ELASTIC ENERGY STORAGE IN THE PEDIPALPAL JOINTS OF SCORPIONS AND SUN-SPIDERS (ARACHNIDA, SCORPIONES, SOLIFUGAE)

Andrew T. Sensenig and **Jeffrey W. Shultz**:   Department of Entomology, University of Maryland, College Park, MD 20742, USA. E-mail: sensenig@wam.umd.edu

ABSTRACT.   Certain joints in the pedipalps of scorpions and sun-spiders lack extensor muscles but have elastic transarticular sclerites that store energy during flexion and return energy as elastic recoil during extension. This study quantifies the extension torque contributed by elastic recoil and hydraulic pressure in the chela (tibia–tarsus) and femur–patella joints of scorpions and the patella–tibia and tibi-tarsus joints of sun-spiders. Extension torque was measured as isolated joints were cycled through a natural range of angles and angular velocities by a computer controlled stepper motor. Resilience (efficiency of elastic energy return) of transarticular sclerites in the absence of internal fluid pressure was about 60% in scorpion joints and 80% in sun-spider joints. Elastic torque increased almost linearly with flexion angle in most joints except in the scorpion chela, where elastic torque decreased rapidly as the fully closed joint began to open, increased gradually and then decreased again near the fully open position. Hydraulic pressure contributed more to extension of pedipalpal joints of scorpions than those of sun-spiders. Our results indicate that mechanical properties of a ''passive'' transarticular sclerite can be changed by altering internal fluid pressure and by capitalizing on the sclerite's intrinsic viscoelasticity.

Keywords: Elasticity, resilience, biomechanics, arthropod, joints

Certain joints in the appendages of arachnids lack extensor muscles and are operated by elevated hemolymph pressure and flexor muscles (Shultz 1989, 1990, 1991), but recent work has shown that elastic mechanisms (springs) can supplement or even replace internal pressure as the principal extensor mechanism in leg joints (Sensenig & Shultz 2003). Specifically, elastic sclerites spanning the arthrodial membrane have been found in certain leg joints of scorpions (Scorpiones), sun-spiders (Solifugae) and harvestmen (Opiliones). Such sclerites appear to be absent in other arachnid orders. These transarticular sclerites are deformed (folded) during joint flexion, and most of the energy used in deforming the sclerite (80–90%) is recovered during extension in sun-spiders and harvestmen. Transarticular sclerites are also present in the pedipalpal joints of scorpions (Alexander 1967) and sun-spiders (original observations) (Figs. 1–4), appendages that are used for a variety of non-locomotor functions (e.g., prey capture, digging, probing, defense). The present work quantifies the relative contributions of elastic and hydraulic mechanisms in pedipalpal movement in scorpions and sun-spiders

and assesses the relative functional complexity of pedal and pedipalpal transarticular elastic sclerites.

In a previous study of elastic mechanisms of arachnid leg joints (Sensenig & Shultz 2003), we showed that forces exerted and recovered during joint movement generally increased monotonically with decreasing joint angle, although the entire force-angle curve could be shifted up or down the force axis by raising or lowering internal fluid pressure, respectively. Further, the difference between the input and output forces at a given joint angle were relatively constant across the normal range of motion, whether or not total force was influenced by internal pressures. The relatively simple structure of the force vs. angle curves for the elastic mechanism at leg joints may reflect the simplicity of the functional demands of locomotion rather than an intrinsic limitation of a passive elastic mechanism. Theoretically, heterogeneity in the structure and composition of a single transarticular sclerite could lead to heterogeneity in the strength, rate, viscoelasticity and resilience of elastic recoil at different joint angles and could affect the way in which internal pres-
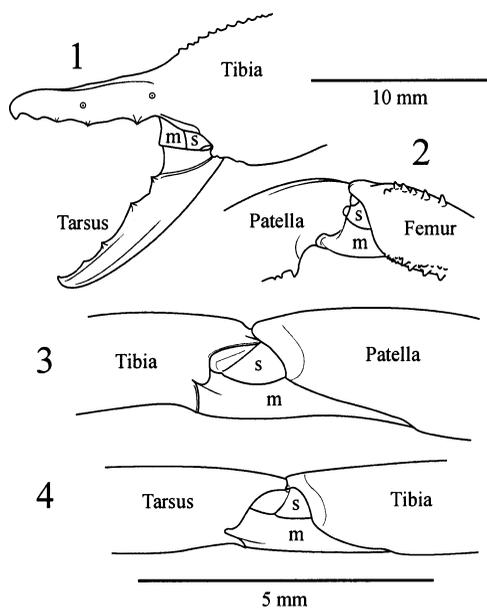
Figures 1–4.—*Heterometrus* pedipalpal joints: 1. chela (tibia–tarsus) joint; 2. femur–patella joint; upper scale bar. *Eremocosta* pedipalpal joints: 3. patella–tibia joint, 4. *Eremocosta*: tibia–tarsus joint; lower scale bar. Abbreviations: m = pliable arthrodial membrane; s = elastic transarticular sclerite.

sure interacts with elasticity. Given the relative functional versatility of pedipalps, we chose to examine the behavior of elastic mechanisms in these appendages with the expectation that functional heterogeneity of transarticular sclerites is more likely to be expressed in pedipalps than in legs.

