Chapter 12

Adhesive Features of the Theraphosid Tarantulas

Fernando Pérez-Miles, Carlos Perafán, and David Ortiz-Villatoro

Abstract Tarantulas are large spiders with adhesive setae on their legs, which enable them to climb on smooth vertical surfaces. The mechanism proposed to explain adhesion in tarantulas is anisotropic friction, where friction is higher when the leg pushes compared to when it pulls. The static friction of live theraphosid spiders on different surfaces and at different inclines was measured and compared between burrowing and arboreal species to test the hypothesis of higher friction in arboreal tarantulas. We analyzed the complementary participation of claw tufts and scopulae of anterior and posterior legs when the tarantula climbs. We also considered the morphology of scopulae and claw tufts setae and compared with similar structures in other families. Adhesive setae, as well as some other setae types found on ventral tarsi are described and characterized. The adhesive face of setae varied in the orientation in different parts of the tarsi, and this variation is more conspicuous in the spiders that have only claw tufts or scopulae. The mechanics of climbing in association with the biological characteristics of the species are analyzed. We discuss the association of adhesive scopulae and claw tufts with burrowing/cursorial mygalomorphs as within Theraphosidae, as was suggested for free-hunter spiders. The morphology, functions, and evolution of scopula and claw tufts are discussed in this chapter.

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12.1 Introduction

Several groups of animals such as arachnids, insects, amphibians, reptiles and mammals, have independently evolved specialized organs on their feet for adhesion (Federle 2006). Adhesive organs are rapidly controllable, can be used repeatedly without any loss of performance, and function on smooth, rough, dirty, and flooded surfaces (Autumn et al. 2014). These organs evolved allowing access to vertical and even inverted surfaces, opening up new habitats (Labonte et al. 2016). The performance of these organs has inspired a considerable amount of work on technical adhesives as they still outperform most artificial adhesives with respect to rapid controllability (Jagota and Hui 2011; Dirks and Federle 2011a). Some researchers also suggest using arthropod-based adhesive mechanisms for more effective tape and binding tools (von Byern and Grunwald 2010; Gorb et al. 2007).

There are two main types of adhesion used by animals: wet adhesion and dry adhesion.

Wet adhesion comprises adhesion mediated by specialized secretions and it is used by insects, amphibians and mammals (Barnes and Jon 2011; Dirks and Federle 2011a; Labonte et al. 2016). Natural chemicals and micromechanical adhesives are often composed of high-molecular compounds containing proteins, polyphenols, lipids, resins, mixtures of long-chain hydrocarbons and mucopolysaccharides, or waxes (von Byern and Grunwald 2010). However, the deep mechanisms are not well understood (von Byern and Grunwald 2010). They are employed for adhesion across many functions such as defense, locomotion, and cocoon building (von Byern and Grunwald 2010).

Dry adhesion relies on van der Waals forces which are intermolecular forces that act between different molecules making them attract or repel. These forces are short-ranging and weak, but if numerous points of close contact are achieved, considerable adhesion forces can be generated (Kesel et al. 2004; IUPAC 2006). Dry adhesive organs have evolved independently at least three times in lizards (Irschick et al. 1996; Williams and Peterson 1982), at least three times in insects (Beutel and Gorb 2001), and occur in some phylogenetically distant groups of spiders and mites (Federle 2006; Wolff et al. 2013; Wolff and Gorb 2016).

Structural differences were found between organs used for wet adhesion in comparison with those used in dry adhesion. As insects employ adhesive substances, the setae in these organs may have relatively blunt tips. On the other hand, lizards and spiders (using only dry adhesion) require setae with extremely fine-spatulated endings (Federle 2006; Wolff and Gorb 2016).

Despite the wide diversity of animals using adhesion (wet or dry), adhesive pads come in only two basic designs: smooth adhesion pads and dense setae adhesion pads (Federle 2006).

12.1.1 Smooth Adhesion Pads

These smooth pads use specialized adhesive substances and have evolved independently in many animal groups such as insects, amphibians, and mammals (Barnes and Jon 2011; Dirks and Federle 2011a; Labonte et al. 2016). Adhesion here is mediated by thin fluid films secreted into the contact zone. As the amount of fluid affects adhesive forces, a control of secretion appears probable (Dirks and Federle 2011b). Some functional principles of smooth pads (adaptability, viscoelasticity, pressure sensitivity) are similar to those known from industrial pressure-sensitive adhesion (Gorb et al. 2007).

Smooth adhesive pads have an internal fibrous structure, are soft and fluid-filled; this way the pad molds to the surface increasing the contact area on rough surfaces (Dirks and Federle 2011a). Adhesive fluid in smooth adhesive systems mainly serves to maximize contact on rough substrates (Bullock et al. 2008).

12.1.2 Setae Adhesion Pads

These pads are composed of specialized setae densely arranged; these setae are covered with specialized setulae or microtrichia. Dense setae adhesion pads are sometimes called “hairy” pads and may use either specialized adhesive secretions or van der Waals forces in order to adhere to a surface (Federle 2006).

In insects, the adhesion of hairy pads is mediated by a liquid secretion, which is released from gland pores at the base of the setae or, in some cases, from an opening under the end-plate at the tip of the hollow adhesive hair (Gorb 1998).

Hairy pads represent an optimized design for surface attachment with increased adhesion, controllable detachment, and can also help to achieve self-cleaning properties (Federle 2006). This could explain why such structures are found among numerous and diverse groups of animals.

12.2 Animal Groups with Adhesive Pads

Amblypygids This group combines structural and functional principles of both smooth and hairy adhesive pads (Beutel and Gorb 2006). Wolff et al. (2015) found a fibrous inner architecture resembling hexagonal structures. These hexagons are rather roof-like with a spatula-like keel. Such thin, spatulate structures are a universal feature of hairy adhesive pads (Wolff et al. 2015). Another interesting feature is the appearance of a viscous fluid (probably lipidic) secretion (Wolff et al. 2015).

Insects Among insects multiple acquisitions of both, dense setae pads and smooth pads can be found (Beutel and Gorb 2006; Gorb 2001; von Byern and Grunwald

2010; Wolff and Gorb 2016). In insects smooth pads or dense setae pads, the adhesion is mediated by a liquid secretion, which is released from gland pores at the base of the setae or, in some cases, from an opening under the end-plate at the tip of the hollow adhesive hair (Gorb 1998).

Amphibia Adhesive pads in frogs are smooth, and like in insects the pads also secrete a fluid. Although the adhesive pads in tree-frogs are generally very similar, it is clear that they have evolved several times independently (Hanna and Barnes 1991). Tree frog toe-pads are made of columnar epithelial cells that are separated from each other at the apices (Barnes and Jon 2011). Pores for mucous glands open into the channels that are between the cells which create a toe pad epithelium that has an array of flat topped cells with mucous filled grooves between them (Barnes and Jon 2011). The purpose of having cells separated at the tip is to allow the toe to conform to the structure it will adhere to (Barnes and Jon 2011). The hexagonal design around the outside of the cells (similar to the crickets) is likely to allow for the mucous to spread evenly over the cell (Barnes and Jon 2011; Hanna and Barnes 1991).

Reptilia Dense setae pads systems of lizards, mainly *Anolis* and Gekkonidae do not produce fluids. Anolids and geckos are very similar and in each case depend upon a profusion of hair-like extensions that can tightly bond onto almost any surface by van der Waals forces (Bullock et al. 2008; Gorb et al. 2007). Geckos have an edge in terms of grip and agility, as they have the ability to fold and unfold their foot-pads allowing a shift from grip to release.

Mammalia Smooth adhesive pads are found in arboreal possums, which are marsupials that glide between trees (Barnes and Jon 2011). The possum is also capable of using smooth adhesive pads to climb vertically, making use of large toe pads (Barnes and Jon 2011). The pads consist of an epidermal layer of stratified squamous epithelium with the outer most layer's cells being flattened (Barnes and Jon 2011). The pad has alternating ridges and grooves with sweat glands emptying into the grooves providing fluid for wet adhesion (Barnes and Jon 2011). Bats have also evolved adhesive pads as an independent acquisition. Some bats make use of an adhesive appendage, which uses wet adhesion (Riskin and Racey 2010).

Araneae Multiple lineages of spiders have independently evolved dense setae adhesive pads (Wolff et al. 2013) that enable them to climb on vertical surfaces (Fig. 12.1). In Araneae adhesive setae are arranged covering ventral surface of tarsi and distal metatarsi (scopulae) and/or in the tip of the tarsi under the claws (claw tufts) (Figs. 12.2 and 12.3). Their pads are much more similar to many lizards and are not like the dense setae pads in insects (Bullock et al. 2008).

