URTICATING SETAE OF TARANTULAS (ARANEAE: THERAPHOSIDAE): MORPHOLOGY, REVISION OF TYPOLGY AND TERMINOLOGY AND IMPLICATIONS FOR TAXONOMY

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Abstract

Tarantula urticating setae are modified setae located on the abdomen or pedipalps, which represent an effective defensive mechanism against vertebrate or invertebrate predators and intruders. They are also useful taxonomic tools as morphological characters facilitating the classification of New World theraphosid spiders. In the present study, the morphology of urticating setae was studied on 144 taxa of New World theraphosids, including ontogenetic stages in chosen species, except for species with urticating setae of type VII. The typology of urticating setae was revised, and types I, III and IV were redescribed. The urticating setae in spiders with type I setae, which were originally among type III or were considered setae of intermediate morphology between types I and III, are newly considered to be ontogenetic derivatives of type I and are described as subtypes. Setae of intermediate morphology between that of body setae and type II urticating setae that were found in Iridopelma hirsutum and Antillena rickwesti may provide another evidence that type II urticating setae evolved from body setae. It is supposed that the fusion of barbs with the shaft may lead to the morphology of type II setae. As the type II setae of Aviculariinae evolved independently to the UrS of Theraphosinae and both subfamilies represent two non-sister groups, this should explain the differences in the morphology of body setae in Aviculariinae and Theraphosinae. The terminology of “barbs” and “reversed barbs” was revised and redefined, newly emphasizing the real direction of barbs.

Introduction

The family Theraphosidae is the most species-rich and the most studied group of mygalomorph spiders [1]. An exclusive defensive mechanism using modified barbed setae called “urticating setae” (UrS) have been recorded in New World representatives belonging to subfamilies Theraphosinae Thorell, 1869 [2], Aviculariinae Simon, 1873 [3] and Psalmopoeinae
The UrS cover either the dorsal abdominal surface in Theraphosinae and Aviculariinae or the prolateral face of the palpal femora in Ephebopus Simon, 1892 (Psalmodoeinae) [5]. When disturbed, spiders frequently disperse their abdominal UrS by moving the posterior legs, or, in the case of palpal setae, by moving the palps along the basal segments of chelicerae and directing these airborne setae towards the intruder [5,6]. Some representatives of Aviculariinae (Avicularia Lamarc, 1818, Iridopelma Pocock, 1901 and Pachistopelma Pocock, 1901) and probably also Kankuamo Perafán et al., 2016 (Theraphosinae) require direct contact with the intruder to release the UrS [7,8,11]. The UrS penetrate the attacker’s skin or mucous membranes, whereby inducing a physical irritation. Some Theraphosinae also use the UrS as an additional component for making egg sacs and the silk mat for moulting as a passive defensive strategy against ants or the larvae of phorid flies [8,9,12].

To date, seven morphological types of UrS have been described (Fig 1). They differ in location, shape, size and orientation of barbs along the shaft, and the length/width ratio. Types I–IV were described and illustrated for the first time by Cooke et al. [6], who noted their value in the systematics of Theraphosidae. Later, Marshall & Uetz [5] described palpal type V in Ephebopus, and Pérez-Miles [13] proposed type VI in the Mexican genus Hemirrhagus Simon, 1903. Most recently, Perafán et al. [11] described the UrS of type VII in the Colombian genus Kankuamo. The occurrence of UrS types in South American genera of Aviculariinae, Psalmopoeinae and Theraphosinae is presented in Table 1.

Some species from the subfamily Theraphosinae have more than one type of UrS and setae of intermediate morphology [10,53]. Types I or IV usually occur in combination with type III [10]. The co-occurrence of types I and IV has not been recorded, nor have any intermediates between type II and types I, III or IV (16; personal observation). Studying the ontogeny of five Uruguayan species, Pérez-Miles [10] found that type III occurred later than the other types present (I or IV). He hypothesised that type III setae represent different types of setae masked by morphological similarity and derived from type I and IV, respectively. Pérez-Miles [10] also found some differences in the morphology of type III setae in species with the co-occurrence of types I+III and III+IV: the basal end of the type III seta in specimens having types I+III has a broad shaft, and at high magnification, this region shows flattened barbs. In specimens with types III+IV, the basal end of the type III seta has no flattened barbs and the shaft is not extended to the tip.

Bertani & Marques [7] and Bertani & Guadanucci [9,53] suggested that the UrS of types II, V and III had evolved independently and that the types I and IV had evolved later from an ancestor type III setae. This hypothesis was supported by the differences in position, structure and the release mechanism of UrS and by the existence of intermediates between types I and III, and III and IV. However, no intermediates between types I and IV were found. Bertani & Guadanucci [9] hypothesised that urticating setae of type II and type III had independently evolved from the relevant body setae and noted 1) the identical manner in which they are inserted into the spider tegument, 2) the resemblance between the truncated basal part of body setae and stalks in UrS, and 3) the morphological similarity of basal barbs in some variants of body setae and UrS. They found body setae setae variants with either type II or III urticating setae, but not with types I and IV [9]. A reconstruction of phylogenetic relationships based on analysis of set of genes [54] confirmed that urticating setae of type II and type III had independently evolved.

Since Pérez-Miles et al. [18] used UrS types in the phylogenetic analysis of Theraphosinae, the typology of the UrS has become an important taxonomical tool. The monophyly of Theraphosinae was reinforced by the presence of the abdominal UrS of types I, III and/or IV [18].
and type VI and VII [11]. Bertani & Marques [7] considered the absence of UrS in the majority of Theraphosidae as a plesiomorphic state.

The aim of this study is 1) to revise the morphological types or subtypes of UrS based on the examination of 144 species of Theraphosidae representing all known South American subfamilies, including their development during ontogeny in chosen species, and also 2) to implicate new findings for taxonomy of Theraphosidae with a support of previously published phylogenetic analyses based on both morphological and molecular data. The aim of the revision is 3) also to critically evaluate what is known in this field of research and 4) to compare the evolutionary hypotheses of UrS development derived from the mentioned phylogenetic analyses.

Fig 1. Abdominal urticating setae of types I, II, III, IV, VI and VII with their supporting stalks, and palpal urticating setae of the type V with the insertion socket.

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Table 1. Distribution of urticating setae types according to the previously published papers or unpublished observations.

| Genus                      | URTICATING SETAE TYPES | References |
|----------------------------|------------------------|------------|
|                            | I | II | III | IV | V | VI | VII |                  |
| **AVICULARIINAE**          |   |    |     |    |   |    |     |                  |
| *Antilena* Fukushima & Bertani, 2017 | – | + | – | – | – | – | – | [14]          |
| *Avicula* Lamarch, 1818    | – | + | – | – | – | – | – | [15]          |
| *Caribena* Fukushima & Bertani, 2017 | – | + | – | – | – | – | – | [14]          |
| *Iridopelma* Pocock, 1901  | – | + | – | – | – | – | – | [15]          |
| *Pachistopelma* Pocock, 1901 | – | + | – | – | – | – | – | [15]          |
| *Typhochlaena* C. L. Koch, 1850 | – | + | – | – | – | – | – | [15]          |
| *Ybyrapora* Fukushima & Bertani, 2017 | – | + | – | – | – | – | – | [14]          |
| **PSALMOPOEINAE**          |   |    |     |    |   |    |     |                  |
| *Epehopus* Simon, 1892     | – | – | – | – | + | – | – | [5]           |
| *Psalmopoeus* Pocock, 1895 | – | – | – | – | – | – | – | [16]          |
| *Pseudoclamoris* Hüsser, 2018 | – | – | – | – | – | – | – | [17]          |
| *Tapinauchenius* Ausserer, 1871 | – | – | – | – | – | – | – | [6,16]        |
| **THERAPHOSINAE**          |   |    |     |    |   |    |     |                  |
| *Acanthoscurria* Ausserer, 1871 | + | – | + | – | – | – | – | [18]          |
| *Acentropelma* Pocock, 1901 a | + | – | ? | – | – | – | – | [19,20]      |
| *Aenigmarchae* Schmidt, 2005 | – | – | – | – | – | + | – | [21]          |
| *Agnostopelma* Pérez-Miles & Weinmann, 2010 | – | – | + | – | – | – | – | [22]          |
| *Aguaapanela* Perafán & Cifuentes, 2015 | – | – | + | + | – | – | – | [23]          |
| *Aphonopelma* Pocock, 1901  | + | – | – | – | – | – | – | [6,18,24]   |
| *Bistriopelma* Kaderka, 2015 | – | – | + | – | – | – | – | [25]          |
| *Bonnetina* Vol, 2000      | – | – | + | – | – | – | – | [26]          |
| *Brachypelma* Simon, 1891  | + | – | + | – | – | – | – | [18]          |
| *Bumba* Pérez-Miles, Bonaldo & Miglio, 2014 | – | – | + | – | – | – | – | [27]          |
| *Cardiopelma* Vol, 1999    | ? | ? | + | ? | ? | ? | ? | J. I. Mendoza Marroquin, pers commun. |
| *Catanduba* Yamamoto et al., 2012 | – | – | + | – | – | – | – | [28]          |
| *Chromatopelma* Schmidt, 1995 | – | – | + | – | – | – | – | [16]          |
| *Citharacanthus* Pocock, 1901 | + | – | – | – | – | – | – | [18]          |
| *Clavopelma* Chamberlin, 1940 | + | – | – | – | – | – | – | [16]          |
| *Cotzeteliana* Mendoza Marroquin, 2012 | + | – | – | – | – | – | – | [29]          |
| *Crassicros* Reichling & West, 1996 | + | – | – | – | – | – | – | [16]          |
| *Cubanana* Ortiz, 2008     | + | – | + | – | – | – | – | [30]          |
| *Cyclolampros* Ausserer, 1871 | – | – | + | – | – | – | – | [18]          |
| *Cryosimus* Simon, 1903    | – | – | + | – | – | – | – | [31,32]      |
| *Cytrophilus* Simon, 1892  | + | – | + | – | – | – | – | types I, III [6]; type III [16]; type I [18] |
| *Dassus* Cambridge, 1892   | – | – | + | – | – | – | – | [16,19]      |
| *Eucnemus* Ausserer, 1875  | – | – | + | – | – | – | – | [33]          |
| *Eupalaeus* Pocock, 1901    | + | – | + | – | – | – | – | [18]          |
| *Eurypholnella* Strand, 1907 a | + | – | ? | – | – | – | – | [19,20]      |
| *Grammostola* Simon, 1892  | – | – | + | – | – | – | – | [6]; as *Phrixotrichus* in [18] |
| *Hapalopus* Ausserer, 1875 b | – | – | + | – | – | – | – | [18], [31] |
| *Hapalotremus* Simon, 1903  | – | – | + | – | – | – | – | [18]          |
| *Hemirrhagus* Simon, 1903  | – | – | – | – | + | – | – | [13,34,35]  |
| *Homoeoarma* Ausserer, 1871 | – | – | + | – | – | – | – | [18]          |
| *Kankuamo* Perafán et. al., 2016 | – | – | – | – | + | – | – | [11]          |
| *Kochiana* Fukushima et al., 2008 | – | – | + | – | – | – | – | [36]          |

