

## A New Troglomorphic, Leaf-litter Scorpion from Ecuador (Troglotayosicidae: *Troglotayosicus*)

RICARDO BOTERO-TRUJILLO,<sup>1, 2</sup> JOSÉ A. OCHOA,<sup>3</sup> AND LORENZO PRENDINI<sup>1</sup>

### ABSTRACT

For several decades, *Troglotayosicus* Lourenço, 1981, remained an enigmatic, monotypic scorpion genus believed to be troglobitic. The discovery and description in recent years of several endogean species of the genus, inhabiting the leaf litter of tropical rainforests in Colombia and Ecuador, advanced knowledge about these scorpions. The known distribution of *Troglotayosicus* was considerably expanded along the Andes, and it was demonstrated that, despite the absence of median ocelli, the genus is composed primarily of species that inhabit leaf litter. In the present study, *Troglotayosicus ballvei*, sp. nov., is described from Sacha Huagra Lodge, adjacent to Archidona Municipality, in Napo Province, Ecuador, raising the number of *Troglotayosicus* species to six, three each in Colombia and Ecuador. An updated map of the known distribution of the genus is presented.

### INTRODUCTION

Collecting scorpions in the field is seldom a difficult task. In the countries of northwestern South America, such as Colombia and Ecuador, fieldwork normally results in the collection of at least one scorpion species, typically belonging to the diverse and widespread family Buthidae C.L. Koch, 1837, and frequently additional species belonging to the same or other families.

<sup>1</sup> Scorpion Systematics Research Group, Division of Invertebrate Zoology, American Museum of Natural History.

<sup>2</sup> División Aracnología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires.

<sup>3</sup> Facultad de Ciencias, Universidad Nacional de San Antonio Abad del Cusco; Sección Aracnología, Museo de Biodiversidad del Perú, Cusco.

Species of other families, such as Chactidae Pocock, 1893, are often collected, especially if several collection methods are applied to all habitats occurring in the study area. One family is rarely collected, however, no matter how thoroughly an area is surveyed. That family, considered by some the most enigmatic scorpion family in the New World, is Troglotayosicidae Lourenço, 1998 (Ochoa et al., 2010).

As currently defined, Troglotayosicidae contains a single genus, *Troglotayosicus* Lourenço, 1981, with five species, to which a sixth is added in the present study. The validity and rank of Troglotayosicidae, which previously also included the genus *Belisarius* Simon, 1879, endemic to the Pyrenees of France and Spain and presently accommodated in Belisariidae Lourenço, 1998, have been discussed on numerous occasions by different authors (Lourenço, 1981, 1998; Stockwell, 1989, 1992; Sissom and Cokendolpher, 1998; Sissom, 2000a, 2000b; Soleglad and Fet, 2003; Coddington et al., 2004; Fet and Soleglad, 2005; Prendini and Wheeler, 2005; Prendini et al., 2010; Tropea and Onnis, 2020) and will not be addressed here. Despite doubts about its validity and rank, the family Troglotayosicidae will continue to be recognized until a rigorous test of its phylogenetic position has been presented.

Lourenço (1981) created *Troglotayosicus* to accommodate *Troglotayosicus vachoni* Lourenço, 1981, an enigmatic, troglomorphic scorpion with a distinct combination of characters including the absence of median ocelli, the presence of two pairs of lateral ocelli, and a unique pattern of pedipalp trichobothria. Almost half a century after its discovery, *T. vachoni* remains known only from the holotype, an adult female collected during a British-Ecuadorian expedition to the Los Tayos Caves, in the Amazonian Region of southeastern Ecuador (fig. 1), in 1976.

For almost three decades, *T. vachoni* was the only known species of the genus until *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009, was discovered on the western slopes of the Andes Cordillera at La Planada, in the Nariño Department (Ricaurte Municipality) of southwestern Colombia, near the border with Ecuador (Botero-Trujillo and Francke, 2009). *Troglotayosicus humiculum* was subsequently recorded from an additional locality, nearby (Ochoa et al., 2010). Shortly thereafter, *Troglotayosicus hirsutus* Botero-Trujillo et al., 2012, was described from Buesaco, also in the Nariño Department (Buesaco Municipality), ca. 90 km northeast of the closest record of *T. humiculum*, on the Andes (Botero-Trujillo et al., 2012). This was followed by the discovery of *Troglotayosicus meijdeni* Botero-Trujillo et al., 2017, at Vereda Agua Caliente, in the Huila Department (Rivera Municipality) of Colombia, on the western slopes of the Cordillera Oriental of the Andes, several hundred kilometers northeast of the other species, and currently the northernmost record for the genus (Botero-Trujillo et al., 2017). Recently, a fifth species, *Troglotayosicus muranunkae* Lourenço et al., 2020, was discovered at Las Orquídeas, in the Zamora Chinchipe Province of Ecuador, ca. 125 km southwest of the type locality of *T. vachoni*, on the slopes of the Cordillera del Condor, between the Andes and Amazonia, becoming the second species recorded from Ecuador and extending the known distribution of the genus further south (Sánchez-Vialas et al., 2020). The known distribution of *Troglotayosicus* now extends ca. 862 km from the northernmost record in Colombia (*T. meijdeni*) to the southernmost record in Ecuador (*T. muranunkae*).

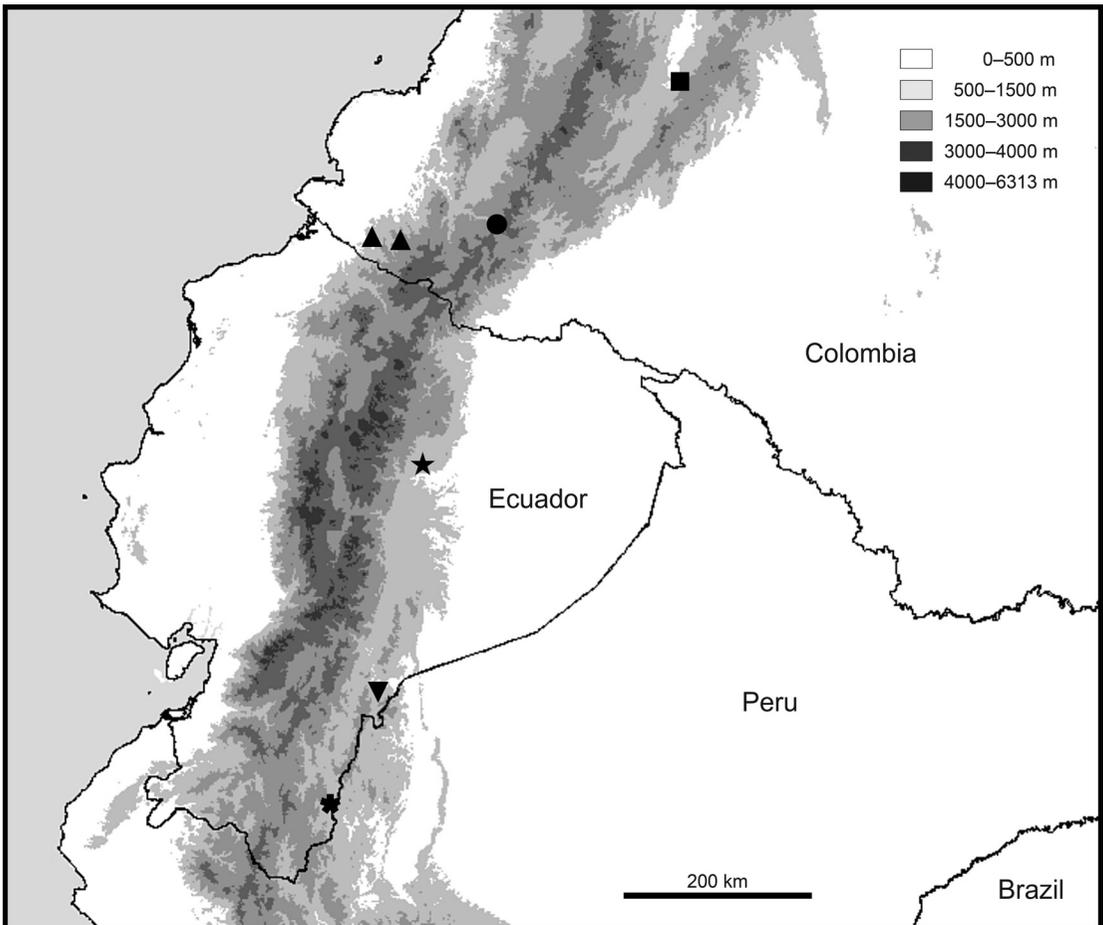


FIGURE 1. Map of northwestern South America, plotting known locality records of *Troglotayosicus* Lourenço, 1981: *Troglotayosicus ballvei*, sp. nov. (star); *Troglotayosicus hirsutus*, Botero-Trujillo et al., 2012 (circle); *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009 (triangles); *Troglotayosicus meijdeni* Botero-Trujillo et al., 2017 (square); *Troglotayosicus muranunkae* Lourenço et al., 2020 (asterisk); *Troglotayosicus vachoni* Lourenço, 1981 (inverted triangle).

Despite the presence of troglomorphies, notably the absence of median ocelli and the presence of two pairs of lateral ocelli, only *T. vachoni*, the type species of *Troglotayosicus*, was collected inside a cave. All other specimens were collected in the leaf litter of tropical rainforests, implying an endogean rather than hypogean lifestyle, as in some eyeless, depigmented species of Typhlochactidae Mitchell, 1971, known only from forest leaf litter, e.g., *Typhlochactas mitchelli* Sisson, 1988, *Typhlochactas sissomi* Francke et al., 2009, and *Typhlochactas sylvestris* Mitchell and Peck, 1977 (Vignoli and Prendini, 2009; Prendini et al., 2010). Sánchez-Vialas et al. (2020: 613, 617) questioned whether *T. vachoni* is exclusively hypogean (i.e., troglobitic); this species may also inhabit leaf litter on the forest floor outside the Los Tayos Caves.

In the present study, *Troglotayosicus ballvei*, sp. nov., is described from male and female specimens collected at Sacha Huagra Lodge, adjacent to the Archidona Municipality, in the Amazonian



FIGURE 2. *Troglotayosicus ballvei*, sp. nov., habitat at type locality in Sacha Huagra Lodge, Napo Province, Ecuador. **A.** Tropical humid forest. **B.** Exposed remnants of collapsed caves inside forest.

part of Napo Province, Ecuador (figs. 1, 2), ca. 250 km from the nearest congeners to the north and south. The new species raises the number of *Troglotayosicus* species to six, three each in Colombia and Ecuador.

#### MATERIAL AND METHODS

Specimens of the new species described herein were hand collected by disturbing leaf litter at night with ultraviolet light (Stahnke, 1972).

Material is deposited in the following collections: the American Museum of Natural History (AMNH), including the Ambrose Monell Cryocollection for Molecular and Microbial Research (AMCC), New York; the Arachnological Collection of the Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá; the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina; the Museo Javeriano de Historia Natural “Lorenzo Uribe, S.J.,” Pontificia Universidad Javeriana (MPUJ), Bogotá, Colombia; the Museo de Biodiversidad del Perú (MUBI), Cusco; the Museo de Zoología (QCAZ), Pontificia Universidad Católica del Ecuador, Quito.

Style and terminology for the species description mostly follows Ochoa et al. (2010). Morphological terminology follows Vachon (1952) and Prendini (2000) for pedipalp carinae,



FIGURE 3. *Troglotayosicus ballvei*, sp. nov., live habitus of adults. A. Paratype ♂ (AMNH IZC 325052). B. Holotype ♀ (QCAZ).