On rough surfaces spiders may use their claws as attachment devices; on a smooth surface adhesion is achieved by the adhesive setae on the distal leg segments (Kesel et al. 2004). This is possible due to the miniaturization and multiplication of contact elements (setules) which rely in van der Waal forces (Kesel et al. 2004). Studies on *Evarcha arcuata* (Araneae, Salticidae) have calculated that a single setule can produce an adhesive force of 41 nN perpendicular to a surface, and this

Fig. 12.1 *Psalmopoeus ecclesiasticus* female resting head down on a tree in its natural habitat, Colombian foggy forest

Fig. 12.2 Adhesive pads on the ventral surface of spiders legs, leg IV of *Grammostola anthracina*. *Sc* scopula, *CT* claw tufts (lateral view)

species possesses a safety factor of 173 (meaning the force can support 173 times the weight of the spider) (Kesel et al. 2004). This has been highly overestimated by the authors, as they assume that all visible setules are in contact with the substrate surface (Wolff and Gorb 2013, 2016).

Specialization in Mygalomorphs Morphology and arrangement of scopulae has been widely used in the taxonomy of Mygalomorphae to diagnose families, subfamilies, and even genera (Simon 1892; Pérez-Miles 1994; Guadanucci 2005). Pérez-Miles et al. (2017) described five morphological types of setae forming scopulae and claw tufts in Mygalomorphae. Adhesive setae are present in claw tufts, lateral bands of scopulae in species with divided scopula, and throughout the ventral face of tarsi in species with entire scopula, mostly in burrower/cursorial families (Pérez-Miles et al. 2017).

Fig. 12.3 Adhesive pads of tarsus I of *Grammostola anthracina*. *Sc* scopula, *CT* claw tufts (ventral view)

Adhesive setae are present in the following Mygalomorph families: Barychelidae, Cyrtauchenidae, Dipluridae, Euctenizidae, Idiopidae, Microstigmatidae, Nemesidae, Paratropididae, Theraphosidae (Pérez-Miles et al. 2017). At least three types of adhesive setae have been described by Pérez-Miles et al. (2017), for Mygalomorphs:

- Lamellate setae: subcylindrical setae with the distal third widened and apically curved. Apical third is densely covered by spatulate microtrichia mainly on adhesive face. This type of setae appears on the Barychelidae, Theraphosidae, and Paratropididae families.
- Lamellate crested setae: similar to the lamellate type but differs by an apical longer conspicuous microtrichia. Only found on some genera of Theraphosidae.
- Lance-shaped setae: These setae are subcylindrical with the distal third curved and not so widened as in the lamellate type, the apex is pointed. The distal half is densely covered by microtrichia on adhesive face. Present in Nemesidae, Idiopidae, Microstigmatidae, Cyrtauchenidae, and Dipluridae.

12.3 Adhesion Structures in Tarantulas

The spider leg is subdivided in sclerotized podomeres (=articles), which are articulated to each other via movable joints. These joints are operated by muscles inserting on the rim of the distal podomere, immediately after the joint (eudesmatic joints) (Shultz 1989; Ferreti et al. 2017). However, in spiders as well as in other arachnids, there is an additional articulation without muscle insertions (adesmatic joints), dividing the arachnid tip of the leg into two pseudopodomeres, the metatarsus and tarsus (= basitarsus and telotarsus, respectively) (Labarque et al. 2017). The adhesion capacity in tarantulas allows the spiders to climb on vertical surfaces (Fig. 12.1) or even inverted surfaces. This high adhesion is due to the presence of adhesive pads on the ventral surface along the tarsus and metatarsus (scopulae) and under the claws (claw tufts) (Figs. 12.2 and 12.3). The adhesive setae under the claws are organized in two plates; each claw tuft is inserted on an articulate claw tuft plate separated from the tarsus by a movable suture or membrane, thus allowing the claw tuft to move according to changes in haemolymph pressure (Wolff et al. 2013).

The adhesive pads of the scopula and claw tufts consist of a dense array of numerous flexible adhesive setae (Fig. 12.4), composed of thousands of hair-like extensions of the cuticle with spatula-like tips, called setules (Kesel et al. 2003) or microtrichia (Richards and Richards 1979).

The adhesive setae are lamelliform, subcylindrical shape with the distal third widened and apically curved. The basal third of the setae are glabrous, while the median third has sparse microtrichia and apical third is densely covered by spatulate microtrichia on one side (adhesive face) (Fig. 12.4) (Rovner 1978; Wolff et al. 2013; Lapinski et al. 2015; Pérez-Miles et al. 2017). This means these setae exhibit a bi-hierarchical spatula structure, conferring a high capacity of adhesion. Spatula-like microstructures recruit adhesive forces by generating a close contact with the substrate due to elastic deformation (Wolff and Gorb 2016). The curved apical region facilitates movements for the contact of microtrichia and due to only one side being covered with the spatulate microtrichia, friction is highly anisotropic (Niederegger and Gorb 2006; Wolff and Gorb 2013, 2016). These lamelliform setae have a similar morphology to those found in some burrower and weaver mygalomorphs and some cursorial araneomorphs (Wolff et al. 2013; Lapinski et al. 2015; Pérez-Miles et al. 2017). Likewise, among arachnids, spatulate setae occur in the distal tarsomeres of some harvestmen of the sub-order Laniatores and in hooded tickspiders (Ricinulei) (Wolff and Gorb 2016).

The microtrichia of the adhesive setae are lateral extensions of the setae; they have a subcylindrical shape with the basis slightly widened and the apex widened and laterally flattened (Pérez-Miles et al. 2017). The shape of the microtrichia apex varies taxonomically; it can be sub-circular, sub-triangular, or sub-rhomboid (Pérez-Miles et al. 2017). Contrary, the nonadhesive distal face in the adhesive setae has longer and strongly curved microtrichia, not distally widened (not spatulated) and arranged in approximately longitudinal bands (Fig. 12.5) (Pérez-Miles et al. 2017).

The orientation of the adhesive face varies in different areas of the scopula and claw tufts, favoring the adhesion in distinct directions. The adhesive face is oriented on the ventral side of the claw tuft setae (the side normally directed toward the body) and on the dorsal side of the scopula setae (the side directed distally). Additionally, on the tip of the legs (scopula apex or claw tufts base) occurs a slight rotation of the setae with the adhesive face oriented to the axis of the leg (Fig. 12.6) (Pérez-Miles et al. 2017). This anisotropic difference in the orientation of the adhesive setae plays an important role for friction control, a central feature for hunting

