Jumping spider feet (Araneae, Salticidae)

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1. Preface

My study of the feet of jumping spiders began more than 30 years ago, leading to the publication of one paper on the *pretarsus* of salticids (Hill 1977a), and a second short paper that described the use of foot pads by *Phidippus regius* (Hill 1978). Opinions with respect to the adhesive mechanism of foot pads varied at that time, but the hypothesis of capillary attraction mediated by a thin surface film of H_2O was widely communicated (e.g., Foelix 1996). More recently, two papers that suggested a plausible role for *van der Waals* forces with respect to the adhesive tenent setae (*tenae*) of salticids were published (Kesel, Martin, and Seidl 2003, 2004). In addition, many informative studies of the mechanisms of adhesion associated with the footpads of the Tokay Gecko (Gekkonidae: *Gekko gecko*) have appeared (e.g., Autumn, Sitti, et al 2002), and a very creative discussion of this subject is presently underway. Much of this work relates directly to materials science, and the pursuit of even better adhesives that work at the *nanoscale* (within 2 nm). I suspect that some people may also be tempted to patent some of these devices, *as if they were human inventions*!

The present report is intended to replace my earlier, dated work on the salticid pretarsus. Many new illustrations have been produced for this purpose. Rather than focusing exclusively on the *tenae* (and their adhesive setules, or *tenules*), this report will present an updated view of the function of salticid feet (tarsus and pretarsus) that also includes the role of claws and other specialized setae, as well as the structure of the foot pads that carry these specialized setae. Version 3 includes new video studies (Figure 47) related to pretarsal movement.

2. Summary

Each *foot* of a salticid spider is comprised of the tarsus, proximally articulated to a varying degree of flexibility with a metatarsus, and the pretarsus, articulated with the distal tarsus, and consisting of a dorsal pair of claws articulated to a central claw lever, and a paired (anterior and posterior) set of foot pads. Claws and footpads can be extended and retracted or flexed by means of hydraulic inflation/deflation of the tarso-pretarsal joint, and/or by movement of a dorsal pretarsal levator and an opposing ventral pretarsal depressor. Claws and footpads can be applied to a surface immediately after leg movement, and retracted from that surface immediately before leg movement. Claws and footpads are also capable of independent movement with respect to each other.

Foot pads, anterior scopulae, and posterior scopulae, are comprised of specialized adhesive setae, the *tenae* (or tenant setae). On the footpads, these setae emerge from a more-or-less regular, space-filling array of sockets on the surface of a moveable tenet plate. From top to bottom, the tenae are progressively shorter, so that the entire array of tenae associated with a footpad terminates in a planar tenent surface, comprised of the flattened ends of the array of tenae. Tenae are also braced and/or interlocked by means of specialized setules, the hook-like *hamules* and the *barbules*, to support cohesive, directional application of each foot pad to a surface. The planar orientation of each foot pad on a foot is different. The flattened ends of the tenae bear a regular hexagonal array of bifurcating *tenules*, each bearing a small triangular membrane that can be positioned close to a surface. Adhesion of these tenules may result primarily from *van der Waals forces* acting at a distance of less than 2 nm from the substratum, a form of *dry adhesion*.

Other important setae associated with the feet of at least some salticids include the highly specialized *pilosae* that can appear as a ventral scopular tract on the tarsi of salticids. The function of pilosae is not known, but they may play a role in the ability of these spiders to wind up a silk dragline as they climb it. The *spondylae* are presumed chemoreceptors comprised of vertebra-like spondyls. A preliminary working catalog of setae and setules is also presented here.

Photographic study of the movement of salticids supports the general view that the claws play an important role in the handling of silk lines under tension. This analysis also confirms the ability of these spiders to flexibly position their foot pads, and to pivot and apply force through these foot pads at the same time that the legs and body of an upside-down spider, under tension, are suspended by the tenules of these foot pads (or at the same time that the legs and body of a right side-up spider, under compression, are raised off of the surface by the tenules).

3. Materials and methods

For scanning electron microscopy (SEM), near-adult *Phidippus audax* were collected in the vicinity of Iowa City, Iowa. Both complete animals and dissected exuviae were used. Adult and near-adult *P. audax* specimens were cryofractured in liquid nitrogen prior to fixation with glutaraldehyde and osmium tetroxide, and critical-point drying. Methanol-preserved specimens of a variety of other salticids were also subjected to glutaraldehyde and osmium tetroxide fixation and critical point drying and examined. Cuticle was treated with the ligand thiocarbohydrazide (TCH) (Kelley, Dekker, and Bluemink 1973) in alternation with osmium tetroxide to reduce charging effects. All specimens were coated with 10-30 nm of gold prior to examination with a Cambridge Stereoscan S4.

A low-power (10-50x) wide-field binocular microscope was used for close observation of animals in the laboratory. Field photographs of spiders moving in vegetation were made with a 90mm macro lens and 3x bellows attached to a 35 mm single-lens reflex camera. These photographs were subsequently enlarged for examination. For the analysis of motion, walking and turning spiders were filmed in the laboratory at a resolution of 640x480x30fps with a Canon Powershot A640 camera equipped with a Bower Digital Camera Adapter Tube (A52B610C) and a 52mm Crystal Vue High Definition +10 Macro Lens. Commercially available Canon ZoomBrowserEX software was used for single frame capture from digital motion pictures.

Identification of *Phidippus* jumping spiders follows Edwards (2004).

4. Introduction

Jumping spiders have collected and have continued to refine an impressive array of devices over their long evolutionary history. Along with other arachnids, they use internal fluid pressure changes to power their respiration, to ingest their food, and to extend their legs. Unique, cartilage-like internal skeletal elements help them to do this. Along with the other spiders, they are masters of silk, and have adapted the fused rear-most segments of the body (the *telsoma*, or *opisthosoma*) into a versatile appendage to support the use of this silk. Among spiders, salticids are distinguished by the remarkable resolution of their anterior medial eyes, and the sophistication of their visually-mediated behavior. This visually-mediated behavior includes the ability to execute targeted jumps, to capture prey or to reach a sighted position, with uncanny accuracy.

Like the Salticidae, many other spiders, including the so-called "primitive" theraphosids, also have pretarsal foot pads, and/or tarsal scopulae. Paired claws, foot pads, and the remarkable adhesive setae (the *tenae*) associated with these foot pads are not unique to the Salticidae (Foelix 1996).

If we assume that salticids evolved from longer-legged ancestors similar to the present-day salticid *Lyssomanes* in appearance, then they can claim at least one remarkable innovation. This is the fact that, for the most part, the relatively short-legged salticids crouch and walk *on the tips of their toes* (their flexible pretarsi), with only limited flexion at each metatarso-tarsal joint. The great majority of salticids are very adept at rapid movement, including the execution of jumps, from a *crouched* position with the legs drawn close to the body.

The Salticidae as a group are ancient, and the many, diverse lineages continue to evolve. Just how ancient this group is cannot be said at the present time, but it is quite possible that the salticid clade predates the radiation of the "class" Aves. Recent discoveries of Mesozoic fossils corresponding to modern spider families and genera (Penney 2004a, 2004b, Penney and Ortuno 2006) support this idea.

The present study is focused on the structure and function of the feet of the relatively large jumping spiders of the genus *Phidippus*, a genus that has diversified greatly on the North American continent. The only other salticid genus with a comparable level of diversity in North America is *Habronattus*. Although they receive little treatment here, *Habronattus* differ significantly from *Phidippus*, and some modifications of their feet (yet to be studied in detail) may reflect this. Relative to their size, *Habronattus* tend to have large foot pads and claws. Like *Phidippus*, they walk on their pretarsi, with limited movement at the metarso-tarsal joint. However, early observations suggest that they may have less capability to retract their relatively large claws. Whereas *Phidippus* and many other salticids usually power their jumps through extension of legs IV, *Habronattus* obtain most of their power for jumps through the retrograde movement and extension of their greatly enlarged legs III. This may give *Habronattus* a strong component of vertical thrust, supporting a ground-dwelling life style that involves frequent jumps directly off of the ground, as a primary mode of locomotion.

In the future, many more comparative studies will be available, and these will reveal much more diversity with respect to the functional morphology of salticid legs, feet, and associated setae. There is a great opportunity for future students of the Salticidae to observe related structures in much greater detail, to complete relevant physiological experiments, and to correlate these observations with the diverse life styles of these remarkable animals.

5. Presentation

Terminology and general review of foot structure

Terminology applied to the distal leg segments of spiders and other arachnids has not been consistent over time. Here, the two tarsal segments are called the *metatarsus* and *tarsus*, respectively (Figure 1), in agreement with the most popular usage of these terms. In some accounts, these have been described as a single segment, separated into a *basitarsus* (the metatarsus) and a *telotarsus* (the tarsus), following similar usage in the description of other arachnids. The term *distitarsus* has occasionally been used in place of telotarsus. What is important is recognition of the fact that the metatarsus and tarsus are fully separate and articulated segments, and that movement of the tarsus relative to the metatarsus is very important with respect to the precise positioning of the *feet* of these spiders on a surface.

Although the term *foot* is decidedly anthropomorphic and thus can be misleading when applied to spiders, it is a useful term to apply to the tarsus and pretarsus collectively, particularly since we also use the anthropomorphic term *leg*. In many respects, the tarsus is analogous to a human foot, and the pretarsal structures are analogous to human toes or the distal portion of the human foot that is responsible for most of the *ground force* that we exert during locomotion.

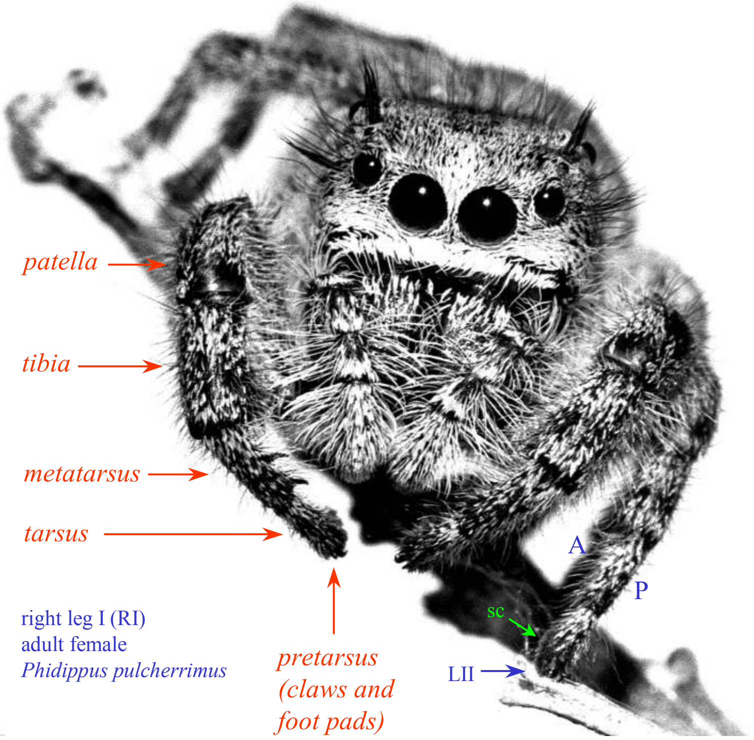


Figure 1. Articulated components of the distal portion of the salticid leg. Claws of legs I were extended and held a strand of silk (not visible) in this picture. The two foot pads (but not scopulae, *sc*) of left leg II (LII) were planted securely on a small twig in front of this spider (blue arrow). Note also the definition of the anterior (A) to posterior (P) axis of the leg, depicted here for LII.

At the same time, an observer should not forget that the set of eight legs of the spider are *also* analogous to the set of ten *fingers* that we bear on two hands, when it comes to grasping and holding! I will continue to use the term *legs* here.

The *pretarsus* consists of discrete, movable structures (*claws* attached to a *claw lever*, in turn supported by *lateral struts*, and two separate *foot pads*) that are *articulated* with the end of the tarsus, in the same sense that the tarsus is articulated with the end of the metatarsus. Some authors have depicted these as part of the tarsus (or telotarsus), but this belies the fact that pretarsal structures are quite separate from the tarsus, and they can be moved independently by the spider.

The *foot pads* have most often been called *claw tufts*, a term that relates primarily to the way that they appear under the microscope. Tufts of *tenae* (tenent setae) are indeed associated with each of the two (anterior and posterior) foot pads on each leg, but each foot pad is also comprised of a discrete and movable basal plate (*tenent plate*). Foot pads are not scopulae.

A *scopula* consists of a tract of specialized, usually flattened, setae most often associated with the ventral, distal tarsus. This term does not apply to the *pretarsus*. Although it is true that some scopulae are comprised of tenae, not all are, and it is not appropriate to call the tenae that are associated with the foot pads *scopula hairs*.

Some araneologists have described the presence of a single scopula on a spider leg. Here, each tract of similar setae is considered to be a separate scopula. Thus (Figure 2) the forelegs of *Phidippus audax* are depicted here with three separate scopulae, two (anterior and posterior) consisting of tenae, and one (ventral) consisting of an altogether different kind of seta, the *pilosa*.

The terms *prolateral* and *retrolateral* have been introduced in the past to describe, respectively, the *anterior* and *posterior* sides of the leg. Since the former terms were originally defined by reference to the latter terms, they are superfluous, and the terms *anterior* and *posterior* will be used directly to describe the two sides of each leg. There is a high degree of bilateral symmetry between the anterior and posterior sides of a leg, but the violations of this symmetry (e.g., the distinction between anterior and posterior claws) are also of great interest.

Most of the descriptions here are derived from work on the relatively large and robust jumping spiders of the genus *Phidippus*, spiders that also have relatively large foot pads and also tend to have scopulae, particularly on the front legs. A working terminology for the setae and setules of salticids will be presented here, but it is understood that substantial additions and modifications to this terminology will be required when we know more about these animals.

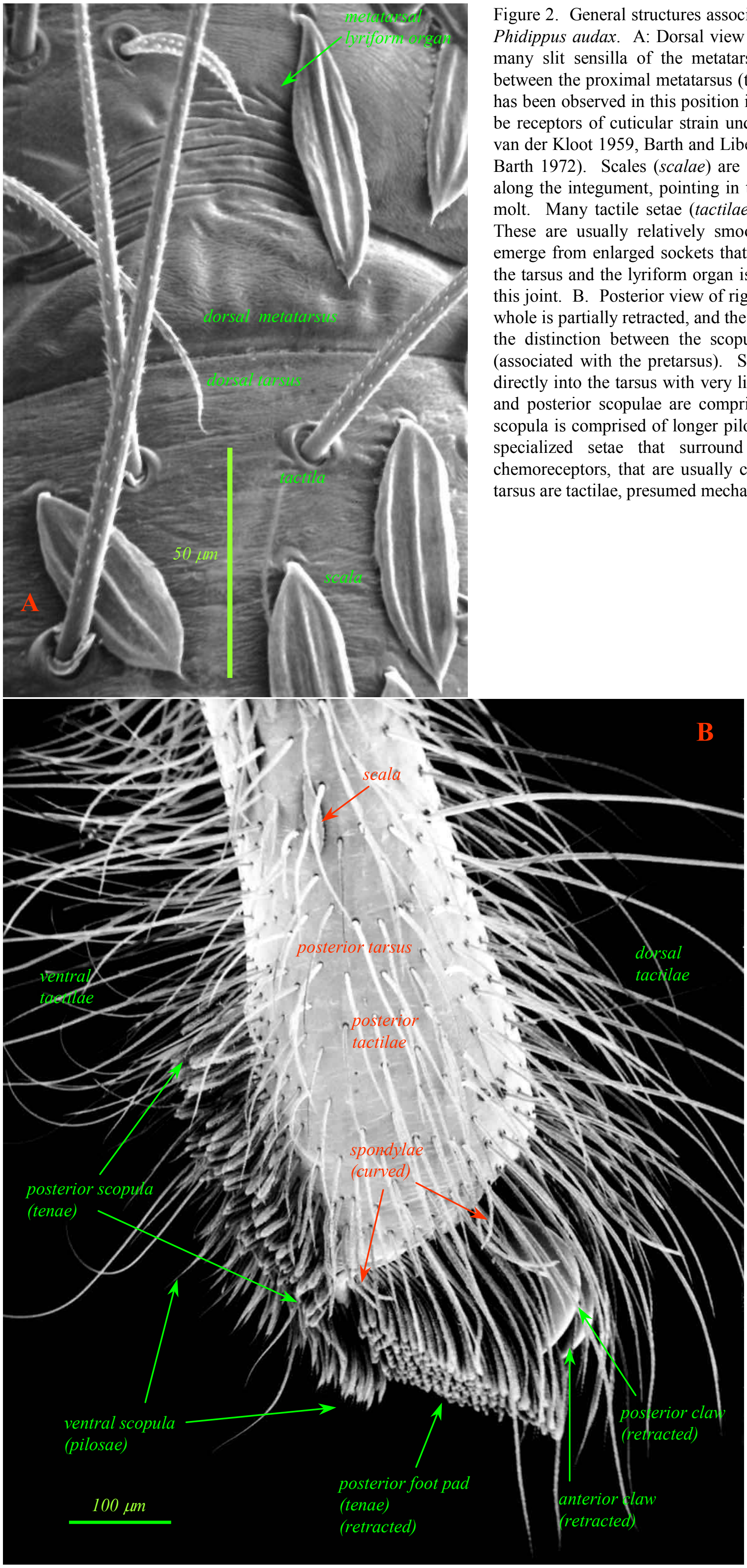


Figure 2. General structures associated with salticid feet, based on SEM photographs of *Phidippus audax*. A: Dorsal view of left leg I (LI) of an immature spider, showing the many slit sensilla of the metatarsal lyriform organ that is associated with the joint between the proximal metatarsus (top) and the distal tarsus (bottom). A lyriform organ has been observed in this position in many spider families, and slit sensilla are known to be receptors of cuticular strain under tension (Kaston 1935, Pringle 1955, Walcott and van der Kloot 1959, Barth and Libera 1970, Barth 1971, 1972, 2002, 2004, Seyfarth and Barth 1972). Scales (*scalae*) are specialized setae that are bent at the base to lie flat along the integument, pointing in the direction that the old cuticle is removed during a molt. Many tactile setae (*tactilae*, presumed mechanoreceptors) are also visible here. These are usually relatively smooth with smaller spinules on the surface, and they emerge from enlarged sockets that permit a degree of movement at the base. Between the tarsus and the lyriform organ is an area of flexible cuticle that permits movement at this joint. B. Posterior view of right leg I (RI) of an adult male. Here the pretarsus as a whole is partially retracted, and the anterior foot pad is also not visible in this view. Note the distinction between the scopulae (associated with the tarsus) and the foot pads (associated with the pretarsus). Scopular setae can bend, but they are also articulated directly into the tarsus with very little if any basal flexibility. The anterior (not visible) and posterior scopulae are comprised of relatively short, isolated tenae. The ventral scopula is comprised of longer pilosae, each bearing a long plumule at the apex. Other specialized setae that surround the pretarsus include the spondylae, presumed chemoreceptors, that are usually curved as shown here. The many larger setae of the tarsus are tactilae, presumed mechanoreceptors.

Dynamics of the pretarsus

SEM views of the major structures associated with the pretarsus are presented in Figures 3 and 4. The general configuration of pretarsal structures is also depicted in Figure 5.

Based on direct observation of living *Phidippus* under the microscope, I have recently been able to extend my earlier observations (Hill 1978) related to the ability of these spiders to extend and to retract not only the claws, but also the tenent plates. The respective roles of the pretarsal levator and depressor in rotating this apparatus were described previously for salticids (Hill 1977a).

A schematic view of the mechanics of this pretarsal movement is presented in Figure 6.

The hypothesis presented in Figure 6 with respect to the roles of the pretarsal levator and depressor generally agrees with the model presented by Speck and Barth (1982, also shown in Barth 2002) for the pretarsus of the ctenid *Cupiennius salei*, with several notable exceptions.

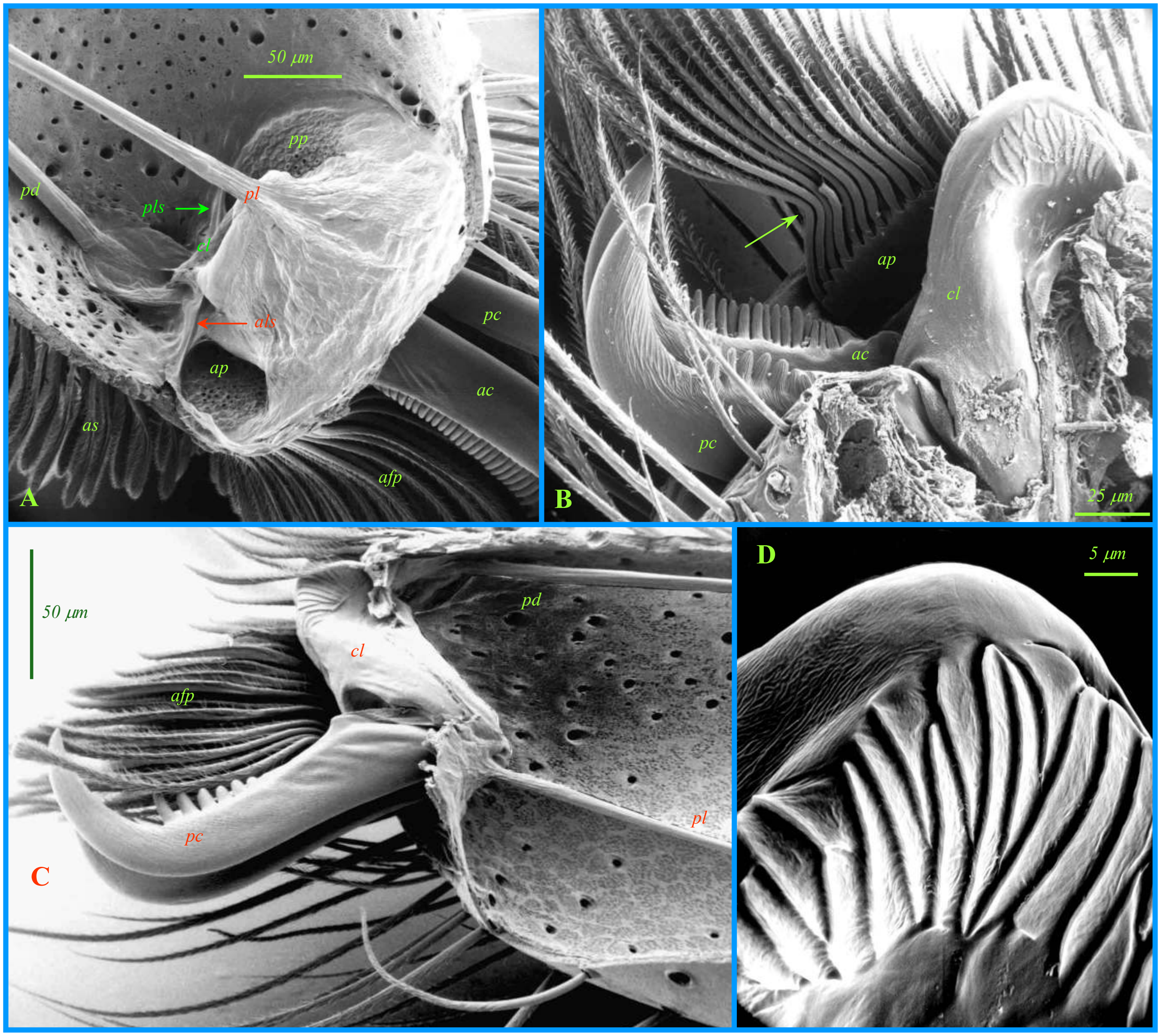


Figure 3. Views of the pretarsus of *Phidippus audax*. A: Interior view of pretarsus from exuvium of immature spider. The claw lever (cl) connects the pretarsal levator (pl) and pretarsal depressor (pd) tendons. The anterior and posterior lateral struts (als and pls, respectively) provide a rigid fulcrum for the action of the claw lever, and are located close to pretarsal depressor tendon. The interior of the anterior and posterior tenent plates (ap and pp, respectively) can be seen, on either side of the claw lever. Tenae of the anterior foot pad (afp) and the anterior scopula (as) can also be seen. Other symbols are: ac, anterior claw, and pc, posterior claw. B: Cryofracture of pretarsus from one of the legs of an adult *P. audax*, as seen from the rear with the posterior tenent plate removed. The claws are in a retracted position. Note the many, smaller teeth of the anterior claw (ac) as compared to those of the posterior claw (pc). The interior wall of the anterior tenent plate (ap) is completely smooth, as are the adjacent surfaces of the medial tenae associated with this plate. Note the extreme curvature of the dorsal tenae (tenent setae) on this plate (arrow). The distal, adhesive tenent pads are to the right of each tena, as seen from this perspective. Note also the flexible articulation of the claws with the claw lever (cl), as well as the pleated cuticular plates on the anterior side of this lever near the ventral side (to the right), where it joins the pretarsal depressor tendon. C: View from the rear of a dissected exuvium of an immature *P. audax*, with the posterior tarsal wall and the posterior foot pad removed. The posterior claw (pc) is partially disarticulated from the claw lever (cl). Other symbols: afp, anterior foot pad, pd, tendon of pretarsal depressor, and pl, tendon of pretarsal depressor. D: Detail of pleated cuticle associated with the ventral portion of the claw lever, from an adult male *P. audax*. Both anterior and posterior sides of the claw lever exhibit this pleated structure.