We examined the mechanical properties of transarticular sclerites at the femur–patella and tibia–tarsus (chela) joints in the pedipalps of two scorpion species and the patella–tibia and tibia–tarsus joints of a sun-spider. The elastic mechanism of the scorpion chela showed considerable mechanical plasticity. The force vs. angle curve was substantially more complex than that observed in the legs and in the pedipalpal femur–patella joint and was affected by the magnitude of internal pressure and by the rate of joint movement. In contrast, the mechanical properties of the pedipalpal transarticular sclerite of the sun-spider were very similar to those of its legs; that is, the sclerite had a simple force vs. angle curve, showed less response to changes in internal pressure, and had no measured viscoelastic properties over the observed rates of

movement. These results show that transarticular elastic sclerites can be constructed with a variety of mechanical properties.

METHODS

Animals.—Desert hairy scorpions, *Hadrurus arizonensis* Ewing 1928 (Scorpiones, Iuridae) (*n* = 3, animal mass = 6.5 ± 1.4 g (mean ± S.D.)), Asian forest scorpions, *Heterometrus spinifer* Ehrenberg 1828 (Scorpiones, Scorpionidae) (*n* = 5, animal mass = 7.2 ± 1.8 g), and sun-spiders *Eremocosta gigasella* (Muma 1970) (Solifugae, Eremobatidae) (*n* = 5, mass = 1.50 ± 0.33 g) were purchased and housed in plastic shoe boxes. One voucher specimen of each species was deposited at the Denver Museum of Nature and Science. Water was provided ad libitum in either open petri dishes or glass vials plugged with cotton, and animals were fed one cricket per week for several weeks. Animals were killed by freezing to −80 °C and preserved at this temperature until used in an experiment. Fresh and frozen joints showed no differences in their relevant material properties.

Kinematic analysis of scorpion chelae.—Chelae of live, intact scorpions and amputated chelae were videotaped (Peak Performance High Speed 120 Hz Video System) so that joint extension occurred in the plane essentially parallel to that of the camera lens. Live scorpions were suspended by their metasomata to evoke a defensive posture in which the chelae were apparently opened to their greatest angle. Each chela was videotaped while the joint axis was held as perpendicular to the camera lens as possible. Several seconds of video were analyzed for each chela, and the maximum measured joint angle in the sequence was recorded as the maximum extension.
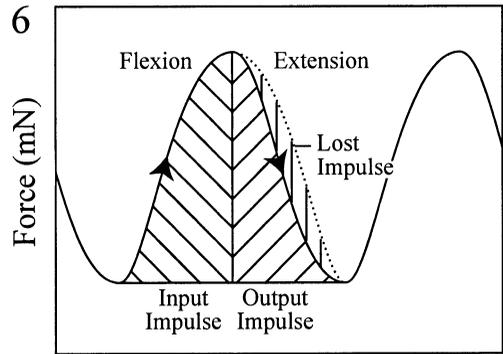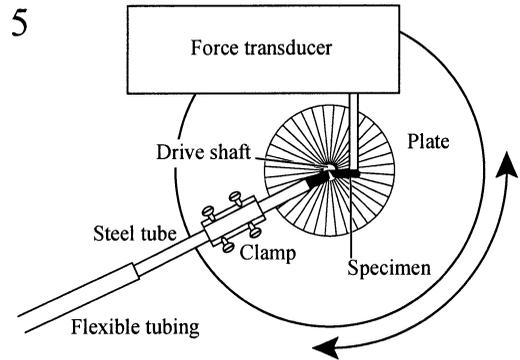
Isolated chelae were videotaped while opening under induced internal pressures of 0, 2.5 and 5 kPa. A motion analysis system (Motus version 6.0, Peak Performance Technologies, Inc.) was used to reconstruct the angular motion of the chela joint. The visible joint condyle, tip of the tarsus (mobile finger), and tip of the tibia (fixed finger) were digitized manually. Resolution of a typical video image was about 28 pixels mm^{-2}.