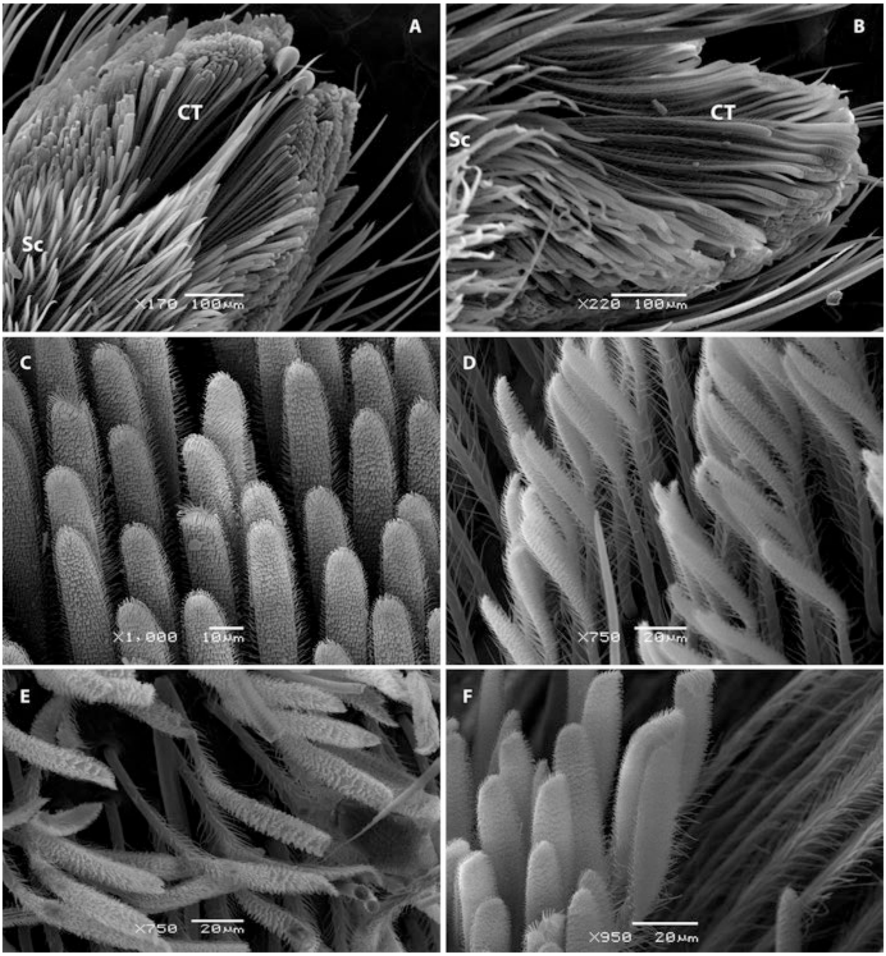

Fig. 12.4 Adhesive lamellate setae of adhesive pads on Theraphosidae. (**a**, **b**) detail of scopula (Sc) and claw tuft (CT) (**a**) *Hapalopus formosus* (**b**) *Holothele longipes*. (**c**–**f**) Close up of adhesive face on the lamellate setae (**c**) *Eupalaestrus weijenberghi* (**d**) *H. formosus* (**e**) *Plesiopelma longisternale* (**f**) *Aphonopelma seemanni* (After Pérez-Miles et al. 2017)

spiders (Wolff and Gorb 2013; Pérez-Miles et al. 2017). This particularity allows the theraphosids to climb, rest head down, and manipulate agile prey.

The scopula is present on ventral surface of all the length tarsi and can be also present on part or whole metatarsi. The morphology and arrangement of the scopula has been widely used in taxonomy and phylogeny of Mygalomorphae, being especially important in Theraphosidae (Simon 1892; Raven 1985; Pérez-Miles 1994; Guadanucci 2005; Bond et al. 2012; Wolff et al. 2013). The condition of scopula and claw tuft on all legs is a distinctive characteristic of Theraphosidae, with few exceptions, and its characteristics has been considered a good taxonomic tool and

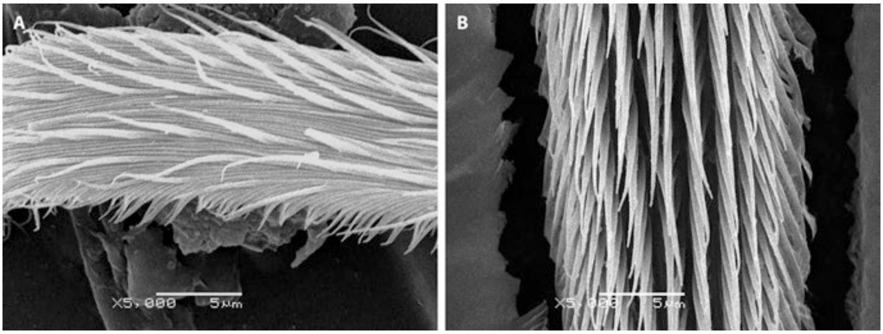

Fig. 12.5 Nonadhesive face of lamellate setae on Theraphosidae. (**a**) *Aphonopelma seemanni* (**b**) *Avicularia* sp. (After Pérez-Miles et al. 2017)

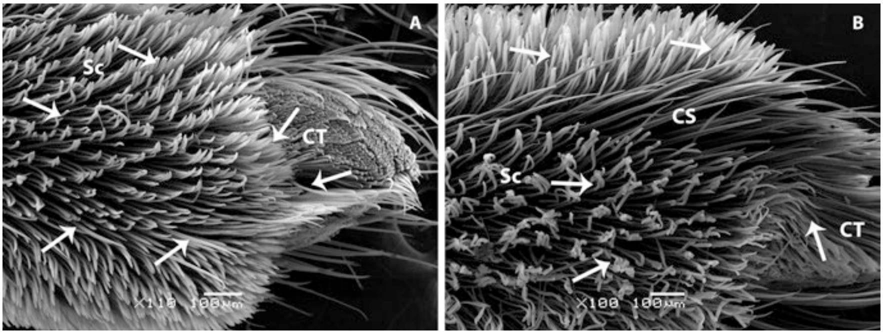

Fig. 12.6 Tips of tarsi showing the orientation of adhesive setae on leg I. (**a**) *Hapalopus formosus* (**b**) *Holothele longipes*. Diagram of the distal part of the tarsus illustrating different orientation of adhesive face of lamellate setae (modified of Wolff and Gorb 2013). Arrows indicate the orientation of adhesive face. *Sc* scopula, *CS* conical setae, *CT* claw tuft

has already been used to diagnose genera and species groups in Theraphosidae. *Agnostopelma* (Pérez-Miles and Weinmann 2010) has an unusual tarsal scopula condition. It has been the only Theraphosinae taxa described with absence of scopula in tarsus IV (Pérez-Miles and Weinmann 2010).

The density, extension, and arrangement of scopula generally vary gradually from front to back, being the front legs denser and more extensive. Additionally, the tarsal scopula can be entire or divided. Entire tarsal scopulae have homogeneous spatulate setae while divided scopulae have a longitudinal band of conical setae (Rovner 1978; Lapinski et al. 2015; Pérez-Miles et al. 2017). These conical setae are longer and thicker than spatulate types (Fig. 12.7). Microtrichia on conical setae are arranged in longitudinal rows, along the entire setae; they are dense, short, and filiform (not spatulated) (Fig. 12.7). Conical setae seem to be more related to traction or propulsion during locomotion (Rovner 1978; Pérez-Miles 1994; Wolff et al. 2013; Pérez-Miles et al. 2017).

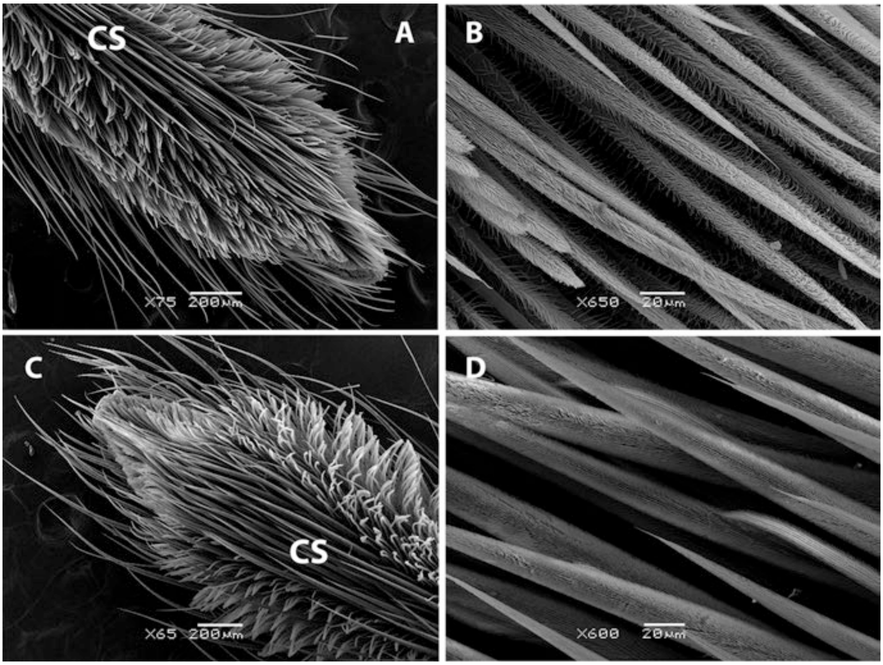

Fig. 12.7 Conical setae (CS). (**a**, **b**) *Hapalopus formosus* (**a**) tarsus IV (**b**) close up of conical setae (**c**, **d**) *Holothele longipes* (**c**) tarsus IV (**d**) close up of conical setae (After Pérez-Miles et al. 2017)

The band of conical setae increases in width from anterior to posterior legs. Consequently, the lateral bands of adhesive setae are reduced toward hind legs. Additionally, other proximal–distal gradations occur. In several theraphosids the median band of conical setae is progressively widening toward the distal part of the tarsi from forelegs to hind legs, while in some theraphosids (e.g., *Ami, Kankuamo*) the anterior–posterior gradation is inverse, on leg I the conical setae are distal in a rhomboid field, and toward the hind legs this field is progressively widening toward the proximal part of tarsi (Fig. 12.8) (Pérez-Miles et al. 2017).