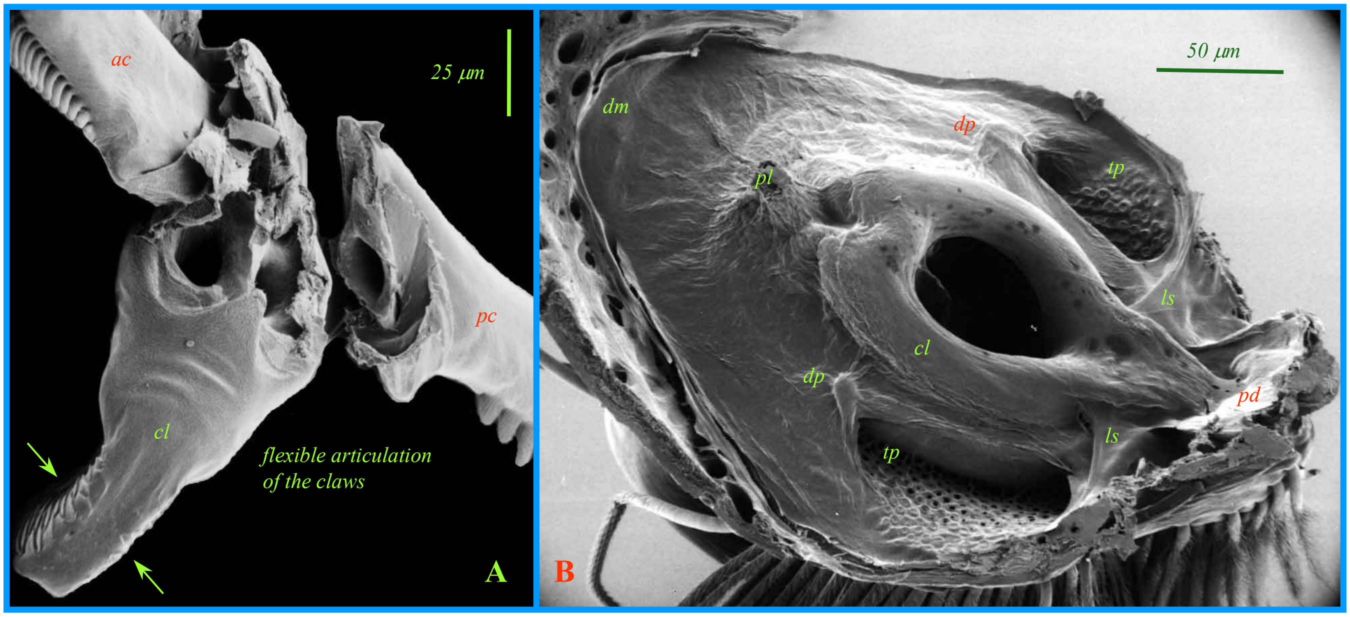


Figure 4. Views of the pretarsus of *Phidippus audax*. A: Disarticulated claw lever (cl) and claws (ac and pc), from dissected exuvium of immature spider. Note the pleated cuticle (arrows) on the anterior (left) and posterior (right) sides of the relatively narrow, ventral end of the claw lever. B: Inside view of the pretarsus from an immature exuvium, almost fully separated from the tarsus (upper left). Note the large area of relatively smooth and flexible cuticle to the right of the dorsal margin (dm) of the pretarsus. The relationship of the two lateral struts (ls) to the claw lever (cl) can be seen clearly in this view. Connection points for the pretarsal levator tendon (pl) and the pretarsal depressor tendon (pd) can also be seen. Dorsal processes (dp) project inwards from the acute dorsal corner of each tenent plate (tp), and may be associated with the action of the pretarsal levator. The ventral margins of the tenent plates are relatively fixed through their proximity to the lateral struts that serve as a fulcrum for the action of the claw lever.

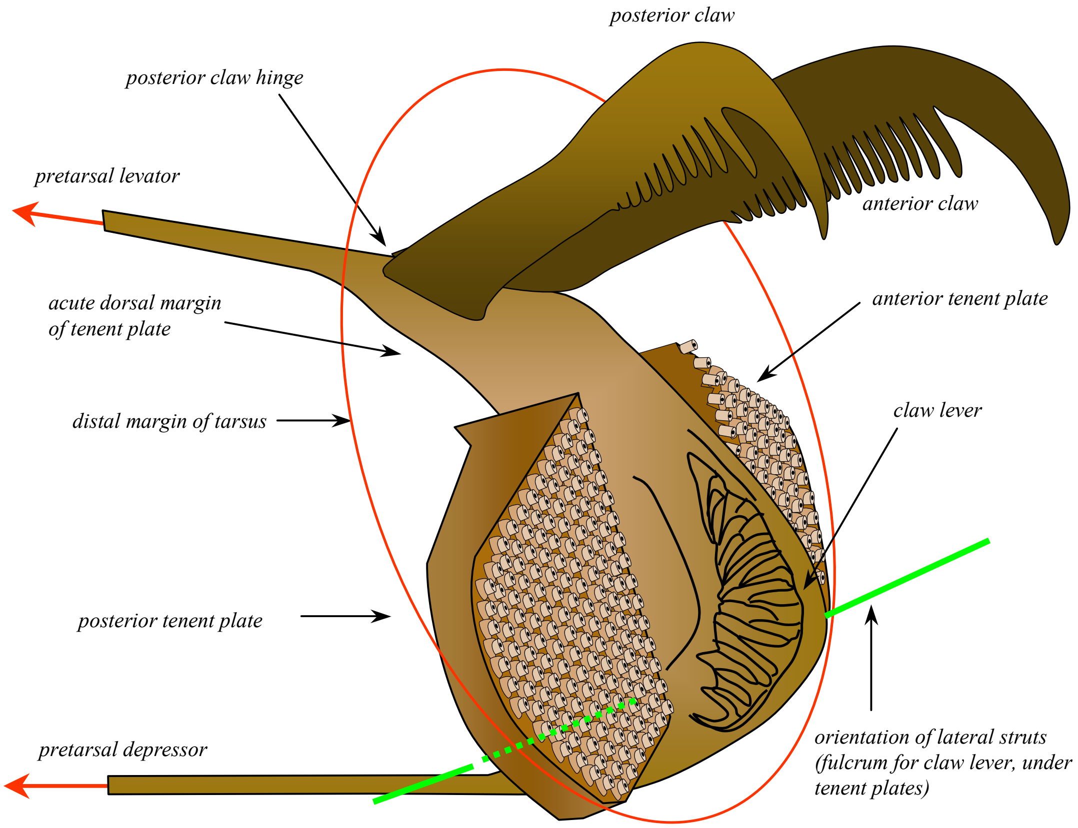


Figure 5. Schematic diagram of the pretarsus, as seen from the rear. The rigid distal margin of the tarsus is indicated with a red ellipse. Within this ellipse, the structures of the pretarsus are primarily connected to the tarsus by a relatively thin and flexible membrane. The most rigid connection between the two is made by the strong lateral struts (position indicated with green line), that also serve as a fulcrum for movement of the claw lever. The exterior sides of the two claw plates are smooth. Each claw articulates separately, and flexibly, with the relatively wide dorsal portion of the claw lever.

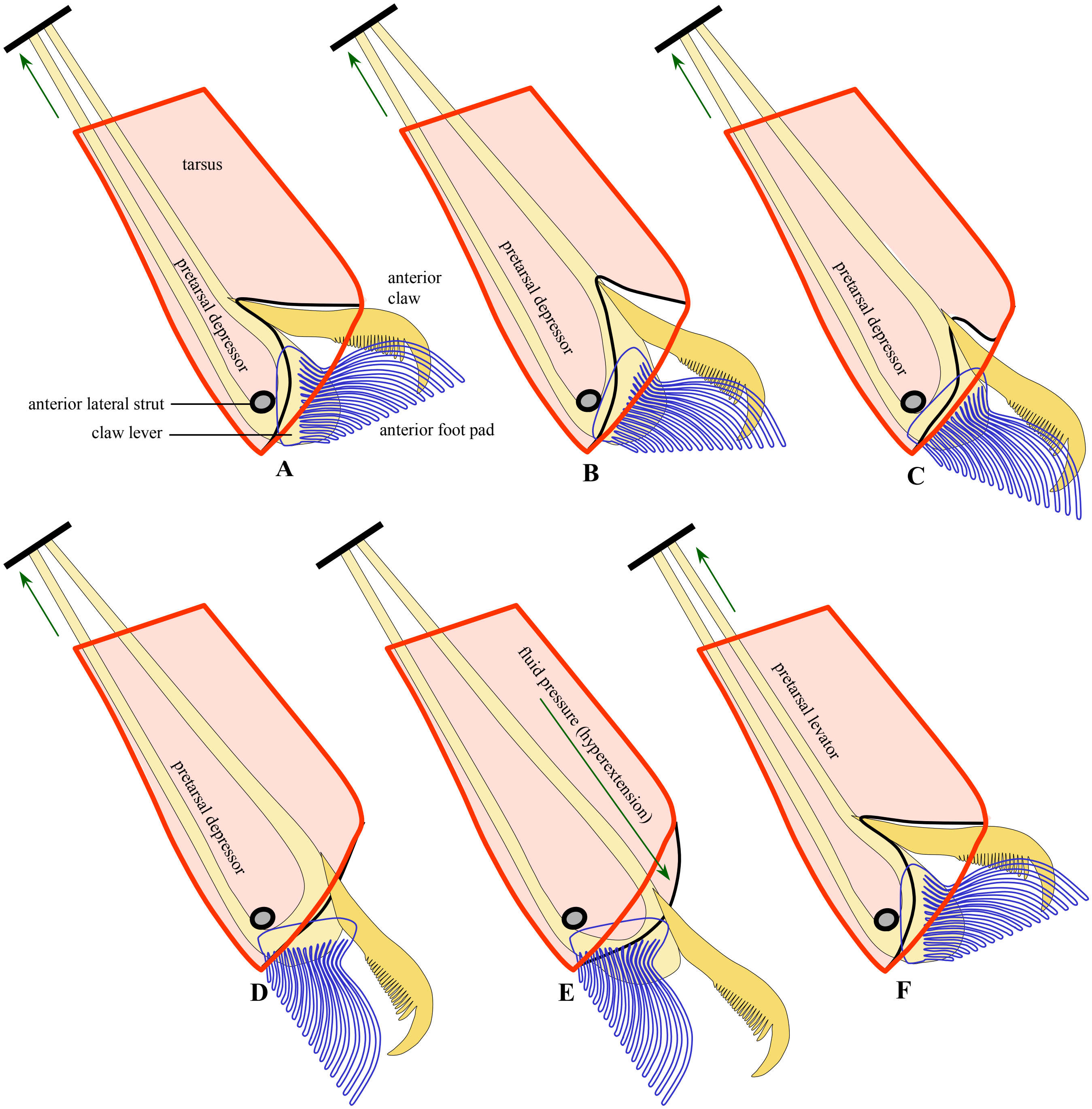


Figure 6. Hypothetical action of the pretarsal apparatus, as viewed from the front. Only the anterior claw and foot pad are shown. A-D: Progressive rotation of the pretarsus through the action of the pretarsal depressor, assisted by internal fluid pressure that tends to inflate the pretarsus. Progressive and relative relaxation of the levator (in opposition) allows this rotation. E: Extension of the claws associated with an increase in internal fluid pressure. Tension on a silk line held by the claws could have a similar effect. F: Retraction of pretarsus through action of the pretarsal levator. This would be facilitated by a simultaneous reduction in internal fluid pressure. At any stage, tension on the depressor could lock the rotation of the pretarsus in place, and allow the spider to move the claws up and down relative to the rest of the pretarsus through adjustment of relative tension of the levator. Additional tension would cause the pleated portion of the claw lever to stretch. Hyperextension under increased fluid pressure (E) could also be associated with further separation of the tenent plates as the claw lever itself is pushed further out. Variable hydrostatic pressure (*hydraulic transmission*) could allow the spider to *shift gears* with respect to the relative effects of tension on the depressor and levator, and the actual control mechanism should be much more sophisticated than this simple model would suggest. In addition, it is likely that elastic rebound associated with the tarso-pretarsal membrane (heavy black line), and recoil of the *torsion springs* represented by the anterior and posterior lateral struts, play an important role in the fine control of movement. Movement here is based on observation of *Phidippus* jumping spiders, and not all salticids may be capable of the same degree of movement of both claws and foot pads. Compare this hypothesis to the SEM views in Figures 3 and 4.

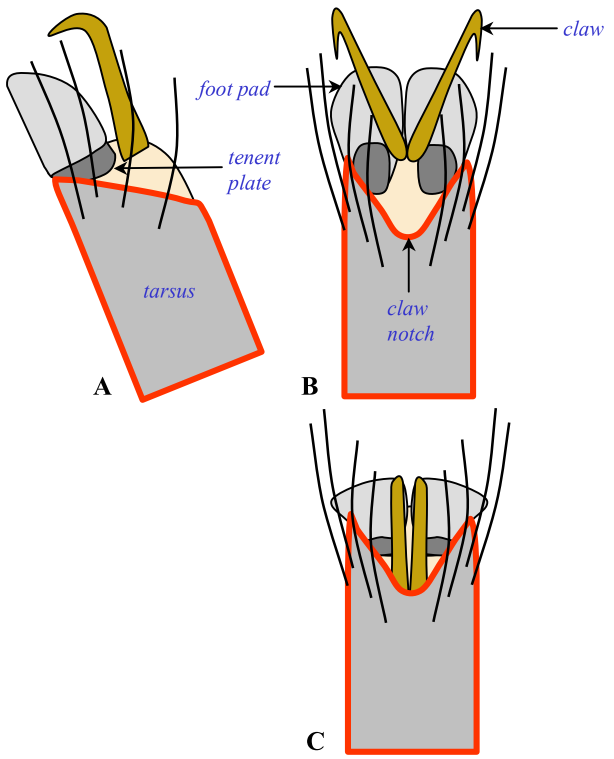


Figure 7. Schematic views of pretarsus of right leg IV (RIV) of a salticid spider, showing retraction of the claws into the distal tarsus. A: Anterior view of extended pretarsus. B: Dorsal view of extended pretarsus. C: Dorsal view of retracted pretarsus with flexed foot pads, showing how the retracted claws can be pulled together into the claw notch.

Speck and Barth described the respective roles of the pretarsal levator and depressor, as well as the impact of internal fluid pressure, in movement of the claws by *Cupiennius*. This action of the pretarsal levator and depressor with respect to the claw apparatus has also been described for other spider families, including the Theraphosidae (Dillon 1952, Sherman and Luff 1971), the Araneidae (Frank 1957), and the Theridiidae (Whitehead and Rempel 1959). Ellis (1944) also demonstrated the function of the levator and depressor muscles directly through electrical stimulation.

All of this work did not cover the dynamics of pretarsal foot pads, or the dynamics of *retractable* claws, found in at least some salticids (including *Phidippus*). As one example of this difference, a strong pull on the pretarsal levator (dorsal tendon) of *Cupiennius* lifted the claws up to a high position. Pull on the levator of a salticid would likewise raise the claw hooks, but it would also *retract* the claws into the distal tarsus. The base articulation of the claws of *Phidippus* rotates ventrally, and the claws pull together against the dorsal margin of the pretarsus and flex against the claw lever, as the claws are retracted (Figure 3B, C).

The pretarsus of salticids not only supports extension and retraction of the claws (Figure 7), but it also supports extension and flexion (retraction) of the foot pads. I have also observed some independent movement (raising and lowering) of the claws relative to the foot pads by *Phidippus*. A simple model of pretarsal extension and retraction by means of the depressor and levator, respectively, is thus insufficient, and further study will be necessary to resolve the respective roles of internal fluid pressure and the muscles associated with the pretarsus.

As one hypothesis, I would suggest that the pretarsal levator and depressor are primarily responsible for *rotation* of all pretarsal components as depicted in Figure 6, at the same time that internal fluid pressure plays a role in their extension. This idea is supported by the proximity of the internal margin of each tenent plate with the claw lever (Figure 4B).

Whereas internal fluid pressure might facilitate action of the depressor, fluid pressure definitely opposes the tendency of the levator to retract the pretarsus. Further extension may be accomplished by an increase in internal fluid pressure, which would tend to inflate the dorsal membrane of the pretarsal articulation and thus could push the claw tips out to a position beyond the extended tenent setae (Figure 6E, also see SEM views in Figure 15A, B). Differential but simultaneous tension on the two tendons may allow for some independence of claw and foot pad movement. The pleating on either side of the claw lever (Figures 3D, 4A) also suggests that this lever stretches under the tension of these tendons.

Other considerations for future study include the observation that the tenae of *Phidippus* and other salticids tend to spread out laterally as the foot pads are extended, and the foot pads appear to separate, even if they do not contact a surface. This suggests that there is some rotation of each tenent plate in a plane perpendicular to the long axis of the leg, when the pretarsus is inflated. Dunlop (1995) described similar lateral movement of the setae associated with the extended claw tufts of the theraphosid spider *Grammostola cala*, in association with depression of the claws. He attributed this to the physical connection between the claw articulation and the tenent plates, and suggested that internal fluid pressure could also play a role in this extension. It is an open and very interesting question whether foot pads and foot pad mobility evolved only once in the Araneae.

The two lateral (anterior and posterior) struts that bind each pretarsus to the distal tarsus (Figure 3A) definitely look like a pair of elastic *torsion springs*, pulling the pretarsus back into a resting position when other sources of tension are removed, along a defined axis of rotation. It is notable that these struts provide the only rigid or semi-rigid articulation between the pretarsus and the tarsus.

Examples of extension and retraction of the pretarsus of *Phidippus* are shown in Figures 8-10. Discrete extension and retraction movements of the pretarsus (both the claws and the foot pads) have been observed for both *Phidippus* and *Platycryptus* salticids in the absence of contact with either silk or a surface, but these direct observations of independent movement are infrequent. Most often these movements are either slight, or very rapid, and they accompany movement of the legs. This makes them difficult to observe directly.

As shown in Figures 8-10, the foot pads of *Phidippus* can be rotated through an angle of about 90° relative to the long axis of the tarsus. With relatively inflexible metatarso-tarsal joints, salticids like *Phidippus* can be said to *walk on their toes*.

In comparison, the salticid *Lyssomanes viridis* (Figure 16), like many other spiders, has very flexible metatarso-tarsal joints, and has more of a tendency to use rotation at these joints to align the foot pads to a surface. *Phidippus* and other salticids do have about 30° of flexibility at these joints (Figure 8), but appear to rely much more on rotation of the pretarsal foot pads to establish and maintain contact with plant surfaces and structures.

Photographs presented in Figures 8-10 also show how *Phidippus* retract the pretarsus when walking on the upper surface of a leaf, and extend the pretarsus to hold on to the edge of a leaf, or to maintain contact with a surface as a leg is extended. The entire pretarsus is very flexibly articulated for dorso-ventral movement to accommodate the orientation of the substratum, and to allow the legs to pivot freely and still maintain contact as the spider moves.

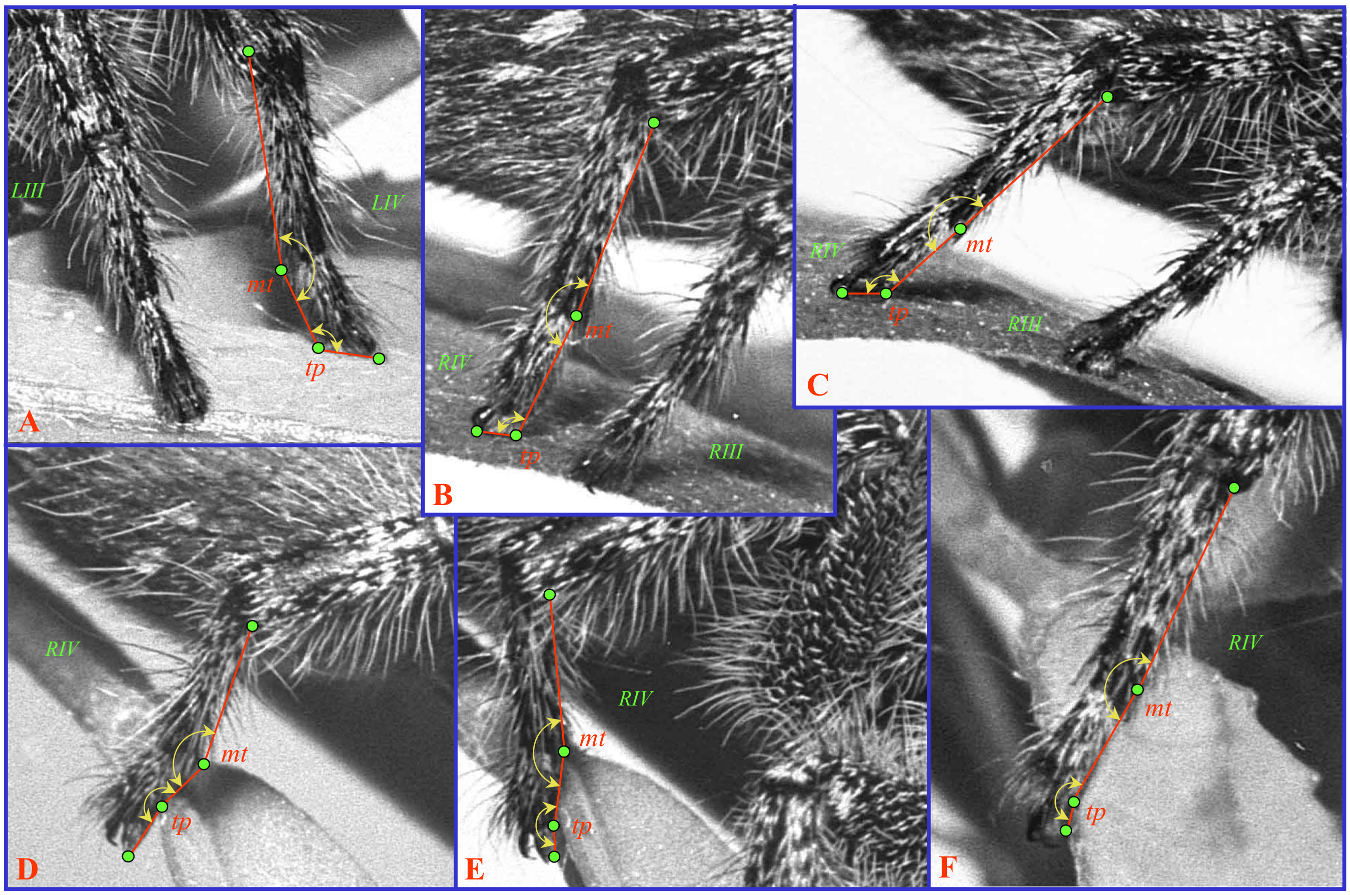


Figure 8. Photographs of legs IV of an adult female *Phidippus pulcherrimus* moving on vegetation, to illustrate flexibility of the metatarsus-tarsus joint (mt) and the tarsus-pretarsus joint (tp). Both joints permit only dorso-ventral rotation. A-C: Examples where the spider was walking on top of a leaf. The angle between the tarsus and the pretarsal foot pad surfaces (tp) was considerably less than 180°, approaching 100° in B. The angle between the metatarsus and the tarsus (mt) was either 180°, or somewhat less. The metatarsus-tarsus joint permits only about 20-30° of movement in *Phidippus*, but significantly impacts the positioning of the foot as shown here. D-F: Examples where the spider was holding the edge of a leaf. As shown by these examples, the angle between the tarsus and the pretarsal foot pad surfaces can exceed 180° when the pretarsus is extended. Note the extended claws in these examples, approximately parallel to the orientation of the long axis of the tarsus and the foot pad surfaces.

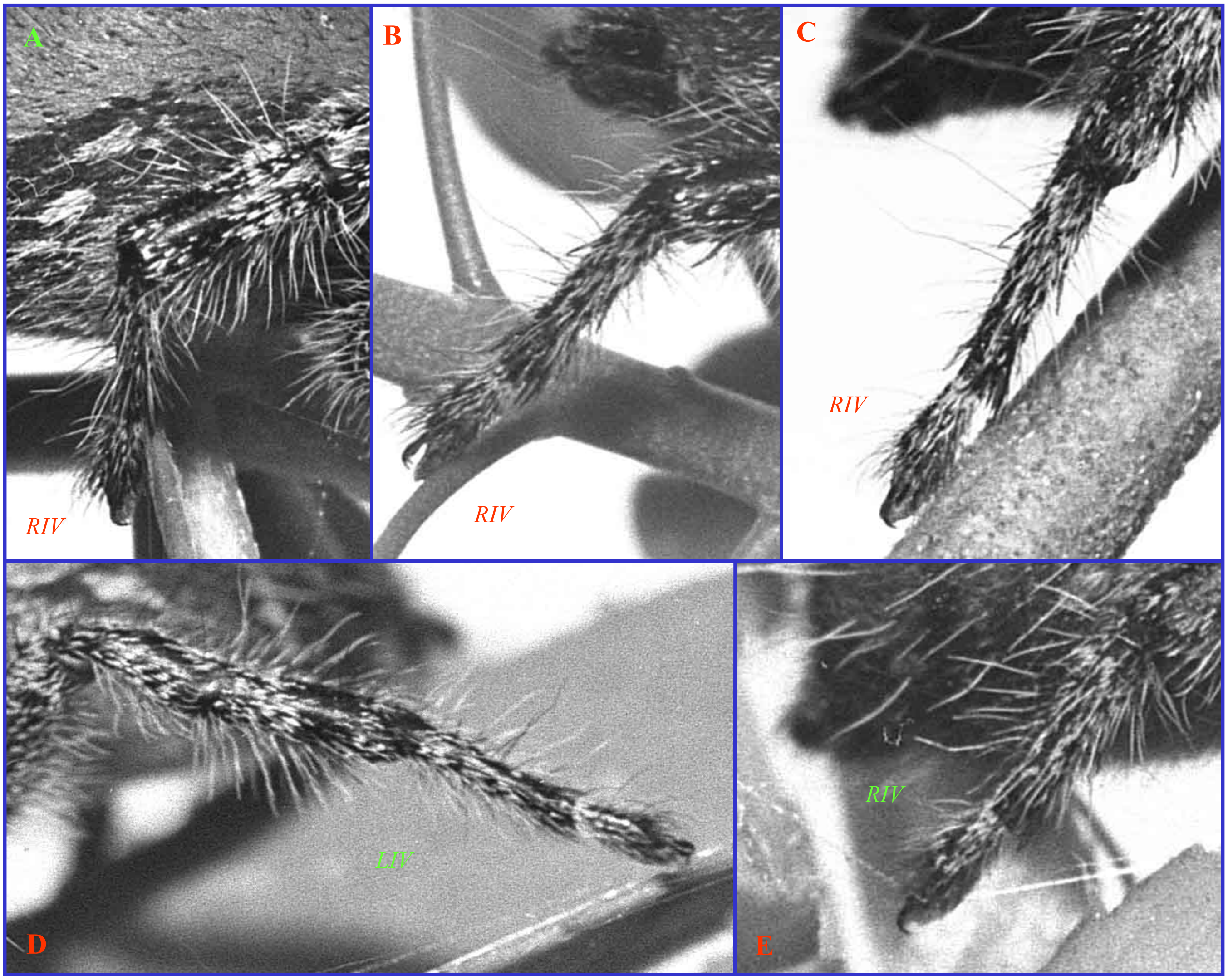


Figure 9. Photographs of the extended pretarsus of legs IV of a walking adult female *Phidippus pulcherrimus*. In each case, the angle between the long axis of the tarsus and the foot pad surfaces of the pretarsus was close to 180°. A: Leg flexed around a small branch, apparently held in place by metatarsal spines (macrosetae). B: Foot pads extended to hold the petiole of a leaf. The extended claws can be seen clearly in this photograph. The pair of extended foot pads often look like a cloven hoof, and one tip was visible beneath the claws in this view. C: Foot pads extended to accommodate the orientation of a branch. Note the difference in elevation of the claws from B to C. D: Extended leg under tension as the extended claws pulled on several strands of silk near the edge of a leaf. Note how the claws extended beyond the foot pads to obtain an unobstructed hold on the silk lines. E: Foot pads resting directly on silk lines, with the claws extended well beyond the foot pads.

