tool. Appendix E, titled "New taxa and combinations in Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) from Central and South America, with notes on additional taxa" was published in the peer-reviewed open-access journal *Insecta Mundi* by Nearns & Tavakilian in March 2012. In this work we described a new genus and five new species of longhorned beetle in the tribe Onciderini, proposed three synonymies, five new combinations, and added 13 new country records in the subfamilies Cerambycinae and Lamiinae. Finally, Appendix F, titled "A new genus and five new species of Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) from South America, with notes on additional taxa" was published in the peer-reviewed open-access journal *Insecta Mundi* by Nearns & Tavakilian in December 2012. In addition to the six new taxa of longhorned beetles described in this work, we also added eight new country records in the tribe Onciderini.

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CHAPTER 1

Molecular Phylogenetic Analysis of the Longhorned Beetle Subfamilies Prioninae and Parandrinae (Insecta: Coleoptera: Cerambycidae)

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Abstract

The phylogenetic relationships among the tribes and genera of longhorned beetle subfamilies Prioninae Latreille and Parandrinae Blanchard (Coleoptera: Cerambycidae) were inferred from DNA sequence data. Four genes (12S rRNA, 28S rRNA, cytochrome oxidase I, and histone III) were sequenced for 60 taxa representing the outgroup cerambycoid family Disteniidae Thomson and four cerambycid subfamilies: Cerambycinae Latreille, Lamiinae Latreille, Lepturinae Latreille, and Spondylidinae Audinet-Serville. The monophyly of Prioninae was tested using parsimony and Bayesian analyses. Prioninae (including Parandrinae and the cerambycine genus *Plectogaster*) was recovered as a monophyletic group in the Bayesian analysis. In the parsimony analysis, Prioninae (including Parandrinae but excluding two prionine genera) was recovered as a monophyletic group. Both analyses recovered the subfamilies Lamiinae, Lepturinae, and Spondylidinae as monophyletic groups, as well as the Parandrinae + Prioninae clade as sister to Cerambycinae. Relationships among prionine tribes had low support values in

both analyses, likely due to missing sequence data for a majority of included taxa, as well as relatively sparse taxonomic coverage (23 of 200 described genera, 11 of 18 tribes included).

Introduction

The longhorned wood boring beetles (family Cerambycidae Latreille), are a charismatic and economically important group of insects. With an estimated 4,000 genera and more than 35,000 described species worldwide (Lawrence, 1991; Tavakilian & Chevillotte, 2012), the longhorned beetles are one of the most diverse families of beetles and are found on all continents except Antarctica (Fig. 1). Nearly all longhorned beetles are phytophagous, feeding within living, dying, or decaying wood as larvae. Longhorned beetles are among the most serious wood boring pest species in the world, affecting various agricultural crops, ornamental trees, and lumber products, causing millions of dollars in damage each year (Solomon, 1995). This group is a favorite among amateur collectors and hundreds of new species are described each year. Despite an abundance of regional guides to longhorned beetles (e.g., Adlbauer, 2001 (Namibia); Bleuzen, 1994 (S. America); Cerda, 1974 (Chile); Lingafelter, 2007 (E. USA); Quentin & Villiers, 1975 (Madagascar); and Zayas, 1975 (Cuba)), higher-level classification within the family is poorly resolved (Švácha & Lawrence, in review). In addition, relatively few phylogenetic studies have been conducted which include Cerambycidae (e.g., Hunt *et al*., 2007; Lawrence *et al*, 2011; Linsley, 1961; Napp, 1994; Švácha & Danilevsky, 1987), and there is no consensus among experts even on the number of subfamilies (ranging from 7–11), their monophyly, or their relationships to one another. Although modern

catalogues and checklists exist for the Neotropical fauna (e.g., Monné, 2006; Monné & Bezark, 2012), catalogues for other regions are lacking, and no modern world catalogue exists (but see Tavakilian & Chevillotte, 2012). The lack of a stable higher-level classification of the longhorned beetles is surprising for such an important and conspicuous group of beetles and dramatically inhibits a more comprehensive, and much-needed understanding of the group's diversity on a world level.

With approximately 1,000 described species in 200 genera, the Prioninae Latreille are the third largest subfamily of longhorned beetles worldwide (Švácha & Lawrence, in review). This group contains relatively small species (~7 mm) as well as the largest known beetle species, *Titanus giganteus* (Linnaeus, 1771), which may attain a length of 17 cm (Fig. 2b). Although most abundant in tropical and subtropical regions, prionines are found in a diverse range of habitats, ranging from deserts to high elevation cloud forests. Most prionines are nocturnal and obscurely-colored, although brightly colored, diurnal genera are also known (e.g., Anacolini Thomson (Fig. 2c), Mallaspini Thomson (Fig. 2a, e), and Solenopterini Lacordaire). The Prioninae also includes several economically important genera such as *Prionus* Geoffrey, 1762 and *Stenodontes* Audinet-Serville, 1832, which are pests of lumber products (Linsley, 1962; Solomon, 1995). Invasive species such as the Asian Longhorned Beetle (*Anoplophora glabripennis* (Motschulsky, 1854)), which was unintentionally imported into the USA via wooden shipping material from China in 1996 (Lingafelter & Hoebeke, 2002), pose a serious threat to agricultural crops, ornamental trees, and lumber products in the USA.

The subfamily Parandrinae Blanchard is a relatively small subfamily of about 100 described species in 10 genera. Members of this subfamily are distributed worldwide but

mainly in warmer regions (Švácha & Lawrence, in review). The subfamily is classified into two tribes: Erichsoniini Thomson with a single species (*Erichsonia dentifrons* Westwood, 1849), known from Central America, and Parandrini Blanchard known from the Australasian, Indomalayan, and Neotropical Regions (Bouchard *et al*., 2011; Švácha & Lawrence, in review). Parandrines are generally nocturnal and may be found under bark of dead trees or within tree hollows.

Many prionine species are strongly sexually dimorphic, especially in the mandibular and antennal morphology, which may be conspicuously modified in males (e.g., Fig 2a–i) and likely evolved in response to sexual selection. Whereas nearly all longhorned beetle species have 11 antennal segments (plesiomorphic condition in beetles), some prionines have as few as eight and as many as 30 (Švácha & Lawrence, in review). These antennal modifications have been interpreted as indirect evidence of the use of volatile pheromones (chemical signals used in conspecific communication) for mate and host plant location. Current research on the role of volatile pheromones for mate and host plant location in the longhorned beetles (e.g., Allison *et al*., 2004; Barbour *et al*., 2006; Cervantes *et al*., 2006; and Hanks, 1999) would benefit greatly from a better understanding of the relationships within the Prioninae (J. Millar, pers. comm.).

The subfamilies Prioninae and Parandrinae have long been considered the sister group to the rest of Cerambycidae (e.g., Crowson, 1960; Hunt *et al*., 2007; Lawrence *et al*, 2011; Linsley, 1959, 1961; Napp, 1994), making them a good starting point for long-term comprehensive phylogenetic work on the entire family. As with most of Cerambycidae, there is no consensus among taxonomists on tribal classification within Prioninae (e.g., Švácha & Lawrence, in review). Despite their ecological and species

diversity, interesting biology, and critical economic importance, a phylogenetic analysis of world Prioninae and Parandrinae has never been conducted and relationships among the 18 tribes and approximately 200 genera are unknown.

The objective of this work is to present the first formal phylogeny of world Prioninae and Parandrinae inferred from DNA sequence data. A robust phylogeny will allow us to test the monophyly of the groups, help to stabilize tribal and generic classification, and begin to place the classification of these subfamilies, and other Cerambycidae, into a world-wide context that has heretofore been lacking.

Materials and Methods

Taxon Sampling

Ingroup Taxa

Most prionines and parandrines are attracted to lights and readily collected. However, some prionines are diurnal and more difficult to sample. The ingroup included 31 prionine and parandrine species, including representative taxa from 12 tribes and 24 genera (Table 1). Of the 18 prionine tribes listed by Bousquet *et al*. (2009), 11 are represented in the analysis (Table 1). Representative specimens from seven tribes (Aegosomatini Thomson, Cacoscelini Thomson, Cantharocnemini Thomson, Ergatini Fairmaire, Eurypodini Gahan, Remphanini Lacordaire, and Vesperoctenini Vives) were unavailable for inclusion in this study. Only a single species of parandrine was included (representing the tribe Parandrini), so monophyly of that subfamily was not tested. Specimens representing the other parandrine tribe (Erichsoniini) were unavailable for study. Not all species were identified beyond genus (e.g., CER259 *Rhaphipodus* sp. 1)

and three ingroup taxa were represented by two individuals: *Derobrachus* sp. (CER318, CER630); *Tithoes* sp. (CER738, CER739); and *Xixuthrus axis* Thomson, 1877 (CER10, CER311) (Table 1). All specimens used in this study were preserved in 95% ethanol. All specimen and DNA vouchers are deposited in the Division of Arthropods frozen tissue collection, the Museum of Southwestern Biology, the University of New Mexico (MSBA, K.B. Miller, curator).

Outgroup Taxa

The 29 outgroup species included representative taxa from two longhorned beetle families (Cerambycidae, Disteniidae Thomson) and four cerambycid subfamilies (Cerambycinae Latreille, Lamiinae Latreille, Lepturinae Latreille, Spondylidinae Audinet-Serville), representing 25 tribes and 27 genera from four geographic regions (Table 1).

Data

Thoracic muscle tissue was excised from specimens preserved in 95% ethanol. DNA was extracted using Qiagen DNeasy (Valencia, CA, USA) protocol for animal tissue and specimens were retained for vouchering purposes.

Four genes were used in the analysis: 12S rRNA (12S, 380 bp), 28S rRNA (28S, 2985 bp), cytochrome oxidase I (COI, 953 bp), and histone III (H3, 328 bp). The primer sequences utilized are provided in Table 3 and amplification conditions were as follows: hot start 94° C (12 min), denature 94° C (1 min), anneal 56° C (1 min), elongation 70° C (1 min 30 s), final elongation 70° C (7 min), 35 cycles.

DNA fragments were amplified using PCR with TaKaRa Ex Taq (Takara Bio Inc., Otsu, Shiga, Japan) on an Eppendorf Mastercycler ep gradient S Thermal Cycler (Eppendorf, Hamburg, Germany) and visualized by gel electrophoresis. PCR purification was done using ExoSAP-IT (USB-Affymetrix, Cleveland, OH, USA) and cycle-sequenced using ABI Prism Big Dye v3.1 (Fairfax, VA, USA) with the same primers used for amplification. Sequencing reaction products were purified using Sephadex G-50 Fine (GE Healthcare, Uppsala, Sweden) and sequenced with an ABI 3130xl Genetic analyzer (Molecular Biology Facility, University of New Mexico). All gene regions were sequenced in both directions.

Data Analysis

Alignment

Sequence fragments were imported into Sequencher 4.1 (Genecodes, 1999) for nucleotide editing and contig assembly. Alignments of H3 and COI were based on conservation of codon reading frame and performed by eye. Alignments of 12S and 28S were performed in MUSCLE (Edgar, 2004). Aligned genes were concatenated in a text editor to form a single character matrix by gene. The resulting aligned dataset was 4,646 bp in length. Completeness of data was calculated for each taxon and gene to provide percentages of data coverage across the sampled taxa (Table 1). The overall data coverage for each gene was: 12S, 100% of characters; H3, 93% of characters; COI, 55% of characters; and 28S, 52% of characters. Twenty-nine of 60 taxa included had less than 40% data coverage, 11 of which were outgroup taxa (Table 1).

Parsimony Analysis

A parsimony analysis was conducted using the program NONA (Goloboff, 1995) as implemented by WinClada (Nixon, 2002). The "Ratchet" option was implemented using the following parameters: 500 (# of iterations/rep), 1 (# trees held/iteration), 464 (# characters to sample), amb-poly, and 10 (random constraint level). The resulting trees then were resubmitted to NONA and TBR branch swapping was executed to search for additional equally parsimonious trees. Branch support (bootstrap) was calculated in NONA using the following parameters: 1000 (number of replications), 10 (number search reps (Mult*N)), 1 (starting tree per rep (hold/)), don't do max* (TBR), and "save consensus" of each replication.

Bayesian Analysis

A partitioned Bayesian analysis of molecular data was conducted using MrBayes v3.2.1 (Huelsenbeck & Ronquist, 2001) implemented on the University of Alaska Fairbanks Life Science Informatics Portal. Ribosomal sequences (12S, 28S) were partitioned by gene and protein coding genes (COI, H3) were partitioned by codon. Models were fit to molecular data using the program MrModeltest2 (Nylander, 2004). The following models of molecular evolution were implemented per partition: 12S and 28S (GTR+I+Γ), COI codon positions 1 and 2 (GTR+I+Γ), COI codon position 3 (GTR+Γ), H3 codon position 1 (GTR+I), H3 codon position 2 (JC), and H3 codon position 3 (HKY+I+Γ). Four Markov Chain Monte Carlo runs were conducted for 20,000,000 generations sampled every 10,000th generation. The first 25% of sampled

trees (500) were discarded in each run as burn-in. A majority rule consensus tree was calculated from the set of trees remaining after burn-in.

Results

Sequence length variability, uncorrected p-distance, and number of nucleotide differences were calculated for each gene in Mega 5.1.0 (Tamura *et al*., 2009). For 12S, sequence data varied in length among sampled taxa from 312–359 bp, aligned sequence length was 380 bp, uncorrected p-distance was 0.21, and the number of nucleotide differences was 52.46. For 28S, sequence data varied in length among sampled taxa from 1861–2572 bp, aligned sequence length was 2985 bp, uncorrected p-distance was 0.041, and the number of nucleotide differences was 72.392. For COI, sequence data varied in length among sampled taxa from 718–806 bp, aligned sequence length was 953 bp, uncorrected p-distance was 0.26, and the number of nucleotide differences was 147.071. For H3, sequence data varied in length among sampled taxa from 269–328 bp, aligned sequence length was 328 bp, uncorrected p-distance was 0.18, and the number of nucleotide differences was 42.766.

The parsimony analysis resulted in two equally parsimonious trees, with the poorly resolved strict consensus (Length = 9,324; CI = 33; RI = 38) shown in Fig. 4. Low consistency and retention index values indicate considerable homoplasy in the data. The subfamily Prioninae was recovered as a monophyletic group with the inclusion of the Parandrinae and exclusion of two prionine exemplars (CER71 *Sarmydus antennatus* Pascoe, 1867 and CER4 *Aesa nearnsi*, new species). The single exemplar from the subfamily Parandrinae (CER365 *Parandra* (*Tavandra*) *polita* Say, 1835) was recovered

as sister to a pair of exemplars in the prionine tribe Acanthophorini Thomson (Fig. 4). The two exemplars in the subfamily Spondylidinae (CER31 *Arhopalus productus* (LeConte, 1850) and CER263 *Asemum striatum* (Linnaeus, 1758)) were recovered as a clade sister to the rest of the cerambycid subfamilies, and the two exemplars in the subfamily Lepturinae (CER150 *Stictoleptura c. canadensis* (Olivier, 1795) and CER368 *Desmocerus palliatus* (Forster, 1771)) were recovered as a clade sister to the subfamily Lamiinae. The subfamily Cerambycinae was recovered as monophyletic, with the inclusion of two prionine exemplars mentioned above (CER71 *Sarmydus antennatus* Pascoe, 1867 and CER4 *Aesa nearnsi*, new species), and sister to the Prioninae + Parandrinae clade. Bootstrap support values were generally low (Fig. 4). Nodes with a bootstrap value greater than 70% were reported for 11 nodes, including several congeneric exemplars (Fig. 4).

The Bayesian analysis resulted in a well resolved majority rule consensus tree with strong support values across the topology at the level of subfamily relationships (Fig. 5). The subfamily Prioninae was recovered as a monophyletic group with the inclusion of Parandrinae and an exemplar from the subfamily Cerambycinae (CER786 *Plectogaster* sp.) (Fig. 5, 6). In addition, the four cerambycid subfamilies included as outgroup taxa (Cerambycinae, Lamiinae, Lepturinae, and Spondylidinae) were recovered as monophyletic groups (Fig. 5). In general, relationships among the prionine tribes and genera were poorly supported (Fig. 5, 6).

The subfamily Parandrinae was represented by a single exemplar and was therefore not tested for monophyly. However, in both analyses (parsimony and Bayesian), the parandrine exemplar (CER365 *Parandra* (*T.*) *polita*) was recovered within

the prionine clade (Fig. 4–6). Both analyses also recovered the two cerambycoid families (Cerambycidae, Disteniidae) and three cerambycid subfamilies (Lamiinae, Lepturinae, and Spondylidinae) as monophyletic groups. In addition, both analyses recovered the Parandrinae + Prioninae clade as sister to the subfamily Cerambycinae.

Among the 11 prionine tribes included in the analyses, seven were recovered as monophyletic groups in the Bayesian analysis. The tribe Acanthophorini, represented by two congeneric exemplars (CER378 *Tithoes* sp. and CER379 *Tithoes* sp.), was recovered as a monophyletic group and strongly supported (Fig. 6).

The tribe Callipogonini Thomson, represented by two exemplars (CER106 *Orthomegas cinnamomeus* (Linnaeus, 1758) and CER384 *Enoplocerus armillatus* (Linnaeus, 1767)), was recovered as a monophyletic group and strongly supported (Fig. 6).

The tribe Closterini Quentin & Villiers, represented by two exemplars (CER748 *Closterus*? sp. 1 and CER749 *Closterus*? sp. 1), was recovered as a monophyletic group with the inclusion of the tribe Acanthophorini, and was weakly supported (Fig. 6).

The prionine tribe Macrotomini Thomson, represented by 10 exemplars (CER259 *Rhaphipodus* sp. 1; CER286 *Rhaphipodus* sp. 2; CER8 *Archetypus fulvipennis* (Pascoe, 1859); CER311 *Xixuthrus axis*; CER10 *Xixuthrus axis*; CER644 *Aulacotoma t. tenuelimbata* Nonfried, 1892; CER665 *Phlyctenosis*? sp. 1; CER649 *Phlyctenosis*? sp. 2; CER663 *Phlyctenosis*? sp. 3; and CER776 *Prionotoma gestroi* (Lameere, 1903)), was recovered as monophyletic group with the inclusion of three tribes (Macrodontiini, Mallaspini, and Mallodonini), and was weakly supported.

The tribe Mallaspini, represented by two exemplars (CER43 *Hileolaspis auratus* (Linnaeus, 1758) and CER328 *Praemallaspis argodi* (Lameere, 1909)), was recovered as a monophyletic group and strongly supported (Fig. 6).

The tribe Mallodonini Thomson, represented by two exemplars (CER487 *Neomallodon arizonicum* Casey, 1912 and CER741 *Mallodon downesii* Hope, 1843), was recovered as a monophyletic group and strongly supported (Fig. 6).

The tribe Prionini Latreille, represented by six exemplars (CER289 *Apterocaulus heterogama* (Burmeister, 1861); CER318 *Derobrachus* sp.; CER630 *Derobrachus* sp.; CER341 *Prionus* (*Neopolyarthron*) *imbricornis* Linnaeus, 1767; CER904 *Psalidognathus modestus* Fries, 1833; and CER19 *Osphryon wauensis* Nylander, 1998), was recovered as a monophyletic group with the exclusion of one exemplar (CER341) and inclusion of two taxa (the tribe Callipogonini and Macrotomini exemplar CER644), and was weakly supported (Fig. 6).

Four prionine tribes (Anacolini, Macrodontiini Thomson, Meroscelisini Thomson, and Terectini Lameere) were represented by a single exemplar so their monophyly was not tested (Table 1). In the Bayesian analysis, a clade containing two of these tribes (Anacolini and Terectini) was recovered as sister to the clade containing the remainder of Prioninae + Parandrinae, and was strongly supported (Fig. 6). This clade contained the only Anacolini exemplar (CER71 *Sarmydus antennatus*), only Terectini exemplar (CER4 *Aesa nearnsi*), only Plectogasterini Quentin & Villiers exemplar (CER786 *Plectogaster* sp., currently classified in the subfamily Cerambycinae), and a Prionini exemplar (CER341 *Prionus* (*N.*) *imbricornis*). The only exemplar in the tribe Meroscelisini

(CER146 *Microplophorus magellanicus* Blanchard, 1851) was recovered as sister to the remainder of Prioninae + Parandrinae.

Discussion

The first formal phylogeny of world Prioninae and Parandrinae inferred from DNA sequence data recovered these subfamilies as a monophyletic group (Fig. 5, 6). This finding is in agreement with traditional classification of the family Cerambycidae, which has often placed these subfamilies as sister taxa (e.g., Hunt *et al*., 2007; Linsley, 1961; Napp, 1994; Švácha & Lawrence, in review). Historically, Prioninae + Parandrinae have been hypothesized as a basal lineage sister to the rest of the family (Linsley, 1961; Napp, 1994; Švácha & Lawrence, in review). In this study, Prioninae + Parandrinae were recovered as sister to the subfamily Cerambycinae, which in turn was recovered as sister to the subfamily Lamiinae + Lepturinae (in the parsimony analysis) and sister to Lepturinae + Spondylidinae (in the Bayesian analysis) (Fig. 5).

The subfamilies Lepturinae + Spondylidinae were recovered as sister taxa in the Bayesian analysis (Fig. 5), a relationship which has been hypothesized by several authors (e.g., Crowson, 1960; Linsley, 1961; Napp, 1994). In the parsimony analysis, Spondylidinae was recovered as a clade sister to the remaining five cerambycid subfamilies included in the analysis (Fig. 4).

Prionines and parandrines share an important morphological synapomorphy: adults lack the typical cerambycid stridulatory (sound producing) structure consisting of a striated plate on the mesonotum and ridges on ventral face of posterior pronotal margin (Linsley, 1959; Švácha & Lawrence, in review) (e.g., Fig. 19). In addition, adult

prionines differ from most other cerambycids by the presence of lateral pronotal margin; however, this feature is highly variable and nearly lacking in some taxa. Švácha & Lawrence (in review) suggest that Parandrinae may be modified prionines based on adult and larval morphological characters.

The outgroup genus *Plectogaster* Waterhouse (tribe Plectogasterini) was recovered within the subfamily Cerambycinae (in the parsimony analysis) and within the subfamily Prioninae (in the Bayesian analysis) (Fig. 5–6). Recovery of this genus within the subfamily Prioninae is remarkable because this genus is currently classified in Cerambycinae (e.g., Adlbauer & Delahaye, 2006; Tavakilian & Chevillotte, 2012) and has had an interesting taxonomic history. For example, Gahan (1906, p. 5) points out that the genus *Plectogaster* was previously classified within the prionine tribe Anacolini by Lameere, but argues that the genus should instead be classified in the subfamily Cerambycinae due to the presence of several morphological characters. Gahan (1906) noted the following morphological characters to support his assertion: that the prothorax lacks a "true lateral margin" (a typically prionine character), that the mesonotum has a "large undivided stridulatory area" (the lack of a stridulatory area is a synapomorphy for the subfamilies Prioninae and Parandrinae), and that the wing venation "resembles that of no true Prioninae." I conducted a morphological study of the dissected hind wing and mesonotum of the exemplar included in this analysis (CER786 *Plectogaster* sp.) and found that both structures conform to the typical cerambycine form (i.e., hind wing lacking the typical prionine wedge cell and the mesoscutum with stridulatory area). It should be noted that sequence data for COI was missing for this exemplar (Table 1).

Relationships among prionine tribes were well resolved in both the parsimony and Bayesian analyses (Fig. 4–6). Support values were generally low in the parsimony analysis (Fig. 4), and low for several clades in the Bayesian analysis (Fig. 5–6). Seven of the 11 prionine tribes included in the study were recovered as monophyletic groups, with the inclusion or exclusion of a few taxa (see Results above). This finding indicates that current tribal classification within the subfamily may not be as artificial as many experts believe (e.g., Švácha & Lawrence, in review).

Most Prioninae are nocturnal and relatively few diurnal species are known from several tribes. Four exemplars of diurnal prionine species were included in this study, representing three tribes: CER71 *Sarmydus antennatus* (Anacolini), CER43 *Hileolaspis auratus* and CER328 *Praemallaspis argodi* (Mallaspini), and CER904 *Psalidognathus mode*stus (Prionini). The Anacolini exemplar was recovered in a poorly supported clade with three other taxa, representing two prionine tribes (Prionini, Terectini) (Fig. 6). The two Mallaspini exemplars were recovered as a clade within the Macrotomini clade (Fig. 6). Finally, the diurnal Prionini exemplar was recovered within the Prionini clade (Fig. 6).

At least two factors may have contributed to the low support values observed in this study: missing sequence data for a majority of included taxa and relatively sparse taxonomic coverage. Sequence data was missing from 40 of 60 (80%) of included taxa (Table 1). Coverage was especially low for two genes: 28S with 52% of characters and COI with 55% of characters. Also, of the approximately 200 described genera of the subfamily Prioninae, only 23 were included in this analysis (Table 1). Tribal

representation within Prioninae was moderate, with 11 of 18 currently recognized tribes included.

In light of the low support values observed in both the parsimony and Bayesian analyses, as well as the incomplete DNA sequence dataset and sparse taxonomic coverage, it would be premature to recommend taxonomic changes based on the results this study. It may also be premature to make any inferences regarding the biogeography or evolution of characters among the included taxa.

A revised study of this dataset would be improved by the addition of missing sequence data for included exemplars, as well the addition of exemplars from tribes and genera not currently included. To address these deficiencies, DNA has been successfully extracted from an additional 41 cerambycoid taxa to be added to a revised analysis (for a total of 101 taxa). These taxa represent 16 exemplars from the subfamilies Prioninae and Parandrinae (including four tribes not previously included in the study), as well as exemplars from four cerambycid subfamilies (Cerambycinae, Dorcasominae, Lepturinae, Spondylidinae), and the cerambycoid family Disteniidae. Additionally, five outgroup taxa from within the superfamily Chrysomeloidea (but outside the cerambycoid families) will be added to a revised analysis to better test higher-level relationships.

A revised study of this dataset would also be improved by the addition of a morphological dataset. Morphological characters could first be identified from existing literature, and then reevaluated and their homology reassessed. Additional morphological characters could be coded from the mandibles (which are often greatly enlarged in male prionines and parandrines), lateral pronotal carinae, antennae, genitalic structures, and hind wing venation.

The addition of missing sequence data, more ingroup and outgroup taxa, and morphological data should provide for a more complete evolutionary history of Prioninae and Parandrinae and allow for a more robust phylogenetic analysis of the family as a whole.

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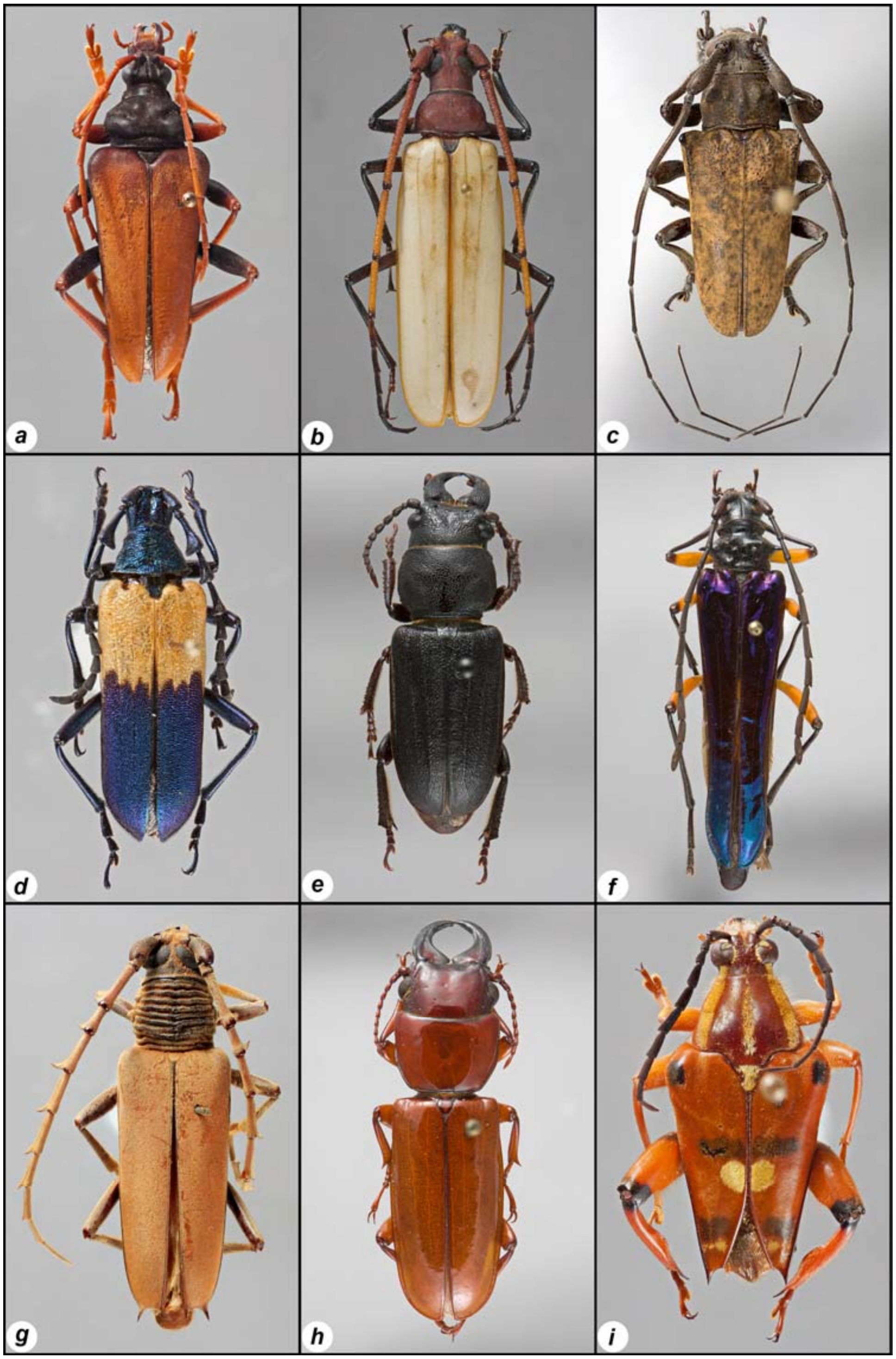

Figure 1. Nine examples of world longhorned beetle (Cerambycidae) diversity. **a)** *Mastododera* (Dorcasominae). **b)** *Aegosoma* (Prioninae). **c)** *Marensis* (Lamiinae). **d)** *Desmocerus* (Lepturinae). **e)** *Spondylis* (Spondylidinae). **f)** *Hephaestion* (Necydalinae). **g)** *Atiaia* (Cerambycinae). **h)** *Parandra* (Parandrinae). **i)** *Trichroa* (Dorcasominae).

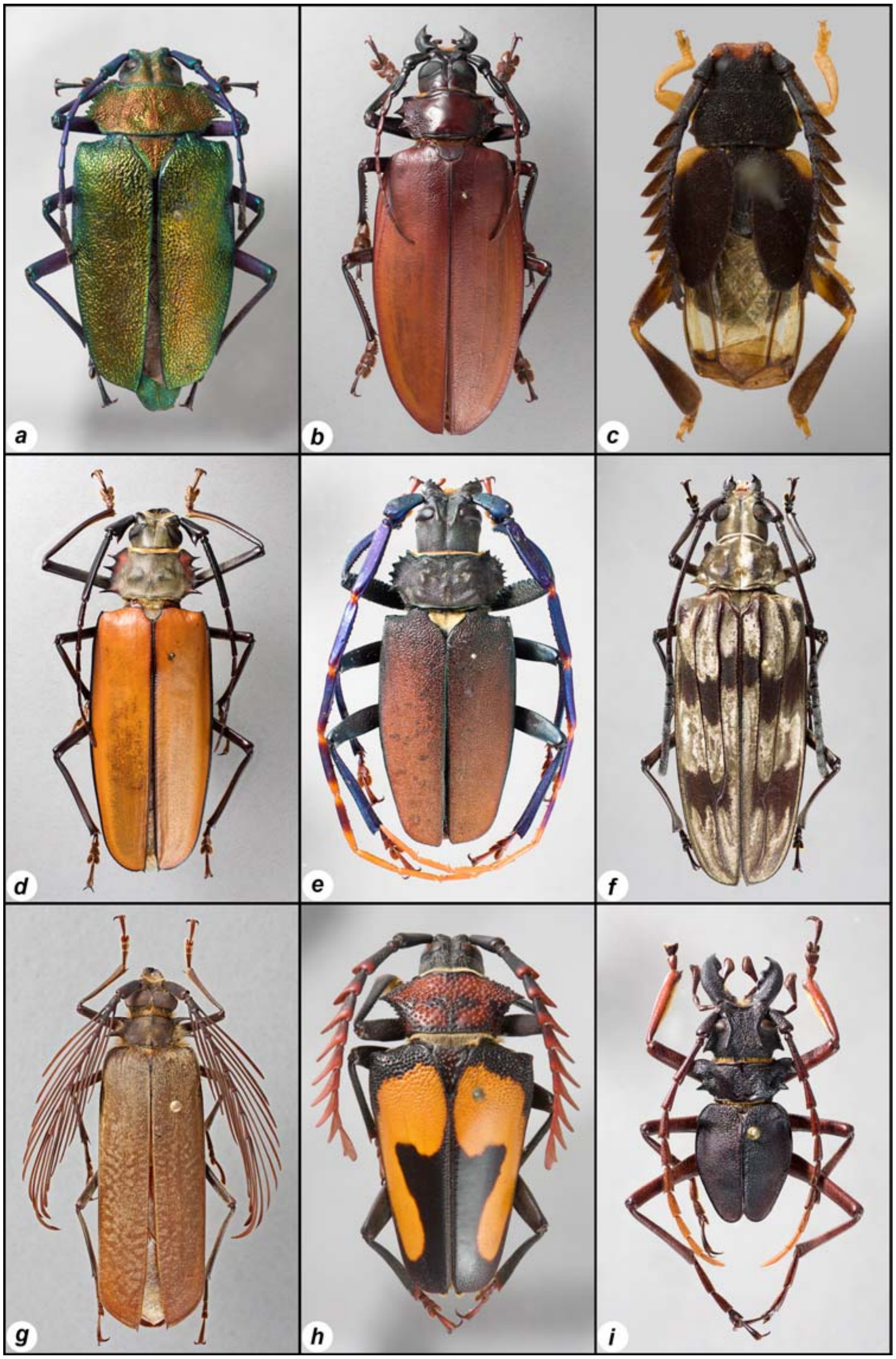

Figure 2. Nine examples of world prionine beetle (Cerambycidae: Prioninae) diversity. **a)** *Pyrodes* (Mallaspini). **b)** *Titanus* (Prionini). **c)** *Myzomorphus* (Anacolini). **d)** *Enoplocerus* (Callipogonini). **e)** *Mallaspis* (Mallaspini). **f)** *Baralipton* (Aegosomatini). **g)** *Sarifer* (Meroscelisini). **h)** *Calocomus* (Calocomini). **i)** *Prionacalus* (Prionini).