Kinetic analysis of isolated joints.—Details of joint preparation, induced joint rota-
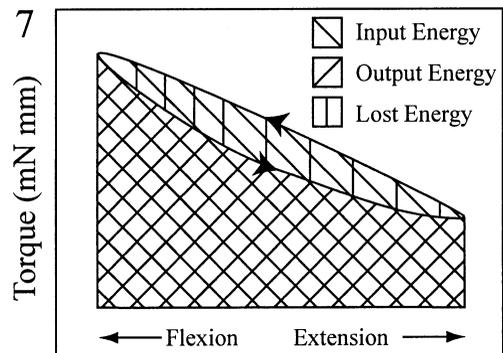
tion, modification of internal fluid pressure, and measurement of torque have been presented in Sensenig & Shultz (2003). In brief, one end of an isolated joint specimen was glued to a metal cylinder clamped to a metal disk, and the free end of the joint was sealed (Fig. 5). The shared lumen of the joint and cylinder was filled with saline (Ringers solution), and internal pressure was modified by changing the fluid level within a vertical titration cylinder connected to the free end of the metal cylinder by a rubber tube. The metal disk was rotated through specified angular excursions and velocities by a computer-controlled stepper motor. With the joint axis aligned with the center of the disk, rotations caused by the stepper motor simulated joint movement. A force transducer was applied to the free end of the joint specimen to measure input forces generated by induced joint flexion and output forces generated by elastic recoil during induced extension. Diagrammatic representations of the data generated by these methods are presented in Figs. 6–7.

Torques generated by joints at static mid-

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Figures 5–7.—Experimental apparatus and graphical explanation of data. 5. Experimental apparatus (diagrammatic) used to obtain dynamic measurements of elastic energy storage. An isolated joint is sealed at one end and glued to a metal cylinder that is clamped to a metal disk. The cylinder and joint are filled with Ringers solution. The rotational axis of the joint is aligned with the rotational axis of the disk and the cylinder fixed into position by a clamp. A stepper motor rotates the disk through a predetermined range, and the steel tube, clamp, and proximal segment of the appendage all move as if they were part of the disk. Force data are recorded by a force transducer contacting the free end of the appendage; 6. Changes in torque through time during a simulated cycle of joint movement. Elastic mechanisms resist flexion (input impulse) but assist extension (output impulse) with the difference representing entropic energy loss; 7. Work loops showing changes in torque over the range of joint angles. Area under the upper (loading) curve represents input energy during flexion, and the area under the lower (unloading) curve represents output energy due to elastic recoil during extension, and the difference represents lost energy. Output energy divided by input energy multiplied by 100 is the percent efficiency of elastic energy storage or resilience.

range angles were measured using the same force transducer, clamp, and rubber tubing used in the dynamic measurements (Fig. 5) but pressure was generated with a syringe (60 cc) and measured by a pressure transducer (Millar Instruments mikro-tip Model PC-360 with Millar Transducer Control Unit Model TCB-100) inserted in the rubber tubing. The pressure transducer was calibrated using the titration cylinder and was accurate to within 0.5 kPa. The two analog data sources (force

and pressure) were collected using an Analog/ Digital Interface Unit and Motus 6.0 software (Peak Performance Technologies) at 600 Hz. Changes in joint volume during flexion and extension were measured by observing fluid movement in a micropipette attached to the joint mounting tube as described by Sensenig & Shultz (2003).

RESULTS

Scorpion chela.—Suspended live *Heterometrus* and *Hadrurus* extended the chela to 45.7 ± 0.5° and 45.7 ± 1.7°, respectively. All chelae generated a characteristic pattern of force as a function of angle (Figs. 8–10, 13). Extension torque at 35° was 27 ± 5 mN mm (mean ± S.D.) in *Heterometrus* and 26 ± 9 mN mm in *Hadrurus*. Resilience of chelae at 0 kPa and 1 Hz was 60 ± 3% for *Heterometrus* and 60 ± 10% for *Hadrurus*. Resilience decreased slightly with increasing cycle frequency (i.e. angular velocity) (Fig. 12). Volume change in *Heterometrus* chelae was 9 ± 1 μl and 2.5 ± 0.5 μl in *Hadrurus*. Handedness in this joint was not apparent. At 4.9 kPa (37 mm Hg) of pressure, extension torque was two to four times higher than that generated by elastic extension alone (Fig. 10). Torque at 35° increased about ninefold in *Heterometrus* as pressure was increased from 0 to 30 kPa and about sixfold in *Hadrurus* (Fig. 14).

Kinematic analysis of isolated chelae (*n* = 4) showed an increase in opening speed with increasing internal pressure (Fig. 13). The maximum acceleration, corresponding to maximum force generation and the "kinks" of the curves in Fig. 13, occurred over a range of 30–35° in the unpressurized joint but occurred at 0–15° when the joint was pressurized.

Destruction of the transarticular sclerite and arthrodial membrane of isolated chelae destroyed all elasticity except in the range of about 0–5°. This elasticity occurred even in several-day-old dessicated claws. Intrinsic elasticity of the hinge thus appeared to govern the opening from 0–5° at 0 kPa. Chelae of resting scorpions were usually open to about 5° (original observation).