(Continued)
Materials and methods

For the morphological analyses, the UrS were removed from four different areas (anterior, central, posterior and lateral, see Fig 2) using forceps, placed in alcohol, and subsequently
examined and measured using an Olympus BH2-RFCA binocular microscope. The samples for measurement were taken from the central area of the urticating setae patch only. The setae without supporting stalks were measured along the shaft and the seta curvature was interpolated. After the collection of each sample, the forceps were cleaned to avoid contamination by the setae from the previous sample. After dehydration in a CPD 030 critical point dryer (BAL-TEC GmbH, Schalkmühle, Germany) and gold coating in a SCD 030 ion sputtering device (BAL-TEC GmbH, Schalkmühle, Germany), the selected samples were examined using a JSM-6380LV scanning electron microscope (JEOL Ltd., Akishima-shi, Japan). The UrS barbs were measured in the basal third of the seta. The ontogenetic stage was characterised via the carapace length, which was measured using a calliper. All of the measurements were provided in millimetres. For the material used in morphological studies, see S1 File. The typology of the UrS follows Cooke et al. [6] (in part), Marshall & Uetz [5], Pérez-Miles [13] and Perafán et al. [11]. For morphological repetitions of the basic types of urticating setae we used the term "subtype". The concept of “barbs” and “reversed barbs” proposed by Cooke et al. [6] was revised and unified, newly emphasizing a real direction of barbs. Generally, setal barbs, which point upwards to the apical tip and which are present in the majority of covering setae of spiders, are called “barbs”. The setal barbs pointing upwards are present, for example, in plumose setae or stout plumose stridulatory setae or bristles, tarsal scopula setae, long tactile setae, any types of

[Fig 2. Distribution of urticating setae types (grey zones) on the dorsal abdomen of particular Theraphosinae. (A) Eupalaestrus larae, female from Argentina. (B) Cyrtopholis sp., male from Cuba, Guantánamo. (C) Phormictopus auratus, female from Cuba, Holguín province. (D) Aphonopelma crinifragum, female from Costa Rica, Puntarenas. (E) Magulla obesa, male (according to [39]). (F) Phrixotrichus vulpinus, male from Chile. (G) Chromatopelma cyanopubescens, male from Venezuela. (H) Kochiana brunipes, female. Abbreviations: III/IV = urticating setae of intermediate morphology between types III and IV; III-s = short type III setae, length 0.07–0.08. White circles represent the spots of sampling.](https://doi.org/10.1371/journal.pone.0224384.g002)
urticating setae or in body setae from which urticating setae probably evolved in Aviculariinae and Theraphosinae (Mygalomorphae: Theraphosidae). Barbed setae (sicate, pinnate or arborate setae) is also known, for example, in Gnaphosidae (Araneomorphae) [55]. The barbs of the opposite direction pointing downward to the setal base, are called “reversed barbs” in this study. As they are present only in a few types of UrS, they are considered a derived character.

The terminology of barbs and reversed barbs was herein unified for all setal structures and in the case of type I setae changed for the reasons mentioned below. Cooke at al. [6] described the morphology of type I setae for the first time, including the terms “barbs” and “reversed barbs”. The most extended barbs of the central area (midsection) were called “main barbs” and the basal barbs of the opposite direction were called “reversed barbs”. To put simply, whatever barbs of the opposite direction to the main barbs might be called “reversed barbs”. The term “main barbs” was used by Cooke et al. [6] only for type I setae and this concept of “main barbs” and “reversed barbs” was followed by Perafán et al. [11] in the description of type VII setae in Kankuamo. In types III, IV, and VII, the main barbs are of the same direction to the main barbs in type I, pointing downwards to the basal end of the seta, but in opposite direction to the main barbs of type II, V, and VI, whose barbs are pointing upwards to the apical end. To unify the terminology in all setal structures, we suggest the above mentioned definitions taking into account especially the real direction of barbs. This new concept allows descriptions of all setal types to be unified and mutually comparable in comparison with Cooke et al. [6], whose concept of “barbs” and “reversed barbs” does not allow this.

Consequently, we renamed section C (= basal barbs) and section B (central section without barbs) (according to Cooke et al. [6]) to section B (= basal barbs) and central section C2 (central section without barbs). The section C2 of main barbs corresponds with main barbs according to Cooke et al. [6]. According to Cooke et al. [6], sections “A”, “B” and “C” refer to the measurements in Tables 2–4 (to single columns), and they were not a part of the description of type I setae. We are persuaded that these minor changes in the amended terminology and abbreviations of type I UrS sections do not cause any confusion among other researchers. In this case we recommend to use the non-abbreviated versions referring to single setal sections.

Juveniles were identified according to the morphological characters of their parental pair or the characters after maturation. The designation of postembryonic stages followed Foelix [56]. The phylogenetic concept of Theraphosinae, Aviculariinae, Psalmopoeinae and Stromatopelmatae follows Turner et al. [20], Lüddecke et al. [54] and Hüsser [17]. The nomenclature followed the World Spider Catalog [1], with the following exceptions: the genus Metriopelma (see remark 2 at the end of the chapter Descriptions of basic urticating setae types and their subtypes) is thus far insufficiently diagnosed, and its revision is needed, together with the species provisionally presented here in that genus.

Table 2. Length ranges of basic type I setae.

| Species | Sex | Length of setae |
|---------|-----|----------------|
| Acanthoscurria sp. from Paraguay | ♀ | 0.40–0.52 |
| Aphonopelma seemanni | ♀ | 0.39–0.41 |
| Brachypelma klaasi | ♀ | 0.37–0.43 |
| Eupalaestrus weijenberghi | ♀ | 0.27–0.37 |
| Cyclosternum schmardae | ♀ | 0.52–0.60 |
| Crassicrus lamanai | ♀ | 0.35–0.37 |
| Phormictopus auratus | ♀ | 0.21–0.28 |
| Reversopelma petersi | ♀ | 0.40–0.53 |

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Results

Distribution of UrS on the abdominal surface in Theraphosinae

The dorsal abdominal cuticle of Theraphosinae is covered with UrS varying in the shape, size and even in the area number as some taxa may have two separate lateral areas of UrS, e.g., Bis-triopelma Kaderka, 2015 and Phrixotrichus Simon, 1889, instead of one dorsal area. Generally, the taxa with UrS of types III, IV and III+IV show higher variability in the shape, size and number of urticating setae patches, in comparison to the taxa with type I setae arranged in one dorsal patch (Fig 2; Bertani & Guadanucci [9]: Figs 5–12). Theraphosinae with type I setae may have only one to two patterns and differ from the taxa with types III, IV or III+IV, in which another seven patterns were recognised [9]. The theraphosine genus Magulla Simon 1892 displays another pattern, which consists of type IV setae placed in the central dorsal patch and type III setae present in two separate anterior patches connected by the central patch [39].

Descriptions of basic urticating setae types and their subtypes

Cooke et al. [6] defined type III setae as 0.3–1.2 mm long setae with thin straight shaft, fine point, barbs along at least one-half the length and considerable variation not only in length but also in the size and density of barbs among setae of this type. As the arrangement of barbs in two opposite rows in Acanthoscurria rhodothele Mello-Leitão, 1923 and in the silhouette of type III setae presented by Cooke et al. [6] is typical for type I setae and because Pérez-Miles [10] found some differences in the morphology of type III setae in species with the co-occurrence of types I+III and III+IV, we decided to revise and redefine type III setae.

We suggest a new terminology for type I setae with the phylogenetic support of the molecular analyses carried out by Turner et al. [20] and Lüddecke et al. [54], showing taxa with type I

Table 3. Length ranges of subtype Ia setae.

| Species                        | Sex | Length of setae |
|--------------------------------|-----|-----------------|
| Aenigmarchae sinapophysis      | ♂   | 0.27–0.31       |
| Aphonopelma seemanni           | ♂   | 0.58            |
| Brachypelma klaasi             | ♀   | 0.46–0.57       |
| Brachypelma verdezi            | ♀   | 0.61–0.67       |
| Cyrtopholus sp. from Cuba, Santiago de Cuba province | ♂ | 0.43 |
| Megaphobema mesomelas          | ♂   | 0.55–0.62       |
| Sericopelma melanotarsum       | ♀   | 0.57–0.65       |
| Sphaerothria hoffmanni         | ♂   | 0.55–0.57       |

Table 4. Length ranges of subtype Ib setae.

| Species                        | Sex | Length of setae |
|--------------------------------|-----|-----------------|
| Aenigmarchae sinapophysis      | ♂   | 0.27–0.31       |
| Aphonopelma seemanni           | ♂   | 0.58            |
| Brachypelma klaasi             | ♀   | 0.46–0.57       |
| Brachypelma verdezi            | ♀   | 0.58–0.60       |
| Brachypelma verdezi            | ♀   | 0.45–0.61       |
| Cyrtopholus sp. from Cuba, Santiago de Cuba province | ♂ | 0.42–0.46       |
| Megaphobema mesomelas          | ♂   | 0.35–0.41       |
| Metriopelma sp. from Venezuela, Isla Margarita | ♂ | 0.30–0.37       |
| Neischnocolus sp. from Ecuador | ♀   | 0.53–0.63       |
setae as monophyletic group, and supported by the findings that were demonstrated in the present study in UrS development during ontogeny in 14 species of Theraphosinae. We consider the UrS that were formerly classified as type III or were considered setae of intermediate morphology between those of types I and III in species possessing both of these types to be ontogenetic derivatives of type I setae as they develop later in the ontogenetic development and they are derived from type I seta morphology. They are further described as subtypes of type I. Other than that, the typology of UrS follows Cooke et al. [6], Marshall & Uetz [5], Pérez-Miles [13] and Perafán et al. [11].

**Type I UrS**, including their subtypes as morphological repetitions (Fig 3), are generally characterised by the presence of reversed barbs in the midsection and a broad basal end. The basal barbs are present and may be developed (Fig 4A and 4B), reduced (Fig 4C) or strongly reduced (Fig 4D). The connection of the UrS with a supporting stalk, which is a so-called
break-off zone, is beneath the basal section of non-reversed barbs; the one exception is in subtype Ic.

**Basic type I** (Figs 1, 3, 4A, 4B and 4E; Table 2): it is characterised by a shaft with two axial flexions and four axial sections (from the basal to the apical end): the basal barbs (section B) are arranged in two opposite, concavely arranged rows; in addition, there is a central third row of longitudinally arranged barbs. The following section (section C2, see Fig 3), which was formerly described as a bare shaft [6], has two parallel rows of short confluent reversed barbs or denticles in adults (Fig 4E). This section may be bare in the first nymphal stages. The following
section (section C1, see Fig 3) carries two opposite rows of reversed barbs, which can be arranged helically, in *Reversopelma petersi* Schmidt, 2001, with 1–4 distal pairs of non-reversed barbs. The tapering apical section (section A, see Fig 3) has only two rows of small reversed denticles. Length of setae: 0.21–0.60.