TABLE 1. Measurements (mm) for type specimens of *Troglotayosicus ballvei*, sp. nov. Material deposited in American Museum of Natural History (AMNH), New York, and Museo de Zoología (QCAZ), Pontificia Universidad Católica del Ecuador, Quito. Abbreviations: L, length; W, width; H, height.

		Holotype ♀ QCAZ	Paratype ♂ AMNH IZC 325052
Total body L <sup>1</sup>		23.45	21.57
Carapace	L	3.22	2.87
	Anterior W	2.01	1.76
	Posterior W	3.02	2.79
Mesosoma	Total L <sup>2</sup>	6.89	5.71
Metasoma	Total L <sup>3</sup>	13.34	12.99
Metasomal segment I	L	1.21	1.14
	W	2.35	2.15
	H	1.92	1.84
Metasomal segment II	L	1.35	1.35
	W	2.33	2.23
	H	1.87	1.82
Metasomal segment III	L	1.56	1.60
	W	2.36	2.18 <sup>4</sup>
	H	1.89	1.83
Metasomal segment IV	L	2.33	2.28
	W	2.41	2.22
	H	1.94	1.77
Metasomal segment V	L	3.54	3.42
	W	2.34	2.16
	H	1.75	1.70
Telson	L	3.35	3.20
	Vesicle W	1.40	1.27
	Vesicle H	0.96	0.91
Pedipalp	Total L <sup>5</sup>	10.28	9.37
Femur	L	2.50	2.30
	W	0.93	0.89
	H	0.83	0.74
Patella	L	3.07	2.75
	W	1.05	1.01
	H	1.05	0.99
Chela	L	4.71	4.32
	W	1.44	1.40
	H	1.51	1.39
	Fixed finger L <sup>6</sup>	1.85	1.67
	Movable finger L	2.52	2.30
	Palm L	2.29	2.10
Pectines	L <sup>7</sup>	1.62	1.55
Lateral ocelli <sup>8</sup>	PLMa diameter	0.21	0.18
	PDMi diameter	0.12	0.11
	Eyespot diameter	0.06	0.04

<sup>1</sup> Sum of prosoma, mesosoma, and metasoma.

<sup>2</sup> Sum of pre- and posttergites I–VII, measured along midline.

<sup>3</sup> Sum of metasomal segments I–V and telson.

<sup>4</sup> Approximate, right aspect anomalous.

<sup>5</sup> Sum of femur, patella, and chela.

<sup>6</sup> Measured from movable finger condyle to fingertip.

<sup>7</sup> Measured along marginal lamella.

<sup>8</sup> Terminology follows Loria and Prendini (2014).

replacing “external” and “internal” with “retrolateral” and “prolateral,” respectively, abbreviated as follows: promedian (PM), digital (DI), prodorsal (PD), dorsomedian (DM), retrodorsal (RD), dorsomarginal (DMA), dorsal secondary (DS), retrolateral (RL), retromedian (RM), retroventral (RV), ventromedian (VM), proventral (PV), dorsal patellar process (DPP), ventral patellar process (VPP); Vachon (1963) for cheliceral dentition notation, replacing “external” and “internal” with “retrolateral” and “prolateral,” respectively; Vachon (1974) for trichobothrial notation, applied to the reinterpretation of *Typhlochactas* trichobothrial patterns proposed by Prendini and Wheeler (2005) and Vignoli and Prendini (2009); a modified version of Prendini (2004) for tergal, sternal, and metasomal carinae, abbreviated as follows: dorsosubmedian (DSM), dorsolateral (DL), lateral supramedian (LSM), median lateral (ML), lateral inframedian (LIM), ventrolateral (VL), ventrosubmedian (VSM), ventromedian (VM); Loria and Prendini (2014) for notation of the lateral ocelli; and Stahnke (1970) for other characters.

Photographs of preserved specimens, taken and processed at the MACN, were obtained with a Leica DFC 290 digital camera mounted on a Leica M165 C stereomicroscope, and the extended focal range images composed with Helicon Focus 6.2.2 Pro software (<http://www.heliconsoft.com/heliconsoft-products/helicon-focus>). Measurements, in mm (table 1), were obtained following the methodology of Sissom et al. (1990), except when otherwise specified, using an ocular micrometer fitted to a Leitz Wetzlar stereomicroscope at the MACN.

The type locality was georeferenced in the field with a portable Garmin 64s GPS Navigation System. The distribution map was produced using DIVA-GIS Version 5.4 (<http://www.diva-gis.org>) by superimposing georeferenced point locality records on a digital elevation dataset from the CGIAR Consortium for Spatial Information (CGIAR-CSI) available online (<http://srtm.csi.cgiar.org>).

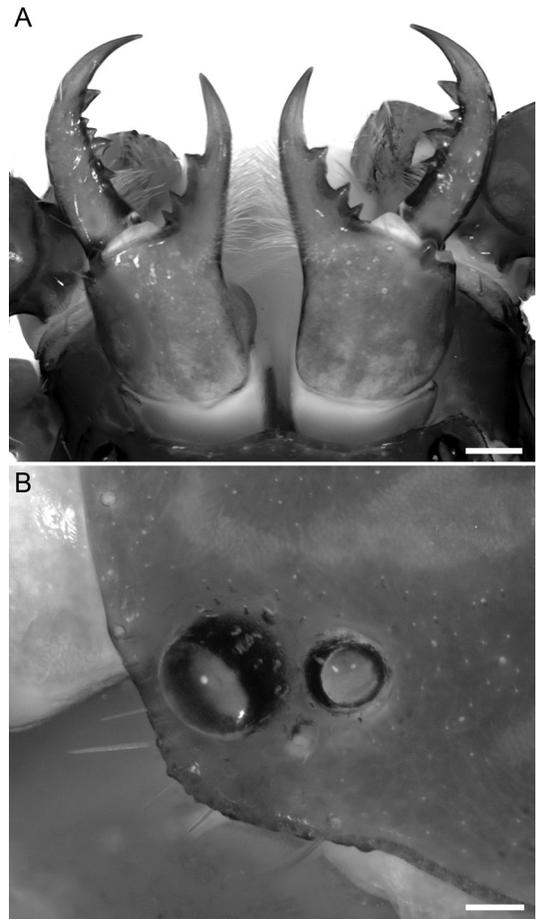


FIGURE 4. *Troglotayosicus ballvei*, sp. nov., prosoma. **A.** Holotype ♀ (QCAZ), chelicerae, dorsal aspect. **B.** Paratype ♂ (AMNH IZC 325052), carapace, dorso-lateral aspect, illustrating sinistral lateral ocelli and eyespot. Scale bars = 0.3 mm (A), 0.1 mm (B).

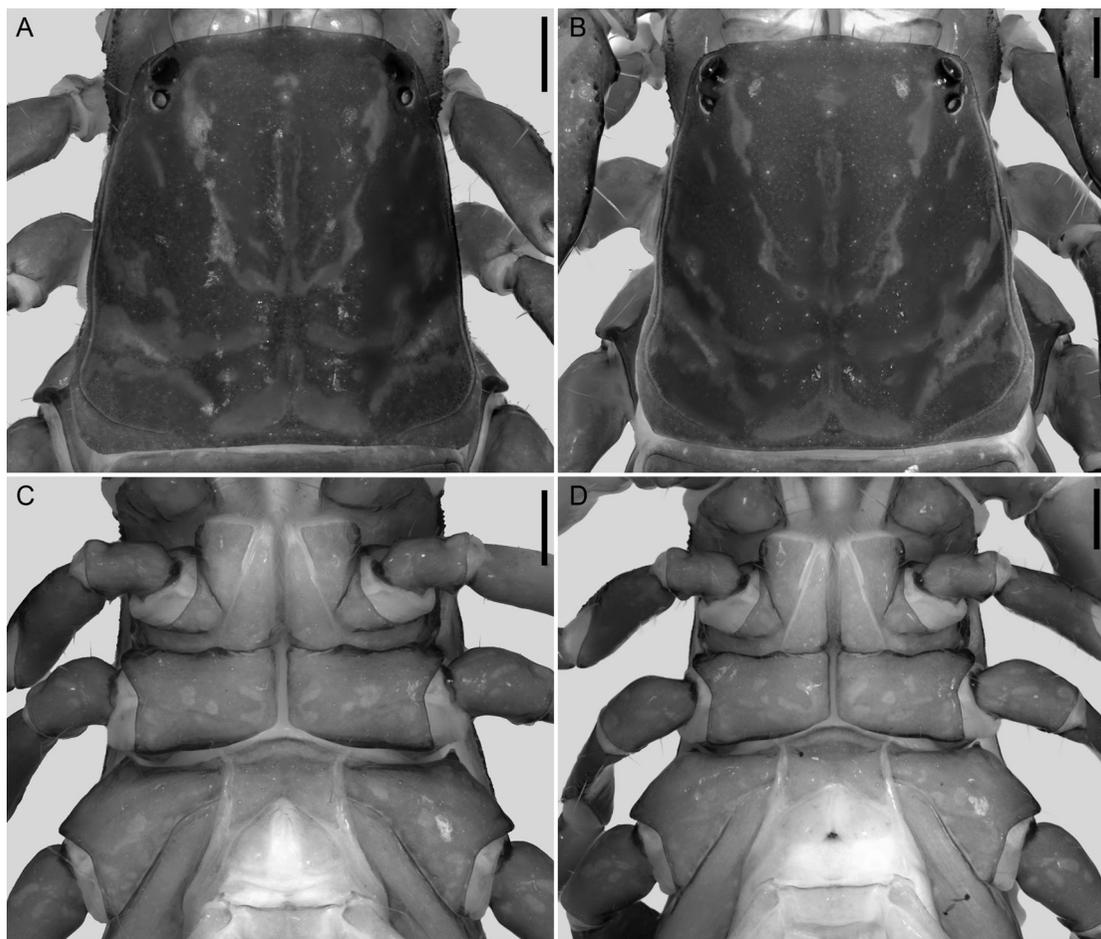


FIGURE 5. *Troglotayosicus ballvei*, sp. nov., prosoma: A, B, carapace, dorsal aspect, and C, D, coxae and sternum, ventral aspect. A, C. Paratype ♂ (AMNH IZC 325052). B, D. Holotype ♀ (QCAZ). Scale bars = 0.5 mm.

