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The pretarsus of salticid spiders

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The pretarsus of *Phidippus audax* (Hentz) consists of two claws flexibly articulated to a central claw lever which is flanked on either side by a curved plate of tenent setae. The claw apparatus allows for retraction of the claws by means of a dorsal cuticular cable of the pretarsal levator, while extension involves the pull of the pretarsal depressor on a ventral cable attached to the claw lever. A series of slit sensilla are strategically situated on either side of this lever. The anterior and posterior claws of the pretarsus differ in the number and spacing of their constituent teeth. The claw tufts are composed of specialized setae which account for the mechanical traction of the foot-pads. Whorled and filamentous setae of the distal tarsus are associated with the pretarsus. Comparable structures are found on other salticids.

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INTRODUCTION

Jumping spiders (Araneae: Salticidae) are distinguished among the spiders as a group by their superb vision. On favorable days a salticid will embark upon a visual search for prey, a search which typically involves movement on all of the surfaces afforded by the local vegetation, regardless of the specific orientation of those surfaces. In pursuit, jumping spiders may run along the underside of a leaf, or climb a vertical stem with equal ease. The pretarsal structures which account for this observed ability to cling to a variety of surfaces while on the run are probably better developed in the Salticidae than in any other family of spiders. The degree of development of adhesive structures of the pretarsus is

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commensurate with the importance of searching behavior on complex surfaces to the survival of these spiders.

In addition to providing the adhesion required for normal locomotion in the supra-terrestrial environment, structures associated with the pretarsus are also involved in the handling of silk lines as well as in locomotion upon the various fabrics produced by these spiders.

Apart from the visual sensorium which dominates the searching behavior of jumping spiders, these spiders often engage in what is apparently a chemotactic, exploratory behavior by tapping the substrate, or various objects, with the pedipalps and forelegs. Both mechanoreceptors and chemoreceptors are apparently associated with the pretarsus.

Clearly, the pretarsus is the site of most spider-substrate interactions, while the pedipalps and spinnerets provide several notable exceptions to this rule. The cuticular structures of the pretarsus are difficult to observe in any detail with conventional methodology. Thus the present study is an attempt to elucidate the functional morphology of the salticid pretarsus by means of scanning electron microscopy.

MATERIALS AND METHODS

Near-adult *Phidippus audax* (Hentz), collected in the vicinity of Iowa City, Iowa, provided the bulk of material for this study. Alcohol-preserved specimens of a variety of salticids, notably *P. rimator* (Walckenaer), *Salticus scenicus* (Clerck), and *Sassacus papenhoei* Peckham, were also examined.

The distal portion of each leg was fixed in glutaraldehyde and osmium tetroxide prior to critical-point drying. Treatment of cuticle with thiocarbohydrazide (THC) (Kelley, Dekker & Bluemink, 1973) in alternation with osmium tetroxide greatly reduced charging effects, particularly where high resolution was required.

Both fixed specimens and dissected exuviae were coated with 10-30 nm of gold prior to examination with a Cambridge Stereoscan S4.

ORGANIZATION OF THE PRETARSUS

The pretarsus consists of a series of structures which articulate with each distal tarsus of the spider (Fig. 1). As indicated in Fig. 2A, the salticid pretarsus consists of two claws articulated with a central claw lever, which is flanked by two plates of tenent setae, or claw tufts.

Each plate (Plates 1C and 2A) is actually a curved wafer containing the bases of the tenent setae. The straight medial edge of each plate articulates with the claw lever by means of a flexible cuticle, while laterally the plates articulate more rigidly with the wall of the tarsus. As may be seen in Plate 2A, the tenent plates retain their position at the rim of the tarsus when the claws are retracted. Thus it is only the claw apparatus that is capable of considerable movement.

The antero-posterior symmetry of the pretarsus is evident.

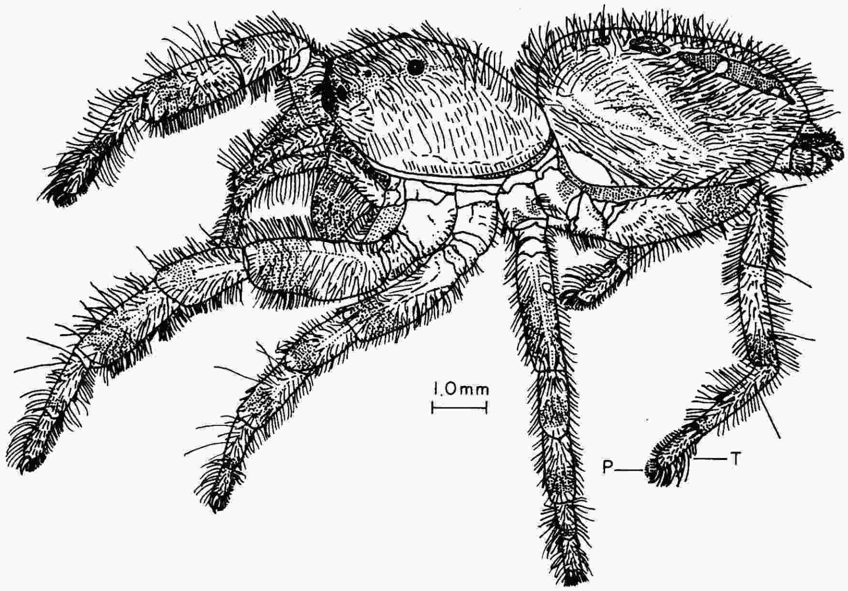


Figure 1. Adult female *Phidippus rimator* (Walckenaer), lateral view. Salticid spiders usually have relatively short limbs which are covered with setae and scales. Substrate-adherent setae of each tarsus and pretarsus provide a secure foot-hold as the jumping spider moves through vegetation in search of prey. This species is typically a denizen of undisturbed grasslands (x7): T, tarsus; P, pretarsus. Adapted after Hill (1975).

