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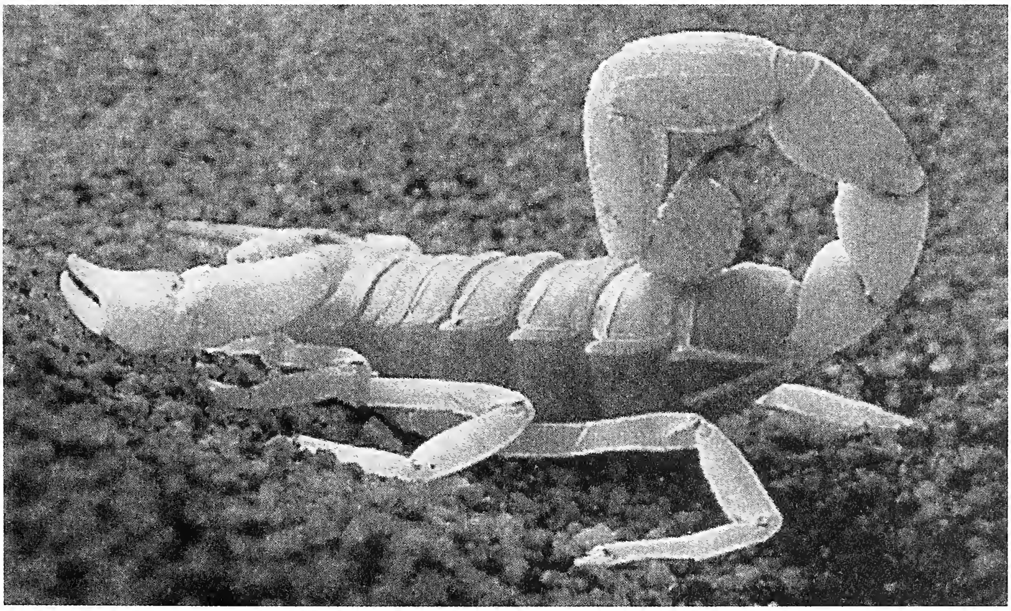

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ELASTIC ENERGY STORAGE IN THE PEDIPALPAL JOINTS OF SCORPIONS AND SUN-SPIDERS (ARACHNIDA, SCORPIONES, SOLIFUGAE)

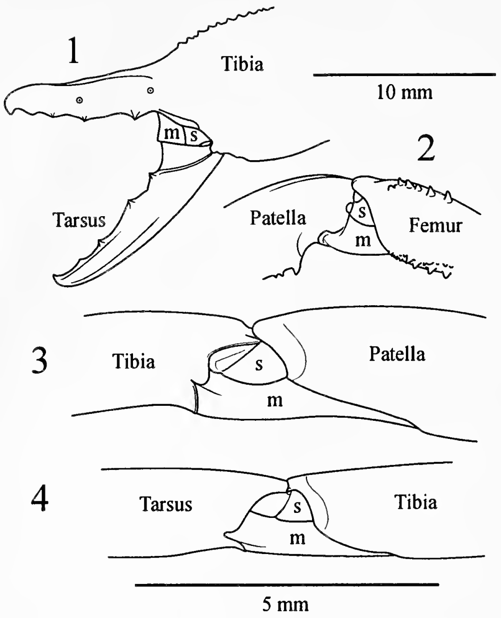
Andrew T. Sensenig and **Jeffrey W. Shultz**: Department of Entomology, University of Maryland, College Park, MD 20742, USA. E-mail: sensenig@wam.umd.edu

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 visco-elastic 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 rotation, 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-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

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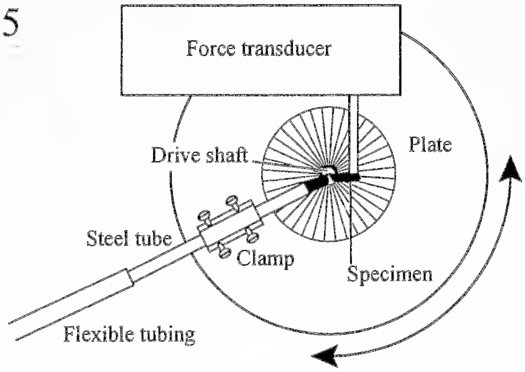

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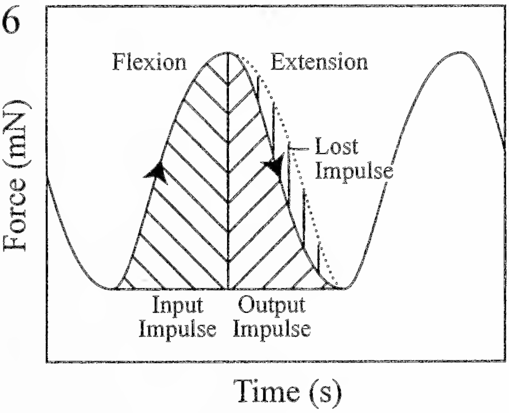

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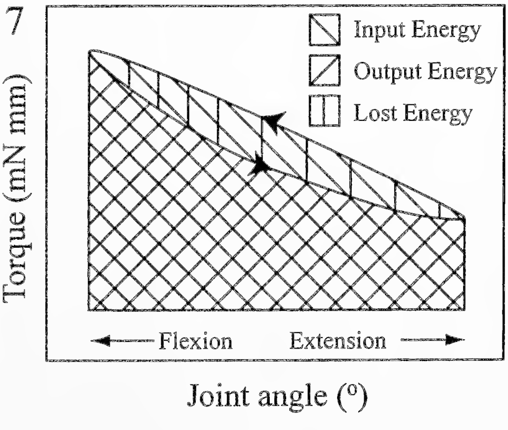

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Figures 5–7.—Experimental apparatus and graphical explanation of data. 5. Experimental apparatus (diagrammatic) used to obtain dynamic measurements of elastic energy storage. An isolated joint is sealed at one end and glued to a metal cylinder that 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.

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).

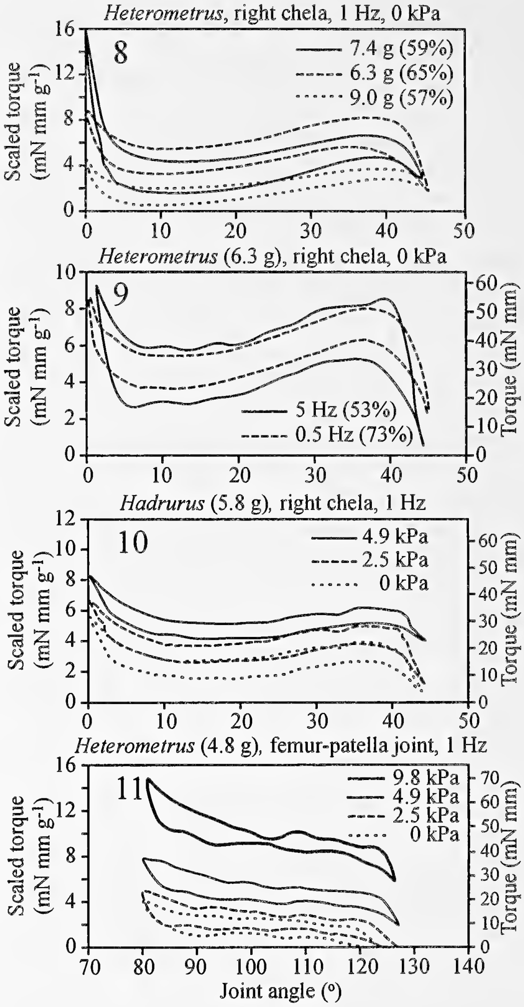
RESULTS

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).

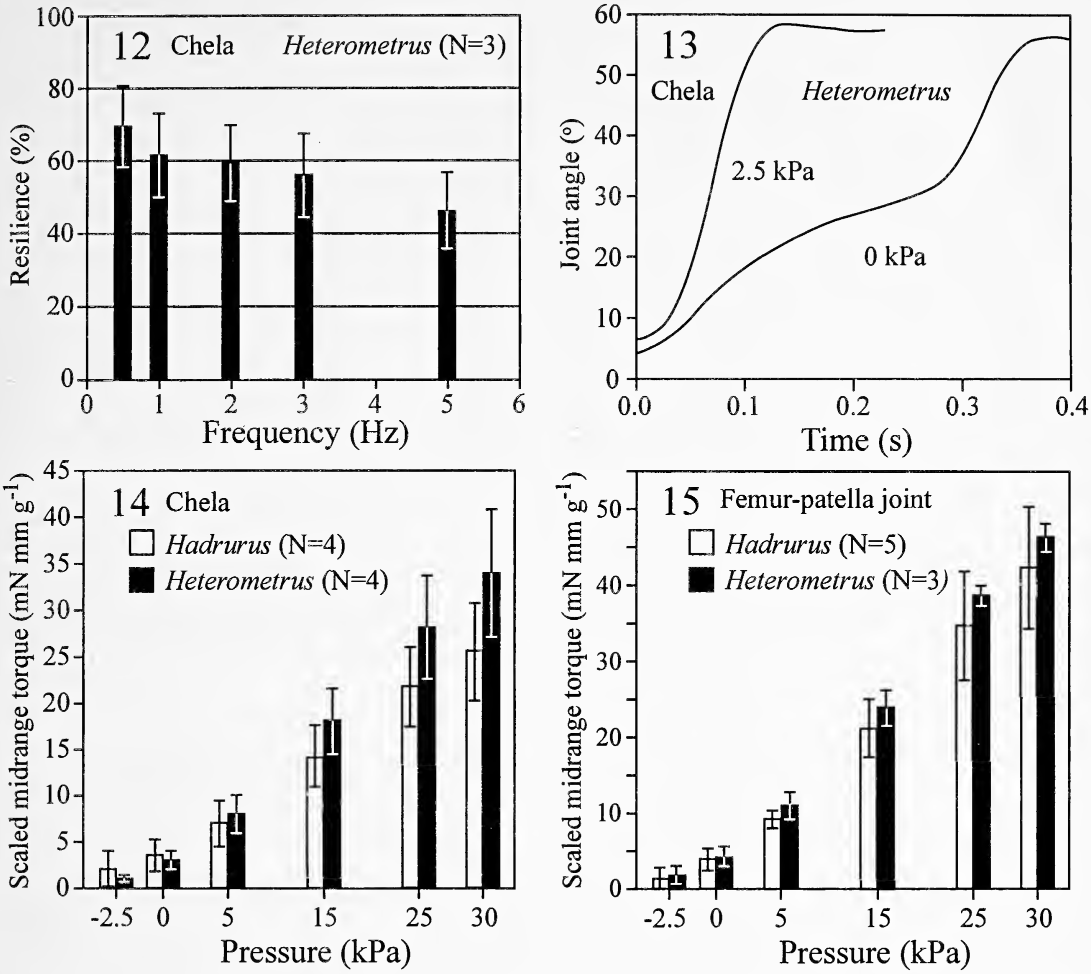
Kinematic analysis of isolated chelae ($n = 4$) showed an increase in opening speed with increasing internal pressure (Fig. 13). The maximum acceleration, corresponding to maximum force generation and the "kinks" of the curves in Fig. 13, occurred over a range of 30–35° in the unpressurized joint but 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 *Heterometrus* ($n = 5$, 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 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.



