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SYSTEMATIC REVISION OF THE NEOTROPICAL  
CLUB-TAILED SCORPIONS, *PHYSOCTONUS*,  
*RHOPALURUS*, AND *TROGLORHOPALURUS*,  
REVALIDATION OF *HETEROCTENUS*, AND  
DESCRIPTIONS OF TWO NEW GENERA AND THREE  
NEW SPECIES (BUTHIDAE: RHOPALURUSINAE)

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LAUREN A. ESPOSITO, HUMBERTO Y. YAMAGUTI,  
CLÁUDIO A. SOUZA, RICARDO PINTO-DA-ROCHA,  
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LAUREN A. ESPOSITO

*Graduate School and University Center,  
City University of New York;  
Scorpion Systematics Research Group,  
Division of Invertebrate Zoology,  
American Museum of Natural History;  
Institute for Biodiversity Science and Sustainability;  
California Academy of Sciences, San Francisco*

HUMBERTO Y. YAMAGUTI

*Departamento de Zoologia, Instituto de Biociências,  
Universidade de São Paulo, Brazil*

CLÁUDIO A. SOUZA

*Laboratório Especial de Coleções Zoológicas,  
Instituto Butantan, São Paulo, Brazil*

RICARDO PINTO-DA-ROCHA

*Departamento de Zoologia, Instituto de Biociências,  
Universidade de São Paulo, Brazil*

LORENZO PRENDINI

*Scorpion Systematics Research Group,  
Division of Invertebrate Zoology,  
American Museum of Natural History*

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## ABSTRACT

The Neotropical “club-tailed” scorpions of the genus *Rhopalurus* Thorell, 1876, and two related genera in family Buthidae C.L. Koch, 1837, i.e., *Physoctonus* Mello-Leitão, 1934, and *Troglorhopalurus* Lourenço et al., 2004, are revised, based on a simultaneous phylogenetic analysis of 90 morphological characters and 4260 aligned DNA nucleotides from three mitochondrial and two nuclear gene loci. The monophyletic New World buthid subfamily Rhopalurusinae Bücherl, 1971, to which these scorpions were originally assigned, is redefined, revised diagnoses and a key to identification of its genera and species (except for *Centruroides* Marx, 1890) provided, and their distributions mapped. The paraphyly of *Rhopalurus* Thorell, 1876, which comprises several monophyletic groups congruent with its disjunct distribution, justifies its relimitation and that of *Troglorhopalurus* Lourenço et al., 2004, the revalidation of *Heteroctenus* Pocock, 1893, and creation of *Ischnotelson*, gen. nov. (type species: *Rhopalurus guanambiensis* Lenarducci, Pinto-da-Rocha and Lucas, 2005) and *Jaguajir*, gen. nov. (type species: *Rhopalurus agamemnon* C.L. Koch, 1839). Ten new combinations are proposed: *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov.; *Heteroctenus bonettii* (Armas, 1999), comb. nov.; *Heteroctenus garridoi* (Armas, 1974), comb. nov.; *Heteroctenus gibarae* (Teruel, 2006), comb. nov.; *Heteroctenus princeps* (Karsch, 1879), comb. nov.; *Ischnotelson guanambiensis* (Lenarducci, Pinto-da-Rocha and Lucas, 2005), comb. nov.; *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov.; *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov.; *Jaguajir rochae* (Borelli, 1910), comb. nov.; *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov. Three new species are described: *Ischnotelson peruassu*, sp. nov. (type locality: Parque Estadual do Peruassu, Minas Geras, Brazil); *Physoctonus striatus*, sp. nov. (type locality: Castelo do Piauí, Piauí, Brazil); *Rhopalurus ochoai*, sp. nov. (type locality: San Agustín, Edo. Zulia, Venezuela). Fifteen new junior subjective synonyms are proposed: *Rhopalurus acromelas* Lutz and Mello, 1922, *Rhopalurus melleipalpus* Lutz and Mello, 1922, *Rhopalurus iglesiasi* Werner, 1927, *Rhopalurus lambdophorus* Mello-Leitão, 1932, *Rhopalurus dorsomaculatus* Prado, 1938, and *Rhopalurus goiasensis* Prado, 1940 = *Jaguajir agamemnon* (C.L. Koch, 1839); *Rhopalurus pinto* *kourouensis* Lourenço, 2008 = *Jaguajir pinto* (Mello-Leitão, 1932); *Rhopalurus crassicauda* Caporiacco, 1947, *Rhopalurus amazonicus* Lourenço, 1986, and *Rhopalurus crassicauda paruiensis* Lourenço, 2008 = *Rhopalurus laticauda* Thorell, 1876; *Rhopalurus melloleitaoi* Teruel and Armas, 2006, and *Rhopalurus aridicola* (Teruel and Armas, 2012) = *Heteroctenus junceus* (Herbst, 1800); *Rhopalurus granulimanus* Teruel, 2006 = *Heteroctenus gibarae* (Teruel, 2006); *Rhopalurus virkii* Santiago-Blay, 2009 = *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987); *Rhopalurus brejo* Lourenço, 2014 = *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997).

## INTRODUCTION

The Neotropical “club-tailed” scorpions of the genus *Rhopalurus* Thorell, 1876, and two related genera in family Buthidae C.L. Koch, 1837, i.e., *Physoctonus* Mello-Leitão, 1934, and *Troglorhopalurus* Lourenço et al., 2004, are a morphologically heterogeneous group of mostly large-bodied, often strikingly colored scorpions, usually with a broad metasoma that becomes noticeably wider posteriorly and an incrassate pedipalp chela in the adult male (fig. 1). Although usually occurring under stones in

areas of open vegetation, e.g., savanna and semidesert (Lourenço and Pinto-da-Rocha, 1997, Lourenço, 2002; fig. 2A–F), some species inhabit caves within those formations (fig. 2G, H). The distribution of these scorpions encompasses the Greater Antilles (Cuba and Hispaniola, West Indies), the Guiana Shield of northern South America (Colombia, the Guianas, and Venezuela) and northeastern Brazil (Fet and Lowe, 2000; Teruel, 2006; Lourenço, 2008; Prendini et al., 2009; Teruel and Roncallo 2008; Santiago-Blay, 2009; figs. 3–9), a disjunction that raises questions concerning their mono-

phyly and historical biogeography. Many of these scorpions possess the unique ability to stridulate audibly by scraping nodules and/or ridges on the dorsal surfaces of their pectines against granules on the ventral surfaces of mesosomal sternite III (Hjelle, 1990; McCormick and Polis, 1990; figs. 10–12), a remarkable behavior that presumably functions to deter would-be predators (Pocock, 1904; Lourenço and Cloudsley-Thompson, 1995; Lourenço, 2007; Prendini et al., 2009).

No subfamilial classification of Buthidae is currently in widespread use (Fet and Lowe, 2000) because the monophyly of buthid subfamilies has never been rigorously tested. However, the presence in *Centruroides* Marx, 1890, and the above-mentioned genera of pro- and retrolateral accessory (supernumerary) denticles in the median denticle rows of the pedipalp chela fingers, unique within the family (Sissom, 1990), represents a potential synapomorphy for subfamily Rhopalurusinae Bücherl, 1971. Rhopalurusinae was originally created (as Rhopalurinae Bücherl, 1971) to accommodate *Centruroides* and *Rhopalurus*, and defined by the presence of accessory denticles. Prior to the research presented here, however, neither the monophyly of Rhopalurusinae nor that of its component genera had been tested. The generic distinction between *Rhopalurus* and *Centruroides*, the most speciose genus of the subfamily, comprising 90 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 (Hoffmann, 1932; Sissom and Lourenço, 1987; Gantenbein et al., 2001), was particularly unclear. 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).

*Rhopalurus* was originally created to accommodate *Rhopalurus laticauda* Thorell, 1876, from northern South America, and diagnosed

on the basis of the posteriorly increasing metasomal width. Soon thereafter, Kraepelin (1891) mistakenly synonymized *Rhopalurus* with *Centrurus* C.L. Koch, 1838, a name later determined to be a junior synonym of *Heterometrus* Ehrenberg, 1828, in family Scorpionidae Latreille, 1802 (Braunwalder and Fet, 1998; Fet and Lowe, 2000). Another genus, *Heteroctenus* Pocock, 1893, was meanwhile described from the West Indies, but subsequently synonymized with *Rhopalurus* when the latter was revalidated by Pocock (1902a). Later, *Rhopalurus* was erroneously considered a junior synonym of *Centruroides*, although the older name, *Rhopalurus*, had precedence (Meise, 1934). This synonymy was short-lived, as Mello-Leitão (1945) considered *Centruroides* and *Rhopalurus* distinct genera. Several decades later, Lourenço (1979, 1982a) conducted a more thorough assessment, differentiating the two genera on the basis of five morphological characters, only two of which (the position of trichobothrium *db* on the fixed finger of the pedipalp chela and the proportions of the male metasoma) continue to be used. Curiously, the presence of a pecten-sternite stridulation organ in *Rhopalurus* was not mentioned by Lourenço (1979). However, Lourenço (1986a) considered this character to be synapomorphic for the genus in a manual cladistic analysis of 10 species, based on eight morphological characters, polarized a priori using ontogenetic data from *Rhopalurus princeps* (Karsch, 1879).

*Centruroides* are currently 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 vary interspecifically 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).

The monotypic genus *Physoctonus*, long regarded a junior synonym of *Rhopalurus* (Francke, 1977a), was recently revalidated by Lourenço (2007). Although considerably smaller (20–25 mm), the type species, *Physoctonus debilis* (C.L. Koch, 1840), from northeastern Brazil resembles the epigeal species of *Rhopalurus* from South America in general appearance and morphometrics, raising doubts as to whether its revalidation might render *Rhopalurus* paraphyletic. *Troglorhopalurus*, a second monotypic genus related to *Rhopalurus*, was described on the basis of a single, troglomorphic specimen from a Brazilian cave (Lourenço et al., 2004). In comparing *Troglorhopalurus* 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 *Troglorhopalurus* might be a junior synonym of *Rhopalurus*. A troglophile species, *Rhopalurus lacrau* Lourenço and Pinto-da-Rocha, 1997, had been described from caves belonging to the same subterranean formation in Brazil and, in the description of *Troglorhopalurus*, Lourenço et al. (2004) suggested the relationship between these taxa should be investigated using molecular data.

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. Over the past decade, several publications have proposed taxonomic changes and described new species (Lenarducci et al., 2005; Teruel, 2006; Teruel and Armas, 2006, 2012a, 2012b; Lourenço, 2007, 2008, 2014; Teruel and Roncallo, 2008; Teruel and Tietz, 2008; Prendini et al., 2009; Santiago-Blay, 2009; Flórez, 2012; Teruel and Roncallo, 2013). Unfortunately, much of

this work was based on one or few specimens, with flimsy evidence and little or no quantitative analysis, resulting in rampant confusion. For example, *Rhopalurus caribensis* Teruel and Roncallo, 2008, *Rhopalurus crassicauda* Caporiacco, 1947, and *Rhopalurus pinto* Mello-Leitão, 1932, were each synonymized and then revalidated. The validity of *R. crassicauda*, its subspecies, and *Rhopalurus virkki* Santiago-Blay, 2009, have been questioned by several authors (Prendini et al., 2009; Teruel and Armas, 2012b).

The need to improve upon the limitations of previous treatments of *Rhopalurus* and related genera prompted a quantitative analysis of rhopalurusine phylogeny (Esposito et al., in review). Simultaneous analysis of 90 morphological characters and 4260 aligned DNA nucleotides from three mitochondrial and two nuclear gene loci, with comprehensive taxon sampling rigorously tested the monophyly and composition of the subfamily and its component genera. Whereas Rhopalurusinae and *Centruroides* were consistently monophyletic, *Rhopalurus* was consistently paraphyletic with respect to *Centruroides*, *Physoctonus*, and *Troglorhopalurus*, comprising several monophyletic groups congruent with its disjunct distribution (fig. 13), and justifying the revised classification presented here (table 1).

The present contribution implements the taxonomic discoveries of Esposito et al. (in review). The monophyletic subfamily Rhopalurusinae Bücherl, 1971, is redefined, revised diagnoses and a key to identification of its genera and species (except for *Centruroides* Marx, 1890) provided, and their distributions mapped. *Heteroctenus* is revalidated, and two new genera described. Ten new combinations are created by transferring species, formerly placed in *Rhopalurus*, to other genera, three new species are described, and 15 new synonyms are presented. The South American genera recognized herein are consistent with the diploid chromosome numbers presented in an independent study of Brazilian Rhopalurusinae by Ubinski et al. (2016), reproduced in table 2.

TABLE 1

**Revised classification of the New World buthid Subfamily Rhopalurusinae Bücherl, 1971  
(excluding *Centruroides* Marx, 1890), with countries of distribution.**

<i>Heteroctenus abudi</i> (Armas and Marcano Fondeur, 1987), comb. nov.	Dominican Republic, Puerto Rico (Mona Is.)
<i>Heteroctenus bonettii</i> (Armas, 1999), comb. nov.	Dominican Republic
<i>Heteroctenus garridoi</i> (Armas, 1974), comb. nov.	Cuba
<i>Heteroctenus gibarae</i> (Teruel, 2006), comb. nov.	Cuba
<i>Heteroctenus junceus</i> (Herbst, 1800)	Cuba
<i>Heteroctenus princeps</i> (Karsch, 1879), comb. nov.	Dominican Republic, Haiti
<i>Ischnotelson guanambiensis</i> (Lenarducci et al., 2005), comb. nov.	Brazil
<i>Ischnotelson peruassu</i> , sp. nov.	Brazil
<i>Jaguajir agamemnon</i> (C.L. Koch, 1839), comb. nov.	Brazil
<i>Jaguajir pinto</i> (Mello-Leitão, 1932), comb. nov.	Brazil, ?French Guiana, Guyana
<i>Jaguajir rochae</i> (Borelli, 1910), comb. nov.	Brazil
<i>Physoctonus debilis</i> (C.L. Koch, 1840)	Brazil
<i>Physoctonus striatus</i> , sp. nov.	Brazil
<i>Rhopalurus caribensis</i> Teruel and Roncallo, 2008	Colombia
<i>Rhopalurus laticauda</i> Thorell, 1876	Brazil, Colombia, Guyana, Venezuela
<i>Rhopalurus ochoai</i> , sp. nov.	Venezuela
<i>Troglorhopalurus lacrau</i> (Lourenço and Pinto-da-Rocha 1997), comb. nov.	Brazil
<i>Troglorhopalurus translucidus</i> Lourenço et al., 2004	Brazil

## MATERIAL AND METHODS

Specimens collected by the authors were located at night using portable ultraviolet (UV) lamps. Portable Garmin® GPS devices were used for recording the geographical coordinates of collection localities in the field. Material is deposited in the following collections: American Museum of Natural History (AMNH), New York, incorporating the Alexis Harington (AH) Collection; Centro Oriental de Ecosistemas y Biodiversidad (BIOECO), Museo de Historia Natural “Tomás Romay,” Santiago de Cuba; Natural History Museum, London (BMNH); Instituto Butantan, São Paulo (IBSP), Brazil; Instituto de Ecología y Sistemática (IES), Havana, Cuba; Instituto Oswaldo Cruz (IOC), Belo Horizonte, Brazil; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Instituto de Zoología de la Academia de Ciencias de Cuba

(IZACC), Havana, Cuba; Laboratório de Estudos Subterrâneos (LES), Universidade Federal de São Carlos, Brazil; Museo ed Instituto di Zoologia Sistemática della Università, Torino (MIZT), Italy; Museum National d’Histoire Naturelle (MNHN), Paris; Museo Nacional de Río de Janeiro (MNRJ), Universidade Federal de Río de Janeiro; Museu de Zoologia da Universidade São Paulo (MZSP), Brazil; Museo Zoologico “La Specola” dell’Università de Firenze (MZUF), Florence, Italy; Natal Museum (NM), Pietermaritzburg, South Africa; Naturhistoriska Museet, Göteborg (NMG), Sweden; Naturhistorisches Museum Wien (NMW), Vienna, Austria; Museum of Natural History, Oxford University (OUMNH), U.K.; Rolando Teruel Ochoa (RTO) Private Collection, Santiago de Cuba; South African Museum (SAM), Cape Town; Natur-Museum Senckenberg, Frankfurt (SMF), Germany; Universidade Fed-

TABLE 2

**Diploid chromosome numbers (2n) for Brazilian species of Rhopalurusinae from Ubinski et al., (2016) with corresponding genera indicated.**

Species (this study)	Species (Ubinski et al., 2016)	2n
<i>Ischnotelson guanambiensis</i>	<i>Rhopalurus guanambiensis</i>	25
<i>Ischnotelson peruassu</i>	<i>Rhopalurus</i> sp. n. 1	26
<i>Ischnotelson</i> sp. nov.	<i>Rhopalurus</i> sp. n. 2	26
<i>Jaguajir agamemnon</i>	<i>Rhopalurus agamemnon</i>	28
<i>Jaguajir pinto</i>	<i>Rhopalurus pinto</i>	28
<i>Jaguajir rochae</i>	<i>Rhopalurus rochai</i>	28
<i>Physoctonus debilis</i>	<i>Rhopalurus debilis</i>	26
<i>Rhopalurus laticauda</i>	<i>Rhopalurus crassicauda</i>	22
<i>Troglorhopalurus lacrau</i>	<i>Rhopalurus lacrau</i>	20
<i>Troglorhopalurus translucidus</i>	<i>Troglorhopalurus translucidus</i>	20–22

eral de Minas Gerais (UFMG), Belo Horizonte, Brazil; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB), Germany; Zoologisches Museum der Universität Hamburg (ZMH), Germany; Zoology Museum of the University of Puerto Rico, Río Piedras (ZMUPR-RP), Puerto Rico. Tissue samples used for DNA isolation are stored (in the vapor phase of liquid nitrogen at  $-150^{\circ}\text{C}$ ) in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH.

Morphological examination of specimens was conducted using a Nikon SMZ1500 dissection stereomicroscope. Specimens were measured using Mitutoyo digital calipers and an ocular micrometer. Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2001a). Nomenclature of general anatomy follows Hjelle (1990) and Sissom (1990), trichobothria follows Vachon (1974), carination of the carapace, tergites, and metasoma follows Vachon (1952), pedipalp carination follows Prendini (2000), ovariuterine anatomy follows Volschenk et al. (2008), and book lung anatomy follows Kamenz and Prendini (2008).

Photographs were taken in visible light as well as under long wave UV light using a Microptics™

ML-1000 digital imaging system or a Canon EOS camera with MP-E 65 mm or 100 mm EF macro-lenses. UV fluorescence images were taken to enhance visualization of surface macrosculpture (Prendini, 2003; Volschenk, 2005). Scanning electron micrographs of pectines were taken using a Zeiss EVO60 VPSEM at the AMNH and a ZEISS DSM 940 at the Instituto de Biociencias, Universidade de São Paulo. Material fixed in 70% ethanol was cleaned with an ultrasonic device, and subsequently dehydrated in acetone. Pectines were fixed to a stub, oven-dried at  $40^{\circ}\text{C}$  for approximately 8 hours, and gold coated using a Balzer SCD 50 sputter-coater.

All records of sufficient accuracy were isolated from the material examined and published literature to create a point locality geographical dataset for mapping distributional ranges. Records for which geographical coordinates were previously entered by the collector were checked for accuracy and coordinates for the remaining records traced using the GEOnet Names Server ([http://164.214.2.59/gns/html/cntry\\_files.html](http://164.214.2.59/gns/html/cntry_files.html)) and the Fuzzy Gazetteer ([http://dma.jrc.it/new\\_site/default.asp](http://dma.jrc.it/new_site/default.asp)).

Distribution maps were produced using ArcView GIS Version 10.4 (Environmental Sys-



tems Research Institute, Redlands, CA), by superimposing point locality records on spatial datasets depicting the topography (500 m contour interval) and political boundaries. A topographic contour coverage was created from the GTOPO30 raster grid coverage, obtained from the website of the U.S. Government Public Information Exchange Resource (<http://edcdaac.usgs.gov/gtopo30/gtopo30.html>).

### SYSTEMATICS

FAMILY BUTHIDAE C.L. Koch, 1837

Subfamily Rhopalurusinae Bücherl, 1971

Rhopalurusinae Bücherl, 1971: 325, type genus

*Rhopalurus* Thorell, 1876, by original designation; Fet and Lowe, 2000: 55, 57; Fet et al., 2003b: 23, 24.

Rhopalurusinae Fet et al., 2003b: 23, 24; Loria and Prendini, 2014: 14, 21.

**DIAGNOSIS:** The following combination of characters distinguishes the species of subfamily Rhopalurusinae, New World Buthidae with accessory (supernumerary) denticles in median denticle rows of pedipalp chela fingers, from other buthid scorpions: chelicerae, movable finger with transverse row of granules; cheliceral fixed finger with dorsobasal setation; pedipalp femur, dorsal surface trichobothria with  $\alpha$ -configuration, trichobothrium  $d_2$  situated on prolateral surface; pedipalp patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; pedipalp chela, fixed and movable fingers, median denticle rows with pro- and retrolateral accessory (supernumerary) denticles; legs without tibial spurs; leg I telotarsus, prolateral pedal spur bifurcating (reduced in *Physoctonus*).

**INCLUDED TAXA:** This New World buthid subfamily includes seven genera (*Centruroides*, *Heteroctenus*, *Ischnotelson*, gen. nov., *Jaguajir*, gen. nov., *Physoctonus*, *Rhopalurus*, and *Troglorhopalurus*), 108 described species, and three subspecies.

**DISTRIBUTION:** Subfamily Rhopalurusinae is endemic to the New World and distributed from North America (the midwestern United States) throughout Central America and the Caribbean islands (Greater and Lesser Antilles) to central-northern South America and the Galapagos Islands.

**REMARKS:** Bücherl's (1971) original name, Rhopalurinae, was a junior homonym of Rhopaluridae Stunkard, 1937, derived from the orthonectid genus *Rhopalura* Girard, 1877, and thus unavailable (Fet and Lowe, 2000). A 2003 ruling by the International Commission on Zoological Nomenclature amended Rhopalurinae to Rhopalurusinae Bücherl, 1971 (Fet et al., 2003b).

### KEY TO GENERA AND SPECIES (EXCLUDING *CENTRUROIDES*) OF NEW WORLD BUTHID SUBFAMILY RHOPALURUSINAE

1. Leg I, prolateral pedal spur simple; sternite V, surface without smooth, raised area posteromedially in male.....2 (*Physoctonus*)
- Leg I, prolateral pedal spur bifurcate; sternite V, surface with smooth, raised area posteromedially in male (fig. 10D).....3
2. Total body length, 23–30 mm; mesosomal tergites uniform in color; metasomal segment V similar in color to preceding segments; pedipalp chela fixed finger trichobothrium *db* situated between trichobothria *est* and *et* .....*Physoctonus debilis*
- Total body length, 22–26 mm; mesosomal tergites with dark transverse bands; metasomal segment V darker than preceding segments; pedipalp chela fixed finger trichobothrium *db* aligned with trichobothrium *et*.....*Physoctonus striatus*, sp. nov.
3. Metasoma of male extremely elongate and narrow, much longer than sum of prosoma and mesosoma; pedipalp patella, prodorsal and proventral carinae adjacent .....*Centruroides*
- Metasoma of male not elongate, similar in length to sum of prosoma and mesosoma

- (figs. 28, 37, 43, 54); pedipalp patella, prodorsal and proventral carinae well separated.....4
4. Scorpions cavernicolous and troglomorphic (fig. 1G, H); pectinal peg sensilla elongate and acuminate .....5 (*Troglorhopalurus*)
- Scorpions epigeal and not troglomorphic (fig. 1A-G); pectinal peg sensilla peg shaped, short, and rhomboid.....6
5. Pedipalp chela fixed finger, median denticle row with eight subrows of primary denticles; pedipalp 4.5× longer than carapace; pedipalp patella 3.8× longer than wide; metasomal segment V 2.7× longer than wide.....*Troglorhopalurus lacrau*, comb. nov.
- Pedipalp chela fixed finger, median denticle row with nine subrows of primary denticles; pedipalp 6.5× longer than carapace; pedipalp patella 6× longer than wide; metasomal segment V 4.5× longer than wide .....*Troglorhopalurus translucidus*
6. Telson laterally compressed, vesicle width about half its height (fig. 22C); mesosoma width similar to carapace (figs. 39, 40); pectinal plate with two depressions laterally; book lung spiracles short, width less than 3× their length (fig. 19A, B).....7 (*Ischnotelson*, gen. nov.)
- Telson rounded, vesicle width similar to height; mesosoma wider than carapace; pectinal plate with one median depression or without depressions; book lung spiracles long, width more than 5× their length (figs. 19C, D, F, 20C-F).....8
7. Total body length, 35–45 mm; pedipalp chela fingers noticeably darker than chela manus; sternite III elevated anteriorly.....*Ischnotelson guanambiensis*, comb. nov.
- Total body length, 48–59 mm; pedipalp chela fingers similar in color to chela manus; sternite III not elevated anteriorly .....*Ischnotelson peruassu*, sp. nov.
8. Sternite III, surface with large, acuminate and evenly distributed granules (fig. 19C, D, F); pedipalp chela manus, proventral carina present; pectinal plate, anterior margin without furrow.....9 (*Jaguajir*, gen. nov.)
- Sternite III, surface finely granular or with small, irregularly distributed granules; pedipalp chela manus, proventral carina absent; pectinal plate, anterior margin with furrow (figs. 18A-E; 20D-F);.....11
9. Mesosoma coloration pale to dark yellow; metasoma of male becoming slightly wider posteriorly; pedipalp chela, fixed and movable fingers of male slightly curved, creating small proximal gap between them; fixed finger of male with prominent proximal lobe .....*Jaguajir rochae*, comb. nov.
- Mesosoma coloration brown to black; metasoma of male becoming markedly wider posteriorly; pedipalp chela, fixed and movable fingers of male markedly curved, creating large proximal gap between them; fixed finger of male with proximal lobe reduced or absent .....10
10. Color of carapace, tergites, metasoma, telson, and pedipalps dark brown to black, sternites, legs, and telson somewhat lighter, reddish brown; metasomal segments, dorsolateral carinae comprising blunt spiniform granules, increasing in size posteriorly, especially prominent on metasomal segments III and IV; segment V almost as wide as long; telson vesicle, subaculear tubercle very reduced, forming small protuberance.....*Jaguajir pintoii*, comb. nov.
- Color of carapace and tergites I–VI brown, tergite VII, metasoma, telson, pedipalps, and legs lighter, somewhat orange; metasomal segments, dorsolateral carinae comprising small, acuminate granules; metasomal segment V approximately 1.5× longer than wide; telson vesicle, subaculear tubercle well developed and spinoid.....*Jaguajir agamemnon*, comb. nov.
11. Telson vesicle, subaculear tubercle present (fig. 21H–J); carapace, central lateral and posteromedian carinae fused (fig. 16C–F); pectinal plate without

- depressions (fig. 20C-F); occurs in South America.....12 (*Rhopalurus*)
- Telson vesicle, subaculear tubercle absent (fig. 21A-B); carapace, central lateral and posteromedian carinae separate (fig. 14A-E); pectinal plate with single median depression; occurs in the Greater Antilles.....14 (*Heteroctenus*)
12. Metasoma ventromedial surface with single, broad band of pigmentation; carapace, tergites, metasoma V, and telson often markedly infusate, contrasting with pale pedipalps, legs and metasomal segments I-IV.....*Rhopalurus laticauda*
- Metasoma ventromedial surface with two or three narrow stripes of pigmentation; carapace, tergites, metasomal segments I-IV, pedipalps, and legs pale and immaculate or lightly infusate, metasoma V, and telson slightly darker than preceding segments.....13
13. Metasoma ventromedial surface with three distinct, narrow stripes of pigmentation (a ventromedial stripe flanked on either side by a ventrosubmedian stripe).....*Rhopalurus caribensis*
- Metasoma ventromedial surface with two distinct, narrow ventrosubmedian stripes of pigmentation....*Rhopalurus ochoai*, sp. nov.
14. Occurs on Hispaniola and adjacent islets....15
- Occurs on Cuba and adjacent islets.....17
15. Pedipalp chela similar in male and female, manus of male only slightly incrassate and fingers not curved proximally, connecting along most of their length with little to no gap present between them proximally, when closed.....*Heteroctenus bonettii*, comb. nov.
- Pedipalp chela dimorphic in male and female, manus of male markedly incrassate and fingers strongly curved proximally, such that only distal portion of fingers connect and distinctive gap present between them proximally, when closed .....16
16. Color predominantly dark; carapace, tergites, metasomal segments I-III, and legs infusate; metasomal segments long and narrow (2× longer than wide) .....*Heteroctenus abudi*, comb. nov.
- Color predominantly pale; carapace, tergites, metasomal segments I-III, and legs immaculate; metasomal segments short and broad (almost equal in length and width).....*Heteroctenus princeps*, comb. nov.
17. Total body length, 64-110 mm; base color light brown to dark reddish brown; entire carapace or only interocular surface infusate; carapace, mesosoma, and metasoma (especially, segments IV and V) noticeably darker than pedipalps and legs.....*Heteroctenus juncus*
- Total body length, 56-86 mm; base color yellow to yellowish brown; entire carapace immaculate (at most, interocular surface bordered by narrow line forming V-shape); carapace, mesosoma, and metasoma not noticeably darker than pedipalps and legs.....18
18. Carapace, metasoma and telson uniformly yellow; pedipalp chela manus similar in color or only slightly darker than femur and patella.....*Heteroctenus garridoi*, comb. nov.
- Carapace interocular surface bordered by two narrow lines forming V-shape; metasomal segments IV and V darkening to blackish-brown posteriorly; telson reddish; pedipalp chela manus darker than femur and patella .....*Heteroctenus gibarae*, comb. nov.

*Centruroides* Marx, 1890

*Buthus exilicauda* Wood, 1863 (= *Centruroides exilicauda* (Wood, 1863)), type species by monotypy.

*Centruroides* (*nec* Ehrenberg, 1829): Thorell, 1876a: 9; Thorell, 1876b: 83; Karsch, 1879a: 18; Pocock, 1890: 120, 121, 127; Kraepelin, 1891: 119-124 (part); Pocock, 1893: 375, 385, 386; Laurie, 1896: 131; Lönnberg, 1897: 196, 197, 208; Kraepelin, 1899: 87 (part); Banks, 1900: 425; Borelli, 1909: 222; Comstock, 1912: 25, 27, fig. 31; Birula, 1917a: 164; Birula, 1917b: 54, 107; Ochoterena,

1920: 223; Mello-Campos, 1924a: 246; 1924b: 312; Comstock, 1940: 27, fig. 31 (*lapsus calami*); Millot and Vachon, 1949: 427; Díaz Nájera, 1966: 110, 111, pl. 1; 1970: 113. *Centruro*: Karsch, 1879b: 120 (*lapsus calami*). *Centruroides* Marx, 1890: 211; Pocock, 1902a: 19, 20; 1902b: 365; Kraepelin, 1912: 69–71; 1914: 22; Hoffmann, 1932: 244, 245; Mello-Leitão, 1932: 27; 1934a: 4, 5; Franganillo, 1936: 158; Hoffmann, 1937: 201–203; Moreno, 1939a: 63; Comstock, 1940: 25, 27; Moreno, 1940a: 164; Mello-Leitão, 1942: 126; 1945: 240, 250–252; Scorza, 1954a: 190; Bücherl, 1964: 59; 1967: 113; Muma, 1967: 2, 4; Bücherl, 1969: 767; Aguilar and Meneses, 1970: 3; Bücherl, 1971: 327; Stahnke, 1971: 282; 1972: 125, fig. 9; Armas, 1974a: 25; Vachon, 1974: 906, 908; 1975: 1598; Francke, 1977b: 75; Stahnke and Calos, 1977: 111; Vachon, 1977: 294; Lourenço, 1979: 214; Williams, 1980: 2, 4; Armas, 1984: 2; González-Sponga, 1984: 64, 65; Francke and Stockwell, 1987: 7; Armas, 1988: 44, 91, 95; Stockwell, 1988: 3; Sissom, 1990: 94, 101; Nenilin and Fet, 1992: 9, 12–14; Stockwell, 1992: 412, 419; Francke, 1985: 7, 15; González-Sponga, 1996: 118, 119, 124, 125, figs. 285–287, 289, 292; Armas, 1998: 50; Kovařík, 1998: 106; Fet and Lowe, 2000: 98–122; Towler et al., 2001: 161–163; Prendini and Wheeler, 2005: 481, table 10; Kamenz and Prendini, 2008: 6, 8, 22, 40, tables 1, 2, pl. 13–17; Volschenk et al., 2008: 654, 656, 658, 659, 663, 664, 674, fig. 1C, tables 1, 2; Armas et al., 2012: 106, 112; Loria and Prendini, 2014: 3, 9, 10, 24, 25, fig. 2D, table 5; Ponce Saavedra and Francke, 2014: 54, figs. 11, 14; *Centruroides* (*Centruroides*): Werner, 1934: 273. *Centruroides*: Díaz Nájera, 1970: 117 (*lapsus calami*). *Centruroides*: Lourenço and Eickstedt, 1988: 7 (*lapsus calami*).

**DIAGNOSIS:** *Centruroides* differs from *Heteroctenus*, *Ischnotelson* gen. nov., *Jaguajir*, gen. nov.,

and *Rhopalurus* by the linear, parallel-sided metasoma that does not increase markedly in width posteriorly; from *Heteroctenus*, *Jaguajir*, gen. nov., and *Rhopalurus* by the absence of a pecten-sternite stridulatory organ; and from *Physoctonus* and *Rhopalurus* by the separate (unfused) central lateral and posterior central submedian carinae of the carapace. *Centruroides* differs further from *Heteroctonus* by the presence or absence of two lateral depressions on the pectinal plate and the absence of macrosetae on the dorsobasal surface of the pectinal teeth; from *Ischnotelson* by the separate (unfused) lateral ocular and central lateral carinae of the carapace, and the telson vesicle not laterally compressed; from *Jaguajir* by the separate (unfused) lateral ocular and anterior central submedian carinae of the carapace; from *Physoctonus* by the bifurcate prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; and from *Troglophthalurus* by the distinct retromedian carina on the pedipalp chela manus, and the adjacent prodorsal and proventral carinae of the pedipalp patella.

**DESCRIPTION:** A revision of *Centruroides* will be presented elsewhere. The following general description outlines characters common to the species of this diverse genus.

**Total length:** Varying from small, gracile to very large, robust scorpions (total length, 35–110 mm).

**Color:** Varying from uniformly pale yellow to uniformly black, often maculate or variegated; legs and pedipalps often paler in color than carapace, tergites, metasoma, and telson; coxosternal region, pectines, and sternites usually paler than carapace, tergites, metasoma, and telson; telson may be darker or paler than metasomal segments.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle raised; two median ocelli; three pairs of lateral macrocelli; one pair of lateral microcelli. Anteromedian,

median ocular and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular, central lateral, anterior central submedian and posterior central submedian carinae distinct, finely to coarsely granular or costate-granular and separate (unfused).

*Pedipalps:* Pedipalp femur retrolateral accessory carinae usually absent. Pedipalp chela manus of adult male slender to slightly incrassate, fixed and movable fingers may be slightly curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, small gap present between fingers proximally, when closed, manus of female not incrassate, fixed and movable fingers not curved proximally, such that proximal dentate margin sublinear, little or no gap present between them proximally, when closed; fixed and movable fingers, median denticle rows each comprising 7–9 oblique subrows of primary denticles flanked closely by pro- and retrolateral accessory (supernumerary) denticles; movable finger with proximal lobe. Pedipalps orthobothriotaxic Type A,  $\alpha$  configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  aligned with or distal to trichobothrium *et*.

*Legs:* Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with irregular tufts of fine, acuminate macrosetae.

*Pectines:* Pectinal plate with or without two lateral depressions (male), anterior margin with sulcus. Pectines not proximally expanded; proximal dorsal fulcra setose or asetose; pectinal teeth almost straight, slightly curved laterally, proximal teeth not enlarged, dorsal surfaces without nodules or striations, dorsobasal surfaces without macrosetae; pectinal sensillae peg shaped.

*Mesosoma:* Tergites IV–VI same width or wider than I–III and VII; I–VI tricarinate, dorsomedian and dorsosubmedian carinae granular to costate-granular, restricted to posterior two

thirds of segment. Tergite VII pentacarinata, dorsomedian carina restricted to anterior two thirds. Sternites smooth, carinae obsolete, more developed on VI and VII; sternite III, lateral margins not forming smooth, raised carina, ventromedian carina not elevated anteriorly, ventrosubmedian surfaces not forming paired depressions, finely and irregularly granular; respiratory spiracles (stigmata) width more than 5 $\times$  length.

*Metasoma:* Metasoma slender, usually not increasing in width posteriorly, segments I and V similar width in both sexes. Segment I with 10 distinct, granular to costate-granular carinae, II with eight or 10 distinct, granular to costate-granular carinae, III and IV each with eight distinct, granular to costate-granular carinae, V with seven distinct but less pronounced, granular carinae; dorsosubmedian carinae absent or obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV; dorsolateral carinae complete on segments I–IV, often terminating in prominent, spiniform granules posteriorly on III and IV, absent on V; lateral supramedian carinae complete on segments I–V; lateral infra-median carinae complete on segment I, partial or absent on II, absent on III–V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third or absent on V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely granular.

*Telson:* Vesicle spherical to elongate, not laterally compressed, usually similar in width or slightly narrower than metasoma V; anterodorsal lateral lobes reduced or absent; lateral and ventral surfaces smooth or granular; subaculear tubercle usually present.

*Hemispermaphore:* Flagelliform.

**DISTRIBUTION:** *Centruroides* is widely distributed from the United States, throughout Mexico, Central America, and the West Indies, to northern South America. One species is endemic to the Galápagos Islands. The list of countries and territories from which *Centruroides* has been recorded is as follows: Anguilla; Antigua and Aruba; Barbuda; Bahamas; Belize; British Virgin

Islands; Colombia; Costa Rica; Cuba; Curaçao; Dominican Republic; Dominica; Ecuador (including the Galápagos Islands); El Salvador; Guadeloupe; Guatemala; Haiti; Honduras; Jamaica; Mexico (Aguascalientes, Baja California, Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Distrito Federal, Durángo, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Tlaxcala, Yucatán, Veracruz, Zacatecas); Martinique; Netherlands Antilles (Bonaire, Saba, St. Eustatius); Nicaragua; Panama; Puerto Rico; St. Barthélemy; St. Kitts and Nevis; St. Martin/Sint Maarten; Turks and Caicos; Venezuela; and the United States of America (Alabama, Arizona, Arkansas, California, Colorado, Florida, Georgia, Illinois, Kansas, Kentucky, Louisiana, Mississippi, Missouri, Nebraska, New Mexico, Nevada, South Carolina, Tennessee, Texas, Utah, U.S. Virgin Islands, with introduced populations in New Jersey, North Carolina, and Virginia). Records from Argentina and Peru (Fet and Lowe, 2000) are dubious.

**ECOLOGY:** *Centruroides* occur in diverse habitats ranging from semidesert to tropical rainforest, from sea level to 1700 m elevation. All species of the genus are eurytopic, most being lapidicolous or corticolous (Prendini, 2001b), sheltering under stones, peeling tree bark, cracks and crevices in rock faces and earthen walls, and holes in tree trunks.

**INCLUDED SPECIES:** The genus *Centruroides* currently includes 90 described species and three subspecies: *Centruroides alayoni* Armas, 1999; *Centruroides alta-graciae* Teruel, Armas and Kovařík, 2015; *Centruroides anchorellus* Armas, 1976; *Centruroides arctimanus* Armas, 1976; *Centruroides baergi* Hoffmann, 1932; *Centruroides balsasensis* Ponce-Saavedra and Francke, 2004; *Centruroides bani* Armas and Marcano Fondeur, 1987; *Centruroides baracoae* Armas, 1976; *Centruroides barbudensis* Pocock, 1898; *Centruroides bertholdii* (Thorell, 1876); *Centruroides bicolor* (Pocock, 1898); *Centruroides*

*des bonito* Quijano-Ravell, Teruel and Ponce-Saavedra, 2016; *Centruroides caral* Armas and Trujillo, 2013; *Centruroides chamela* Ponce-Saavedra and Francke, 2011; *Centruroides chamulaensis* Hoffmann, 1932; *Centruroides chiapanensis* Hoffmann, 1932; *Centruroides edwardsii* (Gervais, 1843); *Centruroides elegans* (Thorell, 1876); *Centruroides elegans insularis* Pocock, 1902; *Centruroides exilicauda* (Wood, 1863); *Centruroides exilimanus* Teruel and Stockwell, 2002; *Centruroides exsul* (Meise, 1933); *Centruroides fallassimus* Armas and Trujillo, 2010; *Centruroides farri* Armas, 1976; *Centruroides flavopictus* (Pocock, 1898); *Centruroides flavopictus meridionalis* Hoffmann, 1932; *Centruroides franckei* Santibañez-López and Contreras-Félix, 2013; *Centruroides fulvipes* (Pocock, 1898); *Centruroides galano* Teruel, 2001; *Centruroides gracilis* (Latreille, 1804); *Centruroides granosus* (Thorell, 1876); *Centruroides griseus* (C.L. Koch, 1845); *Centruroides guanensis* Franganillo, 1930; *Centruroides hentzi* (Banks, 1900); *Centruroides hirsuticauda* Teruel, 2011; *Centruroides hirsutipalpus* Ponce-Saavedra and Francke, 2009; *Centruroides hoffmanni* Armas, 1996; *Centruroides huichol* Teruel, Ponce-Saavedra and Quijano-Ravell, 2015; *Centruroides infamatus* (C.L. Koch, 1844); *Centruroides insulanus* (Thorell, 1876); *Centruroides ixil* Trujillo and Armas, 2016; *Centruroides jara-gua* Armas, 1999; *Centruroides jorgeorum* Santiago-Blay, 2009; *Centruroides koesteri* Kraepelin, 1912; *Centruroides limbatus* (Pocock, 1898); *Centruroides limpidus* (Karsch, 1879); *Centruroides luceorum* Armas, 1999; *Centruroides lucidus* Teruel, Armas and Kovařík, 2015; *Centruroides marcanoi* Armas, 1981; *Centruroides margaritatus* (Gervais, 1841); *Centruroides mariaorum* Santiago-Blay, 2009; *Centruroides mascota* Ponce-Saavedra and Francke, 2011; *Centruroides meisei* Hoffmann, 1938; *Centruroides melanodactylus* Teruel, 2001; *Centruroides navarroi* Teruel, 2001; *Centruroides nigrescens* (Pocock, 1898); *Centruroides nigrimanus* (Pocock, 1898); *Centruroides nigropunctatus* Teruel, 2006; *Centruroides nigrovariatus*

(Pocock, 1898); *Centruroides nitidus* (Thorell, 1876); *Centruroides nitidus taino* Armas and Marcato Fondeur, 1987; *Centruroides noxius* Hoffmann, 1932; *Centruroides ochraceus* (Pocock, 1898); *Centruroides orizaba* Armas and Martín-Frías, 2003; *Centruroides ornatus* Pocock, 1902; *Centruroides pallidiceps* Pocock, 1902; *Centruroides panamensis* Quintero and Esposito, 2014; *Centruroides platnicki* Armas, 1981; *Centruroides pococki* Sissom and Francke, 1983; *Centruroides polito* Teruel, 2007; *Centruroides poncei* Teruel et al., 2015; *Centruroides rileyi* Sissom, 1995; *Centruroides robertoi* Armas, 1976; *Centruroides rodolfoi* Santibañez-López and Contreras-Félix, 2013; *Centruroides ruana* Quijano-Ravell and Ponce-Saavedra, 2016; *Centruroides sanandres* Armas, Sarmiento and Flórez, 2012; *Centruroides sasae* Santiago-Blay, 2009; *Centruroides schmidti* Sissom, 1995; *Centruroides sculpturatus* Ewing, 1928; *Centruroides serrano* Santibañez-López and Ponce-Saavedra, 2009; *Centruroides simplex* (Thorell, 1876); *Centruroides sissomi* Armas, 1996; *Centruroides spectatus* Teruel, 2006; *Centruroides stockwelli* Teruel, 2001; *Centruroides suffusus* (Pocock, 1902); *Centruroides tapachulaensis* Hoffmann, 1932; *Centruroides tecomanus* Hoffmann, 1932; *Centruroides testaceus* DeGeer, 1778; *Centruroides thorellii* (Kraepelin, 1891); *Centruroides tuxtla* Armas, 1999; *Centruroides underwoodi* Armas, 1976; *Centruroides villegasi* Baldazo-Monsivaiz, Ponce-Saavedra and Flores-Moreno, 2013; *Centruroides vittatus* (Say, 1821).

REMARKS: The name *Centruroides* was first introduced by Marx (1890: 211) for two species: *Centruroides exilicauda* (Wood, 1863) and *Centruroides luctifer* Marx, 1890. Because *C. luctifer* is a nomen nudum, *C. exilicauda* is the type species by monotypy (Fet and Lowe, 2000). As Marx (1890) also used the name *Centrurus*, *Centruroides* was not introduced as a replacement name for *Centrurus*.

The name "*Centrurus* Ehrenberg, 1829" was incorrectly used for many years to denote species of *Centruroides* Marx, 1890. However, these two names are not synonymous (Braunwalder

and Fet, 1998; Fet and Lowe, 2000). The type species of *Centrurus* was not originally designated by Ehrenberg (1829), and therefore *Centrurus* Ehrenberg, 1829, is a nomen nudum (Francke, 1985). Thorell (1876a: 9) designated *Androctonus biaculeatus* Lucas, 1835 (= *Centruroides gracilis* (Latreille, 1804)), as the type species. However, the priority in type designation belongs to C.L. Koch (1838) who first used the name in combination with the description of a species, *Centrurus galbineus* C.L. Koch, 1838, a junior synonym of *Heterometrus longimanus* (Herbst, 1800). Therefore, the correct designation and synonymy is *Centrurus* C.L. Koch, 1838 = *Heterometrus* Ehrenberg, 1828 (Scorpionidae).

#### *Heteroctenus* Pocock, 1893

Figures 1A, 2A, B, 3, 4, 11A, B, 12B, 14A–E, 17A, 18A–E, 21A, B, 22A, B, 23A–N, 25–35

*Scorpio junceus* Herbst, 1800 (= *Heteroctenus junceus* (Herbst, 1800)), type species by subsequent designation.

*Scorpio* (part): Herbst, 1800: 65–67, pl. III, fig. 2; Latreille, 1804: 126, 127.

*Scorpio* (*Atreus*) (part): Gervais, 1843: 130; 1844a: 218, fig. 18; 1844b: 39, 54; Lucas, 1851: 70, pl. V, fig. 5–5c; Gervais, 1859: 41, pl. I, fig. 2, 2a–b.

*Rhopalurus* (part): Karsch, 1879b: 119, 121, 122; Pocock, 1902a: 36–38, pl. VIII, fig. 5, 5a, pl. IX, fig. 1, 1a; Banks, 1909: 172; Herrera, 1917: 271; Lampe, 1917: 197; Franganillo, 1930a: 95, figs. 19–21; 1930b: 119; Mello-Leitão, 1932: 14, 15; Meise, 1934: 29, 32, 38; Franganillo, 1935: 21; 1936: 164, figs. 86, 87; Moreno, 1939a: 65–67, pl. 6, fig. 3; 1939b: 124–128, pl. XIX–XXI; 1940b: 129–130, pl. XXII; Prado, 1940: 26–28; Roewer, 1943: 219; Jaume, 1954: 1090, 1091; Esquivel de Verde, 1968: 67; Esquivel de Verde and Machado-Allison, 1969: 33; Bücherl, 1971: 327; Armas, 1973: 7; 1974b: 2–6, figs. 1A, B,

2A, B, 3A, B, 4, table 1; 1977: 3; Stahnke and Calos, 1977: 119; Lourenço, 1979: 215, 216, fig. 8; Armas, 1981a: 52; 1981b: 2–5, figs. 1, 2, table 1; 1982a: 4; 1982b: 5, table 2; Lourenço, 1982a: 108, 110–112, 114–116, 134–138, figs. 2–11, 14–24, 78, table 1; Armas, 1983: 3, fig. 1; 1984: 8; Lourenço, 1984a: 169, 170; 1986a: 133, 135, 136, figs. 17, 18; 1986b: 165, fig. 7; Armas and Marciano Fondeur, 1987: 19, 20, 23, pl. II, fig. 4, tables 10, 11; Armas, 1988: 68–71, 93, 97, figs. 27, 36; Lourenço, 1992: 55; Rudloff, 1994: 9; Lourenço and Cloudsley-Thompson, 1995: 424, 426; Lourenço, 1997a: 590; Lourenço and Pinto-da-Rocha, 1997: 181; Kovařík, 1997: 181; 1998: 118; Armas, 1999: 127; Armas et al., 1999: 30–32; Lourenço et al., 2000: 141–143; Fet and Lowe, 2000: 217, 219–221; Armas, 2001: 246, table 1; Fet et al., 2003a: 2, 3, 6, 10, table 1; Teruel, 2003: 149, 150, figs. 1, 2; 2005: 165; Teruel and Montano, 2005: 221–223, 225–227, figs. 10, 14, tables 2, 4; Armas, 2006: 6; Teruel, 2006: 43–53, figs. 1–10, 12A, E, tables 1, 2; Teruel and Armas, 2006: 175–179, figs. 1–4, tables 1, 2; Teruel et al., 2006: 219–223, fig. 1; Lourenço, 2007: 359, 361, 362; Kamenz and Prendini, 2008: 9, table 2, pl. 41, 43; Perez-Gelabert, 2008: 68; Volschenk et al., 2008: 654, 658, 659, 663, 664, 674, fig. 1B, tables 1, 2; Prendini et al., 2009: 206–223, figs. 1, 2, 4, 5A, B, E, F, 6A, C, 7A, C, 8, 10, 11, tables 1, 3; Santiago-Blay, 2009: 115, 116, 119, 122, 125, figs. 10, 31; Teruel and Armas, 2012a: 153–167, figs. 1–16, tables 1–7; 2012b: 209, 210, 212, 214–217, figs. 1–7, tables 1–3; Teruel and Kovařík, 2012: 116–141, figs. 29, 40, 41, 48, 253–305, 534–565, 636; Rodríguez-Cabrera and Teruel, 2014: 121; Lourenço and Armas, 2015: 228, 229; Rodríguez-Cabrera et al., 2015: 85, 86, fig. 1; Santos et al., 2016: 3, 9, tables 1, figs. 1Ñ, 2B, 3D.

*Centrurus* (part): Karsch, 1879b: 121, 122; Kraepelin, 1891: 123, 135–137, 139, figs. 30, 33;

Pocock, 1893: 385, 391; Thorell, 1893: 372, 373; Kraepelin, 1895: 95; 1899: 89, 94, 95; 1901: 270; 1908: 187, 190, 193, 194; Werner, 1927: 357.

*Heteroctenus* Pocock, 1893: 375, 391, 392; Laurie, 1896: 131; Lönnberg, 1897: 197, 208.

*Centruroides* (*Rhopalurus*) (part): Werner, 1934: 274, fig. 33b.

DIAGNOSIS: *Heteroctonus* differs all from other rhopalurusine genera by the presence of a single, deep, median depression in the male pectinal plate. It differs further from *Ischnotelson*, gen. nov., *Jaguajir*, gen. nov., *Physoctonus*, *Rhopalurus*, *Trogloorhopalurus*, and many species of *Centruroides* by the absence of a subaculear tubercle on the telson; from *Centruroides*, *Ischnotelson*, *Physoctonus*, and *Trogloorhopalurus* by the presence of a pecten-sternite stridulatory organ (proximal pectinal teeth often enlarged, dorsal surfaces with multiple nodules and regular striations, sternite III, lateral margins forming smooth, raised carina, ventromedian carina elevated anteriorly, ventrosubmedian surfaces forming paired depressions, finely and irregularly granular); from *Ischnotelson* and *Rhopalurus*, by the separate (unfused) central lateral and posterior central submedian carinae of the carapace; from *Centruroides* by the presence of macrosetae on the dorsobasal surface of the pectinal teeth; from *Ischnotelson*, by the separate (unfused) lateral ocular and central lateral carinae of the carapace, and the telson vesicle not being laterally compressed; from *Jaguajir* by the separate (unfused) lateral ocular and anterior central submedian carinae of the carapace; from *Physoctonus* by the larger size (30–70 mm), the more distinct carapacial carinae, the setose proximal dorsal fulcra of the pectines, the incrassate pedipalp chela manus of the adult male, the bifurcate prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; and from *Trogloorhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of the adult male





FIG. 1. Representative species in the New World buthid scorpion family Rhopalurusinae Bücherl, 1971, habitus in life. **A.** *Heteroctenus abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂, Isla Mona, Puerto Rico. **B.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂, Guanambi, Bahia, Brazil. **C.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♀, Parque Zoobotânico de Teresina, Piauí, Brazil. **D.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♂, Jeremoabo, Bahia, Brazil. **E.** *Physoctonus debilis*, ♀, Guanambi, Bahia, Brazil. **F.** *Rhopalurus laticauda* Thorell, 1876., ♀, Alter do Chão, Santarem, Pará, Brazil. **G.** *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀, Lapa do Bode, Itaeté, Bahia, Brazil. **H.** *Troglorhopalurus translucidus* Lourenço et al., 2004, ♀, Gruta Rio dos Pombos, Igatu, Andaraí, Bahia, Brazil.