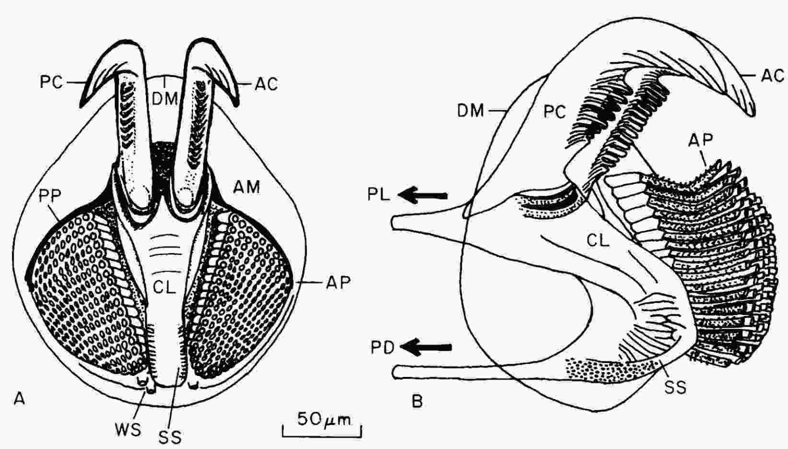
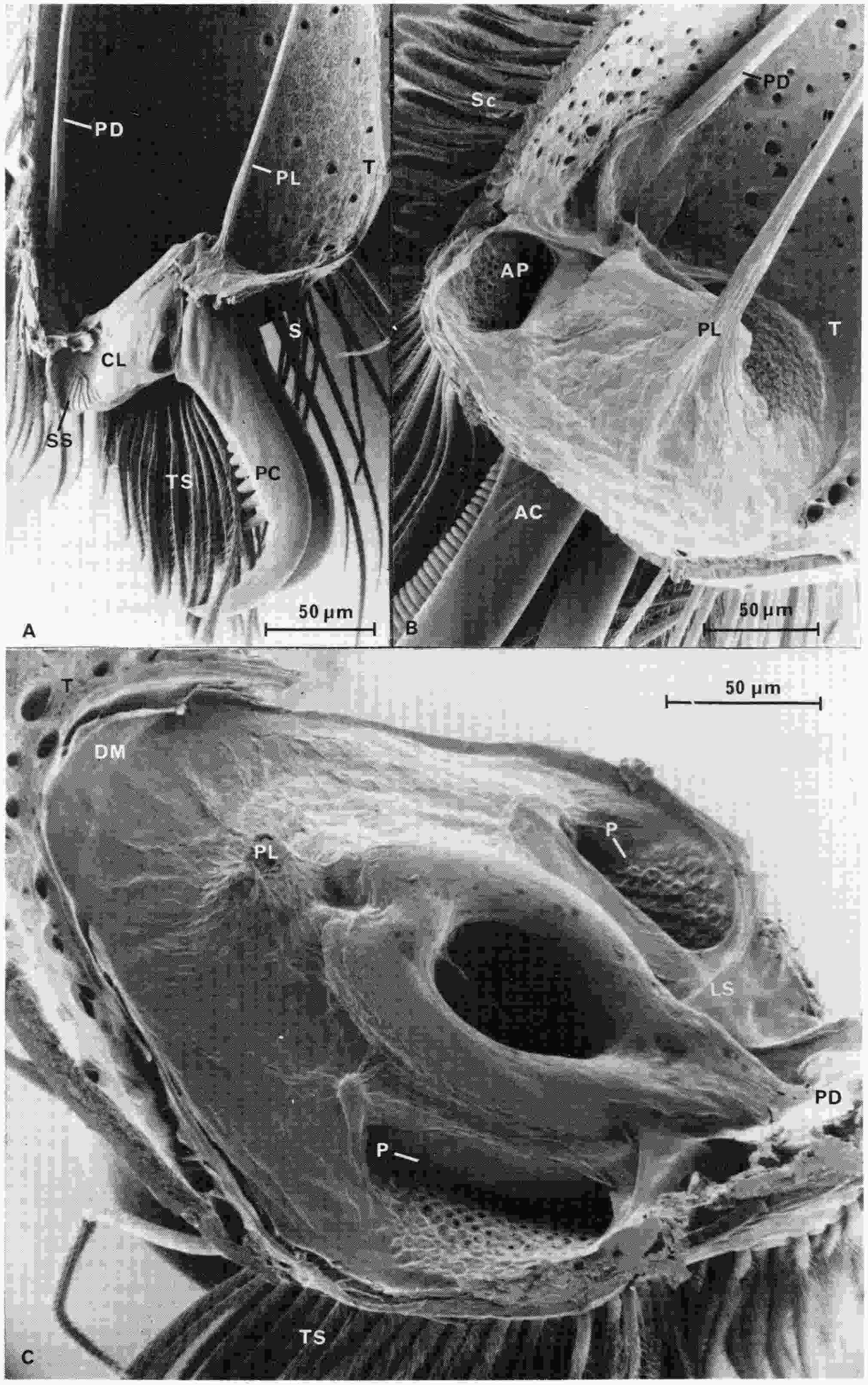


Figure 2. Organization of the pretarsus of *Phidippus audax* (x200): A. Distal projection, showing the bilateral symmetry of the pretarsus about a vertical axis: AC, anterior claw; AM, flexible cuticular articulation of the pretarsus with the tarsus; AP, anterior plate of tenent setae; CL, claw lever; DM, dorsal margin of pretarsus; PC, posterior claw; PP, posterior plate of tenent setae; SS, slit sensilla; WS, sockets of several whorled setae at the ventral margin of the pretarsus. B. Postero-lateral view with the posterior plate of tenent setae removed. Arrows indicate the opposing action of the dorsal cable of the pretarsal levator (PL) and the ventral cable of the pretarsal depressor (PD). The claw articulation with the claw lever (CL) permits a considerable dorso-ventral flexure of the claws. Other symbols as in Fig. 2A.


PD
PL
T
CL
SS
S
TS
PC
50 µm
A
Sc
PD
AP
PL
T
AC
50 µm
B
T
50 µm
DM
PL
P
LS
PD
P
TS
C

THE CLAW APPARATUS

The equivalent of a pretarsal depressor muscle and a pretarsal levator muscle has been described in the Theraphosidae (Dillon, 1952; Sherman & Luff, 1971), the Araneidae (Frank, 1957), and the Theridiidae (Whitehead & Rempel, 1959). In each case the levator and depressor originate with the dorsal wall of the proximal metatarsus and the tibia, while they insert upon what Dillon described as "tendons" in some way connected to the claws. Ellis (1944) demonstrated, by means of direct electrical stimulation of the muscles, the opposing action of the levator and the depressor in the raising and lowering of the claws. The contraction of both the depressor and the levator may serve to extend a portion of the leg (Dillon, 1952; Whitehead & Rempel, 1959), although hydraulic pressure is the more likely means of extending the leg as a whole (Parry & Brown, 1959a).

The claw apparatus of *Phidippus* (Fig. 2B) articulates with the tarsus by means of a thin, flexible cuticle, except for a pair of rigid lateral struts (Plate 1C, LS) which act as a fulcrum for the claw lever. The two claws are separately and flexibly articulated (Plates 2A and 3D) with the claw lever, and press against the lever when retracted.

The levator and depressor tendons (Plate 1A,B) are actually rigid cuticular cables. The levator cable is attached to the claws and runs meso-dorsally through the tarsus. The depressor cable is attached to the ventral margin of the claw lever and runs meso-ventrally through the tarsus. Pull of the levator results in retraction of the claws into the tarsus, while pull of the depressor results in claw extension.

The specific functions of the claws in salticid spiders are not known for certain. Curiously, Foelix (1970b) could not ascertain any definitive function for the claws of the araneid *Araneus diadematus* with ablation experiments. The fact that the claws may be alternately extended and retracted suggests that they are useful only for specialized purposes and that they are employed in specific behaviors, most likely those which involve the handling of silk.

The anterior and posterior claws of each of the legs of *Phidippus* differ greatly in tooth structure (Plate 3). The many closely-spaced teeth of the anterior claw are of the correct spacing to hold the drag-line cables (composed of individual fibres approximately 1.0 μm in diameter) of this spider securely, while the open V-shaped notches between the teeth of the posterior claw should give the spider a tentative grip on the silk, allowing for its subsequent release.

While dangling from a drag-line by the spinnerets, *Phidippus* catch the line with a hind-leg and use this hold to turn about completely. Subsequently the spider winds up the vertical line with the first two pairs of legs while it climbs; at the end of the climb the rolled silk is discarded. This vertical climbing