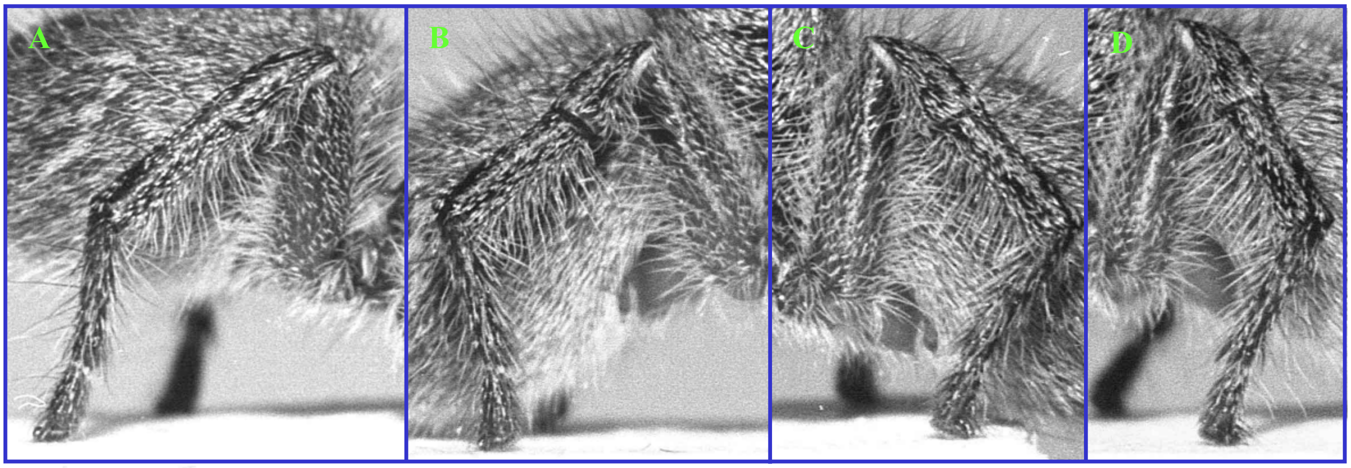


Figure 10. Starting positions for leg IV during jumps from the top of a horizontal surface by an adult female *Phidippus princeps*. Leg IV was cocked and then rapidly extended by means of internal fluid pressure to launch these spiders towards their targets (Parry and Brown 1959a, 1959b, Hill 2006). The angle between the long axis of the tarsus and the foot pads was close to 90°. A: When the spider was jumping down from its position, leg IV was more extended, and the entire surface of the foot pads was brought into contact with the substratum. B-D: To jump up from the surface, the footpads were positioned in front of the tibio-metatarsal joint, apparently near their limit of retraction relative to the tarsus. As shown here, the ventral portion of each foot pad was detached from the surface to accommodate these leg positions, and only the dorsal tenae of these foot pads were in contact at the start of the launch.

The claws

As shown in Figure 4A, the two claws on each leg of *Phidippus* and other salticids are flexibly articulated with the dorsal part of the claw lever. When retracted into the pretarsus, the claws are pulled together, but when extended they are free to separate and orient in different directions (Figure 7). Tension on the claws is conveyed most directly through the tendon of the pretarsal levator.

For *Phidippus* jumping spiders, the anterior claw has many more teeth, smaller teeth, and much tighter spaces between the teeth, than does the posterior claw of each leg (Figure 11, also Hill 1977a, 1978). This difference is characteristic of the great majority of the Salticidae, comprising the *Salticoida* (Maddison and Hedin 2003). Only the smaller Sparteinae and Lyssomaninae subfamilies of the Salticidae are not placed in the Salticoida. I have not yet been able to establish a specific role for the differentiation between anterior and posterior claws in the Salticoida. The hypothesis that the anterior claws are used to tightly grasp silk lines, and that the posterior claws are used to traverse these lines without a tight grasp, is still viable.

In Figure 12, the physical dimensions of structural silk and the fabric of the inner liners of the resting sac are compared to the claw teeth of *Phidippus*. The tight interstices between the anterior claw teeth are of the right size to secure silk lines tightly, particularly if these are associated with the dragline or related structural lines produced by these spiders.

In an earlier publication (Hill 1977a), I suggested that the claws supported movement by these spiders on silk lines, and that the anterior claws might play a role in grasping these lines, as the posterior claws helped to traverse these lines. At that time, even the function of the claws of orb-weaving spiders that depend on silk for prey capture was open to question (Foelix 1970b, *Araneus diadematus*, Araneidae). Later (1978) I was able to observe the use of the claws by *Phidippus regius* walking within a resting sac.

I have recently made many observations of *P. princeps* under the microscope as they extended and used their claws to pull on silk lines, or as they walked on the silk fabric lining their resting sacs. These spiders use claws to hold onto silk within the resting sac, but, when in the preferred right side-up orientation within the resting sac, they also walk directly on their foot pads, on top of the inner fabric of the sac.

The large *claw hooks* (Figure 11A) are used as general-purpose *grappling hooks* by *Phidippus*, and are very effective when these spiders grip the edge of a leaf (Figures 8A, 8B). The teeth may primarily (or exclusively) support the handling and securing of silk lines. Not all silk lines are secured by the teeth, however, and the claw hooks, or even other parts of the leg, are often sufficient for this purpose.

Phidippus use their claws to hold on to their draglines (Figure 9D). When suspended in the air after a predatory jump, these spiders will reach back with a leg IV to secure their dragline (Hill 2006). If they missed the prey, they flip around and climb up the dragline quickly with legs I and IV, wrapping up the silk in the process. The role of the claws in this ascent is not known. However, if they capture a large prey item, they can quickly climb backward up the dragline with their legs IV while holding the prey with legs I and II.

Gorb and Barth (1994) reported the use of the claws of a single leg IV by the pisaurid *Dolomedes*, to secure the dragline while rotating around the attachment disk of that dragline, floating on the water. Few related observations have been documented, but it is likely that the use of the claws to hold the dragline is fairly general within the Araneae.

Gillespie (1991) reported a most interesting use of specialized anterior claws to impale prey, by the tetragnathid *Doryonychus raptor*. These spiders can move quickly enough to impale insects in flight. I have not encountered any similar descriptions related to the use of claws in predation. In salticids, it appears that the macrosetae and the fangs of the chelicerae are the principal attack weapons.

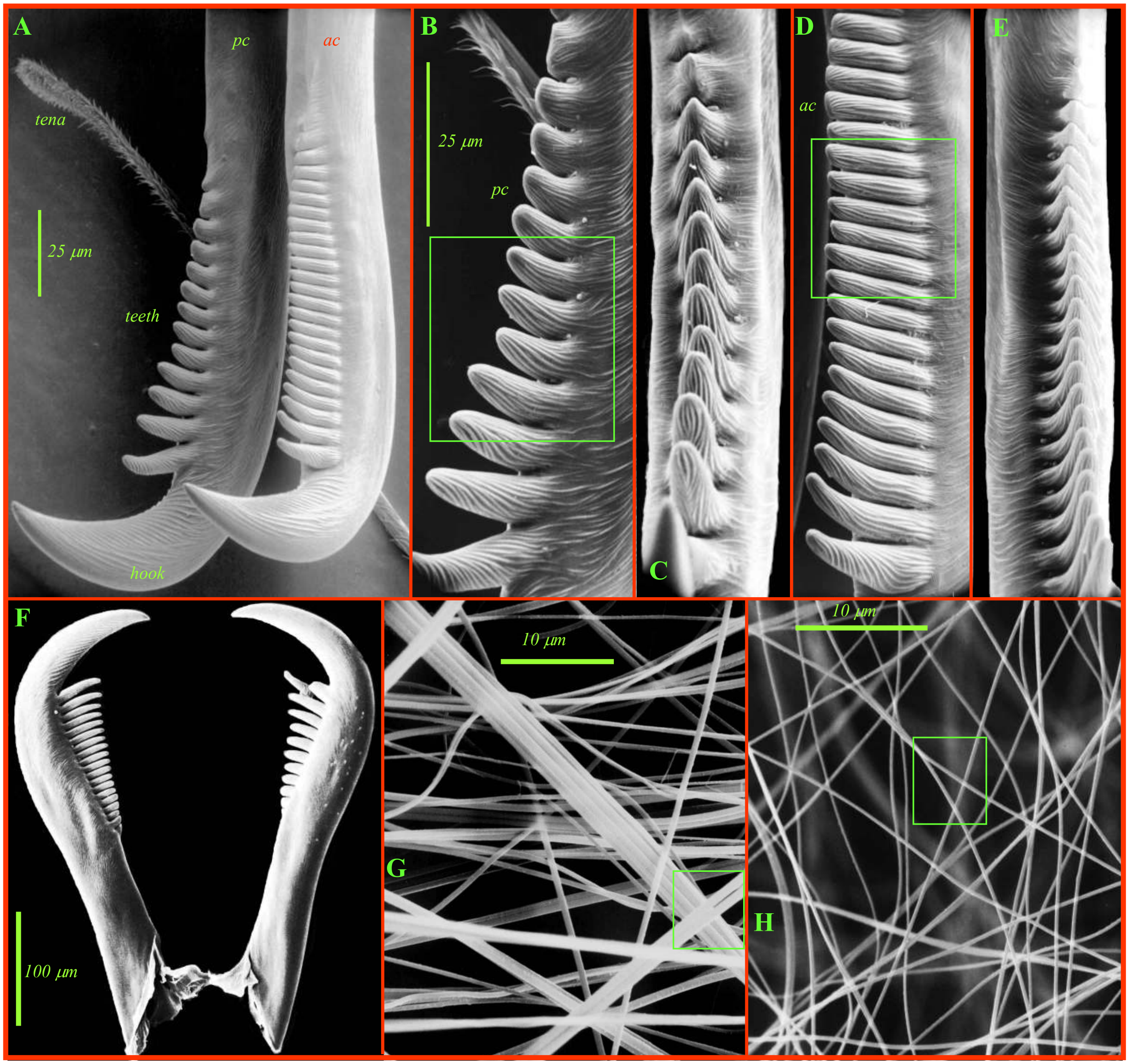


Figure 11. SEM photographs of the claws and silk of *Phidippus audax*. The green inset rectangles correspond to close-up views shown in Figure 8. A: Claws of left leg IV (LIV), from immature (dissected exuvium). Note the relative size of spacing of the *teeth* on the anterior (ac) and posterior (pc) claws, and the distinction between the many claw teeth and the apical *hook* of each claw. B-C: Two detailed views of the posterior claw from (A). D-E: Two detailed views of the anterior claw from (A). F: View of a different pair of claws from the exuvium of an immature spider. Here the full extent of the claws, including the articulating ends (at bottom), can be seen. The anterior claw is to the left. G: Outer or structural silk fibers from the outer layers of the resting sac of a penultimate female *P. audax*. The thicker fibers are the size of dragline fibers, and may have the same source in the major ampullate glands of the anterior spinnerets. H: Layer of fabric consisting of uniform fibers of smaller diameter, from the inside of the resting sac of a penultimate female *P. audax*. Resting or molting sacs of *Phidippus* are lined with multiple layers of fabric like the one seen here. A second layer can be seen, out of focus, in the background.

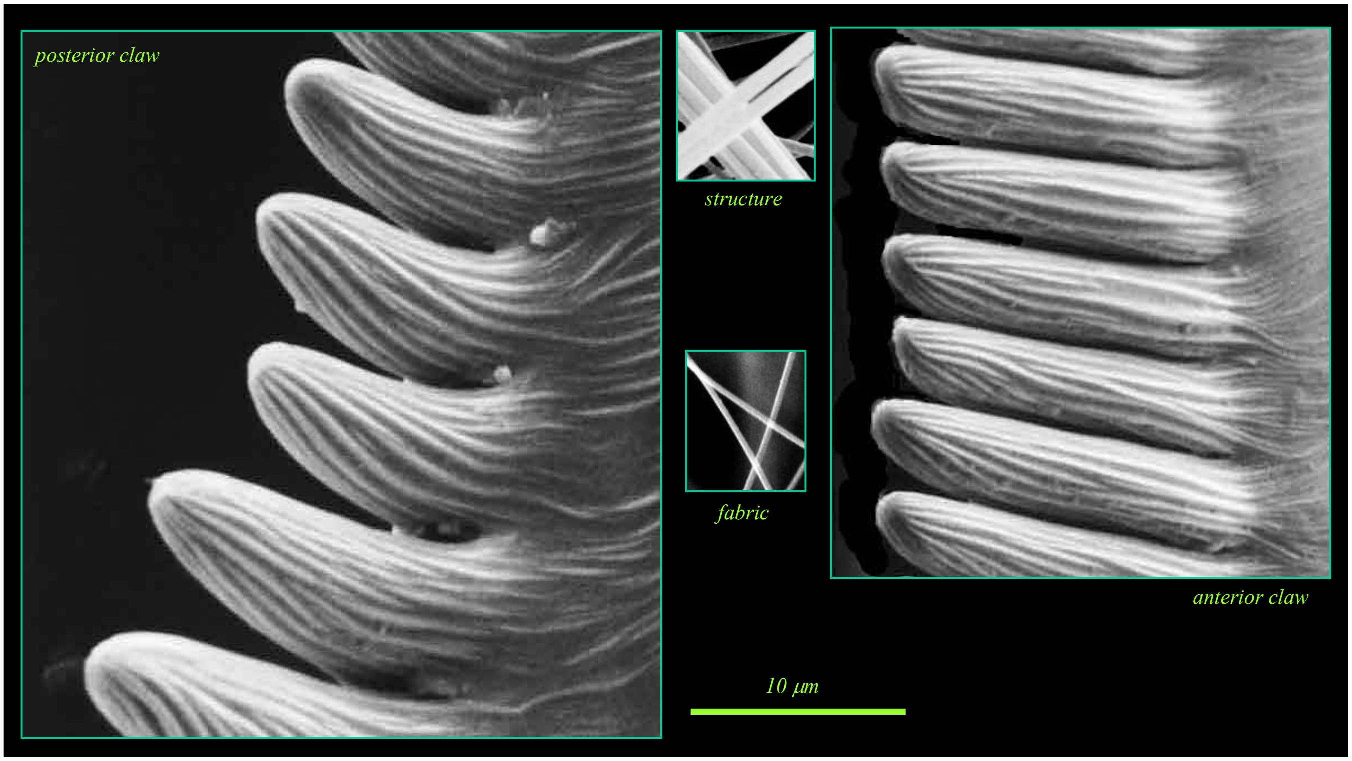


Figure 12. Close-up views of the claws and silk of *Phidippus audax* shown in Figure 11, shown to scale for comparison. Each of the four pictures is identified as a green inset rectangle in Figure 11. Teeth of the posterior claw are more conical, with a gradually narrowing interstices that could accommodate silk fibers across a wide range of dimensions. The curvature of the posterior teeth may also be useful in hooking and pulling on silk lines without holding them tightly. This curvature should also promote the rapid release of silk lines. The long, narrow interstices between the more cylindrical teeth of the anterior claw would support a tight hold on silk lines and these teeth do not appear to be adapted for the rapid release of these lines.

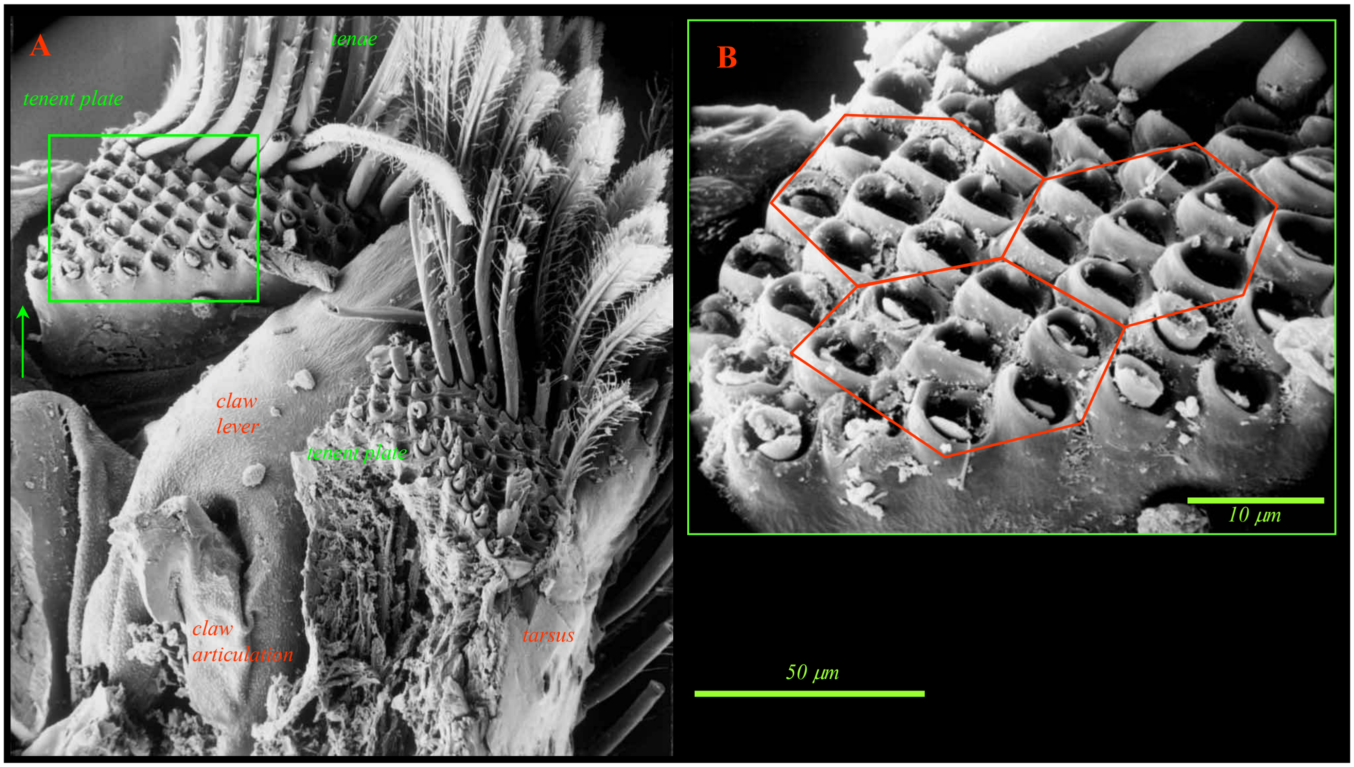
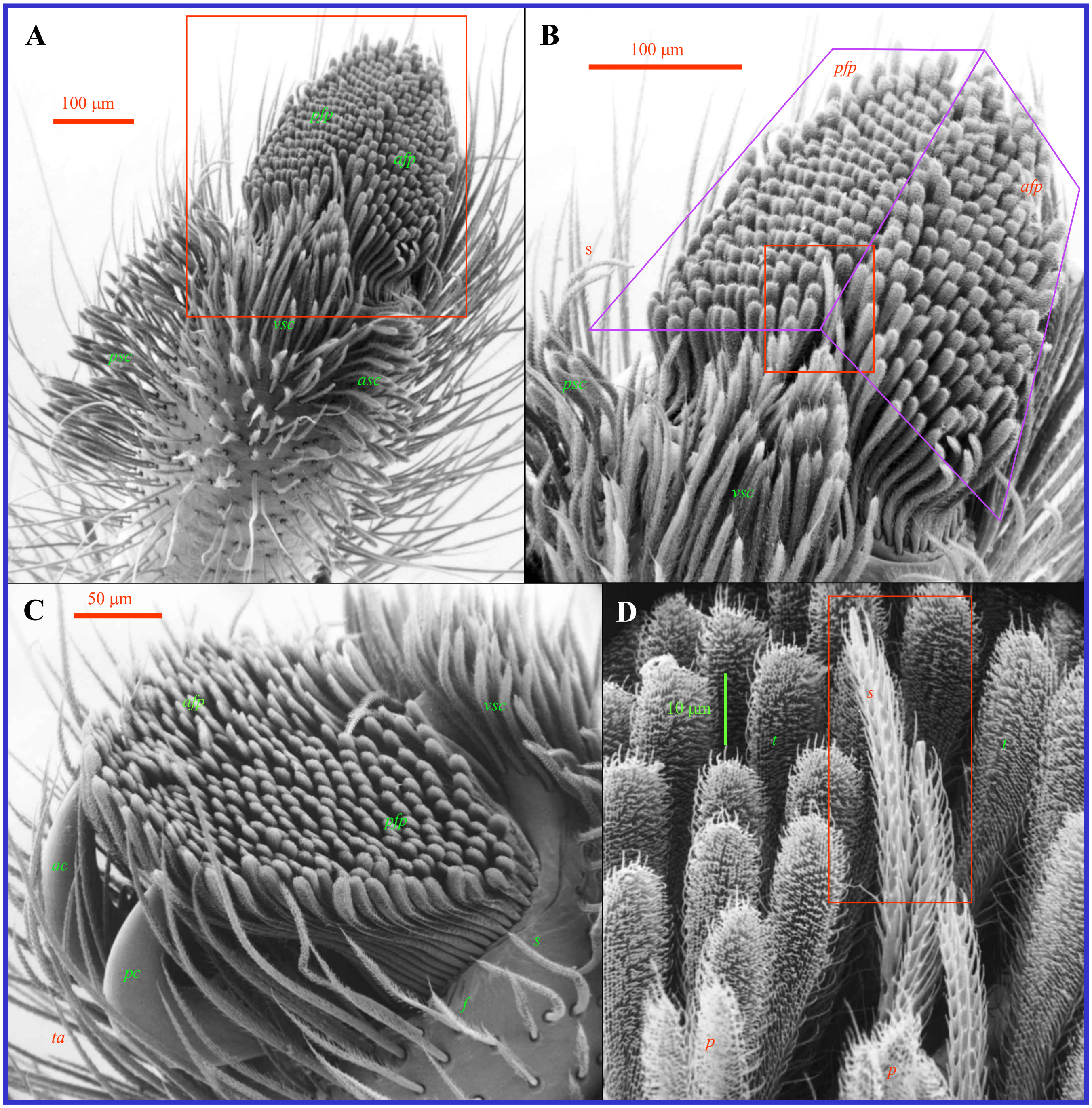


Figure 13. Cryofracture of the pretarsus of an adult male *Phidippus audax*. A: Each of the two food pads is comprised of a tenent plate bearing an array of tenae (tenent setae). Here many of the tenae have been broken off to expose a space-filling, hexagonal array of sockets, lined up in tiers of successively higher elevation, from left (dorsal) to right (ventral). To the right, the non-adhesive side of several tenae, each supported by a brace, can be seen still attached to one of the tenent plates. Note the smooth inside wall of the tenent plate at top left, and the acute (~60°) angle of the dorsal corner of this plate (arrow). Cryofractured soft tissue can be seen beneath the tenent plate in this view. This is not present beneath the cuticular portion of the tenent plates associated with dissected exuviae (Figure 4B). B: Detail from A (inset) highlighting the space-filling, tiered, hexagonal array of sockets from which the tenae of the foot pads emerge.

The foot pads

The relationship of the two foot pads of each foot to the pretarsus was previously depicted, in Figures 5 and 6. A dissected SEM view of the tenent plates supporting the tenae (tenent setae) of these foot pads is shown in Figure 13, for an adult *Phidippus audax*. The sockets bearing the tenae are closely packed and tiered, in a space-filling array. The shape and length of individual tenae also varies across the length and breadth of each footpad, so that the ventral tenae tend to be much shorter than the dorsal tenae, creating a relatively flat surface comprised of the distal, tenent pads of the entire collection of tenae (Figure 14).

Figure 14. SEM views of the right leg I of an adult male *Phidippus audax*. A: Ventral view, showing the relatively flat surfaces of exposed tenent pads (facing the viewer) of tenae of the anterior (afp) and posterior (pfp) foot pads, respectively. The three tarsal scopulae can also be seen clearly in this view: the ventral scopula (vsc) comprised of pilosae, and the anterior (asc) and posterior (psc) scopulae comprised of isolated tenae very similar to those of the foot pads, but not articulated in movable plates. B: Detail from inset in (A), highlighting the separate planes defined by the ends of the tenae of each of the two tenent plates. Notice that the flattened surfaces of the tenae tend to be oriented in a proximal direction, but also tend to face the median line somewhat toward the ventral margin of the pretarsus (near the ventral scopula, vsc, at bottom). C: Posterior view, also showing several *fringilae* (f, fringe setae) of the distal tarsus, facing the pretarsus. Note how the dorsal tenae are much longer than the ventral tenae. D: Detail from inset in (B) showing a distinctive group of *spondylae* (s, presumed chemoreceptors) that emerge between the two foot pads. Other symbols: ac, anterior claw, p, pilosa, pc, posterior claw, t, tena, ta, tactila.