The differentiation of the scopula pattern can be related with ontogenetic status or with spider size. The scopula is divided in most of juvenile theraphosids and becoming entire in adults of some groups (Pocock 1897; Gerschman de Pikelin and Schiapelli 1973; Pérez-Miles 1994), and the condition of scopula divided is related frequently with taxa of small size in Theraphosinae (Pérez-Miles 1994). On the contrary, Guadanucci (2005) found that in the Ischnocolinae, scopula condition appears to have no relation with spider size and should provide useful information for phylogenetic analysis.

Other chemosensory setae appear mixed sparsely with adhesive scopula setae, and present morphological variations between taxa (Fig. 12.9) (Pérez-Miles et al.

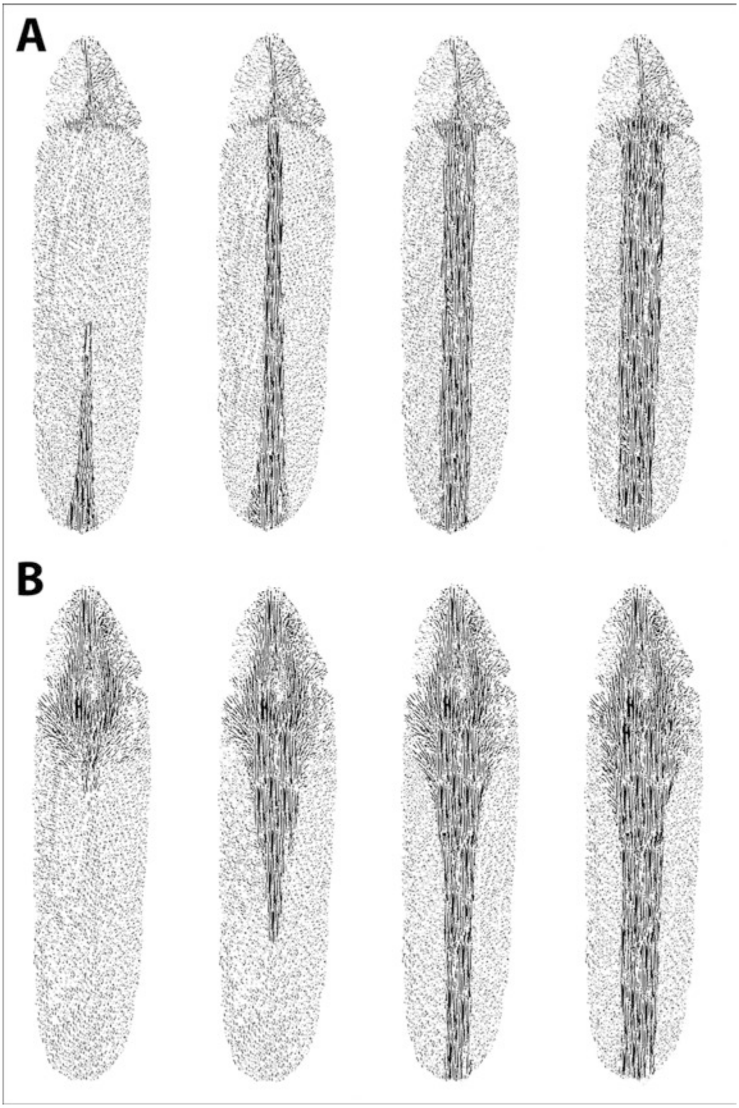

Fig. 12.8 Schematic representation of scopula division: proximal/distal and anterior (left)–posterior (right) gradation (**a**) the median band of conical setae is progressively widening toward the distal part of the tarsi from forelegs to hind legs (**b**) the conical setae are distal in a rhomboid field, and toward the hind legs this field is progressively widening toward the proximal part of tarsi (After Pérez-Miles et al. 2017)

2017). Chemoreception in spiders has been clearly established (Foelix 1970, 2011; Foelix and Chu-Wang 1975; Harris and Mill 1973). Under natural conditions chemoreception is used for testing the quality of food and in recognizing the opposite sex. Chemosensory setae are distinctly curved, blunt-tipped and possess a double

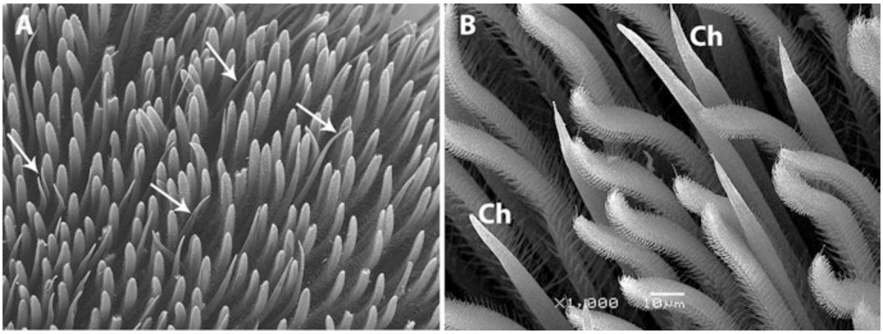

Fig. 12.9 Chemosensory setae (Ch). (**a**) Scopula setae of *Vitalius* sp. Scale bar = 100 µm (**b**) detail of chemosensory setae on scopula of *Plesiopelma longisternale*. Arrows show the chemosensory setae (After Pérez-Miles et al. 2017)

lumen. The smaller circular lumen is entered by dendrites which run up to the open tip (Foelix 1970, Foelix et al. 2013). The outer larger hair lumen does not contain any cellular elements but is filled with some fluid that was called "receptor lymph" (Foelix et al. 2012a).

12.3.1 Function of Scopula and Claw Tuft

In Theraphosidae the dense scopulae and claw tufts occur together (Raven 1985). Scopulae and claw tufts have two important functions in theraphosids: prey capture and locomotion (Homann 1957; Rovner 1978, 1980; Dunlop 1994; Foelix 2011; Pekar et al. 2011; Bond et al. 2012; Foelix et al. 2012b; Niederegger 2013; Wolff and Gorb 2012a, 2015; Wolff et al. 2013; Lapinski et al. 2015; Eggs et al. 2015; Pérez-Miles et al. 2017).

Scopulae and claw tufts consist of thousands of specialized setae that are apically broadened and cover the ventral surfaces of tarsi metatarsi and the tips of the legs under the paired claws (Pérez-Miles et al. 2015). These setae are oriented at a greater angle to the leg axis than covering setae (Pérez-Miles et al. 2015). Setae of scopulae and claw tufts are covered on their distal part by setules with spatula-shaped endings, which increase adhesion. They have a very similar structure but differ in length and density (Foelix et al. 2012b; Wolff et al. 2013; Pérez-Miles et al. 2015).

When the scopula is splayed and pressed against the surface, adhesion comes as the product of each individual setae interacting with the substrate (Peattie et al. 2011). This enables spiders with scopulae to climb even sheer, smooth surfaces such as glass.

12.3.2 Mechanism of Adhesion of the Scopula and Claw Tuft

The original mechanism proposed to explain adhesion in tarantulas is anisotropic friction (Fig. 12.10), where friction is higher when the leg pushes than when it pulls (Niederegger and Gorb 2006). However, Wohlfart et al. (2014) found complementary adhesion in *Cupiennius salei* on glass disabling anterior and posterior legs. In *Cupiennius salei* the direction of highest friction is opposite in claw tufts when compared to scopula (Wolff and Gorb 2013). The specifics of how different pads (scopula and claw tufts) are used by spiders remained unclear for long time (Pérez-Miles et al. 2015).

When a tarantula captures prey the anterior legs are pulled toward the body, so adhesion would be necessary. However, the predator also needs to be able to get rid of the prey very quickly if it turns out to be too large or too dangerous to be handled. In these cases, the ability to push is important (Pérez-Miles et al. 2015).

Pérez-Miles et al. (2015) studied static friction in live theraphosids, to test their climbing abilities on different surfaces and at different inclines and comparing burrower with arboreal species. They found a complementary participation of claw tufts and scopula of anterior and posterior legs when the tarantula climbs. They also tested differences in friction by mixing higher adhesion substrate with a lower one, and comparing friction (Pérez-Miles et al. 2015). This was to test whether an anisotropic friction was responsible of the adhesion as proposed by Niederegger and Gorb (2006) or the alternatives indicated by Wolff and Gorb (2013) and Wohlfart et al. (2014).