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 laboratory 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,

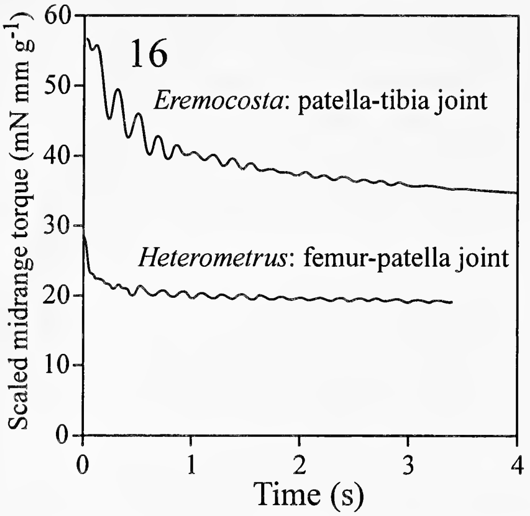
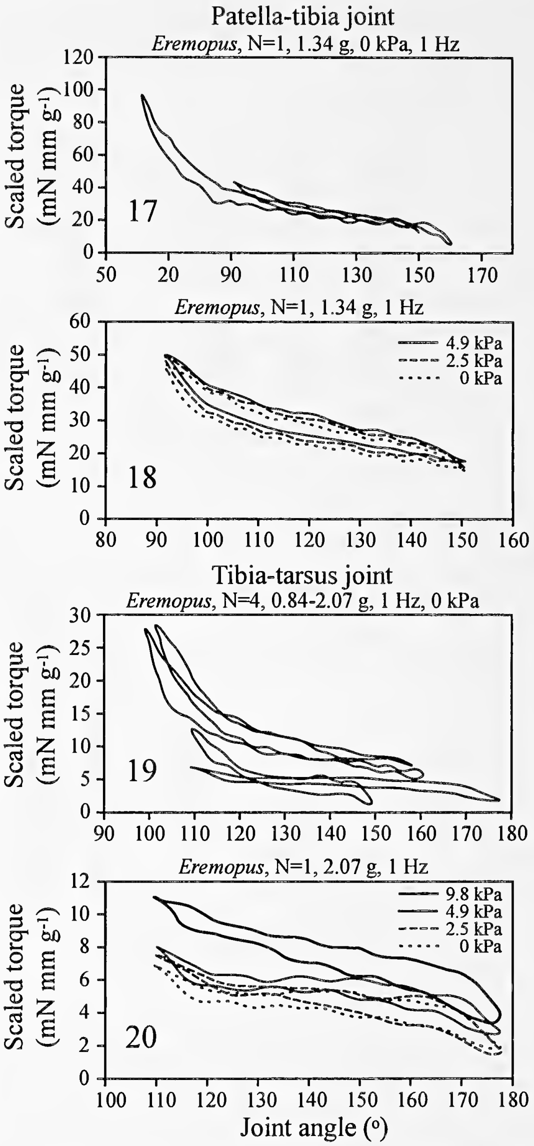


Figure 16.—Examples of the time course of the decay of elastic torque in joints held at a static position under 0 kPa internal pressure. The graph indicates that transarticular sclerites have a viscoelastic property which may reduce energy used to maintain a particular posture.



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 ± 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-

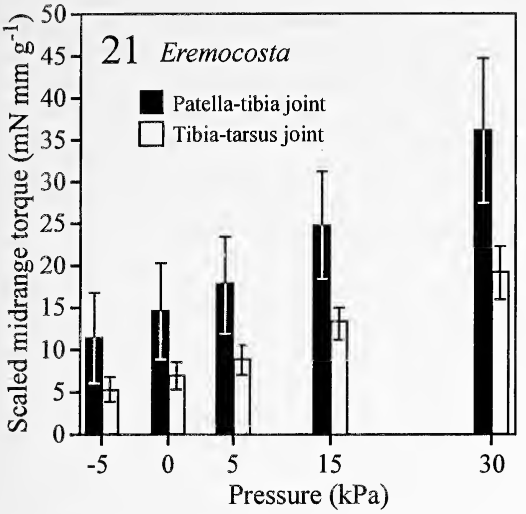


Figure 21.—Scaled midrange torques at applied internal fluid pressures. Midrange torques are those torques generated by a joint at an angle located midway between the maximum and minimum angles. Error bars represent 95% confidence intervals around the mean.

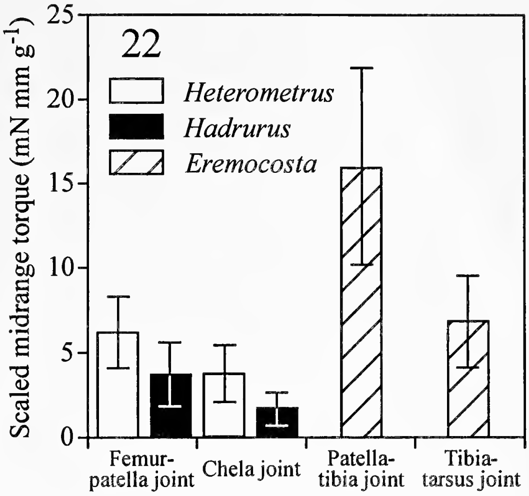


Figure 22.—Scaled midrange torque (torque divided by body mass) generated by elastic transarticular sclerites at 0 kPa internal fluid pressure. Note that proximal joints produce higher torques than distal joints within a species and that the sun-spider *Eremocosta* produces substantially greater scaled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

Alexander, A.J. 1967. Problems of limb extension in the scorpion, *Opisthophthalmus latimanus* Koch. Transactions of the Royal Society of South Africa 37:165–181.

Bennet-Clark, H.C. & E.C.A. Lucey. 1967. The jump of the flea: a study of the energetics and a model of the mechanism. Journal of Experimental Biology 47:59–76.

Ewing, H.E. 1928. The scorpions of the western part of the United States. United States National Museum, Washington 73:27–30.

Govindarajan, S. & G.S. Rajulu. 1974. Presence of resilin in a scorpion *Palamnaeus swammerdami* and its role in the food-capturing and sound-producing mechanism. Experientia 15:908–909.

Hemprich, F.W. & C.G. Ehrenburg. 1828. Plates I & II in Symbolae Physicae seu Icones et Descriptiones Animalium Evertebratorum sepositis Insectis quae ex itinere per Africum borealum et Asiam occidentalem. Friderici Guilelmi Hemprich et Christiani Godofredi Ehrenberg, studio novae aut illustratae redierunt. Percensuit edidit Dr. C.G. Ehrenberg. Decas. I. Berolini ex officina Academica, venditur a Mittlero: Index and Plates.

Koch, C.L. 1836–45. Die Arachniden. 12 vols. Nuremburg.

Muma, M.H. 1970. A synoptic review of North American, Central American and West Indian Solpugida (Arthropoda, Arachnida). Arthropods of Florida and Neighboring Land Areas 5:1–62.

Neff, D., S.F. Frazier, L. Quimby, R.-T. Wang & S. Zill. 2000. Identification of resilin in the leg of cockroach, *Periplaneta americana*: confirmation by a simple method using pH dependence of UV fluorescence. Arthropod Structure & Development 29:75–83.

Punzo, F. 1998. The Biology of Camel-Spiders. Kluwer Academic Publishers, Boston.

Sensenig, A.T. & J.W. Shultz. 2003. Mechanics of cuticular elastic energy storage in leg joints lacking extensor muscles in arachnids. Journal of Experimental Biology 206:771–784.

Shultz, J.W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. Zoological Journal of the Linnean Society 97:1–56.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.

Shultz, J.W. 1991. Evolution of locomotion in Arachnida: the hydraulic pressure pump of the giant whipscorpion, *Mastigoproctus giganteus* (Uropygi). Journal of Morphology 210:13–31.

Shultz, J.W. 1992. Muscle firing patterns in two arachnids using different methods of propulsive leg extension. Journal of Experimental Biology 162:313–329.

Simon, E. 1872. Etudes sur les scorpions. Revue et Magazine de Zoologie 2(1, 2):1–13,51–59,97–101.

