# SYSTEMATICS AND BIOGEOGRAPHY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE)

By

LAUREN A. ESPOSITO

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

2011

© 2011

LAUREN A. ESPOSITO

All Rights Reserved

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

| | |
|---|---|
| Date | **Chair of Examining Committee**<br>Dr. Lorenzo Prendini, American Museum of Natural History |
| Date | **Executive Officer**<br>Dr. Laurel A. Eckhardt |
| | Dr. Susan L. Perkins, American Museum of Natural History |
| | Dr. Frank Burbrink, College of Staten Island |
| | Dr. Valerie Schawaroch, Baruch College |
| | Dr. W. David Sissom, West Texas A&M University |

**Supervisory Committee**

The City University of New York

ABSTRACT: SYSTEMATICS AND BIOGEOGRAPHY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE)

By: Lauren A. Esposito

Advisor: Dr. Lorenzo Prendini

*Background*: The New World scorpion genus *Centruroides* Marx, 1890 (family Buthidae Koch, 1837) is a morphologically diverse and highly venomous taxon. *Centruroides* is among the most complex scorpion genera in the New World, comprising 71 described species and 5 subspecies in addition to several undescribed species. These scorpions are sexually dimorphic, the males typically exhibiting elongation of the metasoma and telson and longer, more slender pedipalp chelae. The greatest diversity of *Centruroides* occurs in Mexico; however the genus is distributed from the southern United States into northern South America and the Galapagos, and throughout the Caribbean. The genus includes the only scorpions of medical importance in North America, with six species that are potentially lethal to humans.

*Historical Taxonomic Problems*: *Centruroides* species are problematic for systematists for several reasons. The morphological characters traditionally used (morphometrics and color) often overlap between closely related species or are vaguely defined, and many have been shown to vary within populations making the identification of species difficult. Many researchers have studied and revised small groups of species, but no comprehensive modern taxonomic treatment of the entire genus exists. The positions of *Centruroides* within the New World buthids, its relationship to its putative sister genus *Rhopalurus* Thorell, 1890, and its monophyly have never been tested. Few modern

analytical methods have been applied to the genus, a problem that extends to both phylogenetic and biogeographical analysis.

*Aims*: The broader vision of this dissertation project was to investigate and evaluate the systematics and biogeographic patterns that have resulted in one of the largest, least understood and most medically important genera of New World buthid scorpions. This was accomplished through: (1) conducting fieldwork in regions of *Centruroides* diversity to gather fresh material for morphological and genetic studies; (2) conducting molecular and morphological phylogenetic analyses to test the monophyly of the genus and determine its relationship to other New World Buthid genera, identify the major clades and test the validity of the currently hypothesized species groups; (3) testing biogeographic hypotheses to explain the present distributions and species diversity.

*Conclusions:* The buthid subfamily Rhopalurusinae Bücherl, 1971, comprising *Centruroides*, *Rhopalurus* Thorell, 1876, *Physoctonus* Mello-Leitao, 1934, *Troglorhopalurus* Lourenço, Baptista & Giupponi, 2004, is supported with molecular and morphological evidence. *Rhopalurus* is paraphyletic with respect to *Centruroides*, forming two clades: one endemic to South America and the other endemic to the Greater Antilles. *Centruroides* is monophyletic, sister to the Greater Antilles *Rhopalurus*. The genus *Heteroctenus* Pocock, 1893 is resurrected for the Greater Antilles *Rhopalurus* species. *Centruroides* contains four, geographically delimited clades: a Caribbean clade, a North American clade, a Mesoamerican clade, and a Yucatan/Chortis block clade. A fossil-calibrated phylogeny of New World buthids dates the separation of the Greater Antilles *Rhopalurus* + *Centruroides* at {29.0, 42.9} mya. Ancestral distribution reconstruction infers this node to be South America and the Greater Antilles. The

ancestral distribution of *Centruroides* is inferred to be North America. Both the dating and the ancestral distribution reconstruction are congruent with the GAARlandia hypothesis, which has been proposed to explain similar disjunct distributions in large mammals. The Greater Antilles distributed sister taxon of *Centruroides* provides evidence for a Caribbean ancestor for the genus, which subsequently colonized North and Meso-America and re-colonized the Caribbean.

**TABLE OF CONTENTS**

**PAGE**

INTRODUCTION: HISTORICAL OVERVIEW AND PROJECT AIMS ..... 1

CHAPTER 1: A PHYLOGENETIC ASSESSMENT OF THE NEW WORLD BUTHID SCORPION SUBFAMILY RHOPALURUSINAE BÜCHERL, 1971 (SCORPIONES: BUTHIDAE) ..... 8
- Introduction ..... 10
- Material and Methods ..... 18
- Results ..... 25
- Discussion ..... 46
- Taxonomy ..... 52
- Acknowledgments ..... 61

CHAPTER 2: MOLECULAR PHYLOGENY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 INFERRED FROM NUCLEAR AND MITOCHONDRIAL LOCI ..... 63
- Introduction ..... 65
- Material and Methods ..... 74
- Results ..... 80
- Discussion ..... 88
- Acknowledgments ..... 93

CHAPTER 3: A TOTAL EVIDENCE PHYLOGENETIC ANALYSIS OF THE SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE) WITH IMPLICATIONS FOR WIDESPREAD CRYPTIC DIVERSITY ..... 95
- Introduction ..... 97
- Material and Methods ..... 104
- Results ..... 114
- Discussion ..... 140
- Acknowledgments ..... 144

CHAPTER 4: A DISJUNCT DISTRIBUTION REVEALS EVIDENCE FOR AN ISLAND ANCESTOR IN THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 ..... 146
- Introduction ..... 147
- Material and Methods ..... 154
- Results ..... 163
- Discussion ..... 175
- Acknowledgments ..... 180

SUMMARY AND SYNTHESIS ..... 181

APPENDICES ..... 192

REFERENCES ..... 294

DISCLAIMER ..... 308

## LIST OF TABLES

**PAGE**

CHAPTER 1: A PHYLOGENETIC ASSESSMENT OF THE NEW WORLD BUTHID SCORPION SUBFAMILY RHOPALURUSINAE BÜCHERL, 1971 (SCORPIONES: BUTHIDAE)

Table 1. Primers used for gene amplification in phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 21
Table 2. Best-fitting models of nucleotide substitution for five loci as calculated in MrModelTest v2.3 (Nylander, 2008) ..... 24

CHAPTER 2: MOLECULAR PHYLOGENY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 INFERRED FROM NUCLEAR AND MITOCHONDRIAL LOCI

Table 3. Primers used for PCR amplification of five gene loci used in a phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 76
Table 4. Best-fitting models of nucleotide substitution for five loci as calculated in MrModelTest v2.3 (Nylander, 2008) for incorporation into a phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 79
Table 5. Major clades in the buthid scorpion genus *Centruroides* Marx, 1890, identified in phylogenetic analyses of molecular data, and the species assigned to each ..... 84

CHAPTER 3: A TOTAL EVIDENCE PHYLOGENETIC ANALYSIS OF THE SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE) WITH IMPLICATIONS FOR WIDESPREAD CRYPTIC DIVERSITY

Table 6. Currently recognized species and subspecies in the buthid scorpion genus *Centruroides* Marx, 1890 ..... 98
Table 7. Proposed Mexican species groups in the buthid scorpion genus *Centruroides* Marx, 1890 ..... 103
Table 8. Arthropod primers used for gene amplification of five loci in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 110
Table 9. Major clades in the buthid scorpion genus *Centruroides* Marx, 1890, recovered in a phylogenetic analysis of morphological characters ..... 128

CHAPTER 4: A DISJUNCT DISTRIBUTION REVEALS EVIDENCE FOR AN ISLAND ANCESTOR IN THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890

Table 10. Primers used for amplification of 12S, 16S, 18S, 28S and Cox1 in a fossil-calibrated biogeographical analysis of the New World scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 156
Table 11. Calibration points and sources of dates for divergence time dating analysis of New World buthid scorpions in BEAST (Drummond & Rambaut, 2007) ..... 160
Table 12. Key geological events in the dispersal of organisms between North and South America ..... 162
Table 13. Results of the Lagrange (Ree *et al*., 2005) analyses of the relative importance of dispersal and vicariance in the present distribution of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 176

**LIST OF FIGURES**

**PAGE**

CHAPTER 1: A PHYLOGENETIC ASSESSMENT OF THE NEW WORLD BUTHID SCORPION SUBFAMILY RHOPALURUSINAE BÜCHERL, 1971 (SCORPIONES: BUTHIDAE)

Figure 1. Approximate distribution of the buthid scorpion genus *Rhopalurus* Thorell, 1876 ..... 13
Figure 2. Approximate distribution of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 16
Figure 3A. Strict consensus of four equally parsimonious trees for the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 obtained from an equal weights analysis of morphology performed in TNT (Goloboff *et al*., 2008) ..... 27
Figure 3B. Alternate topology for the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 obtained from an equal weights parsimony analysis of morphology performed in TNT (Goloboff *et al*, 2008) ..... 29
Figure 4A. Cladogram of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, obtained from a strict consensus (k=1–2) of three equally parsimonious trees in an implied weighting analysis ..... 31
Figure 4B. Cladogram of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, obtained from a strict consensus of three most parsimonious trees (k=3–6) in an implied weighting parsimony analysis of 90 morphological characters ..... 33
Figure 5. Results of the leaf stability analysis on taxa from the scorpion buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 36
Figure 6. Strict consensus of 14 equally parsimonious trees of the buthid scorpion subfamiliy Rhopalurusinae Bücherl, 1971 recovered in an analysis of five concatenated loci ..... 38
Figure 7. Phylogram of the maximum clade credibility Bayesian tree from an analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 using combined molecular and morphological data ..... 41
Figure 8. Strict consensus parsimony phylogram of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, inferred from molecular and morphological data ..... 44

CHAPTER 2: MOLECULAR PHYLOGENY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 INFERRED FROM NUCLEAR AND MITOCHONDRIAL LOCI

Figure 9. Representative species of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 66
Figure 10. Approximate distribution of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 68
Figure 11. Parsimony cladogram for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from five nuclear and mitochondrial loci in TNT (Goloboff *et al*, 2008) ..... 81

Figure 12. Maximum clade credibility tree for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from five nuclear and mitochondrial loci in MrBayes (Ronquist & Huelsenbeck, 2003) 85

CHAPTER 3: A TOTAL EVIDENCE PHYLOGENETIC ANALYSIS OF THE SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE) WITH IMPLICATIONS FOR WIDESPREAD CRYPTIC DIVERSITY

Figure 13. Trends in primary taxonomy publications in the buthid scorpion genus *Centruroides* Marx, 1890 since 1890 101
Figure 14. Geographical coverage of species sampling for phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 107
Figure 15A-D. Parsimony cladograms of four well-supported clades of the buthid scorpion *Centruroides* Marx, 1890 computed in TNT (Goloboff *et al.*, 2008) with Navajo rug sensitivity analyses of relative gene support for each node 116
Figure 16. Strict consensus of 4 equally parsimonious trees for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from morphological data in TNT (Goloboff *et al.*, 2008) 128
Figure 17. Single most parsimonious tree of the scorpion genus *Centruroides* Marx, 1890 resulting from a parsimony analysis of morphology and five nuclear and mitochondrial gene loci in TNT v1.1 (Goloboff *et al*., 2008) 132
Figure 18. Maximum clade credibility tree computed from post burn-in trees in a Bayesian analysis of morphology and five nuclear and mitochondrial gene loci inferred in MrBayes (Ronquist & Huelsenbeck, 2003) 135

CHAPTER 4: A DISJUNCT DISTRIBUTION REVEALS EVIDENCE FOR AN ISLAND ANCESTOR IN THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890

Figure 19. Map of the Caribbean region highlighting geologically distinct island formations 150
Figure 20. Maximum likelihood phylogram of New World buthid genera, with an emphasis on the scorpion genus *Centruroides* Marx, 1890 164
Figure 21. Fossil-calibrated maximum clade credibility phylogram of New World buthid scorpions inferred in BEAST (Drummond & Rambaut, 2007) 168
Figure 22. Ancestral distribution reconstruction of New World buthid scorpions under parsimony dispersal-vicariance criteria computed in RASP (Yu *et al.*, 2011) 171
Figure 23. Ancestral distribution reconstruction of New World buthid scorpions under Bayesian dispersal-vicariance criteria computed in RASP (Yu *et al*., 2011) 173

SUMMARY AND SYNTHESIS

Figure 24. Phylogram of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, computed under Bayesian optimality criteria in MrBayes (Ronquist & Huelsenbeck, 2003) 184
Figure 25. Summary phylogram of the buthid scorpion genus *Centruroides*

Marx, 1890, computed under Bayesian and parsimony optimality criteria in MrBayes (Ronquist & Huelsenbeck, 2003) and TNT (Goloboff *et al.*, 2008) respectively, depicting four geographically aligned clades within the genus ..... 188

## LIST OF APPENDICES

**PAGE**

CHAPTER 1: A PHYLOGENETIC ASSESSMENT OF THE NEW WORLD BUTHID SCORPION SUBFAMILY RHOPALURUSINAE BÜCHERL, 1971 (SCORPIONES: BUTHIDAE)

Appendix 1. Specimens and Genbank accession numbers used in phylogenetic analysis of buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 192
Appendix 2. Morphological characters and character states used in the study of buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 194
Appendix 3. Morphology matrix used in phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 208
Appendix 4. Additional material examined for study of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 212

CHAPTER 2: MOLECULAR PHYLOGENY OF THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890 INFERRED FROM NUCLEAR AND MITOCHONDRIAL LOCI

Appendix 5. Localities and GenBank accession numbers for specimens used in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 218

CHAPTER 3: A TOTAL EVIDENCE PHYLOGENETIC ANALYSIS OF THE SCORPION GENUS *CENTRUROIDES* MARX, 1890 (SCORPIONES: BUTHIDAE) WITH IMPLICATIONS FOR WIDESPREAD CRYPTIC DIVERSITY

Appendix 6. Morphological characters and character states used in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 224
Appendix 7. Morphological character matrix for the buthid scorpion genus *Centruroides* Marx, 1890 ..... 236
Appendix 8. Material examined for phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890 ..... 257

CHAPTER 4: A DISJUNCT DISTRIBUTION REVEALS EVIDENCE FOR AN ISLAND ANCESTOR IN THE NEW WORLD SCORPION GENUS *CENTRUROIDES* MARX, 1890

Appendix 9. Specimen codes, localities and GenBank accession numbers for specimens used in a fossil-calibrated phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 ..... 291

Dedicated to my loving parents Jon and Ellen, sister Gena and wife Micah.

# INTRODUCTION

The New World scorpion genus *Centruroides* Marx, 1890 (Family Buthidae Koch, 1837) is a highly venomous and morphologically diverse taxon. Some *Centruroides* species inhabit woody vegetation and are often found under bark on trees, hence the common name 'bark scorpion' (Polis, 1990). Many *Centruroides* species, however, are fairly plastic in terms of their microhabitat retreats: often residing in cracks and crevices in rock faces, undersides of rocks and other surface cover, in leaf litter at the bases of vegetation, under loose tree bark, or in bromeliads (Polis, 1990; Francke, personal communication; Sissom, personal communication). Their affinity for dark, humid microhabitats attracts them to debris in and around urban areas, creating a higher potential for envenomation (Simard & Watt, 1990). *Centruroides* is among the most complex scorpion genera in the New World, comprising 71 described species and 5 subspecies (Fet & Lowe, 2000; Teruel 2001, 2006, 2007; Teruel & Stockwell, 2002; Armas & Martin-Frias, 2003; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009; Armas & Trujillo, 2010). These scorpions are sexually dimorphic, the males typically exhibiting elongation of the metasoma and telson and long, slender pedipalp chelae (Polis & Sissom, 1996). The greatest diversity of *Centruroides* occurs in Mexico; however the genus is distributed from southwestern Canada into northern South America and throughout the Caribbean (Hoffmann, 1932; Gantenbein *et al.*, 2001; Sissom & Lourenço, 1987). Fossil (amber) *Centruroides* are known from the Dominican Republic (Oligocene) and Chiapas, Mexico (Miocene/Oligocene) (Schawaller, 1979; Santiago-Blay & Poinar, 1993). The genus includes the only scorpions of medical importance in North America; six species are potentially lethal to humans (Dehesa-Davila & Possani, 1994).

**Systematics**

The genus *Centruroides* is problematic for systematists for several reasons. The morphological characters traditionally used (morphometrics and color) often overlap between closely related species or are vaguely defined (Gantenbein *et al.*, 2001). Many commonly used characters vary within populations, hindering the identification of species. Several species have extremely large distributions, suggesting they may be complexes of cryptic species (Gantenbein *et al.*, 2001). These include "species" with discontinuous distributions, and those for which traditional characters have proven unreliable for delimitation (Sissom & Lourenço, 1987; Lourenço & Sissom, 2000; Gantenbein *et al.*, 2001). Various researchers have studied and revised small groups of species, but no comprehensive modern taxonomic treatment of the entire genus exists (Gantenbein *et al.*, 2001; Towler *et al.*, 2001). More than 50% of the currently recognized species of *Centruroides* were described prior to 1900, and many old species have recently been synonymized (Fet and Lowe, 2000; Armas *et al.*, 2003; Córdova-Athanasiadis & Francke, 2007; Teruel & Kovařík, 2010). Some revisionary efforts have been made in the group. Stahnke and Calos (1977) produced a key, not meant to serve as a revision, which contained the 37 species recognized at the time. The most comprehensive treatment was presented by Ponce-Saavedra and Moreno-Barajas (2005), but only included the Mexican species and claimed to include molecular evidence, which was neither provided nor accessioned in any public database. Others revised species restricted to particular geographic areas: Costa Rica (Francke & Stockwell, 1987), South America (Sissom & Lourenço, 1987), Cuba (Teruel, 2007), Dominican Republic (Teruel, 2005), Honduras

(Teruel & Stockwell, 2002). According to Lourenço & Sissom (1996) "techniques such as electrophoresis, karyotyping, and DNA extraction may be essential to understanding species in this complex genus". Few modern analytical methods have been applied to the genus, a problem that extends to both phylogenetic analysis and biogeographical analysis. Teruel *et al.* (2006) used molecular data from a single gene (16S rDNA) to create a phylogeny of thirteen species, and concluded that the genus was not monophyletic. Unfortunately, single-gene phylogenetic analyses are problematic; the use of multiple loci, including at least one from the nuclear genome, is widely recommended (Brower & DeSalle, 1994; Brower *et al.*, 1996; Doyle & Davis, 1998; Gatesy *et al.*, 2007).

The scorpion family Buthidae contains almost all medically important species and is sister to all other scorpion families (non-buthids) (Coddington *et al.*, 2004). *Centruroides* is one of ten New World genera of Buthidae (Fet & Lowe, 2000). The position of *Centruroides* within the monophyletic New World buthid clade is unclear, although the genus is probably monophyletic on the basis of pedipalp chela finger dentition and relative trichobothrial position. *Centruroides* are separated from the New World Buthid genus *Tityus* Koch, 1837 on the basis of nine or fewer oblique median granular rows, plus a short apical row on the movable finger of the pedipalp; and from the genus *Rhopalurus* Thorell, 1876 by the pedipalp fixed-finger trichobothrium *db* situated in line with or basal to *et*, an elongated fifth metasomal segment in males, and the absence of a stridulation organ on the mesosomal sternites (Sissom, 1996). The relationship between *Rhopalurus* and *Centruroides* has been extensively discussed (Pocock, 1890; Kraepelin, 1899; Werner, 1939; Meise, 1934; Mello-Leitão, 1945; Francke, 1978; Lourenço, 1979). *Rhopalurus* is generally considered the sister group of

*Centruroides*, but the distinction between the two genera remains unclear (Lourenço, 1979). Species have been transferred back and forth between genera and the generic definitions have been revised several times (Francke, 1978). The position of *Centruroides* within the New World buthids, its relationship to *Rhopalurus*, and its monophyly have never been rigorously tested.

There are currently seven recognized species groups within *Centruroides* (Teruel, 2001; Ponce-Saavedra & Moreno-Barajas, 2005). Teruel (2007) recognized three groups endemic to Cuba: "*arctimanus*", "*anchorellus*", and "*robertoi*". They may be paraphyletic in the context of the entire genus, however. Two groups are recognized among the Mexican species: "the striped group " (which contains two subgroups "limpidus-elegans" and "suffusus-infamatus"), and the "no-striped group" ( which contains three subgroups "the *bertholdii* subgroup", "the *gracilis* subgroup", and "the *thorellii* subgroup" (Hoffmann, 1932; Ponce-Saavedra & Moreno-Barajas, 2005). Although the Mexican groups may contain valid relationships, they may not be monophyletic due to morphological convergence as a result of similar ecological constraints.

**Medical Importance**

*Centruroides* is the most notorious North American scorpion genus due its medical importance. The venom of six species, five endemic to Mexico, is lethal to adult humans (Dehesa-Davila & Possani, 1994). Annually 100,000–200,000 *Centruroides* envenomations in Mexico result in up to 1,000 deaths (Dehesa-Davila & Possani, 1994),

and clearly pose a severe public health problem. The problem is compounded by the difficulty in obtaining accurate identifications of species because of vague descriptions.

*Centruroides* has also gained attention within the medical field for the pharmacological potential of its mammal-specific neurotoxic venom peptides. *In vivo* experimentation with peptides isolated from *Centruroides* has shown promise in the development of novel immunosuppressants and brain cancer treatments (Lewis & Garcia, 2003; Fu *et al.*, 2007). Additionally, they may be effective in therapy aimed at autoimmune diseases such as multiple sclerosis, type I diabetes, psoriasis, and rheumatoid arthritis (Lewis & Garcia, 2003).

**Caribbean Biogeography**

Scorpions are ideal model systems for understanding biogeographical relationships for several reasons. Scorpions represent one of the oldest invasions of terrestrial habitats by arthropods (Sissom, 1990). This makes them good candidates for vicariance models since their presence on contemporary land formations predates many geological events. *Centruroides* live in an around vegetation which makes them good potential rafters for questions concerning dispersal (Polis, 1990). These scorpions are often opportunistic, with minimal habitat requirements, making them exceptionally good colonizers (Polis, 1990). Other scorpion groups, such as members of the genus *Rhopalurus*, have more specialized habitat requirements (savanna), and so are more likely to display patterns of vicariance (Lourenço, 1987). Lastly, scorpions have sufficient representation in the fossil record (Schawaller, 1979; Santiago-Blay & Poinar, 1993) to allow for fossil-calibrated molecular phylogenies to be inferred which could be used to calculate divergence times

and test competing biogeographical hypotheses. However, to date, there have been few scorpion biogeography publications utilizing molecular techniques or modern analytical tools.

**Project Aims**

The broader vision of this dissertation project is to investigate and evaluate the systematics and biogeographical patterns that have resulted in one of the largest, least understood and most medically important genera of New World buthid scorpions. This was accomplished through: (1) conducting fieldwork in regions of *Centruroides* diversity to gather fresh material for morphological and genetic studies; (2) conducting molecular and morphological phylogenetic analyses to test the monophyly of the genus and determine its relationship to other New World Buthid genera, identify the major clades and test the validity of the currently hypothesized species groups; (3) testing biogeographical hypotheses to explain the present distributions and species diversity.

**CHAPTER ONE:** Congruence of molecules, morphology and geographical distributions in the New World buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 (Scorpiones: Buthidae)

**Abstract:** Buthid scorpions are represented in the New World by 13 genera and 403 species. However, the phylogenetic relationships both within and among the two proposed subfamilies, Tityinae Bücherl, 1971 and Rhopalurusinae Bücherl, 1971, have never been tested. Furthermore, the monophyly of the disjunctly distributed genus *Rhopalurus* Thorell, 1876 has never been tested. Five nuclear and mitochondrial loci (12S, 16S, 18S, 28S, Cox1) and ninety morphological characters analyzed separately and in combination was used to test: monophyly of the New World buthid subfamily Rhopalurusinae, relationships among the genera of Rhopalurusinae, and the monophyly of the scorpion genus *Rhopalurus*. Results from molecular, morphological and combined datasets are congruent and support the monophyly of both subfamilies, recover a paraphyletic *Rhopalurus* that is congruent with its disjunct distribution, and a monophyletic *Centruroides* Marx, 1890 sister to the clade of *Rhopalurus* endemic to the Greater Antilles.

## Introduction

The family Buthidae is the most speciose scorpion family, comprised of approximately 88 genera and 914 described species (Fet and Lowe, 2000; Kovařík, 2001, 2002, 2003; Navidpour, 2008; Volschenk *et al.*, 2008; Lourenço and Duhem, 2009; Lourenço *et al.*, 2010; Lowe, 2010). Globally distributed, with the exception of New Zealand and Antarctica, buthid species vary from habitat generalists capable of rapid dispersal to highly endemic specialists often restricted to relictual areas (Prendini, 2003; Qi and Lourenço, 2007; Lourenço *et al.*, 2010). Buthids (Buthoidea) are the putative sister to all other scorpion families (non-buthids) (Coddington *et al.*, 2004), however intrafamilial phylogenetic relationships remain largely untested.

Buthid species are uniquely capable among scorpions of producing mammalian-specific neurotoxins (Simard & Watt, 1990), and several species are known to be medically important (Simard & Watt, 1990). In some regions of the world, lethal scorpion envenomations pose a severe public health hazard (Celis *et al.*, 2007; Jahan *et al.*, 2007; Shahbazzadeh *et al.*, 2009). Globally, there are an estimated 1.2 million scorpion stings annually resulting in 3250 deaths (Chippaux *et al.*, 2010). As a result, buthid scorpions have garnered considerable attention from medical and biomedical researchers, investigating the production of antivenins as well as therapeutic uses for scorpion venoms (Cheong *et al.*, 2010; Kievit *et al.*, 2010).

In the New World there are currently 13 recognized buthid genera and approximately 403 described species representing two monophyletic radiations and one introduction (*Isometrus maculatus* (DeGeer, 1778)) (Fet & Lowe, 2000). The "Gondwanan buthids" (Fet *et al.*, 2003) are represented in the New World by one South

American genus: *Ananteris* Thorell, 1891. The second radiation, the Centrurini Kraepelin, 1891, is endemic to the New World and comprised of the genera *Tityus* C.L. Koch, 1836, *Rhopalurus* Thorell, 1876, *Centruroides* Marx, 1896, *Mesotityus* Gonzalez-Sponga, 1981, *Alayotityus* Armas, 1973, *Microtityus* Kjellesvig-Waering, 1966, *Tityopsis* Armas, 1974, *Physoctonus* Mello-Leitao, 1934, *Troglorhopalurus* Lourenço, Baptista & Giupponi, 2004 and *Zabius* Thorell, 1893. However, the name Centrurini is not available as it is based on the genus *Centrurus* Ehrenberg, 1829, a junior synonym of *Heterometrus* Ehrenberg, 1828, in the family Scorpionidae Latrielle, 1802 (Fet & Lowe, 2000). For consistency with the Zoological Code of Nomenclature, this monophyletic group of genera will be subsequently be referred to as the "New World buthids".

The monophyly of the New World buthids is supported by evidence from multiple independent sources. Recent comparative morphology studies of the booklungs (Kamenz and Prendini, 2008) and the ovariuterine structure (Volschenk *et al.*, 2008) have revealed synapomorphies supporting the group. Furthermore, toxicological studies have demonstrated the presence of a unique toxin class (ß toxins) in New World buthid species, which is absent in all other buthids (Froy *et al.*, 1999; Coddington *et al.*, 2004). Phylogenetic analyses of molecular data have also supported New World buthid monophyly, recovering the group as sister to all other buthids (Fet *et al.*, 2003; Coddington *et al.*, 2004).

Bücherl (1971) proposed two subfamilies of New World buthids: Tityinae Bücherl, 1971, containing the genera *Tityus* and *Zabius*; and Rhopalurusinae Bücherl, 1971, containing the genera *Rhopalurus* and *Centruroides*. Rhopalurinae was the name originally proposed by Bücherl (1971), however it is a junior homonym of Rhopaluridae

Stunkard, 1937, derived from the orthonectid genus *Rhopalura* Girard, 1877, and thus was not an available name (Fet *et al.*, 2000). A 2003 ruling by the ICZN amended Rhopalurinae to the correct spelling of Rhopalurusinae Bücherl, 1971 (Fet *et al.*, 2003).) The *Rhopalurus* group is comprised of three genera (*Physoctonus*, *Troglorhopalurus*, and *Rhopalurus*), 20 species and three subspecies, which have a disjunct distribution in the Greater Antilles (Cuba and Hispaniola), the Guyana shield of northern South America (Colombia, Guyana, and Venezuela) and Western Brazil (Prendini *et al.*, 2009) (Fig 1). They are unique in possessing the ability to stridulate audibly by scraping nodules and/or ridges on the dorsal surfaces of their pectines against granules on the ventral surfaces of mesosomal sternite III, a remarkable behavior that presumably functions to deter would-be predators (Pocock 1904; Lourenço & Cloudsley-Thompson 1995; Lourenço 2007, Prendini *et al.*, 2009). Lourenço (1986) considered the stridulatory organ to be synapomorphic for the *Rhopalurus* group. However, neither this hypothesis nor the monophyly of the *Rhopalurus* group or the three genera has yet to be tested.

*Centruroides*, the other genus in Bücherl's (1971) Rhopalurusinae, is a morphologically diverse taxon. *Centruroides* scorpions primarily inhabit woody and decaying vegetation and are often found under bark on trees, hence the common name 'bark scorpion' (Polis, 1990). *Centruroides* is among the most diverse scorpion genera in the New World, comprising 71 described species and 5 subspecies (Fet & Lowe, 2000; Teruel 2001, 2006, 2007; Teruel & Stockwell, 2002; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009). These scorpion species are sexually dimorphic, the males typically exhibiting elongation of the metasoma and telson and longer, more slender pedipalp chelae (Polis & Sissom, 1990). The greatest

Figure 1. Approximate distribution of the buthid scorpion genus *Rhopalurus* Thorell, 1876.

**Figure 1**

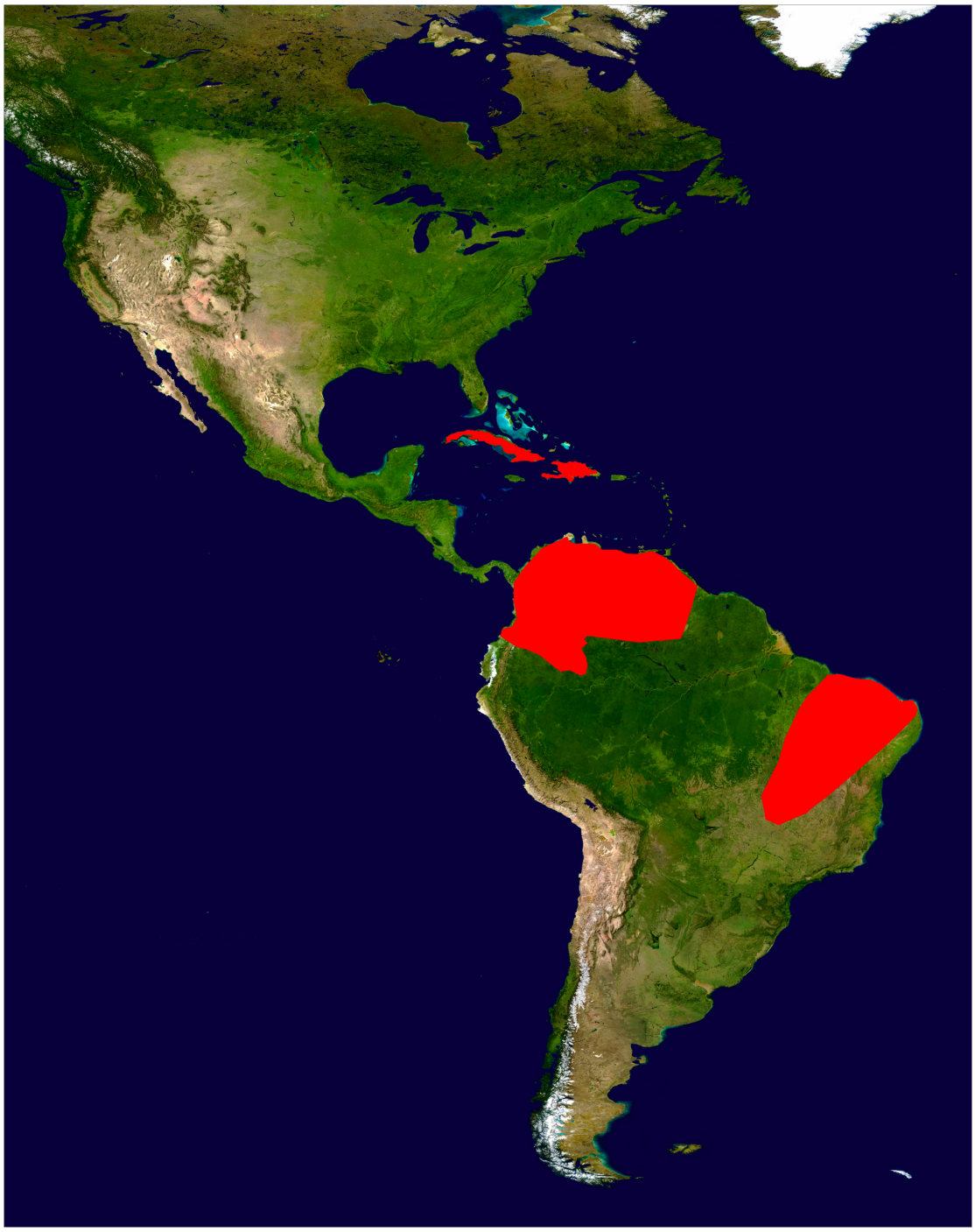


diversity of *Centruroides* occurs in Mexico; however the genus is distributed from the Midwestern United States into northern South America (Colombia, Venezuela, Ecuador, and possibly Peru), throughout the Caribbean, and the Galápagos (Fig 2) (Hoffmann, 1932; Gantenbein *et al.*, 2001; Sissom & Lourenço, 1987). The genus includes the only scorpions of medical importance in North America; six species are potentially lethal to humans (Dehesa-Davila & Possani, 1994). Taxonomically, *Centruroides* is in shambles. Various researchers have studied and revised small groups of species, but there has been no comprehensive modern taxonomic treatment of the entire genus (Gantenbein *et al.*, 2001; Towler *et al.*, 2001).

The morphological basis for Bücherl's (1971) proposal of Rhopalurusinae is the presence of supernumerary granules on the internal surfaces of the fingers of the pedipalp chela. While this character may be phylogenetically useful, it has yet to be cladistically demonstrated as synapomorphic. Historically, species have been transferred back and forth between *Centruroides* and *Rhopalurus*, and the generic definitions have been revised several times (Lourenço, 1979; Meise, 1934; Mello-Leitão, 1945, Pocock, 1890; Werner, 1939). *Centruroides* species are currently separated from species of the *Rhopalurus* group by a combination of the following characters: the pedipalp fixed-finger trichobothrium *db* situated in line with or basal to *et*, an elongated fifth metasomal segment in males, and the absence of a stridulation organ. These characters are problematic: the trichobothrial positions are variable within the genus; the extent of the fifth metasomal segment elongation is variable; and the absence of a stridulation organ is plesiomorphic. A phylogenetic study of Cuban scorpions using a single mitochondrial DNA marker (16S rDNA), found that *Centruroides* was

Figure 2. Approximate distribution of the buthid scorpion genus *Centruroides* Marx, 1890.

**Figure 2**



paraphyletic with respect to the *Rhopalurus* group (Fet *et al.*, 2003). Ovariuterine data, however, suggests the opposite scenario: a paraphyletic *Rhopalurus* group with respect to *Centruroides* (Volschenk *et al.*, 2008).

The objectives of this study are: to test the validity of the buthid subfamily Rhopalurusinae; to test the monophyly of the genera *Rhopalurus*, *Centruroides*, *Troglorhopalurus*, and *Physoctonus*. Phylogenetic analyses were conducted using morphological data, a combined molecular dataset of three mitochondrial and two nuclear DNA loci, and a combined morphological and molecular data matrix. Presented herein are the results of these analyses, and a recommendation to restore *Heteroctenus* Pocock, 1893, a genus of Caribbean scorpions previously synonymized with *Rhopalurus*.

## Methods

### *Taxon Sampling*

In order to evaluate Rhopalurusinae and test the monophyly of the *Rhopalurus* group, all species of *Rhopalurus*, *Troglorhopalurus*, and *Physoctonus* were included with the exception of two Cuban endemics, which could not be obtained: *R. gibarae* Teruel, 2006 and *R. granulimanus* Teruel, 2006. Six species of *Centruroides* were selected to sample the diversity and geographic range of the genus.

Representative species of the New World buthid subfamily Tityinae were included as outgroups. Species of *Tityus* were selected in order to sample the diversity of the genus, using the proposed subgenera (Lourenço, 2006) as a proxy. Two of the three described species of the genus *Zabius* were included on the basis of its inclusion in Tityinae. Finally, the Australasian buthid taxon *Isometrus maculatus* was included as root

for all analyses on the basis that the Isometrinae buthid subfamily is the putative sister to the Centrurinae (Kraepelin, 1899; Fet *et al.*, 2004).

***Morphology***

Morphological characters were taken from various published (27 characters) and unpublished (33 characters) matrices (Lamoral, 1978, 1980; Stockwell, 1989; Jeram, 1994, 1998; Prendini, 2000, 2001, 2004; Dunlop & Braddy, 2001; Soleglad & Sissom, 2001; Soleglad & Fet, 2001, 2003; Giribet *et al.*, 2002; Volschenk *et al.*, 2008; E.S. Volschenk & L. Prendini, unpublished), appended with additional novel characters (30), and assembled into a combined morphological matrix. The combined matrix was scored for exemplars (Prendini, 2001d) from 24 ingroup species and 9 outgroup species (Appendix 1). Analyses of combined molecular and morphological data that include more than one sample for any given species were scored using the exemplar approach (Prendini, 2001d).

The morphological matrix was assembled and scored in Mesquite v2.74 (Maddison & Maddison, 2010). The matrix is composed of 43% prosomal characters, 33% mesosomal characters, and 23% metasomal characters. Of these, 54% of the characters are derived from carination and surface macrosculpturing, 21% are morphometric and shape based, 13% are from macrosetae and trichobothria, 9% are internal and external anatomical characters, and 3% are color-based characters. The primary source of each character is listed along with the 90 characters and states for each character in Appendix 2. The coded matrix is given in Appendix 3.

Nomenclature of general anatomy follows Hjelle (1990) and Sissom (1990), trichobothria follows Vachon (1974), tergite and pedipalp carination follows Prendini (2001b), carapace and metasomal carination follows Vachon (1974), and ovariuterine anatomy follows Volschenk *et al.* (2008). Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2001b). Morphological examination of specimens was conducted using a Nikon SMZ1500 dissection stereomicroscope. Specimens were measured using Mitutoyo digital calipers and an ocular micrometer.

***Field Methods***

Specimens were collected in the field using ultraviolet light and preserved by submersion of live animals in 95% ethanol, and subsequently injected with ethanol to improve the internal preservation. Specimens are stored at -20°C at the American Museum of Natural History.

***Laboratory Methods***

Genomic DNA was extracted muscle tissue from the fourth leg of each specimen using a Qiagen DNEasy Blood and Tissue extraction kit according the manufacturers protocols. Extracted DNA was amplified for five gene regions in overlapping fragments using universal eukaryote and scorpion specific primers (Table 1). Five gene loci were selected for this study, based on their ability to provide resolution at various taxonomic levels: a mitochondrial protein-coding gene (CoxI), mitochondrial structural genes (12S rDNA, 16S rDNA), and nuclear structural genes (18S rDNA, 28S rDNA) (Arnedo *et al.*, 2002; Giribet *et al.*, 2001; Harrison *et al.*, 1987; Hayashi, 1996; Hillis & Dixon, 1991;

**Table 1.** Primers used for gene amplification in a phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971.

| Gene | Primer | Sequence | References (other names) |
|---|---|---|---|
| 12S | 12Sai | AAACTAGGATTAGATACCCTATTAT | Kocher *et al.*, 1989; Simon *et al.*, 1994 (SR-N-14588) |
| | 12Sbi | AAGAGCGACGGGCGATGTGT | Kocher *et al.*, 1989; Simon *et al.*, 1994 (SR-J-14233) |
| 16S | 16Sar | CGCCTGTTTATCAAAAACAT | Simon *et al.*, 1994 (LR-N-13398) |
| | 16Sbr | CTCCGGTTTGAACTCAGATCA | Simon *et al.*, 1994 (LR-J-12887) |
| 18S | 18S1F | TACCTGGTTGATCCTGCCAGTAG | Prendini *et al.*, 2005 |
| | 18S5R | CTTGGCAAATGCTTTCGC | Prendini *et al.*, 2005 |
| | 18S3F | GTTCGATTCCGGAGAGGGA | Prendini *et al.*, 2005 |
| | 18Sbi | GAGTCTCGTTCGTTATCGGA | Prendini *et al.*, 2005 |
| | 18SA2.0 | ATGGTTGCAAAGCTGAAAC | Prendini *et al.*, 2005 |
| | 18S9R | GATCCTTCCGCAGGTTCACCTAC | Prendini *et al.*, 2005 |
| 28S | 28Sa | GACCCGTCTTGAAGCACG | Nunn *et al.*, 1996 (D3A |
| | 28Sbout | CCCACAGCGCCAGTTCTGCTTACC | Prendini *et al.*, 2005 |
| Cox1 | LCO | GGTCAACAAATCATAAAGATATTGG | Folmer *et al.*, 1994 (LCO-1490-J-1514) |
| | HCOoutout | GTAAATATATGRTGDGCTC | Prendini *et al.*, 2005 |
| | LE1R | TCCATTCCCACAGTAAACATATG | |
| | HCOEXTERNA | GAAGTTTATATTTTAATTTTACCTGG | |
| | HCOEXTERNB | CCTATTGAWARAACATARTGAAAATG | |

Wahlberg & Zimmermann, 2000). Polymerase Chain Reaction was performed on an Epicenter thermocycler (Eppendorf) using GoTaq polymerase (Promega). Reactions were verified on a 1.2% agarose gel stained with Sybrsafe DNA gel stain (Invitrogen), and subsequently purified using the Ampure DNA (Agencourt) purification system on a Biomek NX robot (Beckman-Coulter). Cycle sequencing was conducted using Big Dye v1.1 and automated Sanger sequencing of single stranded DNA performed on an Applied Biosystems Inc. Prism™ 3730x. Paired strand reads were aligned using Sequencher™ and edited by hand. Sequences are accessioned in Genbank (Appendix 1).

***Phylogenetic Methods***

Morphological characters were equally weighted *a priori* and analyzed under parsimony in TNT v1.1 (Goloboff *et al.*, 2003) using the New Technology Search option with 10,000 random addition replicates. An implied character weighting (Goloboff, 1993) scheme was employed to evaluate the robustness of the topology in response to character weighting. Six values for the concavity constant, *k*, were investigated. The Australasian buthid species, *Isometrus maculatus*, was used to root all trees. Bootstrap measures of node support were calculated in TNT.

In order to identify rogue taxa (Sanderson & Schaffer, 2002) which may have an impact on either the resulting topologies (Thompson & Schaffer, 2010) or the measures of support (Pattengale *et al.*, 2010) the leaf stability index (Thorley & Page, 2000) was calculated from the resulting trees in Phyutility v2.2 (Smith & Dunn, 2008).

Multiple sequence alignments for individual gene partitions was performed in MAFFT (Katoh *et al.*, 2005) using the G-INS-i strategy (recommended by the authors

for less than 200 sequences with global homology) and PAM1/K=2 matrix parameter (recommended by the authors for aligning closely related sequences). All loci were aligned, however there was no length variation in Cox1, negligible length variation in 18S and 28S (<10 nucleotides), and little length variation in 12S and 16S (<20 nucleotides). The resulting alignments were then concatenated and the matrices were assembled in Geneious v5.1 (Biomatters, Ltd.).

Molecular data from individual gene partitions (12S, 16S 18S, 28S, CoxI) were concatenated and analyzed under parsimony in TNT v1.1. The 'New Technology Search' option with 10,000 random addition replicates, 'Tree Drift' (Goloboff, 1999), and 'Ratchet' (Nixon, 1999) was used to identify the single most parsimonious tree.

A total evidence dataset of morphological and concatenated molecular data was analyzed under Bayesian and parsimony criteria. All analyses were rooted, as before, on *Isometrus maculatus*. The parsimony analysis was conducted using TNT. The Bayesian analysis was performed in MrBayes (Ronquist and Hulsenbeck, 2003) on the CIPRES supercomputing cluster (Miller *et al.*, 2009) in two independent runs for 50 million generations, sampling every 1000 generations. MrModeltest2 v2.3 (Nylander, 2004), employing Akaike information criteria, (Akaike, 1973) was used to determine the best fitting model of DNA substitution for each gene and codon position (CoxI) (Table 2). In cases where the best fitting model included both the Γ and invariable sites (I) parameters, the next best fitting model was selected to avoid issues stemming from the non-independence of the Γ and I parameters. Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (Rambaut and Drummond, 2007), and convergence was assessed by the standard deviations of the split frequencies in AWTY (Nylander *et al.*,

**Table 2.** Best-fitting models of nucleotide substitution for five loci as calculated in MrModelTest2 v2.3 (Nylander, 2008) for a phylogenetic analysis of the buthid subfamily Rhopalurusinae Bücherl, 1971. For Cytochrome *c* oxidase subunit I (Cox1), the best model was determined for each codon position. The partitions indicated with an asterisk (*) are the second best model following the exclusion of models that included both the Γ and I parameters.

| **Locus/ Partition** | **AIC Model** |
|---|---|
| 12S | GTR+G* |
| 16S | HKY+G* |
| 18S | GTR+I |
| 28S | GTR+I |
| CoxI/ 1 | GTR+G* |
| CoxI/ 2 | GTR+G* |
| CoxI/ 3 | GTR+G* |

2008). A maximum clade credibility tree was computed from the post-burn-in trees in TreeAnnotator v1.6.1 (Rambaut & Drummond, 2007). Resulting phylogenies were manipulated and rendered in FigTree v1.2.2 (Rambaut, 2009).

## Results

### *Morphological Analysis*

The morphological analysis resulted in five equally parsimonious phylogenies with a length (T.L.) of 380, exhibiting two islands of tree topologies. In all of the trees, the genera *Tityus* and *Zabius* are recovered as a monophyletic group, with *Zabius* nested within *Tityus*. *Rhopalurus* and *Centruroides* form a monophyletic group containing eight primary clades: a clade containing *Rhopalurus lacrau* Lourenço & Pinto-da-Rocha 1997 and *Troglorhopalurus translucidus* Lourenço *et al*., 2004; a clade of *Physoctonus debilis* (C.L. Koch, 1840) and an undescribed *Physoctonus* species; a clade of *Rhopalurus guanambiensis* Lenarducci *et al*., 2005 and an undescribed species; a northern South America *Rhopalurus* clade (*R. crassicauda* Caporiacco, 1947, *R. amazonicus* Lourenço, 1986, *R. laticauda* Thorell, 1876, *R. caribensis* Teruel & Roncallo, 2008); a Brazilian *Rhopalurus* clade (*R. amazonicus* Lourenço, 1986, *R. pintoi* Mello-Leitão, 1933, *R. rochae* Borelli, 1910); a Greater Antilles *Rhopalurus* clade (*R. bonettii* Armas, 1999, *R. junceus* (Herbst, 1800), *R. abudi* Armas & Marcano Fondeur, 1987, *R. princeps* (Karsch, 1879), *R. garridoi* Armas, 1974); and a *Centruroides* clade (*C. bani* Armas & Marcano Fondeur, 1987, *C. exilicauda* (Wood, 1863), *C. infamatus* (C.L. Koch, 1844), *C. gracilis* (Latreille, 1804), *C. margaritatus* (Gervais, 1841), *C. schmidti* Sissom, 1995). The

recovered phylogenies differ in their relationships among the clades of *Rhopalurus* and *Centruroides.*

Four of the phylogenies had nearly identical topologies with only slight rearrangements of taxa within the terminal clades. A strict consensus of the four phylogenies (Fig 3A) resulted in a tree with T.L. 384, Consistency Index (C.I.) of 0.32, and Retention Index (R.I.) of 0.61. In these four phylogenies as well as in the strict consensus tree, *Centruroides* is recovered as sister to the *Rhopalurus* group. The *Troglorhopalurus* and *Physoctonus* clades fall outside of *Rhopalurus*. The *Rhopalurus laticauda* complex (*R. laticauda*, *R. caribensis*, *R. amazonicus*, *R. agamemnon*) is resolved as sister to the Brazilian + Greater Antilles clades. The fifth most parsimonious (MP) tree recovered (T.L. 380, C.I. 0.32, R.I. 0.62) in the equal weighting analysis (Fig 3B) has a different topology from the other MP trees. As before, the *Troglorhopalurus* and *Physoctonus* clades fall outside of *Rhopalurus. Centruroides* is nested within *Rhopalurus*, and is recovered as sister to the Greater Antilles clade of *Rhopalurus*. The *R. laticauda* complex is recovered as sister to the Brazilian *Rhopalurus* complex.

The implied weighting analyses recovered a single MP tree for each *k* value (1–6). As in the equal weighting analysis, there were two primary topologies among the trees: the first was recovered for *k*=1–2 (Fig 4A), the second recovered for *k*=3–6 (Fig 4B). In all of the implied weighting analyses, *Rhopalurus* is paraphyletic with respect to *Centruroides*. The two topologies differ in their relative position of *Centruroides*. The strict consensus of the *k*=1–2 phylogenies places *Centruroides* as sister to all *Rhopalurus* species. The *Physoctonus* and *Troglorhopalurus* clades fall outside of *Rhopalurus* + *Centruroides*, rendering the *Rhopalurus* group paraphyletic. The strict consensus of the

Figure 3A. Strict consensus of four equally parsimonious trees for the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 obtained from an equal weights analysis of morphology performed in TNT (Goloboff *et al*., 2008). Branch labels correspond to character state changes, character numbers from the matrix correspond to the upper annotations of hash marks on the branches, state for a given character is indicated below the branch.

# Figure 3A

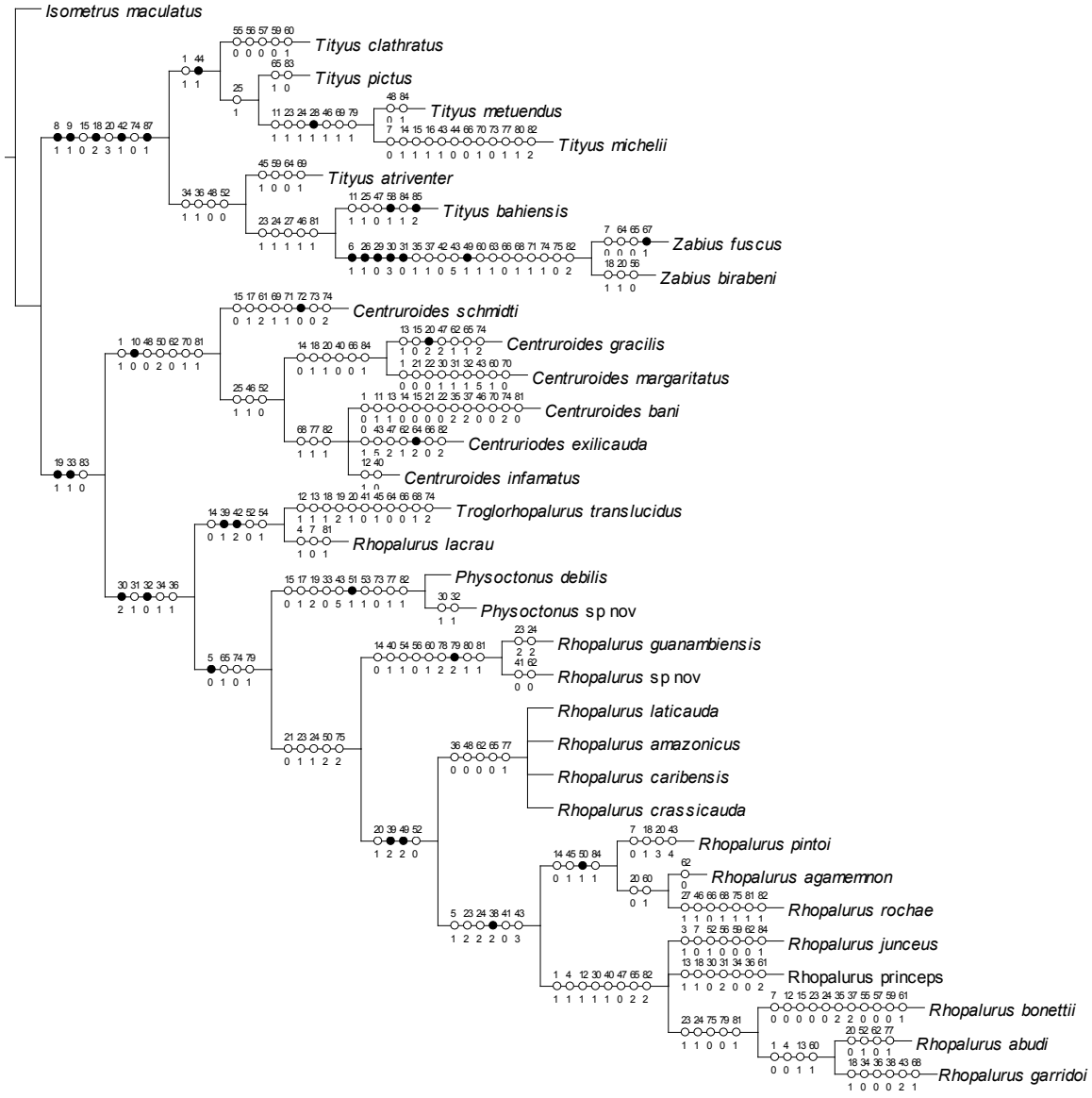

Isometrus maculatus
Tityus clathratus
Tityus pictus
Tityus metuendus
Tityus michelii
Tityus atriventer
Tityus bahiensis
Zabius fuscus
Zabius birabeni
Centruroides schmidti
Centruroides gracilis
Centruroides margaritatus
Centruroides bani
Centruriodes exilicauda
Centruroides infamatus
Troglorhopalurus translucidus
Rhopalurus lacrau
Physoctonus debilis
Physoctonus sp nov
Rhopalurus guanambiensis
Rhopalurus sp nov
Rhopalurus laticauda
Rhopalurus amazonicus
Rhopalurus caribensis
Rhopalurus crassicauda
Rhopalurus pintoi
Rhopalurus agamemnon
Rhopalurus rochae
Rhopalurus junceus
Rhopalurus princeps
Rhopalurus bonettii
Rhopalurus abudi
Rhopalurus garridoi

Figure 3B. Alternate topology for the buthid subfamily Rhopalurusinae Bücherl, 1971 obtained from an equal weights parsimony analysis of morphology performed in TNT (Goloboff *et al.,* 2000). Branch labels correspond to character state changes, character numbers from the matrix correspond to the upper annotations of hash marks on the branches, state for a given character is indicated below the branch.

# Figure 3B

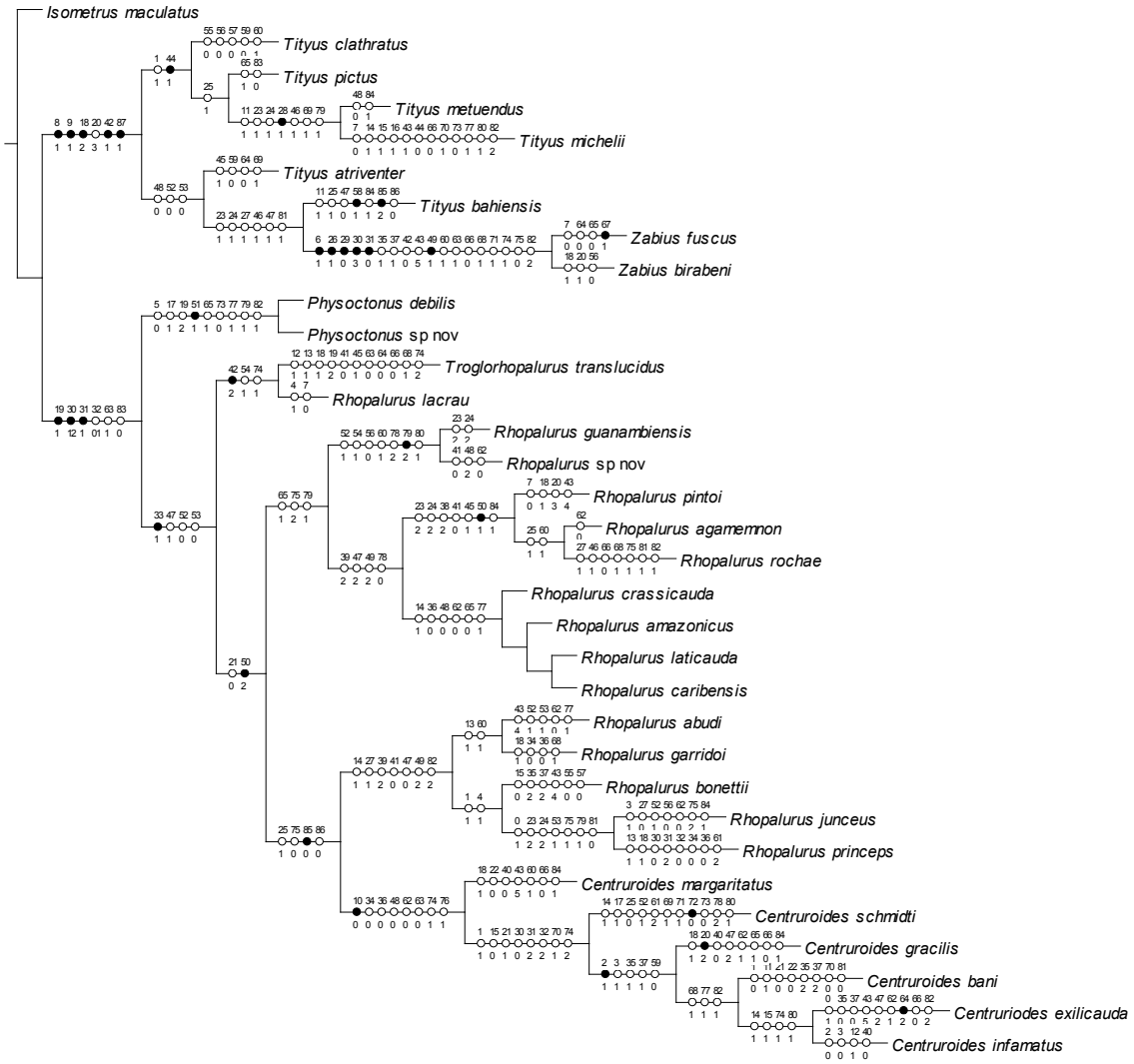

Isometrus maculatus
Tityus clathratus
Tityus pictus
Tityus metuendus
Tityus michelii
Tityus atriventer
Tityus bahiensis
Zabius fuscus
Zabius birabeni
Physoctonus debilis
Physoctonus sp nov
Troglorhopalurus translucidus
Rhopalurus lacrau
Rhopalurus guanambiensis
Rhopalurus sp nov
Rhopalurus pintoi
Rhopalurus agamemnon
Rhopalurus rochae
Rhopalurus crassicauda
Rhopalurus amazonicus
Rhopalurus laticauda
Rhopalurus caribensis
Rhopalurus abudi
Rhopalurus garridoi
Rhopalurus bonettii
Rhopalurus junceus
Rhopalurus princeps
Centruroides margaritatus
Centruroides schmidti
Centruroides gracilis
Centruroides bani
Centruriodes exilicauda
Centruroides infamatus

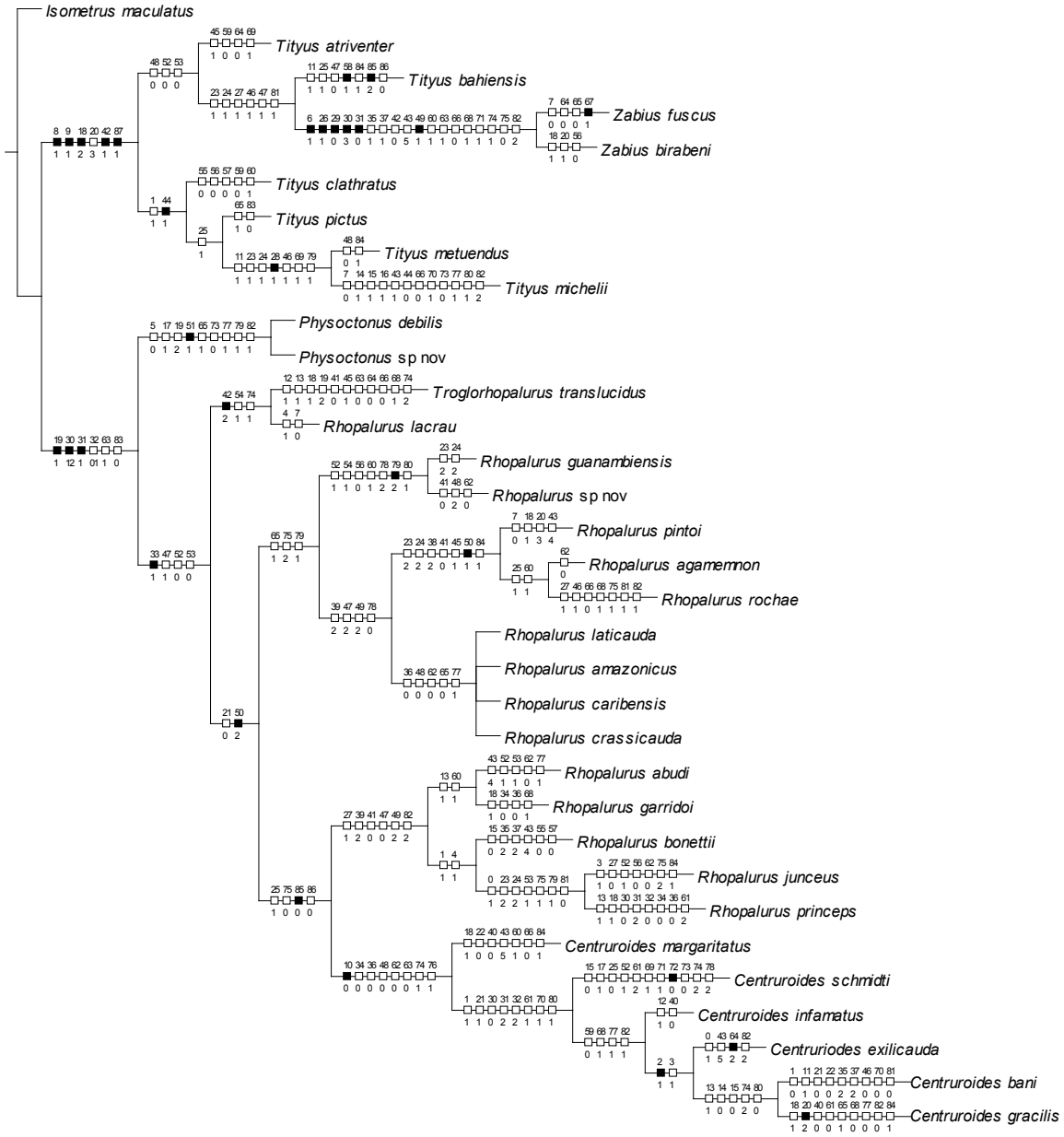
Figure 4A. Cladogram of the scorpion buthid subfamily Rhopalurusinae Bücherl, 1971, obtained from a strict consensus (k=1–2) of three equally parsimonious trees in an implied weighting analysis. Analysis performed in TNT (Goloboff *et al.*, 2000), branch labels correspond to character state changes, character numbers from the matrix correspond to the upper annotations of hash marks on the branches, state for a given character is indicated below the branch.

# Figure 4A


Isometrus maculatus
Zabius fuscus
Zabius birabeni
Tityus atriventer
Tityus clathratus
Tityus pictus
Tityus bahiensis
Tityus metuendus
Tityus michelii
Physoctonus debilis
Physoctonus sp nov
Troglorhopalurus translucidus
Rhopalurus lacrau
Centruroides margaritatus
Centruroides schmidti
Centruroides infamatus
Centruriodes exilicauda
Centruroides bani
Centruroides gracilis
Rhopalurus guanambiensis
Rhopalurus sp nov
Rhopalurus amazonicus
Rhopalurus caribensis
Rhopalurus laticauda
Rhopalurus crassicauda
Rhopalurus abudi
Rhopalurus garridoi
Rhopalurus agamemnon
Rhopalurus rochae
Rhopalurus pintoi
Rhopalurus bonettii
Rhopalurus junceus
Rhopalurus princeps

Figure 4B. Cladogram of the scorpion buthid subfamily Rhopalurusinae Bücherl, 1971, obtained from a strict consensus of three most parsimonious trees (k=3–6) in an implied weighting parsimony analysis of 90 morphological characters. Analysis was performed in TNT (Goloboff *et al.*, 2000), branch labels correspond to character state changes, character numbers from the matrix correspond to the upper annotations of hash marks on the branches, state for a given character is indicated below the branch.

# Figure 4B


Isometrus maculatus
Tityus atriventer
Tityus bahiensis
Zabius fuscus
Zabius birabeni
Tityus clathratus
Tityus pictus
Tityus metuendus
Tityus michelii
Physoctonus debilis
Physoctonus sp nov
Troglorhopalurus translucidus
Rhopalurus lacrau
Rhopalurus guanambiensis
Rhopalurus sp nov
Rhopalurus pintoi
Rhopalurus agamemnon
Rhopalurus rochae
Rhopalurus laticauda
Rhopalurus amazonicus
Rhopalurus caribensis
Rhopalurus crassicauda
Rhopalurus abudi
Rhopalurus garridoi
Rhopalurus bonettii
Rhopalurus junceus
Rhopalurus princeps
Centruroides margaritatus
Centruroides schmidti
Centruroides infamatus
Centruriodes exilicauda
Centruroides bani
Centruroides gracilis

phylogenies of the *k*=3–6 analyses places *Centruroides* as sister to the Greater Antilles *Rhopalurus*, nested within the *Rhopalurus* group, a topology congruent with that of the fifth tree from the equal weights analysis.

The leaf stability analysis of all resulting phylogenies is shown in Figure 5. The outgroup taxa (*Tityus* and *Zabius*) had consistently stable leaf stability indices greater than 0.98, indicating the monophyly of the *Rhopalurus* group + *Centruroides* is stable and the majority of the rearrangements occur within the monophyletic group. The leaf stability indices for all *Rhopalurus* group and *Centruroides* species were between 0.8 and 0.88.

***Molecular Characters***

The molecular matrix of concatenated aligned loci was comprised of 87 terminals (73 ingroup samples and 14 outgroup samples) and 4,250 characters. Of these, 3104 characters were constant, 167 variable characters were parsimony-uninformative, and 979 variable characters were parsimony-informative. The nucleotide composition was as follows: adenine- 25%, cytosine- 18.5%, guanine- 25%, thyamine- 31.5%.

***Molecular Analysis***

Parsimony analysis of the concatenated molecular dataset resulted in 14 equally parsimonious trees (T.L. 6688). The only topological differences among the trees were within terminal species clades, which are collapsed in the strict consensus (Fig. 6): *R. princeps*, *P. debilis*, *R. laticauda*, *R. amazonicus*, and *R. crassicauda*.

Figure 5. Results of leaf stability analysis on taxa from the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971 and plotted on the preferred topology from implied and equal weights parsimony analyses of 90 morphological characters. Calculated in Phyutility (Smith & Dunn, 2008), terminal branches are colored according to taxon stability index: 100>Black>90, 90>Dark grey>85, 85>Light grey>80.

**Figure 5**

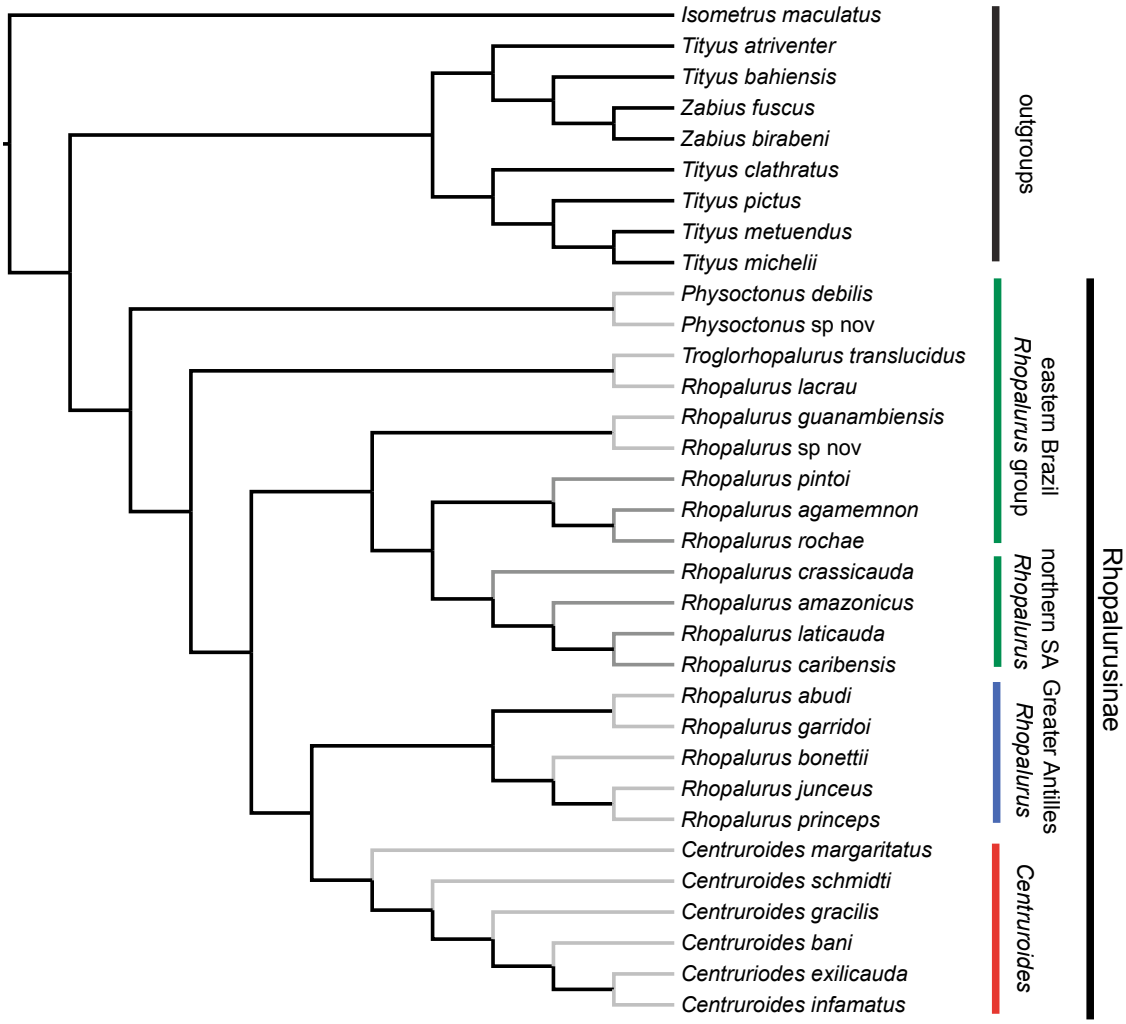
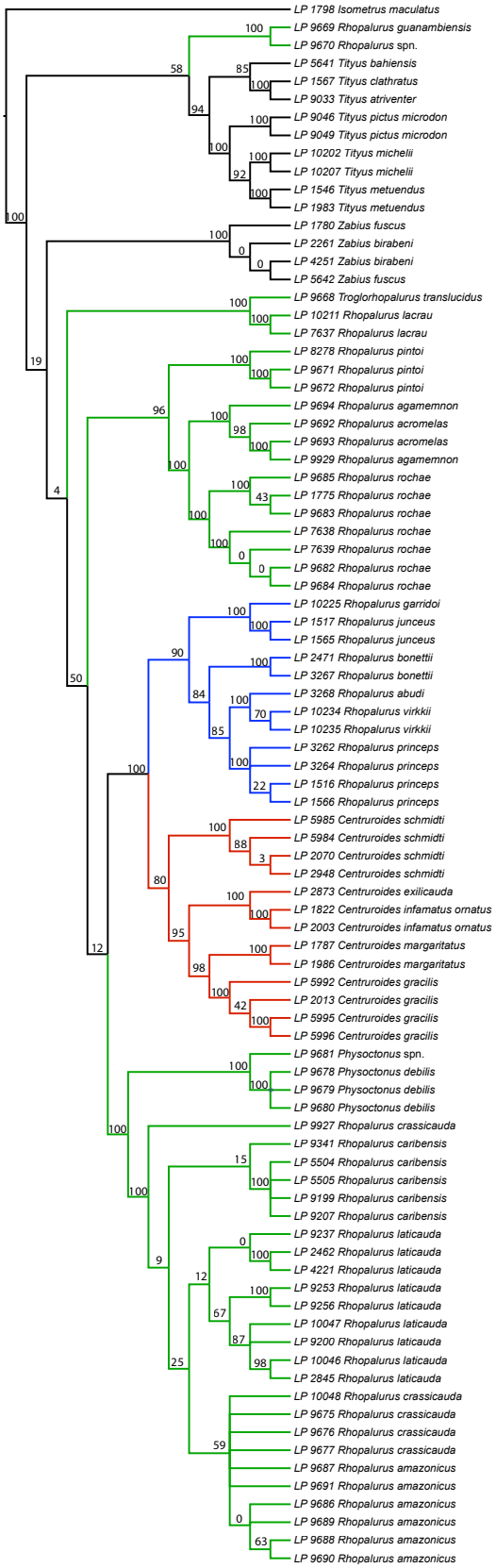

Isometrus maculatus
Tityus atriventer
Tityus bahiensis
Zabius fuscus
Zabius birabeni
Tityus clathratus
Tityus pictus
Tityus metuendus
Tityus michelii
Physoctonus debilis
Physoctonus sp nov
Troglorhopalurus translucidus
Rhopalurus lacrau
Rhopalurus guanambiensis
Rhopalurus sp nov
Rhopalurus pintoi
Rhopalurus agamemnon
Rhopalurus rochae
Rhopalurus crassicauda
Rhopalurus amazonicus
Rhopalurus laticauda
Rhopalurus caribensis
Rhopalurus abudi
Rhopalurus garridoi
Rhopalurus bonettii
Rhopalurus junceus
Rhopalurus princeps
Centruroides margaritatus
Centruroides schmidti
Centruroides gracilis
Centruroides bani
Centruriodes exilicauda
Centruroides infamatus
outgroups
eastern Brazil Rhopalurus group
northern SA Rhopalurus
Greater Antilles Rhopalurus
Centruroides
Rhopalurusinae

Figure 6. Strict consensus of 14 equally parsimonious trees of the buthid scorpion subfamiliy Rhopalurusinae Bücherl, 1971 inferred from molecular and morphological data TNT (Goloboff *et al.*, 2000). Node support values are bootstraps. For ingroup taxa (Rhopalurusinae), branches are colored according to genus and distibution: South American *Rhopalurus* Thorell, 1876 group (green), Greater Antilles *Rhopalurus* (blue), *Centruroides* Marx, 1890 (red).

# Figure 6


LP 1798 Isometrus maculatus
LP 9669 Rhopalurus guanambiensis
LP 9670 Rhopalurus spn.
LP 5641 Tityus bahiensis
LP 1567 Tityus clathratus
LP 9033 Tityus atriventer
LP 9046 Tityus pictus microdon
LP 9049 Tityus pictus microdon
LP 10202 Tityus michelii
LP 10207 Tityus michelii
LP 1546 Tityus metuendus
LP 1983 Tityus metuendus
LP 1780 Zabius fuscus
LP 2261 Zabius birabeni
LP 4251 Zabius birabeni
LP 5642 Zabius fuscus
LP 9668 Troglorhopalurus translucidus
LP 10211 Rhopalurus lacrau
LP 7637 Rhopalurus lacrau
LP 8278 Rhopalurus pintoi
LP 9671 Rhopalurus pintoi
LP 9672 Rhopalurus pintoi
LP 9694 Rhopalurus agamemnon
LP 9692 Rhopalurus acromelas
LP 9693 Rhopalurus acromelas
LP 9929 Rhopalurus agamemnon
LP 9685 Rhopalurus rochae
LP 1775 Rhopalurus rochae
LP 9683 Rhopalurus rochae
LP 7638 Rhopalurus rochae
LP 7639 Rhopalurus rochae
LP 9682 Rhopalurus rochae
LP 9684 Rhopalurus rochae
LP 10225 Rhopalurus garridoi
LP 1517 Rhopalurus junceus
LP 1565 Rhopalurus junceus
LP 2471 Rhopalurus bonettii
LP 3267 Rhopalurus bonettii
LP 3268 Rhopalurus abudi
LP 10234 Rhopalurus virkkii
LP 10235 Rhopalurus virkkii
LP 3262 Rhopalurus princeps
LP 3264 Rhopalurus princeps
LP 1516 Rhopalurus princeps
LP 1566 Rhopalurus princeps
LP 5985 Centruroides schmidti
LP 5984 Centruroides schmidti
LP 2070 Centruroides schmidti
LP 2948 Centruroides schmidti
LP 2873 Centruroides exilicauda
LP 1822 Centruroides infamatus ornatus
LP 2003 Centruroides infamatus ornatus
LP 1787 Centruroides margaritatus
LP 1986 Centruroides margaritatus
LP 5992 Centruroides gracilis
LP 2013 Centruroides gracilis
LP 5995 Centruroides gracilis
LP 5996 Centruroides gracilis
LP 9681 Physoctonus spn.
LP 9678 Physoctonus debilis
LP 9679 Physoctonus debilis
LP 9680 Physoctonus debilis
LP 9927 Rhopalurus crassicauda
LP 9341 Rhopalurus caribensis
LP 5504 Rhopalurus caribensis
LP 5505 Rhopalurus caribensis
LP 9199 Rhopalurus caribensis
LP 9207 Rhopalurus caribensis
LP 9237 Rhopalurus laticauda
LP 2462 Rhopalurus laticauda
LP 4221 Rhopalurus laticauda
LP 9253 Rhopalurus laticauda
LP 9256 Rhopalurus laticauda
LP 10047 Rhopalurus laticauda
LP 9200 Rhopalurus laticauda
LP 10046 Rhopalurus laticauda
LP 2845 Rhopalurus laticauda
LP 10048 Rhopalurus crassicauda
LP 9675 Rhopalurus crassicauda
LP 9676 Rhopalurus crassicauda
LP 9677 Rhopalurus crassicauda
LP 9687 Rhopalurus amazonicus
LP 9691 Rhopalurus amazonicus
LP 9686 Rhopalurus amazonicus
LP 9689 Rhopalurus amazonicus
LP 9688 Rhopalurus amazonicus
LP 9690 Rhopalurus amazonicus

*Rhopalurus* is recovered as paraphyletic with respect to all other New World buthids. *Rhopalurus guanambiensis* is sister to *Tityus*, forming a clade that is sister to all other New World buthids. However, the placement of these two genera as sister may be the result of long-branch attraction. *Zabius* is nested between the *Tityus* +*R. guanambiensis* clade and the remainder of *Rhopalurus* group + *Centruroides*. As in the morphological analysis, *Troglorhopalurus* forms a monophyletic clade with *Rhopalurus lacrau*. The Brazilian *Rhopalurus* species, *R. pintoi*, *R. rochae*, and the *R. acromelas/agamemnon* complex, form a monophyletic clade sister to the remaining *Rhopalurus* and *Centruroides*. *Centruroides* is recovered as sister to the Caribbean *Rhopalurus*, and *Physoctonus debilis* is recovered as sister to the *R. laticauda* complex.

***Total evidence analysis***

The maximum clade credibility tree from the MrBayes analysis is given in Figure 7. The tree is well supported with *Tityus* + *Zabius* recovered as sister to *Centruroides* + *Rhopalurus* group (PP=0.91). *Rhopalurus* is paraphyletic with respect to *Centruroides*, which forms a sister group (PP=1) to the Greater Antilles *Rhopalurus.* Both *Centruroides* and the Greater Antilles *Rhopalurus* are recovered as strongly supported monophyletic groups (PP=1). The Brazilian *Rhopalurus* form a monophlyletic clade (PP=1) sister to a well-supported clade (PP=1) comprised of monophyletic *Physoctonus* (PP=1) + monophyletic *R. laticauda* complex (PP=1).

Parsimony analysis resulted in 39 equally parsimonious trees (TL 7097). A strict consensus (Figure 8) of the 39 trees resulted in a phylogeny with TL 7183, RI 0.75 and CI 0.30. Though a majority of the discordance among the topologies was the result of

Figure 7. Phylogram of the maximum clade credibility Bayesian tree from an analysis of the scorpion subfamily Rhopalurusinae Bücherl, 1971 using combined molecular and morphological data. Analysis performed in MrBayes (Ronquist & Huelsenbeck, 2003), node support values are posterior probabilities. For ingroup taxa (Rhopalurusinae), branches are colored according to genus and distibution: South American *Rhopalurus* Thorell, 1876 group (green), Greater Antilles *Rhopalurus* (blue), *Centruroides* Marx, 1890 (red).