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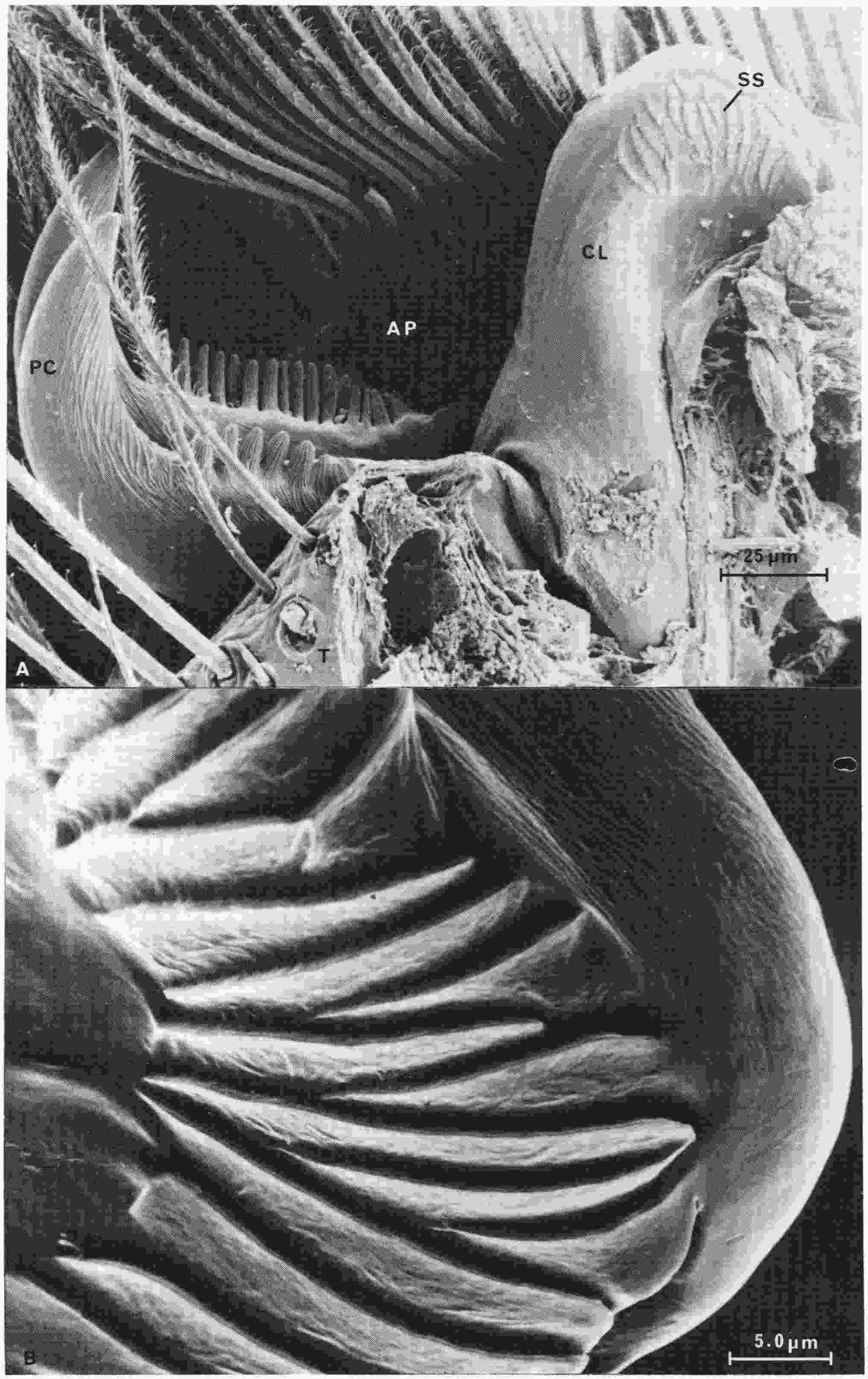
Plate 1. Organization of the pretarsus, exuviae of ***Phidippus audax***. A. Posterior view of pretarsus, with a portion of the tarsal wall removed (x310). B. Dorsal view of pretarsus, exposed by breaking away a portion of the tarsal wall (x320). C. Interior view of the pretarsus (x450). AC, Anterior claw; AP, interior wall of the anterior, plate of tenent setae; CL, claw lever; DM, dorsal margin of the pretarsus; LS, lateral strut; P, plates of tenent setae; PC, posterior claw; PD, cable of pretarsal depressor; PL, cable of pretarsal levator; S, large setae of the dorso-distal tarsus; Sc, scopula setae; SS, slit sensilla; T, tarsus; TS; tenent setae.


SS
CL
AP
PC
25 μm
T
A
B
5.0 μm

behavior should, at least in its initiation, require the grip afforded by the anterior claw.

In traversing a horizontal cable, however, the cable remains intact as the spider travels. Here the posterior claw should be of greater use.

The claws are quite likely of additional use in either walking within the silken molting chamber or resting-sac, or in opening and closing this sac. The presence of a clawed pretarsus in the first instar, which remains within the brood-sac of the female, suggests the utility of claws in maneuvering upon the silken fabric. In summary, the claws may relate to locomotion either by means of or upon silk, while the claw tufts definitely relate to locomotion upon a relatively smooth, non-silk, substrate.

SLIT SENSILLA

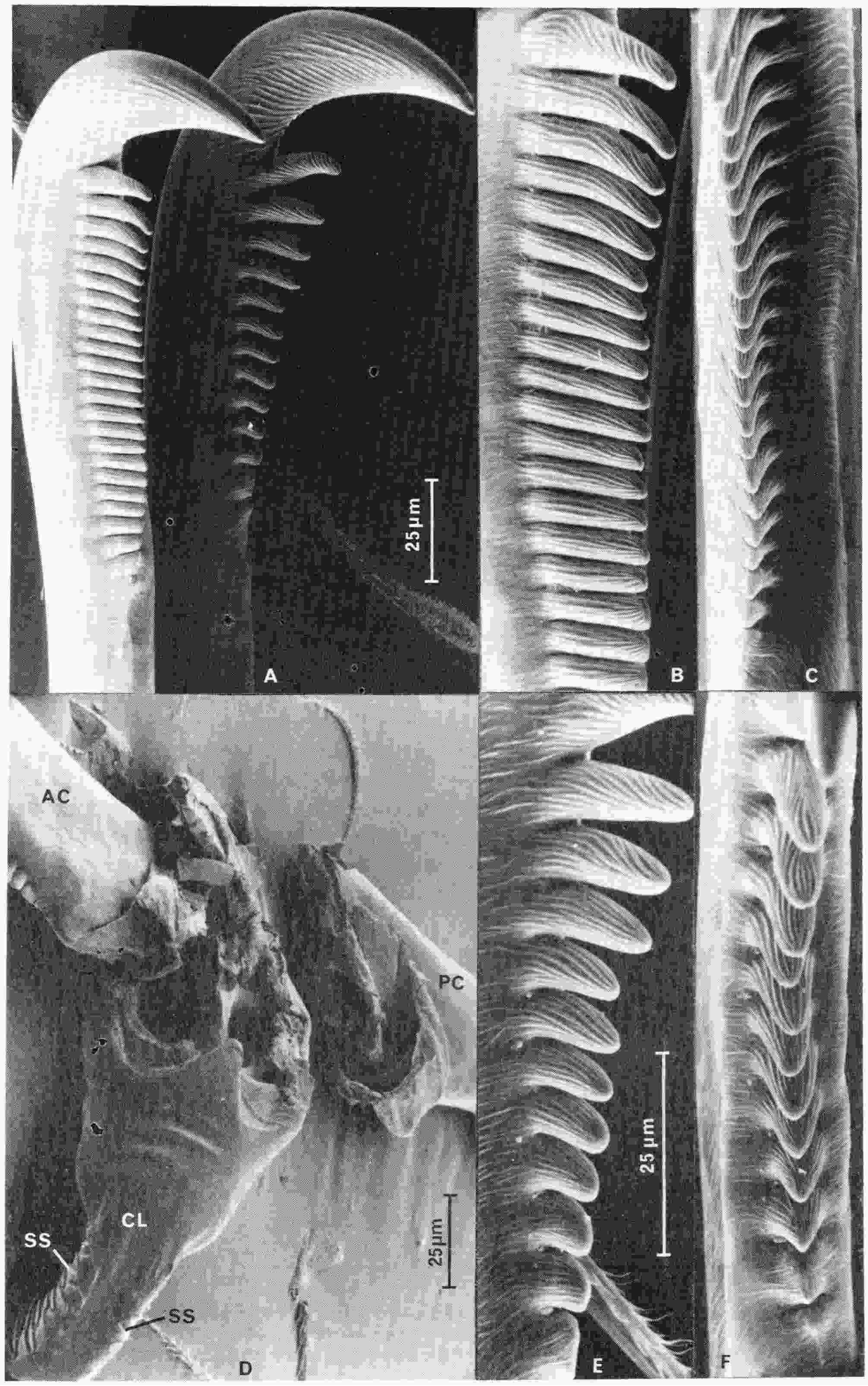
A series of slit sensilla (or lyriform organs; Fig. 2; Plate 2) are located on either side of the ventral portion of the pretarsal lever which projects beyond the rim of the tarsus. This notable group of slit sensilla was not figured by Kaston (1935) on the leg of *Phidippus audax,* probably because of the difficulty of observing pretarsal structures which are obscured by the many setae of this region. A single slit in this position is reported for the ctenid *Cupiennius salei* (Barth & Libera, 1970), while Foelix (1970b: figs 16, 17) apparently figures a series of slit sensilla in this position for *Araneus diadematus* (Araneidae), without noting their presence.

Barth (1971) provides an excellent description of the morphology of slit sensilla, while others (Pringle, 1955; Walcott & van der Kloot, 1959) have provided good evidence for the function of arachnid slit sensilla as mechano-receptors. The slit sensilla of the spider are thought to provide information in regard to cuticular stress, particularly when that stress is perpendicular to the sensillum and the deformation of the cuticle (strain) is maximized (Barth, 1972; Seyfarth & Barth, 1972).

The situation of pretarsal slit sensilla in salticids agrees with the presumed role of these organs as mechano-receptors. The series of slits are clearly oriented in an array perpendicular to the line of rotation of the pretarsal lever. The symmetry of the two groups of slit sensilla, one on either side of the claw lever is striking.