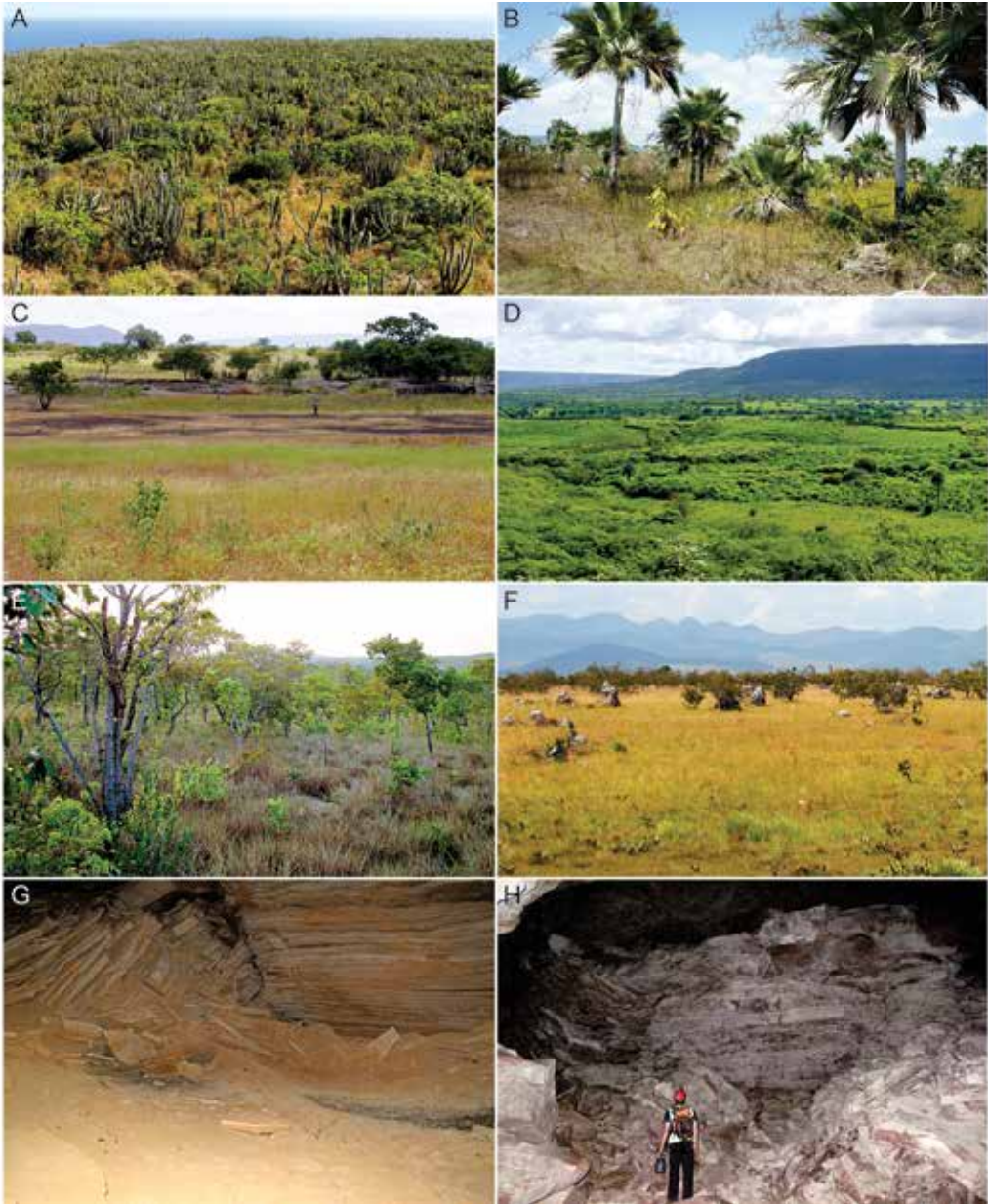


FIG. 2. Representative habitats of species in the New World buthid scorpion family Rhopalurusinae Bücherl, 1971. **A.** Isla Mona, Puerto Rico, habitat of *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov. **B.** Sierra de Cubitas, Camagüey, Cuba, habitat of *Heteroctenus junceus* (Herbst, 1800), comb. nov. **C.** Guanambi, Bahia, Brazil, habitat of *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., and *Jaguajir rochae* (Borelli, 1910), comb. nov. **D.** Exu, Pernambuco, Brazil, habitat of *J. rochae* and *Physoctonus debilis* (C.L. Koch, 1840). **E.** Santarém, Pará, Brazil, habitat of *Rhopalurus laticauda* Thorell, 1876. **F.** Normandia, Roraima, Brazil, habitat of *R. laticauda*. **G.** Lapa do Bode, Itaeté, Bahia, Brazil, habitat of *Troglohopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov. **H.** Gruta do Lapão, Lençóis, Bahia, Brazil, habitat of *Troglohopalurus translucidus* Lourenço et al., 2004.



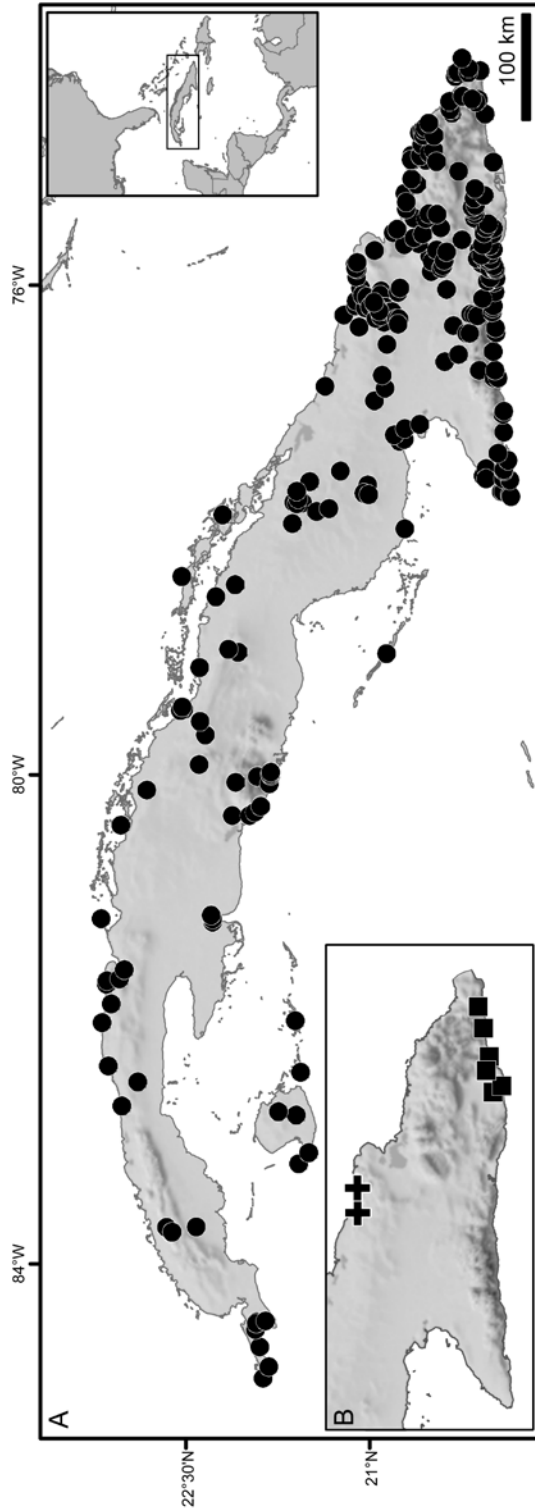


FIG. 3. Map of Cuba and neighboring islets, plotting known locality records of three species of *Heteroctenus* Pocock, 1893: *A. H. junceus* (Herbst, 1800) (circles). *B. H. garridoi* (Armas, 1974), comb. nov. (squares); *H. gibbarae* (Teruel, 2006), comb. nov. (crosses).

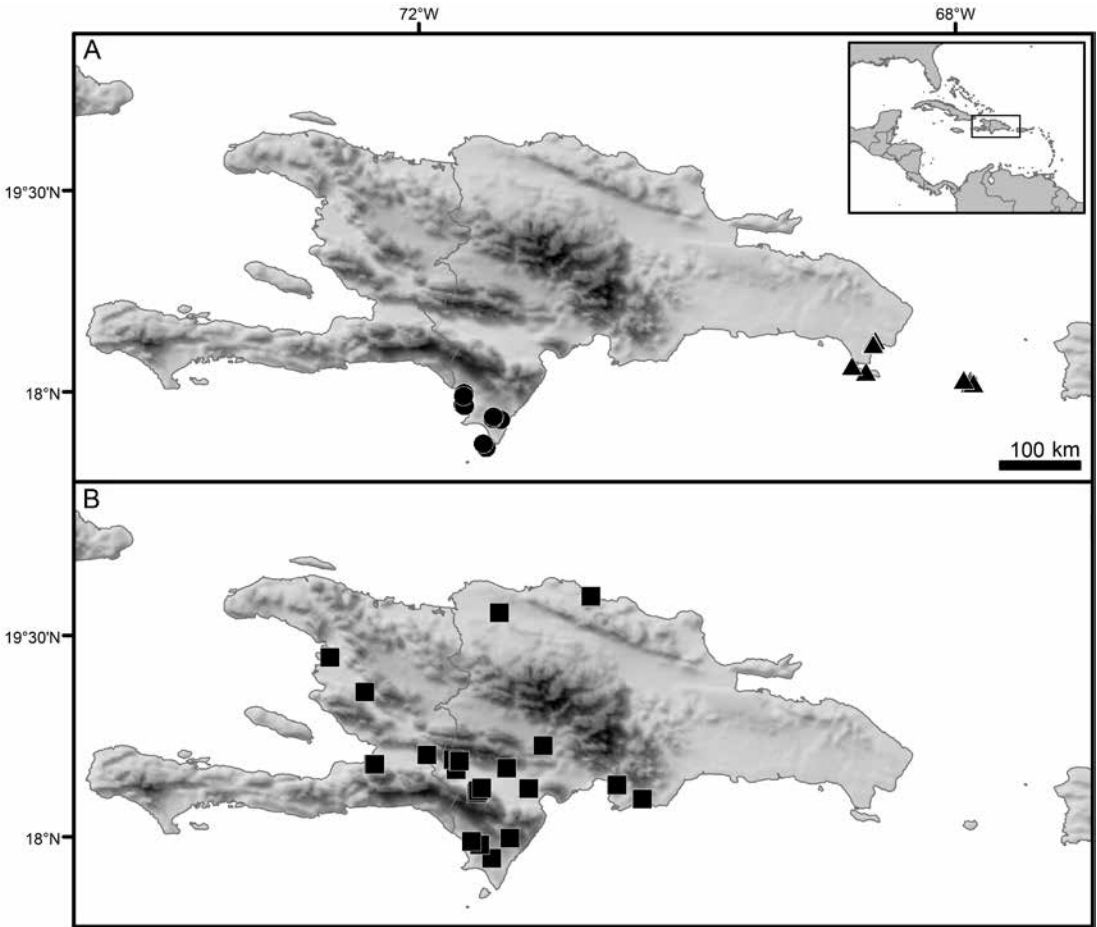


FIG. 4. Map of Hispaniola and neighboring islets, plotting known locality records of three species of *Heteroctenus* Pocock, 1893: A. *H. abudi* (Armas and Marcano Fondeur, 1987), comb. nov. (triangles); *H. bonettii* (Armas, 1999), comb. nov. (circles). B. *H. princeps* (Karsch, 1879), comb. nov. (squares).

emarginate, with a distinct gap evident between them, when closed.

**DESCRIPTION:** The following general description outlines characters common to the species of *Heteroctenus*. Descriptions of hemispermatoophores are based on *H. abudi*, *H. bonettii*, *H. junceus*, and *H. princeps*.

**Total length:** Large, robust scorpions (total length, 50–70 mm).

**Color:** Carapace and tergites I–VI light brown, tergite VII yellowish (fig. 1A). Coxosternal region, pectines and sternites pale yellow. Metasomal segments, dorsal surfaces yellow (segments I–III) to brown (IV and V); ventral surfaces darker; seg-

ments IV and V darker than preceding segments, with V darker than IV. Telson reddish brown, aculeus almost black. Chelicerae and legs yellowish. Pedipalps yellow with chela fingers darker than manus, reddish-brown.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle raised (fig. 14A–E); two median ocelli; three pairs of lateral macrocelli; one or two pairs of lateral microcelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular, central lateral, anterior central submedian, and posterior

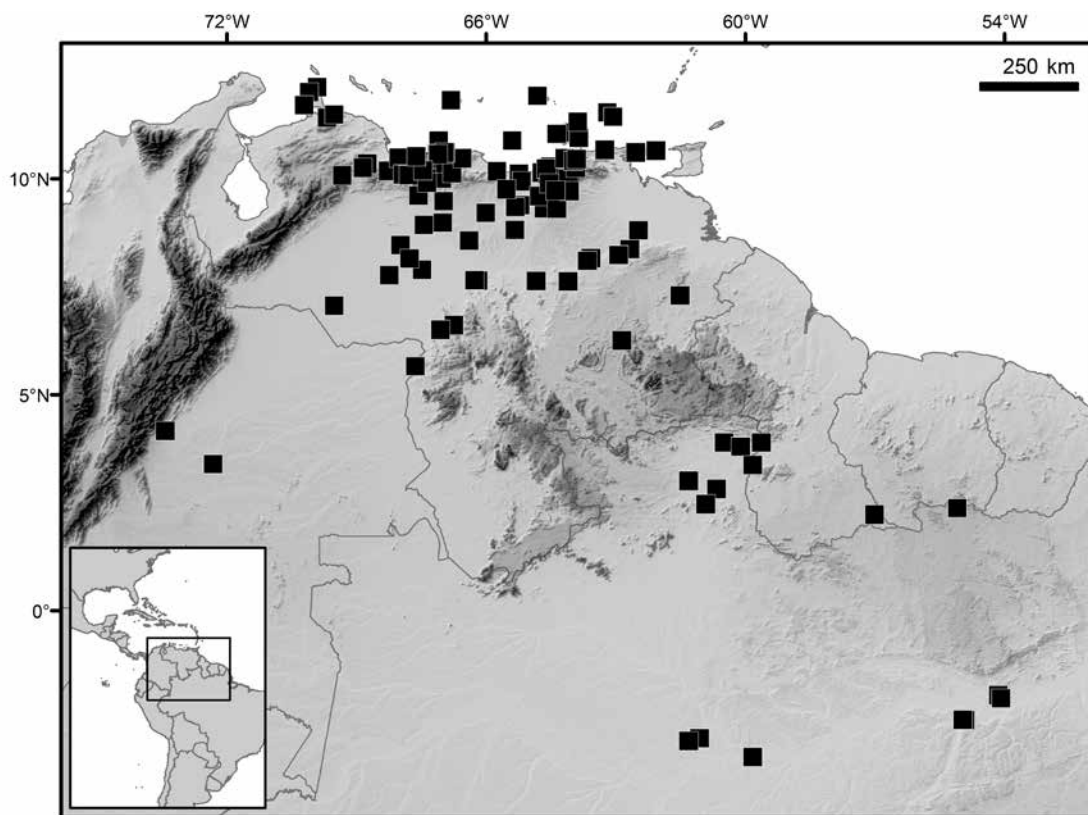


FIG. 5. Map of northern South America, plotting known locality records of *Rhopalurus laticauda* Thorell, 1876 (squares).

central submedian carinae distinct, coarsely granular to costate-granular and separate (unfused).

**Pedipalps:** Pedipalp femur retrolateral accessory carinae absent. Pedipalp chela manus of adult male incrassate, fixed and movable fingers curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, distinct gap present between fingers proximally, when closed (figs. 25–27), manus of female not incrassate, fixed and movable fingers not curved proximally, such that proximal dentate margin sublinear, little or no gap present between them proximally, when closed; manus, proventral and promedian (except in *H. bonettii*) carinae absent; fixed and movable fingers, median denticle rows each comprising eight or nine oblique

subrows of primary denticles flanked closely by pro- and retrolateral accessory (supernumerary) denticles; movable finger with proximal lobe (fig. 17A). Pedipalps orthobothriotaxic Type A,  $\alpha$  configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  aligned with or distal to trichobothrium *et*.

**Legs:** Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with irregular tufts of fine, acuminate macrosetae.

**Pectines:** Pectinal plate with single median depression (male), anterior margin with sulcus (fig. 18A–E). Pectines often proximally expanded,

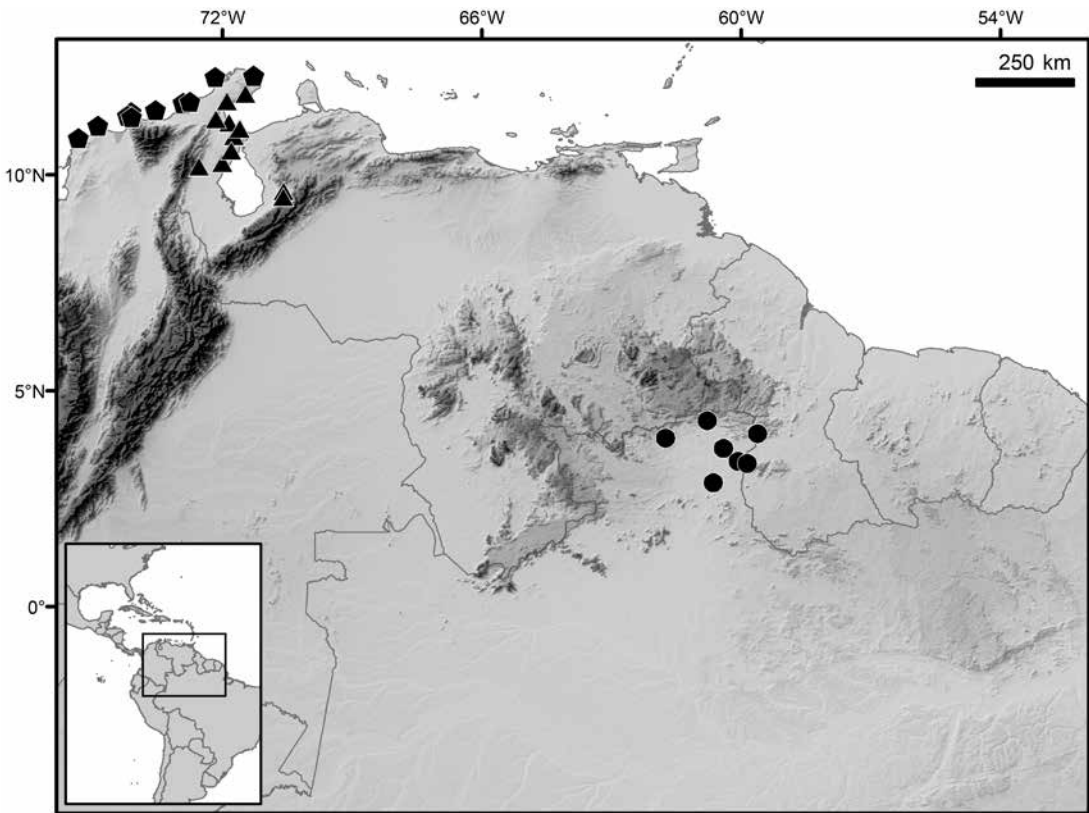


FIG. 6. Map of northern South America, plotting known locality records of *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov. (circles), *Rhopalurus caribensis* Teruel and Roncallo, 2008 (pentagons), and *Rhopalurus ochoai*, sp. nov. (triangles).

at least  $1.5\times$  wider proximally than medially; proximal dorsal fulcra setose; pectinal teeth almost straight, slightly curved laterally, proximal teeth often enlarged, dorsal surfaces with multiple nodules and regular striations (figs. 11B, 12B), dorsobasal surfaces with macrosetae; pectinal sensillae peg shaped.

**Mesosoma:** Tergites IV–VI wider than I–III and VII (figs. 31–35); I–VI tricarinate, dorsomedian and dorsosubmedian carinae granular to costate-granular, restricted to posterior half on I–VI, dorsosubmedian carinae more prominent on IV–VI. Tergite VII pentacarinate, dorsomedian carina restricted to anterior two thirds of segment. Sternites smooth, carinate obsolete, more developed on VI and VII; sternite III, lateral margins forming smooth, raised carina, ventromedian carina ele-

vated anteriorly, ventrosubmedian surfaces forming paired depressions, finely and irregularly granular; respiratory spiracles (stigmata) width more than  $5\times$  length (fig. 11A, B).

**Metasoma:** Metasoma robust, but not increasing markedly in width posteriorly, segment V slightly wider than I in adult male, I and V usually similar width in adult female (figs. 28–30). Segments I and II each with 10 distinct, costate-granular carinae, III and IV each with eight distinct, costate-granular carinae, V with seven distinct but less pronounced, granular carinae; dorsosubmedian carinae obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV, more pronounced on segment I; dorsolateral carinae complete on segments I–IV, and terminating in prominent, spiniform granules posteriorly on III and IV, absent on V; lateral suprime-

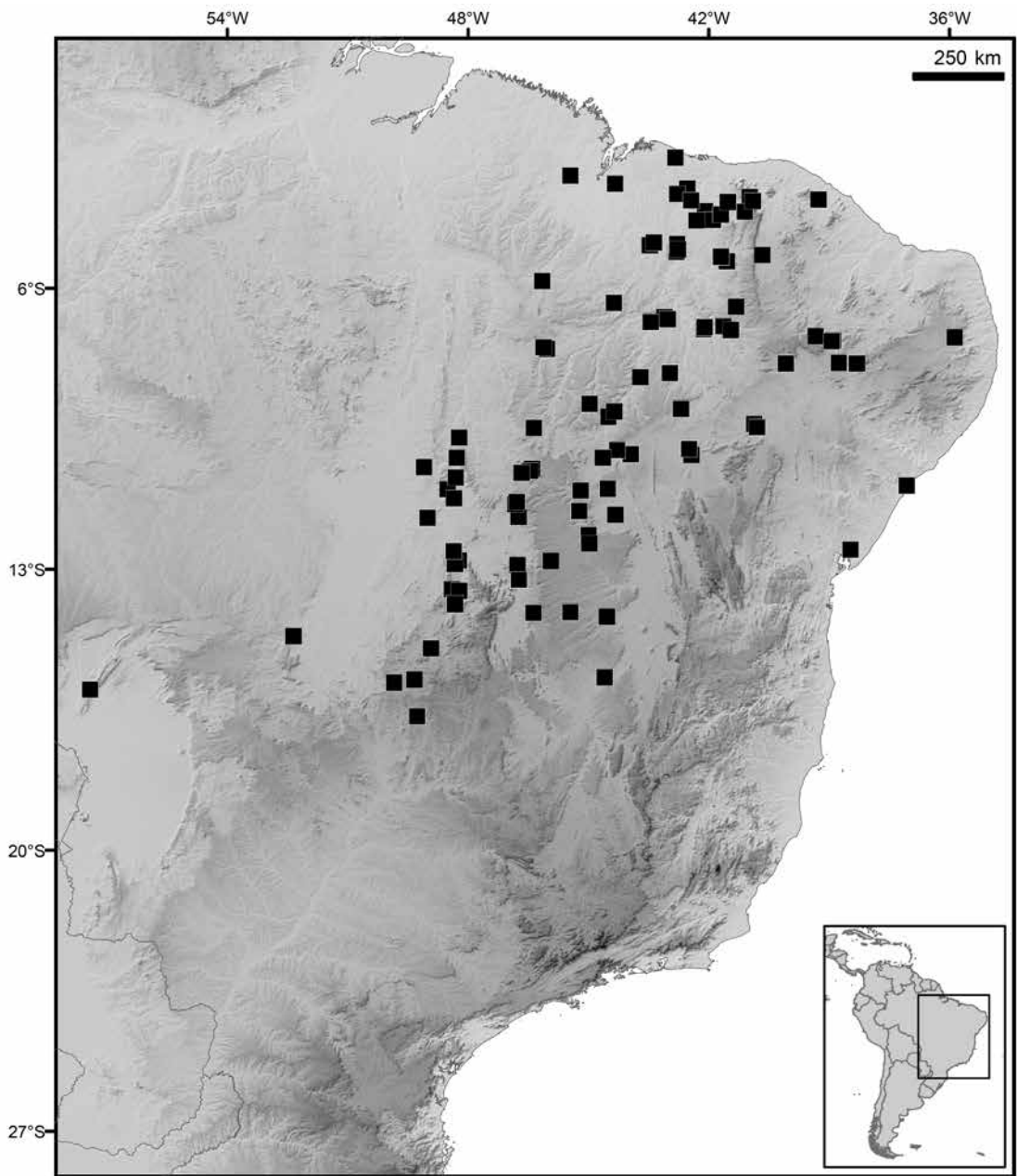


FIG. 7. Map of northeastern South America, plotting known locality records of *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov. (squares).

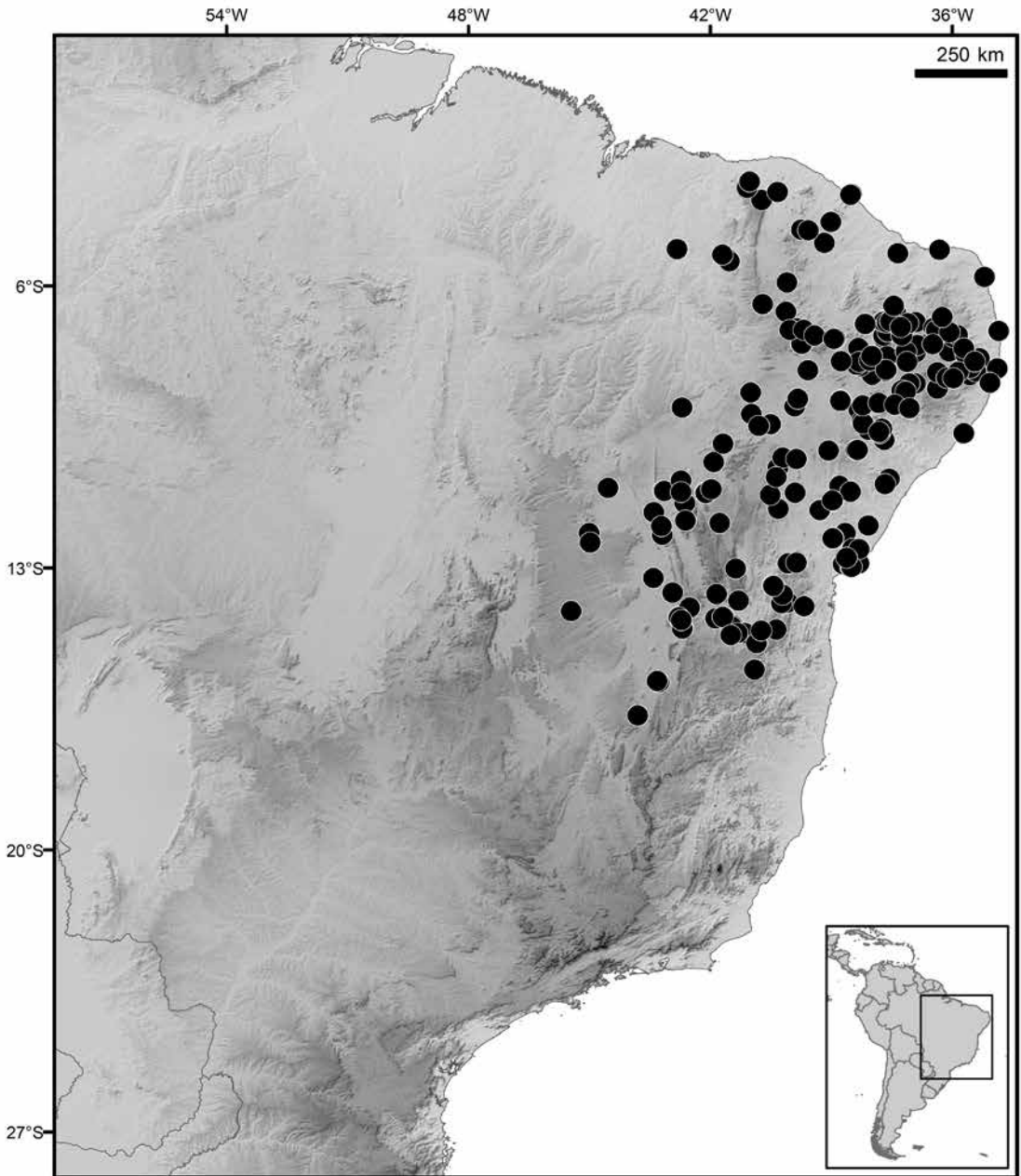


FIG. 8. Map of northeastern South America, plotting known locality records of *Jaguajir rochae* (Borelli, 1910), comb. nov. (circles).



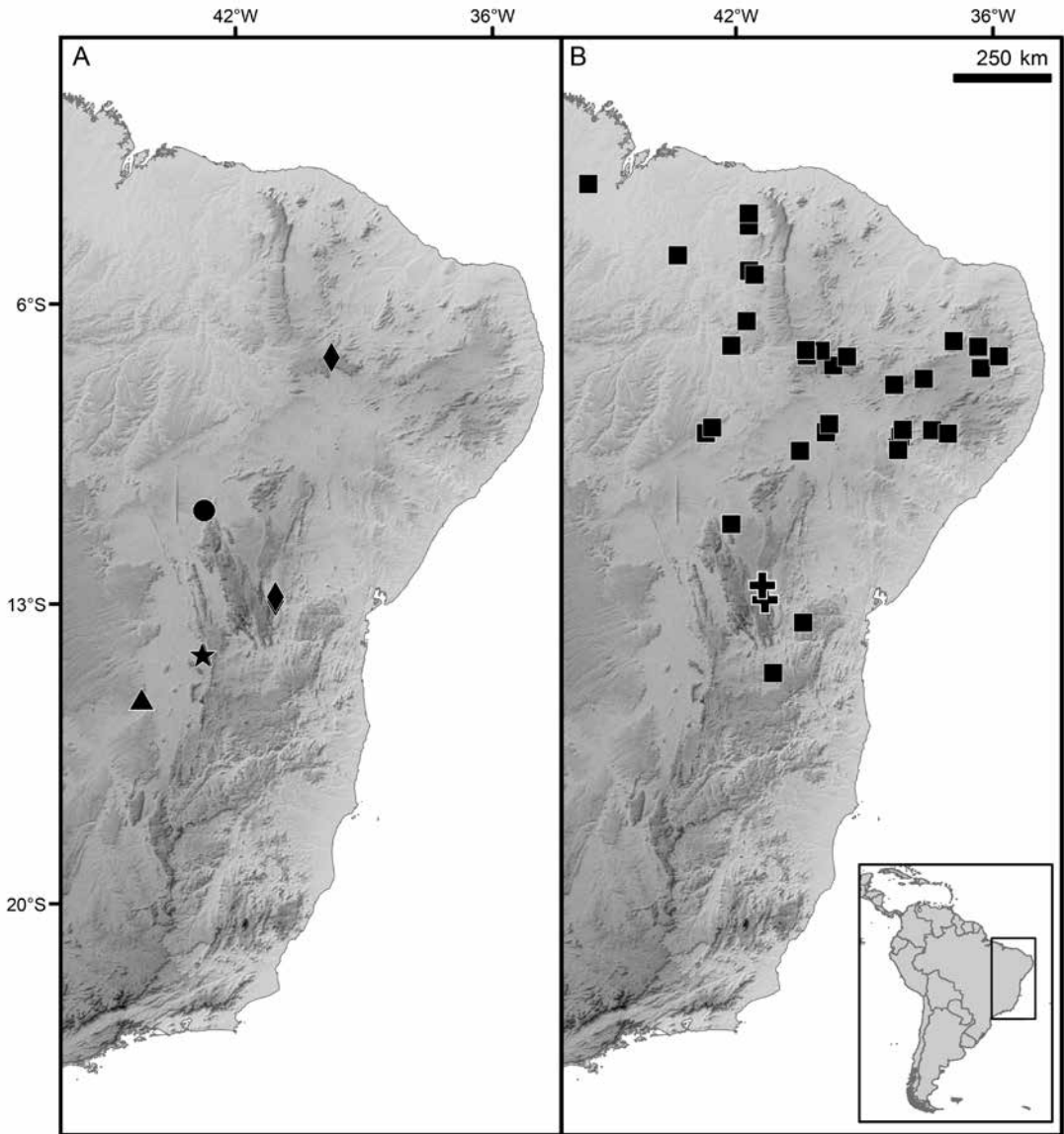


FIG. 9. Map of northeastern South America, plotting known locality records of six species of Rhopalurusinae Bücherl, 1971: **A.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov. (star), *Ischnotelson peruassu*, sp. nov. (triangle), *Physoctonus striatus*, sp. nov. (circle), *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov. (diamonds). **B.** *Physoctonus debilis* (C.L. Koch, 1840) (squares), *Troglorhopalurus translucidus* Lourenço et al., 2004 (crosses).

dian carinae complete on segments I–V; lateral inframedian carinae complete on segment I, partial on II, absent on III–V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third of V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely to coarsely granular, less so on dorsal surfaces, especially on V.

*Telson*: Vesicle slightly elongate, length ca. 1.5× width, not laterally compressed, similar in width or slightly narrower than metasoma V; anterodorsal lateral lobes reduced or absent; lateral and ventral surfaces granular, with distinct ventromedian carina; subaculear tubercle absent.

*Hemispermatothore*: Flagelliform; flagellum, elongate and narrow (fig. 23A–N); trunk markedly concave; three lobules, ental (LI), ectal (LE), and basal (LB); LI continuous until flagellar base; flagellar base narrow, half (*H. abudi* and *H. bonettii*) to one-third (*H. junceus* and *H. princeps*) the maximum width of trunk; LE ca. half (*H. abudi*, *H. junceus* and *H. princeps*) to one third (*H. bonettii*) the length of LI and may be spiniform (*H. bonettii*); LB very short with sharp (*H. abudi*) or setalike (acuminate) (*H. bonettii*) tip.

**INCLUDED SPECIES**: *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov.; *Heteroctenus bonettii* (Armas, 1999), comb. nov.; *Heteroctenus junceus* (Herbst, 1800); *Heteroctenus garridoi* (Armas, 1974), comb. nov.; *Heteroctenus gibarae* (Teruel, 2006), comb. nov.; *Heteroctenus princeps* (Karsch, 1879), comb. nov.

**DISTRIBUTION**: The species of *Heteroctenus* are endemic to the Greater Antilles of the Caribbean (figs. 3, 4): Cuba, Hispaniola (Haiti and the Dominican Republic), and Puerto Rico (Isla Mona). The known locality records range in altitudes from below sea level to 1200 m (Rodríguez-Cabrera and Teruel, 2014).

**ECOLOGY**: Whereas *Heteroctenus* primarily inhabit open vegetation formations (fig. 2A, B), in common with *Rhopalurus* and the South American genera (Lourenço, 1986a, 2008), they also occur in semideciduous forests (Armas, 2001). In the karst limestone landscapes where they occur,

these lapidicolous scorpions shelter under stones or any other available surface debris.

**REMARKS**: This genus accommodates species previously assigned to *Rhopalurus* from the Greater Antilles, the monophyly of which was consistently recovered in the analyses by Esposito et al. (in review), resulting in four new combinations. *Rhopalurus aridicola*, *R. melloleitaoi*, and *R. virkkii* are newly synonymized based on morphological and, in the case of *R. virkkii*, molecular evidence. The validity of *H. gibarae* will need to be reassessed when material becomes available for study.

***Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov.**

Figures 1A, 2A, 4A, 14A, 18A, 21A, 22A, 23A–D, 25A, 26A, 28A, 29A, 30A, 31

*Rhopalurus abudi* Armas and Marcano Fondeur, 1987: 19, 20, fig. 4, pl. II, table 10; Rudloff, 1994: 9; Lourenço and Pinto-da-Rocha, 1997: 181; Kovařík, 1998: 118; Armas, 1999: 127; Armas et al., 1999: 30–32; Armas, 2001: 246, table 1; Fet and Lowe, 2000: 217; Fet et al., 2003a: 3, table 1; Teruel, 2005: 165; Armas, 2006: 6; Teruel, 2006: 50, 51, fig. 12E; Teruel et al., 2006: 220, 221, 223, fig. 1; Perez-Gelabert, 2008: 68; Volschenk et al., 2008: 654, 658, 659, 663, 664, 674, fig. 1D, tables 1, 2; Prendini et al., 2009: 206–209, 211–220, 222, figs. 1, 2, 5A, B, 6A, 7A, 8, 11, table 1; Teruel and Armas, 2012b: 215–217, fig. 7; Santos et al., 2016: 9, fig. 1Ñ.

*Rhopalurus virkkii* Santiago-Blay, 2009: 115, 116, 122, figs. 10, 31; Teruel and Armas, 2012b: 216–217, fig. 7; syn. nov.

**TYPE MATERIAL**: *Rhopalurus abudi*: Holotype ♀ (IES 3.2912), **DOMINICAN REPUBLIC**: *La Altagracia Prov.*: Catuano, Isla Saona, 27.i.1980, E. de J. Marcano Fondeur. *Rhopalurus virkkii*: Holotype ♂ (ZMUPR-RP), **PUERTO RICO**: Isla Mona, Camino del Diablo, approximately 2 km

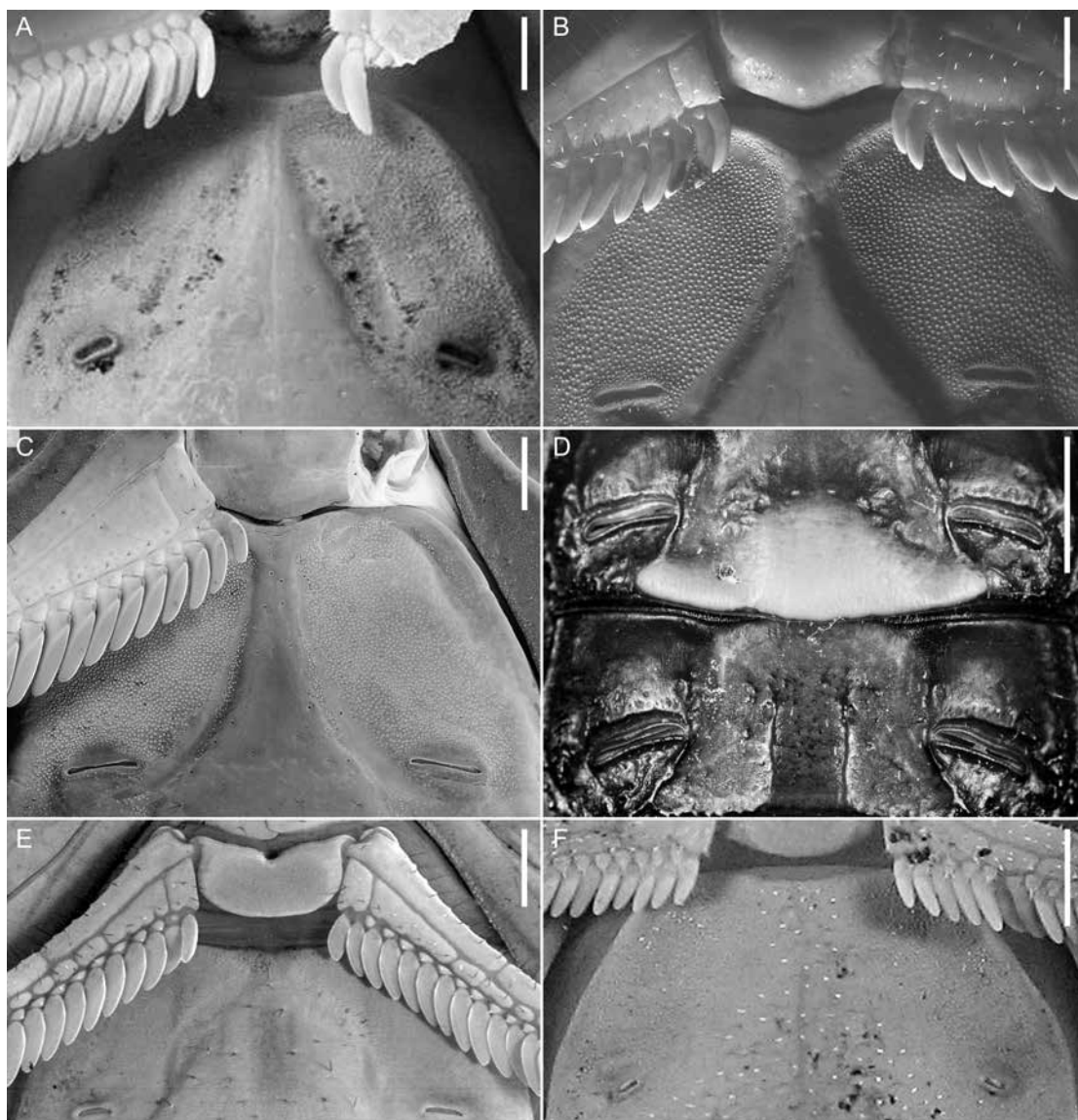


FIG. 10. Rhopalurusinae Bücherl, 1971, sternites III (A–C, E, F), V and VI (D), ventral aspect. **A.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **B.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♀ (MZSP). **C, D.** *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). **E.** *Physoctonus debilis* (C.L. Koch, 1840), ♂ (MZSP). **F.** *Trogloorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). Scale bars = 1 mm (A, E, F), 2 mm (B, C, D).

from Pájaros, 21.i.1982, J.A. Santiago-Blay; 2 ♂, 2 ♀, 2 ♂ subad., 1 ♀ subad., 1 ♂ juv., 1 ♀ juv. paratypes (ZMUPR-RP), El Faro, Pájaros to Uveros, Bajura de los Cerezos.

**DIAGNOSIS:** *Heteroctenus abudi* is most closely related to *H. princeps*, with which it shares pronounced sexual dimorphism of the pedipalp chelae, and differs in this respect from the third *Heteroctenus* species occurring on Hispaniola, *H. bonettii*. The chela manus of the adult male *H. abudi* is incrassate and the fingers strongly curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that only the distal portion of the fingers connect and a distinctive gap is present between them proximally, when closed (fig. 25A). The chela manus of the female is not incrassate and the fingers are not curved proximally, such that the fingers connect along most of their length and little to no gap is present between them proximally, when closed (fig. 26A). However, the pedipalp chela manus of *H. abudi* is longer and more slender, with more strongly developed carinae, than that of *H. princeps*.

Other characters in which *H. abudi* differs from *H. bonettii* and *H. princeps* are as follows. The carapace of *H. abudi* is longer and narrower than that of *H. princeps* (fig. 14A, E). The carapace and tergites are more coarsely and densely granular in *H. abudi* than in *H. bonettii* but less so than in *H. princeps*. The pectines of *H. abudi* are broader basally, with a more pronounced basal plate than in *H. princeps*, but narrower basally, with a less-pronounced basal plate than in *H. bonettii* (fig. 18A, B). The pectinal teeth are similar in size in *H. abudi* whereas the first 6–7 pectinal teeth are noticeably larger in *H. bonettii*. The carapace and tergites are less coarsely and densely granular in *H. abudi* than *H. princeps* but more so than in *H. bonettii*. The submedian sulci of sternite III are convergent in *H. abudi* but subparallel in *H. bonettii* (fig. 18A, B). The pale, raised posteromedial surface of sternite V in the male is less prominent in *H. abudi* than in *H. bonettii*. The metasomal segments of *H. abudi* are longer and narrower, i.e., the width/length ratio

is greater, than in *H. princeps* but shorter and broader, i.e., the width/length ratio is smaller, than in *H. bonettii* (fig. 28A, B). The granulation, ventromedian and ventrolateral carinae of metasomal segment V are less developed, compared with those of the preceding segments in *H. abudi*, such that the segment has a shinier, rounded appearance, as in *H. princeps* (fig. 29A, E).

Unlike *H. bonettii* and *H. princeps*, the coloration of *H. abudi* is predominantly dark, due to extensive infuscation (fig. 31); the carapace, pedipalp chelae, legs, and tergites noticeably infuscate; the metasoma and telson strongly infuscate laterally and ventrally, especially on segments II–IV, becoming more so posteriorly, with each segment darker than the preceding one and segment V darkest. Although the base coloration of specimens from Isla Mona is markedly paler than that of typical specimens from the Dominican Republic, the pattern of infuscation is nevertheless similar.

**DISTRIBUTION:** *Heteroctenus abudi* is endemic to the Dominican Republic (La Altagracia Province) and Puerto Rico. It is known from three populations (fig. 4A), one at the extreme southeastern end of Hispaniola, another on Isla Saona (both falling within the Parque Nacional del Este), and a third on Isla Mona, an islet between Hispaniola and Puerto Rico, also a protected area. The known localities range in altitude from 3 to 68 m.

**ECOLOGY:** *Heteroctenus abudi* inhabits dense canopy, humid coastal forest in the southeast of Hispaniola and adjacent Isla Saona (Prendini et al., 2009) and much drier habitat, ranging from scrub forest and cactus to desert grassland dominated by organ cactus and tall grasses, on Isla Mona (fig. 2A). The difference in habitat may explain the paler coloration of the material from Isla Mona. Most specimens of *H. abudi* were collected at night using UV light detection on karst limestone. The holotype was collected from under a stone (Armas and Marcano Fondeur, 1987). The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). *Heteroctonus abudi* was sympatric with

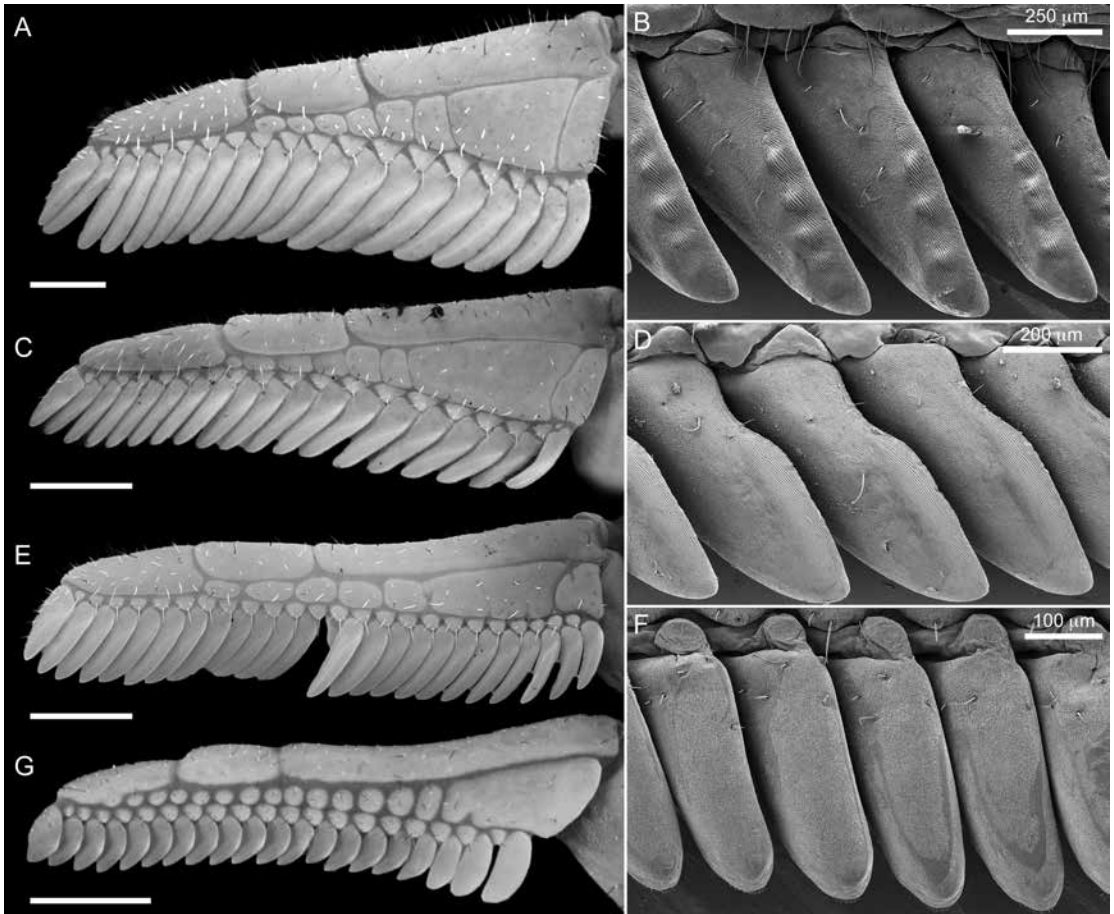


FIG. 11. Rhopalurusinae Bücherl, 1971, dextral pecten, ventral aspect (A, C, E, G) and pectinal teeth, dorsal aspect (B, D, F). A. *Heteroctenus junceus* (Herbst, 1800), ♂ (AMNH). B. *Heteroctenus bonettii* (Armas, 1999), comb. nov., ♀ (AMNH). C. *Rhopalurus laticauda* Thorell, 1876, ♂ (MZSP). D. *Jaguajir rochae* (Borelli, 1910), comb. nov., (AMNH). E. *Rhopalurus laticauda* Thorell, 1876, ♂ (AMCC [LP 2845]). F. *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha 1997), comb. nov., ♀ (AMCC [LP 3260]). G. *Physoctonus debilis* (C.L. Koch, 1840), ♀ (MZSP).

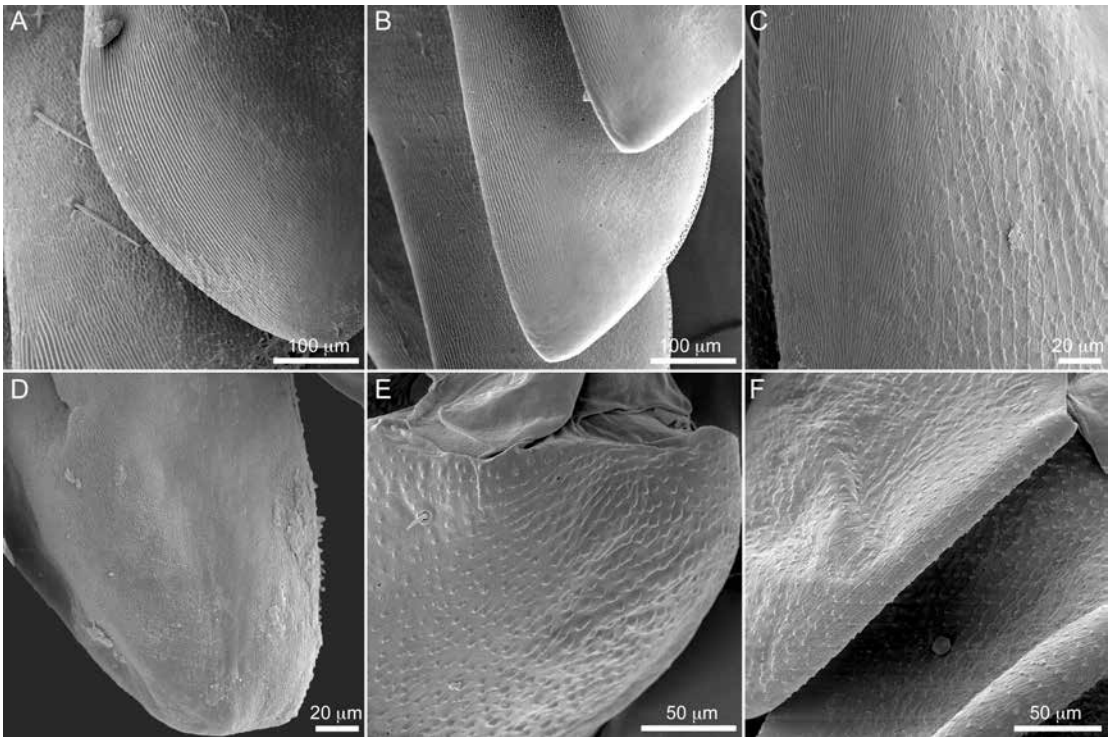


FIG. 12. Rhopalurusinae Bücherl, 1971, pectinal teeth, dorsal aspect, fine structure. A. *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., (MZSP). B. *Heteroctenus princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). C. *Rhopalurus laticauda* Thorell, 1876, (MZSP). D. *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha 1997), comb. nov., ♀ (MZSP). E. *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). F. *Physoctonus debilis* (C.L. Koch, 1840), ♀ (MZSP).

the buthids *Centruroides bani* and *Microtityus consuelo* Armas and Marcano Fondeur, 1987, and the diplocentrid *Cazierius cicero* (Armas and Marcano Fondeur, 1987), in Parque Nacional del Este, and with *C. bani* and the diplocentrid *Cazierius garridoi* Armas, 2005, on Isla Mona.

REMARKS: Lourenço and Pinto-da-Rocha (1997) suggested this species may be a variety of *R. princeps*. Prendini et al. (2009) demonstrated that the two species are distinct, however. Except for paler coloration, populations from Isla Mona, described as *Rhopalurus virkkii* by Santiago-Blay (2009), are morphologically identical to *H. abudi* from the southeastern Dominican Republic, with low genetic divergence between them (Esposito et al., in review), justifying the synonymy: *Rhopalurus virkkii* Santiago-Blay, 2009 = *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), syn. nov.