**Figure 7- Part 1**

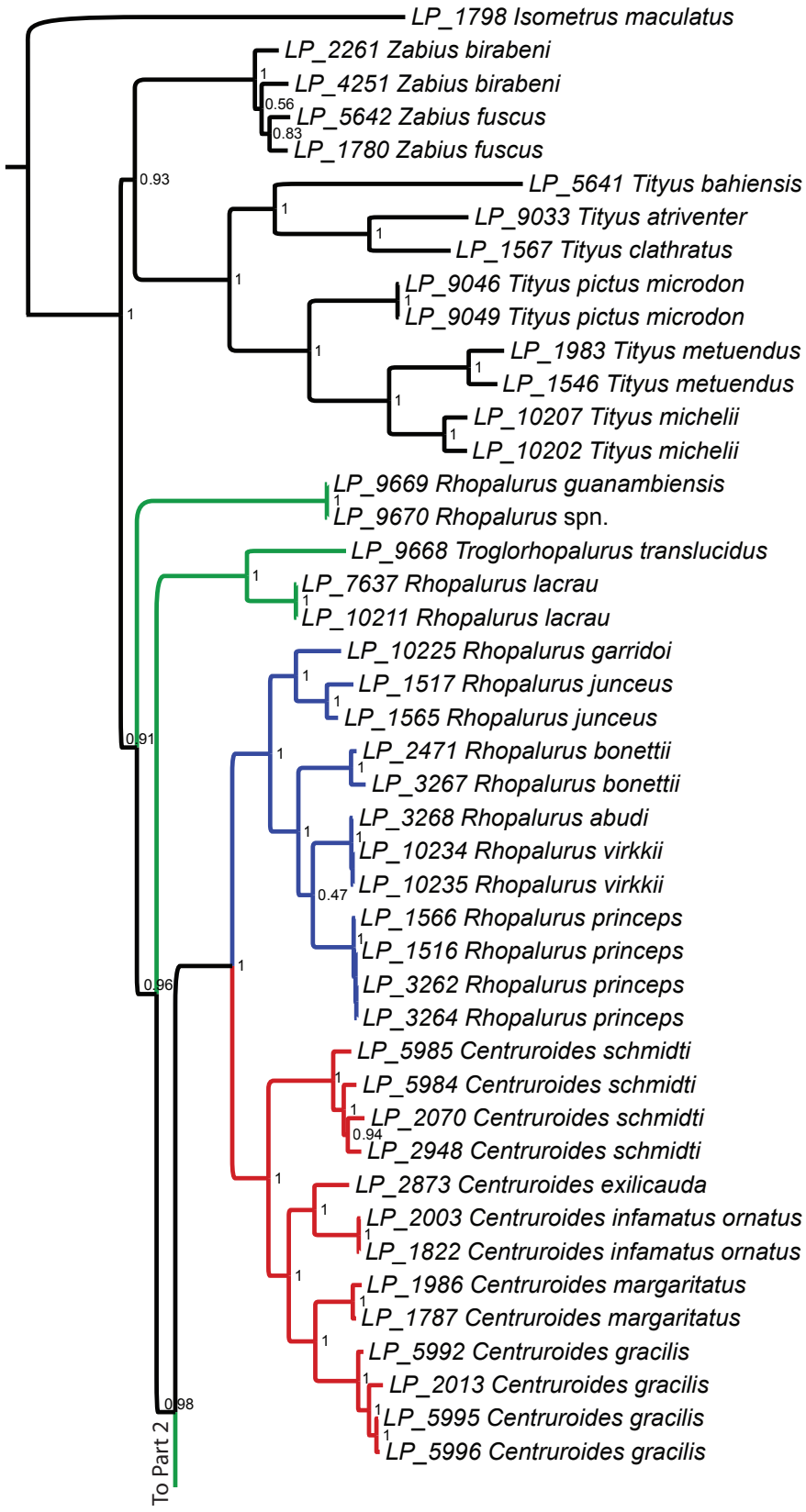


**Figure 7- Part 2**

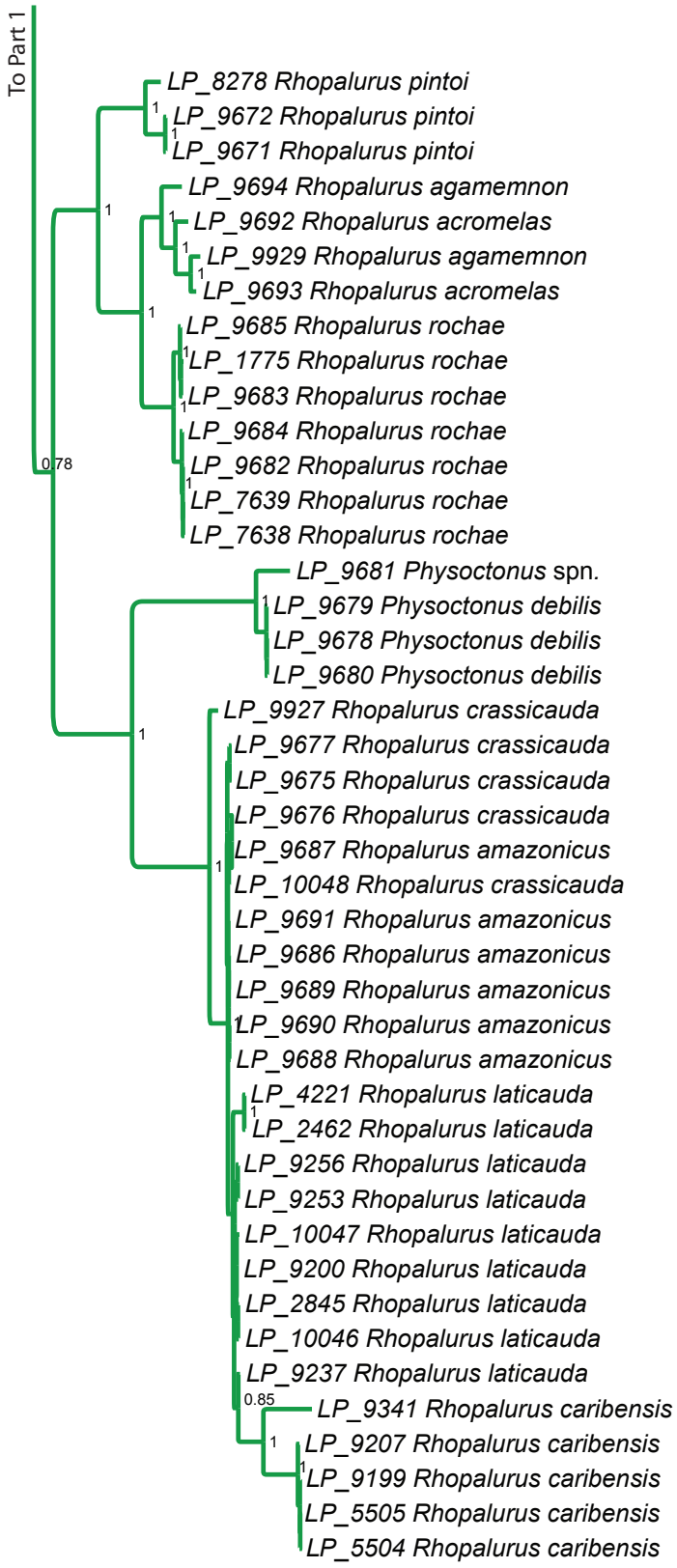
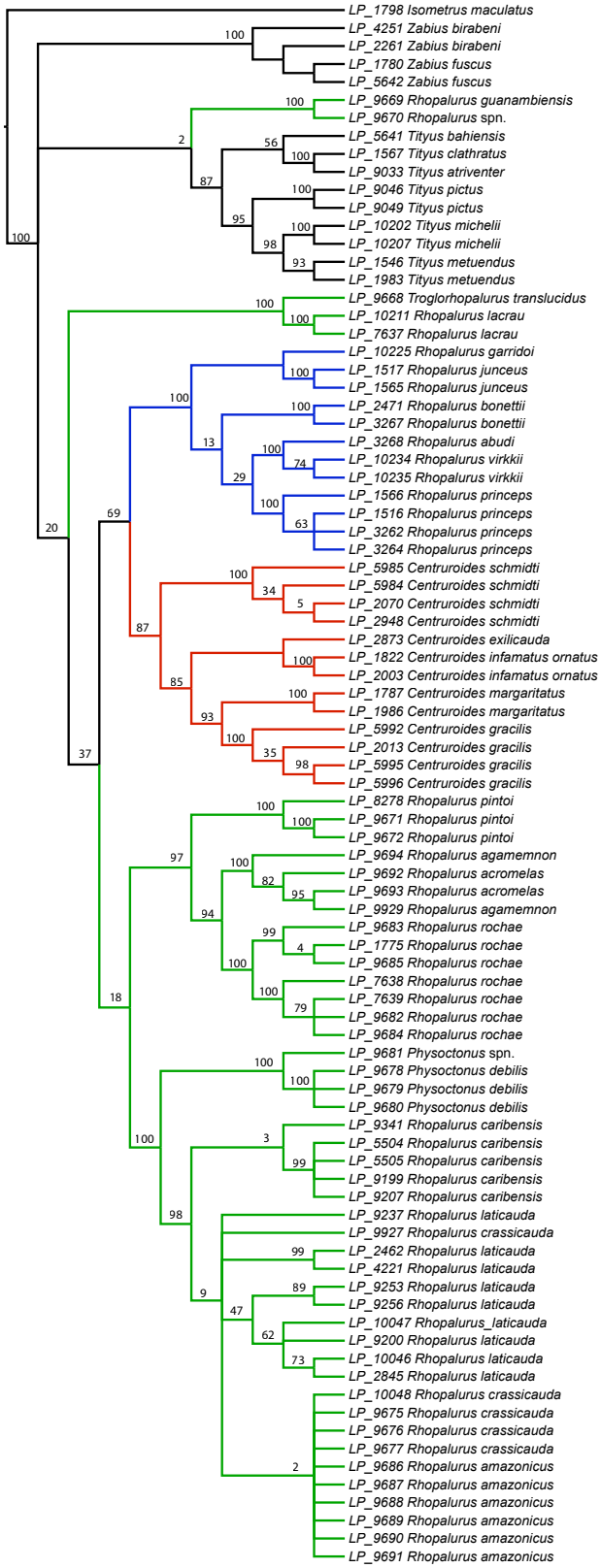


Figure 8. Strict consensus parsimony phylogram of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, inferred from molecular and morphological data. Consensus of 39 equally parsimonious trees from an analysis performed in TNT (Goloboff *et al.,* 2000), node labels are bootstraps. For ingroup taxa (Rhopalurusinae), branches are colored according to genus and distibution: South American *Rhopalurus* Thorell, 1876 group (green), Greater Antilles *Rhopalurus* (blue), *Centruroides* Marx, 1890 (red).

# Figure 8


LP_1798 Isometrus maculatus
LP_4251 Zabius birabeni
LP_2261 Zabius birabeni
LP_1780 Zabius fuscus
LP_5642 Zabius fuscus
LP_9669 Rhopalurus guanambiensis
LP_9670 Rhopalurus spn.
LP_5641 Tityus bahiensis
LP_1567 Tityus clathratus
LP_9033 Tityus atriventer
LP_9046 Tityus pictus
LP_9049 Tityus pictus
LP_10202 Tityus michelii
LP_10207 Tityus michelii
LP_1546 Tityus metuendus
LP_1983 Tityus metuendus
LP_9668 Troglorhopalurus translucidus
LP_10211 Rhopalurus lacrau
LP_7637 Rhopalurus lacrau
LP_10225 Rhopalurus garridoi
LP_1517 Rhopalurus junceus
LP_1565 Rhopalurus junceus
LP_2471 Rhopalurus bonettii
LP_3267 Rhopalurus bonettii
LP_3268 Rhopalurus abudi
LP_10234 Rhopalurus virkkii
LP_10235 Rhopalurus virkkii
LP_1566 Rhopalurus princeps
LP_1516 Rhopalurus princeps
LP_3262 Rhopalurus princeps
LP_3264 Rhopalurus princeps
LP_5985 Centruroides schmidti
LP_5984 Centruroides schmidti
LP_2070 Centruroides schmidti
LP_2948 Centruroides schmidti
LP_2873 Centruroides exilicauda
LP_1822 Centruroides infamatus ornatus
LP_2003 Centruroides infamatus ornatus
LP_1787 Centruroides margaritatus
LP_1986 Centruroides margaritatus
LP_5992 Centruroides gracilis
LP_2013 Centruroides gracilis
LP_5995 Centruroides gracilis
LP_5996 Centruroides gracilis
LP_8278 Rhopalurus pintoi
LP_9671 Rhopalurus pintoi
LP_9672 Rhopalurus pintoi
LP_9694 Rhopalurus agamemnon
LP_9692 Rhopalurus acromelas
LP_9693 Rhopalurus acromelas
LP_9929 Rhopalurus agamemnon
LP_9683 Rhopalurus rochae
LP_1775 Rhopalurus rochae
LP_9685 Rhopalurus rochae
LP_7638 Rhopalurus rochae
LP_7639 Rhopalurus rochae
LP_9682 Rhopalurus rochae
LP_9684 Rhopalurus rochae
LP_9681 Physoctonus spn.
LP_9678 Physoctonus debilis
LP_9679 Physoctonus debilis
LP_9680 Physoctonus debilis
LP_9341 Rhopalurus caribensis
LP_5504 Rhopalurus caribensis
LP_5505 Rhopalurus caribensis
LP_9199 Rhopalurus caribensis
LP_9207 Rhopalurus caribensis
LP_9237 Rhopalurus laticauda
LP_9927 Rhopalurus crassicauda
LP_2462 Rhopalurus laticauda
LP_4221 Rhopalurus laticauda
LP_9253 Rhopalurus laticauda
LP_9256 Rhopalurus laticauda
LP_10047 Rhopalurus_laticauda
LP_9200 Rhopalurus laticauda
LP_10046 Rhopalurus laticauda
LP_2845 Rhopalurus laticauda
LP_10048 Rhopalurus crassicauda
LP_9675 Rhopalurus crassicauda
LP_9676 Rhopalurus crassicauda
LP_9677 Rhopalurus crassicauda
LP_9686 Rhopalurus amazonicus
LP_9687 Rhopalurus amazonicus
LP_9688 Rhopalurus amazonicus
LP_9689 Rhopalurus amazonicus
LP_9690 Rhopalurus amazonicus
LP_9691 Rhopalurus amazonicus

rearrangements within the *R. laticauda* clade, there were some basal rearrangements as well. A basal polytomy results in a lack of resolution among *Zabius*, *Tityus* and the *Rhopalurus* group + *Centruroides*. As in the molecular parsimony analysis, *Tityus* and *R. guanambiensis* form a weakly supported monophyletic clade. This relationship may weaken support for clades, resulting in a basal polytomy. There is, however, congruence among the topologies within the *Rhopalurus* group. *Troglorhopalurus* + *R. lacrau* is the basal clade. *Centruroides* is recovered as sister to the Greater Antilles *Rhopalurus.* The central Brazilian *Rhopalurus* are recovered as a monophyletic group sister to the *R. laticauda* group + *Physoctonus*.

**Discussion**

The results of the various analytical and sampling methods are largely congruent. The results of the molecular analysis and the combined analyses are largely congruent with the island of trees from the morphological analysis containing the alternate topology from the equal weights analysis and the $k$=3–6 consensus tree from the implied weighting analysis. This congruence provides support for these trees as the preferred topology (Figures 3B, 4B, 5, 7).

The monophyly of the *Rhopalurus* group plus *Centruroides* supports Bücherl's (1971) proposal of the New World buthid subfamily Rhopalurusinae. The results of the analyses agree that the presence of supernumary granules on the internal surfaces of the pedipalp fingers is synapomorphic for the group. Additionally, cheliceral characters proved to be synapomorphic, including the presence of dorsobasal setation on the fixed cheliceral finger, the presence of a transverse row of median tubercles on the chelicerae,

and the presence of a bifurcated prolateral pedal spur on leg I, although this is reduced in the genus *Physoctonus*.

Contrary to findings from other researchers (Teruel *et al.*, 2006), *Centruroides* is always recovered as a well-supported monophyletic group. Several synapomorphies support the genus: the internoventral and internodorsal carinae on the pedipalp femur converge on one another as if they have been pinched together, trichobothrium *db* on the fixed finger of the pedipalp chela is either distal to or roughly in line with trichobothrium *et*, trichobothrium *est* on the fixed finger of the pedipalp chela is either between *db* and *et* or basal to *et*, and metasomal segment V is elongated (length > 2.5X width).

Within *Rhopalurus* there are several consistently recovered, and well-supported clades: a Brazilian clade that includes *R. agamemnon*, *R. pintoi* and *R. rochae*; a Greater Antilles clade that includes all of the species present in the Greater Antilles (*R. bonettii*, *R. junceus*, *R. abudi* (and *R. virkkii)*, *R. princeps*, *R. garridoi*); a clade from northern South America that includes the type species, *R. laticauda*, as well as *R. caribensis*, *R. amazonicus*, and *R. acromelas*; a clade containing *R. guanambiensis* and an undescribed species; a clade containing the troglobite *Troglorhopalurus translucidus* and the trogloxene *Rhopalurus lacrau*; and finally a clade containing the monotypic genus *Physoctonus* and an undescribed species. The species comprising each clade come as no surprise, as many species group relationships had been previously proposed (Teruel & Tietz, 2008; Lourenço, 2008; Teruel & Roncallo, 2008).

The taxonomy of the *Rhopalurus* group has long been debated in the literature. The genus is comprised of mostly large, robust, charismatic scorpions. Their size and the stridulatory ability of many of the species garners attention, however, their taxonomy is

in shambles. In the past decade alone, there have been several major publications addressing taxonomic changes in nearly every clade. *Rhopalurus laticauda*, the type species of *Rhopalurus*, has had recent taxonomic changes, including the description of a morphologically similar species: *R. caribensis* (Teruel & Roncallo, 2008). The monotypic genus *Physoctonus*, formerly in synonymy with *Rhopalurus*, has been revalidated (Lourenço, 2007). A troglomorphic species was discovered in a Brazilian cave and described from a single specimen as a new genus and species, *Troglorhopalurus translucidus* (Lourenço *et al.*, 2004). The species *Rhopalurus piceus* was described and then subsequently synonymized with *R. pintoi*, which had been erroneously declared *nomen nudum* (Teruel & Tietz, 2008). The validity of *R. crassicauda* has been doubted and subsequently reaffirmed (Lourenço, 2008; Teruel & Tietz, 2008).

Among the Greater Antilles species, the taxonomy has not fared much better. Three species have been described, two from localities in Cuba less than 25 km apart (*Rhopalurus gibarae* Teruel, 2006, *Rhopalurus granulimanus* Teruel, 2006), and a third from Isla Mona, a small island between Hispaniola and Puerto Rico (Santiago-Blay, 2010). Male specimens of the Hispaniolan species *R. abudi* were discovered and formally described (Prendini *et al.*, 2008).

Many of the current taxonomic problems within *Rhopalurus* can be clarified by the results of the present investigation. *Rhopalurus* is unequivocally paraphyletic. Pocock (1893) described the genus *Heteroctenus* Pocock, 1893, designating the type species as *Heteroctenus junceus* (author, date), and assigning *R. agamemnon* and *R. princeps* to it. Pocock also stated in the description that the genus was closely allied with *Centruroides*. However a few years later, Pocock (1903) synonymized the genus with *Rhopalurus*.

Pocock's (1893) original definition of *Heteroctenus* was made on the basis of expanded proximal pectinal lamellae, an enlarged pectinal plate, and the presence of an enlarged median ridge on sternite III. The synapomorhic characters for *Heteroctenus* proposed by Pocock were recovered in this analysis, and we find on the basis of both morphological and molecular evidence that the genus *Heteroctenus* is valid and should be restored. There are several additional synapomorphies for the genus: the dorsal surfaces of the proximal pectinal teeth have regular striations with multiple nodules, the lateral margins of sternite III form a smooth keel, and the telson lacks a subaculear tubercle.

The two minor genera within the *Rhopalurus* group are clearly evidenced to be valid on the basis of both morphology and molecular data. The consistent placement of *Rhopalurus lacrau* as sister to the monotypic genus *Troglorhopalurus* comes as no surprise. Both taxa are from caves belonging to the same subterranean formation in Brazil (Lourenço *et al.*, 2004), and in the description of *Troglorhopalurus* the authors suggested that this relationship be investigated using molecular data (Lourenço *et al.*, 2004). Our formal recommendation is to transfer *Rhopalurus lacrau* to *Troglorhopalurus*. There are several synapomorphies for the genus: the structure of the peg sensillae are elongate and acuminate (C. Kamenz & L. Prendini, in prep.), the width of the telson vesicle is approximately equal to the width of metasomal segment V; the telson is slightly ovate (length approximately 1.5X width), and metasomal segment V is elongated (length > 2.5X width). The metasomal and telson characters are similar to those of *Centruroides*, and are generally associated with elongation of the metasoma. However, in the case of *Troglorhopalurus* these characters are likely an adapatation to cave dwelling and thus a case of convergence (Prendini *et al.*, 2009).

*Physoctonus debilis*, together with an undescribed species of *Physoctonus* (H. Yamaguti *et al.*, in prep.), are consistently recovered as a monophyletic group. Their relative position within the *Rhopalurus* group is less certain, morphological and molecular analyses are discordant. Under both equal and implied weighting of morphology, *Physoctonus* always was recovered as sister to all (*Rhopalurus* + *Centruroides*), excluding *Troglorhopalurus*. In all molecular and combined analyses *Physoctonus* is recovered as the sister group to a clade containing *R. laticauda*, *R. amazonicus*, *R. caribensis*, and *R. crassicauda*. Superficially, this is an unexpected relationship, however, given the sympatric distributions of the taxa the relationship could represent an ancient dispersal event. There are several synapomorphies in support of the genus: presence of the external accessory carina of the pedipalp femur, the absence of setae on the proximal dorsal fulcrae of the pectines, a slightly ovate telson (length is approximately 1.5X width), the absence of the ventrosubmedia carinae on metasomal segment V, and relatively flat sternite III (no anterior elevation).

The *R. laticauda* clade, comprised of *R. laticauda*, *R. caribensis*, *R. amazonicus*, and *R. crassicauda*, has recently been the subject of considerable speculation regarding the validity of species (Teruel & Tietz, 2008; Lourenço, 2008; Teruel & Roncallo, 2008). Lourenço (2008) suggested that *R. caribensis* is in fact merely a morph of *R. laticauda* rather than a distinct species. Teruel and Tietz (2008) suggested that *R. crassicauda* is a junior synonym of *R. laticauda*, but didn't formally propose the synonymy due to a lack of specimens to examine. Our morphological analysis failed to identify any consistent morphological differences among the three species. Additionally, there was very little genetic differentiation among them. These species are savannah specialists, and all

allopatrically distributed in northern South America. *Rhopalurus amazonicus* is found in "island" savannahs surrounded by the Amazon rainforest (Lourenço, 2008). *Rhopalurus caribensis* is found in the Llanos of the Magdalena, separated from *R. laticauda* by the Andes (Lourenço, 2008). One possible explanation for the lack of synapomorphies or genetic differentiation among these species is the short time period since the last glacial maximum, during which time the northern South American savannahs expanded and came into contact with one another (Lourenço, 2008). A second explanation is that the species distributions are not allopatric and there is still substantial gene flow between populations.

Though there is little genetic differentiation among the species in the *R. laticauda* complex, there are three distinct clades recovered in the both the molecular and combined parsimony analyses: *R. laticauda*, *R. caribensis*, and a clade containing *R. amazonicus* and *R. crassicauda*. While there is some genetic structure among clades, *R. amazonicus* and *R. crassicauda* are indistinguishable genetically or morphologically. We therefore recommend that *R. amazonicus* be considered a junior synonym of *R. crassicauda*.

The remaining species of *Rhopalurus* from central Brazil form two clearly defined, monophyletic clades. The large-bodied species, *R. rochae*, *R. pintoi*, and *R. agamemnon*, form a single clade. The remaining two species: *R. guanambiensis* and an undescribed species related to it (H. Yamaguti *et al.*, in prep), also form a monophyletic clade. Morphologically, *R. guanambiensis* is affiliated with the central Brazilian *Rhopalurus*. The topologies of the molecular and combined analyses differ regarding the placement of *R. guanambiensis*. The phylogenies recovered under parsimony criteria place *R. guanambiensis* sister to *Tityus*. The Bayesian total evidence analysis places *R.*

*guanambiensis* sister to the *Rhopalurus* group + *Centruroides*. This placement is more biologically realistic; the taxon is morphologically unusual for the group with its small body size and extremely modified (autapomorphic) telson shape, but is undoubtedly *Rhopalurus*-like. *Rhopalurus* is paraphyletic under its current definition; however, the Brazilian clades of the genus are currently under revision (H. Yamaguti *et al.*, in prep).

The importance of a clear understanding of the rhopalurusine species and relationships among them cannot be understated. Their unique stridulatory ability, disjunct biogeographic patterns, and the medical potential of their venoms are all candidates for future evolutionary, biogeographic and biomedical research. The distribution of the Rhopalurusinae in some of the most environmentally sensitive areas of the world (i.e. savannahs surrounding the Amazon Basin) make them prime candidates for studies on the impact of recent and future climate change.

**Taxonomy**

Subfamily **Rhopalurusinae** Bücherl, 1971

*Etymology*

Derived from the generic name *Rhopalurus* Thorell, 1876.

*Distribution*

Midwestern United States through northern South America (Belize, Colombia, Costa Rica, Ecuador (including the Galápagos), El Salvador, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela); western Brazil; Caribbean islands

(Bahamas, Cuba, Dominican Republic, Haiti, Jamaica, Lesser Antilles, Puerto Rico, US Virgin Islands).

*Diagnosis*

This New World buthid subfamily includes the following genera: *Centruroides*, *Rhopalurus*, *Heteroctenus*, *Physoctonus*, and *Troglorhopalurus*. The following characters can distinguish species belonging to this group: alpha-configuration of dorsal pedipalp femur trichobothria; presence of supernumerary granules on the internal surfaces of the fingers of the pedipalp chela; presence of a transverse row of median tubercles on the chelicerae; dorsobasal setation of the cheliceral fixed finger; tibial spurs absent; bifurcating prolateral spurs on the telotarsus (reduced in *Physoctonus*).

*Included Taxa*

*Centruroides* Marx, 1890; *Heteroctenus* Pocock, 1897; *Physoctonus* Mello-Leitao, 1934; *Rhopalurus* Thorell, 1890; *Troglorhopalurus* Lourenço, Baptista & Giupponi, 2004

## Genus ***Heteroctenus*** Pocock, 1897

*Etymology*

*hetero* = different, *cteni* = comb

*Distribution*

Greater Antilles: Cuba; Haiti; Dominican Republic (including Isla Saona); Puerto Rico: Isla Mona

*Diagnosis*

Large (50–70 mm), robust scorpions possessing a stridulatory organ on the dorsal surface of the pectinal combs. They can be readily identified on the basis of nine or more oblique

denticular rows with supernumerary granules on the pedipalp fingers and a robust metasoma that has slight to pronounced distal widening. The dorsal surfaces of the proximal pectinal teeth have regular striations with multiple nodules, and the pectines are proximally widened. They can be further separated from the genus *Centruroides* using a combination of the following characters: the presence of a basal lobe on the fixed finger of the pedipalp manus; dilation of the proximal pectinal lamellae; the presence of distinct, large and regular striations on the dorsal surface of the pectinal teeth; the presence of macrosetae on the dorsobasal surface of the pectinal teeth; a single, deep, median depression in the male pectinal plate; the lateral margins of sternite III form a smooth, raised keel; the absence of a subaculear tubercle on the telson.

*Type species*

The type species by original designation is *Heteroctenus junceus* (Herbst, 1800).

*Included Taxa*

We recognize the validity of the Greater Antilles genus *Heteroctonus* and transfer to it all species formerly assigned to *Rhopalurus* from the Greater Antilles: *Heteroctenus abudi* (Armas & Marcano Fondeur, 1987), **comb. nov.**; *Heteroctenus bonettii* (Armas, 1999), **comb. nov.**; *Heteroctenus garridoi* (Armas, 1974), **comb. nov.**; *Heteroctenus gibrarae* (Teruel, 2006), **comb. nov.**; *Heteroctenus granulimanus* (Teruel, 2006), **comb. nov.**; *Heteroctenus junceus* (Herbst, 1800), **comb. nov.**; *Heteroctenus princeps* (Karsch, 1879), **comb. nov.** *Rhopalurus virkkii* Santiago-Blay, 2010 is morphologically indistinguishable from *H. abudi*, with the exception of a slightly paler coloration. Furthermore, populations of *R. virkkii* from Isla Mona and *H. abudi* from western Dominican Republic are genetically identical. We therefore regard *R. virkkii* as a junior synonym of *H. abudi*:

*Rhopalurus virkkii* Santiago-Blay, 2010 = *Heteroctenus abudi* (Armas & Marcano Fondeur, 1987), **syn. nov.** We were unable to obtain specimens of the recently described Cuban species, *H. gibrarae* and *H. granulimanus*, for morphological examination or molecular analysis, and they were therefore omitted from the analyses. However, given the support for the monophyly of all species from the Greater Antilles they are most certainly assignable to *Heteroctenus*.

## Genus ***Centruroides*** Marx, 1890

*Etymology*

*kentri* = pointed apex, *ura* = tail, -*oides* = in the form of

*Distribution*

Midwestern United States through northern South America (Belize, Colombia, Costa Rica, Ecuador (including the Galápagos), El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela); Caribbean islands (Bahamas, Cuba, Dominican Republic, Haiti, Lesser Antilles, Puerto Rico, US Virgin Islands).

*Diagnosis*

Species belonging to this genus can be diagnosed on the basis of the following characters: converging internoventral and internodorsal carinae on the pedipalp patella; eight or more oblique denticular rows with supernumerary granules on the pedipalp fingers; pedipalp chela trichobothria *et* in line with *db* or between *db* and *est*; straight moveable pedipalp finger; proximal dentate margin of pedipalp fingers straight with fingers closed; dorsal surface of metasomal segment I is weakly granular; metasoma segment V length greater

than 2.5 times the width; metasoma length in males is more than 1.5 times the length of the prosoma and carapace.

*Type species*

*Centruroides exilicauda* (Wood, 1863)

*Included taxa*

*Centruroides alayoni* Armas, 1999; *Centruroides anchorellus* Armas, 1976; *Centruroides arctimanus* (Armas, 1976); *Centruroides baergi* Hoffmann, 1932; *Centruroides balsasensis* Ponce-Saavedra & Francke, 2004; *Centruroides bani* Armas & Marcano Fondeur, 1987; *Centruroides baracoae* Armas, 1976; *Centruroides barbudensis* (Pocock, 1898); *Centruroides bertholdii* (Thorell, 1876); *Centruroides bicolor* (Pocock, 1898); *Centruroides chamulaensis* Hoffmann, 1932; *Centruroides chiapanensis chiapanensis* Hoffmann, 1932; *Centruroides chiapanensis tapachualaensis* Hoffmann, 1932; *Centruroides elegans elegans* (Thorell, 1876); *Centruroides elegans insularis* Pocock, 1902; *Centruroides exilicauda* (Wood, 1863); *Centruroides exilimanus* Teruel & Stockwell, 2002; *Centruroides exsul* (Meise, 1934); *Centruroides fallassisimus* Armas & Trujillo, 2010; *Centruroides farri* Armas, 1976; *Centruroides flavopictus flavopictus* (Pocock, 1898); *Centruroides flavopictus meridionalis* Hoffmann, 1932; *Centruroides fulvipes* (Pocock, 1898); *Centruroides galano* Teruel, 2001; *Centruroides gracilis* (Latreille, 1804); *Centruroides griseus griseus* (C. L. Koch, 1844); *Centruroides griseus borinquensis* Armas, 1982; *Centruroides guanensis* Franganillo, 1930; *Centruroides hentzi* (Banks, 1900); *C. hirstutipalpus* Ponce-Saavedra & Francke, 2009; *C. hoffmanni* Armas, 1996; *Centruroides infamatus* (C.L. Koch, 1844); *Centruroides insulanus* (Thorell, 1876); *Centruroides jaragua* Armas, 1999; *Centruroides jorgeorum* Santiago-

Blay, 2009; *Centruroides koesteri* Kraepelin, 1912; *Centruroides limbatus* (Pocock, 1898); *Centruroides limpidus* (Karsch, 1879); *Centruroides luceorum* Armas, 1999; *Centruroides mahnerti* Lourenço, 1983; *Centruroides marcanoi* Armas, 1981; *Centruroides margaritatus* (Gervais, 1841); *Centruroides mariaorum* Santiago-Blay, 2009; *Centruroides meisei* (Hoffmann, 1939); *Centruroides melanodactylus* Teruel, 2001; *Centruroides morenoi* (Mello-Leitao, 1945); *Centruroides navarroi* Teruel, 2001; *Centruroides nigrescens* (Pocock, 1898); *Centruroides nigrimanus* (Pocock, 1898); *Centruroides nigropunctatus* Teruel, 2006; *Centruroides nigrovariatus* (Pocock, 1898); *Centruroides nitidus nitidus* (Thorell, 1876); *Centruroides nitidus taino* Armas & Marcano Fondeur, 1987; *Centruroides noxius* Hoffman, 1932; *Centruroides ochraceus* (Pocock, 1898); *Centruroides orizaba* Armas & Martin-Frias, 2003; *Centruroides ornatus* Pocock, 1902; *Centruroides pallidiceps* Pocock, 1902; *Centruroides platnicki* Armas, 1981; *Centruroides pococki* Sissom & Francke, 1983; *Centruroides polito* Teruel, 2007; *Centruroides rileyi* Sissom, 1995; *Centruroides robertoi* Armas, 1976; *Centruroides sasae* Santiago-Blay, 2009; *Centruroides schmidti* Sissom, 1995; *Centruroides sculpturatus* (Ewing, 1928); *C. serrano* Santibanez-Lopez & Ponce-Saavedra, 2009; *Centruroides sissomi* Armas, 1996; *Centruroides spectatus* Teruel, 2006; *Centruroides stockwelli* Teruel, 2001; *Centruroides suffusus* (Pocock, 1902); *Centruroides tecomanus* Hoffmann, 1932; *Centruroides testaceus testaceus* (DeGeer, 1778); *Centruroides testaceus arubensis* (Bakker, 1963); *Centruroides thorellii* (Kraepelin, 1891); *Centruroides tuxtla* Armas, 1999; *Centruroides underwoodi* Armas, 1976; *Centruroides vittatus* (Say, 1821)

## Genus ***Rhopalurus*** Thorell, 1890

*Etymology*

*rhopalo* = club, *ura* = tail

*Distribution*

South America: Brazil, Colombia, Guyana, Venezuela

*Diagnosis*

Species belonging to this genus exhibit a considerable range in size (30–110 mm), and can be diagnosed on the basis of the following characters: eight or more oblique denticular rows with supernumerary granules on the pedipalp fingers and a robust metasoma that has slight to pronounced distal widening, and the presence of a stridulatory organ on the dorsal surfaces of the pectines and the ventral surfaces of sternite III. The following characters are indicative of a stridulatory organ in *Rhopalurus*: dorsal surfaces of pectinal teeth have regular striations, but lack nodules; sternite III anteriolaterally granular. The following additional characters can be used to identify species belonging to this genus: metasomal segment II has complete lateral-median carinae; metasomal segment III has complete or reduced lateral-median carinae; the telson is spherical and always narrower than metasonal segment V. The fixed finger of the pedipalp chela has trichobothrium *db* situated between trichobothria *est* and *et*. Species can be further separated from *Physoctonus* on the basis of the following characters: in males the moveable finger of the pedipalp is ventrally curved when the fingers are closed, and the manus is incrassate; setae present on the proximal dorsal fulcra of the pectines.

*Type species*

*Rhopalurus laticauda* Thorell, 1876

*Included taxa*

*Rhopalurus agamemnon* (C.L. Koch, 1839); *Rhopalurus caribensis* Teruel & Roncallo, 2008; *Rhopalurus crassicauda* Caporiacco, 1947; *Rhopalurus guanambiensis* Lenarducci *et al*., 2005 *Rhopalurus lacrau* Lourenço & Pinto-da-Rocha 1997; *Rhopalurus laticauda* Thorell, 1876; *Rhopalurus pintoi* Mello-Leitão, 1933; *Rhopalurus rochae* Borelli, 1910. We regard *R. amazonicus* as a junior synonym of *R. crassicauda*: *Rhopalurus amazonicus* Lourenço, 1986 =*Rhopalurus crassicauda* Caporiacco, 1947, **syn. nov.** Morphological and molecular evidence obtained in this study suggest this genus is paraphyletic and requires further investigation. A manuscript on the taxonomy of this genus is in preparation by colleague Humberto Yamaguti at the University of Sao Paulo, Brazil, and has been submitted as part of his doctoral dissertation.

## Genus ***Physoctonus*** Mello-Leitao, 1934

*Etymology*

*physo* = inflate, *-ctonus* = killer

*Distribution*

South America: Brazil: Bahía, Piauí

*Diagnosis*

Species belonging to this genus are relatively small (20–25 mm), and can be diagnosed on the basis of the following characters: small, evenly spaced and sized supernumary granules on the pedipalp fingers; pedipalp trichobothrium *db* is situated between *est* and *et* or in line with *et*; in males the the pedipalps are not incrassate and the proximal dentate

margin is linear when the pedipalp fingers are closed; external accessory carinae of the pedipalp femur is present; presence of a simple (non-bifurcating) prolateral pedial spur; males do not have a smooth, raised area on sternite V; lateral median carinae on metasomal segments II and III are posteriorly restricted; metasomal segment V ventral submedian carinae are absent; telson is slightly ovate, length is approximately 1.5 times the width. These species lack stridulatory organs, the absence of which is indicated by the absence of striations on the dorsal surface of the proximal pectinal teeth, the ventrosubmedian surface of sternite III is smooth or weakly granular, and there is no anterior elevation on the ventral median carinae of sternite III. Additionally, the proximal dorsal fulcra of the pectines do not have setae.

*Type species*

*Physoctonus debilis* (C.L. Koch, 1840)

*Included taxa*

*Physoctonus debilis* (C.L. Koch, 1840)

## Genus ***Troglorhopalurus*** Lourenço, Baptista & Giupponi, 2004

*Etymology*

*troglo-* = cave, *rhopalurus* = after the genus *Rhopalurus* Thorell, 1890

*Distribution*

South America: Brazil: Bahía: Serra do Cristal cave formation

*Diagnosis*

Species belonging to the genus are cave dwelling and may exhibit troglomorphic characteristics. They are medium-sized (35–40 mm) and can be diagnosed on the basis of

the following characters: the presence of supernumary granules on the pedipalp fingers; pedipalp trichobothrium *db* is situated between *est* and *et* or in line with *et*; in males the the pedipalps are not incrassate and the proximal dentate margin is linear when the pedipalp fingers are closed; external accessory carinae of the pedipalp femur is present; the spiracle width is less than 3x the length; metasomal segment II lateral median carinae are present (complete or reduced); metasomal segment III is absent; metasomal segment V is elongate, length is  greater than 2.5 times the width. They do not possess a stridulatory organ, recognized by the presence of irregular striations on the proximal dorsal pectinal surfaces, and the ventrosubmedian surface of sternite III is smooth.

*Type species*

*Troglorhopalurus translucidus* Lourenço, Baptista & Giupponi, 2004

*Included taxa*

*Troglorhopalurus lacrau* Lourenço & Pinto-da-Rocha 1997, **comb. nov.**;

*Troglorhopalurus translucidus* Lourenço, Baptista & Giupponi, 2004. We formally transfer *R. lacrau* to *Troglorhopalurus* based on evidence presented above.

**Acknowledgements**

I would like to thank the following people for assistance with fieldwork and providing specimens: Ricardo Pinto de Rocha, Humberto Yamaguti, Francisca Almeida, Oscar Francke, Jeremy Huff, Kelvin Guerrero, Erich Volschenk, Camilo Mattoni, Adriano Kury, Jose Ochoa, and Alexander Tietz. I would like to thank the following people for assistance in lab work: Gena Esposito, Sarah Schoenbrun, Sylvia Johnson, Michelle Yim,

Ofelia Delgado and Tricia Rubi. A very special thank you to former post-doctoral researcher Erich Volschenk and Lorenzo Prendini who allowed the use of characters defined for an unpublished revision of the family Buthidae and contributed DNA sequences, and to Carsten Kamenz for allowing the use of unpublished SEM micrographs of pectines shown in the appendix. Humberto Yamaguti contributed a tremendous amount of effort in creating and scoring the morphological matrix and sequencing. Additionally, I would like to thank the following sources of funding for providing support for fieldwork, labwork and graduate fellowships: NSF Doctoral Dissertation Improvement Grant (0910147) to the Lorenzo Prendini and I, NSF GK-12 Fellowship to the last author, NSF DEB Grant (0413453) to Lorenzo Prendini, City University of New York/NSF AGEP Grant to the author, City University of New York Presidential Fellowship to the author, City University of New York College Now Fellowship to the author, Museum of Comparative Zoology Ernst Mayr Award to the author, American Museum of Natural History Theodore Roosevelt Award to the author, and a Richard Lounsbery Foundation award to Lorenzo Prendini.

**CHAPTER TWO:** Molecular phylogeny of the New World scorpion genus *Centruroides* Marx, 1890 inferred from nuclear and mitochondrial loci

**Abstract:** The scorpion genus *Centruroides* Marx, 1890 contains 71 species and 5 subspecies making it one of the most speciose scorpion genera worldwide. It is distributed from the southern United States to northern South America, throughout the Caribbean and the Galapagos. Historically, the genus has been taxonomically problematic due to a lack of diagnostic morphological characters and convergent ecomorphs. Several species groups have been proposed, however the neither the monophyly of the genus nor the relationships among the species has ever been tested phylogenetically. Five nuclear and mitochondrial loci were used to infer the first molecular phylogeny of the entire genus, confirming the monophyly and identifying four geographically delimited clades.

## Introduction

The New World scorpion genus *Centruroides* Marx, 1890 (family Buthidae Koch, 1837) is a morphologically diverse taxon (Fig. 9) that includes several highly venomous species (Dehesa-Davila and Possani, 1994). *Centruroides* scorpions primarily inhabit woody vegetation and are often found under bark on trees, hence the common name 'bark scorpion' (Polis, 1990). *Centruroides* is among the most diverse scorpion genera in the New World, comprising 71 described species and 5 subspecies in addition to several undescribed species (Fet & Lowe, 2000; Teruel 2001, 2006, 2007; Teruel & Stockwell, 2002; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009). These scorpions are sexually dimorphic, the males typically exhibiting elongation of the metasoma and long, slender pedipalp chelae; while females are generally more robust and carinate (Polis & Sissom, 1996). The greatest diversity of *Centruroides* occurs in Mexico; however, the genus is distributed from the southern United States throughout Central America to northern South America, the Galápagos, and throughout the Caribbean (Fig. 10) (Hoffmann, 1932; Gantenbein *et al.*, 2001; Sissom & Lourenco, 1987). Fossil *Centruroides* are known from amber from the Dominican Republic (Oligocene) and Chiapas, Mexico (Miocene/Oligocene) (Santiago-Blay and Poinar, 1993; Schawaller, 1979).

*Centruroides* is the most notorious North American scorpion genus due its medical importance. Six species, five endemic to Mexico, are known to be capable of lethal envenomations (Dehesa-Davila & Possani, 1994). Their affinity for dark, humid microhabitats often attracts them to debris in and around human dwellings, where their probability of interactions with humans increases (Simard & Watt, 1990). Annually

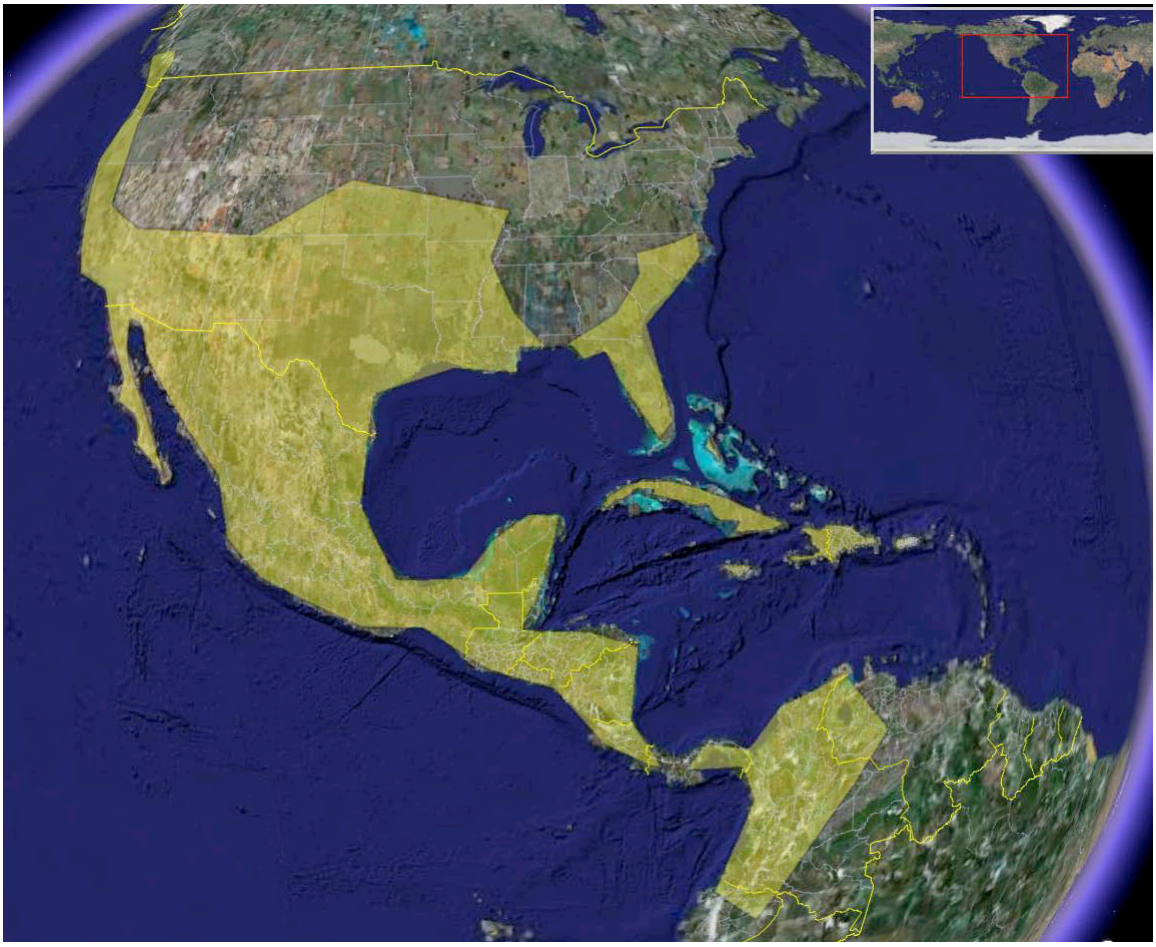
Figure 9. Representative species of the buthid scorpion genus *Centruroides* Marx, 1890. Top to bottom left: *C. thorellii* (Kraepelin, 1891), *C. hentzi* (Banks, 1900), C. *gracilis* Latreille, 1804, *C. limbatus* Pocock, 1898. Top to bottom right: *C. chamulaensis* Hoffmann, 1932, *C. nigrimanus* (Pocock, 1898), *C. sculpturatus* (Ewing, 1928), *C. vittatus* (Say, 1821).

**Figure 9**



Figure 10: Approximate distribution of the buthid scorpion genus *Centruroides* Marx, 1890.

**Figure 10**



100,000–200,000 *Centruroides* envenomations in Mexico result in up to 1,000 deaths (Dehesa-Davila and Possani, 1994). *Centruroides* envenomations clearly pose a severe public health problem. Species of *Centruroides* have also gained attention within the medical field for the pharmacological potential of their mammal-specific neurotoxic venom peptides (Lewis & Gracia, 2003; Fu *et al.*, 2007). *In vivo* experimentation with peptides isolated from *Centruroides* has shown promise in the development of novel immunosuppressants and brain cancer treatments (Lewis & Garcia, 2003; Fu *et al.*, 2007). Additionally, they may be effective in therapy aimed at autoimmune diseases such as multiple sclerosis, type I diabetes, psoriasis, and rheumatoid arthritis (Lewis and Garcia, 2003).

***Systematics***

The taxonomic history of *Centruroides* is long and complex, beginning with the generic name. Marx (1890) first published the name *Centruroides*, however for many years both preceding and subsequent to this publication, the name *Centrurus* Ehrenberg, 1829 was widely used in combination with species assignable to *Centruroides* (Francke, 1984; Fet & Lowe, 2000). Unfortunately, Ehrenberg (1829) failed to designate a type species for *Centrurus*. C.L. Koch (1838) subsequently used the name in combination with a species description thus designating *Centrurus galbineus* Koch, 1838 the type species. This designation further confounded the taxonomy of *Centruroides* however, as *Centrurus galbineus* is a junior synonym of the scorpionid species *Heterometrus* Ehrenberg, 1828 (Francke, 1984; Fet & Lowe, 2000). Adding to the complex taxonomic history of the group is the fact that many *Centruroides* species have either been described

as or transferred to and from the genus *Rhopalurus* Thorell, 1876 (Francke, 1978) because the two genera were never clearly distinguished from one another.

*Centruroides* has been problematic for taxonomists for additional reasons. The morphological characters traditionally used (morphometrics and color) often overlap between closely related species, are vaguely defined (Williams, 1980), or have been used rather *ad hoc* in geographically limited groups of species (Moreno, 1940; Muma, 1967; Armas, 1981, 1982, 1983; Sissom & Lourenço, 1987; Teruel & Stockwell, 2002; Teruel, 2005; Santiago-Blay, 2010). Many commonly used characters (i.e. subaculear tubercle development, granulation, pectinal tooth count, pedipalp denticular rows) vary within populations, hindering species identifications (Stahnke, 1971; Walker, 1973). Several species have extremely large distributions, suggesting they may be complexes of cryptic species, e.g. *Centruroides exilicauda* (Wood, 1863) and *Centruroides margaritatus* (Gervais, 1841) (Gantenbein *et al.*, 2001; Sissom & Lourenco, 1987). These include "species" with very discontinuous distributions, in which traditional characters have proven unreliable for delimitation (Gantenbein *et al.*, 2001; Sissom & Lourenco, 1987).

Historically, there have been few attempts made at revising *Centruroides*. Hoffmann (1932), considering all of the Mexican endemic species, published the most comprehensive revision of the genus, and proposed two subgroups: the "striped" group (*especies rayadas*), meaning those species with longitudinal stripes or bands along their tergites; and the "non-striped" group (*especies non-rayadas*), meaning those species with uniformly colored tergites. The non-striped group was comprised of 9 species and 6 subspecies and was divided into two subgroups based on the pedipalp finger dentition (Hoffmann, 1932). The striped group was comprised of 10 species and 8 subspecies and

was also divided into two subgroups based primarily on the pigmentation of the carapace (Hoffmann, 1932). Hoffman's (1932) revision was quite detailed and included identification keys, diagnoses, and photographs for all of the Mexican species. This revision was subsequently expanded upon to include additional described species, first by Gonzalez-Santillán (2004) and later by Ponce-Saavedra and Moreno-Barajas (2005). Although Hoffmann's (1932) groups may contain valid relationships, they may not be monophyletic due to morphological convergence as a result of similar ecological constraints.

In the next treatment of the genus, Stahnke and Calos (1977) produced the first key containing all recognized *Centruroides* species. The authors clearly stated, however, that they did not intend for their publication to serve as a revision of the group (Stahnke & Calos, 1977).

Several other publications have revised regional groups of *Centruroides*. Teruel (2001) revised the Cuban species and recognized three additional groups: "*arctimanus*", "*anchorellus*", and "*robertoi*". While these relationships may be valid within Cuba, paraphyly in the context of the entire genus is possible.

Other geographically-restricted revisions of *Centruroides* include: Costa Rica (Francke & Stockwell, 1987), South America (Sissom & Lourenço, 1987), Cuba (Moreno, 1940), the Dominican Republic (Armas, 1982; Teruel, 2005), Honduras (Teruel & Stockwell, 2002), Puerto Rico (Santiago-Blay, 2010), the Bahamas (Armas, 1981), Florida and the Keys (Muma, 1967) and the Lesser Antilles (Armas, 1983). Although many of these regional studies have been thorough, they have been limited by the omission of extralimital species and by a failure to consider the biological reality of

species with distributions extending beyond the geopolitical boundaries of the study. To date, there has been no comprehensive revision of *Centruroides* that considers the entire distribution and all of the described species.

According to Lourenço and Sissom (2000: P 117), "techniques such as electrophoresis, karyotyping, and DNA extraction may be essential to understanding species in this complex genus". Few modern analytical methods have been applied to the genus, a problem that extends to both phylogenetic analysis and biogeographical analysis. Teruel *et al.* (2006) used molecular data from a single gene (16S rDNA) to create a phylogeny of thirteen Cuban species, and concluded that the genus was not monophyletic. Towler *et al.* (2001), in a similar approach, used a single gene (16S) to propose a molecular phylogenetic hypothesis of 5 species from central Mexico. Unfortunately, single-gene phylogenetic analyses are problematic; the use of multiple loci, including at least one from the nuclear genome, is widely recommended (Brower *et al.*, 1994; Brower *et al.*, 1996; Doyle & Davis, 1998; Gatesy *et al.*, 2007). Ponce-Saavedra and Moreno-Barajas (2007) also made an attempt at using modern techniques for the Mexican species, but the molecular evidence indicated in their manuscript was neither provided nor accessioned in any public database. The same issues that have affected the taxonomic revisions have been carried over into the publications utilizing modern techniques: conducting an analysis of a paraphyletic group of species from a geopolitical region and then attempting to draw conclusions from the resulting phylogenetic hypothesis.

This study presents a solution to the problematic taxonomic history of *Centruroides*. Using molecular evidence we will test the monophyly of the genus and the

relationships among the species. We propose herein the first comprehensive phylogenetic hypothesis for the genus *Centruroides*.

## Materials and Methods

### *Taxon Sampling*

Each described species in the genus *Centruroides* was sampled from the type locality, or close vicinity (Appendix 5). Wherever possible, an additional specimen from an alternate locality was included. Excluded from this study are species from Cuba that could not be obtained due to permit restrictions by the Cuban government (*C. navarroi* Teruel, 2001, *C. melanodactylus* Teruel, 2001, *C. galano* Teruel, 2001, *C. polito* Teruel, 2007, *C. spectatus* Teruel, 2006, *C. baracoae* (Armas, 1976), *C. stockwelli* Teruel, 2001, *C. nigropunctatus* Teruel, 2006, *C. robertoi* Armas, 1976, *C. alayoni* Armas 1999); *Centruroides exsul* (Meise, 1934) from the Galápagos; and *Centruroides underwoodi* Armas, 1976 from Jamaica, only known from two specimens. All described species from the sister genus *Heteroctenus* Pocock, 1897 were also included except two Cuban endemics which could not be obtained: *Heteroctenus granulimanus* (Teruel, 2008) and *Heteroctenus gibrarae* (Teruel, 2008). Additionally, we selected outgroups from other New World buthid genera on the basis of the proposed monophyly of the New World buthids (Fet *et al.*, 2003): *Tityus* C.L. Koch, 1836, *Rhopalurus* Thorell, 1876, and *Zabius* Thorell, 1893. The Australasian buthid species *Isometrus maculatus* (DeGeer, 1778) was used to root all trees. This taxon belongs to the buthid sufamily Isometrini Kraepelin, 1891, the putative sister to the New World buthids (Kraepelin, 1899; Fet *et al.,* 2003).

### *Field methods*

Specimens were collected in the field using ultraviolet lights and preserved by submersion of live animals in 95% ethanol, and subsequently injected with ethanol to improve the internal preservation. Specimens were then stored at -20°C at the American Museum of Natural History.

### *Laboratory methods*

Genomic DNA was extracted from muscle tissue from the fourth leg of each specimen using a Qiagen DNEasy Blood and Tissue extraction kit according to the manufacturer's protocol. Extracted DNA was amplified for five gene regions in overlapping fragments using universal eukaryote and scorpion-specific primers (see Table 3). Five gene loci were selected for this study, based on their ability to provide resolution at various taxonomic levels and their proven utility in other studies of scorpions (Prendini *et al.*, 2003): a mitochondrial protein-coding gene (Cox1), mitochondrial structural genes (12S rDNA, 16S rDNA), and nuclear structural genes (18S rDNA, 28S rDNA) (Arnedo *et al.*, 2002; Giribet *et al.*, 2001; Harrison *et al.*, 1987; Hayashi, 1996; Hillis & Dixon, 1991; Wahlberg & Zimmermann, 2000). Polymerase Chain Reaction was performed on an Epicenter thermocycler (Eppendorf) using GoTaq polymerase (Promega). Reactions were verified on a 1.2% w/v agarose gel stained with SYBR Safe DNA gel stain (Invitrogen), and subsequently purified using the Ampure (Agencourt) DNA purification kit on a Biomek NX robot (Beckman–Coulter). Cycle sequencing was conducted using Big Dye v1.1 chemistry kit and automated Sanger

**Table 3:** Primers used for PCR amplification of five gene loci used in a phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890.

| Gene | Primer | Sequence | References (other names) |
|---|---|---|---|
| 12S | 12Sai | AAACTAGGATTAGATACCCTATTAT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-N-14588) |
| | 12Sbi | AAGAGCGACGGGCGATGTGT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-J-14233) |
| 16S | 16Sar | CGCCTGTTTATCAAAAACAT | Simon *et al.,* 1994 (LR-N-13398) |
| | 16Sbr | CTCCGGTTTGAACTCAGATCA | Simon *et al.,* 1994 (LR-J-12887) |
| 18S | 18S1F | TACCTGGTTGATCCTGCCAGTAG | Prendini *et al.,* 2005 |
| | 18S5R | CTTGGCAAATGCTTTCGC | Prendini *et al.,* 2005 |
| | 18S3F | GTTCGATTCCGGAGAGGGA | Prendini *et al.,* 2005 |
| | 18Sbi | GAGTCTCGTTCGTTATCGGA | Prendini *et al.,* 2005 |
| | 18SA2.0 | ATGGTTGCAAAGCTGAAAC | Prendini *et al.,* 2005 |
| | 18S9R | GATCCTTCCGCAGGTTCACCTAC | Prendini *et al.,* 2005 |
| 28S | 28Sa | GACCCGTCTTGAAGCACG | Nunn *et al.,* 1996 (D3A |
| | 28Sbout | CCCACAGCGCCAGTTCTGCTTACC | Prendini *et al.,* 2005 |
| Cox1 | LCO | GGTCAACAAATCATAAAGATATTGG | Folmer *et al.,* 1994 (LCO-1490-J-1514) |
| | HCOoutout | GTAAATATATGRTGDGCTC | Prendini *et al.,* 2005 |
| | LE1R | TCCATTCCCACAGTAAACATATG | |
| | HCOEXTERNA | GAAGTTTATATTTTAATTTTACCTGG | |
| | HCOEXTERNB | CCTATTGAWARAACATARTGAAAATG | |

sequencing of single-stranded DNA performed on an Applied Biosystems, Inc. [ABI] DNA Analyzer 3730xl (Sanger *et al.*, 1997). Paired strand reads were aligned using Sequencher v4.8 (Gene Codes Corp.) and edited by hand. Sequences are accessioned in GenBank (Appendix 5).

Multiple sequence alignments for individual gene partitions was performed in MAFFT (Katoh *et al.*, 2005) using the G-INS-i strategy (recommended by the authors for less than 200 sequences with global homology) and PAM1/K=2 matrix parameter (recommended by the authors for aligning closely related sequences). All loci were aligned, however there was no length variation in Cox1, negligible length variation in 18S and 28S (<10 nucleotides), and little length variation in 12S and 16S (<20 nucleotides). The resulting alignments were then concatenated and the matrices were assembled in Geneious v5.1 (Biomatters, Ltd.).

***Phylogenetic analysis methods***

Molecular data from the five loci (12S, 16S 18S, 28S, Cox1) was concatenated and analyzed under Bayesian and parsimony criteria. Geneious v5.1 (Biomatters, Ltd.) was used to concatenate the loci datasets and construct matrices.

A parsimony analysis was conducted in TNT v1.1 using the 'New Technology Search' option with 10,000 random addition replicates, 'Tree Drift' (Goloboff, 1999), and 'Ratchet' (Nixon, 1999). Nodal support values were calculated from 1000 non-parametric bootstrap replicates computed in TNT.

The Bayesian analysis was performed in MrBayes (Ronquist and Huelsenbeck, 2003) on the CIPRES supercomputing cluster (Miller *et al.,* 2009) in two independent

runs for 50 million generations, with 4 chains, sampling every 5000 generations. MrModeltest2 v2.3 (Nylander, 2004), employing Akaike information criteria, (Akaike, 1973) was used to determine the best fitting model of DNA substitution for each gene and codon position (*CoxI*) (Table 4). In cases where the best fitting model included both the Γ and invariable sites (I) parameters, the next best fitting model was selected to avoid issues stemming from the non-independence of the Γ and I parameters (Stamatakis, 2006). Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (Rambaut & Drummond, 2007), and convergence was assessed by the standard deviations of the split frequencies in AWTY (Nylander *et al.*, 2008). The first 5 million generations was discarded as burn-in. A maximum clade credibility tree was computed from the post-burn-in trees in TreeAnnotator v1.6.1 (Rambaut & Drummond, 2007).

In order to identify rogue taxa (Sanderson & Schaffer, 2002), which may have an impact on either the resulting topologies (Thompson & Schaffer, 2010) or the measures of support (Pattengale *et al.*, 2010), the Leaf Stability Index (LSI) (Thorley & Page, 2000) was calculated from the resulting trees in Phyutility v2.2 (Smith & Dunn, 2008). The effect of the individual gene partitions on the concatenated parsimony tree was assessed using Partitioned Bremer Support metrics (Baker & DeSalle, 1997) using TreeRot v3 (Sorenson & Franzosa, 2007) implemented in PAUP* v4b10 (Swofford, 2002). Resulting phylogenies were manipulated and rendered in FigTree v1.2.2 (Rambaut, 2009).

**Table 4.** Best-fitting models of nucleotide substitution for five loci as calculated in MrModelTest2 v2.3 (Nylander, 2008) for incorporation into a phylogenetic analysis of buthid scorpion genus *Centruroides* Marx, 1890. For Cytochrome *c* oxidase subunit I (*Cox1*), the best model was determined for codon position. The partitions indicated with an asterisk (*) are the second best model following the exclusion of models that included both the Γ and I parameters.

| Partition | Model | -lnL | K | AIC | delta | Weight | CumWeight |
|---|---|---|---|---|---|---|---|
| COI-1* | GTR+G | 7681.7861 | 9 | 15381.5723 | 125.4102 | 3.63E-28 | 1 |
| COI-2* | GTR+G | 7682.0879 | 9 | 15382.1758 | 124.1113 | 7.11E-28 | 1 |
| COI-3* | GTR+G | 7718.0913 | 9 | 15454.1826 | 126.6641 | 2.04E-28 | 1 |
| 12S* | GTR+G | 3123.1851 | 9 | 6264.3701 | 0.4082 | 0.4378 | 0.9748 |
| 16S* | HKY+G | 4110.4077 | 5 | 8230.8154 | 24.3926 | 2.55E-06 | 1 |
| 18S | GTR+I | 2680.2502 | 9 | 5378.5005 | 0 | 0.3848 | 0.3848 |
| 28S | GTR+I | 995.896 | 9 | 2009.792 | 0 | 0.5883 | 0.5883 |

**Results**

A total of 131 terminals (109 ingroup samples, 22 outgroup samples) were included in the analyses. The aligned length of the concatenated dataset was 4,250 nucleotides, and included 3,083 constant characters, 180 variable parsimony-uninformative characters, and 943 variable parsimony-informative characters. The average nucleotide composition of the concatenated dataset was as follows: 26% adenine, 18% cytosine, 25% guanine, and 31% thymine.

Parsimony analysis of the concatenated dataset in TNT returned a single most parsimonious tree with a length of 9824, a consistency index of 0.20, and a retention index of 0.62 (Fig. 11). The topology of the most parsimonious tree was congruent with the topology recovered under Bayesian criteria, however there were some rearrangements among the outgroup taxa and in the placement of *Centruroides koesteri* Kraepelin, 1912. The Bayesian analysis of the concatenated dataset, partitioned by loci and by codon for Cox1 was run for 50-million generations, with the first 10-million generations discarded as burn-in. The equivalent sample size for all post-burnin parameters was >300. The maximum clade credibility (MCC) tree with posterior probabilities of clade support from the Bayesian analysis conducted in MrBayes is shown in Figure 12.

*Centruroides* is recovered as a highly supported monophyletic group in all analyses, sister to the genus *Heteroctenus. Centruroides* is comprised of four distinct, geographically delimited clades, each with strong support (Table 5, Fig. 11). An early divergence within *Centruroides* gives rise to two groups: a clade of species from landmasses on or bordering the Caribbean plate (Greater Antilles, Yucatan Peninsula and Chortis Block) and a continental clade of species from North America and Mesoamerica.

Figure 11: Parsimony cladogram for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from five nuclear and mitochondrial loci in TNT (Goloboff *et al.*, 2000). Partitioned Bremer support (Baker & DeSalle, 1997) node label diagrams below each node. Support for gene partition is black if positive, white if zero or negative. Order of loci indicated in each node diagram (left to right): Top row: 12s, 16s, Cox1. Bottom row: 18s, 28s. Nodal support values to the right of each node are non-parametric bootstraps. Taxa colored in red have reported lethal envenomations.

**Figure 11- Part 1**

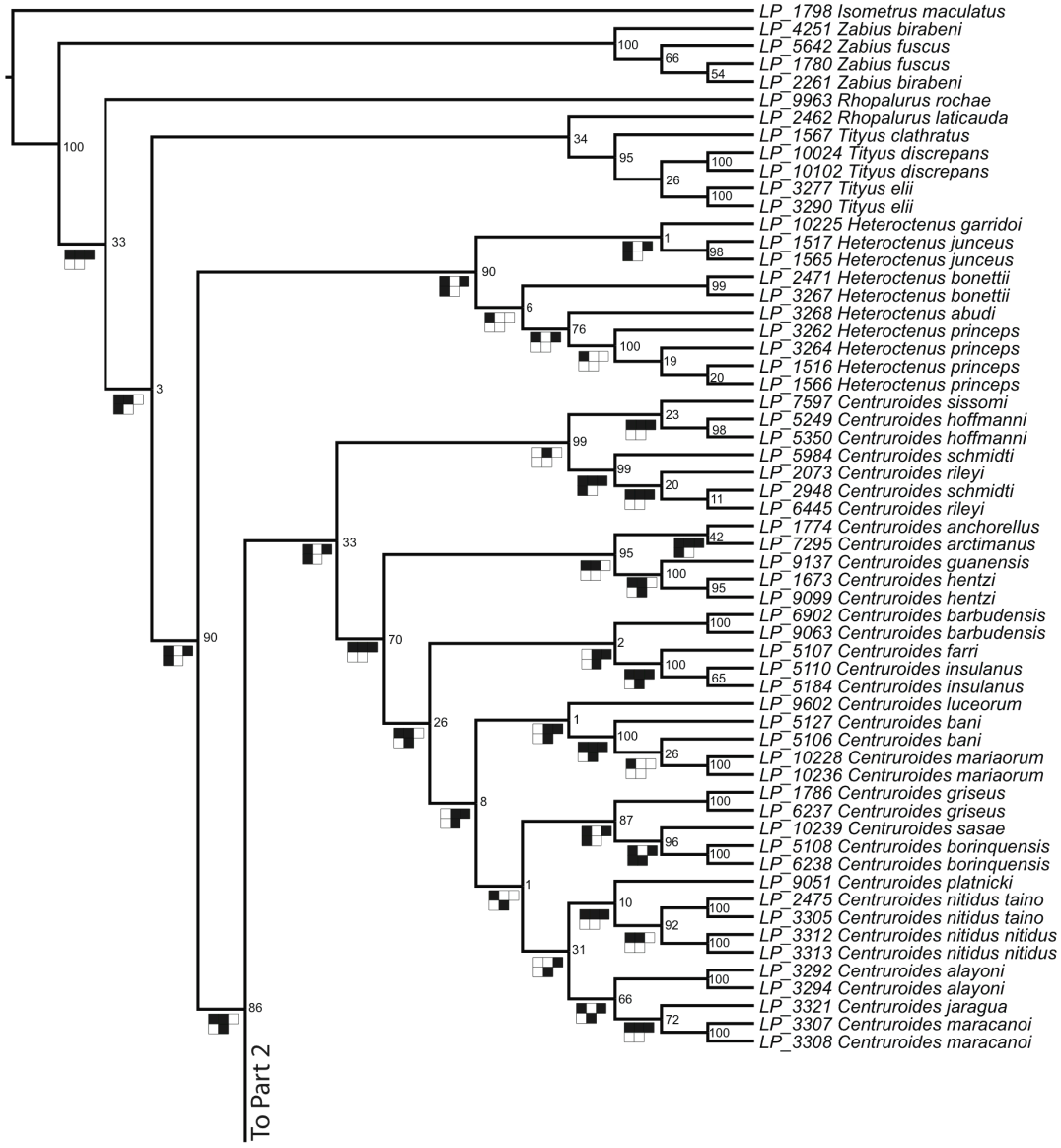


**Figure 11- Part 2**

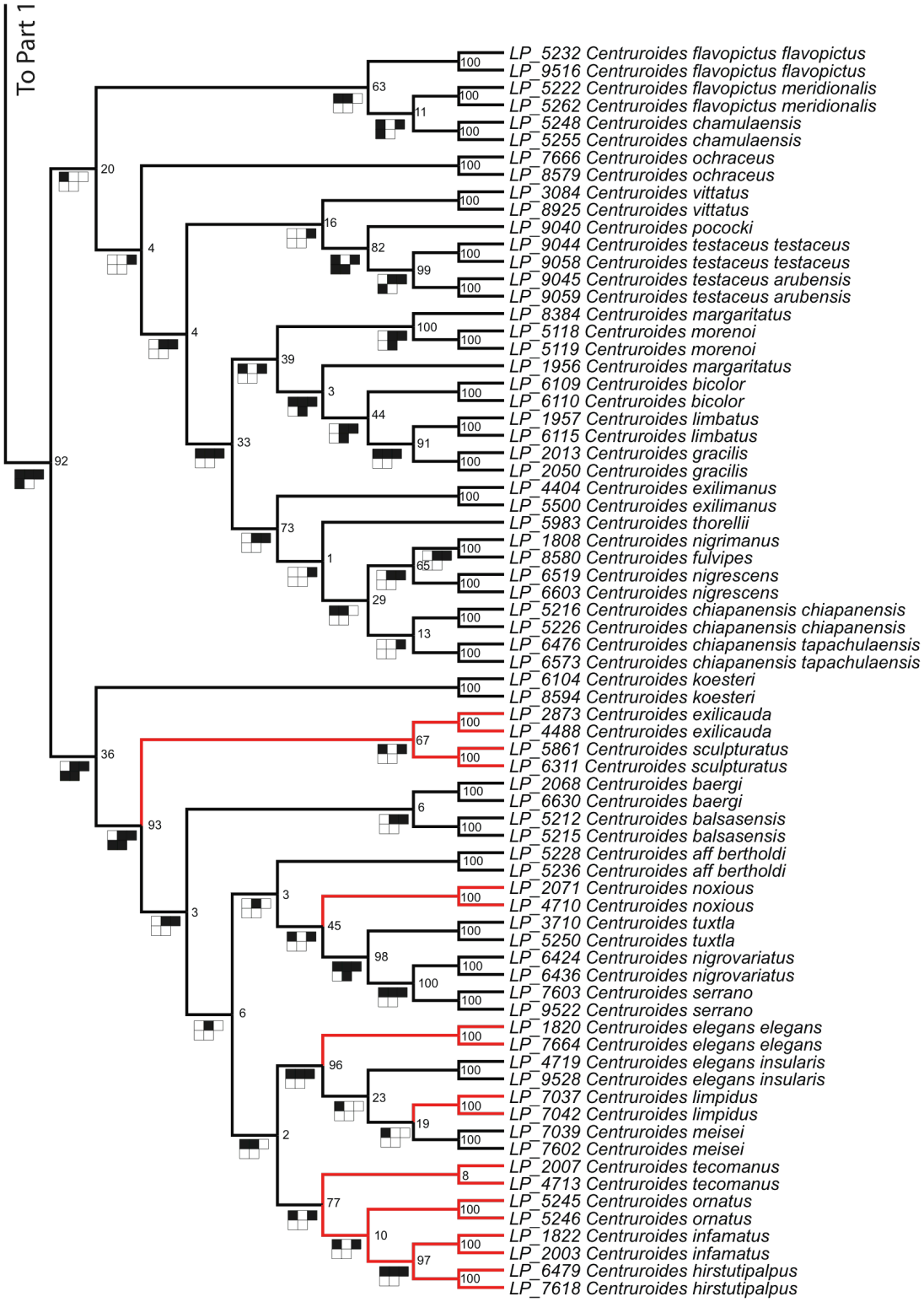


**Table 5.** Major clades in the buthid scorpion genus *Centruroides* Marx, 1890, identified in phylogenetic analyses of molecular data, and the species assigned to each. Species not included in the analyses are indicated with an asterisk. The species groups defined by Hoffmann are indicated next to the relevant species with the following codes: striped *limpidus-elegans* (LE), striped *suffusus-infamatus* (SI), non-striped *bertholdii* (NB), non-striped *gracilis* (NG), non-striped *thorellii* (NT).

**North American Clade**

*C. baergi* Hoffmann, 1932
*C. balsasensis* Ponce-Saavedra & Francke, 2004
*C. elegans elegans* (Thorell, 1876) [LE]
*C. elegans insularis* Pocock, 1902 [LE]
*C. exilicauda* (Wood, 1863) [SI]
*C. hirstutipalpus* Ponce-Saavedra & Francke, 2009
*C. infamatus* (C.L. Koch, 1844) [SI]
*C. limpidus* (Karsch, 1879) [LE]
*C. meisei* (Hoffmann, 1939) [LE]
*C. nigrovariatus* (Pocock, 1898) [SI]
*C. noxius* Hoffman, 1932 [NB]
*C. orizaba* Armas & Martin-Frias, 2003 *
*C. ornatus* Pocock, 1902 [SI]
*C. pallidiceps* Pocock, 1902 [LE]
*C. sculpturatus* (Ewing, 1928)
*C. serrano* Santibanez-Lopez & Ponce-Saavedra, 2009
*C. suffusus* (Pocock, 1902) [SI]
*C. tecomanus* Hoffmann, 1932
*C. tuxtla* Armas, 1999

**Mesoamerican Clade**

*C. bicolor* (Pocock, 1898)
*C. chamulaensis* Hoffmann, 1932 [NT]
*C. chiapanensis chiapanensis* Hoffmann, 1932 [NB]
*C. chiapanensis tapachualaensis* Hoffmann, 1932 [NB]
*C. exilimanus* Teruel & Stockwell, 2002
*C. fallassisimus* Armas & Trujillo, 2010
*C. flavopictus flavopictus* (Pocock, 1898) [NB]
*C. flavopictus meridionalis* Hoffmann, 1932 [NB]
*C. fulvipes* (Pocock, 1898) [NG]
*C. gracilis* (Latreille, 1804) [NG]
*C. limbatus* (Pocock, 1898)
*C. mahnerti* Lourenço, 1983
*C. margaritatus* (Gervais, 1841) [NB]
*C. morenoi* (Mello-Leitao, 1945)
*C. nigrescens* (Pocock, 1898) [NG]
*C. nigrimanus* (Pocock, 1898) [NG]
*C. ochraceus* (Pocock, 1898) [NB]
*C. pococki* Sissom & Francke, 1983
*C. testaceus testaceus* (DeGeer, 1778)
*C. testaceus arubensis* (Bakker, 1963)
*C. thorellii* (Kraepelin, 1891) [NT]
*C. vittatus* (Say, 1821) [SI]

Figure 12: Maximum clade credibility tree for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from five nuclear and mitochondrial loci in MrBayes (Ronquist & Huelsenbeck, 2003). Node values are posterior probabilities. Branch color's indicate the major *Centruroides* clades recovered: Red- Yucatan/Chortis Block, Blue- Greater Antilles, Orange- Mesoamerica, Green- North America. Columns to the right of taxon labels: Left column- leaf stability index (black, 1.0; dark gray, 0.95–1.0; white, <0.95); Right column- specimen localities (black: Australasia, white: South America, green: North America, yellow: Lesser Antilles, blue: Greater Antilles, red: Yucatan/Chortis Block, orange: Central America).

# Figure 12- Part 1

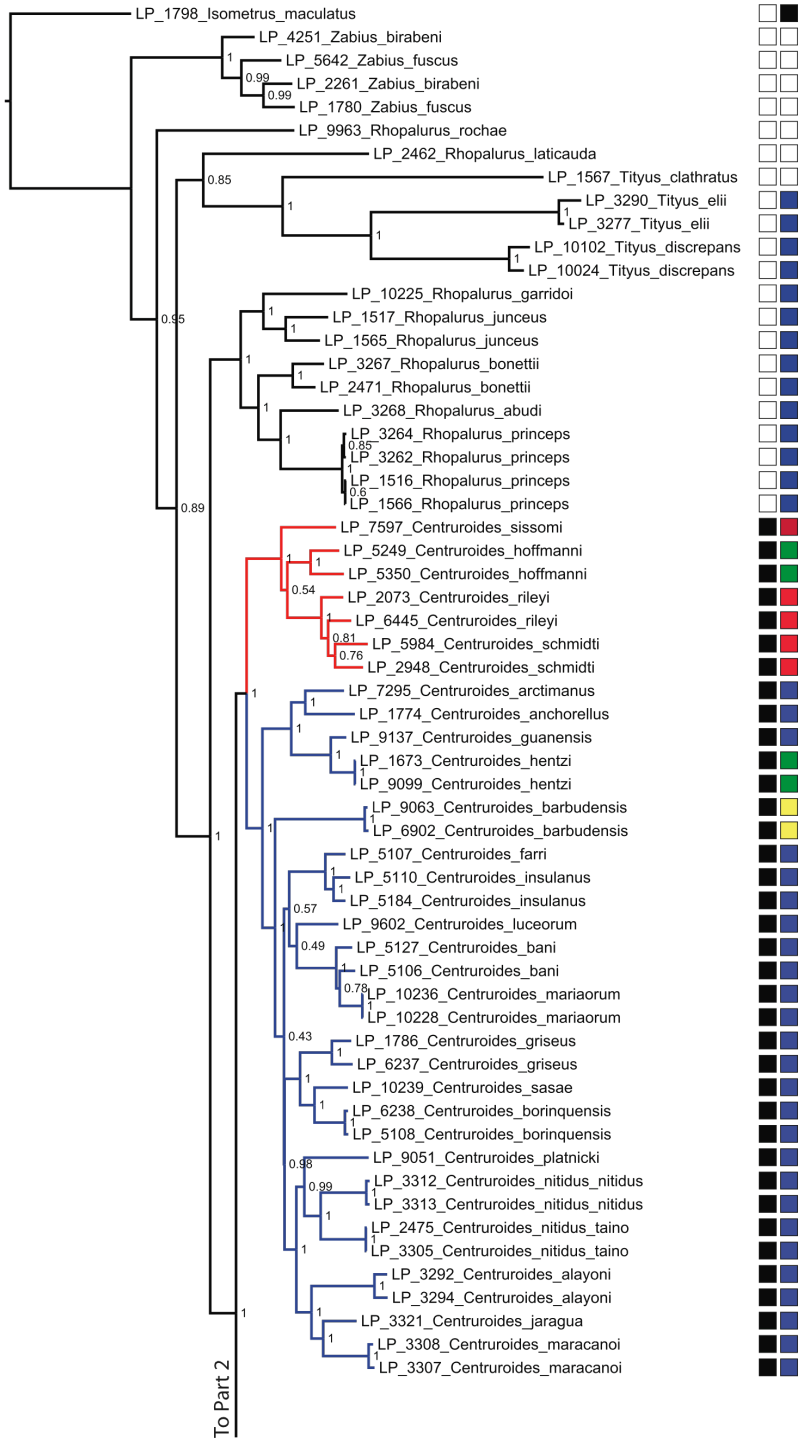
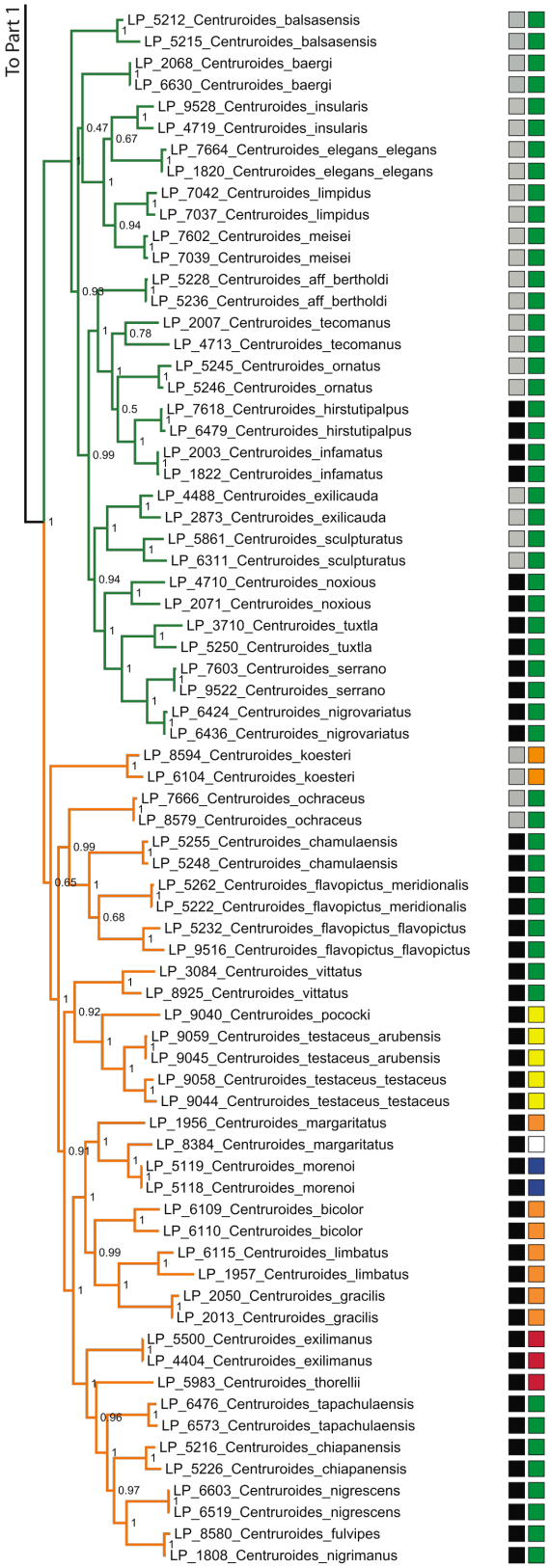


**Figure 12- Part 2**



The Caribbean plate is further divided into a clade of Greater Antilles species, sister to a clade restricted to the Yucatan Peninsula and the Chortis Block. The Chortis Block is defined as the part of Central America south of the Motagua fault of Guatemala and north of latitude 12°30' N (Dengo, 1969; Dengo & Bohnenberger, 1969). The political boundaries of Honduras, El Salvador, northern Nicaragua and southeastern Guatemala are included in the Chortis Block. The continental clade is also divided into two clades: a clade of species from Mesoamerica and the Lesser Antilles, recovered as sister to a clade of species from North America (north of the Isthmus of Tehuantepec). There was very little discordance among the resulting ingroup topologies from the Bayesian and parsimony criteria.

