Chapter 11
Cuticular Structures of New World Tarantulas: Ultramorphology of Setae and Other Features

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Abstract Studying morphology of Theraphosidae spiders can be very challenging, especially if the main objective is assembling characters for systematics. Such spiders present a homogeneous morphology, which, according to some specialists, has driven the attention of systematists to other groups of Araneae. Nevertheless, a great diversity of cuticular structures has been overlooked until the widespread use of scanning electron microscopy (SEM) in the last years for theraphosids. Among all mygalomorphs, Theraphosidae spiders possess the greatest variety of cuticular features. Data regarding cuticular features are still incipient, but we have been gathering massive quantity of SEM images of all parts of the spider body, revealing interesting structures to be used in systematics and investigated for functional morphology. In addition to the well-known tarsal adhesive setae of theraphosids and the urticating setae of Theraphosinae, we found putative chemosensitive setae, a great variety of stridulating setae, distinct morphologies of leg and palpal structures, including cuticular projections, labial and maxillary cuspules, trichobothria, as well as other enigmatic features. In this chapter, we aim to present a comprehensive revision of cuticular features of New World Theraphosidae spiders, with descriptions and micrographs.

11.1 Introduction

Spiders, as a member of the Phylum Arthropoda, have their whole body embraced by a hard body shell, named exoskeleton. The exoskeleton is made of the cuticle, a stiff material composed of lipids and waxes, glycosylated and unglycosylates proteins, the polysaccharide chitin and catecholamines. The cuticle provides protection against both desiccation and predators, maintains the shape and structure of the

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body, allowing locomotion (Moussian 2013). Spiders and insects have cuticles of similar composition (Foelix 1996), and differ from the crustaceans as they may incorporate calcite (Moussian 2013). Spiders also have a mesocuticle, which is absent in insects (Foelix 1996). Rather than a smooth layer, although its lamellate organization, the cuticle bears a great diversity of outgrowths and textures with many distinct functions, e.g., sensitive, adherent and covering setae, bristles, scales, spines, claws, stridulatory ridges and lyrae, among many others.

Tarantulas (Theraphosidae) are notoriously "hairy" spiders, especially when compared to trapdoor or sheet-web mygalomorphs (Fig. 11.1a–d). Not only do they possess greater quantity of setae on their bodies, but they also bear greater diversity of setal forms (Pérez-Miles et al. 2017), providing them with adhesive bristles (adhesive scopula, claw tufts), structural color patterns (Hsiung et al. 2015), urticating setae (Bertani and Guadanucci 2013), stridulating apparatus (Galleti-Lima and Guadanucci 2018), mixed (adhesive and chemosensitive) scopula of males (Pérez-Miles et al. 2017), clavate trichobothria (Guadanucci 2012), tibial apophysis, labial cuspules (Pérez-Miles and Montes de Oca 2005), spigots and epiandrous glands (Ferretti et al. 2017) and other unknown and/or unnamed structures. Recent advances, as in the references cited above, have shown a great diversity of structures, which could only be accessed with scanning electron microscopy, revealing designs and textures not visible under optical microscope.

Fig. 11.1 Habitus, live specimens. Tarantulas and trapdoor spider habitus. (**a**) *Actinopus rufipes*, female. (**b**) *Idiops* sp., male. (**c**) *Homoeomma brasilianum*, female. (**d**) *Dolichothele mottai*, female

Theraphosidae systematics has been greatly influenced by the presence of a stridulatory apparatus since the first records of these setae by Simon (1892) and Pocock (1895). These apparatuses are usually composed by groups of setae (tuft or bristle) inserted on opposite faces (prolateral/retrolateral) of proximal leg and palp articles, such as coxae, trochanters, and femora. The current classification of Theraphosidae at subfamily level greatly relies on the presence, position, and ultrastructure of these setae (e.g., plumose setae, lyra, pegs, thorns). Regarding the Neotropical tarantulas, especially the Theraphosinae, their stridulatory setae have been extensively used as taxonomic characters at generic level, e.g., Ferretti et al. (2011), Bertani et al. (2008), Galleti-Lima and Guadanucci (2018), Gargiulo et al. (2018). To date, different types of stridulating setae have already been found in several theraphosine genera (Figs. 11.2, 11.3, and 11.4) (Pérez-Miles et al. 1996; Galleti-Lima and Guadanucci 2018; pers. obs.). Beyond Theraphosinae, the New World tarantulas belonging to the aviculariinae genus *Psalmopoeus* Pocock, 1895 possess a lyra on prolateral maxillae (West et al. 2008; Fukushima and Bertani 2017), which can be rubbed against a few stiff setae on prolateral chelicerae, acting as a stridulating apparatus.

Theraphosinae and Avicularinae spiders are also notorious for their urticating setae (Chap. 9), a specific detachable kind of seta from which the urticarious reaction has been reported since the naturalists of the nineteenth century (Cooke et al. 1972; Pérez-Miles 2002; Bertani and Guadanucci 2013). Starting with the morphological comprehensive survey by Cooke et al. (1972), a few studies were carried out regarding their morphology and systematics (Marshall and Uetz 1990a; Pérez-Miles 1998; Perafán and Perez-Miles 2010; Bertani and Guadanucci 2013) and usage and behavior (Marshall and Uetz 1990b; Pérez-Miles and Prandi 1991; Pérez-Miles and Costa 1994; Bertani and Marques 1995; Bertani et al. 2003). The two Neotropical endemics Theraphosinae and Aviculariinae are the only spiders that possess these urticating setae, which are lacking in the remaining theraphosids. While in the abdomen of theraphosines one may find types I, III, IV, and VI, Aviculariinae spiders possess type II (abdomen) and type V (palpal femora of *Ephebopus* Simon, 1892). Spiders of these two subfamilies also differ on the way they use the urticating setae: the theraphosines frequently release them by rubbing their hind legs against the abdominal setae patch when disturbed. Their spinose tibia and metatarsi III and IV may have an important role in the mechanism of setae releasing. Type II urticating setae are transferred by contact (except for *Avicularia versicolor,* see Bertani et al. 2003) or by scratching the palpal femur against the chelicera, in *Ephebopus*. The leg spines are numerous in Theraphosinae spiders, and limited to just a few (up to three) apical ones on posterior tibia and metatarsi or completely absent in Aviculariinae. The remaining New World tarantulas, belonging to the subfamilies Schismatothelinae and Ischnocolinae sensu strictu (Guadanucci 2014) lack any kind of urticating setae and have moderate number of leg spines, especially on legs III and IV.