MATERIAL EXAMINED: **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 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 from Sardiniera to Punta Capitan, 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, 10 ♂, 9 ♀,

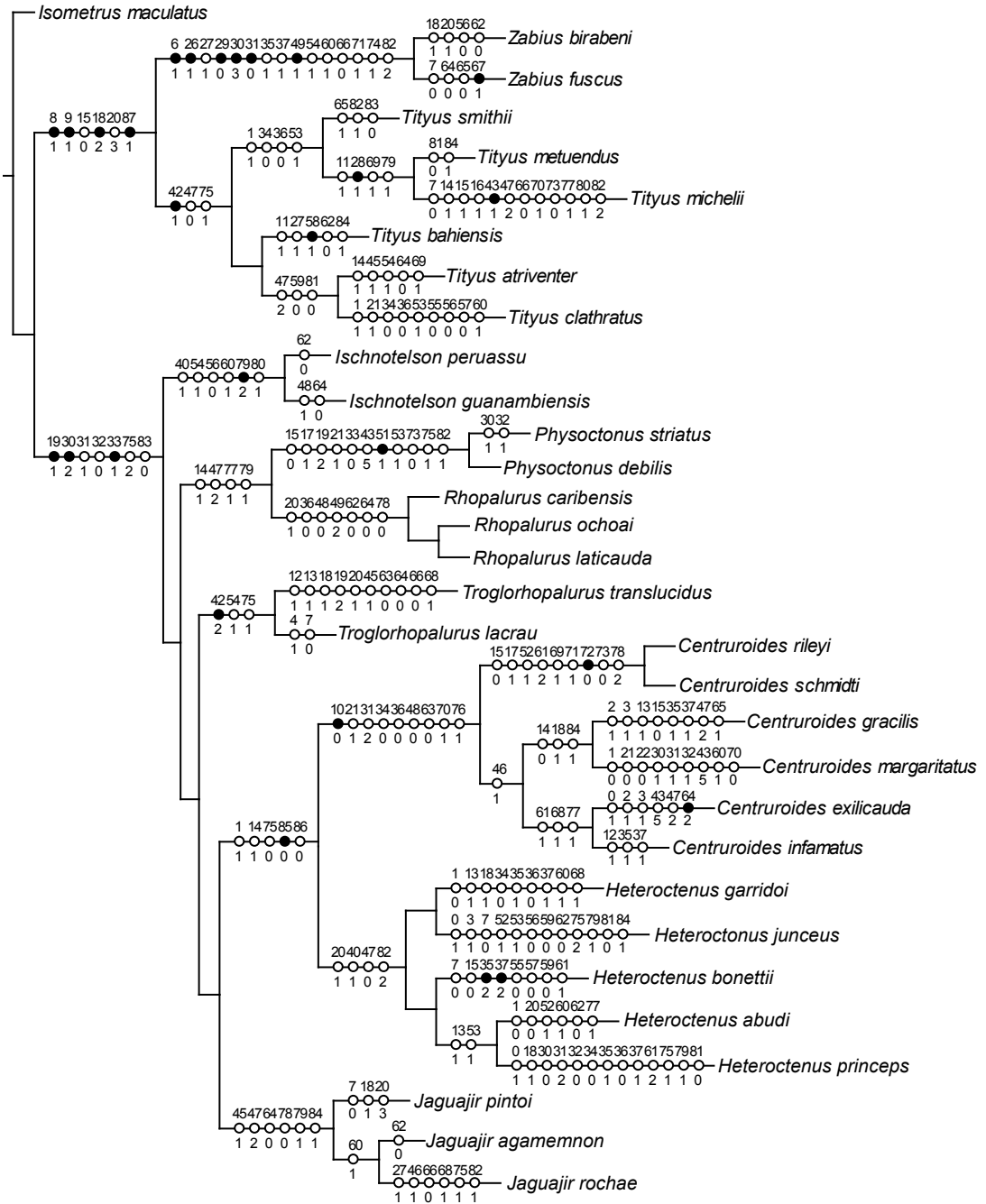


FIG. 13. Phylogeny of the New World buthid scorpion subfamily Rhopalurusinae Bücherl, 1971, obtained by simultaneous phylogenetic analysis of 90 morphological characters and 4260 aligned DNA nucleotides from three mitochondrial and two nuclear gene loci. Maximum clade credibility tree with synapomorphies optimized by accelerated transformation. Black circles indicate uniquely derived apomorphic states, white bars parallel derivations of apomorphic states. Numbers above indicate characters, and below indicate states (appendix 1).

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), comb. nov.**

Figures 4, 11B, 14B, 18B, 23E–G, 25B, 26B, 28B, 29B, 30B, 32

*Rhopalurus bonettii* Armas, 1999: 126–129, fig. 12A–B, table 1; 2006: 6, 10, fig. 8A–D; Kamenz and Prendini, 2008: 9, table 2, pl. 40; Perez-Gelabert, 2008: 68; Prendini et al., 2009: 206, 207, 209, 211–213, 215, 218, 220, 222, 223, figs. 1, 3, 5C, D, 6B, 7B, 9, table 2; Teruel and Armas, 2012b: 216, fig. 7; Santos et al., 2016: 9, 16, fig. 2A.

*Rhopalurus bonettii* Armas, 1999: 126–129, fig. 12A–B, table 1; 2006: 6, 10, fig. 8A–D; Kamenz and Prendini, 2008: 9, table 2, pl. 40; Perez-Gelabert, 2008: 68; Prendini et al., 2009: 206, 207, 209, 211–213, 215, 218, 220, 222, 223, figs. 1, 3, 5C, D, 6B, 7B, 9, table 2; Teruel and Armas, 2012b: 216, fig. 7; Santos et al., 2016: 9, 16, fig. 2A.

**TYPE MATERIAL:** *Rhopalurus bonettii*: Holotype ♂ (IES, IZACC-3.2908), **DOMINICAN REPUBLIC:** *Pedernales Prov.:* Beata Island (NW), Playa del Coco, 10.iii.1999, L.F. de Armas and K. Polanco.

**DIAGNOSIS:** *Heteroctenus bonettii* differs from the other two species of *Heteroctenus* occurring on Hispaniola, *H. abudi* and *H. princeps*, in the less-pronounced sexual dimorphism of the pedipalp chelae. The chelae of the male and female of *H. bonettii* are similar, the manus of the male only slightly incrassate relative to the female, and the fingers not curved proximally, such that the fin-

gers connect along most of their length and little to no gap is present between them proximally, when closed (figs. 25, 26).

Other characters by which *H. bonettii* differs from *H. abudi* and *H. princeps* are as follows. The carapace of *H. bonettii* is longer and narrower than that of *H. princeps* (fig. 14B, E). The carapace and tergites are more finely and sparsely granular in *H. bonettii* than in *H. abudi* and *H. princeps*. The pectines of *H. bonettii* are very broad basally, with a more pronounced basal plate than in *H. princeps* and, to a lesser extent, *H. abudi*. The first 6–7 pectinal teeth are noticeably larger than the rest in *H. bonettii*, unlike *H. abudi* and *H. princeps* in which the teeth are similar in size (fig. 18B). The submedian sulci of sternite III are subparallel in *H. bonettii* but convergent in *H. abudi* and *H. princeps* (fig. 18A, B, E). The pale, raised posteromedial surface of sternite V in the male is more prominent in *H. bonettii* than in *H. abudi* and *H. princeps*. The metasomal segments of *H. bonettii* are longer and narrower, i.e., the width/length ratio is greater, than in *H. princeps* and, to a lesser extent, *H. abudi* (fig. 28A, B, E). The granulation, ventromedian and ventrolateral carinae of metasomal segment V are more developed, compared with those of the preceding segments, such that the segment has a matte, angular appearance in *H. bonettii* (fig. 19B).

Unlike *H. abudi*, the coloration of *H. bonettii* is predominantly pale (fig. 32); the carapace, pedipalp chelae, legs, and tergites immaculate; the metasoma (segments III–V or IV and V only) and telson weakly infuscate. In this respect, *H. bonettii* resembles *H. princeps* except for the pedipalp chelae, which are typically infuscate in the latter.

**DISTRIBUTION:** *Heteroctenus bonettii* is endemic to Pedernales Province south of the Sierra de Baoruco in the western part of mainland Dominican Republic and Isla Beata, the type locality (fig. 4A). Most of the known locality records fall within the Parque Nacional Jaragua, at altitudes ranging from 14 to 92 m.



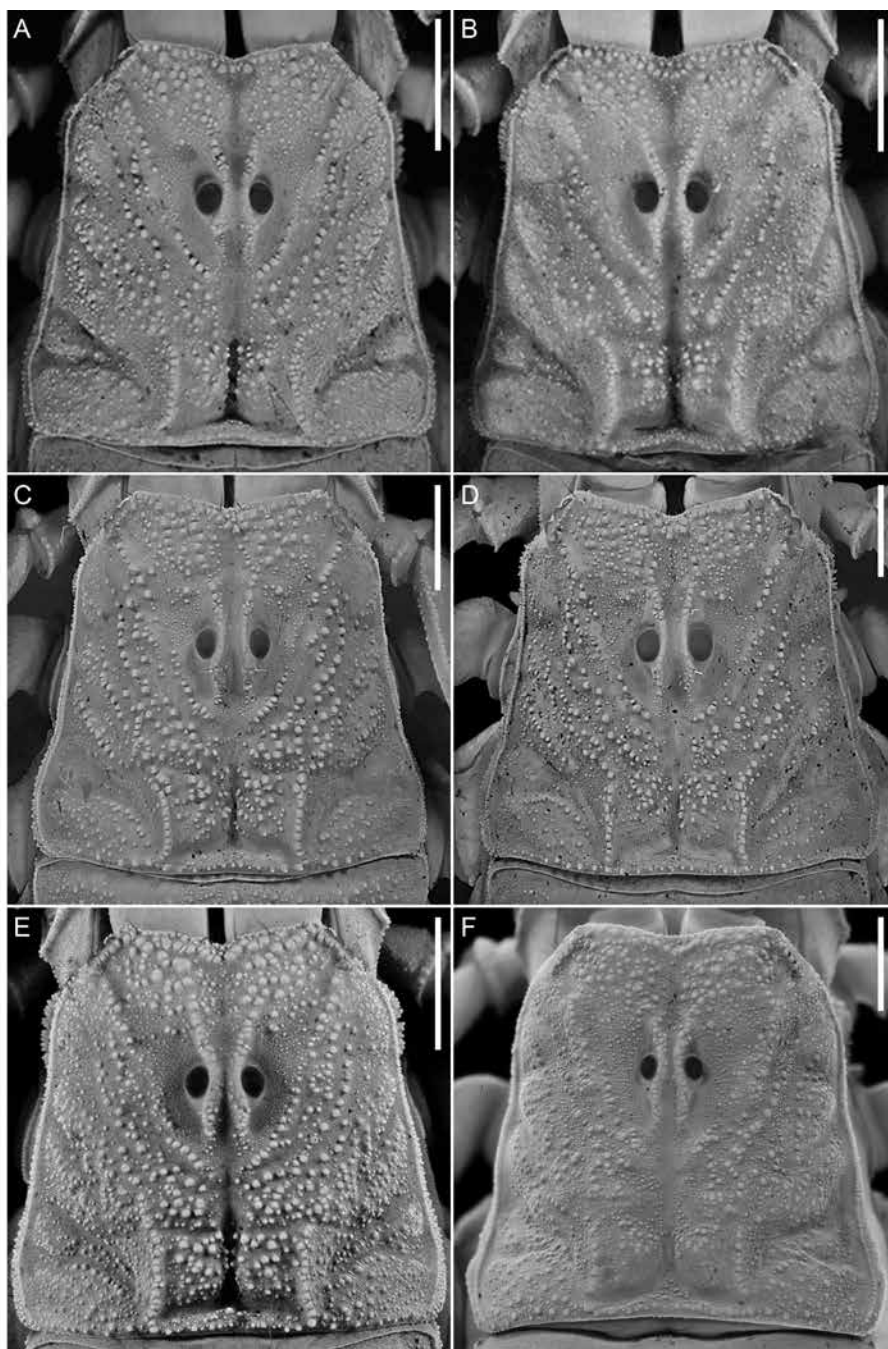


FIG. 14. Rhopalurusinae Bücherl, 1971, carapace, dorsal aspect. **A.** *Heteroctenus abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *Heteroctenus bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). **C.** *Heteroctenus garridoi* (Armas, 1974), comb. nov., ♂ (AMNH). **D.** *Heteroctenus junceus* (Herbst, 1800), comb. nov., ♀ (AMNH). **E.** *Heteroctenus princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). **F.** *Troglophalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). Scale bars = 2 mm.

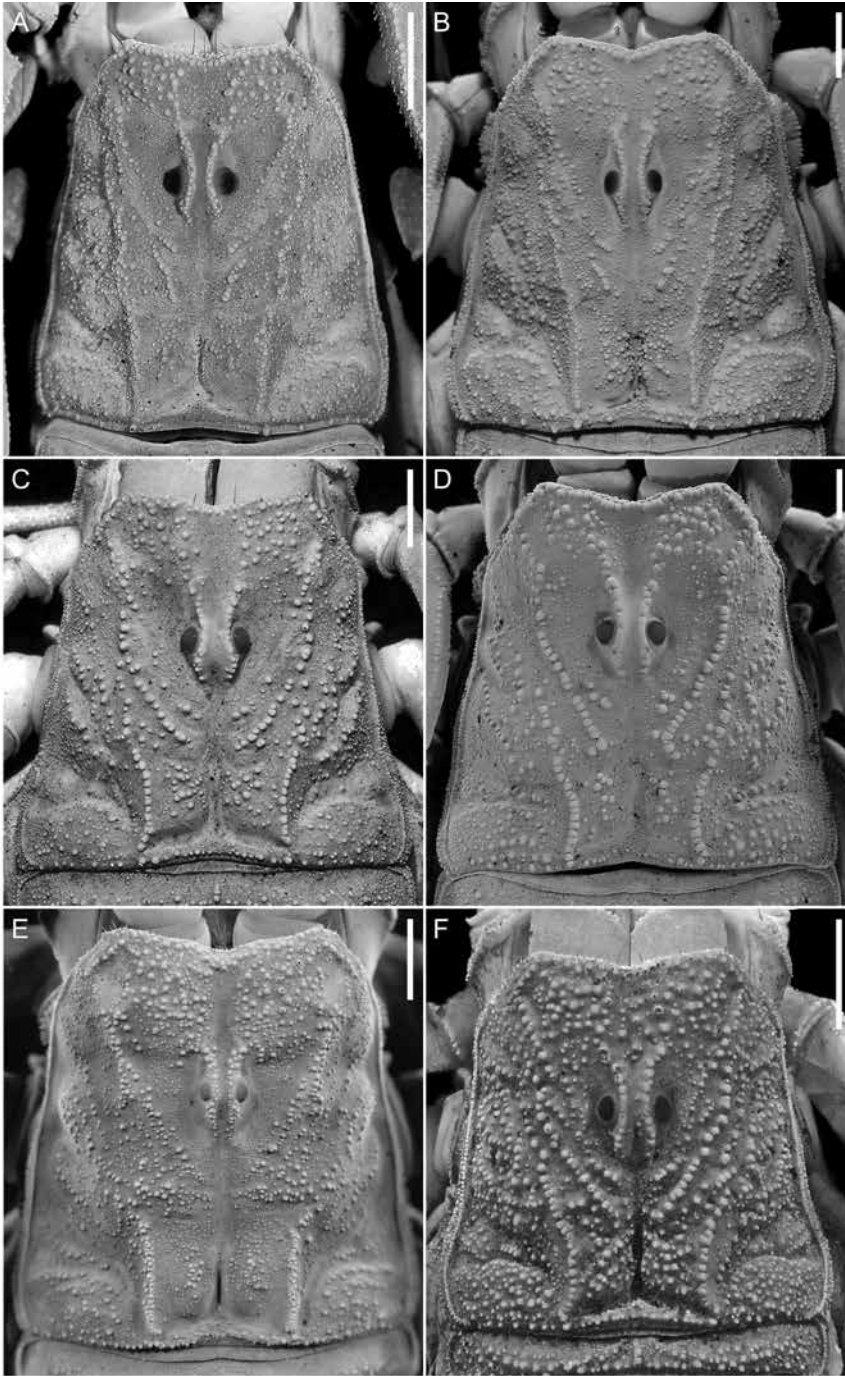


FIG. 15. Rhopalurusinae Bücherl, 1971, carapace, dorsal aspect. **A.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **B.** *Ischnotelson peruassu*, sp. nov., paratype ♂ (MZSP). **C.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). **D.** *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov., ♀ (MZSP). **E.** *Troglorhopalurus translucidus* Lourenço et al., 2004, ♀ (MZSP). **F.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♂ (AMNH). Scale bars = 2 mm.

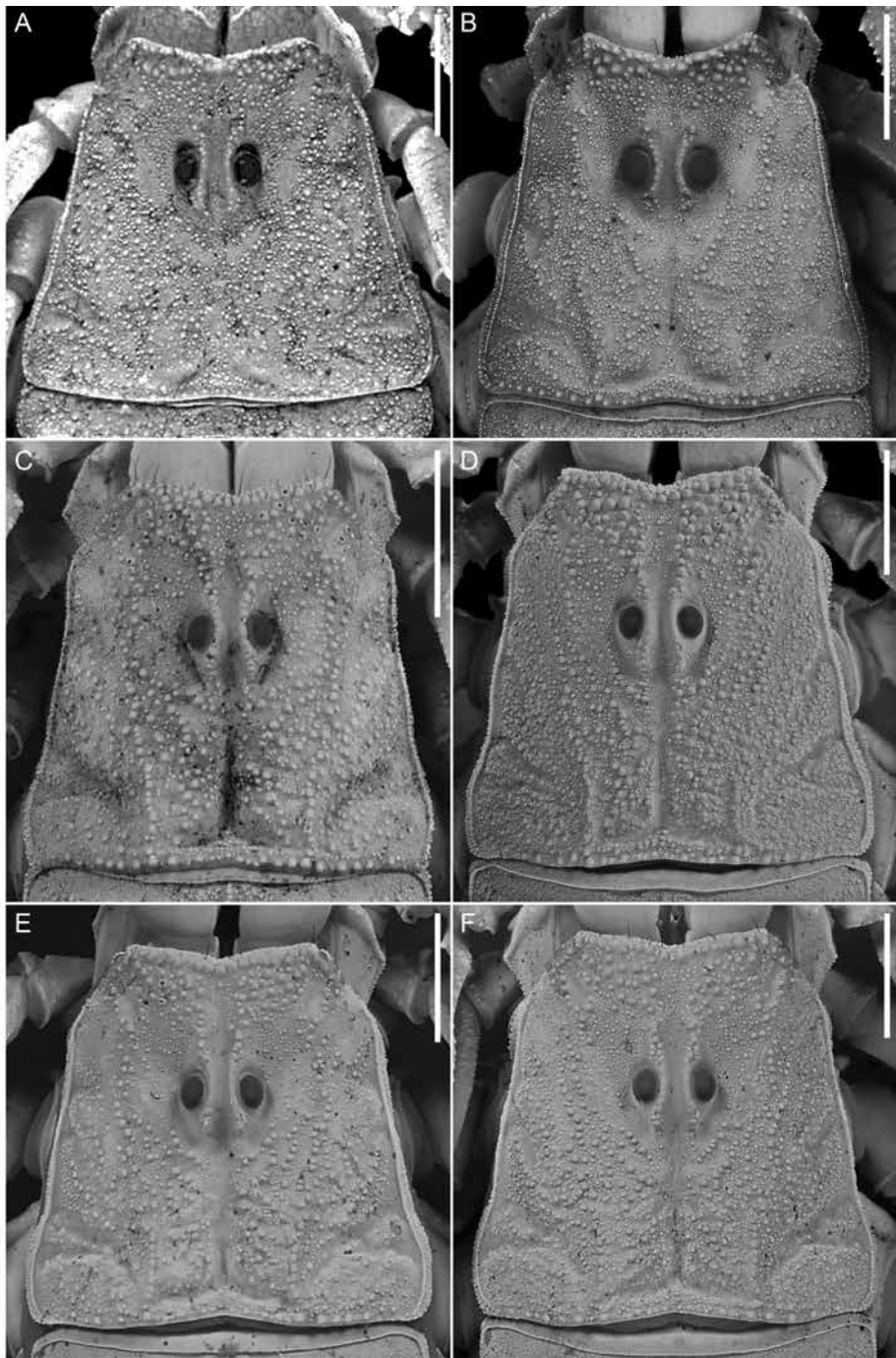


FIG. 16. *Rhopalurusinae* Bücherl, 1971, carapace, dorsal aspect. A. *Physoctonus debilis* (C.L. Koch, 1840), ♀ (MZSP). B. *Physoctonus striatus*, sp. nov., paratype ♂ (MZSP). C. *Rhopalurus caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). D. *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH), Laguna Canaima, Venezuela. E. *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH), Guatire, Venezuela. F. *Rhopalurus ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 1 mm (A, B), 2 mm (C-F).

**ECOLOGY:** *Heteroctenus bonettii* is restricted to deciduous spiny forest and thorn scrub with cacti on karst limestone (Prendini et al., 2009). Scorpions were commonly found sheltering between slabs of rock (though never under bark or wood) by day, and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). *Heteroctenus bonettii* was sympatric with the buthids *Centruroides alayoni*, *C. jaragua*, *C. lucidus*, *Microtityus iviei* Armas, 1999, and *Microtityus lantiguai* Armas and Marcano Fond-eur, 1992, and the diplocentrid *Heteronebo oviedo* (Armas, 1999).

**MATERIAL EXAMINED: 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 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, 2 ♀ (AMCC [LP 2471, 3265]); unmarked track into park between Manuel Goya and Oviedo, 17°48'41.5"N 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 with blacklights, 15 ♂, 8 ♀, 1 subad., 1 juv. (AMNH), 1 juv. [pedipalps] (AMCC [LP 3266]).

***Heteroctenus garridoi* (Armas, 1974),  
comb. nov.**

Figures 3B, 14C, 25C, 26C, 28C, 29C, 30C, 33

*Rhopalurus garridoi* Armas, 1974b: 2–5, figs. 1B, 2B, 3B, 4, table 1; 1982a: 4; 1982b: 5, table 2; Lourenço, 1982a: 114, 115, 135; Armas, 1984: 8; Lourenço, 1984a: 169, 170; 1986b: 165, fig. 7; Armas, 1988: 70, 93; Lourenço,

1992: 55; Rudloff, 1994: 9; Kovařík, 1998: 118; Fet and Lowe, 2000: 219; Teruel, 2006: 43, 44, 46, 52–53, figs. 1–4, 10, 12A, table 1; Teruel and Armas, 2006: 179; 2012b: 209, 214, 215, figs. 6, 7; Prendini et al., 2009: 222; Teruel and Kovařík, 2012: 117–121, figs. 253–266, 556–559, 636.

*Rhopalurus princeps*: Lourenço, 1982a: 114, 136, figs. 2–9, 24, 78, table 1 (part).

*Rhopalurus garridoi*: Armas, 1988: 97 (*lapsus calami*).

**TYPE MATERIAL:** *Rhopalurus garridoi*: Holotype ♀ (IES, IZACC-3.616), 1 ♂, 1 ♀, 5 subad. paratypes (IES), **CUBA:** *Guantánamo Prov.*: Baitiquiri, Guantánamo, xii.1971, O.H. Garrido.

**DIAGNOSIS:** *Heteroctenus garridoi* is most closely related to *H. gibarae*. The two species resemble one another, and differ from the third Cuban species, *H. junceus*, in their smaller size and paler coloration. *Heteroctenus garridoi* and *H. gibarae* vary from 56–86 mm in total length, whereas *H. junceus* varies from 64–110 mm. *Heteroctenus garridoi* and *H. gibarae* are more uniformly yellow to yellowish brown in color, with less contrast between the appendages and the carapace, mesosoma, and metasoma, whereas *H. junceus* varies from light brown to dark reddish brown, with the entire carapace or only the interocular surface infusate, and the carapace, mesosoma, and metasoma (especially, segments IV and V) noticeably darker than the pedipalps and legs. Additionally, the chela is less markedly sexually dimorphic in *H. garridoi* and *H. gibarae*, because the curvature of the fixed and movable fingers of the adult male is less pronounced, resulting in a much smaller gap between them proximally, when closed (fig. 25C), and the manus of the adult female is relatively more incrassate than in *H. junceus*. The basal expansion of the pectines is also less pronounced in *H. garridoi* and *H. gibarae* than in *H. junceus*. Finally, *H. garridoi* and *H. gibarae* differ from *H. junceus* in the more finely granular intercarinal surfaces of the carapace and the pedipalp chela manus.

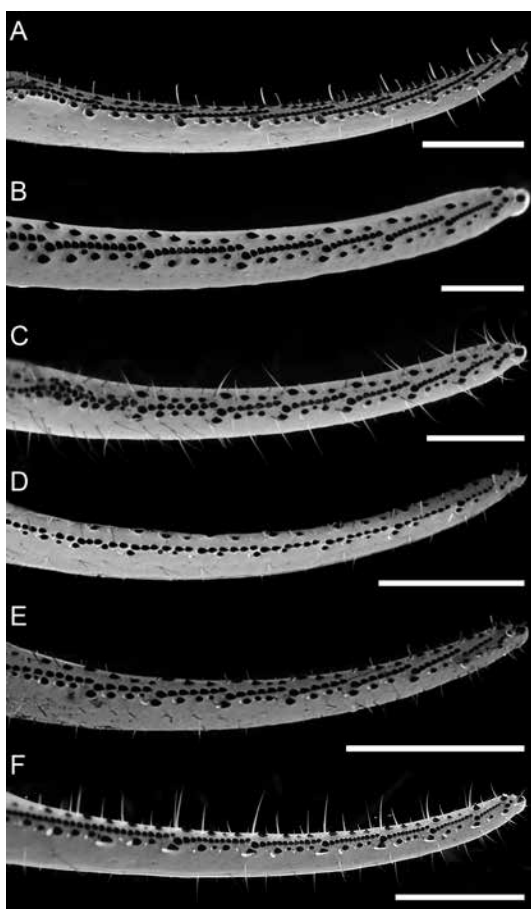


FIG. 17. Rhopalurusinae Bücherl, 1971, pedipalp chela movable finger, dorsal aspect, illustrating dentition (denticle rows). **A.** *Heteroctenus junceus* (Herbst, 1800), comb. nov., ♀ (AMNH). **B.** *Ischnotelson peruassu*, sp. nov., paratype ♀ (MZSP). **C.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♂ (MZSP). **D.** *Physoctonus striatus*, sp. nov., paratype ♂ (MZSP). **E.** *Rhopalurus ochoai*, sp. nov., paratype ♀ (AMNH). **F.** *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). Scale bars = 2 mm.

*Heteroctenus garridoi* appears to differ from *H. gibarae* primarily on the basis of color. *Heteroctenus garridoi* is uniformly yellow whereas *H. gibarae* is uniformly yellowish brown, the carapace bordered by two narrow lines forming a V-shape around the interocular surface, metasomal segments IV and V darkening to blackish brown posteriorly, and the telson reddish. As in *H. junceus*, the pedipalp chela manus of *H. garridoi* is similar in color or only slightly darker than the pedipalp femur and patella, whereas the manus of *H. gibarae* is darker than the femur and patella. The ventrolateral and ventrosubmedian carinae of the metasoma are infuscate in *H. garridoi* but immaculate in *H. gibarae*.

**DISTRIBUTION:** *Heteroctenus garridoi* is endemic to Guantánamo Province in southeastern Cuba (fig. 3B).

**ECOLOGY:** *Heteroctenus garridoi* inhabits semidesert habitats below 150 m in the coastal and subcoastal regions of eastern Cuba (Teruel, 2006). The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). The species is typically found under stones, tree trunks, and inside *Yucca* spp. or cactus (*Ritterocereus* spp.) plants (Teruel, 2006). *Heteroctenus garridoi* has been collected in sympatry with the buthids *Centruroides robertoi*, *H. junceus*, *Microtityus guantanamo* Armas, 1984, and the diplocentrid *Cazierius gundlachii* (Karsch 1880) (see Teruel, 2006).

**MATERIAL EXAMINED:** **CUBA:** *Guantánamo Prov.:* Guantánamo, x.2009, ex G. Molisani, 1 ♀ (AMCC [LP 10225]). *U.S. Guantánamo Bay Naval Base:* Guantánamo 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 gibarae* (Teruel, 2006),  
comb. nov.**

Figure 3B

*Rhopalurus gibarae* Teruel, 2006: 46–49, 52, 53, figs. 5–7, 10, table 2; Teruel and Armas,

2006: 179; 2012b: 209, 215, figs. 6, 7; Prendini et al., 2009: 222; Teruel and Kovařík, 2012: 122, figs. 560–563.

*Rhopalurus granulimanus* Teruel, 2006: 49, 50, 52, 53, figs. 8–10, table 2; Teruel and Armas, 2006: 179; 2012b: 209, 215, figs. 6, 7; Prendini et al., 2009: 222; Teruel and Kovařík, 2012: 122, 123, figs. 564, 565; syn. nov.

TYPE MATERIAL: **CUBA:** *Holguín Prov.:* *Rhopalurus gibarae*: Holotype ♂ (RTO), Municipio Gibara: Sierra de Gibara, 2 km ESE of Gibara (21°04'58"N 75°57'00"W), 26.i.1993, R. Teruel. Paratypes: same data except 18.viii.1992, R. Teruel and R. Ermus, 5 juv. (RTO), 26.i.1993, R. Teruel, 1 ♀ (RTO), 18.x.2001, D. Díaz, 1 ♂, 1 ♀ (RTO). *Rhopalurus granulimanus*: Holotype ♂ (RTO), Municipio Rafael Freyre: Bahía Naranjo, 1 km NE of Estero Ciego (21°05'37"N 75°56'00"W), 25.i.1995, R. Teruel and N. Navarro.

DIAGNOSIS: *Heteroctenus gibarae* is most closely related to *H. garridoi*. The two species resemble one another, and differ from the third Cuban species, *H. junceus*, in their smaller size and paler coloration. *Heteroctenus garridoi* and *H. gibarae* vary from 56–86 mm in total length, whereas *H. junceus* varies from 64–110 mm. *Heteroctenus garridoi* and *H. gibarae* are more uniformly yellow to yellowish brown in color, with less contrast between the appendages and the carapace, mesosoma, and metasoma, whereas *H. junceus* varies from light brown to dark reddish brown, with the entire carapace or only the interocular surface infusate, and the carapace, mesosoma, and metasoma (especially segments IV and V) noticeably darker than the pedipalps and legs. Additionally, the chela is less markedly sexually dimorphic in *H. garridoi* and *H. gibarae*, because the curvature of the fixed and movable fingers of the adult male is less pronounced, resulting in a much smaller gap between them proximally, when closed, and the manus of the adult female is relatively more incrassate than in *H. junceus*. The basal expansion of the pectines is also less pronounced in *H. garridoi* and *H. gibarae* than in *H. junceus*. Finally, *H.*

*garridoi* and *H. gibarae* differ from *H. junceus* in the more finely granular intercarinal surfaces of the carapace and pedipalp chela manus.

*Heteroctenus gibarae* appears to differ from *H. garridoi* primarily on the basis of color. *Heteroctenus gibarae* is uniformly yellowish brown, the carapace bordered by two narrow lines forming a V-shape around the interocular surface, metasomal segments IV and V darkening to blackish brown posteriorly, and the telson reddish, whereas *H. garridoi* is uniformly yellow. The pedipalp chela manus of *H. gibarae* is darker than the pedipalp femur and patella whereas the manus of *H. garridoi* is similar in color or only slightly darker than the femur and patella, as in *H. junceus*. The ventrolateral and ventrosulmedian carinae of the metasoma are immaculate in *H. gibarae* but infusate in *H. garridoi*.

DISTRIBUTION: *Heteroctenus gibarae* is endemic to Holguín Province in southeastern Cuba, where it is known from two populations, the type locality in the Sierra de Naranjo, Gibara, and the type locality of *R. granulimanus*, in Bahía Naranjo, Rafael Freyre (fig. 3B). The two localities are fewer than 50 km apart.

ECOLOGY: *Heteroctenus gibarae* inhabits coastal deciduous dry forest and secondary forest below 25 m in elevation. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). The species is primarily found in limestone rock piles covered in leaves and humus. It has been collected in sympatry with the buthids *Alayotityus* spp., *Centruroides arctimanus*, *C. baracoae*, *H. junceus*, and *Microtityus trinitensis* Armas, 1974.

REMARKS: *Heteroctenus gibarae* and *R. granulimanus* are known from five adult specimens collectively, and the type and only known localities are fewer than 50 km apart. Based on the published descriptions and illustrations, there is no convincing evidence that these specimens represent two distinct species. The putative diagnostic differences outlined for the holotype and only known specimen of *R. granulimanus* fall within the range of intraspecific variation for *H. gibarae*, to the extent that this can be assessed

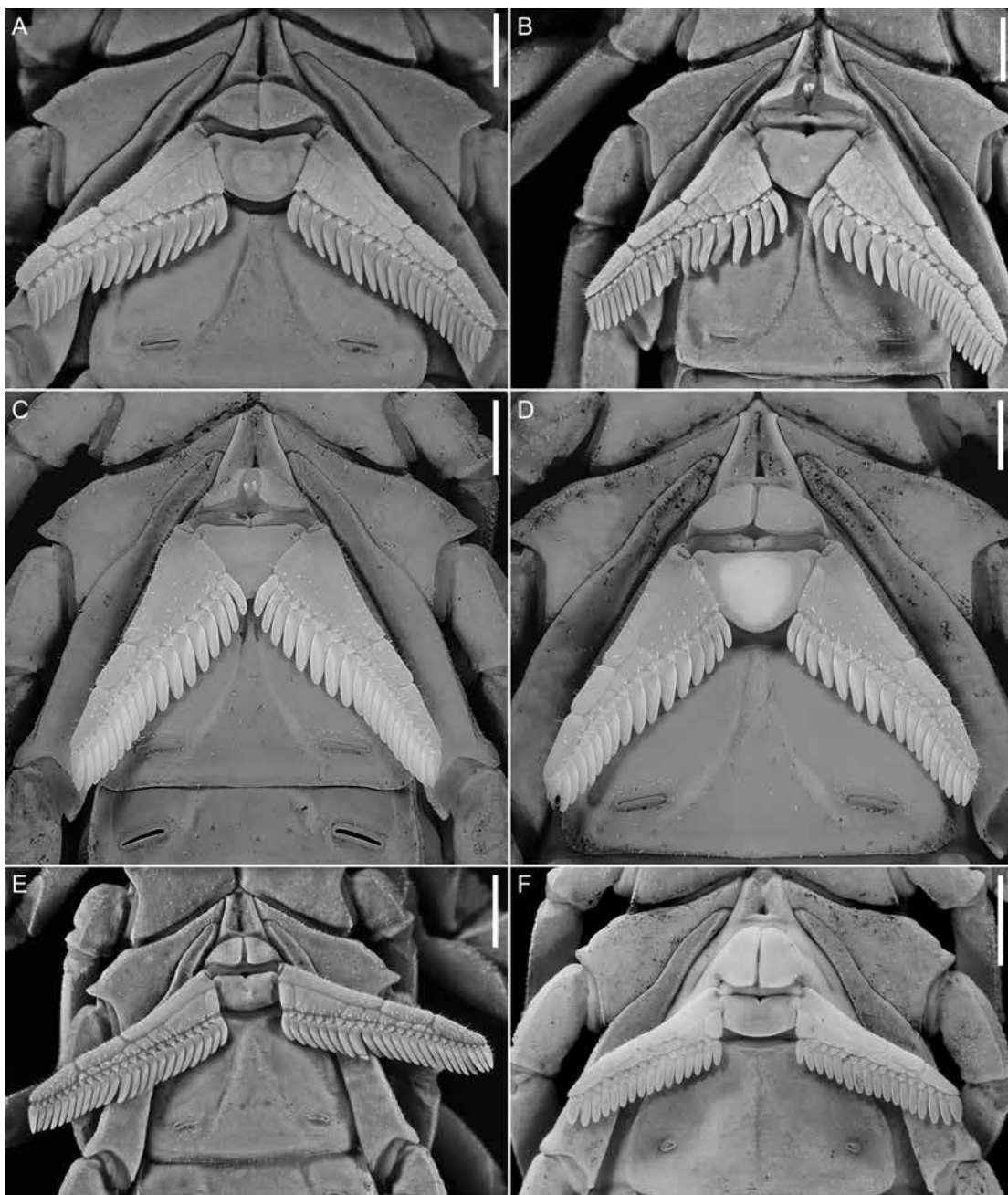


FIG. 18. Rhopalurusinae Bücherl, 1971, sternum, pectines and sternite III, ventral aspect. A. *Heteroctenus abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂ (AMNH). B. *Heteroctenus bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). C. *Heteroctenus junceus* (Herbst, 1800), comb. nov., ♂ (AMNH). D. *Heteroctenus junceus* (Herbst, 1800), ♀ (AMNH). E. *Heteroctenus princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). F. *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). Scale bars = 2 mm.



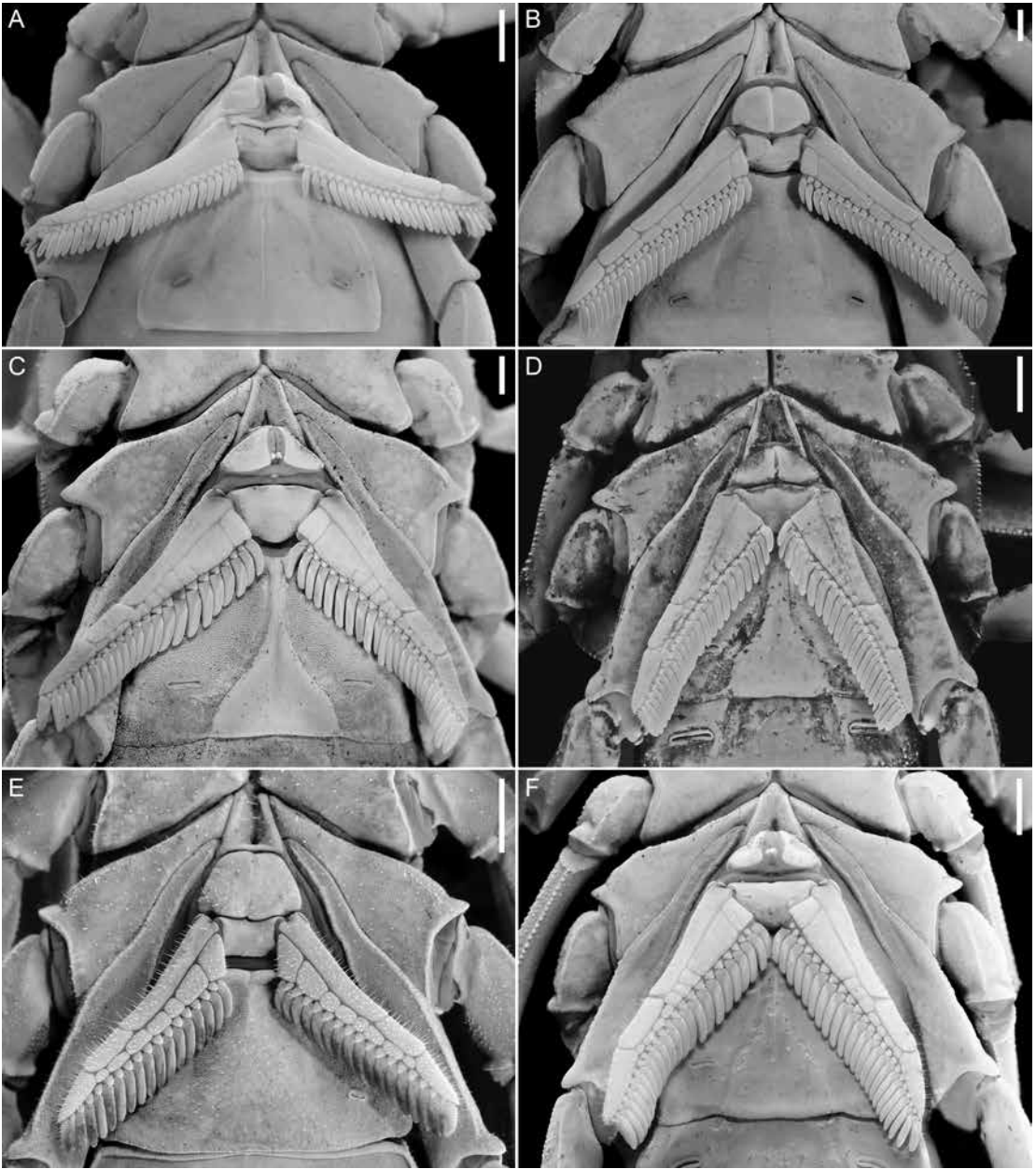


FIG. 19. Rhopalurusinae Bücherl, 1971, sternum, pectines and sternite III, ventral aspect. **A.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♀ (MZSP). **B.** *Ischnotelson peruassu*, sp. nov., paratype ♂ (MZSP). **C.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). **D.** *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). **E.** *Trogloorhopalurus translucidus* Lourenço et al., 2004, ♀ (MZSP). **F.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♂ (MZSP). Scale bars = 2 mm.



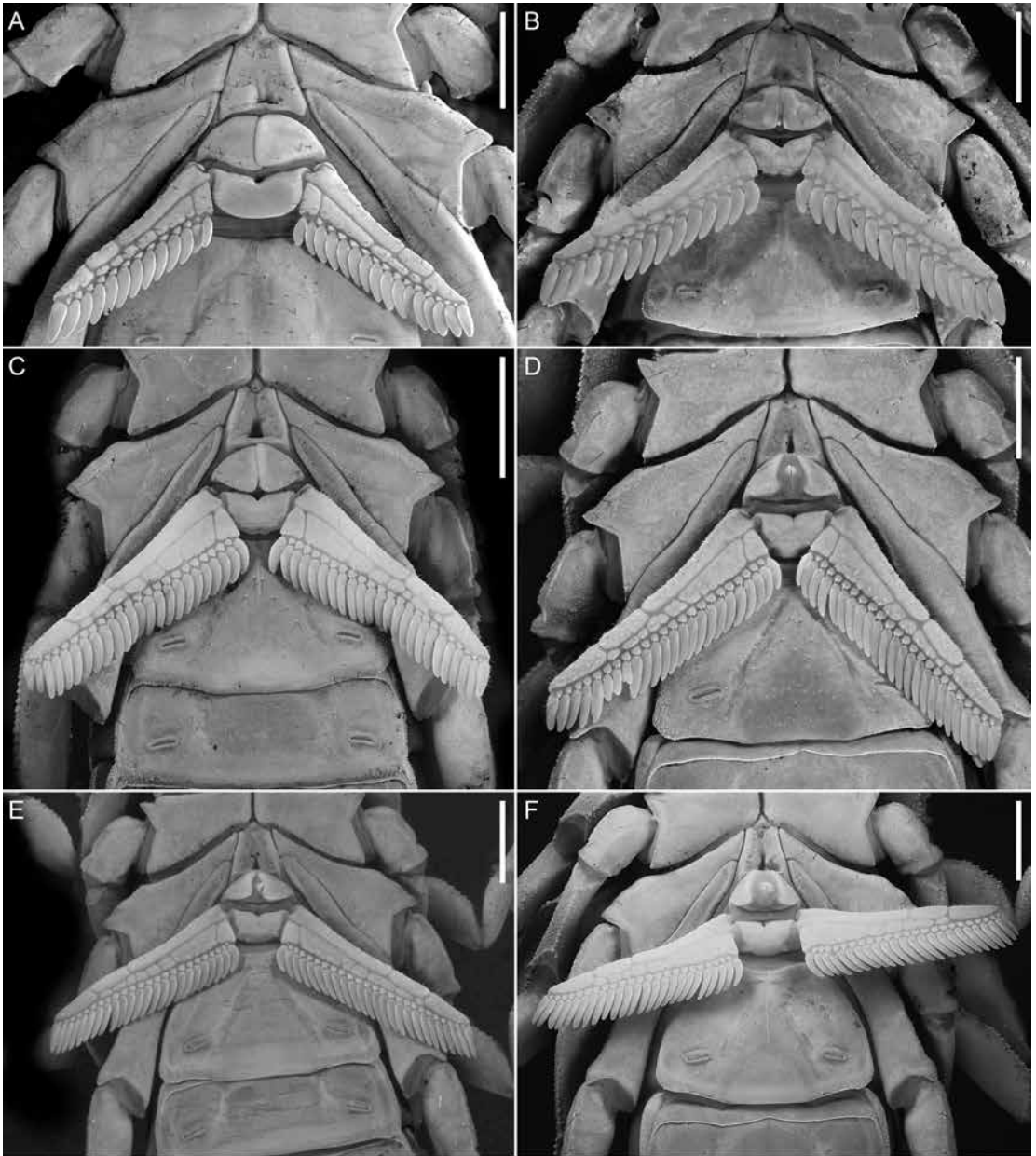


FIG. 20. Rhopalurusinae Bücherl, 1971, sternum, pectines and sternite III, ventral aspect. **A.** *Physoctonus debilis* (C.L. Koch, 1840), ♂ (MZSP). **B.** *Physoctonus striatus*, sp. nov., paratype ♂ (MZSP). **C.** *Rhopalurus caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **D.** *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH), Laguna Canaima, Venezuela. **E.** *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH), Puerto Colombia, Venezuela. **F.** *Rhopalurus ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 2 mm.

given the small sample size ( $n = 4$ ) for the latter. For example, the difference in total length for the males of *H. gibarae* (65–66 mm) and *R. granulimanus* (56 mm), cited among the putatively diagnostic characters, is similar to the size range of males in other Cuban species (*H. garridoi*, 56–69 mm; *H. junceus*, 54–97 mm); as is the range for the length to width ratio of the pedipalp chela (*H. gibarae*, 4.2–4.39; *R. granulimanus*, 4.96; *H. junceus*, 3.5–4.7); and the male pectinal tooth count (*H. gibarae*, 20–21; *R. granulimanus*, 22; *H. garridoi*, 21–24, *H. junceus*, 17–23).

Based on the absence of convincing morphological differences, the limited sample size, and the geographical proximity of the type localities, we consider *R. granulimanus* conspecific with *H. gibarae* and synonymize it accordingly: *Rhopalurus granulimanus* Teruel, 2006 = *Heteroctenus gibarae* (Teruel, 2006), syn. nov. The validity of *H. gibarae*, as distinct from *H. garridoi*, will also need to be reassessed when material becomes available for study as the putative differences between them appear rather minor.

*Heteroctenus junceus* (Herbst, 1800)

Figures 2B, 3A, 11A, 14D, 17A, 18C, D, 21B, 22B, 23H–K, 27A, C, 28D, 29D, 30D, 34

*Scorpio junceus* Herbst, 1800: 65–67, pl. III, fig. 2; Latreille, 1804: 126–127.

*Scorpio (Atreus) hemprichii* Gervais, 1844a: 218, fig. 18 (synonymized by Pocock, 1893: 392); Gervais, 1843: 130 (*nomen nudum*); 1844b: 39, 54; Lucas, 1851: 70, pl. V, fig. 5–5c; Gervais, 1859: 41, pl. I, fig. 2, 2a–b.

*Rhopalurus hemprichii*: Karsch, 1879b: 119.

*Centrurus hemprichii*: Kraepelin, 1891: 123, 135–137, figs. 30, 33; Thorell, 1893: 372, 373.

*Centrurus junceus*: Kraepelin, 1891: 135, figs. 30, 33; Thorell, 1893: 372; Kraepelin, 1895: 95; 1899: 89, 94; 1901: 270; 1908: 187, 190, 193, 194.

*Heteroctenus junceus*: Pocock, 1893: 392.

*Rhopalurus junceus*: Pocock, 1902a: 37, 38, pl.

VIII, fig. 5, 5a, pl. IX, fig. 1, 1a; Banks, 1909:

172; Herrera, 1917: 271; Lampe, 1917: 197; Franganillo, 1930a: 95; 1930b: 119; Mello-Leitão, 1932: 14; Meise, 1934: 29; Franganillo, 1935: 21; 1936: 164, figs. 86, 87; Prado, 1940: 26–28; Roewer, 1943: 219; Esquivel de Verde, 1968: 67; Esquivel de Verde and Machado-Allison, 1969: 33; Bücherl, 1971: 327; Armas, 1974b: 2, figs. 1A, 2A, 3A; 1977: 3; Stahnke and Calos, 1977: 119; Lourenço, 1979: 215, fig. 8; Armas, 1982a: 4; 1982b: 5, table 2; Lourenço, 1982a: 110, 114, 136, figs. 10, 11, 14–23, 78, table 1; Armas, 1983: 3, fig. 1; Lourenço, 1986a: 133, fig. 17; 1986b: 165, fig. 7; Armas, 1988: 68–70, 93, figs. 27, 36; Lourenço, 1992: 55; Rudloff, 1994: 9; Kovařík, 1997: 181; Lourenço, 1997a: 590; Kovařík, 1998: 118; Fet and Lowe, 2000: 219, 220; Teruel, 2003: 149, 150, figs. 1, 2; 2006: 51–53; Teruel and Armas, 2006: 179; 2012a: 153–167, figs. 1–16, tables 1–7; 2012b: 215, fig. 7; Kamenz and Prendini, 2008: 9, table 2, pl. 41; Prendini et al., 2009: 222, 223; Teruel and Kovařík, 2012: 123–140, figs. 29, 40, 41, 48, 265, 267–302, 534–545; Rodríguez-Cabrera and Teruel, 2014: 121; 2015: 85, 86, fig. 1.

*Rhopalurus junceus ravidus* Franganillo, 1930a: 95, figs. 19–21 (synonymized by Lourenço, 1982a: 114); 1935: 21; 1936: 164; Moreno, 1939a: 65–66; Jaume, 1954: 1091.

*Centruroides (Rhopalurus) junceus*: Werner, 1934: 274, fig. 33b.

*Rhopalurus junceus junceus*: Moreno, 1939a: 65; 1939b: 124–128, pl. XIX–XXI; Jaume, 1954: 1090; Armas, 1973: 7.

*Rhopalurus junceus cadenasi* Moreno, 1939a: 66–67, pl. 6, fig. 3 (synonymized by Lourenço, 1982a: 114); 1940b: 129–130, pl. XXII; Jaume, 1954: 1090.

*Rhopalurus melloleitaoi* Teruel and Armas, 2006: 175–179, figs. 1–4, tables 1, 2; Armas, 1974b: 6; 1981a: 52 (part); 1982a: 4; Teruel and Montano, 2005: 221–223, 225–227, figs. 10, 14, tables 2, 4; Prendini et al., 2009: 222;

Teruel and Armas, 2012b: 215, figs. 6, 7;  
 Teruel and Kovařík, 2012: 141, figs. 303–  
 305, 552–555; syn. nov.

*Rhopalurus aridicola* Teruel and Armas, 2012b:  
 210, 212, 214, 215, figs. 1–6, tables 1–3;  
 Armas, 1974b: 6; 1982a: 4; Prendini et al.,  
 2009: 222; Teruel and Kovařík, 2012: 116,  
 figs. 546–551; syn. nov.

TYPE MATERIAL: **CUBA:** *Scorpio (Atreus) hemprichii*, holotype [sex?] (MNHN). *Scorpio junceus*: Holotype [lost], “Brazil” [dubious]; ♂ neotype, *Villa Clara Prov.*: Municipio Placetas: Loma del Vigía. *Rhopalurus j. ravidus*: Holotype [sex?] (IZACC) [lost], *Pinar del Río Prov.*: Sierra del Cuzco, Pinar del Río. *Rhopalurus j. cadenasi*: subad. ♀ holotype (IZACC), *Havana Prov.*: Loma de la Universidad, La Habana. *Rhopalurus meloleitai*: *Granma Prov.*: Municipio Niquero: Holotype ♂, paratype ♀ (RTO), El Guafe (19°57'18"N 6°45'27"W), 2 km N of Cabo Cruz, 50 m, 19. iv.1996; N. Navarro, A. Fernández, and L.M. Díaz. Paratypes: same data except 8–12.vii.2000, R. Teruel, L. Montano, Y. Cala, and R. Escalona, 1 ♀, 1 juv. (IES), 1 juv. (BIOECO), 1 juv. (RTO), 27. vi.2001, L. Montano and R. Escalona, 1 juv. (RTO), 4.iv.2002, L. Montano and R. Escalona, 1 juv. (RTO), 23.i.2003, L. and M. Montano, 1 juv. (RTO); Bosque Castillo (19°54'14"N 77°31'15"W), Alegría de Pío, 270 m, iii.2002, Jacinto, 1 juv. (RTO); Los Muertos (19°54'05"N 77°30'33"W), Alegría de Pío, 280 m, 20.vi.2002, L. Montano, R. Escalona and Y. Cala, 2 juv. (RTO); Sendero Morlotte-Fustete (19°52'48"N 77°33'08"W), 5 km SW of Alegría de Pío, 150 m, 21.vi.2002, Y. Cala and Jacinto, 2 juv. (RTO); Ensenada del Real (19°51'14"N 77°35'40"W), 5 m, 19.iv.1996, N. Navarro, A. Fernández, and L. Díaz, 1 juv. (RTO), iii.2002, Jacinto, 1 ♂, 1 ♀, 1 juv. (RTO). *Rhopalurus aridicola*: *Guantánamo Prov.*: Holotype ♂ (RTO), Municipio Maisí: Punta de Maisí (20°14'42"N 74°08'38"W), 18–19.iv.1998, 5 m, R. Teruel, A. Sánchez, N. Navarro, and A. Fong. Paratypes: Municipio Baracoa: Dolina de la Cueva de La Majana (20°20'14"N 74°27'22"W), 50 m, 10.xi.2007, R. Teruel, 1 juv. (BIOECO). Municipio

Maisí: Sabana, Santa Rosa (20°17'35"N 74°15'45"W), 14.iv.1998, R. Teruel, 1 ♂ (RTO); Punta de Maisí (20°14'42"N 74°08'38"W), 20.iv.1969, O. Tapia, 1 ♀ (RTO), 6.x.1973, L.F. de Armas and L.R. Hernández, 2 ♂, 2 ♀, 1 juv. (IES), viii.1979, L.F. de Armas, 1 ♂ (IES), 18–19.iv.1998, R. Teruel, A. Sánchez, N. Navarro, and A. Fong, 3 ♂, 8 ♀, 1 ♀ with 15 1st instars, 4 juv. (RTO), 6–8. viii.1999, A. Fong, A. Sánchez, and D. Maceira, 1 ♀ with 41 1st instars (BIOECO Sc-104), 6 juv. (BIOECO Sc-105), 8.ii.2004, A. Sánchez, 2 juv. (BIOECO); Punta de Maisí, Cueva El Molino, 31.i.2006, D. de la Nuez, 1 ♀ (IES); Bahía de Ovando, Punta Negra (20°05'39"N 74°14'46"W), 8.viii.1998, A. Sánchez, D. Maceira, and A. Fong, 1 juv. (BIOECO Sc-103).