Weis-Fogh, T. 1959. Elasticity in arthropod locomotion: a neglected subject, illustrated by the wing system of insects. Proceedings of the Fifteenth International Congress on Zoology (1958):393–395.

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TAXONOMIC VARIATION AMONG SPIDERS IN THE ABILITY TO REPEL WATER: SURFACE ADHESION AND HAIR DENSITY

Robert B. Suter: Department of Biology, Vassar College, 124 Raymond Avenue, Poughkeepsie, New York 12604 USA. E-mail: suter@vassar.edu

Gail E. Stratton: Department of Biology, University of Mississippi, University, Mississippi 38677 USA

Patricia R. Miller: Department of Biology, Northwest Mississippi Community College, Senatobia, Mississippi 38668 USA

ABSTRACT. A variety of arthropods forage and avoid predators via locomotion on the surfaces of ponds and streams. For these animals, cuticular hydrophobicity functions to keep them dry and well supported by the water's surface tension, and also allows them to move easily between wet and dry habitats. Among spiders, members of the family Pisauridae exemplify this semi-aquatic lifestyle and, not surprisingly, these spiders remain entirely dry even when submerged. In the current study, we sought to quantify the degree to which spiders in a variety of families resist wetting by liquid water. Two properties of a spider's cuticular hairs are predominant in determining this resistance: adhesion energy (a consequence of molecular interactions between the hair surface and water) and hair density. When hair density is low, the adhesion energy of the cuticle itself also plays a role. Among the ten families we studied, pisaurids and pholcids defined the ends of the spectrum of resistance, with the pisaurids nearly 50 times more resistant to wetting than the pholcids. We discuss both the impact of this variation on spiders' potential for aquatic locomotion and the variety of selective forces that may have contributed to this impressive variation in capabilities.

Keywords: Cuticle, adhesive forces, hydrophobicity, evolution

Fishing spiders (Pisauridae) are conspicuously adept at life on the water. They move easily across the water surface (Gorb & Barth 1994; McAlister 1959; Shultz 1987; Suter et al. 1997), males can find females by following the females' pheromone-impregnated draglines on the water surface (Roland & Rovner 1983) and both sexes detect prey by decoding the surface waves created as insects struggle to escape the adhesive energy of the surface tension (Bleckmann 1985). We expect pisaurids to possess a suite of attributes that facilitate their lifestyle, whether these attributes antedated the move to a semi-aquatic habit or, as adaptations, were subsequent modifications. Among the expected attributes is a surface (both of legs and body) that remains dry when in contact with liquid water (Fig. 1). The rationale for this expectation has several parts. First, other arthropods such as water striders (Insecta: Gerridae and Veliidae) under similar circumstances share the trait (e.g., Andersen 1976); second, aquatic locomotion is substantially enhanced when the legs providing the propulsion remain dry (Suter & Wildman 1999); third, access to oxygen when submerged is strongly facilitated by plastron respiration (e.g., Rovner 1986; Hebets & Chapman 2000) which, in turn, requires a surface covered with hydrophobic hairs (Cheng 1973); and fourth, small organisms find it very difficult to extricate themselves from capillary adhesion if their surfaces are wetted (Fig. 1) (Vogel 1988).

The dangers of capillary adhesion (being unable to climb out of a small puddle, or having several legs stuck to each other by a few drops of water) are not restricted to spiders that live on the water surface. Ballooning spiders can descend into ponds and streams or even into drops of water, raindrops can fall on spiderlings and a stiff breeze can dislodge a spider from vegetation or its web and cause it to land in a puddle or pond. Thus in this con-

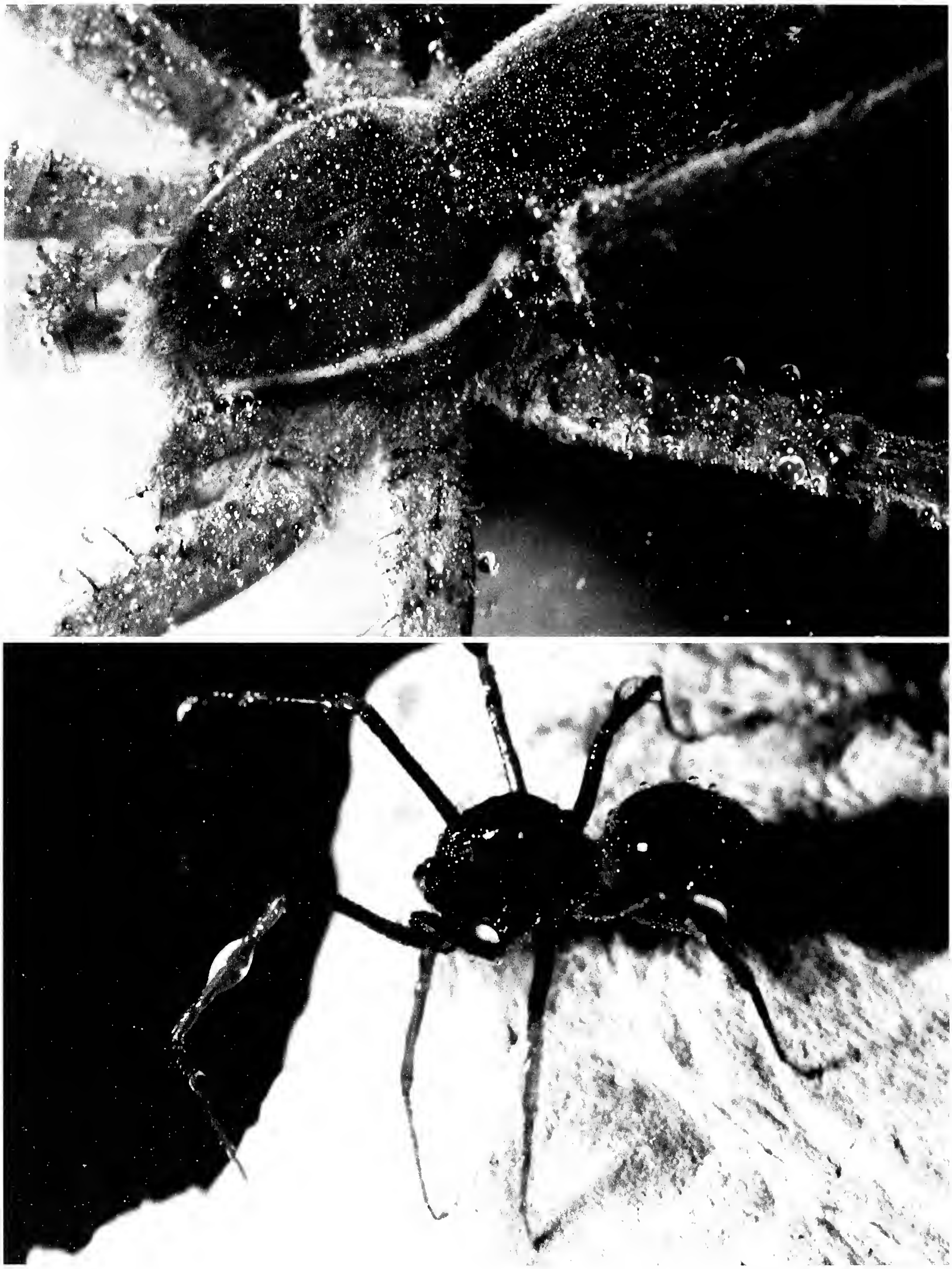

Figure 1.—The surfaces of spiders vary both in hair density (hairs/mm) and in the chemical composition of the cuticle and its hairs. At one end of the spectrum are spiders in the family Pisauridae (top) with strongly hydrophobic hairs that are also very dense. Near the other end of the spectrum are the spitting spiders (Scytodidae, bottom) with very few, relatively hydrophilic, hairs. Water droplets on hydrophobic surfaces are approximately spherical while those on hydrophilic surfaces spread widely.

text, a strongly hydrophobic covering would apparently serve spiders in all but the most xeric of environments. To the contrary, our recent survey of water surface locomotion in spiders (Suter et al. in press; Stratton et al. in press) suggested that strong hydrophobicity is far less common than would be expected if susceptibility to entrapment by capillary adhesion were the only selective force influencing cuticular surface chemistry. In the study reported here, we have measured the functional hydrophobicity of spiders in ten families to help us understand the relationship between cuticular hydrophobicity and the selective forces that may have contributed to its evolution and maintenance.

METHODS

Spiders.—We tested 41 spiders in 25 species distributed among 10 families (Table 1). Pisaurids and scytodids were drawn from captive populations maintained in the laboratory of R. Suter, and spiders in the other families were captured in the field for use in this and a related study (Stratton et al. in press). Each field-captured spider was held for up to 4 days in a plastic vial under the high humidity provided by a wet paper towel pad attached to the inside surface of the vial.

We tested a single leg from each spider. To remove a leg for testing, we inserted forceps into the holding container and grasped a single leg (II or III) approximately in the middle of the femur. Most of the individuals tested readily and promptly (after < 3 s) autotomized the grasped leg and survived the leg removal with no other detectable detriment. A few spiders did not promptly autotomize the grasped leg. We immediately released these from the grasp of the forceps, cooled and then froze them at -15 °C, and removed the leg with iris scissors. The still-frozen spider was then preserved in alcohol.

Voucher specimens for this study are deposited in the Mississippi Entomological Museum.

Functional hydrophobicity.—The two surface attributes that contribute to functional hydrophobicity are hair density and the molecule-level physical interaction between the hair or cuticle surface and water. To measure hair density, we digitized a lateral view of each test leg (Olympus SZX12 stereo dissecting microscope, Panasonic GP-KR222 video camera, Sony DCR-TRV900 used as a digital recorder) and imported the image into NIH Image (shareware from NIH) on a Macintosh G4 computer (Apple Computer, Inc.). In Image, we drew three transects on the metatarsus, each perpendicular to the long axis of the leg segment, then measured the length of the transect and the number of hairs transected. Our measure of hair density for that test leg was the average of the densities (hairs/mm) of the three transects.