The pretarsal slit sensilla may convey information in regard to the position of the claw apparatus or, more likely, they allow the spider to assess the tension on silk cables handled by the claws. Salticids always check the tension on bridging cables (originally formed by ballooning silk) before beginning a traverse.

Plate 2. The claw apparatus, adult male *P. audax*: A. Posterior view of pretarsus with a portion of the tarsus and the posterior plate of tenent setae removed (x610): AP, anterior plate of tenent setae; CL, claw lever; PC, posterior claw; SS, slit sensilla; T, tarsus. B. Slit sensilla of the claw lever (x3000).


25 µm
A
B
C
AC
PC
CL
SS
SS
25 µm
D
25 µm
E
F

SENSORY SETAE

Most of the setae of spiders are innervated by three neurites and probably serve as mechanoreceptors (Foelix & Chu-Wang, 1973a), with the plausible exception of the tenent setae. In *Phidippus*, these "ordinary" setae vary greatly in regard to absolute size and the relative length of the decurrent filaments which project from each shaft (Plate 6). Those with long filaments are termed filamentous setae (Plate 6C). Many of the filamentous setae which surround the pretarsus bear filaments only on the pretarsal margin of the shaft (FS) (Plates 5A and 6B) and these are termed fringe setae. The dorsal aspect of each distal tarsus bears many long and thick setae (S) (Plate 4A) which surround the claws. All of the setae of the jumping spider, as well as the scales which are essentially modified setae, exhibit a fused-fiber composition when observed in detail.

A similar variation in regard to filament (Microseta) length is found in the Anyphaenidae and the Clubionidae (Platnick & Lau, 1975).

The whorled setae (WS) (Fig. 3; Plates 4C and 6E) are readily identified by the flexible, segmented structure of the distal portion of the shaft. Each of the whorled setae of *Phidippus* is characterized by a long apical filament and a blunt apical cone. The cone may bear a single pore near its apex, although this feature has not been observed clearly. The seta probably bends freely, and is oriented in a manner which suggests that the apical cone comes into contact with the substrate.

Whorled setae are present around the distal margin of the tarsus, on the ventral side, on each leg. Invariably in the salticids which have been examined, several whorled setae originate at the ventral margin of the pretarsus and these setae (WS) (Plate 4C) extend beyond the tenent setae, between the claw tufts. In addition, whorled setae are abundant near the tips of the spinnerets and they are present in great numbers in special pits at the tip of each pedipalp of the adult male *P. audax*, just where the pedipalps come into contact with the substrate.

Whorled setae of similar form are found in the Dictynidae (Harris & Mill, 1973), the Lycosidae (Foelix & Chu-Wang, 1973b), the Clubionidae and the Anyphaenidae (Platnick & Lau, 1975).

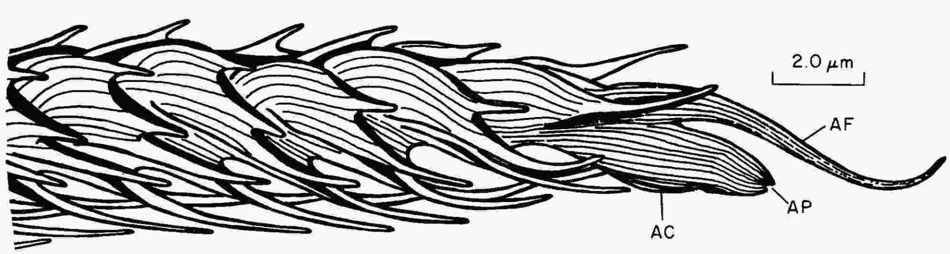
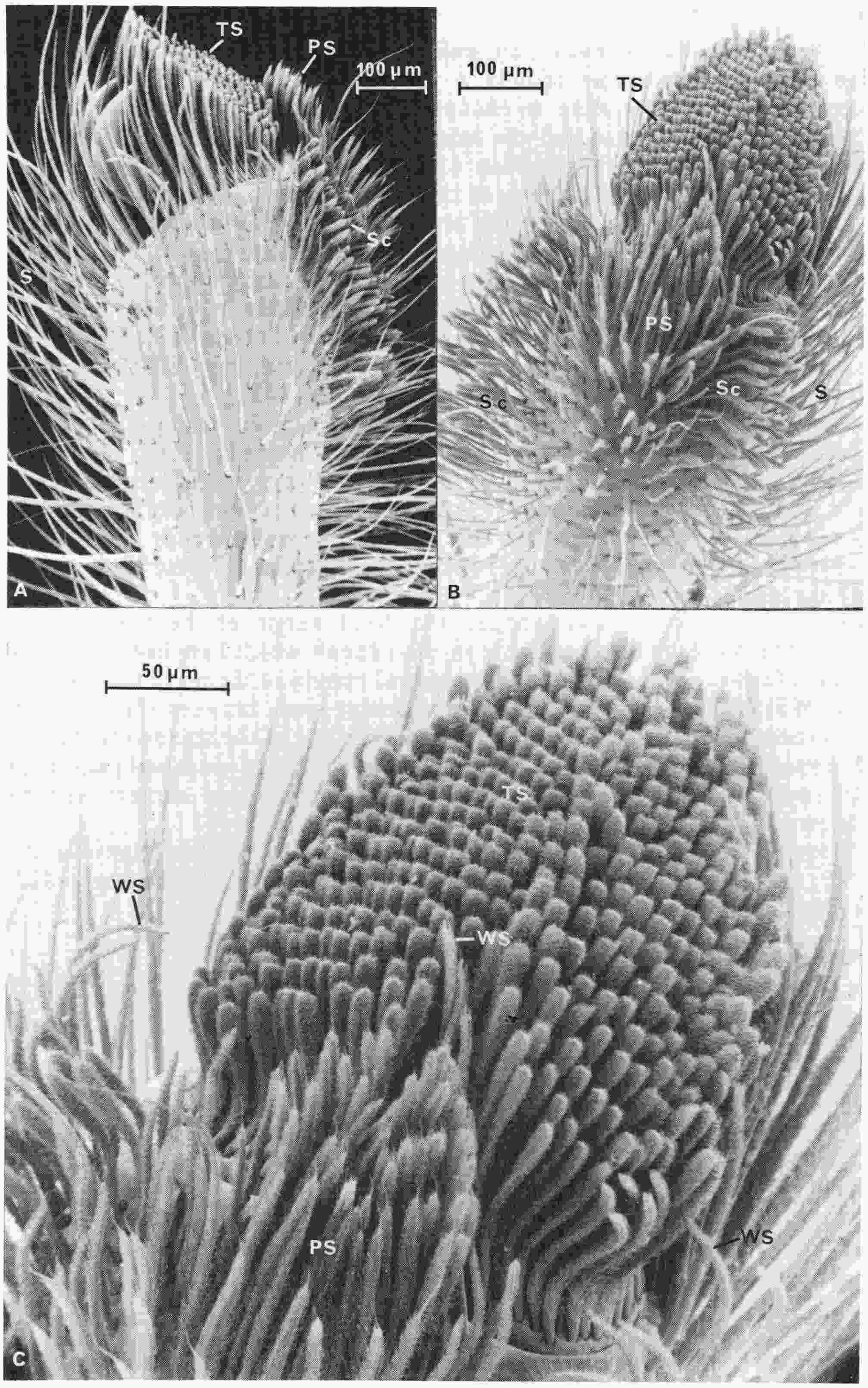


Figure 3. Structure of the apical portion of a whorled seta (x6000): AC, apical cone; AF, apical filament; AP, surface discontinuity of the cone which probably represents an apical pore.

Plate 3. The pretarsal claws, exuviae of *P. audax*. A. The claws of left leg IV (x570). The anterior claw (left) bears more teeth. B, C. Teeth of the anterior claw (x1150). D. Articulation of claws with the claw lever (x540): AC, anterior claw; CL, claw lever; PC, posterior claw: SS, slit sensilla. E, F. Teeth of the posterior claw (x1150).