#### SYSTEMATICS

Family Troglotayosicidae Lourenço, 1998

*Troglotayosicus* Lourenço, 1981

Figures 1–16; table 1

*Troglotayosicus* Lourenço, 1981: 650, 651, type species by original designation: *Troglotayosicus vachoni* Lourenço, 1981; Francke, 1985: 14, 16, 20; Sissom, 1990: 54, 55, 57; Nenilin and Fet, 1992: 28; Stockwell, 1992: 410, 411; Kovařík, 1998: 142; Lourenço, 1998: 135–137; Sissom and Cokendolpher, 1998: 285; Fet and Sissom, 2000: 502; Prendini, 2000: 55; Soleglad and Sissom, 2001: 28, 29, 40, 57, 67–69, 88; Soleglad and Fet, 2003: 28, 32, 36, 40, 61, 66, 67, 68, 81, 82, 85, 86, 88, 93, 106, 107, 108, 141, 146, figs. 116, 117; Fet and Soleglad, 2005: 12; Prendini and Wheeler, 2005: 448, 451, 454, 463, 468, 470, 473, 476, 482, 492, 494; Dupré, 2007: 11; Botero-Trujillo and Francke, 2009: 2, 3, map 1; Vignoli and Prendini, 2009: 3, 10, 14, 16; Ochoa et al., 2010: 1, 2, 11, 15, fig. 12;

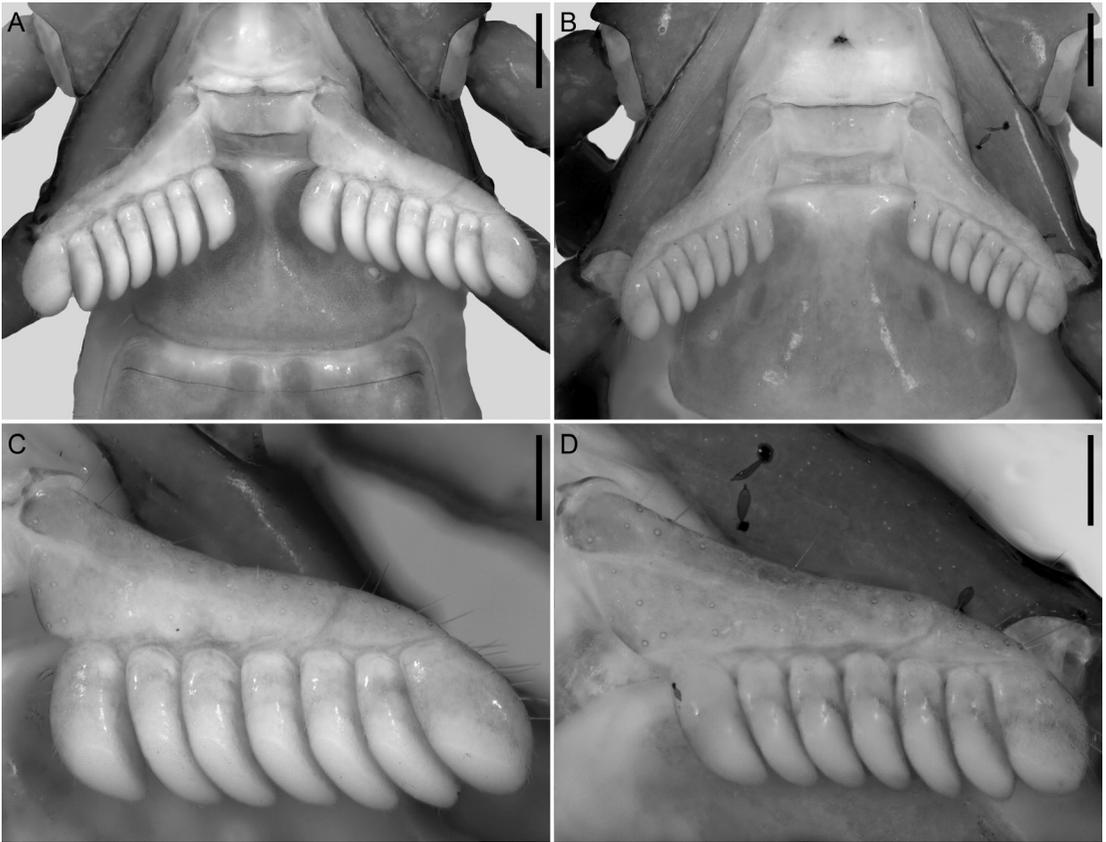


FIGURE 6. *Troglotayosicus ballvei*, sp. nov., pectines, ventral aspect: **A, B**. pectinal area and **C, D**. closeup of sinistral pecten. **A, C**. Paratype ♂ (AMNH IZC 325052). **B, D**. Holotype ♀ (QCAZ); note thalli of fungi (Ascomycota: Laboulbeniomyces: Laboulbeniales Lindau, 1898) on sinistral coxa of leg IV and basal pectinal tooth. Scale bars = 0.5 mm (**A, B**), 0.3 mm (**C, D**).

Prendini et al., 2010: 122, 130, 132; Botero-Trujillo et al., 2012: 63–65, 75, fig. 1; Loria and Prendini, 2014: 5, 20, 22, 24, 25; Botero-Trujillo et al., 2017: 568–570, 580, 581, fig. 1; Loria and Prendini, 2018: 184, 188; Francke, 2019: 16; Sánchez-Vialas et al., 2020: 612–617, fig. 1; Tropea and Onnis, 2020: 6; Prendini et al., 2021: 16, 129, 130.

**DIAGNOSIS:** Cheliceral movable finger with well-developed serrula ventrally. Carapace with weak to moderate anteromedian epistome; without median ocelli; lateral ocelli pattern Type 2B, with two ocelli (PLMa and PDMi) present and four ocelli (ALMa, MLMa, ADMi, and PLMi) absent; lateral eyespot ventral to lateral ocelli. Sternum subpentagonal. Pedipalp chela with DS, DI, RL, RV, PV, DMA, and PD carinae identified by subtle differences in angles between adjacent surfaces, smooth or with DS, DMA, and PD granular; median denticle row of fixed finger comprising six oblique primary subrows of denticles, terminal denticle larger than others and hooklike; median denticle row of movable finger comprising seven oblique primary subrows of denticles, terminal denticle larger and hooklike, accommodated in subdistal diastema of fixed finger; pedipalp fingertips interlocking unevenly when closed such that movable

finger displaced retrolaterally, relative to fixed finger. Pedipalps with three trichobothria on femur, 19 on patella, and 26 on chela, as illustrated (figs. 7–9). Legs without tibial spur; basitarsi with rows of brushlike spinules distally. Posttergites I–VI finely granular or predominantly smooth, acarinate; VII finely granular, posterior half with scattered granules in position of DSM carinae and with DL carinae terminating in tubercle comprising four or five granules. Mesosoma with rounded book lung spiracles; male and female pectines with 7 or 8 teeth, without fulcra. Metasoma with VL and VSM carinae absent on segments I and II, and occasionally also on III and IV; LIM carinae present on segments I–III, present or absent on IV, and indistinct on V; segment V with paired DL, LSM, ML, VL, and VSM carinae, and single VM carina, comprising discontinuous granules not arranged into distinct rows. Telson vesicle without subaculear tubercle; aculeus stout basally, slightly tapering distally. Hemispermaphore lamelliform. Lamina with elongate apex, without crests, articular flexure present; basal portion and foot well developed, similar in length to lamina. Capsule simple, with ectal and ental lobes; IL more pronounced than EL, with sclerotized ectal spurlike projection. Hemispermaphores of *T. meijdeni*, *T. muranunkae*, and *T. vachoni* unknown.

INCLUDED SPECIES: Six species: *Troglotayosicus ballvei*, sp. nov.; *Troglotayosicus hirsutus* Botero-Trujillo et al., 2012; *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009; *Troglotayosicus meijdeni* Botero-Trujillo et al., 2017; *Troglotayosicus muranunkae* Lourenço et al., 2020; *Troglotayosicus vachoni* Lourenço, 1981.

DISTRIBUTION: Colombia, Ecuador.

REMARKS: Sánchez-Vialas et al. (2020) reported only two pairs of lateral ocelli in the two species previously described from Ecuador, *T. muranunkae* and *T. vachoni*, and three in the remaining species. In addition to the PLMa and PDMi lateral ocelli, the three Colombian species exhibit a moderate to large, depigmented area corresponding to the lateral eyespot *sensu* Loria and Prendini (2014), which was referred to as a third pair of ocelli by previous authors (Botero-Trujillo and Francke, 2009; Ochoa et al., 2010; Botero-Trujillo et al., 2012). Although not described, a lateral eyespot is evident in the illustration of *T. muranunkae* (Sánchez-Vialas et al., 2020: 615, fig. 2C), suggesting it may also be present in *T. vachoni*. Two pairs of lateral ocelli and an eyespot are assumed to be present in all species of the genus.

### *Troglotayosicus ballvei*, sp. nov.

Figures 1–16; table 1

TYPE MATERIAL: Holotype ♀ (QCAZ), **ECUADOR**: *Napo Province*: Río Hollín, on way to Santo Domingo, 5 km SE of Archidona, Sacha Huagra Lodge, 00°57'19.6"S 77°44'58.7"W, 660 m, 15–16.iii.2014, J.A. Ochoa and R. Botero-Trujillo. Paratypes: 1 ♂ (AMNH IZC 325052), 1 subad. ♂ (MUBI), 2 juv. (AMCC [LP 12767], QCAZ), same data.

DIAGNOSIS: *Troglotayosicus ballvei* differs from other species in the genus as follows. The body and appendages are not remarkably hirsute in *T. ballvei* (fig. 3), unlike *T. hirsutus*. The median projection (epistome) on the anterior margin of the carapace is weak (shallow) in *T. ballvei* (fig. 5A, B), but pronounced in *T. hirsutus* and *T. vachoni*. The lateral eyespot on the

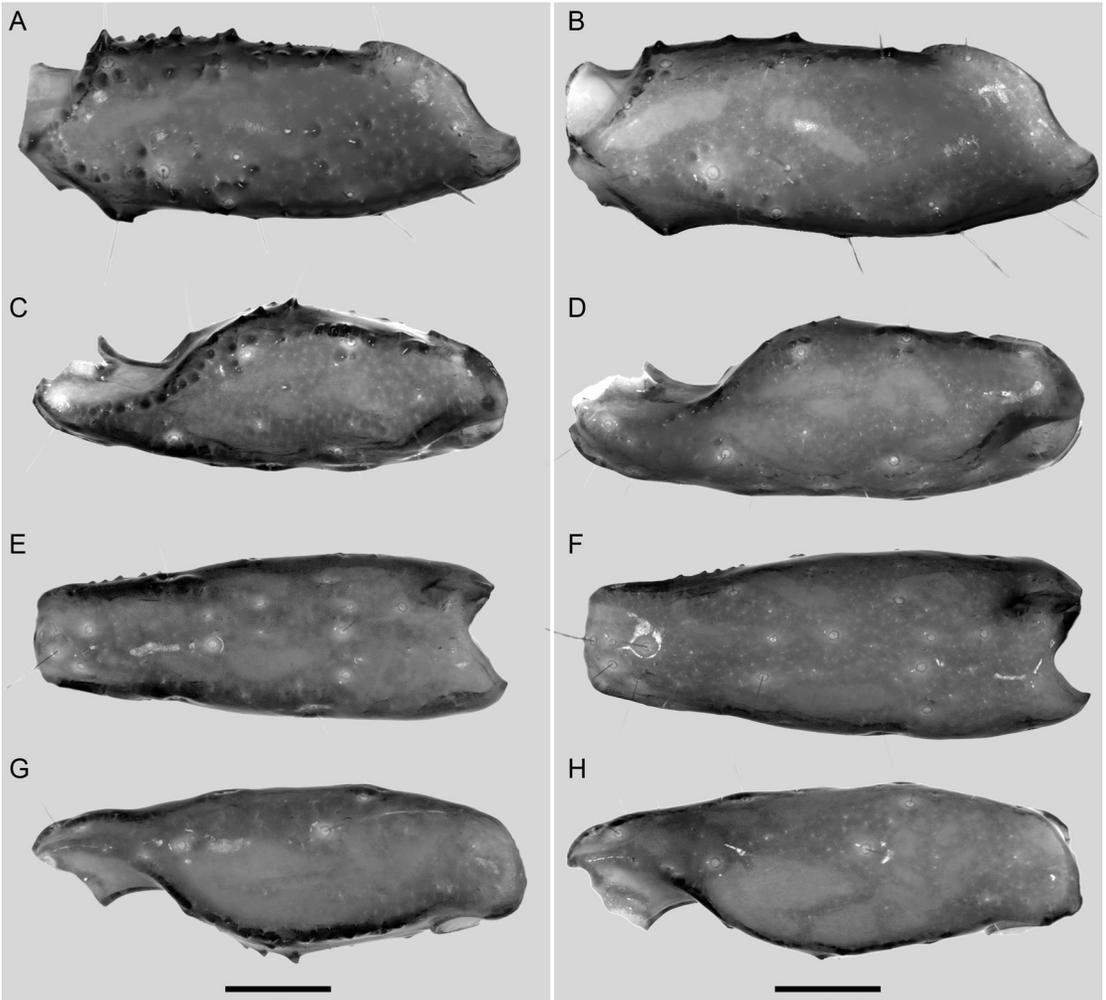


FIGURE 7. *Troglotayosicus ballvei*, sp. nov., dextral pedipalp femur and patella: **A, B**, femur, dorsal aspect, and **C–H**, patella: **C, D**, dorsal, **E, F**, retrolateral, and **G, H**, ventral aspects. **A, C, E, G**, Paratype ♂ (AMNH IZC 325052). **B, D, F, H**, Holotype ♀ (QCAZ). Scale bars = 0.5 mm.