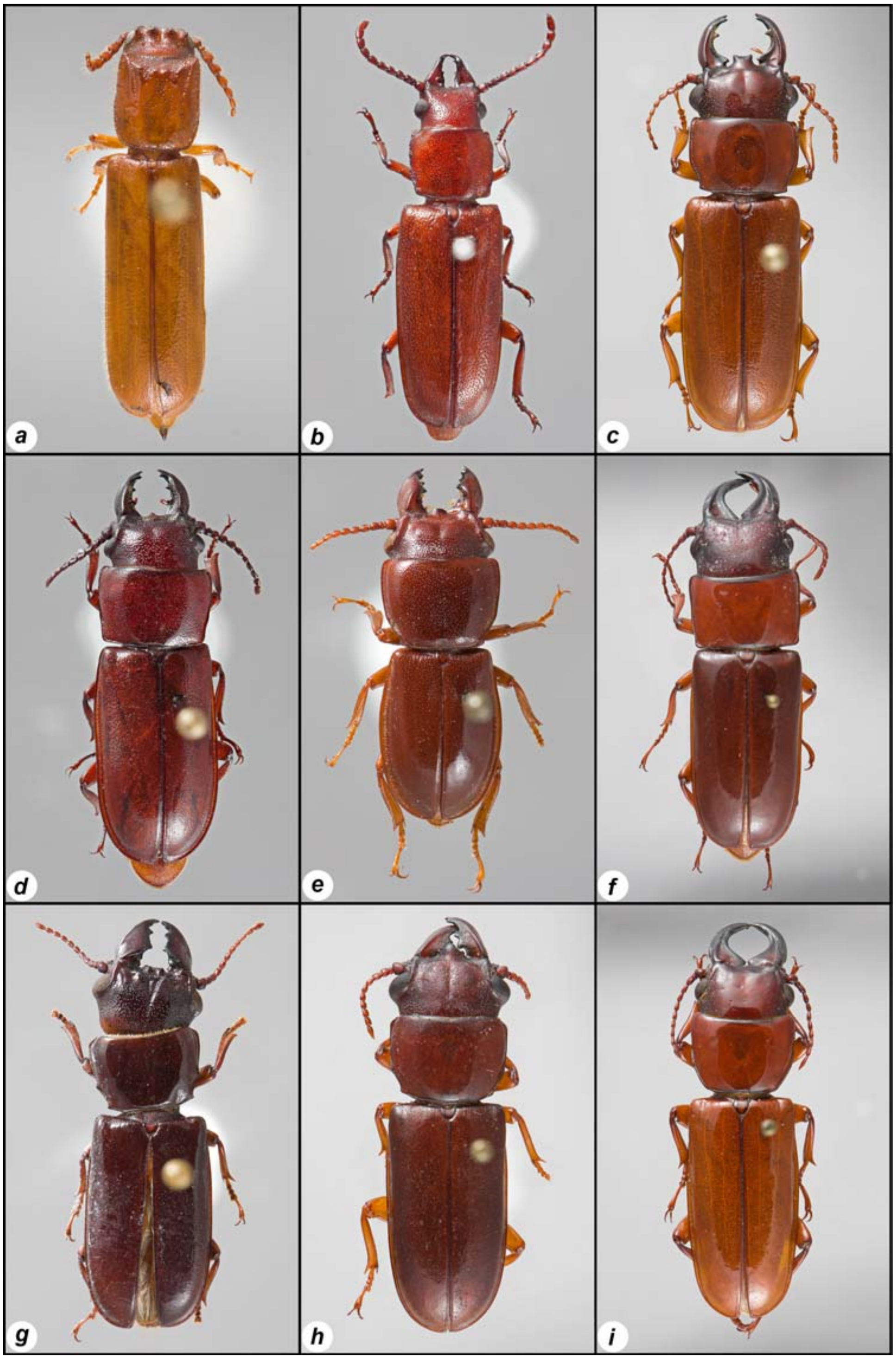

Figure 3. Nine examples of world parandrine beetle (Cerambycidae: Parandrinae) diversity. **a)** *Erichsonia dentifrons*. **b)** *Stenandra kolbei*. **c)** *Birandra* (*Y*.) *latreillei*. **d)** *Neandra brunnea*. **e)** *Storeyandra frenchi*. **f)** *Archandra caspia*. **g)** *Caledonandra passandroides*. **h)** *Melanesiandra solomonensis*. **i)** *Parandra* sp.

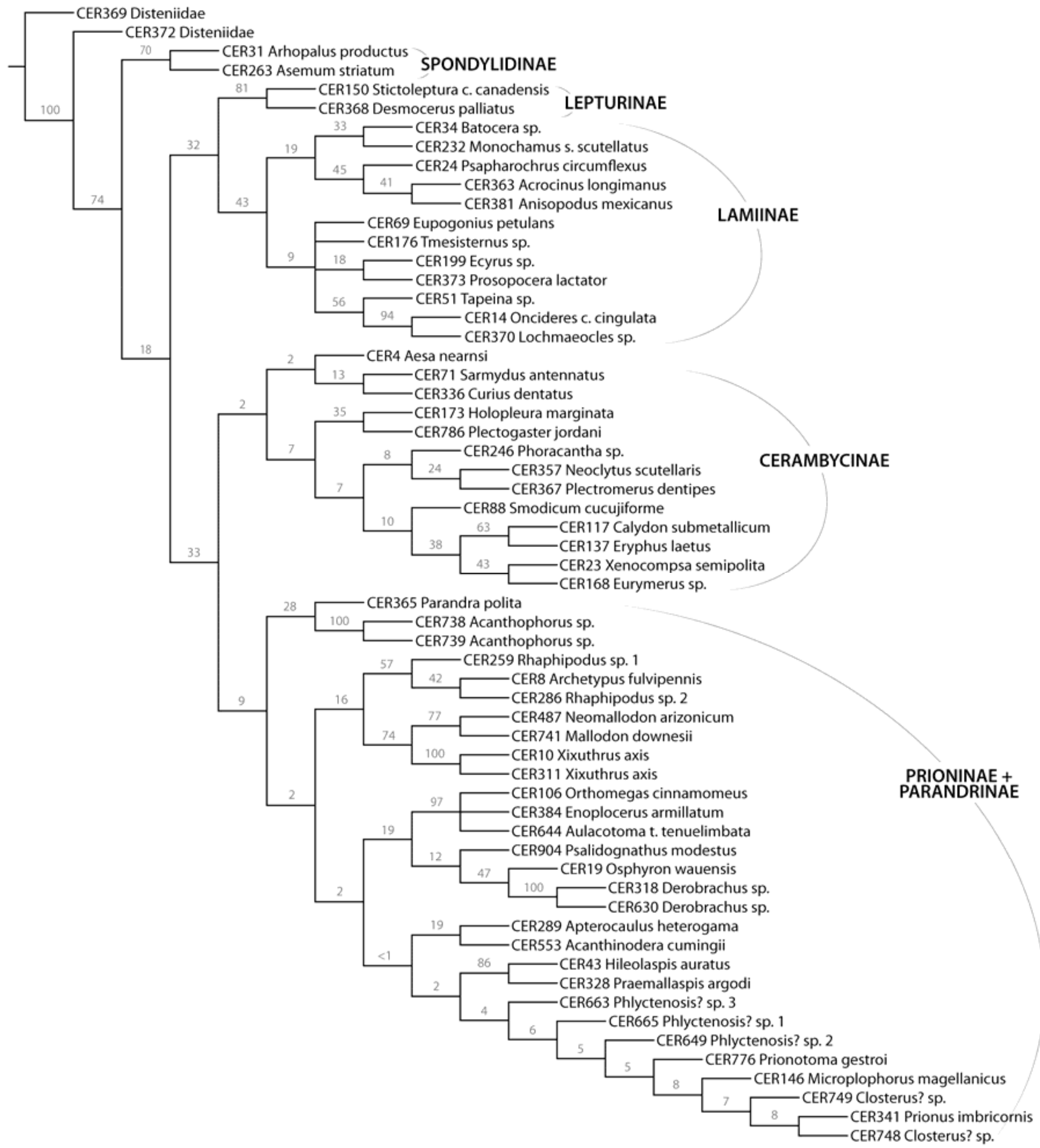

Figure 4. Strict consensus cladogram from two equally most parsimonious trees (L = 9,324; CI = 33; RI = 38) resulting from analysis of six longhorned beetle (Cerambycidae) subfamilies. Numbers at branches are bootstrap values.

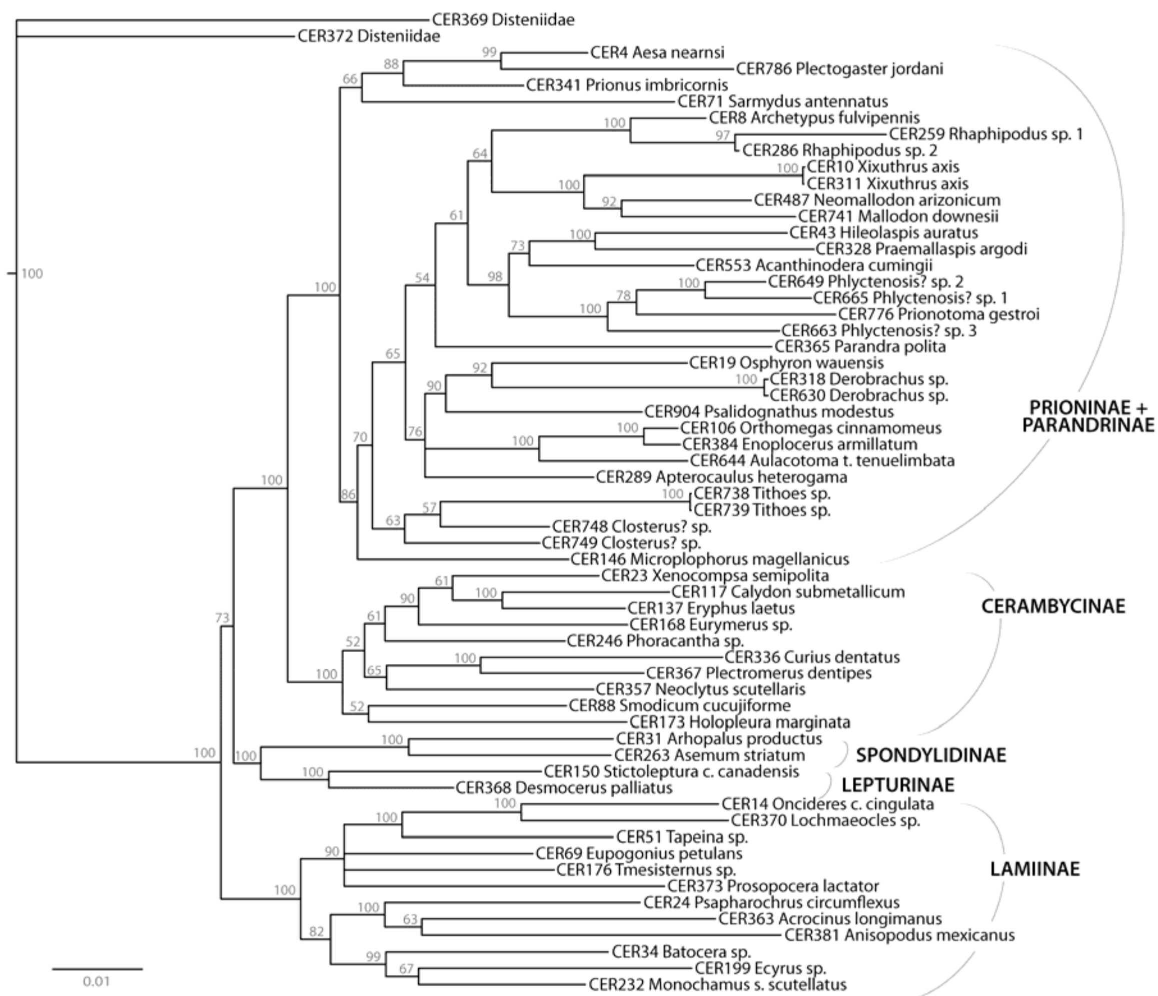

Figure 5. Majority rule consensus tree resulting tree resulting from Bayesian analysis of six longhorned beetle (Cerambycidae) subfamilies. Numbers at branches are posterior probability percentages.

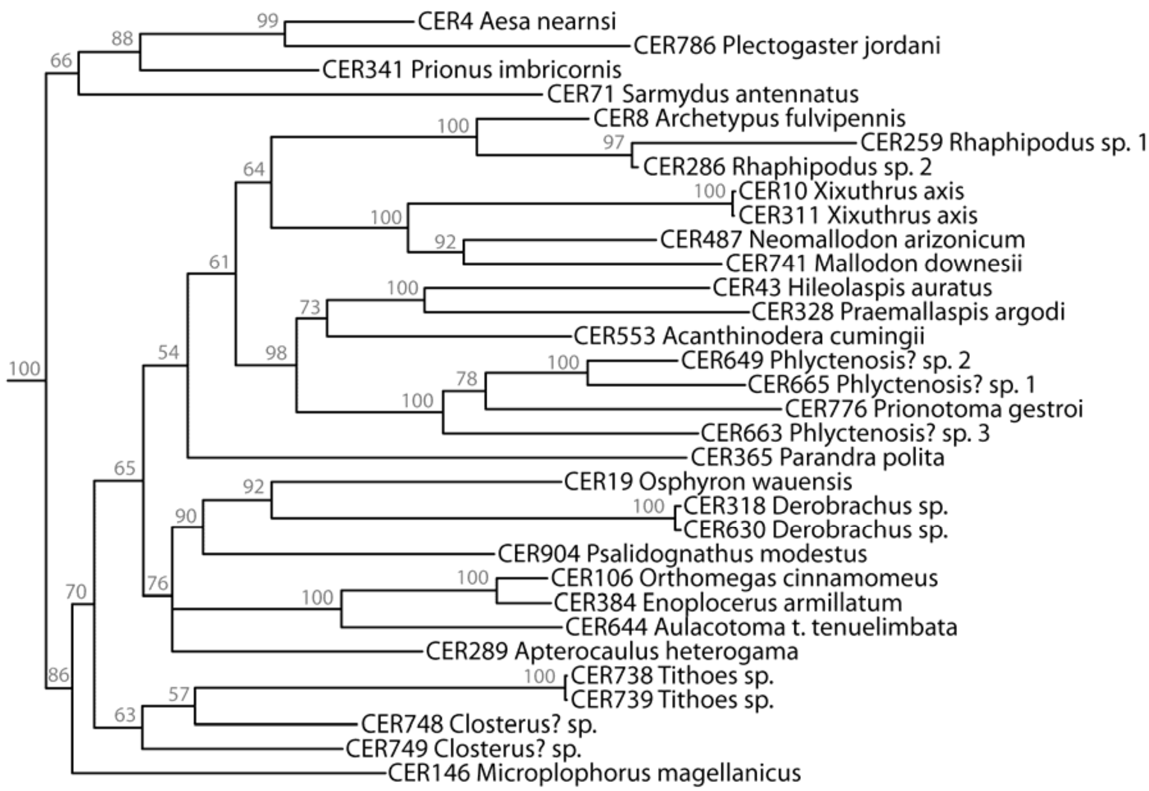

Figure 6. Detail of Prioninae + Parandrinae clade in majority rule consensus tree resulting from Bayesian analysis of six longhorned beetle (Cerambycidae) subfamilies. Numbers at branches are posterior probability percentages.

Family	Subfamily	Tribe	Species	12S	28S	COI	H3
Cerambycidae	Cerambycinae	Achrysonini	CER23 *Xenocompsa semipolita*	100%	100%	0%	100%
Cerambycidae	Cerambycinae	Callidiini	CER117 *Calydon submetallicum*	100%	0%	100%	100%
Cerambycidae	Cerambycinae	Clytini	CER357 *Neoclytus scutellaris*	100%	75%	0%	100%
Cerambycidae	Cerambycinae	Curiini	CER336 *Curius dentatus*	100%	0%	0%	100%
Cerambycidae	Cerambycinae	Ectenessini	CER168 *Eurymerus* sp.	100%	100%	100%	100%
Cerambycidae	Cerambycinae	Heteropsini	CER137 *Eryphus laetus*	100%	100%	0%	100%
Cerambycidae	Cerambycinae	Holopleurini	CER173 *Holopleura marginata*	100%	100%	0%	100%
Cerambycidae	Cerambycinae	Phoracanthini	CER246 *Phoracantha* sp.	100%	100%	100%	100%
Cerambycidae	Cerambycinae	Plectogasterini	CER786 *Plectogaster* sp.	100%	100%	0%	100%
Cerambycidae	Cerambycinae	Plectromerini	CER367 *Plectromerus dentipes*	100%	0%	0%	100%
Cerambycidae	Cerambycinae	Smodicini	CER88 *Smodicum cucujiforme*	100%	0%	0%	100%
Cerambycidae	Lamiinae	Acanthocinini	CER381 *Anisopodus mexicanus*	100%	100%	0%	100%
Cerambycidae	Lamiinae	Acanthoderini	CER24 *Psapharochrus circumflexus*	100%	100%	100%	100%
Cerambycidae	Lamiinae	Acrocinini	CER363 *Acrocinus longimanus*	100%	100%	0%	100%
Cerambycidae	Lamiinae	Batocerini	CER34 *Batocera* sp.	100%	100%	100%	100%
Cerambycidae	Lamiinae	Desmiphorini	CER69 *Eupogonius petulans*	100%	0%	0%	100%
Cerambycidae	Lamiinae	Monochamini	CER232 *Monochamus s. scutellatus*	100%	100%	100%	100%
Cerambycidae	Lamiinae	Onciderini	CER14 *Oncideres c. cingulata*	100%	0%	0%	100%
Cerambycidae	Lamiinae	Onciderini	CER370 *Lochmaeocles* sp.	100%	0%	0%	100%
Cerambycidae	Lamiinae	Pogonocherini	CER199 *Ecyrus* sp.	100%	0%	0%	100%
Cerambycidae	Lamiinae	Prosopocerini	CER373 *Prosopocera lactator*	100%	0%	0%	100%
Cerambycidae	Lamiinae	Tapeinini	CER51 *Tapeina* sp.	100%	100%	0%	100%
Cerambycidae	Lamiinae	Tmesisternini	CER176 *Sphingnotus?* sp.	100%	0%	100%	100%
Cerambycidae	Lepturinae	Desmocerini	CER368 *Desmocerus palliatus*	100%	100%	0%	100%
Cerambycidae	Lepturinae	Lepturini	CER150 *Stictoleptura c. canadensis*	100%	75%	0%	100%
Cerambycidae	Parandrinae	Parandrini	CER365 *Parandra* (*Tavandra*) *polita*	100%	0%	0%	100%
Cerambycidae	Prioninae	Acanthophorini	CER738 *Tithoes* sp.	100%	0%	0%	100%
Cerambycidae	Prioninae	Acanthophorini	CER739 *Tithoes* sp.	100%	100%	0%	100%
Cerambycidae	Prioninae	Anacolini	CER71 *Sarmydus antennatus*	100%	100%	100%	0%
Cerambycidae	Prioninae	Callipogonini	CER106 *Orthomegas cinnamomeus*	100%	100%	0%	100%
Cerambycidae	Prioninae	Callipogonini	CER384 *Enoplocerus armillatutus*	100%	100%	100%	100%
Cerambycidae	Prioninae	Closterini	CER749 *Closterus*? sp. 1	100%	0%	0%	100%
Cerambycidae	Prioninae	Closterini	CER748 *Closterus*? sp. 2	100%	0%	0%	100%
Cerambycidae	Prioninae	Macrodontiini	CER553 *Acanthinodera cumingii*	100%	100%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER259 *Rhaphipodus* sp. 1	100%	100%	0%	100%
Cerambycidae	Prioninae	Macrotomini	CER286 *Rhaphipodus* sp. 2	100%	0%	0%	100%
Cerambycidae	Prioninae	Macrotomini	CER8 *Archetypus fulvipennis*	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER311 *Xixuthrus axis*	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER10 *Xixuthrus axis*	100%	75%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER644 *Aulacotoma t. tenuelimbata*	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER665 *Phlyctenosis*? sp. 1 Madag.r	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER649 *Phlyctenosis*? sp. 2 Madag.	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER663 *Phlyctenosis*? sp. 3 Madag.	100%	0%	100%	100%
Cerambycidae	Prioninae	Macrotomini	CER776 *Prionotoma gestroi*	100%	100%	0%	100%
Cerambycidae	Prioninae	Mallaspini	CER43 *Hileolaspis auratus*	100%	0%	100%	100%
Cerambycidae	Prioninae	Mallaspini	CER328 *Praemallaspis argodi*	100%	100%	100%	100%
Cerambycidae	Prioninae	Mallodonini	CER487 *Neomallodon arizonicum*	100%	100%	0%	100%
Cerambycidae	Prioninae	Mallodonini	CER741 *Mallodon downesii*	100%	0%	100%	100%
Cerambycidae	Prioninae	Meroscelisini	CER146 *Microplophorus magellanicus*	100%	100%	100%	100%
Cerambycidae	Prioninae	Prionini	CER289 *Apterocaulus heterogama*	100%	100%	100%	100%
Cerambycidae	Prioninae	Prionini	CER318 *Derobrachus* sp.	100%	100%	100%	100%
Cerambycidae	Prioninae	Prionini	CER630 *Derobrachus* sp.	100%	0%	100%	100%
Cerambycidae	Prioninae	Prionini	CER341 *Prionus* (*N.*) *imbricornis*	100%	0%	0%	100%
Cerambycidae	Prioninae	Prionini	CER904 *Psalidognathus modestus*	100%	0%	0%	100%
Cerambycidae	Prioninae	Prionini	CER19 *Osphryon wauensis*	100%	0%	100%	100%
Cerambycidae	Prioninae	Terectini	CER4 *Aesa nearnsi* new species	100%	0%	100%	0%
Cerambycidae	Spondylidinae	Asemini	CER31 *Arhopalus productus*	100%	100%	100%	100%
Cerambycidae	Spondylidinae	Asemini	CER263 *Asemum striatum*	100%	0%	0%	100%
Disteniidae	Disteniinae	Disteniini	CER369 *Distenia* sp.	100%	100%	0%	0%
Disteniidae	Disteniinae	Disteniini	CER372 Genus sp. Zambia	100%	100%	0%	0%

Table 1. List of 60 ingroup and outgroup taxa used in analyses of Prioninae + Parandrinae (Cerambycidae), with percentage of data coverage per gene sequenced.

Family	Subfamily	Tribe	Species
Cerambycidae	Cerambycinae	Compsocerini	CER1134 *Compsocerus violaceus*
Cerambycidae	Cerambycinae	Eburiini	CER1084 Eburia haldemani
Cerambycidae	Cerambycinae	Eburiini	CER1065 Eburia sp. 1 DR
Cerambycidae	Cerambycinae	Eburiini	CER1072 Eburia sp. 2 DR
Cerambycidae	Cerambycinae	Eburiini	CER950 Genus sp. Panama
Cerambycidae	Cerambycinae	Erlandiini	CER1142 *Erlandia inopinata*
Cerambycidae	Cerambycinae	Platyarthrini	CER1109 *Platyarthron chilensis*
Cerambycidae	Cerambycinae?	Unknown	CER580 Genus sp. Zambia
Cerambycidae	Cerambycinae	Unknown	CER1070 Genus sp. Zambia
Cerambycidae	Dorcasominae	Apatophyseini	CER648 *Mastododera nodicollis*?
Cerambycidae	Dorcasominae	Apatophyseini?	CER642 Genus sp. 1 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini?	CER674 Genus sp. 2 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini?	CER1149 Genus sp. 3 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini?	CER1150 Genus sp. 4 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini?	CER673 Genus sp. 5 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini?	CER745 Genus sp. 6 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini	CER672 Genus sp. 7 Madagascar
Cerambycidae	Dorcasominae	Apatophyseini	CER675 Genus sp. 8 Madagascar
Cerambycidae	Lepturinae	Lepturini	CER1148 Genus sp. USA
Cerambycidae	Parandrinae	Erichsoniini	CER1153 *Erichsonia dentifrons*
Cerambycidae	Parandrinae	Parandrini	CER1061 *Birandra (Y.) latreillei*
Cerambycidae	Parandrinae	Parandrini	CER1114 Genus sp. CR
Cerambycidae	Prioninae	Anacolini	CER1012 *Sceleocantha* sp. Australia
Cerambycidae	Prioninae	Callipogonini	CER1044 *Trichocnemis s. neomexicanus*
Cerambycidae	Prioninae	Macrotomini	CER1009 *Archetypus*? sp. Australia
Cerambycidae	Prioninae	Macrotomini	CER1010 *Paroplites*? sp. Australia
Cerambycidae	Prioninae	Macrotomini	CER1011 *Xixuthrus*? sp. Australia
Cerambycidae	Prioninae	Mallaspini	CER1106 *Scatopyrodes* sp.
Cerambycidae	Prioninae	Macrodontiini	CER552 *Acanthinodera cumingii*
Cerambycidae	Prioninae	Meroscelisini	CER1123 *Sarifer seabrai*
Cerambycidae	Prioninae	Meroscelisini	CER1023 *Tragosoma* sp.
Cerambycidae	Prioninae	Solenopterini	CER1057 *Elateropsis* sp.
Cerambycidae	Prioninae	Unknown	CER1008 *Agrianome*? sp. Australia
Cerambycidae	Prioninae	Unknown	CER1007 Genus sp. 1 Australia
Cerambycidae	Prioninae?	Unknown	CER1051 Genus sp. 2 Australia
Cerambycidae	Spondylidinae	Atimiini	CER1132 *Atimia* sp.
Cerambycidae	Spondylidinae	Saphanini	CER1129 *Michthisoma heterodoxum*
Cerambycidae	Spondylidinae	Saphanini	CER670 *Opsamates*? sp.
Cerambycidae	Disteniinae	Disteniini	CER1086 Genus sp. 1 Nicaragua
Disteniidae	Disteniinae	Disteniini	CER1051 Genus sp. 2 Nicaragua
Disteniidae	Disteniinae	Disteniini	CER1052 Genus sp. 3 Nicaragua

Table 2. List of taxa for which DNA has been successfully extracted and to be added to analysis of Prioninae + Parandrinae (Cerambycidae).

Gene	Primer	Sequence
12S	ai	5’ - AAACTACGATTAGATACCCTATTAT - 3’
	bi	5’ - AAGAGCGACGGGCGATGTGT - 3’
28S (AB)	Rd1a	5’ - CCCSCGTAAYTTAGGCATAT - 3’
	Rd4b	5’ - CCTTGGTCCGTCTTTCAAGAC - 3’
28S (BD)	Rd3a	5’ - AGTACGTGAAACCGTTCAGG - 3’
	Rd5b	5’ - CCACAGCGCCAGTTCTGCTTAC - 3’
28S (DE)	Rd4.5a	5’ - AAGTTTCCCTCAGGATAGCTG - 3’
	Rd6b	5’ - AACCRGATTCCCTTTCGCC - 3’
28S (EF)	Rd5a	5’ - GGYGTTGGTTGCTTAAGACAG - 3’
	Rd7b1	5’ - GACTTCCCTTACCTACAT - 3’
COI	Jerry	5’ - CAACATTTATTTTGATTTTTTGG - 3’
	Pat	5’ - TCCAATGCACTAATCTGCCATATTA - 3’
H3	Hf	5’ - ATGGCTCGTACCAAGCAGACVGC - 3’
	Hr	5’ - ATATCCTTRGGCATRATRGTGAC - 3’

Table 3. Primer sequences used in parsimony and Bayesian analyses of Prioninae + Parandrinae (Cerambycidae).

CHAPTER 2

Morphological Study and Phylogenetic Analysis of the Twig Girdlers (Insecta: Coleoptera: Cerambycidae: Onciderini)

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Abstract

A morphological study and phylogenetic analysis of the tribe Onciderini Thomson (Cerambycidae: Lamiinae) is presented. Members of this tribe are commonly referred to as the "twig girdlers" due to the peculiar behavior exhibited by adult females of at least four described genera. For the morphological study, specimens representing 74 of the 80 described genera of Onciderini were disarticulated and dissected. Twenty-three morphological characters were illustrated and studied, including the head, mandible, ligula, pronotum, prosternum, mesonotum, metendosternite, hind wing, and aedeagus. Seventy-four ingroup taxa and three outgroup taxa were scored for 23 morphological characters. Results of both the cladistic and Bayesian analyses suggest that the tribe is monophyletic with respect to the outgroup taxa chosen and supported by one unambiguous synapomorphy (pronotum transverse, from 1.2–1.5× as long). Relationships among the species of Onciderini included were poorly resolved and support values were low.

Introduction

The tribe Onciderini (Cerambycidae: Lamiinae) is attributed to Thomson (1860) (Bousquet *et al*., 2009). This large tribe currently consists of 489 described species in 80 genera (Table 4) (Nearns & Tavakilian, 2012b; Monné & Bezark, 2012). The type genus, *Oncideres* Lacordaire, 1830 (Fig. 12f), is the most species-rich in the tribe with 124 described species. Six additional genera contain more than 20 species (*Cacostola* Fairmaire & Germain (32), *Hypsioma* Audinet-Serville (31), *Lochmaeocles* Bates (25), *Hesychotypa* Thomson (23), *Trestonia* Buquet (22), and *Tulcus* Dillon & Dillon (21)) and together these seven genera account for 278 of 489 (57%) described species of Onciderini (Table 4). In addition, 51 of 80 genera (64%) are either monotypic or contain only two species.

Onciderini is widely distributed in the New World from North America to southern South America. Nearly all genera in the tribe (77 of 80) are known from South America, with most occurring in Brazil (71 of 80) (Monné 2005; Monné & Bezark 2012; Nearns *et al*. 2011). Twenty five genera are known from Central America (including Mexico). Thirteen genera are known from Mexico; Costa Rica and Panama each have 21 genera recorded. Although two twig girdlers were originally described from Chile in 1859, this is believed to be an error as no members of this group have been collected there since (J.E. Barriga, pers. comm.). Only three genera are known to occur in the USA (*Cacostola* (Fig. 7g), *Lochmaeocles* (Fig. 11e), and *Oncideres* (Fig. 12f)). *Taricanus* (Fig. 14e) has been recorded from the USA, but this is likely an erroneous record (J.E. Wappes, pers. comm.). See Monné & Bezark (2012) for current geographic distribution.

In 1860, Thomson created the group "Onciderite" (now Onciderini) and later (1868) published a revision of the "groupe de oncidérites" which included 28 genera and 151 species. The most recent revision of the tribe was undertaken by Dillon & Dillon (1945, 1946) who recognized 63 genera and 260 species. This important contribution provided dorsal habitus illustrations of 251 taxa, nearly all of which were illustrated for the first time, as well as dichotomous keys to genera and species. One major flaw in their study must be noted: Dillon & Dillon did not examine type specimens of many taxa deposited in European museums. Given the concurrence of their revision with World War II, this is understandable; however, this omission has caused several taxonomic problems at both the generic and species level.

