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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ABSTRACT


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; Pendini 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 Rhopalura Buchlerl, 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 Centruroides 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-stermire 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 ovarioterine 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 epigean 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 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. A troglobile 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 pintoi 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 rhopalurusan 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 Rhopalurusanae 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 Rhopalurusanae 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 Rhopalurusanae by Ubinski et al. (2016), reproduced in table 2.
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 Sistematica della Università, Torino (MIZT), Italy; Museum National d’Histoire Naturelle (MNHN), Paris; Museo Nacional de Rio de Janeiro (MNRJ), Universidade Federal de Rio de Janeiro; Museu de Zoologia da Universidade São Paulo (MZSP), Brazil; Museo Zoologico “La Specola” dell’Università di Firenze (MZUF), Florence, Italy; Nataal 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 1

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Country</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Heteroctenus abudi</em> (Armas and Marcano Fonseur, 1987), comb. nov.</td>
<td>Dominican Republic, Puerto Rico (Mona Is.)</td>
</tr>
<tr>
<td><em>Heteroctenus bonettii</em> (Armas, 1999), comb. nov.</td>
<td>Dominican Republic</td>
</tr>
<tr>
<td><em>Heteroctenus garridoi</em> (Armas, 1974), comb. nov.</td>
<td>Cuba</td>
</tr>
<tr>
<td><em>Heteroctenus gibarae</em> (Teruel, 2006), comb. nov.</td>
<td>Cuba</td>
</tr>
<tr>
<td><em>Heteroctenus junceus</em> (Herbst, 1800)</td>
<td>Cuba</td>
</tr>
<tr>
<td><em>Heteroctenus princeps</em> (Karsch, 1879), comb. nov.</td>
<td>Dominican Republic, Haiti</td>
</tr>
<tr>
<td><em>Ischnotelson guanambiensis</em> (Lenarducci et al., 2005), comb. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Ischnotelson peruassu</em>, sp. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Jaguaír agamemnon</em> (C.L. Koch, 1839), comb. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Jaguaír pintoi</em> (Mello-Leitão, 1932), comb. nov.</td>
<td>Brazil, ?French Guiana, Guyana</td>
</tr>
<tr>
<td><em>Jaguaír rochae</em> (Borelli, 1910), comb. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Physoctonus debilis</em> (C.L. Koch, 1840)</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Physoctonus striatus</em>, sp. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Rhopalurus caribensis</em> Teruel and Roncallo, 2008</td>
<td>Colombia</td>
</tr>
<tr>
<td><em>Rhopalurus laticauda</em> Thorell, 1876</td>
<td>Brazil, Colombia, Guyana, Venezuela</td>
</tr>
<tr>
<td><em>Rhopalurus ochoai</em>, sp. nov.</td>
<td>Venezuela</td>
</tr>
<tr>
<td><em>Troglorhopalurus lacrau</em> (Lourenço and Pinto-da-Rocha 1997), comb. nov.</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>Troglorhopalurus translucidus</em> Lourenço et al., 2004</td>
<td>Brazil</td>
</tr>
</tbody>
</table>
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°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° 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 data-set 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) and the Fuzzy Gazetteer (http://dma.jrc.it/new_site/default.asp).

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

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

<table>
<thead>
<tr>
<th>Species (this study)</th>
<th>Species (Ubinski et al., 2016)</th>
<th>2n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ischnotelson guanambiensis</td>
<td>Rhopalurus guanambiensis</td>
<td>25</td>
</tr>
<tr>
<td>Ischnotelson peruassu</td>
<td>Rhopalurus sp. n. 1</td>
<td>26</td>
</tr>
<tr>
<td>Ischnotelson sp. nov.</td>
<td>Rhopalurus sp. n. 2</td>
<td>26</td>
</tr>
<tr>
<td>Jaguajir agamemnon</td>
<td>Rhopalurus agamemnon</td>
<td>28</td>
</tr>
<tr>
<td>Jaguajir pintoi</td>
<td>Rhopalurus pintoi</td>
<td>28</td>
</tr>
<tr>
<td>Jaguajir rochae</td>
<td>Rhopalurus rochae</td>
<td>28</td>
</tr>
<tr>
<td>Physoctonus debilis</td>
<td>Rhopalurus debilis</td>
<td>26</td>
</tr>
<tr>
<td>Rhopalurus laticauda</td>
<td>Rhopalurus crassicauda</td>
<td>22</td>
</tr>
<tr>
<td>Troglorhopalurus lacrau</td>
<td>Rhopalurus lacrau</td>
<td>20</td>
</tr>
<tr>
<td>Troglorhopalurus translucidus</td>
<td>Troglorhopalurus translucidus</td>
<td>20–22</td>
</tr>
</tbody>
</table>
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 GTOP03 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 Rhopalurinae Bücherl, 1971