carapace is considerably smaller than the PDMi ocellus in *T. ballvei* (fig. 4B), but similar to or larger than the PDMi ocellus in *T. meijdeni*. The pedipalp chela does not exhibit any obvious sexual dimorphism, i.e., the chela shape is similar in the adults of both sexes in *T. ballvei* (figs. 8, 9), unlike *T. hirsutus* and *T. humiculum*, which exhibit pronounced sexual dimorphism in chela shape, with the chela manus noticeably more incrassate in the adult male. The pedipalp chela DS, DI, RL, RV, and PV carinae are smooth, and the DMA and PD carinae weakly granular (♂) or smooth (♀) in *T. ballvei* (figs. 8, 9), whereas the DMA, PD and, to a lesser extent, DS carinae are granular in *T. humiculum* and the DMA and PD carinae coarsely granular distally in *T. meijdeni*. Trichobothrium *Db* is situated proximally on the pedipalp chela manus, only slightly distal to trichobothrium *Eb*<sub>3</sub>, in *T. ballvei* (figs. 8A, B, 9A, B), whereas *Db* is situated submedially on the manus, approximately midway between the *Eb* and *Et* trichobothrial series, in *T. muranunkae*.

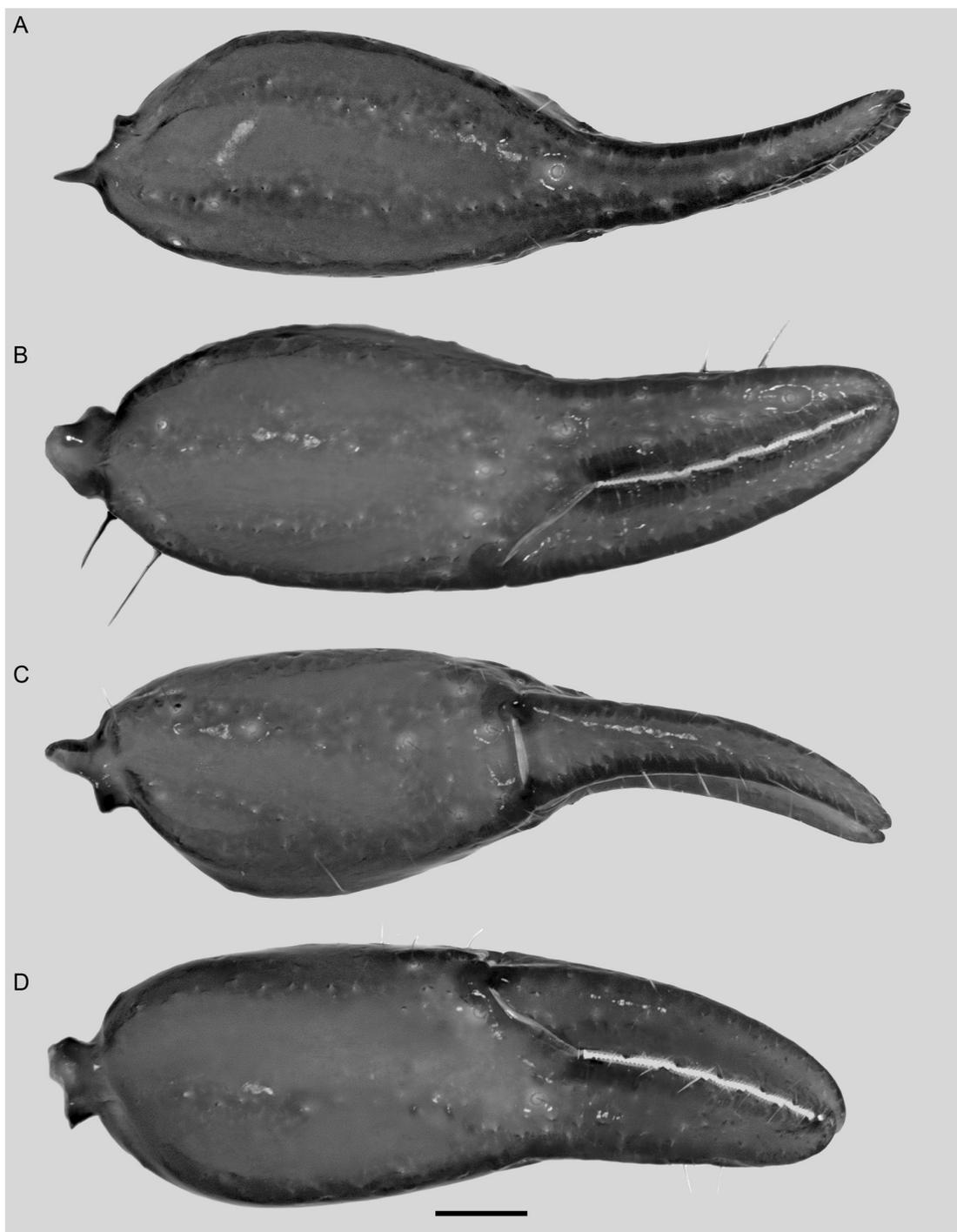


FIGURE 8. *Troglotayosicus ballvei*, sp. nov., paratype ♂ (AMNH IZC 325052), dextral pedipalp chela: A. dorsal, B. retrolateral, C. ventral, and D. prolateral aspects. Scale bar = 0.5 mm.

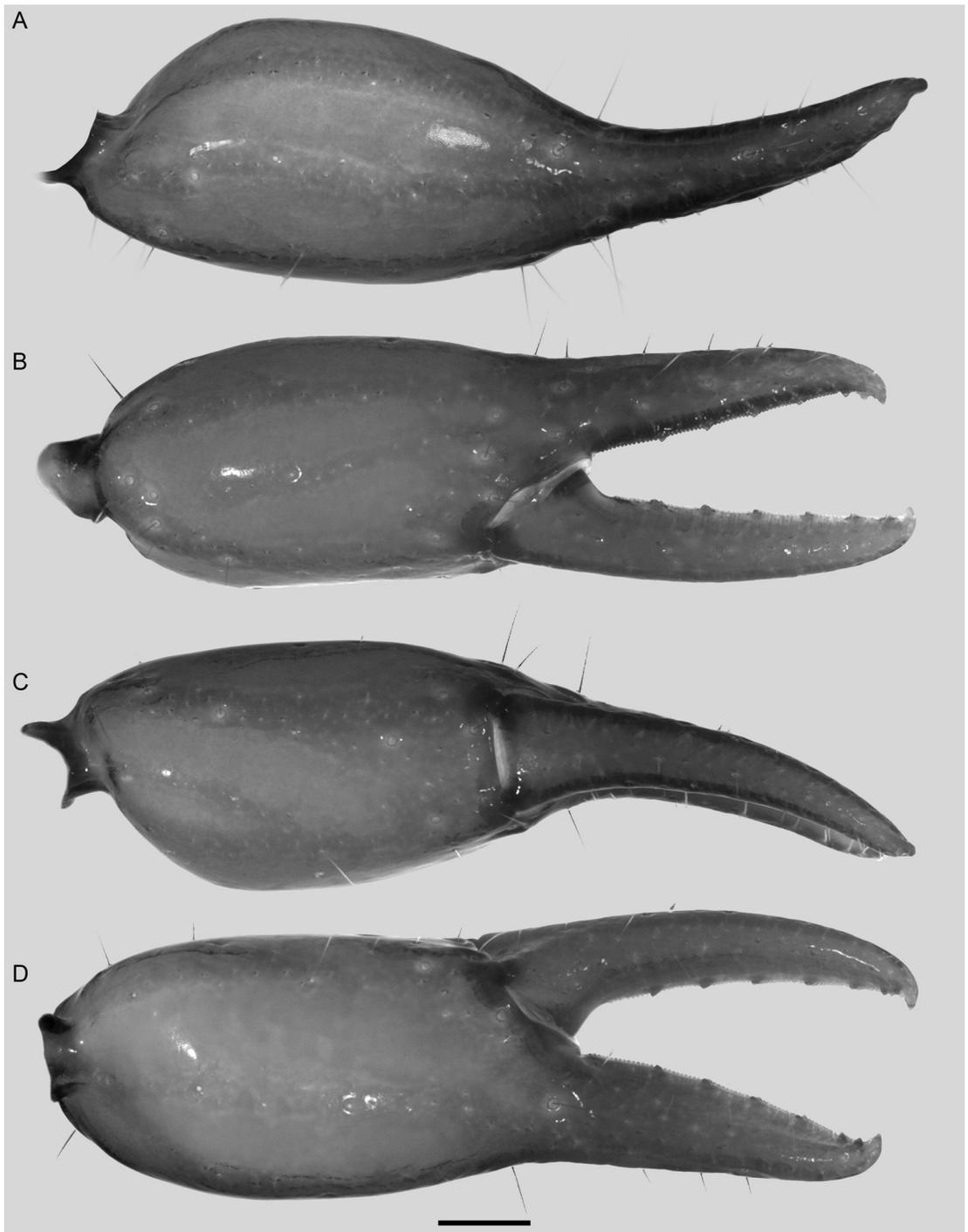


FIGURE 9. *Troglotayosicus ballvei*, sp. nov., holotype ♀ (QCAZ), dextral pedipalp chela: A. dorsal, B. retro-lateral, C. ventral, and D. pro-lateral aspects. Scale bar = 0.5 mm.



FIGURE 10. *Troglotayosicus ballvei*, sp. nov., holo-type ♀ (QCAZ), dextral pedipalp chela fingers, illustrating median denticle rows: **A**. movable finger, dorsal aspect, **B**. fixed finger, ventral aspect. Scale bar = 0.3 mm.