DIAGNOSIS: *Heteroctenus junceus* differs from the other two species of *Heteroctenus* occurring on Cuba, *H. garridoi* and *H. gibarae*, primarily in its larger size and typically darker coloration. *Heteroctenus junceus* varies from 54–107 mm in total length, whereas *H. garridoi* and *H. gibarae* vary from 56–69 mm. *Heteroctenus junceus* varies from yellow to dark reddish brown, typically the interocular surface is infuscate, and the metasomal segments IV and V are noticeably darker than segments I–III, whereas *H. garridoi* and *H. gibarae* are more uniformly yellow to yellowish brown in color, with less contrast between the metasomal segments. Additionally, in *H. junceus*, there is a ventral infuscate stripe on metasomal segments I–III which is not the case in *H. garridoi* and *H. gibarae*. As in *H. garridoi*, the pedipalp chela manus of *H. junceus* is similar in color or only slightly darker than the pedipalp femur and patella, unlike *H. gibarae*, in which the manus is darker than the femur and patella. Additionally, the chela of *H. junceus* is more markedly sexually dimorphic, because the curvature of the fixed and movable fingers of the adult male is more pronounced, resulting in a larger gap between them proximally, when closed (fig. 27A), and the manus of the adult female is relatively more slender, than in *H. garridoi* and *H. gibarae*. The basal expan-

sion of the pectines is also more pronounced in *H. junceus* than in *H. garridoi* and *H. gibarae*. Finally, *H. junceus* differs from *H. garridoi* and *H. gibarae* in the more coarsely granular intercarinal surfaces of the carapace and pedipalp chela manus.

**DISTRIBUTION:** *Heteroctenus junceus* is endemic to Cuba, and has been recorded across the island and on several offshore islets in the following provinces: Camagüey, Cienfuegos, Ciego de Avila, Granma, Guantánamo, Havana, Holguín, Isla de la Juventud, Las Tunas, Matanzas, Pinar del Río, Santiago de Cuba, Sancti Spíritus, Villa Clara. The known localities range in elevation from 55 to 716 m (fig. 3A). Historical reports from Haiti, Puerto Rico and Venezuela (see, e.g., Fet and Lowe, 2000: 220) are erroneous (Armas, 2001; Prendini et al., 2009).

**ECOLOGY:** *Heteroctenus junceus* inhabits a wide range of habitats across the island, including human-altered environments, savanna, secondary vegetation, wetlands, broadleaf forest, and deciduous dry forest (fig. 2B; Teruel and Armas, 2012a). It has been found in elevations ranging from sea level to 1175 m (Rodríguez-Cabrera and Teruel, 2014). This species is typically found in rock crevices, under stones or logs, and under the bark of trees (Teruel and Armas, 2012a). Its habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). On account of its broad distribution, many Cuban scorpion species have been recorded in sympatry with *H. junceus*.

**REMARKS:** The evidence supporting *R. aridicola* and *R. melloleitaoi*, as distinct from *H. junceus*, is underwhelming. *Rhopalurus aridicola*, described from four localities, overlapping known records of *H. junceus*, appears to be morphologically indistinguishable from the latter except for its dark reddish color and more granular carapace and tergites, characters known to be variable in the widespread *H. junceus*. Teruel and Armas (2012b) offer the additional evidence that the pectinal tooth counts of *R. aridicola* are

greater than those of *H. junceus*, yet the counts provided for the two species (19–25 and 15–23, respectively), are statistically insignificant. Little genetic divergence was evident between topotypes of *R. aridicola* and other samples conspecific with *H. junceus* (Esposito et al., in review). *Rhopalurus melloleitaoi*, described from a single locality in close proximity to many known locality records of *H. junceus*, appears to differ from the latter solely on the basis of coloration, the pedipalp chelae being darker than the patella and femur, which is to be expected because the habitat in which it was collected has a dark, red substrate (L.A.E., personal obs.). Based on the lack of convincing morphological differences between *R. aridicola*, *R. melloleitaoi*, and *H. junceus*, their overlapping distributions and, in the case of *R. aridicola*, the low genetic divergence between topotypes thereof and other samples conspecific with *H. junceus* (see Esposito et al., in review), we propose the following synonyms: *Rhopalurus melloleitaoi* Teruel and Armas, 2006 = *Heteroctenus junceus* (Herbst, 1800), syn. nov.; *Rhopalurus aridicola* Teruel and Armas, 2012 = *Heteroctenus junceus* (Herbst, 1800), syn. nov.

**MATERIAL EXAMINED:** “Antillen?” 1 ♂, 2 ♀ (ZMB 7370). “Portorico” [erroneous], Stahl, 2 ♀, 1 juv. (ZMB 7280). **CUBA:** Gundlach, 1 ♂, 1 ♀ (ZMB 738), 2 ♀ (ZMB 2637), 1 juv. (ZMB 7343); vii.2007, C. Hamilton, 1 juv. (AMCC [LP 7009]). Oriente Prov., 1938, P. Thumb, 4 ♀ (ZMH). *Artemisa* Prov.: near Baños [probably Santiago del 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, 2 ♂ (AMCC [LP 12619, 12620]), 2 subad. ♀ (AMCC [LP 12621, 12622]), 1 juv. ♂ (AMCC [LP 12623]). *Guantánamo* 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

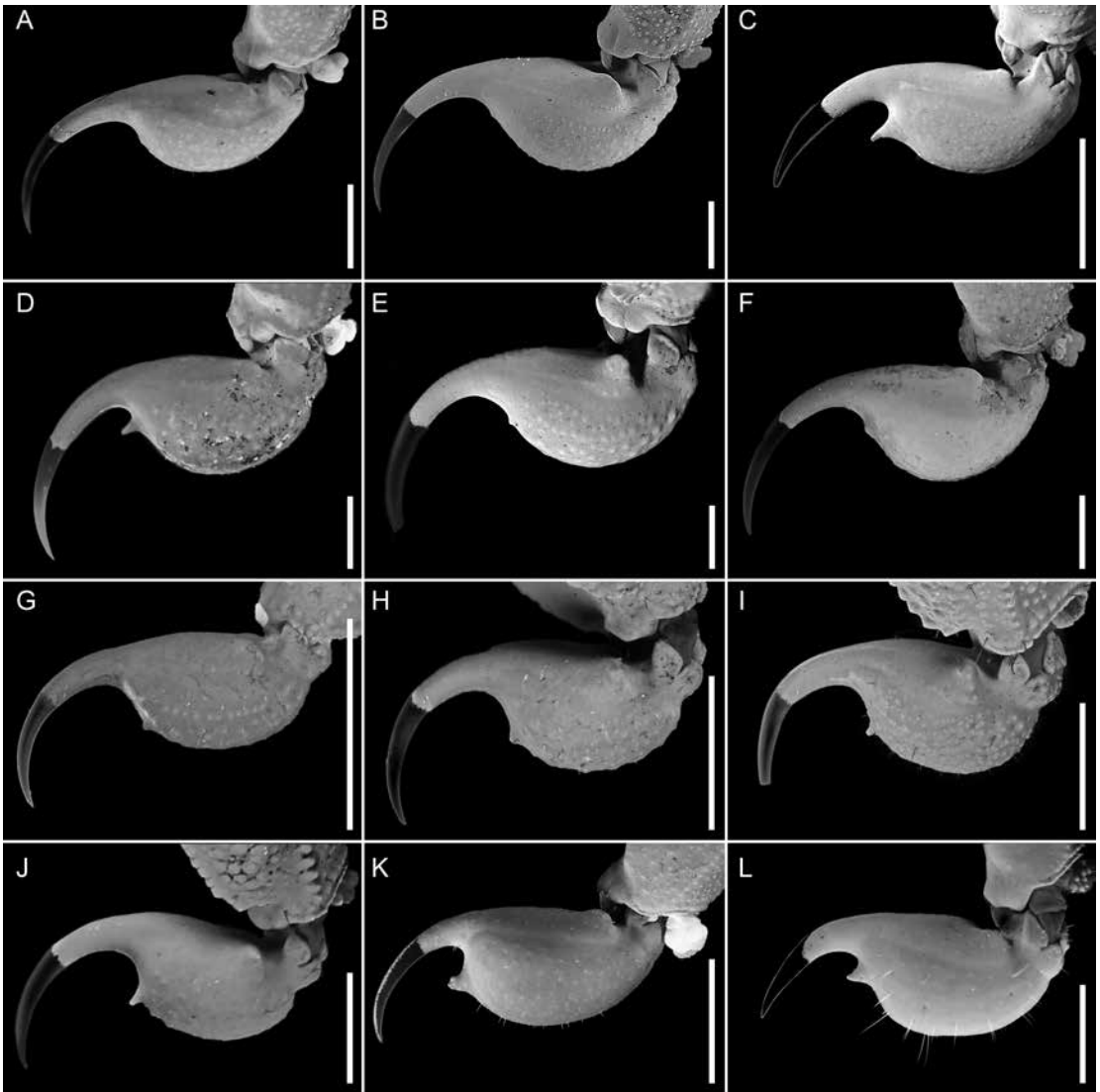


FIG. 21. Rhopalurusinae Bücherl, 1971, telson, lateral aspect. **A.** *Heteroctenus abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *Heteroctenus junceus* (Herbst, 1800), ♂ (AMNH). **C.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **D.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♀ (AMNH). **E.** *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). **F.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♀ (AMNH). **G.** *Physoctonus debilis* (C.L. Koch, 1840), ♀ (AMNH). **H.** *Rhopalurus caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **I.** *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH), Laguna Canaima, Venezuela. **J.** *Rhopalurus ochoai*, sp. nov., holotype ♂ (AMNH). **K.** *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). **L.** *Troglorhopalurus translucidus* Lourenço et al., 2004, ♀ (MZSP). Scale bars = 2 mm.

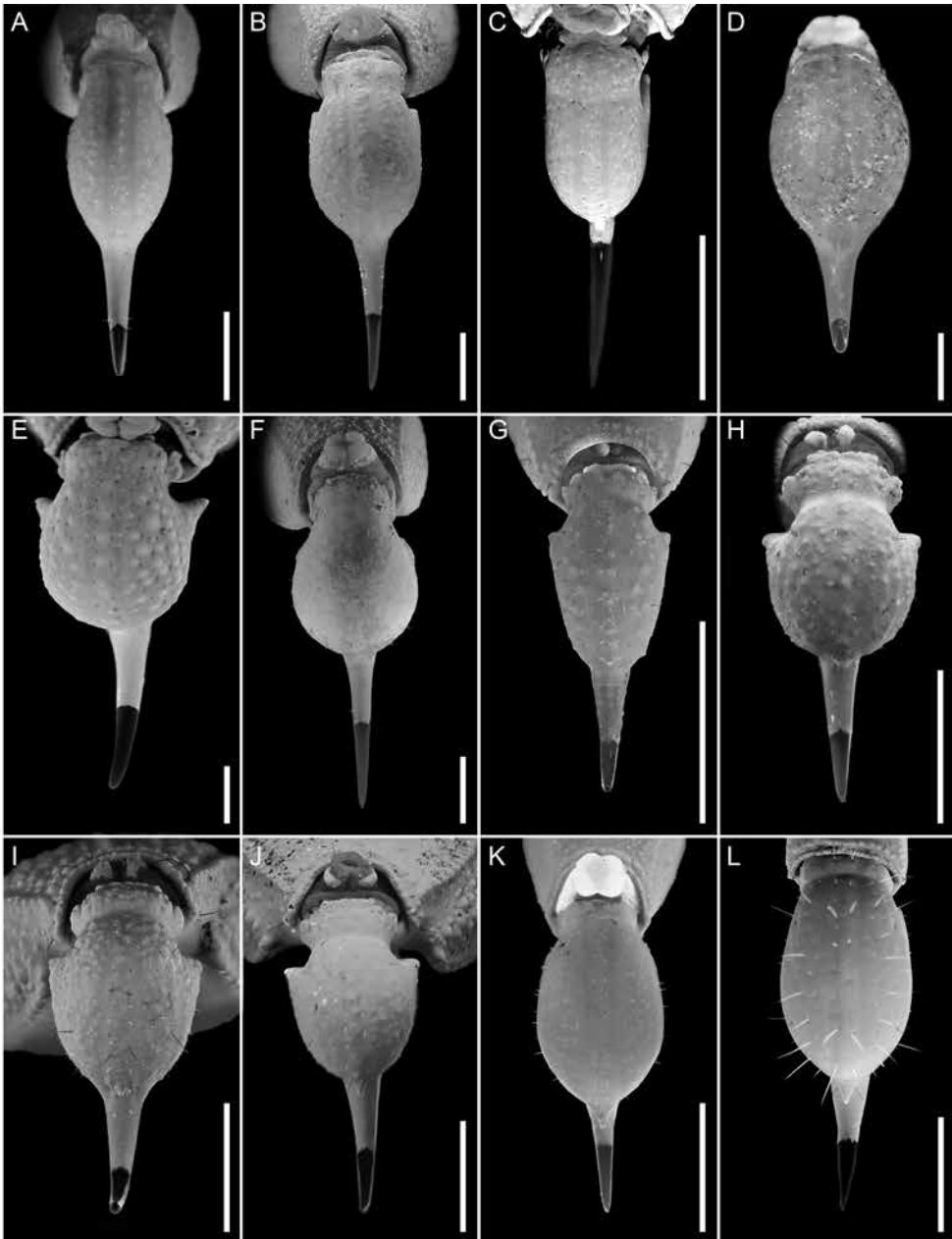


FIG. 22. Rhopalurusinae Bücherl, 1971, telson, ventral aspect. **A.** *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *Heteroctenus junceus* (Herbst, 1800), ♂ (AMNH). **C.** *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **D.** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♀ (AMNH). **E.** *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). **F.** *Jaguajir rochae* (Borelli, 1910), comb. nov., ♀ (AMNH). **G.** *Physoctonus debilis* (C.L. Koch, 1840), ♀ (AMNH). **H.** *Rhopalurus caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **I.** *Rhopalurus laticauda* Thorell, 1876, ♂ (AMNH). **J.** *Rhopalurus ochoai*, sp. nov., holotype ♂ (AMNH). **K.** *Trogloorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (AMNH). **L.** *Trogloorhopalurus translucidus* Lourenço et al., 2004, ♀ (MZSP). Scale bars = 2 mm.

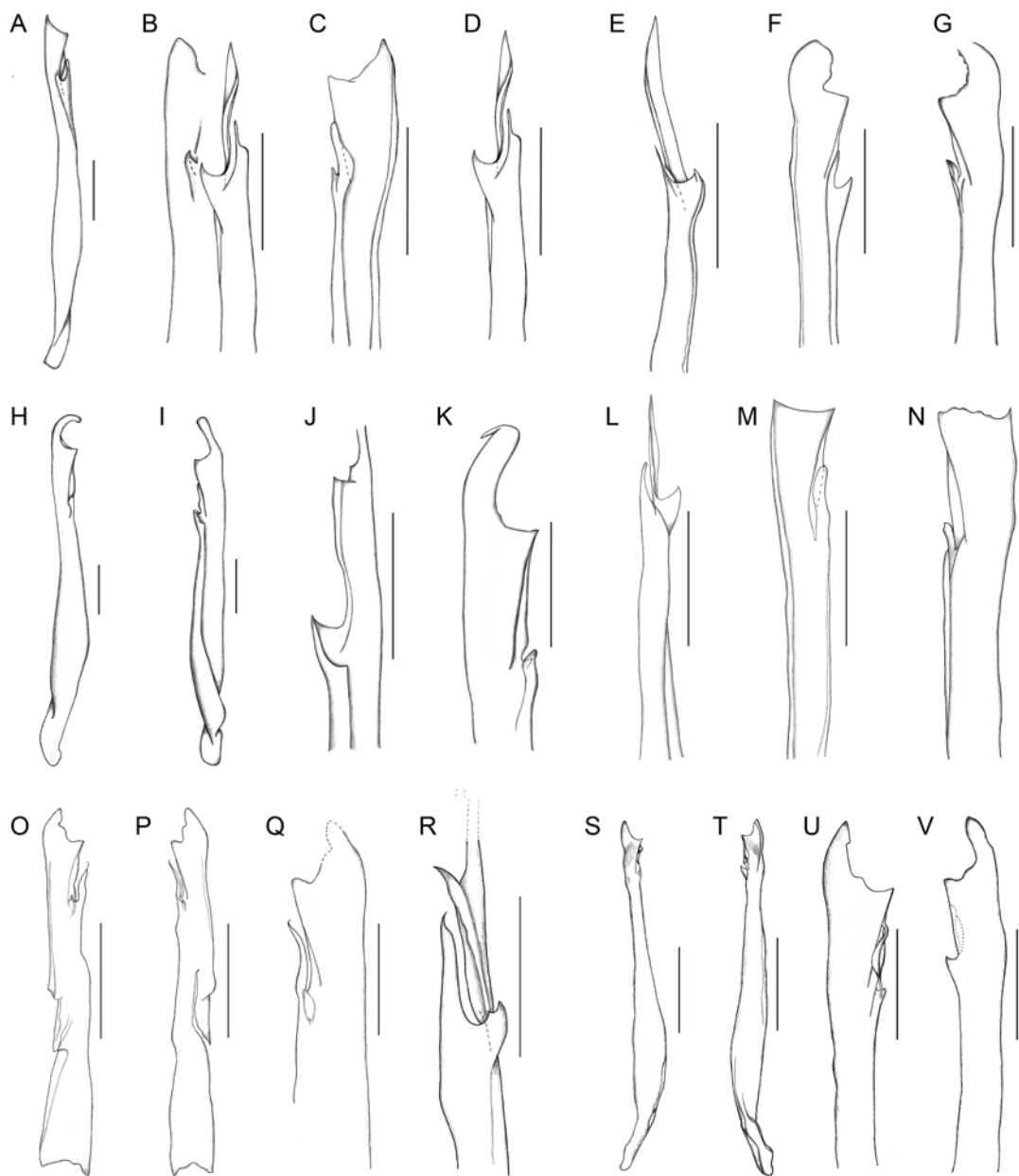


FIG. 23. Rhopalurusinae Bücherl, 1971, hemispermatophores, dorsal aspect (E), dorsal aspect, detail (D, L, R), ectal aspect (A, F, H, O, T), ectal aspect, detail (B, K, M, V), ental aspect (G, I, P, S) and ental aspect, detail (C, J, N, Q, U). A–D. *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov., ♂ (AMNH). E–G. *Heteroctenus bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). H–K. *Heteroctenus junceus* (Herbst, 1800), ♂ (AMNH). L–N. *Heteroctenus princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). O–R. *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). S–V. *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). Scale bars = 1 mm.

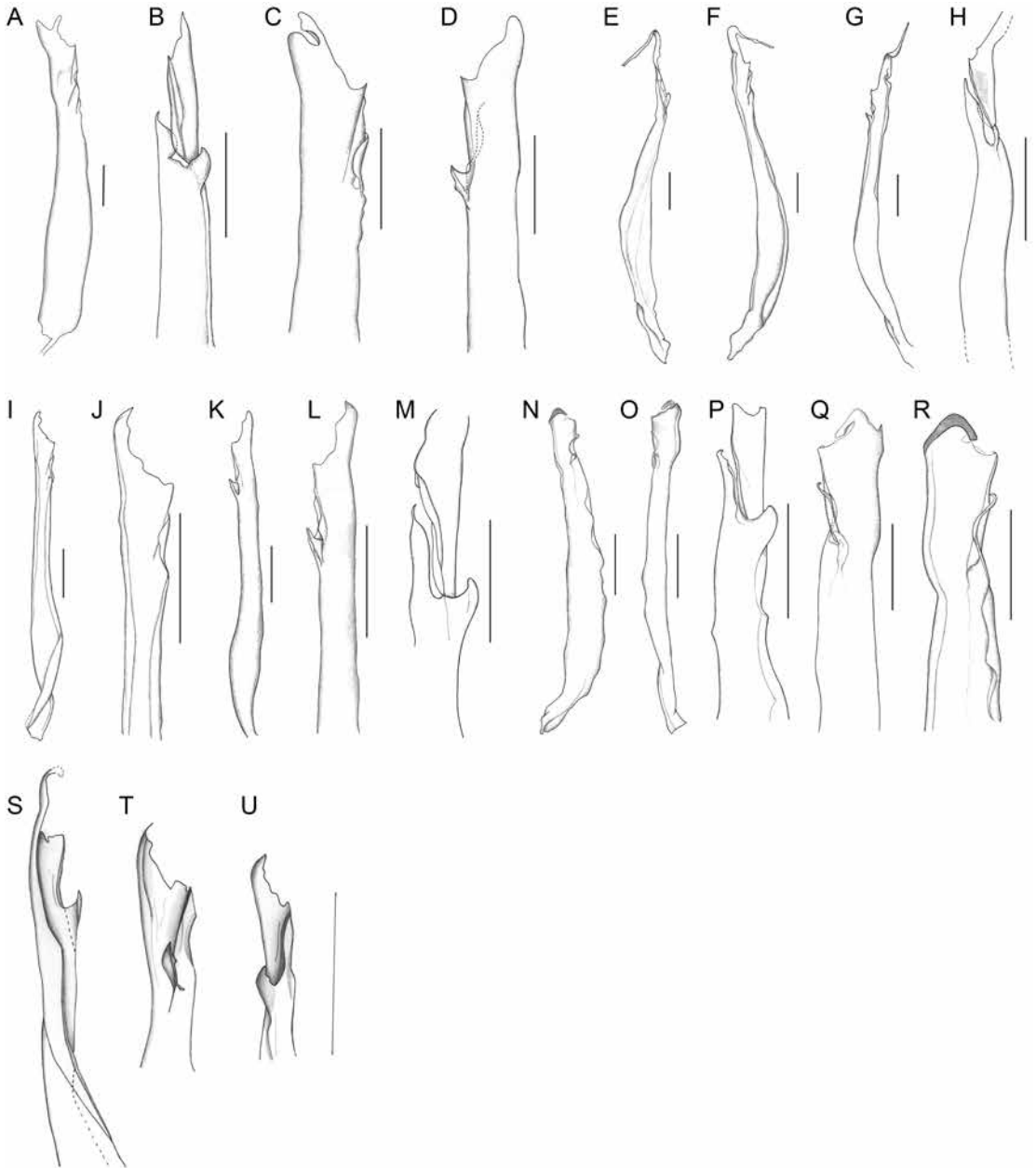


FIG. 24. *Rhopalurusinae* Bücherl, 1971, hemispermatophores, dorsal aspect (E), dorsal aspect, detail (B, H, M, P), ectal aspect (F, I, N, S), ectal aspect, detail (D, J, R, T, U), ental aspect (A, G, K, O), and ental aspect, detail (C, L, Q). A–D. *Jaguajir pintoii* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). E–H. *Jaguajir rochae* (Borelli, 1910), comb. nov., ♂ (MZSP). I–M. *Rhopalurus laticauda* Thorell, 1876, ♂ (MZSP). N–R. *Rhopalurus caribensis* Teruel and Roncallo, 2008, ♂ (MZSP). S–U. *Physoctonus debilis* (C.L. Koch, 1840), ♂ (MZSP). Scale bars = 1 mm.



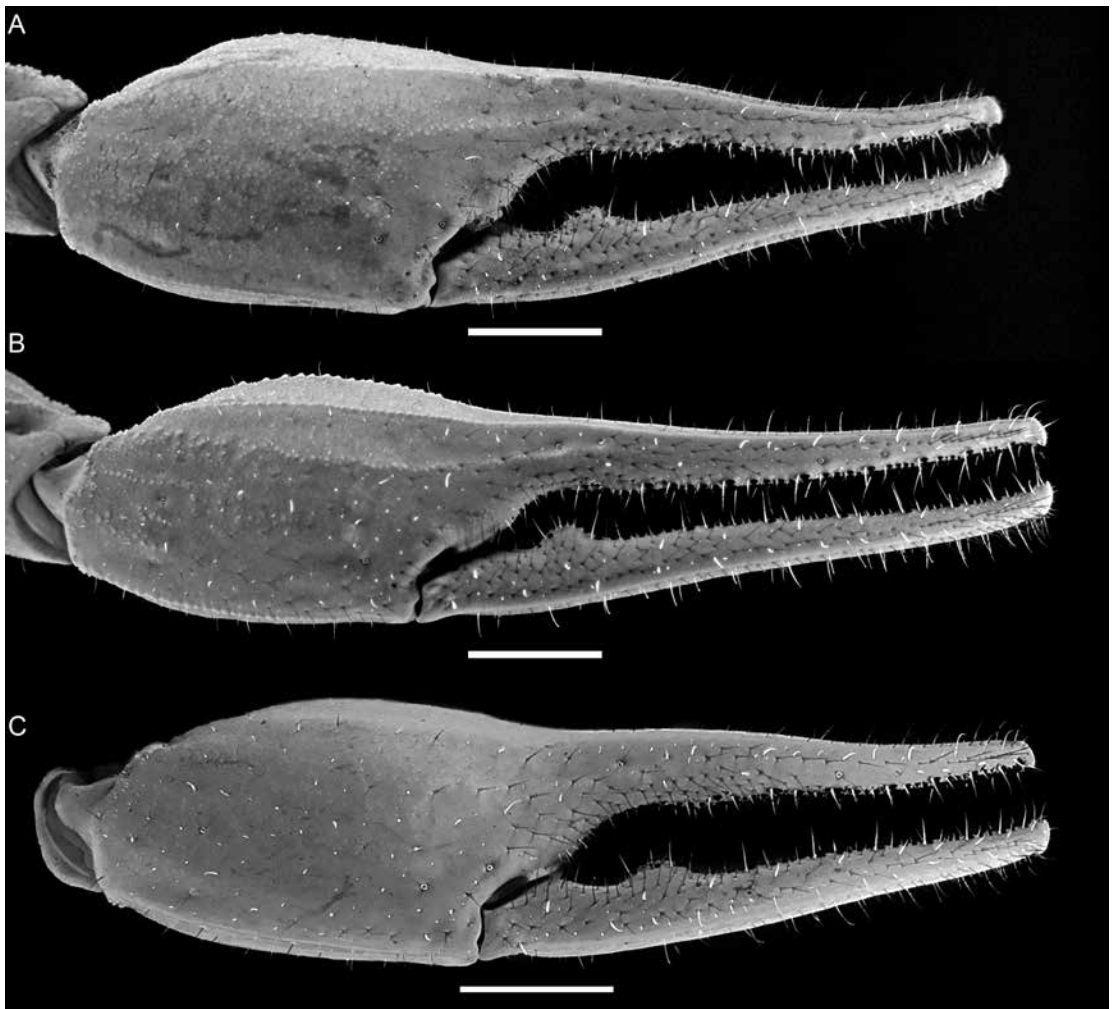


FIG. 25. *Heteroctenus* Pocock, 1893, pedipalp chela, retrolateral aspect. **A.** *H. abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *H. bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). **C.** *H. garridoi* (Armas, 1974), comb. nov., ♂ (AMNH). Scale bars = 2 mm.



FIG. 26. *Heteroctenus* Pocock, 1893, pedipalp chela, retrolateral aspect. **A.** *H. abudi* (Armas and Marcano Fondeur, 1987), comb. nov., ♀ (AMNH). **B.** *H. bonettii* (Armas and Marcano Fondeur, 1987), comb. nov., ♀ (AMNH). **C.** *H. garridoi* (Armas, 1974), comb. nov., ♀ (AMNH). Scale bars = 2 mm.



FIG. 27. *Heteroctenus* Pocock, 1893, pedipalp chela, retrolateral aspect. A. *H. junceus* (Herbst, 1800), comb. nov., ♂ (AMNH). B. *H. princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). C. *H. junceus* (Herbst, 1800), ♀ (AMNH). D. *H. princeps* (Karsch, 1879), comb. nov., ♀ (AMNH). Scale bars = 2 mm.

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); Santiago de las Caballeros, 1936, P. Thumb, 1 ♂ (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); Sierra del Rosario, near Aspuru, xi.1937, H.H. Voelckers, 1 ♂, 1 ♀, 1 juv. ♀ (ZMH); 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]); Viñales 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),  
comb. nov.**

Figures 4B, 12B, 14E, 18E, 23L–N, 27B, D, 29E,  
30E, 35

*Centrurus princeps* Karsch, 1879b: 121, 122;  
Kraepelin, 1891: 123, 139; Pocock, 1893:

385, 391; Kraepelin, 1899: 89, 95; Werner,  
1927: 357.

*Rhopalurus princeps*: Pocock, 1902a: 37; Mello-Leitão, 1932: 15; Stahnke and Calos, 1977: 119; Armas, 1981b: 2–5, figs. 1, 2, table 1; 1982a: 4; 1982b: 5, table 2; Lourenço, 1982a: 114, 136, figs. 2–9, 24, 78, table 1 (part); 1984a: 169, 170; 1986b: 165, fig. 7; Armas and Marcano Fondeur, 1987: 20, 23, fig. 4, pl. II, tables 10, 11; Armas, 1988: 70, 71, 93; Lourenço, 1992: 55; Rudloff, 1994: 9; Lourenço, 1997a: 590; Kovařík, 1998: 118; Fet and Lowe, 2000: 221; Armas, 2001: 246; Kamenz and Prendini, 2008: 9, table 2, pl. 43; Perez-Gelabert, 2008: 68; Volschenk et al., 2008: 654, 658, 659, 663, 664, 674, fig. 1B, tables 1, 2; Prendini et al., 2009: 206, 207, 209–213, 216, 219, 220, 222, 223, figs. 1, 4, 5E, F, 6C, 7C, 10, table 3; Lourenço and Armas, 2015: 228, 229; Santos et al., 2016: 3, 9, fig. 2B.

*Rhopalurus testaceus princeps*: Meise, 1934: 32,  
38.

TYPE MATERIAL: *Centrurus princeps*, holotype ♂ (ZMB 116), **HAITI**: Dept. Ouest: Port-au-Prince [examined].

DIAGNOSIS: *Heteroctenus princeps* is most closely related to *H. abudi*, with which it shares pronounced sexual dimorphism of the pedipalp chelae, and differs from the third *Heteroctenus* species occurring on Hispaniola, *H. bonettii*. The chela manus of the adult male *H. princeps* is incrassate and the fingers strongly curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that only the distal portion of the fingers connect and a distinctive gap is present between them proximally, when closed (fig. 27B). The chela manus of the female is not incrassate and the fingers not curved proximally, such that they connect along most of their length and little to no gap is present between them proximally, when closed (fig. 27D). However, the pedipalp chela manus of *H. princeps* is shorter and more incrassate, with



FIG. 28. *Heteroctenus* Pocock, 1893, metasoma and telson, dorsal aspect. **A.** *H. abudi* (Armas and Marcato Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *H. bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). **C.** *H. garridoi* (Armas, 1974), comb. nov., ♂ (AMNH). **D.** *H. junceus* (Herbst, 1800), ♂ (AMNH). **E.** *H. princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). Scale bars = 5 mm.



FIG. 29. *Heteroctenus* Pocock, 1893, metasoma and telson, ventral aspect. A. *H. abudi* (Armas and Marcato Fondour, 1987), comb. nov., ♂ (AMNH). B. *H. bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). C. *H. garridoi* (Armas, 1974), comb. nov., ♂ (AMNH). D. *H. junceus* (Herbst, 1800), ♂ (AMNH). E. *H. princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). Scale bars = 5 mm.



FIG. 30. *Heteroctenus* Pocock, 1893, metasoma and telson, lateral aspect. **A.** *H. abudi* (Armas and Marcano Fondeur, 1987), comb. nov., ♂ (AMNH). **B.** *H. bonettii* (Armas, 1999), comb. nov., ♂ (AMNH). **C.** *H. garridoi* (Armas, 1974), comb. nov., ♂ (AMNH). **D.** *H. junceus* (Herbst, 1800), ♂ (AMNH). **E.** *H. princeps* (Karsch, 1879), comb. nov., ♂ (AMNH). Scale bars = 5 mm.

more weakly developed carinae, than that of *H. abudi*.

Other characters by which *H. princeps* differs from *H. abudi* and *H. bonettii* are as follows. The carapace of *H. princeps* is shorter and broader than that of *H. abudi* and *H. bonettii* (fig. 14A, B, E). The carapace and tergites are more coarsely and densely granular in *H. princeps* than in *H. bonettii* and, to a lesser extent, *H. abudi*. The pectines of *H. princeps* are narrower basally, with a less-pronounced basal plate than in *H. bonettii* and, to a lesser extent, *H. abudi* (fig. 18A, B, E). The pectinal teeth are similar in size in *H. princeps* whereas the first 6–7 pectinal teeth are noticeably larger in *H. bonettii*. The carapace and tergites are more coarsely and densely granular in *H. princeps* than in *H. abudi* and *H. bonettii*. The submedian sulci of sternite III are convergent in *H. princeps* but subparallel in *H. bonettii* (fig. 18B, E). The pale, raised posteromedial surface of sternite V in the male is less prominent in *H. princeps* than in *H. bonettii*. The metasomal segments of *H. princeps* are shorter and broader, i.e., the width/length ratio is smaller, than *H. bonettii* and, to a lesser extent, *H. abudi* (fig. 28A, B, E). The granulation, ventromedian and ventrolateral carinae of metasomal segment V are less developed, compared with those of the preceding segments in *H. princeps*, such that the segment has a shinier, rounded appearance, as in *H. abudi* (fig. 29A, E).

Unlike *H. abudi*, the coloration of *H. bonettii* is predominantly pale (fig. 35); the carapace, legs, and tergites immaculate; the pedipalp chelae, metasoma (segments IV and V only) and telson infusate. In this respect, *H. princeps* resembles *H. bonettii* except for the pedipalp chelae, which are typically immaculate in the latter.

**DISTRIBUTION:** *Heteroctenus princeps* is endemic to Hispaniola and inhabits the central part of the island (fig. 4B), including the valley of the Yaque del Norte River, the Neiba Valley, the Sierra de Baoruco, Sierra de Martín García, and Sierra de Ocoa (Teruel, 2006). Although the type locality is in Haiti (Département du l'Ouest), most of the known localities are in the Dominican Republic (Azua, Barahona, Baoruco, Inde-

pendencia, Montecristi, Pedernales, and Peravia provinces) at altitudes ranging from below sea level at Isla Cabritos to 485 m in the Sierra de Baoruco. Records from Cuba listed by Fet and Lowe (2000: 221) are erroneous.

**ECOLOGY:** *Heteroctenus princeps* inhabits dry scrub on mixed substrata. It has been collected by day under bark, wood, and stones, as well as in dead and dry agave plants, and at night with UV light detection. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). The buthid, *C. bani*, has been collected in sympatry.

**MATERIAL EXAMINED: 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 Station, 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),



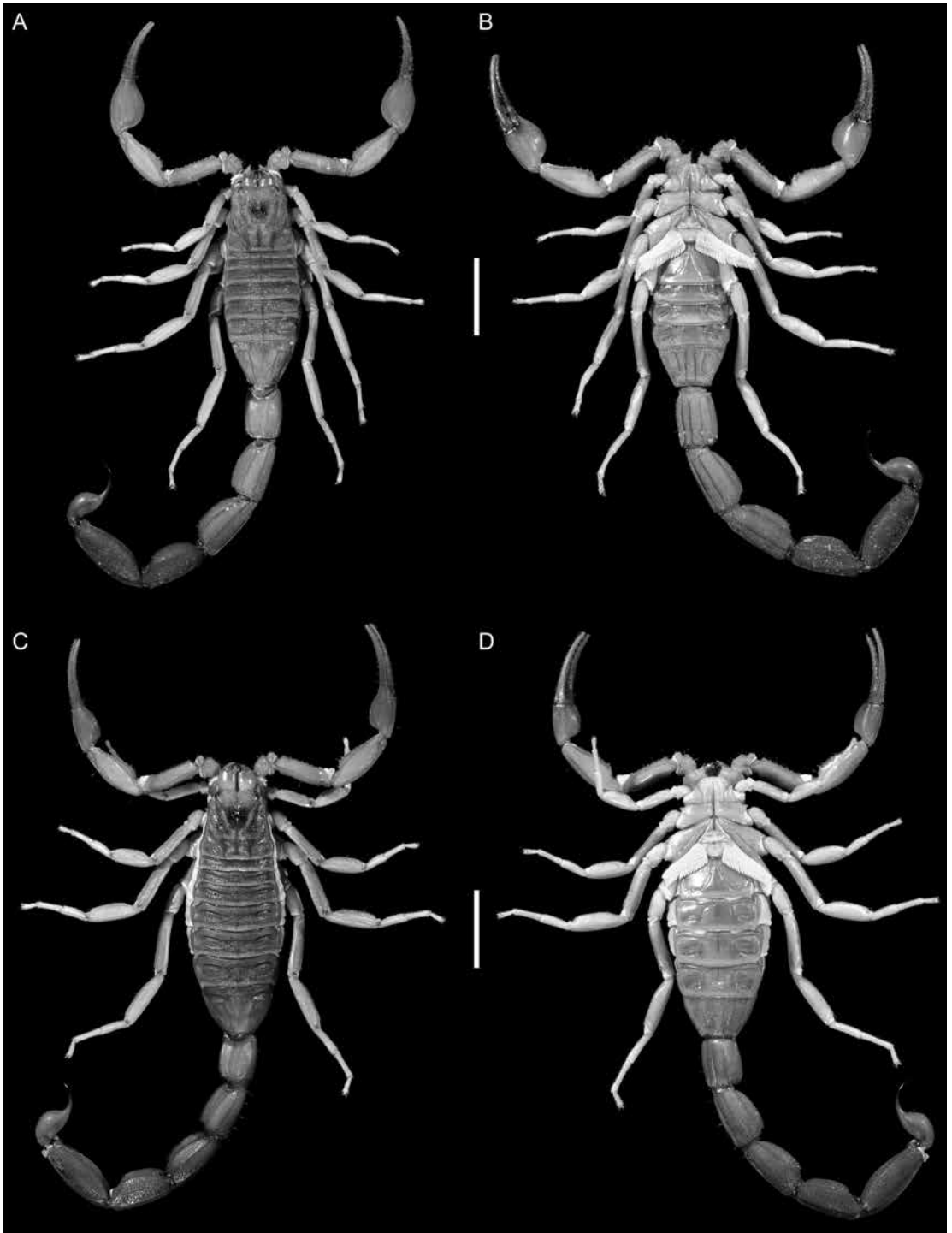


FIG. 31. *Heteroctenus abudi* (Armas and Marcano Fondeur, 1987), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 10 mm.



FIG. 32. *Heteroctenus bonettii* (Armas, 1999), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 10 mm.

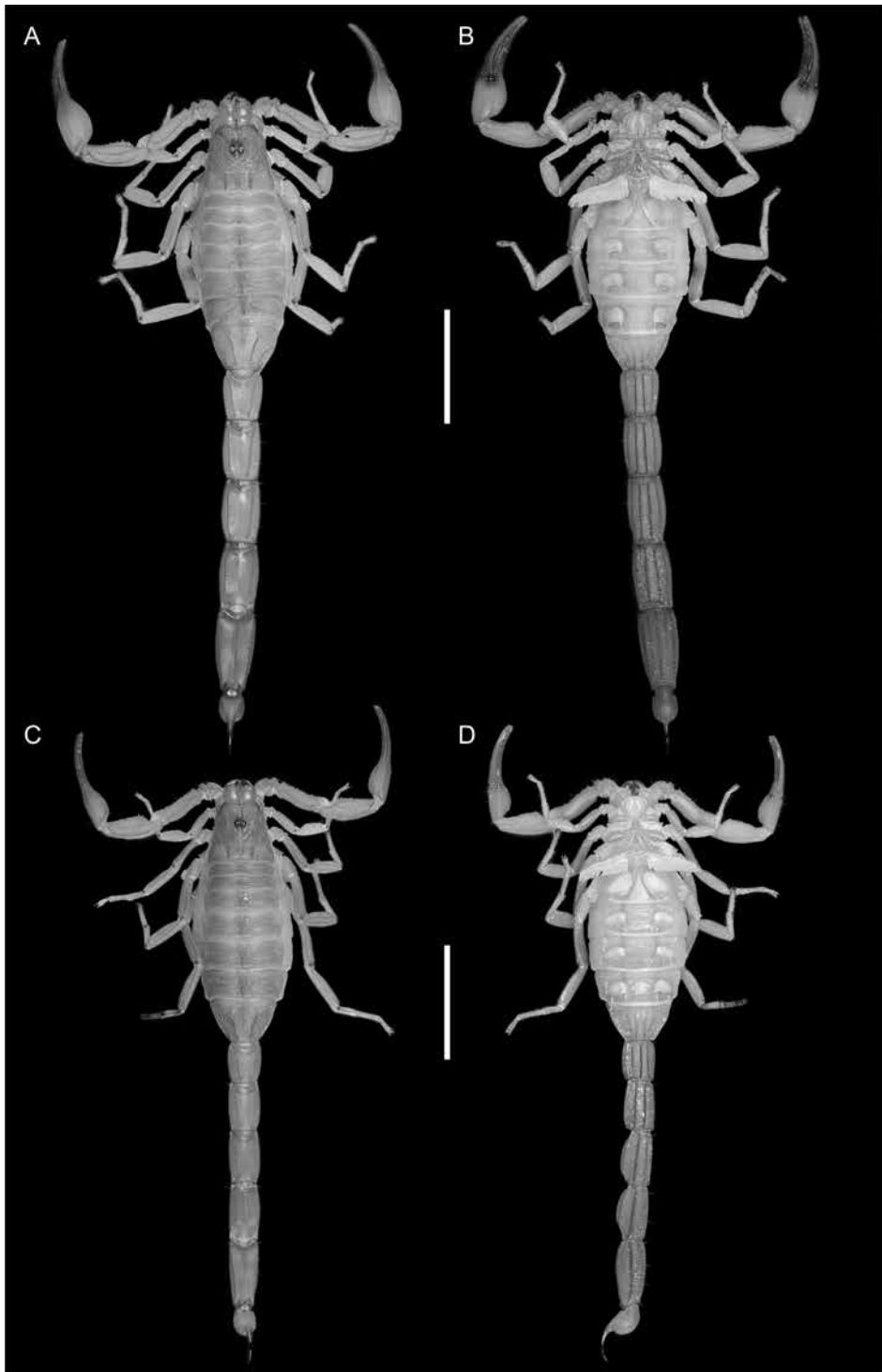


FIG. 33. *Heteroctenus garridoi* (Armas, 1974), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (CAS). C, D. ♀ (CAS). Scale bars = 10 mm.

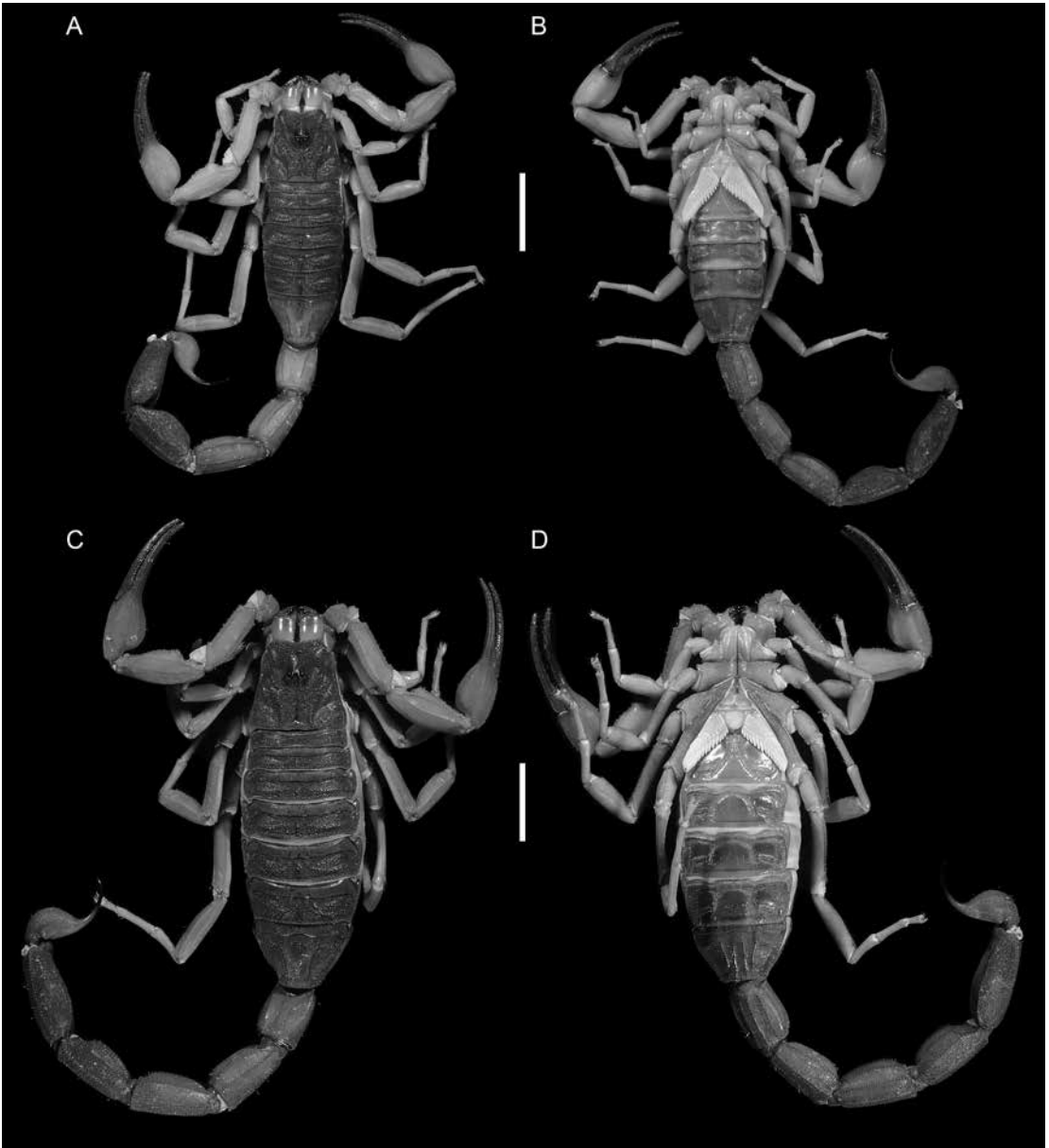


FIG. 34. *Heteroctenus junceus* (Herbst, 1800), habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 10 mm.

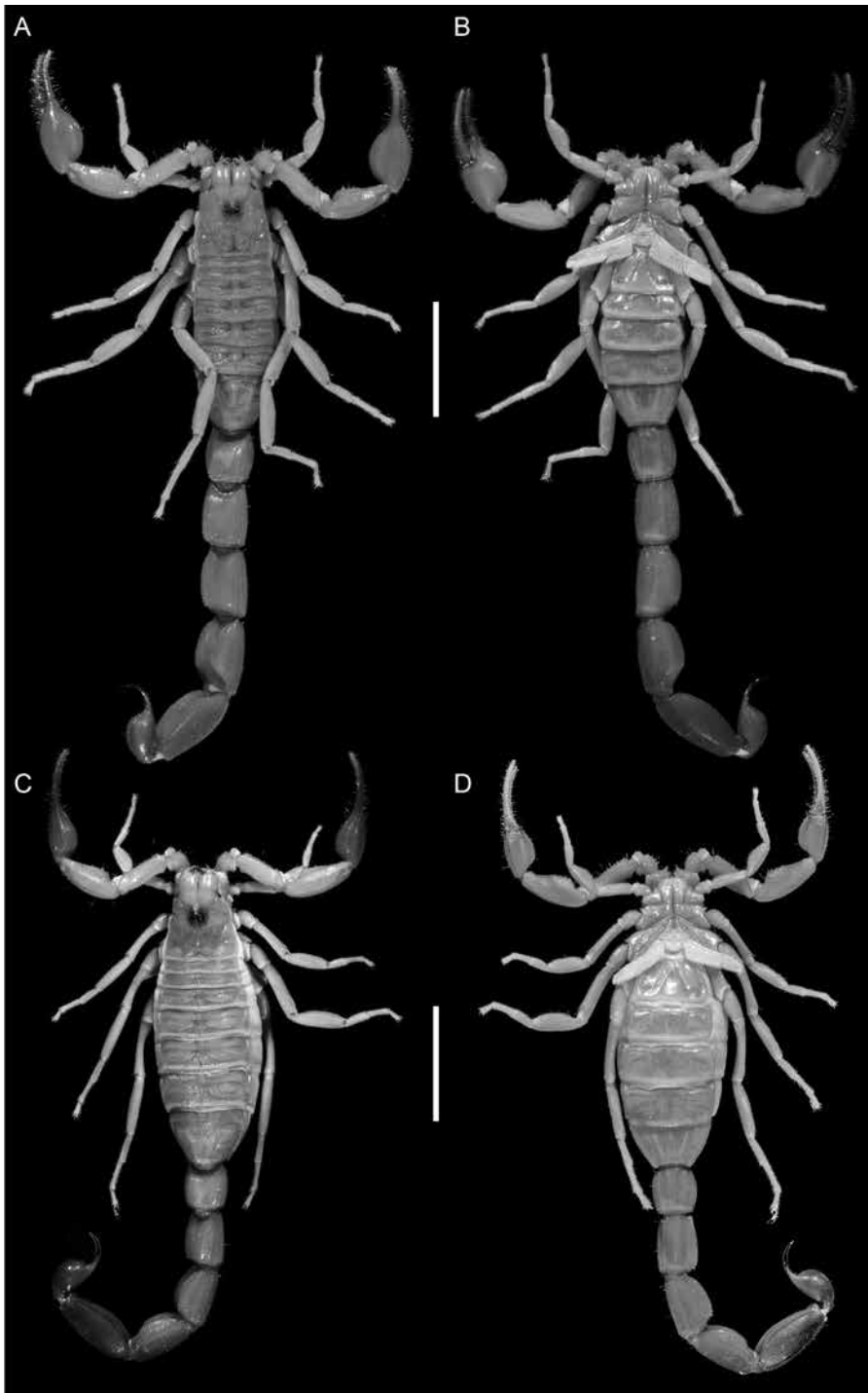


FIG. 35. *Heteroctenus princeps* (Karsch, 1879), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 10 mm.

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]).

***Ischnotelson*, gen. nov.**

Figures 1B, 2C, 9A, 10A, 12E, 15A, B, 17B, 19A, B, 21C, 22C, 23O–R, 36–40

*Rhopalurus guanambiensis* Lenarducci et al., 2005 (= *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov.), type species, here designated.

*Rhopalurus* (part): Lenarducci et al., 2005: 1–7, figs. 1–11; Teruel, 2006: 52; Lourenço, 2007: 359; 2008: 3; Prendini et al., 2009: 222; Brazil and Porto, 2010: 50; Porto et al., 2010: 293, 295, table 1; Lourenço, 2014: 69; Ubiniski et al., 2016: 122.

**DIAGNOSIS:** *Ischnotelson*, gen. nov., differs from all other *rhopalurusine* genera by the fused lateral ocular, central lateral and posterior central submedian carinae of the carapace, and the laterally compressed telson vesicle. It differs further from *Heteroctenus*, *Jaguajir*, gen. nov., and *Rhopalurus* by the absence of a pecten-sternite stridulatory organ; from *Centruroides* and *Troglo-rhopalurus* by the robust metasoma, increasing in width posteriorly (more so in the adult male); from *Heteroctonus* by the presence of two lateral depressions in the male pectinal plate; from *Jaguajir* by the separate (unfused) lateral ocular and anterior central submedian carinae of the carapace; from *Physoctonus* by the larger size (30–70 mm), the more distinct carapacial carinae, the setose proximal dorsal fulcra of the pectines, the incrassate pedipalp chela manus of the adult male, the bifurcate prolateral pedal spur

of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; and from *Troglo-rhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of the adult male emarginate, with a distinct gap evident between them, when closed.

**ETYMOLOGY:** A fusion of the Greek words *ischnos*, meaning “thin” or “slender,” and *telson*, referring to the remarkable, laterally compressed telson of the two species in this genus. Masculine in gender.

**DESCRIPTION:** The following general description outlines characters common to both species of *Ischnotelson*, gen. nov.

**Total length:** Medium-sized scorpions (total length, 30–44 mm).

**Color:** Carapace and tergites I–VI brown, tergite VII yellow (fig. 1B). Coxosternal region, pectines and sternites pale yellow. Metasomal segments, dorsal surfaces yellowish (segments I–III) to brown (IV and V); ventral surfaces darker; segments IV and V darker than preceding segments, with V darker than IV, almost black. Telson dark orange, aculeus dark brown to black. Legs and chelicerae yellowish. Pedipalps yellow with chela fingers darker than manus, reddish brown.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle relatively shallow (fig. 15A–B); two median ocelli; three pairs of lateral macrocelli; one pair of lateral microcelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular, central lateral and posterior central submedian carinae distinct, finely granular to costate-granular and fused (posterior end of one carina connected to anterior end of subsequent carina) forming single nearly continuous, oblique carina, extending along almost entire length of carapace; anterior central submedian carinae distinct, finely granular and separate.