TS
PS
100 µm
Sc
S
A
100 µm
TS
PS
Sc
Sc
S
B
50 µm
TS
WS
WS
PS
WS
C

In *Araneus diadematus* (Araneidae), the whorled setae lack filaments, but are in all other respects comparable. Each whorled seta is innervated by 21 neurites, 2 of which terminate at the base of the seta and presumably serve as mechanoreceptors, and 19 of which terminate in the apical cone and appear to function as contact chemoreceptors (Foelix & Chu-Wang, 1973b). A similar innervation by the neurites of bipolar sensory cells situated in the hypodermis is found in *Ciniflo ferox* (Dictynidae; Harris & Mill, 1973). Foelix (1970a)cites evidence for the role of whorled setae as contact chemoreceptors, an appraisal which is based upon spider behavior, structure of the whorled setae, and the distribution of these setae.

In salticids as well, the whorled setae are strategically situated to serve as contact chemoreceptors when either the pedipalps, spinnerets, or walking legs are brought into contact with the substrate. In salticids, the whorled setae are more abundant at the tips of the forelegs than on the other legs, a distribution which agrees with the substrate-tapping exploratory function of the forelegs.

STRUCTURE AND FUNCTION OF SUBSTRATE-ADHERENT SETAE

Each foot-pad or claw-tuft of the jumping spider consists of an array of flattened tenent setae (TS) (Plate 4C). As the bases of the tenent setae are isolated by a wall of cuticle (P) (Plate 1C), it is unlikely that these setae are innervated. The individual tenent seta (Plate 1A) is flattened distally and supported dorsally by a strut which resists the flexure of the seta below the flattened apex. These setae bear many recurved and outstretched filaments

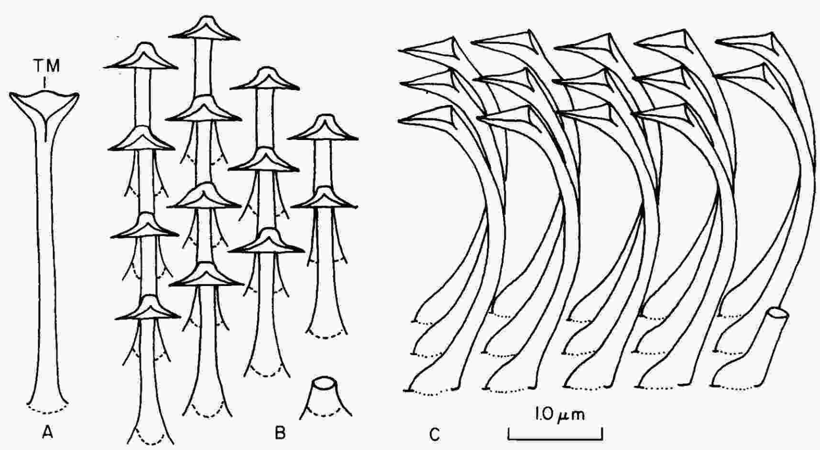
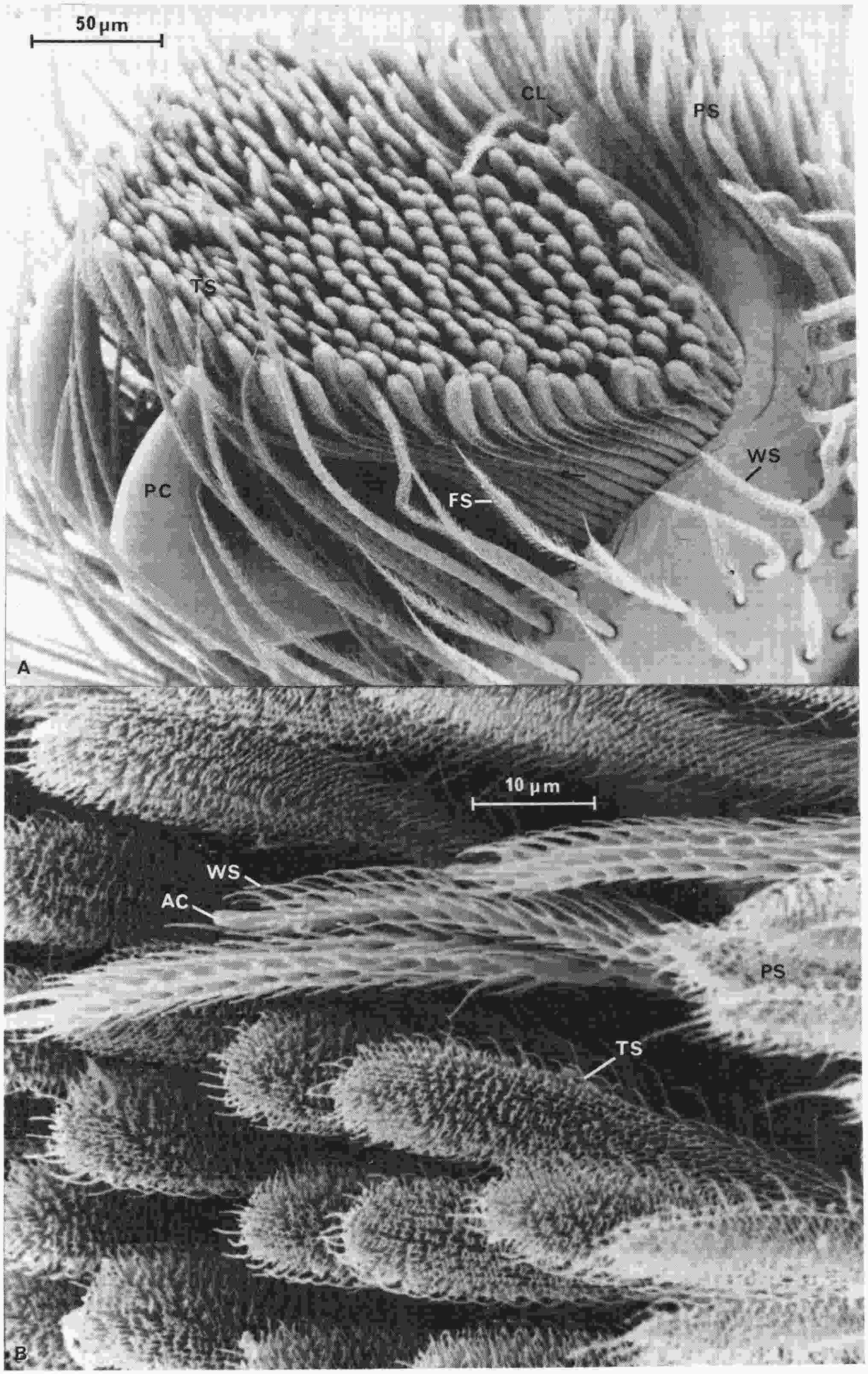


Figure 4. The bifid filaments of the tenent setae (x12,000) A. A single bifid filament, exhibiting a long flexible shaft which bifurcates near the apices. The two apices are connected by a thin, flexible membrane of thin cuticle (TM). B. Vertical projection of a portion of the ventral or tenent surface of a tenent seta, showing the regular alternation of filaments between rows which results in a hexagonal array of filaments. C. Lateral view of the tenent filaments, which are recurved in a proximal direction (to the left) on the ventral surface of a tenent seta.

Plate 4. Distal portion of the right foreleg, adult male *P. audax*: A. Posterior (lateral) view (x105). B. Ventral view (x130). C. Detail from (B) (x360). PS, Plume setae; S, setae; Sc, scopula (tenent) setae; TS, tenent setae of the foot-pads; WS, whorled setae.