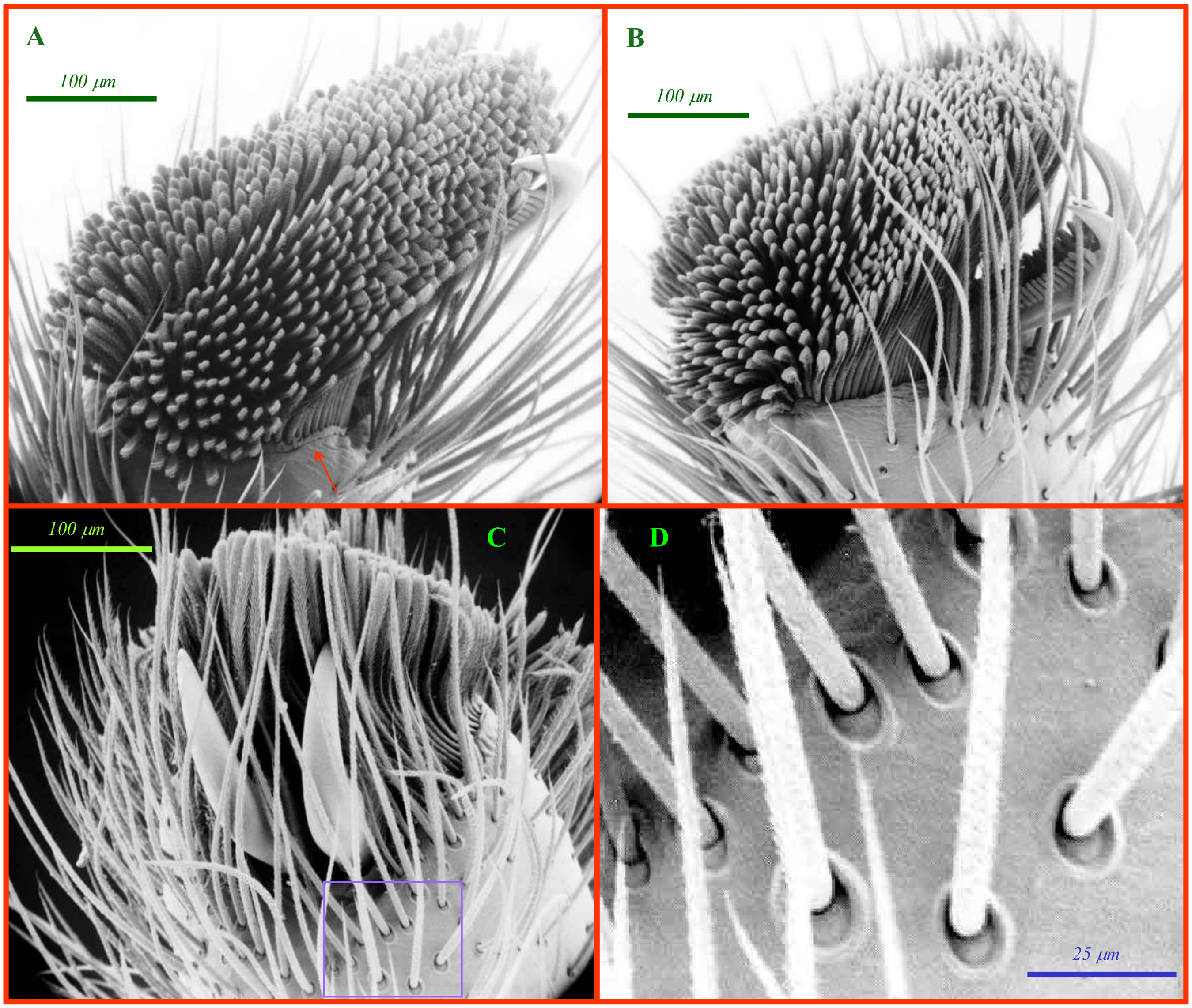


Figure 15. SEM views of the pretarsus of adult male *Phidippus audax* spiders. A-B: Two views of the footpads of the right leg IV (RIV), from two different spiders. The tenae face toward the ventral median of the pretarsus. Note again the regular dorso-ventral variation in the length of individual tenae. Each foot pad bears about 300 individual tenae. The many prominent, plumed setae of the ventral scopula that can be seen here have not been characterized, but the tract that they occupy is comprised exclusively of pilosae on legs I, and these may also be pilosae. Note that relative to (B), (A) is in a more extended position, and the upper margin of the anterior tenent plate can be seen to extend beyond the distal margin of the tarsus (red arrow). C: Dorsal view of pretarsus of the right leg I, showing the many large tactilae (presumed tactile mechanoreceptors) that surround the pretarsus. D: Detail of the bases of tactilae from the inset rectangle in (C) , showing the expanded socket membranes that permit movement of the base of each tactila in a direction away from the pretarsus. It is likely that these tactilae are in a resting position here, with each tactila adjacent to the distal (toward the pretarsus) margin of its socket.

In addition to the regular increase in the length of individual tenae as one moves from the ventral to the dorsal side of each foot pad, the shape of individual tenae varies considerably, as can be seen in Figure 3B. The longer tenae near the acute dorsal margin of each plate are bent significantly in a manner that suggests that they are *directionally* flexible and resilient when applied to a surface.

Figure 15 shows the foot pads of legs IV of an adult male *P. audax*. Each foot pad of leg IV appears to contain far more tenae (about 300) than does each foot pad of leg I (about 180). The dorsal and lateral areas of the distal tarsus, surrounding each pretarsus, also bear many tactilae (tactile setae, presumed mechanoreceptors), as shown in Figure 11.

Legs I and II of *Phidippus* tend to bear scopulae on the ventral surfaces of their tarsi, whereas legs III and IV bear many large setae (not examined in detail here), but not the organized tracts of tenae and pilosae seen on the front legs.

Variation in pretarsus and foot pad development in the Salticidae

The Salticidae is a very diverse group, and considerable variation in the development of the foot pads and the scopulae can be expected. When compared to *Phidippus*, most salticids are considerably smaller, with much smaller foot pads (Figure 16).

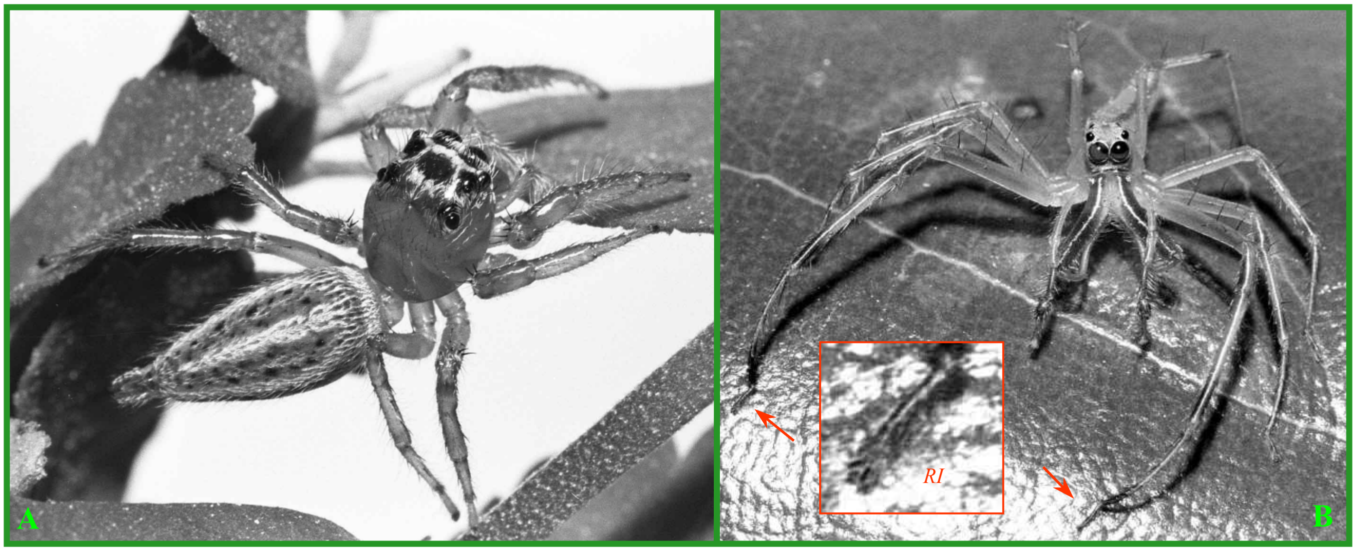


Figure 16. Two smaller salticids with much smaller foot pads than *Phidippus*. Both spiders were photographed in Gainesville, Florida. A: This adult female *Thiodina sylvana* used its small foot pads to secure a foothold near the edge of each leaf as it stepped between them. Like *Phidippus*, *Thiodina* do not tend to flex the metatarso-tarsal joint to a great extent. B: Adult male *Lyssomanes viridis* on the upper surface of an evergreen *Magnolia grandiflora* leaf, a plant highly favored by this species in the southeast. Note how *Lyssomanes* can hold the entire foot (tarsus and pretarsus) against the surface as they walk (arrows, inset detail). Compared to most salticids, they have a very flexible metatarso-tarsal joint, and use rotation at that joint to align each pair of very small, elongated foot pads, to a surface. Immatures that I have observed recently did not have scopulae on the tarsi, but relied on these very small foot pads.

The metatarso-tarsal joint of *Lyssomanes* is highly flexible, as it is in many if not most non-salticid spiders, and these spiders often rest the entire tarsus against the surface as they walk (Figure 16B). Rotation of the tarsus relative to the metatarsus (rather than extensive pretarsal rotation) facilitates alignment of the very small, elongated foot pads of these spiders with a surface. *Lyssomanes* tend to live on the surface of plants with broad, waxy (hydrophobic), flat leaves, and their legs are relatively long and extended almost all of the time.

As noted earlier, only the claws of the Salticoida are known to be highly differentiated. Foelix et al (1984) described the presence of tracts of unusual tenae or tena-like setae comprising anterior and posterior scopulae on the legs of the salticid *Portia*. These were unusual in that their tenent surfaces were oriented in a distal direction, and they could be inflated by increased internal fluid pressure. These setae were thought to be associated primarily with prey capture, as *Portia* normally walk on their foot pads.

Variations in the size of the adhesive *tenules* associated with the tenae of salticid spiders will be discussed in a subsequent section.

As shown in Figures 17 and 18, the basic layout of the pretarsus, and the distribution of associated setal types, have been consistent in the salticids that I have examined in detail. With the exception of *Salticus*, however, all of these were members of a single subfamily, the Dendryphantinae.

Figure 17. Anterior view of ventral margin of the pretarsus of the left leg I of an adult male *Pelegrina* sp. Although the foot pads of this small dendryphantine spider carried a relatively small number of tenae when compared to *Phidippus*, the types of setae that were present, and their relative distribution, were comparable. Symbols: b, barbata or hamata cl, claw lever (note pleating), p, pilosa, s, spondyla, and t, tena associated with the anterior foot pad.

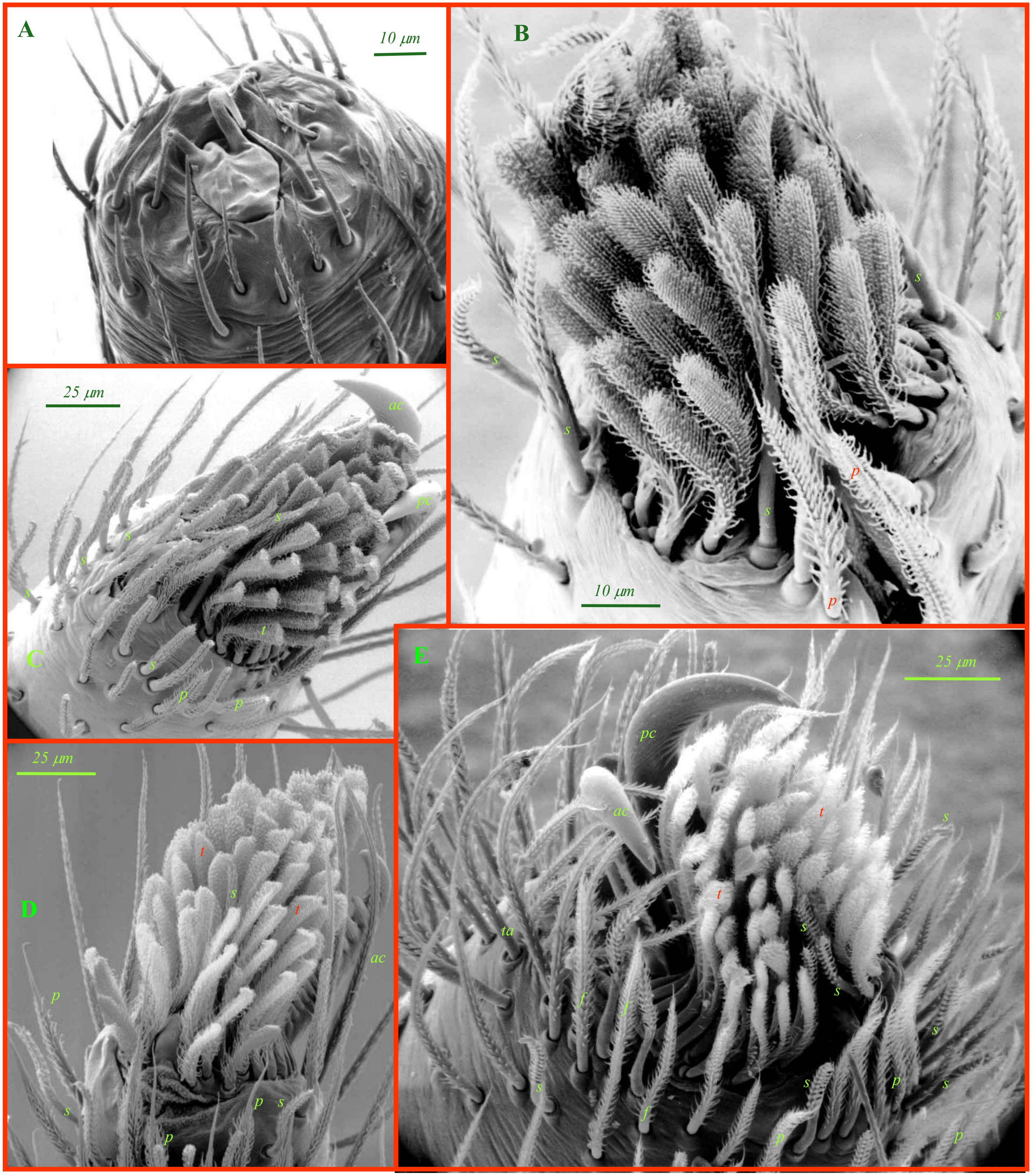


Figure 18. SEM views of the pretarsus of various salticids, all captured in the vicinity of Corvallis, Oregon. A: End of left leg I (LI) of first instar (*larval*) *Phidippus clarus*. The pretarsus was a distinctive segment at the end of the leg, but bears only a simple pair of hooks, and no foot pads. The diminuitive setae were not examined in detail. B: End of left leg I (LI) of second instar *P. clarus*. C: End of left leg I (LI) of adult male *Sassacus papenhoei*. Although scopulae (tracts of setae) were not present, insolated pilosae (p) were visible in this view. D: End of right leg IV (RIV) of adult male *Sassacus papenhoei*. Note the prominent pilosae (p) of the ventral tarsus, and the close spacing of teeth on the anterior claw(ac). E: End of left leg I (LI) of immature *Salticus scenicus*. Symbols: ac, anterior claw, f, fringila, p, pilosa, pc, posterior claw, s, spondyla, t, tena, ta, tactila.

Development of the feet

SEM views of the pretarsus of first instar and second instar *Phidippus clarus* are shown in Figure 18. Newly hatched first instars have a distinctive pretarsus bearing two simple claws without teeth, and no foot pads (A). The first instars use these simple claws to move about in the nest. After these spiders molt to the second instar, they are fully equipped to emerge from the nest with small foot pads, each bearing about 15 small tenae. Toothed claws and smaller numbers of other, smaller setae are also present.

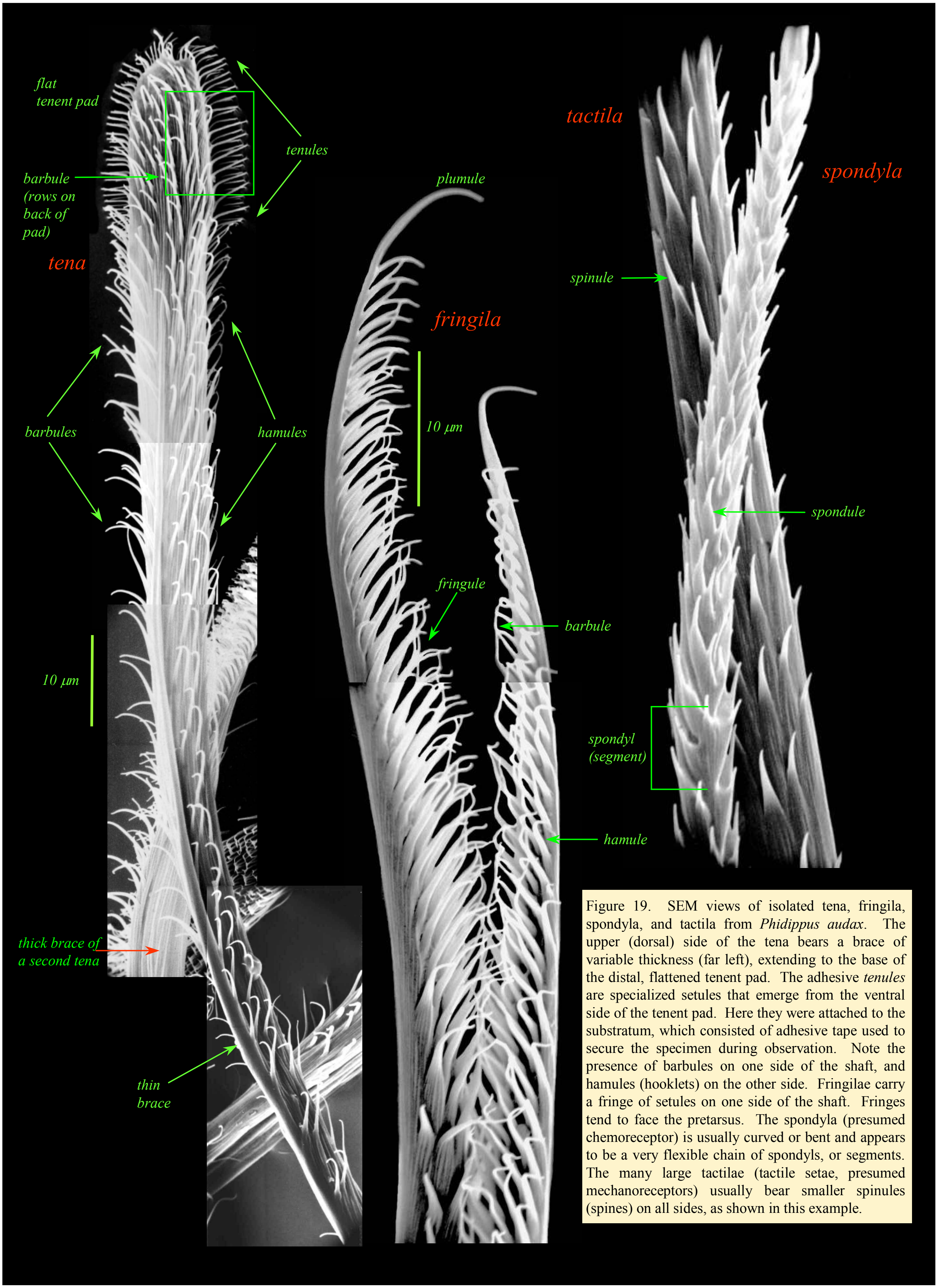


Figure 19. SEM views of isolated tena, fringila, spondyla, and tactila from *Phidippus audax*. The upper (dorsal) side of the tena bears a brace of variable thickness (far left), extending to the base of the distal, flattened tenent pad. The adhesive *tenules* are specialized setules that emerge from the ventral side of the tenent pad. Here they were attached to the substratum, which consisted of adhesive tape used to secure the specimen during observation. Note the presence of barbules on one side of the shaft, and hamules (hooklets) on the other side. Fringilae carry a fringe of setules on one side of the shaft. Fringes tend to face the pretarsus. The spondyla (presumed chemoreceptor) is usually curved or bent and appears to be a very flexible chain of spondyls, or segments. The many large tactilae (tactile setae, presumed mechanoreceptors) usually bear smaller spinules (spines) on all sides, as shown in this example.

The tena and its tenules

As noted previously, each foot pad consists of an array of tenae, or tenent setae, emerging from a movable plate. The anterior and posterior scopulae (tracts) of *Phidippus* are also comprised of isolated tenae that emerge from sockets in the tarsus.

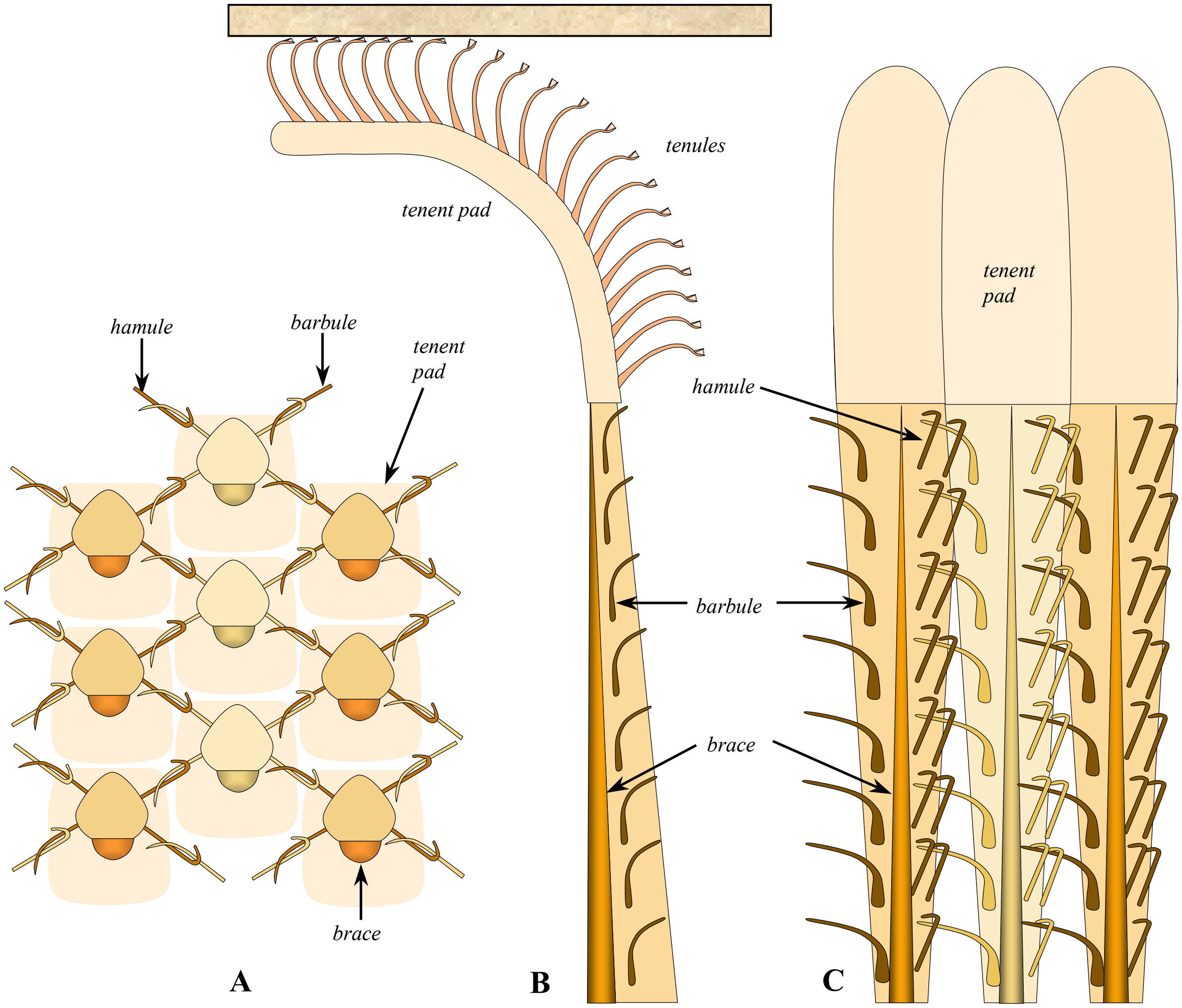
The tena shown in Figure 19 carried barbules on one side, and hamules (hooklets) on the other side. As shown in Figure 20, these allow a tena to interlock with adjacent tenae in the footpad, reinforcing the strength of the entire footpad as it is pushed against a surface, and also maintaining the regular spacing of the flattened tenent pads of the tenae (Figure 14).

The arrangement of barbules and hamules along the shaft of a *Phidippus* tena is very similar to the arrangement of *barbules* and *hooklets* with respect to each *barb* of a bird feather. The array of tenae is *three-dimensional*, however, whereas feather barbs are aligned in a single plane. Just as birds preen their feathers, salticids may also preen their foot pads and tenae (Figure 32D).

The apex of each tena is flattened into a tenent pad bearing many specialized adhesive *tenules* on one side. As convention, the side of the tena that bears these tenules and contacts the substratum will be called the *ventral* side, or the *underside*. Each tena is supported on its dorsal side by a *brace* of variable length and thickness. This brace terminates apically at the base of the flattened tenent pad, allowing that pad to be bent into a position parallel to a surface, as the foot pad is pressed against that surface (Figure 21).

Detailed SEM views of tenules on the underside of the tenent pads are shown in Figure 22. Tenules emerge from the tenent pad in alternating positions on linear, lengthwise rows on the ventral side of each tenent pad, thus forming a hexagonal array (Figures 22, 23).

Figure 20. Schematic views of tenae. A: Hypothetical cross section through the shafts of multiple tenae in a foot pad, showing how barbules and hamules of adjacent tenae could interlock to form a strong meshwork of mutually reinforcing setae, below the level of the tenent pads. This picture assumes that each tena attaches to two adjacent tenae on either side. It is also possible that each tena attaches to only one tena on either side, or that the pattern of attachment is much more variable, according to the specific position of a tena within a foot pad. Barbules may also serve as spacers, to maintain a minimum distance between adjacent tenae. B: Schematic view of tenent pad bending against a surface as the tenules are applied to that surface. C: dorsal schematic of three interlocked tenae.



