Systematics and biogeography of the subfamily Tillinae (Coleoptera: Cleridae) in the New World

by

Alan Fernando Burke

B.A., Autonomous University of Puebla, Mexico, 2001
M.S., Autonomous University of Chapingo, Mexico, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2017

Abstract

The subfamily Tillinae is composed of approximately 700 species with a cosmopolitan distribution. In the New World, the group is composed of 164 species classified in 12 genera. Tillinids are generalist predators of other insects but there is some ecological specificity among related species (i.e. predation on bark and wood-boring beetles). The systematics and biogeography of the subfamily have never been studied. Several genera inhabiting the New World have never been revised, a number of species in the group were described more than 50 years ago, and many of those descriptions were inadequate. Consequently, I present here the first systematic and biogeographic study of the Tillinae in the New World. First, a revision of the New World Tillinae, excluding the species-rich *Cymatodera* Gray is presented. The diagnosis and redescription of 26 species from 11 of the 12 tillinid genera from the New World are given; a new synonym, keys to genera and species, and distribution maps for all the genera treated here are also given. Collection data for all species examined is presented. A new genus was described based on this work in a separate publication. Second, a phylogenetic analysis based on 91 morphological characters and a molecular phylogenetic study based on the analysis of three loci, 16S rDNA, COI and 28S rDNA, for 89 taxa in 37 genera is presented. Results were compared with previous classifications at the subfamily level. Results are generally consistent, recovering Tillinae as a derived and monophyletic group; Old World tillinids were found to be basal groups and sister to New World Tillinae; the New World genus *Onychotillus* was found to be sister to remaining New World Tillinae; the small genera *Barrotillus, Callotillus, Monophylla* and *Neocallotillus* were recovered as basal lineages within the New World Tillinae with intergeneric relations not fully resolved; and the species-rich *Cymatodera* was found to be a paraphyletic group by the inclusion of the genera *Araeodontia*, *Bogcia*, *Cymatoderella* and *Lecontella*. A

phylogeny was also constructed based on a concatenated molecular + morphology dataset; the topology obtained from this analysis is generally consistent with the molecular- and morphology-based phylogenies, separately. Finally, a hypothesis of the historical biogeography of *Cymatodera*, the most species-rich genus in the subfamily Tillinae, is presented. The genus is endemic to, but broadly distributed, in the New World. The principal aim of the study was to infer the age of origin of the group. Hypotheses regarding the center of origin, patterns of distribution, and putative processes that led to the widespread distribution of this group are presented. A phylogenetic analysis of 50 New World tillinid species was constructed using the markers 16S rDNA, COI, and 28S rDNA. A relaxed molecular clock calibrated with three secondary dates derived from other time-calibrated phylogenies is presented. Biogeographic processes were studied using a Bayesian Binary Markov Chain Monte Carlo analysis in the software Reconstruct Ancestral State in Phylogenies. Results obtained here indicate that *Cymatodera* emerged approximately 71.5 MYA during the mid-Cretaceous in what is now southwestern USA and northern Mexico. Two major dispersal events occurred during the evolution of the *Cymatodera* lineage, the first, an eastern migration process, and the second, a southern migration event, the latter route had a greater impact on the diversification of the group. Overall, this research provides a solid foundation for studying the systematics and biogeography of the world Tillinae. Species with recent shared ancestry tend to have similar functional traits for exploiting similar resources. A robust phylogenetic analysis can help elucidate prey preferences or other biological traits for species whose biology is poorly known. This study will also serve as a foundation to investigate broader evolutionary aspects of the subfamily, such as predator-prey associations, mimicry, and the emergence and diversification of pheromone reception, one of the most interesting aspects within the evolutionary history of the group.

Systematics and biogeography of the subfamily Tillinae (Coleoptera: Cleridae) in the New World

by

Alan Fernando Burke

B.A., Autonomous University of Puebla, Mexico, 2001
M.S., Autonomous University of Chapingo, Mexico, 2010

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2017

Approved by:

Major Professor
Gregory Zolnerowich

Abstract

The subfamily Tillinae is composed of approximately 700 species with a cosmopolitan distribution. In the New World, the group is composed of 164 species classified in 12 genera. Tillinids are generalist predators of other insects but there is some ecological specificity among related species (i.e. predation on bark and wood-boring beetles). The systematics and biogeography of the subfamily have never been studied. Several genera inhabiting the New World have never been revised, a number of species in the group were described more than 50 years ago, and many of those descriptions were inadequate. Consequently, I present here the first systematic and biogeographic study of the Tillinae in the New World. First, a revision of the New World Tillinae, excluding the species-rich *Cymatodera* Gray is presented. The diagnosis and redescription of 26 species from 11 of the 12 tillinid genera from the New World are given; a new synonym, keys to genera and species, and distribution maps for all the genera treated here are also given. Collection data for all species examined is presented. A new genus was described based on this work in a separate publication. Second, a phylogenetic analysis based on 91 morphological characters and a molecular phylogenetic study based on the analysis of three loci, 16S rDNA, COI and 28S rDNA, for 89 taxa in 37 genera is presented. Results were compared with previous classifications at the subfamily level. Results are generally consistent, recovering Tillinae as a derived and monophyletic group; Old World tillinids were found to be basal groups and sister to New World Tillinae; the New World genus *Onychotillus* was found to be sister to remaining New World Tillinae; the small genera *Barrotillus, Callotillus, Monophylla* and *Neocallotillus* were recovered as basal lineages within the New World Tillinae with intergeneric relations not fully resolved; and the species-rich *Cymatodera* was found to be a paraphyletic group by the inclusion of the genera *Araeodontia*, *Bogcia*, *Cymatoderella* and *Lecontella*. A

phylogeny was also constructed based on a concatenated molecular + morphology dataset; the topology obtained from this analysis is generally consistent with the molecular- and morphology-based phylogenies, separately. Finally, a hypothesis of the historical biogeography of *Cymatodera*, the most species-rich genus in the subfamily Tillinae, is presented. The genus is endemic to, but broadly distributed, in the New World. The principal aim of the study was to infer the age of origin of the group. Hypotheses regarding the center of origin, patterns of distribution, and putative processes that led to the widespread distribution of this group are presented. A phylogenetic analysis of 50 New World tillinid species was constructed using the markers 16S rDNA, COI, and 28S rDNA. A relaxed molecular clock calibrated with three secondary dates derived from other time-calibrated phylogenies is presented. Biogeographic processes were studied using a Bayesian Binary Markov Chain Monte Carlo analysis in the software Reconstruct Ancestral State in Phylogenies. Results obtained here indicate that *Cymatodera* emerged approximately 71.5 MYA during the mid-Cretaceous in what is now southwestern USA and northern Mexico. Two major dispersal events occurred during the evolution of the *Cymatodera* lineage, the first, an eastern migration process, and the second, a southern migration event, the latter route had a greater impact on the diversification of the group. Overall, this research provides a solid foundation for studying the systematics and biogeography of the world Tillinae. Species with recent shared ancestry tend to have similar functional traits for exploiting similar resources. A robust phylogenetic analysis can help elucidate prey preferences or other biological traits for species whose biology is poorly known. This study will also serve as a foundation to investigate broader evolutionary aspects of the subfamily, such as predator-prey associations, mimicry, and the emergence and diversification of pheromone reception, one of the most interesting aspects within the evolutionary history of the group.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I am especially thankful to Dr. Gregory Zolnerowich for being a great mentor to me. His constant support and enthusiasm gave me the opportunity to develop myself as a scientist. Dr. Zolnerowich is the most approachable person, always keen to discuss new ideas. He was always willing to help me during rough spots, both professionally and personally. I am greatly impressed how Dr. Zolnerowich always has time to help and guide students. I have learned a great deal under his tutelage. Lastly, but not less important, Dr. Greg is one of the best fishing companions I have ever had; his fishing knowledge is almost comparable to his experience as a professor.

I am also thankful to the committee members. Dr. Carolyn Ferguson, for encouraging and giving me ideas during the development of my research project and during the courses I took under her instruction. Dr. Yooseong Park, for allowing me to work in his laboratory, day and night, and all the useful advices and comments during the preparation of the molecular sections of Chapter 4 and 5 of this research. And Dr. John Ruberson who always had time for listening my doubts, ideas and thoughts, and continuously willing to provide valuable advice, for writing all those recommendation letters, and find a solution to any problem that came about during my studies.

I want to express my gratitude to all the individuals and institutions for the loan of material, and particularly to my friend Jacques Rifkind for his important contributions and advices during the preparation of Chapter 2, Jacques was always more than willing to share his knowledge on the checkered beetles of the New World. To Weston Opitz for his friendship and support throughout the development of this research. I am also thankful to John Leavengood, for co-authoring publications emerged from this study, John was always present and willing to discuss interesting topics about the systematics of beetles, and making me laugh during difficult times.

Finally, I also want to thank the Department of Entomology, Kansas State University, for the financial support, the Kansas State University Open Access Publishing Fund for the economical help given for the publication of a number of articles emanated from this research, and the Mexican National Council for Science and Technology (CONACyT), for the funding that made possible to undergo my doctoral studies.

Dedication

I want to dedicate my work to my mother, I cannot thank her enough for all her love and encouragement over all the years she was next to me. I also want to dedicate my work to my wife, Lorena; living with me hasn't been very easy, especially not during those harsh moments, and although the difficulties we have gone through, she has always been next to me, unconditionally.

Chapter 1 - Introduction

1.1 The infraorder Cucujiformia Lameere, 1938, and the superfamily Cleroidea Latreille, 1802

The infraorder Cucujiformia includes the vast majority of herbivorous beetles. The group currently includes the superfamilies Chrysomeloidea, Cleroidea, Cucujoidea, Curculionoidea, Lymexyloidea, and Tenebrionoidea. Lameere (1938) was the first to propose this taxonomic grouping. Crowson (1955) initially included the Bostrichiformia in his Cucujiformia series. Lawrence & Newton (1995) redefined this arrangement to the current classification. The superfamily Cleroidea was first established in the larval system developed by Böving & Craighead (1931a), in which the families Trogossitidae (Clavicornia) and Cleridae-Melyridae (Malacodermata) were grouped together. In addition to those families, the authors included the Dermestidae, Cisidae, Catogenidae (now separated as Cucujidae and Passandridae) and the Bothrideridae (now separated into Bothrideridae and Colydiidae). Interestingly, the striking similarities between larvae of Trogossitidae and Cleridae-Melyridae were overlooked by the entomologists of that time. Sharp and Muir (1912) were the first to speculate about possible relationships between adult forms of Trogossitidae and Cleridae-Melyridae. Subsequently, Crowson (1955, 1964) redefined the superfamily Cleroidea in a new sense by removing Bothrideridae, Cisidae, Colydiidae, Cucujidae, Dermestidae and Passandridae from Cleroidea. In the most recent classification of the Cleroidea of the world by Lawrence & Newton (1995), the authors indicated that the superfamily should be composed of Phloiophilidae, Trogossitidae, Chaetosomatidae, Cleridae, Acanthocnemidae, Phycosecidae, Prionoceridae and Melyridae.

Other authors (Majer, 1994; 1995; Kolibàč, 1992; 1997) added the families Attalomidae, Dasytidae, Gietellidae, Malachidae, Mauroniscidae, Metaxinidae and Thanerocleridae: however, this classification has not been widely accepted.

1.2 The family Cleridae Latreille, 1804

Cleridae is the second largest cleroid family after Melyridae. The group is mainly composed of individuals with predatory habits, but some saprophagous and polliniphagous species can be found. The latest classification of the Cleridae includes 13 subfamilies. Adults of Cleridae are readily distinguished from other members of the superfamily by the presence of a postgular plate or postgular process (see Fig. 2.6 A-B from Chapter 2) and the laterolacinia may be reduced to a lacinial inflection (Opitz, 2010). Larvae of Cleridae are distinguished from other families of Cleroidea by the strongly prognathus mouthparts with transverse stipes and the elongate gular region, which is heavily sclerotized at the epicranial region (Foster & Lawrence, 1991). Larval stages are also active predators on a wide variety of insects. Clerid species are associated with woody and hervaceous plants and can be found on or under the bark, in tunnels of wood and cone borers, in galls, or on plant foliage. Several species of the genera *Enoclerus* and *Thanasimus* are important predators of various bark and ambrosia beetle species in coniferous forests. Adults of different subfamilies, especially Clerinae, are found on flowers, where they feed on pollen. Members of the subfamily Tillinae are strongly attracted to light. The genus *Necrobia* is composed of scavenger species.

The first significant taxonomic treatments on Cleridae were done by Spinola (1841, 1844a, b) and Klug (1842), which incorporated species descriptions numbering in the hundreds. Later

on, much descriptive work was done by LeConte, Gorham, Horn, Melsheimer, and Chevrolat, coleopterists who contributed to the knowledge of this family through the end of the 19th century. The modern classification of the Cleridae is fundamentally based on the work of Corporaal (1950) and Crowson (1964). Corporaal published the first edition of the world clerid catalog in which he proposed a seven-subfamily system to accommodate approximately 3,300 species in 290 genera. Much of the work done by Corporaal remains unrevised and some authors have questioned the validity of several genera and species within Corporaal's catalog. However, this is the most comprehensive work to date and remains a highly useful reference for further systematic works. This classification is based largely on the morphology of the antenna, elytra, and abdominal characters. Considering the highly homoplastic nature of antennal morphology, significant changes have been made in recent years to Corporaal's classification.

Barr (1962), in a non-revisionary work, recommended the use of only two subfamilies within Cleridae, with each of those subdivided into tribes. These subfamilies are the Clerinae, represented by the tribes Tillini, Phyllobaenini, Thaneroclerini and Clerini, and the Korynetinae, characterized by the tribes Epiphloeini, Enopliini and Korynetini. Opitz (2002) commented that the current assignment of supraspecific groups in Cleridae was highly subjective and often lacked sufficient morphological, molecular, and zoogeographical bases. Thus, he considered a classification in which all of the tribes listed by Barr (1962) should be recognized as subfamilies, and the Tarsosteninae to be added as a subfamily pending further work (Kolibàč, 1997; Gerstmeier et al., 1999).

Morphological (Kolibàč, 1992; Opitz, 2010) and molecular (Gunter et al., 2013) classifications of the Cleridae have been proposed, with partial disagreement in terms of the phylogenetic position of a number of subfamilies. In spite of such disagreement in the higher classification of the Cleridae, the morphology-based phylogenies presented by Kolibàč (1992) and Opitz (2010) are relatively congruent with Gunter's molecular-based classification, with the exception of the position of Anthicoclerinae. Currently, there is general consensus in terms of the taxonomic state of the family. Thirteen subfamilies are recognized: Clerinae, Enopliinae, Epiphloeinae, Hydnocerinae, Korynetinae, Tarsosteninae, Thaneroclerinae, Tillinae, Neorthopleurinae, Tarsosteninae, Peloniinae and Anthilcolerinae (Opitz, 2010; Gunter et al., 2013).

Böving & Craighead (1931a, b) described various clerid larvae of the world as they were known at that time. Despite this valuable information, little work has been done concerning clerid larvae since then. A few authors, such as Foster, have worked on the larvae of Thaneroclerinae (1976a), the larvae of Tillinae (1976b) and the larval stages of *Trichodes* (1976c). No comprehensive revisionary work has focused on larval clerids and their potential use in inferring phylogenetic relationships has not been studied further.

Relatively little molecular work has been done with the Cleridae compared to other beetle groups, except for a few studies on widely known predaceous members due to their significance as predators of economically important bark and ambrosia beetles. However, most of these studies were only at an intraspecific level. For example, Schrey et al. (2005) determined the levels of genetic differentiation and the amount of gene flow among different populations

throughout the native rage of *Thanasimus dubius* (Fabricius), a predator of various bark beetles in temperate forests. Molecular data have proven to be extremely useful in determining phylogenetic relationships in many organisms. Recently, Gunter et al. (2013) developed a phylogenetic analysis of the world Cleridae based on both mitochondrial and nuclear DNA; this phylogenetic hypothesis provides a solid framework for resolving other taxonomic issues within the classification of the Cleridae.

1.3 The subfamily Tillinae Leach, 1815

The subfamily Tillinae is the second largest subfamily of checkered beetles after Clerinae. Tillinids can be distinguished from other clerid subfamilies by the fusion of the procryptosternum with the pronotal extension, a synapomorphic character that distinguishes this group of checkered beetles from remaining Cleridae (see Fig. 2.6 C-D from Chapter 2). Secondary characters that readily distinguish Tillinae from other congeners are: body oblong, narrow to robust; mouthparts most commonly prognathous; eyes most often coarsely faceted; antennae composed of 10 to 11 antennomeres; pronotum campanulate to bisinuate; procoxal cavities closed posteriorly (intercoxal process joins the pronotal projections); one longitudinal carina on the anterior portion of each metacoxal cavity; dorsolateral ridge absent; tarsal formula 5-5-5.

Most Tillinae are generalist predators of various groups of insects, but it is suspected that there is some specificity at the ecological level (i.e. predation almost exclusively on wood-boring beetles). Members of the Tillinae are commonly associated with lignicolous environments. Coarsely faceted eyes in several species indicate nocturnal activity. Beeson (1926) stated that

Cylidroctenus chalybaeum (Westwood) has been associated with the tree *Dicterocarpus turbinatus* Gaertner, infested with the wood borer *Heterobostrichus aequalis* (Waterhouse). Gardener (1937) mentioned that *Tillus succintus* Chevrolat has been reared from the bamboo plant *Dendrocalmus strictus* (Roxburgh) Nees infested with bostrichid species. A comprehensive review of the predatory activity of the genus *Lecontella* Wolcott & Chapin is given by Mawdsley (2002). *Cymatodera bicolor* (Say) has been observed to prey on the cerambycid beetle *Chyptophorus verrucosus* (Olivier) feeding on *Cornus florida* L. (Opitz, 2010). A number of *Cymatodera* species are known to prey on economically important insect pests, such as the naval orangeworm, *Amyelois transitella* Walker in *Juglas regia* L. (Michelbacher & Davis, 1961), and the galls of the cynipid *Disholcapis mamma* Kinsey found on several species of *Quercus* (Balduf, 1935). Burke et al. (2011) identified a number of *Cymatodera* species attracted to bark beetle aggregation pheromones in forest stands affected by *Dendroctonus* and *Ips* species in central and south Mexico. Due to the coarsely faceted nature of their eyes, a number of Tillinae species are nocturnal or crepuscular. Rifkind (2006) mentioned that some *Cymatodera* species are capable of stridulating. This behavior may be the result of auditory Batesian mimicry. Rifkind hypothesized that many *Cymatodera* species resemble nocturnal mutillid wasps that, when threatened, emit a stridulatory sound before stinging its attacker, a behavior known as deimatic stridulation. Optiz (2010), citing Rifkind's observations, made further comments, stating that the perpendicular carina observed on the metacoxal cavities, a character observed in many tillinid species (see Fig. 3.12-D from Chapter 3), in conjunction with the metacoxal transverse carinae, when rubbing against each other, may function as the plectrum point capable of producing such stridulatory sounds.

Tillinae has a global distribution; however, the greatest species richness is found in the sub-temperate to subtropical, thorny and scrub forests of North America, and the tropical regions of Africa and Madagascar. In his *Coleopterum Catalogus Suplementa*, Corporaal (1950) recorded 51 genera with approximately 521 species worldwide. Opitz (2010) included 543 described species in 67 genera. Presently, the subfamily is composed of almost 700 species classified in 68 genera (Corporaal, 1950; Opitz, 2010; Burke et al., 2015). In the New World, Tillinae is distributed from south Canada to South America (see Fig. 2.21-A from Chapter 2).

In the New World, Tillinae is composed of 12 genera and approximately 160 species (Corporaal, 1950; Opitz, 2010; Burke et al., 2015; Burke & Zolnerowich, 2016). Much of the confusion regarding the systematics of the New World Tillinae comes from *Cymatodera* Gray, the most speciose genus of New World tillinids. This genus is composed of approximately 130 species (Burke et al., 2015) but many species are yet to be described and several synonyms exist. *Cymatodera* is restricted to the New World, with a high concentration of species found in southwestern USA and northern Mexico, and some representatives extending to South America. Undescribed species are frequently found, especially from Mexico and Central America. Overall, *Cymatodera* is in dire need of revisionary work and there is particular need in defining the morphological characters that define the group. In addition to this, *Cymatodera* is closely related to the smaller genera *Lecontella* Wolcott & Chapin, *Bogcia* Barr, and *Araeodontia* Barr, making difficult the separation of these genera. Finally, the rarity of many specimens and the lack of adequate study material and comparisons with type material makes the study of the group more difficult. The lack of hypothesized phylogenetic relationships and the considerable amount of variation within this genus hinder a better understanding and proper classification of the Tillinae

of the New World. Remaining genera within the Tillinae in the New World are relatively small genera composed of no more than six species.

Overall, the subfamily Tillinae is in dire need of revisionary work, and there is critical necessity to explore and evaluate morphological characters that properly define and delimit a number of genera and species within the group. Much of the confusion regarding the systematics of the Tillinae comes from the large genera *Cladiscus* Chevrolat, *Cylidrus* Latreille, *Cymatodera* Gray, *Pallenis* Laporte de Castelnau, *Stenocylidrus* Spinola, and *Tillus* Olivier. These genera alone represent approximately 50% of the total number of described species, they were erected during the eighteenth and nineteenth centuries, and have not been revised since. Other groups within the Tillinae are relatively small genera that include roughly 300 species. Finally, little is known about the biology, ecology, and biogeography of these beetles, and several species are seldom mentioned in the literature.

This study proposes a robust phylogenetic hypothesis for the New World Tillinae and provides revisions of small genera within the New World Tillinae, information that has not been updated in more than 50 years. Presently, there are no comprehensive keys to genera and species. Several checkered beetle species are commonly found in bark and ambrosia beetle and other secondary boring insect outbreaks (Mawdesly, 2002). The appropriate use of the checkered beetles as biological control agents heavily relies on the proper identification of these beetles.

Finally, the biogeographic analysis given here presents a hypothesis about the center of origin and the distribution patterns the speciose genus *Cymatodera* has undergone. This study

serves as a basis for future research related to the ecology and biology of other New World

Tillinae genera and may also serve as a foundation for similar studies for remaining clerid

subfamilies.

2. References

Balduf, W. V. (1935) Cleridae. Checkered Beetles. pp 109-111. *In*: W.V. Balduf (Ed.), The

    bionomics of entomophagous Coleoptera. John S. Swift Co. New York. 220 pp.

Barr, W. F. (1962) A key to the genera and a classification of the North American Cleridae

    (Coleoptera). The Colleopterists Bulletin 16: 121-127.

Beeson, C. F. C. (1926) On some Indian Cleridae (Coleoptera (Part II)) Note on the biology of

    the Cleridae. The Indian Forest Records 12(8): 217-231.

Böving, A. G., and F. C. Craighead (1931a) An illustrated synopsis of the principal larval forms

    of the order Coleoptera. Entomológica Americana 11(1): 1-80.

Böving, A. G., and F. C. Craighead (1931b) An illustrated synopsis of the principal larval forms

    of the order Coleoptera. Entomológica Americana 11(4): 275-351.

Burke, A. F., D. Cibrián-Tovar, C. Llanderal-Cázares, A. Plascencia-Gonzáles and I. López-

    Pérez (2011) Adiciones y aportaciones para el género *Enoclerus* Gahan (coleoptera:

cleridae) en bosques de clima templado de México. Acta Zoologica Mexicana 27(1): 145-167.

Burke, A. F., J. M. Leavengood Jr. and G. Zolnerowich (2015) A checklist of the New World species of Tillinae (Coleoptera: Cleridae), with an illustrated key to genera and new country records. Zookeys 4059(1): 1-39.

Burke, A. F. and G. Zolnerowich (2016) Taxonomic revision of the New World genus *Callotillus* Wolcott (Cleridae, Tillinae), with the description of the new genus *Neocallotillus*, and an illustrated key of identification to species. ZooKeys 617: 65–89.

Corporaal, J. B. (1950) Cleridae. In W. D. Hincks (editor) Coleopterum Catalogus Suplementa. Pars 23 (Editio secunda) Gravenhage. 373 pp

Crowson, R. A. (1955) The natural classification of the families of Coleoptera. Nathaniel Lloyd and Co. Ltd, London, 187 pp.

Crowson, R. A. (1964) A review of the classification of Cleridae (Coleoptera) with description of two new genera of Peltidae and of several new larval types. Transactions of the Royal Entomological Society of London 116: 275: 5-649.

Foster, D. E. (1976a) A review of the North American Tilliniae larvae (Coleoptera: Cleridae). University of Idaho, Department of Entomology Anniversary Publication 19: 133-138.

Foster, D. E. (1976b) North American Thaneroclerinae larvae (Coleoptera: Cleridae) Coleopterists Bulletin 30(1): 75-80.

Foster, D. E. (1976c) Revision of North American *Trichodes* (Herbst) (Coleoptera: Cleridae). Special Publications of the Museum of Texas Tech University 11: 1-86.

Foster, D. E. and J. F. Lawrence (1991) Cleridae. Including Corynetidae, Korynetidmichelae. In F. W. Stehr (editor), Immature Insects Vol. 2. Kendall/Hunt Publishing, USA. 975 pp.

Gardener, J. C. M. (1937) Immature stages of Indian Coleoptera (21) Cleridae. Indian Forest Record (New Series) 3(2): 31-47.

Gerstmeier, R., J. Halperin, and V. Chekatunov (1999) An annotated list of Cleridae and Thanerocleridae (Coleoptera) of Israel. Phytoparasitica 27: 27-33.

Gunter, N. L., J. M. Leavengood, J. S. Bartlett, E. G. Chapman and S. L. Cameron (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera; Cleridae). Systematic Entomology 38(3): 626-636.

Klug, J. C. F. (1842) Versuch einer systematischen Bestimmung und Ausein-andertzung der Gatuggen und arten der Clerii. In Gerstmeier (1998) Checkered Beetles, Illustrated Key to the Cleridae of the Western Palearctic. Magraf Verlag. 258 pp.

Kolibàč, J. (1992) Revision of the Thanerocleridae n. stat. (Coleoptera: Cleridae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 65: 303-340.

Kolibàč, J. (1997) Classification of the subfamilies of Cleridae (Coleoptera: Cleroidea) Acta Musei Moraviae Scientia Naturales 81: 307-361.

Lameer, A. 1938. Evolution des Coleoptera. Bulletin Annales Societe Entomologique de Belgique 78: 355-362.

Lawrence, J. F. and A. F. Newton Jr. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, refereneces and data on family group names). *In* Pakulak S. A. and S. A. Slipinski (*eds.*): Biology, Phylogeny and Classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson, 779-1006.

Majer, K. (1994) Gietellidae, full family status for Melyridae: Gietellinae (Coleoptera: Cleroidea). Entom. Probl. 25(1): 65-72.

Majer, K. (1995) Revision of the family Mauroniscidae (Insecta: Coleoptera: Cleroidea). Ent. Abh. Mus. Tierkd. Dresden 57(3): 57-89.

Mawdsley, J. R. (2002) Comparative ecology of the genus *Lecontella* Wolcott and Chapin (Coleoptera: Cleridae: Tillinae), with notes on chemically defended species of the beetle family Cleridae. Proceedings of the Entomological Society of Washington 104(1), 164-167.

Michelbacher, A.E. & Davis, C.S. (1961) The navel orangeworm in northern California. Journal of Economic Entomology, 54, 559–562.

Opitz, W. (2002) Family 73. Cleridae. p. 267-280. *In*: R. H. Arnett, Jr., M. C. Thomas, P. E. Skelley, and J. H. Frank (eds.). American Beetles, Vol. 2. CRC Press; Boca Raton, FL. 861 pp.

Opitz, W. (2010) Classification, natural history, Phylogeny and subfamily composition of the Cleridae and generic content of the subfamilies. Entomologica Basiliensia et Collectionis Frey. 32: 31-128.

Rifkind, J. (2006) Stridulation in *Cymatodera* Gray, 1832 (Coleoptera: Cleridae). The Pan-Pacific Entomologist 82(2): 258– 261.

Schrey, N., J. Reeve and F. Anderson. (2005) Mitochondrial DNA analysis of the bark predator *Thanasimus dubius* L. (Coleoptera: Cleridae) reveals regional genetic differentiation. Molecular Ecology 14(11) 3317-3324.

Sharp, D. and F. Muir (1912) The comparative anatomy of the male genitalia tube in Coleoptera. Transactions of the Entomological Society of London 3: 477-642.

Spinola, M. (1841) Monographie des Trediles. Revue Zologique, par La Societe Cuvierienne. 4: 70-76.

Spinola, M. (1844a) Essai monographique sur les clerites. Tome premier. Genes: Freres

    Ponthenier.

Spinola, M. (1844b) Essai monographique sur les clerites. Tome second. Genes: Freres

    Ponthenier.

Chapter 2 - Taxonomic revision of the New World Tillinae Leach (Coleoptera: Cleridae), excluding the genus *Cymatodera* Gray

Abstract

The New World genera of Tillinae Leach *sensu lato*, except *Cymatodera* Gray, are revised. A diagnosis and redescription of the species of *Araeodontia* Barr, *Barrotillus* Rifkind, *Bogcia* Barr, *Callotillus* Wolcott, *Cylidrus* Latreille, *Cymatoderella* Barr, *Lecontella* Wolcott & Chapin, *Monophylla* Spinola, *Neocallotillus* Burke and *Onychotillus* Chapin are presented. *Bogcia oaxacae* Barr is proposed as a junior synonym of *Bogcia disjuncta* Barr. The following species are redescribed: *Araeodontia isabellae* (Wolcott), *A. marginallis* Barr, *A. peninsularis* (Schaeffer), *Barrotillus kropotkini* Rifkind, *Bogcia disjuncta* Barr, *Callotillus bahamensis* Vaurie, *C. eburneocinctus* Wolcott, *Cylidrus abdominalis* Klug, *Cymatoderella collaris* (Spinola), *C. morula* Rifkind, *C. patagoniae* (Knull), *Lecontella brunnea* (Spinola), *L. gnara* Wolcott, *L. striatopunctata* (Chevrolat), *Monophylla californica* (Fall), *M. pallipes* Schaeffer, *M. terminata* (Say), *Neocallotillus elegans* (Erichson), *N. intricatus* Wolcott, *Onychotillus vittatus* Chapin, and *O. cubana* De Zayas. Transcriptions of the original descriptions of *Araeodontia picipennis* Barr, *Bostrichoclerus bicornis* Van Dyke, *Neocallotillus crusoe* (Wolcott) and *Monophylla cinctipennis* (Chevrolat) are presented. Collection data are provided for all species revised. Keys to New World genera and species are given. Taxonomic characters of relevant importance are presented and discussed, and distribution maps for all New World genera are given.

1. Introduction

1.1 Classification and species numbers of the family Cleridae and the subfamily Tillinae

Cleridae is the second largest family within the superfamily Cleroidea. Clerids, commonly known as checkered beetles, can be distinguished from other cleroid beetles based on the presence of a postgular plate or postgular process, members of other cleroid families do not possess that character state (Fig. 2.6 A-B). The current classification of Cleridae divides the family in 13 subfamilies (Opitz, 2010; Gunter et al., 2013). Tillinae, the second largest subfamily within Cleridae, was originally erected by Leach (1815). Tillinae has a cosmopolitan distribution with approximately 700 described species in 69 genera (Corporaal, 1950; Gerstmeier and Weiss, 2009; Gerstmeier and Eberle, 2011; Opitz, 2010). In the New World, Tillinae is distributed from southern Canada to central South America, including the West Indies (Fig. 2.21 A-L), and is represented by 12 genera: *Araeodontia* Barr, *Barrotillus* Rifkind, *Bogcia* Barr, *Bostrichoclerus* Van Dyke, *Callotillus* Wolcott, *Cylidrus* Latreille, *Cymatodera* Gray, *Cymatoderella* Barr, *Lecontella* Wolcott & Chapin, *Monophylla* Spinola, *Neocallotillus* n. gen. Burke, and *Onychotillus* Chapin. *Cymatodera* is the most speciose genus of all clerid beetles in the New World, and by itself, represents almost 20% of all described Tillinae species. The taxonomic status of many *Cymatodera* species is uncertain and the genus as a whole has never been revised. A revision of the genus would be difficult because many species are poorly represented in public and private collections, numerous species are rare in nature, and comparisons with types are particularly difficult due to the rarity and unavailability of this material. The vast majority of *Cymatodera* species inhabit the USA and Mexico, with some species extending to Central America and a few into South America (Fig. 2.21-G). Due to the large number of *Cymatodera* species, this genus is excluded from this revisionary work. The rest of the genera within the New

16

World are small groups with less than 10 described species each, and with three monotypic genera: *Barrotillus* Rifkind, *Bogcia* Barr, and *Bostrichoclerus* Van Dyke.

1.2 Biology of the subfamily Tillinae

The natural history of the Tillinae is largely unknown, however, as a general rule, they are generalist predators of various groups of insects. Tillinids are commonly found inhabiting lignicolous environments. Coarsely faceted eyes in several species indicate nocturnal activity and most genera are attracted to light. A number of species in the genus *Cymatodera* Gray have been observed feeding on wood-boring beetles (Burke et al., 2011), solitary and gall wasps (Michelbacher and Davis, 1961), the larvae of numerous lepidopterous species (Balduf, 1935), and aphids and scales (Opitz, 2010); many of these insects are considered sanitary pests of moderate to minor importance. *Cymatodera bicolor* (Say) has been observed feeding on the cerambycid *Chrysophorus verrucosus* (Olivier) a wood boring beetle found inside the Floridian dogwood *Cornus florida* L. (Opitz, 2010). In the Old World, *Tillus succintus* Spinola has been reared in the bamboo plant *Dendrocalamus stricta* Gaertner (Gardener, 1937); Beeson (1926) indicated that *Cylidroctenus chalybaeum* (Westwood) has been observed to prey on the bostrichid beetle *Heterobostrichus aequalis* (Waterhouse).

1.3 Taxonomy of the subfamily Tillinae

Historically, the description and classification of species within Tillinae have been based on external morphological characters, primarily using antennal gestalt, elytral configuration, pygidial shape, and overall integument color. Many species within the New World Tillinae are difficult to identify due to intraspecific morphological variation, a situation particularly common

for the speciose *Cymatodera,* where more than 130 species have been described (Burke et al, 2015), with many undescribed species. Most of the species descriptions and keys to species are based on one or a few specimens, and intraspecific variation has not been examined in detail. Six revisionary works (Barr, 1952a; Burke & Zolnerowich, 2016, Gerstmeier and Seintner, 2013; Gerstmeier and Weiss, 2009; Gerstmeier and Huesmann, 2004; Solervicens, 1996) pertaining to Tillinae have been conducted, and only those of Barr (1952a, b) and Burke & Zolnerowich (2016) addressed tillinid species inhabiting the New World. Corporaal (1950) published the first comprehensive world catalogue of the Cleridae; in this work, he provided many biographical references. Corporaal's catalogue is outdated and many species have been described since then. In the New World, very few taxonomic studies of the Tillinae have been conducted, with authors such as Barr (1947, 1950a, 1950b, 1952a, 1952b, 1962, 1972, 1975, 1978), Chapin (1927, 1945), Knull (1934, 1940, 1946, 1951) , Rifkind (1993a, 1993b, 1995, 1996, 2015), Schaeffer (1904, 1905, 1908, 1917), and Wolcott (1909, 1910, 1911, 1921, 1923, 1927, 1947) being the principal contributors to the current knowledge of the subfamily in the Americas.

The work presented here is intended to be the first part of a series of revisionary works which will include all Tillinae members in the New World. The Tillinae as a whole is in dire need of taxonomic revision. The majority of New World tillinid genera have not been revised, many species remain new to science, and generic and specific limits are currently a taxonomic conundrum. In this analysis, all lesser groups within the New World Tillinae are revised. Due to the complex taxonomic status and the number of species comprising *Cymatodera*, this genus will be revised separately in future works.

2. Material and methods

2.1 Taxonomic sampling

Twenty-six species, representing 11 of the 12 tillinid genera inhabiting the New World are here treated. *Cylidrus abdominalis* Klug, a species established in Brazil by Corporaal (1950), and very likely an introduction from the Old World (Gorham, 1876), is redescribed. Material from the monotypic species *Bostrichoclerus bicornis* Van Dyke and *Araeodontia picipennis* Barr, *Neocallotillus crusoe* Wolcott, and *Monophylla cinctipennis* (Chevrolat) were not available during the analysis, but the original descriptions are transcribed below.

If more than one male per species was available, and upon permission from the corresponding repository collections or private owners, male genitalia were extracted and dissected from selected specimens. Genitalia extraction and dissection procedures are similar to those outlined by Ekis (1977). Most morphological terminology follows the work of Ekis (1977), Rifkind (1993b), and Opitz (2010). Specimens were examined with a Leica MZ7.5 stereomicroscope. Images were taken and measured using a Leica DFC 500 digital camera, and stacked using the software Zerene Stacker V. 1.04. Scanning electron photographs were taken using a Hitachi 3500N variable pressure scanning electron microscope.

2.2 Collection repositories of specimens examined

The following codens refer to public or private collections from which material was obtained and examined for this revisionary work: American Museum of Natural History, Washington D.C. (AMNH); University of Arizona Insect Collection, Tucson, Arizona (UAIC); British Museum of Natural History Collection, London, UK (BMNH); California Academy of

Sciences Insect Collection, Sacramento, CA (CASC); Colección de Insectos de la Universidad Autónoma de Morelos, Cuernavaca, Morelos (UAMC); Colección Nacional de Insectos UNAM, Distrito Federal, México (CNIN); Colorado State University Insect Collection, Fort Collins, Colorado (CSUC); Field Museum of Natural History Collection, Chicago, IL (FMNH); Florida State Collection of Arthropods, Gainesville, FL (FSCA); Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBIO); Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB); Jacques Rifkind Collection, Valley Village, CA (JNRC); James E. Wappes Collection, San Antonio, TX (JEWC); Kansas State University Museum of Entomological and Prairie Arthropod Research Collection, Manhattan, KS (KSUC); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Natural History Museum of Los Angeles, California (LACM); Ohio State University Collection, Columbus, Ohio (OSUC); Robert H. Turnbow Collection, Enterprise, AL (RHTC); Texas A&M Insect Collection, College Station, TX (TAMU); Università di Firenze Collezione, Florence, Italy (UFBI); University of Arizona Insect Collection, Tucson, AZ (UAIC); University of California, Essig Museum of Entomology, California, Berkeley (EMEC); University of Georgia Insect Collection, Athens, GA (UGCA); University of Kansas, Snow Entomological Museum, Lawrence, KS (SEMC); Utah State University Collection (USUC), Weston Opitz Collection, Salina, KS (WOPC), William F. Barr Museum, University of Idaho, Moscow, ID (WFBM).

3. Systematics

Tillinae Leach, 1815

Type genus: *Tillus* Oliver, 1790.

Synonyms: *Tilloides* Spinola 1841 (pars) Rev. Zool. IV, p. 71; *Cleroides* Spinola 1844 (pars) Clérites I, p. 48; Cleridae Desmarest 1860 (pars) in Chenu; Encycl. d'Hist. Nat. Col. II, p 231; Tillini Lhde 1900, Ent. Zeitig., LXI, P. 6; Tillinae Schenkling 1906. Deutsche Ent. Zeitschr., p. 242.

Differential diagnosis: Tillinae is characterized by a fusion of the procryptosternum with the pronotal extension, a synapomorphic character that distinguishes this group of checkered beetles from other Cleridae (Fig. 2.6 C-D). Secondary characters that readily differentiate Tillinae from other clerid subfamilies are: body oblong, narrow to robust (2.1-2.5); eyes most often coarsely faceted (Fig. 2.12-A); antennae composed of 9 to 11 antennomeres (Figs. 2.8-2.11); pronotum campanulate to bisinuate (Figs. 2.5-E, 2.7 C-D); procoxal cavities closed posteriorly (Fig. 2.6-D), one longitudinal carina on the anterior portion of each metacoxal cavity (see Fig. 3.12-D from Chapter 3); dorsolateral ridge absent; and tarsal formula 5-5-5 (See Fig. 3.13-F from Chapter 3).

Redescription. Body form: slender to moderately robust, oblong, elongate to short. Pronotum: oblong, long, constricted posteriorly and sometimes anterior to frontal margin producing sinuous lateral margins. Size: 3 – 40 mm. Integument color: from black to piceous and light piceous with some metallic tones; elytral fasciae with predominant hues of brown, red and yellow. Head: large to very large; epistomal sutures parallel to feebly sinuate, well developed and extended posteriorly; clypeus well developed; eyes small to very large, always emarginate

anteriorly, slightly to coarsely faceted; gula broad, extended posteriorly, postgular process well developed, antennae composed of 9 to 11 antennomeres, from filiform to pectinate, with various degrees of serration observed, rarely capitate; mandibles well developed, stout; maxilla with well-developed laterolacinia, terminal labial palpi digitiform to cylindrical; terminal maxillary palpi cylindrical to securiform; labium developed. Thorax: pronotum ranging from long bisinuate to campanulate to subquadrate, dorsolateral carinae absent; abdominal sutures complete; prosternum longitudinally expanded anteriorly; prointercoxal process expanded anteriorly, closed internally and posteriorly; mesosternum cylindrical; most punctations on elytral disc bearing setae, punctations may reach apex or not; epipleural fold moderately to strongly developed and positioned laterally; anterior carina usually present; legs with tarsal pulvilli well developed, tarsal formula 5-5-5, fourth tarsomere never reduced; tarsal claw well developed, with one or two tarsal denticles; tibia and femora about the same length; tibial spur formula 2-2-2, 0-2-2, 2-1-1, or 0-0-0; tarsal pulvilliar formula 4-4-4, 4-4-3, 4-3-3, or 4-2-1; posterior wing venation well developed. Abdomen: Six visible ventrites; first ventrite almost always longitudinally carinate proximal to metacoxal cavities; sixth visible ventrite incised distally or not; spicular fork well developed, plates developed, intraspicular plate expanded anteriorly; aedeagus moderately to strongly sclerotized, phallobasic apodeme complete, phallobase acuminate distally; internal ovipositor elongate, usually as long as length of abdomen.

3.1 Key to New World genera.

1. Anterior coxal cavities opened internally and posteriorly (Fig. 2.6-C) .... **non-Tillinae Cleridae**

- Anterior coxal cavities closed internally and posteriorly (Fig. 2.6-D) .... **Tillinae** (2)

2 (1). Frons with a pair of prominent horns arising immediately above eyes .... *Bostrichoclerus*

- Frons without a pair of prominent horns 3

3 (2). Head conspicuously enlarged throughout its length, as wide as or wider than pronotum; body integument feebly clothed (Figs. 2.3-A and 2.5-D)..*Cylidrus*

- Head not conspicuously enlarged throughout its length (Fig. 2.3 B-F); body moderately to conspicuously clothed (Fig. 2.2 C-D).. 4

4 (3). Last antennomere flattened laterally, much longer than length of preceding antennomeres combined (Figs. 2.10 C-D and 2.4-D))... *Monophylla*

- Last antennomere not flattened laterally, not enlarged; length of last antennomere shorter than length of preceding antennomeres combined (Figs. 2.8 and 2.9) 5

5 (4). Antennae composed of 10 antennomeres (Fig. 2.11 A, C-D) 6

- Antennae composed of 11 antennomeres (Fig. 2.10 G-H) 7

6 (5). Slender species; elytra in lateral view flat (Figs. 2.13-A; 2.2 B-C) .... *Neocallotillus*

- Robust species; elytra in lateral view moderately to strongly compressed medially (Figs. 2.13-B; 2.2 D-E) ....*Callotillus*

7 (5). Antennomeres 4–10 strongly serrate (Fig. 2.8-C); length of specimens approximately 7 to 10 mm ....*Bogcia*

- Antennomeres 4-10 slightly to moderately serrate (Fig. 2.9 E-F and 2.10 E-H); length of specimens 2-40 mm 8

8 (7). Tarsal claws with one inner denticle ....*Onychotillus*

- Tarsal claws with two inner denticles (Fig. 2.7-B) 9

9 (8). Basal denticle of tarsal claw digitiform (Fig. 2.6-E)...***Araeodontia***

- Basal denticle of tarsal claw trigonal (Fig. 2.7-B)..10

10 (9). Elytral punctations coarse, elytral striae extending to apex of elytra (Fig. 2.7.G; 2.3 E-F)…………… ....***Lecontella***

- Elytral punctations moderately to very feebly impressed, elytral striae not extending to apex of elytra (Fig. 2.1 A-D) 11

11 (10). Elytral disc with a pair of pale, moderately oblique, elevated fasciae, and a pair of pale, elevated maculae (Fig. 2.1-E), small specimens ....***Barrotillus***

- Elytral disc without elevated fasciae or maculae, small to very large specimens (Fig. 2.1 D, F) 12

12 (11). Ommatidia finely faceted, small specimens (Fig. 2.6-F) ....***Cymatoderella***

- Ommatidia coarsely faceted, small to very large specimens (Fig. 2.12-A) ....
 ....***Cymatodera***

3.2 Araeodontia Barr, 1952a.

Type species: *Cymatodera peninsularis* (Schaeffer, 1904), original designation.

(Distribution shown in Fig. 2.21-B)

Differential diagnosis. The distinctive light testaceous to brownish color on the elytral disc (Fig. 2.1 A-D), in combination with the structure of the basal denticle of the protarsal claw (Fig.

2.6-E), will serve to distinguish members of this genus from the similar *Cymatodera*. Specifically, the basal denticles in *Araeodontia* are digitiform, while members of *Cymatodera* have this basal denticle trigonal (Fig. 2.7-B).

Redescription. Size: 6-12 mm. Color: light testaceous to dark brown, fasciae on elytral disc ranging from testaceous to dark brown. Body: winged species, moderately elongate, robust. Head: including eye width wider than pronotum; integument smooth to moderately punctate; eyes large, coarsely faceted, feebly emarginate anteriorly; antennae filiform to moderately serrate, composed of 11 antennomeres, reaching posterior half of pronotum; frons can be bi-impressed or not; terminal labial palpi securiform; terminal maxillary palpi cylindrical, compressed laterally. Thorax: pronotum smooth to feebly punctate, widest at middle, sides more constricted behind middle; prosternum smooth to slightly punctate; mesosternum feebly to moderately punctate; metasternum slightly punctate, glabrous to moderately vested; metaventral process not compressed anteriorly; metepisternum concealed throughout its length in lateral view. Elytra: elongate, subparallel, slightly broader behind middle, feebly to moderately punctate, punctations extending to posterior third but never reach apex; scutellum ovoid, not compressed; moderately vested; epipleural fold complete, narrowing toward apex. Legs: moderately to coarsely rugose; profemora slightly swollen; tarsal formula 4-4-4; tibial spur formula 4-4-4, pulvillar formula 4-4-4; two tarsal denticles, tarsal denticles digitiform in shape (Fig. 2.6-E); moderately to strongly vested. Abdomen: six visible ventrites; ventrites 1-5 impressed laterally or not; pygidium of males moderately differentiated from that of females (Fig. 2.16 A-D); males with sixth ventrite moderately, narrowly, V-shaped emarginate (Fig. 2.16-B); pygidium of females simple, broadly rounded (Figs. 2.16 C-D). Aedeagus: moderately

sclerotized; length of aedeagus shorter than the length of abdomen; tegmen triangular; phallobasic apodeme elongate, as long as or longer than phallus; endophallic struts, enlarged distally (Fig. 2.18 A-C). Male and female pygidium shape is not variable for all the species in the genus.

Remarks. The genus is currently composed of five species. Barr (1952) conducted a revisionary work of those *Cymatodera* species possessing digitiform tarsal denticles (Fig. 2.6-E). Barr assumed that, based on the state of the tarsal denticles, these species should be assigned to a different genus. The tarsal denticles of *Cymatodera* are triangular (Fig. 2.7-B); however, this character was inconsistent in three species originally assigned to *Cymatodera* occurring in northern Mexico, Lower California and the southwestern United States. As a result, Barr erected *Araeodontia* and described two new species, *Araeodontia picta* and *A. marginalis*. In addition to those differences found in the structure of the tarsal denticles, the distinctive integument color of the genus is probably an adaptation to the arid environments where these species occur (Fig. 2.1 A-D). Barr (1952) indicated that *Araeodontia* can be further divided into two separate groups, one solely composed of *A. picta* Barr, and the second composed of the remaining species, based on differences in the structure of the protarsal denticles.

In this revisionary work, I have revised a significant number of specimens from all species, except *A. picipennis*, and while differences in the size of the protarsal denticles exist, they are subtle and there is not a clear division of two separate groups within the genus. Additionally, male pygidium in all *Araeodontia* species is similar, so that character cannot be used to separate them. Male genitalia, in combination with the elytral marking, can serve to separate species.

Key to species of *Araeodontia*

1. Elytra immaculate, uniformly brown to dark brown.............................. ***Araeodontia picipennis***

- Elytra with an array of markings that range from prominent fasciae to maculae, elytral disc light testaceous to dark brown 2

2 (1). Elytral disc light testaceous to testaceous; each elytron with a longitudinal light brown macula on the posterior third of the elytron (Fig. 2.1-A)................................***Araeodontia isabellae***

- Elytral disc light brown to brown; each elytron adorned with a pair of light testaceous to testaceous fasciae that extend from anterior margin of elytra to elytral apex (Fig. 2.1 B-D)..........3

3 (2). Integument color of head brown to dark-brown, darker than the rest of the body; two longitudinal fasciae on each elytron, the first located on elytral suture and the second along epipleural fold, these fasciae may be interconnected on elytral apex or not (Fig. 2.1-B)..................

.... ***Araeodontia marginalis***

Integument color of head the same color as the rest of the body...4

4 (3). Elytra with an anterior pair of maculae reaching epipleural fold, these maculae more proximal to the humeri (Fig. 2.1-C)..***Araeodontia peninsularis***

- Elytra with an anterior pair of maculae that do not reach the epipleural fold, these maculae are more distal to the humeri (Fig. 2.1-D)...***Araeodontia picta***

3.1 Araeodontia isabellae (Wolcott, 1910).

Figs. 2.1-A, 2.18-A.

Synonyms: *Cymatodera isabellae* Wolcott, 1910. Field Museum Natural History, zool. Ser., vol. 7, no. 10, 9 345. Wickham and Wolcott, 1912 University of Iowa Bulletin Laboratory of Natural History, vol. 6, no. 3 p. 52. Wolcott, 1921 Proc. U.S. Natl. Mus., vol. 59, p. 285. Barr, 1950, Proc. California Acad. Of Sci., ser. 4, vol. 24, no. 12, p. 496.

Type material not examined.

Type locality: United States: Utah, St. George, Washington Co. Type depository: National Museum of Natural History (USNM).

Distribution: USA: AZ, CA, NV, TX, UT.

Differential diagnosis: *Araeodontia isabellae* is most similar to *A. picipennis*. The two species can be readily distinguished based on the color of the elytral disc and elytral patterning. Specifically, *A. isabellae* has the elytral disc pale testaceous to testaceous and possesses two brown to light brown maculae on each elytron (Fig. 2.1-A), while *A. picipennis* has the elytra uniformly brown to dark brown and lacks maculae on the elytral disc.

Redescription. Male. Form: somewhat slender, slightly elongate. Color: head, mouthparts and pronotum light testaceous to brown; thorax, elytra, abdomen and legs light testaceous to testaceous; two longitudinal brown to testaceous maculae on the posterior half of each elytron, the first located proximate to the elytral suture, the second adjacent to the epipleural fold, neither

of these maculae reach the apex, these maculae can be almost absent in some specimens (Fig. 2.1-A).

Head: moderately vested by erect setae; surface moderately to densely punctate; frons bi-impressed; eyes enlarged, bulging, coarsely faceted; antennae extending to posterior half of pronotum, antennomeres 2-3 reduced in length, fourth antennomere about 2× the length of third antennomere, antennomeres 4-10 about the same length as fourth antennomere, antennomeres 4-10 somewhat slender, feebly serrate, eleventh antennomere robust, sub-acuminate.

Thorax: pronotum slightly punctate; faintly rugose laterally, smooth; moderately vested by erect and semi-erect setae; broadest at middle; disc flat, indistinctly impressed in front of middle, sub-basal tumescence absent. Mesosternum: very slightly punctate, smooth. Metasternum convex, puncticulate; covered with fine erect and semi-erect setae. Scutellum subquadrate, notched posteriorly.

Legs: vested with short, recumbent setae intermixed with long, erect setae that become more densely arranged on the distal half of the tibia; femora rugulose, moderately, finely punctate; tibiae transversely rugose, coarsely punctate, vested with short, recumbent setae intermixed with semi-erect setae.

Elytra: humeri rounded, indicated; sides subparallel; base wider than pronotum; widest behind middle; disc flattened apically; apices subtriangular, very slightly dehiscent; disc convex, surface rugulose; moderately vested, vestiture composed of erect and semi-erect setae; sculpture consisting of small, coarse punctations arranged in striae that are gradually reduced in size behind middle and do not reach elytral apex; interstices smooth, 3.0× the width of punctuation at anterior margin.

Abdomen: ventrites 1-4 rugulose, moderately vested with short, recumbent setae and some long, semi-erect setae, indistinctly, finely punctate; first visible ventrite approximately 1.5× the length of second; fifth visible ventrite small, convex, lateral margins subparalle, posterior margin broadly, feebly emarginate; sixth visible ventrite subquadrate, surface somewhat excavated medially, convex laterally; slightly punctate, lateral margins oblique; posterior margin broadly, deeply emarginate , emargination V-shaped, posterolateral angles rounded; fifth tergite slightly convex; finely punctate, rugulose, lateral margin subparallel, posterior margin broadly, shallowly, very feebly, emarginate ; sixth tergite subtriangular; rugulose; surface convex; longer than broad; moderately, finely punctate; inconspicuously covered with short, recumbent setae; lateral margins oblique; posterior margin narrowly, very shallowly emarginate; hind angles rounded. Posterior margin of sixth tergite fully covering sixth visible ventrite and produced ventrally.

Aedeagus: Phallobasic apodeme present; phallus with copulatory piece rounded at apex; phallic plate devoid of denticles; intraspicular plate absent; phallobasic apodeme long, expanded distally; phallobase trigonal; parameres free; tegmen complete, fully covering phallus; parameres pointed anteriorly; endophallic struts long, at least the length of tegmen; endophallic struts slender distally (Fig. 2.18-A).

Sexual dimorphism: Females differ from male specimens on the structure of the last abdominal segment. In females of *A. isabellae* the last abdominal segment is broadly rounded and moderately convex to almost flat; males have this segment broadly and deeply emarginate posteriorly. The structure of the sixth abdominal segment is very consistent for all female species within *Araeodontia*, and there is very little variation among all species in this genus.

Material examined: 2 males, 3 females: Phoenix, AZ, VIII-23-1932, D. K. Duncan; 2 males, 2 females: Nevada, VII-24-1950; 1 male: Texas, VI-2-1950; 1 male: Phoenix, AZ, 5409, Chas Palm; 2 males: Imperial Co., CA, Calipatria, VI-4-1962, Kilgore; 1 male, 2 females: Riverside Co., CA, Palm Canyon 1000, VII-21-1973, W. Barr; 1 female: Clark Co., NV, Logandale, IX-13-1984, Riley, Nelson and Wheeler; 5 females: Yuma Co., AZ, Morelos Dam, VI-22-197, E. Giesbert; 1 male, 3 female: Yuma, AZ, Laguna Dam, VIII-9-1954, Butler and Tuttle; 2 males, 1 female: Riverside Co., CA, Blythe, VII-30, 31-1956, Truxal, Honey and Menke; 2 females: Riverside Co., CA, 15 mi N Blythe, VII-12-1977, Schuster and Smith; 3 males: Riverside Co., CA, 12 mi N Blythe, VII-12-1977, P. Bertrand; 3 males: Phoenix, AZ, VIII-31-1935, Parker; 1 female: El Centro [CA], IX-5-1953, Parker; 1 female: 12 mi E of Herbert, V-12-1956, T. R. Haig; 4 males, 5 females: Phoenix AZ, VIII-31-1953, no collector data; 2 males: Clark Co., NV, Logandale, IX-2-1959, E. D. Parker; 1 male: San Diego Co., CA, Anza-Borrego Springs National Park, VI-5-1971, Sweet and Sweet; 3 males, 3 females: Phoenix, AZ, VIII-31-1935, F. H. Parker; 1 female: Riverside Co., CA, 15 mi N of Blythe, VII-12-1977, R. C. Schuster and N. J. Smith; 1 male: Riverside Co., CA, 12 mi N Blythe, VII-12-1977, R. C. Schuster and N. J. Smith; 2 females: Plumas Co., CA, Johnsville, VIII-8-1959, J. S. Buckett; 1 female: Needles, CA, VII-13-1977, R. C. Schuster and N. J. Smith; 5 males, 2 females: Phoenix, AZ, VIII-31-1935, Parker; 2 females: Imperial Co., CA, 12 mi E of Heber, 12-V-1956, T. R. Haig; 1 female: Clarke Co., NV, Logandale, 2-IX-1959, F. D. Parker; 2 males, 2 females: La Paz Co., AZ, 19-VI-1996, Cibola NWR, D. Anderson.

Araeodontia marginalis Barr, 1952.

Figs. 2.1-B, 2.18-B.

One male paratype examined.

Type locality: Mexico, Samalayuca, Chihuahua. Type depository: American Museum of Natural History (AMNH).

Distribution: USA: TX; Mexico: Chihuahua, Coahuila, Sonora.

Differential diagnosis: *Araeodontia marginalis* is most similar to *A. isabellae.* The fascia pattern on the elytral disc can be used to separate them without difficulty. *Araeodontia marginalis* has two longitudinal fasciae that extend from the elytral base to the apex, the first band is located adjacent to the elytral suture and the second runs along the epipleural fold; for some individuals, the latter band can be absent on the anterior half of the elytral disc; both fasciae are interconnected at the apex (Fig. 2.1-B). *Araeodontia isabellae* has the elytral disc uniformly light testaceous and each elytron has two testaceous maculae (Fig. 2.1-A).

Redescription. Male. Form: body relatively stout, fairly elongate. Color: head, anterior margin of pronotum and mouthparts brown to dark brown; pronotum, thorax, elytra, abdomen and legs testaceous to light brown; two brown, longitudinal fasciae on each elytron, the first located on the elytral suture, and extends from anterior margin of elytra and reaches apex, this fascia abruptly reduced in width on second and last fourth, the second adjacent to epipleural fold, and also extends from anterior margin of elytron and reaches apex, this fascia may be reduced to absent on the anterior half of elytral length, both fasciae may be interconnected at the elytral apex (Fig. 2.1-B).

Head: feebly vested by recumbent, light setae; surface weakly punctate; frons bi-impressed; eyes enlarged, bulging, coarsely faceted; antennae extending to anterior third of elytra; third antennomere about twice the length of second antennomere; antennomeres 3-10 about the same length; antennomeres 4-10 somewhat robust, slightly serrate; eleventh antennomere robust, sub-acuminate.

Thorax: pronotum scarcely punctate; faintly rugose laterally, smooth; moderately vested by semi-erect seta interspersed with fine, recumbent setae; broadest at middle; disc flat, very feebly impressed in front of middle, more strongly constricted behind middle, sub-basal tumescence absent. Mesosternum: very finely vested, smooth. Metasternum: smooth, convex, puncticulate; covered with fine, semi-recumbent setae. Scutellum subquadrate, notched posteriorly.

Legs: moderately vested with short, recumbent setae intermixed with long, erect and semi-erect setae; femora rugulose, moderately, finely punctate; tibiae longitudinally rugose, moderately punctate, vested with short, recumbent setae intermixed with semi-erect setae.

Elytra: humeri rounded, indicated; sides subparallel, widest behind middle; base wider than pronotum; disc flattened apically; apices subtriangular, slightly dehiscent; disc convex, moderately vested, vestiture composed of stiff, erect and semi-erect setae intermixed with stiff, semi-recumbent setae; sculpturing consisting of small, shallow punctations arranged in striae that gradually reduce in size on middle third and do not reach elytral apex; interstices smooth, 4.0× the width of punctuation at anterior margin.

Abdomen: ventrites 1-4 rugulose, feebly vested with short, recumbent setae, indistinctly, finely punctate; first visible ventrite about the same length of second ventrite, ventrite 3-4 subquadrate, smooth, feebly vested with fine recumbent setae; fifth visible ventrite reduced, convex, lateral margins subparallel, posterior margin broadly, slightly emarginate; sixth visible

ventrite subquadrate, surface somewhat concave medially, convex laterally; feebly punctate, lateral margins oblique; posterior margin broadly, moderately deeply emarginate, emargination V-shaped, posterolateral angles rounded; fifth tergite convex; finely punctate, rugulose, lateral margin subparallel, posterior margin broadly, shallowly, slightly, emarginate ; sixth tergite subtriangular; surface convex; longer than broad; moderately, finely punctate; scarcely covered with short, recumbent setae; lateral margins oblique; posterior margin narrowly, very shallowly emarginate; hind angles rounded. Posterior margin of sixth tergite produced ventrally, fully covering sixth visible ventrite.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece expanded at apex; phallic plate without denticles; intraspicular plate present, moderately elongate; phallobasic apodeme long, expanded distally; phallobase trigonal; parameres free; tegmen complete, covering phallus; parameres pointed anteriorly; endophallic struts long, the length of tegmen; endophallic struts slender distally (Fig. 2.18-B).

Sexual dimorphism: The female of *A. marginalis* can be separated from males based on the structure of the last abdominal segment. In females, the lateral and posterior margins of the sixth tergite and the sixth visible ventrite are broadly rounded, making a single semicircular margin; males have the sixth tergite and the sixth visible ventrite subquadrate in shape, and the posterior margin narrowly, shallowly emarginate, the emargination seen in the sixth visible ventrite is slightly deeper than that observed in the sixth tergite. Remaining characters are similar.

Material examined: PARATYPE: 1 male: Pine Springs, TX, VII-12-16-1928, W. Benedict.

Additional material examined: USA: 1 male: Hudspeth Co., TX, 9 mi SW Dell City, VII-31-1950, R. F. Smith; 2 males: Valentine, TX, VI-25-1947, R. H. Beawer. MEXICO: 1 male, 1 female: Sonora, Mexico, near San Jose beach, Ciudad Obregon, 40 mi SW of V-16-23-1961, Howden and Martin; 1 female: Coahuila, Mexico, sand dunes, near Bilbao, 8 mi N of Viesca, V-30-31-1981, J. Doyen and J. Liebherr.

Araeodontia peninsularis (Schaeffer, 1904).

Figs. 2.1-C, 2.6-E, 2.8-A, 2.16 A-D, 2.18-C.

Synonyms: *Cymatodera peninsularis.* Schaeffer, 1904, Jour. New York Ent. Soc., vol. 12, p 214. Wolcott, 1910, Filed Museum of Natural History, zool. Ser., vol. 7, no. 10, p. 34; 1921, Proc. U.S. Natl. Mus., vol. 59, p. 286. Chapin, 1949, Smithsonian Misc. Coll., vol. 111, no. 4, p. 9. Barr 1950, Proc. California Acad. Of Sci., ser. 4, vol. 24, no. 12, p. 496.

Type material not examined.

Type locality: Mexico, San Felipe, Baja California Sur, Cape region. Type depository: National Museum of Natural History (USNM).

Distribution: USA: AZ, CA, NM; Mexico: Baja California, Sinaloa, Sonora.

Differential diagnosis: *A. peninsularis* is most similar to *A. picta*. Differences in the size and position of the maculae on the elytral disc will help to distinguish these species. The anterior

pair of testaceous maculae on the elytral disc of *A. peninsularis* reach the epipleural fold and these spots are more closely approximate to the anterior margin on the anterior half of the elytral disc (Fig. 2.1-C). The elytral disc of *A. picta* possesses two maculae that do not reach the epipleural fold, and these spots are more distant from the anterior margin on the anterior half of the elytral disc (Fig. 2.1-D). Moreover, antennomeres 3-10 on *A. peninsularis* are shorter in length than those found on *A. picta*.

Redescription. Male. Form: body somewhat slender, somewhat elongate. Color: head, pronotum, thorax, abdomen, mouthparts and legs testaceous to light brown, elytra brown to dark brown; mandibles in lateral view brown with posterior half black; two irregular, testaceous maculae on each elytron, the first located on the anterior half, reaching middle third of elytral disc, and the second maculae adjacent to epipleural apex (Fig. 2.1-C).

Head: feebly vested by semi-erect setae; surface weakly punctate; frons bi-impressed; eyes large, bulging, coarsely faceted; antennae extending to anterior third of elytra; third antennomere about 1.5× the length of second antennomere; antennomeres 3-10 about the same length; antennomeres 4-10 moderately robust; eleventh antennomere robust, sub-acuminate, slightly longer than previous antennomere (Fig. 2.8-A).

Thorax: pronotum moderately punctate; somewhat rugose laterally, disc smooth; vested by stiff semi-erect seta interspersed with fine, recumbent setae; broadest at middle; disc flat, moderately impressed in front of middle, more strongly constricted behind middle, sub-basal tumescence absent. Mesosternum: very finely vested, smooth. Metasternum: smooth, convex, puncticulate; covered with fine, semi-recumbent and recumbent setae. Scutellum subquadrate, notched posteriorly.

Legs: femora rugulose, finely punctate, moderately vested with short, recumbent setae intermixed with long, semi-erect setae; tibiae longitudinally rugose, moderately punctate, vested with short, recumbent setae intermixed with semi-erect setae.

Elytra: humeri indicated; sides subparallel, widest behind middle; base wider than pronotum; disc flattened apically; apices subtriangular, moderately dehiscent; disc convex, vestiture on elytral disc composed of stiff, abundant, semi-erect setae intermixed with less numerous, stiff, semi-recumbent setae and some erect setae scattered throughout elytral disc; sculpturing consisting of deep punctations arranged in regular striae that gradually reduce in size on posterior third and do not reach elytral apex; interstices smooth, 2.5 to 3.0 $\times$ the width of punctuation at anterior margin.

Abdomen: ventrites 1-4 rugulose, feebly vested with short, recumbent setae; indistinctly, finely punctate; first visible ventrite about twice the length of second ventrite; ventrite 2-4 subquadrate, short, smooth, feebly vested with fine recumbent setae; fifth visible ventrite reduced, convex, lateral margins subparalle, posterior margin broadly, deeply emarginate; sixth visible ventrite subquadrate, surface somewhat concave medially, convex laterally; slightly punctate, lateral margins oblique; posterior margin broadly, shallowly emarginate, emargination V-shaped, posterolateral angles rounded (Fig. 2.16-B); fifth tergite convex; finely punctate, rugulose, lateral margins subparallel, posterior margin broadly, shallowly, feebly, emarginate; sixth tergite subtriangular; surface convex; longer than broad; moderately, finely punctate; scarcely vested with some short, recumbent setae; lateral margins oblique; posterior margin narrowly, very shallowly emarginate; hind angles rounded (Fig. 2.16-A). Posterior margin of sixth tergite partially produced ventrally, fully covering sixth visible ventrite.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece rounded apically; phallic plate devoid of denticles; intraspicular plate present, somewhat elongate; phallobasic apodeme long, conspicuously expanded distally; phallobase trigonal; parameres free; tegmen complete, fully covering phallus; parameres pointed anteriorly; endophallic struts long, as long as the length of tegmen; endophallic struts slender distally (Fig. 2.18-C).

Sexual dimorphism: Females of this species can be distinguished from male individuals based on the structure of the last abdominal segment. Females have the lateral and posterior margins of the sixth tergite and the sixth visible ventrite broadly rounded, forming a single semicircular margin (Fig. 2.16 C-D). Males have the sixth tergite and the sixth visible ventrite subquadrate in shape, and the posterior margin narrowly, shallowly emarginate, the emargination observed in the sixth visible ventrite is somewhat deeper than in the sixth tergite (Fig. 2.16 A-B). Remaining characters are similar for both sexes in this species.

Material examined: 2 females: Baboquivari Mts. AZ, Baboquivari Canyon, VII-17-1949, F. Werner and W. Nutting; 2 males, 3 females: Tucson, AZ, VIII-5-1935, Bryant; 1 male, 2 females: Hualpai Mts. AZ, VII-4-19, D. J. Knull and J. N. Knull; 1 male, 1 female: Tucson AZ, VII-12-19, Knull and J. N. Knull; 1 male: Santa Rita Mts., AZ, VII-13, [Compared with Type], Knull and J. N. Knull; 1 male, 1 female: Carlsbad, NM, VII-27, Knull and J. N. Knull; 1 male, 1 female: Globe, AZ., V-1939, D. K. Duncan; 1 male, 1 female: Globe, AZ, VII-20-1939, Parker; 2 males: Tucson, AZ, VIII-10-1939, Bryant; 2 females: Pima Co., AZ, Sabina Canyon, VII-17-1973, E. Giesbert; 1 male: Baboquivari Mts., AZ, sweeping slash, in desert, VII-31-1950, R. H. Arnett; 1 male, 3 females: Pima Co., AZ, 1 mi S of Kits Peak rd., IX-10-1974, J. M. Cicero; 1

female: Sta. Catalina Mts., AZ, Mouth of Bear Cn., VII-3-1961, Werner and Nutting; 2 males: foothills Sta. Catalina Mts., AZ, VII-2-1975, K. Stephan; 1 female: Riverside Co. CA, Palm Desert, V-15-1970, A. Mayor; 2 males: Riverside Co., CA, Deep Cyn., Des. Res. Center Sec. 17, R6E, T6S, 116° 22' 36'' W, 33° 36' 19'' N, 10 year Malaise trap study, VI-24-27-1980, J. D. Pinto and S. I. Frommer; 2 males, 3 females: Santa Cruz Co., AZ, Madera Cyn. 4880 ft., VII-23-1963, V. L. Vesterby; 1 female: Pima Co., AZ., Sabino Cyn. Vi-25-1963, F. D. Parker and L. A. Stange; 2 males, 1 female: San Diego Co., CA, 6 mi E Banner, VII-13-1963, T. Bolton; 1 male: Baboquivari Mts. AZ., Baboquivari Cyn., VII-17-1949; 2 females: Mohave Co., AZ, Mohave Valley, VI-10-1980; 1 female: Globe, AZ, [September], D. K. Duncan; 2 males: Baboquivari Mts. AZ, Brown Cyn., VIII-4-1961, U. V. lt., W. Nutting; 1 female: Pima Co. AZ, IBP site, Sta. Rita Range Res., UV trap, VIII-31-1973, W. Nutting; 1 female: Pima Co., AZ, Sta. Rita Ranch, VII, R. Lenczy; 2 males: 3 females: Pima Co., AZ, Organ Pipe Natl. Mon., VI-14-1952, M. Cazier and R. Schrammel; 1 male, 2 females: Pima Co., AZ, 15 mi E. Tucson, 2600 ft., VIII-18-1950, T. Cohn, P. Boone and M. Cazier; 2 males: Hidalgo Co., NM, Cienega Ranch N Rodeo, VII-12-1948, C. Vaurie and P. Vaurie; 1 male, 2 females: San Carlos, AZ, VIII-13-1933, Parker; 2 males, 1 female: Globe, AZ, VIII-3-1933, Parker; 1 female: Coyote Mts. AZ., VIII-4-7-1916, 31° 50' N 111° 29, W 35000 ft., 2 males: Tucson, AZ, AC. 5409, Palm, no collector data; 1 male, 1 female: Baboguivari Mts., AZ, Near Kits Peak, VIII-7-9-1916, 32° 00' N 11° 36' ~3600; 2 males: Globe, AZ, D. K. Duncan. MEXICO. 1 male, 2 females: Sonora, Mexico, Tastiota, VII-18-1952, C. Vaurie and P. Vaurie; 2 females: Sinaloa, Mexico, 16 miles SW Guamuchi, VI-16-1961, F. D. Parker.

Araeodontia picipennis Barr, 1952

Synonyms: *Cymatodera picipennis* Barr, 1950, Proc. California Acad. Sci., ser. 4, vol. 24, no. 12, p 495.

Type material not examined.

Type locality: Venancio, Lower California. Type depository: CASC. Holotype was not available for study.

Distribution: Mexico: Baja California.

The following is Barr's (1950) original description for *Cymatodera picipennis*.

Female: Medium size, somewhat elongate; piceous; pronotum faintly paler at sides and across middle; elytra with brownish subapical spots, right elytron with a broad, faintly indicated, brownish ante-median area along lateral margin at middle; undersurface dark testaceous. Head finely, somewhat sparsely punctured, finely wrinkled at base, sparsely clothed with short, erect brownish hairs; front feebly bi-impressed; antennae brown, stout, reaching basal fourth of elytra, second segment two-thirds as long as third, third segment slightly longer than fourth, segments five to ten nearly equal in length, longer than those preceding, cylindrical, outer margin of each of these segments broadly rounded, slightly incrassate at apex. Pronotum one-third longer than basal width ; surface finely, sparsely punctured, sparsely clothed with short, fine pale hairs, intermixed with

moderately long, erect brown hairs; ante-scutellar impression wanting. Elytra two and one-half times longer than basal width, nearly twice as wide as pronotum at base ; humeri distinct; sides widest behind middle; apices nearly conjointly rounded; surface with striae consisting of fine punctures, extending to subapical spots, interspaces much wider than punctures, sparsely clothed with short, sub-erect pale hairs. Legs dark testaceous, piceous at apices of femora and bases of tibiae, finely, densely punctured, densely clothed with short, brown hairs; middle tibiae dark. Metasternum finely and very sparsely punctured. Abdomen finely, densely punctured; fifth sternite rounded at apex, deeply incised at middle; sixth sternite narrowly rounded at apex; sixth tergite longer and broader than sixth sternite, narrowly rounded at apex. Length: 7 mm.

Holotype, female (C. A. S. No. 5622) from Venancio, July 17, 1938, collected by Michelbacher and Ross. *C. picipennis* belongs to the Xanti group in Wolcott's key and will run to *C. tuta* Wolcott and *C. laevicollis* Schaeffer. It may be separated from these two species by the dark piceous color with the brown, subapical elytral spots and by the structure of the antennae. This species is described from a single female which is in a somewhat damaged condition, the left antenna is broken off at the fourth segment, one of the hind legs is missing, and several of the tarsi are gone. However, the critical characters are present and the species appears to be sufficiently distinct to warrant a name at this time.

Remarks: specimens from *A. picipennis* were not available for examination for this revisionary work. Barr (1952), in his revision of the genus *Araeodontia*, stated that this species is restricted to an area in the vicinity of San Venancio, Baja California Sur, Mexico, and it is only

known from the female holotype. Barr indicated that *A. picipennis* is most similar to *A. peninsularis*, however, the two species can be differentiated based on the structure of the tarsal claws and the elytral disc pattern; specifically, in *A. picipennis,* the two inner tarsal denticles are slender and closely approximated and the elytral disc is immaculate, in a pale testaceous tone. In *A. peninsularis*, the tarsal denticles are thicker and distinctly separated, and each elytron has two irregular testaceous maculae, the first located on the anterior half, reaching middle third of elytral disc, and the second maculae adjacent to epipleural apex. Barr pointed out that validity of the species is questionable and perhaps its rarity is due to its close resemblance with *A. peninsularis,* with the holotype possibly just a case of the maculae being absent. If so, *A. picipennis* would be treated as a junior synonym of *A. peninsularis*.

Araeodontia picta Barr, 1952.

Fig. 2.1-D.

Two female paratypes examined.

Type locality: Mexico, Chihuahua, Valle de Olivos. Type depository: American Museum of Natural History (AMNH).

Distribution: Mexico: Chihuahua.

Differential diagnosis: *A. picta* is most similar to *A. peninsularis*. The two species can be reliably separated based on the macula on the elytral disc. The anterior pair of testaceous

maculae of *A. picta* are well separated from the anterior margin of the elytral disc and do not reach the epipleural fold (Fig. 2.1-D); these spots are noticeably closer to the anterior portion of the elytral disc in *A. peninsularis* and are in partial or total contact with the lateral margin of the elytra disc (Fig. 2.1-C). In addition, in *A. picta,* the second pair of maculae are somewhat separated from the elytral apex, while these maculae are adjacent to the elytral apex in *A. peninsularis*

Redescription. Female. Form: body relatively slender, feebly elongate, similar in shape to remaining *Araeodontia* species. Color: head, pronotum, thorax, abdomen, mouthparts and legs testaceous to light brown, elytra brown to dark brown; mandibles black; two irregular testaceous maculae on each elytron, the first located on middle of elytral disc, the second adjacent to epipleural apex (Fig. 2.1-D).

Head: feebly vested by semierect, stiff setae mixed with semi-recumbent fine setae; surface weakly punctate; frons slightly bi-impressed; eyes large, bulging, coarsely faceted; antennae extending slightly beyond elytral humeri; third antennomere about $2\times$ the length of second antennomere; third antennomere moderately shorter than fourth antennomere, antennomeres 4-10 somewhat robust, about the same length, feebly serrate; eleventh antennomere robust, sub-acuminate, somewhat longer than previous antennomere.

Thorax: pronotum moderately punctate, more densely punctate than head; disc smooth; lateral sides rugulose; relatively vested with stiff, semi-erect seta interspersed with some moderately fine, recumbent setae; broadest at middle; disc flat, inconspicuously impressed in front of middle, more strongly constricted behind middle, sub-basal tumescence absent; mesosternum: very finely vested, smooth, vestiture consisting of fine, semi-recumbent setae;

metasternum: smooth, convex, puncticulate; covered with fine, semi-recumbent and recumbent setae. Scutellum subquadrate, notched posteriorly.

Legs: femora rugulose, finely punctate, moderately vested with short, recumbent setae; tibiae longitudinally rugose, moderately punctate, more heavily than femora, vestiture consisting of short, semi-recumbent setae intermixed with some semi-erect setae.

Elytra: humeri indicated; sides subparallel, widest behind middle; base wider than pronotum; disc flattened apically; apices subtriangular, moderately dehiscent; disc convex, vestiture on elytral disc consisting of stiff, semi-erect setae intermixed with numerous finer, semi-recumbent setae; sculpturing consisting of shallow punctations arranged in regular striae that gradually reduce in size on middle third and do not reach elytral apex; interstices smooth, about $4.0\times$ the width of punctation at elytral base.

Abdomen: ventrites 1-4 rugulose, feebly vested with short, recumbent setae; indistinctly, finely punctate; first visible ventrite about twice the length of second ventrite, ventrites 2-4 subquadrate, short, smooth, weakly vested with fine, recumbent setae; fifth visible ventrite subtriangular, convex, lateral margins oblique, posterior margin truncate; sixth visible ventrite rugulate, surface slightly concave, moderately punctate, lateral and posterior margins broadly rounded; fifth tergite convex, lateral margins subparallel, posterior margin truncate; sixth tergite rugulate, surface feebly convex, broader than long, lateral and posterior margins broadly rounded. Posterior margin of sixth tergite slightly extending beyond posterior margin of sixth visible ventrite.

Aedeagus: not available.

Sexual dimorphism of this species can be obtained from the original description given by Barr (1952): [Male] densely punctate; sternites 1-4 with a smooth submarginal area, hind margins narrowly membranous; fifth [ventrite] shallowly compressed medially, lateral margins oblique, slightly arcuate, hind margins narrowly broadly, semicircularly emarginate; sixth [ventrite] broader than long, lateral margins nearly parallel, hind angles nearly square, broadly rounded, [posterior] margin more or less broadly arcuate, deeply, nearly semicircularly notched at middle; sixth tergite broader and longer than sixth [ventrite], slightly broader than long, disk feebly convex, lateral margins slightly oblique, hind margin nearly semicircularly rounded, ventral surface with a very distinct, broad, transverse, subapical, V-shaped carina.

Material examined: PARATYPE: 1 female: 20 mi SW Camargo Chihuahua, Mex., 4500 ft., VII-13-1947, Cazier. PARATYPE: 1 female: 63 miles W. of Santa Barbara Chihuahua, Mexico, 5500 ft., VII-20-1947, W. Gertsch and C. D. Michener.
Additional material examined: 2 females: 63 mi. W of Santa Barbara, Chihuahua, Mexico, 5500 ft., VII-02-1947, Michener.

Remarks: Barr (1952), in his revisionary work of the New World genus *Araeodontia*, described *A. picta* as a new species endemic to the south part of Chihuahua, Mexico. In the type material revised by him, he indicated the existence of a single male, in this case, the holotype. Remaining specimens in the type series are females. The species is particularly uncommon in most collections; consequently, it was impossible to obtain male specimens for this revisionary work. For that reason, I describe the female paratype of this species. After the description of the female paratype, I extract information from Barr (1952) concerning relevant characters from the

male holotype, specifically, abdominal segments and male genitalia. Based on Barr's holotype description (1952), and the examination of the female paratype, remaining characters between males and females of this species were found to be constant.

3.3 Barrotillus kropotkini Rifkind, 1996

Figs. 2.1-E, 2.7-D, 2.8-B.

One male paratype examined.

Type locality: Francisco Morazán, Tegucigalpa, Honduras. Type depository: Natural History Museum of Los Angeles (LACM).

Distribution: Francisco Morazán, Honduras.

(Distribution shown in Fig. 2.21-C)

Differential diagnosis: This monotypic species is most closely allied to members of *Neocallotillus*, with a particular resemblance to *Neocallotillus elegans*. A number of characters are useful to separate these species: *B. kropotkini* has the antennae composed of 11 antennomeres with the segments moderately serrate (Fig. 2.1-E and 2.8-B), the anterior portion of the pronotum is strongly constricted posteriorly, and the pronotal disc is coarsely and deeply punctate (Fig. 2.7-D). *Neocallotillus elegans* has the antennae composed of 10 antennomere which are moderately pectinate in males (Fig. 2.8 D-E) and serrate in the female (2.8-F), the pronotal disc

46

is somewhat constricted posteriorly (Fig. 2.2-B), and the punctations on the elytral disc are shallowly and slightly impressed.

Redescription. Male. Form: body: elongate, slender, small size, 5.3 mm. Color: head, dorsal portion of pronotum, elytra, abdomen, legs and labial palpi piceous; ventral and posterior portion of pronotum, prosternum, mesosternum, labrum, mouthparts and posterolateral portion of metasternum rufous, antennae dark-brown; each elytron with one macula and one fascia, both markings white and raised from elytral surface, the macula is located on the median region of the anterior third of the elytral disc and the fascia is located on the median region of the elytral disc, the fascia begins on the epipleural fold and do not reach the elytral suture (Fig. 2.1-E).

Head: including eyes wider than pronotum; integument smooth, moderately punctate; eyes large, finely faceted, anteriorly emarginate; frons not bi-impressed, clothed with semi-erect setae of two sizes, antennae consisting of 11 antennomeres, moderately serrate, reaching humeral angles, antennomeres 2-4 small slightly robust, filiform, antennomeres 5-6 feebly serrate, antennomeres 7-10 moderately serrate, antennomeres 5-10 gradually increasing in size, eleventh antennomere as long as the combined length of antennomeres 8-10, last antennomere moderately compressed at middle (Fig. 2.8-B); terminal labial palpi securiform; terminal maxillary palpi cylindrical.

Thorax: pronotum longer than broad, campanulate, disc convex, sides sinuate, moderately clothed with long, semi-erect setae intermixed with less numerous, long, semi-erect setae; conspicuously constricted posteriorly, moderately, coarsely punctate, widest in front, strongly sloped posteriorly; prosternum smooth, feebly punctate, finely vested with pale, semirecumbent setae; mesosternum smooth, feebly punctate, coarsely deeply punctate, finely vested with some

pale, semi-recumbent setae, metasternum slightly punctate, surface smooth, vested with fine, recumbent and semi-recumbent setae, longitudinal depression and metaventral process absent, metepisternum visible throughout its length in lateral view.

Elytra: humeri indicated, slender, elongate, subparallel, slightly broader on posterior third, convex on anterior third, then moderately compressed in middle third, and conspicuously convex again in posterior third, sinuosity observable on lateral view, sculpturing consisting on shallow punctations irregularly arranged, punctations extending to apex, elytral apices rounded, feebly dehiscent, interstices at elytral base about 2.5× the width of punctation; scutellum subquadrate, profusely vested with fine, recumbent and long setae, not compressed; epipleural fold compete, narrowing toward apex.

Legs: femora shiny, smooth, moderately vested with semi-recumbent setae interspersed with some semi-erect setae, tibiae more profusely vested than femora, vestiture consisting on fine, short, recumbent setae on proximal face of tibiae and semi-erect setae on distal face of tibia, tarsal formula 4-4-4; pulvillar formula 4-3-3; two tarsal denticles, tarsal denticles trigonal in shape.

Abdomen: six visible ventrites; ventrites 1-5 shiny, smooth, subquadrate, feebly vested with fine, short, vested with semi-recumbent and recumbent setae; not compressed laterally; fifth visible ventrite subtriangular, slightly clothed with recumbent setae, lateral margins oblique, posterior margin truncate; sixth ventrite small, shiny, smooth, conspicuously broader than long, lateral margins strongly oblique, posterior margin broadly, shallowly emarginate, posterolateral angles rounded; sixth tergite feebly concave, surface smooth, lateral margins strongly oblique, posterior margin notched medially, posterolateral angles broadly rounded, lateral and posterior

margins clothed with conspicuously long, erect setae; sixth tergite extending beyond apical margin of sixth visible ventrite, fully covering sixth ventrite from dorsal view.

Aedeagus: not available.

Female variation: Rifkind (1996) indicated the presence of sexual dimorphism in the antennal gestalt. The eleventh antennomere of the female is somewhat shorter than that of the male; also, in the female, this segment is not medially compressed. Additional differences between males and females are seen in the sixth sternite, where females have the posterior margin of this segment complete and rounded, rather than notched, as observed in male specimens.

Material examined: PARATYPE: 1 male: Honduras: Francisco Morazán, El Rincón, Tegucigalpa, X-5-1988, R. D. Cave.

Remarks: *Barrotillus* is a monotypic genus with the single species *Barrotillus kropotkini* Rifkind. In the generic description, Rifkind (1996) indicated the close resemblance this genus has with many *Stenocylidrus* species, checkered beetles restricted to the Afrotropical region and some Australasian islands, he further indicated the campanulate state of *B. kropotkini* similar to certain species of *Cladiscus* Chevrolat, *Pseudopallenis* Kuwert and *Eburneocladiscus*. Those genera occur in the tropical regions of Africa and Madagascar. I have found *B. kropotkini* to be most closely allied with New World *Neocallotillus*, with the campanulate state of the pronotum of this species a homoplasy shared with many tillinids, rather than an indication of relatedness. It is yet unknown whether more species within *Barrotillus* occur in Central America; if this is the

case, they certainly have a restricted distribution. The northern portion of Central America has been poorly surveyed, thus, further collection of specimens from of this species and an extensive examination of this material will help to elucidate the current taxonomic relationship this monotypic genus has with other New World Tillinae species.

3.4 Bogcia disjuncta Barr, 1972

Figs. 2.1-F, 2.2-A, 2.7-A, 2.8-C, 2.16 E-F, 2.18 D-E.

Bogcia oaxacae Barr, 1978 syn. n. Taxonomy of the New World Clerid Genus *Bogcia* from Mexico, The Pan-Pacific Entomologist, 54: 287-291. New synonymy.

One male and one female paratypes examined.

Type locality: Mazatlán, Sinaloa, Mexico. Type depository: California Academy of Science Collection (CASC).

Distribution: Mexico: Chiapas, Guerrero, Jalisco, Nayarit, Oaxaca, Sinaloa

(Distribution shown in Fig. 2.21-D).

Differential diagnosis. *Bogcia disjuncta* (Figs. 2.1-F and 2.2-A) most closely resembles *Cymatodera bogcioides* Burke (Fig. 2.4-F). The two species can be readily distinguished based on differences in the structure of the protarsal claw and the antennae. *Bogcia disjuncta* has the

protarsal denticle in close proximity to the protarsal claw (Fig. 2.7-A) and the antennae is strongly serrate (Fig. 2.8-C). *Cymatodera bogcioides* has the protarsal claw conspicuously separated from the protarsal denticle (Fig. 2.7-B) and the antennae is moderately serrated.

Redescription. Male. Form: somewhat robust, moderately wide posteriorly, elongate. Color: head, antennae, mouthparts, thorax legs, elytra and abdomen testaceous to brown; posterior half of mandibles black 2-3 irregularly fuscous. Each elytron with a broad, black to brown oblique fascia located behind median region of elytron with varying degrees of extension, ranging from the epipleural fold to the elytral suture, to two reduced, dark maculae, this fascia is preceded by a narrow, pale region; in addition to the dark fascia there is one small, brown to black humeral macula, this spot is absent in some specimens examined (Fig. 2.1-F, 2.2-A).

Head: measured across eyes wider than pronotum; surface rugose; frons feebly bi-impressed; moderately coarsely punctate. Eyes medium-sized, somewhat rounded, inconspicuously longer than wide, feebly emarginate in front, bulging laterally, separated by approximately 2.5 eye-widths. Antennae: antennomeres 2-3 very slightly serrate; third antennomere about 2× the length of second antennomere; fourth antennomere as long as third antennomere; antennomeres 4-10 strongly serrate, about the same length, as broad as long, posterior distal angle sharply pointed; eleventh antennomere about the same length as the tenth antennomere, with its distal margin moderately oblique (Fig. 2.8-C). Thorax: pronotum moderately rugose; widest behind middle; middle slightly wider than front margin; sides constricted subapically, more strongly constricted behind middle; disc flat, feebly impressed in front of middle; subbasal tumescence moderately pronounced. Prosternum: smooth, slightly to

moderately punctate. Mesosternum rugulose; moderately to coarsely punctate. Scutellum subquadrate; wider than long; notched medially.

Legs: femora shiny, finely transversally rugulose, indistinctly punctate, tibiae coarsely, densely punctate, longitudinally rugose clothed with long, erect setae and some short, recumbent setae.

Elytra: anterior margin bisinuate, wider than pronotum; disc smooth, flattened above; humeri indicated; sides subparallel, widest behind middle; apices weakly dehiscent, feebly triangular, covering sixth tergite; elytral declivity somewhat procurved, female specimens slightly wider than males; sculpturing consisting of coarse punctations arranged in striae that gradually reduce in size behind middle; interstices smooth, about $2\times$ the width of punctation.

Abdomen: six visible ventrites, ventrites 1-4 smooth; moderately, finely punctate posterior margins truncate. First ventrite with a longitudinal carina that reaches the posterolateral angles (Fig. 2.7-E); ventrites 3-4 slightly convex; hind margins truncate. Fifth visible ventrite feebly convex; lateral margins oblique; posterior margin broadly, relatively deeply emarginate; hind angles narrowly rounded. Sixth visible ventrite subtriangular; rugulose; surface puncticulate, feebly to moderately convex; broader than long; lateral margins broadly oblique; posterior margin narrow, truncate; hind angles rounded (Fig. 2.16-F). Fifth tergite rugulose; surface feebly to moderately convex; finely punctate; posterior margin shallowly emarginate. Sixth tergite broadly triangular; rugulose; surface very slightly convex; moderately punctate; lateral margins strongly oblique, narrowing apically, producing a constricted, somewhat acuminate posterior margin (Fig. 2.16-E). Sixth tergite extending beyond the apical margin of sixth visible ventrite.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece tapered at apex; phallic plate unarmed, devoid of denticles; intraspicular plate present, elongate; phallobasic

apodeme short, not expanded distally; phallobase subparallel; parameres free; tegmen incomplete, partially covering phallus; parameres pointed anteriorly; endophallic struts long; endophallic struts slender distally (Fig. 2.18 D-E).