50 µm
CL
PS
TS
WS
PC
FS
A
10 µm
WS
AC
PS
TS
B

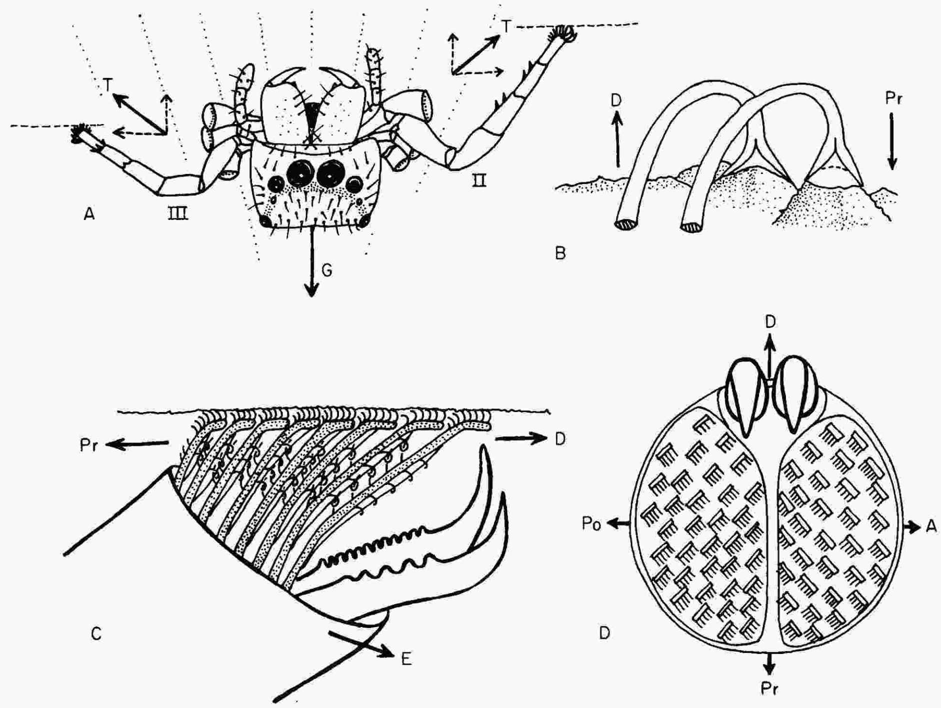


Figure 5. Function of the tenent setae. A. Salticid walking below a horizontal surface: the force of gravity (G) is necessarily balanced by the sum of the vertical components of tension (T) for each of the walking legs in contact with the surface. The balance between antero-posterior and lateral components of leg tension (T) or thrust depends upon the direction in which the spider is moving. *Phidippus* can walk or run in all directions on surfaces in any orientation. For the sake of simplicity only the vertical and lateral components (dashed vectors) of tension exerted by the second leg of the right side (II) and the third leg of the left side (III) are figured here. B. Function of the individual bifid filaments: the forked apex of each filament catches on minute surface irregularities when the tenent seta is pulled against the substrate in a proximal direction (Pr). Presumably the flexible membrane joining the tips of each filament provides the frictional component which accounts for the ability of these spiders to exert the vertical component of leg tension in opposition to gravity. The filaments release their hold on the substrate when moved in a distal direction (D). C. The pretarsal hold on the substrate: the blunt, flattened, and flexible ends of the tenent setae function as a unit on a surface when locked into place by a proximal (Pr) grip of the leg. The bifid filaments of the tenent setae resist displacement in the proximal direction by catching substrate irregularities, but they may be moved in a distal direction (D). Leg extension during walking involves a vertical component of substrate release as well, as indicated by the vector (E). D. Schematic distal projection of the pretarsus. The tenent setae of the anterior and posterior plates are actually oriented in different directions. When locked onto the substrate, both groups of setae strongly resist slippage in the proximal direction as indicated in Fig. 5C. In addition, the anterior plate resists posterior (Po) slippage and the posterior plate resists anterior (A) slippage. Thus the pretarsus resists slippage in all directions except for the distal direction (D).

Plate 5. Distal portion of the right foreleg, adult male *P. audax*. A. Posterior view (x370). B. Detail of setae from plate 4C (x1800). AC, Apical cone of whorled setae; CL, claw lever; FS, fringe seta; PC, posterior claw; PS, plume setae; TS, tenent seta; WS, whorled seta.


10 µm
A
B
C
D
WS
E

which interlock to allow the setae of each plate to function as a collective, inter-supportive unit.

The tenent setae, proximally hollow and circular in section, originate with a regular array of sockets on the curved surfaces of the anterior and posterior pretarsal plates (Fig. 2A). The length of the individual setae is adjusted in such a way that each plate forms a flat surface at the level of the blunt apices of the setae (Fig. 5C; Plate 4C). In this regard, the dorsal setae are considerably longer than are the ventral setae of each plate.

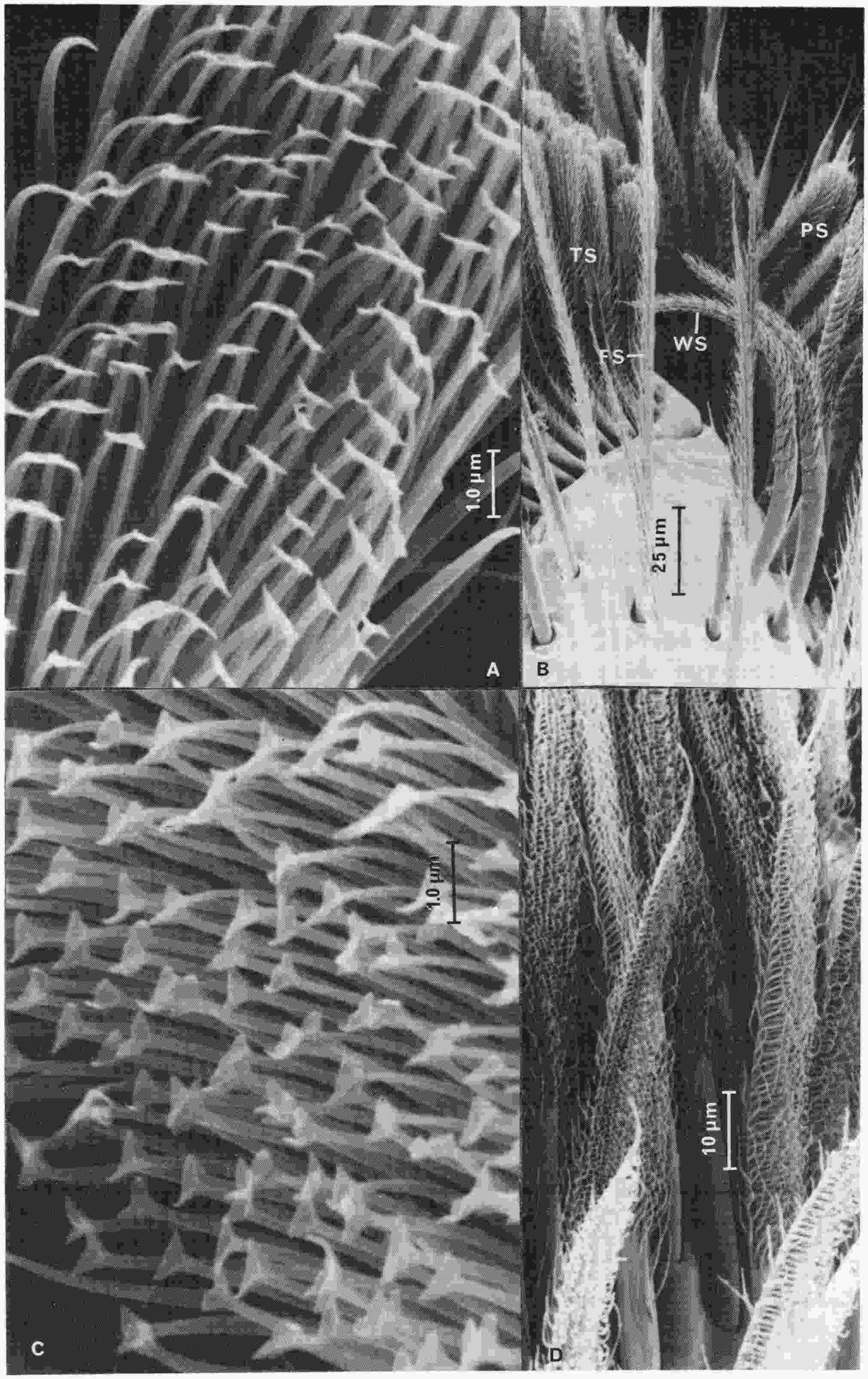
The tenent surface of the individual seta is located on the ventral or proximal side of each flattened apex (Plate 5B). The filaments of this surface are recurved in a proximal direction, and they are arranged in regular rows along the length of the seta, with filaments alternating between adjacent rows to produce a hexagonal array (Fig. 4; Plate 7A,C). Each of the filaments is bifid, with a thin and flexible cuticular membrane connecting the two apices. These bifid filaments are thought to catch on minute irregularities of the substrate, a property which is enhanced by their forked structure (Fig. 5B). The connecting membrane should resist the separation of the apices as the filament is applied to the substrate, putting some tension into the grasp of these minute claws. In addition, the surface of each minute connecting membrane should contribute to the frictional component of leg tension (Fig. 5A), required to overcome the force of gravity when the spider walks on the underside of a horizontal surface. Thus the bifid filaments are devices which facilitate mechanical adhesion to a relatively smooth surface.