Terminal taxon rearrangements in the resulting topologies were assessed using the Leaf Stability Index (LSI) (Fig. 12). The LSI for all *Centruroides* species is relatively high (>0.95), with the exception of *Centruroides koesteri* (0.85). This is largely due to the instability of the position of this species within the resulting topologies.

**Discussion**

Contrary to the findings of Teruel *et al.* (2006), who concluded that *Centruroides* is paraphyletic with respect to the Greater Antilles *Rhopalurus*, the results of the present study conclusively demonstrate the monophyly of *Centruroides*. The study by Teruel *et al.* (2006) was inherently flawed in two respects. It was based on a single gene fragment and limited to taxa occurring in Cuba, a paraphyletic taxon sample.

Additionally, these results unexpectedly identify four geographically delimited monophyletic lineages within *Centruroides*: North American, Mesoamerican, Caribbean,

and Yucatan/Chortis Block. Though morphological similarities among species within each of the four lineages have been observed, it has been difficult using traditional methods to assess whether these similarities were the result of convergence or whether they represented valid relationships (Lourenco & Sissom, 2000). The clade assignments for each species are given in Table 5.

Species of *Centruroides* continue to be described at an ever-increasing rate despite the fact that the genus has never been demonstrated to be monophyletic (Teruel *et al.*, 2006). The only morphological character consistently supporting the monophyly of *Centruroides* is the sexually dimorphic elongation of the male metasoma (Polis & Sissom, 1996). There is considerable variation in this character, however, and some species have weak sexual dimorphism with minimal metasomal elongation (Teruel & Kovařík, 2010).

Perhaps even more surprising than the geographical structure of the *Centruroides* clades, are the few species that are the exceptions to the generalized distribution of the clade to which they belong. These exceptions vividly reveal the convergent evolution of ecomorphotypes within this group of scorpions. *Centruroides vittatus* (Say, 1821) has long been considered the sister taxon of *Centruroides suffusus* Pocock, 1902 on the basis of similar color morphology and a sympatric zone of distribution in the Chihuahuan desert (Armas & Matrin-Fris, 2000; Teruel & Kovařík, 2010). However, the results of the phylogenetic analysis place the two taxa in separate clades with very high support values. *Centruroides vittatus* is grouped well within the Mesomerican clade while *C. suffusus* is a member of the North American clade. This example of convergence of body form in

scorpions occupying the same habitat (ecomorphotype) has been observed in other scorpion groups (Prendini, 2001c).

Another example of ecomorphotype convergence is *C. thorellii* (Kraepelin, 1891), the smallest species in the Mesoamerican clade, which was long considered to belong to a group of small, heavily mottled, and elongate species from the Yucatan Peninsula and the Chortis Block (Sissom, 1995). While little is generally known about the microhabitat usage of scorpions, this group of species, informally termed the "*thorellii* group", is thought to be bromeliad specialists and are often collected from high in the canopy (O. Francke, pers. comm.). The strongly supported placement of *C. thorellii* within the Mesoamerican clade and separate from all the other "*thorellii* group" species is also supported by the lobate telson morphology, which is similar to that of other Mesoamerican species. The remaining species of the "*thorellii* group" form a highly supported clade endemic to the Yucatan Peninsula and Chortis Block, though the "*thorellii* group" is a now an obvious misnomer.

Leaf stability provides a measure of the stability of individual leaves or terminals within a given tree topology or set of trees (Thorley & Page, 2000). In particular, it allows for the identification of phylogenetically unstable taxa (Thorley & Page, 2000). The calculated leaf stability index is displayed as boxes to the right of the taxon names in Figure 12. Black boxes represent a high degree (> 0.95) of stability for that leaf or taxon, gray boxes represent a lower degree of stability, while white represents poor stability. Within *Centruroides*, there is a high degree of stability among the taxa. The only exception to this is *Centruroides koesteri* Kraepelin, 1912, an enigmatic species endemic to Costa Rica and Nicaragua. The taxon is recovered in two positions within

*Centruroides*: sister to the North American clade (parsimony analysis), or sister to the Mesoamerican clade (Bayesian analysis). The highest branch support, indicating the most stable position for *C. koesteri*, is as sister to the Mesoamerican clade. This relationship is more plausible given the Mesoamerican (Costa Rica and Nicaragua) distribution of *C. koesteri* (Francke, 1978; Viquez, 1999), however the addition of morphological data may clarify the placement of this species.

The North American clade contains all of the species implicated in lethal envenomations (Fig. 11, lethal envenomations in red). Relationships among species within the North American clade are incongruent among the analyses and many of the nodes are weakly supported. The low support among species relationships makes it difficult to infer whether there has been repeated evolution of increased venom toxicity or a single evolutionary event followed by subsequent losses of venom toxicity. The toxicity of venom and the recorded lethal envenomations may be confounded by the identifications of the specimens when envenomations occur (Shalita & Wells, 2007). Specimens obtained for this study were frequently (>50%) misidentified using traditional morphological characters and the rate of species misidentification by non-experts is likely considerably greater (Eickstedt *et al.*, 1996). Additionally, toxicological studies of the venom have largely been limited to species from which lethal envenomations have been reported.

The results of this study demonstrate that the *Centruroides* "striped" group, proposed by Hoffmann (1932) and subsequently expanded upon by several others (Gonzalez-Santillán, 2004; Ponce-Saavedra & Moreno-Barajas, 2005), is a valid group and effectively represents the North American clade recovered in this analysis. However

the primary character used to define the group, the presence of a pair of lateral bands or stripes on the tergites, is not a synapomorphy. Additionally, *C. vittatus* must be excluded from the group and *Centruroides noxius* Hoffmann, 1932 must be included. The "striped" subgroups are both invalidated. The "non-striped" group proposed by Hoffmann (1932) is more problematic but effectively represents a combination the Mesoamerican and Yucatan/Chortis clades. The "*thorellii*" subgroup is somewhat congruent with the Yucatan/Chortis clade from this analysis, however nearly half of the taxa currently in the group, *C. thorellii*, *Centruroides chamulaensis* Hoffmann, 1932, and *Centruroides tuxtla* Armas, 1999, must be excluded. The Mesoamerican group is somewhat congruent with the "*bertholdi*" and "*gracilis*" subgroups but neither of these groups includes taxa from the Mesoamerican clade with distributions outside of Mexico.

Within the Caribbean clade there are three major, geographically structured, clades recovered with high support in both analyses: a clade from Cuba and the Bahamas Bank, a clade from Jamaica, and a clade from Hispaniola and Puerto Rico. This pattern of inter-island diversification with little intra-island migration has been observed, to some extent, in other Caribbean endemics including crickets (Oneal, 2009), *Anolis* (Losos, 2009), and spiders (Crews & Gillespie, 2010). The Cuban subgroups proposed by Teruel (2001) could not be evaluated since most of the taxa were not included in this study. However, the endemic Cuban taxa obtained (*Centruroides anchorellus* Armas, 1976 and *Centruroides arctimanus* (Armas, 1976)) formed a monophyletic clade sister to taxa from the Bahamas and Florida (*Centruroides hentzi* (Banks, 1900) and *Centruroides guanensis* Franganillo, 1930).

The aims of this study were to assess the monophyly of the genus *Centruroides* and to determine the major species groups within the genus. Using molecular evidence from mitochondrial and molecular loci, we have conclusively demonstrated that *Centruroides* is a monophyletic genus, and have furthermore identified four major geographically delimited species groups. The identification of the major groups and resolution of the phylogeny represents a major step towards understanding the evolution of this diverse group of scorpions.

**Acknowledgements**

I would like to thank the following people for help in the field and for providing specimens: Lorenzo Prendini, Francisca Almeida, Oscar Francke, Jeremy Huff, Kelvin Guerrero, Camilo Mattoni, Adriano Kury, and Alexander Tietz. I would like to thank the following people for assistance in lab work: Gena Esposito, Sarah Schoenbrun, Sylvia Johnson, Michelle Yim, Ofelia Delgado, and Tricia Rubi. I would like to thank the following sources of funding for providing support for fieldwork, labwork and graduate fellowships: NSF Doctoral Dissertation Improvement Grant (0910147), NSF GK-12 Fellowship, NSF DEB Grant (0413453) awarded to Lorenzo Prendini, City University of New York/NSF AGEP Grant, City University of New York Presidential Fellowship, City University of New York College Now Fellowship, Museum of Comparative Zoology Ernst Mayr Award, American Museum of Natural History Theodore Roosevelt Award, and the Richard Lounsbery Foundation, awarded to Lorenzo Prendini. Last but not least,

thank you to my doctoral advisor, Lorenzo Prendini, whose support and guidance made this work possible.

**CHAPTER THREE:** A total evidence phylogenetic analysis of the scorpion genus *Centruroides* Marx, 1890 (Scorpiones: Buthidae) with implications for widespread cryptic diversity

**Abstract:** The taxonomy of the scorpion genus *Centruroides* Marx, 1890 has been hampered by conservative morphology. The characters traditionally used to define *Centruroides* species rely heavily on morphometrics and color, and a complete revision of the genus has not been undertaken in over a century. In order to undertake a comprehensive phylogenetic analysis of the genus, a barcoding approach was used to define OTUs for morphological character scoring. The approach utilized reciprocal illumination of molecular, morphological and locality information to identify 98 OTUs, scored for 112 morphological characters. Parsimony analysis of the morphological dataset failed to recover the four clades identified in a previous analysis of molecular data. Topologies obtained by analyses of total evidence (morphological and molecular datasets) under Bayesian and parsimony optimality criteria differed in the placements of *Centruroides exsul* (Meise, 1934) and *Centruroides koesteri* Kraepelin, 1912, and in recovering a monophyletic (Bayesian) or paraphyletic (parsimony) Mesoamerican Clade B. The Bayesian total evidence analysis recovered four clades identified in previous molecular phylogenies, with high nodal support values. The results of the analyses suggest a considerable amount of cryptic diversity within the genus.

## Introduction

The buthid scorpion genus *Centruroides* Marx, 1890 is a diverse taxon, distributed from northern South America to the southern United States, throughout the Caribbean islands and the Galápagos (Hoffmann, 1932; Gantenbein *et al.*, 2001; Sissom & Lourenco, 1987). With 71 species and 5 subspecies currently recognized (Table 6), it is the largest buthid genus in North America and the second largest in the New World (Fet & Lowe, 2000; Teruel 2001, 2006, 2007; Teruel & Stockwell, 2002; Armas & Martin-Frias, 2003; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009; Armas & Trujillo, 2010). *Centruroides*, commonly known as 'bark scorpions', reside in microhabitat retreats during the day and generally sit or actively forage on vegetation and rock faces at night (Polis, 1990). *Centruroides* species are fairly plastic in terms of their retreats: often residing in cracks and crevices in rock faces, undersides of rocks and other surface cover, in leaf litter at the bases of vegetation, under loose tree bark, or in bromeliads (Polis, 1990; O.F. Francke & W.D. Sissom, pers. comm.). The venom of several species—notably *Centruroides elegans elegans* (Thorell, 1876), *Centruroides limpidus* (Karsch, 1879), *Centruroides infamatus* (CentruroidesL. Koch. 1844), *Centruroides noxius* Hoffmann, 1932, *Centruroides ornatus* Pocock, 1902, *Centruroides suffusus* Pocock, 1902, *Centruroides sculpturatus* (Ewing, 1928)—is potentially lethal to adult humans, resulting in as many as 1,000 fatalities per year in Mexico (Mazzotti & Bravo-Becherelle, 1963; Dehesa-Davila & Possani, 1994).

Pocock (1902) published the last morphological revision of the genus to include all of the species described at the time. The taxonomy of the group has undergone

**Table 6.** Currently recognized species and subspecies of the buthid scorpion genus *Centruroides* Marx, 1890. Species not included in the molecular analysis are indicated with an *, species not included in the morphological analysis are indicated with a #.

*C. alayoni* Armas, 1999
*C. anchorellus* Armas, 1976
*C. arctimanus* (Armas, 1976)
*C. baergi* Hoffmann, 1932
*C. balsasensis* Ponce-Saavedra & Francke, 2004
*C. bani* Armas & Marcano Fondeur, 1987
*C. baracoae* Armas, 1976 *#
*C. barbudensis* (Pocock, 1898)
*C. bertholdii* (Thorell, 1876) *#
*C. bicolor* (Pocock, 1898)
*C. chamulaensis* Hoffmann, 1932
*C. chiapanensis chiapanensis* Hoffmann, 1932
*C. chiapanensis tapachulaensis* Hoffmann, 1932
*C. elegans elegans* (Thorell, 1876)
*C. elegans insularis* Pocock, 1902
*C. exilicauda* (Wood, 1863)
*C. exilimanus* Teruel & Stockwell, 2002
*C. exsul* (Meise, 1934) *
*C. fallassisimus* Armas & Trujillo, 2010
*C. farri* Armas, 1976
*C. flavopictus flavopictus* (Pocock, 1898)
*C. flavopictus meridionalis* Hoffmann, 1932
*C. fulvipes* (Pocock, 1898)
*C. galano* Teruel, 2001 *#
*C. gracilis* (Latreille, 1804)
*C. griseus griseus* (C. L. Koch, 1844)
*C. griseus borinquensis* Armas, 1982
*C. guanensis* Franganillo, 1930
*C. hentzi* (Banks, 1900)
*C. hirstutipalpus* Ponce-Saavedra & Francke, 2009
*C. hoffmanni* Armas, 1996
*C. infamatus* (C.L. Koch, 1844)
*C. insulanus* (Thorell, 1876)
*C. jaragua* Armas, 1999
*C. jorgeorum* Santiago-Blay, 2009 *#
*C. koesteri* Kraepelin, 1912
*C. limbatus* (Pocock, 1898)
*C. limpidus* (Karsch, 1879)
*C. luceorum* Armas, 1999
*C. mahnerti* Lourenço, 1983
*C. marcanoi* Armas, 1981
*C. margaritatus* (Gervais, 1841)
*C. mariaorum* Santiago-Blay, 2009
*C. meisei* (Hoffmann, 1939)
*C. melanodactylus* Teruel, 2001 *#
*C. morenoi* (Mello-Leitao, 1945)
*C. navarroi* Teruel, 2001 *#
*C. nigrescens* (Pocock, 1898)
*C. nigrimanus* (Pocock, 1898)
*C. nigropunctatus* Teruel, 2006 *#
*C. nigrovariatus* (Pocock, 1898)
*C. nitidus nitidus* (Thorell, 1876)
*C. nitidus taino* Armas & Marcano Fondeur, 1987
*C. noxius* Hoffmann, 1932
*C. ochraceus* (Pocock, 1898)
*C. orizaba* Armas & Martin-Frias, 2003 *#

*C. ornatus* (Pocock, 1902)
*C. pallidiceps* Pocock, 1902
*C. platnicki* Armas, 1981
*C. pococki* Sissom & Francke, 1983
*C. polito* Teruel, 2007 *#
*C. rileyi* Sissom, 1995
*C. robertoi* Armas, 1976 *
*C. sasae* Santiago-Blay, 2009
*C. schmidti* Sissom, 1995
*C. sculpturatus* (Ewing, 1928)
*C. serrano* Santibanez-Lopez & Ponce-Saavedra, 2009
*C. sissomi* Armas, 1996
*C. spectatus* Teruel, 2006 *#
*C. stockwelli* Teruel, 2001 *#
*C. suffusus* (Pocock, 1902)
*C. tecomanus* Hoffmann, 1932
*C. testaceus testaceus* (DeGeer, 1778)
*C. testaceus arubensis* (Bakker, 1963)
*C. thorellii* (Kraepelin, 1891)
*C. tuxtla* Armas, 1999
*C. underwoodi* Armas, 1976 *#
*C. vittatus* (Say, 1821)

considerable change in the century since (Fig. 13). For many years following the description of the genus, there was confusion regarding the generic name, and *Centrurus* Ehrenberg, 1828 was used interchangeably with *Centruroides* (Francke, 1984; Fet & Lowe, 2000). The type species of *Centrurus* was designated by C.L. Koch (1838) as *Centrurus galbineus* C.L. Koch, 1838, a species subsequently synonymized under the scorpionid taxon *Heterometrus longimanus* (Herbst, 1800) (Fet & Lowe, 2000). Therefore, the use of *Centrurus* in reference to any North American buthid species is incorrect.

The greatest efforts to assign *Centruroides* species to morphological groups were made several researchers working on Mexican species (Hoffmann, 1932; González-Santillán, 2001; Ponce & Moreno-Barajas, 2005). Among the Mexican distributed species, the most recent proposal (Ponce & Moreno-Barajas, 2005) included five species groups (Table 7): the striped group with two subgroups (*limpidus-elegans* subgroup and *suffusus-infamatus* subgroup) and the non-striped group with three subgroups (the *bertholdii* subgroup, the *gracilis* subgroup and the *thorellii* subgroup). The validity of these species groups has never been tested using modern analytical methods.

There are few proposed hypotheses of relationships or species groups among the non-Mexican species of *Centruroides* (Gantenbein *et al.*, 2000; Teruel, 2001, Teruel *et al.*, 2006). Some effort has been made to define groups among the Cuban species (Teruel, 2001), including the definition of three endemic groups: "*arctimanus*", "*anchorellus*", and "*robertoi*". However, these species groups do not consider other Caribbean taxa and may be paraphyletic in context of the entire genus.

Figure 13. Trends in primary taxonomy publications in the buthid scorpion genus *Centruroides* Marx, 1890.

**Figure 13**

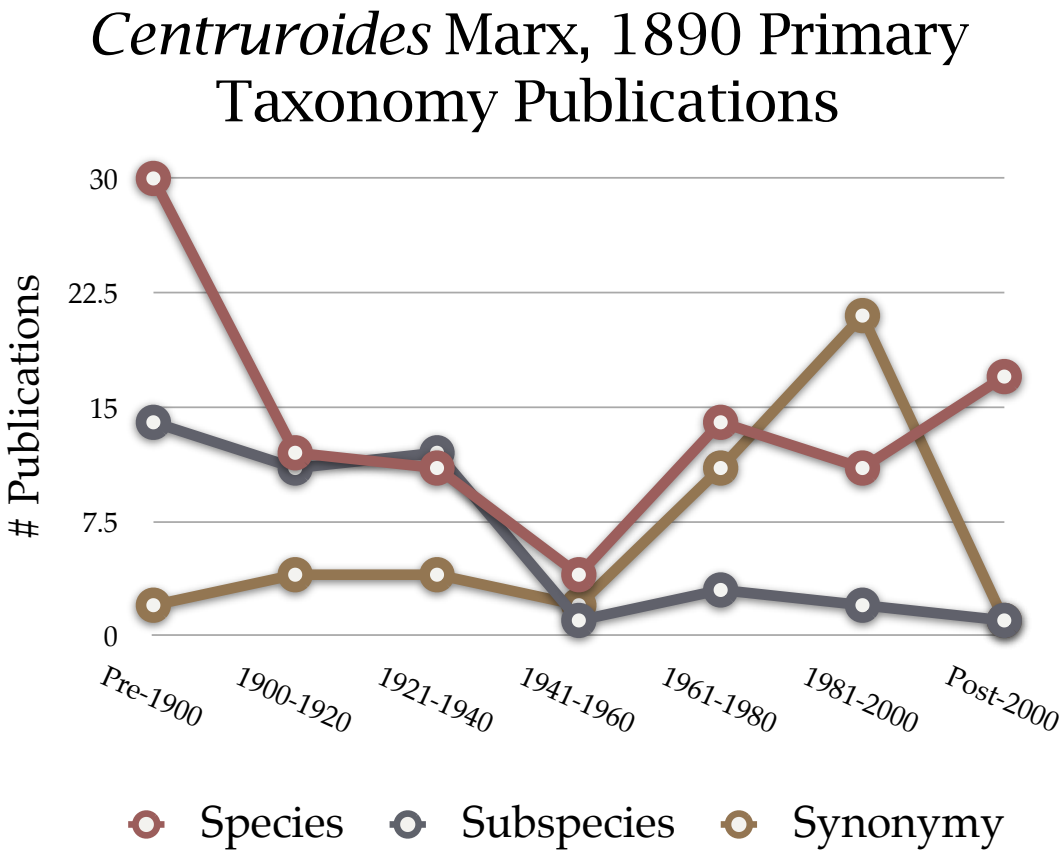

*Centruroides* Marx, 1890 Primary Taxonomy Publications
# Publications
30
22.5
15
7.5
0
Pre-1900
1900-1920
1921-1940
1941-1960
1961-1980
1981-2000
Post-2000
Species
Subspecies
Synonymy

**Table 7.** Proposed Mexican species groups in the buthid scorpion genus *Centruroides* Marx, 1890. Follows Ponce-Saavedra & Moreno-Barajas (2005).

| |
|---|
| **The "Striped" Group** |
| **subgroup *limpidus-elegans*** |
| *Centruroides elegans elegans* (Thorell, 1876) |
| *Centruroides elegans insularis* Pocock, 1902 |
| *Centruroides tecomanus* Hoffmann, 1932 |
| *Centruroides meisei* Hoffmann, 1938 |
| *Centruroides pallidiceps* (Pocock, 1902) |
| *Centruroides balsasensis* Ponce & Francke, 2004 |
| *Centruroides limpidus* (Karsch, 1879) |
| **subgroup *suffusus-infamatus*** |
| *Centruroides baergi* Hoffmann, 1932 |
| *Centruroides exilicauda* (Wood, 1863) |
| *Centruroides infamatus* (Koch, 1844) |
| *Centruroides ornatus* Pocock, 1902 |
| *Centruroides nigrovariatus* Pocock, 1902 |
| *Centruroides suffusus* Pocock, 1902 |
| *Centruroides vittatus* (Say, 1821) |
| **The "Non-striped' Group** |
| **subgroup *bertholdii*** |
| *Centruroides bertholdii* (Thorell, 1876) |
| *Centruroides chiapanensis chiapanensis* Hoffmann, 1932 |
| *Centruroides chiapanensis tapachulaensis* Hoffmann, 1932 |
| *Centruroides flavopictus flavopictus* Pocock, 1898 |
| *Centruroides flavopictus meridionalis* Hoffmann, 1932 |
| *Centruroides margaritatus* (Gervais, 1841) |
| *Centruroides noxius* Hoffmann, 1932 |
| *Centruroides ochraceus* (Pocock, 1898) |
| **subgroup *gracilis*** |
| *Centruroides fulvipes* (Pocock, 1898) |
| *Centruroides gracilis* (Latrielle, 1804) |
| *Centruroides nigrescens* (Pocock, 1898) |
| *Centruroides nigrimanus* (Pocock, 1898) |
| **subgroup *thorellii*** |
| *Centruroides thorellii* (Kraepelin, 1891) |
| *Centruroides chamulaensis* Hoffmann, 1932 |
| *Centruroides hoffmanni* Armas, 1996 |
| *Centruroides rileyi* Sissom, 1995 |
| *Centruroides schmidti* Sissom, 1995 |
| *Centruroides sissomi* Armas, 1996 |
| *Centruroides tuxtla* Armas, 1999 |

Much of the revisionary work done on *Centruroides* species is geographically restricted (Moreno, 1940, 1967; Armas, 1981, 1982, 1983; Francke & Stockwell, 1987; Sissom & Lourenço, 1987; Teruel & Stockwell, 2002; Teruel, 2005; Santiago-Blay, 2010). The characters traditionally used to define *Centruroides* species rely heavily on morphometrics and color (Gantenbein *et al.*, 2000). Species are inadequately defined, and many of the types are damaged or in poor condition, making redescriptions difficult. A phylogeny constructed from objective morphological characters is critical to resolving species groups and subsequently redefining species.

Previous research using molecular data has demonstrated the presence of four geographically delimited clades within *Centruroides* (L.A. Esposito & L. Prendini, in prep.). This study presents a comprehensive molecular phylogeny for each of the four clades, incorporating undescribed species as well as most of the currently described species in the genus (61/71). Exemplars specimens (Prendini, 2001d) were scored for all described and putative species, and a phylogenetic analysis of the morphological data performed. The morphological dataset was then combined with the molecular data, and a total evidence phylogenetic analysis is presented for the entire genus. Herein we present a phylogenetic approach to defining the species groups within *Centruroides*, thereby providing a path toward a comprehensive revision of the group.

## Materials and Methods

### *Species Concept*

For this study we use the phylogenetic species concept (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981). To identify operational taxonomic units (OTUs) for

morphological scoring, we used reciprocal illumination of morphological, molecular and locality data (Hennig, 1966). A previous molecular phylogeny, sampling most *Centruroides* species from one or two specimens, identified four geographically delimited clades within the genus (L.A. Esposito & L. Prendini, in prep.). Four clade-specific phylogenetic analyses were conducted, expanding the sampling to all available specimens for each clade (Appendix 8). The 'taxonomic circle' approach (DeSalle *et al.*, 2005) was then applied to the resulting phylogenies to identify OTUs. For paraphyletic species, only the clade containing specimens from the type or approximate type locality that matched the original species description, was assigned to that species, subsequently referred to as the 'type clade'. The remaining clades were then verified against the type clade for morphological and/or geographical distinctiveness, assigned an OTU code, generally "*C. aff. speciesX_1*, *2*, ...", and scored independently for the morphological matrix. Sub-clades from monophyletic species were also examined for morphological distinctiveness. If clades were determined to be morphologically distinct, they were each assigned an OTU species code, "*C. speciesX_1*, *2*, ...", and scored individually for morphology. If sub-clades were not found to be morphologically distinct, then a single OTU for that species was confirmed. At the end of this process, exemplar specimens from each phenotypically and genotypically distinct clade, or OTU, were scored for morphology.

***Taxon Sampling***

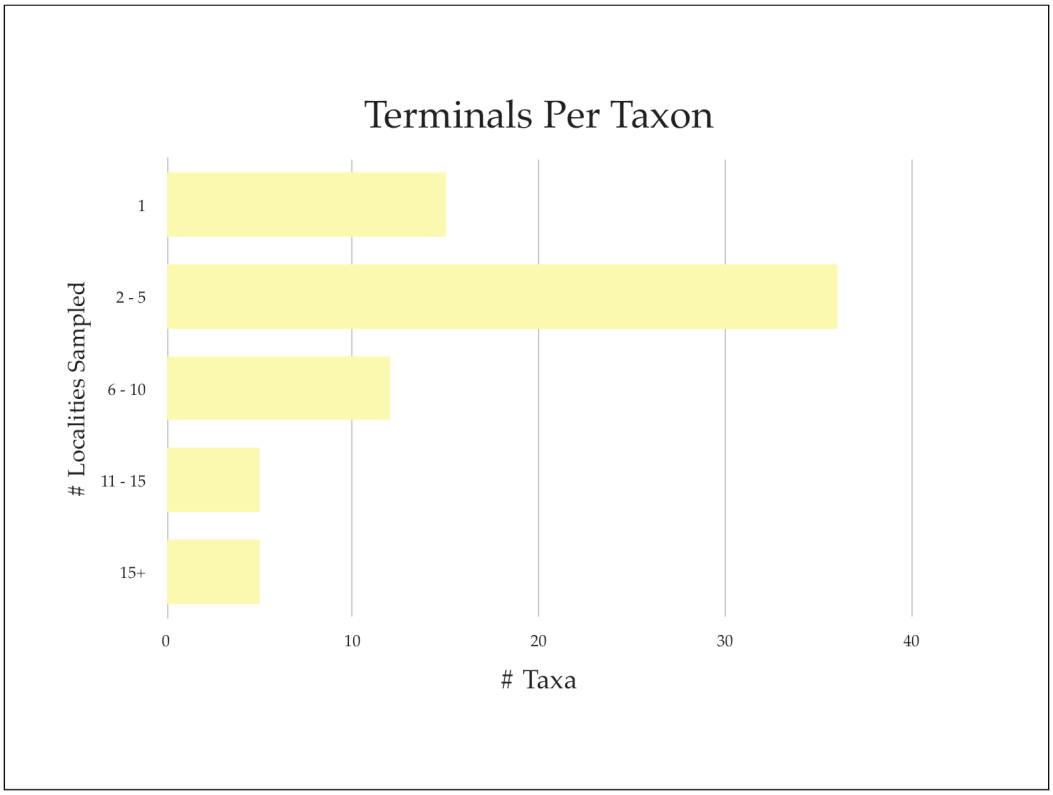
For clade-specific analyses, the ingroup sampling used all available *Centruroides* samples belonging to a given clade. To the extent possible, species were sampled from

multiple localities across their distributions (Fig. 14). Clade assignments were made using a well-resolved molecular phylogeny from L.A. Esposito & L. Prendini (in prep.). The four clades identified are A- North American taxa, B- Mesoamerican taxa, C- Caribbean taxa, and D- taxa from the Yucatan peninsula and the Chortis Block (Nicaragua and Honduras). The appropriate letter (A-D) in Table 6 indicates clade assignments for each species. Two representative species from the remaining three clades were included as outgroups in each clade-specific analysis. *Heteroctenus junceus* (Herbst, 1800), the type species of *Heteroctenus* Pocock, 1897, sister genus of *Centruroides*, was also included as an outgroup.

The morphological and total evidence (morphology and molecules) analyses included all described species in the genus *Centruroides* with the exception of those indicated with asterisks in Table 6. Previous studies have demonstrated that *Heteroctenus* is the sister group to *Centruroides* (Esposito *et al.*, in prep). The following species from the sister genus *Heteroctenus* were included as outgroups: *H. junceus*, *Heteroctenus princeps* (Karsch, 1879), *Heteroctenus bonettii* (Armas, 1999), *Heteroctenus abudi* (Armas & Marcano Fondeur, 1987), *Heteroctenus garridoi* (Armas, 1974). Additional outgroup specimens were included from *Rhopalurus*, on the basis of its position within the New World buthid subfamily Rhopalurusinae Bücherl, 1971 (L.A. Esposito *et al.*, in prep.): the western Brazilian species, *Rhopalurus rochae* Borelli, 1910, and the type species from northern South America, *Rhopalurus laticauda* Thorell, 1876.

Figure 14. Geographical coverage of *Centruroides* Marx, 1890 species sampling for phylogenetic analysis.

**Figure 14**


Terminals Per Taxon
# Localities Sampled
1
2 - 5
6 - 10
11 - 15
15+
0
10
20
30
40
# Taxa

### *Field Methods*

All included specimens were collected in the field, preserved by submersion of live animals in 95% ethanol, and subsequently injected with ethanol to improve the internal preservation. Specimens were then stored at -20°C at the American Museum of Natural History.

### *Laboratory Methods*

Genomic DNA was extracted from muscle tissue from of the fourth leg of each specimen using a Qiagen DNEasy Blood and Tissue extraction kit according the manufacturer's protocols.

Extracted DNA was amplified for five gene regions in overlapping fragments using universal eukaryote and scorpion specific primers (Table 8). Five gene loci were selected for this study, based on their ability to provide resolution at various taxonomic levels: a mitochondrial protein-coding gene (Cox1), mitochondrial structural genes (12S rDNA, 16S rDNA), and nuclear structural genes (18S rDNA, 28S rDNA) (Arnedo *et al.*, 2002; Giribet *et al.*, 2001; Harrison *et al.*, 1987; Hayashi, 1996; Hillis & Dixon, 1991; Wahlberg & Zimmermann, 2000). Polymerase Chain Reaction was performed on an Epicenter thermocycler (Eppendorf) using GoTaq polymerase (Promega). Reactions were verified on a 1.2% agarose gel stained with Sybr safe DNA gel stain (Invitrogen), and subsequently purified using the Ampure DNA (Agencourt) purification system on a Biomek NX robot (Beckman-Coulter). Cycle sequencing was conducted using Big Dye v1.1 and automated Sanger sequencing of single stranded DNA performed on an Applied Biosystems Inc. Prism™ 3730x.

**Table 8.** Arthropod primers used for gene amplification of five loci in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890

| Gene | Primer | Sequence | References (other names) |
|---|---|---|---|
| 12S | 12Sai | AAACTAGGATTAGATACCCTATTAT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-N-14588) |
| | 12Sbi | AAGAGCGACGGGCGATGTGT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-J-14233) |
| 16S | 16Sar | CGCCTGTTTATCAAAAACAT | Simon *et al.,* 1994 (LR-N-13398) |
| | 16Sbr | CTCCGGTTTGAACTCAGATCA | Simon *et al.,* 1994 (LR-J-12887) |
| 18S | 18S1F | TACCTGGTTGATCCTGCCAGTAG | Prendini *et al.,* 2005 |
| | 18S5R | CTTGGCAAATGCTTTCGC | Prendini *et al.,* 2005 |
| | 18S3F | GTTCGATTCCGGAGAGGGA | Prendini *et al.,* 2005 |
| | 18Sbi | GAGTCTCGTTCGTTATCGGA | Prendini *et al.,* 2005 |
| | 18SA2.0 | ATGGTTGCAAAGCTGAAAC | Prendini *et al.,* 2005 |
| | 18S9R | GATCCTTCCGCAGGTTCACCTAC | Prendini *et al.,* 2005 |
| 28S | 28Sa | GACCCGTCTTGAAGCACG | Nunn *et al.,* 1996 (D3A |
| | 28Sbout | CCCACAGCGCCAGTTCTGCTTACC | Prendini *et al.,* 2005 |
| Cox1 | LCO | GGTCAACAAATCATAAAGATATTGG | Folmer *et al.,* 1994 (LCO-1490-J-1514) |
| | HCOoutout | GTAAATATATGRTGDGCTC | Prendini *et al.,* 2005 |
| | LE1R | TCCATTCCCACAGTAAACATATG | |
| | HCOEXTERNA | GAAGTTTATATTTTAATTTTACCTGG | |
| | HCOEXTERNB | CCTATTGAWARAACATARTGAAAATG | |

Paired strand reads were aligned using Sequencher™ and edited by hand. Sequences are accessioned in Genbank (Appendix 8). Multiple sequence alignments for individual gene partitions was performed in MAFFT (Katoh *et al.*, 2005) using the G-INS-i strategy (recommended by the authors for less than 200 sequences with global homology) and PAM1/K=2 matrix parameter (recommended by the authors for aligning closely related sequences). All loci were aligned, however there was no length variation in Cox1, negligible length variation in 18S and 28S (<10 nucleotides), and little length variation in 12S and 16S (<20 nucleotides). The resulting alignments were then concatenated and the matrices were assembled in Geneious v5.1 (Biomatters, Ltd.).

***Molecular Clade Analyses***

For each clade-specific analysis, molecular data from the five loci (12S, 16S, 18S, 28S, Cox1) was concatenated and analyzed under parsimony criteria in TNT v1.1 (Goloboff *et al.*, 2003). The 'New Technology Search' option with 10,000 random addition replicates, 'Tree Drift' (Goloboff, 1999), and 'Ratchet' (Nixon, 1999) was used to identify the single most parsimonious tree.

These analyses were conducted in order to identify OTUs for morphological scoring. To test the utility of the OTUs for morphological scoring versus scoring specimens on the basis of their locality and morphology-based identifications, analyses constraining genetic-based OTUs and locality/morphology-based species identifications were conducted for each clade in TNT using the 'force +' command. The same search strategies as the original analyses were employed. The unconstrained trees were then compared to the two sets of constrained trees using the Wilcoxon signed ranks test

(Templeton, 1983), the 'winning-sites' test (Prager & Wilson, 1988), and the Shimodaira-Hasegawa test (Shimodaira & Hasegawa, 1999) as implemented in PAUP* v4b10 (Swofford, 2002).

In order to assess the topological congruence of loci, individual analyses of each locus was also conducted using the same search strategy as the concatenated analyses. 'Navajo rugs' (Giribet, 2003), or nodal sensitivity plots, using the five resulting gene trees were created in Cladescan v1.0 (Sanders, 2010) for the four clade-specific analyses. For each node, the 'Navajo rug' depicts whether that node was recovered in each gene tree.

***Morphological Data***

Morphological characters were taken from various published and unpublished matrices (Lamoral, 1978, 1980; Stockwell, 1989; Jeram, 1994, 1998; Prendini, 2000, 2001, 2004; Dunlop & Braddy, 2001; Soleglad & Sissom, 2001; Soleglad & Fet, 2001, 2003; Giribet *et al.*, 2002; Volschenk *et al.*, 2008; Kamenz & Prendini, 2008 E.S. Volschenk & L. Prendini, unpublished data) appended with additional novel characters, and assembled into a combined morphological matrix (Appendix 6). The primary source of each character is listed along with the 109 characters and states for each character in Appendix 7. Exemplar specimens (Prendini, 2001d) from 121 OTUs were scored for morphological characters. Nomenclature of general anatomy follows Hjelle (1990) and Sissom (1990), trichobothria follows Vachon (1974), tergite and pedipalp carination follows Prendini (2001b), carapace and metasomal carination follows Vachon (1974), and ovariuterine anatomy follows Volschenk *et al.* (2008).

Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2001b). Morphological examination of specimens was conducted using a Nikon SMZ1500 dissection stereomicroscope. Specimens were measured using Mitutoyo digital calipers and an ocular micrometer.

### *Morphological analysis*

Morphological characters were equally weighted *a priori* and analyzed with parsimony in TNT v1.1 using the New Technology Search option with 10,000 random addition replicates. *Rhopalurus laticauda* author, date, the type species, was used to root all trees. Nodal support was assessed using 1000 non-parametric bootstrap replicates, calculated in TNT.

### *Total Evidence Analysis*

A combined dataset of morphological and concatenated molecular data was analyzed under Bayesian and parsimony criteria. All analyses were rooted on *R. laticauda*. The parsimony analysis was conducted using TNT v1.1. The Bayesian analysis was performed in MrBayes (Ronquist and Huelsenbeck, 2003) on the CIPRES supercomputing cluster (Miller *et al.*, 2009) in two independent runs for 70 million generations, with 4 chains, sampling every 5000 generations. MrModeltest2 v2.3 (Nylander, 2004), employing Akaike (1973) information criteria, was used to determine the best fitting model of DNA substitution for each gene and codon position (CoxI). In cases where the best fitting model included both the Γ and invariable sites (I) parameters, the next best fitting model was selected to avoid issues stemming from the non-

independence of the Γ and I parameters (Stamatakis, 2006). The Lewis (2001) model was used for the morphology (standard) data partition. Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (Rambaut & Drummond, 2007), and convergence was assessed by the standard deviations of the split frequencies in AWTY (Nylander *et al.*, 2008). The first 5 million generations were discarded as burn-in. A maximum clade credibility tree was computed from the post-burn-in trees in TreeAnnotator v1.6.1 (Rambaut & Drummond, 2007).

## Results

### *Datasets*

A total of 385 samples (372 ingroup samples and 13 outgroup samples) were included in the analyses. The concatenated and aligned molecular dataset of 4,240 nucleotides was comprised of 26% adenine, 18% cytosine, 25% guanine, and 31% thymine. This consisted of 3,177 constant characters, 142 parsimony-uninformative variable characters, and 931 parsimony-informative characters.

The morphological dataset was comprised of 112 characters, of which 8 were constant and 104 were parsimony-informative. The characters were divided among the prosoma (32%), the mesosoma (31%) and the metasoma (26%). These characters were distributed among ratio/shape (12%), color (26%), surface macrosculpture (25%), carinae (26%), setae (4%), and anatomy (7%).

***Clade Analyses***

Individual parsimony analyses of each major *Centruroides* clade were conducted. Clade A refers to a group of North American species distributed north of the Isthmus of Tehuantepec, Clade B refers to a group of species distributed in the primarily Mesoamerican neotropics, Clade C refers to a group of species endemic to the Caribbean Islands and Florida, and Clade D refers to a group of arboreal species endemic to the Yucatan Peninsula (including the Mayan block) and the Chortis block. These four clades were consistently recovered with high support in previous molecular analyses of *Centruroides* (L.A. Esposito & L. Prendini, in prep.).

An unconstrained parsimony analysis of the concatenated molecular dataset (12S, 16S, 18S, 28S, Cox1) for Clade A resulted in 191 equally parsimonious trees. A majority-rule consensus of the trees (Fig. 15A) resulted in a tree with length (TL) 6609, Consistency Index (CI) 0.24, and Retention Index (RI) 0.71. Thirty OTUs were identified after morphological examination of the specimens from the resulting clades. Two constrained parsimony analyses were also performed, one constraining the samples in each OTU and another constraining the samples to the species identifications made on the basis of morphology and locality information. Three statistical tests were performed to compare the topologies from the constrained analyses to those obtained in the unconstrained analysis: the Wilcoxon signed ranks test (Templeton, 1983), the 'winning-sites' test (Prager & Wilson, 1988), and the Shimodaira-Hasegawa test (Shimodaira & Hasegawa, 1999). There was no significance for any of the tests among the OTU constrained topologies and the unconstrained topologies, however there was significant

Figure 15A. Majority-rule consensus of 191 equally parsimonious trees resulting from an unconstrained parsimony analysis, conducted in TNT v1.1 (Goloboff *et al.*, 2003), of concatenated molecular data (12S, 16S, 18S, 28S, Cox1) for Clade A, a clade of *Centruroides* Marx, 1890 scorpions distributed in North America. (Length 6609, Consistency Index 0.24, and Retention Index 0.71) The values to the right of nodes are nonparametric bootstraps. Navajo rug diagrams are depicted below the nodes and indicate topological congruence in individual gene analyses (left to right: 12S, 16S, 18S, 28S, Cox1). If the node was recovered in an individual gene analysis then the appropriate square will be black, if the node was not recovered then the appropriate square will be white.

**Figure 15A- Part 1**

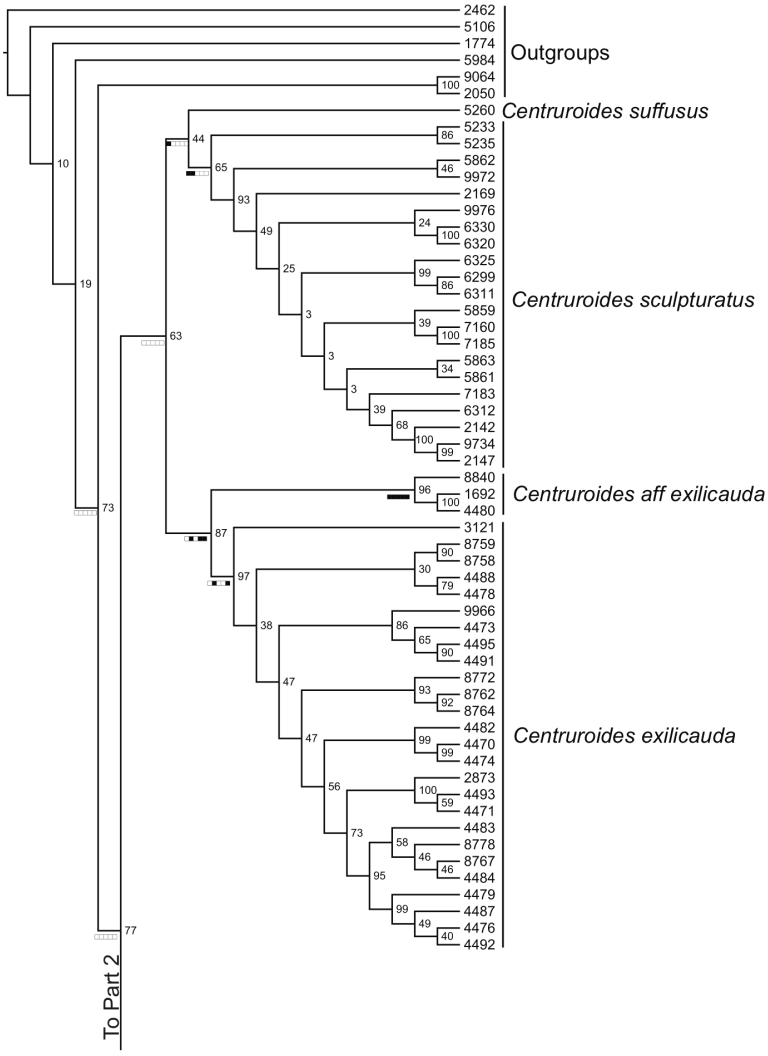
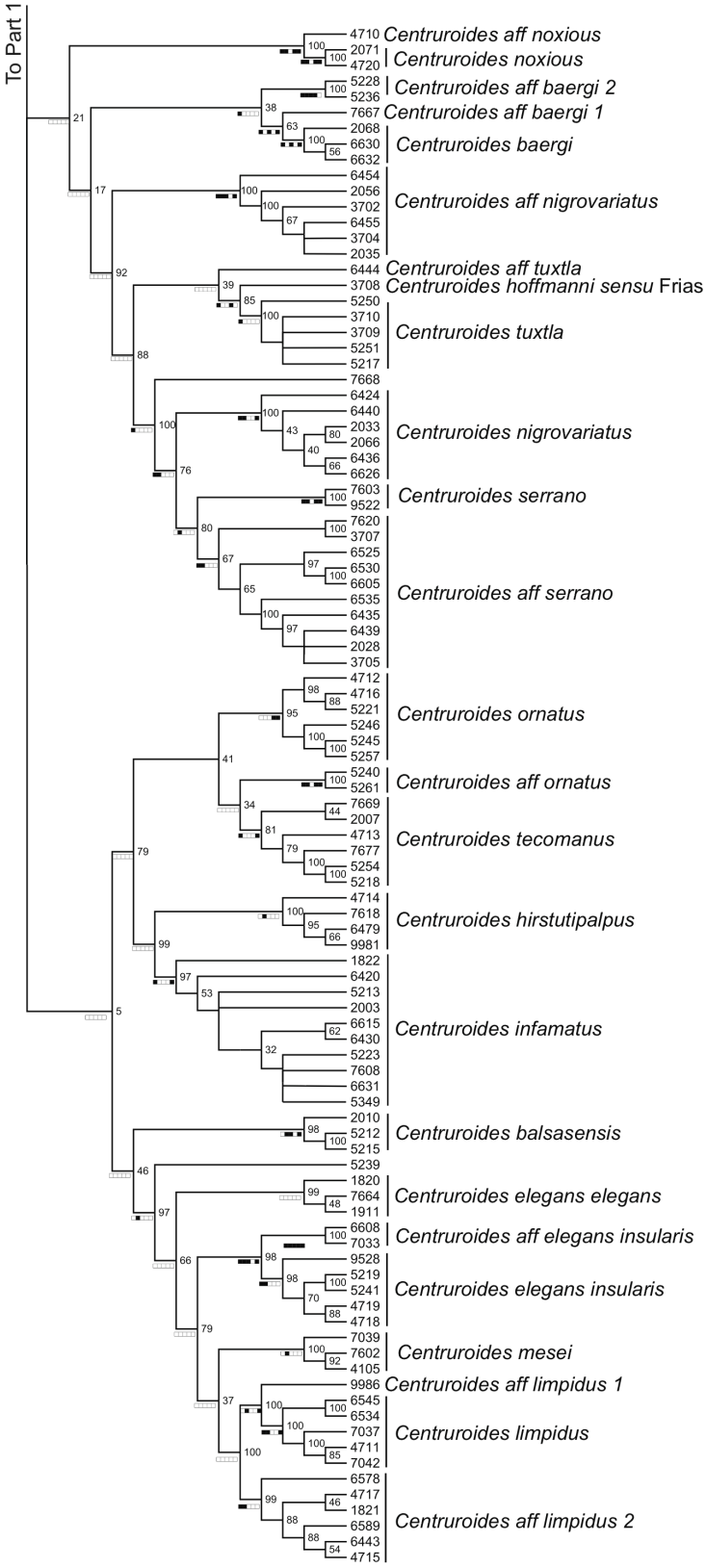


**Figure 15A- Part 2**



difference in all three tests ($P < 0.05$) comparing the unconstrained topologies and the species constrained topologies.

An unconstrained parsimony analysis of the concatenated molecular dataset (12S, 16S, 18S, 28S, Cox1) for Clade B resulted in 23 equally parsimonious trees. A majority-rule consensus of the trees (Fig. 15B) resulted in a phylogeny with TL 6518, CI 0.28, and RI 0.74. Thirty-five OTUs were identified after morphological examination of the specimens from the resulting clades. Two constrained parsimony analyses were also performed, one constraining the samples in each OTU and another constraining the samples to the species identifications made on the basis of morphology and locality information. Three statistical tests were performed to compare the topologies from the constrained analyses to those obtained in the unconstrained analysis (Wilcoxon signed ranks test, 'winning-sites' test, Shimodaira-Hasegawa test). There was no statistical significance for any test among the OTU constrained topologies and the unconstrained topologies. There was, however, significant difference in all three tests ($P < 0.05$) comparing the unconstrained topologies and the species constrained topologies.

An unconstrained parsimony analysis of the concatenated molecular dataset (12S, 16S 18S, 28S, Cox1) for Clade C resulted in 38 equally parsimonious trees. A majority-rule consensus of the trees (Fig. 15C) resulted in a phylogeny with TL 4841, CI 0.43, and RI 0.59. Twenty-eight OTUs were identified after morphological examination of the specimens from the resulting clades. Two constrained parsimony analyses were also performed, one constraining the samples for each OTU and another constraining the samples to the species identifications made on the basis of morphology and locality information. Three statistical tests were performed to compare the topologies from the

Figure 15B. Majority-rule consensus of 23 equally parsimonious trees resulting from an unconstrained parsimony analysis, conducted in TNT v1.1 (Goloboff *et al.*, 2003), of concatenated molecular data (12S, 16S, 18S, 28S, Cox1) for Clade B, a clade of *Centruroides* Marx, 1890 scorpions distributed in Mesoamerica. (Length 6518, Consistency Index 0.28, and Retention Index 0.74) The values to the right of nodes are nonparametric bootstraps. Navajo rug diagrams are depicted below the nodes and indicate topological congruence in individual gene analyses (left to right: 12S, 16S, 18S, 28S, Cox1). If the node was recovered in an individual gene analysis then the appropriate square will be black, if the node was not recovered then the appropriate square will be white.

**Figure 15B- Part 1**

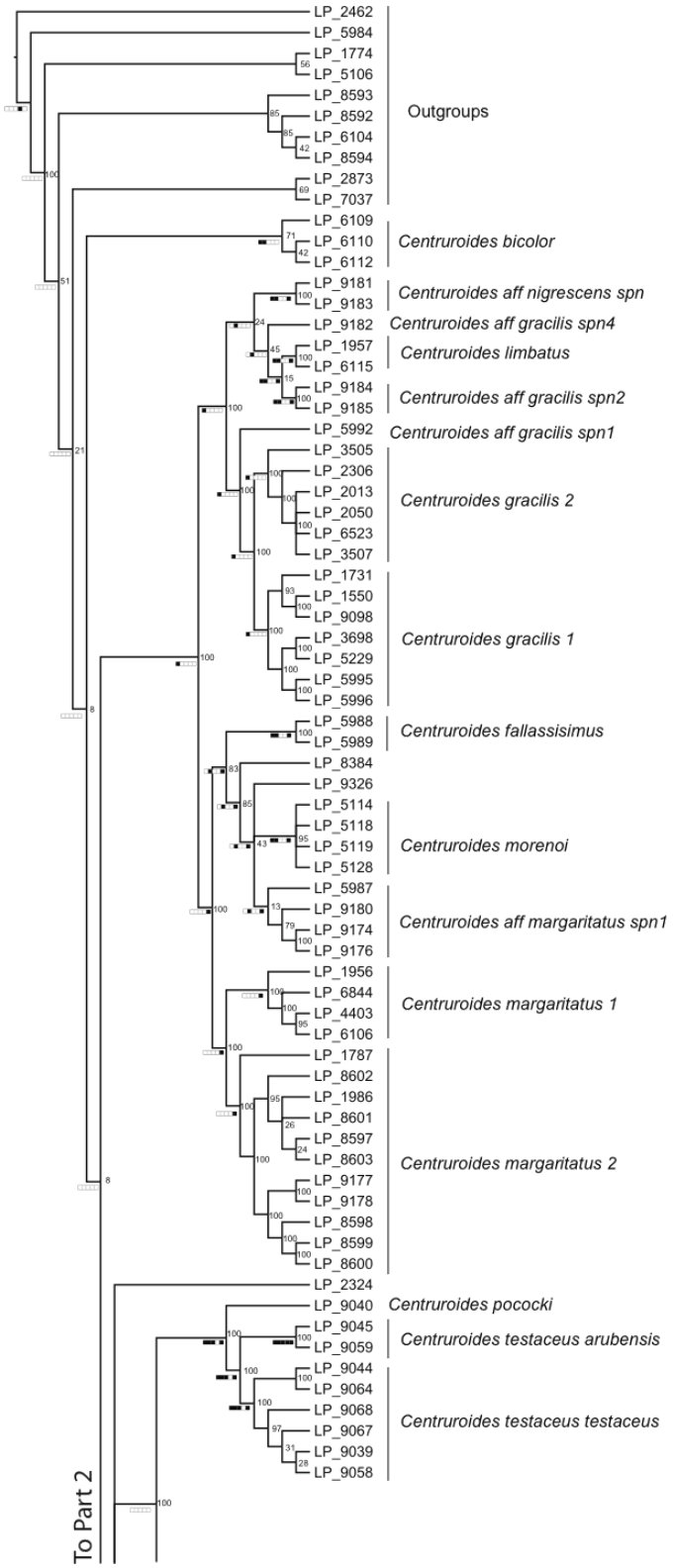


**Figure 15B- Part 2**

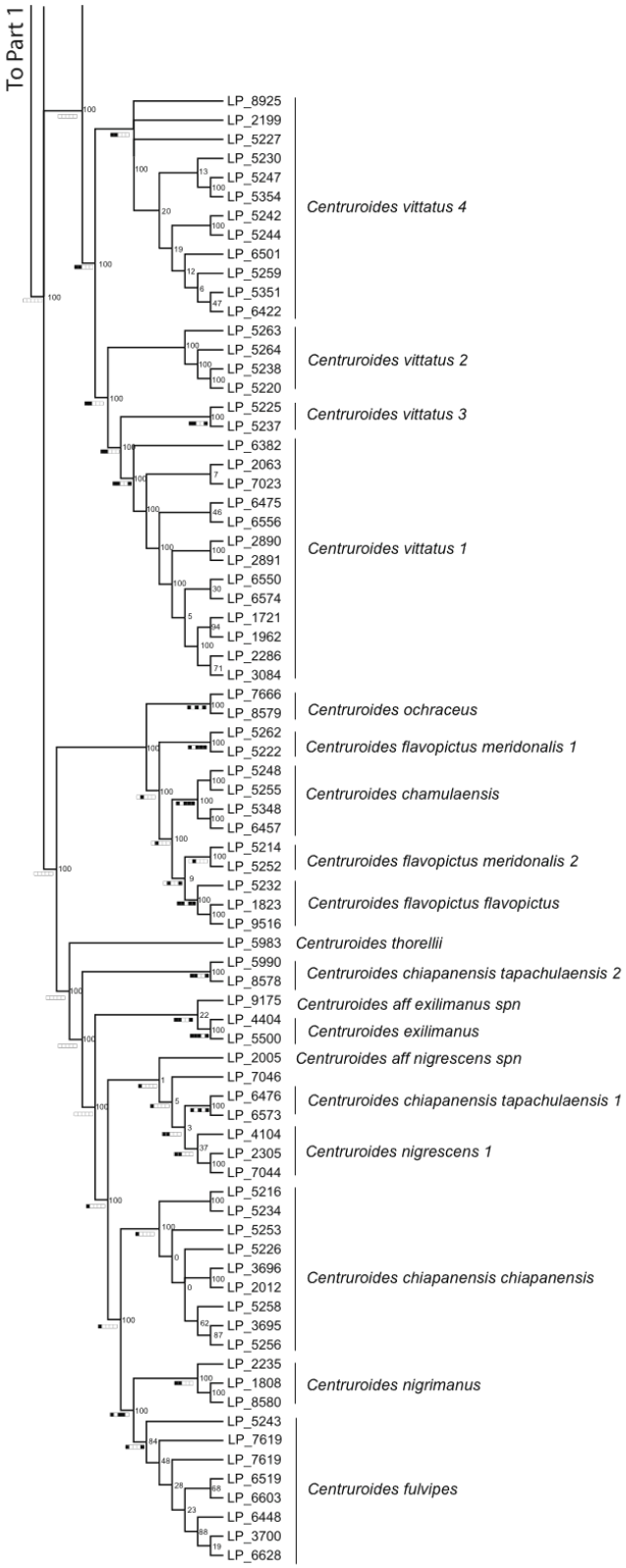
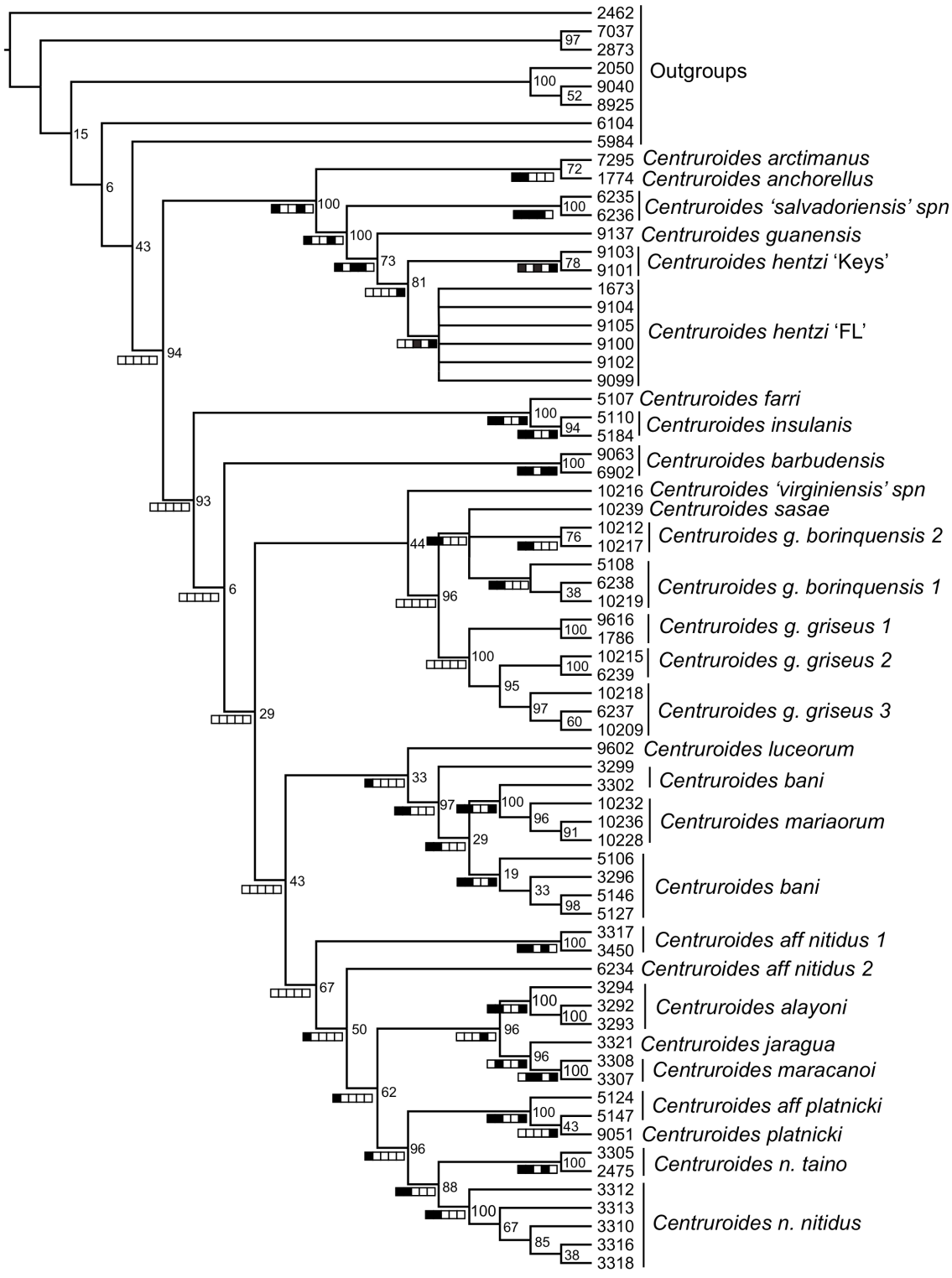


Figure 15C. Majority-rule consensus of 38 equally parsimonious trees resulting from an unconstrained parsimony analysis, conducted in TNT v1.1 (Goloboff *et al.*, 2003), of concatenated molecular data (12S, 16S, 18S, 28S, Cox1) for Clade C, a clade of *Centruroides* Marx, 1890 scorpions distributed in the Caribbean. (Length 4841, Consistency Index 0.43, and Retention Index 0.59) The values to the right of nodes are nonparametric bootstraps. Navajo rug diagrams are depicted below the nodes and indicate topological congruence in individual gene analyses (left to right: 12S, 16S, 18S, 28S, Cox1). If the node was recovered in an individual gene analysis then the appropriate square will be black, if the node was not recovered then the appropriate square will be white.

**Figure 15C**


2462
7037
2873
2050
9040
8925
Outgroups
6104
5984
7295 Centruroides arctimanus
1774 Centruroides anchorellus
6235
6236
Centruroides 'salvadoriensis' spn
9137 Centruroides guanensis
9103
9101
Centruroides hentzi 'Keys'
1673
9104
9105
9100
9102
9099
Centruroides hentzi 'FL'
5107 Centruroides farri
5110
5184
Centruroides insulanis
9063
6902
Centruroides barbudensis
10216 Centruroides 'virginiensis' spn
10239 Centruroides sasae
10212
10217
Centruroides g. borinquensis 2
5108
6238
10219
Centruroides g. borinquensis 1
9616
1786
Centruroides g. griseus 1
10215
6239
Centruroides g. griseus 2
10218
6237
10209
Centruroides g. griseus 3
9602 Centruroides luceorum
3299
3302
Centruroides bani
10232
10236
10228
Centruroides mariaorum
5106
3296
5146
5127
Centruroides bani
3317
3450
Centruroides aff nitidus 1
6234 Centruroides aff nitidus 2
3294
3292
3293
Centruroides alayoni
3321 Centruroides jaragua
3308
3307
Centruroides maracanoi
5124
5147
Centruroides aff platnicki
9051 Centruroides platnicki
3305
2475
Centruroides n. taino
3312
3313
3310
3316
3318
Centruroides n. nitidus

constrained analyses to those obtained in the unconstrained analysis (Wilcoxon signed ranks test, 'winning-sites' test, Shimodaira-Hasegawa test). There was no statistical significance for any test among the OTU constrained topologies and the unconstrained topologies. There was, however, significant difference in all three tests ($P < 0.05$) comparing the unconstrained topologies and the species constrained topologies.

An unconstrained parsimony analysis of the concatenated molecular dataset (12S, 16S, 18S, 28S, Cox1) for Clade D resulted in 5 equally parsimonious trees. A majority-rule consensus of the trees (Fig. 15D) resulted in a phylogeny with TL 2250, CI 0.55, and RI 0.48. Seven OTUs were identified after morphological examination of the specimens from the resulting clades. Two constrained parsimony analyses were also performed, one constraining the samples in each OTU and another constraining the samples to the species identifications made on the basis of morphology and locality information. Three statistical tests were performed to compare the topologies from the constrained analyses to those obtained in the unconstrained analysis (Wilcoxon signed ranks test, 'winning-sites' test, Shimodaira-Hasegawa test). There was no statistical significance for any test among the OTU constrained topologies and the unconstrained topologies. There was, however, significant difference in all three tests ($P < 0.05$) comparing the unconstrained topologies and the species constrained topologies.

***Morphological Analysis***

The parsimony analysis of morphological data resulted in four equally parsimonious trees. A strict consensus of the four trees resulted in a tree (Fig. 16) with TL 1738, CI 0.10, and RI 0.54. Consistent with the low retention index, bootstrap support

Figure 15D. Majority-rule consensus of 5 equally parsimonious trees resulting from an unconstrained parsimony analysis, conducted in TNT v1.1 (Goloboff *et al.*, 2003), of concatenated molecular data (12S, 16S, 18S, 28S, Cox1) for Clade D, a clade of *Centruroides* Marx, 1890 scorpions distributed in the Yucatan peninsula or the Chortis Block. (Length 2250, Consistency Index 0.55, and Retention Index 0.48) The values to the right of nodes are nonparametric bootstraps. Navajo rug diagrams are depicted below the nodes and indicate topological congruence in individual gene analyses (left to right: 12S, 16S, 18S, 28S, Cox1). If the node was recovered in an individual gene analysis then the appropriate square will be black, if the node was not recovered then the appropriate square will be white.

**Figure 15D**

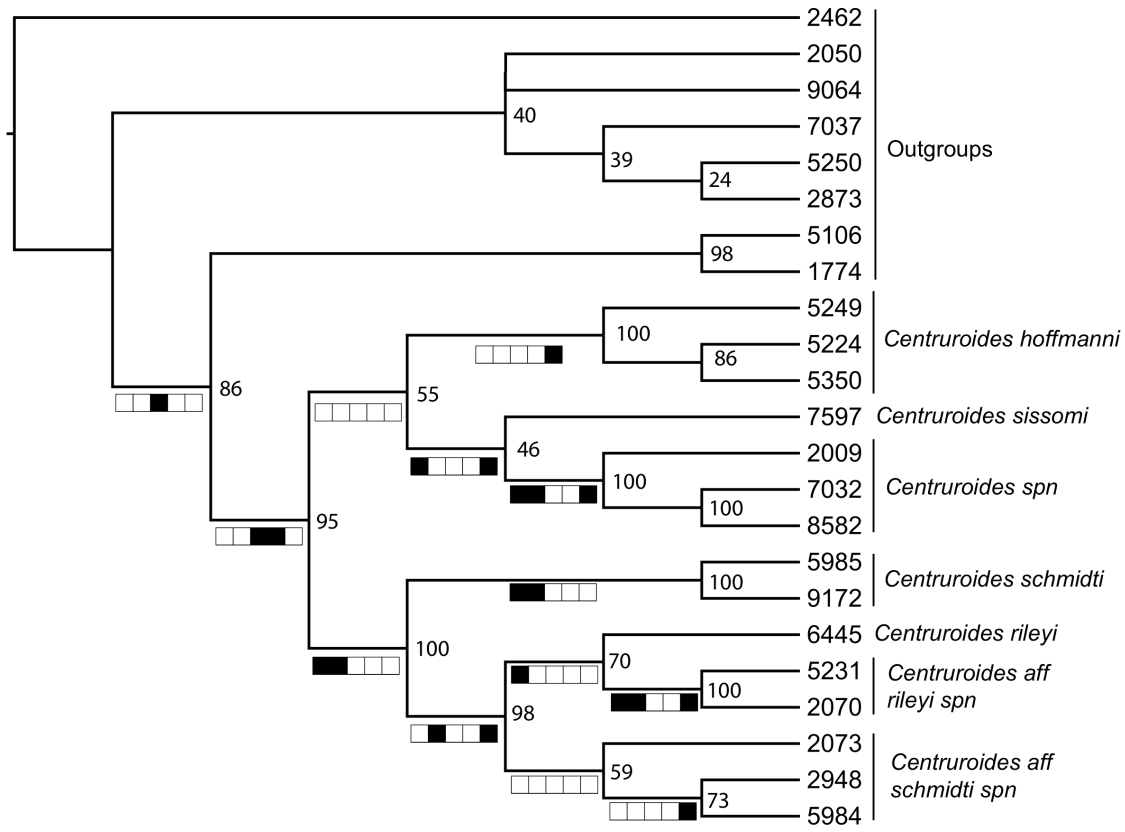

2462
2050
9064
7037
5250
2873
5106
1774
Outgroups
5249
5224
5350
Centruroides hoffmanni
7597
Centruroides sissomi
2009
7032
8582
Centruroides spn
5985
9172
Centruroides schmidti
6445
Centruroides rileyi
5231
2070
Centruroides aff rileyi spn
2073
2948
5984
Centruroides aff schmidti spn
40
39
24
98
86
55
100
86
46
100
100
95
100
70
100
98
59
73

Figure 16. Strict consensus of 4 equally parsimonious trees for the buthid scorpion genus *Centruroides* Marx, 1890 inferred from morphological data in TNT (Goloboff *et al.*, 2008). Hash marks on branches are character state changes, characters indicated above branches, states indicated below. Node values are nonparametric bootstraps. Shading signifies relation to clades recovered in an analysis of molecular data: Clade A- Blue, Clade B- Red, Clade C- Green, Clade D- Yellow.

**Figure 16- Part 1**

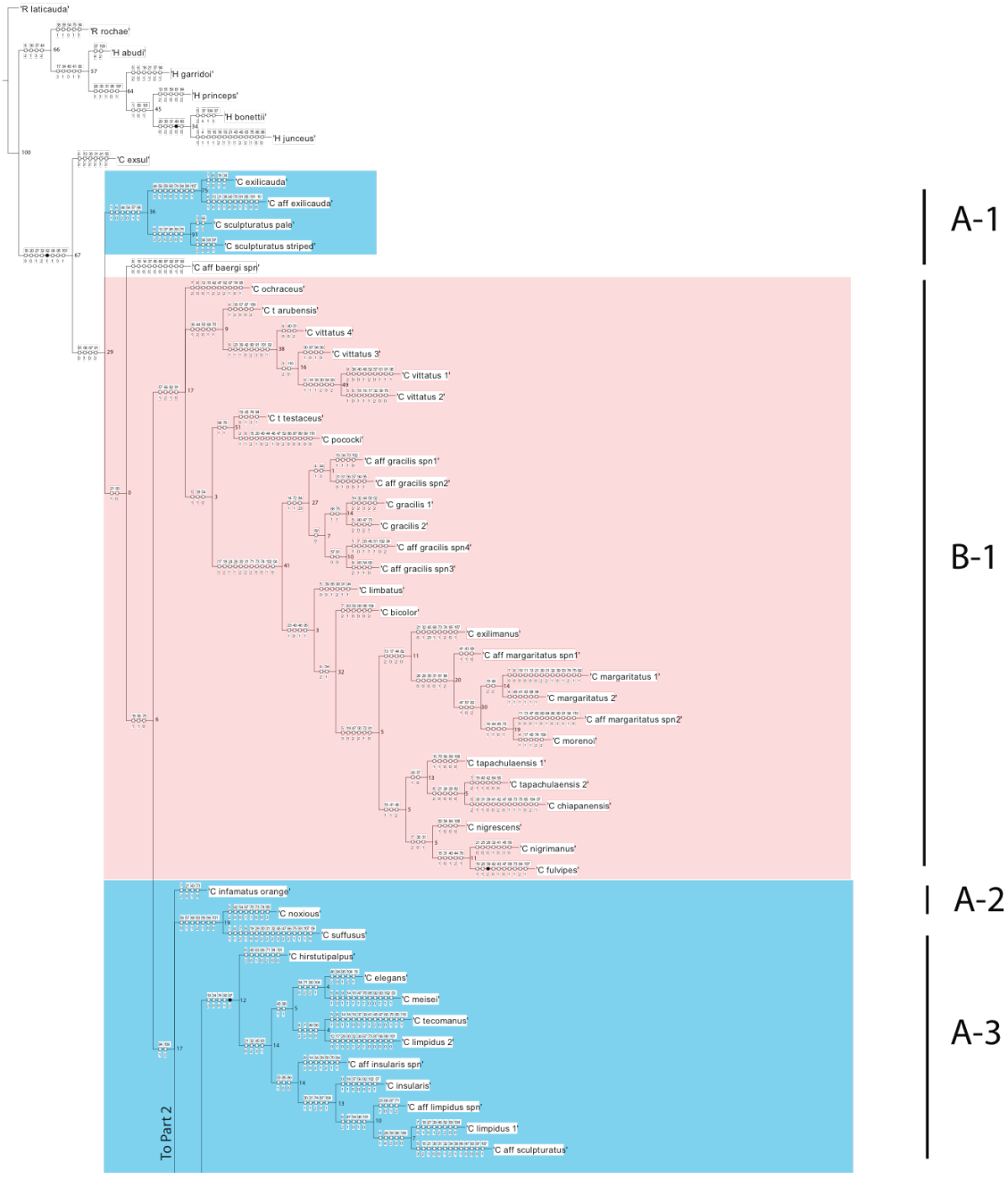
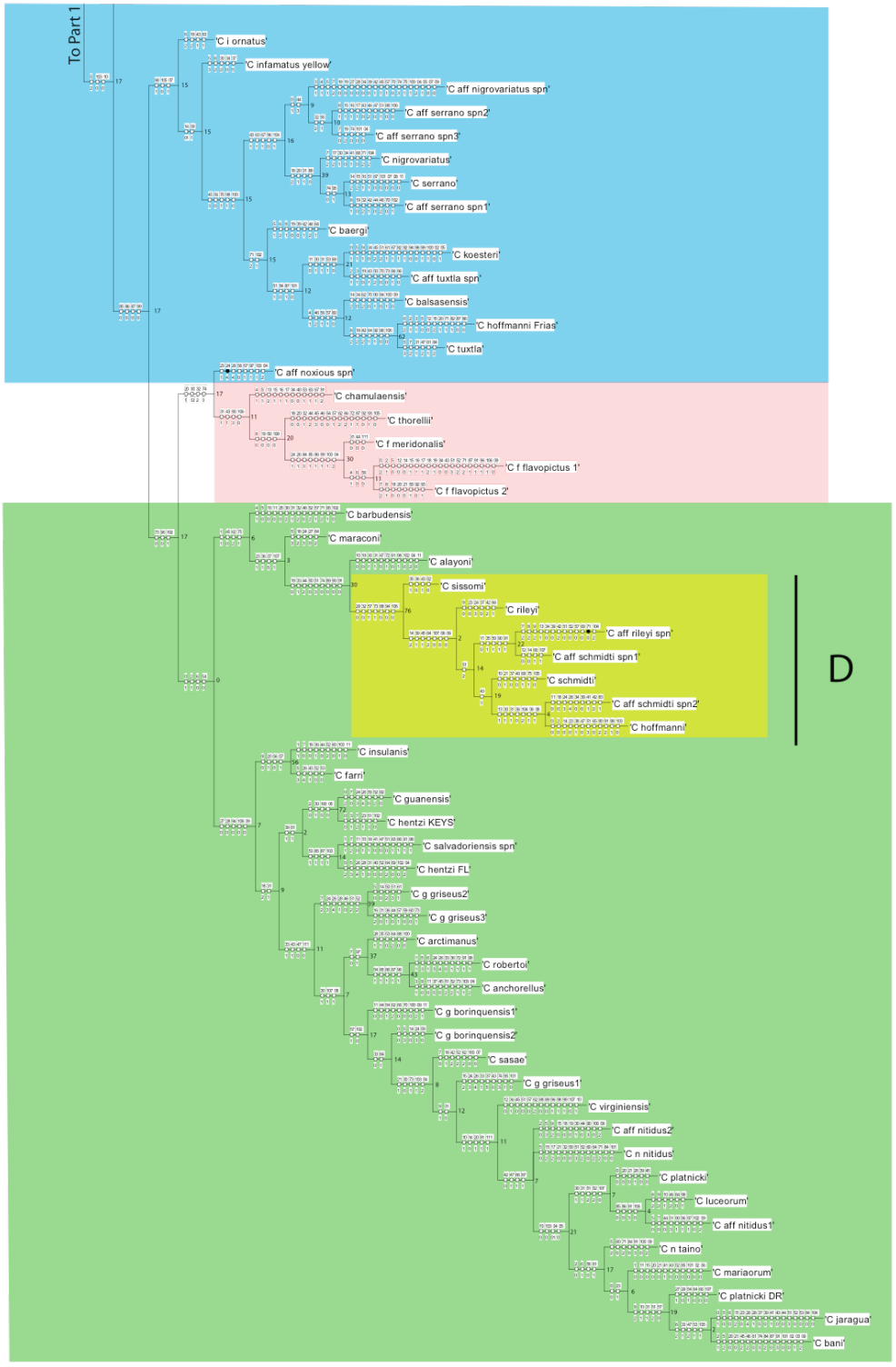


**Figure 16- Part 2**



values are quite low throughout the tree. *Centruroides* was recovered as a monophyletic clade, sister to *Heteroctenus* + *Rhopalurus rochae*.

Only one of the four clades of *Centruroides* recovered in previous molecular analyses was recovered in its entirety (Clade D, the Yucatan/Chortis Block species). Clades C (Caribbean species) and D formed a monophyletic group with the two clades sister to one another. As with previous molecular analyses, a monophyletic group containing all Clade C and D species was recovered in the morphological analysis; however, Clade C was rendered paraphyletic by Clade D.

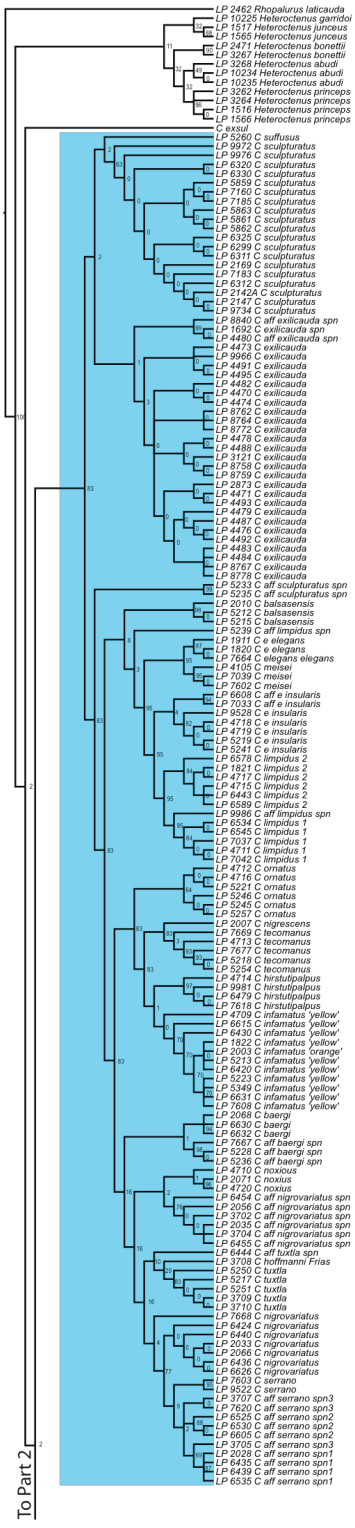
Clades A (North American species) and B (Mesoamerican species) from previous molecular analyses were both recovered as paraphyletic. All of the species formed six clades (Fig. 16, Table 9), and four of the six clades recovered belong to Clade A. The species forming Clade B were recovered in two clades, paraphyletic with respect to the Clade A species.

***Total Evidence Analysis***

The total evidence (morphology + molecular datasets) parsimony analysis resulted in a single most parsimonious tree (MP) with TL 16993, CI 0.12, and RI 0.78 (Fig. 17). Bayesian analysis of the dataet performed in MrBayes was run for 70 million generations with the first 15 million generations discarded as burn-in. Effective sample size for all parameters after burn-in was >200. A maximum clade credibility tree from the post burn-in trees was computed in TreeAnnotator v1.6.1 (Rambaut & Drummond, 2010) (Fig. 18). The topologies resulting from the two optimality criteria were discordant.

Figure 17. Single most parsimonious tree of the scorpion genus *Centruroides* Marx, 1890 resulting from a parsimony analysis of morphology and five nuclear and mitochondrial gene loci in TNT v1.1 (Goloboff *et al*., 2008) (length 16993, consistency index 0.12, and retention index 0.78). Node values are bootstraps. Shading signifies relation to clades recovered in an analysis of molecular data: Clade A- Blue, Clade B- Red, Clade C- Green, Clade D- Yellow.

# Figure 17- Part 1



# Figure 17- Part 2

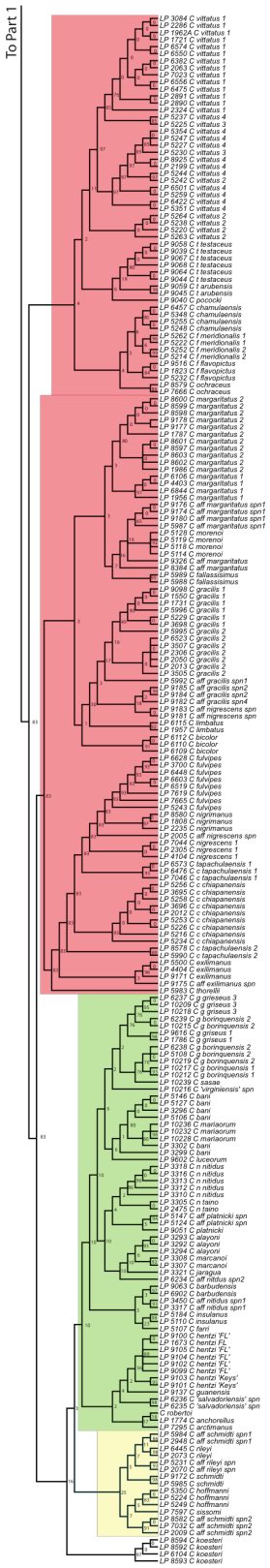


Figure 18. Maximum clade credibility tree computed from post burn-in trees in a Bayesian analysis of morphology and five nuclear and mitochondrial gene loci inferred in MrBayes (Ronquist & Huelsenbeck, 2003). Analysis was run for 70 million generations with the first 15 million generations discarded as burn-in. Effective sample size for all parameters after burn-in was >200. Node values are posterior probablitites, shading signifies relation to clades recovered in an analysis of molecular data: Clade A- Blue, Clade B- Red, Clade C- Green, Clade D- Yellow.