Female variation: Females differ from males by having the posterior margin of the first and second visible ventrites truncate (Fig. 2.7-E), rather than acuminate (Fig. 2.7-F) as observed in males. Females have the fifth visible ventrite rugose, lateral margins oblique and the posterior margin truncate; sixth visible ventrite rugulose, semicircular, surface feebly convex, broader than long, lateral and posterior margins broadly rounded; the fifth tergite rugulose, lateral margins oblique, posterior margin truncate; and the sixth tergite rugulose, broader than long, surface inconspicuously convex, lateral and posterior margins strongly oblique and slightly acuminate posteriorly, giving the appearance of an almost semicircular margin.

Material examined: PARATYPES: 1 male, 1 female: 23 mi S of Matias Romero, Oaxaca, Mexico, 6-IV-1962, F. D. Parker and L. A. Stange.

Additional material examined: 2 males, 3 females: Jalisco, Mexico, Estación de Biologia Chamela, VIII-21-1991, E. Ramirez; 3 females: Jalisco, Mexico, Estacion de Biología Chamela, trampa de luz, VII-15-1986, R. A. Usela; 1 female: Jalisco, Mexico, Estación de Biología Chamela, trampa de luz, VII-13- 1986, R. A. Usela; 3 females: Jalisco, Mexico, Estación de Biología Chamela, trampa de luz, VII-9- 1986, R. A. Usela; 2 males, 1 female: Jalisco, Mexico, Estacion de Biologia Chamela, trampa de luz, VII-3- 1986, F. A. Noguera; 2 males, 3 females: Jalisco, Mexico, Estacion de Biologia Chamela, VII-15- 1986, R. A. Usela; 2 males: Jalisco, Mexico, Estacion de Biologia Chamela, atraido a la luz, VII-15- 1986, F. A. Noguera; 3 males, 1

female: Jalisco, Mexico, Chamela, VI-17- 1990, A la luz, F. A. Noguera; 2 males, 3 females: Jalisco, Mexico, Chamela, VI-15- 1990, A la luz, F. A. Noguera; 1 male: Mexico, Jalisco, Chamela, atraido a la luz, VII-7- 1986, F. A. Noguera; 2 males, 2 females: Jalisco, Mexico, Estacion de Biol. Chamela, VII-15-23-1987, F. T. Hovore, at UV and MV light; 3 males, 2 females: Jalisco, Mexico, Chamela, vic. UNAM, VII-9-19-1993, J. E. Wappes; 3 females: Jalisco, Mexico, vic. Estacion de Biologia Chamela, UNAM, VII-9-14-1993, Black light, Morris, Huether, Wappes; 2 males, 4 females: Jalisco, Mexico, Est. Biol. Chamela, VII-10-20-1985, E. Giesbert; 3 males, 2 females: Jalisco, Mexico, Chamela, vic. UNAM, VII-9-19-1993, J. Wappes; 2 males: Mexico, Jalisco, Estacion Biologica Chamela, VII-10-10-1985, E. Giesbert; 3 males, 1 female male: Jalisco, Mexico, Est. Biologica Chamela, VII-9-1981, Curoecol, trampa de luz, no collector data.

Remarks: *Bogcia* was originally erected by Barr (1978). The genus most closely resembles the diverse *Cymatodera.* In his descriptive work, Barr described *Bogcia disjuncta* and *B. oaxacae* from the Pacific coast of Mexico, with *Bogcia disjuncta* designated as the type species. One species, *C. obliquefasciata* Schaeffer, is frequently misidentified as a member of *Bogcia* due to the moderately to strongly serrate condition of the antennae, a character observed in other *Cymatodera* species such as *C. conflagrata* (Klug) and *C. limatula* Burke. Presently, *B. disjuncta* and *B. oaxacae* are the only representatives of the genus. After an extensive examination of a number of *B. disjuncta* and *B. oaxacae*, including one male and one female paratype of *B. oaxaca,* I have concluded that the characters provided by Barr to separate these species are not of sufficient value to retain them as separate species. Interspecific variation in integument color and fasciae arrangement is a very common condition among numerous clerid species and various

descriptive works of New World Tillinae species (Wolcott, 1909; 1921; Rifkind, 1993; Leavengood, 2008; Burke & Zolnerowich, 2014; Rifkind et al., 2010; Burke, 2013; Burke & Zolnerowich, 2014; Burke et al., 2015) have shown abdominal and aedeagal differences are the most reliable morphological characters used for delineating interspecific boundaries within Cleridae. Considerable variation was observed in the morphology of the specimens examined here. The integument color and fasciae pattern from specimens identified as *B. disjuncta* and *B. oaxacae* were highly variable and many intermediate forms were observed (Figs. 2.1-F, 2.2-A). Aedeagal and pygidial structures from a number of specimens identified as *B. disjuncta* and *B. oaxacae* were very similar and consistent (Fig. 2.18 E-D). The majority of specimens examined were identified as *B. oaxacae*; this is very likely due to the lack of morphological characters which can reliably differentiate these species. As a result, here, I designate *B. oaxacae* as a junior synonym of *B. disjuncta*.

3.5 Bostrichoclerus Van Dyke, 1938

Type locality: Palm Cañon, Angel de la Guardia, Golf of California, Mexico. Type depository: California Academy of Sciences Collection (CASC).

Distribution: USA: CA; Mexico: Baja California.

(Distribution shown in Fig. 2.21-E)

Due to the rarity of the species, this unusual clerid was not examined in this revisionary work; however, in order to complement the revision of the Tillinae in the New World, the descriptive work of Van Dyke (1938) is given here.

[Diagnosis] The species is most similar to *Cymatodera*. It, however, does not look like any species of the latter genus, but at first sight rather like a large species of the genus *Polycaon* of the family Bostrichidae, also because of its size and general appearance somewhat suggests *Natalis* [Cleridae: Clerinae]. Its distinctive peculiarities are the prominent horns, the type of antennae and the glabrous elytra.

Description. Large, elongate, very finely and sparsely pilose. Head large; eyes large, transverse, coarsely granular, feebly emarginate in front, and very prominent; antennae long, eleven segmented, scape robust, segments 2-5 about twice as long as broad, feebly clavate and quite glabrous, a few stiff hairs only being evident, segments 6-10 moderately serrate, eleventh fusiform, the free angles of 6-8 densely clothed with fine silky pile and the three following segments completely clothed; a prominent horn, laterally compressed and bifid at apex, arising from in front of each eye and just within the insertion antennae giving the latter the appearance of arising from their base; mandibles robust; maxillary palpi four segmented, labial palpi three segmented, the terminal segments of both sets securiform, that of the labial palpi the larger, and almost an equilateral triangle. Prothorax robust, somewhat longer than broad, broadly constricted at sides in front of middle and narrowed posteriorly, basal margin a complete and well defined bead; coxal cavities rounded and narrowly opened behind. Elytra almost 3× as broad as prothorax, two and a half times as long as

broad. Finely, densely and irregularly punctured and without striae except for fine sutural striae close to the suture and extending from about the middle almost to the apex. Anterior coxae conical, very narrowly separated, trochantine not visible; middle coxae feebly conical well separated and with evident trochantine; hind coxae transverse. Abdomen with five free ventral segments. Legs long and moderately slender; tibiae with short terminal spurs; tarsal segments all well developed, flattened dorsally, 1-4 broad yet longer than broad, with usual membranous appendages and densely papillose beneath, the fifth with sides somewhat papillose; claws simple.

Bostrichoclerus bicornis Van Dyke, 1938.

Description: Holotype: unique from Palm Cañon, Angel de La Guardia Island, Gulf of California, collected May 3, 1921, by J. C. Chamberlin, from beneath bark. Moderately large, dark brown and somewhat shining. Head flattened in front, densely punctured above, smooth and sparsely punctured anteriorly, with a faint medial, longitudinal impression on front and sparsely pilose. Prothorax about a sixth longer than broad, base lobed at middle and sinuate each side, apex broadly arcuate and overhanging, disk irregularly punctured, more closely and deeply so in front and with short, reclinate hairs widely scattered about, and broadly and feebly impressed at middle. Scutellum semicircular, densely punctured, rugose and concave. Elytra moderately convex, with pronounced though well rounded humeri, sides almost parallel and disc somewhat dull as the result of the dense punctations and fine rugoseness. Beneath somewhat shining, densely punctured anteriorly and sparely behind. Legs with apices of tibiae beneath and undersurfaces of the tarsal segments from 1-

57

4 densely clothed with short, silky, orange pile. Length 20 mm. with head flexed, breadth 6.5 mm.

Remarks: *Bostrichoclerus* was erected as a monotypic genus by Van Dyke (1938). The species is remarkably different from other congeners in the New World. Van Dyke indicated that, based on the coarsely faceted structure of the eyes, the genus should be placed within Tillinae. He thought *Bostrichoclerus was* closely related to *Cymatodera*, but *Bostrichoclerus* is very different from all known forms of *Cymatodera*. According to Van Dyke, *Bostrichoclerus bicornis* is easily identified based on the prominent frontal horns, the shape of the antennae, and the completely glabrous elytral disc. The species is extremely uncommon among collections. *Bostrichoclerus bicornis* was described by Van Dyke (1938) based on single specimen collected in Isla Angel de la Guardia in the Golf of California, Baja California, Mexico. Later on, a second specimen was collected in southern California (Barr, 1957, Burke et al, 2015). No more specimens have been collected since.

3.6 Callotillus Wolcott, 1911

Type species. *Callotillus eburneocinctus* Wolcott, 1911, original designation.

(Distribution shown in Fig. 2.21-F)

Differential diagnosis. *Callotillus* is similar to the recently described genus *Neocallotillus* (Burke & Zolnerowich, 2016). These checkered beetles can be differentiated from *Neocallotillus*

based on the following combination of characters: Males of *Callotillus* have antennomeres 1-2 filiform; the third antennomere is moderately serrate; antennomeres 4-9 are strongly serrate and approximately equal in length; and the tenth antennomere is broadly ovoid and about the same length as antennomeres 8-9 combined (Figs. 2.9-B, 2.11-A). The antennal structure of females is similar to that of males, except antennomeres 4-9 are moderately serrate and the tenth antennomere is cylindrical to moderately ovoid (Figs. 2.9-C, 2.11-C). In *Neocallotillus* species the male has antennomeres 1-2 filiform; the third antennomere is moderately serrate; antennomeres 4-9 are strongly pectinate; and the tenth antennomere is ovoid in shape and laterally compressed (Fig. 2.8 D-E); the length of the tenth antennomere may vary by species. Females have antennomeres 1-3 filiform; the fourth antennomere is moderately serrate; and antennomeres 4-9 are robust, moderately, and gradually increasing is size toward the distal end (Figs. 2.8-F, 2.9-A); the tenth antennomere of females is similar to that of the males. In addition, *Callotillus* species are conspicuously more robust (Fig. 2.2 D-E) while *Neocallotillus* species are relatively slender and elongate (Fig. 2.13-A). Finally, *Neocallotillus* species lack an elytral swelling present on the anterior third of the elytral disc of *Callotillus* (Fig. 2.13-B).

Redescription. Size: 6–10 mm. Color: Testaceous and ferrugineous to almost black; fasciae on elytral disc may be present or not, if present, ranging from light testaceous to brown. Body moderately robust, expanded posteriorly.

Head: Moderately small, longer than wide; eyes inconspicuously bulging laterally (Fig. 2.14-B), strongly emarginate at antennal insertion; clypeus feebly emarginate medially; antennae composed of 10 antennomeres; sexual dimorphism observable in antennal composition, with antennomeres 2-9 in males conspicuously serrate (Figs. 2.9-B, 2.11-A) but moderately serrate in

59

females (Figs. 2.9-C, 2.11-C), last antennomere compressed laterally in both sexes; labrum moderately constricted laterally, subquadrate; terminal maxillary palpi sub-cylindrical; terminal labial palpi securiform.

Thorax: Pronotum moderately to conspicuously globose, narrower than anterior margin of elytra; disc moderately to strongly convex, inconspicuously broader at middle, slightly sinuate behind middle, then feebly to moderately constricted on last fourth; anterior depression and antescutellar impression absent. Prosternum: smooth to feebly puncticulate; conspicuously wider than long. Mesoventrite smooth, slightly to moderately puncticulate; metepisternum partially visible in lateral view, not fully concealed by elytron (Fig. 2.12-D). Metaventrite moderately to strongly convex; surface variously punctate.

Elytra: Moderately robust, elongate, expanded posteriorly; median region of elytral disc feebly to moderately compressed in lateral view; subbasal elytral swellings present; elytral apex declivity slightly to moderately steep; transverse fasciae may be present on elytral disc or not, if present elevated from elytral disc.

Legs: Femora wide; surface rugulose to smooth. Tibiae rugulose, moderately expanded posteriorly; tibial spur formula 2-2-2. Two tarsal denticles, inner tarsal denticles trigonal, outer tarsal denticles digitiform.

Abdomen: Six ventrites; surface smooth, moderately convex; ventrites 1-5 with lateral margins parallel and posterior margins truncate; male pygidium moderately differentiated form that of females.

Aedeagus: Slender and moderately sclerotized; phallobasic apodeme robust distally; endophallic struts short, robust throughout their length (Fig. 2.15-D).

Remarks. In this revision, I treat *Callotillus* as a genus containing two species: *C. bahamensis* Vaurie (Fig. 2.2 D), a species currently recorded from the Bahamas and the Cayman Islands, and *C. eburneocinctus* Wolcott (Fig. 2.2-E), which is restricted to the southernmost tip of the Florida peninsula, including the Florida Keys.

Key to the species of *Callotillus*.

1. Pronotal disc dark testaceous to rufous; anterior half of elytral disc same color as pronotum, posterior half piceous, color transition interrupted by a median, transverse, pale fascia that extends from epipleural fold to elytral suture; median region of elytral disc compressed in lateral view (Fig. 2.2-E) .... ***Callotillus eburneocinctus***
– Pronotal integument piceous; elytral disc same color as pronotum, except humeral area testaceous to almost ferrugineous; elytral disc lacking any fascia or maculation; median region of elytral disc feebly compressed in lateral view (Fig. 2.2-D).......................... ***Callotillus bahamensis***

Callotillus bahamensis Vaurie, 1952
Figs. 2.2-D, 2.11-A, C.

One female allotype examined.

Type locality: South Bimini Island, Bahamas, British West Indies. Type depository. American Museum of Natural History (AMNH).

Distribution. The Bahamas, Cayman Islands.

Differential diagnosis. *Callotillus bahamensis* is most similar to *C. eburneocinctus*. The two species can be differentiated with ease based on the color pattern on the elytral disc. *Callotillus bahamensis* has the elytral disc predominantly piceous, except a light testaceous area surrounding the humeral angles, this testaceous area extends from the anterior fourth of the epipleural fold and may reach the scutellum or not (Fig. 2.2-D). *Callotillus eburneocinctus* has the anterior half of the elytral disc rufous and the posterior portion fuscous, this coloration shift is interrupted by a transverse, moderately elevated, pale band which runs from the elytral suture to the epipleural fold (Fig. 2.2-E).

Redescription. Male. Form: Moderately robust; elytra gradually expanded toward apex, then abruptly narrowing behind distal fourth. Color: Anterior portion of femora, trochanters, coxae, and anterior fourth of the elytral disc light testaceous, this testaceous pattern on the elytral disc reaches the humeral region laterally and the scutellum internally; the rest of the body uniformly fuscous; elytral disc devoid of any bands or fasciae (Fig. 2.2-D).

Head: Including eyes not wider than pronotum; eyes taller than wide, not bulging laterally, moderately small, finely faceted, strongly sub-triangularly emarginate; integument rugose, feebly punctate, punctuation small; antennal notch located in front of emargination; frons not bi-impressed. Antennae of males composed of 10 antennomeres; second antennomere short, robust, beadlike in shape; third antennomere about 2× the length of previous antennomere, moderately serrate; fourth antennomeres slightly longer than third antennomere; antennomeres 4-9 about the

same length, strongly serrate; last antennomere elongate, about 2.5× the length of ninth antennomere, slightly ovoid in shape, laterally compressed (Fig. 2.11-A).

Thorax: Pronotum globose, slightly broader than long; surface shiny, finely, deeply punctate; sides subparallel, then abruptly constricted on posterior fourth; disc strongly convex; anterior transverse depression and subbasal tumescence absent. Prosternum wider than long; surface smooth. Mesoventrite rugulose; surface finely punctate, feebly vested with fine, pale, semi-erect setae. Metepisternum partially visible in lateral view; conspicuously clothed with recumbent, pale setae. Metaventrite globose; strongly convex; surface shiny; longitudinal depression present; metaventral process absent.

Elytra: Convex, robust; humeri indicated, gradually expanding toward elytral apex, then abruptly narrowing behind humeri; conspicuously vested with fine, pale, recumbent and semi-recumbent setae, vestiture density is reduced on humeri, where elytral disc acquires a testaceous tone; elytral disc rugulose throughout the surface; elytral apices rounded, moderately dehiscent; epipleural fold complete, narrowing toward apex.

Legs: Femora swollen anteriorly; surface shiny, smooth, very finely rugulose. Tibiae longitudinally rugulose; two tarsal denticles, outer denticle digitiform, interior denticle triangular in shape.

Abdomen: Ventrites 1-4 broadly convex, smooth, subquadrate, feebly punctate, not compressed laterally. Fifth visible ventrite convex, shiny and moderately compressed medially; lateral margins subparallel; posterior margin broadly truncate. Sixth ventrite triangular in shape; small; moderately excavated; shiny; slightly punctate; conspicuously broader than long; lateral margins strongly oblique, feebly arcuate; posterior margin small, broadly, deeply emarginate; posterolateral angles broadly rounded. Fifth tergite subquadrate; strongly convex; rugulose;

slightly punctate; posterior margin truncate. Sixth tergite subquadrate; rugulose; wider than long; surface moderately convex; coarsely punctate; lateral margins oblique, posterior margin truncate; posterolateral angles rounded. Sixth tergite extending beyond apical margin of sixth ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: Not available.

Sexual dimorphism: Females of *C. bahamensis* can be distinguished from male specimens based on the antennal structure and the shape of the last abdominal segment. Females have antennomeres 4-9 moderately serrate (Fig. 2.11-C), rather than strongly serrate, as observed in males (Fig. 2.11-A). Additionally, the last ventrite and the last tergite are subquadrate in shape, and not emarginate, as in males.

Material examined. ALLOTYPE: 1 female: South Bimini Island, Bahamas, B. W. I., VI-1951, M. Cazier and C and P Vaurie, handwritten red label, allotype depository: SMNH. Additional material examined. 1 male, 1 female: Cayman, Little Cayman, 3 km SE of Spot Bay, 27-V-2009, R. Turnbow.

Remarks. In her original description, Vaurie (1952) suggested that *C. bahamensis* is most closely related to *C. crusoe*. After examination of specimens of *C. bahamensis*, this species is most similar to *C. eburneocinctus*. Based on Wolcott's description (1921), *C. crusoe* is here placed within *Neocallotillus*. Examination of material of *C. crusoe* will be essential to clarify the status of this rare species.

Callotillus eburneocinctus Wolcott, 1911

Figs. 2.2-E, 2.9 B-C, 2.12-D, 2.13-B, 2.14-B, 2.15-D.

Type material not examined.

Type locality: Key West, Monroe Co., Florida. Type depository. United States National Museum of Natural History (USNM).

Distribution. USA: FL.

Differential diagnosis. *Callotillus eburneocinctus* is most similar to *C. bahamensis*. Characters to distinguish these species appear in the diagnosis section of *C. bahamensis.*

Redescription. Male. Form: Body moderately elongate, robust; head and pronotum somewhat slender; elytra gradually expanded toward apex, then abruptly narrowing behind distal fourth. Color: head, antennae, mouthparts, pronotum, and anterior half of elytral disc testaceous to rufous; legs brunneous; distal end of mandibles, abdomen and posterior half of elytral disc fuscous; thorax bicolored, metaventrite anteriorly ferrugineous, posteriorly and distally fuscous; each elytron with a transverse, median, pale fascia that runs from the epipleural fold to the elytral suture, this band may be raised in most individuals (Fig. 2.2-E).

Head: Including eyes not wider than pronotum; eyes small, taller than wide, not bulging laterally, finely faceted, strongly, sub-triangularly emarginate; surface integument corrugate; antennal notch located in front of antennal emargination; frons not bi-impressed. Antennae of

males consisting of 10 antennomeres; second antennomere short, robust; third antennomere about 2× the length of previous antennomere, moderately serrate; fourth antennomeres slightly longer than third antennomere; antennomeres 4-9 about the same length, strongly serrate; last antennomere elongate, about 2× the length of ninth antennomere, slightly ovoid in shape, laterally compressed (Fig. 2.9-B). Anterior portion of clypeus narrow, approximately 2× the length of eye emargination (Fig. 2.14-B).

Thorax: Pronotum globose, as broad as long; surface rugulose, profusely, finely punctate; punctations narrow, shallow; sides subparallel in dorsal view, then abruptly constricted on posterior fourth; disc strongly convex; anterior transverse depression and subbasal tumescence absent. Prosternum wider than long; surface smooth, rugulose, glabrous. Mesoventrite smooth, shiny, glabrous; surface very finely punctate. Metaventrite strongly convex; surface smooth, feebly, finely punctate; longitudinal depression present; metaventral process absent.

Elytra: Robust; humeri indicated, gradually expanding toward elytral apex; surface convex on anterior third, then moderately compressed on middle third, and conspicuously convex again on posterior third; a pair of long, stiff, erect tuft of dark setae located on the anterior fourth each elytron; surface of elytral disc rugulose; sculpturing absent; elytral apices rounded, moderately dehiscent; epipleural fold complete, narrowing toward apex.

Legs: Femora moderately swollen; surface shiny, smooth. Tibiae longitudinally rugulose; two tarsal denticles, outer denticle digitiform in shape, interior denticle triangular.

Abdomen: Ventrites 1-3 broadly convex, smooth, shiny, subquadrate, feebly punctate, not compressed laterally. Fourth ventrite moderately punctate, medially compressed. Fifth ventrite shiny, strongly excavated; lateral margins subparallel; posterior margin broadly, shallowly emarginate. Sixth ventrite triangular in shape; small; moderately excavated; slightly punctate;

conspicuously broader than long; lateral margins strongly oblique, moderately arcuate; posterior margin shallowly, narrowly emarginate; posterolateral angles rounded. Fifth tergite subquadrate; moderately, coarsely punctate; posterior margin truncate. Sixth tergite subtriangular in shape; feebly convex; wider than long; surface moderately punctate; lateral margins strongly oblique, moderately arcuate; posterior margin very shallowly, narrowly emarginate; posterolateral angles broadly rounded. Sixth tergite extending beyond apical margin of sixth ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: Phallobasic apodeme present; phallus with copulatory piece feebly swollen at apex, petiolate; phallobase subparallel; phallic plate armed with one irregular row of denticles; intraspicular plate present, elongate; phallobasic lobes free; tegmen complete, fully covering phallus; phallobasic lobes rounded distally; phallobasic apodeme moderately short, expanded distally; endophallic struts short, robust distally (Fig. 2.15-D).

Sexual dimorphism: The structure of the antennae will help to differentiate females of *C. eburneocinctus* from males. Females have the third antennomere feebly serrate and the antennomeres 4-9 are moderately serrate (Fig. 2.9-C), males have the third antennomere moderately serrate and antennomeres 4-9 are strongly serrate (Fig. 2.9-B). Females also have the sixth ventrite subquadrate in shape and the posterior margin is broadly truncate, males have this segment subtriangular in shape with the posterior margin narrow and slightly emarginate.

Material examined. 2 males, 3 females: Monroe Co., FL, Big Pine Key, 17-IV-1978, E. Giesbert; 1 male, 1 female: Monroe Co., FL, Everglades Nat. Park, Flamingo, 16-V-1991, R. Morris; 1 male, 2 females: FL, Miami, 13-VI-1963, B. K. Dozier; 1 female: FL, Tavernier, on Key Largo,

19-VI-1970, beating *Laguncularis racemosa* (L.), G. H. Nelson; 2 males, 3 females: FL, Miami, Virginia Key, 23-VI-1970, beating *Conocarpus erecta* L., G. H. Nelson. 1 male: Miami-Dade Co., FL, Miami, 25- VI-1965, B.K. Dozier; 4 specimens: FL, No Name Key, 29-V-1997, R. Turnbow, ex. *Metopium toxiferum* L., emerged 31-III-1979, R. Turnbow; 1 specimen: FL, Sugarloaf Key, 2-V-2000, 30-V-1997, R. Turnbow; 4 males, 9 females: Monroe Co., FL, Big Pine Key, reared from wood, E. Giesbert.

3.7 Cylidrus abdominalis Klug 1842

Fig. 2.3-A.

Synonyms: *Cylidrus fasciatus* var. *spinolai* Schenkling, Clerites II, 1844, p. 122.

Type locality: Santa Catarina, Brazil. Type depository: Germany, Berlin, Museum für Naturkunde der Humboldt-Universität (ZMHB).

Distribution: States of Espirito Santo, Mato Grosso do Sul, and Santa Catarina, Brazil.

Differential diagnosis: *Cylidrus abdominalis* is extremely similar to the African *C. fasciatus*. Based on an extensive revision of material identified as *C. fasciatus* from the Central African Republic, Cameroon and Congo, Gorham's suggestion (1876) that the fairly common *C. fasciatus* was introduced to South America and eventually became adapted to its new environment seems plausible. The four Brazilian specimens I have examined here do not differ from *C. fasciatus*, a finding contrary to Gorham's observations on elytral fasciae differences

between these two entities. The fasciae observed in the specimens examined here under the name *C. fasciatus* display slight differences in the shape, color, and pattern (Figs. 2.3-A, 2.5-D); specifically, these fasciae can range from dark testasceous to almost albus, can extend from the elytral suture to the epipleural fold, to only a pair of spots on the median region of the elytral disc. The Brazilian specimens examined here are consistent with these variations. Remaining characters were not variable for material corresponding to both species.

Redescription: Female. Form: Body moderately elongate, slender, elytra subparallel. Color: head, thorax, elytral fuscus; legs, mouthparts and abdomen testaceous; antennomeres 1-5 dark testaceous, antennomeres 6-11 fuscus. Each elytron with a median, transversal, testaceous fascia, this fascia initiates at the elytral suture and does not reach the epipleural fold (Fig. 2.3-A).

Head longer than wide; enlarged throughout its length; including eyes moderately wider than pronotum; eyes small, taller than wide, not bulging laterally, finely faceted, feebly emarginate posteriorly; antennal notch located in front of eye emargination; frons not bi-impressed; clypeus crenulate posteriorly; gena carinate, encircling eyes; submentum moderately rugose, somewhat shiny; gular sutures parallel, slightly marked; integument feebly punctate, rugose, more strongly rugose below eyes puctations fine and shallow, moderately clothed with fine, pale, short, recumbent setae; antennae composed of 11 antennomeres; first antennomere slender, second antennomere slightly shorter than first antennomere, third antennomer moderately longer than second antennomere, fourth antennomere about the same length as second antennomere, fifth antennomere about the same length as fourth antennomere, sixth antennomere about the same length as fifth antennomeres, antennomeres 6-10 about the same length, clavate, last antennomere moderately longer than preceding antennomere, elongate,

moderately robust, obtusely rounded, slightly longer than tenth antennomere (2.8-G); terminal labial palpi subsecuriform, terminal maxillary palpi, slender, cylindrical.

Thorax: lateral margins of pronotum parallel, sides very feebly narrowing apically, strongly compressed in behind anterior margin; surface shiny, feebly rugose, clothed with some fine, moderately short, pale, semi-erect setae and some long, pale erect setae, vestiture more abundant laterally; very finely, scarcely punctate, punctations small and shallow. Prosternum convex, wider than long; smooth; polished, very feebly punctate, puctations small and shallow. Mesosternum as long as wide, concave; strongly rugose; slightly vested with fine, pale, semi-erect setae; scarcely punctate, punctations coarse and deep. Metasternum: strongly convex, surface finely rugose, inconspicuously vested with fine, pale, semirecumbent setae; longitudinal depression and metaventral process absent; metepisternum exposed throughout its length. Scutellum ovoid, compressed medially, glabrous.

Elytra: slightly broader than pronotum; sinuate in lateral view; moderately elongate; humeri feebly indicated, rounded; sides parallel, broader at middle; disc flat above; surface shiny, smooth; apices subtriangular, dehiscent; elytral declivity conspicuously gradual almost imperceptible; surface moderately clothed with fine, short, dark, semirecumbent setae interspersed with very few scattered moderately long, semi-erect setae; surface feebly punctate, punctations fine and shallow, sculpturing irregularly arranged throughout the elytral length; punctations at elytral base absent; epipleural fold fine and narrow, gradually narrowing toward distal end, absent on posterior fourth. Elytra not covering last two abdominal segments.

Legs: femora shiny, smooth; slightly punctate, consciously swollen, moderately compressed laterally; swollen; moderately clothed with some pale, fine, semirecumbent and semi-erect setae uniformly located throughout femoral surface; tibiae moderately slender

broadening toward distal end, moderately punctate, longitudinally rugose, vestiture consisting of pale, semirecumbent setae intermixed with some semi-erect setae. Tarsal Formula 4-4-4, tibial spur formula, tarsal pulvillar formula 4-3-3.

Abdomen: six visible ventrites; first visible ventrite moderately longer than second visible ventrite, ventrites 1-4 quadrate, shiny, smooth, convex, subquadrate, moderately, finely punctate, weakly clothed with fine, long, pale, recumbent setae, not compressed laterally, posterior margins truncate. Fifth visible ventrite quadrate; shiny; smooth; polished; surface moderately convex; weakly clothed with fine, long, recumbent setae; lateral margins parallel; posterior margin moderately broadly, shallowly emarginate, emargination V-shaped. Sixth visible ventrite subquadrate smooth, shiny, convex, almost flat; inconspicuously punctate; clothed with some erect and semierect, long, piceous setae, vestiture more abundant on anterolateral margins; lateral margins feebly oblique; posterior margin broadly rounded to almost truncate. Fifth tergite subquadrate, conspicuously concave; rugulose; glabrous; feebly punctate; posterior margin truncate. Sixth tergite subquadrate; slightly rugulose; longer than wide; posterolateral margins conspicuously vested with long and short erect setae, posterior margin more strongly vested; surface moderately, minutely punctate; lateral margins slightly oblique, posterior margin slightly rounded to almost truncate. Sixth tergite extending slightly beyond apical margin of sixth visible ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: not available.

Sexual dimorphism: no males available for this species.

Material examined: 1 female: Espirito Santo, [Brazil], Schmidt, 100 m, 1905; 1 male, 1 female: Mato Grosso do Sul, Brasil, Selvíria, UNESP Farm, ex Hevea brasiliensis bole, VII-10-1990, S. R. Rodrigues; 1 female: Nova Teutonia, Santa Catarina, Brazil, VIII-7-1944, F. Plaumann; 1 female: Brazil, Nova Teutonia, IX-1973, F. Plaunmann.

Remarks: *Cylidrus* was described by Latreille (1829). According to Corporaal (1950), the genus is composed of 19 species and seven subspecies. *Cylidrus* has a worldwide distribution with a large number of species occurring in the tropical regions of African and Oceania. Gorham (1876) indicated that *Cylidrus abdominalis* is particularly similar to *Cylidrus fasciatus* Laporte, a species inhabiting central and southern Africa, and was probably transported from the Old World and became established in the Brazilian region. In this revision, specimens of *C. abdominalis* and *C. fasciatus* were examined and no morphological differences were observed. *Cylidrus abdominallis* is here redescribed from five specimens collected in the southeastern Brazilian provinces of Espirito Santo, Mato Grosso do Sul and Santa Catarina. Regardless of its origin, whether a natural occurrence or an introduced species, the specimens examined here confirm the existence of this genus in the New World.

3.8 Cymatoderella Barr, 1962

Type species: *Tillus collaris* Spinola, 1844. Original designation.

Synonyms: *Tillus collaris* Spinola, 1844. Clérites I, Lec. Ann. Lyc. Nat. Hist. New York V, 1849. *Tillus patagoniae* Knull, 1946. A new species of *Tillus* from Arizona (Coleoptera: Cleridae). Ohio Journal. Sc. 46(2):72 1951.

(Distribution shown in Fig. 2.21-H)

Differential diagnosis: *Cymatoderella* is most similar to various *Cymatodera* species of moderate size. The two genera can be easily recognized based on the structure of the ommatidia. *Cymatoderella* species have the diameter of the ommatidia somewhat small (Fig. 2.6-F) if compared with *Cymatodera* species (Fig. 2.12-A). Additionally, the bicolored composition of the integument in *Cymatoderella*, with a testaceous to ferrugineous coloration on the head and pronotum and a piceous tone on the rest of the body(Fig. 2.3 B-D), except *C. patagoniae*, where the pygidium is also testaceous to ferruginous, can also serve to separate these genera; *Cymatodera bicolor* (Say) is the only *Cymatodera* species with a similar color pattern, but it has an elongate and narrow body shape (Fig. 2.5-E), not a robust one, as observed in *Cymatoderella* (Fig. 2.3 B-D).

Redescription: Size: 3-7 mm. Body: Small, relatively robust specimens. Color: pronotum bicolored, testaceous to ferruginous in the median region and piceous on the margins to uniformly testaceous to ferruginous; legs, antennae, thorax, elytra and abdominal segments piceous; head and mouthparts can be testaceous, ferruginous, or with an array of piceous tones; for *C. patagoniae*, visible ventrites 4-6 can be testaceous to ferruginous. Form: small sized individuals, body short, robust, elytra subparallel to moderately expanded posteriorly.

Head: eyes medium sized, moderately taller than wide, moderately bulging laterally, feebly emarginate; sculpturing variously impressed; vestiture variable; antennal insertion located in front of emargination; clypeus moderately emarginate medially; antennae composed of 11 antennomeres; sexual dimorphism slightly difficult to observe in the last abdominal segment; terminal maxillary palpi cylindrical; terminal labial palpi securiform (Fig. 2.3- B-D).

Thorax: pronotum narrower than elytral base; widest at middle; sides constricted subapically; more strongly constricted behind middle; disc moderately convex; anterior depression feebly indicated; antescutelar impression absent; posterior margin conspicuously constricted transversally. Prosternum smooth, variously punctate and vested. Mesosternum wider than long; shiny, variously punctate. Metasternum convex, smooth, shiny moderately clothed. Legs: femora moderately swollen; tibia slender rugose to rugulose; tibial spur formula 2-2-2, pulvillar formula 4-4-4. Elytra: broad; robust; gradually expanded behind middle; humeri strongly indicated; elongate; surface convex, expanded behind middle; moderately to coarsely sculptured; sculpturing arranged in regular striae; elytral declivity moderately steep; epipleural fold complete, narrowing toward apex; pygidium concealed in dorsal view.

Abdomen: six visible ventrites; first visible segment shiny; smooth; 1.5× longer than remaining segments; visible segments 2-4 subquadrate; smooth; shiny; variously impressed and clothed; lateral margins parallel; posterior margins truncate; fifth visible ventrite subquadrate; variously vested; lateral margins moderately oblique; posterior margin truncate; sixth visible ventrite subtriangular, displaying a degree of sexual dimorphism; lateral margins strongly oblique; posterior margin rounded to moderately emarginate. Fifth tergite subquadrate; posterior margin truncate; sixth ventrite subtriangular.

Remarks: *Cymatoderella* was established by Barr (1962) to hold *Tillus collaris* Spinola and *T. patagoniae* Knull, two New World species originally designated within *Tillus* (Oliver), a widely distributed genus with a concentration of species in Africa and Oceania. Rifkind (1993) described a third representative, *Cymatoderella morula.* To date, *Cymatoderella* is composed of three species, *C. collaris* (Spinola), *C. morula* Rifkind, and *C. patagoniae* (Knull). *Cymatoderella collaris* is widely distributed throughout North and Central America; the species ranges from the eastern and southern United States, extending southward to Mexico and the Central American countries of Guatemala, Honduras and El Salvador. *Cymatoderella morula* and *C. patagoniae* are species with a limited distributional range. *Cymatoderella collaris* inhabits regions of southern Mexico, Guatemala and Honduras (Rifkind, 1993), and *C. patagoniae* is restricted to southern Arizona (Knull, 1946) and Sonora, Mexico.

Key to species of *Cymatoderella* Barr

1. Last abdominal segment ferruginous, remaining abdominal segments testaceous to almost piceous; elytral disc conspicuously clothed with pale, short, semirecumbent setae (Fig. 2.3-D); elytra robust; distribution restricted to Arizona and Sonora, Mexico....***Cymatoderella patagoniae***

- Last abdominal segment piceous to dark testaceous, the same color as remaining segments; distribution more widespread 2

2 (1). Antennomeres 2-4 subequal in length, short, cylindrical; antennomeres 5-10 robust, moderately serrate (Fig. 2.9-D); widely distributed, from east and south USA south to Honduras and El Salvador..***Cymatoderella collaris***

- Antennomeres 2-3 subequal in length, short, cylindrical; antennomeres 4-10 robust, moderately serrate (Fig. 2.9-E); distribution from south Mexico to Guatemala and Honduras ....
....***Cymatoderella morula***

Cymatoderella collaris (Spinola, 1844)

Figs. 2.3-B, 2.6-D, 2.9-D, 2.19-B.

Synonyms: *Tillus collaris* Spinola, 1844. Clérites I, Lec. Ann. Lyc. Nat. Hist. New York V, 1849.

Type material not examined.

Type locality: L'Amérique Septentrionale. Type depository: Italy, Torino, Museo Regionale di Scienze Naturali (MRSN).

Distribution: USA: AL, FL, GA, KY, LA, MD, MS, OH, SC, TN, TX; Mexico: Chiapas, Estado de Mexico, Jalisco, Nayarit, Nuevo Leon, San Luis Potosi, Sinaloa, Tamaulipas, Veracruz.

Differential diagnosis: *Cymatoderella collaris* is most similar to *C. morula*. The two species can be readily differentiated based on the structure of the antennae. Antennomeres 2-4 of *C. collaris* are short and subequal in length, and antennomeres 5-10 are elongate, robust and moderately serrate (Fig. 2.9-D). In contrast, *Cymatoderella morula* has antennomeres 2-3 short and subequal in length and the antennomeres 4-10 are elongate, robust and moderately serrate (Fig. 2.9-E). The geographic distribution of these species may also serve to differentiate them; *C. collaris* is widely distributed from eastern and southern USA south to El Salvador, while *C. morula* is restricted to southwest Mexico, Guatemala, Honduras and Nicaragua.

Redescription. Male. Form: body short, robust, elytra gradually expanded toward apex, then abruptly narrowing behind distal fourth. Color: pronotum uniformly testasceous to ferruginous throughout its surface to bicolored, if bicolored, ranging from testaceous to ferruginous in the median region and piceous on the margins; legs, antennae, thorax, elytra piceous; abdomen piceous to dark testaceous; head and mouthparts with various of piceous tones. Elytral disc devoid of any bands or fasciae (Fig. 2.3-B).

Head: including eyes moderately wider than pronotum; eyes of moderate size, taller than wide, conspicuously bulging laterally, finely faceted, emarginate posteriorly; antennal notch located in front of emargination; frons impressed; integument shiny, feebly punctate, puctations moderately coarse, sparsely clothed with fine, pale, semirecumbent and semi-erect setae; antennae composed of 11 antennomeres; antennae clothed with short, recumbent, fine setae; antennomeres 2-4 short, robust, subequal in length; fourth antennomere about 2.5× the length of fifth antennomere, antennomeres 5-10 robust, moderately serrate; approximately the same size;

last antennomere elongate, moderately robust, obtusely rounded, slightly longer than tenth antennomere (Fig. 2.9-D); terminal labial palpi securiform.

Thorax: pronotum bisinuate, widest at middle; sides constricted sub apically, more strongly constricted behind middle, moderately constricted in front of middle; surface shiny, smooth, moderately vested with fine, long pale, semirecumbent setae intermixed with some long semierect, fine, pale setae, in some individual vestiture is more abundant on the posterolateral area of the pronotum; finely to moderately punctate; punctations small and shallow; anterior transverse depression and subbasal tumescence absent, abruptly compressed on posterior margin. Prosternum conspicuously wider than long; smooth; polished, devoid of punctation in most individuals, some individuals very feebly punctate, punctations coarse and shallow; moderately vested with fine, pale, semi-erect setae. Mesosternum shiny, smooth, feebly vested with fine, pale, semi-erect setae; moderately punctate. Metasternum: strongly convex, surface shiny to finely rugulose, inconspicuously vested with fine, pale, recumbent setae; longitudinal depression and metaventral process present; metepisternum hidden throughout its length. Scutellum ovoid, compressed medially, clothed with pale, fine, recumbent setae to glabrous.

Elytra: broader than pronotum, moderately elongate; broader than long; humeri indicated, rounded; sides subparallel, gradually broadening toward distal end, broadest behind middle, then abruptly narrowing toward apex on posterior fourth; disc flat above; surface shiny to moderately rugulose; apices subtriangular; inconspicuously dehiscent; elytral declivity moderately steep; surface moderately clothed with fine, short, recumbent, pale setae interspersed with some pale, fine, long, semi-erect setae; surface strongly, coarsely punctate; sculpture consisting of coarse, deep punctations arranged in regular striae that gradually reduce in size toward elytral apex and

disappear on posterior fourth; interstices at elytral base about 3 to 4 × the width of punctation; interstices shiny to moderately rugulose.

Legs: femora shiny, smooth; feebly punctate, posterior and middle femora feebly swollen, anterior femora more swollen; moderately clothed with some pale, fine, semirecumbent and semi-erect setae uniformly located throughout the femoral surface; tibiae slender, moderately punctate, longitudinally rugose, vestiture consisting of pale, recumbent setae interspersed with semi-erect setae.

Abdomen: six visible ventrites; ventrites 1-4 shiny, smooth, convex, subquadrate, feebly punctate, moderately vested with fine, long, pale, recumbent setae; not compressed laterally; posterior margins truncate. Fifth visible ventrite subtriangular; shiny; smooth; polished; surface convex; weakly clothed with fine, long, recumbent setae; lateral margins strongly oblique, arcuate; posterior margin broadly, shallowly emarginate to almost truncate in some individuals. Sixth visible ventrite small, rugulose; feebly convex; moderately, finely punctate; clothed with some erect and semierect, long, piceous setae; conspicuously broader than long; lateral margins strongly oblique; posterior margin broadly, shallowly emarginate to almost truncate; posterolateral angles broadly rounded. Fifth tergite subquadrate, convex; rugulose; glabrous; slightly punctate; posterior margin truncate. Sixth tergite subtriangular; rugulose; wider than long; moderately convex; clothed with fine, pale, recumbent setae; surface moderately punctate; lateral margins oblique, posterior margin truncate to moderately rounded; posterolateral angles moderately to strongly rounded; some long, erect, pale, stout setae located along the posterior margin. Sixth tergite extending beyond apical margin of sixth visible ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece moderately tapered at apex; phallic plate unarmed, denticles absent; intraspicular plate present, elongate, moderately rounded; phallobasic apodeme short, expanded distally; phallobase subparallel; parameres free; tegmen incomplete, partially covering phallus; parameres pointed distally; endophallic struts long, the length of tegmen; endophallic struts in horizontal position in relation to tegmen when in horizontal view; endophallic struts robust distally (Fig. 2.19-B).

Sexual dimorphism: Females of *C. collaris* can be distinguished from male specimens based on the shape of the last abdominal segment. Females have the sixth visible ventrite conspicuously long and broad, appearing as a semicircle, rather than short in length, and broadly, shallowly emarginate, as observed in males.

Material examined: USA: 5 males, 9 females: Hidalgo Co., TX, III-26-1953, D. J. and J. N. Knull; 2 females: Hidalgo Co., TX, III-26-1956, D. J. and J. N. Knull; 1 male, 1 female: Hidalgo Co., TX, 07-IV-1961, D. J. and J. N. Knull; 3 females: Hidalgo Co., TX, IV-03-1961, D. J. and J. N. Knull; 1 male, 3 females: Mobile, AL, V-20-1922, H. P. Loding; 2 males, 4 females: Starr Co., TX, III-20-1952, D. J. and J. N. Knull; 1 male: Spring Hills, AL, 10-V-1918, H. P. Loding; 1 female: Gadsden Co., FL, V-8-1939, D. J. and J. N. Knull; 1 female: TX, Apple Springs, 13-V-1974, R. Reeve; 1 male: Jefferson Co., AL, Birmingham, 5-VII-1956, H. R. Steeves Jr., at light; 1 female: Ft. Mount, GA, IX-7-1937, P. W. Fatting; 2 female: Hidalgo Co., TX, 07-V-1957, D. J. and J. N. Knull; 1 males: Morehead, KY, 21-VI-1949, D. J. and J. N. Knull; 1 male, 2 females: Great Smoky Mountains Nat. Park, TN, VI-14-1942, D. J. and J. N. Knull; 2 males: Hidalgo Co., TX, III-29-1953, D. J. and J. N. Knull; 6 males, 1 female: Starr Co., TX, III-28-1950, D. J. and J.

N. Knull; 1 male: Stone Mt., GA, VI-17-1949; P. W. Fattig; 1 male: Jefferson Co., AL, Vestavia, VII-18-1981, T. King, at light; 1 female: Starr Co., TX, III-31-1963, D. J. and J. N. Knull; 1 male, 2 females: Jefferson Co., AL, Birmingham, Shades Mts., VI-15-1982, T. King, at light; 1 male: Walker Co., AL, Jasper, X-09-1978, T. King, at light; 1 female: Walker Co., AL, nr. Jasper, Devil's Ladder, 04-VII-1981, T. King, at light; 2 females: Clinch Co., GA, N of Homerville at Atkins Co. line, V-28-2004; beating in cypress bog, P. Skelley; 1 male: Liberty Co., FL, Torreya State Park, VII-17-1987, Matthews and Skelley, at light; 1 male: Dixie Co., FL, 3.5 mi N of Old Town, RT. 349, IV-27-1980, M. C. Thomas; 1 male: Alachua Co., FL, Hwy. 241 at Santa Fe River, IV-5-1989, C. W. Mills III, on bark on *Carya illionensis*; 2 females: Starr Co., TX, IV-5-1963, D. J. and J. N. Knull; 1 male: Liberty Co., FL, Torreya State Park, V-6-1989, R. Turnbow; 2 males, 1 female: Bexar Co., TX, Leon Valley, VI-14-1971, G. H. Nelson, beating *Diospytos texana.* MEXICO: 2 females: Mexico, San Luis Potosi, 41 mi N of San Luis Potosi, 26-VI-1965,G. H. and D. E. Nelson; 1 male, 1 female: Mexico, San Luis Potosi, 25.7 km W of Rio Verde, 4100', 2-VI-1987; 1 male: Chiapas, Mexico, La Sepultura, V-2-2008, A. Burke; 2 males: Veracruz, Mexico, 2 km S Jalapa, VII-1985, J. Peña; 1 male: Jalisco, Mexico, Mismaloya River, 5 km E of Hwy. 200, VI-8-1991, W. B. Warner; 1 female: Estado de Mexico, Mexico, Temascaltepec, Bejucos, VII-1993, H. E. Hinton, R. L. Usinger; 1 male, 1 female: Nayarit, 3 mi NW Santa Maria del Oro, June 27, 1963, J. Doyen. 2 males, 1 female: Nuevo Leon, Mexico, 28 km SW Linares, VIII-12-2009, A. Burke, D. Cibrián.

Remarks: Despite the broad geographical distribution of *C. collaris*, a species that ranges from the eastern and southern USA to continental Mexico, Guatemala, and Honduras (Rifkind, 1993), an extensive examination of material collected throughout the range shows the

morphology of the species is consistent throughout its geographical range. Certain characters, however, may vary in accordance to the collecting locality; this variation is apparent when comparing individuals collected in southeastern USA and the Florida peninsula with specimens collected elsewhere. Such variation is observable in the abdomen's integument color of both sexes. Specifically, specimens collected in the southeast USA and the Florida peninsula have the abdomen uniformly piceous, while those individuals collected in midsouthern USA and Mexico presented a moderately fuscous to dark-testasceous coloration. Remaining characters were not variable for all the specimens examined.

Cymatoderella morula Rifkind, 1993

Figs. 2.3-C, 2.9-E, 2.19-C.

Two male paratypes examined.

Type locality: Mexico, Oaxaca, Sierra de Miahuatlán. Type depository: California Academy of Science Collection (CASC).

Distribution: Mexico: Oaxaca; Central America: Guatemala, Honduras.

Differential diagnosis: *Cymatoderella morula* is most similar to *C. collaris*. Characters to distinguish these species appear in the diagnosis section of *C. collaris*.

Redescription. Male. Form: small and robust individuals, elytra gradually expanded toward apex, then abruptly narrowing behind distal fourth. Color: pronotum uniformly testasceous to ferruginous throughout its surface to bicolored, if bicolored, can range from testaceous to ferruginous in the median region and piceous on the margins; legs, thorax and elytra piceous; abdomens dark testaceous; antennae uniformly piceous, or with scape and pedicel dark testasceous to piceous and remaining antennomeres piceous; head and mouthparts with various tones of piceous to brown tones. Elytral disc devoid of any bands or fasciae (Fig. 2.3-C).

Head: including eyes slightly wider than pronotum; eyes of moderate size, taller than wide, conspicuously bulging laterally, finely faceted, posteriorly emarginate; antennal notch located in front of emargination; frons feebly bi-impressed; integument shiny, smooth, finely, sparsely punctate, punctations small, shallow; moderately clothed with fine, pale, semirecumbent setae interspersed with some semi-erect setae; antennae composed of 11 antennomeres; antennae clothed with short, recumbent, fine setae; antennomeres 2-3 short, robust, subequal in length; third antennomere about $2.5 \times$ the length of fourth antennomere, antennomeres 4-10 robust, moderately serrate; subequal in length; last antennomere elongate, moderately robust, obtusely rounded, slightly longer than tenth antennomere (Fig. 2.9-E).

Thorax: pronotum bisinuate, widest at middle; sides constricted subapically, more strongly constricted behind middle and moderately constricted in front of middle; surface shiny, rugulose, moderately vested with fine, short, pale, recumbent setae intermixed with some long and very long, erect, fine, pale setae, the latter setae located on the lateral margins of the pronotum; finely to moderately punctate; punctations small and shallow; anterior transverse depression and subbasal tumescence absent, moderately compressed on posterior margin. Prosternum: conspicuously wider than long; smooth; polished; moderately carinate; devoid of punctation;

glabrous. Mesosternum: shiny, smooth, feebly vested with fine, pale, semi-erect setae; slightly punctate, punctations coarse and deep. Metasternum: strongly convex, surface shiny, smooth, inconspicuously vested with fine, pale, recumbent setae; longitudinal depression and metaventral process present. Metepisternum hidden throughout its length. Scutellum elongate, compressed medially, feebly clothed with pale, fine, semirecumbent setae.

Elytra: broader than pronotum; moderately short; broader than long; humeri indicated, rounded; sides subparallel, gradually broadening toward distal end; broadest behind middle, then abruptly narrowing toward apex behind posterior third; disc flat above; surface shiny, smooth; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity moderately steep; surface clothed with fine, short, pale, recumbent setae interspersed with some scattered pale, fine, long, erect setae; surface strongly, coarsely punctate; sculpturing consists of coarse, deep, punctations arranged in regular striae that gradually reduce in size toward elytral apex and completely disappear on posterior fifth; interstices at elytral base about $2 \times$ the width of punctation; interstices shiny, smooth.

Legs: femora shiny, smooth, swollen, anterior femora conspicuously more swollen than middle and posterior femora; moderately clothed with some pale, fine, semirecumbent and semi-erect setae; tibiae feebly rugulose, vestiture similar to that observed on femora, some individuals have tibiae more strongly vested than femora.

Abdomen: six visible ventrites; ventrites 1-4 shiny, convex, smooth, subquadrate, punctate, moderately clothed with fine, long, pale, recumbent setae; not compressed laterally; posterior margins truncate. Fifth visible ventrite subtriangular; shiny; smooth; polished; surface moderately convex; clothed with fine, long, pale, recumbent setae; lateral margins strongly oblique, arcuate; posterior margin narrowly, shallowly emarginate. Sixth visible ventrite small,

shiny, smooth; feebly convex; moderately, finely punctate; sparsely clothed with some short, pale, fine, semi-erect setae; conspicuously broader than long; lateral margins strongly oblique, arcuate; posterior margin broadly, shallowly emarginate; posterolateral angles broadly rounded. Fifth tergite subquadrate, convex; glabrous; feebly punctate; posterior margin truncate. Sixth tergite subtriangular; rugose; wider than long; convex; sparsely clothed with fine, pale, recumbent setae; surface moderately, finely punctate; lateral margins oblique, posterior margin moderately rounded; posterolateral angles strongly rounded; some long, erect, dark, stout setae located along the posterior margin and posterolateral angles. Sixth tergite extending beyond apical margin of sixth visible ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece conspicuously swollen at apex; phallic plate unarmed, devoid of denticles; intraspicular plate present, moderately short and rounded; phallobasic apodeme short, expanded distally; phallobase subparallel; parameres free; tegmen incomplete, partially covering phallus; parameres moderately pointed distally; endophallic struts long, the length of tegmen; endophallic struts slender distally (Fig. 2.19-C).

Sexual dimorphism: Females of *C. morula* can be distinguished from male individuals based on the shape of the last abdominal segment. Female specimens have the sixth visible ventrite broadly rounded posteriorly, rather than subtriangular in shape and broadly, shallowly emarginate, as observed in male specimens.

Material examined: PARATYPE: 1 male: Oaxaca, Mexico, Sierra de Miahuatlán, 5500', Highway 175 10 km S of Miahuatlán, VII-5-1989, on dry oak forest, E. Barchert, A. Evans, J.

Rifkind. PARATYPE: 1 male: Honduras, vic. L. Yojoa, Montaña de Pozo Azul, 28-V-1979, E. Giesbert.

Additional material examined: 1 male: Departamento de Alta Verapaz, Guatemala, 57 km N of El Rancho, on new Cobán highway, V-30-1973, 1463 m, W. Opitz; 1 female: Granada, Nicaragua, Reserva Natural Volcan Mombacho, 11° 50' 04" N, 85° 58' 48" W 1100 m, V-19-2000, m.v. light. Smith, Ocampo, Cave, Cordero.

Cymatoderella patagoniae Knull, 1946

Figs. 2.3-D, 2.17 C-D, 2.19-D.

Eighteen male and twelve female paratypes examined.

Type locality: Arizona, Patagonia Mountains, Santa Cruz Co. Type depository: Field Museum of Natural History Collection (FMNH).

Distribution: USA: Arizona; Mexico: Jalisco, Sonora.

Differential diagnosis: *Cymatoderella patagoniae* can be differentiated from other congeners based on the color of the pygidium and the elytral vestiture. *Cymatoderella patagoniae* has the pygidium testaceous to ferrugineous (Fig. 2.17 C-D), and the elytral vestiture is pale to whitish, fine, recumbent and moderately abundant (Fig. 2.3-D), while *C. collaris* and *C. morula* possess the last abdominal segment black to brown, and the elytral disc is moderately clothed with pale, yellowish to testaceous, semirecumbent setae interspersed with some semi-

erect setae. The distribution of these species may further serve to separate *C. patagoniae* from its congeners. *Cymatoderella patagoniae* is restricted to south Arizona and north Sonora; while *C. collaris* is distributed from eastern and southern USA down to Mexico and Central America, and *C. morula* is found in south Mexico, Guatemala, Honduras and Nicaragua.

Redescription. Male. Form: small and robust, elytra gradually expanded toward apex, abruptly narrowing behind the posterior fourth. Color: head and scutellum ranging from uniformly testasceous, ferruginous, with different tones of dark testaceous, light brown, to completely piceous integument; mouthparts with various tones of piceous to brown tones; pronotum uniformly testasceous; legs, thorax and elytra piceous; abdominal segments 1-5 dark testaceous to ferrugineous, pygidium testaceous to ferrugineous; antennae uniformly piceous, Elytral disc devoid of any bands or fasciae (Fig. 2.3-D).

Head: including eyes wider than pronotum; eyes of moderate size, taller than wide, bulging laterally, finely faceted, emarginate posteriorly; antennal notch located in front of emargination; frons bi-impressed; integument shiny, finely, sparsely punctate, puctations small, shallow; conspicuously clothed with fine, whitish, semirecumbent setae interspersed with some erect, pale setae located around eyes; antennae composed of 11 antennomeres; antennae moderately vested with short, recumbent, fine, whitish setae; antennomeres 2-4 short, robust, subequal in length; fourth antennomere about 3× the length of fifth antennomere, antennomeres 5-10 robust, moderately serrate; subequal in length; last antennomere elongate, moderately robust, obtusely rounded, 1.5× longer than tenth antennomere.

Thorax: pronotum bisinuate, widest at middle; sides constricted subapically, more strongly constricted behind middle and constricted in front of middle; surface shiny, rugulose, profusely

clothed with fine, short, pale, semirecumbent setae intermixed with some long, erect, fine, pale setae; moderately punctate; punctations wide and shallow; anterior transverse depression moderately impressed, subbasal tumescence absent; moderately compressed posteriorly. Prosternum: conspicuously wider than long; smooth; polished; feebly carinate; devoid of punctatation; glabrous. Mesosternum: rugulose, vested with fine, pale, semi-erect setae; moderately punctate, punctations coarse and deep. Metasternum: strongly convex, surface shiny, rugulose, inconspicuously vested with fine, pale, recumbent setae; longitudinal depression and metaventral process present. Metepisternum hidden throughout its length. Scutellum elongate, feebly clothed with pale, fine, semirecumbent setae.

Elytra: broader than pronotum; moderately elongate, broader than long; humeri indicated, rounded; sides gradually broadening toward distal end, broadest on posterior fourth, then abruptly narrowing toward apex behind posterior fourth; disc flat above; surface shiny, smooth; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity relatively gradual; surface conspicuously vested with fine, short, whitish, recumbent setae sporadically interspersed with some whitish, fine, long, erect setae; surface punctate, punctations arranged in regular striae; sculpturing consists moderately coarse, shallow, punctations arranged in regular striae that gradually reduce in size and depth toward elytral apex and completely disappear on posterior sixth; interstices at elytral base about 2.5 × the width of punctation; interstices shiny, rugulose.

Legs: femora shiny, rugulose, feebly swollen, clothed with some whitish, fine, semirecumbent and semi-erect setae; tibiae longitudinally rugulose, vestiture similar to but more abundant than femora.

Abdomen: six visible ventrites; ventrites 1-4 shiny, smooth, polished, convex, subquadrate, moderately punctate, clothed with fine, long, yellowish pale, recumbent setae; not compressed

laterally; posterior margins truncate. Fifth visible ventrite subtriangular; shiny; smooth; polished; surface convex; vested with fine, long, pale, recumbent setae; lateral margins strongly oblique, arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite small, moderately to strongly rugulose; surface flat, moderately, finely punctate; clothed with short, pale, fine, semi-erect setae intermingled with some long, pale, erect setae; conspicuously broader than long; lateral margins strongly oblique, arcuate; posterior margin broadly, somewhat deeply emarginate; posterolateral angles broadly rounded (Fig. 2.17-D). Fifth tergite subquadrate, convex; glabrous; feebly punctate; posterior margin truncate. Sixth tergite subquadrate; moderately rugose; wider than long; convex; clothed with fine, pale, recumbent setae; surface finely punctate; lateral margins oblique, posterior margin truncate to semicircularly emarginate, posterolateral angles rounded; some long, erect, dark, stout setae located along the posterolateral margins (Fig. 2.17-C). Sixth tergite extending beyond apical margin of sixth visible ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece tapered at apex; phallic plate unarmed, devoid of denticles; intraspicular plate present, elongate; phallobasic apodeme short, expanded distally; phallobase subparallel; parameres free; tegmen incomplete, partially covering phallus; parameres moderately pointed distally; endophallic struts long, slightly longer the length of tegmen; endophallic struts in horizontal position in relation to tegmen when in horizontal view; endophallic struts robust distally (Fig. 2.19-D).

Sexual dimorphism: females have the sixth visible abdominal segment broadly rounded posteriorly, rather than broadly, shallowly emarginate, as observed in male specimens.

89

Material examined: PARATYPES: 18 males, 12 females: Patagonia Mountains, AZ, VII-2-3, D. J. and J. N. Knull.

Additional material examined: USA: 1 male, 1 female: Peloncillos Mountains, AZ, 33 mi E of Douglas, VII-17-1973, S. McCleve. MEXICO: 2 males, 3 female: Sonora, Mexico, Highways 15, 12 mi N of Hermosillo, 14-VIII-1965, G. H. Nelson, on *Olneya tesota* Gray; 1 male: Jalisco, Mexico, 22 km SW Llano Grande, 270 m, VI-28-1995, R. L. Westcott.

Remarks: Rifkind (1993) examined two specimens tentatively identified by him as *C. patagoniae* which were collected in the western portion of the Mexican state of Jalisco. I had the opportunity to examine one of these specimens and compared it with the extensive type series Knul (1946) designated as *C. patagoniae.* This specimen certainly falls well into Klug's original description; therefore, I have listed this specimen as part of the material examined in this revisionary work; for that reason, the geographic range of the species is extended to Jalisco, Mexico.

3.9 Lecontella Wolcott & Chapin, 1918

Type species *Cymatodera (Lecontella) cancellata* LeConte, 1854, original designation.

(Distribution shown in Fig. 2.21-I)

Differential diagnosis: The genus *Lecontella* is most similar to *Cymatodera*. A number of morphological characters can be used to differentiate them. Members of *Lecontella* have the

pronotum and the elytral disc coarsely punctate (Figs. 2.3 E-F, 2.4-A, 2.7-G, 2.12-F), the striae on the elytral disc extend to the apex, the antennae are moderately serrate, and antennomeres 2-10 are conspicuously compacted (Figs. 2.9-F, 2.10 A-B). Species of *Cymatodera* have the pronotum and the elytral disc moderately punctate and the striae almost never reach the elytral apex (Figs. 2.4-F, 2.5-E, and see Figs. 3.3-F, 3.3 A-F and 3.18 B-C from Chapter 3), the antennal shape ranges from filiform to moderately serrate, and antennomeres 2-10 are not compacted (Fig. 2.10 G-H). Various keys of identification have previously used the conspicuously long eleventh antennomere of *Lecontella* as a diagnostic character to differentiate this genus from the closely allied *Cymatodera*; however, I have found that a number of species in *Cymatodera* (Fig. 2.10-H) share this character state with *Lecontella*.

Redescription: Size: 8-28 mm. Color: Body uniformly fuscous to testaceous except abdomen, slightly lighter than rest of the body, integument can range from brown-testaceous to almost ferrugineous in some individuals. Elytral disc with fasciae or maculae absent. Body: winged species, elongate, feebly to moderately robust.

Head: including eye slightly wider than pronotum; integument coarsely punctate, punctations vary from narrow to wide; eyes large, coarsely faceted, feebly emarginate anteriorly conspicuously bulging laterally; antennae moderately to strongly serrate, consisting of 11 antennomeres; antennomeres 2-10 moderately to conspicuously compacted (Fig. 2.9-F, 2.10 A-B); frons bi-impressed or not; terminal labial palpi securiform; terminal maxillary palpi cylindrical, compressed laterally. Sexual dimorphism observable in eleventh antennomere, males have this segment conspicuously longer than that of females.

Thorax: pronotum deeply punctate, punctation may range from moderately narrow to conspicuously wide (Fig. 2.12 E-F); pronotum widest at middle, sides more constricted behind middle. Mesepisternum fully covered by elytron in lateral view (Fig. 2.12-C). Prosternum rugose to smooth, moderately punctate, punctation coarse. Mesosternum wider than long, smooth, moderately punctate, punctations coarse. Metasternum wider than long, surface conspicuously punctate; punctation moderately wide. Metaventral process compressed anteriorly; metepisternum hidden by elytra throughout its length in lateral view.

Elytra: elongate, subparallel, slightly broader on posterior third; surface coarsely punctate (Fig. 2.7-G), punctations arranged in striae, punctations extending to apex; scutellum ovoid, compressed; moderately vested; epipleural fold complete, narrowing toward apex. Legs: femora moderately to coarsely rugose; moderately swollen; tibiae slender rugulose to rugose; tarsal formula 4-4-4; pulvillar formula 4-4-4; two tarsal denticles, tarsal denticles trigonal in shape; moderately to strongly vested.

Abdomen: six visible ventrites; ventrites 1-4 not impressed laterally; pygidium of males feebly differentiated form that of females. Aedeagus: sclerotized; length of aedeagus shorter than the length of abdomen; tegmen triangular; phallic plate devoid of denticles; phallobasic apodeme short, as long as or longer than phallus; endophallic struts enlarged feebly swollen distally.

Remarks: *Lecontella* was originally described by Wolcott a&Chapin (1918), with *Lecontella* (*Cymatodera*) *cancellata* (LeConte) as the type species; later on, *L. cancellata* was later synonymized by Ekis (1975) with *L. brunnea* (Spinola). The genus is currently composed of three species: *L. brunnea* (Spinola), a species originally described as *Cymatodera longicornis* var. *brunnea* Melsheiner 1846, later on transferred to *Lecontella* by Wolcott & Chapin (1918) the

92

current type species for the genus; *L. gnara* Wolcott, 1927; and *L. striatopunctata,* a species originally describe as *Cymatodera striatopunctata* (Chevrolat, 1876), and subsequently transferred to *Lecontella* by Wolcott (1927). The genus is widely distributed in the USA and Mexico, with one species extending to Central America. Mawdsley (2002) indicated that larvae of *L. brunnea* are parasites in nests of solitary bees and wasps, and on immature stages of Cerambycidae and Buprestidae inside tunnels in fallen trees constructed by larvae of various species of those two beetle families. Adults of *Lecontella* species are regularly collected by light traps. Females of *Lecontella brunnea* and *L. striatopunctata* are indistinguishable from each other and are identified based on geographic range.

Key to species of *Lecontella* Wolcott & Chapin

1. Punctation on pronotal disc coarse, deep and wide (Fig. 2.12-B) ....***Lecontella gnara***
- Punctations on pronotal disc small, fine and shallow (Fig. 2.12-E) 2
2 (1). Male antennomeres 2-10 moderately compacted and robust, last antennomere of males cylindrical, elongate, flattened apically, at least 4-5× the length of tenth antennomere (Fig. 2.9-F); antennae as long as combined length of head and pronotum; ....male ***Lecontella brunnea***
- Male antennomeres 2-10 conspicuously compacted and robust, last antennomere of males cylindrical, robust, moderately elongate, not flattened apically, at least 3-4 × the length of tenth antennomere (Fig. 2.10-B); antennae shorter than combined length of head and pronotum; ....male ***Lecontella striatopunctata***

Lecontella brunnea (Spinola, 1844)

Figs. 2.3-E, 2.9-F, 2.12-E, 2.19-E.

Synonyms: *Cymatodera longicornis* var. *brunnea* (Melsheimer, 1846) nec Spinola 1844, Proc.
Acad. Philad., II-12, 1844-45 (1846) p. 306 (*Cymatodera*) Synonymized by LeConte (1854), and
transferred to *Lecontella* by Wolcott & Dybas (1918); *Cymatodera cancellata* LeConte, 1854,
Proc. Acad. Philad. VII, 1854, p. 81 (*Cymatodera*) Synonymized by Wolcott (1920).

Type material not examined.

Type locality: Brownsville, Texas. Type depository: Italy, Torino, Museo Regionale di Scienze
Naturali (SCUT).

Distribution: USA: AR, FL, GA, IA, IN, KS, ME, MI, MO, NC, NJ, OH, OK, PA, TX, VA;
Mexico: Baja California, Jalisco, Michoacan, Morelos, Nayarit, Nuevo Leon, Oaxaca, Sinaloa,
Sonora, Tamaulipas.

Differential diagnosis: *Lecontella brunnea* is most similar to *L. gnara*. The two species are
partially sympatric but they can be identified based on the punctations on the pronotal surface.
Pronotal punctations on *L. brunnea* are small and conspicuously numerous (Fig. 2.12-E), while
the pronotal punctations of *L. gnara* are coarser, deeper, and broader than of observed in *L.
brunnea* (Fig. 2.12-F). Antennomeres 2-10 of *L. brunnea* are somewhat slender, inconspicuously
compacted and moderately serrated, and the serration increasing toward the distal end (Fig. 2.9-

F); while *L. gnara* has antennomeres 2-10 somewhat robust and moderately compacted, and feebly serrated (Fig. 2.10-A).

Redescription. Male. Form: medium-sized to large, moderately robust individuals. Color: head, pronotum, thorax, scutellum, legs and antennae brown to brunneous; elytra light brown to brunneous; mouthparts fuscous, posterior half of mandibles piceous; abdominal segments brown to light testaceous; elytral disc devoid of any bands or fasciae (Fig. 2.3-E).

Head: including eyes wider than pronotum; eyes large, moderately taller than wide, bulging laterally, coarsely faceted, moderately emarginate posteriorly; antennal notch located in front of emargination; frons bi-impressed; integument coarsely, conspicuously, deeply punctate; moderately clothed with fine, whitish, semirecumbent setae interspersed with some erect, pale setae; antennae composed of 11 antennomeres; antennae moderately vested with short, recumbent, fine, whitish setae; antennomeres robust, antennomeres 2-10 about same length, gradually increasing in width toward distal end, last antennomere of males sexually dimorphic, conspicuously elongate, moderately robust, parallel, cylindrical, posterior portion rounded 4-6× longer than length of tenth antennomere.

Thorax: pronotum bisinuate, widest at middle, moderately short in length; sides constricted subapically, tapered, widest in the middle; surface rugulose, conspicuously punctate, punctations moderately small and deep (Fig. 2.12-E), moderately clothed with fine, short, pale, recumbent setae intermixed with some long, erect, fine, pale setae, long setae more abundant on lateral area of pronotum; anterior transverse depression moderately impressed, subbasal tumescence absent; posterior margin of pronotum compressed. Prosternum: conspicuously wider than long; smooth; polished; very feebly punctate to absent; surface vested to glabrous. Mesosternum: surface

rugulose, feebly vested with fine, pale, semi-erect setae; coarsely, conspicuously punctate, punctations moderately wide and deep. Metasternum: surface rugulose, moderately convex; numerously, coarsely punctate; moderately vested with fine, pale, recumbent setae; longitudinal depression and metaventral process present. Scutellum elongate, feebly clothed with pale, fine, semirecumbent setae, moderately compressed medially.

Elytra: broader than pronotum; elongate; humeri indicated, rounded; sides inconspicuously broadening toward distal end, broadest on posterior third, then abruptly narrowing toward apex at posterior fourth; disc flat above; surface rugose to rugulose; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity moderately steep; surface conspicuously vested with fine, short, whitish, recumbent setae sporadically interspersed with some whitish, fine, long, erect setae; conspicuously, coarsely punctate, punctations arranged in regular striae; sculpturing consisting of coarse, deep, wide punctations arranged in regular striae of the same size through the length of the striae, punctation reaching the elytral apex; interstices at elytral base about $0.5 \times$ the width of punctation; interstices rugulose. Epipleural fold gradually narrowing toward apex, last sixth feebly to moderately crenulate.

Legs: femora rugose, feebly swollen, clothed with some whitish, fine, semirecumbent and semi-erect setae, surface conspicuously punctate, punctations small and shallow; tibiae rugulose, moderately punctate, punctations shallow and small, vestiture consisting of stiff recumbent and semirecumbent setae.

Abdomen: six visible ventrites; ventrites 1-4 shiny, smooth, polished, convex, subquadrate, moderately punctate, clothed with fine, long, yellowish pale, recumbent setae; not compressed laterally; posterior margins truncate. Posterior margin of first visible ventrite conspicuously elevated with a transverse carina originating next to posterolateral angles producing a broad,

deep, arcuate emargination. Fifth visible ventrite subtriangular; shiny; surface rugulose, convex, moderately punctate, punctations shallow and moderately small; vested with fine, short pale, recumbent setae; lateral margins strongly oblique, moderately arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite small shape triangular; moderately to strongly rugulose; surface convex, moderately, finely punctate; clothed with short, pale, fine, semi-erect setae; broader than long; lateral margins strongly oblique, moderately arcuate; posterior margin short, broadly, deeply, V-shaped emarginate. Fifth tergite subtriangular, surface convex, shiny, conspicuously rugulose; feebly punctate; posterior margin truncate. Sixth tergite strongly triangular; moderately rugose; longer than wide; surface convex; moderately clothed with fine, pale, recumbent setae; surface finely punctate; lateral margins strongly oblique, posterior margin small, nearly acuminate, inconspicuously truncate. Sixth tergite slightly extending beyond apical margin of sixth visible ventrite, fully covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece conspicuously swollen at apex; phallic plate unarmed, devoid of denticles; intraspicular plate present, elongate; phallobasic apodeme long, feebly expanded distally; phallobase subparallel; parameres free; tegmen complete, fully covering phallus; parameres pointed distally; endophallic struts long, slender distally (Fig. 2.19-E).

Sexual dimorphism: Females of *L. brunnea* can be differentiated from male specimens based on the structure of the last abdominal segment. The sixth visible segment in females is broadly rounded, while males have this segment somewhat triangular in shape; moderately to strongly rugulose, convex, broader than long, the lateral margins are moderately to strongly oblique, and the posterior margin is short and broadly, deeply, V-shaped emarginate.

Additionally, females have the eleventh antennomere short, moderately robust, obtusely rounded, moderately longer than tenth antennomere, but males have the last antennomere cylindrical, not compressed medially and conspicuously longer than that of females.

Material examined: USA: 12 males, 16 females: San Bernardino Co., CA, Joshua Tree Nat. Park, 12-V to 25-VIII-2010, Black light, E. Sadler; 2 females: New Braunfels, TX, VI7, H. Mittendorf; 1 male: Bethel, TX, [no collecting date]; 1 female: S. Pines, NC, VI-29-1919, A. H. Manee; 1 female: Harrisburg, PA, VII-3-1936, J. N. Knull; 2 females: Rockville, PA, V-25-1919, J. L. Knull; 1 female: Starr Co., TX, V-25-1951, D. J. and J. N. Knull; 1 female: Mont Alto, Pennsylvania, 1-VII-1931, A. Champlain; 1 female: Uvalde Co., TX VIII-4-1934, D. J. and J. N. Knull; 2 males: Brownsville, TX, V-11-1934, J. N. Knull; 1 female: Archbold Biol. Sta., Highlands Co. FL, IX-11-1958, S. W. Frost; 1 female: Yuma, AZ, [no collecting date], W. Lipe; 1 female: Benton Co., AR, VII-5-1942, M. W. Sanderson; 1 male, 2 females: Hidalgo Co., TX, VI-8-1958, D. J. and J. N. Knull; 1 female: Alpine, TX, VIII-6 (no collecting date), D. Larsen; 1 female: El Paso, TX, VI-8-1914; F. Larsen; 1 female: Texas [no data available]; 1 male, 1 female: Fedor, TX, [no collecting data], J. D. Sherman; 1 female: TX, 1918, C. V. Riley; 1 female: TX, [no collecting date], G. Wells; 2 males: TX, 1939 [no collecting date], New Hampshire, J. D. Sherman; 1 male: Lee Co., TX, [no collection date]; 1 female: Cameron Co., TX, Sabal Palm Groove Audubon Sanctuary, VI-2-6-1986, R. M. Brattain; 1 female: Warren Co., IN, VI-1970 [no collector data]; 1 male: Brooks Co., TX, 12 m, W of Rachal, V-8-1986, N. M. Downie; 1 male: Comal Co., TX, Bulverde, mv + bl, VI-1-1998, R. Turnbow; 2 females: Kinney Co., TX, 7 mi NE Brackettville, mv + bl, VI-23-2000, R. Turnbow; 1 female: Hidalgo Co., TX, Santa Ana Ref., VI-10-1975, J. E. Wappes; 1 female: Cameron Co., TX, Near

Brownsville, VI-28-1989; R. L. Heitman; 1 male, 2 females: Jackson Co., MO, Raytown, VII-4-1978, G. H. Nelson; 1 female: Jackson Co., MO, Blue Springs, at UV light, G. H. Nelson; 1 male: Starr Co., TX, Falcon Heights, at lite, VI-12-1975, H. Turnbow; 1 female: Grantsburg, IN, at black light, VII-4-1964, D. Eckert; 2 males: Monroe Co., FL, Flamingo, Everglades National Park, VII-8-1977 [no collector data]; 1 female: Aransas Co., TX, Goose Island State Park, North of Aransas Pass, VI-14-1969, R. L. Heitzman; 1 female: Highlands Co., FL, Arch Biol. Sta., IX-15-1978, L. L. Lampert, Jr; 1 male: Cameron Co., TX, Brownsville, V-22-1967, W. H. Tyson: 1 female: Columbia, MO, VI-27-1966, S. Poe; 2 males: Monroe Co., FL, Big Pine Key, 19-VI-1975, J. B. Heppner; 1 female: Lancaster Co., NE, VII-19-1984, L K. Rieske; 1 male: Comanche Co., OK, Fort Sill, West Range Near Strip 15, VII-19-2006, B. Kondratieff and W. Cranshaw; 1 male, 2 females: Comanche Co., OK, Fort Sill, Quanah Range, near twin gates, VIII-2-2006, B. Kondratieff, M. Camper and J. Owens; 1 male, 2 females: Comanche Co., OK, Fort Sill, Quanah Range, Quanah Cr., IX-16-2006; 1 male: Comanche Co., OK, Fort Sill, East Range, Nat. Res. Building, VIII-2-2006, B. Kondratieff, M. Camper and J. Owens; 1 male, 8 females: Starr Co., TX, Round Mountain, [no collecting date], Riley; 1 female: Gonzalez Co., TX, Seguin, VII-16-18-1984, K. W. Vick, bl trap; 1 female: TX, Hidalgo Co., Bentsen-Rio Grande State park, VII-1-1961, R. H. Arnett Jr and E. Van Tassell; 1 female: Pima Co., AZ, Sonoran desert Mus., IX-2-1975, R. Turnbow; 2 males: Jeff Davis Co., TX, Davies Mt., St. Park, VII-18-21-1973, F. T. Hovore; 1 female: Johnson Co., TX, Cleburne, St. Park, 7-VII-1971, G. H. Nelson and Family; 2 females: Bexar Co., TX, Leon Valley, IV-4-1971, G. H. Nelson, on *Prosopis chilensis*; 2 males, 2 females: FL, Myakka River State Park, VII-25-2000, funnel trap; Ford Co., TX, Highway 6 at Wichita River, VIII-3-6-1996, S. P. Holmes; 1 male, 1 female: Comal Co., TX, Bulverde, VI-21-26-1993, J. E. Wappes; 1 male: Hidalgo Co., TX, Anzulduas Park, Hg light, V-27-1986, Morris

and Morris; 2 females: Hidalgo Co., TX, Bentsen- Rio Grande State Park, VIII-10-1996, D. J. Heffern; MEXICO: 1 female: Apatzingan [Michoacan], Mexico, VIII-5-1942, H. Hoogstraag; 2 males, 1 female: Jalisco, Mexico, 14 km N Guadalajara, Ruta 54, Posada San Isidro, VI-23, R. Miller and L. Stange; 1 male: Nayarit, Mexico, Rio Santiago, Las Andujas, VII-11-13-1991, E. Barrera; 2 males, 1 female: Oaxaca, Mexico, Dominguillo, 760 msnm, N 17 38 907 O 96 54 703, VIII-20-1998, S. Zaragoza

Lecontella gnara Wolcott, 1927

Figs. 2.3-F, 2.7-G, 2.10-A, 2.12 C, F, 2.19-F.

Synonyms: *Cymatodera cilindrocollis* Spinola, 1844, nec. Chevrolat, 1833, no. 11 (*Cymatodera*). "Mexique" Synonymized by Ekis, 1975.

Two female paratypes examined.

Type locality: Sabinas Canyon, Tucson, Arizona. Type depository: FMNH (Chicago Field Museum of Natural History).

Distribution: USA: AZ, CA, NM, NV, TX, UT; Mexico: Baja California, Sonora.

Differential diagnosis: *Lecontella gnara* is most closely related to *L. brunnea*. Characters to distinguish these species is given in the diagnosis section of *L. brunnea.*

Redescription. Male. Form: medium-sized to large, moderately robust individuals. Color: head, pronotum, thorax, scutellum, legs and antennae brown to brunneous; elytra testaceous to brunneous; mouthparts fuscous, last fourth of mandibles piceous to black; abdominal segments testaceous to piceous; elytral disc devoid of any bands or fasciae (Fig. 2.3-F).

Head: including eyes wider than pronotum; eyes large, moderately taller than wide, bulging laterally, coarsely faceted, moderately emarginate posteriorly; antennal notch located in front of emargination; frons bi-impressed; integument coarsely, conspicuously, deeply punctate; moderately clothed with fine, pale, recumbent setae interspersed with some erect, pale setae; antennae composed of 11 antennomeres; antennae vested with short, recumbent, fine, pale setae; antennomeres 2-10 moderately robust, about the same length, gradually increasing in width toward distal end, antennomeres 1-4 cylindrical; serration in antennomeres 5-10 gradually increasing toward distal end; last antennomere of males sexually dimorphic, conspicuously elongate, moderately robust, parallel, cylindrical, posterior portion rounded 4-6× longer than length of tenth antennomere (Fig. 2.10-A).

Thorax: pronotum bisinuate, widest at middle, moderately short in length; sides constricted subapically, more strongly constricted behind middle and feebly constricted in front of middle; surface conspicuously punctate, elytral disc with punctations coarse, deep interspersed with a smooth disc (Fig. 2.12-F); moderately clothed with fine, short, pale, recumbent setae intermingled with some long, erect, fine, pale setae, long setae more abundant on anterior and lateral area of pronotum; anterior transverse depression moderately impressed, subbasal tumescence absent; posterior margin of pronotum compressed. Prosternum: conspicuously wider than long; moderately to strongly punctate, punctation fine, deep; surface vested to glabrous. Mesosternum: surface rugulose, very feebly vested with fine, pale, semi-erect setae; coarsely top

very coarsely punctate, punctations wide, deep. Metasternum: surface smooth to rugulose, convex; numerously, moderately punctate, punctations moderately coarse, shallow to deep; vested with fine, pale, recumbent setae; longitudinal depression and metaventral process present. Scutellum elongate, feebly clothed with pale, fine, semirecumbent setae, moderately compressed medially.

Elytra: broader than pronotum; elongate; humeri indicated, rounded; sides inconspicuously broadening toward distal end, broadest on posterior third, then abruptly narrowing toward apex at posterior fourth; disc flat above; surface rugose to rugulose at interstices; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity moderately steep; surface moderately vested with fine, short, pale, recumbent setae interspersed with some pale, fine, long, erect setae; conspicuously, coarsely punctate, punctations consisting of coarse, deep, wide punctations arranged in regular striae of the same size that decrease in size at elytral declivity, punctation reach the elytral apex (Fig. 2.7-G); interstices at elytral base as wide as the width of punctation; interstices smooth. Epipleural fold gradually narrowing toward apex, last sixth feebly to moderately crenulate.

Legs: femora rugulose to moderately rugose, feebly swollen posteriorly, clothed with some whitish, fine, semirecumbent and semi-erect setae, surface conspicuously punctate, punctations small and shallow; tibiae rugulose, moderately punctate, punctations shallow and small, vestiture consisting of short, recumbent and semirecumbent setae.

Abdomen: six visible ventrites; first ventrite coarsely rugose to rugulose, ventrites 2-4 moderately rugulose, convex, subquadrate, moderately punctate, clothed with fine, long, yellowish pale, recumbent setae; not compressed laterally; posterior margins truncate. Posterior margin of first and second visible ventrites moderately elevated with a transverse carina

originating next to posterolateral angles producing a broad, moderately elevated arcuate emargination. Fifth visible ventrite subtriangular; shiny; surface rugulose, convex, moderately punctate, punctations shallow, small; vested with fine, pale, recumbent setae; lateral margins oblique, feebly arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite small shape subtriangular; rugulose to rugose; surface convex, moderately, finely punctate; clothed with short, pale, fine, recumbent setae; broader than long; lateral margins moderately oblique, arcuate; posterior margin short, broadly, shallowly, emarginate. Fifth tergite subquadrate, surface convex, shiny, finely rugulose; punctate; posterior margin truncate. Sixth tergite subquadrate; rugulose to rugose; wider than long; surface convex; moderately clothed with fine, pale, recumbent setae; surface punctate; lateral margins oblique; posterior margin broadly, feebly emarginate. Sixth tergite extending beyond apical margin of sixth visible ventrite, covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece swollen at apex; phallic plate unarmed; intraspicular plate present, moderately elongate; phallobasic apodeme long, slightly expanded distally; phallobase subparallel; parameres free; tegmen complete, completely covering phallus; parameres pointed distally; endophallic struts long, slender distally (Fig. 2.19-F).

Sexual dimorphism: Females of *L. gnara* can be differentiated from male specimens based on the shape of the last abdominal segment. The sixth visible segment in females is broadly rounded, while male individuals have this segment somewhat subquadrate with the posterior margin broadly, very shallowly emarginate. Additionally, female specimens of *L. gnara* have the eleventh antennomere short, moderately robust, obtusely rounded, moderately longer than tenth

antennomere; males have the last antennomere cylindrical, not compressed medially and conspicuously longer than that of females.

Material examined: PARATYPE: 1 female: Sabino Canyon, Tucson, Arizona, 15-VII-1915, L. Liebeck; PARATYPE: 1 female: Copper Basin, near Prescott, Arizona, 9-IX-1907, J. A. Krusche;

Additional Material examined: 1 female: Arnett Creek, AZ, S. W. Superior, VIII-13-1972, L. J. Bayer; 1 male: Chiricahua Mountains, AZ, VII-20-1953, D. J. and J. N. Knull; 2 males: Chiricahua Mountains, AZ, VII-22-1957, D. J. and J. N. Knull; 1 male: Chiricahua Mountains, AZ, VII-17-1957, D. J. and J. N. Knull; 1 male, 1 female: Chiricahua Mountains, AZ, VIII-8-1952, D. J. and J. N. Knull; 1 male: Chiricahua Mountains, AZ, VIII-26, D. J. and J. N. Knull; 1 male, 3 females: Chiricahua Mountains, AZ, VII-9-1959, D. J. and J. N. Knull; 1 female: Chiricahua Mountains, AZ, VII-14-1957, D. J. and J. N. Knull; 2 males, 1 female: Chiricahua Mountains, AZ, VII-15-1961, D. J. and J. N. Knull; 3 females: Chiricahua Mountains, AZ, VII-22-1961, D. J. and J. N. Knull; 1 male, 3 females: Chiricahua Mountains, AZ, VIII-28-1962, D. J. and J. N. Knull; 2 males, 1 female: Tucson, AZ, VII-29, J. N. Knull; 2 males: Tucson, AZ, VIII-10, J. N. Knull; 2 females: Chiricahua Mountains, AZ, VII-11, D. J. and J. N. Knull; 1 female: Chiricahua Mountains, AZ, VIII-12-1952, D. J. and J. N. Knull; 2 male, 3 females: Tucson, AZ, VIII-27, D. J. and J. N. Knull; 2 females: Chiricahua Mountains, AZ, VII-27-1953, D. J. and J. N. Knull; 1 male: Chisos Mountains, TX, Oak Spring, VIII-15-1962, C. A. Triplehorn; 2 females: Chiricahua Mountains, AZ, VIII-2-1952, D. J. and J. N. Knull; 1 female: Chiricahua Mountains, AZ, VIII-28, D. J. and J. N. Knull; 1 female: Tucson, AZ, VIII-13; J. N. Knull; 1 female: Tucson, AZ, VIII-27, D. J. and J. N. Knull; 1 female: Tucson, AZ, VII-11, J. N.

Knull; 2 males: Tucson, AZ, VII-14, J. N. Knull; 2 males: Chiricahua Mountains, AZ, VIII-21-1962, D. J. and J. N. Knull; 1 male: Tumacacori Mountains, AZ, VIII-2-1962; D. J. and J. N. Knull; 2 females: Sabino Canyon, AZ, VIII-15-1945, Tucker; 1 female: Tucson, AZ, VIII-6, J. N. Knull; 1 male: Wickenburg, AZ, VII-25, D. J. and J. N. Knull; 1 male: Tucson, AZ, VIII-6-1913, J. N. Knull; 1 female: Tucson, AZ, 26-VII-1920, J. N. Knull; 2 females: Huachuca Mountains, AZ, 25-VII, J. N. Knull; 3 female: Chiricahua Mountains, AZ, IX-4-1962, D. J. and J. N. Knull; 1 male, 2 females: Chiricahua Mountains, AZ, VII-30-1959, D. J. and J. N. Knull; 2 females: Chiricahua Mountains, AZ, VIII-7-1959, D. J. and J. N. Knull; 1 male, 1 female: Chiricahua Mountains, AZ, VII-10-1961, D. J. and J. N. Knull; 4 males, 2 females: Chiricahua Mountains, AZ, VIII-10-1961, D. J. and J. N. Knull; 1 male: Chiricahua Mountains, AZ, VII-18-1961, D. J. and J. N. Knull; 1 female: Chiricahua Mountains, AZ, IX-11-1962, D. J. and J. N. Knull; 2 females: Sabino Canyon, AZ, VIII-7-1962, D. J. and J. N. Knull; 1 male, 2 females: Chiricahua Mountains, AZ, VIII-14-1962, D. J. and J. N. Knull; 1 female: Tucson, AZ, VII-1929, J. N. Knull, 1 female: Tucson, AZ, VIII-1910, J. N. Knull; 1 female: Tucson, AZ, VIII-1927, J. N. Knull; 1 male: Pecos, TX, 15-VIII-1962, N. M. Downie; 1 female: Globe, AZ, 1-VII-1933, F. H. Parker; 2 males: Santa Cruz Co., AZ, Yanks Spring, 4 m SE Ruby, Pajaritos, Mountains, 4,000 ft, IX-5-1950, T. Cohn, P. Boone and M. Cazier; 1 male: Pima Co., AZ, El Mirador Ranch, 4 mi NW Sasabe, Baboquivari Mts., 3,900 ft, IX-3-1950, T. Cohn, P. Boone and M. Cazier; 2 females: Pima Co., AZ, Sabino Canyon, Santa Catalina Mts., 5,000 ft, VIII-6-1948, G. E. Ball; 1 male: Pima Co., AZ, 15 mi E Tucson, 2600 ft, VIII-18-1950, T. Cohn, P. Boone and M. Cazier; 1 male, 1 female: Pima Co., AZ, Madrona Canyon, Ranger Station, Rincon Mts, VIII-24-1952, 3,300 ft, G. M. Bradt; 3 males: Pima Co., AZ, Continental, VII-29-1948, G. E. Ball; 2 females: Patagonia, AZ, VII-6-1936, M. Cazier; 2 males: Hidalgo Co., NM, 18 mi N

Rodeo, VII-7-1956; 1 male: Pima Co., AZ, Tucson, VII-1953, G. M. Bradt; 1 female: Patagonia, AZ, VII-6-1936, M. Cazier; 1 female: Tucson, AZ, VIII-26-1949, 2,700, G. M. Bradt; 1 female: Globe, AZ, VIII-28-1952, F. H. Parker; 1 female: Huachuca Mountains, AZ, 5,400, on palm, Chass; 1 male: Gila Bend, AZ, [no collecting date and collector data]; 2 females: Baboquivari Mountains, AZ, VII-23-1949; F. H. Parker; 1 male, 1 female: Coyote Mountains, AZ, VII-4-VIII-1916, 31° 59' N 11° 29', 3,500, [no collector data]; 1 female: Patagonia mountains, AZ, VIII-20-1949, F. H. Parker; 1 female: Huachuca Mountains, AZ, VIII-15-1949, F. H. Parker; 1 female: Pima Co., AZ, Lowell Ranger Station, VI-20-VII-1916; 1 female: Globe, AZ, VIII-26-1935, C. Parker; 1 female: Santa Cruz Co., AZ, Pajarito Mts., Pena Blanca, Canyon, VII-27-1978, 1191 m, at light, S. McCleve; 1 male, 1 female : Cochise Co., AZ, Texas Canyon, 5,300', black lite, VIII-12-1974, S. McCleve; 1 female: Cochise Co., AZ, San Bernardino Ranch, VIII-14-1976, S. McCleve; 2 female: Cochise Co., AZ, Leslie Canyon, VIII-17-1978, S. McCleve; 1 male: Cochise Co., AZ, Texas Canyon, 5300', black lite, VIII-12-1974; 1 female: Graham Co., AZ, Aravaipa Canyon, Turkey Creek, VIII-11-1998, MV and blacklight, F. W. Skillman Jr; 1 male, 1 female: Tortilla Mounatins, AZ, 12 mi N of Tucson, Pima Co., VII-16-1966; 1 female: Pima Co., AZ, Collsal Cave Park, VIII-25-1970, K. Stephan; 1 female: Cochise Co., AZ, South Western Res. Sta., VII-6-1980, UV light, L. L. Lampert Jr; 2 males: Cochise Co., AZ, Cottonwood Canyon, mercury vapor + black light, VII-16-2000, R. Turnbow; 1 male, 1 female: La Paz Co., AZ, 12-VI-1996, Cibola NWR, D. Anderson. MEXICO: 1 male: Sonora, Mexico, Tastiota, VII-18-1952, C. and P. Vaurie; 1 male: Durango, Mexico, Rodeo, San Juan del Rio, 4,700 ft, VII-29-1947; 2 females: Sonora, Mexico, Obregon, VII-29-1952, C. P. Vaurie; 1 male, 1 female: Sonora, Mexico, Minas Nuevas, 7-VIII-1952, C. and P. Vaurie.

