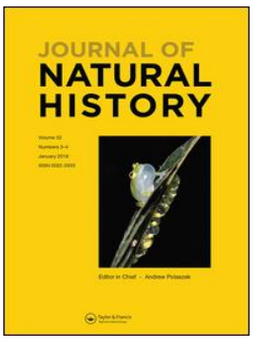

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The Neotropical genus *Hapalotremus* Simon, 1903 (Araneae: Theraphosidae), with the description of seven new species and the highest altitude record for the family

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ABSTRACT

New specimens of the genus *Hapalotremus* (Theraphosinae) are revised based on the examination of types and additional material collected in Argentina, Bolivia and Peru. A new generic diagnosis is proposed. New information and illustrations are provided for known species and seven new species were recognized and are newly described and illustrated. Hence, *Hapalotremus* comprises 10 valid species, distributed along the Andes and Yungas in western South America. All species are keyed and mapped. New taxonomic features are included in the descriptions and the detail of embolus keels morphology and positions are described for the first time for the genus. Information on species habitat is included. The highest altitude record for a Theraphosidae spider, living at 4524 m above sea level, is reported.

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Introduction

Theraphosidae is the most speciose family among Mygalomorphae, which comprises 143 genera and 959 nominal species (World Spider Catalog [Internet] 2017) and includes some of the largest spiders in the world. Theraphosinae contains about half of all known theraphosid species and is known only from the New World, primarily the Neotropics (Pérez-Miles et al. 2008; Ortiz and Francke 2017).

Hapalotremus Simon, 1903 comprises tarantula species found at altitudes between 1300 and 4500 m in the biogeographic regions of Puna and Yungas from Argentina, Bolivia and Peru. In 1903, Simon described *Hapalotremus albipes* Simon, 1903 without a specific locality other than Bolivia, based on a single adult male. Remarkably, this species shows a white spot pattern on the dorsal surface of the abdomen and white pubescence on the dorsal surface of the legs (Simon 1903). Gerschman de Pikelín and Schiapelli (1973) revised the holotype of

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H. albipes and illustrated the palpal bulb and the tibial apophysis of leg I. In 1993, Schmidt described a female of *H. albipes* based on a single specimen from Bolivia with no further details on specific locality. In addition, this author illustrated the spermatheca for the first time, comprising a single spermathecal receptacle with superior lateral edges of equal width to the bases (Schmidt 1993). Pérez-Miles and Locht (2003) revised the genus *Hemirrhagus* Simon, 1903 and transferred *Hemirrhagus major* Chamberlin, 1916, a species from Cusco Valley in southern Peru, at c. 2800 m to *Hapalotremus* because it lacked the diagnostic features of *Hemirrhagus*. Recently, Cavallo and Ferretti (2015) described one new species from Argentina, *Hapalotremus martinorum* Cavallo and Ferretti, 2015, based on specimens from Salta Province. In 1923, Mello-Leitão established three genera from Brazil: *Dolichothele* Mello-Leitão, 1923 with *Dolichothele exilis* Mello-Leitão, 1923 as type species, based on a female from the state of Paraíba; *Goniodontium* Mello-Leitão, 1923 with *Goniodontium muticum* Mello-Leitão, 1923 as type species, based on a female from the state of Bahia; and *Cyclothorax* Mello-Leitão, 1923, type species *Cyclothorax cyclothorax* Mello-Leitão, 1923, based on a male from the state of Rio de Janeiro. Then, Strand (1929) replaced the name *Cyclothorax* with *Cyclothoracoides*, because the former was pre-occupied. Later, Raven (1985) considered the three genera as junior synonyms of *Hapalotremus* after the examination of the holotypes. Schmidt (2002) stated that *Dolichothele* is not a synonym of *Hapalotremus*, and considered the genus as *incertae sedis* belonging to the Ischnocolinae, because the description of the genus was based on a female. However, the transfer was not accepted by Platnick (2002). Recently, Cavallo and Ferretti (2015) proposed *Hapalotremus cyclothorax* (Mello-Leitão, 1923) as a junior synonym of *Homoeomma montanum* (Mello-Leitão, 1923) and *Hapalotremus scintillans* (Mello-Leitão, 1929) as a junior synonym of *Pachistopelma rufonigrum* Pocock, 1901. Unfortunately, these authors made no comments about the synonymy of *Cyclothoracoides* with *Homoeomma* Ausserer, 1871. However, Lucas and Indicatti (2015) considered *Cyclothoracoides* as a junior synonym of *Homoeomma*, so confirming the synonymy proposed by Cavallo and Ferretti (2015). Moreover, Lucas and Indicatti (2015), through the examination of the holotypes, revalidated *Dolichothele* and its type species, therefore *D. exilis* was restored. Also, *Hapalotremus muticus* is considered a junior synonym of *D. exilis* (Lucas and Indicatti 2015). In 1948, the genus *Sickius* Soares and Camargo, 1948, was established, and named the type species *Sickius longibulbi* Soares and Camargo, 1948, based on a single male from the state of Mato Grosso, Brazil. Later, Raven (1985, p. 159) considered *Sickius* to be a junior synonym of *Hapalotremus* for 'which it shared conformation of the tibial spur and the associated bent metatarsus (both of the first leg)'; however, he stated that the type was never examined. In 2002, Bertani and da Silva examined the type species and revalidated *Sickius* and its type species, transferring the monotypic genus from the subfamily Theraphosinae to Ischnocolinae.

Examination of theraphosid material collected in Argentina, Bolivia and Peru from several institutions revealed undescribed material of *Hapalotremus*. Seven new species were recognized from this material and are newly described from Huancarayoc, Michi Michani Cunca, Ollachea–Corani, Upis and Usicayos–Quetapalo from Peru; Sacaba from Bolivia; and Tafí del Valle from Argentina. Moreover, a new generic diagnosis is proposed for *Hapalotremus* to include newly discovered taxonomic features, along with amendments to the diagnosis of three previously described species. An identification key to the males and females of the genus is provided, herein. Distribution maps for all the species are presented.

Material and methods

Morphology

The general descriptive format follows Bertani (2001) and Raven (2005). For morphometrics, the measurements were taken with an ocular micrometre (Olympus SZ40 stereomicroscope) and a digital caliper to the nearest 0.001 mm. All measurements were taken by N. Ferretti, P. Cavallo and D. Ríos-Tamayo. All appendage measurements were taken on the left side and dorsal views. Lengths of leg articles were taken from the mid-proximal point of articulation to the mid-distal point of the article (*sensu* Coyle 1995; fig. 1 and Bond 2012; figs 11–16). Terminology for tibial apophyses (or spurs) follows the general usage in Theraphosidae and it includes the prolateral apophysis (or apophysis branch) and retrolateral apophysis (e.g. Bertani 2001; Pérez-Miles et al. 2008). Male palpal organ keel terminology follows Bertani (2000). Female genitalia were dissected and cleared in concentrated lactic acid for 60–120 minutes and spermathecae were photographed from their dorsal view. Urticating setae terminology follows Cooke et al. (1972) and Bertani and Guadanucci (2013). Trichobothrial terminology and position follows Guadanucci (2012). Number and disposition of spines are counted from the proximal third to the distal third (modified from Petrunkevitch 1925). Photographs by N. Ferretti were taken with a Leica S8 APO and with a SONY Hv200v digital camera mounted to an Olympus SZ stereoscopic microscope, scanning electron micrographs were taken with a JEOL 35CF. Photographs by R. West were taken with an OMAX 9 MP digital camera mounted to an AmScope SM-3TZ-54S-5M trinocular stereomicroscope, aided by Helicon Focus 6 stacking software. Photographs by D. Ríos-Tamayo were taken with a 2500 Moticam 5 MP digital camera mounted to a Motic SMZ168 trinocular stereomicroscope. Photographs and most of the data of the type specimens of *H. albipes* were provided by Fernando Pérez-Miles and Fabian Vol. Maps were made by N. Ferretti using the Geographical System Information software QGIS 2.18 Las Palmas (available at www.qgis.org).

Abbreviations of characters used in theraphosid morphological studies

A, apical keel; AK, accessory keel; ALE, anterior lateral eyes; ALP, apical lateral projections; AME, anterior median eyes; BP, basal projection; D, dorsal; DMR, dorsal median region; P, prolateral; PB, prolateral branch of tibial apophysis; PI, prolateral inferior keel; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; PME, posterior median eyes; PMS, posterior median spinnerets; PS, prolateral superior keel; R, retrolateral; RB, retrolateral branch of tibial apophysis.

Materials from the following institutions were examined

AMNH, American Museum of Natural History, New York, USA; LZI, Laboratorio de Zoología de Inverterbrados II, Universidad Nacional del Sur, Bahía Blanca, Argentina. MACN-Ar, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard, USA; MHNC–B,

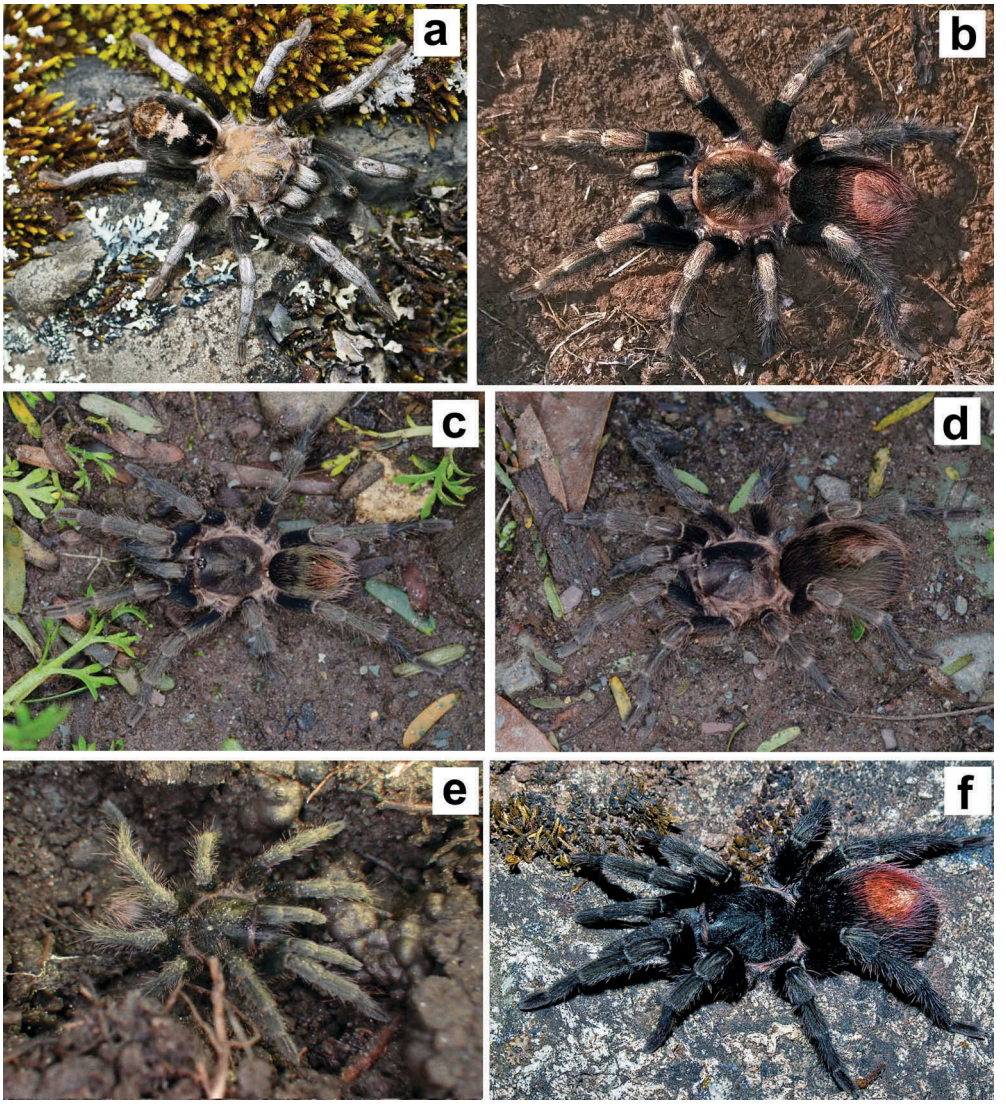

Figure 1. (a–f) *Hapalotremus* spp. habitus. (a) *Hapalotremus albipes*, female. (b) *Hapalotremus major*, female. (c, d) *Hapalotremus martinorum*. (c) Male. (d) Female. (e) *Hapalotremus chasqui* sp. nov., juvenile. (f) *Hapalotremus marcapata* sp. nov., female. Photos: a: Mauricio Pacheco Suarez; b: Juan Chaparro; c, d: Patricio Cavallo; e: Laura Montes de Oca; f: Josh Richards.

Museo Nacional de Historia Natural, Bolivia; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MLP, Museo de La Plata, La Plata, Argentina; MUBI, Museo de Biodiversidad del Peru, Cusco, Peru (this collection was part of Museo de Historia Natural, Universidad Nacional de San Antonio Abad, Cusco, Peru); MUSM-ENT, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; SMF, Senckenberg Museum, Frankfurt am Main, Germany.

Taxonomy

Family **THERAPHOSIDAE** Thorell, 1869
Subfamily **THERAPHOSINAE** Thorell, 1870
Genus ***HAPALOTREMUS*** Simon, 1903
(Figures 1–37)

Dolichothele Mello-Leitão, 1923: 120; Raven 1985: 152.
Goniodontium Mello-Leitão, 1923: 127. Raven 1985: 153.
Cyclothoracoides Strand 1929: 17; Raven 1985: 151.

Type species

Hapalotremus albipes Simon, 1903 by monotypy.

Species included

Hapalotremus albipes Simon, 1903, *Hapalotremus carabaya* sp. nov., *Hapalotremus chasqui* sp. nov., *Hapalotremus chespiritoi* sp. nov., *Hapalotremus kuka* sp. nov., *Hapalotremus major* (Chamberlin, 1916), *Hapalotremus marcapata* sp. nov., *Hapalotremus martinorum* Cavallo and Ferretti, 2015, *Hapalotremus perezmilesi* sp. nov., *Hapalotremus vilcanota* sp. nov.

Etymology

The Greek adjective *Hapal*, followed by the Greek connective vowel *o*, followed by the Greek noun *trêma*, followed by the Latin suffix *us* meaning of or pertaining to. Hence, the derivative compound name *Hapalotremus* 'of the soft hole', possibly refers to the way it lives in a soft hole in the ground. Gender would be masculine.

Generic diagnosis

Hapalotremus resembles *Hapalopus* Ausserer, 1875 and *Davus* Pickard-Cambridge, 1892 by having the metatarsus I strongly curved (Pérez-Miles et al. 1996; Bertani 2000; Gabriel 2016). However, males of *Hapalotremus* differ from those of *Davus* in the shape of male palpal bulb without a twisted embolus and from those of *Hapalopus* by having a longer and curved embolus with a continuous PI (split in two in *Hapalopus*), also by a shorter tibia I and by the shape of the spermathecae on females without having a membranous base. *Hapalotremus* also resembles *Schizopelma* Pickard–Cambridge, 1897; since females have one single spermathecal receptacle (Pérez-Miles et al. 1996; Gabriel 2016), but differ in male characteristics: lacking a bifid embolus on palpal bulb and tibial apophysis with two branches. Additionally, representatives of *Hapalotremus* can be characterized by the combination of the following characters: presence of red or white setae on the dorsum of the abdomen (Figures 1, 2) and a labium bearing a reduced number of cuspules (about 4 to 12) (Figure 5d, e), excepting on *H. martinorum*, *H. chasqui* sp. nov. and *H. kuka* sp. nov. (more than 20 cuspules). Males and females are also characterized by presenting a slightly developed scopula or no scopulae on apical metatarsus IV (Figure 6c) and by having a small field of strong short spiniform setae on basal

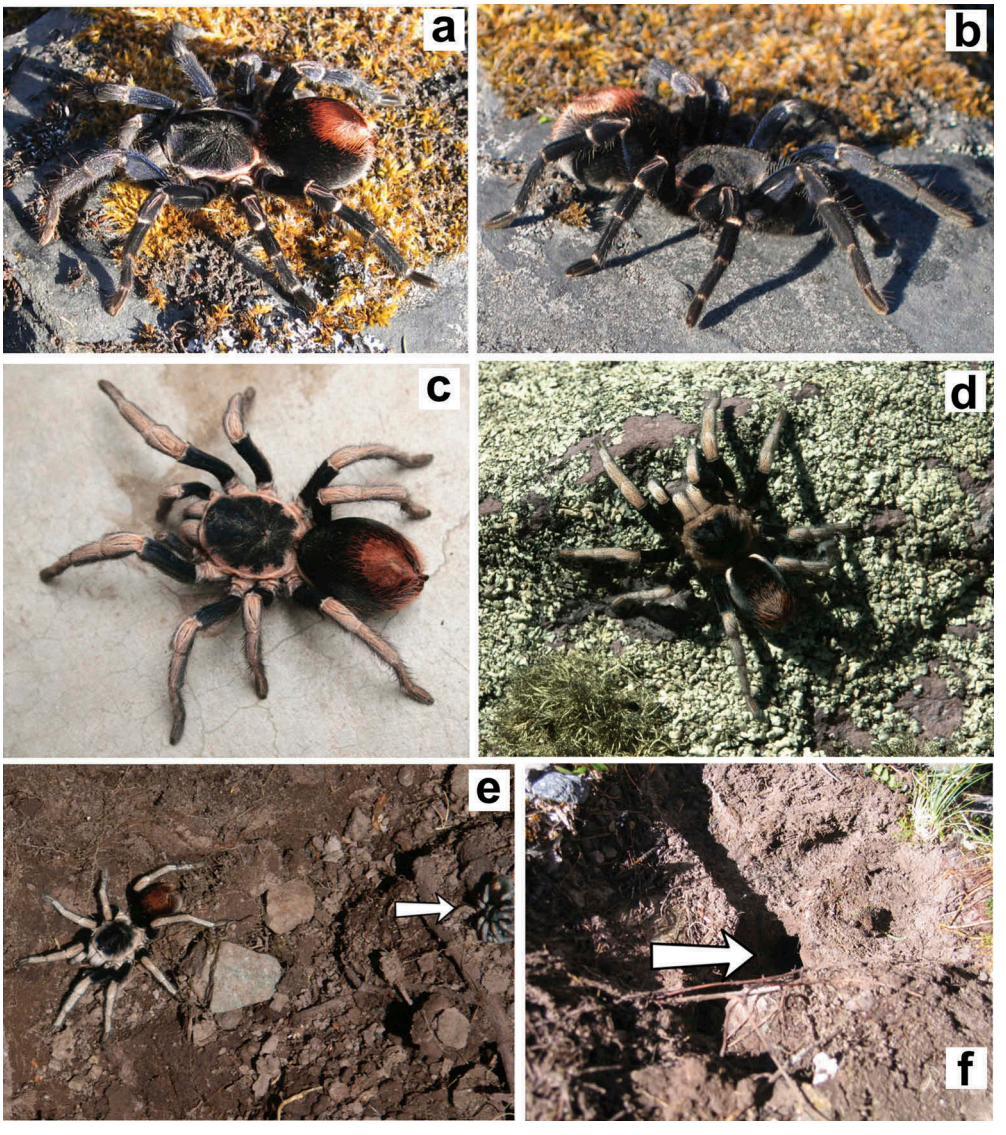

Figure 2. (a–f) *Hapalotremus* spp. Habitus. (a, b) *Hapalotremus carabaya* sp. nov., female holotype. (c, d) *Hapalotremus vilcanota* sp. nov., female. (e) *Hapalotremus vilcanota* sp. nov., female and juvenile (white arrow) found under the same stone. (f) *Hapalotremus vilcanota* sp. nov. burrow. Photos: a, b, d–f: Tracie Seimon; c: Josh Richards.

retrolateral coxal face of palp and legs I–IV (Figure 6b). Additionally, males are further distinguished by showing the following combination of characters: short tibia I, more than 10% shorter than metatarsus I (Figure 7g) with the exception of *H. martinorum* (Figure 13g) and *H. major* (Figure 10g) (tibia I roughly the same length as metatarsus I or longer), tibia I with two apophyses which originate from a common base (Figures 7f, 10f), curved metatarsus I (Figures 7g, 10g), presence of a rounded retrolateral process on male palpal tibia (Figures 7h,i, 11c,d, 13h,i), palpal bulb with digitiform apophysis (Figure 8b) and prolateral inferior keel presenting a ventral crest (blunt or pointed)

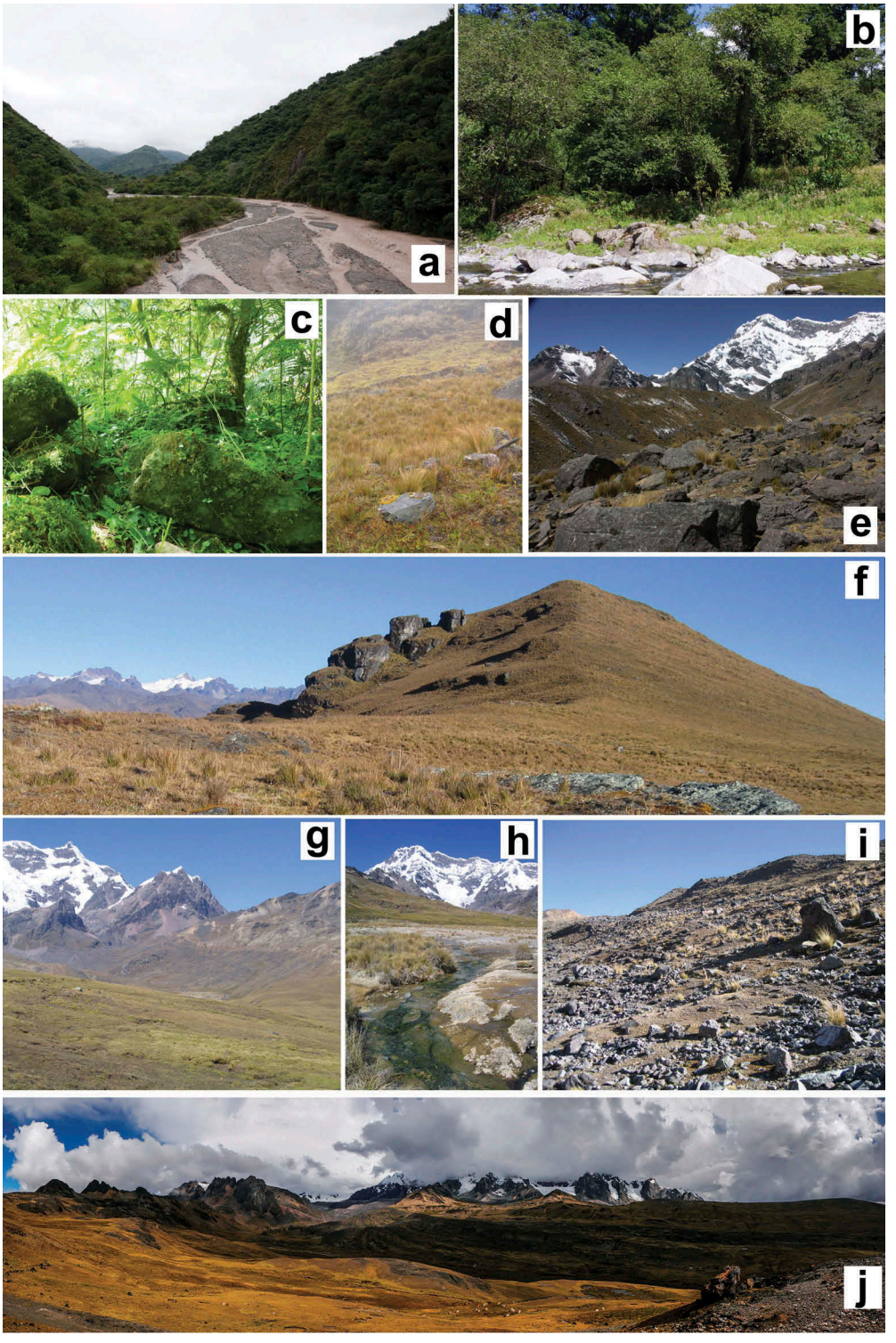

Figure 3. (a–j) *Hapalotremus* spp. habitat. (a) Escoipe River, next to route 33, Salta Province, Argentina, type locality of *Hapalotremus martinorum*. (b, c) Los Sosa River, next to route 307, Tucumán Province, Argentina, habitat of *Hapalotremus chasqui* sp. nov. (d, f) Cordillera Carabaya, Michi Michani Cunca, type locality of *Hapalotremus carabaya* sp. nov. (e, g–j) Cordillera Vilcanota, Upis, type locality of *Hapalotremus vilcanota* sp. nov. Photos: a: Patricio Cavallo; b: Gabriel Pompozzi; c: Laura Montes de Oca; d–i: Tracie Seimon; j: Josh Richards.

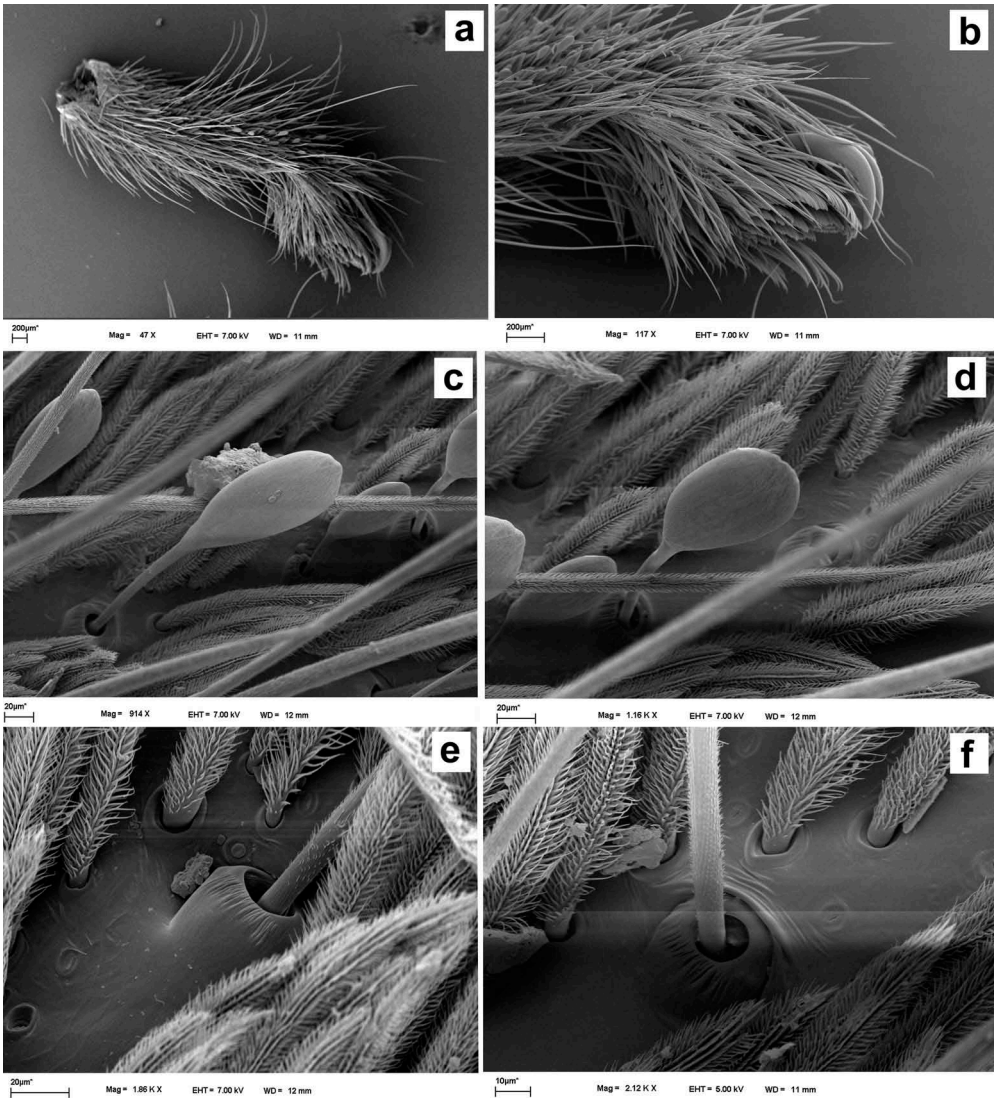

Figure 4. (a–f) *Hapalotremus vilcanota* sp. nov., female paratype (MUSM-ENT 0508680). (a, b) Tarsus IV, prolateral view. (c, d) Non-plumose clavate tarsal trichobothria. (e, f) Filiform tarsal trichobothria. Photos: Nelson Ferretti.