**Figure 18- Part 1**

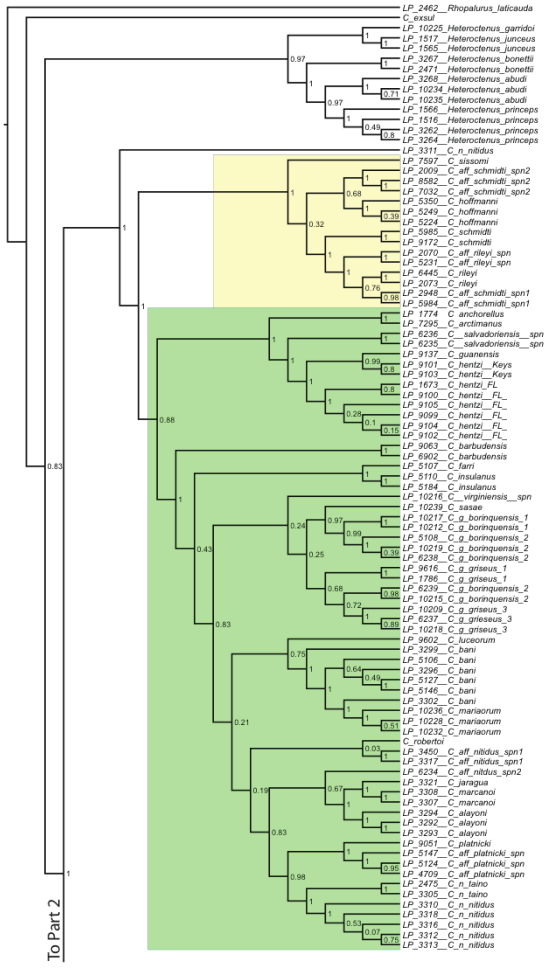
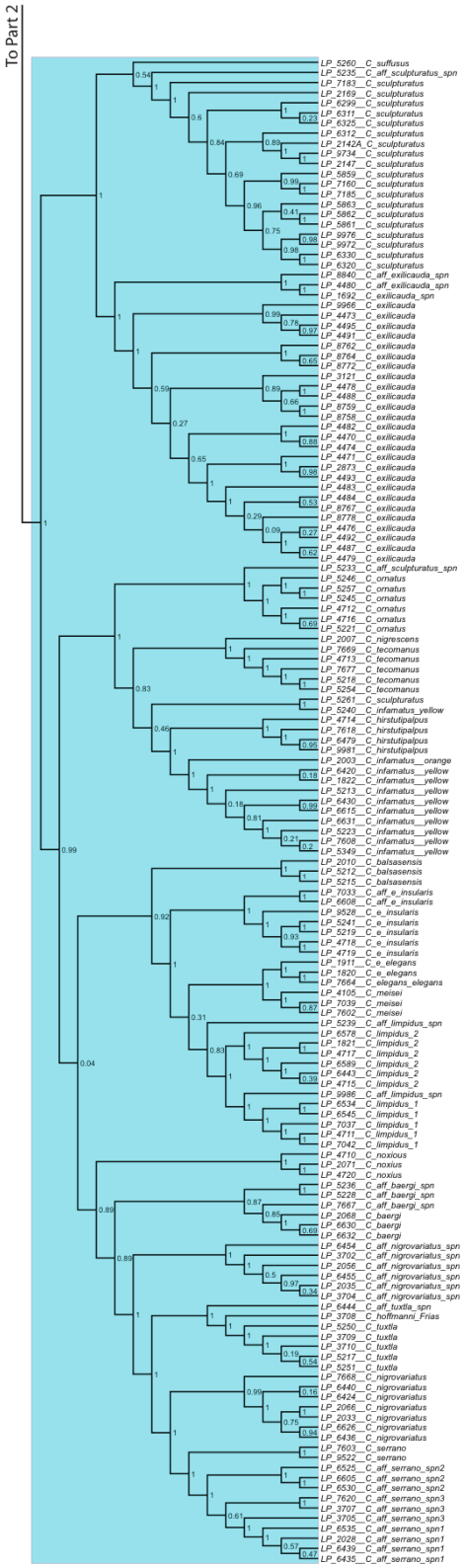


**Figure 18- Part 2**



**Figure 18- Part 3**



The total evidence parsimony analysis resulted in a topology differing significantly from phylogenies inferred from the separate analyses of molecular and morphological data. *Centruroides* was recovered as a weakly supported monophyletic group, sister to *Heteroctenus*. *Centruroides exsul* (Meise, 1934), endemic to the Galápagos, was recovered as the basal-most taxon, sister to all other *Centruroides*, a relationship based on morphological data alone. Clade A, the North American clade, was recovered as a monophyletic group with moderate support (Bootstrap= 83). In disagreement with the molecular phylogeny but congruent with the morphological phylogeny, Clade B, the Mesoamerican clade, was recovered in two parts: one clade containing species endemic to Mexico and the Lesser Antilles, and another containing both widely distributed species and Central American endemics. Clade B was paraphyletic with respect to Clades C and D. *Centruroides koesteri* Kraepelin, 1912, endemic to Costa Rica and Nicaragua, is recovered as sister to Clades C and D, which form a monophyletic group. Clade C, the Caribbean clade, is monophyletic, albeit weakly supported. Sister to Clade C, is Clade D, the Yucatan/Chortis Block clade, also weakly supported.

The Bayesian total evidence phylogeny differed from the parsimony phylogeny in the placements of *C. exsul* and *C. koesteri*, and in recovering the monophyly of Mesoamerican Clade B. *Centruroides exsul* was recovered as basal to *Centruroides* + *Heteroctenus*, rendering *Centruroides* paraphyletic with respect to *Heteroctenus*. All other *Centruroides* were recovered as a well-supported (posterior probablility (PP)=1) monophyletic group, sister to *Heteroctenus*. Four well supported primary clades were recovered within *Centruroides*, arranged in two bifurcating sister clades, one containing

Clades A and B, the other containing Clades C and D. *Centruroides koesteri* was recovered as sister to Clades A and B with high support (PP=1).

Of the subgroups previously proposed, the "striped group" was recovered in its entirety in both analyses with two exceptions: the exclusion of *Centruroides vittatus* (Say, 1821), and the inclusion of *Centruroides noxius* Hoffmann, 1932. One of the two proposed subgroups within the "striped group" was also recovered, the "*limpidus-elegans*" subgroup (with the exception of *Centruroides tecomanus* Hoffmann, 1932). Within the non-striped group, the "*thorellii"* subgroup was recovered in both analyses to the exclusion of two taxa: *C. thorellii* and *C, chamulaensis*. Neither the "*bertholdii*" subgroup nor the "*gracilis*" subgroup were recovered, however. The taxa contained in both subgroups, with the exception of *C. noxius*, were recovered in Clade B (paraphyletic in the Bayesian analysis).

**Discussion**

Previous analyses of molecular data demonstrated the presence of four geographically delimited clades within *Centruroides* (Esposito & Prendini, in prep). Clade-specific phylogenetic analyses of molecular data provide strong evidence for widespread cryptic speciation within the group (Figs. 15-18). The extent of cryptic species diversity within *Centruroides* was expected. Many of the species, as currently defined, are polymorphic and have thus represented taxonomic problems (Sissom & Lourenco, 1987; Lourenco & Sissom, 1996). Among closely related species, it should be anticipated that species occupying the same habitat type exhibit some degree of morphological similarity or convergence. This has likely been the source of taxonomic

confusion within *Centruroides*. A clearer picture of the species diversity will enable descriptions of species as discrete, diagnosable phylogenetic units.

The strategy employed in this study allows for the identification of OTUs using molecular data for subsequent morphological scoring. The OTUs identified do not represent taxonomic decisions, but rather allow for the determination of appropriate exemplars (Prendini, 2001d) in order to construct a morphological matrix that accurately reflects both inter- and intraspecific variation. This approach results in morphological coverage at the population and species levels as well as allowing for the inclusion of potentially undescribed species.

This morphological analysis is the first phylogenetic analysis of morphological characters ever performed on *Centruroides*. The morphological matrix incorporates traditionally used characters, such as color, by categorizing patterns in a systematic and objective manner across all species. In some cases, these characters are phylogenetically meaningful, such as with Hoffman's (1932) '*limpidus-elegans*' subgroup, defined by four discrete lines on the carapace and tergites. In other cases, such as the presence of a pair of lateral band on the tergites used to define the 'striped' group (Hoffmann, 1932), the character is not phylogenetically informative.

The species groups defined from Mexico (Hoffmann, 1932; Ponce-Saavedra & Moreno-Barajas, 2005) were partially recovered in the morphological analysis. The "*limpidus-elegans*" subgroup was recovered as Clade A-3 (Table 9) with the exception of *C. balsasensis*. Specimens identified tentatively as *C. pallidiceps* were genetically identical to *C. exilicauda*, and the validity of the taxon could not be further verified. The "*suffusus-infamatus*" subgroup was also partially recovered in the morphological analysis

(Fig. 16, Clade A-4) with the exception of *C. exilicauda*, which formed a monophyletic clade with *C. sculpturatus* (Fig. 16, Clade A-1), *C. vittatus*, which falls within the clade B-1, and *C. suffusus*, which forms a clade with *C. noxius* (Fig. 16, Clade A-2). The "*thorellii*" group (Ponce Saavedra & Moreno Barajas, 2005), a misnomer due to the fact that *C. thorellii* is not a part of the clade, was also recovered in part (Fig. 16, Clade D). However, neither *C. chamulaensis*, which is within clade B-2, or *C. tuxtla*, which is within cladeA-4, belong to this group. Neither the "*gracilis*" nor the "*bertholdii*" (Hoffmann, 1932; Ponce Saavedra & Moreno Barajas, 2005) groups were recovered, although both belong in part to Clade B (1&2).

The results of total evidence analyses (combined morphological and molecular data) based on parsimony and Bayesian optimality criteria differed in several important respects. The correct placement of *C. koesteri* has been difficult to discern using molecular data (L.A. Esposito & L. Prendini, in prep.). The taxon has been recovered in three possible positions: sister to Clade A + B, sister to Clade A, or sister to Clade B. In the parsimony analysis of combined data, a new position for the taxon was recovered: as sister to Clades C and D. There was low support for this position, however, and the Bayesian analysis recovered the taxon as sister to Clades A and B with high support (PP=1). This is the most plausible position for the species, given its distribution (endemic to Costa Rica and Nicaragua) and general morphology (moderately large, stongly curved aculeus, ventral metasomal stripe absent).

Another source of incongruence is the placement of *C. exsul*. In the parsimony analysis, this species is recovered as sister to all other *Centruroides*, and in the Bayesian analysis it is recovered as sister to *Centruroides* + *Heteroctenus*. The absence of

molecular data for this species may have affected its placement (Novacek, 1992; Weins & Moen, 2008), determined exclusively on the basis of morphology.

The most notable difference between the total evidence topologies obtained is in the monophyly and placement of Clade B, rendered paraphyletic with respect to Clades C and D in the parsimony analysis. However, the bootstrap support for the basal nodes of the *C. vittatus* clade was very low. The Bayesian analysis recovered a highly-supported (PP=1) monophyletic Clade B, sister to Clade A (PP=1). This placement is better supported and congruent with previous molecular analyses.

The phylogeny resulting from the Bayesian analysis is the preferred topology. The inter-clade relationships are consistent with those recovered in previous analyses, consistently well supported, and biologically meaningful. The placement of *C. koesteri* is congruent with previous results. The biggest difference between the total evidence Bayesian topology and the results of all other analyses conducted is the placement of *C. exsul*, rendering *Centruroides* paraphyletic. The possibility that this placement is an artefact of the absence of molecular data for this species cannot be disregarded, but its basal position in the morphological analysis, taken together with its isolated distribution in the Galapagos, merit further investigation.

Traditionally, the greatest diversity of *Centruroides* has been in Mexico (Hoffmann, 1932; Ponce-Saavedra & Moreno-Barajas, 2005). There are currently 71 recognized species and 5 recognized subspecies in the genus (Fet & Lowe, 2000; Teruel 2001, 2006, 2007; Teruel & Stockwell, 2002; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009). However, the results of this study suggest that not only is there greater species-level diversity across the genus

than previously recognized, but the diversity in other regions of the distribution is equal to that of the Mexican fauna. At least 98 morphologically and genetically unique OTUs can be recognized from the material examined in this research. In many cases there was insufficient material available to decide whether all of the OTUs identified are new species. The diversity of the genus would increase by 25 percent, should they prove to be.

This study is the first comprehensive phylogenetic study of the genus *Centruroides*. The analyses have identified four major clades and 98 OTUs, which have implications for a considerable amount of cryptic diversity within the genus. A major taxonomic revision of the genus, resulting from this information obtained through study, is currently underway.

**Acknowledgements**

I would like to thank the following people for help in the field and for providing specimens: Lorenzo Prendini, Francisca Almeida, Oscar Francke, Jeremy Huff, Kelvin Guerrero, Camilo Mattoni, Jose Ochoa, Sarah Crews, Edmundo Gonzalez, Adriano Kury, and Alexander Tietz. Thank you to Lorenzo Prendini and Erich Volschenk for providing unpublished characters for the morphology matrix. A huge thank you to Edmundo Gonzalez for providing input and his tremendous knowledge on the Mexican species and geography. I would like to thank the following people for assistance in lab work: Gena Esposito, Sarah Schoenbrun, Sylvia Johnson, Michelle Yim, Ofelia Delgado, and Tricia Rubi. Last, but not least I would like to acknowledge the following sources of funding for providing support for fieldwork, labwork and graduate fellowships: NSF Doctoral

Dissertation Improvement Grant (0910147), NSF GK-12 Fellowship, NSF DEB Grant (0413453) awarded to Lorenzo Prendini, City University of New York/NSF AGEP Grant, City University of New York Presidential Fellowship, City University of New York College Now Fellowship, Museum of Comparative Zoology Ernst Mayr Award, American Museum of Natural History Theodore Roosevelt Award, and the Richard Lounsbery Foundation (awarded to Lorenzo Prendini).

**CHAPTER FOUR:** A disjunct distribution reveals evidence for an island ancestor in the New World buthid scorpion genus *Centruroides* Marx, 1890

**Abstract:** This study investigates the biogeographic patterns in the New World buthid scorpion genera *Rhopalurus* Thorell, 1876, *Heteroctenus* (Pocock, 1897), and *Centruroides* Marx, 1890; tests the relative roles of vicariance and dispersal in explaining the present disjunct distribution of the genera; and determines the ancestral distribution of the scorpion genus *Centruroides*. A fossil-calibrated phylogeny was estimated to infer the dates of key speciation events. The relative likelihood of vicariance or dispersal in explaining the present distributions of taxa was calculated. Bayesian and parsimony optimality criteria were used to infer ancestral distributions of the genera. *Centruroides* was recovered as sister to the Greater Antilles endemic genus *Heteroctenus*, rendering the *Rhopalurus* group paraphyletic. The date of the ancestral node for the *Heteroctenus* + *Centruroides* clade has a 95% confidence interval of {29.0, 42.9} mya. There was no significant difference among models emphasizing vicariance or dispersal. The ancestral distribution of the *Heteroctenus* + *Centruroides* clade is inferred to be South America and the Greater Antilles. The ancestral distribution of *Centruroides* is inferred to be North America. The likelihood models of distribution analyzed in Lagrange support dispersal versus vicariance. However, the inferred ancestral distributions are also congruent with GAARlandia, as this is the most parsimonious explanation for a South America-Greater Antilles distribution. The Greater Antilles distributed sister taxon of *Centruroides* provides evidence for a Caribbean ancestor for the genus, which subsequently colonized North and Mesoamerica before re-colonizing the Caribbean.

## Introduction

Scorpions are a largely untapped resource for understanding biogeographical patterns. They represent one of the oldest invasions of terrestrial habitats by arthropods (Sissom, 1990). Their presence on contemporary land formations predates many geological events (Kjellesvig-Waering, 1986), making them good candidates for vicariance models. Additionally, different lineages of scorpions have different dispersal abilities. Some lineages are narrowly endemic, have specialist habitat requirements. Others are opportunistic, with generalist habitat requirements, making them good colonizers. Scorpions have sufficient representation in the fossil record (Kjellesvig-Waering, 1986) allowing for the inference of fossil-calibrated molecular phylogenies that could be used to calculate divergence times and test competing biogeographical hypotheses. Despite all of this, there have been few peer-reviewed scorpion biogeography publications utilizing molecular techniques or modern analytical tools (Yamashita & Fet, 2001; Gantenbein *et al.*, 2007).

The New World contains some of the most dangerous and diverse genera in the scorpion family Buthidae. The genus *Centruroides* Marx, 1809 is distributed from the southern United States, México, Central America and the Caribbean to northern South America. These scorpions often live in and around vegetation, which suggests they may be good potential rafters (Sissom, 1990). The buthid genera *Heteroctenus* (Pocock, 1897) and *Rhopalurus* Thorell, 1876, have narrower habitat requirements (savannah), and a disjunct distribution attributable to vicariance (Teruel, 2006). They are distributed in the open-grasslands of eastern Brazil, northwestern South America and the Greater Antillian islands of Cuba and Hispaniola (Prendini *et al.*, 2009). The paraphyly of *Rhopalurus* with

respect to *Centruroides* was recently demonstrated (Esposito *et al.*, in prep.), the results of which led to the revalidation of *Heteroctenus*, and suggested that the interplay between taxa on the Caribbean islands (*Heteroctenus*, *Centruroides*), North America (*Centruroides*) and South America (*Rhopalurus*) were pivotal in the formation of the present-day diversity of the genera. However, questions concerning the importance of dispersal and vicariance have not yet been explored. We present a fossil-calibrated phylogeny for *Centruroides*, *Rhopalurus* and *Heteroctenus*, which will be used to infer the relative role of vicariance and dispersal in forming the present day distributions of these taxa.

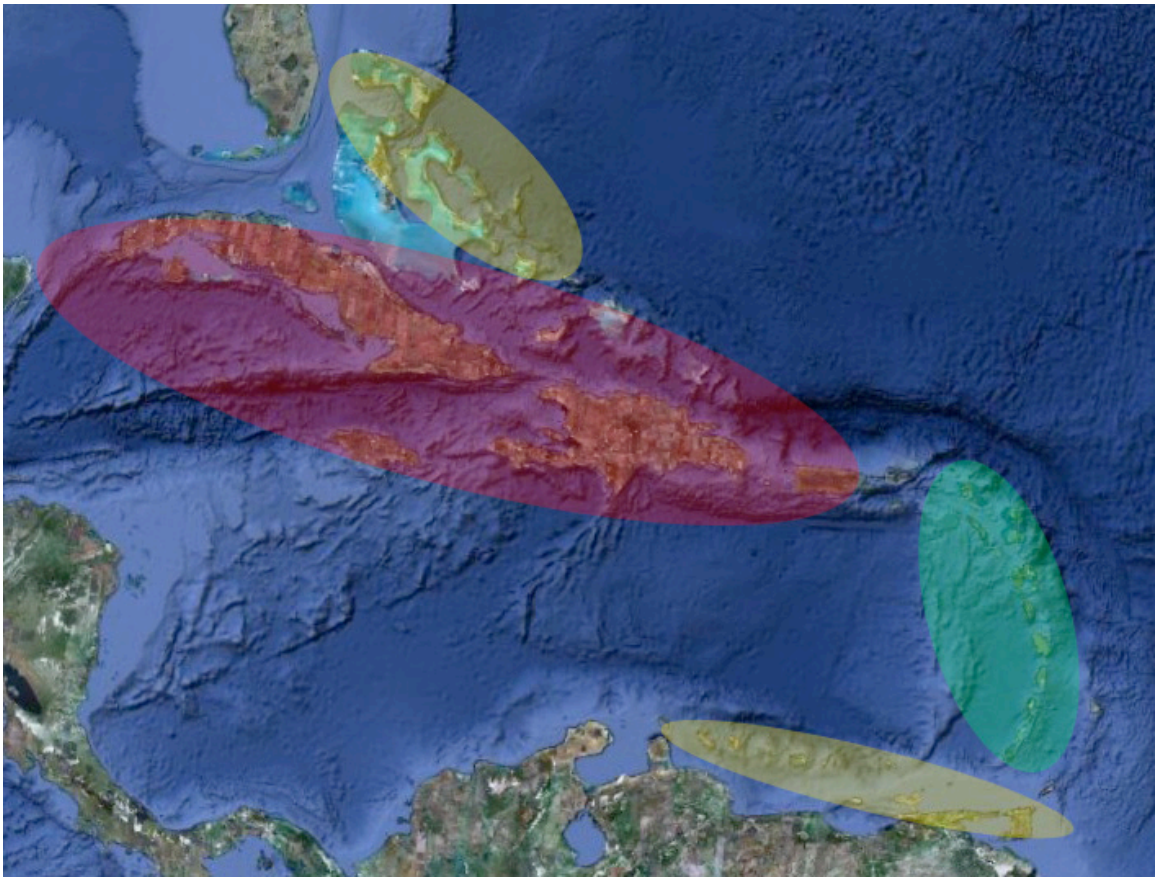
***Caribbean Biogeography***

The biodiversity of the Caribbean region is a complex assemblage of organisms resulting from vicariance and dispersal events between North and South America. The Caribbean contains over 7000 islands and is nearly 4000 km long, with ecosystems ranging (often on a single island) from desert to evergreen forest. It is comprised, principally, of three island groups: the Greater Antilles, the Lesser Antilles, and the Bahamian islands (Fig. 19).

The Greater Antilles consists of the ‘fragment islands’ of Jamaica, Puerto Rico, Hispaniola and Cuba. While western Cuba and western Jamaica are likely fragments of Continental origin (Iturralde-Vinent and MacPhee, 1999), the remainder of the present day Greater Antilles originated as the ‘proto Greater Antilles’. Their formation originated with the subduction of the oceanic lithosphere between the North and South American plates, creating a hotspot of island formation in the Cretaceous (145–65 mya) (Ladd,

Figure 19. Map of the Caribbean region highlighting geologically distinct island formations. Red- Greater Antilles fragment islands, Green- Lesser Antilles Darwinian islands, Yellow- platform islands.

**Figure 19**



1976; Coney, 1982; Santiago-Valentin and Olmstead, 2004). As the Caribbean plate moved eastward between the North and South American continents, the proto-Greater Antilles began to drift, and the subsequent eastward movement of the Caribbean plate broke the moving landmass into smaller islands (Iturralde-Vinent & MacPhee, 1999; Mann *et al.*, 2002). Eventually colliding with the shallow Bahamas bank in the northern Caribbean basin, the now fragmented proto-Greater Antilles entered a renewed period of subduction, volcanism, and orogeny (Lewis & Draper, 1990; Santiago-Valentin & Olmstead, 2004). The formation of the Cayman trench, a major fault south of Cuba, pushed western Jamaica, a fragment of the Chortis Block (present-day Nicaragua, Guatemala, Honduras), towards the Greater Antilles. The present configuration of the landmasses of the Greater Antilles have had various configurations in the past, adding to the complexity of their historical biogeography (Ricklefs & Bermingham, 2008).

The Lesser Antilles are a considerably younger (~20 mya) formation of 'Darwinian islands' (Mann *et al.*, 2002) comprised of an active volcanic arc to the west, and a series of islands to the east created by the uplifting of marine sediment during the movement of the Caribbean plate (Ricklefs & Bermingham, 2008). With the exception of a few small groups connected by shallow banks, there have been no connections among the Lesser Antilles or the continental crust (Ricklefs & Bermingham, 2008). The Bahamian islands are an old, stable, geologically distinct chain of 'platform islands' formed from the accumulation of carbonate marine sediments (Meyerhoff *et al.*, 1974; Mullins & Lynts, 1977).

Within this geological context, three major categories of hypotheses have been postulated to explain the present patterns of diversity in the Caribbean region: (1)

connections via land bridges, (2) vicariance events, and (3) overwater dispersal from continents and between islands. Evidence from herpetofauna (principally *Anolis)* (Williams, 1989; Crother & Guyer, 1996; Hegdes, 1996a, 1996b, 1996c; Hedges & Heinicke, 2007; Heinicke *et al.*, 2007), as well as multiple plant lineages (Michelangeli *et al.*, 2008) has been used to argue that the absence of lineages older than the breakup of the proto-Antilles precludes a vicariance origin. Stemming from these lines of evidence, researchers argue for the initial colonization of most taxa via overwater dispersal on flotsam. In contrast, other studies suggested that vicariance played a larger role than dispersal in the initial colonization of the Caribbean, for example in lizards (Crother & Guyer, 1996; Iturralde-Vinent & MacPhee, 1999; Van Ee *et al.*, 2008) and some plants (Van Ee *et al.*, 2008).

One vicariance hypothesis was proposed to explain the disjunct distribution of some mammal groups in the Greater Antilles and South America: the GAARlandia (Greater Antilles + Aves Ridge) hypothesis (Iturralde-Vinent and MacPhee, 1999). Using geological data, including fossil evidence, Iturralde-Vinent and MacPhee (1999) demonstrated the likely existence of a land bridge connecting South America to the Greater Antilles during the Eocene Oligocene transition 35–33 million years ago. The proposed subsequent break-up of the proto-Antilles emphasizes the role of vicariance in the colonization of the Greater Antilles. The GAARlandia hypothesis was tested using molecular evidence from several mammal (Dávalos, 2004), plant (van Ee *et al.*, 2008; Fritsch & McDowell, 2009; Lavin *et al.*, 2001; Lavin & Matos, 2008; Francisco-Ortega *et al.*, 2008), and arachnid (Teruel, 2006; Crews & Gillespie, 2010) lineages, with conflicting results. Results from some lineages were consistent with the model, however

others did not fit the predictions of divergence times required. Dávalos (2004), drawing from mammal data, concluded that a general biogeographic pattern for the initial colonization of the Greater Antilles does not exist, and patterns should be treated on a taxon-by-taxon basis. We test the GAARlandia hypothesis on the phylogeny of *Centruroides*, *Rhopalurus* and *Heteroctenus*, and infer the distributions of ancestral nodes.

## Methods

### *Taxon Sampling*

Each described species in the genus *Centruroides* was sampled from the type locality, or vicinity (Appendix 9). Wherever possible, one additional specimen from an alternate locality was also included. Excluded from this study are *C. exsul* (Meise, 1934) from the Galápagos; *C. underwoodi* Armas, 1976 from Jamaica, known only from two specimens; and ten species endemic to Cuba that could not be obtained: *C. navarroi* Teruel, 2001; *C. melanodactylus* Teruel, 2001; *C. galano* Teruel, 2001; *C. polito* Teruel, 2007; *C. spectatus* Teruel, 2006; *C. baracoae* Armas, 1976; *C. stockwelli* Teruel, 2001; *C. nigropunctatus* Teruel, 2006; *C. robertoi* Armas, 1976; *C. alayoni* Armas 1999. All described Greater Antilles species from the genus *Heteroctenus* were included except two Cuban endemics which could not be obtained: *Heteroctenus granulimanus* (Teruel, 2008) and *Heteroctenus gibrarae* (Teruel, 2008). Additionally, we included outgroup species from the New World buthid genera *Tityus* C.L. Koch, 1836, South American *Rhopalurus*, and *Zabius* Thorell, 1894. Outgroup taxa were selected on the basis of their inclusion in the New World buthid lineage (Fet *et al.*, 2003; Coddington *et al.*, 2004). The

cosmopolitan buthid species *Isometrus maculatus* (DeGeer, 1778) was used as a root on the basis of the proposed relationship between the New World buthids and the buthid subfamily Isometrinae Birula, 1917 (Kraepelin, 1899; Fet *et al.*, 2003).

### *Field Methods*

Specimens were collected in the field using ultraviolet light and preserved by submersion of live animals in 95% ethanol, and subsequently injected with ethanol to improve the internal preservation. Specimens are stored at -20°C at the American Museum of Natural History.

### *Laboratory Methods*

Genomic DNA was extracted from muscle tissue of the fourth leg of each specimen using a Qiagen DNEasy Blood and Tissue extraction kit according the manufacturer's protocols. Extracted DNA was amplified for five gene regions in overlapping fragments using universal eukaryote and scorpion specific primers (see Table 10). Five gene loci were selected for this study based on their ability to provide resolution at various taxonomic levels: a mitochondrial protein-coding gene (Cox1), mitochondrial structural genes (12S rDNA, 16S rDNA), and nuclear structural genes (18S rDNA, 28S rDNA) (Arnedo *et al.*, 2002; Giribet *et al.*, 2001; Harrison *et al.*, 1987; Hayashi, 1996; Hillis & Dixson, 1991; Wahlberg & Zimmerman, 2000). PCR was performed using an Epicenter thermocycler (Eppendorf) using GoTaq polymerase (Promega). Reactions were verified on a 1.2% agarose gel stained with Sybr safe DNA gel stain (Invitrogen), and subsequently purified using the Ampure DNA (Agencourt) purification system on a

**Table 10.** Primers used for amplification of 12S, 16S, 18S, 28S and Cox1 in a fossil-calibrated biogeographical analysis of the New World scorpion subfamily Rhopalurusinae Bücherl, 1971.

| Gene | Primer | Sequence | References (other names) |
|---|---|---|---|
| 12S | 12Sai | AAACTAGGATTAGATACCCTATTAT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-N-14588) |
| | 12Sbi | AAGAGCGACGGGCGATGTGT | Kocher *et al.,* 1989; Simon *et al.,* 1994 (SR-J-14233) |
| 16S | 16Sar | CGCCTGTTTATCAAAAACAT | Simon *et al.,* 1994 (LR-N-13398) |
| | 16Sbr | CTCCGGTTTGAACTCAGATCA | Simon *et al.,* 1994 (LR-J-12887) |
| 18S | 18S1F | TACCTGGTTGATCCTGCCAGTAG | Prendini *et al.,* 2005 |
| | 18S5R | CTTGGCAAATGCTTTCGC | Prendini *et al.,* 2005 |
| | 18S3F | GTTCGATTCCGGAGAGGGA | Prendini *et al.,* 2005 |
| | 18Sbi | GAGTCTCGTTCGTTATCGGA | Prendini *et al.,* 2005 |
| | 18SA2.0 | ATGGTTGCAAAGCTGAAAC | Prendini *et al.,* 2005 |
| | 18S9R | GATCCTTCCGCAGGTTCACCTAC | Prendini *et al.,* 2005 |
| 28S | 28Sa | GACCCGTCTTGAAGCACG | Nunn *et al.,* 1996 (D3A |
| | 28Sbout | CCCACAGCGCCAGTTCTGCTTACC | Prendini *et al.,* 2005 |
| Cox1 | LCO | GGTCAACAAATCATAAAGATATTGG | Folmer *et al.,* 1994 (LCO-1490-J-1514) |
| | HCOoutout | GTAAATATATGRTGDGCTC | Prendini *et al.,* 2005 |
| | LE1R | TCCATTCCCACAGTAAACATATG | |
| | HCOEXTERNA | GAAGTTTATATTTTAATTTTACCTGG | |
| | HCOEXTERNB | CCTATTGAWARAACATARTGAAAATG | |

Biomek NX robot (Beckman-Coulter). Cycle sequencing was conducted using Big Dye v1.1 and automated Sanger sequencing of single stranded DNA performed on an Applied Biosystems Inc. Prism™ 3730x. Paired strand reads were aligned using Sequencher™ and edited by hand. Sequences are accessioned in GenBank (Appendix 9).

### *Phylogenetic Methods*

Multiple sequence alignments for individual gene partitions were performed in MAFFT (Katoh *et al.*, 2002, 2005) using the G-INS-i strategy and PAM1/K=2 matrix parameter. All loci were aligned, however there was no length variation in Cox1, negligible length variation in 18S and 28S (<10 nucleotides), and little length variation in 12S and 16S (<20 nucleotides). The resulting alignments were manually edited in Geneious (Biomatters, Ltd.).

The concatenated dataset, partitioned by gene and codon position, was analyzed in raxmlHPC v7.0.4 (Stamatakis, 2006). Each partition was analyzed under the GTR+Γ model (Yang, 1994). RAxML employs a rapid search algorithm that quickly searches tree space, but does not always recover the tree with the best likelihood, thus multiple runs (2) were performed in combination with the 'rapid bootstrap' algorithm.

### *Divergence Time Estimation*

A fossil-calibrated phylogeny was estimated in BEAST v1.6.1 using a relaxed molecular clock with unlinked partitions (Drummond *et al.*, 2006). Each partition was analyzed under the GTR+Γ model. The resulting best tree from the RAxML analysis was transformed into an ultrametric tree using nonparametric rate smoothing over the branch

lengths in TreeView v1.0 (Page, 1996). The tree was then rooted and scaled to reflect the age and topological constraints imposed on the Bayesian priors and used as a starting tree for the BEAST analysis. An uncorrelated lognormal tree prior was used for dating, with a Yule speciation tree prior. Models and molecular clocks for each partition were unlinked. A lognormal distribution was used for fossil calibration points with the mean age of the fossil equal to the lognormal mean and the fossil dating error equal to the lognormal standard deviation.

The analysis was run for 50 million generations, sampling every 5000$^{th}$ generation. Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (Rambaut and Drummond, 2007), and convergence was assessed by the standard deviations of the split frequencies. The first 5 million generations were discarded as burn-in. A maximum clade credibility tree was computed from the post-burn-in trees in TreeAnnotator v1.6.1 (Rambaut & Drummond, 2007).

Fossils of *Centruroides* are known from Dominican amber deposits dating to the early Miocene (Grimaldi & Engel, 2005). Some authors have assigned these fossils to extant taxa (Armas, 1988). This is unlikely given the age of the fossils, although they are morphologically similar to many Caribbean species and can be assigned with a high degree of certainty to this clade. Fossils of *Tityus* have also been described from Dominican amber (Santiago-Blay & Poinar, 1988). An additional fossil has been described from Chiapas amber deposits, contemporaneous with Dominican amber (Santiago-Blay & Poinar, 1993; Grimaldi & Engel, 2005). The Chiapas amber specimen was only putatively assigned to *Centruroides* upon description and no additional assessment of this placement has ever been published. The photographs and descriptions

of the specimen clearly relate it to a group of small, arboreal species from northern Mesoamerica, including *Centruroides schmidti* author, date and other species with an ovate telson, a prominent, ridge-like subaculear tubercle, and elongated pedipalps and metasoma. Minimum age calibration points for the BEAST analysis were taken from a combination of the amber fossils (minimum age constraints) and the date of South America's separation from Antarctica in the Eocene, the last possible connection between Isometrinae and the New World buthids via the Trans-Antarctic exchange (Table 11) (Sanmartin & Ronquist, 2004).

### *Ancestral Distribution Reconstruction*

Ancestral distributions were reconstructed under both Bayesian and Maximum Parsimony criteria in RASP (Yu *et al.*, 2011). RASP requires three input files: a tree set (distribution of trees), a file providing the distribution of each taxon, and a consensus tree or preferred topology. In this case, the post-burnin trees from the BEAST analysis were used for the tree set, and the Maximum Clade Credibility (MCC) tree was specified as the consensus tree. Taxa were assigned to one or more of five geographical regions based on their known distributions: Australasia, South America (south of the Panamá Canal), Central America (north of the Panamá Canal, south of the Isthmus of Tehuantepec), North America (north of the Isthmus of Tehuantepec), and the Caribbean.

### *Biogeographical Hypothesis Testing*

Lagrange (Ree *et al.*, 2005; Ree & Smith, 2008) was used to test competing hypotheses of vicariance and dispersal. Lagrange uses likelihood models that consider

**Table 11.** Calibration points and sources of dates for divergence time dating analysis of New World buthid scorpions in BEAST (Drummond & Rambaut, 2007).

| Source | Clade | Minimum age |
|---|---|---|
| Dominican amber subfossil | Caribbean *Centruroides* | 15 my |
| Dominican amber subfossil | *Tityus* | 15 my |
| Chiapas amber subfossil | "*thorellii* group" | 15 my |
| South America-Antarctica Break | Centrurinae | 30 my |

differences in dispersal and extinction at various time periods, accounting for external information such as dispersal potential and the geologic history of a region. Given the complexity of the Caribbean, it is critical that this information be considered.

The analysis follows that of Crews and Gillespie (2010) who, examining spiders of the genus *Selenops* Latreille, 1890 with a distribution similar to that of *Centruroides*, identified six geological events in the Caribbean Basin critical to forming a route for dispersal between North and South America (Table 12). The relative importance of vicariance and dispersal to explain the present distribution of *Centruroides* was tested as follows: A) colonization via dispersal only (GAARlandia absent), with probability of colonization via dispersal dependant on distance; B) colonization via dispersal or vicariance (GAARlandia present), with probability of dispersal dependent on distance; C) colonization via dispersal, with probability of colonization via dispersal equal regardless of distance (GAARlandia absent); D) colonization via dispersal or vicariance (GAARlandia present), with probability of dispersal not dependent on distance (all equal); E) colonization with little dispersal (GAARlandia absent); F) colonization with little dispersal (GAARlandia present). The likelihood parameters for each hypothesis take into account the Caribbean geography for time periods corresponding to the six key events (Table 12), such that the probability of dispersal to any given landmass is dependent upon its existence at that time. For example, if the island of Grenada had not yet formed during a given time slice, then the probability of dispersal to that island is 0.

The Lagrange analysis requires the definition of geographic regions to which distributions of taxa can be assigned. Five regions were defined for this analysis: South America, south of the Panamá Canal, plus Aruba, Curaçao and Bonaire; North and

**Table 12.** Key geological events in the dispersal of organisms between North and South America.

| MYA | Geologic Event |
|---|---|
| 3.0 | Closing of the Isthmus of Panamá |
| 5.0 | Most recent appearance of Northern Lesser Antilles |
| 12.0 | Most recent appearance of Southern Lesser Antilles |
| 33.0 | Disappearance of GAARlandia |
| 35.0 | Appearance of GAARlandia |
| 55.0 | Time after which land was available in the Greater Antilles region |

Central America, north of the Panamá Canal; Greater Antilles, i.e. the Caribbean islands of Cuba, Hispaniola, Puerto Rico, and the Bahamas Bank; northern Lesser Antilles, i.e. the Lesser Antilles volcanic arc north of Martinique; southern Lesser Antilles, i.e. the Lesser Antilles volcanic arc south of Dominica.

Six analyses (A-F) were conducted using the fossil-calibrated phylogeny resulting from the analysis in BEAST. Models were constructed using dispersal matrices for each time slice in each analysis, incorporating constraints of the hypothesis and landmass availability for each time slice. The fit of each model to the fossil-calibrated phylogeny was reported as a likelihood score.

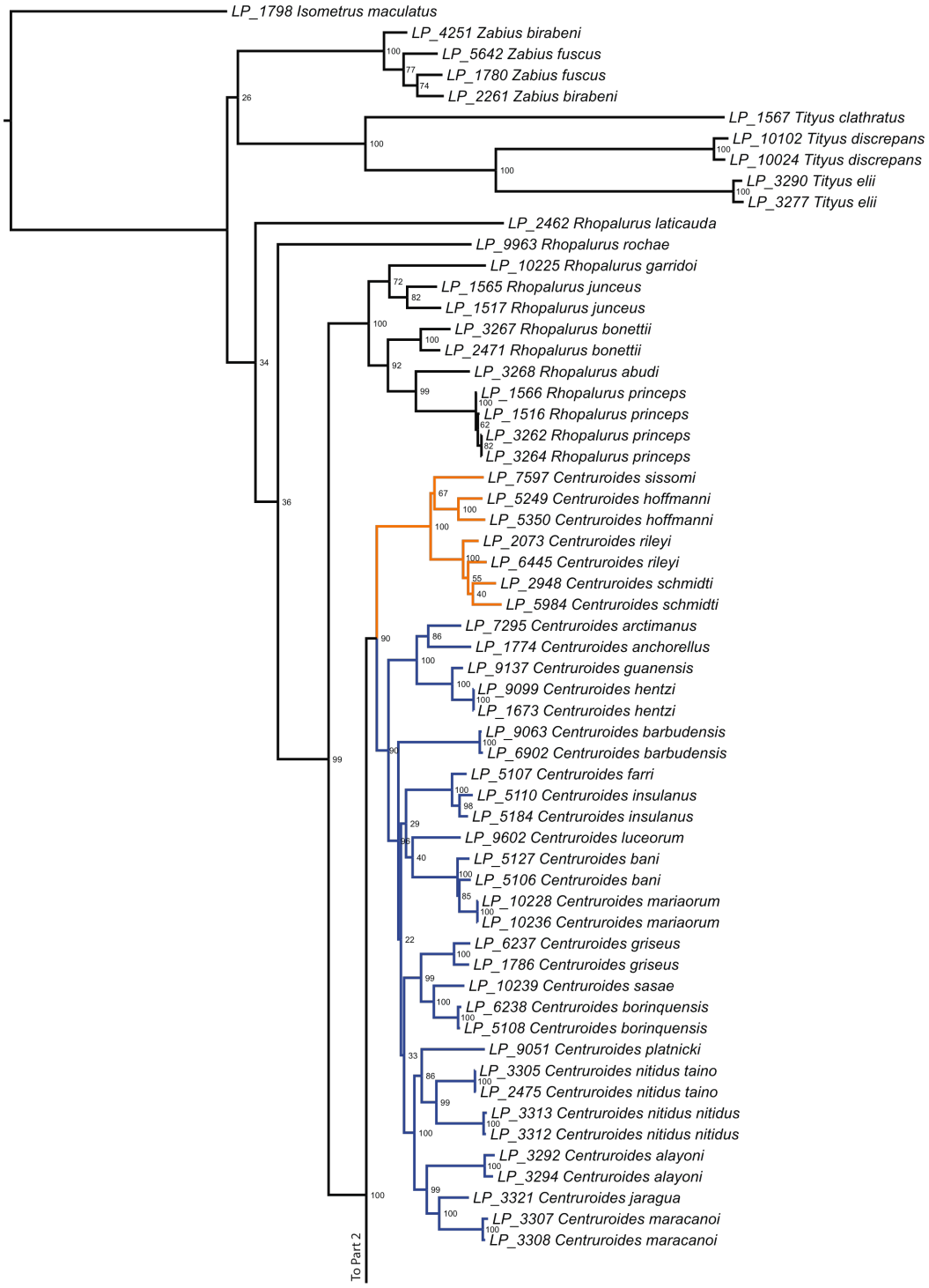
## Results

### *Phylogeny*

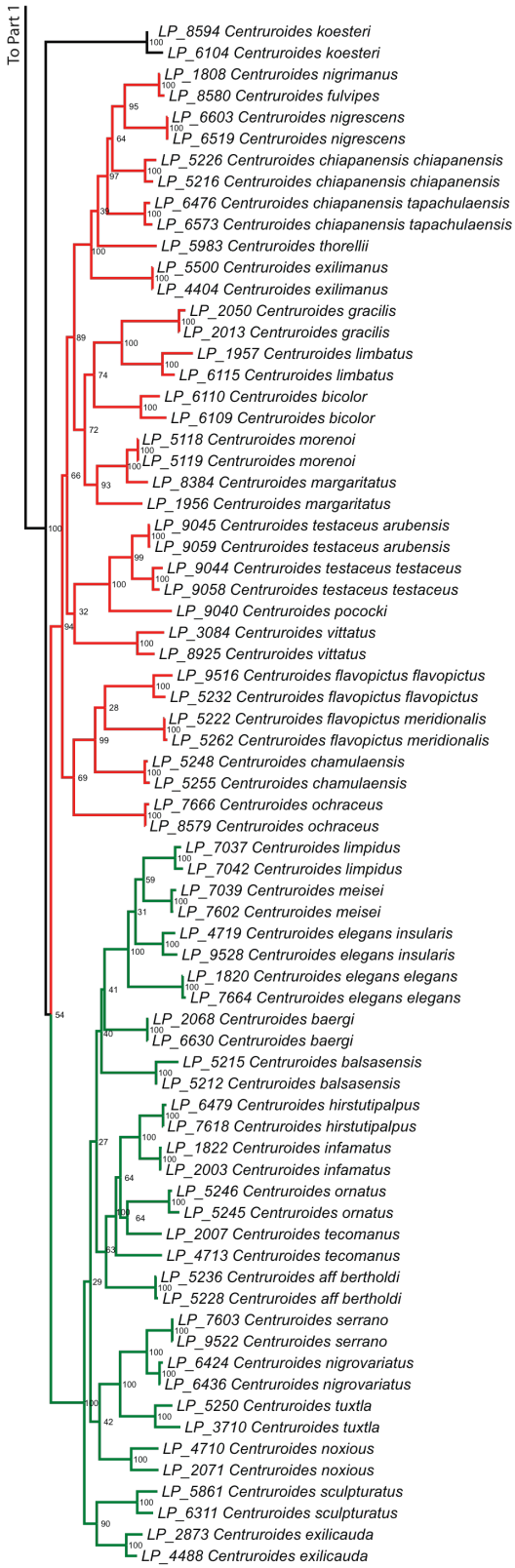
The results of the two independent RAxML runs were congruent, indicating that the tree with the highest likelihood (-47574.55) was successfully recovered (Fig. 20). The genera *Centruroides* and *Heteroctenus* were each recovered as monophyletic with high bootstrap support (BS=100). As in previous analyses, they were recovered as well-supported sister groups (BS=99). Within *Centruroides*, four distinct clades were recovered with high support: a North American clade (BS=100), a Central American clade (BS=94), a Caribbean clade (BS=90), and a clade representing the Yucatan Peninsula/Chortis Block (BS=99), where Chortis block is defined as the part of Central America south of the Motagua fault of Guatemala and north of latitude 12°30'N (Dengo, 1969; Dengo & Bohnenberger, 1969).

Figure 20. Maximum likelihood phylogram of New World buthid genera, with an emphasis on the scorpion genus *Centruroides* Marx, 1890. Phylogram inferred from five loci (12S, 16S, 18S, 28S, Cox1) under maximum likelihood optimality criteria in RAxML (Stamatakis, 2006). Node labels are bootstrap values. Red: North American *Centruroides* clade, Green: Mesoamerican *Centruroides* clade, Orange: Yucatan/Chortis Block *Centruroides* clade, Blue: Caribbean *Centruroides* clade

# Figure 20- Part 1



# Figure 20- Part 2



***Divergence Time Estimation***

The results of the fossil-calibrated phylogeny estimated in BEAST are depicted in Figure 21. Effective sample size for all parameters was >300. Nodes of interest are indicated with letters on the phylogeny. Node A depicts the split between New World Buthids and *Isometrus*, and was constrained with a minimum age in the analysis. The 95% confidence interval recovered for the age of node was {38.6, 58.6} mya. Node B depicts the split between *Heteroctenus* + *Centruroides* and the remaining New World buthids, and has a 95% confidence interval of {29.0, 42.9} mya. Node C depicts the split between *Heteroctenus* and *Centruroides* with a 95% confidence interval of {24.7, 36.7} mya. Node D depicts the split between the Caribbean clade and the Yucatan/Chortis Block clade of *Centruroides* with a 95% confidence interval of {19.8, 27.4} mya. Lastly, Node E depicts the North American clade of *Centruroides* with a 95% confidence interval of {14.3, 21.2} mya.

***Ancestral Distribution Reconstruction***

Ancestral distributions inferred under parsimony (Fig. 22) and Bayesian criteria (Fig. 23) were largely congruent. The New World buthid ancestral node was reconstructed as South American in both analyses. The distribution of (*Heteroctenus* + *Centruroides*) ancestral node was unresolved in the parsimony (MP) analysis, but was found to have a South America + Caribbean distribution in the Bayesian analysis. The *Centruroides* ancestral distribution was also unresolved in the MP analysis but found to be a North American distribution in the Bayesian analysis. All ancestral clade distributions within *Centruroides* were unresolved in the MP analysis, except for the

Figure 21. Fossil-calibrated maximum clade credibility phylogram of New World buthid scorpions inferred in BEAST (Drummond & Rambaut, 2007). Blue node bars are 95% confidence intervals of dates. Labels to the right of nodes are median ages. Nodes indicated with black asterisks have >95 posterior probability, one asterisk indicates 90< posterior probability <95, two asterisks indicates posterior probability <90. Nodes of interest, discussed in the manuscript are referred to with letters. Calibration points are indicated with red asterisks.

# Figure 21- Part 1



**Figure 21- Part 2**

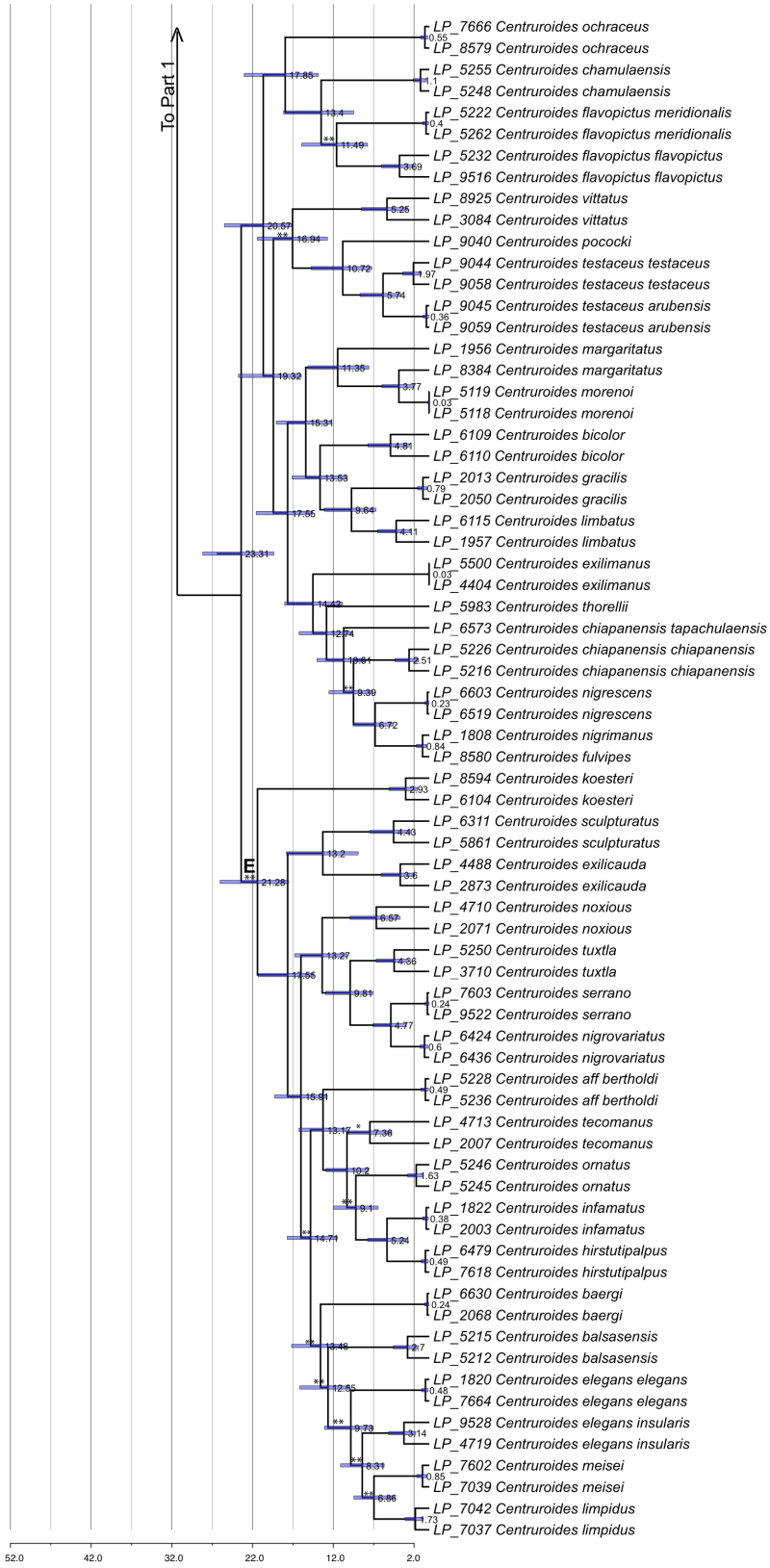


Figure 22. Ancestral distribution reconstruction of New World buthid scorpions under parsimony dispersal-vicariance criteria computed in RASP (Yu *et al.*, 2011). Node colors correspond to geographic areas as indicated in the legend.

**Figure 22**

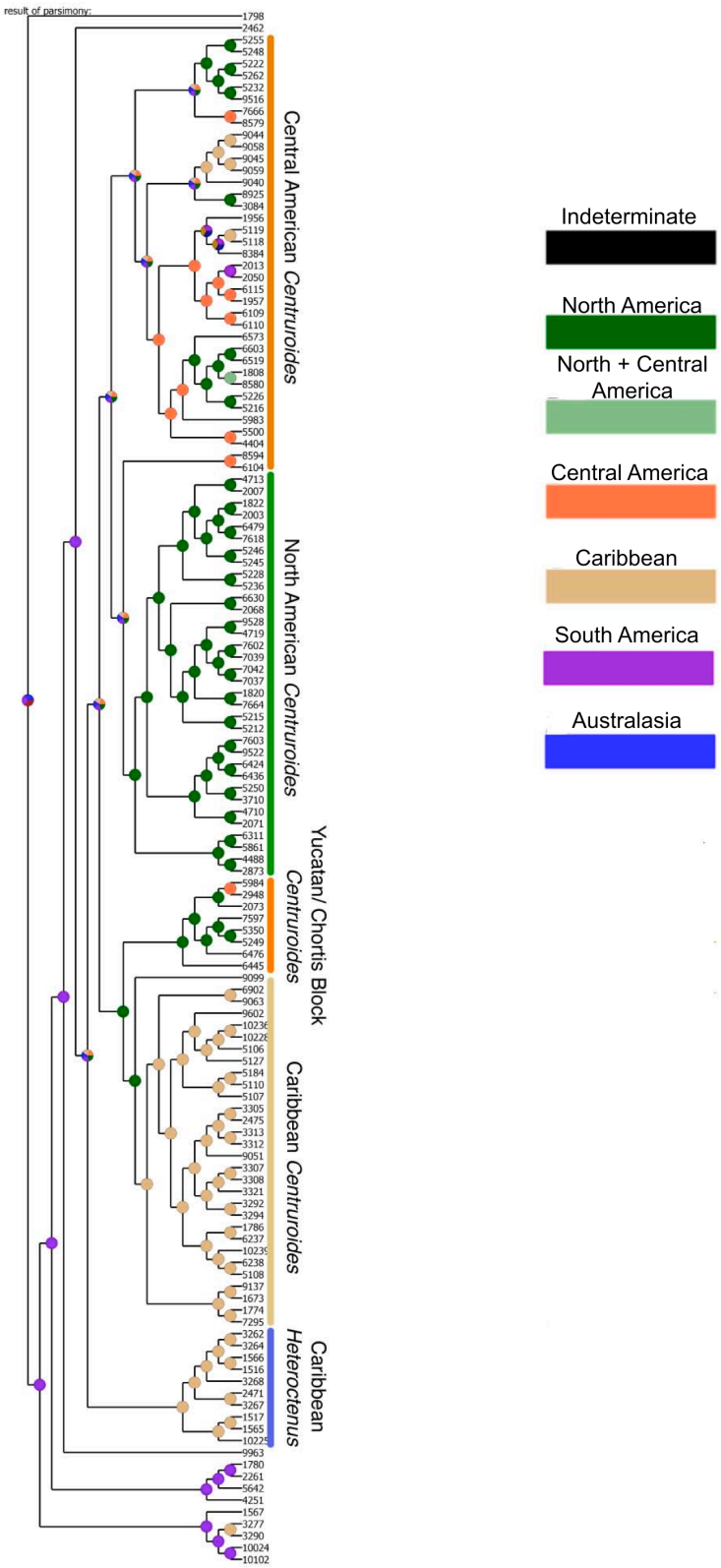
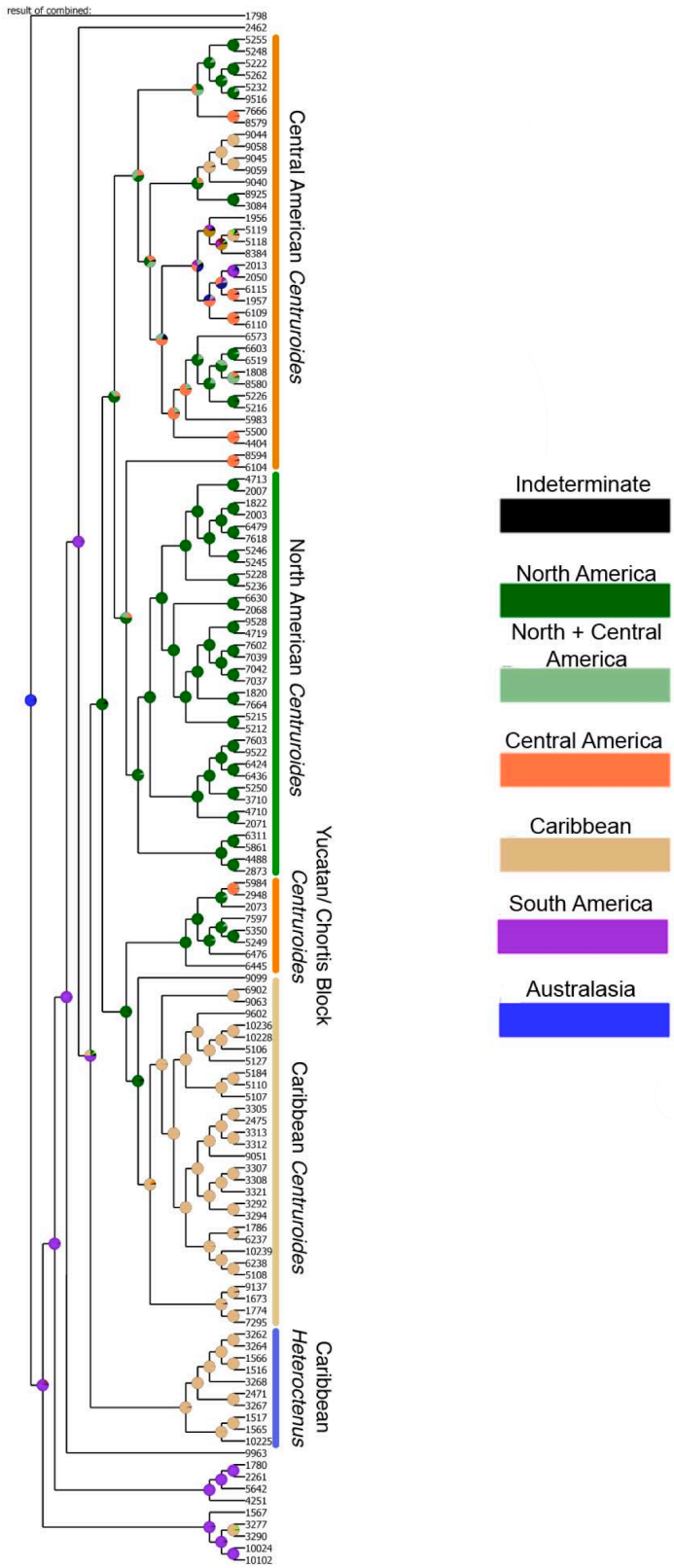

result of parsimony:
Central American Centruroides
North American Centruroides
Yucatan/ Chortis Block Centruroides
Caribbean Centruroides
Caribbean Heteroctenus
Indeterminate
North America
North + Central America
Central America
Caribbean
South America
Australasia

Figure 23. Ancestral distribution reconstruction of New World buthid scorpions under Bayesian dispersal-vicariance criteria computed in RASP (Yu *et al.*, 2011). Node colors correspond to geographic areas as indicated in the legend.

**Figure 23**


result of combined:
Central American Centruroides
North American Centruroides
Yucatan/ Chortis Block Centruroides
Caribbean Centruroides
Caribbean Heteroctenus
Indeterminate
North America
North + Central America
Central America
Caribbean
South America
Australasia

Yucatan/Chortis Block and Caribbean clades, both of which have an ancestral North American distribution. The Bayesian analysis recovered the same North American ancestral distribution for the Yucatan/Chortis Block and Caribbean clades, and additionally recovered an ancestral distribution of Central America + North America for both the North American and Central American clades.

### *Biogeographical Hypothesis Testing*

Results of the biogeographical hypothesis testing in Lagrange are given in Table 13. There was no significant difference in any pair of hypotheses. The likelihood values for dispersal-only models were equally probable to dispersal + vicariance (GAARlandia) models. There was however, significant difference in the likelihood values among the models with varying dispersal influence: the models with dispersal had significantly better likelihood scores than models without dispersal. The models where dispersal was dependant on distance had slightly better likelihood scores than the models where dispersal was independent of distance.

## Discussion

Questions concerning the origin and diversification of lineages in the Americas are fascinating because of the interplay of the complex geological history of the Caribbean islands, the proximity of landmasses with dramatically different biota (South, Central, and North America), and their varying dispersal abilities. The proximity of some Caribbean islands to major continental landmasses affords a dynamic interaction and interchange of biota between continents and islands. Historically, island biogeography

**Table 13.** Results of the Lagrange (Ree *et al.*, 2005) analyses of the relative importance of dispersal and vicariance in the present distribution of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971.

| Model | -ln(L) | Dispersal | Extinction |
|---|---|---|---|
| Distance dependant dispersal without GAARlandia | -68.28 | 0.0036 | 0.002 |
| Distance dependant dispersal with GAARlandia | -69.18 | 0.0036 | 0.002 |
| Dispersal without GAARlandia | -69.86 | 0.0039 | 0.002 |
| Dispersal with GAARlandia | -69.82 | 0.0039 | 0.002 |
| No dispersal without GAARlandia | -76.68 | 0.0276 | 0.0018 |
| No dispersal with GAARlandia | -75.32 | 0.0283 | 0.0018 |

and metapopulation theory (Hanksi, 1999) have viewed island-continental biotic interchange as a strictly one-way route, with larger landmasses acting as sources and islands as sinks for biodiversity (Wilson, 1961; MacArthur & Wilson, 1967). However, increasing evidence (Heaney, 2007) points to a paradigm shift where islands, at least in the Caribbean, are no longer considered the end of the road (Ricklefs & Bermingham, 2008). 'Reverse colonization', the colonization of continents from islands, has been recently been demonstrated in birds (Sturge *et al.*, 2009).

Beginning at the base of the phylogeny from the BEAST analysis (Fig. 21, Node A), there is congruence with the node age and the rifting of South America from Antarctica in the Eocene (56–34 mya). Diversification of the major lineages of New World Buthids likely occurred in South America during the late Eocene and early Oligocene. The first dispersal event out of South America occurs in the genus *Heteroctenus*, distributed in the Greater Antilles. This pattern of distribution is congruent with the GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999), which proposes a land bridge existed between South America and the proto-Greater Antilles when the Aves Arc briefly emerged between 33 and 35 mya. The node (B) reflecting the split between the Greater Antilles *Heteroctenus* and the South American *Rhopalurus* has a median age of 35.5 +/- 6.5 mya, congruent with the proposed timing of GAARlandia. This is also supported in the Bayesian ancestral distribution reconstruction which indicates that the ancestral node of *Heteroctenus* + *Centruroides* had a South American-Caribbean distribution. Given that the islands in the Lesser Antilles did not emerge until after 12 mya, a land bridge providing a route of dispersal between the Greater Antilles and South America would explain the reconstructed distribution. However, the Lagrange analysis

failed to reject dispersal-only hypotheses. In fact models that assumed dispersal only scenarios had greater likelihood scores than those assuming vicariance only. In the Crews and Gillespie (2010) study on *Selenops* spiders, the same parameters were used on a similarly distributed dataset and resulted in a rejection of the dispersal-only hypotheses in favor of GAARlandia. Teruel (2006) also invoked the GAARlandia hypothesis to explain the present distributions of the *Rhopalurus* group, but did not offer any biogeographical analysis to support his assertions. These results suggest that dispersal played a greater role in shaping the present distributions of *Centruroides*, and alternative hypotheses to GAARlandia could be further evaluated.

The split between *Centruroides* and *Heteroctenus* occurred in the late Oligocene, and the diversification of the major lineages of *Centruroides* occurred during the early Miocene. This was a period of considerable geological activity in the Greater Antilles, as the Caribbean plate moved into the present day Caribbean basin, towards North America, before eventually coming to rest against the Bahamas Bank (Iturralde-Vinent & MacPhee, 1999). Geological details of the islands during this period are complex, and beyond the scope of this discussion. However, island breakups in combination with submersions, collisions, and changes in sea level resulted in ample opportunity for the diversification of lineages in the region (Ricklefs & Bermingham, 2008).

The dating analysis and ancestral distribution reconstruction point to an “out of Cuba” (Glor, 2005) model of *Centruroides* cladogenesis. The sister group relationship between *Centruroides* and *Heteroctenus* from the Greater Antilles suggests *Centruroides* cladogenesis resulted from dispersal or vicariance into North America from the Greater

Antilles. The ancestral distribution reconstructed (in the Bayesian analysis only) for the basal node of *Centruroides* is North America.

The close relationship between the Greater Antilles clade of *Centruroides* and the Yucatan/Chortis Block clade suggests a likely route for colonization of the Americas, considering the proximity of both landmasses (Yucatan and Chortis) to Cuba during the eastward migration of the Caribbean plate (Iturralde-Vinent & MacPhee, 1999; Heinecke *et al.*, 2010). This proximity provided ample opportunity for dispersal to and from the Greater Antilles to the Yucatan peninsula and the Chortis Block. The plausibility of a Caribbean re-colonization by *Centruroides* is further suggested by the basal position of the Cuban *Centruroides* species within the Greater Antilles clade.

The pattern suggested here, that *Centruroides* colonized and diversified into northern Mesoamerica via dispersal from the Greater Antilles, is observed in eleutherodactyline frogs (Heinecke *et al.*, 2010). The arboreal habitat preference of *Centruroides* may have been important to their successful colonization, and could explain the absence of savannah specialists, *Heteroctenus*, who were unable to colonize the subtropical habitats encountered.

In the absence of competition from their larger competitors and predators (i.e., *Heteroctenus*) on the American continents, two major *Centruroides* radiations appear to have occurred: one southward, through Central America and into northern South America; and the other northward, through Mexico to the southwestern United States, where *Centruroides* diversified in the newly forming habitat of the North American deserts at the end of the last glacial maximum. The dating of the North American desert

species is consistent with the emergence of these habitats in the last 15 my (Fig. 21, Node E) (Wilson & Pitts, 2010).

In addition to these northward- and southward-trending dispersals, *Centruroides* radiated into their new habitat, *Centruroides* may have also returned eastward successfully re-colonizing the Caribbean, as suggested for some other taxa (give citations if possible). This 'reverse colonization' event demonstrates the importance of islands for creating and maintaining continental biodiversity.

**Acknowledgements**

The author would like to thank the following people for assistance with fieldwork and providing specimens: Francisca Almeida, Oscar Francke, Jeremy Huff, Kelvin Guerrero, Camilo Mattoni, Ricardo Pinto-da-Rocha, Adriano Qury, Alex Tietz, Rolando Teruel, and Edmundo Gonzalez. She would like to thank the following people for assistance in lab work: Gena Esposito, Sarah Schoenbrun, Sylvia Johnson and Michelle Yim. Special thanks to Sarah Crews for providing specimens and considerable help setting up the Lagrange analysis, to Humberto Yamaguti for providing specimens and feedback on initial ideas, and to Dave Grimaldi for providing high-resolution photographs of amber-preserved specimens. Thank you to Jessica Ware and Sarah Crews for feedback on this manuscript. Most importantly, thank you to my advisor Lorenzo Prendini who provided specimens, funding, advice and patience.

# SUMMARY AND SYNTHESIS

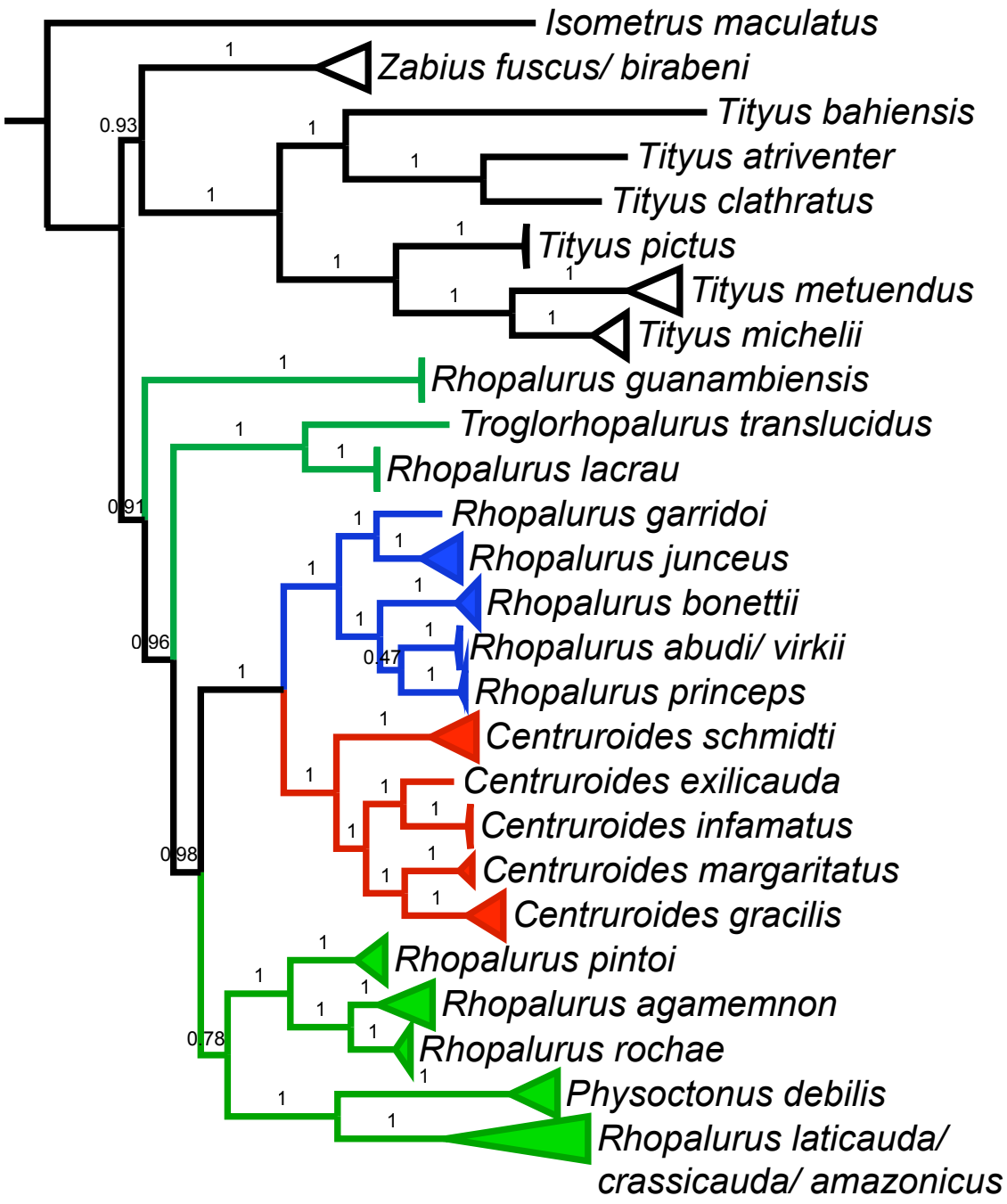
The focus of this dissertation is the systematics of the New World buthid scorpion subfamily the Rhopalurusinae Bücherl, 1971, with an emphasis on the genus *Centruroides* Marx, 1890. Prior to this study, the monophyly of the genus, the subfamily, and their positions within the New World buthids had never been rigorously tested (Fet & Lowe, 2000). This dissertation represents the largest phylogenetic analysis of buthid scorpions, in terms of both sampling and characters, ever performed. The specific aims of this project were to: 1) test the monophyly of subfamily Rhopalurusinae using morphological and molecular data; 2) test the monophyly of the genera within Rhopalurusinae: *Centruroides*, *Rhopalurus* Thorell, 1876, *Physoctonus* Mello-Leitao, 1934, and *Troglorhopalurus* Lourenço *et al.*, 2004 and determine their relationship to other New World Buthid genera using morphological and molecular data; (3) conduct molecular and morphological phylogenetic analyses to test the validity of the currently hypothesized species groups with *Centruroides* and define major groups based on monophyly; (4) test biogeographical hypotheses that can explain the present distributions and species diversity of *Centruroides* and *Rhopalurus*.

Bücherl (1971) proposed two subfamilies of New World buthids: Tityinae Bücherl, 1971, containing the genera *Tityus* C.L. Koch, 1836 and *Zabius* Thorell, 1893; and Rhopalurusinae, containing the genera *Rhopalurus* and *Centruroides*. The synapomorphic character differentiating the subfamilies is the presence, in Rhopalurusinae, of supernumary granules on the internal surfaces of the fingers of the pedipalp chelae (Bücherl, 1971). On the basis of this character, two subsequently described genera should be placed within the Rhopalurusinae: *Troglorhopalurus* and *Physoctonus*. The monophyly of Rhopalurusinae and its contained genera was tested

using morphological (90 characters) and molecular data (5 loci, 4,250 characters), analyzed both separately and in combination under Bayesian and parsimony optimality criteria. The results from all analyses were congruent: Rhopalurusinae are monophyletic (Figure 24). However, long-branch attraction (Felsenstein, 1978) appears to play a role when molecular data is analyzed under parsimony, placing *Rhopalurus guanambiensis* Lenarducci *et al.*, 2005 sister to the genus *Tityus*, and rendering Rhopalurusinae paraphyletic.

Historically, species have been transferred back and forth between *Centruroides* and *Rhopalurus*, and the generic definitions have been revised several times (Pocock, 1890; Werner, 1939; Meise, 1934; Mello-Leitão, 1945; Lourenço, 1979). A phylogenetic study of Cuban scorpions using a single molecular marker (16S rDNA), found that *Centruroides* was paraphyletic with respect to the *Rhopalurus* group (Teruel *et al.*, 2006). Ovariuterine data, however, suggests the opposite scenario: a paraphyletic *Rhopalurus* subgroup with respect to *Centruroides* (Volschenk *et al.*, 2008). The findings of the study presented here were congruent with those of Volschenk *et al.* (2008), and recovered *Rhopalurus* as paraphyletic with respect to *Centruroides*, *Troglorhopalurus*, and *Physoctonus*. The *Rhopalurus* species endemic to the Greater Antilles formed a monophyletic clade sister to *Centruroides*. Contrary to the findings of Teruel *et al.* (2006), *Centruroides* was recovered as monophyletic. The species of *Rhopalurus* endemic to South America were recovered as a monophyletic group sister to *Physoctonus*. There were two exceptions: the trogloxene species *Rhopalurus lacrau* Lourenço & Pinto-da-Rocha 1997 was recovered as sister to the monotypic troglobite *Troglorhopalurus*; and *Rhopalurus guanambiensis* was recovered as the basal member of

Figure 24: Phylogram of the New World scorpion subfamily Rhopalurusinae Bücherl, 1971 (Buthidae), computed under Bayesian optimality criteria in MrBayes (Ronquist & Huelsenbeck, 2003). Outgroup taxa are depicted in black, *Rhopalurus* Thorell, 1876 species endemic to South America are depicted in green, *Rhopalurus* species endemic to the Greater Antilles are depicted in blue, and *Centruroides* Marx, 1890 species are depicted in red. Values on branches are posterior probabilities.


Isometrus maculatus
Zabius fuscus/ birabeni
Tityus bahiensis
Tityus atriventer
Tityus clathratus
Tityus pictus
Tityus metuendus
Tityus michelii
Rhopalurus guanambiensis
Troglorhopalurus translucidus
Rhopalurus lacrau
Rhopalurus garridoi
Rhopalurus junceus
Rhopalurus bonettii
Rhopalurus abudi/ virkii
Rhopalurus princeps
Centruroides schmidti
Centruroides exilicauda
Centruroides infamatus
Centruroides margaritatus
Centruroides gracilis
Rhopalurus pintoi
Rhopalurus agamemnon
Rhopalurus rochae
Physoctonus debilis
Rhopalurus laticauda/
crassicauda/ amazonicus
0.93
0.91
0.96
0.47
0.98
0.78

Rhopalurusinae in the Bayesian analysis of combined data. To correct for the paraphyly of *Rhopalurus*, it was recommended that the genus *Heteroctenus* Pocock, 1897 be restored for the Greater Antilles species of *Rhopalurus*, and that the species *Rhopalurus lacrau* author, date be transferred to *Troglorhopalurus*.

The buthid scorpion genus *Centruroides* Marx, 1890 is a diverse and highly venomous taxon, distributed from northern South America to the southern United States, throughout the Caribbean islands and the Galapagos (Hoffmann, 1932; Sissom & Lourenco, 1987; Gantenbein *et al.*, 2001). With 71 species and 5 subspecies currently recognized, it is the largest buthid genus in North America and the second largest in the New World Fet & Lowe, 2000; Teruel & Stockwell, 2002; Teruel 2001, 2006, 2007; Armas & Martin-Frias, 2003; Ponce-Saavedra & Francke, 2004, 2009; Santiago-Blay, 2009; Santibanez-Lopez & Ponce-Saavedra, 2009; Armas & Trujillo, 2010). These scorpions are sexually dimorphic, the males typically exhibiting elongation of the metasoma and longer, more slender pedipalp chelae; while females are most robust and carinate (Polis & Sissom, 1996). Fossil *Centruroides* are known from amber from the Dominican Republic (Oligocene) and Chiapas, Mexico (Miocene/Oligocene) (Santiago-Blay & Poinar, 1993; Schawaller, 1979).

Pocock (1902) published the last morphological revision of the genus to include all of species known at the time. The characters traditionally used to define *Centruroides* species rely heavily on morphometrics and color (Gantenbein *et al.*, 2001). Species are often inadequately defined, and many of the types are damaged or in poor condition, making redescriptions difficult. Adding urgency to this problem, the venom of several

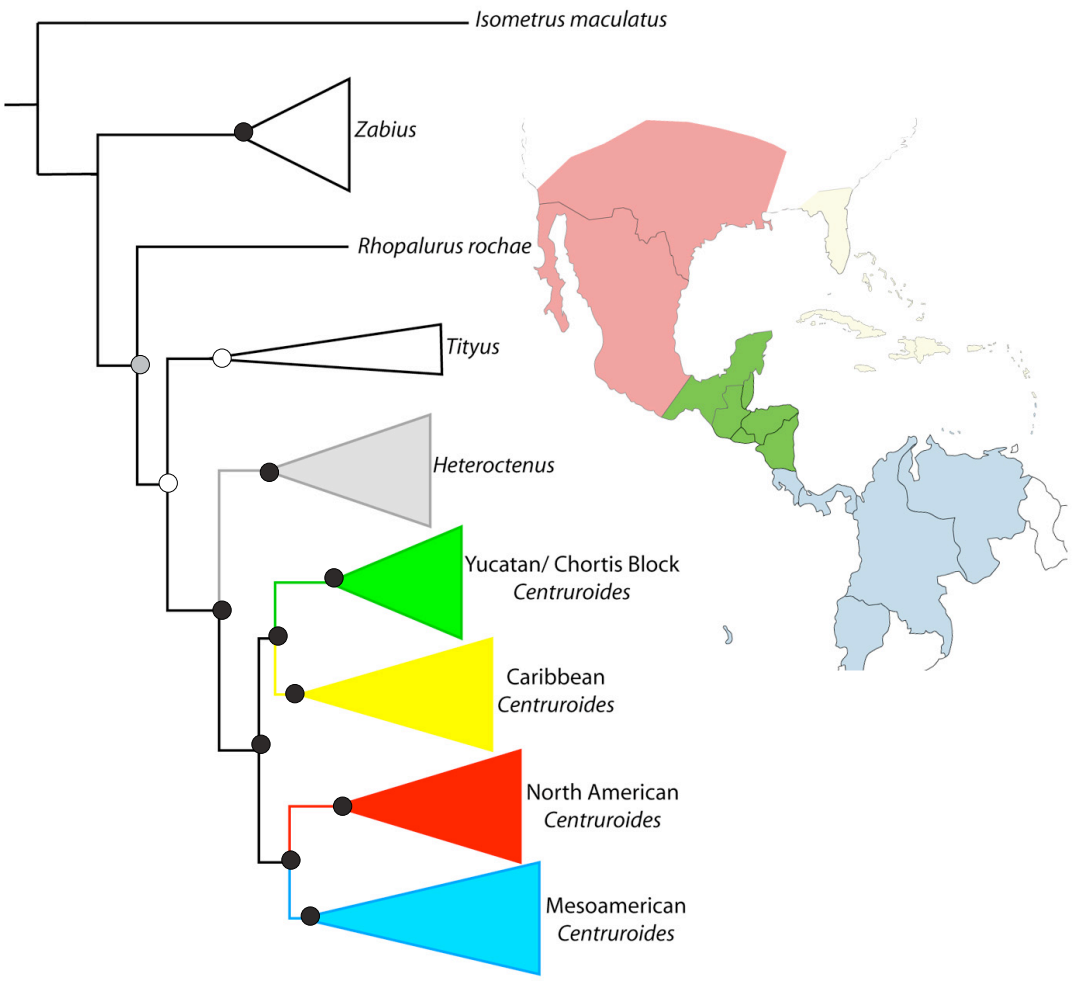
species is potentially lethal to adult humans, resulting in as many as 1,000 fatalities per year in Mexico (Mazzotti & Bravo-Becherelle, 1963; Ponce-Saavedra & Francke, 2009).