The macrosetae on the telotarsi of legs I–IV are regularly arranged into a pair of parallel ventrosubmedian rows in *T. ballvei* (fig. 11E), but not arranged into rows in *T. muranunkae* and *T. vachoni*. The ventral and ventrolateral surfaces of the telson are distinctly, coarsely granular in *T. ballvei* (fig. 15), but smooth in *T. muranunkae*. The metasomal LSM carinae are weakly developed, yet distinct, in *T. ballvei* (figs. 12, 13), but obsolete in *T. muranunkae*. The VL and VSM carinae are absent on metasomal segment III and comprise coarse granules in the medial third of segment IV, in *T. ballvei* (figs. 12, 13), whereas both carinae are present on segments III and IV in *T. humiculum*, and absent on the two segments in the other four species. The hemispermatophore of the new species differs from that of the other *Troglotayosicus* species for which adult males are known. The lamina is

broad proximally and medially, forming two obtuse angles along the dorsal margin in its proximal half, in *T. ballvei* (fig. 16), as in *T. hirsutus*, but markedly expanded medially, not forming angles, in *T. humiculum*. The apex of the lamina is more elongate in *T. ballvei* than in other species and slightly coiled, whereas it terminates in a small dilation in *T. hirsutus*. The ectal lobe (EL) is well developed, with a dorsal process in *T. ballvei*, similar to that of *T. humiculum*, but the EL is vestigial and does not possess a dorsal process in *T. hirsutus*.

**ETYMOLOGY:** The species name is dedicated to Oscar F. Francke Ballvé, formerly of the Universidad Nacional Autónoma de México, on the occasion of his retirement and in recognition to his contributions to the knowledge of troglomorphic and troglobitic arachnids.

**DESCRIPTION:** The following description is based on the type material. The description of legs III and IV is based on the male as the carinae are less pronounced in females and immature stages. Measurements in table 1.

**COLOR:** Color in life as in figure 3. Following description based on preserved specimens. Base color, chelicerae, and legs yellowish to chestnut; carapace, tergites, metasoma, and pedipalps yellowish (juveniles) or carapace, tergites, and pedipalps orange to chestnut, with metasomal segments becoming darker (adults); sternites and coxosternal region yellowish; pectines whitish. PLMa and PDMi ocelli surrounded by black pigment (fig. 4B). Carapace and coxosternal region with pale yellowish stripes and spots, mostly along sulci; pedipalp chela manus with darker areas along positions of carinae, more obvious in adults (figs. 8, 9); remaining areas predominantly unpigmented.

**CHELICERAE:** Manus, dorsal and retrolateral surfaces predominantly smooth, sparsely setose (fig. 4A); prolateral and ventral surfaces densely setose. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal); median and basal teeth separate, not fused into

bicusp. Movable finger, dorsal margin with five teeth, prodistal, two small subdistal, median, and basal; prodistal and retrodistal teeth not opposable, prodistal tooth at most partially overlapping retrodistal tooth in dorsal aspect; ventral surface with long, well-developed serula, and vestigial retrobasal denticle at base.

**CARAPACE:** Anterior margin sublinear, with weak median projection (epistome) and approximately six macrosetae (fig. 5A, B); posterior margin linear, with few macrosetae. Median ocelli absent; two pairs of lateral ocelli, PLMa and PDMi (fig. 4B), PLMa larger; small eyespot ventral to lateral ocelli. Median longitudinal sulcus shallow but evident, not reaching anterior margin; posterolateral and posterior transverse sulci obsolete. Surfaces acarinate, finely granular, and sparsely setose.

**STERNUM:** Shape subpentagonal with rounded apex (fig. 5C, D); lateral margins subparallel, slightly converging anteriorly such that posterior width greater than length; posterior depression shallow. Surface with 6–8 macrosetae and additional microsetae.

**PEDIPALPS:** Carinae well developed (adults) or obsolete (juveniles). Femur tetracarinate ( $\delta$ ) or tricarinate ( $\varphi$ ) (fig. 7A, B); PD carina complete ( $\delta$ ) or discontinuous ( $\varphi$ ), granular; RD carina restricted to proximal two-thirds of segment ( $\delta$ ) or discontinuous ( $\varphi$ ), granular; PV carina complete, granular (more pronounced in  $\delta$ ); RV carina incomplete, restricted to proximal third of segment ( $\delta$ ) or absent ( $\varphi$ ); dorsal intercarinal surface with few scattered granules ( $\delta$ ) or predominantly smooth ( $\varphi$ ); retrolateral surface smooth; prolateral surface densely ( $\delta$ ) or sparsely ( $\varphi$ ) granular; ventral surface smooth; surfaces sparsely setose. Patella tricarinate ( $\delta$ ) or bicarinate ( $\varphi$ ) (fig. 7C–H); PD and PV carinae granular (more so in  $\delta$ ), complete ( $\delta$ ) or discontinuous ( $\varphi$ ); DPP comprising three or four granules proximally (more pronounced in  $\delta$ ); VPP comprising one to three small gran-

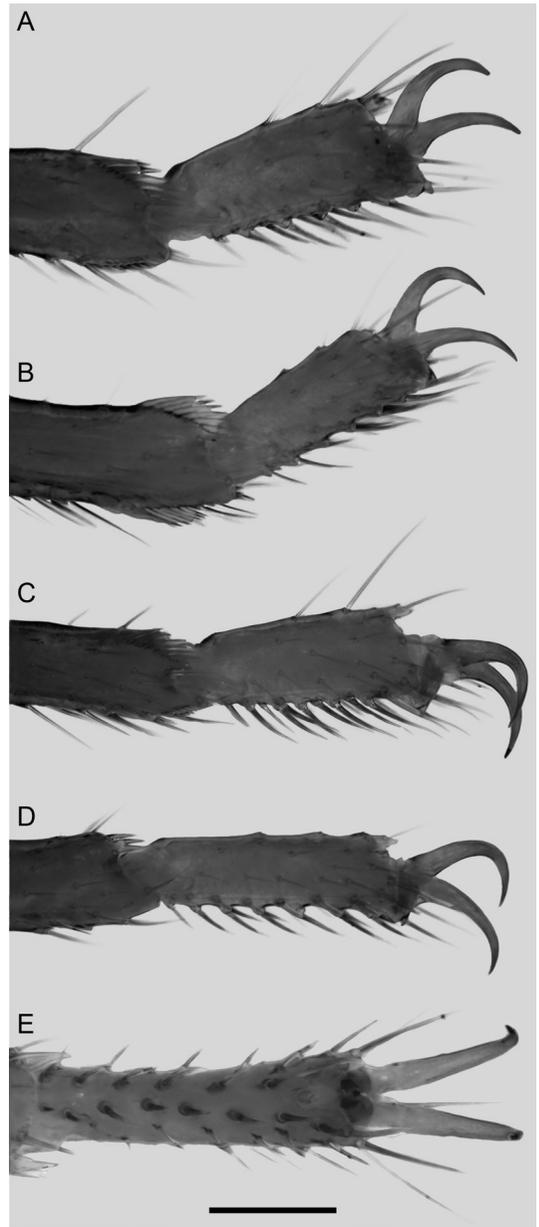


FIGURE 11. *Troglotayosicus ballvei*, sp. nov., legs I–IV, telotarsi and distal end of basitarsi. **A–D.** Paratype  $\delta$  (AMNH IZC 325052), dextral legs I–IV, retrolateral aspect. **E.** Holotype  $\varphi$  (QCAZ), sinistral leg IV, ventral aspect. Scale bar = 0.3 mm.

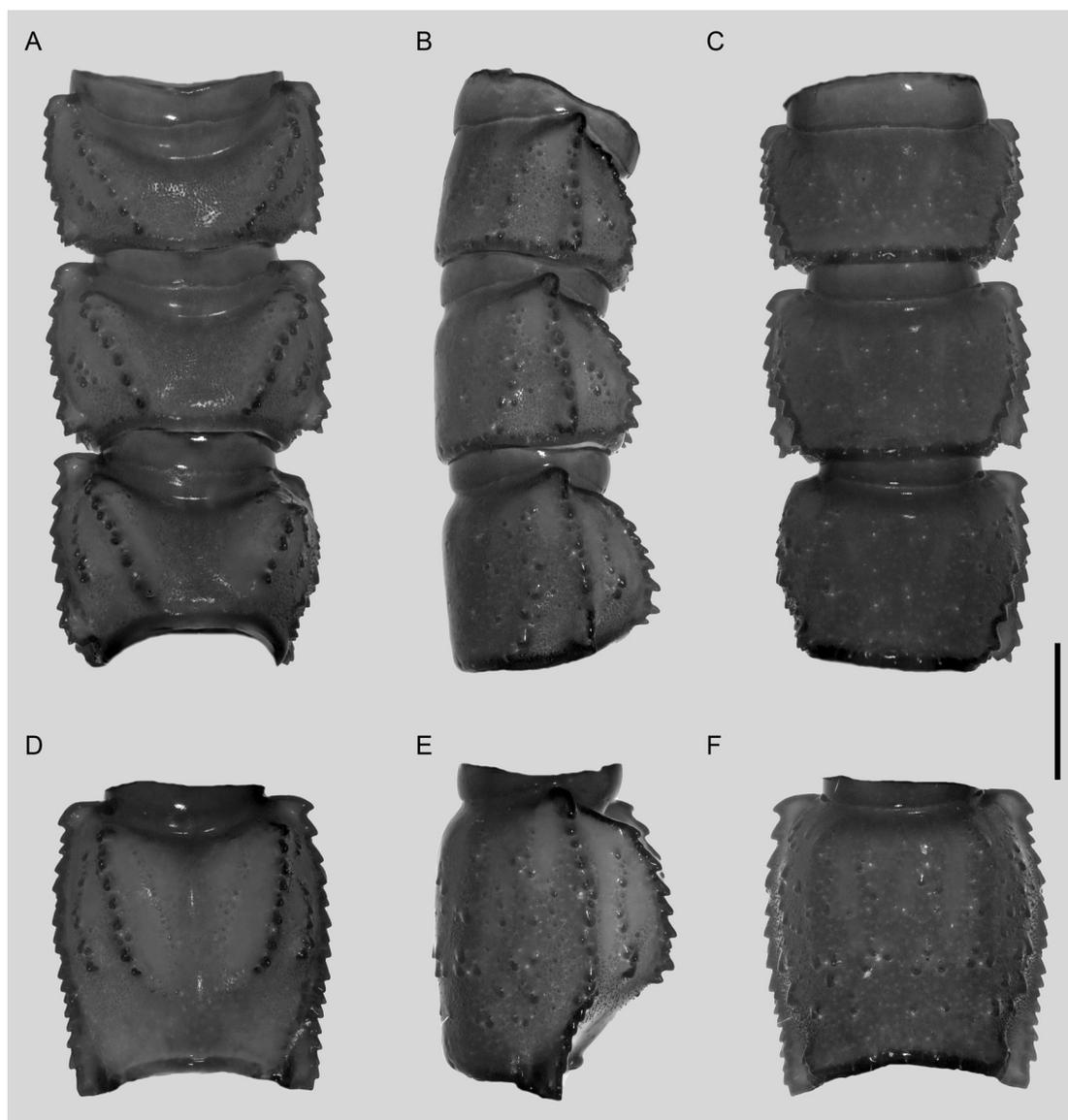


FIGURE 12. *Troglotayosicus ballvei*, sp. nov., paratype ♂ (AMNH IZC 325052), metasomal segments: A–C, segments I–III and D–F, IV: A, D, dorsal, B, E, lateral, and C, F, ventral aspects. Scale bar = 1 mm.

ules proximally; RD carina obsolete, incomplete, comprising small, discontinuous granules (♂) or absent (♀); all other carinae absent; intercarinal surfaces smooth; patellar carinae less developed in immature stages. Chela manus slightly incrassate (figs. 8, 9), longer than fixed finger, shorter than movable finger (table 1). Chelal carinae obsolete; positions of DS, DI, RL, RV, and PV carinae identified by subtle differences in angles between adjacent surfaces (slightly more pronounced in ♂); PD and DMA weakly granular (♂) or smooth (♀). Intercarinal surfaces smooth, with some macro- and microsetae, mostly along carinae, becoming more abundant on fingers. Fixed finger, median denticle row comprising six oblique, slightly imbricate primary