(Figure 6d, f). Females are distinguished by having a single oblong spermathecal receptacle with a basal portion usually wider than apically and the presence of basal and apical lateral projections (Figure 6e).

Distribution and habitat

The genus is endemic to South America and is mostly distributed in the western Andean region from central Peru in the north to northwestern Argentina in the south (Figures 36, 37). Specimens of *Hapalotremus* clearly show habitat preferences involving high-altitude cloud forests (Figure 3a–c) and grassy rocky mountains (Figure 3d–j). Specimens can be

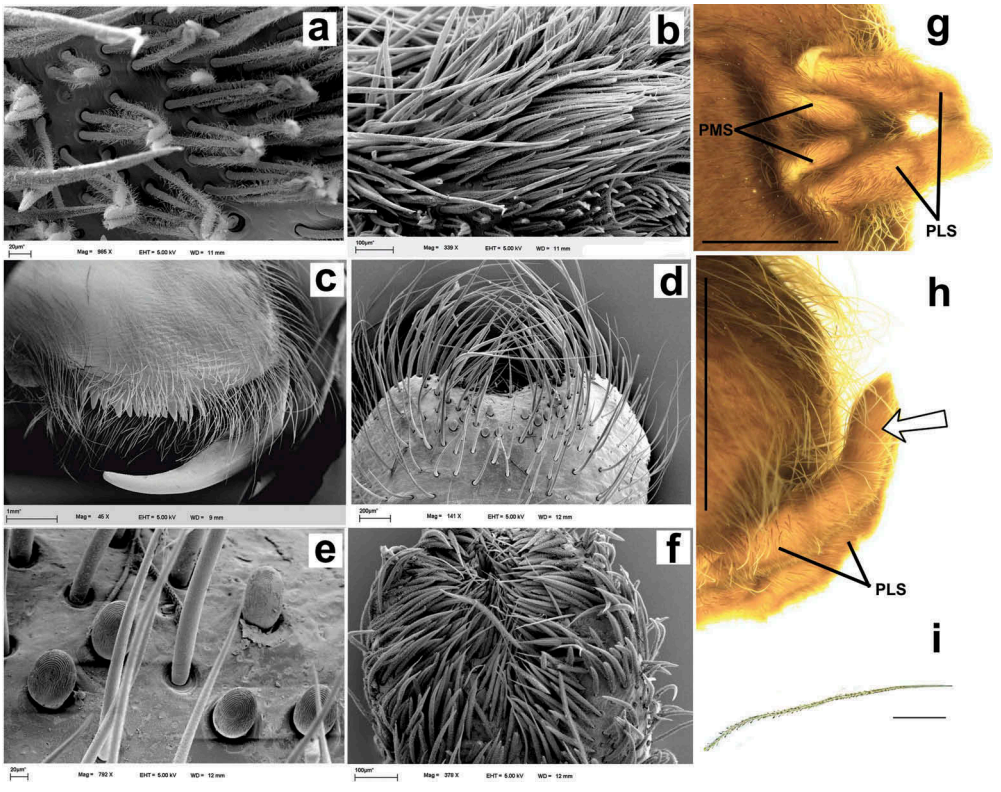

Figure 5. (a–i) *Hapalotremus vilcanota* sp. nov., female paratype (MUSM-ENT 0508680). (a, b) Ventral tarsus IV. (a) Detail of scopulae. (b) Detail of long conical setae dividing the scopulae. (c) Right chelicerae. (d) Labium. (e) Cuspules. (f) Posterior median spinnerets, apical end. (g) Ventral view of spinnerets. (h) Lateral view of posterior lateral spinnerets (arrow indicates the apical segment). (i) Type III urticating setae. PLS, posterior lateral spinnerets; PMS, posterior median spinnerets. Scale bara: g, h: 1 mm; i: 0.1 mm. Photos: Nelson Ferretti.

found among fallen logs or under rocks; they make short burrows like other theraphosid spiders (Figure 2e, f), with one or more co-existing. Some species can be found at very high altitudes in the Andean region, with records of more than 4500 m above sea level (a.s.l.) (Figure 3d–j). As far as we know, *Hapalotremus* are the only known theraphosid spiders in the world found living at such high elevation (up to 4524 m a.s.l.). Some of the highest elevations recorded for Theraphosidae are those of *Haplocosmia himalayana* (Pocock, 1899) (about 2100 m a.s.l.) (Pocock 1899), *Aguapanela arvi* Perafán, Cifuentes and Estrada–Gómez, 2015 (up to 2400 m a.s.l.) (Perafán et al. 2015), *Cyriocosmus* spp. (up to 3000 m a.s.l.) (Pérez-Miles and Weinmann 2009), *Euathlus* spp. (up to 3200 m a.s.l.) (Perafán and Pérez-Miles 2014; Ferretti 2015) and recently described species of *Bistriopelma* Kaderka, 2015 with elevation records up to 4398 m a.s.l. (Kaderka 2015).

Description

Chelicerae without rastellum (Figure 5c). Clypeus narrow. Overall shape of eye group rectangular (Figures 9g, 10d, 12c, 13d). Eye tubercle elevated, wider than long. Anterior

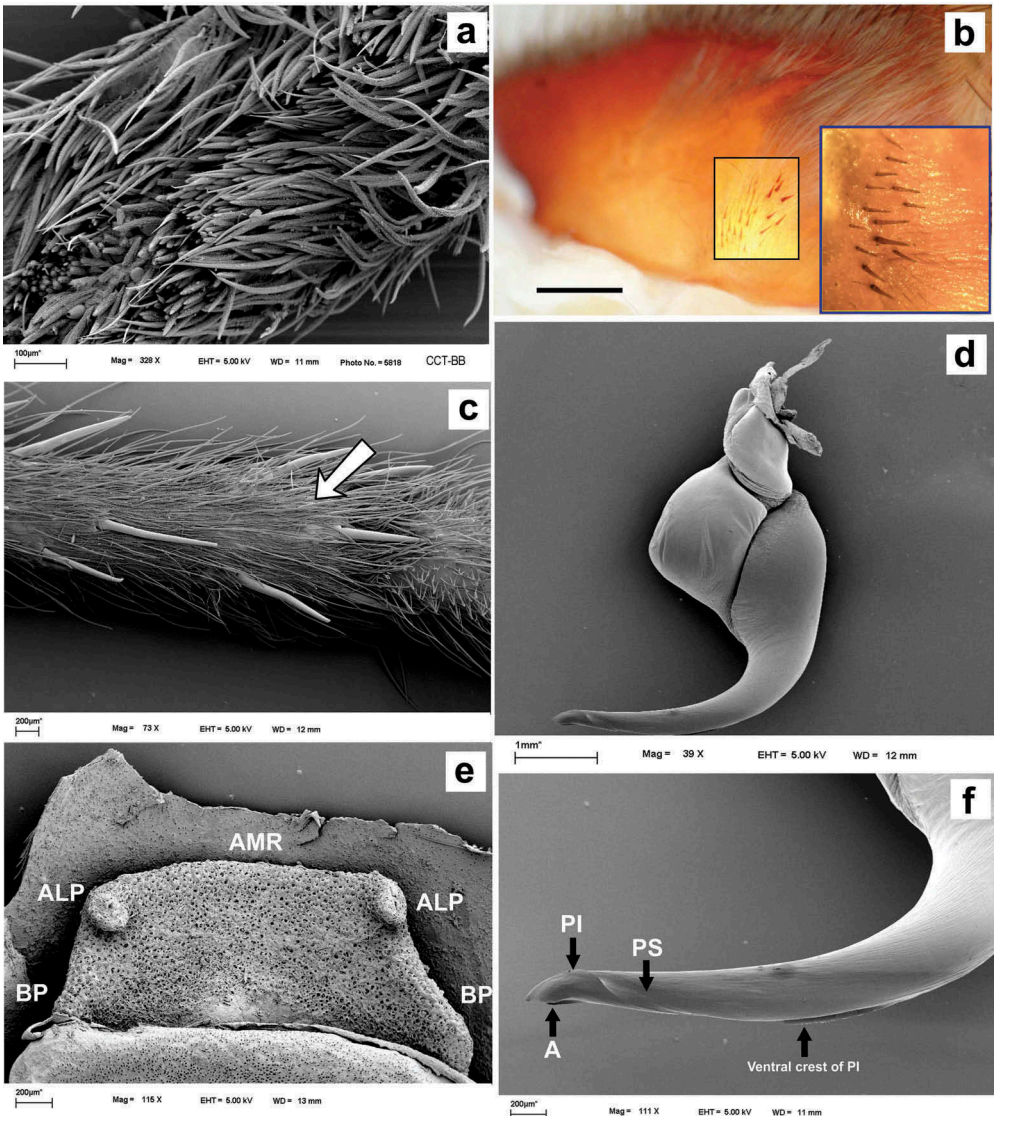

Figure 6. (a–c, e) *Hapalotremus vilcanota* sp. nov., female paratype (MUSM-ENT 0508680). (d, f) *Hapalotremus perezmilesi* sp. nov., holotype male (MUBI). (a) Posterior lateral spinneret, distal segment. (b) Retrolateral view of palpal coxae. (c) Ventral metatarsus IV. (d) Male right palpal bulb, prolateral view. (e) Spermathecae, ventral view. (f) Detail of embolus: A: apical keel, PI: prolateral inferior keel, PS: prolateral superior keel. ALP, apical lateral projection; AMR, apical median region; BP, basal projection. Scale bar: b: 1 mm. Photos: Nelson Ferretti.

eye row procurved, posterior recurved. Males and females with oval carapace, both with fovea straight or slightly procurved (Figures 7a, 9a, 12a). Intercheliceral tumescence absent. One row of big teeth on cheliceral promargin furrow and a group of small teeth on retromargin (Figure 5c). Labium slightly wider than long or subequal, with about 4–27 conspicuous blunt cuspules on the subapical margin (Figure 5d, e). Endites with distinct anterior lobe, with 53–126 blunt cuspules on inner basoventral surface. Sternum oval, six

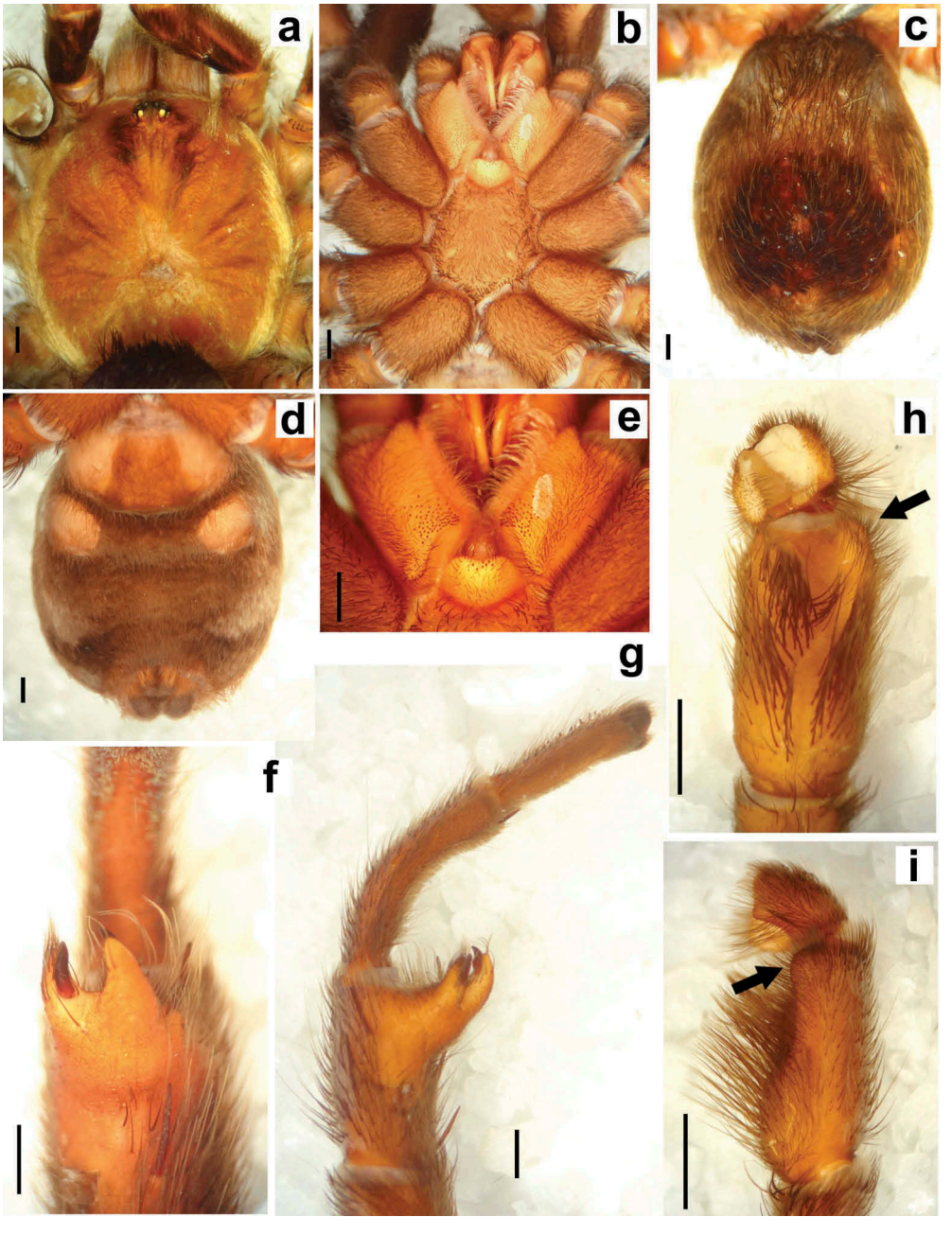

Figure 7. (a–i) *Hapalotremus albipes*, male from Botijlaca, Bolivia (AMNH). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. (e) Labium and maxillae, ventral view. (f) Tibial apophysis, ventral view. (g) Leg I, lateral view. (h) Palpal tibia, ventral view. (i) Palpal tibia, retrolateral view. Arrows indicate the rounded process. Scale bar: 1 mm. Photos: Nelson Ferretti.

sternal sigillae, median and posterior away from margin by about one length or next to margin, oval-elongated or oval-rounded in *H. carabaya* sp. nov. Urticating hairs: typical type III (Figure 5i) occurring in a patch on central dorsum of the abdomen (Figures 1, 2a–d).

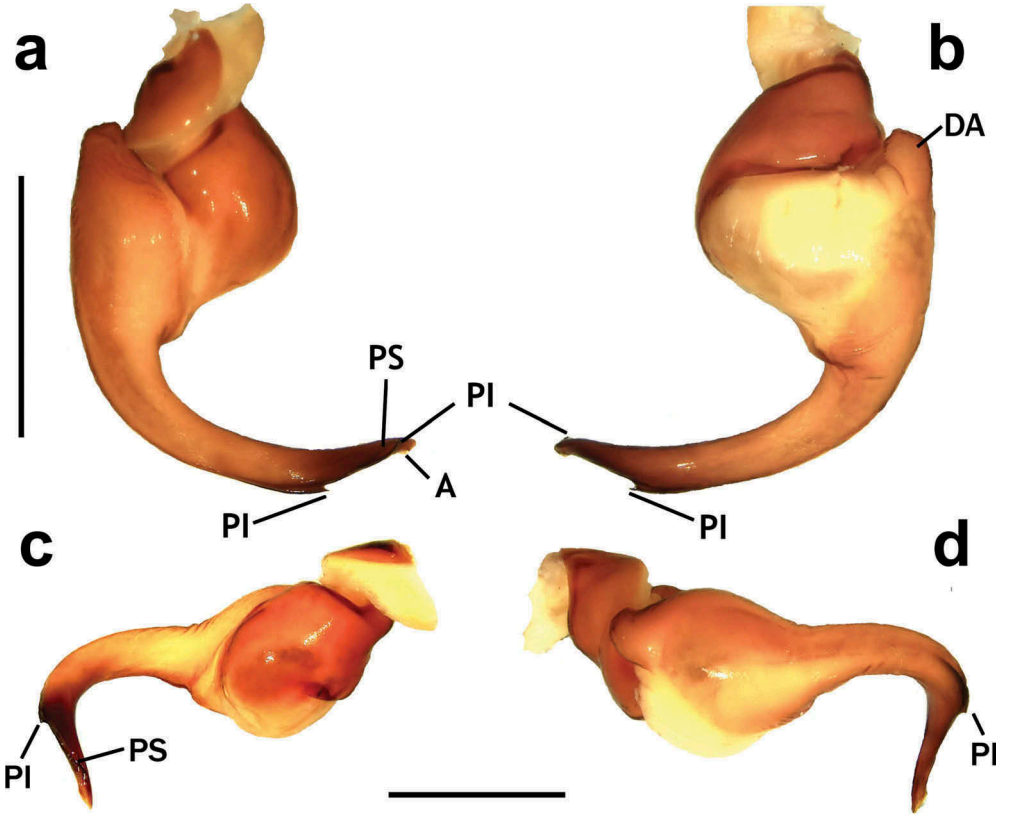

Figure 8. (a–d) *Hapalotremus albipes*, male from Botijlaca, Bolivia (AMNH). Male left palpal bulb. (a) Prolateral view. (b) Retrolateral view. (c) Dorsal view. (d) Ventral view. A, apical keel; DA, digitiform apophysis; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Nelson Ferretti.

Stridulatory apparatus absent. Trichobothria: tarsi I–IV (males and females): dorsally, two parallel rows of non-plumose clavate trichobothria (Figure 4c,d) interspersed with filiform (Figure 4e, f), separated by a row of long, thin setae. On metatarsi and tibia only filiform trichobothria. All tarsi without pseudosegmentation (Figure 4a, b). Males and females, scopulae: ventrally, all tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV (Figure 5a, b). Metatarsi I–III scopulate, entire or divided by conical long setae; metatarsus IV with no scopulae, almost inconspicuous (Figure 6c) or well-developed apical scopulae (only in *H. kuka* sp. nov.) (Figure 27f). Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV (Figure 6b). Female palpal claw without teeth. Superior tarsal claw of all tarsi with one row with few small teeth. Third claw absent on all tarsi. Claw tufts well-developed on all tarsi (Figure 4b). Four spinnerets (Figure 5g): posterior lateral spinnerets three-segmented with digitiform apical segment (Figure 5g, h); posterior median spinnerets entire (Figure 5f, g). Tibia I of males usually short (shorter than metatarsus I) (Figure 7g) with tibial apical apophysis originated from a common base, protruded and formed by two branches (prolateral and retrolateral) (Figure 7f, 10f, 13g, 19e, 23g, 30f), which are subequal or retrolateral slightly larger (except in *H. martinorum* with a

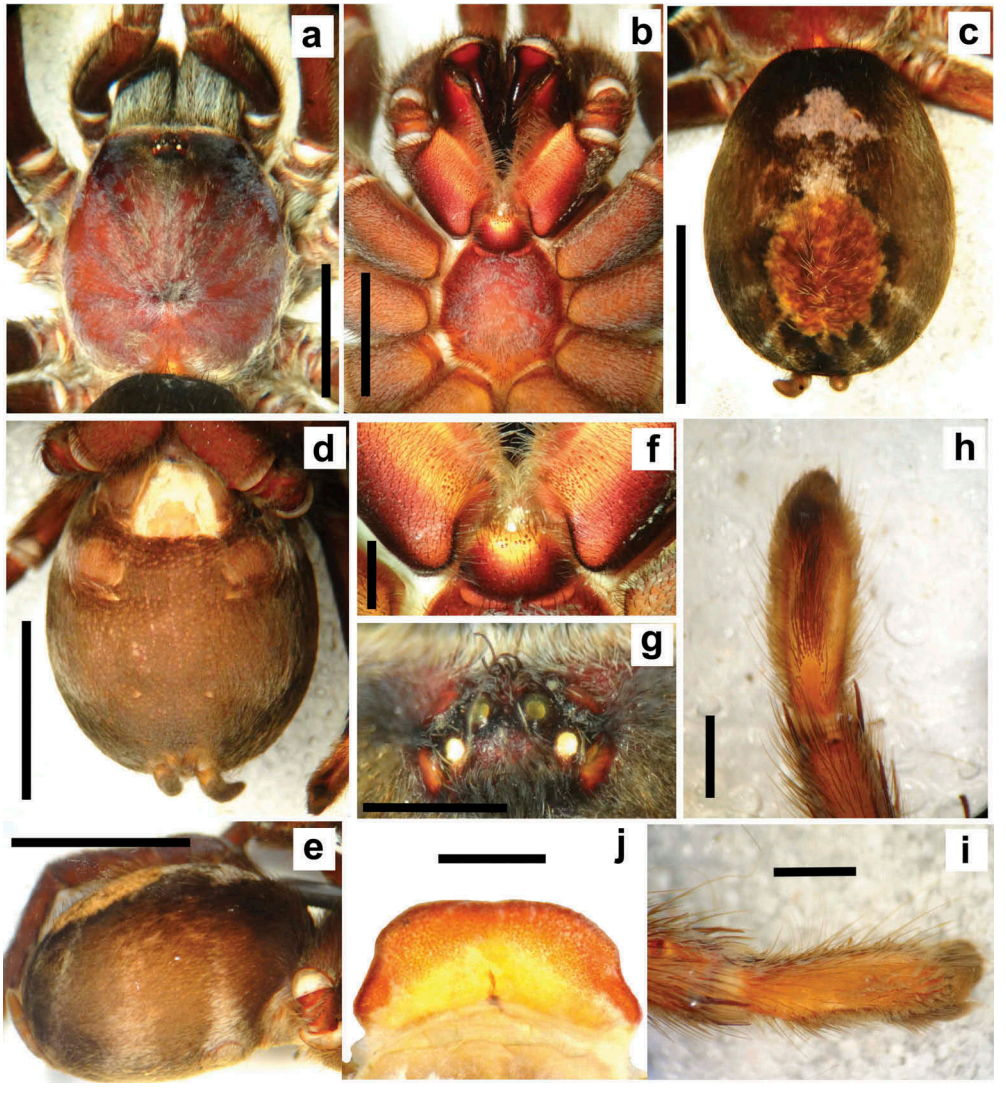

Figure 9. (a–j) *Hapalotremus albipes*, female from La Paz, Bolivia (MHNC–B). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. (e) Abdomen, lateral view. (f) Labium and maxillae, ventral view. (g) Eyes, dorsal view. (h) Tarsus IV, ventral view. (i) Tarsus IV, prolateral view. (j) Spermathecae, dorsal view. Scale bars: a–e: 5 mm; f–j: 1 mm. Photos: Nelson Ferretti.

noticeably larger retrolateral branch, Figure 13f, g). Prolateral branch with a basal ventral strong spine, and retrolateral with a shorter spine on inner face (except in *H. chasqui* sp. nov. bearing two spines). Metatarsus I curved and close outside the tibial apophysis branches (*H. albipes*, *H. chasqui* sp. nov. and *H. martinorum*) or between the two branches (*H. chespiritoi* sp. nov., *H. major* and *H. perezmilesi* sp. nov.). Male with palpal tibia with a retrolateral rounded process (Figure 7h, i). Palpal bulb globose at base with a large extended subtegulum. A basal digitiform apophysis well-developed (*H. albipes*, *H. major*, *H. martinorum* and *H. chespiritoi* sp. nov.) (Figure 8b) or absent (*H. chasqui* sp. nov. and

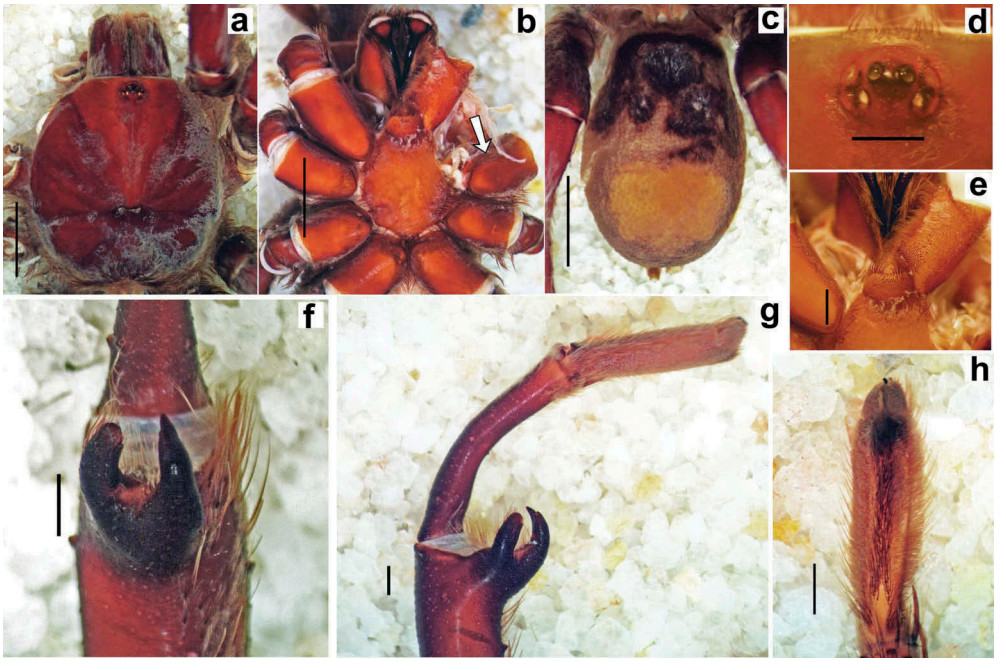

Figure 10. (a–h) *Hapalotremus major*, male holotype (MCZ 142). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Eyes, dorsal view. (e) Labium and maxillae. (f) Tibial apophysis, ventral view. (g) Leg I, lateral view. (h) Tarsus IV, ventral view. Arrow indicates the spiniform setae on coxa. Scale bars: a–c: 5 mm; d–h: 1 mm. Photos: Rick West.

H. perezmilesi sp. nov.) (Figure 20a) on male palpal bulb. Embolus thick, subcylindrical, strongly curved to the retrolateral side, bearing two prolateral keels (superior and inferior) with a slight development (Figure 31a–d) or well-developed and strong (Figure 8a–d). The prolateral inferior keel presents a ventral crest blunt (Figure 31a, b) or pointed (Figure 24a, b). Genitalia of females consists of one oval (Figure 29e) or oblong (Figure 33e) receptacle with an apical median region domed (Figure 29e), straight (Figure 33e) or depressed (Figure 9j) and apical lateral projections varying in a more lateral (Figure 26e) or apical location (Figure 22e) and in development (Figure 6e).

Hapalotremus albipes Simon, 1903
(Figures 1a, 7–9, 36)

Hapalotremus albipes: Simon, 1903: 930, fig. 1083. Gerschman De Pikelín and Schiapelli 1973: 72, figs 63–67. Schmidt 1986: 41, fig. 12. Schmidt 1993: 10, figs 1–6. Schmidt, 1993: 66, figs 101–103. Pérez-Miles et al. 1996: 52, fig. 23. Schmidt, 1997: 16, figs 76–79. Vol 1999: 11, fig. K. Schmidt 2003: 127, figs 111–114. Cavallo and Ferretti 2015: 878, fig. 3c.