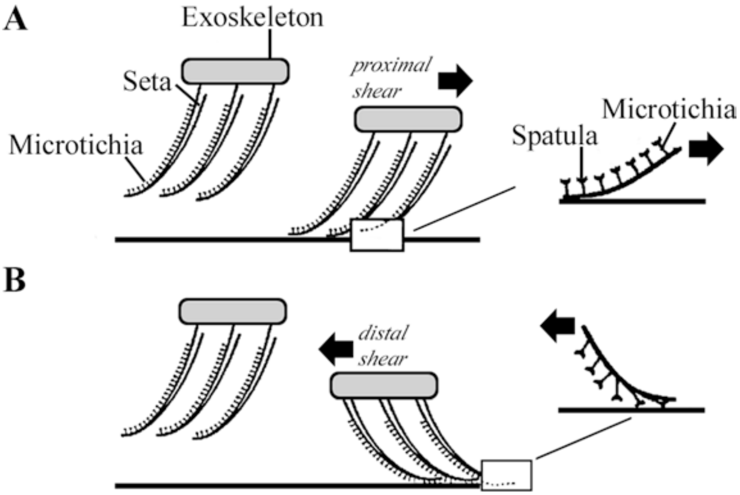

Fig. 12.10 Schematic representation of scopula adhesive setae on tarsus with the microtrichia. (**a**) when the leg pulls toward the body, the nonadhesive face of the setae contacts the substrate. (**b**) when the leg pushes distally, the scopula setae bends backward and the microtrichia enter in contact with the substrate (After Niederegger and Gorb 2006, with permission of the authors)

Pérez-Miles et al. (2015) observed no differences between the main friction of forelegs or hind legs. These results partially agree with the morpho-functional explanation given for both scopulae and claw tufts by Niederegger and Gorb (2006). These authors propose that the scopulae or claw tuft setae are curved in the proximal direction when pushed. Scopulae made contact with the substrate when the leg pushed, while claw tufts made contact when the leg pulled or during locomotion on a horizontal plane (Pérez-Miles et al. 2015).

Considering this observation together with the morphology of scopulae and claw tufts, they may function in a different way: scopulae produce adhesion when the leg pushes while claw tufts produce adhesion when the leg pulls. This observation is congruent with the opposite direction in friction forces of scopula and claw tufts found in *Cupiennius salei* and *Aphonopelma seemanni* (Niederegger and Gorb 2006; Wolff and Gorb 2013). These results could be explained by the opposite arrangement of adhesive setules, which are present on the dorsal (facing substrate) part of scopula setae, as reported by Foelix and Chu-Wang (1975) and Niederegger and Gorb (2006), and on the ventral (facing body) part (Hill 2010; Wolff and Gorb 2012a, b, 2013) of claw tuft setae.

Foelix et al. (2012b) suggested that adhesive setules are on opposite faces on the claw tufts and tarsal scopula setae, but with a different arrangement (ventral for scopulae and dorsal for claw tufts). Wolff and Gorb (2013) also found that the orientation of setae gradually changes in distal and lateral directions of claw tufts and scopula, which could influence the direction of friction force in relation to the part of the leg in contact with the substrate. This factor could optimize the complementary friction of claw tufts and scopulae including lateral components of leg movement (Pérez-Miles et al. 2015, 2017).

In adhesive scopula and claw tufts, the adhesive face is on the ventral side of claw tuft setae (the side normally directed toward the body) and on the dorsal side of the setae on the scopula (the side directed distally). On the tip of the legs (apical scopula or claw tufts) occurs a slight rotation of the setae with the adhesive face oriented to the axis of the leg (Pérez-Miles et al. 2017).

The orientation of the anisotropic adhesive setae differs between proximal tarsus in comparison with the tip of the tarsus (apical scopula or claw tuft), due to different anisotropy in the location of the microtrichia (Pérez-Miles et al. 2017). This is similar to what has been reported for large araneomorph hunting spiders (Wolff and Gorb 2013). This specific arrangement has been hypothesized to play an important role for friction control (Pérez-Miles et al. 2017). Considering the morphology, it is expected that distal setae produce adhesion when the leg pulls while proximal setae produce adhesion when the leg pushes. This hypothetical mechanism is congruent with the observations of Pérez-Miles et al. (2015), but differs from results by Niederegger and Gorb (2006) who found higher adhesion of the scopula when the leg pushes in the theraphosid *Aphonopelma seemanni*.

Pushing adhesion mechanisms are in conflict with the use of adhesive setae for prey capture, at least in the first steps of prey grabbing, because for prey attraction the adhesion must be produced when the forelegs pull the prey toward the chelicerae. However, once capture is advanced and the spider is above the prey and with legs at the sides and below, pushing adhesion may be effective.

Another interpretation is related to the full control of prey by the predator due to the mechanics of moveable setae (Rovner 1978; Eggs et al. 2015; Pérez-Miles et al. 2017). This is also possible in theraphosids since claw tufts setae are moveable (Dunlop 1994; Labarque et al. 2017). Additionally, Wolff and Gorb (2012a) stressed the importance for the predator to release the prey if it turns out to be hazardous, which should be facilitated by the control of adhesion.

Pulling adhesion is expected in claw tufts or distal tarsal scopula, so these features could be involved in both prey capture and locomotion. When the spider climbs vertically upward, adhesion may be produced by distal adhesive setae of forelegs pulling and proximal scopula of hind legs pushing (Pérez-Miles et al. 2015) with a similar dynamics as proposed by Wolff and Gorb (2013) and Wohlfart et al. (2014).

When locomotion is oriented downward, anterior scopulae push and posterior claw tufts (or distal scopulae) pull. Resting position in arboreal theraphosids is usually head down. This behavior could explain the anterior–posterior gradation of scopula indicated by Raven (1985) who observed an increasing development of such features in anterior direction. Obviously front legs are mainly involved in prey capture, as the first explanation for anterior–posterior gradations (Wolff and Gorb 2012a; Eggs et al. 2015). Perhaps mainly tarsal tips are involved in initial stages of prey capture while both tip and most part of tarsi are involved in climbing and late stages of prey capture.

12.3.3 Silk as an Adhesive Fluid?

As far as we know, all spiders secret silk through spigots located on specialized abdominal appendages, the spinnerets. Males also have spigots near the ventral genital opening to build the sperm web (Marples 1967; Ferretti et al. 2017). Singularly, spitting spiders of the genus *Scytodes* could eject a mixture of silk, glue, and venom through their fangs, from cheliceral-prosomatic glands (Monterroso 1928; Millot 1930).

Surprisingly, some years ago Gorb et al. (2006) reported that tarantulas can also secrete silk from their feet and argued that this would provide additional adhesion during climbing locomotion, and avert catastrophic falls, suggesting a third attachment mechanism. They reported that during climbing on vertical smooth surfaces if the tarantula started to slip, silk was secreted as a viscous fluid that solidifies, gluing the thread to the substrate (Gorb et al. 2006; Rind et al. 2011). According to Gorb et al. (2006), the tarsal silk resembles the silk used to cement draglines to substrates described by Vollrath and Knight (2001).

These events were later questioned by Pérez-Miles et al. (2009), who observed tarantulas climbing with free and experimentally sealed spinnerets. When the spinnerets were sealed, they did not observe silk threads on any surface, discarding leg secretion of silk.

Rind et al. (2011) fueled the controversy of tarsal silk by inducing a slight slipping of the tarsi and observing fine silk threads that emerge from ribbed “spigots” on the ventral tarsi. These structures were also reported by Gorb et al. (2006), but Pérez-Miles et al. (2009) found no structures interpretable as silk glands or silk conduits with transverse cuts.

Pérez-Miles and Ortiz-Villatoro (2012) revisited the tarsal silk controversy, testing several species of tarantulas (including an arboreal one). These authors used tarantulas with both free and sealed spinnerets on larger vertical surfaces and induced them to slip, shaking gently the surfaces. They confirmed the results by Pérez-Miles et al. (2009), denying the presence of a silk trail on the legs (when the spinnerets are sealed) and suggested that silk is a light sticky fiber that can easily adhere to a surface. Consequently, passive contamination with spinneret silk is the most likely explanation to the traces found in the studies of Gorb et al. (2006) and Rind et al. (2011).

Peattie et al. (2011) found fluid footprints when arachnids climbed on vertical surfaces, apparently originating from tarsal setae, but their silken nature was not confirmed. These fluids were examined by Pérez-Miles and Ortíz-Villatoro (2012) who determined that this substance clearly differs from silk because they are made up of groups of droplets.

The data presented by Peattie et al. (2011) for spiders show an extreme wetting of the setae, such that the spatulae are submerged in the fluid. Adhesion models show that in hairy pads, secretion enhances adhesion, only if it wets the space between the spatula and the substrate (Huber et al. 2005). If the fluid film is thicker than the spatula, slipping occurs (Bullock et al. 2008; Wolff and Gorb 2012b). In the cases of fluid appearance, the setal tips were completely wetted and the pad slid along the surface. Hence, adhesion was obviously reduced.