The manner in which the tenent setae grip the surface is shown in Fig. 5C. The jumping spider secures a grip on the substrate by flexing the leg in a direction indicated here by (Pr), while release is readily accomplished by extending and lifting the leg as indicated by (E). When a surface is quite smooth the spider will flex its legs until the bifid filaments have caught upon surface irregularities in a manner sufficient to resist a further slippage in the proximal direction.

Phidippus jump in essentially the same way that *Sitticus* jumps, as described by Parry & Brown (1959b). Legs I and II are raised, while legs IV are flexed (Fig. 1) in preparation for the hydraulic extension which provides the requisite thrust for the jump. Thus the pretarsus of each fourth leg is actually removed from the surface beforehand, and only the third pair of legs remains in contact with the substrate at the time of the jump. The adhesion provided by the third legs is essential if the spider is jumping from anything other than an upper, horizontal surface. By means of multiple-flash photography, Parry & Brown found that, as *Sitticus* jumps, the third legs are moved laterally just before the release of the substrate. This observation agrees with the notion that leg extension is required for substrate release.

The anterior and posterior plates of tenent setae are oriented in slightly different directions, a device which provides a lock against lateral slippage of the leg against a smooth substrate, regardless of the orientation of the spider (Fig. 5D).

Plate 6. Setae associated with the pretarsus of *P. audax* (x2200). A. Dorsal view of the distal half of a tenent seta. B. Fringe setae. C. Filamentous setae. D. Whorled seta. E. Whorled seta (WS) compared with ordinary setae.


1.0 µm
A
TS
PS
WS
FS
25 µm
B
1.0 µm
C
10 µm
D

Tenent setae are not restricted to the pretarsus of *Phidippus*, but are also found in the form of two ventrolateral scopulae on the distal portion of each tarsus (Sc) (Plate 4B), particularly on the forelegs of older spiders.

In addition, large flattened fringe setae, or plume setae (PS) (Plates 4C and 7D) are found in a mid-ventral tract of the distal tarsus between the scopulae. The plume setae resemble tenent setae: They are supported by a dorsal strut, and the decurrent filaments of plume setae occur primarily on the ventral or proximal surface. The filaments are simple, however, and each plume seta bears a single large apical filament. The specific function of these setae is not known, but they may facilitate either the handling of or walking upon silk, or locomotion upon a highly irregular surface where the regular array of tenent setae is of little use. As a leg is flexed, the plume setae must have the first opportunity to grip the substrate. Perhaps if this grip is insufficient, further flexure brings the tenent setae into play.

Plume setae may also facilitate thrust when rapid locomotion, rather than substrate adhesion, is of the greatest priority. In any case, the flattened, reinforced structure and orientation of plume setae suggests a role in substrate adhesion.

Tenent setae are found in many spider families, although the filaments of those tenent setae which have been examined in detail are simple rather than bifid. The tenent (lamelliform) setae of clubionids and anyphaenids are similar to those of salticids, but each filament terminates as a blunt knob (Platnick & Lau, 1975). Tenent setae with simple filaments are associated with the pretarsus of the gnaphosid *Callilepis* (Platnick, 1975).

POSTEMBRYONIC DEVELOPMENT OF THE PRETARSUS

The pretarsus of a first instar *Phidippus rimator* bears only a single pair of simple claws (Plate 8E) which facilitate the movement of these blind spiders within the brood-sac. Once the spider has molted to the second instar (Plate 8F), the pretarsus appears in the adult pattern, complete with an array of functional tenent setae, whorled setae, and filamentous setae. At this stage of development the spiderlings (nymphs) emerge from the brood-sac to embark upon an independent, self-supportive way of life.

Each time the spider molts, the setae associated with the pretarsus increase in both size and number, commensurate with the increased size of the spider.

THE PRETARSUS OF OTHER SALTICIDS

Although this study deals primarily with *Phidippus audax*, most of the generalizations set forth should apply to the Salticidae as a group.

In certain details, however, there is a great deal of inter-specific variation. In general the number, but not the absolute width, of the individual tenent setae

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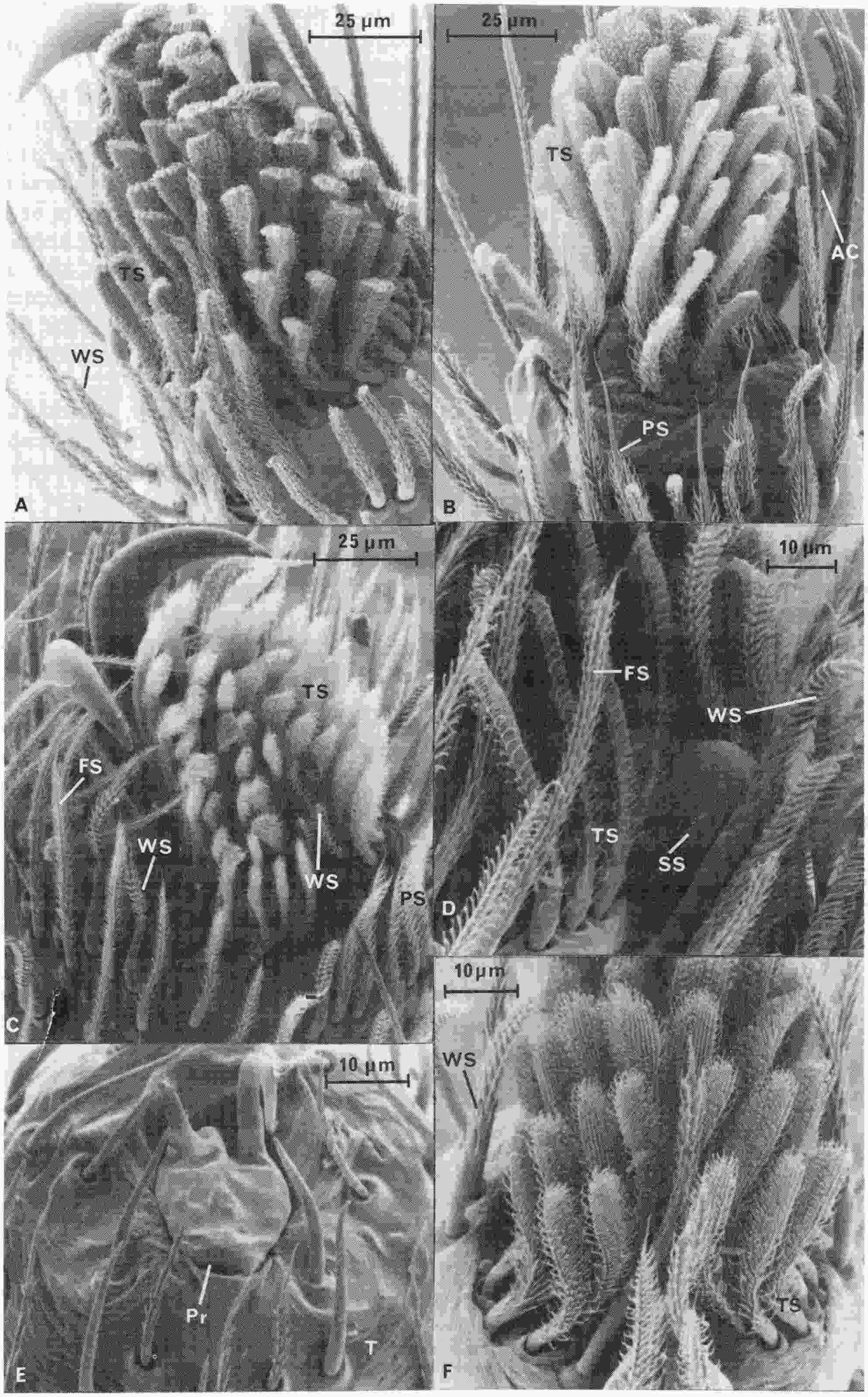
Plate 7. Setae associated with the pretarsus of *P. audax*. A. Ventral view of the distal portion of a tenent seta, showing the regular rows of bifid filaments (x10,000). B. Ventral margin of the pretarsus (x525): FS, fringe seta; PS, plume seta; TS, tenent setae; WS, whorled seta. C. The bifid filaments of the tenent setae (x12,000). D. Ventral (Proximal) view of plume setae (x1100).