**Subtype I a** (Fig 3; Bertani [47]: Fig 5; Table 3): it differs from the basic type I in the absence of the section C2; a third central row of basal barbs or denticles is present. Length of setae: 0.37–0.67. Length of reversed barbs: 0.005–0.030.

**Subtype I b** (Figs 3, 5A and 5B; Table 4): it is characterised by a nearly straight shaft or a shaft with one axial flection and three axial sections (from the basal to the apical end): the reduced basal section (section B) carries two opposite rows of barbs that are reduced in length and confluent with the shaft, or the barbs are absent. Section C2 is absent. Two rows of opposite reversed barbs on section C1 can be complemented by a third row in the proximal part. The tapering apical section (section A) carries denticles arranged in two opposite rows. Length of setae: 0.27–0.63. Length of reversed barbs: 0.007–0.011.

**Subtype I c** (Figs 3, 4C and 4D; Pérez-Miles [10]: Fig 6, basal section; Table 5): it is characterised by a long, almost straight shaft or a shaft with one axial flection and three axial sections (from the basal to the apical end): the reduced basal section B carries short barbs, which strongly adhere to the shaft, or the barbs are absent. Section C2 is absent. The following central
section, C1, carries thin and long reversed barbs, which are less dense than in the other subtypes, arranged in two longitudinal rows, and complemented by additional one or two rows in the proximal part only. The tapering apical section (section A) carries reversed denticles arranged in two opposite rows. This subtype is clearly longer than the other type I subtypes.

Subtype Ic differs from Ib in total length (Ic > Ib), lower density of barbs and larger size (in Ic 2–6 times as long as in Ib). It was formerly misinterpreted as a type III seta due to the morphological resemblance, but it differs in the incrassate shaft at the basal end, which carries flattened barbs visible at high magnification (approximately 2000×) [10]. This subtype always occurs with basic type I or another subtype of the type I seta. Length of setae: 0.52–1.64. Length of reversed barbs: 0.022–0.050.

Subtype Id (Figs 3 and 5D; Table 6): it is characterised by a shaft with one axial flection and four axial sections (from the basal to the apical end): the basal barbs (section B) are arranged in two opposite rows, concavely arranged rows, with a central third row of longitudinal barbs. The following section (section C2), has two parallel rows of short confluent reversed barbs or denticles in adults. It is unusually long, with the C2/C1 ratio higher than 3.0 (up to 9.0). Section C1 is basally flexed, with two opposite rows of reversed barbs. Length of setae: 0.31–0.68. This subtype was found in the genera Citharacanthus Pocock, 1901 and Neischnocolus Petrunkevitch, 1925.

Subtype If (Figs 3 and 6A; Table 7): it is characterised by its very small size. The setae have one axial flection and four axial sections (from the basal to the apical end): the section of basal barbs (section B) carries three rows of barbs that have a T-shape in cross-section. The following cylindrical C2 section is smooth and stout in comparison to the If subtype. The following short C1 section has two opposite rows of reversed barbs and the tapering apical section (section A) carries two opposite rows of small reversed denticles. Length of setae: 0.11–0.15. Length of reversed barbs: up to 0.011. This subtype was found only in the females of Metriopelma sp. from Margarita Island, Venezuela.

### Table 5. Length ranges of subtype Ic setae.

| Species                      | Sex | Length of setae  |
|------------------------------|-----|------------------|
| Acanthoscurria geniculata    | ♀   | 0.67–0.87        |
| Acanthoscurria suina         | ♂   | 0.58–0.67        |
| Brachypelma auratum          | ♀   | 1.10–1.27        |
| Brachypelma baumgarteni      | ♀   | 1.56–1.64        |
| Brachypelma klaasi           | ♀   | 0.81–0.98        |
| Brachypelma albiceps         | ♀   | 0.73–0.81        |
| Eapalaestrus larae           | ♀   | 0.66–0.74        |
| Nhandu tripepii              | ♀   | 0.71–0.75        |
| Phormictopus auratus         | ♀   | 0.52–0.58        |
| Phormictopus cubensis        | ♀   | 0.61–0.87        |
| Phormictopus sp. from Cuba, Guanabo | ♀ | 0.73–0.84 |
| Sericopelma melanotarsum     | ♀   | 0.73–0.75        |

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### Table 6. Length ranges of subtype Id setae.

| Species                                | Sex | Length of setae  |
|----------------------------------------|-----|------------------|
| Citharacanthus longipes                | ♀   | 0.51–0.56        |
| Neischnocolus sp. from Costa Rica      | ♂   | 0.64–0.77        |
| Neischnocolus sp. from Venezuela       | ♀   | 0.31–0.68        |
| Neischnocolus weinmanni                | ♂   | 0.59             |

https://doi.org/10.1371/journal.pone.0224384.t006
**Subtype I** (Figs 3 and 6B; Table 8): it is characterised by a smaller size and an extremely narrow and flattened shaft in section C2, which has a rough surface. The setae have two axial flections and four axial sections (from the basal to the apical end): section B is arranged in two opposite rows, and the third central row of longitudinal basal barbs is present. Section C2 represents a zone in which the seta breaks off. Scale bar = 20 μm.

![Image of uroticating setae of type I and its subtypes Ie and If.](https://doi.org/10.1371/journal.pone.0224384.g006)

**Table 7. Length ranges of subtype Ie setae.**

| Species                      | Sex | Length of setae |
|------------------------------|-----|-----------------|
| *Metriopelma* sp. from Venezuela, Isla Margarita | ♀   | 0.11–0.15       |

https://doi.org/10.1371/journal.pone.0224384.t007
Type II UrS (Figs 1, 7A–7E, 8 and 9; Table 9): it is characterised by a stout and almost straight shaft with a basal and apical penetrating tip and with two axial sections (from the basal to the apical end): the basal section is equipped with short barbs or scale-like barbs (Fig 9C), which are restricted to the basal third only, with the exception of the UrS of *Caribena versicolor* (Walckenaer, 1837) and *C. laeta* (C. L. Koch, 1842) [14], whose barbs are longer and scattered along the whole shaft except the apex. The tapering apical section is bare. The morphology of UrS in two studied nymphs of *C. versicolor* (length of carapace (car.) 2.5 and 3.5) (Fig 7B, 7D and 7E) is congruent with that of the adults. The basal tips of the tested Aviculariinae were slightly curved upwards.

Type II urticating setae are typical for some Aviculariinae genera such as *Antillena* Fukushima & Bertani, 2017, *Avicularia* Lamarck, 1818, *Caribena* Fukushima & Bertani, 2017, *Iridopelma* Pocock, 1901, *Pachistopelma* Pocock, 1901, *Typhochlaena* C. L. Koch, 1850, and *Ybyrapora* Fukushima & Bertani, 2017 [14,15].

In most of Aviculariinae with type II setae, the UrS can be dispersed through direct contact with the intruder [6,7], or may be airborne (recorded in *C. versicolor*; [8]). The shafts of airborne setae carrying well-developed barbs are much longer and narrower than those of the setae released by direct contact [8]. Bertani et al. [8] supposed that the airborne setae represent a homoplastic character shared with Theraphosinae and are a derived character for the Aviculariinae genera *Avicularia*, *Iridopelma* and *Pachistopelma*. According to Cooke et al. [6] and Bertani & Marques [7], the penetrating tip is located basally near the supporting stalk; the mechanism of release of type II UrS was described and determined by the latter authors. In the present study we observed that type II setae also penetrated the target through their apical tips in two Aviculariinae (females of *Avicularia* sp. from Bolivia and *Pachistopelma bromelicola* Bertani, 2012). Both females were stimulated and irritated by the oval piece of polystyrene hold in tweezers. The distribution area of type II setae covers the northern part of South America, including some Caribbean islands (Kaderka [57]: Fig 1).

The setae of intermediate morphology between the body setae and the type II urticating setae (Fig 8B), which were found in *Iridopelma hirsutum* Pocock, 1901 and *Antillena rickwesti* (Bertani & Huff, 2013), provide another evidence that type II UrS evolved from the body setae (Figs 9B and 10). These setae have a scale morphology restricted to the basal end only and are up to one fifth of the seta length. The apical section is densely covered with short barbs arranged in many longitudinal rows. In addition, they are nearly the same length as the body setae. Length of UrS: 0.45–1.66. Length of setae of intermediate morphology: 0.48–0.51. Length of body setae: 0.47–0.53.

**Type III UrS** (Figs 1, 11A–11D, 12A and 12B; Table 10): the seta is characterised by an almost straight shaft and by two axial sections: the long basal section has reversed barbs that are usually arranged in 4–5 longitudinal rows, the basal end of the shaft is slightly tapered. The connection of the seta with a supporting stalk is between the tips and basal ends of the

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**Table 8. Length ranges of subtype I**

| Species                  | Sex  | Length of setae |
|--------------------------|------|-----------------|
| *Pseudhapalopus* sp. from Colombia juv. | ♂   | 0.18–0.21       |

https://doi.org/10.1371/journal.pone.0224384.t008
basalmost reversed barbs. The short, tapering apical section lacks barbs but has reversed denticles. Length of setae: 0.07–1.25. Length of reversed barbs: 0.003–0.013. Setae of this type are usually arranged in one dorsal patch (most Theraphosinae) or in two dorsolateral patches, e.g., in *Phrixotrichus*, *Bistriopelma*, *Magulla* [39], and *Tmesiphantes hypogeus* Bertani, Bichuette & Pedroso, 2013 [58].

**Type IV UrS** (Figs 1, 12C and 12D; Table 11): the seta is characterised by a small size (up to 0.20) and a bent shaft. The basal section has strong reversed barbs (the diameter of the barbs at the basal end is comparable to the diameter of the shaft at the connection site). The central section has small reversed barbs arranged asymmetrically along the shaft. The tapering apical
section has two opposite rows of reversed denticles. The connection of the seta with a supporting stalk is between the tips and basal ends of the well-developed basalmost reversed barbs. Length of setae: 0.08–0.21. Length of reversed barbs: 0.004–0.009. According to Bertani & Guadanucci [9], type IV UrS can be better characterised by the barbs pointing towards the convex side of the seta. The occurrence of this type is restricted to the South American Theraphosinae only (see Table 1).