Since Dillon & Dillon's revision, taxonomic contributions have been provided by several authors, including Dillon & Dillon (1949, 1952), Fragoso (1967, 1970, 1971), Galileo & Martins (1990, 1991, 2001, 2003, 2007, 2008a, 2008b), Giorgi (1998, 2001a, 2001b), Martins (1975, 1979, 1981a, 1981b), Martins & Galileo (1990, 1995, 1996, 2005a, 2005b, 2007, 2008, 2009a, 2009b, 2010), Martins *et al*. (2006, 2008, 2009), Monné & Fragoso (1984), Nearns & Tavakilian (2012a, 2012b), Nearns & Swift (2011), Nearns *et al*. (2011), Noguera (1993), and Noguera & Chemsak (1993).

Known as the "twig girdlers" in the USA and as the "corta palo" [cuts wood] (Bosq, 1950), "serrador" [one who saws], or "serruchador" [sawyer] (Delgado & Couturier, 2004) in Latin America, adult females of at least four genera in the tribe Onciderini (*Ecthoea* (Fig. 9a), *Lochmaeocles* (Fig. 11e), *Oncideres* (Fig. 12f), and *Psyllotoxus* (Fig. 14a)) are known to "girdle" living branches by chewing a V-shaped groove with their mandibles completely around the branch or main trunk, through the

bark and phloem (Fig. 63a–c). Females then oviposit into the newly cut host material which usually falls to the forest floor. By girdling a living branch or trunk, females weaken a part of the healthy host tree, circumventing plant defense mechanisms and ensuring that valuable nutrients such as nitrogen remain trapped within the branch for the benefit of their larvae (Dillon & Dillon, 1945; Forcella, 1981; Forcella, 1984; Rice, 1995; Rogers, 1977) (e.g., Fig. 63c). This peculiar girdling by adult females appears to be unique to Onciderini. More than 50 different woody plant families have been recorded as hosts for Onciderini, including many economically and agriculturally important crops such as avocado, cocoa, coffee, guava, grape, peach, pecan, and sweet potato (Monné, 2005; Nearns *et al*., 2011).

In the USA, the biology of the "hickory girdler," *Oncideres c. cingulata* (Say, 1826), has been studied extensively by several authors (Dillon & Dillon, 1945; Forcella, 1981; Forcella, 1984; Rice, 1995; Rogers, 1977). Adults of this species (Fig. 12f) emerge from late August to early October (Solomon, 1995) and the life cycle is usually completed in one year (Linsley, 1940; Linsley & Chemsak, 1984).

The biology of another North American species, the "huisache girdler," *Oncideres pustulata* LeConte, 1854 has been studied by several authors (e.g., High, 1915; Hovore & Penrose, 1982; Rice, 1986; Rice, 1989). Additional studies on the biology of *Oncideres* were conducted by Duffy (1960) and Linsley (1961). Hovore & Penrose (1982) and Touroult (2004) recorded non-Onciderini Cerambycidae species which emerged from branches girdled by *Oncideres*.

Several recent studies have found that girdling by *Oncideres* species can severely affect the size and architecture of host trees. For example, Romero *et al*. (2005) and

studied the effects of *O. humeralis* Thomson, 1868 on the number and size structure of its host plants in Brazil. In a related study, Neto *et al*. (2005) evaluated host plant selection and patterns of host use by the same species in Brazil. Calderon-Cortes *et al*. (2011) studied the effect of ecosystem engineering by a species of *Oncideres* on the arthropod community of a tropical dry forest in Mexico. Caraglio *et al*. (2001) provided observations on the links between girdling activity by a species of *Oncideres* and the architecture of a species of tree in French Guiana.

Given that at least four genera of Onciderini are known to girdle branches, and that more than 50 different woody plant families have been recorded (including many economically and agriculturally important crops), the potential exists for an onciderine to become an invasive pest species. An interactive identification tool to Onciderini ("Oncid ID") was recently developed and freely available to both US Department of Agriculture (USDA) port identifiers and the general public (Nearns *et al*., 2011). However, the monophyly of Onciderini has never been tested and additional studies are needed.

The objective of this study is to present the first morphological study and phylogenetic analysis of the Onciderini. A comprehensive morphological study and robust phylogeny will aid in identification and discovery of new taxa, allow for the discovery of relationships among genera and species, test the monophyly of the tribe, and help to stabilize generic classification.

Materials and Methods

Specimens and photographs from the following collections were examined: American Coleoptera Museum, San Antonio, Texas, USA; The Natural History Museum,

London, United Kingdom; Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; Cornell University Insect Collection, Ithaca, New York, USA; Denis Faure Private Collection, Kourou, French Guiana; Edmund F. Giesbert Collection (at FSCA), Gainesville, Florida, USA; Eugenio H. Nearns Private Collection, Albuquerque, New Mexico, USA; Florida State Collection of Arthropods, Gainesville, Florida, USA; Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Heredia, Costa Rica; Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; Ian P. Swift Private Collection, Orange County, California, USA; Jean-Louis Giuglaris Private Collection, Matoury, French Guiana; Julien Touroult Private Collection, Soyaux, France; Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; Departamento de Historia Natural, Museo Nacional de Costa Rica, San José, Costa Rica; Muséum National d'Histoire Naturelle, Paris, France; Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima, Peru; Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; Swedish Museum of Natural History, Stockholm, Sweden; Naturhistorisches Museum Basel, Basel, Switzerland; Pierre-Henri Dalens Private Collection, Rémire-Montjoly, French Guiana; Nationaal Natuurhistorische Museum, Leiden, Netherlands; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany; National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA; Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; Bavarian State Collection of Zoology, Munich, Germany; and Zoological Museum University of Copenhagen, Copenhagen, Denmark.

Classification and distributional data are based on Monné (2005) and Monné & Bezark (2012). Observations of whole specimens were made using a Max Erb stereomicroscope with 10× eyepieces. Structures cleared in KOH were placed in a watch glass containing 95% ethyl alcohol under a Zeiss (Oberkochen, Germany) Achromat S stereo dissecting microscope fitted with a drawing tube. Photographs were taken with a Visionary Digital (Dun Inc., Palmyra, VA, USA) Passport Storm imaging system fitted with a Canon (Lake Success, NY, USA) EOS 40D. Illustrations were completed using Adobe (Mountain View, CA, USA) Illustrator CS5 software with a Wacom (Vancouver, WA, USA) Bamboo drawing tablet.

Specimen Preparation

Specimens were prepared for disarticulation and dissection by soaking in warm water for 1–3 hours. Disarticulated structures were placed in 10% KOH solution and heated for 30 minutes at 90 C. Hind wings were mounted on white card stock for photography.

Taxon Sampling for Morphological Study

Specimens from 74 of 80 (93%) described genera of Onciderini were disarticulated and dissected for morphological study. Whenever possible, the type species for each genus in the tribe was selected for study. In addition, when available, specimens of both sexes were dissected for study to account for sexually dimorphic characters. Morphological characters which exhibited significant intraspecific variation were excluded from the study. A morphological atlas was prepared (Fig. 16) and the

following morphological characters were studied: head (Figs. 17, 23a–dd, 24a–dd, 25a–r, 39a–c, 40a–b, 41a–b, 44a–c, 45a–c, 46a–c); ligula (Figs. 18, 26a–dd, 27a–y, 48a–b); mandible (Figs. 42a–b, 43a–b); pronotum (Figs. 28, 55a–c); prosternum (Fig. 29); mesonotum (Figs. 19, 30a–dd, 31a–ii, 52a–c, 53a–b); metendosternite (Figs. 21, 32a–dd, 33a–n, 54a–b); hind wing (Figs. 20, 36a–r, 37a–r, 38a–p, 60a–c); aedeagus (tegmen and parameres) (Figs. 22, 34a–dd, 35a–dd, 61a–b, 62a–b). Terminology for the ligula and hind wing follows Lawrence *et al*., (2011); and for the aedeagus Sharp & Muir (1912).

Representative specimens for six onciderine genera were unavailable for dissection: *Carenesycha* Martins & Galileo (Fig. 7h), *Neohylus* Monné (Fig. 12d) (partial specimen available for dissection), *Priscatoides* Dillon & Dillon (Fig. 13e) (known from only two specimens), *Psyllotoxoides* Breuning (Fig. 13i) (known only from the female holotype), *Tritania* Dillon & Dillon (Fig. 15b), and *Xylomimus* Bates (Fig. 15h).

Taxon Sampling for Phylogenetic Analyses

Ingroup Taxa

The ingroup taxa consisted of 74 of 80 described genera of Onciderini, including the type genus of the tribe, *Oncideres* (Table 7). Representative specimens for six genera were not available for dissection (see above) and were not included in the morphological study or phylogenetic analyses.

Outgroup Taxa

A total of three outgroup taxa were selected from two tribes traditionally near Onciderini in the subfamily Lamiinae. *Saperda lateralis* Fabricius, 1775 (Saperdini) and

two species from the tribe Agapanthiini were included: *Hippopsis lemniscata* (Fabricius, 1801), *Pachypeza joda* Dillon & Dillon, 1945 (Table 7).

Data for Phylogenetic Analyses

Characters and Their States

A total of 23 morphological were coded (12 binary, 11 multistate). Eleven characters (29 states) were coded from the head, including eyes and antennae; two characters (seven states) from the prothorax; two characters (six states) from the mesothorax; one character (two states) from the metathorax; five characters (13 states) from the elytra and hind wing; two characters (four states) from male genitalic structures. All characters were run as unweighted and nine characters were treated as additive (Table 5, 6).

Tables 5 and 6 provide definitions of the morphological characters and their states used in the phylogenetic analyses. Morphological characters were coded from both males and females unless indicated otherwise. Character and character state numbers refer to data coded in the data matrix for each taxon (Table 7). The data matrix was constructed and edited using the program WinClada (Nixon, 2002). Inapplicable data were coded as missing data (Strong & Lipscomb, 1999).

Parsimony Analysis

A parsimony analysis was conducted using the program TNT (Goloboff *et al.*, 2005) as implemented by WinClada heuristics (Nixon, 2002). The following commands were used to find the most parsimonious trees: ratchet (“20000: # of interations/rep”, “4:

UPweight percentage", "4: DOWNweight percentage"), drift ("5000: # of iterations/rep"), tree fusion ("5000: # rounds"), sectorial search, TBR-max, and "1,000,000: # total trees to hold." Unsupported nodes were collapsed in all trees using WinClada. Consistency Index (CI) and Retention Index (RI) were calculated in WinClada. Branch support (bootstrap) values were calculated in NONA as implemented by WinClada using the following commands: 1000 replications, 10 search reps (MULT*N), 5 starting tree per replication (HOLD/), and don't do max* (TBR), and save consensus of each replication.

Bayesian Analysis

A Bayesian analysis was conducted using the program MrBayes v3.2.1 (Huelsenbeck & Ronquist, 2001) implemented on the University of Alaska Fairbanks Life Science Informatics Portal. The same nine characters as in the parsimony analysis were treated as additive (ordered) and the model accounted for only parsimony-informative characters sampled (Ronquist *et al*., 2011).

Results

A morphological study of specimens representing 74 of 80 described genera of Onciderini resulted in 23 characters with potential utility for tribal- and generic-level diagnoses, as well as phylogenetic analyses. Morphological variation was found in characters from the head, mandible, ligula, pronotum, prosternum, mesonotum, metendosternite, hind wing, and aedeagus.

A cladistic analysis of 74 species of Onciderini, three outgroup taxa, and 23 characters produced 70,468 most parsimonious trees of length 232. The strict consensus of most parsimonious trees (L = 377 steps, CI = 10, RI = 23) is poorly resolved and supports the tribe Onciderini as a monophyletic group with respect to the outgroup taxa chosen (Fig. 64). Low consistency and retention index values indicate considerable homoplasy in the data. Characters were mapped in WinClada using ACCTRAN (fast) optimization (Fig. 64). The Onciderini clade is characterized by one unambiguous synapomorphy (pronotum transverse, from 1.2–1.5× as long). Relationships among the 74 ingroup taxa were almost completely unresolved and bootstrap support values were low for all clades (none greater than 70% recorded).

A Bayesian analysis of 77 taxa and 23 morphological characters resulted in a poorly resolved majority rule consensus tree (Fig. 65). The tribe Onciderini was a monophyletic group with respect to the outgroup taxa chosen. As in the parsimony analysis, relationships among the 74 ingroup taxa were almost completely unresolved and poorly supported (Fig. 65).

Discussion

Relatively few morphological atlases have been produced for Cerambycidae (e.g., Galileo, 1987a; Galileo, 1987b; Lingafelter & Hoebeke, 2002) or Coleoptera (e.g., McHugh *et al*. 1997). However, a detailed morphological study of a taxon can be a valuable tool, aiding in the discovery of new taxa, relationships among genera and species, as well as characters associated with particular behaviors or modes of life.

A morphological study of Onciderini specimens representing 74 of 80 described genera resulted in the identification of 23 characters which may be of utility for tribal- and generic-level diagnoses, as well as phylogenetic analyses.

Characters of the head have long been employed in the diagnosis of Onciderini (e.g., Dillon & Dillon, 1945). Significant variation was found in several relationships, such as the size of the eye compared to the gena, the width of the frons between the lower lobes of the eyes, and the relative width between antennal tubercles (Figs. 17, 23a–dd, 24a–dd, 25a–r, 39a–c, 40a–b, 41a–b, 44a–c, 45a–c, 46a–c). Several characters of the head which exhibited significant intraspecific variation were excluded from the study (e.g., the number of ommatidia connecting the upper and lower eye lobes).

Mandibles dissected from 74 of 80 described genera of Onciderini (Figs. 42a–b, 43a–b) showed significant variation in the incisor edge, which was either smooth or dentate. Mandibles with dentate incisor edges were either unidentate or multidentate. In a few genera studied this character was found to be sexually dimorphic. In each case, males were found to have the incisor edge dentate while females of the same species were found to have the incisor edge smooth. Female specimens of the four genera known to girdle branches (*Ecthoea*, *Lochmaeocles*, *Oncideres*, and *Psyllotoxus*) were consistently found to have mandibles with a smooth incisor edge.

The maxilla and labium were also studied for 74 genera and variation was found in the shape of the lobes of the ligula. Specifically, lobes of the ligula were found to vary from broadly rounded to obliquely subtruncate. In addition, the level of emargination between the lobes was also variable (Figs. 18, 26a–dd, 27a–y, 28a–r, 48a–b).

The shape and proportions of the pronotum (Figs. 28, 55a–c) varied significantly among the 80 genera studied, ranging from subcylindrical to subconical, and with or without lateral tubercles. Similarly, the prosternum (Fig. 29), as well as the shape and proportions of the prosternal process between the procoxae, varied significantly.

Several characters of the mesonotum were also found to vary. Specifically, the size and shape of the stridulatory file, the shape of the apex of the mesoscutum, and the overall proportions of the mesonotum (e.g., distinctly transverse, subquadrate, or distinctly elongate) varied among genera (Figs. 19, 30a–dd, 31a–ii, 52a–c, 53a–b). Additional studies are required to determine if the shape and size of the stridulatory file varies intraspecifically.

The metendosternite (also known as the metafurca) is an internal structure which serves as an attachment point for various thoracic muscles. This structure has been important to the study of Coleoptera since Crowson's studies (1938, 1944). Various characters of the metendosternite were recently employed in the phylogenetic analysis of Coleoptera conducted by Lawrence *et al*. (2011). Within the taxa studied, the metendosternite in Onciderini is typical for Lamiinae, consisting of a stalk which forks into two lateral arms. At the base of the lateral arms are the laminae and projecting forward are the anterior tendons. Variation was found in the shape of the lateral arms and laminae, as well as the area between the tendons (Figs. 21, 342a–dd, 33a–n, 54a–b). Additional studies are required to determine if the shape and size of the lateral arms and laminae exhibit intraspecific variation.

Hind wings dissected from 74 of 80 described genera of Onciderini were typical for the subfamily (with a distinct radial cell, R-M loop, medial spur, medial embayment,

and no wedge cell) and lacked significant variation. However, wing pigmentation was found to vary with from nearly clear to darkly pigmented (Figs. 20, 36a–r, 37a–r, 38a–p, 60a–c). Additional studies are required to determine if the level of pigmentation varies intraspecifically.

Characters of the male genitalia were also studied for 74 genera and variation was found in the parameres (lateral lobes) and tegmen. Specifically, the width of the parameres at the base compared to the apex was found to vary from about as wide to distinctly narrower (tapering to apex). In addition, the length of the tegmen compared to the length of the parameres was also variable (Figs. 22, 34a–dd, 35a–dd, 61a–b, 62a–b).

In light of the poorly resolved consensus trees and low support values observed in both phylogenetic analyses, it would be premature to infer any biological implications from this study. Since girdling behavior is unknown (unobserved) for all but species of four genera (*Ecthoea*, *Lochmaeocles*, *Oncideres*, and *Psyllotoxus*), this behavior was not utilized in this study and the evolution of this character remains unresolved.

The objective of this study was to present the first morphological study and phylogenetic analysis of the Onciderini. Based on the results of this study, additional morphological characters and states as well as addition representative species may be needed to resolve the relationships among the 74 described genera. The addition of DNA sequence data may also be helpful in resolving relationships.

Acknowledgments

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Genus	# Species	Distribution	Genus	# Species	Distribution
Agaritha	1	SA	*Lochmaeocles*	25	CA, NA, SA
Alexera	2	SA	*Lydipta*	4	SA
Apamauta	1	SA	*Marensis*	1	SA
Apocoptoma	1	SA	*Microcanus*	1	CA
Bacuris	1	CA, SA	*Midamiella*	1	SA
Bucoides	3	SA	*Monneoncideres*	1	SA
Cacostola	32	A, CA, NA, SA	*Neocherentes*	1	SA
Carenesycha	2	SA	*Neodillonia*	2	SA
Cherentes	1	CA, SA	*Neohylus*	2	SA
Chitron	1	SA	*Neolampedusa*	2	SA
Cicatrodea	2	SA	*Oncideres*	124	A, CA, NA, SA
Cipriscola	1	SA	*Oncioderes*	2	SA
Clavidesmus	10	SA	*Paratrachysomus*	1	SA
Cnemosioma	1	SA	*Paratritania*	1	SA
Cordites	2	SA	*Pericasta*	1	SA
Cydros	2	CA, SA	*Periergates*	3	CA
Cylicasta	7	CA, SA	*Peritrox*	5	SA
Delilah	2	SA	*Plerodia*	2	SA
Ecthoea	1	CA, SA	*Priscatoides*	1	SA
Ephiales	1	SA	*Prohylus*	1	SA
Esonius	1	SA	*Proplerodia*	2	SA
Eudesmus	7	CA, SA	*Pseudobeta*	4	SA
Eupalessa	1	SA	*Psyllotoxoides*	1	SA
Euthima	4	SA	*Psyllotoxus*	4	SA
Furona	3	CA, SA	*Sternycha*	7	CA, SA
Glypthaga	8	SA	*Strioderes*	1	SA
Hesycha	12	SA	*Sulpitus*	1	SA
Hesychotypa	23	CA, SA	*Taricanus*	2	CA
Hypselomus	1	SA	*Tibiosioma*	4	SA
Hypsioma	31	CA, LA, SA	*Touroultia*	3	SA
Iaquira	1	SA	*Trachysomus*	17	CA, SA
Ischiocentra	10	CA, SA	*Trestoncideres*	3	CA, SA
Ischioderes	2	SA	*Trestonia*	22	CA, LA, SA
Ischiosioma	2	SA	*Tritania*	1	SA
Jamesia	11	SA	*Tulcoides*	2	SA
Lachaerus	1	SA	*Tulcus*	21	CA, SA
Lachnia	1	SA	*Tybalmia*	9	CA, SA
Lesbates	5	SA	*Typhlocerus*	1	SA
Leus	1	SA	*Venustus*	2	CA, SA
Lingafelteria	1	SA	*Xylomimus*	1	SA

Table 4. Eighty genera currently classified in the tribe Onciderini (Cerambycidae: Lamiinae). Distribution abbreviations as follows: A = Antilles, CA = Central America, LA = Lesser Antilles, NA = North America, SA = South America.

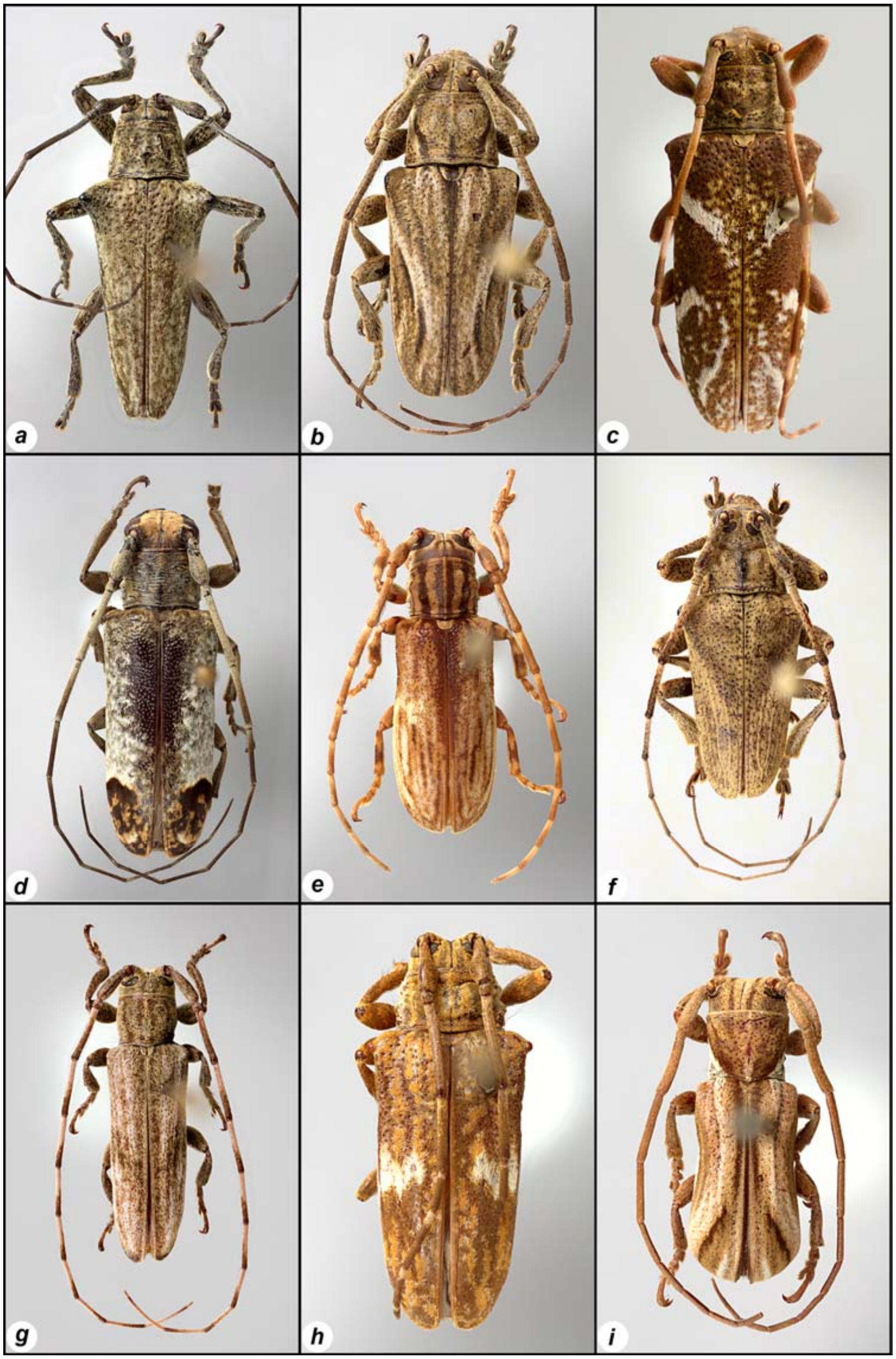

Figure 7. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Apocoptoma*. **e)** *Bacuris*. **f)** *Bucoides*. **g)** *Cacostola*. **h)** *Carenesycha*. **i)** *Cherentes*.

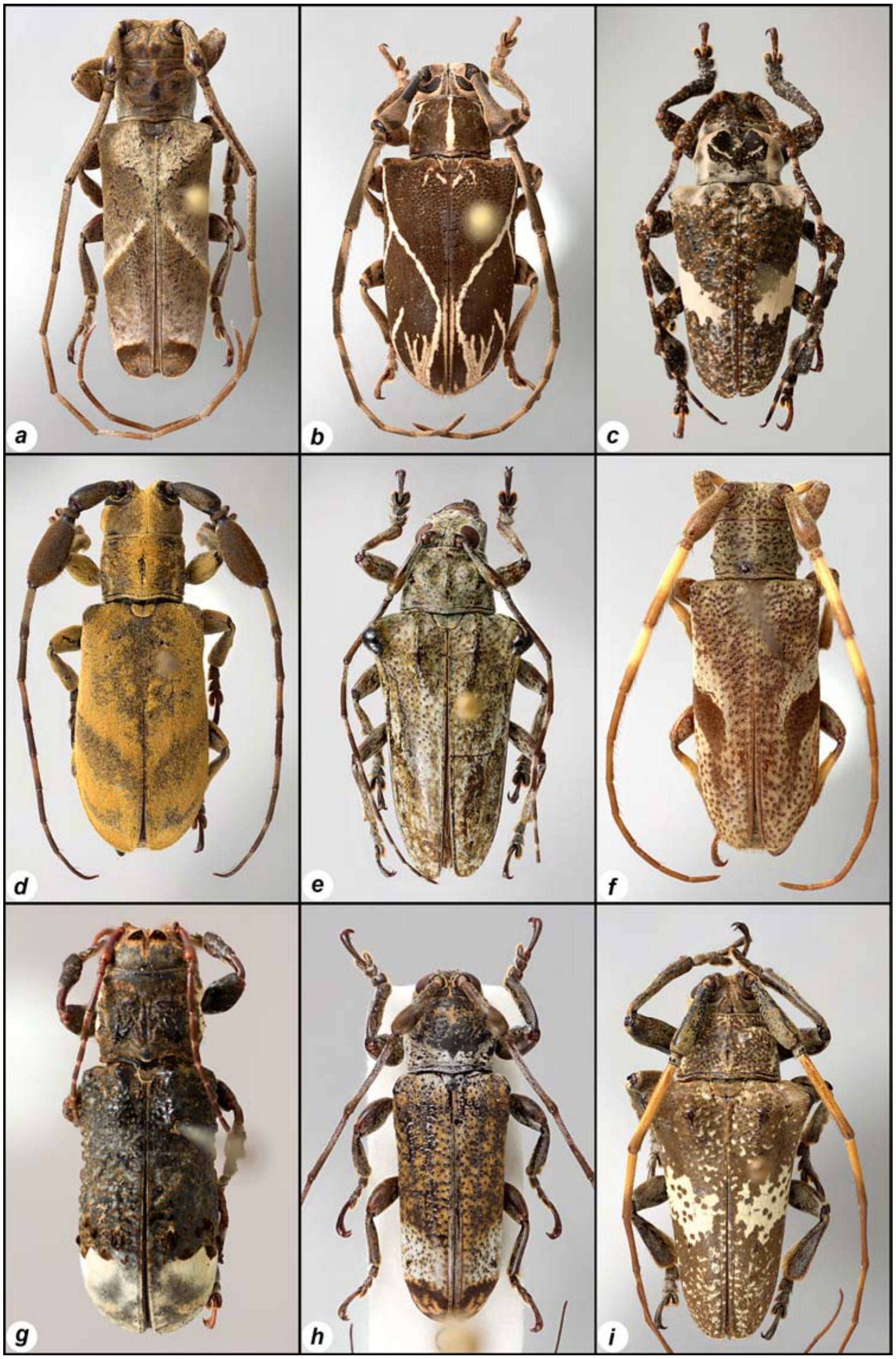

Figure 8. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Chitron*. **b)** *Cicatrodea*. **c)** *Cipriscola*. **d)** *Clavidesmus*. **e)** *Cnemosioma*. **f)** *Cordites*. **g)** *Cydros*. **h)** *Cylicasta*. **i)** *Delilah*.

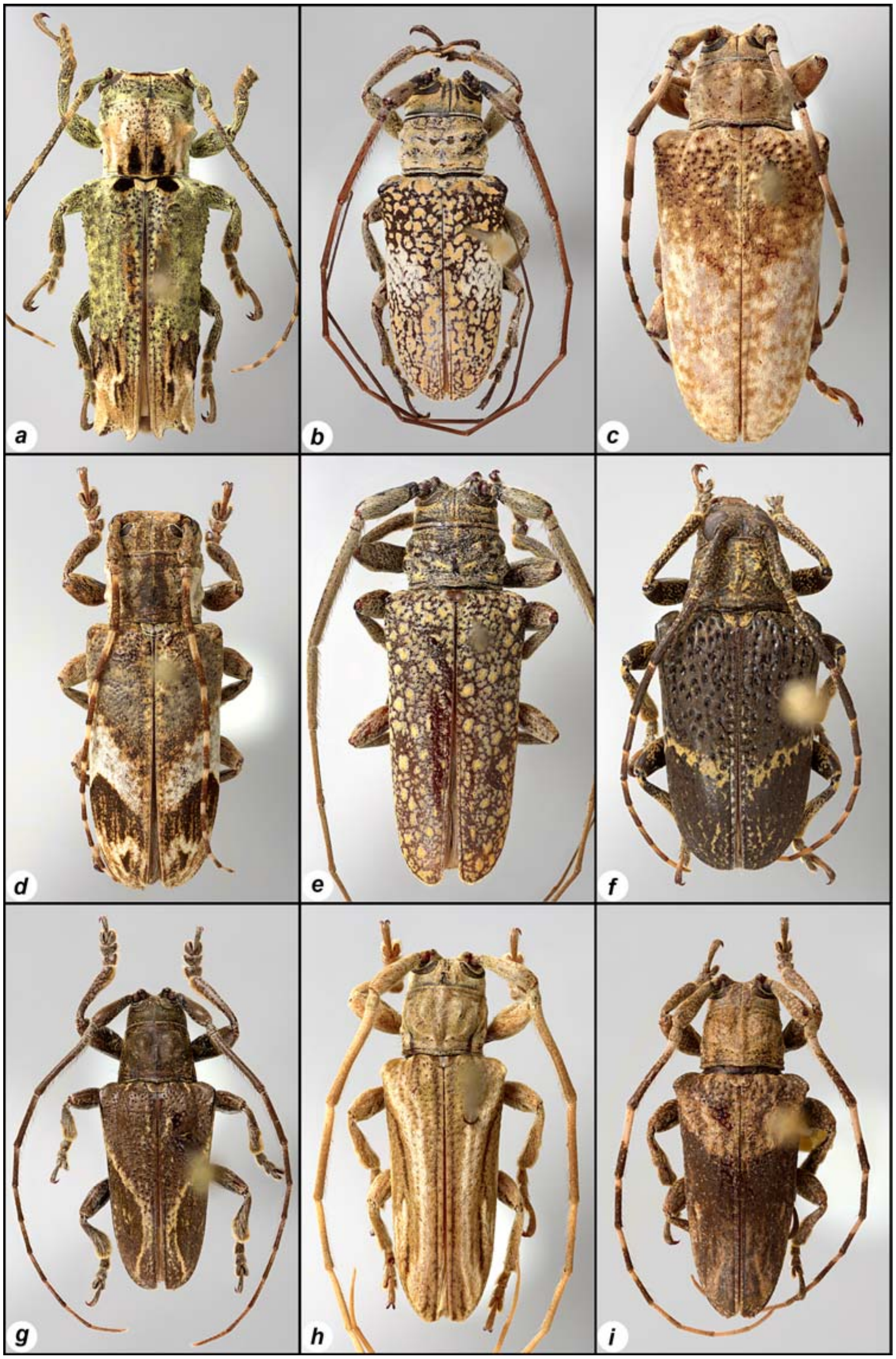

Figure 9. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Ecthoea*. **b)** *Ephiales*. **c)** *Esonius*. **d)** *Eudesmus*. **e)** *Eupalessa*. **f)** *Euthima*. **g)** *Furona*. **h)** *Glypthaga*. **i)** *Hesycha*.