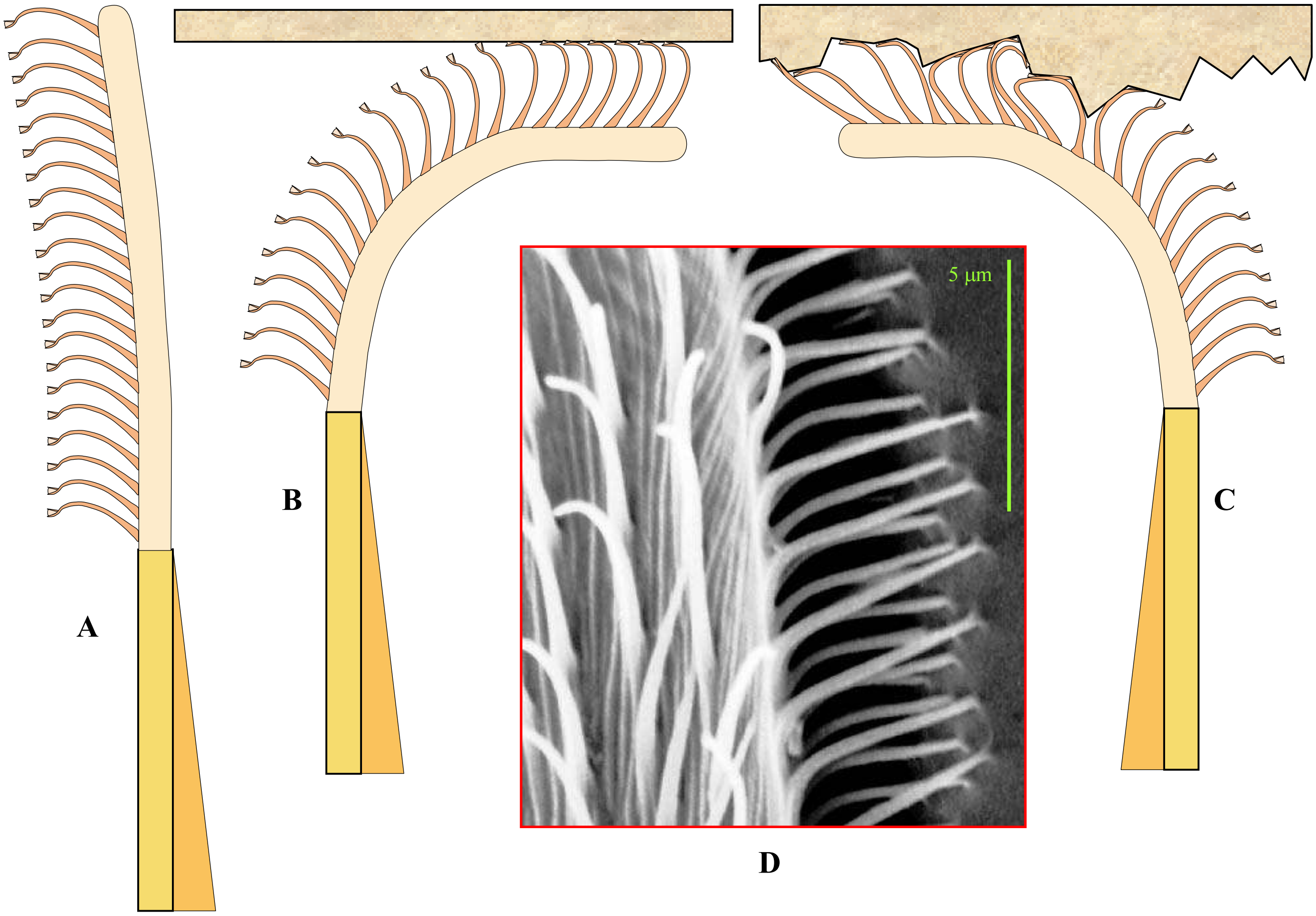


Figure 21. Application of the tenent pad and tenae to a surface. A: Schematic lateral view of the distal end of a tena. When not in use, the tenent pad can fold forward, bringing the recurved tenules on its underside closer to each other. B: Tena applied to a smooth surface. As shown here, the direction of application of the tenent pad to a surface suggests that the surface is usually contacted by the distal side of each tenule (the side toward the apex of the tena), but this is only hypothetical.. As shown here, the number of tenules that are actually brought into proximity with a surface depends on the extent to which the tenent pad is applied to that surface. C: Tena applied to an irregular surface. Depending on the flexibility and resilience of individual tenules, these may be able to fit into the interstices of an irregular surface, and may adhere on either side (proximal or distal) of the tenule, as shown here. D: Detail of tenent pad applied to a surface, from Figure 15. This is my best picture of tenules applies to a surface, although the fact that the surface in this case consisted of adhesive tape does not suggest a natural situation. This does show the ability of the tenules to bend, to stretch, or even to twist, and to thereby make contact with the surface at many points. From this view it is somewhat ambiguous whether the proximal or distal sides of the tenules are involved in this adhesion.

Adhesive capability of salticid tenules

As shown in Figure 22, each tenule narrows and then bifurcates near the apex, supporting a very thin membrane at its end. Recently Kesel, Martin, and Seidl (2003, 2004) studied the tenae and tenules of the salticid *Evarcha arcuata*. Their more recent publication (2004) contains updated numbers that will be cited here. By means of atomic force microscopy (AFM), they measured an average adhesive force (pull-off force) of ~41 nN per tenule. Related measurements, approximations, and calculations are summarized in Figure 24, with a comparison to *Phidippus audax*.

The comparison to *P. audax* was based on the theoretical scaling effect described in Figure 23C, as well as other considerations that are documented in Figure 24.

The large *safety factors* presented in Figure 24 may suggest that these spiders have far more adhesive capacity than they require, but this is not the case. There are many factors that may contribute to a jumping spider's need for more adhesive capacity, included those listed here:

[1] Even when walking under a smooth surface, many if not most of the legs are not in contact with a surface at the same time.

[2] Surfaces in nature are not ideal or smooth, and the ability of tenules to contact these surfaces varies greatly.

[3] The water film coating many surfaces, particularly under conditions of high humidity, may actually need to be pushed aside by the tenules to make close contact with a surface, if tenules are indeed hydrophobic.

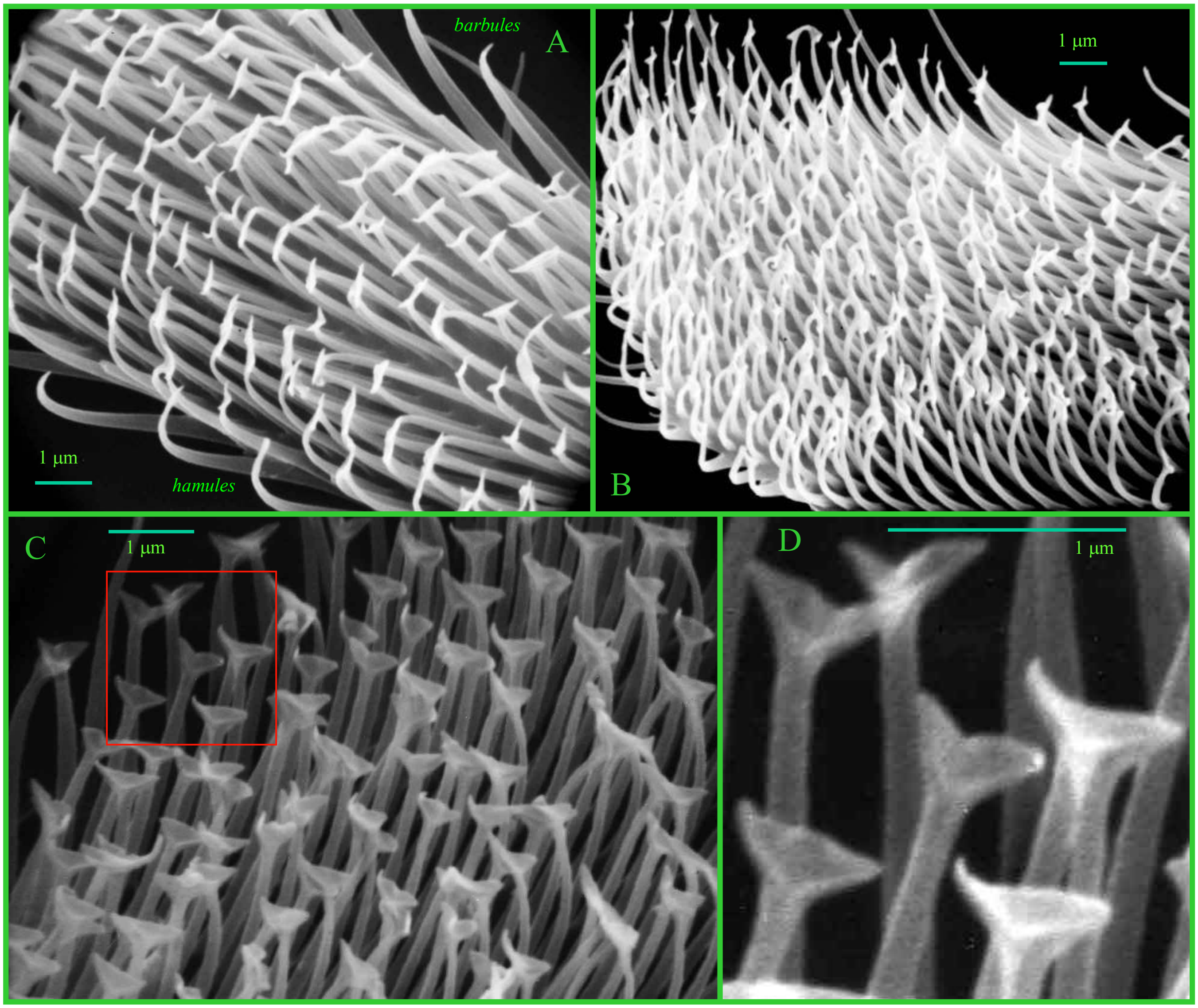


Figure 22. SEM views of the tenules associated with the underside of the the tenent pads of adult or near-adult *Phidippus audax*. The many tenules are recurved toward the base of the tena, bringing the triangular membrane at the end of each tenule into a near-perpendicular orientation with respect to the surface of the tenent pad. A: Lower portion of a tenent pad, showing lateral barbules and hamules. B: Widest, apical portion of a tenent pad. C: Detailed view of tenules, looking toward the apex of a tena (upper right). D: Detail of inset from (C), showing the narrow neck, bifurcation and connecting membrane at the apex of each tenule.

[4] Salticids do not appear to preload or press their foot pads against a surface to anything close to their full capacity, and the proximal or basal tenules may see very limited action.

[5] Even stationary salticid legs pivot and rotate as they are used to apply ground force by a moving salticid, exposing different sets of tenules, aligned in different planes with respect to the surface. As shown in Figure 14, anterior and posterior foot pads on each leg have different orientations, as do individual tenae.

[6] The weight of prey can greatly exceed the weight of the spider itself.

[7] Movement of the spider can greatly increase related forces and the tension on the legs.

[8] The legs of these spiders are seldom aligned with the force of gravity, and resulting tensions are much greater.

The last point is easily overlooked. Even when a spider is not moving, the resultant tension on the legs can greatly exceed the force of gravity. As shown in Figures 25 and 26, when a salticid is resting beneath a surface, both the ground force and the ground reaction force play on the tensile strength of the tenae and their tenules. It is likely that forces working to pull tenules from the surface often have a relatively small normal (perpendicular to the surface) component, as compared to a relatively large shear (parallel to the surface) component. Tensile force would be applied along the shaft of each tenule. All of the measurements of adhesion reported by Kesel et al (2003, 2004) were based on instrumental application of force *normal* to tenule membranes. The pull-off force that they measured for a tenule should correspond to the maximum tension that can be applied to a tenule shaft.

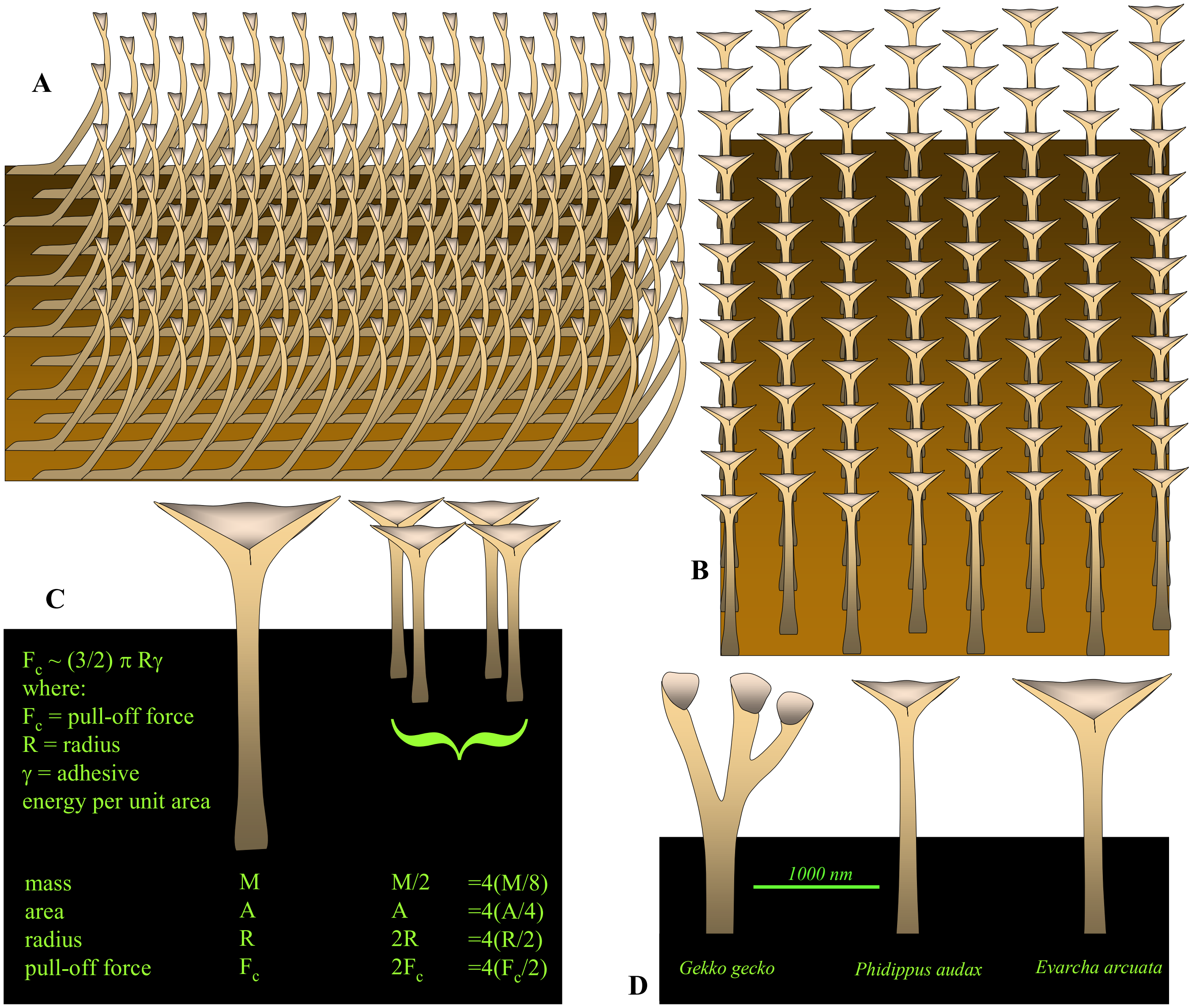


Figure 23. Schematic views of tenent pads and their associated tenules. A: As viewed from the side, tenules emerge from the surface of the tenent pad in alternating positions on parallel linear arrays, creating a space-filling, hexagonal pattern. When not in use, the apical membranes of the tenules are aligned in a position that is nearly perpendicular to the plane of the tenent pad. B: As seen in an end-on view, the regular array of triangular surfaces associated with the apices of the many tenules of a tenent pad does not fill all of the available area, but allows for some separation between the individual tenules. C: Comparison of the pull-off force (F_C) of one large tenule, with four tenules scaled to 1/2 of its linear dimensions, after Arzt, Gorb, and Spolenak (2003). Although the adhesive energy (pull-off energy, or energy required to separate a tenule from a surface) of a tenule is proportionate to its surface area, the pull-off force (or *force* required to pull the tenule from a surface) is proportionate to the linear dimensions of a small surface. Thus the four smaller tenules have twice the pull-off force of the single tenule. This *scaling effect* is thought to be responsible for the fact that larger animals that employ tenules tend to have smaller tenules than do smaller animals. D: Comparison of tenule surfaces of the Tokay Gecko (*spatulae* of *Gekko gecko,* based on Autumn, Sitti, et al 2002) with those of the salticid spiders *Phidippus audax* (either adult or near-adult) and *Evarcha arcuata* (based on Kesel, Martin, and Seidl 2003, 2004). The smaller size of the tenules of the much larger and heavier *P. audax*, when compared to those of *E. arcuata*, is consistent with the predicted *scaling effect*.

Some of these important points will be reviewed in a subsequent section, as part of a discussion on salticid movement.

Nature of the adhesive force (comparative studies)

Because of the relatively small size of these structures, Kesel, Martin, and Seidl (2003, 2004) suggested that *dry van der Waals* forces (effective within 2 nm) could be the source of their adhesion, but they could neither confirm this nor rule out a role for *wet* capillary forces.

Many studies related to the tenules of gecko lizards (Squamata, Gekkonidae, *Gekko gecko* in particular) have been published recently (e.g., Autumn, Sitti et al 2002, Autumn and Peattie 2002, Huber et al 2005, Autumn, Dittmore et al 2006, Autumn, Hseih et al, 2006, Autumn, Majedi et al 2006). The relatively small scale (~200 nm) of the adhesive surfaces (*spatulae*) of the branching tenent setae of these animals is shown in Figure 23D. These setae clearly represent convergent evolution with respect to the tenae of spiders, and it is very likely that they use the same adhesive mechanism.

	Evarcha arcuata	(source)	***Phidippus audax***	(source)
adhesive or pull-off force per tenule	41 nN	Kesel et al 2004	24 nN	application of *E. arcuata* results to scaling effect
area of tenule membrane	170,000 nm²	Kesel et al 2004	58,000 nm²	calculation assumes similarity of *E. arcuata* tenules
width of tenule membrane	1200 nm	based on measurement from photograph in Kesel et al 2004	700 nm	Hill 1978, and this study
estimated tenule count	624,000	Kesel et al 2004	1,500,000	new estimate, based on average of 250 tenae per foot pad, and 750 effective tenules per tena, not including scopulae
total adhesive or pull-off force, F_a	25.6 mN	Kesel et al 2004	36.0 mN	product of pull-off force per tenule and count of tenules
sotal contact area	0.106 mm²	Kesel et al 2004	0.087 mm²	product of area of setule membrane and count of tenules
tenacity or tensile strength (**Pa**scal=N/m²)	0.24 MPa	Kesel et al 2004	0.41 MPa	ratio of pull-off force to contact area
weight	15.1 mg	Kesel et al 2004	150 mg	based on Hill 2006
gravitational force, F_m	0.148 mN	product of weight and g = 980 cm/sec²	1.47 mN	product of weight and g = 980.7cm/sec²
safety factor	173	Kesel et al 2004	24	ratio of F_a to F_m

Figure 24. Comparison of estimated adhesion capabilities of *Evarcha arcuata* (based on Kesel et al 2004) with those of *Phidippus audax*. Sources for respective estimates are given in the table. All counts shown here need to be corroborated with more detailed studies. Based on photographs provided by Kesel et al, I would estimate that there are only about 40 tenae per foot pad in *E. arcuata*, and the larger size of the tenules also suggests that their density is much less than in *Phidippus*. Based on these considerations, the comparable count of effective tenules for *E. arcuata* could be much lower than the estimate shown here. In comparison, Roscoe and Walker (1991) found that *Salticus scenicus* only had about 211,000 tenules.

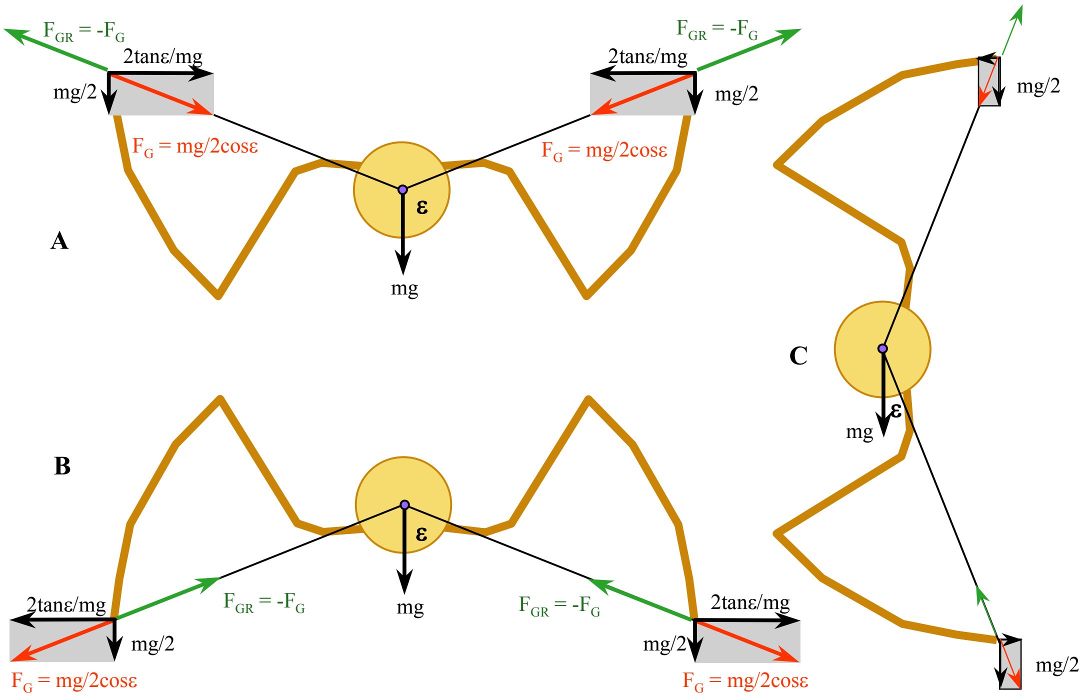


Figure 25. Schematic view of ground force (F_G) and ground reaction force (F_{GR}) on legs of a stationary spider. In this static view, the spider is supported on only two legs, one on either side of the body. Only net forces on the mass (yellow circle at center) and the extended, fixed legs (brown lines) are shown. Each leg is treated as a simple strut conveying ground force between the mass of the spider and the substratum. A: Standing upside-down, under a surface. When the spider is upside-down, the ground force is compressive (red vectors), and the equal and opposite ground reaction force (green vectors) is tensile, with respect to the legs. Note that the horizontal components of ground force are directed toward the spider. Because of this, the legs of a spider in this position that is losing its traction (substrate resistance to applied force) will move toward the spider. As a leg is moved closer to the spider, the horizontal component of ground force is reduced. B: Standing right side-up, on top of a surface. In this case, the ground force is tensile, and the ground reaction force is compressive, with respect to the legs. C: Standing sideways, on a vertical surface. The ground force on the uphill leg is compressive, and the ground force on the downhill leg is tensile. Movement involves additional application of compressive or tensile ground forces, in three dimensions.

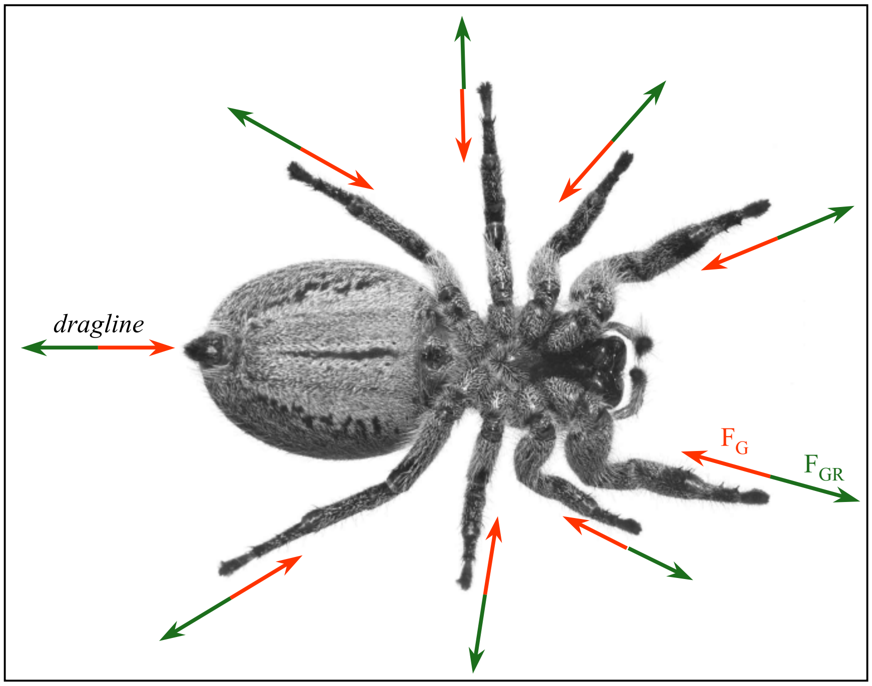


Figure 26. Photograph of adult female *Phidippus texanus* clinging to the underside of a horizontal glass plate with all eight claw tufts, as viewed from above. This is a relatively large and heavy salticid spider. Because the legs are close to horizontal in orientation, the ground force associated with the weight of this stationary spider (F_G, red vectors) is compressive with respect to the extended legs and also primarily horizontal (pointing somewhat into the page). Equal and opposite ground reaction forces (F_{GR}, green vectors) are tensile with respect to the extended legs, and also primarily horizontal (pointing somewhat out of the page). These tensions can greatly exceed the force of gravity, as shown in Figure 21. Note that the dragline force (red vector) also carries some of the weight of the spider, and is coupled with an equal and opposite dragline reaction force (green vector). The ground force is created by the spider pulling the substratum with the tenules of its tenent setae. The ground reaction force is created by the substratum pulling the spider through these tenules.

The question of whether the adhesion of gecko feet is based on *van der Waals* forces or capillary attraction has received a considerable amount of attention. *Van der Waals* forces constitute what is called a *dry* adhesion mechanism, as these forces depend only on the close proximity of molecules, and not on the intervening action of dipole moments associated with a thin molecular layer of H_2O (*capillary attraction*, whereby both surfaces are attracted to the water layer).

A strong argument has been developed for the role of *van der Waals* forces in gecko adhesion (Autumn, Sitti et al 2002, Liang et al 2000). Adhesion is impacted by the size and shape of the contact surfaces, and the small (200 nm) spatulae at the end of gecko tenules adhere equally to both hydrophobic and hydrophilic surfaces as long as these can be polarized. The β-keratin of gecko setae is hydrophobic. On the other hand, Huber et al (2005) more recently demonstrated that humidity significantly increased the pull-off force associated with single spatulae of geckos, and suggested that a monolayer of H_2O molecules on the surface could account for this effect. Sun et al (2005) also proposed that *capillary force* would be more important if surfaces were not smooth, or if the relative humidity were high.