Diagnosis: The following combination of characters distinguishes the species of subfamily Rhopalurinae, 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 α-configuration, trichobothrium d2 situated on prolateral surface; pedipalp patella trichobothrium d3 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 Troglorhopalus), 108 described species, and three subspecies.

Distribution: Subfamily Rhopalurinae 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.


KEY TO GENERA AND SPECIES (EXCLUDING CENTRUROIDES) OF NEW WORLD BUTHID SUBFAMILY RHOPALURINAE

1. Leg I, prolateral pedal spur simple; sternite V, surface without smooth, raised area postero-medially in male.2 (Physoctonus) – Leg I, prolateral pedal spur bifurcate; sternite V, surface with smooth, raised area posteromedially in male (fig. 10D).…..............................Phsyoctonus debilis

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 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. Scorpions cavernicolous and troglomorphic (fig. 1G, H); pectinal peg sensilla elongate and acuminate.  
5. 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).  
6. 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.  
7. Total body length, 35–45 mm; pedipalp chela fingers noticeably darker than chela manus; sternite III elevated anteriorly.  
8. Sternite III, surface with large, acuminate and evenly distributed granules (fig. 19C, D, F); pedipalp chela manus, proventral carinae fused (fig. 16C–F); pectinal plate, anterior margin without furrow.  
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.  
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.  
11. Telson vesicle, subaculear tubercle present (fig. 21H–J); carapace, central lateral and posteroventral 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); pectoral plate with single median depression; occurs in the Greater Antilles.............

12. Metasoma ventromedial surface with single, broad band of pigmentation; carapace, tergites, metasoma V, and telson often markedly infuscate, 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 infuscate, metasoma V, and telson slightly darker than preceding segments..................13

13. Metasoma ventromedial surface with three distinct, narrow stripes of pigmentation (a ventromedian 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..........................Heteroctenus abudi, comb. nov.

16. Color predominantly dark; carapace, tergites, metasomal segments I–III, and legs infuscate; metasomal segments long and narrow (2× longer than wide) ..............

17. Total body length, 64–110 mm; base color light brown to dark reddish brown; entire carapace or only interocular surface infuscate; carapace, mesosoma, and metasoma (especially, segments IV and V) noticeably darker than pedipalps and legs..............Heteroctenus princeps, 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 garridoi, comb. nov.

Centruroides Marx, 1890

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

Centrurus (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,


Diagnosis: Centruroides differs from Heteroctenus, Ischnotelson gen. nov., Jaguaquir, gen. nov., and Rhopalurus by the linear, parallel-sided metasoma that does not increase markedly in width posteriorly; from Heteroctenus, Jaguaquir, gen. nov., and Rhopalurus by the absence of a pecten-stermite 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 Heteroctenus 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 Jaguaquir 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 Troglorhopalurus 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 macroocelli; one pair of lateral microocelli. 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, α 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 fulcrum 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 pentacarinate, 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× 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 costategranular 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 inframedian 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; subacicular tubercle usually present.