Apart from stridulatory and urticating setae of New World tarantulas, few other cuticular structures received attention and were studied in a comparative framework at the ultramorphological level, and will be dealt with in more detail further below. Trichobothria of Theraphosidae and Barychelidae were described in their

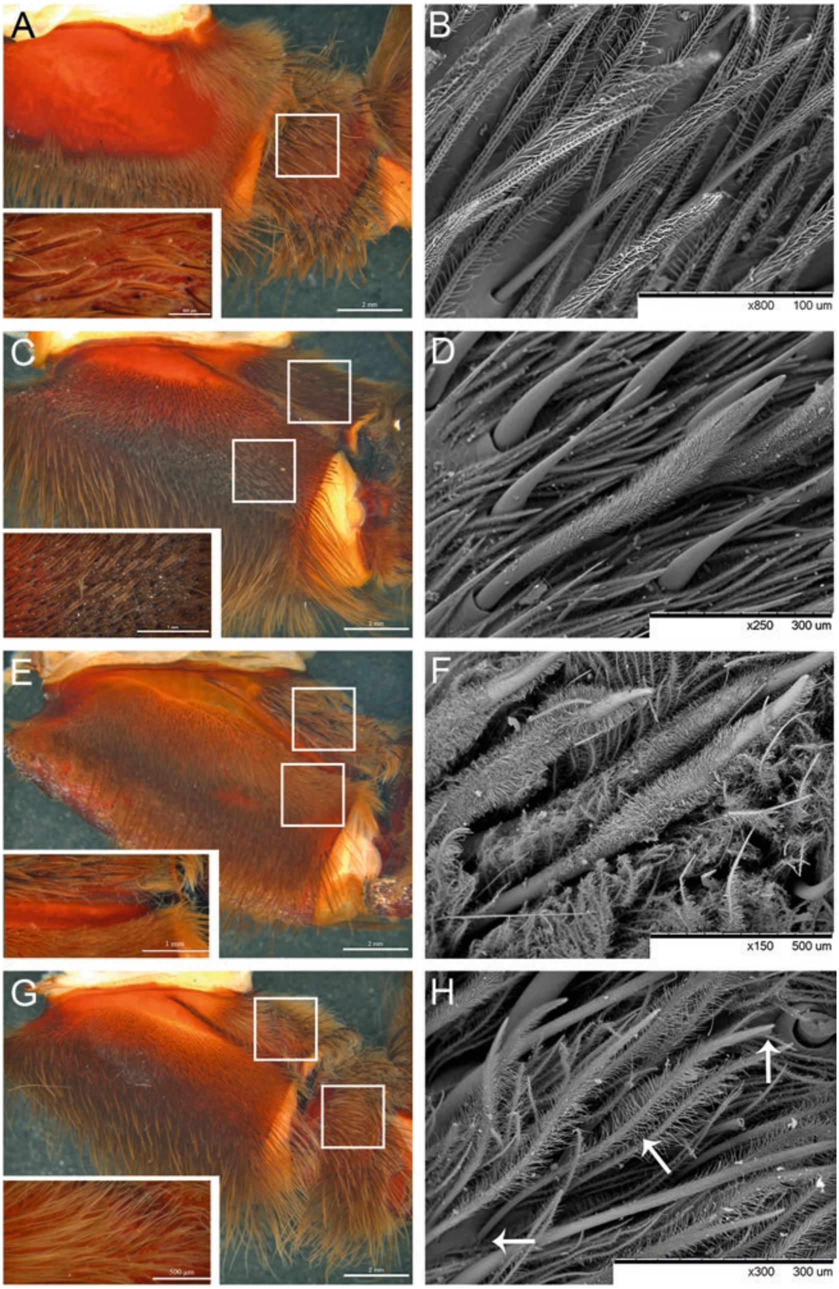

Fig. 11.2 Stridulating setae. (**a**) Retrolateral view of coxae and trochanter of palp in *Acanthoscurria gomesiana*, detail showing claviform stridulating setae. (**b**) Claviform stridulating setae, SEM micrography. (**c**) Prolateral view of coxae I in *Grammostola* sp., detail showing rough stridulating setae. (**d**) Rough stridulating setae, SEM micrography. (**e**) Prolateral view of coxae I in *Lasiodora* sp., detail showing velvet stridulating setae. (**f**) Velvet stridulating setae, SEM micrography. (**g**) Prolateral view of coxae and trochanter I in *Vitalius* sp., detail showing plumose stridulating setae. (**h**) Plumose stridulating setae, SEM micrography

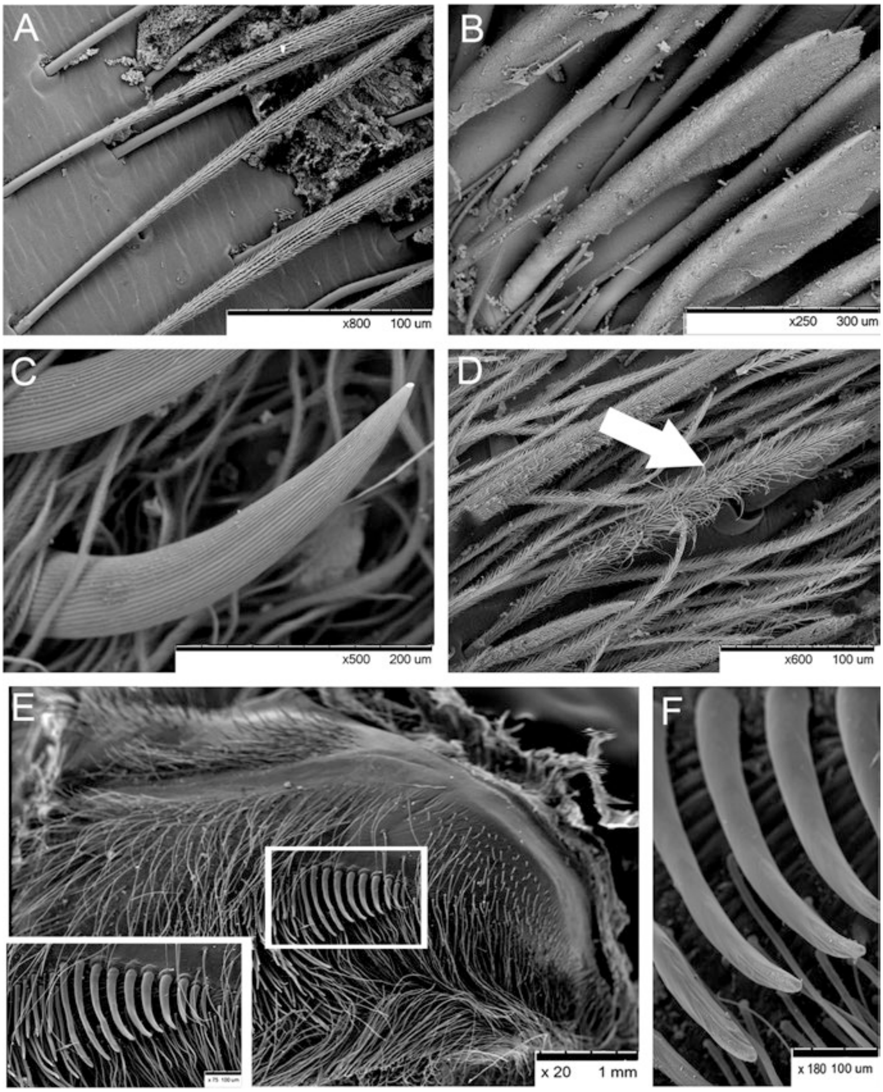

Fig. 11.3 Stridulating setae (cont.). (**a**–**f**) SEM micrographs of distinct types of stridulating setae. (**a**) Sectioned stridulating setae. (**b**) Spatuliform stridulating setae. (**c**) Spiniform stridulating setae. (**d**) Pilose stridulating setae (arrow). (**e**) Prolateral view of maxilla in *Psalmopoeus* sp., showing the maxillary lyra in the detailed square. (**f**) Maxillary lyra, detail of setae, in *Psalmopoeus* sp.

ultrastructure and disposition by Guadanucci (2012); Pérez-Miles et al. (2017) presented data on adhesive tarsal setae (scopula and claw tufts) and recognized the mixed scopula of Theraphosidae males, composed of chemosensitive and adhesive setae; labial and maxillary cuspules are conspicuous cuticular structures shared by Theraphosidae and many other mygalomorph families (except Mecicobothriidae,