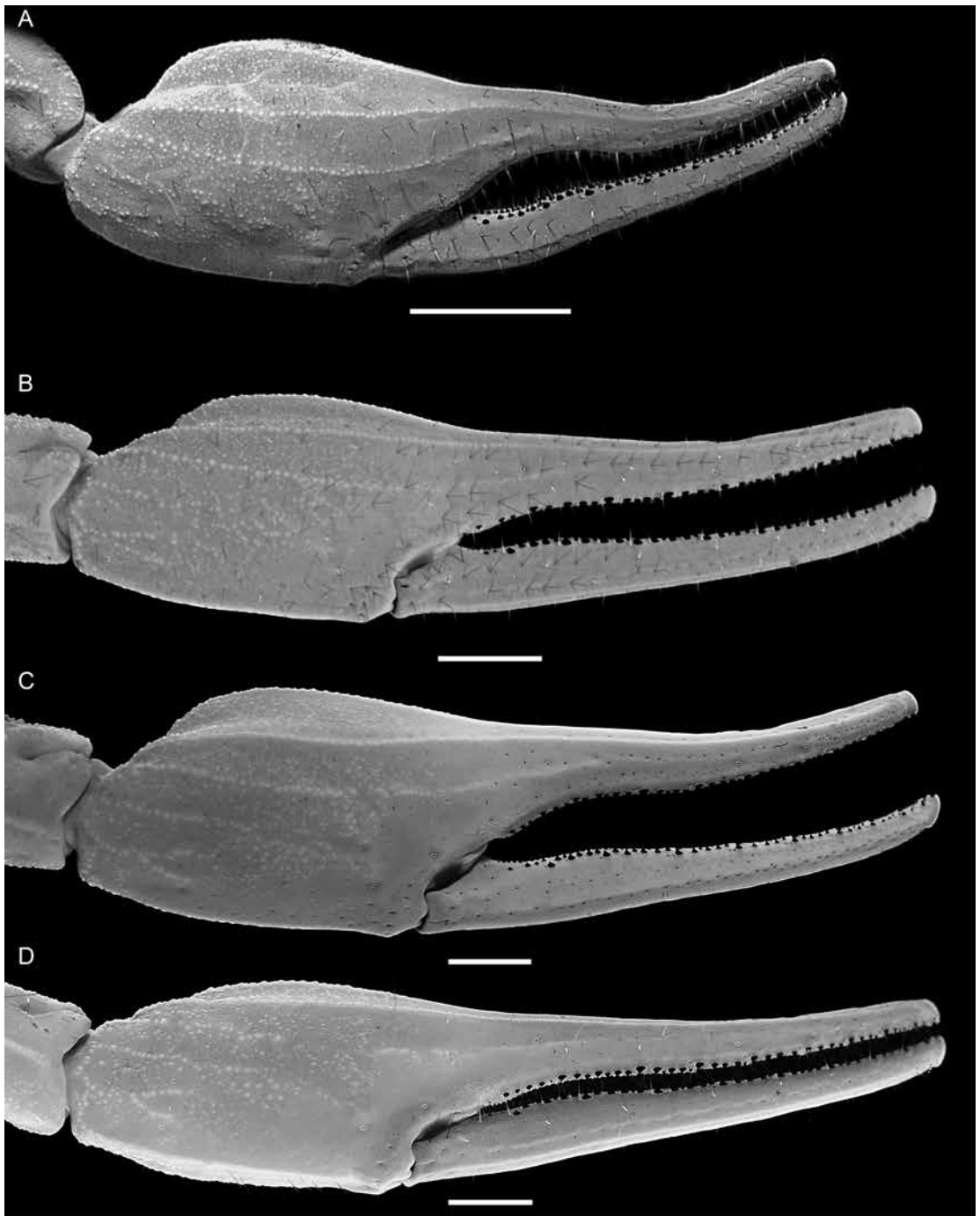


FIG. 36. *Ischnotelson*, gen. nov., pedipalp chela, retrolateral aspect. **A.** *I. guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **B.** *I. guanambiensis* (Lenarducci et al., 2005), comb. nov., ♀ (MZSP). **C.** *Ischnotelson peruassu*, sp. nov., holotype ♂ (MZSP). **D.** *Ischnotelson peruassu*, sp. nov., paratype ♀ (MZSP). Scale bars = 2 mm.

**Pedipalps:** Pedipalp femur retrolateral accessory carinae absent. Pedipalp chela manus of adult male incrassate, fixed and movable fingers curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, distinct gap present between fingers proximally, when closed (fig. 36), manus of female not incrassate, fixed and movable fingers not curved proximally, such that proximal dentate margin sublinear, little or no gap present between them proximally, when closed; manus, proventral carina present, promedian carina absent; fixed and movable fingers, median denticle rows each comprising eight oblique subrows of primary denticles flanked closely by pro- and retrolateral accessory (supernumerary) denticles; movable finger without proximal lobe (fig. 17B). Pedipalps orthobothriotaxic Type A,  $\alpha$  configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  proximal to trichobothrium  $et$ .

**Legs:** Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with distinct pro- and retroventral rows of fine, acuminate macrosetae.

**Pectines:** Pectinal plate with two lateral depressions (male), anterior margin with sulcus (fig. 19A–B). Pectines not proximally expanded, at least  $1.5\times$  wider proximally than medially; proximal dorsal fulcra setose; pectinal teeth almost straight, slightly curved laterally, proximal teeth, dorsal surfaces covered with small denticles, without striations, dorsobasal surfaces with macrosetae absent or present; pectinal sensillae peg shaped (fig. 12E).

**Mesosoma:** Tergites III–V slightly wider than I and II in female; I–VI tricarinate, dorsosubmedian carinae finely granular, absent on I and II, restricted to posterior quarter on III–VI; dorsomedian carinae finely granular, vestigial on I and II, restricted to posterior third on III–VI. Tergite VII pentacarinata, dorsome-

dian carina restricted to anterior two thirds of segment. Sternites smooth, carinae absent or obsolete; sternite III, lateral margins not forming smooth, raised carina, ventromedian carina not elevated anteriorly, ventrosubmedian surfaces not forming paired depressions, finely and irregularly granular (figs. 10A, 19A–B); respiratory spiracles (stigmata) width less than  $3\times$  length.

**Metasoma:** Metasoma robust, increasing in width posteriorly, segment V wider than I, more markedly so in adult male (figs. 37, 38). Segments I–III each with 10 distinct, costate-granular carinae, IV with eight distinct, costate-granular carinae, V with seven distinct but less pronounced, granular carinae; dorsosubmedian carinae obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV, more pronounced on segment I; dorsolateral carinae complete on segments I–IV, and terminating in prominent, spiniform granules posteriorly on III and IV, absent on V; lateral suprmedian carinae complete on segments I–V; lateral inframedian carinae complete on segments I and II, complete but obsolete on III, absent on IV and V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third of V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely granular, less so on dorsal surfaces, especially on segment V.

**Telson:** Vesicle small, slightly elongate and laterally compressed, width ca. half height, considerably narrower than metasoma V, width less than half metasoma V (fig. 22C); anterodorsal lateral lobes reduced; lateral and ventral surfaces smooth, without ventromedian carina; subaculear tubercle pronounced and spinoid.

**Hemispermaphore:** Flagelliform; flagellum, elongate and narrow (fig. 23O–R); trunk markedly concave; three lobules, ental (LI), ectal (LE), and basal (LB); LI inclined sinistrally relative to axis of trunk and continuous until flagellar base; flagellar base wide (half maximum width of trunk); LE length ca. two thirds that of LI, with curved tip ending in small protuberance, width



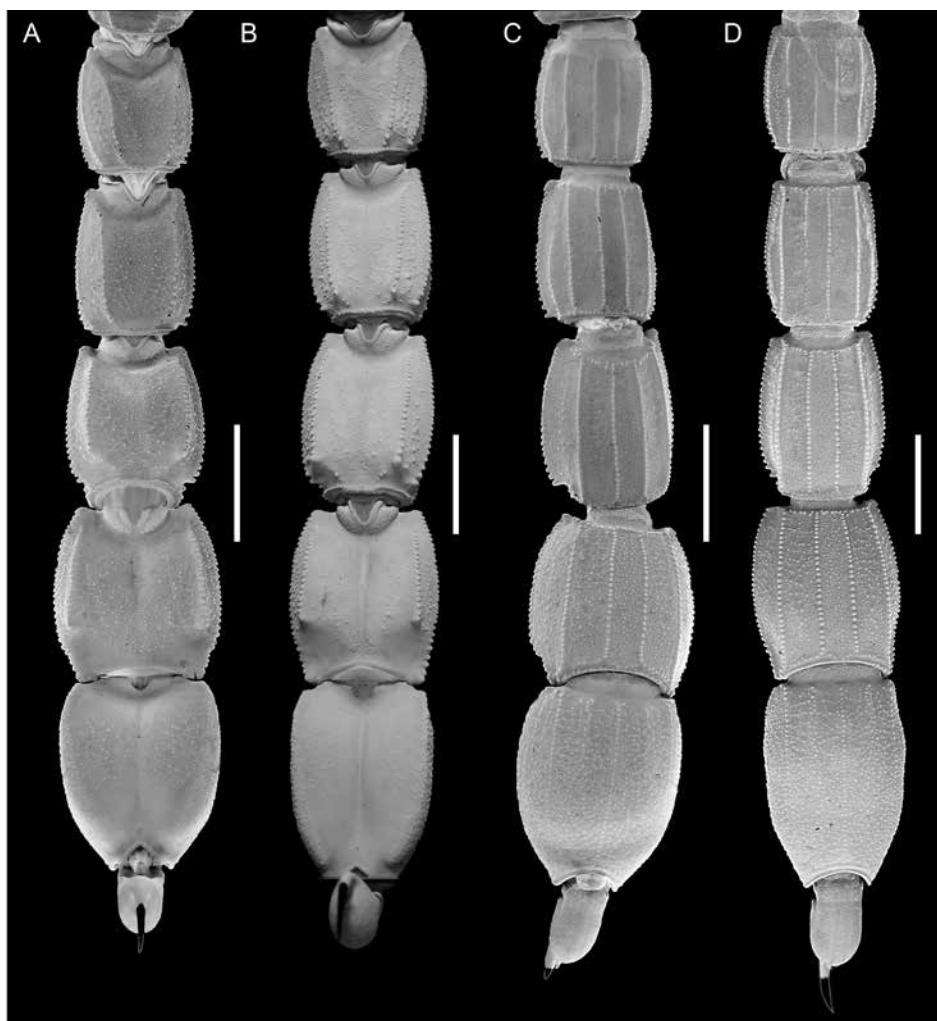


FIG. 37. *Ischnotelson*, gen. nov., metasoma and telson, dorsal (A, B) and ventral (C, D) aspects. A, C. *I. guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). B, D. *I. peruassu*, sp. nov., holotype ♂ (MZSP). Scale bars = 5 mm.

ca. two thirds that of LB; LB short, carina shaped with sharp tip, ca. 60° angle between LB and LE.

**Cytogenetics:** The diploid chromosome number of *I. guanambiensis* is  $2n = 25$  and of *I. peruassu*, sp. nov., is  $2n = 26$  (table 2) (Ubinski et al., 2016).

**INCLUDED SPECIES:** *Ischnotelson guanambiensis* (Lenarducci, Pinto-da-Rocha and Lucas, 2005), comb. nov.; *Ischnotelson peruassu*, sp. nov.

**DISTRIBUTION:** *Ischnotelson*, gen. nov., is endemic to northeastern Brazil. The type and only known locality of *I. guanambiensis* is in the state of Bahia, whereas the two known localities of *I. peruassu*, sp. nov., are close to each other (fig. 9A) in the state of Minas Gerais.

**ECOLOGY:** The known localities of *Ischnotelson*, gen. nov., occur at the ecotone of Brazilian caatinga and cerrado (fig. 2C).



FIG. 38. *Ischnotelson*, gen. nov., metasoma and telson, lateral aspect. **A.** *I. guanambiensis* (Lenarducci et al., 2005), comb. nov., ♂ (MZSP). **B.** *I. peruassu*, sp. nov., holotype ♂ (MZSP). Scale bars = 5 mm.

**REMARKS:** The consistent paraphyly of *Rhopalurus* in the analyses by Esposito et al. (in review) and the identification of a well defined, monophyletic group comprising *R. guanambiensis* and the new species described below, justifies the creation of the new genus and the transfer of *R. guanambiensis* to it, resulting in a new combination (fig. 13). The recognition of a new genus is consistent with the cytogenetic study of Ubinski et al. (2016) which identified a diploid chromosome number of  $2n = 25$  for *R. guanambiensis* and  $2n = 26$  for *I. peruassu*, sp. nov., and a third, as yet undescribed species (table 2).

***Ischnotelson guanambiensis* (Lenarducci, Pinto-da-Rocha and Lucas, 2005), comb. nov.**

Figures 1B, 2C, 9A, 10A, 12E, 15A, 19A, 21C, 22C, 23O–R, 36A, B, 37A, C, 38A, 39

*Rhopalurus guanambiensis*: Lenarducci et al., 2005: 1, 2, 7, tables 1, 2, figs. 1–11; Lourenço, 2008: 3; Prendini et al., 2009: 222; Brazil and Porto, 2010: 50; Porto et al., 2010: 293, 295, table 1; Lourenço, 2014: 69; Ubinski et al., 2016: 122.

**TYPE MATERIAL:** *Rhopalurus guanambiensis*: Holotype ♂ (IBSP-SC 3404), 3 ♂ paratypes

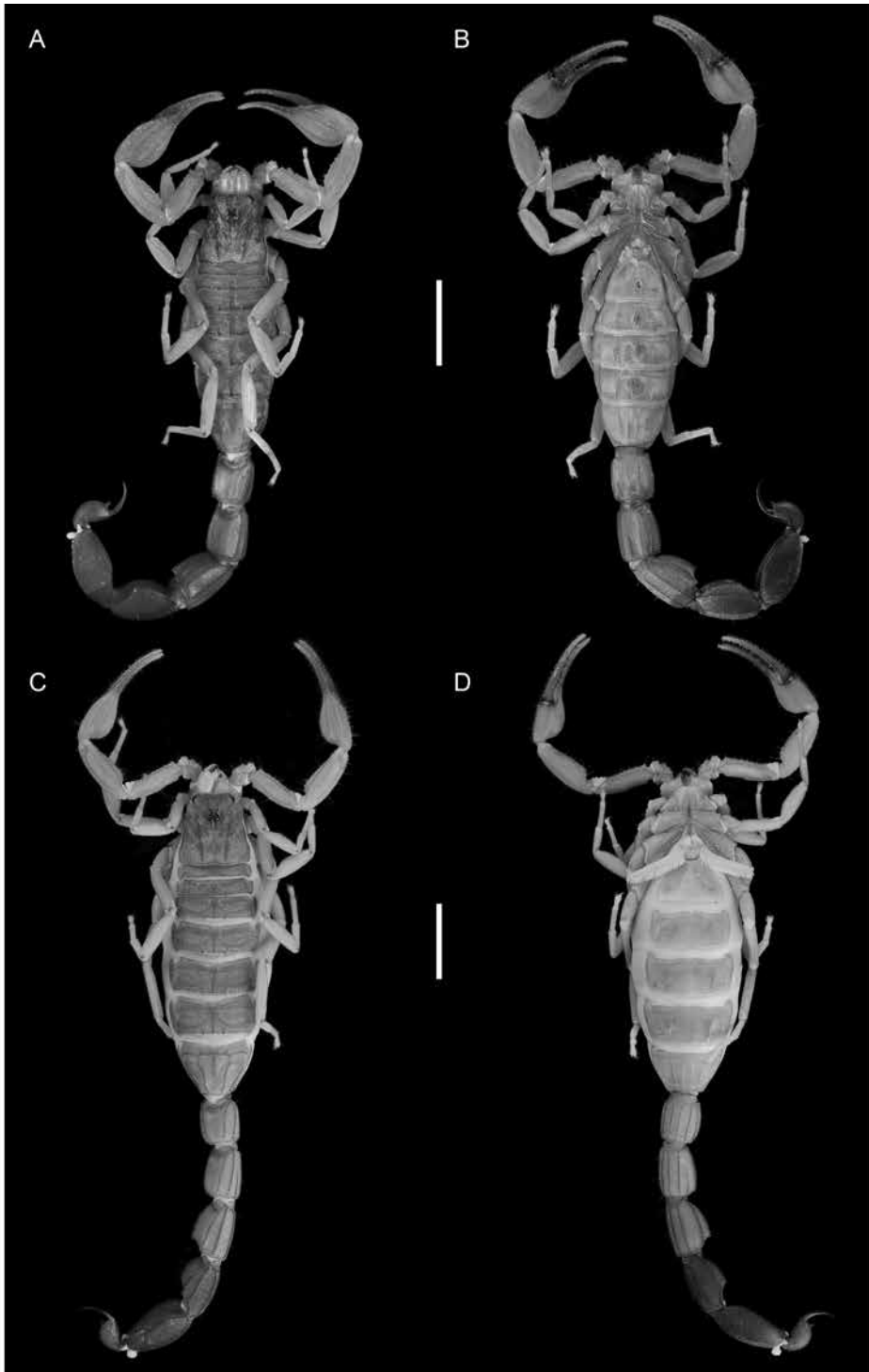


FIG. 39. *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (MZSP). C, D. ♀ (MZSP). Scale bars = 10 mm.

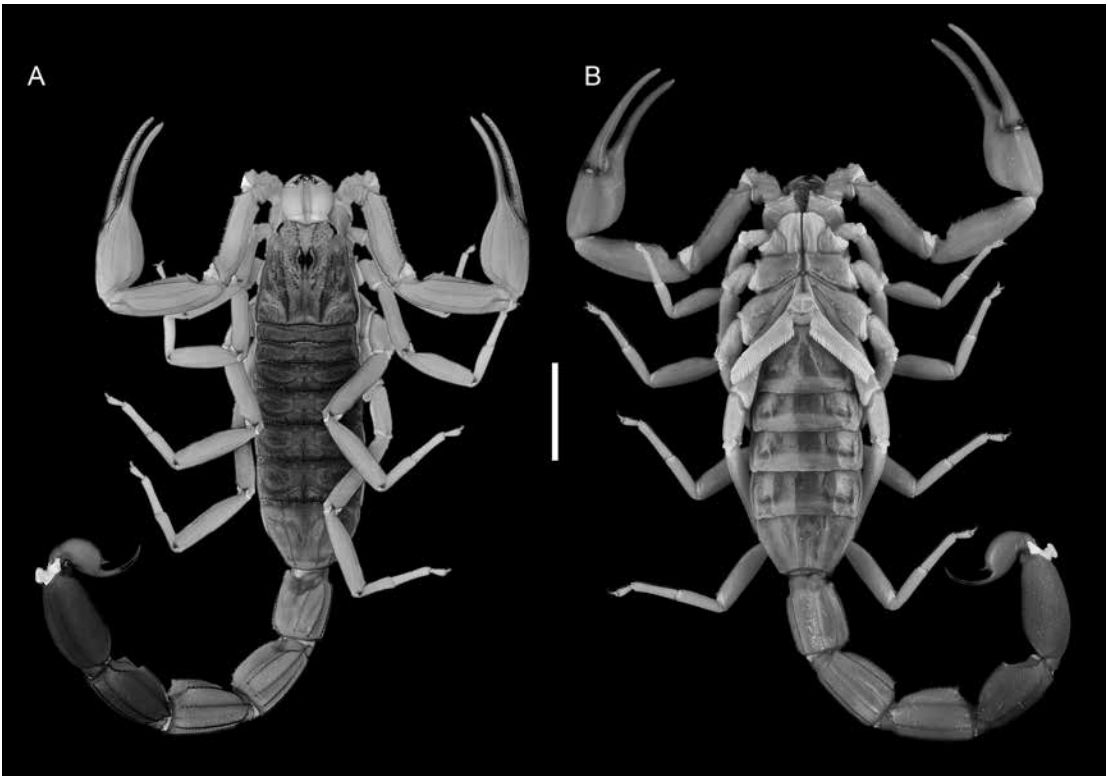


FIG. 40. *Ischnotelson peruassu*, sp. nov., holotype ♂ (MZSP), habitus, dorsal (A) and ventral (B) aspects. Scale bar = 10 mm.

(IBSP-SC 3406-3407, MZSP-22590), paratype ♀ (IBSP-SC 3405), **BRAZIL:** *Bahía:* Guanambi, 14°11'15"S 42°48'45"W, 1985, V.F. Neves.

**DIAGNOSIS:** *Ischnotelson guanambiensis* differs from its sister species, *I. peruassu*, sp. nov., as follows. *Ischnotelson guanambiensis* is smaller, varying from 35–45 mm in total length, than *I. peruassu*, which varies from 48–59 mm. Metasomal segments IV, V, and telson are darker in *I. guanambiensis* than in *I. peruassu*. The pedipalp chela fingers are noticeably darker than the chela manus in *I. guanambiensis*, but similar in color to the manus in *I. peruassu*. The pedipalps and legs are covered by fine setae in *I. guanambiensis*, but sparsely setose in *I. peruassu*. The granulation of the carapace of *I. guanambiensis* is coarser than that of *I. peruassu*, and the dorsal intercarinal surfaces of the metasoma are shagreened in *I. guanambiensis*, but smooth in *I. peruassu*. The

carinae of the carapace are more pronounced in *I. guanambiensis* than in *I. peruassu*. Sternite III is elevated anteriorly in *I. guanambiensis* unlike in *I. peruassu* (fig. 10A). Finally, the sexual dimorphism of the adult male *I. guanambiensis* is more pronounced than that of the adult male *I. peruassu*: the pedipalps are more incrassate, the fixed and movable fingers of the pedipalp chela are markedly curved proximally and the posterior broadening of the metasoma is more pronounced in the former.

**DISTRIBUTION:** *Ischnotelson guanambiensis* is endemic to the Brazilian state of *Bahía*, and known only from the type locality, near the city of Guanambi.

**ECOLOGY:** The type and only known locality is situated on the ecotone of Brazilian caatinga and cerrado (fig. 2C). Personally collected specimens were found at night with UV light detection. The

habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**MATERIAL EXAMINED: BRAZIL:** *Bahía*: Município Ceraíma: Aeroporto de Guanambi, Guanambi, 14°13'00"S 42°46'60"W, 15.viii.2007, H.Y. Yamaguti et al., 1 ♀ (MZSP 70872), 17.xii.2007, H.Y. Yamaguti et al., 1 subad. ♀ (MZSP 30864/AMCC [LP 9669]), 1 subad. ♂ (MZSP 30865/AMCC [LP 9670]), 21.i.2009, H.Y. Yamaguti et al., 1 ♂ (MZSP 70873).

*Ischnotelson peruassu*, sp. nov.

Figures 9B, 15B, 17B, 19B, 36C, D, 37B, D, 38B, 40

*Rhopalurus* sp. n. 1: Ubinski et al., 2016: 122.

**TYPE MATERIAL: BRAZIL:** *Minas Gerais*: Município Januária: Januária, Parque Nacional Cavernas do Peruaçu: Holotype ♂ (MZSP 31138/AMCC [LP 9937]), 15°07'26"S, 44°14'28"W, 4–25.i.2009, R.S. Recoder and M. Teixeira, Jr. Paratypes: 1 ♀ (UFMG 4820), 1 subad. ♀ (UFMG 4818), 1 juv. ♂, 1 juv. ♀ (UFMG 4824), 15°09'09"S 44°14'30"W, 17–22.x.2010, G.F.B.P. Ferreira.

**DIAGNOSIS:** *Ischnotelson peruassu*, sp. nov., differs from its sister species, *I. guanambiensis*, as follows. *Ischnotelson peruassu* is larger, varying from 48–59 mm in total length, than *I. guanambiensis*, which varies from 35–45 mm. Metasomal segments IV, V, and telson are paler in *I. peruassu* than in *I. guanambiensis*. The pedipalp chela fingers are similar in color to the chela manus in *I. peruassu* but noticeably darker than the manus in *I. guanambiensis*. The pedipalps and legs are sparsely setose in *I. peruassu*, but covered by fine setae in *I. guanambiensis*. The carinae of the carapace are less pronounced in *I. peruassu* than in *I. guanambiensis* and the carapace more finely granular in *I. peruassu* than in *I. guanambiensis*. The dorsal intercarinal surfaces of the metasoma are smooth in *I. peruassu* and shagreened in *I. guanambiensis*. Sternite III is not elevated anteriorly in *I. peruassu* unlike in *I. guanambiensis*. Finally, the sexual dimorphism of the adult male *I. peruassu*

is less pronounced than that of the adult male *I. guanambiensis*: the fixed and movable fingers of the pedipalp chela are shallowly curved proximally and the posterior broadening of the metasoma is less pronounced in the former.

**ETYMOLOGY:** The specific epithet is a noun in apposition, referring to the type locality, a Brazilian state park covered by savanna that protects important caves.

**DESCRIPTION:** The following description is based on the holotype male unless otherwise noted (for measurements, see table 3). Only characters that differ from the generic description are noted.

*Total length:* Medium-sized scorpions (total length, 48–59 mm).

*Color:* Carapace and tergites I–VI brown, tergite VII and metasomal segments I–III dark yellow, metasomal segments IV, V, and telson darker than preceding segments, reddish brown (fig. 40); telson vesicle paler than metasomal segments IV and V, aculeus black; carinae of carapace, tergites, and metasoma dark brown. Sternites yellow. Chelicerae pale yellow; pedipalps yellow, chela fingers similar in color to chela manus; legs yellow, slightly paler than pedipalps.

*Carapace:* Shape trapezoidal (fig. 15B). Width of anterior margin approximately two thirds that of posterior margin. Anteromedian, median ocular, and posteromedian sulci shallow but well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular carinae present but weakly developed, central lateral and posterior central submedian carinae distinct, finely granular to costate-granular and fused, forming single nearly continuous, oblique carina, extending along almost entire length of carapace; anterior central submedian carinae distinct, finely granular and separate. Carapace anterior margin with large spinoid granules.

*Pedipalps:* Pedipalp fingers each with seven oblique subrows (fused basal subrows) of primary denticles and short subrow of terminal denticles (fig. 17B). Chela manus slightly incrassate, with fixed and movable fingers shallowly curved proximally, in male. Carinae

TABLE 3

**Meristic data for type material of *Ischnotelson peruassu*, sp. n., *Physoctonus striatus*, sp. n., and *Physoctonus debilis* (C.L. Koch, 1840).**

Measurements follow Prendini (2000, 2003, 2004). <sup>1</sup>Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; <sup>2</sup>sum of metasomal segments I–V and telson; <sup>3</sup> measured from base of condyle to tip of fixed finger.

		<i>I. peruassu</i>		<i>P. debilis</i>		<i>P. striatus</i>	
		Holotype	Paratype			Holotype	Paratype
		♂	♀	♂	♂	♂	♂
		MZSP	UFMG	MZSP	MZSP	MZSP	MZSP
		31138	4818	30866	31158	31128	30869
Total length <sup>1</sup>		58.7	48.6	26.5	28.1	25.9	22.5
Prosoma	length	7.0	6.2	3.1	3.4	3.1	2.9
	ant. width	4.2	3.8	2.2	2.3	1.3	1.3
	post. width	7.2	6.2	3.7	4.0	3.3	3.0
Mesosoma	total length	16.5	12.0	7.8	7.7	7.4	6.2
Metasoma	total length <sup>2</sup>	35.2	30.4	15.6	17.0	15.4	13.4
Segment I	length	4.7	4.0	2.1	2.2	2.3	1.5
	width	4.1	3.5	1.9	2.0	1.7	1.3
	height	3.4	2.9	1.6	1.6	1.3	1.3
Segment II	length	5.3	4.5	2.3	2.5	2.6	2.3
	width	4.2	3.6	1.8	1.9	1.6	1.6
	height	3.4	3.0	1.5	1.6	1.3	1.3
Segment III	length	5.7	4.8	2.5	2.7	2.4	2.3
	width	4.7	3.6	1.9	2.0	1.8	1.7
	height	3.6	3.0	1.5	1.5	1.4	1.3
Segment IV	length	6.1	5.3	2.7	3.1	2.7	2.6
	width	5.2	4.0	2.1	2.2	2.1	2.0
	height	3.6	3.0	1.5	1.6	1.4	1.3
Segment V	length	7.2	6.3	3.2	3.4	3.0	2.8
	width	4.9	3.8	2.0	2.2	2.2	1.9
	height	3.2	2.7	1.5	1.6	1.3	1.3
Telson	total length	6.2	5.5	2.8	3.1	2.4	1.9
Vesicle	length	3.6	3.3	1.8	1.9	1.4	1.2
	width	1.7	1.7	1.1	1.2	1.1	0.9
	height	2.1	2.0	1.1	1.1	1.0	0.9
Aculeus	length	3.4	2.9	1.4	1.6	1.3	1.0
Pedipalp	total length	26.9	23.4	12.5	13.8	11.9	10.9
Femur	length	6.9	6.0	3.0	3.2	2.9	2.4
	width	2.0	1.8	0.9	1.0	0.8	0.8
	height	1.4	1.3	0.7	0.8	0.7	0.7
Patella	length	7.7	6.6	3.4	3.8	3.3	2.9
	width	2.5	2.3	1.3	1.5	1.1	1.2
	height	2.1	1.7	0.9	1.0	1.0	0.7
Chela	length <sup>3</sup>	12.3	10.8	6.1	6.8	5.7	5.6
Manus	width	3.2	2.1	1.4	1.5	1.3	1.4
	height	3.2	2.2	1.3	1.2	1.1	1.2
Mov. finger	length	8.2	7.3	4.3	4.8	4.0	4.0
Pectines	total length	5.2	4.9	2.2	2.5	2.5	2.0
	basal width	1.8	1.4	0.9	1.0	0.9	0.9
	tooth count	26/26	27/27	14/13	14/15	15/15	17/17

granular to costate-granular except femur and patella prolateral carinae comprising spiniform granules; chela manus proventral and promedian carinae absent.

*Legs*: Legs III and IV, tibial spurs absent; I–IV, surfaces carinate; basitarsi each with bifurcate prolateral pedal spur; telotarsi each with irregular tufts of fine, acuminate macrosetae.

*Sternum*: Subtriangular. Median longitudinal sulcus deep throughout, extending from anterior margin to posterior margin.

*Genital operculum*: Genital opercula suboval, completely divided longitudinally; genital papillae present (♂).

*Pectines*: Tooth count, 26/26 (♂), 27/27 (♀). Pectinal plate rectangular, width approximately 2× length, median anterior notch present.

*Mesosoma*: Tergites similar to posterior width of carapace, I–III similar in width, IV and V slightly wider than I–III. Dorsomedian carina absent on I, restricted to posterior half on II–IV, posterior third on VI and V; dorso-submedian carinae absent on segments I and II, restricted to posterior quarter on III–VI. Tergite VII pentacarinata, dorsomedian carinae present on anterior third but weakly granular. Sternite III not distinctly elevated anteriorly (fig. 19B). Spiracles on sternite III ovoid, width approximately 2× length. Surface of sternites III–VI smooth, sternite VII granular, with four granular carinae.

*Metasoma*: Metasomal segments longer than wide, but increasing in width posteriorly such that segment V is one third wider than segment I (fig. 37B, D). Carinae well developed, segments I and II with 10 carinae, lateral inframedian carinae of segment III weakly developed; segment IV with 8 carinae; segment V with 5 carinae.

*Hemispermaphore*: Flagelliform.

*Sexual dimorphism*: Adult males and females differ as follows. Males are smaller than females in total length. The carinae of the carapace, metasoma, and pedipalps are more finely granular in males than females. The pedipalp chela manus of males is incrassate and the fixed fingers slightly curved proximally (fig. 36D). The

chela manus of females is not incrassate (fig. 36D). The metasomal segments are proportionally broader in males, exaggerating the posterior increase in metasomal width, compared to females, in which the metasomal segments are more similar in width. Metasomal segments IV and V, though darker than the preceding segments in both sexes, are relatively paler in females than males.

*DISTRIBUTION*: This species is known from only two adjacent localities within the Parque Nacional Cavernas do Peruaçu, in the Município Januária of northern Minas Gerais state, Brazil (fig. 9B).

*ECOLOGY*: The known localities are situated on the ecotone of Brazilian caatinga and cerrado, a semiarid environment along the Peruaçu River, close to São Francisco River, which exhibits several microclimates due to topographical variation and the presence or absence of waterbodies. The type specimens were collected on calcareous sandy soil with sparse vegetation, at arid, high-elevation localities within the park. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

### *Jaguajir*, gen. nov.

Figures 1C, D, 2D, 6–8, 10B–D, 11D, 12A, 15C, D, F, 17C, 19C, D, F, 21D–F, 22D–F, 23S–V, 24A–H, 41–47

*Androctonus agamemnon* C.L. Koch, 1839 (= *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov.), type species, here designated.

*Androctonus* (part): C.L. Koch, 1839: 103–105, pl. CCV, fig. 506.

*Tityus* (part): C.L. Koch, 1850: 91; Pocock, 1902b: 377.

*Heteroctenus* (part): Pocock, 1893: 393; Meise, 1934: 42.

*Centrurus* (part): Kraepelin, 1895: 95; 1899: 89, 94; 1908: 187, 190, 194; Penther, 1913: 240–243, figs. 1–4; Werner, 1927: 358; Mello-Leitão, 1945: 286.



*Rhopalurus* (part): Pocock, 1902a: 37; 1902b:

377, 378; Borelli, 1910: 3–5; Lutz and Mello, 1922a: 25, 26; 1922b: 25; Penther, 1913: 242, 243, figs. 3, 4; Lutz and Mello, 1922b: 25; Mello-Campos, 1924a: 252, 275–286, pl. 5, fig. 27, pl. 8, fig. 34, pl. 10, fig. 35, 36, pl. 11, figs. 37–39; 1924b: 318, 341, 342–349, 351, 352, pl. 5, fig. 27, pl. 8, fig. 34, pl. 10, figs. 35, 36, pl. 11, figs. 37–39; Werner, 1927: 357, 358, fig. 2a–2d; Mello-Leitão, 1932: 11–15, 30, 31, 38, 39, 46, fig. 2a–2c, 8a–8c; Vellard, 1932: 556; Meise, 1934: 42; Viquez, 1935: 111, fig. 40; Prado, 1938: 347–349, figs. 1, 2; 1939: 6; 1940: 25–36, fig.; Roewer, 1943: 219; Mello-Leitão, 1945: 266–272, 274–279, 284–293, figs. 113–115, 118–121; Jaume, 1954: 1090; Bücherl, 1959: 268, 269; 1967: 112; 1969: 767; 1971: 327; Lucas and Bücherl, 1971: 635–637; 1972: 252, 262, 263, 276, 282, 283, pl. 11, fig. 38; Stahnke and Calos, 1977: 119; Lourenço, 1979: 215, fig. 7; Araújo, 1981: 235; Lucas et al., 1981: 128, 129, tables 1, 2; Lourenço, 1982a: 107, 108, 115–117, 122, 123, 128, 129, 133–139, figs. 1, 25–28, 39–62, 64–78, table 1; 1982b: 74, figs. 1–3; 1984b: 14; 1986a: 133, figs. 10, 11, 15; 1986b: 165, 170, fig. 7; 1990: 161; 1992: 55; 1997a: 590; Lourenço and Cloudsley-Thompson, 1995: 423–425, 428, figs. 1, 3–7; Lourenço and Pinto-da-Rocha, 1997: 183–185, figs. 4, 6, 8, 10, 12, 13, 15–21; Kovařík, 1998: 118; Fet and Lowe, 2000: 217, 218, 221, 222; Lourenço et al., 2000: 143; Lourenço, 2002: 92, 93, 104–106, 110, 111, 304–305, figs. 39, 192–204, 232–250; Manzanilla and Sousa, 2003: 9; Lourenço et al., 2004: figs. 9–10; Lenarducci et al., 2005: 7, table 2; Lira-da-Silva et al., 2005: 2; Teruel, 2006: 50–52; Lourenço, 2007: 359–361, fig. 1; Kamenz and Prendini, 2008: 9, table 2, pl. 44; Lourenço, 2008: 1, 3, 4–7, 9–12, figs. 2–4, 10–17, table 1; Teruel and Tietz, 2008: 1–3, 5–8, figs. 1–4, 7, table 1, 2; Volschenk et al., 2008: 651, 652, 654, 660, 661, 663,

664, 674, fig. 2E, tables 1, 2; Outeda-Jorge et al., 2009: 44, 46, 48, 49, fig. 4; Prendini et al., 2009: 222–224; Brazil and Porto, 2010: 25, 50, 59, 66, figs. 5B, 7A; Porto et al., 2010: 292–296, fig. 2A, B, table 1; Lourenço, 2014: 69; Ubinski et al., 2016: 122.

*Centruroides* (part): Werner, 1927: 357; 1934: 274, fig. 33a.

DIAGNOSIS: *Jaguajir*, gen. nov., differs from all other *rhopalurus* genera by the fused lateral ocular and anterior central submedian carinae of the carapace. It differs further from *Centruroides*, *Ischnotelson*, gen. nov., *Physoctonus*, and *Troglo-rhopalurus* by the presence of a pecten-sternite stridulatory organ (proximal pectinal teeth, dorsal surfaces without nodules but with regular striations, sternite III, ventromedian carina elevated anteriorly, ventrosubmedian surfaces forming paired depressions, covered by large, regularly spaced acuminate granules, lateral margins forming smooth, raised carina); from *Rhopalurus* and *Ischnotelson* by the separate (unfused) central lateral and posterior central submedian carinae of the carapace; from *Centruroides* and *Troglo-rhopalurus* by the robust metasoma, increasing in width posteriorly (more so in the adult male); from *Centruroides* by the presence of macrosetae on the dorsobasal surface of the pectinal teeth; from *Heteroctenus* by the absence of depressions in the male pectinal plate and the presence of a subaculear tubercle on the telson; from *Ischnotelson* by the separate (unfused) lateral ocular and central lateral carinae of the carapace and the telson vesicle not laterally compressed; from *Physoctonus* by the larger size (30–70 mm), the more distinct carapacial carinae, the setose proximal dorsal fulcra of the pectines, the incrassate pedipalp chela manus of the adult male, the bifurcate prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; and from *Troglo-rhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of

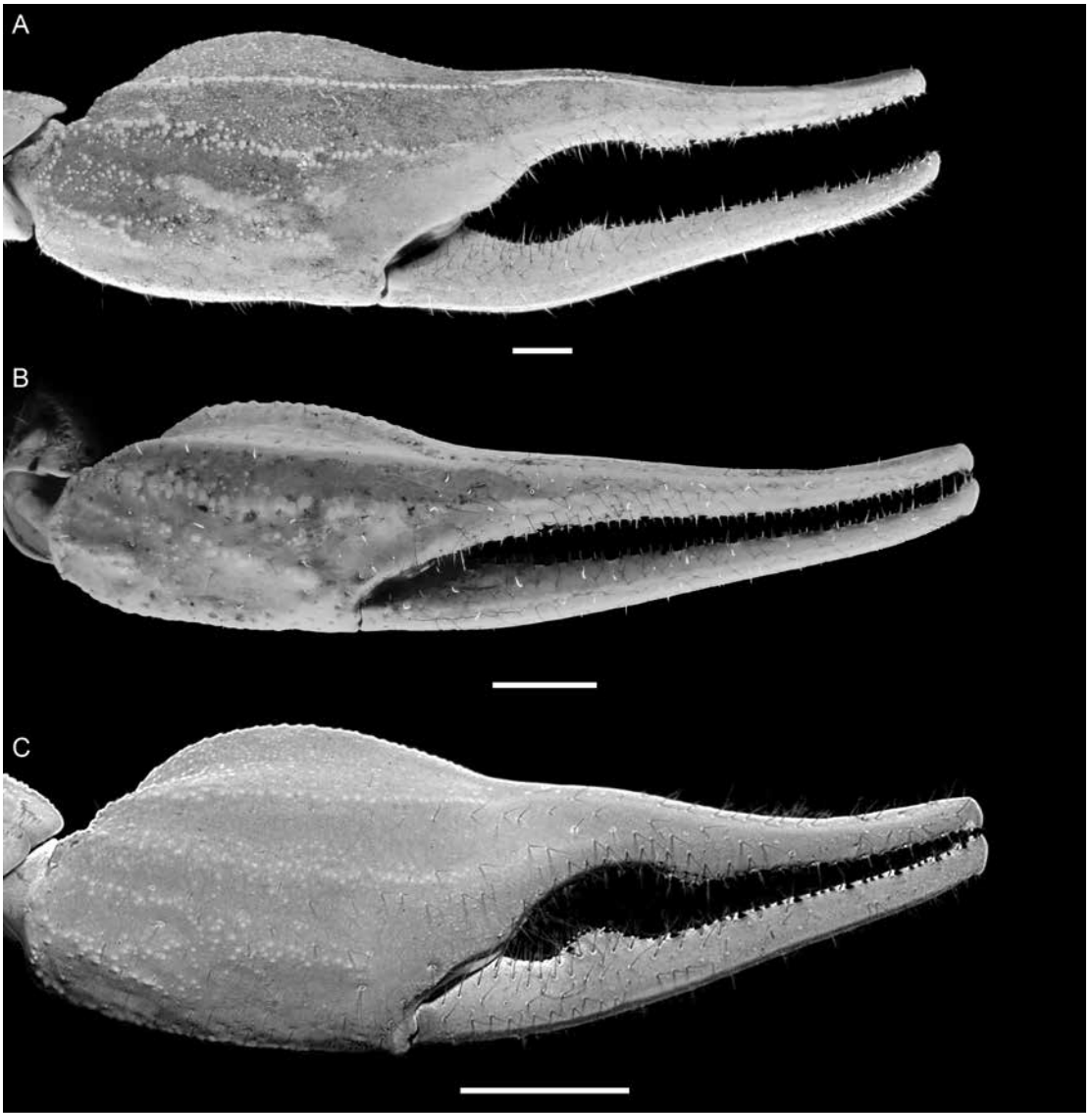


FIG. 41. *Jaguajir*, gen. nov., pedipalp chela, retrolateral aspect. A. *J. agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). B. *J. pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). C. *J. rochae* (Borelli, 1910), comb. nov., ♂ (MZSP). Scale bars = 2 mm.

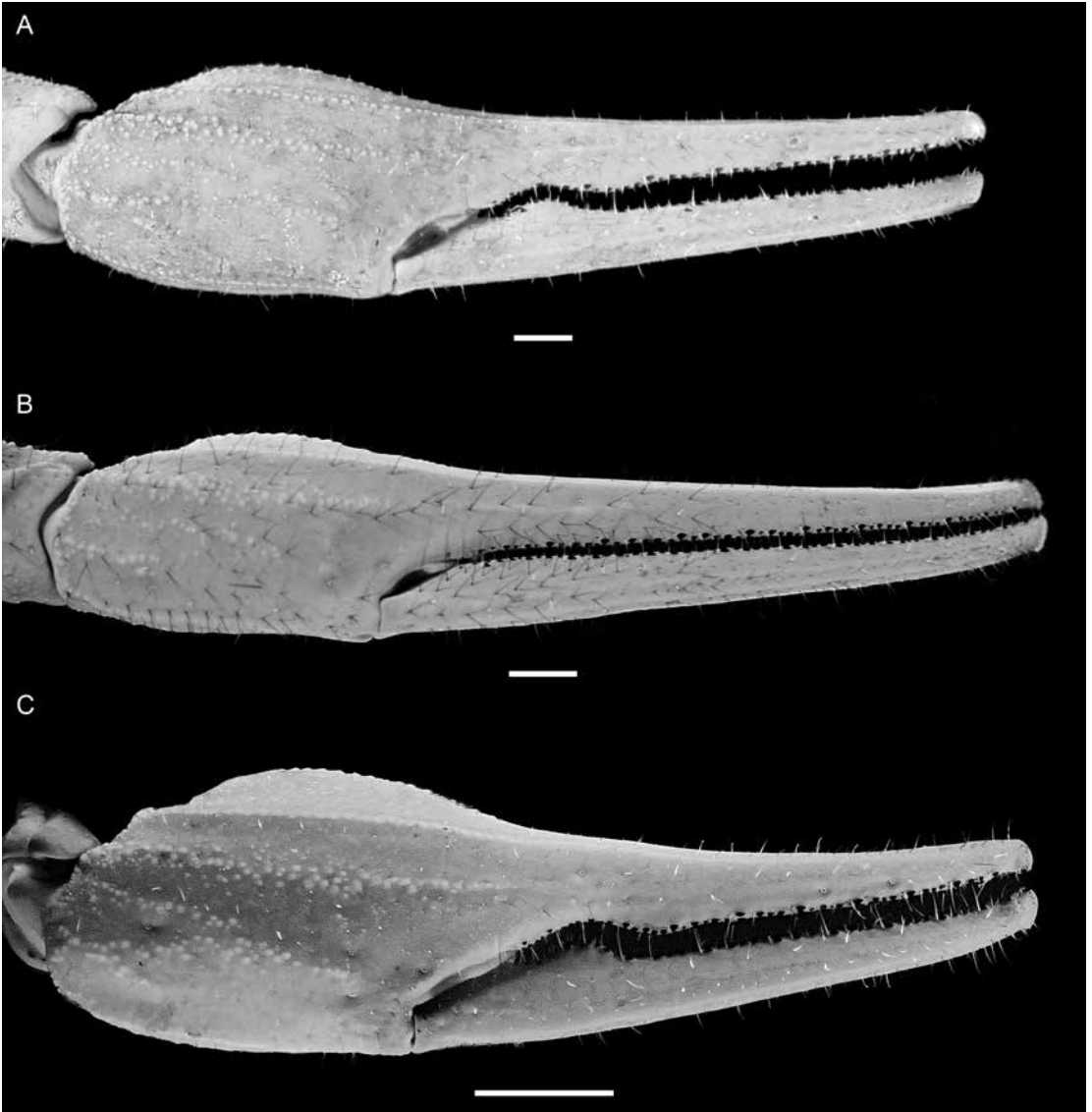


FIG. 42. *Jaguajir*, gen. nov., pedipalp chela, retrolateral aspect. A. *J. agamemnon* (C.L. Koch, 1839), comb. nov., ♀ (MZSP). B. *J. pinto* (Mello-Leitão, 1932), comb. nov., ♀ (MZSP). C. *J. rochae* (Borelli, 1910), comb. nov., ♀ (AMNH). Scale bars = 2 mm.

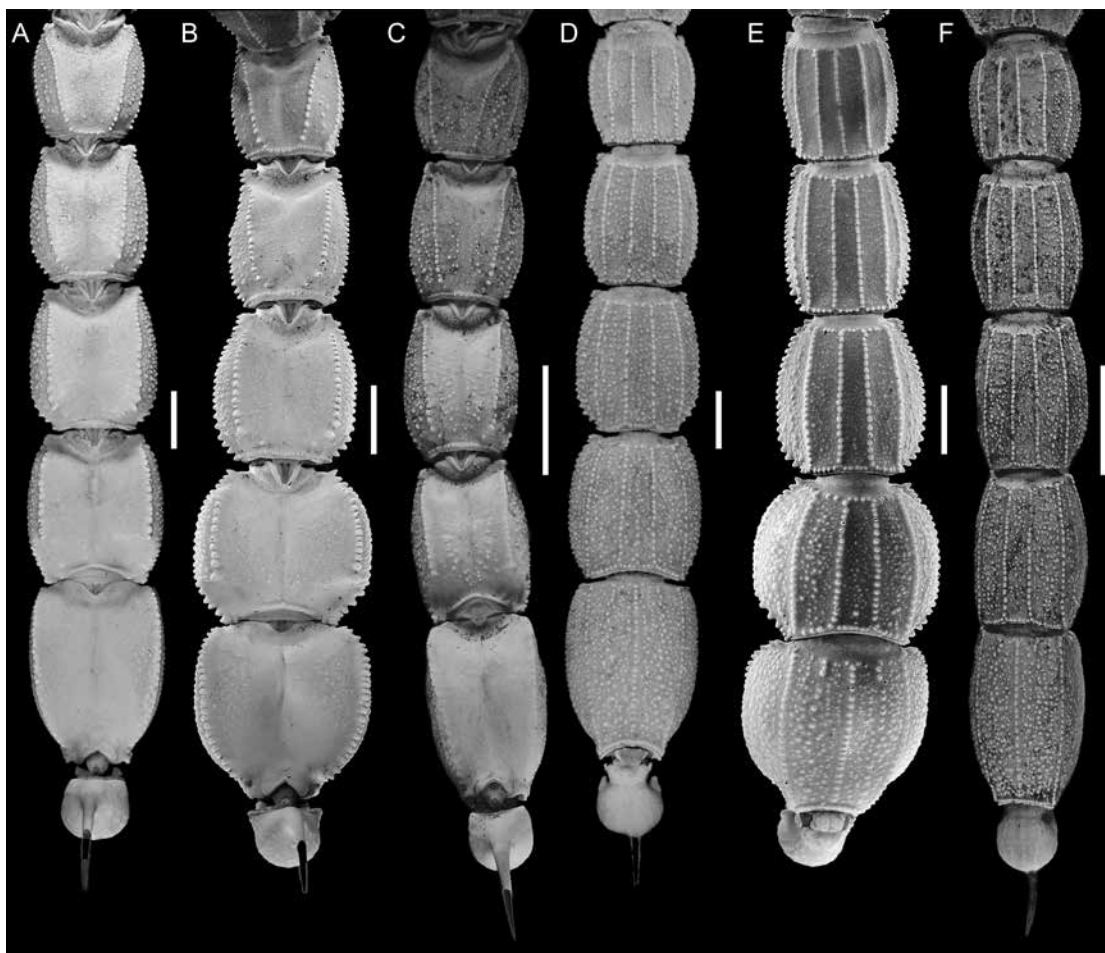


FIG. 43. *Jaguajir*, gen. nov., metasoma and telson, dorsal (A–C) and ventral (D–F) aspects. A, D. *J. agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). B, E. *J. pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). C, F. *J. rochae* (Borelli, 1910), comb. nov., ♂ (AMNH). Scale bars = 5 mm.

the adult male emarginate, with a distinct gap evident between them, when closed.

**ETYMOLOGY:** The name is taken from the Tupi word *jaguajira*, meaning “scorpion,” or “one who devours” (Von Martius, 1867). It is masculine in gender.

**DESCRIPTION:** The following general description outlines characters common to the species of *Jaguajir*, gen. nov.

**Total length:** Large, robust scorpions (total length, 50–110 mm).

**Color:** Coloration varies considerably among the three species of the genus (fig. 1C, D), with *J.*

*pinto* predominantly dark brown to black, *J. rochae* predominantly pale to dark yellow, and *J. agamemnon* bicolored, with carapace and tergites I–VI brown, and tergite VII, metasoma, telson, pedipalps, and legs lighter, somewhat orange. Despite the differences, in all three species, the pectines are paler than the carapace, tergites, and metasoma; the legs, chelicerae, and pedipalps similar to or paler than the carapace, tergites, and metasoma; the coxosternal region and sternites slightly paler than the carapace, tergites, and metasoma; and sternite VII is slightly darker than the preceding sternites.

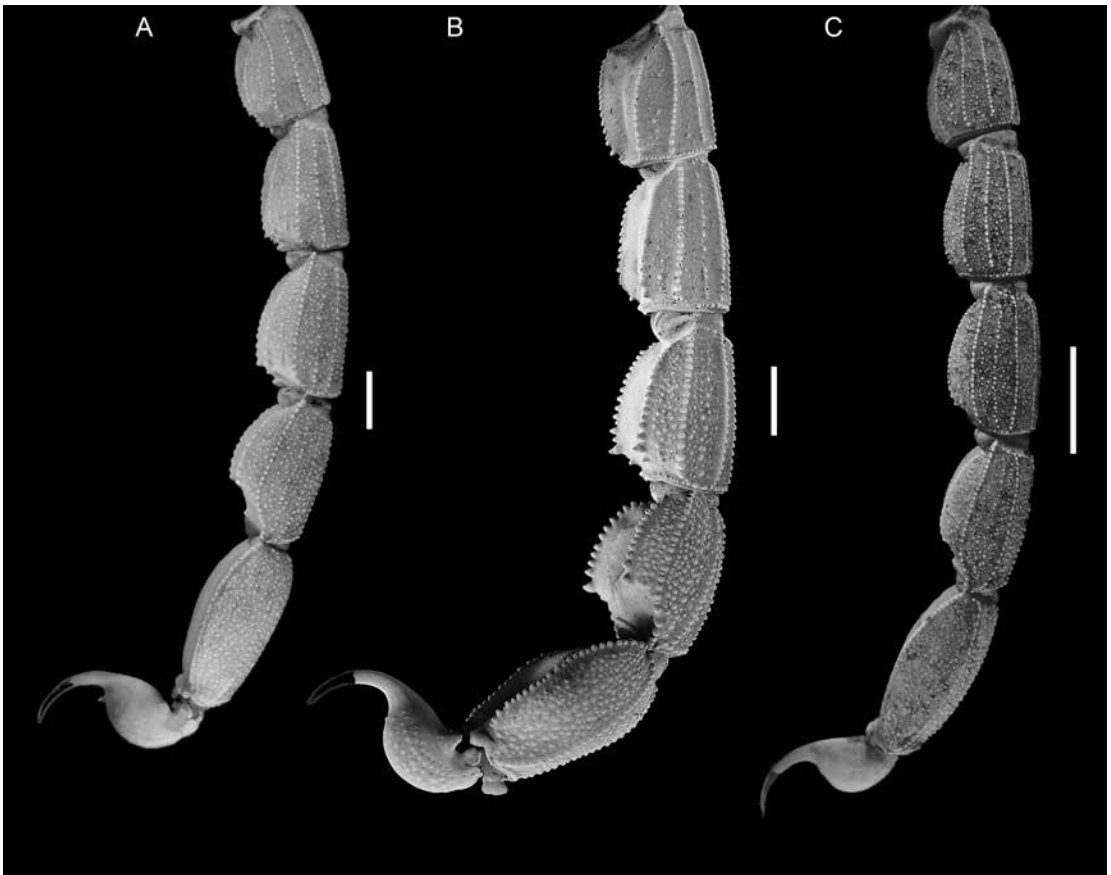


FIG. 44. *Jaguajir*, gen. nov., metasoma and telson, lateral aspect. A. *J. agamemnon* (C.L. Koch, 1839), comb. nov., ♂ (MZSP). B. *J. pinto* (Mello-Leitão, 1932), comb. nov., ♂ (MZSP). C. *J. rochae* (Borelli, 1910), comb. nov., ♂ (AMNH). Scale bars = 5 mm.