To quantify the molecule-level interaction between water and the exposed surface of the leg (cuticle per se or cuticular hairs), we measured the contact angles formed between very small droplets of distilled water and the relevant surfaces on the legs of spiders. The rationale for this use of the contact angle is as follows. Ignoring gravity, the forces acting on liquid water resting on a solid surface are the forces of cohesion, attributable to the attraction of water molecules to each other, and adhesion, attributable to the mutual attraction of water molecules and the molecules at the surface of the solid. Conceptually, when the cohesive forces are much greater than the adhesive forces, the water takes on a nearly spherical form and one infers that the solid surface is quite hydrophobic. In contrast, when the cohesive forces are much smaller than the adhesive forces, the water spreads out on the solid surface and one infers that the solid surface is hydrophilic. This relationship was first understood and formalized by Laplace and Young in 1805 as

$$W_a = W_c(1 + \cos \theta_c)/2 = \gamma(1 + \cos \theta_c) \quad (1)$$

(Denny 1993, Eq. 12.1), in which W_a is the energy of adhesion, W_c is the energy of cohesion, θ_c is the angle of contact between the solid and the liquid, and γ is the surface tension of the liquid. The convenient algebraic dependence of W_a on θ_c (Eq. 1) made it possible for us to estimate the relative hydrophobicity of even a very small and curved surface, that of a cuticular hair, by measuring the static contact angle in digital images.

To measure contact angles, we mounted each test leg at the edge of a microscope slide positioned so that the tarsus and metatarsus extended beyond the edge of the glass. Using an inverted compound microscope (Nikon Diaphot), we digitized images of small sections of the leg (as above, or using a Nikon

Table 1.—Identities and properties of subjects used in this study. Families are listed in phylogenetic order after Platnick (2002). The pressure index is a function of both the adhesion energy and the hair density (Eq. 2). Values in the three final columns are averages over N individuals.

Family	Genus and species	Individuals N	Adhesion energy W_a (joules)	Hair density (h/mm)	Pressure index
Scytodidae	*Scytodes* sp. A Latreille 1804	3	0.482	20.956	7.690
	Scytodes sp. B Latreille 1804	1	0.603	16.273	2.796
Pholcidae	*Crossopriza lyoni* (Blackwall 1867)	2	0.719	37.619	1.324
	Pholcus phalangioides (Fuesslin 1775)	3	0.777	40.913	−1.731
Theridiidae	*Theridion* sp. Walckenaer 1805	2	0.605	30.469	6.728
	Tidarren sisyphoides (Walckenaer 1842)	2	0.320	23.277	13.050
Tetragnathidae	*Leucauge argyra* (Walckenaer 1842)	3	0.442	31.978	12.201
	Tetragnatha versicolor Walckenaer 1842	3	0.211	66.994	47.359
Araneidae	*Araneus trifolium* (Hentz 1847)	1	0.560	36.989	8.531
	Larinia directa (Hentz 1847)	3	0.607	42.791	8.251
	Mangora placida (Hentz 1847)	1	0.923	28.973	−7.760
Lycosidae	*Geolycosa rogersi* Wallace 1942	1	0.204	40.432	29.125
	Rabidosa carrana (Bryant 1934)	1	0.189	53.439	39.601
	Trochosa terricola Thorell 1856	2	0.486	56.299	18.256
Pisauridae	*Dolomedes tenebrosus* Hentz 1844	1	0.136	53.091	43.182
	Dolomedes triton (Walckenaer 1837)	1	0.115	45.115	37.995
	Dolomedes vittatus Walckenaer 1837	1	0.263	80.192	51.248
Agelenidae	*Agelenopsis* sp. Giebel 1869	1	0.256	28.892	18.727
	Agelenopsis naevia (Walckenaer 1842)	1	0.196	32.535	23.769
	Agelenopsis pennsylvanica (Koch 1843)	1	0.325	48.544	26.860
Thomisidae	*Misumena vatia* (Clerck 1757)	2	0.217	22.205	15.533
	Misumenoides formosipes (Walckenaer 1837)	1	0.323	29.940	16.654
Salticidae	*Habronattus hallani* (Richman 1973)	1	0.274	39.872	24.878
	Phidippus audax (Hentz 1845)	1	0.135	39.158	31.907
	Phidippus regius Koch 1846	2	0.253	29.779	19.615

D100 SLR camera), with cuticular hairs in silhouette, immediately after exposing the leg to a stream of microscopic water droplets. The stream of water droplets, generated by an ultrasonic humidifier (Welbilt MW-500T/88 filled with distilled water), flowed first through a 1.5 m long plastic tube, then through a 0.25 m long glass tube (diameter =

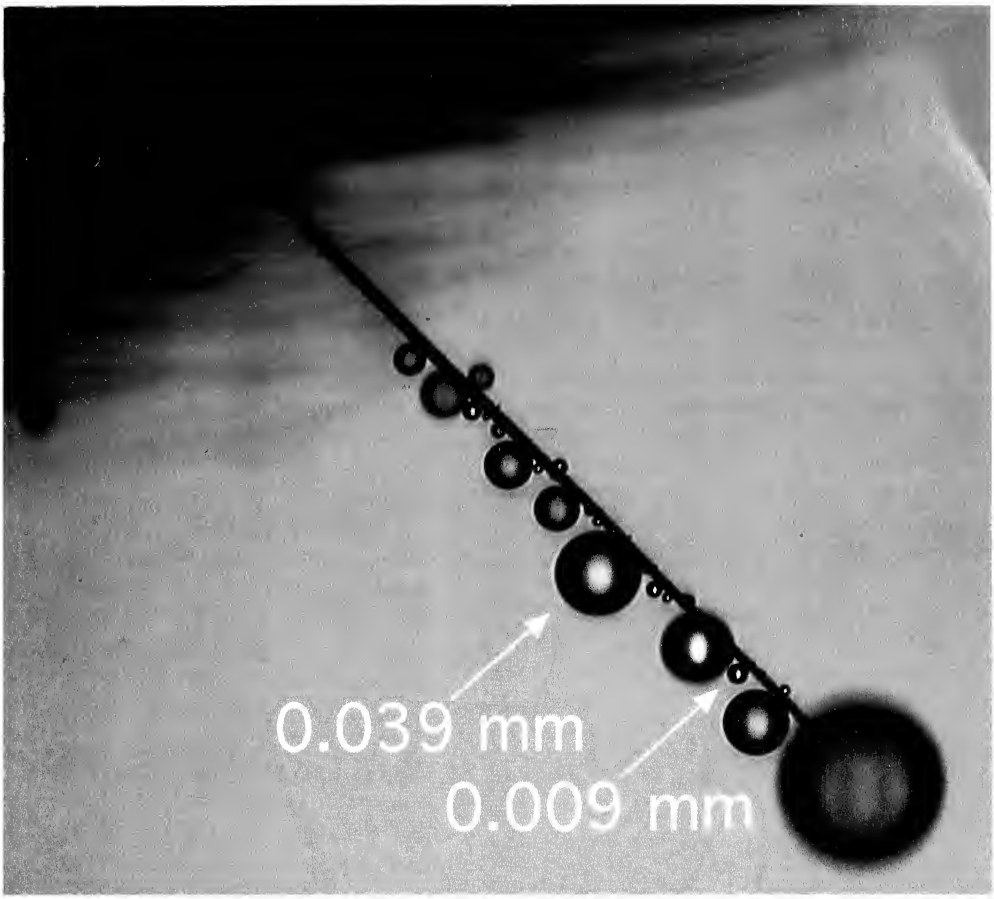

Figure 2.—Micro-droplets deposited on a trichobothrium of *Dolomedes triton*. Droplet size was small enough (3.1×10^{-5} μl and 3.8×10^{-7} μl above) to render the effects of gravity negligible.

5.5 mm), and finally across the 6 cm that separated the tube's opening and the spider's leg. The droplets in the supply stream were so small that they appeared, in aggregate, to be steam, but were at room temperature (21–23 °C).

During the application of the supply stream, water accumulated on the surfaces of cuticular hairs (Fig. 2) or on the cuticle itself. The accumulated water took the form of droplets with shapes that depended upon the ratio of adhesive to cohesive forces acting upon the water. We measured droplets that had diameters < 0.3 mm to avoid any influence of gravity on our measurements (Denny 1993).

We analyzed the digitized images using the angle measurement tool (Fig. 3) in NIH Image (see specifications above). We included in our analysis any droplet for which (a) the intersection between it and the supporting surface was in focus, (b) the plane defined by that axis and the geometric center of the droplet was perpendicular to the camera's focal plane and (c) the diameter of the droplet was < 0.3 mm. Under these criteria, for the 41 spiders tested, we measured 187 contact angles for droplets on cuticular hairs and 25 contact angles for droplets on the cuticles themselves. For one spider we had only a single measurement of leg-hair contact angle. For all of the others, measurements per spider ranged from 2–13.