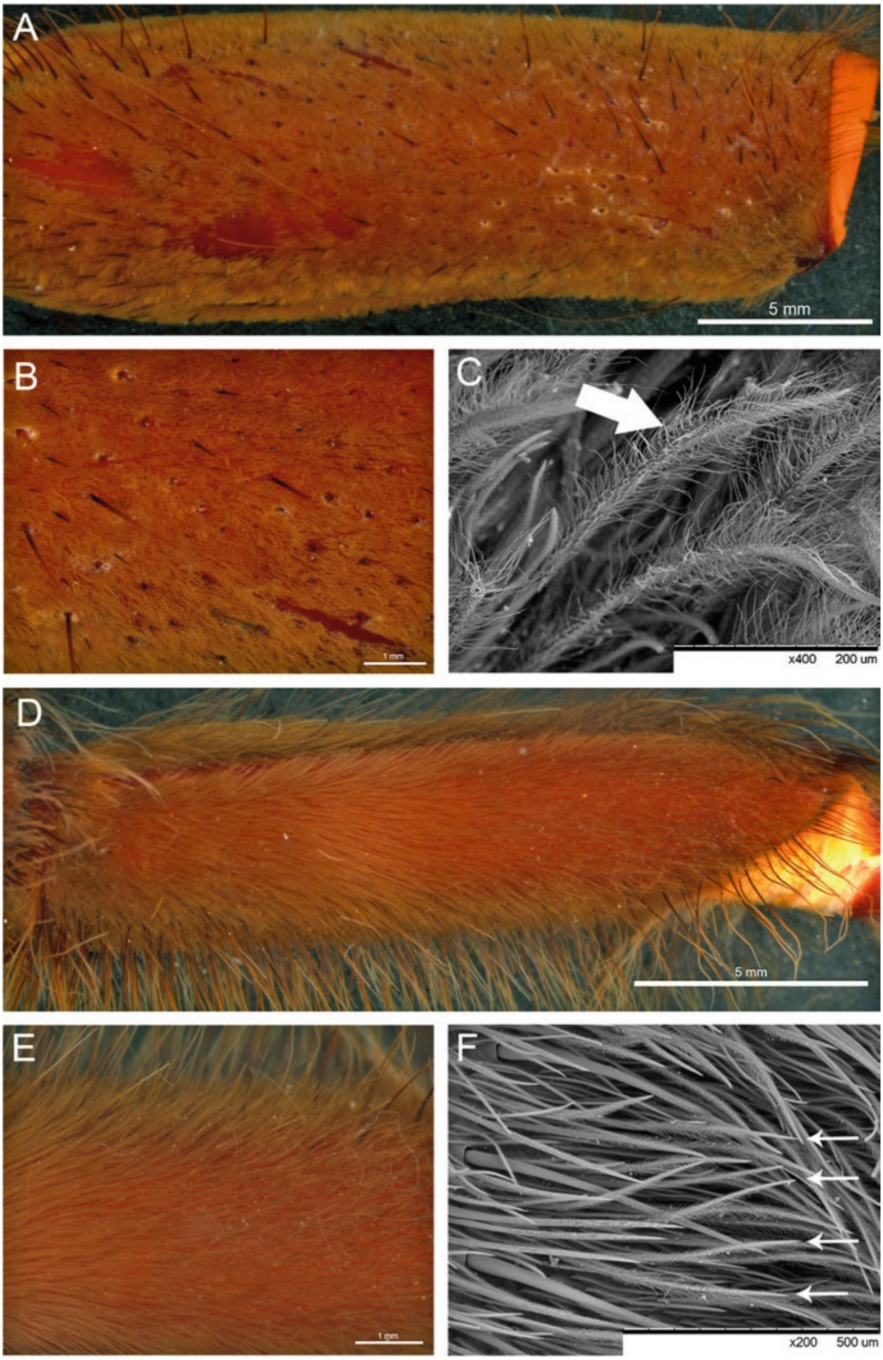

Fig. 11.4 Femoral scopulae. (**a**) Retrolateral view of femur IV in *Theraphosa blondi*. (**b**) Femoral scopula of leg IV in *Theraphosa blondi*. (**c**) Claviform stridulating setae (arrow) of femoral scopulae of leg IV, SEM micrography. (**d**) Retrolateral view of femur IV in *Vitalius* sp. (**e**) Femoral scopulae of leg IV in *Vitalius* sp. (**f**) Plumose stridulating setae (arrows) of femoral scopulae of leg IV, SEM micrography

Hexurellidae, Megahexuridae and Antrodietidae), and they were studied in a few number of theraphosine and aviculariine genera by Pérez-Miles and Montes de Oca (2005). Ferretti et al. (2017) published the first comparative study of the epiandrous apparatus for mygalomorph spiders, which comprises a group of additional silk glands (epiandrous spigots) located at the anterior margin of the genital furrow of males, and included a few New World tarantula spiders; Hsiung et al. (2015) recognized a diversity of nanostructural mechanisms that produces blue reflectance in tarantulas. Except from the ones cited above, no other cuticular feature has received much attention from arachnologists in the last few years, except by some particular taxonomic works for the purpose of morphological description. Recent publications and unpublished surveys have yielded great diversity of cuticular structures that were examined under the SEM, where magnifications above 500× can reveal conspicuous differences in well-known structures (e.g., stridulating setae, tufts, leg scopula, chemosensory setae) and other newly discovered structures for which, at the moment, we can only speculate about their functions.

11.1.1 **Stridulating Setae*: Coxae, Trochanters, Femora (Figs. 11.2, 11.3, and 11.4)***

Stridulating apparatus are fairly well known in spiders. A single spider individual (Fam. Zodariidae) has been reported with six stridulating apparatus, according to Jocqué (2005), who also listed many types of stridulatory organs described at least for 22 families of spiders. The production of a hissing sound by some Theraphosidae spiders is well reported (Legendre 1963; Uetz and Stratton 1982; Marshall et al. 1995) and very well known among tarantula hobbyists. Although the detailed mechanism of stridulating has never been elucidated, different authors (Pérez-Miles et al. 2005; Bertani et al. 2008; Galleti-Lima and Guadanucci 2018) agree that the possession of stiff setae, spines, ridges, or pegs on opposite surfaces comprises the apparatus behind the production of sound, caused by the attrition between such structures (Uetz and Stratton 1982). In the case of New World Tarantulas, the stridulating apparatus can be located on distinct proximal palp and legs articles, such as coxae, trochanters and femora, and they are usually composed by a group of setae, with long or short barbs (Figs. 11.2a–h and 11.3a, b) (most genera), short spines (Fig. 11.3c) (*Theraphosa* and *Pamphobeteus*), or peg-like setae forming the lyra (*Psalmopoeus*) (Fig. 11.3e, f).