**Type V UrS** (Figs 1, 13A and 13B; Table 12): the seta is characterised by an almost straight shaft and by two axial sections. The long basal section (80–90% of the seta length) has barbs arranged asymmetrically along the shaft; the angle between the shaft and the barbs is approximately 10–30˚ and the barbs are more confluent on the base. The short, tapering apical section is bare. Type V setae are inserted in the sockets on the palpal cuticle, and supporting stalks are absent. The seta break-off zone is inside the socket. Length of setae: 0.55–0.67. Length of barbs: 0.009–0.011. This type of urticating setae is located distally on the prolateral face of the palpal femora of *Ephebopus* spp. [59,60]. The setae are densely packed and uniformly arranged (Fig 13). This unique morphological characteristic is considered a generic characteristic of *Ephebopus* [59]. According to Bertani & Marques [7], there is no reason to consider this type of setae as homologous to the abdominal setae in Aviculariinae or Theraphosinae.

**Type VI UrS** (Figs 1, 14A–14E and 15; Pérez-Miles [13]: Figs 1–4; Table 13): this seta, with an almost straight shaft, is connected to the abdominal surface by cylindrical supporting stalks (Fig 14A). The barbs are subbasally short and more confluent to the shaft (for approximately 10% of the seta length) and longer and more protruding on the rest of the seta (the angle between the shaft and the barbs is approximately 30˚). The apical section (approximately 10%
of the seta length) can be bare (Pérez-Miles [13]: Figs 1–4) or can have well-developed protruding barbs reaching the apex, and causing the absence of the apical tip. Reversed barbs are absent on type VI setae. Length of setae: 0.64–1.21. Length of barbs (measured in apical region): 0.007–0.010. The setae can be arranged in one dorsomedial patch, two dorsal paramedian patches, or in two lateral patches [35]. This type was found only in the Mexican genus *Hemirrhagus*, with the exception of some troglobitic species [35]. Type VI setae are distinguished from the very similar type II setae by the presence of long barbs in the apical half. The morphology of the basal half is congruent.

**Type VII UrS** (Perafán et al. [11]: Figs 2 and 8): the seta is straight and has small reversed subtriangular barbs or denticles along the entire shaft. These barbs are not homogenous in size or density and they are longer in the basal part. A small oval patch of lanceolated barbs is
located in the apical quarter near the penetrating tip. The lanceolated barbs are longer, broader and less acute than the reversed barbs. The length/width ratio of the shaft is approximately 34:1. The setae are connected to the abdominal surface by thinner stalks. Type VII setae resembles type II but differs in the presence of the patch of lanceolated barbs and in the presence of reversed barbs scattered along the shaft [11]. These setae were found exclusively in Kankuamo [11].

The urticating setae types found at the examined specimens are listed in Table 14.

### Ontogeny of urticating setae in Theraphosinae

We studied the ontogeny in two groups of Theraphosinae. Group A comprised the taxa Acanthoscurria geniculata C. L. Koch, 1841, Brachypelma albopilosum Valerio, 1980, Cyrtopholus flavostriatus Schmidt, 1995, Eupalaestrus weijenberghi (Thorell, 1894), Nhandu coloratovillosus (Schmidt, 1998), Nhandu tripepii (Dresco, 1984), Phormictopus auratus Ortiz & Bertani, 2005 and Phormictopus cubensis Chamberlin, 1917, with type I setae. The occurrence of UrS types in the chosen species during ontogeny is presented in Table 14. This group always showed the basic type I setae in the first nymphal stages. Subtypes I\textsubscript{a} and/or I\textsubscript{b} and/or I\textsubscript{c} only co-occurred in the later instars, with exceptions only found in two juveniles of Phormictopus spp. from the Dominican Republic (car. 3.2–3.3), in which the co-occurrence of basic type I with subtypes I\textsubscript{a} and I\textsubscript{b} was recorded.

Group B included the taxa Cyriocosmus perezmilesi Kaderka, 2007, Davus sp. (2), Theraphosa blondi (Latreille, 1804), Kochiana brunnipes (C. L. Koch, 1842), Phrixotrichus vulpinus (Karsch, 1880) and Grammostola sp. (3) from Chile. They possessed type III or IV UrS in the first nymphal stages. The occurrence of UrS types in the selected species during their ontogeny is presented in Table 14. In the Cyriocosmus perezmilesi nymph (car. 1.5; the first nymphal stage) neither UrS nor other types of abdominal setae were found in the patch where they normally are in the later instars. In the subsequent developmental stage (car. 2.2), ontogenetic precursors of the type III setae were found (Fig 11A).

In the Davus sp. (2) nymph (car. 2.0), an ontogenetic precursor of type III setae (0.11–0.13 long) was found, with barbs of the opposite direction and was restricted to the basal half of the shaft only. In the higher instars (car. 2.9, 4.4), a few type III setae were found that were of
similar length as in the previous stage, but with the last two reversed barbs abnormally elongated and protruding as in type IV. In the next instar (car. 6.9), normal type III setae (length 0.18–0.25) were found.

In *Theraphosa blondi*, type III setae of two discrete length categories were recognised in all of the instars (car. 5.5, 6.5, 8.0, 10.0, 12.0, 14.0, 20.0 in ♀, car. 34.0 in ♂): long setae (0.28–0.32) and short setae (0.07–0.08) (Fig 12A and 12B), whose length corresponded to the length range in type IV setae. Two length categories of type III were also found in a mature female of *Kochiana brunnipes*: a visible central patch of long type III setae was bordered by a narrow band of short type III setae (Fig 2).

In the *P. vulpinus* juvenile (car. 2.2; UrS length 0.23–0.24) and an adult male (UrS length 0.47–0.53), only type III setae occurred in both lateral patches, type IV setae were found only in the adult female (UrS length 0.49–0.57).
In *Grammostola* sp. (3) from Chile, the early instars (car. 3.2, 3.9) possessed only type IV setae. In the later instars (car. 4.8, 5.5, 6.7), setae of intermediate morphology between types III and IV were also found. The adult male possessed both types, including intermediate forms. The ontogeny in this group was characterised by the presence of type III or IV UrS in the early instars. In species with only type III setae (e.g., *Cyriocosmus*, *Davus*, *Hapalopus*, *Kochiana*, and *Theraphosa*), the UrS morphology was relatively constant during ontogeny. In species with types III and IV in the terminal instars, the missing type, type III or IV, as well as the UrS of intermediate morphology, appeared later during ontogeny. In the species with both types III and IV, a high degree of variability in the total length and curvature of the setae was recorded, just as in the length and diameter of the basal barbs. Both types III and IV represent the extremes of a morphological continuum.
Fig 12. Urticating setae of type III and IV. (A) Theraphosa blondi, female. Long seta of type III, basal section, total length 0.28–0.32. Scale bar = 20 μm. (B) Theraphosa blondi, female. Short seta of type III, total length 0.07–0.08. Scale bar = 20 μm. (C) Chromatopelma cyanopubescens, female. Type IV with reversed barbs in the basal section and reversed denticles in the apical section. Scale bar = 10 μm. (D) Chromatopelma cyanopubescens, female. Type IV, basal end, the arrow shows the connection to a supporting stalk, located between the last two basal barbs. Scale bar = 5 μm.

https://doi.org/10.1371/journal.pone.0224384.g012
The ontogenies of UrS types VI and VII were not studied because such material was unavailable to us.

**Systematics**

Order Araneae Clerck, 1757 [62]
Infraorder Mygalomorphae Pocock, 1892 [63]
Family Theraphosidae Thorell, 1869 [2]
Subfamily Theraphosinae Thorell, 1869 [2]

Theraphosinae Thorell, 1869 –Nova Acta Regiae Societatis Scientiarum Upsaliensis, (3) 7: 161–164.

Diagnosis: The subfamily Theraphosinae distinguishes itself from all other theraphosids by the presence of abdominal urticating setae of type I or VI or VII or III and/or IV, together with a large and extended subtegulum and keels present on the embolus of the male palpal bulb (modified from Pérez-Miles et al. [18], following Perafán et al. [11]).

**Table 10. Length ranges of type III setae.** juv. = juvenile specimen. car. = length of carapace.

| Species                        | Sex | Length of setae |
|--------------------------------|-----|-----------------|
| Bonnetina rudolffi             | ♂   | 0.43–0.49       |
| Bonnetina sp. from Mexico      | ♂   | 0.37–0.47       |
| Chromatopelma cyanopubescens  | ♂   | 0.36–0.41       |
| Cyriocosmus perezmilesi       | ♂   | 0.30–0.36       |
| Cyriocosmus perezmilesi       | ♂   | 0.20–0.27       |
| Cyriocosmus venezuelensis      | ♂   | 0.20–0.24       |
| Cyriocosmus venezuelensis      | ♂   | 0.20–0.27       |
| Davus sp. (1)                 | ♂   | 0.36–0.41       |
| Davus pentaloris from Mexico  | ♂   | 0.34–0.48       |
| Davus ruficeps                | ♂   | 0.39–0.48       |
| Euaathlus sp. from Chile, Volcán Chilán | ♂   | 0.35–0.46       |
| Grammostola sp. from Argentina| ♂   | 0.33–0.47       |
| Grammostola sp. from Chile     | ♂   | 0.37–0.49       |
| Hapalotremus sp. from Peru     | ♂   | 0.96–1.25       |
| Phrixotrichus vulpinus         | ♂   | 0.47–0.53       |
| Phrixotrichus vulpinus         | ♂   | 0.49–0.57       |
| Phrixotrichus vulpinus (car. 2.2) | juv. | 0.23–0.24       |
| Schizopelma sp. from Mexico    | ♂   | 0.32–0.38       |
| Theraphosa blandi              | ♂   | short 0.07–0.08  |
| Theraphosa blandi              | ♂   | long 0.28–0.32   |
| Thrixopelma ockerti            | ♂   | 0.44–0.61       |
| Tmesiphantes hypogeus          | ♂   | 0.32            |

https://doi.org/10.1371/journal.pone.0224384.t010

**Table 11. Length ranges of type IV setae.**

| Species                        | Sex | Length of setae |
|--------------------------------|-----|-----------------|
| Chromatopelma cyanopubescens  | ♂   | 0.10–0.12       |
| Euaathlus sp. from Chile, Volcán Chilán | ♂   | 0.11–0.13       |
| Grammostola sp. from Argentina | ♂   | 0.13–0.21       |
| Grammostola sp. from Chile     | ♂   | 0.08–0.15       |
| Phrixotrichus vulpinus         | ♂   | 0.15–0.19       |
| Thrixopelma ockerti            | ♂   | 0.10–0.14       |

https://doi.org/10.1371/journal.pone.0224384.t011
Urticating setae of tarantulas
Fig 13. Palpal urticating setae of type V in an immature female of *Ephebopus cyanognathus*. (A) Type V urticating setae connected with the palpal surface by insertion sockets. Scale bar = 10 μm. (B) Prolateral face of the right palp with a limited area of insertion sockets without urticating setae. Scale bar = 100 μm.

https://doi.org/10.1371/journal.pone.0224384.g013

Distribution: North, Central and South America.