Type material
Male holotype (MNHN) from Bolivia, Chaco. Male holotype not examined, only photos provided by F. Vol.

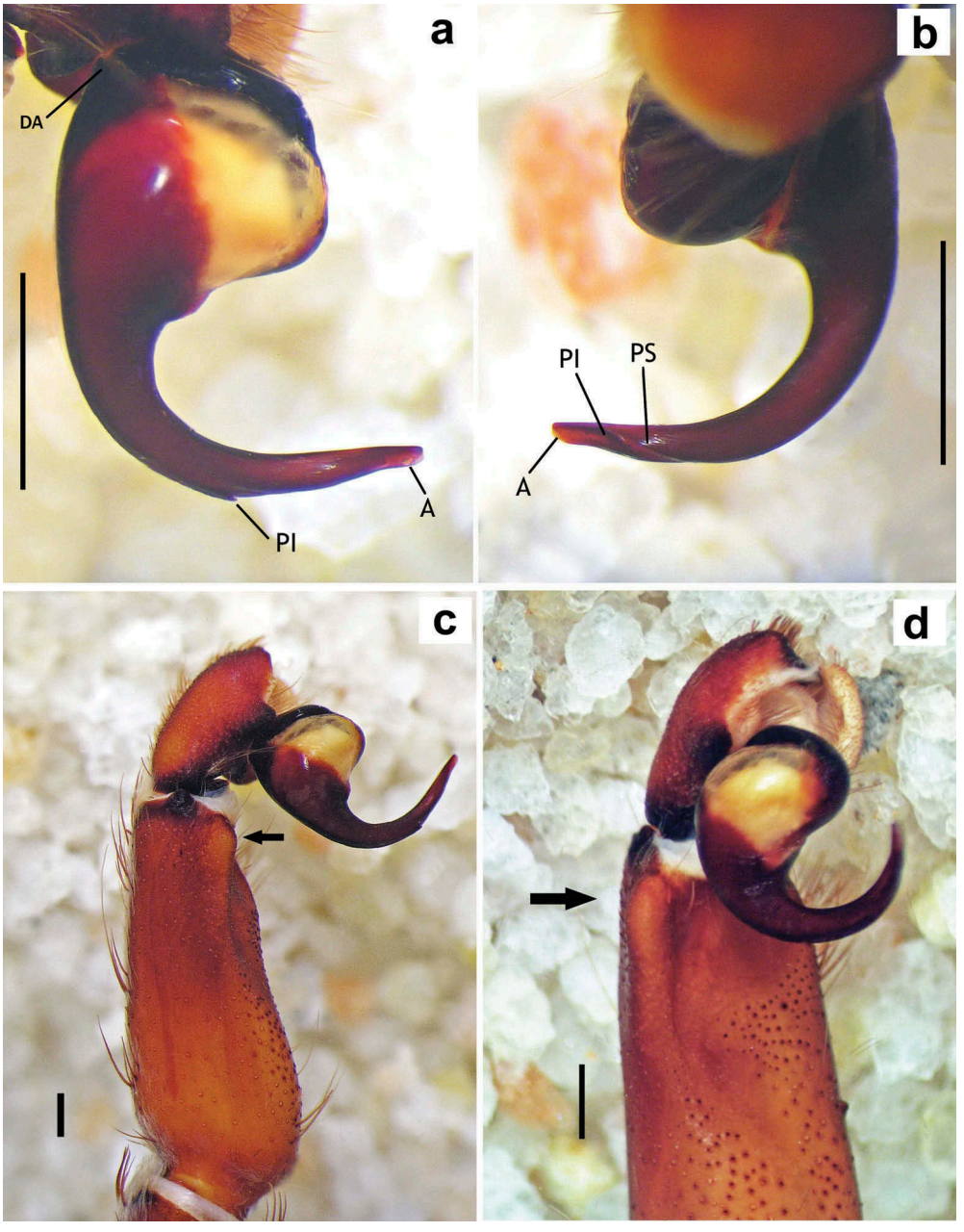

Figure 11. (a–d) *Hapalotremus major*, male holotype (MCZ 142). (a, b) Male right palpal bulb. (a) Retrolateral view. (b) Prolateral view. (c. d) Palpal tibia. (c) Palpal tibia, retrolateral view. (d) Palpal tibia, ventral view. Arrows indicate the rounded process. A, apical keel; DA, digitiform apophysis; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Rick West.

Additional material examined

Three females (SMF37093) from Bolivia, P. Klass col, only illustrations provided by F. Pérez-Miles; one female (MHNC–B) from Bolivia, La Paz, Murillo, Pongo, 3 km from Unduavi, 3600 m a. s.l., 7 July 1991, E. Peñaranda col.; two females (MHNC–B) from Bolivia, La Paz, Sud Yungas

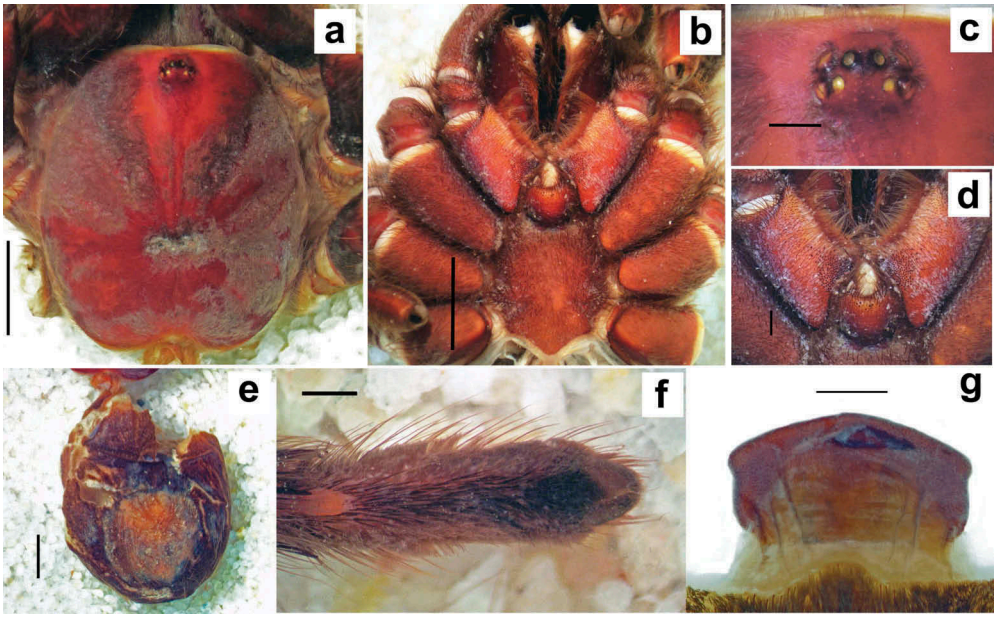

Figure 12. (a–g) *Hapalotremus major*, female paratype (MCZ 143). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Eyes, dorsal view. (d) Labium and maxillae. (e) Abdomen, dorsal view. (f) Tarsus IV, ventral view. (g) Spermathecae, dorsal view. Scale bars: a–b, e: 5 mm; c–d, f–g: 1 mm. Photos: Rick West.

Province, Unduavi, 3660 m a.s.l., 1 November 1990, E. Peñaranda col.; six females and 10 immatures (AMNH) from Bolivia, Oruro, from a point between Coscapa to La Paz, 3200 m a.s.l., 24 October 1984, L. E. Peña col.; one male (AMNH) from Bolivia, La Paz, Pacajes, Botijlaca (-16.1919 S, -68.1403 W), 3600 m a.s.l., 2 October 1984, L. E. Peña col.

Etymology

A compound word whose first element is the Latin adjective *albus* meaning white, and the second element is the genitive Latin noun *pes* meaning foot, that refers to the distinctive white-legged coloration (Simon 1903).

Amended diagnosis

The following character combination, modified from Schmidt (1993), is diagnostic for *H. albipes*. Carapace and legs entirely covered dorsally with white setae, except femora of legs and palps, which are dark grey (Figures 1a, 7a, 9a), abdomen dark with rounded dorsal median patch of reddish-orange urticating setae, and two or three white spots dorsally (more noticeably on females), the bigger spot is arrow-shaped, and with three or four white lines posterior laterally in each side of abdomen, reaching the urticating patch (Figures 1a, 9c, d). Labium wider than long bearing a reduced number of cuspules (6–13) (Figures 7e, 9b, f). Absence of spiniform setae on pro- and retrolateral coxal faces of legs I–IV. Metatarsi IV with no scopulae (Figure 9h). Male tibia I very short, more than 20% shorter than metatarsus I (Figure 7g). Male palpal tibia with retrolateral rounded process developed (Figure 7h, i). Palpal bulb base with a basal digitiform apophysis well-developed (Figure 8a–d); embolus

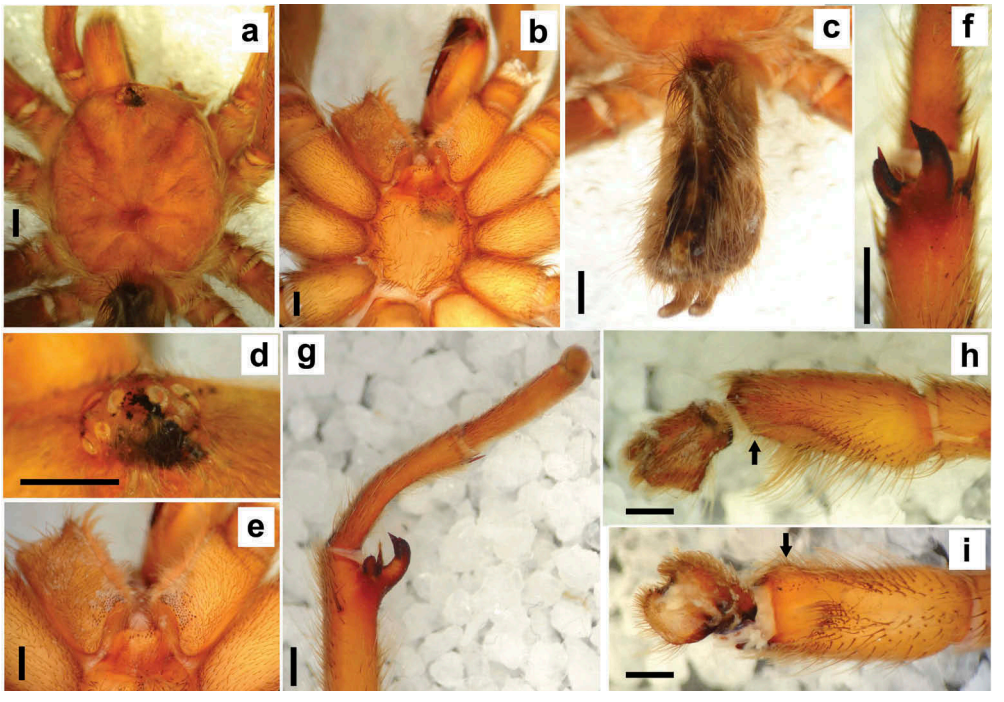

Figure 13. (a–i) *Hapalotremus martinorum*, male holotype (MLP 19152). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Eyes, dorsal view. (e) Labium and maxillae, ventral view. (f) Tibial apophysis, ventral view. (g) Leg I, lateral view. (h) Palpal tibia, retrolateral view. (i) Palpal tibia, ventral view. Arrows indicate the rounded process. Scale bar: 1 mm. Photos: Nelson Ferretti.

thick and very curved to the retrolateral face and prolateral keels slightly developed; PI bearing a ventral medial crest pointed at distal end and located half way forward of embolus (Figure 8a, b). Female spermathecae consist of one receptacle with basal portion slightly wider than apical, apical lateral projections slightly developed and apical median region depressed (Figure 9j). Urticating setae: type III present on male and female and arranged in a dorsal median patch on the abdomen (Figures 7c, 9c).

Variation (from additional material examined)

Total length, females (n = 3): 26.7–29.8 (mean = 28.3 ± 1.5SD); carapace length, females: 12.4–13.8 (13.1 ± 0.7); length of palp and legs, females: palp 17.8–20.4 (18.9 ± 1.3), I 25.4–31.5 (27.9 ± 3.1), II 24.2–28.3 (26 ± 2.07), III 23.6–25.5 (24.8 ± 1.04), IV 31.4–33.4 (32 ± 1.15). Labial cuspules, females 10–13, maxillary cuspules, right 91–120, left 96–118.

Distribution and habitat

The holotype male described by Simon (1903) gives no indication other than 'Chaco' for the type locality and this involves a large region in Bolivia. In the same way, Schmidt (1993) described the female of *H. albipes* for the first time but did not provide a locality for those specimens, only 'Bolivia'. A specimen of *H. albipes* is shown in Figure 1a and was located in La Paz (Bolivia) at about 4252 m a.s.l., near the type locality. Here, we provide records of this

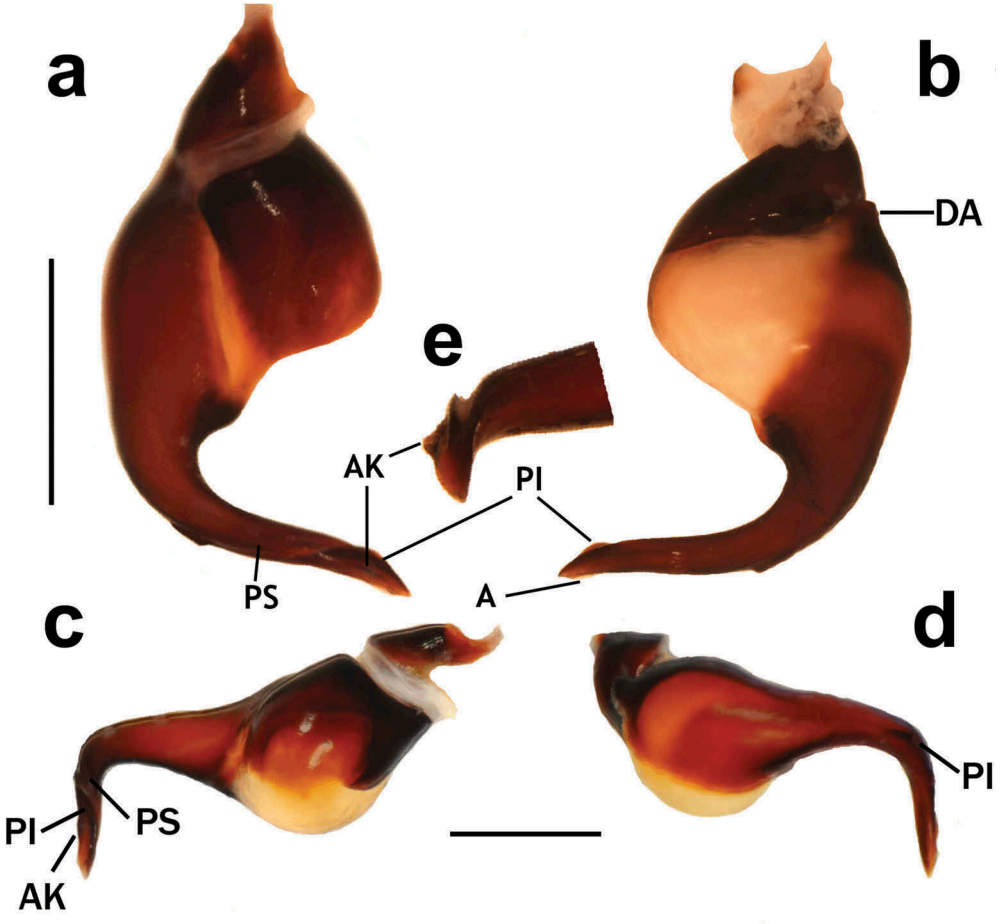

Figure 14. (a–e) *Hapalotremus martinorum*, male holotype left palpal bulb (MLP 19152). (a) Prolateral view. (b) Retrolateral view. (c) Dorsal view. (d) Ventral view. (e) Embolus showing keels. A, apical keel; AK accessory keel; DA, digitiform apophysis; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Nelson Ferretti.

species for Unduavi, Coscapa and Botijlaca (among 3200 and 3600 m a.s.l.), Bolivia (Figure 36). These sites are located east of Cordillera Real on the edge of the Yungas region, which constitutes a transition between the highlands of the Andes and the tropical lowlands of the Amazon rainforests. The annual average temperature of this area is 17.4°C with monthly average values ranging from 15°C in June and 19°C in December. The average annual precipitation is 725 mm, with a dry season from May to August and a wet season from December to February (www.censosbolivia.ine.gob.bo).

Hapalotremus major (Chamberlin, 1916)
(Figures 1b, 10–12, 36)

Hemirrhagus major: Chamberlin, 1916: 198, fig. 8. Pérez-Miles and Locht, 2003: 366.

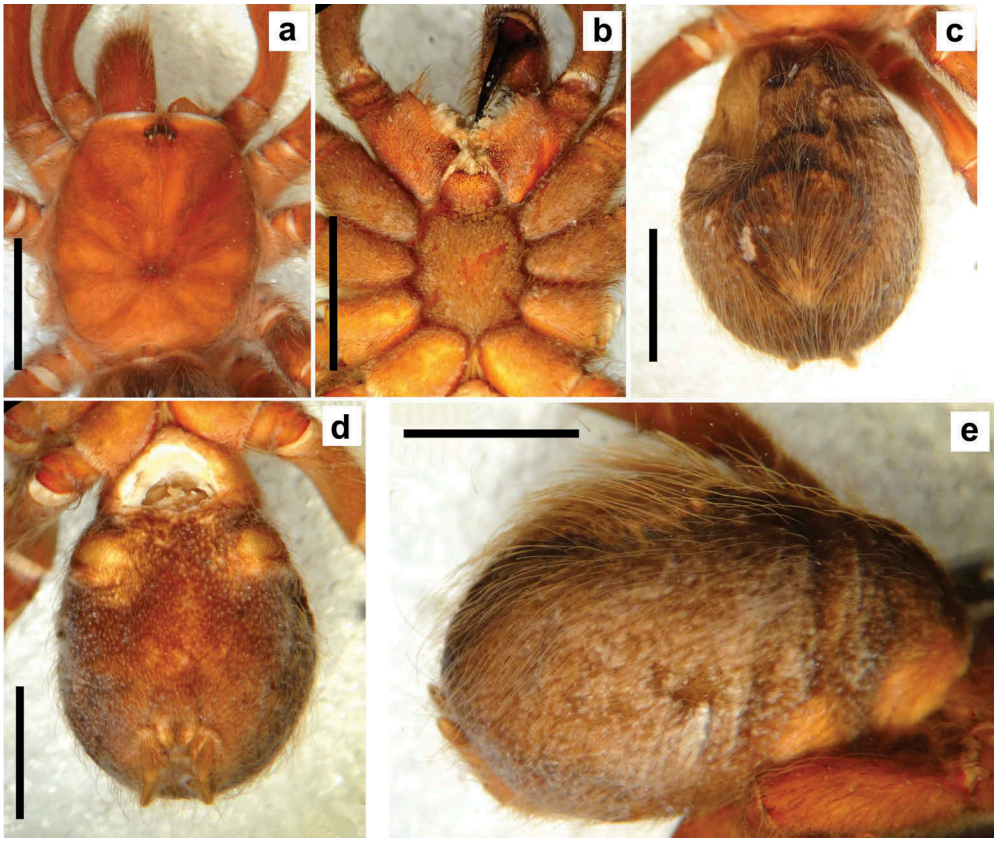

Figure 15. (a–e) *Hapalotremus martinorum*, female paratype (MLP 19153). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. (e) Abdomen, lateral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Type material

Male holotype (MCZ 142) from Peru, Cusco, Cusco Valley (Cuzco), E.D. Flint col. (A. Agassiz, April 1875), missing left palp and embolus, examined; one paratype female (MCZ 143) from Peru, Cusco, Cusco Valley (Cuzco), E.D. Flint col. (A. Agassiz, April 1875), examined.

Etymology

A Latin adjective meaning greater or larger (Chamberlin 1916).

Notes

Data labels of *H. major* holotype male (MCZ 142) and paratype female (MCZ 143) state 'Peru: Cuzco Valley, Coll.: E. D. Flint (rec.'d per A. Agassiz, Apr. 1875)'. Alexander Agassiz was curator of the Museum of Comparative Zoology, Cambridge, between 1874 and 1885, and made collection trips to Peru during that period. It is possible that the collector, E.D. Flint, either presented these two specimens to Alexander Agassiz while he was at the MCZ, or while he was in Peru. Both specimens were later described by Chamberlin (1916) in *Bulletin of the Museum of Comparative Zoology* entitled '*Results of the Yale Peruvian Expedition of 1911. The*

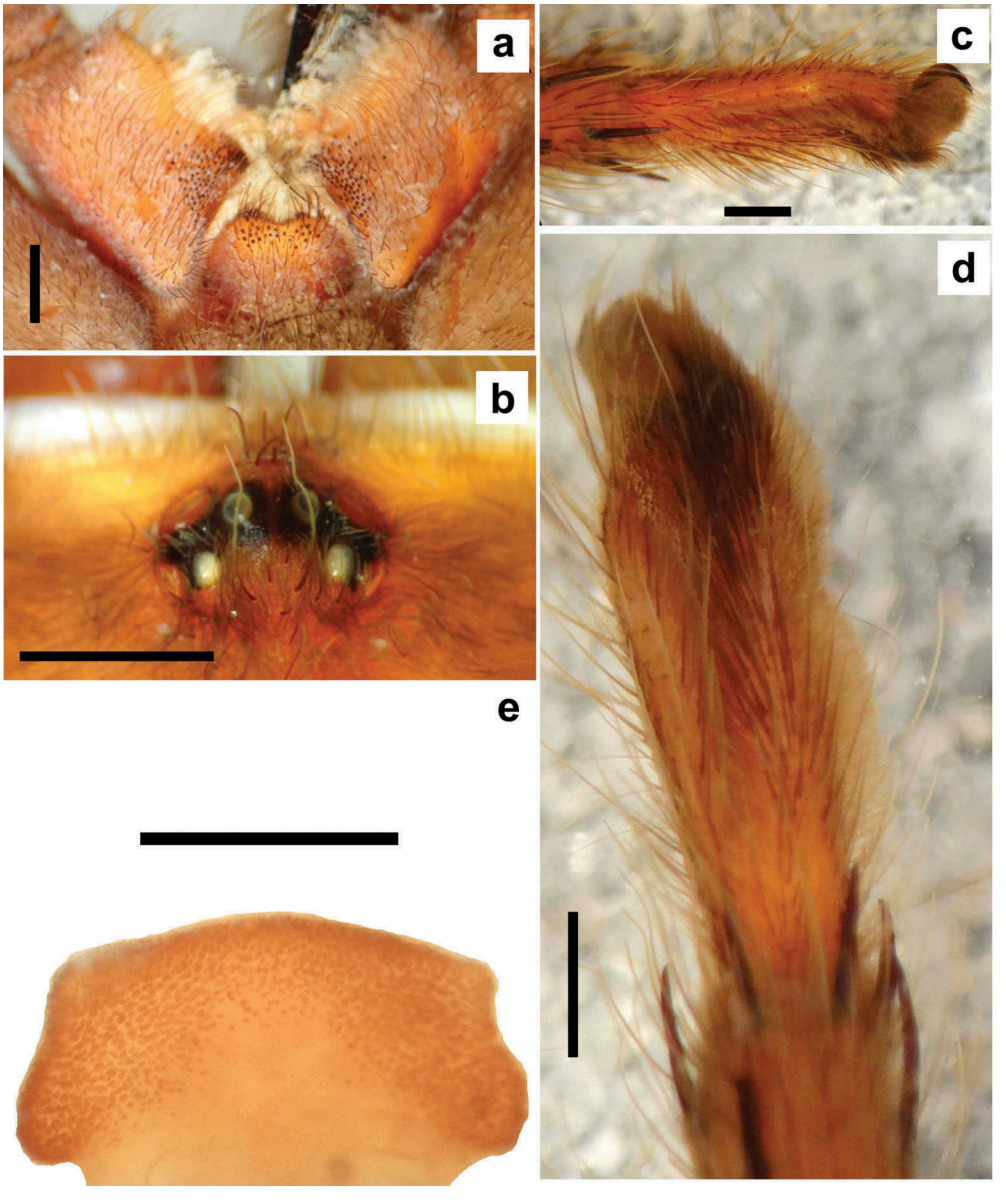

Figure 16. (a–e) *Hapalotremus martinorum*, female paratype (MLP 19153). (a) Labium, ventral view. (b) Eyes, dorsal view. (c) Tarsus IV, prolateral view. (d) Tarsus IV, ventral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

Arachnida'. It seems likely that these two specimens were not collected on the Yale Peruvian Expedition of 1911. Chamberlin (1916) states that most of the 1911 Yale Peruvian Expedition specimens were collected by Professor H.W. Foote (p. 177). The data label for the *H. major* non-type female (MCZ 144) states that it was collected on the Yale Peruvian Expedition of 1911, however, no collector is cited on the label. In addition, this specimen was not collected at the type locality of Cuzco Valley, but rather at Urubamba Valley, and examination found this specimen to be an immature male (R.C. West, pers. obs.).

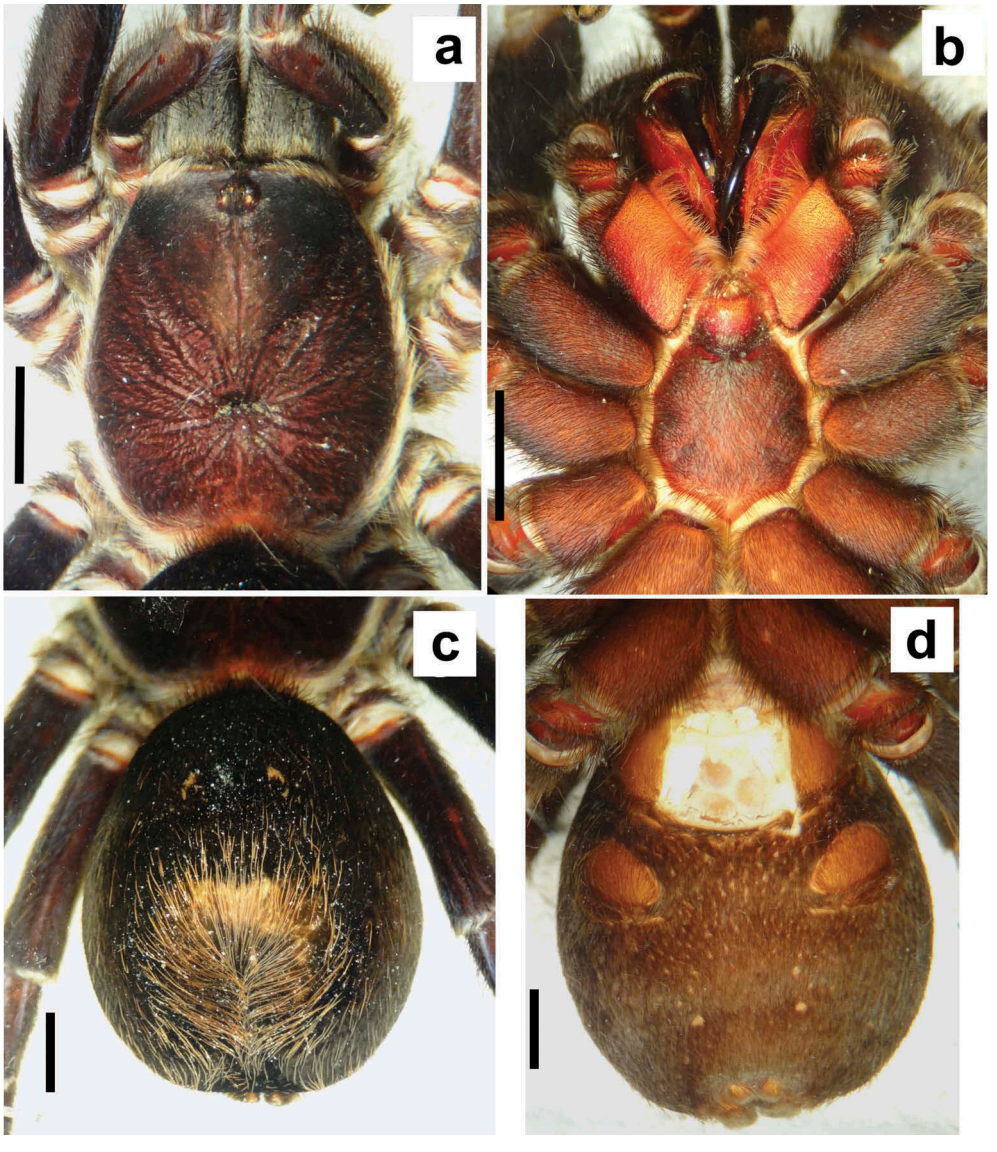

Figure 17. (a–d) *Hapalotremus carabaya* sp. nov., female holotype (MUSM-ENT 0508676). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Additional material examined

One immature male (MCZ 144) from Peru, Cusco, Urubamba, Urubamba (-13.3061 S, -72.1194 W), 2895 m a.s.l., July 1911, Yale Peruvian Expedition.