The few authors that proposed relationship hypothesis among Theraphosinae spider genera in the last years have used the presence of a stridulating apparatus as a systematic character (Pérez-Miles et al. 1996; Bertani 2001; Perafán and Perez-Miles 2014; Bertani et al. 2011). The presence of such a stridulatory apparatus appears as apomorphic for some genera (e.g., *Lasiodora*, *Grammostola*, *Acanthoscurria*, *Cyrtopholis*, *Theraphosa*) and they were all considered of the same morphological type and treated as same character state by the authors above, differing only on where they are located (coxae and/or trochanters). More recent papers have verified the presence of new types of stridulatory setae, some of these setae types are present on spiders for which they were unreported before (although a stridulating apparatus was already known): *Hemirrhagus* (Marroquín 2014), *Pamphobeteus* (Bertani et al. 2008), *Longilyra* (Gabriel 2014), *Aguapanela* (Perafán et al. 2015). Not until the comparative survey on the ultrastructure of the setae on the coxae and trochanters of Theraphosinae (Galleti-Lima and Guadanucci 2018) did we know about the diversity of forms of stridulatory setae. Interestingly, Bücherl (1957) anticipated this diversity, recognized and illustrated differences in the setae of *Acanthocurria*, *Grammostola*, and *Lasiodora*. According to Galleti-Lima and Guadanucci (2018), and also our unpublished data, the diversity of stridulatory setae found on coxae and trochanters of Theraphosidae spiders fits into the following nine types: claviform (Fig. 11.2b), rough (Fig. 11.2d), velvet (Fig. 11.2f), plumose (Fig. 11.2h), sectioned (Fig. 11.3a), spatuliform (Fig. 11.3b), spiniform (Fig. 11.3c), pilose (Fig. 11.3d), and liriform (see Gabriel 2014: Figs. 1–3). Among the Theraphosinae, spiders that have been reported with stridulatory setae on coxae and/or trochanters are listed on Table 11.1.

Table 11.1 Types and location of stridulating setae found on coxa and/or trochanter on Theraphosinae genera

Genera	Type of stridulating setae	Location
Acanthoscurria	Claviform (Fig. 11.2b)	Trochanter
Aguapanela	Plumose (Fig. 11.2h)	Coxa + trochanter
Aphonopelma	Sectioned (Fig. 11.3a)	Coxa + trochanter
Brachypelma	Claviform	Coxa + trochanter
Citharacanthus	Sectioned	Trochanter
Cotztetlana	Spiniform (Fig. 11.3c)	Coxa + trochanter
Crassicrus	Plumose	Trochanter
Cyrtopholis	Claviform	Trochanter
Grammostola	Rough (Fig. 11.2d)	Coxa
Hemirrhagus[a]	Sectioned/spatuliform (Fig. 11.3b)/pilose (Fig. 11.3d)	Coxa + trochanter
Lasiodora	Plumose + velvet (Fig. 11.2f)	Coxa + trochanter
Longilyra	liriform (Gabriel 2014: Figs. 1–3)	Trochanter
Megaphobema	Plumose	Coxa + trochanter
Nesipelma	Claviform	Trochanter
Nhandu	Plumose	Coxa + trochanter
Pamphobeteus	Spiniform	Coxa
Phormictopus	Claviform	Coxa + trochanter
Proshapalopus	Plumose	Coxa + trochanter
Pterinopelma	Plumose	Coxa + trochanter
Theraphosa	Claviform + spiniform	Coxa + trochanter
Umbyquyra	Claviform	Trochanter
Vitalius	Plumose	Coxa + trochanter

[a] Spiders of the genus *Hemirrhagus* have been recorded with distinct types in different species

Nevertheless, Theraphosinae is the most diverse Neotropical group of mygalomorphs, and there is still a great number of spiders to have their coxae and trochanter examined under the SEM, thus reaching enough magnifications to detect these morphological attributes. We are far from a consensus about Theraphosinae relationships and, consequently, far from understanding the evolution of these setae. Few papers suggested the use of stridulation in sexual and defensive behaviors (Legendre 1963; Uetz and Stratton 1982; Marshall et al. 1995). In fact, sexual courtship of theraphosids (and of mygalomorphs in general, see Ferretti et al. 2013) is strongly based on mechanical signals, with legs and body vibrations performed by both males and females. These vibrations, which sometimes are associated with a hissing audible sound, together with those of defensive behaviors, have an important adaptive value, and thus supporting the hypothesis of multiple acquisitions across Theraphosinae (Pérez-Miles et al. 1996; Bertani 2001; Bertani et al. 2008; Galleti-Lima and Guadanucci 2018). The various types of stridulating setae support the hypothesis of multiple acquisitions, following the proposal of Galleti-Lima and Guadanucci (2018) that stridulating setae are modifications of regular body seta. Apart from the Theraphosinae, the only New World theraphosid bearing stridulatory apparatus are spiders of the genus *Psalmopoeus*, showing a conspicuous lyra on the prolateral surface of the maxillae (Fig. 11.3e, f). These peg-like structures that form the lyra are curved, with very short barbs on the apex (Fig. 11.3f—detail), and disposed as a series of parallel setae of increasing length (from basal to apical). For many years, *Psalmopoeus* was included in the Selenocosmiinae, due to the presence of these clavate setae (bacillae) on the prolateral maxillary surface (Raven 1985; West et al. 2012), and thus comprising the sole representative of this subfamily in the Neotropics. *Psalmopoeus* is currently placed within Aviculariinae, and its stridulatory apparatus differ from that of selenocosmiines by having fewer setae (from 9 to 14), while the lyra of selenocosmiines is an oval patch of many setae [obs: the whole organ, composed by the group of setae on prolateral maxillae, has been named lyra by some authors (Raven 1985; West et al. 2012; Mendoza-Marroquín 2014), contrary to Gabriel and Sherwood (2018) that named each setae as lyra.].

The scopula on the retrolateral surface of femur IV (Fig. 11.4a–f) has also been given great weight in Theraphosinae phylogenetics (Raven 1985; Pérez-Miles et al. 1996; Bertani 2001) and its presence is a good taxonomic character for genera diagnosing (pers. obs.). These authors cited above did not draw any attention concerning the presence of a scopula on femora I–III. The femoral scopula is very similar to that on tarsi: it has a rug-like appearance, occupying the whole lateral (pro and/or retrolateral) surface, and it can be intermixed with long setae. Perafán et al. (2016) detected the femoral scopula in species of the following genera: *Acanthoscurria*, *Cyrtopholis*, *Eupalaestrus* Pocock, 1901, *Lasiodora*, *Megaphobema* Pocock, 1901, *Metriopelma* Becker, 1878, *Nhandu*, *Pamphobeteus*, *Phormictopus*, *Schizopelma* F. O. Pickard-Cambridge, 1897, *Sericopelma* Ausserer, 1875, *Theraphosa*, *Vitalius* and *Xenesthis* Simon, 1891, and we report herein the presence of the same structure in *Proshapalopus* and *Pterinopelma*. The femoral scopula is composed of claviform setae (Fig. 11.4a–c) in *Theraphosa* and *Brachypelma*, or plumose setae in the remaining genera cited above. Spiders of the genera *Lasiodora*, *Brachypelma*, and

Table 11.2 Types and location of femoral scopula setae on Theraphosinae genera

Genera	Type of setae	Location (femur)
Acanthoscurria	Plumose (Fig. 11.4f)	I (prolateral) + IV (retrolateral)
Brachypelma	Claviform (Fig. 11.4c)	All legs
Cyrtopholis	Plumose	I (prolateral) + IV (retrolateral)
Eupalaestrus	Plumose	I (prolateral) + IV (retrolateral)
Lasiodora	Plumose	All legs
Megaphobema	Plumose	I (prolateral) + IV (retrolateral)
Metriopelma	Plumose	I (prolateral) + IV (retrolateral)
Nhandu	Plumose	I (prolateral) + IV (retrolateral)
Pamphobeteus	Plumose	I (prolateral) + IV (retrolateral)
Phormictopus	Plumose	I (prolateral) + IV (retrolateral)
Proshapalopus	Plumose	I (prolateral) + IV (retrolateral)
Pterinopelma	Plumose	I (prolateral) + IV (retrolateral)
Schizopelma	Plumose	I (prolateral) + IV (retrolateral)
Sericopelma	Plumose	I (prolateral) + IV (retrolateral)
Theraphosa	Claviform	All legs
Vitalius	Plumose	I (prolateral) + IV (retrolateral)
Xenesthis	Plumose	I (prolateral) + IV (retrolateral)

Theraphosa are the only ones that possess femoral scopula on all legs. Otherwise, in the remaining, these setae are present on femora I (prolateral) and IV (retrolateral) (Table 11.2).