The greatest efforts to assign *Centruroides* species to morphological groups were made several researchers working on Mexican species (Hoffmann, 1932; González-Santillian, 2001; Ponce-Saavedra & Moreno-Barajas, 2005). Among the Mexican species, the most recent proposal (Ponce-Saavedra & Moreno-Barajas, 2005) included five species groups: the striped group with two subgroups (*limpidus-elegans* subgroup and *suffusus-infamatus* subgroup), and the non-striped group with three subgoups (*bertholdii* subgroup, *gracilis* subgroup, *thorellii* subgroup). The validity of these species groups has never been tested using modern analytical or phylogenetic methods.

In order to assess the monophyly of *Centruroides* and the proposed species groups, morphological and molecular datasets were generated and analyzed which included 451 samples from 7 genera, 85 species and 7 subspecies. This taxon sample includes 3 genera, 71 species, and 6 subspecies not previously included in any published phylogenetic analysis. Most of the described species (61/71) in the genus *Centruroides* were sampled.

As in previous analyses from this study, *Centruroides* was recovered as monophyletic (Fig. 25) and contained four well supported, geographically delimited clades: a clade from Mesoamerica, northern South America and the southern Lesser Antilles; a clade from North America; a clade from the Greater Antilles, the northern Lesser Antilles and Florida; and a clade from the Yucatan peninsula and the Chortis block. The clades from the molecular analysis were not recovered in their entirety using morphology alone.

Figure 25: Summary phylogeny of the New World buthid genus *Centruroides* Marx, 1890, computed under Bayesian and parsimony optimality criteria in MrBayes (Ronquist & Huelsenbeck, 2003) and TNT (Goloboff *et al.*, 2003) respectively, depicting four geographically aligned clades within the genus. Map depicts the area ranging from southern North America through northern South America, and includes the Galapagos and the Caribbean; the approximate distribution of *Centruroides*. Clade colors correspond to map colors, although the Mesoamerican *Centruroides* clade and the Yucatan/Chortis *Centruroides* clade are sympatric in the green region depicted on the map. Outgroups are depicted in black, and the Greater Antilles disributed sister taxon, *Heteroctenus* Pocock, 1897, is depicted is grey. Circles on the nodes represent posterior probabilities: black=1, $1 \leq$ grey $\geq 0.95$, $0.95 >$ white $\leq 0.90$.


Isometrus maculatus
Zabius
Rhopalurus rochae
Tityus
Heteroctenus
Yucatan/ Chortis Block
Centruroides
Caribbean
Centruroides
North American
Centruroides
Mesoamerican
Centruroides

The species groups proposed by previous authors (Hoffmann, 1932; González-Santillian, 2001; Ponce-Saavedra & Moreno-Barajas, 2005) were partially recovered in both molecular and morphological analyses. The striped group (Hoffmann, 1932; González-Santillian, 2001; Ponce-Saavedra & Moreno-Barajas, 2005), endemic to Mexico and the USA, was recovered in its entirety in the total evidence analyses. One of the two striped subgroups, the *limpidus-elegans* subgroup (Hoffmann, 1932; González-Santillian, 2001; Ponce-Saavedra & Moreno-Barajas, 2005), was recovered in its entirety with the exception of one taxon in both the morphological and molecular analyses. All of the other proposed groups were partially recovered, however they were either paraphyletic or polyphyletic in the context of the entire phylogeny.

To investigate the biogeographical patterns in the New World scorpion genera *Rhopalurus* Thorell, 1876 and *Centruroides* Marx, 1890, a fossil-calibrated phylogeny was estimated in Beast (Drummond *et al.*, 2006) to infer the dates of key events. The relative likelihood of vicariance and dispersal in explaining the present distributions of taxa was calculated in Lagrange (Ree *et al.*, 2005; Ree & Smith, 2008), and ancestral distributions of the genera were inferred using DIVA (parsimony and Bayesian) in the software package RASP (Yu *et al.*, 2011). The date of the ancestral node of the Greater Antilles *Rhopalurus* plus *Centruroides* clade was recovered with a 95% confidence interval of {29.0, 42.9} mya. There was no significant difference among models including or excluding the GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999). There was, however, a significantly higher likelihood score in the models that emphasized distance-dependent. The ancestral distribution of the Greater Antilles *Rhopalurus* (= *Heteroctenus*) + *Centruroides* clade was inferred to be South America and

the Greater Antilles, and the ancestral distribution of *Centruroides* was inferred to be North America.

The node separating the Greater Antilles *Rhopalurus* from the South American *Rhopalurus* is congruent with the GAARlandia hypothesis, which has been proposed to explain similar disjunct distributions in large mammals (Iturralde-Vinent & MacPhee, 1999; Davalos, 2004). The inferred ancestral distribution (South America-Greater Antilles) is also congruent with GAARlandia. Crews and Gillespie (2010) obtained similar results in a study on *Selenops* spiders.

Both the dating analysis and the ancestral distribution reconstruction point to an "out of Cuba" (Glor, 2005) model of *Centruroides* cladogenesis. *Centruroides* appear to have dispersed from the Greater Antilles into northern Mesoamerica, a pattern observed in eleutherodactyline frogs (Heinecke *et al.*, 2010), and from there colonized North and South America. 'Reverse colonization', the colonization of continents by island species, has recently been proposed as an important mechanism for generating biodiversity in the Americas (Ricklefs & Bermingham, 2008). *Heteroctenus,* the Greater Antilles distributed sister taxon of *Centruroides*, provides direct evidence of a Caribbean ancestor for the genus, demonstrating the importance of islands for creating and maintaining continental biodiversity.

**Appendix 1.** Specimens and Genbank accession numbers used in phylogenetic analysis of the buthid subfamily Rhopalurusinae Bücherl, 1971.

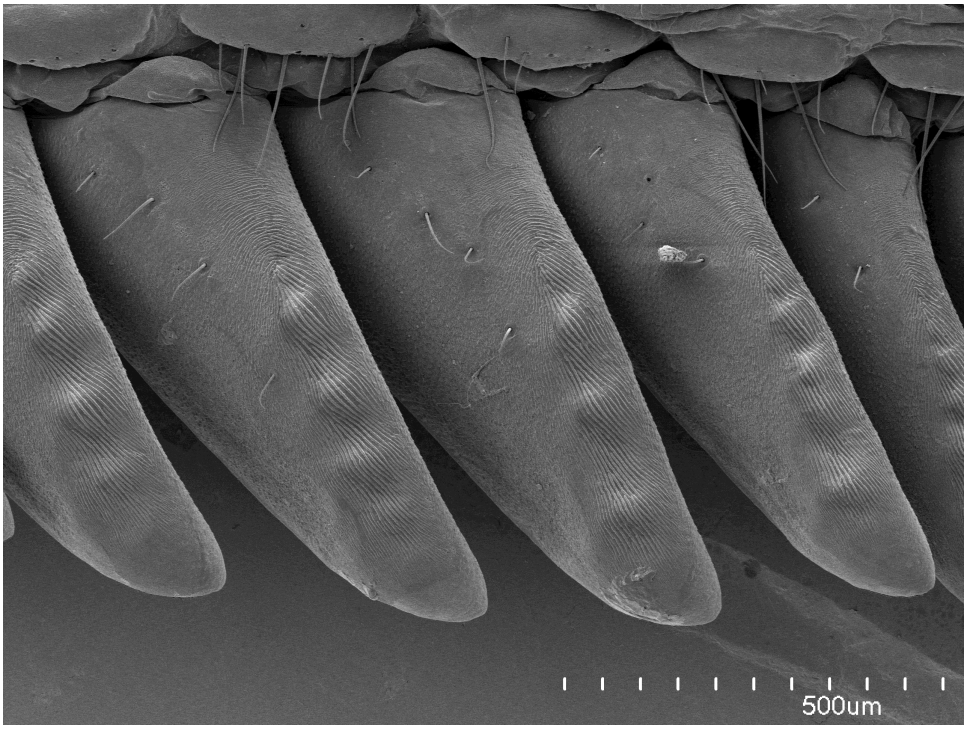
| Specimen ID | *Species* | Author, Date | Genbank Accession Number | | | | |
|---|---|---|---|---|---|---|---|
| | | | 12S | 16S | 18S | 28S | CoxI |
| LP 2873 | *Centruroides exilicauda* | (Wood, 1863) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5992 | *Centruroides gracilis* | (Latreille, 1804) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5995 | *Centruroides gracilis* | (Latreille, 1804) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5996 | *Centruroides gracilis* | (Latreille, 1804) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2013 | *Centruroides gracilis* | (Latreille, 1804) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1822 | *Centruroides infamatus ornatus* | Pocock, 1902 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2003 | *Centruroides infamatus ornatus* | Pocock, 1902 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1787 | *Centruroides margaritatus* | (Gervais, 1841) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1986 | *Centruroides margaritatus* | (Gervais, 1841) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 6445 | *Centruroides rileyi* | Sissom, 1995 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2070 | *Centruroides schmidti* | Sissom, 1995 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2948 | *Centruroides schmidti* | Sissom, 1995 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5984 | *Centruroides schmidti* | Sissom, 1995 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5985 | *Centruroides schmidti* | Sissom, 1995 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2286 | *Centruroides vittatus* | (Say, 1821) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1798 | *Isometrus maculatus* | (DeGeer, 1778) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9678 | *Physoctonus debilis* | (C.L. Koch, 1840) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9679 | *Physoctonus debilis* | (C.L. Koch, 1840) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9680 | *Physoctonus debilis* | (C.L. Koch, 1840) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9681 | *Physoctonus* sp. nov. | | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 3268 | *Rhopalurus abudi* | Armas & Marcano Fondeur, 1987 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9692 | *Rhopalurus acromelas* | Lutz & Mello, 1922 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9693 | *Rhopalurus acromelas* | Lutz & Mello, 1922 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9694 | *Rhopalurus agamemnon* | (C.L. Koch, 1839) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9929 | *Rhopalurus agamemnon* | (C.L. Koch, 1839) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9686 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9687 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9688 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9689 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9690 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9691 | *Rhopalurus amazonicus* | Lourenço, 1986 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2471 | *Rhopalurus bonettii* | Armas, 1999 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 3267 | *Rhopalurus bonettii* | Armas, 1999 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9341 | *Rhopalurus caribensis* | Teruel & Roncallo, 2008 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10048 | *Rhopalurus crassicauda* | Caporiacco, 1947 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9675 | *Rhopalurus crassicauda* | Caporiacco, 1947 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9676 | *Rhopalurus crassicauda* | Caporiacco, 1947 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9677 | *Rhopalurus crassicauda* | Caporiacco, 1947 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9927 | *Rhopalurus crassicauda* | Caporiacco, 1947 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10225 | *Rhopalurus garridoi* | Armas, 1974 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9669 | *Rhopalurus guanambiensis* | Lenarducci et al., 2005 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9937 | *Rhopalurus guanambiensis* | Lenarducci et al., 2005 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1517 | *Rhopalurus junceus* | (Herbst, 1800) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1565 | *Rhopalurus junceus* | (Herbst, 1800) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10211 | *Rhopalurus lacrau* | Lourenço & Pinto-da-Rocha 1997 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 7637 | *Rhopalurus lacrau* | Lourenço & Pinto-da-Rocha 1997 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2462 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2845 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 4221 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5504 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5505 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9199 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9200 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9207 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9237 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9253 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9256 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10046 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10047 | *Rhopalurus laticauda* | Thorell, 1876 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 8278 | *Rhopalurus pintoi* | Mello-Leitao, 1932 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9671 | *Rhopalurus pintoi* | Mello-Leitão, 1933 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9672 | *Rhopalurus pintoi* | Mello-Leitão, 1933 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 3264 | *Rhopalurus princeps* | (Karsch, 1879) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |

| Specimen ID | *Species* | Author, Date | Genbank Accession Number | | | | |
|---|---|---|---|---|---|---|---|
| | | | 12S | 16S | 18S | 28S | CoxI |
| LP 1516 | *Rhopalurus princeps* | (Karsch, 1879) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1566 | *Rhopalurus princeps* | (Karsch, 1879) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 3262 | *Rhopalurus princeps* | (Karsch, 1879) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1775 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 7638 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 7639 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9682 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9683 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9684 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9685 | *Rhopalurus rochae* | Borelli, 1910 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9670 | *Rhopalurus* sp. nov. | | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10234 | *Rhopalurus virkkii* | Santiago-Blay, 2009 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10235 | *Rhopalurus virkkii* | Santiago-Blay, 2009 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9033 | *Tityus atriventer* | Pocock, 1897 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5641 | *Tityus bahiensis* | (Perty, 1833) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1567 | *Tityus clathratus* | C.L. Koch, 1844 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1546 | *Tityus metuendus* | Pocock, 1897 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1983 | *Tityus metuendus* | Pocock, 1897 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10202 | *Tityus michelii* | Armas, 1982 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 10207 | *Tityus michelii* | Armas, 1982 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9046 | *Tityus pictus microdon* | Pocock, 1893 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9049 | *Tityus pictus microdon* | Pocock, 1893 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 9668 | *Troglorhopalurus translucidus* | Lourenço et al., 2004 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 2261 | *Zabius birabeni* | Mello-Leitão, 1938 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 4251 | *Zabius birabeni* | Mello-Leitão, 1938 | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 5642 | *Zabius fuscus* | (Thorell, 1876) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |
| LP 1780 | *Zabius fuscus* | (Thorell, 1876) | 12345ABC | 12345ABC | 12345ABC | 12345ABC | 12345ABC |

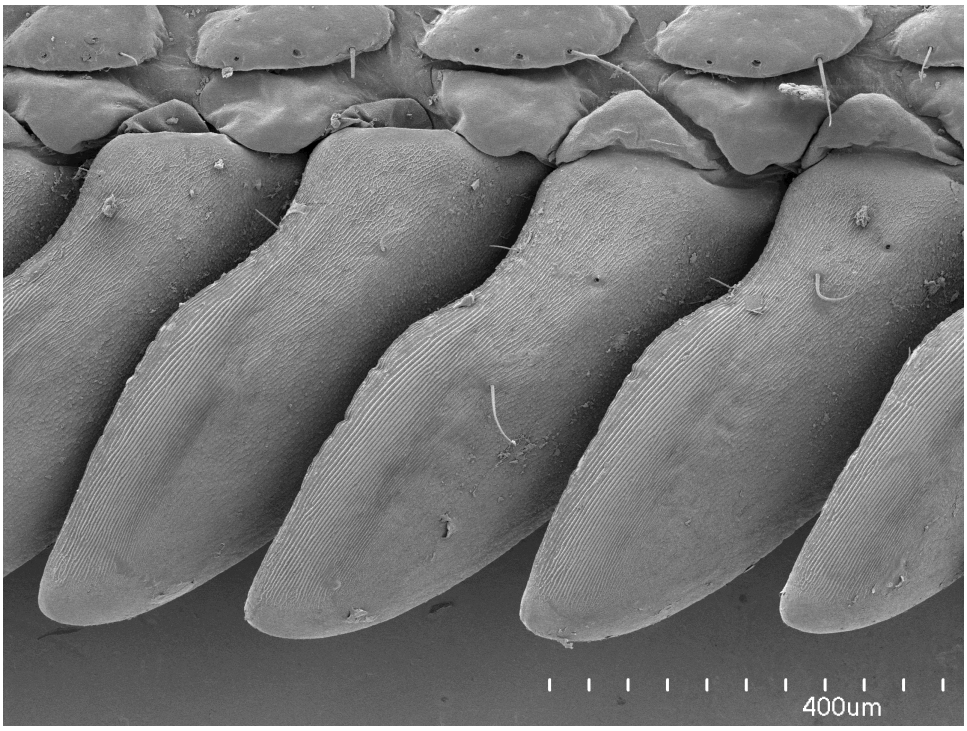
**Appendix 2.** Morphological characters and character states used in the study of buthid scorpion subfamily Rhopalurusinae Bücherl, 1971.

Nomenclature of general anatomy follows Hjelle (1990) and Sissom (1990), trichobothria follows Vachon (1974), tergite and pedipalp carination follows Prendini (2001b), carapace and metasomal carination follows Vachon (1974), ovariuterine anatomy follows Volschenk *et al.* (2008) and book lung anatomy follow Kamenz & Prendini (2008). Pectinal stridulatory characters are illustrated in the diagrams below (SEM micrographs courtesy of Carsten Kamenz):

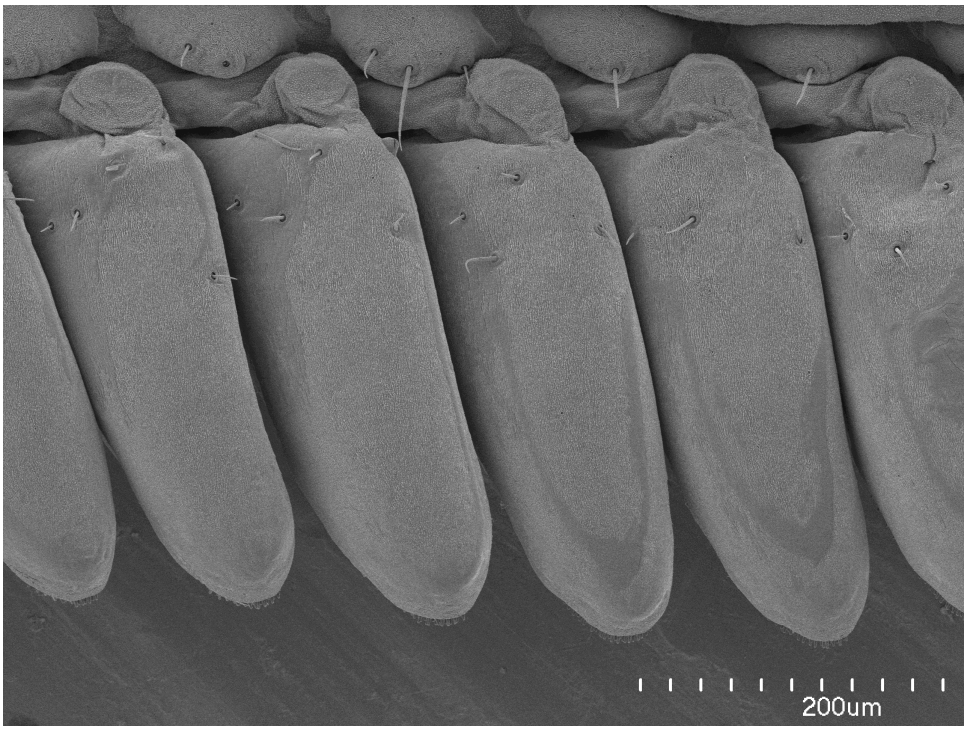
A) Scanning electron micrograph of *Heteroctenus bonnetti* (Armas, 1999) illustrating the proximal dorsal surfaces of the pectines. Stridulatory striations are present, nodules are present, shape of the pectinal tooth is straight, more than six macrosetae present on proximal pectinal fulcra, macrosetae on the dorsobasal surface of the pectinal teeth present.



C) Scanning electron micrograph of *Rhopalurus rochae* Borelli, 1910 illustrating the proximal dorsal surfaces of the pectines. Stridulatory striations are present, nodules are absent, shape of the pectinal tooth is sinuate, three macrosetae present on proximal pectinal fulcra, macrosetae on the dorsobasal surface of the pectinal teeth present.



D) Scanning electron micrograph of *Troglorhopalurus lacrau* (Lourenço & Pinto-da-Rocha 1997) illustrating the proximal dorsal surfaces of the pectines. Stridulatory striations are irregular, nodules are absent, shape of the pectinal tooth is straight, one macrosetae present on proximal pectinal fulcra, macrosetae on the dorsobasal surface of the pectinal teeth present.



Characters:

1. Prosoma, carapace, lateral ocular carina (Volschenk & Prendini, unpublished)
   0 present
   1 absent

2. Prosoma, carapace, centrolateral carina (Volschenk & Prendini, unpublished)
   0 present
   1 absent

3. Prosoma, carapace, anterior centrosubmedian carina (Volschenk & Prendini, unpublished)
   0 present
   1 absent

4. Prosoma, carapace, posterior centrosubmedian carina (Volschenk & Prendini, unpublished)
   0 present
   1 absent

5. Prosoma, carapace, relation of anterior and posterior centrosubmedian carinae
   0 not fused
   1 fused

6. Prosoma, carapace, relation of lateral ocular carina with posterior centrosubmedian carina (Volschenk & Prendini, unpublished)
   0 fused
   1 not fused

7. Prosoma, carapace, macro-ocelli of the lateral ocular tubercle (Stockwell, 1989; Jeram, 1994; Prendini, 2000; Giribet *et al.*, 2002; Soleglad & Fet, 2003; Volschenk & Prendini, unpublished)
   0 three ocelli
   1 two ocelli

8. Prosoma, carapace, lateral ocular tubercles, posterior micro ocellus (Stockwell, 1989; Jeram, 1994; Prendini, 2000; Giribet *et al.*, 2002; Soleglad & Fet, 2003; Volschenk & Prendini, unpublished)
   0 present
   1 absent

9. Prosoma, chelicerae, fixed finger, dorsobasal setation
   0 present
   1 absent

10. Prosoma, chelicerae, position of the median tubercles

0 transverse row
1 spread

11. Prosoma, pedipalp patella, internoventral and internodorsal association (Volschenk & Prendini, unpublished)
0 converging, pinched together
1 separate, clearly defined

12. Prosoma, pedipalp chela, dorsal accessory carina (Volschenk & Prendini, unpublished)
0 granular
1 nongranular

13. Prosoma, pedipalp chela, median carina (Volschenk & Prendini, unpublished)
0 present
1 absent or obsolete

14. Prosoma, pedipalp chela, ventral accessory carina (Volschenk & Prendini, unpublished)
0 present
1 absent or obsolete

15. Prosoma, pedipalp chela, internoventral carina (Volschenk & Prendini, unpublished)
0 present
1 absent

16. Prosoma, pedipalp chela, internomedian carina (Volschenk & Prendini, unpublished)
0 present
1 absent

17. Prosoma, pedipalp chela, internodorsal carina (Volschenk & Prendini, unpublished)
0 present
1 absent

18. Prosoma, pedipalp femur, external accessory carina (Volschenk & Prendini, unpublished)
0 absent
1 present

19. Prosoma, pedipalp chela, fixed finger, number of primary denticular rows (Volschenk & Prendini, unpublished)
0 eight
1 nine
2 thirteen or more

20. Prosoma, pedipalp chela, fixed finger, supernumerary granules (Soleglad & Fet, 2003; Volschenk & Prendini, unpublished)
    0 absent
    1 present
    2 small and widely spaced

21. Prosoma, pedipalp chela, movable finger, number of primary denticular rows (Soleglad & Fet, 2003; Prendini, 2004; Volschenk & Prendini, unpublished)
    0 eight
    1 nine
    2 eleven
    3 thirteen or more

22. Prosoma, pedipalp chela, shape (male) (Prendini, 2001, 2004)
    0 incrassate
    1 not incrassate

23. Prosoma, pedipalp chela, shape (female) (Prendini, 2001)
    0 incrassate
    1 not incrassate

24. Prosoma, pedipalp chela, fixed finger, shape (male) (Prendini, 2001, 2004)
    0 straight, proximal dentate margin linear when fingers closed
    1 slightly curved dorsally
    2 strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers closed

25. Prosoma, pedipalp chela, movable finger, shape (male) (Prendini, 2001, 2004)
    0 straight, proximal dentate margin linear when fingers closed
    1 slightly curved ventrally
    2 strongly curved ventrally, proximal dentate margin distinctly emarginate when fingers closed

26. Prosoma, pedipalp chela, movable finger, basal lobe (male) (Prendini, 2001)
    0 absent
    1 present

27. Prosoma, pedipalp chela, movable finger, median lobe (male) (Prendini, 2004)
    0 absent
    1 present

28. Prosoma, pedipalp chela, fixed finger, basal lobe (male) (Prendini, 2001)
    0 absent
    1 present

29. Prosoma, pedipalp chela, fixed finger, median lobe (male) (Prendini, 2004)

0 absent
1 present

30. Prosoma, pedipalp femur, dorsal surface, trichobothrium $d_2$ (Soleglad & Fet, 2001, 2003; Volschenk & Prendini, unpublished)
    0 absent (four *d* group trichobothria)
    1 present (five *d* group trichobothria)

31. Prosoma, pedipalp chela, fixed finger, trichobothrium *db* placement (Volschenk & Prendini, unpublished)
    0 distal to *et*
    1 roughly inline with *et*
    2 between *est* and *et*
    3 roughly inline with *est*

32. Prosoma, pedipalp chela, fixed finger, trichobothrium *est* placement (Volschenk & Prendini, unpublished)
    0 approximately inline with *db*
    1 between *db* and *et*
    2 basal to *et*

33. Prosoma, pedipalp chela, fixed finger, *et* placement (Volschenk & Prendini, unpublished)
    0 between *dt* and *db*
    1 inline with *db*
    2 between *db* and *est*

34. Prosoma, leg I, prolateral pedal spur
    0 simple
    1 bifurcating

35. Prosoma, leg I, telotarsal setation (Volschenk & Prendini, unpublished)
    0 tufts of setae
    1 two discrete rows

36. Prosoma, leg I, telotarsal setae form (Volschenk & Prendini, unpublished)
    0 fine and acuminate setae
    1 thickened acuminate setae
    2 short stout setae

37. Prosoma, leg IV, telotarsal setation (Volschenk & Prendini, unpublished)
    0 tufts of setae
    1 two discrete rows

38. Prosoma, leg IV, telotarsal setae form (Volschenk & Prendini, unpublished)
    0 fine and acuminate setae

1 thickened acuminate setae
2 short stout setae

39. Mesosoma, pectines, tooth shape (See appendix figures A-C)
0 straight, with sides almost parallel
1 rounded
2 dorsal surface sinuate

40. Mesosoma, pectines, proximal teeth, dorsal surface (See appendix figures A-C)
0 smooth or slightly granular
1 with irregular striations
2 large and regular striations

41. Mesosoma, pectines, proximal teeth, nodules on dorsal surface (See appendix figures A-C)
0 one nodule
1 multiple nodules
2 nodules absent

42. Mesosoma, pectines, macrosetae on the dorsobasal surface of the teeth (See appendix figures A-C)
0 present
1 absent

43. Mesosoma, pectines, structure of the peg sensillae (Kamenz & Prendini, unpublished)
0 short and blunt
1 elongate and blunt
2 elongate and acuminate

44. Mesosoma, pectines, proximal dorsal fulcra setae (See appendix figures A-C)
0 one
1 two
2 three
3 four
4 six or more
5 absent

45. Mesosoma, pectines (females), proximal median lamellae (Prendini, 2001, 2004; Volschenk & Prendini, unpublished)
0 not dilated
1 dilated

46. Mesosoma, pectines, anterior margin of the pectinal plate, sulcus
0 present
1 absent

47. Mesosoma, pectines (males), posterior margin of the pectinal plate
    0 curved
    1 straight

48. Mesosoma, pectines (males), pectinal plate depressions
    0 single median depression
    1 two lateral depressions
    2 absent

49. Mesosoma, pectines, ventral median carinae
    0 broad anterior raised region
    1 narrow, elevated anterior keel
    2 no elevation anteriorly

50. Mesosoma, sternite III, lateral margins
    0 not raised or granular
    1 granular keel
    2 smooth keel

51. Mesosoma, sternite III, ventrosubmedian surface
    0 smooth or slightly granular
    1 large, regularly spaced granules (stridulatory)
    2 small, irregular granules

52. Mesosoma sternite V, posteromedian surface (male) (Prendini, 2004; Volschenk & Prendini, unpublished)
    0 with raised, smooth area
    1 unmodified

53. Mesosoma, sternite VI, ventrosubmedian carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

54. Mesosoma, sternite VI, ventrolateral carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

55. Mesosoma, sternites III-VI, spiracle shape (Kamenz & Prendini, 2008)
    0 wide, width more than 5X the length
    1 compact, width less than 3X the length

56. Mesosoma, tergite I, dorsolateral carinae (Volschenk & Prendini, unpublished)
    0 reduced
    1 absent

57. Mesosoma, tergite I, dorsosubmedian carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

58. Mesosoma, tergite II, dorsolateral carinae (Volschenk & Prendini, unpublished)
    0 reduced
    1 absent

59. Mesosoma, tergite II, dorsomedian carina (Volschenk & Prendini, unpublished)
    0 present
    1 absent

60. Mesosoma, tergites III-VI, dorsolateral carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

61. Mesosoma, tergites III-VI, dorsosubmedian carinae (Prendini, 2004)
    0 absent
    1 present

62. Mesosoma, tergite VII, dorsomedian carina (Volschenk & Prendini, unpublished)
    0 narrow granular ridge
    1 granular mound, no ridge
    2 non-granular mound, no ridge

63. Mesosoma, tergite VII, coloration
    0 paler than preceding tergites
    1 same as other tergites

64. Metasoma, segment I, dorsal surface
    0 weakly granular
    1 distinctly granular

65. Metasomal segment II, median lateral carina (Prendini, 2004; Volschenk & Prendini, unpublished)
    0 continuous
    1 posteriorly confined
    2 absent

66. Metasoma, segment III, median lateral carina (Prendini, 2004; Volschenk & Prendini, unpublished)
    0 continuous
    1 posteriorly confined
    2 absent

67. Metasoma, segment III, dorsolateral carinae
    0 distal granules similar in size
    1 distal granules larger and spiniform

68. Metasoma, segment IV, median lateral carinae
    0 absent or obsolete
    1 present

69. Metasoma, segments IV and V, ventral coloration
    0 darker than preceding segments
    1 similar to preceding segments

70. Metasoma, segment V, anal rim granulation (Volschenk & Prendini, unpublished)
    0 present
    1 absent

71. Metasoma, segment V, dorsolateral carina (Volschenk & Prendini, unpublished)
    0 present
    1 absent

72. Metasoma, segment V, median lateral carinae
    0 absent
    1 present

73. Metasoma, segment V, ventromedian carina
    0 absent
    1 present

74. Metasoma, segment V, ventrosubmedian carinae
    0 absent
    1 present

75. Metasoma, segment V, ratio of segment length to width
    0 slightly elongated, length less than 2x width
    1 elongated, length 2.5-3X width
    2 pronounced elongation, length more than 3X the width

76. Metasoma, segments I-IV, width (Lamoral, 1978; Prendini, 2001, 2003)
    0 narrowing distally, segment I wider than segment IV
    1 slight widening distally, segment I slightly narrower than segment IV
    2 pronounced widening distally, segment I much narrower than the segment V

77. Metasoma, length (males)
    0 similar to prosoma + mesosoma length, <1.5X length
    1 much longer than prosoma + mesosoma length, ≥1.5X length

78. Metasoma, segments I-V, coloration, dark ventromedian stripe
    0 absent
    1 present

79. Telson, shape
    0 spherical, length similar to width
    1 slightly ovate, length approximately 1.5X width
    2 ovate, length more than 2X width

80. Telson, Telson vesicle, width relative to width of metasomal segment V (Lamoral, 1978; Prendini, 2001, 2003)
    0 approximately equal
    1 somewhat narrower
    2 considerably narrower, less than half the width

81. Telson, ventromedian carina (Volschenk & Prendini, unpublished)
    0 present
    1 absent

82. Telson, lateral surface granulation (Volschenk & Prendini, unpublished)
    0 granular
    1 smooth

83. Telson, subaculear tubercle (Lamoral, 1980; Stockwell, 1989; Prendini, 2000, 2004; Soleglad & Fet, 2003; Volschenk & Prendini, unpublished)
    0 pronounced, pointed tooth
    1 nub-like eminence
    2 absent

84. Telson, subaculear tubercle, dorsal granules
    0 absent
    1 present

85. Relation of male and female body size
    0 males smaller or approximately equal
    1 males much larger (>1.5X)

86. Mesosoma, ovariuterus, number of loops (Volschenk *et al.*, 2008)
    0 8
    1 9
    2 2

87. Mesosoma, ovariuterus, form (Volschenk *et al.*, 2008)
    0 simple
    1 complex bridged

88. Mesosoma, booklungs, lamellar surface (Kamenz and Prendini, 2008)
    0 slender venation
    1 ribbed venation

89. Mesosoma, booklungs, lamellar edge (Kamenz and Prendini, 2008)
    0 thorns
    1 smooth or slightly wrinkled

90. Mesosoma, booklungs, posterior spiracle edge (Kamenz and Prendini, 2008)
    0 hillocks
    1 subconical

**Appendix 3.** Morphology matrix used in phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Isometrus maculatus* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Zabius fuscus* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 3 | 0 |
| *Zabius birabeni* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | - | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 3 | 0 |
| *Tityus atriventer* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Tityus bahiensis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 |
| *Tityus clathratus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Tityus metuendus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 |
| *Tityus michelii* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 |
| *Tityus pictus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Centruroides bani* | 0 | 0 | 1 | 1 | - | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Centruriodes exilicauda* | 1 | 1 | 1 | 1 | - | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Centruroides gracilis* | 0 | 1 | 1 | 1 | - | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Centruroides infamatus* | 0 | 1 | 0 | 0 | - | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Centruroides margaritatus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Centruroides schmidti* | 0 | 1 | 0 | 0 | 0 | - | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Physoctonus debilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Physoctonus* sp nov | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Troglorhopalurus translucidus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus lacrau* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | - | 1 | - | - | - | - | - | - | 1 | 2 | 1 |
| *Rhopalurus guanambiensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus* sp nov | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | - | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus laticauda* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus amazonicus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus caribensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus crassicauda* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus agamemnon* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus rochae* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 1 |
| *Rhopalurus pintoi* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Rhopalurus abudi* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Rhopalurus bonettii* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Rhopalurus garridoi* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Rhopalurus junceus* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Rhopalurus princeps* | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 2 |
| Steps | 2 | 4 | 1 | 3 | 2 | 3 | 1 | 6 | 1 | 1 | 1 | 3 | 4 | 4 | 8 | 6 | 2 | 2 | 8 | 3 | 9 | 5 | 5 | 7 | 7 | 5 | 1 | 4 | 1 | 1 | 6 | 4 |
| Consistency Index | 0.50 | 0.25 | 1.00 | 0.33 | 0.50 | 0.33 | 1.00 | 0.17 | 1.00 | 1.00 | 1.00 | 0.33 | 0.25 | 0.25 | 0.13 | 0.17 | 0.50 | 0.50 | 0.25 | 0.67 | 0.33 | 0.20 | 0.20 | 0.29 | 0.29 | 0.20 | 1.00 | 0.25 | 1.00 | 1.00 | 0.50 | 0.50 |
| Retention Index | 0.50 | 0.70 | 1.00 | 0.50 | 0.67 | 0.71 | 1.00 | 0.00 | 1.00 | 1.00 | 1.00 | 0.33 | 0.40 | 0.40 | 0.53 | 0.58 | 0.00 | 0.50 | 0.50 | 0.90 | 0.65 | 0.50 | 0.00 | 0.69 | 0.69 | 0.73 | 1.00 | 0.57 | 1.00 | 1.00 | 0.82 | 0.85 |

| Character | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Isometrus maculatus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 5 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Zabius fuscus* | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 5 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Zabius birabeni* | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 5 | ? | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Tityus atriventer* | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | ? | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Tityus bahiensis* | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Tityus clathratus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Tityus metuendus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Tityus michelii* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Tityus pictus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Centruroides bani* | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Centruriodes exilicauda* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 5 | 0 | 0 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Centruroides gracilis* | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Centruroides infamatus* | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Centruroides margaritatus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Centruroides schmidti* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 |
| *Physoctonus debilis* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 5 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Physoctonus* sp nov | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 5 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Troglorhopalurus translucidus* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | ? | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Rhopalurus lacrau* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 0 | - | - | 2 | 0 | 0 | - | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Rhopalurus guanambiensis* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Rhopalurus* sp nov | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Rhopalurus laticauda* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Rhopalurus amazonicus* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Rhopalurus caribensis* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Rhopalurus crassicauda* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Rhopalurus agamemnon* | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 3 | 0 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Rhopalurus rochae* | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 3 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Rhopalurus pintoi* | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 4 | 0 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Rhopalurus abudi* | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Rhopalurus bonettii* | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Rhopalurus garridoi* | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Rhopalurus junceus* | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Rhopalurus princeps* | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 |
| Steps | 5 | 1 | 5 | 7 | 6 | 7 | 3 | 3 | 5 | 5 | 3 | 11 | 2 | 3 | 7 | 9 | 7 | 3 | 2 | 1 | 6 | 4 | 4 | 2 | 4 | 2 | 1 | 5 | 6 | 5 | 10 | 4 |
| Consistency Index | 0.40 | 1.00 | 0.20 | 0.29 | 0.17 | 0.29 | 0.33 | 0.67 | 0.40 | 0.20 | 0.67 | 0.45 | 0.50 | 0.33 | 0.14 | 0.22 | 0.29 | 0.67 | 1.00 | 1.00 | 0.17 | 0.25 | 0.25 | 0.50 | 0.25 | 0.50 | 1.00 | 0.20 | 0.17 | 0.40 | 0.10 | 0.25 |
| Retention Index | 0.82 | 1.00 | 0.67 | 0.17 | 0.67 | 0.17 | 0.67 | 0.92 | 0.63 | 0.60 | 0.83 | 0.45 | 0.50 | 0.50 | 0.40 | 0.53 | 0.69 | 0.92 | 1.00 | 1.00 | 0.55 | 0.67 | 0.50 | 0.00 | 0.25 | 0.00 | 0.00 | 0.43 | 0.44 | 0.25 | 0.31 | 0.77 |

| Character | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Isometrus maculatus* | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Zabius fuscus* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | - | 0 | 1 | 1 | 1 | 1 | 1 |
| *Zabius birabeni* | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | - | ? | ? | ? | ? | ? | ? |
| *Tityus atriventer* | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? |
| *Tityus bahiensis* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 |
| *Tityus clathratus* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | ? | ? | 1 | 1 | 1 |
| *Tityus metuendus* | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | ? | ? |
| *Tityus michelii* | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | - | 0 | ? | ? | ? | ? | ? |
| *Tityus pictus* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? |
| *Centruroides bani* | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? |
| *Centruriodes exilicauda* | 2 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | - | 0 | 0 | 0 | 0 | 1 | 1 |
| *Centruroides gracilis* | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Centruroides infamatus* | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? |
| *Centruroides margaritatus* | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | ? | ? | 0 | 1 | 1 |
| *Centruroides schmidti* | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | ? | ? | 0 | 1 | 1 |
| *Physoctonus debilis* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? |
| *Physoctonus* sp nov | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? |
| *Troglorhopalurus translucidus* | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? |
| *Rhopalurus lacrau* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? |
| *Rhopalurus guanambiensis* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? |
| *Rhopalurus* sp nov | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? |
| *Rhopalurus laticauda* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 1 | 0 |
| *Rhopalurus amazonicus* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? |
| *Rhopalurus caribensis* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? |
| *Rhopalurus crassicauda* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? |
| *Rhopalurus agamemnon* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | ? | ? | 0 | 1 | 1 |
| *Rhopalurus rochae* | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Rhopalurus pintoi* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | ? | ? | ? | ? | ? |
| *Rhopalurus abudi* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | - | 0 | 0 | 0 | ? | ? | ? |
| *Rhopalurus bonettii* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | - | 0 | ? | ? | 0 | 1 | 0 |
| *Rhopalurus garridoi* | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | - | 0 | ? | ? | ? | ? | ? |
| *Rhopalurus junceus* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | - | 1 | ? | ? | 0 | 1 | 0 |
| *Rhopalurus princeps* | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | - | 0 | 0 | 0 | 0 | 1 | 1 |
| Steps | 6 | 6 | 7 | 1 | 7 | 3 | 3 | 2 | 1 | 3 | 7 | 7 | 2 | 6 | 7 | 5 | 4 | 9 | 9 | 2 | 6 | 2 | 2 | 1 | 1 | 4 |
| Consistency Index | 0.33 | 0.33 | 0.14 | 1.00 | 0.14 | 0.33 | 0.33 | 0.50 | 1.00 | 0.33 | 0.29 | 0.29 | 0.50 | 0.17 | 0.29 | 0.40 | 0.25 | 0.11 | 0.22 | 0.50 | 0.17 | 1.00 | 0.50 | 1.00 | 1.00 | 0.25 |
| Retention Index | 0.60 | 0.67 | 0.14 | 0.00 | 0.25 | 0.33 | 0.50 | 0.50 | 0.00 | 0.33 | 0.44 | 0.74 | 0.83 | 0.50 | 0.62 | 0.77 | 0.40 | 0.47 | 0.46 | 0.75 | 0.29 | 1.00 | 0.50 | 1.00 | 0.00 | 0.00 |

**Appendix 4.** Additional material examined for the study of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971.

Specimens are deposited in the following collections: American Museum of Natural History (AMNH), New York, U.S.A., incorporating the Alexis Harington (AH) Collection; Natur-Museum Senckenberg, Frankfurt (SMF), Germany; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB), Germany; Zoologisches Museum der Universität Hamburg (ZMH), Germany. "LP" numbers are provided on labels with the specimens and correspond to entries in the molecular specimen database of Lorenzo Prendini at the AMNH. "ESV" numbers are provided on labels with the specimens and correspond to entries in the specimen database of Erich Volschenk.

***Physoctonus debilis* (C.L. Koch, 1840):** BRAZIL: *Pernambuco*: Exu, 5 km N, 1 ♀ (AMNH), 4 October 1977, L.J. Vitt; 1 ♀ (AMNH),18 January 1978, L.J. Vitt & K.E. Streilein; Exu, 18 km N, 1 ♀ (AMNH), 5 March 1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat; Fazenda Batente, 13 km E Exu, 1 ♀ (AMNH), 10 November 1977, L.J. Vitt & K.E. Streilein; Fazenda Caterino, 10 km NE Exu, 1 ♀ (AMNH), 9 July 1977, L.J. Vitt; 1 ♀ (AMNH), 25 September 1977, L.J. Vitt; *Bahia:* Xique-Xique, 1 ♂ (AMNH [LP 9950]), 10 March 2008, T.J. Porto; Xique-Xique, 1 ♂ (AMNH [LP 9681]), 10 February 2008, T.J. Porto; *Piauí*: proximo ao P.N. Sete Cidades, Brasileira e Piracuruca, 04°10'02S, 41°41'56.7W, 1 ♀ (AMNH [LP 9679]), 16 August 2008, R. Pinto-da-Rocha & L.S. Carvalho; Castelo do Piauí, 05°13'43S, 41°41'57W, 2 ♀, (AMNH [LP 9680, LP 9931)], 13 August 2008, R. Pinto-da-Rocha *et al.*; Oeiras, 06°58'28S, 42°06'31W, 2 ♀, 1 subadult ♂ (AMNH [LP 9678, LP 9940, LP 9962]), 2-3 June 2008, H. Yamaguti *et al.*

***Rhopalurus abudi* Armas & Marcano Fondeur, 1987:** DOMINICAN REPUBLIC: *La Altagracia Province*: Parque Nacional del Este: Cabo Flaso (entrance zone), 18°22'25"N, 68°37'01"W, 1 ♂ (AMNH [ESV6091]), 14 July 2004, E.S. Volschenk & J. Huff, 67.7 m; Track between ranger station (at Boca de Yuma) and Punta Faustino, 18°21'17.2"N, 68°36'52.3"W, 1 ♀, 48 first instars (AMNH [ESV6010]), 1 ♀, 22 first instars (AMNH [ESV6019]), 1 ♀ 32 first instars (AMNH [ESV6039]), 11 ♂, 4 ♀, 1 subad. ♂, 1 subad. ♀, 2 juv. (AMNH [ESV6072]), 1 ♂, 1 ♀ (AMNH [ESV7110]), 1 ♂, 1 ♀ (AMNH [ESV7117]), 1 ♂, (AMNH [ESV7120]), 1 ♂, 1 ♀ (AMNH [ESV7242]), 1 ♂, 1 ♀ (AMNH [ESV7303]), 1 ♀ (AMNH [ESV7306]), 1 ♂, 1 ♀ (AMNH [ESV7705]), 1 ♂, 1 ♀ (AMNH [ESV7937]), 3 juv. (AMNH), 1 juv. (AMNH [LP 3268]), 14 July 2004, E.S. Volschenk & J. Huff, 3.3 m, dense canopy humid forest, hand collected at night with blacklights, from limestone outcrops, especially along an old rock wall along the start of the track.

***Rhopalurus acromelas* Lutz & Mello, 1922:** BRAZIL: *Maranhão*: Municipio de Loreto: Santa Barbara, on shore of Rio Parnoiba, 1 ♂ (AMNH), June 1962, G. Eiten; *Pernambuco*: Exu, 10 km N, 1 ♀, 1 subad. ♀, 4 juv. (AMNH), 13 March 1977, L.J. Vitt,

rocky habitat within thorn scrub forest, 1 ♂, 1 ♀ (AMNH [ESV7532]), 14 March 1977, L.J. Vitt, rocky habitat in thorn scrub; Exu, 10 km NE, 1 ♂, 1 ♀, 2 subad. ♀, 2 subad., 1 juv. (AMNH), 28 April 1977, L.J. Vitt; 1 ♂, 1 ♀ (AMNH [ESV7244]), 25 September 1977, L.J. Vitt; Exu, 15 km NE, 1 subad. ♀ (AMNH), 14 May 1977, L.J. Vitt, high caatinga, under bark of tree; Exu, 20 km E, 1 juv. ♂ (AMNH), 30 March 1977, L.J. Vitt; Fazenda Caterino, 10 km NE Exu, 1 subad. ♂ (AMNH), 9 July 1977, L.J. Vitt; 1 juv. ♂ (AMNH) 1 August 1977, L.J. Vitt; *Piauí:* Barras, 04°19'04S, 42°18'26W, 1 subadult ♂ (AMNH [LP 9693)], 18 August 2008, R. Pinto-da-Rocha *et al.*; Sítio Ouro Verde, Teresina, 04°54'13.9S, 42°47'27.1W, 1 subadult ♂ (AMNH [LP 9695]), 27 July 2008, L.S. Carvalho, 27, 7, 2008; 1 subadult ♂ (AMNH [LP 9960)], 27 June 2008, L.S. Carvalho; *Maranhão*: Caxias, 04°56'26S, 43°27'59W, 2 subadult ♂ (AMNH [LP 9692, LP 9936]), 15-16 August 2008, R. Pinto-da-Rocha *et al.*; Castelo do Piauì, 05°13'43S, 41°41'57W, 1♀ (AMNH [LP 9696]), 13 August 2008, R. Pinto-da-Rocha *et al.*; 2 subadult ♂ (AMNH [LP 9933, LP 9939]); *Tocantins*: Mateiros, Jalapão, 10°33.811'S, 46°27.409'W, 1 subadult ♀ (AMNH [LP 9934]), 17 April 2009, S. Outeda-Jorge & F. Marques; 1 subadult ♂, 1 ♂ (AMNH [LP 9958, LP 9938)], 8 April 2009, S. Outeda-Jorge & F. Marques.

***Rhopalurus agamemnon* (Herbst, 1800):** BRAZIL: *Piauí:* Piracuruca, proximo ao P.N. Sete Cidades, 04°10'07S, 41°41'56.7W, 1♂ (AMNH [LP 9949]), 16 August 2008, R. Pinto-da-Rocha & L.S. Carvalho; Teresina, Campus UFPI, 05°02'43.5S, 42°46'13.4W, 1♂ (AMNH [LP 9929]), 16 August 2008, UFPI; Oeiras, 06°58'28S, 42°06'31W, 1♂, 1♀ (AMNH [LP 9954, LP 9942]), 2-3 April 2008, H.Y. Yamaguti *et al.*; *Maranhão:* Balsas, 07°28'44S, 46°07'09W, ]) 1 juvenile ♂, 1♀ (AMNH [LP 9932, LP 9948)], 4 June 2008, H.Y. Yamaguti *et al.*; *Tocantins:* Rio da Conceição, estrada para E.E. Serra Geral, 11°22'26S, 46°49'11W, 1♀ (AMNH [LP 9694]), 7 June 2008, H.Y. Yamaguti *et al.*; 1 subadult ♂ (AMNH [LP 9935]), 7 April 2008, H.Y. Yamaguti, M.B. da Silva & T.J. Porto.

***Rhopalurus amazonicus* Lourenço, 1986:** BRAZIL: *Parà*: Alter do Chão, Santarèm, 02°31'36S, 54°54'19W, 1 ♂, 1 subadult ♂, 3 juveniles (AMNH [LP 9686, LP 9688, LP 9689, LP 9690, LP 9691]), 28 October 2008, R. Pinto-da-Rocha & H. Yamaguti; Monte Alegre, 01°56'32S, 54°08'13W, 2 ♀ (AMNH [LP 9687, LP 9924]), 31 October 2008, R. Pinto-da-Rocha & H. Yamaguti.

***Rhopalurus bonettii* Armas, 1999:** DOMINICAN REPUBLIC: *Pedernales Province*: Parque National Jaragua: Cabo Rojo, 17°53'45.2"N, 71°39'35.8"W, 9 July 2004, E.S. Volschenk & J. Huff, 15 m, dry cactus and spiny forest on limestone karst, hand collected at night with blacklights, 3 ♂, 10 ♀, 4 subad., 2 juv. (AMNH [ESV6005]), 1 ♂ (AMNH [ESV7126]), 1 ♂, 1 ♀ (AMNH [ESV7127]), 1 subad. ♂ (AMNH), 1 juv. ♂ (AMNH [LP 3267]); Road to Fondo Paradi, 1.8 km from Highway 44, 17°48.692'N, 71°26.600'W, 12 January 2004, J. Huff, 302 ft, found between rocks, 1 ♀ (AMNH [LP 2471]), 1 ♀ (AMNH [LP 3265]); Track into park, between Manuell Goa and Oviedo, 17°48'41.5"N, 71°26'35.9"W, 9 July 2004, E.S. Volschenk & J. Huff, 83.3 m, deciduous forest and thorny scrub, hand collected from between stones during the day and with

blacklights at night, 13 ♂, 7 ♀, 1 subad., 1 juv. (AMNH [ESV6011]), 1 ♂, 1 ♀ (AMNH [ESV7112]), 1 ♂ (AMNH [ESV7129]), 1 juv. (AMNH [LP 3266]).

***Rhopalurus caribensis*** **Teruel & Roncallo, 2008:** COLOMBIA: *Magdalena Department*: Bahia de Guairaca, Tayrona Park, 1 ♀ (SMF 37027), 31 October 1985, H.-G. Muller; Pozo Colorado, 11 km W Santa Marta, 1 ♀, 1 subad., 19 first instars (AMNH), 18–30 April 1968, B. Malkin; Puente de Los Clavos, 15 km E Pueblo Bello, Sierra Nevada de Santa Marta, 1 subad. ♀ (AMNH), 13 June 1968, B. Malkin, 1500 m; Santa Marta, 2 ♀ (SMF 39120), 29 June–31 July 1966; Santa Marta, Finca Las Delicias, 1 ♂ (AMNH [LP 9341]), 17 May 2008, J.A. Noriega, 80 m; VENEZUELA: *Trujillo*: Motatan, San Miguel, ca. Represa Agua Viva, 09º30.225'N, 70º34.914'W, 1 juvenile (AMNH [LP 9199]), 23 September 2008, J.A. Ochoa & S. Bazo, 195 m, dry Forest; Valera Region, 1 ♀ (AMNH [LP 5504]), 1 ♀ (AMNH [LP 5505]), October 2005, S.E. Bazo Abreu; *Zulia:* Jesus Enrique Lozada, San Agustín, 10º45.841'N, 71º44.108', 1 subadult ♀ (AMNH [LP 9207]), 2 ♀, 3 ♂ (AMNH), 28 September 2008, J.A. Ochoa & S. Bazo, 44 m, dry forest.

***Rhopalurus crassicauda*** **Caporiacco, 1947:** BRAZIL: *Amazonas*: Rio Branco, Amazonasgebiet, 1 juv. ♀ (ZMB 14867), 1912, E. Ule; *Roraima*: Mt. Roraima, 2 ♂, 1 ♀, 1 subad. (AMNH); Alto Alegre, 02°56'34N, 61°03'09W, 1 juvenile ♂ (AMNH [LP 9927]), 10 November 2008, H.Y. Yamaguti & R. Pinto-da-Rocha; Alto Alegre, 03°00'10N, 61°18'08W, 1♂ (AMNH [LP 9952]), 10 November 2008, H.Y. Yamaguti & R. Pinto-da-Rocha; Bonfim, 03°22'45N, 59°49'18W, 1 ♂ (AMNH [LP 9677]), 1 subadult ♂ (AMNH [LP 9925]), 13 November 2008, H. Yamaguti & R. Pinto-da-Rocha; Mucajaì, 02°27'38N, 60°54'24W, 1 ♂ (AMNH [LP 9676]), 12 November 2008, H. Yamaguti & R. Pinto-da-Rocha; Normandia, 03°53'44N, 59°37'40W, 1 ♀ (AMNH [LP 9675]), 1 ♂ (AMNH [LP 9959]), 14 November 2008, H. Yamaguti & R. Pinto-da-Rocha; VENEZUELA: *Bolivar:* Gran Sabana, Parque Nacional Canaima: Laguna Canaima, Isla Anatoly, 06°15.191'N, 62°50.945'W, 1 juvenile (AMNH [LP 10048]), 27 July 2009, L. Prendini & J.A. Ochoa, 395 m, savanna and forest.

***Rhopalurus junceus*** **(Herbst, 1800):** CUBA: 1 juv. (AMNH [LP 7009]), July 2007, C. Hamilton,; 'Antillen?,' 1 ♂, 2 ♀ (ZMB 7370); 'Portorico', 2 ♀, 1 juv. (ZMB 7280 [ESV7001]), Stahl; 2 ♀ (ZMB 2637), 1 ♂, 1 ♀ (ZMB 7380 [ESV7224]), 1 juv. (ZMB, 7343), Gundlach; Arroyo Bermejo, near Fibacoa, 1 ♂ (ZMB 31020), 31 May 1967, Kleiderschrank; im zelt. wiese auf sandboden, 1 ♀ (ZMB 31021), 15 June 1967; 1 juv. (ZMB 31022), June 1967; Santiago de las Caballeros, 1 ♂ (ZMH),1936, P. Thumb; *Havana Province*: Havana, 1 ♀ (AMNH), April 1941, Dr E. Weiss, 1 ♀, 1 subad. (AMNH). *Holguín Province*: captive bred, 1 juv. (AMNH [LP 1928]), August 2000, Heist; near Baños [Banes], 2 ♂ (AMNH), May 1918; Guardalavaca, captive bred, 1 ♂ (AMNH [LP 1565]), 29 March 1993, W. Altmann; Mountains near Guisa, 1 ♀, 28 juv. (ZMH), October 1936, P. Thumb; Moa, 1 ♂ (ZMH), September 1937, P. Thumb; 4 ♀ (ZMH), 1938, P. Thumb; *Isla de la Juventud Province*: Isle of Pines, 1 ♂ (AMNH). *Pinar del Rio Province*: Guanahacabiles, Akadstat. El Beral, 1 subad. (ZMB 31023), December 1967, G. Peters; Sierra de Anafe, 2 subad. (AMNH), 23 February 1947, M. Barro; Vinales Valley, 1 ♀ (AMNH), 1940, Osorio. *Santiago de Cuba Province*: La

Socapa, 10 km SW of Santiago de Cuba, 1 ♂ (AMNH), 1 ♀ (AMNH [LP 1509]), 1 juv. ♀ (AMNH [LP 1517]), 1 ♀ (AMNH [LP 1518]), 9 April 1999, R. Teruel; Santiago de Cuba, 1 ♂, 2 juv. (AMNH); *Sancti Spiritus Province*: Trinidad, 1 ♂ (AMNH AH 4514 [ESV7041]), August 1978, B. Acosta.

***Rhopalurus garridoi* Armas, 1974:** CUBA: *Guantanamo*: (AMNH [LP 10225]) 1 ♀, G. Molisani, October, 2009.

***Rhopalurus guanambiensis* Lenarducci *et al.*, 2005:** BRAZIL: *Bahìa*: Municìpio Ceraìma, Aeroporto de Guanambi, Guanambi, 14°13'00S, 42°46'60W 1 subadult ♀ (AMNH [LP 9669]), 1 ♂ (AMNH [LP 9937]), 17 December 2007, H. Yamaguti *et al.*; *Minas Gerais*: Januaria, P.N. Cavernas do Peruaçu, 15.12383°S, 44.24111°W, 1 subadult ♂ (AMNH [LP 9670]), 4-25 January 2009, R.S. Recoder & M. Teixeira-Jùnior.

***Rhopalurus junceus* (Herbst, 1800):** CUBA: 1 juvenile (AMNH [LP 7009]), July 2007, C. Hamilton; *Holguin*: Guardalavaca, captive bred, 1 ♂ (AMNH [LP 1565]), 29 March 1993, W. Altmann; Heist, captive bred 1 juvenile (AMNH [LP 1928]), August 2000, B. Striffler; *Santiago de Cuba*: La Socapa, 10 km SW of Santiago de Cuba, 1 juvenile (AMNH [LP 1517]), 1 ♀ (AMNH [LP 1518]), 1 ♂, 1 ♀ (AMNH [LP 1509]), 9 April 1999, R. Teruel.

***Rhopalurus lacrau* Lourenço & Pinto-da-Rocha, 1997:** BRAZIL: *Bahia*: Município Itaeté: Trail between Caves 'Lapa do Bode' and 'Lapa Escondida,' 12°56'9.1"S, 41°3'56.2"W, 2 ♀ (AMNH), 1 subad. ♀, 4 juv. (AMNH [LP 7637]), 21 January 2007, C.I. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, under rocks; Municipio Itaeté, Lapa do Bode, 1 juvenile (AMNH [LP 10211]), 24 January 2007, C.I. Mattoni, R. Pinto-da-Rocha & H. Yamaguti.

***Rhopalurus laticauda* Thorell, 1876:** 2 ♀ (ZMB 14865); 'Mexico', Dr v. Hubl, 1 ♂ (ZMB 14866). VENEZUELA: 1 ♂, 1 ♀ (ZMB 8226), F. Kummerow; San Jose de Guaviare, 1 ♀ (SMF 39252), December 1955, Meden; *Aragua*: 1 subad. ♂ (SMF 29208), Maracay; 1 ♂, 1 ♀, 1 subad. (SMF 8876/218), Fahrenholz; *Bolívar*: Ciudad Bolivar, 2 ♀ (ZMH), 20 February 1903; La Paragua, M.A. de Verde, 1 ♂ (AMNH); Upata, 1 ♀ (AMNH), February 1973, A. Bordes; *Carabobo*: Valencia, 1 ♀ (ZMB 31024), 29 December 1904, F. Kummerow; 2 ♀ (ZMH), September 1958, H. Ardelt; *Distrito Federal*: Caracas, 2 ♀, 20 first instars (AMNH [ESV7444], March 1999, C. Siederman; 1 ♂ (AMNH [LP 2462]), 2001, C. Siederman; *Guarico*: Calabozo and San Fernando de Apure (about halfway between), 1 ♀ (AMNH), 30 November 1967, M.A. de Verde; 'Hato Masaguarat,' 45 km S Calabozo, 1 ♂ (AMNH [ESV7816]), 7 April 1978, Y. Lubin; Guatire, 1 ♂, 1 ♀ (AMNH [LP 2845]), 29 April 2004, R.C. West, under rocks, dry forest. *Mérida*: Mérida, 2 ♂, 3 ♀ (SMF 5712/27); *Miranda*: Guatire, 1 ♂ (AMNH [LP 2845]), 1 ♀ (AMNH), 29 April 2004, R.C. West, under rocks, dry forest; Hda. Santa Rosa, 3 km N Guatire, 1 ♂, 1 ♀, 2 juv. (AMNH), 10 January 1973, M.A. González-Sponga, 450 m; *Nueva Esparta*: Isla Margarita, N of Peninsula de Macanao, 11°02.618'N, 64°21.542'E, 1 ♀ (AMNH [LP 4221]), 4 September 2005, S. Huber; *Apure:*

Elorza, 10 km SO Elorza, road to San Felipe, 07º03.749'N, 69º30.249'W, 1 juvenile (AMNH [9200]), 5 October 2008, J.A. Ochoa & S. Bazo, 89 m, llanos; *Bolívar:* Cedeño, ca. Los Pijiguaos, 06º29.878'N, 67º02.600'W, 1 juvenile (AMNH [LP 9237]), 12 October, 2008, J.A. Ochoa & S. Bazo, 76 m, llanos; Ciudad Bolívar, ca. Bolivar city, 07º37.486'N, 64º05.924'W, 1 juvenile (AMNH [LP 9256]), 24 October 2008, J.A. Ochoa & S. Bazo, 117 m, llanos; Cedeño, Comunidad Corosal, ca. Pijiguaos, 1 subadult ♀ (AMNH [LP 9253]), 25 October 2008, J.A. Ochoa, 80 m, forest.

***Rhopalurus pintoi* Mello-Leitão, 1933:** GUYANA: *Roraima Province*: Rununui region, SW Guyana, near Venezuelan border, 1 juv. ♂ (AMNH [LP 8278]), March 2008, ex A. Tietz; Vila Tepequèm, Amajari, 03°47'54N, 61°44'57W, 1♀ (AMNH [LP 9671]), 17 November 2008, H. Yamaguti & R. Pinto-da-Rocha; Vila Tepequém, Amajari, 03°47'54N, 61°43'08W, 1♀ (AMNH [LP 9672]), 11 November 2008, H. Yamaguti & R. Pinto-da-Rocha; Normandia, 03°53'44N, 59°37'40W, 1 juvenile ♂ (AMNH [LP 9928]), 1 juvenile ♂ (AMNH [LP 9944]), 14 November 2008, H.Y. Yamaguti & R. Pinto-da-Rocha.

***Rhopalurus princeps* (Karsch, 1879):** DOMINICAN REPUBLIC: *Independencia Province*: Isla Cabritos, 18°30.019'N, 71°43.228'W, 1 ♂, 1 ♀, 16 juv. (AMNH), 5 ♂, 3 ♀, 3 subad., 1 juv. (AMNH), 3 juv. (AMNH [LP 2470]), 1 subad., 2 juv. (AMNH [LP 3260]), 7 January 2004, J. Huff, 110 ft, under rock, coral; Ranger station for Parque Nacional Isla Cabritos, 18°33'45"N, 71°41'50"W, 3 ♂, 7 ♀, 5 subad., 2 juv. (AMNH [ESV6006]), 1 subad. ♂ (AMNH), 1 subad. (AMNH [LP 3264]), 8 July 2004, E.S. Volschenk & J. Huff, -19 m, dry forest, hand collected from under stones and logs, and with blacklights; Parque Nacional Isla Cabritos, behind Ranger Station, 18.56287°N, 71.69762°W, 2 ♂, 8 ♀, 1 subad. ♀, 32 first instars (AMNH), 2 ♂, 1 subad. ♀ (AMNH), 1 ♂ (AMNH [LP 5102]), 8 August 2005, L. Esposito, -23 m, mixed dry forest with succulents, UV detection; Parque Nacional Sierra de Baoruco, road between Rabo de Gato and Duverge, 18°19'38"N, 17°33'55"W, 3 ♂, 3 ♀, 3 juv. (AMNH [ESV6033]), 1 juv. (AMNH), 1 ♀ (AMNH [LP 3263]), 7 July 2004, E.S. Volschenk & J. Huff, 447 m, arid thorny scrub, hand collected from under stones and in dead and dry agaves; Puerto Escondido, Sierra de Baoruco, 18°19.762'N, 71°33.502'W, 1 ♂, 3 ♀, 1 juv. (AMNH), 1 juv. (AMNH [LP 3261]), 6 January 2004, J. Huff, 1592 ft, under dead agave; Road to Puerto Escondido, 18°20.376'N, 71°33.345'W, 1 ♀ (AMNH), 1 juv. (AMNH [LP 3262]), 6 January 2004, J. Huff, 1388 ft, under rocks in gravel quarry; *Pedernales Province*: Manuel Goja, 3.9. km N, 1 ♂ (AMNH [LP 1566]), 9 May 1998, D. Huber; Oviedo to Pedernales, 11.5 km N, 1 ♂ (AMNH [LP 1516]), 8 May 1998, D. Huber; HAITI: *Departement de l'Ouest*: Port-au-Prince, holotype ♂ (ZMB 116), Ehrenberg.

***Rhopalurus rochae* Borelli, 1910:** BRAZIL: *Bahia*: Município Ceraíma: Guanambí, 7 km S, 14°17'5.6"S, 42°47'2.2"W, 1 juv. (AMNH [LP 7638]), 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 533 m, UV sampling, modified savanna, cloudy and raining; Fazenda du Fabiano, 8 km NE Guanambí, 14°10'17.6"S, 42°43'56.4"W, 1 ♂, 2 juv. (AMNH [LP 7639]), 1 ♀ (AMNH), 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 539 m, under rocks, rocky hill and surrounds, open savanna modified; Guanambí, 16 km SE, 14°17'19"S, 42°41'31.1"W, 1

juv. (AMNH [LP 7655]), 25 January 2007, C. Mattoni, R. Pinto-da-Rocha, H. Yamaguti, 559 m, UV sampling and under leaf litter, banana plantation and surrounds; *Paraíba*: Soledade, 07°02.118'S, 36°27.311'W, 1 ♂ (AMNH [LP 1581]), 1 ♀ (AMNH [LP 1582]), 1 ♂ (AMNH [LP 1775]), 16 March 1999, A. Kury & A. Giupponi, 575 m. *Pernambuco*: Escola Aquicola, Exu, 1 ♂ (AMNH [ESV7248]), 30 March 1977, L.J. Vitt, caatinga; 1 ♂ (AMNH), 27 June 1977, L.J. Vitt; Exu, 3 km NW, 2 ♂, 1 ♀, 3 juv. (AMNH), 10 March 1977, L.J. Vitt; Exu, 3 km W, 2 ♂, 4 ♀, 4 juv. (AMNH), 30 May 1977, L.J. Vitt, 1 June 1977; 1 ♀ (AMNH), L.J. Vitt,; Exu, 5 km N, 1 ♂, 1 juv. (AMNH), 6 April 1977, L.J. Vitt, caatinga; 1 juv. (AMNH), 18 January 1978, L.J. Vitt & K.E. Streilein; Exu, L.J. Vitt, 1 juv. (AMNH), 5 km E, 8 May 1977; Exu, 6 km N, 1 ♀, 1 juv. ♂ (AMNH), 15 March 1977, L.J. Vitt, open fields (cotton), under fallen logs; Exu, 6 km NE, 1 ♀, 49 first instars (AMNH), 16 March 1977, L.J. Vitt, under rock on larger rock, caatinga habitat; Exu, 18 km E, 1 ♀, 29 first instars (AMNH), 1 ♀, 39 first instars (AMNH [ESV7210]), 5 March 1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat; Exu, 20 km E, 1 ♂, 1 ♀ (AMNH [ESV7625]), 30 March 1977, J.L.Vitt,; Fazenda Batente, 5 km NE Exu, 1 juv. (AMNH), 29 March 1977, L.J. Vitt; Fazenda Caterino, 10 km NE Exu, 2 ♂, 3 juv. (AMNH), 5 ♂, 3 ♀ (AMNH), 1 August 1977, L.J. Vitt; Fazenda Chelonia, 8 km S Exu, 2 juv. (AMNH), 28 July 1977, L.J. Vitt; Fazenda Guarani, 3 km N Exu, 1 ♂, 3 ♀, 1 subad. 3 juv. (AMNH), 14 July 1977, L.J. Vitt; Fazenda Guarani, 5 km N Exu, 1 ♀, 3 juv. (AMNH), 29 July 1977, L.J. Vitt; 1 ♀ (AMNH) 19 February 1978, L.J. Vitt; *Sergipe*: Municipio Lagarto: near Genipapo, 1 ♂, 2 ♀ (AMNH), July 1982, O.F. Francke.

***Rhopalurus virkkii*** **Santiago-Blay, 2009**: U.S.A.: *Puerto Rico*: Isla Mona, road to El Faro, 18.06389°N, 67.86857°W 1♂ 3♀ (AMNH), 1 juvenile (AMNH [LP 10234]), U.S.A, Puerto Rico, Isla Mona, road to El Faro, 17 October 2009, L. Esposito & H. Yamaguti, blacklighting, Vegetation primarily desert grassland dominated by organ cactus and tall grasses; trail #1 to Punta Capitan from Sardiniera, 18.08823°N, 67.93815°W, 10♂ 10♀ (AMNH), 2 juveniles (AMNH [LP 10235]), 16 October 2009, L. Esposito & H. Yamaguti, blacklighting - trail is primarily scrub forest and cactus.

**Appendix 5.** Localities and GenBank accession numbers for specimens used in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890

| Species | Locality | 12S | 16S | 18S | 28S | CoxI |
|---|---|---|---|---|---|---|
| *Centruroides alayoni Armas, 1999* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides alayoni Armas, 1999* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides anchorellus Armas, 1976* | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides arctimanus Armas, 1976* | Cuba, Holguín | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides baergi Hoffmann, 1932* | Mexico, Oaxaca, Municipio Cuicatlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides baergi Hoffmann, 1932* | Mexico, Oaxaca, Santa María Ixcatlán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides balsasensis Ponce & Francke, 2004* | México, Michoacán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides balsasensis Ponce & Francke, 2004* | México, Michoacán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bani Armas & Marcano Fonduer, 1987* | Dominican Republic, Barahona Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bani Armas & Marcano Fonduer, 1987* | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides barbudensis Pocock, 1898* | Saba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides barbudensis Pocock, 1898* | St. Kitts and Nevis, Nevis | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides aff bertholdi Pocock, 1902* | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides aff bertholdi Pocock, 1902* | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bicolor (Pocock, 1898)* | Costa Rica, Puntarenas Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bicolor (Pocock, 1898)* | Costa Rica, Puntarenas Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus borinquensis Armas, 1982* | U.S.A., Puerto Rico | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus borinquensis Armas, 1982* | U.S.A., Puerto Rico | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chamulaensis Hoffmann, 1932* | México, Chiapas, Municipio San Juan Chamula | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chamulaensis Hoffmann, 1932* | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chiapanensis Hoffmann, 1932* | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chiapanensis Hoffmann, 1932* | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans elegans (Thorell, 1876)* | Mexico, Jalisco, Municipio Las Huertas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans elegans (Thorell, 1876)* | Mexico, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilicauda (Wood, 1863)* | México, Baja California | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilicauda (Wood, 1863)* | Mexico, Baja California Sur, Municipio La Paz | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilimanus Teruel & Stockwell, 2002* | Honduras? | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilimanus Teruel & Stockwell, 2002* | Honduras? | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides farri? (Thorell, 1876)* | Jamaica, St. Elizabeth Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | 12S | 16S | 18S | 28S | CoxI |
|---|---|---|---|---|---|---|
| *Centruroides flavopictus flavopictus (Pocock, 1898)* | México, Veracruz, Municipio Catemaco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus flavopictus (Pocock, 1898)* | Mexico, Oaxaca, Municipio de Santa Maria Jacatepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus meridionalis Hoffmann, 1932* | México, Chiapas, Municipio Comitan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus meridionalis Hoffmann, 1932* | México, Chiapas, Municipio Comitan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides fulvipes (Pocock, 1898)* | Mexico, Oaxaca | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides gracilis (Latreille, 1804)* | México, Hidalgo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides gracilis (Latreille, 1804)* | México, San Luis Potosi | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus (C.L. Koch, 1844)* | U.K., British Virgin Islands, Guana Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus (C.L. Koch, 1844)* | U.S.A., Puerto Rico, Culebra | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides guanensis Franganillo, 1930* | U.S.A., Florida, Monroe County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hentzi (Banks, 1900)* | U.S.A., Florida | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hentzi (Banks, 1900)* | U.S.A., Florida, Alachua County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hirstutipalpus Ponce-Saavedra & Francke, 2009* | México, Colima, Minatitlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hirstutipalpus Ponce-Saavedra & Francke, 2009* | Mexico, Colima | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hoffmanni Armas, 1996* | México, Chiapas, Municipio Tzimol | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hoffmanni Armas, 1996* | México, Chiapas, Municipio Villaflores | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides infamatus Pocock, 1902* | Mexico, Michoacan, Municipio Tinqambato | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides infamatus Pocock, 1902* | Mexico, Michoacan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides insulanus (Thorell, 1876)* | Jamaica, St. Thomas Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides insulanus (Thorell, 1876)* | Jamaica, St. Ann Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans insularis Pocock, 1902* | Mexico, Nayarit, Municipio Tuxpan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans insularis Pocock, 1902* | Mexico, Nayarit | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides jaragua Armas, 1999* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides koesteri Kraepelin, 1912* | Costa Rica, Guanacaste Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides koesteri Kraepelin, 1912* | Nicaragua, León, La Paz Centro | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limbatus (Pocock, 1898)* | Costa Rica, Hacienda Barú, Barú | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limbatus (Pocock, 1898)* | Costa Rica, Limon Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limpidus (Karsch, 1879)* | México, Guerrero, Tepecoacuilco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limpidus (Karsch, 1879)* | México, Guerrero, Buena Vista de Cuellar | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides luceorum Armas, 1999* | U.S.A., Navassa Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides maracanoi Armas, 1981* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides maracanoi Armas, 1981* | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| Centruroides margaritatus (Pocock, 1898) | Costa Rica, Esterillos Centro | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | 12S | 16S | 18S | 28S | CoxI |
|---|---|---|---|---|---|---|
| Centruroides margaritatus (Pocock, 1898) | Ecuador, Loja, Catamayo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides mariaorum Santiago-Blay, 2009* | U.S.A, Puerto Rico, Isla Mona | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides mariaorum Santiago-Blay, 2009* | U.S.A, Puerto Rico, Isla Mona | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides meisei Hoffmann, 1938* | Mexico, Guerrero, Municipio Copala | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides meisei Hoffmann, 1938* | Mexico, Guerrero, Municipio Copala | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides morenoi Mello-Leitao, 1945* | Jamaica, St. Andrews Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides morenoi Mello-Leitao, 1945* | Jamaica, St. Andrews Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrescens (Pocock, 1898)* | Mexico, Oaxaca, Miahuatlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrescens (Pocock, 1898)* | Mexico, Oaxaca, Magdalena Mixtepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrimanus Pocock, 1898* | Mexico, Oaxaca, Municipio Santiago Astata | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrovariatus (Pocock, 1898)* | Mexico, Oaxaca, San Sebastián de las Grutas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrovariatus (Pocock, 1898)* | Mexico, Oaxaca, Magdalena Mixtepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus nitidus (Thorell, 1876)* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus nitidus (Thorell, 1876)* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus taino Armas & Marcano Fondeur, 1987* | Dominican Republic | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus taino Armas & Marcano Fondeur, 1987* | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides noxious Hoffmann, 1932* | Mexico, Nayarit | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides noxious Hoffmann, 1932* | Mexico, Nayarit, Municipio Huajicori | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ochraceus (Pocock, 1898)* | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ochraceus (Pocock, 1898)* | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ornatus Pocock, 1902* | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ornatus Pocock, 1902* | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides platnicki Armas, 1981* | Turks and Caicos, Caicos, Providenciales | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides pococki Sissom & Francke, 1983* | St. Kitts and Nevis, St. Kitts | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides rileyi Sissom, 1995* | Mexico, Veracruz | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides rileyi Sissom, 1995* | Mexico, San Luis Potosi, Axtlan de Terrazas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sasae Santiago-Blay, 2009* | U.S.A, Puerto Rico, Isla Caja de Muertos | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides schmidti Sissom, 1995* | Mexico, Chiapas, Municipio Ococingo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides schmidti Sissom, 1995* | Guatemala, Izabal | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sculpturatus Ewing, 1928* | U.S.A., Arizona, Pima County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sculpturatus Ewing, 1928* | Mexico, Sonora, Municipio Soyopa | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides serrano Santibanez-Lopez & Ponce-Saavedra, 2009* | Mexico, Oaxaca, Municipio Villa Alta | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | 12S | 16S | 18S | 28S | CoxI |
|---|---|---|---|---|---|---|
| *Centruroides serrano Santibanez-Lopez & Ponce-Saavedra, 2009* | Mexico, Oaxaca, Municipio Villa Alta | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sissomi Armas, 1996* | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tapachulaensis Hoffmann, 1932* | Mexico, Oaxaca, San Pedro Juchatengo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tapachulaensis Hoffmann, 1932* | Mexico, Oaxaca, San Sebastián de las Grutas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tecomanus Hoffmann, 1932* | Mexico, Michoacan, Municipio de Aquila | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tecomanus Hoffmann, 1932* | Mexico, Jalisco, Municipio Talpa de Allende | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus arubensis Backer, 1963* | Dutch Antilles, Aruba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus arubensis Backer, 1963* | Dutch Antilles, Aruba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus testaceus DeGeer, 1778* | Dutch Antilles, Curacao | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus testaceus DeGeer, 1778* | Dutch Antilles, Bonaire | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides thorellii (Kraepelin, 1891)* | Guatemala, Sacatepéquez | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tuxtla Armas, 1999* | Mexico, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tuxtla Armas, 1996* | México, Chiapas, Municipio Arriaga | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides vittatus (Say, 1821)* | U.S.A., Texas, Terrell County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides vittatus (Say, 1821)* | U.S.A., Texas, Brewster County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus abudi Armas & Marcano Fondeur, 1987* | Dominican Republic, La Altagracia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus bonettii Armas, 1999* | Dominican Republic, Pedernales Provence, N | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus bonettii Armas, 1999* | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus garridoi Armas, 1974* | Cuba, Guantanamo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus (Herbst, 1800)* | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus (Herbst, 1800)* | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus (Herbst, 1800)* | Cuba, Holguin | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus laticauda Thorell, 1876* | Venezuela, Caracas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps (Karsch, 1879)* | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps (Karsch, 1879)* | Dominican Republic, Oviedo to Pedernales | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps (Karsch, 1879)* | Dominican Republic, Pedernales Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps (Karsch, 1879)* | Dominican Republic | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus rochae Borelli, 1910* | Brazil, Bahia | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus clathratus C.L. Koch, 1844* | Trinidad & Tobago, Trinidad, Gaspar Grande Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus discrepans (Karsch, 1879)* | Venezuela, Distrito Federal, Caracas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus discrepans (Karsch, 1879)* | Venezuela, Miranda, Los Salias | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus elii Armas & Marcano Fondeur, 1992)* | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | 12S | 16S | 18S | 28S | CoxI |
|---|---|---|---|---|---|---|
| *Tityus elii Armas & Marcano Fondeur, 1992* | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius birabeni Mello-Leitão, 1938* | Argentina, La Pampa Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius birabeni Mello-Leitão, 1938* | Argentina, San Juan Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius fuscus (Thorell, 1876)* | Argentina, Córdoba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius fuscus (Thorell, 1876)* | Argentina | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

**Appendix 6.** Morphological characters and character states used in phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890.