Scorpion femur–patella joints.—The working angles of the femur–patella joint of the pedipalp were approximately 80–130° in living animals under provocation. Femur–patella joints from the right pedipalp of *Heter-*
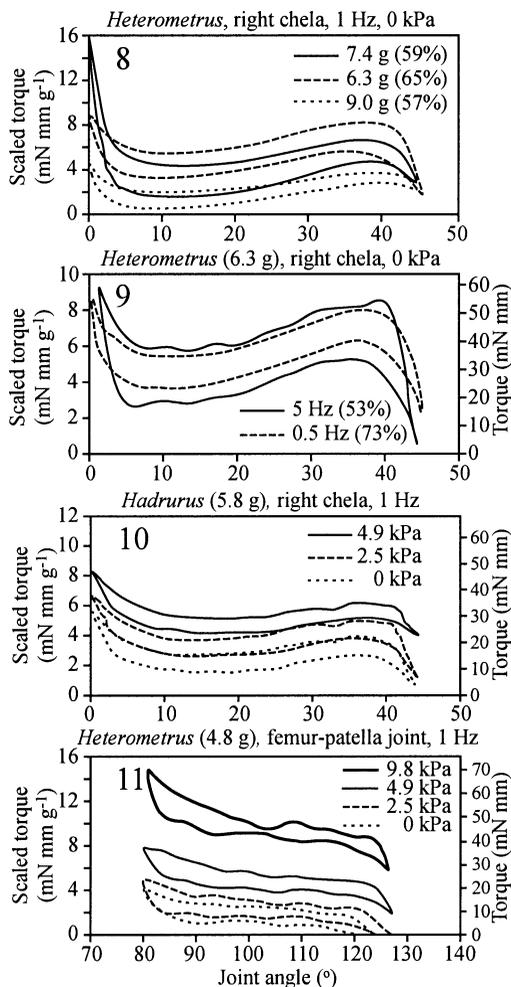
Figures 8–11.—Work loops showing the relationship between scaled torque and joint angle during representative cycles of flexion and extension. Scaled torque is torque divided by body mass. Percent elastic energy return or resilience is indicated for some work loops.

ometrus (*n* = 5, animal mass = 7.2 ± 1.8 g, volume change = 11 ± 1 μl) and *Hadrurus* (*n* = 3, animal mass = 6.5 ± 1.4 g, volume change = 8.5 ± 0.5 μl) were used. The transducer input tube contacted the joint between 6 and 8 mm from the axis of rotation. Resilience at 1 Hz was 64 ± 11% for *Hadrurus* and 76 ± 10% for *Heterometrus*. Force generation during flexion and extension was unimodal (Fig. 11) for the femur–patella joint, in contrast to the chela (Fig. 8–10). Torque at 105° during unloading was 41 ± 29 mN mm for *Heterometrus* and 33 ± 17 mN mm for
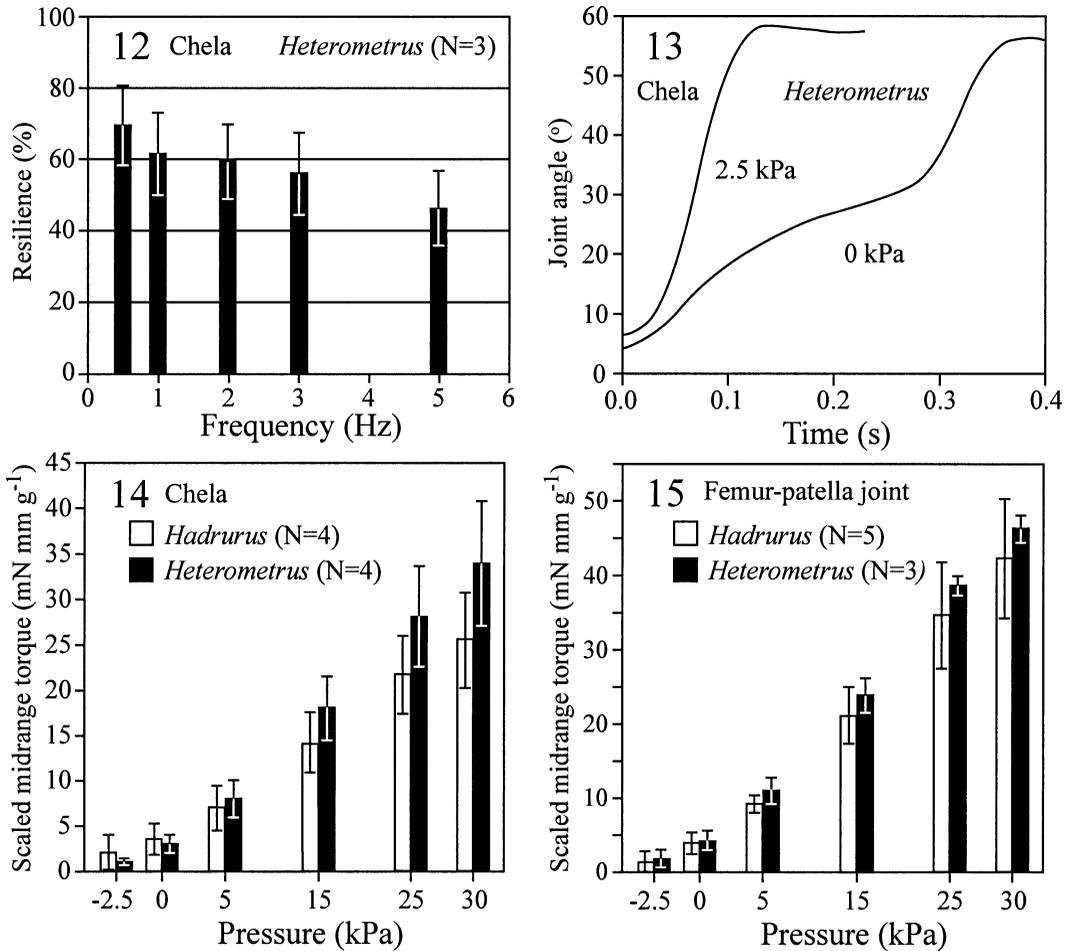
Figures 12–15.—Effects on cycle frequency and internal fluid pressure on resilience and torque in the pedipalpal joints of scorpions. 12. Resilience decreases with increasing cycle frequency in the chela joint of *Heterometrus*; 13. Internal fluid pressure increases the rate of opening at the chela joint and lowers the angle at which maximum acceleration occurs (the slope of the curves represent the rate of opening, while the ''kinks'' represent acceleration); 14. Scaled midrange torque increases with internal fluid pressure in the chela joint.; 15. Scaled torque increases with internal fluid pressure in the femur-patella joint. Error bars represent 95% confidence intervals around the mean.

