

Plucking with the plectrum: phylogeny of the New World buthid scorpion subfamily Centruroidinae Kraus, 1955 (Scorpiones: Buthidae) reveals evolution of three pecten-sternite stridulation organs

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Abstract. All New World buthid scorpions except one South American genus, *Ananteris* Thorell, 1891, comprise a monophyletic group. The monophyly of two subfamilies, Centruroidinae Kraus, 1955 (= Rhopalurusinae Bücherl, 1971) and Tityinae Bücherl, 1971, proposed to accommodate a subset of these genera, has never been tested. The genera accommodated within Centruroidinae are diverse and poorly defined. Prior to the research presented here, *Rhopalurus* Thorell, 1876 had a disjunct distribution in the Greater Antilles, the Guiana Shield of northern South America, and northeastern Brazil, where *Physoctonus* Mello-Leitão, 1934 and *Troglophopalurus* Lourenço et al., 2004 also occur. The generic distinction between *Rhopalurus* and *Centruroides* Marx, 1890, the most speciose genus of Centruroidinae, distributed from the midwestern United States to northern South America, and throughout the Caribbean, was also unclear. Previous studies suggested *Centruroides* was paraphyletic with respect to *Rhopalurus* and vice versa. The study presented here, the first rigorous test of the monophyly of Centruroidinae and its component genera, is based on 90 morphological characters and 4,260 aligned base-pairs of DNA sequence from three mitochondrial and two nuclear DNA loci for 102 terminal taxa, representing 24 species in seven ingroup genera, and nine species in three outgroup genera. Molecular and morphological data, analyzed separately and simultaneously, yielded congruent results. Centruroidinae was monophyletic whereas Tityinae was paraphyletic. *Centruroides* was monophyletic whereas *Rhopalurus* was paraphyletic, comprising several monophyletic groups congruent with its disjunct distribution. The results of this analysis justify the redefinition of *Rhopalurus* and *Troglophopalurus*, the revalidation of *Heteroctenus* Pocock, 1893, and the recently created genera *Ischnotelson* Esposito et al., 2017 and *Jaguajir* Esposito et al., 2017. The phylogeny indicates that three distinct types of pecten-sternite stridulation organ evolved in *Heteroctenus*, *Jaguajir* and *Rhopalurus*.

Key words. New World, savannah, Arachnida, *Rhopalurus*, systematics.

1. Introduction

The family Buthidae C.L. Koch, 1837, comprising 89 genera and approximately 1,110 described species of extant scorpions, is distributed worldwide and includes most of the world's medically important scorpions. Although the intrafamilial phylogenetic relationships of Buthidae remain largely untested, there is general agreement that

all New World buthids except one genus occurring in South America, *Ananteris* Thorell, 1891 (*Microananteris* Lourenço, 2003 was justifiably synonymized with *Ananteris* by BOTERO-TRUJILLO & NORIEGA 2011), comprise a monophyletic group, referred to hereafter as the “New World buthids” (CODDINGTON et al. 2004). This diverse

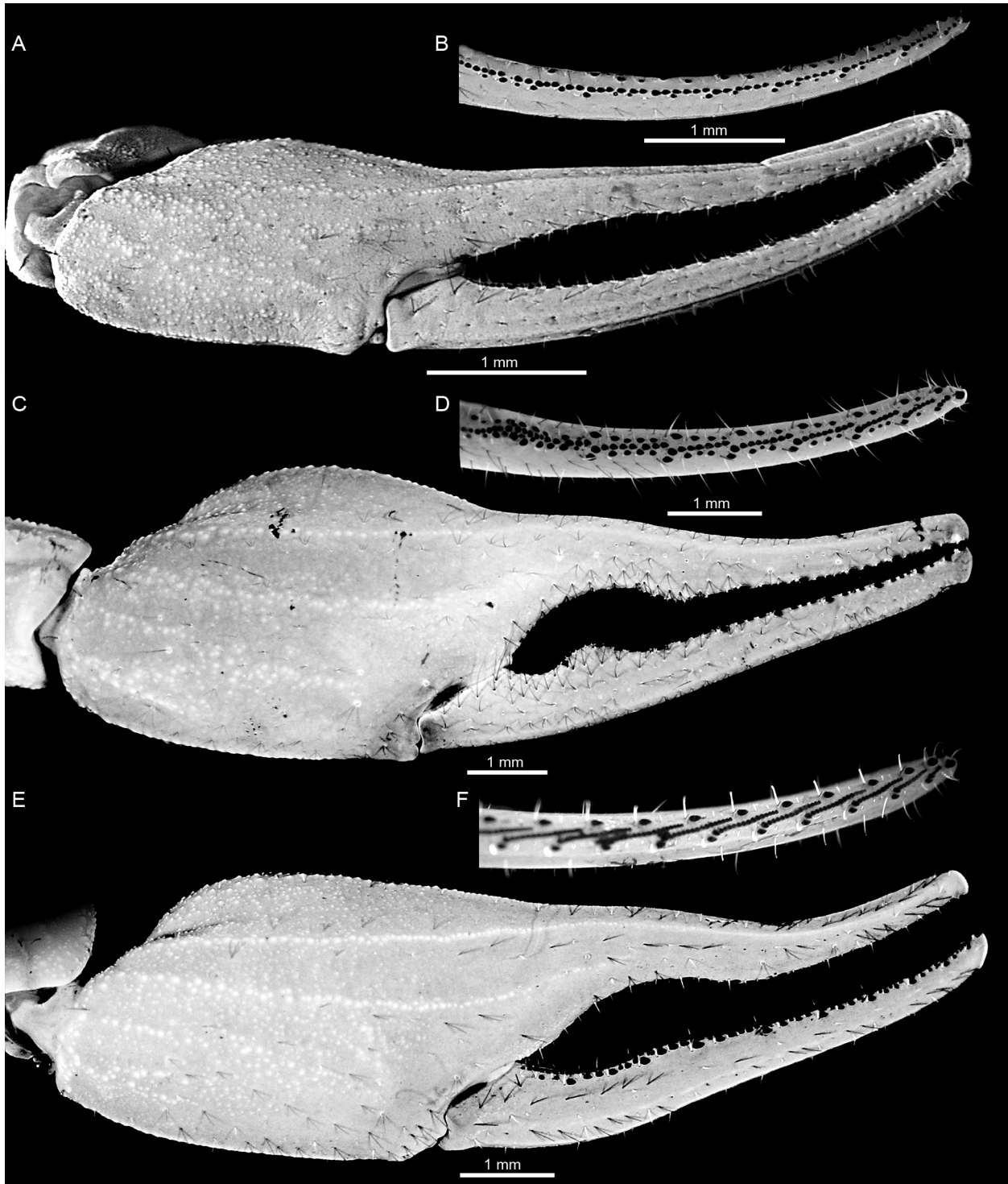


Fig. 1. Male pedipalp chela, retrolateral aspect, and movable finger, dorsal aspect of species in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955, illustrating shapes and denticle rows. **A:** *Physoctonus debilis* (C.L. Koch, 1840). **B:** *Physoctonus striatus* Esposito et al., 2017. **C, D:** *Jaguajir rochae* (Borelli, 1910). **E:** *Ischnotelson guanambiensis* (Lenarducci et al., 2005). **F:** *Tityus serrulatus* Lutz & Mello, 1922.

group, originally named Centrurini Kraepelin, 1891, is endemic to the New World and comprises approximately 398 described species in 14 genera: *Alayotityus* Armas, 1973; *Centruroides* Marx, 1890; *Chaneke* Francke et al., 2014; *Heteroctenus* Pocock, 1893; *Ischnotelson* Esposito et al., 2017; *Jaguajir* Esposito et al., 2017; *Mesotityus* Gonzalez-Sponga, 1981; *Microtityus* Kjellesvig-Waer-

ing, 1966; *Physoctonus* Mello-Leitão, 1934; *Rhopalurus* Thorell, 1876; *Tityopsis* Armas, 1974; *Tityus* C.L. Koch, 1836; *Troglohopalurus* Lourenço et al., 2004; *Zabius* Thorell, 1893.

The monophyly of New World buthids, excluding *Ananteris*, is supported by evidence from multiple independent sources. Comparative morphological studies of

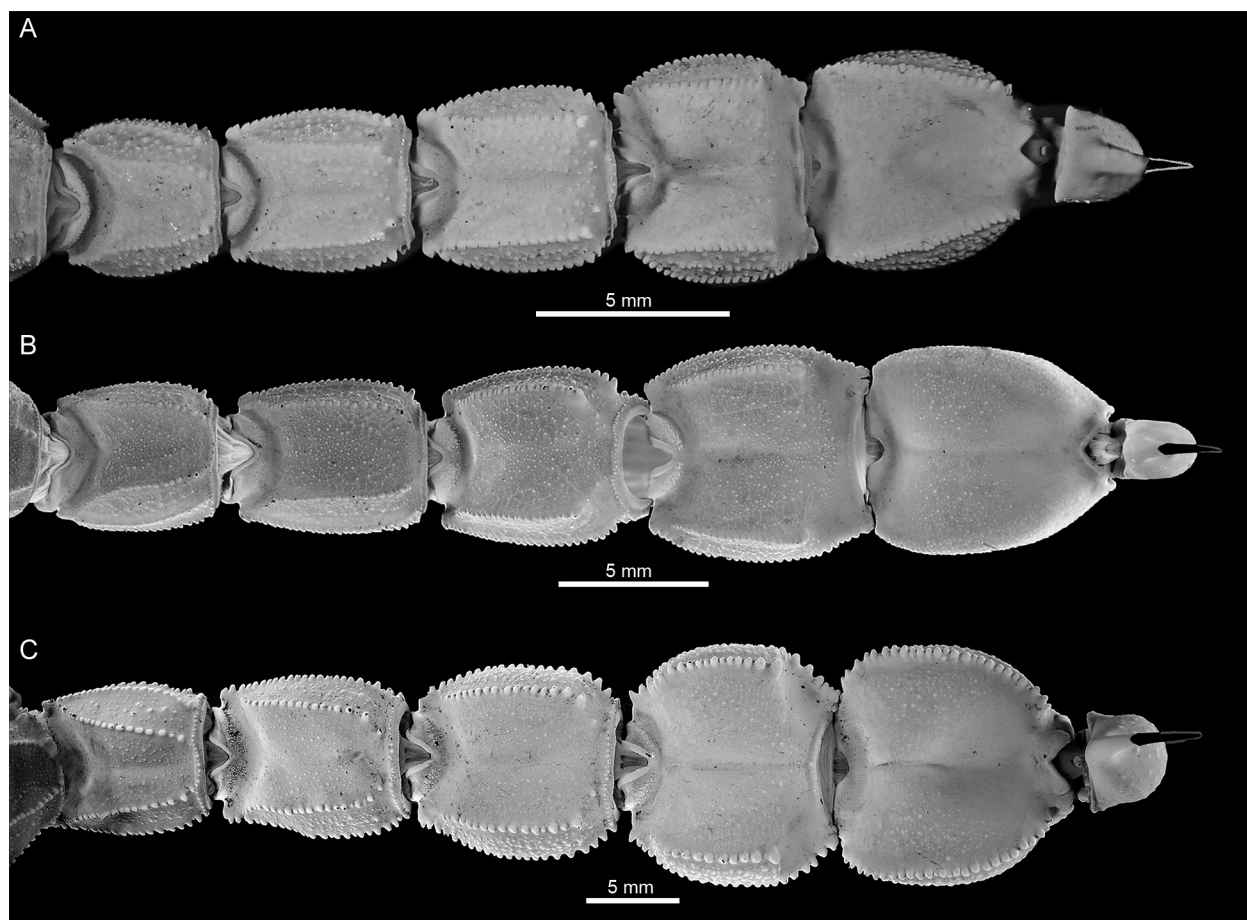


Fig. 2. Male metasoma, dorsal aspect, of species in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955, illustrating posterior widening. **A:** *Rhopalurus ochoai* Esposito et al., 2017. **B:** *Ischnotelson guanambiensis* (Lenarducci et al., 2005). **C:** *Jaguajir pinto* (Mello-Leitão, 1932).

pedipalp trichobothrial patterns (FET et al. 2005), book lungs (KAMENZ & PRENDINI 2008), and ovariuterine structure (VOLSCHENK et al. 2008) revealed potential synapomorphies, toxicological studies demonstrated the presence of a unique toxin class (β toxins), absent in other buthids (FROY et al. 1999), and phylogenetic analyses of transcriptomes (SHARMA et al. 2015) and nuclear and/or mitochondrial DNA sequences recovered its monophyly (FET et al. 2003a; CODDINGTON et al. 2004; BORGES & GRAHAM 2016; OJANGUREN-AFFILASTRO et al. 2017).

Although the monophyly of New World buthids has never been contested, there is less agreement about the names applied to the clade. BÜCHERL (1971) proposed two subfamilies to accommodate the four genera of New World buthids recognized at the time. Rhopalurinae, comprising *Centruroides* and *Rhopalurus*, was defined by the presence of pro- and retrolateral accessory (or supernumerary) denticles in the median denticle rows of the pedipalp chela fingers (Fig. 1B,D), whereas Tityinae Bücherl, 1971, comprising *Tityus* and *Zabius*, was defined by their absence (Fig. 1F). A great deal of confusion has surrounded the nomenclature for the New World buthid clade containing the genera *Centruroides* and *Rhopalurus*. KRAEPELIN (1891) first proposed Centrurini, subsequently emended to Centrurinae (KRAEPE-

LIN 1899), on *Centrurus* Ehrenberg, 1829. KRAEPELIN (1894) later synonymized *Centrurus* with *Heterometrus* Ehrenberg, 1828 of family Scorpionidae Latreille, 1802. *Centruroides* Marx, 1891 was meanwhile proposed, not as a replacement name for *Centrurus*, but for *Buthus exilicauda* Wood, 1863, a North American species, and another species that was named but not described (FET & LOWE 2000: 98). The name *Centrurus* was incorrectly used for many years to denote species of *Centruroides* because of an erroneous understanding and placement of *Centrurus*. Centruroidinae was considered a *nomen nudum* because it was first proposed after 1930 and ROEWER (1943) omitted a description from the designation, hence FET & LOWE (2000: 57) suggested Rhopalurinae should be used instead. FET et al. (2003b) emended Rhopalurinae to Rhopalurusinae to avoid homonymy. ESPOSITO et al. (2017), following FET & LOWE (2000) and FET et al. (2003b), used Rhopalurusinae. Soon after, ARMAS (2017) synonymized Rhopalurusinae with Centruroidinae and considered KRAUS (1955) the author of the latter, based on a brief description published in a footnote. Following arguments set forth in more detail in Appendix 1, the valid subfamily name is Centruroidinae Kraus, 1955, and the names Rhopalurinae and Rhopalurusinae, are junior synonyms thereof. On the other hand, Centruri-

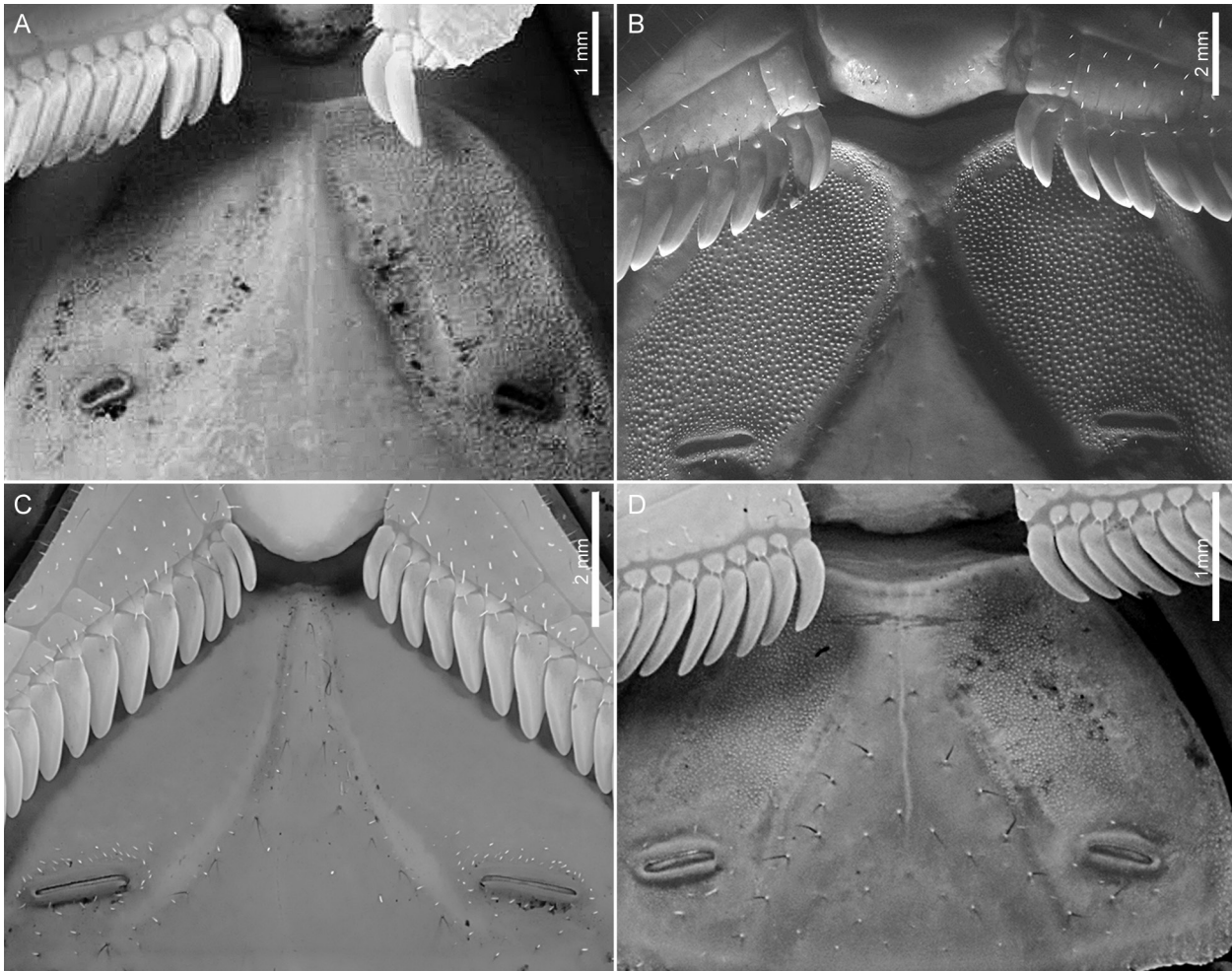


Fig. 3. Sternite III, ventral aspect, illustrating *pars stridens* of pecten-sternite stridulation organs of species in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955. **A:** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), ♂ (MZSP). **B:** *Jaguajir agamemnon* (C.L. Koch, 1839), ♀ (MZSP). **C:** *Heteroctenus junceus* (Herbst, 1800), ♀ (AMNH). **D:** *Rhopalurus ochoai* Esposito et al., 2017, holotype ♂ (AMNH).

nae is synonymous with Scorpionidae not Buthidae, as it is based on *Centrurus*, an available junior synonym of *Heterometrus* (BRAUNWALDER & FET 1998; FET 2000; FET & LOWE 2000). *Centrurus* is not a senior synonym of *Centruroides* or a *nomen nudum* as FRANCKE (1985) suggested (see also ICZN 1986: 144, 145).

Additional genera, described after the creation of these subfamilies, were not formally accommodated within them. No subfamilial classification of Buthidae is in widespread use (FET & LOWE 2000) as the monophyly of buthid subfamilies has never been rigorously tested. Four studies, each using a different data source and taxon sample, and in each case representing a very small sample of the taxonomic diversity within the family, recovered different results (FET et al. 2003a; SHARMA et al. 2015; BORGES & GRAHAM 2016; OJANGUREN-AFFILASTRO et al. 2017). It has long been suspected that the group of taxa herein referred to Centruroidinae may be monophyletic, however, due to the presence of accessory denticles in the median denticle rows of the pedipalp chela fingers, unique to these taxa among Buthidae (SISSON 1990).

Prior to the research presented here, the genera accommodated within Centruroidinae were also poorly defined. The ‘club-tailed’ scorpions of the genus *Rhopalurus* and the related genera, *Physoctonus* and *Trogloorhopalurus*, were a morphologically heterogeneous group of mostly large-bodied, often strikingly colored scorpions, usually with a broad metasoma that becomes noticeably wider posteriorly and an incrasate pedipalp chela in the adult male (Figs. 1, 2). *Rhopalurus* comprised 23 species and two subspecies whereas *Physoctonus* and *Trogloorhopalurus* were monotypic (Table 1). The unique ability to stridulate audibly by scraping nodules and/or ridges on the dorsal surfaces of the pectinal teeth against granules on the ventral surfaces of mesosomal sternite III (Figs. 3–5), a remarkable behavior that presumably functions to deter would-be predators (POCOCK 1904; LOURENÇO & CLOUDSLEY-THOMPSON 1995; LOURENÇO 2007; PRENDINI et al. 2009), was considered synapomorphic for *Rhopalurus* by LOURENÇO (1986) although this had not been tested quantitatively.

Physoctonus, long regarded a junior synonym of *Rhopalurus* (FRANCKE 1977), was recently resurrected (LOU-

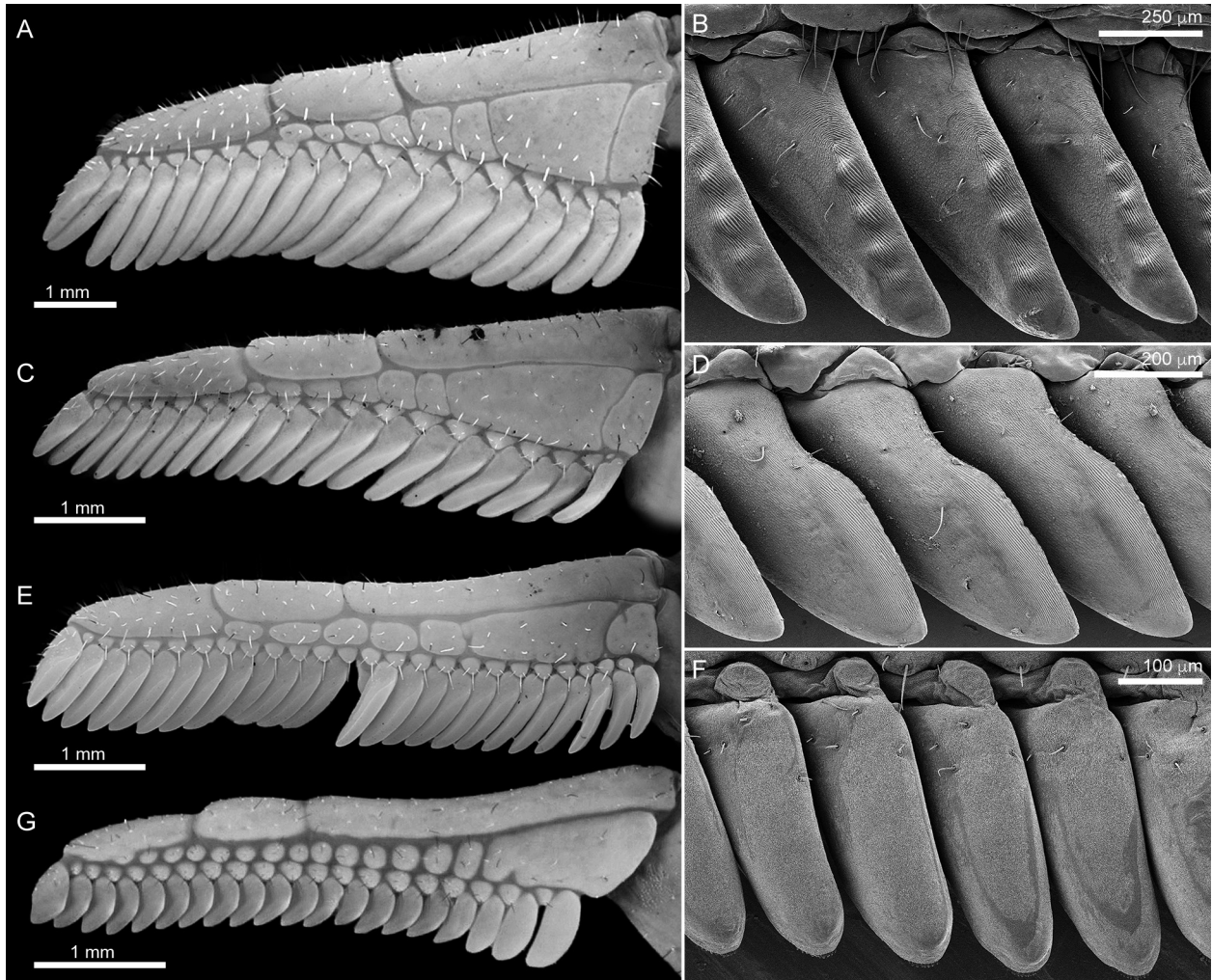


Fig. 4. Dextral pecten, ventral aspect (A, C, E, G), and pectinal teeth, dorsal aspect (B, D, F), illustrating *plectrum* of pecten-sternite stridulation organs of species in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955. **A:** *Heteroctenus junceus* (Herbst, 1800), ♂ (AMNH). **B:** *Heteroctenus bonettii* (Armas, 1999), ♀ (AMNH). **C:** *Rhopalurus laticauda* Thorell, 1876, ♂ (MZSP). **D:** *Jaguajir rochae* (Borelli, 1910), (AMNH). **E:** *Rhopalurus laticauda* Thorell, 1876, ♂ (AMCC [LP 2845]). **F:** *Troglorhopalurus lacrau* (Lourenço & Pinto-da-Rocha, 1997), ♀ (AMCC [LP 3260]). **G:** *Physoctonus debilis* (C.L. Koch, 1840), ♀ (MZSP).