1. Prosoma, Carapace, Lateral Ocular Carinae (Volschenk & Prendini, unpublished)
    0 present
    1 reduced to several granules
    2 absent

2. Prosoma, Carapace, Centrolateral Carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

3. Prosoma, Carapace, Anterior Centrosubmedian carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

4. Prosoma, Carapace Posterior Centrosubmedian Carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

5. Prosoma, Carapace, Anterior median notch
    0 present
    1 absent

6. Prosoma, Carapace, granulation
    0 non-granular
    1 sparse granules
    2 densely granular medially
    3 densely granular

7. Prosoma, carapace, granular form
    0 weak, shagreened
    1 large, round
    2 large, conical
    3 none

8. Prosoma, Carapace, anterior median furrow
    0 absent
    1 present, wide
    2 present, narrow, deep

9. Prosoma, Carapace, median occular furrow

0 absent
1 present, wide
2 present, narrow, deep

10. Prosoma, Carapace, posterior median furrow
0 absent
1 present, wide
2 present, narrow, deep

11. Prosoma, Carpace, posterior marginal furrow
0 absent
1 present

12. Prosoma, Carapace, posterior lateral furrows
0 absent
1 present

13. Prosoma, Carapace, anterior margin, carination
0 none
1 smooth keel
2 granular

14. Prosoma, Carapace, lateral margins, carination
0 none
1 smooth keel
2 granular

15. Prosoma, Carapace, posterior margin, carination between posterior centrosubmedian carinae
0 none
1 smooth keel
2 granular

16. Prosoma, Pedipalp, chela, dorsointernal carina (Volschenk & Prendini, unpublished)
0 granular
1 non-granular
2 absent

17. Prosoma, Pedipalp, chela, dorsoexternal carina (Volschenk & Prendini, unpublished)
0 granular
1 non-granular
2 absent

18. Prosoma, Pedipalp, chela, externomedian carina (Volschenk & Prendini, unpublished)
0 granular

1 non-granular
2 absent
3 reduced to several granules

19. Prosoma, Pedipalp, chela, externoventral dorsal accessory carina (Volschenk & Prendini, unpublished)
0 complete
1 reduced
2 absent

20. Prosoma, Pedipalp, chela, externoventral carina
0 granular
1 non-granular

21. Prosoma, Pedipalp, chela, internodorsal accessory carina
0 present
1 absent

22. Prosoma, Pedipalp, chela, internoventral accessory carina
0 present
1 absent

23. Prosoma, pedipalp, patella, dorsal median carina
0 present
1 absent

24. Prosoma, Pedipalp, femur, external median carina
0 small granules
1 large, conical granules

25. Prosoma, Pedipalp, fixed finger, number of denticular rows
0 eight
1 nine
2 10 or more
3 seven plus fused basal row
4 six plus fused basal row

26. Prosoma, Pedipalp, fingers, supernumary granules (Soleglad & Fet, 2003; Volschenk & Prendini, unpublished)
0 absent
1 present

27. Prosoma, Pedipalp, movible finger, number of denticular rows (Soleglad & Fet, 2003; Prendini, 2004; Volschenk & Prendini, unpublished)
0 eight
1 nine

2 eleven
3 thirteen or more
4 seven plus fused basal row

28. Prosoma, Pedipalp, chela (males) (Prendini, 2001, 2004)
0 incrassate
1 not incrassate

29. Prosoma, Pedipalp, chela (females) (Prendini, 2001)
0 incrassate
1 not incrassate

30. Prosoma, Pedipalp, movable finger, basal lobe (males) (Prendini, 2001)
0 absent
1 present

31. Prosoma, Leg I, tarsi, tuft setal form (Volschenk & Prendini, unpublished)
0 dense, short
1 dense, long, accuminate
2 sparse

32. Prosoma, Leg IV, tarsi, setal form (Volschenk & Prendini, unpublished)
0 dense, short
1 dense, long, accuminate
2 sparse

33. Prosoma, Leg IV, trochanter, margins
0 no keel, flat
1 smooth keel
2 granular keel

34. Mesosoma, pectines, pectinal tooth shape
0 elongate, with parallel sides
1 rounded, spade-like

35. Mesosoma, pectines, proximal teeth, nodules on dorsal surface
0 one nodule
1 multiple nodules
2 nodules absent

36. Mesosoma, pectines, dorsal fulcra
0 present
1 reduced

37. Mesosoma, pectines, tympanum-like expansion between lamellae and teeth
0 absent

1 present

38. Mesosoma, pectines, setation of the dorsal proximal fulcra
    0 one
    1 two
    2 three
    3 four
    4 six or more
    5 absent

39. Mesosoma, pectines (males), anterior margin of the pectinal plate, sulcus
    0 present
    1 absent

40. Mesosoma, pectines (males), posterior margin of the pectinal plate
    0 straight
    1 convex
    2 concave

41. Mesosoma, pectines (males), median pectinal plate depression
    0 present
    1 absent

42. Mesosoma, pectines (males), lateral pectinal plate depressions
    0 present
    1 absent

43. Mesosoma, pectines (males), pectinal plate shape
    0 square
    1 rectangular
    2 trapezoid

44. Mesosoma, pectines (females), anterior margin of the pectinal plate, sulcus
    0 present
    1 absent

45. Mesosoma, pectines (females), posterior margin of the pectinal plate
    0 straight
    1 slightly convex
    2 prominently rounded
    3 concave

46. Mesosoma, pectines (females), pectinal plate depressions
    0 none
    1 single median wide depression
    2 paired lateral depressions

3 single median small, deep depression (pinhole)

47. Mesosoma, Sternite VI, ventromedian carina (Volschenk & Prendini, unpublished)
0 absent
1 present, granular
2 present, non-granular

48. Mesosoma, Sternite V (males), setation
0 absent
1 un-pitted setae
2 pitted setae

49. Mesosoma, Sternite VI, ventrolateral carina (Volschenk & Prendini, unpublished)
0 absent
1 reduced to single granule
2 present

50. Mesosoma, Tergites III-VI, lateral carinae (Volschenk & Prendini, unpublished)
0 present
1 absent

51. Mesosoma, Tergites III-VI, submedian carinae (Prendini, 2004)
0 absent
1 reduced
2 present

52. Mesosoma, Tergite VII, median carina (Volschenk & Prendini, unpublished)
0 narrow granular ridge
1 wide granular keel
2 wide non-granular keel
3 reduced to nub

53. Metasoma, Segment II, lateral median carinae (Prendini, 2004; Volschenk & Prendini, unpublished)
0 complete
1 posteriorly restricted
2 absent

54. Metasoma, Segment III, lateral median carinae (Prendini, 2004; Volschenk & Prendini, unpublished)
0 complete
1 posteriorly restricted
2 absent

55. Metasoma, Segment III, dorsolateral carinae
0 distal granules similar in size

1 distal granules larger and accuminate

56. Metasoma, Segment IV, median lateral carinae
0 absent or obsolete
1 present

57. Metasoma, Segment V, posterior margin granulation (Volschenk & Prendini, unpublished)
0 present
1 absent

58. Metasoma, Segment V, dorsolateral carinae
0 present
1 absent

59. Metasoma, Segment V, median lateral carinae
0 absent or obsolete
1 present

60. Metasoma, Segment V, ventrolateral carinae
0 absent
1 present

61. Metasoma, Segment V, ventromedian carinae
0 absent or obsolete
1 present

62. Metasoma, Segment V, ventral submedian carinae
0 absent or obsolete
1 present

63. Metasoma, Segment V (males), ratio of segment length to width
0 slightly elongated, length less than 2x width
1 elongated, length 2.5-3X width
2 pronounced elongation, length more than 3X the width

64. Metasoma, Segments I-IV, width (Lamoral, 1978; Prendini, 2001, 2003)
0 narrowing distally, segment I slightly wider than segment IV
1 slight widening distally, segment I slightly narrower than segment IV
2 pronounced widening distally, segment I much narrower than the segment V

65. Metasoma, length (males)
0 similar or slightly greater than the length of the rest of the body
1 1.5-2X the length of the body
2 more than 2x the length of the body

66. Metasoma, length (females)
    0 similar or slightly greater than the length of the rest of the body
    1 1.5-2X the length of the body
    2 more than 2x the length of the body

67. Telson (males), length
    0 spherical, length similar to the width
    1 slightly ovate, length approximately 1.5X the width
    2 ovate, length more than 2X the width

68. Telson (males), width in relation to the width of metasomal segment V (Lamoral, 1978; Prendini, 2001, 2003)
    0 similar
    1 more narrow
    2 much narrower, less than half the width of metasomal segment V

69. Telson, ventral median carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

70. Telson, ventral lateral carinae (Volschenk & Prendini, unpublished)
    0 present
    1 absent

71. Telson, aculeus
    0 pointing up, 90 degree angle to telson
    1 pointing out, less than 90 degree angle to telson

72. Telson, notch at ventrolateral proximal margin
    0 absent
    1 present, unmodified
    2 present, dorsally projecting

73. Telson, lateral lobes
    0 absent
    1 present

74. Telson, ventral surface
    0 granular
    1 smooth

75. Telson, subaculear tubercle (Lamoral, 1980; Stockwell, 1989; Prendini, 2000, 2004; Soleglad & Fet, 2003; Volschenk, unpublished)
    0 developed, singular
    1 developed, bifurcated
    2 slight protuberance

3 absent

76. Relation of male and female total length
    0 males smaller or similar
    1 males much larger

77. Mesosoma, Ovariuterus, number of loops (Volschenk *et al.*, 2008)
    0 8
    1 9

78. Mesosoma, Ovariuterus (Volschenk *et al.*, 2008)
    0 simple
    1 complex bridged

79. Mesosoma, Booklungs, Lamellar surface (Kamenz & Prendini, 2008)
    0 slender venation
    1 ribbed venation

80. Mesosoma, Booklungs, Lamellar edge (Kamenz & Prendini, 2008)
    0 thorns
    1 smooth or wrinkled

81. Mesosoma, Booklungs, Posterior spiracle edge (Kamenz & Prendini, 2008)
    0 hillocks
    1 subconical

82. Prosoma, pedipalp patella internal setation
    0 dense, long setae
    1 sparse, short setae

83. Prosoma, legs, tarsal claws
    0 long, slightly curved
    1 hooked

84. Prosoma, Chelicerae, reticulated coloration
    0 present
    1 laterally restricted
    2 absent

85. Prosoma, Pedipalps, coloration
    0 equally colored
    1 manus darker
    2 manus and patella darker
    3 manus lighter

86. Prosoma, Pedipalp, femur, mottling

0 present
1 absent

87. Prosoma, Pedipalp, patella, mottling
0 present
1 absent

88. Prosoma, Pedipalp, manus, mottling
0 present
1 absent

89. Prosoma, Pedipalp, fingers, mottling
0 present
1 absent

90. Mesosoma, Tergites I-VI, mottling
0 present
1 absent

91. Mesosoma, Tergites I-VI, lateral band shape
0 none
1 narrow
2 distinct, rectangular
3 wide, nearly touching margins

92. Mesosoma, Tergites I-VI, lateral band intensity
0 absent
1 faint
2 mottled
3 distinct

93. Mesosoma, Tergites I-VI, coloration
0 eye-shaped pattern
1 absent

94. Mesosoma, Tergites I-VI, lateral margin coloration
0 distinct black line
1 none

95. Mesosoma, Tergites I-VI, median stripe
0 absent
1 present

96. Mesosoma, Tergite VII, coloration
0 same as other tergites
1 lighter than other tergites

97. Prosoma, Carpace, mottling
    0 present
    1 absent

98. Prosoma, Carapace, banding
    0 absent
    1 two distinct bands
    2 four lines

99. Prosoma, Carapace, interoccular triangle coloration
    0 present
    1 absent

100. Metasoma, I-V, ventral mottling
    0 present
    1 absent

101. Metasoma, I-V, lateral mottling
    0 present
    1 absent

102. Metasoma, I-V, ventral stipe
    0 present
    1 absent

103. Metasoma, V, coloration
    0 same as other segments
    1 darker than other segments

104. Telson, lateral bands
    0 present
    1 absent

105. Telson, median stripe
    0 complete
    1 posteriorly confined
    2 absent

106. Telson, mottling
    0 present
    1 absent

107. Mesosoma, Sternites III-VI, mottling
    0 present
    1 absent

108. Mesosoma, Sternite V (male), coloration
    0 pale patch present
    1 pale patch absent

109. Mesosoma, Sternite V (female), coloration
    0 pale patch present
    1 pale patch absent

110. Mesosoma, Sternite VII, coloration
    0 same as other sternites
    1 lighter than other tergites
    2 darker than other tergites

111. Prosoma, legs I-IV, dorsal mottling
    0 present
    1 absent

112. Prosoma, legs I-IV, ventral mottling
    0 present
    1 absent

**Appendix 7.** Morphological character matrix for the buthid scorpion genus *Centruroides* Marx, 1890

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_aff_baergi_spn'* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *'C_aff_exilicauda'* | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *'C_aff_gracilis_spn1'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_gracilis_spn2'* | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_gracilis_spn3'* | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_gracilis_spn4'* | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_insularis_spn'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_aff_limpidus_spn'* | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_aff_margaritatus_spn1'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| *'C_aff_margaritatus_spn2'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *'C_aff_nigrovariatus_spn'* | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *'C_aff_nitidus1'* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_aff_nitidus2'* | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *'C_aff_noxious_spn'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_rileyi_spn'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 2 | 2 | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_aff_schmidti_spn1'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_aff_schmidti_spn2'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_aff_sculpturatus'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_serrano_spn1'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 |
| *'C_aff_serrano_spn2'* | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *'C_aff_serrano_spn3'* | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 |
| *'C_aff_tuxtla_spn'* | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_alayoni'* | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_anchorellus'* | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 2 | 1 | 2 | 2 | 1 | 0 | 0 | 0 |
| *'C_arctimanus'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 2 | 1 | 2 | 2 | 1 | 0 | 0 | 0 |
| *'C_baergi'* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_balsasensis'* | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *'C_bani'* | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_barbudensis'* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_bicolor'* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_chamulaensis'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_chiapanensis'* | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 3 | 2 | 0 | 0 | 0 | 0 |
| *'C_elegans'* | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_exilicauda'* | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_exilimanus'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_exsul'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_f_flavopictus_1'* | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_f_flavopictus_2'* | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_f_meridonalis'* | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| *'C_farri'* | 1 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| *'C_fulvipes'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 0 |
| *'C_g_borinquensis1'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_g_borinquensis2'* | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | [12] | [02] | 2 | 1 | 0 | 0 | 0 |
| *'C_g_griseus1'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 1 | 0 |
| *'C_g_griseus2'* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_g_griseus3'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_gracilis_1'* | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_gracilis_2'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_guanensis'* | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *'C_hentzi_FL'* | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 2 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *'C_hentzi_KEYS'* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *'C_hirstutipalpus'* | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 |
| *'C_hoffmanni_Frias'* | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_hoffmanni'* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_i_ornatus'* | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 |
| *'C_infamatus_orange'* | 1 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_infamatus_yellow'* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *'C_insulanis'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'C_insularis'* | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_jaragua'* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_koesteri'* | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_limbatus'* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'C_limpidus_1'* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_limpidus_2'* | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_luceorum'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_maraconi'* | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_margaritatus_1'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_margaritatus_2'* | 0 | 0 | 0 | 0 | 1 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_mariaorum'* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_meisei'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_morenoi'* | 0 | 0 | 0 | 0 | 1 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 |
| *'C_n_nitidus'* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 1 | 0 | 0 |
| *'C_n_taino'* | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_nigrescens'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 0 |
| *'C_nigrimanus'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 3 | 2 | 0 | 0 | 0 | 0 |
| *'C_nigrovariatus'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 |
| *'C_noxious'* | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *'C_ochraceus'* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *'C_platnicki_DR'* | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_platnicki'* | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_pococki'* | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| *'C_rileyi'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_robertoi'* | 1 | 1 | 1 | 0 | 0 | 3 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *'C_salvadoriensis_spn'* | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 1 | 0 | 2 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_sasae'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 |
| *'C_schmidti'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *'C_sculpturatus_pale'* | 2 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_sculpturatus_striped'* | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_serrano'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_sissomi'* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_suffusus'* | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *'C_t_arubensis'* | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_t_testaceus'* | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *'C_tapachulaensis_1'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 3 | 1 | 0 | 0 | 1 | 0 |
| *'C_tapachulaensis_2'* | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 3 | 2 | 1 | 0 | 0 | 0 |
| *'C_tecomanus'* | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_thorellii'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *'C_tuxtla'* | 0 | 1 | 0 | 0 | 1 | 3 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *'C_virginiensis'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *'C_vittatus_1'* | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *'C_vittatus_2'* | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *'C_vittatus_3'* | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_vittatus_4'* | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'H_abudi'* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 3 | 1 | 1 | 1 | 0 | 0 |
| *'H_bonettii'* | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 |
| *'H_garridoi'* | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 3 | 1 | 0 | 1 | 1 | 0 |
| *'H_junceus'* | 2 | 1 | 0 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 3 | 2 | 1 | 0 | 1 | 0 |
| *'H_princeps'* | 2 | 1 | 0 | 0 | 0 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 3 | 1 | 0 | 1 | 0 | 0 |
| *'R_laticauda'* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| Steps | 24 | 16 | 10 | 9 | 15 | 40 | 16 | 27 | 31 | 23 | 14 | 12 | 7 | 9 | 23 | 27 | 21 | 22 | 31 | 20 | 14 | 24 | 0 |
| Consistency Index | 0.08 | 0.06 | 0.10 | 0.11 | 0.07 | 0.08 | 0.13 | 0.07 | 0.06 | 0.09 | 0.07 | 0.08 | 0.14 | 0.22 | 0.09 | 0.07 | 0.14 | 0.18 | 0.06 | 0.05 | 0.07 | 0.04 | 0.00 |
| Retention Index | 0.56 | 0.58 | 0.71 | 0.00 | 0.33 | 0.46 | 0.77 | 0.24 | 0.37 | 0.38 | 0.19 | 0.15 | 0.00 | 0.30 | 0.50 | 0.31 | 0.57 | 0.62 | 0.49 | 0.57 | 0.46 | 0.54 | 0.00 |

| Character | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_aff_baergi_spn'* | 0 | 0 | 1 | 0 | ? | 1 | ? | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 5 | ? | ? | ? | ? | ? | 0 |
| *'C_aff_exilicauda'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_aff_gracilis_spn1'* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *'C_aff_gracilis_spn2'* | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 2 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 |
| *'C_aff_gracilis_spn3'* | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_aff_gracilis_spn4'* | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 2 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 |
| *'C_aff_insularis_spn'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_limpidus_spn'* | 1 | 0 | 1 | 0 | 1 | ? | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | ? |
| *'C_aff_margaritatus_spn1'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_aff_margaritatus_spn2'* | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_aff_nigrovariatus_spn'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *'C_aff_nitidus1'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *'C_aff_nitidus2'* | 0 | 0 | 1 | 0 | ? | 0 | ? | 1 | 1 | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *'C_aff_noxious_spn'* | 1 | 4 | 1 | 4 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 |
| *'C_aff_rileyi_spn'* | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 5 | 0 | 0 | 1 | 0 | 2 | 0 |
| *'C_aff_schmidti_spn1'* | 1 | 0 | 1 | 0 | 1 | ? | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 5 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_schmidti_spn2'* | 1 | 3 | 1 | 4 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 2 | ? |
| *'C_aff_sculpturatus'* | 0 | 0 | 1 | 4 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_aff_serrano_spn1'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| *'C_aff_serrano_spn2'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_serrano_spn3'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_aff_tuxtla_spn'* | 0 | 0 | 1 | 0 | ? | 1 | ? | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 5 | ? | ? | ? | ? | ? | 1 |
| *'C_alayoni'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 0 | 0 |
| *'C_anchorellus'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_arctimanus'* | 0 | 0 | 1 | 0 | ? | 1 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | ? | 0 | 0 | 1 | 1 | 1 | ? |
| *'C_baergi'* | 0 | 0 | 1 | 0 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_balsasensis'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_bani'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_barbudensis'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_bicolor'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *'C_chamulaensis'* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'C_chiapanensis'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| *'C_elegans'* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *'C_exilicauda'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |

| Character | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_exilimanus'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_exsul'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_f_flavopictus_1'* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 |
| *'C_f_flavopictus_2'* | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 |
| *'C_f_meridonalis'* | 0 | 1 | 1 | 1 | ? | 1 | ? | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 |
| *'C_farri'* | 0 | 0 | 1 | 4 | ? | 0 | ? | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 |
| *'C_fulvipes'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 |
| *'C_g_borinquensis1'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_g_borinquensis2'* | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *'C_g_griseus1'* | 0 | 3 | 1 | 4 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_g_griseus2'* | 0 | 3 | 1 | 4 | ? | 1 | ? | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 |
| *'C_g_griseus3'* | 0 | 3 | 1 | 4 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_gracilis_1'* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_gracilis_2'* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *'C_guanensis'* | 0 | 3 | 1 | 4 | 0 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | ? |
| *'C_hentzi_FL'* | 0 | 0 | 1 | 4 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| *'C_hentzi_KEYS'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *'C_hirstutipalpus'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_hoffmanni_Frias'* | 0 | 0 | 1 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 5 | 0 | 1 | 1 | 0 | 2 | ? |
| *'C_hoffmanni'* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 5 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'C_i_ornatus'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *'C_infamatus_orange'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *'C_infamatus_yellow'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_insulanis'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| *'C_insularis'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_jaragua'* | 0 | 0 | 1 | 4 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 0 | 0 |
| *'C_koesteri'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_limbatus'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_limpidus_1'* | 0 | 0 | 1 | 4 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_limpidus_2'* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *'C_luceorum'* | 0 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | 2 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 |
| *'C_maraconi'* | 1 | 3 | 1 | 4 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 0 | 0 |
| *'C_margaritatus_1'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_margaritatus_2'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |

| Character | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_mariaorum'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *'C_meisei'* | 0 | 0 | 1 | 0 | 0 | ? | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? |
| *'C_morenoi'* | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | [01] | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_n_nitidus'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_n_taino'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_nigrescens'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'C_nigrimanus'* | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_nigrovariatus'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *'C_noxious'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *'C_ochraceus'* | 0 | 0 | 1 | 0 | 1 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | ? |
| *'C_platnicki_DR'* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_platnicki'* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *'C_pococki'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *'C_rileyi'* | 0 | 3 | 1 | 4 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 |
| *'C_robertoi'* | 0 | 3 | 1 | 4 | ? | 0 | ? | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | ? | ? | ? | ? | ? | 1 |
| *'C_salvadoriensis_spn'* | 0 | 0 | 1 | 0 | ? | 0 | ? | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_sasae'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 |
| *'C_schmidti'* | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_sculpturatus_pale'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 |
| *'C_sculpturatus_striped'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 |
| *'C_serrano'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_sissomi'* | 1 | 0 | 1 | 4 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 1 |
| *'C_suffusus'* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_t_arubensis'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *'C_t_testaceus'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| *'C_tapachulaensis_1'* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| *'C_tapachulaensis_2'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *'C_tecomanus'* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_thorellii'* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *'C_tuxtla'* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 5 | 0 | 1 | 1 | 0 | 2 | 0 |
| *'C_virginiensis'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| *'C_vittatus_1'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_vittatus_2'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *'C_vittatus_3'* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |

| Character | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_vittatus_4'* | 1 | 0 | 1 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | ? |
| *'H_abudi'* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'H_bonettii'* | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'H_garridoi'* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'H_junceus'* | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'H_princeps'* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 |
| *'R_laticauda'* | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| Steps | 12 | 15 | 2 | 19 | 13 | 10 | 9 | 32 | 30 | 23 | 7 | 20 | 3 | 10 | 18 | 5 | 23 | 16 | 22 | 32 | 28 | 27 | 22 |
| Consistency Index | 0.08 | 0.20 | 0.50 | 0.11 | 0.08 | 0.10 | 0.11 | 0.06 | 0.07 | 0.09 | 0.14 | 0.10 | 0.33 | 0.10 | 0.28 | 0.20 | 0.09 | 0.06 | 0.05 | 0.06 | 0.04 | 0.11 | 0.18 |
| Retention Index | 0.66 | 0.52 | 0.00 | 0.50 | 0.65 | 0.59 | 0.43 | 0.43 | 0.49 | 0.51 | 0.63 | 0.28 | 0.33 | 0.53 | 0.41 | 0.00 | 0.54 | 0.38 | 0.32 | 0.33 | 0.43 | 0.49 | 0.44 |

| Character | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_aff_baergi_spn'* | 1 | 3 | 1 | ? | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_aff_exilicauda'* | 3 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_aff_gracilis_spn1'* | 3 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_aff_gracilis_spn2'* | 3 | 1 | 2 | ? | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | ? | ? | 0 | ? |
| *'C_aff_gracilis_spn3'* | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_aff_gracilis_spn4'* | 1 | 1 | 1 | ? | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | ? | ? | ? | 0 | ? |
| *'C_aff_insularis_spn'* | 1 | 3 | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_aff_limpidus_spn'* | ? | ? | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | ? | 0 |
| *'C_aff_margaritatus_spn1'* | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |
| *'C_aff_margaritatus_spn2'* | 1 | 0 | 1 | 0 | 2 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 |
| *'C_aff_nigrovariatus_spn'* | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_nitidus1'* | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 0 | 0 |
| *'C_aff_nitidus2'* | 0 | 1 | 2 | ? | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_aff_noxious_spn'* | 1 | 1 | 2 | ? | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | ? | ? | ? | 0 | ? |
| *'C_aff_rileyi_spn'* | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 1 | 2 |
| *'C_aff_schmidti_spn1'* | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 0 | 0 | 2 | 0 | 2 | ? | 1 |
| *'C_aff_schmidti_spn2'* | ? | ? | 1 | 2 | 2 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 1 | 0 | 2 | 0 | 2 | 1 | 2 |
| *'C_aff_sculpturatus'* | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_aff_serrano_spn1'* | 0 | 3 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_aff_serrano_spn2'* | 3 | 3 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_serrano_spn3'* | 3 | 3 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *'C_aff_tuxtla_spn'* | 1 | 3 | 1 | ? | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | ? | ? | ? | ? |
| *'C_alayoni'* | 2 | 0 | 2 | 0 | 2 | 1 | 0 | 3 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_anchorellus'* | 1 | 0 | 2 | 0 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_arctimanus'* | ? | ? | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | ? | 1 |
| *'C_baergi'* | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| *'C_balsasensis'* | 1 | 3 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 |
| *'C_bani'* | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_barbudensis'* | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_bicolor'* | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_chamulaensis'* | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| *'C_chiapanensis'* | 1 | 1 | 2 | 0 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_elegans'* | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_exilicauda'* | 3 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 |

| Character | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_exilimanus'* | 2 | [23] | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_exsul'* | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| *'C_f_flavopictus_1'* | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 3 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_f_flavopictus_2'* | 1 | 1 | 1 | ? | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_f_meridonalis'* | 0 | 1 | 1 | ? | 2 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_farri'* | 1 | 1 | 1 | ? | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_fulvipes'* | 2 | 1 | 2 | 0 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_g_borinquensis1'* | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 0 |
| *'C_g_borinquensis2'* | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_g_griseus1'* | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_g_griseus2'* | 1 | 1 | 0 | ? | 2 | 1 | 2 | 3 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | ? | 0 | ? | ? | ? |
| *'C_g_griseus3'* | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 2 |
| *'C_gracilis_1'* | 3 | 1 | 2 | 0 | 2 | 1 | 2 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_gracilis_2'* | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_guanensis'* | ? | ? | 2 | 2 | 2 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | ? | 2 |
| *'C_hentzi_FL'* | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 2 |
| *'C_hentzi_KEYS'* | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 3 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |
| *'C_hirstutipalpus'* | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *'C_hoffmanni_Frias'* | ? | ? | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | ? | 1 |
| *'C_hoffmanni'* | 2 | 1 | 1 | 0 | 2 | 1 | 0 | 3 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 0 | 0 | 2 | 0 | 2 | 0 | 2 |
| *'C_i_ornatus'* | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_infamatus_orange'* | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_infamatus_yellow'* | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_insulanis'* | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_insularis'* | 2 | 3 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_jaragua'* | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *'C_koesteri'* | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *'C_limbatus'* | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 |
| *'C_limpidus_1'* | 1 | 3 | 2 | 1 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_limpidus_2'* | 1 | 3 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *'C_luceorum'* | 1 | 1 | 2 | ? | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | ? | ? | ? | 0 | ? | 0 | ? |
| *'C_maraconi'* | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 0 | 2 |
| *'C_margaritatus_1'* | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |
| *'C_margaritatus_2'* | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |

| Character | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_mariaorum'* | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *'C_meisei'* | ? | ? | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | ? | 1 |
| *'C_morenoi'* | 1 | 0 | 1 | 1 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |
| *'C_n_nitidus'* | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 3 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 |
| *'C_n_taino'* | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *'C_nigrescens'* | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_nigrimanus'* | 2 | 3 | 2 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_nigrovariatus'* | 1 | 3 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_noxious'* | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 |
| *'C_ochraceus'* | ? | ? | 2 | 2 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | ? | 2 |
| *'C_platnicki_DR'* | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| *'C_platnicki'* | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *'C_pococki'* | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_rileyi'* | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 3 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 1 | 0 | 2 | 0 | 2 | 0 | 1 |
| *'C_robertoi'* | 1 | 1 | 2 | ? | 2 | 1 | 2 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_salvadoriensis_spn'* | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *'C_sasae'* | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_schmidti'* | 2 | 1 | 2 | 2 | 2 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 2 |
| *'C_sculpturatus_pale'* | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_sculpturatus_striped'* | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_serrano'* | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_sissomi'* | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 3 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 2 |
| *'C_suffusus'* | 1 | 3 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 2 |
| *'C_t_arubensis'* | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_t_testaceus'* | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_tapachulaensis_1'* | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 0 | ? | 0 | ? |
| *'C_tapachulaensis_2'* | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_tecomanus'* | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| *'C_thorellii'* | 2 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_tuxtla'* | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 |
| *'C_virginiensis'* | 1 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 |
| *'C_vittatus_1'* | 2 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 |
| *'C_vittatus_2'* | 2 | 3 | 2 | 1 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |
| *'C_vittatus_3'* | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 |

| Character | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_vittatus_4'* | ? | ? | 2 | 1 | 2 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | ? | 2 |
| *'H_abudi'* | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'H_bonettii'* | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'H_garridoi'* | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'H_junceus'* | 2 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 |
| *'H_princeps'* | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'R_laticauda'* | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 |
| Steps | 33 | 31 | 0 | 1 | 20 | 29 | 26 | 12 | 18 | 0 | 16 | 25 | 0 | 8 | 9 | 9 | 15 | 8 | 19 | 4 | 25 | 12 | 15 |
| Consistency Index | 0.06 | 0.06 | 0.00 | 1.00 | 0.10 | 0.10 | 0.08 | 0.17 | 0.06 | 0.00 | 0.06 | 0.04 | 0.00 | 0.13 | 0.11 | 0.11 | 0.13 | 0.25 | 0.11 | 0.25 | 0.08 | 0.08 | 0.07 |
| Retention Index | 0.46 | 0.49 | 0.00 | 1.00 | 0.51 | 0.45 | 0.27 | 0.23 | 0.63 | 0.00 | 0.62 | 0.56 | 0.00 | 0.13 | 0.27 | 0.67 | 0.72 | 0.45 | 0.54 | 0.25 | 0.53 | 0.27 | 0.62 |

| Character | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_aff_baergi_spn'* | ? | 0 | 1 | 1 | 2 | 0 | 1 | 2 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |
| *'C_aff_exilicauda'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *'C_aff_gracilis_spn1'* | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_gracilis_spn2'* | 0 | 0 | 1 | 0 | 2 | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_gracilis_spn3'* | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_gracilis_spn4'* | 0 | 0 | 1 | 0 | 2 | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_insularis_spn'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_aff_limpidus_spn'* | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'C_aff_margaritatus_spn1'* | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_aff_margaritatus_spn2'* | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 3 |
| *'C_aff_nigrovariatus_spn'* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 1 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_aff_nitidus1'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_aff_nitidus2'* | ? | 0 | 1 | 1 | 1 | 0 | 0 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 3 |
| *'C_aff_noxious_spn'* | ? | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_aff_rileyi_spn'* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *'C_aff_schmidti_spn1'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *'C_aff_schmidti_spn2'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_aff_sculpturatus'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'C_aff_serrano_spn1'* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_aff_serrano_spn2'* | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_aff_serrano_spn3'* | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_aff_tuxtla_spn'* | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 |
| *'C_alayoni'* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | ? | ? | ? | ? | ? | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *'C_anchorellus'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_arctimanus'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_baergi'* | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_balsasensis'* | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *'C_bani'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | [01] |
| *'C_barbudensis'* | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_bicolor'* | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_chamulaensis'* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3 |
| *'C_chiapanensis'* | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_elegans'* | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_exilicauda'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 3 | 0 | ? | ? | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |

| Character | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_exilimanus'* | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_exsul'* | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_f_flavopictus_1'* | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 3 |
| *'C_f_flavopictus_2'* | ? | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 |
| *'C_f_meridonalis'* | ? | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 |
| *'C_farri'* | ? | 0 | 1 | 1 | 1 | 0 | 0 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_fulvipes'* | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_g_borinquensis1'* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_g_borinquensis2'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | [01] | 0 | 0 | 1 | 1 | 2 |
| *'C_g_griseus1'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 3 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |
| *'C_g_griseus2'* | ? | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_g_griseus3'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_gracilis_1'* | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_gracilis_2'* | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_guanensis'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_hentzi_FL'* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 |
| *'C_hentzi_KEYS'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_hirstutipalpus'* | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *'C_hoffmanni_Frias'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_hoffmanni'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *'C_i_ornatus'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_infamatus_orange'* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_infamatus_yellow'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_insulanis'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_insularis'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'C_jaragua'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| *'C_koesteri'* | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *'C_limbatus'* | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_limpidus_1'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *'C_limpidus_2'* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *'C_luceorum'* | ? | 0 | 1 | 1 | 1 | 0 | 0 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *'C_maraconi'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| *'C_margaritatus_1'* | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | ? | ? | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_margaritatus_2'* | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | ? | ? | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 0 |

| Character | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_mariaorum'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | [01] |
| *'C_meisei'* | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 |
| *'C_morenoi'* | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 0 |
| *'C_n_nitidus'* | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_n_taino'* | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_nigrescens'* | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_nigrimanus'* | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_nigrovariatus'* | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_noxious'* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 3 |
| *'C_ochraceus'* | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_platnicki_DR'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_platnicki'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_pococki'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *'C_rileyi'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_robertoi'* | ? | 0 | 1 | 1 | 1 | 1 | 0 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_salvadoriensis_spn'* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 |
| *'C_sasae'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |
| *'C_schmidti'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | ? | ? | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_sculpturatus_pale'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_sculpturatus_striped'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| *'C_serrano'* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *'C_sissomi'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *'C_suffusus'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_t_arubensis'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| *'C_t_testaceus'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_tapachulaensis_1'* | 0 | 0 | 1 | 1 | 2 | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_tapachulaensis_2'* | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'C_tecomanus'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *'C_thorellii'* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 3 |
| *'C_tuxtla'* | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *'C_virginiensis'* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| *'C_vittatus_1'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'C_vittatus_2'* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 2 |
| *'C_vittatus_3'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 |

| Character | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_vittatus_4'* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 |
| *'H_abudi'* | 0 | 0 | 1 | 1 | 2 | ? | 1 | 2 | 0 | 0 | 0 | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'H_bonettii'* | 0 | 0 | 1 | 1 | 2 | ? | 1 | 2 | 0 | ? | ? | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'H_garridoi'* | 0 | 0 | 1 | 1 | 2 | ? | 1 | 2 | 0 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'H_junceus'* | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 1 | ? | ? | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 |
| *'H_princeps'* | 1 | 0 | 1 | 1 | 2 | ? | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| *'R_laticauda'* | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| Steps | 7 | 22 | 14 | 5 | 24 | 24 | 14 | 1 | 1 | 0 | 0 | 2 | 4 | 12 | 11 | 19 | 13 | 17 | 15 | 8 | 3 | 21 | 18 |
| Consistency Index | 0.14 | 0.05 | 0.14 | 0.20 | 0.04 | 0.13 | 0.07 | 1.00 | 0.00 | 0.00 | 0.00 | 0.50 | 0.25 | 0.08 | 0.18 | 0.16 | 0.15 | 0.06 | 0.07 | 0.13 | 0.33 | 0.24 | 0.17 |
| Retention Index | 0.00 | 0.48 | 0.71 | 0.76 | 0.54 | 0.60 | 0.28 | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 | 0.80 | 0.79 | 0.67 | 0.47 | 0.78 | 0.70 | 0.69 | 0.56 | 0.78 | 0.73 | 0.69 |

| Character | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_aff_baergi_spn'* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | ? | 1 | 0 | 1 | 1 |
| *'C_aff_exilicauda'* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_aff_gracilis_spn1'* | 1 | ? | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_aff_gracilis_spn2'* | 1 | ? | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | ? | 1 | 0 | 1 | 1 |
| *'C_aff_gracilis_spn3'* | 1 | ? | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_aff_gracilis_spn4'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | ? | 1 | 0 | 1 | 1 |
| *'C_aff_insularis_spn'* | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 1 |
| *'C_aff_limpidus_spn'* | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 |
| *'C_aff_margaritatus_spn1'* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_aff_margaritatus_spn2'* | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_aff_nigrovariatus_spn'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_aff_nitidus1'* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | [01] | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 |
| *'C_aff_nitidus2'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | ? | 1 | 2 | 0 | 1 |
| *'C_aff_noxious_spn'* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | ? | 1 | 2 | 0 | 1 |
| *'C_aff_rileyi_spn'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *'C_aff_schmidti_spn1'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | ? | 0 | 0 | 1 |
| *'C_aff_schmidti_spn2'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_aff_sculpturatus'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_aff_serrano_spn1'* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_aff_serrano_spn2'* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 |
| *'C_aff_serrano_spn3'* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_aff_tuxtla_spn'* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_alayoni'* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 |
| *'C_anchorellus'* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *'C_arctimanus'* | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *'C_baergi'* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | ? | 1 | 2 | 0 | 1 |
| *'C_balsasensis'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_bani'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_barbudensis'* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | [02] | 0 | 1 | 0 | 1 | 2 | 0 | 1 |
| *'C_bicolor'* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_chamulaensis'* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 |
| *'C_chiapanensis'* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 |
| *'C_elegans'* | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_exilicauda'* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |

| Character | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_exilimanus'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'C_exsul'* | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_f_flavopictus_1'* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_f_flavopictus_2'* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | ? | 0 | 2 | 0 | 1 |
| *'C_f_meridonalis'* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | ? | 0 | 2 | 0 | 0 |
| *'C_farri'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_fulvipes'* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 |
| *'C_g_borinquensis1'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_g_borinquensis2'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *'C_g_griseus1'* | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *'C_g_griseus2'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *'C_g_griseus3'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | [01] | [02] | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *'C_gracilis_1'* | 1 | ? | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_gracilis_2'* | 1 | ? | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_guanensis'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_hentzi_FL'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_hentzi_KEYS'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_hirstutipalpus'* | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 |
| *'C_hoffmanni_Frias'* | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 1 | 2 | 0 | 1 |
| *'C_hoffmanni'* | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_i_ornatus'* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_infamatus_orange'* | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | ? | 1 | 2 | 1 | 1 |
| *'C_infamatus_yellow'* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_insulanis'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *'C_insularis'* | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_jaragua'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_koesteri'* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_limbatus'* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_limpidus_1'* | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_limpidus_2'* | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 |
| *'C_luceorum'* | 1 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 1 |
| *'C_maraconi'* | 1 | 0 | [01] | 0 | 0 | 0 | 0 | 0 | [01] | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_margaritatus_1'* | 1 | ? | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *'C_margaritatus_2'* | 1 | ? | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |

| Character | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_mariaorum'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *'C_meisei'* | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 |
| *'C_morenoi'* | 1 | ? | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 |
| *'C_n_nitidus'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_n_taino'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_nigrescens'* | 1 | ? | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 |
| *'C_nigrimanus'* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_nigrovariatus'* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *'C_noxious'* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_ochraceus'* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'C_platnicki_DR'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_platnicki'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_pococki'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *'C_rileyi'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *'C_robertoi'* | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | [01] | 0 | 0 | 1 | 1 | ? | 1 | 0 | 0 | 0 |
| *'C_salvadoriensis_spn'* | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *'C_sasae'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *'C_schmidti'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | [01] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *'C_sculpturatus_pale'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_sculpturatus_striped'* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_serrano'* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *'C_sissomi'* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 |
| *'C_suffusus'* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'C_t_arubensis'* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 |
| *'C_t_testaceus'* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_tapachulaensis_1'* | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *'C_tapachulaensis_2'* | 1 | ? | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'C_tecomanus'* | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'C_thorellii'* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| *'C_tuxtla'* | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 |
| *'C_virginiensis'* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'C_vittatus_1'* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_vittatus_2'* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *'C_vittatus_3'* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |

| Character | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *'C_vittatus_4'* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'H_abudi'* | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *'H_bonettii'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *'H_garridoi'* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'H_junceus'* | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'H_princeps'* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *'R_laticauda'* | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| Steps | 10 | 10 | 17 | 19 | 13 | 11 | 20 | 13 | 15 | 17 | 22 | 22 | 28 | 12 | 9 | 24 | 10 | 24 | 8 | 7 |
| Consistency Index | 0.10 | 0.10 | 0.12 | 0.05 | 0.08 | 0.18 | 0.05 | 0.08 | 0.20 | 0.06 | 0.09 | 0.14 | 0.14 | 0.08 | 0.11 | 0.04 | 0.10 | 0.08 | 0.13 | 0.14 |
| Retention Index | 0.40 | 0.53 | 0.63 | 0.42 | 0.77 | 0.57 | 0.62 | 0.76 | 0.52 | 0.43 | 0.55 | 0.62 | 0.54 | 0.63 | 0.47 | 0.43 | 0.55 | 0.50 | 0.83 | 0.45 |

**Appendix 8.** Material examined for phylogenetic analysis of the buthid scorpion genus *Centruroides* Marx, 1890

Specimens are deposited in the following collections: American Museum of Natural History (AMNH), New York, U.S.A., incorporating the Alexis Harington (AH) Collection; California Academy of Sciences (CAS) California, U.S.A. "LP" numbers are provided on labels with the specimens and correspond to entries in the molecular specimen database of Lorenzo Prendini at the AMNH.

***Centruroides alayoni* Armas, 1999**: Dominican Republic, Pedernales Provence, Oviedo, W, roadside near rubbish dump: ♂2 , sex indeterminant 1 juv.(AMNH[LP 3292]), collected by E.S. Volschenk & J. Huff, 6/vii/2004, 17.8131°N71.4186°W, 42 m, Spiny scrub with limestone boulders; hand collected from under rocks and logs. Dominican Republic, Pedernales Provence, Parque Nacional Jaragua, Cabo Rojo: ♂1, ♀2 (AMNH[LP 3293]), collected by E.S. Volschenk & J. Huff, 9/vii/2004, 17.8958°N71.6600°W, 15 m, Dry cactus and spiny forest on limestone karst; hand collected from under stones and logs, and with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Sierra de Baoruco, from Cabo Rojo: ♀2 , sex indeterminant 1 subad. (AMNH[LP 3294]), collected by E.S. Volschenk & J. Huff, 10/vii/2004, 18.0900°N71.5108°W, 1271 m, Pine forest and dense lower storey; hand collected from under stones of visitors car park and along walking tracks, and with blacklights.

***Centruroides anchorellus* Armas, 1976:** Cuba, Santiago de Cuba Province, San Juan, 1 km E Santiago de Cuba: ♂2, ♀2 (AMNH[LP 1774]), collected by R. Teruel, 22/iv/1999.

***Centruroides arctimanus* (Armas, 1976):** Cuba, Holguín: ♂1 (AMNH[LP 7296]), sex indeterminant 2 juv.(AMNH[LP 7295]), 3/x/2007.

***Centruroides baergi* Hoffmann, 1932:** Mexico, Oaxaca, Municipio Cuicatlan, Tomellin: ♂2, ♀3 (AMNH[LP 2067]), collected by L. Prendini, O. Francke, E. Gonzalez and J. Ponce, 23/vii/2002, 17°45.180'N 96°57.237'W, 605 m; desert; collected at night with UV light.; ♂1, ♀3 , sex indeterminant 1(AMNH[LP 2068]), collected by L. Prendini, O. Francke, E. Gonzalez and J. Ponce, 23/vii/2002, 17°45.180'N 96°57.237'W, 605 m; desert; collected at night with UV light. Santa María Ixcatlán, Camino a Ixcatlan, 5 km NW Cuicatlan: ♂1 (AMNH[LP 6630]), collected by O. Francke, M. Cordova, A. Jaimes & G. Montiel, 8/xi/2005, 17.81523°N 97.00539°W, 702 m. San Juan Bautista Cuicatlán, 33 km S Cuicatlan, Carretera Cuicatlan-Oaxaca: sex indeterminant 1(AMNH[LP 6632]), collected by O. Francke, M. Cordova, G. Montiel & A. Jaimes, 9/xi/2005, 17.58191°N 96.94879°W, 1574 m. San Juan Atepec, Rio Grande: sex indeterminant 1 juv.(AMNH[LP 9530]), collected by O.F. Francke, A. Quijano & C. Santibañez, 3/vii/2008, 17.41395°N 96.57108°W, 1327 m. Puebla, 2 km E Tehuacan: ♂1 , sex indeterminant 1(AMNH[LP 2047]), collected by L. Prendini, O. Francke, E. Gonzalez and J. Ponce, 25/vii/2002, 18°24.002'N 97°22.867'W, in burrows and under stones; semi-

desert scrub; 1435 m. Puebla, Valle de Puebla: sex indeterminant 1(AMNH[LP 2075]), collected by J. Ponce, 17/vii/2002, dry limestone slope; scrub; under stone.

***Centruroides balsasensis*** **Ponce-Saavedra & Francke, 2004:** Mexico, Michoacan, Churumuco: ♀1 (AMNH[LP 2010]), collected by J. Ponce S., 17/iii/2001;♀1 (AMNH[LP 2011]), collected by J. Ponce S., 17/iii/2001. Tepalcatepec, 1 km al SW El Taixtan: ♂1 (AMNH[LP 7048]), collected by Francke, Ponce *et al.*, 18/v/2007, 19° 01.719'N 102°55.706 W, 980 m. La Huacana, El Vado: ♀1 (AMNH[LP 7049]), collected by Francke, Ponce *et al.*, 20/v/2007, 18° 48.908'N 101°54.976 W, 198 m. Highway Caracuaro-Huetamo, 125 km: ♀1 (AMNH[LP 5212]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 14/vii/2005, 18°56.231'N 101°02.906'W, 724 m. Álvaro Obregon: subadult ♀ 1, ♀ 1 (AMNH[LP 5215]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 11/vii/2005, 19°02.310'N 102°58.405'W, 462 m.

***Centruroides bani*** **Armas & Marcano Fondeur, 1987:** Dominican Republic, Barahona Prov., Azua, 14 km W: ♂2, ♀3 , sex indeterminant 1 subad., 1 juv.(AMNH[LP 5106]), collected by L. Esposito, 10/viii/2005, 18.46288°N070.97374°W, 149 m, dry shrublands with succulents, UV detection, 35°C. Independencia Province, Parque Nacional Isla Cabritos, behind Ranger Station: ♂2 , sex indeterminant 1 subad.(AMNH[LP 5127]), collected by L. Esposito, 8/viii/2005, 18.56287°N071.69762°W, -23 m, mixed dry forest with succulents, UV detection, 35°C. Isla Cabritos: sex indeterminant juv.(AMNH[LP 2474]), collected by J. Huff, 7/i/2004, 18°30.019'N71°43.228'W, 110 ft; ♂4, ♀2 , sex indeterminant 4 juv.(AMNH[LP 3295]), collected by J. Huff, 7/i/2004, 18°30.019'N71°43.228'W, 110 ft, under rock, coral. Parque Nacional Sierra de Bauruco, road between Rabo de Gato and Duverge: ♂1, ♀1 , sex indeterminant 2 juv.(AMNH[LP 3300]), collected by E.S. Volschenk & J. Huff, 7/vii/2004, 18.3272°N71.5653°W, 447 m, Arid thorny scrub; hand collected from under stones and in dead and dry agaves. Isla Cabritos, at Park station: sex indeterminant 2 juv.(AMNH[LP 3301]), collected by E.S. Volschenk & J. Huff, 8/vii/2004, 18.5622°N71.6973°W, -19.821 m, Dry forest; hand collected from under stones and logs, and with blacklights. La Altagracia Province, Parque Nacional del Este, track between ranger station at Boca de Yuma and Punta Faustino: ♀1 (AMNH[LP 3303]), collected by E.S. Volschenk & J. Huff, 14/vii/2004, 18.3547°N68.6144°W, 3.25 m, Dense canopy humid forest; hand collected from under stones and blacklighting, especially along an old rock wall along the start of the track. Monte Cristi Prov., Monte Cristi, National Park Property: sex indeterminant 1 subad., 3 juv.(AMNH[LP 5146]), collected by L. Esposito, 4/viii/2005, 19.84955°N071.63910°W, 100 m, mixed dry shrubland with succulents, UV detection. Puerto Escondido, Sierra de Baoruco: ♀2 , sex indeterminant juv.(AMNH[LP 3296]), collected by J. Huff, 6/i/2004, 18°19.762'N71°33.502'W, 1592 ft, under dead agave. Valle de Neiba, Salt flood plain, Hwy 46 near Mella: ♀1 (AMNH[LP 3299]), collected by J. Huff, 6/i/2004, 18°19.594'N71°21.739'W, 22 ft. Road to Polo (via Cabral): ♀2 , sex indeterminant juv.(AMNH[LP 3297]), collected by J. Huff, 5/i/2004, 18°11.738'N71°15.035'W, 1091 ft, under rocks, dead agave. Dominican Republic, Hwy 46, W of Neiba: ♂1, ♀1 , sex indeterminant juv.(AMNH[LP 3298]), collected by J. Huff, 7/i/2004, 18°31.948'N71°36.611'W, 19 ft, under bark in horse field of low scrub.

***Centruroides barbudensis*** **(Pocock, 1898):** Saba, Sandy Cruz at Hell's Gate, All Too Far Sulfur Mine Trail: ♂1 (AMNH[LP 6902]), collected by S. Crews, 17/ii/2007, under bark.

St. Kitts and Nevis, Nevis, Trail behind Golden Rock Inn: ♀1 (AMNH[LP 9063]), collected by L. Esposito & D. Schiff, 1/vii/2008, 17.143°N62.567°W, tropical forest, UV detection.

***Centruroides bicolor* (Pocock, 1898):** Costa Rica, Puntarenas Prov., Cerro Nara, Londres, Quepos: ♀1 , sex indeterminant 1(AMNH[LP 6109]), collected by V. Vignoli, C. Viquez & H. Ajuria, 19/v/2006, 09°28'40"N84°02'49"W, 161 m. Fundación Neotropica, Agua Buena de Rincón, Península de Osa: ♂1 (AMNH[LP 6110]), collected by V. Vignoli, C. Viquez & H. Ajuria, 23/v/2006, 08°42'02"N83°30'47"W, 86 m; ♀1 (AMNH[LP 6111]), collected by V. Vignoli, C. Viquez & H. Ajuria, 23/v/2006, 08°42'02"N83°30'47"W, 86 m. Curré, close to River Caño Blancal, Cajón: ♀2 (AMNH[LP 6112]), collected by V. Vignoli, C. Viquez & H. Ajuria, 20/v/2006, 08°57'46"N83°24'57"W, 55 m. U.S.A,

***Centruroides griseus borinquensis* Armas, 1982:** Puerto Rico, Bosque Estatal de Guanica (Bosque Seco), Route 333, 3.4 km E of intersection with Route 116: sex indeterminant 3 juv.(AMNH[LP 10210]), collected by L. Prendini, J. Huff & A. Nieves, 20/x/2009, 17°57.269'N66°54.264'W, 33 m, tropical dry forest on limestone/karst outcrops and low hills; acacias and spiny trees, cercus columnar cactus dominant; UV detection on warm, still, moonless night. U.S.A, Puerto Rico, Area Natural del Suroeste de Puerto Rico, Bosque de Boqueron, peninsula at El Faro de Cabo Rojo: sex indeterminant 2 juv.(AMNH[LP 10212]), collected by L. Prendini, J. Huff & A. Nieves, 20/x/2009, 17°56.142'N67°11.495'W, 5 m, tropical dry forest on limestone/karst outcrops and low hills; acacias and spiny trees, cercus columnar cactus dominant; UV detection on warm, still, moonless night. U.S.A, Puerto Rico, Bosque Estatal de Guanica (Bosque Seco), Route 333, 8.7 km E of intersection with Route 116: sex indeterminant 1 juv.(AMNH[LP 10214]), collected by L. Prendini, J. Huff & A. Nieves, 20/x/2009, 17°57.511'N66°51.717'W, 27 m, tropical dry forest on limestone/karst outcrops and low hills; acacias and spiny trees, cercus columnar cactus dominant; UV detection on warm, still, moonless night. U.S.A, Puerto Rico, Bosque Estatal de Maricao, 3.8 mi S of intersection with Route 366 on Route 120 (km 5 marker from Sabana Grande): sex indeterminant 1 subad.(AMNH[LP 10217]), collected by L. Prendini & J. Huff, 20/x/2009, 18°07.017'N66°56.903'W, 450 m, montane rainforest along roadside; rock faces covered with roots and dense leaf litter in places; UV detection on cool, still, moonless night after rain, ground fairly wet. U.S.A, Puerto Rico, Bosque Estatal Susua, 2.7 mi from entrance gate/campsite: sex indeterminant 1 subad., 1 juv.(AMNH[LP 10219]), collected by L. Prendini & J. Huff, 19/x/2009, 18°04.522'N66°55.947'W, 168 m, UV detection on cool, still, humid night; rocky roadcut, humid savanna on rock wall. U.S.A, Puerto Rico, Area Natural del Suroeste de Puerto Rico, Bosque de Boqueron, Morllos (ruins) de Cabo Rojo (El Faro de Cabo Rojo): sex indeterminant 2 juv.(AMNH[LP 10220]), collected by L. Prendini, J. Huff & A. Nieves, 20/x/2009, 17°56.710'N67°11.539'W, 0 m, salt flats and mangroves on Cabo Rojo peninsula; UV detection. U.S.A, Puerto Rico, Bosque Estatal Susua, old campsite, trail leading into forest: sex indeterminant 2 juv.(AMNH[LP 10221]), collected by L. Prendini & J. Huff, 19/x/2009, 18°04.045'N66°53.839'W, 180 m, dry forest with extensive leaf litter layer; wet and humid after earlier rain; UV detection at night and hand collecting in morning under rocks and logs. U.S.A., Puerto Rico, Bosque Estatal de Guanica: Punta Jacinto: ♂1, ♀1 (AMNH[LP 5108]), collected by L. Esposito, 11/vii/2005, 17.95401°N066.85544°W,

1.2 m, desert scrub 50 m from beach, under vegetation, UV detection, 35°C. U.S.A., Puerto Rico, Susua State Forest, N of Sabana Grande: ♀1 (AMNH[LP 6238]), collected by S. Crews & A. Puente-Rolon, 10/vi/2006, 18°04'15.0"N66°54'31.6"W, ca. 207 m, dry serpentine forest, under rocks.

***Centruroides chamulaensis* Hoffmann, 1932:** Mexico, Chiapas, Comitán de Domínguez, 2.2 km hacia Zaragoza de la Montana: ♂1 (AMNH[LP 6457]), collected by O. Francke, A. Valdez, A. Ballesteros & H. Montaño, 22/x/2006, 16°23.16N 92°13.265W, 2049 m. México, Chiapas, Municipio San Juan Chamula, Paraje Loma, deviation to San Juan Chamula: ♀1 (AMNH[LP 5248]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 2/ix/2005, 16°15.237'N 93°35.774'W, 1132 m. México, Chiapas, San Cristobal de las Casas, near intersection to Ocosingo: ♀1 , sex indeterminant 2(AMNH[LP 5255]), collected by O. Francke, M. Córdova, A. Jaimes & J. Ballesteros, 28/v/2005, 16°40.803'N 93°35.077'W, 2136 m. México, Chiapas, Municipio Comitan, Highway Tepisca-Comitan, 133 km: ♀1 (AMNH[LP 5348]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 3/ix/2005, 16°30.432'N 92°21.069'W, 2213 m.

***Centruroides chiapanensis chiapanensis* Hoffmann, 1932:** Mexico, Chiapas, Ocozocoautla: ♂1 (AMNH[LP 2012]), collected by , 17/vi/2002. Mexico, Chiapas, Toll Highway Tuxtla Gutierrez-Mexico, km 192.5, Reserva el Ocote, SW : juvenile ♀ 1 (AMNH[LP 3695]), collected by R. Paredes, O. Francke and G. Villegas, 4/xi/2004, 16°48'04.8"N 93°20'42.1"W, 1041 m, rock rolling. Mexico, Chiapas, Villacorzo-Tuxtla Gutierrez road, km 53, turnoff to Parral 2 km S: juvenile ♀ 1 (AMNH[LP 3696]), collected by R. Paredes, O. Francke and G. Villegas, 6/xi/2004, 16°20'35.8"N 92°58'45.7"W, 648 m, UV light detection at night. México, Chiapas, Las Delicias: ♂1 (AMNH[LP 5216]), collected by O. Francke, M. Córdova, J. Ballesteros & A. Jaimes, 29/iii/2005. México, Chiapas, Rabasa ground camp, Reserva del Ocote: sex indeterminant 1(AMNH[LP 5226]), collected by O. Francke, M. Córdova, A. Jaimes & J. Ballesteros, 24/v/2005, 16°54.583'N 93°36.683'W, 758 m. México, Chiapas, Municipio Tzimol, Highway Comitan-Tzimol Santa Rosa: sex indeterminant 1(AMNH[LP 5234]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 2/ix/2005, 16°11.056'N 92°16.988'W, 730 m. México, Chiapas, El Aguacero : sex indeterminant 1(AMNH[LP 5253]), collected by O. Francke, M. Córdova, A. Jaimes & J. Ballesteros, 25/v/2005, 16°45.374'N 93°31.468'W, 764 m. México, Chiapas, Municipio Tuxtla Gutierrez, Miradores del Parque Nacional Canon del Sumidero: ♀1 (AMNH[LP 5256]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 29/viii/2005, 16°49.654'N 93°05.702'W, 1248 m. México, Chiapas, Municipio Venustiano Carranza, Highway La Rosa-Teopisca: (AMNH[LP 5258]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 3/ix/2005, 16° 24.631'N 92° 23.769'W, 1494 m. México, Chiapas, Municipio Villaflores, California Ejido, 1 km SE, Reserva de La Biosfera La Sepultura: sex indeterminant 2(AMNH[LP 5243]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 30/viii/2005, 16°15.237'N 93°35.774'W, 1132 m. Mexico, Chiapas, Municipio Ococingo, Frontera Corozal, 2 km SE: ♂2 (AMNH[LP 3634]), collected by R. Paredes & J.L. Castelo, 28/iv/2004, 16°48'12.7"N 90°52'11.2"W, 150 m. Mexico, Chiapas, "La vuelta del alacran" 4.8 km from km 27 on road from Ocozocuautla to Villa Flores: ♂1, ♀1 (AMNH[LP 3694]), collected by O. Francke, R. Paredes and G. Villegas, /x/2004, 16°32'35.2"N

93°129'09.8"W, 781 m, UV light detection at night. Mexico, Chiapas, El Aguacero y Rio Subterraneo, road Ocozocoautla-Cintalapa km 106: ♀1, ♀ 1 (AMNH[LP 3697]), collected by R. Paredes, O. Francke and G. Villegas, 2/xi/2004, 16°45'29.4"N 93°31'30.6"W, 616 m, UV light detection at night. Mexico, Oaxaca, Municipio Mixes, 7 km terciese San Juan Juquile, Mixes-Acatlancito: sex indeterminant 1 juv.(AMNH[LP 7665]), collected by O. Francke, A. Ballesteros, H. Montano, C. Santibanez & A. Valdez, 18/vii/2007, 16°54.595'N 95°55.711'W, 1388 m.

***Centruroides elegans elegans*** **(Thorell, 1876):** Mexico, Jalisco, Municipio Las Huertas, Estacion de Biologia Chamela, UNAM: ♀1 (AMNH[LP 1820]), collected by E. Gonzalez Santillan, 26/iii/2000. Mexico, Jalisco, La Huerta, Estacion Biol. Chamela: ♂1 (AMNH[LP 7664]), collected by O. Francke *et al.*, 30/viii/2007, 19°29.875'N 105°02.608'W, 97 m. México, Jalisco, Rio San Nicolas and Highway 200: ♂1, ♀2 (AMNH[LP 1911]), collected by N.O. Palomera, 6/vii/2001.

***Centruroides exilicauda*** **(Wood, 1863):** Mexico, Baja California, Municipio Ensenada, Route 1, 21 km marker: sex indeterminant 19(AMNH[LP 4470]), collected by E. González, R. Mercurio, L. Prendini & W.E. Savary, 2/vii/2005, 30°20.469′N 115°49.019′W, 45 m, UV detection at night. Mexico, Baja California, Municipio Ensenada, Punta Prieta, 37 km N, off Route 1: ♀1 (AMNH[LP 4471]), collected by L. Prendini & R. Mercurio, 13/vii/2005, 29°15.116′N 114°10.100′W, 588 m, UV detection at night. Mexico, Baja California, Municipio Ensenada, Punta Banda, between El Rincon and La Bufadora, ca. 1 km SE of Pico Banda off BCN 23: subadult ♀ 1, ♀ 7 , sex indeterminant 7(AMNH[LP 4474]), collected by E. González, W.E. Savary, L. Prendini & R. Mercurio, 1/vii/2005, 31°44′N 116°43.025′W, 139 m, UV detection at night. Mexico, Baja California, Municipio Ensenada, Misión San Borja: ♂1 (AMNH[LP 4482]), collected by E. González & W.E. Savary, 13/vii/2005, 28°44.607′N 113°45.233′W, 433 m, UV detection at night. Mexico, Baja California, Municipio Ensenada, 4 km along gravel road to Calamajué from junction with Route 1: ♀2 (AMNH[LP 4493]), collected by R. Mercurio & L. Prendini, 13/vii/2005, 29°15.116′N 114°08.366′W, 623 m, UV detection at night. Mexico, Baja California, Municipio de Ensenada, Bahía Tortugas 10 km NW: ♀1 (AMNH[LP 8778]), collected by H. Montaño & E. Gonzalez, 7/vii/2008, 27°45.389'N 114°57.103'W, 110 m, Arroyo sand banks on cutting edges/ UV detection during night. Mexico, Baja California, Municipio Ensenada, La Bufadora, ca. 1.5 km SE: ♀2, subadult ♀ 5 , sex indeterminant 20(AMNH[LP 4497]), collected by L. Prendini, E. González, R. Mercurio & W.E. Savary, 1/vii/2005, 31°43.052′N 116°42.473′W, 117 m, burrow excavation by day. Mexico, Baja California, Municipio Ensenada , Pico Banda: ♀1 (AMNH[LP 4498]), collected by E. González, L. Prendini, W.E. Savary & R. Mercurio, 1/vii/2005, 31°44.304′N 116°43.295′W, 260 m, UV detection at night. Mexico, Baja California, Municipio de Ensenada, Misión de San Francisco de San Borja de Adac: sex indeterminant 1(AMNH[LP 8761]), collected by H. Montaño & E. Gonzalez, 30/vi/2008, 28°44.604'N 113°45.224'W, 437 m, Thorn and scrub with cacti, stones and boulders, disturvance by cattle/ UV detection during night. Mexico, Baja California, Municipio de Ensenada, El Arenoso, ca 100 km S El Rosario: ♀1 (AMNH[LP 8766]), collected by H. Montaño & E. Gonzalez, 3/vii/2008, 30°02.821'N 115°17.734'W, 535 m, Agave and acti, stones/ Rock rolling and chopping dead agave. Mexico, Baja California, Municipio de Ensenada, San Borja, 27 km W from Rosarito (Misión de San Francisco de San Borja de Adac): sex indeterminant

1(AMNH[LP 8769]), collected by H. Montaño & E. Gonzalez, 30/vi/2008, 28°40.919'N 113°58.927'W, 171 m, Hills with agave and cacti, stones/ Rock rolling, chopping dead agave . Mexico, Baja California, Municipio de Ensenada, Misión de San Francisco de San Borja de Adac, 5 km W: ♂1 (AMNH[LP 8773]), collected by H. Montaño & E. Gonzalez, 30/vi/2008, 28°44.558'N 113°47.935'W, 380 m, Thorn and scrub with cacti, stones and boulders/ UV detection during night. Mexico, Baja California Sur, Ciudad Constitución, 32 km SW: ♂1, ♀1 (AMNH[LP 3120]), collected by O. Francke, W. Savary, E. González & A. Valdez, 11/vii/2004, 24°55'17"N 111°58'5.5"W, 26 m, UV light detection at night. Mexico, Baja California Sur, Todos los Santos, S of: ♂1, ♀1 (AMNH[LP 3121]), collected by O. Francke, W. Savary, E. González & A. Valdez, 10/vii/2004, 23°25'47.6"N 110°11'36.1"W, 80 m, UV light detection at night. Mexico, Baja California Sur, Municipio Comondú, El Cayuco Fish Camp, sand dunes S: subadult ♀ 6, ♀ 2 (AMNH[LP 4473]), collected by W.E. Savary, E. Gonzalez, L. Prendini & R. Mercurio, 11/vii/2005, 24°34.666′N 111°40.633′W, 6 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, San Ignacio, 3 km S on road to La Laguna: ♂1 (AMNH[LP 4476]), collected by E. Gonzalez, W.E. Savary, L. Prendini & R. Mercurio, 12/vii/2005, 27°16.533′N 112°53.366′W, 167 m, UV detection at night. Mexico, Baja California Sur, Municipio La Paz, La Paz, ca. 5 km N junction Route 1 and road to San Juan de la Costa: ♀ 4 (AMNH[LP 4478]), collected by R. Mercurio, W.E. Savary, L. Prendini & E. González, 9/vii/2005, 24°08.500′N 110°28.566′W, 30 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, Guerrero Negro, 11 km SE, W side Route 1: ♂1 (AMNH[LP 4479]), collected by L. Prendini & R. Mercurio, 4/vii/2005, 27°54.916′N 113°55.333′W, 18 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé , Microondas San Lucas: ♀1 (AMNH[LP 4483]), collected by W.E. Savary & R. Mercurio, 5/vii/2005, 27°11.550′N 112°14.150′W, 185 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé , Mulegé, sand dunes ca. 4 km S: ♂1 (AMNH[LP 4484]), collected by W.E. Savary & R. Mercurio, 6/vii/2005, 26°53.166′N 111°56.550′W, 3 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, Route 1, 7 km SW turnoff to Punta Abreojos: ♂2 (AMNH[LP 4487]), collected by L. Prendini, E. González, W.E. Savary & R. Mercurio, 5/vii/2005, 27°17.05′N 113°09.866′W, 76 m, UV detection at night. Mexico, Baja California Sur, Municipio La Paz, La Paz, ca. 10 km SE on BCS 286 to San Juan de los Planes: ♀1 (AMNH[LP 4488]), collected by L. Prendini & R. Mercurio, 9/vii/2005, 24°08.433′N 110°15.333′W, 106 m, UV detection at night. Mexico, Baja California Sur, Municipio Loreto, Loreto, 25 km S, on gravel road just off Route 1: ♀2 (AMNH[LP 4491]), collected by E. González, W.E. Savary, L. Prendini & R. Mercurio, 7/vii/2005, 25°48.666′N 111°19.266′W, 6 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, San Ignacio, 28 km E on Route 1: ♂1 (AMNH[LP 4492]), collected by L. Prendini, & R. Mercurio, 8/vii/2005, 27°23.730′N 112°39.540′W, 303 m, UV detection at night. Mexico, Baja California Sur, Municipio Comondú, San José de Comondú: ♀1 (AMNH[LP 4495]), collected by L. Prendini, R. Mercurio, E. González & W.E. Savary, 7/vii/2005, 26°03.542′N 111°48.985′W, 293 m, UV detection at night. Mexico, Baja California Sur, Municipio de La Paz, Isla Cerralvo, SW side : ♂1 (AMNH[LP 8758]), collected by I.G. Nieto Castaneda and E. Gonzalez, 27/v/2008, 24°10'56.66"N 109°53'14.7"W, 0–50 m, Arroyo wash, stones and boulders/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Isla Espíritu Santo,

Playa Bonanza: sex indeterminant 1(AMNH[LP 8759]), collected by I.G. Nieto Castaneda and E. Gonzalez, 31/v/2008, 24°27.364'N 110°18.471'W, 0–50 m, Bajada with cacti and scrub/UV detction during night. Mexico, Baja California Sur, Municipio de La Paz, Isla San José Fishing camp Palma Sola : sex indeterminant 2(AMNH[LP 8762]), collected by I.G. Nieto Castaneda and E. Gonzalez, 3/vi/2008, 25°03.091'N 110°40.037'W, 0–50 m, Arroyo wash, stones and boulders, thorn-scrub and cacti, sandy area, cliffs and compacted sand hills/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Isla San José W side: ♀1 (AMNH[LP 8764]), collected by I.G. Nieto Castaneda and E. Gonzalez, 2/vi/2008, 24°56.722'N 110°38.908'W, 0–50 m, Arroyo wash, stones and boulders, thorn-scrub and cacti/ UV detection during night. Mexico, Baja California Sur, Municipio de Loreto, Isla Danzante S, Punta Faro: sex indeterminant 1(AMNH[LP 8767]), collected by I.G. Nieto Castaneda and E. Gonzalez, 12/vi/2008, 25°46.295'N 111°15.001'W, 0–50 m, Stones and boulders, thorn-scrub and cacti/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Isla Santa Cruz, by the light house: sex indeterminant 1(AMNH[LP 8772]), collected by I.G. Nieto Castaneda and E. Gonzalez, 5/vi/2008, 25°15.697'N 110°43.669'W, 0–50 m, Stones and boulders, thorn-scrub and cacti, hills with strong slope / UV detection during night and turning rocks. Mexico, Baja California Sur, Municipio de La Paz, San Juan de la Costa, 60 km NE: subadult ♀ 1 (AMNH[LP 9966]), collected by M.M Correa & I.G. Nieto, 20/ix/2008, 24°36´09.7´´N 110°44´22.4´´W, sea level, UV lighting, rocky cliffs by the sea. Mexico, Baja California Sur, Municipio La Paz, La Paz, ca. 38 km N, 1 km off Route 1 on Ley Federal de la Reforma Agraria: sex indeterminant 2(AMNH[LP 4472]), collected by W.E. Savary & E. González, 9/vii/2005, 24°03.609′N 110°36.777′W, 256 m, UV detection at night. Mexico, Baja California Sur, Municipio Loreto, Loreto, 25 km S, on gravel road ca. 250 m E Route 1: ♀1 (AMNH[LP 4475]), collected by W.E. Savary, L. Prendini, R. Mercurio & E. González, 7/vii/2005, 25°48.666′N 111°19.266′W, 6 m, UV detection at night. Mexico, Baja California Sur, Municipio Loreto, Loreto, S, ca. 8 km along gravel road to San Javier, from junction with Route 1: ♀1 (AMNH[LP 4477]), collected by L. Prendini, E. González, R. Mercurio & W.E. Savary, 8/vii/2005, 25°59.733′N 111°25.116′W, 120 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, Sierra de San Francisco, 8 km SW at La Presa junction: ♂1 (AMNH[LP 4485]), collected by E. González & L. Prendini, 6/vii/2005, 27°35.178′N 113°03.579′W, 1170 m, UV detection at night. Mexico, Baja California Sur, Municipio Loreto, Loreto, S, ca. 3 km along gravel road to San Javier, from junction with Route 1: subadult ♀ 1 (AMNH[LP 4486]), collected by E. González, R. Mercurio, W. E. Savary & L. Prendini, 8/vii/2005, 25°59.800′N 111°19.250′W, 38 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé , San José de Comondú to Loreto, along road: subadult ♀ 1 (AMNH[LP 4489]), collected by L. Prendini, W.E. Savary, E. González & R. Mercurio, 7/vii/2005, 26°01.055′N 111°45.180′W, 293 m, UV detection at night. Mexico, Baja California Sur, Municipio Mulegé, Cueva del Raton, 5 km SW Sierra de San Francisco: ♀4 , sex indeterminant 17(AMNH[LP 4490]), collected by E. González & L. Prendini, 6/vii/2005, 27°35.491′N 113°01.441′W, 1130 m, UV detection at night. Mexico, Baja California Sur, Municipio La Paz, La Paz, ca. 20 km N junction Route 1 and road to San Juan de la Costa: sex indeterminant 1(AMNH[LP 4494]), collected by L. Prendini, E. González & R. Mercurio, 9/vii/2005, 24°13.383′N 110°35.766′W, 20 m, UV detection at night. Mexico, Baja California Sur, Municipio

Mulegé, Microondas el Abulon: ♂1 (AMNH[LP 4496]), collected by W.E. Savary & E. González, 12/vii/2005, 27°17.483′N 113°01.916′W, 141 m, UV detection at night. Mexico, Baja California Sur, Municipio de Mulegé, Bahía Tortugas 10 km NE: sex indeterminant 2(AMNH[LP 8760]), collected by H. Montaño & E. Gonzalez, 5/vii/2008, 27°45.216'N 114°50.602'W, 17 m, San dunes with spots of small stones, no vegetation/ UV detection during night. Mexico, Baja California Sur, Municipio de Comondú, San José de Comondú, 30 km N, between Rosarito and San Isidro: ♀1 (AMNH[LP 8763]), collected by H. Montaño & E. Gonzalez, 27/vi/2008, 26°21.252'N 111°50.109'W, 258 m, Bottom of a canyon, boulders and cliffts, sandy area, thorny vegetation/ UV detection during night. Mexico, Baja California Sur, Municipio de Mulegé, Sierra del Placer, 21 km to junction Bahía Tortugas and Bahía Asunción, 98 km E of Vizcaino towards Bahía Tortugas: subadult ♀ 1 (AMNH[LP 8765]), collected by H. Montaño & E. Gonzalez, 28/vi/2008, 27°28.928'N 114°17.093'W, 262 m, Stabilized sand dunes, compacted sand dunes and rocky spots, scrub vegetation/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Microwaves antenna, La Paz, libramiento to Pichilingue beach: subadult ♀ 1, ♀ 1 (AMNH[LP 8768]), collected by I.G. Nieto Castaneda and E. Gonzalez, 9/vi/2008, 24°07.872'N 110°16.987'W, 224 m, Stones and boulders, thorn-scrub and cacti/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, El Pilar, ca 20 km NE of Las Pocitas: ♀1 (AMNH[LP 8770]), collected by H. Montaño & E. Gonzalez, 25/vi/2008, 24°28.762'N 111°01.125'W, 92 m, Oasis, carved walls of compacted sand and granitic walls, stones and boulders/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Las Cruces 4 km NW: ♀1 (AMNH[LP 8771]), collected by H. Montaño & E. Gonzalez, 24/vi/2008, 24°13.511'N 110°07.410'W, 31 m, Stones, granitic sand and pebbles, thorn-scrub and cacti/ UV detection during night. Mexico, Baja California Sur, Municipio de Loreto, Loreto, 13 km W to San Javier, provisional dirty road : ♀1 (AMNH[LP 8774]), collected by H. Montaño & E. Gonzalez, 26/vi/2008, 25°58.817'N 111°27.211'W, 176 m, Arroyo wash, stones and boulders, thorn-scrub and cacti, sandy area/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, Libramiento to Pichilingue marker km 4, by the Termoelectrica Punta Prieta: sex indeterminant 1(AMNH[LP 8775]), collected by M. Correa, I.G. Nieto Castaneda and E. Gonzalez, 23/vi/2008, 24°12.843'N 110°16.214'W, 105 m, Arroyo wash, stones and boulders, thorn-scrub and cacti, sandy area, cliffs and compacted sand hills/ UV detection during night. Mexico, Baja California Sur, Municipio de Comondú, San José de Comondú, 12 km N: ♂1 (AMNH[LP 8776]), collected by H. Montaño & E. Gonzalez, 8/vii/2008, 26°08.729'N 111°47.326'W, 504 m, Rocky area scrub-thorn vegetation, disturbance by cattle/ UV detection during night. Mexico, Baja California Sur, Municipio de Comondú, San José de Comondú, 9 km NW, Cerro el Pabellón: sex indeterminant 1(AMNH[LP 8777]), collected by H. Montaño & E. Gonzalez, 9/vii/2008, 26°05.949'N 111°53.688'W, 742 m, Scoria and basalt rocks, cliffs/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, San Evaristo, 10-15 km S, dirty road: ♂1 (AMNH[LP 8830]), collected by H. Montaño & E. Gonzalez, 12/vii/2008, 24°47.757'N 110°40.502'W, 27–50 m, Scrub-thorn and cacti, arroyo and sand banks/ UV detection during night. Mexico, Baja California Sur, Municipio de La Paz, San Evaristo, 5 km S: sex indeterminant 2(AMNH[LP 8834]), collected by H. Montaño & E. Gonzalez, 12/vii/2008, 24°52.901'N 110°41.404'W, 5–50 m, Sand dunes/ UV detection during night. México, Baja California, Bahia de Los

Angeles, N of Programa Tortuga Marina: ♀1 (AMNH[LP 2873]), collected by R. Mercurio, M. Nishiguchi, *et al.*, 27/v/2004, 28°55.0'N 113°31.0'W, 3 m, UV light detection. México, Baja California Sur, Juncalito: ♂6, ♀3, ♀ 2 (AMNH[LP 2872]), collected by R. Mercurio, M. Nishiguchi, *et al.*, 20/v/2004, 25°49.892'N 111°19.691'W, 5 m, UV light detection. México, Baja California Sur, Municipio Comondú, S of El Cayuco "Fish Camp": ♂11, ♀7 , sex indeterminant 6 subad.(AMNH[LP 2874]), collected by R. Mercurio, M. Nishiguchi, *et al.*, 24/v/2004, 24°34.672'N 111°40.645'W, 23 m, UV light detection. México, Baja California Sur, El Tecolote: ♂3, ♀8 , sex indeterminant 3 juv.(AMNH[LP 2875]), collected by R. Mercurio, M. Nishiguchi, *et al.*, 21/v/2004, 24°20.259'N 110°18.580'W, 2 m, UV light detection.

***Centruroides exilimanus* Teruel & Stockwell, 2002:** El Salvador, Martin Perez, Golfo de Fonseca, La Union: ♀1 (AMNH[LP 9171]), collected by E. Echeverria, 16/viii/2001, 13°16'38"N87°44'11"W, 10 m. Honduras?, : sex indeterminant 1 subad.(AMNH[LP 4404]), collected by , /viii/2005. Honduras?, : ♂1 (AMNH[LP 5500]), collected by , /ii/2006.

***Centruroides exsul* (Meise, 1934):** Venezuela, Galapagos, Isla Pinta, southern coast: 3, 2, 2, 2, 5 (CAS[9027472]), collected by D.O. Cavagnaro, 25/v/1964.

***Centruroides fallassisimus* Armas & Trujillo, 2010:** Guatemala, Zacapa, Aldea Casas de Pinto, near turnoff for Zacapa at Rio Hondo: ♂2, ♀1, subadult ♀ 1, ♀ 2, juvenile ♀ 1 , sex indeterminant 1(AMNH[LP 5988]), collected by J. Huff, C. Viquez & D. Ortiz, 13/vii/2006, N 15°01'37.1" W 89°36'57.2" , 77 m, Semi-arid region with scrub forest and cacti. Collected under rocks in shaded areas and at night using UV. Guatemala, Zacapa, Huite, Antombran, Cerro Malpais: ♀2, ♀ 1, juvenile ♀ 1 , sex indeterminant 1(AMNH[LP 5989]), collected by J. Huff, C. Viquez & D. Ortiz, 14/vii/2006, N 14°56'35.1" W 89°44'34.7" , 81 m, Semi-arid region with scrub forest and cacti. Collected under rocks in shaded areas. Honduras, Departamento de Lempira, Municipio de La Iguala?, La Telegrafía, side of road going to Gracias, before reach Santa Rita: ♂1 (AMNH[LP 9176]), collected by C. Viquez & M. Branstetter, 28/ix/2008, 14.76599°N88.24193°W, 466 m, day, under rocks in Quercus forest. Honduras, Departamento de Lempira, Municipio de Gracias, Road to Santa Rosa de Copán, just out of Gracias: ♂1 (AMNH[LP 9180]), collected by C. Viquez & M. Branstetter, 29/ix/2008, 14.663533°N88.59829°W, 642 m, night, side of road in a bean crop, under rocks and UV. Honduras, Departamento de Santa Barbara, Municipio de Santa Barbara, San Antonio, 1 km NE de Río Grande de Otoro: juvenile ♀ 1 (AMNH[LP 9174]), collected by C. Viquez & M. Branstetter, 28/ix/2008, 14.77435°N88.17076°W, 355 m, day, under rocks in a maize crop.

***Centruroides farri* Armas, 1976:** Jamaica, St. Elizabeth Parish, Lover's Leap, 1 km E: sex indeterminant 2 juv.(AMNH[LP 5107]), collected by L. Esposito, 24/vii/2005, 17°52.270'N077°39.114'W, 62 m, evergreen drought-deciduous shrubland with succulents, high bluffs, UV detection, 35°C. Jamaica, St. Elizabeth Parish, Lover's Leap, 1 km E: ♀1 (AMNH[LP 5112]), collected by L. Esposito, 24/vii/2005, 17°52.270'N077°39.114'W, 62 m, evergreen drought-deciduous shrubland with succulents, high bluffs, UV detection, 35°C.

***Centruroides flavopictus flavopictus* (Pocock, 1898):** Mexico, Oaxaca, Municipio de Santa Maria Jacatepec, Vega de Sol: ♂1 (AMNH[LP 9516]), collected by O.F. Francke,

R. Botero, C. Santibañez & A. Valdez, 5/vi/2008, 17.812655°N 96.21521°W, 46 m. Mexico, Veracruz, Municipio Santiago Tuxtla, Cerro Blanco, 6 km Camino hacia Cerro Vigia: ♂1 (AMNH[LP 1823]), collected by E. Gonzalez Santillan, 28/Enero?/2001. Mexico, Veracruz, Municipio Santiago Tuxtla, Cerro Blanco, 6 km Camino hacia Cerro Vigia: ♂1 (AMNH[LP 1824]), collected by E. Gonzalez Santillan, 28/Enero?/2001. Mexico, Veracruz, Estacion de Biologia 'Los Tuxtlas', UNAM: sex indeterminant 1(AMNH[LP 2069]), collected by E. Gonzalez Santillan and L. Prendini, 19/vii/2002, lowland rainforest; collected at night with UV light. México, Veracruz, Municipio Catemaco, Estacion de Biologia los Tuxtlas: ♀1 (AMNH[LP 5232]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 26/viii/2005, 18°35.058'N 93°04.491'W, 134 m.