**Hemispermatophore:** 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, Durango, 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, 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 altagraciae* Teruel, Armas and Kovařík, 2015; *Centruroides anchorellus* Armas, 1976; *Centruroides arctimanus* Armas, 1976; *Centruroides baergi* Hoffmann, 1932; *Centruroides bonalearis* Ponce-Saavedra and Francke, 2004; *Centruroides bani* Armas and Marcano Fondec, 1987; *Centruroides baracae* Armas, 1976; *Centruroides barbodensis* Pocock, 1898; *Centruroides bertholdii* (Thorell, 1876); *Centruroides bicolor* (Pocock, 1898); *Centruroides 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 fallassiim Armas and Trujillo, 2010; *Centruroides farr* Armas, 1976; *Centruroides flavopictus* (Pocock, 1898); *Centruroides flavopictus meridionalis* Hoffmann, 1932; *Centruroides francesi* 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 jaragua* Armas, 1999; *Centruroides Jorgeorum* Santiago-Blay, 2009; *Centruroides koesteri* Kraepelin, 1912; *Centruroides limbatis* (Pocock, 1898); *Centruroides limpidus* (Karsch, 1879); *Centruroides luceorum* Armas, 1999; *Centruroides lucidus* Teruel, Armas and Kovařík, 2015; *Centruroides marcano Armas, 1981; *Centruroides margaritatus* (Gervais, 1841); *Centruroides mariaorum* Santiago-Blay, 2009; *Centruroides mascota* Ponce-Saavedra and Francke, 2011; *Centruroides meesi* Hoffmann, 1938; *Centruroides nigrimanus* (Pocock, 1898); *Centruroides nigropunctatus* Teruel, 2006; *Centruroides nigrovariatus
(Pocock, 1898); *Centruroides nitidus* (Thorell, 1876); *Centruroides nitidus taino* Armas and Marciano Fonseca, 1987; *Centruroides noxius* Pocock, 1902; *Centruroides palliceps* Pocock, 1902; *Centruroides panamensis* Quintero and Esposito, 2014; *Centruroides platnicki* Armas, 1981; *Centruroides polito* Teruel, 2007; *Centruroides poncei* Teruel et al., 2015; *Centruroides rileyi* Sissom, 1995; *Centruroides robertoi* Armas, 1976; *Centruroides racineus* 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 Contreras-Félix, 2013; *Centruroides ruana* Quijano-Ravell and Ponce-Saavedra, 2016; *Centruroides sanandres* Armas, Sarmiento and Flórez, 2012; *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 thorelli* (Kraepelin, 1891); *Centruroides tuxtla* Armas, 1999; *Centruroides underwoodi* Armas, 1976; *Centruroides villegasi* Baldazo-Monsivais, 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 *C. 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).
Diagnosis: *Heteroctonus* differs all from other rhopalurine genera by the presence of a single, deep, median depression in the male pectinal plate. It differs further from *Ischnotelson*, *Jaguajir*, *Physoctonus*, *Rhopalurus*, *Troglorhopalurus*, and many species of *Centruroides* by the absence of a subaculear tubercle on the telson; from *Centruroides*, *Ischnotelson*, *Physoctonus*, and *Troglorhopalurus* 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 pectines; 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, and from *Centruroides* 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 *Troglorhopalurus* by the proximal dentate margin of the chela fixed and movable fingers of the adult male
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 juncus* (Herbst, 1800), comb. nov. C. Guanambi, Bahía, Brazil, habitat of *Ischnotelson guanambiensis* (Lenarducci et al., 2005), comb. nov., and *Jaguarjir rochae* (Borelli, 1910), comb. nov. D. Exu, Pernambuco, Brazil, habitat of *J. rochae* and *Physcoionus debilis* (C.L. Koch, 1840). E. Santarém, Pará, Brazil, habitat of *Rhopalurus laticauda* Thorell, 1876. F. Norman-dia, Roraima, Brazil, habitat of *R. laticauda*. G. Lapa do Bode, Itaeté, Bahía, Brazil, habitat of *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997), comb. nov. H. Gruta do Lapão, Lençóis, Bahía, Brazil, habitat of *Troglorhopalurus translucidus* Lourenço et al., 2004.
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 hemispermatophores 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; segments 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 ocelloi; three pairs of lateral macroocelli; one or two pairs of lateral microocelli. 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, 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 orthothriotaxic Type A, α 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,
at least 1.5× 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. Stermites 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, finely and irregularly granular; respiratory spiracles (stigmata) width more than 5× 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 suprame-
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 Rhopalurinae 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.

**Hemispermatophore:** 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. 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.


**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 (Rodriguez-Cabrera and Teruel, 2014).

**Ecology:** Whereas *Heteroctenus* primarily inhabit open vegetation formations (fig. 2A, B), in common with *Rhopalus* 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 *Rhopalus* 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. *Rhopalus 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.