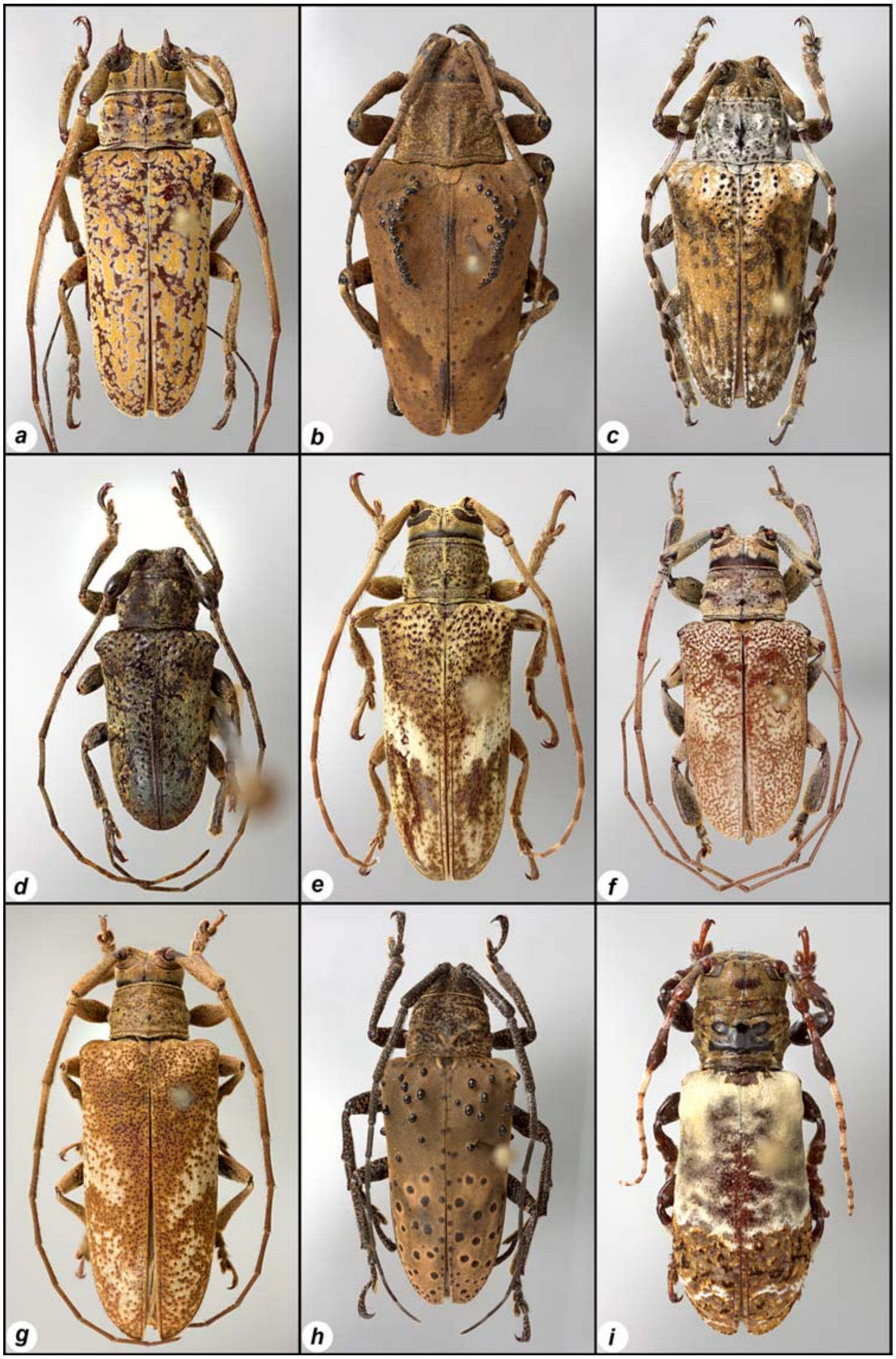

Figure 10. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Hesychotypa*. **b)** *Hypselomus*. **c)** *Hypsioma*. **d)** *Iaquira*. **e)** *Ischiocentra*. **f)** *Ischioderes*. **g)** *Ischiosioma*. **h)** *Jamesia*. **i)** *Lachaerus*.

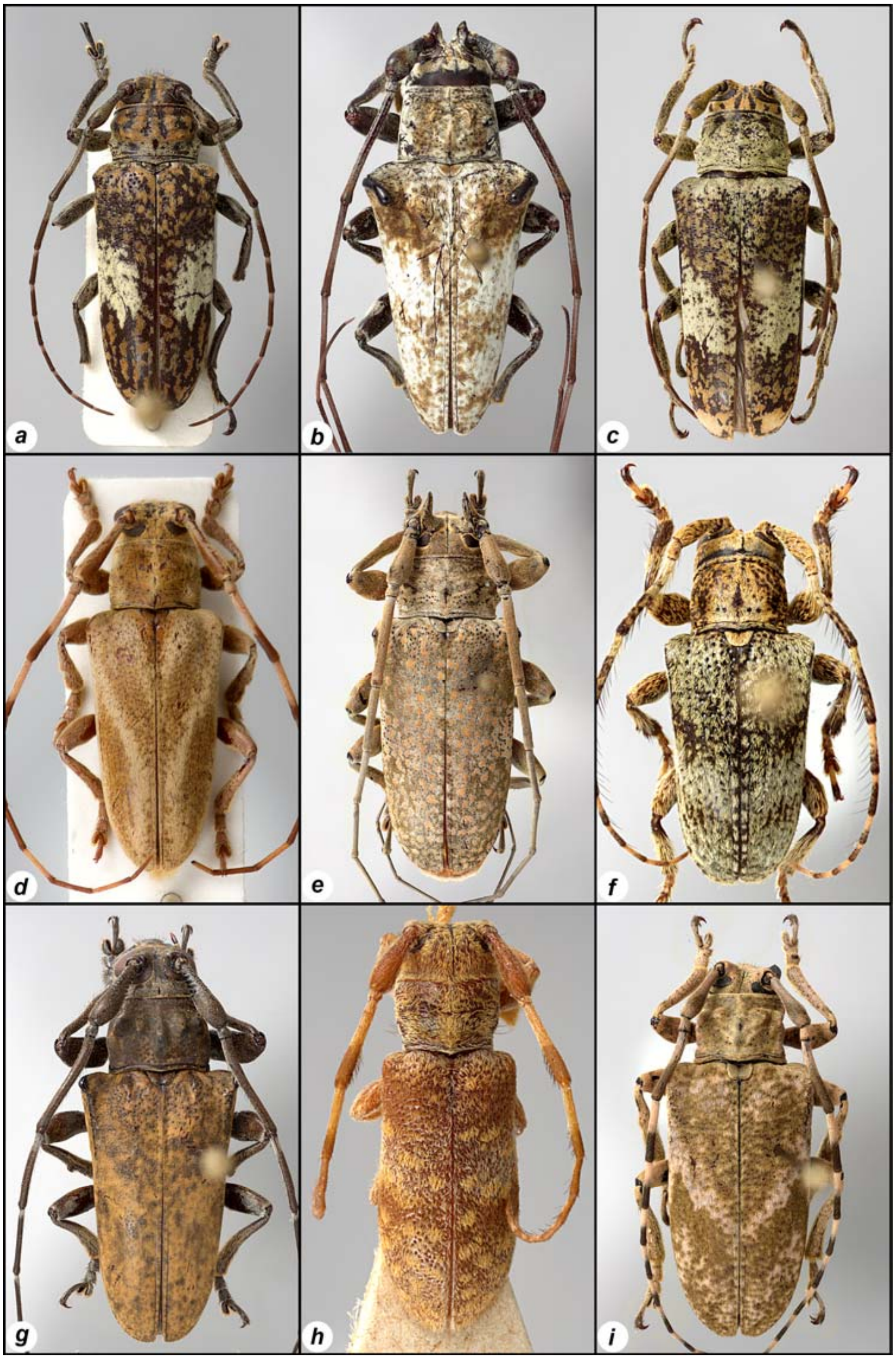

Figure 11. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Lachnia*. **b)** *Lesbates*. **c)** *Leus*. **d)** *Lingafelteria*. **e)** *Lochmaeocles*. **f)** *Lydipta*. **g)** *Marensis*. **h)** *Microcanus*. **i)** *Midamiella*.

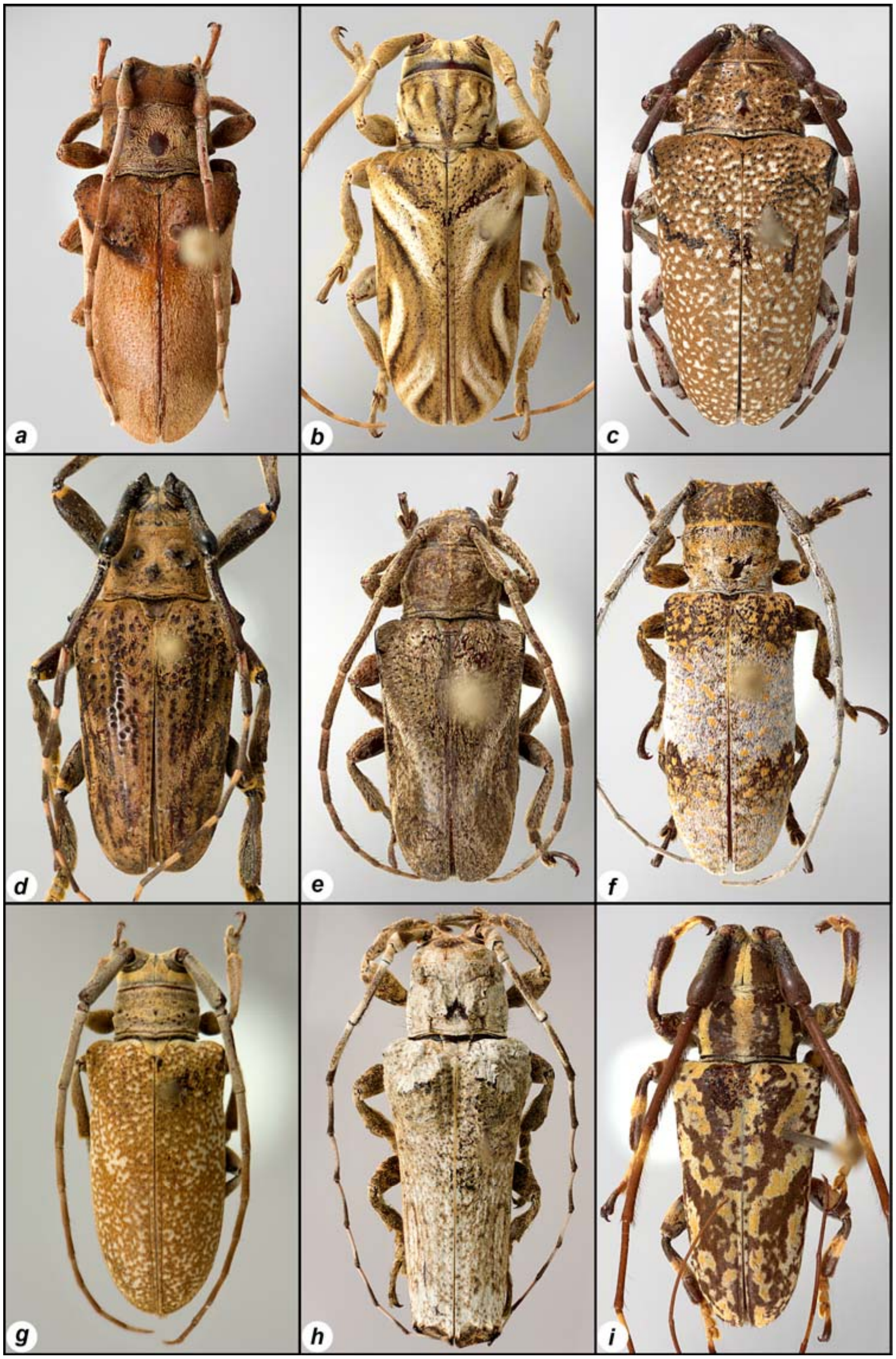

Figure 12. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Monneoncideres*. **b)** *Neocherentes*. **c)** *Neodillonia*. **d)** *Neohylus*. **e)** *Neolampedusa*. **f)** *Oncideres*. **g)** *Oncioderes*. **h)** *Paratrachysomus*. **i)** *Paratritania*.

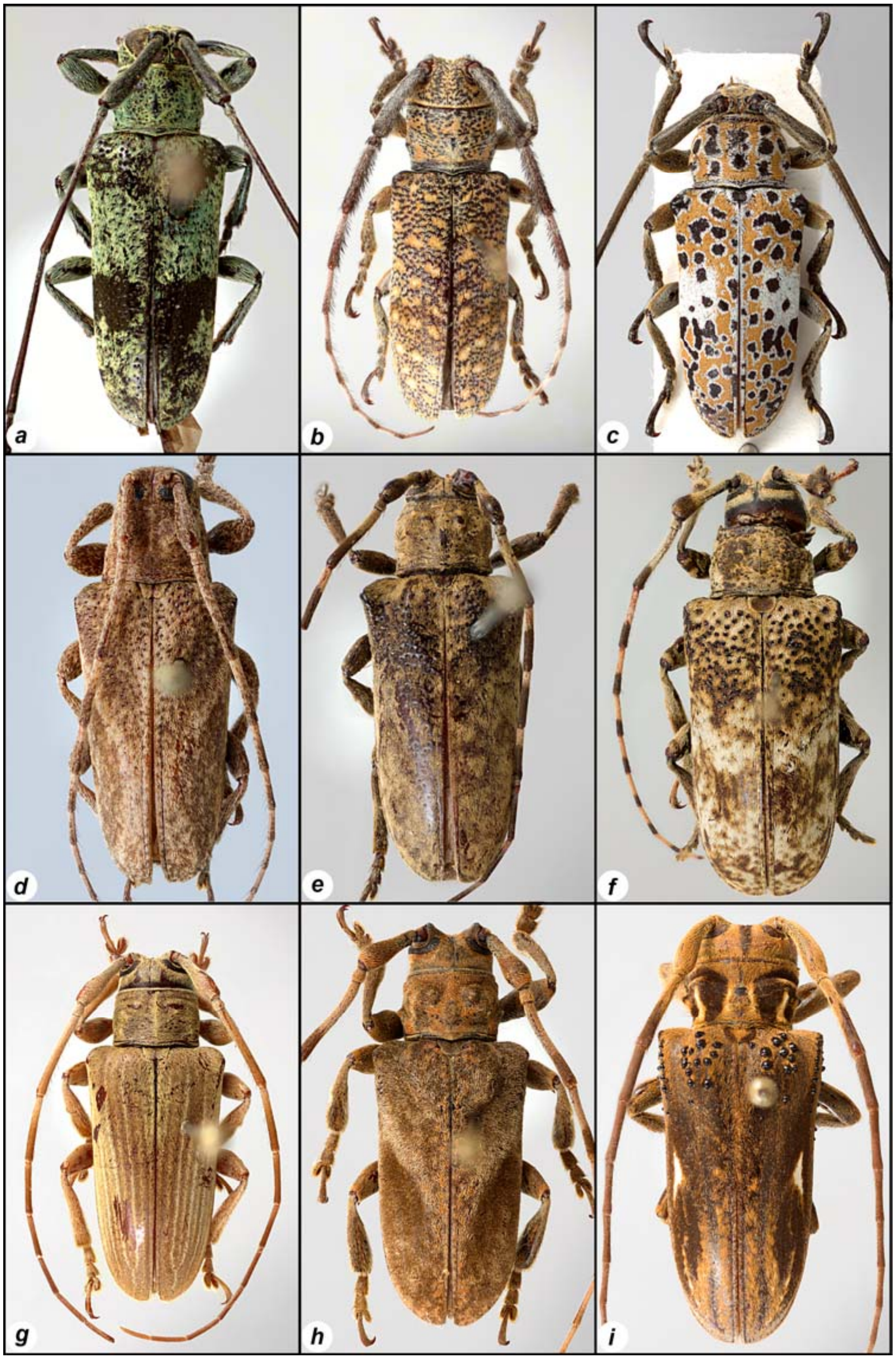

Figure 13. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Pericasta*. **b)** *Periergates*. **c)** *Peritrox*. **d)** *Plerodia*. **e)** *Priscatoides*. **f)** *Prohylus*. **g)** *Proplerodia*. **h)** *Pseudobeta*. **i)** *Psyllotoxoides*.

Figure 14. Nine genera of Onciderini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Psyllotoxus*. **b)** *Sternycha*. **c)** *Strioderes*. **d)** *Sulpitus*. **e)** *Taricanus*. **f)** *Tibiosioma*. **g)** *Trachysomus*. **h)** *Touroultia*. **i)** *Trestoncideres*.

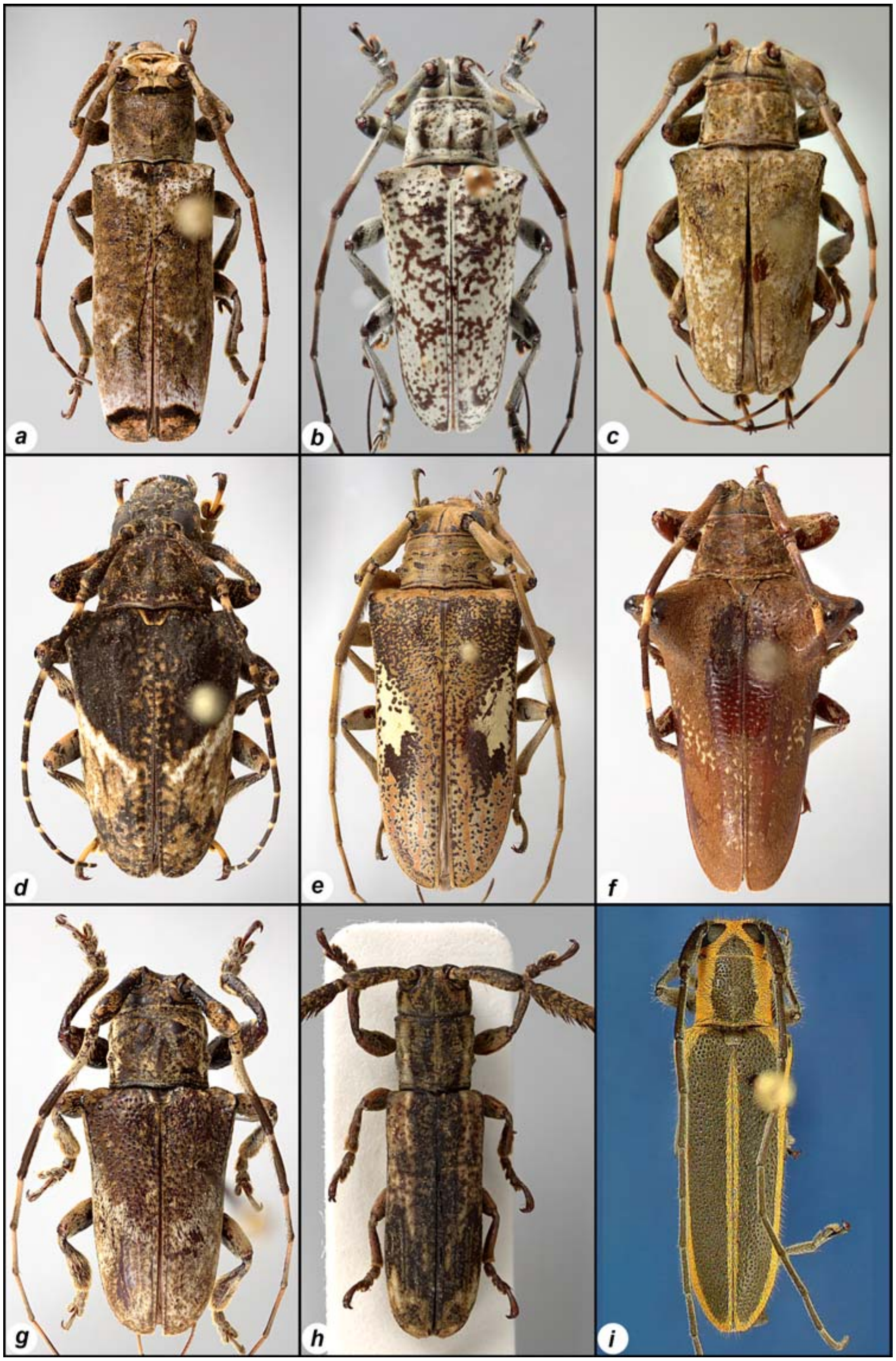

Figure 15. Eight genera of Onciderini and one genus of Saperdini (Cerambycidae: Lamiinae), dorsal habitus photographs. **a)** *Trestonia*. **b)** *Tritania*. **c)** *Tulcoides*. **d)** *Tulcus*. **e)** *Tybalmia*. **f)** *Typhlocerus*. **g)** *Venustus*. **h)** *Xylomimus*. **i)** *Saperda*.

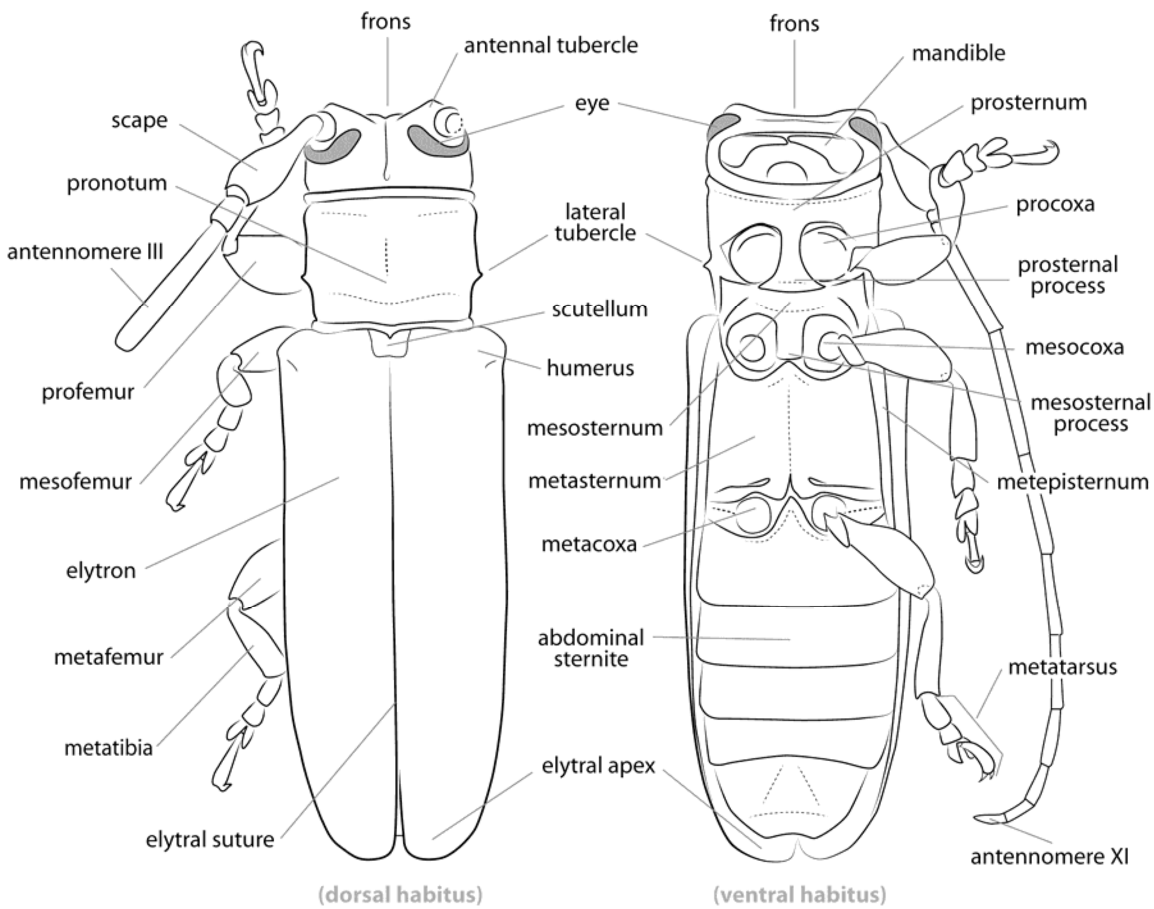

Figure 16. Morphological atlas showing dorsal and ventral structures in Onciderini (Cerambycidae: Lamiinae).

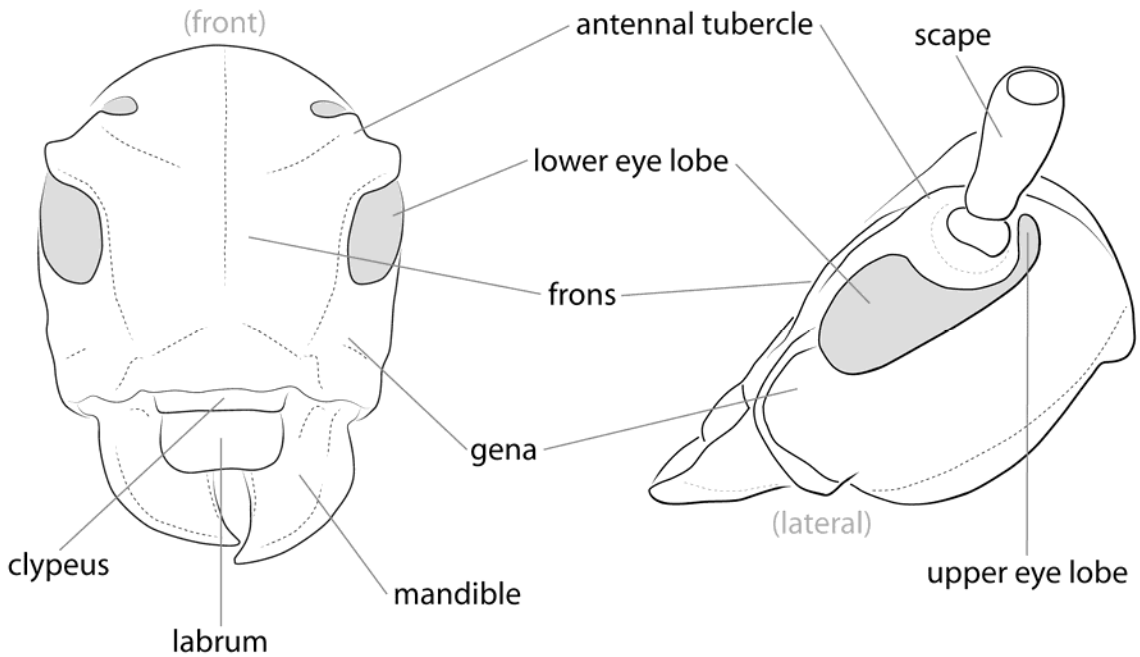

Figure 17. Head morphology in Onciderini (Cerambycidae: Lamiinae).

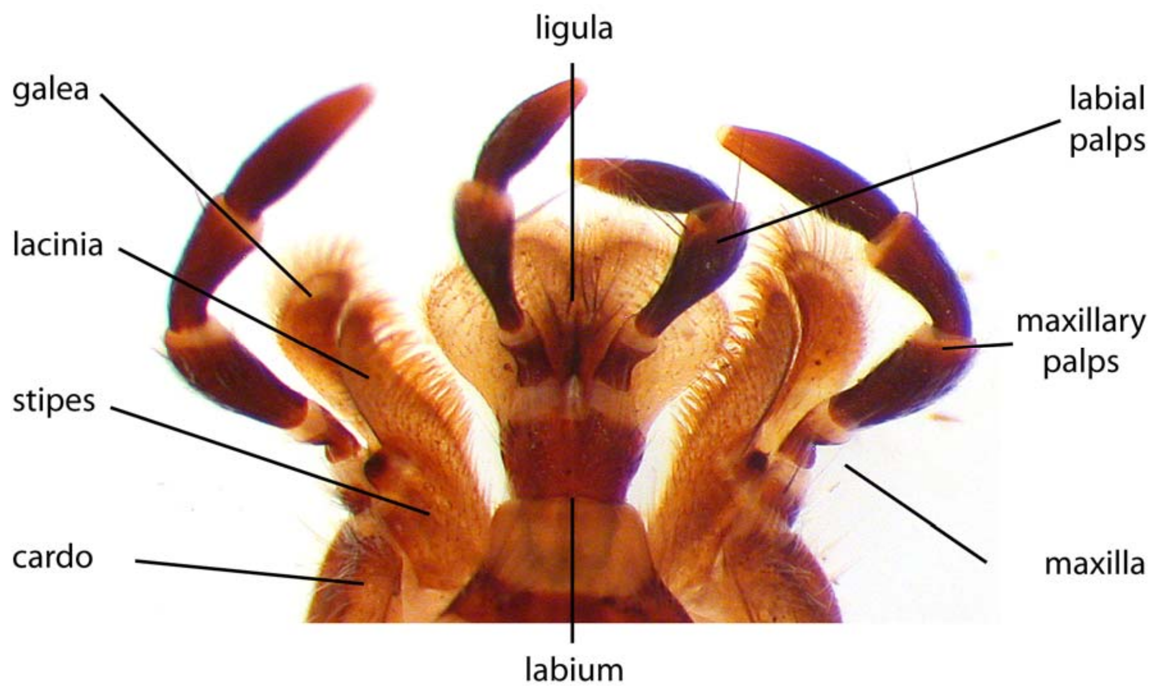

Figure 18. Maxilla and labium morphology in Onciderini (Cerambycidae: Lamiinae) (*Hypsioma*).

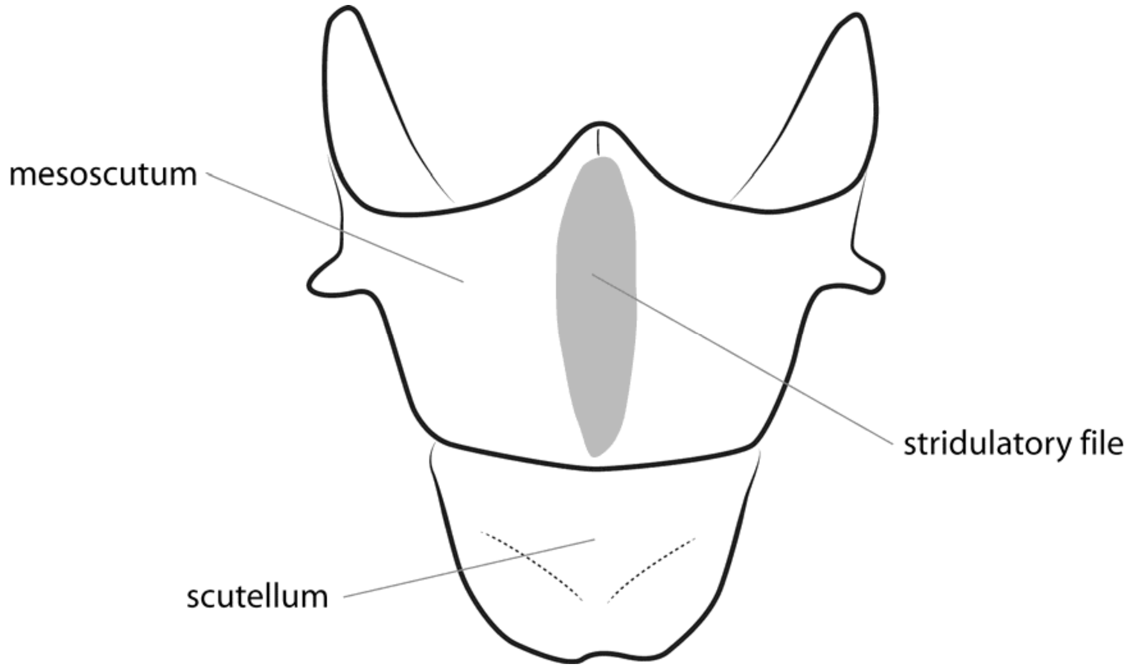

Figure 19. Mesonotum morphology in Onciderini (Cerambycidae: Lamiinae).

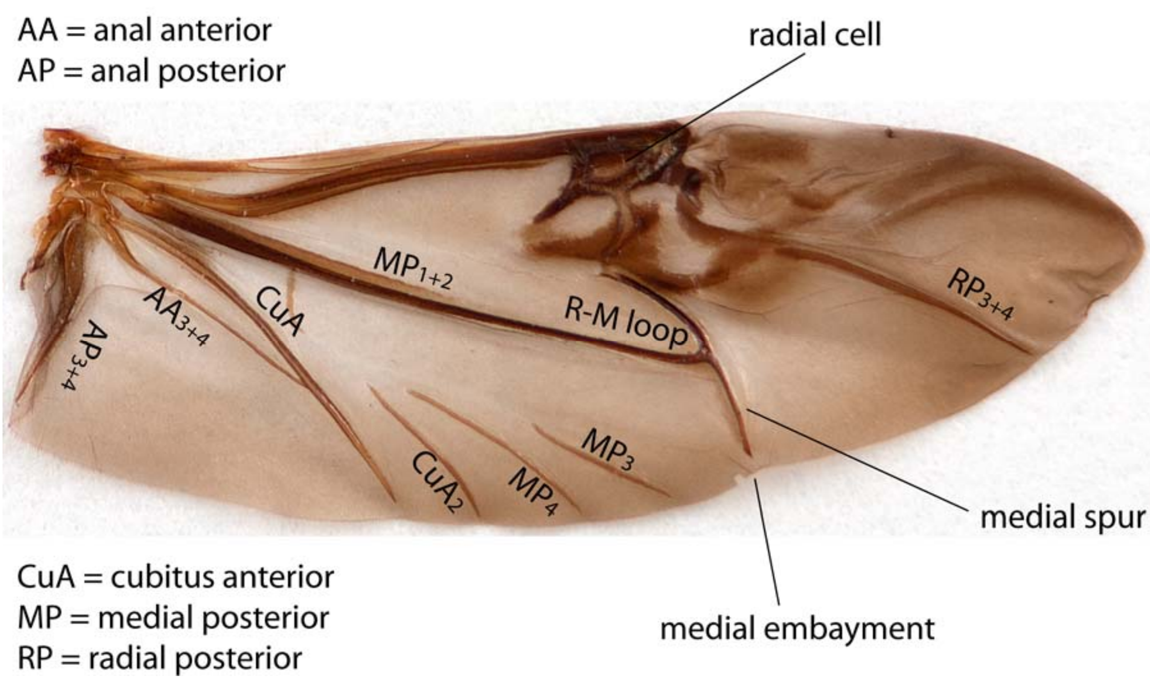

Figure 20. Hind wing morphology of Onciderini (Cerambycidae: Lamiinae) (*Agaritha*).