Amended diagnosis

Males and females of *H. major* can be distinguished from those of *H. albipes* by the presence of long spiniform setae on entire pro- and retrolateral coxal face of legs I–IV (Figure 10b) and

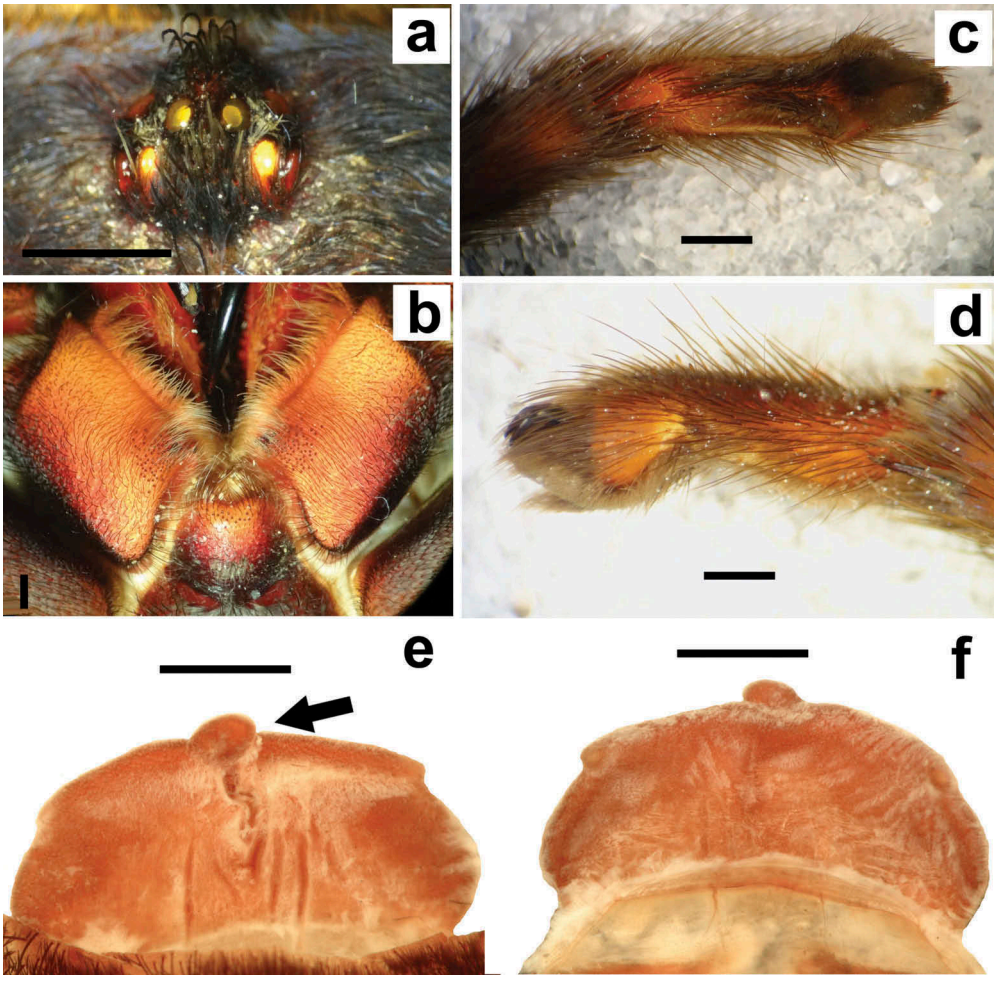

Figure 18. (a–f) *Hapalotremus carabaya* sp. nov., female holotype (MUSM-ENT 0508676). (a) Eyes, dorsal view. (b) Labium, ventral view. (c) Tarsus IV, ventral view. (d) Tarsus IV, prolateral view. (e) Spermathecae, dorsal view. (f) Spermathecae, ventral view. Scale bar: 1 mm. Photos: Nelson Ferretti.

absence of any white setal pattern on dorsum of abdomen (Figure 1b). Additionally, males of *H. major* differs from those of *H. albipes* by: presence of palpal tibia having the retrolateral rounded process more developed (Figure 11c, d), tibia I roughly the same length as metatarsus I, and digitiform apophysis less developed (Figure 11a); embolus longer and thinner than *H. albipes*, very curved to the retrolateral face of the palpal bulb (Figure 11a, b); prolateral keels less developed with ventral medial crest located more basally than in *H. albipes* (Figure 11a, b). *Hapalotremus major* male with 16 (Figure 10e) and female with 5 (Figure 12d) labial cuspules. Females of *H. major* can be easily distinguished from those of *H. albipes* by the spermathecae basal portion narrower than apical portion, domed apical median region and apical lateral projections more developed (Figure 12g). Urticating setae: type III present on male (Figure 10c) and female (abdomen of female in bad condition) and arranged in a dorsal median patch on the abdomen (Figure 12e).

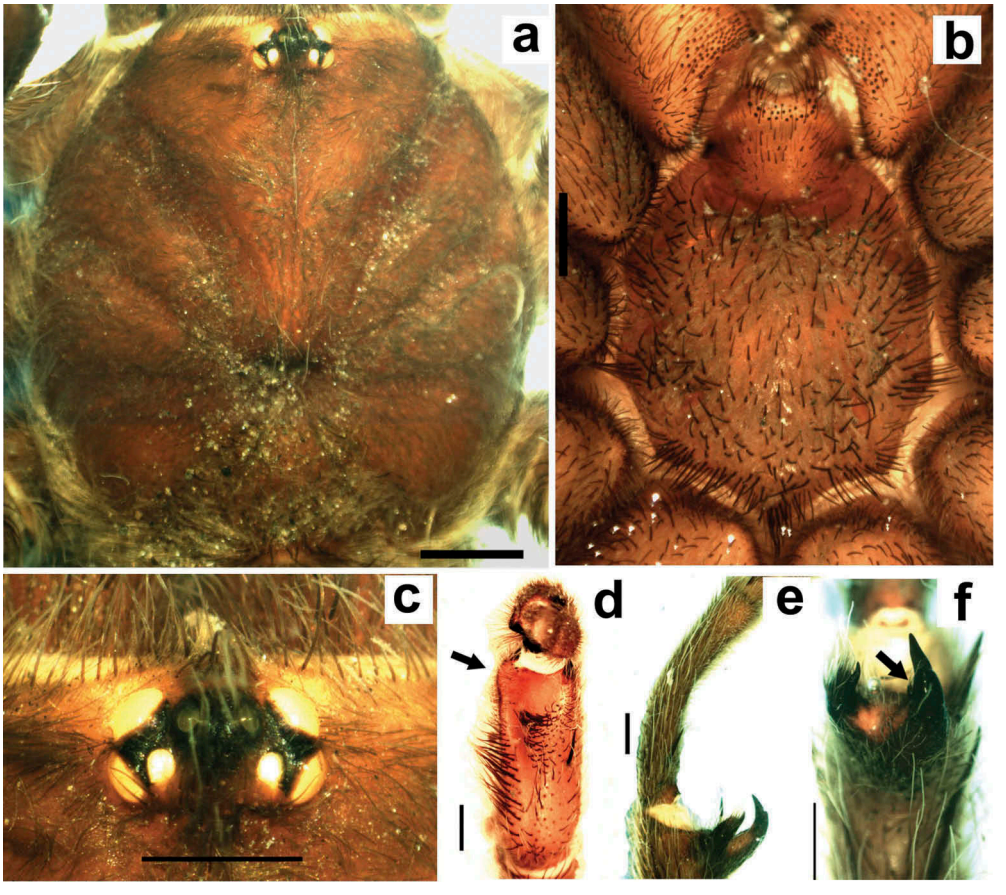

Figure 19. (a–f) *Hapalotremus chasqui* sp. nov., male holotype (MACN-Ar 36632). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Eyes, dorsal view. (d) Palpal tibia, ventral view (arrow indicates the rounded process). (e) Leg I, lateral view. (f) Tibial apophysis, ventral view (arrow marks the second spine on branch). Scale bar: 1 mm. Photos: Duniesky Ríos-Tamayo.

Distribution and habitat

Known only from Cusco Valley, Peru, at about 2500 m a.s.l. (Figure 37). A specimen of *H. major* (Figure 1b) has been found near the type locality inhabiting crevices under big rocks (J. C. Chaparro, pers. obs.).

Hapalotremus martinorum Cavallo and Ferretti, 2015 (Figures 1c, d, 13–15, 36)

Hapalotremus martinorum: Cavallo and Ferretti, 2015: 876, figs 1a, b, 2a–f, 3a–c, 5c.

Type material

Male holotype (MLP19152) from Argentina, Salta, Chicoana, near provincial route 33, adjacent to Escoipe River (-25.1500 S, -65.6000 W), 1496 m a.s.l., 20 April 2011, Patricio E. Cavallo, Martin Hüsser and Martin Gamache cols.; paratype female (MLP19153), same data as holotype. Examined.

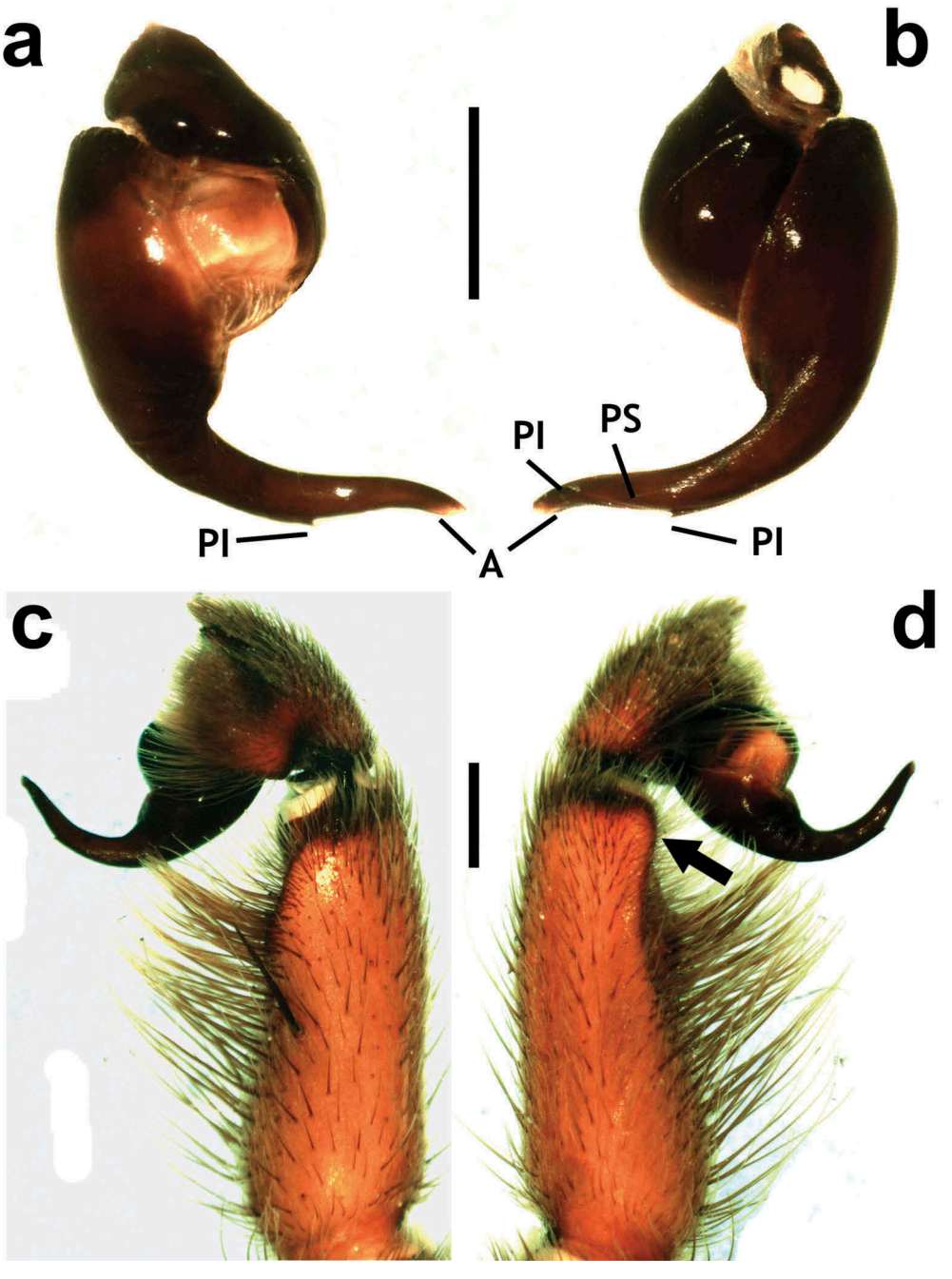

Figure 20. (a–d) *Hapalotremus chasqui* sp. nov., male holotype (MACN-Ar 36632). (a, b) Male right palpal bulb. (a) Retrolateral view. (b) Prolateral view. (c, d) Male palpal bulb and tibia. (c) Prolateral view. (d) Retrolateral view. Arrow indicates the rounded process. A, apical keel; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Duniesky Ríos-Tamayo.

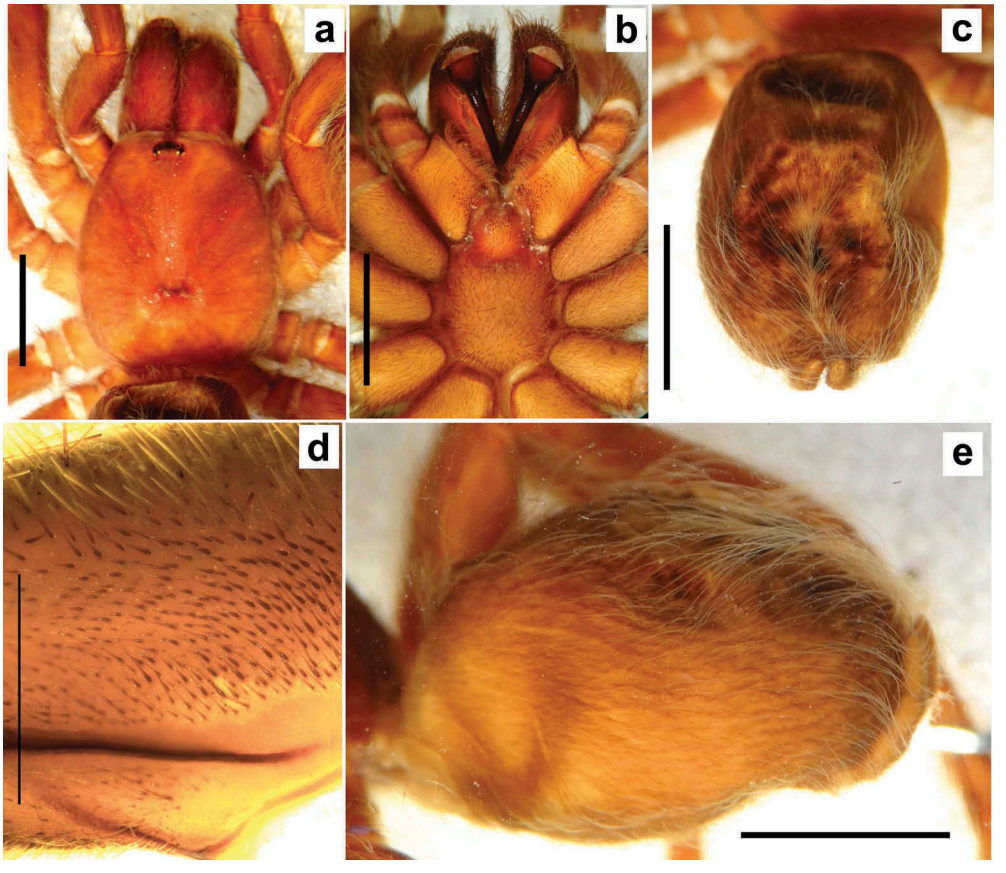

Figure 21. (a–e) *Hapalotremus chasqui* sp. nov., female paratype (MACN-Ar 35596). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Detail of long spiniform setae on prolateral face of coxa I. (e) Abdomen, lateral view. Scale bars: a–c, e: 5 mm; d: 1 mm. Photos: Nelson Ferretti.

Additional material examined

Female (MACN–Ar 38174) from Argentina, Salta, Rosario de Lerma, Campo Quijano (-24.9075 S, -65.6442 W), 29 September 1967, A. Fornes col.; female (MACN–Ar 38207) from Argentina, Salta, Salta, San Lorenzo Hill (-24.7269 S, -65.5044 W), 16 July 1924, A. Frers col.

Notes

In the original description of the species (Cavallo and Ferretti 2015), the ventral crest of the prolateral inferior keel was described as a subapical keel due to its triangular shape and position. However, a more detailed examination of the male holotype and the comparison with the other species of *Hapalotremus* led us to identify a continuous PI very well-developed along the embolus having a ventral expansion or crest, as found in all known species.

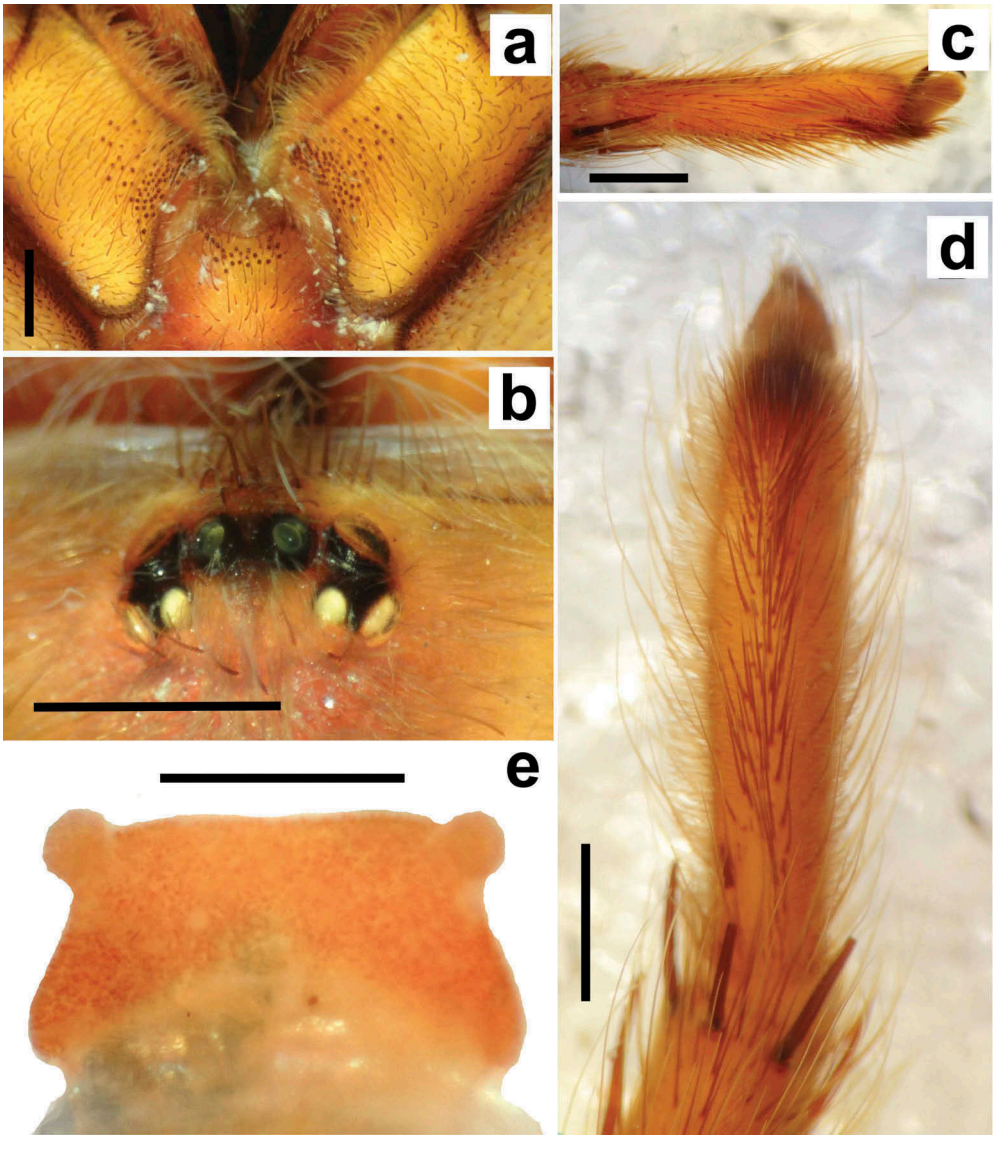

Figure 22. (a–e) *Hapalotremus chasqui* sp. nov., female paratype (MACN-Ar 35596). (a) Labium, ventral view. (b) Eyes, dorsal view. (c) Tarsus IV, prolateral view. (d) Tarsus IV, ventral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

Amended diagnosis

Hapalotremus martinorum is characterized by a distinct green pubescence between the patella and tarsi of legs and on the lateral faces of the abdomen in combination with red setae on the urticating patch (Figure 1c, d). Males of *H. martinorum* can be distinguished from those of *H. albipes* and *H. major* by a large number of labial cuspules (more than 20), tibia I about 10% longer than metatarsus I (Figure 13g), by having a slightly

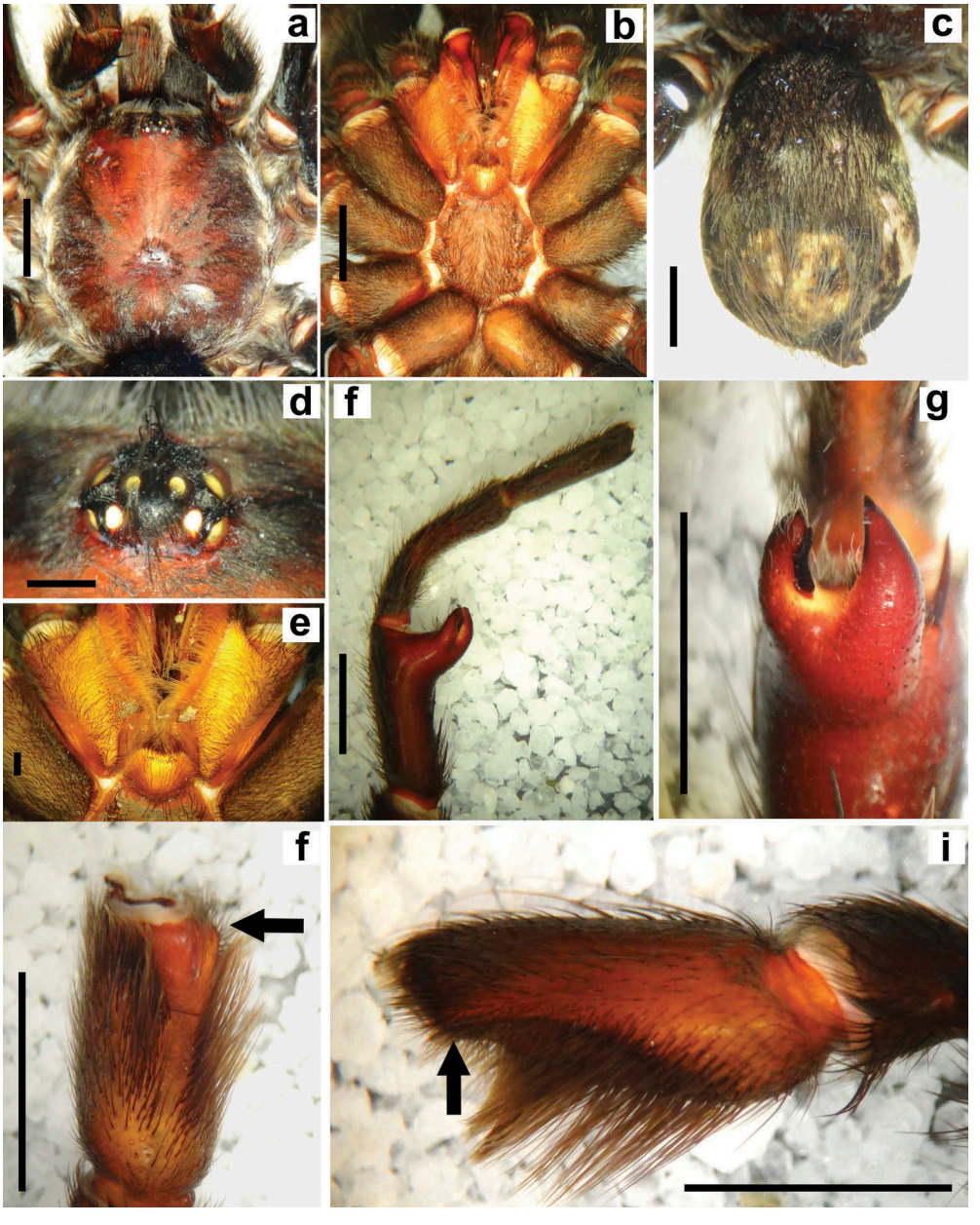

Figure 23. (a–i) *Hapalotremus chespiritoi* sp. nov., male holotype (MUBI). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Eyes, dorsal view. (e) Labium and maxillae, ventral view. (f) Leg I, lateral view. (g) Tibial apophysis, ventral view. (h) Palpal tibia, ventral view. (i) Palpal tibia, retrolateral view. Arrows indicate the rounded process. Scale bar: a–c, g: 5 mm. d–f, h–i: 1 mm. Photos: Nelson Ferretti.

developed retrolateral rounded process on palpal tibia (Figure 13h, i), unequal sizes of tibial apophysis branches (PB smaller than RB) (Figure 13f, g) and slower curvature of metatarsus I (Figure 13g). Palpal bulb resembles that of *H. major*, but it differs by the

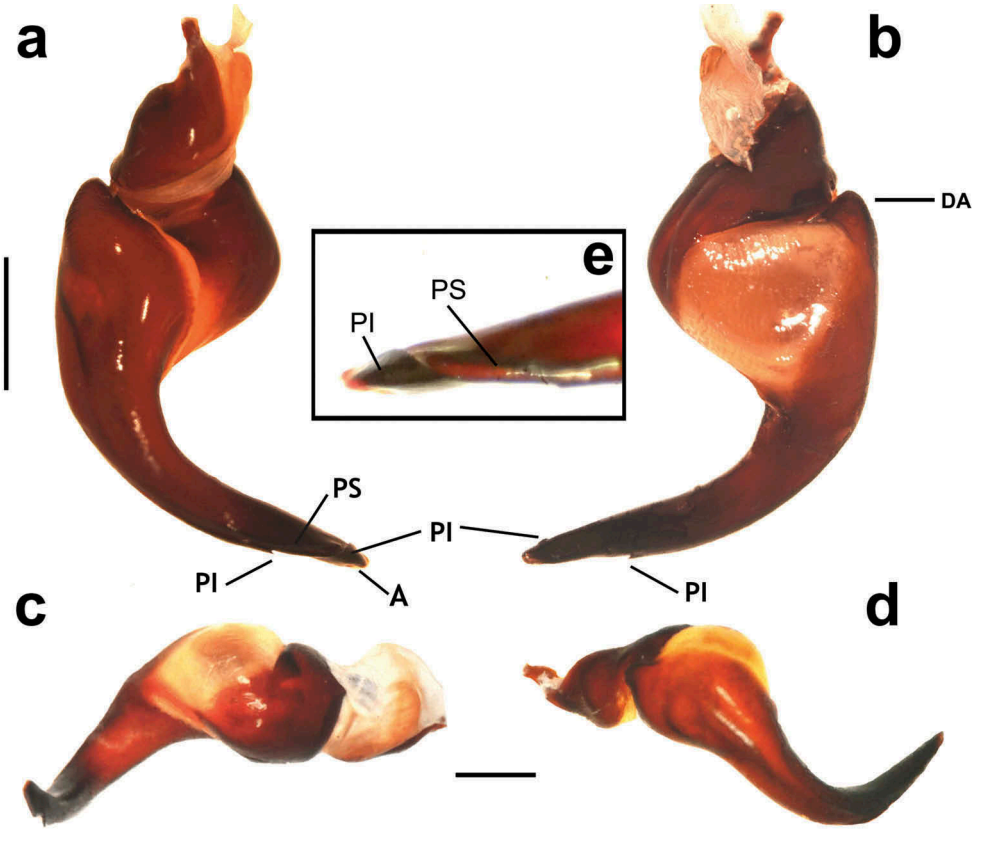

Figure 24. (a–e) *Hapalotremus chespiritoi* sp. nov., male holotype left palpal bulb (MUBI). (a) Prolateral view. (b) Retrolateral view. (c) Dorsal view. (d) Ventral view. (e) Embolus showing keels. A, apical keel; DA, digitiform apophysis; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Nelson Ferretti.

more developed digitiform apophysis (Figure 14a–d) and prolateral keels (Figure 14a–d). Females of *H. martinorum* can be distinguished from those of *H. albipes* and *H. major* by the larger number of cuspules on labium (more than 25 cuspules) (Figures 15b, 16a). Additionally, males of *H. martinorum* differ from all *Hapalotremus* species by the presence of an accessory keel (AK) on palpal embolus located among PI and A (Figure 14a, e). Also, females of *H. martinorum* can be characterized by the shape of the spermathecae, with basal portion wider than apical, apical lateral projections slightly developed and protrude from the apical median region (Figure 16e).