***Centruroides gracilis* (Latreille, 1804):** Guatemala, Petén, Rio Secoyo ♂ km marker 335, approx. 15km south of St. Luis. Collected along highway bordered on each side by small mountains: sex indeterminant 1(AMNH[LP 5993]), collected by J. Huff, C. Viquez & D. Ortiz, 9&12/vii/2006, N 16°01’37.7” W 89°19’24.0” , 278 m, Habitat with many limestone rocks on a slope with heavy leaf litter and well shaded. Guatemala, Petén, Cerro Cahui on Lake Petén Itza: ♂2, ♀1 (AMNH[LP 5994]), collected by J. Huff, C. Viquez & D. Ortiz, 9/vii/2006, N 16°59’53.0” W 89°42’14.9” , 118 m, Tropical forest reserve with many trails. Collected using UV at night. México, Chiapas, Crossroad Frontera Corozal-Sierra de la Cojolita: ♂3, ♀2 (AMNH[LP 3699]), collected by O. Francke & H. Montano, 8/xi/2004, 16°45'57.4"N 91°01'42.6"W, 208 m, UV light detection at night. México, Chiapas, Ocosingo, Crossroad to Bonampak, 1 km SE: ♂2, ♀1 (AMNH[LP 3701]), collected by O. Francke & H. Montano, 10/xi/2004, 16°48'14.9"N 90°52'17.1"W, 93 m, UV light detection at night. México, Chiapas, El Encaño, Sierra Cojolita: ♀ 1 (AMNH[LP 4103]), collected by A. Valdez, O. Francke & A. Ballesteros, 8/iv/2005, 16°48.677'N 91°04.646'W, 165 m. U.S.A., Florida, Florida Keys: ♂1 (AMNH[LP 1901]), collected by , /iv/2002. U.S.A., New Jersey, Middlesex County, Geerlings Green Houses, 486 William St., Piscataway: ♀1 (AMNH[LP 3009]), collected by , 13/viii/2004, 40.57191°N74.47991°W. México, Hidalgo, 24 km SE Tamazunchale: ♂1 , sex indeterminant 2(AMNH[LP 2013]), collected by L. Prendini and E. Gonzalez, 3/viii/2002, 21°11'14"N 98°54'16"W, under stones on grassy hillside (deforested). México, San Luis Potosi, Antena de Microondas de Ciudad Valles: ♀7 , sex indeterminant 3(AMNH[LP 2050]), collected by L. Prendini, J. Soriano and E. Gonzalez, 2/viii/2002, 21°58'55"N 99°08'58"W, 340 m; forest (disturbed); collected at night with UV light. México, San Luis Potosi, Antena de Microondas de Ciudad Valles: ♂4, ♀3 , sex indeterminant 3(AMNH[LP 2051]), collected by L. Prendini, J. Soriano and E. Gonzalez, 2/viii/2002, 21°58'55"N 99°08'58"W, 340 m; forest (disturbed); collected at night with UV light. México, San Luis Potosí, Municipio Ciudad Valles, Sótano de Yerbaniz: ♀2 (AMNH[LP 3506]), collected by O. Francke, 14/ix/2004, 22.1854°N 98.9869°W, surface near cave. México, San Luis Potosí, Municipio Ciudad Valles, Sótano de Yerbaniz: ♂6, ♀5 , sex indeterminant 1 juv.(AMNH[LP 3507]), collected by O. Francke, 14/ix/2004, 22.1854°N 98.9869°W, surface near cave. México, Tamaulipas, La Pilita, Area Aldama: ♀1 (AMNH[LP 2306]), collected by P. Sprouse, 3/i/2003. México, Veracruz, Municipio de Atoyac, Grutas de Atoyac: ♂1 , sex indeterminant 1 juv.(AMNH[LP 3505]), collected by O. Francke, 22/ix/2004, 18.9215°N 96.7653°W, 460 m, collected on surface. México, Veracruz, Puente Nacional, Los Idolos: sex

indeterminant 1(AMNH[LP 6523]), collected by O. Francke, P. Berea & A. Ballesteros, 5/v/2006, 19.42915°N 96.53677°W, 112 m. Guatemala, Petén, Yax Há Mayan Archeological Site: sex indeterminant 3(AMNH[LP 5995]), collected by J. Huff, C. Viquez & D. Ortiz, 11/vii/2006, N 17°04’11.7” W 89°23’59.1” , 274 m, collected around the ruins and surrounding forest. Collected under rocks, logs and bark and at night using UV. Guatemala, Petén, Km 325 on highway CA 13, north of Rio Dulce: ♀1 (AMNH[LP 5996]), collected by J. Huff, C. Viquez & D. Ortiz, 12/vii/2006, N 16°00’42.4” W 89°18’10.9” , 287 m, collected under rocks along highway. México, Chiapas, Ocosingo, San Javier crossroad, 1 km S: ♂2, ♀3 (AMNH[LP 3698]), collected by O. Francke, 9/xi/2004, 17°48'21.7"N 91°04'58.6"W, 207 m, UV light detection at night. México, Chiapas, El Aserradero: sex indeterminant 1(AMNH[LP 5229]), collected by , 4/vi/2005, 16°47.160'N 91°02.228'W, 196 m. U.S.A., Florida, : sex indeterminant 6 juv.(AMNH[LP 1731]), collected by , /vii/1998. U.S.A., Florida, Monroe County, Dry Tortugas, Garden Key, Fort Jefferson: ♂1 (AMNH[LP 9098]), collected by D.H. & T.D. Desoer, 27/ix/2008, 24˚37'42"N82˚52'24"W, 20:30–21:30, 26˚C, UV blacklight, Fort walls, courtyard and internal passages. Venezuela, La Guaira: ♀1 , sex indeterminant 1 juv.(AMNH[LP 1550]), collected by M.A. Gonzalez-Sponga, /xi/1998. Ecuador, Loja, Catamayo , Border Parque Predesur, 2 km NE Catamayo: ♀1 , sex indeterminant 1 juv(AMNH[LP 8384]), collected by J.A. Ochoa, 6/ii/2008, 03°57.542'S79°23.428'W, 1240 m, dry forest, collected at night with UV light.

***Centruroides griseus grisues*** **(C. L. Koch, 1844):** U.K., British Virgin Islands, Guana Island: ♀1 (AMNH[LP 1786]), collected by J. Lazell, 12/x/2000. U.K., British Virgin Islands, Virgin Gorda Island: ♀1 (AMNH[LP 9616]), collected by , 15/iv/2009. U.S.A, Puerto Rico, Bosque Estatal Cambalache, 3.9 mi W intersection with Route 681 on Route 682: sex indeterminant 1 subad., 1 juv.(AMNH[LP 10215]), collected by L. Prendini, J. Huff, L. Esposito & H. Yamaguti, 15/x/2009, 18°27.537'N66°35.877'W, 417 m, dry forest on low limestone outcrops; extensive leaf litter layer; limestone outcrops and loose stones; hand collected during day and UV detection on warm, still, humid night, no moon. U.S.A, U.S. Virgin Islands, St. John, Virgin Islands National Park, Yawzi Point Trail: sex indeterminant 1 juv.(AMNH[LP 10209]), collected by L. Prendini & J. Huff, 17/x/2009, 18°19.162'N64°43.521'W, 42 m, subtropical dry forest with agave, cereus, coloumn cacti and barrel cacti on promontory (Yawzi Point); many loose rocks; UV detection. U.S.A, U.S. Virgin Islands, St. John, Virgin Islands National Park, 0.5 mi E of turnoff to Yawzi Point Trail: sex indeterminant 2 juv.(AMNH[LP 10213]), collected by L. Prendini & J. Huff, 17/x/2009, 18°19.054'N64°43.119'W, 18 m, primary subtropical forest, UV detection on warm, still, very humid, moonless night, immediately after rain. U.S.A, U.S. Virgin Islands, St. John, Virgin Islands National Park, Lameshur Bay Trail, parking lot and first few hundred meters of trail: sex indeterminant 1 juv.(AMNH[LP 10218]), collected by L. Prendini & J. Huff, 17/x/2009, 18°19.242'N64°43.641'W, 22 m, subtropical forest (primary) near seashore; taken under stones; UV detection on cool to warm night. U.S.A., Puerto Rico, Culebra, Brava Beach Trail: ♂1, ♀1 (AMNH[LP 6237]), collected by S. Crews & G. Oliviere, 12/vi/2006, 18°19'38.9"N65°16'54.1"W, ca. 9 m, dry forest, under bark. U.S.A., Puerto Rico, Arecibo, Arenalejos, Carretera 657, km 1.9: sex indeterminant 1 subad.(AMNH[LP 6239]), collected by S. Crews, A. Puente-Rolon & M. Nevaraez, 7/vi/2006, 18°25'15.9"N66°40'35.2"W, ca. 141 m, under bark of iron wood and Bursera.

***Centruroides guanensis* Franganillo, 1930:** U.S.A., Florida, Monroe County, Long Key State Park: ♂1 (AMNH[LP 9137]), collected by K. Crouch, 4/xi/2008, 24°48.484'N80°50.060'W, inside ranger station. U.S.A., Florida, : ♂1 (AMNH[LP 1673]), collected by , 16/v/2000.

***Centruroides hentzi* (Banks, 1900):** U.S.A., Florida, Alachua County, Paynes Prarie State Park, main rd. near river trail: ♀1 (AMNH[LP 9099]), collected by D.H. & T.D. Desoer, 5/x/2008, 29˚32'07"N82˚17'16"W, 20 m, 20:15–21:00, 24˚C, UV blacklight, on bark of pines just off of road. U.S.A., Florida, St. Johns County, FDOT Rest Area, I-95 S exit 304: ♀1 (AMNH[LP 9100]), collected by D.H. & T.D. Desoer, 24/ix/2008, 29˚43'00"N81˚20'07"W, 8 m, 20:00–21:00, 23˚C, UV blacklight, on pine trees with moderate undergrowth; pine trees on mown lawn at edge of denser forest. U.S.A., Florida, Monroe County, Everglades National Park, Long Pine Key Campground: sex indeterminant 1 juv.(AMNH[LP 9101]), collected by D.H. & T.D. Desoer, 30/ix/2008, 25˚24'00"N80˚39'21"W, 21:20–23:00, 24 ˚C, UV blacklight, primarily slash pine, on bark or near base on low plants or logs . U.S.A., Florida, Sarasota County, Oscar Scherer State Park, around Blue Trail: ♀1 (AMNH[LP 9102]), collected by D.H. & T.D. Desoer, 2/x/2008, 27˚10'46"N82˚27'55"W, 2 m, 20:15–21:15, 26–20˚C, UV blacklight, pine trees and ground debris. U.S.A., Florida, Monroe County, Dry Tortugas, Loggerhead Key, N of lighthouse: ♀ 1 , sex indeterminant 1 juv.(AMNH[LP 9103]), collected by D.H. & T.D. Desoer, 28/ix/2008, 24˚38'02"N82˚55'11"W, 20:30–22:00, 26˚C, UV blacklight, lee side of decayed Casuarina stumps, shrubs and driftwood during light rain and moderate wind (4–5 Bf). U.S.A., Florida, Leon County, Tall Timbers Research Station, gulley behind Sloan house: sex indeterminant 2 juv.(AMNH[LP 9104]), collected by D.H. & T.D. Desoer, 3/x/2008, 30˚39'35"N84˚12'36"W, 54 m, 21:00–23:30, 21–18˚C, UV blacklight, on long leaf pine bark, ground debris, Smilax leaves, Callicarpa leaves. U.S.A., Florida, Gadsden County, FDOT Rest Area, I-10 exit 162: sex indeterminant 1 juv.(AMNH[LP 9105]), collected by D.H. & T.D. Desoer, 4/x/2008, 30˚37'36"N84˚53'35"W, 66 m, 21:20–21:50, UV blacklight, trees surrounded by mown lawn, near picnic area at edge of denser forest.

***Centruroides hirstutipalpus* Ponce-Saavedra & Francke, 2009:** Mexico, Colima, Municipio Manzanillo, El Habillal, 3 km E El Veladero de Camotlán, 6 km from Route 98, along gravel road, SITE 62: ♂1 , sex indeterminant 1(AMNH[LP 4714]), collected by E. González & R. Mercurio, 1/viii/2005, 20°21.674′N 105°08.017′W, 500 m, UV detection at night. Mexico, Colima, Balneario 'El Salto', Minatitlan: ♀1 (AMNH[LP 7618]), collected by O. Francke, H. Montano, A. Valdez, C. Santibanez & A. Ballesteros, 29/viii/2007, 19°22.087'N 104°05.128'W, 650 m. Mexico, Colima, Municipio de Minatitlan, Balneario el Salto: ♀1 (AMNH[LP 9981]), collected by O. Francke, H. Montaño, A. Valdez, C. Santibañez & A. Ballesteros, 29/viii/2007, 19°22.087´N 101°05.128´W, 650 m. México, Colima, Minatitlan, Balneario El Salto : ♂1 (AMNH[LP 6479]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 26/v/2006, 19°22.087N 104°5.128W, 650 m.

***Centruroides hoffmanni* Armas, 1996:** México, Chiapas, Las Delicias: ♀1 (AMNH[LP 5224]), collected by O. Francke, M. Córdova, J. Ballesteros & A. Jaimes, 29/iii/2005. México, Chiapas, Municipio Tzimol, Highway Comitan-Tzimol Santa Rosa: ♂1, ♀1 (AMNH[LP 5249]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 2/ix/2005, 16°11.056'N 92°16.988'W, 730 m. México, Chiapas, Municipio

Villaflores, Ejido California, 1 km SE, Reserva de La Biosfera La Sepultura: ♂1 (AMNH[LP 5350]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 30/viii/2005, 16°15.237'N 93°35.774'W, 1132 m.

***Centruroides infamatus* (C.L. Koch, 1844):** Mexico, Guanajuato, Acámbaro, 2 km N Pueblo San Luis de los Agustinos: ♂2 (AMNH[LP 6631]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 25/iii/2006, 20.20775°N 100.6895°W, 2450 m. Mexico, Jalisco, Mazamitla, Carretera Mazamitla-Jiquilpan: ♂1 (AMNH[LP 6430]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 31/v/2006, 19°57.516N 103°0.768W, 2097 m. Mexico, Jalisco, Tamazula de Gordiano, Carretera Tamazula-Mazamitla: ♀3 , sex indeterminant 1(AMNH[LP 6615]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 30/v/2006, 19.88031°N 103.08298°W, 1825 m. Mexico, Michoacan, Municipio Tinqambato, 4 km W de Tinqambato: ♂1 (AMNH[LP 1822]), collected by E. Gonzalez Santillan, 23/iii/2000, under stones. Mexico, Michoacan, Morelia: ♂1 (AMNH[LP 2003]), collected by R. Cancino M., 8/ii/2002. Mexico, Michoacan, Morelia: ♀1 (AMNH[LP 2004]), collected by E.P. Miranda L., 3/ix/2001. Mexico, Michoacan, Tandamangapio, Los Tabanos: ♀2 (AMNH[LP 6420]), collected by O. Francke, H. Montaño, A. Valdez & A. Ballesteros, 31/v/2006, 19.9749°N 102.84226°W, 223 m. Mexico, Michoacan, Cerro Grande, 1 km S Ecuandoreo: sex indeterminant 1 juv.(AMNH[LP 7608]), collected by O. Francke *et al.*, 1/ix/2007, 20°07.966'N 102°11.713'W, 1884 m. México, Michoacán, Municipio Tangancicuaro, Lago de Camecuaro National Park: ♂1, ♀3 (AMNH[LP 5213]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 3/vii/2005, 19°53.916'N 102°12.450'W, 1730 m. México, Michoacán, Municipio Tangancicuaro, Predio La Beata: sex indeterminant 2(AMNH[LP 5223]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 3/vii/2005, 19°55.648'N 102°10.685'W, 1780 m. México, Michoacán, Churintzio, 4 km N: ♂1 (AMNH[LP 5349]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 4/vii/2005, 20°09.813'N 102°02.845'W, 1904 m. Mexico, Guerrero, Tlapa de Comonfort, 30 km S Olinala: ♀ 1 (AMNH[LP 7034]), collected by Francke *et al.*, 15/vi/2007, 17° 36.524'N 98°44.156 W, 2063 m.

***Centruroides insulanus* (Thorell, 1876):** Jamaica, St. Ann District, Runaway Caves, ca. 1 km E: ♀1 (AMNH[LP 5184]), collected by S. Huber, 15/vi/2005, 18°27'28.9"N77°21'03.2"W, 34 m, under stones in bush. Jamaica, St. Thomas Parish, Morant Bay: ♀1 , sex indeterminant 2 subad.(AMNH[LP 5110]), collected by L. Esposito, 28/vii/2005, 17°52.270'N076°22.362'W, 19 m, mixed herbaceous/woodland/plantation, degraded habitatUV detection, 35°C. Jamaica, St. Thomas Parish, Morant Bay: ♂1 , sex indeterminant 3 juv.(AMNH[LP 5111]), collected by L. Esposito, 28/vii/2005, 17°52.270'N076°22.362'W, 19 m, mixed herbaceous/woodland/plantation, degraded habitatUV detection, 35°C.

***Centruroides elegans insularis* Pocock, 1902:** Mexico, Nayarit, Municipio Compostela, Compostela, ca. 11 km S, on gravel road between Felipe Carrillo Puerto and Zapotán, SITE 60: ♀1 , sex indeterminant 2(AMNH[LP 4718]), collected by E. González & R. Mercurio, 1/viii/2005, 21°07.233′N , 104°50.772′W, 833 m, UV detection at night. Mexico, Nayarit, Municipio Tuxpan, Microondas Peñitas, ca. 10 km E Tuxpan, SITE 57: ♂2, ♀1 (AMNH[LP 4719]), collected by E. González & R. Mercurio, 31/vii/2005,

21°55.843′N 105°12.805′W, 230 m, UV detection at night. Mexico, Nayarit, Isla Maria Madre, Brecha Laguna del Toro, Antena de Microondas: (AMNH[LP 9528]), collected by U. Torres & E. Pagaza, 9/ix/2008, 21°34'56.71"N 106°33'18.19"W. México, Jalisco, Mascota, 1 km E: ♀1 (AMNH[LP 5219]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 9/vii/2005, 20°31.192'N 104°46.301'W, 1281 m. México, Jalisco, Highway Ameca-Mascota, 111 km: ♀1 , sex indeterminant 1(AMNH[LP 5241]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 9/vii/2005, 22°28.820'N 104°45.508'W, 1500 m.

***Centruroides jaragua* Armas, 1999:** Dominican Republic, La Altagracia Province, Forested road cutting in cane fields, near Alto de Chavon: sex indeterminant 1 juv.(AMNH[LP 3320]), collected by E.S. Volschenk & J. Huff, 15/vii/2004, 18.4908°N68.9178°W, 65.5 m, Humid forested cutting flanked by sugarcane fields; hand collected from under stones and logs, and with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Jaragua, Cabo Rojo: ♀1 , sex indeterminant 3 juv.(AMNH[LP 3319]), collected by E.S. Volschenk & J. Huff, 9/vii/2004, 17.8908°N71.6567°W, 10.2 m, Dry area with mostly grassy tussocks and sparse trees; collected with blacklights. Dominican Republic, Pedernales Provence, Floodplain beside road, between Pedernales and Oviedo : ♂1 (AMNH[LP 3321]), collected by E.S. Volschenk & J. Huff, 6/vii/2004, 18.0017°N71.6820°W, 12.9 m, Dry floodplain with cactus, grass tussocks and sparse trees; hand collected with blacklights.

***Centruroides koesteri* Kraepelin, 1912= *Centruroides mahnerti* Lourenço, 1983:** Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♀2 (AMNH[LP 6102]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♂1 (AMNH[LP 6103]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♂1, ♀ 1 (AMNH[LP 6104]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Nicaragua, Chinandega, El Viejo, Santo Thomas, Villa Argentina: ♀1 (AMNH[LP 8592]), collected by C. Viquez & J. Mata, 26/xi/2007, 12°45'00.0"N87°23'45.6"W, 38 m. Nicaragua, Chinandega, El Viejo, Hacienda (Hostal) Cosiguina: ♀1 (AMNH[LP 8593]), collected by C. Viquez & J. Mata, 27/xi/2007, 12°54'33.0”N87°30'40.0”W, 18 m. Nicaragua, León, La Paz Centro, Volcán Momotombo, El Cardón, afloramientos de rocas volcanicas y bosque: ♂1 (AMNH[LP 8594]), collected by C. Viquez & J. Mata, 2/xii/2007, 12°24'57.0”N86°29'16.8”W, 55 m. Costa Rica, Islas Murcielago, Isla San Jose: subadult ♀ 1 (AMNH[LP 8596]), collected by M.M. Chavarria D., 13/xi/2004. Costa Rica?, : ♀1, juvenile ♀ 3 , sex indeterminant 3 juv.(AMNH[LP 8595]).

***Centruroides limbatus* (Pocock, 1898):** Costa Rica, Limon Prov., Reserva Biológica “Hitoy Cerere”, Cahuita: ♀3 (AMNH[LP 6113]), collected by V. Vignoli, C. Viquez & H. Ajuria, 17/v/2006, 09°40'18"N,83°01'30"W, 95 m. Costa Rica, Limon Prov., Reserva Biológica “Hitoy Cerere”, Cahuita: ♀1 , sex indeterminant 14(AMNH[LP 6114]), collected by V. Vignoli, C. Viquez & H. Ajuria, 17/v/2006, 09°40'18"N,83°01'30"W, 95 m. Costa Rica, Limon Prov., Reserva Biológica “Hitoy Cerere”, Cahuita: ♀ 1 (AMNH[LP 6115]), collected by V. Vignoli, C. Viquez & H. Ajuria, 17/v/2006, 09°40'18"N,83°01'30"W, 95 m. Costa Rica, Hacienda Barú, Barú: sex indeterminant 1(AMNH[LP 1957]), collected by A.V.Peretti & M. Montoya, 15/iv/2002.

***Centruroides limpidus* (Karsch, 1879):** Mexico, Guerrero, Cerro de la Coronilla, 2 km E Ahuelican: juvenile ♂ 1 (AMNH[LP 9524]), collected by O.F. Francke, A. Valdez, T. Lopez & C. Quijano, 8/i/2009, 18.01628°N 99.52875°W, 855 m, night collecting. México, Estado de Mexico, Municipio Malinalco, Malinalco, ca. 19 km S, on gravel road off State Route 4, SITE 49: ♂1, ♀3 , sex indeterminant 1(AMNH[LP 4711]), collected by R. Mercurio & E. González , 25/vii/2005, 18°52.197′N099°26.990′W, 1530 m, UV detection at night. México, Guerrero, Tepecoacuilco, 2 km W Ahuehuepan: ♂1 (AMNH[LP 7037]), collected by Francke, Ponce *et al.*, 14/vi/2007, 18° 00.911'N 99°31.407 W, 867 m. México, Guerrero, Buena Vista de Cuellar, El Comal: ♀ 1 , sex indeterminant 1(AMNH[LP 7042]), collected by Francke, Ponce *et al.*, 13/vi/2007, 18° 27.086'N 99°17.139 W, 1749 m. México, Michoacán, Municipio Paracuaro, La Berea: ♂1 (AMNH[LP 5239]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila , 11/vii/2005, 19°08.173'N 102°13.195'W, 445 m. México, Morelos, Tlaquiltenango, 2 km NE Estacion del CEAMISH, Quilamula: ♂1 , sex indeterminant 1(AMNH[LP 6534]), collected by M. Cordova & A. Jaimes, 28/i/2006, 18°30.657N 99°0.798W, 1086 m. México, Puebla, San Pedro Cuayuca, 13 km NE Tlacotepec: ♂2 , sex indeterminant 1(AMNH[LP 6545]), collected by , 29/vi/2005, 18°25.841N 98°14.015W, 1117 m.

***Centruroides luceorum* Armas, 1999:** U.S.A., Navassa Island, United States National Wildlife Refuge, area around lighthouse and adjacent building remains: sex indeterminant 1 juv.(AMNH[LP 9602]), collected by C. Lombard *et al.*, /xii/2008, 18°23'49.88"N75°00'46.33"W, collected with UV.

***Centruroides marcanoi* Armas, 1981:** Dominican Republic, Independencia Province, Parque Nacional Sierra de Baoruco, Rabo de Gato: ♂1 (AMNH[LP 3308]), collected by E.S. Volschenk & J. Huff, 7/vii/2004, 18.3108°N71.5817°W, 408 m, Broadleaf forest with little/no understory; hand collected from under stones and logs, and with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Sierra de Baoruco, from Cabo Rojo: ♀2 (AMNH[LP 3307]), collected by E.S. Volschenk & J. Huff, 10/vii/2004, 18.0900°N71.5108°W, 1271 m, Pine forest and dense lower storey; hand collected from under stones of visitors car park and along walking tracks, and with blacklights.

***Centruroides margaritatus* (Gervais, 1841):** Honduras: ♀1, 1 sex indeterminant (AMNH[LP 2157]), ix/2002. Nicaragua, Granada, Domitila Research Station (Domitila Reserva Silvestre Privada): ♂1 (AMNH[LP 4325]), collected by Chaboo & Shepard, 10/vi/2005, 11°42.54'N85°57.21'W. Nicaragua, Granada, Domitila Research Station (Domitila Reserva Silvestre Privada): ♀1 (AMNH[LP 4326]), collected by C.S. Chaboo, 8/vi/2005, 11°42.54'N85°57.21'W. Costa Rica, Guanacaste, Between Santa Cecilia and Pan-Am. Hwy: ♀2 (AMNH[LP 6843]), collected by J.S. Miller, 29/i/2007. Costa Rica, Guanacaste, Between Santa Cecilia and Pan-Am. Hwy: subadult ♀ 1 (AMNH[LP 6844]), collected by J.S. Miller, 29/i/2007. Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♂1 (AMNH[LP 6105]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♀2 (AMNH[LP 6106]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Guanacaste Prov., Parque National Santa Rosa, Peninsula de Santa Elena: ♂1 (AMNH[LP 6107]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Guanacaste Prov., Parque National Santa

Rosa, Peninsula de Santa Elena: sex indeterminant 1(AMNH[LP 6108]), collected by V. Vignoli & C. Viquez, 29/v/2006, 10°50'22"N85°37'07"W, 309 m. Costa Rica, Esterillos Centro: ♂1, ♀1 , sex indeterminant 1(AMNH[LP 1956]), collected by A.V. Peretti & M. Montoya, 16/iv/2002. Costa Rica, : ♂1 (AMNH[LP 4403]), collected by , /viii/2005. Honduras, Departamento de Francisco Morazán, Municipio de San Antonio de Oriente, E.A.P. Zamorano, Monte Redondo, Acuacultura: juvenile ♂ 1 (AMNH[LP 9177]), collected by C. Viquez, 6/x/2008, 13.99988°N86.98917°W, 773 m, night UV. Honduras, : ♂1 (AMNH[LP 1787]), collected by , /iii/2001. Nicaragua, Chinandega, El Viejo, Santo Thomas, Villa Argentina: juvenile ♂ 1 (AMNH[LP 8599]), collected by C. Viquez & J. Mata, 26/xi/2007, 12°45'00.0"N87°23'45.6"W, 38 m. Nicaragua, Chinandega, El Viejo, Hacienda (Hostal) Cosiguina: juvenile ♂ 1 (AMNH[LP 8600]), collected by C. Viquez & J. Mata, 27/xi/2007, 12°54'33.0”N87°30'40.0”W, 18 m. Nicaragua, Departamento de Estelí, Municipio de Condega, Venecia, Canta Gallo, 21 km NE of Condega to San Sebastian de Yalí: ♀1 (AMNH[LP 9178]), collected by C. Viquez & M. Branstetter, 8/x/2008, 13.41816°N86.25397°W, 1227 m, day, rocks logs and litter search. Nicaragua, Granada, Domitila: (AMNH[LP 1986]), collected by J.M. Maes, 27/v/2002, 55 m. Nicaragua, León, Nagarote, Carretera vieja a León, Finca ganadera a orillas de carretera: ♂1 (AMNH[LP 8597]), collected by C. Viquez & J. Mata, 24/xi/2007, 12°09'41.0"N86°39'35.0”W, 58 m. Nicaragua, León, Telica, Carretera a San Isidro: sex indeterminant 1 juv.(AMNH[LP 8598]), collected by C. Viquez & J. Mata, 25/xi/2007, 12°31'40.8"N86°51'14.4"W, 136 m. Nicaragua, León, El Jicaral, San Rafael, carretera a Matagalpa, en paredones: juvenile ♂ 1 (AMNH[LP 8601]), collected by C. Viquez & J. Mata, 29/xi/2007, 12°40'35.0”N86°25'37.0”W, 110 m. Nicaragua, León, La Paz Centro, Volcán Momotombo, El Cardón, afloramientos de rocas volcanicas y bosque: juvenile ♂ 1 (AMNH[LP 8603]), collected by C. Viquez & J. Mata, 2/xii/2007, 12°24'57.0”N86°29'16.8”W, 55 m. Nicaragua, Matagalpa, San Dionisio, Antes de llegar a San Ramón, frente escuela La Curva: juvenile ♂ 1 , sex indeterminant 2 juv.(AMNH[LP 8602]), collected by C. Viquez & J. Mata, 1/xii/2007, 12°52'15.0”N85°50'01.0”W, 560 m.

***Centruroides mariaorum*** **Santiago-Blay, 2009:** Dominican Republic, La Altagracia Province, Parque Nacional del Este, track between ranger station at Bayahibe and La Toruga: ♂1 , sex indeterminant 6 juv.(AMNH[LP 3302]), collected by E.S. Volschenk & J. Huff, 13/vii/2004, 18.3281°N68.8028°W, 8.54 m, Cactus and spiny scrub on sand and on limestone; hand collected from under stones and logs, and with blacklights. U.S.A, Puerto Rico, Isla Mona, road between Sardiniera and airport: ♂1 (AMNH[LP 10228]), collected by L. Esposito & H. Yamaguti, 18/x/2009, 18.06344°N67.88731°W, blacklighting, tropical coastal forest. U.S.A, Puerto Rico, Isla Mona, road to El Faro: ♀1 (AMNH[LP 10232]), collected by L. Esposito & H. Yamaguti, 17/x/2009, 18.06389°N67.86857°W, blacklighting, Cazierius doorkeeping, population sparse. Vegetation primarily desert grassland dominated by organ cactus and tall grasses. Drier than east coast. U.S.A, Puerto Rico, Isla Mona, trail #1 to Punta Capitan from Sardiniera: sex indeterminant 1 subad., 1 juv.(AMNH[LP 10236]), collected by L. Esposito & H. Yamaguti, 16/x/2009, 18.08823°N67.93815°W, blacklighting - trail is primarily scrub forest and cactus.

***Centruroides meisei*** **(Hoffmann, 1939):** Mexico, Guerrero, Colotlipa, Quechultenango: ♂1 (AMNH[LP 4105]), collected by A. Valdez & H. Montaño, 14/iii/2005. Mexico,

Guerrero, Municipio Copala, Microwaves Fogos: ♂1 (AMNH[LP 7039]), collected by Francke *et al.*, 22/vi/2007, 16° 33.992'N 98°53.301 W, 103 m. Mexico, Guerrero, Municipio Copala, Microondas Fogos: sex indeterminant 1 juv.(AMNH[LP 7602]), collected by O. Francke *et al.*, 22/vi/2003, 16°33.992'N 98°53.301'W, 103 m. Mexico, Guerrero, Municipio Copala, Microndas Fogos: juvenile ♂ 2 (AMNH[LP 8581]), collected by O.F. Francke, H. Montaño & A. Ballesteros, 2/xi/2007, 16°34.360'N 98°53.423'W, 14 m.

***Centruroides flavopictus meridonalis* Hoffmann, 1932:** México, Chiapas, Municipio Comitan, Lagunas de Montebello National Park: sex indeterminant 4(AMNH[LP 5222]), collected by O. Francke, G. Villegas, G. Montiel & S. Rubio, 3/ix/2005, 16°06.677'N 91°43.796'W, 1473 m. México, Chiapas, Municipio Comitan, Lagunas de Montebello National Park: ♀1 (AMNH[LP 5262]), collected by O. Francke, G. Villegas, G. Montiel & S. Rubio, 3/ix/2005, 16°06.677'N 91°43.796'W, 1473 m. México, Chiapas, Rabasa ground camp, Reserva del Ocote: ♀1 (AMNH[LP 5214]), collected by O. Francke, M. Córdova, A. Jaimes & J. Ballesteros, 24/v/2005, 16°54.538'N 93°36.683'W, 758 m. México, Chiapas, Municipio Tuxtla Gutierrez, Microwave Station Canon del Sumidero: ♀1 (AMNH[LP 5252]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 29/viii/2005, 16°48.151'N 93°05.450'W, 1104 m, UV detection at night .

***Centruroides morenoi* (Mello-Leitao, 1945):** Jamaica, Manchester Parish, Alligator Pond, 10 km W: ♂1 (AMNH[LP 5114]), collected by L. Esposito, 23/vii/2005, 17°51.275'N077°32.103'W, 18.6 m, lowland semi-deciduous forest with succulents pristine habitat, under rock, 36°C. Jamaica, Manchester Parish, Alligator Pond, 10 km W: ♂5, ♀1 , sex indeterminant 2 subad., 2 juv.(AMNH[LP 5116]), collected by L. Esposito, 23/vii/2005, 17°51.275'N077°32.103'W, 18.6 m, lowland semi-deciduous forest with succulents pristine habitat, under rock, 36°C. Jamaica, St. Andrews Parish, Yallahs, 10 km W, Quarry Lot: ♂1 (AMNH[LP 5118]), collected by L. Esposito, 30/vii/2005, 17.92318°N 076.64048°W, 85 m, degraded, lowland semi-deciduous forest, UV detection, 35°C. Jamaica, St. Andrews Parish, Bull Bay: ♂2, ♀1 (AMNH[LP 5119]), collected by L. Esposito, 29/vii/2005, 17.94180°N076.67900°W, 17 m, hillside, lowland semi-deciduous forest with succulents UV detection, 36°C. Jamaica, St. Andrews Parish, Bull Bay, Surf Camp: ♀1 (AMNH[LP 5125]), collected by L. Esposito, 29/vii/2005, 17.94130°N076.68774°W, 23 m, near a rock wall along the beach, UV detection, 36°C. Jamaica, St. Catherine Parish, Salt River, 1 km S Jon's House: ♀1 (AMNH[LP 5128]), collected by L. Esposito, 21/vii/2005, 17°49.814'N077°10.875'W, 16.2 m, evergreen drought-deciduous shrubland with succulents, limestone near salt water marsh, degraded habitat, UV detection, 35.5°C.

***Centruroides nigrescens* (Pocock, 1898):** Mexico, Guerrero, Copala, Microwaves Fogos: sex indeterminant 1(AMNH[LP 7046]), collected by Francke *et al.*, 22/vi/2007, 16° 33.992'N 98°53.301 W, 103 m. Mexico, Guerrero, Copala, Microndas Fogos: juvenile ♂ 1 (AMNH[LP 8576]), collected by O.F. Francke, H. Montaño & A. Ballesteros, 2/xi/2007, 16°34.360'N 98°53.423'W, 14 m. Mexico, Oaxaca, Totolapan, 4 km N: ♂1, ♀2 (AMNH[LP 3700]), collected by G. Villegas, O. Francke and R. Paredes , 1/xi/2004, 16°41'45.9"N 96°18'52.1"W, 1078 m, UV light detection at night. Mexico, Oaxaca, San Cristobal Amatlán, 1 km N San Lorenzo Mixtepec: sex indeterminant 2(AMNH[LP 6448]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 22/vi/2006, 16.29201°N 96.33305°W, 1925 m. Mexico, Oaxaca, Miahuatlan, 4 km E Miahuatlan: sex indeterminant

3(AMNH[LP 6519]), collected by O. Francke G. Villegas, H. Montaño, C. Santibañez & A. Valdez, 23/vi/2006, 16°19.504N 96°32.46W, 1638 m. Mexico, Oaxaca, Magdalena Mixtepec, Magdalena Mixtepec: ♂1 (AMNH[LP 6603]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 19/vi/2006, 16.8804°N 96.85093°W, 1710 m. Mexico, Oaxaca, Oaxaca, Zona Comunal San Felipe: ♀1 (AMNH[LP 6628]), collected by , 12/xi/2005, 17.116294°N 96.714306°W. Mexico, Oaxaca, Mitla, 15 km E: sex indeterminant 1 juv.(AMNH[LP 7619]), collected by O. Francke, H. Montano, A. Valdez, A. Ballesteros & C. Santibanez, 18/vii/2007, 16°56.606'N 96°17.114'W, 2081 m, pine-oak woodland. Mexico, Guerrero, Municipio de Chilpancingo, Acahuizotla: ♂1 (AMNH[LP 2305]), collected by P. Sprouse, 28/xii/2002. Mexico, Guerrero, Colotlipa, Quechultenango: ♀2 , sex indeterminant 1(AMNH[LP 4104]), collected by A. Valdez & H. Montaño, 14/iii/2005. Mexico, Guerrero, Chilpancingo, Amojileca: sex indeterminant 1(AMNH[LP 7044]), collected by Francke *et al.*, 20/vi/2007, 17° 34.090'N 99°34.145 W, 1484 m. Mexico, Michoacan, Municipio de Aquila, Faro de Bucerias: ♀1 (AMNH[LP 2005]), collected by M.A. Villaseñor R., 15/i/2002.

***Centruroides nigrimanus* (Pocock, 1898):** Mexico, Oaxaca, Municipio Santiago Astata, 4 km N Zimatan, El Chorro de Mazatan: ♂1 (AMNH[LP 1808]), collected by E. Gonzalez Santillan, 18/ix/2000. Mexico, Oaxaca, Municipio Santiago Astata, 4 km N Zimatan, El Chorro de Mazatan: ♂1 (AMNH[LP 1809]), collected by E. Gonzalez Santillan, 18/ix/2000. Mexico, Oaxaca, Municipio Tehuantepec, Orilla de la Presa Benito Juárez: ♀1 (AMNH[LP 2235]), collected by R. Paredes, 10/viii/2002. Mexico, Oaxaca, Bahia de Huatulco: sex indeterminant 1(AMNH[LP 8580]), collected by IBUNAM, /x/2007.

***Centruroides nigrovariatus* (Pocock, 1898):** Mexico, Oaxaca, Municipio de Etla, 7 km N San Gabriel: ♂2, ♀3 (AMNH[LP 2033]), collected by O. Francke, E. Gonzalez and J. Ponce, 22/vii/2002, SW facing slopes with oaks, 2125 m. Mexico, Oaxaca, Municipio de Etla, 3 km N San Gabriel: ♂3, ♀5 , sex indeterminant 3(AMNH[LP 2066]), collected by E. Gonzalez, O. Francke and J. Ponce, 22/vii/2002, 1900 m; under stones. Mexico, Oaxaca, San Sebastián de las Grutas, Paradero hacia las grutas de San Sebastian de las Grutas: ♂1 (AMNH[LP 6424]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 29/vi/2006, 16.63031°N 96.9691°W, 1625 m. Mexico, Oaxaca, Magdalena Mixtepec, Magdalena Mixtepec: ♂1, subadult ♀ 1 (AMNH[LP 6436]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 19/vi/2006, 16.8804°N 96.85093°W, 1710 m. Mexico, Oaxaca, San Sebastián de las Grutas, San Sebastian de las Grutas: sex indeterminant 2(AMNH[LP 6440]), collected by O. Francke, A. Valdez & H. Montaño, 4/xii/2005, 16°38.061N 96°58.425W, 1874 m. Mexico, Oaxaca, Oaxaca, Campus I.T.U.O: sex indeterminant 1(AMNH[LP 6626]), collected by O. Francke, A. Valdez & H. Montaño, 4/xii/2005, 16.75°N 96.66°W, 1550 m. Mexico, Oaxaca, Municipio Mixes, 7 km terciese San Juan Juquile, Mixes-Acatlancito: sex indeterminant 1 juv.(AMNH[LP 7668]), collected by O. Francke, A. Ballesteros, H. Montano, C. Santibanez & A. Valdez, 18/vii/2007, 16°54.595'N 95°55.711'W, 1388 m. Mexico, Oaxaca, Ixtepeji, El Punto, 8.4 km N: ♀ 1 (AMNH[LP 9519]), collected by O.F. Francke, A. Quijano & C. Santibañez, 4/vii/2008, 17.26765°N 96.58792°W, 2115 m.

***Centruroides nitidus nitidus* (Thorell, 1876):** Dominican Republic, Monte Cristi Prov., Parque Nacional Monte Cristi, hillside behind Ranger Station: ♀4 (AMNH[LP 5113]),

collected by L. Esposito, 3/viii/2005, 19.89294°N071.65692°W, 104 m, drought-deciduous shrubland with succulents, leaf litter and bark, UV detection, 33°C. Dominican Republic, Monte Cristi Prov., Monte Cristi, National Park Property: ♂2, ♀1 , sex indeterminant 8 juv.(AMNH[LP 5117]), collected by L. Esposito, 4/viii/2005, 19.84955°N071.63910°W, 100 m, mixed dry shrubland with succulents, UV detection. Dominican Republic, Pedernales Provence, Oviedo, W, roadside near rubbish dump: ♀2 (AMNH[LP 3312]), collected by E.S. Volschenk & J. Huff, 6/vii/2004, 17.8131°N71.4186°W, 42 m, Spiny scrub with limestone boulders; hand collected from under rocks and logs. Dominican Republic, Pedernales Provence, Parque Nacional Jaragua, unmarked track into Park between Manuell Goa and Oviedo: ♂1, ♀1 , sex indeterminant 1 juv.(AMNH[LP 3313]), collected by E.S. Volschenk & J. Huff, 9/vii/2004, 17.8117°N71.4433°W, 83.3 m, Deciduous forest and thorny scrub; hand collected from under stones and logs and with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Sierra de Baoruco, from Cabo Rojo: ♂1 (AMNH[LP 3316]), collected by E.S. Volschenk & J. Huff, 10/vii/2004, 18.0900°N71.5108°W, 1271 m, Pine forest and dense lower storey; hand collected from under stones of visitors car park and along walking tracks, and with blacklights. Dominican Republic, Pedernales Provence, Floodplain beside road, between Pedernales and Oviedo : ♂1 (AMNH[LP 3318]), collected by E.S. Volschenk & J. Huff, 6/vii/2004, 18.0017°N71.6820°W, 12.9 m, Dry floodplain with cactus, grass tussocks and sparse trees; hand collected with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Jaragua, Cabo Rojo: ♂2 (AMNH[LP 3314]), collected by E.S. Volschenk & J. Huff, 9/vii/2004, 17.9197°N71.6558°W, 10.2 m, Beach with trees and sparse low grass understorey, collected with blacklights. Dominican Republic, Pedernales Provence, Parque Nacional Jaragua, along road between Manuel Golla and Cabo Rojo turn-off: ♂2 (AMNH[LP 3315]), collected by E.S. Volschenk & J. Huff, 9/vii/2004, 17.8892°N71.4989°W, 152 m, old agave plantation on roadside; collected with blacklights. Dominican Republic, W of Oviedo on Hwy 44: ♂1, ♀1 (AMNH[LP 3310]), collected by J. Huff, 12/i/2004, 17°48.771'N71°25.089'W, 195 ft, garbage dump, rock pile, under bark on trees. Dominican Republic, Parque Nacional Jaragua, road to Fondo Paradi, 1.8 km from Highway 44: ♂2, ♀1 (AMNH[LP 3309]), collected by J. Huff, 12/i/2004, 17°48.692'N71°26.600'W, 302 ft, under rocks, bark.

***Centruroides nitidus taino* Armas & Marcano Fondeur, 1987:** Dominican Republic, La Vega Province, Road from Costanza to Reserva Científica Valle Nuevo: sex indeterminant 5 juv.(AMNH[LP 3305]), collected by E.S. Volschenk & J. Huff, 12/vii/2004, 18.8167°N70.6853°W, 2267 m, Hand collected from under stones and logs, and with blacklights. Dominican Republic, La Vega Province, Road from Costanza to Reserva Científica Valle Nuevo: ♀1 , sex indeterminant 20 juv.(AMNH[LP 3306]), collected by E.S. Volschenk & J. Huff, 23/vii/2004, 18.7772°N70.6447°W, 2334 m, Pine forest; hand collected from under bark of pine logs. Dominican Republic, Reserva Cientifica Valle Nuevo, Cordillera Central: ♀2 (AMNH[LP 2475]), collected by J. Huff, 10/i/2004, 18°42.259'N70°36.115'W, 7849 ft, under rocks and bricks around abandoned building in pine forest. Dominican Republic, Reserva Cientifica Valle Nuevo, Cordillera Central: ♂1 (AMNH[LP 2473]), collected by J. Huff, 10/i/2004, 18°42.259'N70°36.115'W, 7849 ft, under rocks and bricks around abandoned building in pine forest. Dominican Republic, Reserva Cientifica Valle Nuevo, Cordillera Central:

♂3, ♀3 , sex indeterminant 7 juv.(AMNH[LP 3304]), collected by J. Huff, 10/i/2004, 18°47.131'N70°39.033'W, 7586 ft, under pine bark on dead Pinus occidentalis. Dominican Republic, Reserva Cientifica Valle Nuevo, Cordillera Central: ♀1 (AMNH[LP 3377]), collected by J. Huff, 10/i/2004, 18°42.259'N70°36.115'W, 7849 ft, under rocks and bricks around abandoned building in pine forest.

***Centruroides noxius*** **Hoffman, 1932:** Mexico, Nayarit, Pantanal: ♀2 (AMNH[LP 2071]), collected by , /vii/2002. Mexico, Nayarit, Municipio Huajicori, Huajicori ca. 20 km NE, on gravel road to San Andres Milpillas, SITE 55: ♂1 , sex indeterminant 1(AMNH[LP 4710]), collected by R. Mercurio & E. González , 30/vii/2005, 22°41.647′N 105°12.208′W, 1070 m, UV detection at night. Mexico, Nayarit, Municipio Compostela, Compostela, ca. 11 km S, on gravel road between Felipe Carrillo Puerto and Zapotán: ♂1, subadult ♀ 1 (AMNH[LP 4720]), collected by R. Mercurio & E. González , 1/viii/2005, 21°07.233′N , 104°50.772′W, 834 m, UV detection at night. Mexico, Nayarit, Municipio Compostela, south of Compostela: ♀1 (AMNH[LP 8668]), collected by R.C. West, 1/vii/2008, 21°12'59.78"N 104°56'19.09"W, 3205 ft., under dry cow manure in pasture.

***Centruroides ochraceus*** **(Pocock, 1898):** Mexico, Quintana Roo, Puerto Morelos, Jardin Botanico 'Alfredo Barrera': ♂1 (AMNH[LP 7666]), collected by G. Montiel-Parra, R. Paredes, M. Ramirez, D. Chibras & G. Bonilla, 4/vii/2007, 20.84504°N86.90357°W, 38 m. Mexico, Quintana Roo, Puerto Morelos, Botanical Gardens: subadult ♀ 1 (AMNH[LP 8579]), collected by G. Montiel & R. Paredes, 4/viii/2007, 20.84504°N86.90357°W, 38 m.

***Centruroides ornatus*** **Pocock, 1902:** Mexico, Nayarit, Municipio Santa María del Oro, Santa María del Oro, 8 km NE, near La Laguna, on road to El Buruato, SITE 51: ♂1, ♀1 (AMNH[LP 4712]), collected by E. González & R. Mercurio, 28/vii/2005, 21°23.090′N 104°32.507′W, 564 m, rock rolling by day. México, Jalisco, Highway Los Volcanes-Aquila, 37 km: ♀1 , sex indeterminant 1(AMNH[LP 5245]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 9/vii/2005, 20°15.241'N 104°28.834'W, 1886 m. México, Jalisco, Puerta de Barro, 2 km N, La Grulla: sex indeterminant 1(AMNH[LP 5246]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 9/vii/2005, 19°51.509'N 104°13.420'W, 1059 m. México, Jalisco, Mascota, 32 km E: ♂1, ♀1 (AMNH[LP 5257]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 9/vii/2005, 20°24.177'N 104°38.202'W, 1710 m. México, Nayarit, Municipio del Nayar, Tepic, ca. 30 km NE, near El Vicentiño, SITE 52: sex indeterminant 1(AMNH[LP 4716]), collected by R. Mercurio & E. González , 28/vii/2005, 21°46.744′N 104°52.235′W, 152 m, rock rolling by day. México, Zacatecas, Jalpa, 5 km SW: ♂3, ♀2 (AMNH[LP 5221]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 7/vii/2005, 21°38.569'N 103°03.425'W, 1564 m.

***Centruroides platnicki*** **Armas, 1981:** Turks and Caicos, Caicos, Providenciales, Malcolm’s Road: 12 km NW lighthouse: sex indeterminant 1 juv.(AMNH[LP 9051]), collected by L. Esposito, D. Schiff & D. Jones, 3/viii/2008, 21.823°N72.296°W, desert scrub on limestone with no soil, UV detection. Turks and Caicos, Caicos, Providenciales, Malcolm’s Road: 12 km NW lighthouse: subadult ♀ 1 (AMNH[LP 9053]), collected by L. Esposito, D. Schiff & D. Jones, 4/viii/2008, 21.823°N72.296°W, desert scrub on

limestone with no soil, UV detection. Dominican Republic, Monte Cristi Prov., Monte Cristi, 8 km E: ♀1 , sex indeterminant 3 juv.(AMNH[LP 5124]), collected by L. Esposito, 3/viii/2005, 19.81941°N071.59999°W, 102 m, mixed dry shrubland with succulents, rocky, sandy substrate, UV detection, 33°C. Dominican Republic, Santiago Prov., Parque Nacional Armando Bermudez, behind Ranger Station: sex indeterminant 1 juv.(AMNH[LP 5147]), collected by L. Esposito, 7/viii/2005, 19.06721°N070.86301°W, 1087 m, dry forest, under bark, 30°C.

***Centruroides pococki* Sissom & Francke, 1983:** St. Kitts and Nevis, St. Kitts, St. Kitts: Southeast Peninsula: Half Moon Bay: juvenile ♀ 1 (AMNH[LP 9040]), collected by L. Esposito & D. Schiff, 3/vii/2008, 17.273°N62.600°W, dry thorn scrub with volcanic boulders, UV detectionectection.

***Centruroides rileyi* Sissom, 1995:** Mexico, San Luis Potosi, Axtlan de Terrazas, Axtlan de Terrazas: ♂1 (AMNH[LP 6445]), collected by O. Francke, A. Valdez, G. Villegas & R. Paredes, 28/iv/2006, 21.42601°N 98.87821°W, 100 m. Mexico, Veracruz, Camino a Cañada Blanca: ♂1 (AMNH[LP 2073]), collected by J. Ponce, 18/vii/2002, 18°55.707'N 96°51.434'W, coffee plantation in lowland rainforest; collected at night with UV light.

***Centruroides robertoi* Armas, 1976:** Cuba, Oriente, Baracoa, Punta Maisi: 1 paratype ♀ AMNH, collected by C. Fundora, 6/x/1976.

***Centruroides sasae* Santiago-Blay, 2009:** U.S.A, Puerto Rico, Isla Caja de Muertos, along road from Carrucho Point to Visitor's Center to El Faro 1887: ♂1 (AMNH[LP 10239]), collected by L. Esposito & H. Yamaguti, 23/x/2009, 17.89999°N to 17.88630°N66.51748°W to 66.52740°W, Tropical dry forest and dry scrub dominated by thorn trees and cactus. Blacklighting and under stones. U.S.A, Puerto Rico, Isla Caja de Muertos, along road from Carrucho Point to Visitor's Center to El Faro 1887: sex indeterminant 2 juv.(AMNH[LP 10242]), collected by L. Esposito & H. Yamaguti, 23/x/2009, 17.89999°N to 17.88630°N66.51748°W to 66.52740°W, Tropical dry forest and dry scrub dominated by thorn trees and cactus. Blacklighting and under stones.

***Centruroides schmidti* Sissom, 1995:** Guatemala, Zacapa, Aldea Casas de Pinto, near turnoff for Zacapa at Rio Hondo: sex indeterminant 1(AMNH[LP 5985]), collected by J. Huff, C. Viquez & D. Ortiz, 13/vii/2006, N 15°01’37.1” W 89°36’57.2” , 77 m, Semi-arid region with scrub forest and cacti. Collected under rocks in shaded areas and at night using UV. Honduras, Departamento de Francisco Morazán, Municipio de San Antonio de Oriente, E.A.P. Zamorano, Monte Redondo, Acuacultura: sex indeterminant 8 juv.(AMNH[LP 9172]), collected by C. Viquez, 23/ix/2008, 13.99988°N86.98917°W, 773 m, night UV.

***Centruroides sculpturatus* (Ewing, 1928):** Mexico, Chihuahua, Municipio Temosachi, Highway Mex16 km 333 between Maytona (Sonora) and Cahuisori (Chihuahua): ♀2 (AMNH[LP 6312]), collected by E. Gonzalez & P. Berea, 25/vi/2006, N 28° 27. 324’W 108°25.830’, 1927 m, rolling rocks during day. Mexico, Sonora, Pelican Point, Puerto Peñasco: ♀1 (AMNH[LP 2169]), collected by M. Nishiguchi *et al.*, 9/x/2002, ~9:30 pm, UV lighting, on wall of house. Mexico, Sonora, Municipio Soyopa, Plutarco Elias Calles Damp, Ejido el Novillo: ♂1 , sex indeterminant 2(AMNH[LP 6299]), collected by P. Berea & E. Gonzalez, 22/vi/2006, N 28° 58. 827’W 109°30.160’, 258 m, rolling rocks during day. Mexico, Sonora, Municipio Soyopa, Sierra el Encinal, 9 km from crossroad in highway Mex16 to El Encinal: subadult ♀ 1 (AMNH[LP 6311]), collected by E.

Gonzalez & P. Berea, 24/vi/2006, N 28° 35. 412’W 109°27.148’, 380 m, UV detection at night. Road cut wall, near by creek with tropical vegetation. Lots of flying insects. Mexico, Sonora, Municipio Hermosillo, Bay New Kino, 5 km: ♂1 (AMNH[LP 6320]), collected by P. Berea & E. Gonzalez, 28/vi/2006, N 28° 53. 415’W 112°02.010’, 30 m, UV detection at night. Mexico, Sonora, Municipio Guaymas, Microwave antenna at Guaymas: subadult ♀ 1 (AMNH[LP 6325]), collected by P. Berea & E. Gonzalez, 29/vi/2006, N 27° 56. 624’W 110°54.103’, 389 m, UV detection at night. Mexico, Sonora, Municipio Hermosillo, Bay New Kino, 16 km NW dirty road: juvenile ♀ 1 (AMNH[LP 6330]), collected by E. Gonzalez, 2/vii/2006, N 28° 55. 249’W 112°02.572’, 116 m, UV detection at night. Mexico, Sonora, Municipio de Navojoa, Microwaves Cerro Prieto, ca. 15 km E of Navojoa, Site 3: ♂2 (AMNH[LP 9972]), collected by E. González & J. L. Castelo, 23/ix/2009, 27.08228°N 109.29058°W, 375 m, UV detection at night, volcanic outcrop with deciduous tropical forest. Mexico, Sonora, Municipio de Navojoa, Microwaves Cerro Masiaca, ca. 35 km SW of Navojoa, Site 1: ♂1, ♀1 (AMNH[LP 9976]), collected by E. González & J. L. Castelo, 21/ix/2009, 26°46´30.32´´N 109°17´59.17´´W, 193 m, UV detection at night, volcanic outcrop, thorny forest. U.S.A., Arizona, Chandler: ♀1 (AMNH[LP 10078]), collected by A. Hicks, /viii/2009, 33.30030N 111.79005W. U.S.A., Arizona, Yavapai County, Bradshaw Mountains: Black Canyon, Horsethief Basin Recreation Area, Black Canyon Creek, Exit 248 off I17 near Bumble Bee, 4.3 mi W I17: ♀1 (AMNH[LP 5859]), collected by R. Mercurio, W. Savary & ATS group, 16/vi/2006, 34°11.526'N 112°09.740'W, 758 m, UV light detection at night. U.S.A., Arizona, Santa Cruz County, Coronado National Forest: Santa Rita Mountains, Gardner Canyon, Gardner Canyon Road: sex indeterminant 1 juv.(AMNH[LP 5860]), collected by R. Mercurio & W. Savary, 19/vi/2006, 31°42.663'N 110°47.837'W, 1718 m, UV light detection at night. U.S.A., Arizona, Pima County, Vail, 15400 E Collassal Cave Road, dry rocky wash: sex indeterminant 1 juv.(AMNH[LP 5861]), collected by J. Cowles, B. Savary, W. Savary & R. Mercurio, 20/vi/2006, 32°02.180'N 110°39.914'W, 1007 m, UV light detection at night. U.S.A., Arizona, Pima County, Coronado National Forest: Santa Catalina Mountains, Catalina highway, Windy Point Vista, granitic rocky road cut slopes: sex indeterminant 1 juv.(AMNH[LP 5862]), collected by R. Mercurio & W. Savary, 22/vi/2006, 32°22.122'N 110°42.996'W, 2011 m, UV light detection at night. U.S.A., Arizona, Cochise County, Coronado National Forest: Dragoon Mountains, Middle March Canyon, Middle March Canyon Road, 2.1 mi from turnoff to Pearce towards China Peak, rocky road cut slopes: sex indeterminant 3 juv.(AMNH[LP 5863]), collected by R. Mercurio & W. Savary, 23/vi/2006, 31°53.611'N 109°58.769'W, 1976 m, UV light detection at night. U.S.A., Arizona, Maricopa County, Sunflower, turnoff to Bushnell Tanks: juvenile ♂ 1 (AMNH[LP 7160]), collected by L. Prendini & J. Huff, 6/ix/2007, 33°52'08.8"N 111°27'54.4"W, 1057 m, Sonora desert, oak scrub/chaparral transition in foothills of Mazatzal Mountains, low rocky ridge along dry wash. U.S.A., Arizona, Santa Cruz County, Atascosa Mountains: ♂2 (AMNH[LP 7183]), collected by M. Rubio, 14/ix/2007, 31°24.574'N 111°09.435'W, 4780 ft, UV detection at night. U.S.A., Arizona, Gila County, Tonto National Forest: El Oso Road, Mazatzal Mountains: subadult ♀ 1 (AMNH[LP 7185]), collected by L. Prendini & J. Huff, 6/ix/2007, 33°44'29.0"N 111°21'29.9"W, 1785 m, pine-oak scrub on coarse, granitic sandy loam. U.S.A., Arizona, Pima County, Vail, 2.83 mi ESE, on heading of 106°, property of W.P. Savary & J. Cowles: ♂1 (AMNH[LP 4378]), collected by W.E. Savary

*et al.*, 1/viii/1996, 32°02'12.7"N 110°39'52.2"W, 3300 ft. U.S.A., New Mexico, Hidalgo County, Geronimo Pass, Peloncillo Mountains, Coronado National Forest: (AMNH[LP 2133]), collected by L. Prendini, L. Esposito and Y. Rodriguez, 13/ix/2002, 31°30.885'N 109°01.510'W, 5757 ft, Oak-pine scrub on rocky hills; collected at night with UV; sympatric with D. peloncillensis, V. spinigerus. U.S.A., New Mexico, Hidalgo County, Geronimo Pass, Peloncillo Mountains, Coronado National Forest: sex indeterminant 2(AMNH[LP 2141B]), collected by L. Prendini, L. Esposito and Y. Rodriguez, 13/ix/2002, 31°30.885'N 109°01.510'W, 5757 ft, Oak-pine scrub on rocky hills; collected at night with UV; sympatric with D. peloncillensis, V. spinigerus. U.S.A., New Mexico, Hidalgo County, Geronimo Pass, Peloncillo Mountains, Coronado National Forest: (AMNH[LP 2142A]), collected by L. Prendini, L. Esposito and Y. Rodriguez, 13/ix/2002, 31°30.885'N 109°01.510'W, 5757 ft, Oak-pine scrub on rocky hills; collected at night with UV; sympatric with D. peloncillensis, V. spinigerus. U.S.A., New Mexico, Hidalgo County, Granite Gap Ghost Town, 11.5 mi S Road Forks: sex indeterminant 1(AMNH[LP 2147]), collected by L. Prendini, L. Esposito and Y. Rodriguez, 13/ix/2002, 32°04.974'N 108°58.962'W, Chihauhaun desert scrub, rocky granite slopes with barrel cacti, Cholla and Ocoteo; under stone. U.S.A., New Mexico, Sierra County, Caballo Lake State Park: ♀1 (AMNH[LP 9734]), collected by J. Huff, 30/iv/2009, 32°54'25.54"N 107°18'41.5"W, 1288 m. U.S.A., New Mexico, Hidalgo County, Granite gap, 9 miles south of I-10 along NM State Rt 80: ♀ 1 (AMNH[LP 3010]), collected by S.J. Burchfield, /iv/2004. U.S.A., New Mexico, Hidalgo County, Granite gap, 9 miles south of I-10 along NM State Rt 80: ♂1 (AMNH[LP 3011]), collected by S.J. Burchfield, /iv/2004. U.S.A., New Mexico, Hidalgo County, Granite Gap on hwy 80, N of Rodeo: ♂1, ♀ , sex indeterminant 2(AMNH[LP 7024]), collected by J. Huff, 22/vii/2007, N 32°05’34.2”W 108°58’12.1” , 1367 m, UV detection on and around rock outcrops. U.S.A., New Mexico, Hidalgo County, Granite Gap, Peloncillo Mountains: sex indeterminant 2 juv.(AMNH[LP 7099]), collected by L. Prendini & J. Huff, 4/ix/2007, 32°05'43.1"N 108°58'13.7"W, 1367 m, Sonora desert with coarse granitic sandy loam and large granite outcrops.

***Centruroides serrano*** **Santibanez-Lopez & Ponce-Saavedra, 2009:** Mexico, Oaxaca, Municipio Villa Alta, San Andres Zoolaga, 6 km S: ♂1 (AMNH[LP 7603]), collected by O. Francke, H. Montano, A. Valdez, C. Santibanez & A. Ballesteros, 21/vii/2007, 17°15.472'N 96°14.393'W, 1119 m. Mexico, Oaxaca, Municipio Villa Alta, San Andres Zoolaga, 6 km S: ♀1 (AMNH[LP 9522]), collected by O.F. Francke *et al.*, /vii/2007, 17°15.472'N 96°14.393'W.

***Centruroides sissomi*** **Armas, 1996:** Mexico, Quintana Roo, Puerto Morelos, Jardin Botanico 'Alfredo Barrera': ♂1 (AMNH[LP 7597]), collected by G. Montiel-Parra, R. Paredes, M. Ramirez, D. Chibras & G. Bonilla, 4/vii/2007, 20.84504°N86.90357°W, 38 m. Mexico, Guerrero, Copala, Microwaves Fogos: ♂1 (AMNH[LP 7032]), collected by Francke *et al.*, 22/vi/2007, 16° 33.992'N 98°53.301 W, 103 m.

***Centruroides suffusus*** **(Pocock, 1902):** Mexico, Oaxaca, San Pedro Juchatengo, 3 km W San Pedro Juchatengo: sex indeterminant 2(AMNH[LP 6476]), collected by , 27/vi/2006, 845 m.

***Centruroides chiapanensis tapachualaensis*** **Hoffmann, 1932:** Mexico, Oaxaca, San Sebastián de las Grutas, Paradero hacia las grutas de San Sebastian de las Grutas: ♀1

(AMNH[LP 6573]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 29/vi/2006, 16.63031°N 96.9691°W, 1625 m. Mexico, Colima, Municipio Coquimatlan, Los Ameales: sex indeterminant 1 juv.(AMNH[LP 7669]), collected by O. Francke *et al.*, 28/viii/2007, 19°00.962'N 103°50.015'W, 296 m.

***Centruroides tecomanus* Hoffmann, 1932:** Mexico, Jalisco, Municipio Talpa de Allende, El Tuito, ca. 24 km along gravel road to Talpa de Allende, SITE 61: sex indeterminant 2(AMNH[LP 4713]), collected by R. Mercurio & E. González , 2/viii/2005, 20°21.674′N 105°08.017′W, 1863 m, rock rolling by day. Mexico, Jalisco, Municipio La Huerta, Estacion de Biologia Chamela, Cutzmala, Instituto de Biologia, UNAM: ♂1 (AMNH[LP 7677]), collected by O. Francke *et al.*, 30/viii/2007, 19°29.875'N 105°02.608'W, 97 m. Mexico, Michoacan, Municipio de Aquila, Faro de Bucerias: ♂1 (AMNH[LP 2006]), collected by M.A. Villaseñor R., 15/i/2002, Selva baja caducifolia. Mexico, Michoacan, Municipio de Aquila, Faro de Bucerias: ♀1 (AMNH[LP 2007]), collected by M.A. Villaseñor R., 16/i/2002, Selva baja caducifolia. México, Jalisco, Estación de Biología Chamela, Chachalacas Trail : ♂1 (AMNH[LP 5218]), collected by J. L. Castelo & L. Gutierrez, 17/viii/2005, 19°29.620'N 105°02.799'W. México, Jalisco, Estación de Biología Chamela, el Tejon Trail: sex indeterminant 2(AMNH[LP 5254]), collected by J. L. Castelo, 18/viii/2005, 19°29.836'N 105°02.491'W.

***Centruroides testaceus arubensis* (Bakker, 1963):** Dutch Antilles, Aruba, Arikok National Park: Trail to Jamanota: ♂ 5, ♀ 5 (AMNH[LP 9045]), collected by L. Esposito & D. Schiff, 24/vii/2008, 12.493°N69.934°W, desert scrub dominated by organ pipe cactus and acacia, UV detection. Dutch Antilles, Aruba, Hill behind Baby Beach: ♀ 1 (AMNH[LP 9059]), collected by L. Esposito & D. Schiff, 24/vii/2008, 12.423°N69.887°W, rocky hill with no vegetation, under stones.

***Centruroides testaceus testaceus* (DeGeer, 1778):** Dutch Antilles, Bonaire, Dos Pos: Trail behind Windmill: ♂ 5, ♀ 5 subadult ♀ 1 (AMNH[LP 9039]), collected by L. Esposito & D. Schiff, 27/vii/2008, 12.239°N 68.356°W, dry tropical forest, under stones. Tolo: Southern Coastal Highway inland from Dive Site 9, Karpata: ♀1 (AMNH[LP 9058]), collected by L. Esposito & D. Schiff, 26/vii/2008, 12.211°N68.325°W, desert scrub, under pipelines, UV detection. Hato: Southern Coastal Highway inland from Dive Site 25, Petrie's Pillar: subadult ♀ 1 (AMNH[LP 9067]), collected by L. Esposito & D. Schiff, 26/vii/2008, 12.204°N68.307°W, arid thorn forest, UV detection. Washikemba: near salt lagoon and mangroves,: ♂1 (AMNH[LP 9068]), collected by L. Esposito & D. Schiff, 27/vii/2008, 12.116°N68.241°W, dry tropical forest, UV detection. Curacao, Hook's Restaurant Marina near the Carmabi Foundation: ♀1 (AMNH[LP 9044]), collected by L. Esposito & D. Schiff, 20/vii/2008, 12.122°N68.969°W, desert scrub, UV detection. Rei Rinken Park: ♀1 (AMNH[LP 9064]), collected by L. Esposito & D. Schiff, 21/vii/2008, 12.183°N60.965°W, manchineel forest, UV detection.

***Centruroides thorellii* (Kraepelin, 1891):** Guatemala, Sacatepéquez, Parque Senderos de Alux, 15-20 km west of Guatemala City: ♂10, ♀20 , sex indeterminant 4(AMNH[LP 5983]), collected by J. Huff, C. Viquez, E. Agreda & D. Ortiz, 30/vi/2006, N 14°36'39.2" W 90°38'21.1" , 2256 m, Pine dominated forest, collected at night using UV and during the day under bark.

***Centruroides tuxtla* Armas, 1999:** Mexico, Chiapas, "La vuelta del alacran" 4.8 km from km 27 on road from Ocozocuautla to Villa Flores: ♂1, ♀1 (AMNH[LP 3709]), collected by R. Paredes, O. Francke and G. Villegas, /x/2004, 16°32'35.2"N 93°129'09.8"W, 781 m, UV light detection at night. Mexico, Chiapas, Altamira Ranch, Ocozocuatla, ~7 km N: ♀1 , sex indeterminant 2(AMNH[LP 3710]), collected by G. Villegas, O. Francke and R. Paredes , 4/xi/2004, 16°48'41.2"N 93°24'2.5"W, 925 m, rock rolling. México, Chiapas, Municipio Villaflores, Ejido California, 1 km SE, Reserva de La Biosfera La Sepultura: ♂1 (AMNH[LP 5217]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 31/viii/2005, 16°15.786'N 93°36.513'W, 971 m. México, Chiapas, Municipio Arriaga, Arriaga, 4 km NE: ♂1 (AMNH[LP 5250]), collected by O. Francke, M. Córdova, A. Jaimes & H. Montaño, 1/ix/2005, 16°15.69'N 93°51.96'W, 163 m. México, Chiapas, Municipio Villaflores, Ejido California, 1 km SE, Reserva de La Biosfera La Sepultura: ♀1 (AMNH[LP 5251]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 30/viii/2005, 16°15.237'N 93°35.774'W, 1132 m.

***Centruroides vittatus* (Say, 1821):** Mexico, Coahuila, General Cepéda, 14 km S El Nogal, Sierra de la Concordia: sex indeterminant 2(AMNH[LP 6432]), collected by W.D. Sissom & B. Hendrixson, 22/vii/2006, 25°14.426N 101°25.826W, 1915 m. Mexico, Coahuila, General Cepéda, 19 km S El Nogal, Sierra de la Concordia: sex indeterminant 1(AMNH[LP 6509]), collected by E. González & M. Cordova, 22/vii/2006, 25.21792°N 101.43623°W, 2078 m. Mexico, Coahuila, General Cepéda, 2 km S El Nogal, Sierra de la Concordia: sex indeterminant 1(AMNH[LP 6560]), collected by O. Francke, S. Grant & A. Ballesteros, 22/vii/2006, 25°16.788N 101°25.775W, 1730 m. Mexico, Coahuila, Cuatrocienegas, Dunas de Yeso Cuatrociénegas: subadult ♀ 1 (AMNH[LP 6627]), collected by O. Francke, W.D. Sissom, M. Córdova, A. Jaimes & A. Ballesteros, 18/vii/2006, 26°51.765'N 102°10.476'W, 776 m. Mexico, Tamaulipas, Jaumave, 26 km N Jaumave: sex indeterminant 1(AMNH[LP 6543]), collected by O. Francke, W.D. Sissom, G. Casper, T. Anton, V. Totti, H. Montaño, C. Santibañez & A. Ballesteros, 24/viii/2006, 23°36.996'N 99°17.288'W, 956 m. U.S.A., Texas, : ♀1 (AMNH[LP 1741]), collected by , 16/v/2000. U.S.A., Texas, Culberson County, Indio Research Station, near Van Horn: ♂1, ♀4 (AMNH[LP 2140B]), collected by L. Esposito, /ix/2002, collected at night with UV light. México, Durángo, Higway 137, between Once de Marzo and San Juan del Río, San Francisco de Lajas, 4 km: ♂1, ♀1 , sex indeterminant 2(AMNH[LP 5220]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 10/viii/2005, 24°51.764´N 104°38.846´W, 1893 m, Rock rolling by day. México, Durángo, La Mina, Highway 137, between Panuco de Colorado and San Jose de Avino: sex indeterminant 4(AMNH[LP 5238]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 9/viii/2005, 24°31.809'N 104°18.941'W, 2217 m, UV detection at night . México, Durángo, Highway 36, 9 km between crossroad San Andres Atotonilco and La Laguna de la Chaparra: sex indeterminant 4(AMNH[LP 5263]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 11/viii/2005, 25°05.306'N 105°31.530'W, 2095 m, Rock rolling by day. México, Durángo, Peñon Blanco, 8 km N: ♂1 (AMNH[LP 5264]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 11/viii/2005, 24°51.148'N 104°01.989'W, 1667 m, UV detection at night . Mexico, Coahuila, Parras, Sierra Parras ca. 8 km S Parras: ♀1 (AMNH[LP 6422]), collected by B.

Hendrixson, K. Mc West, E. González & S. Grant, 21/vii/2006, 25°22.974N 102°11.145W, 1922 m. Mexico, Coahuila, Sierra Mojada, Sierra Mojada I: sex indeterminant 1(AMNH[LP 6501]), collected by W.D. Sissom, E. González & B. Hendrixson , 20/vii/2006, 27°19.188'N 103°43.135'W, 1605 m. México, Chihuahua, Highway Guachochi-Balleza, 55 km: sex indeterminant 1(AMNH[LP 5227]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 4/viii/2005, 26°57.757'N 106°25.401'W, 1657 m, Rock rolling by day. México, Chihuahua, Coyame grutas: sex indeterminant 1(AMNH[LP 5230]), collected by W.D. Sissom, K. McWest, C. Lee & L. Jarvis , 30/vii/2005, 29°25.714'N 105°07.284'W, 1293 m, Large rocks, Creosote, Mariola, Lechuguilla, Opuntia, Thelosperma. México, Chihuahua, Sierra del Nido, on the way to Las Varas: ♀1 , sex indeterminant 3(AMNH[LP 5242]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee & J. Ballesteros , 30/vii/2005, 29°21.415'N 106°29.666'W, 1710 m, UV detection at night . México, Chihuahua, On the way to Namiquimipa: sex indeterminant 1(AMNH[LP 5244]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Duran, 31/vii/2005, 29°04.145'N 106°33.011'W, 2268 m, Rock rolling by day. México, Chihuahua, Highway Guasache-El Parral, 90 km, crossroad Guasarache: ♀1 , sex indeterminant 2(AMNH[LP 5247]), collected by W.D. Sissom, K. McWest, C. Lee & C. Durán-Barrón , 3/viii/2005, 26°57.312'N 106°41.199'W, 2356 m, UV detection at night . México, Chihuahua, Highway Belleza-Hidalgo del Parral, 12 km: sex indeterminant 1(AMNH[LP 5354]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 4/viii/2005, 25°51.197'N 106°06.756'W, 2202 m, Rock rolling by day. México, Durángo, Dinamita: ♂1, ♀1 (AMNH[LP 5259]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 29/vii/2005, 25°44.089'N 103°40.401'W, 1328 m, UV detection at night . México, Durángo, Municipio Tlahualilo, Highway 49, at deviation Montes Claros-Tlahualilo de Zaragoza: ♂1 , sex indeterminant 2(AMNH[LP 5351]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 6/viii/2005, 26°09.242'N 103°31.284'W, 1107 m, UV detection at night . U.S.A., Texas, Hudspeth County, Indio Ranch: (AMNH[LP 2199]), collected by L. Esposito, /xi/2002, 30°16'36"N 105°00'58"W, collected at night with UV light. U.S.A., Texas, Brewster County, Big Bend National Park: Castolon: ♀2 (AMNH[LP 8925]), collected by W.D. Sissom , 1/viii/2008, on house and on grounds of compound. Mexico, Coahuila, San Buenaventura, Rancho las Esparzas: ♀1 (AMNH[LP 6382]), collected by C. Savvas, 24/i/2006, 90°N 99°W. Mexico, Coahuila, General Cepéda, 5 km S El Nogal, Sierra de la Concordia: sex indeterminant 2(AMNH[LP 6550]), collected by O. Francke, S. Grant & A. Ballesteros, 22/vii/2006, 25°16.250N 101°25.634W, 1804 m. Mexico, Coahuila, Cuatrocienegas, Ojo de Agua, Ejido El Oso: ♀1 (AMNH[LP 6574]), collected by O. Francke, W.D. Sissom, K. McWest, B. Hendrixson, S. Grant, A. Jaimes M. Córdova, E. González & A. Ballesteros, 19/vii/2006, 27.05599°N 102.22636°W, 1039 m. Mexico, Nuevo León, Santa Catarina, Cañon de la Huasteca: subadult ♀ 1 (AMNH[LP 6475]), collected by O. Francke, W.D. Sissom, K. McWest, B. Hendrixson, S. Grant, A. Jaimes, M. Cordova, E. González & A. Ballesteros, 24/vii/2006, 25.61456°N 100.47551°W, 780 m. Mexico, Nuevo León, Linares, W de Santa María ca. 77 km W de Linares m x 58: ♀1 (AMNH[LP 6556]), collected by K. McWest, B. Hendrixson & S. Grant, 25/vii/2006,

24°41.614'N 100°05.490'W, 1896 m. Mexico, Tamaulipas, 8 km SE Jaumave: ♀1 (AMNH[LP 2063]), collected by E. Gonzalez Santillan, 27/vii/2002, 23°21.977'N 99°27.366'W, 975 m; foothills of Sierra Madre Oriental; arid, rocky (limestone) W-facing slope with cacti and cycads; under stone. U.S.A., Illinois, Monroe County, : ♀1 (AMNH[LP 1721]), collected by T. Anton, 3/viii/1998. U.S.A., Illinois, Monroe County, : ♀1 (AMNH[LP 1722]), collected by T. Anton, 3/viii/1998. U.S.A., New Mexico, Las Cruces: ♀1 (AMNH[LP 2324]), collected by M.K. Nishiguchi, /vi/2000. U.S.A., New Mexico, Queen, Lincoln National Forest, Guadaloupe Mountains: ♂1, ♀4 (AMNH[LP 2890]), collected by J. Huff & R. West, 13/vi/2004, 32°12.085'N 104°41.798'W, under rocks around pond. U.S.A., New Mexico, Bottomless Lakes, on plateau above lakes: ♂1, ♀2 (AMNH[LP 2891]), collected by J. Huff & R. West, 13/vi/2004, 33°20.233'N 104°19.524'W, 3663 ft, scrub desert, collected with UV. U.S.A., Oklahoma, Bryan County, Caddo: ♂1 (AMNH[LP 1962A]), collected by W. Lu, 25/v/2002. U.S.A., Texas, Buda: ♂1, ♀1 (AMNH[LP 2286]), collected by P. Sprouse, /iii/2003, in house. U.S.A., Texas, Terrell County, Sanderson: sex indeterminant juvs(AMNH[LP 3084]), collected by B.R. Tomberlin & S.J. Burchfield, /viii/2004, under trash at railroad dump. U.S.A., Texas, backside of Government Canyon State Park along rock cut on hwy. 211, just past San Antonio city limit. : ♂ , ♀ , sex indeterminant 1(AMNH[LP 7023]), collected by J. Huff, 20/vii/2007, N 29°32’15.5”W 98°48’37.8” , 318 m, UV detection on rock road cut. México, Durángo, Highway 241, Vicente Guerrero-Guadalupe Victoria, between Cieneguillas and Francisco Zarco: ♂1 , sex indeterminant 2(AMNH[LP 5237]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 9/viii/2005, 29°05.129'N 104°02.614'W, 2125 m, Rock rolling by day. México, Zacatecas, Highway Sombrerete-Durángo, 184.5 km: sex indeterminant 2(AMNH[LP 5225]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 9/viii/2005, 23°44.719'N 103°47.779'W, 2357 m, Rock rolling by day.

***Centruroides*** **spp. undetermined:** Mexico, Jalisco, just south of El Tuito, : ♂1 (AMNH[LP 8669]), collected by R.C. West, 1/vii/2008, 20°21'20.80"N 105°18'35.21"W, 2514 ft., pine/oak forest, under fallen logs. Mexico, Oaxaca, Mancuernas, 8 km W: juvenile ♂ 1 (AMNH[LP 9523]), collected by O.F. Francke, A. Quijano & C. Santibañez, 30/vi/2008, 16.37059°N 98.18100°W, 230 m. México, Durángo, Highway Durángo-El Salto, 45.5 km Puente Mimbres: ♀1 , sex indeterminant 1(AMNH[LP 5260]), collected by O. Francke, W.D. Sissom, K. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis & C. Durán-Barrón, 8/viii/2005, 23°55.605'N 104°57.118'W, 2289 m, Rock rolling by day. *Centruroides “hoffmanni” sensu* Frias *et al.*, 2008: Mexico, Oaxaca, San Miguel Tenango, 0.5 km W: ♂40, ♀27, subadult ♀ 6, juv ♀ 9 (AMNH[LP 3706]), collected by R. Paredes, O. Francke and G. Villegas, 2/xi/2004, 16°15'30.9"N 95°35'57.2"W, 256 m, UV light detection at night. San Miguel Tenango, 0.5 km W: ♀4 (AMNH[LP 3708]), collected by O. Francke, R. Paredes and G. Villegas, 2/xi/2004, 16°15'30.9"N 95°35'57.2"W, 1571 m, UV light detection at night. *Centruroides aff baergi*: Mexico, Guerrero, Municipio Olinala, Olinala, 16 km S: 1 sex indeterminant (AMNH[LP 7667]), collected by O. Francke, J. Ponce, M. Cordas, H. Montano & A. Ballesteros, 16/vi/2007, 17°41.988'N 98°44.690'W, 2183 m. Jalisco, Mezquitic Road, between Mezquitic and Hojuelos: ♀1 (AMNH[LP 5228]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila , 7/vii/2005, 22°21.601'N 103°38.622'W, 2089 m.