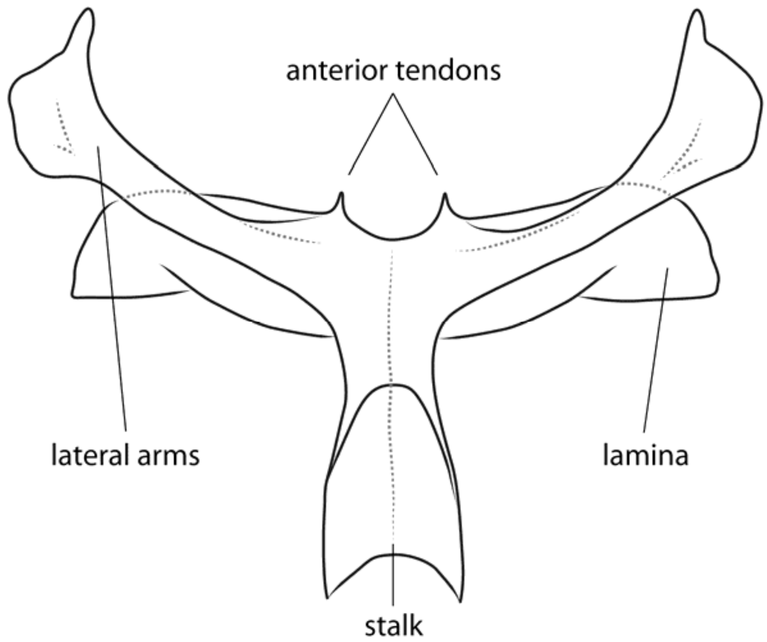

Figure 21. Metendosternite morphology of Onciderini (Cerambycidae: Lamiinae).

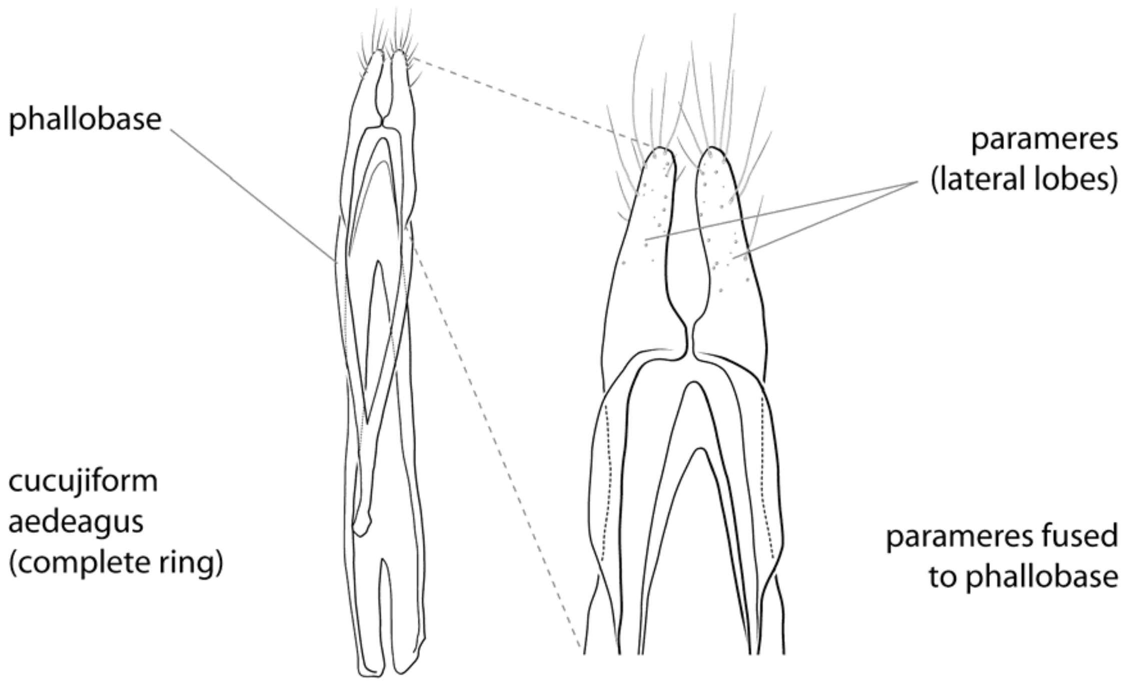

Figure 22. Male genitalia (aedeagus) morphology in Onciderini (Cerambycidae: Lamiinae).

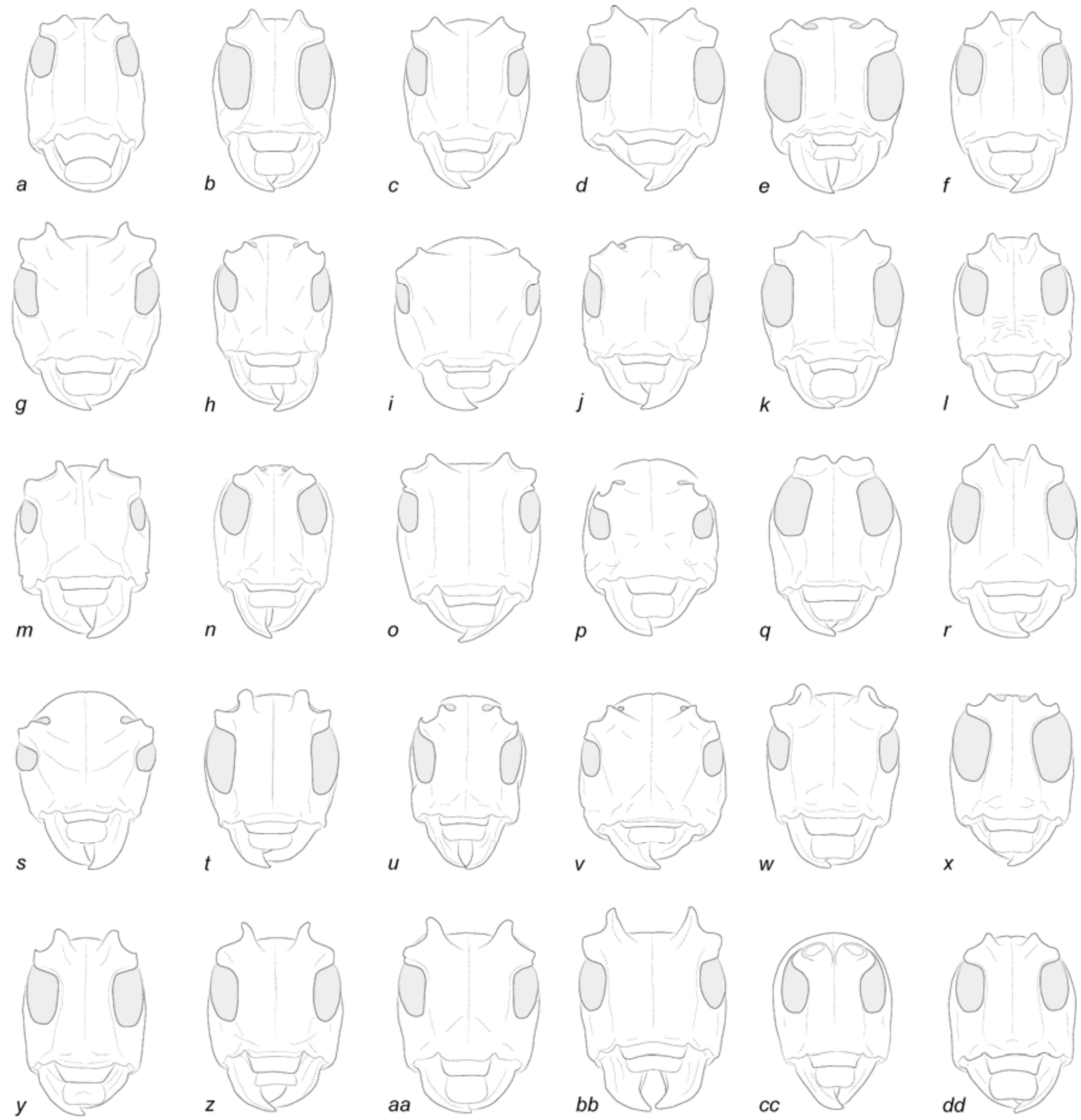

Figure 23. Thirty genera of Onciderini (Cerambycidae: Lamiinae), head illustrations. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Apocoptoma*. **e)** *Bacuris*. **f)** *Bucoides*. **g)** *Cacostola*. **h)** *Carenesycha*. **i)** *Cherentes*. **j)** *Chitron*. **k)** *Cicatrodea*. **l)** *Cipriscola*. **m)** *Clavidesmus*. **n)** *Cnemosioma*. **o)** *Cordites*. **p)** *Cydros*. **q)** *Cylicasta*. **r)** *Delilah*. **s)** *Ecthoea*. **t)** *Ephiales*. **u)** *Esonius*. **v)** *Eudesmus*. **w)** *Eupalessa*. **x)** *Euthima*. **y)** *Furona*. **z)** *Glypthaga*. **aa)** *Hesycha*. **bb)** *Hesychotypa*. **cc)** *Hypselomus*. **dd)** *Hypsioma*.

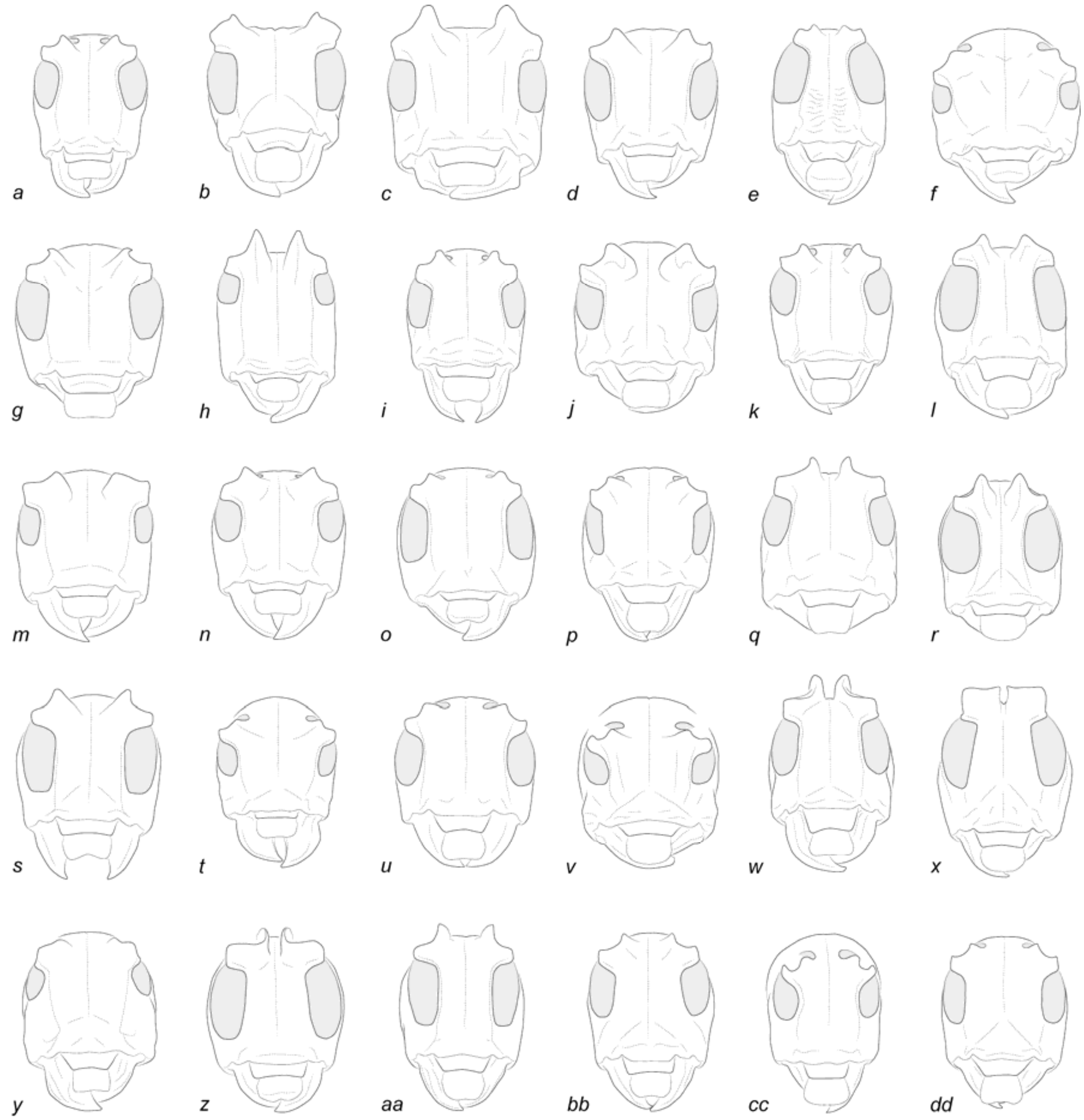

Figure 24. Thirty genera of Onciderini (Cerambycidae: Lamiinae), head illustrations. **a)** *Iaquira*. **b)** *Ischiocentra*. **c)** *Ischioderes*. **d)** *Ischiosioma*. **e)** *Jamesia*. **f)** *Lachaerus*. **g)** *Lachnia*. **h)** *Lesbates*. **i)** *Leus*. **j)** *Lochmaeocles*. **k)** *Lydipta*. **l)** *Marensis*. **m)** *Microcanus*. **n)** *Midamiella*. **o)** *Monneoncideres*. **p)** *Neocherentes*. **q)** *Neodillonia*. **r)** *Neohylus*. **s)** *Neolampedusa*. **t)** *Oncideres*. **u)** *Oncioderes*. **v)** *Paratrachysomus*. **w)** *Paratritania*. **x)** *Pericasta*. **y)** *Periergates*. **z)** *Peritrox*. **aa)** *Plerodia*. **bb)** *Priscatoides*. **cc)** *Prohylus*. **dd)** *Proplerodia*.

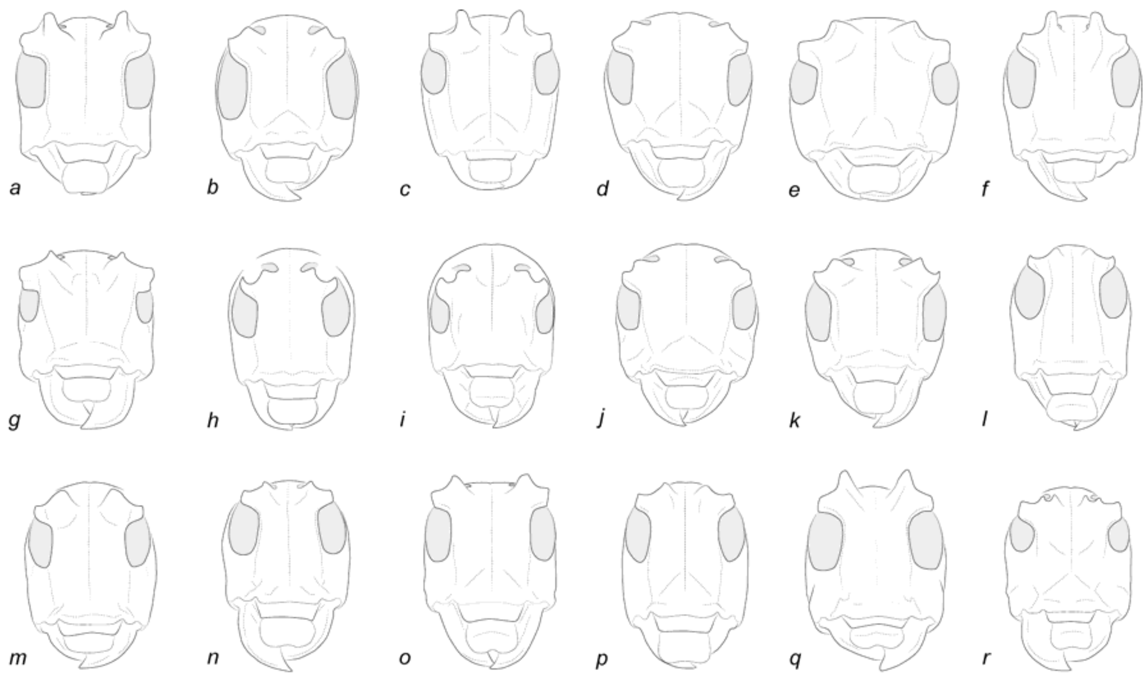

Figure 25. Eighteen genera of Onciderini (Cerambycidae: Lamiinae), head illustrations. **a)** *Pseudobeta*. **b)** *Psyllotoxoides*. **c)** *Psyllotoxus*. **d)** *Sternycha*. **e)** *Strioderes*. **f)** *Sulpitus*. **g)** *Taricanus*. **h)** *Tibiosioma*. **i)** *Trachysomus*. **j)** *Trestoncideres*. **k)** *Trestonia*. **l)** *Tritania*. **m)** *Tulcoides*. **n)** *Tulcus*. **o)** *Tybalmia*. **p)** *Typhlocerus*. **q)** *Venustus*. **r**) *Xylomimus*.

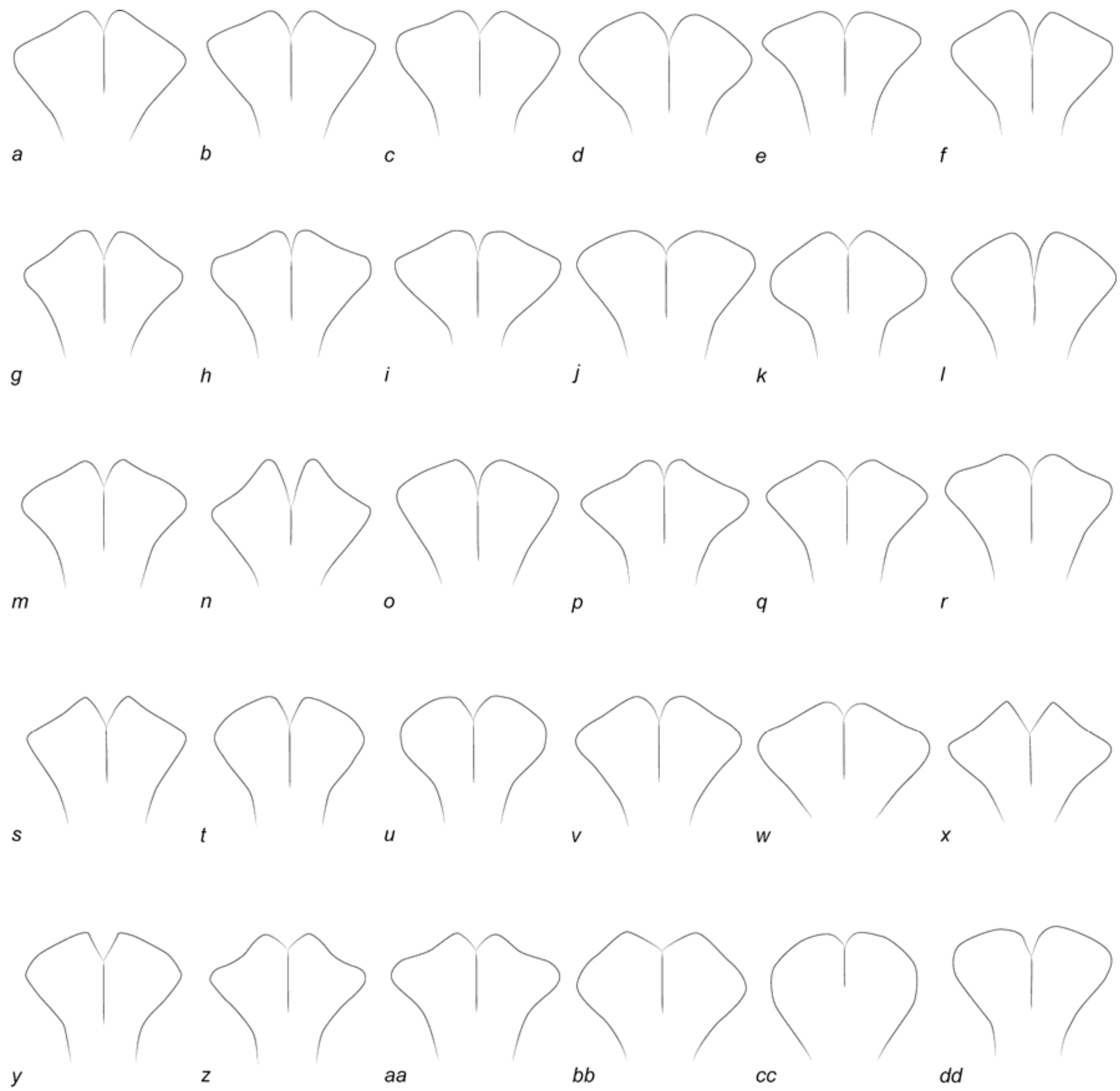

Figure 26. Thirty genera of Onciderini (Cerambycidae: Lamiinae), ligula illustrations. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Apocoptoma*. **e)** *Bucoides*. **f)** *Cicatrodea*. **g)** *Cipriscola*. **h)** *Clavidesmus*. **i)** *Cordites*. **j)** *Cydros*. **k)** *Cylicasta*. **l)** *Delilah*. **m)** *Ecthoea*. **n)** *Ephiales*. **o)** *Esonius*. **p)** *Eudesmus*. **q)** *Eupalessa*. **r)** *Furona*. **s)** *Hesychotypa*. **t)** *Hypselomus*. **u)** *Hypsioma*. **v)** *Iaquira*. **w)** *Ischiocentra*. **x)** *Ischiosioma*. **y)** *Jamesia*. **z)** *Lachnia*. **aa)** *Lesbates*. **bb)** *Lydipta*. **cc)** *Marensis*. **dd)** *Microcanus*.

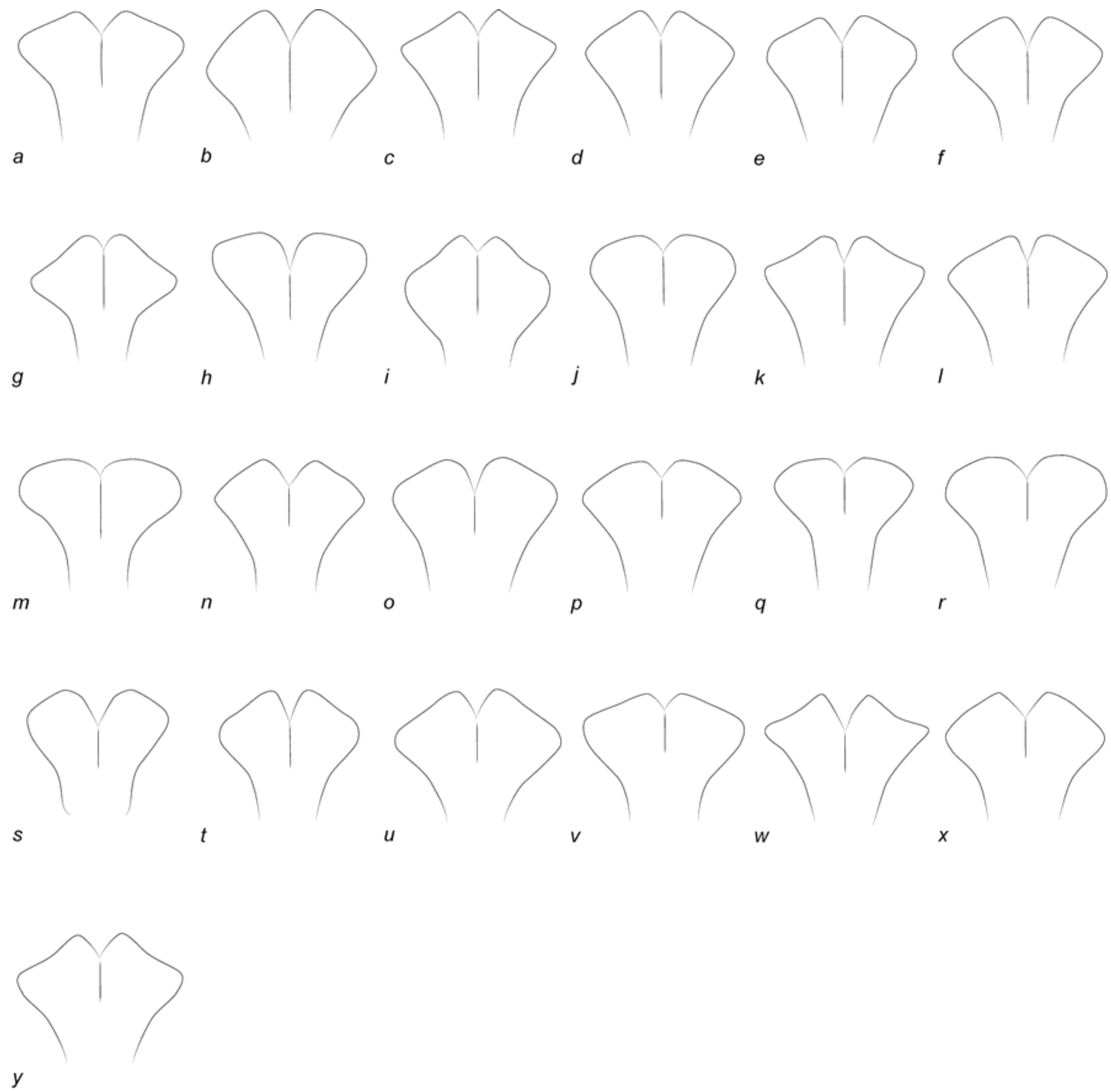

Figure 27. Twenty-five genera of Onciderini (Cerambycidae: Lamiinae), ligula illustrations. **a)** *Midamiella*. **b)** *Neocherentes*. **c)** *Neodillonia*. **d)** *Neolampedusa*. **e)** *Oncioderes*. **f)** *Paratritania*. **g)** *Pericasta*. **h)** *Periergates*. **i)** *Peritrox*. **j)** *Plerodia*. **k)** *Prohylus*. **l)** *Pseudobeta*. **m)** *Psyllotoxus*. **n)** *Sternycha*. **o)** *Strioderes*. **p)** *Sulpitus*. **q)** *Taricanus*. **r)** *Trachysomus*. **s)** *Trestoncideres*. **t)** *Trestonia*. **u)** *Tulcoides*. **v)** *Tulcus*. **w)** *Tybalmia*. **x)** *Typhlocerus*. **y)** *Venustus*.

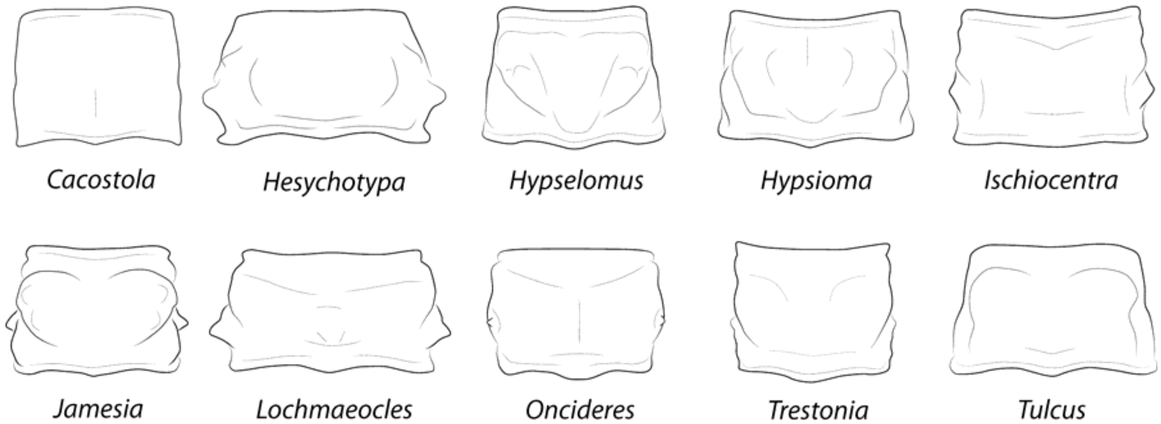

Figure 28. Ten genera of Onciderini (Cerambycidae: Lamiinae), pronotum illustrations.

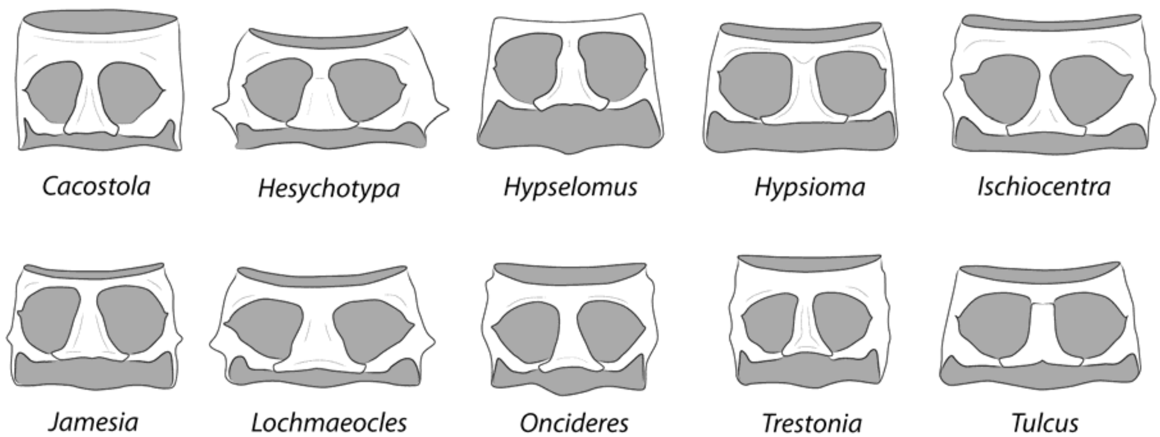

Figure 29. Ten genera of Onciderini (Cerambycidae: Lamiinae), prosternum illustrations.

Figure 30. Thirty genera of Onciderini (Cerambycidae: Lamiinae), mesonotum illustrations. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Apocoptoma*. **e)** *Bucoides*. **f)** *Cacostola*. **g)** *Cherentes*. **h)** *Cicatrodea*. **i)** *Cipriscola*. **j)** *Clavidesmus*. **k)** *Cordites*. **l)** *Cydros*. **m)** *Cylicasta*. **n)** *Delilah*. **o)** *Ecthoea*. **p)** *Ephiales*. **q)** *Esonius*. **r)** *Eudesmus*. **s)** *Eupalessa*. **t)** *Furona*. **u)** *Hesychotypa*. **v)** *Hypselomus*. **w)** *Hypsioma*. **x)** *Iaquira*. **y)** *Ischiocentra*. **z)** *Ischioderes*. **aa)** *Ischiosioma*. **bb)** *Jamesia*. **cc)** *Lachaerus*. **dd)** *Lachnia*.

Figure 31. Thirty-three genera of Onciderini, one genus of Saperdini, and one genus of Agapanthiini (Cerambycidae: Lamiinae), mesonotum illustrations. **a)** *Lesbates*. **b)** *Leus*. **c)** *Lochmaeocles*. **d)** *Lydipta*. **e)** *Marensis*. **f)** *Microcanus*. **g)** *Midamiella*. **h)** *Neocherentes*. **i)** *Neodillonia*. **j)** *Neolampedusa*. **k)** *Oncideres*. **l)** *Oncioderes*. **m)** *Paratritania*. **n)** *Pericasta*. **o)** *Periergates*. **p)** *Peritrox*. **q)** *Plerodia*. **r)** *Prohylus*. **s)** *Proplerodia*. **t)** *Pseudobeta*. **u)** *Psyllotoxus*. **v)** *Sternycha*. **w)** *Strioderes*. **x)** *Sulpitus*. **y)** *Taricanus*. **z)** *Trachysomus*. **aa)** *Trestoncideres*. **bb)** *Trestonia*. **cc)** *Tulcoides*. **dd)** *Tulcus*. **ee)** *Tybalmia*. **ff)** *Typhlocerus*. **gg)** *Venustus*. **hh)** *Saperda*. **ii)** *Hippopsis*.