Distribution and habitat

Known from Salta Province, northwestern Argentina (Figure 36). Specimens were found in high-cloud forests of the Yungas region (Figure 3a). These spiders occupy short burrows or crevices under stones and usually the stones, where individuals can be found, are covered with mosses and small ferns (see more details of natural history in Cavallo and Ferretti 2015).

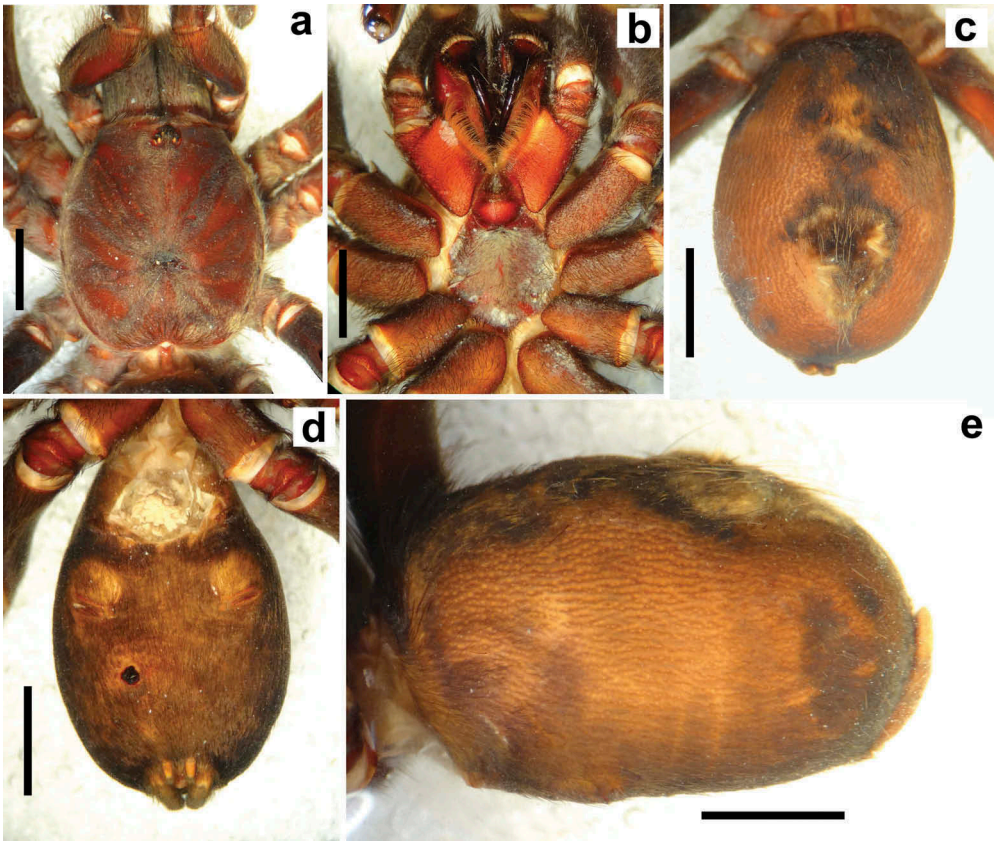

Figure 25. (a–e) *Hapalotremus chespiritoi* sp. nov., female paratype (MUBI). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. (e) Abdomen, lateral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Hapalotremus carabaya sp. nov.
(Figures 2a, b, 3d, f, 17–18, 37)

Type material
Female holotype (MUSM–ENT 0508676) from Peru, Quispicanchi, Cusco, Michi Michani Cunca, Cordillera Carabaya (-13.5792 S, -70.5778 W), 4057 m a.s.l., 30 June 2006, Severino Crispin Huanca col.

Additional material examined
Immature (MUSM–ENT 0508678) from Peru, Quispicanchi, Cusco, Michi Michani Cunca, Cordillera Carabaya (-13.5792 S, -70.5778 W), 3947 m a.s.l., 28 June 2006, Tracie Seimon col.

Etymology
The specific epithet refers to the type locality where the species was found and also to the Cordillera Carabaya which is a mountain chain located in the southeast of Peru. It

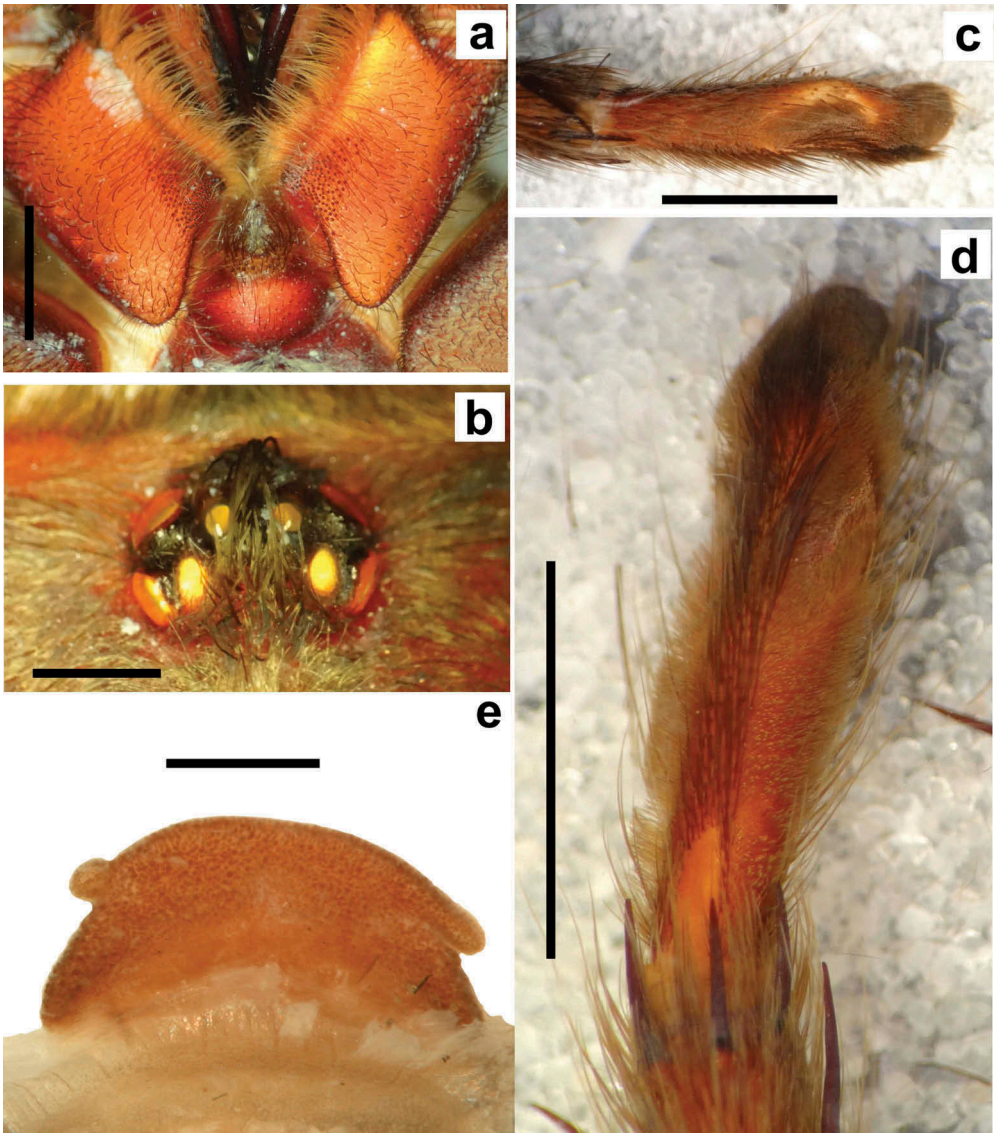

Figure 26. (a–e) *Hapalotremus chespiritoi* sp. nov., female paratype (MUBI). (a) Labium, ventral view. (b) Eyes, dorsal view. (c) Tarsus IV, prolateral view. (d) Tarsus IV, ventral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

forms part of the Eastern Cordillera of the Andes and extends in a northwest–southeast direction for about 95 km, from the department of Puno. It also presents a glacier surface of 100 km^2 with its maximum elevation reaching 5780 m a.s.l.

Diagnosis

Females of *H. carabaya* sp. nov. can be easily distinguished from those of all other species of *Hapalotremus* by the spermathecae bearing an additional well-developed

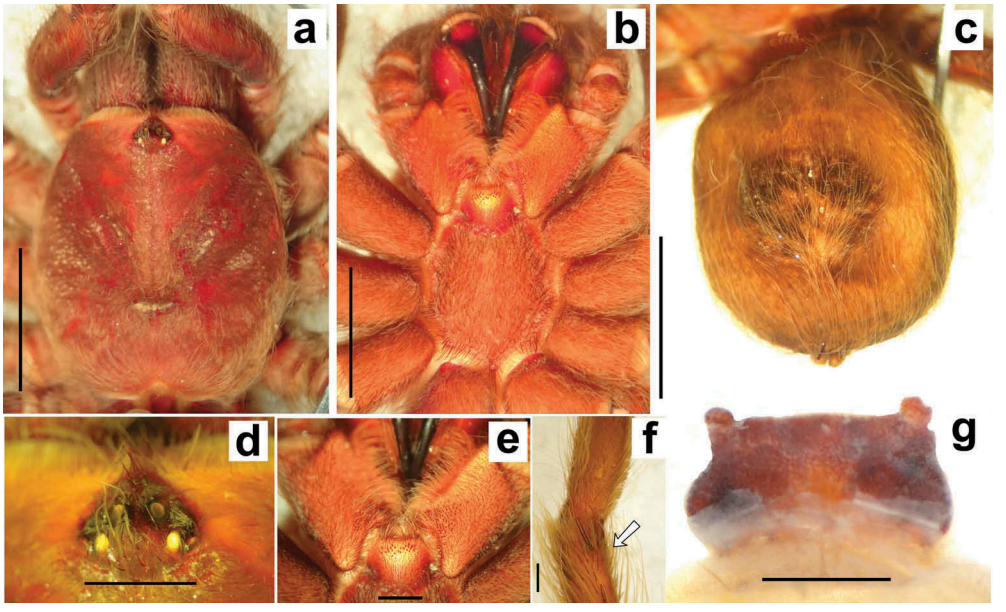

Figure 27. (a–g) *Hapalotremus kuka* sp. nov., female holotype (AMNH). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Eyes, dorsal view. (e) Labium and maxillae, ventral view. (f) Metatarsus and tarsus IV, lateral view. (g) Spermathecae, dorsal view. Arrow indicates the scopulae on ventral metatarsus IV. Scale bars: a–c: 5 mm. d–g: 1 mm. Photos: Nelson Ferretti.

apical median projection with a long thin wavy groove extending downward dorsal median from this projection (Figure 18e, f). Male unknown.

Description

Holotype female (MUSM–ENT 0508676): Total length (not including chelicerae and spinnerets) 36.9. Carapace: length, 15.7; width 13.6. Abdomen: length 20.2. Fovea: procurved, width 2.1.

Colour pattern (live specimen): carapace dark, with pink setae on margins; legs dark with stripes on patellae distinct; abdomen black with red setae on urticating patch (Figure 2a, b).

Eyes: anterior eye row procurved, posterior recurved (Figure 18a). Eyes sizes and interdistances: AME 0.19, ALE 0.23, PME 0.28, PLE 0.24, AME–AME 0.30, AME–ALE 0.18, PME–PME 0.91, PME–PLE 0.11, ALE–PLE 0.24. Ocular tubercle: length, 1.60; width, 1.75. Clypeus: length, 0.25. Labium: length, 2.5; width, 3.0, with 16 cuspules (Figures 17b, 18b). Maxillae: right with 112 cuspules, left with 108 cuspules. Sternum: length, 6.4; width, 5.8. Three pairs of sternal circular sigillae, first pair hardly visible, second and third pairs visible, third pair about its length from the margin (Figure 17b). Chelicerae: with 13 well-developed teeth on promargin of furrow and 19 small teeth on the retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 11.3, 6.8, 8.0, 6.8, 4.6, 37.5; II: 9.6, 5.8, 6.5, 6.1, 4.5, 32.5; III: 8.3, 5.3, 5.8, 7.8, 5.1, 32.3; IV: 10.7, 6.5, 8.2, 11.0, 5.5, 41.9; palp: 8.0, 5.2, 6.1, –, 5.8, 25.1. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 1.5 long; PLS, three-segmented, 5.3 long.

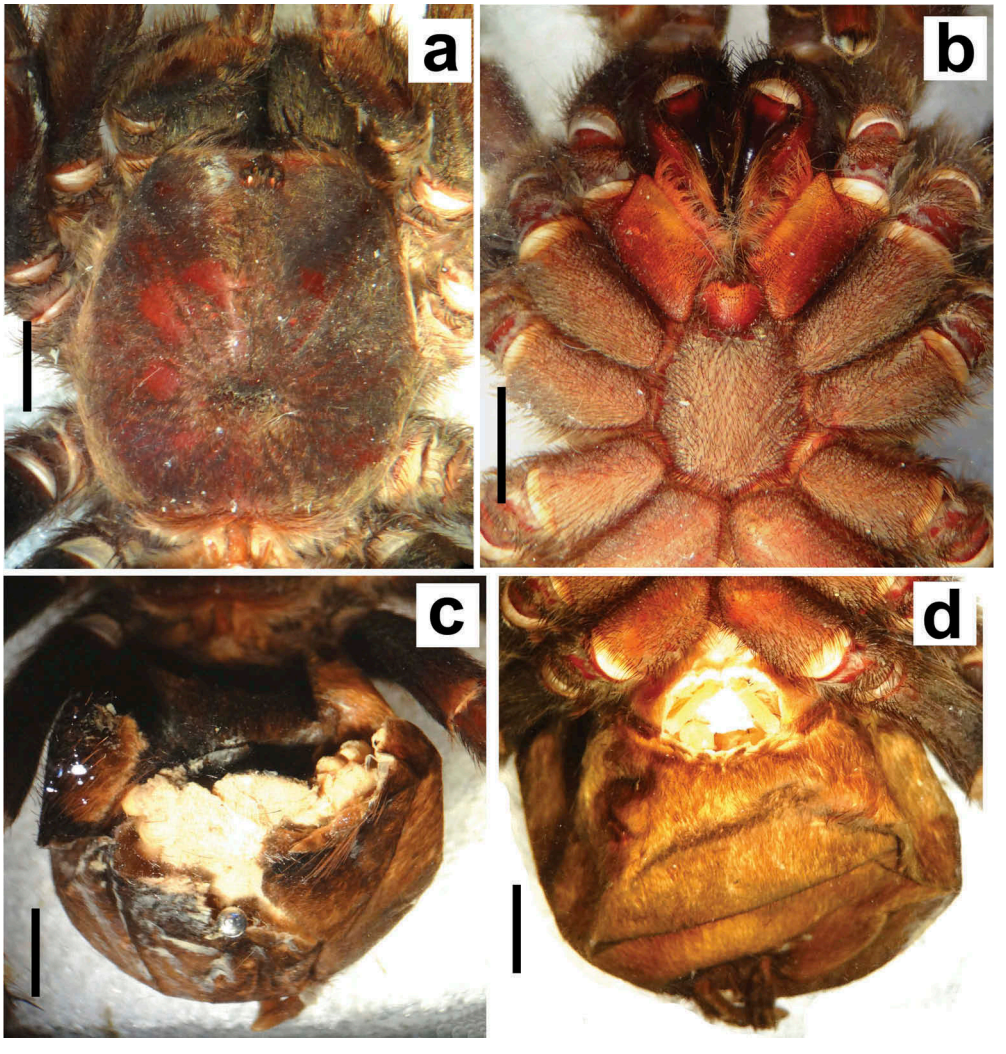

Figure 28. (a–d) *Hapalotremus marcapata* sp. nov., female holotype (MUBI). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Scopulae: Ventrally, all tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I 1/2 scopulate divided by one row of setae, II 1/2 scopulate divided by three rows of setae, III 1/4 scopulate divided by more than three rows of setae, IV with no scopulae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora: palp 0; I 2d; II 0; III 0; IV 0. Patellae: palp and legs I–IV 0. Tibiae: palp 1-2v; I 1v; II 1-2v, 1-1-1p, 1-1r; III 2-1-2v, 1-1-1p, 1-1r; IV 1-2-2v, 1p, 1-1-1r. Metatarsi: I 1-1v; II 1-2v, 1r; III 2d, 1-1-2v, 1-2-2-2-2p, 1-1-1r; IV 2d, 2-1-3v, 1-1-1-2p, 1-1-1-1r. Tarsi: I–IV 0.

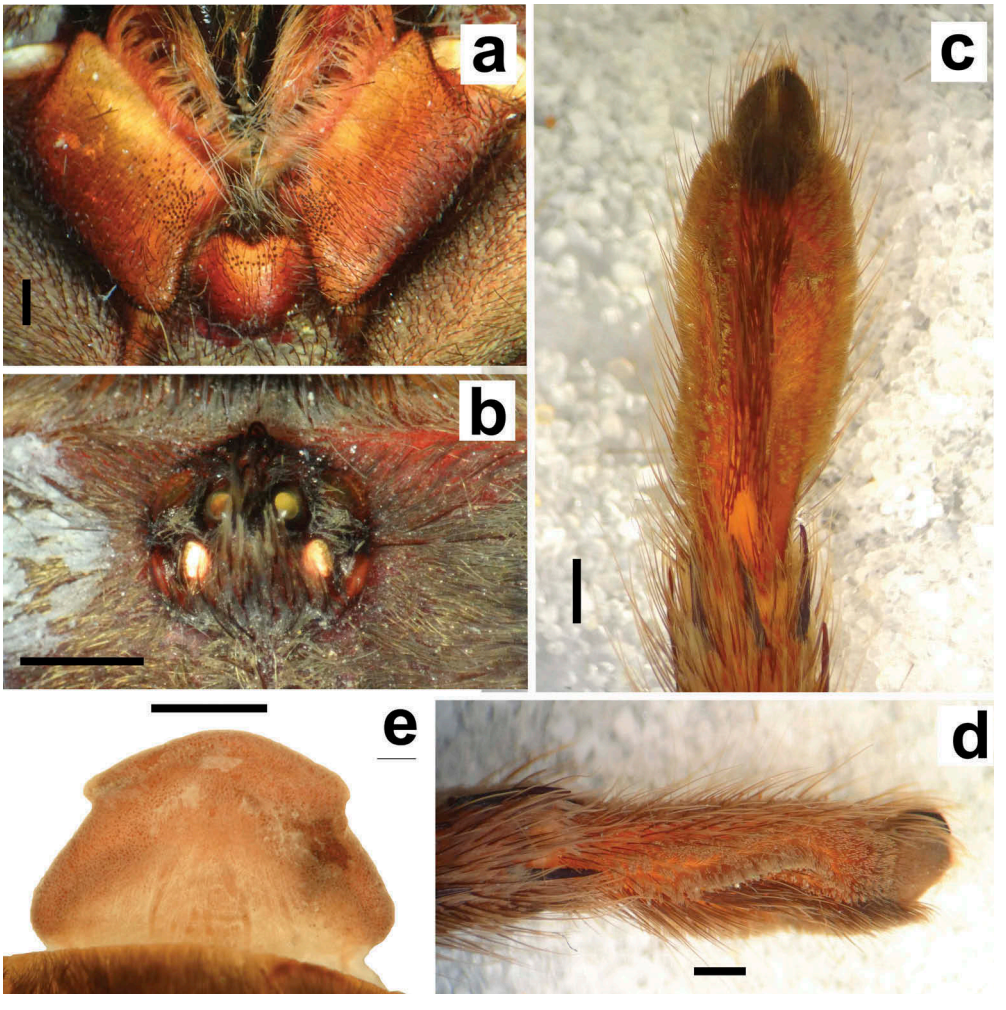

Figure 29. (a–e) *Hapalotremus marcapata* sp. nov., female holotype (MUBI). (a) Labium, ventral view. (b) Eyes, dorsal view. (c) Tarsus IV, ventral view. (d) Tarsus IV, prolateral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

Genitalia: Spermathecal receptacle with basal portion much wider than apical; apical median region rounded and apical lateral projections slightly developed; presence of an additional well-developed apical median projection with a long thin wavy groove extending downward dorsal median from this projection (Figure 18e, f).

Urticating setae: Type III present and arranged in one big dorsal median patch on the abdomen (Figure 17c).

Distribution and habitat

Known only from type locality (Figure 37). Specimens were found on a hill under different rocks in close proximity to each other at about 4000 m a.s.l. (Figure 3d, f). Spiders were located at 2:02 pm under misty weather conditions with drizzle. Day temperature on 30 June 2006 was 8°C but dropped to an overnight low of about −3.3°C.

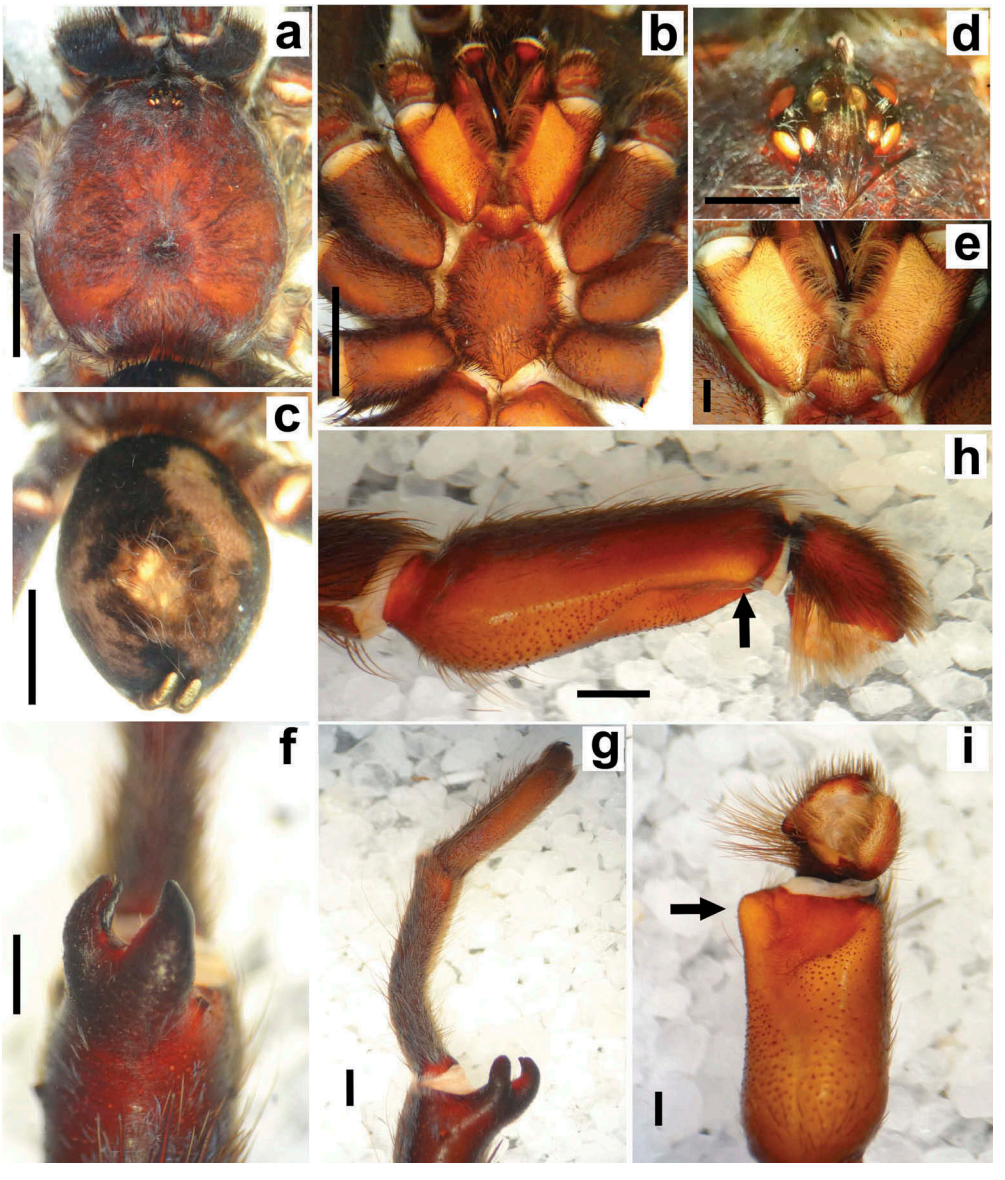

Figure 30. (a–i) *Hapalotremus perezmilesi* sp. nov., male holotype (MUBI). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Eyes, dorsal view. (e) Labium and maxillae, ventral view. (f) Tibial apophysis, ventral view. (g) Leg I, lateral view. (h) Palpal tibia, prolateral view. (i) Palpal tibia, ventral view. Arrows indicate the rounded process. Scale bars: a–c: 5 mm. d–i: 1 mm. Photos: Nelson Ferretti.