Functional hydrophobicity in the current context, that is, the ability of a hair-covered leg to resist the intrusion of liquid water into the space between the leg and the hairs, depends both on hair density and on the energy of adhesion of the hair surfaces. Hairs with a low energy of adhesion (and thus a high contact angle) can be spaced relatively far apart and still resist the water's intrusion, whereas

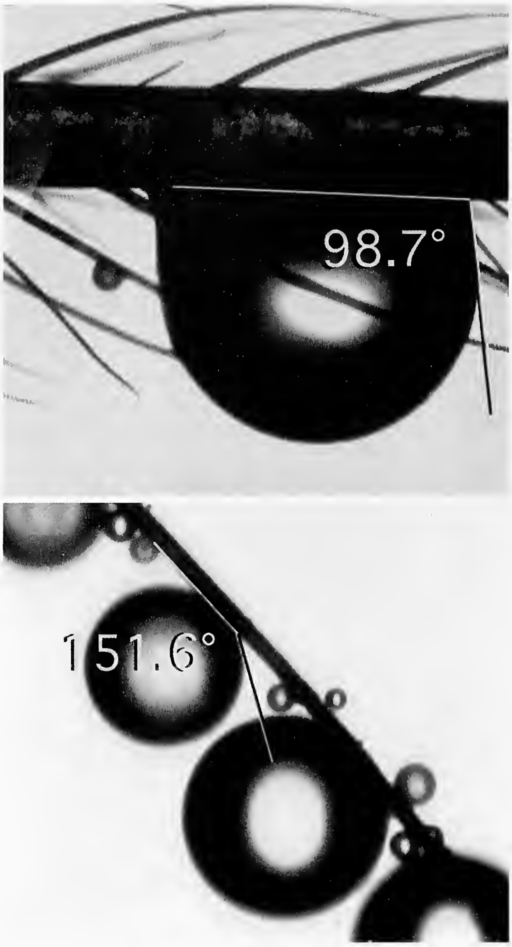

Figure 3.—Contact angles of droplets on the leg cuticle of *Scytodes* sp. (top) and on a trichobothrium of *D. triton* (bottom). Angles > 90° indicate that the energy of cohesion among the water molecules exceeds the energy of adhesion between the spider surface and the water molecules.

hairs with a high W_a must be spaced closer together to achieve the same resistance to intrusion. Denny (1993, p. 265) provides a clear explication, derived from the work of Crisp & Thorpe (1948), of this relationship:

$$\Delta p = \frac{\gamma \cos(\theta_c + \phi)}{\frac{l}{2} - r \cos \phi} \qquad (2)$$

where the sustainable pressure difference is Δp, l is the center-to-center distance between hairs, and ϕ is the angle between the center-to-center line and the location, on a hair, where the air-water interface makes contact. Because of the very small scale at which we were working, we could not measure ϕ, so we adopted the following as our pressure index:

$$I_p = \frac{\cos \theta_c}{l} \qquad (3)$$

which shares with Eq. 2 the property that it is directly proportional to cos θ_c and inversely proportional to l (the inverse of hair density).

RESULTS

Spiders in this study showed conspicuous differences in the ways liquid water interacted with their surfaces (Table 1). These differences were visible at a macroscopic level, for example, in the spherical beads of distilled water that accumulated on the hairy surfaces of pisaurids and in the more flattened drops of water that accumulated on the nearly hairless surfaces of scytodids (Fig. 1). The deposition of microscopic droplets of distilled water onto cuticular hairs (Fig. 2) and onto the cuticular surfaces themselves revealed a similar range of differences in contact angles (Fig. 3) and consequently in the underlying property of the surface, the adhesion energy. The adhesion energies of cuticular hairs (Fig. 4, top) varied from the lowest values in the pisaurids to the highest values in the pholcids and araneids, with an 8-fold difference between the extremes when viewed species by species (Table 1). That is, the hairs of the pisaurids were the most resistant to wetting, the most hydrophobic, and the hairs of the pholcids and araneids were the least resistant to wetting, the most hydrophilic. For 14 spiders spread among 5 families (Araneidae, Pholcidae, Scytodidae, Tetragnathidae, Theridiidae), we measured adhesion energy not only on cuticular hairs but also on the cuticle surfaces themselves. In every case, the adhesion energy of the cuticle exceeded that of the cuticular hairs (mean difference, 0.431 j; paired $t = -6.631$; two-tailed $P < 0.0001$).

Hair density, like adhesion energy, also varied over a wide range among spiders in the 10 families tested (Fig. 4, middle). Pisaurids had the highest densities (59.5 ± 10.6, mean ± S.E.) and scytodids had the lowest (19.8 ± 2.4), with a 4.9-fold difference between the extremes when viewed species by species (Table 1).

Our estimate of functional hydrophobicity, the pressure index (Eq. 3), varied as expected given the variations in adhesion energy and

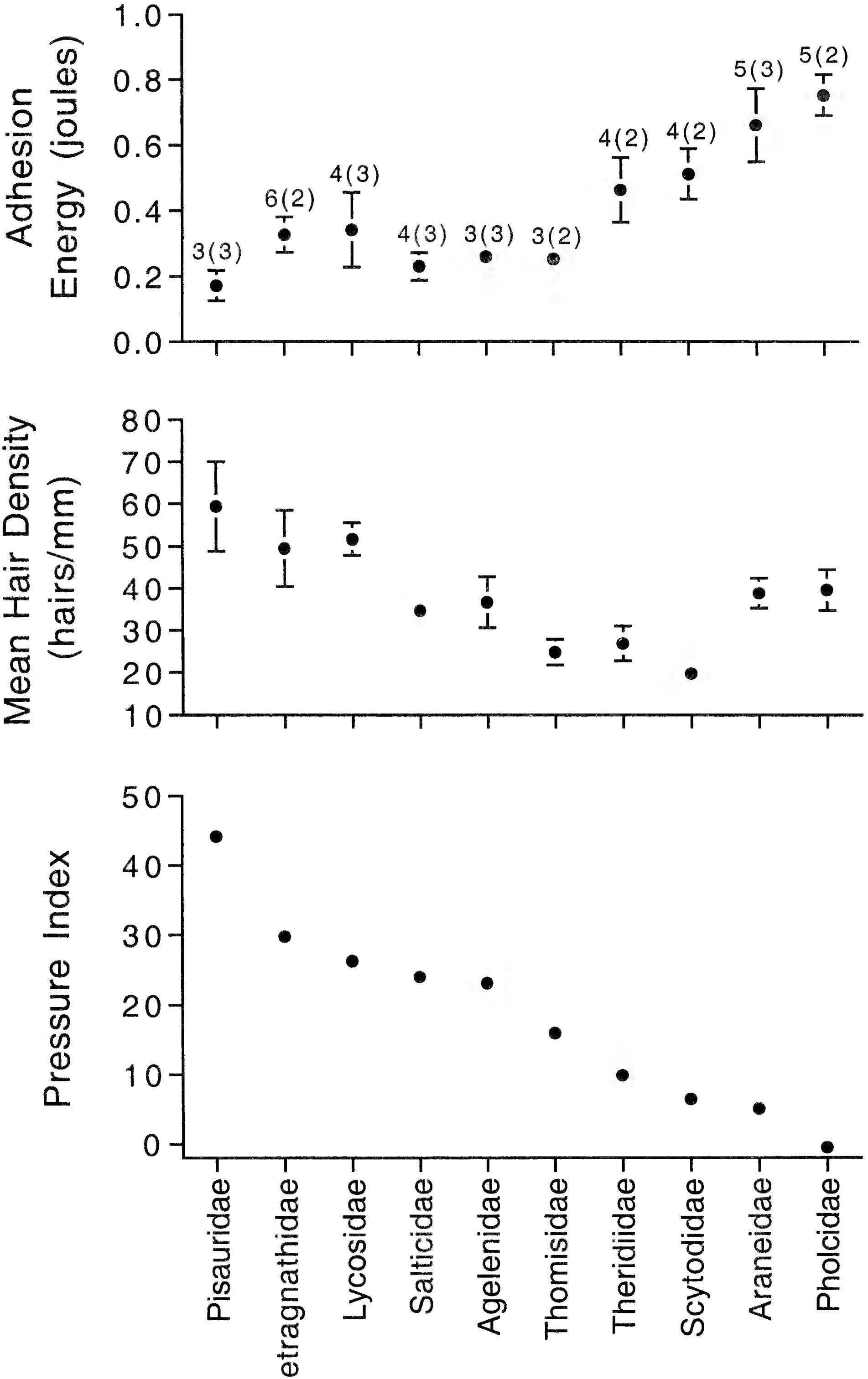

Figure 4.—Variation in resistance to wetting (pressure index, bottom) among 10 families of spiders. The observed variation is a consequence both of the adhesion energy of the hair surfaces (top) and of the spacing of the hairs (middle). Associated with each family in the top graph is a number signifying the number of individuals tested followed by a number in parentheses signifying the number of species tested.