11.1.2 Adhesive Setae*: Scopula and Claw Tufts (Fig. 11.5a, c–e, g, h)*

Many published papers investigated various aspects of these remarkable adhesive setae, providing climbing and prey-capturing skills [see Pérez-Miles et al. (2017) and references cited therein and also Chap. 12], mainly focused on araneomorph spiders. Theraphosids in general are characterized by the possession of claw tufts and dense tarsal scopulae (Raven 1985) (Fig. 11.5a, c–e, g, h), those of which are composed by the same type of adhesive setae, and are similar to those of araneomorphs (Ramírez 2014). They are microtriched setae (spatulated microtrichia), with the difference that those of claw tufts are longer and inserted into tarsal pads located below the claws (Fig. 11.5e). Pérez-Miles et al. (2017) identified two variants of adhesive setae in theraphosids, lamellate and lamellate-crested. Large spiders, as the big theraphosines (e. g., *Theraphosa*, *Pamphobeteus*, *Xenesthis*) bear very dense tarsal scopula, while small theraphosids have a less dense scopula, which can be even less dense in the hind legs. Simon (1892) used the condition of the tarsal scopula (entire or divided by a band of setae) in Theraphosidae to distinguish his tribe Ischnocolea (current subfamily Ischnocolinae) (divided scopula) from the

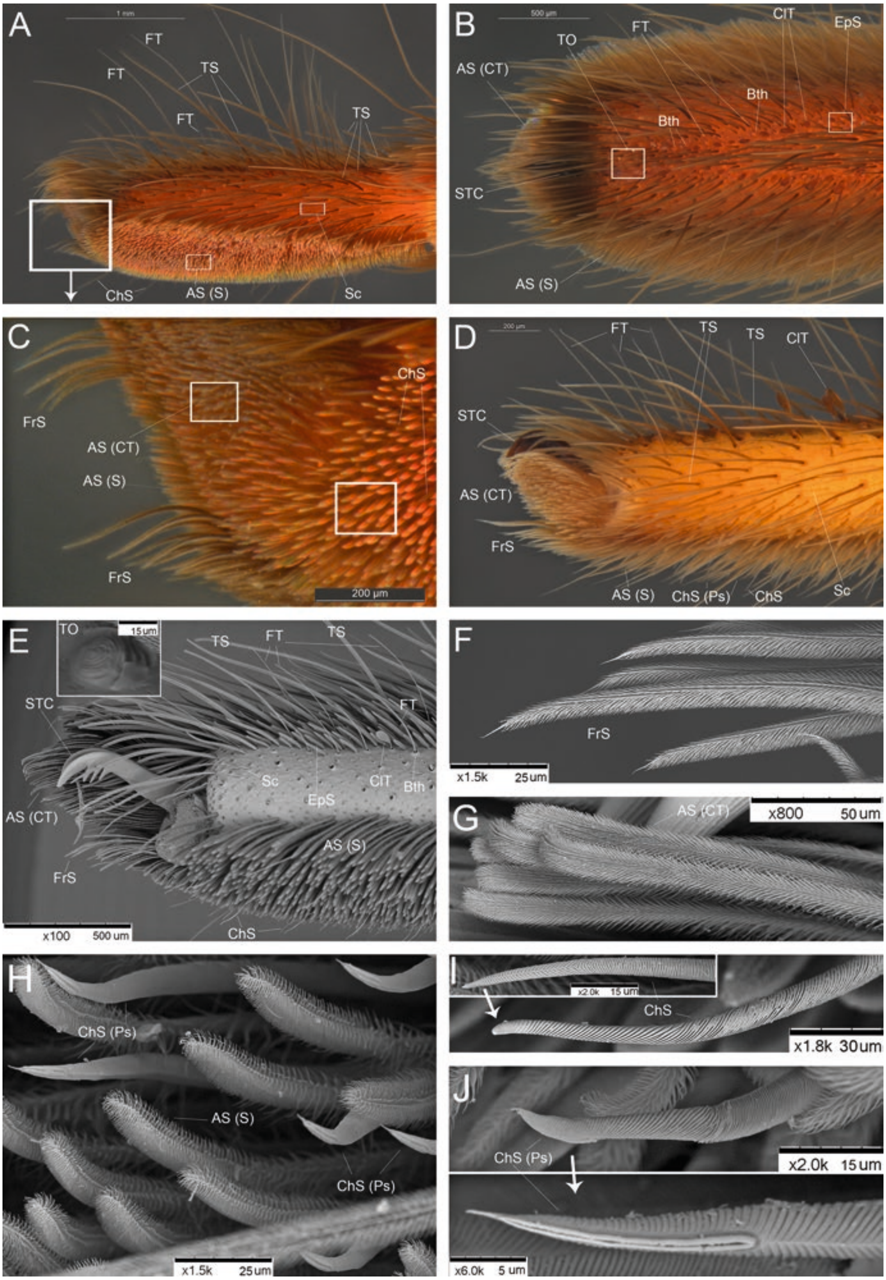

Fig. 11.5 Scopula, pseudoscopula, claw tufts. (**a**–**c**). Female tarsus I, *Guyruita cerrado*. (**d**) Male tarsus I, *Tmesiphantes riopretano*. (**e**) Female tarsus I, detail of the tarsal organ, *Guyruita* sp. (**f**) Frictional setae, female tarsus I, *Sickius longibulbi*. (**g**) Adhesive setae (claw tufts), female tarsus IV, *Heterothele* sp. (**h**) Scopulae on male tarsi I, *Typhochlaena paschoali*. (**i**) Chemosensory seta, lateral view, male tarsi IV, *Guyruita* sp.; detail, dorsal view. (**j**) Chemosensory seta (male pseudoscopula), lateral view, *Heterothele* sp.; detail, ventral view, *Guyruita* sp. Acronyms: *AS (CT)* adhesive setae (claw tufts), *AS (S)* adhesive setae (scopulae), *Bth* bothrium, *ClT* clavate trichobothrium, *ChS* chemosensory setae, *ChS (Ps)* chemosensory setae (male pseudoscopula), *Sc* scales, *EpS* epitrichobothrial setae, *FT* filiform trichobothrium, *FrS* frictional setae, *STC* superior tarsal claws, *TS* tactile setae (striated setae), *TO* tarsal organ

remaining (entire scopula). Pérez-Miles (1994) verified the ontogenetic differentiation (from divided to entire) and its relation to spider size (divided condition in small spiders) for Theraphosinae. In fact, in theraphosids with divided scopula, there is an anterior-posterior gradation of the width of the band dividing the scopula, being wider on hind legs (Guadanucci 2005; Pérez-Miles et al. 2017). Pérez-Miles et al. (2015) found no differences in friction between species with divided and entire tarsal scopula. However, their results on testing friction of tarantulas' adhesive pads suggested that claw tufts produce adhesion when the legs pull, while scopula functions when legs push, which is in agreement with previous studies with *Cupiennius salei* (Ctenidae) and *Aphonopelma seemani* (Theraphosidae) (Niederegger and Gorb 2006). Many authors have suggested differential usages of these adhesive setae, but it is clear that they are involved both in adhesion for locomotion and in prey capture (Pérez-Miles et al. 2017). Within Mygalomophae, the scopula seems to have been acquired independently by Crassitarsae and Euctenizoidina (Pérez-Miles et al. 2017).