*Chelicerae*: Base, dorsal surface with medial transverse row of well-developed tubercles.

*Carapace*: Median ocular tubercle raised (fig. 15C, D, F); two median ocelli; three pairs of lateral macroocelli; one pair of lateral microocelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular and anterior central submedian carinae distinct, coarsely granular to costate-granular, and fused; central lateral and posterior central submedian carinae distinct, coarsely granular to costate-granular, and separate (unfused).

*Pedipalps*: Pedipalp femur retrolateral accessory carinae absent. Pedipalp chela manus of

adult male incrassate, fixed and movable fingers curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, distinct gap present between fingers proximally, when closed (fig. 41), manus of female not incrassate, fixed and movable fingers not curved proximally, such that proximal dentate margin sublinear, little or no gap present between them proximally, when closed (fig. 42); manus, proventral carina present, promedian carina absent; fixed and movable fingers, median denticle rows each comprising eight oblique subrows of primary denticles (*J. agamemnon* and *J. rochae*), or nine and 13 subrows, respectively (*J. pinto*), flanked closely by



FIG. 45. *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (MZSP). C, D. ♀ (MZSP). Scale bars = 10 mm.

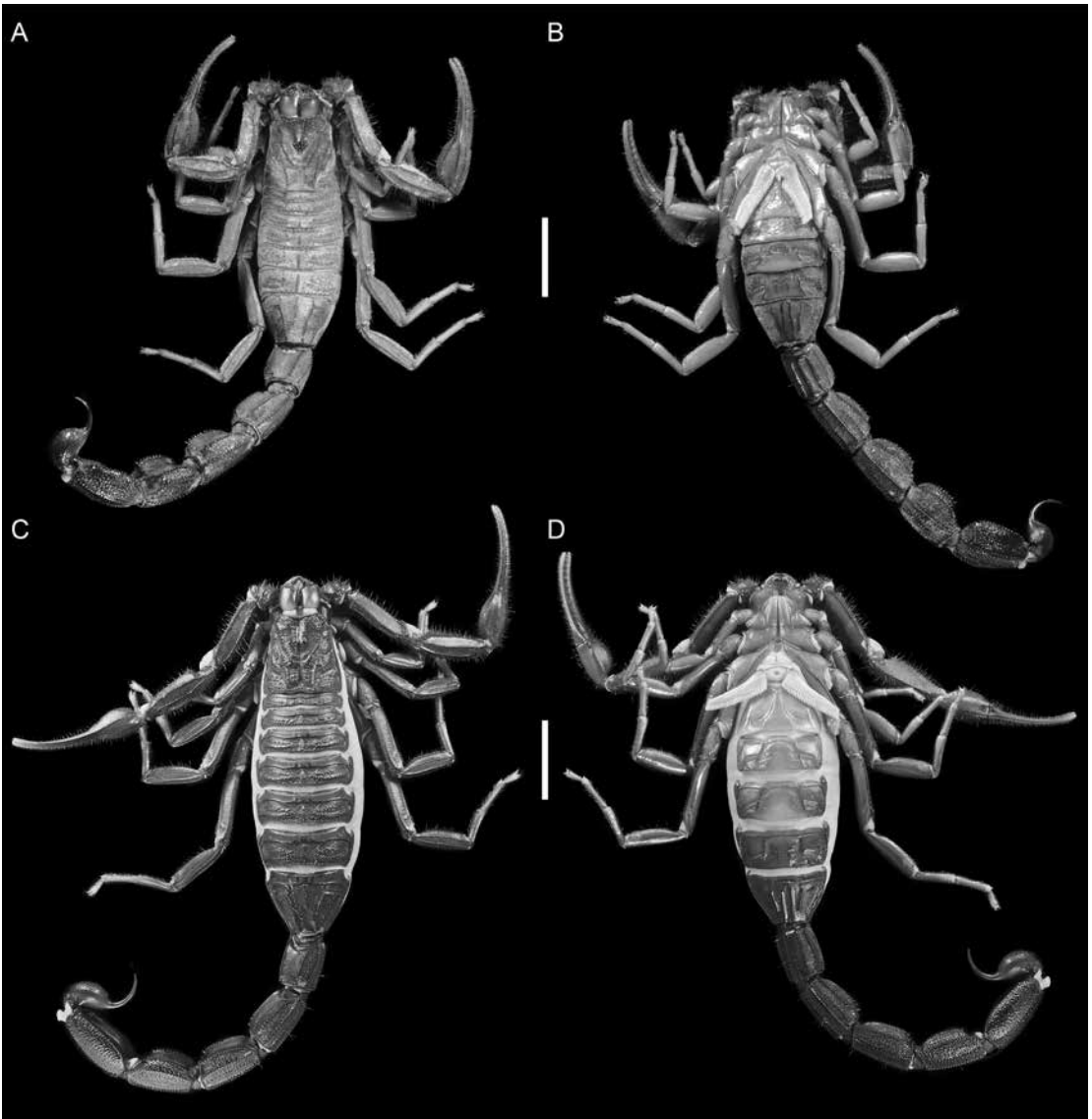


FIG. 46. *Jaguajir pintoï* (Mello-Leitão, 1932), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (MZSP). C, D. ♀ (OUMNH). Scale bars = 10 mm.

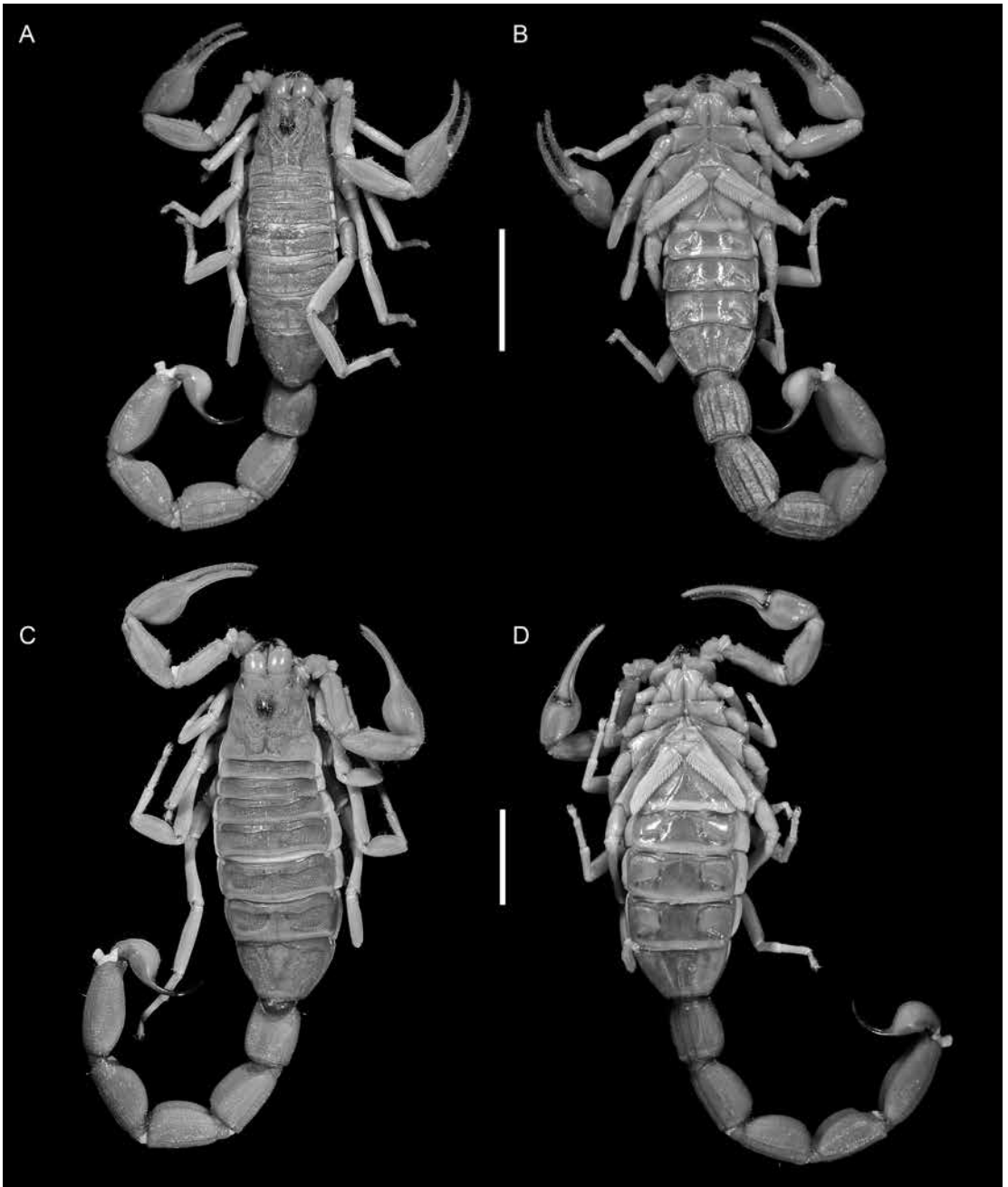


FIG. 47. *Jaguajir rochae* (Borelli, 1910), comb. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 10 mm.



pro- and retrolateral accessory (supernumerary) denticles; movable finger with or without proximal lobe (fig. 17C). Pedipalps orthobothriotaxic Type A,  $\alpha$  configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  proximal to trichobothrium  $et$ .

**Legs:** Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with distinct pro- and retroventral rows of fine, acuminate macrosetae.

**Pectines:** Pectinal plate without median depressions (male), anterior margin without sulcus (figs. 11D, 19C, D, F). Pectines proximally expanded, at least 1.5 $\times$  wider proximally than medially; proximal dorsal fulcra setose; pectinal teeth almost straight, slightly curved laterally, proximal teeth, dorsal surfaces sinuous, due to presence of distal elevation, covered with striations, dorsobasal surfaces with macrosetae; pectinal sensillae peg shaped (fig. 12A).

**Mesosoma:** Tergites IV and V wider than I–III (figs. 45–47); I–VI tricarinate, dorsomedian carinae finely granular, restricted to posterior two thirds on I–V, complete on VI; dorsosubmedian carinae finely granular, restricted to posterior third on I–III, restricted to posterior quarter on IV–VI. Tergite VII pentacarpinate, dorsomedian carina restricted to anterior third of segment. Sternites smooth, carinate obsolete, more developed on VI and VII; sternite III, lateral margins forming smooth, raised carina, ventromedian carina elevated anteriorly, ventrosubmedian surfaces forming paired depressions covered by large, regularly spaced acuminate granules; respiratory spiracles (stigmata), width more than 5 $\times$  length (figs. 10 B–D).

**Metasoma:** Metasoma robust, increasing slightly to markedly in width posteriorly, segment V slightly or considerably wider than I in adult male, similar or slightly wider than I in adult female (figs. 43, 44). Segments I–III each with 10 distinct, costate-granular carinae, IV with eight distinct, costate-granular carinae, V with seven

distinct but less pronounced, granular carinae; dorsosubmedian carinae obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV, more pronounced on segment I; dorsolateral carinae complete on segments I–IV, and terminating in prominent, spiniform granules posteriorly on II and, to a greater extent, III on IV, absent on V; lateral suprmedian carinae complete on segments I–V; lateral inframedian carinae complete on segments I–III, absent on IV and V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third of V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely to coarsely granular.

**Telson:** Vesicle subspherical, not laterally compressed, narrower than metasoma V; anterodorsal lateral lobes prominent (*J. pinto*) or reduced (*J. agamemnon* and *J. rochae*); lateral and ventral surfaces granular or smooth, with shallow ventromedian carina; subaculear tubercle present, prominent and spinoid (*J. agamemnon*) or vestigial (*J. pinto* and *J. rochae*).

**Hemispermaphore:** Flagelliform; flagellum, elongate and narrow (figs. 23S–V, 24A–H); trunk markedly concave; three lobules, ental (LI), ectal (LE), and basal (LB); LI inclined slightly to sinistral side relative to axis of trunk and continuous until flagellar base; flagellar base narrow, half (*J. pinto* and *J. rochae*) to one third (*J. agamemnon*) maximum width of trunk; LE length ca. half (*J. pinto*) to two thirds (*J. agamemnon* and *J. rochae*) that of LI, with sharp tip and base width similar to that of LB; LB short, carina shaped, with sharp tip (*J. pinto*), angle between LB and LE 45° (*J. agamemnon* and *J. rochae*) to 80° (*J. pinto*).

**Cytogenetics:** The diploid chromosome number of *J. agamemnon*, *J. pinto*, and *J. rochae* (table 2) is  $2n = 28$  (Ubinski et al., 2016).

**INCLUDED SPECIES:** *Jaguajir agamemnon* (C.L. Koch, 1839), comb. nov.; *Jaguajir pinto* (Mello-Leitão, 1932), comb. nov.; *Jaguajir rochae* (Borelli, 1910), comb. nov.

**DISTRIBUTION:** *Jaguajir* is endemic to north and northeastern South America (figs. 6–8). Confirmed locality records occur in Brazil and Guyana, but the genus may also occur in Ven-

ezueta (Prendini et al., 2009). A single from record from Kourou, French Guiana (Lourenço, 2008) remains to be confirmed.

**ECOLOGY:** The three species of this genus are typically associated with open vegetation (caatinga and cerrado; fig. 2D), and have been collected under stones during the day and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**REMARKS:** The consistent paraphyly of *Rhopalurus* in the analyses by Esposito et al. (in review) and the identification of a well-defined, monophyletic group, comprising three species from northern and northeastern Brazil, i.e., *R. agamemnon*, *R. pinto*, and *R. rochae*, justifies the creation of the new genus and the transfer of those species to it, resulting in three new combinations (fig. 13). The recognition of a new genus is consistent with the cytogenetic study of Ubinski et al. (2016) which identified a diploid chromosome number of  $2n = 28$  for *R. agamemnon*, *R. pinto*, and *R. rochae* (table 2).

***Jaguajir agamemnon* (C.L. Koch, 1839),  
comb. nov.**

Figures 1C, 7, 10B, 12A, 15C, 19C, 21D, 22D,  
23S–V, 41A, 42A, 43A, D, 44A, 45

*Androctonus agamemnon* C.L. Koch, 1839: 103–  
105, pl. CCV, fig. 506.

*Tityus agamemnon*: C.L. Koch, 1850: 91; Pocock,  
1902b: 377.

*Heteroctenus agamemnon*: Pocock, 1893: 393.

*Centrurus agamemnon*: Kraepelin, 1895: 95;  
1899: 89, 94; 1908: 187, 190, 194; Penther,  
1913: 240.

*Rhopalurus borellii* Pocock, 1902b: 377, 378 (syn-  
onymized by Lourenço, 1982a: 128); 1902a:  
37; Mello-Campos, 1924a: 276, 285, 286;  
1924b: 318, 342, 351, 352; Werner, 1927:  
358; Prado, 1939: 6; Mello-Leitão, 1945: 266,  
270, 272; Bücherl, 1959: 268; Lucas et al.,  
1981: 129, table 2.

*Rhopalurus agamemnon*: Pocock, 1902a: 37; Mello-  
Campos, 1924a: 252, 275, 276; 1924b: 318,  
341, 342; Mello-Leitão, 1932: 14, 30; Prado,  
1940: 25, 27; Mello-Leitão, 1945: 267, 269, 270;  
Bücherl, 1959: 268; 1971: 327; Lucas and  
Bücherl, 1972: 263; Stahnke and Calos, 1977:  
119; Lourenço, 1982a: 123, 136, figs. 1, 64–76,  
78, table 1; 1986a: 133, fig. 15; 1986b: 165, fig.  
7; 1990: 161; 1992: 55; Kovařík, 1998: 118; Fet  
and Lowe, 2000: 218; Lenarducci et al., 2005:  
7, table 2; Lourenço, 2008: 6; Prendini et al.,  
2009: 222, 223; Brazil and Porto, 2010: 41, 50,  
59, 66, figs. 2A, 5A; Porto et al., 2010: 292–  
295, table 1; Ubinski et al., 2016: 122.

*Centrurus intermedius* Penther, 1913: 240 (syn-  
onymized by Lourenço, 1982a: 123).

*Rhopalurus acromelas* Lutz and Mello, 1922a: 25,  
26; Mello-Campos, 1924a: 252, 276, 282,  
283, pl. 11, fig. 38; 1924b: 318, 342, 347, 348,  
pl. 11, fig. 38; Werner, 1927: 358; Mello-  
Leitão, 1932: 15, 31; Meise, 1934: 42; Prado,  
1940: 26, 29; Mello-Leitão, 1945: 266, 267–  
269; Bücherl, 1959: 268; 1971: 327; Lou-  
renço, 1982a: 128, 129, 135, 137, figs. 77, 78,  
table 1; 1986a: 133, fig. 11; 1986b: 165, fig. 7;  
1990: 161; 1992: 55; Kovařík, 1998: 118; Fet  
and Lowe, 2000: 217, 218; Lenarducci et al.,  
2005: 7, table 2; Kamenz and Prendini, 2008:  
9, table 2; Lourenço, 2008: 1; Prendini et al.,  
2009: 222, 223; Porto et al., 2010: 292, 295,  
table 1; syn. nov.

*Rhopalurus melleipalpus* Lutz and Mello, 1922b:  
25 (previously synonymized with *R. acrome-  
las* by Lourenço, 1982a: 129); Mello-Cam-  
pos, 1924a: 252, 275, 283, pl. 11, fig. 37;  
1924b: 318, 341, 348, 349, pl. 11, fig. 37;  
Werner, 1927: 358; Mello-Leitão, 1932: 15,  
31; Meise, 1934: 42; Prado, 1940: 26, 32;  
Lourenço, 1982a: 129; syn. nov.

*Rhopalurus borelli*: Mello-Campos, 1924a: 252;  
Mello-Leitão, 1932: 15, 31; Prado, 1938: 347–  
349, fig. 2; 1940: 27, 35, 36; Bücherl, 1971: 327;  
Lucas and Bücherl, 1972: 262, 263, map;  
Araújo, 1981: 235; Lourenço, 2008: 6.

- Rhopalurus iglesiasi* Werner, 1927: 357, 358, fig. 2a–d (synonymized with *R. borellii* by Lucas and Bücherl, 1972: 262); Mello-Leitão, 1932: 15, 31; Meise, 1934: 42; Prado, 1938: 347–349, fig. 2; 1939: 6; 1940: 26, 33; Roewer, 1943: 219; Mello-Leitão, 1945: 267, 274; Bücherl, 1959: 268; 1971: 327; Lourenço, 1979: 215; 1982a: 128; syn. nov.
- Rhopalurus lambdophorus* Mello-Leitão, 1932: 12–15, 31, 38, 39, fig. 8, 8a–8c (previously synonymized with *R. acromelas* by Lourenço, 1982a: 129); Prado, 1940: 26, 30; Mello-Leitão, 1945: 266, 278, 279; Lourenço, 1982a: 129; syn. nov.
- Rhopalurus intermedius*: Mello-Leitão, 1932: 14; Prado, 1940: 26, 28; Mello-Leitão, 1945: 267, 277, 278; Bücherl, 1959: 268.
- Heteroctenus borellii*: Meise, 1934: 42.
- Centruroides (Rhopalurus) borellii*: Werner, 1934: 274, fig. 33, 33a.
- Rhopalurus dorsomaculatus* Prado, 1938: 347–349, figs. 1, 2 (previously synonymized with *R. borellii* by Lucas and Bücherl, 1972: 262); Prado, 1940: 26, 33, fig.; Lourenço, 1982a: 128; syn. nov.
- Rhopalurus goiasensis* Prado, 1940: 26, 31, 32, fig. (previously synonymized with *R. acromelas* by Lourenço, 1982a: 133); syn. nov.
- Rhopalurus iglesiasi dorsomaculatus*: Mello-Leitão, 1945: 267, 275–277, figs. 113, 114; Bücherl, 1959: 268; Lucas and Bücherl, 1971: 636, figs. 1–4.
- Rhopalurus stenochirus goyasensis*: Mello-Leitão, 1945: 267; Lourenço, 1979: 215.
- Rhopalurus stenochirus melleipalpus*: Mello-Leitão, 1945: 267, 292, 293.
- Rhopalurus stenochirus goiasensis*: Mello-Leitão, 1945: 290–292; Lucas and Bücherl, 1972: 263.
- Rhopalurus borelli borelli*: Jaume, 1954: 1090.
- Rhopalurus stenochirus goiazensis*: Bücherl, 1959: 269.
- Rhopalurus agamemnon*: Porto et al., 2010: 294, fig. 2A.

TYPE MATERIAL: **BRAZIL**: *Androctonus agamemnon*: Holotype [sex?] (ZMB) [lost]. Ceará: *Rhopalurus melleipalpus*: Holotype ♀ [lost], Assare. *Rhopalurus lambdophorus*: Holotype ♂ [lost; original type depository unknown; ?“Museu Rocha, Ceará”], Ceará. Goiás: *Rhopalurus borellii*: 1 ?juv. ♀ lectotype [desig. Lourenço, 1982a: 139] (BMNH 1842.6.20.1), Goiás; paralectotype ♂ (BMNH). *Rhopalurus dorsomaculatus*: Holotype ♀ (IBSP 35), Cana Brava, Nova Roma. *Rhopalurus goiasensis*: 1 juv. ?♂ holotype (IBSP 66), paratype ♀ (IBSP 31), Cana Brava. Piauí: *Centruroides intermedius*: Holotype ♀ (NMW 2246), Barra do Parnaguá. *Rhopalurus acromelas*: 1 ♂, 1 ♀ syntypes [lost], Terezina. *Rhopalurus iglesiasi*: 1 ♂, 8 ♀ syntypes (SMF 5280), Piauí.

DIAGNOSIS: *Jaguajir agamemnon* is most closely related to *J. pinto*. The two species resemble one another, and differ from *J. rochae*, in their darker coloration and broader metasoma. Whereas the base coloration is brown to black, and the metasoma of the male markedly wider posteriorly in *J. agamemnon* and *J. pinto*, the base coloration is pale to dark yellow, and the metasoma of the male slightly wider posteriorly in *J. rochae*. Additionally, the fixed and movable fingers of the pedipalp chela of the male are markedly curved, creating a large proximal gap between them, and the proximal lobe on the fixed finger of the male is reduced or absent in *J. agamemnon* and *J. pinto*, whereas the fixed and movable fingers of the pedipalp chela of the male are slightly curved, creating a small proximal gap between them, and the proximal lobe on the fixed finger of the male exhibits a prominent proximal lobe, in *J. rochae*. Furthermore, the subaculear tubercle of the telson is well developed and spinoid in *J. agamemnon*, but very reduced, forming a small protuberance, in *J. pinto* and *J. rochae*.

*Jaguajir agamemnon* can be further differentiated from *J. pinto* as follows. *Jaguajir agamemnon* is bicolored and generally paler, with the prosoma and tergites I–VI brown and tergite VII, metasoma, telson, pedipalps, and legs lighter, somewhat orange, whereas *J. pinto*, is almost

uniformly dark, with the prosoma, tergites, metasoma, telson, and pedipalps dark brown to black, and the sternites, legs, and telson somewhat lighter, reddish brown. Additionally, the metasoma of *J. agamemnon* is proportionally more slender, with metasomal segment V approximately 1.5× longer than wide, than that of *J. pintoi*, with metasomal segment V almost as wide as long. The dorsolateral carinae of the metasomal segments comprise small, acuminate granules in *J. agamemnon*, whereas the carinae comprise blunt spiniform granules, increasing in size posteriorly, especially prominent on segments III and IV, in *J. pintoi*.

**DISTRIBUTION:** *Jaguajir agamemnon* is endemic to northeastern Brazil and recorded from the states of Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Pernambuco, Piauí, and Tocantins (fig. 7).

**ECOLOGY:** This species inhabits open savannah. Personally collected specimens were found under stones during the day and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**REMARKS:** The evidence and analyses presented by Esposito et al. (in review) demonstrated that *R. acromelas* is conspecific with *J. agamemnon*, justifying its synonymy, and that of its former synonyms, with the latter, resulting in the following new synonyms: *Rhopalurus acromelas* Lutz and Mello, 1922 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.; *Rhopalurus melleipalpus* Lutz and Mello, 1922 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.; *Rhopalurus iglesiasi* Werner, 1927 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.; *Rhopalurus lambdophorus* Mello-Leitão, 1932 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.; *Rhopalurus dorsomaculatus* Prado, 1938 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.; *Rhopalurus goiasensis* Prado, 1940 = *Jaguajir agamemnon* (C.L. Koch, 1839), syn. nov.

**MATERIAL EXAMINED: BRAZIL: Maranhão:** Balsas, 07°28'44"S 46°07'09"W, 4.vi.2008, H.Y. Yamaguti et al., 1 ♀ (MZSP 31132/AMCC [LP

9948]), 1 juv. ♂ (MZSP 31133/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/AMCC [LP 9692]), 04°56'50"S 43°29'45"W, 15.viii.2008, R. Pinto-da-Rocha et al., 1 juv. ♂ (MZSP 31134/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). *Piauí:* Barras, 04°19'04"S 42°18'26"W, 18.viii.2008, R. Pinto-da-Rocha et al., 1 subad. ♀ (MZSP 30884/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/AMCC [LP 9696]), 1 subad. ♂ (MZSP 31157/AMCC [LP 9933]), 1 juv. ♂ (MZSP 31156/AMCC [LP 9939]); Oeiras, 06°58'28"S 42°06'31"W, 2–3.iv.2008, H.Y. Yamaguti et al., 1 ♂ (MZSP 31160/AMCC [LP 9954]), 1 ♀ (MZSP 31161/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/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/AMCC [LP 9695]), 1 juv. ♂ (MZSP 31169/AMCC [LP 9960]); Teresina, Campus UFPI, 05°02'43.5"S 42°46'13.4"W, 16.viii.2008, UFPI, 1 ♂ (MZSP 31170/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/AMCC [LP 9938]), 1 subad. ♀ (MZSP 31180/AMCC [LP 9934]), 1 juv. ♂ (MZSP 31181/

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/AMCC [LP 9694]), 1 subad. ♀ (MZSP 31193/AMCC [LP 9935]).

***Jaguajir pinto* (Mello-Leitão, 1932),**  
comb. nov.

Figures 6, 10C, D, 15D, 19D, E, 21E, 22E, 24A–D, 41B, 42B, 43B, E, 46

*Rhopalurus pinto* Mello-Leitão, 1932: 11, 12, 15, 31, 38, 46, fig. 2a–c; Prado, 1940: 27, 36; Mello-Leitão, 1945: 266, 284, 285, fig. 115 (part); Bücherl, 1967: 112; 1969: 767; Lourenço, 1982a: 107, 108, 115, 117, fig. 78 (part); Kovařík, 1998: 118; Fet and Lowe, 2000: 221; Teruel, 2006: 51, 52; Teruel and Tietz, 2008: 2, 3, 5–9, figs. 1–4, 7, tables 1, 2; Lourenço, 2008: 4, 7, figs. 2–4; Prendini et al., 2009: 222, 223; Ubinski et al., 2016: 122.

*Rhopalurus laticauda pinto*: Lourenço, 1982a: 115–117, 136, figs. 25–28, 39–46, table 1; 1984b: 14; 1986a: 133, fig. 10; 1986b: 170, fig. 7; 1992: 55; 1997a: 590; Fet and Lowe, 2000: 221; Teruel and Tietz, 2008: 8.

*Rhopalurus piceus* Lourenço and Pinto-da-Rocha, 1997: 183, figs. 4, 6, 8, 10, 12, 13, 15–20 (synonymized by Teruel and Tietz, 2008: 2, 8); Kovařík, 1998: 118; Fet and Lowe, 2000: 221; Lourenço, 2002: 104, 105, 110, 111, 304–305, figs. 232–238; Lenarducci et al., 2005: 7, table 2; Teruel, 2006: 52; Teruel and Tietz, 2008: 8; Lourenço, 2008: 3, 6; 2014: 69.

*Rhopalurus pinto kouroensis* Lourenço, 2008: 4–7, 9–12, figs. 2–4, 10–17, table 1; syn. nov.

*Rhopalurus pinto pinto*: Lourenço, 2008: 6.

*Rhopalurus crassicauda kouroensis*: Prendini et al., 2009: 222.

TYPE MATERIAL: **BRAZIL:** *Roraima:* *Rhopalurus pinto*: Holotype ♂ (IOC) [lost], Rio Tacutú.

*Rhopalurus piceus*: Holotype ♀ (MZSP 15173), paratype ♀ (MZSP), Tepequén, 15–22.vi.1993, M. Vanzolini; paratype ♂ (MZSP 10565), Surumu, 04°12'S 60°47'W, 10.vii.1986, C.M. Carvalho; paratype ♀ (MNHN RS-8497), Rio Branco, Surumu, xi.1966, M. Alvarenga. *Rhopalurus pinto kouroensis*: Holotype ♂ (MNHN RS-8631), **FRENCH GUIANA:** *Kourou:* taches forestières de la piste Dejrad, viii.1975, M. Boulard and P. Pompanon.

DIAGNOSIS: *Jaguajir pinto* is most closely related to *J. agamemnon*. The two species resemble one another, and differ from *J. rochae*, in their darker coloration and broader metasoma. Whereas the base coloration is brown to black, and the metasoma of the male markedly wider posteriorly in *J. agamemnon* and *J. pinto*, the base coloration is pale to dark yellow, and the metasoma of the male slightly wider posteriorly in *J. rochae*. Additionally, the fixed and movable fingers of the pedipalp chela of the male are markedly curved, creating a large proximal gap between them, and the proximal lobe on the fixed finger of the male is reduced or absent, in *J. agamemnon* and *J. pinto*, whereas the fixed and movable fingers of the pedipalp chela of the male are slightly curved, creating a small proximal gap between them, and the proximal lobe on the fixed finger of the male exhibits a prominent proximal lobe, in *J. rochae*. Furthermore, the subaculear tubercle of the telson is very reduced, forming a small protuberance, in *J. pinto*, as in *J. rochae*, whereas it is well developed and spinoid in *J. agamemnon*.

*Jaguajir pinto* can be further differentiated from *J. agamemnon* as follows. *Jaguajir pinto* is almost uniformly dark, with the prosoma, tergites, metasoma, telson, and pedipalps dark brown to black, and the sternites, legs, and telson somewhat lighter, reddish brown, whereas *J. agamemnon* is bicolored and generally paler, with the prosoma and tergites I–VI brown and tergite VII, metasoma, telson, pedipalps, and legs lighter, somewhat orange. Additionally, the metasoma of *J. pinto* is proportionally more robust, with metasomal segment V almost as wide as long, than that of *J. agamem-*

*non*, with metasomal segment V approximately 1.5× longer than wide. The dorsolateral carinae of the metasomal segments comprise blunt spiniform granules, increasing in size posteriorly, especially prominent on segments III and IV in *J. pinto*, whereas the carinae comprise small, acuminate granules in *J. agamemnon*.

**DISTRIBUTION:** *Jaguajir pinto* is endemic to northern Brazil (recorded from the states of Amazonas, Pará and Roraima) and Guyana (Roraima Province) (fig. 6). It may also be present in the state of Bolívar in Venezuela (Prendini et al., 2009) but has yet to be recorded there. A single record from Kourou, French Guiana, remains to be confirmed.

**ECOLOGY:** This species inhabits open vegetation formations. Specimens collected by the authors were found under stones during the day and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**REMARKS:** Lourenço (1982a, 1984a, 1986a, b, 1992, 1997a) relegated *R. pinto* to a subspecies of *R. laticauda* and synonymized *R. crassicauda* therewith, but later (Lourenço and 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 and Lowe (2000) continued to list it as a subspecies of *R. laticauda* in accordance with Lourenço (1982a). 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 and 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 that *R. piceus* may yet prove to be valid and rejected the suggestion that *R. crassicauda* is a junior synonym of *R. laticauda*, instead proposing that it might be a subspecies thereof and creating a new subspecies, *R. crassicauda paruiensis*, 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 and Tietz (2008), and the suggestion that *R. crassicauda* is probably a junior synonym of *R. laticauda*. The evidence and analyses presented by Esposito et al. (in review) supported the validity of *J. pinto* as distinct from *R. laticauda*, upheld the synonymy of *R. piceus* therewith, and justified the synonymy: *Rhopalurus pinto kouroensis* Lourenço, 2008 = *Jaguajir pinto* (Mello-Leitão, 1932), syn. nov. *Rhopalurus crassicauda*, on the other hand, was determined to be conspecific with *R. laticauda* and synonymized accordingly, below.

**MATERIAL EXAMINED: 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/AMCC [LP 9928]), 1 juv. ♂ (MZSP 31177/AMCC [LP 9944]); Serra do Tepequem, 31.v–5.vi.2011, Equipe Herpeto USP, 1 ♂, 2 ♀, 1 juv. ♀ (MZSP 54207); Vila Tepequén, Amajari, 03°47'54"N 61°43'08"W, 11.xi.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 1 ♀ (MZSP 30862/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/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), comb. nov.**

Figures 1D, 2D, 8, 11D, 15F, 17C, 19F, 21F, 22F, 24E–H, 41C, 42C, 43C, F, 44C, 47

*Rhopalurus rochae* Borelli, 1910: 3–5; Mello-Leitão, 1932: 31; Meise, 1934: 42; Lourenço, 1982a: 122, 135, figs. 47–62, 78, table 1; 1982b: 74, figs. 1–3; 1986b: 165, fig. 7; 1990: 161; Kovařík, 1998: 118; Fet and Lowe, 2000: 222; Kamenz and Prendini, 2008: 9, table 2, pl. 44; Volschenk et al., 2008: 651, 652, 654, 660, 661, 663, 664, 674, fig. 2E, tables 1, 2; Prendini et al., 2009: 222–224.

- Centrurus stenochirus* Penther, 1913: 240–242, figs. 1, 2 (synonymized by Lourenço, 1982a: 122).
- Centrurus barythenar* Penther, 1913: 242–243, figs. 1, 2 (synonymized by Lourenço, 1982a: 122); Werner, 1927: 358; Mello-Leitão, 1945: 286.
- Rhopalurus barythenar*: Mello-Campos, 1924a: 252, 276, 281, 282, pl. 5, fig. 27, pl. 8, fig. 34; 1924b: 318, 341, 347, pl. 5, fig. 27, pl. 8, fig. 34; Mello-Leitão, 1932: 16, 31; Vellard, 1932: 556; Meise, 1934: 42; Prado, 1940: 26, 34, 35.
- Rhopalurus rochai*: Mello-Campos, 1924a: 252, 276, 279–281, pl. 10, figs. 35, 36; 1924b: 318, 341, 345, 346, pl. 10, figs. 35, 36; Werner, 1927: 358; Mello-Leitão, 1932: 16; Prado, 1940: 26, 34; Mello-Leitão, 1945: 267, 285–288, figs. 118, 119; Bücherl, 1959: 269; 1971: 327; Lucas and Bücherl, 1972: 263; Stahnke and Calos, 1977: 119; Lourenço, 1979: 215, fig. 7; Araújo, 1981: 235; Lucas et al., 1981: 128, table 1; Fet and Lowe, 2000: 222; Brazil and Porto, 2010: 25, 50, 59, 66, figs. 5B, 7A; Porto et al., 2010: 292–294, 296, fig. 2B, table 1; Ubinski et al., 2016: 122.
- Rhopalurus stenochirus*: Mello-Campos, 1924a: 252, 275, 278, 279, pl. 11, fig. 39; 1924b: 318, 341, 343–345, pl. 11, fig. 39; Mello-Leitão, 1932: 15, 31; Meise, 1934: 42; Prado, 1940: 26, 30, 31; Mello-Leitão, 1945: 267, 288–290, figs. 120, 121; Bücherl, 1971: 327; Lucas and Bücherl, 1972: 263; Stahnke and Calos, 1977: 119; Araújo, 1981: 235; Lourenço, 1982a: 122, 123, figs. 49, 50.
- Centruroides stenochirus*: Werner, 1927: 357.
- Ropalurus barythenar*: Viquez, 1935: 111, fig. 40.

TYPE MATERIAL: **BRAZIL**: *Bahía*: *Centrurus barythenar*: 12 ♂ syntypes (NMW 2248), Joazeiro. *Centrurus stenochirus*: 2 ♂, 1 juv. ?♀ syntypes (NMW 2251), Barra. *Ceará*: *Rhopalurus rochae*: Lectotype ♀, paralectotype ♂ [desig. Lourenço, 1982a: 138] (MIZT Sc 421 ex 645), Fortaleza.

DIAGNOSIS: *Jaguajir rochae* can be differentiated from *J. agamemnon* and *J. pinto* by its paler coloration and more slender metasoma. Whereas the base coloration is pale to dark yellow, and the metasoma of the male slightly wider posteriorly in *J. rochae*, the base coloration is brown to black, and the metasoma of the male markedly wider posteriorly in *J. agamemnon* and *J. pinto*. Additionally, the fixed and movable fingers of the pedipalp chela of the male are slightly curved, creating a small proximal gap between them, and the proximal lobe on the fixed finger of the male exhibits a prominent proximal lobe in *J. rochae*, whereas the fixed and movable fingers of the pedipalp chela of the male are markedly curved, creating a large proximal gap between them, and the proximal lobe on the fixed finger of the male is reduced or absent in *J. agamemnon* and *J. pinto*. Furthermore, the subaculear tubercle of the telson is much reduced, forming a small protuberance in *J. rochae*, as in *J. pinto*, but well developed and spinoid in *J. agamemnon*.

DISTRIBUTION: *Jaguajir rochae* is endemic to northeastern Brazil and recorded from the states of Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe (fig. 8). A record from Costa Rica (Viquez, 1935) is based on a misidentification.

ECOLOGY: This species inhabits open savannah (fig. 2D). Specimens collected by the authors were found under stones during the day and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

REMARKS: Borelli (1910) named the species after Francisco Diaz da Rocha, but the original spelling was feminine, *rochae*. Fet and Lowe (2000) noted that the masculine spelling is *rochai* and changed it accordingly. Although the corrected spelling has been adopted by others (e.g., Teruel, 2006: 52), we consider it an unjustified emendation and continue to use Borelli's (1910) original spelling. It is noteworthy that, on the page preceding the description of *R. rochae*, Borelli (1910) described *Tityus duckei* Borelli, 1910, after Mr. Ducke, implying he was aware of

the proper ending for a masculine name and it was not a *lapsus*. If Rocha is considered a Latin name, the proper ending, even if dedicated to a man, is *rochae* (ICZN, 1999: Art. 31.1.1. Examples), which may be what Borelli (1910) intended.

**MATERIAL EXAMINED: BRAZIL:** *Bahía*: Barra, Igarité, 5.vi.2008, 1 ♀ (MZSP 31122/AMCC [LP 9963]); Catu, Ibiraba, 2.viii.2000, 1 ♀ (MZSP 31123/AMCC [LP 9953]); Guanambi, Ceraíma, 14°13'S 42°46'W, 10–17. xii.2007, H.Y. Yamaguti et al., 1 ♂ (MZSP 30881/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 savannah, 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 do 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 savannah modified, 1 ♀ (AMNH), 1 ♂, 2 juv. (AMCC [LP 7639]); Jeremoabo, Espadado de Cima, 10°04'S 38°23'W, 27.v.2008, H.Y. Yamaguti, T.J. Porto, and M.B. da Silva, 1 subad. ♀ (MZSP 30882/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/AMCC [LP 9956]), 1 ♀ (MZSP 31124/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/AMCC [LP 9945]); Várzea do Poço, 19.x.2007, 1 ♀ (MZSP 31127/AMCC [LP 9926]). *Minas Gerais*: Janaúba, 11.xii.2007, H.Y. Yamaguti, S. Outedajorge, and C.A. Souza, 1 juv. ♂ (MZSP 31136/AMCC [LP 9957]); Janaúba, UNIMONTES, Campus Janaúba, 11.xii.2007, H.Y. Yamaguti et al., 1 subad. ♂ (MZSP 30879/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/AMCC [LP 9955]), 1 juv. ♂ (MZSP 31143/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, 2 ♀ (MZSP 31146/AMCC [LP 9943], MZSP 31147/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/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/AMCC [LP 9961]), 1 ♀ (MZSP 31151/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/AMCC [LP 9683]).



*Physoctonus* Mello-Leitão, 1934

Figures 1E, 2D, 9, 10D, 11G, 12F, 16A, B, 17D, 20A, B, 21G, 22G, 24S–U, 48–52

*Vaejovis debilis* C.L. Koch, 1840 [= *Physoctonus debilis* (C.L. Koch, 1840)], type species, by subsequent designation.

*Vaejovis* (part): C.L. Koch, 1840: 21, 22, pl. CCLIX, fig. 605; Kraepelin, 1899: 96.

*Waejovis* (lapsus): Gervais, 1844b: 458.

*Rhopalurus* (part): Borelli, 1910: 5–8, fig. 1;

Mello-Campos, 1924a: 252, 275–277; Mello-Leitão, 1932: 14, 30; Meise, 1934: 42; Prado, 1940: 26, 29, 30; Mello-Leitão, 1945: 266, 272, 273; Bücherl, 1959: 268; 1971: 327; Francke, 1977a: 125, 127–134, figs. 1–15; Lourenço, 1982a: 108, 133, 135–137, fig. 78; Armas, 1984: 8; Lourenço, 1986a: 133, 135, figs. 12, 16; 1986b: 165, fig. 7; 1990: 161; 1992: 55; Kovařík, 1998: 118; Lourenço, 2002: 101, 111, figs. 225, 226; Lira-da-Silva et al., 2005: 1, 2; Teruel, 2006: 51; Ubinski et al., 2016: 122.

*Physoctonus* Mello-Leitão, 1934b: 76, 77, figs.

1–7; 1942: 129; 1945: 129–132, figs. 40, 41; Bücherl, 1967: 115; 1969: 768; Vachon, 1963: 161, 165; Stahnke, 1974: 129; Francke, 1977a: 127; Lourenço, 2007: 359–364; Outeda-Jorge et al., 2009: 43–46; Prendini et al., 2009: 222; Brazil and Porto, 2010: 50, 57.

**DIAGNOSIS:** *Physoctonus* differs from other rhopalurusine genera by the obsolete carapacial carinae, the asetose proximal dorsal fulcra of the pectines, the simple (nonbifurcate) prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked by small, widely spaced prolateral accessory (supernumerary) denticles and sparse retro-lateral accessory denticles. It differs further from *Heteroctenus*, *Ischnotelson*, gen. nov., *Jaguajir*, gen. nov., *Rhopalurus*, and *Trogloorhopalurus* by the small size (total length, 20–25 mm); from *Heteroctenus*, *Ischnotelson*, *Jaguajir*, and *Rhopalurus* by the slender pedipalp chela manus of the

adult male; from *Heteroctenus*, *Jaguajir*, and *Rhopalurus* by the absence of a pecten-sternite stridulatory organ; from *Heteroctenus* by the absence of depressions in the male pectinal plate and the presence of a subaculear tubercle on the telson; from *Ischnotelson* by the separate (unfused) lateral ocular and central lateral carinae of the carapace and the telson vesicle not laterally compressed; and from *Trogloorhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of the adult male emarginate, with a distinct gap evident between them, when closed.

**DESCRIPTION:** The following general description outlines characters common to both species of *Physoctonus* (for measurements, see table 3).

**Total length:** Relatively small scorpions (total length, 20–25 mm).

**Color:** Base color pale to dark yellow (fig. 1E). Carapace immaculate except interocular surface infuscate, forming dark triangle. Tergites immaculate except for dorsomedian band of infuscation, forming longitudinal stripe on mesosoma. Coxosternal region, pectines, and sternites immaculate, pale to dark yellow. Metasomal segments I–III, dorsal surfaces immaculate, yellow, similar color as carapace and tergites, segments IV and V, dorsal surfaces darker than preceding segments; I–III, ventral surfaces slightly darker than dorsal surfaces, IV and V noticeably darker than I–III, V darker than IV; I–IV each with dark ventromedian band of infuscation. Telson vesicle yellow, similar to metasomal segment V, aculeus almost black. Chelicerae, pedipalps, and legs base color yellow, similar to tergites, with reticulate infuscation; chela fingers dark brown.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle low (fig. 16A, B); two median ocelli; three pairs of lateral macroocelli; one pair of lateral microocelli. Anteromedian, median ocular, and posteromedian sulci present, forming single, almost continuous, longitudinal sulcus. Carinae obsolete, finely granular, and barely distinguishable from surface

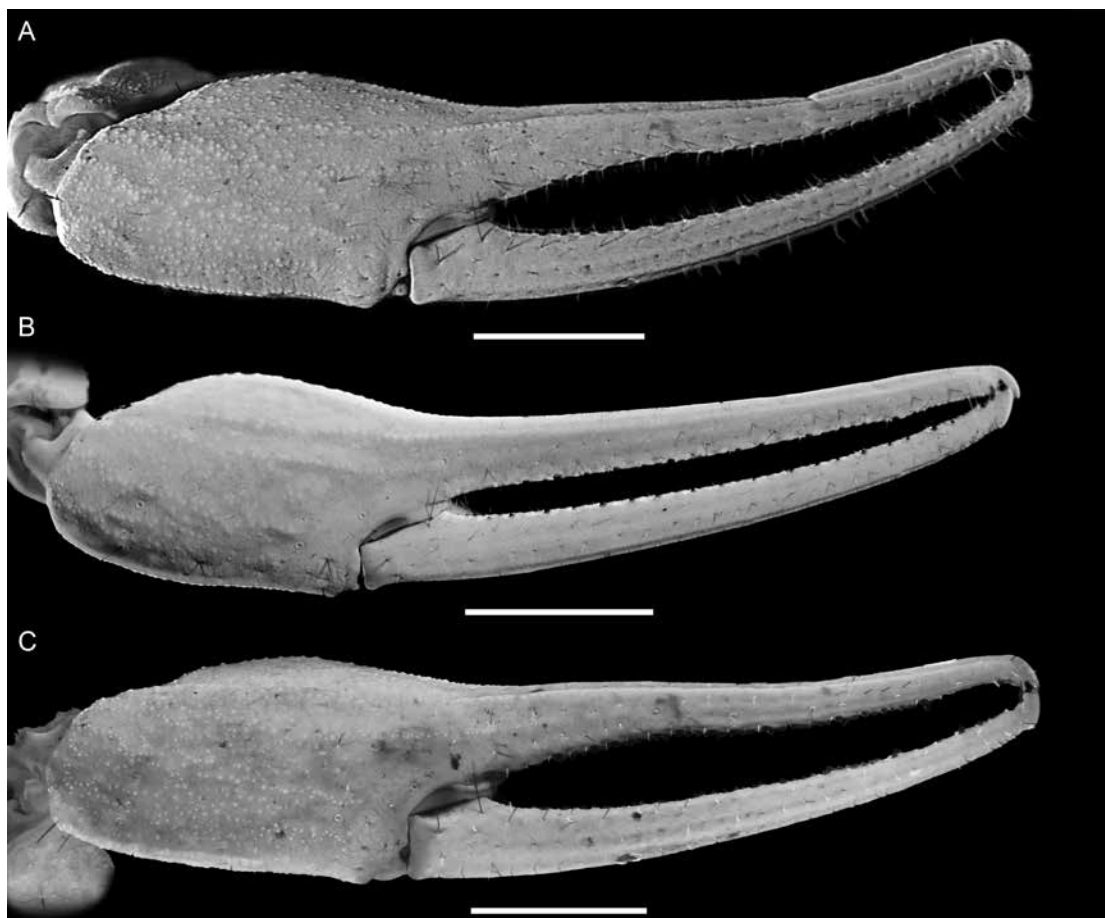


FIG. 48. *Physoctonus* Mello-Leitão, 1934, pedipalp chela, retrolateral aspect. A. *P. debilis* (C.L. Koch, 1840), ♂ (MZSP). B. *P. debilis* (C.L. Koch, 1840), ♀ (MZSP). C. *P. striatus*, sp. nov., ♂ (MZSP). Scale bars = 1 mm.

granulation; lateral ocular and anterior central submedian carinae separate (unfused); central lateral and posterior central submedian carinae fused.

**Pedipalps:** Pedipalp femur retrolateral accessory carinae present. Pedipalp chela manus of adult male slender, proximal dentate margins of fixed and movable fingers slightly curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, slight gap present between fingers proximally, when closed (fig. 48A, C), manus of female not incrassate, fixed

and movable fingers not curved proximally, such that proximal dentate margin sublinear, little or no gap present between them proximally, when closed (fig. 48B); manus, proventral carina absent, promedian carina present; fixed and movable fingers, median denticle rows each comprising eight oblique subrows of primary denticles flanked by small, widely spaced pro-lateral accessory (supernumerary) denticles and sparse retrolateral accessory denticles; movable finger without proximal lobe (fig. 17D). Pedipalps orthobothriotic Type A, a configuration; femur with five dorsal trichobothria,

trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  proximal to or aligned with trichobothrium  $et$ .

**Legs:** Legs III and IV, tibial spurs absent; I and II, basitarsi each with simple prolateral pedal spur; telotarsi each with distinct pro- and retroventral rows of fine, acuminate macrosetae.

**Pectines:** Pectinal plate without depressions (male), anterior margin with sulcus (fig. 20A, B). Pectines not proximally expanded; proximal dorsal fulcra asetose; pectinal teeth almost straight, slightly curved laterally, proximal teeth, dorsal surfaces without striations but covered with small denticles, dorsobasal surfaces without macrosetae; pectinal sensillae short and blunt (figs. 11G, 12F).

**Mesosoma:** Tergites V–VII slightly wider than I–IV; I–VI unicarinate, dorsosubmedian carinae absent, dorsomedian carina reduced to posterior half on I–VI, complete on V and VI. Tergite VII pentacarinata, dorsomedian carina complete (fig. 51). Sternites smooth, carinae absent or obsolete; sternite III, lateral margins not forming smooth, raised carina, ventromedian carina not elevated anteriorly, ventrosubmedian surfaces not forming paired depressions, smooth; respiratory spiracles (stigmata) width less than  $5\times$  length (fig. 10E).

**Metasoma:** Metasoma slender, increasing slightly in width posteriorly, segment V only slightly wider than I in adult male, I and V similar width in adult female (figs. 49, 50). Segments I–III each with 10 distinct, granular carinae, IV with eight distinct, granular carinae, V with five distinct, granular carinae; dorsosubmedian carinae obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV, more pronounced on segment I; dorsolateral carinae complete on segments I–IV, and terminating in slightly larger, subspiniform granules posteriorly on II–IV, absent on V; lateral supramedian carinae complete on segments I–V; lateral inframedian carinae complete on segments I–III, complete but obsolete on IV, and absent on V; ventrosubmedian carinae com-

plete on segments I–IV, absent on V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely and densely granular on lateral and ventral surfaces of segments I–V and dorsal surfaces of I–III.

**Telson:** Vesicle oval, not laterally compressed, narrower than metasoma V; anterodorsal lateral lobes prominent; lateral and ventral surfaces granular, pentacarinata with distinct ventromedian carina; subaculear tubercle vestigial.

**Hemispermatothore:** Flagelliform; flagellum, elongate and narrow (fig. 24S–U); trunk concave; three lobules, ental (LI), ectal (LE), and basal (LB); LI inclined to ental side of trunk and continuous to flagellar base; flagellar base wide, ca. two thirds width of trunk; LE length ca. half that of LI, spiniform with curved tip; LB base wide and slightly elongate, apex thin and curved.

**Cytogenetics:** The diploid chromosome number of *P. debilis* (table 2) is  $2n = 26$  (Ubinski et al., 2016).

**INCLUDED SPECIES:** *Physoctonus debilis* (C.L. Koch, 1840); *Physoctonus striatus*, sp. nov.

**DISTRIBUTION:** *Physoctonus* is endemic to northeastern Brazilian, and has been recorded in the states of Bahia, Ceará, Paraíba, Pernambuco, and Piauí (fig. 9).

**ECOLOGY:** The two species of *Physoctonus* inhabit the semiarid Brazilian caatinga and cerrado (fig. 2D). These small, lapidicolous scorpions have been collected under stones and with UV light detection at night.

**REMARKS:** *Physoctonus*, created to accommodate *Physoctonus physurus* Mello-Leitão, 1934, was synonymized with *Rhopalurus* when Francke (1977a) synonymized *P. physurus* with *Rhopalurus debilis*. *Physoctonus* was later revalidated by Lourenço (2002). Its validity was upheld by the analyses of Esposito et al. (in review), which consistently recovered the monophyly of its two species as distinct from the species of *Rhopalurus* (fig. 13), and the cytogenetic study of Ubinski et al. (2016) which identified a diploid chromosome number of  $2n = 26$  for *R. debilis* (table 2).