The presence of a thin fluid film between the scopula and a smooth substrate may play an important role in the adhesion mechanism (Homann 1957; Wolff and Gorb 2012b; Pérez-Miles and Ortiz-Villatoro 2012). Thus, the secretions observed by Peattie et al. (2011), Wolff and Gorb (2013) and Pérez-Miles and Ortíz-Villatoro (2012) unlikely support adhesion, but may have the function to clean the setae, control (reduce) adhesion, or may even result from unusual behavior of the animals, for example, due to the strong illumination used in such visualization methods (Wolff and Gorb 2013).

According to Foelix et al. (2012b), these footprints may originate from chemosensory setae and can be composed of receptor lymph. This substance can probably appear as fluid and sometimes as dryer filamentous lymph, depending on relative humidity, temperature, and the hydration state of the spider, which could explain the confusion with fibers. Likewise, Foelix et al. (2012b) found that the “silk spigots” reported by Gorb et al. (2006) and Rind et al. (2011) have all diagnostic features of chemosensitive hairs (contact chemoreceptor) in spiders, rather than a silk spigot.

Additionally, Niederegger and Gorb (2006) demonstrated that artificially dried spider scopulae may have diminished adhesion, although this may be due to desiccation of the cuticle (Wolff and Gorb 2013). Experiments with dead specimens of spider legs show that their hairy adhesive pads can generate high adhesion and friction on smooth surfaces even in a dry state (Kesel et al. 2003; Niederegger and Gorb 2006; Wolff and Gorb 2013).

Although the adhesion of tenent setae on the tarsi and claw tufts of legs and pedipalps almost certainly outweighs any potential contribution from the sparsely distributed trails secreted by the ribbed hairs (Foelix et al. 2012b).

12.3.4 Climbing

Pérez-Miles et al. (2015) observed that when climbing upward, palps, legs I and II touched the surfaces only with a part of the claw tufts, while leg pair IV touched the surface with the distal portion of tarsal scopulae and only in rare cases with claw tufts. It was also observed that leg IV was more extended than the resting legs.

When climbing, legs III usually touched the surface with a part of the claw tufts but in some cases, when this leg was extended backwards, it also touched the surface with the distal portion of the tarsal scopulae (Pérez-Miles et al. 2015). During increased inclination the contact area of anterior claw tuft and posterior scopula was increased, while the contact area of posterior claw tufts slightly decreased. Usually, just before a leg was elevated for a step, we observed movements in the tarsal claw tufts (Pérez-Miles et al. 2015).

12.4 Ecological and Evolutionary Aspects of the Adhesion Structures in Tarantulas

The spatulate setae as a mechanism in dry adhesion has evolved multiple times independently within arthropods and reptiles (e.g., in geckoes and anoles, mites of the order Trombidiformes, and hunting spiders) (Peattie and Full 2007; Wolff et al. 2013; Ramírez 2014). The widespread occurrence of powerful adhesive setae suggests their importance in locomotion, mainly to climb on inclined or vertical surfaces, and in prey capture.

A hypothesis has emphasized the locomotory function of the adhesive setae as an evolutionary driver of adhesive structures in spiders, due the impressive climbing ability of the spiders, although this predominantly includes only the distal end of the legs, principally the claw tufts (Foelix and Chu-Wang 1975; Roscoe and Walker 1991; Dunlop 1994; Kesel et al. 2003; Niederegger and Gorb 2006; Wolff and Gorb 2012a, c). An the alternative hypothesis has been proposed: prey capture could be the original evolutionary driving force in the evolution of attachment organs in spiders, and that their use in locomotion was a secondary benefit that led to the occupation of new habitats (Rovner 1978; Miller et al. 1988; Wolff et al. 2013). According to Wolff et al. (2013), this can be regarded as a key innovation that promoted the great radiations of the Dionycha in the Eocene and of the Theraphosidae in the Miocene (Penney and Selden 2011).

In spiders, the use of silk for capturing and immobilizing prey is widespread. However, some lineages never evolved a silk-dependent prey capture mode or have independently abandoned web building and explored alternative hunting strategies. Thus, free hunting lifestyles implicate alternative mechanisms for capturing, securing, and handling of prey. The adhesive pads located on spider ventral apical legs have been hypothesized as an evolutionary alternative to prey capture webs. Wolff et al. (2013) found a close association between the adhesive setae and the free hunter lifestyle in spiders. They suggested that scopulae evolved as a substitute for silk in prey control and that the claw tufts are, in most cases, a secondary development. This transition from webs to active hunting occurred independently in many spider taxa and resulted in multiple origins of remarkably similar sticky hairs (Wolff et al. 2013; Ramírez 2014).

The hypothesis that the claw tufts were derived as a distal specialization from scopula (Wolff et al. 2013) was also supported by Pérez-Miles et al. (2017), when describing the rotation of adhesive face in distal scopula in non-claw-tufted mygalomorph families (some nemesiids, idiopids, microstigmatids, cyrtaucheniids, euctenizids, and diplurids). In these scopulae the adhesive face of setae is oriented dorsally in the proximal tarsus (like a normal scopula) and ventrally in the apical tarsus (like a normal claw tuft).

Rovner (1978), Foelix et al. (1984), Pekar et al. (2011), Wolff et al. (2013), and Eggs et al. (2015) proposed the participation of scopulae in prey manipulation in Araneomorphae. The following observations support the hypothesis that scopulae in spiders are generally an adaptation for prey capture (Wolff et al. 2013): (1) Scopulae are often restricted to or more developed in the anterior legs; (2) Scopulate setae are mainly distributed in the pro- and retro-lateral parts of the tarsus, metatarsus and tibia, whereas at the ventral side they are lacking; (3) Most spiders walk on their pretarsal tips; and (4) The adhesive sides of the scopula setae are often facing away from the ground in resting animals and become erect by increased hemolymph pressure.

On the other hand, the evolution of claw tufts is associated with the formation of a highly sclerotized basal plate in the pretarsal region, thus being articulated with the tarsus; it permits spreading and mobility of the pads and may facilitate control of both attachment and detachment (Speck and Barth 1982; Dunlop 1994; Hill 2010; Labarque et al. 2017). It occurs in the derived lineages of the Dionycha (except gnaphosids, most thomisids, and some salticids), Dysderoidea, Theraphosidae, and Ctenidae (Wolff et al. 2013). Thus, although obviously claw tufts also are used for prey capturing, mating, and grooming, there are some arguments supporting the primary locomotory function of the claw tufts differing from the function of the scopulae (Wolff et al. 2013): (1) Claw tufts typically contact the substrate in walking and climbing spiders; (2) In contrast to the scopulae, claw tufts are always well developed in all the legs of those species which feature them; (3) Whereas scopulae are more developed in the anterior legs, claw tufts are often larger in the posterior legs presumably because these produce the highest forward thrust; and (4) Among free hunting spiders those having claw tufts make up a significantly higher proportion found in above-ground and highly structured habitats such as broad leaf litter, than found at ground level and on even substrates. The last argument interprets the claw tufts as an adaptation to enhance climbing ability.

The orientation of the anisotropic adhesive setae that differs between the proximal tarsus in comparison with the tip of the tarsus (apical scopula or claw tuft), and consequently the different orientation of the microtrichia (Wolff and Gorb 2013; Pérez-Miles et al. 2017) suggest that the explanation of adhesive mechanism and biological function of scopula and claw tuft could be more complex. Considering the morphology, it is expected that distal setae produce adhesion when the leg pulls while proximal setae produce adhesion when the leg pushes (Pérez-Miles et al. 2015, 2017). Theraphosids walk on horizontal surfaces using their tarsal tips, but when climbing on vertical surfaces a close contact exists between most part of tarsi which push on the surface (Pérez-Miles et al. 2015). It should be noted that arboreal species of Theraphosidae show more developed scopulae than terrestrial species.

In this sense, Pérez-Miles et al. (2017) questioned the function of scopulae in prey manipulation in Mygalomorphae and argued that this is only applicable to apical scopula or claw tufts, considering that the adhesive faces of most part of scopula setae are oriented dorsally (distally) facilitating pushing adhesion. Pushing adhesion may be effective once capture is advanced and the spider is above the prey and with legs at the sides and below (Pérez-Miles et al. 2017). Another interpretation is related with the full control of prey by the predator due to the mechanics of moveable setae, as happens in mygalomorphs since claw tufts setae are moveable (Dunlop 1994; Labarque et al. 2017). Rovner (1978) proposed that erectile scopular setae could change of orientation during attack which was confirmed in lycosid spiders by Eggs et al. (2015). This could be an alternative explanation for adhesion during prey capture.