Another important feature concerning the scopula is the condition found in arboreal theraphosids, which for the Neotropical ones are included within Aviculariinae: dense scopula that extends laterally, giving the tarsi a spatulate appearance (Bertani 2012). This condition is also found in those aviculariines that do not have arboreal behavior (*Ephebopus*) and its function if not very well understood (West et al. 2008).

The adhesive setae forming a scopula are also present on ventral metatarsi, varying in density and extension. Except for those few large spiders (e.g., *Xenesthis*, *Theraphosa*, *Pamphobeteus*) with dense metatarsal scopula, the widespread condition is that scopula on metatarsi of hind legs are limited to the distal end (sometimes limited to few sparse setae), whereas the scopula on fore legs can extend from half to the entire article. The condition (extension and density) of the metatarsal scopula has never been closely studied, but it seems plausible to consider this character as an adaptation to prey capture based in two assumptions: (1) the scopula is concentrated on fore legs and (2) the metatarsi do not touch the substrate during locomotion. Wolff et al. (2013), who found a close association between adhesive setae and free hunter lifestyle in spiders, suggesting that the acquisition of a scopula was as an adaption to controlling prey, evolving as a substitute for silk.

11.1.3 Frictional Setae *(Fig. 11.5a, c–f)*

They are conical setae, with no-spatulate microtrichia, inserted on tarsus tip below the claws, and may extend in a median line to the basal portion of the tarsus, dividing the scopula in longitudinal halves (Pérez-Miles 1994; Guadanucci 2005; Pérez-Miles et al. 2017). From lateral view, these setae are easily distinguished from the adhesive ones on apical tarsus, because they stick out from below the dense claw tufts (Fig. 11.5a–d). From ventral view, a patch of plumose set is distinguishable from the dense scopula (Fig. 11.6a). Pérez-Miles (1994) adopted the same terminology proposed by Rovner (1978) for *Lycosa* spp. and named the thick setae that divides the scopula as type B (adhesive setae are type A). Pérez-Miles et al. (2017) considered these as conical setae, and highlighted its presence in the transitional zone between scopula and claws tufts (Fig. 11.6a). They also showed different conditions of the length and width of this band of conical setae, varying from narrow to wide, restricted to either apical or basal portion, or extended along the whole scopula length. Furthermore, Ramírez (2014) recognized in dionychan spiders a morphological intermediate between tenent (adhesive) and plumose setae, and named them pseudotenent setae. The pseudotenent share with frictional setae the position of insertion (below the claws) and the strong morphological similarities, with acute setal shaft and loosely organized expanded barbs (non-spatulate). Ramírez (2014) found these pseudotenent setae in several araneomorph families, as it is present in all Mygalomorphae families (pers. obs.) with the difference that, in Theraphosidae, they have more barbs (plumose aspect) compared to those of other families (except for the barychelids, which whom they share close affinities) with an acute tip (Fig. 11.5f).

A few studies have investigated the adhesive and frictional forces performed by the scopulate spider tarsi (Niederegger and Gorb 2006; Wolff and Gorb 2012, 2013; Wolff et al. 2013; Lapinski et al. 2015), all focused on the typical adhesive setae (claws tufts and scopula setae with spatulate microtrichia). Wolff and Gorb (2012) suggested that these frictional setae play a role in the claw-interlocking mechanism with rough substrates, representing a further adaptation for locomotion on non-horizontal surfaces. However, considering the variation of these setae (disposition and quantity) in tarantulas, it seems that we are still far from a full understanding of the function of these frictional setae.

11.1.4 Chemosensors

Structures that function as chemosensors must have pores or slits, through which any specific substance penetrates and reaches the sensory cells (Barth 2002), that extends inside the setal shaft up to the opening near the tip (Foelix 1996). In spiders, chemoreceptors are concentrated on distal segments of palps and forelegs (Gaskett 2007; Foelix 1996). The most common are chemosensory setae, named hair sensilla by Foelix (1996). In Theraphosidae spiders, as in the remaining mygalomorphs, these chemosensors are more common on tibiae, metatarsus, and tarsus, but they were also found also in proximal palp/leg segments (coxae and trochanters) and spinnerets (pers. obs.). They can be very long setae, slightly curved and usually overpassing in length the surrounding setae, located on all faces of palp and legs (see Fig. 11.5e, few chemosensory setae—ChS, mixed with adhesive scopula). The distal half of these chemosensory setae are ornamented with thin diagonal ridges, resembling the texture of a rope, and the opening is a very small rounded pore (Fig. 11.5i).