**Type Material:** *Rhopalus abudi*: Holotype ♀ (IES 3.2912), DOMINICAN REPUBLIC: La Altagracia Prov.: Catano, Isla Saona, 27.i.1980, E. de J. Marcano Fondeur. *Rhopalus virkkii*: Holotype ♂ (ZMUPR-RP), PUERTO RICO: Isla Mona, Camino del Diablo, approximately 2 km
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 Uvero, 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 in *H. princeps* but more so than in *H. bonettii*. The submedian sulci of sternite III are convergent in *H. abudi* but sub-parallel in *H. bonettii* (fig. 18A, B). The pale, raised postero medial 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

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.


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-Gelbert, 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-Gelbert, 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.


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 fingers 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.
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 Fondeur, 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.


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


**Type Material:** *Rhopalurus garridoi*: Holotype ♀ (IES, IZACC-3.616), 1 ♂, 1 ♀, 5 subad. paratypes (IES), CUBA: Guantánamo Prov.: Baitiquirí, 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 infuscate, 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*, 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*. 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.
**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 sympathy 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 ♀ (AMNH). 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. Droge 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,


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 infuscate, 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 ventrosubmedian carinae of the metasoma are immaculate in H. gibarae but infuscate 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 sympathy with the buthids Alayotityus spp., Centruroides arctimanus, C. baracoae, H. junceus, and Microti-tyus 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.
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 \(R.\ granulinanus\) (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; \(R.\ granulinanus\), 4.96; \(H.\ junceus\), 3.5–4.7); and the male pectinal tooth count (\(H.\ gibarae\), 20–21; \(R.\ granulinanus\), 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 \(R.\ granulinanus\) conspecific with \(H.\ gibarae\) and synonymize it accordingly: \(Rhopalus\) \(granulinanus\) 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)


**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. 1, fig. 2, 2a–b.

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

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


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


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

**Rhopalus 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.;


**Diagnosis:** *Heteroctenus junceus* differs from the other two species of *Heteroctenus* occurring on Cuba, *H. Garridoi* and *H. gibrarae*, primarily in its larger size and typically darker coloration. *Heteroctenus junceus* varies from 54–107 mm in total length, whereas *H. Garridoi* and *H. gibrarae* 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. gibrarae* 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. gibrarae*. 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. gibrarae*, 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. gibrarae*. The basal expan-
sion of the pectines is also more pronounced in *H. junceus* than in *H. garri-doi* and *H. gibarae*. Finally, *H. junceus* differs from *H. garri-doi* 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, Cien-fuegos, Ciego de Ávila, Granma, Guantánamo, Havana, Holguín, Isla de la Juventud, Las Tunas, Matanzas, Pinar del Río, Santiago de Cuba, Sancti Spiritus, 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 lapidico-lous 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. aridi-cola* and *R. melloleitaoi*, as distinct from *H. junceus*, is underwhelming. *Rhopalus 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 toptypes of *R. aridicola* and other samples conspecifc with *H. junceus* (Esposito et al., in review). *Rhopalus 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 habi-tat in which it was collected has a dark, red sub-strate (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 toptypes thereof and other samples conspecific with *H. junceus* (see Esposito et al., in review), we propose the following synonyms: *Rhopalus melloleitaoi* Teruel and Armas, 2006 = *Heterocte-nus junceus* (Herbst, 1800), syn. nov.; *Rhopalus aridicola* Teruel and Armas, 2012 = *Heteroctenus junceus* (Herbst, 1800), syn. nov.

FIG. 22. Rhopalurusinae Bücherl, 1971, telson, ventral aspect. 

B. Heteroctenus junceus (Herbst, 1800), ♂ (AMNH).
C. Ischnotelson guanambiensis (Lenarducci et al., 2005), comb. nov., ♂ (MZSP).
D. Jaguajir agamenon (C.L. Koch, 1839), comb. nov., ♀ (AMNH).
E. Jaguajir pintoi (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. Troglorhopalurus lacrau (Lourenço and Pinto-da-Rocha, 1997), comb. nov., ♀ (AMNH).
L. Troglorhopalurus translucidus Lourenço et al., 2004, ♀ (MZSP). Scale bars = 2 mm.
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.


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
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 pectines 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 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 infuscate. 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, Independence, 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 habits are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). The buthid, *C. bani*, has been collected in sympathy.