It appears that only *van der Waals* forces are required to explain gecko adhesion, and dry adhesion is possible, but the presence of an H_2O monolayer on the surface might also increase the adhesion of the spatules of geckos. There are still many significant questions related to the theory behind both of these mechanisms. An H_2O dipole monolayer might actually facilitate adhesion, but a really wet surface of the kind that biologists usually associate with capillary attraction might interfere with adhesion.

More experiments, and development of related theory, will be necessary to further refine our view of salticid adhesion. The small size of the tenules is definitely consistent with the hypothesis of adhesion by means *van der Waals* forces acting at a distance of less than 2 nm. The fact that H_20 is present on many natural surfaces (Foelix 1996) does not by itself tell us whether this helps or hinders the action of individual tenules. The association of many different hydrophobic (essentially non-polar) lipids with the epicuticle of spiders and other arthropods (e.g., Hadley 1982, Gibbs 1998, Prouvost et al 1999, and Stratten et al 2004) also supports the *dry adhesion hypothesis*.

One of the most interesting features related to the sizing of these contact elements is the *scaling effect* (Figures 23, 24), whereby an increase in the pull-off force can be attained through subdivision of contact elements and surfaces into even smaller surfaces (Arzt et al 2003, Autumn, Sitti et al 2002, Gao and Yao 2004, Federle 2006). This is because the *linear* dimensions of small structures (near 100 nm), rather than their combined surface area, determine the pull-off force. The most satisfactory explanation for this effect lies in the idea that release of small elements is an all-or-nothing edge effect, and once it has started it rapidly proceeds to completion. The net result is that larger animals tend to have smaller contact elements. The observation that *Phidippus audax* have smaller tenules than do *Evarcha arcuata* is consistent with this hypothesis (Figures 23D, 24).

Of course, a smaller salticid could also simply have fewer tenae, or fewer tenules per tena. *Habronattus* have relatively large foot pads and claws, and *Lyssomanes* have relatively small foot pads and claws. The footpads and tenae of many more salticids need to be studied in detail before we can draw any conclusions with respect to the relative roles of tenule size and the number of tenules or tenent setae in a foot pad.

Many other concepts that may be applicable to the Salticidae have emerged from studies of gecko adhesion. For example, the action of pulling the legs toward the midline may be important in the *preloading* of the spatulae, or the positioning of the gecko spatulae close to a surface (Autumn, Hsieh et al 2006). From direct observation it is known that salticid tenules are similarly preloaded as the spider pushes them *into* or *onto* a surface, bending the tenae to bring a greater portion of the ventral surface of the tenent pad into proximity with a surface (Hill 1978). The tenae are braced on the dorsal side, and thus a *very small* movement of the foot pads in a proximal direction *may* accompany this preloading process, but this movement is too small to observe directly. Autumn and Peattie (2002) found that a very small preload force applied normally, followed by a very small (~5 μm) displacement of the spatulae parallel to the surface, greatly increased their attachment. Stalks of the spatulae, like the tenae, are naturally recurved in a resting state. In any case, when salticid foot pads are pressed against a surface, the tenent pads of the tenae can bend, bringing more tenules into proximity with that surface.

Per Autumn, Majidi et al (2006), with reference to gecko foot pads, *setal arrays function as a bed of springs with a directional stiffness, assisting alignment of the adhesive spatular tips with the contact surface during shear loading.* This descriptive statement could just as well apply to the foot pads of salticids.

Salticids can be observed to pull their legs toward their center of gravity when losing traction on a surface. Although this exaggerated movement looks like a form of preloading as described for gecko setae, it is really a result of the tension that normally exists on the legs of a suspended salticid. The diagram in Figure 25A shows how the tension associated with gravitational force tends to pull the outstretched legs of an upside-down spider toward the center of gravity, also reducing the amount of tension in the process. In effect, the suspended spider is pulling the surface toward its center of gravity with its legs (ground force), at the same time that the surface pulls its legs away from that center of gravity (equal and opposite ground reaction force). As shown in Figure 25C, only the elevated legs of a salticid on a vertical surface tend to be pulled toward the center of gravity when it slips.

Adhesion of gecko spatulae is directional, and since these structures are relatively small, removal of one subset at a time may require a relatively small force (Autumn et al 2000). Whereas adhesion may be accomplished through *strength in numbers*, release could be accomplished just as readily through a *divide and conquer* approach. Relatively small changes in the angle of application of the spatulae of geckos to a surface may substantially reduce the pull-off (detachment) force, enabling their rapid release (Autumn, Dittmore et al 2006).

It is possible that the rotation of the pretarsal mechanism (Figure 6), including the normal movement of the pretarsal levator and the pretarsal depressor during leg movement, also facilitates the adhesion and subsequent release of the footpads of salticids. This is an attractive hypothesis, but it remains to be demonstrated. From direct observation, it appears that salticids simply place their feet on a surface, pivot them in place as they exert ground force, and then lift them off with no special effort, as they walk. One might expect that the foot pads would be removed from the surface prior to execution of a jump, but even the foot pads of legs IV that provide forward propulsion to *Phidippus* during a jump remain firmly planted on the surface until they leave that surface in flight (Figure 10, also see Hill 2006).

Hansen and Autumn (2005) described how gecko spatulae clean themselves as a gecko walks, essentially removing obstructing particles through exclusion as they selectively bond to the substratum. The same mechanism may apply to salticid tenules. I do not know if geckos actually preen or clean their feet, but salticids do, by placing their feet in their mouth (Figure 32D).

The pilosae

The ventral scopulae that may be prominent on the distal tarsi of legs I and II of *Phidippus* (Figures 2B, 14) are comprised of a unique kind of seta, the *pilosa* (Figures 27, 28D). Pilosae are broad and compressed in the direction of the long axis of the tarsus, and they are aligned in a distal direction somewhat parallel to that axis. Each pilosa bears a relatively long apical plume. The proximal side, or underside, of each pilosa bears a regular, hexagonal or space-filling array formed by alternating longitudinal rows of s-shaped setules, the *tinules* (tines). Unlike *tenules*, tinules do not bifurcate or bear a thin, adhesive membrane at the tip. Instead, they form a carpet of hooks that can be pressed against a surface.

As shown in Figure 17 and 18, even when an extensive scopular tract of pilosae is not present, isolated groups of pilosae can still be found on the distal-ventral tarsus of many salticids, including *Salticus scenicus*. Their occurrence and position suggests that these distinctive setae play a very important role in *catching something*. One possibility is that they are used to wind up silk as a salticid climbs a vertical silk line rapidly with legs I and II, with legs III and IV outstretched. The role in handling silk is supported by the orientation of the tinules, which would also support rapid release of that silk. Another possibility is that they are used to grasp an irregular or spinous surface (or prey) that would limit the effective use of the tenae. There has been some interest in the effectiveness of microspine arrays in securing a foothold on a surface (Asbeck et al 2005), but the orientation of the tinules (pointing in a distal direction) does not support this hypothesis.

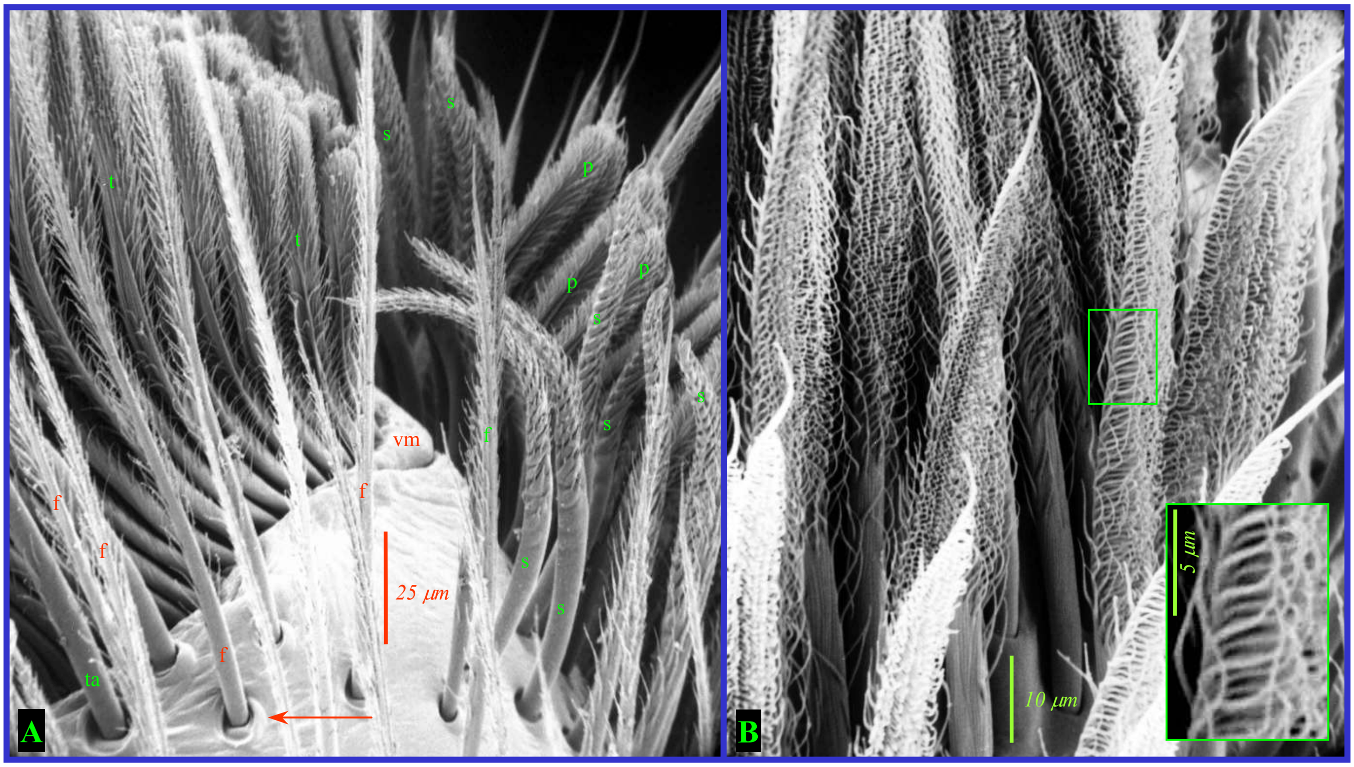


Figure 27. Two SEM views of setae associated with the distal tarsus of an immature *Phidippus audax*, from exuviae. A: Ventral margin (vm) of distal tarsus. Note the curved spondylae (s), which appear to be very flexible and to bend in response to gravity. These are presumed contact chemoreceptors, with several associated mechanoreceptor neurites. The plumed, flattened pilosae (p) comprise a mid-ventral scopular tract. The visible tenae (t) of the pretarsal foot pad are braced against lateral bending. Both the fringilae (f) and the tactilae (ta) emerge from enlarged sockets that support movement, and are presumed mechanoreceptors. Long setules (fringules) borne by the fringilae face toward the pretarsus. B: Detail of ventral scopular tract of pilosae, as seen from the proximal side that contacts the substrate. The inset detail shows the regular, alternating rows of s-shaped tinules (tines) that comprise a shape-filing hexagonal array of these hook-like structures.

As with many other setae of the legs, *Phidippus* often rest their pilosae against surfaces or leaf edges as they move. As important as the pilosae appear to be, the adaptive value of their unique structure for a salticid remains to be demonstrated conclusively.

The spondylae

Previously (Hill 1977a) I called these *whorled setae*. The term spondylae is more descriptive, as it refers to the similarly of each spondyla to a vertebral column (Figures 19, 27A, 28, 29). If these setae are as flexible as they look, then they also represent a form of convergent evolution with the vertebrae of vertebrates, to achieve both strength and flexibility.

Several of these setae usually extend between the foot pads (Figures 14, 28C). They can also be found in considerable numbers on the distal tarsus, usually in a ventral orientation. These are abundant in the *apical pits* of salticid pedipalps (Hill 1977b).

I have not been able to find any additional studies of this presumed chemosensory role in *salticid* spiders.

Anatomic and electrophysiological studies of similar setae in other spider families (Foelix 1970a, Foelix and Chu-Wang 1973b, Harris and Mill 1973, Drewes and Bernard 1976) have demonstrated the presence of many chemosensory neurites associated with an open pore at the tip of the apical cone of each spondyla (see Figure 28C), as well as several mechanoreceptors.

Other setae

Fringilae of the distal tarsus bear fringes of setules on the side facing the pretarsus (Figures 19, 27A). The numerous *tactilae* are larger setae (Figures 19, 29). The *barbatae* are covered with a dense array of barbules, and the *hamatae* are covered with a dense array of hamules or hooklets (Figure 29). All of these may be mechanoreceptors based on deflection at the base (Foelix and Chu-Wang 1973a, Barth 2004).

A preliminary or working catalog of the setae and setules of salticids is presented in Figures 30-31. This is far from complete at the present time.

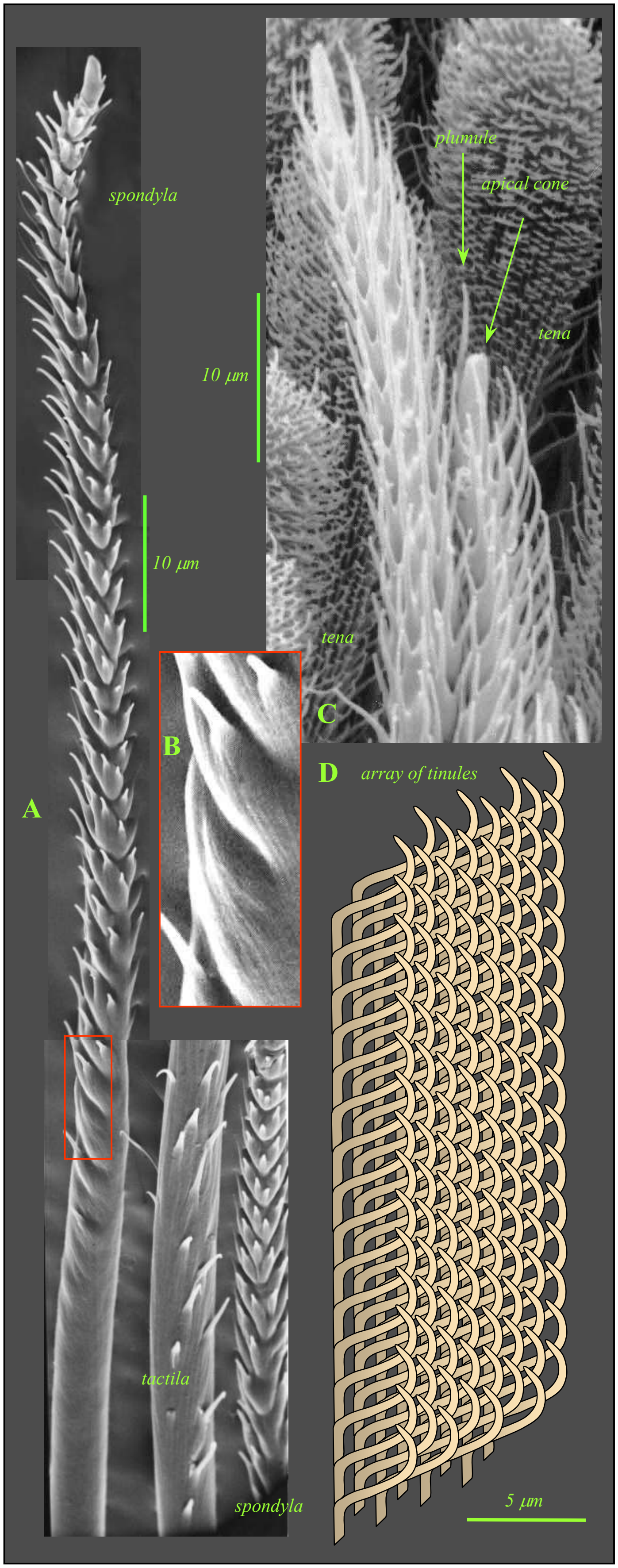
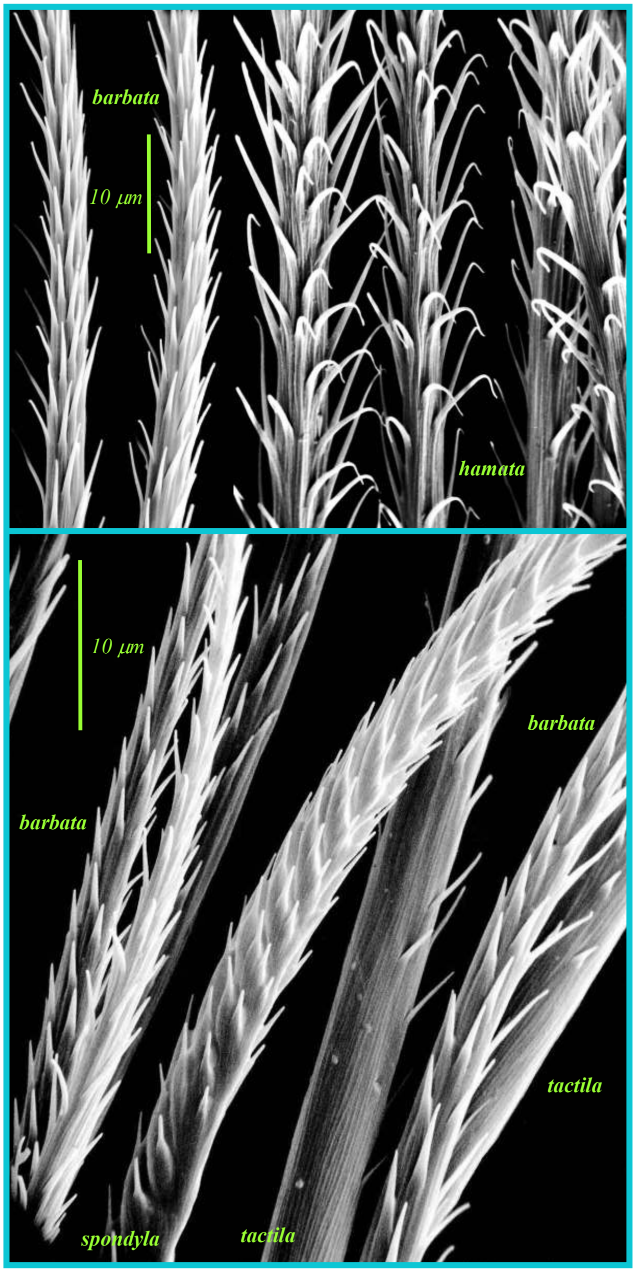


Figure 28. (left) Distinctive setae associated with the distal tarsus of *Phidippus*. A: SEM montage of distal portion of a spondyla from the exuvium of an immature *Phidippus* audax. Regular, repeating segments or *spondyls* of the distal portion of these setae resemble vertebrae and are presumably flexible in the same manner. B: Detail of inset from A, showing texture of surface. C: Detail of spondules between foot pads of leg I of an adult male *P. audax*, from inset depicted in Figure 14 (D). A pore at the end of each apical cone is presumably associated with multiple chemosensory neurites. Each spondyla usually bears an apical *plumule* or plume. D: Schematic diagram of tinule array associated with the proximal side of the flattened pilosae. Each pilosa of the ventral tarsus is aligned in a distal direction, and this represents the side of the pilosa that contacts a surface when the distal tarsus is applied to that surface.

Figure 29. (below) Setae associated with the distal tarsus of *Phidippus audax*, from exuviae of immature spiders. Tactilae (presumed mechanoreceptors) are larger setae with relatively few setules, or shorter scale-like setules. Barbatae bear a regular, repeating array of uniform barbules on all sides. Hamatae similarly carry a fairly regular array of hamules, or hooks, on all sides.



seta	common name	description	location
barbata	barbed seta	smaller seta with dense array of uniform, medium length barbules, otherwise similar to tactila in form	unknown distribution
fringila	fringed seta	small to medium seta with barbules, hamules, or fringules facing one direction, also bearing an apical plumule; oval socket membrane indicative of directional mechanosensory function	when present, on distal tarsus facing the pretarsus with movement at base in direction of pretarsus
hamata	hooked seta, filamentous seta	smaller seta bearing many hamules (hooklets) on more than one side; may also bear barbules that can interlock with hooklets on adjacent setae	unknown distribution
macroseta	spine, bristle, seta	Much thicker and heavier than any other setae, either blunt or sharply pointed but always tapering and covered with a uniform distribution of small spinules; used as weapon of both attack and defense	per species each macroseta occupies a specific location on the legs, such as the ventral metatarsus, or the dorsal, distal femur
pilosa	pilose seta, plume seta	large, flattened seta bearing dense array of tinules (tines) on one side, with distinctive apical plumule	when present, a cluster of these distinctive setae often form a ventral scopula, most often on leg I
scala	scale seta, scale	small to large setae with shaft angled at socket to lie flat against surface of body; highly variable in form and often flattened	can be found in various forms and colors on most of the legs and body; always pointing toward direction of molt
spondyla	spondylous seta, whorled seta, chemosensory seta	flexible chemosensory seta with smooth surface proximally leading to series of repeating links resembling vertebrae (spondyls); distal end bears a characteristic cone with apical pore, as well as a terminal plume (plumule) that can prevent direct contact of the pore with the substratum	in small groups or singly on the distal tarsus around the pretarsus and near spinnerets; can be abundant distally on pedipalps, particularly in males
tactila	tactile seta	small to very large uniform, gradually tapering seta, usually bearing shorter spines or barbules; flexible socket membrane within larger socket surrounds the shaft	found all over the body and legs of the spider; large and prominent on dorsum of body and legs
tena	tenent seta lamelliform seta	Medium to large distally flattened setae bearing dense array of tenules (flexible tenent pad) on one side; shaft bears a characteristic brace (strut or buttress) on the side opposite the tenent pad which varies greatly in thickness but resists flexion of the seta below the level of the broad, flattened tenent pad	emerge from pretarsal plates as claw tufts; also may be present on distal tarsus as anterior and posterior scopulae, most often on leg I

Figure 30. (above) Working classification of known salticid setae.

Lamelliform setae in other spider families

The foot pads of clubionids and anyphaenids bear lamelliform setae similar to salticid tenae, but their setules terminate in blunt knobs (Platnick and Lau 1975). Setules of the lamelliform setae of the gnaphosid *Callilepis* are simple barbs (Platnick 1975). Perez-Miles (1994) observed differentiation between anterior, posterior, and ventral tracts of scopular setae in theraphosids, but the setules of these setae were not expanded into distal adhesive membranes, as they are in the Salticidae.

The tenae and tenules of the philodromid *Philodromus aureolus*, as figured by Foelix (1996), are very similar to those of salticids. Tenules ("scopula hairs") of the wolf spider *Lycosa punctulata* were also figured by Foelix, and these are also arranged in a space-filling hexagonal array. Foelix described these as "lacking" typical end feet, but his figure clearly depicts a very small triangular process at the end of each tenule.

setule	common name	description	occurrence
barbule	barb	medium to long process that curves uniformly away from the shaft of a seta, often with less than 90° of total curvature; often not regular or densely packed	found to some extent on many different setae
fringule	fringe setule	wider multithreaded processes that divide into two or more separate processes toward the apex	may be present on fringila, between lateral barbules and hamules
hamule	hook or hooklet	process that is relatively straight but then curves sharply, often more than 90°, near the distal end to form a hook; can interlock with barbules	densely packed on hamata when these occur; may also be found on one side of a tenent seta, capable of interlocking with barbules on an adjacent seta
plumule	filament	apical process of variable length at the distal end of a setae, often very long	very long and distinctive on pilosa, fringila, and spondyla
spinule	microspine, spine	shorter process that can be almost triangular in shape, often adnate or parallel to the shaft of the seta	uniformly distributed on macroseta and tactila, often near the base on other setae; also frequently found under scales, or along the margins of scales
spondule	barb	regular process of variable length occupying a specific position and occurring at repeated intervals along the shaft of a seta	only found on spondyla, appearing in a repeating pattern on each spondyl (segment or link)
tenule	bifid filament	fine, recurved and regular process that tapers to a narrow neck and then bifurcates to two sharp points connected by a thin triangular membrane at the apex	only found on the flattened tenent pad of the tena, where they occur in a dense and regular hexagonal array formed by regular and alternating placement on adjacent, longitudinal tenule rows
tinule	tine decurrent filament	sinuous and regular process of medium and fairly uniform length that is recurved at the base then curves back in the direction of the shaft of the seta; similar to tenule but does not bifurcate and does not bear a thin membrane at the apex	found densely packed on one side of fringila if this occurs, but most notably in a regular hexagonal array formed by regular and alternating placement on adjacent, longitudinal tinule rows of the pilosa

Figure 31. Working classification of salticid setules.

Direct observations related to use of the feet

In addition to their use in locomotion, salticids also use their feet to hold prey, to hold their mates, and to groom (Figure 32). Examples of the use of the feet during movement by adult *Phidippus pulcherrimus* are given in Figures 33-36. The use of the claws to handle silk lines under tension can be seen clearly in Figures 33A and 36. Claws can also be used with the foot pads to secure a hold on the edge of a leaf (Figures 34B, 35).

Figure 34A also shows the application of the ventral scopula to a leaf. RIII in Figure 33B, and RIV in Figure 34A show how far the foot pads can be extended to hold a leaf or twig. Figure 33B, in particular, provides a very good view of the manner in which these spiders can secure themselves with *ground force* applied to a twig or stem to support application of *dragline force* in the opposite direction, particularly when securing a dragline. Dragline force is defined as the force or tension applied by the spider to a dragline. In turn, the dragline applies ground force to the surface to which it is attached, and dragline reaction force to the spider (Hill 2006).

The opposition of ground forces (e.g., LII and RIV on opposite sides of a twig) in Figure 34B provides a good example of the manner by which these spiders balance themselves when walking on complex structures.

Role of foot pads during turns

Land (1971, 1972) previously described the walking or stepping patterns of salticids. In his experiments, spiders were affixed to an apparatus by their carapace, and their legs were free to move as they held and turned a light-weight paper ring. As Land noted, the resulting load or moment of inertia associated with turning in this experiment was about 27 times the normal value for untethered spiders. At the same time, the accuracy of turns that were observed demonstrated clearly that these spiders do not determine how far they turn by measuring the energy that they exert through the application of ground force, but must instead rely on a sense of leg position or the extent of leg movement.