Hadrurus. Scaled torque (torque divided by body mass) at 105° was 7 ± 0.8 mN mm g^{-1} for *Heterometrus* and 3.7 ± 1.9 mN mm g^{-1} for *Hadrurus*. Torque at the femur-patella joint of both *Heterometrus* and *Hadrurus* increased twofold when pressure was increased from 0 to 4.9 kPa (0 to 37 mm Hg) (Fig. 11). Extension torque generated by the static joint at 30 kPa was about ninefold higher than at 0 kPa (Fig. 15). Extension torque decayed 26 ± 6% when the joint was held at 90° for 1 s (Fig. 16).

Sun-spider joints.—*Eremocosta* in the lab-oratory moved their pedipalps in a slow, methodical manner, and the pedipalps showed very little movement during normal locomotion. *Eremocosta* used step frequencies of 2–8 Hz in the fourth leg when moving in the laboratory. While some pedipalp movement such as prey capture may be comparably rapid, most movement appears much slower than leg movement.

The morphology of the patella–tibia joint and observations of living sun-spiders suggested a natural range of motion of 150–90°. The patella–tibia joints of *Eremocosta* (*n* = 5,
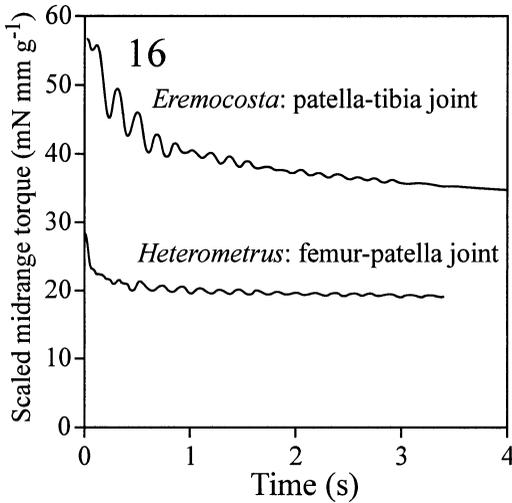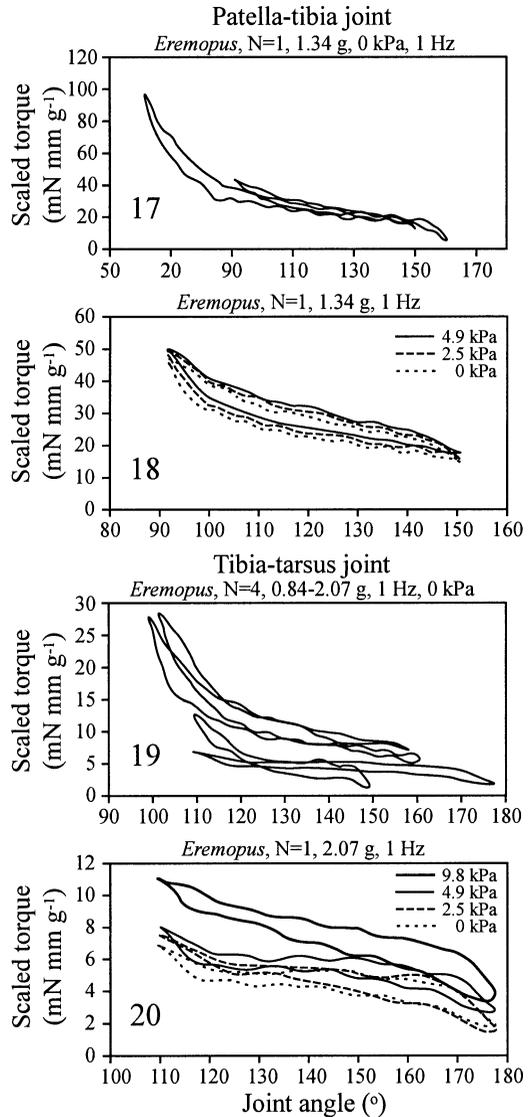
Figure 16.—Examples of the time course of the decay of elastic torque in joints held at a static position under 0 kPa internal pressure. The graph indicates that transarticular sclerites have a viscoelastic property which may reduce energy used to maintain a particular posture.