Remarks: The representatives of this subfamily can be divided into four groups according to the types of UrS possessed:

1) Group A with type I UrS present on the dorsal abdomen, including the following taxa: *Acanthoscurria*, *Aenigmarchne*, *Aphonopelma*, *Brachypelma*, *Citharacanthus*, *Clavopelma*, *Cotzetetlana*, *Crassicrus*, *Cubanana*, *Cyclasternum*, *Cyrtopholis*, *Eupalaestrus*, *Lasiodora*, *Lasiodoridae*, *Longilyra*, *Metriopelma*, *Mygalarachne*, *Neischnocolus*, *Neosternotarsus*, *Nesipelma*, *Nhandu*, *Pamphobeteus*, *Phormictopus*, *Proshapalopus*, *Pseudhapalopus*, *Pterinopelma*, *Reversopelma*, *Scopelobates*, *Sericopelma*, *Sphaerobothria*, *Stichoplastoris*, *Umbyquyra*, *Vitalius*, *Xenesthis*.

2) Group B with type III and/or IV UrS present on the dorsal abdomen, including the following taxa: *Agnostopelma* (III+IV), *Aguapanela* (III+IV), *Bistriopelma* (III), *Bonnetina* (III), *Bumba* (III+IV), *Cardiopelma* (III), *Catanduba* (III), *Chromatopelma* (III+IV), *Cyriocosmus* (III), *Davus* (III), *Euathlus* (III+IV), *Grammostola* (III+IV), *Hapalopus* (III, IV), *Hapalotremus* (III), *Homoeomma* (III+IV, Kovichina (III; short + long version)), *Magulla* (III+IV), *Magnacarina* (III), *Melloleitaoina* (III+IV), *Munduruku* (III+IV), *Phrixotrichus* (III+IV), *Plesiopeilma* (III+IV), *Schizopelma* (III), *Theraphosa* (III; short + long version), *Thrixopelma* (III+IV), *Timensiphantes* (III).

3) Group C with type VI UrS present on the dorsal abdomen, with reversions in some troglobitic species of *Hemirrhagus* [35]. The genus *Hemirrhagus* is the only representative of this group. Pérez-Miles [13] placed *Hemirrhagus* into Theraphosinae based generally on the presence of abdominal UrS, abundant leg spination and the absence of laterally extended scopulae and spatulate scopula setae, which collectively argued against its inclusion in Aviculariinae [13]. According to phylogenetic analysis proposed by Perafán et al. [11], *Hemirrhagus* is in the basal position to the rest of the tested Theraphosinae genera. The morphological similarity of type VI to type II UrS is discussed below.

4) Group D with type VII UrS present on the dorsal abdomen [11]. *Kankuamo* is the only representative of this group.

The monophyly of the groups A and B was supported by the molecular analysis carried out by Turner et al. [20], and three new tribes within Theraphosinae were proposed: Theraphosini Turner et al., 2017 (= group A with *Theraphosa*), Grammostolini Turner et al., 2017 and Hapalopini Turner et al., 2017 (= group B without *Theraphosa*). The tribe Theraphosini was represented by 18 genera (*Acanthoscurria*, *Aphonopelma*, *Brachypelma*, *Citharacanthus*, *Crassicrus*, *Cyrtopholis*, *Eupalaestrus*, *Lasiodora*, *Longilyra*, *Metriopelma*, *Mygalarachne*, *Neischnocolus*, *Neosternotarsus*, *Nesipelma*, *Nhandu*, *Pamphobeteus*, *Phormictopus*, *Proshapalopus*, *Pseudhapalopus*, *Pterinopelma*, *Reversopelma*, *Scopelobates*, *Sericopelma*, *Sphaerobothria*, *Stichoplastoris*, *Umbyquyra*, *Vitalius*, *Xenesthis*; 50% of known genera), and the tribes Grammostolini + Hapalopini by 12 genera (*Bonnetina*, *Bumba*, *Chromatopelma*, *Cyriocosmus*, *Davus*, *Euathlus*, *Grammostola*, *Hapalopus*, *Homoeomma*, *Phrixotrichus*, *Plesiopeilma*, and *Thrixopelma*; 50% of known genera). The monophyly of the

| Species                  | Sex | Length of setae |
|--------------------------|-----|-----------------|
| *Ephebopus cyanognathus* | juv.| 0.60–0.67       |
| *Ephebopus rufescens*    | ♂  | 0.55–0.62       |

https://doi.org/10.1371/journal.pone.0224384.t012
group A with type I UrS was also supported by the molecular analysis carried out by Lüdecke et al. [54]. The authors analysed nuclear and mitochondrial markers of nine genera from the group A (Aphonopelma, Brachypelma, Crassicrus, Lasiodora, Lasiodorides, Megaphobema, Nhandu, Sericopelma, and Xenesthis; 26% of known genera), two genera from the group B...
(Grammostola and Kochiana; only 8% of known genera), together with 37 taxa from other subfamilies of Theraphosidae.

Subfamily Aviculariinae Simon, 1873 [3]
Aviculariinae Simon, 1873 – Mémoires de la Société Royale des Science de Liège, Bruxelles 5 (2): 1–174.

Diagnosis: The subfamily Aviculariinae distinguishes itself from all other theraphosids by the following combination of morphological characters: the presence of abdominal urticating setae of type II; legs aspinose or weakly spinose on ventral tibiae and metatarsi; scopulae on tarsi and metatarsi I and II laterally extended; the presence of separate seminal receptacles in females; the presence of one subapical apophysis or a protuberance ending in numerous spines on male tibia I, except for Typhochlaena, Ybyrapora and some Avicularia spp., which lack this apomorphic character [14,15] (modified from Fukushima and Bertani [14], following the concept of Aviculariinae proposed by Lüdecke et al. [54]).

Distribution: Central America and north of South America.

Table 13. Length ranges of type VI setae. juv. = juvenile specimen. car. = length of carapace.

| Species               | Sex | Length of setae |
|-----------------------|-----|-----------------|
| Hemirrhagus coztic    | ♂   | 0.82–0.88       |
| Hemirrhagus eros      | ♂   | 1.13–1.21       |
| Hemirrhagus papalotl  | ♂   | 0.74–1.04       |
| Hemirrhagus papalotl (car. 9.0) | juv. ♂ | 0.64–0.80 |

https://doi.org/10.1371/journal.pone.0224384.t013
Table 14. Distribution of urticating setae types in studied material.

| Species                  | Locality                      | Sex, stage | I | Ia | Ic | Ie | If | II | III | IV | V | VI |
|--------------------------|-------------------------------|------------|---|----|----|----|----|----|-----|----|---|----|
| **ISCNOCOLINAE**         |                               |            |   |    |    |    |    |    |     |    |   |    |
| Holothele sp.            | Peru, Rio Napo                | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Holothele sp.            | Venezuela, Aragua             | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Holothele sp.            | Venezuela, State of Bolivar   | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Holothele sp.            | Venezuela, State of Bolivar   | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Holothele sp.            | Venezuela, State of Carabobo  | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Neoholothele sp.         | Venezuela, Isla Margarita     | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Neoholothele sp.         | Venezuela, Isla Margarita     | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| **SCHISMATOTHELINAEN**   |                               |            |   |    |    |    |    |    |     |    |   |    |
| Euthycaelus colonicus    | Venezuela, State of Carabobo  | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Neoholothele sp.         | Colombia                      | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Neoholothele sp.         | Venezuela, Isla Margarita     | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Neoholothele sp.         | Venezuela, Isla Margarita     | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Bolivar   | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Bolivar   | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Merida    | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Guarico   | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Guarico   | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Schismatothele sp.       | Venezuela, State of Aragua, Maracay | ♂      | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| **PSALMOPOEINAE**        |                               |            |   |    |    |    |    |    |     |    |   |    |
| Ephebopus cyanognathus   | French Guyana juv. (car. 6.0) |            | – | –  | +  | –  | –  | –  | +   | –  | + | –   |
| Ephebopus rufescens      | French Guyana                 | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Psalmopoeus cambridgei   | unknown origin                | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Psalmopoeus irminia      | unknown origin                | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Psalmopoeus reducens     | unknown origin                | ♂          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Tapinauchenius sp.       | Colombia, Puerto Arica juv. (car. 2.2) | ♂      | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Tapinauchenius sp.       | Colombia, Puerto Arica        | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Tapinauchenius sp.       | Venezuela, State of Delta Amacuro | ♀      | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| Tapinauchenius sp.       | Peru                          | ♀          | – | –  | –  | –  | –  | –  | –   | –  | – | –   |
| **AVICULARINAE**         |                               |            |   |    |    |    |    |    |     |    |   |    |
| Antillena rickwesti      | Dominican Republic            | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Avicularia hirschi       | Ecuador                       | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Avicularia hirschi       | Ecuador juv. (car. 3.0)       | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Avicularia sp.           | Bolivia, Beni province        | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Avicularia sp.           | Peru, Puerto Maldonado        | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Avicularia sp.           | Venezuela                     | ♂          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Caribena versicolor (1)  | unknown origin                | ♂          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Caribena versicolor (2)  | unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Caribena versicolor (3)  | unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Iridopelma hirsutum      | Brazil, Pernambuco, Recife    | ♂          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Pachistopelma bromelicola| Brazil                        | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| **THERAPHOSINAE**        |                               |            |   |    |    |    |    |    |     |    |   |    |
| Acanthoscurria geniculata| unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria geniculata| unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria geniculata| unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria geniculata| unknown origin                | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria sp.       | Paraguay, Terr. Foncière       | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria sp.       | Peru, Puerto Maldonado        | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |
| Acanthoscurria sp.       | Peru, Puerto Maldonado        | ♀          | – | –  | –  | –  | –  | –  | +   | –  | – | +   |