RENÇO 2007), whereas *Heteroctenus*, the name once applied to the Antillean species of *Rhopalurus*, remained in synonymy. As defined at the outset of this research, *Rhopalurus* was distributed in the Greater Antilles (Cuba and Hispaniola), the Guiana Shield of northern South America (Colombia, the Guianas, and Venezuela) and northeastern Brazil, where *Physoctonus* and *Troglorhopalurus* also occur (Fig. 6; FET et al. 2000; TERUEL 2006; LOURENÇO 2008; PRENDINI et al. 2009; TERUEL & RONCALLO 2008; SANTIAGO-BLAY 2009), but the monophyly of its disjunct components had not been tested quantitatively, either.

The generic distinction between *Rhopalurus* and *Centruroides* was also unclear (ESPOSITO et al. 2017). *Centruroides* is the most speciose genus of Centruroidinae, comprising 91 described species and three subspecies, distributed from the midwestern United States to northern South America (Colombia, Venezuela, Ecuador, and possibly Peru) and throughout the Caribbean (Fig. 6; HOFFMANN 1932; GANTENBEIN et al. 2001; SISSOM &

LOURENÇO 1987). Historically, several species had been transferred between *Centruroides* and *Rhopalurus*, and the generic definitions revised multiple times (POCOCK 1890; WERNER 1939; MEISE 1934; MELLO-LEITÃO 1945; LOURENÇO 1979). *Centruroides* were separated from *Rhopalurus* by the following combination of characters: pedipalp chela fixed finger trichobothrium *db* aligned with or proximal to trichobothrium *et*, fifth metasomal segment elongated in adult males, and the absence of a pecten-sternite stridulation organ. However, trichobothrial positions and the length of the fifth metasomal segment are interspecifically variable within both genera, and the absence of a stridulation organ is probably plesiomorphic. A phylogenetic analysis of Cuban scorpions based on a single mitochondrial gene locus (16S rDNA) recovered *Centruroides* paraphyletic with respect to *Rhopalurus* (FET et al. 2003a) whereas ovariuterine data suggested *Rhopalurus* was paraphyletic with respect to *Centruroides* (VOLSCHENK et al. 2008). A better understanding of the systematic limits and diagnosis of *Centruroides* is

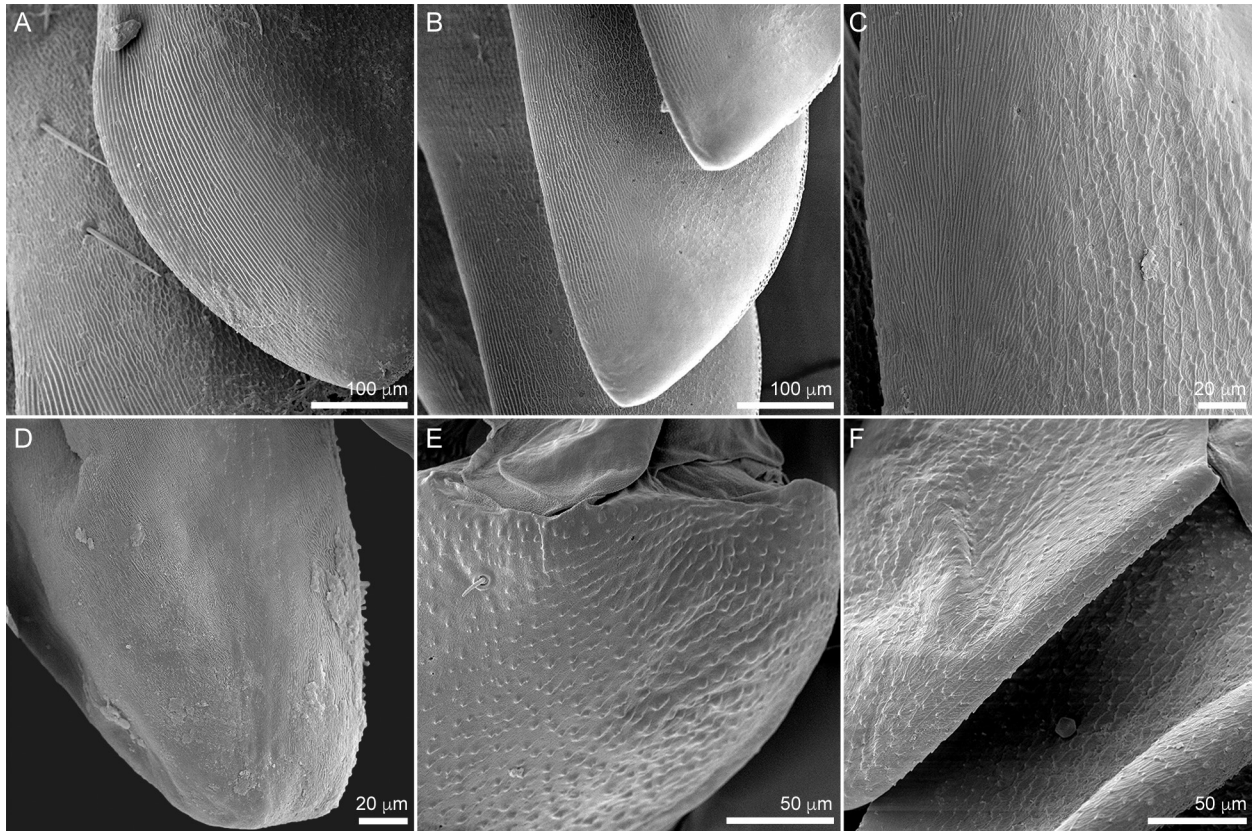


Fig. 5. Pectinal teeth, dorsal aspect, fine structure, illustrating *plectrum* of pecten-sternite stridulation organs of species in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955. **A:** *Jaguajir agamemnon* (C.L. Koch, 1839), (MZSP). **B:** *Heteroctenus princeps* (Karsch, 1879), ♂ (AMNH). **C:** *Rhopalurus laticauda* Thorell, 1876, (MZSP). **D:** *Troglorhopalurus lacrau* (Lourenço & Pinto-da-Rocha, 1997), ♀ (MZSP). **E:** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), ♂ (MZSP). **F:** *Physoctonus debilis* (C.L. Koch, 1840), ♀ (MZSP).

of considerable medical importance because the genus includes the only dangerously venomous scorpions in North America, among them eight species responsible for lethal envenomations in humans (DEHESA-DAVILA & POSSANI 1994; CHÁVEZ-HARO & ORTIZ 2015).

The taxonomy of species previously assigned to *Rhopalurus* was in a similar state of disarray when this research began. Mostly large and colorful, and often with the ability to stridulate audibly, these charismatic scorpions have attracted considerable attention. In the past decade alone, several publications proposed taxonomic changes and described new species (LENARDUCCI et al. 2005; TERUEL 2006; TERUEL & ARMAS 2006, 2012; LOURENÇO 2007, 2008, 2014; TERUEL & RONCALLO 2008, 2013; TERUEL & TIETZ 2008; PRENDINI et al. 2009; SANTIAGO-BLAY 2009; FLÓREZ 2012), often increasing, rather than decreasing, the taxonomic confusion. For example, *Rhopalurus caribensis* Teruel & Roncallo, 2008, *Rhopalurus crassicauda* Caporiacco, 1947 and *Rhopalurus pintoii* Mello-Leitão, 1932 were each synonymized and then resurrected. The validity of *R. crassicauda*, its two subspecies, and *Rhopalurus virkki* Santiago-Blay, 2009 was questioned by several authors (PRENDINI et al. 2009; TERUEL & ARMAS 2012).

The study presented here is the first rigorous test of the monophyly of Centruroidinae and its component taxa, based on phylogenetic analysis of 90 morphologi-

cal characters and 4,260 aligned base-pairs of DNA sequence from three mitochondrial and two nuclear DNA loci for 102 terminal taxa, representing 24 species in seven ingroup genera, and nine species in three outgroup genera. The integration of morphological and genomic data provides the benefits of simultaneously testing alternative sources of evidence for the monophyly of Centruroidinae and its component genera, and recognizing diagnostic morphological synapomorphies for their identification. A revised classification of Centruroidinae (Table 2), as Rhopalurusinae, was presented by ESPOSITO et al. (2017). The present study also investigates, for the first time, the evolution of the pecten-sternite stridulation organs of these scorpions, revealing that three distinct types evolved in *Heteroctenus*, *Jaguajir* and *Rhopalurus*.

2. Material and methods

2.1. Taxon sampling

The classification of Centruroidinae employed here follows ESPOSITO et al. (2017) (Table 2). In order to test the monophyly of the subfamily and its component genera,

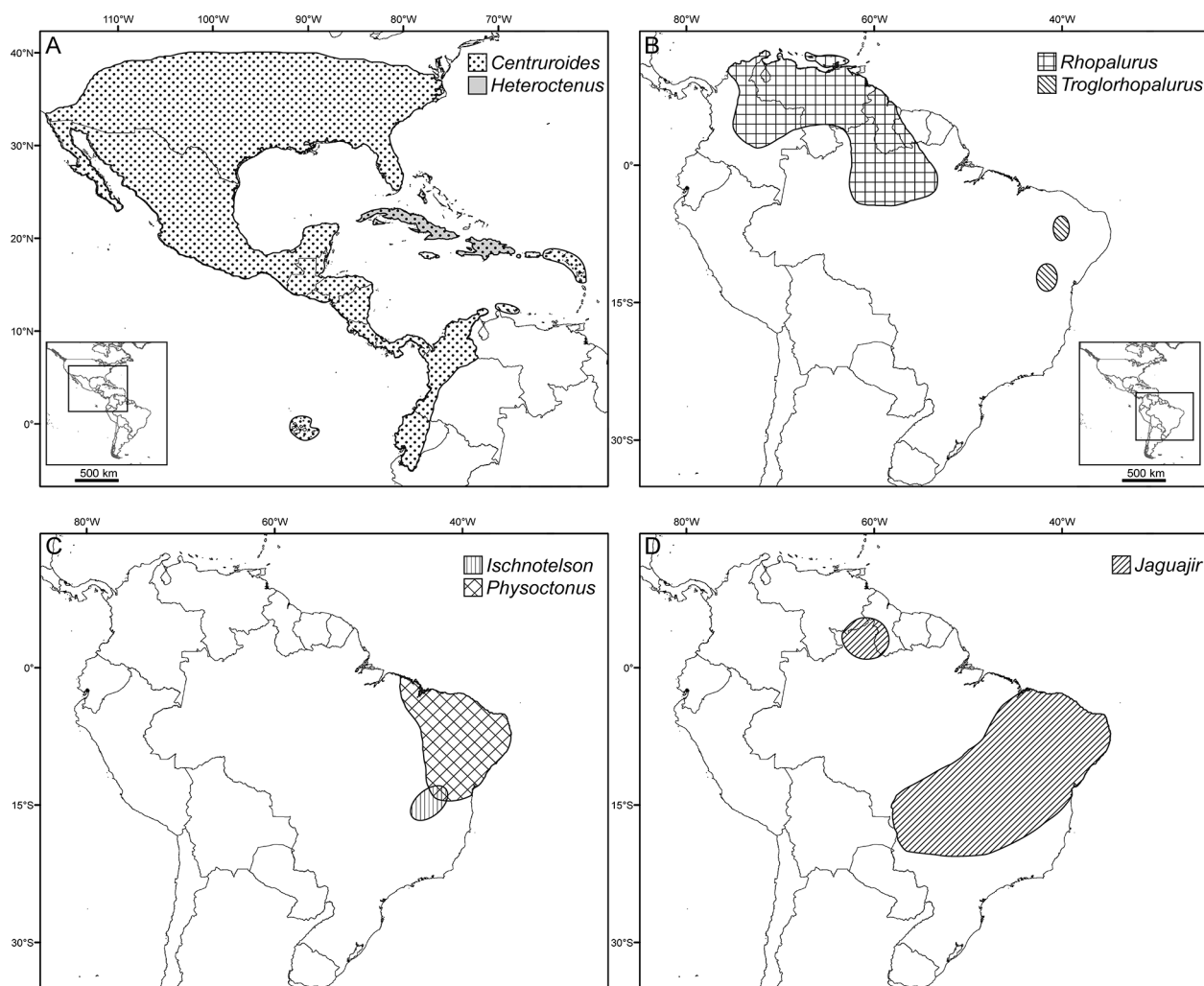


Fig. 6. Approximate distributions of genera in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955: **A:** *Centruroides* Marx, 1890 and *Heteroctenus* Pocock, 1893. **B:** *Rhopalurus* Thorell, 1876 and *Troglorhopalurus* Lourenço et al., 2004. **C:** *Ischnotelson* Esposito et al., 2017 and *Physoctonus* Mello-Leitão, 1934. **D:** *Jaguajir* Esposito et al., 2017.

as well as the validity of species previously assigned to *Physoctonus*, *Rhopalurus*, and *Troglorhopalurus*, samples were obtained from across the known distributions of as many current and previously recognized species and subspecies as possible, with an emphasis on obtaining material from the proximity of type localities to accurately assign names to populations (Appendix 2). The sample included topotypes of seven infrageneric taxa listed in synonymy by ESPOSITO et al. (2017): *Centruroides stenochirus* Penther, 1913; *Rhopalurus acromelas* Lutz & Mello, 1922; *Rhopalurus amazonicus* Lourenço, 1986; *Rhopalurus laticauda sachsi* Karsch, 1879; *Rhopalurus piceus* Lourenço & Pinto-da-Rocha, 1997; *Rhopalurus virkkii* Santiago-Blay, 2009; *Rhopalurus aridicola* Teruel & Armas, 2012. Six exemplar species (PRENDINI 2001b) of *Centruroides* were selected to represent the taxonomic and geographical diversity of this speciose genus (ESPOSITO 2011).

Six infrageneric taxa, five of which were synonymized by ESPOSITO et al. (2017), were omitted from the ingroup because fresh material was unavailable for DNA extraction. Four of these taxa are restricted to Cuba and could

not be obtained for study: *Heteroctenus gibarae* (Teruel, 2006) and its junior synonym, *Rhopalurus granulimanus* Teruel, 2006; *Rhopalurus melloleitaoi* Teruel & Armas, 2006, a junior synonym of *Heteroctenus junceus* (Herbst, 1800). *Rhopalurus brejo* Lourenço, 2014, known only from the holotype, is a junior synonym of *Troglorhopalurus lacrau* (Lourenço & Pinto-da-Rocha, 1997). *Rhopalurus crassicauda parauensis* Lourenço, 2008 and *Rhopalurus pintoii kourouensis* Lourenço, 2008 are junior synonyms of *Rhopalurus laticauda* Thorell, 1876 and *Jaguajir pintoii* (Mello-Leitão, 1932), respectively.

Exemplar species from two genera of Tityinae were included as outgroups: six species of *Tityus*, selected to represent four of its five subgenera (LOURENÇO 2006), and two of the three described species of *Zabius*. Trees were rooted on the cosmopolitan buthid, *Isometrus maculatus* (DeGeer, 1778). The final taxon sample therefore comprised 24 ingroup species and nine outgroup species, considered satisfactory for testing the monophyly of Centruroidinae and polarizing the morphological characters of its component genera, the aims of this study.

Table 1. Previous classification of the buthid scorpion species assigned to genera *Physcoctonus* Mello-Leitão, 1934, *Rhopalurus* Thorell, 1876 and *Trogloorhopalurus* Lourenço et al., 2004 with countries of distribution (PRENDINI et al. 2009; LOURENÇO 2014).

<i>Physcoctonus debilis</i> (C.L. Koch, 1840)	Brazil
<i>Rhopalurus abudi</i> Armas & Marcato Fondeur, 1987	Dominican Republic
<i>Rhopalurus acromelas</i> Lutz & Mello, 1922	Brazil
<i>Rhopalurus agamemnon</i> (C.L. Koch, 1839)	Brazil
<i>Rhopalurus amazonicus</i> Lourenço, 1986	Brazil
<i>Rhopalurus aridicola</i> Teruel & Armas, 2012	Cuba
<i>Rhopalurus bonettii</i> Armas & Marcato Fondeur, 1987	Dominican Republic
<i>Rhopalurus brejo</i> Lourenço, 2014	Brazil
<i>Rhopalurus caribensis</i> Teruel & Roncallo, 2008	Colombia
<i>Rhopalurus crassicauda</i> Caporiacco, 1947	Brazil, Guyana
<i>Rhopalurus crassicauda parvensis</i> Lourenço, 2008	Brazil
<i>Rhopalurus garridoi</i> Armas, 1974	Cuba
<i>Rhopalurus gibarae</i> Teruel, 2006	Cuba
<i>Rhopalurus granulimanus</i> Teruel, 2006	Cuba
<i>Rhopalurus guanambiensis</i> Lenarducci et al., 2005	Brazil
<i>Rhopalurus junceus</i> (Herbst, 1800)	Cuba
<i>Rhopalurus lacrau</i> Lourenço & Pinto-da-Rocha 1997	Brazil
<i>Rhopalurus laticauda</i> Thorell, 1876	Colombia, Venezuela
<i>Rhopalurus melloleitai</i> Teruel & Armas, 2006	Cuba
<i>Rhopalurus pinto</i> Mello-Leitão, 1932	Brazil, Guyana
<i>Rhopalurus pinto kourouensis</i> Lourenço, 2008	French Guiana
<i>Rhopalurus princeps</i> (Karsch, 1879)	Dominican Republic, Haiti
<i>Rhopalurus rochae</i> Borelli, 1910	Brazil
<i>Rhopalurus virkkii</i> Santiago-Blay, 2009	USA (Mona Is., Puerto Rico)
<i>Trogloorhopalurus translucidus</i> Lourenço et al., 2004	Brazil

Whereas DNA sequences were generated for multiple conspecific individuals of thirteen ingroup species, resulting in a final sample of 102 terminal taxa (Appendix 2), morphological characters were scored for only one terminal taxon per species (i.e., 33 terminal taxa) and extrapolated to all conspecific individuals in the simultaneous analyses with molecular data, because none of the morphological characters were assessed to be intraspecifically polymorphic (PRENDINI 2001b).

2.2. Morphological data

Twenty-seven morphological characters were adopted from published matrices on various scorpion taxa (LAMORAL 1978, 1980; JERAM 1994, 1998; PRENDINI 2000, 2001a, 2004; SOLEGLAD & SISSOM 2001; SOLEGLAD & FET 2001, 2003; VOLSCHENK et al. 2008), 33 from unpublished matrices (STOCKWELL 1989; E.S. Volschenk & L. Prendini unpublished data), and 30 new characters were added for a total of 90 characters, comprising 38 (43%) characters from the prosoma, 25 (33%) from the mesosoma, and 21 (23%) from the metasoma. 54% of the characters were derived from carination and surface macrosculpture, 21% from shape and morphometrics, 13% from macrosetae and trichobothria, 9% from internal and external anatomy, and 3% from coloration (Appendix 3).

Nomenclature follows HJELLE (1990) and SISSOM (1990), except for carapace, tergite and metasomal

Table 2. Revised classification (ESPOSITO et al. 2017) of the buthid scorpion species previously assigned to genera *Physcoctonus* Mello-Leitão, 1934, *Rhopalurus* Thorell, 1876 and *Trogloorhopalurus* Lourenço et al., 2004 with countries of distribution.

<i>Heteroetenus abudi</i> (Armas & Marcato Fondeur, 1987) (= <i>Rhopalurus virkkii</i> Santiago-Blay, 2009)	Dominican Republic, USA (Mona Is., Puerto Rico)
<i>Heteroetenus bonettii</i> (Armas & Marcato Fondeur, 1987)	Dominican Republic
<i>Heteroetenus garridoi</i> (Armas, 1974)	Cuba
<i>Heteroetenus gibarae</i> (Teruel, 2006) (= <i>Rhopalurus granulimanus</i> Teruel, 2006)	Cuba
<i>Heteroetenus junceus</i> (Herbst, 1800) (= <i>Rhopalurus melloleitai</i> Teruel & Armas, 2006, <i>Rhopalurus aridicola</i> Teruel & Armas, 2012)	Cuba
<i>Heteroetenus princeps</i> (Karsch, 1879)	Dominican Republic, Haiti
<i>Ischnotelson guanambiensis</i> (Lenarducci et al., 2005)	Brazil
<i>Ischnotelson peruassu</i> Esposito et al., 2017	Brazil
<i>Jaguajir agamemnon</i> (C.L. Koch, 1839) (= <i>Rhopalurus acromelas</i> Lutz & Mello, 1922)	Brazil
<i>Jaguajir pinto</i> (Mello-Leitão, 1932) (= <i>Rhopalurus pinto kourouensis</i> Lourenço, 2008)	Brazil, French Guiana, Guyana
<i>Jaguajir rochae</i> (Borelli, 1910)	Brazil
<i>Physcoctonus debilis</i> (C.L. Koch, 1840)	Brazil
<i>Physcoctonus striatus</i> Esposito et al., 2017	Brazil
<i>Rhopalurus caribensis</i> Teruel & Roncallo, 2008	Colombia
<i>Rhopalurus laticauda</i> Thorell, 1876 (= <i>Rhopalurus crassicauda</i> Caporiacco, 1947, <i>Rhopalurus amazonicus</i> Lourenço, 1986, <i>Rhopalurus crassicauda parvensis</i> Lourenço, 2008)	Brazil, Colombia, Venezuela
<i>Rhopalurus ochoai</i> Esposito et al., 2017	Venezuela
<i>Trogloorhopalurus lacrau</i> (Lourenço & Pinto-da-Rocha, 1997) (= <i>Rhopalurus brejo</i> Lourenço, 2014)	Brazil
<i>Trogloorhopalurus translucidus</i> Lourenço et al., 2004	Brazil

carination (VACHON 1952), pedipalp carination (PRENDINI 2001a), pedipalp trichobothria (VACHON 1974), ovariuterine anatomy (VOLSCHENK et al. 2008), and book lung ultrastructure (KAMENZ & PRENDINI 2008). Measurements follow STAHNKE (1970), LAMORAL (1979), and PRENDINI (2001a). Morphological examination of specimens (Appendix 3) was conducted using a Nikon SMZ1500 dissection stereomicroscope. Specimens were measured using Mitutoyo digital calipers and an ocular micrometer. The morphological matrix (Table 3) was assembled and scored in Mesquite v2.74 (MADDISON & MADDISON 2010).