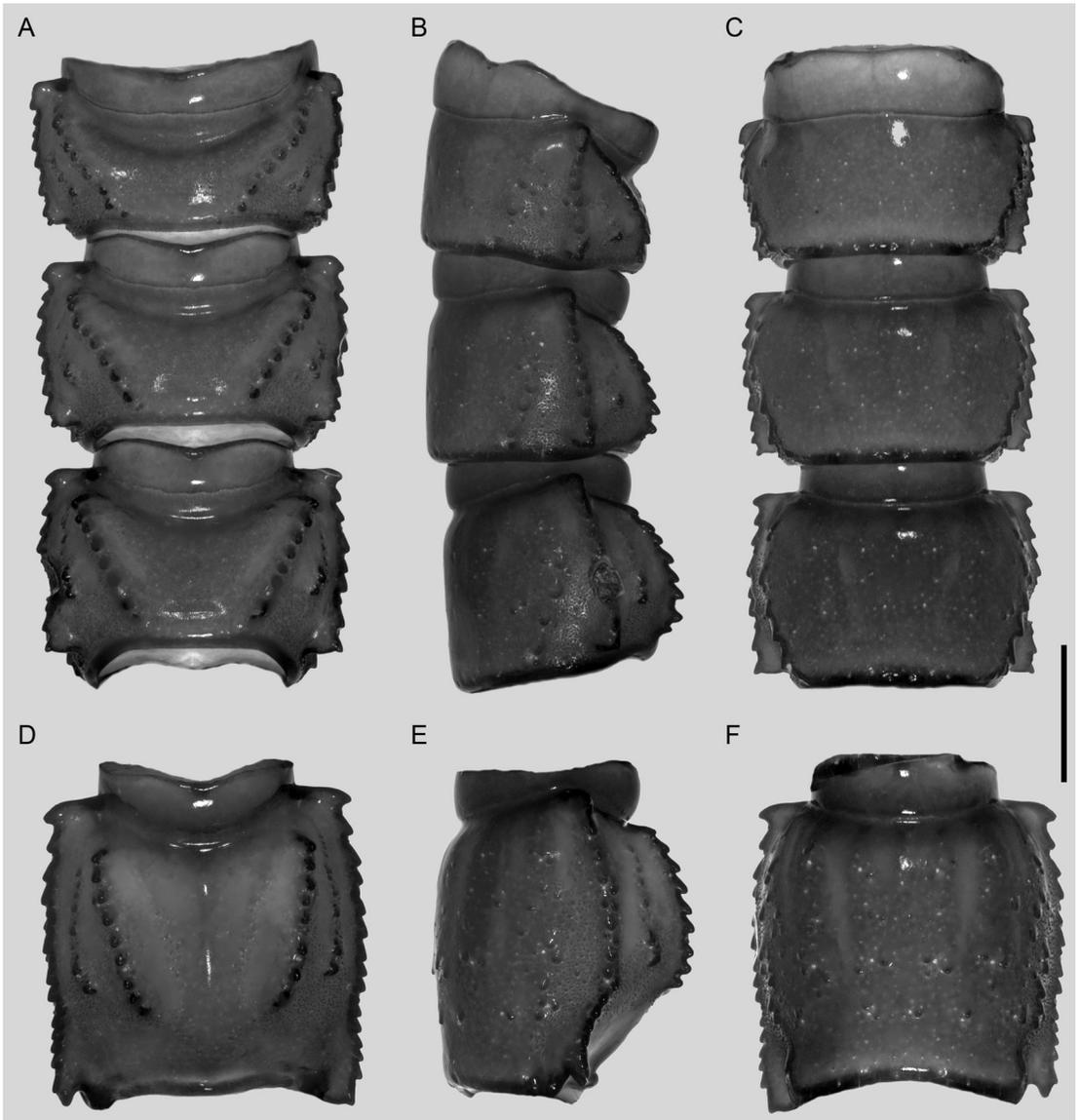


FIGURE 13. *Troglotayosicus ballvei*, sp. nov., holotype ♀ (QCAZ), metasomal segments: A–C. segments I–III and D–F. IV: A, D. dorsal, B, E. lateral, and C, F. ventral aspects. Scale bar = 1 mm.

subrows of denticles, flanked by five retrolateral and six prolateral denticles (fig. 10B); terminal denticle considerably larger than preceding denticles, hooklike; fingertips interlocking unevenly when closed such that movable finger displaced retrolaterally. Movable finger, median denticle row comprising seven oblique, slightly imbricate primary subrows of denticles, flanked by six retrolateral and seven prolateral denticles (fig. 10A); terminal denticle enlarged, hooklike, accommodated in subdistal diastema of fixed finger.

TRICHOBOTHRIA: Femur with three trichobothria (fig. 7A, B): one on retrolateral surface (*e*), one on dorsal surface (*d*), one on prolateral surface (*i*). Patella with 19 trichobothria (fig. 7C–H),

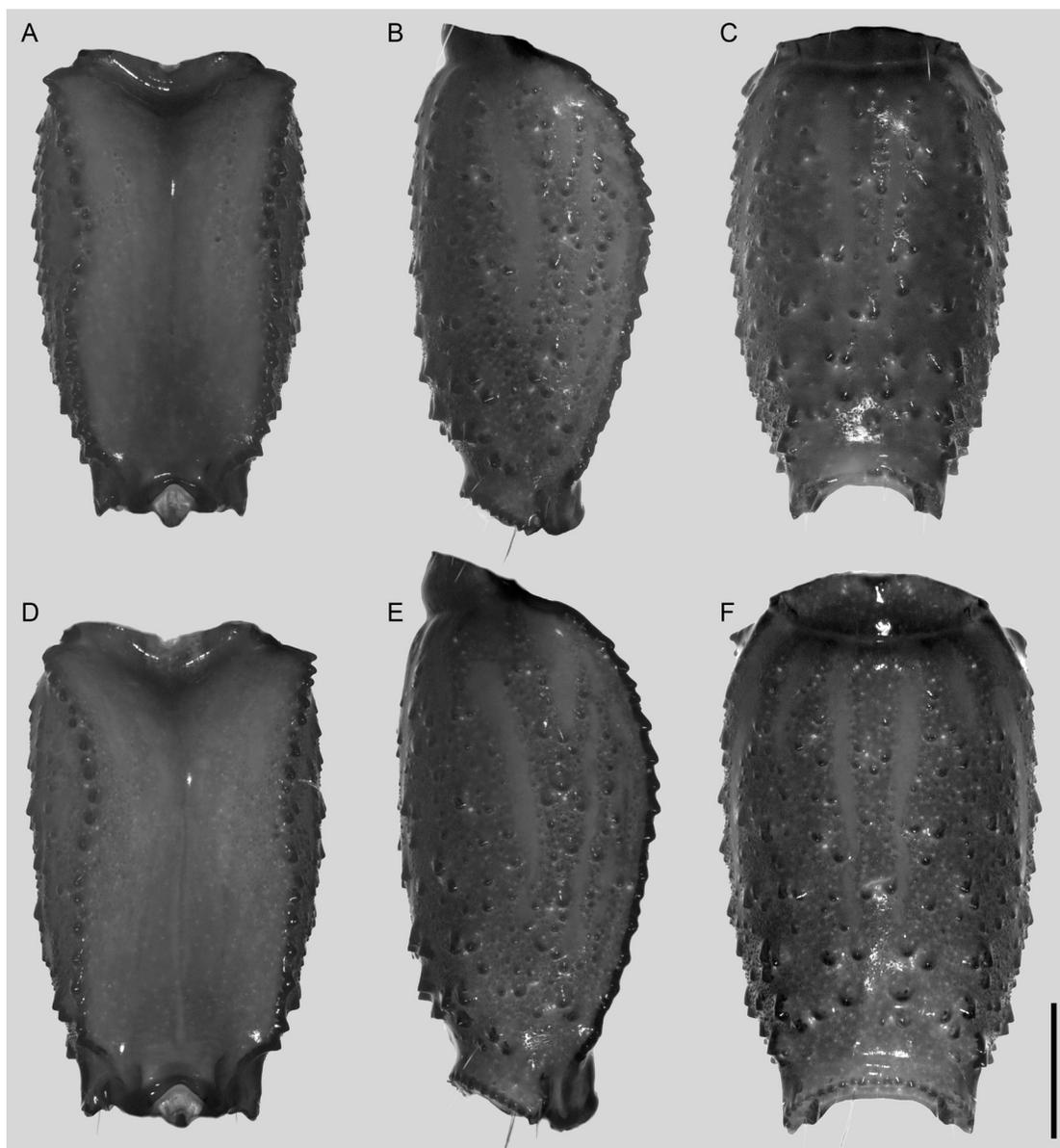


FIGURE 14. *Troglotayosicus ballvei*, sp. nov., metasomal segment V: A, D, dorsal, B, E, lateral, and C, F, ventral aspects. A–C. Paratype ♂ (AMNH IZC 325052). D–F. Holotype ♀ (QCAZ). Scale bar = 1 mm.

two petite ( $et_2$ ,  $esb_2$ ), one accessory ( $em_3$ ): two on ventral surface ( $v_1$ ,  $v_2$ ); 14 on retrolateral surface ( $et_1$ – $et_3$ ,  $est$ ,  $em_1$ – $em_3$ ,  $esb_1$ ,  $esb_2$ ,  $eb_1$ – $eb_5$ ); two on dorsal surface ( $d_1$ ,  $d_2$ ); one on prolateral surface ( $i$ ). Chela with 26 trichobothria (figs. 8, 9), five petite ( $Db$ ,  $dsb$ ,  $Et_4$ ,  $Et_5$ ,  $Esb$ ), one accessory ( $dm$ ): 15 on manus, four on ventral surface ( $V_1$ – $V_4$ ), ten on retrolateral surface ( $Et_1$ – $Et_5$ ,  $Est$ ,  $Esb$ ,  $Eb_1$ – $Eb_3$ ), one on dorsal surface ( $Db$ ); 11 on fixed finger, four on retrolateral surface ( $et$ ,  $est$ ,  $esb$ ,  $eb$ ), five on dorsal surface ( $dt$ ,  $dst$ ,  $dm$ ,  $dsb$ ,  $db$ ), two on prolateral surface ( $it$ ,  $ib$ ).