Lecontella striatopunctata (Chevrolat, 1876)

Figs. 2.4-A, 2.10-B, 2.10-A.

Synonyms: *Cymatodera striatopunctata* Chevrolat, 1876, Mémoire sur la famille des Clérites. Buquet, Paris, 51 p.

Type material not examined.

Type locality: "Mexique". Type depository: Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Distribution: Mexico: Jalisco, Morelos, Nayarit, Oaxaca; Central America: Guatemala.

Differential diagnosis: *Lecontella striatopunctata* is most similar to *L. brunnea*. These two species are parapatric and often misidentified as each other. However, these species can be readily identified based on the structure of the antennae. Males of *L. striatopunctata* have antennomeres 2-10 conspicuously compacted and robust, last antennomere 3-4× the length of tenth antennomere (Fig. 2.10-A). Males of *L. brunnea* have the antenna moderately compacted and the antennomeres gradually increasing in width toward the distal end, last antennomere 4-5× the length of tenth antennomere (Fig. 2.9-F). Both sexes of the two species can also be differentiated based on the posterior portion of the epipleural fold, specifically, *L. striatopunctata* have the last sixth of the epipleural fold smooth, while *L. brunnea* has the posterior sixth of the epipleural fold feebly to moderately crenulate.

Redescription. Male. Form: small to large individuals, moderately robust. Color: head, pronotum, thorax, scutellum, legs and antennae brown to brunneous; elytra testaceous to almost black; mouthparts fuscous, last fourth of mandibles piceous to black; abdominal segments testaceous to piceous; elytral disc devoid of any bands or fasciae (Fig. 2.4-A).

Head: including eyes wider than pronotum; eyes large, moderately taller than wide, bulging laterally, coarsely faceted, moderately emarginate posteriorly; antennal notch located in front of emargination; frons bi-impressed; integument coarsely, conspicuously, shallowly punctate; moderately clothed with fine, pale, recumbent setae intermixed with some erect, pale setae; antennae composed of 11 antennomeres; antennae vested with short, recumbent, fine, pale setae; antennomeres; second antennomere moderately robust, slightly shorter than third antennomere; antennomeres 3-10 serrate, conspicuously robust and compacted, about the same length; last antennomere of males sexually dimorphic, conspicuously elongate, moderately robust, parallel, cylindrical, posterior portion rounded 4-5 × longer than length of tenth antennomere.

Thorax: pronotum bisinuate, widest at middle, moderately short in length; sides constricted subapically, more strongly constricted behind middle and feebly constricted in front of middle; surface conspicuously punctate, elytral disc with punctations small, moderately shallow, interspersed with a smooth disc; moderately clothed with fine, short, pale, recumbent setae interspersed with some long, semierect, fine, pale setae; long setae more abundant on anterior and lateral area of pronotum; anterior transverse depression moderately impressed, subbasal tumescence absent; posterior margin of pronotum feebly to moderately compressed. Prosternum: conspicuously wider than long; moderately to strongly punctate, punctation fine, deep; surface very feebly vested to glabrous. Mesosternum: surface smooth, vested with fine, pale, semi-erect setae; moderately to coarsely punctate, punctations wide, deep. Metasternum: surface smooth to

finely rugulose, convex; numerously, coarsely to moderately punctate, punctations moderately coarse, shallow; clothed with fine, pale, recumbent setae; longitudinal depression and metaventral process present. Scutellum wide, clothed with pale, fine, semirecumbent setae, moderately compressed medially.

Elytra: broader than pronotum; elongate; humeri indicated, rounded; sides inconspicuously broadening toward distal end, broadest on posterior 1/4, then abruptly narrowing toward apex at posterior 1/4; surface rugose to rugulose at interstices; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity moderately steep; surface vested with fine, short, pale, recumbent setae and some pale, fine, long, erect setae; conspicuously, coarsely punctate, punctations arranged in regular striae; sculpturing consisting of coarse, deep, wide punctations arranged in regular striae that decrease in size in posterior fourth, punctation reaching elytral apex; interstices at elytral base $0.5 \times$ the width of punctation; interstices smooth. Epipleural fold gradually narrowing toward apex, not crenulate.

Legs: femora rugose, moderately swollen on distal end, clothed with some pale, fine, semirecumbent setae mixed with some semi-erect setae, surface conspicuously punctate, punctations moderately small, shallow. Tibiae rugulose, punctate; punctations shallow and small; vestiture consisting of fine, recumbent and semirecumbent setae.

Abdomen: six visible ventrites; first ventrite moderately rugose to rugulose, ventrites 2-4 moderately to strongly rugulose, convex, subquadrate, punctate, vested with fine, long, pale, recumbent setae; not compressed laterally; posterior margins truncate. Posterior margin of first and second visible ventrites moderately elevated with a transverse carina originating next to posterolateral angles producing a broad, moderately elevated arcuate emargination. Fifth visible ventrite subtriangular; surface rugulose, convex, moderately punctate, punctations shallow,

small; vested with fine, pale, recumbent setae; lateral margins oblique, feebly arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite small shape triangular; rugulose to rugose; surface convex, moderately, finely punctate; clothed with short, pale, fine, recumbent setae; as broad as long; lateral margins strongly oblique, arcuate; posterior margin short, somewhat acuminate, very shallowly emarginate. Fifth tergite subquadrate, surface convex, rugulose; posterior margin truncate. Sixth tergite subtriangular; finely to moderately rugulose; surface feebly convex; clothed with fine, pale, recumbent setae; lateral margins oblique; posterior margin truncate. Sixth tergite extending beyond apical margin of sixth visible ventrite, covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece moderately swollen at apex; phallic plate unarmed, devoid of denticles; intraspicular plate present, elongate; phallobasic apodeme long, expanded distally; phallobase subparallel; parameres free; tegmen complete, covering phallus; parameres pointed distally; endophallic struts long, slender distally (Fig. 2.20-A).

Sexual dimorphism: Females of *L. striatopunctata* differ from males in the shape of the last abdominal segment. Females have the lateral and posterior margins of the sixth abdominal segment broadly rounded. Males have the lateral margins of the sixth abdominal segment strongly oblique and the posterior margin is short, almost acuminate, and shallowly emarginate. Additionally, females have the eleventh antennomere short, moderately robust, obtusely rounded, and moderately longer than tenth antennomere; while males have the last antennomere cylindrical, not compressed medially and 4-5× longer than tenth antennomere.

Material examined: 1 male, 1 female: Morelos, Mexico, Tepalcingo, N El Limón, 18° 32' 18.3"
N 98° 56' 01.7" W, 1272 m, Selva baja caducifolia, trampa de luz, VI-6-2008, M. De León; 1
male: Mexico, Jalisco, Estacion Biologica Chamela, VIII-1-2-1991, E. Giesbert; 1 female:
Guerrero, Mexico, Highway 95, 5.6 km S Milpillas, [no collector data]; 3 females: Jalisco,
Mexico, Estacion Biologica Chamela, VII-10-20-1985, E. Giesbert; 1 male, 1 female: Jalisco,
Mexico, Estacion Biologica Chamela, X-1-2-1991, E. Giesbert; 1 male: El Progreso, Guatemala,
Highway 17, vic. Morazán, 1700', V-29 to VI-2-1989, E. Giesbert; 1 female: Zacapa,
Guatemala, 12-14 km S San Lorenzo, 1000-2000', VI-3-6-1989, E. Giesbert; 1 male: Jalisco,
Mexico, Estacion Biologica Chamela, X-15-21-1987, E. Giesbert; 1 male, 1 female: Mex.,
Jalisco, Mexico, Chamela Estacion UNAM, X-1-2-1991, J. E. Wappes; 2 males: Jalisco, Mexico,
Chamela vic. E. B. UNAM, VII-9-19-1993, J. E. Wappes; 3 females: Jalisco, Mexico, vic
Chamela, 15-VII-1990, J. E. Wappes; 1 female: Zacapa, Guatemala, 12-14 km S San Lorenzo, 1-
2000', VI-3-6-1989; 1 female: Mexico, Jalisco, 17.6 km N Chamela, VII-16-1987, R. Turnbow,
2 males: Mexico, Jalisco, vic Estacion de Biologia Chamela UNAM, VII-9-14-1993, Black
Light, Morris, Huether, Wappes.

3.10 Monophylla Spinola, 1841.

Synonyms: *Macrotelus* Klug 1842, type species: *Tillus terminatus* Say (monotypic),
synonymized by LeConte (1849); *Elasmocerus* LeConte 1849, type species: *Monophylla
terminata* Say (original designation), unnecessary replacement name for Monophylla (Say,
1849).

Type species *Cymatodera megatoma* Spinola, 1841 (monotype), synonymized as *Monophylla* (*Tillus*) *terminata* (Say, 1835).

(Distribution shown in Fig. 2.21-J)

Diagnosis: The genus *Monophylla* is noticeably different to the rest of the New World tillinids genera. Several morphological characters are unique to this genus. The most characteristic feature is the size of the last antennomere, and species have this antennomere conspicuously longer than the other antennomeres combined (Fig. 2.10 C-D). This character is similar to certain males of the genus *Teloclerus* Schenkling (Cleridae: Tillinae), a genus distributed in Africa and Madagascar. The conspicuously enlarged and feebly emarginate eyes of *Teloclerus* (Fig. 2.4-E) may serve to separate this genus from members of the New World *Monophylla,* where the eyes are conspicuously emarginate, almost dividing them into two portions (Fig. 2.12-B). Additional characters that will serve to separate *Monophylla* from other New World Tillinae genera are the rectangular shape and strongly rugulose surface of the pronotum (Fig. 2.7-C) and the exposed pygidium in male individuals (Fig. 2.4-C).

Redescription: Size: 4-10 mm. Color: Body ranging from fuscous to ferrugineous; some individuals may possess one pale fascia on each elytron (Fig. 2.4 B-D). Body: Winged species, elongate, slender, subparallel.

Head: including eye slightly narrower than pronotum; integument numerously, coarsely punctate, punctations vary from narrow to wide and shallow to deep; eyes moderately small, finely faceted, strongly emarginate, emargination almost dividing each eye into two separate

halves (Fig. 2.12-B); inconspicuously bulging laterally; number of antennomeres variable, last antennomere as long as or conspicuously longer than the length of remaining antennomeres combined (Fig. 2.10 C-D); frons feebly to moderately bi-impressed; terminal labial palpi securiform; terminal maxillary palpi cylindrical, compressed laterally. Sexual dimorphism observable in last antennomere, males have this segment conspicuously longer than that of females.

Thorax: Pronotum coarsely punctate, punctations may range from narrow to wide, depending on species; lateral margins subparallel, slightly constricted posteriorly (Fig. 2.7-C). Prosternum enlarged, smooth to rugose, variously punctate. Mesosternum wider than long, smooth to rugulose, moderately punctate. Metasternum wider than long, surface conspicuously punctate to almost smooth. Metaventral process not compressed anteriorly; metepisterna largely exposed, the elytra do not coverer these plates.

Elytra: elongate, subparallel, surface coarsely punctate, punctations numerous, irregularly arranged, punctations extending to apex; scutellum ovoid, not compressed, wider than long; epipleural fold complete, narrowing toward apex. Legs: Femora moderately to coarsely rugose; moderately swollen; tibiae slender; tarsal formula 4-4-4; pulvillar formula 4-4-4; two tarsal denticles, inner tarsal denticles trigonal in shape.

Abdomen: Six visible ventrites; ventrites 1-5 not impressed laterally; pygidium of males moderately differentiated from that of females; females with sixth ventrite broadly rounded, pygidium simple, pygidium not covered by elytra in male specimens.

Aedeagus: feebly sclerotized; length of aedeagus shorter than the length of abdomen; tegmen triangular; phallic plate devoid of denticles; phallobasic apodeme long, longer than phallus; endophallic struts enlarged conspicuously swollen distally (Fig. 2.20 B-D).

Remarks: *Monophylla* was described by Spinola in (1841), with *Monophylla megatoma* Spinola as the type species, a species later synonymized as *Monophylla terminata* (Say), as the type species. Synonyms for the genus were subsequently proposed by Klug (1842) and LeConte (1849). Klug erected *Macrotelus* (1842) to designate *Tillus terminatus* Say as a different entity outside of species of *Tillus.* LeConte (1849) erected the monotypic genus *Elasmocerus* to synonymize *Tillus* (*Macrotelus*) *terminatus* Say. Both names were unnecessary replacement names for *Monophylla* and are now considered junior synonyms. Currently, the genus is composed of four species distributed in the United States, Mexico, Central America and Cuba. Three of the four recognized species are here covered. Due to the lack of material, *Monophylla cinctipennis* (Chevrolat, 1874), a species restricted to Cuba, is not redescribed in this revisionary work. The author is unaware of any material that has been collected since the original description. The relatively short description given by Chevrolat (1874) is translated from French and presented below.

Sexual dimorphism is noticeable in all species comprising the genus. The form of the antennae, the number of antennomeres, and differences in the shape of the pygidium will help to separate male individuals from females (Fig. 2.10 C-D). Due to this sexual dimorphism, keys for identification to *Monophylla* species are given for males and females, separately. It is advisable to determine the sex of the specimens before using the keys provided here. Sex determination can be achieved upon observation of the last antennomeres; specifically, male individuals have the last antennomere conspicuously elongate and dilated, with the remaining segments remarkably reduced (Fig. 2.10-C). Females have the last antennomere moderately enlarged, the last antennomere is slightly longer than remaining antennomeres combined, and antennomeres 7-

10 or 6-10 are strongly serrate (Fig. 2.10-D). Additionally, the pygidium of males is emarginate posteriorly (Fig. 2.17 E-F) while females have this segment broadly rounded posteriorly (Fig. 2.17 G-H).

Key to male species of *Monophylla* Spinola.

1. Large individuals, ~8 mm long; antennae composed of eleven antennomeres; integument color mostly black, except the elytral suture and margins testaceous, and scutellum brown; head and pronotum coarsely, heavily punctate; restricted to Cuba..........................***Monophylla cinctipennis***

- Smaller individuals, 4-8 mm; antennae composed of nine or ten antennomeres; integument color not as above; head and pronotum variously punctate, species not found in Cuba 2

2. (1). Pronotum bicolored, outer region of pronotal disc testaceous to ferrugineous, median region of pronotal disc piceous to black (Figs. 2.4-D; 2.4-D); antennomeres 3-9 robust, antennomeres 6-9 serrate, gradually increasing in size toward distal end...***M. terminata***

- Pronotum not as above; antennae not as above, antennomeres 7-9 serrate or compacted 3

3. (2). Antennae composed of nine antennomeres; antennomeres 3-6 reduced, conspicuously compacted and difficult to distinguish, antennomeres 7-8 serrate; pronotum uniformly brown to dark testaceous except the anterior and posterior edge with a narrow tint of testaceous to ferrugineous color (Fig. 2.4-B)..***M. californica***

- Antennae composed of ten antennomeres; antennomeres 3-9 compacted, moderately robust, serration on antennomeres 4-9 gradually increasing toward distal end; pronotum uniformly brown to dark testaceous except the anterior and posterior edge with a shade of testaceous to ferrugineous color (Fig. 2.4-C)..***M. pallipes***

Key to female species of *Monophylla* Spinola.

1. Antennae composed of nine antennomeres; antennomeres 6-8 serrate, serration gradually increasing toward distal end; ninth antennomere slightly longer than the length of remaining antennomeres combined..***M. californica***

- Antennae composed of ten antennomeres 2

2. (1). Pronotum brown to almost piceous, a dark testaceous, narrow band of the anterior and posterior margins………………………………………………………………………….***M. pallipes***

- Pronotum bicolored, outer region of pronotal disc testaceous to ferrugineous, median region of pronotal disc piceous to black ....***M. terminate***

Note: Chevrolat, in his descriptive work of *Monophylla cinctipennis* (1876), does not provide any reference or character for the female of this species, as a result, this species is excluded from the key to female *Monophylla* species.

Monophylla californica (Fall, 1901)

Figs. 2.4-B, 2.12-B, 2.20-B.

Synonyms: *Elasmocerus californicus* Fall, 1901, Papers Calif. Acad. VIII, 251 (Elasmocerus).

Type material not examined.

Type locality: Santa Cruz Mountains, Santa Cruz Co., CA. Type depository: Museum of Comparative Zoology, Harvard University (MCZC).

Distribution: USA: AZ, CA, NV, OR, TX, UT, WY; Mexico: Baja California, Baja California Sur, Sonora, Morelos.

Diagnosis: *Monophylla californica* is most similar to *M. pallipes*. The two species have a broad, sympatric distribution and they can be easily misidentified. These species, however, can be separated with relative ease based on their antennae. The antennae of *M. californica* are composed of nine antennomeres, while the antennae of *M. pallipes* have ten antennomeres.

Redescription. Male. Form: small to moderately large, slender individuals. Color: head, antennae, scutellum and legs testaceous to fuscus; pronotum testaceous to almost black, the anterior and posterior margins of the pronotum have a narrow to moderately wide ferrugineous to testaceous band; thorax fuscous to almost black; elytra light testaceous to almost black, each elytron with a pale, moderately narrow fascia on the median region of the elytral disc that initiates on the epipleural fold but does not reach the elytral suture; mouthparts fuscous, abdominal segments light testaceous to piceous (Fig. 2.4-B).

Head: including eyes narrower than pronotum; eyes moderately small, taller than wide, slightly bulging laterally, antennal notch located in front of emargination (Fig. 2.12-B); integument coarsely to moderately punctate; moderately clothed with fine, pale, semi-erect setae intermixed with erect, pale setae; antennae composed of nine antennomeres; antennae vested with very short, semi-erect fine, dark setae; second antennomere robust, short, antennomeres 3-6 small, conspicuously compacted; antennomeres 7-8 short, serrate, ninth antennomere noticeably

117

enlarged, conspicuously compressed laterally, much longer that remaining antennomeres combined; last antennomere of males sexually dimorphic.

Thorax: pronotum subparallel, widest at middle, feebly to moderately constricted toward posterior margin; surface conspicuously punctate, rugose; elytral disc flat; clothed with fine, moderately short, pale, recumbent setae interspersed with some long and very long, semi-erect and erect, dark setae, these setae are more abundant on lateral area of pronotum; anterior transverse depression feebly to moderately impressed, subbasal tumescence absent. Prosternum: as long as wide; moderately to strongly punctate, punctation fine, shallow; surface vested to glabrous. Mesosternum: surface moderately to coarsely punctate, vested with fine, pale, semi-erect setae; moderately punctate, punctations wide, deep, metepisterna visible throughout their length, not covered by elytra. Metasternum: surface smooth medially, moderately to strongly punctate laterally, punctation wide and shallow; clothed with fine, pale, recumbent setae; longitudinal depression present, metaventral process absent. Scutellum wide, clothed with pale, fine, semirecumbent setae, moderately compressed medially.

Elytra: anterior margin slightly broader than pronotum; elongate; subparallel, humeri feebly indicated, rounded; sides broadening toward distal end, widest on middle third then gradually narrowing toward apex; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity gradual; surface moderately vested with fine, short, pale and dark, semi-erect setae some pale, fine, long, semi-erect setae, the latter more abundant toward epipleural fold; conspicuously, conspicuously punctate, punctations small and shallow, punctations arranged irregularly arranged that reach the elytral apex; interstices smooth. Epipleural fold gradually narrowing toward apex.

Legs: femora feebly rugulose to smooth, widest on middle half, laterally compressed, clothed with some pale, fine, semirecumbent setae mixed with some semi-erect setae, surface feebly punctate, punctations small and shallow. Tibiae rugulose, slender, punctate; punctations shallow and small; vestiture consisting of fine, semi-erect setae.

Abdomen: six visible ventrites, ventrites 1-4 convex, smooth, shiny; first visible ventrite longer than second ventrite, moderately rugulose; ventrites 2-4 moderately subquadrate, punctate, vested with fine, long, pale, recumbent setae and some long semi-erect setae; not compressed laterally; posterior margins truncate. Fifth visible ventrite strongly convex, subquadrate, surface rugulose, moderately punctate, punctations shallow, small; vested with fine, pale, recumbent setae; lateral margins subparallel, feebly arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite subtriangular; surface slightly to moderately rugulose, convex to almost flat, finely punctate; vested with moderately long and long, erect setae, vestiture more abundant on anterolateral margins; lateral margins oblique, strongly arcuate; posterior margin broadly, deeply emarginate, U-shaped emargination, posterolateral angles rounded. Fifth tergite subquadrate, surface convex; posterior margin truncate. Sixth tergite subquadrate; finely to moderately rugulose; surface convex posterior median region compressed; clothed with fine, pale, recumbent setae; lateral margins oblique; posterior margin broadly, deeply emarginate, U-shaped emargination, posterolateral angles rounded. Sixth tergite extending beyond apical margin of sixth visible ventrite, covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece swollen at apex; phallic plate armed with a row of denticles; intraspicular plate present, elongate; phallobasic apodeme conspicuously short, moderately expanded distally; phallobase trigonal; parameres free;

tegmen incomplete, partially covering the phallus; parameres pointed anteriorly; endophallic struts long, truncate distally (Fig. 2.20-B).

Sexual dimorphism: Females of *M. californica* can be differentiated from males based on the length of the last antennomere; specifically, the ninth antennomere is moderately shorter in females than in males; also, antennomeres 8-6 are larger, triangular in shape and moderately serrate in females, but conspicuously reduced and compressed in male individuals. In addition to antennal differences, the last abdominal segment in females is broadly rounded, rather than emarginate posteriorly, as in males.

Material examined: USA: 1 male, 2 females: San Diego Co., CA, 3 mi E of Jacumba, VII-14-1984, G. H. Nelson; 1 male: San Diego Co., CA, 5 mi E Jacumba, VI-29-1984, on Acacia greggii, G. H. Nelson; 1 male: Los Angeles Co., CA, Mount Baldy, VI-23-1973, E. Giesbert; 1 male: Imperial Co., CA, 15 mi E Calexico, VI-6-1961, [no collector data]; 1 female: Globe, AZ, IX-1-1933, F. H. Parker; 2 males, 1 female: Riverside Co., CA, VIII-4-1939, A. T. McClay; 2 males: Cochise Co., AZ, 2 mi S of Portal, VII-2-1960, M. Statham; 1 female: Warners, CA, X-12-1924, R. C. Casselberry; 3 females: Imperial Co., CA, Fish Springs, I-1-1939; A. T. McClay; 1 male, 1 female: Riverside Co., CA, 4-VII-1939, beating mesquite, A. T. McClay; 1 female: Pima Co., AZ, [no collecting date and collector]; 1 male: Los Angeles Co., CA; Westwood Hills, X-5-1939; 2 males, 1 female: Huachuca Mountains, AZ, VIII-19-1950, J. N. Knull; 2 females: Yuma, AZ, IV-1-1924, J. N. Knull; 2 males, 1 female: Cottonwood, AZ, VIII-18, J. N. Knull; 2 females: Cave Creek, AZ, VIII-20-1959, J. N. Knull; 8 males, 6 females: Oak Creek Canyon, AZ, VIII-15, D. J. and J. N. Knull; Grand Teton National Park, WY, VII-14-1939, D. J. and J. N.

Knull; 2 males, 2 females: Valverde Co., TX, V-6-1941, D. J. and J. N. Knull; 1 male: Calipatria, CA, II-29-1924, J. N. Knull; 1 female: Palm Springs, CA, V-19-1941, D. J. and J. N. Knull; Mecca, CA, VI-19-1948, D. J. and J. N. Knull; 1 male, 1 female: Jacumba, CA, VI-24-1954, D. J. and J. N. Knull; 3 males, 1 female: Winterhaven, CA, VI-25-1952, D. J. and J. N. Knull; 1 male, 2 females: Tucson, AZ, D. J. and J. N. Knull; 1 male, 2 female: Palm Springs, CA, VI-30-1946, D. J. and J. N. Knull; 1 male: Santa Monica Co., CA, 1942, Rivers; 4 females: Santa Cruz Co., CA, Glenwood, VI-16-1968, Tyson; 1 male: Upper City, CA, VI-5-1932, A. T. McClay; 1 female: Imperial Co., CA, I-11-1934, D. J. and J. N. Knull; Riverside Co., CA, VIII-4-1939, A. T. McClay; 2 males: Tucson, AZ, VI-20-1935, Bryant; 1 male: Globe, AZ, VII-30-1949, F. H. Parker. MEXICO: 1 male, 1 female: Baja California [Sur], Mexico, 5 mi S La Paz; VIII-24-1976, E. Giesbert; 2 female: Baja California Mexico, V-29-1987, riparian palm oasis, G. H. Nelson; 1 male: Lower California, [Mexico], Santa Rosa, [missing collecting locality and date]; 1 male: Sonora, Mexico, Minas Nuevas, VIII-7-1952, C. P. Vaurie; 2 males, 1 female: Santa Rosa, Lower California, VII, D. J. and J. N. Knull; 3 males: Morelos, Mexico, Tlaquiltenango, Huaxtla, 18. 37917° N 99.04581° W, Trampa de luz, V-23-2009, V. H. Toledo; 1 male: Morelos, Mexico, Tepalcingo, El Limón, 18° 31' 55.8" N 98°, 56' 17.2" W, trampa de luz, II-17-2007, V. H. Toledo and M. A. Corona.

Remarks: I have examined a number of specimens of *M. californica* collected in Morelos, Mexico, which would indicate a considerable range expansion for this species. Additional samples are needed to show if this species has a disjunct range or the present known distribution is the result of a lack of collecting.

Monophylla cinctipennis (Chevrolat, 1874)

Synonyms: *Macrotelus cinctipennis* Chevrolat, Rev. et Mag. Zool., 1874, p. 281.

Type locality: Cuba. Type depository: Instituto Cubano de Zoología, Museo D. Gundlach.

Distribution: Cuba.

The original description given by Chevrolat (1874) is given below for further references.

[Description:] Color and shape: head black, elongate, prothorax, femora (knees fourth ahtica), elytra in the suture and on the margin yellow; densely [punctate], striped [striae] elongate; eyes and antennae black; head rounded, [frons] between the eyes convex, furrow [setae] thin; prothorax scarcely longer than broad, widening; form semicylindrical, truncate; [on] hind [area] slightly rounded, long, arching, trifossulato??; scutellum punctiform brown; elytra elongate, parallel, rounded, posteriorly, the legs black. Antennae eleven articulate [antennomeres], first article [antennomere] elongate striped; second [antennomere] short, third [antennomere] the length of the first, a little less than fourth [antennomer], fifth conical, [antennomere] 6-10 subnodosis [robust], short, last [eleventh antennomere] long, cylindrical, spongiose??

Remarks: Wolcott (1910), in his notes from Chevrolat's description of *Macrotelus cinctipennis*, mentioned the rarity of the species; he further indicated that this species was unknown to him and he had not encountered.

Monophylla pallipes Schaeffer, 1908

Figs. 2.4-C, 2.20-C.

Type material not examined.

Type locality: Brownsville, Texas. Type depository: United States National History Museum (USNM).

Holotype lost. Lectotype designated by Chapin (1949).

Distribution: USA: AZ, CA, TX; Mexico: Chiapas, Jalisco, Morelos, Quintana Roo, San Luis Potosi, Sinaloa, Tamaulipas, Yucatan. Central America: Costa Rica, Guatemala, Honduras. South America: Chile (introduced).

Diagnosis: *Monophylla pallipes* is very similar to *M. californica.* The two species are sympatric in distribution; therefore, they can be misidentified when collected simultaneously. Diagnostic characters are provided in the diagnosis of *M. californica.*

Redescription. Male. Form: small to moderately large, slender individuals. Color: head, antennae, pronotum, scutellum and legs dark testaceous to almost piceous; the anterior and posterior margins of the pronotum have a narrow ferrugineous to testaceous band; thorax ferrugineous to almost black; elytra testaceous to piceous, each elytron with a pale to yellowish fascia on the median region of the elytral disc that initiates on the epipleural fold and does not reach the elytral suture; mouthparts fuscous, abdominal segments light testaceous to fuscous (Fig. 2.4-C).

Head: including eyes narrower than pronotum; eyes moderately small, taller than wide, feebly bulging laterally, antennal notch in front of eye emargination; integument coarsely to moderately punctate; clothed with fine, pale, semirecumbent and semi-erect setae intermixed with some scattered erect, pale setae; antennae composed of 10 antennomeres; antennae vested with very short, semi-erect fine, dark setae; second antennomeres robust, moderately short, antennomeres 3-4 small, conspicuously compacted; antennomeres 5-9 serrate, serration and size gradually increasing toward distal end, last antennomeres noticeably enlarged, conspicuously compressed laterally, much longer than remaining antennomeres combined; last antennomere sexually dimorphic.

Thorax: pronotum subparallel, widest at middle, feebly to moderately constricted toward posterior margin; pronotal surface moderately to conspicuously punctate, rugose to rugulose; pronotal disc flat; clothed with fine, moderately short, pale and dark, semirecumbent setae interspersed with some long and very long, erect, dark setae; anterior transverse depression feebly to moderately impressed, subbasal tumescence absent. Prosternum: as long as wide; moderately to strongly punctate, punctation fine, shallow; surface feebly to moderately clothed. Mesosternum: surface moderately to coarsely punctate, vested with fine, pale, semi-erect setae;

moderately o coarsely punctate, punctations wide, deep; metepisterna visible throughout their length, not covered by elytra. Metasternum: convex, surface moderately to strongly punctate laterally, punctation wide and shallow; moderately clothed with fine, pale, recumbent setae; longitudinal depression present, metaventral process absent. Scutellum wide, clothed with pale, fine, recumbent setae, compressed medially.

Elytra: anterior margin slightly broader than pronotum; elongate; subparallel, humeri feebly indicated, rounded; sides gradually expanding toward distal end, widest on middle third then narrowing toward apex; elytral apices subtriangular; inconspicuously dehiscent; elytral declivity gradual; surface clothed with fine, short, pale and dark, semi-erect and erect setae; conspicuously punctate, punctations small and shallow, irregularly arranged, punctations reaching the elytral apex; interstices smooth, narrow. Epipleural fold gradually narrowing toward apex.

Legs: femora rugulose to smooth, moderately expanded behind middle, laterally compressed, moderately clothed with some pale, fine, semi erect setae, surface feebly, shallowly punctate. Tibiae rugulose, slender, puncticulate; punctations shallow and small; vestiture consisting of fine, pale, semi-erect setae mingled with some pale, semirecumbent setae.

Abdomen: six visible ventrites, ventrites 1-4 convex, smooth, shiny; first visible ventrite longer than second visible ventrite, feebly to moderately rugulose; ventrites 2-4 subquadrate, punctate, moderately vested with fine, long, pale, recumbent setae; not compressed laterally; posterior margins truncate. Fifth visible ventrite convex, subquadrate, surface rugulose, moderately puncticulate, punctations shallow, small; vested with fine, pale, recumbent setae; lateral margins subparallel, arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite subquadrate; surface slightly to moderately rugulose, feebly convex to almost flat, feebly compressed on the median-posterior region; moderately clothed with some long, erect

125

setae, vestiture more abundant on anterolateral margins; lateral margins oblique, moderately arcuate; posterior margin broadly, deeply emarginate, U-shaped emarginate, posterolateral angles round. Fifth tergite subquadrate, surface convex; posterior margin truncate. Sixth tergite subquadrate; finely to moderately rugulose; surface convex posterior median region compressed; clothed with long, fine, pale and dark recumbent setae; lateral margins oblique; posterior margin broadly, moderately deeply emarginate, U-shaped emargination, posterolateral angles rounded. Sixth tergite slightly extending beyond apical margin of sixth visible ventrite, covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece swollen at apex; phallic plate armed with a row of denticles; intraspicular plate present, elongate; phallobasic apodeme conspicuously short, moderately expanded distally; phallobase moderately sinuate; parameres free; tegmen incomplete, partially covering the phallus; parameres pointed anteriorly; endophallic struts long, conspicuously robust distally (Fig. 2.20-C).

Sexual dimorphism: Females of *M. pallipes* differ from male specimens based on the following respects: the tenth antennomere of females is shorter than in males; antennomeres 6-9 are larger and moderately serrate in females, but conspicuously reduced and compressed in males; and females have the last abdominal segment broadly rounded to feebly truncate, while males have this segment moderately emarginate posteriorly.

Material examined: 2 males, 2 females: Hidalgo Co., TX, IV-7-1950, D. J. and J. N. Knull; 2 males, 6 females: Brownsville, TX, V-25-1934, D. J. and J. N. Knull; 2 males, 5 females: Brownsville, TX, V-14, D. J. and J. N. Knull; 1 female: Brewster Co., TX, V-26-1948; 1 female:

Cameron Co., TX, VI-4-1950, D. J. and J. N. Knull; 2 females: Corpus Christy, TX, III-30-1961, D. J. and J. N. Knull; l male: Gillespie Co., TX, IV-23, D. J. and J. N. Knull; 1 male, 2 females: Hidalgo Co., TX, III-20-1952, D. J. and J. N. Knull; 1 male, 1 female: Hidalgo Co., TX, III-29-1963, D. J. and J. N. Knull; 1 male: Hidalgo Co., TX, III-26-1953, D. J. and J. N. Knull; 1 male, 1 female: Starr Co., TX, IV-9-1963, D. J. and J. N. Knull; 2 males: Starr Co., TX, III-20-1952, D. J. and J. N. Knull; 1 female: Hidalgo Co., TX, 7-IV-1950, D. J. and J. N. Knull; 1 male, 1 female: Hidalgo Co., TX, V-23-1953, D. J. and J. N. Knull; 2 males: Jackson Co., TX, V-22, D. J. and J. N. Knull; 2 males, 1 female: Brownsville, TX, V-19, D. J. and J. N. Knull; 3 males, 2 females: Uvalde Co., TX, VI-13-1949, J. N. Knull; 1 female: Santa Cruz Co., CA, Glenwood road, VI-16-1968, W. H. Tyson; 1 female: Gillespie Co., TX, VI-1, J. N. Knull; 1 male: Brownsville, TX, V-12, D. J. and J. N. Knull; 1 male: Brownsville, TX, V-5, D. J. and J. N. Knull; 1 female: Brownsville, TX, XI-19-1911, in pasture, Garden; 1 female: Cameron Co., TX, 2 mi E Los Indios, V-13-1978, N. M. Downie; 1 female: Cameron Co., TX, Sabal Palm Grove, IV-20-30-1986, D. H. Heffern; 2 males, 3 females: San Patricio Co., TX, Welder Wildlife Ref., VII-10-20-1981, R. H. Turnbow; 3 males: Cameron Co., TX, Sabal Palm Grove Sanctuary, III-16-1981, R. H. Turnbow; 2 males: Cameron Co., TX, Palm Groove Sanctuary, Brownsville, I-1977, F. T. Hovore; 1 female: Hidalgo Co., TX, Santa Ana National Refugee vic., Willow Lake, T. C. MacRae; 1 male: Starr Co., TX, Rio Grande City, X-10-1972, E. Giesbert; 1 female: San Patricio Co., TX, Welder Wildlife Refuge, V-10-12-1977, E. Giesbert; 1 male: TX, reared from mesquite logs, emerged X-10-1955, H. F. Howden; 1 male, 1 female: TX, Lake Corpus Christy State Park, VI-19-1971; G. H. Nelson; 1 male: Cameron Co., TX, Sabal Palm Grove Sanctuary, III-20-1982, R. Turnbow. MEXICO: 1 male: Sinaloa, Mexico, 3 km E El Marmol, VIII-8-1983, E. Giesbert; 1 male, 2 females: San Luis Potosí, Mexico, 69.5 km N Tamazunchale, VI-5-1987,

R. H. Turnbow; 2 males, 3 females: Jalisco, Mexico, 1.2 km S of La Cumbre, VII-19-2011, R. H. Turnbow; 2 males, 1 female: Tamaulipas, Mexico, 1-2 mi E Nuevo Morelos, VI-2-1982, R. H. Turnbow; 1 male: Guerrero, Mexico, 7.3 km NW Ixtapa, VII-17-1985, R. Turnbow; 2 males, 2 females: Quintana Roo, Mexico, highway 186, 17 km S jct. 307, V-30-1984, R. Turnbow; 1 female: Yucatan, Mexico, 2 km E Chichen Itza, V-26-1984, R. Turnbow; 1 female: Chiapas, Mexico, 4 mi NW of Pueblo Nuevo River Bajada, VII-15-1965, G. H. Nelson. CENTRAL AMERICA: 1 female: El Paraiso, Honduras, 31.5 km W Danli, VII-20-1995, R. Turnbow.

Remarks: The holotype of *M. pallipes* was lost and a lectotype was designated by Chapin (1949).

Monophylla terminata (Say, 1835)

Figs. 2.4-D, 2.7-C, 2.10-C, 2.10-D, 2.17-E, 2.17-F, 2.17-G, 2.17-H, 2.20-D.

Synonyms: *Tillus* (*Macrotelus*) *terminatus* Say, 1835, Original designation, Bost. Journ. Nat. Hist. Mus., p. 160. Synonymized by Wolcott (1910). *Elasmocerus terminates* (Say, 1835) designated by LeConte, 1849.

Type material not examined.

Type locality: "near Council Bluff, on the Missouri River". Type depository: Type material destroyed, no lectotype has been designated.

Distribution: Canada: Ontario; USA: AL, AR, AZ, DC, FL, GA, IA, IL, IN, KS, KY, LA, MD, MI, MO, MS, NC, NE, NJ, NY, OK, OH, PA, RI, SC, TX, VA, WV. Mexico: Chihuahua, Sinaloa.

Differential diagnosis: *Monophylla terminata* is most similar to *M. pallipes*, the two species can be recognized based on the structure of the antennae and integument color. In males of *M. terminata*, antennomeres 3-6 are robust and compacted and antennomeres 7-9 are serrate (Fig. 2.10-C). In *M. pallipes*, antennomeres 3-4 are robust and clavate and antennomere 5-9 are serrate; additionally, for males and females, the pronotum of *M. terminata* is bicolored, the outer region of the pronotal disc is testaceous to ferrugineous and the median region is piceous to black. In *Monophylla pallipes* the pronotum predominantly dark testaceous to piceous, with the anterior and posterior margins narrowly dark ferrugineous, this coloration may be absent in some specimens and the pronotum is completely dark ferrugineous to almost black.

Redescription. Male. Form: small to moderately large, slender individuals. Color: head, antennae, legs and scutellum dark testaceous to almost piceous; thorax bicolored, outer region of pronotal disc testaceous to ferrugineous, median region of pronotal disc piceous to black; prosternum testaceous to ferrugineous to almost black; meso and metathorax bicolored, testaceous to ferrugineous and piceous to black; elytra fuscous to black, the anterior half of the epipleural fold testaceous to ferrugineous, some individuals with a pale to yellowish fascia on the median region of the elytral disc that initiates on the epipleural fold and does not reach the elytral suture; abdomen light testaceous to ferrugineous; mouthparts testaceous (Fig. 2.4-D).

Head: including eyes feebly narrower than pronotum; eyes medium-sized, taller than wide, feebly bulging laterally, antennal notch in front of eye emargination; integument conspicuously punctate, punctation moderately wide and shallow; moderately vested with fine, pale, semi-erect and erect setae; antennae composed of 10 antennomeres; antennae vested with very short, semi-erect fine, dark setae; second antennomere robust, moderately short, antennomeres 3-6 small, robust, conspicuously compacted; antennomeres 7-9 compacted, serrate, serration gradually increasing toward distal end, last antennomere noticeably enlarged, conspicuously compressed laterally, much longer that remaining antennomeres combined; last antennomere sexually dimorphic.

Thorax: pronotum subparallel, moderately expanded at middle, then constricted before posterior margin; pronotum with surface moderately to conspicuously punctate, feebly to moderately rugulose; pronotal disc flat; clothed with fine, moderately short, pale and dark, semi-erect setae interspersed with some long and very long, erect, dark setae; anterior transverse depression feebly impressed to absent, subbasal tumescence absent (Fig. 2.7-C). Prosternum: rugose, as long as wide; moderately punctate, punctation fine to moderately coarse, shallow; surface moderately clothed, vestiture consisting of fine, long, semi-erect setae. Mesosternum: surface moderately to coarsely punctate, punctation coarse and shallow, interstices smooth, shiny; vested with fine, pale, semi-erect setae; metepisterna visible throughout their length, not covered by elytra. Metasternum: strongly convex; surface feebly to moderately punctate, punctation small and shallow; clothed with fine, pale, semirecumbent setae; longitudinal depression present, metaventral process absent. Scutellum wide, clothed with pale, fine, recumbent setae.

Elytra: anterior margin slightly broader than pronotum; elongate; subparallel, humeri feebly indicated, rounded; sides gradually expanding toward distal end, moderately wider on middle third, then narrowing toward apex; elytral apices subtriangular to moderately rounded; inconspicuously dehiscent to almost confluent; elytral declivity gradual; surface clothed with fine, short, pale and dark, erect setae, intermingled with some scattered long, erect setae; conspicuously punctate, punctations wide and shallow, irregularly arranged, punctations reaching the elytral apex; interstices smooth to feebly rugulose, narrow; epipleural fold gradually narrowing toward apex.

Legs: surface of femora smooth, shiny, expanded medially, laterally compressed; feebly to moderately clothed with some pale, fine, semi-erect setae, surface shallowly punctate. Tibiae shiny, slender, puncticulate; punctations shallow and small; vestiture consisting of fine, pale, erect and semi-erect setae.

Abdomen: six visible ventrites, ventrites 1-4 convex, smooth, shiny, subquadrate, slightly punctate, moderately vested with fine, moderately short, pale, appressed setae; segments not compressed laterally; posterior margins truncate. Fifth visible ventrite convex, subquadrate, surface smooth, shiny, feebly to moderately punctate, punctations wide and shallow; feebly to moderately vested with fine, pale, recumbent setae; lateral margins moderately oblique, arcuate; posterior margin broadly, shallowly emarginate. Sixth visible ventrite small, subquadrate; conspicuously wider than long; surface slightly to moderately rugulose, almost flat; moderately clothed with some long, erect setae, vestitures more abundant on anterolateral margins; lateral margins strongly oblique, moderately arcuate; posterior margin broadly, deeply emarginate, U-shaped emargination; posterolateral angles round (Fig. 2.17-F). Fifth tergite subquadrate, surface feebly convex; posterior margin broadly, very feeble emarginate. Sixth tergite subquadrate;

finely to moderately rugulose; surface convex; clothed with some long, fine, pale, dark recumbent setae; lateral margins moderately oblique; posterior margin broadly, moderately deeply emarginate, with a U-shaped emargination, posterolateral angles rounded (Fig. 2.17-E). Sixth tergite slightly extending beyond apical margin of sixth visible ventrite, covering sixth ventrite in dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece swollen at apex; phallic plate armed with a row of ell developed denticles; intraspicular plate present, elongate; phallobasic apodeme moderately short, expanded distally; phallobase moderately sinuate; parameres free; tegmen incomplete, partially covering the phallus; parameres pointed anteriorly; endophallic struts truncate distally (Fig. 2.20-D).

Sexual dimorphism: Females of *M. terminata* show a number of differences with respect to males. The most apparent is the length of the last antennomere; specifically, this antennomere is somewhat shorter in females compared with that of males; additionally, antennomeres 6-9 are moderately large and moderately serrate in females (Fig. 2.10-D), but conspicuously reduced and compressed in males (Fig. 2.10-C). Finally, the last abdominal segment of females is broadly rounded, and not emarginate posteriorly, as in males.

Material examined: 1 female: Taney Co., MO, on wood pile, V-6-1955, B. Miller; 2 females: Brewster Co., TX, Chisos Mountains Basin, Big Bend Nat. Park, VI-15-1948, M. Cazier; 1 female: Terrell Co., TX, Sanderson, VI-12-1948, M. Cazier, 1 male, 1 female: Dimmit Co. TX, Catarina, , VI-10-1948, M. Cazier; 1 female: NY, F. Montgomery, VI-17-1910, F. M. Schott; 1 female: Berks Co., PA, Virginville, VI-6-1968, P. Vaurie; 2 males, 1 female: Dekalb Co., GA,

reared on *Vitis* sp., 1971, J. E. W.; 1 male, 1 female: TN, Coll. Chass Palm, [no collecting date, no collector data]; 1 male: 1 female: Encinal, TX, IX-13-1955, L. Downs; 1 male: Westfield, NJ, VI-8-1956, G. R. Ferguson, 4 males, 4 females: Fort Lee, NJ, 1912, [no collector data]; 1 female: Nutley, NJ, VIII-12, E. L. Dickenson; Denville, NJ, VII-1-1924, F. M. Schott; Greenwood, New Jersey, V-1930, J. A. Grossbeck; 1 male, 3 females: TX, 4 mi E of Mission, on mesquite, IV-16-1974, G. H. Nelson; 1 female: Southern Pines, NC, V-1-1923, A. H. Manee; 1 male: NY, 7-VIII-1886, [no collector data]; 1 male: Comal Co., TX, VI-12-1910, [no collector data]; 1 female: Washington, NJ, VII-16-1958, [no collector data]; 7 males, 5 females: Hummelstown, PA, VI-20-1920, J. N. Knull; 2 males, 1 female: Harrisburg, PA, V-12-1910, J. N. Knull; 1 male, 2 females: Mont Alto, PA, 29-V-1931, J. N. Knull; 1 female: N. Cumberland, PA, [no collecting data], A. Champlain; 1 male: Columbus, OH, VIII-1-1924, J. N. Knull; 4 females: Hocking Co., OH, VI-4-16, J. N. Knull; 4 males, 2 females: Key Largo, FL, V-13, J. N. Knull; 1 female: Lake Corpus Christi, TX, III-3-1961, D. J. and J. N. Knull; 1 female: Delaware Co., OH, 4-VI, D. J. and J. N. Knull; 1 female: Starr Co., TX, IV-5-1963, D. J. and J. N. Knull; 1 male: Brooks, TX, IV-10-1950, D. J. and J. N. Knull; 1 male: Uvalde Co., TX, VIII-25-1947, D. J. and J. N. Knull; 1 female: Gillespie Co., TX, V-7-1946, D. J. and J. N. Knull; 1 female: Valley, NE, VI-30-1938, D. J. and J. N. Knull; 2 males: Lemoyne, PA, III-12-1911, D. J. and J. N. Knull; 1 male: Brownsville, TX, III-15, J. N. Knull; 2 males: New York, NY, [no collecting date]; G. Beyer; 1 female: Stillwater, OK, V-21-1995, M. Gates; 1 female: Starr Co., TX, 7 mi E El Sauz, V-8-1986, N. M. Downy; 1 male: USA, Marion Co., FL, SR40, at Lynne, IV-17-2007, F. W. Skillman Jr, beating slash; 2 females: San Antonio, TX, VII-4-1968, G. H. Nelson family; Gambier, OH, VI-19-1940, [no collector data]; 2 males, 1 female: Berrien Co., GA, 3 mi E Alapaha, IV-2-4-1973, R. Turnbow; 1 female: Starr Co., TX, Falcon Heights, abandoned park,

farm road 2098, [no collecting date], T. C. MacRae; 1 female: Alachua Co., FL, Gainesville, IX-24-1990, M. C. Thomas; 2 males: Taney Co., MO, Henning Cons. Area, White River Balds National Area, T. C. [no collecting date], MacRae; 1 male: Greenbrier Co., WV, Rupert, VIII-31-1992, S. F. Hutchinson; 2 males: Lawrence, KS, summer-1952, attracted to light, S. L. Wood; 1 female: Osage Co., OK, West Bartlesville, V-5-1981, K. Burnham; 1 male: Brazos Co., TX, IV-16-1960, J. N. Knull; 3 males, 4 females: Philadelphia Co., PA, [no collecting date], H. W. Wenzel; 3 males, 2 females: Hummelstown, PA, [no collecting date], J. N. Knull; 1 male: Franklin Co., OH, Columbus, VII-14-1968, [no collector data]; 1 male, 1 female: Carlisle, PA, VI-27-1917, H. R. Kirk; 1 male, 1 female: Benchley, TX, IV-30-1941, D. J. and J. N. Knull; 1 female: Columbus, OH, VI-24-1967, C. A. Triplehorn; 1 male: Kennedy, TX, IV-1944, R. Klieforth; 2 females: Cameron Co., TX, IV-3-1964, D. J. and J. N. Knull; 1 male: Lake Corpus Christy, TX, III-24-1965; 2 females: Seneca Co., OH, VII-25-1955, H. W. Hintz; 1 male: Dubuque, IA, VI-16-1955, H. Hintz; 1 male: Essex Co., Ontario, Wheatly, VI-9-1967, K. Stephan; 1 female: Ela, NC, Swan Co., 20-VIII-1954, G. B. Merrill; 1 female: Zapata Co., TX, 4 mi N San Ygnacio, VI-13-1975, R. Turnbow; 1 male: Latimer Co., OK, V-1986, K. Stephan; 1 male: Oxford, MS, V-15-1949, H. V. Weems Jr.; 1 female: Highlands Hamm Station Park, FL, III-5-1957, H. V. Weems Jr.

3.11 Neocallotillus Burke, 2016

Type species. *Neocallotillus elegans* (Erichson, 1847)

(Distribution shown in Fig. 2.21-L)

Differential diagnosis. *Neocallotillus* most closely resembles *Callotillus*. This genus can be differentiated from *Callotillus* based on the following characters: In males of *Neocallotillus* the first and second antennomeres are filiform; the third antennomere is moderately serrate; antennomeres 4-9 are strongly pectinate; and the tenth antennomere is ovoid in shape and laterally compressed (Fig. 2.8 D-E); the length of the tenth antennomere may vary by species. Females of *Neocallotillus* have antennomeres 1-3 filiform; the fourth antennomere is moderately serrate; and antennomeres 4-9 are robust and gradually increasing in size toward distal end (Figs. 2.8-F, 2.9-A); the tenth antennomere of females is similar to that of males. On the other side, males of *Callotillus* have antennomeres 1-2 small and filiform; third antennomere moderately serrate; antennomeres 4-9 strongly serrate and approximately equal in length; and tenth antennomere broadly ovoid and approximately the same length as antennomeres 8-9 together (Figs. 2.9-B, 2.11-A). The antennal structure of females is similar to that of males, except the antennomeres 4-9 are moderately serrate and the tenth antennomere is cylindrical to moderately ovoid (Figs. 2.9-C, 2.11-C). *Neocallotillus* species are also more slender (Fig. 2.2 D-E) than *Callotillus* (Fig. 2.2 D-E) and *Neocallotillus* species lack an elytral swelling which is present on the anterior third of the elytral disc of *Callotillus* (Fig. 2.13 A-B). *Neocallotillus* also resembles *Barrotillus* Rifkind (Fig. 2.1-E); however, the antenna of *Neocallotillus* is composed of 10 antennomeres (Fig. 2.8 D-E), while the antenna of *Barrotillus* has 11 antennomeres (Fig. 2.8-B). The restricted distribution of *Barrotillus*, recorded only from a confined locality in Honduras, will also serve to separate it from the widely distributed *Neocallotillus*.

Description. Size: 3–7 mm. Color: Light testaceous to dark brown (Figs. 2.2 B-C, 2.5-C); costae on elytral disc variously adorned, ranging from light testaceous to brown. Form: small to medium sized individuals; body elongate; elytra subparallel to moderately expanded posteriorly.

Head: Eyes medium sized, moderately taller than wide, conspicuously bulging laterally, strongly emarginate at antennal insertion; diameter of ommatidia small (Fig. 2.13-A); clypeus approximately 3× the width of eye emargination and moderately emarginate medially. Antennae composed of 10 antennomeres; sexual dimorphism observable in antennal shape, where the antennae are moderately pectinate and strongly compressed dorsoventrally in males (Fig. 2.8 D-E), but serrate and somewhat compressed dorsoventrally in females (Figs. 2.8-F, 2.9-A); tenth antennomere ovoid in both sexes. Labrum elongate, subquadrate; terminal maxillary palpi conical, acuminate posteriorly; terminal labial palpi securiform.

Thorax: Shape of pronotum scutiform, rounded laterally, narrower than anterior margin of elytra; disc feebly to moderately convex; inconspicuously broader at middle, feebly sinuate, conspicuously constricted on last fourth; anterior depression and antescutellar impression absent. Tibial spur formula 2-2-2, pulvillar formula 4-4-4. Prosternum: Smooth to feebly puncticulate; conspicuously wider than long. Mesoventrite: smooth, puncticulate. Metepisternum visible throughout its length in lateral view, not concealed by elytron. Metaventrite: moderately to strongly convex; variously punctate.

Elytra: Slender, expanded posteriorly, elongate; median region of elytral disc feebly compressed in lateral view; sides subparallel to moderately expanded posteriorly in dorsal view; elytral declivity feebly to moderately gradual; elytral markings always present in various shapes, may be elevated or not.

Legs: Femora smooth, variably vested. Tibiae moderately rugulose, weakly expanded posteriorly, variously vested. Two tarsal denticles conspicuously separated from each other, inner tarsal denticles trigonal, outer tarsal denticles digitiform.

Abdomen: Smooth to glossy, moderately vested, feebly to moderately convex, with six visible ventrites; lateral margins of ventrites 1-5 parallel, posterior margins truncate; sixth ventrite triangular to subquadrate in shape; male pygidia moderately differentiated from female pygidia (Figs. 2.16 G-L, 2.17 A-B).

Aedeagus: Moderately robust; phallobasic apodeme short, slender distally; endophallic struts elongate, slender throughout their length (2.15 A-C).

Remarks. Expressing tentative assignment of some of his species to *Callotillus*, Wolcott (1923) wrote: "*Callotillus crusoe*, as well as *C. elegans* and *C. vafer*, are placed in *Callotillus* provisionally only, as it differs from the other members of the genus in several important characters. No doubt, eventually, the creation of a new genus will be necessary for the reception of this new species and *C. elegans* and *C. vafer*. In *C. eburneocinctus*, the terminal segment of the maxillary palpi is sub-cylindrical, the eyes are emarginate internally and the abdomen has but five segments. In *C. elegans*, *C. vafer*, and *C. crusoe* the maxillary palpi have the terminal segment conical, the eyes are deeply emarginate anteriorly, and the abdomen has six distinct well developed segments". The morphological differences listed by Wolcott, together with the presence of pectinate antennae on males of *Neocallotillus* (Fig. 2.8 D-E) versus serrate antennae on males of *Callotillus* (Figs. 2.9-B, 2.11-A), and an elytral swelling present in *Callotillus* but absent in *Neocallotillus* (Fig. 2.13 A-B), support the recognition of two genera within the group. The monotypic *Barrotillus* (Fig. 2.1-E) was also examined in this study in order to assess

possible congenericity with *Neocallotillus* (Fig. 2.2 B-C). The structure of the antennae and number of antennomeres serve as evidence to conclude that these closely related genera should be considered as separate taxa (Fig. 2.8-B, D-E).

Key to species of *Neocallotillus*

1. Elytral disc finely punctate, punctations irregularly arranged; median region of each elytron adorned with a transverse, light testaceous to almost whitish, slightly elevated fascia, and one elevated macula on the anterior half of the elytral disc, this macula can be absent in some specimens, length 2-5 mm (Fig. 2.2 B-C) .... ***Neocallotillus elegans***
− Elytral disc devoid of punctations; fasciae pattern not as above, elytral disc variously adorned but not as above, larger individuals 2
2 (1). Each elytron with a testaceous, broad and procurved fascia that initiates at the elytral suture and extends from the median region of the elytral disc to the elytral apex, and small, narrow, moderately oblique marking at the median region of the elytral disc; posterior third of elytral disc with a semicircular macula (Fig. 2.5-F) .... ***Neocallotillus crusoe***
− Each elytron adorned with a pair of elaborate, pale fasciae, and one macula arranged as follows: macula located on the anterior fourth, posterior to the humeral angle; one fascia located on anterior half of elytral disc, and strongly procurved, initiating on elytral suture and ending just before epipleural fold; second fascia moderately oblique, located immediately posterior to the other fascia, initiating at the epipleural fold and not reaching the elytral suture (Fig. 2.2-F)......................
.... ***Neocallotillus intricatus***

Neocallotillus elegans (Erichson, 1847)

Figs. 2.2 B-C, 2.5-C, 2.8 D-F, 2.9-A, 2.13-A, 2.14-A, 2.15 A-B, 2.16 G-L, 2.17 A-B, 2.19-A.

Synonyms: *Tillus elegans* Erichson; Arch Naturgesch, 13, 1847: 85. *Callotillus occidentallis* Gorham; Biologia Centrali-Americana, 3 (2), 129. *Callotillus vafer* Wolcott syn. n.; Proceedings of the United States National Museum, 59, 270.

One female paratype examined.

Ttype locality: "Republica Peruana". Type depository. Zoologisches Museum Berlin, Germany (ZMB).

Distribution. USA: AZ, CA, LA, NM, NV, TX, UT; Mexico: Baja California, Baja California Sur, Chiapas, Chihuahua, Guerrero, Jalisco, Morelos, Nayarit, Oaxaca, Sonora, Tamaulipas, Yucatan; Central America: Costa Rica, Guatemala, Honduras, Nicaragua.

Differential diagnosis. *Neocallotillus elegans* can be differentiated from similar species based on the integument color, fascia pattern, and wide geographic distribution. The species is most similar to *N. intricatus* but can be easily differentiated from the latter based on the fasciae pattern on the elytral disc. *Neocallotillus elegans* has the elytra adorned with a light testaceous to almost whitish median, longitudinal, slightly elevated fascia, and a pair of elevated maculae on the anterior half near the humeral angles (Figs. 2.2 B-C, 2.5-C), these maculae may be absent in some individuals. *Neocallotillus intricatus* has the elytral disc decorated with an intricate design

of light testaceous fasciae and a pair of maculae arranged in the following manner: each elytron with one macula situated posterior to the humeral angle; one strongly procurved fasciae located on the anterior half of the elytral disc, this fascia initiates on the elytral suture and do not reach the epipleural fold; and a second fascia situated immediately posterior to the first, this band is strongly oblique, initiating on the epipleural fold and not reaching the elytral suture (Fig. 2.2-F). The geographic distribution of these species can also serve to separate them. *Neocallotillus elegans* is found from the USA to Costa Rica while *N. intricatus* is restricted to Costa Rica and Panama.

Redescription. Male. Form: Small individuals, feebly to moderately slender (Figs. 2.2 B-C, 2.5-C). Body: elongate, slender. Color: body integument variously colored, from piceous to ferruginous, with tones ranging from fuscous to testaceous; each elytron with one macula and one fascia, both markings ranging from almost albus to testaceous; the fascia is located on the median region of the elytral disc and can range from conspicuously wide to almost imperceptible; the macula is located on the median region of the anterior third of the elytral disc, initiating on the epipleural fold and almost reaching the elytral suture; these markings can be medially interconnected or not. The maculae may be absent in some specimens.

Head: Including eyes wider than pronotum; eyes conspicuously bulging laterally, taller than wide, large, finely faceted, very strongly emarginate; emargination subtriangular, extending 3/4 the eye width; integument moderately to strongly punctate; antennal notch located in front of antennal emargination; frons slightly to moderately bi-impressed. Antennae consisting of 10 antennomeres; antennomeres 2-3 small, beadlike; fourth antennomere strongly serrate, robust; antennomeres 4-9 pectinate, gradually increasing in size toward distal end; last antennomere

enlarged, ovoid in shape, laterally compressed (Fig. 2.8 D-E). Anterior portion of clypeus wide, approximately 3× the length of eye emargination (Fig. 2.13-A).

Thorax: Pronotum longer than broad, moderately to strongly punctate, punctations ranging from coarse and deep to moderately shallow and fine; sides subparallel in dorsal view, then abruptly constricted on posterior fourth; disc feebly convex. Prosternum smooth, punctate; punctations coarse, finely to moderately vested with pale, recumbent setae. Mesoventrite smooth, feebly punctate; finely vested with some pale, semi-recumbent to recumbent setae. Metaventrite moderately punctate; strongly convex; surface smooth, vested with fine, recumbent and semi-recumbent setae; longitudinal depression present; metaventral process absent.

Elytra: Humeri indicated, slender, elongate; lateral margins subparallel, slightly to moderately broader on posterior third, then moderately to strongly compressed on middle third, and conspicuously convex again on posterior third; sculpture consisting on shallow, irregularly arranged punctations; elytral apices subtriangular to almost rounded, feebly dehiscent; interstices at elytral base about 3× the width of punctuation; scutellum subquadrate, not compressed; epipleural fold complete, narrowing toward apex.

Legs: Femora swollen on posterior half; shiny; very feebly rugulose; weakly clothed with some semi-recumbent setae. Tibiae more profusely vested than femora.

Abdomen: Six ventrites; ventrites 1-5 shiny, smooth, subquadrate, not compressed laterally. Fifth ventrite subquadrate; lateral margins subparallel; posterior margin broadly, shallowly emarginate. Sixth ventrite small, conspicuously excavated, moderately, coarsely punctate, conspicuously broader than long; lateral margins strongly oblique, procurved; posterior margin broadly, moderately deeply, U-shaped emarginate; posterolateral angles broadly rounded (Fig. 2.16-L). Fifth tergite subquadrate, moderately, coarsely punctate; posterior margin broadly,

shallowly emarginate. Sixth tergite concave, wider than long; surface smooth; lateral margins moderately oblique; posterior margin broadly, moderately deeply, U-shaped emarginate. Posterolateral angles broadly rounded, fully covering sixth ventrite from dorsal view (Fig. 2.16-K.

Aedeagus: Phallobasic apodeme present; phallus with copulatory piece moderately swollen at apex; phallic plate devoid of denticles; intraspicular plate present, elongate; phallobasic apodeme short, expanded distally; phallobase subparallel; phallobasic lobes free; tegmen complete, fully covering phallus; phallobasic lobes pointed anteriorly; endophallic struts long, extending beyond the length of tegmen; endophallic struts slender throughout their length, weakly robust distally (Figs. 2.15 A-B, 2.19-A).

Sexual dimorphism: Females can be distinguished from males based on the antennal structure and the shape of the last abdominal segment. The antennal shape of females is moderately to strongly serrate; antennomeres 2-3 are slender, filiform; antennomeres 4-9 are serrate, the serrations gradually increasing in size toward distal end (Fig. 2.8-F). The posterior margin of the sixth ventrite of females is strongly procurved, producing a semicircular pygidium (Fig.2.17 A-B).

Material examined. PARATYPE: 1 female: [*Callotillus occidentalis* Gorham], Pantaleon, 1700 ft., Champion.

Additional material examined. 2 males: SW Hidalgo Co., TX, 17-III-1946, George B. Vogt, beating flowers and foliage, on *Prosonis juliflora* DeCandolie; 1 male, 3 females: Riverside Co., CA, Chuckawalla Mts., Corn Spg. Campground, 25-IV-1987, A. J. Mayor; 1

female: Imperial Co., CA, 9 mi N Winterhaven, 2-IV-1997, F. G. Andrews and A. J. Gilbert, sweeping *Prosopis*; 1 female: TX, 12 mi W Guthrie, 14-VII-1969, K. Polk; 1 male, 1 female: Hidalgo Co., TX, Sta. Ana Natl. Refuge, vic. Willow Lake, T. C. McRea; 1 male, 1 female: Val Verde Co., TX., Pecos River, 29-VIII-1970, no collector data; 1 male: Rio Grande City, Starr Co., TX, on *Prosopis*; 1 male: NM, 12 mi W Carlsbad, 25-IV-1971, on mesquite, C. R. Ward; 1 male: San Diego Co., CA, Borrego State Park, 17-20-IV-1969, no collector data; 1 female: Painted Canyon, Riverside Co., Calif., 25-III-1962, F. G. Andrews; 1 male: N. M., Hidalgo Co., Coronado Natl. Forest, 26-V-1976, W. Iselin; 3 males, 2 females: AZ, Sta. Catalina Mts., Pima Canyon, 7-IX-1970, K. Stephan; 1 female: TX, 5 mi NW of Alpine, 17-VI-1965, on *Sapindus drummondii*, G. H. Nelson; 2 males: Starr Co., TX, 2 mi W of Sullivan City, reared from *Pithecelobium flexicaule*, G. H. Nelson; 1 female: Socorro Co., NM, Bosque de Apache Nat. Wildlife Ref., 2-VII-2000, F. W. Skillman Jr.; 2 females: AZ, Sta. Catalina Mts., Pima Canyon, Bred ex Palo Verde, K. Stephan; 1 female AZ, Sta. Catalina Mts., Sabino Canyon, 11-VIII-1961, G. H. Nelson;; 1 female: CA, Imperial Co., 7 mi N of Glamis, 29-VIII-1987, on *Cercidium floridum,* Wood; 2 males, 1 female: Imperial Co., CA, Frink Spr., 7-VII-1993, on Olneya tesota, G. H. Nelson; 1 female: San Diego Co., CA, 3 mi E of Jacumba, reared *Acacia greggii*, 22-V-1987, G. H. Nelson; 1 male, 3 females: AZ, Pima Co., GreenValley, 15-VII-976, no collector data; 1 male, 1 female: Eddy Co., NM, 26 mi E of Carlsbad, 2-VI-1977, no collector data; 1 female: Dona Ana Co., NM, 9 miles west of Santa Teresa, 8-V-1999, J. C. Schaffner; 1 female: Bastrop Co., TX, Bastrop, 3-VI- 1997, S. G. Wellso; 1 female: Cochise Co., AZ, 12 mi N of Douglas, 24-VII-1982, J. E. Wappes; 1 male: TX, 3 mi southeast Presidio, 12-IV-1968, J. G. Hafernik; 1 male, 1 female: Pima Co., AZ, Mt. Lemon, V-17-1976, R. Lenczy; 1 male: Cochise Co., AZ, Wilcox Dry Lake, 6-VI-1970, A. R. Hardy; 1 male: TX, Brownsville, VII-1937, H. S.

Barber; 2 males: AZ, Tucson, VIII-193[ ], Bryant; 1 female: Riverside Co., CA, 25-III- 1962, F. G. Andrews; 10 males, 5 females: CA, Mecca, 20-V-1924, B. Warwick; 1 female: CA, Calipatria, 6-V-1924, B. Warwick; 1 female: CA, Calipatria, 1-V-1924, B. Warwick; 1 male: CA, Calipatria, 10-V-1924, B. Warwick; 10 females: Hidalgo Co., TX, J. N. Knull, 28-III-1954; 3 males, 4 females: TX, Brownsville, , 25-V-1934, J. N. Knull; 2 females: Cameron Co., TX, 25-III-1952, J. N. Knull; 5 males, 3 females: Hidalgo Co., TX, 26-III-1957, J. N. Knull; 6 males, 6 females: Hidalgo Co., TX, 20- III-1952, D. J. and J. N Knull; 1 male: AZ, Huachuca Mt., 5-VI D. J. and J. N. Knull; 2 females: Starr Co., TX, D. J. and J. N. Knull, 28-III-1950; 1 male: Uvalde Co., TX, 20-V, D. J. Knull; 1 male, 2 females: Hidalgo Co., TX, 29-III-1968, D. J. and J. N Knull; 2 females: Hidalgo Co., TX, 26-III-1953, D. J. and J. N. Knull; 1 male, 1 female: Hidalgo Co., TX, 24-III-1954, D. J. and J. N. Knull; 1 male: Hidalgo Co., TX, 28-III-1954, D. J. and J. N. Knull; 1 male, 4 females: CA, Santa Rosa L., VIII, J. L. Knull; 3 males, 1 female: AZ, Wilcox, 4-VII-1951, D. J. and J. N. Knull; 2 males: AZ, Wilcox, 6-VI-1954, D. J. and J. N. Knull; 1 female: AZ, Patagonia Mts., 2-VII- 1953, D. J. and J. N. Knull; 1 male: Culberson Co., TX, 9-VII-1953, D. J. and J. N. Knull; 2 male, 2 females: Pima Co., AZ, 9-VII-1975, N. M. Downy; 1 male: Bell Co., TX, Holland, 12-VII-1988, S. G. Wellso; 2 males: Hidalgo Co. TX, Sta. Ana Natl. Refugee, VIII-1977, J. E. Wappes; 1 male, 1 female: Calipatria Co., CA, 15-VII-1925, B. Warwick; 1 female: Uvalde Co., TX, VII-27, J. N. Knull; 1 female: CA, Mecca, 12-V-1924, B. Warwick; 4 males, 1 female: CA, Calipatria, 1-6-V-1924, B. Warwick; 15 males, 9 females: AZ, Chiricahua Mts., 1-3-VI, J. N. Knull; 1 male, 2 females: AZ, Tucson, VIII-19, J. N. Knull; 2 females: Hidalgo Co., NM, 24-III-1954; D. J. and J. N. Knull; AZ, Wilcox, 11-VI-1954, D. J. and J. N. Knull; 2 males: Imperial Co., CA, 15 mi W of Calexico, 5-6-VI-1961, light trap, H. F. Howden; 1 female: CA, Palm Springs, 15-VI-1948, D. J. and J. N. Knull; 1 female: TX,

Davis Mts., 24-VI-1957, D. J. and J. N. Knull; 4 males, 7 females: TX, Chisos Mts., V-25, J. N. Knull; 2 males: Jeff Davis Co., TX, 20-VI-1957, D. J. and J. N. Knull; 1 male: TX, on live oak, 17- V-1965, J. L. Bottmer; 2 males: AZ, Mt. Huachuca, 5-8-VI, D. J. and J. N. Knull; 3 males: Hidalgo Co., TX, 20-IV-1968, D. J. and J. N Knull; 4 males, 6 females: Jim Wells Co., TX, 8 mi S of Alice, 6-8-April-1984, S. G. Wellso; 2 females: Jim Wells Co., TX, Alice, 15-IV-1986, S. G. Wellso; 1 male: Brewster Co., TX, Castolon, 14- IV-1983, S. G. Wellso; 1 female: Brewster Co., TX, Big Bend Natl. Park, 16-IV-1983, S. G. Wellso; MEXICO: 1 male, 1 female: Chiapas, Mex., 4 mi NW of Pueblo Nuevo River Bajada, 15-VII-1965, G. H. Nelson; 1 male: Baja Calif. S., Mex., 4 mi S La Paz, 14-IX-1978, B. K. Dozier; 1 male: Baja Calif., Mex., Catavina, riparian palm oasis, on *Acacia greggii*, G. H. Nelson; 1 male, 2 females: Baja Calif. S., Mex., La Paz, 29-VI- 1973, B. F. Chamberlain; 2 females: Baja Calif. S., Mex., 1-3 mi E Cabo San Lucas, G. Riley; 1 female: Baja Calif. Sur, Mex, 9 mi N San Jose del Cabo, G. Riley; 2 males: Baja Calif. S., Mex., 66 km NE Insurgentes nr. Ultima Agua, on *Prosopis articulata*, 13-IV-1994, D. Yanega; 2 males: Morelos, Mex., Tlaquiltenango, Huaxtla, 18.37598 N, 99.04804 W, 1053 m, 13-XII-2009, V. H. Toledo; 1 male: Sonora, Mex., 29 km SE Tecoripa y 3 km S Rancho Las Peñitas, 733 m, on *Acacia* sp., 22-IV-2004, V. H. Toledo; 2 males, 1 female: Baja Calif. S., Mex., Las Barrancas, 27-V-1984, P. DeBach, Malaise trap; 1 female: Yucatan, Mex., Tekom, 04-VIII-1940, I. Sanderson; 1 male: Baja Calif., Mex., Santa Rosa, 08-10-I-1914, G. Beyer; 1 male, 2 females: Chiapas, Mex., 4 mi NW of Pueblo Nuevo, 15-VII-1968, G. H. Nelson; 1 male: Tamaulipas, Mex., El Encino, 15-IV-1984, S. G. Wellso. 8 males, 3 females: Baja Calif. S., Mex. 6 km E of San Antonio, 350 m, on *Prosopis articulata*, 11-IV-1994, no collector data; CENTRAL AMERICA: 2 males: Guanacaste, [Costa Rica], Cerro El Hacha, 800m, 12 km SE La Cruz, 320000, 364000, 1998; 1 male: Heredia Province, Costa Rica, Sarapiqui, Chilamate, La

145

Marita Farm, 26-II-1992, R. L. Johnson and R. Ochoa; 1 female: Rivas, Nicaragua, San Juan del Sur, 11' 15° N, 82' 52° W, 10-III-1998, L. J. Clark; 1 female: Granada, Nicaragua, Volcan Mombacho, Finca San Joaquin, 15-V- 1998, malaise trap, in organic coffee, J. M. Maes.

Remarks. The species *Callotillus occidentalis*, described by Gorham (1882) for individuals collected in Guatemala and Nicaragua, was later synonymized with *C. elegans* by Schenkling (1903). I examined one female paratype of *C. occidentallis* and agree with Schenkling's synonomy. Barr (1950) proposed that *Callotillus vafer* be reclassified as a subspecies of *C. elegans* on the basis of integument color, geographic distribution discontinuity, and differences in the structure of the elytral punctation. Individuals inhabiting Arizona, California, Nevada, New Mexico, western Texas, Utah, and the Baja California peninsula were classified by Barr as *C. e. vafer* while specimens from western Louisiana, eastern Texas, Mexico and Central America were recognized as *C. e. elegans*. Barr also indicated the existence of intermediate forms of these subspecies in the USA and Baja California; however, I have found intermediate forms exist throughout much of the geographic range of the species. It is possible to find both color morphos (Fig. 2.2 B-C), including intermediate forms (Fig. 2.5-C), as well as conspicuously similar antennal forms throughout North and Central America. Aside from integument variation, no other morphological evidence was found to differentiate these subspecies as separate taxa. As more material from these subspecies has been accumulated, *N. elegans* is a species with a wide spectrum of color variation throughout an extensive geographic distribution.

Neocallotillus crusoe (Wolcott, 1921)

Fig. 2.15-F.

Type material not examined.

Type locality: Camuy, Puerto Rico. Type depository. American Museum of Natural History (AMNH).

Distribution. Puerto Rico.

Differential diagnosis. *N. crusoe* is similar to *N. elegans* but differs from the latter species by the absence of seriate elytral punctures, its larger size, its broader form, and the impunctate metaventrite and abdomen. The differently formed and arranged raised fasciae or maculae are also distinguishing characters. The head and pronotum in *N. crusoe* are densely pubescent, sparsely so in the *N. elegans* species; the antennae are differently formed, having a greater number of triangular segments; the color pattern is unique; the arrangement of the pubescence in basal half of elytra is distinctive; and the densely pilose elytral tubercles are present only in *C. eburneocinctus*.

The following is Wolcott's original description.

Form: Moderately slender. Color: Black. Dorsal surface feebly shining; ventral surface very shining; front of head narrowly rugulose; antenna (apical two segments black) and labrum at sides testaceous; elytra black with the apical half in large part pale yellow; a large, ovate, ante-apical, black maculation; sides at middle with an oblique, elevated, white

maculation; a similar minute, slightly transverse maculation at basal fourth at middle of width of each elytron.

Head: Including the not prominent eyes, equal in width to pronotum at apex; surface coarsely rugoso-punctate; pubescence dense, semi-recumbent, grayish white. Antennae slightly longer than head and prothorax, ten-segmented; basal segment short, very stout; second small, subtriangular; third to ninth triangular, their apices acute; ninth and tenth forming an elongate ovate mass; tenth narrower than eighth, nearly as long as seventh and eighth together; color testaceous; ninth and tenth segments black, the former narrowly testaceous at base.

Pronotum: Slightly longer than wide; apical margin truncate; sides parallel to slightly behind the middle, then strongly arcuately narrowing to about basal fourth, thence subparallel to base; base truncate, the extreme edge with a fine elevated margin; subapical constriction wanting; subapical transverse impression nearly obsolete, only faintly indicated in certain lights; surface with sculpture same as that of head; pubescence same as that of head but with long, sparse, erect, black hairs intermixed.

Elytra: Base nearly twice as wide as pronotum at base; humeri obtusely rounded; sides from humeri to middle straight, nearly parallel, behind the middle gradually broadening to apical fourth, thence arcuately narrowing to the conjointly rounded apices; color black, apical half pale yellow, anterior margin of yellow portion convex; in apical third a large, elongate ovate, common, sutural maculation, extending very nearly to apical margin, black; sides slightly anterior to middle with a feebly arcuate, linear, elevated, white maculation, this extending obliquely and attenuate forward from lateral margin halfway to suture; at basal fourth a minute, slightly transverse, elevated, white maculation midway

between the lateral margin and the suture; base with a broad triangular area, having one angle on suture, and an oblique fascia each side, extending from immediately behind the humeri to the suture at a point slightly before the middle, composed of dense, coarse, grayish-white pubescence; a large, feebly elevated, subbasal tubercle, midway between lateral margin and suture, densely clothed with a tuft of long, black hairs; black portions densely clothed with short, semi-recumbent, black pubescence, longer and erect in humeral region; the yellow portion densely clothed with pale yellowish pubescence, a few nearly erect, long, black hairs intermixed; surface finely and sparsely punctate at extreme base, becoming closer at about basal fourth, and a little coarser toward the apex; punctuation irregular throughout, showing no tendency to become seriate.

Abdomen: Impunctate; very sparsely clothed with long, black hairs. Meso[ventrite] sternum smooth; moderately clothed with semi-recumbent, grayish-white pubescence. Legs rather short and stout; moderately clothed with rather long, white hairs. Length, 4.2 mm.

Remarks. Wolcott (1923) described *Callotillus crusoe* from a single male specimen collected near Camuy, Puerto Rico. Wolcott concluded that this species was allied to *C. elegans* and *C. vafer* but could be differentiated from the latter two based on the absence of elytral punctations, a relatively larger size and broader body shape, and the absences of punctations on the metaventrite and abdomen. Based on Wolcott's illustration and his descriptive work, the shape of the antennae appear to be serrate, and the species seems to be comparatively larger and broader than other *Neocallotillus* species. These characteristics may suggest a relationship to *Callotillus*. Due to the absence of material of *N. crusoe*, a redescription of this species is not presented in this study. Based on Wolcott's assessment, *C. crusoe* was moved to *Neocallotillus*.

Neocallotillus intricatus (Wolcott, 1947)

Figs. 2.2-F, 2.11 B-D, 2.15-C.

One male paratype examined.

Type locality: Farm La Caja, 8 km. west of San Jose, Costa Rica. Type depository. Naturalis Biodiversity Center, Leiden, The Netherlands (RMNH).

Distribution. Costa Rica, Panama.

Differential diagnosis. *N. intricatus* is most similar to *N. elegans*. The two species can be differentiated based on the fasciae pattern on the elytra disc. *Neocallotillus intricatus* has the elytral disc decorated with an intricate design of light testaceous fasciae and a pair of maculae arranged in the following manner: Each elytron with one macula situated posterior to the humeral angle; one strongly procurved fasciae located on the anterior half of the elytral disc, this fascia initiates on the elytral suture and do not reach the epipleural fold; and a second fascia situated immediately posterior to the first, this band is strongly oblique, initiating on the epipleural fold and not reaching the elytral suture (Fig. 2.2-F). *Neocallotillus elegans* has the elytra adorned with a light testaceous to almost whitish median, longitudinal, slightly elevated fascia, and a pair of elevated maculae on the anterior half near the humeral angles (Fig. 2.2 B-C), these maculae may be absent in some individuals. The geographic distribution of these species can also serve to separate them. *Neocallotillus intricatus* is limited to Costa Rica and Panama, while *Neocallotillus elegans* is found from the USA to Costa Rica.

Redescription. Male. Form: Body elongate; head, pronotum and anterior half of elytra slender, feebly expanded behind middle half of elytral margins. Color: Head, pronotum, thorax, abdominal segments 1-4 and femora griscent to fuscous; anterior margin of pronotum, antennae, mouthparts, tibiae, abdominal segments 5-6 and elytral apex light-ferruginous. Elytra adorned with an intricate array of two pale-testaceous fasciae and a pair of maculae of the same color, the position of these elytral markings is as follows: the first fascia is located on the anterior half of the elytral disc, this band is strongly procurved, initiating on the elytral suture and not reaching the epipleural fold; the second fascia is located immediately posterior to the first band and is moderately oblique, initiating on the epipleural fold and not reaching the elytral suture; the two macuale are located posterior to the humeral angles. Elytral pattern not elevated from elytral disc (Fig. 2.2-F).

Head: Including eyes not wider than pronotum; eyes strongly emarginate, taller than wide, feebly bulging laterally, small, finely faceted; emargination subtriangular; integument moderately punctate; antennal notch anterior to antennal emargination; frons moderately bi-impressed. Antennae of male consisting of 10 antennomeres; antennomeres 2-3 small, beadlike; fourth antennomere serrate; antennomeres 4-9 pectinate, gradually increasing in size toward distal portion of antenna; last antennomer enlarged, as long as ninth antennomere, ovoid in shape, laterally compressed.

Thorax: Pronotum longer than broad; surface rugulose and strongly, finely punctate; punctations numerous, shallow; sides subparallel in dorsal view, then abruptly constricted on posterior fourth; disc convex. Prosternum feebly convex; surface smooth; conspicuously punctate, punctations shallow. Mesoventrite smooth; surface slightly punctate; finely vested. Metaventrite globate; surface smooth, strongly convex and finely punctate; longitudinal

depression and metaventral process absent; metepisternum exposed but profusely covered with short, fine, pale setae observable in lateral view. Scutellum ovoid in shape.

Elytra: Humeri indicated; slender on anterior half and then gradually expanding behind middle; surface convex on anterior third, then strongly compressed on middle third, and then conspicuously convex on posterior third; elytral sinuosity observable in lateral view; sculpture on elytral disc consisting on abundant, very shallow, irregularly arranged punctations almost imperceptible in some individuals; elytral apices rounded, moderately dehiscent; interstices on elytral base about 2× the width of punctuation; epipleural fold complete, narrowing toward apex.

Legs: Femora swollen; surface shiny, smooth; vestiture consisting of some semi-recumbent setae, then abruptly vested with numerous pale, semi-recumbent, stout setae on distal face. Tibiae more profusely vested than femora; vestiture consisting on stout, pale, short, recumbent setae interspersed with some semi-erect setae.

Abdomen: Six ventrites; ventrites 1-4 broadly convex, smooth, rugulose, subquadrate, not compressed laterally; posterior margins truncate. Fifth ventrite shiny; lateral margins moderately obtuse; posterior margin broadly, shallowly emarginate. Sixth ventrite small; surface moderately excavated, shiny, feebly punctate, conspicuously broader than long; lateral and posterior margins strongly oblique, semicircular. Fifth tergite sub-quadrate; surface moderately, coarsely punctate; posterior margin broadly, shallowly emarginate. Sixth tergite concave, wider than long; surface smooth; lateral margins moderately oblique; posterior margin truncate; posterolateral angles subquadrate. Sixth tergite extending beyond apical margin of sixth ventrite, fully covering sixth ventrite from dorsal view.

Aedeagus: Moderately robust; distal portion of phallus petiolate; phallobasic apodeme present; phallus with copulatory piece moderately swollen distally; intraspicular plate present,

152

elongate; phallobasic lobes moderately procurved; tegmen complete, fully covering phallus; phallobasic lobes acuminate distally (Fig. 2.15-C).

Sexual dimorphism: The antennal shape of females is strongly serrate (Fig. 2.11-D), rather than pectinate, as observed in males (Fig. 2.11-B). Females have antennomeres 1-3 slender, antennomeres 4-5 are moderately serrate, and antennomeres 6-9 are strongly serrate, the serration gradually increasing in size toward the distal end. Females also have the lateral and posterior margins of the sixth ventrite subquadrate, producing a somewhat semicircular pygidium. All females in the material examined were moderately larger than males.

Material examined. PARATYPE: 1 male: Farm La Caja, 8 km W San José, Costa Rica, Eing, 12-VI to 20-VII-1924, hand written red label.
Additional material examined. 2 females: Costa Rica, Guanacaste, 3 km SW of R. Naranjo, 11-18-III-1992, F. D. Parker; 1 male, 3 females: Costa Rica, Guanacaste, 14 km S Cañas, 2-III-1990, F. D. Parker; 1 male, 2 females: Panama, Coclé province, El Valle [Anton], 19-II-1999, W. E. Wappes.

Remarks. Wolcott & Dybas (1947) described *Callotillus intricatus* based on two specimens, one male and one female, collected from a single locality 8 km west of San Jose, Costa Rica. This species was transferred to *Neocallotillus* based on the pectinate antennae of male individuals (Fig. 2.11-B) and the feebly pectinate to almost serrate antennae in females (Fig. 2.11-D), those antennal shapes are very similar to those observed on *N. elegans* males (Figs. 2.8 D-E) and females (Fig. 2.8-F, 2.9-A). Other characters that are similar in these species

are general body shape, elytral sculpturing, and the conical shape of the terminal segment of the maxillary palpi.

3.12 Onychotillus Chapin, 1945

Type species: *Onychotillus vittatus* Chapin. Original designation.

(Distribution shown in Fig. 2.21-K)

Redescription. Size: 3-12 mm. Color: Body ranging from light fuscous to ferrugineous; some individuals may possess one pale, median fascia on each elytron. Body: Winged species, short, moderately robust individuals, somewhat subparallel (Fig. 2.5 A-B).

Head: Including eye slightly narrower than pronotum; integument moderately to coarsely punctate, punctations vary from narrow to wide; eyes large, finely faceted, feebly emarginate posteriorly; moderately bulging laterally; eleven antennomeres, antennae extending beyond posterior margin of pronotum; last antennomere as long as or conspicuously longer than ninth antennomere (Fig. 2.10 E-F); frons feebly to moderately bi-impressed; terminal labial palpi securiform; terminal maxillary palpi cylindrical, compressed laterally.

Thorax: Pronotum smooth and shiny to moderately punctate, punctation may range from narrow to moderately wide; lateral margins subparallel, slightly constricted anteriorly, feebly to conspicuously wider posteriorly. Prosternum much wider than long, smooth to rugose, variously punctate. Mesosternum moderately wider than long, smooth, feebly to moderately punctate. Metasternum convex, wider than long, surface conspicuously punctate to almost smooth.

Metaventral process compressed anteriorly; metepisterna largely exposed, the elytra do not coverer these plates.

Elytra: Moderately short to elongate, subparallel, widest on middle half, surface moderately to coarsely punctate, punctations arranged in regular striae, punctations do not extend to apex; epipleural fold compete, narrowing toward apex. Legs: femora smooth to rugose; moderately swollen distally; tibiae rugose to rugulose; tarsal formula 4-4-4; pulvillar formula 4-4-4; one tarsal denticle, tarsal denticle trigonal in shape.

Abdomen: Six visible ventrites; visible ventrites 1-5 not impressed laterally; pygidium of males feebly differentiated from that of females; females with sixth ventrite broadly rounded, pygidium simple.

Aedeagus: moderately sclerotized; length of aedeagus short, not longer than the length of abdomen; tegmen triangular; phallic plate devoid of denticles; phallobasic apodeme short, shorter than phallus; endophallic struts reduced.

Remarks: *Onychotillus* was described by Chapin (1945). The genus is most similar to *Cymatodera*. *Onychotillus* is currently composed of five species, all inhabiting the West Indies. Of the five valid species, three are thought to be restricted to Cuba (De Zayas, 1988), while the original descriptions of *O. cubana* De Zayas and *O. vittatus* Chapin indicate that these species are restricted to Cuba (De Zayas, 1988) and Jamaica (Chapin, 1945), respectively. Based on the limited descriptive work given by De Zayas (1988), where no keys for identification for the new species were provided, I have examined material of what would be *O. cubana*. None of the specimens belonging to this species were collected in Cuba, so I tentatively place these specimens within De Zayas' *O. cubana*, pending further material to be examined. It is important

to note that De Zayas' descriptions were based, in most cases, on single specimens, and access to that material has shown to be particularly difficult. Additionally, I have examined a number of specimens from *O. vittatus* which were collected in the Dominican Republic and the Cayman Islands, and all of those represent new distributional records for the species. Material collected in the type locality was also revised here. In this revisionary work, the genus *Onychotillus* and two species: *O. cubana* De Zayas and *O. vittatus* Chapin are redescribed. Due to the lack of availability of material and the poorly detailed descriptions conducted by De Zayas (1988), three species are excluded from this revision; *O. trinitatis* De Zayas, *O. minuta* De Zayas, and *O. dimidiata*, De Zayas, all of them endemic to Cuba (De Zayas, 1988).

Key to species of *Onychotillus*.

1. Pronotal disc piceous to almost black, with or without a metallic hue (Fig. 2.5-B); last antennal segment about the same length as two preceding antennomeres combined (Fig. 2.10-F) ....***Onychotillus vittatus***
− Pronotal disc light testaceous to ferrugineous, without a metallic hue (Fig. 2.5-A); last antennal segment about the same length as three to four preceding antennomeres combined (Fig. 2.10-E) ....***Onychotillus cubana***

Onychotillus cubana De Zayas, 1988
Figs. 2.5-A, 2.10-E.

Type material not examined.

Type locality: Pico Turquino, Cuba. Type depository: Unknown.

Distribution: Cayman Islands, Cuba, Dominican Republic.

Differential diagnosis: *Onychotillus cubana* can be differentiated from the congeneric *O. vittatus* based in the integument color, structure of the eleventh antennomere, and body size. In *O. cubana* the pronotum and prosternum integument is light testaceous to ferrugineous (Fig. 2.5-A); the last antennomere is approximately 4× the length of the previous antennomere (Fig. 2.10-E); and the body size is minute, 3-5 mm in length. *Onychotillus vittatus* has the pronotum and prosternum integument metallic blue to almost piceous (Fig. 2.5-B), the eleventh antennomere is about the same length as the previous antennomere (Fig. 2.10-F), and individuals of this species are longer compared to *O. cubana*, with a body length ranging from 6 to 11 mm. A differential diagnosis for the rest of the species not covered in this revisionary work is more difficult, however, based on De Zayas descriptions (1988), none of the species restricted to Cuba have the same color pattern observed in *O. cubana* and *O vittatus*.

Redescription. Male. Form: moderately robust, short individuals. Color: Head, antennae, mouthparts, elytra, legs, meso and metathorax light fuscous to almost piceous; pronotum and prosternum testaceous to ferrugineous, mesosternum and abdomen, except anterior portion of first visible ventrite, testaceous; legs, metasternum and anterior portion of first visible ventrite brown. Each elytron adorned with five longitudinal, moderately regular, fuscous fasciae; fasciae becoming paler and narrower toward epipleuron; fasciae 2-4 not reaching elytral apex; first and fifth fasciae interconnected at posterior portion of elytra, reaching apex (Fig. 2.5-A).