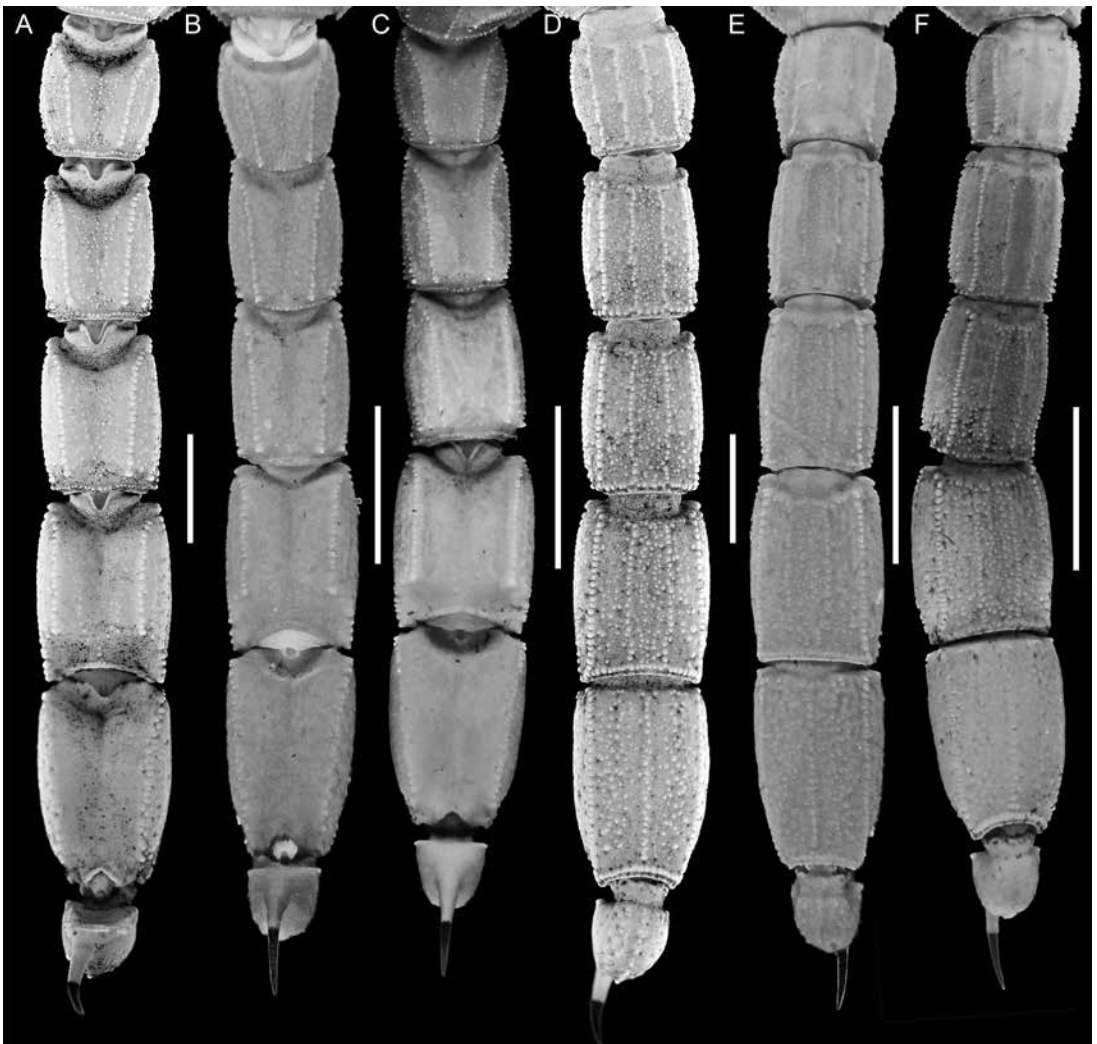


FIG. 49. *Physoctonus debilis* (C.L. Koch, 1840), metasoma and telson, dorsal (A–C) and ventral (D–F) aspects. A, C, D, F. 2 ♂ (MZSP). B, E. ♀ (AMNH). Scale bars = 2.5 mm.



FIG. 50. *Physoctonus debilis* (C.L. Koch, 1840), metasoma and telson, lateral aspect. A, C. 2♂ (MZSP). B. ♀ (AMNH). Scale bars = 2.5 mm.

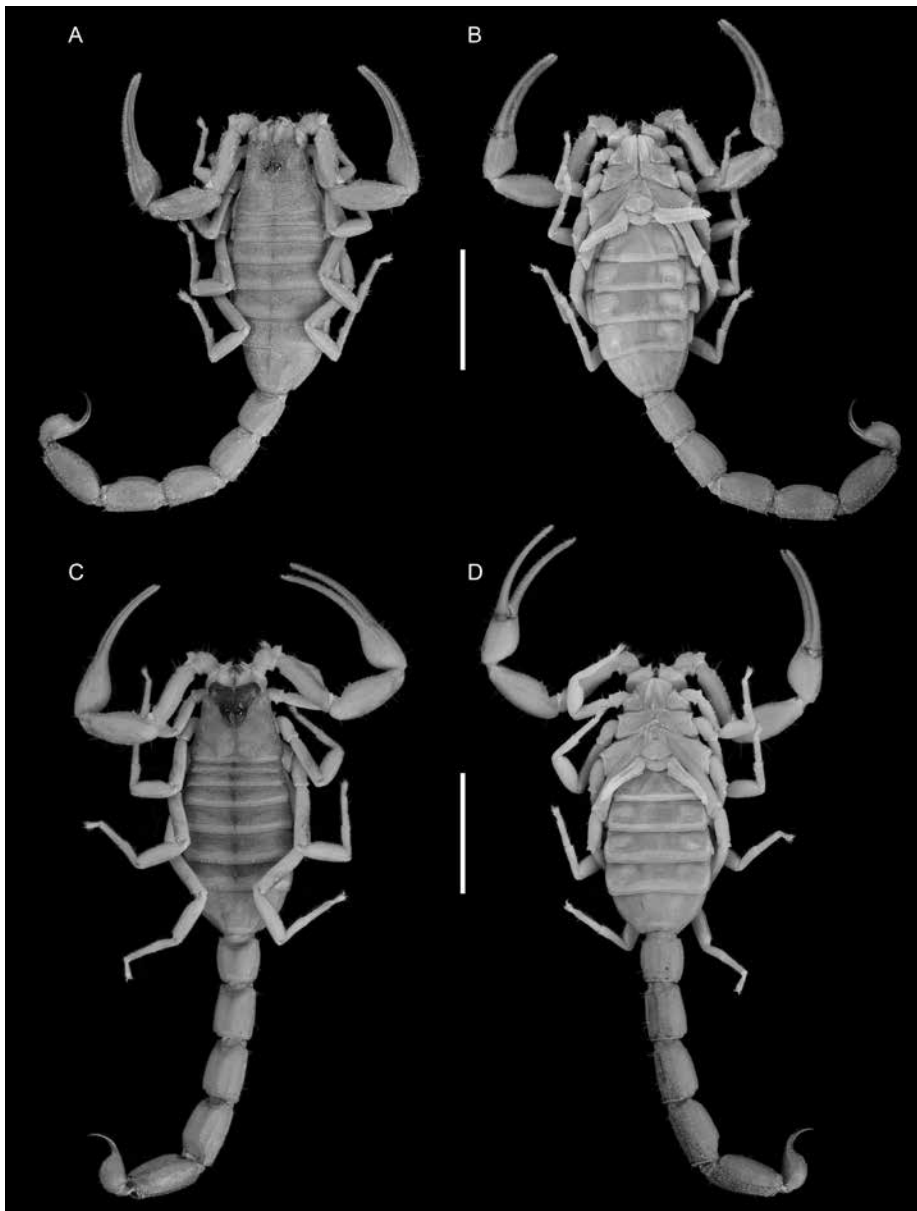


FIG. 51. *Physoctonus debilis* (C.L. Koch, 1840), 2 ♀ (AMNH), habitus, dorsal (A, C) and ventral (B, D) aspects. Scale bars = 1 mm.

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

Figures 1E, 2D, 9B, 10D, 11G, 12F, 16A, 20A, 21G, 22G, 24S–U, 48A, B, 49–51; table 3

*Vaejovis debilis* C.L. Koch, 1840: 21, 22, pl.

CCLIX, fig. 605; 1850: 89; Kraepelin, 1899: 96.

*Vaejovis debilis*: Gervais, 1844b: 458.

*Rhopalurus debilis*: Borelli, 1910: 5–8, fig. 1;

Mello-Campos, 1924a: 252, 275, 276, 277;

1924b: 318, 341, 342, 343; Mello-Leitão,

1932: 14, 30; Meise, 1934: 42; Prado, 1940:

26, 29–30; Mello-Leitão, 1945: 266, 272, 273;

Bücherl, 1959: 268; 1971: 327; Francke,

1977a: 127–134, figs. 1–15; Lourenço, 1982a:

133, 136, fig. 78; 1986a: 133, figs. 12, 16;

1986b: 165, fig. 7; 1990: 161; 1992: 55;

Kovářík, 1998: 118; Fet and Lowe, 2000: 219;

Ubinski et al., 2016: 122.

*Physoctonus physurus* Mello-Leitão, 1934b: 76,

77, figs. 1–7 (synonymized by Francke,

1977a: 127); 1942: 129; 1945: 129–132, figs.

40, 41; Bücherl, 1967: 115; 1969: 768;

Stahnke, 1974: 129.

*Physoctonus debilis*: Lourenço, 2007: 360, figs.

4–5, 14–25; Prendini et al., 2009: 222; Brazil

and Porto, 2010: 50; Porto et al., 2010: 293,

295, fig. 1F, table 1.

**TYPE MATERIAL: BRAZIL:** *Vaejovis debilis*: Holotype ?♀ (ZSM) [lost]. *Physoctonus physurus*: Holotype ♂ (MNRJ), *Paraíba*: Santa Luzia.

**DIAGNOSIS:** *Physoctonus debilis* differs from its sister species, *P. striatus*, sp. nov., as follows. The mesosomal tergites of *P. debilis* are uniformly pale, except for the infusate dorsomedian carinae, which form a thin stripe longitudinally, whereas the tergites of *P. striatus* are darker, with transverse bands of infuscation. The intercarinal surfaces of the carapace and metasomal segments II–IV are more coarsely and densely granular in *P. debilis* but weakly granular to smooth in *P. striatus*. The carinae of the carapace, pedipalps, and metasoma are more pronounced in *P. debilis*

than in *P. striatus*: for example, the lateral inframedian carinae of metasomal segments II and III are complete in *P. debilis* but restricted to the posterior third of the segment in *P. striatus*; and the retromedian and secondary accessory carinae of the pedipalp chela manus are complete and granular in *P. debilis* but vestigial or absent in *P. striatus*. Pedipalp chela fixed finger trichobothrium *db* is situated distal to trichobothrium *et* in *P. debilis* but aligned with *et* in *P. striatus*.

**DISTRIBUTION:** *Physoctonus debilis* is endemic to Brazil, where it has been recorded in the states of Ceará, Paraíba, Pernambuco, and Piauí (fig. 9B).

**ECOLOGY:** The known locality records are situated in the Brazilian caatinga (fig. 2D). Specimens collected by the authors were found under stones during the day or with UV light detection at night. The habitus is consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**REMARKS:** *Physoctonus debilis* was originally placed in the nonbuthid genus *Vaejovis* C.L. Koch, 1836, but was transferred to *Rhopalurus* by Borelli (1910), where it remained until Lourenço (2002) revalidated the genus *Physoctonus*. As noted by Fet and Lowe (2000), the true date of publication of C.L. Koch's name is 1840 (see Brignoli, 1985), not 1841 as commonly quoted. This species has a junior homonym, *Vaejovis debilis* L. Koch, 1865, from Mexico, the identity of which is unknown.

**MATERIAL EXAMINED: 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., 2 ♀ (MZSP 30868/AMCC [LP 9680]), MZSP 31158/AMCC [LP 9931]; Oeiras, 06°58'28"S 42°06'31"W, 2–3. vi.2008, H.Y. Yamaguti et al., 1 ♀ (MZSP 31162/AMCC [LP 9940]), 1 subad. ♀ (MZSP 31164/AMCC [LP 9962]), 3.vi.2008, H.Y. Yamaguti et al.,

1 ♀ (MZSP 30866/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/AMCC [LP 9679]).

*Physoctonus striatus*, sp. nov.

Figures 9A, 16B, 17D, 20B, 48C; table 3

*Physoctonus debilis*: Porto et al., 2010: 295, table 1 (part).

TYPE MATERIAL: **BRAZIL**: *Bahia*: Xique-Xique, 10°49'60"S 42°43'60"W: Holotype ♂ (MZSP 30869/AMCC [LP 9681]), 2.x.2008, T.J. Porto. Paratype ♂ (MZSP 31128/AMCC [LP 9950]), same data except 3.x.2008, T.J. Porto.

DIAGNOSIS: *Physoctonus striatus*, sp. nov., differs from its sister species, *P. debilis*, as follows. The mesosomal tergites of *P. striatus* are dark, with transverse bands of infuscation, whereas the tergites of *P. debilis* are uniformly pale, except for the infusate dorsomedian carinae, which form a thin stripe longitudinally. The carinae of the carapace, pedipalps, and metasoma are less pronounced in *P. striatus* than in *P. debilis*: for example, the lateral inframedian carinae of metasomal segments II and III are restricted to the posterior third of the segment in *P. striatus*, but complete in *P. debilis*; and the retromedian and secondary accessory carinae of the pedipalp chela manus are vestigial to absent in *P. striatus*, but complete and granular in *P. debilis*. Pedipalp chela fixed finger trichobothrium *db* is aligned with trichobothrium *et* in *P. striatus* but situated distal to *et* in *P. debilis*.

ETYMOLOGY: The species name refers to the transverse bands of infuscation on the mesosomal tergites.

DESCRIPTION: The following description is based on the holotype male unless otherwise noted (for measurements, see table 3). Only characters that differ from the generic description are noted.

*Total length*: Small scorpions, 22–26 mm.

*Color*: Base color dark yellow to light brown. Carapace immaculate except interocular surface infusate, forming dark triangle, almost reaching anterior margin, and thin, dark line of infuscation around margins. Tergites each with infusate median carina forming a thin dark line longitudinally, with transverse band of infuscation, and a dark line of infuscation around margins. Coxosternal region, pectines, and sternites immaculate, dark yellow. Metasomal segments I–IV, dorsal surfaces immaculate, similar in color to carapace and tergites; II–IV, ventral surfaces infusate, forming a longitudinal stripe; V completely infusate. Telson vesicle similar to metasomal segment V dorsal surface, aculeus almost black. Chelicerae, pedipalps, and legs brown, entirely infusate.

*Carapace*: Pentagonal in shape, anterior width approximately two thirds posterior width. Median ocular tubercle low; median sulci shallow; lateral ocular carinae continuous with posterior median carinae. Carinae obsolete, finely granular and barely distinguishable from surface granulation; anterior margin with large round granules.

*Pedipalps*: Pedipalp femoral and patellar carinae coarsely granular; chelal carinae more finely granular (fig. 48C). Chela fixed finger trichobothrium *db* aligned with trichobothrium *et*. Retromedian carina vestigial, restricted to distal quarter of chela manus; secondary accessory carina of chela manus absent.

*Legs*: Legs III and IV, tibial spurs absent; I–IV, surfaces carinate; basitarsi each with simple prolateral pedal spur; telotarsi each with distinct pro- and retroventral rows of fine, acuminate macrosetae.

*Sternum*: Subtriangular. Median longitudinal sulcus shallow anteriorly, deep, wide posteriorly.

*Genital operculum*: Genital opercula suboval, completely divided longitudinally; genital papillae present (♂).

*Pectines*: Tooth count, 15/15 (♂). Pectinal plate trapezoid, with deep anterior notch (fig. 20B).

*Mesosoma*: Tergites IV–VI slightly wider than I–III; I–VI unicarinate, dorsosubmedian



carinae absent, dorsomedian carina reduced to posterior half on I–VI. Tergite VII pentacarinata, dorsomedian carina reduced. Sternites III–VI smooth, carinae absent or obsolete; sternite III, lateral margins not forming smooth, raised carina, ventromedian carina not elevated anteriorly, ventrosubmedian surfaces not forming paired depressions, smooth; sternite VII with four granular carinae; respiratory spiracles (stigmata) width more than  $5\times$  length.

*Metasoma*: Metasomal segments I–III each with 10 carinae, IV with eight carinae, V with five carinae; lateral inframedian carinae complete on segment I, restricted to posterior third of segment on II and III, absent on IV and V. Ventral intercarinal surfaces of segments I–IV coarsely granular, dorsal and lateral surfaces weakly granular or smooth, segment V smooth. Metasoma increasing slightly in width posteriorly, segments IV and V wider than I in adult male.

*Telson*: Vesicle pentacarinata; subaculear tubercle vestigial.

*Hemispermaphore*: As for genus.

*Sexual dimorphism*: Females are unknown.

**DISTRIBUTION**: This species is known only from the type locality in the Brazilian state of Bahia (fig. 9A).

**ECOLOGY**: The type locality is situated in the Brazilian caatinga, a very dry environment with sandy soil. Specimens were collected under stones during the day or with UV light detection at night. The habitus is consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

*Rhopalurus* Thorell, 1876

Figures 1F, 2E, 5, 6, 11C, E, 12C, 16C–F, 17E, 20C–F, 21H–J, 22H–J, 24I–R, 52–60

*Rhopalurus laticauda* Thorell, 1876, type species by original designation.

*Rhopalurus* Thorell, 1876a: 9; 1876b: 143–145; Karsch, 1879a: 18; 1879b: 118, 119, 122; Mello-Campos, 1924a: 252, 253, 267, 283–285, pl. 7, fig. 31; Werner, 1927: 357; Lutz,

1928: 72, 73, figs. 1–3; Mello-Leitão, 1932: 15; Meise, 1934: 32; Prado, 1940: 27, 35; Prado and Rios-Patiño, 1940: 41; Hummelinck, 1940: 139; Mello-Leitão, 1940: 51; Roewer, 1943: 219; Mello-Leitão, 1945: 266, 280–284, figs. 115–117; Caporiacco, 1947: 20; 1951: 4; Scorza, 1954a: 190, 201, figs. 15, 16; 1954b: 160; 1954c: 166; Bücherl, 1959: 268; 1967: 112; 1969: 767; Esquivel de Verde and Machado-Allison, 1969: 33; Bücherl, 1971: 327; Lucas and Bücherl, 1972: 263; Francke, 1977a: 133, fig. 12; Stahnke and Calos, 1977: 119; Vachon, 1977: 300, figs. 24, 28; González-Sponga, 1978: 201, figs. 9, 277, 278; Lourenço, 1979: 215, figs. 1, 3, 4; 1981: 545, fig. 2; 1982a: 108, 115, 117, 134–136, 138, figs. 12, 13, 25–46, 78; Cekalovic, 1983: 190; González-Sponga, 1984: 72–74; Lourenço, 1984b: 14; 1986a: 132–134, figs. 3–9, 13, 14; 1986b: 170, fig. 7; 1988: 169, figs. 13, 15; Lourenço and Flórez, 1990: 71; Lourenço, 1991a: 282, fig. 5; 1991b: 117; Flórez, 1991: 119; Lourenço, 1992: 55; 1994: 157; González-Sponga, 1996: 118, 137, figs. 314–319; Lourenço, 1997b: 67, figs. 9, 10, 12, 14, 15; Lourenço and Pinto-da-Rocha, 1997: 184, 185, fig. 21; Kovařík, 1998: 118; Lourenço et al., 2000: 141; Manzanilla and Sousa, 2003: 3–12; Fet and Lowe, 2000: 219–221; Lourenço, 2002: 96, 98, 99, 111, figs. 205–224; Fet et al., 2003b: 23, 24; Lenarducci et al., 2005: 2, 7; Prendini and Wheeler, 2005: 481, table 10; Teruel, 2006: 50–52; Rojas-Runjaic and Sousa, 2007: 6; Lourenço, 2007: 359; Kamenz and Prendini, 2008: 9, table 2, pl. 40–44; Lourenço, 2008: 1, 2, 3, 5, 7, 12, figs. 1, 4–9; Teruel and Roncallo, 2008: 1, 2, 5, 8, 10, figs. 1–7; Teruel and Tietz, 2008: 1, 6, 8, 10, 11, figs. 5–9; Volschenk et al., 2008: 651, 652, 654, 658–661, 663, 664, 674, figs. 1B, D, 2E, tables 1, 2; Prendini et al., 2009: 222, 223; Outeda-Jorge et al., 2009: 44–46; Brazil and Porto, 2010: 57, 79; Teruel and Roncallo, 2013: 112,



FIG. 52. *Rhopalurus* Thorell, 1876, pedipalp chela, retrolateral aspect. **A.** *R. caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **B, C.** *R. laticauda* Thorell, 1876. **B.** ♂ (AMNH), Laguna Canaima, Venezuela. **C.** ♀ (AMNH), Guatire, Venezuela. **D.** *R. ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 2 mm.

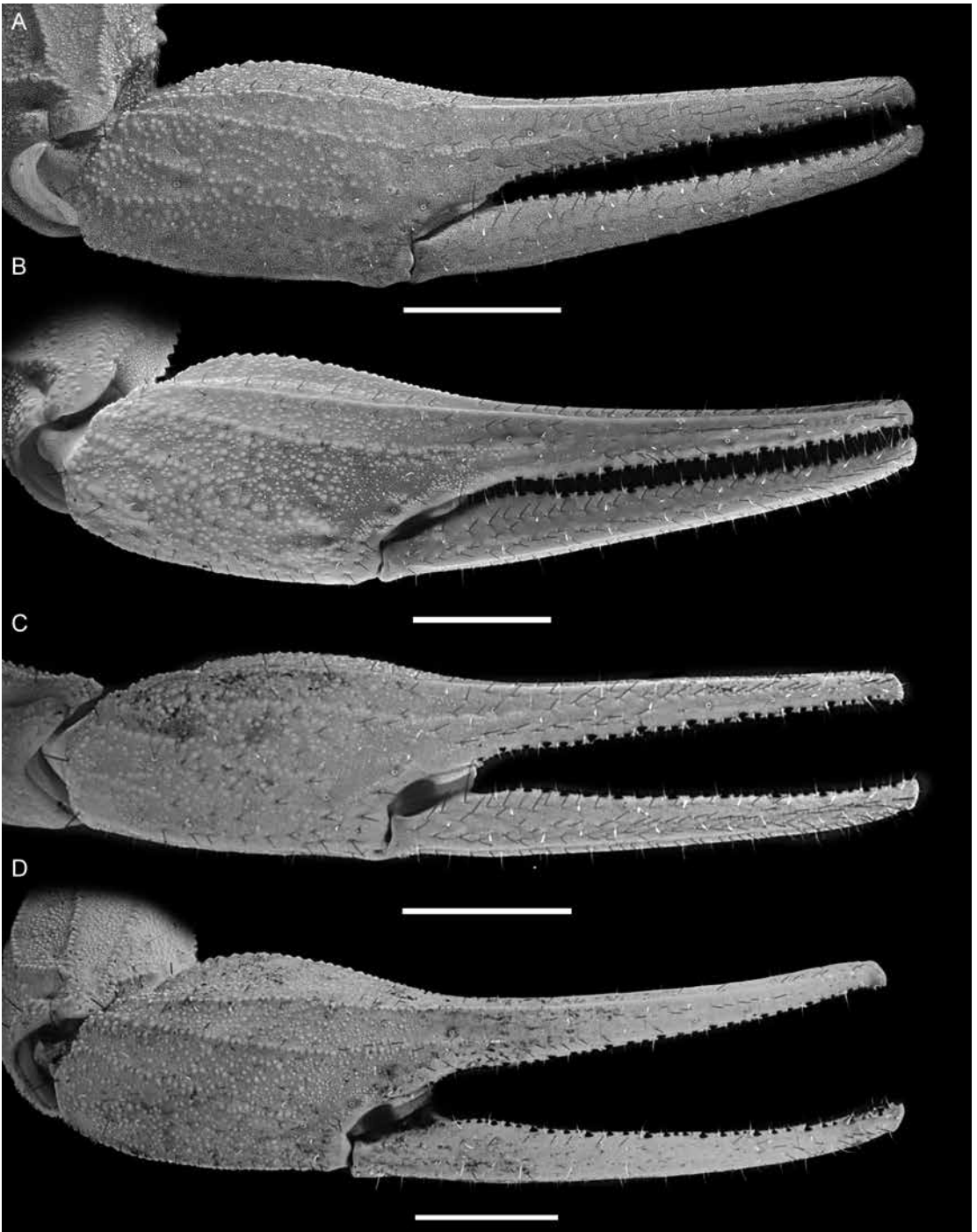


FIG. 53. *Rhopalurus* Thorell, 1876, pedipalp chela, retrolateral aspect. A. *R. caribensis* Teruel and Roncallo, 2008, ♀ (SMF). B. *R. laticauda* Thorell, 1876, ♀ (AMNH), Laguna Canaima, Venezuela. C. *R. laticauda* Thorell, 1876, ♀ (AMNH), Puerto Colombia, Venezuela. D. *R. ochoai*, sp. nov., paratype ♀ (AMNH). Scale bars = 2 mm.



FIG. 54. *Rhopalurus* Thorell, 1876, metasoma and telson, dorsal aspect. **A.** *R. caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **B, C.** *R. laticauda* Thorell, 1876. **B.** ♂ (AMNH), Laguna Canaima, Venezuela. **C.** ♂ (AMNH), Puerto Colombia, Venezuela. **D.** *R. ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 5 mm.

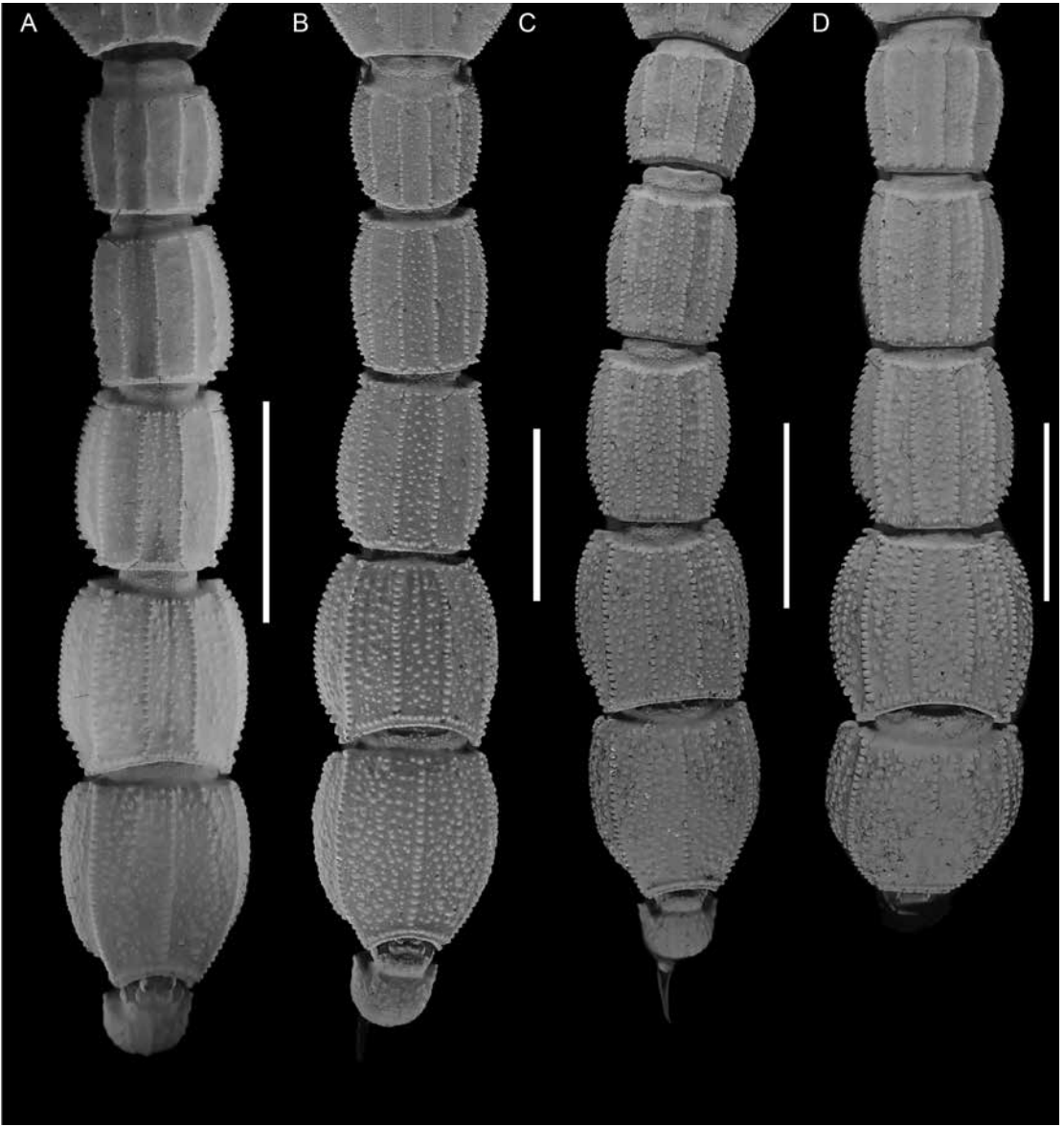


FIG. 55. *Rhopalurus* Thorell, 1876, metasoma and telson, ventral aspect. **A.** *R. caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **B.** *R. laticauda* Thorell, 1876, ♀ (AMNH), Laguna Canaima, Venezuela. **C.** *R. laticauda* Thorell, 1876, ♀ (AMNH), Puerto Colombia, Venezuela. **D.** *R. ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 5 mm.



FIG. 56. *Rhopalurus* Thorell, 1876, metasoma and telson, lateral aspect. **A.** *R. caribensis* Teruel and Roncallo, 2008, ♂ (AMNH). **B.** *R. laticauda* Thorell, 1876, ♀ (AMNH), Laguna Canaima, Venezuela. **C.** *R. laticauda* Thorell, 1876, ♀ (AMNH), Puerto Colombia, Venezuela. **D.** *R. ochoai*, sp. nov., holotype ♂ (AMNH). Scale bars = 5 mm.

113; Teruel and Cozijn, 2013: 1; Loria and Prendini, 2014: 25, table 5; Lourenço, 2014: 69, 74, 75; Ubinski et al., 2016: 122.

*Centrurus* (part): Kraepelin, 1891: 123, 137–139; Kraepelin, 1899: 89, 95; 1908: 187, 190, 194; Penther, 1913: 240; Waterman, 1950: 168.

**DIAGNOSIS:** *Rhopalurus* differs from *Centruroides*, *Heteroctenus*, *Jaguajir*, gen. nov., and *Troglo-rhopalurus* by the fused central lateral and posterior central submedian carinae of the carapace; from *Centruroides*, *Ischnotelson*, gen. nov., *Physoconus* and *Troglo-rhopalurus* by the presence of a pecten-sternite stridulatory 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); from *Centruroides* and *Troglo-rhopalurus* by the robust metasoma, increasing in width posteriorly (more so in the adult male); from *Heteroctenus* by the absence of depressions in the male pectinal plate and the presence of a subaculear tubercle on the telson; from *Ischnotelson* by the separate (unfused) lateral ocular and central lateral carinae of the carapace and the telson vesicle not laterally compressed; from *Jaguajir* by the separate (unfused) lateral ocular and anterior central submedian carinae of the carapace; from *Physoconus* by the larger size (30–70 mm), the more distinct carapacial carinae (at least the posterior central submedian carinae), the setose proximal dorsal fulcra of the pectines, the incrassate pedipalp chela manus of the adult male, the bifurcate prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; and from *Troglo-rhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of the adult male emarginate, with a distinct gap evident between them, when closed.

**DESCRIPTION:** The following general description outlines characters common to the species of *Rhopalurus*.

**Total length:** Medium-sized, compact scorpions (total length, 30–70 mm).

**Color:** Carapace and tergites I–VI dark brown, tergite VII light brown (fig. 1F). Coxosternal region, pectines and sternites pale yellow. Metasomal segments I–III, dorsal surfaces yellowish to orange, IV and V, dorsal surfaces brown, darker than preceding segments; I–III, ventral surfaces darker than dorsal surfaces, IV and V, ventral surfaces darker than I–III, V almost black, darker than IV; I–IV each with dark ventromedian and/or ventrosubmedian stripes or solid band of pigmentation. Telson vesicle brown, paler than metasomal segment V, aculeus almost black. Chelicerae and legs brown, similar to carapace. Pedipalps yellowish to orange, chela fingers dark brown.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle raised (fig. 16C–F); two median ocelli; three pairs of lateral macroocelli; one pair of lateral microocelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular and anterior central submedian carinae indistinct, finely granular and separate (unfused); central lateral and posterior central submedian carinae distinct, finely granular, and fused into single slightly oblique carina, extending almost two thirds the length of carapace.

**Pedipalps:** Pedipalp femur retrolateral accessory carinae absent. Pedipalp chela manus of adult male incrassate, fixed and movable fingers curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that proximal dentate margin emarginate, distinct gap present between fingers proximally, when closed (fig. 52), manus of female not incrassate, fixed and movable fingers not curved proximally, such that proximal dentate margin sub-linear, little or no gap present between them proximally, when closed (fig. 53); manus, proventral and promedian carinae absent; fixed and movable fingers, median denticle rows respectively comprising eight and nine oblique sub-

rows of primary denticles flanked closely by pro- and retrolateral accessory (supernumerary) denticles; movable finger without proximal lobe (fig. 17E). Pedipalps orthobothriotaxic Type A,  $\alpha$  configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  proximal to trichobothrium *et*.

*Legs:* Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with irregular tufts of fine, acuminate macrosetae.

*Pectines:* Pectinal plate without depressions (male), anterior margin with sulcus (fig. 20C–F). Pectines proximally expanded, at least 1.5 $\times$  wider proximally than medially; proximal dorsal fulcra setose; pectinal teeth straight, proximal teeth, dorsal surfaces without nodules but with regular striations (figs. 11C, E, 12C), dorsobasal surfaces without macrosetae; pectinal sensillae peg shaped.

*Mesosoma:* Tergites IV–VI wider than I–III (figs. 57–60); I–VI tricarinate, dorsosubmedian carinae vestigial or absent; dorsomedian carinae vestigial, reduced to posterior third of I–VI. Tergite VII pentacarinata, dorsomedian carina complete. Sternites smooth, carinae absent or obsolete; sternite III, lateral margins forming smooth, raised carina, ventromedian carina elevated anteriorly, ventrosubmedian surfaces forming paired depressions, finely and irregularly granular anterolaterally; respiratory spiracles (stigmata) width more than 5 $\times$  length.

*Metasoma:* Metasoma robust, increasing in width posteriorly, segment V ca. 2 $\times$  width of segment I in adult male, only slightly wider than I in adult female (figs. 54–56). Segments I–III each with 10 distinct, costate-granular carinae, IV with eight distinct, costate-granular carinae, V with seven distinct, costate-granular carinae; dorsosubmedian carinae obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV, more pronounced on segment I; dorsolateral carinae complete on

segments I–IV, and terminating in prominent, spiniform granules posteriorly on II–IV, absent on V; lateral suprmedian carinae complete on segments I–V; lateral inframedian carinae complete on segments I–III, absent on IV and V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third of V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces densely and coarsely granular, especially on dorsal surfaces of segments I–III and ventral surfaces of I–V.

*Telson:* Vesicle subspherical, not laterally compressed, narrower than metasoma V; anterodorsal lateral lobes prominent; lateral and ventral surfaces granular, acarinate, or with obsolete ventromedian carina; subaculear tubercle vestigial to subspinoid.

*Hemispermaphore:* Flagelliform; flagellum, elongate and narrow (fig. 24I–R); trunk markedly concave; three lobules, ental (LI), ectal (LE), and basal (LB); LI inclined slightly to sinistral side relative to axis of trunk and continuous until flagellar base; flagellar base narrow, one third maximum width of trunk; LE length approximately two thirds that of LI, with sharp tip and varying from very curved (in *R. caribensis*) to straight (in *R. laticauda*), width half that of LB; LB short, carina shaped with rhomboid tip, angle between LB and LE 75° (*R. caribensis*) to 80° (*R. laticauda*).

*Cytogenetics:* The diploid chromosome number of *R. laticauda* (table 2) is  $2n = 22$  (Ubinski et al., 2016).

INCLUDED SPECIES: *Rhopalurus caribensis* Teruel and Roncallo, 2008; *Rhopalurus laticauda* Thorell, 1876; *Rhopalurus ochoai*, sp. nov.

DISTRIBUTION: The genus *Rhopalurus* is endemic to the Guiana Shield of northern South America and recorded from Brazil, Colombia, Guyana, Venezuela, and several islands and island archipelagos in the southern Caribbean (Venezuelan territory): Isla Coche; Isla Cubagua; Isla Margarita; Isla La Peche, Archipiélago de Los Frailes; Isla La Tortuga; Isla Pico [Morro Pando], Archipiélago de Los Hermanos; Archipiélago de



Los Roques; Angoleta and Isla Conejo, Archipiélago de Los Testigos (figs. 5, 6).

**ECOLOGY:** The species of *Rhopalurus* inhabit open savanna-grassland vegetation, including caatinga and cerrado formations, and large tree clearings in the tropical rain forests of Amazonia (fig. 2E, F). The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**REMARKS:** The consistent paraphyly of *Rhopalurus* in the analyses by Esposito et al. (in review) and the identification of several well-defined, monophyletic groups, comprising species formerly assigned to *Rhopalurus*, justifies its redefinition and restriction to three species from northern South America (fig. 13). This finding is also consistent with the cytogenetic study of Ubinski et al. (2016), which identified a diploid chromosome number of  $2n = 22$  for *R. laticauda* (table 2).

*Rhopalurus caribensis* Teruel and Roncallo, 2008

Figures 6, 16C, 20C, 21H, 22H, 24N–R, 52A, 53A, 54A, 55A, 56A, 57

*Rhopalurus laticauda*: Lourenço, 1982a: 107, 108, 113, 115, 133–138, figs. 12, 13, 78, table 1 (misidentification: specimens from Magdalena); 1991a: 282; fig. 5 (misidentification: specimens from Magdalena); Flórez, 2001: 28 (misidentification: records from Magdalena and La Guajira); Botero-Trujillo and Fagua, 2007: 129–131, 133, figs. 4–6 (misidentification: specimen from Atlántico and records from Magdalena and La Guajira); Teruel and Roncallo, 2007: 6 (misidentification: record from La Guajira); Flórez, 2012 (part): 1, 2, figs. 1, 2, table 1.

*Rhopalurus caribensis* Teruel and Roncallo, 2008: 3–11, figs. 1–7, tables 1, 2; Lourenço, 2008: 5, 7, fig. 4; Prendini et al., 2009: 222, 223; Teruel and Roncallo, 2010: 2–4, 11, figs. 2, 11 (part), table 1; 2013: 112, 113, tables 1, 2; Teruel and Cozijn, 2013: 2.

**TYPE MATERIAL:** **COLOMBIA:** *La Guajira Dept.*: Holotype ♂ (RTO Sco.0358), Riohacha, Barrio “Adelaida,” 18.xii.2006, C.A. Roncallo. Paratypes: 2 ♂, 1 ♀, 1 juv. ♂ (RTO Sco.0359), Riohacha, Colegio “Sagrado Corazón,” km 1 via Maicao, 27.xi.2006, C.A. Roncallo; 1 ♀, 1 juv. ♂ (RTO Sco.0373), Serranía de Macuira, 3 km W of Nazareth, 14.vii.2007, J. Echavarría.

**DIAGNOSIS:** *Rhopalurus caribensis* is most closely related to *R. ochoai*, sp. nov. It resembles *R. ochoai* and typical populations of *R. laticauda* from the northwestern part of the distribution in its predominantly pale yellow-tan color, with light infuscation on the carapace and mesosoma, and metasoma V and telson slightly darker than the preceding segments. However, *R. caribensis* can be consistently differentiated from *R. laticauda* and *R. ochoai* by the color pattern on the ventral surface of the metasoma. Whereas *R. caribensis* displays three distinct, narrow stripes (a ventromedian stripe flanked on either side by a ventrosubmedian stripe) of pigmentation along the ventral surface, all three stripes are fused into a single, broad band of pigmentation (more pronounced in populations from the southeast of the distribution) in *R. laticauda*, and only two narrow ventrosubmedian stripes are present in *R. ochoai*. As with *R. ochoai*, *R. caribensis* differs further from populations of *R. laticauda* occurring in the southeastern part of the distribution (previously referable to *R. amazonicus*) in the considerably paler mesosoma, metasoma V, and telson. Additionally, the subaculear tubercle of the telson is vestigial in *R. caribensis*, small and blunt in *R. laticauda*, and subspinoid in *R. ochoai*.

**ECOLOGY:** Specimens for which data are available were collected with UV light detection at night in dry forest. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

**DISTRIBUTION:** This species appears to be endemic to the Llanos of the Magdalena, Colombia, separated from the nearest populations of *R. laticauda* and *R. ochoai*, sp. nov., by the Cordillera de Perijá (fig. 6). The known locality records occur in the Colombian departments of Atlántico, La

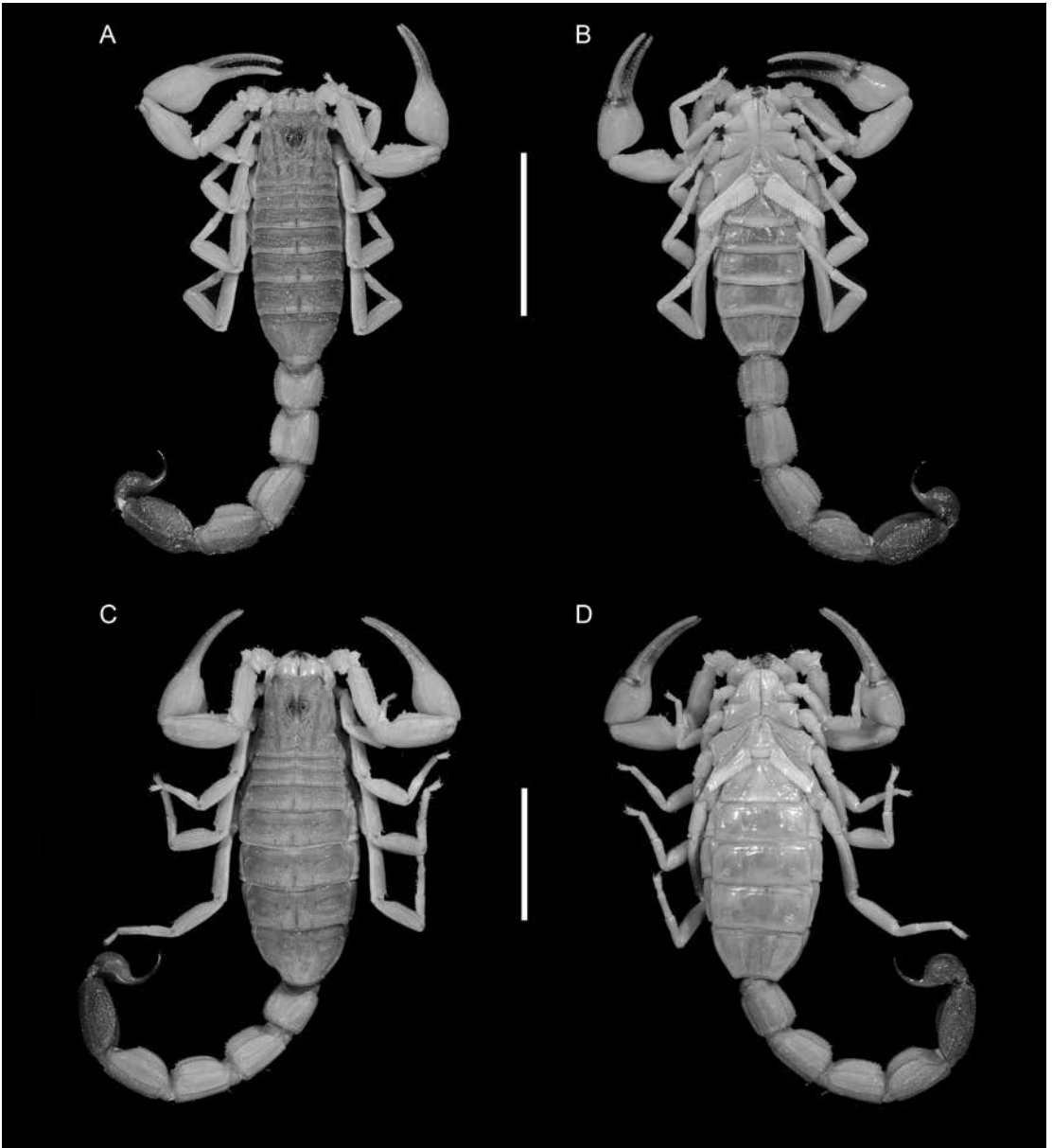


FIG. 57. *Rhopalurus caribensis* Teruel and Roncallo, 2008, habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (SMF). Scale bars = 1 mm.

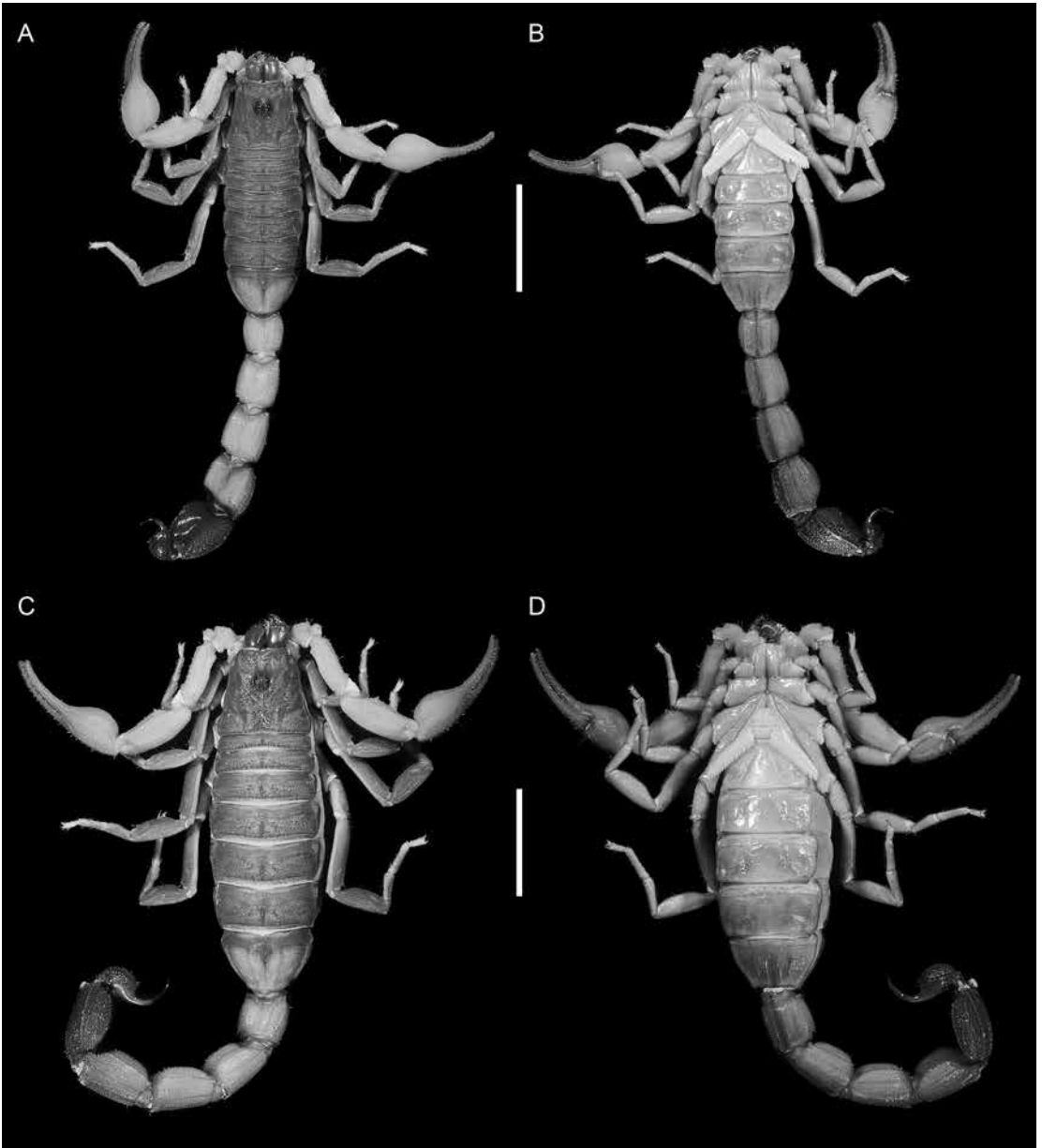


FIG. 58. *Rhopalurus laticauda* Thorell, 1876, Laguna Canaima, Venezuela, habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 1 mm.



FIG. 59. *Rhopalurus laticauda* Thorell, 1876, Puerto Colombia, Venezuela, habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. ♂ (AMNH). C, D. ♀ (AMNH). Scale bars = 1 mm.



FIG. 60. *Rhopalurus ochoai*, sp. nov., habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. Holotype ♂ (AMNH). C, D. Paratype ♀ (AMNH). Scale bars = 1 mm.

Guajira, and Magdalena. Material reported from the Venezuelan state of Zulia (Rojas-Runjaic and Becerra, 2008; Teruel and Roncallo, 2008, 2010) is referable to *R. ochoai*.

REMARKS: The status of *R. caribensis* has been the subject of controversy. Lourenço (2008) suggested it is a morph of *R. laticauda* and might be more appropriately recognized as a subspecies thereof. Flórez (2012) synonymized *R. caribensis* with *R. laticauda* based in part on images of *Tityus* alleged to be *R. caribensis*. Teruel and Roncallo (2013) subsequently revalidated *R. caribensis*. The analyses by Esposito et al. (in review) supported the validity of *R. caribensis* based on genetic divergence from *R. laticauda* (fig. 13). The two species are also morphologically diagnosable based on the character combinations described above.

MATERIAL EXAMINED: **COLOMBIA:** *Magdalena Dept.*: Municipio Santa Marta: Bahía de Guairaca, Tayrona Park, 31.x.1985, H.-G. Muller, 1 ♀ (SMF 37027); Corregimiento de Bonda, Vereda Girocasaca, Finca Guaipi, 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

Figures 1F, 2E, F, 5, 11C, E, 12C, 16D, E, 20D, E, 21I, 22I, 24I–M, 52B, C, 53B, C, 55B, C, 56B, C, 58, 59

*Rhopalurus laticauda* Thorell, 1876a: 9; 1876b: 143–145; Karsch, 1879a: 18; Mello-Campos, 1924a: 252, 253, 276, 283–285, pl. 7, fig. 31; 1924b: 318, 342, 349–351, pl. 7, fig. 31; Werner, 1927: 357; Lutz, 1928: 72, 73, figs. 1–3;

Mello-Leitão, 1932: 15; Prado, 1940: 27, 35; Prado and Rios-Patiño, 1940: 41, fig.; Hummelinck, 1940: 139, table 20; Mello-Leitão, 1940: 51; Roewer, 1943: 219; Mello-Leitão, 1945: 266, 280–284, figs. 115–117; Caporiacco, 1951: 4; Scorza, 1954a: 190, 201, figs. 15, 16; 1954b: 160; 1954c: 166; Bücherl, 1959: 268; 1967: 112; 1969: 767; Esquivel de Verde and Machado-Allison, 1969: 33; Bücherl, 1971: 327; Lucas and Bücherl, 1972: 263; Francke, 1977a: 133, fig. 12; Stahnke and Calos, 1977: 119; Vachon, 1977: 300, figs. 24, 28; González-Sponga, 1978: 201, figs. 9, 277, 278; Lourenço, 1979: 215, figs. 1, 3, 4; 1981: 545, fig. 2, tables 5–8; 1982a: 115, 136, figs. 12–13, 25–46, 78, table 1; Cekalovic, 1983: 190; González-Sponga, 1984: 72–74, fig.; Lourenço, 1984b: 14; 1986b: 170, fig. 7; Lourenço and Flórez, 1990: 71; Lourenço, 1991a: 282, fig. 5; Flórez, 1991: 119; Lourenço, 1991b: 117; 1992: 55; 1994: 157; González-Sponga, 1996: 118, 137, figs. 314–319; Lourenço, 1997b: 67, figs. 9, 10, 12, 14, 15; Kovařík, 1998: 118; Fet and Lowe, 2000: 220, 221; Flórez, 2001: 28 (records from Arauca, Casanare, and Meta); Botero-Trujillo and Fagua, 2007: 129–131, 133, figs. 4–6 (specimens from Vichada and records from Arauca, Casanare, and Meta); Kamenz and Prendini, 2008: 9, table 2, pl. 42; Lourenço, 2008: 3, 4, 5, 7, 12, table 1, fig. 4; Teruel and Roncallo, 2008: 2–5, 11, fig. 2; Prendini et al., 2009: 222, 223; Flórez, 2012 (part): 1, 2, figs. 1, 2, table 1; Teruel and Roncallo, 2013: 112, 113. *Rhopalurus laticauda sachsii* Karsch, 1879b: 118, 119, 122 (synonymized by Kraepelin, 1891: 137).

*Centrurus laticauda*: Kraepelin, 1891: 123, 137–139; 1899: 89, 95; 1908: 187, 190, 194; Penzance, 1913: 240; Waterman, 1950: 168.

*Rhopalurus testaceus laticauda*: Meise, 1934: 32. *Rhopalurus crassicauda* Caporiacco, 1947: 20; 1948: 609, 610, figs. 1–3; Lourenço, 2002:

36, 98–100, 110, 111, figs. 214–224; Teruel, 2006: 51, 52; Teruel and Tietz, 2008: 8, 9–11, figs. 5–9; Lourenço, 2008: 4–8, table 1, fig. 4; Prendini et al., 2009: 222, 223; Brazil and Porto, 2010: 50; Ubinski et al., 2016: 122; syn. nov.