(Continued)
| Species                        | Locality                      | Sex, stage | I | I₂ | I₃ | I₄ | I₅ | I₆ | I₇ | I₈ | I₉ | I₁₀ |
|-------------------------------|-------------------------------|------------|---|----|----|----|----|----|----|----|-----|-----|
| *Acanthoscurria suina*        | Uruguay                       | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Acanthoscurria theraphosoides*| Brazil                        | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Aenigmarachne sinapophysis*  | Costa Rica                    | ♂          | – | +  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Agnostopelma gardel*         | Col. Boyacá, Belen            | ♂          | – | +  | –  | –  | –  | –  | –  | –  | –    | +    |
| *Aphonopelma bicoloratum*     | Mexico                        | ♂          | – | +  | –  | –  | –  | –  | –  | –  | –    | –    |
| *Aphonopelma bicoloratum*     | Mexico                        | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Aphonopelma bicoloratum*     | Mexico                        | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Aphonopelma bicoloratum*     | Mexico                        | ♂          | + | +  | +  | –  | –  | –  | –  | –  | –    | –    |
| *Bistriopelma lamasi*         | Peru, Ayacucho province       | ♂          | – | –  | –  | –  | –  | –  | +  | –  | –    | +    |
| *Bistriopelma lamasi*         | Peru, Ayacucho province       | ♂          | – | –  | –  | –  | –  | –  | –  | +  | –    | +    |
| *Bistriopelma matuskai*       | Peru, Apurímac province       | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | +    |
| *Bistriopelma matuskai*       | Peru, Apurímac province       | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | +    |
| *Bonnetina rudloffi*          | Mexico                        | ♂          | – | –  | –  | –  | –  | –  | +  | –  | –    | +    |
| *Bonnetina sp.*               | Mexico                        | ♂          | – | –  | –  | –  | –  | –  | –  | –  | –    | +    |
| *Brachypelma albiceps*        | unknown origin                | ♂          | – | –  | –  | –  | –  | –  | –  | –  | –    | +    |
| *Brachypelma albopilosum*     | unknown origin                | ♂          | – | +  | –  | –  | –  | –  | –  | –  | –    | +    |
| *Brachypelma auraaturn*       | Mexico                        | ♂          | – | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Brachypelma baumgarteni*     | Mexico                        | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Brachypelma baumgarteni*     | Mexico                        | ♂          | + | –  | –  | +  | –  | –  | –  | –  | –    | –    |
| *Brachypelma fossorium*       | Costa Rica, Guanacaste province| ♂          | + | +  | –  | –  | –  | –  | –  | –  | –    | –    |
| *Brachypelma klaasi*          | Mexico                        | ♂          | – | +  | +  | –  | –  | –  | –  | –  | –    | –    |
| *Brachypelma smithi*          | Mexico                        | ♂          | + | –  | +  | –  | –  | –  | –  | –  | –    | –    |
| *Brachypelma verdezi*         | Mexico                        | ♂          | + | –  | +  | –  | –  | –  | –  | –  | –    | –    |
| *Brachypelma verdezi*         | Mexico                        | ♂          | + | –  | +  | –  | –  | –  | –  | –  | –    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |
| *Chromatopelma cyanopubescens*| Venezuela                     | ♂          | – | –  | –  | –  | –  | +  | –  | +    | –    |

(Continued)
Table 14. (Continued)

| Species                        | Locality                     | Sex, stage        | URTICATING SETAE TYPES |
|--------------------------------|------------------------------|-------------------|------------------------|
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 4.0)   | I  Ia Ic Ie Ih Ij II III IV V VI |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 5.0)   | - - - - - - + + - - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 6.0)   | - - - - - - + + - - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 7.5)   | - - - - - - - - + + - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 9.2)   | - - - - - - - - + - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 10.5)  | - - - - - - - - - - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 13.2)  | - - - - - - - - - - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | juv. (car. 15.0)  | - - - - - - - - - - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | ♂ (car. 16.5)     | - - - - - - - - + - - - |
| Chromatopelma cyanopubescens   | Venezuela                    | ♂ (car. 4.5)      | - - - - - - - - + + - - |
| Citharacanthus cyaneus         | Cuba, Granma                 | ♂                | + + - - - - - - - - - - |
| Citharacanthus livingstoni     | Guatemala, Livingston        | ♂                | - - - - - - + - - - - - |
| Citharacanthus longipes        | Mexico, State of Chiapas     | ♂                | - - - - - - + - - - - - |
| Citharacanthus longipes        | Mexico, State of Chiapas     | ♂                | - - - - - - + - - - - - |
| Citharacanthus sp.             | Mexico, State of Veracruz    | ♂                | - - - - - - + - - - - - |
| Affinity to Citharacanthus b   | Costa Rica, Guapiles        | ♂                | - - - - - - + - - - - - |
| Affinity to Citharacanthus b   | Costa Rica, Guapiles        | ♂ (car. 2.1)     | - - - - - - + - - - - - |
| Affinity to Citharacanthus b   | Costa Rica, Guapiles        | ♂ (car. 10.5)    | - - - - - - + - - - - - |
| Affinity to Citharacanthus b   | Costa Rica, Guapiles        | ♂                | - - - - - - + - - - - - |
| Crassicrus lamanai             | unknown origin               | ♂                | - - - - - - + - - - - - |
| Cyclosternum schmardae         | Ecuador, Cordillera          | ♂                | - - - - - - + - - - - - |
| Cyclosternum sp.               | Peru, Puerto Maldonado       | ♂                | - - - - - - + - - - - - |
| Cyclosternum sp.               | Peru, Ucayali, Pucallpa      | ♂                | - - - - - - + - - - - - |
| Cyriocosmus leetzii            | Venezuela, State of Táchira  | ♂                | - - - - - - + - - - - - |
| Cyriocosmus perezmilesi (1)    | Bolivia, Beni province       | ♂                | - - - - - - + - - - - - |
| Cyriocosmus perezmilesi (2)    | Bolivia, Beni province       | ♂                | - - - - - - + - - - - - |
| Cyriocosmus perezmilesi (3)    | Bolivia, Beni province       | juv. (car. 1.5)  | - - - - - - + - - - - - |
| Cyriocosmus perezmilesi (3)    | Bolivia, Beni province       | juv. (car. 2.2)  | - - - - - - + - - - - - |
| Cyriocosmus rogerioi           | Peru, Kuelap near Chachapoyas| ♂                | - - - - - - + - - - - - |
| Cyriocosmus venezuelensis      | Venezuela, State of Lara     | ♂                | - - - - - - + - - - - - |
| Cyriocosmus venezuelensis      | Venezuela, State of Lara     | ♂                | - - - - - - + - - - - - |
| Cyrtopholis flavostriatus (1)  | Guano, Lesser Antilles       | ♂                | + + - - - - - - - - - - |
| Cyrtopholis flavostriatus (2)  | unknown origin               | juv. (car. 7.5)  | + - - - - - - - - - - - |
| Cyrtopholis flavostriatus (2)  | unknown origin               | juv. (car. 18.0) | + + - - - - - - - - - - |
| Cyrtopholis sp.                | Cuba, Guantánamo             | ♂                | + + - - - - - - - - - - |
| Cyrtopholis sp.                | Cuba, Holguin province       | ♂                | + + - - - - - - - - - - |
| Cyrtopholis sp. (1)            | Cuba, Santiago de Cuba province, Baconao | juv. ♂    | - - - - - - + - - - - - |
| Cyrtopholis sp. (1)            | Cuba, Santiago de Cuba province, Baconao | ♂    | - + - - - - - - - - - - |
| Cyrtopholis sp. (2)            | Cuba, Santiago de Cuba province, Baconao | ♂    | - + + - - - - - - - - - |
| Cyrtopholis sp. (2)            | Cuba, Trinidad               | ♂                | - - - - - - + - - - - - |
| Cyrtopholis sp.                | Dominican Republic, La Vega province | ♂    | - - - - - - + - - - - - |
| Cyrtopholis sp. (1)            | Dominican Republic, Pedernales province | ♂    | - - - - - - + - - - - - |
| Cyrtopholis sp. (2)            | Dominican Republic, Pedernales province | juv. (car. 2.7) | - - - - - - + - - - - - |
| Davus pentaloris               | Mexico, State of Oaxaca      | ♂                | - - - - - - + - - - - - |
| Davus ruficeps                 | Costa Rica, Peninsula de Nicoya | ♂    | - - - - - - + - - - - - |
| Davus sp. (1)                  | unknown origin               | ♂                | - - - - - - + - - - - - |

(Continued)
| Species | Locality | Sex, stage | I | Iₐ | Iₕ | Iₖ | Iₗ | II | III | IV | V | VI |
|---------|----------|------------|---|----|----|----|----|----|-----|----|----|----|
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
| Davus sp. (2) unknown origin juv. | ♂ | – – – – – – – – + – – – | |
### Table 14. (Continued)

| Species                  | Locality                                             | Sex, stage | URTICATING SETAE TYPES |
|--------------------------|------------------------------------------------------|------------|------------------------|
| *Hemirrhagus coztic*     | Mexico, Morelos, Tepoztlán, Cueva del Diablo         | ♀          | – – – – – – – – – – – + |
| *Hemirrhagus eros*       | Mexico, Oaxaca, El Punto                            | ♀          | – – – – – – – – – – – + |
| *Hemirrhagus ocellatus*  | Mexico, Estado de Mexico, Cueva Peña Blanca          | –          | – – – – – – – – – – – + |
| *Hemirrhagus papalotl*   | Mexico, Guerrero, Gruta de Aguacacihil, Taxco         | ♀          | – – – – – – – – – – – + |
| *Hemirrhagus papalotl*   | Mexico, State of Guerrero, Cave La Joya              | juv. ♀     | – – – – – – – – – – – + |
| *Homoeomma*              | Chile                                                | ♀          | – – – – – – – – – – – + |
| *Homoeomma*              | Chile                                                | ♀          | – – – – – – – – – – – + |
| *Kochiana brunnipes*     | unknown origin                                       | ♀          | – – – – – – – – – – – + |
| *Kochiana brunnipes*     | unknown origin juv. (car. 1.0)                       | ♀          | – – – – – – – – – – – + |
| *Kochiana brunnipes*     | unknown origin juv. (car. 3.1)                       | ♀          | – – – – – – – – – – – + |
| *Kochiana brunnipes*     | unknown origin juv. (car. 10.3)                      | ♀          | – – – – – – – – – – – – |
| *Lasiodora isabellina*   | Brazil, Rio de Janeiro                               | ♀          | – – – – – – – – – – – + |
| *Magnacarina*            | Mexico, State of Oaxaca, Bahías de Huautulco         | ♀          | – – – – – – – – – – – + |
| *Megaphobema mesomelas*  | unknown origin                                       | ♀          | – – – – – – – – – – – + |
| *Megaphobema robustum*   | unknown origin                                       | ♀          | + – – + – – – – – – – – |
| *Megaphobema velvetosoma*| unknown origin                                       | ♀          | – – – – – – – – – – – + |
| *Metriopelma* sp.        | Costa Rica, Alajuela province                        | ♀          | – – – – – – – – – – – + |
| *Metriopelma* sp.        | Costa Rica, Alajuela province                        | ♀          | – – – – – – – – – – – – |
| *Metriopelma* sp.        | Venezuela, Isla Margarita                            | ♀          | – – – – – – + – – – – – |
| *Metriopelma* sp.        | Venezuela, Isla Margarita                            | ♀          | – – – – – – – – – – – – |
| *Metriopelma* sp.        | Venezuela, State of Barinas                          | ♀          | – – – – – – + – – – – – |
| *Metriopelma* sp.        | Venezuela, State of Aragua                           | ♀          | – – – – – – + – – – – – |
| *Mygalarachne brevipes*  | Honduras                                             | ♀          | – – – – – – + – – – – – |
| *Neischnocolus armiuariensis* | Peru, Cuzco province                               | ♀          | – – – – – – + – – – – – |
| *Neischnocolus*          | Colombia, Ibagué Tolima                              | ♀          | – – – – – – + – – – – – |
| *Neischnocolus*          | Costa Rica                                           | ♀          | – – – – – – + – – – – – |
| *Neischnocolus*          | Ecuador, Imbabura / Carchi province                  | ♀          | + – – – + – – – – – – – |
| *Neischnocolus*          | Venezuela, State of Guarico                          | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin                                       | ♀          | – – – – – – – – – – – + |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 3.7)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 6.0)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 7.4)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 9.1)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 11.2)                      | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 14.3)                      | ♀          | + – – – + – – – – – – – |
| *Nhandu coloratovillosus*| unknown origin juv. (car. 17.0)                      | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin                                       | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin juv. (car. 3.7)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin juv. (car. 6.5)                       | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin juv. (car. 10.0)                      | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin juv. (car. 21.0)                      | ♀          | + – – – + – – – – – – – |
| *Nhandu tripepii*        | unknown origin                                       | ♀          | + + + + + – – – – – – – |
| *Phormictopus cf. atrichomatus* | Dominican Republic, Barahona province             | ♀          | + + + + + – – – – – – – |
| *Phormictopus cf. atrichomatus* | Dominican Republic, Barahona province              | ♀          | + + + + + – – – – – – – |
| *Phormictopus cf. atrichomatus* | Dominican Republic, Barahona province               | ♀          | + + + + + – – – – – – – |