2.3. Molecular data

Field-collected specimens were injected with and preserved in 95% ethanol, and stored at -20°C . Genomic DNA was extracted from muscle tissue dissected from the fourth leg using a Qiagen DNEasy Blood and Tissue extraction kit according the manufacturers protocols.

Extracted DNA was amplified for five gene loci, selected based on their ability to provide resolution at various taxonomic levels (ARNEDO et al. 2002; GIRIBET et al. 2001; HARRISON et al. 1987; HAYASHI 1996; HILLIS & DIXON 1991; WAHLBERG & ZIMMERMANN 2000), in overlap-

Table 4. Primers used to amplify DNA sequences of two nuclear and three mitochondrial gene markers for phylogenetic analysis of the New World buthid subfamily Centruroidinae Kraus, 1955.

Primer Name	Primer Sequence (5' to 3')	Citation
18S rDNA		
18Sa2.0	ATGGTTGCAAAGCTGAAAC	WHEELER et al. (1993)
18Sbi	GAGTCTCGTTCGTTATCGGA	WHEELER et al. (1993)
18S1F	TACCTGGTTGATCCTGCCAGTAG	GIRIBET et al. (1996)
18S3F	GTTGATTCCGGAGAGGGA	GIRIBET et al. (1996)
18S5R	CTTGGCAAATGCTTTCGC	GIRIBET et al. (1996)
18S9R	GATCCTTCCGCAGGTTACCTAC	GIRIBET et al. (1996)
28S rDNA		
28Sa	GACCCGTCTTGAAGCACG	NUNN et al. (1996)
28Sb	TCGGAAGGAACCAGCTAC	NUNN et al. (1996)
28Sbout	CCCACAGCGCCAGTCTGCTTACC	PRENDINI et al. (2005)
12S rDNA		
12Sai	AAACTAGGATTAGATACCCATTAT	KOCHER et al. (1989)
12Sbi	AAGAGCGACGGCGATGTGT	KOCHER et al. (1989)
16S rDNA		
16Sbr	CTCCGGTTTGAATCAGATCA	SIMON et al. (1994)
16Sar	CGCCTGTTTATCAAAAACAT	SIMON et al. (1994)
Cytochrome c Oxidase I		
HCO	TAAACTTCAGGGTGACCAAAAAATCA	FOLMER et al. (1994)
HCOoutout	GTAAATATATGRTGDGCTC	PRENDINI et al. (2005)
LCO	GGTCAACAAATCATAAAGATATTGG	FOLMER et al. (1994)
Nancy (C1-N-2191)	CCCGGTAAAATTTAAAATATAAACTTC	HARRISON et al. (1987)
C1-J-1718	GGNGGATTTGGAAATGRTTRGTTC	HARRISON et al. (1987)
C1-N-2776	GGATAATCAGAATANCGNCGAGG	HARRISON et al. (1987)
CruzR	CATACCCAAAGARCCAAAAGG	VALDEZ-CRUZ et al. (2004)
LE1R	TCCATTCCACAGTAAACATATG	ESPOSITO (2011)
HCOEXTa	GAAGTTTATATTTAATTTTACCTGG	SIMON et al. (1994)
HCOEXTb	CCTATTGAWARAACATARTGAAAATG	SIMON et al. (1994)

DNA performed on an Applied Biosystems Inc. Prism™ 3730×. Paired-strand reads were aligned using Sequencher™ and edited by hand. A total 506 DNA sequences were generated (Table 5). The sequences of 98 individuals were complete for all 5 gene loci.

2.4. Phylogenetic analysis

Morphological characters were equally weighted *a priori* and analyzed with parsimony in TNT v1.1 (GOLOBOFF et al. 2003) using the New Technology Search option with 10,000 random addition replicates. Implied character weighting (GOLOBOFF 1993) was employed to evaluate the robustness of the topology to character weighting. Six values for the concavity constant, *k*, were investigated. Bootstrap measures of node support were calculated in TNT.

The leaf stability index (THORLEY & PAGE 2000) was calculated from the resulting trees in Phytutility v2.2 (SMITH & DUNN 2008) to identify rogue taxa (SANDERSON & SCHAFFER 2002) which may have an impact on the topology (THOMPSON & SCHAFFER 2010) or measures of support (PATTENGAL et al. 2010).

Multiple sequence alignments for individual gene partitions were performed in MAFFT (KATO et al. 2005) using the G-INS-i strategy, recommended by the authors for less than 200 sequences with global homology, and

the PAM1/K = 2 matrix parameter, recommended by the authors for aligning sequences of closely related taxa. The resulting alignments were manually edited in Geneious v5.1 (Biomatters, Ltd.).

Aligned sequence data from the five gene loci (18S, 28S, 12S, 16S, COI) were concatenated to produce a molecular data matrix comprising 87 terminals and 4,250 characters, 3,104 of which were invariant, 167 variable but uninformative, and 979 variable and informative. The nucleotide composition was 25% A, 18.5% C, 25% G and 31.5% T.

The concatenated DNA sequence alignments were analyzed simultaneously in TNT v1.1, using equal weights in the New Technology Search option comprising 10,000 random addition replicates of Tree Drift (GOLOBOFF 1999) and Ratchet (NIXON 1999) to identify the most parsimonious tree. The concatenated dataset, partitioned by gene and codon position, were analyzed under Bayesian (MrBayes v3.2.1) (HUELSENBECK & RONQUIST 2001; RONQUIST & HUELSENBECK 2003) and likelihood (RaxML) (STAMATAKIS 2006) criteria. 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 (COI) (Table 6). When the best fitting model included both the Γ and invariable sites (I) parameters, the next best fitting model was selected to avoid issues resulting from non-

Table 5. Genbank accession codes for vouchers, deposited at the American Museum of Natural History, New York (AMNH), and the Museu de Zoologia da Universidade São Paulo, Brazil (MZSP), and tissue samples, deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH, from which DNA was extracted and sequenced for phylogenetic analysis of the New World buthid subfamily Centruroidinae Kraus, 1955. Type localities (TL) of taxa currently recognized or in synonymy [] denoted by ‘Y’. Provenience data are provided in Appendix 1.

Species	TL	Voucher	AMCC	18S	28S	12S	16S	COI
<i>Isometrus maculatus</i>		AMNH	LP 1798	KY982016.1	KY982111.1	KY981825.1	KY981921.1	KY982207.1
<i>Tityus atriventer</i>		AMNH	LP 9033	KY982074.1	KY982169.1	KY981883.1	KY981978.1	KY982264.1
<i>Tityus bahiensis</i>		AMNH	LP 5641	KY982075.1	KY982170.1	KY981884.1	KY981979.1	KY982265.1
<i>Tityus clathratus</i>		AMNH	LP 1567	KY982076.1	KY982171.1	KY981885.1	KY981980.1	KY982266.1
<i>Tityus discrepans</i>		AMNH	LP 1547	KY982077.1	KY982172.1	KY981886.1	KY981981.1	KY982267.1
<i>Tityus kuryi</i>		AMNH	LP 7659	KY982078.1	KY982173.1	KY981887.1	KY981982.1	KY982268.1
<i>Tityus metuendus</i>		AMNH	LP 1546	KY982079.1	KY982174.1	KY981888.1	KY981983.1	KY982269.1
<i>Tityus smithii</i>		AMNH	LP 9046	KY982081.1	KY982176.1	KY981890.1	KY981985.1	KY982271.1
<i>Tityus riverai</i>		AMNH	LP 10202	KY982080.1	KY982175.1	KY981889.1	KY981984.1	KY982270.1
<i>Zabius birabeni</i>		AMNH	LP 4251	KY982082.1	KY982177.1	KY981891.1	KY981986.1	KY982272.1
<i>Zabius fuscus</i>		AMNH	LP 5642	KY982083.1	KY982178.1	KY981892.1	KY981987.1	KY982273.1
<i>Centruroides exilicauda</i>		AMNH	LP 1692	KY981988.1	KY982084.1	KY981797.1	KY981893.1	KY982179.1
<i>Centruroides gracilis</i>		AMNH	LP 2013	KY981989.1	KY982085.1	KY981798.1	KY981894.1	KY982180.1
<i>Centruroides infamatus</i>		AMNH	LP 1822	KY981990.1	KY982086.1	KY981799.1	KY981895.1	KY982181.1
<i>Centruroides margaritatus</i>		AMNH	LP 1986	KY981991.1	KY982087.1	KY981800.1	KY981896.1	KY982182.1
<i>Centruroides rileyi</i>		AMNH	LP 6445	KY981992.1	KY982088.1	KY981801.1	KY981897.1	KY982183.1
<i>Centruroides schmidtii</i>		AMNH	LP 9172	KY981993.1	KY982089.1	KY981802.1	KY981898.1	KY982184.1
<i>Centruroides vittatus</i>		AMNH	LP 2286	KY981994.1	KY982090.1	KY981803.1	KY981899.1	KY982185.1
<i>Heteroctenus abudi</i>		AMNH	LP 3268	KY981997.1	KY982093.1	KY981806.1	KY981902.1	KY982188.1
[= <i>Rhopalurus virrkii</i>]	[Y]	AMNH	LP 10234	KY981995.1	KY982091.1	KY981804.1	KY981900.1	KY982186.1
	[Y]	AMNH	LP 10235	KY981996.1	KY982092.1	KY981805.1	KY981901.1	KY982187.1
<i>Heteroctenus bonettii</i>	Y	AMNH	LP 2471	KY981998.1	KY982094.1	KY981807.1	KY981903.1	KY982189.1
	Y	AMNH	LP 3267	KY981999.1	KY982095.1	KY981808.1	KY981904.1	KY982190.1
<i>Heteroctenus garridoi</i>	Y	AMNH	LP 10225	KY982000.1	KY982096.1	KY981809.1	KY981905.1	KY982191.1
<i>Heteroctenus junceus</i>		AMNH	LP 1517	KY982007.1	KY982103.1	KY981816.1	KY981912.1	KY982198.1
		AMNH	LP 1565	KY982008.1	KY982104.1	KY981817.1	KY981913.1	KY982199.1
[= <i>Rhopalurus aridicola</i>]	[Y]	AMNH	LP 12613	KY982001.1	KY982097.1	KY981810.1	KY981906.1	KY982192.1
	[Y]	AMNH	LP 12618	KY982002.1	KY982098.1	KY981811.1	KY981907.1	KY982193.1
<i>Heteroctenus princeps</i>		AMNH	LP 12622	KY982003.1	KY982099.1	KY981812.1	KY981908.1	KY982194.1
		AMNH	LP 12624	KY982004.1	KY982100.1	KY981813.1	KY981909.1	KY982195.1
		AMNH	LP 12627	KY982005.1	KY982101.1	KY981814.1	KY981910.1	KY982196.1
		AMNH	LP 1516	KY982010.1	KY982106.1	KY981819.1	KY981915.1	KY982201.1
		AMNH	LP 1566	KY982011.1	KY982107.1	KY981820.1	KY981916.1	KY982202.1
		AMNH	LP 3262	KY982012.1	KY982108.1	KY981821.1	KY981917.1	KY982203.1
		AMNH	LP 3264	KY982013.1	–	KY981822.1	KY981918.1	KY982204.1
		AMNH	LP 12478	KY982009.1	KY982105.1	KY981818.1	KY981914.1	KY982200.1
<i>Ischnotelson guanambiensis</i>	Y	MZSP 30864	LP 9669	KY982014.1	KY982109.1	KY981823.1	KY981919.1	KY982205.1
		MZSP 30865	LP 9670	KY982015.1	KY982110.1	KY981824.1	KY981920.1	KY982206.1
<i>Ischnotelson peruassu</i>	Y	MZSP 31138	LP 9937	KY982017.1	KY982112.1	KY981826.1	KY981922.1	KY982208.1
<i>Jaguajir agamemnon</i>		MZSP 30883	LP 9692	KY982018.1	KY982113.1	KY981827.1	KY981923.1	KY982209.1
		MZSP 30884	LP 9693	KY982019.1	KY982114.1	KY981828.1	KY981924.1	KY982210.1
		MZSP 30885	LP 9694	KY982020.1	KY982115.1	KY981829.1	KY981925.1	KY982211.1
		MZSP 30886	LP 9695	KY982021.1	KY982116.1	KY981830.1	KY981926.1	KY982212.1
		MZSP 30887	LP 9696	KY982022.1	KY982117.1	KY981831.1	KY981927.1	KY982213.1
[= <i>Rhopalurus acromelas</i>]	[Y]	MZSP 31170	LP 9929	KY982023.1	KY982118.1	KY981832.1	KY981928.1	KY982214.1
		MZSP 31133	LP 9932	KY982024.1	KY982119.1	KY981833.1	KY981929.1	KY982215.1
		MZSP 31157	LP 9933	KY982025.1	KY982120.1	KY981834.1	KY981930.1	KY982216.1
		MZSP 31161	LP 9942	KY982026.1	KY982121.1	KY981835.1	KY981931.1	KY982217.1
		MZSP 31167	LP 9949	KY982027.1	KY982122.1	KY981836.1	KY981932.1	KY982218.1
		MZSP 31181	LP 9958	KY982028.1	KY982123.1	KY981837.1	KY981933.1	KY982219.1
<i>Jaguajir pintoii</i>								
[= <i>Rhopalurus crassicauda</i>]	[Y]	AMNH	LP 8278	KY982029.1	KY982124.1	KY981838.1	KY981934.1	KY982220.1
[= <i>Rhopalurus piceus</i>]	[Y]	MZSP 30863	LP 9671	KY982030.1	KY982125.1	KY981839.1	KY981935.1	KY982221.1
	[Y]	MZSP 30862	LP 9672	KY982031.1	KY982126.1	KY981840.1	KY981936.1	KY982222.1
		MZSP 31176	LP 9928	KY982032.1	KY982127.1	KY981841.1	KY981937.1	KY982223.1

Table 5 continued.

Species	TL	Voucher	AMCC	18S	28S	12S	16S	COI
<i>Jaguajir rochae</i>		AMNH	LP 1775	KY982033.1	KY982128.1	KY981842.1	KY981938.1	KY982224.1
		AMNH	LP 7638	KY982034.1	KY982129.1	KY981843.1	KY981939.1	KY982225.1
		AMNH	LP 7639	KY982035.1	KY982130.1	KY981844.1	KY981940.1	–
		MZSP 30879	LP 9682	KY982036.1	KY982131.1	KY981845.1	KY981941.1	KY982226.1
		MZSP 30880	LP 9683	KY982037.1	KY982132.1	KY981846.1	KY981942.1	KY982227.1
		MZSP 30881	LP 9684	KY982038.1	KY982133.1	KY981847.1	KY981943.1	KY982228.1
		MZSP 30882	LP 9685	KY982039.1	KY982134.1	KY981848.1	KY981944.1	KY982229.1
		MZSP 31127	LP 9926	KY982040.1	KY982135.1	KY981849.1	KY981945.1	KY982230.1
		MZSP 31151	LP 9941	KY982041.1	KY982136.1	KY981850.1	KY981946.1	KY982231.1
		MZSP 31146	LP 9943	KY982042.1	KY982137.1	KY981851.1	KY981947.1	KY982232.1
		MZSP 31148	LP 9946	KY982043.1	KY982138.1	KY981852.1	KY981948.1	KY982233.1
		MZSP 31124	LP 9947	KY982044.1	KY982139.1	KY981853.1	KY981949.1	KY982234.1
		MZSP 31143	LP 9951	KY982045.1	KY982140.1	KY981854.1	KY981950.1	KY982235.1
	MZSP 31123	LP 9953	KY982046.1	KY982141.1	KY981855.1	KY981951.1	KY982236.1	
[= <i>Centruurus stenochirus</i>]	[Y]	MZSP 31122	LP 9963	KY982047.1	KY982142.1	KY981856.1	–	KY982237.1
<i>Physoctonus debilis</i>		MZSP 30866	LP 9678	KY982048.1	KY982143.1	KY981857.1	KY981952.1	KY982238.1
		MZSP 30867	LP 9679	KY982049.1	KY982144.1	KY981858.1	KY981953.1	KY982239.1
		MZSP 30868	LP 9680	KY982050.1	KY982145.1	KY981859.1	KY981954.1	KY982240.1
<i>Physoctonus striatus</i>	Y	MZSP 30869	LP 9681	KY982051.1	KY982146.1	KY981860.1	KY981955.1	KY982241.1
<i>Rhopalurus caribensis</i>	Y	AMNH	LP 9341	KY982053.1	KY982148.1	KY981862.1	KY981957.1	KY982243.1
		AMNH	LP 13167	KY982052.1	KY982147.1	KY981861.1	KY981956.1	KY982242.1
<i>Rhopalurus laticauda</i>		AMNH	LP 2462	KY982057.1	KY982152.1	KY981866.1	KY981961.1	KY982247.1
[= <i>Rhopalurus laticauda sachsi</i>]	[Y]	AMNH	LP 2845	KY982058.1	KY982153.1	KY981867.1	KY981962.1	KY982248.1
		AMNH	LP 4221	KY982059.1	KY982154.1	KY981868.1	KY981963.1	KY982249.1
		AMNH	LP 9200	KY982060.1	KY982155.1	KY981869.1	KY981964.1	KY982250.1
		AMNH	LP 9237	KY982061.1	KY982156.1	KY981870.1	KY981965.1	KY982251.1
		AMNH	LP 9253	KY982062.1	KY982157.1	KY981871.1	KY981966.1	KY982252.1
		AMNH	LP 9256	KY982063.1	KY982158.1	KY981872.1	KY981967.1	KY982253.1
		MZSP 30876	LP 9675	KY982064.1	KY982159.1	KY981873.1	KY981968.1	KY982254.1
		MZSP 30877	LP 9676	KY982065.1	KY982160.1	KY981874.1	KY981969.1	KY982255.1
		MZSP 30878	LP 9677	KY982066.1	KY982161.1	KY981875.1	KY981970.1	KY982256.1
		MZSP 30870	LP 9686	KY982067.1	KY982162.1	KY981876.1	KY981971.1	KY982257.1
[= <i>Rhopalurus amazonicus</i>]		MZSP 30871	LP 9687	KY982068.1	KY982163.1	KY981877.1	KY981972.1	KY982258.1
	[Y]	MZSP 30872	LP 9688	KY982069.1	KY982164.1	KY981878.1	KY981973.1	KY982259.1
	[Y]	MZSP 30873	LP 9689	KY982070.1	KY982165.1	KY981879.1	KY981974.1	KY982260.1
	[Y]	MZSP 30874	LP 9690	KY982071.1	KY982166.1	KY981880.1	KY981975.1	KY982261.1
	[Y]	MZSP 30875	LP 9691	KY982072.1	KY982167.1	KY981881.1	KY981976.1	KY982262.1
		MZSP 31172	LP 9927	KY982073.1	KY982168.1	KY981882.1	KY981977.1	KY982263.1
		AMNH	LP 10046	KY982054.1	KY982149.1	KY981863.1	KY981958.1	KY982244.1
		AMNH	LP 10047	KY982055.1	KY982150.1	KY981864.1	KY981959.1	KY982245.1
		AMNH	LP 10048	KY982056.1	KY982151.1	KY981865.1	KY981960.1	KY982246.1
	<i>Rhopalurus ochoai</i>	Y	AMNH	LP 5504	MF508621.1	MF508628.1	–	MF402014.1
		AMNH	LP 5505	MF508622.1	MF508629.1	–	MF402015.1	MF508636.1
		AMNH	LP 9199	MF508623.1	MF508630.1	–	MF402016.1	MF508637.1
		AMNH	LP 9207	MF508624.1	MF508631.1	–	MF402017.1	MF508638.1
<i>Troglorhopalurus lacrau</i>		AMNH	LP 7637	MF508626.1	MF508633.1	MF508616.1	MF508619.1	MF508640.1
	Y	AMNH	LP 10211	MF508625.1	MF508632.1	MF508615.1	MF508618.1	MF508639.1
<i>Troglorhopalurus translucidus</i>	Y	MZSP 30888	LP 9668	MF508627.1	MF508634.4	MF508617.1	MF508620.1	MF508641.1

independence of the Γ and I parameters. The Bayesian analysis was performed on the CiPRES supercomputing cluster (MILLER et al. 2009) in four independent runs for 60 million generations, sampling every 1000 generations. Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (RAMBAUT & DRUMMOND 2007) and convergence assessed by the standard deviations of split frequencies in AWTY (NYLANDER et al. 2008). A maximum

clade credibility tree was computed from the post-burn-in trees with TreeAnnotator v1.6.1 (RAMBAUT & DRUMMOND 2007). The concatenated dataset was also analyzed in raxmlHPC v7.0.4 (STAMATAKIS 2006). Each partition was analyzed under the GTR+ Γ model (YANG 1994).

The morphological character matrix and concatenated DNA sequence alignments were analyzed simultaneously with parsimony and Bayesian Inference. Par-

simony analysis was conducted using TNT with equal weighting. The Bayesian analysis was performed in MrBayes v.3.2.1 on the CiPRES supercomputing cluster in two independent runs for 50 million generations, sampling every 1000 generations. Burn-in times were determined by eye using ln-likelihood in Tracer v1.5 (RAMBAUT & DRUMMOND 2007) and convergence assessed by the standard deviations of split frequencies in AWTY (NYLANDER et al. 2008). A maximum clade credibility tree was computed from the post-burn-in trees in TreeAnnotator v1.6.1 (RAMBAUT & DRUMMOND 2007).

2.5. Stridulation

The pecten-sternite stridulation organ was examined and standardized images prepared of the pectines and sternite III of seventeen species of Centruroidinae, using material in the collections of the University of São Paulo (USP) and the American Museum of Natural History: *Heteroctenus abudi* (Armas & Marcano Fondeur, 1987); *Heteroctenus bonettii* (Armas, 1999); *Heteroctenus garridoi* (Armas, 1974); *H. junceus*; *Heteroctenus princeps* (Karsch, 1879); *Ischnotelson guanambiensis*

Table 6. Best-fitting models of nucleotide substitution calculated for five loci in phylogenetic analysis of the New World buthid subfamily Centruroidinae Kraus, 1955. The best model was determined for each codon position for Cytochrome *c* Oxidase subunit I (COI). Partitions indicated with an asterisk are the second-best model following the exclusion of models that included both the *T* and *I* parameters.

Locus: Partition	AIC Model
18S rDNA	GTR+I
28S rDNA	GTR+I
12S rDNA	GTR+G*
16S rDNA	HKY+G*
COI: 1 st position	GTR+G*
COI: 2 nd position	GTR+G*
COI: 3 rd position	GTR+G*

(Lenarducci et al., 2005); *Ischnotelson peruassu* Esposito et al., 2017; *Jaguajir agamemnon* (C.L. Koch, 1839); *J. pintoii*; *Jaguajir rochae* (Borelli, 1910); *R. caribensis*; *R. laticauda*; *Rhopalurus ochoai* Esposito et al., 2017; *T. lacraui*; *Trogloorhopalurus translucidus* Lourenço et al., 2004; *Physoctonus debilis* (C.L. Koch, 1840); *Physoctonus striatus* Esposito et al., 2017.

Table 7. Length (steps), consistency indices (CI) and retention indices (RI) of 90 morphological characters on the most parsimonious tree obtained by equal weights and implied weighting ($k = 3-6$) for phylogenetic analysis of the New World buthid subfamily Centruroidinae Kraus, 1955.