25 µm
TS
WS
A
25 µm
TS
AC
PS
B
25 µm
TS
FS
WS
WS
PS
C
10 µm
FS
WS
TS
SS
D
10 µm
Pr
T
E
10µm
WS
TS
F

varies in proportion to the size of the spider. Although each category of setae is clearly recognizable in various species (Plate 8), the detailed structure of these setae varies. For example, the apical filaments of the plume setae of *Sassacus papenhoei* (PS) (Plate 8B) are proportionately much greater in length than are those of *P. audax*. Certainly one could tabulate a broad series of variations on this scale.

Each claw of *S. papenhoei* bears a combination of loosely-spaced distal teeth and tightly-spaced proximal teeth (AC) (Plate 8B). This arrangement contrasts to that seen in *P. audax* where teeth of a particular sort are restricted to either the anterior or posterior claw.

In general, despite certain variations in form, both the organization of the pretarsus and the arrangement of its component setae are essentially the same in all those salticids which have been examined.

DISCUSSION

Foelix (1970b) provides a good description of the araneid pretarsus for comparison. *Araneus* lacks tenent setae, but is equipped with a third claw and a set of serrated bristles for the handling of silk.

There has been some question in regard to the mode of action of certain adhesive organs in insects. The arolia of cockroaches are thought to function by means of an adhesive, waxy surface film of the exocuticle which is applied against the substrate (Roth & Willis, 1952; Arnold, 1974). In *Rhodnius,* the surface tension of a secreted substance may promote adhesion of the tenent hairs (Gillett & Wigglesworth, 1932).

On the basis of this study, it is difficult to rule out the possibility that the cuticle of the bifid filaments is coated with an adhesive. Certainly no difference between fixed spiders and exuviae was found. With structures of this minute size, even electrostatic phenomena cannot be neglected. While there is no evidence for the secretion of adhesive substances by the tenent setae, saliva applied to the foot-pads by the spider while grooming may promote adhesion.

Mechanical adhesion is advantageous in that it provides for a rapid release of the substrate by a moving spider. Even if the cuticle of the bifid filaments were adhesive, certain mechanical considerations could not be neglected. The fact that these filaments maintain their spacing and do not adhere to each other suggests a mechanical function. *Phidippus* cannot adhere to extremely smooth surfaces, and these spiders maintain a better grip on rough surfaces than on relatively smooth surfaces. Different species of jumping spiders vary in their ability to cling to particular surfaces.

Thus it appears that the tenent setae of salticids function mechanically by grasping or applying force against minute surface irregularities.

Plate 8. The pretarsus of various salticids. A. Left leg I of adult male *Sassacus papenhoei* Peckham (x640). B. Left leg IV of adult male *S. papenhoei* (x640). C. Left leg I of immature *Salticus scenicus* (Clerck) (x600). D. Ventral margin of the pretarsus, left leg I of adult male *Metaphidippus* sp. (x1020). E. Left leg I of first instar (larval) *Phidippus rimator* (Walckenaer) (x1200). F. Left leg I of second instar *P. rimator* (x1070). AC, Anterior claw; FS, filamentous setae; Pr, pretarsus; PS, plume setae; SS, slit sensilla; T, tarsus; TS, tenent setae; WS, whorled setae.

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REFERENCES

ARNOLD, J. W., 1974. Adaptive features on the tarsi of cockroaches (Insecta: Dictyoptera). *International Journal of Insect Morphology and Embryology, 3:* 317-34.

BARTH, F. G., 1971. Der sensorische Apparat der Spaltsinnesorgane (*Cupiennius salei* Keys., Araneae). *Zeitschrift für Zellforschung und mikroskopische Anatomie, 112:* 212-46.

BARTH, F. G., 1972. Die Physiologie der Spaltsinnesorgane. I. Modellversuche zur Rolle des cuticularen Spaltes beim Reiztransport. *Journal of Comparative Physiology, 78:* 315-36.

BARTH, F. G. & LIBERA, W., 1970. Ein Atlas der Spaltsinnesorgane von *Cupiennius salei* Keys. *Zeitschrift für Morphologie und Ökologie der Tiere, 68:* 343-69.

DILLON, L. S., 1952. The myology of the araneid leg. *Journal of Morphology 90:* 467-80.

ELLIS, C. H., 1944. Mechanisms of extension in the legs of spiders. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 86:* 41-50.

FOELIX, R. F., 1970a. Chemosensitive hairs in spiders. *Journal of Morphology, 132:* 313-34.

FOELIX, R. F., 1970b. Structure and function of the tarsal sensilla in the spider *Araneus diadematus. Journal of Experimental Zoology, 175:* 99-124.

FOELIX, R. F. & CHU-WANG, I-WU, 1973a. The morphology of spider sensilla. I. Mechanoreceptors. *Tissue and Cell, 5:* 451-60.

FOELIX, F. F. & CHU-WANG, I-WU, 1973b. The morphology of spider sensilla. II. Chemoreceptors. *Tissue and Cell, 5:* 461-78.

FRANK, H., 1957. Untersuchungen zur funktionellen Anatomie der lokomotorischen Extremitäten von *Zygiella x-notata,* einer Radnetzspinne. *Zoologische Jahrbücher (Anatomie), 76:* 423-60.

GILLETT, J. D. & WIGGLESWORTH, V. B., 1932. The climbing organ of an insect, *Rhodnius prolixus* (Hemiptera: Reduviidae). *Proceedings of the Royal Society (B), 111:* 364-76.

HARRIS, D. J. & MILL, P. J., 1973. The ultrastructure of chemoreceptor sensilla in *Ciniflo* (Araneida, Arachnida). *Tissue and Cell, 5:* 679-89.

HILL, D. E., 1975. The structure of the central nervous system of jumping spiders of the genus *Phidippus* (Araneae: Salticidae). M.S. Thesis, Oregon State University, Corvallis Oregon: 94p.

KASTON, B. J., 1935. The slit sense organs of spiders. *Journal of Morphology, 58:* 189-210.

KELLEY, R. O., DEKKER, R. A. F. & BLUEMINK, J. G., 1973. Ligand-mediated osmium binding: Its application in coating biological specimens for scanning electron microscopy (SEM). *Journal of Cell Biology, 59:* 165a.

PARRY, D. A. & BROWN, R. H. J. 1959a. The hydraulic mechanism of the spider leg. *Journal of Experimental Biology, 36:* 423-33.

PARRY, D. A. & BROWN, R. H. J., 1959b. The jumping mechanism of salticid spiders. *Journal of Experimental Biology, 36:* 654-64.

PLATNICK, N. I., 1975. A revision of the holarctic spider genus *Callilepis* (Araneae, Gnaphosidae). *American Museum Novitates, 2573:* 1-32.

PLATNICK, N. I. & LAU, A., 1975. A revision of the *celer* group of the spider genus *Anyphaena* (Araneae, Anyphaenidae) in Mexico and Central America. *American Museum Novitates, 2575:* 1-36.

PRINGLE, J. W. S., 1955. The function of the lyriform organs of arachnids. *Journal of Experimental Biology, 32:* 270-78.

ROTH, L. M. & WILLIS, E. R., 1952. Tarsal structure and the climbing ability of cockroaches. *Journal of Experimental Biology, 119:* 483-517.

SEYFARTH, E. A. & BARTH, F. G., 1972. Compound slit sense organs on the spider leg: Mechanoreceptors involved in kinesthetic orientation. *Journal of Comparative Physiology, 78:* 176-91.

SHERMAN, R. G. & LUFF, A. R., 1971. Structural features of the tarsal claw muscles of the spider *Eurypelma marxi* Simon. *Canadian Journal of Zoology, 49:* 1549-56.

WALCOTT, C. & VAN DER KLOOT, W. G., 1959. The physiology of the spider vibration receptor. *Journal of Experimental Zoology, 141:* 191-244.

WHITEHEAD, W. F. & REMPEL, J. G., 1959. A study of the musculature of the black widow spider, *Latrodectus mactans* (Fabr.). *Canadian Journal of Zoology, 37:* 831-70.