Figures 17–20.—Work loops of pedipalpal joints in the sun-spider *Eremocosta*.

mass = 1.50 ± 0.33 g, volume change = 1.0 ± 0.5 μl) at 1 Hz were highly resilient (82 ± 6 %) with an approximately linear increase in elastic force over the range of 150–90° (Figs. 17, 18). When rotated through more than 90°, the force curve showed an increase in slope at this high flexion (Fig. 17). At extension greater than 150°, the force of extension drops off abruptly to 0 N, and the isolated joint only opens to about 160°. Torque at 120° (midrange) extension while unloading was 17 ± 8 mN mm. Scaled torque at 120° while unloading was 15 ± 10 mN mm g^{-1}. Resilience was not significantly different over frequencies of 0.2 to 8 Hz. Fluid pressure of 4.9 kPa (37 mm Hg) increased torque by about 20% (Fig. 21), and torque generated at 30 kPa was about twofold higher than at 0 kPa (Fig. 21). Decay in extension torque after 1 s from flexion to 90° was about 40% (Fig. 16).

The natural range of motion of the tibia-tarsus joint for *Eremocosta* ($n = 4$, body mass $= 1.54 \pm 0.48$ g, volume change approximately 0.5 μl) was estimated to be 160–100° from joint morphology. The tibia–tarsus joint was smaller in diameter than the patella–tibia joint and generated lower extension torques. Torque at the midrange angle of 130° was 10 ± 2.1 mN mm, with resilience of 78 ± 9% at 1 Hz (Figs. 19, 20). Scaled torque at the midrange angle of 130° was 7 ± 2.8 mN mm g^{-1}. An internal pressure of 4.9 kPa (37 mm Hg) increased torque at midrange by about 30% of that generated by the transarticular sclerite alone (Fig. 21). Increasing pressure from 0 to 30 kPa resulted in an approximately three-fold increase in extension torque (Fig. 21).

DISCUSSION

Mechanics of joint extension in arachnids.—Extension generated partially or entire-
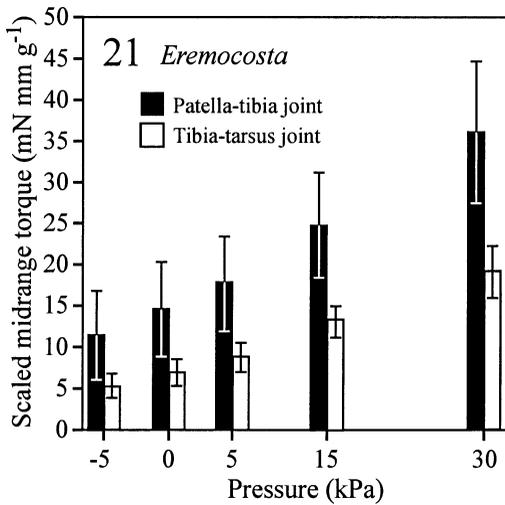
Figure 21.—Scaled midrange torques at applied internal fluid pressures. Midrange torques are those torques generated by a joint at an angle located midway between the maximum and minimum angles. Error bars represent 95% confidence intervals around the mean.
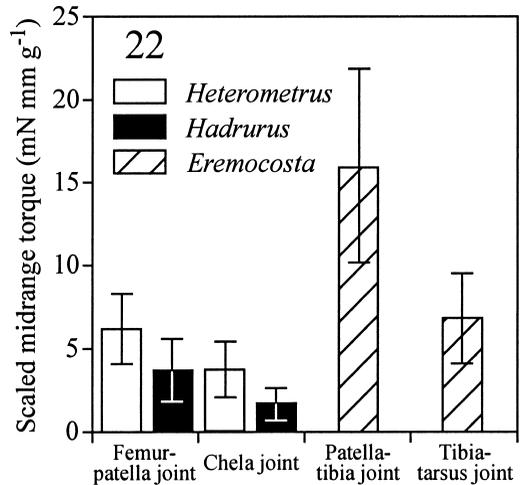