Char.	Steps	CI	RI	Char.	Steps	CI	RI	Char.	Steps	CI	RI
1	2	0.50	0.50	31	6	0.50	0.82	61	6	0.17	0.44
2	4	0.25	0.70	32	4	0.50	0.85	62	5	0.40	0.25
3	1	1.00	1.00	33	5	0.40	0.82	63	10	0.10	0.31
4	3	0.33	0.50	34	1	1.00	1.00	64	4	0.25	0.77
5	2	0.50	0.67	35	5	0.20	0.67	65	6	0.33	0.60
6	3	0.33	0.71	36	7	0.29	0.17	66	6	0.33	0.67
7	1	1.00	1.00	37	6	0.17	0.67	67	7	0.14	0.14
8	6	0.17	0.00	38	7	0.29	0.17	68	1	1.00	0.00
9	1	1.00	1.00	39	3	0.33	0.67	69	7	0.14	0.25
10	1	1.00	1.00	40	3	0.67	0.92	70	3	0.33	0.33
11	1	1.00	1.00	41	5	0.40	0.63	71	3	0.33	0.50
12	3	0.33	0.33	42	5	0.20	0.60	72	2	0.50	0.50
13	4	0.25	0.40	43	3	0.67	0.83	73	1	1.00	0.00
14	4	0.25	0.40	44	11	0.45	0.45	74	3	0.33	0.33
15	8	0.13	0.53	45	2	0.50	0.50	75	7	0.29	0.44
16	6	0.17	0.58	46	3	0.33	0.50	76	7	0.29	0.74
17	2	0.50	0.00	47	7	0.14	0.40	77	2	0.50	0.83
18	2	0.50	0.50	48	9	0.22	0.53	78	6	0.17	0.50
19	8	0.25	0.50	49	7	0.29	0.69	79	7	0.29	0.62
20	3	0.67	0.90	50	3	0.67	0.92	80	5	0.40	0.77
21	9	0.33	0.65	51	2	1.00	1.00	81	4	0.25	0.40
22	5	0.20	0.50	52	1	1.00	1.00	82	9	0.11	0.47
23	5	0.20	0.00	53	6	0.17	0.55	83	9	0.22	0.46
24	7	0.29	0.69	54	4	0.25	0.67	84	2	0.50	0.75
25	7	0.29	0.69	55	4	0.25	0.50	85	6	0.17	0.29
26	5	0.20	0.73	56	2	0.50	0.00	86	2	1.00	1.00
27	1	1.00	1.00	57	4	0.25	0.25	87	2	0.50	0.50
28	4	0.25	0.57	58	2	0.50	0.00	88	1	1.00	1.00
29	1	1.00	1.00	59	1	1.00	0.00	89	1	1.00	0.00
30	1	1.00	1.00	60	5	0.20	0.43	90	4	0.25	0.00

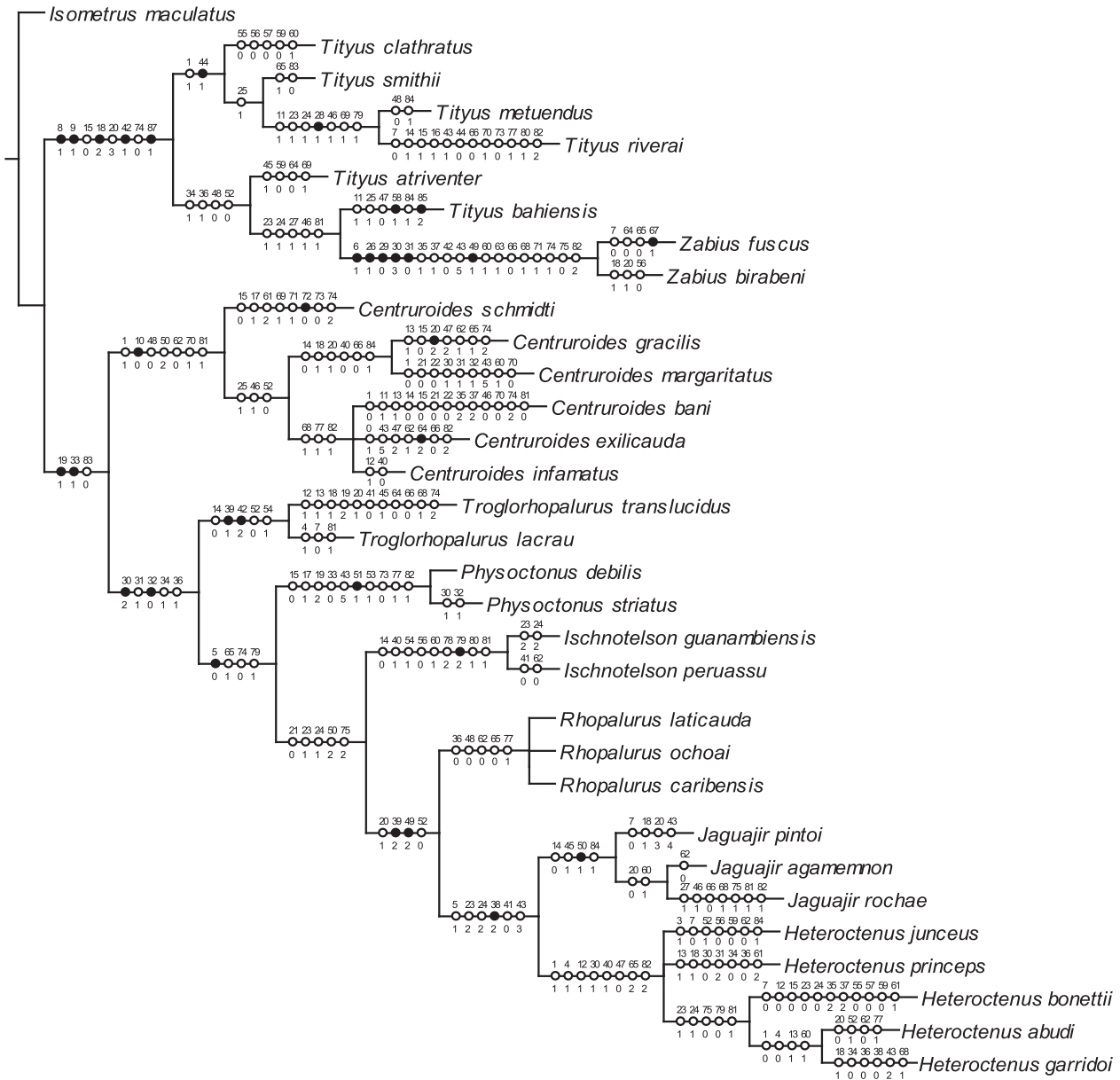


Fig. 7. Phylogeny of the New World buthid scorpion subfamily Centruroidinae Kraus, 1955 obtained by separate analysis of 90 morphological characters with parsimony. Strict consensus of four most parsimonious trees (MPTs) obtained by analysis under equal weighting. Synapomorphies optimized with accelerated transformation. Black circles indicate uniquely derived apomorphic states, white circles indicate parallel derivations of apomorphic states, numbers above indicate characters, and numbers below indicate states. Refer to Appendix 2 for character descriptions.

Material fixed in 70% ethanol was cleaned using a sonicator, and subsequently dehydrated with acetone. One pecten per species was dissected, fixed on a stub, and dried in an oven for approximately 8 hours. The material was covered with gold using a Sputter Coater Balzer SCD 50, and images of the pectines prepared using a ZEISS DSM 940 scanning electronic microscope at USP. Ultraviolet fluorescence images of sternite III were also prepared, using a Microoptics ML-1000 digital imaging system (PRENDINI 2003a; VOLSCHENK 2006).

Stridulation behavior was observed and recorded in ten species: *H. abudi*; *I. guanambiensis*; *J. agamemnon*; *J. pintoii*; *J. rochae*; *T. translucidus*; *T. lacrau*; *P. debilis*; *P. striatus*; *R. crassicauda*.

3. Results

3.1. Separate morphological analyses

Parsimony analysis of the morphological character matrix with equal weighting obtained five most parsimonious trees (MPTs) with a length of 380 steps, Consistency Index (CI) of 0.32, and Retention Index (RI) of 0.62, in two islands of tree topologies (Table 7). *Tityus* and *Zabius* consistently formed a monophyletic group, with *Zabius* monophyletic, and *Tityus* paraphyletic with respect to *Zabius*. Centruroidinae was consistently monophyletic and comprised seven primary clades corresponding to



Fig. 8. Phylogeny of the New World buthid scorpion subfamily Centruroidinae Kraus, 1955 obtained by separate analysis of 90 morphological characters with parsimony. Single MPT with alternative topology obtained by analysis under equal weighting and implied weighting with mild concavity ($k = 3-6$). Synapomorphies optimized with accelerated transformation. Black circles indicate uniquely derived apomorphic states, white circles indicate parallel derivations of apomorphic states, numbers above indicate characters, and numbers below indicate states. Refer to Appendix 2 for character descriptions.

genera *Centruroides*, *Heteroctenus*, *Ischnotelson*, *Jaguajir*, *Physoctonus*, *Rhopalurus* and *Troglorhopalurus*. Four of the MPTs were almost identical, exhibiting only minor rearrangements among the species of *Centruroides* and *Rhopalurus*, as indicated by the strict consensus (Fig. 7). These topologies placed *Centruroides* sister to the remaining six centruroidine genera, all previously accommodated within *Rhopalurus*: (*Centruroides* (*Troglorhopalurus* (*Physoctonus* (*Ischnotelson* (*Rhopalurus* (*Heteroctenus* + *Jaguajir*)))))). The fifth MPT recovered by the equal weighting analysis differed from the other MPTs by reversing the positions of *Physoctonus* and *Troglorhopalurus*, and placing *Centruroides* in a clade with *Heteroctenus*, sister to a clade comprising *Ischno-*

telson, *Jaguajir* and *Rhopalurus* (Fig. 8): (*Physoctonus* (*Troglorhopalurus* ((*Ischnotelson* (*Jaguajir* + *Rhopalurus*)) (*Centruroides* + *Heteroctenus*))))).

Analyses with implied weighting under $k = 1-6$ obtained a single MPT in each case. As in the equal weighting analysis, *Tityus* and *Zabius* consistently formed a clade, with *Zabius* monophyletic, and *Tityus* paraphyletic with respect to *Zabius*. Centruroidinae was consistently monophyletic and comprised seven primary clades corresponding to the abovementioned genera. However, two alternative topologies were recovered, depending on the strength of weighting against homoplasy (the concavity constant, k). The topology obtained by analyses with mild concavity ($k = 3-6$) was identical to the fifth MPT ob-

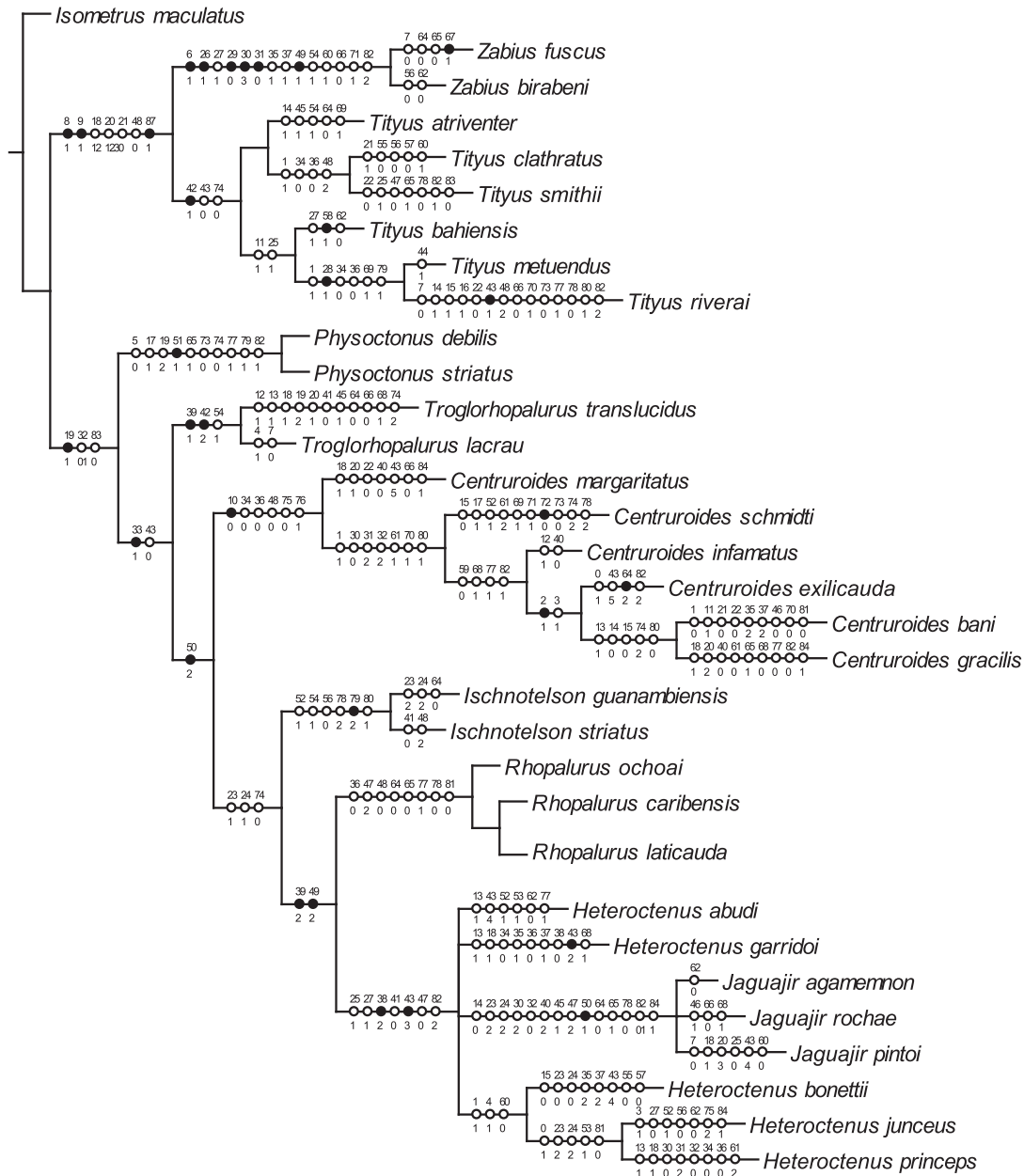


Fig. 9. Phylogeny of the New World buthid scorpion subfamily Centruroidinae Kraus, 1955 obtained by separate analysis of 90 morphological characters with parsimony. Single most parsimonious tree obtained by analysis under implied weighting with strong concavity ($k = 1-2$). Synapomorphies optimized with accelerated transformation. Black circles indicate uniquely derived apomorphic states, white circles indicate parallel derivations of apomorphic states, numbers above indicate characters, and numbers below indicate states. Refer to Appendix 2 for character descriptions.

tained by the analysis with equal weighting (Fig. 8). The topology obtained by the analyses with strong concavity ($k = 1$ or 2) recovered *Tityus* monophyletic and placed *Centruroides* sister to a clade comprising *Heteroctenus*, *Ischnotelson*, *Jaguajir* and *Rhopalurus*, to the exclusion of *Physoctonus* and *Troglorhopalurus* (Fig. 9): (*Physoctonus* (*Troglorhopalurus* (*Centruroides* (*Heteroctenus* (*Ischnotelson* (*Jaguajir* + *Rhopalurus*)))))). *Heteroctenus* was paraphyletic with respect to *Jaguajir*.

Leaf stability indices of the topology obtained by separate analyses of the morphological character matrix with equal weighting and implied weighting under $k = 3-6$ were greater than 0.98 for the outgroup taxa (*Tityus* and

Zabius) indicating that the monophyly of Centruroidinae is stable and most rearrangements occur among its component genera. Leaf stability indices for the seven genera were also high, varying between 0.80 and 0.88, indicating that the monophyly of these genera is well supported, despite some uncertainty regarding their relative positions.

3.2. Separate molecular analyses

Parsimony analysis of the concatenated molecular dataset produced 14 MPTs of 6,688 steps, CI of 0.33 and RI of 0.75. The only topological disagreement concerned

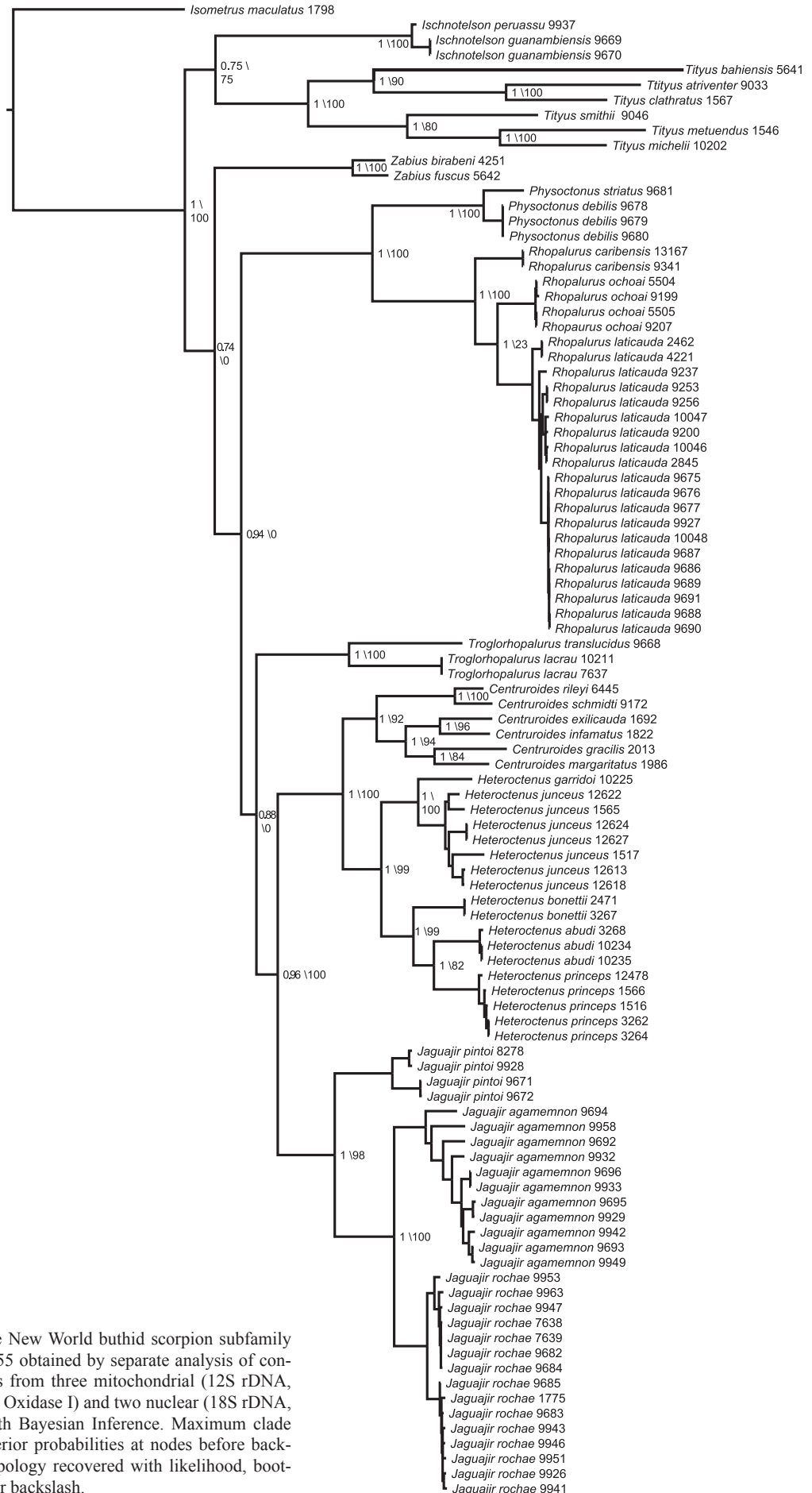


Fig. 10. Phylogeny of the New World buthid scorpion subfamily Centruroidinae Kraus, 1955 obtained by separate analysis of concatenated DNA sequences from three mitochondrial (12S rDNA, 16S rDNA, Cytochrome *c* Oxidase I) and two nuclear (18S rDNA, 28S rDNA) gene loci with Bayesian Inference. Maximum clade credibility tree with posterior probabilities at nodes before backslash. Nearly identical topology recovered with likelihood, bootstrap support at nodes after backslash.

prising *Physoctonus* and *Rhopalurus*, to the exclusion of *Jaguajir* and *Troglorhopalurus*: (*Troglorhopalurus* (*Jaguajir* ((*Centruroides* + *Heteroctenus*) (*Physoctonus* + *Rhopalurus*))))).

Likelihood analysis of the molecular dataset again recovered the monophyly of all genera, including *Tityus*, and the clades comprising *Centruroides* and *Heteroctenus*, and *Physoctonus* and *Rhopalurus*. Unlike the parsimony analysis, however, Centruroidinae was monophyletic, with the following relationships among its component genera: (*Ischnotelson* ((*Physoctonus* + *Rhopalurus*) (*Troglorhopalurus* (*Jaguajir* (*Centruroides* + *Heteroctenus*))))).

3.3. Simultaneous analyses

Simultaneous analysis of the morphological character matrix and the concatenated molecular dataset with equal weights parsimony retrieved 39 MPTs of 7,097 steps, CI 0.30 and RI 0.75 (Fig. 11). *Tityus*, *Zabius* and the seven centruroidine genera were each consistently monophyletic with high support. As in the parsimony analyses of the molecular dataset, however, Centruroidinae was rendered paraphyletic by the placement of *Zabius* sister to *Tityus*, to the exclusion of *Ischnotelson* (Fig. 11). Alternative hypotheses for the relative positions of these three groups resulted in a basal polytomy between *Zabius*, a weakly supported clade comprising *Ischnotelson* and *Tityus*, and a clade comprising the remaining genera of Centruroidinae. Relationships among the remaining centruroidine genera were better supported and mostly congruent with the topologies recovered by the separate analyses of the morphological and molecular data. *Jaguajir* was placed sister to a clade comprising *Physoctonus* and *Rhopalurus*, which together was sister to a clade comprising *Centruroides* and *Heteroctenus*, to the exclusion of *Troglorhopalurus*: (*Troglorhopalurus* ((*Centruroides* + *Heteroctenus*) (*Jaguajir* (*Physoctonus* + *Rhopalurus*))))).

The maximum clade credibility tree obtained from the simultaneous analysis with MrBayes was well supported (Fig. 11). *Tityus*, *Zabius*, and the seven centruroidine genera were each monophyletic with posterior probabilities (PP) = 1. *Tityus* and *Zabius* formed the monophyletic sister group (PP = 0.96) of a monophyletic Centruroidinae (PP = 0.72). Relationships among the genera of Centruroidinae resembled those obtained by the simultaneous analysis with parsimony, except for the placement of *Ischnotelson*. *Jaguajir* was placed sister to a clade comprising *Physoctonus* and *Rhopalurus* (PP = 1), in turn placed sister to a clade comprising *Centruroides* and *Heteroctenus* (PP = 1), to the exclusion of *Troglorhopalurus*.