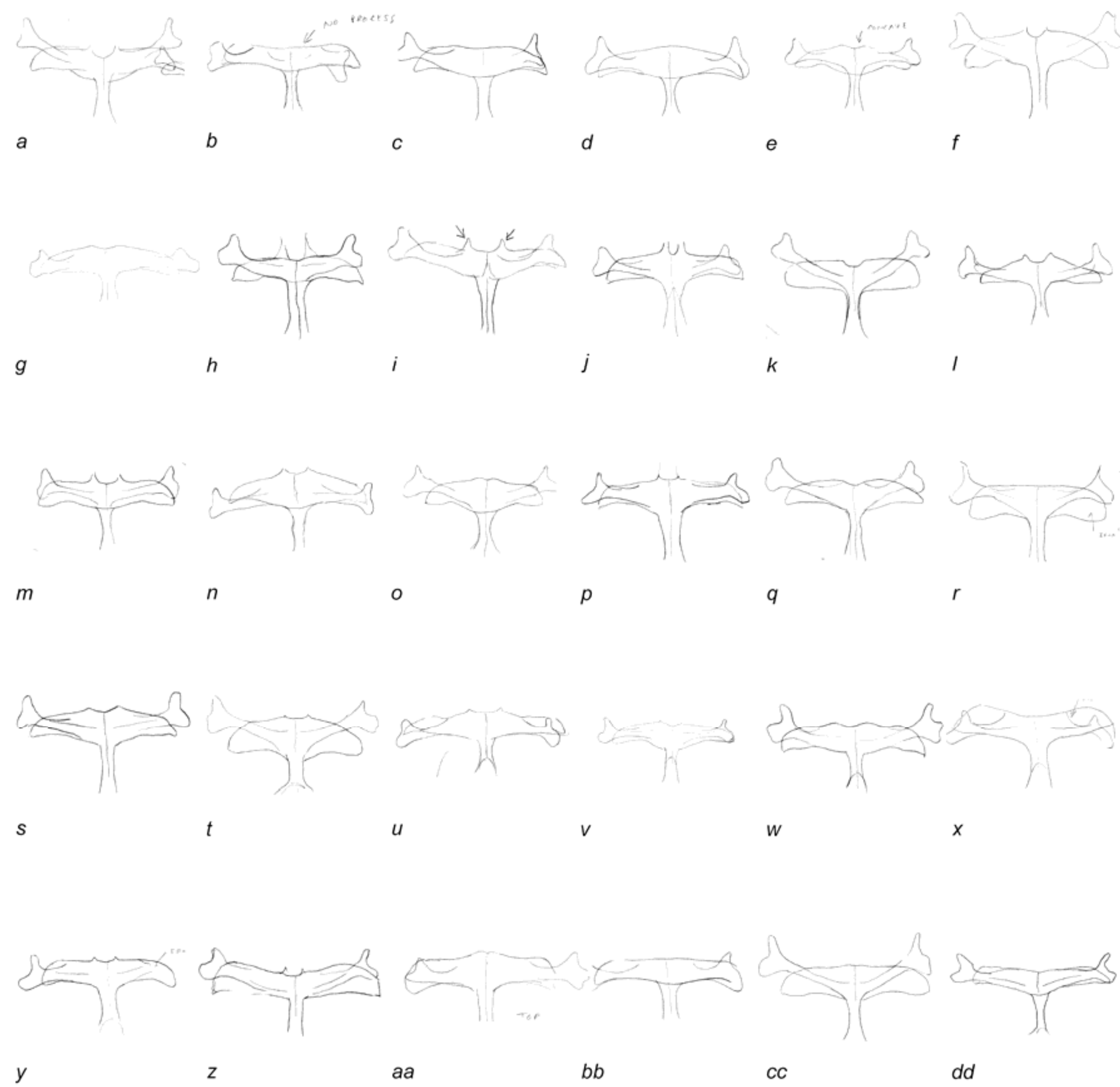

Figure 32. Thirty genera of Onciderini (Cerambycidae: Lamiinae), metendosternite illustrations. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Apocoptoma*. **e)** *Bucoides*. **f)** *Cacostola*. **g)** *Cherentes*. **h)** *Cicatrodea*. **i)** *Clavidesmus*. **j)** *Cordites*. **k)** *Cydros*. **l)** *Cylicasta*. **m)** *Delilah*. **n)** *Ecthoea*. **o)** *Ephiales*. **p)** *Esonius*. **q)** *Eudesmus*. **r)** *Eupalessa*. **s)** *Furona*. **t)** *Hesychotypa*. **u)** *Hypselomus*. **v)** *Hypsioma*. **w)** *Iaquira*. **x)** *Ischioderes*. **y)** *Ischiosioma*. **z)** *Lachaerus*. **aa)** *Lachnia*. **bb)** *Lesbates*. **cc)** *Lochmaeocles*. **dd)** *Lydipta*.

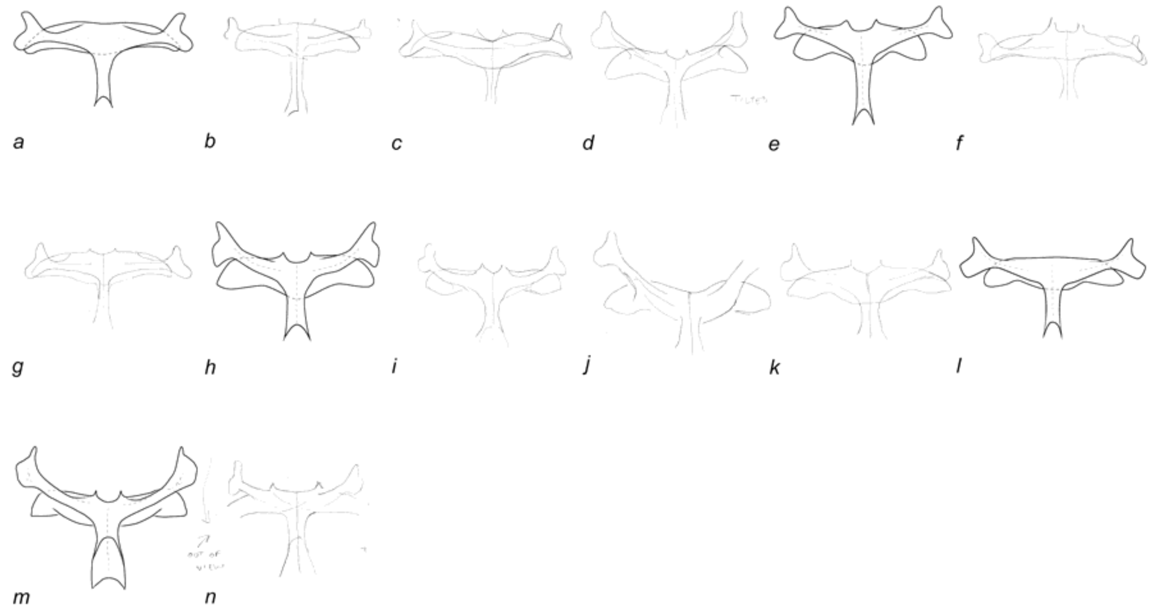

Figure 33. Thirteen genera of Onciderini and one genus of Saperdini (Cerambycidae: Lamiinae), metendosternite illustrations. **a)** *Marensis*. **b)** *Microcanus*. **c)** *Midamiella*. **d)** *Neodillonia*. **e)** *Neolampedusa*. **f)** *Oncioderes*. **g)** *Periergates*. **h)** *Peritrox*. **i)** *Prohylus*. **j)** *Proplerodia*. **k)** *Pseudobeta*. **l)** *Sulpitus*. **m)** *Trachysomus*. **n)** *Saperda*.

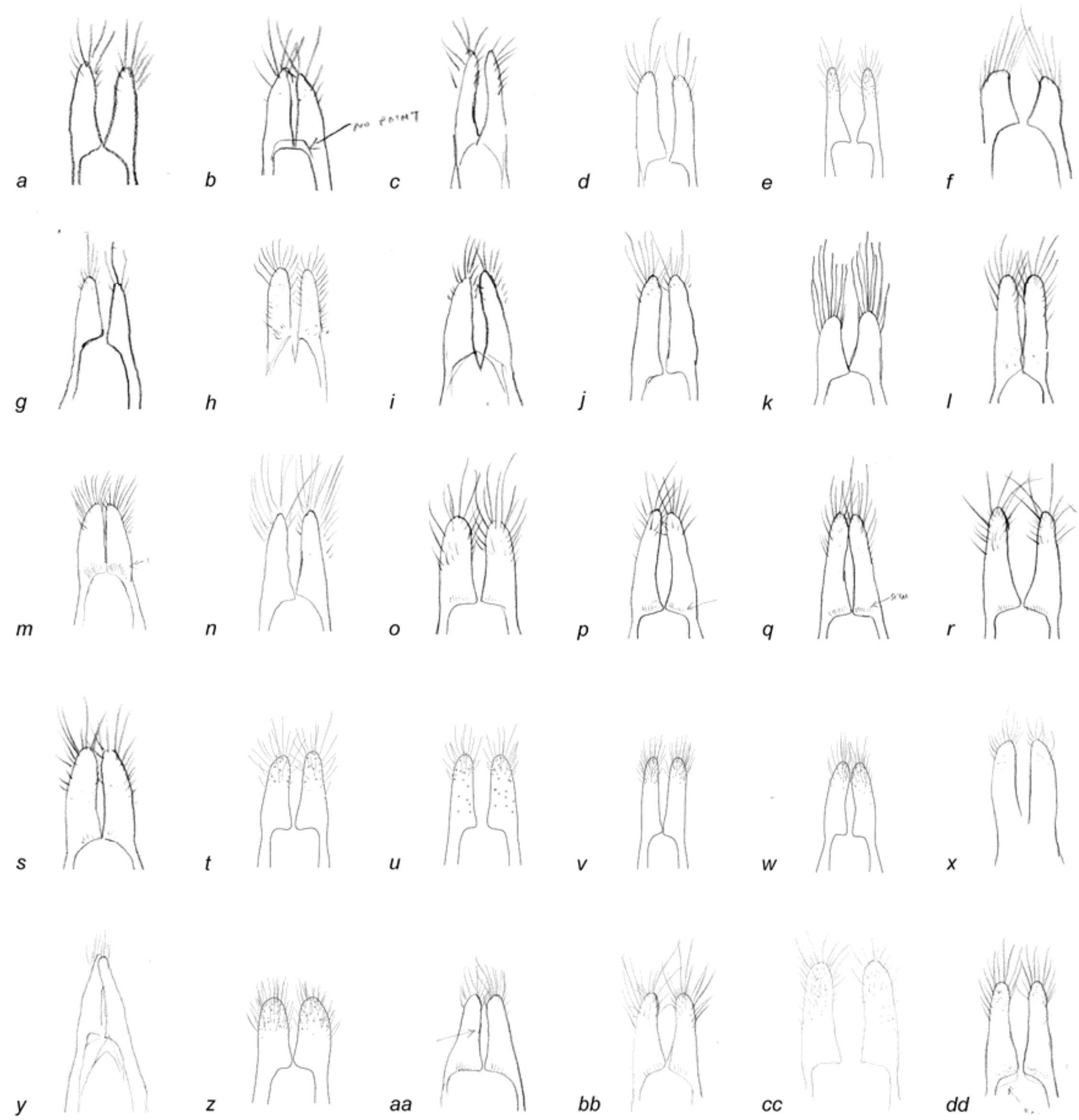

Figure 34. Thirty genera of Onciderini (Cerambycidae: Lamiinae), tegmen and parameres illustrations. **a)** *Alexera*. **b)** *Apamauta*. **c)** *Apocoptoma*. **d)** *Bucoides*. **e)** *Cacostola*. **f)** *Cherentes*. **g)** *Cicatrodea*. **h)** *Cipriscola*. **i)** *Clavidesmus*. **j)** *Cordites*. **k)** *Cydros*. **l)** *Cylicasta*. **m)** *Delilah*. **n)** *Ecthoea*. **o)** *Ephiales*. **p)** *Esonius*. **q)** *Eudesmus*. **r)** *Eupalessa*. **s)** *Furona*. **t)** *Hesychotypa*. **u)** *Hypselomus*. **v)** *Hypsioma*. **w)** *Ischiocentra*. **x)** *Ischioderes*. **y)** *Ischiosioma*. **z)** *Jamesia*. **aa)** *Lachaerus*. **bb)** *Lachnia*. **cc)** *Lesbates*. **dd)** *Leus*.

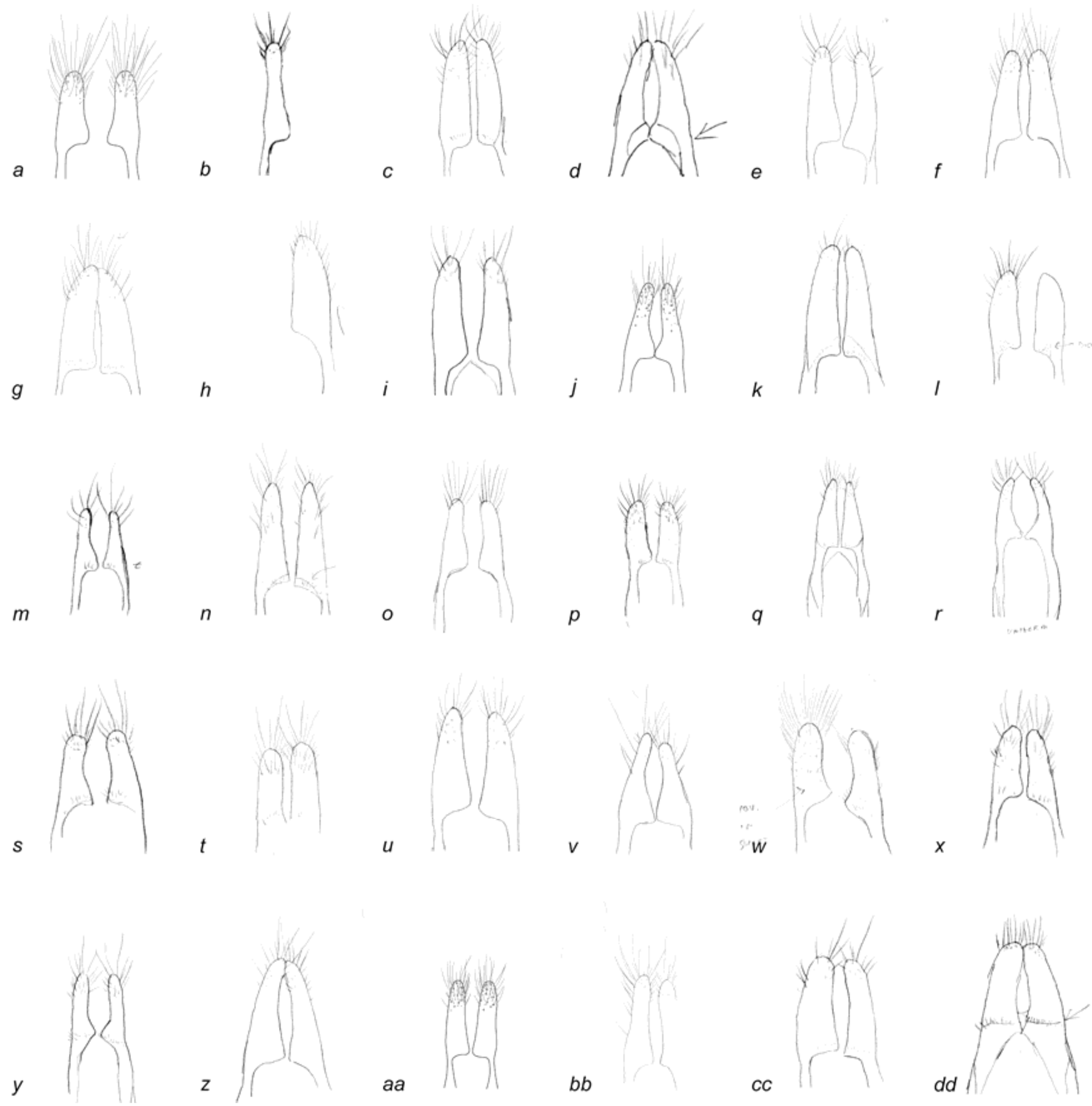

Figure 35. Twenty-nine genera of Onciderini and one genus of Saperdini (Cerambycidae: Lamiinae), tegmen and parameres illustrations. **a)** *Lochmaeocles*. **b)** *Lydipta*. **c)** *Marensis*. **d)** *Microcanus*. **e)** *Midamiella*. **f)** *Neocherentes*. **g)** *Neodillonia*. **h)** *Neohylus*. **i)** *Neolampedusa*. **j)** *Oncideres*. **k)** *Oncioderes*. **l)** *Paratritania*. **m)** *Pericasta*. **n)** *Periergates*. **o)** *Peritrox*. **p)** *Plerodia*. **q)** *Proplerodia*. **r)** *Pseudobeta*. **s)** *Psyllotoxus*. **t)** *Strioderes*. **u)** *Sulpitus*. **v)** *Taricanus*. **w)** *Trachysomus*. **x)** *Trestoncideres*. **y)** *Trestonia*. **z)** *Tulcoides*. **aa)** *Tulcus*. **bb)** *Tybalmia*. **cc)** *Venustus*. **dd**) *Saperda*.

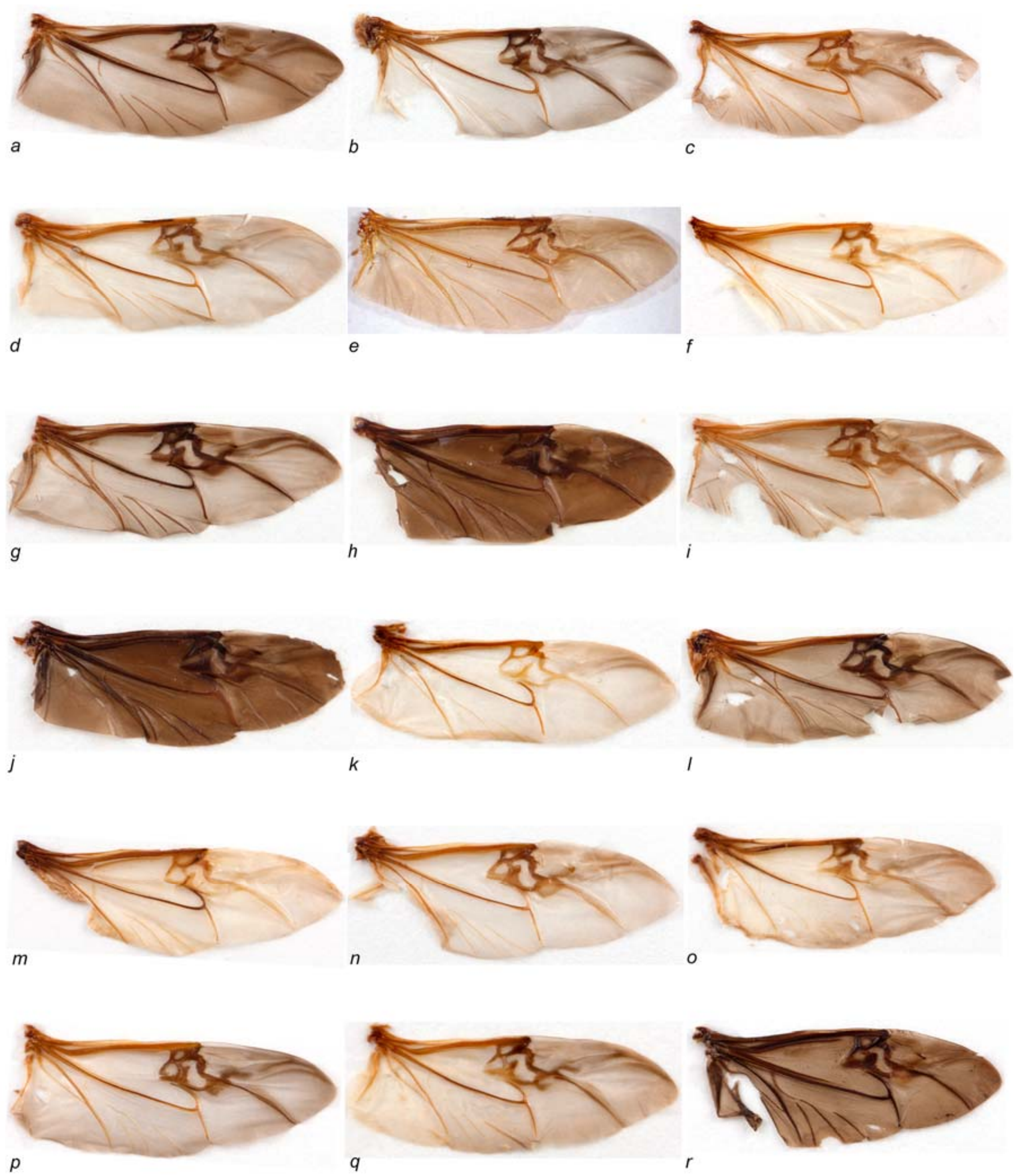

Figure 36. Eighteen genera of Onciderini (Cerambycidae: Lamiinae), hind wing photographs. **a)** *Agaritha*. **b)** *Alexera*. **c)** *Apamauta*. **d)** *Bucoides*. **e)** *Cacostola*. **f)** *Chitron*. **g)** *Cipriscola*. **h)** *Clavidesmus*. **i)** *Cordites*. **j)** *Cydros*. **k)** *Cylicasta*. **l)** *Delilah*. **m)** *Ecthoea*. **n)** *Ephiales*. **o)** *Esonius*. **p)** *Eudesmus*. **q)** *Furona*. **r)** *Hesychotypa*.

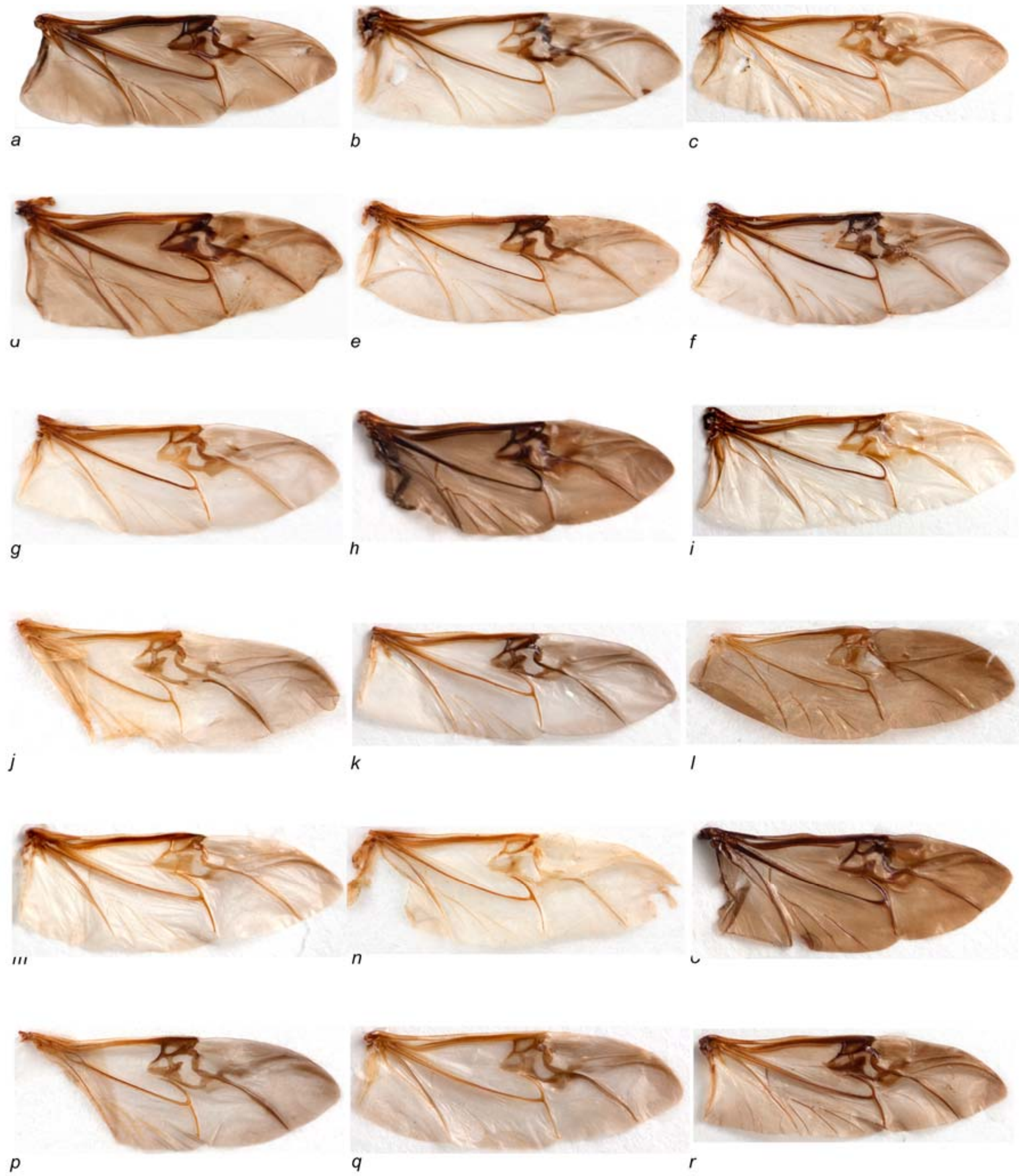

Figure 37. Eighteen genera of Onciderini (Cerambycidae: Lamiinae), hind wing photographs. **a)** *Hypselomus*. **b)** *Hypsioma*. **c)** *Ischiocentra*. **d)** *Ischioderes*. **e)** *Ischiosioma*. **f)** *Jamesia*. **g)** *Lachnia*. **h)** *Lesbates*. **i)** *Lochmaeocles*. **j)** *Lydipta*. **k)** *Marensis*. **l)** *Microcanus*. **m)** *Midamiella*. **n)** *Neocherentes*. **o)** *Neodillonia*. **p)** *Neolampedusa*. **q)** *Oncioderes*. **r)** *Paratritania*.

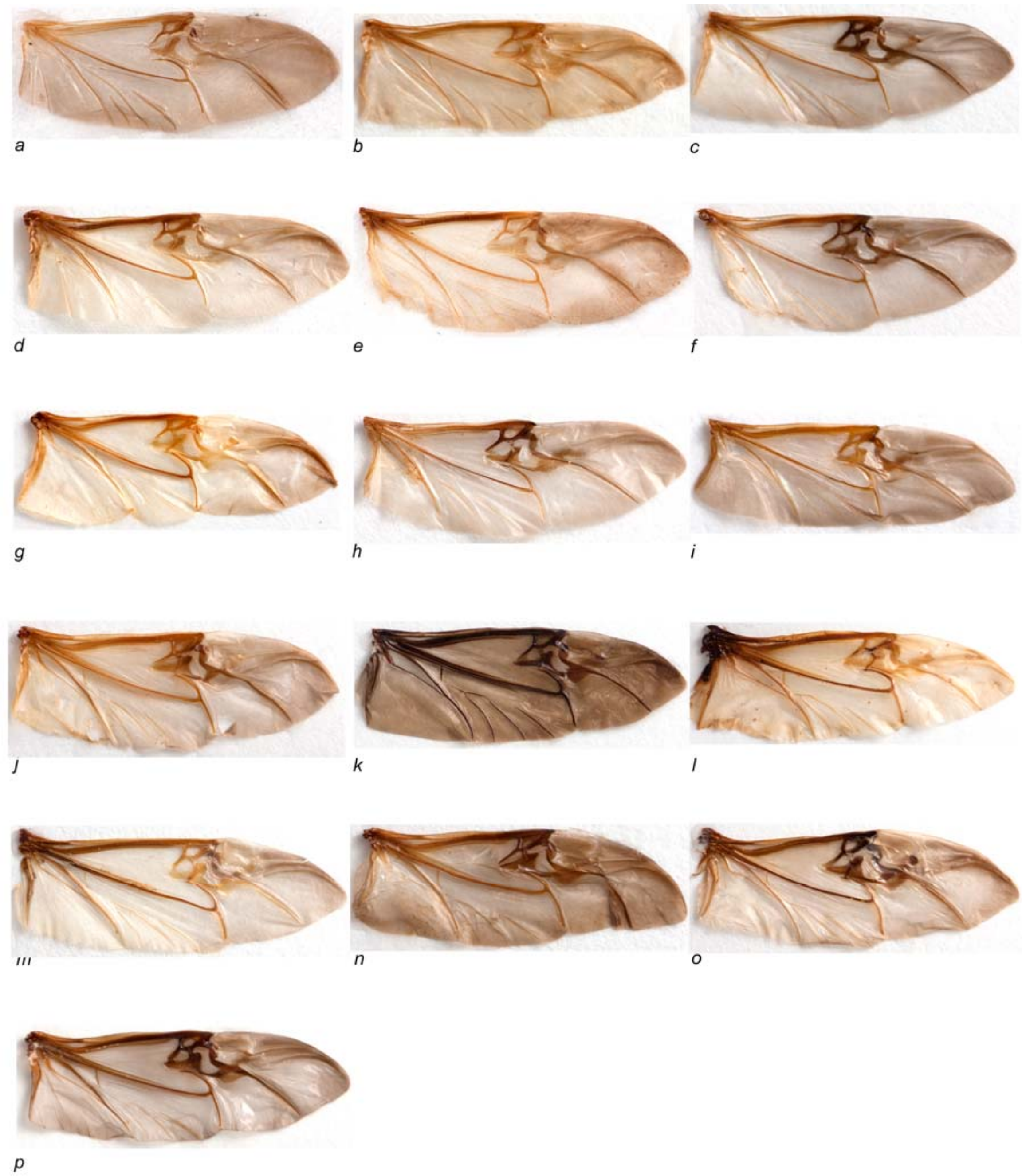

Figure 38. Sixteen genera of Onciderini (Cerambycidae: Lamiinae), hind wing photographs. **a)** *Pericasta*. **b)** *Periergates*. **c)** *Peritrox*. **d)** *Plerodia*. **e)** *Proplerodia*. **f)** *Pseudobeta*. **g)** *Psyllotoxus*. **h)** *Sternycha*. **i)** *Strioderes*. **j)** *Sulpitus*. **k)** *Taricanus*. **l)** *Trachysomus*. **m)** *Trestonia*. **n)** *Tulcoides*. **o)** *Tulcus*. **p)** *Tybalmia*.

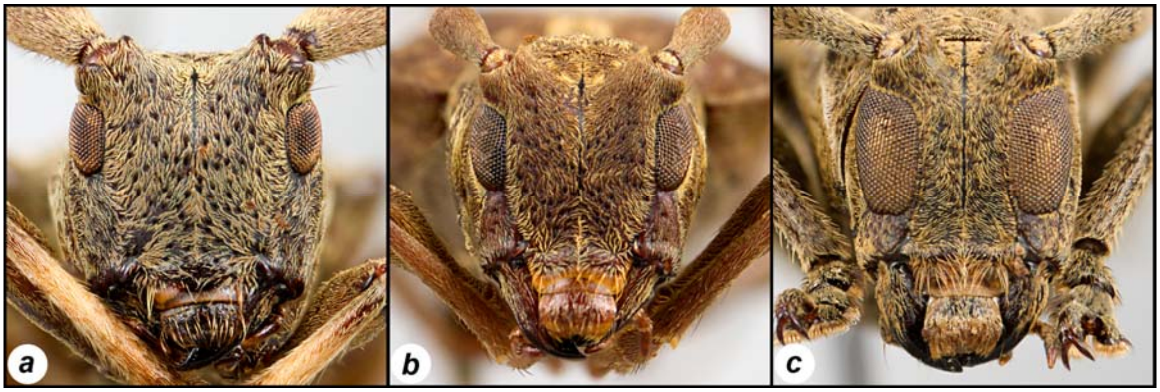

Figure 39. Character 1: Eye lower lobe height compared to gena. **a)** Shorter, 0.7× or more (*Cordites*). **b)** About the same (*Apamauta*). **c)** Taller, 1.3× or more (*Alexera*).

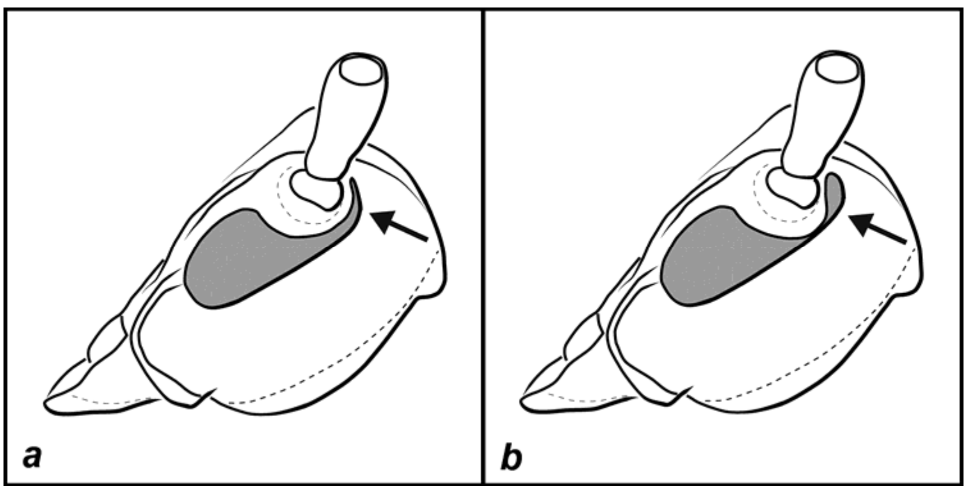

Figure 40. Character 2: Eyes divided into upper and lower lobes. **a)** Absent. **b)** Present.