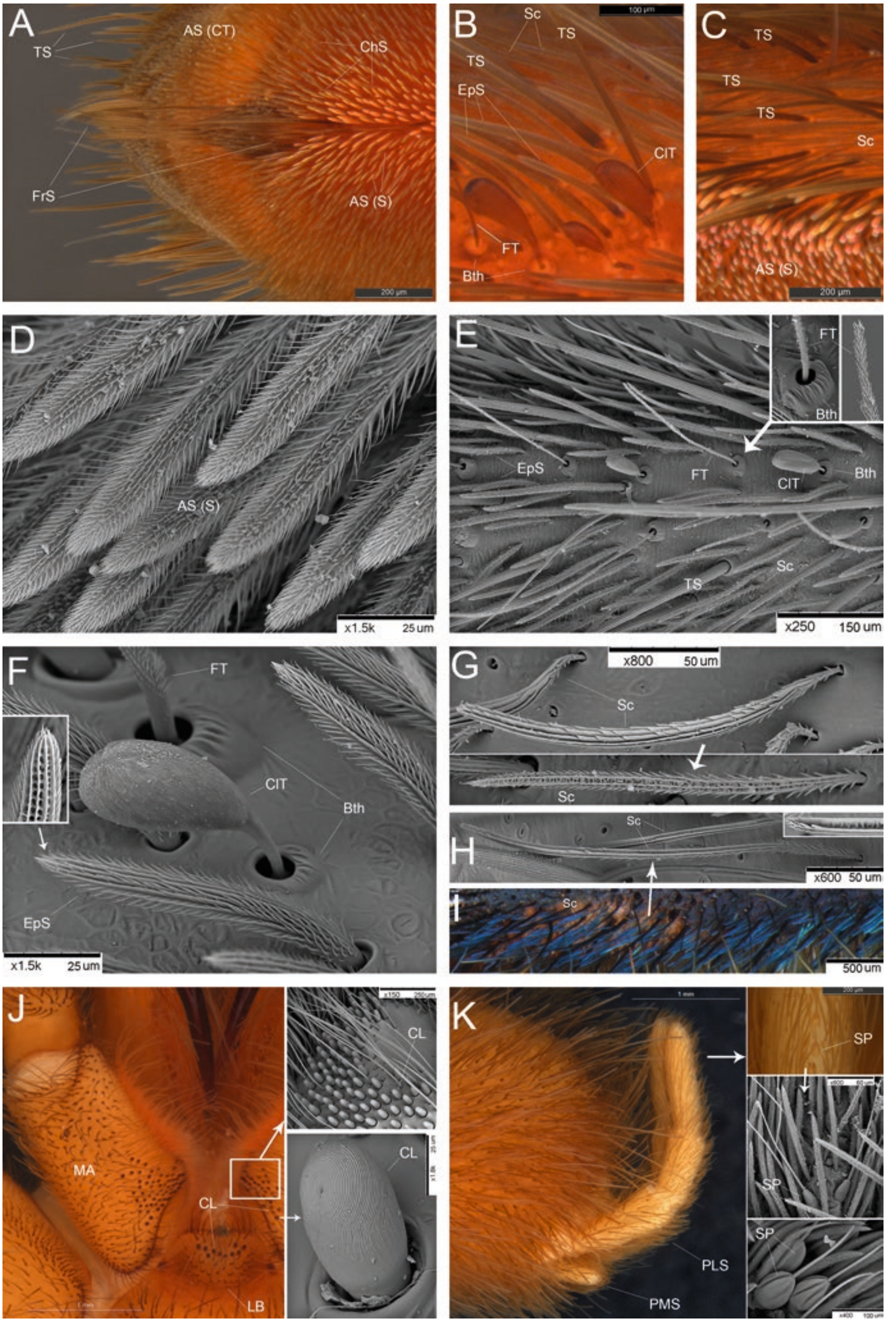

Fig. 11.6 Trichobothria, scales, cuspules, spigots. (**a**–**c**) Female tarsus I, *Guyruita cerrado*: (**a**) Claw tufts and scopulae, ventral view; (**d**) Female tarsus I, *Guyruita* sp. (**e**) Male tarsus I, dorsal view, *Tmesiphantes riopretano*. (**f**) Female tarsus I, lateral view, *Sickius longibulbi*; detail, dorsal

Recently, Foelix et al. (2010) found a scopula-like concentration of putative chemosensory setae on ventral tarsi of males *Liphistius* and *Idiops*. More recently, Pérez-Miles et al. (2017) reported the same type of chemosensory setae only in males of all mygalomorphs, located ventrally on tarsi and, in a few cases, apical metatarsi (more numerous in forelegs). In mygalomorphs lacking adhesive scopula, these setae form the pseudoscopula, named by Pérez-Miles et al. (2017) to differ from the adhesive scopula, present both in males and females. In Theraphosidae (Fig. 11.5h), and other spiders with adhesive scopula (e.g., diplurines, barychelids, nemesiids and some cyrtaucheniids), these putative chemosensory setae are interspersed with adhesive setae to form the mixed scopula (Pérez-Miles et al. 2017) and are characterized by a similar texture of the surface, similar to the long chemosensory setae described above, and with a distinct subapical opening. In Theraphosidae, the apical portion is slightly swollen with a thin and long opening slit, and a well-marked rim (Fig. 11.5j), condition shared with Barychelidae (pers. obs.).

Foelix et al. (2010) reported a scopula-like structure on ventral tarsi of *Liphistius* (Mesothelae) and *Idiops pylorus* Schwendinger, 1991 (Mygalomorphae), for which they suggested to be probable contact chemoreceptors. Years before Foelix et al. (2010), Gorb et al. (2006) reported to have found tarsal spigots in a female *Aphonopelma seemanni*, and also suggested that the tarsal silk production by these spigots would help the spiders climb vertical surfaces providing extra adhesion. The pictures provided by the author for the alleged spigots are in fact the long chemosensory setae that are present in both sexes, as they share the exact same ultrastructure (blunt tip and thin diagonal ridges). After a few replies (Pérez-Miles et al. 2009; Gorb et al. 2009) and extra morphological and experimental studies (Rind et al. 2011; Pérez-Miles and Ortíz-Villatoro 2012; Foelix et al. 2010), Foelix et al. (2012) showed that they probably comprise chemoreceptors.

The tarsal organ has also been interpreted as a chemoreceptor, although never experimentally tested for this function, and received little attention throughout the years. Raven (1985) described the overall morphology of tarsal organ in mygalomorphs as low or slightly raised, domed, with concentric ridges, located at the median dorsal line close to tarsal anterior margin. Due to the great amount of setae on their body, especially on the legs, the tarsal organ of theraphosids is of difficult visualization, unless some apical setae are removed. The first work regarding the tarsal organ was done by Blumenthal (1935), and the ultrastructural description was performed by Foelix and Chu-Wang (1973). The tarsal organ of theraphosids, which

view. (**g**–**i**) Scales: (**g**) Male tarsus I, lateral view, *Holothele longipes*; dorsal view, *T. riopretano*. (**h**, **i**) Male tarsus I, dorsal view, *Dolichothele diamantinensis*. (**i**) Live specimen. (**j**) Labial and maxillary cuspules, *T. riopretano*, male; detail of the maxilla, *Typhochlaena paschoali*, male; cuspule detail, *D. diamantinensis*, male. (**k**) Spinnerets, lateral view, *T. riopretano*, male; spigots details, ventral view: *T. riopretano*, male; *S. longibulbi*, female; *T. costae*, male. Acronyms: *AS (CT)* adhesive setae (claw tufts), *AS (S)* adhesive seta (scopulae), *Bth* bothrium, *CL* cuspule, *ClT* clavate trichobothrium, *ChS* chemosensory seta, *Sc* scale, *EpS* epitrichobothrial seta, *FT* filiform trichobothrium, *LB* labium, *MA* maxilla (palpal coxae), *PLS* posterior lateral spinnerets, *PMS* posterior median spinnerets, *FrT* frictional setae, *SP* spigot, *TS* tactile seta (striated setae) fits in the description above, seems not to be of great value in systematics since it does not show much variation.

11.1.5 Trichobothria*: Clavate, Thickened, Filiform*

Various terrestrial arthropods are equipped with mechanosensitive sensilla named trichobothria, characterized by a cup-shaped cuticular structure (bothrium), in which a seta is inserted (Reissland and Görner 1985). The trichobothria in theraphosid spiders vary from filiform, thickened, and clavate (club-shaped) (Guadanucci 2012). As in other mygalomorph spiders, these trichobothria are present on dorsal tarsi, retrolateral (basal to mid length) and dorsal (distal) metatarsus, and lateral (basal retro and prolateral) and dorsal (from basal extending to apical in two parallel rows) (Raven 1985). Simon (1892) was the first to note the presence of clavate trichobothria in mygalomorph spiders. All known theraphosids bear clavate trichobothria (Fig. 11.6b, e, f) on all tarsi (including the adult male cymbium), and they vary in its ultramorphology, as plumose and non-plumose (i.e., barbed and unbarbed) (Guadanucci 2012). Other mygalomorphs (*Conothele* spp. and *Ummidia* spp., family Halonoproctidae) and *Liphistius* (Mesothelae, Liphistiomorphae) include representatives with clavate trichobothria, but this shared presence with Theraphosidae is considered a convergence (Murphy and Platnick 1981; Raven 1985; Goloboff 1993). Some Barychlidae also bear clavate trichobothria on tarsi, differing in size (smaller than in Theraphosidae) and disposition (few trichobothria in a compact group, rather than in a row as in theraphosids). This shared presence of clavate trichobothria on tarsi is considered synapomorphic, due to the close phylogenetic relationship between Theraphosidae and Barychelidae (Raven 1985; Goloboff 1993; Bond et al. 2012; Guadanucci 2014). Guadanucci (2012) described the following disposition patterns for Neotropical Theraphosidae: two parallel rows in Theraphosinae, Schismatothelinae, *Dolichothele*, *Acanthopelma*, and *Holothele*; two diverging rows (U-shaped row) in Aviculariinae; short apical row in *Catumiri*. The sensitivity to air currents is well known for filiform trichobothria (Foelix 1996; Barth 2002), while the clavate trichobothria have been suggested to be adapted to the detection of vibrations of the soil (Den Otter 1973). Quirici and Costa (2005) demonstrated that seismic communication plays an important role during courtship of two tarantulas from Uruguay (*Eupalaestrus weijenberghi* and *Acanthoscurria cordubensis).* The clavate trichobothria on tarsi of *Sericopelma rubronitens* Ausserer, 1875 (Theraphosinae) showed response to vibrations on a table during electrophysiological experiments, and the removal of these trichobothria resulted in the absence of any stimulus (Den Otter 1973).