3.4. Preferred hypothesis

The tree topologies obtained from separate and simultaneous analyses using various analytical and sampling methods were mostly congruent. The preferred hypothe-

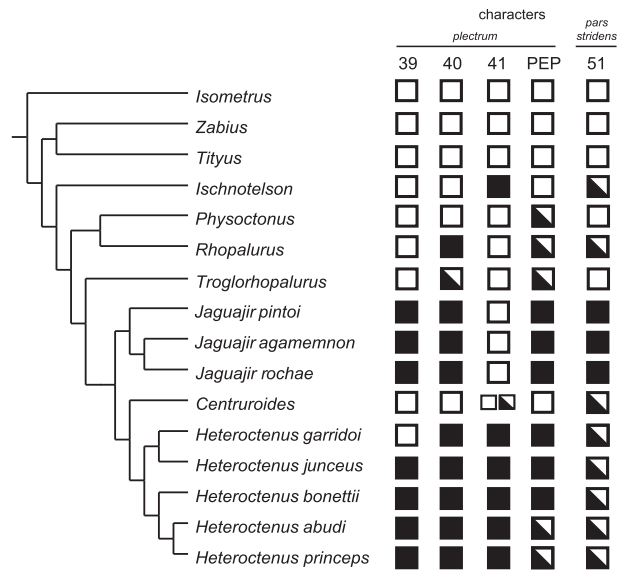


Fig. 12. Characters associated with pecten-sternite stridulation (Table 3, Appendix 2) in the New World buthid scorpion subfamily Centruroidinae Kraus, 1955. PEP = proximally expanded pectines. White squares = stridulatory state absent (plesiomorphic state). Bicolored squares = intermediate state. Black squares = stridulatory state present (apomorphic state). Two squares = both character states present

sis for the relationships among the genera of Centruroidinae is the topology recovered by simultaneous analysis of the molecular and morphological data, likelihood analysis of the molecular dataset, and one of the topologies recovered in the parsimony analysis morphology dataset (Fig. 11). This topology was mostly congruent with the consensus of the MPTs obtained from the separate morphological analyses with equal weights and implied weights under mild concavity ($k = 3-6$).

3.5. Stridulation

The morphology of the pecten-sternite stridulation organ varies among the species of Centruroidinae (Table 8, Figs. 3–5, 12). A stridulation organ was considered present in species that possess granular depressions on sternite III (*pars stridens*) and regular (i.e., continuous and approximately parallel) striations on the dorsal surfaces of the pectinal teeth (*pectrum*). Stridulation does not occur in *Alayotityus*, *Ischnotelson*, *Isometrus*, *Mesotityus*, *Physoctonus*, *Tityus*, and *Troglorhopalurus*, due to the absence of one or both structures.

The *pars stridens* is synapomorphic for the Centruroidinae, but exhibits varying levels of development among the genera, e.g., the granules are small in most genera, but large in *Jaguajir*. Its absence in some *Centruroides*, *Physoctonus* and *Troglorhopalurus* is considered an independent secondary loss in each case. A dorsal ridge on the pectinal teeth arose independently in *Jaguajir* and some *Heteroctenus*.

The *pectrum* arose within the centruroidine clade that excludes *Ischnotelson*. The striations reverted to ir-

Table 8. Morphological characteristics of the pecten-sternite stridulation organ of the species of the New World buthid genera *Heteroctenus* Pocock, 1893, *Ischnotelson* Esposito et al., 2017, *Jaguajir* Esposito et al., 2017, *Physoctonus* Mello-Leitão, 1934, *Rhopalurus* Thorell, 1876, and *Troglohopalurus* Lourenço et al., 2004. Characters that define the presence of a stridulation organ indicated in boldface. Numbers in parentheses refer to character numbers in the morphological matrix (Table 3, Appendix 2).

		<i>Pars stridens</i>		<i>Plectrum</i>		
		Sternite III Lateral Depressions (51)	Proximally Expanded Pectines	Pectinal Teeth Striations (40)	Pectinal Teeth Dorsal Keel (39)	Pectinal Teeth Nodules (41)
Type IV-A	<i>J. agagemnon</i>	Present, large granules	> 2 × medial	Present, parallel	Present	Absent
	<i>J. pinto</i>	Present, large granules	> 2 × medial	Present, parallel	Present	Absent
	<i>J. rochae</i>	Present, large granules	> 2 × medial	Present, parallel	Present	Absent
Type IV-B	<i>H. abudi</i>	Present, small granules	1.5 × medial	Present, parallel	Present	Present
	<i>H. bonettii</i>	Present, small granules	> 2 × medial	Present, parallel	Present	Present
	<i>H. junceus</i>	Present, small granules	> 2 × medial	Present, parallel	Present	Present
	<i>H. princeps</i>	Present, small granules	1.5 × medial	Present, parallel	Present	Present
	<i>H. garridoi</i>	Present, small granules	> 2 × medial	Present, parallel	Absent	Present
Type IV-C	<i>R. laticauda</i>	Present, small granules	1.5 × medial	Present, parallel	Absent	Absent
	<i>R. caribensis</i>	Present, small granules	1.5 × medial	Present, parallel	Absent	Absent
	<i>R. crassicauda</i>	Present, small granules	1.5 × medial	Present, parallel	Absent	Absent
Absent	<i>T. lacrau</i>	Absent, irregular	1.5 × medial	Present, irregular	Absent	Absent
	<i>T. translucidus</i>	Absent, irregular	1.5 × medial	Present, irregular	Absent	Absent
	<i>I. guanambiensis</i>	Present, small granules	Absent	Absent	Absent	Present
	<i>I. peruassu</i>	Present, small granules	Absent	Absent	Absent	Present
	<i>P. debilis</i>	Absent	1.5 × medial	Absent	Absent	Absent
	<i>P. striatus</i>	Absent	1.5 × medial	Absent	Absent	Absent

regular in *Centruroides* and were lost in *Physoctonus*.

Pronounced proximal expansion of the pectinal lamellae, observed in the clade containing *Centruroides*, *Heteroctenus*, and *Jaguajir*, was secondarily reduced in some *Heteroctenus* (e.g., *H. princeps*) and lost in *Centruroides*.

4. Discussion

4.1. Centruroidinae and *Centruroides* monophyletic

Centruroides, *Physoctonus*, *Troglohopalurus* and the species previously assigned to *Rhopalurus* (ESPOSITO et al. 2017) were monophyletic and well-supported in all except two topologies, confirming the monophyly of Centruroidinae. Among Buthidae, the presence of prolateral accessory denticles in the median denticle rows of the pedipalp chela fingers is uniquely synapomorphic for the subfamily (Fig. 1). Additional synapomorphies include a transverse row of median tubercles on the chelicerae, dorsobasal setation on the cheliceral fixed finger, and a bifurcated prolateral pedal spur on leg I, reduced in *Physoctonus*.

Centruroides was also consistently monophyletic and well-supported in the analyses presented, contradicting the findings of TERUEL et al. (2006), in which Cuban species of *Centruroides* were paraphyletic with respect to Cuban species of *Rhopalurus*, currently placed in *Heteroctenus* (ESPOSITO et al. 2017). Morphological synapomorphies of *Centruroides* include convergence

of the prodorsal and proventral carinae of the pedipalp patella, trichobothrium *db* of the fixed finger of the pedipalp chela aligned with or distal to trichobothrium *et*, trichobothrium *est* of the fixed finger situated between trichobothria *db* and *et* or proximal to *et*, and metasomal segment V elongate, particularly in adult males (length > 2.5 × width).

4.2. *Rhopalurus* s.l. paraphyletic

The group of species assigned to *Rhopalurus* by previous authors (FET & LOWE 2000; TERUEL 2006; TERUEL & ARMAS 2006, 2012; LOURENÇO 2007, 2008, 2014; TERUEL & RONCALLO 2008, 2013; TERUEL & TIETZ 2008; PRENDINI et al. 2009; SANTIAGO-BLAY 2009; FLÓREZ 2012) was consistently paraphyletic in the analyses presented here, contradicting the suggestion by LOURENÇO (1986) that these species are united by the presence of a pecten-sternite stridulation organ (Figs. 3–5). The components of *Rhopalurus sensu lato* consistently formed six well-supported monophyletic groups, the species composition of which comes as little surprise, given their disjunct distributions (Fig. 6).

Heteroctenus, removed from synonymy with *Rhopalurus* by ESPOSITO et al. (2017), comprises all former species of *Rhopalurus* occurring in the Greater Antilles, and represented in the analyses by the type species, *H. junceus*, and five species transferred from *Rhopalurus* by ESPOSITO et al. (2017): *H. abudi* and its junior synonym, *R. virkkii*; *H. bonettii*; *H. garridoi*; *H. gibarae*; *H. princeps*.

Two genera, recently created by ESPOSITO et al. (2017), accommodate two distinct groups of species, all

except two of which were transferred from *Rhopalurus* by ESPOSITO et al. (2017). *Ischnotelson* comprises two species characterized by a very narrow telson, *I. guanambiensis* and *I. peruassu*, from the caatinga and cerrado of northeastern Brazil. *Jaguajir* comprises three large-bodied species from northern Brazil: *J. pinto* from savanna formations on the Guiana Shield, and *J. agamemnon* and *J. rochae* from the caatinga and cerrado of northeastern Brazil.

Physoctonus comprises two small epigeal species from the arid caatinga of northeastern Brazil, *P. debilis*, transferred to *Rhopalurus* by FRANCKE (1977) and reinstated by LOURENÇO (2007), and *P. striatus*.

Rhopalurus comprises three compact species with moderately pale coloration, from savanna formations on the Guiana Shield of northern South America, the type species, *R. laticauda*, *R. caribensis*, and *R. ochoai*.

Troglochorpalurus comprises two species from caves in northeastern Brazil, the troglobite *T. translucidus* and the troglophile *T. lacrau*, transferred from *Rhopalurus* by ESPOSITO et al. (2017).

4.3. *Heteroctenus* revalidated

POCOCK (1893) created *Heteroctenus* to accommodate three species that were, at the time, placed in *Centrurus* (later transferred to *Centruroides*), designated the Cuban species, *H. junceus*, as type species and noted in the description that *Heteroctenus* was closely allied with *Centrurus*. POCOCK (1902) synonymized *Heteroctenus* with *Rhopalurus*. However, in the analyses presented here, the characters on which *Heteroctenus* was originally defined, i.e., proximally expanded pectinal lamellae, enlarged pectinal plate, and pronounced median carina on mesosomal sternite III, were found to be synapomorphic for the Caribbean species of *Rhopalurus* and form the justification, in combination with additional morphological and molecular evidence, for revalidating *Heteroctenus* and transferring the Caribbean species to it. Additional morphological synapomorphies for the genus include: dorsal surfaces of proximal pectinal teeth with regular striations and multiple nodules, lateral margins of sternite III with smooth carina, and telson without subaculear tubercle.

The analyses presented here also clarified the status of *R. virkkii*, described from Isla Mona, an islet between Hispaniola and Puerto Rico (SANTIAGO-BLAY 2009). TERUEL & ARMAS (2012) suggested *R. virkkii* might be synonymous with *R. abudi*, described from Isla Saona, Dominican Republic, off the southwestern coast of Hispaniola, and later reported from mainland Hispaniola (PRENDINI et al. 2009), but were unable to examine material from Isla Mona. Based on evidence presented here, *R. virkkii* is merely a pale color form of *H. abudi*, with little genetic divergence from the mainland population thereof, justifying the synonymy by ESPOSITO et al. (2017).

The validity of four Cuban taxa, referable to *Heteroctenus*, merits further discussion. ESPOSITO et al. (2017)

synonymized *R. aridicola* and *R. melloleitaoi* with *H. junceus*, based on the absence of convincing morphological differences or evidence of geographical isolation from the latter and, in the case of *R. aridicola*, on the low genetic divergence between topotypes thereof and samples conspecific with *H. junceus*, presented here. *Rhopalurus granulimanus* was synonymized with *H. gibarae* based on the absence of convincing morphological differences, the limited sample size, and the observation that the type localities of the two taxa are less than 25 km apart (ESPOSITO et al. 2017). Approximately nine days after publication of these synonyms, ARMAS (2017) published a rebuttal in an online journal that claims to be peer-reviewed, revalidating the three taxa synonymized by ESPOSITO et al. (2017), and formally transferring each to *Heteroctonus*. The arguments presented by ARMAS (2017) are unconvincing, however, for the following reasons.

In justifying the revalidation of *H. aridicola*, ARMAS (2017) presented four arguments, to which we respond in turn. (1) *Heteroctenus aridicola* differs from *H. junceus* based on the presence of (i) stronger metasomal carinae; (ii) a more attenuated metasoma in the male; and (iii) a very small proximal gap between the pedipalp chela fingers of the male (ARMAS 2017). In our experience, a wide range of variation in granulation/carination, metasomal width, and size of the proximal gap between the pedipalp chela fingers of the male is evident across the distribution of *H. junceus*, and in other widespread species of *Heteroctenus*, and the variation described for *H. aridicola* falls well within this range. As such, these characters are unreliable for species diagnosis, especially when comparing small samples. (2) *Heteroctenus aridicola* and *H. junceus* are sympatric and syntopic (ARMAS 2017). The reasoning behind this argument is circular. These concepts, by definition, assume the presence of more than one species and therefore cannot be used to justify the existence of more than one species a priori. (3) In the laboratory, *H. aridicola* and *H. junceus* are capable of interbreeding but immatures resulting from those breedings died prior to reaching adulthood, suggesting postzygotic reproductive isolation (ARMAS 2017). Failure to reach adulthood in captivity is not proof of reproductive isolation. The immatures from those breedings may have died for other reasons. Furthermore, data presented herein includes specimens matching the description of *H. aridicola* and collected from within the range defined for that species, yet which cannot be distinguished genetically from specimens collected elsewhere across the range of *H. junceus*, falsifying the hypothesis of reproductive isolation. (4) *Heteroctenus aridicola* is endemic to the xerophytic coastal area between Punta Negra and Punta de Maisí, whereas specimens from Santa Rosa and Baracoa appear to be accidental introductions (ARMAS 2017). This argument appears to contradict the argument based on sympatry (2) and, as stated, a sample from Baracoa was genetically indistinguishable from other samples of *H. junceus*, suggesting panmixis.

Concerning the synonymy of *H. melloleitaoi*, ARMAS (2017) presented three arguments, to which we respond

in turn. (1) *Heteroctenus melloleitai* was described from five localities in the Niquero Municipality of Granma Province not “a single locality” (ARMAS 2017). Nevertheless, the distance between the furthest localities of *H. melloleitai* is less than 15 km, and all five localities occur within the Parque Nacional Desembarco del Granma, throughout which *H. junceus* is also distributed (ESPOSITO et al. 2017). (2) *Heteroctenus melloleitai* was collected syntopically with *H. junceus* not “in close proximity to many known locality records of *H. junceus*” (ARMAS 2017). As stated above, the reasoning behind this argument is circular. This concept, by definition, assumes the presence of more than one species and therefore cannot be used to justify the existence of more than one species a priori. (3) *Heteroctenus melloleitai* differs from *H. junceus* in the metasoma and pedipalps being more attenuated, mainly in the females, and the significantly higher pectinal tooth count (ARMAS 2017). As previously stated, variation in meristics and other characters is observed across the distribution of *H. junceus* and other widespread species of *Heteroctenus*. The pectinal tooth count allegedly diagnostic for *H. melloleitai* does not differ statistically from that of *H. junceus*.

With respect to ARMAS' (2017) criticism that the type material was not examined, it should be noted that the decisions of ESPOSITO et al. (2017) were based on data presented in the published diagnoses and accompanying illustrations of these taxa, which are presumed to be sufficient to document the variation (indeed, L.F. de Armas and colleagues regularly publish taxonomic decisions based solely on literature and/or photographs of specimens unavailable for loan to Cuba). Based on the available evidence, the following synonyms are therefore upheld: *Rhopalurus granulimanus* Teruel, 2006 = *Heteroctenus gibarae* (Teruel, 2006); *Rhopalurus melloleitai* Teruel & Armas, 2006 and *Rhopalurus aridicola* Teruel & Armas, 2012 = *Heteroctenus junceus* (Herbst, 1800). The validity of *H. gibarae*, as distinct from *H. garridoi*, will be reassessed when material becomes available for study.

4.4. Additional genera from Brazil

The species formerly assigned to *Rhopalurus* from northern and northeastern Brazil formed two clearly defined, monophyletic groups in the analyses presented here, justifying the creation of two genera by ESPOSITO et al. (2017). *Ischnotelson* accommodates two unusual Brazilian species, *R. guanambiensis* and a second, allopatric species, which share a uniquely narrow telson in addition to fused lateral ocular, central lateral, and posterior central submedian carinae of the carapace. *Jaguajir* accommodates three morphologically diverse, large-bodied species, *R. agamemnon*, *R. pinto*, *R. rochae*, united by the possession of fused lateral ocular and anterior central submedian carinae on the carapace.

Although unequivocally monophyletic, the phylogenetic positions of *Ischnotelson* and, to a lesser extent,

Jaguajir were unstable in the analyses presented here. Whereas the two genera formed a monophyletic group with *Rhopalurus* in the separate morphological analyses, these genera were not monophyletic with one another or with *Rhopalurus* in the separate parsimony and likelihood analyses of the molecular dataset, which placed *Ischnotelson* sister to *Tityus*, rendering Centruroidinae paraphyletic, or in the combined analyses, which placed *Ischnotelson* sister to a group comprising all other Centruroidinae. The placement of *Ischnotelson* sister to all other centruroidine genera is the most plausible reconstruction, based on the presence of accessory denticles in the median denticle rows of the pedipalp chela fingers, an incrassate pedipalp chela manus in the adult male, and a posterior widening of the metasoma. *Jaguajir* was consistently placed sister to *Rhopalurus* or (*Heteroctenus* + *Centruroides*), except for one topology resulting from the morphological analysis, in which it rendered *Heteroctenus* paraphyletic. Its consistent placement sister to (*Heteroctenus* + *Centruroides*) in topologies recovered by the separate and combined analyses is the most plausible hypothesis.

The analyses presented here also clarified the status of several infrageneric taxa assigned to *Jaguajir* by ESPOSITO et al. (2017), the validity of which was previously confused. LOURENÇO (1982, 1984, 1986a,b, 1992, 1997) relegated *R. pinto* to a subspecies of *R. laticauda* and synonymized *R. crassicauda* therewith but later (LOURENÇO & PINTO-DA-ROCHA 1997) described another species, *R. piceus*, from the vicinity of the type locality of *R. pinto*. KOVAŘÍK (1998) listed *R. pinto* at the rank of species but FET & LOWE (2000) continued to list it as a subspecies of *R. laticauda* in accordance with LOURENÇO (1982). LOURENÇO (2002) formally reinstated *R. pinto* and removed *R. crassicauda* from synonymy. TERUEL (2006) suggested *R. pinto* might be a senior synonym of *R. piceus*. TERUEL & TIETZ (2008) formally synonymized *R. piceus*, erroneously declaring *R. pinto* to be a *nomen nudum*, and questioned whether *R. crassicauda* is distinct from *R. laticauda*. LOURENÇO (2008) suggested *R. piceus* may yet prove to be valid and rejected the suggestion that *R. crassicauda* is a junior synonym of *R. laticauda*, instead proposing it might be a subspecies thereof, and creating a new subspecies, *R. crassicauda paruensis*, along with a new subspecies of *R. pinto*. PRENDINI et al. (2009), however, agreed with the synonymy of *R. piceus* with *R. pinto* by TERUEL & TIETZ (2008), and the suggestion that *R. crassicauda* is probably a junior synonym of *R. laticauda*. The evidence and analyses presented here supported the validity of *J. pinto* as distinct from *R. laticauda*, upheld the synonymy of *R. piceus* therewith, and justified the synonymy of *R. piceus* and *R. pinto kouroensis* by ESPOSITO et al. (2017). *Rhopalurus crassicauda*, on the other hand, was determined to be conspecific with *R. laticauda* and synonymized by ESPOSITO et al. (2017). Additionally, *R. acromelas* was demonstrated to be conspecific with *J. agamemnon*, justifying its synonymy, and that of its previous synonyms, *Rhopalurus melleipalpus* Lutz & Mello, 1922, *Rhopalurus iglesiasi* Werner, 1927, *Rhopalurus lambdophorus* Mello-Leitão, 1932, *Rho-*

palurus dorsomaculatus Prado, 1938, and *Rhopalurus goiasensis* Prado, 1940, by ESPOSITO et al. (2017).

4.5. *Physoctonus* validated

Physoctonus debilis was originally placed in the non-buthid genus *Vaejovis* C.L. Koch, 1836 but was transferred to *Rhopalurus* by BORELLI (1910) where it remained until LOURENÇO (2002) resurrected *Physoctonus*. *Physoctonus*, created to accommodate *Physoctonus physurus* Mello-Leitão, 1934, was synonymized with *Rhopalurus* when FRANCKE (1977) synonymized *P. physurus* with *Rhopalurus debilis*.

Physoctonus debilis and a second species described by ESPOSITO et al. (2017) were consistently monophyletic in the analyses presented here, justifying LOURENÇO's (2002) decision to reinstate the genus. *Physoctonus* is supported by several morphological synapomorphies: pedipalp femur with retrolateral accessory carina; pectinal proximal dorsal fulcræ asetose; telson slightly ovate (length ca. $1.5 \times$ width), metasomal segment V without ventrosubmedian carina; sternite III surface planar, i.e., without anterior elevation.

The phylogenetic position of *Physoctonus* within Centruroidinae remains somewhat uncertain. *Physoctonus* was consistently placed sister to *Rhopalurus* in the separate analyses of the molecular data and the simultaneous analyses of the morphological and molecular data, an unexpected relationship, given the allopatric distributions of these taxa. In contrast, separate analyses of the morphological data consistently placed *Physoctonus* sister to a monophyletic group comprising all centruroidine genera except *Troglorhopalurus*.

4.6. *Rhopalurus* redefined

As redefined by ESPOSITO et al. (2017), *Rhopalurus* comprises only three species, *R. caribensis*, *R. laticauda*, and *R. ochoai*, united by the following morphological synapomorphies: fused central lateral and posterior central submedian carinae of the carapace, and the presence of a pecten-sternite stridulation organ (proximal pectinal teeth, dorsal surfaces without nodules but with regular striations, sternite III, ventromedian carina elevated anteriorly, ventrosubmedian surfaces forming paired depressions, finely and irregularly granular, lateral margins forming smooth, raised carina). *Rhopalurus* are savanna specialists, endemic and allopatrically distributed in savanna formations on the Guiana Shield of northern South America.

The status of *R. caribensis*, occurring in the Llanos of the Magdalena, Colombia, and separated from the nearest populations of *R. laticauda* by the Cordillera de Mérida (Andes), has been the subject of controversy. LOURENÇO (2008) suggested *R. caribensis* is a morph of *R. laticauda* rather than a distinct species. FLOREZ (2012) adopted this suggestion and synonymized *R. caribensis* with *R. laticauda* based in part on images of *Tityus* alleged to be

R. caribensis. TERUEL & RONCALLO (2013) subsequently revalidated *R. caribensis*. The analyses presented here supported the validity of *R. caribensis* based on genetic divergence from *R. laticauda*. Although morphologically similar, the two species can be consistently diagnosed by the color pattern on the ventral surface of the metasoma. Whereas *R. caribensis* displays three distinct, narrow stripes of pigmentation along the ventral surface (a ventromedian stripe flanked on either side by a ventrosubmedian stripe), these stripes are fused into a single, broad band of pigmentation (more pronounced in populations from the southeast of the distribution, formerly referable to *R. amazonicus*) in *R. laticauda*.

Unlike *R. caribensis*, no evidence was found to support the continued recognition of *R. amazonicus*, justifying its synonymy with *R. laticauda* by ESPOSITO et al. (2017). According to LOURENÇO (2008), *R. amazonicus* inhabits savanna “islands” surrounded by rainforest, but the genetic results presented here indicate substantial gene flow between these populations. The noticeably darker and more contrasting coloration of populations referable to *R. amazonicus*, compared with typical populations of *R. laticauda* to the north and west, was found to represent a difference in the intensity, rather than the pattern, of pigmentation. For example, these populations exhibit the single, broad band of pigmentation along the ventral surface of the metasoma, only more pronounced than observed in typical populations of *R. laticauda*.