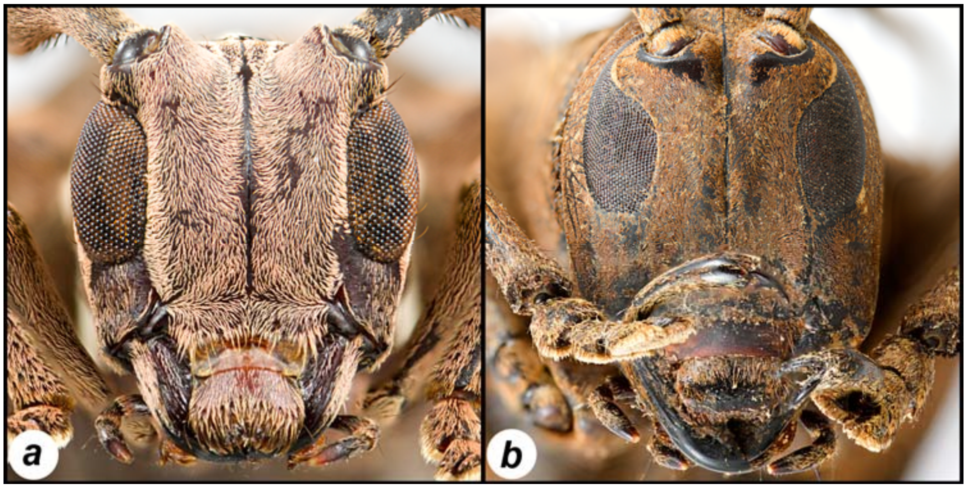

Figure 41. Character 3: Eyes confluent with head capsule (not protruding). **a)** Absent (*Cicatrodea*). **b)** Present (*Hypselomus*).

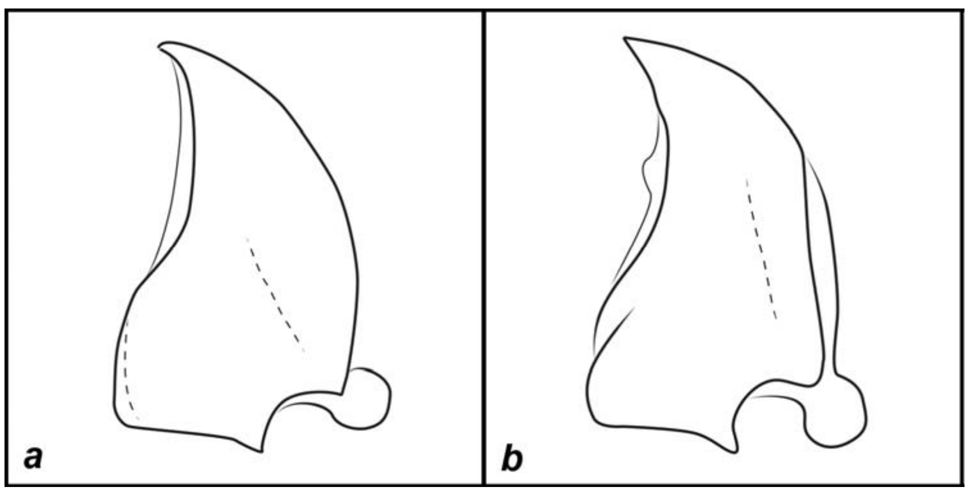

Figure 42. Character 4: Mandible incisor edge in males. **a)** Smooth. **b)** Dentate.

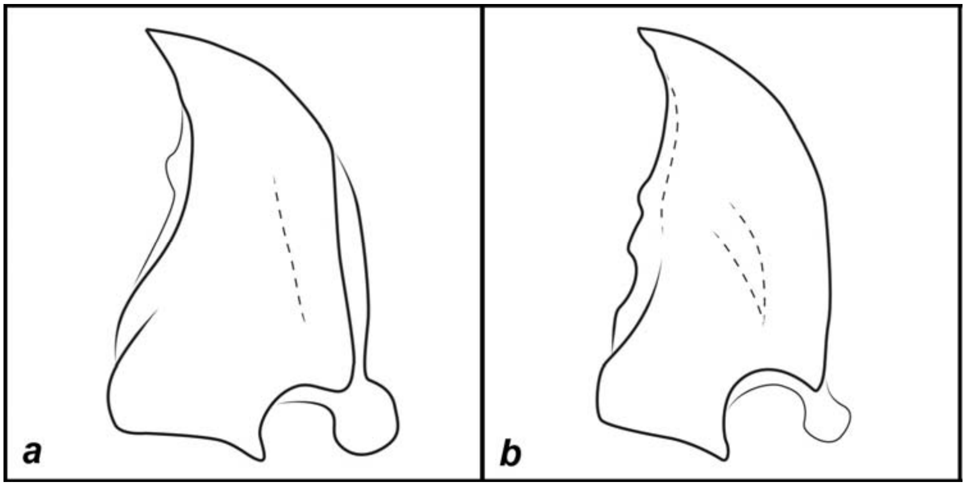

Figure 43. Character 5: If mandible incisor edge dentate in males, then incisor edge as follows. **a)** Unidentate. **b)** Multidentate.

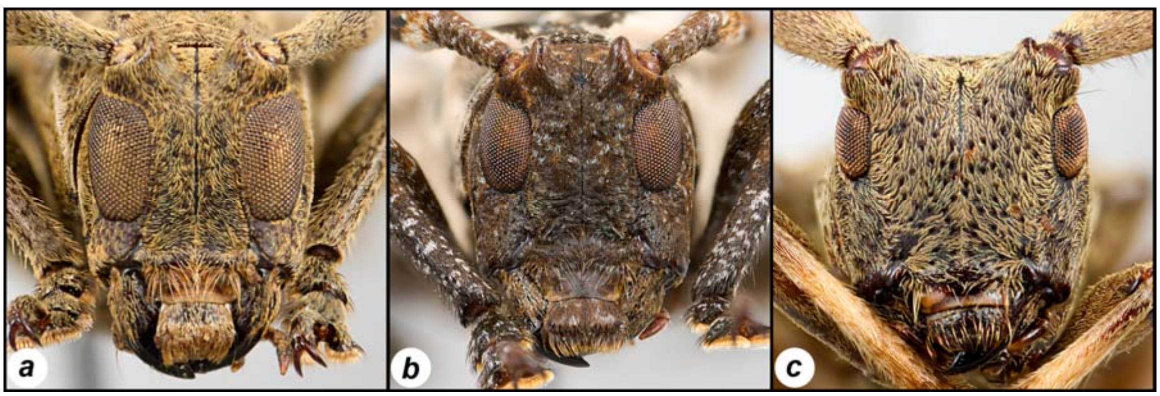

Figure 44. Character 6: Head, width of frons between lower eye lobes. **a)** Narrow, less than 2 lower eye lobe widths (*Alexera*). **b)** Moderate, between 2–4 widths (*Cipriscola*). **c)** Wide, more than 4 lower eye lobe widths (*Cordites*).

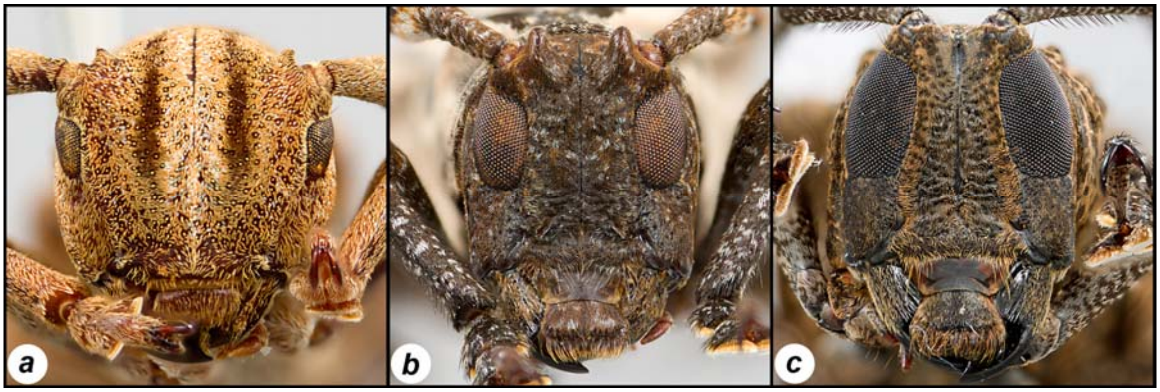

Figure 45. Character 7: Frons, height compared to width. **a)** Transverse: 0.5–0.8× taller (*Cherentes*). **b)** Subquadrate: 0.9–1.2× taller (*Cipriscola*). **c)** Elongate: 1.3–1.6× taller (*Jamesia*).

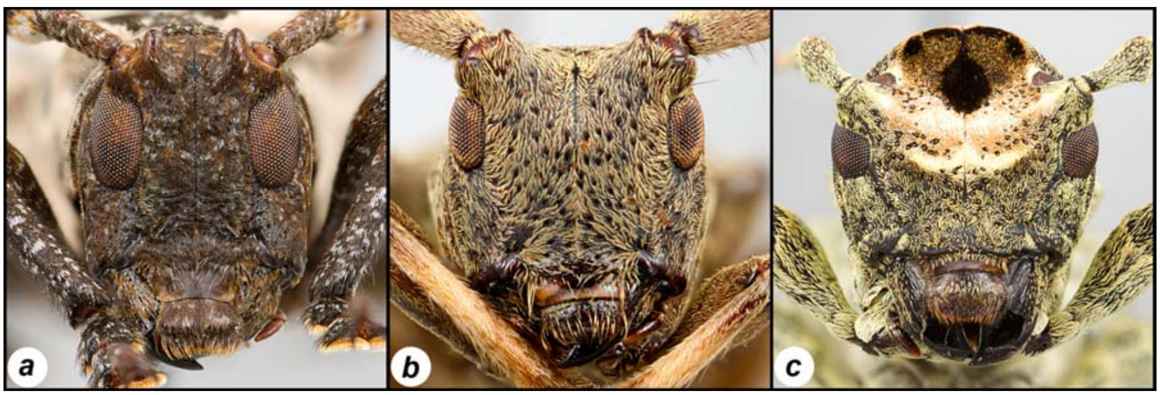

Figure 46. Character 8: Antennal tubercles, width apart at socket. **a)** narrowly separated, less than 2 antennal socket widths (*Cipriscola*). **b)** at least 2, but less than 4 antennal socket widths (*Cordites*). **c)** 4 antennal socket widths or more (*Ecthoea*).

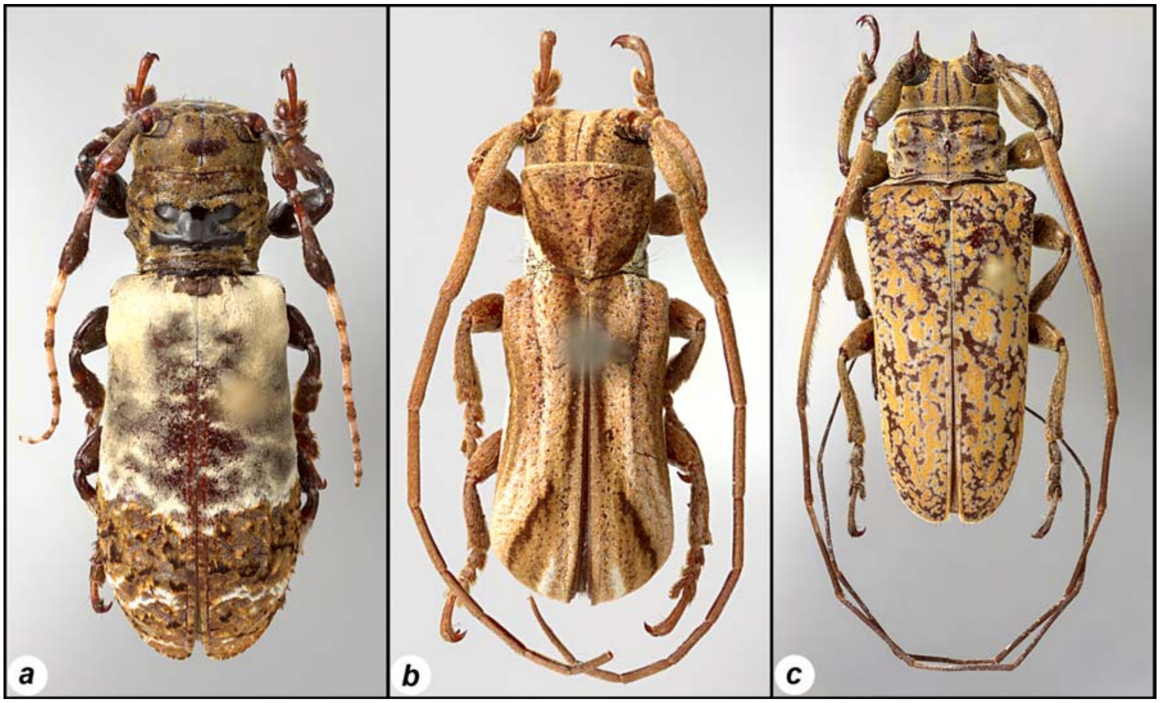

Figure 47. Character 9: Antennal length in males. **a)** Short, not reaching elytral apices (*Lachaerus*). **b)** Moderate, attaining elytral apices (*Cherentes*). **c)** Long, distinctly surpassing elytral apices (*Hesychotypa*).

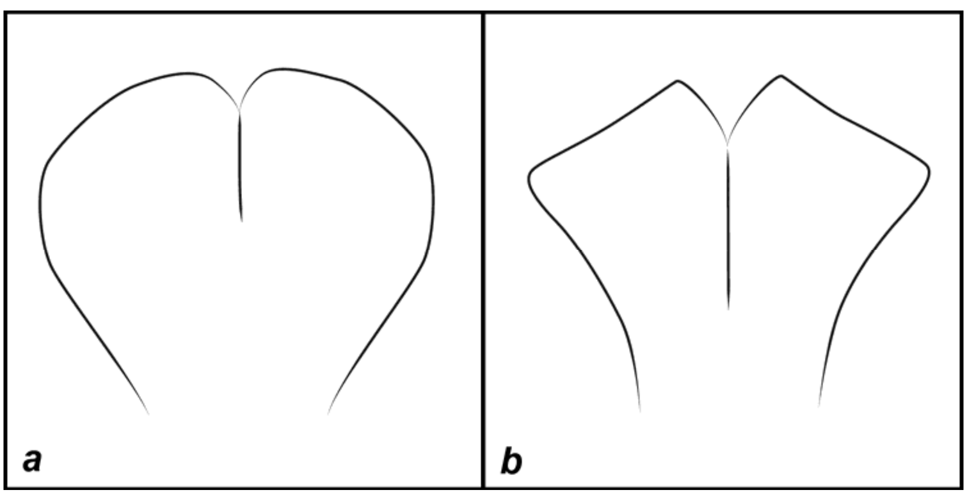

Figure 48. Character 10: Mouthparts, ligula lobe shape. **a)** Rounded. **b)** Subtruncate.

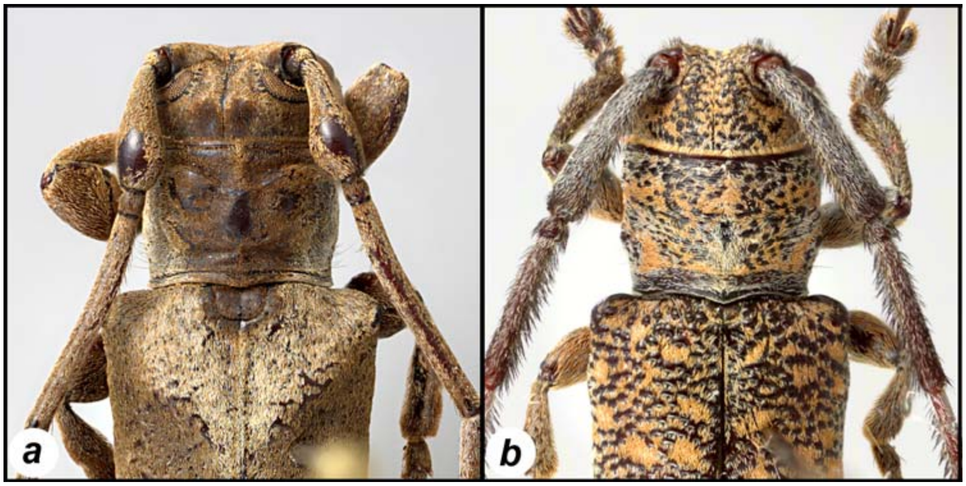

Figure 49. Character 11: Antennomere III. **a)** Without dense setae beneath (*Cordites*). **b)** With dense setae beneath (*Periergates*).

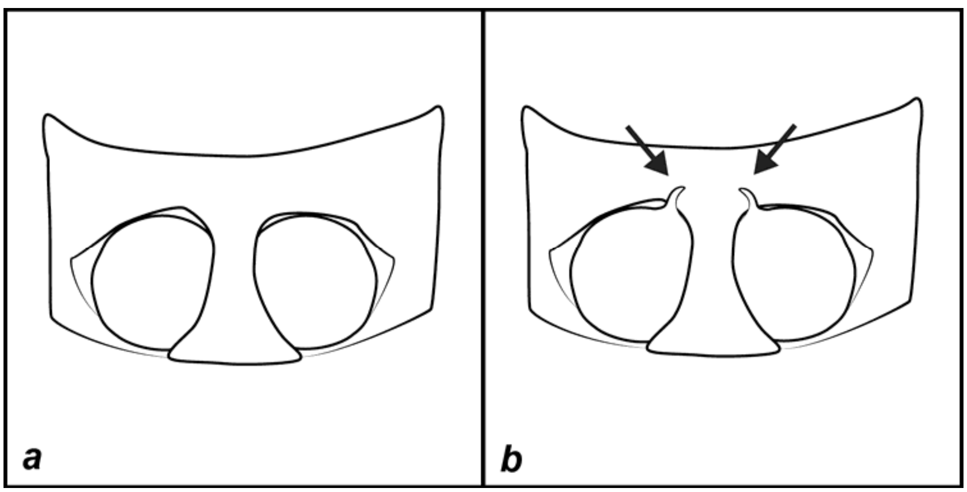

Figure 50. Character 12: Procoxae in males. **a)** Not modified. **b)** Modified with curved hook.

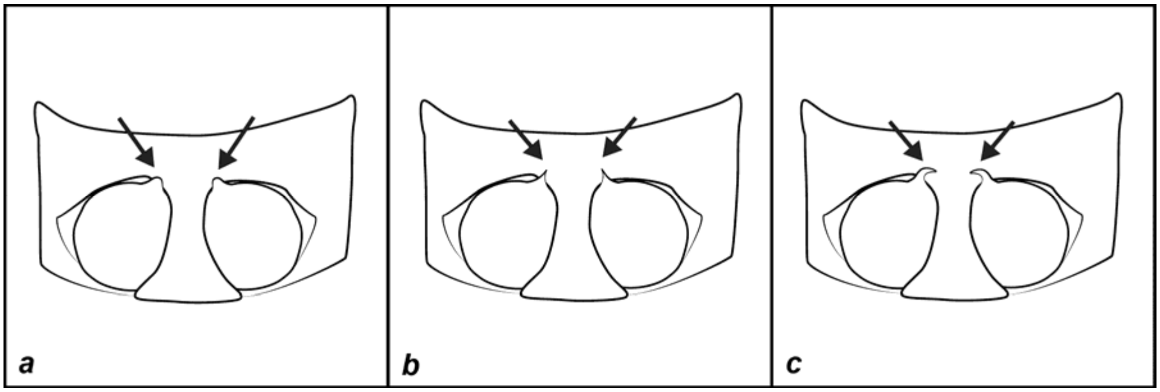

Figure 51. Character 12 (continued): procoxae in males. **a)** Modified with blunt protuberance. **b)** Modified with acute projection. **c)** Modified with curved hook.

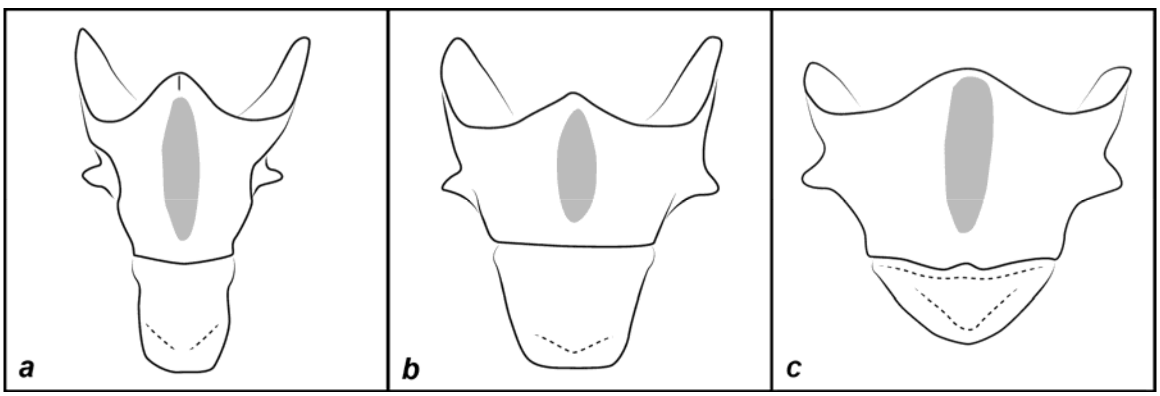

Figure 52. Character 13: Mesonotum, width compared to height. **a)** Elongate. **b)** Subquadrate. **c)** Transverse.

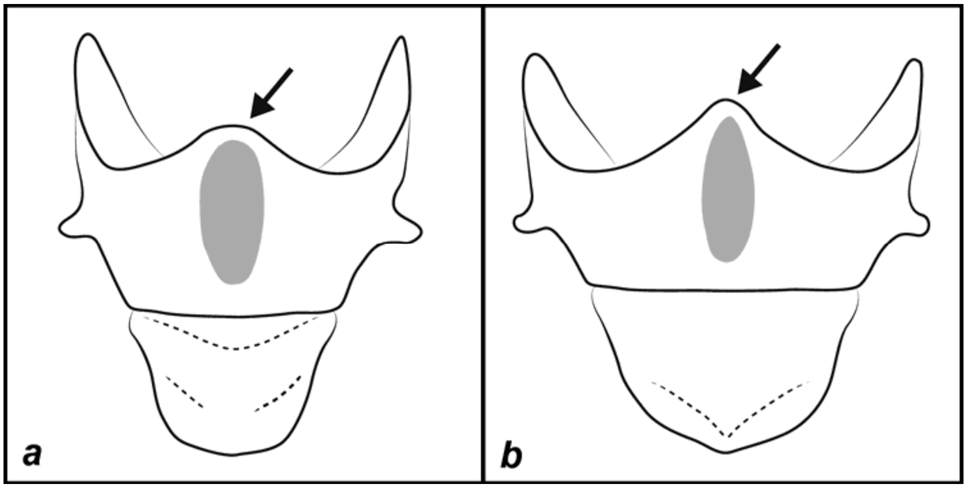

Figure 53. Character 14: Mesoscutum shape at apex. **a)** Broadly rounded. **b)** Not broadly rounded (narrowly rounded, acute or subtruncate).

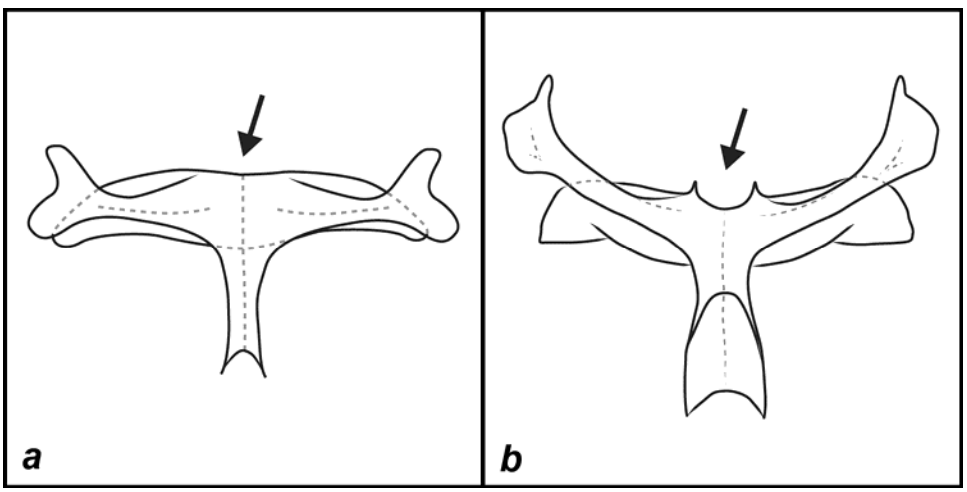

Figure 54. Character 15: Metendosternite, shape of anterior area at midline. **a)** Nearly straight. **b)** Distinctly concave.

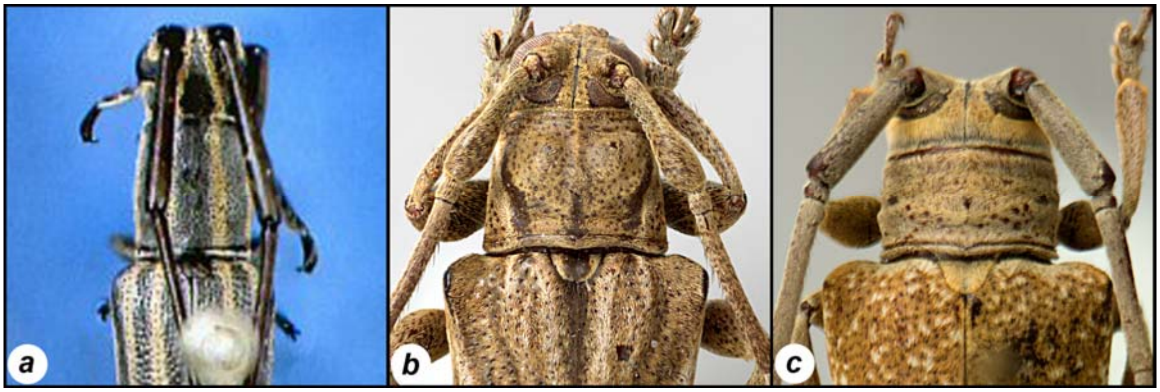

Figure 55. Character 16: Pronotal width (at widest) compared to pronotal length. **a)** Subquadrate, from 0.8–1.1× as long (*Hippopsis*). **b)** Transverse, from 1.2–1.5× as long (*Alexera*). **c)** Transverse, from 1.6–1.9× as long (*Oncioderes*).

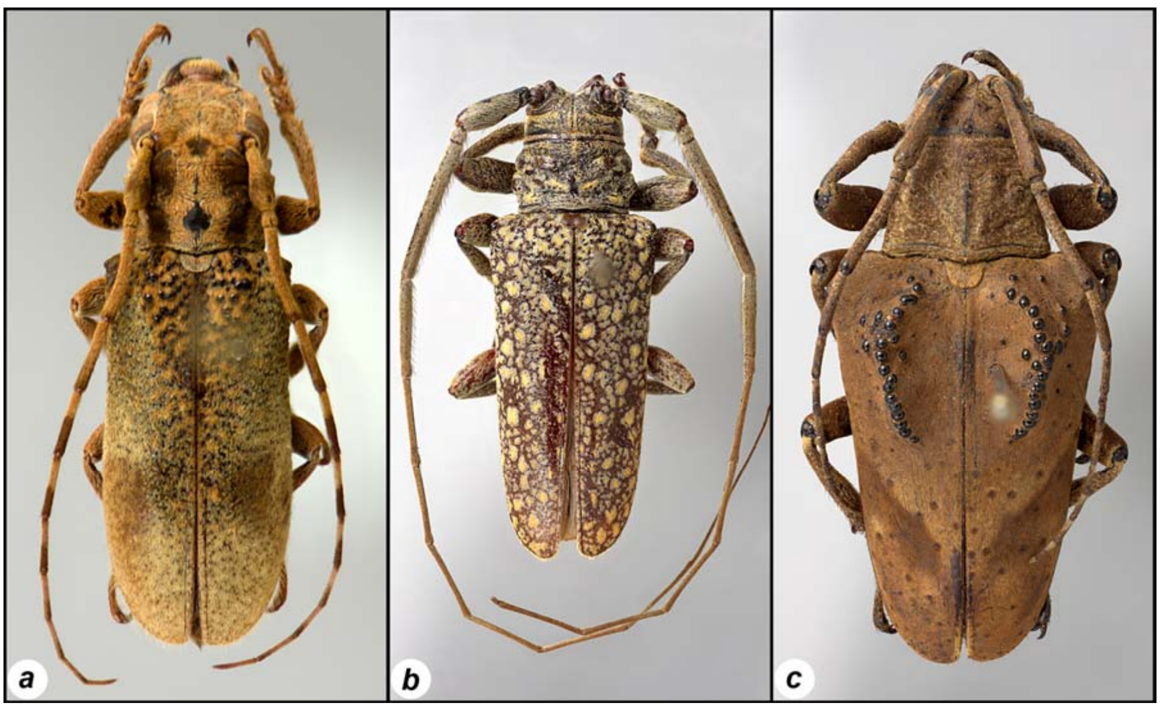

Figure 56. Character 17: Elytral width measured across humeri compared to pronotal width (at widest). **a)** 1.2× wider or less (*Trestoncideres*). **b)** 1.3–1.6× wider (*Eupalessa*). **c)** 1.7× or more (*Hypselomus*).

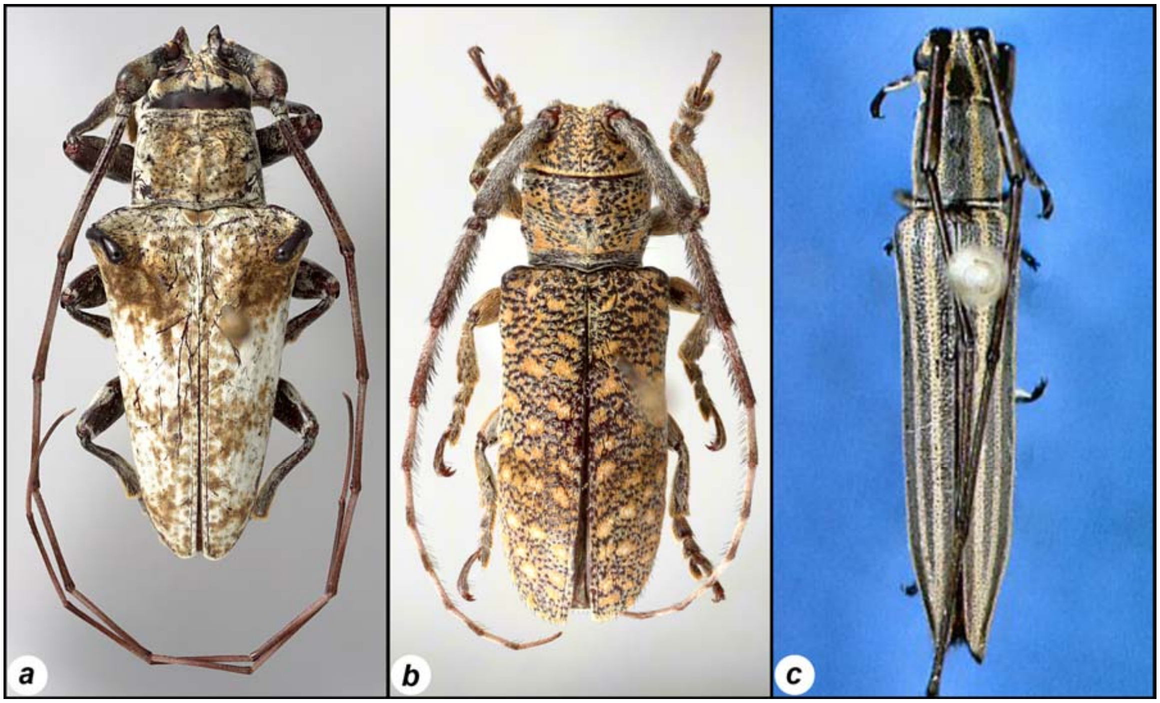

Figure 57. Character 18: Elytral length compared to width at humeri. **a)** 1.5× or less (*Lesbates*). **b)** 1.6–2.4× longer (*Periergates*). **c)** 2.5× or more (*Hypselomus*).