Figure 22.—Scaled midrange torque (torque divided by body mass) generated by elastic transarticular sclerites at 0 kPa internal fluid pressure. Note that proximal joints produce higher torques than distal joints within a species and that the sun-spider *Eremocosta* produces substantially greater scaled midrange torques than scorpions.

ly by elastic recoil occurs in joints of several arachnid groups, where it functions in locomotion, prey capture, climbing, and burrowing. Comparisons of elastic energy storage among joints within and among species highlights the important role of elasticity in the pedipalps of the sun-spider *Eremocosta*, in which the transarticular sclerites are highly resilient and generate proportionally large extension forces. The pedipalpal patella–tibia joint in *Eremocosta* generated about 30 μJ (20 μJ g^{-1}) by elastic extension, while the pedipalpal tibia–tarsus joints and pedal patella–tibia joints generated about 10 μJ (7 μJ g^{-1}). By comparison, the chela joint of the more massive *Heterometrus* generated about 30 μJ (5 μJ g^{-1}) and the femur–patella joint generated about 60 μJ (10 μJ g^{-1}). It is noteworthy that the larger and more powerful of the two elastic joints in sun-spider and scorpion pedipalps is also the more proximal (Fig. 22) and stored two to three times more energy than the distal sclerite. The tendency to have larger proximal sclerites may be important in *Eremocosta* for reducing total limb inertia and in allowing for finer motor control by the antagonistic flexor muscles at the tip of the pedipalp.

Resilience of the elastic sclerites in *Eremocosta* is very high (up to 90%), which suggests that these structures are comprised of resilin or some similar rubber. Resilin is a highly resilient protein of arthropods and is known to return large proportions of energy in the jumping mechanism of fleas (Bennet-Clark & Lucey 1967), to increase energetic efficiency of flight in locusts (Weis-Fogh 1959), and to serve as an antagonist to muscles at distal joints in roaches (Neff et al. 2000). Resilin has been identified in the cuticle of the chela (tibia–tarsus) joint of the scorpion *Heterometrus swammerdami* Simon 1872 (Govindarajan & Rajulu 1974).

Scorpion chela.—Folding of the transarticular sclerite during flexion is responsible for almost all of the energy stored in the chela at 0 kPa, although a very small amount may be stored in the arthrodial membrane itself. From the geometry of folding, Alexander (1967) reasoned that most of the extension force would be generated at an intermediate joint angle, where the vector of 'sclerite force' would be most optimal for opening the chela. Alexander identified three phases in the opening of the chela characterized by different angular velocities. Rapid opening occurred from 0–6°, slow opening from 6–25° and rapid opening ("click") from 25–50°. The present study measured high torques over the ranges

at which Alexander observed rapid extension. We agree with Alexander (1967) that high forces at small angles (0–5°) are probably due to intrinsic elasticity of the hinge and that high force at larger angles (30–42°) are due to maximum effectiveness of the folded sclerite. This observation may explain why resting scorpions typically maintain the chelal angle in the 5–10° range, as this would minimize the effort expended by flexor muscles. These mechanical properties might be expected to occur at all joints with transarticular sclerites but were actually observed only in the chela.

Resilience of the chela joint decreased as the frequency of movement increased. We attribute this to the low torque produced by the elastic sclerite in this joint. The elastic torque must overcome both the internal friction of the joint and accelerate the tarsus, and thus the joint would have a natural rate of extension. When the induced extension was rapid, this speed was closer to the limit at which the joint could naturally extend, and hence the force exerted by the joint on the force transducer was lower. By analogy to the animal, no other extension mechanism other than the elastic sclerite is needed to open the chela at low speeds, but it is likely that most situations require faster movements assisted by hydraulics.

The large diameters of the pedipalpal segments and the bulging membrane of the femur–patella joint in scorpions under stimulation suggest that hydraulic extension may be used at the pedipalpal joints. *Opistophthalmus latimanus* Koch 1837 generated maximum pressure of 27 kPa (200 mm Hg) and torque of about 200 mN mm in the chela during stimulation (Alexander 1967). These values are consistent with our measurements of isolated chelae (Figs. 8–10, 14). Even at relatively low pressure (2.5 kPa) most of the work during extension of the chela would be performed by pressure. The contribution of the elastic mechanism is still apparent during pressurized extension, as evidenced by the characteristic variation in force over joint angle (Figs. 8–10). Hydraulics and cuticular elasticity are both used in the chela, and the elastic contribution is minimal when the animal generates high torque through high pressure. Alexander suggested that scorpions may be generating pressure for extension within the pedipalp because pressures in the prosoma of scorpions are much lower than those observed in the appendages, but a mechanism of local pressure generation has not been found.