Head: measured across eyes moderately wider than pronotum; surface rugose; moderately, coarsely punctate; clothed with moderately long, recumbent setae and some semirecumbent setae behind the eyes; frons bi-impressed; eyes large, rounded, slightly taller than wide, bulging laterally. Antennae extending slightly beyond base of elytra; second antennomere short, robust; third antennomere slightly longer than third antennomere; fourth antennomere about the same length as second antennomere, antennomeres 5-10 subequal in length, about half the length of fourth antennomere; antennomere 2–4 subcylindrical; antennomeres 5–10 feebly serrate; last antennomere cylindrical, acuminate posteriorly, approximately $3.5 \times$ the length of tenth antennomere (Fig. 2.10-E).

Thorax: pronotum short, as wide as long; sides feebly constricted anteriorly and subapically; widest in front of middle; disc feebly convex; anterior transverse depression and subbasal tumescence absent; surface moderately clothed with short and long, semi-erect setae; surface feebly rugulose to shiny, conspicuously less rugose than head; moderately, shallowly punctate. Prosternum rugulose to shiny; punctation absent to very feebly punctate. Mesosternum feebly convex; conspicuously, coarsely punctate, feebly clothed with long, semirecumbent setae. Metasternum conspicuously wider than long; strongly concave; rugulose; moderately, shallowly punctate; moderately vested with fine, pale, recumbent setae.

Legs: Femora and tibiae moderately clothed with fine, semirecumbent setae interspersed with long, semi-erect setae; surface of femora rugulose to smooth; tibiae transversally, moderately rugose; fourth tarsomeres with pulvilli not incised medially.

Elytra: base wider than pronotum; humeri indicated; sides subparallel; widest behind middle; disc feebly convex; surface rugose; apices subtriangular; feebly dehiscent; moderately clothed with long and short, erect setae; sculpture consisting of coarse punctations arranged in

158

regular striae that gradually become smaller toward apex, striae reaching elytral apex; interstices at elytral base about 2.5× the width of punctuation.

Abdomen: Six visible ventrites; first visible ventrite medially elevated, lateral areas feeble excavated; ventrites 1–4 moderately rugose, subquadrate, moderately, shallowly punctate, vested with long, fine, pale, recumbent setae. Fifth visible ventrite subquadrate; surface convex; moderately, coarsely punctate; lateral margins subparallel; posterior margin truncate. Sixth visible ventrite subquadrate, broader than long; surface rugulose; moderately, coarsely punctate; lateral margins conspicuously oblique, posterior margin broadly rounded, producing a rounded posterolateral margin. Fifth tergite rugulose, lateral margins subparallel; posterior margin truncate, with a narrow, shallow, triangular emargination on median region. Sixth tergite subtriangular, broader than long; surface rugulose; lateral margins feebly arcuate, oblique; posterior margin short, rounded, the lateral and posterior angles producing a rounded posterolateral margin; Sixth tergite extending beyond posterior margin of sixth visible ventrite, fully covering the sixth visible ventrite from dorsal view.

Aedeagus: phallobasic apodeme present; phallus with copulatory piece tapered posteriorly; phallic plate armed with a row of fine and small denticles; intraspicular plate present, somewhat elongate; phallobasic apodeme long, expanded distally; phallobase sinuate laterally; parameres free; tegmen incomplete, partially leaving phallus exposed; parameres pointed at distal end; endophallic struts long, slender distally.

Sexual dimorphism: The single female specimen examined differs from males by having the last abdominal segment broadly rounded and inconspicuously convex to almost flat, rather than subtriangular with the surface moderately convex as seen in males, and the eleventh

antennomere is moderately shorter compared to the same antennomere in males. Remaining characters do not vary for both sexes.

Material examined: 2 males, 1 female: Cayman Islands, Brac Brac Paradise Subdivision, 19° 44.688' N 79° 44.55' W, 6-VI-2008, M. C. Thomas, R. H. Turnbow and B. K. Dozier, blacklight trap; 1 female: Cayman Islands, Major Donald Dr., 4 km E jct. Ashton Reid Dr., 22-V-2009, M. C. Thomas, R. H. Turnbow; 1 male: Dominican Republic, Independencia, Sierra de Neiva, just south of crest, 5 km SW of Angel Feliz, 1780 m, 18° 41' N 71° 47' W, 13-15-X-1991, J. Rawlings, R. Davidson, C. Young and S. Thomas.

Onychotillus vittatus Chapin, 1945

Figs. 2.5-B, 2.10-F, 2.17-I.

Type material not examined.

Type locality: Great Goat, Jamaica. Type depository: National Museum of Natural History (NMNH).

Distribution: Dominican Republic, Jamaica.

Differential diagnosis: *Onychotillus vittatus* is most similar to *O. cubana* and characters to distinguish these species are given above in the diagnosis of *O. cubana*.

Description. Male. Form: slender, moderately small, elongate individuals. Color: head, pronotum, antennae, mouthparts, elytra, meso and metathorax metallic blue to almost piceous; legs with femora bicolored, anterior portion light testaceous to pale yellow, posterior portion metallic blue to almost black, tibiae uniformly metallic blue to almost black. Abdomen uniformly piceous to black. Elytral disc without fasciae or bands (Fig. 2.5-B).

Head: measured across eyes moderately narrower than pronotum; surface rugose; moderately punctate; punctures broad and shallow, clothed with moderately long, recumbent setae and some semirecumbent setae; frons bi-impressed; eyes large, rounded, slightly taller than wide, moderately bulging laterally, finely faceted. Second antennomere short, robust; third antennomere slightly longer than second antennomere; antennomeres 4-5 about the same length as third antennomere, sixth antennomere slightly shorter than fifth antennomere, antennomeres 6-10 subequal in length; antennomere 2–5 subcylindrical; antennomeres 6–10 feebly serrate; last antennomere cylindrical, acuminate posteriorly, slightly compressed medially, approximately $2 \times$ longer than the length of tenth antennomere, eleventh segment moderately longer in males than in females (Fig. 2.10-F).

Thorax: pronotum short, as wide as long to slightly longer than wide; sides weakly constricted anteriorly and subapically; conspicuously widest in front of middle; disc feebly convex; anterior transverse depression and subbasal tumescence absent; surface moderately clothed with short, recumbent setae intermixed with some long, semi-erect setae; surface rugulose to rugose; conspicuously punctate, punctations somewhat small and shallow. Prosternum shiny; with a longitudinal carina that divides this plate, moderately excavated laterally, feebly punctate. Mesosternum; moderately, coarsely punctate, punctations wide and deep, glabrous to slightly clothed with long, semirecumbent setae. Metasternum conspicuously

wider than long; strongly concave; moderately rugose; moderately, shallowly punctate; vested with fine, pale, recumbent setae.

Legs: Femora feebly rugose, shiny, moderately clothed with fine, pale recumbent and semirecumbent setae; tibiae transversally, moderately rugose, more conspicuously vested than femora; fourth tarsomeres with pulvilli not incised medially.

Elytra: base wider than pronotum; humeri indicated; sides subparallel; widest at middle; disc moderately convex; surface rugose to moderately rugulose; apices rounded; slightly dehiscent; clothed short, semirecumbent setae intermingled with some long, erect setae; sculpturing consists of coarse punctations arranged in regular striae that gradually become smaller toward apex, striae reaching elytral apex; interstices at elytral base about 2.5× the width of punctuation.

Abdomen: Six visible ventrites; first visible ventrite feebly elevated medially, anterolateral region very feeble excavated; ventrites 1–5 moderately rugose, subquadrate, moderately, shallowly punctate, vested with long, fine, pale, recumbent setae. Fifth visible ventrite with the lateral margins subparallel and the posterior margin truncate. Sixth visible ventrite small, subquadrate, broader than long; surface moderately rugose; moderately punctate; lateral margins conspicuously oblique, posterior margin broadly rounded (2.17-I). Fifth tergite broadly convex, rugulose, lateral margins subparallel; posterior margin truncate. Sixth tergite subquadrate, as broader as long; surface rugulose; lateral margins slightly oblique; posterior margin triangular, acuminate distally (Fig. 2.17-I). Sixth tergite extending beyond posterior margin of sixth visible ventrite, fully covering the sixth visible ventrite from dorsal view.

Aedeagus: not available.

Sexual dimorphism: females of *O. vittatus* differ from male specimens by having the last antennomere 2× longer than the previous antennomere, rather than 3× longer, as in males. The lateral and posterior margins of the sixth visible ventrite are broadly rounded, giving the appearance of a semicircular margin, rather than subtriangular and posteriorly acuminate, as seen in males (Fig. 2.17-I).

Material examined: 1 male, 2 females: Dominican Republic, Provincia La Vega, La Cienega de Manabao Park Headquarter, 3-5-VII-1999, 3000', R. E. Woodruff, backlight; 1 female: Constanza, Santo Domingo, 5000', IX-1922, [no collector data]; 2 females: Jamaica, Bull Run, St. Andrew Park, 19-IV-1959, Farr and Sanderson.

4. References

Balduf, W. V. (1935) Cleridae: Checkered Beetles. Pp 109-111. In W. V. Balduf (Editor) The Binomics of entomophagous Coleoptera. New York: John S. Swift Co.

Barr, W. F. (1947) New species of *Cymatodera* from the southwestern United States and northern Mexico (Coleoptera: Cleridae). American Museum Novitates 1572: 1–9.

Barr, W. F. (1950a) Systematic and synonymical notes on the New World clerid beetles (Coleoptera). Entomologische Berichten 13, 61–62.

Barr, W. F. (1950b) Contributions toward a knowledge of the insect fauna of Lower California (Coleoptera: Cleridae). Proceedings of the California Academy of Science, Series 4, Series, 24(12): 485–519.

Barr, W. F. (1952a) A revision of the species belonging to the new clerid genus *Araeodontia* (Coleoptera). American Museum Novitates 1573: 1–17.

Barr, W. F. (1952b) New species of *Cymatodera* from the southwestern United States and northern Mexico (Coleoptera: Cleridae). American Museum Novitates 1572: 1–9.

Barr, W. F. (1962) A key to the genera and a classification of the North American Cleridae (Coleoptera). Coleopterists Bulletin 16:121-127.

Barr, W. F. (1972) New species of North American *Cymatodera* (Coleoptera: Cleridae). Entomologische Arbeiten aus dem Museum Georg Frey 787: 1–32.

Barr, W. F. (1975) Family Cleridae. In: Arnett, R.H. (Ed.), Checklist of the beetles of North and Central America and the West Indies. Vol. 4. Family 73. Flora and Fauna Publications, Gainesville, pp. 1–18.

Barr, W. F. (1978) Taxonomy of the new clerid genus *Bogcia* from Mexico. The Pan-Pacific Entomologist 54: 87-291.

Beeson, C. F. C. (1926) On some Indian Cleridae (Coleoptera (Part II) Note on the biology of the Cleridae. The Indian Forest Records 12(8): 217-231.

Burke, A. F. (2013) Six new species of *Cymatodera* from Mexico and Central America and the retention of *Cymatodera obliquefasciata* as a valid name (Cleridae, Tillinae). ZooKeys 299: 49-75.

Burke, A. F., J. M. Leavengood Jr. and G. Zolnerowich (2015) A checklist of the New World species of Tillinae (Coleoptera: Cleridae), with an illustrated key to genera and new country records. Zootaxa 4059(1): 1–39.

Burke, A. F. and G. Zolnerowich (2014) *Cymatodera ochlera* Barr, a junior synonym of *Cymatodera wolcotti* Barr, with a comparison to similar species (Coleoptera: Cleridae). Zootaxa, 3847(3): 423-430.

Burke, A. F. and G. Zolnerowich (2016) Taxonomic revision of the New World genus *Callotillus* Wolcott (Cleridae, Tillinae), with the description of the new genus *Neocallotillus*, and an illustrated key of identification to species. ZooKeys 617: 65–89.

Burke, A. F., D. Cibrián-Tovar, C. Llanderal-Cázares, A. Plascencia-Gonzáles and I. López-Pérez (2011) Adiciones y aportaciones para el género *Enoclerus* Gahan (coleoptera: cleridae) en bosques de clima templado de México. Acta Zoologica Mexicana 27(1): 145-167.

Chapin, E. A. (1927) Notes on North American Tillinae, with description of a new *Cymatodera* (Col.: Cleridae). Proceedings of the Biological Society of Washington 40: 143–146.

Chapin, E. A. (1945) A genus and species of clerid beetles from Jamaica. 1945. Transactions of the Connecticut Academy of Arts and Sciences, 36: 595-599.

Chevrolat, M. A. (1874) Catalogue des Clerides de la colleciòn de M.A. Chevrolat. Revue et Magasin de Zoologie (Series 3) 2(6): 252-329.

Corporaal, J. B. (1950) Coleopterorum Catalogus, Supplementa. Pars 2: Cleridae. W. Junk, Gravenhage.

De Zayas, F. (1988) Familia Cleridae. In: Entomofauna Cubana. Orden Coleoptera. Separata Descripción de Nuevas Especies, J. F. Valdés-Montero (Ed.), Editorial Científico-Técnica, La Habana, Cuba.

Ekis, G. (1977) Classification, phylogeny and zoogeography of the genus *Perylipus* (Coleoptera: Cleridae). Smithsonian Contributions to Zoology 227.

Gardener, J. C. M. (1937) Immature stages of Indian Coleoptera (21) Cleridae. Indian Forest Record (New Series) 3(2): 31-47.

Gerstmeier, R. and J. Eberle (2011) Definition and revision of the *Orthrius*-group of genera (Coleoptera, Cleridae, Clerinae). ZooKeys 92: 35-60.

Gerstmeier, R. and A. Huesmann (2004) Revision of the Afrotropical species of the genus Trichodes Herbst, 1792 (Coleoptera, Cleridae). Zootaxa 694, 1-22.

Gerstmeier, R. and M. Seitner (2013) Revision of the checkered beetle genus Eunatalis Schenkling, 1909 (Coleoptera: Cleridae: Clerinae). Zootaxa 3698 (1), 1-77.

Gerstmeier, R. and Weiss, I. (2009) Revision of the genera Diplocladus Fairmaire, 1885 and Strotocera Schenkling, 1902 (Coleoptera: Cleridae: Tillinae). Zootaxa 2242, 1-54.

Gorham, H. S. (1882-1883) Insecta, Coleoptera, Cleridae. Biologia Centrali-Americana 3(2): 113-168 (1882), 169-224 (1883).

Gorham, H.S. (1876) Notes on the coleopterous family Cleridae with descriptions of new genera and species. Cistula Entomologica, 2 (1875–82), 57–106.

Gunter, N. L., J. M. Leavengood Jr, J. S. Bartlett, E. G. Chapman and S. L. Cameron (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera; Cleridae). Systematic Entomology 38(3): 626-636.

Klug, J. C. F. (1842) Versuch einer systematischen Bestimmung und Auseinandersetzung der

    Gattungen und Arten der Clerii, einer Insektenfamilie aus der Ordung der Coléoptère n.

    Abhandlungen der Koniglichen Akademie der Wissenschaften in Berlin 1840-1842 (1842):

    259-397.

Knull, J. N. (1934) Five new species of Coleoptera (Cleridae, Elateridae, Buprestidae and

    Cerambycidae). Entomological News 45: 9–13.

Knull, J. N. (1940) Four new species of western Coleoptera (Cleridae, Buprestidae, and

    Cerambycidae). Annals of the Entomological Society of America 33: 555–559.

Knull, J. N. (1946) New Species of *Tillus* from Arizona (Coleoptera: Cleridae). The Ohio Journal

    of Science. 46(2): 72.

Knull, J. N. (1951) The checkered beetles of Ohio (Coleoptera: Cleridae). Ohio Biological

    Survey Bulletin 8(42): 268–350.

Leavengood, J. M. (2008) *Enoclerus knabi* (Wolcott), a junior synonym of *Enolcerus*

    ichneumoneous (Fabricius) (Coleoptera: Cleridae). Insecta Mundi 289(57): 1-2.

LeConte, J. L. (1849) Synopsis of the Coleopterous insects of the group Cleridae which inhabit

    the United States. Annals of the Lyceum of Natural History of New York 5(1851-1852): 9-

    35.

Mawdsley, J. R. (2002) Comparative ecology of the genus *Lecontella* Wolcott and Chapin (Coleoptera: Cleridae: Tillinae), with notes on chemically defended species of the beetle family Cleridae. Proceedings of the Entomological Society of Washington 104(1), 164-167.

Michelbacher, A. E. and C. S. Davis (1961) Orchard and plant affect control of naval orangeworm. California Agriculture, September 1961, 12-13.

Opitz, W. (2010) Classification, natural history, phylogeny and subfamily composition of the Cleridae and generic content of the subfamilies (Coleoptera, Cleridae). *Entomologica Basiliensia et Collectionis Frey* 32: 31-128.

Rifkind, J. (1993a) A New Species of *Cymatoderella* Barr (Coleoptera: Cleridae) from Mexico and Central America, with a Key and Distributional Data for the Genus. The Coleopterists Bulletin, 47: 279-284.

Rifkind, J. (1993b) A new species of *Cymatodera* from Oaxaca, Mexico (Coleoptera: Cleridae). The Coleopterists Bulletin, 47 (1): 83-88.

Rifkind, J. (1995) Additions to the checkered beetle fauna of Belize with the description of a new species (Coleoptera: Cleridae) and a nomenclatural change. Insecta Mundi 9(1-2): 17–24.

Rifkind, J. (1996) A new genus and species of checkered beetle from Honduras with additions to the Honduran Fauna. *Contributions in Science* 461: 1-10.

Rifkind, J. (2015) New species of *Cymatodera* Gray (Coleoptera: Cleridae: Tillinae) from México and Central America, with notes on others. Zootaxa 3946(4): 519–552.

Rifkind, J., V. H. Toledo and A. M. Corona (2010). New species of Cleridae (Coleoptera) from Morelos, Mexico. Zootaxa 2659: 53-59.

Schaeffer, C. W. (1904) New genera and species of Coleoptera. Journal of the New York Entomological Society 12(4): 197–236.

Schaeffer, C. W. (1905) Some additional new genera and species of Coleoptera found within the limits of the United States. Bulletin of the Brooklyn Institute of Arts and Sciences 1(7), 141–179.

Schaeffer, C. W. (1908) On new and known Coleoptera of the families Coccinellidae and Cleridae. Journal of the New York Entomological Society 16, 125–135.

Schaeffer, C. W. (1917) On some North American Cleridae (Coleoptera). Journal of the New York Entomological Society 25: 129–134.

Schenkling, S. (1906) Zur systematik der Cleriden. Deutsche Ent. Zeitschr. p. 241-320.

Solervicens, J. (1996) Taxonomic revision of the genus *Notocymatodera* Schenkling, 1907 (Coleoptera: Cleridae). Acta Entomológica Chilena, 20: 99-106.

Spinola, M. M. (1841) Monographie des Terediles. Table au synoptique des Clairons. Revue Zoologique pat la Société Cuvierienne 4: 70-76.

Van Dyke, E. (1934) New species of the Pacific coast Coleoptera. Entomological News of the Natural History Museum of Chicago, 49: 189-195.

Vaurie, P. (1952) The checkered beetles of the Bahama Islands, British West Indies. American Museum Novitates, 1547: 1-5.

Wolcott, A. B. (1909) The Cleridae of the Public Museum of Milwaukee. Bulletin of the Wisconsin Natural History Society 7(3–4): 93–102.

Wolcott, A. B. (1910) Note on some Cleridae of Middle and North America with descriptions of new species. Field Museum of Natural History, Zoological Series, 7(10): 339-401.

Wolcott, A. B. (1911) New American Cleridae, with notes on others (Coleoptera). Entomological News 22: 115–125.

Wolcott A. B. (1921) North American Predaceous beetles of the tribe Tillini in the United States National Museum. Proceedings of the United States National Museum 59: 269-290.

Wolcott, A. B. (1923) Two new species of West Indian Cleridae (Coleoptera). American Museum Novitates, 59: 1-3.

Wolcott, A. B. (1927) A review of the Cleridae of Costa Rica. Coleopterological Contributions, 1(10): 1-104.

Wolcott, A. B. (1947) Catalogue of North American beetles of the family Cleridae. Fieldiana: Zoology 32(2): 59-105.

Wolcott, A. B. and H. S. Dybas (1943) Two new beetles from Costa Rica and Australia, with a description of a new genus (Coleoptera, Cleridae). Fieldiana. Zoology, 31(18): 143-148.

Wolcott, A. B., and E. A. Chapin. (1918) Notes on Cleridae. Bulletin of the Brooklyn Entomological Society 13:107-108.
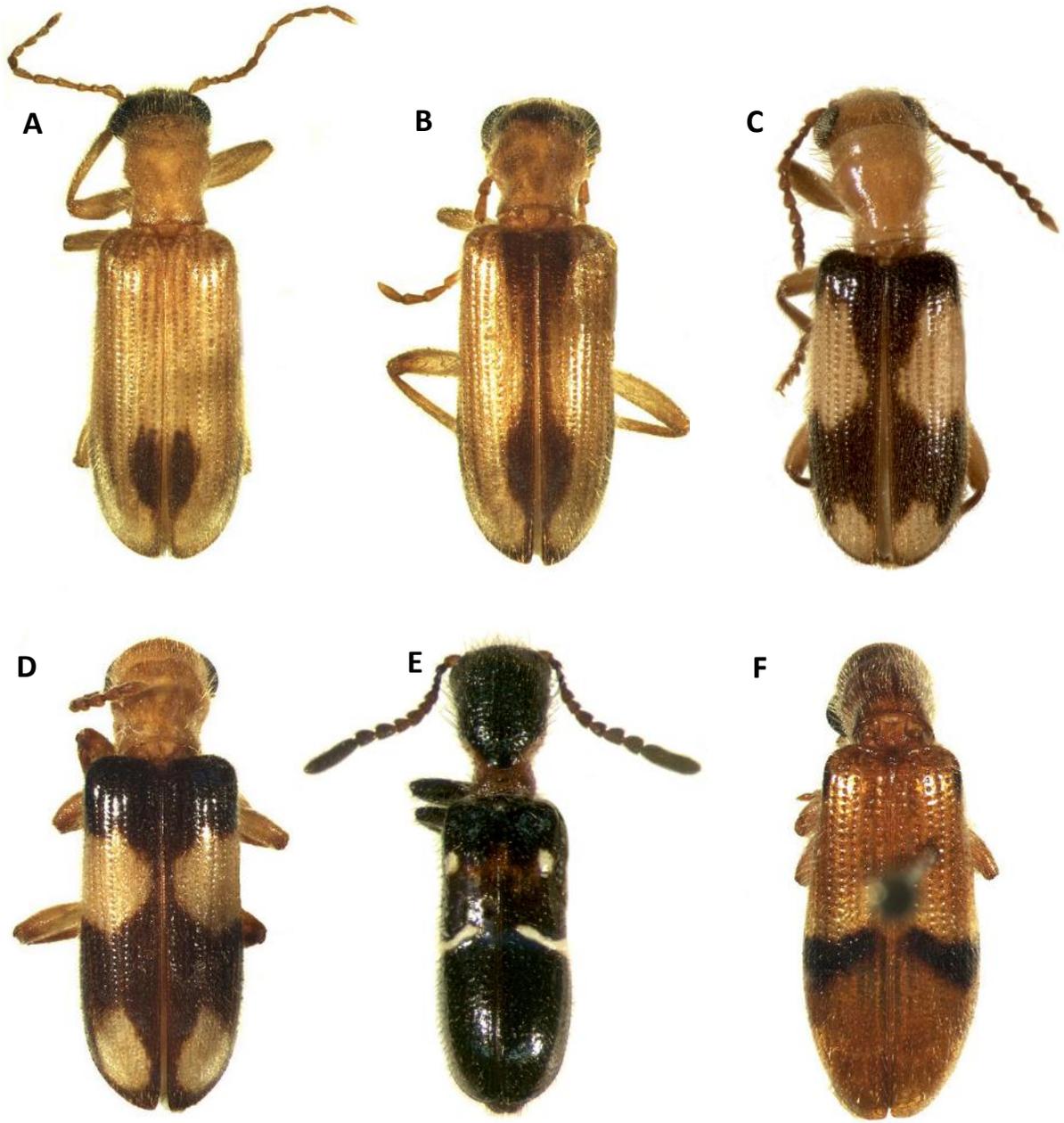
Fig. 2.1 Habitus of: A. *Araeodontia isabellae*; B. *Araeodontia marginalis*; C. *Araeodontia peninsularis*; D. *Araeodontia picta*; E. *Barrotillus kropotkini*; F. *Bogcia disjuncta*.
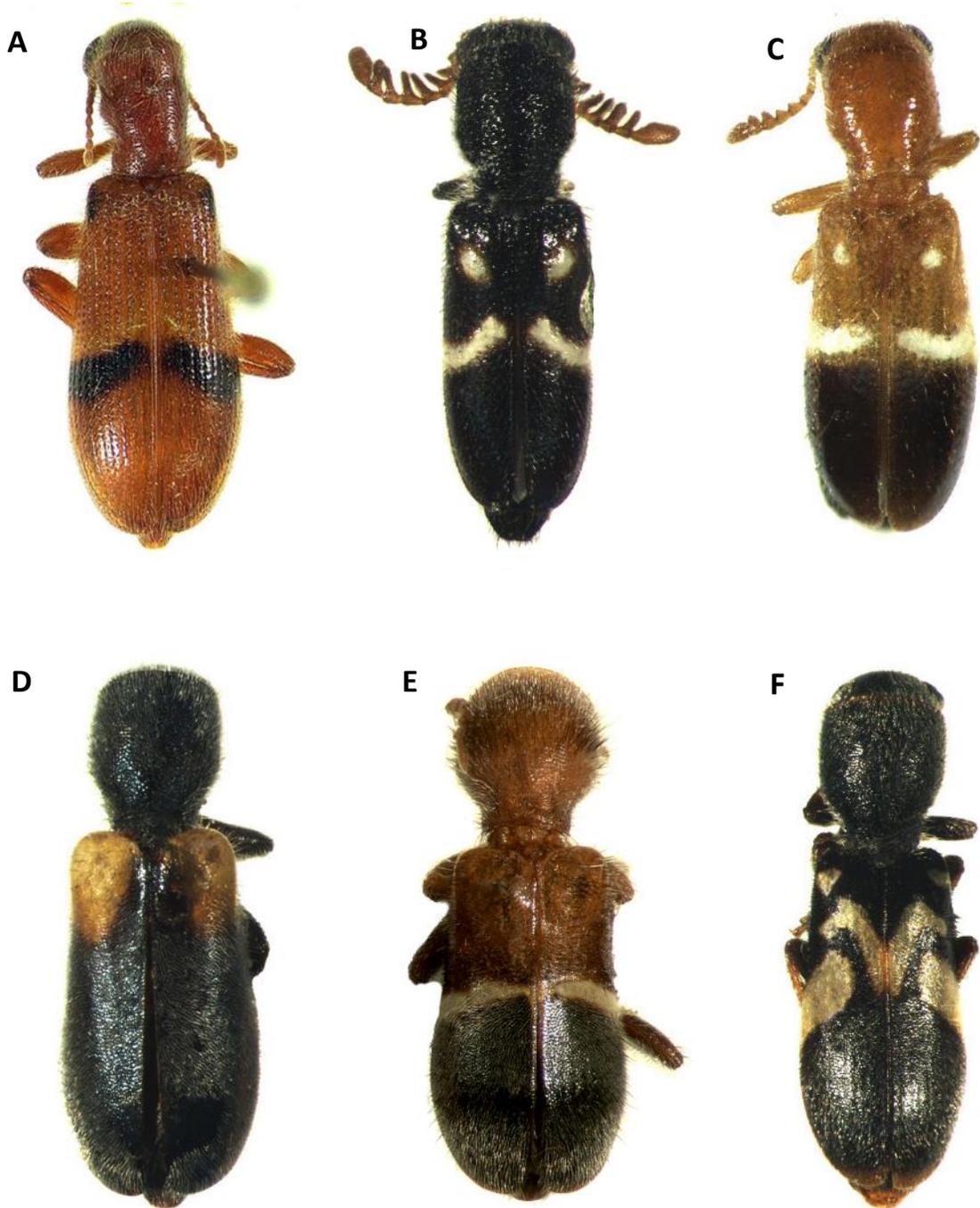
Fig. 2.2 Habitus of: A. *Bogcia oaxacae* syn. n.; B. *Neocallotillus elegans* (*elegans*); C. *Neocallotillus elegans* (*vafer*); D. *Callotillus bahamensis;* E. *Callotillus eburneocinctus*; F. *Neocallotillus intricatus.*
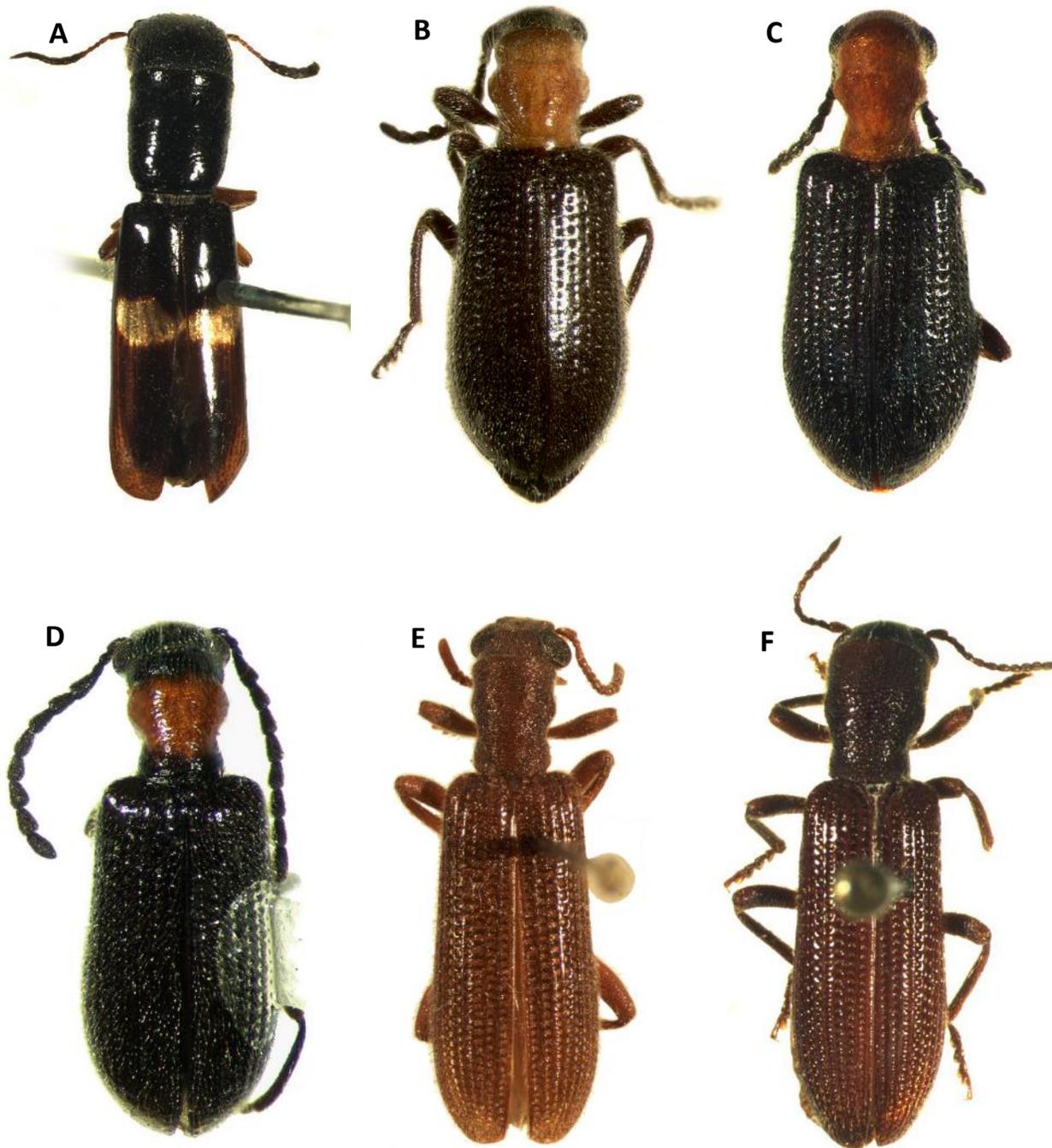
Fig. 2.3 Habitus of: A. *Cylidrus abdominalis*; B. *Cymatoderella collaris;* C. *Cymatoderella morula*; D. *Cymatoderella patagoniae*; E. *Lecontella brunnea;* F. *Lecontella gnara*.
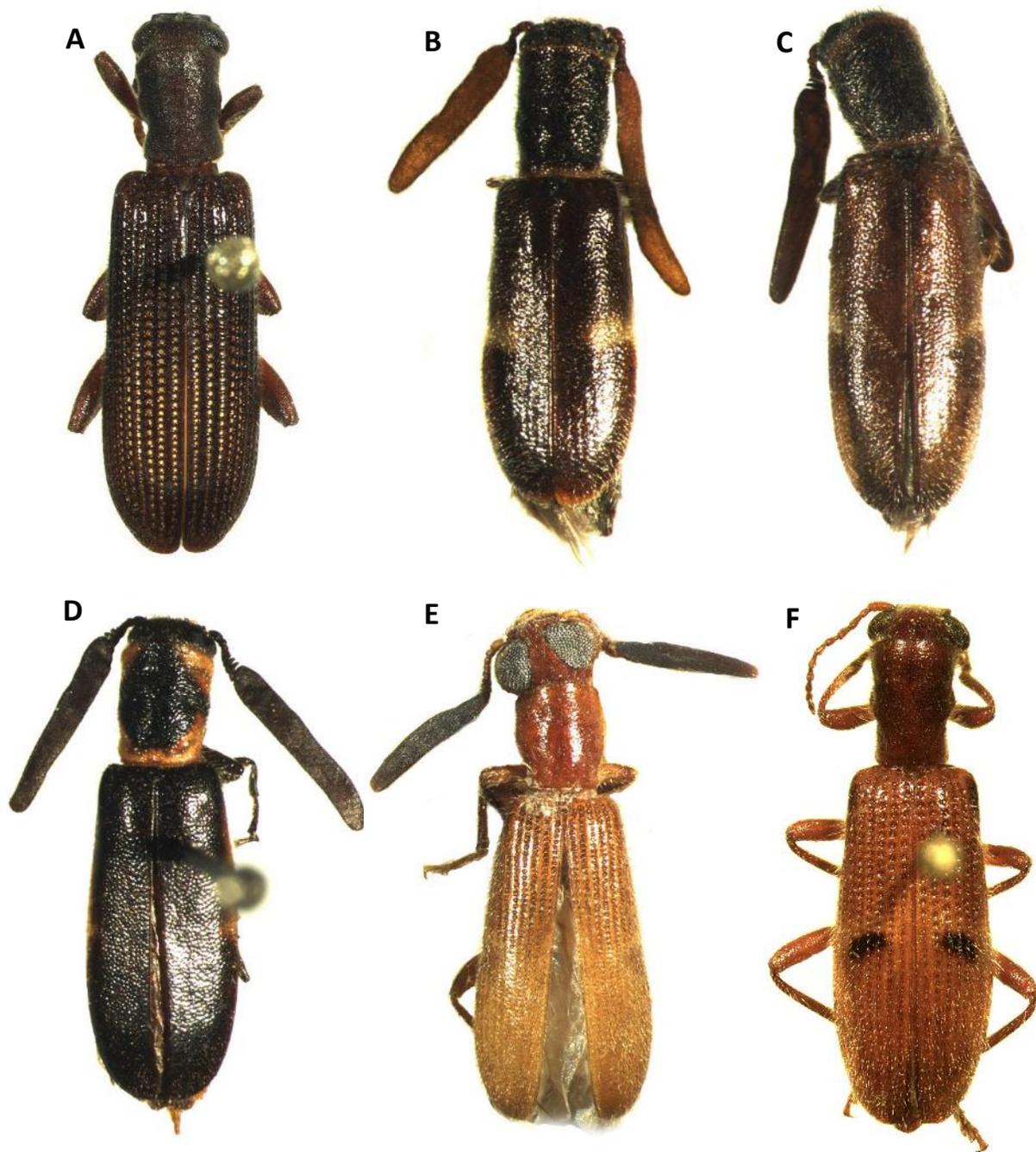
Fig. 2.4 Habitus of: A. *Lecontella striatopunctata*; B. *Monophylla californica*; C. *Monophylla pallipes*; D. *Monophylla terminata*; E. *Teloclerus compresicornis*; F. *Cymatodera bogcioides*.
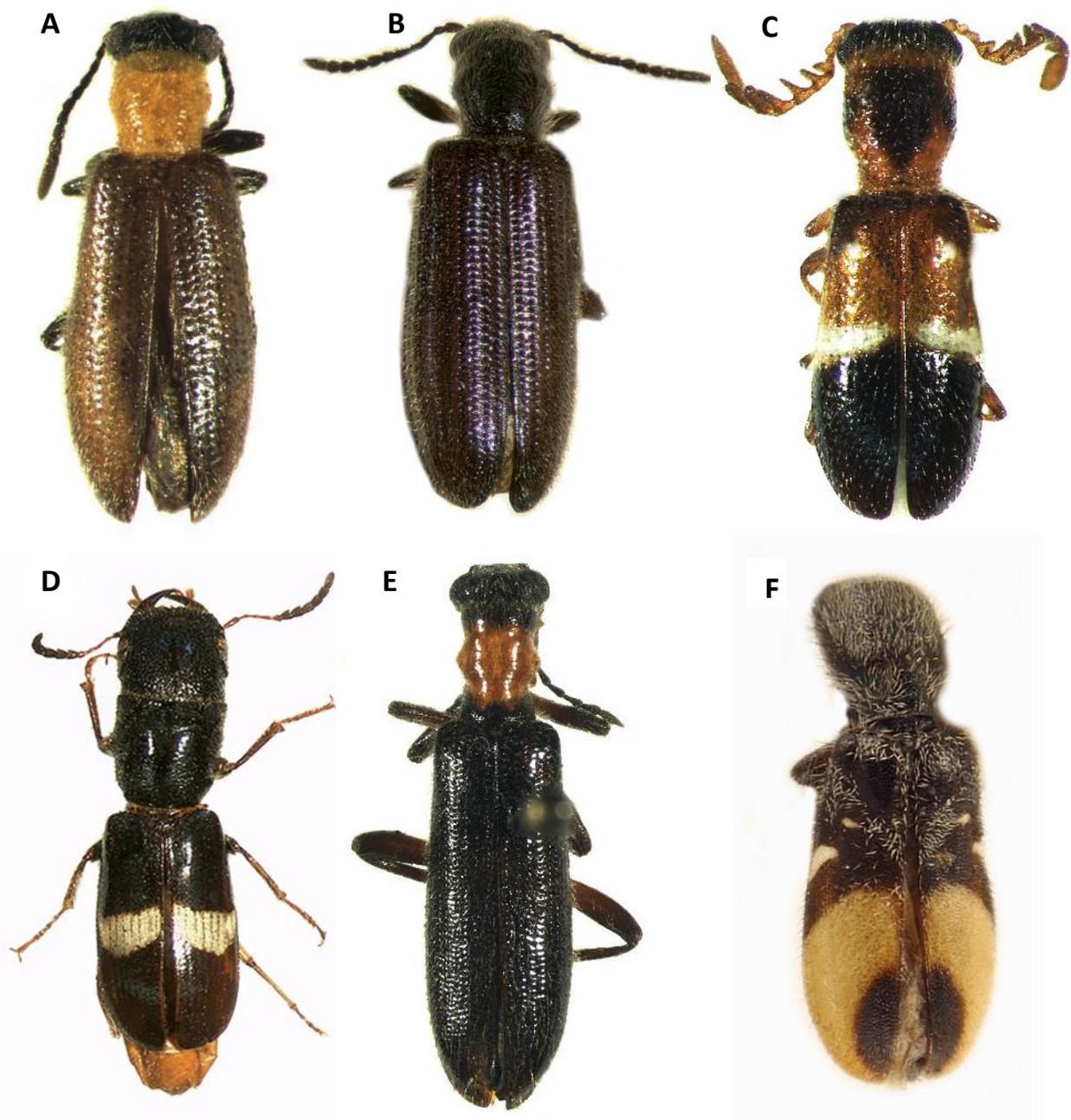
Fig. 2.5 Habitus of: A. *Onychotillus cubana*; B. *Onychotillus vittatus*; C. *Neocallotillus elegans*; D. *Cylidrus fasciatus*; E. *Cymatodera bicolor;* F. *Neocallotillus crusoe* (image courtesy of The American Museum of Natural History, New York).
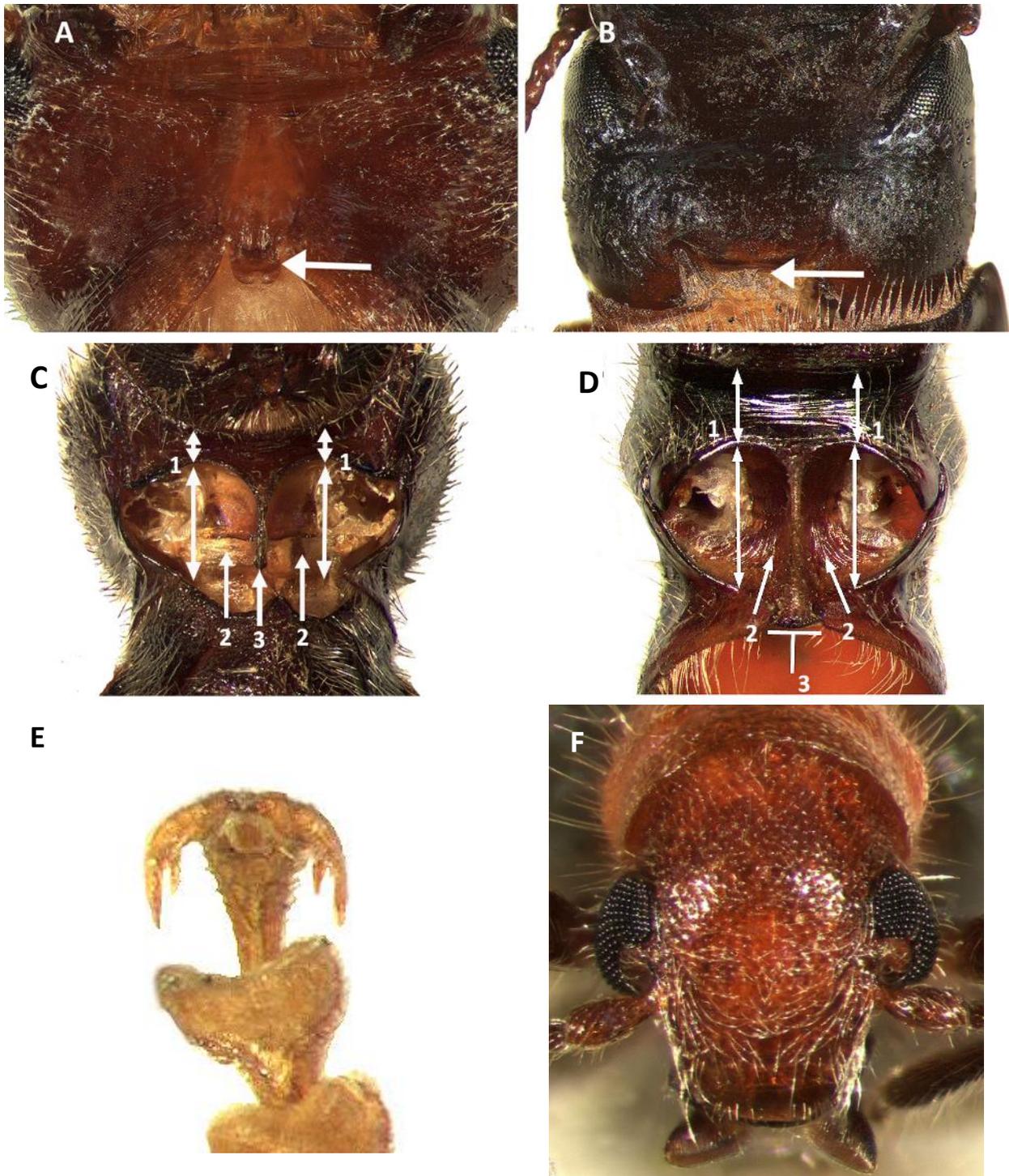
Fig. 2.6 A-B Gular structure of: A. *Cymatodera californica* (Cleridae), arrow indicates pos-gular process present; B. *Temnoscheila virescens* (Trogossitidae), arrow indicates post-gular process absent; C-D Procoxal cavities of: C. *Enoclerus zonatus*; D. *Cymatodera sallei*; arrows 1 indicate longitudinal length of procoxal cavities in relation to longitudinal length of prosternum; arrows 2 indicate interior portion of procoxal cavities; arrow 3 indicates intercoxal process. E. Tarsal claw of *Araeodontia peninsularis*; F. Eye structure of *Cymatoderella collaris*.
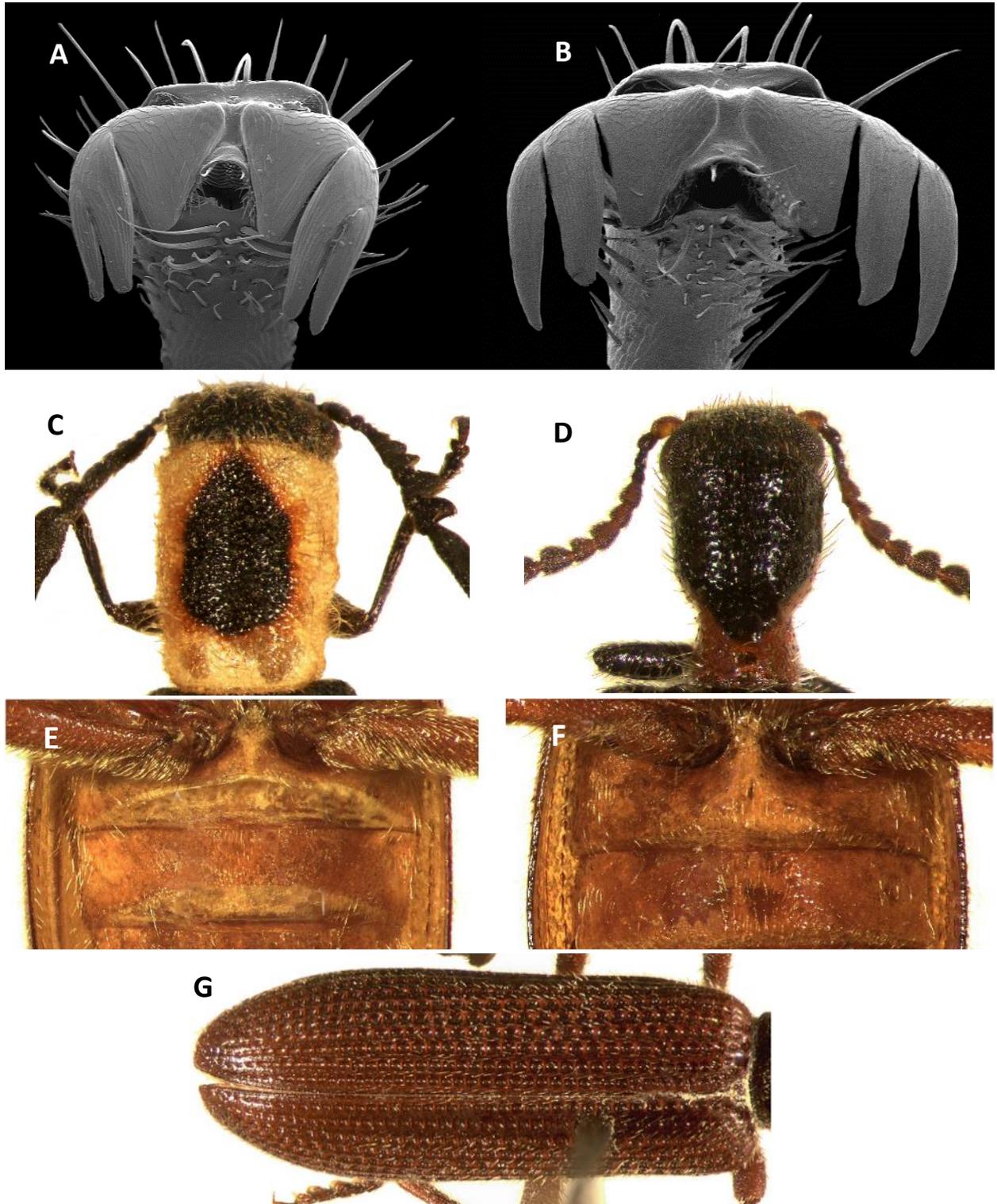
Fig. 2.7 A-B Tarsal claws of: A. *Bogcia oaxacae*; B. *Cymatodera balteata*. Prothorax in dorsal view of: C-D Pronotal structure of: C. *Monophylla terminata*; D. *Barrotillus kropotkini*; E-F First and second visible ventrite of: E. *Cymatodera mitae* (male); F. *Cymatodera mitae* (female); G. Elytral ground of *Lecontella gnara.*

A

B

C
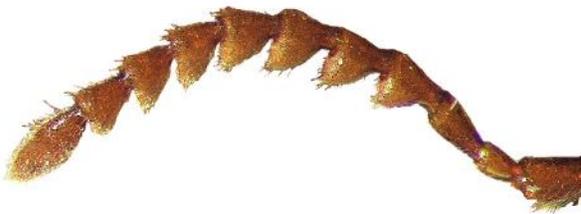
D

E

F

G

Fig. 2.8 Antennae of: A. *Araeodontia peninsularis* (male); B. *Barrotillus kropotkini* (male); C. *Bogcia oaxacae* (male); D. *Neocallotillus elegans* (*elegans*) (male); E. *Neocallotillus elegans* (*vafer*) (male); F. *Neocallotillus elegans* (*elegans*) (female); G. *Cylidrus abdominalis* (male).
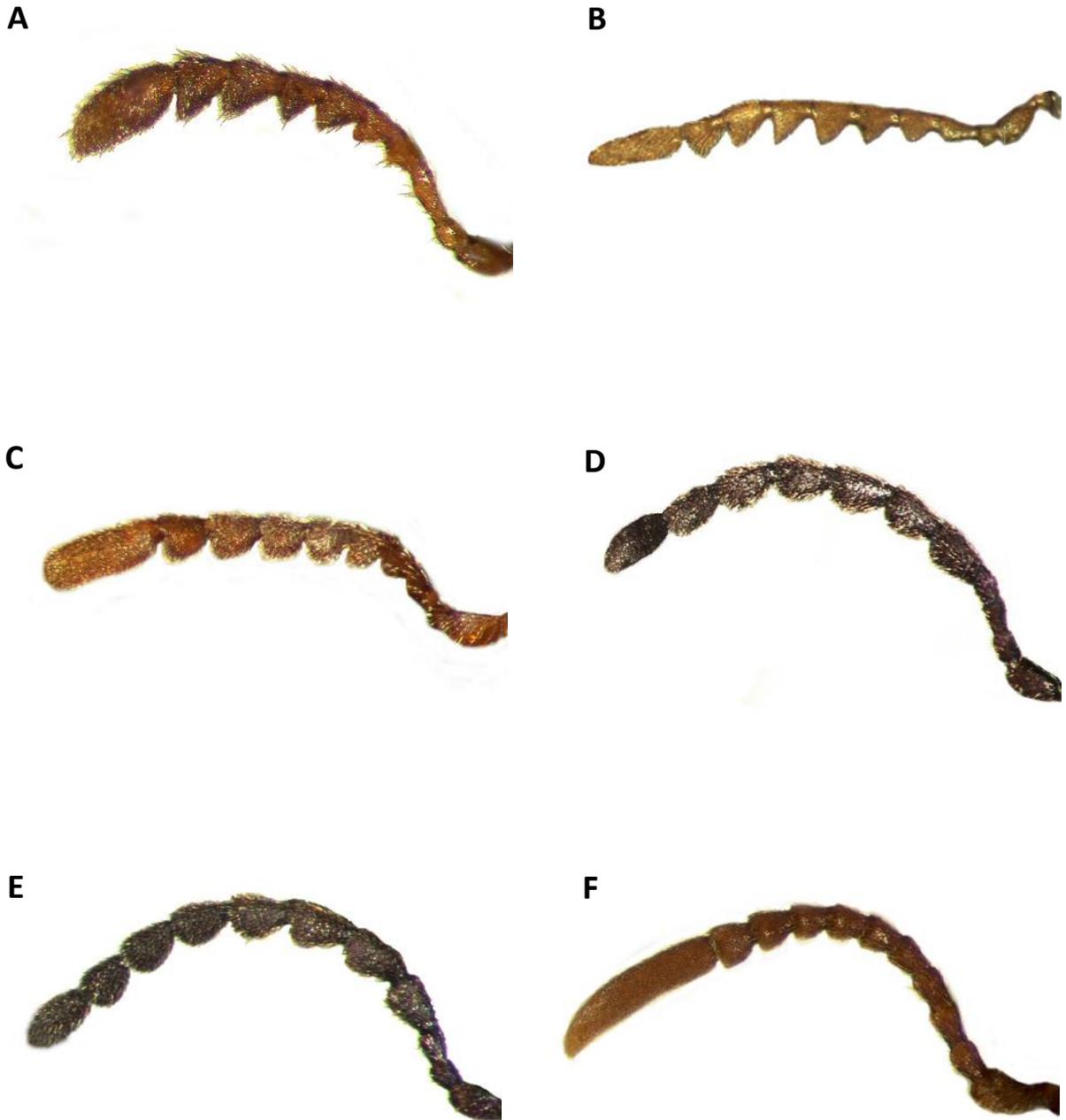
Fig. 2.9 Antennae of: A. *Neocallotillus elegans* (*vafer*) (female); B. *Callotillus eburneocinctus* (male); C. *Callotillus eburneocinctus* (female) D. *Cymatoderella collaris* (male); E. *Cymatoderella morula* (male); F. *Lecontella brunnea* (male).
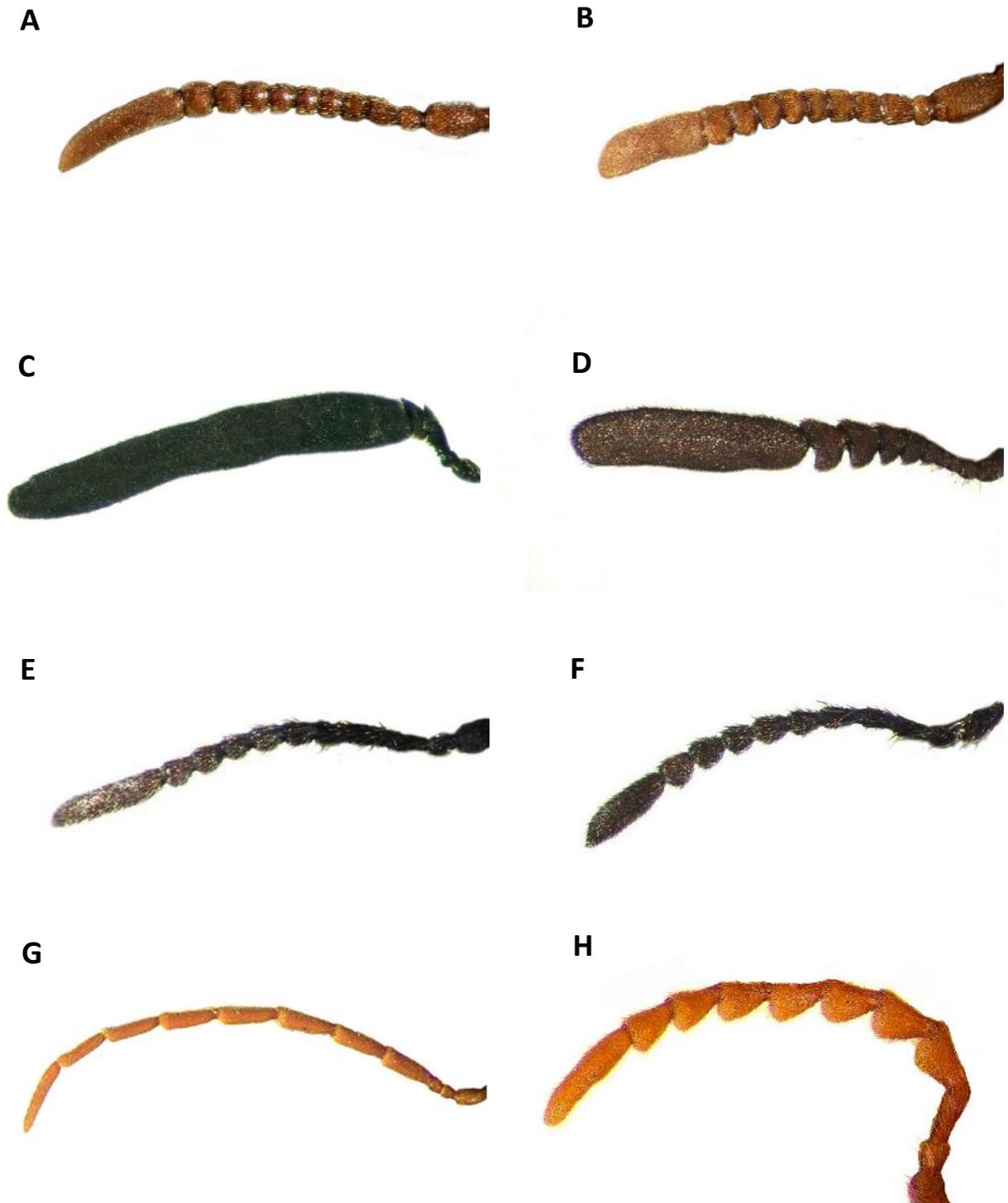
Fig. 2.10 Antennae of: A. *Lecontella gnara* (male); B. *Lecontella striatopunctata* (male); C. *Monophylla terminata* (male); D. *Monophylla terminata* (female); E. *Onychotillus cubana* (male); F. *Onychotillus vittatus* (male); G. *Cymatodera longicornis* (male); H. *Cymatodera limatula* (male).
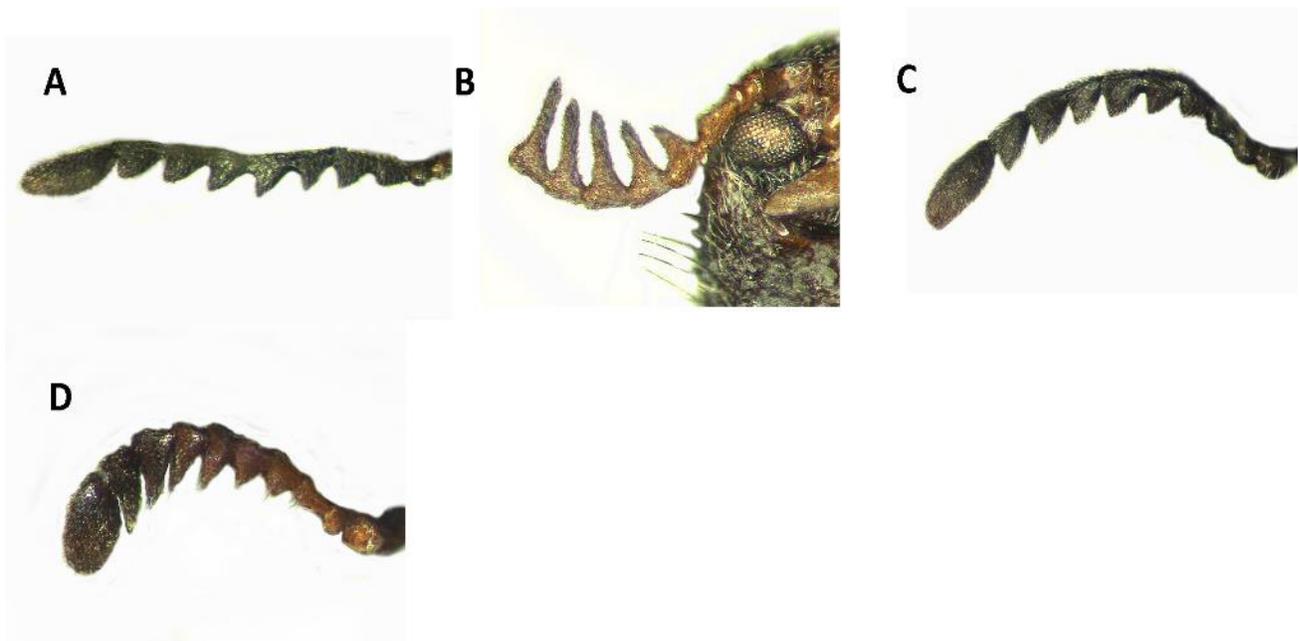
Fig. 2.11. Antennae of: A. *Callotillus bahamensis* (male); B. *Neocallotillus intricatus* (male); C. *C. bahamensis* (female); D. *N. intricatus* (female).
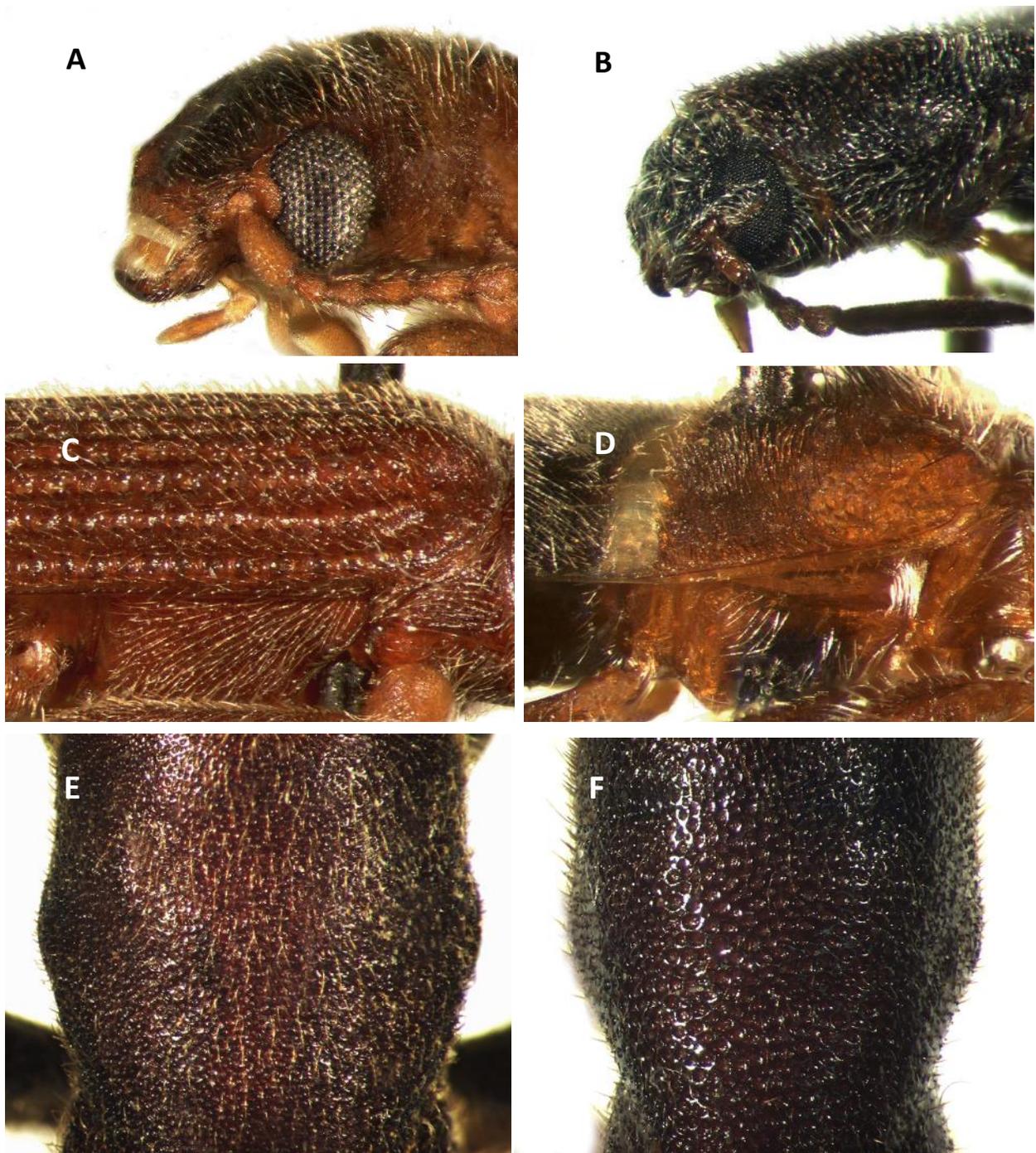
Fig. 2.12 A-B Eye structure of: A. *Cymatodera laevicolis*; B. *Monophylla californica*; C-D Mesepisternum: C. Hidden throughout its length in *Lecontella gnara*; D. Visible throughout its length in *Callotillus eburneocinctus*; E-F Pronotal surface of: E. *Lecontella brunnea*; F. *Lecontella gnara*.

Fig. 2.13 Habitus in lateral view of: A. *Neocallotillus elegans,* male; B. *Callotillus eburneocinctus,* male.
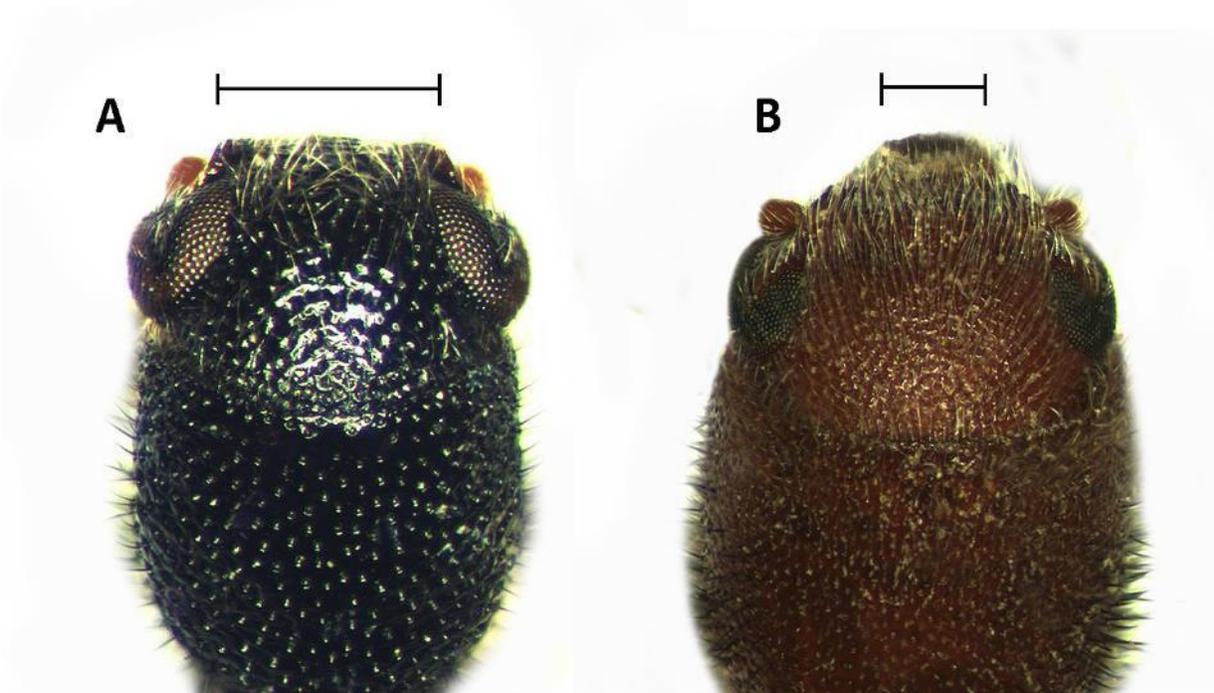
Fig. 2.14 Head of: A. *Neocallotillus elegans*; B. *Callotillus eburneocinctus*. Bars indicate width of frons.

Fig. 2.15 Aedeagus of: A. *Neocallotillus elegans* (*elegans*); B. *N. elegans* (*vafer*); C. *N. intricatus* (*C. intricatus*); D. *Callotillus eburneocinctus*.
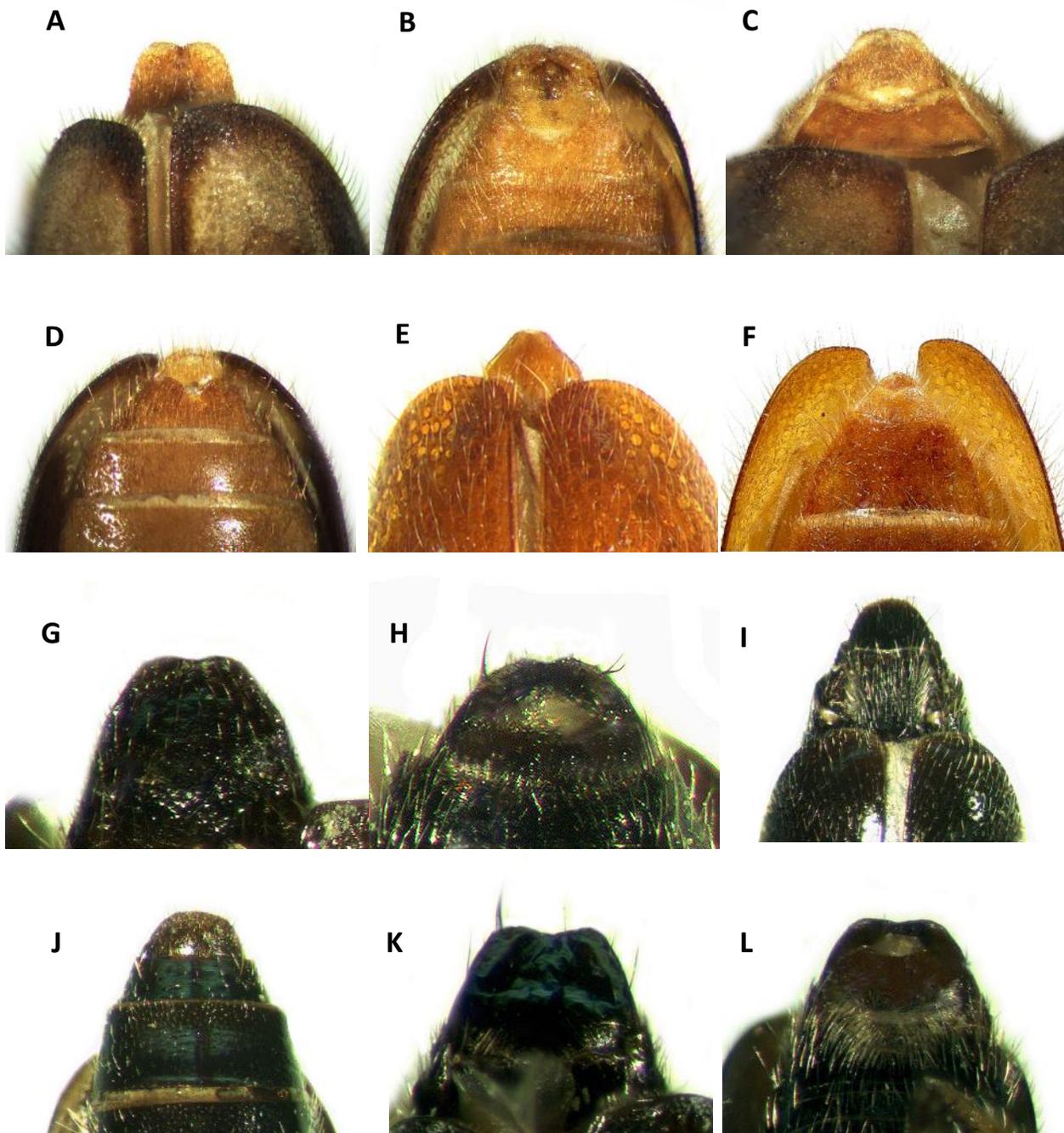
Fig. 2.16 Pygidium of: A. *Araeodontia peninsularis* dorsal view (male); B. *Araeodontia peninsularis* ventral view (male); C. *Araeodontia peninsularis* dorsal (female); D. *Araeodontia peninsularis* ventral (female); E. *Bogcia disjuncta* dorsal (male); F. *Bogcia disjuncta* ventral (male); G. *Neocallotillus elegans* (*elegans*) dorsal (male); H. *Neocallotillus elegans* (*elegans*) ventral (male); I. *Neocallotillus elegans* (*elegans*) dorsal (female); J. *Neocallotillus elegans* (*elegans*) ventral (female); K. *Neocallotillus elegans* (*vafer*) dorsal (male); L. *Neocallotillus elegans* (*vafer*) ventral (male).
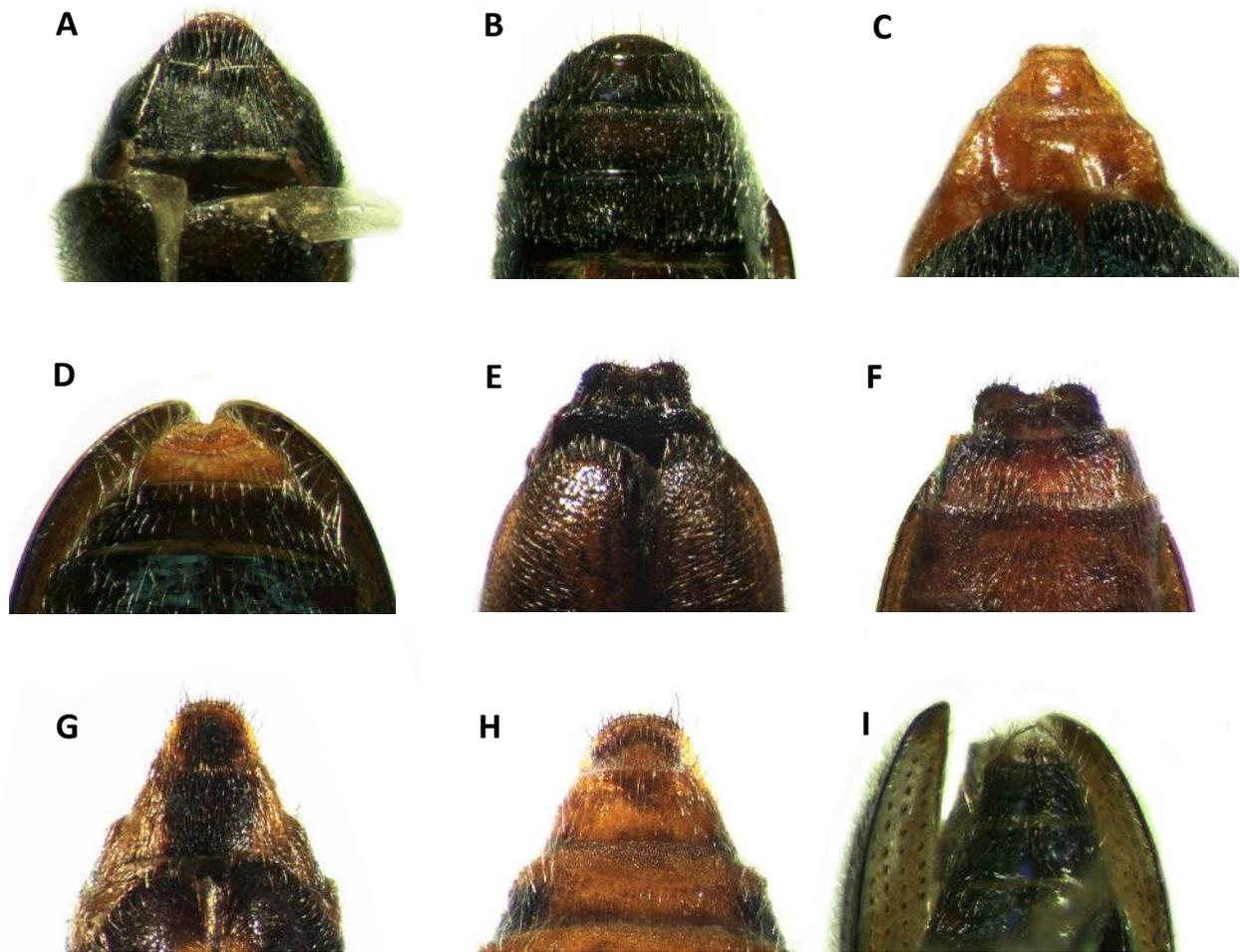
Fig. 2.17 Pygidium of: A. *Neocallotillus elegans* (*vafer*) dorsal (female); B. *Neocallotillus elegans* (*vafer*) ventral (female); C. *Cymatoderella patagoniae* dorsal (male); D. *Cymatoderella patagoniae* ventral (male); E. *Monophylla terminata* dorsal (male); F. *Monophylla terminata* ventral (male); G. *Monophylla terminata* dorsal (female); H. *Monophylla terminata* ventral (female); I. *Onychotillus vittatus* ventral (male).

Fig. 2.18 Male genitalia of: A. *Araeodontia isabellae*; B. *Araeodontia marginallis*; C. *Araeodontia peninsularis*; D. *Bogcia disjuncta*; E. *Bogcia oaxacae* syn. n.
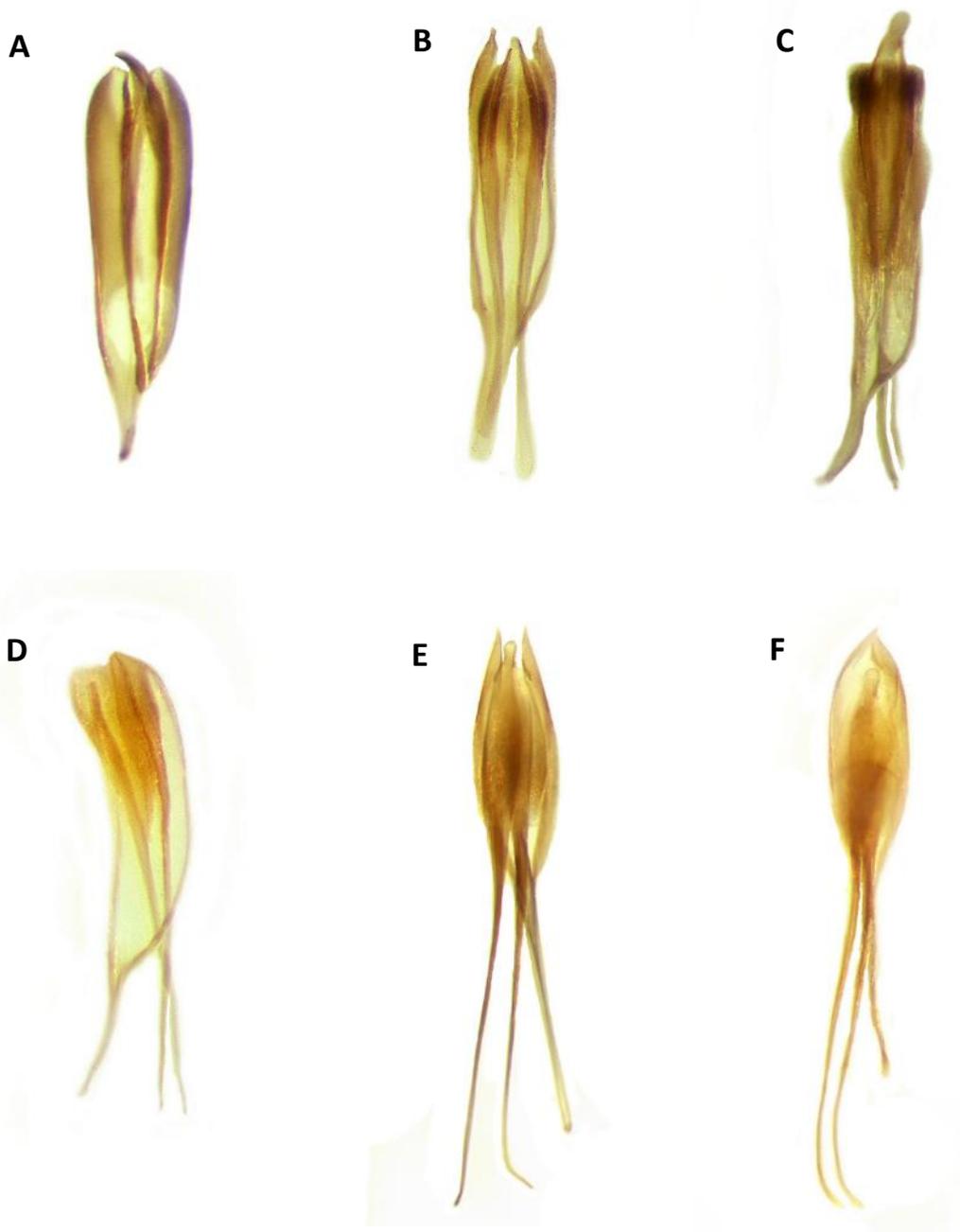
Fig. 2.19 Male genitalia of: A. *Neocallotillus elegans* (*vafer*); B. *Cymatoderella collaris*; C. *Cymatoderella morula*; D. *Cymatoderella patagoniae*; E. *Lecontella brunnea*; F. *Lecontella gnara*.
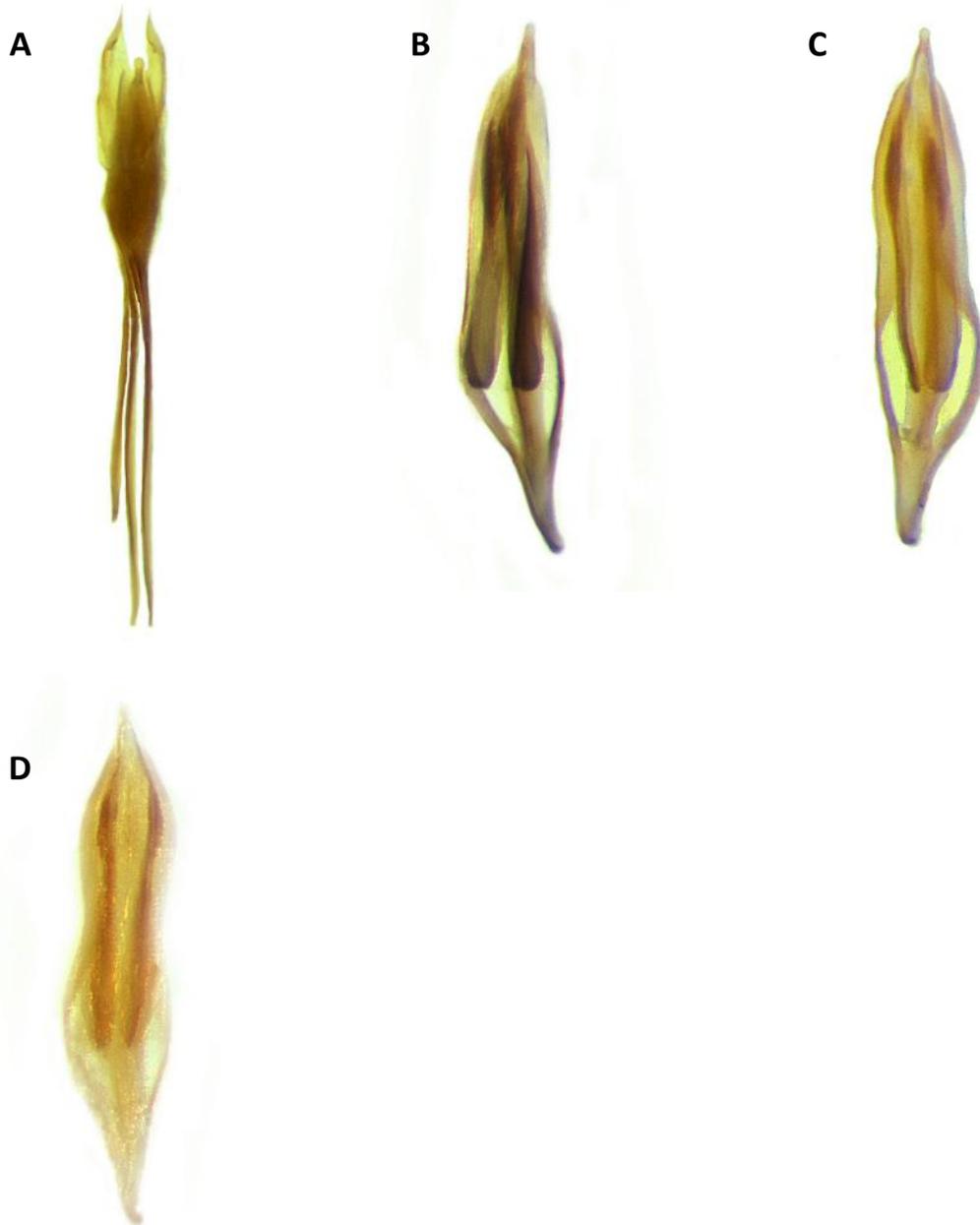
Fig. 2.20 Male genitalia of: A. *Lecontella striatopunctata*; B. *Monophylla californica*; C. *Monophylla pallipes*; D. *Monophylla terminata*.
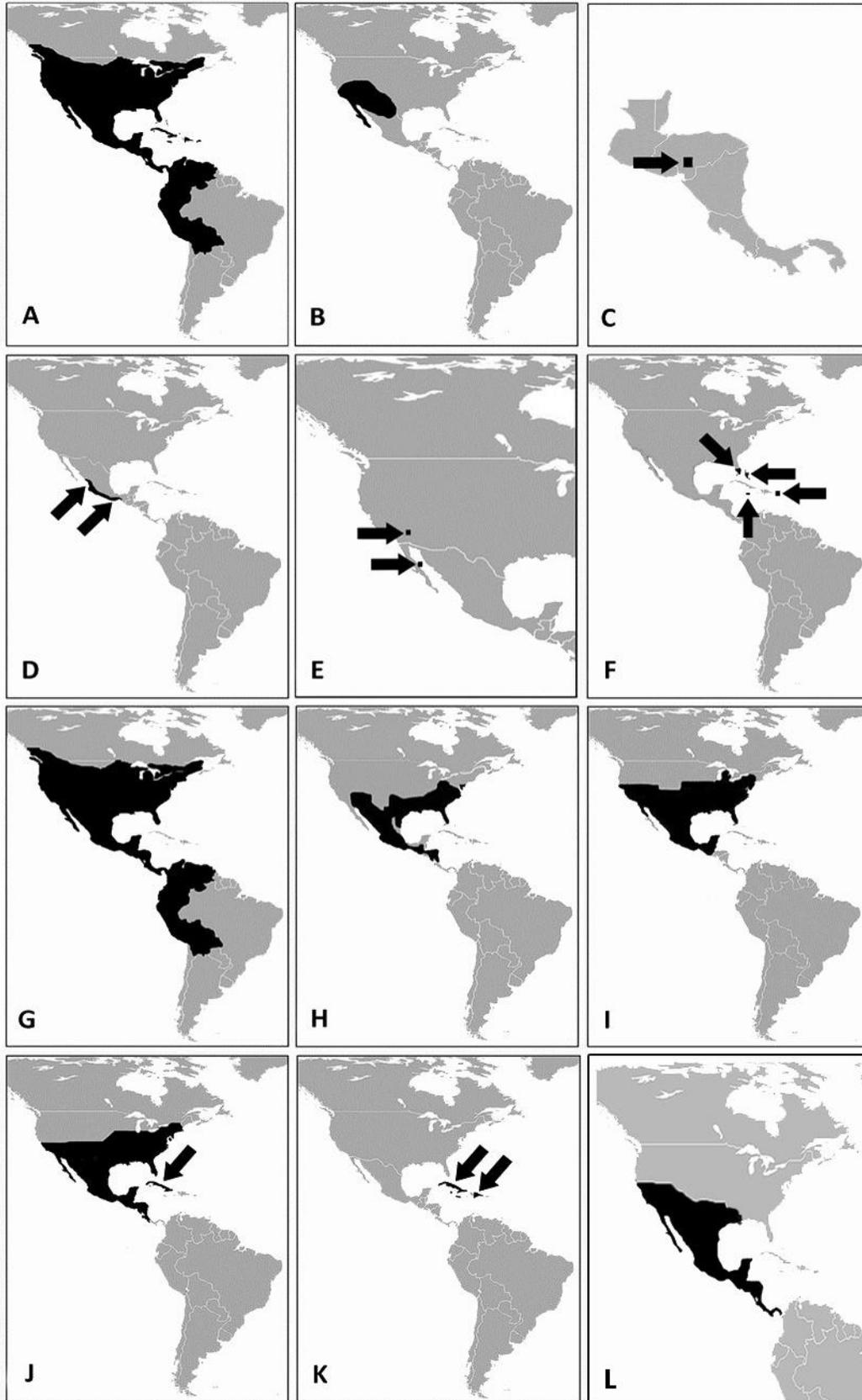
Fig. 2.21 Distribution in the New World of: A. Tillinae Leach, B. *Araeodontia* Barr, C. *Barrotillus* Rifkind, D. *Bogcia* Barr, E. *Bostrichoclerus* Van Dyke, F. *Callotillus* Wolcott, G. *Cymatodera* Gray (not treated here), H. *Cymatoderella* Barr, I. *Lecontella* Wolcott & Chapin, J. *Monophylla* Spinola, K. *Onychotillus* Chapin, L. *Neocallotillus* Burke.

Chapter 3 - Phylogenetic analysis of the subfamily Tillinae (Coleoptera: Cleridae) in the New World based on morphological characters, with biogeographic considerations

Abstract

The relationships of the clerid subfamily Tillinae inhabiting the New World are studied here through a morphology-based phylogenetic analysis. Ninety-one morphological characters from 66 New World tillinid species, representatives of seven tillinid genera from the Old World, 13 species from seven non-tillinid subfamilies within Cleridae, and members of Melyridae and Trogossitidae were carefully selected. Phylogenies were reconstructed using maximum parsimony and Bayesian approaches. Interfamilial relationships were not fully resolved. Results indicate that Tillinae is a monophyletic group. Old World tillinids are recovered as basal taxa in the phylogeny of the Tillinae. Intergeneric relationships obtained in the analysis suggest that *Onychotillus* Chapin is sister to remaining New World Tillinae. Intergeneric relations for the small genera *Callotillus* Wolcott, *Monophylla* Spinola and *Neocallotillus* Burke were not fully resolved. The small genus *Cymatoderella* Barr was found to be the sister group of *Cymatodera*. The speciose genus *Cymatodera* Gray was obtained as paraphyletic by the inclusion of the small genera *Araeodontia, Bogcia* and *Lecontella.* The *Cymatodera* group is further subdivided into two major clades reflecting differences in the male pygidium. Six major species groups for the mainly *Cymatodera* group are proposed. Based on collecting locality data obtained from approximately 7,000 specimens, and in combination with the phylogenetic results, a hypothesis for the center of origin and distribution patterns for the New World tillinids is presented. A list of

characters used in the analysis, together with the corresponding character-state data matrix are provided. Characters of relevance used in the analysis are described and imaged in detail. The results obtained here should be corroborated by the incorporation of a molecular-based phylogenetic analysis. The characters and character-states used in this study may function as framework for the selection of morphological characters of taxonomic value for further phylogenetic analyses of other clerid subfamilies.