Figure 58. Character 19: Elytra with glabrous granules. **a)** Absent (*Hesychotypa*). **b)** Present (*Jamesia*).

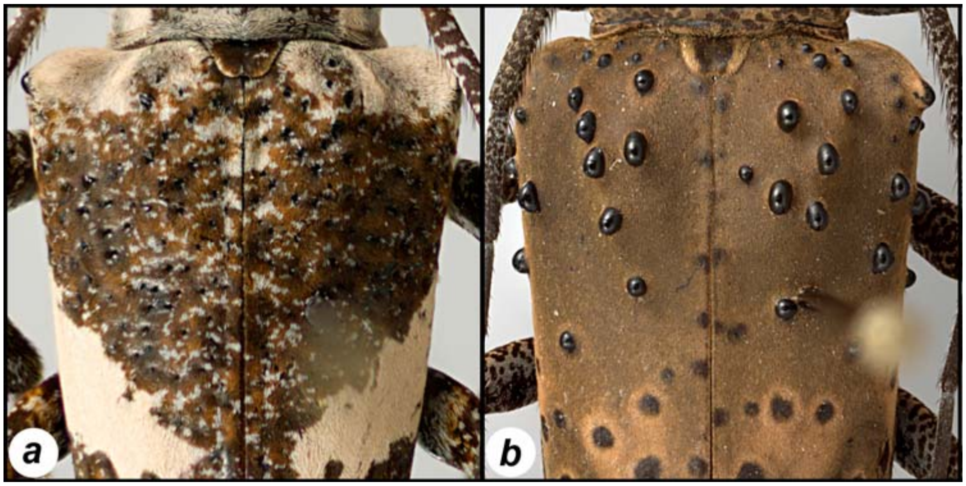

Figure 59. Character 20: If elytra with glabrous granules, then granules as follows. **a)** Granulate-punctate (*Cipriscola*). **b)** Granules without punctures (*Jamesia*).

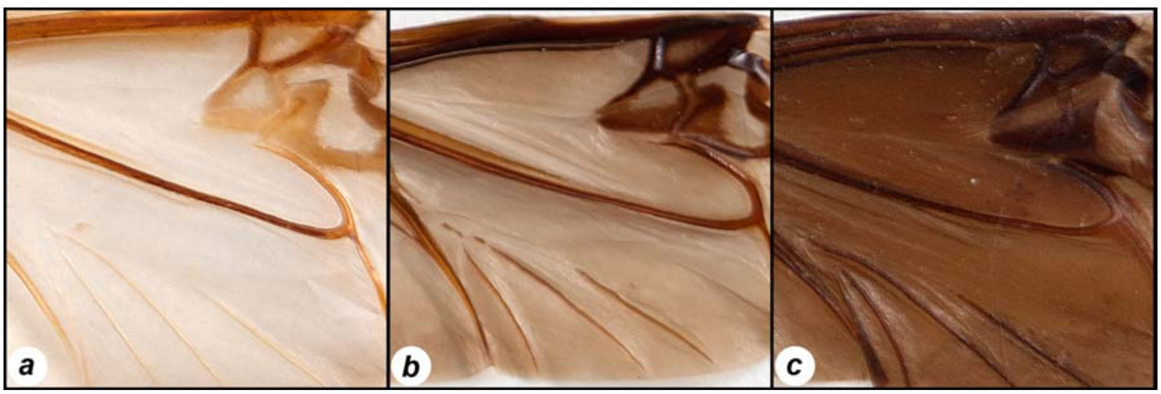

Figure 60. Character 21: Hind wing pigmentation. **a)** Clear (*Lachnia*). **b)** Moderately pigmented (*Hypselomus*). **c)** Darkly pigmented (*Cydros*).

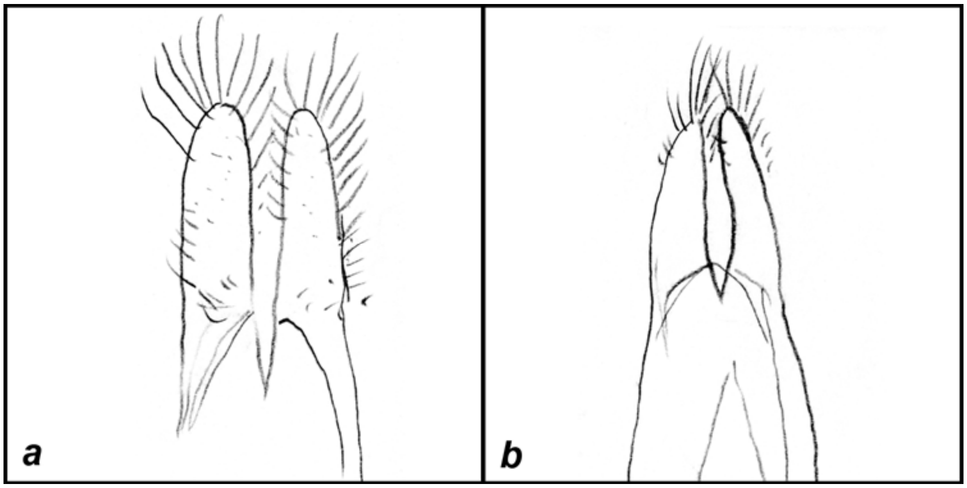

Figure 61. Character 22: Male genitalia, width of parameres at base compared to apex. **a)** About the same. **b)** Distinctly narrower.

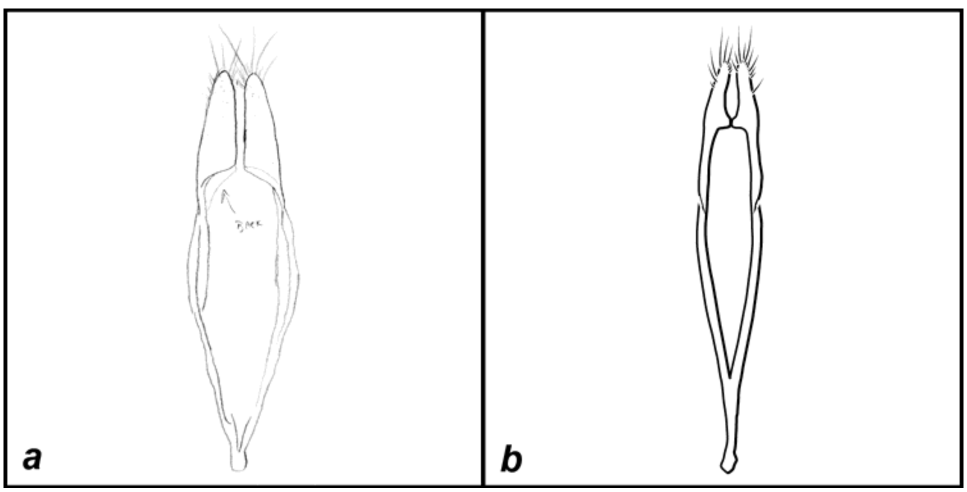

Figure 62. Character 23: Male genitalia, length of tegmen compared to length of parameres. **a)** Moderately long. **b)** Elongate, 3× or more.

Figure 63. Three examples of girdling by Onciderini (Cerambycidae: Lamiinae), Santa Cruz, Bolivia. **a)** Adult female *Oncideres* sp. on recently girdled branch. **b)** Girdled tree trunk (approx. 8 cm diameter). **c)** Girdled branch which has been opened to expose Onciderini larva inside (approx. 20 mm long).

#	Character description and states
1	Eye lower lobe height compared to gena 0 = shorter, 0.7× or less (Fig. 39a) 1 = about the same (Fig. 39b) 2 = taller, 1.3× or more (Fig. 39c) This character is treated as additive
2	Eyes divided into upper and lower lobes 0 = absent (Fig. 40a) 1 = present (Fig. 40b)
3	Eyes confluent with head capsule (not protruding) 0 = absent (protruding) (Fig. 41a) 1 = present (confluent) (Fig. 41b)
4	Mandible incisor edge in males 0 = smooth (Fig. 42a) 1 = dentate (Fig. 42b)
5	If mandible incisor edge dentate in males, then incisor edge as follows 0 = unidentate (Fig. 43a) 1 = multidentate (Fig. 43b)
6	Head, width of frons between lower eye lobes 0 = narrow, less than 2 lower eye lobe widths (Fig. 44a) 1 = moderate, between 2–4 widths (Fig. 44b) 2 = wide, more than 4 lower eye lobe widths (Fig. 44c) This character is treated as additive
7	Frons, height compared to width 0 = transverse: 0.5–0.8× taller (Fig. 45a) 1 = subquadrate: 0.9–1.2× taller (Fig. 45b) 2 = elongate: 1.3–1.6× taller (Fig. 45c) 3 = strongly elongate: 1.7–2.0 times taller 4 = distinctly elongate: 2.1–2.4 times taller This character is treated as additive
8	Antennal tubercles, width apart at socket 0 = narrowly separated, less than 2 antennal socket widths (Fig. 46a) 1 = at least 2, but less than 4 antennal socket widths (Fig. 46b) 2 = 4 antennal socket widths or more (Fig. 46c) This character is treated as additive
9	Antennal length in males 0 = short, not reaching elytral apices (Fig. 47a) 1 = moderate, attaining elytral apices (Fig. 47b) 2 = long, distinctly surpassing elytral apices (Fig. 47c) This character is treated as additive
10	Mouthparts, ligula lobe shape 0 = rounded (Fig. 48a) 1 = subtruncate (Fig. 48b)
11	Antennomere III 0 = without dense setae beneath (e.g., Fig. 49a) 1 = with dense setae beneath (e.g., Fig. 49b)
12	Procoxae in males 0 = not modified (Fig. 50a) 1 = modified with blunt protuberance (Fig. 51a) 2 = modified with acute projection (Fig. 51b) 3 = modified with curved hook (Fig. 51c)

Table 5. Definition of morphological characters 1–12 used in analyses of Onciderini (Cerambycidae: Lamiinae).

#	Character description and states
13	Mesonotum, width compared to height 0 = elongate (Fig. 52a) 1 = subquadrate (Fig. 52b) 2 = transverse (Fig. 52c)
14	Mesoscutum shape at apex 0 = broadly rounded (Fig. 53a) 1 = narrowly rounded (Fig. 53b) 2 = narrowly subtruncate (Fig. 31cc)
15	Metendosternite, shape of anterior area at midline 0 = nearly straight (Fig. 54a) 1 = distinctly concave (Fig. 54b)
16	Pronotal width (at widest) compared to pronotal length 0 = subquadrate, from 0.8–1.1× as long (Fig. 55a) 1 = transverse, from 1.2–1.5× as long (Fig. 55b) 2 = transverse, from 1.6–1.9× as long (Fig. 55c) This character is treated as additive
17	Elytral width measured across humeri compared to pronotal width (at widest) 0 = 1.2× wider or less (Fig. 56a) 1 = 1.3–1.6× wider (Fig. 56b) 2 = 1.7× or more (Fig. 56c) This character is treated as additive
18	Elytral length compared to width at humeri 0 = 1.5× or less (Fig. 57a) 1 = 1.6–2.4× longer (Fig. 57b) 2 = 2.5× or more (Fig. 57c) This character is treated as additive
19	Elytra with glabrous granules 0 = absent (Fig. 58a) 1 = present (Fig. 58b)
20	If elytra with glabrous granules, then granules as follows 0 = granulate-punctate (Fig. 59a) 1 = granules without punctures (Fig. 59b)
21	Hind wing pigmentation 0 = clear (Fig. 60a) 1 = moderately pigmented (Fig. 60b) 2 = darkly pigmented (Fig. 60c) This character is treated as additive
22	Character Male genitalia, width of parameres at base compared to apex 0 = about the same (Fig. 61a) 1 = distinctly narrower (Fig. 61b)
23	Male genitalia, length of tegmen compared to length of parameres 0 = moderately long, less than 3× (Fig. 62a) 1 = elongate, 3× or more (Fig. 62b)

Table 6. Definition of morphological characters 13–23 used in analyses of Onciderini (Cerambycidae: Lamiinae).

	000000000 123456789 + ++++	1111111111 0123456789 +++	2222 0123 +
Agaritha iolaia	010??1211	10?1111210	?1??
Alexera barii	2100?0311	1031101110	?000
Apamauta lineolata	1100?2112	1031101210	?000
Apocoptoma chabrillacii	1100?1112	1030101110	?100
Bacuris sexvittatus	2100?0111	1001011110	?0??
Bucoides erichsoni	110101202	1031111110	?000
Cacostola rugicollis	1100?1112	1001111120	?000
Cherentes niveilateris	0100?2021	1001111110	?110
Chitron mniszechii	1100?2112	1001101110	?001
Cicatrodea bahia	110100102	1031001111	0010
Cipriscola fasciata	110100201	1021101101	0100
Clavidesmus heterocerus	1100?2011	1001111110	?210
Cnemosioma innominata	110??031?	10?2001210	?0??
Cordites armillata	010102112	1031011110	?100
Cydros leucurus	1100?1010	1000011010	?211
Cylicasta nysa	1100?0402	1001211110	?001
Delilah gilvicornis	110101202	1032111101	0110
Ecthoea quadricornis	1100?2021	1001101010	?001
Ephiales cretacea	1100?1112	1101111110	?001
Esonius panopus	1100?1111	1031101111	0000
Eudesmus posticalis	1100?2011	1001111110	?000
Eupalessa attenuata	110112112	1131102111	0000
Euthima rodens	110100411	1031111110	?000
Furona degenera	110100311	1131111110	?000
Glypthaga xylina	110111112	10?1111110	?010
Hesycha bimaculata	1100?1111	1032001110	?001
Hesychotypa miniata	110101012	1011112110	?110
Hippopsis lemniscata	2100?0212	0000000120	?000
Hypselomus cristatus	101110201	1010011201	1100
Hypsioma steinbachi	110100212	0031111111	0001
Iaquira viridis	1100?0212	1001111110	?0??
Ischiocentra monteverdensis	210101112	1030111110	?000
Ischioderes oncioderes	110101012	1031002110	?110
Ischiosioma obliquata	1100?1111	1001011210	?000
Jamesia globifera	101100402	1001011111	1010
Lachaerus fascinus	1100?2020	1001011110	?000
Lachnia subcincta	110101112	1001102110	?011
Lesbates acromii	011101212	1031101200	?110
Leus ramuli	110101111	1002101110	?001
Lingafelteria giuglarisi	2100?1111	1001011110	?011

Table 7. Data matrix for 77 taxa and 23 morphological characters used in analyses of Onciderini (Cerambycidae: Lamiinae). Characters marked with "+" are additive, inapplicable character states are marked with '-' and unobserved character states with '?'

	000000000 123456789 + ++++	1111111111 0123456789 +++	2222 0123 +
Lochmaeocles callidryas	110101012	1011102111	0010
Lydipta pumilio	110101211	1101001110	?000
Marensis simplex	111100202	0021001110	?001
Microcanus minor	1100?2011	1021101110	?100
Midamiella hecabe	1100?1111	1021101110	?010
Monneoncideres cristata	1110?1111	1001101111	1011
Neocherentes dilloniorium	110112011	1021001110	?000
Neodillonia albisparsa	1100?1102	1021012100	?100
Neolampedusa obliquator	110101111	1021011110	?000
Oncideres c. cingulata	1100?1022	?012011111	1001
Oncioderes rondoniae	1100?1011	1002112110	?000
Pachypeza joda	1100?0202	1101000020	?000
Paratrachysomus huedepohli	110??102?	1001101110	?0??
Paratritania alternans	110101202	1111101111	0000
Pericasta virescens	1110?0302	1001101110	?011
Periergates rodriguezi	010102112	1111111111	0001
Peritrox nigromaculatus	210100212	1011111110	?000
Plerodia singularis	110100211	0001101110	?000
Prohylus phanthasma	110??1111	1000011111	00??
Proplerodia piriana	1100?1111	?031001110	?010
Pseudobeta seabrai	110101111	1031111110	?010
Psyllotoxus griseocinctus	110101112	0010101111	0001
Saperda lateralis	2100?0121	0000000120	?010
Sternycha paupera	110111021	1001101110	?000
Strioderes peruanus	110102010	0011111110	?010
Sulpitus lilla	1100?1112	1031001110	?010
Taricanus truquii	010102012	0111011111	0211
Tibiosioma remipes	1100?1111	1021001110	?000
Touroultia swifti	2100?0111	1011011210	?000
Trachysomus camelus	1100?2021	0001012100	?001
Trestoncideres albiverntris	1100?1121	1001112011	0000
Trestonia pulcherrima	1100?1022	1031111110	?010
Tulcoides pura	110101211	1032201110	?000
Tulcus lycimnius	1100?1211	1031112100	?000
Tybalmia pupillata	110101112	1131102111	0000
Typhlocerus prodigiosus	110??1201	1031112210	?2??
Venustus zeteki	1100?0211	1011101100	?000

Table 7 (continued). Data matrix for 77 species and 23 morphological characters used in analyses of Onciderini (Cerambycidae: Lamiinae). Characters marked with “+” are additive, inapplicable character states are marked with ‘-’ and unobserved character states with ‘?’

Figure 64. Strict consensus of the 70,468 most parsimonious trees (L = 377 steps, CI = 10, RI = 23) resulting from cladistic analysis of 74 species of Onciderini (Cerambycidae: Lamiinae) and three outgroup taxa, with characters mapped using ACCTRAN (fast) optimization. Black hash marks indicate unambiguous changes, white hash marks indicate homoplasious changes or reversals. Numbers above hash marks are character numbers, those below hash marks are character states.

Figure 65. Majority rule consensus tree resulting from Bayesian analysis of 74 species of Onciderini (Cerambycidae: Lamiinae). Numbers at branches are posterior probability percentages.

APPENDIX A

Published in: Nearns, E.H. & K.B. Miller. 2009. A new species of *Plectromerus* Haldeman from Central America and description of the female of *Plectromerus dezayasi* Nearns & Branham (Coleoptera, Cerambycidae, Cerambycinae, Plectromerini). *ZooKeys*, 24: 55–62. Available from: http://cerambycids.com/pdf/Nearns&Miller_2009.pdf

Abstract

A new species, *Plectromerus roncavei*, sp. n. (Coleoptera, Cerambycidae, Cerambycinae, Plectromerini), from Honduras and Nicaragua is described and illustrated. Features distinguishing the new species from its congeners as well as a modified key to *Plectromerus* species are presented. In addition, the previously unknown female of *Plectromerus dezayasi* Nearns & Branham is described and illustrated.

APPENDIX B

Published in: Nearns, E.H., Lord, N.P., & K.B. Miller. 2011. Oncid ID: Tool for diagnosing adult twig girdlers (Cerambycidae: Lamiinae: Onciderini). The University of New Mexico and Center for Plant Health Science and Technology, USDA, APHIS, PPQ. Available from: http://cerambycids.com/oncidid/

Abstract

Designed for use by a wide variety of individuals, Oncid ID provides support for the identification of adult "twig girdlers," a large group of longhorned beetles in the tribe Onciderini (Cerambycidae: Lamiinae). This tribe currently contains 79 genera and 481 species which are widely distributed in the Nearctic and Neotropical regions. Members of this group are known to attack a number of economically important woody plant species. The potential introduction of exotic twig girdler species into the USA poses a serious risk. The interactive key featured in Oncid ID was developed in Lucid version 3.5 software. Oncid ID is a fully illustrated identification tool, featuring a gallery page with habitus images of representatives of each genus, as well as head illustrations for each genus. The fact sheets feature detailed descriptions, diagnostic features, geographic distribution, synonymies, and references. Each fact sheet also includes a variety of high-quality images, including dorsal and lateral habitus shots and close-ups of the heads of a number of representative species. Many of the images are of the type specimens, and images of both sexes are included where possible. The fact sheets also include information on host plants and girdling behavior, when available. The tool also features a morphological atlas to help users who may not be completely familiar with all the

morphological terminology featured in the tool. A glossary is also provided within the tool to provide more specific definitions to terms used in the key and fact sheets.

APPENDIX C

Published in: Nearns, E.H. & I.P. Swift. 2011. New taxa and combinations in Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae). *Insecta Mundi*, 0192: 1–27. Available from: http://www.cerambycids.com/pdf/Nearns&Swift_2011.pdf

Abstract

Monneoncideres, a new genus of Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) is described and illustrated. Six new species of Onciderini are also described and illustrated: *Hesycha tavakiliani* from Brazil; *Lesbates milleri* from Venezuela; *Monneoncideres cristata* from Ecuador and Peru; *Neodillonia waltersi* from Ecuador; *Tibiosioma martinsi* from Ecuador; and *Trestonia wappesi* from Panama. Keys to the known species of *Lesbates* Dillon & Dillon, 1945 and *Tibiosioma* Martins & Galileo, 1990 are provided. The genus *Ophthalmocydrus* Aurivillius, 1925 (Onciderini) is transferred to Pteropliini (Lamiinae); and *Xylomimus* Bates, 1865 (Apomecynini) is transferred to Onciderini. The following new synonymies are proposed: *Kuauna* Martins & Galileo, 2009 = *Ophthalmocydrus* Aurivillius, 1925; *Kuauna schmidi* Martins & Galileo, 2009 = *Ophthalmocydrus semiorbifer* Aurivillius, 1925; *Paraplerodia* Martins & Galileo, 2010 = *Tibiosioma* Martins & Galileo, 2007; *Paraplerodia acarinata* Martins & Galileo, 2010 = *Tibiosioma maculosa* Martins & Galileo, 2007; and *Ischiomaeocles* Franz, 1954 = *Lochmaeocles* Bates, 1880. The following new combination is proposed: *Lochmaeocles salvadorensis* (Franz, 1954), transferred from *Ischiomaeocles*. The following 37 new country records are reported: *Alexera barii* (Jekel, 1861) (Bolivia, Ecuador); *Bacuris sexvittatus* (Bates, 1865) (Panama); *Cacostola brasiliensis* Thomson,

1868 (Argentina); *Cherentes niveilateris* (Thomson, 1868) (French Guiana); *Cicatrodea monima* Dillon &Dillon, 1946 (Ecuador); *Clavidesmus metallicus* (Thomson, 1868) (Ecuador, Peru); *Cydros leucurus* Pascoe, 1866 (Brazil); *Ecthoea quadricornis* (Olivier, 1792) (Ecuador); *Eudesmus grisescens* Audinet-Serville, 1835 (Ecuador, Trinidad and Tobago, Venezuela); *Euthima variegata* (Aurivillius, 1921) (Ecuador); *Hesychotypa heraldica* (Bates, 1872) (Belize, Guatemala); *Hesychotypa punctata* Martins, 1979 (Peru); *Lochmaeocles basalis* Dillon &Dillon, 1946 (Ecuador, Trinidad and Tobago); *Lochmaeocles zonatus* Dillon & Dillon, 1946 (Venezuela); *Lydipta conspersa* (Aurivillius, 1922) (Peru); *Neocherentes dilloniorum* Tippmann, 1960 (Brazil); *Neolampedusa obliquator* (Fabricius, 1801) (Ecuador); *Peritrox perbra* Dillon & Dillon, 1945 (Ecuador); *Priscatoides tatila* Dillon & Dillon, 1945 (Bolivia); *Strioderes peruanus* Giorgi, 2001 (Brazil); *Trachysomus apipunga* Martins & Galileo, 2008 (Peru); *Trachysomus camelus* Buquet, 1852 (Venezuela); *Trachysomus peregrinus* Thomson, 1858 (Ecuador); *Trachysomus thomsoni* Aurivillius, 1923 (Venezuela); *Trestoncideres laterialba* Martins & Galileo, 1990 (Brazil); *Trestonia exotica* Galileo & Martins, 1990 (Ecuador); *Trestonia fulgurata* Buquet, 1859 (Grenada, Trinidad and Tobago); *Tritania dilloni* Chalumeau, 1990 (Venezuela); *Tulcus paganus* (Pascoe, 1859) (Ecuador); *Xylomimus baculus* Bates, 1865 (French Guiana). *Theobroma cacao* Linnaeus (Sterculiaceae) is recorded as a new host plant record for *Eudesmus grisescens*.

APPENDIX D

Published in: Nearns, E.H., Lord, N.P., Lingafelter, S.W., Santos-Silva, A., & K.B. Miller. 2012. Longicorn ID: Tool for diagnosing cerambycoid families, subfamilies, and tribes. The University of New Mexico and Center for Plant Health Science and Technology, USDA, APHIS, PPQ. Available from: http://cerambycids.com/longicornid/

Abstract

Cerambycoid beetles include the large family Cerambycidae and three smaller families: Disteniidae, Oxypeltidae, and Vesperidae. Together, these families are a charismatic and economically important group of beetles with an estimated 4,000 genera and more than 35,000 described species worldwide. When all three phases are complete, Longicorn ID will provide identification support to the four families, 14 subfamilies, and 250 tribes. Cerambycoids (also known as “longhorned beetles” or simply “longicorns”) are among the most serious wood-boring pest species in the world, affecting various agricultural crops, ornamental trees, and lumber products, causing millions of dollars in damage each year. Due to the large size of this group of beetles, the development of Longicorn ID has been broken up into three phases. The first phase, available now, contains identification keys to the families and subfamilies, as well as keys to the tribes of cerambycoid beetles except for the three largest subfamilies of Cerambycidae: Lamiinae, Lepturinae, and Cerambycinae. Together, these three subfamilies comprise about 90% of the species diversity of the family. Identification keys to the tribes of Lamiinae and Lepturinae are scheduled for release in December 2013, and a key to the tribes of Cerambycinae is scheduled for release in December 2014. Longicorn ID is a

fully illustrated identification tool, featuring a gallery page with habitus images of representatives of each group within the tool. The gallery is filterable, allowing you to view images of representatives from an entire family, each subfamily, or a specific tribe. There are fact sheets for each taxonomic level, each featuring descriptions, diagnostic features, geographic distribution, and biology and economic importance information. Each tribe fact sheet also includes high-quality zoom-able images of a number of exemplar species, including dorsal and lateral habitus shots and close-ups of the heads. The tool also includes a wide variety of other resources to help support identification within this large group of beetles. Longicorn ID features a morphological atlas to help users who may not be completely familiar with all the morphological terminology featured in the tool. In addition to the dorsal and ventral habitus atlas shown at right, there are atlases that demonstrate other unique features of this group of beetles. A glossary is also provided within the tool to provide more specific definitions to terms used in the key and fact sheets. Due to its relatively broad scope, Longicorn ID includes a number of keys. There are several simple, image-based dichotomous keys, one to help you quickly determine which family of cerambycoid beetles your species belongs to and several for the smaller subfamilies that only have a few tribes. There are also a number of matrix-based interactive keys. In phase 1, there are Lucid keys for the cerambycoid families and subfamilies, tribe keys for the smaller subfamilies of Cerambycidae, and tribe keys for the two larger non-cerambycid families, Disteniidae and Vesperidae. Each key is illustrated and provides links to the relevant fact sheets.

APPENDIX E

Published in: Nearns, E.H. & G.-L. Tavakilian. 2012. New taxa and combinations in Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) from Central and South America, with notes on additional taxa. *Insecta Mundi*, 0231: 1–24. Available from: http://www.cerambycids.com/pdf/Nearns&Tavakilian_2012.pdf

Abstract

Touroultia, a new genus of Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) is described and illustrated. Five new species of Onciderini are also described and illustrated: *Jamesia ramirezi* from Costa Rica; *Peritrox marcelae* from French Guiana; *Touroultia swifti* from Ecuador; *Touroultia lordi* from French Guiana; *Trestoncideres santossilvai* from Brazil. Keys to the known species of *Peritrox* Bates, 1865; *Touroultia* gen. nov.; and *Trestoncideres* Martins & Galileo, 1990 are provided. The following new synonymies are proposed: *Calliphenges* Waterhouse, 1880 (Colobotheini) = *Malthonea* Thomson, 1864 (Desmiphorini); *Paraclytemnestra* Breuning, 1974 (Onciderini) = *Jamesia* Jekel, 1861 (Onciderini); *Orteguaza* Lane, 1958 (Apomecynini) = *Clavidesmus* Dillon & Dillon, 1946 (Onciderini). The following new combinations are proposed: *Clavidesmus funerarius* (Lane, 1958) (Onciderini); *Clavidesmus lichenigerus* (Lane, 1958) (Onciderini); *Ischiocentra insulata* (Rodrigues & Mermudes, 2011); *Malthonea cuprascens* (Waterhouse, 1880) (Desmiphorini); *Touroultia obscurella* (Bates, 1865) (Onciderini). The following species is restored to original combination: *Jamesia lineata* Fisher, 1926 (Onciderini). The following 13 new country records are reported: *Ataxia hovorei* Lingafelter & Nearns, 2007 (Pteropliini)

(Haiti); *Carterica soror* Belon, 1896 (Colobotheini) (Ecuador); *Colobothea lunulata* Lucas, 1859 (Colobotheini) (Colombia); *Curius punctatus* (Fisher, 1932) (Curiini) (Haiti); *Cyclopeplus lacordairei* Thomson, 1868 (Anisocerini) (Colombia); *Iarucanga mimica* (Bates, 1866) (Hemilophini) (Ecuador); *Pirangoclytus latithorax* (Martins & Galileo, 2008) (Clytini) (Costa Rica); *Porangonycha princeps* (Bates, 1872) (Hemilophini) (Colombia); *Trestonia lateapicata* Martins & Galileo, 2010 (Onciderini) (Brazil); *Tulcus dimidiatus* (Bates, 1865) (Onciderini) (Colombia); *Unaporanga cincta* Martins & Galileo, 2007 (Hemilophini) (Colombia); *Zeale dubia* Galileo & Martins, 1997 (Hemilophini) (Colombia); *Zonotylus interruptus* (Olivier, 1790) (Trachyderini) (Colombia).

APPENDIX F

Published in: Nearns, E.H. & G.-L. Tavakilian. 2012. A new genus and five new species of Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) from South America, with notes on additional taxa. *Insecta Mundi*, 0266: 1–23. Available from: http://www.cerambycids.com/pdf/Nearns&Tavakilian_2012b.pdf

Abstract

Lingafelteria, a new genus of Onciderini Thomson, 1860 (Coleoptera: Cerambycidae: Lamiinae) is described and illustrated. Five new species of Onciderini are also described and illustrated: *Cylicasta mariahelenae*, *Lingafelteria giuglarisi*, *Psyllotoxus dalensi*, *Psyllotoxus faurei* from French Guiana; *Trestonia solangeae* from Bolivia. Keys to the known species of *Psyllotoxus* Thomson, 1868 are provided. *Psyllotoxoides albomaculata* Breuning, 1961 is redescribed; and the first known females of *Strioderes peruanus* Giorgi, 2001 and *Tibiosioma martinsi* Nearns & Swift, 2011 are described. The following eight new country records are reported: *Peritrox marcelae* Nearns & Tavakilian, 2012 (Brazil); *Pseudobeta ferruginea* Galileo & Martins, 1990 (French Guiana); *Tibiosioma martinsi* Nearns & Swift, 2011 (Brazil, Peru); *Trestonia exotica* Galileo & Martins, 1990 (French Guiana); *Trestonia morrisi* Martins & Galileo, 2005 (French Guiana); *Tritania dilloni* Chalumeau, 1990 (French Guiana, Suriname).

CONCLUSION

The longhorned wood boring beetles are a diverse and economically important group of insects in need of systematic expertise in order to resolve higher-level classification and provide a robust phylogenetic framework within which to explore and answer evolutionary questions regarding their diversity, ecology, conservation, and management. My dissertation incorporates several aspects of systematic entomology: field work, morphological study, scientific illustration, macro photography, new species discovery, molecular analysis, ecology, and the development of interactive identification tools.

In Chapter 1, I presented the first formal phylogeny of longhorned beetle subfamilies Prioninae Latreille and Parandrinae Blanchard (Coleoptera: Cerambycidae) inferred from DNA sequence data. In both the parsimony and Bayesian analyses, Prioninae + Parandrinae were recovered as a monophyletic group and sister to the subfamily Cerambycinae. Relationship among the prionine tribes and genera were poorly resolved, likely due to missing sequence data for a majority of included taxa, as well as relatively sparse taxonomic coverage.

In Chapter 2, I presented the first morphological study and phylogenetic analysis of the tribe Onciderini Thomson (Cerambycidae: Lamiinae). Onciderini were recovered as a monophyletic group with respect to the outgroup taxa chosen. Relationships among the 74 species of onciderines included were poorly resolved in both the parsimony and Bayesian analyses.

In Appendices A–F, I listed six works published in partial fulfillment of this dissertation. Included in these six works are four publications in which a total of 20 new

cerambycid taxa are described, 58 new country records are recorded, and identification keys to the species of six genera are presented. The remaining two published works ("Oncid ID: Tool for diagnosing adult twig girdlers," and "Longicorn ID: Tool for diagnosing cerambycoid families, subfamilies, and tribes") are identification tools developed for port identifiers via competitive grant funding from the US Department of Agriculture - Animal and Plant Health Inspection Service (USDA-APHIS).