Pulling adhesion is expected in claw tufts or in the distal part of tarsal scopula, so these features could be involved in both prey capture and adhesion for locomotion. When the spider climbs vertically upward, adhesion may be produced by apical adhesive setae of forelegs pulling and proximal scopula of hind legs pushing (Pérez-Miles et al. 2015). Inversely, when the locomotion is oriented downward, anterior scopulae push and posterior claw tufts (or distal scopulae) pull. Resting position in arboreal theraphosids is usually head down. This behavior could be explained by the anterior–posterior gradation of scopula indicated above. Although, obviously front legs are mainly involved in prey capture, and is the first explanation for anterior–posterior gradations.

Among the Mygalomorphae the adhesive setae have been also reported in Barychelidae, Cyrtaucheniidae, Idiopidae, Paratropididae, Nemesiidae (Wolff et al. 2013), and in females of the idiopids *Misgolas*, *Euoplos* and *Aganippe*, diplurids *Diplura*, *Trechona* and *Linothele*, and some euctenizids (Pérez-Miles et al. 2017). Some of them use a sheet-web for prey capture or inhabit burrows with wafer-lid trapdoors; therefore, these groups may be exceptions to the hypothesis that suggest that scopulae evolved as a substitute for silk (Wolff et al. 2013). Mygalomorph foraging webs employ silk either in a sheet web or at a burrow entrance to detect, localize, and manipulate prey (Coddington et al. 2019). However, in mygalomorphs silk is not adhesive enough for prey capture as in most araneomorphs, so the participation of adhesive setae would be necessary.

According to Pérez-Miles et al. (2017), adhesive scopulae were acquired in the Crassitarsae, in the Euctenizidae and in some idiopids (*Misgolas*, *Euoplos*, and *Aganippe*) (based on the phylogenetic hypothesis of Bond et al. (2012)), and the presence of adhesive scopula has a relationship with cursorial/burrower taxa, despite of their exceptional presence in some trapdoors and Diplurinae.

Pérez-Miles et al. (2017) hypothesize two scenarios for the origin of adhesive scopulae in Mygalomorphae: (1) two independent acquisitions of adhesive scopula in Crassitarsae and Euctenizoidina with few generic reversions or (2) its acquisition in the Bipectina with a reversion in the Ctenizoidina. According to first hypothesis, the adhesive scopula of Crassitarsae and Euctenizoidina is not homologous (Bond and Opell 2002; Pérez-Miles et al. 2017), and its association with the burrower or cursorial lifestyle indicates that it probably evolved together with ecological characteristics.

The claw tufts are much more restricted in Mygalomorphae than in Araneomorphae. They are present only in Theraphosidae and Barychaelidae with a parallelism in *Melloina* (Paratropididae), but in this last case without scopula (Raven 1985; Pérez-Miles et al. 2017). According to Pérez-Miles et al. (2017) and Wolff et al. (2013), claw tufts seem to be acquired twice in Mygalomorphae, just in cursorial/burrower spiders, and they were derived from scopula.

References

Autumn K, Niewiarowski PH, Puthoff JB (2014) Gecko adhesion as a model system for integrative biology, interdisciplinary science, and bioinspired engineering. Ann Rev Ecol Evol Syst 45:445–470

Barnes W, Jon P (2011) Functional morphology and design constraints of smooth adhesive pads. MRS Bull 32:479–485

Beutel RG, Gorb SN (2001) Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. J Zool Syst Evol Res 39:177–207

Beutel RG, Gorb SN (2006) A revised interpretation of the evolution of attachment structures in Hexapoda with special emphasis on Mantophasmatodea. Arthropod Syst Phylo 64:3–25

Bond JE, Opell BD (2002) Phylogeny and taxonomy of the genera of south-western North American Euctenizinae trapdoor spiders and their relatives (Araneae: Mygalomorphae, Cyrtaucheniidae). Zool J Linn Soc Lond 136:487–534

Bond JE, Hendrixson BE, Hamilton CA, Hedin M (2012) A reconsideration of the classification of the spider infraorder Mygalomorphae (Arachnida: Araneae) based on three nuclear genes and morphology. PLoS One 7(6):e38753. https://doi.org/10.1371/journal.pone.0038753

Bullock JM, Drechsler P, Federle W (2008) Comparison of smooth and hairy attachment pads in insects: friction, adhesion and mechanisms for direction-dependence. J Exp Biol 211:3333–3343

Coddington JA, Agnarsson I, Hamilton CA, Bond JE (2019) Spiders did not repeatedly gain, but repeatedly lost, foraging webs. PeerJ 7:e6703. https://doi.org/10.7717/peerj.6703

Dirks JH, Federle W (2011a) Fluid-based adhesion in insects—principles and challenges. Soft Matter 7:11047

Dirks JH, Federle W (2011b) Mechanisms of fluid production in smooth adhesive pads of insects. J R Soc Interface 8:952–960

Dunlop JA (1994) Movements of scopulate claw tufts at the tarsus tip of a tarantula spider. Neth J Zool 45:513–520

Eggs B, Wolff JW, Khun-Nentwig L, Gorb SN, Nentwig W (2015) Hunting without a web: how lycosoid spiders subdue their prey. Ethology 121:1166–1177

Federle W (2006) Why are so many adhesive pads hairy? J Exp Biol 209:2611–2621

Ferretti N, Pompozzi G, Copperi S, Wehitt A, Galíndez E, González A, Pérez-Miles F (2017) A comparative morphological study of the epiandrous apparatus inmygalomorph spiders (Araneae, Mygalomorphae). Micron 93:9–19

Foelix RF (1970) Structure and function of tarsal sensilla in the spider *Araneus diadematus*. J Exp Zool 175:99–124

Foelix RF (2011) Biology of spiders, 3rd edn. Oxford University Press, New York, pp 188–217

Foelix RF, Chu-Wang IW (1975) The structure of scopula hairs in spiders. In: Proc 6th Int Congr Arachnol, Amsterdam, pp 56–58

Foelix R, Erb B, Rast B (2013) Alleged silk spigots on tarantula feet: Electron microscopy reveals sensory innervation, no silk. Arthropod Structure and Development 42:209–217

Foelix RF, Jackson RR, Henksmeyer A, Hallas S (1984) Tarsal hairs specialized for prey capture in the salticid Portia. Rev Arachnol 5:329–334

Foelix RF, Rast B, Erb B (2012a) Hafthaare bei Vogelspinnen: Vergleich einer bodenlebenden Brachypelma mit einer baumlebenden *Poecilotheria*. Arachne 17:16–23

Foelix R, Rast B, Peattie AM (2012b) Silk secretion from tarantula feet revisited: alleged spigots are probably chemoreceptors. J Exp Biol 215:1084–1089

Gerschman de Pikelin BS, Schiapelli RD (1973) La subfamilia "Ischnocolinae" (Araneae: Theraphosidae). Rev Mus Arg C Nat "Bernardino Rivadavia", Entomologia 4:43–77

Gorb SN (1998) The design of the fly adhesive pad: distal tenent setae are adapted to the delivery of an adhesive secretion. Proc R Soc Lond B 265:747–752

Gorb SN (2001) Attachment devices of insect cuticle. Kluwer Academic, Dordrecht

Gorb SN, Niederegger S, Hayashi CY, Summers AP, Vötsch W, Walther P (2006) Silk-like secretion from tarantula feet. Nature 443:407

Gorb SN, Sinha M, Peressadko A, Daltorio KA, Quinn RD (2007) Insects did it first: a micropatterned adhesive tape for robotic applications. Bioinspir Biomim 2:117–125

Guadanucci JPL (2005) Tarsal scopula significance in Ischnocolinae phylogenetics (Araneae, Mygalomorphae, Theraphosidae). J Arachnol 33:456–467

Hanna G, Barnes WJP (1991) Adhesion and detachment of the toe pads of tree frogs. J Exp Biol 155:103–125

Harris DJ, Mill PJ (1973) The ultrastructure of chemoreceptor sensilla in *Ciniflo* (Araneida, Arachnida). Tissue Cell 5:679–689

Hill DE (2010) Jumping spider feet (Araneae, Salticidae). Peckhamia 85:1–41

Homann H (1957) Haften Spinnen an einer Wasserhaut? Naturwissenschaften 44:318–319