**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 4740]), 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, 35ºC, 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.i.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.v.2004, E.S. Volschenk and J. Huff, arid thorny scrub, hand collected from under stones and in dead and dry agaves, 3 ♀, 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, 7.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. 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.


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


**Diagnosis:** *Ischnotelson*, gen. nov., differs from all other rhopalurusine genera by the fused lateral ocular, central lateral and posterior central submedian carinæ 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 carinæ of the carapace; from *Physoctonus* by the larger size (30–70 mm), the more distinct carapacial carinæ, 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 macroocelli; one pair of lateral microocelli. Anteromedian, median ocular, and posteromedian sulci well developed, forming single, almost continuous, longitudinal sulcus. Lateral ocular, central lateral and posterior central submedian carinæ 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 carinæ distinct, finely granular and separate.
**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, α 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 retroversal 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× 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 pentacarinate, dorsomedian 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× 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 supramedian 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; subacicular tubercle pronounced and spinoid.

**Hemispermatophore:** 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
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).
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.


*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. 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.](image-url)
(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 incassate, 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′00″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]), 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.


**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. Stermites 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).

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<td>3.8</td>
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<td>2.2</td>
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<tr>
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<td>height</td>
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<td>6.8</td>
<td>5.7</td>
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<td>2.1</td>
<td>1.4</td>
<td>1.5</td>
<td>1.3</td>
<td>1.4</td>
<td></td>
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<tr>
<td></td>
<td>height</td>
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<td>2.2</td>
<td>1.3</td>
<td>1.2</td>
<td>1.1</td>
<td>1.2</td>
<td></td>
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<td>length</td>
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<td>7.3</td>
<td>4.3</td>
<td>4.8</td>
<td>4.0</td>
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<td></td>
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<tr>
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<td>total length</td>
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<td>4.9</td>
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<td>2.5</td>
<td>2.5</td>
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<td>1.4</td>
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<td>0.9</td>
<td>0.9</td>
<td></td>
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<td>tooth count</td>
<td>26/26</td>
<td>27/27</td>
<td>14/13</td>
<td>14/15</td>
<td>15/15</td>
<td>17/17</td>
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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; dorsal-submedian carinae absent on segments I and II, restricted to posterior quarter on III–VI. Tergite VII pentacarinate, 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.

**Hemispermatophore:** 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 ecotope 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).

**Jagua spiralis gen. nov.**


**Androctonus agamemnon** C.L. Koch, 1839 (= *Jagua spiralis 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.

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; Mello-Campos, 1924b: 25; 1924c: 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: 25–36, fig.; Roewer, 1943: 219; Mello-Leitão, 1945: 341, 342–349, 351, 352, pl. 5, fig. 37–39; Werner, 1927: 357; 1934: 274, fig. 33a.

Diagnosis: Jaguajír, gen. nov., differs from all other rhopalurine 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 subaculbar 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...
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 *Jagujir*, 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. pintoi* 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.

**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. pintoi), flanked closely by

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pro- and retrolateral accessory (supernumerary) denticles; movable finger with or without proximal lobe (fig. 17C). Pedipalps orthobothriotaxic Type A, α configuration; femur with five dorsal trichobothria, trichobothrium \( d_2 \) situated on prolateral surface; patella trichobothrium \( d_1 \) 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× 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 pentacarinate, 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× 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 supramedian 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 (\( J. pintoi \)) or reduced (\( J. agamemnon \) and \( J. rochae \)); lateral and ventral surfaces granular or smooth, with shallow ventromedian carina; subacicular tubercle present, prominent and spinoid (\( J. agamemnon \)) or vestigial (\( J. pintoi \) and \( J. rochae \)).

**Hemispermatophore:** 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 (\( J. pintoi \) and \( J. rochae \)) to one third (\( J. agamemnon \)) maximum width of trunk; LE length ca. half (\( J. pintoi \)) 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 (\( J. pintoi \)), angle between LB and LE 45° (\( J. agamemnon \) and \( J. rochae \)) to 80° (\( J. pintoi \)).

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

**Included Species:** \( Jaguajir agamemnon \) (C.L. Koch, 1839), comb. nov.; \( Jaguajir pintoi \) (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-
ezuela (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. pintoi, 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. pintoi, 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.