At the same time, the leg positions required to hold a ring, and the forces associated with the legs and feet as they held a ring, were different from those associated with walking on a surface. Since the ring moved as the spider turned, it did not provide the ground *resistance* that a spider would encounter in a normal situation. One result of this was that turns were measured as stepping movements, when in fact many turns that require the exertion of ground force against resistance do not involve any stepping movements. Salticids can *pivot* in place (Figures 37, 38).

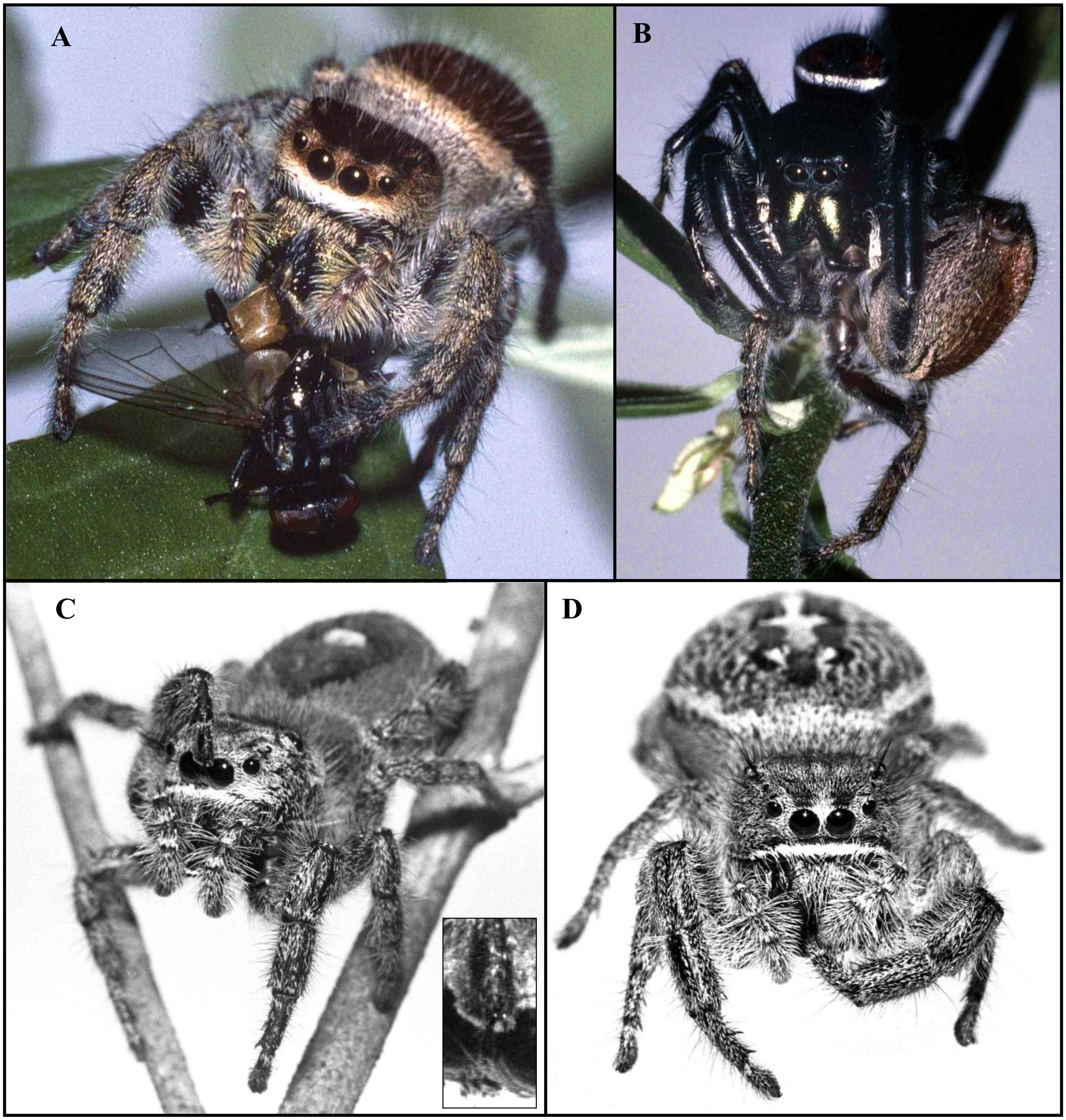


Figure 32. Some non-locomotory applications of feet by *Phidippus* jumping spiders. A: Adult female *P. clarus* from Florida holding its prey securely during feeding. Foot pads associated with LI were applied directly to the smooth thorax of this fly. B. Male *P. clarus* from Florida holding a female *P. clarus* with legs I during mating. Note the use of foot pads by the female to maintain a hold on the stem. C: Adult female *P. pulcherrimus* from Florida rubbing between the anterior medial eyes (AME) with what appears to be the ventral scopula (see detail in inset) of RI. During grooming, legs are often used to rub other legs. Specialized setae on the inside of each pedipalp are also used to clean the cornea of each eye (Hill 1977b). D: Adult female *P. texanus* grooming the end of LI with its mouthparts. Each leg can be groomed in this manner, in turn. This represents the most frequently observed grooming behavior of *Phidippus* and many other salticids, including *Lyssomanes viridis*.

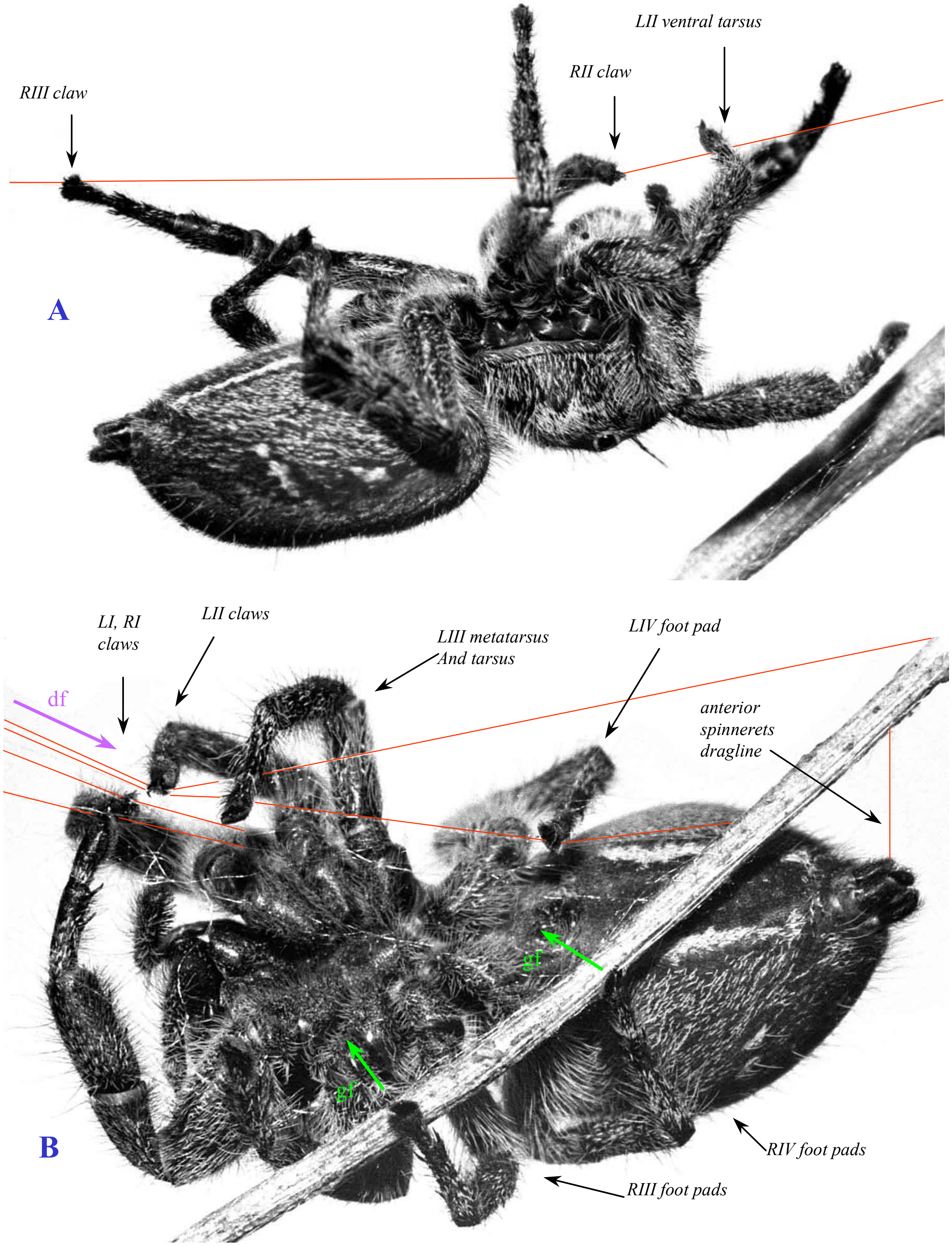


Figure 33. Use of claws, foot pads, and legs by a moving adult female *Phidippus pulcherrimus* hanging from silk lines. Silk lines that were captured on film are marked with red lines. A. Hanging upside down during traverse of an attached dragline. At this point the spider was supported by claws of right legs II and III (RII and RIII, respectively), and by a hold on the line by the ventral tarsus of left leg II. B. Grasping silk lines at the start of a traverse. Claws of legs I and II engaged the lines directly, as right legs III and IV were held firmly against the *opposite* side of the small twig (gf, ground force) to support the equal and opposite dragline force (df) exerted by the spider as it pulled on the draglines. At this point he foot pad of leg IV was also pushing on a silk line. The taut dragline released by the anterior spinnerets may have also provided some support for the weight of the telsoma (opisthosoma). Note how the extended and separated foot pads of RIII spread out laterally.

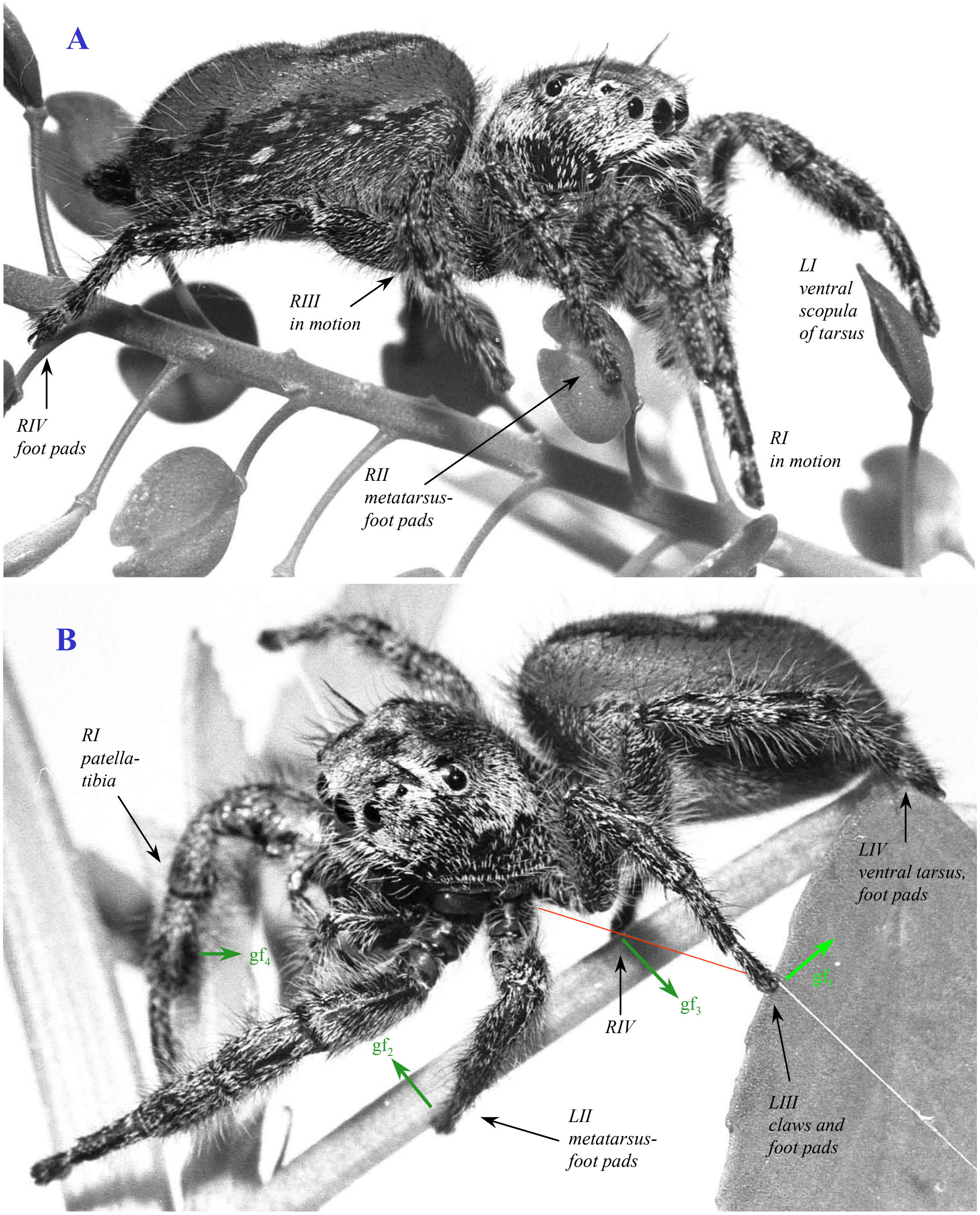


Figure 34. Examples of the use of foot pads, claws, and legs by an adult female *Phidippus pulcherrimus* moving rapidly on top of plant structures. A: Simultaneous movement of alternating legs by the rapidly moving spider. B: Spider crossing a silk line during rapid movement. The line did not provide support, but was pushed back by LIII (gf_1 exerted against the line and the leaflet) as shown here. Note the use of the ventral tarsus (LIV) for support. Opposing ground forces (gf_2 with LII and gf_3 with RIV) gave this spider a secure grasp of this leaf petiole. Leg RI (patella to tibia) rested against a small vertical leaflet, in position to provide thrust (gf_4) during continued forward movement.

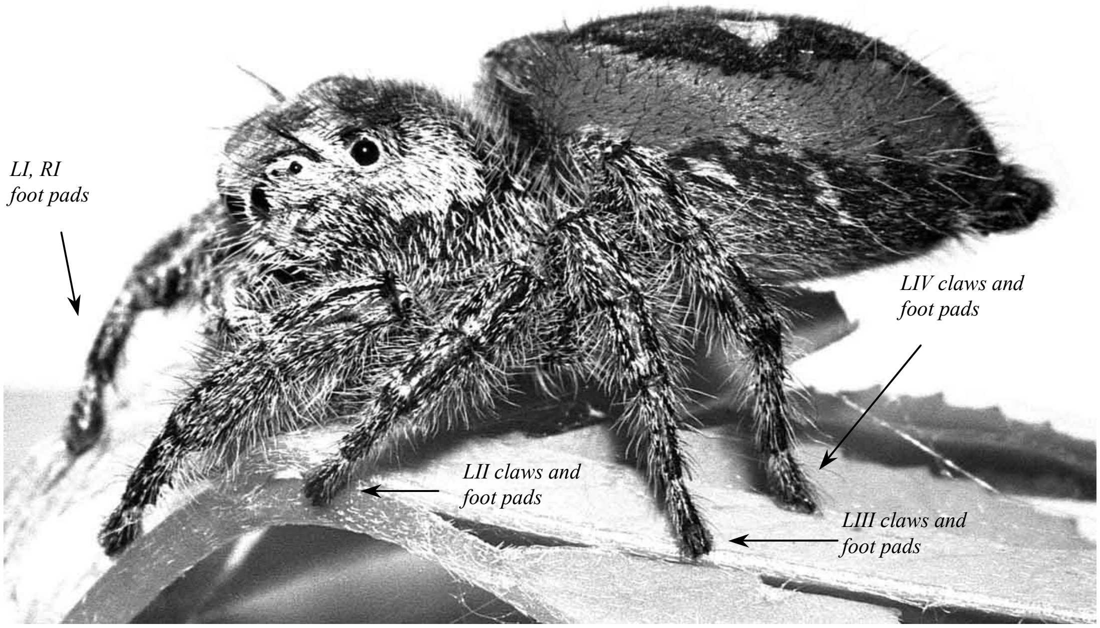


Figure 35. Use of claws and foot pads by an adult female *Phidippus pulcherrimus* resting on top of a leaf cluster. The edges of leaves and other structures were frequently grasped with the claws as shown here, even when the foot pads were also applied to the surface.

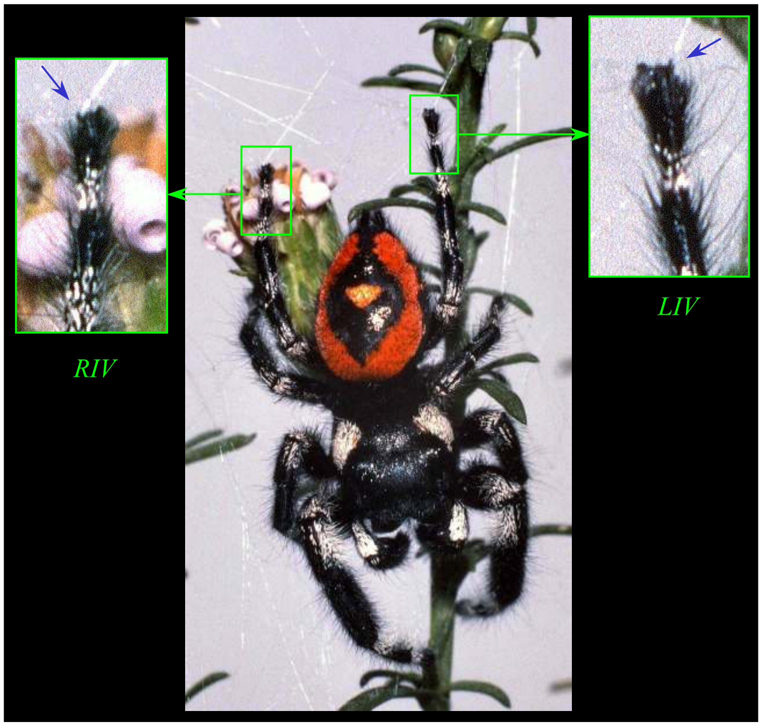


Figure 36. Adult male *Phidippus pulcherrimus* suspended from a skein of silk draglines. Inset detail shows how the claws of legs IV held these silk lines under tension.

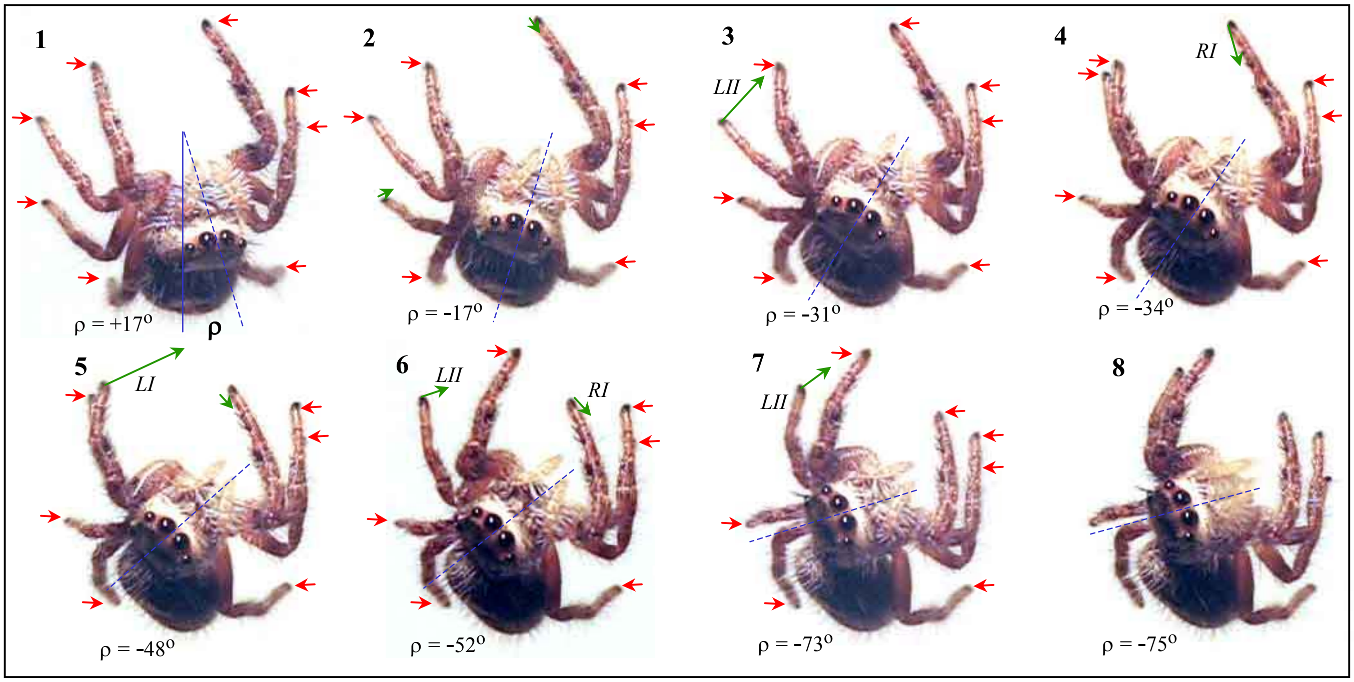


Figure 37. Completion of a series of ρ turns (Hill 2006) by an immature *Phidippus princeps* on a vertical surface, as seen from above. Serial frames 1-8 were taken from a motion picture of these turns, as the spider attempted to maintain its alignment with the visual surround as it was rotated. To record these pictures, the spider, the camera, and a transparent, vertical plastic substratum were rotated together. Note that considerable repositioning or pivoting of the foot pads took place with respect to the surface during these turns, but very few steps were taken (green arrows). As a convention, stationary feet are identified in each frame with a short red arrow, and each movement vector is drawn with a green arrow.

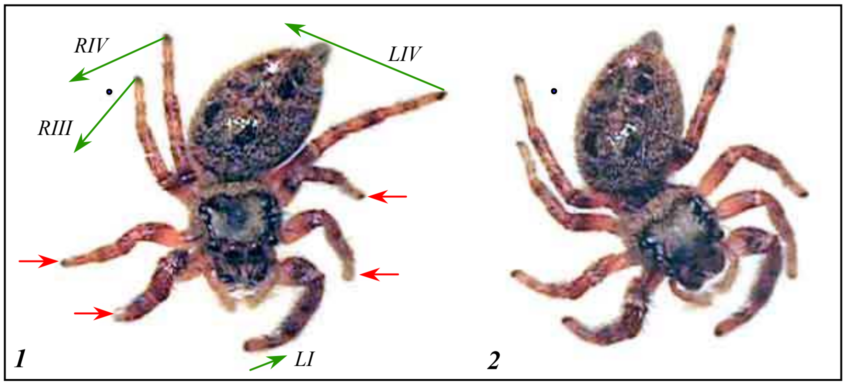


Figure 38. Completion of an α turn (Hill 2006) by an immature *P. princeps*. Three of the hind legs were taken off of the surface and moved simultaneously to complete this turn (green movement vectors). A net clockwise ground force (torque) was exerted through the four footpads that pivoted in place (red arrows), to support counter-clockwise movement of this spider. Resistance of the substratum was required to generate the net counter-clockwise ground reaction force (torque). In a real-life situation, the relationship of stepping movements to pivoting movements depends greatly on the proximity and orientation of available surfaces in a complex structural environment. When the spider is on a vertical (or upside-down) surface, continued attachment by means of the foot pads, as they exert ground force, is required.

Examples of turns completed by *Phidippus* on the underside of a smooth, plastic surface are shown in Figures 39-42. Alternation of legs on opposite sides of the body was fairly loose. Land previously described how spiders generally moved legs on opposite sides of the body in different directions during these turns (forward on one side, and backward on the other side), although each turn may be better described in terms of movement of some or all of the legs in either a clockwise, or a counter-clockwise direction. Spiders were careful to maintain a foothold on the surface during these turns, and rarely fell off of a surface. As shown in Figure 42, when holding a large prey item, a *Phidippus* would either move one leg at a time, or they would slide their foot pads on the smooth surface, to maintain this attachment. After falling off of this surface, a spider rapidly regained its position by climbing *backwards* up the dragline with the hind legs, holding the prey with legs I and II. It then rapidly attached the dragline, and then each of the two legs IV in succession.

In a real-life situation, it is expected that the sequence of leg movement during a turn would depend greatly on the relationship of the feet to a number of different, more complex plant surfaces. During each turn, the alignment of each foot pad applied to the surface changes considerably as the spider pivots. As discussed previously, much of the observed flexibility with respect to the application of foot pads to a surface is the result of their extension. An additional degree of flexibility is attained by pivoting from the posterior to the anterior foot pad as the leg is moved from front to rear. Supplemental anterior and posterior scopulae comprised of tenae (Figure 2B) also allow the front legs to attach when they are in a more sideways or laterigrade orientation with respect to a surface.