1. Introduction

The superfamily Cleroidea is composed of 13 families (Lawrence & Leschen, 2010; Lawrence et al., 2011). Cleridae is the second largest cleroid family, after Melyridae *sensu* Lawrence & Leschen (2010). Interfamilial relationships for the cleroid assemblage are inconclusive. Hunt et al. (2007) recovered Trogossitidae as the sister group of a clade composed of Cleridae + Melyridae. Lawrence et al. (2011), in a morphological phylogenic analysis of the Coleoptera, found Cleroidea to be a paraphyletic group, and only after adding the monotypic family Metaxinidae and the small Chaetosomatidae was it possible to obtain a monophyletic group. Lawrence et al. (2011) recovered Melyridae as the sister to all Cleroidea families. Gunter et al. (2013), in their molecular-based phylogenetic analysis of the Cleridae, found a melyrid lineage formed by Rhadalidae + Mauroniscidae + Prionoceridae + Melyridae + Dasytidae + Malachiidae, together with Trogossitidae (*sensu lato*), as the sister to Cleridae.

Cleridae is composed of approximately 3,500 species classified into nearly 300 genera (Gerstmeier, 2000), with most of its members having a predatory behavior, but some pollinophagous and scavenger species are known. The first systematic treatments of the Cleridae

were carried out during the nineteenth century by authors such as Spinola (1841, 1844) and

Lacordaire (1857); later on, Schenkling (1903, 1910), Gahan (1910), Chapin (1924), Böving &

Craighead (1931), Crowson (1955, 1964), Winkler (1964, 1980), Kolibàč (1992, 1997, 1998)

and Opitz (1997) greatly increased the knowledge at all taxonomic levels; and more recently,

Kolibàč (2004), Opitz (2004, 2005, 2006, 2007, 2008a, 2008b, 2008c, 2009, 2010) and Gunter et

al. (2013) have made substantial contributions to the systematics of the family. Based on the

work done by Crowson (1964), eight subfamilies were traditionally recognized: Clerinae,

Korynetinae, Enopliinae, Epiphloeinae, Phyllobaeninae (now treated as a junior synonym of

Hydnocerinae), Tarsosteninae, Thaneroclerinae and Tillinae. Kolibáč (1992, 1997) made

substantial rearrangements within the clerid lineage and, based on the size of the fourth

tarsomere, proposed the division of Cleridae into two separate families, the Thanerocleridae

(possessing a reduced fourth tarsomere), including three tribes Isoclerini, Thaneroclerini, and

Zenodosini; and the Cleridae (with the fourth tarsomere not reduced), comprised of the

subfamilies Korynetinae, Hydnocerinae, Clerinae and Tillinae.

According to the most recent treatments of Cleridae, 13 subfamilies are currently accepted

(Opitz, 2010, Gunter et al., 2013); however, some differences exist concerning the status of the

Thanerocleridae. Leschen (2010) gave family status to this group of beetles, while Opitz (2010)

rejected it, considering Thaneroclerinae a subfamily. Gunter et al. (2013) recovered

Thaneroclerinae as monophyletic and nested within Cleridae, supporting Opitz's (2010) findings

of Thaneroclerinae being a subfamily within Cleridae, while the concept of Thaneroclerinae

sensu Opitz was found to be paraphyletic. Other results obtained by Gunter et al. (2013) indicate

that Tillinae represents the sister group to remaining clerids. This finding differs from the

morphology based classifications given by Kolibáč (1992, 1997) and Opitz (2010) recovering Thaneroclerinae as the sister group to all clerids. Gunter et al. (2013) obtained two major clades for remaining Cleridae subfamilies: the first composed of Thaneroclerinae + Korynetinae + Epiphloeinae + Peloninae + Neourthopleurinae + Tarsosteninae + Enopliinae + Epiclininae *subf. n.*, and the second including Hydnocerinae + Clerinae (in part) and Clerinae (in part). The authors also recovered the Korynetinae lineage (Korynetinae + Tarsosteninae + Peloniinae + Neorthopleurinae + Epiphloeinae) as paraphyletic, and only Epiclininae, formed by the genera *Epiclanes* + *Eleale* + *Cleromorpha* (these formerly placed within Clerinae), was recovered as monophyletic.

Tillinae, the second largest subfamily after Clerinae, it is represented by approximately 700 species in 69 genera (Corporaal, 1950; Rifkind, 1993a, 1993b, 1996; Rifkind et al., 2010; Opitz, 2010; Burke, 2013; Burke & Zolnerowich, 2014, Burke et al., 2015). The tillinid fauna is well represented in the North American temperate and sub-temperate zones, the Neotropics, and the Paleotropic region of Africa, with an important concentration of genera and species in Madagascar and Central Africa (Opitz, 2010). Based on a literature revision, to date, approximately 160 described species classified into 12 genera are found in the Americas (Corporaal, 1950; Barr, personal communication, 1979; Rifkind, 1993*a*; 1993*b;* 1996; Rifkind et al.; 2010; Burke, 2013; Burke & Zolnerowich, 2014, Burke et al., 2015, Burke & Zolnerowich, 2016). These genera are: *Araeodontia* Barr, *Barrotillus* Rifkind, *Bogcia* Barr, *Bostrichoclerus* Van Dyke, *Callotillus* Wolcott, *Cylidrus* Latreille, *Cymatodera* Gray, *Cymatoderella* Barr, *Lecontella* Wolcott & Chapin, *Monophylla* Spinola *Neocallotillus* Burke & *Onychotillus* Chapin (Table 1).

Here, the first morphology-based phylogeny of the New World Tillinae is presented. The use of various morphological characters is proposed for phylogenetic purposes. Geographic data at the species level are also presented. Finally, species groups for the speciose genus *Cymatodera* are proposed. This analysis is the first step toward a better understanding of the subfamily, and can be useful for identifying and highlighting taxa in need of taxonomic revision.

2. Materials and Methods

2.1 Taxonomic sampling

The sampling consisted of 66 species, representing 10 of the 12 tillinid genera inhabiting the New World (Table 1), and seven Old World species. The monotypic species *Bostrichoclerus bicornis* Van Dyke, and *Cylidrus abdominalis* Klug, reported from Brazil by Corporaal (1950), could not be obtained and were not examined for the study. The sampling also included thirteen representatives of non-tillinid clerids from the subfamilies Neorothopleurinae, Hydnocerinae, Korynetinae, Tarsosteinae, Epiphloeinae and Peloniinae (sensu Opitz, 2010). Two non-Cleridae families, Melyridae and Trogossitidae, with two species for each family, were also included as outgroups. *Cymatodera* is represented in this study by 44 species inhabiting the New World, totaling approximately 30% of all described species. Remaining genera in the analysis were well represented, with at least 60% of their representatives included in the analysis. The current number of described species per genus, number of examined species in the analysis per genus, and the corresponding percentages of species examined in this analysis in relation to the total number of taxa per genus are given in Table 1. The data matrix (Table 3) was constructed based on the examination and comparison of adult specimens and resulted in 91 morphological

characters (58 binary and 33 multistate) from the head, thorax, abdomen, male and female terminalia, and male genitalia.

2.2 Collection repositories and specimens examined

The following codens refer to public and private collections from which material was obtained: American Museum of Natural History, Washington D.C. (AMNH); British Museum of Natural History Collection, London, UK (BMNH); California Academy of Sciences Insect Collection, Sacramento, CA (CASC); Colección Nacional de Insectos UNAM, México (CNIN); Field Museum of Natural History Collection, Chicago, IL (FMNH); Florida State Collection of Arthropods (FSCA); Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBIO); Institut Royal des Sciences Naturelles de Belgique (IRSNB); Jacques Rifkind Collection (JNRC); James E. Wappes Collection (JEWC); Kansas State University Museum of Entomological and Prairie Arthropod Research Collection, Manhattan, KS (KSUC); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Robert H. Turnbow Collection, Enterprise, AL (RHTC); Texas A&M Insect Collection, College Station, TX (TAMU); Università di Firenze Collezione, Florence, Italy (UFBI); and Weston Opitz Collection, Salina, KS (WOPC).

Identified taxa used in the analysis (by genus and species) are: *Araeodontia isabellae* (Wolcott) (FSCA), *A. marginallis* Barr (FCCA), *A. peninsularis* (Schaeffer) (FSCA), *Barrotillus kropotkini* Rifkind (JNRC), *Bogcia disjuncta* Barr (JEWC)), *B. oaxacae* Barr (CNIN), *Callotillus bahamensis* Vaurie (AMNH), *C. eburneocinctus* Wolcott (FSCA), *Chariessa pillosa* (Forster) (KSUC), *Collops bipunct*atus (Say) (KSUC), *C. quadrimaculatus* (Fabricius) (KSUC), *Cylidrus*

fasciatus ab. *bimaculatus* Spinola (IRSNB), *Cylidroctenus chalybaeum* (Westwood), *Cymatodera aegra* (WOPC), *C. angulifera* Gorham (FSCA), *C. balteata* LeConte (FMNH), *C. barri* Rifkind (JNRC), *C. bicolor* (Say) (WOPC), *C. bipunctata* Gorham (FSCA), *C. californica* Horn (FSCA), *C. championi* Gorham (INBIO), *C. conflagrate* (Klug) (WOPC), *C. delicatula* (Fall) (FSCA), *C. depauperata* Gorham (TAMU), *C. fascifera* LeConte (FSCA), *C. floridana* Barr (FSCA), *C. fuchsia* Schaeffer (FSCA), *C. guatemalensis* Schenkling (RHTC), *C. hoegei* Gorham (RHTC), *C. hopei* Gray (FSCA), *C. hornei* Wolcott (FSCA), *C. inornata* (Say) (FMNH), *C. latefascia* Schaeffer (FMNH), *C. limatula* Burke (FSCA), *C. linsleyi* Barr (FSCA), *C. marmorata* (JEWC), *C. mitchelli* Chapin (FSCA), *C. neomexicana* (FSCA), *C. obliquefasciata* Schaeffer (TAMU), *C. pallida* (BMNH), *C. prolixa* (Klug) (INBIO), *C. pseudotsugae* Barr (FMNH), *C. punctate* LeConte (FMNH), *C. puncticollis* Bland (FMNH), *C. rosalinae* Burke (USNM), *C. sallei* Thomson (INBIO), *C. sericans* Gorham (INBIO), *C. tuta* Wolcott (FMNH), *C. usta* LeConte (FSCA), *C. vagemaculata* Thomson (CNIN), *C. vandyki* Schaeffer (FSCA), *C. venusta* Wolcott (INBIO), *C. werneri* Barr (FSCA), *C. xanti* Horn (BMNH), *C. xaviera* Horn (FSCA), *Cymatoderella collaris* (Spinola) (WOPC), *C. morulla* Rifkind (JNRC), *C. patagoniae* Knull (WOPC), *Enoclerus abdominallis* (Chevrolat) (KSUC), *E. nigripes* (Say) (KSUC), *Lecontella brunea* (Spinola) (WOPC), *L. gnara* Wolcott (WOPC), *L. striatopunctata* (Chevrolat) (CNIN*), Madoniella dislocate* (Say) (KSUC), *Monophylla californica* (Fall) (WOPC), *M. pallipes* Schaeffer (FSCA), *M. terminate* (Say) (FSCA), *Necrobia rufipes* (De Geer) (KSUC), *Neocallotillus elegans* (Erichson) (WOPC), *N. elegans* (*elegans*) Wolcott (WOPC), *N. elegans* (*vafer*) Wolcott (WOPC), *N. elegans* (*intermediate*) Wolcott (WOPC), *N. intricatus* Wolcott & Dybas (FSCA), *Neorthopleura thorasica* (Say) (KSUC*), Pellonium leucophaeum* (Klug) (KSUC), *Phyllobaenus humerallis* (Say) (KSUC), *P. pallipes*

(Say) (KSUC), *Priocera castanea* (Newman) (KSUC), *Onychotillus cubana* (RHTC), *Onychotillus vittatus* Chapin (WOPC), *Stenocylidrus dispar* Fairmaire (WOPC), *Strotocera grandis* Schenkling (MNHN), *Tilloidea transversalis* (Charpentier) (MRAC), *Trichodes nutalli* Kirby (KSUC), *Zenodosus sanguineous* (Say) (TAMU). Unidentified taxa used in the analysis (by genus and species): *Gastrocentrum* sp. (UFBI) and *Orthocladiscus* sp. (IRSNB).

2.3 Data reconstruction and phylogenetic analyses

A data matrix (Table 3) was constructed and edited using Mesquite version 2.75 for Windows (Maddison & Maddison, 2011). Question marks (?) in the matrix indicate missing data and/or inapplicable character states. Three characters shown in italics in Table 2 were ultimately excluded from the analysis because they were parsimony uninformative. Morphological terminology primarily follows Barr (1972), Ekis (1977), Rifkind (1993*a*) and Opitz (2010). A single parsimony search was performed using the software PAUP (Phylogenetic Analysis Using Parsimony) version 4.0b10 (Swofford, 2002) for Macintosh. Due to the relatively large number of taxa, a heuristic search using a Tree-Bisection-Reconnection procedure was performed. All characters were initially unordered and unweighted. The MulTrees option was in effect during the analysis. Clade support was assessed by a full bootstrapping analysis with a total of 200 replicates with random addition sequence per replicate.

The software MrBayes has been shown to be useful for analyzing morphological and partitioned morphological-molecular datasets using the Mk1 model modeling rate heterogeneity among characters using gamma distribution (Lewis, 2001), and various phylogenetic analyses have implemented this approach with positive results (Wiens et al., 2005; Bernhard et al., 2009;

Bochkov & Mironov, 2011; Mlambo et al., 2012; Kits *et al.* 2013; Ruhfel et al., 2013; Klaczko et al., 2014); as a result, a Bayesian analysis using the software MrBayes version 3.2.2 for Windows (Huelsenbeck & Ronquist, 2011) was also performed. Two independent runs with eight MCMC chains each, two cold and six heated chains, were used with 10^6 generations sampled every 1,000 generations (Marshall et al. 2006). Illustration and editing of the resulting trees were carried out with the software Mesquite version 2.75 for Windows (Maddison & Maddison, 2011).

2.4 Geographic data

To investigate the center of origin and distribution patterns the New World Tillinae have undergone, collecting locality information from all tillinid species examined was obtained from approximately 7,000 specimens gathered throughout the Americas and the Old World. The geographic regions used in this study were the following: 1) Old World species; 2) north USA-Canada species; 3) east and central USA species; 4) southwest USA species; 5) USA – north Mexico species; 6) Mexico species; 7) Mexico – Central America species; 8) Central America species; 9) Caribbean islands species; and 10) Mexico – Central – South America species. The differentiation of north Mexico and Mexico is justified by the fact that north Mexico is part of the southernmost portion of the Nearctic region, while central and south Mexico, here treated as Mexico, are part of the Neotropical region (Undvardy, 1975). The Rocky Mountains were set as the limit between the eastern and western USA. Species found in north Mexico and the western USA do not extend to Canada. Species with a wide Nearctic distribution (USA-Canada) never reach north Mexico. The geographic records of the taxa examined in the analysis do not

represent conclusive species distribution and are too tentative to make ecological assumptions or hypotheses. Knowledge of the geographic distribution of the New World Tillinae is still scarce.

3. Results

From a dataset of 91 characters, 88 of which are parsimony informative (Table 3.2), a single heuristic search was performed, producing 2461 most parsimonious trees of 677 steps. A strict consensus tree was constructed from these trees (Figs. 3.1, 3.2). When supported, >50% bootstrap values are indicated above branches (Fig. 3.1). Consistency indices for all retained trees are relatively far from random (Consistency Index=0.21), a situation very likely caused by a very high rate of homoplasies (Homoplasy Index= 0.8).

The Bayesian analysis achieved stationarity of the dataset after 2.5 million generations, and the 50% majority-rule consensus tree of the 20% post burn-in posterior distribution is shown in Fig. 3.3. Posterior probability values are indicated above branches. The Bayesian analysis reveals a consensus tree comparable to the strict consensus tree based on maximum parsimony. The Bayesian topology obtained relatively high retention indices for interfamilial relationships and higher tillinid taxa, providing good support for the monophyly of the New World Tillinae. Poor intergeneric resolution is observed at the interspecific level, indicating high levels of homoplasy among tillinid species.

Within Cleridae, the subfamily Thaneroclerinae *sensu* Opitz (2010) was found to be sister to remaining clerid subfamilies (Figs. 3.1, 3.2). The subfamilies Epiphloeinae, Peloniinae, Korynetinae and Neorthopleurinae were recovered as basal lineages. The Clerinae and

Hydnocerinae are paraphyletic subfamilies, with inconclusive relationships at the intergenic level for these subfamilies. Tillinae was obtained as a derived clade, with Old World Tillinae taxa recovered as basal groups within the Tillinae lineage. *Onychotillus* (New World) was found to be sister to remaining New World Tillinae (clade 1 in Fig 3.2). A monophyletic clade consisting of *Monophylla, Barrotillus, Neocallotillus* and *Callotillus* was recovered (clade 2 in Fig. 3.2). This group was subdivided into two sub-clades, one composed of *Monophylla* species, and the other formed by *Barrotillus, Neocallotillus* and *Callotillus. Cymatoderella* was found to be sister to a large clade composed of *Cymatodera* and related genera (clade 3 in Fig. 3.2). A large, monophyletic group (clade 4 + clade 5) can be subdivided into two major lineages, the first composed of species with a simple male pygidium (clade 4), and the second group of species with a highly modified male pygidium (clade 5). Based on the interspecific relationships observed within the large clade composed of *Cymatodera* and related genera (clade 4 + clade 5), it is possible to designate 6 species-groups (Fig. 3.2): the *aegra –werneri* group, *hoegei – guatemalensis* group, *hopei – horni* group, *floridana – depauperata* group, *oaxacae* group, and *tricolor* group.

4. Discussion

Results at the interfamily level obtained in this analysis should be taken with care due to the lack of a broad family taxon-sampling, leaving inconclusive relationships outside of the clerid lineage. The analysis recovered Trogossitidae as the sister group of all Cleridae (Figs. 3.3), with Melyridae a separate lineage within Cleroidea. This finding is similar to that obtained by Hunt et al. (2007), where Trogossitidae was the sister to a clade composed of Cleridae + Melyridae. Lawrence et al. (2011) found Melyridae to be the sister group of all Cleroidea. Gunter

et al. (2013), in their molecular phylogeny, found a melyrid lineage (*sensu* Majer, 1994) composed of Rhadalidae + Mauroniscidae + Prionoceridae + Melyridae + Dasytidae + Malachiidae, together with Trogossitidae (in part), to be the sister to Cleridae.

The analyses recovered *Zenodosus sanguineus* (Say) (Thaneroclerinae) as the sister to remaining clerid taxa; this finding supports those of Opitz (2010) and Gunter et al. (2013), where Thaneroclerinae was recovered as part of the Cleridae, rather than as a separate family, as proposed by Koliváč (1997). Epiphloeinae, Peloniinae, Korynetinae and Neorthopleurinae are basal lineages in the clerid phylogeny, which is consistent with the results of Opitz (2010) and Gunter (2013). Clerinae and Hydnocerinae are derived but paraphyletic groups. The affinity between Clerinae and Hydnocerinae has been previously demonstrated by Opitz (2010) and Gunter et al. (2015); the latter study further recovered these subfamilies as largely paraphyletic, supporting the findings obtained here.

Gunter et al. (2013) and Hunt et al. (2007) obtained Tillinae as the most basal lineage, while the present study recovered Tillinae as a derived group, as did Opitz (2010) and Koliváč (1997). This finding is supported by the presence of the procoxal cavities closed internally (the fusion of the procryptosternum with the posterior portion of the pronotal extension, as described by Opitz, (2010), and the proepimera completely surrounding the procoxal cavities externally (Fig. 3.11 B-C). The structural composition of the procoxal cavities is unique among Tillinae species, and it is only observed outside of Cleridae in the trogossitid subfamily Rentoniinae (Gunter *et al*., 2013). This character can be considered a synapomorphy for the tillinid clade. Remaining Cleridae subfamilies have the procoxal cavities opened internally and posteriorly

(Fig. 3.11-A). Any adaptive advantage of this character state to the tillinids is unclear but it may deliver certain advantage when handling large prey.

4.1 Consistencies found between parsimony and Bayesian analyses

The parsimony and Bayesian analyses found the Taneroclerinae to be the sister group to remaining clerids (Figs. 3.1, 3.3), a result consistent with Kolibáč (1992) and Opitz (2010). Subfamily relationships were not fully resolved for both parsimony and Bayesian inferences. Despite these findings, it was possible to observe highly resolved relationships among certain subfamilies. Specifically, the clades Korynetine + Neorthopleurinae, Epiphloeinae + Peloniinae, and Clerinae + Hydnocerinae were recovered as closely related and with high bootstrap and posterior probability values (Figs. 3.1, 3.3). These major groups are in partial disagreement with Opitz's classification (2010), in which he indicated two major clades, the first composed of Thaneroclerinae + Isoclerinae, sister of remaining clerids, and a second subdivided into two monophyletic groups, the first formed by Hydnocerinae + Anthicoclerinae + Tillinae + Clerinae, and the second composed of Epiphloeinae + Tarsosteninae + Peloniinae + Enopliinae + Neorthopleurinae + Korynetinae. Despite the partial disagreement between Opitz's classification and these results, Clerinae *sensu lato* was found to be closely related to Hydnocerinae, two groups also recovered as closely related by Gunter et al. (2013). The clade Clerinae + Hydnocerinae was recovered as sister to the Tillinae, a result similar to that of Opitz (2010). This analysis did not cover all subfamilies used by Opitz (2010) and Gunter et al. (2013), and different taxon sampling could explain why the results here are different from theirs.

The parsimony and Bayesian inferences obtained Old World species as basal groups in the tillinid lineage. A clade composed of *Cylidrus fasciatus + Cylidroctenus chalybaum + Stenocylidrus dispar* was recovered as the most basal clade within the Tillinae by the parsimony analysis, with interspecific relationships for remaining Old World tillinids unresolved (Figs. 3.1, 3.2). Conversely, the Bayesian approach recovered *Cylidrus fasciatus + Cylidroctenus chalybaum* as the most basal clade of all tillinid species, with *Stenocylidrus dispar* part of a group of Old World tillinid species with unresolved interspecific relationships.

Three widely distributed morphotypes of *Neocallotillus elegans* (Erichson) (Fig. 3.5-E and see Figs. 2.2 B-C and 2.5-C from Chapter 2) were examined and, for both analyses, these taxa were unresolved within a single clade.

Despite poor intergeneric resolution in the Bayesian tree, which produced a major polytomy for the New World Tillinae, two major clades were recovered. The first is a clade composed of *Barrotillus + Callotillus + Monophylla + Neocallotillus* (clade 2 in Fig. 3.2) with a posterior provability value of 0.99. The second clade is a group composed of exclusively *Cymatodera* species (clades 5 in Fig. 3.2). This group was recovered with a posterior probability value of 0.71, supporting interspecific relationships (Fig. 3.1). These groups were also recovered in the parsimony analysis.

4.2 Differences between parsimony and Bayesian studies

The Bayesian analysis revealed a consensus tree with a topology generally similar to the unweighted maximum parsimony tree (Figs. 3.1, 3.3). However, a number of clades in the

208

Bayesian analysis were included in a major polytomy. Clades within this polytomy were recovered with low posterior probability values (less than 50%) and, as a result, were collapsed in the analysis. Low posterior probability values for these clades could be due to the relatively high homoplasy rate found at the specific level. This rate was also observed in the maximum parsimony analysis, with a homoplasy index of 0.8. Following, major differences between the parsimony and Bayesian analyses are discussed.

Results from the parsimony analysis divide the subfamily Tillinae into seven major groups: 1) *Cylidroctenus + Cylidrus + Stenocylidrus,* 2) *Orthocladiscus + Strotocera + Cladiscus*, 3) *Monophylla + Barrotillus + Neocallotillus + Callotillus*, 4) *Onychotillus,* 5) *Cymatoderella,* 6) *Cymatodera sensu lato + Araeodontia + Bogcia + Lecontella,* and 7) *Cymatodera sensu lato.* These clades are supported by moderate to high bootstrap values. However, the Bayesian analysis resulted in a clade composed of *Cylidroctenus + Cylidrus* and inconclusive relationships for a group composed of *Orthocladiscus + Strotocera + Cladiscus + Stenocylidrus.*

The parsimony analysis produced *Onychotillus* as sister to remaining tillinid genera (clade 1 in Fig. 3.2), this clade is supported by moderately high bootstrap value, while no sister group to the Cleridae could be inferred from the Bayesian analysis (Fig. 3.3).

The parsimony approach recovered a clade (clade 2 in Fig. 3.2) composed of *Barrotillus*, *Callotillus, Monophylla* and *Neocallotillus* with moderate to high bootstrap values. This group was subdivided into two separate lineages, one composed of all *Monophylla* species*,* and the second formed by *Barrotillus + Callotillus + Neocallotillus;* the latter clade with interspecific

relationships partially resolved. The Bayesian inference obtained the *Monophylla + Barrotillus + Neocallotillus + Callotillus* as unresolved (Fig. 3.3).

The parsimony analysis indicates that *Cymatoderella* represents the sister group to *Cymatodera* and related genera (clades 4 + 5 in Fig. 3.2) with a high bootstrap value. *Cymatoderella* can be distinguished from *Cymatodera* and related genera by the moderately protruding, finely faceted, small eyes (Fig. 3.10-A), an indication of diurnal activity. Small eye size and reduced ommatidia diameter (Fig. 3.10-A) may represent a plesiomorphic character for the New World Tillinae, supporting *Cymatoderella* as the sister to *Cymatodera* and allied genera. The Bayesian inference recovered a major polytomy for all major New World Tillinae taxa.

The parsimony analysis produced a resolved lineage composed of *Cymatodera* (in part) + *Araeodontia + Bogcia + Lecontella,* (clade 4) and *Cymatodera* (in part, clade 5 in Fig. 3.2). Conversely, the Bayesian topology shows poor resolution at the specific level for this major lineage, and was unresolved for clade 4 (Figs. 3.2, 3.3).

4.3 Classification and diagnosis of major Tillinae groups

Morphological characters that readily separate all major clades obtained in the analysis and their composition and relevance are described below.

Tillinae (clades 1-5 in Fig. 3.2) is characterized by the fusion of the procryptosternum with the pronotal extension (Fig. 3.11 B-C), a synapomorphic character which separates Tillinae from remaining clerid subfamilies. Secondary characters that readily differentiate tillinids from other

congeners are: body oblong (Figs. 3.4 C-D, F, 3.5 C-F, 3.6-D, 3.6 A-F, 3.7 A-F), narrow (Figs. 3.4 C-F, 3.5-D) to robust (Figs. 3.4 B, E, 3.5-F, 3.6-B, 3.7-B); mouthparts predominantly prognathous (Fig. 3.9 A-D); eyes most often coarsely faceted (Figs. 3.9-C, 3.10-D); antennae composed of 10 (Fig. 3.15-F) to 11 antennomeres (Fig. 3.15 C-D); pronotum straight, campanulate to bisinuate (Fig. 3.16 B-D); the procoxal cavities closed posteriorly, that means, the intercoxal process joins the pronotal projections (Fig. 3.11 B-C); a pair of conspicuously marked to feebly elevated carinae on the anterior portion of each metacoxal cavity (Fig. 3.12-D) the dorsolateral ridge is absent (Fig. 3.14-A); tarsal formula 5-5-5 (Fig. 3.11-D); and aedeagus feebly to strongly sclerotized (Figs. 3.22 A-D, 3.23 A-D).

Seven species inhabiting the Old World were selected for analysis (Fig. 3.4 A-F): *Cylidrus fasciatus* Laporte (Belgian Congo, now Central African Republic)*, Cylidroctenus chalybaeum* Westwood (Sinepung, Nepal)*, Gastrocentrum sp.* (North Borneo, Indonesia, and Brunei)*, Orthocladiscus sp.* (Papua New Guinea)*, Stenocylidrus dispar* Fairmaire (Fampanambo, Madagascar), *Strotocera grandis* Schenkling (Mt. Sabah, Malaysia)*,* and *Tilloidea transversalis* (Charpentier) (Bulgaria and Macedonia). Morphological examination of this material indicates plesiomorphic male genitalia, where the phallobasic denticles are absent in all specimens examined, the only exception was observed in *Gastrocentrum* sp., where two short rows of denticles are found near the apical portion of the parameres. Phallobasic denticles are moderately to strongly present in all *Cymatodera* and related taxa (Fig. 3-22 A-D, 3.23 A-D), but feebly present to absent in basal New World taxa (Fig. 3.22-E). The absence of phallobasic denticles may be a plesiomorphic character in the tillinid lineage, hence the position of Old World taxa in the phylogeny, and the affinity these taxa have with basal New World tillinids. Other

morphological characters observed in Old World tillinids the male pygidium being poorly differentiated from that of females. *Stenocylidrus dispar* represents the only exception to this observation, where the male pygidium is moderately differentiated from female specimens. Species possessing bright, conspicuous or metallic integument coloration also had smaller eyes and reduced ommatidia diameter, this combination of characters may indicate diurnal activity. Aposematic coloration may be advantageous for species with diurnal activity. Conversely, species with dull coloration possess enlarged eyes and wide ommatidial diameter, these characters suggests crepuscular to nocturnal activity. Finally, the carina found on the anterior portion of each metacoxal cavity, conspicuous in all New World Tillinae (Fig. 3.12-D), was from moderately present to absent in Old World tillinids. Specifically, *Cylidrus fasciatus* and *Cylidroctenus chalybaeum* have a reduced carina, giving the appearance of an enlarged tubercle; *Gastrocentrum* sp.*, Tilloidea transversalis* and *Stenocylidrus dispar* have a shallow but complete carina somewhat similar to that observed in Old World tillinid taxa, while *Strotocera grandis* and *Orthocladiscus* sp. lack these carinae.

Clade 1, *Onychotillus* (Fig. 3.5-C), is a group supported by both parsimony and Bayesian inferences. The genus is composed of 5 species inhabiting the West Indies. Species in the group are small, less than 7 mm in length, reddish to bluish, to dark metallic integument, small head, as wide as pronotum, antennae moderately serrate, with the eleventh antennomere at least 2× the length of tenth antennomere, slender body, and posterior wings fully developed. Four *Onychotillus* species inhabiting Cuba have been described by De Zayas (1988), from these, only *O. cubana* was examined. The remaining species were not examined due to the absence of material in all collections from which material was borrowed. The presence of a single tarsal

denticle on all legs is the only morphological character that clearly distinguish the genus from remaining tillinids and can be considered a synapomorphy for the group. All other New World tillinid genera have two tarsal denticles.

Clade 2, *Monophylla* + *Barrotillus* + *Neocallotillus* + *Callotillus* (Fig. 3.2). Four genera with moderate intraspecific support are included in this clade. Clade 2 can be further separated into two sub-clades: 1) *Monophylla* and 2) *Barrotillus* + *Neocallotillus* + *Callotillus*. *Monophylla* can be distinguished from remaining tillinids by the enlarged last antennomere (Fig. 3.15-A), this antennal form is not found in other New World species. General characters of the genus are: body slender; relatively small individuals, less than 10 mm; head of moderate size, as wide as pronotum; lateral margins of pronotum subparallel (Fig. 3.16-B); elytra asperate with indistinguishable striae (Fig. 3.5-D); and the reduced procoxae and procoxal cavities (Fig. 3.11-C). *Monophylla* is most closely allied to *Callotillus* Wolcott, *Barrotillus* Rifkind, and *Neocallotillus* Burke. The group is morphologically identified by the strongly serrate to pectinate condition of the antennae (Fig. 3.15-F and see Figs. 2.8 D-F, 2.9 A-E, 2.11 A-D) and the campanulate to scutiform shape of the pronotum (Figs. 3.16-C). The group was recovered by the parsimony and Bayesian analyses. Interspecific relationships are partially resolved (see inconsistencies for parsimony and Bayesian analyses section and Figs. 3.2, 3.3).

Clade 3, *Cymatoderella* (Fig. 3.6-B) has three described species, *C. collaris* (Spinola)*, C. morula* Rifkind and *C. patagoniae* (Knull). The group was originally erected by Barr (1962) to accommodate those species belonging to *Tillus* Olivier inhabiting the New World. Differences in the structure of the eyes will help to separate *Tillus* from *Cymatoderella*. Specifically, in *Tillus*

the ommatidia are wide and coarse, while in *Cymatoderella* the ommatidia are reduced in

diameter (Fig. 3.10-A). The genus is distributed from the northern USA to Honduras and El

Salvador. Secondary characters are: small size, robust body (Fig. 3.6-B), and antennomeres 4-11

moderately serrate (see Fig. 2.9 D-E from Chapter 2). Eye structure in the group is indicative of

diurnal activity, and it is shared with all basal New World taxa. The parsimony inference found

Cymatoderella as the sister group of the largest and most derived *Cymatodera* lineage (clades 4

+ 5, Fig 3.2).

Clades 4 + 5 *Cymatodera* lineage (Fig. 3.2). *Cymatodera* is the largest tillinid genus in the

New World, and one of the most species-rich in the world. To date, there are approximately 130

described species (Burke et al. 2015) (Table 1). The genus is distributed from south Canada to

South America, with its southernmost limit northern Bolivia (Leavengood, *personal

communication*). *Cymatodera* is absent in the West Indies. The genus is most similar to

Araeodontia, Bogcia, and *Lecontella*. *Cymatodera* and allied groups can be separated from other

tillinids by the structure of the male genitalia, where the parameres are partially to totally fused

and create a sheath that completely encircles the phallus (Fig. 3.23 A-D), this character can be

considered synapomorphic in *Cymatodera* and related genera. In contrast, parameres of other

tillinids are partially to totally free (see Fig. 2.20 B-D from Chapter 2). The following

combination of secondary characters will serve separate *Cymatodera* and allied groups from

other tillinids: body length 4.0 mm to over 30.0 mm; antenna serrate (Fig. 3.15-D) to filiform

(Fig. 3.15-C), last antennomere circular in cross section, as long as (Fig. 3.15-D), or shorter than

the length of preceding three antennomeres (Fig. 3.15 C, D), basal denticle of tarsal claws

trigonal (Fig. 3.12-B), eyes coarsely faceted (Fig. 3.10-D), and elytral disc with striated

punctuations (Fig. 3.18 B-F), punctations may be regularly (Fig. 3.18-E) or irregularly arranged (Fig. 3.18-F). *Cymatodera* is separated into two major clades (clade 4 and 5 in Fig. 3.2).

Clade 4: *Cymatodera sensu lato + Araeodontia + Bogcia + Lecontella.* The genus *Araeodontia*, is composed of five species distributed in south USA and north Mexico. *Araeodontia* is distinguished from *Cymatodera* by the shape of the basal denticles, in *Araeodontia* this denticle is digitiform in all members (see Fig. 2.6-E from Chapter 2); conversely, *Cymatodera* has the basal denticle trigonal (Fig. 3.12-B). The genus *Lecontella* is composed of three species distributed in North and Central America, the genus can be readily separated from *Cymatodera* by the sculpturing on the elytral ground, where nine rows of coarse punctations reach the elytral apex (Fig. 3.18-D). *Bogcia* is distinguishable from all *Cymatodera* species by the structure of the protarsal unguis, where the basal denticle of the tarsal claw is closely approximated to the denticle (Fig. 3.12-A), rather than conspicuously separated, as observed in *Cymatodera* (Fig. 3.12-B). Clade 4 can be differentiated from remaining *Cymatodera* congeners by the structure of the pygidium, where males in the clade have the last abdominal segment poorly modified and very similar to that of females (Fig. 3.21-E). Three species-groups are proposed in this clade, and morphological characters supporting these species-groups are the following:

1) *Tricolor* group: The *tricolor* group is the most basally nested lineage in clade 4. Species in this group have the male genitalia moderately sclerotized, and possess two parallel rows of denticles on each paramere (Fig. 3.23 A-C). Species in the group can be readily separated from other *Cymatodera* species if they possess moderately to conspicuously

large and rounded eyes (Fig. 3.9-C), fully developed posterior wings, and the absence of tubercles or carinae on the mesal area of the metasternum (Fig. 3.17 A-C). Sexual dimorphism is observed in species in this group, specifically, the posterior portion of the elytral margins is more expanded posteriorly in females of these species.

2) *Aegra – werneri* group. Species in this group can be separated from other *Cymatodera* species by their reduced size and the conspicuously bulging and large eyes in relation to the dimension of the head. The following combination characters distinguish this group: stout individuals, comparatively small size (smallest *Cymatodera* species are found in this group), umbones pronounced; elytra length conspicuously short in relation to the head and pronotum length (Fig. 3.7-B), and elytral declivity noticeably steep.

3) *Disjuncta* group. Members of this group can be separated from other *Cymatodera* species based on the structure of the male genitalia with phallobasic denticles feebly to moderately sclerotized and the aedeagus slightly sclerotized. Small phallobasic denticles may represent a plesiomorphic state in the group (Fig. 3.2). The parameres are reduced, and the endophallic struts are conspicuously long and slender (Fig. 3.22 A, F). This combination of characters is not found in other *Cymatodera* species. Other diagnostic characters are the serrate (Fig. 3.15-D), and/or closely joined antennal segments (Fig. 3.15-G), the eleventh antennomere moderately to conspicuously enlarged (Fig. 3.15 D, G), the frons narrow and bi-impressed, and the pronotum somewhat robust (Fig. 3.6 D, E). The group is widely distributed from the south USA to Central America, with a high concentration of species in the western portion of Mexico.

Clade 5: *Cymatodera sensu lato*. The group is species-rich, with many undescribed taxa in the mountainous regions of central and southern Mexico and Central America. This clade was recovered as monophyletic in the parsimony analysis, and it is supported by the presence of males with a moderately to well differentiated last abdominal segment when compared with that of females (Fig. 3.21-F). Secondary characters in this clade are enlarged body size, tegmen elongate with sclerotized phallus (Figs. 3.22 C-D, 3.23 A, D), and, in most species, the presence of tubercles or carinae on the mesal area of the metasternum (3.17 B-C). It has been proposed that these carinae/tubercles may be used for stridulatory purposes (Rifkind, 2006). I propose three major species groups for this clade, these are well supported by parsimony and Bayesian results. Morphological characters supporting these species-groups and their phylogenetic relationships with other congeners are discussed below.

1) *hopei – hornei* group. This is the most basally nested group in clade 5 (Fig. 3.2). Members in the group have a Nearctic distribution. These species can be characterized by the possession of the following morphological characters: relatively slender antennae (Fig. 3.15-C, E); comparatively large members (largest *Cymatodera* species are found in this group); integument sparsely covered with short setae; relatively long elytra in relation to head-pronotal length; methatorax and posterior wings fully developed; and absence of a pair of tubercles/carinae on metasternal surface (Fig. 3.17-A).

2) *depauperata -floridana* group. Various species in the group show brachyptery on the posterior pair of wings. Species with poorly developed posterior wings have a reduced

anterior margin of the elytral disc (Fig. 3.18 C, F) if compared with species possessing

fully developed posterior wings (Fig. 3.18 B, D, E). In the order Coleoptera, flight muscles

are located in the metathorax and are covered by the scutum; thus, the reduction of the

anterior elytral margin in a number of *Cymatodera* species in the group is caused by the

reduction of the scutum, wing muscles, and wing size. Brachyptery is observed in other

beetle families, such as ground beetles (Liebherr, 1988; Zalewski and Ulrich, 2006; Hartley

et al., 2007), and may indicate an adaptation to evolutionary changes in rapidly changing

environments, specifically, ecological islands where isolation has taken place. In addition,

males of various species in the group have a pair of tubercles on the mestarternal area of

the methatorax (Fig. 3.17-B). Wing reduction in some species may have resulted in the

appearance of these tubercles, which are present only in males and presumably used for

stridulatory purposes (Rifkind, 2006).

3) *hoegei – guatemalensis* group. The group was equally recovered in the parsimony and

Bayesian analyses. Morphological evidence indicates that this clade is closely allied to the

depauperata –floridana group. The presence of a spicule on the anterior portion of the

phallus (Fig. 3.22-C-3) is a unique character that separate species in the *hoegei –*

guatemalensis group from other *Cymatodera* species in clade 5 (Fig. 3.2). Most species in

the group are confined to Mexico and Central America with one species, *C. championi*

Gorham, extending to the northern portion of South America. Secondary characters useful

to separate members of this group from other species are: body slender, head

conspicuously enlarged (Fig. 3.7-F), antennae elongate and filiform (Fig. 3.15-E),

methatorax and posterior wings fully developed, elytral margins straight, and a pair of

tubercles or carinae present on mesal area of metasternum of males (Fig. 3.17-B, C). The group was recovered as the most derived lineage in clade 5.

4.4 Clades with morphological inconsistencies and insufficient phylogenetic evidence.

- A clade composed of *Barrotillus + Neocallotillus + Callotillus* (clade 2 in Fig. 3.2) was recovered with partially resolved relationships. Insufficient phylogenetic signal for the wide variety of *Neocallotillus elegans* morphotypes is the likely cause of the polytomy observed here. These findings confirm that these morphotypes belong to a single species, *Neocallotillus elegans*.

- Two groups nested in clade 4 were recovered as monophyletic: *C. sericans + C. angulifera + Araedontoia isabellae + A. marginalli + A. penninsularis,* and *C. conflagrate + C. bicolor + C. inornata*. Despite their monophyletic status, these clades are not proposed as species-groups due to morphological inconsistencies. A number of taxa in clade 4 appear to be related to no other species-groups proposed, these are: *Cymatodera tuta, C. latefascia, C. antennata,* and *C. fascifera* (Figs. 3.1, 3.2). Particularly interesting is *C. antennata,* where morphological evidence clearly places this species together with *C. tuta* and *C. xanti,* but it was recovered as distantly related to the latter species. These inconsistencies could be resolved with the inclusion of more taxa to the dataset.

4.5 Geographic considerations

Knowledge of the origin, dispersion, and current distribution of the Tillinae is scarce. Many species descriptions were published during the late nineteenth and early twentieth

centuries, and distribution records for these descriptive works were poorly referenced at best, and, in most cases, had no specific locality data available. In the best cases, country data was the only information provided. Later collections that include detailed locality data can be used as a starting point for developing hypotheses about the origin and distribution of Tillinae species.

In this section, I present a brief discussion about the origin and distribution of the New World Tillinae. Data records were collected for 66 species, a figure that represents approximately 40% of all described New World Tillinae species. The information comes from locality labels for approximately 7,000 specimens collected throughout the Americas and examined during the study, including type material for some species. Geographic information for the New World Tillinae was not published previously; thus, this could be used as a foundation for subsequent works to study the distribution patterns of other groups of checkered beetles.

A number of New World tillinid species have a broad distribution while others occur on isolated populations in remote areas. In many instances, access to these areas is limited and difficult. Collecting expeditions are frequently carried out in an irregular fashion, and a limited number of regions have been extensively collected while many more have been poorly surveyed. As a result, acquisition of data from collecting localities is by no means the preferable approach to follow when developing studies dealing with distributional patterns. However, locality data, in combination with phylogenetic information, can be used to shed some light on the center of origin and dispersal pattern organisms have followed. In this case, the combination of both sources of information may help to develop hypotheses of biogeographic patterns for these checkered beetles. The geographic distribution of all major clades proposed in the phylogenetic

analysis is broadly described. The phylogenetic position of theses taxa is also discussed. Based on the phylogenetic position and current geographical distribution of these taxa, a general hypothesis of the origin and distribution for these clades is proposed.

Seven species of Old World Tillinae are included in the phylogenetic analysis to test the relationships these taxa have with New World Tillinae species. Old World taxa were selected in order to include a broad geographic area, and consequently have morphological characteristics sufficiently dissimilar to those observed in the lineage of New World Tillinae. Old World taxa were recovered as the most basal groups in Tillinae lineage. Their position suggests that New World tillinid species are a relatively recent lineage in the evolutionary history of the subfamily. Due to the reduced taxon sampling of tillinids inhabiting the Old World, it is unknown which lineage of Old World tillinids gave origin to New World taxa. The most remarkable similarities found between the Old World tillinids examined and the basal tillinid groups inhabiting the New World is a poorly sclerotized and unarmed male genitalia (absence of denticles on the phallic plate, see Fig. 2.13 A, C-D), and the male pygidium poorly differentiated from that of females.

Barrotillus, Callotillus, Monophylla, Neocallotillus and *Onychotillus* were recovered as basal lineages in the phylogeny. The parsimony analysis recovered *Onychotillus* as the sister to remaining tillinids. *Onychotillus* is restricted to the Caribbean Islands (see Fig. 2.21-K from Chapter 2). Morphological evidence indicates similarity with *Cymatodera* and related genera, where the antennal shape is feebly serrate to filiform, the pronotal shape in dorsal view is bisinuate, and the elytral sculpturing is arranged in regular striae. The most recent common ancestor of *Onychotillus* could have originated in continental America, with an eventual

221

transition toward a more isolated distribution, reaching in the Caribbean Islands, and eventually

separating from other tillinids in the Americas. *Monophylla* is composed of four described

species. The group is primarily found in the Nearctic region of the New World, with one species

endemic to Cuba, and two species extending to central and southern Mexico and north Central

America (see Fig. 2.21-J from Chapter 2). The monotypic *Barrotillus* is currently restricted to a

small region in the department of Francisco Morazán, Honduras (see Fig. 2.21-C from Chapter

2). *Callotillus* is limited to the southernmost portion of the Florida peninsula and also found in

Puerto Rico and the Bahamas (see Fig. 2.21-F from Chapter 2). *Neocallotillus* is widely

distributed in North and Central America, with one species extending to the West Indies (see Fig.

2.21-L from Chapter 2). *Barrotillus, Callotillus, Neocallotillus* and *Monophylla* were recovered

as closely allied in the analysis (clade 2 in Fig. 3.2). The most common ancestor of this group

could have had a continental origin, with a subsequent migration of some species to insular

areas, while others expanded their geographic range in continental North America.

    Cymatoderella is widely distributed throughout United States, Mexico and northern Central

America (see Fig. 2.21-C from Chapter 2). The group is distinguishable from *Cymatodera* only

by its relatively small eyes and reduced ommatidial diameter. These characters are shared with

remaining basal groups in the New World Tillinae lineage and are also found in many Old World

Tillinae. Evans (1980) mentioned that adaptive forces are most obviously reflected by structures

(or organs) that are of immediate importance for survival, rather than other structures with no

immediate survival repercussions to the species, and compound eye *gestalt* would be such a

structure. Nocturnal behavior probably emerged independently in a number of tillinids, with

many *Cymatodera* species in the New World possessing large eyes and enlarged ommatidia.

Morphological examination and the current geographic distribution of the species composing *Cymatoderella* indicates that the group is closely related *Cymatodera* (clades 4 and 5). The phylogenetic position of *Cymatoderella*, recovered as sister to *Cymatodera* and related groups, is tentatively only, as it is hypothesized that this genus is closely allied to the *aegra-werneri* group.

Within *Cymatodera*, the *tricolor* and *hopei – horni* species-groups were recovered as basal lineages in clades 4 and 5, respectively (Fig. 3.2). Species in these groups have a predominantly Nearctic distribution while species recovered as more derived, such as those in the *hoegei - guatemalensis* group, have a distribution almost exclusively limited to the Neotropics. Interestingly, the *hoegei – guatemalensis* group is particularly speciose in central and southern Mexico as well as Central America, with some species in the group extending to South America. Species groups with an intermediate position in the topology (*oaxaca*, *aegra – werneri* and *floridana – depauperata* groups) are represented by species distributed from the central, south and southwestern USA to Central America. The *oaxaca* species-group is restricted to Mexico; species in the *agegra – weneri* are found mostly in the southwest USA and north Mexico; and the *floridana – depauperata* group is more uniformly distributed throughout North and Central America.

Based on the locality data obtained from specimens of *Cymatodera* and related taxa examined and their phylogenetic position, it is hypothesized that species recovered as derived taxa (Fig. 3.2) entered South America after the emergence of the Isthmus of Panama 12-15 million years ago (Bacon et al., 2015; Montes et al., 2015; O'Dea et al., 2016), during the great American biotic interchange. New World tillinids, and particularly *Cymatodera* and related taxa,

have succeeded in arid, semiarid, sub-tropical, and temperate and sub-temperate mid and high-altitude mountainous environments, where xeric scrublands, thorny forests, coniferous sub-tropical to temperate forests, and mixed pine-broadleaved forests predominate (Opitz, 2010; Burke et al., 2015; Rifkind, 2015). The number of *Cymatodera* species inhabiting tropical habitats is markedly small. Xeric scrublands, thorny forests and coniferous sub-tropical to temperate forests become less common moving south, and are replaced by more tropical settings. Simpson and Neff (1985) indicate that the tropical flora found in Central America and southern Mexico derives from southern elements. The migration of this tropical flora to North America occurred shortly after the closure of the Panamanian seaway. This is supported by the fact that many genera and species found in the Panamanian and Costa Rican tropical forests are species-rich in the tropical regions of South America, where they originated (Graham, 1973). Simpson and Neff (1985) point out that, in combination with this floral migration, a number of pollinators common in the Amazonian rain forests moved northward, accompanying their natural plants migrants. It is hypothesized that as more suitable prey items colonized Central America, predatory invertebrates, such as New World tillinids, could have colonized and thrived in these new habitats. Tillinids inhabiting sub-tropical and tropical environments were recovered as more derived taxa, while those occupying more arid, semiarid and sub-temperate environments were found to be part of basal lineages. Lineages recovered in the phylogeny at an intermediate position are predominately found in sub-tropical to sub-temperate mountainous environments. These findings may indicate that New World tillinids originated in a Nearctic environment and subsequently moved southward, and eventually began to occupy various Neotropical habitats, including sub-tropical mountainous environments, and eventually entering north and northwestern South America in recent geological time.

5. Conclusions

Results from the morphology-based phylogenetic analysis of the New World Tillinae support the subfamily as a monophyletic group. It is uncertain whether Tillinae represents the sister group of remaining clerids (Gunter *et al*. 2013), or if it is a derived clade closely related to Clerinae and Hydnocerynae, with Thaneroclerinae the most basal group of the clerid lineage (Kolibáč, 1997; Opitz, 2010). The results obtained here partially support Kolibáč's and Opitz's findings. Moreover, the taxon sampling outside of Tillinae was limited. Hence, the conclusions should be tested against a molecular-based analysis, and a partitioned molecular-morphological analysis (see Chapter 4). Despite low intraspecific resolution, the use of a Bayesian approach implementing the Mk1 modeling of substitution for morphological data was tested and provided additional support for the monophyly of the Tillinae.

The results indicate that the genera *Barrotillus, Callotillus*, *Monophylla, Neocallotillus* and *Onochotillus* are basal groups in the New World Tillinae lineage, these taxa are more closely related to Old World tillinids included in the analysis, taxa that, in turn, were recovered as the most basal lineages in the phylogeny of the Tillinae. The parsimony analysis recovered *Cymatoderella* as sister to the species-rich *Cymatodera* lineage, a result that was inconclusive in the Bayesian analysis (fig. 3.3). This result could indicate the genus is closely related to the *aegra-werneri* group (Fig. 3.2). *Cymatodera sensu stricto* was recovered as a paraphyletic group. *Cymatodera*, together with the lesser and closely allied *Araeodontia, Bogcia* and *Lecontella*, comprised a monophyletic group. Species-groups for the large *Cymatodera* are proposed for the first time. These groups are morphologically supported and were recovered with moderate to high bootstrap values. A number of clades were composed of species without clear

morphological similarities; as a result, these clades were not proposed as species-groups. The addition of more taxa may change the phylogenetic position of these taxa or increase resolution.

Geographic data obtained from collecting localities indicates high species-richness in the southwestern USA and Mexico, with a less diversity southward, with only three species recorded from South America. The *Cymatodera* lineage probably originated somewhere in southwest USA or northern Mexico and eventually moved to south Mexico and Central America before the closure of the Panamanian seaway, and into the eastern USA separately. *Cymatodera* species richness in south Mexico and Central America may indicate a rapid radiation of species due to the appearance of various groups of prey that entered Central America during the emergence of the Panamanian isthmus and subsequently moved northward. *Cymatodera* entered South America in a recent geological time, after the closure of the Panamanian Isthmus, 12-15 million years ago. This may explain the reduced number of *Cymatodera* species found in South America.

The findings obtained in the analysis should be corroborated with a molecular-based phylogenetic analysis.

6. References

Barr, W. F. (1962) A key to the genera and a classification of the North American Cleridae (Coleoptera) The Coleopterists Bulletin 16: 121-127.

Barr, W. F. (1972) New species of North American *Cymatodera* (Coleopteran: Cleridae). Entomologische Arbeiten Aus Dem Museum G. Frey 787: 1-32.

Bacon, C. D., D. Silvestro, C. Jaramillo, B. T. Smith, P. Chakrabarty and A. Antonelli (2015) Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proceedings of National Academy of Sciences 112: 6110–6115.

Bernhard, D., I. Rivera, A. Komarek, and R. G. Beutel (2009) Phylogenetic analysis of Hydrophiloidea (Coleoptera: Polyphaga) based on molecular data and morphological characters of adults and immature stages. Insect Systematics & Evolution 40 (2009) 3–41.

Bochkov, A. V. and S. V. Mironov (2011) Phylogeny and systematics of mammal-associated psoroptidian mites (Acariformes: Astigmata : Psoroptidia) derived from external morphology. Invertebrate Systematics 25(1) 22-59.

Böving, A. G. and F. C. Craighead (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana (n. s.) 11(1930): 1-351.

Burke, A. F. (2013) Six new species of *Cymatodera* from Mexico and Central America and the retention of *Cymatodera obliquefasciata* as a valid name (Coleoptera: Cleridae). ZooKeys 299: 49-75.

Burke, A. F. and G. Zolnerowich (2014) Four new species of *Cymatodera* Gray from Mexico.
Zookeys 387: 33-49.

Burke, A. F., J. M. Leavengood Jr. and G. Zolnerowich (2015) A checklist of the New World
species of Tillinae (Coleoptera: Cleridae), with an illustrated key to genera and new
country records. Zootaxa 4059(1): 1–39.

Burke, A .F. and G. Zolnerowich (2016) Taxonomic revision of the New World genus *Callotillus*
Wolcott (Cleridae, Tillinae), with the description of the new genus *Neocallotillus*, and an
illustrated key of identification to species. ZooKeys 617: 65–89.

De Zayas, F. (1988) Orden Coleoptera. Separata Descripción de Nuevas Especies. *In*
Entomofauna Cubana. Editorial Científico-Técnica. La Habana, Cuba.

Chapin, E. A. (1924) Classification of the Philippine components of the coleopterous family
Cleridae. The Philippine journal of Science 25: 159-286, 5 pls.

Corporaal, J. B. (1950) Coleopterorum Catalogus, Supplementa. Pars 2: Cleridae. W. Junk,
Gravenhage.

Crowson, R. A. (1955) The natural classification of the families of Coleoptera. Nathaniel Lloyd
& C. Ltd., London.

Crowson, R. A. (1964) A review of the Classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types. The transactions of the Royal Entomological Society of London 116: 275-327.

Ekis, G. (1977) Classification, phylogeny and zoogeography of the genus *Perylipus* (Coleoptera: Cleridae). Smithsonian Contributions to Zoology 227.

Gahan, C. J. (1910) Notes on Cleridae and descriptions of some new genera and species of this family of Coleoptera. Annals and Magazine of Natural History 5: 55-79.

Gerstmeier, R. (2000) Aktueller Stand der Buntkäfer-Forschung (Coleoptera, Cleridae, Thanerocleridae). Entomologica Basiliensa 22, 169-179.

Graham, A. (1973) History of the arborescent temperate element in the northern Latin American biota, in Vegetation and Vegetation History of Northern Latin America. A. Graham (ed.), pp. 301-314, Elsevier, New York.

Gunter, N. L., J. M Leavengood., J. S. Bartlett, E. G. Chapman and S. L. Cameron (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera; Cleridae). Systematic Entomology 38(3): 626-636.

Hartley, D. J., M. J. Koivula, R. H. Spence, R. Pelletier and G. E. Ball (2007) Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. Ecography 30: 673-684.

Huelsenbeck, J. P. and F. Ronquist (2001) MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754-755.

Hunt, T., Bergsten, J., Levkanicova, J., Papadopoulou, A., St. John, O., Wild, R., Hammond, P. R., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. y Vogler, A. P. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science 318: 1913-1916.

Kits, J. H., S. A. Marshall and J. H. Skevington (2013) Phylogeny of the Archiborborinae (Diptera: Sphaeroceridae) Based on combined morphological and molecular analysis. PLoS ONE 8(1): e51190. doi:10.1371/journal.pone.0051190

Klaczko, J., G. G. Montingelli and H. Zaher (2014) A combined morphological and molecular phylogeny of the genus *Chironius* Fitzinger, 1826 (Serpentes: Colubridae). Zool J Linn Soc. 171: 656–667. doi:10.1111/zoj.12147

Kolibáč, J. (1992) Revision of Thanerocleridae N. Stat. (Coleoptera, Cleridae). Mitteilungen der Schweizerischen Entomologischen Gesellschafat 65: 303-340.

Kolibáč, J. (1997) Classification of the subfamilies of Cleridae (Coleoptera: Cleroidae). Acta
Musei Moraviae Scientiae Naturales 81: 307-361.

Kolibáč J. (1998) Classification of the subfamily Hydnocerinae Spinola, 1844 (Coleoptera:
Cleridae). Acta Musei Moraviae, Scientiae biologicae, 83: 127–210.

Kolibáč, J. (2004) Metaxinidae fam. nov., a new family of Cleroidea (Coleoptera). Entomologica
Basiliensia, 26: 239–268.

Lacordaire, T. (1857) Famille XLI. Clérides. Historie Naturalle des insectes. Genera des
Coléoptéres: ou exposéméthodique et critique de tous les Genres proposés jusque 'ici dans
cet ordre d'insectes, Vol. Tome IV, pp 415-496. Libraire Encyclopédique de Roret, Paris.

Lawrence, J. F. and R. A. B. Leschen (2010) Melyridae. Handbook of Zoology, Coleoptera,
Beetle, Morphology and Systematics, Vol. 2: Handbook of Zoology (ed. by R. A. B.
Leschen, R. G. Beutel and J. F. Lawrence), pp. 237-280. Walter de Gruyter, Berlin.

Lawrence, J. F., S. A. Slipinski, A. E. Seago, M. K. Thayer, A. F. Newton and A. E. Marvaldi
(2011) Phylogeny of the Coleoptera based on morphological characters of adults and larva.
Annales Zoologici (Warzawa) 61: 1-217.

Leschen, R. A. B. (2010) Cleroidea. Handbook of Zoology, Coleoptera, Beetles. Morphology and Systematics, Vol. 2: Handbook of Zoology (ed. by R. A. B. Leschen, R. G. Beutel and J. F. Lawrence), pp. 237-280. Walter de Gruyter, Berlin.

Lewis, P. O. (2001) A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. Systematic Biology 50: 6.

Liebherr, J. K. (1988) Brachyptery and phyletic size increase in Carabidae (Coleoptera). Annals of the Entomological Society of America 81(2): 151-159.

Maddison, W. P. and Maddison D. R. (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75 http://mesquiteproject.org

Majer, K. (1994) A review of the classification of the Melyridae and related families (Coleoptera: Cleroidea). Entomologica Basiliensia 17: 319-390.

Marshall, D. C., C. Simon and T. R. Buckley (2006) Accurate branch length estimation in partitioned Bayesina analysis requires accommodation of among-partition rate variation and attention to branch length priors. Systematic Biology 55: 993.

Mlambo, S, C. L. Sole and C. H. Scholtz (2012) Phylogeny of the African ball-rolling dung beetle genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). Invertebrate Systematics 25(3): 197-207.

Montes, C., A. Cardona, C. Jaramillo, A. Pardo, J. C. Silva, V. Valencia, C. Ayala, L. C. Pérez-Angel, L. A. Rodriguez-Parra, V. Ramirez, and H. Niño (2015) Middle Miocene closure of the Central American Seaway. Science 348: 226–229.

O'Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O. Aguilera, M. P. Aubry, W. A. Berggren, A. F. Budd, M. A. Cozzuol, S. E. Coppard, H. Duque-Caro, S. Finnegan, G. M. Gasparini, E. L. Grossman, K. G. Johnson, L. D. Keigwin, N. Knowlton, E. G. Leigh, J. S. Leonard-Pingel, P. B. Marko, N. D. Pyenson, P. G. Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Todd, G. J. Vermeij, and J. B. C. Jackson (2016) Formation of the Isthmus of Panama. Science advances 2(8): 1-12.

Opitz, W. (1997) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part I. The genera of Epiphloeinae. *Insecta Mundi* 11(1): 51-96.

Opitz, W. (2004) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part II. The genera *Caetophloeus* Opitz and *Plocamocera* Spinola. Bulletin of the American Museum of Natural History 280: 1-82.

Opitz, W. (2005) Classification, natural history, and evolution of the genus Aphelocerus Kirsch (Coleoptera: Cleridae: Clerinae). Bulletin of the American Museum of Natural History 293: 1-128.

Opitz, W. (2006) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part III. The genera *Parvochaetus* n. gen., *Amboakis* n. gen. and *Ellipotom*a Spinola. Insecta Mundi 20(3-4): 97-164.

Opitz, W. (2007) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part IV. The genera Pyticeroides Kuwert and Diapromeces Opitz. Entomologica Basiliensia et Collectionis *Frey* 29: 77-166.

Opitz, W. (2008a) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part V. Decorosa Opitz, a new genus of checkered beetles from Hispaniola with description of its four new species. American Museum Novitates 3628: 1-29.

Opitz, W. (2008b) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part VI. The genera *Epiphlaeus* Spinoal and *Opitzius* Barr. Annales Zologici 58(1): 1-34.

Opitz, W. (2008c) Classification, natural history, and evolution of the Epiphloeinae (Coleoptera Cleridae) Part VII. The genera *Hapsidopteris* Opitz, *Iontoclerus* Opitz, *Katamyurus* Opitz, *Megatrachys* Opitz, *Opitzia* Nemésio, *Pennasolis* Opitz, new genus, *Pericales* Opitz, new genus, *Pteroferus* Opitz, new genus, and *Turbophloeous* Opitz, new genus. Zootaxa 1754: 1-40.

Opitz, W. (2009) Classification, natural history, and evolution of the Neorthopleurinae Opitz, new subfamily (Coleoptera Cleridae) Part I. Generic composition of the subfamily and key to genera. Entomologica Basiliensia Frey 31: 135-207.

Opitz, W. (2010) Classification, natural history, phylogeny and subfamily composition of the Cleridae and generic content of the subfamilies (Coleoptera, Cleridae). Entomologica Basiliensia et *Collectionis Frey* 32: 31–128.

Rifkind, J. (1993a) A new species of *Cymatodera* from Oaxaca, Mexico (Coleoptera: Cleridae) The Coleopterists Bulleti*n* 47(1): 83-88.

Rifkind, J. (1993b) A new species of *Cymatoderella* Barr (Coleoptera: Cleridae) from Mexico and Central America, with a key and distribution data for the genus. The Coleopterists Bulletin 47(3): 279-284.

Rifkind, J. (1996) A new genus and species of checkered beetle from Honduras with additions to the Honduran Fauna. Contributions in Science 461: 1-10.

Rifkind, J. (2006) Stridulation in *Cymatodera* Gray, 1832 (Coleoptera: Cleridae). The Pan-Pacific Entomologist 82(2): 258-261.

Rifkind, J. (2015) New species of *Cymatodera* Gray (Coleoptera: Cleridae: Tillinae) from México and Central America, with notes on others. Zootaxa 3946(4): 519-552.

Rifkind, J., V. H. Toledo, and A. M. Corona (2010) New species of Cleridae (Coleoptera) from
Morelos, Mexico. Zootaxa 2659: 53-59.

Ruhfel, B. R., P. F. Stevens and C. C. Davis (2013) Combined morphological and molecular
phylogeny of the Clusioid clade (malpighiales) and the placement of the ancient Rosid
macrofossil paleoclusia. Int. J. Plant Sci. 174(6): 910-936. DOI: 10.1086/670668

Schenkling, S. (1903). Coleptera. Malacodermata. Fam. Cleridae. Genere Insectorum (Wytsman
Brussels) 13: 1-124.

Schenkling, S. (1910) Pars. 23. Cleridae. Coleopterum Catalogus (ed. by S Schenkling). W.
Junk, Berlin.

Simpson, B. B. and J. L. Neff (1985) Plants, their pollinating bees, and the great American
interchange. *In* The Great American Biotic Interchange. F. G. Stehli and S. D. Webb *(eds.)*
pp. 427-449. Plenum Press, New York.

Spinola, M. (1841) Monographie des Térédiles. Revue Zoologique par La Societé Cuvierienne 4:
70-76.

Spinola, M. (1844) Essai monographique sur les Clérites. Insectes Coléoptéres. Imprimerioe de
fréres Ponthenier. Genes.

Swofford, D. L. (2002) PAUP V 4.08 b10. Phylogenetic Analysis Using Parsimony (and other methods). Sinauer, Sunderland, MA, USA.

Udvardy, M. D. F. (1975) A classification of the biogeographical provinces of the world. IUCN Occasional Paper no. 18. Morges, Switzerland: IUCN.

Wiens, J. J., J. B Fetzner, Jr., C. L. Parkinson, and W. Tod (2005) Hylid Frog Phylogeny and Sampling Strategies for Speciose Clades. Systematic Biology 54(5): 778-807

Winkler, J. R. (1964) A revision of the genus *Dieropsis* Gahan, 1908, type of a new subfamily Dieropsinae n. subf. (Coleoptera: Cleridae). Acta Universitatis Carolinae – Biologica, 1964: 305-329.

Winkler, J. R. (1980) A revision of the subfamily Cleropiestinae subf. n. Acta Universitatis Carolinae – Biologica 1978: 437-456.

Zalewski, M. and W. Ulrich, (2006) Dispersal as a key element of community structure: the case of ground beetles on lake islands. Diversity Distribution 12: 767-775.

Table 3.1 New World tillinid species per genus, number of species per genus used in the analysis.

Genus	Total number of species described*	Species covered in the analysis	% species covered in the analysis
Araeodontia	5	3	100%
Barrotillus	1	1	100%
Bogcia	1	1	100%
Bostrichoclerus	1	0	0%
Callotillus	2	2	100%
*Cylidrus***	1	0	0%
Cymatodera	~130	44	~30%
Cymatoderella	3	3	100%
Lecontella	3	3	100%
Monophylla	5	3	60%
Neocallotillus	3	2	67%
Onychotillus	5	2	40%
TOTAL	**157**	**64**	**40%**

* Figure obtained from all revised material loaned from collections mentioned in the text, Corporaal 1950, the updated Barr unpublished checklist (1979), and subsequent descriptive works of Rifkind (1993*a*, 1993*b*, 1996), Rifkind *et al.* (2010), Burke (2013), Burke & Zolnerowich, 2014 and Burke et al. (2015).
** Distribution of *Cylidrus* was discussed in Chapter 2.

Table 3.2 Morphological characters and states used in the phylogenetic analysis of the New World Tillinae. Characters in italics were excluded from the analysis because they were parsimony-uninformative.

HEAD:

1. Postgular plate or postgular process: 0, present (Fig. 3.8-A); 1, absent (Fig. 3.8-B)

2. Head measured across eyes: 0, not wider than pronotum (Figs. 3.4-E, 3.5-A, 3.5-B); 1, as wide or wider than pronotum (Figs. 3.4-A, 3.4-F, 3.6-D, 3.7-F)

3. Eyes: Eyes: 0, height less than two times their width (Fig. 3.9-C); 1, height at least two times their width (Fig. 3.9 B, D)

4. Frons of male: 0, not impressed; 1, bi-impressed

5. Clypeus: 0, not emarginate; 1, emarginate

6. Eyes: 0, not protuberant (Figs. 3.4-C, 3.14-C); 1, protuberant (Figs. 3.10 A, B, 3.13 A, D)

7. Anterior eye emargination: 0, absent (Fig. 3.10-C); 1, present (Fig. 3.10 A, B)

8. Eyes: 0, finely faceted (Fig. 3.9-A); 1, strongly faceted (Fig. 3.9-C, 3.10-D)

9. Antennal club: 0, symmetrical (Fig. 3.15-A); 1, asymmetrical (Fig. 3.15-B); 2, absent (Fig. 3.15-C)

10. Scape: 0, short, less than half the length of horizontal eye width (Fig. 3.15-F); 1, elongate, at least half the length of horizontal eye width (Fig. 3.9-C, 3.10-D)

11. Antennal sockets: 0, separated from eyes by less than 0.5 times the horizontal diameter of eye (Fig. 3.10-A); 1, separated from eye by at least 0.5 times the horizontal diameter of eye (Fig. 3.10-B)

12. Last antennomere of male: 0, shorter than the length of two previous antennomeres (Fig. 3.15-C) 3.15-E); 1, at least as long as the length of two previous antennomeres (Fig. 315-D, 3.15-G)

13. Antenna: 0, composed of 11 antennomeres (Fig. 3.15-D, 3.15-E); 1, composed of 10 antennomeres (Fig. 3.15-F)

14. Funicles: 0, tightly articulated (Fig. 3.15-G); 1, loosely articulated (Fig. 3.15-C)

15. *Mandibular denticle: 0, present; 1, absent*

16. Mesal prosternal length: 0, at least the length of procoxal cavity Fig (3.11-C-1); 1, less than the length of procoxal cavity Fig. (3.11-B-1)

17. Antenna of male: 0, do not extend beyond posterior margin of pronotum (Fig. 3.4-F, 3.5 A, B, 3.6-E); 1, extending beyond posterior margin of pronotum (Fig. 3.5-D, 3.6 A, C)

18. Protibia: 0, armed with two spurs; 1, armed with one spur; 2, unarmed

19. Mesotibia: 0, armed with two spurs; 1, armed with one spur; 2, unarmed

20. Metatibia: 0, armed with two spurs; 1, armed with one spur; 2, unarmed

21. Protarsal claw: 0, with two denticles (Fig. 3.12-B), 1, with one denticle; 2, without denticles (Fig. 3.11-E, 3.13-E)

22. Interior protarsal claw: 0, joined to denticle (Fig. 3.12-A); 1, separated from denticle (Fig. 3.12-B)

23. Basal denticle of protarsal claw: 0, triangular with margins straight (Fig. 3.12 A, B); 1, triangular with margins procurved; 2, digitiform (see Fig. 2.6 from Chapter 2)

24. Protarsal pulvilli: 0, absent (Fig 3.13-E); 1, present (Fig. 3.13-F)

25. Protarsus: 0, without pulvillus; 1, with two pulvilli; 2, with three pulvilli; 3, with four pulvilli

26. Mesotarsus: 0, without pulvillus; 1, with two pulvilli; 2, with three pulvilli; 3, with four pulvilli

27. Metatarsus: 0, without pulvillus; 1, with two pulvilli; 2, with three pulvilli; 3, with four pulvilli

28. Fourth protarsomere: 0, not reduced (Figs. 3.11-D, 3.13-F); 1, reduced (Fig. 3.11-E-1)

29. Fourth protarsomere with fourth pulvillus: 0, not incised (Fig. 3.15-H-1); 1, incised (Fig. 3.15-I-1)

30. Tarsal formula: 0, 5-5-5; 1, 5-5-4

31. Terminal labial palp: 0, cylindrical (Fig. 3.13-C-2); 1, subsecuriform (Fig. 3.13-B); 2, securiform (Fig. 3.13-A)

32. Terminal maxillary palp: 0, cylindrical (Fig. 3.13-C-1); 1, subsecuriform (Fig. 3.13-D); 2, securiform (Fig. 3.13-B)

THORAX

33. Anterior coxal cavities: 0, with procryptosternum fused to pronotal extension (Fig. 3.11-B-2); 1, with procryptosternum not fused to pronotal extension (Fig. 3.11-A-2)

34. Pronotum: 0, with subapical sides constricted, narrower than sufrontal sides (Fig. 3.6-A); 1, with subapical sides as broad as subfrontal sides (Fig. 3.6-B)

35. Pronotal trichobotria: 0, absent; 1, present

36. Dorsolateral ridge separating disc from hypomeron: 0, absent (Fig. 3.14-A); 1, incomplete, do not reach base of hypomeron (Fig. 3.14-C); 2, complete, reach base of hypomeron (Fig. 3.14-B)

37. Proepimeron and prosternum: 0, separated at dorsolateral area of procoxa (Fig. 3.14-D); 1, partially separated at dorsolateral area of procoxa but never confluent; 2, confluent at dorsolateral area of procoxa (Fig. 3.14-E)

38. Lateral margin of pronotum in dorsal view: 0, parallel (Fig. 3.16-B); 1, sinuate (Fig. 3.16-A); 2, bisinuate (Fig. 3.16-D); 3, campanulate (Fig. 3.16-C)

39. Pronotum: 0, widest at middle (Fig. 3.6-B); 1, anterior margin of pronotum as wide as middle (Fig. 13.6-D)

40. Anterior transverse depression on pronotal disc: 0, absent (Fig. 3.16-B); 1, present (Fig. 3.16-A)

41. Sub-basal impression on pronotal disc: 0, absent (Fig. 3.16-C); 1; present (Fig. 3.16-D)

42. Posterior portion of proepimerones: 0, fully surrounding procoxal cavities (Fig. 3.11-B, 3.11-C); 1, partially surrounding procoxal cavities (Fig. 3.11-A)

43. Proepimerones behind coxal cavity: 0, present (Fig. 3.11-B); 1, absent (Fig. 3.11-A)

44. Prointercoxal process: 0, complete (Fig. 3.11-B-3); 1, incomplete (Fig. 3.11-A-3)

45. Distal end of prointercoxal process: 0, not expanded laterally Fig. (3.11-A); 1, expanded laterally (Fig. 3.11-B)

46. Prothoracic rest (peduncle): 0, absent (Fig. 3.11-A); 1, present (Fig. 3.11-C-2)

47. Mesosternum: 0, punctate; 1, puncticulate; 2, smooth

48. Longitudinal marking on mesal area of metasternum: 0, absent; 1, present

49. Mesocoxal cavities: 0, not projecting; 1, projecting

50. *Mesosternum: 0, wider than long; 1, as long as wide; 2, longer than wide*

51. Mesocoxal cavities surrounded by: 0, mesosternum and metasternum; 1, mesosternum, mesepimeron and metasternum; 2, mesosternum, mesepisternum, mesepimeron and metasternum

52. Mesotrochantines: 0, exposed; 1, concealed; 2, absent

53. Metasternum: 0, wider than long; 1, longer than wide

54. Metasternum of males: 0, unarmed (Fig. 3.17-A); 1, articulated with a pair of tubercles (Fig. 3.17-B); 2, articulated with a pair of carinae (Fig. 3.17-C)

55. Metasternum: 0, punctate, 1, puncticulate; 2, smooth

56. Longitudinal marking on mesal area of metathorax: 0, not impressed; 1, impressed

57. Metepisternum: 0, visible throughout its length (Fig. 3.17-D); 1, covered by elytron (Fig. 3.17-E)

ELYTRA

58. Elytral ground: 0, glabrous (Fig. 3.4-A); 1, vested (Fig. 3.7-D)

59. Elytral punctations: 0, arranged in regular striae (Fig. 3.18-E); 1, arranged in irregular straie Fig. 3.18-F); 2, absent (Fig. 3.18-A)

60. Elytral disc: 0, without ridges or elevations (Fig. 3.6-B, 3.6-D); 1, with at least one ridge or a pair of elevations (Fig. 3.5-E, 3.6-A)

61. Anterior margin of elytral disc: 0, smooth (Fig. 3.19-C); 1, moderately punctate, interstices at least as broad as punctuation (Fig. 3.19-B); 2, coarsely punctate, interstices narrower than punctuation (Fig. 3.19-A)

62. Lateral margins of male elytra: 0, subparallel (Fig. 3.6-C, 3.7-B, 3.7-C); 1, expanded on second half (Fig. 3.6-E, 3.7 A, E)

63. Punctations on elytral disc: 0, extending to apex (Fig. 3.18-D); 1, extend beyond half but do not reach apex (Fig. 3.18-C); 2, do not extend beyond first half (Fig. 3.18-B)

64. Elytral apices: 0, triangular (Fig. 3.20-C); 1, subquadrate (Fig. 3.20-D); 2, notched (Fig. 3.20-F); 3, rounded (Fig. 3.20-E)

65. Elytral disc: 0, glabrous; 1, with setae of one size; 2, with setae of two sizes; 3, with setae of three sizes

66. Elytral base: 0, with complete transversal carina (Fig. 3.20-B); 1, with incomplete transversal carina (Fig. 3.19-D); 2, without transverse carina (Fig. 3.20-A)

67. Humeri: 0, indicated (Fig. 3.5-A, 3.5-B); 1, not indicated (Fig. 3.7-E)

68. Elytral apices: 0, confluent (Fig. 3.12-C); 1, not confluent (Fig. 3.20-E)

69. Epipleural fold: 0, complete, not narrowing toward apex; 1, gradually narrowing toward apex; 2, incomplete

ABDOMEN

70. Ventrites 1-5: 0, not marked laterally (Fig. 3.18-G); 1, marked laterally (Fig. 3.18-H)

71. Metacoxal cavities; 0, not carinate 1, carinate (Fig. 3.12-D)

72. Ventrites 1-4 of male: 0, with intersegmental membranes absent; 1, with intersegmental membranes in at least one segment but not all; 2, with intersegmental membranes in all segments

73. Fifth visible ventrite of male: 0, not emarginate (Fig. 3.21-C); 1, emarginate (Fig. 3.21-D)

74. Fifth visible ventrite of female: 0, not emarginated (Fig. 3.21-A); 1, emarginated (Fig. 3.21-B)

75. Sixth visible segment of males: 0, not modified, unspecialized (Fig. 3.21-E); 1, modified, specialized (Fig. 3.21-F)

76. Pygidium of male: 0, concealed in dorsal view (Fig. 3.21-A) 1, exposed in dorsal view (Figs. 3.7 D-F, 3.21-B)

77. Wing folding microthrichia: 0, absent in all visible tergites; 1, present in at least one tergite

AEDEAGO

78. *Phallobasic apodema: 0, absent; 1; present* (Fig. 3.23-A, 3.23-C)

79. Phallus with copulatory piece: 0, tapered at apex (Fig. 3.22-A-1, 22-F-1); 1, swollen at apex (Fig. 3.22-B-1); 2, rounded at apex (Fig. 3.23-D-1); 3, blunt at apex (Fig. 3.22-D-1)

80. Phallic plate: 0, armed with a row(s) of denticles (Fig. 3.23-A-1, C-1, D-2); 1, unarmed (Fig. 3.22-E)

81. Intraspicular plate: 0, absent; 1, present, elongate (Fig. 3.23-E-2); 2, present, short, rounded (Fig 3.23-E-1)

82. Phallic spicula: 0, absent (Figs. 3.22-A, 3.23-B); 1, present (Fig. 3.22-C-3)

83. Phallobasic apodeme: 0, not expanded distally (Fig. 3.22-A-3, B-2); 1, expanded distally (Fig. 3.23-C-2)

84. Phallobasic apodeme: 0, long, at least one third length of tegmen (Fig. 3.22-B-3); 1, less than one third length of tegmen (Figs. 3.22-C-1, 3.23-A-2)

85. Phallobase: 0, subparallel (Figs. 3.22-D, 3.23-D); 1, trigonal (Fig. 3.22-A, F); 2, sinuate (Fig. 3.22-E)

86. Parameres: 0, fused (Figs. 3.22-C, 3.23-D); 1, free (Figs. 3.22-A, F, 3.23-B)

87. Tegmen: 0, complete, fully covering phallus (Fig. 3.22-C, 3.23-D); 1, incomplete, partially covering phallus (Figs. 3.22-A, F, 3.23-B)

88. Parameres: 0, pointed anteriorly (Fig. 3.23-B-1); 1, rounded anteriorly (Fig. 3.23-A-3; 2, swollen anteriorly (Fig. 3.22-D-2)

89. Endophallic struts: 0, short, less than the length of tegmen (Fig. 3.22-E-2); 1, long, at least the length of tegmen (Fig. 3.22-F-3)

90. Endophallic struts: 0, in vertical position in relation to tegmen when in horizontal view; 1, in horizontal position in relation to tegmen when in horizontal view

91. Endophallic struts: 0, truncate distally (Fig. 3.22-E-3); 1, slender distally (Fig. 3.22-C-2); 2, robust distally (Fig. 3.23-B-2)

Table 3.3 Character state data-matrix.