Heteroctenus agamemnon: Pocock, 1893: 393.

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


Rhopalurus melleipalpus Lutz and Mello, 1922b: 25 (previously synonymized with R. acromelas by Lourenço, 1982a: 129); Mello-Campos, 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 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.


Heteroctenus borellii: Meise, 1934: 42.

Centruroides (Rhopalurus) borellii: Werner, 1934: 274, fig. 33, 33a.


Rhopalurus goiasensis Prado, 1940: 26, 31, 32, fig. (previously synonymized with R. acromelas by Lourenço, 1982a: 133); syn. nov.


Rhopalurus stenocephurus melleipalpus: Mello-Leitão, 1945: 267, 292, 293.


Rhopalurus agammnon: Porto et al., 2010: 294, fig. 2A.
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. agamenmon* 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. agamenmon*, whereas the carinae comprise blunt spiniform granules, increasing in size posteriorly, especially prominent on segments III and IV, in *J. pintoi*.

**Distribution:** *Jaguair agamenmon* 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) demonstrate that *R. acrome-las* is conspecific with *J. agamenmon*, justifying its synonymy, and that of its former synonyms, with the latter, resulting in *J. agamenmon*.


Jaguajir pintoi (Mello-Leitão, 1932), comb. nov.

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

Rhopalurus pintoi 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); Kovafík, 1998: 118; Fet and Lowe, 2000: 221; Teruel, 2006: 51, 52; Teruel and Tietz, 2008: 2, 3, 5–9, tables 1, 2; Lourenço, 2008: 4, 7, figs. 2–4; Prendini et al., 2009: 222, 223; Ubiniski et al., 2016: 122.


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


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

Type Material: BRAZIL: Roraima: Rhopalurus pintoi: Holotype ♂ (IOC) [lost], Río Tacutú.


Diagnosis: Jaguajir pintoi 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. pintoi, 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. pintoi, 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. pintoi, as in J. rochae, whereas it is well developed and spinoid in J. agamemnon.

Jaguajir pintoi can be further differentiated from J. agamemnon as follows. Jaguajir pintoi 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. pintoi 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. pintoi, whereas the carinae comprise small, acuminate granules in J. agamennon.

**Distribution:** Jaguajir pintoi 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. pintoi* 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. pintoi*. Kovářík (1998) listed *R. pintoi* 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. pintoi* and removed *R. crassicauda* from synonymy. Teruel (2006) suggested *R. pintoi* might be a senior synonym of *R. piceus*. Teruel and Tietz (2008) formally synonymized *R. pintoi*, erroneously declaring *R. pintoi* 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 paruensis*, along with a new subspecies of *R. pintoi*. Prendini et al. (2009), however, agreed with the synonymy of *R. piceus* with *R. pintoi* 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. pintoi* as distinct from *R. laticauda*, upheld the synonymy of *R. piceus* therewith, and justified the synonymy: *Rhopalurus pintoi kouroensis* Lourenço, 2008 = *Jaguajir pintoi* (Mello-Leitão, 1932), syn. nov. *Rhopalurus crassicauda*, on the other hand, was determined to be conspecific with *R. laticauda* and synonymized accordingly, below.


**Jaguajir rochae** (Borelli, 1910), comb. nov.


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 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.


Diagnosis: Jaguajir rochae can be differentiated from J. agamemnon and J. pintoi 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. pintoi. 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. pintoi. Furthermore, the subaculear tubercle of the telson is much reduced, forming a small protuberance in J. rochae, as in J. pintoi, but well developed and spinoid in J. agamemnon.

Distribution: Jaguajir rochae is endemic to northeastern Brazil and recorded from the states of Bahía, Ceará, Paraíba, Pernambuco, Piauí, Río 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 rochaē (ICZN, 1999: Art. 31.1.1. Examples), which may be what Borelli (1910) intended.

Physoctonus Mello-Leitão, 1934


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.


Diagnosis: Physoctonus differs from other rhopalurine 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 Troglo rhopalurus 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 subacicular 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 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 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
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 prolateral accessory (supernumerary) denticles and sparse retrolateral accessory denticles; movable finger without proximal lobe (fig. 17D). Pedipalps orthobothriotaxic Type A, α 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 $d_b$ 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: Pecetal 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 pentacarinate, dorsomedian carina complete (fig. 51). Stermites smooth, cariniae 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× 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 complete 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, pentacarinate with distinct ventromedian carina; subcircular tubercle vestigial.