The validity of *R. crassicauda*, another species repeatedly confused with *R. laticauda*, has been subject to considerable speculation (LOURENÇO 1982, 2002, 2008; TERUEL & TIETZ 2008; PRENDINI et al. 2009). When LOURENÇO (1982) relegated *R. pinto* to a subspecies of *R. laticauda*, *R. crassicauda* was synonymized therewith. Ten years later, when LOURENÇO (2002) reinstated *R. pinto*, *R. crassicauda* was removed from synonymy. TERUEL & TIETZ (2008) questioned whether *R. crassicauda* is distinct from *R. laticauda* but refrained from a formal synonymy in the absence of material for examination. LOURENÇO (2008) rejected the suggestion that *R. crassicauda* is a junior synonym of *R. laticauda*, proposing instead that it might be a subspecies thereof, and creating a new subspecies, *R. crassicauda paruiensis*. PRENDINI et al. (2009), however, agreed with TERUEL & TIETZ (2008) that *R. crassicauda* is probably a junior synonym of *R. laticauda*, and emphasized the need to clarify the distinction between *R. laticauda*, *R. crassicauda* and its subspecies. Based on the evidence presented here, *R. crassicauda* is indeed conspecific with *R. laticauda* and its subspecies, justifying its synonymy by ESPOSITO et al. (2017).

One possible explanation for the lack of clear diagnostic characters among the species of *Rhopalurus* is the relatively short time period since the last glacial maxima, during which time the northern savannas of South America expanded and reconnected with one another (LOURENÇO 2008). Despite the limited genetic differentiation within *Rhopalurus*, a distinct group of populations, representing a previously unrecognized species, *R. ochoai*, distributed

around Lake Maracaibo, east of the Cordillera de Perijá, and north and west of the Cordillera de Mérida, was identified and described by ESPOSITO et al. (2017).

4.7. *Trogloorhopalurus* redefined

The monotypic genus *Trogloorhopalurus* was created to accommodate *Trogloorhopalurus translucidus* Lourenço et al., 2004, based on a single, troglomorphic specimen from a Brazilian cave. In comparing *Trogloorhopalurus* with *Rhopalurus*, LOURENÇO et al. (2004: 1153, 1156) noted that “all modifications presented by the new troglomorphic scorpion are the result of adaptation to a cave dwelling life,” prompting PRENDINI et al. (2009) to suggest that *Trogloorhopalurus* might be a junior synonym of *Rhopalurus*. A troglophile species, *Rhopalurus lacraui* Lourenço & Pinto-da-Rocha, 1997, had been described from caves belonging to the same subterranean formation in Brazil and, in the description of *Trogloorhopalurus*, LOURENÇO et al. (2004) suggested the relationship between these taxa should be investigated using molecular data. Accordingly, the consistent placement of *R. lacraui* sister to *T. translucidus* in the analyses presented here comes as little surprise, and justifies the transfer of *R. lacraui* (and its junior synonym, *Rhopalurus brejo* Lourenço, 2014) to *Trogloorhopalurus* by ESPOSITO et al. (2017).

Several morphological synapomorphies support *Trogloorhopalurus*, as redefined by ESPOSITO et al. (2017): pectinal peg sensillae elongate and acuminate; metasomal segment V elongate (length > 2.5 × width); telson slightly ovate (length ca. 1.5 × width); telson vesicle width approximately equal to metasomal segment V width. The metasomal and telson characters resemble characters observed in *Centruroides*, and are generally associated with elongation of the metasoma. However, these characters apparently evolved convergently in *Trogloorhopalurus* and are presumed to be an adaptation to life in caves (PRENDINI et al. 2009).

4.8. Evolution of stridulation

Stridulation, defined as the emission of sound by rubbing together different parts of the body – typically a structure, appendix or projection, i.e., the *plectrum*, against a modified surface, i.e., the *pars stridens* – is used for intraspecific (e.g., mating behavior) and/or interspecific (e.g., defense) communication (DUMORTIER 1964a). Stridulation in scorpions is usually associated with defense behavior (DUMORTIER 1964b; ALEXANDER 1958; ACOSTA & MAURY 1990; MCCORMICK & POLIS 1990; LOURENÇO & CLOUDSLEY-THOMPSON 1995; PRENDINI 2001a; PRENDINI et al. 2003). DUMORTIER (1964a) recognized four different types of stridulation organs in scorpions, according to the structures of which they are comprised (DUMORTIER 1964a): type I, pedipalp-leg (scorpionids of the genera *Heterometrus*, *Pandinus* Thorell, 1876 and relatives); type II, chelicera-cephalothorax (scorpionids of the ge-

nus *Opisthophthalmus* C.L. Koch, 1837); type III, metasoma-aculeus (buthids of the genus *Parabuthus* Pocock, 1890); and type IV, pecten-sternite (Centruroidinae). ACOSTA & MAURY (1990) described a fifth type, in which sound is produced by the friction of tergites III–VI, in the bothriurid genus *Timogenes* Simon, 1880; a similar stridulatory apparatus was reported in another bothriurid, *Brachistosternus ehrenbergii* (Gervais, 1841) by OCHOA & OJANGUREN-AFFILASTRO (2007).

Type IV stridulation, caused by friction of nodules and striations on the dorsal surface of the pectinal teeth (*plectrum*) with granulation in depressions on the ventral surface of sternite III (*pars stridens*), was first recorded among Centruroidinae by W.J. Burchell during a visit to Brazil in 1828. Burchell observed the behavior in a species later determined by POCOCK (1904) to be *Rhopalurus borelli*, a junior synonym of *Jaguajir agamemnon* (LOURENÇO & CLOUDSLEY-THOMPSON 1995). The pecten-sternite stridulation organ was historically regarded as a diagnostic character of *Rhopalurus* (LOURENÇO 1982; SISSOM 1990; LOURENÇO & CLOUDSLEY-THOMPSON 1995; LOURENÇO et al. 2000; FET et al. 2000) but is now known to exist in several species of *Heteroctenus*, *Jaguajir*, and *Rhopalurus* (ESPOSITO et al. 2017).

Prior to the present study, the evolution of the pecten-sternite stridulation organ had not been investigated in a phylogenetic context (PRENDINI et al. 2009). As demonstrated by the analyses presented here, the organ is actually a complex of several characters associated with the *pars stridens* and the *plectrum*, which evolved independently in Centruroidinae. Three distinct types of pecten-sternite stridulation organ, first noted by POCOCK (1904), may be recognized.

Type IV-A occurs in *Jaguajir*, the only genus in which audible stridulation accompanied by movement of the pectines has been observed (H.Y. Yamaguti, pers. obs.). This is the most pronounced stridulation organ. The *pars stridens* is characterized by deep lateral depressions on sternite III which are flat and coarsely granular across the surface (Fig. 3B). The pectinal lamellae are expanded proximally (Fig. 4A) such that the proximal width is more than twice the medial width. This membranous widening creates a tympanum-like structure, which might amplify the intensity of stridulation (POCOCK 1904; LOURENÇO & CLOUDSLEY-THOMPSON 1995; PRENDINI et al. 2009). The pectinal teeth each possess a broad ridge on the dorsal surface (Fig. 4D), where deep, parallel striations are concentrated (Fig. 5A), creating a sinuous shape.

Type IV-B occurs in *Heteroctenus* and there are records of audible stridulation in species of the genus (POCOCK 1904; LOURENÇO et al. 2000). This stridulatory apparatus is also well developed. The *pars stridens* is characterized by fine granulation on sternite III (POCOCK 1904; Fig. 3C). Some species, such as *H. princeps*, possess lateral depressions on sternite III with irregular granulation. The pectines are expanded proximally (Fig. 4A) to varying degrees among the different species (Table 6). The striations on the dorsal surface of the pectinal teeth resemble those of Type A (Fig. 4B). Nodules on the stri-

ated surfaces of the pectinal teeth of *Heteroctenus* species may serve to increase the striated area (Fig. 5B), perhaps enhancing the audibility of stridulation (LOURENÇO et al. 2000). However, as the nodules are also found in *I. guanambiensis*, which does not possess a stridulation organ, their presence may not be directly related to stridulation.

Type IV-C occurs in *Rhopalurus*. This is the least developed type of stridulation organ (POCOCK 1904; TERUEL 2006; TERUEL & RONCALLO 2008). The *pars stridens* is characterized by fine granulation on sternite III with shallower sternite depressions than observed in Types IV-A and IV-B (Fig. 3D). The pectinal lamellae are only slightly expanded proximally, such that the proximal width is about $1.5 \times$ the medial width (Figs. 4C,E). The dorsal surfaces of the pectinal teeth are flat (without a ridge) and the striations, although well defined, are less developed than in Types IV-A and IV-B (Fig. 5C). There are no records of pectinal movement or sound production in *Rhopalurus* species, despite the presence of a stridulation organ.

5. Conclusions

This study presents the first rigorous test of the monophyly of Centruroidinae and its component taxa, based on phylogenetic analysis of morphological characters and DNA sequence data from multiple gene loci. The benefits of integrating and simultaneously analysing diverse sources of data are evident in the insights gained concerning the monophyly, diagnostic characters and distributions of these scorpions from the species level on up. The need for improved understanding of the classification of Centruroidinae cannot be understated. Their unique stridulation ability, disjunct biogeographical distributions, and the medical potential of their venoms offer promise for future evolutionary, biogeographical and biomedical research. Their distribution in some of the most environmentally sensitive areas of the world, e.g., savanna surrounding the Amazon rainforest, make them prime candidates for studies on the impact of recent and future climate change.

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8. Appendix 1

Arguments justifying why Centruroidinae Kraus, 1955, not Centurinae Koch, 1837, should be in Buthidae C.L. Koch, 1837, whereas Centurinae Koch, 1837 should be in Scorpionidae Latreille, 1802.

Centrurus Ehrenberg, 1829: 350, originally published with a brief description, is an available name (Article 12.1) regardless of the absence of included species.

The first and only included available species was *Centrurus galbineus* Koch, 1838: 110–112, pl. CXXXIX, fig. 320, fixing it as the type species of *Centrurus* by subsequent monotypy. KOCH (1838) described and illustrated the species, which is evidently an immature *Heterometrus*, and indicated that the locality was unknown. FET & LOWE (2000: 434) reported the type lost.

KRAEPELIN (1894: 34) synonymized *C. galbineus* with *Heterometrus longimanus* (Herbst, 1800), hence *Centrurus* became a junior synonym of *Heterometrus* Ehrenberg, 1828, fixing its current placement in Scorpioninae Latreille, 1802 (Article 61).

KOCH (1837: 38) published and characterized “Centurides” for two genera, *Centrurus* and *Vaejovis* C.L. Koch, 1836. Centurides is an unlatinized, vernacular, family-group name formed from *Centrurus*, which is the type genus (Article 12.2.4). Without latinization, the name is unavailable (Article 11.7.2).

Centurides was latinized as Centurini and generally accepted as valid by subsequent authors (e.g., see PETERS 1861: 512; THORELL 1876: 7; THORELL & LINDSTRÖM 1885: 25; KRAEPELIN 1891: 149), hence Centurini Koch, 1837 was then available (Article 11.7.2). KRAEPELIN (1899) later changed the suffix from that of a tribe to that of a subfamily, Centurinae.

Centurini or Centurinae, when cited in Buthidae C.L. Koch, 1837, are misidentifications, not synonymous with Buthidae (FET & LOWE 2000: 55, 56).

The correct placement of Centurini or Centurinae is in Scorpionidae, where Centurinae should be cited as a synonym of the nominotypical subfamily Scorpioninae (FET 2000: 427).

The type species of *Centrurus* is a junior synonym of *Heterometrus longimanus* (Herbst, 1800) (= *Scorpio longimanus*) (KRAEPELIN 1894: 34; FET 2000: 434), hence *Centrurus* is a junior synonym of *Heterometrus* Ehrenberg, 1828 (FET 2000: 431).

Centrurus is not a senior synonym of *Centruroides* or a *nomen nudum* as FRANCKE (1985) suggested (see also ICZN 1986: 144, 145).

Given the preferred classification of *Centrurus* as a synonym of *Heterometrus* in the Scorpioninae, the family-group name based on *Centrurus* will necessarily have to be applied (as valid or as a synonym) in the Scorpioninae (Article 61).

The Principle of Typification renders it impossible for Centurinae or Centurini to be assigned to any family other than the one that harbors *Centrurus galbineus*.

MARX (1890: 211) established *Centruroides* by including one available species, *Buthus exilicauda* Wood, 1863 (Article 12.2.5). *Centruroides* was proposed as a genus in its own right, not as a replacement name for *Centrurus*. However, due to a misunderstanding of *Centrurus*, the name was often used to refer to species that belonged in *Centruroides* and the latter was erroneously considered a junior synonym of the former. That misunderstanding appears to have precipitated the idea that Centurinae was the correct name of the buthid subfamily.

Early usages of Centruroidinae were invalid because the taxon was undescribed and the name accordingly unavailable (ROEWER 1943: 218; JAUME 1954: 1087). Centruroidinae became available when KRAUS (1955: 101) published a brief description in a footnote. Centruroidinae Kraus, 1955 is the correct name, not Centurinae, Rhopalurinae or Rhopalurusinae.

Article 40.1 states that “When the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family-group name is not to be replaced on that account alone.” It might therefore be argued that Article 40.1 does not make a distinction regarding whether or not the junior synonym belongs to the same family, and therefore requires Centurinae to be the correct name (O.F. Francke, pers. comm.). This argument overlooks The Principal of Typification (Article 61), however, which makes clear that the type of a name determines its placement in a classification and the type of a name cannot be separated from the name.

Article 40.2 states that “If, however, a family-group name was replaced before 1961 because of the synonymy of the type genus, the substitute name is to be maintained if it is in prevailing usage.” The following arguments have been offered to justify that the concept of *Centrurus* and Centurinae was always in Buthidae, not Scorpionidae, and Centruroidinae is not in prevailing usage (O.F. Francke, pers. comm.):

1. Between 1876 and 1900, eighteen species were described in *Centrurus* by THORELL (1876; $n = 4$), KARSCH (1879a,b; $n = 2$), KRAEPELIN (1891, 1898; $n = 2$), POCKOCK (1898; $n = 9$) and BANKS (1900; $n = 1$). All were described in Buthidae, and today are in *Centruroides* and remain in Buthidae. The concept back then of *Centrurus* was of a buthid not a scorpionid. KRAEPELIN (1891) proposed subfamily Centurini within Buthidae and KRAEPELIN (1899) used the proper ending for a subfamily, Centurinae, five years after synonymizing *Centrurus galbineus* (KRAEPELIN 1894); the subfamily concept therefore remained within Buthidae.

2. The species known today as *Centruroides gracilis* (Latreille, 1804) was published as the combination *Centrurus gracilis* by nineteen different authors, always within Buthidae. Similarly, the species known today as *Centruroides margaritatus* (Gervais, 1841) was pub-

lished as *Centrurus margaritatus* twenty times, always within Buthidae.

3. Centruroidinae was used by only four authors between 1943 and 1998 (FET & LOWE 2000) whereas Centruroidinae was used 23 times.

The argument that the concept of *Centrurus* and Centruroidinae has always been in Buthidae neglects the identity and placement of the type species of *Centrurus* and

type genus of Centruroidinae, which are in Scorpionidae. *Centruroides* was not proposed as a replacement name for *Centrurus*, but was proposed for *Buthus exilicauda*, a North American species, and for an undescribed species that was named but not described. The name *Centrurus* was incorrectly used for many years to denote species of *Centruroides* because of an erroneous understanding and placement of *Centrurus*.

9. Appendix 2

Tissue samples from which DNA was extracted and sequenced, and associated voucher specimens and additional material examined for morphological character matrix used in phylogenetic analysis of the New World buthid subfamily Centruroidinae Kraus, 1955, deposited in the following collections: American Museum of Natural History (AMNH), New York, U.S.A., incorporating the Alexis Harington (AH) Collection; Museum National d'Histoire Naturelle (MNHN), Paris, France; Museu de Zoologia da Universidade de São Paulo (MZSP), Brazil; Natal Museum (NM), Pietermaritzburg, South Africa; Museum of Natural History, Oxford University, U.K. (OUMNH); South African Museum (SAM), Cape Town; Natur-Museum Senckenberg, Frankfurt (SMF), Germany; Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Brazil; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB), Germany; Zoologisches Museum der Universität Hamburg (ZMH), Germany. Samples, stored in the Ambrose Monell Cryocollection (AMCC) of the American Museum of Natural History, New York, and vouchers, in the AMNH Collection of Arachnida and Myriapoda, share the same number.

***Centruroides exilicauda* (Wood, 1863):** MEXICO: *Baja California Sur*: Municipio Los Cabos: Cabo San Lucas, 15 mi. E, 22°53.383'N 109°54.933'W, 1.vi.1999, M.E. Soleglad, 1 ♂ (AMCC [LP 1692]); San Bartolo, 6 km SW, 23°41.816'N 109°50.800'W, 100 m, 13.vii.2008, H. Montaña and E. González, mesic vegetation, 1 ♀ (AMCC [LP 8840]).

***Centruroides gracilis* (Latreille, 1804):** MEXICO: *Hidalgo*: Municipio Tamazunchale: Tamazunchale, 24 km SE, 21°11'14"N 98°54'16"W, 3.viii.2002, L. Prendini and E. González, under stones on grassy hillside (deforested), 1 ♂, 2 juv. (AMCC [LP 2013]). *San Luis Potosí*: Antena de Microondas de Ciudad Valles, 21°58'55"N 99°08'58"W, 340 m, 2.viii.2002, L. Prendini, J. Soriano and E. González, forest (disturbed), collected at night with UV light, 4 ♂, 3 ♀, 3 juv. (AMCC [LP 2051]).

***Centruroides infamatus* (C.L. Koch, 1844):** MEXICO: *Michoacán*: Municipio Tandamangapio: Los Tabanos, 19.9749°N 102.84226°W, 223 m, 31.v.2006, O.F. Francke, H. Montaña, A. Valdez and A. Ballesteros, 2 ♀ (AMCC [LP 6420]). Municipio Tinquambato: Tinquambato, 4 km W, 23.iii.2000, E. González, under stones, 1 ♂ (AMCC [LP 1822]).

***Centruroides margaritatus* (Gervais, 1841):** NICARAGUA: *Granada*: Domitila, 55 m, 27.v–1.vi.2002, J.M. Maes, 1 ex. [legs] (AMCC [LP 1986]); Domitila Research Station (Domitila Reserva Silvestre Privada), 11°42.54'N 85°57.21'W, 8.vi.2005,

C.S. Chaboo, 1 ♀ (AMCC [LP 4326]), 10.vi.2005, Chaboo and Shepard, 1 ♂ (AMCC [LP 4325]).

***Centruroides rileyi* Sissom, 1995:** MEXICO: *San Luis Potosí*: Municipio Axtlan de Terrazas: Axtlan de Terrazas, 21.42601°N 98.87821°W, 100 m, 28.iv.2006, O.F. Francke, A. Valdez, G. Villegas and R. Paredes, 1 ♂ (AMCC [LP 6445]).

***Centruroides schmidti* Sissom, 1995:** HONDURAS: *Dept. Francisco Morazán*: Municipio San Antonio de Oriente: E.A.P. Zamorano, Monte Redondo, Acuacultura, 13.999°N 86.989°W, 773 m, 23.ix.2008, C. Viquez, night UV, 8 juv. (AMCC [LP 9172]). *Islas del Bahía*: Municipio Roatán: Cayos Cochinos, Cayos Menor, forest trails, 15°57.448'N 86°30.055'W, 101 m, 2.viii.2012, K. Sagastume and S. Longhorn, scrub oak forest, 1 ♀ (OUMNH); Isla Utila, Utila, wet savannah forest, 16°06.369'N 86°54.135'W, 12 m, 21.vii.2012, K. Sagastume and S. Longhorn, scrub forest/savannah, 1 ♀ (OUMNH).

***Centruroides vittatus* (Say, 1821):** U.S.A.: *Texas*: Hays Co.: Buda, iii.2003, P. Sprouse, in house, 1 ♂, 1 ♀ (AMCC [LP 2286]).

***Heteroctenus abudi* (Armas & Marcano Fondeur, 1987):** DOMINICAN REPUBLIC: *La Altagracia Prov.*: Parque Nacional del Este: Cabo Flaso (entrance zone), 18°22'25"N 68°37'01"W, 67.7 m, 14.vii.2004, E.S. Volschenk and J. Huff, 1 ♂ (AMNH); track between Ranger Station (at Boca de Yuma) and Punta Faustino, 18°21'17.2"N 68°36'52.3"W, 3.3 m, 14.vii.2004, E.S. Volschenk and J. Huff, dense canopy humid forest, hand collected from under stones and blacklighting, especially along an old rock wall along the start of the track, 19 ♂, 15 ♀, 1 subad. ♂, 1 subad. ♀, 5 juv., 102 1st instars (AMNH), 1 juv. (AMCC [LP 3268]); San Rafael de Yuma, 18°21.332'N 68°37.095'W, 46 m, 8.vi.2012, CarBio Team, rock wall, 1 ♂ (AMCC [LP 12463]). U.S.A.: *Puerto Rico*: Isla Mona, trail #1 to Punta Capitan from Sardiniera, 18°05.294'N 67°56.289'W, 16.x.2009, L. Esposito and H.Y. Yamaguti, blacklighting, primarily scrub forest and cactus, on rocks, sympatric with *Centruroides* and *Cazierius*, 10 ♂, 9 ♀, 3 subad., 4 juv. (AMNH), 2 juv. (AMCC [LP 10235]); road to El Faro, 18°03.833'N 67°52.114'W to 18°05.126'N 67°50.871'W, 17.x.2009, L. Esposito and H.Y. Yamaguti, blacklighting, population sparse, vegetation primarily desert grassland dominated by organ cactus and tall grasses, drier than east coast, 2 ♂, 4 ♀, 1 subad., 1 juv. (AMNH), 1 juv. (AMCC [LP 10234]); main road at intersection to trail #26 to Playa India, 18°03.806'N 67°53.239'W, 18.x.2009, L. Esposito and H.Y. Yamaguti, 1 ♂ (AMNH).