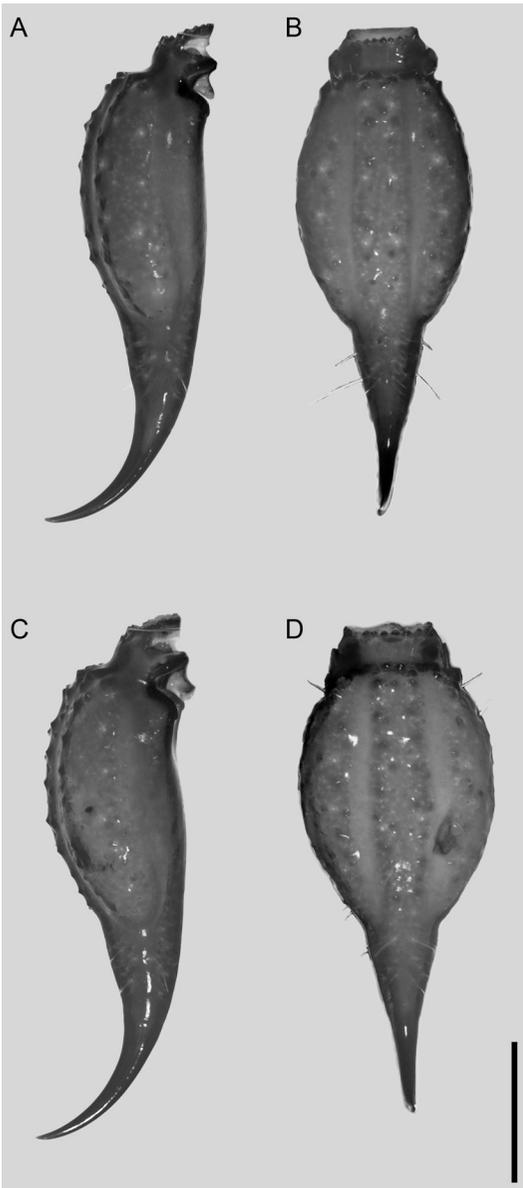


FIGURE 15. *Troglotayosicus ballvei*, sp. nov., telson: **A, C**, lateral and **B, D**, ventral aspects. **A, B**, Paratype ♂ (AMNH IZC 325052). **C, D**, Holotype ♀ (QCAZ). Scale bar = 1 mm.

to lesser extent, proximal tooth larger than others (fig. 6C, D); pectines longer and with larger teeth in ♂.

**STERNITES:** Sternite III, surface finely granular dorsal to pectines (♂) or smooth (♀ and immatures); IV–VI, surfaces smooth; III–VI each with pair of small, rounded spiracles, situated medio-

**LEGS:** Femur with RD carina continuous and incomplete, granular in proximal two-thirds; PV and RV carinae continuous, granular, fusing into single carina in distal third; other carinae absent. Patella predominantly acarinate; RV carina obsolete, comprising row of small, discontinuous granules; other carinae absent. Tibia, basitarsus, and telotarsus acarinate. Tibial spurs absent; prolateral pedal spur present; retrolateral pedal spurs vestigial. Basitarsi of legs I–IV setose; I–III each with retrodorsal, promedian, proventral, and retroventral rows of brushlike spinules distally (fig. 11A–D); retrodorsal brush well developed on all legs; promedian brush well developed on I–III, absent on IV; proventral brush small or obsolete on I, well developed on II and III, absent on IV; retroventral brush small or obsolete, especially on IV. Telotarsi of legs I–IV, dorsomedian lobe with large macroseta; ventral surface without spinules, subspiniform macrosetae regularly arranged into pair of parallel ventrosubmedian rows (fig. 11E), comprising 6 proventral and 7 or 8 retroventral macrosetae on I, 6–7/8 on II, 7–8/8–9 on III, 8/9 on IV; ungues well developed, curved, equal in length; dactyl shorter than ungues.

**TERGITES:** Pretergites smooth. Posttergites I–VI, surfaces finely granular (♂) or predominantly smooth (♀ and immatures), acarinate. Posttergite VII, surface finely granular, posterior half with scattered granules in position of DSM carinae; DL carinae present in posterior half, each terminating in tubercle comprising four or five granules; posterior margin coarsely granular.

**PECTINES:** Pectinal plate wider than long (fig. 6A, B), surface with several macro- and microsetae. Tooth count 7/7; distal tooth and,

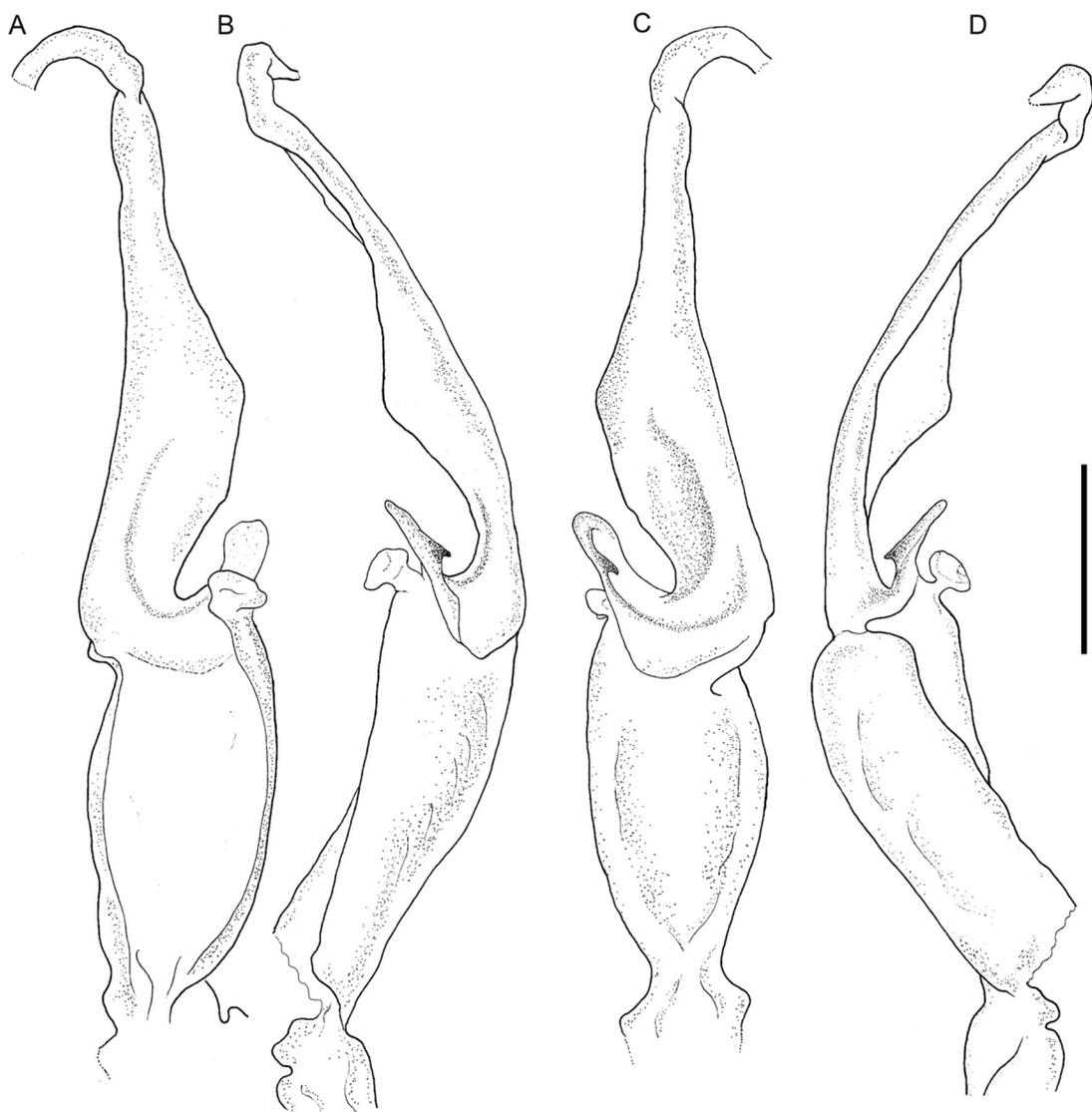


FIGURE 16. *Troglotayosicus ballvei*, sp. nov., paratype ♂ (AMNH IZC 325052), sinistral hemispermaphore: A. ental, B. dorsal, C. ectal, and D. ventral aspects. Scale bar = 0.5 m.

laterally; VII, surface acarinate and entirely smooth (♀ and immatures) or becoming weakly granular laterally (♂); III–VII each densely setose, including along lateral and posterior margins.

**METASOMA:** Segments I–V progressively increasing in length (figs. 12, 13, table 1). Segments I–IV, dorsal intercarinal surfaces finely granular (♂) or predominantly smooth (♀); lateral intercarinal surfaces sparsely granular; ventral intercarinal surfaces smooth on I–III, coarsely to sparsely and finely granular on IV. Segment V, dorsal intercarinal surface sparsely and finely granular; lateral and ventral surfaces densely and coarsely granular, granules increasing in size posteriorly. DL carinae complete, costate-granular, converging posteriorly on segments I–IV (figs. 12A, B, D, E, 13A,

B, D, E), complete, granular on V (fig. 14A, B, D, E); LSM carinae weak, but distinct, each comprising row of granules between DL and ML carinae, in medial third of segments I–V (figs. 12A, B, D, E, 13A, B, D, E, 14B, C, E, F); ML carinae complete, costate-granular on segments I–IV, and complete, but obscured by dense granulation on lateral surfaces of V (figs. 12B, E, 13B, E, 14B, E); LIM carinae less pronounced than DL and LSM carinae, comprising isolated granules, complete on segments I–III, restricted to posterior two-thirds of IV, indistinct on V; VL and VSM carinae absent on segments I–III (figs. 12B, C, 13B, C), comprising discontinuous, coarse granules in medial third of IV (more pronounced in ♂) (figs. 12E, F, 13E, F); VL, VSM, and VM carinae present but indistinct, obscured by granulation, on segment V (figs. 14C, F).

TELSON: Vesicle elongate (fig. 15); anterodorsal lateral lobes present; dorsal and dorsolateral surfaces smooth; ventral and ventrolateral surfaces coarsely granular, with granules arranged in three broad longitudinal stripes (obsolete carinae); with scattered macrosetae and several microsetae. Aculeus long, gently curved, stout basally, slightly tapering distally.

HEMISPERMATOPHORE: Hemispermatophore lamelliform (fig. 16). Lamina translucent and weakly sclerotized, especially distally, broad proximally and medially, and progressively tapering distally; crests absent; apex elongate, terminating in slightly coiled dilation. Capsule simple; ectal lobe (EL) medium sized, with dorsal process, inclined towards ental surface; ental lobe (IL) oval, elongate, larger than EL, with markedly sclerotized ectal spurlike projection; median lobe absent. Articular flexure present; trunk well developed but weakly sclerotized, twice as broad as basal part of lamina.

SUPPLEMENTARY NOTES: The vestigial retrobasal denticle aligned with the base of the serula, reported herein for *T. ballvei*, was mistakenly reported as “vestigial internal basal teeth” in the original description of *T. hirsutus* by Botero-Trujillo et al. (2012: 67).

DISTRIBUTION: *Troglotayosicus ballvei* is known only from the type locality, Sacha Huagra Lodge, 5 km southeast of Archidona, in the Napo Province of Ecuador (fig. 1).

ECOLOGY: The type series of *T. ballvei* was collected at night following rainfall, from the surface of, or slightly below, the leaf litter, inside a dense, primary tropical rainforest (fig. 2A). The habitat at the collection locality is unusual in the presence of what appears to be a system of collapsed underground tunnels or caves (fig. 2B). The soil at the collection site was completely covered by a thick layer of accumulated leaf litter (more than 20 cm deep) and abundant vegetation, some of which had grown on the surface of the “cave” walls that were still erect.

*Troglotayosicus ballvei* is codistributed with three buthids, *Tityus bastosi* Lourenço, 1981, and two species of *Ananteris* Thorell, 1891, *Ananteris ashmolei* Lourenço, 1981, and a smaller unidentified species, and an unidentified species of chactid, *Teuthraustes* Simon, 1878.

ADDITIONAL MATERIAL EXAMINED: **ECUADOR:** *Napo Province:* Río Hollín, on way to Santo Domingo, 5 km SE of Archidona, Sacha Huagra Lodge, 00°57'19.6"S 77°44'58.7"W, 600 m, 29.xi.2009, M.J. Ramírez, C. Grismado, M. Izquierdo, and F. Labarque, 1 juv. (MACN Ar).