*Rhopalurus amazonicus* Lourenço, 1986a: 132–134, figs. 3–9, 13, 14; 1986b: 170, fig. 7; 1988: 169, figs. 13, 15; 1991b: 117; 1992: 55; Lourenço and Pinto-da-Rocha, 1997: 184; Kovařík, 1998: 118; Fet and Lowe, 2000: 218, 219; Lourenço, 2008: 1; Prendini et al., 2009: 222; Brazil and Porto, 2010: 50; Lourenço, 2014: 69; syn. nov.

*Rhopalurus crassicauda parauensis* Lourenço, 2008: 4, 7–8, figs. 4–9, table 1; Prendini et al., 2009: 222; Lourenço, 2014: 69; syn. nov.

*Rhopalurus laticauda laticauda*: Fet and Lowe, 2000: 221.

*Rhopalurus crassicauda crassicauda*: Lourenço, 2008: 6.

*Rhopalurus* cf. *laticauda*: Teruel and Cozijn, 2013: 2–6, figs. 1–4, tables 1, 2.

**TYPE MATERIAL:** *Rhopalurus amazonicus*: Holotype ♀ (INPA), **BRAZIL:** Pará: Alter do Chão-Santarém, v.1984, W. Manson. *Rhopalurus crassicauda*: 2 ♂, 1 ♀ syntypes (MZUF), **GUYANA:** Runununi [Rupununi], British Guiana. *Rhopalurus crassicauda parauensis*: Holotype ♂ (MNHN RS-8630), **BRAZIL:** Pará: Campos de Paru, South of Serra do Tumucumaque, border with Suriname, x.1966, F. Petter. *Rhopalurus laticauda*: Lectotype ♀, paralectotype ♀ (NMG 170) [here designated], **COLOMBIA.** *Rhopalurus laticauda sachsi*: **VENEZUELA:** 2 syntypes [sex?] (ZMB 3020); 1 syntype [sex?] (ZMB 3042), Calaboço; syntype ♂ (ZMB 3043), Caracas.

**DIAGNOSIS:** *Rhopalurus laticauda* can be consistently differentiated from *R. caribensis* and *R. ochoai*, sp. nov., by the color pattern on the ventral surface of the metasoma. Whereas *R. laticauda* displays a single, broad band of pigmentation along the ventral surface, which is more pronounced in populations from the

southeast of the distribution, *R. caribensis* displays three distinct, narrow stripes (a ventro-median stripe flanked on either side by a ventrosubmedian stripe), and *R. ochoai* displays only two narrow ventrosubmedian stripes. Typical populations of *R. laticauda* from the northwestern part of the distribution resemble *R. caribensis* and *R. ochoai* in the predominantly pale yellow-tan color, with light infuscation on the carapace and mesosoma, and metasoma V and telson slightly darker than the preceding segments. However, populations from the southeastern part of the distribution (previously referable to *R. amazonicus*) differ in the markedly infuscate carapace, tergites, metasoma V, and telson, which contrasts with the pale pedipalps, legs, and metasomal segments I–IV (fig. 1F). Additionally, the subaculear tubercle of the telson is small and blunt in *R. laticauda*, vestigial in *R. caribensis*, and subspinoid in *R. ochoai*.

**DISTRIBUTION:** *Rhopalurus laticauda* is endemic to northern South America and several islands and island archipelagos in the southern Caribbean (fig. 5; Teruel and Roncallo, 2008; Teruel and Cozijn, 2013): Isla Coche; Isla Cubagua; Isla Margarita; Isla La Tortuga; Isla La Peche, Archipiélago de Los Frailes; Isla Pico [Morro Pando], Archipiélago de Los Hermanos; Archipiélago de Los Roques; Angoletta and Isla Conejo, Archipiélago de Los Testigos. The known localities occur in Brazil (the states of Amazonas, Pará, and Roraima), Colombia (the departments of Arauca, Boyacá, Casanare, Cesar, Meta, La Guajira, Magdalena, and Vichada), Guyana and Venezuela (the states of Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, D.F., Falcon, Guárico, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Vargas, and Yaracuy).

**ECOLOGY:** Specimens for which data are available were collected with UV light detection at night in savanna or dry forest (fig. 2E, F). The habitat and habitus are consistent with

the lapidicolous ecomorphotype (Prendini, 2001b).

REMARKS: *Rhopalurus laticauda* exhibits phenotypic plasticity in size and the intensity of infuscation on the carapace, tergites, metasoma, and pedipalps, apparently associated with habitat variation across the distribution, which ranges from completely open, semiarid coastal scrub in northwestern South America to tree clearings in the tropical rainforest of the Amazon Basin, much further southeast. When considering limited subsets of the overall distribution, this phenotypic plasticity has led to the false recognition of separate species or subspecies for regional variants. For example, Lourenço (1986a, 2008), recognized *R. amazonicus*, *R. crassicauda*, and *R. crassicauda paruensis* for the populations of *R. laticauda* that inhabit savanna “islands” surrounded by rainforest, but the low genetic divergence among samples from these populations recovered by Esposito et al. (in review) indicates substantial gene flow between them. The somewhat darker and more contrasting coloration of populations referable to *R. amazonicus* and *R. crassicauda* from the southeast of the distribution, 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, just more pronounced than in typical populations of *R. laticauda*. In the absence of deep genetic divergence between these populations and consistent combinations of diagnostic morphological characters, we regard *R. amazonicus*, *R. crassicauda*, and *R. crassicauda paruensis* as conspecific with *R. laticauda* and propose the following new synonyms: *Rhopalurus crassicauda* Caporiacco, 1947 = *Rhopalurus laticauda* Thorell, 1876, syn. nov.; *Rhopalurus amazonicus* Lourenço, 1986 = *Rhopalurus laticauda* Thorell, 1876, syn. nov.; *Rhopalurus crassicauda paruensis* Lourenço, 2008 = *Rhopalurus laticauda* Thorell, 1876, syn. nov.

Teruel and Cozijn (2013: 1) tentatively determined *Rhopalurus* records from islands in the southern Caribbean as *Rhopalurus* cf. *laticauda*, noting “their precise identity still warrants further study.” No consistent morphological differences are observed between the island and mainland populations and Esposito et al. (in review) found no significant genetic divergence between samples from Isla Margarita and the Venezuelan mainland. Therefore, we consider the island populations to be conspecific with, and appropriately assigned to *R. laticauda*.

MATERIAL EXAMINED: 2 ♀ (ZMB 14865). “Mexico,” Dr v. Hubl, 1 ♂ (ZMB 14866). **BRAZIL:** F. Kummerow, 1 ♂, 1 ♀ (ZMB 8226). **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/AMCC [LP 9686]), 1 subad. ♂, (MZSP 30872), 1 juv. (AMCC [LP 9688]), 2 juv. ♀ (MZSP 30873/AMCC [LP 9689], MZSP 30874/AMCC [LP 9690]), 1 juv. (MZSP 30875/AMCC [LP 9691]); Monte Alegre, 01°56'32"S 54°08'13"W 31.x.2008, H.Y. Yamaguti and R. Pinto-da-Rocha, 2 ♀ (MZSP 30871/AMCC [LP 9687], MZSP 31141/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/AMCC [LP 9952]), 1 juv. ♂ (MZSP 31172/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/AMCC [LP 9677]), 1 subad. ♂ (MZSP 31175/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/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/AMCC [LP 9959]), 1 ♀ (MZSP 30876/AMCC [LP 9675]); Río Branco, Amazonasgebiet, 1912, E. Ule, 1 juv. ♀ (ZMB 14867). **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, Fahrenholz, 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. Yepez, 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 ♂ meta-soma (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 Anatoly, 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]); Upata, ii.1973, A. Bordes, 1 ♀ (AMNH). *Carabobo:* Municipio Valencia: Valencia, 29.xii.1904, F. Kummerow, 1 ♀ (ZMB 31024), ix.1958, H. Ardelt, 2 ♀ (ZMH), Valencia, Falcon Distr., viii.1992, C. Siederman, 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. González-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. González-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]); Isla Margarita, 2001, C. Siederman, 1 ♀ (AMCC [LP 2462]).

*Rhopalurus ochoai*, sp. nov.

Figures 6, 16F, 17E, 20F, 21J, 22J, 52D, 53D, 54D, 55D, 56D, 60; table 3

*Rhopalurus caribensis:* Rojas-Runjaic and

Becerra, 2008: 465, fig. 1 (misidentification: records from Zulia, Venezuela); Prendini et al., 2009: 222 (misidentification: records from Zulia, Venezuela), 223; Teruel and Roncallo, 2010: 4, 11, fig. 11 (misidentification: records from Zulia, Venezuela).

**TYPE MATERIAL: VENEZUELA:** Holotype ♂ (AMNH), *Zulia:* Municipio Jesus Enrique Lozada: San Agustín, 10°45.841'N 71°44.108'W, 44 m, 28.ix.2008, J.A. Ochoa and S.E. Bazo Abreu, dry forest. Paratypes: *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 ♀ (AMNH), 1 subad. ♀, 1 juv. ♀ (AMCC [LP 9199]). Municipio Valera: Valera region, N, x.2005, S.E. Bazo Abreu, 2 ♀ (AMCC [LP 5504, 5505]). *Zulia:* Municipio Jesus Enrique Lozada: 1 ♂, 2 ♀, 1 subad. ♀ (AMNH), 1 subad. ♀ (AMCC [LP 9207]), same data as holotype.

**DIAGNOSIS:** *Rhopalurus ochoai*, sp. nov., is most closely related to *R. caribensis*. It resembles *R. caribensis* and typical populations of *R. laticauda* from the northwestern part of the distribution, in its predominantly pale yellow-

TABLE 4

**Meristic data for type material of *Rhopalurus ochoai*, sp. n.**

Measurements follow Prendini (2000, 2003, 2004a). <sup>1</sup>Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; <sup>2</sup>sum of metasomal segments I–V and telson; <sup>3</sup>measured from base of condyle to tip of fixed finger.

		Holotype	Paratype	Paratype	Paratype	Paratype	Paratype
		♂	♂	♂	♀	♀	♀
		AMNH	AMNH	AMNH	AMNH	AMNH	AMNH
Total length <sup>1</sup>		46	45	41.9	47.2	48.9	46.6
Prosoma	length	5.8	6.5	5.3	5.6	6.4	5.6
	ant. width	2.9	3.2	2.9	2.8	3	3.2
	post. width	6.1	5.9	5.8	5.9	7.1	6.0
Mesosoma	total length	16.6	15.5	14.1	18.5	16.5	18.7
Metasoma	total length <sup>2</sup>	23.6	23.0	22.5	23.1	26	22.3
Segment I	length	3.9	3.7	3.3	3.5	3.7	3.6
	width	3.6	3.5	3.1	3.3	3.5	3.3
	height	3.0	3.2	2.8	2.7	3.2	2.7
Segment II	length	4.2	4.1	4.1	4.4	4.7	4.0
	width	3.9	3.7	3.3	3.3	3.9	3.4
	height	3.1	3.7	2.7	2.9	3.2	2.6
Segment III	length	4.7	4.5	4.7	4.6	5.4	4.6
	width	4.5	3.9	3.7	3.4	4.2	3.5
	height	3.2	3.0	2.8	2.7	3.2	2.8
Segment IV	length	5.1	5.2	5.3	5.1	5.8	4.8
	width	5.6	4.4	4.3	3.8	44.9	3.7
	height	3.1	2.9	2.6	3	3.3	2.7
Segment V	length	5.7	5.5	5.1	5.5	6.4	5.3
	width	5.5	4.4	4.1	3.7	4.8	3.6
	height	3.2	2.8	2.6	2.6	3.2	2.6
Telson	total length	5.0	5.2	4.6	4.9	5.7	4.5
Vesicle	length	2.9	3.2	2.7	3.1	3.1	2.5
	width	2.2	2.1	2.9	2.1	2.5	2.2
	height	2.0	2.0	1.8	1.8	2.2	2.0
Aculeus	length	3.2	2.8	2.4	2.6	3.7	2.8
Pedipalp	total length	22.1	21.3	18.8	20.9	22.8	21.1
Femur	length	4.8	4.9	4.4	4.9	5.2	4.9
	width	1.7	1.2	1.4	1.7	1.9	1.7
	height	1.3	1.8	1.2	1.1	1.4	1.2
Patella	length	6.5	6.1	4.8	5.6	6.3	6.0
	width	2.5	2.5	2	2.4	2.6	2.3
	height	1.7	1.5	1.7	1.5	1.9	1.4
Chela	length <sup>3</sup>	10.8	10.3	9.6	10.4	11.3	10.2
Manus	width	3.5	2.8	3	2.5	2.8	2.3
	height	3.3	2.7	2.7	2.4	3.1	2.0
Mov. finger	length	6.8	6.7	6.1	6.9	7.2	7.0
Pectines	total length	5.1	3.9	4.6	4.1	4.7	4.4
	basal width	1.1	1.1	1.3	1.3	1.1	1.0
	tooth	24/23	20/21	24/25	21/22	23/23	22/21

tan color, with light infuscation on the carapace and tergites, and metasomal segment V and telson slightly darker than the preceding segments. However, *R. ochoai* can be consistently differentiated from *R. caribensis* and *R. laticauda* by the color pattern on the ventral surface of the metasoma. Whereas *R. ochoai* displays two narrow ventrosubmedian stripes of pigmentation along the ventral surface, three distinct, narrow stripes (a ventromedian stripe flanked on either side by a ventrosubmedian stripe) are present in *R. caribensis*, and all three stripes are fused into a single, broad band of pigmentation (more pronounced in populations from the southeast of the distribution) in *R. laticauda*. As with *R. caribensis*, *R. ochoai* differs further from populations of *R. laticauda* from the southeastern part of the distribution (previously referable to *R. amazonicus*) in the considerably lighter mesosoma, metasoma V, and telson. Additionally, the subaculear tubercle of the telson is subspinoid in *R. ochoai*, small and blunt in *R. laticauda*, and vestigial in *R. caribensis*.

**ETYMOLOGY:** This species name is a patronym, honoring the Peruvian arachnologist, José Antonio Ochoa Camara, who collected most of the type specimens, for his contributions to the study of scorpions.

**DESCRIPTION:** The following description is based on the type material (for measurements, see table 4). Only characters that differ from the generic description are noted.

**Total length:** Medium-sized, compact scorpions (total length, 41–49 mm).

**Color:** Predominantly tan-yellow with pedipalp chela manus, metasomal segment V and telson slightly darker, khaki yellow. Chelicerae with reticulate infuscation. Carapace, pedipalp chela fingers, tergites, metasomal segment V, and telson lightly infuscate. Metasomal segments I–IV, ventral surfaces each with two narrow ventrosubmedian stripes of pigmentation.

**Carapace:** Shape pentagonal, emarginate anteriorly; posterior width greater than anterior width. Median ocular tubercle raised, with

pair of ocelli. Three pairs of lateral macrocelli, one pair of lateral microcelli, situated between the second and third macrocelli. Anteromedian, median ocular and posteromedian sulci well developed, forming single, almost continuous longitudinal sulcus; posteromedian sulcus moderately deep, posterolateral sulci wide, shallow depressions. Intercarinal surfaces coarsely and densely granular; lateral ocular and anterior central submedian carinae indistinct, finely granular and separate (unfused); central lateral and posterior central submedian carinae distinct, finely granular, and fused into single slightly oblique carina, extending almost two thirds the length of carapace. Anterior margin with several macrosetae, remaining surfaces asetose.

**Pedipalps:** Chela manus retrodorsal carina distinct, granular; ventromedian carina obsolete, granular; intercarinal surfaces granular.

**Legs:** Legs III and IV, tibial spurs absent; I–IV, surfaces carinate; basitarsi each with bifurcate prolateral pedal spur; telotarsi each with irregular tufts of fine, acuminate macrosetae.

**Sternum:** Subtriangular. Median longitudinal sulcus shallow anteriorly, deep, narrow posteriorly.

**Genital operculum:** Genital opercula suboval, completely divided longitudinally; genital papillae present (♂), absent (♀).

**Pectines:** Pectinal plate rectangular, without depressions (male), anterior margin with sulcus medially. Tooth count, 20–25 (♂), 21–23 (♀).

**Mesosoma:** Tergites granular, each with median carina, tergite VII pentacarinat. Sternite III with two finely granular lateral depressions and median surface raised, setose; IV–VI granular posterolaterally; VII granular with four carinae.

**Metasoma:** Metasoma robust, increasing in width posteriorly, segment V ca. 2× width of segment I in adult male, only slightly wider than I in adult female (fig. 54D). Ventral intercarinal surfaces finely and sparsely granular on segments I and II, coarsely and densely granular on III and IV (fig. 55D).



FIG. 61. *Troglorhopalurus* Lourenço et al., 2004, pedipalp chela, retrolateral aspect. **A.** *T. lacraui* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (MZSP). **B.** *Troglorhopalurus translucidus* Lourenço et al., 2004, ♀ (MZSP). Scale bars = 2 mm.

*Telson:* Vesicle width ca. half to one third the width of metasomal segment V (males); lateral and ventral surfaces granular with obsolete ventromedian carina; subaculear tubercle small, subspinoid.

*Sexual dimorphism:* Adult males and females differ as follows. Intercarinal surfaces of the carapace, tergites, metasoma, and pedipalps are more coarsely and densely granular in males than females. The pedipalp chela manus of males is incrassate and the fingers curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that only the distal portion of the fingers connect and a distinctive gap is present between them proximally, when closed (fig. 52D). The chela manus of females is not incrassate and the fingers are not curved proximally, such that the fingers connect along most of their length and little to no gap is present between them proximally, when closed (fig. 53D). The metasomal segments are proportionally broader in males, exaggerating the pos-

terior increase in metasomal width, compared to females. In some populations, infuscation of the metasoma, especially segment V, the telson, and the ventral carinae of segments I–IV, is more intense in females.

*DISTRIBUTION:* *Rhopalurus ochoai*, sp. nov., appears to be restricted to northwestern Venezuela, where it has been recorded around Lake Maracaibo in the states of Trujillo and Zulia. The known records fall within an area bordered by the Cordillera de Perijá to the west and the Cordillera de Mérida to the south and east (fig. 6). Records of *R. caribensis* reported from the Venezuelan state of Zulia (Rojas-Runjaic and Becerra, 2008; Teruel and Roncallo, 2008, 2010; Prendini et al., 2009) are referable to *R. ochoai*.

*ECOLOGY:* Specimens for which data are available were collected with UV light detection at night in dry forest. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001b).

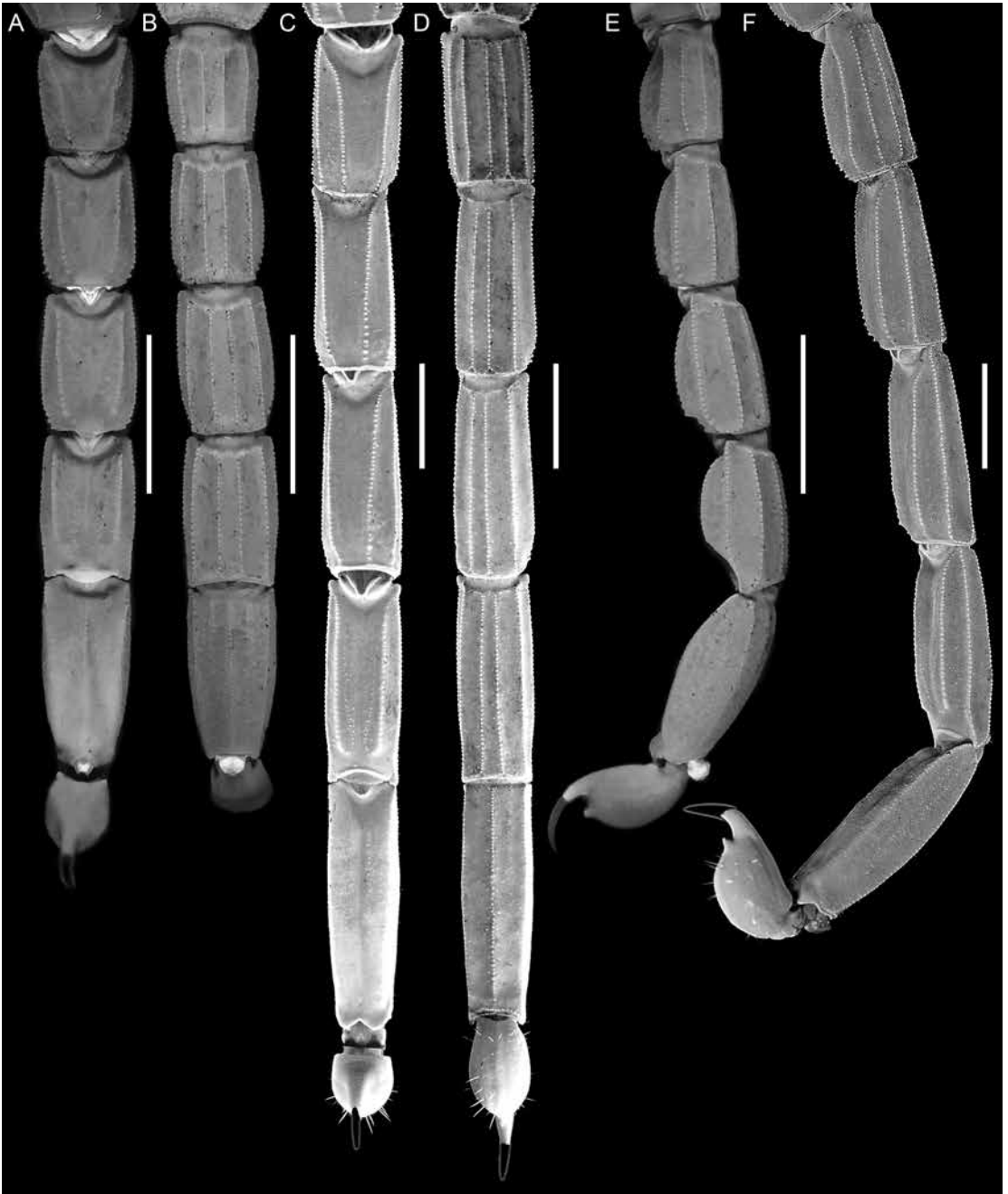


FIG. 62. *Troglophalurus* Lourenço et al., 2004, metasoma and telson, dorsal (A, C), ventral (B, D) and lateral (E, F) aspects. A, B, E. *T. lacrae* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (AMNH). C, D, F. *T. translucidus* Lourenço et al., 2004, ♀ (MZSP).

*Troglorehopalurus* Lourenço, Baptista and Giupponi, 2004

Figures 1G, H, 2G, H, 9, 10E, 11F, 12D, 14F, 15E, 17F, 18F, 19E, 21K, L, 22K, L, 61–63

*Troglorehopalurus translucidus* Lourenço et al., 2004, type species by original designation.

*Troglorehopalurus* Lourenço et al., 2004: 1151–1156, figs. 1–10; Prendini and Wheeler, 2005: 481, table 10; Volschenk and Prendini, 2008: 236, 249; Prendini et al., 2009: 206, 222; Brazil and Porto, 2010: 57; Ochoa et al., 2010: 17; Ubinski et al., 2016: 122.

*Rhopalurus* (part): Lourenço and Pinto-da-Rocha, 1997: 182–188, 191, figs. 1–3, 5, 7, 9, 11, 14; Kovařík, 1998: 118; Fet and Lowe, 2000: 220; Lourenço, 2002: 102, 111, figs. 228–231; Manzanilla and Sousa, 2003: 3; Lourenço et al., 2004: 1152, 1156; Lenarducci et al., 2005: 1, 2, 7; Lira-da-Silva et al., 2005: 2; Teruel, 2006: 52; Lourenço, 2007: 359; 2008: 3; 2008: 3; Prendini et al., 2009: 222, 223; Outeda-Jorge et al., 2009: 44–46, 48, 49; Brazil and Porto, 2010: 50, 62; Porto et al., 2010: 293–295, table 1; Lourenço, 2014: 69–75, figs. 1–12; Gallão and Bichuette, 2016: 2, 3, 9–11, figs. 1, 18; Ubinski et al., 2016: 122.

**DIAGNOSIS:** *Troglorehopalurus* differs from *Heteroctenus*, *Jaguajir*, gen. nov., *Physoctonus*, and *Rhopalurus* by the proximal dentate margins of the chela fixed and movable fingers of the adult male that are linear, with no gap evident between them, when closed; from *Heteroctenus*, *Jaguajir*, and *Rhopalurus* by the absence of a pecten-sternite stridulatory organ; from *Ischnotelson*, gen. nov., and *Rhopalurus* by the separate (unfused) central lateral and posterior central submedian carinae of the carapace; from *Heteroctenus* by the presence of two lateral depressions in the male pectinal plate, and a subaculear tubercle on the telson; from *Ischnotelson* by the separate (unfused) lateral ocular and central lateral carinae of the carapace and the telson vesicle

not being laterally compressed; from *Jaguajir* by the separate (unfused) lateral ocular and anterior central submedian carinae of the carapace; from *Physoctonus* by the larger size (35–40 mm), the more distinct carapacial carinae, the setose proximal dorsal fulcra of the pectines, the bifurcate prolateral pedal spur of leg I, and the oblique subrows of primary denticles on the pedipalp chela fingers flanked closely by pro- and retrolateral accessory (supernumerary) denticles; from *Rhopalurus* by the slender metasoma, not increasing in width posteriorly; and from *Centruroides* by the obsolete retromedian carina on the pedipalp chela manus, and the well-separated dorsointernal and proventral carinae of the pedipalp patella.

**DESCRIPTION:** The following general description outlines characters common to both species of *Troglorehopalurus*.

**Total length:** Medium-sized, gracile scorpions (total length, 35–40 mm) with soma slightly dorsoventrally compressed.

**Color:** Base color predominantly pale brown with pigmentation somewhat reduced, especially in the immature stages (fig. 1G–H). Carapace and tergites similar to or slightly darker than chelicerae, pedipalps, legs, sternites, metasoma and telson vesicle; pedipalp chela fingers darker than chela manus, patella, and femur, carinae darker than intercarinal surfaces; pectines pale yellow; metasomal segments IV and V darker than preceding segments in *T. lacrau*, comb. nov.; metasomal carinae darker than intercarinal surfaces; telson aculeus dark brown to black.

**Chelicerae:** Base, dorsal surface with medial transverse row of well-developed tubercles.

**Carapace:** Median ocular tubercle low (figs. 14F, 15E); two median ocelli reduced, more so in *T. translucidus*; three pairs of lateral macrocelli; one pair of lateral microcelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular, central lateral, anterior central submedian and posterior central submedian carinae somewhat indistinct, finely granular and separate (unfused).

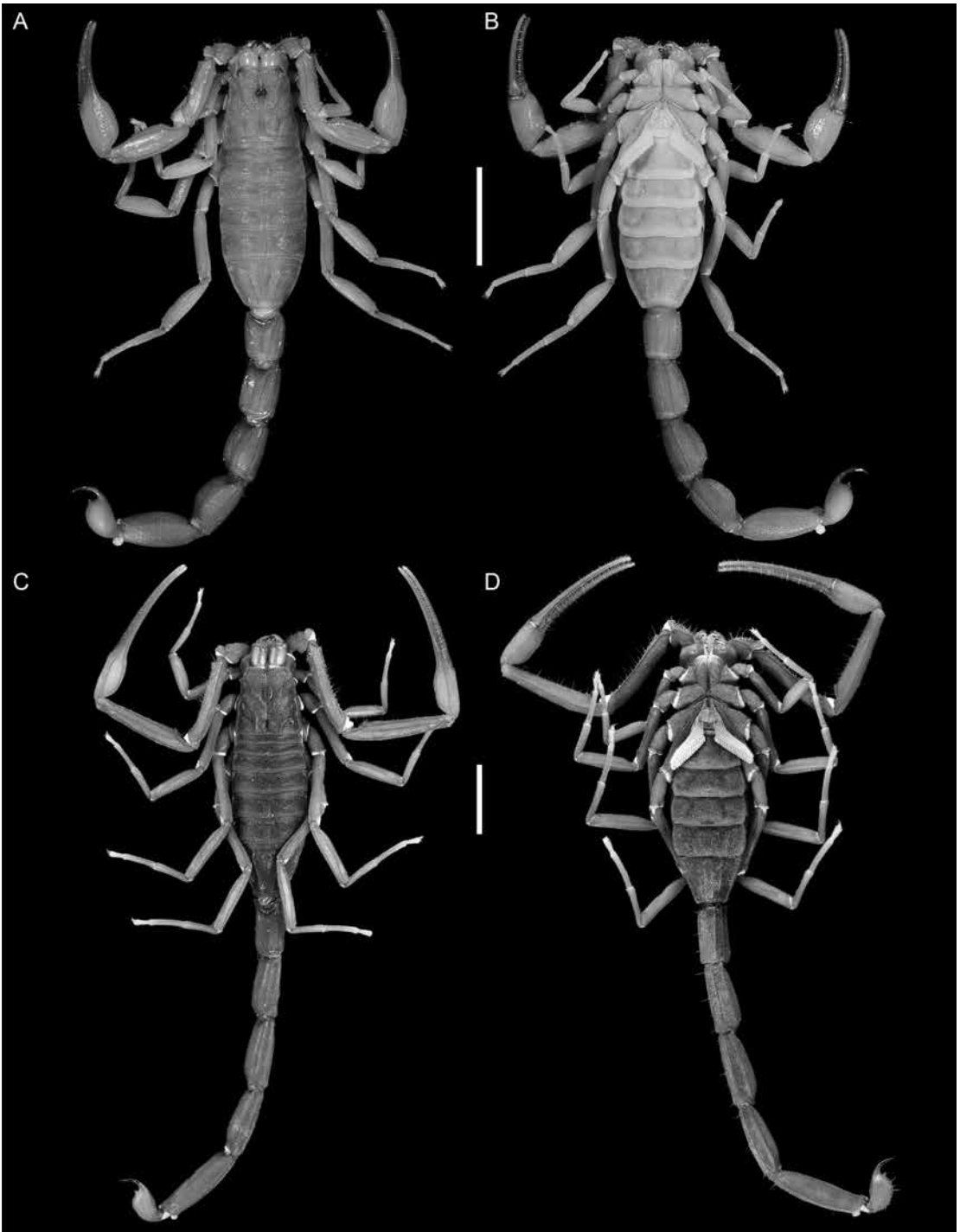


FIG. 63. *Troglorhopalurus* Lourenço et al., 2004, habitus, dorsal (A, C) and ventral (B, D) aspects. A, B. *T. lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (AMNH). C, D. *T. translucidus* Lourenço et al., 2004, ♀ (MZSP). Scale bars = 1 mm.

**Pedipalps:** Pedipalp femur retrolateral accessory carinae absent. Pedipalp chela manus of males incrassate in *T. lacrau*, slender in *T. translucidus* (fig. 61), fixed and movable fingers not curved, such that proximal dentate margin linear, no gap present between fingers proximally, when closed; manus, proventral carina present, promedian carina absent; fixed and movable fingers, median denticle rows each comprising eight (*T. lacrau*) or nine (*T. translucidus*) oblique subrows of primary denticles flanked closely by pro- and retrolateral accessory (supernumerary) denticles, smaller and more sparse in *T. translucidus*; movable finger without proximal lobe (fig. 17F). Pedipalps orthobothriotaxic Type A, a configuration; femur with five dorsal trichobothria, trichobothrium  $d_2$  situated on prolateral surface; patella trichobothrium  $d_3$  situated retrolateral to dorsomedian carina; chela fixed finger trichobothrium  $db$  situated proximal to trichobothrium *et*.

**Legs:** Legs III and IV, tibial spurs absent; I–IV, basitarsi each with bifurcate prolateral pedal spur; telotarsi each with distinct pro- and retroventral rows of fine, acuminate macrosetae.

**Pectines:** Pectinal plate with two lateral depressions (male), anterior margin with or without sulcus (figs. 18F, 19E). Pectines not proximally expanded; proximal dorsal fulcra setose; pectinal teeth almost straight, slightly curved laterally, proximal teeth, dorsal surfaces without nodules and with irregular striations (figs. 11F, 12D), dorsobasal surfaces with or without macrosetae; pectinal sensillae elongate and acuminate.

**Mesosoma:** Tergites IV and VI wider than I–III and VII; dorsosubmedian carinae vestigial or absent, dorsomedian carinae finely granular, vestigial, restricted to posterior margins of segments I–V, complete on VI (fig. 63). Tergite VII pentacarinata, dorsomedian carina restricted to anterior half of segment. Sternites III–V smooth, carinae absent or obsolete, ventromedian carina present on VI and VII; sternite III, lateral margins not forming smooth, raised carina, ventromedian carina not elevated anteriorly, ventrosubmedian surfaces not forming

paired depressions, finely and irregularly granular; respiratory spiracles (stigmata) small and short, width ca.  $2 \times$  length (fig. 10F).

**Metasoma:** Metasoma slender, not increasing in width posteriorly, I and V similar width in both sexes (fig. 62). Segments I and II each with 10 distinct, costate-granular carinae, III and IV each with eight distinct, costate-granular carinae, V with seven distinct but less pronounced, granular carinae; dorsosubmedian carinae absent or obsolete, reduced to rows of granules on dorsal surfaces of segments I–IV; dorsolateral carinae complete on segments I–IV, often terminating in prominent, spiniform granules posteriorly on III and IV, absent on V; lateral suprmedian carinae complete on segments I–V; lateral inframedian carinae complete on segment I, partial on II, absent on III–V; ventrosubmedian carinae complete on segments I–IV, restricted to anterior third on V; ventromedian carina absent on segments I–IV, complete on V. Intercarinal surfaces finely granular.

**Telson:** Vesicle slightly elongate, not laterally compressed, width similar to metasoma V width; anterodorsal lateral lobes reduced or absent; lateral and ventral surfaces granular (*T. translucidus*) or smooth (*T. lacrau*), with distinct ventromedian carina; subaculear tubercle well developed, spinoid.

**Hemispermatothore:** Unknown.

**Cytogenetics:** The diploid chromosome number of *T. lacrau* is  $2n = 20$  and of *T. translucidus*,  $2n = 20$ – $22$  (Ubinski et al., 2016).

**INCLUDED SPECIES:** *Trogloorhopalurus translucidus* Lourenço et al., 2004; *Trogloorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov.

**DISTRIBUTION:** *Trogloorhopalurus* is endemic to northeastern Brazil, where it has been recorded in the states of Bahia and Ceará (fig. 9).

**ECOLOGY:** Both species of *Trogloorhopalurus* occur under stones either inside or in close proximity to caves (fig. 2G, H).

**REMARKS:** *Trogloorhopalurus* was originally monotypic, created to accommodate *T. translucidus*. In comparing *Trogloorhopalurus* with *Rhopal-*



*urus*, Lourenço et al. (2004: 1153, 1156) noted “all modifications presented by the new troglobitic scorpion are the result of adaptation to a cave dwelling life,” prompting Prendini et al. (2009) to suggest that *Troglorhopalurus* might be a junior synonym of *Rhopalurus*. *Rhopalurus lacrau* had earlier been described from caves belonging to the same subterranean formation in Brazil and, in the description of *Troglorhopalurus*, Lourenço et al. (2004) suggested the relationship between these taxa should be investigated using molecular data. Gallão and Bichuette (2016) subsequently identified four morphological characters shared by *R. lacrau* and *T. translucidus*, in addition to their troglomorphic habitus (metasomal carination, pectinal tooth count, pectinal peg sensillar shape, and the absence of a pecten-sternite stridulatory apparatus). A close association between the two species was independently verified in the cytogenetic study of Ubinski et al. (2016) which identified a diploid chromosome number of  $2n = 20$  for *R. lacrau* and  $2n = 20-22$  for *T. translucidus* (table 2). Accordingly, the consistent placement of *R. lacrau* sister to *T. translucidus* in the analyses of Esposito et al. (in review) is rather predictable, and justifies the transfer of *R. lacrau* to *Troglorhopalurus* and the following new combination: *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha 1997), comb. nov. (fig. 13).

***Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov.**

Figures 1G, 2G, 9, 10E, 11F, 12D, 14F, 17F, 18F, 21K, 22K, 61A, 62A, B, E, 63A, B

*Rhopalurus lacrau* Lourenço and Pinto-da-Rocha, 1997: 182–183, figs. 1–3, 5, 7, 9, 11, 14; Kovařík, 1998: 118; Fet and Lowe, 2000: 220; Lourenço, 2008: 3; Prendini et al., 2009: 222, 223; Brazil and Porto, 2010: 50, 62; Porto et al., 2010: 293–295, table 1; Lourenço, 2014: 69, 73–75, fig. 12; Gallão and Bichuette, 2016: 2, 3, 9–11, figs. 1, 18; Ubinski et al., 2016: 122.

*Rhopalurus brejo* Lourenço, 2014: 71–75, figs. 1–12; syn. nov.

TYPE MATERIAL: **BRAZIL:** *Rhopalurus lacrau*: Holotype ♀ (MZSP 15175), *Bahía*: Município Itaeté: Lapa do Bode (inside the cave), 12°56'S 41°04'W, 7.ix.1993, E. Trajluió. *Rhopalurus brejo*: Holotype ♀ (MNHN), *Ceará*: Chapada (serra) do Araripe, Brejo Grande, S of Santana, ii.1964.

DIAGNOSIS: *Troglorhopalurus lacrau* differs from its sister species, *T. translucidus*, as follows. The soma and appendages are shorter and broader in *T. lacrau* than *T. translucidus*, in which the soma and appendages are elongate and slender: total body length is about 40 mm in *T. lacrau* and 60 mm in *T. translucidus*; the pedipalp is 4.5× longer than the carapace in *T. lacrau* but 6.5× longer in *T. translucidus*; the pedipalp chela manus is incrassate and slightly shorter than the chela movable finger in *T. lacrau* but very slender, the manus almost half the length of the movable finger in *T. translucidus*; the pedipalp patella is 3.8× longer than wide in *T. lacrau*, but 6× longer in *T. translucidus*; metasomal segment V is 2.7× longer than wide in *T. lacrau*, but 4.5× longer in *T. translucidus*. The retromedian and secondary accessory carinae of the pedipalp chela manus are weakly granular in *T. lacrau*, and absent in *T. translucidus*. Eight subrows of denticles are present in the median denticle row of the chela fixed finger of *T. lacrau*, whereas nine subrows are present in *T. translucidus*. Macrosetae on the fixed and movable fingers of the pedipalp chela are shorter than the chela width in *T. lacrau*, but longer in *T. translucidus*. Macrosetae of the telson vesicle are shorter than the subaculear tubercle in *T. lacrau*, but longer in *T. translucidus*. The subaculear tubercle of the telson is blunt in *T. lacrau*, but has a sharply pointed tip in *T. translucidus*. The posterior third of the aculeus is curved in *T. lacrau*, but straight in *T. translucidus*.

DISTRIBUTION: *Troglorhopalurus lacrau* is endemic to Brazil, and known from only two populations, in the states of *Bahía* and *Ceará*

(fig. 9A). All except two specimens were collected from two connected caves, Lapa do Bode Cave and Gruta Escondida in the Município Itaeté of Bahia. A single, dead individual was collected from Bob Cave, ca. 20 km northeast (Gallão and Bichuette, 2016), also in Município Itaeté. The second population of *T. lacrau* is represented by the type locality and only known specimen of its junior synonym, *R. brejo*, in the state of Ceará. The two localities are 700 km apart but the region between them, the Serra do Espinhaço, is poorly sampled. Assuming the record from Ceará is reliable, this species may be discovered in the Serra do Espinhaço when it is more thoroughly surveyed.

**ECOLOGY:** Most of the known specimens of *T. lacrau* were collected under stones inside limestone caves. Despite extensive searches, no specimens were found outside the type locality, Lapa do Bode Cave (Gallão and Bichuette, 2016), where this species has a well-established population (fig. 2G). The habitat, distribution and habitus are consistent with the troglophile ecomorphotype (Prendini, 2001b).

**REMARKS:** *Rhopalurus brejo* was poorly described in an obscure journal with distorted plates. The original description and illustrations barely permit us to determine to which genus this taxon belongs. Although the holotype and only known specimen of *R. brejo* was not directly examined during the present investigation, its identity was verified by photographs received from the MNHN (and now publicly available at <https://science.mnhn.fr/institution/mnhn/collection/rs/>). Examination thereof, together with the limited data provided in the original description, leaves no doubt that *R. brejo* is conspecific with *T. lacrau*. *Rhopalurus brejo* shares with *T. lacrau* the presence of distinct pedipalp carinae and eight subrows of denticles in the median denticle row of the chela fixed finger. We therefore propose the following synonym: *Rhopalurus brejo* Lourenço, 2014 = *Troglophalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), syn. nov.

**MATERIAL EXAMINED:** **BRAZIL:** *Bahía:* Município Itaeté: trail connecting caves Lapa do Bode and Gruta 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 Cave, 24.i.2007, C.I. Mattoni, R. Pinto-da-Rocha and H. Yamaguti, 1 subad. ♀ (AMCC [LP 10211]).

*Troglophalurus translucidus*

Lourenço et al., 2004

Figures 1H, 2H, 9B, 15E, 19E, 21L, 22L, 61B, 62C, D, F, 63C, D

*Troglophalurus translucidus* Lourenço et al., 2004: 1153–1156, figs. 1–10; Prendini et al., 2009: 222; Brazil and Porto, 2010: 52, 58, 62, fig. 4F; Porto et al., 2010: 293, 294, 296, fig. 3H, table 1; Gallão and Bichuette, 2016: 3–10, figs. 1–26, tables 1, 2, appendix 1; Ubinski et al., 2016: 122.

**TYPE MATERIAL:** [Subad.] ♂ holotype (MNRJ 4786), **BRAZIL:** *Bahía:* Município Lençóis: Gruta do Lapão, 12.xi.2002, A.P.L. Giupponi and R.L.C. Baptista.

**DIAGNOSIS:** *Troglophalurus translucidus* differs from its sister species, *T. lacrau*, as follows. The soma and appendages are elongate and slender in *T. translucidus* compared with *T. lacrau*, in which the soma and appendages are shorter and broader: total body length is about 60 mm in *T. translucidus* and 40 mm in *T. lacrau*; the pedipalp is 6.5× longer than the carapace in *T. translucidus* but 4.5× longer in *T. lacrau*; the pedipalp chela manus is very slender, the manus almost half the length of the movable finger in *T. translucidus* but incrassate and slightly shorter than the chela movable finger in *T. lacrau*; the pedipalp patella is 6× longer than wide in *T. translucidus*, but 3.8× longer in *T. lacrau*; metasomal segment V is 4.5× longer than wide in *T. translucidus*, but 2.7× longer in *T. lacrau*. The retromedian and secondary acces-

sory carinae of the pedipalp chela manus are absent in *T. translucidus*, but present in *T. lacrau*. Nine subrows of denticles are present in the median denticle row of the chela fixed finger of *T. translucidus*, whereas eight subrows are present in *T. lacrau*. Macrosetae on the fixed and movable fingers of the pedipalp chela are longer than the chela width in *T. translucidus*, but shorter in *T. lacrau*. Macrosetae of the telson vesicle are shorter than the subaculear tubercle in *T. translucidus*, but longer in *T. lacrau*. The subaculear tubercle of the telson has a sharply pointed tip in *T. translucidus*, but is blunt in *T. lacrau*. The posterior third of the aculeus is straight in *T. translucidus*, but curved in *T. lacrau*.

**DISTRIBUTION:** *Troglophopalus translucidus* is endemic to the Brazilian state of Bahia, where it is known only from sandstone caves within the Chapada Diamantina National Park: the type locality, Lapão Cave, and a group of five caves ca. 30 km to the south, Esbirro de Quina Cave, Parede Vermelha Cave, Canal da Fumaça Cave, Lava Pé Cave, and Rio dos Pombos Cave (fig. 9B) (Gallão and Bichuette, 2016).

**ECOLOGY:** All specimens of *T. translucidus* thus far collected have been found within sandstone caves above 500 m (fig. 2H; Gallão and Bichuette, 2016). The habitat and habitus of this species are consistent with the troglobite ecomorphotype (Prendini, 2001b).

**REMARKS:** The pale brown (translucent) coloration of the carapace, tergites, and metasoma of the holotype of *T. translucidus*, indicative in part of reduced sclerotization of the tegument and once thought to be diagnostic for the species (Lourenço et al., 2004), reflect its immature habitus (Gallão and Bichuette, 2016: 9, figs. 20–25). The adults are dark brown, the tegument more sclerotized, as observed in the adults of *T. lacrau* (figs. 1H, 63C, D).

**MATERIAL EXAMINED:** **BRAZIL:** Bahia: Município Lençóis: Gruta do Lapão, Chapada Diamantina, 12°34'00"S 41°22'60"W, 20–29.i.2009, H.Y. Yamaguti et al., 1 subad. ♂ (MZSP/AMCC

[LP 9668]). Município Andaraí: Gruta Canal da Fumaça, 3.IV.2013, M.E. Bichuette, D.M. von Schimonsky, J.E. Gallão, 1 ♀ (LES-4786).

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## APPENDIX 1

### MORPHOLOGICAL CHARACTERS AND CHARACTER STATES USED IN PHYLOGENETIC ANALYSIS OF NEW WORLD BUTHID SUBFAMILY RHOPALURUSINAE BÜCHERL, 1971

Nomenclature follows Hjelle (1990) and Sissom (1990), except for carapace and metasomal carination (Vachon, 1952), tergite and pedipalp carination (Prendini, 2000), pedipalp trichobothria (Vachon, 1974), ovariuterine anatomy (Volschenk et al., 2008), and book lung anatomy (Kamenz and Prendini, 2008).

### Carapace

1. Lateral ocular carina: **0**, present; **1**, absent.
2. Centrolateral carina: **0**, present; **1**, absent.
3. Anterior central submedian carina: **0**, present; **1**, absent.
4. Posterior central submedian carina: **0**, present; **1**, absent.
5. Anterior and posterior centrosubmedian carinae, fusion: **0**, separate; **1**, fused.
6. Central lateral carina and posterior centrosubmedian carina, fusion: **0**, fused; **1**, separate.
7. Lateral ocular tubercle, macroocelli, count (Stockwell, 1989; Prendini, 2000; Soleglad and Fet, 2003): **0**, three; **1**, two.
8. Lateral ocular tubercles, posterior microocellus (Stockwell, 1989; Prendini, 2000; Soleglad and Fet, 2003): **0**, present; **1**, absent.

### Chelicerae

9. Fixed finger, dorsobasal setation: **0**, present; **1**, absent.
10. Base, dorsal tubercles, position: **0**, medially distributed and forming transverse row; **1**, spread.

### Pedipalps

11. Patella internodorsal and proventral carinae: **0**, converging, pinched together; **1**, separate, clearly defined.
12. Chela manus dorsal accessory carina: **0**, granular; **1**, smooth.
13. Chela manus median carina: **0**, present; **1**, absent or obsolete.
14. Chela ventral accessory carina: **0**, present; **1**, absent or obsolete.
15. Chela proventral carina: **0**, present; **1**, absent.
16. Chela promedian carina: **0**, present; **1**, absent.
17. Chela dorsointernal carina: **0**, present; **1**, absent.
18. Femur retrolateral accessory carina: **0**, absent; **1**, present.
19. Chela fixed finger, median denticle row, **0**, primary subrows: 8; **1**, 9; **2**, 13 or more.

20. Chela fixed finger, median denticle row, pro-lateral accessory (supernumerary) granules (Soleglad and Fet, 2003): **0**, absent; **1**, present, large granules; **2**, present, small and widely spaced granules.
21. Chela movable finger, median denticle row, primary subrows (Soleglad and Fet, 2003; Prendini, 2004): **0**, 8; **1**, 9; **2**, 11; **3**, 13 or more.
22. Chela shape (male) (Prendini, 2001c, 2004): **0**, incrassate; **1**, slender.
23. Chela shape (female) (Prendini, 2001c): **0**, incrassate; **1**, slender.
24. Chela fixed finger, shape (male) (Prendini, 2001c, 2004): **0**, straight, proximal dentate margin linear when fingers closed; **1**, slightly curved dorsally; **2**, strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers closed.
25. Chela movable finger, shape (male) (Prendini, 2001c, 2004): **0**, straight, proximal dentate margin linear when fingers closed; **1**, slightly curved ventrally; **2**, strongly curved ventrally, proximal dentate margin distinctly emarginate when fingers closed.
26. Chela movable finger, proximal lobe (male) (Prendini, 2001c): **0**, absent; **1**, present.
27. Chela movable finger, median lobe (male) (Prendini, 2004): **0**, absent; **1**, present.
28. Chela fixed finger, proximal lobe (male) (Prendini, 2001c): **0**, absent; **1**, present.
29. Chela fixed finger, median lobe (male) (Prendini, 2004): **0**, absent; **1**, present.
30. Femur dorsal surface, trichobothrium  $d_2$  (Soleglad and Fet, 2001, 2003): absent (four  $d$  trichobothria); **1**, present (five  $d$  trichobothria).
31. Chela fixed finger, trichobothrium  $db$  position: **0**, situated distal to trichobothrium  $et$ ; **1**, approximately aligned with  $et$ ; **2**, situated between trichobothria  $est$  and  $et$ ; **3**, approximately aligned with  $est$ .
32. Chela fixed finger, trichobothrium  $est$  position: **0**, approximately aligned with trichobothrium  $db$ ; **1**, situated between trichobothria  $db$  and  $et$ ; **2**, situated proximal to  $et$ .
33. Chela fixed finger, trichobothrium  $et$  position: **0**, situated between trichobothria  $dt$  and  $db$ ; **1**, aligned with  $db$ ; **2**, situated between  $db$  and  $est$ .

### Legs

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

### Pectines

39. Pectinal teeth, shape: **0**, straight, sides almost parallel; **1**, rounded; **2**, dorsal surface sinuate.
40. Proximal pectinal teeth, dorsal surface: **0**, smooth or slightly granular; **1**, with irregular striations; **2**, large and regular striations.
41. Proximal pectinal teeth, dorsal surface, nodules: **0**, single; **1**, multiple; **2**, absent.
42. Pectinal teeth, dorsobasal surface, macrosetae: **0**, present; **1**, absent.
43. Pectinal teeth, peg sensillae, shape: **0**, short and blunt; **1**, elongate and blunt; **2**, elongate and acuminate.
44. Proximal dorsal fulcra, setae: **0**, one; **1**, two; **2**, three; **3**, four; **4**, six or more; **5**, absent.
45. Proximal median lamellae (female) (Prendini, 2001c, 2004): **0**, not dilated; **1**, dilated.
46. Pectinal plate, anterior margin, sulcus: **0**, present; **1**, absent.

47. Pectinal plate, posterior margin (male): **0**, curved; **1**, straight.  
 48. Pectinal plate depressions (male): **0**, single median; **1**, two lateral; **2**, absent.

#### Sternites

49. Sternite III, ventral median carinae: **0**, broad anterior raised region; **1**, narrow, elevated anterior carina; **2**, no elevation anteriorly.  
 50. Sternite III, lateral margins: **0**, not raised or granular; **1**, granular carina; **2**, smooth carina.  
 51. Sternite III, ventrosubmedian surface: **0**, smooth or slightly granular; **1**, large, regularly spaced granules (stridulatory); **2**, small, irregular granules.  
 52. Sternite V, posteromedian surface (male) (Prendini, 2004): **0**, with raised, smooth area; **1**, unmodified.  
 53. Sternite VI, ventrosubmedian carinae: **0**, present; **1**, absent.  
 54. Sternite VI, ventrolateral carinae: **0**, present; **1**, absent.  
 55. Sternites III–VI, spiracle shape (Kamenz and Prendini, 2008): **0**, wide, width  $>5\times$  length; **1**, compact, width  $<3\times$  length.

#### Tergites

56. Tergite I, dorsolateral carinae: **0**, reduced; **1**, absent.  
 57. Tergite I, dorsosubmedian carinae: **0**, present; **1**, absent.  
 58. Tergite II, dorsolateral carinae: **0**, reduced; **1**, absent.  
 59. Tergite II, dorsomedian carina: **0**, present; **1**, absent.  
 60. Tergites III–VI, dorsolateral carinae: **0**, present; **1**, absent.  
 61. Tergites III–VI, dorsosubmedian carinae (Prendini, 2004): **0**, absent; **1**, present.  
 62. Tergite VII, dorsomedian carina: **0**, narrow, granular carina; **1**, granular mound, no carina; **2**, smooth mound, no carina.  
 63. Tergite VII, coloration relative to preceding tergites: **0**, paler than; **1**, similar to.

#### Metasoma

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

78. Segments I–V, coloration, dark ventromedian stripe: **0**, absent; **1**, present.

#### Telson

79. Vesicle shape: **0**, spherical, length similar to width; **1**, slightly ovate, length ca. 1.5× width; **2**, ovate, length more than 2× width.

80. Vesicle width relative to width of metasomal segment V (Prendini, 2001c, 2003): **0**, approximately equal; **1**, somewhat narrower; **2**, considerably narrower, less than half.

81. Vesicle ventromedian carina: **0**, present; **1**, absent.

82. Vesicle lateral surface, granulation: **0**, granular; **1**, smooth.

83. Vesicle subaculear tubercle (Lamoral, 1980; Stockwell, 1989; Prendini, 2000, 2004; Soleglad and Fet, 2003): **0**, pronounced, pointed tooth; **1**, nublike eminence; **2**, absent.

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

#### Size

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

#### Ovariuterus

86. Ovariuterine network, number of loops (Volschenk et al., 2008): **0**, 8; **1**, 9; **2**, 2.

87. Ovariuterus type (Volschenk et al., 2008): **0**, simple; **1**, complex bridged.

#### Book lungs

88. Lamellar surface (Kamenz and Prendini, 2008): **0**, slender venation; **1**, ribbed venation.

89. Lamellar edge (Kamenz and Prendini, 2008): **0**, thorns; **1**, smooth or slightly wrinkled.

90. Posterior spiracle edge (Kamenz and Prendini, 2008): **0**, hillocks; **1**, subconical.



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