Mezquitic, 4 km N: ♀2 (AMNH[LP 5236]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 6/vii/2005, 22°24.732'N 103°43.222'W, 1388 m. *Centruroides aff chiapanensis*: Guatemala, Escuintla, Farm 6 km northeast of Puerto San Jose: ♀1, 39 sex indeterminant (AMNH[LP 5990]), collected by J. Huff, C. Viquez & D. Ortiz, 4/vii/2006, N 13°57’28.0” W 90°45’47.2” , 5m, collected in secondary forest around the farm and along the edges of cow pastures, collected at night using UV. Mexico, Chiapas, Municipio Tapachula, Finca Brasil: ♂1 (AMNH[LP 8578]), collected by R. Paredes, 7/i/2008, 15°05'41.7"N 92°18'48.8"W, 470 m. *Centruroides aff elegans insularis*: Mexico, Guerrero, La Union , Majahua, N Zihuatanejo: ♂1, ♀1 (AMNH[LP 6608]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 24/v/2006, 17.79718°N 101.7442°W, 11 m. Michoacan, Aquila, Colola: sex indeterminant 1(AMNH[LP 7033]), collected by Francke *et al.*, 19/v/2007, 18° 18.047'N 103°24.536 W, 42 m. *Centruroides aff exilicauda*: Mexico, Baja California Sur, 15 mi E of Cabo San Lucas: ♂1 (AMNH[LP 1692]), collected by M.E. Soleglad, 1/vi/1999. Municipio Los Cabos, San José del Cabo, ca. 10 km S off Route 1: sex indeterminant 18(AMNH[LP 4480]), collected by W.E. Savary, E. Gonzalez & R. Mercurio, 10/vii/2005, 22°59.766′N 119°44.216′W, 50 m, UV detection at night. San Bartolo, 6 km SW: ♀1 (AMNH[LP 8840]), collected by H. Montaño & E. Gonzalez, 13/vii/2008, 23°41.816'N 109°50.800'W, 100 m, mesic vegetation. *Centruroides aff exilimanus*: Honduras, Departamento de Francisco Morazán, Municipio de Tatumbla, Cerro Uyuca, principal trail to abandoned house: juvenile ♀ 1 (AMNH[LP 9175]), collected by C. Viquez & M. Branstetter, 24/ix/2008, 14.02816°N87.07364°W, 1692 m, afternoon and night, under rocks on the trail and UV. *Centruroides aff gracilis*: Guatemala, Izabal, Rio Sauce, 15km east of El Estor at a picnic area on the river: 4 sex indeterminant (AMNH[LP 5991]), collected by J. Huff, C. Viquez & D. Ortiz, 7/vii/2006, N 15°33’36.7” W 89°17’05.7”, 13m, collected on thatch roof using UV at night. Rio Dulce, Hotel Tijax: ♂1 , 1 sex indeterminant (AMNH[LP 5992]), collected by J. Huff, C. Viquez & D. Ortiz, 8/vii/2006, N 15°40’12.2” W 89°00’27.0” , 49 m, collected along trails through old secondary growth tropical forest using UV at night. Honduras, Departamento de Atlantida, Municipio de La Ceiba, La Ceiba, Pico Bonito Lodge, property with cacao, close to the lodge: ♀1 (AMNH[LP 9185]), collected by C. Viquez & M. Branstetter, 2/x/2008, 15.68947°N86.90344°W, 124 m, under rocks at night with UV. Municipio de Telá, Jardín Botánico, Lancetilla, trail to Represa Vieja: ♀ 1 (AMNH[LP 9184]), collected by C. Viquez & M. Branstetter, 1/x/2008, 15.72585°N87.45128°W, 163 m, afternoon and night, under rocks, logs and UV. Municipio de Meambar, P.N. Cerro Azul Meambar, trail to Quebrada: ♀1 (AMNH[LP 9183]), collected by C. Viquez & M. Branstetter, 26/ix/2008, 14.87122°N87.90525°W, 798 m, night UV. Departamento de Francisco Morazán, Municipio de Tegucigalpa, P.N. La Tigra, trail to view point: ♂1 (AMNH[LP 9181]), collected by C. Viquez & M. Branstetter, 25/ix/2008, 14.21909°N87.08374°W, 1667 m, day, under rocks and logs. Nicaragua, Departamento de Matagalpa, Municipio de Matagalpa, Selva Negra, km 140 Highway Matagalpa-Jinotega, trail El Atajo: ♀1 (AMNH[LP 9182]), collected by C. Viquez & M. Branstetter, 8/x/2008, 12.99807°N85.90996°W, 1267 m, night collecting. *Centruroides aff limpidus*: Mexico, Guerrero, Municipio de Chilpancingo de los Bravo, Omiltemi, 2 km E: ♀ 1 (AMNH[LP 9986]), collected by O. Francke, H. Montaño, T. López, C. Quijano, C. Santibañez y A. Valdez, 23/vii/2009, 17.55447°N 99.65427°W, 2013 m, UV detection at

night. Cutzamala de Pinzón, 3 km N Ixtapilla: ♀3 (AMNH[LP 6589]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 22/v/2006, 18.57365°N 100.62835°W, 297 m. Estado de Mexico, Municipio Zacazonapan, 3 km N Zacazonapan: ♀1 (AMNH[LP 1821]), collected by O. Francke & E. Gonzalez Santillan, 16/xii/2001. Municipio Tejupilco, Parque Nacional Sierra de Nanchititla, ca. 2 km from park office on gravel road, SITE 48: sex indeterminant 2(AMNH[LP 4715]), collected by E. González & R. Mercurio, 24/vii/2005, 18°52.016′N 100°25.383′W, 1765 m, UV detection at night. México, Estado de Municipio Temascaltepec, Temascaltepec, 3 km S, ca. 2 km along gravel road from Route 134, SITE 47: ♀1, ♀ 1 (AMNH[LP 4717]), collected by E. González & R. Mercurio, 23/vii/2005, 19°01.166′N 100°03.900′W, 1909 m, UV detection at night, Pine forest. Guerrero, Cutzamala de Pinzón, 3 km N Ixtapilla: sex indeterminant 2(AMNH[LP 6443]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 22/v/2006, 18.57365°N 100.62835°W, 297 m. Zihuatanejo, Entronque en Km 110 de la carretera Altamirano-Zihuatanejo: sex indeterminant 4(AMNH[LP 6578]), collected by O. Francke, A. Valdez, H. Montaño & A. Ballesteros, 23/v/2006, 17.96675°N 101.21085°W, 1815 m. *Centruroides aff nigrovariatus*: Mexico, Oaxaca, 6 km N Telixtlahuaca: ♂1 (AMNH[LP 2035]), collected by O. Francke, E. Gonzalez and J. Ponce, 22/vii/2002, 17°20.367'N 96°56.121'W, SE slope, dry scrub, 1915 m. 3.7 km N El Moral: ♀1 , sex indeterminant 1(AMNH[LP 2056]), collected by L. Prendini, O. Francke, E. Gonzalez and J. Ponce, 23/vii/2002, 17°30.134'N 96°56.091'W, 2050 m; Oak forest and grassland; under stones. Huitzo, 1.5 km N: ♂10, ♀27 , sex indeterminant 6(AMNH[LP 3703]), collected by O. Francke, R. Paredes and G. Villegas, 31/x/2004, 17°17'28.5"N 96°55'35.9"W, 1890 m, UV light detection at night. Huitzo, 1.5 km N: ♂2, ♀1 (AMNH[LP 3704]), collected by O. Francke, R. Paredes and G. Villegas, 31/x/2004, 17°17'28.5"N 96°55'35.9"W, 1890 m, UV light detection at night. San Antonio Acutla, Km 2 carretera San Cristobal Sochixtlahuaca-Santiago Tejupan : ♂2 (AMNH[LP 6454]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 6/vi/2006, 17.704°N 97.39445°W, 2290 m. San Francisco Telixtlahuaca, Cerro del 20, 46 km N Telixtlahuaca: ♀ 1 (AMNH[LP 6455]), collected by O. Francke, M. Cordova, A. Jaimes & G. Montiel, 9/xi/2005, 1986 m. Puebla, Toll road to Tehuacan, km 21 (n of town): ♀1 (AMNH[LP 3702]), collected by G. Villegas, O. Francke and R. Paredes , 31/x/2004, 18°38'41.1"N 97°27'22.9"W, 2249 m, rock rolling. *Centruroides aff nitidus*: Dominican Republic, La Altagracia Province, Forested road cutting in cane fields, near Alto de Chavon: ♂1, ♀1 (AMNH[LP 3317]), collected by E.S. Volschenk & J. Huff, 15/vii/2004, 18.4908°N68.9178°W, 65.5 m, Humid forested cutting flanked by sugarcane fields; hand collected from under stones and logs, and with blacklights. Parque Nacional del Este, track between ranger station at Bayahibe and La Toruga: ♂1 (AMNH[LP 3450]), collected by E.S. Volschenk & J. Huff, 13/vii/2004, 18.3281°N68.8028°W, 8.54 m, Cactus and spiny scrub on sand and on limestone; hand collected from under stones and logs, and with blacklights. Bahamas, Great Inagua, Old Aerostat Base: ♀1 (AMNH[LP 6234]), collected by S. Crews & H. Nixon, 16/v/2006, 21°06'06.7"N73°39'01.9"W, ca. 2 m, under bark of Casuarina. *Centruroides aff ornatus*: México, Michoacán, Municipio Coalcoman, La Nieve: ♀1 , sex indeterminant 2 (AMNH[LP 5240]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 10/vii/2005, 18°49.070'N 103°02.653'W, 2246 m. Las Cocinas, Highway Nocupetaro-Carácuaro: sex indeterminant 1(AMNH[LP 5261]), collected by O. Francke, J. Ponce, M. Córdova, A.

Jaimes, G. Francke & V. Capovila, 14/vii/2005, 19°01.880'N 101°14.067'W, 672 m. *Centruroides aff rileyi*: México, Veracruz, Municipio Catemaco, Estacion de Biologia 'Los Tuxtlas', UNAM: ♂1 (AMNH[LP 5231]), collected by O. Francke, M. Córdova, A. Jaimes, A. Valdez & H. Montaño, 26/viii/2005, 18°35.058'N 93°04.491'W, 134 m; ♀1 (AMNH[LP 2070]), collected by J. Ponce and O. Francke, 19/vii/2002, collected at night with UV light. *Centruroides aff schmidti*: Guatemala, Izabal, Rio Dulce, Hotel Tijax: ♂1 , sex indeterminant 1(AMNH[LP 5984]), collected by J. Huff, C. Viquez & D. Ortiz, 8/vii/2006, N 15°40’12.2” W 89°00’27.0” , 49 m, collected along trails through old secondary growth tropical forest using UV at night. Mexico, Chiapas, Municipio Ococingo, Frontera Corozal, 2 km SE: ♂2 , 1 sex indeterminant (AMNH[LP 2948]), collected by R. Paredes & J.L. Castelo, 28/iv/2004, 16°48'12.7"N 90°52'11.2"W, 150 m. *Centruroides aff serrano*: Mexico, Oaxaca, S of Ixtlan on Highway 175: ♀1 , sex indeterminant 1(AMNH[LP 2028]), collected by L. Prendini, E. Gonzalez, O. Francke and J. Ponce, 21/vii/2002, 17°15.642'N 96°32.427'W, 2075 m. Mexico, Oaxaca, Mitla, 9 Km W: ♀1 (AMNH[LP 3705]), collected by G. Villegas, O. Francke and R. Paredes , /x/2004, 16°55'40.9"N 96°24'44.7"W, 1688 m, rock rolling. Xaaga, 7 km S, on the road from Mitla to Hierve el Agua: ♀4, juvenile ♀ 1 (AMNH[LP 3707]), collected by G. Villegas, O. Francke and R. Paredes , 1/xi/2004, 16°52'46.6"N 96°18'11.0"W, 2316 m, rock rolling. Tlacolula, 1 km E Yagul: sex indeterminant 2(AMNH[LP 6435]), collected by O. Francke, M. Cordova, A. Jaimes, A. Valdez, G. Montiel & C. Santibañez, 14/xi/2006, 16°57.297N 96°26.461W, 1662 m. Diaz Ordaz, 9.6 km N Diaz Ordaz, Carretera Diaz Ordaz-San Miguel: ♂1 (AMNH[LP 6439]), collected by O. Francke, M. Cordova, A. Jaimes, G. Montiel & C. Santibañez, 14/xi/2005, 17°2.388N 96°28.27W, 2369 m. Miahuatlan, 4 km E Miahuatlan: ♂2 (AMNH[LP 6525]), collected by O. Francke G. Villegas, H. Montaño, C. Santibañez & A. Valdez, 23/vi/2006, 16°19.504N 96°32.46W, 1638 m. San Cristobal Amatlán, 1 km N San Lorenzo Mixtepec: ♀1 (AMNH[LP 6530]), collected by O. Francke G. Villegas, H. Montaño, C. Santibañez & A. Valdez, 23/vi/2006, 16°17.493N 96°20.91W, 2120 m; ♂2, ♀ 1 (AMNH[LP 6605]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 22/vi/2006, 16.29201°N 96.33305°W, 1925 m. Zona Comunal San Felipe: ♀1 (AMNH[LP 6535]), collected by O. Francke, G. Montiel & C. Santibáñez, 12/xi/2005, 17.116294°N 96.714306°W. Mitla, 15 km E: ♂1 (AMNH[LP 7620]), collected by O. Francke, H. Montano, A. Valdez, A. Ballesteros & C. Santibanez, 18/vii/2007, 16°56.606'N 96°17.114'W, 2081 m, pine-oak woodland. Pedro Juchatengo, 3 km W San Pedro Juchatengo: ♂2 (AMNH[LP 6444]), collected by O. Francke, A. Valdez, G. Villegas, H. Montaño & C. Santibañez, 27/vi/2006, 16.36373°N 97.10973°W, 845 m. *Centruroides aff griseus griseus:* U.S.A, U.S. Virgin Islands, St. Croix, Tague Bay, Ridge Road, 0.6 mi from intersection with Route 82: sex indeterminant 1 juv.(AMNH[LP 10216]), collected by L. Prendini & J. Huff, 16/x/2009, 17°44.870'N64°36.132'W, 56 m, rock walls along roadside; UV detection on warm, still, dark, humid night. *Centruroides aff morenoi:* Colombia, Valle , Cali , Antigua via Yumbo: ♀1 (AMNH[LP 9326]), collected by J. Moreno , 8/viii/2008, 03°21'N76°30'W, 1000 m aprox. Guatemala, Santa Rosa, El Papayo: ♀1, ♀ 1 (AMNH[LP 5986]), collected by J. Huff, C. Viquez, D. Ortiz, C. Avila & R. Estrada, 3/vii/2006, N 14°08’17.1” W 90°33’51.8” , 296 m, collected in the village along the road bank and around the farmhouse of C. Avila. Collected under rocks, logs and bark. Guatemala, Santa Rosa, El Papayo: ♀1 , sex indeterminant

60(AMNH[LP 5987]), collected by J. Huff, C. Viquez, D. Ortiz, C. Avila & R. Estrada, 3/vii/2006, N 14°08’05.6” W 90°34’05.6”, 277 m, collected at the edge of town in a cow pasture. Collected under rocks . *Centruroides aff guanensis:* Bahamas, San Salvador, Gerace Field Station, trails behind field station vic.: ♀1 (AMNH[LP 6235]), collected by S. Crews, 19/v/2006, 24°06.9'N74°27.8'W, ca. 3-25 m, under rocks and bark. Bahamas, San Salvador, Gerace Field Station, trails behind field station vic.: sex indeterminant 1 juv.(AMNH[LP 6236]), collected by S. Crews, 19/v/2006, 24°06.9'N74°27.8'W, ca. 3-25 m, under rocks and bark. *Centruroides aff sculpturatus:* México, Chihuahua, Military check point Batopilas: ♀2 (AMNH[LP 5235]), collected by O. Francke, K. McWest, H. Montaño, J. Ballesteros, L. Jarvis, 2/viii/2005, 27°03.502'N 107°43.054'W, 652 m, UV detection at night . México, Jalisco, El Pueblo crossroad, 3 km: ♂1, ♀1 (AMNH[LP 5233]), collected by O. Francke, J. Ponce, M. Córdova, A. Jaimes, G. Francke & V. Capovila, 8/viii/2005, 21°00.597'N 103°10.284'W, 1872 m. *Centruroides aff schmidti:* Mexico, Guerrero, Copala, Microndas Fogos: subadult ♀ 1 (AMNH[LP 8582]), collected by O.F. Francke, H. Montaño & A. Ballesteros, 2/xi/2007, 16°34.360'N 98°53.423'W, 14 m. Mexico, Michoacan, Municipio de Aquila, Faro de Bucerias: ♂1 (AMNH[LP 2009]), collected by J. Ponce and E. Gonzalez, 14/iv/2002, Selva baja caducifolia. Mexico, Chiapas, Huixtla, Hotel Alicia: juvenile ♂ 1 (AMNH[LP 8424]), collected by S. Crews, 22/ix/2004, in bed, stung my back.

***Heteroctenus abudi* (Armas & Marcano Fondeur, 1987):** Dominican Republic: *La Altagracia Province*: Parque Nacional del Este: Cabo Flaso (entrance zone), 18°22'25"N, 68°37'01"W, 1 ♂ (AMNH [ESV6091]),14 July 2004, E.S. Volschenk & J. Huff, 67.7 m; Track between ranger station (at Boca de Yuma) and Punta Faustino, 18°21'17.2"N, 68°36'52.3"W, 1 ♀, 48 first instars (AMNH [ESV6010]), 1 ♀, 22 first instars (AMNH [ESV6019]), 1 ♀ 32 first instars (AMNH [ESV6039]), 11 ♂, 4 ♀, 1 subad. ♂, 1 subad. ♀, 2 juv. (AMNH [ESV6072]), 1 ♂, 1 ♀ (AMNH [ESV7110]), 1 ♂, 1 ♀ (AMNH [ESV7117]), 1 ♂, (AMNH [ESV7120]), 1 ♂, 1 ♀ (AMNH [ESV7242]), 1 ♂, 1 ♀ (AMNH [ESV7303]), 1 ♀ (AMNH [ESV7306]), 1 ♂, 1 ♀ (AMNH [ESV7705]), 1 ♂, 1 ♀ (AMNH [ESV7937]), 3 juv. (AMNH), 1 juv. (AMNH [LP 3268]), 14 July 2004, E.S. Volschenk & J. Huff, 3.3 m, dense canopy humid forest, hand collected at night with blacklights, from limestone outcrops, especially along an old rock wall along the start of the track. U.S.A.: *Puerto Rico*: Isla Mona, road to El Faro, 18.06389°N, 67.86857°W 1♂ 3♀ (AMNH), 1 juvenile (AMNH[LP 10234]), U.S.A, Puerto Rico, Isla Mona, road to El Faro, 17 October 2009, L. Esposito & H. Yamaguti, blacklighting, Vegetation primarily desert grassland dominated by organ cactus and tall grasses; trail #1 to Punta Capitan from Sardiniera, 18.08823°N, 67.93815°W, 10♂ 10♀ (AMNH), 2 juveniles (AMNH[LP 10235]), 16 October 2009, L. Esposito & H. Yamaguti, blacklighting - trail is primarily scrub forest and cactus

***Heteroctenus bonettii* (Armas, 1999):** Dominican Republic: *Pedernales Province*: Parque National Jaragua: Cabo Rojo, 17°53'45.2"N, 71°39'35.8"W, 9 July 2004, E.S. Volschenk & J. Huff, 15 m, dry cactus and spiny forest on limestone karst, hand collected at night with blacklights, 3 ♂, 10 ♀, 4 subad., 2 juv. (AMNH [ESV6005]), 1 ♂ (AMNH [ESV7126]), 1 ♂, 1 ♀ (AMNH [ESV7127]), 1 subad. ♂ (AMNH), 1 juv. ♂ (AMNH [LP 3267]), Road to Fondo Paradi, 1.8 km from Highway 44, 17°48.692'N, 71°26.600'W, 12 January 2004, J. Huff, 302 ft, found between rocks, 1 ♀ (AMNH [LP 2471]), 1 ♀

(AMNH [LP 3265]), Track into park, between Manuell Goa and Oviedo, 17°48'41.5"N, 71°26'35.9"W, 9 July 2004, E.S. Volschenk & J. Huff, 83.3 m, deciduous forest and thorny scrub, hand collected from between stones during the day and with blacklights at night, 13 ♂, 7 ♀, 1 subad., 1 juv. (AMNH [ESV6011]), 1 ♂, 1 ♀ (AMNH [ESV7112]), 1 ♂ (AMNH [ESV7129]), 1 juv. (AMNH [LP 3266]).

***Heteroctenus junceus* (Herbst, 1800):** Cuba: 1 juv. (AMNH [LP 7009]), July 2007, C. Hamilton,; 'Antillen?,' 1 ♂, 2 ♀ (ZMB 7370); 'Portorico', 2 ♀, 1 juv. (ZMB 7280 [ESV7001]), Stahl; 2 ♀ (ZMB 2637), 1 ♂, 1 ♀ (ZMB 7380 [ESV7224]), 1 juv. (ZMB, 7343), Gundlach; Arroyo Bermejo, near Fibacoa, 1 ♂ (ZMB 31020), 31 May 1967, Kleiderschrank; im zelt. wiese auf sandboden, 1 ♀ (ZMB 31021), 15 June 1967; 1 juv. (ZMB 31022), June 1967; Santiago de las Caballeros, 1 ♂ (ZMH),1936, P. Thumb; *Havana Province*: Havana, 1 ♀ (AMNH), April 1941, Dr E. Weiss, 1 ♀, 1 subad. (AMNH). *Holguín Province*: captive bred, 1 juv. (AMNH [LP 1928]), August 2000, Heist; near Baños [Banes], 2 ♂ (AMNH), May 1918; Guardalavaca, captive bred, 1 ♂ (AMNH [LP 1565]), 29 March 1993, W. Altmann; Mountains near Guisa, 1 ♀, 28 juv. (ZMH), October 1936, P. Thumb; Moa, 1 ♂ (ZMH), September 1937, P. Thumb; 4 ♀ (ZMH), 1938, P. Thumb; *Isla de la Juventud Province*: Isle of Pines, 1 ♂ (AMNH). *Pinar del Rio Province*: Guanahacabiles, Akadstat. El Beral, 1 subad. (ZMB 31023), December 1967, G. Peters; Sierra de Anafe, 2 subad. (AMNH), 23 February 1947, M. Barro; Vinales Valley, 1 ♀ (AMNH), 1940, Osorio. *Santiago de Cuba Province*: La Socapa, 10 km SW of Santiago de Cuba, 1 ♂ (AMNH), 1 ♀ (AMNH [LP 1509]), 1 juv. ♀ (AMNH [LP 1517]), 1 ♀ (AMNH [LP 1518]), 9 April 1999, R. Teruel; Santiago de Cuba, 1 ♂, 2 juv. (AMNH); *Sancti Spiritus Province*: Trinidad, 1 ♂ (AMNH AH 4514 [ESV7041]), August 1978, B. Acosta.

***Heteroctenus garridoi* Armas, 1974:** Cuba: *Guantanamo*: (AMNH[LP 10225]) 1♀, G. Molisani, 10, 2009.

***Rhopalurus laticauda* Thorell, 1876:** 2 ♀ (ZMB 14865); 'Mexico', Dr v. Hubl, 1 ♂ (ZMB 14866). Venezuela: 1 ♂, 1 ♀ (ZMB 8226), F. Kummerow; San Jose de Guaviare, 1 ♀ (SMF 39252), December 1955, Meden; *Aragua*: 1 subad. ♂ (SMF 29208), Maracay; 1 ♂, 1 ♀, 1 subad. (SMF 8876/218), Fahrenholz; *Bolívar*: Ciudad Bolivar, 2 ♀ (ZMH), 20 February 1903; La Paragua, M.A. de Verde, 1 ♂ (AMNH); Upata, 1 ♀ (AMNH), February 1973, A. Bordes; *Carabobo*: Valencia, 1 ♀ (ZMB 31024), 29 December 1904, F. Kummerow; 2 ♀ (ZMH), September 1958, H. Ardelt; *Distrito Federal*: Caracas, 2 ♀, 20 first instars (AMNH [ESV7444], March 1999, C. Siederman; 1 ♂ (AMNH [LP 2462]), 2001, C. Siederman; *Guarico*: Calabozo and San Fernando de Apure (about halfway between), 1 ♀ (AMNH), 30 November 1967, M.A. de Verde; 'Hato Masaguarat,' 45 km S Calabozo, 1 ♂ (AMNH [ESV7816]), 7 April 1978, Y. Lubin; Guatire, 1 ♂, 1 ♀ (AMNH[LP 2845]), 29 April 2004, R.C. West, under rocks, dry forest. *Mérida*: Mérida, 2 ♂, 3 ♀ (SMF 5712/27); *Miranda*: Guatire, 1 ♂ (AMNH [LP 2845]), 1 ♀ (AMNH), 29 April 2004, R.C. West, under rocks, dry forest; Hda. Santa Rosa, 3 km N Guatire, 1 ♂, 1 ♀, 2 juv. (AMNH), 10 January 1973, M.A. González-Sponga, 450 m; *Nueva Esparta*: Isla Margarita, N of Peninsula de Macanao, 11°02.618'N, 64°21.542'E, 1 ♀ (AMNH [LP 4221]), 4 September 2005, S. Huber; *Apure:* Elorza, 10 km SO Elorza, road to San Felipe, 07°03.749'N, 69°30.249'W, 1 juvenile (AMNH[9200]), 5 October

2008, J.A. Ochoa & S. Bazo, 89 m, llanos; *Bolívar:* Cedeño, ca. Los Pijiguaos, 06°29.878'N, 67°02.600'W, 1 juvenile (AMNH[LP 9237]), 12 October, 2008, J.A. Ochoa & S. Bazo, 76 m, llanos; Ciudad Bolívar, ca. Bolivar city, 07°37.486'N, 64°05.924'W, 1 juvenile (AMNH[LP 9256]), 24 October 2008, J.A. Ochoa & S. Bazo, 117 m, llanos; Cedeño, Comunidad Corosal, ca. Pijiguaos, 1 subadult ♀ (AMNH[LP 9253]), 25 October 2008, J.A. Ochoa, 80 m, forest

***Heteroctenus princeps*** **(Karsch, 1879):** Dominican Republic: *Independencia Province*: Isla Cabritos, 18°30.019'N, 71°43.228'W, 1 ♂, 1 ♀, 16 juv. (AMNH), 5 ♂, 3 ♀, 3 subad., 1 juv. (AMNH), 3 juv. (AMNH [LP 2470]), 1 subad., 2 juv. (AMNH [LP 3260]), 7 January 2004, J. Huff, 110 ft, under rock, coral; Ranger station for Parque Nacional Isla Cabritos, 18°33'45"N, 71°41'50"W, 3 ♂, 7 ♀, 5 subad., 2 juv. (AMNH [ESV6006]), 1 subad. ♂ (AMNH), 1 subad. (AMNH [LP 3264]), 8 July 2004, E.S. Volschenk & J. Huff, -19 m, dry forest, hand collected from under stones and logs, and with blacklights; Parque Nacional Isla Cabritos, behind Ranger Station, 18.56287°N, 71.69762°W, 2 ♂, 8 ♀, 1 subad. ♀, 32 first instars (AMNH), 2 ♂, 1 subad. ♀ (AMNH), 1 ♂ (AMNH [LP 5102]), 8 August 2005, L. Esposito, -23 m, mixed dry forest with succulents, UV detection; Parque Nacional Sierra de Baoruco, road between Rabo de Gato and Duverge, 18°19'38"N, 17°33'55"W, 3 ♂, 3 ♀, 3 juv. (AMNH [ESV6033]), 1 juv. (AMNH), 1 ♀ (AMNH [LP 3263]), 7 July 2004, E.S. Volschenk & J. Huff, 447 m, arid thorny scrub, hand collected from under stones and in dead and dry agaves; Puerto Escondido, Sierra de Baoruco, 18°19.762'N, 71°33.502'W, 1 ♂, 3 ♀, 1 juv. (AMNH), 1 juv. (AMNH [LP 3261]), 6 January 2004, J. Huff, 1592 ft, under dead agave; Road to Puerto Escondido, 18°20.376'N, 71°33.345'W, 1 ♀ (AMNH), 1 juv. (AMNH [LP 3262]), 6 January 2004, J. Huff, 1388 ft, under rocks in gravel quarry; *Pedernales Province*: Manuel Goja, 3.9. km N, 1 ♂ (AMNH [LP 1566]), 9 May 1998, D. Huber; Oviedo to Pedernales, 11.5 km N, 1 ♂ (AMNH [LP 1516]), 8 May 1998, D. Huber; Haiti: *Departement de l'Ouest*: Port-au-Prince, holotype ♂ (ZMB 116), Ehrenberg.

***Rhopalurus rochae*** **Borelli, 1910:** Brazil: *Bahia*: Município Ceraíma: Guanambí, 7 km S, 14°17'5.6"S, 42°47'2.2"W, 1 juv. (AMNH [LP 7638]), 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 533 m, UV sampling, modified savanna, cloudy and raining; Fazenda du Fabiano, 8 km NE Guanambí, 14°10'17.6"S, 42°43'56.4"W, 1 ♂, 2 juv. (AMNH [LP 7639]), 1 ♀ (AMNH), 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 539 m, under rocks, rocky hill and surrounds, open savanna modified; Guanambí, 16 km SE, 14°17'19"S, 42°41'31.1"W, 1 juv. (AMNH [LP 7655]), 25 January 2007, C. Mattoni, R. Pinto-da-Rocha, H. Yamaguti, 559 m, UV sampling and under leaf litter, banana plantation and surrounds; *Paraíba*: Soledade, 07°02.118'S, 36°27.311'W, 1 ♂ (AMNH [LP 1581]), 1 ♀ (AMNH [LP 1582]), 1 ♂ (AMNH [LP 1775]), 16 March 1999, A. Kury & A. Giupponi, 575 m. *Pernambuco*: Escola Aquicola, Exu, 1 ♂ (AMNH [ESV7248]), 30 March 1977, L.J. Vitt, caatinga; 1 ♂ (AMNH), 27 June 1977, L.J. Vitt; Exu, 3 km NW, 2 ♂, 1 ♀, 3 juv. (AMNH), 10 March 1977, L.J. Vitt; Exu, 3 km W, 2 ♂, 4 ♀, 4 juv. (AMNH), 30 May 1977, L.J. Vitt, 1 June 1977; 1 ♀ (AMNH), L.J. Vitt,; Exu, 5 km N, 1 ♂, 1 juv. (AMNH), 6 April 1977, L.J. Vitt, caatinga; 1 juv. (AMNH), 18 January 1978, L.J. Vitt & K.E. Streilein; Exu, L.J. Vitt, 1 juv. (AMNH), 5 km E, 8 May 1977; Exu, 6 km N, 1 ♀, 1 juv. ♂ (AMNH), 15 March 1977, L.J. Vitt, open fields (cotton), under fallen logs; Exu, 6 km NE, 1 ♀, 49 first instars (AMNH), 16 March 1977,

L.J. Vitt, under rock on larger rock, caatinga habitat; Exu, 18 km E, 1 ♀, 29 first instars (AMNH), 1 ♀, 39 first instars (AMNH [ESV7210]), 5 March 1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat; Exu, 20 km E, 1 ♂, 1 ♀ (AMNH [ESV7625]), 30 March 1977, J.L.Vitt,; Fazenda Batente, 5 km NE Exu, 1 juv. (AMNH), 29 March 1977, L.J. Vitt; Fazenda Caterino, 10 km NE Exu, 2 ♂, 3 juv. (AMNH), 5 ♂, 3 ♀ (AMNH), 1 August 1977, L.J. Vitt; Fazenda Chelonia, 8 km S Exu, 2 juv. (AMNH), 28 July 1977, L.J. Vitt; Fazenda Guarani, 3 km N Exu, 1 ♂, 3 ♀, 1 subad. 3 juv. (AMNH), 14 July 1977, L.J. Vitt; Fazenda Guarani, 5 km N Exu, 1 ♀, 3 juv. (AMNH), 29 July 1977, L.J. Vitt; 1 ♀ (AMNH) 19 February 1978, L.J. Vitt; *Sergipe*: Municipio Lagarto: near Genipapo, 1 ♂, 2 ♀ (AMNH), July 1982, O.F. Francke.

Appendix 9. Specimen codes, localities and GenBank accession numbers for specimens used in a fossil-calibrated phylogenetic analysis of the buthid scorpion subfamily Rhopalurusinae Bücherl, 1971.

| | | Genbank Accession Numbers | | | | |
|---|---|---|---|---|---|---|
| **Species** | **Locality** | **12S** | **16S** | **18S** | **28S** | **COI** |
| *Centruroides alayoni* Armas, 1999 | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides alayoni* Armas, 1999 | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides anchorellus* Armas, 1976 | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides arctimanus* Armas, 1976 | Cuba, Holguín | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides baergi* Hoffmann, 1932 | Mexico, Oaxaca, Municipio Cuicatlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides baergi* Hoffmann, 1932 | Mexico, Oaxaca, Santa María Ixcatlán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides balsasensis* Ponce & Francke, 2004 | México, Michoacán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides balsasensis* Ponce & Francke, 2004 | México, Michoacán | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bani* Armas & Marcano Fonduer, 1987 | Dominican Republic, Barahona Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bani* Armas & Marcano Fonduer, 1987 | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides barbudensis* Pocock, 1898 | Saba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides barbudensis* Pocock, 1898 | St. Kitts and Nevis, Nevis | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides* aff *bertholdi* Pocock, 1902 | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides* aff *bertholdi* Pocock, 1902 | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bicolor* (Pocock, 1898) | Costa Rica, Puntarenas Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides bicolor* (Pocock, 1898) | Costa Rica, Puntarenas Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus borinquensis* Armas, 1982 | U.S.A., Puerto Rico | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus borinquensis* Armas, 1982 | U.S.A., Puerto Rico | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chamulaensis* Hoffmann, 1932 | México, Chiapas, Municipio San Juan Chamula | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chamulaensis* Hoffmann, 1932 | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chiapanensis* Hoffmann, 1932 | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides chiapanensis* Hoffmann, 1932 | México, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans elegans* (Thorell, 1876) | Mexico, Jalisco, Municipio Las Huertas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans elegans* (Thorell, 1876) | Mexico, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilicauda* (Wood, 1863) | México, Baja California | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilicauda* (Wood, 1863) | Mexico, Baja California Sur, Municipio La Paz | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilimanus* Teruel & Stockwell, 2002 | Honduras? | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides exilimanus* Teruel & Stockwell, 2002 | Honduras? | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides farri*? (Thorell, 1876) | Jamaica, St. Elizabeth Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus flavopictus* (Pocock, 1898) | México, Veracruz, Municipio Catemaco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus flavopictus* (Pocock, 1898) | Mexico, Oaxaca, Municipio de Santa Maria Jacatepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus meridionalis* Hoffmann, 1932 | México, Chiapas, Municipio Comitan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides flavopictus meridionalis* Hoffmann, 1932 | México, Chiapas, Municipio Comitan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides fulvipes* (Pocock, 1898) | Mexico, Oaxaca | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides gracilis* (Latreille, 1804) | México, Hidalgo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides gracilis* (Latreille, 1804) | México, San Luis Potosi | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus* (C.L. Koch, 1844) | U.K., British Virgin Islands, Guana Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides griseus* (C.L. Koch, 1844) | U.S.A., Puerto Rico, Culebra | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides guanensis* Franganillo, 1930 | U.S.A., Florida, Monroe County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hentzi* (Banks, 1900) | U.S.A., Florida | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | Genbank Accession Numbers | | | | |
|---|---|---|---|---|---|---|
| | | 12S | 16S | 18S | 28S | COI |
| *Centruroides hentzi* (Banks, 1900) | U.S.A., Florida, Alachua County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hirstutipalpus* Ponce-Saavedra & Francke, 2009 | México, Colima, Minatitlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hirstutipalpus* Ponce-Saavedra & Francke, 2009 | Mexico, Colima | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hoffmanni* Armas, 1996 | México, Chiapas, Municipio Tzimol | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides hoffmanni* Armas, 1996 | México, Chiapas, Municipio Villaflores | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides infamatus* Pocock, 1902 | Mexico, Michoacan, Municipio Tinqambato | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides infamatus* Pocock, 1902 | Mexico, Michoacan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides insulanus* (Thorell, 1876) | Jamaica, St. Thomas Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides insulanus* (Thorell, 1876) | Jamaica, St. Ann Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans insularis* Pocock, 1902 | Mexico, Nayarit, Municipio Tuxpan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides elegans insularis* Pocock, 1902 | Mexico, Nayarit | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides jaragua* Armas, 1999 | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides koesteri* Kraepelin, 1912 | Costa Rica, Guanacaste Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides koesteri* Kraepelin, 1912 | Nicaragua, León, La Paz Centro | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limbatus* (Pocock, 1898) | Costa Rica, Hacienda Barú, Barú | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limbatus* (Pocock, 1898) | Costa Rica, Limon Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limpidus* (Karsch, 1879) | México, Guerrero, Tepecoacuilco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides limpidus* (Karsch, 1879) | México, Guerrero, Buena Vista de Cuellar | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides luceorum* Armas, 1999 | U.S.A., Navassa Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides maracanoi* Armas, 1981 | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides maracanoi* Armas, 1981 | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides margaritatus* (Pocock, 1898) | Costa Rica, Esterillos Centro | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides margaritatus* (Pocock, 1898) | Ecuador, Loja, Catamayo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides mariaorum* Santiago-Blay, 2009 | U.S.A, Puerto Rico, Isla Mona | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides mariaorum* Santiago-Blay, 2009 | U.S.A, Puerto Rico, Isla Mona | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides meisei* Hoffmann, 1938 | Mexico, Guerrero, Municipio Copala | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides meisei* Hoffmann, 1938 | Mexico, Guerrero, Municipio Copala | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides morenoi* Mello-Leitao, 1945 | Jamaica, St. Andrews Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides morenoi* Mello-Leitao, 1945 | Jamaica, St. Andrews Parish | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrescens* (Pocock, 1898) | Mexico, Oaxaca, Miahuatlan | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrescens* (Pocock, 1898) | Mexico, Oaxaca, Magdalena Mixtepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrimanus* Pocock, 1898 | Mexico, Oaxaca, Municipio Santiago Astata | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrovariatus* (Pocock, 1898) | Mexico, Oaxaca, San Sebastián de las Grutas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nigrovariatus* (Pocock, 1898) | Mexico, Oaxaca, Magdalena Mixtepec | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus nitidus* (Thorell, 1876) | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus nitidus* (Thorell, 1876) | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus taino* Armas & Marcano Fondeur, 1987 | Dominican Republic | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides nitidus taino* Armas & Marcano Fondeur, 1987 | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides noxious* Hoffmann, 1932 | Mexico, Nayarit | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides noxious* Hoffmann, 1932 | Mexico, Nayarit, Municipio Huajicori | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ochraceus* (Pocock, 1898) | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ochraceus* (Pocock, 1898) | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ornatus* Pocock, 1902 | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides ornatus* Pocock, 1902 | México, Jalisco | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides platnicki* Armas, 1981 | Turks and Caicos, Caicos, Providenciales | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides pococki* Sissom & Francke, 1983 | St. Kitts and Nevis, St. Kitts | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides rileyi* Sissom, 1995 | Mexico, Veracruz | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

| Species | Locality | Genbank Accession Numbers | | | | |
|---|---|---|---|---|---|---|
| | | 12S | 16S | 18S | 28S | COI |
| *Centruroides rileyi* Sissom, 1995 | Mexico, San Luis Potosi, Axtlan de Terrazas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sasae* Santiago-Blay, 2009 | U.S.A, Puerto Rico, Isla Caja de Muertos | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides schmidti* Sissom, 1995 | Mexico, Chiapas, Municipio Ococingo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides schmidti* Sissom, 1995 | Guatemala, Izabal | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sculpturatus* Ewing, 1928 | U.S.A., Arizona, Pima County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sculpturatus* Ewing, 1928 | Mexico, Sonora, Municipio Soyopa | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides serrano* Santibanez-Lopez & Ponce-Saavedra, 2009 | Mexico, Oaxaca, Municipio Villa Alta | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides serrano* Santibanez-Lopez & Ponce-Saavedra, 2009 | Mexico, Oaxaca, Municipio Villa Alta | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides sissomi* Armas, 1996 | Mexico, Quintana Roo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tapachulaensis* Hoffmann, 1932 | Mexico, Oaxaca, San Pedro Juchatengo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tapachulaensis* Hoffmann, 1932 | Mexico, Oaxaca, San Sebastián de las Grutas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tecomanus* Hoffmann, 1932 | Mexico, Michoacan, Municipio de Aquila | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tecomanus* Hoffmann, 1932 | Mexico, Jalisco, Municipio Talpa de Allende | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus arubensis* Backer, 1963 | Dutch Antilles, Aruba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus arubensis* Backer, 1963 | Dutch Antilles, Aruba | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus testaceus* DeGeer, 1778 | Dutch Antilles, Curacao | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides testaceus testaceus* DeGeer, 1778 | Dutch Antilles, Bonaire | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides thorellii* (Kraepelin, 1891) | Guatemala, Sacatepéquez | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tuxtla* Armas, 1999 | Mexico, Chiapas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides tuxtla* Armas, 1996 | México, Chiapas, Municipio Arriaga | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides vittatus* (Say, 1821) | U.S.A., Texas, Terrell County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Centruroides vittatus* (Say, 1821) | U.S.A., Texas, Brewster County | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus abudi* Armas & Marcano Fondeur, 1987 | Dominican Republic, La Altagracia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus bonettii* Armas, 1999 | Dominican Republic, Pedernales Provence, N | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus bonettii* Armas, 1999 | Dominican Republic, Pedernales Provence | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus garridoi* Armas, 1974 | Cuba, Guantanamo | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus* (Herbst, 1800) | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus* (Herbst, 1800) | Cuba, Santiago de Cuba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus junceus* (Herbst, 1800) | Cuba, Holguin | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus laticauda* Thorell, 1876 | Venezuela, Caracas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps* (Karsch, 1879) | Dominican Republic, Independencia Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps* (Karsch, 1879) | Dominican Republic, Oviedo to Pedernales | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps* (Karsch, 1879) | Dominican Republic, Pedernales Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus princeps* (Karsch, 1879) | Dominican Republic | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Rhopalurus rochae* Borelli, 1910 | Brazil, Bahia | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus clathratus* C.L. Koch, 1844 | Trinidad & Tobago, Trinidad, Gaspar Grande Island | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus discrepans* (Karsch, 1879) | Venezuela, Distrito Federal, Caracas | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus discrepans* (Karsch, 1879) | Venezuela, Miranda, Los Salias | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus elii* Armas & Marcano Fondeur, 1992) | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Tityus elii* Armas & Marcano Fondeur, 1992 | Dominican Republic, La Vega Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius birabeni* Mello-Leitão, 1938 | Argentina, La Pampa Prov. | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius birabeni* Mello-Leitão, 1938 | Argentina, San Juan Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius fuscus* (Thorell, 1876) | Argentina, Córdoba Province | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |
| *Zabius fuscus* (Thorell, 1876) | Argentina | ABC12345 | ABC12345 | ABC12345 | ABC12345 | ABC12345 |

## REFERENCES


Ahola, V., Aittokallio, T., Vihinen, M. & Uusipaikka, E. 2006. A statistical score for assessing the quality of multiple sequence alignments. *BMC Bioinformatics* **7**: 484–503.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Second International Symposium on Information Theory. Budapest: Akademiai Kiado, P. 267–281.

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transacations on Automatic Control* **19**: 716–723.

Armas, L.F. 1981. El género *Centruroides* Marx, 1890 (Scorpiones: Buthidae) en Bahamas y República Dominicana. *Poeyana* **227**: 1–7.

Armas, L.F. 1983. The Lesser Antillean scorpions of the genus *Centruroides.* Uitgaven "Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen", Utrecht, **15**(197), **11**: 55–67.

Armas, L.F. 1988. Sinopsis de los escorpiones antillanos. La Habana: Editorial Cientifico-Tècnica, p. 56–57.

Armas, L.F. & Martin-Frias, E. 2003. Nueva especie de *Centruroides* Marx, 1890 (Scorpiones: Buthidae) del estado de Veracruz, Mexico. *Boletin de la Sociedad Entomologica Aragonesa* **7**: 205–209.

Armas, L.F., Martin-Frias, E. & Estevez–Ramirez, J. 2003 Lista anotida de las especies mexicanas del genero *Centruroides* Marx, 1890 (Scorpiones: Buthidae). *Revisra Ibérica de Aracnología* **9**: 93–98.

Armas, L.F. & Trujillo, R.E. 2010. Nueva especie de *Centruroides* Marx, 1890 (Scorpiones: Buthidae) de Guatemala y Honduras, America Central. *Boletin de la Sociedad Entomologica Aragonesa* **47**: 235–240.

Arnedo, M.A., Oromì, P. & Ribera, C. 2002. Radiation of the spider genus *Dysdera* (Araneae, Dysderidae) in the Canary Islands: cladistic analysis based on multiple data sets. *Cladistics* **17**: 313–353.

Baker, R.H. & DeSalle, R. 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. *Systematic Biology* **46**: 674–698

Borges, A., Bermingham, E., Herrera, N., Alfonso, M.J. & Sanjur, O.I. 2010. Molecular systematics of the neotropical scorpion genus *Tityus* (Buthidae): The historical biogeography and venom antigenic diversity of toxic Venezuelan species. *Toxicon* **55**: 436–454.

Bouckaert, R.R. 2010. DensiTree: Making sense of sets of phylogenetic trees. *Bioinformatics* **26**(10): 1372–1373.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**: 795–803.

Bremer, K. 1994. Branch Support and Tree Stability. *Cladistics* **10**: 295–304.

Brower, A.V.Z. & DeSalle, R. 1994. Practical and theoretical considerations for choice of a DNA sequence region in insect molecular systematics, with a short review of published studies using nuclear gene regions. *Annals of the Entomological Society of America* **87**: 702–716.

Brower, A.V.Z., DeSalle, R. & Vogler, A. 1996. Gene trees, species trees, and systematics: a cladistic perspective. *Annual Review of Ecology and Systematics* **27**: 423– 450.

Bücherl, W. 1971. Classification, biology and venom extraction of scorpions. Pp. 317–348 in Bücherl, W. & Buckley, E.E. (Eds.), *Venomous Animals and Their Venoms*, *3*. Academic Press, New York, NY.

Celis A, Gaxiola-Robles, R., Sevilla-Godínez, E., de Jesús Orozco-Valerio, M. & Armas, J. 2007. Tendencia de la mortalidad por picaduras de alacran en Mexico, 1979–2003. *Pan American Journal of Public Health* **21**(6): 373–379.

Cheong, A., Li, J., Sukumar, P., Kumar, B., Zeng, F., Riches, K., Munsch, C., Wood, I.C., Porter, K.E. & Beech, D.J. 2011. Potent suppression of vascular smooth muscle cell migration and human neointimal hyperplasia by KV1.3 channel blockers. *Cardiovascular Research* **89**(2): 282–289.

Chippaux, J.P. & Goyffon, M. 2010. Epidemiology of scorpionism: A global appraisal. *Acta Tropica* **8**(107): 71–9.

Coddington, J.A., Giribet, G., Harvey, M.S., Prendini, L. & Walter, D.E. 2004. Arachnida. Pp. 296–318 in Cracraft, J. & Donoghue, M.J. (Eds.), *Assembling the Tree of Life*. Oxford University Press, New York, NY.

Coney, P.J. 1982. Plate tectonic constraints on the biogeography of Middle America and the Caribbean region. *Annals of the Missouri Botanical Garden* **69**: 432–443.

Córdova-Athanasiadis, M. & Francke, O.F. 2007. The identity of *Centruroides elegans edentulus*. *Journal of Arachnology* **34**: 634–635.

Crews, S.C. & Gillespie, R.G. 2010. Molecular systematics of *Selenops* spiders (Araneae: Selenopidae) from North and Central America: implications for Caribbean biogeography. *Biological Journal of the Linnean Society* **101**: 288–322.

Crother, B.I. & Guyer, C. 1996. Caribbean historical biogeography: Was the dispersal-vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica* **52**: 440–465.

Davalos, L.M. 2004. Phylogeny and biogeography of Caribbean mammals. *Biological Journal of the Linnean Society* **81**: 373–394.

Dehesa–Davila, M. & Possani, L.D. 1994. Scorpionism and serotherapy in Mexico. *Toxicon* **32**: 1015–1018.

Dengo, G. & Bohnenberger, O. 1969. Structural development of Northern Central America. *American Association of Petroleum Geologists Memoir* **II**.

Dengo, G. 1969. Problems of tectonic relations between Central America and the Caribbean. *Gulf Coast Association of Geological Societies* **XIX**: 311–320.

DeSalle, R., Egan, M.G. & Siddall, M. 2005. The unholy trinity: Taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society B* **360**(1462): 1905–1916.

Doyle, J.J. & Davis, J.I. 1998. Homology on molecular phylogenetics: a parsimony perspective. Pp. 101–131 in Soltis, D.E., Soltis, P.S. & Doyle, J.J. (Eds.), *Molecular Systematics of Plants II: DNA Sequencing*. Kluwer Academis Publishers, Dordrecht, The Netherlands.

Drummond, A.J. & Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7**: 214.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: e88.

Dunlop , J.A. & Braddy, S.J. 2001. Scorpions and their sister–group relationships. Pp. 1–24. in Fet, V. & Selden, P.A. (Eds.) *Scorpions 2001.* In Memoriam *Gary A. Polis.* British Arachnological Society, Burnham Beeches, Bucks, UK.

Eicksted, V.R.D. von, Ribeiro, L.A., Candido, D.M., Albuquerque, M.J. & Jorge, M.T. 1996. Evolution of scorpionism by *Tityus bahiensis* (Perty) and *Tityus serrulatus* Lutz And Mello and geographical distribution of the two species in the state of São Paulo, Brazil. *Journal of Venoms and Animal Toxins* **2**(2): 92–105.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* **39**: 783–791.

Fet, V. & Lowe, G. 2000. Family Buthidae C.L. Koch, 1837. Pp. 54–286 in Fet, V., Sissom, W.D., Lowe, G. & Braunwalder, M.E., *Catalog of the Scorpions of the World (1758–1998)*. New York Entomological Society, New York, NY.

Fet, V., Gantenbein, B., Gromov, A.V., Lowe, G. and Lourenço, W.R. 2003. The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius* **4**: 1–10

Fet, V., Petersen, M.E. & Slyusarev, G.S. 2003. RHOPALURUSINAE Bucherl, 1971 (Arachnida, Scorpiones, BUTHIDAE): Proposed conservation as the correct spelling to remove homonymy with RHOPALURIDAE Stunkard, 1937 (Orthonectida). *Bulletin of Zoological Nomenclature* **60**(1): 23–25.

Fet, V., Sissom, W.D., Lowe, G. & Braunwalder, M.E. 2000. *Catalog of the Scorpions of the World (1758–1998)*. The New York Entomological Society, New York, NY.

Fet, V., Soleglad, M.E. & Barker, M.D. 2001. Phylogenetic analysis of the "hirsutus" group of the genus *Hadrurus* Thorell, 1876 based on morphology and mitochondrial DNA (Scorpiones: Iuridae). Pp. 139–159 in Fet, V. & Selden, P.A. (Eds.), *Scorpions 2001.* In Memoriam *Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, UK.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytocrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology & Biotechnology* **3**: 294–299.

Francisco-Ortega, J., Ventosa, I., Oviedo, R., Jiménez, R.F., Herrera, P., Maunder, M. & Panero, J. 2008. Caribbean Island Asteraceae: Systematics, Molecules, and Conservation on a Biodiversity Hotspot. *Botanical Review* **74**(1): 112–131.

Francke, O.F. 1984. *Centrurus limpidus* Karsch, 1879 and *Centruroides ornatus* Pocock, 1902 (Arachnida, Scorpiones): proposed conservation. Z. N. (S.) 2446. *Bulletin of the Zoological Nomenclature* **41**(2): 97–100.

Francke, O.F. & Stockwell, S.A. 1987. Scorpions (Arachnida) from Costa Rica. *Special Publications of the Museum*, *Texas Tech University* **25**: 1–64.

Franke, O.F. 1978. Redescription of *Centruroides koesteri* Kraepelin (Scorpionida, Buthidae). *Journal of Arachnology* **6**: 65–71.

Fritsch, P.W. & McDowell, T.D. 2009. Biogeography and phylogeny of Caribbean plants, an introduction. *Systematic Botany* **28**(2): 376–377.

Gantenbein, B., Fet, V., Largiadèr, C.R. & Scholl, A. 1999. First DNA phylogeny of Euscorpius Thorell, 1876 (Scorpiones, Euscorpiidae) and its bearing on taxonomy and biogeography of this genus. *Biogeographica* **75**: 49–65.

Gantenbein, B., Largiadèr, C.R. & Scholl, A. 1999. Nuclear and mitochondrial gene variation of *Buthus occitanus* (Amoreux, 1789) across the Strait of Gibraltar. C.R. Zoologia et Botanica 99, Zürich 17–19 February 1999. *Revue suisse de Zoologie* **106**(4): 760.

Gantenbein, B., Fet, V., Barker, M. & Scholl, A. 2000. Nuclear and mitochondrial markers reveal the existence of two parapatric scorpion species in the Alps: *Euscorpius germanus* (C. L. Koch, 1837) and *E. alpha* Caporiacco, 1950, *stat. nov*. (Euscorpiidae). *Revue suisse de Zoologie* **107**: 843–869.

Gantenbein, B., Fet, V. and Barker, M.D. 2001. Mitochondrial DNA reveals a deep, divergent phylogeny in *Centruroides exilicauda* (Wood, 1863) (Scorpiones: Buthidae). Pp. 235–244 in Fet, V. & Selden, P.A. (Eds.), *Scorpions 2001.* In Memoriam *Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, UK.

Gantenbein, M.B., Fet, V. & Blaxter, M. 2007. The effect of model choice on phylogenetic inference using mitochondrial sequence data: Lessons from the scorpions. *Molecular Phylogenetics and Evolution* **43**(2): 583–595.

Gatesy, J., DeSalle, R. & Wahlberg, N. 2007. How many genes should a systematist sample? Conflicting insights from a phylogenomic matrix characterized by replicated incongruence. *Systematic Biology* **56**: 355–363.

Giribet, G. 2003. Stability in phylogenetic formulations and its relationship to nodal support. *Systematic Biology* **52**: 554–564.

Giribet, G. & Wheeler, W.C. 1999. On gaps. *Molecular Phylogenetics and Evolution* **13**: 132–143.

Giribet, G., Edgecombe, G.D. Wheeler, W.C. & Babbitt, C. 2002. Phylogeny and systematic position of Opiliones: A combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* **18**: 5–70.

Giribet, G., Edgecombe, G.D. & Wheeler, W.C. 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature* **413**: 157–161.

Goldman, N., Anderson, J.P., Rodrigo, A.G. 2000. Likelihood-based tests of topologies in phylogenetics. *Systematic Biology* **49**(4): 652–70.

Goloboff, P.A. 1993. Estimating character weights during tree search. *Cladistics*: **9**: 83–91.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* **15**: 415–428.

Goloboff, P.A., Farris, S. & Nixon, K. 2000. *TNT (Tree analysis using New Technology)*, *version BETA 2*, *January 2004*. Published by the authors.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M. & Szumik, C.A. 2003. Improvements to resampling measures of group support. *Cladistics* **19**: 324–332.

Gonzalez-Santillan, E. 2004. Escorpiofauna of Estado de Mexico. Master's thesis. UNAM, Mexico, 141 pp.

Gow, J.L., Peichel, C.L. & Toylor, E.B. 2005. Contrasting hybridization rates between sympatric three-spined sticklebacks highlight the fragility of reproductive barriers between evolutionarily young species. *Molecular Ecology* **15**(3): 739–752.

Grimaldi, D. & Engel, M.S. 2005. *Evolution of the Insects*. New York/Cambridge: Cambridge University Press. 755 pp.

Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, New York, NY.
Harrison, R.G., Rand, D.M. & Wheeler, W.C. 1987. Mitochondrial DNA variation in field crickets across a narrow hybrid zone. *Molecular Biology and Evolution* **24**: 363–371.
Hayashi, C.Y. 1996. Molecular Systematics of Spiders: Evidence from Ribosomal DNA. Unpublished PhD Dissertation, Yale, New Haven, CT.
Heaney, L.R. 2007. Is a new paradigm emerging for oceanic island biogeography? *Journal of Biogeography* **34**(5): 753–757.
Hedges, S.B. 1996a. Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics* **27**: 163–196.
Hedges, S.B. 1996b. The origin of West Indian amphibians and reptiles. Pp. 95–128 in *Contributions to West Indian herpetology: A tribute to Albert Schwartz*, Powell, R. & Henderson, R.W. (eds.). Society for the Study of Reptiles and Amphibians, Ithaca, NY.
Hedges, S.B. 1996c. Vicariance and dispersal in Caribbean biogeography. *Herpetologica* **52**: 466–473.
Hedges, S.B. & Heinicke, M.P. 2007. Molecular phylogeny and biogeography of West Indian frogs of the genus *Leptodactylus* (Anura, Leptodactylidae). *Molecular Phylogenetics and Evolution* **44**(1): 308–314.
Heinicke, M.P., Duellman, W.E. & Hedges, S.B. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences* **104**(24): 10092–10097.
Heled, J. & Drummond, A.J. 2010. Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* **27**(3): 570–80.
Hillis, D.M. & Dixon, M.T. 1991. Ribosomal DNA: Molecular evolution and phylogenetic inference. *Quarterly Review of Biology* **66**: 411–453.
Hjelle, J.T. 1990. Anatomy and Morphology. Pp. 9–63 in Polis, G.A. (Ed.), *The Biology of Scorpions*. Stanford University Press, Stanford, CA.
Hoffmann, C.C. 1932. Monografías para la Entomología Médica de México. Monografía Núm. 2. Los Scorpiones de México. Segunda parte: Buthidae. *Anales del Instituto Biologia*, *México* **3**(4): 283–361.
Huber, D., Gantenbein, B., Fet, V. & Scherabon, B. 2001. *Euscorpius carpathicus* (Lamoral, 1767) in Austria: Phylogenetic position clarified by mitochondrial DNA analysis (Scorpiones: Euscorpiidae). Pp. 273–278 in Fet, V. & Selden, P.A. (Eds.), *Scorpions 2001.* In Memoriam *Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, UK.
Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755.
Iturralde-Vinent, M.A & MacPhee, R.D.E. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* **238**: 1–95.
Jahan, S., Mohammed Al Saigul, A. & Abdul Rahim Hamed, S. 2007. Scorpion stings in Qassim, Saudi Arabia: a 5-year surveillance report. *Toxicon* **50**(2): 302–305.
Jeram, A.J. 1994. Carboniferous Orthosterni and their relationship to living scorpions. *Paleontology* **37**(3): 203–470.

Jeram, A.J. 1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. Pp 17–31 in Selden, P.A. (Ed.), *Proceedings of the 17th European Colloquium of Arachnology*, *Edinburgh*, *1997*. British Arachnological Society, Burnham Beeches, Bucks, UK.

Kamenz, C. & Prendini, L. 2008. An atlas of book lung ultrastructure in the Order Scorpiones (Arachnida). *Bulletin of the American Museum of Natural History* **316**: 1–259.

Katoh, K., Kuma, K., Toh, H. & Miyata, T. 2005. MAFFT version 5: Improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* **33**: 511–518.

Katoh, M. & Kuma, M. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**: 3059–3066.

Kievit, F.M., Veiseh, O., Fang, C., Bhattarai, N., Lee, D., Ellenbogen, R.G. & Zhang, M. 2010. Chlorotoxin labeled magnetic nanovectors for targeted gene delivery to glioma. *ACS Nano* **4**(8): 4587–4594.

Kjellesvig-Waering, E.N. 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica Americana* **55**: 1–257.

Kluge, A.G. 1998. Total evidence or taxonomic congruence: Cladistics or consensus classification. *Cladistics* **14**: 151–158.

Koch, C.L. 1837 (1838). Die Arachniden. Getreu nach der Natur Abgebildet und Beschrieben. C.H. Zeh'schen, Nürnberg.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X. & Wilson, A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences* **86**: 6196–6200.

Kovařík, F. 2001. Catalog of the Scorpions of the World (1758–1998) by V. Fet, W.D. Sissom, G. Lowe, and M. Braunwalder (New York Entomological Society, 2000:690 pp.) Discussion and supplement for 1999 and part of 2000. *Serket* **7**: 78–93.

Kovařík, F. 2002. Co nového u štírů v roce 2000. *Akvárium Terárium* **45**: 55–61.

Kovařík, F. 2003. Co nového u štírů v roce 2001. *Akvárium Terárium* **45**: 55–61.

Kraepelin, K. 1891. Revision der Skorpione. I. Die Familie der Androctonidae. Jarbuch der Hamburgischen Wissenschaftlichen Anstalten 8: 1–144.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. Pp. 1–165 *in* F. Dahl (ed.), Das Tierreich 8 (Arachnoidea), Herausgegeben von der Deutschen Zoologischen Gesellschaft. R. Friedlander und Sohn Verlag, Berlin, Germany.

Ladd, J.W. 1976. Relative motion of South America with respect to North America and Caribbean tectonics. *Geological Society of America Bulletin* **87**: 969–976.

Lambkin, C.L., Lee, M.S.Y., Winterton, S.L. & Yeates, D.K. 2002. Partitioned Bremer support and multiple trees. *Cladistics* **18**: 436–444.

Lamoral, B.H. 1978. Systematics and bionomics of the scorpions of South West Africa (Arachnida, Scorpionida). Ph.D. Thesis, University of Natal, Pietermaritzburg.

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* **23**(3):497–784.

Lamoral, B.H. 1980. Two new psammophile species and new records of scorpions from the northern Cape Province of South Africa (Arachnida: Scorpionida). *Annals of the Natal Museum* **24**: 201–210.

Lavin, M. & Matos, A. 2008. The impact of ecology and biogeography on legume diversity, endemism, and phylogeny in the Caribbean region: A new direction in historical biogeography. *The Botanical Review* **74**(1): 178–196.

Lavin, M., Wojciechowski, M.F., Richman, A., Rotella, J., Sanderson, M.J. & Matos, A.B. 2001. Identifying tertiary radiations of Fabaceae in the Greater Antilles: alternatives to cladistic vicariance analysis. *International Journal of Plant Sciences* **162**: S53–S76.

Lewis, J.F. & Draper, G. 1990. Geological and tectonic evolution of the northern Caribbean margin. Pp. 77–140 in Dengo, G. & Case, J.E. (Eds.), *The Caribbean Region*, *Geology of North America*, *Volume H*. Geological Society of America, Boulder, CO.

Lewis, J.L. & Garcia, M.L. 2003. Theraputic potential of venom peptides. *Nature Reviews: Drug Discovery* **2**: 790–802.

Lewis, P.O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biol*ogy **50**: 913–925.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley, CA.

Lourenço, W.R., Duhem, B. & Cloudsley-Thompson, J.L. 2010. A new relictual buthid scorpion from the region of the Great Rift Valley in Kenya (Scorpiones, Buthidae). *Comptes Rendus Biologies* **333**(3): 280–285.

Lourenço, W.R. & Duhem, B. 2009. Saharo-Sindian buthid scorpions; description of two new genera and species from Occidental Sahara and Afghanistan. *ZooKeys* **14**: 37–54.

Lourenço, W.R. & Cloudsley-Thompson, J.L. 1995. Stridulatory apparatus and the evolutionary significance of sound production in *Rhopalurus* species (Scorpiones: Buthidae). *Journal of Arid Environments* **31**(4): 423–429.

Lourenço, W.R. 1979. A propos de la véritable identité des generes *Rhopalurus* Thorell, 1876 et *Centruroides* Marx, 1899 (Scorpiones, Buthidae). *Revue Arachnologique* **2**: 213–219.

Lourenço, W.R. 1986. Biogéographie et phylogénie des scorpions du genre *Rhopalurus* Thorell, 1876 (Scorpiones, Buthidae). *Mémoires de la Société Royale Belge d'Entomologie* **33**: 129–137.

Lourenço, W.R. 2007. New considerations on the taxonomic status of the genus *Physoctonus* Mello-Leitão, 1934 (Scorpiones, Buthidae). *Boletin de la Sociedad Entomológica Aragonesa* **40**: 359–365.

Lourenço, W.R. & Sissom, W.D. 2000. Scorpiones. Pp. 115–135 in Llorente Bousquets, J.E., García Aldrete, A.N. & González Soriano, E. (Eds.), *Biodiversidad*, *taxonomía y biogeografía de artrópodos de México*: *Hacia una síntesis de su conocimiento*. Universidad Nacional Autonoma de Mexico, Mexico.

Lowe G. 2010. New picobuthoid scorpions (Scorpiones: Buthidae) from Oman. *Euscorpius* **93**: 1–53.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Maddison, W.P. 1997. Gene trees in species trees. *Systematic Biology* **46**: 523–536.

Maddison, W. P. & Maddison, D.R. 2010. *Mesquite: A modular system for evolutionary analysis. Version 2.73.* Published by the authors, available at http://mesquiteproject.org

Mallet, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology and Evolution* **20**(5): 229–237.

Mann, P., Calais, E., Ruegg, J.C., DeMets, C., Jansma, P.E. & Mattioli, G.S. 2002. Oblique collision in the northeastern Caribbean from GPS measurements and geological observations. *Tectonics* **21**: 1057–1083.

Marx, G. 1890. Arachnida. *Proceedings of the United States National Museum* **12**: 207–211.

Mazzotti, L. & Bravo-Becherelle, M.A. 1963. Scorpionism in the Mexican Republic. Pp. 119-131 in Keegan, H.L. & McFarland, W.W. (Eds.), *Venomous and Poisonous Animal and Noxious Plants of the Pacific Area*. Pergamon, New York, NY.

Meise, W. 1934. Scorpiones. *Nyt Magizin for Naturvidenskaberne* **72**: 25–43.

Mello-Leitão, C. 1945. Escorpiões sul-americanos. *Arquivos de Museu Nacional* **XL**: 468.

Meyerhoff, A.A. and C.W. Hatten. 1974. Bahamas salient of North America: Tectonic framework, stratigraphy and petroleum potential. *AAPG Bulletin* **58**: 1201–1239.

Michelangeli, F., Judd, W., Penneys, D., Skean, J., Bécquer-Granados, E., Goldenberg, R. & Martin, C. 2008. Multiple events of dispersal and radiation of the tribe Miconieae (Melastomataceae) in the Caribbean. *The Botanical Review* **74**(1): 53–77.

Miller, M.A., Holder, M.T., Vos, R., Midford, P.E., Liebowitz, T., Chan, L., Hoover, P. & Warnow, T. 2009. The CIPRES Portals. CIPRES. Available at http://www.phylo.org/sub_sections/portal.

Moreno, A. 1940. Contribucíon al estudio de los escorpiónidos Cubanos. Parte III– Familia "Buthidae". Addendus. *Memorias de la Sociedad Historia Natural* **14**(2): 161–164.

Mullins, H.T. & Lynts, G.W. 1977. Origin of the northwestern Bahama platform: Review and reinterpretation. *GSA Bulletin* **88**: 1147–1161.

Muma, M.H. 1967. Scorpions, whipscorpions and wind scorpions of Florida. *Arthropoda of Florida and Neighboring Land Areas* **4** (95): 1–28.

Navidpour, S. & Lowe, G. 2009. Revised diagnosis and redescription of Apistobuthus susanae (Scorpiones, Buthidae). *Journal of Arachnology* **37**(1): 49–59.

Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**: 407–414.

Nixon, K.C. & Wheeler, Q.D. 1990. An amplification of the phylogenetic species concept. *Cladistics* **6**: 211–223.

Novacek MJ. 1992. Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals. *Systematic Biology* **41**: 58–73.

Nuin, P., Wang, Z. & Tillier, E. 2006. The accuracy of several multiple sequence alignment programs for proteins. *BMC Bioinformatics* **7**: 471.

Nunn, G.B., Theisen, B.F., Christensen, B. & Arctander, P. 1996. Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. *Journal of Molecular Evolution* **42**: 211–223.

Nylander, J.A.A. 2004. *MrModeltest v2.* Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Nylander, J.A.A., Wilgenbush, J.C., Warren, D.L. & Swofford, D.L. 2008. AWTY (Are We There Yet?): A system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* **24**: 581–583.

Oneal, E. 2009. Biogeographic and evolutionary mechanisms driving diversification in Caribbean ground crickets (genus *Amphiacusta*). Unpublished PhD Dissertation. University of Michigan, Ann Arbor, MI.

Page, R.D.M. 1996. TREEVIEW: An application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12**: 357–358.

Pattengale, N.D., Alipour, M., Bininda-Emonds, O.R.P., Moret, B.M.E., Gottlieb, E.J. & Stamatakis, A. 2010. How many bootstrap replicates are necessary? *Journal of Computational Biology* **17**(3): 337–354.

Pocock, R.I. 1890. A revision of the genera if scorpions in the family Buthidae, with descriptions of some South-African Species. *Proceedings of the Zoological Society of London* **1890**: 114–141.

Pocock, R.I. 1893. Contributions to our knowledge of the arthropod fauna of the West Indies. Part I. Scorpiones and Pedipalpi, with a supplementary note upon the freshwater Decapoda of St. Vincent. *Journal of the Linnaean Society* **24**: 374–409.

Pocock, R.I. 1902 *Arachnida*, *Scorpiones*, *Pedipalpi and Solifugae. Biologia Centrali-Americana.* Taylor & Francis, London, 71 pp.

Pocock, R.I. 1904. On a new stridulating-organ in scorpions discovered by W.J. Burchell in Brazil in 1828. *Annals and Magazine of Natural History* **7**(13): 56–62.

Polis, G.A. & Farley, R.D. 1979. Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Journal of Zoology* **187**: 517–542.

Polis, G.A. & Sissom, W.D. 1990. Life history. Pp. 161–223 in Polis, G.A. (Ed.), *The Biology of Scorpions*. Stanford University Press, Stanford, CA.

Ponce-Saavedra, J. & Moreno-Barajas, R.J. 2005. El gènero *Centruroides* Marx 1890 (Scorpiones: Buthidae) en Mèxico. *Biològicas* **7**: 42–51.

Ponce-Saavedra, J. & Francke, O.F. 2004. Una nueva especie de alacrán del género *Centruroides* Marx (1890) (Scorpiones: Buthidae) de la depresión del Balsas, México. *Acta Zoológica Mexicana* **20**: 221–232.

Ponce-Saavedra, J. & Francke, O.F. 2009. Description of a new species of scorpion of medical importance of the genus *Centruroides* (Scorpiones: Buthidae) from the state of Colima, Mexico. *Revista Mexicana de Biodiversidad* **80**: 647– 658.

Ponce-Saavedra, J., Francke, O.F., Cano-Camacho, H. & Hernández-Calderón, E. 2009. Evidencias morfológicas y moleculares que validan como especie a *Centruroides tecomanus* (Scorpiones, Buthidae). *Revista Mexicana de Biodiversidad* **80**(1): 71–84.

Posada, D. & Crandall, K.A. 1998. Modeltest: Testing the model of DNA substitution. *Bioinformatics* **14**(9): 817–818.

Prager, E.M. & Wilson, A.C. 1988. Ancient origin of lactalbumin from lysozyme: analysis of DNA and amino acid sequences. *Journal of Molecular Evolution* **27**: 326–335.

Prendini L. 2000a. A new species of *Parabuthus* Pocock (Scorpiones: Buthidae), and new records of *Parabuthus capensis* (Ehrenberg), from Namibia and South Africa. *Cimbebasia* **16**: 31–45.

Prendini, L. 2000b. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. *Cladistics* **16**: 1–78.

Prendini, L. 2001a. Two new species of *Hadogenes* (Scorpiones, Ischnuridae) from South Africa, with a redescription of *Hadogenes bicolor* and a discussion on the phylogenetic position of *Hadogenes*. *Journal of Arachnology* **29**: 146–172.

Prendini L. 2001b. Phylogeny of *Parabuthus* (Scorpiones, Buthidae). *Zoologica Scripta* **30**: 13–35.

Prendini L. 2001c. Substratum specialization and speciation in southern African scorpions: The Effect Hypothesis revisited. Pp. 113–138 in Fet, V. & Selden, P.A. (Eds.), *Scorpions 2001*. In Memoriam *Gary A. Polis.* British Arachnological Society, Burnham Beeches, Bucks, UK.

Prendini, L. 2001d. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology* **50**(2): 290–300.

Prendini, L. 2003. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology* **28**(2): 149–172.

Prendini L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109–186.

Prendini, L., Crowe, T.M. & Wheeler, W.C. 2003. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. *Invertebrate Systematics* **17**: 185–259.

Prendini, L., Weygoldt, P. & Wheeler, W.C. 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): Evidence from behaviour, morphology and DNA. *Organisms*, *Diversity and Evolution* **5**: 203–236.

Prendini, L., Esposito, L.A., Huff, J.C. & Volschenk, E.S. 2009. Redescription of *Rhopalurus abudi* Armas & Marcano Fondeur (Scorpiones: Buthidae), with first description of the male and first record from Hispaniola. *Journal of Arachnology* **37**: 206–244.

Prendini, L., Volschenk, E.S., Maaliki, S. & Gromov, A.V. 2006. A 'living fossil' from Central Asia: The morphology of *Pseudochactas ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position. *Zoologischer Anzeiger* **245**: 211–248.

Prendini, L., Francke, O.F. & Vignoli, V. 2010, Troglomorphism, trichobothriotaxy and typhlochactid phylogeny (Scorpiones, Chactoidea): More evidence that troglobitism is not an evolutionary dead-end. *Cladistics* **26**: 117–142.

Rambaut, A. & Drummond, A.J. 2007. *Tracer v1.4.* Published by the authors, available from http://beast.bio.ed.ac.uk/Tracer.

Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**(11): 2299–2311.

Ricklefs, R. & Bermingham, E. 2008. The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B*, *Biological Sciences* **363**: 2393–2413.

Ronquist, F. & Huelsenbeck, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986. *Akaike information criterion statistics*. Springer, New York, NY.

Sanderson, M.J. & Shaffer, H.B. 2002. Troubleshooting molecular phylogenetic analyses. *Annual Reviews of Ecology and Systematics* **33**: 49–72.

Sanger, F., Nicklen, S. & Coulsen, A.R. 1977. DNA sequencing with chain terminating inhibitors. *Proceedings of the National Academy of Sciences* **74**: 5463–5468.

Sanmartín, I. & Ronquist, F. 2004. Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology* **53**: 216–243.

Santibanez-Lopez, C.E. and Ponce-Saavedra, J. 2009. A new species of *Centruroides* (Scorpiones: Buthidae) from the northern mountains of Oaxaca. *Revista Mexicana de Biodiversidad* **80**: 321– 331.

Santiago-Blay, J.A. 2009. Systematics and some aspects of the biology of the scorpions (Arachnida) of the greater Puerto Rico region: A biosystematic synopsis. *Entomological News* **120**(1): 109–124

Santiago-Blay, J.A. & Poinar Jr., G.O. 1993. First scorpion (Buthidae: *Centruroides*) from Mexican amber (Lower Miocene to Upper Oligocene). *Journal of Arachnology* **18**: 115–117.

Santiago-Valentin, E. & Olmstead, R.G. 2004. Historical biogeography of Caribbean plants: Introduction to current knowledge and possibilities from a phylogenetic perspective. *Taxon* **53**: 299–315.

Schawaller, W. 1979. 1st record of a scorpion from Dominican Amber Collection Stuttgart (Arachnida Scorpionida). *Stuttgarter Beitraege zur Naturkunde Serie B Geologie und Palaeontologie*: 1–15.

Schawaller, W. 1982. Zwei weitere Skorpione in Dominikanischem Berstein. (Stuttgarter Bernsteinsammlung: Arachnida; Scorpionida). *Stuttgarter Beiträge zur Naturkunde- Serie B* **82**:1–14.

Scherabon, B., Gantenbein, B., Fet, V., Barker, M., Kuntner, M., Kropf, C. & Huber, D. 2000. A new species of scorpion for Austria, Italy, Slovenia and Croatia: *Euscorpius gamma* Caporiacco, 1950, *stat. nov*. (Scorpiones, Euscorpiidae). *Ekólogia (Bratislava)* **19**: 253–262.

Shahbazzadeh, D., Amirkhani, A., Djadid, N.D., Bigdeli, S., Akbari, A. & Ahari, H. 2009. Epidemiological and clinical survey of scorpionism in Khuzestan province, Iran. *Toxicon* **53**(4): 454–9.

Shalita, E.A. & Wells, R.D. 2007. Treatment of yellow scorpion (*Leiurus quinquestriatus*) sting: A case report. *Journal of the American Pharmacists Association* **47**(5): 616–619.

Shimodaira, H. & Hasegawa, M. .1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* **16**: 1114–1116.

Simard, J.M. & Watt, D.D. 1990. Venoms and Toxins in Biology of Scorpions. Pp. 414–444 in Polis, G.A. (Ed.), *The Biology of Scorpions*. Stanford University Press, Stanford, CA.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P., 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**: 651–701.

Sissom, W.D. 1990. Systematics, biogeography, and paleontology. Pp. 64–160 in Polis, G.A. (Ed.), *The Biology of Scorpions*. Stanford University Press, Stanford, CA.

Sissom, W.D. & Hendrixson, B.E. 2005. Scorpion biodiversity and patterns of endemism in northern Mexico. Pp. 122–137 in Cartron, J.L.E. & Ceballos, G. (Eds.), *Biodiversity*, *Ecosystems*, *and Conservation in northern Mexico*. Oxford University Press, Oxford, UK.

Sissom, W.D. & Lourenço, W.R. 1987. The genus *Centruroides* in South America (Scorpiones, Buthidae). *Journal of Arachnology* **15**: 11–28.

Smith, S.A. & Dunn, C.W. 2008. Phyutility: A phyloinformatics tool for trees, alignments, and molecular data. *Bioinformatics* **24**: 715–716

Soleglad, M.E. & Fet, V. 2001. Evolution of scorpion orthobothriotaxy- a cladistic approach. *Euscorpius* **1**: 1–38.

Soleglad, M.E. & Fet, V. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius* **11**: 1–175.

Soleglad, M.E. & Sissom, W.D. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: A major revision. Pp. ??? in Fet, V. & Selden, P.A. (Eds.) *Scorpions 2001*. In Memoriam *Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, UK.

Sorenson, M.D. & Franzosa E.A. 2007. *TreeRot*, *version 3*. Boston University, Boston, MA.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. *Entomological News* **81**: 297–316.

Stahnke, H.L. & Calos, M. 1977. A key to the species of the genus *Centruroides* Marx (Scorpionida: Buthidae). *Entomological News* **88**: 111–120.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. *Bioinformatics* **22**(21): 2688–2690.

Stockwell, S.A. 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). Unpublished PhD Dissertation, University of California, Berkeley.

Stockwell, S.A. 1992. Systematic observations on North American Scorpionida with a key and checklist of the families and genera. *Journal of Medical Entomology* **29**: 407–422.

Stunkard, H.W. 1937. The physiology, life-cycles and phylogeny of the parasitic flatworms. *American Museum Novitates* **908**: 1–27.

Sturge, R., Jacobsen, F., Rosensteel, B.B., Neale, R.J. & Omland, K.E. 2009. Colonization of South America from Caribbean Islands confirmed by molecular phylogeny with increased taxon sampling. *Condor* **11**: 575–579.

Swofford, D.L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*, *Version 4*. Sinauer Associates, Sunderland, MA.

Templeton, A.R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* **37**(2): 221–244.

Teruel, R. 2001. Tres nuevas especies de *Centruroides* (Scorpiones: Buthidae) de Cuba. *Revista Ibérica de Aracnologia* **3**: 93–107.

Teruel, R. 2005. Nuevos datos sobre la taxonomía, distribución geográfica y ecología de los escorpiones de la República Dominicana (Scorpiones: Liochelidae, Scorpionidae: Buthidae). *Boletín de la Sociedad Entomológica Aragonesa* **36**: 165–176.

Teruel, R. 2006. Apuntes sobre la taxonomía y biogeografía del género *Rhopalurus* Thorell 1876 (Scorpiones: Buthidae), con la descripción de dos nuevas especies de Cuba. *Boletín de la Sociedad Entomológica Aragonesa* **38**: 43–56.

Teruel, R. 2007. Una nueva especie de *Centruroides* Marx 1890 del groupo "arctimanus" (Scorpiones: Buthidae) de Cuba. *Boletín de la Sociedad Entomológica Aragonesa* **40**: 187–193.

Teruel, R. & Stockwell, S.A. 2002. A review of the scorpion fauna of Honduras, with the description of a new species (Scorpiones: Buthidae, Diplocentridae). *Revista Ibérica de Aracnología* **6**: 111–127.

Teruel, R., Fet, V. & Graham, M.R. 2006. The first mitochondrial DNA phylogeny of Cuban Buthidae (Scorpiones: Buthoidea). *Boletìn Sociedad Entomològica Aragonesa* **39**: 219–226.

Teruel, R. & Kovařík, F. 2010. The true identity of the enigmatic scorpion *Centruroides subgranosus* (Kraepelin, 1898), with some taxonomic comments on *Centruroides vittatus* (Say, 1821) and *Centruroides suffusus* Pocock, 1902 (Scorpiones: Buthidae). *Euscorpius* **97**: 1–11.

Thomson, R.C. & Shaffer, H.B. 2010. Rapid progress on the vertebrate tree of life. *BMC Biology* **8**: 19.

Thorell, T. 1876. Etudes scorpiologiques. *Atti Societe Italienne de Sciences Naturelles* **19**: 75–272.

Thorley, J.L. & Page, R.D. 2000. Radcon: Phylogenetic tree comparison and consensus. *Bioinformatics* **16**: 486–487.

Towler, W.I., Ponce-Saavedra, J., Gantenbein, B. & Fet, V. 2001. Mitochondrial DNA reveals divergent phylogeny in tropical *Centruroides* (Scorpiones: Buthidae) from Mexico. *Biogeographica* **77**(4): 157–172.

Vachon, M. 1973 [1974]. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle* **3**(140): 857–958.

van Ee, B., Berry, P., Riina, R. & Gutiérrez Amaro, J. 2008. Molecular phylogenetics and biogeography of the Caribbean-centered croton subgenus *Moacroton* (Euphorbiaceae s.s.). *The Botanical Review* **74**(1): 132–165.

Viquez, C. 1999. *Escorpiones de Costa Rica*. Santo Domingo, Heredia: INBio, 84 pp.
Volschenk, E.S. 2005. A new technique for examining surface morphosculpture of scorpions. *Journal of Arachnology* **33**: 820–825.
Volschenk, E.S., Mattoni, C.I. & Prendini, L. 2008. Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order. *Zoological Journal of the Linnean Society* **154**: 651–675.
Wahlberg, N. & Zimmermann, M. 2000. Pattern of phylogenetic relationships among members of the tribe Melitaeini (Lepidoptera: Nymphalidae). *Cladistics* **16**: 347–363.
Wiens, J.J. & Moen, D.S. 2008. Missing data and the accuracy of Bayesian phylogenetics. *Journal of Systematics and Evolution* **46**(3): 307–314.
Werner, F. 1939. Ueber einige Skorpione aus dem Museum Alexander Koenig. Festschrift 60. Geburtstag von Professor Embrik Strand **5**: 361–362.
Williams, E.E. 1989. A critique of Guyer and Savage (1986): Cladistic relationships among anoles (Sauria: Iguanidae): Are the data available to reclassify the anoles? Pp. 433–478 in Woods, C.A. (Ed.), *Biogeograpy of the West Indies. Past*, *Present*, *and Future*. Sandhill Crane, Gainesville, FL.
Williams, S.C. 1976. The scorpion fauna of California. *Bulletin for the Society for Vector Ecology* **3**: 14.
Wilm, A., Mainz, I. & Steger, G. 2006. An enhanced RNA alignment benchmark for sequence alignment programs. *Algorithms for Molecular Biology* **1**: 19.
Wilson, E.O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* **95**: 169–193.
Wilson, J.S. & Pitts, J.P. 2010. Illuminating the lack of consensus among descriptions of earth history data in the North American deserts: A resource for biologists. *Progress in Physical Geography* **34**(4): 419–441.
Yamashita, T. & Fet, V. 2001. Molecular approaches to biogeography. Pp. 347–369 In: Brownell P. H., and G. A. Polis (Eds). Scorpion Biology and Research. Oxford University Press, UK.
Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. *Journal of Molecular Evolution* **39**: 306–314.
Yu, Y., Harris, A.J. & He, X.J. 2011. *RASP (Reconstruct Ancestral State in Phylogenies) v1.103*. Published by the authors, available at http://mnh.scu.edu.cn/soft/blog/RASP

## DISCLAIMER

The new species names presented herein are not intended to formally establish new taxonomic names.