Huber G, Mantz H, Spolenak R, Mecke K, Jacobs K, Gorb SN, Arzt E (2005) Evidence for capillarity contributions to gecko adhesion from single spatula nanomechanical measurements. Proc Natl Acad Sci USA 102:16293–16296

Irschick DJ, Austin CC, Petren K, Fisher RN, Losos JB, Ellers O (1996) A comparative analysis of clinging ability among pad-bearing lizards. Biol J Linn Soc 59:21–35

IUPAC (2006) Compendium of chemical terminology, 2nd ed. (the "Gold Book"). Compiled by A. D. McNaught and A. Wilkinson. Blackwell Scientific Publications, Oxford (1997). XML on-line corrected version: http://goldbook.iupac.org. Created by M. Nic, J. Jirat, B. Kosata; updates compiled by A. Jenkins. ISBN 0-9678550-9-8. https://doi.org/10.1351/goldbook

Jagota A, Hui CY (2011) Adhesion, friction, and compliance of bio-mimetic and bio-inspired structured interfaces. Mater Sci Eng Rep 72:253

Kesel AB, Martin A, Seidl T (2003) Adhesion measurements on the attachment devices of the jumping spider *Evarcha arcuata*. J Exp Biol 206:2733–2738

Kesel AB, Martin A, Seidl T (2004) Getting a grip on spider attachment: an AFM approach to microstructure adhesion in arthropods. Smart Mater Struct 13:512–518

Labarque FM, Wolff JO, Michalik P, Griswold CE, Ramírez MJ (2017) The evolution and function of spider feet (Araneae: Arachnida): multiple acquisitions of distal articulations. Zool J Linnean Soc 20:1–34

Labonte D, Clemente CJ, Dittrich A, Kuo CY, Crosby AJ, Irschick DJ, Federle W (2016) Extreme positive allometry of animal adhesive pads and the size limits of adhesion-based climbing. Proc Natl Acad Sci 113:1297–1302

Lapinski W, Walther P, Tschapka M (2015) Morphology reflects microhabitat preferences in an assemblage of neotropical wandering spiders. Zoomorphology 134:219–236

Marples BJ (1967) The spinnerets and epiandrous glands of spiders. Zool J Linn Soc 46:209–223

Miller GL, Miller PR, Brady AR (1988) Adhesive hairs in lycosid spiders of various life styles, including the occurrence of claw tufts in *Lycosa hentzi* banks. Bull Br Arachnol Soc 7:213–216

Millot J (1930) Glandes venimeuses et glandes sèricigènes chez les Sicariides. Bull Soc Zool Fr 55:150–174

Monterroso B (1928) Observazioni preliminar sella del genere *Scytodes* (Walk) (Araneae Verae: Sicariidae). Rend Reale Accad Naz Lincei Ser 6(6):171–174

Niederegger S (2013) Functional aspects of spider scopulae. In: Nentwig W (ed) Spider ecophysiology. Springer, Berlin, pp 57–66

Niederegger S, Gorb SN (2006) Friction and adhesion in the tarsal and metatarsal scopulae of spiders. J Comp Physiol A 192:1223–1232

Peattie AM, Full JR (2007) Phylogenetic analysis of the scaling of wet and dry biological fibrillar adhesives. Proc Natl Acad Sci 104:18595–18600

Peattie AM, Dirks JH, Henriques S, Federle W (2011) Arachnids secrete a fluid over their adhesive pads. PLoS One 6(5):e20485. https://doi.org/10.1371/journal.pone.0020485

Pekar S, Sobotnık J, Lubin Y (2011) Armoured spiderman: morphological and behavioural adaptations of a specialised araneophagous predator (Araneae: Palpimanidae). Naturwissenschaften 98:593–603

Penney D, Selden PA (2011) Fossil spiders: the evolutionary history of a megadiverse order, Monograph series, volume 1. Siri Scientific Press, Manchester, p 128

Pérez-Miles F (1994) Tarsal scopula division in Theraphosinae (Araneae, Theraphosidae): its systematic significance. J Arachnol 22:46–53

Pérez-Miles F, Ortíz-Villatoro D (2012) Tarantulas do not shoot silk from their legs: evidence in four species of New World tarantulas. J Exp Biol 215:1749–1752

Pérez-Miles F, Weinmann D (2010) *Agnostopelma*: a new genus of tarantula without a scopula on leg IV (Araneae: Theraphosidae: Theraphosinae). J Arachnol 38:104–112

Pérez-Miles F, Panzera A, Ortíz-Villatoro D, Perdomo C (2009) Silk production from tarantula feet questioned. Nature 461:E9–E10

Pérez-Miles F, Perafán C, Santamaría L (2015) Tarantulas (Araneae: Theraphosidae) use different adhesive pads complementary during climbing on smooth surfaces: experimental approach in eight arboreal and burrower species. Biol Open 4:1643–1648

Pérez-Miles F, Guadanucci JPL, Jurgilas JP, Becco R, Perafán C (2017) Morphology and evolution of scopula, pseudoscopula and claw tufts in Mygalomorphae (Araneae). Zoomorphology 136:435–459

Pocock RI (1897) On the spiders of the suborder Mygalomorphae from the Ethiopian Region, contained in the collection of the British Museum. Proc Zool Soc London 1897:724–774

Ramírez MJ (2014) The morphology and phylogeny of dionychan spiders (Araneae, Areneomorphae). Bull Am Mus Nat Hist 390:1–374

Raven R (1985) The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bull Am Mus Nat Hist 182:1–180

Richards AG, Richards PA (1979) The cuticular protuberances of insects. Int J Insect Morphol Embryol 8:143–157

Rind FC, Birkett CL, Duncan BJ, Ranken AJ (2011) Tarantulas cling to smooth vertical surfaces by secreting silk from their feet. J Exp Biol 214:1874–1879

Riskin DK, Racey PA (2010) How do sucker-footed bats hold on, and why do they roost head-up? Biol J Linn Soc 99:233–240

Roscoe DT, Walker G (1991) The adhesion of spiders to smooth surfaces. Bull Br Arachnol Soc 8:224–226

Rovner JS (1978) Adhesive hairs in spiders: behavioral functions and hydraulically mediated movement. Symp Zool Soc Lond 42:99–108

Rovner JS (1980) Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). J Arachnol 8:201–215

Shultz JW (1989) Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. Zool J Linnean Soc 97:1–56

Simon E (1892) Histoire Naturelle des Araigneés, vol 1. Roret, Paris, p 256

Speck J, Barth FG (1982) Vibration sensitivity of pretarsal slit sensilla in the spider leg. J Comp Physiol A 148:187–194

Vollrath F, Knight DP (2001) Liquid crystalline spinning of spider silk. Nature 410:541–548

Von Byern J, Grunwald I (eds) (2010) Biological adhesive systems: from nature to technical and medical application. Springer, Wien

Williams EE, Peterson JA (1982) Convergent and alternative designs in the digital adhesive pads of Scincid lizards. Science 215:1509–1511

Wohlfart E, Wolff JO, Arzt E, Gorb SN (2014) The whole is more than the sum of all its parts: collective effect of spider attachment organs. J Exp Biol 217:222–224

Wolff J, Seiter M, Gorb SN (2015) Functional anatomy of the pretarsus in whip spiders (Arachnida, Amblypygi). Arthropod Structure and Development 44:524–540

Wolff JO, Gorb SN (2012a) Comparative morphology of pretarsal scopulae in eleven spider families. Arthropod Struct Dev 41:419–433

Wolff JO, Gorb SN (2012b) The influence of humidity on the attachment ability of the spider *Philodromus dispar* (Araneae, Philodromidae). Proc R Soc B Biol Sci 279:139–143

Wolff JO, Gorb SN (2012c) Surface roughness effects on attachment ability of the spider *Philodromus dispar* (Araneae, Philodromidae). J Exp Biol 215:179–184

Wolff JO, Gorb SN (2013) Radial arrangement of Janus-like setae permits friction control in spiders. Sci Rep 3:1101

Wolff JO, Gorb SN (2015) Adhesive foot pads: an adaptation to climbing? An ecological surveyin hunting spiders. Zoology 118:1–7

Wolff JO, Gorb SN (2016) Attachment structures and adhesive secretions in arachnids. Springer International Publishing, Cham, p 184. https://doi.org/10.1007/978-3-319-45713-0

Wolff JO, Nentwig W, Gorb SN (2013) The great silk alternative: multiple co-evolution of web loss and sticky hairs in spiders. PLoS One 8(5):e62682. https://doi.org/10.1371/journal.pone.0062682