Scorpion femur–patella joint.—The relatively large transarticular sclerites of the femur–patella joint of the scorpion pedipalp were described by Alexander (1967) in *Opistophthalmus latimanus*. Similar sclerites occur throughout Scorpiones but are most obvious in dark-colored scorpions where the dark sclerite contrasts with the lighter arthrodial membrane (Alexander 1967). In the femur–patella joints examined here, torque generation of unpressurized joints decreased abruptly at the beginning of extension (especially in *Hadrurus*), but extension torque was high enough to extend the joint completely.

Alexander (1967) noted two distinct regions of the arthrodial membrane in *O. latimanus*, namely, a pliable pad and a stiffer scute. The pliable pad is compressed at the onset of flexion with little deformation of the membrane, and the scute begins to fold once torque is high enough. This two-part mechanism results in greater uniformity in the elastic torque over the range of joint extension than that produced at the chela. Alexander attributed the evolution of this complexity to the large angular excursions at the femur-patella joint, and the need to prevent overextension and damage. While we were not able to discriminate the two regions of the cuticle in the species we examined, the uniform torque we observed during extension suggests that such a mechanism is present (Fig. 11).

Increasing the internal fluid pressure of isolated femur-patella joints increased extension torque in a manner similar to that observed in the chela. Torque at the femur–patella joint was not measured in living scorpions, but it is likely that torques are produced that are substantially higher than those generated by the elastic mechanism alone. Our measurements of torque as a function of pressure and Alexander's (1967) measurement of a maximum pressure in the pedipalp (27 kPa) suggest that the highest midrange torque possible in the femur-patella joint is about 450 mN mm, whereas maximum elastic torque is about 50 mNmm.

Sun-spider joints.—Transarticular sclerites occur at the patella–tibia and tibia–tarsus joints of all post-cheliceral appendages in sun-spiders. Pedipalps are not typically used in propulsion but are used for probing, grabbing

prey, tamping soil and climbing (Punzo 1998). The presence of elastic joints in both the pedipalp and leg VI suggests that the body of *Eremocosta* could be modeled as a spring operating in the anterior to posterior axis and that simultaneous elastic extension of these joints could be used in tamping or moving debris. Internal fluid pressures have not been reported from sun-spiders, but it is unlikely that that they are high enough to be important in leg extension given that only extremely high pressures have any effect on extension torque (Figs. 17–21). In fact, sun-spiders may be an example of extreme dependence on elastic extension of major joints in both the pedipalp and legs.

Eremocosta, like several species of sun-spiders (Punzo 1998), climbs and can even scale a vertical glass surface using adhesive organs on the tip of the pedipalp (pers. obs.). During this behavior, the flexor muscles of the pedipalp lift the entire body with little assistance from other appendages. This is typically a slow movement (~0.5 Hz) and, due to the fact that it is an attempted escape, may be indicative of the power capabilities of the pedipalpal muscles. Rough calculations suggest that, to lift the body, the flexor muscles perform about ten times the work contained in a flexed pedipalpal sclerite. Elastic extension is relatively powerful in these animals, but the most powerful flexion movements can easily overcome the sclerite's folding resistance and can power movements at levels that would be impossible to attain solely through elastic extension.

Potential advantages of elastic mechanisms in arachnid pedipalps.—The use of elastic extension in arachnids requires explanation in light of its apparent evolutionary derivation from an ancestral hydraulic mechanism (Shultz 1989, 1990, 1991, 1992). Advantages of elastic extension over hydraulics during locomotion include reduction of appendicular inertia, mechanical or physiological efficiency of elastic sclerites over hydraulics, and elastic absorption of potentially destabilizing forces (Sensenig & Shultz 2003). Rapid predatory movements and persistent elevation of the pedipalps during locomotion both call for reduction in pedipalpal mass. While the slender pedipalps of *Eremocosta* are similar to the legs in having a relatively small mass, the pedipalps of scorpions suggest that reduction of weight is not so important as the ability to withstand large forces involved in prey capture and defense. Dessication may be a hazard to many scorpions and sun-spiders, and maintaining some functionality of limbs during environmental extremes would be an advantage of elastic extension. Little extension occurs in heavily dessicated scorpions. While assigning the cause of behavior in such stressed animals to a specific mechanical deficit such as low hydraulic fluid is difficult, some work has suggested that full extension capability returns after Ringers solution is injected into the animal (Alexander 1967).

Transarticular sclerites function as spring-like extensors in the pedipalps of scorpions and sun-spiders. Variation in the size, strength and resilience of elastic transarticular sclerites of the pedipalp and legs in these and other arachnids (Sensenig & Shultz 2003) illustrates evolutionary modification of a passive mechanical structure for diverse biological roles. The transarticular sclerites of sun-spiders appear to be specialized for generating simple but highly resilient patterns of extension torque independent of internal fluid pressure, while those of the scorpion are less resilient but synergistic with internal fluid pressure. It is not yet known whether there are necessary functional trade-offs between the resilience and plasticity in transarticular sclerites.

ACKNOWLEDGMENTS

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