It is remarkable the presence of clavate trichobothria on basal lateral tibia of the great majority of Theraphosidae, which was originally reported by Guadanucci (2012). The aviculariine, the Neotropical arboreal tarantulas (except for *Ephebopus*, which according to West et al. 2008 has lost the arboreal behavior) present a distinctive disposition of tibial clavate trichobothria, which are in a compact group.

Considering their arboreal behavior and the presence of similar trichobothria in cerci of crickets, thought to be gravity receptors (Horn and Bishof 1983), it is possible that this configuration is an adaptation to sense in a 3D environment.

On both sides of all trichobothria row (on tarsi, metatarsi and tibiae), forming two parallel rows, tarantulas have the epitrichobothrial setae (Fig. 11.6b, e, f). They are similar to tactile setae, but shorter than the clavate trichobothria. In the aviculariines, as well as in other subfamilies (e.g., Selenocosmiinae, Ornithoctoninae), the epitrichobothrial setae form a dense patch intermixed with the filiform and clavate trichobothria (Guadanucci 2012).

11.1.6 Scales *(Fig. 11.6c, g–i)*

Townsend and Felgenhauer (1998) and Ramírez (2014) defined scales as setae inserted in small sockets and bent immediately after its insertion, so that the setae overlay close to the surface of the cuticle. According to Townsend and Felgenhauer (1999), scales comprise a specific type of setae because they lack innervation. There has been a great diversity of spider cuticular scales described in araneomorphs (Hill 1979; Townsend and Felgenhauer 1998, 1999, 2001; Ramírez 2014), but just few Theraphosidae taxa were included in these studies. In the case of tarantulas, these setae can be seen, under the microscope, as a whitish sub-layer below the numerous tactile setae. SEM micrographs revealed a unique ultramorphology with longitudinal furrows (named lamellar structure by Foelix et al. 2013) and spike-like ornaments (Fig. 11.6g–i), and they are present in all body parts, including appendages as chelicerae, palps, legs, and spinnerets. Many Neotropical tarantulas are brightly colored, ranging from violet to green, most of them have structural colors (iridescent) (Foelix et al. 2013). The intense blue coloration, depicted in Fig. 11.6i of the tarsus of a female *Dolichothele diamantinensis*, is due to light reflectance of these scales. Hsiung et al. (2015) found that the blue color is the most common in tarantulas and is the result of light reflectance form diverse structures in different spiders. According to their results, the setae showing the highest reflectance are produced by setae with longitudinal furrows (named therein as "bladelike" and "lobe-like" protruding hairs).

11.1.7 Spigots

Theraphosidae spiders have spigots on ventral face of both posterior median spinnerets and posterior lateral spinnerets (all three articles) spinnerets (Raven 1985; Palmer 1990; Murphy and Roberts 2015). In Mygalomorphae, as well as within Theraphosidae, the spigots show a uniform morphology, having a short base and a long articulated shaft ending in a terminal pore (Fig. 11.6k). Along the length of the shaft may be ornamented scale-like ornaments, which is also morphologically uniform across mygalomorphs. These spigots are usually characterized as aciniform gland spigots (AC) (Fig. 11.6k, first two small images), and other trap-door mygalomorph also have MAC (Modified Aciniform Spigot), which are similar to AC, but with the base slightly thicker (Murphy and Roberts 2015). We know of at least two *Typhochlaena* species (*T. seladonia* and *T. paschoali*, Fig. 11.6k, last image) with modified aciniform gland spigots (MAC). These MACs are similar to pumpkniform-shape spigots present in *Stenoterommata* (Pycnothelidae), as they both have an enlarged base with longitudinal wrinkle-like marks. These *Typhochlaena* species have a singular behavior of building their web-retreats on tree trunks enclosed by a thin trapdoor (Andre and Hüsser 2016). In the Neotropics, spiders belonging to different families build trapdoors on their retreats (Nemesiidae, Barychelidae, Cyrtaucheniidae), and some other familes are exclusive trapdoor spiders. However, this is very unique among theraphosids.

11.1.8 Cuspules

Cuspules are globular to conical cuticular outgrowths inserted in distinct sockets on labium and/or maxilla. Under the stereomicroscope they appear as small dark dots, but at higher magnifications (above 1000×—SEM) it is possible to make out their ultrastructural surface with several parallel ridges, similar to fingerprints (Fig. 11.6j). Anterior and posterior faces have distinct ornamentations: anterior face with transverse ridges on apical half, basal half with longitudinal ridges; posterior apical half with concentric ridges that fuse with longitudinal ridges on basal half. This general ultramorphological pattern has very little variation within Theraphosidae (Pérez-Miles and Montes de Oca 2005). The number and distribution of these cuspules, and also their disposition are useful diagnostic characters for some genera and suprageneric groups (e.g., *Dolichothele*, *Catumiri*, *Tmesiphantes*, *Hapalopus*, with few cuspules; the Schismatothelinae with extreme numbers and high density of labial cuspules). No clear function has been experimentally demonstrated for these cuspules, but mechanical, glandular, and sensorial usage have been discussed by Pérez-Miles and Montes de Oca (2005). These authors further suggested that due to their position, ornamentations, and unique presence in mygalomorphs (paraxial fangs), the cuspules could help in prey retention by the opposing force from the chelicerae when the spider holds the food item.

11.1.9 Epiandrous Spigots

Recently, Ferretti et al. (2017) published the first comparative study of the epiandrous apparatus of mygalomorph spiders, which comprises a group of additional silk glands associated with epiandrous spigots located at the anterior margin of the genital furrow of males. They are present in most spiders (Marples 1967) and are a possible synapomorphy for Araneae (Ferretti et al. 2017). Their function is still not clear, but it should act during sperm web building and sperm induction. In theraphosids, the number of spigots may be over 100 in large individuals, and are intermixed with distinct types of plumose setae (Ferretti et al. 2017). These plumose setae are well documented in various micrographs by Ferretti et al. (2017) and are, in fact, the ones referred here as scales and tactile setae. This high density of setae and their conspicuous distribution in a distinct patch (half-moon shaped zone) help distinguishing the sex of live spiders, as it appears as a clear small mark on the epigastric furrow of males (Ferretti et al. 2017). In mygalomorphs these spigots are elongated setae, widened at the base and inserted in sockets. Different from the spigots on spinnerets (Fig. 11.6k), the epiandrous spigots lack a globular base.

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