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Collops bipunctatus	0	0	0	1	0	1	0	0	2	1	0	0	1	1	0	1	1
Collops quadripunctatus	0	0	0	1	0	1	0	0	2	1	0	0	1	1	0	1	1
Temnoscheila virescens	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Tenebroides sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Chariessa pillosa	1	0	1	0	2	1	1	0	0	1	0	0	0	0	0	1	1
Enoclerus zonatus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	1	0
Enoclerus nigripes	1	0	0	1	2	1	1	0	0	1	0	0	0	0	0	1	0
Madoniella dislocata	1	1	0	0	2	1	1	0	0	1	1	0	1	1	0	1	0
Necrobia rufipes	1	0	0	1	2	1	1	0	0	1	0	0	0	1	1	1	0
Neorthopleura thoracica	1	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	1
Pelonium leucophaeum	1	1	0	1	2	1	1	1	0	1	0	0	0	1	0	1	1
Phyllobaenus humeralis	1	1	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0
Phyllobaenus pallipennis	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0
Placopterus thoracicus	1	0	0	1	2	1	1	0	0	1	0	0	0	0	0	1	0
Priocera castanea	1	0	0	0	1	0	1	0	2	1	0	0	0	1	0	1	0
Trichodes nutalli	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0
Zenodosus sanguineus	1	0	0	0	1	1	0	0	2	1	0	0	0	1	0	1	0
Cylidroctenus chalybaum	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1
Cylidrus fasciatus	1	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0
Gastrocentrum sp.	1	0	0	1	1	1	1	1	2	0	0	0	0	0	0	1	0
Orthocladiscus sp.	1	0	0	0	1	1	1	1	2	0	0	0	0	1	0	1	0
Stenocylidrus dispar	1	1	1	0	2	0	1	0	2	0	0	0	0	1	0	1	0
Strotocera grandis	1	0	0	1	1	1	1	1	2	0	0	0	0	1	0	1	0
Tilloidea transversalis	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	1	0
Araeodontia isabellae	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Araeodontia marginallis	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Araeodontia peninsularis	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Barrotillus kropotkini	1	1	1	0	1	1	1	0	2	0	0	1	0	1	0	0	1
Bogcia disjuncta	1	1	0	1	1	1	0	1	2	1	0	1	0	1	0	1	1
Bogcia oaxacae	1	1	0	1	1	1	0	1	2	1	0	1	0	1	0	1	1
Callotillus bahamensis	1	0	1	0	1	0	1	0	2	1	0	1	1	1	0	1	0
Callotillus eburneocinctus	1	0	1	0	1	0	1	0	2	1	0	1	1	1	0	1	0
Neocallotillus elegans	1	1	0	0	1	1	1	0	2	1	0	1	1	1	0	0	1
Neocallotillus elegans (*elegans*)	1	1	0	0	1	1	1	0	2	1	0	1	1	1	0	0	1
Neocallotillus elegans (*vafer*)	1	1	0	0	1	1	1	0	2	1	0	1	1	1	0	0	1
Neocallotillus intricatus	1	0	1	0	1	0	1	0	2	1	0	1	1	1	0	1	0
Neocallotillus elegans (*intermediate*)	1	0	0	0	1	0	1	0	2	1	0	1	1	1	0	1	1
Cymatodera aegra	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera angulifera	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera antennata	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera balteata	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	0	1
Cymatodera barri	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	0
Cymatodera bicolor	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	0	1
Cymatodera bipunctata	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera californica	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera championi	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera conflagrata	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1

Table 3.3 (continued)

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cymatodera delicatula	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera depauperata	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	0	0
Cymatodera fascifera	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera floridana	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	0	1
Cymatodera fuchsii	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera guatemalensis	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera hoegei	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera hopei	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera horni	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera inornata	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera latefascia	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera limatula	1	1	0	1	1	1	1	1	2	1	0	1	0	1	0	1	1
Cymatodera linsleyi	1	1	1	1	1	1	0	1	2	1	0	0	0	1	0	1	1
Cymatodera marmorata	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera mitchelli	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera neomexicana	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera obliquefasciata	1	1	0	1	1	1	1	1	2	1	0	1	0	1	0	1	1
Cymatodera pallida	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera prolixa	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	0	1
Cymatodera pseudotsuga	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera punctata	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera puncticollis	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera rosalinae	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	0
Cymatodera sallei	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera sericans	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	0
Cymatodera tricolor	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera tuta	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera usta	1	1	0	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera vagemaculata	1	1	0	1	1	1	1	1	2	1	0	1	0	1	0	1	0
Cymatodera ovipennis	1	1	1	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera venusta	1	1	1	1	1	0	1	1	2	1	0	0	0	1	0	1	1
Cymatodera werneri	1	1	0	0	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera xanti	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	1
Cymatodera xaviera	1	1	0	1	1	1	1	1	2	1	0	0	0	1	0	1	0
Cymatoderella collaris	1	1	0	1	1	1	1	0	2	1	0	0	0	1	0	1	1
Cymatoderella morula	1	1	0	1	1	1	1	0	2	1	0	0	0	1	0	1	1
Cymatoderella patagoniae	1	1	0	1	1	1	1	0	2	1	0	0	0	1	0	1	1
Lecontella brunnea	1	1	0	1	1	1	0	1	2	1	0	1	0	0	0	1	1
Lecontella gnara	1	1	0	1	1	1	0	1	2	1	0	1	0	1	0	1	1
Lecontella striatopunctata	1	1	0	1	1	1	0	1	2	1	0	1	0	0	0	1	0
Monophylla californica	1	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1
Monophylla pallipes	1	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1
Monophylla terminata	1	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1
Onychotillus vittatus	1	1	0	1	1	1	1	0	2	1	0	1	0	1	0	1	1
Onychotillus cubana	1	1	0	1	1	1	1	0	2	1	0	1	0	1	0	1	1

Table 3.3 (continued)

Taxon \ Character	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Collops bipunctatus	2	2	2	2	?	?	0	0	0	0	0	?	1	0	0	0	1
Collops quadripunctatus	2	2	2	2	?	?	0	0	0	0	0	?	1	0	0	0	1
Temnoscheila virescens	0	0	0	2	?	?	0	0	0	0	0	?	0	0	0	0	0
Tenebroides sp.	0	0	0	2	?	?	0	0	0	0	0	?	0	0	0	0	0
Chariessa pillosa	2	1	1	2	?	?	1	2	2	2	1	0	0	2	2	0	0
Enoclerus zonatus	1	0	0	1	1	0	1	3	3	3	0	1	0	2	1	0	0
Enoclerus nigripes	1	0	0	1	1	0	1	3	3	3	0	1	0	2	0	0	0
Madoniella dislocata	2	1	1	1	1	0	1	2	2	1	1	0	0	0	0	0	1
Necrobia rufipes	0	0	0	1	0	0	1	2	2	2	1	0	0	0	0	0	0
Neorthopleura thoracica	1	0	0	1	0	0	1	2	2	2	1	0	0	0	0	0	1
Pelonium leucophaeum	2	1	1	2	?	?	1	2	2	2	1	0	0	2	2	0	0
Phyllobaenus humeralis	1	0	0	1	?	?	1	3	3	3	0	0	0	2	0	0	1
Phyllobaenus pallipennis	1	0	0	1	1	0	1	3	3	3	0	0	0	2	0	0	1
Placopterus thoracicus	1	0	0	1	1	0	1	3	3	3	0	1	0	2	0	0	0
Priocera castanea	1	0	0	2	?	?	1	3	3	3	0	0	0	2	0	0	0
Trichodes nutalli	1	0	0	2	?	?	1	3	3	3	0	1	0	2	1	0	0
Zenodosus sanguineus	0	0	0	2	0	0	1	0	0	0	1	0	0	1	1	0	0
Cylidroctenus chalybaum	0	0	0	2	1	0	1	3	3	3	0	1	0	2	0	1	0
Cylidrus fasciatus	0	0	0	2	1	0	1	3	3	3	0	1	0	1	0	1	1
Gastrocentrum sp.	2	0	0	1	1	1	1	3	3	3	0	1	0	2	1	1	0
Orthocladiscus sp.	0	0	0	1	1	1	1	3	3	3	0	0	0	2	0	1	0
Stenocylidrus dispar	0	0	0	1	1	0	1	3	3	3	0	1	0	1	1	1	0
Strotocera grandis	0	0	0	1	1	1	1	3	3	3	0	1	0	2	0	1	0
Araeodontia marginallis	0	0	0	0	1	2	1	3	3	3	0	1	0	2	0	1	0
Araeodontia peninsularis	0	0	0	0	1	2	1	3	3	3	0	1	0	2	0	1	0
Barrotillus kropotkini	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Bogcia disjuncta	0	0	0	0	0	0	1	3	3	3	0	1	0	2	0	1	0
Bogcia oaxacae	0	0	0	0	0	0	1	3	3	3	0	1	0	2	0	1	0
Callotillus bahamensis	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Callotillus eburneocinctus	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Neocallotillus elegans	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Neocallotillus elegans (*elegans*)	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Neocallotillus elegans (*vafer*)	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Neocallotillus intricatus	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Neocallotillus elegans (intermediate)	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera aegra	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera angulifera	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera antennata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera balteata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera barri	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera bicolor	0	0	0	0	1	0	1	3	3	3	0	0	0	2	0	1	0
Cymatodera bipunctata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera californica	0	0	0	0	1	0	1	3	3	3	0	0	0	2	0	1	0
Cymatodera championi	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera conflagrata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera delicatula	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera depauperata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera fascifera	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0

Table 3.3 (continued)

Taxon \ Character	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Cymatodera floridana	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera fuchsii	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera guatemalensis	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera hoegei	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera hopei	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera horni	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera inornata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera latefascia	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera limatula	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera linsleyi	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera marmorata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera mitchelli	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera neomexicana	0	0	0	0	1	0	1	3	3	3	0	0	0	2	0	1	0
Cymatodera obliquefasciata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera pallida	0	0	0	0	1	0	1	3	3	3	0	0	0	2	0	1	0
Cymatodera prolixa	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera pseudotsuga	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera punctata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera puncticollis	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera rosalinae	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera sallei	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera sericans	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	1
Cymatodera tricolor	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera tuta	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera usta	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera vagemaculata	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	1
Cymatodera ovipennis	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera venusta	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera werneri	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera xanti	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatodera xaviera	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Cymatoderella collaris	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	1
Cymatoderella morula	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	1
Cymatoderella patagoniae	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Lecontella brunnea	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Lecontella gnara	0	0	0	0	1	0	1	3	3	3	0	1	0	2	0	1	0
Lecontella striatopunctata	0	0	0	0	1	1	1	3	3	3	0	1	0	2	0	1	0
Monophylla californica	0	0	0	0	1	0	1	1	3	3	0	1	0	2	0	1	0
Monophylla pallipes	0	0	0	0	1	0	1	1	3	3	0	1	0	2	0	1	0
Monophylla terminata	0	0	0	0	1	0	1	1	3	3	0	1	0	2	0	1	0
Onychotillus vittatus	0	0	0	1	1	0	1	3	3	3	0	1	0	2	0	1	1
Onychotillus cubana	0	0	0	1	1	0	1	3	3	3	0	1	0	2	0	1	1

Taxon \ Character	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Collops bipunctatus	0	2	1	1	0	0	0	1	1	0	0	1	0	0	1	0	1
Collops quadripunctatus	0	2	1	1	0	0	0	1	1	0	0	1	0	0	1	0	1
Temnoscheila virescens	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 3.3 (continued)

Taxon \ Character	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Tenebroides sp.	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Chariessa pillosa	0	1	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1
Enoclerus zonatus	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	0
Enoclerus nigripes	0	0	0	1	1	1	0	1	1	1	0	0	0	1	1	0	0
Madoniella dislocata	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1
Necrobia rufipes	0	2	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1
Neorthopleura thoracica	1	2	0	0	1	0	0	1	1	1	0	0	2	2	1	0	0
Pelonium leucophaeum	0	2	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1
Phyllobaenus humeralis	0	0	1	1	0	1	0	1	1	1	0	0	0	2	1	0	2
Phyllobaenus pallipennis	0	0	1	1	0	1	0	1	1	1	0	0	0	1	1	0	2
Placopterus thoracicus	0	0	0	1	0	1	0	1	1	1	0	0	2	0	1	0	1
Priocera castanea	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0	1
Trichodes nutalli	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	1
Zenodosus sanguineus	0	2	0	3	1	0	0	1	1	1	1	0	0	0	1	0	0
Cylidroctenus chalybaum	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0	2
Cylidrus fasciatus	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	2
Gastrocentrum sp.	0	0	0	2	1	1	0	1	1	0	0	1	0	1	1	0	1
Orthocladiscus sp.	0	0	0	3	1	1	1	0	1	0	0	0	0	1	1	0	1
Stenocylidrus dispar	0	0	2	1	0	0	1	0	0	0	0	1	1	1	1	0	1
Strotocera grandis	0	0	0	2	0	0	1	0	1	0	1	1	0	1	1	0	1
Tilloidea transversalis	0	0	0	1	0	0	0	1	1	0	1	0	0	1	1	0	1
Araeodontia isabellae	0	0	0	2	1	1	0	1	0	0	1	1	0	1	1	0	0
Araeodontia marginallis	0	0	0	2	1	1	0	1	0	0	1	1	1	1	1	2	0
Araeodontia peninsularis	0	0	0	2	1	1	0	1	0	0	1	1	1	1	1	0	0
Barrotillus kropotkini	0	0	1	3	1	0	0	1	1	0	1	1	0	0	1	0	0
Bogcia disjuncta	0	0	0	2	1	1	0	0	0	0	1	1	0	1	1	0	0
Bogcia oaxacae	0	0	0	2	1	1	0	0	0	0	1	1	0	1	1	0	0
Callotillus bahamensis	0	0	1	3	1	0	0	1	1	0	1	1	1	1	1	0	0
Callotillus eburneocinctus	0	0	1	3	1	0	1	1	1	0	1	1	1	1	1	0	0
Neocallotillus elegans	0	0	1	3	1	0	0	1	1	0	1	1	0	1	1	0	0
Neocallotillus elegans (*elegans*)	0	0	1	3	1	0	0	1	1	0	1	1	0	1	1	0	0
Neocallotillus elegans (*vafer*)	0	0	1	3	1	0	0	1	1	0	1	1	0	1	1	0	0
Neocallotillus intricatus	0	0	1	3	1	0	0	1	1	0	1	1	0	1	1	0	0
Neocallotillus elegans (intermediate)	0	0	1	3	0	0	0	1	1	0	1	1	0	1	1	0	0
Cymatodera aegra	0	0	1	2	0	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera angulifera	0	0	0	2	1	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera antennata	0	0	1	2	1	0	0	0	0	0	1	1	0	1	1	0	0
Cymatodera balteata	0	0	1	2	0	1	0	0	0	0	1	1	0	2	1	0	0
Cymatodera barri	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera bicolor	0	0	1	2	0	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera bipunctata	0	0	0	2	1	0	0	0	0	0	1	1	1	1	1	0	0
Cymatodera californica	0	0	0	2	1	0	0	0	0	0	1	1	0	1	1	0	0
Cymatodera championi	0	0	1	2	1	1	1	0	0	0	1	1	1	2	1	0	0
Cymatodera conflagrata	0	0	1	2	0	1	1	0	0	0	1	1	0	11	1	0	0
Cymatodera delicatula	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera depauperata	0	0	1	2	0	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera fascifera	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera floridana	0	0	2	2	0	1	1	0	0	0	1	1	1	1	1	0	0

Table 3.3 (continued)

Taxon \ Character	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Cymatodera fuchsii	0	0	1	2	0	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera guatemalensis	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera hoegei	0	0	0	2	1	0	1	0	0	0	1	1	0	2	1	0	0
Cymatodera hopei	0	0	0	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera horni	0	0	0	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera inornata	0	0	0	2	0	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera latefascia	0	0	0	2	0	0	0	0	0	0	1	1	0	1	1	0	0
Cymatodera limatula	0	0	0	2	1	1	0	0	0	0	1	1	0	1	1	0	0
Cymatodera linsleyi	0	0	0	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera marmorata	0	0	0	2	0	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera mitchelli	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera neomexicana	0	0	1	2	0	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera obliquefasciata	0	0	0	2	1	1	0	0	0	0	1	1	0	1	1	0	0
Cymatodera pallida	0	0	1	2	1	1	1	0	0	0	1	1	0	1	1	0	0
Cymatodera prolixa	0	0	1	2	0	1	1	0	0	0	1	1	1	1	1	0	0
Cymatodera pseudotsuga	0	0	0	2	0	0	0	0	0	0	1	1	0	1	1	0	0
Cymatodera punctata	0	0	1	2	0	0	1	0	0	0	1	1	0	1	1	0	0
Cymatodera puncticollis	0	0	1	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera rosalinae	0	0	1	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera sallei	0	0	1	2	1	1	1	0	0	0	1	1	1	2	1	0	0
Cymatodera sericans	0	0	0	2	1	1	0	0	0	0	1	1	1	1	1	0	0
Cymatodera tricolor	0	0	1	2	1	0	1	0	0	0	1	1	0	1	1	0	0
Cymatodera tuta	0	0	1	2	0	0	0	0	0	0	1	1	0	1	1	0	0
Cymatodera usta	0	0	1	2	1	1	1	0	0	0	1	1	0	2	1	0	0
Cymatodera vagemaculata	0	0	1	2	1	0	0	0	0	0	1	1	1	1	1	0	0
Cymatodera ovipennis	0	0	1	2	1	0	1	0	0	0	1	1	0	2	1	0	0
Cymatodera venusta	0	0	1	2	1	1	1	0	0	0	1	1	1	1	1	0	0
Cymatodera werneri	0	0	1	2	1	0	1	0	0	0	1	1	0	1	1	0	0
Cymatodera xanti	0	0	1	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatodera xaviera	0	0	1	2	1	0	0	0	0	0	1	1	0	2	1	0	0
Cymatoderella collaris	0	0	0	2	0	0	0	1	0	0	1	1	0	1	1	0	0
Cymatoderella morula	0	0	0	2	0	0	0	1	0	0	1	1	0	1	1	0	0
Cymatoderella patagoniae	0	0	0	2	0	0	0	1	0	0	1	1	0	1	1	0	0
Lecontella brunnea	0	0	0	2	0	0	1	0	0	0	1	1	0	1	1	0	0
Lecontella gnara	0	0	0	2	1	0	1	0	0	0	1	1	0	1	1	0	0
Lecontella striatopunctata	0	0	0	2	1	0	0	0	0	0	1	1	0	1	1	0	0
Monophylla californica	0	0	1	3	1	0	0	1	1	0	1	0	0	1	1	0	1
Monophylla pallipes	0	0	1	3	1	0	0	1	1	0	1	0	0	1	1	0	1
Monophylla terminata	0	0	1	3	1	0	0	1	1	0	1	0	0	1	1	0	1
Onychotillus vittatus	0	0	2	1	0	1	0	1	1	0	1	1	0	1	1	0	1
Onychotillus cubana	0	0	1	1	0	0	0	1	1	0	0	1	0	2	1	0	1

Taxon \ Character	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
Collops bipunctatus	2	0	0	1	0	0	1	1	0	0	0	0	1	2	2	0	0
Collops quadripunctatus	2	0	0	1	0	0	1	1	0	0	1	0	1	2	2	0	0
Temnoscheila virescens	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenebroides sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Table 3.3 (continued)

Taxon \ Character	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
Chariessa pillosa	2	0	0	1	0	0	1	1	0	2	1	0	1	3	0	0	0
Enoclerus zonatus	0	0	0	0	1	0	1	2	0	0	0	2	1	2	2	0	0
Enoclerus nigripes	0	0	0	1	0	0	1	1	0	0	0	0	1	2	2	0	0
Madoniella dislocata	2	0	0	0	0	0	1	0	0	2	1	0	1	2	0	0	0
Necrobia rufipes	0	0	0	0	1	0	1	1	0	1	0	0	0	1	2	0	1
Neorthopleura thoracica	0	0	0	0	0	0	1	0	0	1	0	0	0	2	2	0	1
Pelonium leucophaeum	0	0	0	1	0	0	1	1	0	2	1	0	1	2	0	0	0
Phyllobaenus humeralis	0	0	0	0	0	0	1	1	0	1	0	0	3	2	2	0	1
Phyllobaenus pallipennis	0	0	0	2	0	0	1	1	0	1	0	0	3	2	2	0	1
Placopterus thoracicus	0	0	0	1	0	0	1	2	0	0	0	2	1	1	2	0	0
Priocera castanea	0	0	0	0	0	0	1	0	0	0	0	0	1	3	2	0	1
Trichodes nutalli	0	0	0	1	0	0	1	1	0	0	0	0	1	3	2	0	1
Zenodosus sanguineus	2	0	0	0	0	0	1	1	0	1	0	0	1	1	2	0	0
Cylidroctenus chalybaum	1	0	0	1	0	0	1	1	1	1	0	2	3	2	2	0	1
Cylidrus fasciatus	1	0	0	1	0	0	0	1	0	0	0	2	1	0	2	0	1
Gastrocentrum sp.	1	0	0	0	0	0	1	0	0	1	0	2	0	2	1	0	0
Orthocladiscus sp.	1	0	0	1	0	0	1	1	0	2	0	0	1	2	2	0	1
Stenocylidrus dispar	1	0	1	0	0	1	1	1	0	2	0	0	0	2	0	0	1
Strotocera grandis	1	0	1	1	0	1	1	0	0	2	0	2	1	2	0	0	0
Tilloidea transversalis	1	0	0	0	0	0	1	1	0	2	0	2	0	2	0	0	0
Araeodontia isabellae	1	0	0	1	0	1	1	0	0	2	0	1	0	2	0	0	0
Araeodontia marginallis	1	0	0	1	0	1	1	0	0	1	0	1	0	3	0	0	0
Araeodontia peninsularis	1	0	0	1	0	1	1	0	0	2	0	1	0	3	0	0	0
Barrotillus kropotkini	1	1	0	1	0	0	1	1	1	1	0	0	1	2	2	0	1
Bogcia disjuncta	1	0	0	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Bogcia oaxacae	1	0	0	1	1	1	1	0	0	2	0	1	1	3	0	0	0
Callotillus bahamensis	1	0	0	0	0	0	1	2	0	0	0	1	3	3	2	0	1
Callotillus eburneocinctus	1	0	0	0	0	0	1	2	1	0	0	1	3	3	2	0	1
Neocallotillus elegans	1	1	0	1	0	0	1	1	1	0	0	0	3	2	2	0	1
Neocallotillus elegans (*elegans*)	1	1	0	1	0	0	1	1	1	0	0	0	3	2	2	0	1
Neocallotillus elegans (*vafer*)	1	1	0	1	0	0	1	1	1	0	0	0	3	2	2	0	1
Neocallotillus intricatus	1	0	0	1	0	0	1	2	1	0	0	1	3	3	2	0	1
Neocallotillus elegans (*intermediate*)	1	1	0	1	0	0	1	1	1	0	0	0	3	2	2	0	1
Cymatodera aegra	1	0	0	1	1	1	1	0	0	2	0	1	0	3	0	0	0
Cymatodera angulifera	1	0	0	1	1	1	1	0	0	2	0	1	0	3	0	0	1
Cymatodera antennata	1	0	0	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera balteata	1	0	1	1	1	1	1	0	0	2	0	1	1	3	0	0	0
Cymatodera barri	1	0	1	1	0	1	1	1	0	1	1	1	3	3	0	1	1
Cymatodera bicolor	1	0	0	1	0	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera bipunctata	1	0	0	1	1	1	1	0	0	2	1	2	1	2	0	0	0
Cymatodera californica	1	0	0	1	0	1	1	0	0	2	0	1	2	2	0	0	0
Cymatodera championi	1	0	1	1	1	1	1	0	0	1	0	2	2	2	0	0	1
Cymatodera conflagrata	1	0	0	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera delicatula	1	0	0	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera depauperata	1	0	0	1	0	1	1	1	0	1	1	1	3	2	0	1	1
Cymatodera fascifera	1	0	0	1	0	1	1	1	0	2	0	1	1	2	0	0	0
Cymatodera floridana	1	0	1	1	0	1	1	0	0	1	0	2	3	3	0	0	1
Cymatodera fuchsii	1	0	0	1	0	1	1	0	0	1	0	1	0	3	0	0	0

Table 3.3 (continued)

Taxon \ Character	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
Cymatodera guatemalensis	1	0	1	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera hoegei	1	0	1	1	1	1	1	0	0	2	0	1	1	3	0	0	0
Cymatodera hopei	1	0	0	0	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera horni	1	0	0	0	0	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera inornata	1	0	0	1	0	1	1	0	0	1	1	1	1	2	0	0	0
Cymatodera latefascia	1	0	0	1	1	1	1	0	0	2	0	1	1	3	0	0	0
Cymatodera limatula	1	0	0	1	1	1	1	0	0	2	0	1	1	2	0	0	0
Cymatodera linsleyi	1	0	0	1	0	1	1	0	0	1	1	1	1	3	0	0	0
Cymatodera marmorata	1	0	1	1	1	1	1	1	0	2	0	1	1	2	0	0	0
Cymatodera mitchelli	1	0	2	0	0	1	1	0	0	1	1	1	0	3	2	1	1
Cymatodera neomexicana	1	0	2	0	1	1	1	0	0	1	0	1	1	3	0	0	0
Cymatodera obliquefasciata	1	0	0	0	1	1	1	0	0	2	0	1	1	3	0	0	0
Cymatodera pallida	1	0	0	1	0	1	1	0	0	1	0	1	1	2	0	0	0
Cymatodera prolixa	1	0	1	1	1	1	1	0	0	1	0	1	3	2	0	0	0
Cymatodera pseudotsuga	1	0	0	1	0	1	1	0	0	1	0	2	1	3	0	0	0
Cymatodera punctata	1	0	0	1	0	1	1	0	0	1	0	0	1	2	0	0	0
Cymatodera puncticollis	1	0	0	1	1	1	1	0	0	2	0	1	3	2	0	0	0
Cymatodera rosalinae	1	0	0	0	0	1	1	0	0	1	1	1	1	3	0	0	1
Cymatodera sallei	1	0	1	1	1	1	1	0	0	2	0	1	2	2	0	0	1
Cymatodera sericans	1	0	0	1	1	1	1	0	0	2	0	1	1	3	0	0	0
Cymatodera tricolor	1	0	0	1	0	1	1	0	0	2	0	1	1	3	0	0	1
Cymatodera tuta	1	0	0	1	1	1	1	0	0	1	0	1	1	3	0	0	0
Cymatodera usta	1	0	0	1	0	1	1	0	0	1	0	1	3	2	0	0	1
Cymatodera vagemaculata	1	0	0	1	1	1	1	0	0	2	0	1	3	2	0	0	1
Cymatodera ovipennis	1	0	0	1	0	1	1	0	0	1	1	1	3	3	0	1	1
Cymatodera venusta	1	0	1	1	1	1	0	0	0	1	0	1	3	2	0	0	0
Cymatodera werneri	1	0	0	1	1	1	1	0	0	1	0	1	3	2	0	0	0
Cymatodera xanti	1	0	0	1	1	1	1	0	0	2	0	1	3	3	0	0	1
Cymatodera xaviera	1	0	0	1	0	1	1	0	0	2	0	1	1	3	0	0	1
Cymatoderella collaris	1	0	0	1	1	1	1	0	0	1	0	1	1	2	0	0	0
Cymatoderella morula	1	0	0	1	1	1	1	0	0	1	0	1	1	2	0	0	0
Cymatoderella patagoniae	1	0	0	1	1	1	1	0	0	1	0	1	1	2	0	0	0
Lecontella brunnea	1	0	0	1	1	1	1	0	0	2	0	0	0	2	0	0	0
Lecontella gnara	1	0	0	1	1	1	1	0	0	2	0	0	1	2	0	0	0
Lecontella striatopunctata	1	0	0	0	1	1	1	0	0	2	0	0	1	2	0	0	0
Monophylla californica	?	1	0	0	0	0	1	1	0	0	0	0	1	2	2	0	0
Monophylla pallipes	?	1	0	0	0	0	1	1	0	0	0	0	0	2	2	0	1
Monophylla terminata	?	1	0	1	0	0	1	1	0	0	0	0	0	1	2	0	0
Onychotillus vittatus	?	0	0	0	1	0	1	0	0	1	0	0	1	2	0	0	1
Onychotillus cubana	?	0	0	0	1	0	1	0	0	1	0	0	1	2	2	0	1

Taxon \ Character	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Collops bipunctatus	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0
Collops quadripunctatus	1	0	0	1	1	0	0	0	1	1	0	0	0	0	1	1	2
Temnoscheila virescens	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Tenebroides sp.	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0
Chariessa pillosa	1	0	0	2	1	0	0	1	1	1	0	1	1	0	1	0	0

Table 3.3 (continued)

Taxon \ Character	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Enoclerus zonatus	1	0	0	2	1	0	0	0	1	1	0	1	2	0	1	1	1
Enoclerus nigripes	1	0	0	2	0	0	0	0	1	1	0	1	2	0	0	0	1
Madoniella dislocata	1	0	0	2	0	0	0	0	1	1	2	1	1	0	1	1	0
Neorthopleura thoracica	1	0	0	2	0	0	0	0	1	1	0	1	0	0	1	0	2
Necrobia rufipes	1	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	2
Pelonium leucophaeum	1	1	0	2	0	0	0	1	1	1	0	1	1	0	0	1	2
Phyllobaenus humeralis	1	1	0	1	1	0	0	1	1	1	3	1	0	0	1	0	2
Phyllobaenus pallipennis	1	0	0	2	1	0	0	1	1	1	0	1	0	0	1	0	2
Placopterus thoracicus	1	0	0	2	1	0	0	0	1	1	2	1	2	0	0	1	2
Priocera castanea	1	0	0	2	1	0	0	0	1	1	0	1	0	0	1	1	2
Trichodes nutalli	1	0	0	2	1	1	0	0	1	1	1	1	0	0	1	1	0
Zenodosus sanguineus	1	0	0	1	0	0	0	0	1	?	?	?	?	0	?	?	?
Cylidroctenus chalybaum	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0
Cylidrus fasciatus	1	0	1	2	0	0	0	1	1	1	0	0	0	0	0	0	1
Gastrocentrum sp.	1	1	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0
Orthocladiscus sp.	1	0	0	2	1	0	0	1	1	1	0	0	0	0	0	0	0
Stenocylidrus dispar	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0
Strotocera grandis	1	0	0	2	1	0	0	0	1	1	2	0	0	0	1	0	0
Tilloidea transversalis	1	0	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0
Araeodontia isabellae	1	0	1	2	1	1	0	0	1	1	2	1	1	0	1	0	1
Araeodontia marginallis	1	0	1	2	1	1	0	0	1	1	1	1	1	0	1	0	1
Araeodontia peninsularis	1	0	1	2	1	1	0	0	1	1	2	1	1	0	1	0	1
Barrotillus kropotkini	1	0	1	2	0	?	0	0	1	1	1	?	?	0	?	?	?
Bogcia disjuncta	1	0	1	2	1	0	0	0	1	1	0	1	1	0	0	0	0
Bogcia oaxacae	1	0	1	2	1	0	0	0	1	1	0	1	1	0	0	0	0
Callotillus bahamensis	1	0	1	2	1	0	0	0	1	1	1	0	1	0	1	1	1
Callotillus eburneocinctus	1	0	1	2	1	1	0	1	1	1	1	0	1	0	1	1	0
Neocallotillus elegans	1	0	1	2	1	0	0	0	1	1	1	0	1	0	1	1	0
Neocallotillus elegans (*elegans*)	1	0	1	2	1	0	0	0	1	1	1	0	1	0	1	1	0
Neocallotillus elegans (*vafer*)	1	0	1	2	1	0	0	0	1	1	1	0	1	0	1	1	0
Neocallotillus intricatus	1	0	1	2	0	0	0	1	1	1	1	?	?	0	?	?	?
Neocallotillus elegans (intermediate)	1	0	1	2	1	0	0	1	1	1	1	0	1	0	1	1	0
Cymatodera aegra	1	0	1	2	1	0	0	0	1	1	2	1	1	0	0	0	0
Cymatodera angulifera	1	1	1	2	1	1	0	0	1	1	0	0	1	0	0	0	0
Cymatodera antennata	1	0	1	2	1	0	0	0	1	1	2	1	1	0	1	0	2
Cymatodera balteata	1	1	1	2	1	0	1	1	1	1	0	0	2	0	1	1	0
Cymatodera barri	1	1	1	2	1	1	1	1	0	1	0	0	1	0	0	1	0
Cymatodera bicolor	1	1	1	1	1	0	1	0	1	1	0	0	1	0	0	0	1
Cymatodera bipunctata	1	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	0
Cymatodera californica	1	1	1	2	1	0	1	0	1	1	3	0	1	0	1	1	0
Cymatodera championi	1	1	1	2	1	1	1	1	1	1	2	0	2	1	1	1	0
Cymatodera conflagrata	1	0	1	1	1	0	0	0	1	1	0	1	1	0	1	0	0
Cymatodera delicatula	1	0	1	2	1	0	0	0	1	1	2	1	1	0	1	0	0
Cymatodera depauperata	1	1	1	2	1	1	1	1	0	1	0	0	1	0	1	1	0
Cymatodera fascifera	1	0	1	2	1	0	0	1	1	1	0	0	1	0	1	0	0
Cymatodera floridana	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	0
Cymatodera fuchsii	1	0	1	2	1	1	1	1	1	1	2	0	2	0	1	1	0
Cymatodera guatemalensis	1	1	1	2	1	1	1	1	1	1	2	0	2	1	1	1	0

Table 3.3 (continued)

Taxon \ Character	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Cymatodera hoegei	1	1	1	2	1	1	1	1	1	1	2	0	2	1	1	1	0
Cymatodera hopei	1	1	1	2	1	0	1	1	1	1	2	0	1	0	1	1	0
Cymatodera horni	1	1	1	2	1	0	1	1	1	1	2	0	1	0	1	1	0
Cymatodera inornata	1	1	1	1	1	0	0	0	1	1	0	1	1	0	0	1	1
Cymatodera latefascia	1	0	1	2	1	0	0	0	1	1	1	0	1	0	1	0	1
Cymatodera limatula	1	0	1	2	1	0	0	0	1	1	0	1	1	0	0	0	0
Cymatodera linsleyi	1	1	1	2	1	1	1	0	1	1	2	0	1	0	1	1	0
Cymatodera marmorata	1	1	1	2	1	1	1	1	1	1	4	1	2	1	1	1	0
Cymatodera mitchelli	1	1	1	2	1	1	1	1	0	1	0	0	2	0	0	1	0
Cymatodera neomexicana	1	1	1	2	1	1	1	1	1	1	2	0	2	0	1	1	0
Cymatodera obliquefasciata	1	0	1	2	1	0	0	0	1	1	0	1	1	0	0	1	0
Cymatodera pallida	1	0	1	2	1	0	0	0	1	1	2	1	1	0	1	0	0
Cymatodera prolixa	1	1	1	2	1	1	1	1	1	1	2	0	2	1	1	1	0
Cymatodera pseudotsuga	1	0	1	2	1	1	1	0	1	1	0	0	1	0	1	1	0
Cymatodera punctata	1	0	1	2	1	1	1	0	1	1	0	0	2	0	1	1	0
Cymatodera puncticollis	1	0	1	2	1	0	0	0	1	1	0	1	1	0	1	0	0
Cymatodera rosalinae	1	0	1	2	1	1	0	0	1	1	0	0	1	0	1	0	0
Cymatodera sallei	1	1	1	2	1	1	1	1	1	1	0	0	2	1	1	1	0
Cymatodera sericans	1	1	1	2	0	0	0	0	1	1	0	1	1	0	1	0	0
Cymatodera tricolor	1	1	1	2	1	0	0	0	1	1	0	0	1	0	1	0	0
Cymatodera tuta	1	0	1	2	1	0	0	0	1	1	2	0	1	0	1	0	0
Cymatodera usta	1	0	1	2	1	0	0	0	1	1	0	1	2	0	0	1	0
Cymatodera vagemaculata	1	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0
Cymatodera ovipennis	1	1	1	2	1	1	1	1	0	1	0	0	1	0	1	1	0
Cymatodera venusta	1	1	1	2	1	1	1	1	1	1	2	0	2	1	1	1	0
Cymatodera werneri	1	0	1	2	1	0	0	0	1	1	2	1	1	0	1	0	0
Cymatodera xanti	1	0	1	2	1	0	0	0	1	1	2	1	1	0	1	0	1
Cymatodera xaviera	1	0	1	2	1	1	0	0	1	1	0	0	2	0	1	0	0
Cymatoderella collaris	1	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0
Cymatoderella morula	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	1	0
Cymatoderella patagoniae	1	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0
Lecontella brunnea	1	0	1	2	1	0	0	0	1	1	1	1	1	0	0	0	0
Lecontella gnara	1	0	1	2	1	0	0	0	1	1	1	1	1	0	0	0	0
Lecontella striatopunctata	1	0	1	2	0	0	0	0	1	1	1	1	1	0	0	0	0
Monophylla californica	2	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1
Monophylla pallipes	2	1	1	1	1	0	0	1	1	1	1	0	1	0	1	1	2
Monophylla terminata	2	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	2
Onychotillus vittatus	1	0	1	1	1	0	0	0	0	1	?	?	?	0	?	?	?
Onychotillus cubana	1	0	1	2	1	0	0	0	0	1	0	0	1	0	1	0	2

Taxon \ Character	86	87	88	89	90	91
Collops bipunctatus	0	0	2	1	0	1
Collops quadripunctatus	0	0	2	1	0	2
Temnoscheila virescens	1	0	2	1	1	2
Tenebroides sp.	1	0	2	1	1	2
Chariessa pillosa	0	1	1	1	1	1

Table 3.3 (continued)

Taxon \ Character	86	87	88	89	90	91
Enoclerus zonatus	0	0	1	1	1	0
Enoclerus nigripes	0	0	0	1	1	0
Madoniella dislocata	1	0	1	1	1	1
Necrobia rufipes	1	1	2	1	1	1
Neorthopleura thoracica	1	1	1	1	1	1
Pelonium leucophaeum	0	1	1	1	1	2
Phyllobaenus humeralis	1	0	2	1	1	1
Phyllobaenus pallipennis	1	0	1	1	1	1
Placopterus thoracicus	1	0	1	1	1	0
Priocera castanea	1	0	1	1	1	1
Trichodes nutalli	1	0	2	1	1	1
Zenodosus sanguineus	?	?	?	?	?	?
Cylidroctenus chalybaum	0	0	1	1	1	1
Cylidrus fasciatus	0	0	0	1	1	0
Gastrocentrum sp.	1	0	0	0	1	0
Orthocladiscus sp.	1	1	1	1	1	0
Stenocylidrus dispar	0	0	0	0	1	1
Strotocera grandis	0	1	1	1	1	1
Tilloidea transversalis	1	1	0	0	1	1
Araeodontia isabellae	1	0	1	1	1	0
Araeodontia marginallis	1	0	1	1	1	0
Araeodontia peninsularis	1	0	1	1	1	0
Barrotillus kropotkini	?	?	?	?	?	?
Bogcia disjuncta	0	1	1	1	1	0
Bogcia oaxacae	0	1	1	1	1	0
Callotillus bahamensis	0	0	0	1	1	1
Callotillus eburneocinctus	0	0	0	1	1	1
Neocallotillus elegans	1	0	1	1	1	1
Neocallotillus elegans (*elegans*)	1	0	1	1	1	1
Neocallotillus elegans (*vafer*)	1	0	1	1	1	1
Neocallotillus intricatus	?	?	?	?	?	?
Neocallotillus elegans (*inter.*)	1	0	1	1	1	1
Cymatodera aegra	0	0	1	1	1	1
Cymatodera angulifera	0	0	1	1	1	0
Cymatodera antennata	0	1	1	1	1	1
Cymatodera balteata	0	0	1	1	1	0
Cymatodera barri	0	0	1	1	1	0
Cymatodera bicolor	0	1	1	1	1	0
Cymatodera bipunctata	0	1	1	1	1	0
Cymatodera californica	0	0	0	1	1	1
Cymatodera championi	0	0	0	1	1	0
Cymatodera conflagrata	0	0	1	1	1	1
Cymatodera delicatula	0	0	1	1	1	1
Cymatodera depauperata	0	0	1	1	1	0
Cymatodera fascifera	0	0	1	1	1	1
Cymatodera floridana	0	0	1	1	1	0
Cymatodera fuchsii	0	0	1	1	1	0
Cymatodera guatemalensis	0	0	0	1	1	0

Table 3.3 (continued)

Taxon \ Character	86	87	88	89	90	91
Cymatodera hoegei	0	0	0	1	1	0
Cymatodera hopei	0	0	0	1	1	1
Cymatodera horni	0	0	0	1	1	1
Cymatodera inornata	0	0	1	1	1	0
Cymatodera latefascia	0	0	1	1	1	1
Cymatodera limatula	0	1	1	1	1	0
Cymatodera linsleyi	0	1	2	1	1	0
Cymatodera marmorata	0	0	0	1	1	0
Cymatodera mitchelli	0	0	1	1	1	0
Cymatodera neomexicana	0	0	0	1	1	0
Cymatodera obliquefasciata	0	1	1	1	1	0
Cymatodera pallida	0	1	1	1	1	1
Cymatodera prolixa	0	0	0	1	1	0
Cymatodera pseudotsuga	0	0	2	1	1	1
Cymatodera punctata	0	0	1	1	1	1
Cymatodera puncticollis	0	0	1	1	1	1
Cymatodera rosalinae	0	1	1	1	1	1
Cymatodera sallei	0	0	2	1	1	0
Cymatodera sericans	0	1	1	1	1	0
Cymatodera tricolor	0	1	1	1	1	1
Cymatodera tuta	0	1	1	1	1	1
Cymatodera usta	0	1	1	1	1	1
Cymatodera vagemaculata	0	1	1	1	1	0
Cymatodera ovipennis	0	0	0	1	1	0
Cymatodera venusta	0	0	0	1	1	0
Cymatodera werneri	0	0	1	1	1	1
Cymatodera xanti	0	1	1	1	1	1
Cymatodera xaviera	0	1	1	1	1	1
Cymatoderella collaris	0	1	1	1	1	1
Cymatoderella morula	0	1	1	1	1	0
Cymatoderella patagoniae	0	1	1	1	1	1
Lecontella brunnea	0	0	1	1	0	0
Lecontella gnara	0	0	1	1	0	0
Lecontella striatopunctata	0	0	1	1	0	0
Monophylla californica	1	1	1	0	1	2
Monophylla pallipes	1	1	1	0	1	1
Monophylla terminata	1	1	1	0	1	0
Onychotillus vittatus	?	?	?	?	?	?
Onychotillus cubana	1	1	1	1	1	0
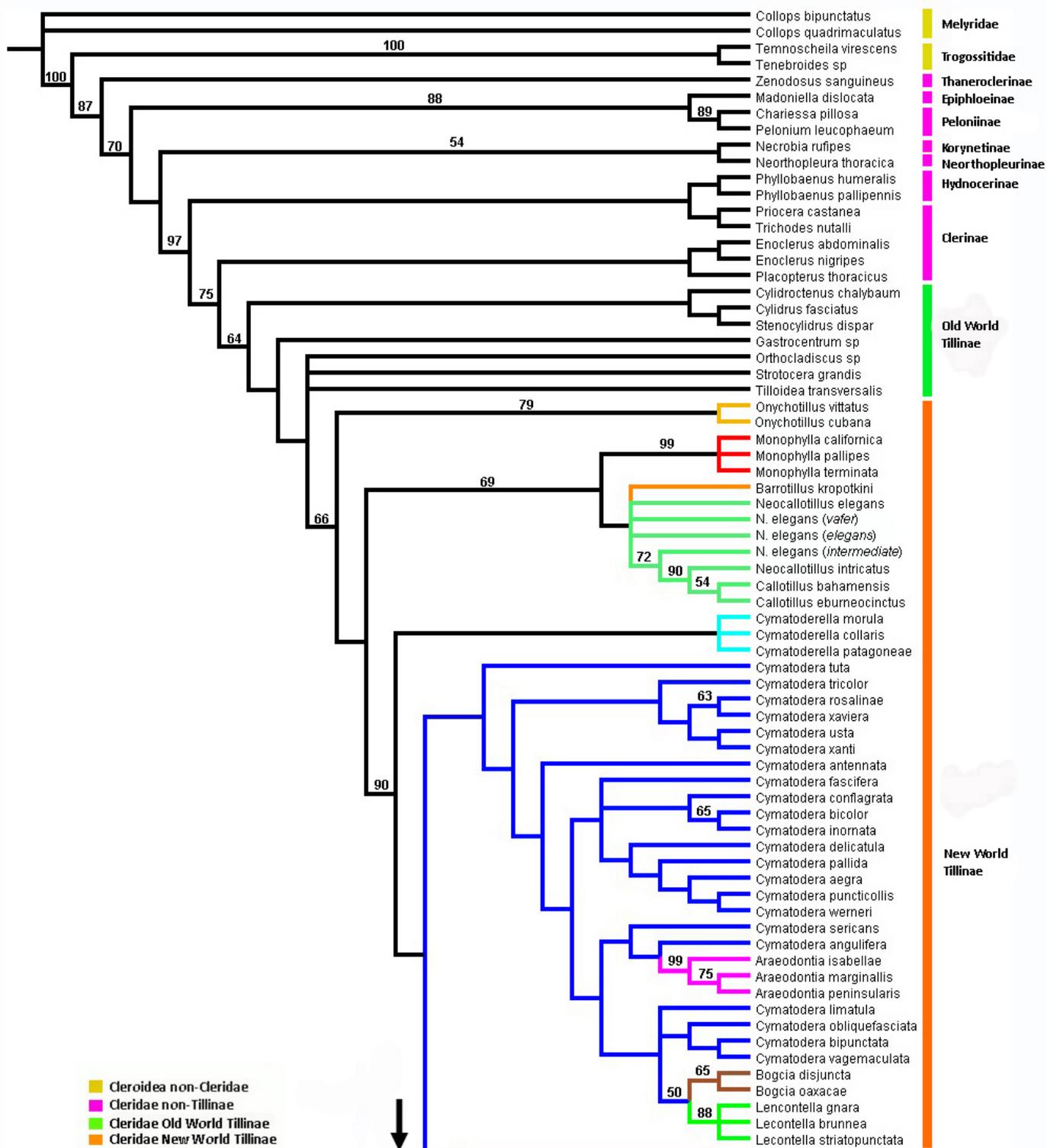
Tree continues on next page. Legends are shown on next page.
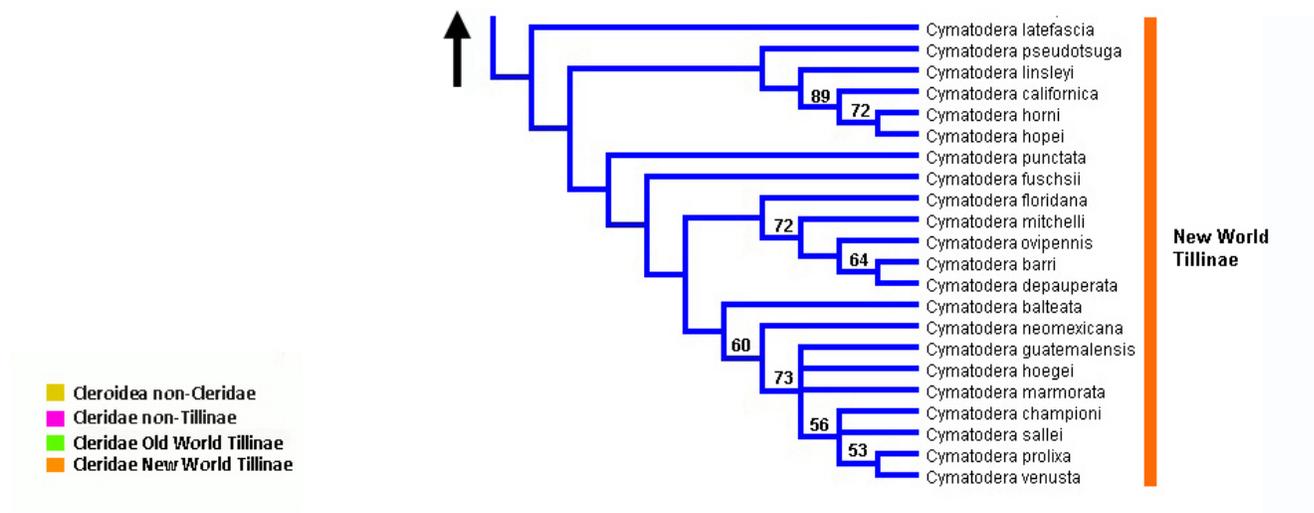
Fig. 3.1 Strict consensus tree of 2667 equally most parsimonious trees found for unordered and unweighted dataset. Non-Cleridae (yellow) and Non-Tillinae (pink squares) indicate outgroup, and Old World Tillinae (Green) and New World Tillinae (orange) represent ingroup. Color branches represent diversification of genera within Tilliniae. When supported, bootstrap values are shown above branches. The legend is shown at the lower left corner of the topology.
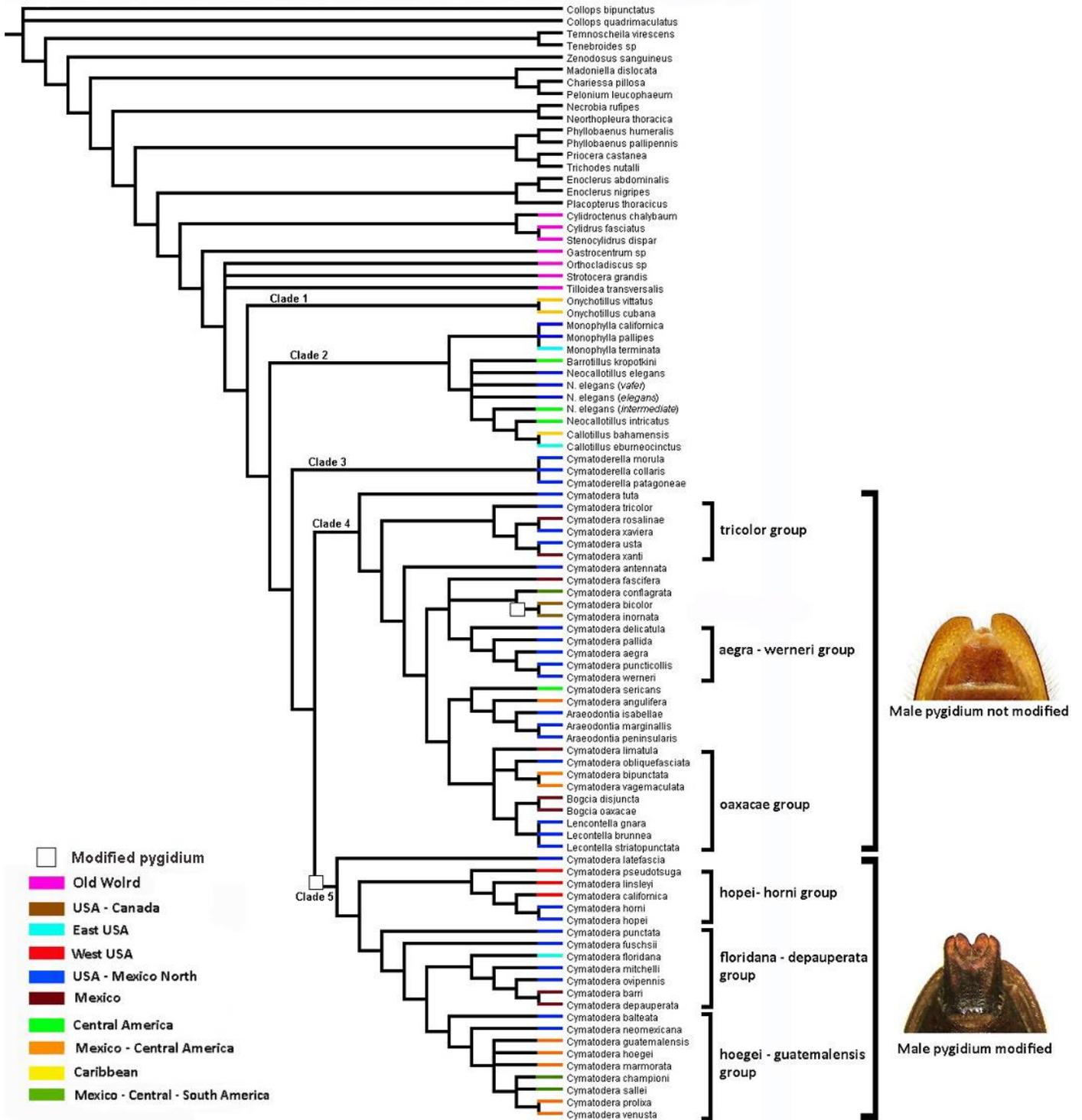
Fig. 3.2 Strict consensus tree generated by parsimony inference indicating six major species groups for the *Cymatodera + Araeodontia + Bogcia + Lecontella* lineage (Clades 4 + 5). Two major lineages for this clade can be inferred based on the male pygidium, those clades are shown with an illustration of a representative male pygidium. Colored branch tips represent distribution of the Tillinae in ten major geographical regions indicated at the lower left corner of the topology. Distribution of Old World tillinids is not detailed.
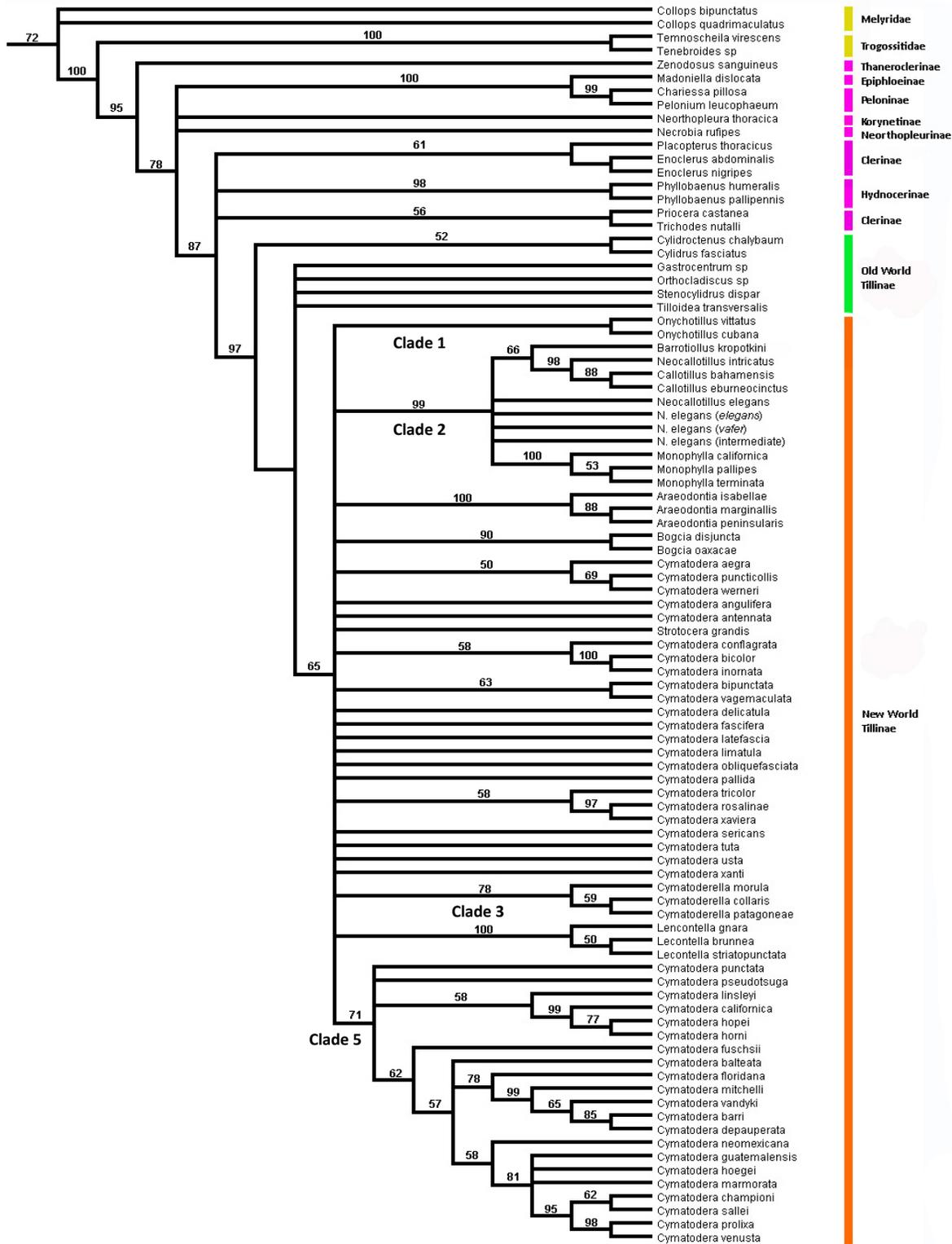
Fig. 3.3 50% majority-rule consensus tree resulting from Bayesian analysis (standard discrete model).When supported, numbers above branches represent posterior probability values. Clades obtained from maximum parsimony analysis, when supported, are indicated below branches.
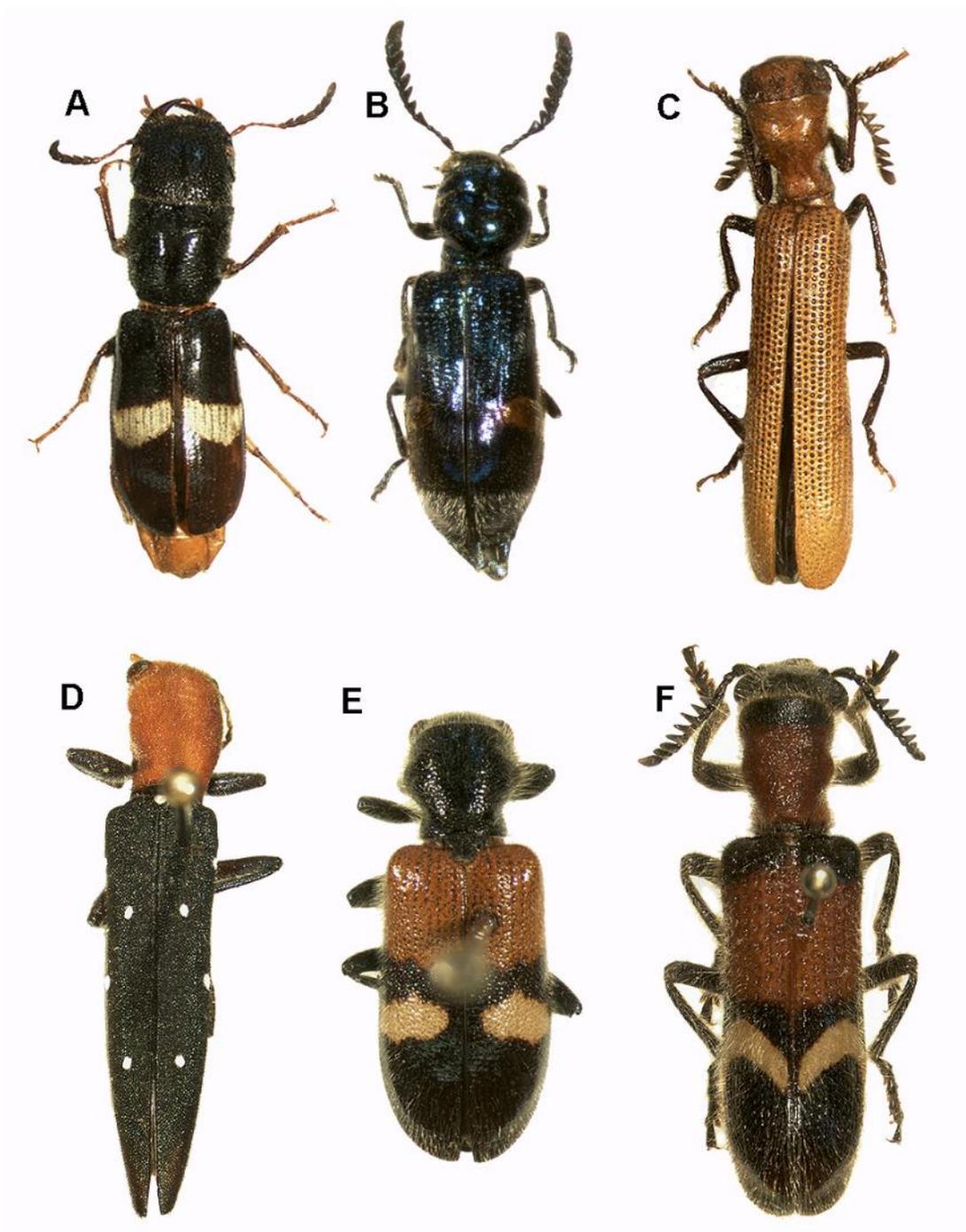
Fig. 3.4 Habitus of: A. *Cylidrus fasciatus* (male); B. *Cylidroctenus chalybaeum* (male); C. *Orthocladiscus sp.* (male); D. *Stenocylidrus dispar* (male); E. *Tilloidea transversalis* (male); F. *Strotocera grandi*s (male).
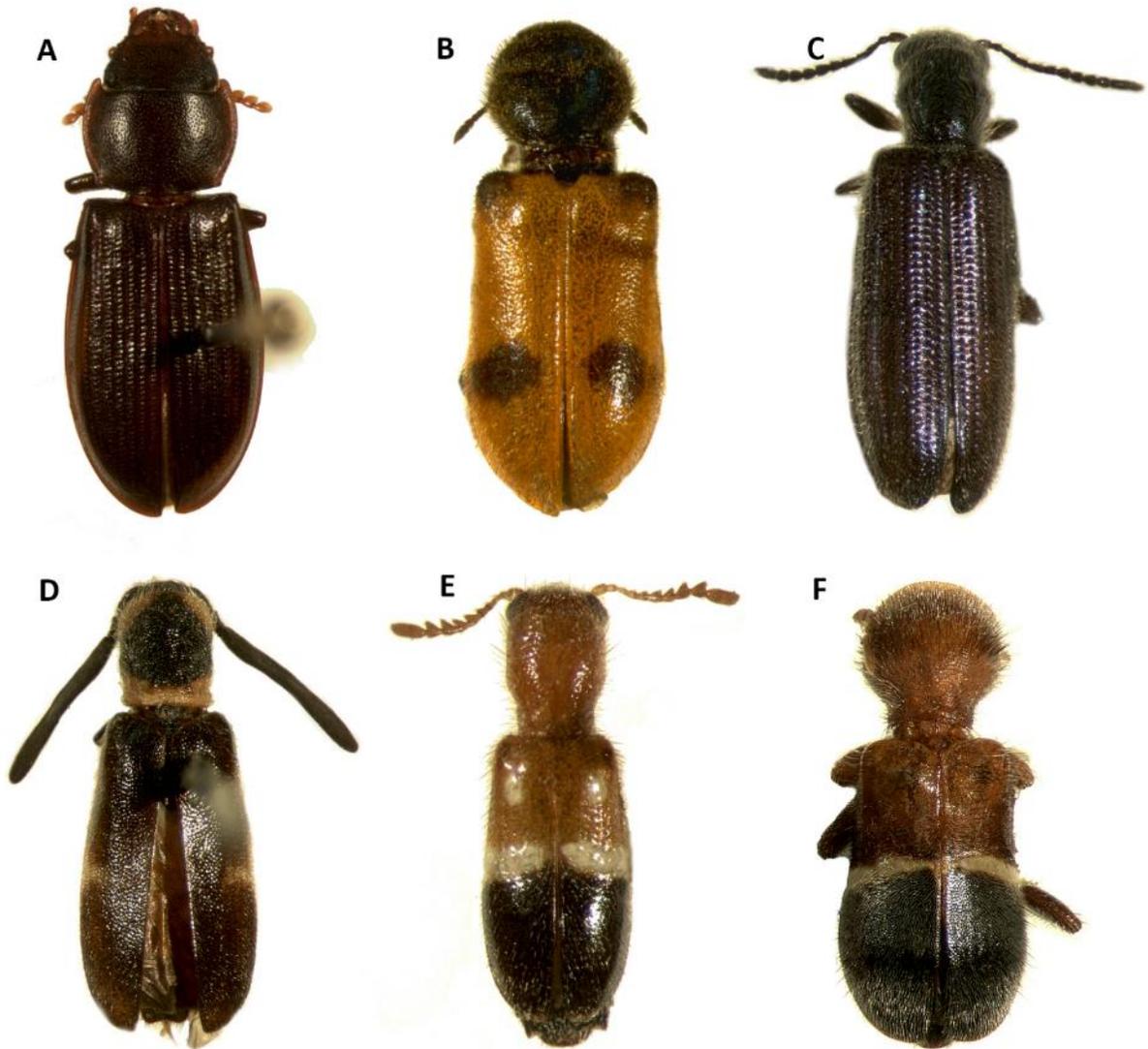
Fig. 3.5 Habitus of: A. *Tenebroides americanus* (male); B. *Enoclerus zonatus* (male); C. *Onychotillus vittatus* (male); D. *Monophylla terminata* (male); E. *Neocallotillus elegans* (male); F. *Callotillus eburneocinctus* (male).
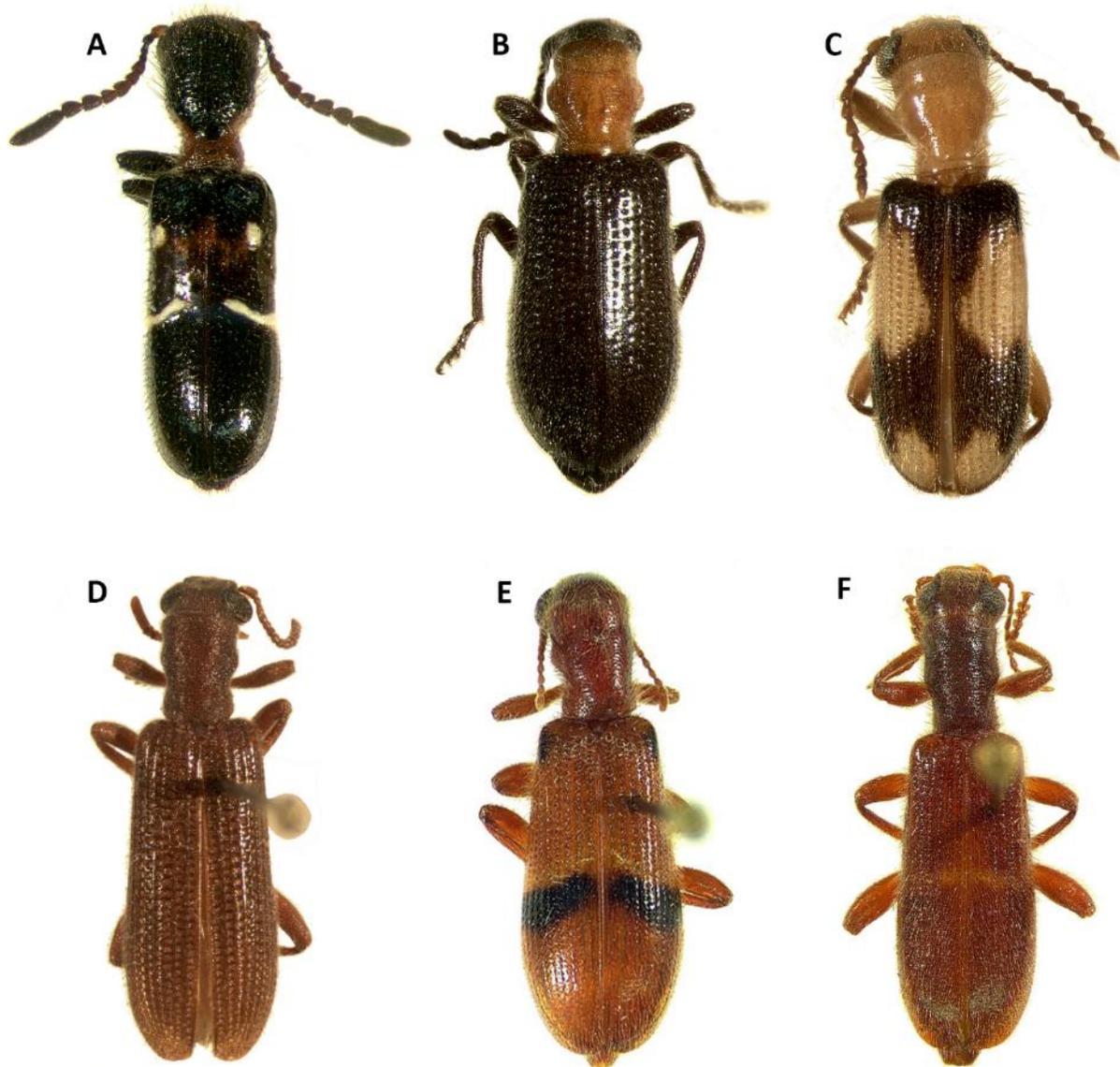
Fig. 3.6 Habitus of: A. *Barrotillus kropotkini* (male); B. *Cymatoderella collaris* (male); C. *Araeodontia peninsularis* (male); D. *Lecontella brunea* (male); E. *Bogcia oaxacae* (male); F. *Cymatodera rosalinae* (male).
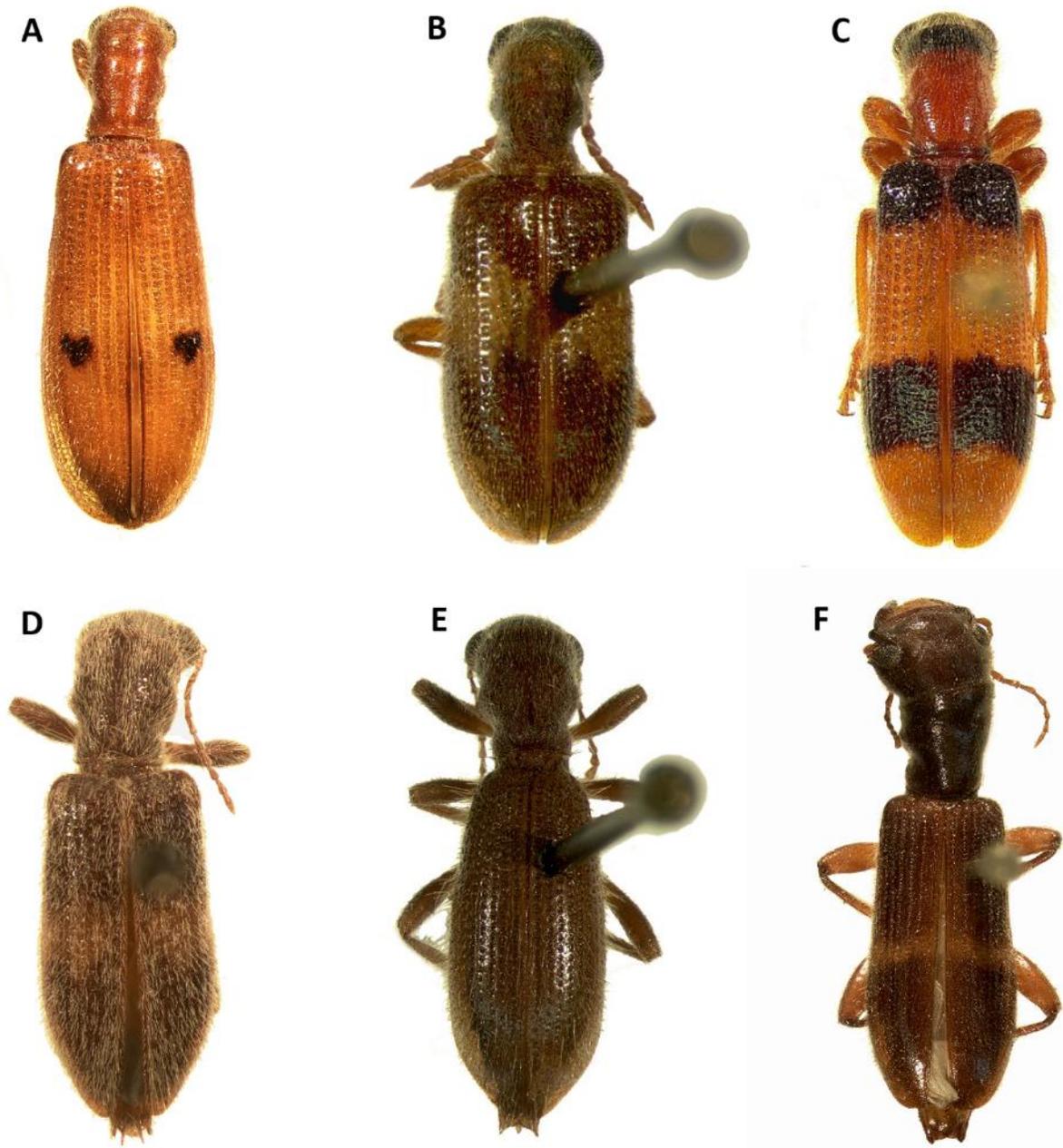
Fig. 3.7 Habitus of: A. *Cymatodera bipunctata* (male); B. *C. aegra* (male); C. *C. limatula* (male); D. *C. fuchsii* (male); E. *C. ovipennis* (male); F. *C. hoegei* (male).
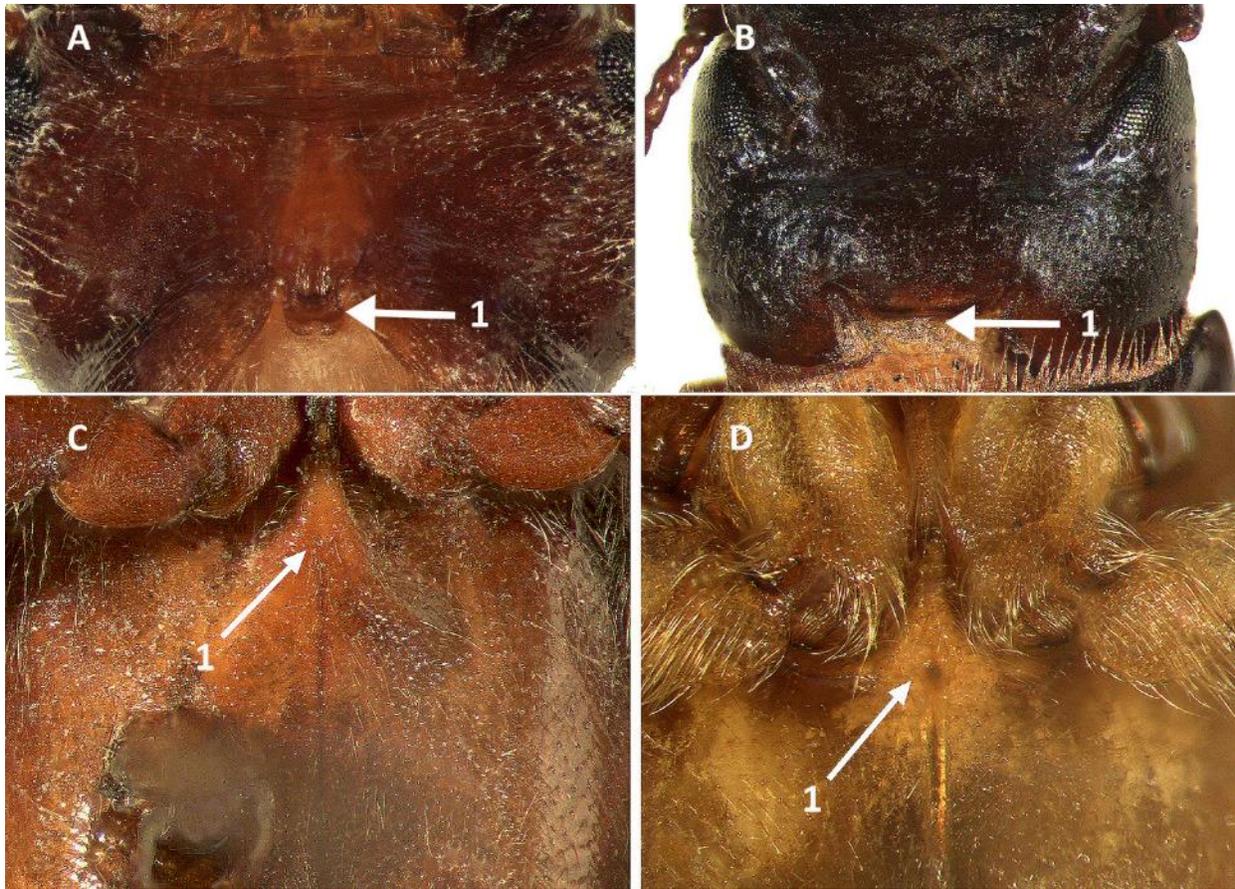
Fig. 3.8 A-B Gular structure: A. Arrow 1 indicates post-gular process present in *Cymatodera californica*; B. arrow 1 indicates post-gular process absent in *Temnoscheila virescens*; C-D Anterior portion of metasternum: C. arrow 1 indicates metaventral process not depressed in *Cymatodera linsleyi*; D. arrow 1 indicates metaventral process depressed in *Cymatodera balteata*.
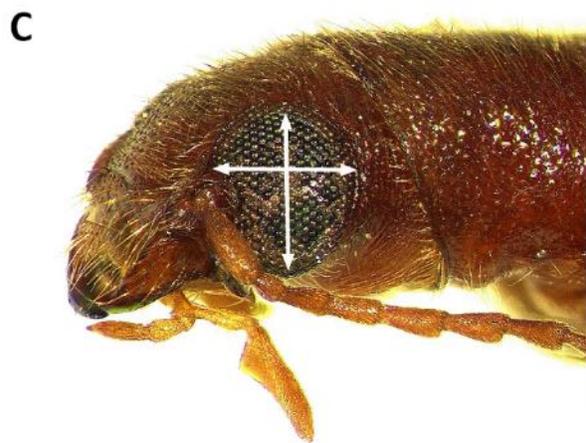
Fig. 3.9 A-B Ommatidia of: *Enoclerus zonatus*; B. *Cymatodera venusta.* C-D. Size of eyes of: C. *Cymatodera rosalinae*; D. *C. venusta;* arrows indicate vertical length in relation to horizontal length.
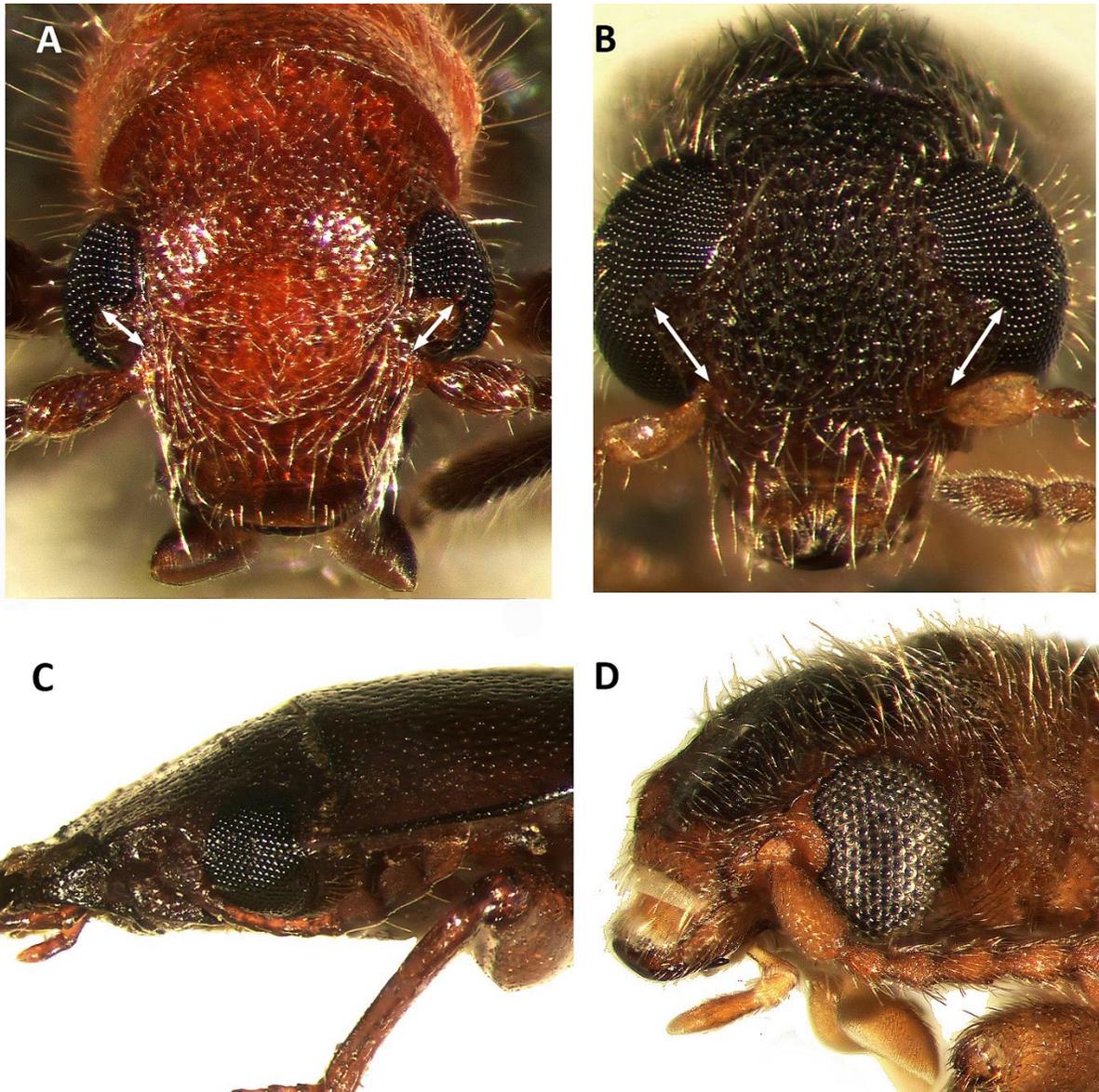
Fig. 3.10 A-B Position of antennal sockets of: A. *Cymatodera patagoniae*; B. *Madoniella dislocata*. Arrows indicate distance between antennal sockets and eyes; C-D Eye emargination of: C. *Tenebroides americanus*; D. *Cymatodera laevicolis*.
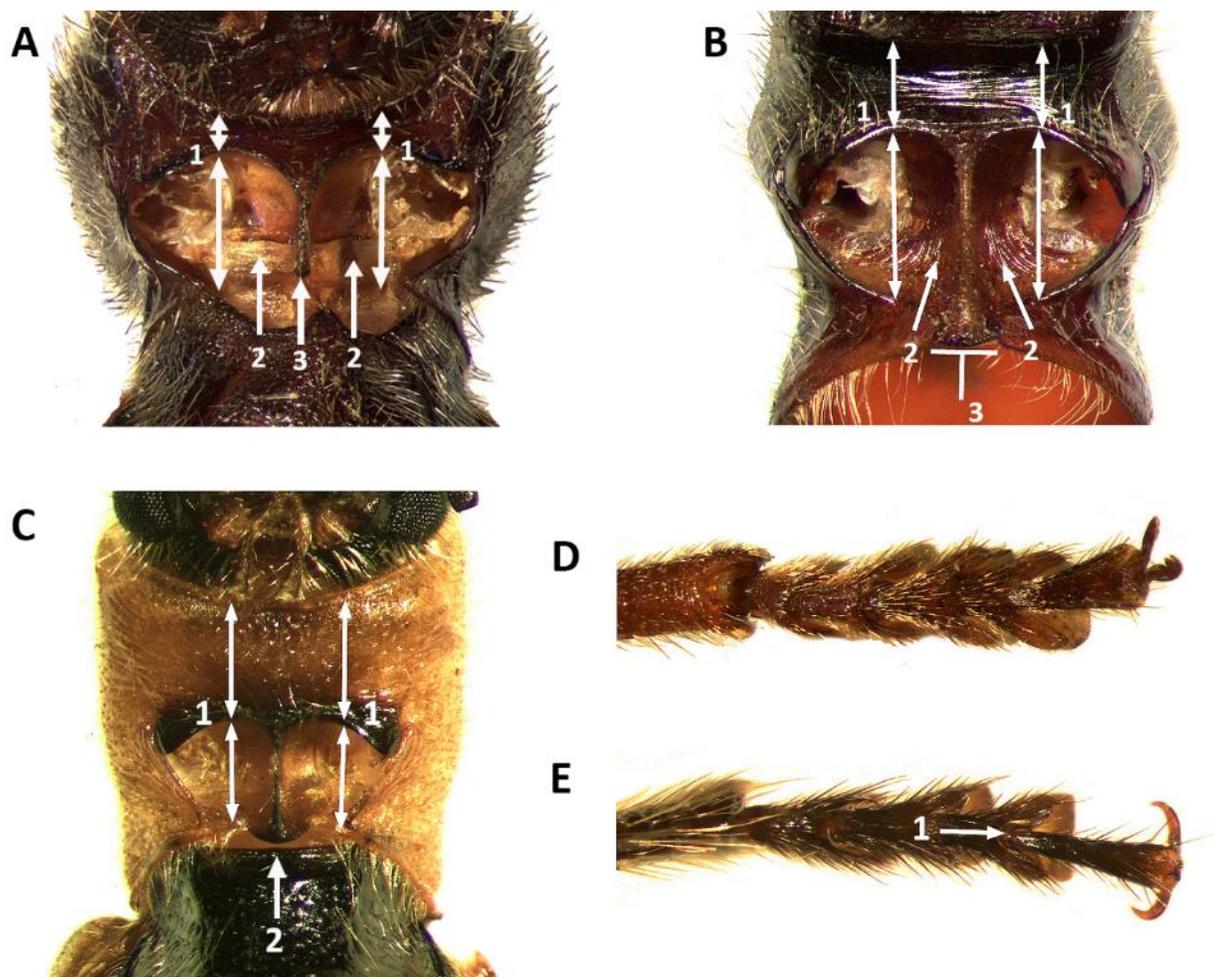
Fig. 3.11 A-D Procoxal cavities of: A. *Enoclerus zonatus*; B. *Cymatodera sallei*; C. *Monophylla terminate*. Arrows 1 indicate longitudinal length of procoxal cavities in relation to longitudinal length of prosternum; arrows 2 indicate interior portion of procoxal cavities; arrow 3 indicates intercoxal process. D-E Protarsomeres of: D. *Cymatodera tricolor*; E. *Chariessa pillosa;* arrow indicates size of fourth protarsomere.
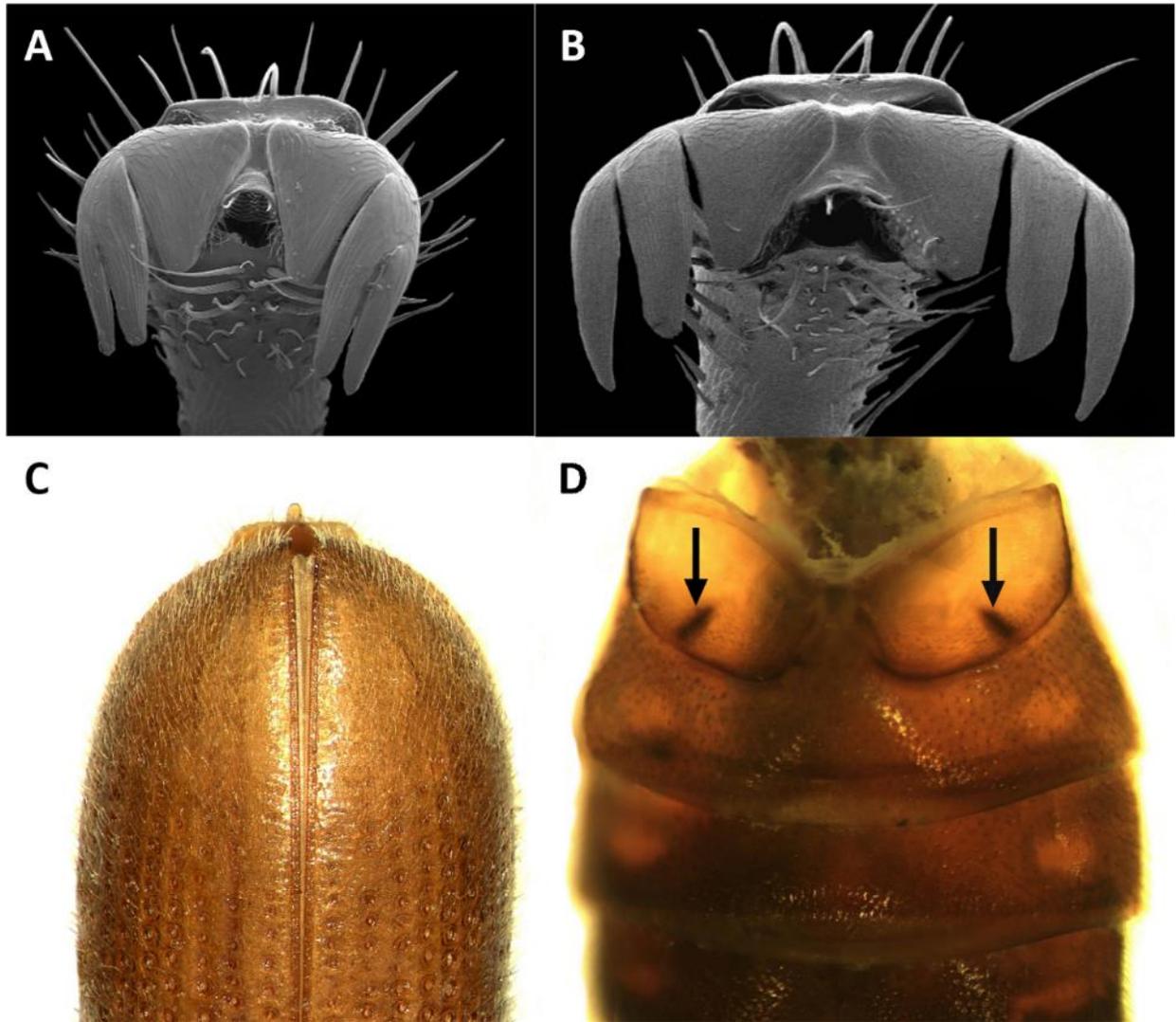
Fig. 3.12 A-B Protarsal claws of: A. *Bogcia oaxacae*; B. *Cymatodera rosalinae*. C. Posterior portion of elytra of *Cymatodera antennata;* D. Abdomen of *C. balteata*, arrows indicate first abdominal segment bearing a pair of carinae.
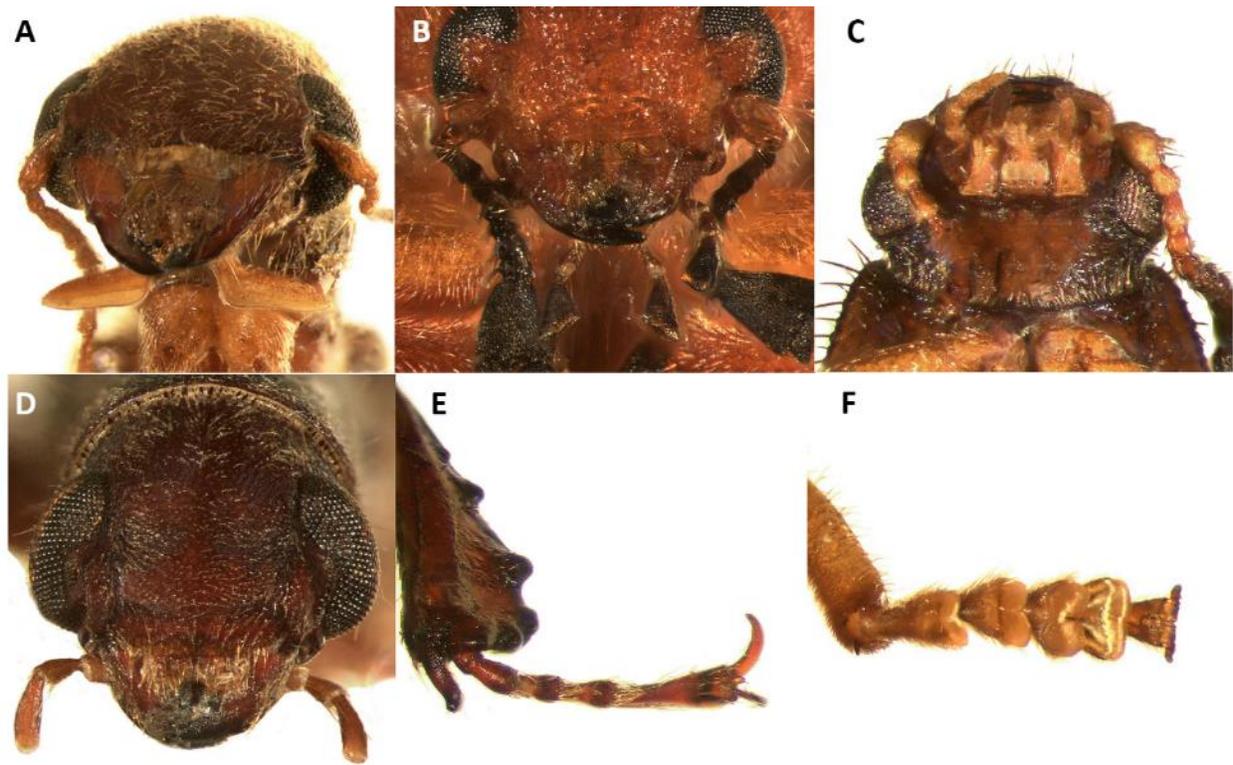
Fig. 3.13 A-D Labial and maxillary palpi of: A. *Cymatodera sallei*; B. *Chariessa pillosa*; C. *Necrobia rufipes*; D. *Cymatodera horni*. E-F Protarsomeres of: E. *Temnoscheila virescens*; F. *Cymatodera tuta.*
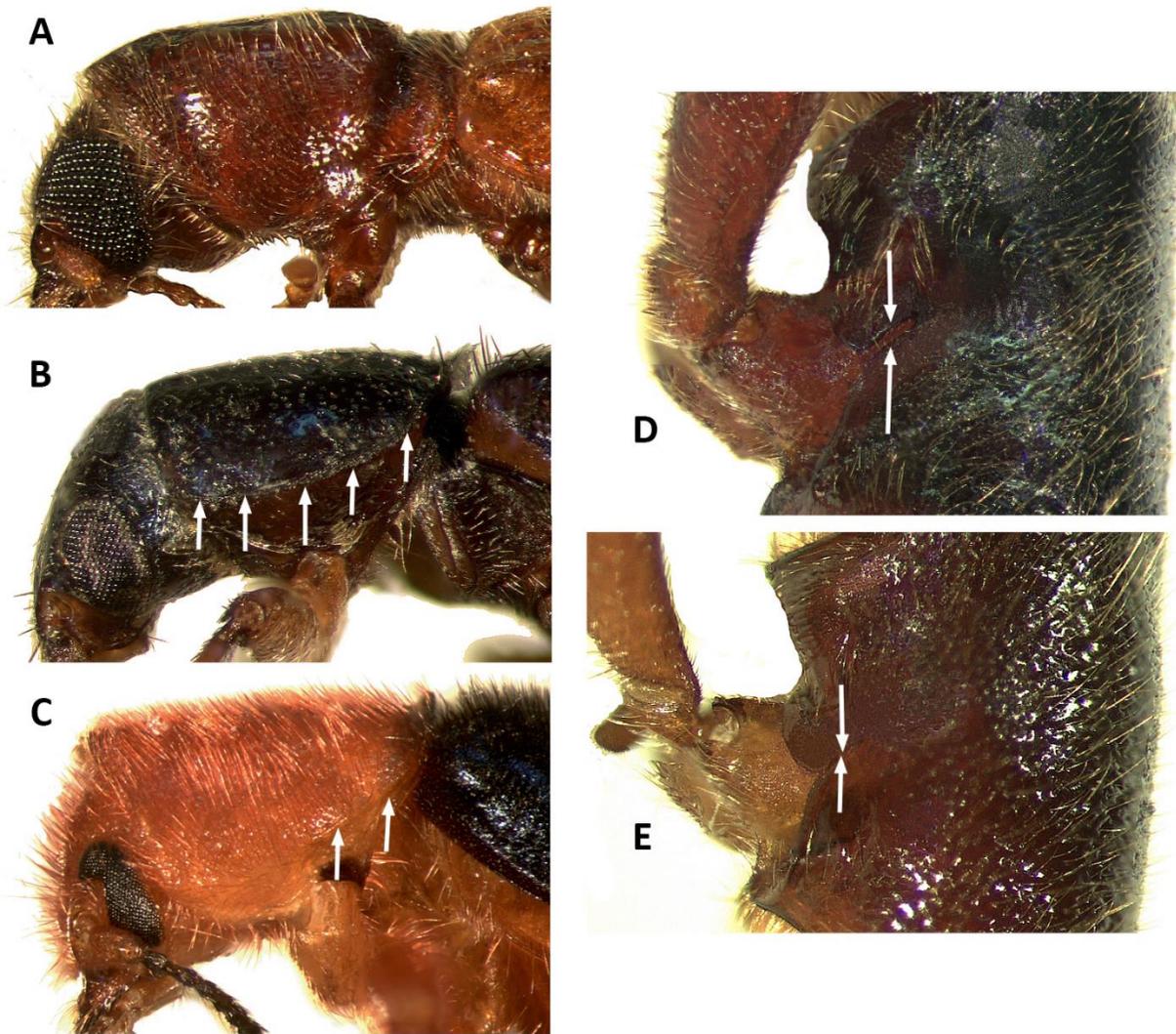
Fig. 3.14 A-C Lateral view of: A. *Priosera castanea*; B. *Necrobia rufipes*; C; *Chariessa pillosa*; arrows indicate extension of dorsolateral carina. D-E Lateral suture on the confluence of the prosternum and the proepimeron of: D. *Cymatodera californica,* arrows indicate suture is open; E. *C. championi*, arrows indicate suture closed.
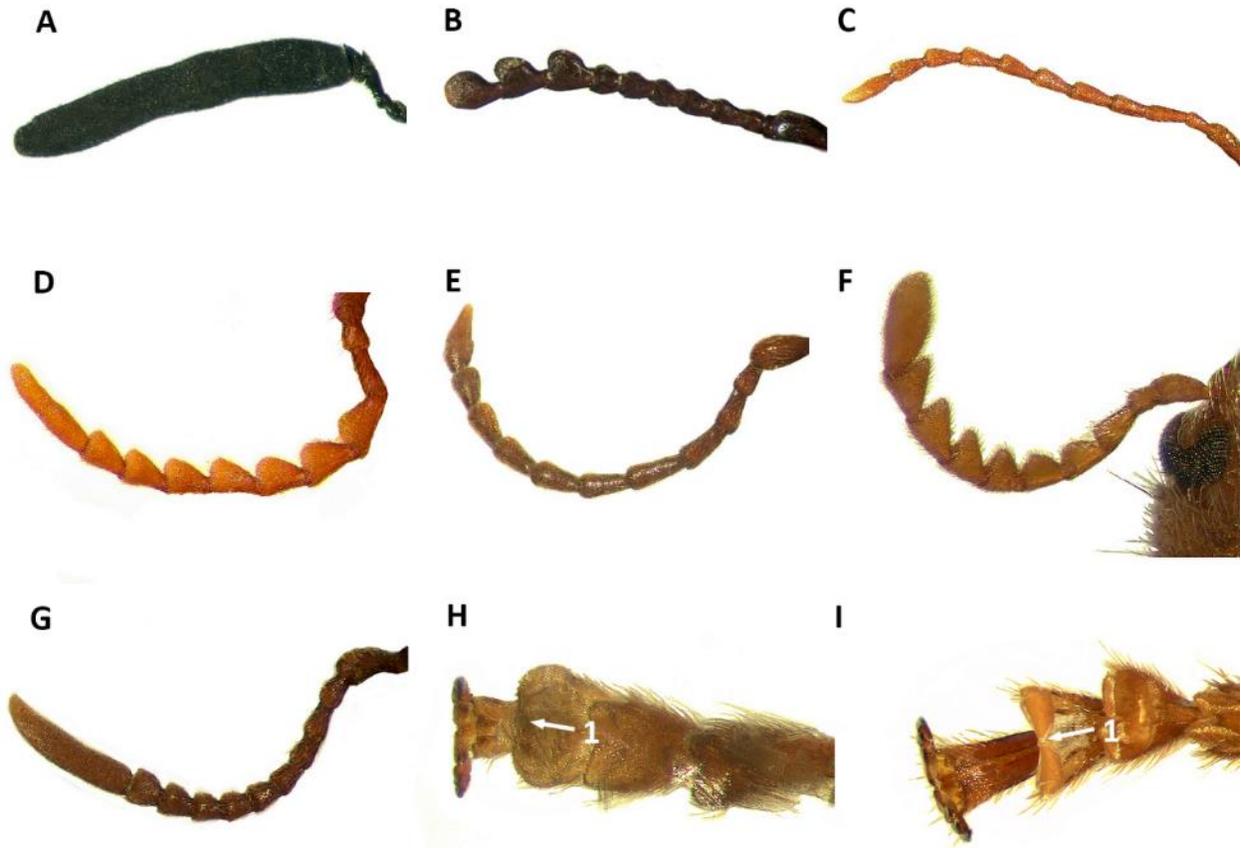
Fig. 3.15 A-G Antennae of: A. *Monophylla terminate*; B. *Temnoscheila virescens*; C. *Cymatodera rosalinae*; D. *C. limatula*; E. *C. balteata*; F. *Neocallotillus intricatus*; G. *Lecontella brunea*. H-I Fourth protarsomere of: H. *Araeodontia isabellae*, arrow indicates posterior portion of fourth protarsomere not incised; I. *Cymatodera championi*, arrow indicates posterior portion of fourth protarsomere not incised.
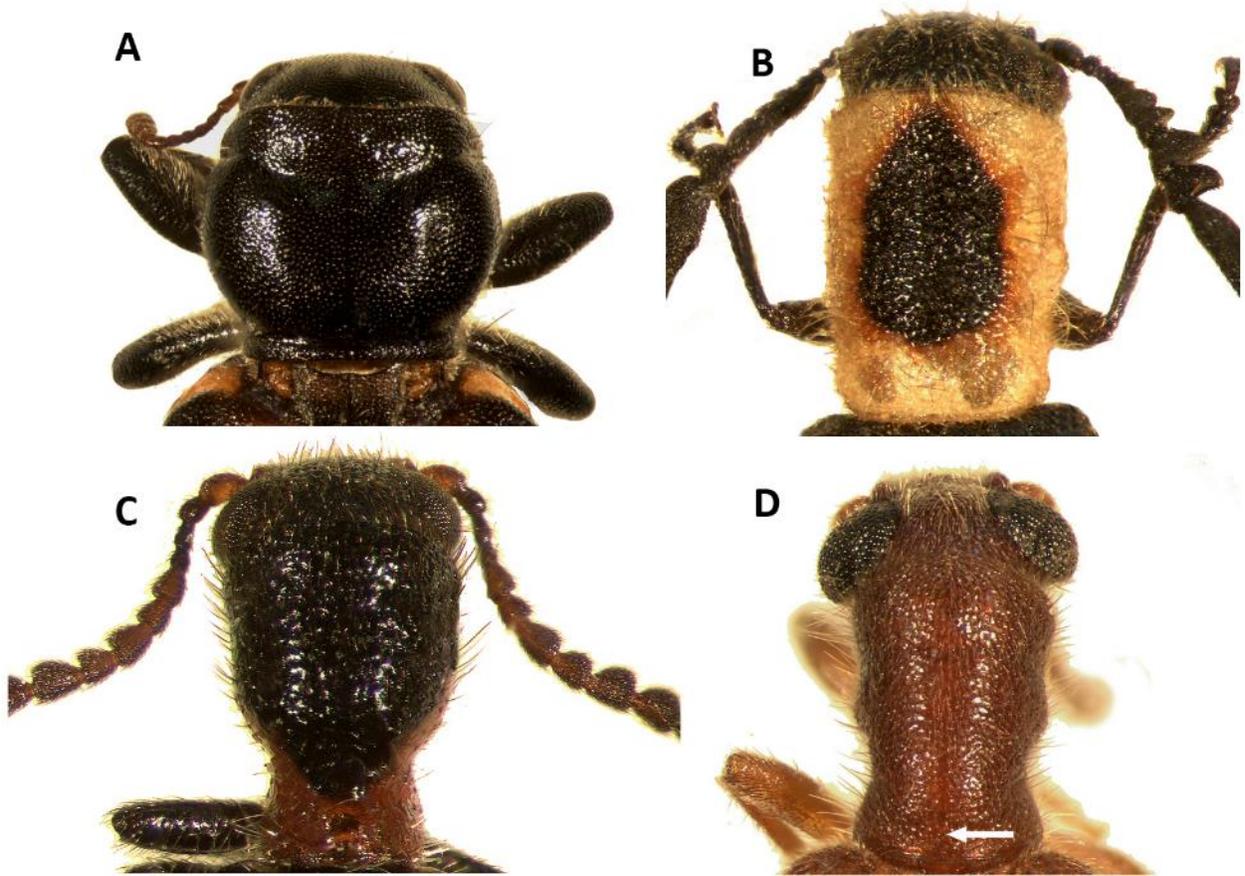
Fig. 3.16 A-D Pronotal shape in dorsal view of: A. *Enoclerus zonatus*; B. *Monophylla terminata*; C. *Barrotillus kropotkini*; D. *Cymatodera antennata*, arrow indicates position of sub-basal impression.
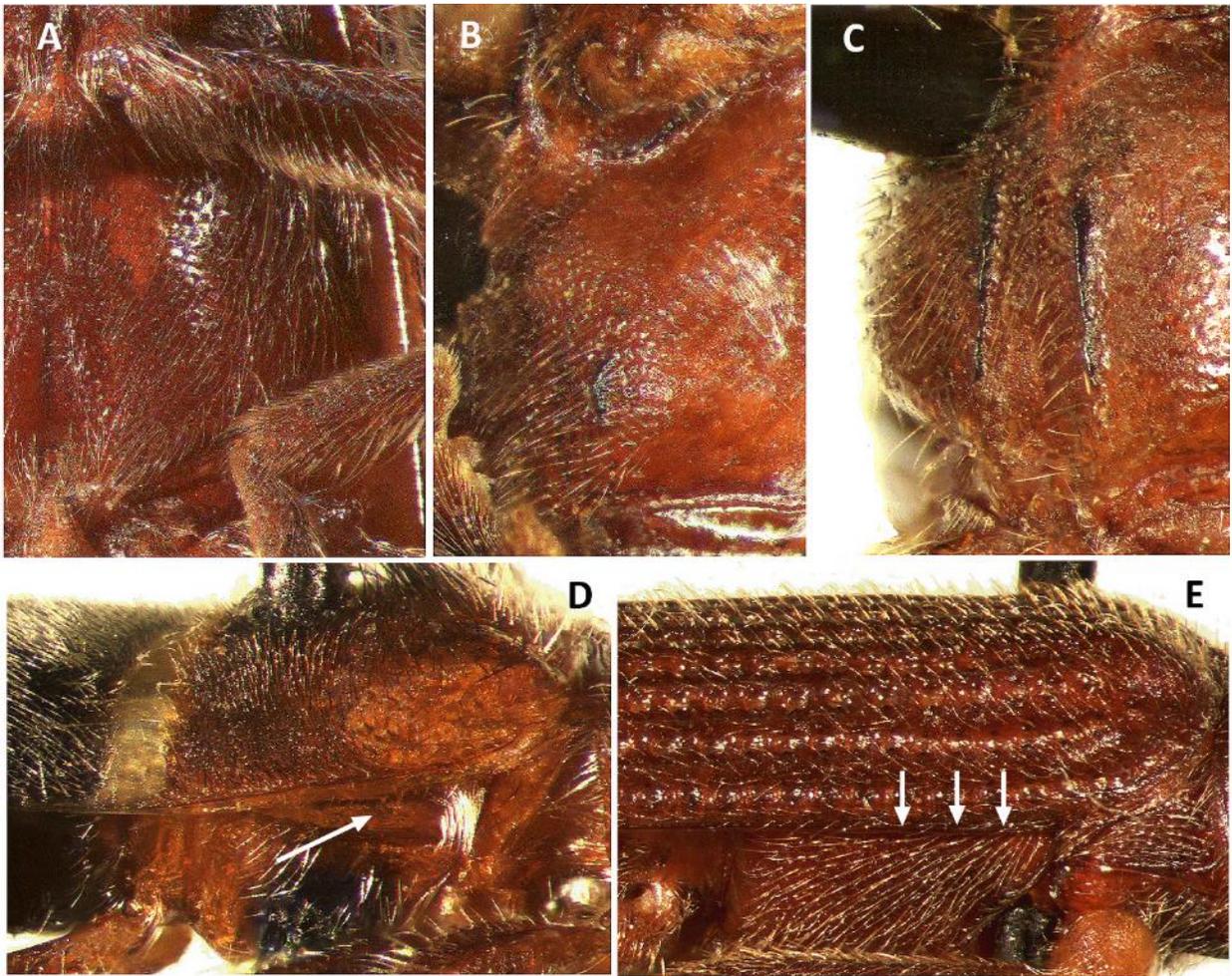
Fig. 3.17 A-C Metasterna of: A. *Lecontella gnara*; B. *Cymatodera balteata*; C. *C. neomexicana*. D-E Lateral view of mesothorax of: D. *Callotillus eburneocinctus*, arrow indicates metepisternum visible, not covered by elytron; E. *Lecontella gnara*, arrows indicate elytron covering metepisternum.
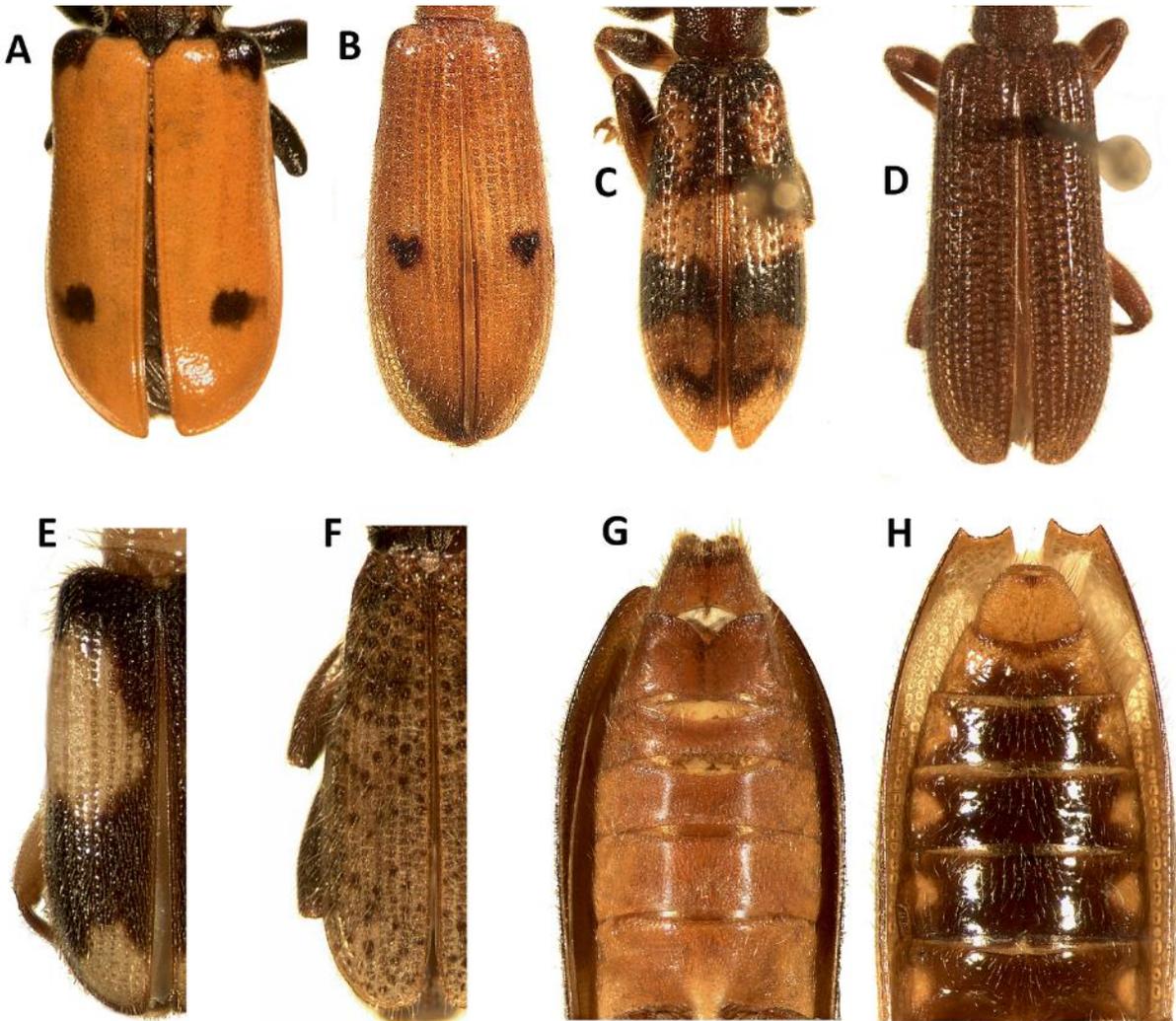
Fig. 3.18 A-D Elytral punctations of: A. *Enoclerus zonatus*; B. *Cymatodera bipunctata*; C. *C. balteata*; D. *Lecontella gnara*. E-F Striae on elytra of: E. *Araeodontia peninsularis*; F. *Cymatodera barri*; G-H Abdomen of: G. *Cymatodera californica*; H. *C. sallei*.
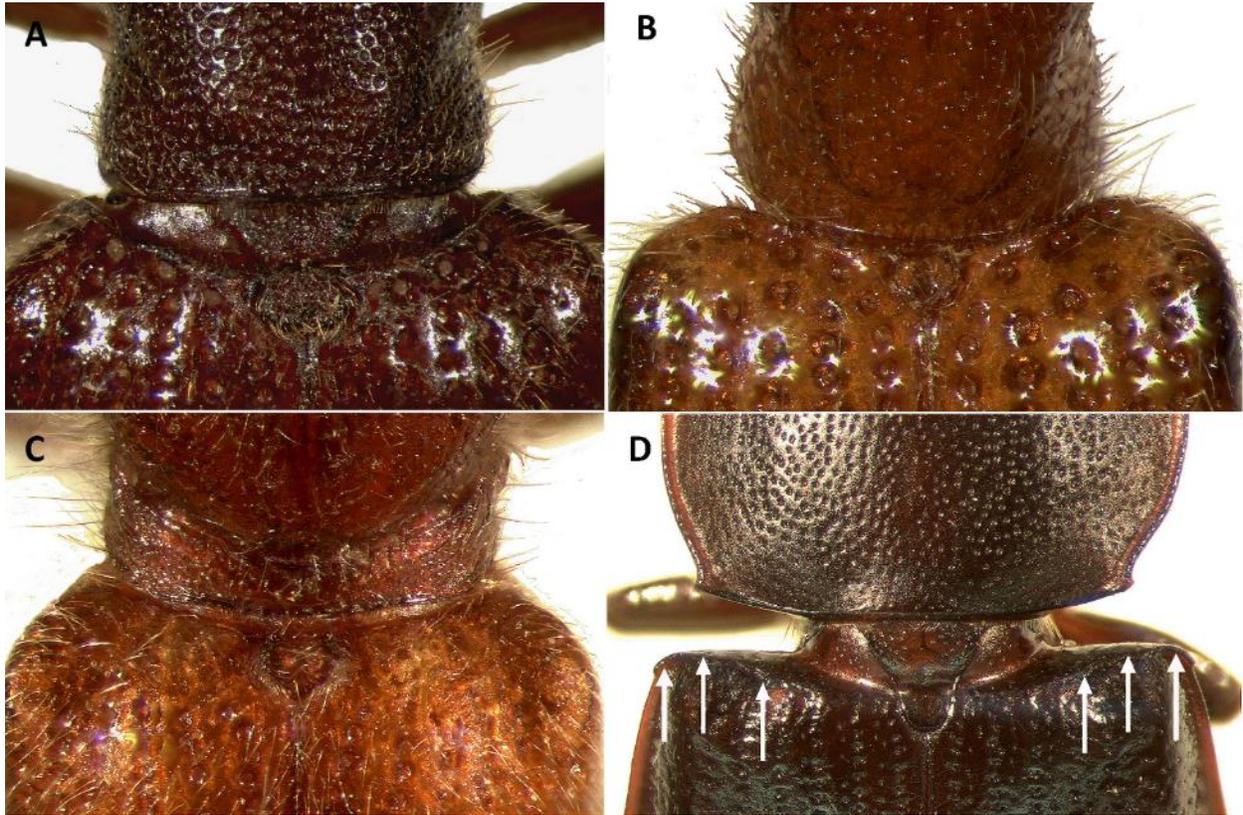
Fig. 3.19 A-C Interstices on the elytral base of: A. *Lecontella gnara*; B. *Bogcia oaxacae*; C *Priocera castanea*. D. Anterior elytral margin of *Tenebroides americanus*, arrows indicate extension of carinae on elytral base.
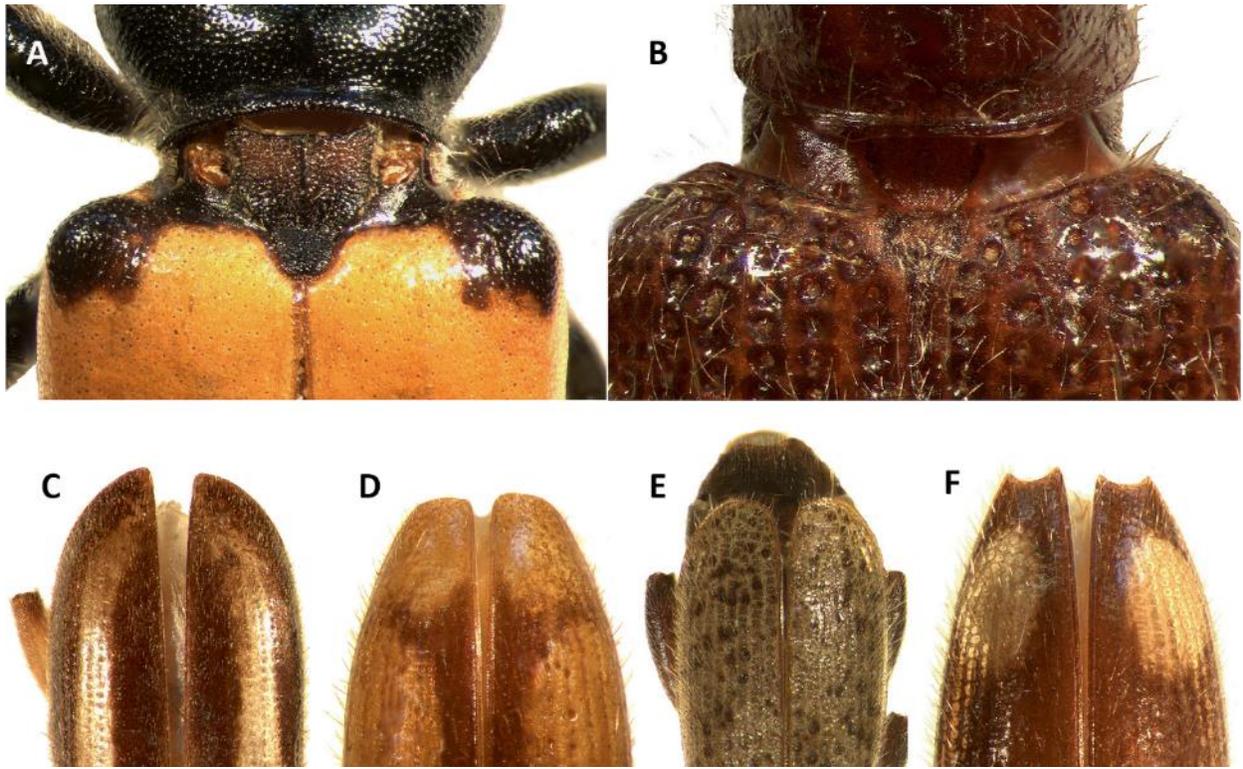
Fig. 3.20 A-B Anterior elytral margin of: A. *Enoclerus zonatus*; B. *Cymatodera guatemalensis*. C-D Elytral apex shape of: C. *Araeodontia marginalis*; D. *Cymatodera venusta*; E. *C. barri*; F. *C. championi*.
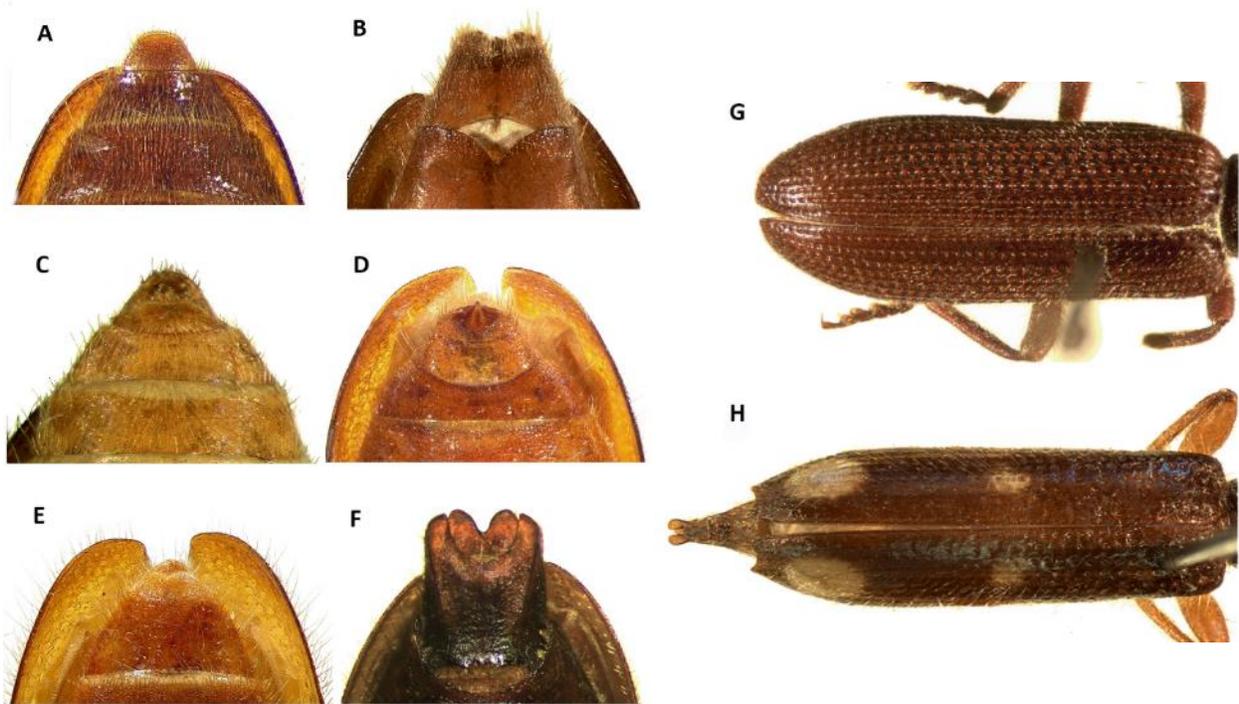
Fig. 3.21 A-H. Pygidium of: A. *Bogcia oaxacae* (female); B. *Cymatodera californica* (female); C. *Enoclerus nigripes* (male); D. *Cymatodera rosalinae* (male); E. *Cymatodera limatula* (male); F. *Cymatodera marmorata* (male). G-H View of pygidium in dorsal position of: A. *Lecontella gnara*, pygidium concealed B. *Cymatodera sallei,* pygidium exposed.
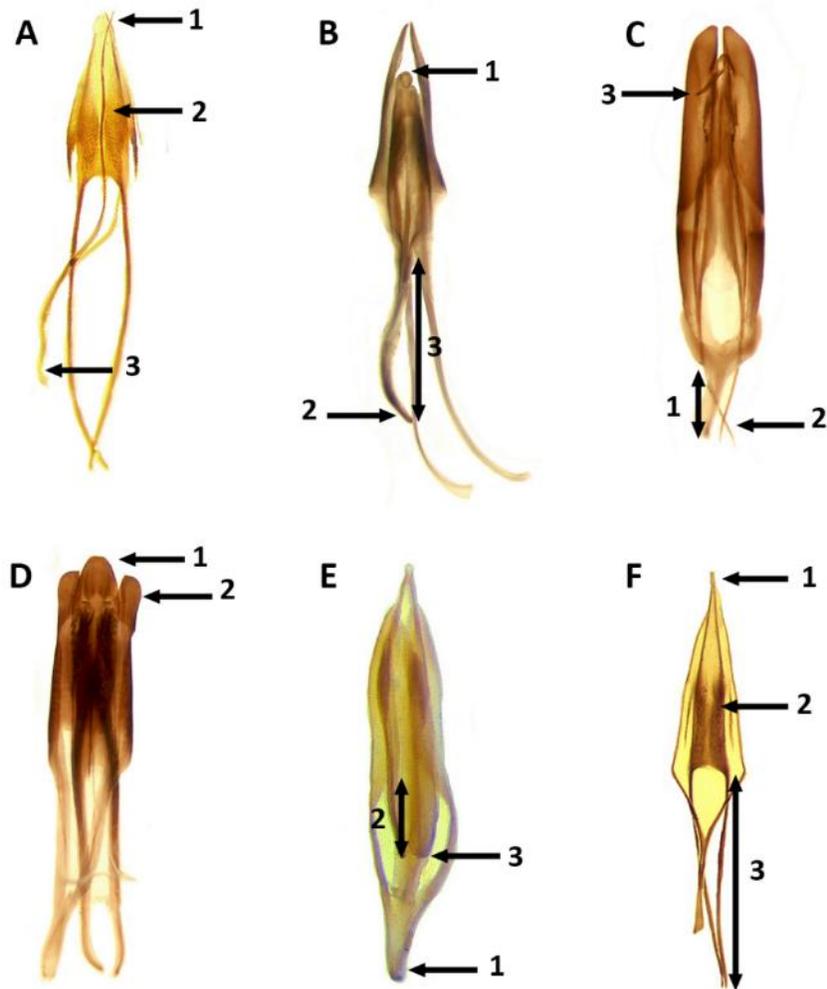
Fig. 3.22 A-F Male genitalia of: A. *Cymatodera limatula*, 1 copulatory piece tapered, 2 phallic plate devoid of denticles, 3 phallobasic apodeme slender distally; B. *Araeodontia peninsularis*, 1 copulatory piece swollen distally, 2 phallobasic apodeme slender distally, 3 phallobasic apodeme long; C. *Cymatodera hopei*, 1 phallobasic apodeme short, 2 endophalloc struts slender, 3 phallic spicule; D. *Cymatodera californica,* 1 copulatory piece blunt, 2 parameres swollen distally; E. *Monophylla terminata*, 1 phallobasic apodeme distally robust, 2 endophallic struts short, 3 endophallic struts truncate distally; F. *Bogcia oaxacae*, 1 copulatory piece tapered, 2. phallic plate devoid of denticles, 3 endophallic struts long.
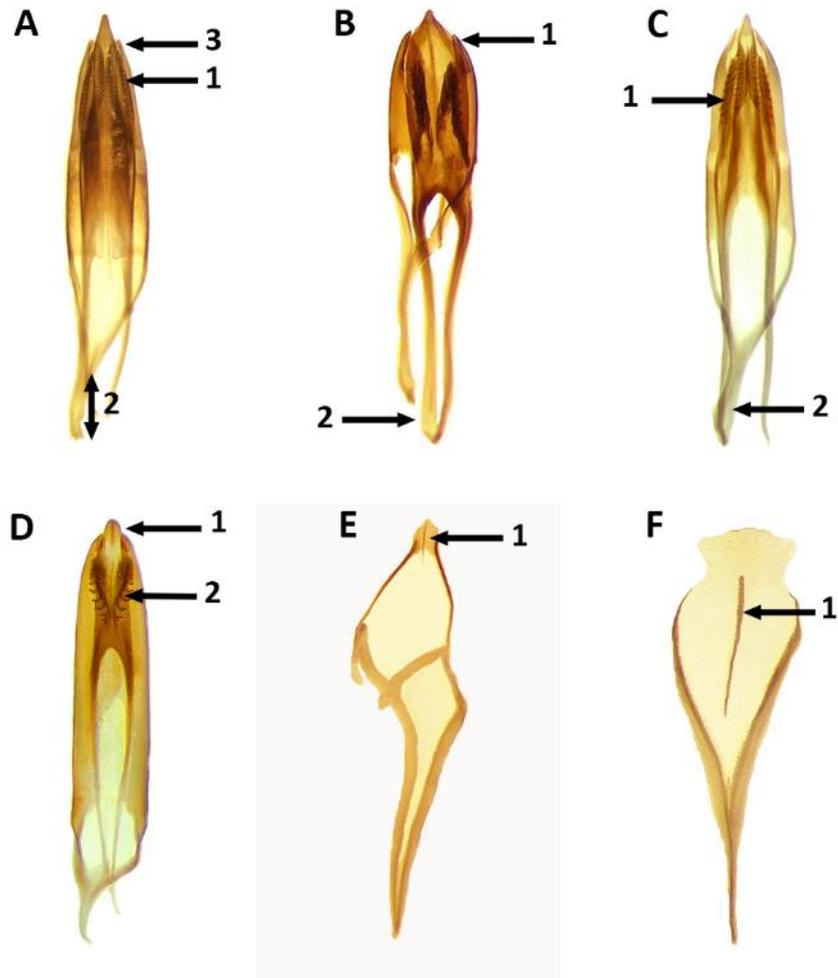
Fig. 3.23 A-D Male genitalia of: A. *Cymatodera balteata*, 1 phallic plate armed with denticles, 2 phallobasic apodeme short, 3 parameres rounded distally; B. *C. rosalinae*, 1 parameres rounded distally, 2 endophallic struts robust distally; C. *C. floridana*, 1 phallic plate armed with denticles, 2 phallobasic apodeme robust distally; D. *C. barri*, 1 copulatory piece rounded distally, 2 phallic plate armed with denticles. E-F Spicular fork of: E. *Cymatodera championi*, 1 intraspicular plate narrow and short; F. *C. californica*, 1 intraspicular plate wide and elongate.