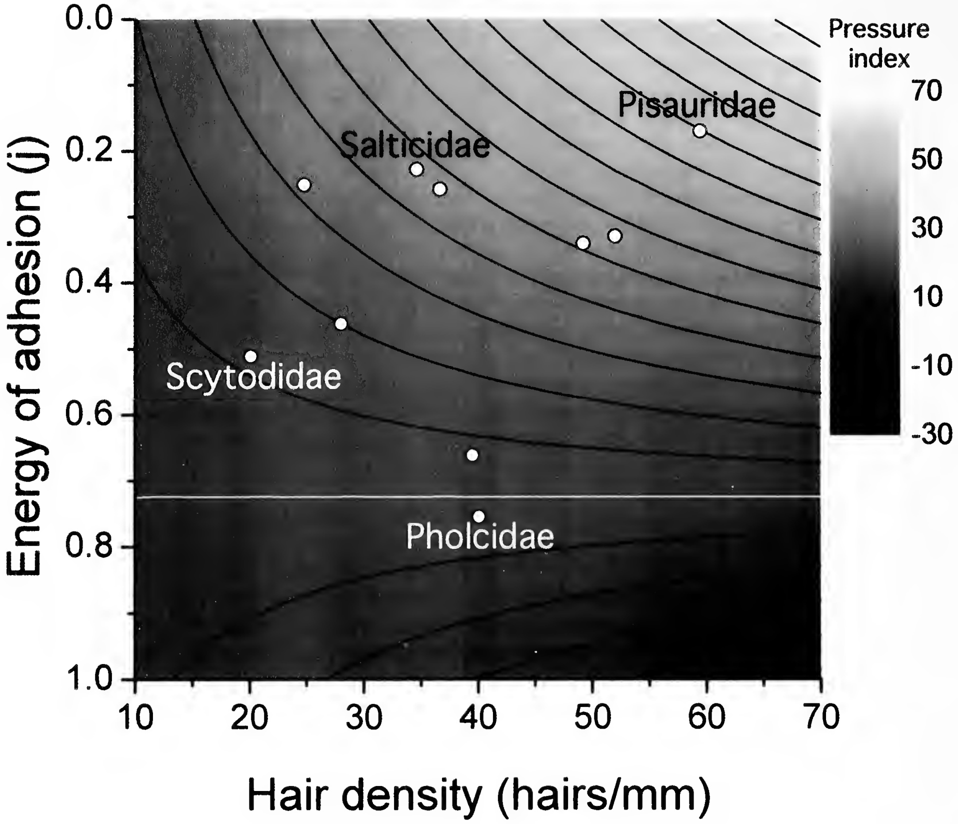

Figure 5.—The influence of hair density and energy of adhesion on the pressure index (z-axis, joules). The data shown here are the same as those in Fig. 4, arranged to emphasize two points. First, hair density and energy of adhesion are not significantly correlated ($r = -0.262$, $P = 0.465$). Second, a variety of combinations of moderately low energies of adhesion (e.g. < 0.4 j) can render a spider well protected from wetting if hair density is sufficiently high (e.g., > 30 hairs/mm). Lines on the graph are pressure index isoclines, with 0 j in white (horizontal line) and those $\neq 0$ shown at intervals of 5 j in black. Data points for all ten families are shown, with labels appended to four for illustrative purposes.

hair density that are its component parts. The surfaces of pisaurids were markedly more functionally hydrophobic than the surfaces of any of the other families of spiders and had a functional hydrophobicity that was nearly 50 times as great as that of the pholcids (Fig. 4, bottom).

The coincidence of very high hair density and very low adhesion energy in the Pisauridae suggests that these two properties may be inversely correlated among species or among families, but that is not the case. A plot of energy of adhesion vs. hair density (Fig. 5) shows that among the families tested there is no significant relationship between the two variables ($r = -0.262$, $P = 0.465$). This absence of a significant correlation is repeated in a comparison of the two variables among species ($r = -0.286$, $P = 0.166$).

DISCUSSION

It would be surprising if fishing spiders (Pisauridae), many of which inhabit riparian environments and actively use the water surface during foraging, searching for mates, and escaping from predators, did not shed water easily from their surfaces (see introduction). Our data indicate, as expected, that their surfaces are strongly hydrophobic, being densely packed with hairs that have very little affinity for liquid water (Figs. 1, 4, 5). Indeed, in the sample of 10 families represented in this study, the functional hydrophobicity of the next highest family, Tetragnathidae, was only two thirds that of the pisaurids (Fig. 4).

The five families at the low end of the scale of functional hydrophobicity include three (Thomisidae, Theridiidae, Pholcidae; Fig. 4) that, in a more comprehensive study of behavior on the water surface, appear to have no capacity to stay afloat when placed on water (Stratton et al. in press). In that same study, the other two families (Scytodidae, Araneidae) had some members with sufficient hydrophobicity to make water surface locomotion possible in theory, and among the araneids it is evident that at least one species is quite adept at aquatic locomotion (Suter et al. in press). Thus the range of functional hydrophobicities that we found in this study includes, at the low end, spiders for which water surface locomotion is morphologically and biochemically insupportable.

We are tempted, and perhaps justified, to view the coincidence of high hair density and low adhesion energy in the pisaurids as an adaptive suite as it is of substantial current benefit to these spiders not only in aquatic locomotion (e.g., Suter 1999; Suter & Wildman 1999) but also in predator evasion (Suter 2003) and in respiration when submerged (Hebets & Chapman 2000; Rovner 1986; Thorpe 1950). The justification for this view is augmented by at least one striking intrafamilial comparison. In the Tetragnathidae, the two species tested (*T. versicolor, L. argyra*) were very far apart in functional hydrophobicity (Table 1), and the one with the much higher functional hydrophobicity is in a genus, *Tetragnatha*, known for its accomplished swimmers (Suter et al. in press).

We find it less easy to explain the substantial variation in functional hydrophobicity in the Tetragnathidae and among the other eight non-pisaurid families tested in this study. Some of that variation is attributable to differences in hair density (Fig. 5; Table 1), and hairs are known to serve sensory, adhesive, and locomotor functions (see text and references in Foelix 1996) as well as visual signaling (e.g., Hebets & Uetz 2000) and defensive (e.g., Marshall & Uetz 1990) functions. But much of the variation is attributable to differences in the energy of adhesion at the interface between the surfaces of the cuticular hairs and liquid water (Fig. 5), and we are uncertain about the functions of hydrophilic hairs. At the core of our quandary is the following question: What benefits accrue to terrestrial arthropods that, like the pholcids in this study, have relatively hydrophilic surfaces?

We offer three general hypotheses for consideration. First, adhesion to substances other than water can play a variety of important roles in the lives of small organisms; because of their relatively high ratio of surface area to volume, small organisms are far more influenced by surface forces than are larger creatures for which inertia is predominant (Vogel 1994). (This is the same scaling effect that causes small organisms to be so vulnerable to being trapped by water's surface tension.) Biological adhesion has attracted substantial attention recently as examples of its importance have come to light. For example, because of the adhesive properties of their tarsi, certain ants can run well on waxy plant surfaces while most cannot (Federle et al. 2000), flies easily walk on inverted smooth surfaces (Gorb 1998) as do many spiders possessing scopulae (Rovner 1978; Foelix 1996, p. 18), and some staphylinid beetles capture springtails with a sticky, protrusible, rod-like labium (Bauer & Pfeiffer 1991). In the current context, the propensity of cuticular hairs to adhere to other substances certainly might drive selection away from hydrophobicity, depending upon the specific circumstances. For example, surface alterations could enhance adhesion to prey surfaces, could reduce susceptibility to surface binding by the spores of pathogens, the eggs of parasitoids, or the silk of other spiders, or could facilitate locomotion on smooth surfaces.

Our second general hypothesis concerns metabolic costs. The hydrophobic properties of the cuticle and hairs of terrestrial arthropods are thought to be attributable to the orderly deposition, either during development or as an ongoing process, of a waxy or oily epicuticular layer (Holdgate 1955). Both the production of this layer and its maintenance through grooming or other mechanisms could be metabolically costly. If that were the case, then selection might favor a decline in hydrophobicity. Testing this hypothesis would be difficult, not because assessing metabolic costs would be daunting but because weighing the cost savings against correlated cost increases would be very complicated. For example, the waxy epicuticle of terrestrial arthropods is credited with a substantial reduction in transpirational water loss (Crawford 1981), a protection that spiders in xeric environments could ill afford to lose.

Finally, an alternative to both of these hypotheses is the possibility that in some families of spiders grooming is relatively rare. Long periods between grooming bouts would allow the degradation of an otherwise strongly hydrophobic surface due to an accumulation of chemical and particulate debris. Such degradation is known to occur in insects, especially those that inhabit stored grains (Holdgate 1955), but the frequent grooming commonly seen in spiders (personal observation) suggests that this explanation for the variation reported here is unlikely to be correct.

We find none of these hypotheses to be particularly compelling, which leaves us unable to explain why spiders show such a range of capacities to shed water. That same range of capacities, however, does lead to a conclusion about the kinds of preadaptations that are likely to have facilitated the move, by some groups of spiders, into the niche defined by the air-water interface.

Functional hydrophobicity sufficient to allow a spider to move about on the surface of water is far more widespread among spiders than are gaits specialized for aquatic locomotion (Suter et al. in press; Stratton et al. in press). From this we infer that functional hydrophobicity was a preadaptation that facilitated aquatic locomotion (e.g., among the Pisauridae) rather than an adaptation that arose as the ancestors of present-day semi-aquatic spiders began their shift to the more aquatic existence. It follows, therefore, that few theridiids, scytodids, araneids, or pholcids, all of which had indices of hydrophobicity < 10 in this study (Fig. 4), are likely to evolve effective modes of aquatic locomotion in the future. Despite this impediment, we know of one species of araneid, *Larinioides cornutus* (Clerck 1757), that not only is functionally hydrophobic but also adopts a rowing gait much like that of *Dolomedes* when it finds itself on the surface of water (Suter et al. in press).

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LITERATURE CITED

Anderson, N.M. 1976. A comparative study of locomotion on the water surface in semiaquatic bugs (Insects, Hemiptera, Gerromorpha). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 139:337–396.

Bauer, T. & M. Pfeiffer. 1991. 'Shooting' springtails with a sticky rod: the flexible hunting behaviour of *Stenus comma* (Coleoptera: Staphylinidae) and the counter-strategies of its prey. Animal Behaviour 41:819–828.

Bleckmann, H. 1985. Discrimination between prey and non-prey wave signals in the fishing spider *Dolomedes triton* (Pisauridae). Pp. 215–222. *In* Acoustic and Vibrational Communication in Insects. (K. Kalmring & N. Elsner, eds.). Paul Parey, Berlin.

Cheng, L. 1973. Marine and freshwater skaters: differences in surface fine structures. Nature 242: 132–133.

Crawford, C.S. 1981. Biology of Desert Invertebrates. Springer-Verlag, New York. 314 pp.