Hapalotremus chasqui sp. nov.
(Figures 1e, 19–22, 36)

Type material

Male holotype (MACN–Ar 36632) from Argentina, Tucumán, Tafí del Valle, road to Tafí del Valle, 4.5 km west of 'El Indio', 14 October 1994, P. Goloboff col.; paratype female

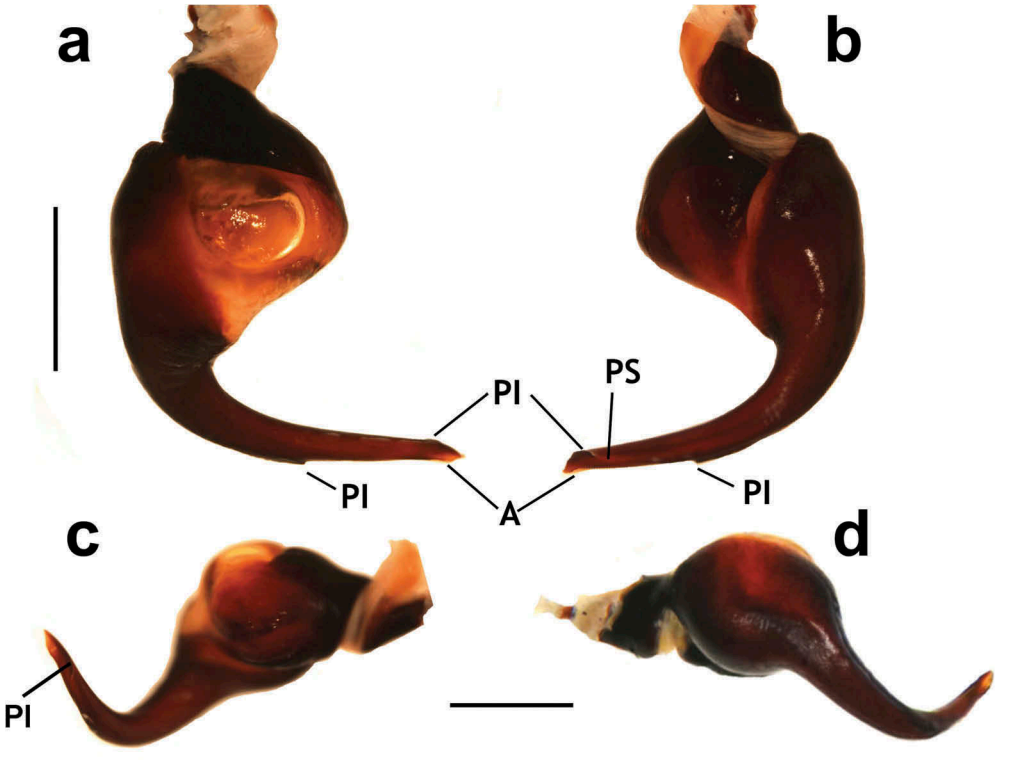

Figure 31. (a–d) *Hapalotremus perezmilesi* sp. nov., male holotype right palpal bulb (MUBI). (a) Retrolateral view. (b) Prolateral view. (c) Dorsal view. (d) Ventral view. A, apical keel; PI, prolateral inferior keel; PS, prolateral superior keel. Scale bar: 1 mm. Photos: Nelson Ferretti.

(MACN–Ar 35596) from Argentina, Tucumán, Tafí del Valle, El Indio (road to Tafí del Valle), 17 January 1981, A. Roig col.

Additional material examined

Immature male (LZI 542) from Argentina, Tucumán, Tafí del Valle, route 307, El Aluvión, road to Tafí del Valle (-27.0208 S, -65.6581 W), 1349 m a.s.l., under stone, 15 February 2017, Nelson Ferretti col.; female (MACN–Ar 38151) from Argentina, Jujuy, Ledesma, Calilegua (-23.6714 S, -64.8661 W), October 1968, M. E. Galiano col.; female (MACN–Ar 38192) from Argentina, Salta, General José de San Martín, Bermejo River, 80 km southern Embarcación (-23.1806 S, -64.1414 W), February 1948, M. Lillo col.

Etymology

The specific epithet is a noun taken in apposition and refers to the personal messengers of the Inca, named '*chasqui*' in Quechua language, which means young runner. The *chasqui* ran from one post to another to deliver messages or objects (Academia Mayor de Lengüa Quechua 2005).

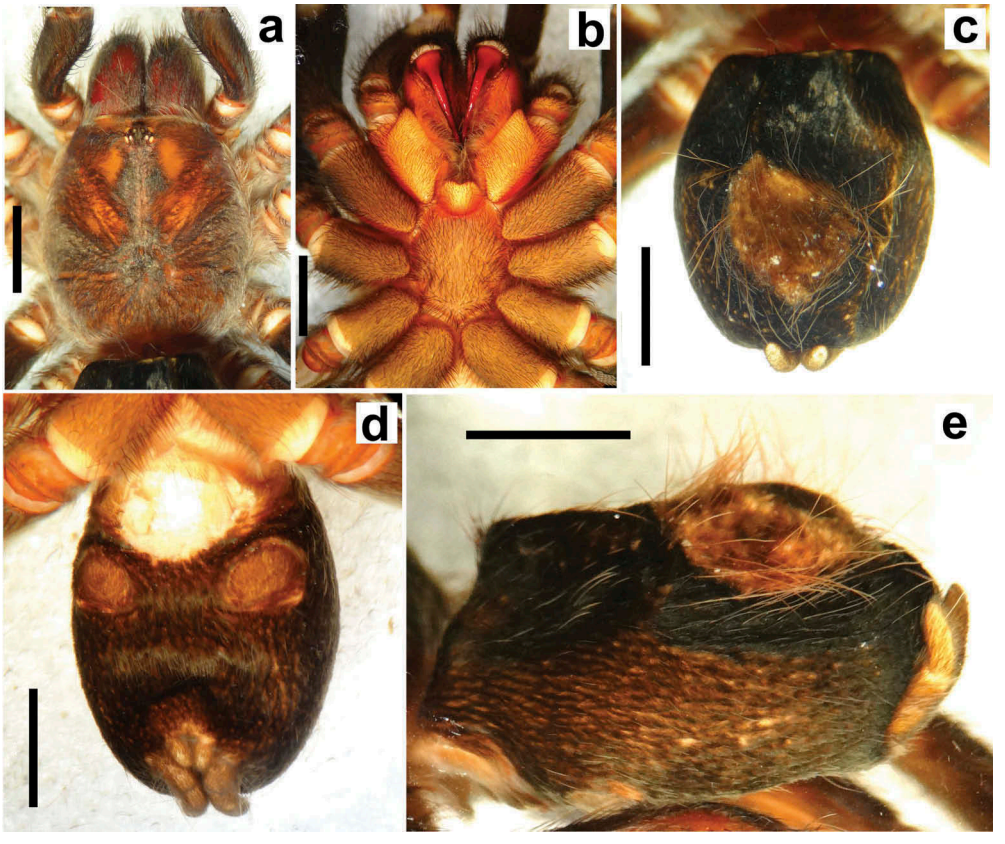

Figure 32. (a–e) *Hapalotremus perezmilesi* sp. nov., female paratype (MUBI). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, dorsal view. (d) Abdomen, ventral view. (e) Abdomen, lateral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Diagnosis

Males and females resemble those of *H. martinorum* and *H. kuka* sp. nov. by their small size (about 2 cm long) and the large number of labial cuspules (more than 25), but differ from them by the presence of long spiniform setae on prolateral coxal face of legs I–IV (Figure 21d). Males can be distinguished from those of *H. martinorum* by the presence of two spines on the retrolateral branch of tibial apophysis (Figure 19f), by lacking the digitiform apophysis on the bulb (Figure 20a, b) and by the absence of an accessory keel on embolus (Figure 20a, b); also by the pointed ventral crest on PI, located more apically on embolus (Figure 20a, b). Females can also be distinguished from those of all other species by the spermathecae with basal portion wider than apical, apical median region straight and apical lateral projections well-developed (Figure 22e).

Description

Holotype male (MACN–Ar 36632): Total length (not including chelicerae and spinnerets) 21.26, carapace length 10.06, width 9.40, abdomen 11.20 long. Fovea transverse, small and straight, width 1.10.

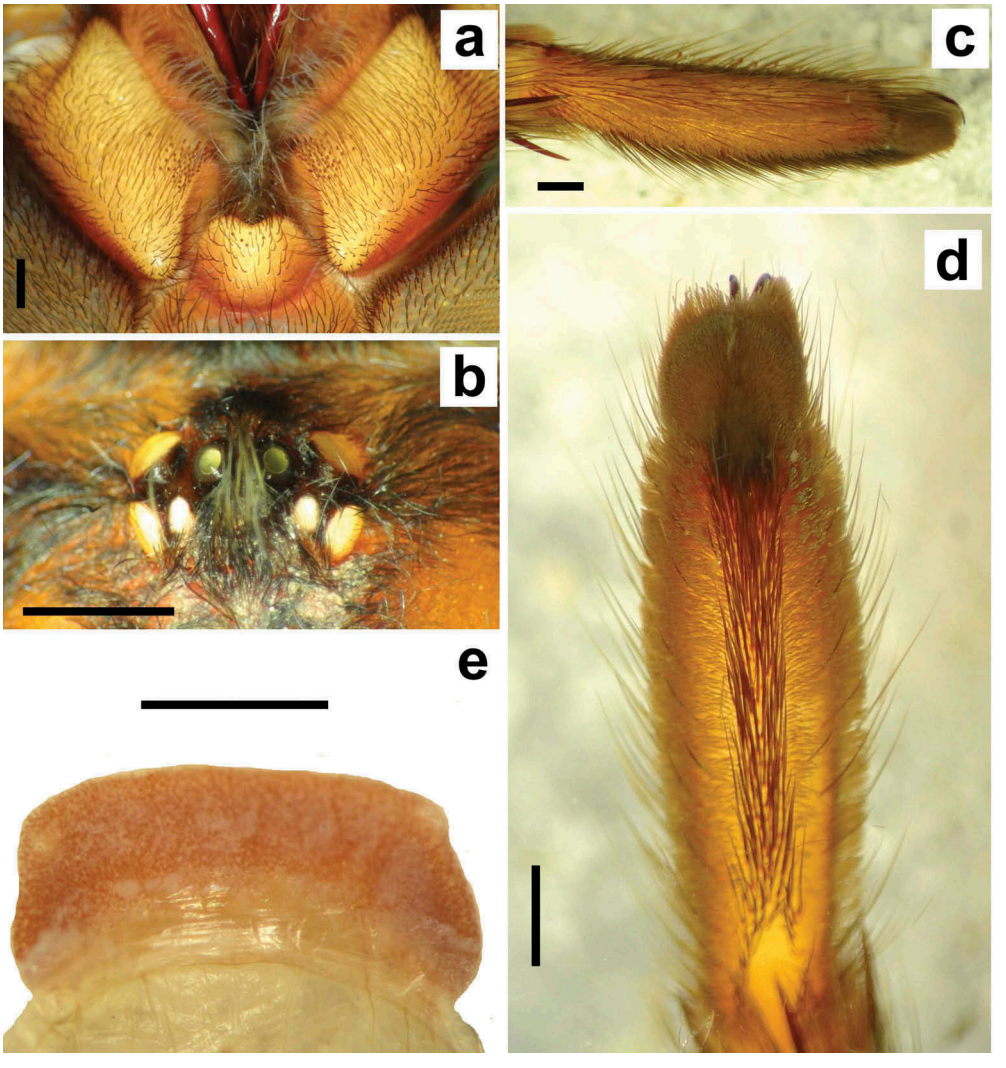

Figure 33. (a–e) *Hapalotremus perezmilesi* sp. nov., female paratype (MUBI). (a) Labium, ventral view. (b) Eyes, dorsal view. (c) Tarsus IV, prolateral view. (d) Tarsus IV, ventral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

Colour pattern (in alcohol): carapace reddish brown with white long setae on margins (Figure 19a), legs like carapace with fine white setae on coxae, abdomen brown with long light yellow setae and an urticating setae patch.

Eyes: anterior eye row procurved, posterior recurved (Figure 19a, c). Eyes sizes and interdistances: AME 0.15, ALE 0.44, PME 0.20, PLE 0.40, AME–AME 0.25, AME–ALE 0.11, PME–PME 0.53, PME–PLE 0.08, ALE–PLE 0.09. Ocular tubercle length 0.81, width 1.37, clypeus 0.24. Labium length 1.40, width 2.10 with 26 cuspules (Figure 19b). Maxillae: right with 104 cuspules, left with 96 cuspules. Sternum length 4.40, width 4.30. Three pairs of sternal oval sigillae, third pair about its length and a half from the margin (Figure 19b). Chelicerae with 13 well-developed teeth on promargin of furrow and 5 small teeth on retromargin.

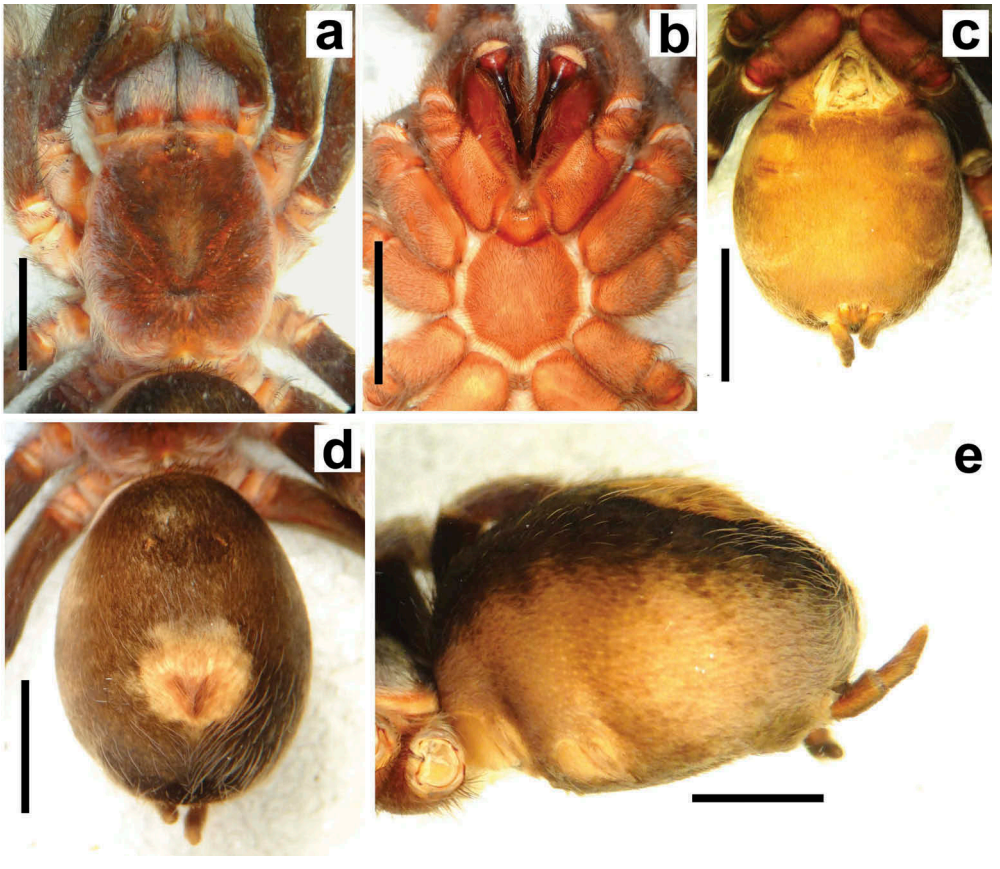

Figure 34. (a–e) *Hapalotremus vilcanota* sp. nov., female holotype (MUSM-ENT 0508677). (a) Carapace, dorsal view. (b) Sternum, ventral view. (c) Abdomen, ventral view. (d) Abdomen, dorsal view. (e) Abdomen, lateral view. Scale bar: 5 mm. Photos: Nelson Ferretti.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 9.40, 5.20, 7.30, 6.60, 4.20, 32.70; II: 9.40, 4.70, 6.60, 7.00, 4.20, 31.90; III: 8.20, 4.20, 6.10, 8.30, 4.20, 31.00; IV: 10.30, 4.70, 8.00, 10.20, 5.20, 38.40; palp: 6.60, 3.60, 5.60, –, 2.80, 18.60. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 1.80 long; PLS, three-segmented, 1.80 basal, 1.20 middle, 1.90 distal long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I–II 1/2 divided by two lines of setae, III 1/3 scopulate divided by three lines of setae, IV with no scopulae. Dorsal face of all tarsi and cymbium with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side, leg I of the left side missing): Femora; palp 1p; I 1p; II 1-1-1p; III 1-1p, 1-1-1r; IV 1p, 1r; patellae; palp 0; I 1v; II 1v; III 1-2p; IV 1v; tibiae: palp 1p; I 2-3-1-1v, 1-1p; II 2-3-1-4v, 1-1-1p, 1r; III 2-2-1-2v, 2-1-2-2-1p, 1-1-1r; IV 2-1-2-1-2v, 2-1-1-1-1p, 1-1r; metatarsi I 2-0-2v; II 1-1-1-1-2-3v, 1-1p, 1-1r; III 2-1-2-1-2-2-3v, 1-1-1-1p, 1-1-1r; IV 3-1-1-2-2-2v, 1-1-1-1p, 1-2-1r; tarsi I–IV, 0.

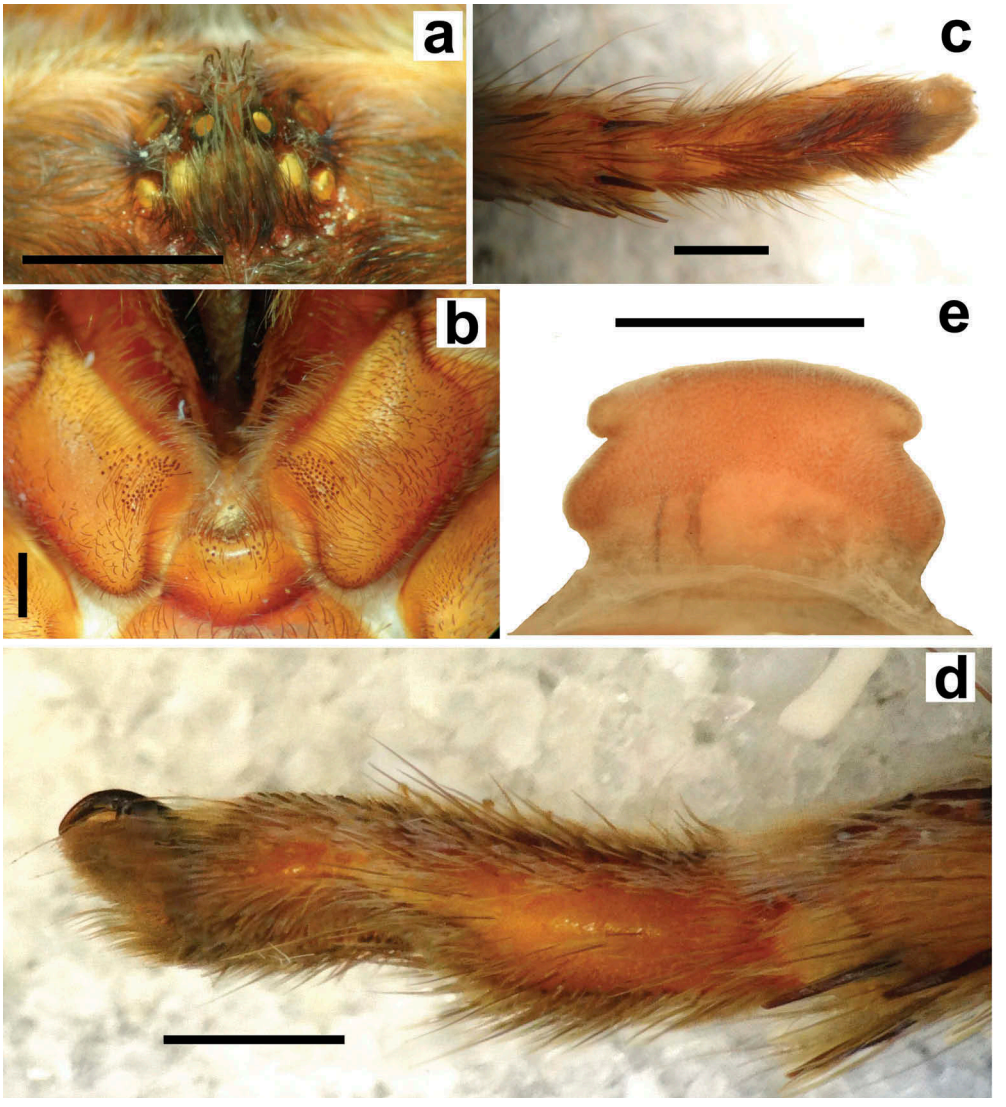

Figure 35. (a–e) *Hapalotremus vilcanota* sp. nov., female holotype (MUSM-ENT 0508677). (a) Eyes, dorsal view. (b) Labium, ventral view. (c) Tarsus IV, ventral view. (d) Tarsus IV, prolateral view. (e) Spermathecae, dorsal view. Scale bar: 1 mm. Photos: Nelson Ferretti.

Tibia I about 10% shorter than metatarsus I. Tibia I with two apophyses, prolateral branch with a long black thorn on inner side, slightly curved at tip and longer than the spur, retrolateral branch with a small spine on the base of the inner side, a robust and long black spine inserted on ventral side of the spur (Figure 19e, f). Metatarsus I curved at middle area, flexion on the outside of the two branches (Figure 19e).

Palp: palpal tibia with a developed retrolateral rounded process (Figures 19d, 20d). Palpal bulb base without digitiform apophysis, embolus subcylindrical, strongly curved

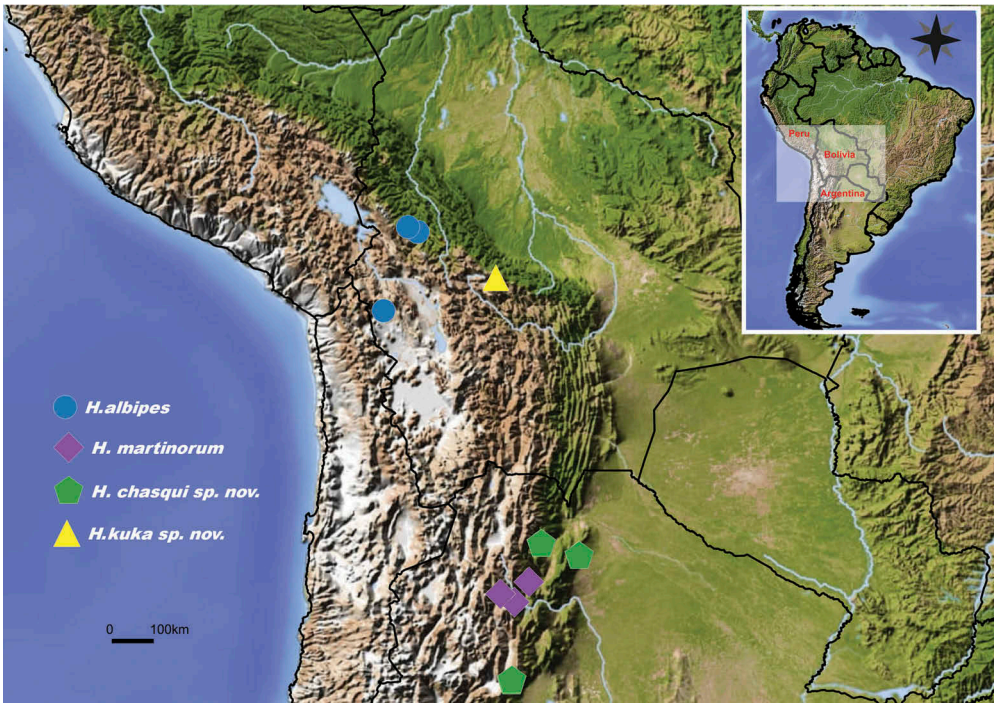

Figure 36. Distribution map of *Hapalotremus* species from Argentina and Bolivia.

to the retrolateral side. Prolateral keels well-developed, PI with ventral medial crest pointed distally and apical keel (A) slightly developed (Figure 20a, b).

Urticating setae: type III present and arranged in one dorsal posterior patch on the abdomen.

Paratype female (MACN–Ar 35596): Total length (not including chelicerae and spinnerets), 24.3, carapace length, 11.5, width 8.4, abdomen 11.3 long. Fovea procurved, width 1.3.

Colour pattern (in alcohol): carapace and legs pale brown, abdomen brown with long white setae on dorsal area (Figure 21a–e).

Eyes: anterior eye row procurved, posterior recurved (Figure 22b). Eyes sizes and interdistances: AME 0.16, ALE 0.25, PME 0.15, PLE 0.16, AME–AME 0.23, AME–ALE 0.14, PME–PME 0.58, PME–PLE 0.08, ALE–PLE 0.12. Ocular tubercle length 0.8, width 1.25, clypeus 0.15. Labium length 1.55, width 1.50 with 22 cuspules (Figure 22a). Maxillae: right with 97 cuspules, left with 83 cuspules. Sternum length 4.0, width 4.1. Three pairs of sternal oval sigillae, pairs visible, third pair about its length from the margin (Figure 21b). Chelicerae with 13 well-developed teeth on promargin of furrow and 11 small teeth on the retromargin.

Leg formula: IV > II > III > I. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 4.9, 3.4, 5.1, 3.1, 3.2, 19.7; II: 6.2, 3.5, 4.3, 4.7, 3.5, 22.2; III: 5.2, 3.6, 4.4, 5.1, 3.2, 21.5; IV: 7.0, 3.6, 6.4, 7.2, 3.1, 27.3; palp: 3.2, 2.2, 3.7, –, 3.1, 12.2. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 1.1 long; PLS, three-segmented, 3.8 long.

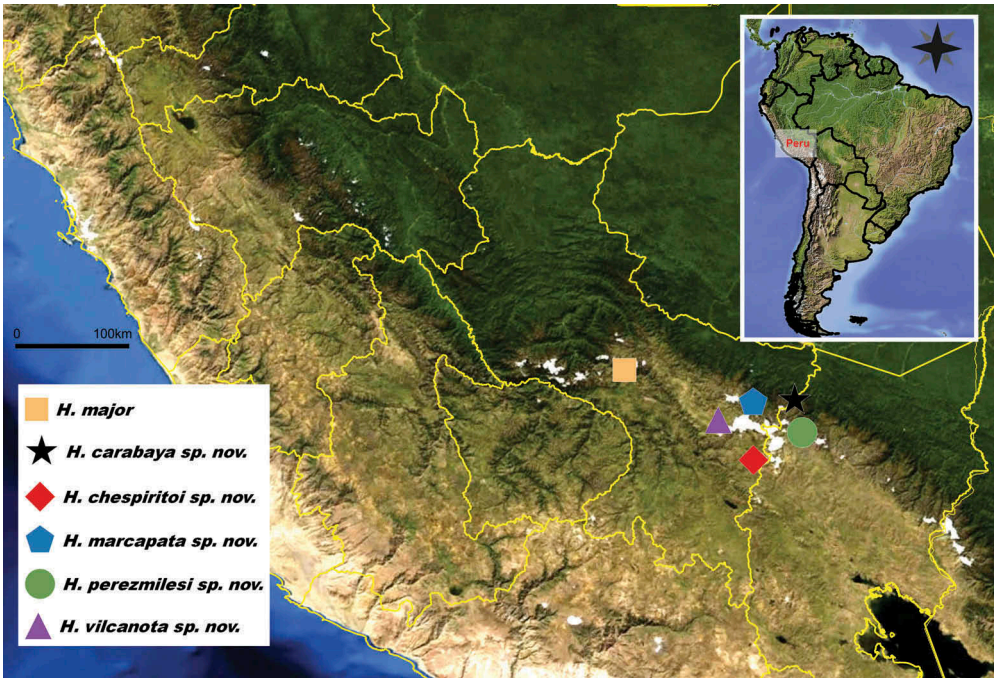

Figure 37. Distribution map of *Hapalotremus* species from Peru.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I 1/2 scopulate entire, II 1/3 scopulate entire, III 1/3 scopulate divided by three lines of setae, IV with no scopulae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora of legs and palp 1d; patellae of legs and palp 0; tibiae: palp 1-2v, 1-1p; I 1-2v, 1r; II 1-2v, 1p; III 1-1-2v, 1-1-1p, 1-1r; IV 1-2-2v, 1-1-1p, 1-1r; metatarsi: I 2-2v, 1r; II 1-1v, 1-1-1r, 1-1p; III 1-1-1v, 2-2-1-2p, 1-1-2-1r; IV 1-1d, 1-1-2v, 2-1-2p, 1-1-2-1-2r; tarsi I–IV, 0.