***Heteroctenus bonettii* (Armas, 1999):** DOMINICAN REPUBLIC: *Pedernales Prov.*: Parque Nacional Jaragua: Cabo Rojo, 17°53'45.2"N 71°39'35.8"W, 15 m, 9.vii.2004, E.S. Volschenk and J. Huff, dry cactus and spiny forest on limestone karst, hand collected from under stones and logs, and with blacklights, 5 ♂, 11 ♀, 5 subad., 2 juv. (AMNH), 1 juv. ♂ (AMCC [LP 3267]); road to Cabo Rojo, 0.6 km S of DR 44, 17°58.201'N 71°39.036'W, 14 m, 7.vii.2010, J. Huff and S. Schoenbrun, karst limestone,

- 1 ♂, 1 ♀, 1 subad. ♂ (AMNH), 1 subad. ♂ (AMCC [LP 10524]); road to Fondo Paradi, 1.8 km from Highway 44, 17°48.692'N 71°26.600'W, 302 ft, 12.i.2004, J. Huff, found between rocks, 1 ♀ (AMCC [LP 2471]), 1 ♀ (AMCC [LP 3265]); unmarked track into park between Manuell Goa and Oviedo, 17°48'41.5" 71°26'35.9"W, 83.3 m, 9.vii.2004, E.S. Volschenk and J. Huff, deciduous forest and thorny scrub, hand collected from under stones and logs and with blacklights, 15 ♂, 8 ♀, 1 subad., 1 juv. (AMNH), 1 juv. [pedipalps] (AMCC [LP 3266]).
- Heteroctenus garridoi* (Armas, 1974):** CUBA: *Guantanamo Prov.*: Guantanamo, x.2009, ex G. Molisani, 1 ♀ (AMCC [LP 10225]). *U.S. Guantanamo Bay Naval Base*: Guantanamo Bay, Graffiti Hill, 19°55'00.48"N 75°06'08.64"W, 7.v.2010, P. Tolson, S. Droege and S. Brady, native scrub, 1 ♂ (AMNH).
- Heteroctenus juncea* (Herbst, 1800):** Antillen?, 1 ♂, 2 ♀ (ZMB 7370). Porto Rico [erroneous], Stahl, 2 ♀, 1 juv. (ZMB 7280). Santiago de las Caballeros [Dominican Republic, erroneous], 1936, P. Thumb, 1 ♂ (ZMH). CUBA: Gundlach, 1 ♂, 1 ♀ (ZMB 738), 2 ♀ (ZMB 2637), 1 juv. (ZMB 7343). vii.2007, C. Hamilton, 1 juv. (AMCC [LP 7009]). *Pinar del Río Prov.*: Sierra del Rosario, near Aspuru, xi.1937, H.H. Voelckers, 1 ♂, 1 ♀, 1 juv. ♀ (ZMH). *Artemisa Prov.*: near Baños [probably Santiago de los Baños], v.1918, 2 ♂ (AMNH). *Camagüey Prov.*: Sierra de Cubitas, Limones-Tuabaquey Ecological Reserve, area around field station, 21°32.887'N 77°46.705'W, 55 m, 13–14.iv.2012, CarBio Team, 1 ♂ (AMCC [LP 12619]), 1 ♂ (AMCC [LP 12620]), 1 subad. ♀ (AMCC [LP 12621]), 1 subad. ♀ (AMCC [LP 12622]), 1 juv. ♀ (AMCC [LP 12623]). *Guantanamo Prov.*: Alejandro Humboldt National Park: near El Yunque de Baracoa, 20°19.907'N 74°34.151'W, 74 m, 4.iv.2012, CarBio Team, 1 ♀, 26 juv. (AMCC [LP 12432]), 20°20.701'N 74°33.985'W, 370 m, 5.iv.2012, CarBio Team, 1 ♂ (AMCC [LP 12613]), 20°19.64'N 74°35.59'W, 530 m, 6–7.iv.2012, CarBio Team, 1 ♂, 2 ♀ (AMNH), 1 ♂ (AMCC [LP 12614]), 4 ♀ (AMCC [LP 12615–12618]). *Havana Prov.*: Havana, 1 ♀ (AMNH), iv.1941, E. Weiss, 1 ♀, 1 subad. (AMNH). *Holguín Prov.*: viii.2000, Heist, captive bred, 1 juv. (AMCC [LP 1928]); Guardalavaca, 29.iii.1993, W. Altmann, captive bred, 1 ♂ (AMCC [LP 1565]); Mayari, Parque Nacional "Mensura-Piloto", 1 km después de la carretera al Hotel "Mayari", 716 m, 10.v.2013, F. Cala-Riquelme and A. Deler-Hernández, secondary riverine forest with abundance of pines, collected in the evening and at night on vegetation and trunks, 1 juv. ♂ (AMCC [LP 12896]). *Isla de la Juventud Prov.*: Isle of Pines, 1 ♂ (AMNH). *Mayabeque Prov.*: Arroyo Bermejo, near Fibacoa [Jibacoa], 15.vi.1967, 1 ♀ (ZMB 31021), vi.1967, 1 juv. (ZMB 31022), 31.v.1967, Kleiderschrank, 1 ♂ (ZMB 31020); Guisa, mountains near, x.1936, P. Thumb, 1 ♀, 28 juv. (ZMH), Moa, ix.1937, P. Thumb, 1 ♂ (ZMH). *Oriente Prov.*: 1938, P. Thumb, 4 ♀ (ZMH). *Pinar del Río Prov.*: Guanahacabiles, Akad.-stat. El Beral, xii.1967, G. Peters, 1 subad. (ZMB 31023); Sierra de Anafe, 23.ii.194, M. Barro, 2 subad. (AMNH); Viñales National Park, near Dos Hermanas, 22°37.265'N 83°44.3'W, 130 m, 18.iv.2012, CarBio Team, 2 juv. ♂ (AMCC [LP 12624, 12625]), 1 juv. ♀ (AMCC [LP 12626]), 22°39.424'N 83°42.097'W, 280 m, 20–21.iv.2012, CarBio Team, 6 juv. ♂ (AMCC [LP 12627–12632]), 1 juv. ♀ (AMCC [LP 12633]); Vinales Valley, 1940, Osorio, 1 ♀ (AMNH). *Sancti Spiritus Prov.*: Trinidad, viii.1978, B. Acosta, 1 ♂ (AMNH [AH 4514]). *Santiago de Cuba Prov.*: La Socapa, 10 km SW of Santiago de Cuba, 9.iv.1999, R. Teruel, 1 ♂ (AMNH), 3 ♀ (AMCC [LP 1509, 1517, 1518]); Santiago de Cuba, 1 ♂, 2 juv. (AMNH).
- Heteroctenus princeps* (Karsch, 1879):** DOMINICAN REPUBLIC: *Independencia Prov.*: Parque Nacional Isla Cabritos: Isla Cabritos, 18°30.019'N 71°43.228'W, 110 ft, 7.i.2004, J. Huff, under rock, coral, 6 ♂, 4 ♀, 3 subad., 17 juv. (AMNH), 3 juv. (AMCC [LP 2470]), 1 subad., 2 juv. (AMCC [LP 3260]); Ranger station, 18°33'45"N 71°41'50"W, –19 m, 8.vii.2004, E.S. Volschenk and J. Huff, dry forest, hand collected from under stones and logs, and with blacklights, 3 ♂, 7 ♀, 6 subad., 2 juv. (AMNH), 1 subad. (AMCC [LP 3264]); behind Ranger Sta-
- tion, 18.56287°N 71.69762°W, –23 m, 8.viii.2005, L. Esposito, mixed dry forest with succulents, UV detection, 35°C, 3 ♂, 8 ♀, 2 subad. ♀, 32 1st instars (AMNH), 1 ♂ (AMCC [LP 5102]); park entrance to Lago Enriquillo, 18°33.772'N 71°41.859'W, 18 m, 21.ii.2012, J. Huff and R.C. West, 1 juv. ♂ (AMCC [LP 12102]). Parque Nacional Sierra de Bahoruco: road between Rabo de Gato and Duverge, 18°19'38"N 71°33'55"W, 447 m, 7.vii.2004, E.S. Volschenk and J. Huff, arid thorny scrub, hand collected from under stones and in dead and dry agaves, 3 ♂, 3 ♀, 4 juv. (AMNH), 1 ♀ (AMCC [LP 3263]); Puerto Escondido, Sierra de Bahoruco, 18°19.762'N 71°33.502'W, 1592 ft, 6.i.2004, J. Huff, under dead agave, 1 ♂, 3 ♀, 1 juv. (AMNH), 1 juv. (AMCC [LP 3261]); Puerto Escondido, 6 km NNE, 18°21.084'N 71°32.048'W, 240 m, 6.vii.2010, J. Huff and S. Schoenbrun, 1 subad. ♂ (AMCC [LP 10523]); Road to Puerto Escondido, 18°20.376'N 71°33.345'W, 1388 ft, 6.i.2004, J. Huff, under rocks in gravel quarry, 1 ♀ (AMNH), 1 juv. (AMCC [LP 3262]). *La Altagracia Prov.*: San Rafael, El Morro Monte Cristi, 19°47.34'N 70°43.02'W, 40 m, 22.vi.2012, CarBio Team, 1 ♀ (AMCC [LP 12479]), 1 subad. ♂ (AMCC [LP 12478]). *Pedernales Prov.*: Manuel Goja, 3.9 km N, 17°50'20.81"N 71°27'18.84"W, 9.v.1998, D. Huber, 1 ♂ (AMCC [LP 1566]); Oviedo to Pedernales, 11.5 km N, 17°56'18.69"N 71°32'37.25"W, 8.v.1998, D. Huber, 1 ♂ (AMCC [LP 1516]). HAITI: *Dept. Ouest*: Port-au-Prince, 18°32'21.15"N 72°19'44.39"W, Ehrenberg, holotype ♂ (ZMB 116).
- Ischnotelson guanambiensis* (Lenarducci et al., 2005):** BRAZIL: *Bahia*: Ceraíma: Guanambi, Aeroporto de Guanambi, 14°13'00"S 42°46'60"W, 17.xii.2007, H.Y. Yamaguti et al., 1 subad. ♀ (MZSP 30864), [leg] (AMCC [LP 9669]), 1 subad. ♂ (MZSP 30865), [leg] (AMCC [LP 9670]).
- Ischnotelson peruassu* Esposito et al., 2017:** BRAZIL: *Minas Gerais*: Januária: Parque Nacional Cavernas do Peruaçu, 15°07.43'N 44°14.467'W, 4–25.i.2009, R.S. Recoder and M. Teixeira-Júnior, paratype ♂ (MZSP 31138), [leg] (AMCC [LP 9937]).
- Isometrus maculatus* (DeGeer, 1778):** SRI LANKA: Wellawaya, 24.ii.2000, D. Huber, 1 ♂, 1 ♀ (AMCC [LP 1798]).
- Jaguajir agamemnon* (C.L. Koch, 1839):** BRAZIL: *Maranhão*: Balsas, 07°28'44"S 46°07'09"W, 4.vi.2008, H.Y. Yamaguti et al., 1 ♀ (MZSP 31132), [leg] (AMCC [LP 9948] ex), 1 juv. ♂ (MZSP 31133), [leg] (AMCC [LP 9932]); Caxias, 04°56'26"S 43°27'59"W, 16.viii.2008, R. Pinto-da-Rocha et al., 1 juv. ♂ (MZSP 30883), [leg] (AMCC [LP 9692]), 04°56'50"S 43°29'45"W, 15.viii.2008, R. Pinto-da-Rocha et al., 1 juv. ♂ (MZSP 31134), [leg] (AMCC [LP 9936]); Santa Barbara, on shore of Rio Parnaíba, vi.1962, G. Eiten, 1 ♂ (AMNH). *Pernambuco*: Exu, 10 km N, 13.iii.1977, L.J. Vitt, rocky habitat within thorn scrub forest, 1 ♀, 1 subad. ♀, 4 juv. (AMNH), 14.iii.1977, L.J. Vitt, rocky habitat in thorn scrub, 1 ♂, 1 ♀ (AMNH); Exu, 10 km NE, 28.iv.1977, L.J. Vitt, 1 ♂, 1 ♀, 2 subad. ♀, 2 subad., 1 juv. (AMNH), 25.ix.1977, L.J. Vitt, 1 ♂, 1 ♀ (AMNH); Exu, 15 km NE, 14.v.1977, L.J. Vitt, high caatinga, under bark of tree, 1 subad. ♀ (AMNH); Exu, 20 km E, 30.iii.1977, L.J. Vitt, 1 juv. ♂ (AMNH); Fazenda Caterino, 10 km NE Exu, 1.viii.1977, L.J. Vitt, 1 juv. ♂ (AMNH), 25.ix.1977, L.J. Vitt, 1 ♀ (AMNH), 9.vii.1977, L.J. Vitt, 1 subad. ♂ (AMNH). *Pi-auí*: Barras, 04°19'04"S 42°18'26"W, 18.viii.2008, R. Pinto-da-Rocha et al., 1 subad. ♀ (MZSP 30884), [leg] (AMCC [LP 9693]); Castelo do Piauí, 05°13'43"S 41°41'57"W, 13.viii.2008, R. Pinto-da-Rocha et al., 1 ♀ (MZSP 30887), [leg] (AMCC [LP 9696]), 1 subad. ♂ (MZSP 31157), [leg] (AMCC [LP 9933]), 1 juv. ♂ (MZSP 31156), [leg] (AMCC [LP 9939]); Oeiras, 06°58'28"S 42°06'31"W, 2–3.iv.2008, H.Y. Yamaguti et al., 1 ♂ (MZSP 31160), [leg] (AMCC [LP 9954]), 3 ♀ (MZSP 31161), [leg] (AMCC [LP 9942]); Piracuruca, near Parque Nacional Sete Cidades, 04°10'07"S 41°41'56.7"W, 16.viii.2008, R. Pinto-da-Rocha and L.S. Carvalho, 1 ♂ (MZSP 31167), [leg] (AMCC [LP 9949]); Sítio Ouro Verde, Teresina, 04°54'13.9"S 42°47'27.1"W, 27.vii.2008, L.S. Carvalho, 1 subad. ♂ (MZSP

- 30886), [leg] (AMCC [LP 9695]), 1 juv. ♂ (MZSP 31169), [leg] (AMCC [LP 9960]); Teresina, Campus UFPI, 05°02'43.5"S 42°46'13.4"W, 16.viii.2008, UFPI, 1 ♂ (MZSP 31170), [leg] (AMCC [LP 9929]). *Tocantins*: Mateiros, Jalapão, 10°33.811'S 46°27.409'W, 17.iv.2009, S. Outeda-Jorge and F. Marques, 1 ♂ (MZSP 31182), [leg] (AMCC [LP 9938]), 1 subad. ♀ (MZSP 31180), [leg] (AMCC [LP 9934]), 1 juv. ♂ (MZSP 31181), [leg] (AMCC [LP 9958]); Rio da Conceição, estrada para E.E. Serra Geral, 11°22'26"S 46°49'11"W, 7.vi.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♀ (MZSP 30885), [leg] (AMCC [LP 9694]), 1 subad. ♀ (MZSP 31193), [leg] (AMCC [LP 9935]).
- Jaguajir pintoí (Mello-Leitao, 1932):** BRAZIL: *Roraima*: Normandia, 03°53'44"N 59°37'40"W, 14.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 juv. ♂ (MZSP 31176), [leg] (AMCC [LP 9928]), 1 juv. ♂ (MZSP 31177), [leg] (AMCC [LP 9944]); Vila Tepequém, Amajari, 03°47'54"N 61°43'08"W, 11.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♀ (MZSP 30862), [leg] (AMCC [LP 9672]), 03°47'54"N 61°44'57"W, 17.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♀ (MZSP 30863), [leg] (AMCC [LP 9671]). GUYANA: Upper Takutu–Upper Essequibo Region: Rupununi region, SW Guyana, near Venezuelan border, iii.2008, 1 juv. ♂ (AMCC [LP 8278]), 24.ix.2008, imported L. Arden, 9 ♀, 3 juv. (OUMNH 2009-001).
- Jaguajir rochae (Borelli, 1910):** BRAZIL: *Bahia*: Barra, Igarité, 5.vi.2008, 1 ♀ (MZSP 31122), [leg] (AMCC [LP 9963]); Catu, Ibiraba, 2.viii.2000, 1 ♀ (MZSP 31123), [leg] (AMCC [LP 9953]); Ceraíma, Guanambi, 14°13'00"S 42°46'60"W, 10–17.xii.2007, H.Y. Yamaguti et al., 1 ♂ (MZSP 30881), [leg] (AMCC [LP 9684]); Guanambi, 7 km S, 14°17'5.6"S 42°47'2.2"W, 533 m, 24.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, UV sampling, modified savanna, cloudy and raining, 1 juv. (AMCC [LP 7638]); Guanambi, 16 km SE, 14°17'19"S 42°41'31.1"W, 559 m, 25.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, UV sampling and under leaf litter, banana plantation and surrounds, 1 juv. (AMCC [LP 7655]); Fazenda du Fabiano, 8 km NE Guanambi, 14°10'17.6"S 42°43'56.4"W, 539 m, 24.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, under rocks, rocky hill and surrounds, open savanna modified, 1 ♀ (AMNH), 1 ♂, 2 juv. (AMCC [LP 7639]); Espadado de Cima, Jeremoabo, 10°04'S 38°23'W, 27.v.2008, H.Y. Yamaguti, T.J. Porto and M.B. da Silva, 1 subad. ♀ (MZSP 30882), [leg] (AMCC [LP 9685]); Ibotirama, 12°10'34"S 43°11'33"W, 8.vi.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♂ (MZSP 31125), [leg] (AMCC [LP 9956]), 1 ♀ (MZSP 31124), [leg] (AMCC [LP 9947]); Jeremoabo, 10°04'S 38°23'W, 25.v.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♂ (MZSP 31126), [leg] (AMCC [LP 9945]); Várzea do Poço, 19.x.2007, 1 ♀ (MZSP 31127), [leg] (AMCC [LP 9926]). *Minas Gerais*: Janaúba, 11.xii.2007, H.Y. Yamaguti, S. Outeda-Jorge and C.A. Souza, 1 juv. ♂ (MZSP 31136), [leg] (AMCC [LP 9957]); UNIMONTES, campus Janaúba, Janaúba, 11.xii.2007, H.Y. Yamaguti et al., 1 subad. ♂ (MZSP 30879), [leg] (AMCC [LP 9682]). *Paraíba*: Soledade, 07°02.118'S 36°27.311'W, 575 m, 16.iii.1999, A. Kury and A. Giupponi, 3 ♂ (AMCC [LP 1581, 1582, 1775]). *Pernambuco*: Escola Aquícola, Exu, 30.iii.1977, L.J. Vitt, caatinga, 1 ♂ (AMNH), 27.vi.1977, L.J. Vitt, 1 ♂ (AMNH); Exu, 07°26'44"S 39°44'21"W, 1.vi.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♀ (MZSP 31144), [leg] (AMCC [LP 9955]), 1 juv. ♂ (MZSP 31143), [leg] (AMCC [LP 9951]); Exu, 18 km E, 5.iii.1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat, 2 ♀, 68 1st instars (AMNH); Exu, 20 km E, 30.iii.1977, L.J. Vitt, 1 ♂, 1 ♀, 2 juv. (AMNH); Exu, 3 km NW, 10.iii.1977, L.J. Vitt, 2 ♂, 1 ♀, 3 juv. (AMNH); Exu, 3 km W, 30.v.1977, L.J. Vitt, 2 ♂, 4 ♀, 4 juv. (AMNH), 1.vi.1977, L.J. Vitt, 1 ♀ (AMNH); Exu, 5 km E, 8.v.1977, L.J. Vitt, 1 juv. (AMNH); Exu, 5 km N, 6.iv.1977, L.J. Vitt, caatinga, 1 ♂, 1 juv. (AMNH), 18.i.1978, L.J. Vitt and K.E. Streilein, 1 juv. (AMNH); Exu, 6 km N, 15.iii.1977, L.J. Vitt, open fields (cotton), under fallen logs, 1 ♀, 1 juv. ♂ (AMNH); Exu, 6 km NE, 16.iii.1977, L.J. Vitt, under rock on larger rock, caatinga habitat, 1 ♀, 49 1st instars (AMNH); Fazenda Batente, 5 km NE Exu, 29.iii.1977, L.J. Vitt, 1 juv. (AMNH); Fazenda Caterino, 10 km NE Exu, 1.viii.1977, L.J. Vitt, 7 ♂, 3 ♀, 3 juv. (AMNH); Fazenda Chelonia, 8 km S Exu, 28.vii.1977, L.J. Vitt, 2 juv. (AMNH); Fazenda Guarani, 3 km N Exu, 14.vii.1977, L.J. Vitt, 1 ♂, 3 ♀, 1 subad., 3 juv. (AMNH); Fazenda Guarani, 5 km N Exu, 29.vii.1977, L.J. Vitt, 1 ♀, 3 juv. (AMNH), 19.ii.1978, L.J. Vitt, 1 ♀ (AMNH); Serra Talhada, 07°58'11"S 38°19'16"W, 30.v.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♀ (MZSP 31146), [leg] (AMCC [LP 9943]), 1 ♀ (MZSP 31147), [leg] (AMCC [LP 9930]); Vitória do Santo Antão, 08°07'S 35°25'W, 28.v.2008, H.Y. Yamaguti, M.B. da Silva and T.J. Porto, 1 ♀ (MZSP 31148), [leg] (AMCC [LP 9946]). *Piauí*: Castelo do Piauí, 05°13'43"S 41°41'57"W, 13.viii.2008, R. Pinto-da-Rocha and L.S. Carvalho, 1 ♂ (MZSP 31150), [leg] (AMCC [LP 9961]), 1 ♀ (MZSP 31151), [leg] (AMCC [LP 9941]). *Sergipe*: near Genipapo, vii.1982, O.F. Francke, 1 ♂, 2 ♀ (AMNH); UHE Xingó, Canindé de São Francisco, 22.viii.2007, Arnaldo Jr., 1 ♀ (MZSP 30880), [leg] (AMCC [LP 9683]).
- Physoctonus debilis* (C.L. Koch, 1840):** BRAZIL: *Pernambuco*: Exu, 18 km N, 5.iii.1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat, 1 ♀ (AMNH); Exu, 5 km N, 4.x.1977, L.J. Vitt, 1 ♀ (AMNH), 18.i.1978, L.J. Vitt and K.E. Streilein, 1 ♀ (AMNH); Fazenda Batente, 13 km E Exu, 10.xi.1977, L.J. Vitt and K.E. Streilein, 1 ♀ (AMNH); Fazenda Caterino, 10 km NE Exu, 9.vii.1977, L.J. Vitt, 1 ♀ (AMNH), 25.ix.1977, L.J. Vitt, 1 ♀ (AMNH). *Piauí*: Castelo do Piauí, 05°13'43"S 41°41'57"W, 13.viii.2008, R. Pinto-da-Rocha et al., 1 ♀ (MZSP 30868), [leg] (AMCC [LP 9680]), 1 ♀ (MZSP 31158), [leg] (AMCC [LP 9931]); Oeiras, 06°58'28"S 42°06'31"W, 2–3.vi.2008, H.Y. Yamaguti et al., 1 ♀ (MZSP 31162), [leg] (AMCC [LP 9940]), 1 subad. ♀ (MZSP 31164), [leg] (AMCC [LP 9962]), 3.vi.2008, H.Y. Yamaguti et al., 1 ♀ (MZSP 30866), [leg] (AMCC [LP 9678]); near Parque Nacional Sete Cidades, Brasileira e Piracuruca, 04°10'02"S 41°41'56.7"W, 16.viii.2008, R. Pinto-da-Rocha and L.S. Carvalho, 1 ♀ (MZSP 30867), [leg] (AMCC [LP 9679]).
- Physoctonus striatus* Esposito et al., 2017:** BRAZIL: *Bahia*: Xique-Xique, 10°49'60"S 42°43'60"W, 2.x.2008, T.J. Porto, paratype ♂ (MZSP 30869), [leg] (AMCC [LP 9681]), 3.x.2008, T.J. Porto, paratype ♂ (MZSP 31128), [leg] (AMCC [LP 9950]).
- Rhopalurus caribensis* Teruel & Roncallo, 2008:** COLOMBIA: *Magdalena Dept.*: Município Santa Marta: Bahía de Guairaca, Tayrona Park, 31.x.1985, H.-G. Muller, 1 ♀ (SMF 37027); Corregimiento de Bonda, Vereda Girocasaca, Finca Guaipe, 11°13'05.5"N 74°06'14.3"W, 173 m, 21–24.viii.2014, J.A. Moreno and W. Galvis, nocturnal, manual collection with UV light, 1 ♂ (AMCC [LP 13167]), 1 subad. ♂ (AMNH); Finca Las Delicias, 80 m, 17.v.2008, J.A. Noriega, 1 ♂ (AMCC [LP 9341]); Pozo Colorado, 11 km W Santa Marta, 18–30.iv.1968, B. Malkin, 1 ♀, 1 subad., 19 1st instars (AMNH); Puente de Los Clavos, 15 km E Pueblo Bello, Sierra Nevada de Santa Marta, 1500 m, 13.vi.1968, B. Malkin, 1 subad. ♂ (AMNH); Santa Marta, 29.vi–31.vii.1966, 2 ♀ (SMF 39120).
- Rhopalurus laticauda* Thorell, 1876:** 2 ♀ (ZMB 14865). "Mexico", Dr v. Hubl, 1 ♂ (ZMB 14866). BRAZIL: F. Kummerow, 1 ♂, 1 ♀ (ZMB 8226). *Acre*: Rio Branco, Amazonasgebiet, 1912, E. Ule, 1 juv. ♀ (ZMB 14867). *Pará*: Alter do Chão, Santarém, 02°31'36"S 54°54'19"W, 28.x.2008, R. Pinto-da-Rocha and H.Y. Yamaguti, 1 ♂ (MZSP 30870), [leg] (AMCC [LP 9686]), 1 subad. ♂ (MZSP 30872), 1 juv. (AMCC [LP 9688]), 1 juv. ♀ (MZSP 30873), [leg] (AMCC [LP 9689]), 1 juv. ♀ (MZSP 30874), [leg] (AMCC [LP 9690]), 1 juv. (MZSP 30875), [leg] (AMCC [LP 9691]); Monte Alegre, 01°56'32"S 54°08'13"W 31.x.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♀ (MZSP 30871), [leg] (AMCC [LP 9687]), 1 ♀ (MZSP 31141), [leg] (AMCC [LP 9924]). *Roraima*: Alto Alegre, 02°56'34"N 61°03'09"W, 10.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♂ (MZSP 31173), [leg] (AMCC [LP 9952]), 1 juv. ♂ (MZSP 31172), [leg] (AMCC [LP 9927]); Bonfim,