Hemispermatophore: 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 Bahía, Ceará, Paraíba, Pernambuco, and Piauí (fig. 9).

Ecology: The two species of Physoctonus inhabit the semi-arid 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. ♂ (MZSP). B, E. ♀ (AMNH). Scale bars = 2.5 mm.
FIG. 50. *Physoctonus debilis* (C.L. Koch, 1840), metasoma and telson, lateral aspect. **A, C.** ♂ (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.

Vaejovis debilis C.L. Koch, 1840: 21, 22, pl. CCLIX, fig. 605; 1850: 89; Kraepelin, 1899: 96.

Waejovis debilis: Gervais, 1844b: 458.


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.


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 infuscate 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.

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).


**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 infuscate 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 infuscate, forming dark triangle, almost reaching anterior margin, and thin, dark line of infuscation around margins. Tergites each with infuscate 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 infuscate, forming a longitudinal stripe; V completely infuscate. Telson vesicle similar to metasomal segment V dorsal surface, aculeus almost black. Chelicerae, pedipalps, and legs brown, entirely infuscate.

**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* in *P. striatus*. 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 single prosternal lateral 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 uniarinate, dorsosubmedian
carinae absent, dorsomedian carina reduced to posterior half on I–VI. Tergite VII pentacarinate, 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× 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 pentacarinate; subacicular tubercle vestigial.

Hemispermatophore: As for genus.

Sexual dimorphism: Females are unknown.

Distribution: This species is known only from the type locality in the Brazilian state of Bahía (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


Rhapalurus laticauda Thorell, 1876, type species by original designation.

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


**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., Physoctonus and Troglorhopalurus 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 Troglorhopalurus 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 subacicular 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 (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 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 tegrites I–VI dark brown, tegrite 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 sublinear, 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, α 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× 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 pentacarinate, 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× length.

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 (figs. 54–56). Segments I–III each with 10 distinct, costate-granulate carinae, IV with eight distinct, costate-granulate carinae, V with seven distinct, costate-granulate 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 supramedian 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.

Hemispermatophore: 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; Angoletta and Isla Conejo, Archipélago 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


*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.


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 subsinoid 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. 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 Bondia, 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); 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


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


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


**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 ventromedian 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; Angloleta 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.


**Rhopalurus ochoaui**, 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).


**Diagnosis:** *Rhopalurus ochoaui*, 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-
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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*. 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 ventro-submedian 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 macroocelli, one pair of lateral microocelli, situated between the second and third macroocelli. Antero-median, 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 distinctive, 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 pentacarinate. 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).
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 posterior 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).
Troglorhopalurus Lourenço, Baptista and Giupponi, 2004


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

Troglorhopalurus 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.


Diagnosis: Troglorhopalurus 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-stermite 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 subacicular 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 Troglorhopalurus.

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 macroocelli; one pair of lateral microocelli. 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).
**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).

**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, dorsosubmedian carinae finely granular, vestigial, restricted to posterior margins of segments I–V, complete on VI (fig. 63). Tergite VII pentacarinate, dorsosubmedian 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× 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 supramedian 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.

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

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

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

**Remarks:** *Troglorhopalurus* was originally monotypic, created to accommodate *T. translucidus*. In comparing *Troglorhopalurus* 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.


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


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 Bahia 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 Bahía. 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 troglobile 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 = Troglorhopalurus lacrau (Lourenço and Pinto-da-Rocha, 1997), syn. nov.


Troglorhopalurus translucidus
Lourenço et al., 2004

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

Troglorhopalurus 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.


Diagnosis: Troglorhopalurus 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 longer than the subaculear tubercle in *T. translucidus*, but shorter 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:** *Troglorhopalurus translucidus* is endemic to the Brazilian state of Bahía, 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:** Bahía: 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 manus median 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, present; 1, absent.
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 (supernumery) 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.


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 $d$: (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 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× length; 1, compact, width <3× 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× width; 1, elongated, length 2.5–3× width; 2, pronounced elongation, length more than 3× 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×); 1, much greater (≥1.5×).
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.