Genitalia: Single spermathecal receptacle with basal portion wider than apical; apical median region straight and apical lateral projections well developed (Figure 22e).

Urticating setae: Type III present and arranged in one big dorsal median patch on the abdomen (Figure 21c).

Distribution and habitat

This is the second species reported for Argentina, after *H. martinorum*. *Hapalotremus chasqui* sp. nov. distributed at about 1300–2000 m a.s.l. in the Yungas region (Figure 3b, c) (Figure 36) at Tucumán, Jujuy and Salta Provinces. The prevailing climate in this area is temperate with low humidity and winter snowfalls. The average maximum temperature in summer (January) is about 26°C, whereas in winter (July) it is about 16°C, with temperatures dropping as low as −10°C being common. East of this area, in Tucumán Province, is moist and consists of grasslands with groves of conifer, deciduous and

pepper trees, while west of this area is less moisture, favouring the presence of scattered cacti such as '*cardón*'.

Hapalotremus chespiritoi sp. nov.
(Figures 23–26, 37)

Type material
Male holotype (MUBI) from Peru, Canchis, Cusco, Sicuani, between Usicayos and Quetapalo (near Patambuco, 34 km northeast of Sicuani) (-14.1225 S, -70.9517 W), 3773 m a.s.l., 5 February 2007, Juan C. Chaparro col.; paratype female (MUBI), same data as holotype.

Etymology
The specific name is in honour of Roberto Gómez Bolaños (1929–2014), commonly known by his pseudonym 'Chespirito'. He was a Mexican screenwriter, actor, comedian, film and television director, widely regarded as one of the most important Spanish-language humorists of the twentieth century. Curiously, the shape of the spermatheca of female of *H. chespiritoi* sp. nov. resembles the small vinyl antennae of 'Chapulín Colorado', a comical and bungling superhero created by R.G. Bolaños.

Diagnosis
Males of *H. chespiritoi* sp. nov. can be distinguished from those of the other species by the palpal bulb with a slightly curved and very thick embolus and a well-developed basal digitiform apophysis (Figure 24a–d). Females can be distinguished from those of all other species by the shape of the spermathecae with a basal portion much wider than apical; rounded apical median region and apical lateral projections very well developed (Figure 26e).

Description
Holotype male (MUBI): Total length (not including chelicerae and spinnerets) 34.6, carapace length 16.4, width 15.0, abdomen 17.5 long. Fovea transverse, straight, width 2.0.

Colour pattern (in alcohol): carapace pale brown with white long setae on margins, legs black with white setae on coxae, abdomen black with white setae on distal dorsal region and light yellow setae on urticating patch (Figure 23a–c).

Eyes: anterior eye row procurved, posterior recurved (Figure 23d). Eyes sizes and interdistances: AME 0.17, ALE 0.22, PME 0.20, PLE 0.18, AME–AME 0.32, AME–ALE 0.19, PME–PME 0.66, PME–PLE 0.13, ALE–PLE 0.10, Ocular tubercle length 1.6, width 2.0, clypeus 0.25. Labium length 2.0, width 2.5 with 14 cuspules (Figure 23e). Maxillae: right with 99 cuspules, left with 119 cuspules. Sternum length 6.3, width 6.2. Three pairs of sternal oval sigillae, first pair hardly visible, second and third pairs visible, third pair less than half its length from the margin (Figure 23b). Chelicerae with 12 well-developed teeth on promargin of furrow and 26 small teeth on retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 12.5, 8.0, 9.2, 10.2, 7.3, 47.2; II: 12.2, 6.8, 9.2, 9.3, 7.5, 45.0; III:

11.5, 6.6, 8.9, 10.9, 6.4, 44.3; IV: 13.8, 7.6, 11.5, 16.3, 7.2, 56.4; palp: 9.7, 6.0, 7.6, –, 4.2, 27.5. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 1.1 long; PLS, three-segmented, 6.6 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I 2/3 scopulate and entire, II 3/4 scopulate and entire, III 1/4 scopulate and entire, IV with no scopulae. Dorsal face of all tarsi and cymbium with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora of palp and legs I–IV, 0; patellae; palp 0; I 1-1-2v; II 1v; III 1v; IV 1v, 1p, 1r; tibiae: palp 0; I 2-1-2-1v, 1-1r; II 2-1-1-1-2v, 1-1-1r; III 1-1d, 2-1-1-2v, 1-1-3-1-2-1p, 2-1-1-2r; IV 2-1-1-2v, 1-1-1-1-1p, 1-1-2-1-1-2-1r; metatarsi I 1v; II 1-1-2v, 1-1p, 2-2-1r; III 2d, 1-1-2v, 1-1-2p, 1-1-1-1-1r; IV 3-3-1-3v, 1-2-1-1p, 1-3-2-1r; tarsi I–IV, 0. Metatarsus I very curved at middle area (Figure 23f). Tibia I about 10% shorter than metatarsus I. Tibia I with two apophyses, which originated from a common base and branches are of almost equal size. The retrolateral branch conical bearing a short and strong spine on inner side; the prolateral branch digitiform bearing a short and strong spine on retrolateral side (Figure 23g). Flexion of metatarsus I between the two branches.

Palp: palpal tibia with a small retrolateral rounded process (Figure 23h, i). Palpal bulb base with a well-developed digitiform apophysis (Figure 24a–d); embolus very thick curved to the retrolateral face and prolateral keels strong and well-developed; PI well-developed beginning at basal ventral portion of embolus bearing a ventral medial crest pointed distally; PS less developed than PI (Figure 24a, b, e). Apical keel small, located below the apex of embolus (Figure 24a).

Urticating setae: Type III present and arranged in one dorsal posterior patch on the abdomen (Figure 23c).

Paratype female (MUBI): Total length (not including chelicerae and spinnerets), 34.8, carapace length, 15.6, width 13.0, abdomen 18.8 long. Fovea slightly procurved, width 2.1.

Colour pattern (in alcohol): carapace pale brown with white short setae on margins, legs black with white setae on coxae, abdomen light brown lacking most of setae and with light yellow setae on urticating patch (Figure 25a–e).

Eyes: anterior eye row procurved, posterior recurved (Figure 26b). Eyes sizes and interdistances: AME 0.20, ALE 0.32, PME 0.20, PLE 0.27, AME–AME 0.30, AME–ALE 0.25, PME–PME 0.68, PME–PLE 0.05, ALE–PLE 0.09. Ocular tubercle length 1.5, width 1.75, clypeus 0.25. Labium length 3.05, width 2.75 with 12 cuspules (Figure 26a). Maxillae: right with 116 cuspules, left with 111 cuspules. Sternum length 5.3, width 6.0. Three pairs of sternal oval sigillae, first pair hardly visible, second and third pairs visible, third pair almost next to the margin (Figure 25b). Chelicerae with 12 well-developed teeth on promargin of furrow and 23 small teeth on the retromargin.

Leg formula: IV > I > III > II. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 10.1, 7.0, 8.0, 7.5, 5.2, 37.8; II: 8.6, 6.1, 6.9, 7.3, 5.4, 34.3; III: 8.4, 5.8, 6.7, 8.9, 5.4, 35.2; IV: 9.8, 6.5, 9.5, 13.0, 7.1, 45.9; palp: 7.4, 4.5, 5.5, –, 6.6, 35.9. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 1.25 long; PLS, three-segmented, 4.0 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I 1/2 scopulate divided by three lines of setae, II 1/2

scopulate divided by four lines of setae, III 1/4 scopulate divided by four lines of setae, IV with no scopulae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora; palp 0; I 0; II 0; III 1-1d; IV 1d, 1-1p; patellae; palp 0; I 0; II 0; III 0; IV 1p; tibiae: palp 1-2v, 1r; I 0; II 1v; III 1-1-2v, 2-2p, 1-1r; IV 1-1-1-2v, 1-1-1p, 1-1-1r; metatarsi: I 1v; II 1-2v; III 1-1-1-2v, 1-1-1-1p, 1-1-1r; IV 1d, 1-1-3v, 1-1p, 1-1-2-1r; tarsi I–IV, 0.

Genitalia: Single spermathecal receptaculum with basal portion wider than apical; rounded apical median region and apical lateral projections well developed (Figure 26e).

Urticating setae: Type III present and arranged in one dorsal posterior patch on the abdomen (Figure 25c).

Distribution and habitat

Know only from the type locality at about 3700 m a.s.l. (Figure 37).

Hapalotremus kuka sp. nov.
(Figures 27, 36)

Type material

Female holotype (AMNH) from Bolivia, Chapare, Cochabamba, northeast of Sacaba (-17.4036 S, -62.0406 W), 3300 m a.s.l., 29 January 1976, L. E. Peña col.

Additional material examined

One female and three immatures (AMNH) from Bolivia, Chapare, Cochabamba, northeast of Sacaba (-17.4036 S, -62.0406 W), 3300 m a.s.l., 29 January 1976, L. E. Peña col.

Etymology

The specific name is a noun in apposition formed by the Quechua and Aymara word *kuka*, which means 'coca', referring to the plant species *Erythroxylum coca* Lam. 1786 originated from the Amazon Andes and used by Pre-Inca and Inca cultures for rituals in relation to men and nature (Academia Mayor de Lengüa Quechua 2005).

Diagnosis

Females of *H. kuka* sp. nov. resemble those of *H. chasqui* sp. nov. and *H. martinorum* by the large number of labial cuspules (more than 25 cuspules), but differ by the presence of scopulae on metatarsi IV (Figure 27f) in combination with spermathecae having apical lateral projections well developed, elongated and located more apically than in *H. chasqui* sp. nov. and *H. martinorum* (Figure 27g). Male unknown.

Description

Holotype female (AMNH): Total length (not including chelicerae and spinnerets) 26.51. Carapace: length, 11.11; width 9.37. Abdomen length 13.73. Fovea: slightly procurved, width 1.7.

Colour pattern (in alcohol): carapace reddish brown with white short setae on margins and basal, legs brown with very long white setae on coxae, trochanter and femora, abdomen light brown with light yellow setae on urticating patch (Figure 27a–c).

Eyes: anterior eye row procurved, posterior recurved (Figure 27d). Eyes sizes and inter-distances: AME 0.12, ALE 0.19, PME 0.10, PLE 0.14, AME–AME 0.18, AME–ALE 0.12, PME–PME 0.43, PME–PLE 0.05, ALE–PLE 0.11. Ocular tubercle: length, 0.92; width, 0.64. Clypeus: length, 0.2. Labium: length, 1.34; width, 1.79, with 27 cuspules (Figure 27e). Maxillae: right with 115 cuspules, left with 112 cuspules. Sternum: length, 5.15; width, 4.76. Three pairs of sternal oval sigillae, all pairs hardly visible (Figure 27b). Chelicerae: with 9 well-developed teeth on promargin of furrow and 19 small teeth on the retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 7.09, 5.15, 5.1, 3.94, 3.31, 24.59; II: 6.79, 4.64, 4.42, 4.69, 3.79, 24.3; III: 5.12, 3.9, 4.24, 5.04, 3.7, 22.0; IV: 8.3, 5.35, 6.01, 7.68, 3.98, 31.3; palp: 5.56, 3.7, 4.12, -, 3.84, 17.2. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 0.8 long; PLS, three-segmented, 4.2 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV. Metatarsi I 1/2 scopulate divided by three rows of setae, II 1/3 scopulate divided by three rows of setae, III 2/3 scopulate divided by approximately six rows of setae, IV 1/4 apical scopulate divided by approximately eight rows of setae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora: Palp 1d; III 1d; legs I, II and IV, 0. Patellae of palp and Legs I–IV, 0. Tibiae: palp 1-2v, 1-1r; I 1-2v; II 1-2v, 1p, III 2-1-2v, 1-1-1p, 1r; IV 1-1-2v, 1-1r. Metatarsi: I 1-3v; II 2-3v; III 1-2-3v, 2-1p, 1-2-1-1r; IV 2-2-1-2v, 1-1-1r, 1-1-1p. Tarsi: I–IV 0.

Genitalia: Single spermathecal receptacle with basal portion wider than apical and basal projections well-developed, in combination with apical lateral projections well-developed, elongated and located apically (Figure 27g).

Urticating setae: Type III present and arranged in one dorsal posterior patch on the abdomen (Figure 27c).

Distribution and habitat

Known only from the type locality, at about 3300 m a.s.l. (Figure 36).

Hapalotremus marcapata sp. nov.
(Figures 1f, 28, 29, 37)

Type material

Female holotype (MUBI) from Peru, Quispicanchis, Cusco, Marcapata, Huancarayoc (Marcapata Valley) (-13.6028 S, -70.9542 W), 3368 m a.s.l., 20 February 2006, Juan C. Chaparro col.

Etymology

The specific epithet 'Marcapata' corresponds to the Quechuan word, which means on the summit; and also to Marcapata Valley, located in the Andes in southern Peru, Cusco Department, which belongs to the Vilcanota mountain chain.

Diagnosis

Females of *H. marcapata* sp. nov. differ from those of all other species of *Hapalotremus* by the colour pattern, being entirely black with red setae on dorsal abdomen urticating patch (Figure 1f). Additionally, females of *H. marcapata* sp. nov. can be distinguished from those of all other species by the femora of palp and legs I–IV bearing a single dorsal spine, in combination with the shape of the spermathecae having its basal portion much wider than apical; noticeably domed apical median region and apical lateral projections slightly developed (Figure 29e). Male unknown.

Description

Holotype female (MUBI): Total length (not including chelicerae and spinnerets) 40.0. Carapace: length, 17.3; width 15.2. Abdomen in bad condition: length 22.0. Fovea: slightly procurved, width 2.3.

Colour pattern (live specimen): entirely black with pink hairs on margin of carapace and with red setae on dorsal abdomen urticating patch (Figure 1f).

Eyes: anterior eye row procurved, posterior recurved (Figures 28a, 29b). Eyes sizes and interdistances: AME 0.26, ALE 0.28, PME 0.30, PLE 0.19, AME–AME 0.38, AME–ALE 0.29, PME–PME 0.87, PME–PLE 0.16, ALE–PLE 0.24, Ocular tubercle: length, 1.4; width, 1.9. Clypeus: length, 0.3. Labium: length, 2.0; width, 2.6, with 18 cuspules (Figure 29a). Maxillae: right with 126 cuspules, left with 112 cuspules. Sternum: length, 7.6; width, 7.2. Three pairs of sternal elongated sigillae, all pairs hardly visible (Figure 28b). Chelicerae: with 13 well-developed teeth on promargin of furrow and 18 small teeth on the retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 11.9, 7.5, 8.4, 7.3, 5.0, 40.1; II: 11.6, 6.2, 5.8, 8.3, 5.1, 37; III: 10.1, 5.6, 6.5, 8.8, 5.4, 36.4; IV: 12.7, 6.5, 10.1, 13.5, 7.0, 49.8; palp: 7.7, 4.9, 6.0, –, 6.2, 24.8. Field of spiniform setae on basal retrolateral face of palp and legs I–IV. Spinnerets: PMS, 1.1 long; PLS, three-segmented, 5.8 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV (Figure 29c, d). Metatarsi I 2/3 scopulate divided by three rows of setae, II 1/2 scopulate divided by three rows of setae, III 1/4 scopulate divided by approximately six rows of setae, IV with no scopulae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora of palp and Legs I–IV, 1d. Patellae of palp and Legs I–IV, 0. Tibiae: palp 2v, 1p; I 1p; II 1-1v, 1-1p, III 1-1-2v, 1-2-1p, 1-1r; IV 1-1-2v, 1-1-2-1p, 1-2-2-1r. Metatarsi: I 1-2v; II 1-2v, 1p; III 2-2-1v, 1-1-2-2p, 2-2-2r; IV 1-1-2v, 2-2-1-2-2r, 2-1-1-1-2-2p. Tarsi: I–IV 0.

Genitalia: Single spermathecal receptacle with basal portion much wider than apical; noticeably domed apical median region and apical lateral projections slightly developed (Figure 29e).

Urticating setae: Type III present, abdomen in bad condition (Figure 28c).

Distribution and habitat

Known only from the type locality, at about 3300 m a.s.l. (Figure 37).

Hapalotremus perezmilesi sp. nov.
(Figures 30–33, 37)

Type material
Male holotype (MUBI) from Peru, Carabaya, Puno, Ollachea, between Ollachea and Corani (-13.8892 S, -70.5106 W), 3859 m a.s.l., 4 February 2007, Juan C. Chaparro col.; four paratypes females (MUBI), same data as holotype.

Etymology
The specific name is a patronym in honour of Fernando Pérez-Miles for his great contributions to the knowledge of systematics, biogeography, ecology and behaviour of Neotropical Theraphosidae.

Additional material examined
Immature (MUBI) from Peru, Carabaya, Puno, Ollachea, between Ollachea and Corani (-13.8892 S, -70.5106 W), 3859 m a.s.l., 4 February 2007, Juan C. Chaparro col.

Diagnosis
Males and females resemble those of *H. chespiritoi* sp. nov. by the body size (about 3 cm long) but differ by the reduced number of labial cuspules (4–8) (Figure 30e). Males resemble those of *H. martinorum* by the shape of palpal bulb and the much curved embolus but differ from them by the absence of an accessory keel (AK) on apical embolus (Figure 31a–d). Females can be easily distinguished from those of the other species by the spermathecae being oblong with basal portion slightly wider than apical, the apical median region almost straight and apical lateral projections inconspicuous (Figure 33e).

Description
Holotype male (MUBI): Total length (not including chelicerae and spinnerets) 28.5, carapace length 13.0, width 12.3, abdomen 13.6 long. Fovea transverse, straight, width 1.5.

Colour pattern (in alcohol): carapace brown with white long setae on margins, legs black with white setae on coxae, abdomen black with long light yellow setae on a dorsal posterior urticating patch (Figure 30a–c).

Eyes: anterior eye row procurved, posterior recurved (Figure 30d). Eyes sizes and interdistances: AME 0.24, ALE 0.31, PME 0.18, PLE 0.35, AME–AME 0.22, AME–ALE 0.16, PME–PME 0.56, PME–PLE 0.08, ALE–PLE 0.18, Ocular tubercle length 1.0, width 1.5, clypeus 0.75. Labium length 1.5, width 2.5 with four cuspules (Figure 30e). Maxillae: right with 71 cuspules, left with 65 cuspules. Sternum length 6.5, width 5.0. Three pairs of sternal oval sigillae, first pair hardly visible, second and third pairs visible, third pair about its length from the margin (Figure 30b). Chelicerae with 11 well-developed teeth on promargin of furrow and six small teeth on retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 10.8, 6.4, 7.0, 8.4, 5.8, 38.4; II: 10.0, 5.6, 6.8, 7.8, 6.0, 36.2; III: 8.9, 5.0, 6.5, 9.0, 6.1, 35.5; IV: 11.3, 5.4, 8.7, 12.4, 6.7, 44.5; palp: 8.3, 5.0, 7.5, –, 3.3, 24.1. Field of

spiniform setae on basal retrolateral face of palp and legs I–IV. Spinnerets: PMS, 1.5 long; PLS, three-segmented, 4.4 long.

Scopulae: All tarsi densely scopulate and divided ventrally by conical long setae increasing in number from tarsus I to IV. Metatarsi I 2/3 divided by two lines of setae, II 1/2 scopulate divided by three lines of setae, III 1/3 scopulate divided by three lines of setae, IV almost inconspicuous apical scopulate, hardly visible and divided by numerous conical setae. Dorsal face of all tarsi and cymbium with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora; palp 1d; I 1d; II 0; III 2-1-1d, 1r; IV 1-1d; patellae; palp 1d; I 0; II 1v; III 1v, 1r; IV 1d,; tibiae: palp 0; I 3v, 1p; II 3-2-1-2v,1-1p, 1-1r; III 1d, 2-1-2v, 2-2-1-1p, 1-1-1-1r; IV 1d, 2-2-2v, 1-1p, 1-1-1-1r; metatarsi I 3v, 1p, 1r; II 1-1d, 1-2-3v, 1-1p, 1-1r; III 1-2-3d, 1-2-3v, 1-2p, 1-2r; IV 1d, 2-1-1v, 2-1-1-1-1-2-1p, 1-1-1-1r; tarsi I–IV, 0.

Metatarsus I very curved at middle area (Figure 30g). Tibia I about 10% shorter than metatarsus I. Tibia I with two apophyses, which originated from a common base, and branches of equal size. The retrolateral branch conical; the prolateral branch digitiform bearing a short and strong spine on retrolateral side (Figure 30f, g). Flexion of metatarsus I between the two branches.

Palp: palpal tibia with a well-developed retrolateral rounded process (Figure 30h, i) on apex. Palpal bulb base lacking a digitiform apophysis (Figure 31a). Embolus thin and curved to the retrolateral face with prolateral keels well-developed; PI beginning at basal ventral portion of embolus bearing a blunt medial crest; PS less developed than PI, hardly visible (Figure 31a–d). Apical keel small, located below the apex of embolus.

Urticating setae: Type III present and arranged in one dorsal posterior patch on the abdomen (Figure 30c).

Paratype female (MUBI): Total length (not including chelicerae and spinnerets), 30.0, carapace length, 14.0, width 12.5, abdomen 14.5 long. Fovea slightly procurved, width 1.75.

Colour pattern (in alcohol): carapace pale brown with white short setae on dorsal central area and margins, legs brown with white setae on coxae, abdomen dark with orange setae on urticating patch, spinnerets pale brown (Figure 32a–e).

Eyes: anterior eye row procurved, posterior recurved (Figure 33b). Eyes sizes and interdistances: AME 0.20, ALE 0.25, PME 0.22, PLE 0.23, AME–AME 0.31, AME–ALE 0.22, PME–PME 0.76, PME–PLE 0.07, ALE–PLE 0.13, Ocular tubercle length 1.25, width 1.75, clypeus 0.75. Labium length 1.75, width 2.50 with five cuspules (Figure 33a). Maxillae: right with 65 cuspules, left with 67 cuspules. Sternum length 6.1, width 5.0. Three pairs of sternal oval sigillae, first pair hardly visible, second and third pairs visible, third pair about its length from the margin (Figure 32b). Chelicerae with 11 well-developed teeth on promargin of furrow and 8 small teeth on the retromargin.

Leg formula: IV > I > III > II. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 9.8, 6.6, 7.2, 6.4, 4.8, 34.8; II: 8.7, 5.3, 6.0, 6.7, 5.2, 31.9; III: 8.6, 5.3, 5.5, 7.5, 5.6, 32.5; IV: 10.2, 5.2, 8.2, 10.4, 6.8, 40.8; palp: 6.9, 5.3, 5.9, –, 6.0, 24.1. Field of spiniform setae on basal retrolateral face of palp and legs I–IV. Spinnerets: PMS, 1.2 long; PLS, three-segmented, 4.4 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV (Figure 33c, d). Metatarsi I 3/4 scopulate divided by three lines of setae, II 1/2 scopulate divided by four lines of setae, III 1/3 scopulate divided by more than four lines of setae, IV almost inconspicuous apical scopulate, hardly visible and divided by numerous conical setae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae (Figure 33c).

Chaetotaxy (left side): Femora; palp 0; I 0; II 0; III 1d; IV 0; patellae of palp and legs 0; tibiae: palp 4v; I 1v, 1r; II 1-3v, 1r; III 2-3v, 1r; IV 2-1-2v, 1-1p, 1-1r; metatarsi: I 1-3v; II 2-1-1-3v, 1r; III 1d, 2-2-3v, 1-1-1-1p, 1-1-1r; IV 1-2-2-1-2v, 1-1-1-1p, 1-1-1-1r; tarsi I–IV, 0.

Genitalia: Single spermathecal receptaculum oblong with basal portion slightly wider than apical; apical median region almost straight and apical lateral projections not developed (Figure 33e).

Urticating setae: Type III present and arranged in one dorsal posterior patch on the abdomen (Figure 32c).

Variation

Total length, females (n = 4): 25.1–33.6 (mean = 30.1 ± 3.6SD), carapace length, females: 11.2–16.4 (13.8 ± 2.1). Length of palp and legs, females: palp 15.3–24.1 (20.4 ± 4.03), I 22.2–36.1 (30.8 ± 6.2), II 20.6–32.4 (28.5 ± 5.4), III 20.1–32.5 (28 ± 5.6), IV 25.8–42 (36.4 ± 7.3). Labial cuspules, females 5–8, maxillary cuspules, right 53–84, left 58–91.

Distribution and natural history

Know only from the type locality at about 3800 m a.s.l. (Figure 37).

Hapalotremus vilcanota sp. nov.
(Figures 2c–f, 3e, g–j, 34, 35, 37)

Type material

Female holotype (MUSM–ENT 0508677) from Peru, Upis, Cordillera Vilcanota (-13.7594 S, -71.2703 W), 4524 m a.s.l., 4 July 2006, Tracie Seimon col.; two paratypes females (MUSM–ENT 0508680, 0508681), same data as holotype.

Additional material examined

Immature (MUSM–ENT 0508679) from Peru, Upis, Cordillera Vilcanota (-13.7594 S, -71.2703 W), 4485 m a.s.l., 4 July 2006, Tracie Seimon col.

Etymology

The specific epithet refers to the type locality where this species was found and also to the Cordillera Vilcanota which is a mountain chain located at southeastern Peru; the range extends for about 120 km through Puno and Cusco Departments. It is the second largest snowy concentration in Peru, with 469 glaciers in an area of about 418 km^2. It reaches its maximum altitude in the snowy Ausangate, with 6372 m a.s.l. (Salzmann et al. 2013).

Diagnosis

Females of *H. vilcanota* sp. nov. differ from those of the other species of *Hapalotremus* by the colour pattern, with carapace dark with white setae on margins almost reaching cephalic area and on the fovea; legs and palp with dark femora, the remaining segments white and abdomen ventrally and laterally white almost to dorsal region (Figure 2c, d, 34a–e). Additionally, females of *H. vilcanota* sp. nov. can be distinguished from those of all species by the spermathecae with basal portion wider than apical and with a noticeable constriction on median lateral area; apical median region domed, and apical lateral projections well developed and laterally located (Figure 35e). Male unknown.

Description

Holotype female (MUSM–ENT 0508677): Total length (not including chelicerae and spinnerets) 24.4. Carapace: length, 9.3; width 8.2. Abdomen: length 15.0. Fovea: procurved, width 2.0.

Colour pattern (live specimen): carapace dark, with whitish setae on margins reaching almost cephalic area and on the fovea; chelicerae with white setae; legs and palp with dark femora, the remaining segments white; abdomen dorsally black with red setae on urticating patch, abdomen ventrally and laterally white (Figure 2c, d).