- 03°22'45"N 59°49'18"W, 13.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♂ (MZSP 30878), [leg] (AMCC [LP 9677]), 1 subad. ♂ (MZSP 31175), [leg] (AMCC [LP 9925]); Mt. Roraima, 2 ♂, 1 ♀, 1 subad. (AMNH [29180]); Mucajaí, 02°27'38"N 60°54'24"W, 12.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♂ (MZSP 30877), [leg] (AMCC [LP 9676]); Normandia, 03°53'44"N 59°37'40"W, 14.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♂ (MZSP 31178), [leg] (AMCC [LP 9959]), 1 ♀ (MZSP 30876), [leg] (AMCC [LP 9675]). COLOMBIA: *Guaviare Dept.*: San José del Guaviare, xii.1955, Meden, 1 ♀ (SMF 39252). VENEZUELA: *Apure*: Elorza, 10 km SW, road to San Felipe, 07°03.749'N 69°30.249'W, 89 m, 5.x.2008, J.A. Ochoa and S.E. Bazo Abreu, llanos, 3 ♂, 3 ♀, 1 subad. ♂, 3 juv. ♂ (AMNH), 1 juv. (AMCC [LP 9200]). *Aragua*: Cagua, 10°11'N 67°27'W, 1903, 1 ♂, 1 ♀ (SAM 6512); Maracay, Fahrenheit, 1 ♂, 1 ♀, 1 subad. (SMF 8876/218), 1 subad. ♂ (SMF 29208); Parque Nacional Henri Pittier: Puerto Colombia, Cristo Mirador, 10°30.572'N 67°36.253'W, 1–10 m, 1.viii.2009, F. Rojas-Runjaic, A. Ferrer, L. Prendini and J.A. Ochoa, dry area, hill near to beach, 1 ♂, 3 ♀ (AMNH), 1 juv. (AMCC [LP 10046]). *Bolívar*: A.C. La Ceiba, between Puerto Ordaz and Ciudad Bolívar, 08°14.023'N 62°55.562'W, 102 m, 15.vii.2009, A. Yopez, M. Blanco and J.A. Ochoa, llanos, 1 ♂ (AMNH), 1 juv. (AMCC [LP 10047]); Cedeño ca. Los Pijiguaos, 06°29.878'N 67°02.600'W, 76 m, 12.x.2008, J.A. Ochoa and S.E. Bazo Abreu, llanos, 2 ♀, 1 subad. ♀ (AMNH), 1 juv. (AMCC [LP 9237]); Ciudad Bolívar, 20.ii.1903, 2 ♀ (ZMH), 07°37.486'N 64°05.924'W, 117 m, 24.x.2008, J.A. Ochoa and S.E. Bazo Abreu, llanos, 1 ♂, 3 ♀, 1 subad. ♀, 1 juv. ♂, 1 ♂ metasoma (AMNH), 1 juv. (AMCC [LP 9256]); Comunidad Corosal, ca. Pijiguaos, 80 m, 25.x.2008, J.A. Ochoa, forest, 1 ♂, 4 ♀, 2 subad. ♀ (AMNH), 1 subad. ♀ (AMCC [LP 9253]); Gran Sabana, 88 km, xi.2005–ii.2006, C. Siederman, 2 ♂ (AMNH); La Paragua, M.A. de Verde, 1 ♂ (AMNH); Parque Nacional Canaima: Laguna Canaima, Isla Anatóly, 06°15.191'N 62°50.945'W, 395 m, 27.vii.2009, L. Prendini and J.A. Ochoa, savanna and forest, 3 ♂, 2 ♀ (AMNH), 1 juv. (AMCC [LP 10048]); Uputa, ii.1973, A. Bordes, 1 ♀ (AMNH). *Distrito Federal*: Caracas, iii.1999, C. Siederman, 2 ♀, 20 1st instars (AMNH). *Guarico*: between Calabozo and San Fernando de Apure (about halfway), 30.xi.1967, M.A. de Verde, 1 ♀ (AMNH); Hato Masaguarat, 45 km S Calabozo, 7.iv.1978, Y. Lubin, 1 ♂ (AMNH). *Mérida*: Mérida, 2 ♂, 3 ♀ (SMF 5712/27). *Miranda*: Guatire, 15.xii.1975, M.A. Gonzalez-Sponga, 1 ♂, 1 ♀ (NM 16431), 29.iv.2004, R.C. West, under rocks, dry forest, 1 ♂ (AMCC [LP 2845]), 1 ♀ (AMNH); Hacienda Santa Rosa, 3 km N Guatire, 450 m, 10.i.1973, M.A. Gonzalez-Sponga, 1 ♂, 1 ♀, 2 juv. (AMNH). *Nueva Esparta*: Isla Margarita, N of Peninsula de Macanao, 11°02.618'N 64°21.542'E, 4.ix.2005, S. Huber, 1 ♀ (AMCC [LP 4221]); probably Isla Margarita, 2001, C. Siederman, 1 ♀ (AMCC [LP 2462]).
- Rhopalurus ochoai Esposito et al., 2017:** VENEZUELA: *Carabobo*: Municipio Valencia: Valencia, 29.xii.1904, F. Kummerow, paratype ♀ (ZMB 31024), ix.1958, H. Ardel, 2 ♀ paratypes (ZMH), Valencia, Falcon Distr., viii.1992, C. Siederman, paratype ♂ (AMNH). *Trujillo*: Municipio Motatan: San Miguel, ca. Represa Agua Viva, 09°30.225'N 70°34.914'W, 195 m, 23.ix.2008, J.A. Ochoa and S.E. Bazo Abreu, dry forest, 1 ♂, 1 ♀ paratypes (AMNH), 1 subad. ♀, 1 juv. ♀ paratypes (AMCC [LP 9199]). Municipio Valera: Valera region, N, x.2005, S.E. Bazo Abreu, paratype ♀ (AMCC [LP 5504]), paratype ♀ (AMCC [LP 5505]). *Zulia*: Municipio Jesus Enrique Lozada: San Agustín, 10°45.841'N 71°44.108', 44 m, 28.ix.2008, J.A. Ochoa and S.E. Bazo Abreu, dry forest, holotype ♂, 1 ♂, 2 ♀, 1 subad. ♀ paratypes (AMNH), 1 subad. ♀ paratype (AMCC [LP 9207]).
- Tityus atriventer Pocock, 1897:** GRENADA: *St. Andrew Parish*: Balthazar Estate, 12.124°N 61.660°W, 18.vii.2008, L. Esposito and D. Schiff, agricultural land, under stones, 1 ♀ (AMCC [LP 9033]).
- Tityus bahiensis (Perty, 1833):** ARGENTINA: *Misiones Prov.*: San Ignacio, road to Playas del Sol, 27°16'15"S 55°44'35"W, 60 m, 7.ii.2006, C.I. Mattoni and D. Vrech, UV on paranaense forest, in base of tree, 1 ♀ (AMCC [LP 5641]). BRAZIL: *São Paulo*: São Paulo, 13.vi.1893, J. Wiengreen, 1 ♂, 2 ♀ (ZMH).
- Tityus clathratus C.L. Koch, 1844:** SURINAM: Paramaribo, 27.x.1909, C. Heller, 2 ♂, 1 ♀, 1 subad. ♂ (ZMH). TRINIDAD AND TOBAGO: *Trinidad*: Gaspar Grande Island, 7.vii.1999, L. Prendini, collected at night with UV light, 8 ♀ (AMCC [LP 1567]).
- Tityus discrepans (Karsch, 1879):** VENEZUELA: *Distrito Federal*: Caracas, xi.1998, M.A. Gonzalez-Sponga, 1 ♀, 1 juv. (AMCC [LP 1547]). *Miranda*: Municipio Los Salias: San Antonio de los Altos, Quebrada Aguas Blancas, 10°22.088'N 66°58.033'W, 1391 m, 22.viii.2009, S. Foghin, F. Rojas-Runjaic and J.A. Ochoa, secondary forest, 1 ♂ (AMCC [LP 10102]).
- Tityus kuryi Lourenço, 1997:** BRAZIL: *Bahia*: Mucugé, 10 km NE, 12°57'30.7"S 41°19'30.1"W, 1163 m, 20.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, UV sampling, hills with open rocky savanna, 1 juv. (AMCC [LP 7659]); road to Iगतú, south access, 12°54'11.9"S 41°18'26.2"W, 900 m, 21.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, UV sampling, hills with open rocky savanna, 1 ♀ (AMCC [LP 7656]).
- Tityus metuendus Pocock, 1897:** GUYANA: Essequibo River, 01°36'45.7"N 58°38'14.6"W, 240 m, 15.vii.1999, M. Kuntner, primary forest, collected on tree trunk, 1 ♂ (AMCC [LP 1546]). PERU: *Loreto*: Rio Orosa, E of Iquitos, 12.vi.2002, S. Gonzales, on tree trunk at night, 2 ♀ (AMCC [LP 1983]).
- Tityus smithii Pocock, 1893:** ST. VINCENT AND THE GRENADINES: *Bequia*: Old Road to Hope Beach, 13.006°N 61.221°W, 14.vii.2008, L. Esposito and D. Schiff, tropical forest, UV detection, 1 subad. ♀ (AMCC [LP 9046]); Cinnamon Garpoan, 13°01.322'N 61°14.126'W, 170 m, 5.v.2013, CarBio Team, dry scrub, 1 ♂ (AMCC [LP 12976]); Princess Margaret Beach, 13°00.13'N 61°14.377'W, 20 m, 5.v.2013, CarBio Team, coastal vegetation, 1 ♀ (AMCC [LP 12977]).
- Tityus riverai Teruel & Sanchez, 2009:** U.S.A.: *Puerto Rico*: Municipio Mayagüez: Zoo Dr. Juan A. Rivero, Barrio Miradero, xi.2008, W. Vargas, on avian warehouse, found dead, 1 ♂, 1 ♀ (AMNH); Mayagüez, Zoologico de Puerto Rico (Mayagüez Zoo), 18°12.948'N 67°08.008'W, 30 m, 22.x.2009, L. Prendini, J. Huff and L. Figueroa, lowland tropical forest in zoological gardens, UV detection on warm, very humid, moonless night, taken on tree trunks and tree holes mostly near bird aviary, some several meters high, 1 subad., 1 juv. (AMCC [LP 10202]).
- Troglohopalurus lacraui (Lourenço & Pinto-da-Rocha, 1997):** BRAZIL: *Bahia*: Itaeté: Trail between Caves "Lapa do Bode" and "Lapa Escondida", 12°56'9.1"S 41°03'56.2"W, 21.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H.Y. Yamaguti, under rocks, 2 ♀ (AMNH), 1 subad. ♀, 4 juv. (AMCC [LP 7637]); "Lapa do Bode", 24.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H. Yamaguti, 1 subad. ♀ (AMCC [LP 10211]).
- Troglohopalurus translucidus Lourenço et al., 2004:** BRAZIL: *Bahia*: Andaraí: Gruna Canal da Fumaça, GPS, J.E. Gallao, D. Schimonsky and M.E. Bichuette, date, 1 ♂ (LES-4786). Lençóis: Gruta do Lapão, Chapada Diamantina, Lençóis, 12°34'00"S 41°22'60"W, 20–29.i.2009, H.Y. Yamaguti et al., 1 ♂ (MZSP), [pedipalp and two legs] (AMCC [LP 9668]).
- Zabius birabeni Mello-Leitão, 1938:** ARGENTINA: *La Pampa Prov.*: Lihuel Calel, 6.i.2003, A.A. Ojanguren-Affilastro, 1 ♀ (AMCC [LP 2261]). *San Juan Prov.*: plains near Caucete, base of Sierra de Pie de Palo, 31°42'37.5"S 68°08'24.2"W, 817 m, 28.i.2005, C.I. Mattoni and A.A. Ojanguren-Affilastro, UV sampling, 1 ex. [chela] (AMCC [LP 4251]).
- Zabius fuscus (Thorell, 1876):** ARGENTINA: *Córdoba Prov.*: Capilla de Olaen, ca. 11 km W of Molinari, 31°09'44.46"S 64°36'24.336"W, 1096 m, 29.xii.2005, C.I. Mattoni, A. Peretti, P. Carreras, M. Zerda and D. Vrech., grassland with granitic rocks, under stones and UV, 2 juv. (AMCC [LP 5642]); La Cumbre, iii.2000, K. Biondo, 1 ♂ (AMCC [LP 1869]); Puesto del Cura, 1917, Lillo, 2 ♀ (MNHN RS 3587).

10. Appendix 3

Morphological characters and character states used in phylogenetic analysis of New World buthid subfamily Centruroidinae Kraus, 1955. Nomenclature follows HJELLE (1990) and SISSOM (1990), except for carapace and metasomal carination (VACHON 1974; PRENDINI 2003b), tergite and pedipalp carination (PRENDINI 2001b), pedipalp trichobothria (VACHON 1974), ovariterine anatomy (VOLSCHEK et al. 2008), and book lung anatomy (KAMENZ & PRENDINI 2008).

Carapace

1. Lateral ocular carina: present (0); absent (1).
2. Central lateral carina: present (0); absent (1).
3. Anterior central submedian carina: present (0); absent (1).
4. Posterior central submedian carina: present (0); absent (1).
5. Anterior and posterior central submedian carinae, fusion: separate (0); fused (1).
6. Central lateral carina and posterior central submedian carina, fusion: fused (0); separate (1).
7. Lateral ocular tubercle, macro-ocelli, count (STOCKWELL 1989; PRENDINI 2000; SOLEGLAD & FET 2003): three (0); two (1).
8. Lateral ocular tubercles, posterior micro-ocellus (STOCKWELL 1989; PRENDINI 2000; SOLEGLAD & FET 2003): present (0); absent (1).

Chelicerae

9. Fixed finger, dorsobasal setation: present (0); absent (1).
10. Median tubercles on the dorsal surface of the trunk, pattern of arrangement: transverse row (0); spread (1).

Pedipalps

11. Patella, association between prodorsal and proventral carinae: converging (0); separate, clearly defined (1).
12. Chela dorsal accessory carina: granular (0); smooth (1).
13. Chela median carina: present (0); absent or obsolete (1).
14. Chela ventral accessory carina: present (0); absent or obsolete (1).
15. Chela ventrointernal carina: present (0); absent (1).
16. Chela internomedian carina: present (0); absent (1).
17. Chela dorsointernal carina: present (0); absent (1).
18. Femur retrolateral accessory carina: absent (0); present (1).
19. Chela fixed finger, median denticle row, primary subrows: 8 (0); 9 (1); 13 or more (2).
20. Chela fixed finger, median denticle row, prolateral accessory (supernumerary) granules (SOLEGLAD & FET 2003): absent (0); present, well developed (1); present, weak and widely spaced (2).

21. Chela movable finger, median denticle row, number of primary subrows (SOLEGLAD & FET 2003; PRENDINI 2004): 8 (0); 9 (1); 11 (2); ≥ 13 (3).
22. Chela shape (male) (PRENDINI 2001b, 2004): incrassate (0); slender (1).
23. Chela shape (female) (PRENDINI 2001b): incrassate (0); slender (1).
24. Chela fixed finger, shape (male) (PRENDINI 2001b, 2004): straight, proximal dentate margin linear when fingers closed (0); slightly curved dorsally (1); strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers closed (2).
25. Chela movable finger, shape (male) (PRENDINI 2001b, 2004): straight, proximal dentate margin linear when fingers closed (0); slightly curved ventrally (1); strongly curved ventrally, proximal dentate margin distinctly emarginate when fingers closed (2).
26. Chela movable finger, proximal lobe (male) (PRENDINI 2001b): absent (0); present (1).
27. Chela movable finger, median lobe (male) (PRENDINI 2004): absent (0); present (1).
28. Chela fixed finger, proximal lobe (male) (PRENDINI 2001b): absent (0); present (1).
29. Chela fixed finger, median lobe (male) (PRENDINI 2004): absent (0); present (1).
30. Femur dorsal surface, trichobothrium d_2 (SOLEGLAD & FET 2001, 2003): absent (four d trichobothria) (0); present (five d trichobothria) (1).
31. Chela fixed finger, trichobothrium db position: situated distal to trichobothrium et (0); approximately aligned with et (1); situated between trichobothria est and et (2); approximately aligned with est (3).
32. Chela fixed finger, trichobothrium est position: approximately aligned with trichobothrium db (0); situated between trichobothria db and et (1); situated proximal to et (2).
33. Chela fixed finger, trichobothrium et position: situated between trichobothria dt and db (0); aligned with db (1); situated between db and est (2).

Legs

34. Leg I, prolateral pedal spur: simple (0); bifurcating (1).
35. Leg I, telotarsal setae, arrangement: tufts (0); two discrete rows (1).
36. Leg I, telotarsal setae, form: fine, acuminate (0); thick, acuminate (1); short, stout (2).
37. Leg IV, telotarsal setae, arrangement: tufts (0); two discrete rows (1).
38. Leg IV, telotarsal setae, form: fine, acuminate (0); thickened acuminate (1); short, stout (2).

Pectines

39. Pectinal teeth, shape: straight, sides almost parallel (0); sides slightly concurve, not straight (1); dorsal surface strongly concurve, sinuate (2).

40. Proximal pectinal teeth, dorsal surface, sculpture: smooth or slightly granular (0); with irregular striations (1); large and regular striations (2).
41. Proximal pectinal teeth, dorsal surface, nodules: single (0); multiple (1); absent (2).
42. Pectinal teeth, dorsobasal surface, macrosetae: present (0); absent (1).
43. Pectinal teeth, peg sensillae, shape: short and blunt (0); elongate and blunt (1); elongate and acuminate (2).
44. Proximal dorsal fulcra, setae: one (0); two (1); three (2); four (3); six or more (4); absent (5).
45. Proximal median lamellae, shape (female) (PRENDINI 2001b, 2004): not dilated (0); dilated (1).
46. Pectinal plate, anterior margin, sulcus: present (0); absent (1).
47. Pectinal plate, posterior margin (male): curved (0); straight (1).
48. Pectinal plate depressions (male): single median (0); two lateral (1); absent (2).

Sternites

49. Sternite III, ventral median carinae: broad anterior raised region (0); narrow, elevated anterior carina (1); no elevation anteriorly (2).
50. Sternite III, lateral margins, sculpture: not raised or granular (0); granular carina (1); smooth carina (2).
51. Sternite III, ventrosubmedian surface, sculpture: smooth or slightly granular (0); large, regularly spaced granules (1); small, irregular granules (2). — Granules as characterized in state (1) are known to have a stridulatory function in all/some species where this state was observed.
52. Sternite V, raised, smooth area on posteromedian surface (male) (PRENDINI 2004): present (0); absent (1).
53. Sternite VI, ventrosubmedian carinae: present (0); absent (1).
54. Sternite VI, ventrolateral carinae: present (0); absent (1).
55. Sternites III–VI, spiracle shape (KAMENZ & PRENDINI 2008): wide, width $> 5 \times$ length (0); compact, width $< 3 \times$ length (1).

Tergites

56. Tergite I, dorsolateral carinae: restricted to anterior 2/3 or less (0); absent (1).
57. Tergite I, dorsosubmedian carinae: present (0); absent (1).
58. Tergite II, dorsolateral carinae: restricted to anterior 2/3 or less (0); absent (1).
59. Tergite II, dorsomedian carina: present (0); absent (1).
60. Tergites III–VI, dorsolateral carinae: present (0); absent (1).
61. Tergites III–VI, dorsosubmedian carinae (PRENDINI 2004): absent (0); present (1).
62. Tergite VII, dorsomedian carina: narrow, granular carina (0); granular mound, no carina (1); smooth mound, no carina (2).

63. Tergite VII, coloration relative to preceding tergites: paler (0); similar (1).

Metasoma

64. Segment I, dorsal surface, granulation: sparsely granular (0); densely granular (1).
65. Segment II, lateral inframedian carina (PRENDINI 2004): continuous (0); posteriorly confined (1); absent (2).
66. Segment III, lateral inframedian carina (PRENDINI 2004): continuous (0); posteriorly confined (1); absent (2).
67. Segment III, dorsolateral carinae, posterior granules, size relative to anterior granules: similar (0); larger and spiniform (1).
68. Segment IV, lateral inframedian carinae: absent or obsolete (0); distinctly present and well developed (1).
69. Segments IV and V, ventral coloration relative to preceding segments: darker (0); similar (1).
70. Segment V, anal rim granulation: present (0); absent (1).
71. Segment V, dorsolateral carina: present (0); absent (1).
72. Segment V, lateral inframedian carinae: absent (0); present (1).
73. Segment V, ventromedian carina: absent (0); present (1).
74. Segment V, ventrosubmedian carinae: absent (0); present (1).
75. Segment V, ratio of length to width: slightly elongate, length $< 2 \times$ width (0); elongate, length $2.5\text{--}3 \times$ width (1); strongly elongate, length $> 3 \times$ width (2).
76. Segments I–IV, relative width (LAMORAL 1978; PRENDINI 2001b, 2003b): narrowing posteriorly, segment I wider than IV (0); slight widening posteriorly, segment I slightly narrower than IV (1); pronounced widening posteriorly, segment I much narrower than IV (2).
77. Segments I–V, summed length relative to prosoma + mesosoma length (male): similar ($< 1.5 \times$) (0); much greater ($\geq 1.5 \times$) (1).
78. Segments I–V, coloration, dark ventromedian stripe: absent (0); present (1).

Telson

79. Vesicle shape: spherical, length similar to width (0); slightly ovate, length ca. $1.5 \times$ width (1); ovate, length more than $2 \times$ width (2).
80. Vesicle width relative to width of metasomal segment V (LAMORAL 1978; PRENDINI 2001b, 2003b): approximately equal (0); somewhat narrower (1); considerably narrower, less than half (2).
81. Vesicle ventromedian carina: present (0); absent (1).
82. Vesicle lateral surface, granulation: granular (0); smooth (1).
83. Vesicle subaculear tubercle (LAMORAL 1980; STOCKWELL 1989; PRENDINI 2000, 2004; SOLEGLAD & FET 2003): pronounced, pointed tooth (0); nub-like eminence (1); absent (2).

84. Vesicle subaculear tubercle, dorsal granules: absent (0); present (1).

Size

85. Male body length, relative to female: smaller or approximately equal (0); much larger ($> 1.5 \times$) (1).

Ovariuterus

86. Ovariuterine network, number of loops (VOLSCHENK et al. 2008): 8 (0); 9 (1); 2 (2).
87. Ovariuterus type (VOLSCHENK et al. 2008): simple (0); complex bridged (1).

Book lungs

88. Lamellar surface (KAMENZ & PRENDINI 2008): slender venation (0); ribbed venation (1).
89. Lamellar edge (KAMENZ & PRENDINI 2008): thorns (0); smooth or slightly wrinkled (1).
90. Posterior spiracle edge (KAMENZ & PRENDINI 2008): hillocks (0); subconical (1).

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