(Continued)
### URTICATING SETAE TYPES

| Species                          | Locality                        | Sex, stage | I | I₂ | I₃ | I₄ | I₅ | I₆ | III | IV | V | VI |
|---------------------------------|---------------------------------|------------|---|----|----|----|----|----|-----|----|----|----|
| Phormictopus auratus (1)        | Cuba, Holguín province          | ♀          | + | –  | –  | +  | –  | –  | –   | –  | –  | –  |
| Phormictopus auratus (2)        | Cuba, Santiago de Cuba          | ♀          | + | –  | +  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus auratus (3)        | Cuba, Holguín province          | juv. σ (car. 16.0) | + | +  | +  | +  | –  | –  | –   | –  | –  | –  |
| Phormictopus auratus (4)        | Cuba, Holguín province          | juv. (car. 1.9) | – | –  | –  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus auratus (4)        | Cuba, Holguín province          | juv. (car. 3.0) | + | –  | –  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus cancerides         | Dominican Republic, Bahoruco province | juv. (car. 3.3) | + | –  | +  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus cubensis (1)       | Cuba, Pinar del Río province    | ♀          | + | +  | +  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus cubensis (2)       | Cuba, Pinar del Río province    | ♀          | + | –  | –  | +  | –  | –  | –   | –  | –  | –  |
| Phormictopus cubensis (3)       | Cuba, Pinar del Río province    | juv. (car. 1.9) | + | –  | +  | –  | –  | +   | –   | –  | +  | –  |
| Phormictopus cubensis (3)       | Cuba, Pinar del Río province    | juv. (car. 9.2) | + | –  | –  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus sp.                | Cuba, Yumuri River              | ♀          | + | –  | +  | –  | –  | –  | –   | –  | –  | –  |
| Phormictopus sp.                | Cuba, Guanabo                   | ♀          | + | –  | –  | –  | –  | –  | –   | –  | –  | –  |
| Phrixotrichus vulpinus (1)      | Chile                           | σ           | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Phrixotrichus vulpinus (2)      | Chile                           | σ           | – | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Phrixotrichus vulpinus (3)      | Zimbabwe                        | juv. (car. 2.2) | – | –  | –  | –  | –  | +  | –   | –  | –  | +  |
| Pseudohapalopus sp.             | Colombia                        | juv. σ      | – | –  | –  | –  | +  | –  | +   | –  | –  | –  |
| Plesiopelma sp.                 | Uruguay                         | ♀           | – | –  | –  | +  | –  | –  | –   | –  | –  | –  |
| Pterinopelea sazimai            | Brazil                          | σ           | + | +  | –  | –  | –  | –  | –   | +  | –  | –  |
| Pterinopelea sazimai            | Brazil                          | juv. σ      | – | –  | –  | +  | –  | –  | –   | –  | –  | –  |
| Reversopelma petersi            | Ecuador, Peru                   | σ           | – | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Reversopelma petersi            | Ecuador, Peru                   | ♀           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Schizopelma sp.                 | Mexico, Guerrero                | σ           | – | –  | –  | +  | –  | –  | –   | –  | –  | –  |
| Sericopela melanotarsum (1)     | Costa Rica                      | ♀           | + | +  | +  | –  | –  | +   | –   | –  | +  | –  |
| Sericopela melanotarsum (2)     | Costa Rica                      | juv. σ      | + | +  | –  | –  | –  | –  | –   | +  | –  | –  |
| Sericopela rubronitens          | Panama                          | σ           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Sericopela sp.                  | Costa Rica, Limon province      | ♀           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Sphaerobothria hoffmanni (1)    | Costa Rica, San José            | σ           | + | +  | +  | –  | –  | –  | –   | –  | –  | –  |
| Sphaerobothria hoffmanni (2)    | Costa Rica                      | σ           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Stichoplasteris sp.             | Costa Rica, Las Juntas          | ♀           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Stichoplasteris sp.             | Costa Rica, Las Juntas          | σ           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |
| Theraphosa blondi (1)           | unknown origin                  | ♀           | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 3.5) | – | –  | –  | –  | –  | –  | +   | –  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 6.5) | – | –  | –  | –  | –  | –  | +   | –  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 8.0) | – | –  | –  | –  | –  | –  | –   | +  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 10.0) | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 12.0) | – | –  | –  | –  | –  | –  | –   | +  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 14.0) | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Theraphosa blondi (2)           | unknown origin                  | juv. σ (car. 20.0) | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Theraphosa apophysis            | Venezuela, Autana River         | ♀           | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Thrixopelma ockerti (1)         | Peru, Loreto                    | ♀           | – | –  | –  | –  | –  | +  | –   | –  | –  | –  |
| Thrixopelma ockerti (2)         | Peru, Loreto                    | juv. σ (car. 3.9) | – | –  | –  | –  | –  | –  | +   | –  | –  | –  |
| Thrixopelma ockerti (2)         | Peru, Loreto                    | juv. σ (car. 7.8) | – | –  | –  | –  | –  | +  | –   | –  | –  | +  |
| Thrixopelma ockerti (2)         | Peru, Loreto                    | juv. σ (car. 15.0) | – | –  | –  | –  | –  | +  | –   | +  | –  | –  |
| Thrixopelma ockerti (3)         | Peru, Loreto                    | juv. (car. 3.2) | – | –  | –  | –  | –  | –  | +   | –  | –  | +  |
| Vitalius paranaensis (1)        | unknown origin                  | σ           | + | +  | –  | –  | –  | –  | –   | –  | –  | –  |

(Continued)
Genera included: Antillena, Avicularia, Caribena, Iridopelma, Pachistopelma, Typhochlaena, Ybyrapora.

Remarks: The monophyly of this subfamily was supported by previously published phylogenetic analyses [14,15,17,20,54,60]. This subfamily does not represent a sister group to the South American genera Psalmopoeus, Tapinauchenius and Ephebopus or the African genera Stromatopelma Karsch, 1881 and Heteroscodra Pocock, 1899 [15,20], as was previously proposed by West et al. [60], who transferred all of the mentioned genera to Aviculariinae, considering only well-developed and laterally extended scopulae on the tarsi and metatarsi I and II as a basic phylogenetic criterion but omitting the separation of Africa from the South American continent more than 110 Mya [64]. Later, Lüdecke et al. [54] revealed that the African genera Stromatopelma and Heteroscodra represent a sister group to African subfamily Harpactirinae Pocock, 1897 [65]. Following the concept of Aviculariinae proposed by Lüdecke et al. [54] we added the presence of type II setae to the diagnosis of Aviculariinae.

Subfamily Psalmopoeinae Samm & Schmidt, 2010 [4]
Psalmopoeinae Samm & Schmidt, 2010 –Tarantulas of the World, 142: 35–41.

Diagnosis: The subfamily Psalmopoeinae distinguishes itself from all other theraphosids by the following combination of morphological characters: the presence of two subapical apophyses on male tibia I; scopulae on tarsi and metatarsi I and II laterally extended giving a spatulate appearance; legs aspinose on tibiae and metatarsi; abdominal urticating setae are absent; the presence of separate seminal receptacles in females (modified from Hüsser [17] and Samm and Schmidt [4]).

Distribution: Central America and north of South America.

Genera included: Psalmopoeus, Pseudoclamoris, Tapinauchenius, Ephebopus.

Remarks: The monophyly of this subfamily is supported by previously published phylogenetic analyses [14,15,60], which all have a congruent topology Ephebopus + (Psalmopoeus + Tapinauchenius). It is also supported by molecular analyses carried out by Turner et al. [20], Lüdecke et al. [54], and Hüsser [17]. Ephebopus is the only genus within Psalmopoeinae, which possesses urticating setae but in contrast to abdominal urticating setae found in Theraphosinae they are located dor-sally at the base of the retrolateral tibial apophysis (Fig 16).

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Table 14. (Continued)

| Species             | Locality       | Sex, stage | URTICATING SETAE TYPES |
|---------------------|----------------|------------|------------------------|
| Vitalius paranaensis (2) | unknown origin | juv. (car. 5.2) | + – – – – – – – – – – – – – – – – – – – – |

σ = adult male; Ψ = adult female; juv. = juvenile specimen, car. = length of carapace; “+” = present; “–” = absent. The number in parenthesis following the scientific name of the particular species refers to the particular specimen in the group.

a The modified type I UrS found in the holotype of Aenigmarachne sinapophysis Schmidt, 2005 were erroneously interpreted as type VI in the original description.
b Affinity to Citharacanthus Pocock, 1901, the material has the same type of UrS (type I, subtype Ia), three keels, PS, PI and A (sensu Bertani [61]), on the embolus of the male palpal bulb and separate seminal receptacles with distinct apical lobes in females but plumose stridulatory bristles on the prolateral face of trochanter I are absent. Based on personal observation, the number, size and density of stridulatory plumose bristles on trochanter I vary in different Citharacanthus species; e.g., C. longipes (Cambridge, 1897) has few well-developed stout bristles whereas in C. meermanni Reichling & West, 2000 the bristles are distinctly smaller, narrower but denser.
c Affinity to Metroipelma Becker, 1878, the material possesses type I urticating setae and lacks the subapical apophyses on male tibia I. The studied species share the presence of two separate seminal receptacles with extended apical lobes. The stage of this character is not known in Metroipelma because the female of Metroipelma breyeri Becker, 1878 (generic type) from Guanajuato, Mexico is still unknown. The placement of the Venezuelan and Costa Rican species in Metroipelma is provisional, and revision is needed.
Subfamily Stromatopelminae Schmidt, 1993 [66], revalidated
Stromatopelminae Schmidt, 1993 – Landbuch Verlag, Hannover: 112.