Crisp, D.J. & W.H. Thorpe. 1948. The water-protecting properties of insect hairs. Discussions of the Faraday Society 3:210–220.

Denny, M.W. 1993. Air and Water: The Biology and Physics of Life's Media. Princeton University Press, Princeton. 341 pp.

Federle, W., K. Rohrseitz & B. Hölldobler. 2000. Attachment forces of ants measured with a centrifuge: better 'wax-runners' have a poorer attachment to a smooth surface. Journal of Experimental Biology 203:505–512.

Foelix, R.F. 1996. Biology of Spiders (2nd ed.). Oxford University Press, Oxford. 330 pp.

Gorb, S.N. 1998. The design of the fly adhesive pad: distal tenent setae are adapted to the delivery of an adhesive secretion. Proceedings of the Royal Society of London B 265:747–752.

Gorb, S.N. & F.G. Barth. 1994. Locomotor behavior during prey-capture of a fishing spider, *Dolomedes plantarius* (Araneae: Araneidae): galloping and stopping. Journal of Arachnology 22:89–93.

Hebets, E.A. & R.F. Chapman. 2000. Surviving the flood: plastron respiration in the non-tracheate arthropod *Phrynus marginemaculatus* (Amblypygi: Arachnida). Journal of Insect Physiology 46:13–19.

Hebets, E. & G.W. Uetz. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 47:280–286.

Holdgate, M.W. 1955. The wetting of insect cuticles by water. Journal of Experimental Biology 32: 591–617.

Marshall, S.D. & G.W. Uetz. 1990. Incorporation of urticating hairs into silk: a novel defense mechanism in two neotropical tarantulas (Araneae, Theraphosidae). Journal of Arachnology 18:143–149.

McAlister, W.H. 1959. The diving and surface-walking behaviour of *Dolomedes triton sexpunctatus* (Araneida: Pisauridae). Animal Behaviour 8:109–111.

Platnick, N.I. 2002. The world spider catalog, version 3.0. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81-87/index.html.

Roland, C. & J.S. Rovner. 1983. Chemical and vibratory communication in the aquatic pisaurid spider *Dolomedes triton* (Araneae, Pisauridae). Journal of Arachnology 11:77–85.

Rovner, J.S. 1978. Adhesive hairs in spiders: behavioral functions and hydraulically mediated movement. Symposia of the Zoological Society of London 42:99–108.

Rovner, J.S. 1986. Spider hairiness: air stores and low activity enhance flooding survival in inland terrestrial species. Acta X International Congress of Arachnology Jaca/Espana: 123–129.

Shultz, J.W. 1987. Walking and surface film locomotion in terrestrial and semi-aquatic spiders. Journal of Experimental Biology 128:427–444.

Stratton, G., R.B. Suter & P.R. Miller. In press. Evolution of water surface locomotion by spiders: a comparative approach. Biological Journal of the Linnean Society.

Suter, R.B. 1999. Cheap transport for fishing spiders: the physics of sailing on the water surface. Journal of Arachnology 27:489–496.

Suter, R.B. 2003. Trichobothrial mediation of an aquatic escape response: directional jumps by the fishing spider, *Dolomedes triton*, foil frog attacks. Journal of Insect Science 3:16.

Suter R.B., O. Rosenberg, S. Loeb, H. Wildman & J. Long, Jr. 1997. Locomotion on the water surface: propulsive mechanisms of the fisher spider, *Dolomedes triton*. Journal of Experimental Biology 200:2523–2538.

Suter, R.B., G.E. Stratton & P.R. Miller. In press. Water surface locomotion by spiders: distinct gaits in diverse families. Journal of Arachnology.

Suter, R.B. & H. Wildman. 1999. Locomotion on the water surface: hydrodynamic constraints on rowing velocity require a gait change. Journal of Experimental Biology 202:2771–2785.

Thorpe, W.H. 1950. Plastron respiration in aquatic insects. Biological Review 25:344–390.

Vogel, S. 1988. Life's Devices: The Physical World of Animals and Plants. Princeton University Press, Princeton. 367 pp.

Vogel, S. 1994. Life in Moving Fluids: The Physical Biology of Flow (second edition). Princeton University Press, Princeton. 467 pp.

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BEHAVIORAL REPERTORY OF THE NEOTROPICAL HARVESTMAN *ILHAIA CUSPIDATA* (OPILIONES, GONYLEPTIDAE)

Wilton Pereira, Abner Elpino-Campos and **Kleber Del-Claro**: Laboratório de Ecologia Comportamental e de Interações (LECI), Instituto de Biologia, Universidade Federal de Uberlândia, CP 593, 38400-902 Uberlândia, MG, Brazil

Glauco Machado[1]: Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, 13083-970 Campinas, SP, Brazil

ABSTRACT. In this study, we provide an ethogram for the harvestman *Ilhaia cuspidata* and describe the daily activity pattern of captive individuals. We also provide a comparison between the behavioral repertory of this species with that of the syntopic *Discocyrtus oliverioi.* Five females and four males of *I. cuspidata* were maintained in the same terrarium from November 1999–November 2000 for qualitative and quantitative observations. Twenty behavioral acts were recorded, classified in seven categories and the relative frequency of each was determined: exploration (69.8%), resting (16.7%), feeding (6.3%), grooming (4.4%), social interactions (2.6%), reproduction (0.1%) and others (0.3%). There was a marked difference in the frequency of the behavioral categories between sexes: females fed more frequently than males and males were involved in social interactions more frequently than females. During most of the daylight hours, individuals remained inside shelters and became active from 19:00–09:00 h. Although *I. cuspidata* and *D. oliverioi* showed almost the same behavioral acts, there were quantitative differences in their repertories: the relative frequency of behavioral categories "resting" and "social interactions" were higher for *I. cuspidata* whereas "reproduction" and "grooming" were higher for *D. oliverioi.* The main qualitative difference between these two species was related to the forms of parental care: females of *D. oliverioi* guard their eggs and first instar juveniles, whereas females of *I. cuspidata* scatter their eggs in time and space and do not actively protect their offspring. Since both species share the same habitats (sometimes in multi-species aggregations), the behavioral differences between them may be explained by particular morphological and physiological characteristics of the species, as well as by phylogenetic constraints.

Keywords: Activity pattern, defensive behavior, *Discocyrtus*, ethogram, gregariousness, parental care

The Opiliones constitutes a highly diversified order in terms of morphology and habits, and includes approximately 5000 species widespread throughout the world (Adis & Harvey 2000). Harvestmen are particularly suitable for behavioral studies because individuals of many species are abundant and easy to observe, both in the field and laboratory. Selected species may be good model organisms for experimental manipulations since they allow researchers to test hypotheses about the ecological meaning of certain behavioral patterns (e.g. Mora 1990; Machado & Oliveira 1998; Machado et al. 2002). Representatives of the suborder Laniatores may be maintained in captivity, where they behave in a similar way to that observed in the field (e.g. Capocasale & Bruno-Trezza 1964; Elpino-Campos et al. 2001; Willemart 2001), facilitating quantitative and qualitative comparisons between species.

An ethogram is a set of comprehensive descriptions of the behavioral repertory of a species (Brown 1975). Allied with field observations, ethograms are important starting points for any ethological research and for understanding the biology and ecology of a wide range of animals (Lehner 1940). *Discocyrtus oliverioi* H. Soares 1945 (Gonyleptidae, Pachylinae) was the first harvestman to have its behavioral repertory studied and is so far the only species available for comparison (El-

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[1] Author for correspondence.

pino-Campos et al. 2001). This harvestman species showed 25 behavioral acts that were divided into six major categories: exploration, resting, foraging, social interactions, self-grooming, and reproduction. The individuals were inactive during the day and foraged and interacted with other individuals at night. Females reproduced in captivity and showed maternal care toward the eggs and newly hatched offspring (Elpino-Campos et al. 2001).

Discocyrtus oliverioi is very abundant in urban areas of Uberlândia, state of Minas Gerais, Brazil, where it occurs syntopically with two other harvestmen, *Discocyrtus* sp. and *Ilhaia cuspidata* Roewer 1913 (Elpino-Campos et al. 2001). In this paper, we provide a detailed ethogram for *I. cuspidata* (Gonyleptidae, Gonyleptinae) and describe the daily activity pattern of captive individuals. Some comments on the foraging, defense, gregariousness, and reproduction of this harvestman are also presented for the first time. In addition, we have made qualitative and quantitative comparisons between the behavioral repertories of *I. cuspidata* and *D. oliverioi*.

METHODS

Collection of harvestmen and maintenance in the laboratory.—Individuals of *I. cuspidata* were collected in the Experimental Garden of the Universidade Federal de Uberlândia (18° 53′S, 48° 15′W; 863 m ele.), an urban area in the state of Minas Gerais, southeastern Brazil. The behavioral observations were based on nine individuals (5 females and 4 males) maintained in the same terrarium (20.5 × 44.5 cm × 27.5 cm high) containing soil, leaves and two pieces of tree fern trunk (8 × 10 cm each) as shelters. The shelters had the shape of a gabled roof, so that the individuals could slip under them, finding protection against light. Temperature and moisture conditions in the laboratory were similar to those in the field (nearly 25 °C and 70–80% relative humidity). In addition, nine individuals of *D. oliverioi* and one of *Discocyrtus* sp. were also placed in the same terrarium. The harvestmen were fed live termite workers (Insecta, Isoptera), freshly chopped pieces of earthworms (Annelida, Oligochaeta), honey solution and an artificial diet for ants (Bhatkar & Whitcomb 1970). A light schedule of 14L: 10D was maintained in the laboratory, simulating the natural lighting at the time of the study.