Chapter 4 - Molecular phylogeny of the New World Tillinae (Coleoptera: Cleridae): testing the monophyly of the group and intergeneric relationships

Abstract

Tillinae is the second largest subfamily within Cleridae, after Clerinae, and the phylogeny of the subfamily has never been analyzed with molecular data. The monophyly of the New World Tillinae was inferred and intergeneric relationships were examined using approximately 3600 nt of both nuclear and mitochondrial rDNA. The phylogenetic analysis was based on three loci: the mitochondrial genes 16S rDNA and cytochrome *c* oxidase subunit I (COI), and the nuclear gene 28S (LSU) rDNA. These loci were amplified for 89 taxa in 37 genera. Data were analyzed using a Bayesian approach. Maximum parsimony and maximum likelihood inferences were also tested to compare with the results obtained from the Bayesian analysis. The molecular- and molecular + morphology-based analyses recovered Trogossitidae as a paraphyletic group closely allied to Phloiophilidae. A clade composed of Dasytidae + Malachidae + Melyridae was recovered as a derived monophyletic group in the cleroid lineage. The identity of the sister group of all Cleridae was not fully recovered. Clerinae, Hydnocerinae and Epiclininae were always rendered as paraphyletic groups. Tillinae was found to be a derived and monophyletic. Within Tillinae, Old World tillinids were generally recovered as basal taxa. A group composed of the Old World *Cladiscus* Chevrolat, *Cylidrus* Latreille, *Spinoza* Lewis, *Tilloidea* Laporte *and Tillus* Olivier,

together with the New World genera *Neocallotillus* Burke and *Monophylla* Spinola, were

recovered as the sister to other New World Tillinae. All analyses rendered *Cymatodera* Gray as

monophyletic only when the small *Araeodontia* Barr, *Cymatoderella* Barr *and Lecontella*

Wolcott & Dybas were included. The classification of *Cymatodera* and related groups is

discussed in detail. A concatenated molecular + morphological phylogeny was constructed. The

topology obtained increased the taxon-sampling to 134 species in 48 genera. Results obtained in

this analysis are generally consistent with the molecular-based topology. Similarities and

differences among these methods are discussed, as are differences in Chapter 3 results and

molecular results presented here.

1. Introduction

1.1 Distribution and checklist.

The subfamily Tillinae has a cosmopolitan distribution (Opitz, 2010). In his *Coleopterum

Catalogus Supplementa*, Corporaal (1950) listed 51 genera with approximately 521 species

worldwide. Opitz (2010) included 543 described species in 67 genera. The highest diversity of

tillinid species is found in North American temperate and sub-temperate zones and the equatorial

regions of Africa and Madagascar. Despite this diversity, little is known about the biogeography

of the subfamily. Distribution records of New World Tillinae have been reported in some works

since the eighteenth century; early works include those of Spinola (1844), Gemminger & Harold

(1869), Lohde (1900), Schenkling (1910), Wolcott (1947), Corporaal (1950), Papp (1960) and

Barr (1975). A modern synthesis of this information is given by Burke et al. (2015). In

Corporaal's catalogue, 121 tilline species were recorded from the Americas. Barr (1975) listed

282

131 species of Tillinae in North and Central America and the West Indies. Papp (1960) recorded

115 tilline species inhabiting North America, but that work did not cover those species inhabiting

the Caribbean Islands. More recently, Opitz (2010) presented a distribution map of the checkered

beetles of the world (by subfamily, not by genus or species) and listed 67 tilline genera, 11 of

which are found in the New World. Later on, Burke & Zolnerowich (2016) erected the genus

Neocallotillus, thus, there are 12 recognized genera in the New World.

1.2 Systematics

According to the higher-level morphological classification of the Cleridae given by Kolibàč

(1992) and Opitz (2010) (Fig. 4.1 A-B), the Tillinae was recovered as a derived group in the

clerid lineage, closely related to Clerinae and Hydnocerinae. The molecular phylogenetic

analysis by Gunter et al. (2013) recovered Tillinae as the most basal lineage within the Cleridae,

and the sister group of all other clerids (Fig. 4.1-C). The state of the procoxae, where the fusion

of the procryptosternum with the pronotal extension produces a closed cavity, may represent an

apomorphy for the Tillinae (Opitz, 2010), but a plesiomorphic state in Gunter's classification

(2013).

In this study, a molecular phylogenetic analysis to examine the monophyly of the Tillinae

and the phylogenetic relationships of a number of genera was undertaken. In addition, a

molecular + morphological phylogeny was reconstructed to increase taxon sampling and to

obtain greater resolution at the genus and species level.

2. Materials and Methods

2.1. Taxon sampling

The complete dataset consisted of 89 species from 36 genera and included six genera of New World Tillinae and five genera of Old World Tillinae, representatives of 9 clerid subfamilies (*sensu* Opitz, 2010), and 11 taxa from 4 non-clerid subfamilies from the superfamily Cleroidea as outgroups (Table 4.1). Five genera from the Old World Tillinae were included in the analysis; although reduced in nature, this taxon-sampling was carefully selected so tillines from the four continents with evident morphological differences could be represented. Due to the rarity of material suitable for DNA, four New World genera were not included in this analysis, they are the monotypic *Barrotillus, Bostrichoclerus* and *Bogcia*, and *Onychotillus*, with five described species. The speciose *Cymatodera* was well represented in the analysis, with 42 species, almost a third of all described taxa (Burke et al., 2015). A profile of amplification for each individual gene and reference of sequences acquired from GenBank when applicable, is given in Table 4.2 for all taxa.

2.2 Molecular + Morphology-based dataset

The inclusion of a morphological dataset expanded the taxon-sampling to 134 species from 48 genera. The new dataset included representatives of 13 taxa from the cleroid families Dasytidae, Malachidae, Melyridae, Phloiophilidae and Trogossitidae as outgroups. The clerid taxon sampling included species from eight of the 12 subfamilies accepted by Opitz (2010) and the subfamily Epiclininae proposed by Gunter (2013). The Tillinae taxon sampling comprised 10 Old World Tillinae genera and eleven of the 12 genera inhabiting the New World. The *Cymatodera* taxon sampling was expanded to 64 species, almost half of all described species (Burke et al., 2015). A list of taxa, distribution, and collecting localities is provided in Table 4.1.

2.3 DNA amplification and gene sequencing

DNA was extracted from total body, head and/or thorax of specimens using the QIAGEN DNeasy tissue kit as per standard protocols. The mitochondrial genes 16S rDNA and cytochrome *c* oxidase subunit I (COI), and the nuclear gene 28S (large subunit) rDNA, were amplified. The 16S rDNA locus was amplified as a single fragment with the primers '16S-F1' and '16S-R1', but in some cases it was amplified using the primer pairs '16c' and '12sB'. COI was amplified in two smaller fragments using the primer pairs 'LCO-1490' to 'HCO-700ME' and 'Jerry' and 'Pat'. Partial 28S sequences also were generated using the primer pairs '28Sff' to '28Sdd'. Primer sequences and references are listed in Table 5.3. Sequences were aligned to form contigs and edited using Geneious (V. 7.1; Drummond et al., 2012). Amplifications were conducted in the Laboratory of Molecular Entomology at the Department of Entomology, Kansas State University, as follows: amplifications were conducted using the QIAGEN Fast Cycling PCR Kit with the following reaction composition: 10 µL of QIAGEN Fast Cycling PCR Master Mix, 2 µL of 10x CoralLoad Fast Cycling Dye, 1 µL of each primer at a 1 µM concentration, 4 µL of RNase-free water, and 1 µL of template producing 20 µL of reaction volume. Typical PCR reactions were performed under the following conditions: initial activation 5 m at 95°C; 3-step cycle: denaturation 30s at 96°C; annealing 1 m at 45°C; extension 30s at 68°C (40 cycles); final extension 10 m at 72°C. Annealing temperature between 40°C to 50°C according to the locus to be amplified. Detailed thermocycling conditions are given in Table 4.4. PCR products were purified using ZYMO DNA (PCR) Clean and Concentrator Kit. Cleaned PCR products were sent to the DNA Sequencing and Genotyping Facility, Department of Plant Pathology, Kansas State University, for sequencing. Sequences were edited using Geneious (V 7.1; Drummond et al., 2012).

2.4 Multiple alignment and phylogenetic analysis

Sequences of each gene were aligned separately using default parameters of MUSCLE in Geneious (V. 7.1; Drummond et al., 2012). Each alignment was edited by manual inspection before concatenation of the dataset. Gaps were treated as missing data. The program jModelTest (Darriba et al., 2012) was used to find the best substitution model for each single-gene dataset (Table 4.5). Single-gene phylogenies were estimated through Maximum Parsimony (MP) implemented in PAUP (Swofford, 2016), Maximum Likelihood (ML) implemented in PhyML in Geneious (Drummond et al., 2012) and/or PAUP (Swofford, 2016), and Bayesian inference (BI) implemented in MrBayes 3.2 (Huelsenbeck & Ronquist 2001) to check for potential conflicts between gene trees. Subsequently, single-gene datasets were concatenated using Geneious 7.1.9 (V. 7.1; Drummond et al., 2012) to produce a combined matrix spanning ~3600 nt. The program PartitionFinder (Lanfear et al., 2012) was used to determine the best partitioning strategy and nucleotide substitution models for the concatenated dataset; the optimal partitioning scheme divided the dataset in five partitions, separating the genes 16S rDNA and 28S(LSU) rDNA, and subdividing the separate codon positions of COI (Table 4.7); other partition strategies were also tested (Table 4.6).

For the Maximum Parsimony analysis, a heuristic search using a Tree-Bisection-Reconnection procedure was performed. All characters were initially unordered and unweighted. The MulTrees option was in effect during the analysis and a strict consensus tree was generated from the best trees produced. For the Maximum Likelihood analysis, a heuristic search using a Subtree-Pruning-Regrafting topology search was conducted implementing the general time reversible substitution model, with proportion of invariable sites and gamma distribution fixed; a

strict consensus tree was generated from the best topologies obtained in the analysis. For the

Bayesian analysis, the dataset was partitioned as predicted by PartitionFinder (Lanfear et al.,

2012), three partition strategies were tested (Table 4.6); the analysis was conducted using

MrBayes V 3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), and each

analysis consisted of 10 million generations with a random starting tree, and two simultaneous

runs with four Markov chains sampled every 1000 generations with unlinked partitions.

Stationarity in MCMC chains was determined in Tracer (Rambaut & Drummond, 2007), twenty

percent of the generations were discarded as burn-in. A 50% consensus tree was obtained from

the two combined runs to establish the posterior probabilities of clades.

2.5 Molecular + morphology-based phylogenetic analysis

A phylogenetic analysis based on a concatenated DNA dataset and a morphology-based

dataset (see Tables 3.2, 3.3 from Chapter 3) was performed in a Bayesian Inference framework.

The concatenated DNA and molecular-based datasets were merged using Mesquite V 2.75 for

Windows (Maddison & Maddison, 2011) producing a matrix of 134 taxa from 48 genera. This

included seven genera of New World Tillinae, five genera of Old World Tillinae, members of 11

non-Tillinae subfamilies and eight genera of non-clerid Cleroidea (Table 4.2 and see Table 3.2

from Chapter 3). The new Nexus file was then edited manually to specify the corresponding

character-states and substitution models. For the molecular dataset, the substitution models

implemented were those obtained from PartitionFinder (Lanfear et al., 2012) (Table 4.7); for the

morphology-based dataset, the Mk1 model modeling rate heterogeneity among characters using

gamma distribution (Lewis, 2001) was implemented. Alternative schemes were also tested

(Table 4.6). The phylogenetic analysis was performed in MrBayes V. 3.2.1 (Huelsenbeck &

Ronquist, 2001; Ronquist & Huelsenbeck, 2003) and consisted of 10 million generations with a random starting tree, and two simultaneous runs with four Markov chains sampled every 1000 generations with unlinked partition (Drummond et al., 2006; Drummond and Rambaut, 2007). Substitution models were unlinked among partitions. Twenty percent of the generations were discarded as burn-in and a 50% consensus tree was obtained from the two combined runs to establish the posterior probabilities of clades.

3. Phylogenetic results

The amplified fragments varied in length from 614 to 1466 nt for COI, 318 to 539 nt for 16S, and 536 to 1465 nt for 28S. The total length of the dataset was of approximately 3600 nt. Nucleotide frequencies of single-gene datasets were as follows: COI: A: 28.1%, C: 19.5%, G: 16.5% and T: 36.0%; 16S: A: 35.6%, C: 9.6%, G: 15.9%, and T: 39.1%; and 28S: A: 25.6%, C: 26.6%, G: 29.9%, and T: 18.9%. Base frequencies were relatively equal in the nuclear gene 28S, while the mitochondrial regions 16S and COI showed higher A-T bias.

PartitionFinder (Lanfear et al., 2012) selected five partitions (16S, 28S, COI first codon position, COI second codon position, and COI third codon position) as the optimal partitioning scheme with the nucleotide substitution model GTR+I+G for 16S, 28S, and COI first codon position; GTR+I for COI second codon position; and SYM+I+G for COI third codon position. In addition to the selected scheme, alternative partitioning strategies were also tested (Table 4.7).

Overall, for the single-gene topologies, as well as the concatenated DNA dataset, major clades for all resulting topologies using MP, ML, and BI were generally equally recovered and

with moderate to high posterior probability values (Figs. 4.2-3, 4.5). The single-gene dataset corresponding to the COI locus produced the widespread discordance when compared with other loci, recovering the Tillinae as an unresolved clade, together with all major clerid subfamily taxa (Fig. 4.4). However, when the COI-based matrix was concatenated with other matrices, the final product was a majority-rule topology highly congruent with the 16S and 28S topologies, and was supported by high posterior probability values (Fig. 4.5). Unless stated otherwise, results discussed here are from the DNA-based concatenated analysis.

3.1 Phylogenetic results of the molecular-based analysis

Results of the phylogenetic analysis are: the genus *Temnoscheila* (Trogossitidae) was recovered as sister to all other cleroid subfamilies. Trogossitidae was not recovered as a monophyletic group, with close relationship to Phloiophilidae. High posterior probability values support the paraphyly of Trogossitidae. A clade composed of Dasytidae + Malachidae + Melyridae was always recovered as monophyletic in all DNA topologies with high posterior probability values. The sister to Cleridae was not resolved. *Madoniella dislocatus* (Say) (Epiphloeinae) was recovered as the sister to other Cleridae for the single-gene 16S (Fig. 4.2); the topology based on the 28S locus obtained *Cregya oculata* (Say) (Peloniinae) as the sister to other clerids (Fig. 4.3); the COI topology obtained a large polytomy for the clerid lineage (Fig. 4.4); while the concatenated dataset recovered a polytomy composed of *C. oculata* (Say) and *M. dislocatus* as sister to other Cleridae (Fig. 4.5). The subfamily Thaneroclerinae was recovered as part of Cleridae in all analyses. A clade composed of Thaneroclerinae + Neorthopleurinae + (Korynetinae, Peloniinae) + Enopliinae were consistently recovered as early lineages of the Cleridae. Single-gene topologies, excluding COI, and the concatenated dataset indicate that

neither Clerinae nor Hydnocerinae nor Epiclininae *sensu* Gunter et al. (2013) are monophyletic groups. The concatenated dataset found Hydnocerinae as a clade nested within a group of clades containing Clerinae and Epiclininae.

Clerinae was recovered as paraphyletic by the inclusion of Epiclininae and Hydnocerinae. The Tillinae was recovered as a monophyletic subfamily based on most datasets, except for the COI single-gene topology (Fig. 4.4), and can be divided in five major groups: 1) a clade composed of Old World Tillinae, *Neocallotillus* and *Monophylla* species; 2) *Lecontella* species; 3) a clade comprising *Cymatodera* (in part) species, *Cymatoderella* species and *Araeodontia* species; 4) a clade composed of *Cymatodera xavierae* Knull and related *Cymatodera* (in part) species; and 5) a clade comprising derived *Cymatodera* (in part) species (Fig. 4.5). These groups were also recovered for the 16S single-gene topologies (Fig. 4.2), but were not fully recovered for the 28S single-gene phylogeny (Figs. 4.3). The 16S and concatenated-based topologies recovered Old World species and the New World Tillinae *Neocallotillus* and *Monophylla* as basal taxa and as a sister clade to all other New World tillinids. These results were not found in the 28S-based analysis, with Old World tillinids and the New World *Neocallotillus* and *Monophylla* recovered at different positions in the topology (Fig. 4.3). The cause of this discrepancy is thought to be due to incomplete lineage sorting, where ancestral tillinid species probably were polymorphic for the 28S gene and, over time and due to selection and genetic drift, polymorphism for that gene was probably lost in some species but retained in others; consequently, species maintaining more than one allele of the same gene will appear to be more closely related than they are, depending on the inherited allele.

In all analyses, the speciose *Cymatodera* was obtained as paraphyletic by the inclusion of *Araeodontia*, *Lecontella* and *Cymatoderella*. Two major lineages within the large *Cymatodera* were generally recovered with moderately to high posterior probability values; morphological characters (See Figs. 3.3 and 3.21 from Chapter 3) support the split of the large *Cymatodera* group into these clades.

3.2 Phylogenetic results of the molecular + morphology-based analysis

A molecular + morphology-based phylogenetic analysis using the concatenated DNA-based and the morphology-based datasets, constructed in Chapter 3, was performed. The taxon-sampling consisted of 134 taxa from 48 genera (Table 4.2 and see Table 3.3 from Chapter 3). Results here suggest that *Temnsocheila in part* (Trogossitidae) is the sister to other cleroid groups. Trogossitidae was not recovered as monophyletic and had a close relationship with Phloiophilidae. A clade composed of Malachidae + Dasytidae + Trogossitidae *in part* + Melyridae was recovered as a derived clade in the cleroid lineage. Relationships among Dasytidae, Malachidae and Trogossitidae (in part), are not fully resolved.

Within Cleridae, Taneroclerinae (*Zenodosus sanguineus*) was obtained as sister to remaining clerids. The Enopliinae, Epiphloeinae, Neorthopleurinae, Korynetinae, Peloniinae lineages were recovered as basal groups in the clerid lineage. Peloniinae was found to be polyphyletic, separating *Cregya* and *Pelonium + Chariessa*. Clerinae, Epiclininae, Hydnocerinae and Tillinae were rendered as derived clades. A polytomy containing Clerinae, Epiclininae, Hydnocerinae was found, thus, those subfamily relationships could not be resolved.

Tillinae was recovered as monophyletic with an Old World Tillinae clade composed of

Tillus + *Tilloidea* + *Cladiscus* + *Gastrocentrum* + *Orthocladiscus* + *Strotocera* + *Cylidroctenus* + *Clydrus* + *Stenocylidrus*, as sister to all Tillinae. Two clades composed of *Spinoza* (Old World) + (*Onychotillus* + *Neocallotillus*) + *Barrotillus* were obtained as sister to all other New World tillinids. *Cymatodera* was rendered as paraphyletic clade with the presence of *Araeodontia, Bogcia, Cymatoderella* and *Lecontella* in a large clade. Finally, within this large clade, interspecific relationships are partially resolved, with three major groups: 1) an arrangement of clades composed of *Cymatodera tricolor* and related taxa, *Cymatodera serena* and related taxa, *Cymatodera bicolor* and related taxa, and *Bogcia, Lecontella* and related taxa. Those clades can be grouped together based on morphological similarities such as the feebly to moderately sclerotized aedeagus, and moderate to large size; 5) *Araeodontia* and related taxa, these species can be morphologically grouped based on the simple male pygidium, feebly sclerotized aedeagus and small size; and 6) *Cymatodera mitchelli* Chapin*, C. californica* Horn*, C. championi* Gorham and related species, these taxa are morphologically grouped together based on their elaborate male pygidium, coarsely sclerotized aedeagus and large size (Fig. 4.7).

4. Discussion

The first comprehensive molecular phylogeny of the Tillinae is presented here, with DNA data for 89 cleroid species. The DNA-based and the molecular + morphology-based analyses recovered Trogossitidae as a paraphyletic group, with the small family Phloiophilidae always closely related to Trogossitidae. Similar results were also obtained by Hunt et al. (2007); Gunter et al. (2013); and McKenna et al. (2015), supporting the hypothesis that Trogossitidae is a paraphyletic group. A melyrid lineage consisting of Dasytidae + Malachidae + Melyridae was

always recovered as derived in the cleroid lineage. This result is consistent with Gunter et al. (2013), supporting the general notion of the close relationship among these families, with a melyrid lineage (*sensu* Majer, 1994) composed of Rhadalidae + Mauroniscidae + Prionoceridae + Melyridae + Dasytidae + Malachiidae, together with Trogossitidae (in part) consistently obtained in their analysis. Similar results were obtained by Bocakova et al. (2011), who recovered strongly supported family-level clades within this large monophyletic group.

The clerid lineage was always recovered as monophyletic, but interfamily relationships were not fully resolved. Kolibáč (1997) synonymized the subfamilies Tarsosteninae, Enopliinae and Epiphloeinae with Korynetinae, grouping all species with a reduced fourth tarsomere within Korynetinae; in addition, he assigned family status to the subfamily Thaneroclerinae (Kolibáč, 1992) containing two tribes, Thaneroclerini and Zenodosini. Bouchard et al. (2011) elevated these tribes to subfamily level. Opitz (2010) divided Korynetinae *sensu* Kolibáč (1997) into six subfamilies: Korynetinae, Neorthopleurinae, Enopliinae, Peloniinae, Tarsosteninae and Epiphloeinae; in the same study, he rejected Thanerocleridae as a separate family (Kolibáč, 1992), indicating that this group would be considered as a subfamily within Cleridae. Gunter et al. (2013) recovered Thaneroclerinae as part of the Cleridae lineage, however, the authors indicated that the division of Korynetinae *sensu* Kolibáč (1997) in six subfamilies given by Opitz (2010) is debatable, rendering these subfamilies as paraphyletic groups. In this study, all molecular-based analyses, including the molecular + morphology-based topology, recovered Thaneroclerinae as part of the Cleridae lineage; this finding corroborates the view of Opitz (2010) of treating Thaneroclerinae as a subfamily within Cleridae, rather than elevating the group to the family level, as stated by Kolibáč (1992) and Bouchard et al. (2011). The division of

Korynetinae *sensu* Kolibáč (1997) in six subfamilies proposed by Opitz (2010) was not supported in this study, but rather, the findings obtaining here are congruent with Kolibáč (1997) in that Korynetinae represents a single subfamily. This result supports Gunter et al. (2013) in finding Korynetinae *sensu* Kolibáč (1997) to be a monophyletic group, thus disagreeing with Opitz's (2010) treatment of Korynetinae.

The sister group to all other Cleridae cannot be fully established in this study. The subfamily Epiphloeinae (*Madoniella dislocatus*) was recovered as sister to all other clerids in the single-gene 16S phylogeny. The single-gene 28S phylogeny found Peloniinae (*Cregya oculata*) as the sister to all other clerids. The concatenated dataset rendered Epiphloeinae + Peloninae as sister to the Cleridae, while the molecular + morphology-based analysis recovered Thaneroclerinae (*Zenodosus sanguineus*) as the sister to all clerid subfamilies (Figs. 4.2-4.5). These findings differ from those found by Gunter et al. (2013), who found Tillinae to be the sister to all other clerids. The results obtained here show partial agreement with the findings obtained by Opitz (2010), with Thaneroclerinae as sister to all other clerids.

The COI-based phylogenetic analysis recovered Cleridae as a large polytomy comprised of all major clerid subfamilies with little resolution (Fig. 4.4) producing conflicting relationships and collapsed branches. An explanation for the discrepancies obtained from the COI dataset could be that COI is a locus undergoing fast substitution rates (i.e. much of the variation may be homoplasious). In addition, it has been shown that the pattern of mitochondrial mutation rates is strikingly different not only among higher taxonomic levels, but also at the species level (Montooth & Rand, 2008). Thus, certain taxa within the same family, or even the same genus,

can have remarkably different substitution rates in the COI locus. It is possible that New World tillinids are undergoing a rapid process of speciation, evidence of this process is demonstrated after analyzing the results obtained from the application of a relaxed molecular clock (see Fig. 5.4 from Chapter 5). That chapter discusses how *Cymatodera* has undergone numerous speciation events and rapid diversification in the last 20-40 million years. Therefore, it is suspected that due to the rapid speciation process tillinids are currently undergoing, the COI locus is accumulating a high number of mutations, which can result in long branches. Branch lengths can be easily measured in the single-gene COI phylogram (note branch length scale in lower left of Fig. 4.4). This figure shows relatively long branches for most Tillinae species, indicating a high number of changes per site have occurred for those taxa. In contrast, for other phylograms obtained (Figs. 5.2-3, 5-6), branch lengths are relatively shorter when compared with the single-gene COI phylogram. Based on this result, it is highly advised that phylogenetic analyses based on molecular data should include more than one genetic region as source of data, so potential disagreement(s) among gene trees can be detected and, if possible, ameliorated.

In their molecular analysis of the Cleridae, Gunter et al. (2013) erected a new subfamily, Epiclininae, which is morphologically similar to Clerinae. While the authors indicated that no morphological synapomorphies are known for the group, the separation of Epiclininae from Clerinae was based on the position of a number of Australasian clerids in their topology. The Epiclininae clade was recovered early in the evolutionary history of Cleridae, with close relationship with Korynetinae and Neorthopleurinae, rather than closely related to Clerinae. Here, a clade composed of Clerinae + Hydnocerinae + Epiclininae was recovered in both DNA-based and molecular + morphology-based analyses, with high posterior probability values,

suggesting a close relationship between Epiclininae and Clerinae. Results given here support the hypothesis given by Gunter et al. (2013), with neither Clerinae nor Hydnocerinae represent monophyletic lineages. Intergeneric relationships of these taxa were recovered with high resolution in the 16S and the concatenated analyses, with three lesser clades nested within this group: the first one is composed of Clerinae *in part* + Epiclininae, the second encompassing Hydnocerinae, and the third group including Clerinae *in part* (Fig. 4.5). Only the 28S analysis recovered two clades: Clerinae + Epiclininae and Hydnocerinae (Fig. 4.3). Similarly, Gunter et al. (2013) subdivided the Clerinae + Hydnocerinae lineage in three nested clades, one composed of Clerinae *in part*, the second grouping Clerinae *in part* + Hydnocerinae *in part*, and a third clade composed of Clerinae *in part* + Hydnocerinae *in part*. The molecular + morphology-based analysis did not resolve intergeneric relationships of this clade, producing a large polytomy composed of Clerinae + Hydnocerinae + Epiclininae (Figs. 4.6 and 4.7).

All DNA-based and the molecular + morphology-based analyses recovered Tillinae as monophyletic (Figs. 4.2, 4.3, 4.6). The monophyly of Tillinae proposed by Gunter et al. (2013) is confirmed here. The position of Tillinae in the Cleridae lineage is contentious, however. Tillinae was generally recovered as a derived clade in the clerid lineage, most closely related to a clade composed of Clerinae + Hydnocerinaa + Epiclininae, in this analysis. This result differs from that of Gunter et al. (2013) and Hunt et al. (2007), obtaining Tillinae as the sister to other Cleridae. However, their analyses were based on smaller groups of taxa, with only 7 taxa and a single taxon, respectively. The hypothesis of Tillinae as a derived group was also obtained by Opitz (2010), whose morphological analysis showed Tillinae as a derived group closely allied to

Clerinae. More recently, McKenna et al. (2015), in their comprehensive molecular analysis, also recovered Tillinae as a derived clade closely related to Clerinae.

Old World tillinids were equally recovered as basal taxa and allied closely to *Neocallotillus* and *Monophylla* (and *Onychotillus* and *Barrotillus* in the molecular + morphology-based analysis); this clade was obtained as sister to all other New World Tillinae. In the molecular + morphology-based topology, a clade composed of Old World tillinids was recovered as sister to all other Tillinae and the New World *Neocallotillus, Barrotillus, Monophylla* and *Onychotillus* were recovered as basal lineages of the New World Tillinae. These findings suggest that the New World genera *Barrotillus, Neocallotillus, Monophylla* and *Onychotillus* are more closely related to Old World tillinids than to all other New World species. Although the identity of the sister clade to the New World Tillinae was not fully resolved, these results suggest that the New World Tillinae *per se* is a paraphyletic group, as the Old World genera *Spinoza* and *Cylidrus* were nested in the same clade with *Neocallotillus* and *Monophylla*. For the molecular + morphology-based analysis, only *Spinoza* was recovered in the same clade with *Barrotillus, Neocallotillus, Monophylla* and *Onychotillus*, supporting the notion of New World tillinids as a paraphyletic group.

A large clade composed of *Araeodontia + Cymatodera + Cymatoderella + Lecontella* was recovered in all DNA-based phylogenies. The molecular + morphology-based phylogeny recovered the small genus *Bogcia* as part of this major clade. These results suggest that there is close relatedness between the small *Araeodontia, Bogcia, Cymatoderella* and *Lecontella* with the speciose *Cymatodera*. Moreover, *Cymatodera sensu stricto* was rendered as paraphyletic, and

only after including the lesser *Araeodontia, Bogcia, Cymatodera, Cymatoderella* and *Lecontella*

the group can be considered as monophyletic. These results are consistent with the morphology-

based phylogenetic analysis (see Fig. 3.2 from Chapter 3), which showed those genera nested

inside the major *Cymatodera* group. The close relationship between *Araeodontia, Bogcia,*

Cymatoderella and Lecontella with the speciose *Cymatodera* is morphologically apparent (see

Figs 3.6-7; 3.10 A-C; 3.18 and 3.21 from Chapter 3) and is discussed in detail in Chapter 3.

Based on the DNA-based topology, the *Cymatodera* lineage can be subdivided into four

clades with high posterior probability values (Fig. 4.5). These clades were also partially obtained

in the molecular + morphology-based analysis (Figs. 4.6 and 4.7). These are: 1) A *Lecontella*

clade; the group was also recovered in the molecular + morphology-based analysis, but in that

case, *Lecontella* is closely allied to *Bogcia disjuncta* Barr*,* and *C. obliquefasciata* Schaeffer, but

those taxa were not sampled for the molecular phylogeny. Species in this clade can be

morphologically grouped based on the strong serration of their antennae (see Figs. 3.15 D, G

from Chapter 3), and this clade was recovered as the sister to all other *Cymatodera* species. 2) A

clade containing small species with a simple male pygidium (Fig. 4.7 and see Figs. 3.2, 3.6 B-C,

3.7 B, and 3.21 from Chapter 3), with females sometimes difficult to separate from males based

on external characters. These species are found mostly in semi-arid habitats of the southwestern

USA and northern Mexico, except *Cymatoderella collaris* (Spinola) and *Cymatodera conflagrate*

(Klug), two species broadly distributed from central Mexico to South America. This clade was

also recovered in the molecular + morphology-based topology with high posterior probability

values. 3) A clade composed of *Cymatodera rosalinae* Burke + *C. xaviera* Knull + *C. hoegei*

Gorham + *C. morosa* LeConte + *C. serena* Barr; these species are distributed in the

southwestern USA and northerb to central Mexico. Morphologically, the group can be recognized by the clear sexual dimorphism these species have, with females larger and more robust, and the male pygidium moderately differentiated from females (Fig. 4.7 and see Fig. 3.21-D from Chapter 3). This clade was partially recovered in the molecular + morphology-based analysis, with three separate clades: *C. xaviera* and related species*, C. serena* and related taxa, *C. bicolor* and allied species, and *C. limatula* and related species (Fig. 4.6). 4) A clade encompassing *Cymatodera* species with a derived pygidium (Fig. 4.7 and see Figs. 3.2 and 3.21 B, F, H from Chapter 3), which makes males easily identifiable from females, and moderately large to large size. Species found in this clade are broadly distributed in the Americas, ranging from the southwestern USA to South America. This clade also was recovered in the molecular + morphology-based analysis with interspecific relationships well resolved and moderately high posterior probability values. Seven *Cymatodera* species were nested outside the three species groups proposed in the molecular + morphology-based analysis. These are *Cymatodera angulifera* Gorham*, C. angustata* Spinola*, C. bipunctata* Gorham*, C. fascifera* LeConte*, C. sericans* Gorham, *C. undulata* (Say) *and C. vagemaculata* Thomson (Fig. 4.6). The inclusion of more intensive taxon sampling may render a more accurate placement of these species within the *Cymatodera* lineage.

The DNA- (Fig. 4.5) and morphology-based (see Figs. 3.2 and 3.3 from Chapter 3) analyses generally agree with the results obtained from the molecular + morphology-based topology (Figs. 4.6 and 4.7). For practical purposes, a mirrored phylogenetic tree was generated to elucidate differences and similarities between the DNA- and morphology-based topologies (Fig. 4.8-A). Overall, both approaches equally recovered all major tillinid groups, but a number

299

of differences were found. Both analyses were consistent in 1) Thaneroclerinae *sensu* Opitz

(2010) or Zenodosini *sensu* Kolibáč (1992) was recovered as part of the clerid lineage in all

DNA-based analyses, the molecular + morphology-based topology, and the morphology-based

topology. 2) The subfamilies Enopliinae, Korynetinae, Neorthopleurinae, Peloniinae and

Thaneroclerinae were recovered as basal lineages in all DNA-based phylogenies, including the

molecular + morphology-based analysis; a similar result was obtained in the morphology-based

study. 2) Old World tillinids were always recovered as basal taxa in the Tillinae lineage. 3)

Neocallotillus and *Monophylla* were generally recovered as sister to all New World Tillinae in

the DNA-based topologies (except 28S); for the molecular + morphology-based and

morphology-based analyses, the genera *Onychotillus* and *Barrotillus*, together with

Neocallotillus and *Monophylla,* were also recovered as basal taxa of New World tillinids. 4) A

large clade composed of *Araeodontia + Cymatodera + Cymatoderella + Lecontella* was equally

recovered in all DNA-based analyses. For the molecular + morphology and morphology-based

analyses, the genus *Bogcia* was included in this large clade, and this finding suggests that

Cymatodera sensu stricto is a paraphyletic group. And 4) The morphology-based phylogenetic

analysis divided the large clade composed of *Cymatodera* and related genera in two major

groups, the first composed of taxa with males possessing a "simple" pygidium and non-

sclerotized aedeagus (see Figs. 3.3, 3.6 B-C, 3.21-E and 3.22 A-B from Chapter 3), and a second

that includes taxa with a derived male pygidium and sclerotized aedeagus (see Figs. 3.3, 3.7 D-F,

3.21-F and 3.23 A-D from Chapter 3). Overall, these groups were recovered in the DNA-based

concatenated analyses (Fig. 4.6) and the molecular + morphology-based topology, but for the

latter analysis, a third group was also identified. These appear in Fig. 4.7 as: group A, composed

of taxa of medium to large size, male pygidium moderately elaborate, and aedeagus feebly to

moderately sclerotized; group B, composed of taxa of minute to small size, with a simple

pygidium, and the aedeagus is slender and feebly sclerotized; and group C, composed of taxa of

moderate to very large size, with an elaborate pygidium, and a robust and sclerotized aedeagus.

Some other differences also were found, such as the position of certain "unresolved" taxa

like *Cymatodera undulata* (Say) and *C. vagemaculata* (Thomson); however, the majority of the

taxa composing this large clade show consistency with the arrangement originally recovered in

the morphology-based analysis (see Fig. 3.3 from Chapter 3). Differences between the analyses

include: 1) the DNA-based analysis recovered *Temnoscheila* (Trogossitidae) as the sister to other

Cleroidea families while the morphology-based analysis recovered Melyridae as the sister group

to all cleroids. 2) A clade composed of Dasytidae + Malachidae + Melyridae was recovered in

the DNA-based analysis, but this clade was not observed in the morphology-based topology. 3)

A polytomy consisting of *Cregya disjuncta* (Peloniinae) and *Madoniella dislocata*

(Epiphloeinae) was found to be the sister to all Cleridae taxa by the DNA-based topology while

Zenodosus sanguineus (Thaneroclerinae) was shown as the sister to all Cleridae in the

morphology-based analysis. 4) The DNA-based analysis recovered a polytomy encompassing the

subfamilies Clerinae, Epiclininae and Hydnocerinae, and this finding suggests that none of these

subfamilies represent monophyletic lineages. The results divide those group in three clades, one

composed of Clerinae *in part* + Epiclininae, the second including Hydnocerinae, and the third

encompassing Clerinae *in part*. This grouping was not obtained in the morphology-based

analysis, where Clerinae was recovered as paraphyletic group by the inclusion of Hydnocerinae.

5) The DNA-based results showed *Cymatoderella* as part of a clade composed of species sharing

a plesiomorphic pygidium and a non-sclerotized aedeagus (Fig. 4.7) while the sister to all other

New World tillinids was a clade composed of *Neocallotillus + Monophylla.* In contrast, *Cymatoderella* was recovered as sister to the large clade composed of *Cymatodera* and related groups in the morphology-based analysis (see Fig. 3.3 from Chapter 3). 6) The DNA-based analysis recovered *Lecontella* as a closely related, but separate lineage, from *Cymatodera* and related genera (Fig. 4.5). The morphology-based analysis recovered *Lecontella* as part of a clade composed of *Bogcia disjuncta* Barr*, Cymatodera obliquefasciata* Schaeffer*, C. limatula* Burke and *C. bipunctata* Gorham (Fig. 4.6 and see Fig. 3.3 from Chapter 3).

5. Conclusions

This study represents the first attempt to understand the phylogenetic relationships of the New World Tillinae. The classification of the Tillinae tends to follow traditional methods of classification based on morphological similarities used to divide or group taxa, a phenomenon that may result in inaccurate classifications. The results given here serve as a basis to assess natural relationships of the New World Tillinae based on molecular, and molecular + morphological data. Taxon-sampling at the species level was relatively ample for *Cymatodera*, the most species-rich tillinid genus. The loci used in this study were selected in a way that shallow as well as deeper levels of divergence could be tested for all genera and species included in the analyses. Results here support the hypothesis given by Hunt et al. (2007), Bocakova et al. (2011), Gunter et al. (2013), and McKenna et al. (2013) that Trogossitidae is a paraphyletic group closely allied to Phloiophilidae. A clade composed of Dasytidae + Malachydae + Melyridae was generally obtained in all analyses; this result is consistent with the findings obtained by Bocakova et al. (2011) and Gunter et al. (2013). Thaneroclerinae (Thaneroclerini *sensu* Kolibáč (1992)) was always recovered as part of the Cleridae lineage. Interfamily

302

relationships of Korynetinae *sensu* Opitz (2010) were not fully resolved; however, due to the

poor taxon-sampling for these subfamilies, it is premature to reject the classification of

Korynetinae given by Opitz (2010). Neither Clerinae, nor Hydnocerinae nor Epiclininae

represent monophyletic lineages, a result that partially agrees with Gunter et al. (2013), where

Hydnocerinae is nested within a grade of clades containing most clerid taxa. *Eleale lepida*

(Epiclininae *sensu* Gunter et al., 2013) was recovered in all analyses as part of the clade

composed of Clerinae + Hydnocerinae, as opposed to results obtained by Gunter et al. (2015).

They recovered *Eleale* and related groups (all endemic to Australia) as a separate lineage closely

allied to Korynetinae *sensu* Kolibáč (1997). In this study, the taxon-sampling for the Epiclininae

(*sensu* Gunter et al., 2013) was reduced, hence, it is premature to draw conclusions about the

nature of the subfamily.

Old World Tillinae were consistently recovered as basal groups within the Tillinae lineage.

The existence of a well-developed carina in each metacoxal cavity in all New World Tillinae

(see Fig. 3.12-D from Chapter 3), but weak to almost absent carina in Old World tillinids

examined, supports this hypothesis. *Neocallotillus* and *Monophylla* (including *Onychotillus* and

Barrotillus in the molecular + morphology-based analysis) were recovered as sister to all other

New World Tillinae. The speciose *Cymatodera* was rendered as paraphyletic. The small genera

Araeodontia, Bogcia, Cymatoderella and *Lecontella* were nested in a large clade encompassing

the speciose *Cymatodera*, indicating a close relationship among these genera. This result is

supported by the following morphological characters: pronotum laterally bi-impressed; one tarsal

denticle and a pair of tarsal claws on distal tarsomeres; labial palpi securiform; a well-developed

carina on each metacoxal cavity; and the elytra coarsely to moderately impressed (Figs. 3.12 A-B

and D, and 3.18 B-F from Chapter 3). Morphological data has previously identified two major

groups within the large *Cymatodera* clade, one group composed of species with males having a

simple pygidium and a weakly sclerotized aedeagus, and another group with species where males

possess a derived pygidium and a sclerotized aedeagus. That finding is supported by results

obtained from the DNA- (Figs. 4.5) and molecular + morphology-based (Fig. 4.7) analyses.

The family Cleridae is a moderately diverse group of predatory beetles, with slightly less

than 4,000 species and many more yet to be described. The topologies obtained here can serve as

a foundation to start answering evolutionary or ecological questions about the group. A robust

phylogeny can test whether Tillinae evolved from an ancestral generalist or a specialized

predator that have developed pheromone identification to locate their prey, and determine if

reversals from specialization to generalist feeding have occurred. The phylogeny can also be

used to address questions such as the evolution of stridulation and mimicry in species of Tillinae.

Numerous clerid species that potentially attack economically important insect pests should

exist within this large group. Because species with recent shared ancestry tend to have similar

functional traits for exploiting similar resources, the phylogenetic position of poorly known

species may reveal the predatory preferences that may be applied against pests such as bark and

ambrosia beetles.

6. References

Barr, W. F. (1975) Family Cleridae. In: Arnett, R.H. (Ed.), Checklist of the beetles of North and Central America and the West Indies. Vol. 4. Family 73. Flora and Fauna Publications, Gainesville, pp. 1–18.

Bocakova, M., R. Constantin, and L. Bocak (2011) Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). Cladistics 27: 1–13.

Bouchard, P., Y. Bousquet, A. E. Davies, M. A. Alonso-Zarazaga, J. F. Lawrence, C. H. C. Lyal, A. F. Newton, C. A. M. Reid, M. Schmitt, S. A. Slipinski, A. B. T. Smith (2011) Family-group names in Coleoptera (Insecta). ZooKeys, 2011, 88: 1-972. doi: 10.3897/zookeys.88.807

Breton, S., G. Burger, D. T. Stewart and P. U. Blier (2006) Comparative analysis of gender associated complete mitochondrial genomes in marine mussels (*Mytilus* spp.). Genetics 172: 1107–1119.

Burke, A. F., D. Cibrián-Tovar, C. Llanderal-Cázares, A. Plascencia-Gonzáles and I. López-Pérez. (2010) Additions and contributions for the genus *Enoclerus* Gahan (Coleoptera: Cleridae) on temperate climate forests of Mexico. Acta Zoologica Mexicana 27(1): 145-167.

Burke, A. F., J. M. Leavengood Jr. and G. Zolnerowich (2015) A checklist of the New World species of Tillinae (Coleoptera: Cleridae), with an illustrated key to genera and new country records. Zookeys 4059 (1): 1-039.

Burke, A. F. and G. Zolnerowich (2016) Taxonomic revision of the New World genus *Callotillus* Wolcott (Cleridae: Tillinae), with the description of the new genus *Neocallotillus*, and an illustrated key of identification to species. ZooKeys 617: 65-89.

Corporaal, J. B. (1950) Cleridae. In: W. D. Hinks (Ed.). Coleopterorum catalogus supplementa, Pars 23 (editio secunda). W. Junk; The Hague. 373 p.

Darriba, D. G., L. Taboada, R. Doallo and D. Posada (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9(8): 772.

Drummond, A. J., B. Ashton, S. Buxton, M. Cheung, A. Cooper, C. Duran, M. Field, J. Heled, M. Kearse, S. Markowitz, R. Moir, S. Stones-Havas, S. Sturrock, T. Thierer, and A. Wilson (2012) Geneious V. 7.1. Available from http://www.geneious.com/

Folmer, O, M. Black, W. Hoeh, R. Lutz and R. Vrijenhoek (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5):294-9.

Gemminger, M. and E. Harold (1869) Catalogus Coleopterorum hucuque descriptorum synonymicus et systematicus. Sumptu E. H. Gummi 12: 1–3822.

Gunter, N. L., J. M. Leavengood Jr, J. S. Bartlett, E. G. Chapman and S. L. Cameron (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera; Cleridae). Systematic Entomology 38(3): 626-636.

Huelsenbeck, J. P., and F. Ronquist (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754-755.

Hunt, T., J. Bergsten, Z. Levkanicova, A. Papadopoulou, O. St. John, R. Wild, P. M. Hammond, D. Ahrens, M. Balke, M. S. Caterino, J. Gómez-Zurita, I. Ribera, T. G. Barraclough, M. Bocakova, L. Bocak, and A. P. Vogler (2007) A Comprehensive Phylogeny of Beetles Reveals the Evolutionary Origins of a Superradiation. Science 318: 1913-1916.

Inward, D. G. (2003) The evolution of dung beetle assemblages. Ph.D. thesis, Imperial College, London.

Kolibàč, J. (1992) Revision of Thaneroscleridae n. stat. (Coleoptera, Cleroidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 65: 303–340.

Kolibàč, J. (1997) Classification of the subfamilies of Cleridae (Coleoptera: Cleroidea) Acta Musei Moraviae Scientia Naturales 81: 307-361.

Lanfear, R., B. Calcott, S.Y.W. Ho and S. Guindon (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695-1701.

Lewis, P. O. (2001) A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data, Systematic Biology 50: 6.

Lohde, R. (1900) Cleridarum Catalogus. Stettiner Entomologische Zeitung, 61: 3–148.

Maddison, W. P. and D. R. Maddison (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75 http://mesquiteproject.org

McKenna, D. D., A. Wild, K. Kanda, C. Bellamy, R. G. Beutel, M. S. Caterino, C. W. Farnum, D. C. Hawks, M. A. Ivie, M. L. Jameson, R. A. B. Leschen, A. E. Marvaldi, J. C. McHugh, A. F. Newton, J. A. Robertson, M. K. Thayer, M. F. Whiting, J. F. Lawrence, A. Ślipiński, D. F. Maddison and B. D. Farrell (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology 40: 835‑880.

Montooth, K. L. and D. R. Rand (2008) The Spectrum of Mitochondrial Mutation Differs across Species. PLOS Biology 6(8): e213. doi:10.1371/journal.pbio.0060213

National Center for Biotechnology Information http://www.ncbi.nlm.nih.gov/genbank/ (last accessed 20 June 2016).

Opitz, W. (2010) Classification, natural history, phylogeny and subfamily composition of the Cleridae and generic content of the subfamilies. Entomologica Basiliensia et Collectionis Frey 32: 31-128.

Papp, C. (1960) The Cleridae of North America. Part I: The geographical distribution of the Cleridae of North America, north of the Panama Canal. Southern California Academy of Sciences Bulletin 59(2): 76–88.

Rambaut, A. and A. J. Drummond (2007) Tracer V. 1.4 http://beast.bio.ed.ac.uk/Tracer.

Ronquist, F. and J. P. Huelsenbeck (2003) Mrbayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Schenkling, S. (1910) Cleridae. In: Schenkling, S. (Ed.), Coleoptorum Catalogus, Pars 23. W. Junk, Berlin, 174 pp.

Simon, C., F. Frati, A. Beckenbach, B. Crespi, H. Liu and P. Flook (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87: 651–702.

Spinola, M. M. (1844) Essai monographique sur les Clerites: Insectes Coléoptères. 2 vols.

    Imprimiere der frères Ponthenier, Genoa, 386 pp.

Swofford, D. L. (2016) PAUP: Phylogenetic analysis using parsimony (and other methods).

    Version 4.0a150. http://people.sc.fsu.edu/~dswofford/paup_test/

Wolcott, A. B. (1947) Catalogue of North American beetles of the family Cleridae. Fieldiana

    Zoology 32 (2), 59–105.

Table 4.1 Clerid species, locality data, and distribution, including outgroups, used in the phylogenetic analysis.

No.	Taxon	Author	Locality information	Distribution
1	*Apteropilo humerofuscus**	Bartlett, 2009	Queensland, Australia	Outgroup
2	*Araedontia peninsularis*	(Schaeffer, 1904)	Tucson, AZ, USA	West USA – north Mexico
3	*Carphurus malaccanus*	Pic, 1917	Queensland, Australia	Outgroup
4	*Chariessa pillosa**	(Forster, 1781)	Dallas, Texas	Outgroup
5	*Cladiscus obeliscus*	(Lewis, 1892)	Manoboly, India	Old World (Asia)
6	*Colyphus rutilus*	(Gorgham, 1882)	Oaxaca, Mexico	Outgroup
7	*Collops bipunctatus***	(Say, 1823)	Manhattan, KS, USA	Outgroup
8	*Cregya oculata**	(Say, 1835)	Mobile, Alabama	Outgroup
9	*Cylidrus centralis*	Pascoe, 1860	Queensland, Australia	Old World (Oceania)
10	*Cymatodera aegra*	Wolcott, 1921	Fort Davis, TX, USA	West USA – north Mexico
11	*Cymatodera angustata*	Spinola, 1844	Refugio, CA, USA	West USA
12	*Cymatodera antennata*	Schaeffer, 1908	Santa Cruz Co., AZ, USA	West West USA – north Mexico
13	*Cymatodera balteata*	LeConte, 1854	Uvalde, TX, USA	West USA – north Mexico
14	*Cymatodera bicolor*	(Say, 1825)	Talladega, AL, USA	USA - Canada
15	*Cymatodera californica*	Horn, 1868	Los Angeles Co, CA, USA	West USA
16	*Cymatodera championi*	Gorham, 1882	Chiriquí, Panama	Central - South America
17	*Cymatodera conflagrata*	(Klug, 1842)	Chamela, Jalisco, Mexico	Mexico - Central - South America
18	*Cymatodera decipiens*	Fall, 1906	Joshua Tree Nat. Park. CA, USA	West USA
19	*Cymatodera dietrichi*	Barr, 1952	Portal, AZ, USA	West USA – north Mexico
20	*Cymatodera fuchsii*	Schaeffer, 1904	Joshua Tree Nat. Park. CA, USA	West USA – north Mexico
21	*Cymatodera hoegei (Costa Rica)*	Gorham, 1882	Monteverde, Costa Rica	Mexico - Central America
22	*Cymatodera hoegei (Mexico)*	Gorham, 1882	Chamela, Jalisco, Mexico	Mexico
23	*Cymatodera hopei*	Gray, 1832	Texcoco, Mexico	Mexico
24	*Cymatodera horni*	Wolcott, 1910	Cochise Co. AZ, USA	West USA – north Mexico
25	*Cymatodera inornata*	(Say, 1835)	Latimer Co., OK, USA	East USA
26	*Cymatodera intermedia*	Barr, 1950	Los Cabos, Baja Cal. Sur, Mexico	Mexico
27	*Cymatodera latefascia*	Schaeffer, 1904	Pima Co., AZ, USA	West USA – north Mexico
28	*Cymatodera lisnleyi*	Barr, 1972	Joshua Tree Nat. Park. CA, USA	West USA

No.	Taxon	Author	Locality information	Distribution
29	*Cymatodera lorenae*	sp. n.	Pinotepa Nacional, Oaxaca, Mexico	Mexico
30	*Cymatodera marmorata*	(Klug, 1842	Patzcuaro, Michoacan, Mexico	Mexico - Central America
31	*Cymatodera mexicana*	Rifkind, 2015	Sierra Huautla, Oaxaca, Mexico	Mexico
32	*Cymatodera mitchelli*	Chapin, 1927	Joshua Tree Nat. Park. CA, USA	West USA
33	*Cymatodera morelensis*	sp. n	El Limon, Morelos , Mexico	Mexico
34	*Cymatodera morosa*	LeConte, 1858	Santa Rita Mts., AZ, USA	West USA – north Mexico
35	*Cymatodera neomexicana*	Knull, 1934	Carrizozo, NM, USA	West USA
36	*Cymatodera oblita*	Horn, 1886	Pima Co., AZ, USA	West USA
37	*Cymatodera pallida*	Schaeffer, 1908	Joshua Tree Nat. Park. CA, USA	West USA – north Mexico
38	*Cymatodera pseudotsugae*	Barr, 1947	Mt Hamilton, CA, USA	West USA
39	*Cymatodera punctata*	LeConte, 1852	Cochise Co. AZ, USA	West USA – north Mexico
40	*Cymatodera puncticollis*	Bland, 1863	Joshua Tree Nat. Park. CA, USA	West USA – north Mexico
41	*Cymatodera rosalinae*	Burke, 2013	Chamela, Jalisco, Mexico	Mexico
42	*Cymatodera serena*	Barr, 1872	Sonora, Mexico	West USA – north Mexico
43	*Cymatodera sirpata*	Horn, 1885	Hidalgo Co., TX, USA	West USA – north Mexico
44	*Cymatodera sobara*	Barr, 1960	Coahuila, Mexico	West USA – north Mexico
45	*Cymatodera tortuosa*	Burke & Rifkind, 2014	Queretaro, Mexico	Mexico
46	*Cymatodera turbata*	Horn, 1865	Hidalgo Co., TX, USA	West USA – north Mexico
47	*Cymatodera tuta*	Wolcott, 1910	Pima Co., AZ, USA	West USA – north Mexico
48	*Cymatodera tutoides*	Barr, 1972	Los Saenz, Starr Co., TX	West USA – north Mexico
49	*Cymatodera undulata*	(Say, 1825)	Near Lexington, KY, USA	USA - Canada
50	*Cymatodera vagemaculata*	Thomson, 1860	Cañon del Sumidero, Chiapas, Mexico	Mexico - Central America
51	*Cymatodera werneri*	Barr, 1952	Catalina Mt, AZ, USA	Mexico - Central America
52	*Cymatodera xaviera*	Knull, 1940	Tucson, AZ, USA	West USA – north Mexico
53	*Cymatoderella collaris*	(Spinola, 1844)	Matehuala, SLP, Mexico	USA - Mexico - Central America
54	*Dasytes areatus***	Stephens 1829	Europe	Outgroup
55	*Eleale lepida**	Pascoe, 1860	Queensland, Australia	Outgroup
56	*Enoclerus moestus* *	(Klug, 1842)	Sta Catalina, AZ, USA	Outgroup
57	*Enoclerus rosmarus**	(Say, 1823)	Pillbury Cross, KS, USA	Outgroup
58	*Isoclerus cipisek**	(LeConte, 1849)	Queensland, Australia	Outgroup

No.	Taxon	Author	Locality information	Distribution
59	*Isohydnocera tabida**	(LeConte, 1849)	Wichita, KS, USA	Outgroup
60	*Lecontella brunnea*	Kolibac, 1998	Joshua Tree Nat. Park. CA, USA	USA - Mexico
61	*Lecontella gnara*	Wolcott, 1927	Pima Co., AZ, USA	West USA – north Mexico
62	*Lemidia accincta*	(Newman, 1842)	Queensland, Australia	Outgroup
63	*Madoniella dislocata**	(Say, 1825)	Lexington, KY	Outgroup
64	*Malachius bipustulatus***	(Linnaeus, 1758)	Frankfurt, Germany	Outgroup
65	*Monophylla californica*	(Fall, 1901)	Imperial Co., CA, USA	West USA - Mexico _Central America
66	*Monophylla terminata*	(Say, 1835)	Val Verde Co., TX, USA	Canada - USA - north Mexico
67	*Necrobia ruficollis**	(Fabricius, 1775)	Europe	Outgroup
68	*Necrobia rufipes**	(Fabricius, 1781)	Manhattan, KS, USA	Outgroup
69	*Neocallotillus elegans*	(Erichson, 1847)	Riverside Co., CA, USA	West USA - Mexico
70	*Neorthopleura thoracica**	(Say, 1823)	Aiken Co. , SC, USA	Outgroup
71	*Ostoma ferruginea***	(Linnaeus, 1758)	Queretaro, Mexico	Outgroup
72	*Opilo pallidus**	(Olivier, 1795)	Germany	Outgroup
73	*Pelonides sp.*	****	Guadalupe Co., TX, USA	Outgroup
74	*Pelonium leucophaeum**	(Klug, 1842)	Victoria Co., TX, USA	Outgroup
75	*Peltis grossa***	(Linnaeus, 1758)	Europe	Outgroup
76	*Perilypus sp.**	****	Jim Wells Co., TX, USA	Outgroup
77	*Phloiophilus edwardsii***	Stephens, 1830	Europe	Outgroup
78	*Phyllobaenus guatemalae**	(Gorham, 1877)	El Aguacero, Chiapas, Mexico	Outgroup
79	*Phyllobaenus cf cinctus**	(Spinola, 1844)		Outgroup
80	*Priocera sp.*	****	Mexico	Outgroup
81	*Priocera castanea**	(Newman, 1838)	Lee Co., AL, USA	Outgroup
82	*Spinoza sp.*	****	Japan	Old World (Asia - Oceania)
83	*Temnoscheila acuta***	(LeConte, 1858)	Joshua Tree Nat. Park. CA, USA	Outgroup
84	*Temnoscheila caerulea***	(Olivier, 1790)	Europa	Outgroup
85	*Temnoscheila virescens***	(Fabricius, 1775)	Hidalgo, Mexico	Outgroup
86	*Tilloidea transversalis*	(Charpentier, 1825)	Bulgaria, Europa	Old World (Europe - Middle East)
87	*Tillus elongatus*	(Linnaeus, 1758)	Europe	Old World (Europe)
88	*Trichodes ornatus**	(Linsley & MacSwain, 1943)	Inyo Co., CA, USA	Outgroup
89	*Zenodosus sanguineus**	(Say, 1835)	Near Lexington, KY, USA	Outgroup

Table 4.2 Profile of amplification for each individual gene or reference of sequences.

No.	Taxon name	Famly/subfamily	16S	28S	COI
1	*Apteropilo humerofuscus**	Cleridae: Tarsestoninae	Gunter *et al.*	Gunter *et al.*	Gunter *et al.*
2	*Araedontia peninsularis*	Cleridae: Tillinae	This study	This study	This study
3	*Carphurus malaccanus*	Melyridae	Bocakova et al.	Bocakova et al.	Bocakova et al.
4	*Chariessa pillosa**	Cleridae: Peloniinae	Gunter et al.	Gunter et al.	Gunter et al.
5	*Cladiscus obeliscus*	Cleridae: Tillinae	Bocakova et al.	Bocakova et al.	Bocakova et al.
6	*Colyphus rutilus*	Cleridae: Clerinae	This study	This study	This study
7	*Collops bipunctatus***	Melyridae	Cline et al.	Cline et al.	Cline et al.
8	*Cregya oculata**	Cleridae: Peloniinae	Gunter et al.	Gunter et al.	Gunter et al.
9	*Cylidrus centralis*	Cleridae: Tillinae	Gunter et al.	Gunter et al.	Gunter et al.
10	*Cymatodera aegra*	Cleridae: Tillinae	This study	This study	This study
11	*Cymatodera angustata*	Cleridae: Tillinae	This study	This study	This study
12	*Cymatodera antennata*	Cleridae: Tillinae	This study	This study	-
13	*Cymatodera balteata*	Cleridae: Tillinae	This study	This study	This study
14	*Cymatodera bicolor*	Cleridae: Tillinae	This study	This study	This study
15	*Cymatodera californica*	Cleridae: Tillinae	This study	McKenna et al.	This study
16	*Cymatodera championi*	Cleridae: Tillinae	This study	This study	This study
17	*Cymatodera conflagrata*	Cleridae: Tillinae	This study	This study	-
18	*Cymatodera decipiens*	Cleridae: Tillinae	This study	This study	This study
19	*Cymatodera dietrichi*	Cleridae: Tillinae	This study	This study	This study
20	*Cymatodera fuchsii*	Cleridae: Tillinae	This study	This study	This study
21	*Cymatodera hoegei (Costa Rica)*	Cleridae: Tillinae	This study	-	-
22	*Cymatodera hoegei (Mexico)*	Cleridae: Tillinae	This study	This study	This study
23	*Cymatodera hopei*	Cleridae: Tillinae	This study	This study	This study
24	*Cymatodera horni*	Cleridae: Tillinae	This study	-	This study
25	*Cymatodera inornata*	Cleridae: Tillinae	This study	This study	This study
26	*Cymatodera intermedia*	Cleridae: Tillinae	This study	This study	-
27	*Cymatodera latefascia*	Cleridae: Tillinae	This study	This study	This study
28	*Cymatodera lisnleyi*	Cleridae: Tillinae	This study	-	This study

No.	Taxon name	Famly/subfamily	16S	28S	COI
29	*Cymatodera lorenae* sp. n.	Cleridae: Tillinae	This study	-	This study
30	*Cymatodera marmorata*	Cleridae: Tillinae	This study	This study	This study
31	*Cymatodera mexicana*	Cleridae: Tillinae	This study	This study	This study
32	*Cymatodera mitchelli*	Cleridae: Tillinae	This study	This study	This study
33	*Cymatodera morelensis* sp. n.	Cleridae: Tillinae	This study	-	This study
34	*Cymatodera morosa*	Cleridae: Tillinae	This study	This study	This study
35	*Cymatodera neomexicana*	Cleridae: Tillinae	This study	This study	This study
36	*Cymatodera oblita*	Cleridae: Tillinae	This study	This study	This study
37	*Cymatodera pallida*	Cleridae: Tillinae	This study	This study	-
38	*Cymatodera pseudotsugae*	Cleridae: Tillinae	-	-	This study
39	*Cymatodera punctata*	Cleridae: Tillinae	This study	This study	This study
40	*Cymatodera puncticollis*	Cleridae: Tillinae	This study	This study	This study
41	*Cymatodera rosalinae*	Cleridae: Tillinae	This study	This study	This study
42	*Cymatodera serena*	Cleridae: Tillinae	This study	This study	-
43	*Cymatodera sirpata*	Cleridae: Tillinae	This study	This study	This study
44	*Cymatodera sobara*	Cleridae: Tillinae	-	-	This study
45	*Cymatodera tortuosa*	Cleridae: Tillinae	This study	This study	This study
46	*Cymatodera turbata*	Cleridae: Tillinae	This study	This study	This study
47	*Cymatodera tuta*	Cleridae: Tillinae	This study	This study	This study
48	*Cymatodera tutoides*	Cleridae: Tillinae	This study	-	This study
49	*Cymatodera undulata*	Cleridae: Tillinae	This study	This study	This study
50	*Cymatodera vagemaculata*	Cleridae: Tillinae	This study	This study	This study
51	*Cymatodera werneri*	Cleridae: Tillinae	This study	This study	-
52	*Cymatodera xaviera*	Cleridae: Tillinae	This study	This study	This study
53	*Cymatoderella collaris*	Cleridae: Tillinae	This study	This study	This study
54	*Dasytes areatus***	Dasitydae	Bocakova et al.	-	Hendrich et al.
55	*Eleale lepida**	Cleridae: Epiclininae	Gunter *et al.*	Gunter *et al.*	Gunter *et al.*
56	*Enoclerus moestus* *	Cleridae: Clerinae	Gunter *et al.*	Gunter *et al.*	Gunter *et al.*
57	*Enoclerus rosmarus**	Cleridae: Clerinae	Gunter *et al.*	Gunter *et al.*	Gunter *et al.*
58	*Isoclerus cipisek**	Cleridae: Isoclerinae	-	Gunter et al.	Gunter et al.

No.	Taxon name	Famly/subfamily	16S	28S	COI
59	*Isohydnocera tabida**	Cleridae: Hydnocerinae	This study	This study	This study
60	*Lecontella brunnea*	Cleridae: Tillinae	This study	This study	This study
61	*Lecontella gnara*	Cleridae: Tillinae	Gunter et al.	This study	Gunter et al.
62	*Lemidia accincta*	Cleridae: Hydnocerinae	Gunter et al.	Gunter et al.	Gunter et al.
63	*Madoniella dislocata**	Cleridae: Epiphloeinae	Gunter et al.	-	Dewaard et al.
64	*Malachius bipustulatus***	Melyridae	Bocakova et al.	Bocakova et al.	Hendrich et al.
65	*Monophylla californica*	Cleridae: Tillinae	This study	This study	This study
66	*Monophylla terminata*	Cleridae: Tillinae	This study	This study	This study
67	*Necrobia ruficollis**	Cleridae: Korynetinae	Bocakova et al.	-	Bocakova et al.
68	*Necrobia rufipes**	Cleridae: Korynetinae	This study	This study	This study
69	*Neocallotillus elegans*	Cleridae: Tillinae	This study	-	This study
70	*Neorthopleura thoracica**	Cleridae: Neorthopleurinae	Gunter et al.	-	Gunter et al.
71	*Ostoma ferruginea***	Trogossitidae	Hunt et al.	Hunt et al.	Hunt et al.
72	*Opilo pallidus**	Cleridae: Clerinae	Bocakova et al.	-	Bocakova et al.
73	*Pelonides* sp.	Cleridae: Clerinae	-	This study	This study
74	*Pelonium leucophaeum**	Cleridae: Enopliinae	Gunter et al.	-	Gunter et al.
75	*Peltis grossa***	Trogossitidae	Bocakova et al.	Bocakova et al.	Hendrich et al.
76	*Perilypus sp.**	Cleridae: Clerinae	Gunter et al.	Gunter et al.	Gunter et al.
77	*Phloiophilus edwardsii***	Phloiophilidae	Bocakova et al.	Bocakova et al.	Bocakova et al.
78	*Phyllobaenus guatemalae**	Cleridae: Hydnocerinae	-	Gunter et al.	Gunter et al.
79	*Phyllobaenus cf cinctus**	Cleridae: Hydnocerinae	Gunter et al.	Gunter et al.	Gunter et al.
80	*Priocera* sp.	Cleridae: Clerinae	-	Gunter et al.	Gunter et al.
81	*Priocera castanea**	Cleridae: Clerinae	Gunter et al.	Gunter et al.	Gunter et al.
82	*Spinoza* sp.	Cleridae: Tillinae	Bocakova et al.	Bocakova et al.	Bocakova et al.
83	*Temnoscheila acuta***	Trogossitidae	This study	This study	-
84	*Temnoscheila caerulea***	Trogossitidae	Bocakova et al.	Bocakova et al.	Hendrich et al.
85	*Temnoscheila virescens***	Trogossitidae	-	This study	This study
86	*Tilloidea transversalis*	Cleridae: Tillinae	Levkanicova *et al.*	Bocakova et al.	Levkanicova *et al.*
87	*Tillus elongatus*	Cleridae: Tillinae	Bocakova et al.	Bocakova et al.	Hendrich et al.
88	*Trichodes ornatus**	Cleridae: Clerinae	McElrath et al.	Gunter et al.	Dewaard et al.
89	*Zenodosus sanguineus **	Cleridae: Thaneroclerinae	Gunter et al.	Gunter et al.	Gunter et al.