Eyes: anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.14, ALE 0.16, PME 0.20, PLE 0.12, AME–AME 0.26, AME–ALE 0.09, PME–PME 0.52, PME–PLE 0.04, ALE–PLE 0.13, Ocular tubercle: length, 1.0; width, 1.25. Clypeus: length, 0.15. Labium: length, 1.25; width, 2.25, with 12 cuspules (Figure 35b). Maxillae: right with 126 cuspules, left with 117 cuspules. Sternum: length, 4.0; width, 4.1. Three pairs of sternal oval sigillae, first pair hardly visible, second and third pairs visible, third pair less than its length from the margin (Figure 34b). Chelicerae: with 13 well-developed teeth on promargin of furrow and 16 small teeth on the retromargin.

Leg formula: IV > I > II > III. Length of legs and palpal segments (femur, patella, tibia, metatarsus, tarsus, total): I: 6.7, 4.6, 5.1, 4.5, 3.3, 24.2; II: 6.4, 4.0, 4.0, 3.8, 3.2, 21.4; III: 5.2, 3.2, 3.5, 4.1, 3.0, 19.0; IV: 6.9, 4.1, 5.4, 6.2, 3.2, 25.8; palp: 5.2, 3.2, 3.5, –, 3.0, 14.9. Field of spiniform setae on basal retrolateral coxal face of palp and legs I–IV. Spinnerets: PMS, 0.75 long; PLS, three-segmented, 4.0 long.

Scopulae: All tarsi densely scopulate and divided by conical long setae increasing in number from tarsus I to IV (Figure 35c, d). Metatarsi I 1/2 scopulate divided by two rows of setae, II 1/2 scopulate divided by two rows of setae, III 1/3 scopulate divided by more than four rows of setae, IV with no scopulae. Dorsal face of all tarsi with two parallel rows of non-plumose clavate trichobothria interspersed with filiform, separated by a row of long, thin setae.

Chaetotaxy (left side): Femora of palp and Leg I, 1d. Patellae of Leg IV, 1v. Tibiae: palp 0; I 0; II 1v, III 3v, 2-1p, 1-1r; IV 2v, 1p, 1r. Metatarsi: I 2v; II 2v; III 1-2v, 2-1-2-2p, 1-1-1r; IV 2-2-3v, 1-1-1r. Tarsi: I–IV 0.

Genitalia: Single spermathecal receptacle with basal portion wider than apical and with noticeable constriction and bulge on median lateral area; apical median area domed and apical lateral projections well developed (Figure 35e).

Urticating setae: Type III present and arranged in one dorsal median patch on the abdomen (Figure 34d).

Variation

Total length, females (n = 3): 24.4–25.4 (mean = 24.8 ± 0.5SD), carapace length, females: 9.3–11.1 (10.4 ± 0.9). Length of palp and legs, females: palp 12.5–14.9 (14.1 ± 1.3), I 22.5–24.6 (23.7 ± 1.1), II 20.1–22.4 (21.2 ± 1.05), III 17.2–24.2 (20.5 ± 3.5), IV 24.6–25.8 (25.1 ± 0.6). Labial cuspules, females 8–12, maxillary cuspules, right 91–126, left 87–124.

Distribution and habitat

Known only from type locality (Figure 37). This species was found living at about 4500 m a.s.l. (Figure 3e, g–j). At this area, global elevation records have been documented for agricultural and flowering plants, orchids, amphibians, pelecypods and lizards (Seimon et al. 2007, 2017). The Cordillera Vilcanota mountain range is among the highest in Peru, with the highest peak (Nevado Ausangate) at 6384 m a.s.l., and glaciers terminating around 4700–5000 m a.s.l. (Salzmann et al. 2013). Climatically, this area experiences two distinct seasons: a wet and warm (1–2°C higher) season during the summer in southern hemisphere (October–November to April–March) and a dry and cold season (April–May to September–October) (Rabatel et al. 2013). As a result, most of the precipitation falls during the warm and wet season (Hanshaw and Bookhagen 2014). High-alpine ecosystems are unique habitats with extreme conditions and at such elevations, atmospheric pressure is 50–60% that of sea level, and plants are adapted to a lower CO_2 environment (Halloy 1981). Specimens were observed in burrows constructed under big rocks (Figure 2e, f). One adult female was found together with 27 early instar offspring in the same burrow on 4 July 2006.

Identification key to the species of male Hapalotremus

Males of *H. carabaya* sp. nov., *H. kuka* sp. nov., *H. marcapata* sp. nov. and *H. vilcanota* sp. nov. are unknown.

1. Presence of digitiform apophysis at basal tegulum of copulatory bulb (Figure 8b) 2
– Absence of digitiform apophysis (Figures 20a, 31a) 3
2. Numerous labial cuspules (usually more than 20) (Figure 19b)..... ***H. chasqui*** sp. nov.
– Few labial cuspules (about four to eight) (Figure 30e)... ... ***H. perezmilesi*** sp. nov.
3. Embolus with an accessory keel (AK) on tip (Figure 14a, e)..... ..... ***H. martinorum***
– Embolus without an accessory keel on tip 4
4. Long spiniform setae on entire pro- and retrolateral coxal faces of legs I–IV (Figure 10b, see also Figure 21d)..... ..... ***H. major***
– Absence of spiniform setae on coxae of legs 5
5. Embolus almost straight (Figure 24a–d); tibia I as long as metatarsus I (Figure 23f).... ..... ***H. chespiritoi*** sp. nov.
– Embolus very curved (Figure 8a–d); tibia I shorter than metatarsus I (Figure 7g)... ..... ***H. albipes***

Identification key to the species of female Hapalotremus

1. Presence of long spiniform setae on entire pro- and retrolateral coxal faces of legs I–IV (Figure 21b, d) 2

– Absence of such spiniform setae 3
2. Reduced number of labial cuspules (about five) (Figure 12d); basal portion of spermathecae narrower than apical region and lateral projections slightly developed (Figure 12g) ..... ***H. major***
– Numerous labial cuspules (about 25) (Figure 22a); basal portion of spermathecae wider than apical region (Figure 22e) and lateral projections well developed and located apically ..... ***H. chasqui*** sp. nov.
3. Reduced number of labial cuspules (less than 20), usually between 5 and 15 4
– Large number of labial cuspules (more than 20) 9
4. Femora of palp and legs I–IV bearing one dorsal spine ..... ***H. marcapata*** sp. nov.
– Femora of palp and legs I–IV without dorsal spine 5
5. Spermathecae of female with one additional well-developed apical median projection with a long thin wavy groove extending downward dorsal median region from this projection (Figure 18e–f) ..... ***H. carabaya*** sp. nov.
– Spermathecae of female without additional projection 6
6. Spermathecae of female with apical lateral projections well developed (Figures 26e, 35e) 7
– Spermathecae of female with apical lateral projections slightly developed or almost inconspicuous (Figures 9j, 33e) 8
7. Small body size (less than 25 mm in total length); spermathecae with a noticeable constriction and bulge on median lateral area (Figure 35e) ..... ***H. vilcanota*** sp. nov.
– Larger body size (about 35 mm in total length); spermathecae without such constriction and bulge on median lateral area (Figure 26e) ***H. chespiritoi*** sp. nov.
8. Abdomen dark without white spots; spermathecae oblong with apical lateral projections almost inconspicuous (Figure 33e) ..... ***H. perezmilesi*** sp. nov.
– Abdomen dark with two or three white spots, largest spot arrow-shaped, and three or four posterior lateral white lines (Figure 9c); spermathecae with basal portion wider than apical (Figure 9j) ..... ***H. albipes***
9. Spermathecae with lateral projections well-developed and apically oriented (Figure 27g) ..... ***H. kuka*** sp. nov.
– Spermathecae with lateral projections less developed and laterally oriented (Figure 16e) ..... ***H. martinorum***

Discussion

Spiders of the genus *Hapalotremus* Simon 1903 were initially placed in the subfamily Ischnocolinae until Raven (1985) tentatively transferred them to the subfamily Theraphosinae because of their morphological affinites found within that subfamily. However, Schmidt (1993) returned *Hapalotremus* to Ischnocolinae as a 'provisional placement', mainly by the presence of a reduced number of labial cuspules and the metatarsus I curved on males. As a result, from the phylogenetic analysis and taxonomic revision of Theraphosinae made by Pérez-Miles et al. (1996), *Hapalotremus* was placed in the Theraphosinae according to the morphology of the male palpal bulb, with extended subtegulum and conspicuous keels in the embolus, females having a single spermathecal receptaculum and the presence of type III urticating setae. Recently, a new division of

the Theraphosinae was proposed by Turner et al. (2017) under a molecular framework, so positioning *Hapalotremus* into the Hapalopini tribe. This tribe contains multiple genera with only type III urticating hairs (Turner et al. 2017). Pérez-Miles et al. (1996) proposed diagnostic characters to distinguish the genus based only on the morphology of the type species *H. albipes*. Hence, four synapomorphies were proposed for *Hapalotremus*: (i) a reduced number of labial cuspules; (ii) apical region of the bulb subconical; (iii) sclerites II + III of the bulb wide; and (iv) two subequal keels on palpal bulb (Pérez-Miles et al. 1996). With the addition of new species, we observed that one of these characters is not diagnostic for all species, since *H. chasqui* sp. nov., *H. martinorum* and *H. kuka* sp. nov. have a large number of labial cuspules (more than 20). Additionally, with the examination of new material and description of adult specimens, we found some new characters that could constitute new synapomorphies, such as the small field of strong setae located on the basal retrolateral coxal face of palp and legs (Figure 6b); males having a metatarsus I strongly curved (Figure 7g), and the presence of a retrolateral rounded process on male palpal tibia (Figure 7h, i). Moreover, the presence of a prolateral inferior keel extending along almost the entire embolus and having a pronounced crest at the middle (Figure 6f) was observed in all known males. The genera *Hapalopus*, *Metriopelma* and *Chromatopelma* have the PI very well developed, as in *Hapalotremus* (Bertani 2000). However, in *Hapalopus* PI is split in two and *Metriopelma* and *Chromatopelma* have the entire PI presenting a triangular shape (Bertani 2000). Unfortunately, until a cladistics analysis is carried out, it cannot be said that these diagnostic characters are synapomorphies for the genus. To date, *Hapalotremus* has been included in the phylogenetic analysis made by Pérez-Miles et al. (1996) and Pérez-Miles (2000) and the relationships between this genus and other Theraphosinae genera were treated. According to these works, *Hapalotremus* was placed in a derived position within the Theraphosinae. Pérez-Miles et al. (1996) argued that a transformation series in the spermathecae occurs from the primitive condition of two separated spermathecae, to a widely fused condition, and finally to a single receptacle. Thus, an important feature that suggests the derived placement of *Hapalotremus* is the shape of the spermathecae, which in all species consists of a single oval receptacle. From both works, *Hapalotremus* was recovered as closely related to *Hapalopus* given by the presence of a double male tibial apophysis and a metatarsus I strongly curved. Recently, Perafán et al. (2016) analyzed the cladistics relationships of the genus *Kankuamo* Perafán, Galvis and Pérez–Miles, 2016 within the Theraphosinae. The authors included *Hapalotremus* in this cladistics analysis, which occupied a more basal position in the general cladogram and a basal group from the clade conformed by *Euathlus* Ausserer, 1875, *Phrixotrichus* Simon, 1889, *Bumba* Pérez-Miles, Bonaldo and Miglio, 2014, *Melloleitaoina* Gerschman de Pikelín and Schiapelli, 1960, *Tmesiphantes* Simon, 1892b, *Grammostola* Simon, 1892a, *Homoeomma* Ausserer, 1871 and *Plesiopelma* Pocock, 1901, primarily given by the reduced number of labial cuspules and by the curved metatarsus I, the flexion of it, the presence of an apical keel on embolus and the shape of the spermathecae (Perafán et al. 2016). However, from the present study, some new features or character states such as the ventral crest on PI that could be similar to the ventral crest of *Euathlus*, or the number of labial cuspules, the retrolateral process of male palpal tibia (shared also by *Bumba*) or the digitiform apophysis of the bulb (present in *Homoeomma*) could suggest a new placement of *Hapalotremus* within the Theraphosinae.

Bertani (2000) revised and homologized the keels of male palpal bulbs in Theraphosinae. Unfortunately, no specimens of *Hapalotremus* were revised in this work. However, Bertani (2000) came to some conclusions based on the interpretation of male palpal bulb characters carried out in the Pérez-Miles et al. (1996) cladistics analysis. Arguably, Bertani (2000) found incongruence between the character evolution proposed and to that of Pérez-Miles et al. (1996), particularly on the branches including the genera *Schizopelma* Pickard-Cambridge, 1897, *Metriopelma* Becker, 1878, *Hapalopus* and *Hapalotremus*. From the contribution of the present work, all known species studied share the presence of a PI, PS and A keels (noting that *H. martinorum* additionally possess an accessory keel). These keels are found in *Hapalopus* (with the absence of an apical keel) and in *Metriopelma* in agreement with those found by Bertani (2000). This could indicate a more basal placement of *Hapalotremus* within the Theraphosinae (as was found by Perafán et al. 2016), since Bertani (2000) stated that the presence of PI and PS keels on the male palpal bulb are plesiomorphic to Theraphosinae. Although a cladistics analysis of the genus is necessary to clarify the relationships between species and the relations with other Theraphosinae genera, we think this is inapplicable at this stage because of the lack of information on most *Hapalotremus* males.

Species of *Hapalotremus* are distributed mainly along the biogeographic Provinces of Puna (South American Transition Zone) and Yungas (South Brazilian dominion) of western South America (Morrone 2014). Thus, the area distribution of the genus comprises the western slopes of the Andes, between 1300 and 4500 m of altitude, from southern Peru, Bolivia to northwestern Argentina. The lowest and southernmost known record of the genus was that reported for *H. martinorum* (Cavallo and Ferretti 2015). However, with the discovery of *H. chasqui* sp. nov. the southern distribution has been extended about 200 km and the lowest altitude corresponds to about 1300 m a.s.l.

Females of *H. major* and *H. marcapata* sp. nov. presented with the abdomen ruptured, so it was possible to see a small number of large preserved eggs. Those females were originally collected in April and February, respectively. *Hapalotremus* males from the species distributed along the Yungas biogeographic province (*H. albipes* and *H. chasqui* sp. nov.) appear to be active in the month of October and those males of high altitudes along the Puna biogeographic province (*H. major*, *H. chespiritoi* sp. nov. and *H. perezmilesi* sp. nov.) are active on February–April (data from collection labels). From the dates when some males were found, it is probable that the life cycle for most *Hapalotremus* is that males mature and breed with the females at the beginning of the rainy summer season, which extends from November to April, and that females produce their egg sac at the start of the dry winter season, which extends from April to November. Also, according to the extreme habitat conditions in these high-elevation environments (Krajick 2006; Hanshaw and Bookhagen 2014; Seimon et al. 2017), females could produce much larger and fewer ova in an egg sac so that when the young develop and emerge they are large and have a higher chance for survival (possibly a *K* reproductive strategy) (Stubbs 1978; Parry 1981). Moreover, this is consistent with the large instar observed with the maternal female of *H. vilcanota* sp. nov. during July (Tracie Seimon, pers. obs.).

Finally, we recommend and consider it necessary to carry out more fieldwork to collect and describe the males of some *Hapalotremus* species, since most are known only

from females. Consequently, the additional material of the different species of the genus will allow a better understanding of their diversity and their evolutionary relationships.

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References

Academia Mayor de Lengüa Quechua. 2005. Diccionario Quechua – Español. 2da Edición ed. Peru: Cusco; p. 1–479.

Ausserer A. 1871. Beiträge zur Kenntnis der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). Verh K K Zool Bot Ges Wien. 21:117–224.

Ausserer A. 1875. Zweiter Beitrag zur Kenntniss der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). Verh K K Zool Bot Ges Wien. 25:125–206.

Becker L. 1878. Sur un nouveau genre d'Avicularidae. Ann Soc Ent Belg. 21:256–257.

Bertani R. 2000. Male palpal bulbs and homologous features in Theraphosinae (Araneae, Theraphosidae). J Arachnol. 28:29–42.
Bertani R. 2001. Revision, cladistic analysis and zoogeography of *Vitalius, Nhandu* and *Proshapalopus*, with notes on other theraphosine genera (Araneae, Theraphosidae). Arq Zool. 36:265–356.
Bertani R, Guadanucci JPL. 2013. Morphology, evolution, and usage of urticating setae by tarantulas (Araneae: Theraphosidae). Zoologia. 30(4):403–418.
Bond JE. 2012. Phylogenetic treatment and taxonomic revision of the trapdoor spider genus *Aptostichus* Simon (Araneae, Mygalomorphae, Euctenizidae). Zookeys. 252:1–209.
Cavallo P, Ferretti N. 2015. The first *Hapalotremus* Simon, 1903 (Araneae: Theraphosidae) from Argentina: description and natural history of *Hapalotremus martinorum* sp. nov. J Nat Hist. 49 (15–16):873–887.
Chamberlin RV. 1916. Results of the Yale Peruvian Expedition of 1911. Arachnida Bull Mus Comp Zool. 60:177–299.
Cooke JAL, Roth VD, Miller FH. 1972. The urticating hairs of theraphosid spiders. Am Mus Novit. 2498:1–43.
Coyle FA. 1995. A revision of the funnel web mygalomorph spider subfamily Ischnothelinae (Araneae, Dipluridae). Bull Am Mus Nat Hist. 226:1–133.
Ferretti N. 2015. On three new *Euathlus* tarantulas from Argentina and cladistics analysis of the genus. J Arachnol. 43(3):313–326.
Gabriel R. 2016. Revised taxonomic placement of the species in the Central American genera *Davus* O. Pickard-Cambridge, 1892, *Metriopelma* Becker, 1878, and *Schizopelma* F. O. Pickard-Cambridge, 1897, with comments on species in related genera (Araneae: Theraphosidae). Arachnology. 17(2):61–92.
Gerschmande Pikelín BS, Schiapelli RD. 1960. Un nuevo género con una nueva especie de Ischnocolinae (Araneae-Theraphosidae). Physis. 21:200–206.
Gerschman de Pikelín BS, Schiapelli RD. 1973. La subfamilia Ischnocolinae (Araneae: Theraphosidae). Rev Mus Argent Cienc Nat. 4:43–77.
Guadanucci JPL. 2012. Trichobothrial morphology of Theraphosidae and Barychelidae spiders (Araneae, Mygalomorphae). Zootaxa. 3439:1–42.
Halloy SRP. 1981. La presión de anhidrido carbónico como limitante altitudinal de las plantas. Lilloa. 35:159–167.
Hanshaw MN, Bookhagen B. 2014. Glacial areas, lake areas, and snow lines from 1975 to 2012: status of the Cordillera Vilcanota, including the Quelccaya Ice Cap, northern central Andes, Peru. Cryosphere. 9:359–376.
Kaderka R. 2015. *Bistriopelma*, a new genus with two new species from Peru (Araneae, Theraphosidae, Theraphosinae). Rev Peru Biol. 22(3):275–288.
Krajick K. 2006. Living the high life: the mountaintop environment of the Andes harbors a Noah's ark of previously undocumented species. Nat Hist. 115:4–50.
Lamarck J. 1786. Encyclopédie Méthodique, Botanique. Paris; p. 393.
Lucas SM, Indicatti RP. 2015. Revalidation of *Dolichothele* Mello-Leitão and notes on *Hapalotremus* Simon (Araneae, Mygalomorphae, Theraphosidae). Stud Neotrop Fauna Environ. 50(3):204–212.
Mello-Leitão CF de. 1923. Theraphosoideas do Brasil. Rev Mus Paul. 13:1–438.
Mello-Leitão CF de. 1929. Aranhas do Pernambuco colhidas por D. Bento Pickel. An Acad Bras Cienc. 1:91–112.
Morrone JJ. 2014. Biogeographical regionalisation of the Neotropical region. Zootaxa. 3782(1):1–110.
Ortiz D, Francke OF. 2017. Reconciling morphological and molecular systematics in tarantulas (Araneae: Theraphosidae): revision of the Mexican endemic genus *Bonnetina*. Zool J Linn Soc. doi:10.1093/zoolinnean/zlw013
Parry GD. 1981. The meanings of r– and K–selection. Oecologia. 48(2):260–264.
Perafán C, Cifuentes Y, Estrada-Gómez S. 2015. *Aguapanela*, a new tarantula genus from the Colombian Andes (Araneae, Theraphosidae). Zootaxa. 4033(4):529–542.

Perafán C, Galvis W, Gutiérrez M, Pérez-Miles F. 2016. *Kankuamo*, a new theraphosid genus from Colombia (Araneae, Mygalomorphae), with a new type of urticating setae and divergent male genitalia. Zookeys. 601:89–109.
Perafán C, Pérez-Miles F. 2014. The Andean tarantulas *Euathlus* Ausserer, 1875, *Paraphysa* Simon, 1892 and *Phrixotrichus* Simon, 1889 (Araneae: Theraphosidae): phylogenetic analysis, genera redefinition and new species descriptions. J Nat Hist. 48(39–40):2389–2418.
Pérez-Miles F. 2000. *Iracema cabloca* new genus and species of a theraphosid spider from Amazonic Brazil (Araneae, Theraphosinae). J Arachnol. 28:141–148.
Pérez-Miles F, Bonaldo AB, Miglio L.T. 2014. Bumba, a replacement name for Maraca Pérez-Miles, 2005 and Bumba lennoni, a new tarantula species from western Amazonia (Araneae, Theraphosidae, Theraphosinae). ZooKeys. 448:1–8.
Pérez-Miles F, Gabriel R, Miglio L, Bonaldo A, Gallon R, Jimenez JJ, Bertani R. 2008. Ami, a new theraphosid genus from Central and South America, with description of six new species (Araneae: mygalomorphae). Zootaxa. 1915:54–68.
Pérez-Miles F, Locht A. 2003. Revision and cladistics analysis of the genus *Hemirrhagus* Simon, 1903 (Araneae, Theraphosidae, Theraphosinae). Bull Br Arachnol Soc. 12:365–375.
Pérez-Miles F, Lucas SM, Jpi DS, Bertani R. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: theraphosidae). Mygalomorph. 1:33–68.
Pérez-Miles F, Weinmann D. 2009. Two new species of *Cyriocosmus* Simon, 1903 from Peru and the highest altitude record for the genus (Araneae, Theraphosidae, Theraphosinae). Rev Iber Aracnol. 17:29–35.
Petrunkevitch A. 1925. Arachnida from Panama. Trans Conn Acad Arts Sci. 27:51–248.
Pickard-Cambridge O. 1892. Arachnida. Araneida. In: Ducane F, Godman J, Salvin O, editors. Biologia Centrali-Americana, Zoology. London: Porter; p. 89–104
Pickard-Cambridge FO. 1897. Arachnida – araneida and Opiliones. In: Ducane F, Godman J, Salvin O, editors. Biologia Centrali-Americana, Zoology. London: Porter; p. 1–40.
Platnick NI 2002. The world spider catalog, version 3.0. American Museum of Natural History. Available from: https://research.amnh.org/iz/spiders/catalog_3.0/index.html. Accessed on 7 April 2017.
Pocock RI. 1899. Diagnoses of some new Indian Arachnida. J Bomb Nat Hist Soc. 12:744–753.
Pocock RI. 1901. Some new and old Genera of South American Avicullariidae. Ann Mag Nat Hist. 7 (8):540–555.
Rabatel A, Francou B, Soruco A, Gomez J, Cáceres B, Ceballos JL, Basantes R, Vuille M, Sicart JE, Huggel C, et al. 2013. Current state of glaciers in the tropical Andes: a multi-century perspective on glacier evolution and climate change. Cryosphere. 7:81–102.
Raven RJ. 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematic. Bull Am Mus Nat Hist. 182:1–180.
Raven RJ. 2005. A new tarantula species from northern Australia (Araneae, Theraphosidae). Zootaxa. 1004:15–28.
Salzmann N, Huggel C, Rohrer M, Silverio W, Mark BG, Burns P, Portocarrero C. 2013. Glacier changes and climate trends derived from multiple sources in the data scarce Cordillera Vilcanota region, southern Peruvian Andes. The Cryosphere. 7:103–118.
Schmidt G. 1986. Vogelspinnen: lebensweise, Bestimmungsschlüssel, Haltung und Zucht. Minden: Albrecht Philler; p. 1–87.
Schmidt G. 1993. Das Weibchen von *Hapalotremus albipes* Simon 1903 (Araneida: theraphosidae). Arachnologischer Anzeiger. 4:10–14.
Schmidt G. 1997. Bestimmungsschlüssel für die Gattungen der Unterfamilie Theraphosinae (Araneae: Theraphosidae). Arachnologisches Magazin. 3:1–27.
Schmidt G. 2002. *Dolichothele* ist kein Synonym von *Hapalotremus* (Araneae: theraphosidae: Theraphosinae). Tarantulas of the World. 7:16–18.
Schmidt G. 2003. Die Vogelspinnen: eine weltweite Übersicht. Hohenwarsleben: Neue Brehm-Bücherei; p. 1–383.

Seimon T, Seimon A, Daszak P. 2007. Upward range extension of Andean anurans and chytridiomicosis to extreme elevations in response to tropical deglaciation. Glob Change Biol. 13:288–299.

Seimon T, Seimon A, Yager K, Reider K, Delgado A, Sowell P, Tupayachi A, Konecky B, McAloose D, Halloy S. 2017. Long-term monitoring of tropical alpine habitat change, Andean anurans, and chytrid fungus in the Cordillera Vilcanota, Peru: Results from a decade of study. Ecol Evol. 7:1527–1540.

Simon E. 1892a. Etudes arachnologiques. 24e Mémoire. XXXIX. Descriptions d'espèces et de genres nouveaux de la famille des Avicylariidae (suite). Ann Soc Entomol Fr. 61:271–284.

Simon E. 1892b. Histoire naturelle des araignées. Paris; p. 1–256.

Simon E. 1889. Etudes arachnologiques. 21e Mémoire. XXX. Descriptions de quelques arachnides du Chili et remarques synonymiques sur quelques unes des espèces décrites par Nicolet. Ann Soc Entomol Fr. 6(8):217–222.

Simon E. 1903. Histoire naturelle des araignées. Deuxiéme Edition Paris (Roret). 2:669–1080.

Soares BAM, Camargo HF de A. 1948. Aranhas coligidas pela Fundação Brasil-central (Arachnida-Araneae). Bol Mus Para Emílio Goeldi. 10:355–409.

Strand E. 1929. Zoological and palaeontological nomenclatorical notes. Acta Univ Latv. 20:1–29.

Stubbs M. 1978. Density dependence in the life–cycles of animals and its importance in K– and r–strategies. J Anim Ecol. 46:677–688.

Thorell T. 1869. On European spiders. Part I. Review of the European genera of spiders, preceded by some observations on zoological nomenclature. Nova Acta Regiae Soc Sci Upsaliensis. 3(7):1–108.

Thorell T. 1870. On European spiders. Nova Acta Regiae Soc Sci Upsaliensis. 3(7):109–242.

Turner SP, Longhorn SJ, Hamilton CA, Gabriel R, Pérez-Miles F, Vogler AP. 2017. Re-evaluating conservation priorities of New World tarantulas (Araneae: Theraphosidae) in a molecular framework indicates non-monophyly of the genera, *Aphonopelma* and *Brachypelma*. Syst Biodivers. 16 (1):89–107.

Vol F. 1999. A propos d'une spermatheque inhabituelle. Arachnides. 42:1–13.

World Spider Catalog [Internet]. 2017. World Spider Catalog version 18.0. Bern: Natural History Museum. Available from http://wsc.nmbe.ch