Diagnosis: The subfamily Stromatopelminae distinguishes itself from all other theraphosids by the following combination of morphological characters: legs aspinose or weakly spinose; fovea circular and pit-like; the labial cuspules reduced; males without subapical apophysis on leg I (modified from Schmidt [66], Gallon [67], Gallon [68]).

Distribution: Central and Western Africa.

Genera included: Stromatopelma, Heteroscodra.

Remarks: Gallon [67] proposed the following topology for Stromatopelminae: Encyocratella + (Heteroscodra + Stromatopelma). According to the phylogenetic analyses of Bertani [15] and Fukushima & Bertani [14], both based on morphological data, Encyocratella does not represent a sister group of Stromatopelma + Heteroscodra. The monophyly of clade Stromatopelma + Heteroscodra was confirmed by West et al. [60], Bertani [15], Fukushima & Bertani [14] and also Lüdecke et al. [54] who placed this clade as a sister group to the African subfamily Hapactirinae, respecting 110 Myr of independent evolution on both African and South American continent. Following the phylogenetic concept proposed by Lüdecke et al. [54], the subfamily Stromatopelminae, which was previously synonymised with Aviculariinae by West et al. [60], is hereby revalidated.

Discussion

Urticating setae as a defensive mechanism

The defensive strategy using urticating setae against vertebrate and invertebrate predators and intruders has been described. Two uses of UrS have been recorded: the active defence against
potential intruders and the passive defence consisting in the incorporation of UrS into the silk mat for moulting or the egg sac wall, e.g., against phorid larvae (Diptera: Phoridae) [5,6,7,8,9,12]. The abdominal urticating setae of Theraphosinae emerge approximately in the first or second nymphal stage (nomenclature of instars determined after Foelix [56]). The larval stages lack abdominal UrS. The larvae do not use the defensive strategy based on the release of UrS because they live together in the egg sac and later in the security of the mother’s burrow, entirely dependent on yolk reserves. In addition, this defensive mechanism would be inefficient due to the small size and amount of UrS.

In the majority of spiders, moulting ceases at maturity. However, females of mygalomorph spiders continue to moult approximately every year throughout their lives, acquiring a fresh vestment of setae, including defensive urticating setae at each moult [6].

During the study ontogenetic development of UrS in Theraphosinae, we revealed the morphological resemblance between the airborne type III and the airborne subtypes I_{b} and I_{c} of type I setae, consisting in the presence of reversed barbs along the shaft. An explanation was proposed by Pérez-Miles [10]. Presumably, ecological pressures on the large spiders of the New World are similar, and this fact could explain the convergence of any type I subtypes with the type III morphology, probably due to their efficacy for defensive purposes [10].

Hypotheses of evolution of urticating setae

No broadly accepted hypothesis exists despite the attention dedicated to the phylogeny of New World Theraphosidae, based on both morphological and molecular characters, from which the evolutionary hypotheses for UrS may be derived. We analysed the previously published phylogenetic hypotheses [9,11,14,15,18,20,54,60], and derived a few hypotheses of the evolution of urticating setae, complemented by a proposal of a new approach to study of UrS and their evolution.

The diagnosis of Theraphosinae proposed by Pérez-Miles et al. [18] implicitly presumes the existence of a common ancestor, from which descendants carrying abdominal UrS of types I or III and/or IV evolved.

A hypothesis of UrS evolution derived from the Theraphosinae phylogeny published by Pérez-Miles et al. [18] and Bertani & Guadanucci [9] is proposed (Fig 17). The genera with type I setae compose a monophyletic group, together with the ingroup Theraphosa + (Schizopelma + (Davus sensu Gabriel [19] + (Hapalopus + Hapalotremus))) with only type III UrS and unipartite spermatheca; a loss of type I UrS during evolution is presumed.

Another hypothesis of UrS evolution (Fig 18), which is derived from the phylogenetic analysis performed by Perafán et al. [11], indicates, among others, that the type VII UrS of Kan-kuamo evolved from type I, that Theraphosa lost its type I UrS during evolution and that Hemirrhagus represents a basal group to the rest of the tested Theraphosinae genera. The taxa with type I UrS comprise two non-sister groups, in which the independent evolution of type I setae is supposed.

Bertani & Guadanucci [9] suggested that the UrS of types II, V and III had evolved independently, as it was later confirmed by Lüddecke et al. [54], and that the types I and IV had evolved later from an ancestor type III setae; type VI was neither studied nor discussed. This hypothesis was supported by the differences in position, structure and the release mechanism of UrS and by the existence of intermediates between types I and III, and III and IV. However, no intermediates between types I and IV were found [9]. Bertani & Guadanucci [9] hypothesised that urticating setae of type II and type III had independently evolved from the relevant body setae and noted 1) the identical manner in which they are inserted into the spider tegument (Bertani & Guadanucci [9]: Figs 23 and 24), 2) the resemblance between the truncated
basal part of body setae and stalks in UrS, and 3) the morphological similarity of basal barbs in some variants of body setae and UrS. They found body setae variants with either type II or III urticating setae, but not with types I and type IV [9]. Unfortunately, this theory does not offer an explanation of 1) how the morphologically more complicated type I setae evolved from the ancestor type III setae, whose morphology is distinctly different (the differences are mainly due to the presence of basal barbs and their arrangement into three longitudinal rows), 2) why the ancestor type III setae evolved into two different types of urticating setae, 3) why the intermediates between type I and type IV does not exist, if both types evolved from the common ancestor type III setae and 4) why the authors rejected the hypothesis proposed Pérez-Miles [10] that type III setae in taxa with and without type I setae represent two different kinds of non-homologous setae masked by surface similarity. In Fig 15, Bertani & Guadanucci [9] marked by arrow the type I seta intermixed with type III setae. However, their “type III setae” also have basal “reversed” barbs (“reversed” sensu Cooke et al., 1972, “basal” sensu revision in the present study). For that reason they are misinterpreted as type III setae. These basal “reversed” barbs in type III setae have never been recorded in taxa with type III and III+IV. If
type III setae evolved from body setae, another conflict remains. Type III setae in taxa with type I were derived from type I morphology during ontogeny and so they can not be derived from two different morphological structures. If yes, it is an example of homoplasy. In agreement with Bertani & Guadanucci [9] we did not find body setae variants with type I so we could not compare a morphology of body setae in taxa with and without type I setae.

In 2017, Turner et al. [20] used a fragment of mitochondrial genome for the first time to build a gene tree for the inference of a relationships within the family of Theraphosidae (Turner et al. [20]: Figs 2–5), with the following impacts to a contemporary systematics. They recognised three monophyletic groups within Theraphosinae: the tribe Theraphosini Turner et al., 2017, comprising taxa with type I UrS including Theraphosa with only type III UrS, and another two tribes Hapalopini Turner et al., 2017 and Grammostolini Turner et al., 2017, with UrS of type III or III+IV. The basal position of Theraphosa within Theraphosini may be clarified by the addition of further molecular data, both from unsampled genera and new fragments of mitochondrial or nuclear genome. In comparison to the previously published
evolutionary hypotheses of UrS phylogeny (Figs 17 and 18), the hypothesis proposed by Turner et al. [20] (Fig 19) is the most parsimonious, minimising the total number of character-state changes because the taxa with type I UrS comprise a monophyletic group and whatever loss of type I urticating setae during evolution (Fig 16) or a gain of type I setae by two paraphyletic groups (Fig 17) are not supposed.

Bertani & Guadanucci [9] recognised three different types of body setae: a) long tactile setae, b) intermediate-length highly plumose setae and c) short body setae, from which the UrS probably evolved. Studying the abdominal setae in *Grammostola* sp. from Brazil (Bertani & Guadanucci [9]: Fig 25), the authors presumed that type III UrS had evolved from finely plumose body setae. In the same specimen, they also found another type of short body seta (Bertani & Guadanucci [9]: Fig 18), that was non-plumose and 0.16 long, with long bars along one side of the shaft. The length of these setae and the uniform orientation of barbs coincided with the length range of type IV UrS and their arrangement of barbs.

In comparison to both types of short body setae as precursors of UrS found in *Grammostola* sp. [9], we found body setae of different morphology in two Aviculariinae, *Antillena rickwesti* (Fig 10) and *Iridopelma hirsutum* (Fig 9B). We suppose that the fusion of barbs with the shaft may lead to the morphology of type II setae. As the type II setae of Aviculariinae evolved independently to the UrS of Theraphosinae and both subfamilies represent two non-sister groups [54], this should explain the differences in the morphology of body setae in Aviculariinae and Theraphosinae.

Concerning the subfamily Theraphosinae, the only way to reconstruct its phylogeny and to infer the evolution of UrS, is to perform a thorough phylogenomic analysis comprising taxa with all known types of UrS (I, III, III+IV, VI and VII). At the same time, we also propose a new approach to the study of abdominal UrS evolution in Theraphosinae. If type II setae and type III setae were derived from morphologically different body setae, this would indicate that all types of abdominal UrS, probably including types VI and VII, evolved from any type of body setae. If UrS evolved from the same type of body setae but in different ways, then they should be considered homologous. To better understand the evolutionary process consisting of morphological specialisations of body setae and resulting in different types of defensive setae (UrS) in Theraphosinae, it seems crucial to recognise, from which morphological types of body setae different types of UrS evolved and to understand how it occurred. The existence of such types of body setae is presumed based on the existence of already documented intermediates between the particular type of UrS (II or III) and the corresponding body setae.

**Conclusions**

The morphology of UrS was studied on 144 taxa of New World theraphosids, including ontogenetic stages in chosen species, except for species with type VII UrS. Four different types of ontogenetic development of abdominal UrS were recognised within Theraphosinae, two of which were studied in detail. The typology of UrS was revised, and types I, III and IV were redescribed. The UrS in spiders with type I setae, which were originally among type III or were considered setae of intermediate morphology between types I and III, are now considered to be ontogenetic derivatives of type I and its modified forms are described as subtypes. The new terminology coincides with the hypothesis proposed by Pérez-Miles (2002) and also with the phylogenetic hypotheses proposed by Turner et al. [20] (Fig 19), and Lüddecke et al. [54], presenting the genera with type I UrS as a monophyletic group within Theraphosinae for the first time, and the presence of type I setae as a unique synapomorphy of this group. Setae of intermediate morphology between that of body setae and type II urticating setae that were found in *Iridopelma hirsutum* and *Antillena rickwesti* may provide another evidence that type II
urticating setae evolved from body setae. We suppose that the fusion of barbs with the shaft may lead to the morphology of type II setae. As the type II setae of Aviculariinae evolved independently to the UrS of Theraphosinae and both subfamilies represent two non-sister groups [54], this should explain the differences in the morphology of body setae in Aviculariinae and Theraphosinae. The terminology of "barbs" and "reversed barbs" was revised and redefined, newly emphasizing the real direction of barbs.

Supporting information

S1 File. List of examined material, voucher numbers and location information. (DOC)

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