Table 4.3 Primers used for PCR amplification and sequencing.

Marker	Primer Name	Primer Sequence	Reference
16S	16S-R1	TTTAATCCAACATCGAGG	Simon *et al*., 1994
	16S-F1	CGCCTGTTTAACAAAAACAT	Simon *et al*., 1994
	16c	CCCTGATACCCAGGTAC	Gunter *et al*., 2013
	12sb	AAACTAGGATTAGATACCC	Gunter *et al*., 2013
28S			
	28Sff	TTACACACTCCTTAGCGGAT	Inward, 2003
	28Sdd	GGGACCCGTCTTGAAACAC	Inward, 2003
COI			
	LCO-1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*., 1994
	HCO-700ME	TCAGGGTGACCAAAAAATCA	Breton *et al*., 2006
	Jerry	CAACATTTATTTTGATTTTTTGG	Simon *et al*., 1994
	Pat	TCCATTGCACTAATCTGCCATATTA	Simon *et al*., 1994

Table 4.4 Thermocycling conditions used to amplify mitochondrial and nuclear genes using the polymerase chain reaction (PCR). Protocols for 16S were modified from Kambhampati and Smith (1995); protocols for 28S and COI were modified from Gunter et al. (2015).

Gene	PCR Protocol
16S	Initial activation: 5 m at 95°C. 3-step cycle: denaturation 30s at 96°C, annealing 1 m at 45°C, extension: 30S at 68°C (40 cycles). Final extension: 10 m at 72°C.
18S	Initial activation: 5 m at 95°C. 3-step cycle: denaturation 30s at 96°C, annealing 1.5 m at 50°C, extension: 30s at 68°C (40 cycles). Final extension: 10 m at 72°C.
COI	Initial activation: 5 m at 95°C. 3-step cycle*:* denaturation 30s at 96°C, annealing 1 m at 40°C, extension: 30s at 68°C (40 cycles). Final extension: 10 m at 72°C.

Table 4.5 Estimated parameters for Bayesian analysis using jModelTest 2.1.4 (K= Optimized free parameters.

Gene	Selected model	K	-ln likelihood
16S	GTR+I+G	174	8298.9984
28S	GTR+I+G	148	7949.0462
COI	GTR+I+G	154	16836.2352

Table 4.6 Partitions tested for all for Bayesian and maximum-likelihood analyses.

	Partition	
1	Unpartitioned	unpartitioned
2	16S, 28S, COI	by gene
3	16S, 28S, COI_1, COI_2, COI_3	PartitionFinder

Table 4.7 Best partitioning scheme determined by PartitionFinder, the model of molecular evolution and the corresponding subset partition.

Subset	Best model	Subset partition
1	GTR+I+G	16S gene position
2	GTR+I+G	28S gene position
3	GTR+I+G	First codon position COI
4	GTR+G	Second codon position COI
5	SYM+I+G	Third codon position COI
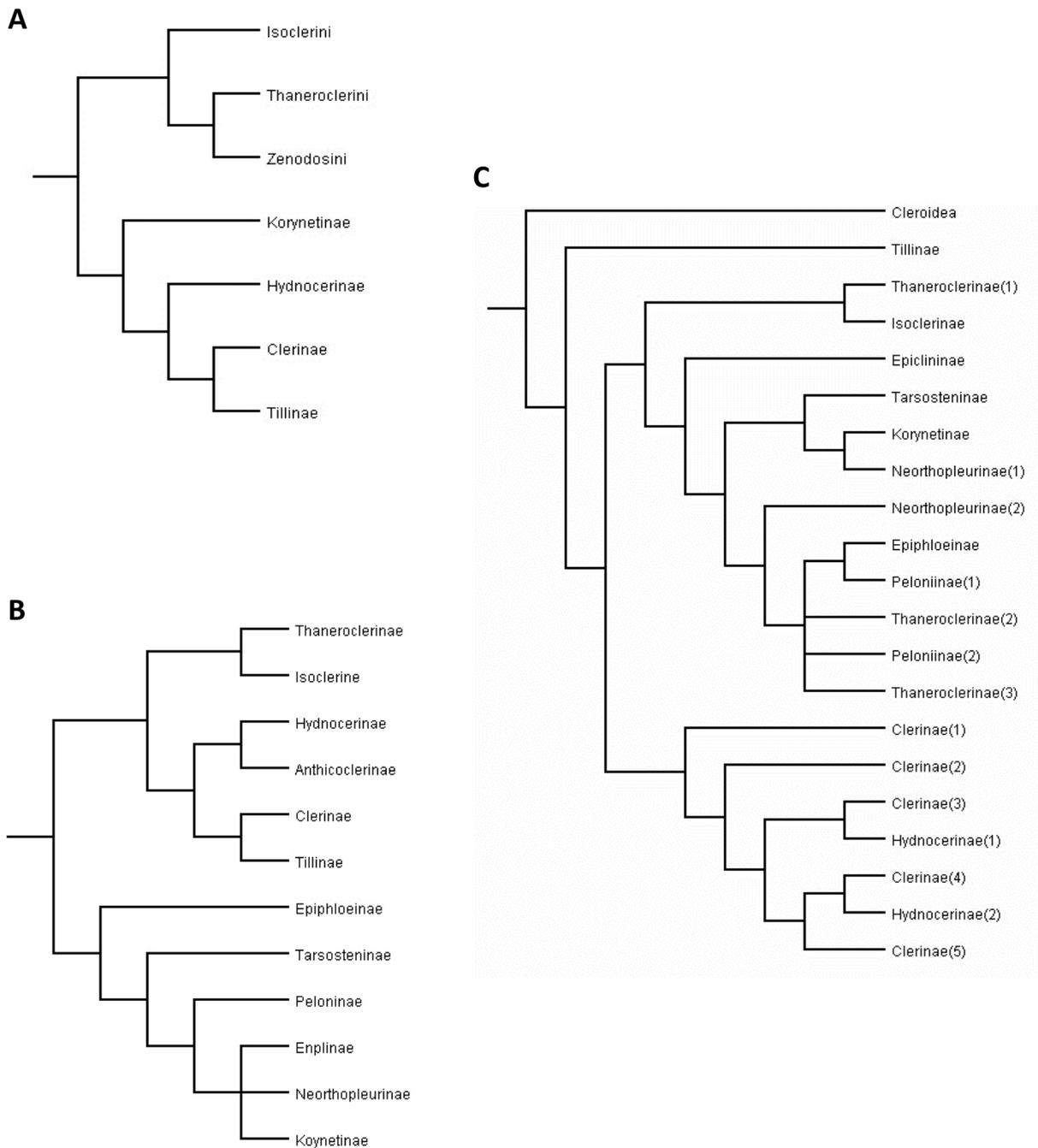
Fig. 4.1 Simplified topologies comparing higher-level classifications of the Cleridae proposed by:
A) Kolibàč (1992). B) Opitz (2010) and C) Gunter et al. *sensu* Opitz (2010). The current
classification of the Cleridae recognizes 13 subfamilies (Opitz, 2010 and Gunter et al., 2013).
Subfamilies marked with numbers in parentheses in Gunter et al. are paraphyletic or polyphyletic.

Temnoscheila acuta
Temnoscheila caerula
0.773
0.773
Phloiophilus_edwardsii
1
Ostoma ferruginea
Peltis grossum
Malachius bipostulatus
1
Dasytes areatus
0.73
Collops bipunctatus
Carphurus malaccanus

Trogossitidae (in part)

Trogossitidae (in part)
+ Phloiophilidae

Dasytidae +
Malachidae +
Melyridae

Madoniella dislocata
1
Necrobia_ruficollis
Necrobia_rufipes
0.588
0.545
Zenodosus sanguineus
0.993
0.585
Neorthopleura thoracica
Cregya oculata
0.914
Apteropilo humerofuscus
0.945
Chariessa pilosa
Pelonium leucophaeum
0.795

Thaneroclerinae + Neorthopleurinae
+ Korynetinae + Peloniinae
+ Enopliinae

Eleale lepida
Opilo_pallidus
Trichodes_ornatus
1
0.753
Phyllobaenus_guatemalae
0.753
Isohydnocera tabida
Perilypus_sp
Phyllobaenus cf cinctus
0.971
Priocera castanea
0.844
Enoclerus rosmarus
0.84
Colyphus rutilus
0.923
Enoclerus moestus

Clerinae +
Epiclininae +
Hydnocerinae

Tilloidea transversalis
0.618
Tillus elongatus
Cladiscus obeliscus
0.997
1
Spinoza sp
Cylidrus centralis

Old World Tillinae

0.999
Neocallotillus elegans
1
Monophylla californica
Monophylla terminata
0.747
1
Lecontella brunnea
Lecontella gnara
0.768
Araeodontia peninsularis
0.737
Cymatodera tuta
0.851
Cymatodera antennata
0.987
Cymatodera intermedia
1
Cymatoderella collaris
0.597
Cymatodera conflagrata
0.888
Cymatodera tutoides
0.999
Cymatodera pallida
0.999
Cymatodera punticollis
Cymatodera turbata
0.999
Cymatodera latefascia
0.973
Cymatodera aegra
0.996
Cymatodera werneri
Cymatodera decipiens
0.751
1
Cymatode morelensis
Cymatodera punctata
Cymatodera tortuosa
0.797
1
Cymatodera xaviera
0.902
Cymatodera_hoegei_(Mexico)
0.601
Cymatodera rosalinae
1
Cymatodera horni
0.941
Cymatodera californica
0.734
Cymatodera linsleyi
Cymatodera hopei
0.806
0.997
Cymatodera balteata
Cymatodera undulata
0.755
Cymatodera vagemaculata
Cymatodera angustata
Cymatodera lorenae
Cymatodera serena
0.815
Cymatodera neomexicana
0.697
Cymatodera oblita
0.995
Cymatodera marmorata
0.997
Cymatodera championi
Cymatodera_hoegei_(C_Rica)
0.957
Cymatodera morosa
0.997
Cymatodera bicolor
1
Cymatodera sirpata
Cymatodera inornata
0.99
Cymatodera dietrichi
0.515
Cymatodera mitchelli
0.767
Cymatodera fuschsii
Cymatodera mexicana

New World Tillinae

0.05

Fig. 4.2. Fifty percent majority rule consensus tree based on the mitochondrial locus 16S resulting from two Bayesian MCMC runs performed in MrBayes. Numbers above branches represent Bayesian posterior probability values.

320

Fig. 4.3. Fifty percent majority rule consensus tree based on the nuclear locus 28S resulting from two Bayesian MCMC runs performed in MrBayes. Numbers above branches represent Bayesian posterior probability values.

321

Fig. 4.4. Fifty percent majority rule consensus tree based on the mitochondrial locus cytochrome oxidase subunit I resulting from two Bayesian MCMC runs performed in MrBayes. Numbers above branches represent Bayesian posterior probability values.

322

Fig. 4.5. Fifty percent majority rule consensus tree from the concatenated dataset based on the optimal partition strategy predicted by Partition Finder resulting from two Bayesian MCMC runs performed in MrBayes. Numbers above branches represent Bayesian posterior probability values.

Temnoscheila acuta
Temnoscheila virescens
Tenebroides sp
0.98
Temnoscheila caerula
Phloiophilus edwardsii
0.94
Ostoma ferrugineum
Peltis grossa
Peltis ferruginea
0.79
Malachius bipustulatus
Dasytes aeratus
0.69
Collops quadrimaculatus
Collops bipunctatus
Carphurus malaccanus
Zenodosus sanguineus
1
Cregya oculata
0.87
Neorthopleura thoracica
1
Necrobia ruficollis
Necrobia rufipes
0.77
Apteropilo humerofuscus
0.88
Madoniella dislocata
1
Pelonium leucophaeum
0.78
Chariessa pilosa
0.57
Pelonides sp
0.91
Eleale lepida
Isohydnocera tabida
Perilypus sp
Colyphus rutilus
Enoclerus moestus
Enoclerus rosmarus
Lemidia accincta
0.86
Priocera sp
1
Enoclerus abdominalis
Enoclerus nigripes
Phyllobaenus humeralis
Phyllobaenus pallipennis
Placopterus thoracicus
0.64
Phyllobaenus guatemalae
Phyllobaenus cf cinctus
0.65
Opilo pallidus
Trichodes ornatus
0.64
Priocera castanea
Trichodes nutalli
1
Tillus elongatus
0.59
Tilloidea transversalis
Cladiscus obeliscus
Gastrocentrum sp
Orthocladiscus sp
Strotocera grandis
0.66
Cylidroctenus chalybaum
0.81
Cylidrus centralis
Cylidrus fasciatus
Stenocylidrus dispar
1
0.78
Spinoza sp
0.75
Onychotillus vittatus
Onychotillus n sp
1
1
Monophylla californica
0.58
Monophylla terminata
Monophylla pallipes
1
Neocallotillus elegans
Barrotillus kropotkini
1
Callotillus intricatus
0.9
Callotillus bahamensis
Callotillus eburneocinctus
Cymatodera angulifera
Cymatodera bipunctata
Cymatodera fascifera
Cymatodera angustata
Cymatodera undulata
0.71
Cymatodera vagemaculata
Cymatodera sericans
0.62
Cymatodera tricolor
0.99
Cymatodera xaviera
Cymatodera rosalinae
0.55
Cymatodera usta
0.62
Cymatodera hoegei Mexico
0.85
Cymatodera morosa
Cymatodera serena
0.74
Cymatodera lorenae
0.96
Cymatodera latefascia
1
Cymatodera bicolor
1
Cymatodera sirpata
Cymatodera inomata
0.77
Cymatodera limatula
Cymatodera obliquefasciata
1
Lecontella striatopunctata
0.6
Lencontella gnara
Lecontella brunnea
0.97
Bogcia disjuncta
Bogcia oaxacae
1
0.78
1

Trogossitidae (in part)

Trogossitidae (in part) + Phloiophilidae

Dasytidae + Malachidae + Melyridae

Thaneroclerinae + Neorthopleurinae + Korynetinae + Peloniinae + Enopliinae

Clerinae + Epiclininae + Hydnocerinae

Old World Tillinae

New World Tillinae

324

Fig. 4.6. Fifty percent majority rule consensus tree of the morphology-based dataset and the concatenated molecular dataset for the New World Tillinae. The topology was based on the optimal partition strategy predicted by PartitionFinder and the Mk1 model, and resulted from two Bayesian MCMC runs performed in MrBayes. Numbers above branches represent Bayesian posterior probability values.
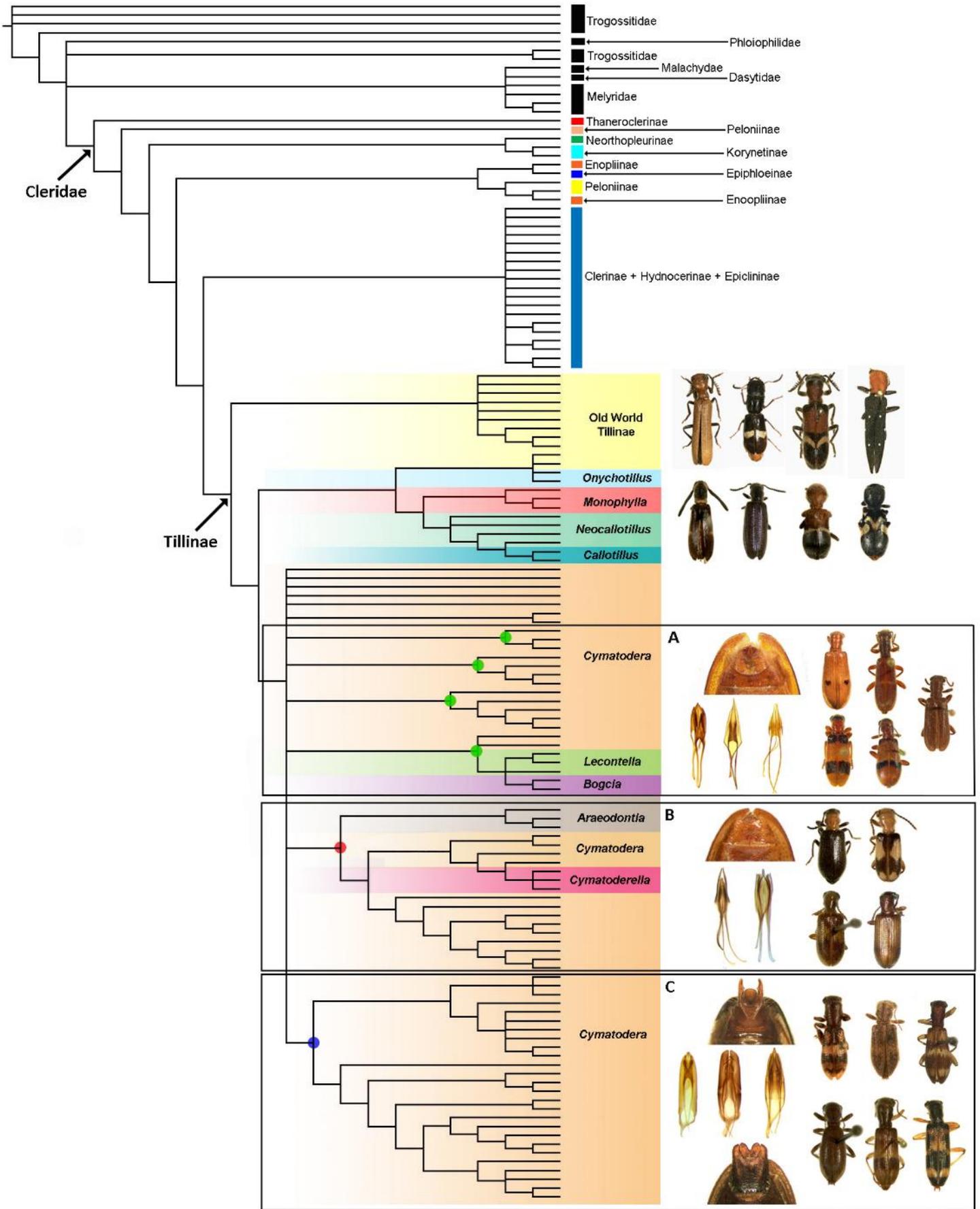
Fig. 4.7. Molecular + morphology-based phylogeny of the New World Tillinae. Black bars along branch tips represent cleroid families used in this study as outgroup taxa. Colored bars along branch tips represent non-tillinid clerid subfamilies *sensu* Opitz (2010) and Gunter et al. (2013). New World Tillinae genera are color-coded to denote intergeneric relationships. Three major groups within the large clade composed of *Cymatodera* and related genera are given: group *A* is an unresolved assemblage of clades composed of taxa of medium to large size, male pygidium moderately elaborate, and aedeagus feebly to moderately sclerotized, clades containing these taxa are marked with green circles; group *B* is a clade composed of taxa of small to moderate size, simple male pygidium, and aedeagus slender and feebly sclerotized, a clade containing these taxa is marked with a red circle; and group *C* is a clade composed of taxa of moderate to very large size, male pygidium conspicuously elaborate, and aedeagus robust and sclerotized, a clade containing these taxa is marked with a blue circle. Images of Tillinae species from each group and taxonomic characters of importance are given at the right of the topology.
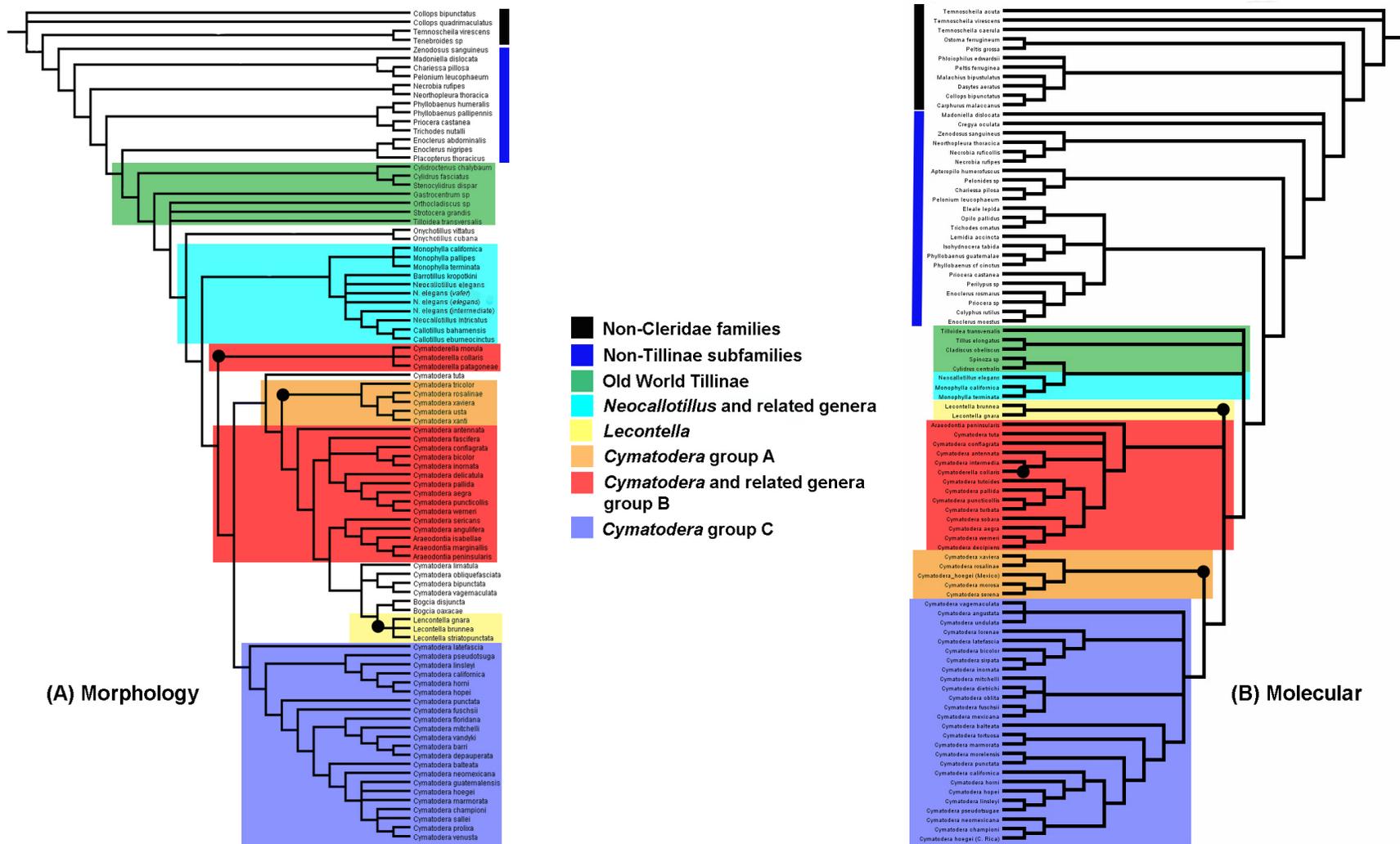
Fig. 4.8. (A) Strict consensus topology of the morphology-based phylogenetic analysis (chapter 3), and (B) Bayesian topology of the concatenated DNA dataset showing position of major groups (see Fig. 4.7). Black circles denote clades not equally supported in both analyses.

Chapter 5 - Historical biogeography and distribution of the checkered beetle genus *Cymatodera* Gray and related genera (Cleridae: Tillinae)

Abstract

The historical biogeography of *Cymatodera* Gray, one of the most species-rich genera within the subfamily Tillinae, is investigated here. The principal aim of the study was to determine the age of origin of these beetles. Hypotheses about the center of origin, patterns of distribution, and processes that led to the widespread distribution of the group are presented. A phylogenetic analysis of 50 New World tillinid species was constructed through maximum likelihood and Bayesian inferences using three molecular loci, the mitochondrial markers 16S rDNA and cytochrome c oxidase subunit I, and the nuclear gene 28S (LSU) rDNA. A relaxed molecular clock using a Bayesian inference, which was calibrated using three secondary dates derived from other time-calibrated phylogenies to estimate lineage divergence times, was developed. Biogeographic processes were studied using the Bayesian Binary Markov Chain Monte Carlo analysis implemented in the software Reconstruct Ancestral State in Phylogenies. The results obtained here suggest that the most recent common ancestor of all extant *Cymatodera* species emerged 71.5 MYA during the mid-Cretaceous in what is now north-central Mexico and the southwest USA, where the highest diversity of species currently occur. Species richness diminishes gradually southward, with only three described species found in South America. *Cymatodera* is a relatively recent genus in Central America and it is hypothesized that the group entered to what is now South America after the closure of the Panamanian Isthmus, 12-15 MYA.

1. Introduction

Vicariance and biological dispersal are the two major biogeographical processes responsible to produce population fragmentation, and eventually, enabling speciation (Newton, 2003). Vicariance is the process where the geographic range of a particular taxon, or groups of taxa, is separated into discontinuous areas of distribution through the appearance of physical barriers, such as the formation lakes or oceans, the uplift of mountains, or the separation of land masses. Most of these events are caused by tectonic processes (Nelson & Platnick, 1981; Cooper et al., 2001 Humphries and Parenti, 2001; Albert and Reis, 2011). The formation of these barriers will eventually lead to the split of the geographic range of species, a halt of gene flow among populations, and the subsequent formation of new taxa. On the other side, biological dispersal is a process where individuals migrate from the parental population across geological barriers, being these barriers older than the parental species, to colonize new habitats. This movement of species can lead to the formation of a new population sufficiently isolated from the original and eventually, to a speciation event (Newton, 2003).

Various studies (Platnick and Nelson, 1978; Humphries and Parenti, 2001; Lieberman, 2005; Newton, 2003; Ree & Smith, 2008; Lomolino et al., 2009; Albert and Crampton 2010) have found that the movment of individuals across pre-existing barriers could properly explain the distribution of closely related taxa with a wide distribution. In the case of *Cymatodera*, a species-rich genus with an extensive distribution, it is hypothesized that biological dispersal is the process responsible of the population fragmentation and extensive speciation the genus has undergone.

Cymatodera is restricted to, but widely distributed, in the New World, ranging from southern Canada to central South America, but absent in the West Indies (Burke et al., 2015) (Fig. 5.3). *Cymatodera* is the most speciose genus within the Tillinae, with approximately 130 described species (Corporaal, 1950, Papp, 1960, Barr, 1975, Burke et al., 2015). A number of *Cymatodera* species have a widespread distribution throughout the Americas, while others are endemic to isolated areas (Burke et al., 2015). The highest diversity of *Cymatodera* species is found in North American (north-central Mexico and southwestern USA) semiarid to temperate and sub-temperate zones. Species diversity gradually diminishes southward, with the fewest number of *Cymatodera* species found in South America.

Ree & Smith (2008) have stated that a robust phylogenetic history currently is the best method to accurately understand the processes producing the widespread distribution of the taxa under investigation. Lomolino et al. (2009) further indicated that this phylogeny must be time-calibrated to allow comparisons of lineage divergence with climatic and geological information. Previous studies (Hunt et al., 2015 and McKenna et al., 2015) have recovered the time of origin of the Cleridae as approximately 95-107 MYA. By this time, continents had already taken the general form observed today, and consequently, major vicariance events could not have been responsible for the diversification of the group.

In this chapter, a molecular-based phylogenetic analysis of *Cymatodera* and related genera was developed. The phylogeny obtained was used to reconstruct ancestral states and the processes underlying the extensive distribution of the *Cymatodera* lineage in the New World. A

chronogram was reconstructed using an uncorrelated relaxed clock model and three calibration dates to infer the time of origin of these checkered beetles. Based on the results obtained, a hypothesis on the origin, diversification and current distribution for the *Cymatodera* lineage is given. This hypothesis is supported by geological events and climatic data.

2. Materials and methods

2.1 Taxon sampling, DNA amplification and gene sequencing

The taxon-sampling consisted of 50 species representing 6 New World Tillinae genera. A list of taxa, distribution, and localities is provided in Table 5.2. DNA was extracted from total body, head and/or thorax of specimens using a QIAGEN DNeasy tissue kit as per standard protocols. Three loci were analyzed: the mitochondrial genes 16S rDNA and cytochrome c oxidase subunit I (COI), and the nuclear gene 28S (LSU) rDNA. The 16S rDNA locus was amplified as a single fragment with the primers '16S-R1' and '16S-R2', but in some cases it was amplified using the primer pairs '16c' and '12sB'. COI was amplified in two smaller fragments using the primer pairs 'LCO-1490' to 'HCO-700ME' and 'Jerry' and 'Pat'. Partial 28S sequences were also generated using the primer pairs '28Sff' to '28Sdd'. Primer sequences and references are listed in Table 5.3. Amplifications were carried out in the Laboratory of Molecular Entomology at the Department of Entomology, Kansas State University as follows: amplifications were carried out using the QIAGEN Fast Cycling PCR Kit with the following reaction composition: 10 μL of QIAGEN Fast Cycling PCR Master Mix, 2 μL of 10x CoralLoad Fast Cycling Dye, 1 μL of each primer at a 1 μM concentration, 4 μL of RNase-free water, 1 μL of template producing 20 μL of reaction volume. Typical PCR reactions were performed under the following conditions: Initial activation: 5 m at 95°C; 3-step cycle: denaturation: 30s at 96°C,

annealing 1 m at 45°C, extension: 30s at 68°C (40 cycles); final extension: 10 m at 72°C.

Annealing temperature between 40°C to 50°C according to the locus to be amplified. Detailed

thermocycling conditions are given in Table 4.4 from Chapter 4. PCR products were purified

using ZYMO DNA (PCR) Clean and Concentrator Kit. Cleaned PCR products were sent to the

DNA Sequencing and Genotyping Facility, Department of Plant Pathology, Kansas State

University, for sequencing. Profile of amplification for each individual gene and reference for

sequences acquired in GenBank, when applicable, is given in Table 5.3.

2.2 Multiple alignment and phylogenetic analysis

Each sequence was aligned by manual inspection to form contigs using Geneious 7.1.9 (V.

7.1; Drummond et al., 2012). Single-gene datasets were concatenated to produce a combined

matrix spanning ~2710 bp using Geneious 7.1.9 (V. 7.1; Drummond et al., 2012). Phylogenetic

analyses of the concatenated dataset were performed using a Bayesian approach (BA), and a

maximum likelihood approach (MLA). Gaps were treated as missing data. For the BA, the

dataset was partitioned as predicted by PartitionFinder (Lanfear et al., 2012) (Table 5.1); the

analysis was carried out using MrBayes V. 3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist &

Huelsenbeck, 2003), each analysis consisted of 10 million generations with a random starting

tree, and two simultaneous runs with four Markov chains sampled every 1,000 generations with

unlinked partitions. Stationarity in Markov Chain Monte Carlo (MCMC) chains was determined

in Tracer (Rambaut & Drummond, 2007). Twenty percent of the generations were discarded as

burn-in; a 50% consensus tree was obtained from the two combined runs to establish the

posterior probabilities of clades. MLA analysis was developed in RaxML V. 7.0.3 (Randomized

Axelerated Maximum Likelihood) (Stamatakis, 2014) implementing the same modeling strategy

used with the BA. A nonparametric bootstrap analysis with a total of 200 replicates with random addition sequence per replicate was conducted to assess nodal support.

2.3 Divergence-time estimation

A Bayesian approach was implemented to reconstruct a time-calibrated chronogram using MrBayes V 3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). An uncorrelated lognormal relaxed clock model (Drummond et al., 2006) was used in the analysis. Substitution models applied for the concatenated dataset were those predicted by PartitionFinder (Lanfear et al., 2012) (Table 5.3). Selected substitution models were unlinked among partitions. The uncorrelated lognormal clock and all trees obtained in the analysis were kept as linked. Three node-based calibration ages obtained by Hunt et al. (2010) and McKenna et al. (2015) were used for the analysis: the crown-group node of all Tillinae species included in this analysis was assigned a fix prior to 107 MYA, the ancestor-node of all New World Tillinae was assigned a long normal prior of (mean) 96 MYA (SD=5), and one calibration point for *Cymatodera* was assigned a truncated normal prior of (mean) 42 MYA (SD=5). Convergence diagnostics were examined in Tracer 1.5. Two independent MCMC searches were performed for 10 million generations. Initial 20% of the generations were discarded from the analysis as burn-in.

2.4 Reconstruction of ancestral area

The current distribution of *Cymatodera* species and related genera was obtained from approximately 7,000 specimens examined, covering all 50 species included in the analysis. Collection locality and current distribution for all species are given in Table 5.2. The geographical regions were divided as follows: 1) Canada (Nearctic), 3) eastern USA (Nearctic),

4) western USA (Nearctic), 5) north Mexico (Nearctic), 6) south Mexico (Neotropic), 7) Central America (Neotropical), and 8) South America (Neotropical). The Nearctic and Neotropical biogeographic regions, when possible, were subdivided into areas delimited by geological and/or natural barriers which could reduce the flow of populations or individuals from one area to another. Although there is not a significant natural barrier dividing Canada and USA, all the species found in northern Mexico and the western USA do not extend to Canada, and species with a USA - Canada distribution never reach northern Mexico. The Rocky Mountains, a geographic barrier, was set as the limit between the eastern and western USA. The western USA and northern Mexico are mostly divided by the Sonora and Chihuahua Deserts. The delimitation of north Mexico and Central Mexico is justified by the fact that north Mexico is part of the southernmost portion of the Nearctic region, while south Mexico is part of the Neotropical region (Undvardy, 1975); these regions are divided by the Trans-Mexican Volcanic Belt. Central and South America were previously separated by the Central American Seaway, the closure of this seaway 15-18 MYA had tremendous effects on the biogeography of adjacent areas.

A Bayesian Binary MCMC (BBM) analysis was implemented to reconstruct ancestral areas using the program Reconstruct Ancestral States in Phylogenies (RASP) (Yu et al., 2013). This approach follows a DIVA (dispersal-vicariance) methodology for estimating the posterior distribution of tree topologies. Furthermore, BBM adopts a Bayesian approach and uses a phylogeny and the current geographic range of the taxa to infer historical areas of origin of ancestors of monophyletic groups (Yu et al., 2013). The topology retrieved by RASP is based on the phylogeny obtained by the MLA executed in RaxML. Topologies containing unresolved clades and/or polytomies are rejected by RASP as sources of information, only fully resolved

trees can be used. The maximum number of areas at each node was retained as 8. The fixed model Jukes-Cantor + Gamma (JC+G) with a null root distribution was implemented in the analysis. Two MCMC chains were run simultaneously for 10 million generations sampled every 1,000 generations.

3. Results

3.1 Phylogenetic analysis of the Cymatodera group

The concatenated matrix consisted of 2710 bp. The COI amplified fragment consisted of 577-681 bp, the 16S dataset contained 465-524 bp, and the 28S fragment consisted of 488-1341 bp. Base frequencies were almost equal in the nuclear gene 28S (A=25.8%, C=24.3%, G=30.5%, T=19.4%), but for the mitochondrial genes 16S (A=35.7%, C=9.0%, G=16.0%, T=39.3%) and COI (A=31.4%, C=16.7%, G=15.5%, T=36.4%) a higher A-T bias was observed. PartitionFinder (Lanfear et al., 2012) selected five partitions (16S, 28S, COI first codon position, COI second codon position, and COI third codon position) as the optimal partitioning scheme with the nucleotide substitution model GTR+I+G for 16S and 28S; the model GTR+G for the COI first codon position; GTR+G for COI second codon position; and SYM+G for the COI third codon position (Table 5.1). The Bayesian analysis obtained Neocallotillus Burke + Monophylla Spinola as sister to all other New World Tillinae while MLA recovered Monophylla as the sister group to a clade composed of *Araeodontia* Barr + *Cymatodera* Gray + *Cymatoderella* Barr and *Lecontella* Wolcott & Dybas. The analyses obtained *Cymatodera* as paraphyletic by the inclusion of *Araeodontia*, *Cymatoderella* and *Lecontella*. Three broad groups from the *Cymatodera* lineage were recovered: Clade 1: a lineage of *Cymatodera* species with a posterior probability value (PP) of 0.85 (clade 1 in Figs. 5.1, 5.2); Group 2: a cluster of clades composed of *Lecontella* and

336

Cymatodera species; and Clade 3: a large clade encompassing derived *Cymatodera* species with a PP of 0.82 (Figs. 5.1, 5.2).

3.2 Estimation of divergence-time events

The most recent common ancestor of *Cymatodera* and related genera originated approximately 71.5 MYA (CI = 61.9-78.6), during the Maastrichtian age in the Early Cretaceous. Two crown groups can be inferred from the chronogram: 1) Clade 1, with an age of 60.4 MYA (CI = 49.4-70.3); and 2) Group 2 + Clade 3, with an age of 67.5 MYA (CI = 58.8-76.2). The oldest lineage in the *Cymatodera* group is represented by the *Lecontella* lineage, that group emerged approximately 67.5 MYA (CI = 58.8-76.2) and is currently distributed in the southwest USA and Mexico. The youngest lineage in the group is formed of *Cymatodera* species inhabiting Central America, with the origin of the most recent common ancestor of this clade approximately 12.3 MYA (CI = 4.2-18.2) (Fig. 5.4).

3.3 Historic biogeography of the Cymatodera group

The BBM analysis recovered southwestern USA and northern Mexico (Nearctic) as the center of origin of all New World Tillinae. Two major dispersal events occurred during the evolution of the group in the New Wolrd. The first event followed a southward direction, while the second dispersal experienced a west-to-east migration. The first migration event, a north-to-south route, had the greatest impact on the current distribution of the group, with many new species diversifying from those species migrating southward. The second migration process had a lesser impact, with fewer species adapting to regions found east and north from the center of origin. The three sub-clades obtained in the phylogenetic analysis also have relatively complex

centers of origin (Fig. 5.3). Clade 1 originated in the southwestern USA and north Mexico, with all species in the group currently distributed in that region, except C. conflagrata, a species widely distributed in the Americas. A grade of clades in group 2 are generally old taxa that originated 30 million years ago or earlier and originated in the western USA and northern Mexico. Clade 3 emerged in the Nearctic; however, because taxa forming this assemblage are present in several areas and form sister relationships with lineages in multiple areas, their center of origin is difficult to establish. According to its center of origin, this clade can be subdivided into two major groups: 1) species in clade 3 currently distributed in the western USA, Mexico, Central and South America, are mostly young lineages, less than 30 million years old (Fig. 5.4), and have a center of origin in west USA and Mexico (Fig. 5.3); and 2) species in clade 3 distributed in the eastern USA, such as *Cymatodera* bicolor (Say) and C. inornata (Say) (clade 3), are also young lineages, however, they have a yet more complex origin, and is not possible to assert with certainty their center of origin.

4. Discussion

4.1 Phylogenetic relationships of the Cymatodera group

    Neocallotillus and *Monophylla* were equally recovered as basal lineages in the BA and MLA analyses. BA produced a polytomy encompassing *Neocallotillus* and *Monophylla* as the sister to all other New World tillinids (Fig. 5.1). MLA retrieved *Neocallotillus* as the most basal lineage in the topology and *Monophylla* as sister to *Cymatodera* and related genera (Fig. 5.2). These results are consistent with the DNA-based and DNA + morphology-based phylogenetic analyses (see Figs. 4.5 and 4.6 from Chapter 4), where *Neocallotillus* and *Monophylla,* together

with Old World tillinids, were recovered as sister to all other New World tillinids.

Cymatodera was recovered as paraphyletic by including *Araeodontia*, *Cymatoderella* and *Lecontella* in the *Cymatodera* lineage. *Araeodontia* and *Cymatoderella* were found to be nested in a clade compose of species were males have a relatively simple pygidium and a feebly to moderately sclerotized aedeagus (Clade 1 in Figs. 5.1, 5.2). *Lecontella* was recovered to be the sister to a group of species with sclerotized pygidium and aedeagus (*Cymatodera* xavierae Knull and related species + Clade 3 in Figs. 5.1, 5.2). In the molecular analysis, *Lecontella* was found to be sister to all other *Cymatodera* species and related genera (see Fig. 4.5 from Chapter 4); remaining genera were equally obtained in both analyses. The monotypic *Bogcia* Barr was also retrieved as part of the large *Cymatodera* clade by the molecular + morphology analysis (see Fig. 4.6 from Chapter 4). Morphological data suggests that *Bogcia* is closely related to *Cymatodera* (see Figs. 3.1, 3.6-E, 3.12-A, 3.22-F from Chapter 3). The relationship between *Cymatodera* and these taxa was previously discussed and illustrated (see Fig. 3.2 from Chapter 3 and Fig. 4.5, 4.7 from Chapter 4) and three major groups from the *Cymatodera* lineage can be equally inferred from the BA and MLA analyses (Fig. 5.1 and 5.2):

- Clade 1) *Cymatodera* aegra Wolcott and related species; a monophyletic group in the *Cymatodera* lineage which can be morphologically characterized by a small to moderately small and robust body size, feebly sclerotized aedeagus, parameres crenulate with a row of fine denticles, and simple male pygidium.

- Group 2) A grade of two clades. The first is composed of *Lecontella gnara* Wolcott *and L. brunnea* (Spinola); this clade was recovered as sister to remaining *Cymatodera* species (see Figs. 5.1, 5.2). The second clade composed of *Cymatodera xaviera* Knull, *C. rosalinae* Burke, *C. morosa* LeConte, *C. serena* Barr, and *C. hoegei* Gorham (Mexico); this group was recovered as sister to a large *Cymatodera* clade (clade 3 in Fig. 5.1, 5.2). It should be noted that the position of *Lecontella* varied between the concatenated DNA-based analysis of Chapter 4 and the analysis in this chapter.

- Clade 3) *Cymatodera* championi and related species is a clade composed exclusively of *Cymatodera* species. These taxa share the following morphological charters: a conspicuously differentiated male pygidium, parameres armed with a row of moderately large to very large denticles, and a sclerotized aedeagus. The largest species in the genus are part of this clade.

These clades are generally congruent with the results obtained by the DNA- and molecular + morphology-based analyses (see Fig. 3.1 from Chapter 3 and Figs. 4.5, 4.6 from Chapter 4).

4.2 Divergence time and historic geography

The application of a molecular clock to the dataset indicates that the most recent common ancestor of the *Cymatodera* lineage originated approximately 70.8 MYA (CI = 61.9 - 78.6). This period coincides with a major radiation of species that all Coleoptera families underwent during the Late Cretaceous (McKenna et al., 2015). This radiation of beetle taxa overlaps with the extensive diversification of flowering plant species, which replaced coniferous species as the

dominant plant group during a period that ranged from 60 to 100 MYA, during period called the

Cretaceous Terrestrial Revolution (Brentnall et al., 2005). The *Cymatodera* lineage subsequently

followed two major diversification events. The first began approximately 67.8 MYA (CI=59.2 -

74.7) and gave rise to a number of species found throughout the Americas; this wave was

probably the most important since it gave rise to ancestors of most present-day species, including

several groups now distributed in central and south Mexico and Central America. The second

diversification event occurred 60.9 MYA (CI=52.2-69.6); this event had a lesser effect on the

diversification of the *Cymatodera* lineage and gave rise to the ancestors of most species currently

inhabiting the southwest USA and north Mexico, with few species subsequently entering south

Mexico and Central America (Fig. 5.4).

A major radiation of *Cymatodera* species is observed between 18-44 MYA. During this

period, most *Cymatodera* clades included in the analysis diversified extensively and produced

almost all lineages observed in the chronogram. This period coincides with the appearance and

diversification of fungus-farming and bark beetles from the subfamily Scolytinae

(Curculionidae) beetles (Jordal and Cognato, 2012). Scolytinae, commonly known as bark

beetles, is a diverse subfamilies within the Curculionidae. These beetles occur worldwide and are

associated to most groups of terrestrial plants. Bark beetles play a fundamental role in the

structure of plant communities, contributing to the natural cycle of various plant ecosystems

(Wegensteiner et al., 2015). It is suspected that clerid beetles, including various *Cymatodera*

species, play an important role in the population dynamics of bark beetles (Wegensteiner et al,

2015). The family Cleridae includes some of the most well-known groups of bark beetle

predators, and many of them can have important impacts on bark beetle populations. Various

clerid species exploit aggregation pheromones and other semiochemical queues emitted by bark beetles and the host tree under attack to locate their prey. The complex interaction between these two groups of beetles undoubtedly took place during millions of years of co-evolution, and it serves as an indication of the close affinity clerids and bark beetles have. Consequently, the diversification of Scolytinae species (20-55 MYA) and related prey items in the New World very likely facilitated the rapid speciation of predatory insects such as *Cymatodera* species, and other clerid predators.

4.3 Ancestral areas and current distribution

    Cymatodera is particularly species-rich in semiarid environments with xeric scrublands and thorny forests, and these types of environment are widespread in the southwest USA and north Mexico. Temperate and sub-temperate, mid and high-altitude mountainous environments with coniferous forests and mixed pine-broadleaved forests are also habitats that support moderately high concentrations of species. According to the BBM analysis, *Cymatodera* originated in what is now the southwest USA and north Mexico, where the highest diversity of species is currently found (Fig. 5.3), during the Late Cretaceous (70.8 MYA). This period was characterized by a dramatic increase in global temperatures, which were approximately 10°C higher than those currently observed (Skelton et al., 2003 and Haywood et al., 2005). The appearance of the *Cymatodera* lineage occurred shortly after the Cretaceous Thermal Maximum, a period where a steep and progressive warming of the planet took place (Wilson et al., 2009). During this period deciduous forests extended to polar regions, replacing vast areas previously covered by coniferous forests, however, islands of conifers remained present at high altitudes throughout much of what is now North America (Peralta-Medina and Falcon-Lang, 2012). The warm

temperatures and abundant vegetation were very likely favorable to various groups of beetles, allowing a slow but steady diversification of beetle taxa, including the first *Cymatodera* species.

A slow but steady diversification of the group was observed in the Paleocene and upper Eocene (50-66 MYA). During this epoch, the climate was slowly but steadily cooling down. Fossil pollen (Frederiksen, 1980) and macrofossils (Dilcher, 1973; Wolfe, 1985) suggest that the climate of southern North America during the Eocene epoch (38-55 MYA) varied between seasonally dry tropical and humid subtropical with a tropical to subtropical flora characterizing this period. As the Rocky Mountains formed (55-80 MYA), coniferous forests characteristic of higher elevations expanded (Axelrod and Raven, 1985; Axelrod, 1986, 1990).

A significant radiation of species took place during the late Eocene- early Oligocene (20-40 MYA) (Fig. 5.4). This period was largely represented by drier habitats at lower elevations and cooler and more humid environments at higher altitudes (Upchurch and Wolfe, 1987; English and Johnston, 2010). These habitats most likely held a rich arthropod fauna with many suitable prey items, and triggered the radiation of various predatory species, such as *Cymatodera* and related genera. Drier climates and colder winters initiated the decline of tropical environments in the North American flora during the late Oligocene (25-27 MYA). At this time, the flora of southwestern North America was predominantly represented by mixed conifer forest and a pinyon-juniper woodland scrub (Wolfe and Schorn, 1989). Various migration waves took place during this radiation of species.

Cymatodera dispersed mainly through two routes, the first one was an eastward migration, and the second and most important route was a southern migration with significant diversification of species throughout the region. For the eastern migration, two dispersal events occurred late in the history of the group, approximately 20-35 MYA ma (Fig. 5.4). Interestingly, this wave of species did not radiate extensively, and presently, only five *Cymatodera* species inhabit the east-southeast USA and southeast Canada (Corporaal, 1950, Papp, 1960, Barr, 1975, Burke et al., 2015). This phenomenon is most likely due to a number of geological and ecological events. *Cymatodera* originated in North America approximately 71.5 MYA; at that time, the continent of North America was divided into two large land masses by the Western Interior Seaway (WIS), the Laramidian subcontinent to the west and the Appalachian subcontinent to the east. This body of water existed during the second half of the Cretaceous to the early Paleogene (Blackey, 2011). The seaway halted the migration of species from west to east. As the WIS was closing, the Rocky Mountains in what is now western USA were slowly but steadily uplifting (55-80 MYA). After the total closure of the WIS (approximately 50-55 MYA), the Rocky Mountains had totally emerged and further prevented the migration of species from west to east (Fig. 5.5). Those species that could crossed or circumvent this area found relatively high temperatures and evergreen tropical to sub-tropical low-altitude woodlands in much part of what is now northeast, east and southeast USA, and high competition with other arthropod predators already established in that region of the continent, preventing the diversification of the group.

For the southward migration, five waves of dispersal events occurred during the evolutionary history of the group and took place at three different times. The oldest wave

occurred approximately 47-55 MYA; this wave gave rise to a number of species inhabiting what is now the southwest USA and north Mexico. The second wave happened 20-33 MYA; this wave gave rise to ancestors of most present-day Mexican species. The third and most recent wave occurred only 10-16 MYA; during this wave the ancestors of most species now inhabiting Central America entered this region (Fig. 5.3). The latest and most recent migration wave had important biogeographic consequences for the group. The results obtained from the BBM analysis (Fig. 5.3) and the age of those species inhabiting meridional latitudes (Fig. 5.4), suggest that *Cymatodera* is a young lineage in South America. The West Indies pathway has been proposed as a probable dispersal route for various groups of fauna between the Nearctic and the Neotropics. These faunas very likely originated in what is now North America, dispersed through the West Indies pathway, and then diversified in South America (Rosen, 1975; Humphries and Parenti, 2001; Ramirez et al., 2010; Condamine et al., 2013). This pathway was probably not the route for *Cymatodera* species to enter South America because no *Cymatodera* species from the West Indies have been described, nor has any fossil been found in that area, while approximately 20-30 described species are currently found in Central America (Burke et al., 2015).

Presently, only three described species are distributed in South America: *Cymatodera conflagrata* (Klug), *C. championi* Gorham, and *C. venusta* Wolcott. The latter two are closely related species nested in a young clade (~14 MYA) composed of taxa distributed from south Mexico to Bolivia (Fig. 5.4 and see Fig. 4.6 from Chapter 4). Due to the age of these species and their current distribution, *Cymatodera* very likely entered to South America after the formation of the Panamanian Isthmus, 12-15 million years ago (Bacon et al., 2015; Montes et al., 2015;

345

O'Dea et al., 2016), during the Great American Interchange. According to Graham (1973), the

Central America peninsula was predominantly covered by sub-tropical scrubland and savannah

vegetation prior to the formation of the Panamanian isthmus. This habitat was suitable for the

first *Cymatodera* species arriving to the region, and after the closure of the Central American

seaway, a new migration wave may have taken a number of species into South America. The

results given here support the geographic conclusions of the morphology-based phylogeny in

Chapter 3. That analysis found species distributed in Central and South America as derived

clades.

Unlike *C. championi* and *C. venusta, C. conflagrata*, the third South American species

known, emerged earlier in the evolutionary history of the group (56.3 MYA) and is nested in a

clade distantly related to the former two taxa (Fig. 5.4). *Cymatodera conflagrata* (Klug) is found

from central Mexico to Colombia and Venezuela and belongs to a clade composed of species

predominantly distributed in southwest USA and north Mexico (Fig. 5.3), suggesting that that

species probably emerged in north or central Mexico earlier than its South American

counterparts, underwent a major migration process, and entered South American after the

formation of the Isthmus of Panama.

5. Conclusions

This is the first study addressing the biogeographic processes that gave rise to the present-

day distribution of the speciose *Cymatodera* genus in the New World. In general, the results

indicate that *Cymatodera* sensu stricto is paraphyletic in nature, and only the inclusion of the

small genera *Araeodontia*, *Cymatoderella* and *Lecontella* will produce a monophyletic group

346

(Fig. 5.1 and 5.2). The *Cymatodera* lineage appeared approximately 71.5 MYA, during the late Cretaceous, a period characterized by higher-than-average temperatures and dense deciduous forests in North America. *Cymatodera* originated in what is now the southwest USA and north Mexico, a region that currently holds the highest diversity of species. One large radiation of species took place approximately 20-35 MYA; during this period, North America was cooling down and many deciduous forests started to disappear, and replaced by drier environments at low elevations and cooler ecosystems at higher altitudes. Two major dispersal routes were followed, a southward and an eastward route. The southward route was the most successful, with a high number of species subsequently diversifying in what is now north and central Mexico and Central America, and subsequently, entering to South America. *Cymatodera* is a young lineage in Central America, with species inhabiting this area emerging 13-25 MYA. It is hypothesized that the genus entered South America approximately 12 MYA, after the closure of the Panamanian seaway. Presently, only three described species are found in South America. The eastern migration had a lesser effect on the *Cymatodera* lineage, with approximately five species currently distributed east of the Rocky Mountains. The limited diversification of species in east North America was caused by the existence of the WIS in North America during the appearance and early diversification of the group, and subsequently, the uplifting of the Rocky Mountains, preventing an east-to-west migration.

The methods followed here could be applied to study the historic biogeography and patterns of distribution of other taxa within the Cleridae lineage. Sampling for further studies on the biogeography of the group must focus on obtaining population level data for all *Cymatodera* species and a more robust taxon-sampling to better understand the migrations routes species in

the group underwent. Finally, by studying the historic geography of the Tillinae and the patterns

of distribution of *Cymatodera*, it is possible to understand the past and present relationships these

taxa have with the plant communities they inhabit, information useful to broaden our

understanding about the ecology, present-day distribution, and evolution of the group.

6. References

Albert, J. S. and W. G. R Crampton (2010) The Geography and Ecology of Diversification in
Neotropical Freshwaters". Nature Education Knowledge. 3(10): 13.

Albert, J. S. and R. E. Reis (2011) Historical Biogeography of Neotropical Freshwater Fishe*s*.
University of California Press. p. 308.

Axelrod, D. I. (1986) Analysis of some palaeogeographic and palaeoecologic problems of
palaeobotany. Palaeobotanist 35: 115-129.

Axelrod, D. I. (1990) Age and origin of the subalpine forest zone. Paleobiology 16 (3): 360–369.

Axelrod, D. I. and P. H. Raven (1985) Origins of the cordilleran flora. Journal of Biogeography
12: 21-47.

Bacon, C. D., D. Silvestro, C. Jaramillo, B. T. Smith, P. Chakrabarty and A. Antonelli (2015)
Biological evidence supports an early and complex emergence of the Isthmus of Panama.
Proceedings of National Academy of Sciences 112: 6110–6115.

Barr, W. F. (1975) Family Cleridae. In: Arnett, R.H. (Ed.), Checklist of the beetles of North and

    Central America and the West Indies. Vol. 4. Family 73. Flora and Fauna Publications,

    Gainesville, pp. 1–18.

Blakey, R. C. (March, 2011) Paleogeography and Geologic Evolution of North America

    http://jan.ucc.nau.edu/rcb7/nam.html. Web site last accessed on 2-22-2017.

Brentnall, S. J., D. J. Beerling, C. P. Osborne and V. E. Wittig (2005) Climatic and ecological

    determinants of leaf lifespan in polar forests of the high CO2 Cretaceous 'greenhouse'

    world. Global Change Biology 11(12): 2177–2195.

Burke, A. F., J. M. Leavengood Jr. and G. Zolnerowich (2015) A checklist of the New World

    species of Tillinae (Coleoptera: Cleridae), with an illustrated key to genera and new

    country records. Zookeys 4059(1): 1-39.

Condamine, F. L., F. A. H. Sperling and G. J. Kergoat (2013) Global biogeographical pattern of

    swallowtail diversification demonstrates alternative colonization routes in the Northern and

    Southern hemispheres. Journal of Biogeography 40: 9–23.

Cooper, A., C. Lalueza-Fox, S. Anderson, A. Rambaut, J. Austin, and R. Ward (2001) Complete

    mitochondrial genome sequences of two extinct moas clarify ratite evolution. Nature 409:

    704–707.

Corporaal, J. B. (1950) Cleridae. In: W. D. Hinks (Ed.). Coleopterorum catalogus supplementa, Pars 23 (editio secunda). W. Junk; The Hague. 373 p.

Dilcher, D. L. (1973) A paleoclimatic interpretation of the Eocene floras of southeastern North America. In: A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam, pp. 39-59.

Drummond, A. J., B. Ashton, S. Buxton, M. Cheung, A. Cooper, C. Duran, M. Field, J. Heled, M. Kearse, S. Markowitz, R. Moir, S. Stones-Havas, S. Sturrock, T. Thierer, and A. Wilson (2012) Geneious V. 7.1. Available from http://www.geneious.com/

English, J. M and S. T. Johnston (2004) The Laramide Orogeny: What Were the Driving Forces? International Geology Review 46(9): 833-838.

Frederiksen, N. O. (1980) Mid-Tertiary climate of southeastern United States: the sporomorph evidence. Journal of Paleontology 54: 728-739.

Graham, A. (1973) History of the arborescent temperate element in the northern Latin American biota, in Vegetation and Vegetation History of Northern Latin America. A. Graham *Ed.*, pp. 301-314, Elsevier, New York.

Haywood, A. M., P. J. Valdes and P. J. Markwick (2005) Cretaceous (Wealden) climates: a

    modelling perspective. Cretaceous Research 25: 303–311.

Huelsenbeck, J. P., and F. Ronquist (2001) MRBAYES: Bayesian inference of phylogenetic

    trees. Bioinformatics 17: 754-755.

Humphries, C. J. and L. R. Parenti (2001) *Cladistic Biogeography. Interpreting Pattern of Plant*

    and Animal Distributions. Oxford Biogeography Series No. 12. Oxford University Press.

Hunt, T., J. Bergsten, Z. Levkanicova, A. Papadopoulou, O. St. John, R. Wild, P. M. Hammond,

    D. Ahrens, M. Balke, M. S. Caterino, J. Gómez-Zurita, I. Ribera, T. G. Barraclough, M.

    Bocakova, L. Bocak, and A. P. Vogler (2007) A Comprehensive Phylogeny of Beetles

    Reveals the Evolutionary Origins of a Superradiation. Science 318: 1913-1916.

Jordal, B. H. and A. I. Cognato (2012) Molecular phylogeny of bark and ambrosia beetles

    reveals multiple origins of fungus farming during periods of global warming. BMC

    Evolutionary Biology 12(133): 1-10.

Lanfear, R., B. Calcott, S. Y. W. Ho, and S. Guindon (2012) PartitionFinder: combined selection

    of partitioning schemes and substitution models for phylogenetic analyses. Molecular

    Biology and Evolution 29: 1695-1701.

Lieberman, B. S. (2005) Geobiology and paleobiogeography: tracking the coevolution of the Earth and its biota. Palaeogeography, Palaeoclimatology and Palaeoecology 219(1-2): 23–33.

Lomolino, M. V., B. R. Riddle and J. H. Brown (2009) *Biogeography*. Sinauer Associates, Inc., Sunderland, MA.

McKenna, D. D., A. Wild, K. Kanda, C. Bellamy, R. G. Beutel, M. S. Caterino, C. W. Farnum, D. C. Hawks, M. A. Ivie, M. L. Jameson, R. A. B. Leschen, A. E. Marvaldi, J. C. McHugh, A. F. Newton, J. A. Robertson, M. K. Thayer, M. F. Whiting, J. F. Lawrence, A. Ślipiński, D. F. Maddison and B. D. Farrell. 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology 40: 835‑880.

Montes, C., A. Cardona, C. Jaramillo, A. Pardo, J. C. Silva, V. Valencia, C. Ayala, L. C. Pérez-Angel, L. A. Rodriguez-Parra, V. Ramirez, and H. Niño (2015) Middle Miocene closure of the Central American Seaway. Science 348: 226–229.

Nelson, G.J. & N. I. Platnick (1981) *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.

Newton, I (2003) The Speciation and Biogeography of Birds. 1st ed. Academic Press, London. 668 p.

O'Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S.

    Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O.

    Aguilera, M. P. Aubry, W. A. Berggren, A. F. Budd, M. A. Cozzuol, S. E. Coppard, H.

    Duque-Caro, S. Finnegan, G. M. Gasparini, E. L. Grossman, K. G. Johnson, L. D. Keigwin,

    N. Knowlton, E. G. Leigh, J. S. Leonard-Pingel, P. B. Marko, N. D. Pyenson, P. G.

    Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Todd, G. J. Vermeij, and J. B. C.

    Jackson (2016) Formation of the Isthmus of Panama. Science advances 2(8): 1-12.

Papp, C. (1960) The Cleridae of North America. Part I: The geographical distribution of the

    Cleridae of North America, north of the Panama Canal. Southern California Academy of

    Sciences Bulletin 59(2): 76–88.

Peralta-Medina, E. and H. J. Falcon-Lang (2012) Cretaceous forest composition and productivity

    inferred from a global fossil wood database. Geology 40(3): 219-222.

Platnick, N. I. and G.J. Nelson (1978) A method of analysis for historical biogeography.

    Systematic Zoology 27, 1–16.

Ramirez, S. R., D. W. Roubik, C. Skov and N. E. Pierce (2010) Phylogeny, diversification

    patterns and historical biogeography of euglossine orchid bees (Hymenoptera: Apidae).

    Biological Journal of the Linnean Society 100: 552–572.

Rambaut, A. and A. J. Drummond (2007) Tracer V. 1.4 http://beast.bio.ed.ac.uk/Tracer.

Ree, R. H. and S. A. Smith (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Systematic Biology 57: 4–14.

Ronquist, F. and J. P. Huelsenbeck (2003) Mrbayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Rosen, D. E. (1975) Vicariance model of Caribbean biogeography. Systematic Zoology 139(2): 431–464.

Skelton, P. W., R. A. Spicer, S. P. Kelly and I. Gilmour (2003) The Cretaceous World. Cambridge University Press. Cambridge.

Stamatakis, A. (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. In Bioinformatics.

Upchurch, G. R., Jr. and J. A. Wolfe (1987) Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. In: E. M. Friis, W. G. Chaloner, and P R. Crane (eds.) The Origins of Angiosperms and Their Biological Consequences. Cambridge University Press, Cambridge, U.K. pp. 75-102.

Wegensteiner, R., B. Wermelinger and M. Herrmann (2012). Natural Enemies of Bark Beetles: Predators, Parasitoids, Pathogens, and Nematodes. *In* Bark Beetles. Biology and Ecology of Native an Invasive Species. F. E. Vega and R. W. Hofstetter (eds.) 1st ed. Elsevier, Academic Press. Oxford. 620 p.

Wilson, P. A., R. D. Norris and M. J. Cooper (2009) Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of the Turonian tropics on Demerara Rise. Geology 30(7): 607-610.

Wolfe, J. A. (1985) Distribution of major vegetational types during the Tertiary. In: E. T. Sundquist and W. S. Broecker (eds.) The Carbon Cycle and Atmospheric CO2: Natural Variations Archean to Present. American Geophysical Union, Washington, D.C. Monograph 32, pp. 357-376.

Wolfe, J. A. and H. E. Schorn (1989) Paleoecologic, paleoclimatic, and evolutionary significance of the Oligocene Creede flora, Colorado. Paleobiology 15: 180- 198.

Yu, Y., A.J. Harris and X. He (2013) RASP (Reconstruct Ancestral State in Phylogenies) 2.1 beta. Available at http://mnh.scu.edu.cn/soft/blog/RASP.

Table 5.1 Best partitioning scheme determined by PartitionFinder, the model of molecular evolution, and the corresponding locus.

Subset	Best model	Subset partition
1	GTR+I+G	16S gene position
2	GTR+I+G	28S gene position
3	GTR+G	First codon position COI
4	GTR+G	Second codon position COI
5	SYM+G	Third codon position COI

Table 5.2 Clerid species, locality data, and distribution, including outgroups, used in the phylogenetic analysis.

No.	Taxon	Author	Locality information	Distribution
1	*Araeodontia peninsularis*	(Schaeffer, 1904)	Tucson, AZ, USA	West USA - North Mexico
2	*Neocallotillus elegans*	(Erichson, 1847)	Riverside Co., CA, USA	West USA - Mexico
3	*Cymatodera aegra*	Wolcott, 1921	Fort Davis, TX, USA	West USA - North Mexico
4	*Cymatodera angustata*	Spinola, 1844	Refugio, CA, USA	West USA
5	*Cymatodera antennata*	Schaeffer, 1908	Santa Cruz Co., AZ, USA	West USA - North Mexico
6	*Cymatodera balteata*	LeConte, 1854	Uvalde, TX, USA	West USA - North Mexico
7	*Cymatodera bicolor*	(Say, 1825)	Talladega, AL, USA	USA - Canada
8	*Cymatodera californica*	Horn, 1868	Los Angeles Co, CA, USA	West USA
9	*Cymatodera championi*	Gorham, 1882	Chiriquí, Panama	Central - South America
10	*Cymatodera conflagrata*	(Klug, 1842)	Chamela, Jalisco, Mexico	Mexico - Central - South America
11	*Cymatodera decipiens*	Fall, 1906	Joshua Tree Nat. Park. CA, USA	West USA
12	*Cymatodera dietrichi*	Barr, 1952	Portal, AZ, USA	West USA – North Mexico
13	*Cymatodera fuchsii*	Schaeffer, 1904	Joshua Tree Nat. Park. CA, USA	West USA - North Mexico
14	*Cymatodera hoegei (Costa Rica)*	Gorham, 1882	Monteverde, Costa Rica	Mexico - Central America
15	*Cymatodera hoegei (Mexico)*	Gorham, 1882	Chamela, Jalisco, Mexico	Mexico
16	*Cymatodera hopei*	Gray, 1832	Texcoco, Mexico	Mexico
17	*Cymatodera horni*	Wolcott, 1910	Cochise Co. AZ, USA	West USA - North Mexico
18	*Cymatodera inornata*	(Say, 1835)	Latimer Co., OK, USA	East USA
19	*Cymatodera intermedia*	Barr, 1950	Los Cabos, Baja Cal. Sur, Mexico	Mexico
20	*Cymatodera latefascia*	Schaeffer, 1904	Pima Co., AZ, USA	West USA - North Mexico
21	*Cymatodera lisnleyi*	Barr, 1972	Joshua Tree Nat. Park. CA, USA	West USA
22	*Cymatodera lorenae*	sp. n.	Pinotepa Nacional, Oaxaca, Mexico	Mexico
23	*Cymatodera marmorata*	(Klug, 1842	Patzcuaro, Michoacan, Mexico	Mexico - Central America
24	*Cymatodera mexicana*	Rifkind, 2015	Sierra Huautla, Oaxaca, Mexico	Mexico
25	*Cymatodera mitchelli*	Chapin, 1927	Joshua Tree Nat. Park. CA, USA	West USA
26	*Cymatodera morelensis*	sp. n.	El Limon, Morelos , Mexico	Mexico
27	*Cymatodera morosa*	LeConte, 1858	Santa Rita Mts., AZ, USA	West USA - North Mexico
28	*Cymatodera neomexicana*	Knull, 1934	Carrizozo, NM, USA	West USA
29	*Cymatodera oblita*	Horn, 1886	Pima Co., AZ, USA	West USA

No.	Taxon	Author	Locality information	Distribution
30	*Cymatodera pallida*	Schaeffer, 1908	Joshua Tree Nat. Park. CA, USA	West USA - North Mexico
31	*Cymatodera pseudotsugae*	Barr, 1947	Mt Hamilton, CA, USA	West USA
32	*Cymatodera punctata*	LeConte, 1852	Cochise Co. AZ, USA	West USA - North Mexico
33	*Cymatodera puncticollis*	Bland, 1863	Joshua Tree Nat. Park. CA, USA	West USA - North Mexico
34	*Cymatodera rosalinae*	Burke, 2013	Chamela, Jalisco, Mexico	Mexico
35	*Cymatodera serena*	Barr, 1872	Sonora, Mexico	West USA - North Mexico
36	*Cymatodera sirpata*	Horn, 1885	Hidalgo Co., TX, USA	West USA - North Mexico
37	*Cymatodera sobara*	Barr, 1960	Coahuila, Mexico	West USA - North Mexico
38	*Cymatodera tortuosa*	Burke & Rifkind, 2014	Queretaro, Mexico	Mexico
39	*Cymatodera turbata*	Horn, 1865	Hidalgo Co., TX, USA	West USA - North Mexico
40	*Cymatodera tuta*	Wolcott, 1910	Pima Co., AZ, USA	West USA - North Mexico
41	*Cymatodera tutoides*	Barr, 1972	Los Saenz, Starr Co., TX	West USA - North Mexico
42	*Cymatodera undulata*	(Say, 1825)	Near Lexington, KY, USA	USA - Canada
43	*Cymatodera vagemaculata*	Thomson, 1860	Cañon del Sumidero, Chiapas, Mexico	Mexico - Central America
44	*Cymatodera werneri*	Barr, 1952	Catalina Mt, AZ, USA	Mexico - Central America
45	*Cymatodera xaviera*	Knull, 1940	Tucson, AZ, USA	West USA - North Mexico
46	*Cymatoderella collaris*	(Spinola, 1844)	Matehuala, SLP, Mexico	USA - Mexico - Central America
47	*Lecontella brunnea*	Kolibac, 1998	Joshua Tree Nat. Park. CA, USA	USA - Mexico
48	*Lecontella gnara*	Wolcott, 1927	Pima Co., AZ, USA	West USA - North Mexico
49	*Monophylla californica*	(Fall, 1901)	Imperial Co., CA, USA	West USA - Mexico - Central America
50	*Monophylla terminata*	(Say, 1835)	Val Verde Co., TX, USA	Canada - USA - North Mexico

Table 5.3 Profile of amplification for each individual gene or reference of sequences.

No.	Taxon name	Family/subfamily	16S	28S	COI
1	*Araeodontia peninsularis*	Cleridae: Tillinae	This study	This study	This study
2	*Neocallotillus elegans*	Cleridae: Tillinae	This study	-	This study
3	*Cymatodera aegra*	Cleridae: Tillinae	This study	This study	This study
4	*Cymatodera angustata*	Cleridae: Tillinae	This study	This study	This study
5	*Cymatodera antennata*	Cleridae: Tillinae	This study	This study	-
6	*Cymatodera balteata*	Cleridae: Tillinae	This study	This study	This study
7	*Cymatodera bicolor*	Cleridae: Tillinae	This study	This study	This study
8	*Cymatodera californica*	Cleridae: Tillinae	This study	McKenna et al.	This study
9	*Cymatodera championi*	Cleridae: Tillinae	This study	This study	This study
10	*Cymatodera conflagrata*	Cleridae: Tillinae	This study	This study	-
11	*Cymatodera decipiens*	Cleridae: Tillinae	This study	This study	This study
12	*Cymatodera dietrichi*	Cleridae: Tillinae	This study	This study	This study
13	*Cymatodera fuchsii*	Cleridae: Tillinae	This study	This study	This study
14	*Cymatodera hoegei* (Costa Rica)	Cleridae: Tillinae	This study	This study	-
15	*Cymatodera hoegei* (Mexico)	Cleridae: Tillinae	This study	This study	This study
16	*Cymatodera hopei*	Cleridae: Tillinae	This study	This study	This study
17	*Cymatodera horni*	Cleridae: Tillinae	This study	-	This study
18	*Cymatodera inornata*	Cleridae: Tillinae	This study	This study	This study
19	*Cymatodera intermedia*	Cleridae: Tillinae	This study	This study	-
20	*Cymatodera latefascia*	Cleridae: Tillinae	This study	This study	This study
21	*Cymatodera lisnleyi*	Cleridae: Tillinae	This study	-	This study
22	*Cymatodera lorenae* sp. n.	Cleridae: Tillinae	This study	-	This study
23	*Cymatodera marmorata*	Cleridae: Tillinae	This study	This study	This study
24	*Cymatodera mexicana*	Cleridae: Tillinae	This study	This study	This study
25	*Cymatodera mitchelli*	Cleridae: Tillinae	This study	This study	This study
26	*Cymatodera morelensis* sp. n.	Cleridae: Tillinae	This study	-	This study
27	*Cymatodera morosa*	Cleridae: Tillinae	This study	This study	This study
28	*Cymatodera neomexicana*	Cleridae: Tillinae	This study	This study	This study
29	*Cymatodera oblita*	Cleridae: Tillinae	This study	This study	This study

| No.	Taxon name	Family/subfamily	16S	28S	COI
30	*Cymatodera pallida*	Cleridae: Tillinae	This study	This study	-
31	*Cymatodera pseudotsugae*	Cleridae: Tillinae	-	-	This study
32	*Cymatodera punctata*	Cleridae: Tillinae	This study	This study	This study
33	*Cymatodera puncticollis*	Cleridae: Tillinae	This study	This study	This study
334	*Cymatodera rosalinae*	Cleridae: Tillinae	This study	This study	This study
435	*Cymatodera serena*	Cleridae: Tillinae	This study	This study	-
36	*Cymatodera sirpata*	Cleridae: Tillinae	This study	This study	This study
37	*Cymatodera sobara*	Cleridae: Tillinae	This study	-	This study
38	*Cymatodera tortuosa*	Cleridae: Tillinae	This study	This study	This study
39	*Cymatodera turbata*	Cleridae: Tillinae	This study	This study	This study
40	*Cymatodera tuta*	Cleridae: Tillinae	This study	This study	This study
41	*Cymatodera tutoides*	Cleridae: Tillinae	This study	-	This study
42	*Cymatodera undulata*	Cleridae: Tillinae	This study	Gunter et al.	This study
43	*Cymatodera vagemaculata*	Cleridae: Tillinae	This study	This study	This study
44	*Cymatodera werneri*	Cleridae: Tillinae	This study	This study	-
45	*Cymatodera xaviera*	Cleridae: Tillinae	This study	This study	This study
46	*Cymatoderella collaris*	Cleridae: Tillinae	This study	This study	This study
47	*Lecontella brunnea*	Cleridae: Tillinae	This study	This study	This study
48	*Lecontella gnara*	Cleridae: Tillinae	Gunter et al.	This study	Gunter et al.
49	*Monophylla californica*	Cleridae: Tillinae	This study	This study	This study
50	*Monophylla terminata*	Cleridae: Tillinae	This study	This study	This study

Fig. 5.1 Fifty percent majority rule consensus Bayesian tree based on 16S, COI and 28S sequences with gap coding. Posterior probability values are given above branches. Three morphologically distinguishable groups are indicated in the phylogeny.
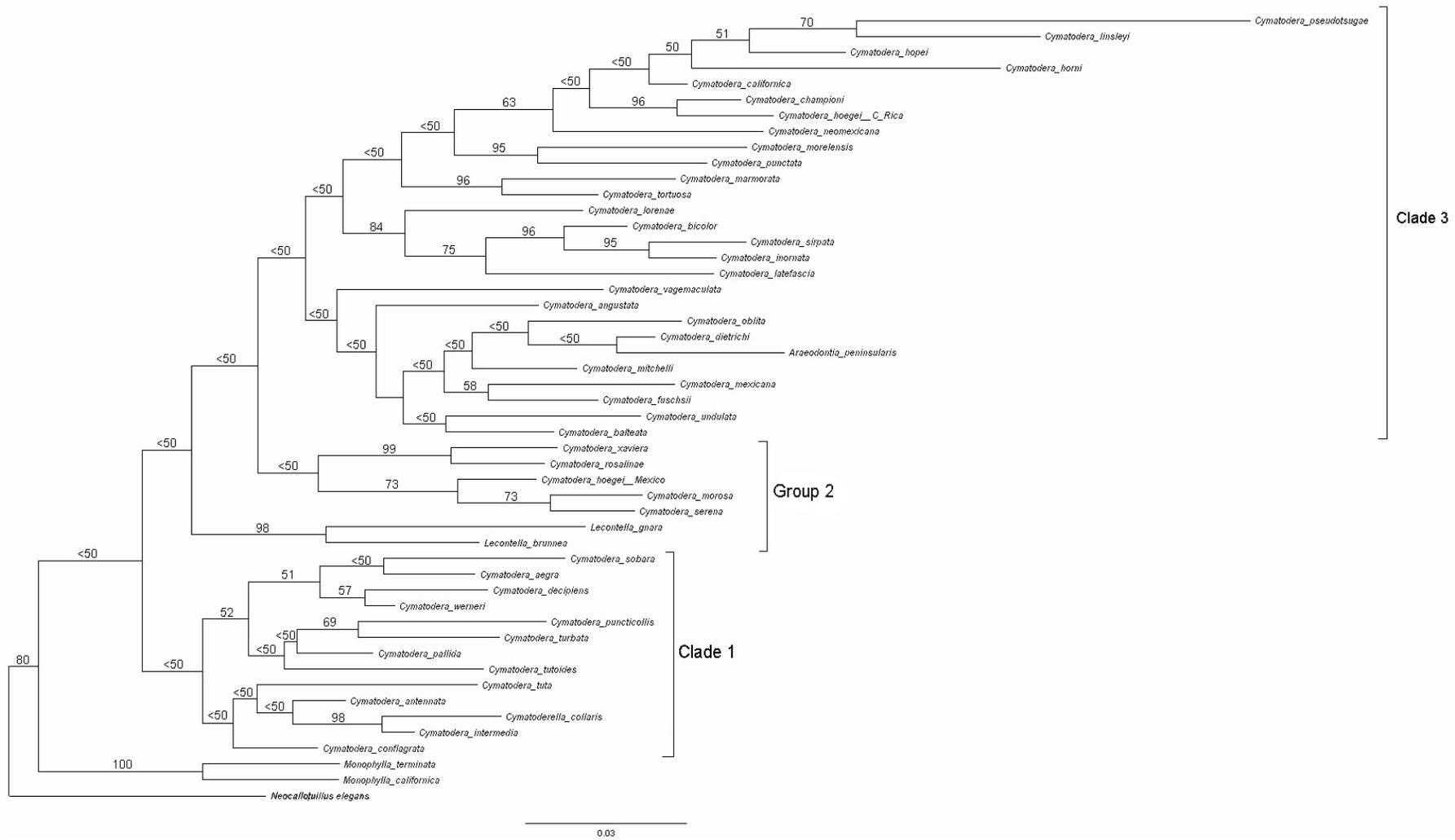
Fig. 5.2 Strict consensus phylogram resulting from maximum likelihood analysis based on 16S, COI and 28S sequences with gap coding. Three morphologically distinguishable groups are indicated in the topology. Bootstrap values are indicated above branches.
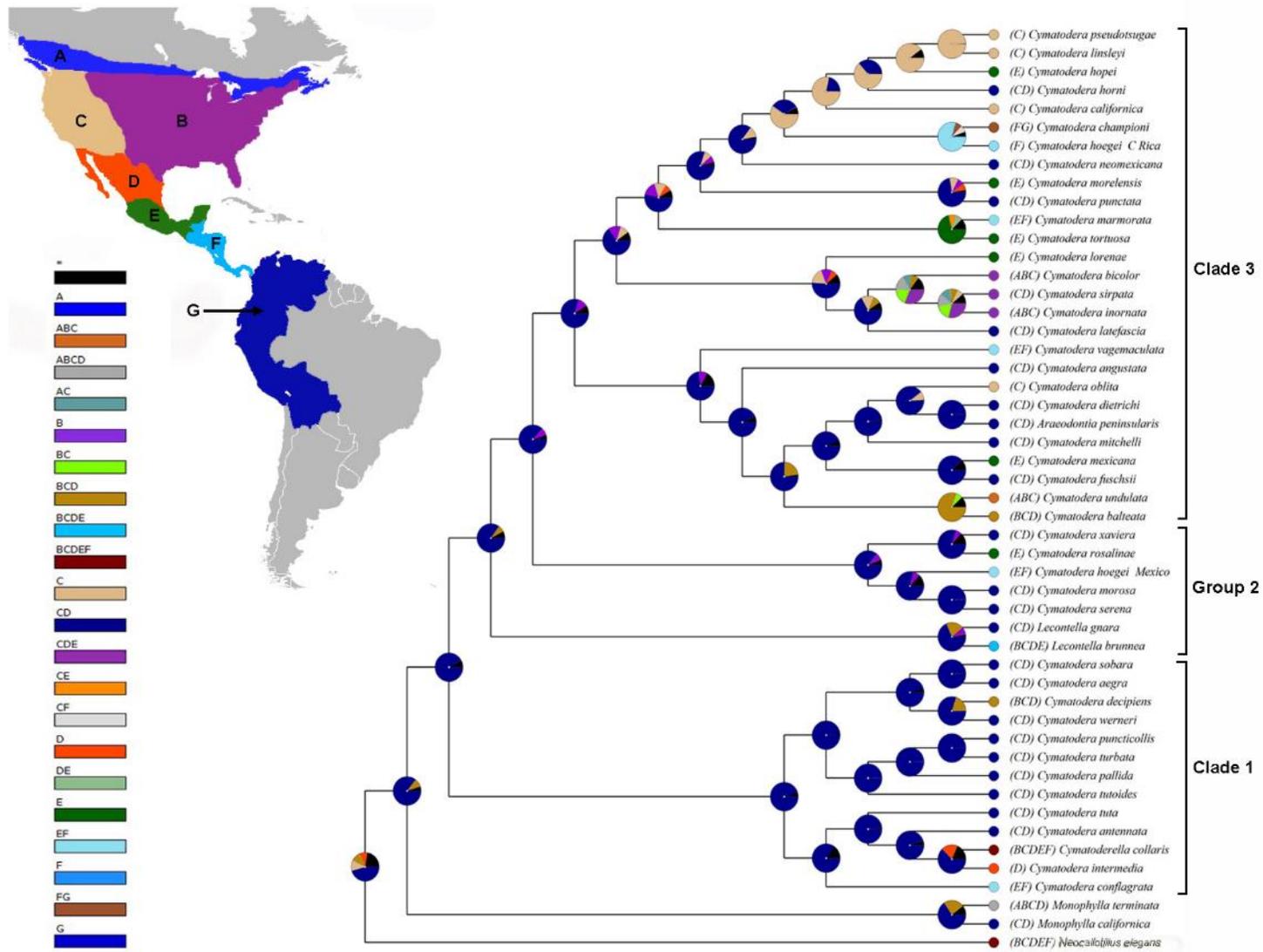
Fig. 5.3 Ancestral area reconstruction with color-coded pie charts at nodes representing 95% confidence intervals of the relative frequencies of ancestral area optimizations across the entire phylogeny. Distribution of all species included in the analysis are color-coded at the tip of each node. A color-coded distribution map and corresponding legends for all areas and combination of areas are given at left of tree.
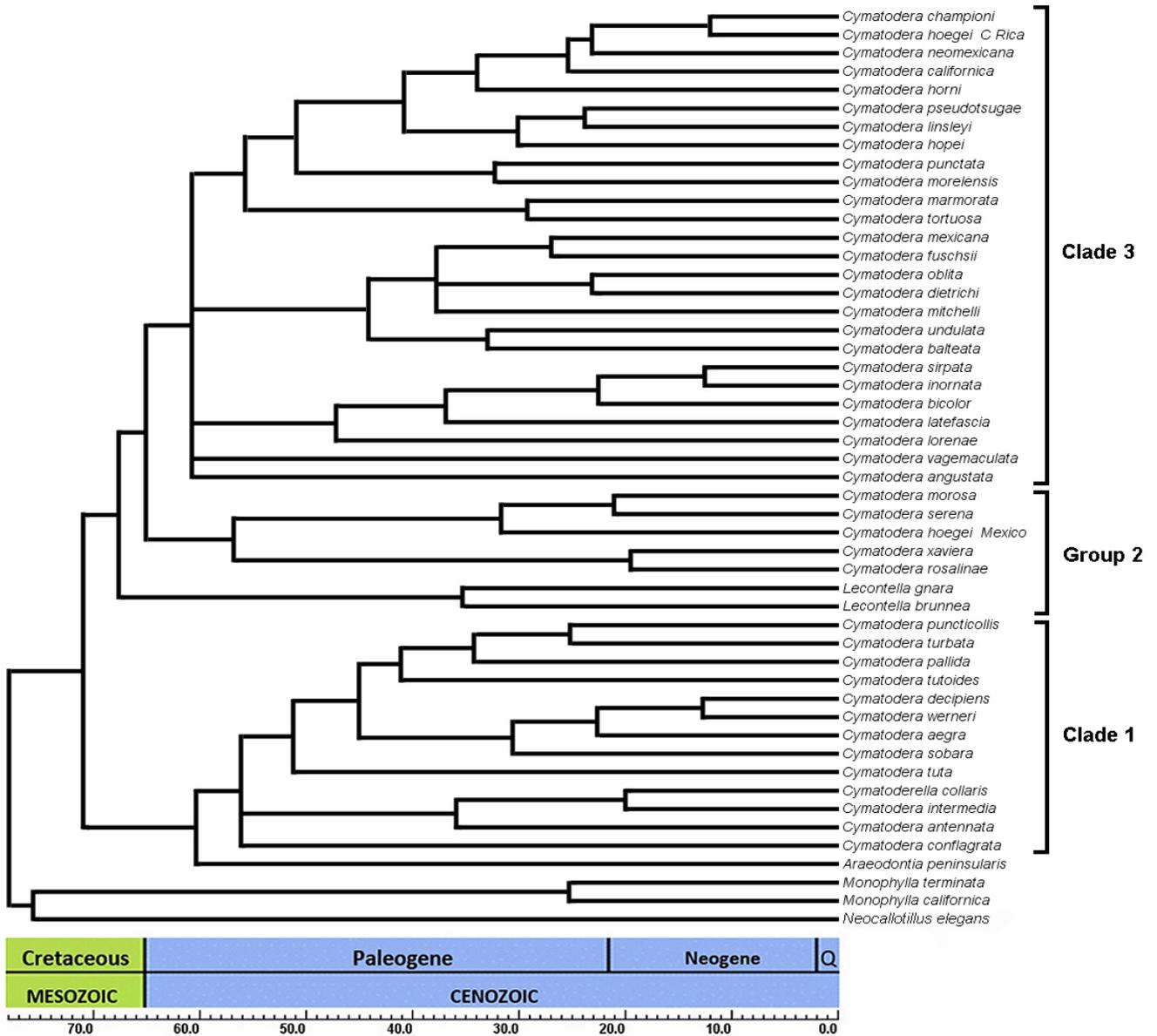
Fig. 5.4 A chronogram applying a relaxed molecular clock using MrBayes indicates that the most recent common ancestor of *Cymatodera* and related genera originated approximately 71.5 ma (CI = 61.9-78.6) with two crown groups: Clade 1, with an age of 60.4 ma (CI = 49.4-70.3); and group 2 + Clade 3, with an age of 67.5 ma (CI = 58.8-76.2). The youngest *Cymatodera* was recovered to be approximately 12.3 million years old (CI = 4.2-18.2). (Q=Quaternary).
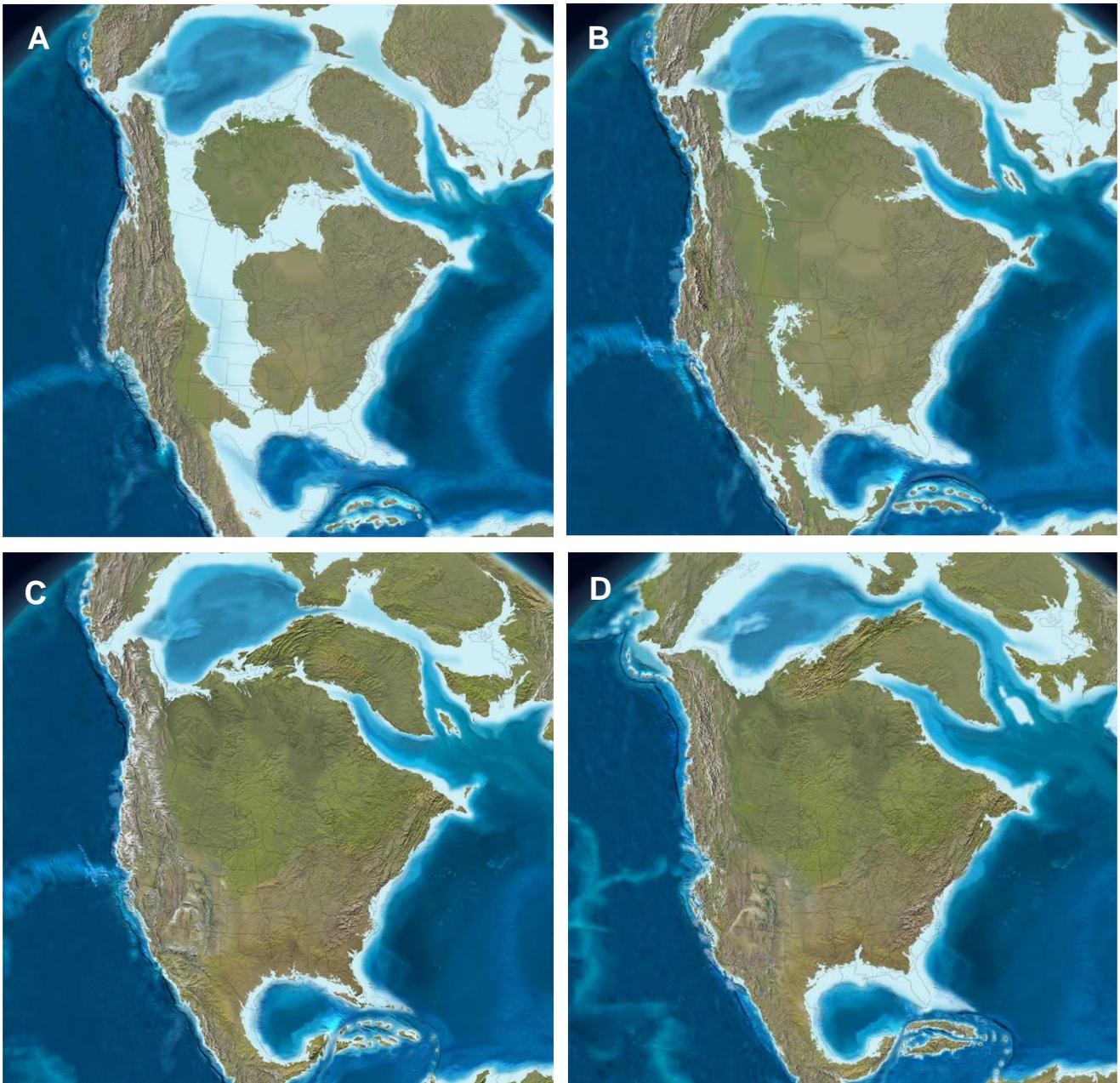
Fig. 5.5 North American A. 75 MYA; B. 65 MYA; C. 60 MYA and D. 50 MYA. Note the closure of the Western Interior Seaway approximately 60 MYA. Images courtesy of Ron Blakey, Professor Emeritus NAU Geology (http://jan.ucc.nau.edu).