#### COMPARATIVE MATERIAL EXAMINED

The following specimens, belonging to other species of *Troglotayosicus*, were examined during the present investigation.

*Troglotayosicus hirsutus* Botero-Trujillo et al., 2012: **COLOMBIA:** *Nariño Department:* Buesaco Municipality: Buesaco, 01°22'39.2"N 77°09'29"W, 1959 m, iii.2011, O.A. Tovar and J.E. Souza, UV light, holotype ♂ (MPUJ SCO 401), paratype ♀ (MPUJ SCO 402); same data, except: J.A. Ochoa, O.A. Tovar, and J.E. Souza, 1–2.xii.2011, 3 juv. ♀ paratypes (MPUJ SCO 405), 1 subad. ♀, 1 juv. ♀ (AMCC [LP 11284]).

*Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009: **COLOMBIA:** *Nariño Department:* Ricaurte Municipality: Vereda Alto Cartagena, Finca Nueva Estrella, 01°13'15.7"N 77°58'08.6"W, 1617 m, 12.ix.2008, R. Botero Trujillo, J.P. Botero, and J.A. Ochoa, 1 ♂, 1 ♀ (MPUJ ENT 46835 old SCO 399), 1 subad. ♀ (AMCC [LP 9311]), 3 juv. (AMCC [LP 9312–9314]).

*Troglotayosicus meijdeni* Botero-Trujillo et al., 2017: **COLOMBIA:** *Huila Department:* Rivera Municipality: Vereda Agua Caliente, area adjacent to Termales Los Ángeles, 880 m, 02°45'06.6"N 75°14'17"W, i.2014, J.C. González Gómez and J.C. Valenzuela Rojas, holotype ♀ (MPUJ ENT 46833), 4 ♀ paratypes (AMCC [LP 13921], ICN AS 1001, MACN Ar), 1 juv. ♂ (MPUJ ENT 46834), 1 juv. ♀ (ICN AS 1002).

#### ACKNOWLEDGMENTS

R.B.-T. was supported by a Theodore Roosevelt Postdoctoral Research Fellowship from the AMNH Richard Gilder Graduate School (RGGS) and U.S. National Science Foundation (NSF) grant DEB 1655050 to L.P. R.B.-T. thanks John J. Flynn (Dean of the RGGS), Rebecca Johnson (RGGS Director of Administration), James M. Carpenter (Chair, AMNH Division of Invertebrate Zoology) and David A. Grimaldi (Acting Chair), and Edward Gaughan (Invertebrate Zoology Administrative Assistant) for support and assistance during the covid-19 pandemic, when this work was completed. The authors thank the curators and managers of institutional collections who loaned material for study: Eduardo Flórez (ICN); Andrés A. Ojanguren-Affilastro, Martín J. Ramírez, and Cristian Grismado (MACN); Dimitri Forero and Giovanny Fagua (MPUJ); Álvaro Barragán and Verónica Crespo Pérez (QCAZ); Steve Thurston (AMNH) for assistance with preparing the plates for this contribution; David Grimaldi and Jessica Ware (AMNH) for identifying the epibionts in figure 6B, D; Martín J. Ramírez and Andrés A. Ojanguren-Affilastro (MACN) for access to space and equipment to R.B.-T. at the MACN; Álvaro Barragán and Emilia Moreno (QCAZ) for assistance and hospitality during the trip to Ecuador; Pío A. Colmenares, Stephanie F. Loria, and Louis N. Sorkin for logistical assistance at the AMNH; Andrés A. Ojanguren-Affilastro and an anonymous reviewer for helpful comments on an earlier draft of the manuscript. Specimens of *T. ballvei* were collected on scientific research authorization (N° 007-14 IC-FAU-DNB/MA) of the Ministry of Environment, Government of Ecuador.

#### REFERENCES

Botero-Trujillo, R., and O.F. Francke. 2009. A new species of troglomorphic leaf litter scorpion from Colombia belonging to the genus *Troglotayosicus* (Scorpiones: Troglotayosicidae). In J.C. Cok-

- endolpher and J.R. Reddell (editors), Studies on the cave and endogean fauna of North America, V. Texas Memorial Museum, Speleological Monographs 7: 1–10. Austin: Texas Memorial Museum, University of Texas.
- Botero-Trujillo, R., J.A. Ochoa, O.A. Tovar, and J.E. Souza. 2012. A new species in the scorpion genus *Troglotayosicus* from forest leaf litter in southwestern Colombia (Scorpiones, Troglotayosicidae). *Zootaxa* 3506: 63–76.
- Botero-Trujillo, R., J.C. González-Gómez, J.C. Valenzuela-Rojas, and L.F. García. 2017. A new species in the troglomorphic scorpion genus *Troglotayosicus* from Colombia, representing the northernmost known record for the genus (Scorpiones, Troglotayosicidae). *Zootaxa* 4244: 568–582.
- Coddington, J.A., G. Giribet, M.S. Harvey, L. Prendini, and D.E. Walter. 2004. Arachnida. In J. Cracraft and M. Donoghue, *Assembling the tree of life*: 296–318. New York: Oxford University Press.
- Dupré, G. 2007. *Conspectus genericus scorpionorum 1758–2006* (Arachnida: Scorpiones). *Euscorpius* 50: 1–31.
- Fet, V., and W.D. Sissom. 2000. Family Troglotayosicidae Lourenço, 1998. In V. Fet, W.D. Sissom, G. Lowe, and M.E. Braunwalder, *Catalog of the scorpions of the world (1758–1998)*: 287–322. New York: New York Entomological Society.
- Fet, V., and M.E. Soleglad. 2005. Contributions to scorpion systematics. I. On recent changes in high-level taxonomy. *Euscorpius* 31: 1–13.
- Francke, O.F. 1985. *Conspectus genericus scorpionorum 1758–1982* (Arachnida: Scorpiones). *Occasional Papers of the Museum, Texas Tech University* 98: 1–32.
- Francke, O.F. 2019. *Conspectus genericus scorpionorum 1758–1985* (Arachnida: Scorpiones) updated through 2018. *Zootaxa* 4657: 1–56.
- Kovařík, F. 1998. Štíři [Scorpiones]. Jihlava, Czech Republic: Madagaskar. [in Czech]
- Loria, S.F., and L. Prendini. 2014. Homology of the lateral eyes of Scorpiones: a six-ocellus model. *PLoS One* 9: e112913.
- Loria, S.F., and L. Prendini. 2018. Ultrastructural comparison of the eyespot and ocelli of scorpions, and implications for the systematics of Chaerilidae Pocock, 1893. *Zoologischer Anzeiger* 273: 183–191.
- Lourenço, W.R. 1981. Scorpions cavernicoles de l'Équateur: *Tityus demangei* n. sp. et *Ananteris ashmolei* n. sp. (Buthidae); *Troglotayosicus vachoni* n. gen., n. sp. (Chactidae), scorpion troglobie. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 3: 635–662.
- Lourenço, W.R. 1998. Panbiogéographie, les distributions disjointes et le concept de famille relictuelle chez les scorpions. *Biogeographica* 74: 133–144.
- Nenilin, A.B., and V. Fet. 1992. Зоогеографический анализ мировой фауны скорпионов (Arachnida Scorpiones) [Zoogeographical analysis of the world scorpion fauna (Arachnida: Scorpiones)]. *Arthropoda Selecta* 1: 3–31. [in Russian; extended English summary]
- Ochoa, J.A., R. Botero-Trujillo, and L. Prendini. 2010. On the troglomorphic scorpion *Troglotayosicus humiculum* (Scorpiones, Troglotayosicidae), with first description of the adults. *American Museum Novitates* 3691: 1–19.
- Prendini, L. 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): an exemplar approach. *Cladistics* 16: 1–78.
- Prendini, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109–186.
- Prendini, L., and W.C. Wheeler. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. *Cladistics* 21: 446–494.

- Prendini, L., O.F. Francke, and V. Vignoli. 2010. Troglomorphism, trichobothriotaxy and typhlochactid phylogeny (Scorpiones, Chactoidea): more evidence that troglobitism is not an evolutionary dead-end. *Cladistics* 26: 117–142.
- Prendini, L., V.L. Ehrenthal, and S.F. Loria. 2021. Systematics of the relictual Asian scorpion family Pseudochactidae Gromov, 1998, with a review of cavernicolous, troglobitic, and troglomorphic scorpions. *Bulletin of the American Museum of Natural History* 453: 1–149.
- Sánchez-Vialas, A., J. Blasco-Aróstegui, J. García-Gila, and W.R. Lourenço. 2020. A new species of *Troglotayosicus* Lourenço, 1981 (Scorpiones: Troglotayosicidae) from southern Ecuador. *Arachnology* 18: 612–618.
- Sissom, W.D. 1990. Systematics, biogeography, and paleontology. In G.A. Polis (editor), *The biology of scorpions*: 64–160. Stanford, CA: Stanford University Press.
- Sissom, W.D. 2000a. Family Chactidae Pocock, 1893. In V. Fet, W.D. Sissom, G. Lowe, and M.E. Braunwalder, *Catalog of the scorpions of the world (1758–1998)*: 287–322. New York: New York Entomological Society.
- Sissom, W.D. 2000b. Family Superstitioniidae Stahnke, 1940. In V. Fet, W.D. Sissom, G. Lowe, and M.E. Braunwalder, *Catalog of the scorpions of the world (1758–1998)*: 496–500. New York: New York Entomological Society.
- Sissom, W.D., and J.C. Cokendolpher. 1998. A new troglobitic scorpion of the genus *Typhlochactas* (Superstitionidae) from Veracruz, Mexico. *Journal of Arachnology* 26: 285–290.
- Sissom, W.D., G.A. Polis, and D.D. Watt. 1990. Field and laboratory methods. In G.A. Polis (editor), *The biology of scorpions*: 445–461. Stanford, CA: Stanford University Press.
- Soleglad, M.E., and V. Fet. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius* 11: 1–175.
- Soleglad, M.E., and W.D. Sissom. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. In V. Fet and P.A. Selden (editors), *Scorpions 2001. In memoriam Gary A. Polis*: 25–111. Burnham Beeches, U.K.: British Arachnological Society.
- Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. *Entomological News* 81: 297–316.
- Stahnke, H. 1972. U.V. light, a useful field tool. *BioScience* 22: 604–607.
- Stockwell, S.A. 1989. Revision of the phylogeny and higher classification of Scorpiones (Chelicerata). Ph.D. dissertation, University of California, Berkeley, 413 pp.
- Stockwell, S.A. 1992. Systematic observations on North American Scorpionida with a key and checklist of the families and genera. *Journal of Medical Entomology* 29: 407–422.
- Tropea, G., and C. Onnis. 2020. A remarkable discovery of a new scorpion genus and species from Sardinia (Scorpiones: Chactoidea: Belisariidae). *Arachnida – Rivista Aracnologica Italiana* 26: 3–25.
- Vachon, M. 1952. Études sur les scorpions. Alger: Institut Pasteur d'Algérie, 482 pp.
- Vachon, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 35: 161–166.
- Vachon, M. 1974 (“1973”) Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 140: 857–958.
- Vignoli, V., and L. Prendini. 2009. Systematic revision of the troglomorphic North American scorpion family Typhlochactidae (Scorpiones: Chactoidea). *Bulletin of the American Museum of Natural History* 326: 1–94.