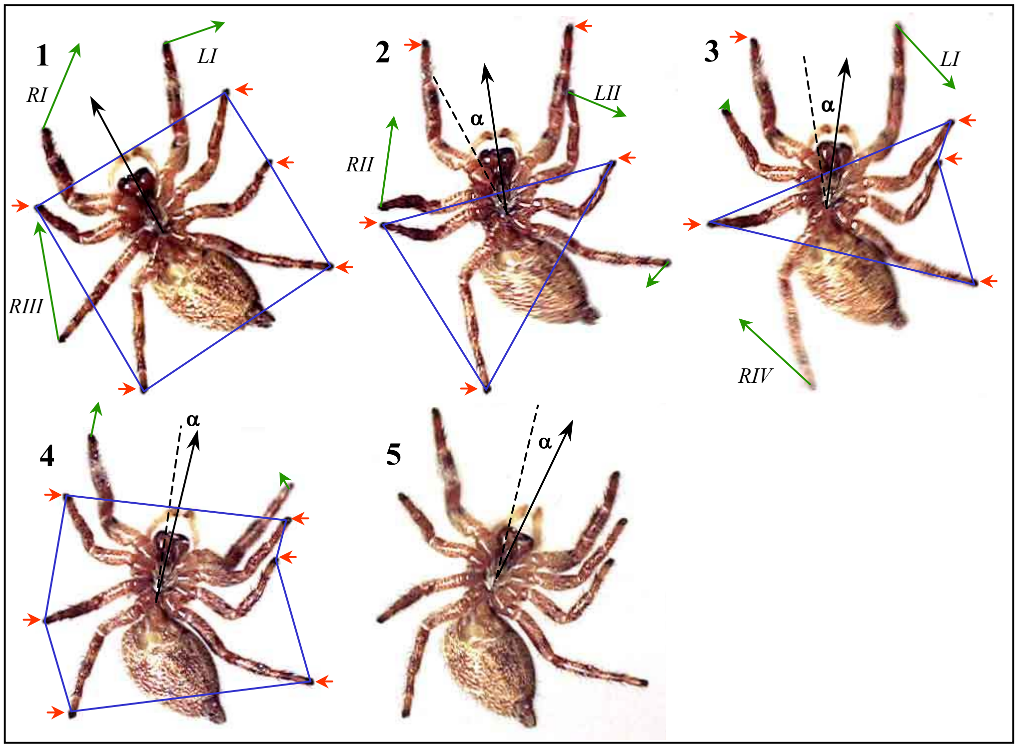


Figure 39. (above) α turn by an immature *Phidippus princeps* on the underside of a clear plastic surface, as viewed from above. Each frame of this motion picture was selected to depict the end of one step of this turn. The balanced platform of attachment and suspension from the surface is depicted in each case as a blue polygon connecting the feet that did not change position during the subsequent step. All legs shown as moving in a single frame were moving at the same time. Note that ground force for this rotation was delivered through the legs that did not change position during each step. LIII was not moved, and LIV was only moved a small distance (2), during this turn. Movement from (4) to (5) involved a pivot of the legs, and only slight movement of legs I as they were held away from the surface.

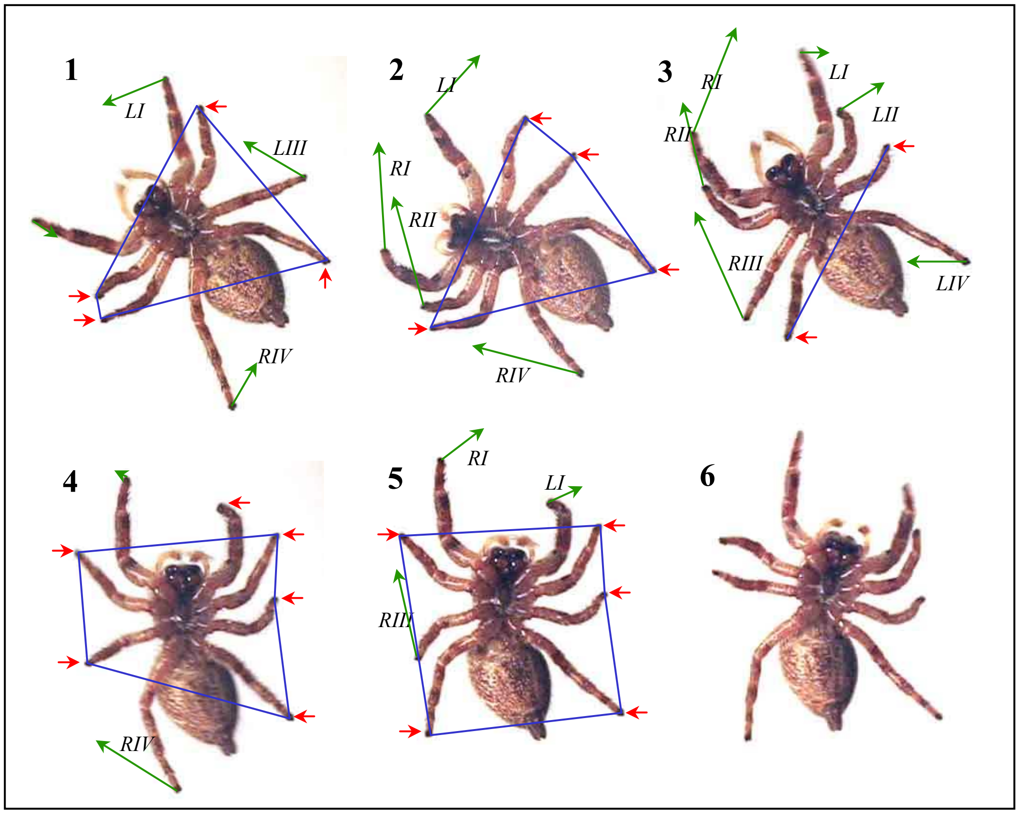


Figure 40. Two sequential α turns by an immature *Phidippus princeps* on the underside of a clear plastic surface, as viewed from above. The first turn (counter-clockwise, from 1 to 2) involved a single step and the simultaneous movement of three legs. The second turn (clockwise, from 2 to 6) required four steps. Note that LIII did not move during the second turn. The attached dragline contributed to the stability of this spider as it moved from position (3).

Figure 41. Two sequential α turns in the same direction by an immature *Phidippus princeps* on the underside of a clear plastic surface, as viewed from above. Each turn (1-3, above, and 3-5, below) was executed in two discrete steps. This spider paused at position (3) between the two turns. Steps did not follow a strict alternation between legs on opposite sides of the body. Note that both legs II were kept in the same position during both steps of the first turn, and RIII was not moved during the second turn.

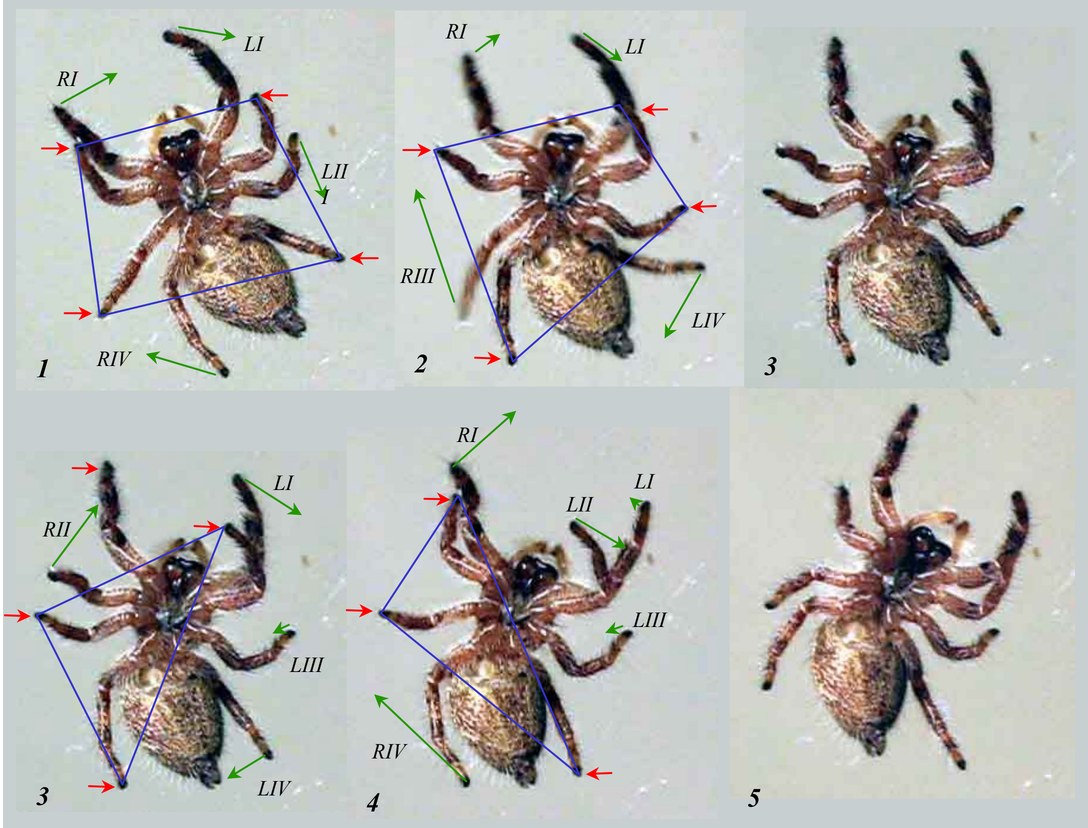
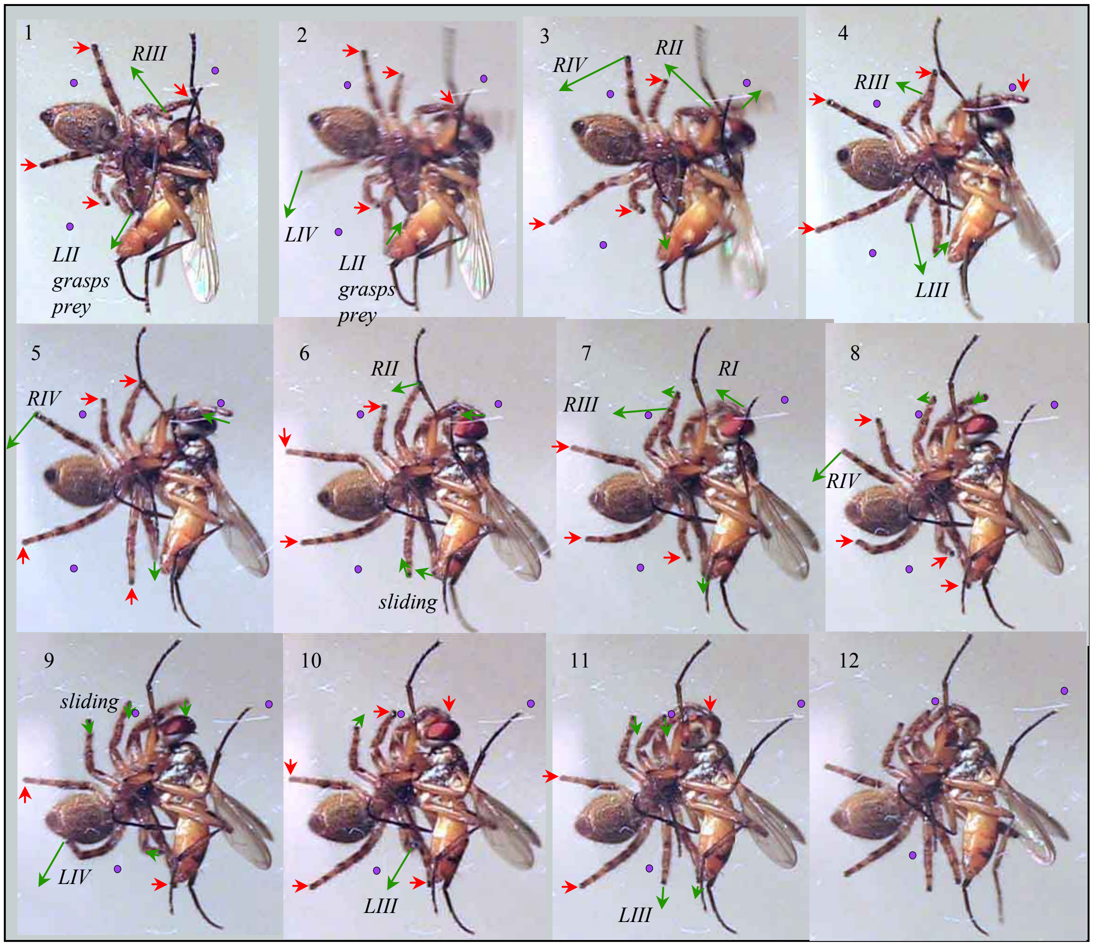


Figure 42. α turn (1-4) followed by slow backward steps (4-12) by an immature *Phidippus (species indet.)* on the underside of a clear plastic surface, as viewed from above. As this relatively large fly was held by legs I and II, single leg steps or small slides were used to accomplish this movement and maintain a secure and balanced attachment to the surface.



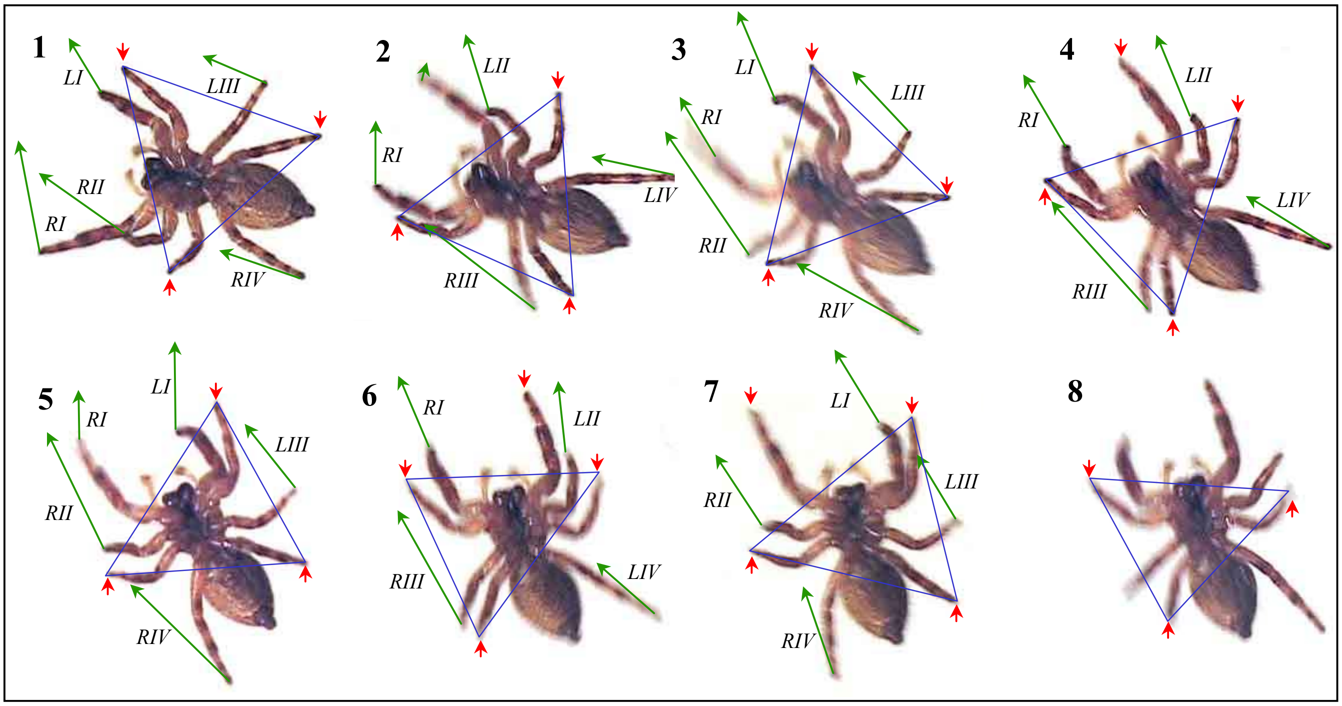


Figure 43. Alternating tripod pattern of movement during a rapid forward walk by an immature *Phidippus princeps* on the underside of a clear plastic surface, as viewed from above. All legs shown moving in a single frame during this sequence (green arrows) were moving simultaneously. During slower movement, this pattern may not be as regular. Note that legs I sometimes moved together, but there was a strict alternation between LII+LIV+RIII and RII+RIV+LIII steps. Note the significant rotation of each leg as it applied ground force against the surface. Note that ground force of a spider suspended below a surface like this is applied as a tension vector from the point of attachment of the tenules of each leg to the center of gravity of the spider. Forward movement adds a backward component to this ground force.

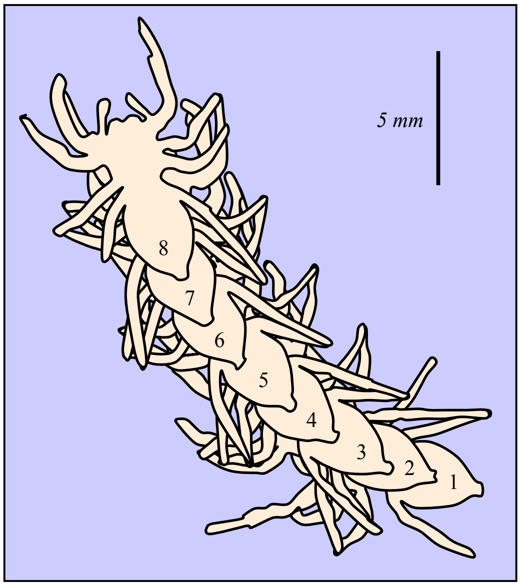


Figure 44. Outline of sequential spider positions (1-8) from Figure 43, to show net forward movement. *Phidippus* can turn continuously like this to face moving prey as they move toward it.

Role of foot pads during a walk

Land (1972) described the loosely alternating tetrapod gait of a walking salticid. With this gait, legs RI, RIII, LII, and LIV would first move, followed by legs LI, LIII, RII, and RIV, and so on in alternation. Typically, however, legs I are held off of the surface during this movement, and the resultant movement can be best described as an alternating tripod (Figures 43-45). This pattern can also be seen in the sideways walk shown in Figure 46. Land described the ability of salticids to walk in all directions, but did not study sideways stepping patterns.

Recent video studies of movement by *Phidippus* jumping spiders (Figure 47) have shown that both the claws and foot pads can be extended to grip a surface after a leg is repositioned, and can also be retracted by the spider to release a surface just before the leg itself is moved. Figure 47A illustrates the ability of these spiders to extend or depress the claws after movement of the foot pads to grip a surface.

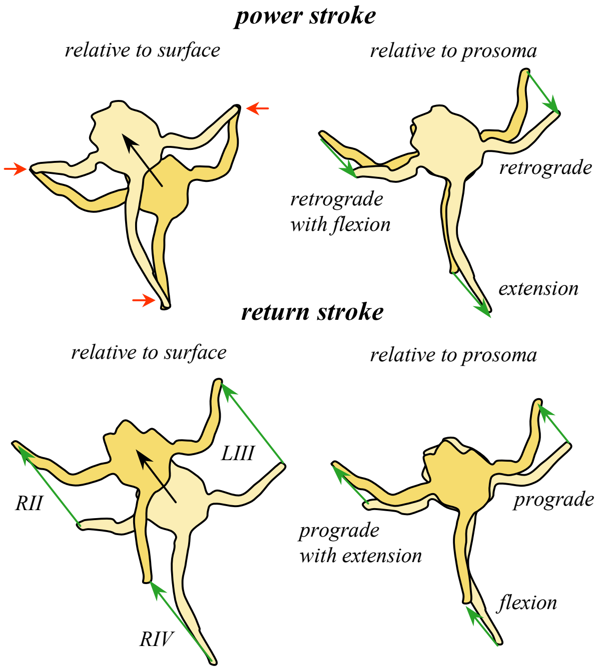
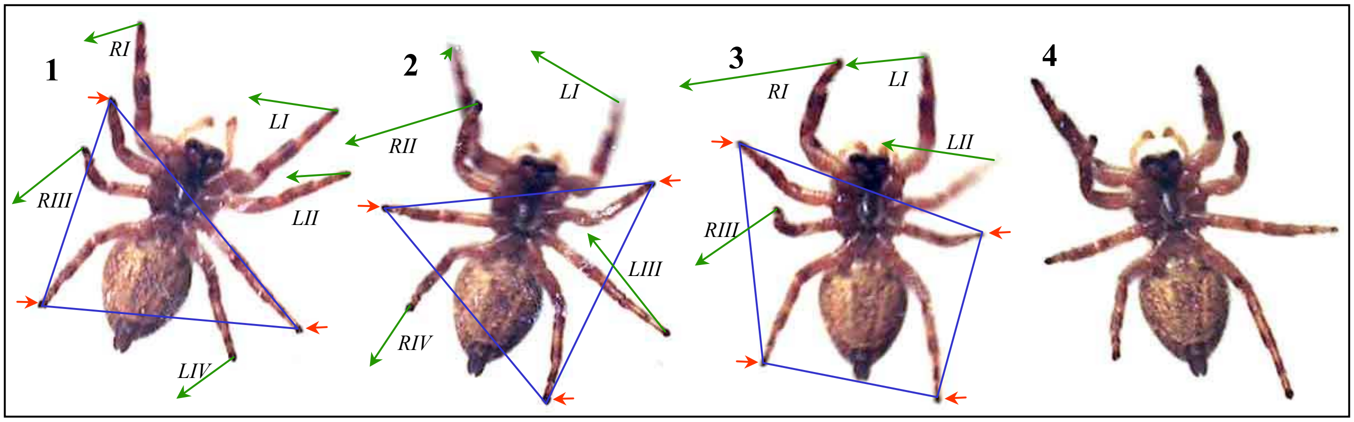


Figure 45. Tracings of the RII-LIII-RIV tripod during part of the rapid forward walk shown in Figure 43. In each case the outline of the prosoma and three of the legs that constitute one of the two tripods is shown. During the power stroke the foot pads of each leg stayed in position on the surface (top left, red arrows), but moved backward relative to the prosoma (top right) to deliver ground force to the substratum in the direction of their movement (green arrows). During the return stroke the three legs were lifted from the surface and moved forward relative to the surface (bottom left), and also reversed their power stroke motion relative to the prosoma (bottom right). In general, the legs II use alternating flexion and extension, coupled with alternating retrograde and prograde motion achieved through rotation relative to the prosoma. Legs III tend to remain extended, with alternating retrograde and prograde motion associated with rotation at the base relative to the prosoma. Legs IV alternately extend and flex as shown here. During a *rapid* walk on a smooth surface, all three of these legs usually move at the same time. Note that about half of the forward movement of these legs during the return stroke was due to forward movement of the prosoma (powered by the opposing tripod), and half (lower right) was due to movement of these legs relative to the prosoma. Thus the legs alternately move the prosoma, and then move relative to the prosoma. This is analogous to the rowing a pair of oars.

6. Acknowledgments

The SEM work in this study was completed with the generous assistance of Dr. C. Y. Shih of the Department of Zoology at the University of Iowa, in the 1975-1976 time frame. This work was sponsored by a grant of the Graduate College of the University of Iowa. I would also like to thank Dr. G. B. Edwards for his useful comments.

Figure 46. Loosely alternating tripod pattern of movement during a sideways walk by an immature *Phidippus princeps* on the underside of a clear plastic surface, as viewed from above. *Phidippus* can walk (and perhaps jump) in all directions on a surface.



A. Anterior view of LIII on the upper surface of a leaf (M1821)

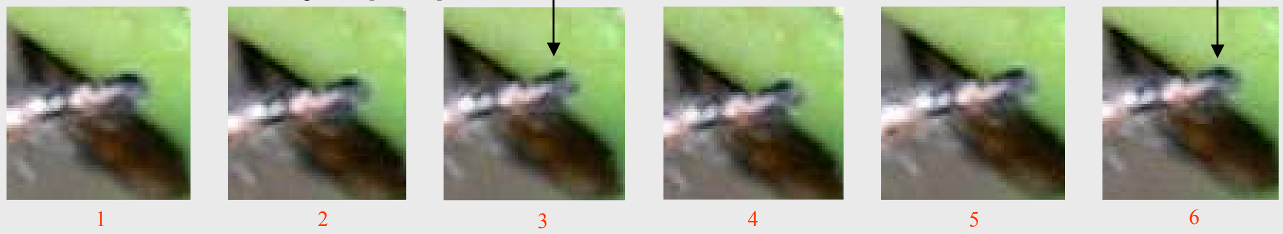
foot pads extended to meet surface

extension and depression of claws continues

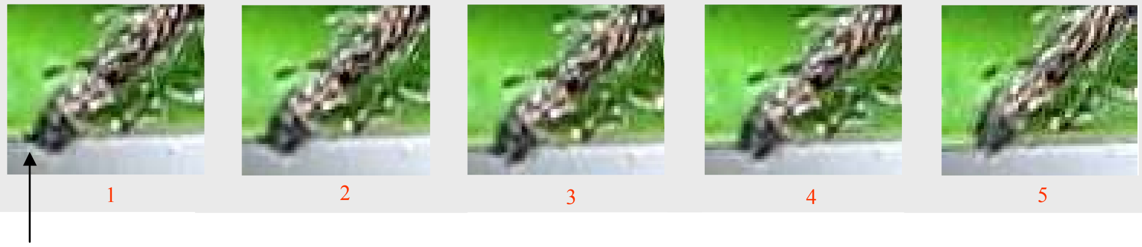
foot pads extended to meet surface

foot pads retracted away from surface

B. Posterior view of LIV under a leaf petiole [M1203]

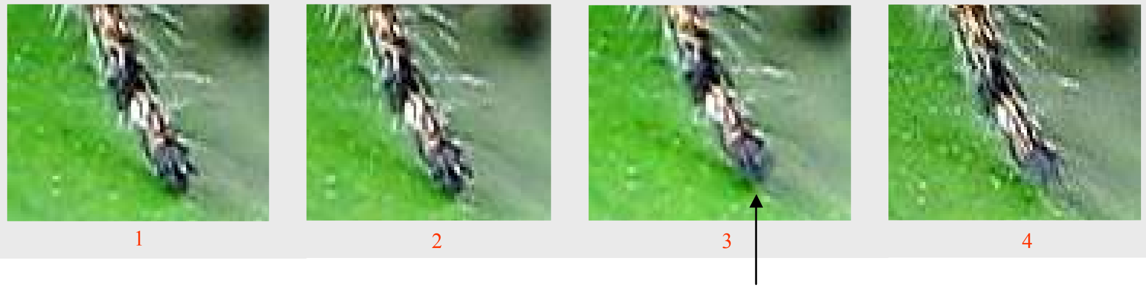


C. Lateral view (anterior is to the left) of LII holding the edge of a leaf [M1318]



claw holding edge of leaf

D. Anterior view of LIV releasing the upper surface of a leaf [M1820]



retraction of foot pads

Figure 47. Sequential frames (30 fps) from four different (A-D) digital videos of moving adult female *Phidippus princeps* captured in southern Greenville County, South Carolina. These sequences illustrate the independence of movement of pretarsal claws and footpads from movement of the entire leg. A: After this leg was brought down on the leaf surface, the foot pads were immediately extended [1-2], followed by depression of the claws [2-6]. B: During rapid movement of this spider as it pursued a running coccinellid beetle, the footpads of this leg were extended to meet the surface of the leaf petiole [1-3], and then retracted [4-5] immediately before the leg was lifted from the surface. C: Initially [1] one of the claws of this leg was extended to hold the edge of this leaf. This claw was retracted [1-5] immediately before the leg was moved. D: Rapid (blurred) retraction of the footpads [3-4] began immediately before this leg was moved from the plant surface.

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