Activity pattern.—The activity schedule of *I. cuspidata* was quantified by observing captive individuals at 1 h intervals during a 24 h period. Sampling at each interval consisted of counting the number of individuals accomplishing the different types of behavioral acts during a 5 min period. These observations were repeated on three non-consecutive days in January 1999 totaling 72 h of sampling. The main aim of these samplings was to determine the relative frequency of the major behavioral categories throughout the day. At this point, we were not interested in determining the biological rhythm of the species.

Behavioral repertory and ethogram.—In order to identify and describe the behavioral acts of *I. cuspidata*, six hours of field observations and another 6 h of observations in the laboratory (20 sessions of 36 min ad libitum sampling, sensu Altmann 1974) were done at night when the animals were most active (18:00–00:00 h) in January 1999. The description of all behavioral acts and their classification into behavioral categories were as described by Elpino-Campos et al. (2001). In addition quantitative data only on captive individuals were obtained in 30 sessions of observations from November 1999–November 2000. Each session consisted of scan samples of all individuals performed at 50 min intervals over 200 min. For each sampling all individuals were scanned twice. These observations were made between 19:00 and 03:00 h with a red lamp to avoid disturbing the animals (cf. Machado & Oliveira 1998; Elpino-Campos et al. 2001). Ten minutes before each behavioral sampling, 10 termite workers and three pieces of earthworm (1 cm each) were offered as food. The data recorded in these samplings were used to construct the ethogram. The absolute frequencies of the major behavioral categories were compared between sexes and between *I. cuspidata* and *D. oliverioi* using a G test (Sokal & Rohlf 1995). The null hypothesis was of no difference between sexes and between species. Some specific behavioral acts (see results) were also compared using a chi square test done on the raw data (Sokal & Rohlf 1995).

Voucher specimens of males and females of *I. cuspidata*, *D. oliverioi*, and *Discocyrtus* sp. were deposited in the Museu de Biodiversi-

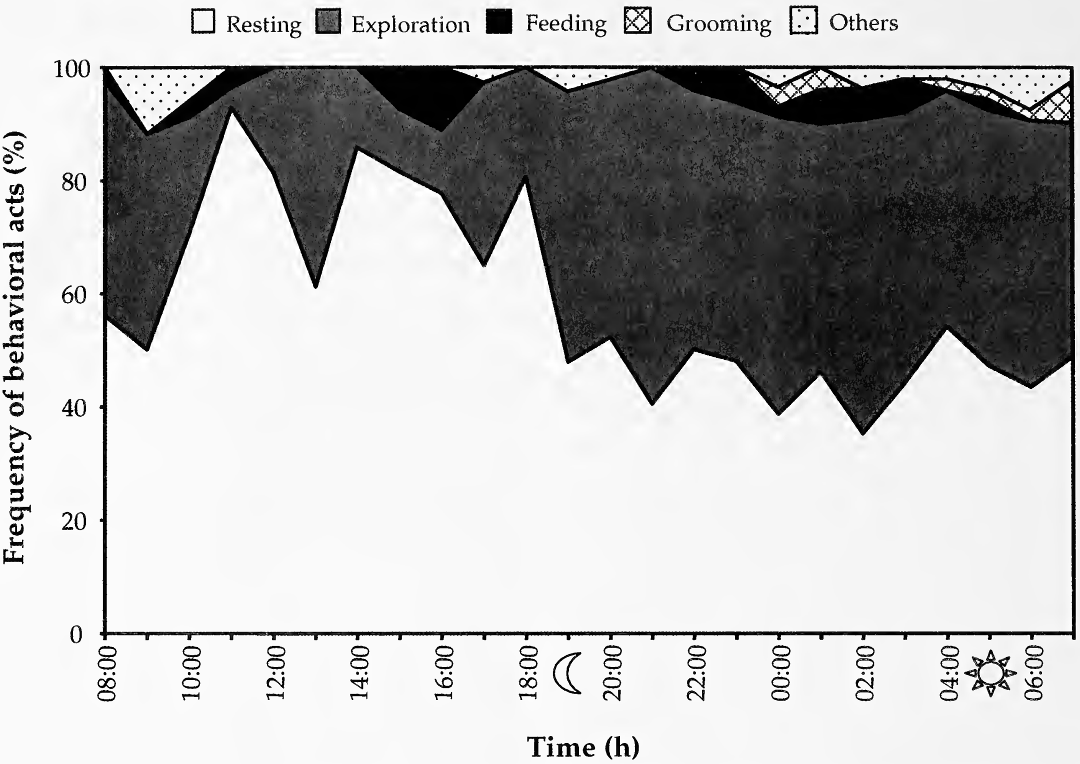

Figure 1.—Daily activity schedule of the harvestman *Ilhaia cuspidata*. The data are based on three different days of sampling and were obtained from nine captive individuals. The moon and the sun indicate dusk and dawn, respectively.

dade do Cerrado (MBC, Uberlândia, MG, Brazil) and at the Museu de Zoologia da Universidade de São Paulo (MZSP, São Paulo, SP, Brazil).

RESULTS

Activity pattern and foraging.—During most of the daylight hours, individuals of *Ilhaia cuspidata* were found hidden inside shelters (Fig. 1). Individuals became active with the onset of darkness (about 18:00 h), when they left the shelters to forage (Fig. 1). They accepted both live (termites) and dead (pieces of worm) animals, with the food item being grasped and taken to the shelter to be consumed. Fights for food and aggressive interactions were observed among conspecifics ($n = 7$) and with *Discocyrtus oliverioi* ($n = 3$) in the shelters. Sometimes, two or more conspecifics were seen feeding simultaneously on the same piece of food ($n = 3$). Most individuals of *I. cuspidata* became inactive at about 9:00 h, i.e., four hours after sunrise (Fig. 1). Notwithstanding, individuals were recorded outside the shelters sometimes during the day, drinking water or walking about (Fig. 1).

Behavioral repertory.—Twenty behavioral acts, classified into seven major groups of activities, were recorded for *I. cuspidata*: feeding, social interactions, resting, exploration, grooming, reproduction and others (Table 1). Exploration was the most common activity, followed by resting and feeding (Table 1). Although field observations indicated that *I. cuspidata* is a gregarious harvestman (see below), in captivity individuals rested alone more frequently than in groups (males and females combined; $\chi^2 = 8.33$; d.f. = 1; $P < 0.01$). Self-grooming activities, known as leg threading in harvestmen (cf. Edgar 1971), involved mainly legs II (males and females combined; $\chi^2 = 12.43$; d.f. = 3; $P < 0.001$) (Table 1). Grooming behavior occurred when the harvestmen were moving around the environment and, more frequently, after feeding (when both legs and pedipalps were cleaned).

There was a marked difference in the frequency of behavioral categories between

Table 1.—Behavioral repertory and frequency of each behavioral act for nine captive individuals of the harvestman *Ilhaia cuspidata*. n = number of individuals observed and, in parentheses, the number of behavioral acts observed for each sex.

	Frequency of behavioral acts (%)		
Behavioral acts	Males (n = 4) (881)	Females (n = 5) (1291)	Total (n = 9) (2172)
FEEDING	5.11	7.05	6.27
Feed on termites	1.82	1.94	1.89
Feed on pieces of worm	2.61	3.87	3.36
Feed on honey solution	0.23	0.31	0.28
Fight for food	0.45	0.93	0.74
SOCIAL INTERACTIONS	4.32	1.47	2.61
Touching conspecific with legs	1.70	0.70	1.10
Touching individual of *D. oliverioi* with legs	0.68	0.23	0.41
Attacking conspecific	1.14	0.54	0.78
Attacking individual of *D. oliverioi*	0.80	0	0.32
RESTING	17.59	16.11	16.72
Alone	10.33	9.14	9.62
In multi-species aggregation	7.26	6.97	7.10
EXPLORATION	68.10	70.73	69.65
Walkabout	18.50	19.60	19.15
Touching the substrate with first legs	16.80	17.82	17.40
Touching the substrate with second legs	32.80	33.31	33.10
SELF-GROOMING	4.54	4.26	4.37
Leg threading—first pair	1.02	0.93	0.97
Leg threading—second pair	1.70	1.63	1.66
Leg threading—third pair	0.68	0.93	0.83
Leg threading—fourth pair	0.80	0.54	0.64
Cleaning the pedipalps	0.34	0.23	0.27
REPRODUCTION	0	0.15	0.11
Oviposition	0	0.15	0.11
OTHER	0.34	0.23	0.27
Pressing the body against the substrate	0.34	0.23	0.27
TOTAL	100.0	100.0	100.0

males and females (G = 20.25; d.f. = 4; $P <$ 0.001). Due to the low frequency of behavioral acts the categories "reproduction" and "others" were not included in this analysis. The frequency of feeding and exploration activities was higher in females than in males, whereas males were involved in social interactions more frequently than females (Table 1).

Notes on natural history.—When disturbed in the field, individuals of *I. cuspidata* remained motionless with the legs retracted over the body. In this position, the dark brown coloration of the animals was extremely cryptic against a dark background. Individuals also showed thanatosis in which the legs were fully extended laterally and the animal became rigid for up to 5 min. Even when persistently mechanically disturbed with forceps or manipulated, the harvestmen rarely released repugnant substances or attacked the aggressor with the pedipalps.

Oviposition of *I. cuspidata* was observed twice (January and February) in the laboratory. The females repeatedly touched a given point on the substrate with the first two pairs of legs before ovipositing. Subsequently, a single egg was laid and the female spent 5–10 s attaching debris and soil particles on the egg surface with the first two pairs of legs. Females abandoned the oviposition site, leaving the egg unprotected. Another four eggs (similar in size and color) were found unprotected in the terrarium and were probably laid by females of *I. cuspidata*. Two eggs were covered by debris, while the other two had no particles attached.

In the field, five multi-species aggregations

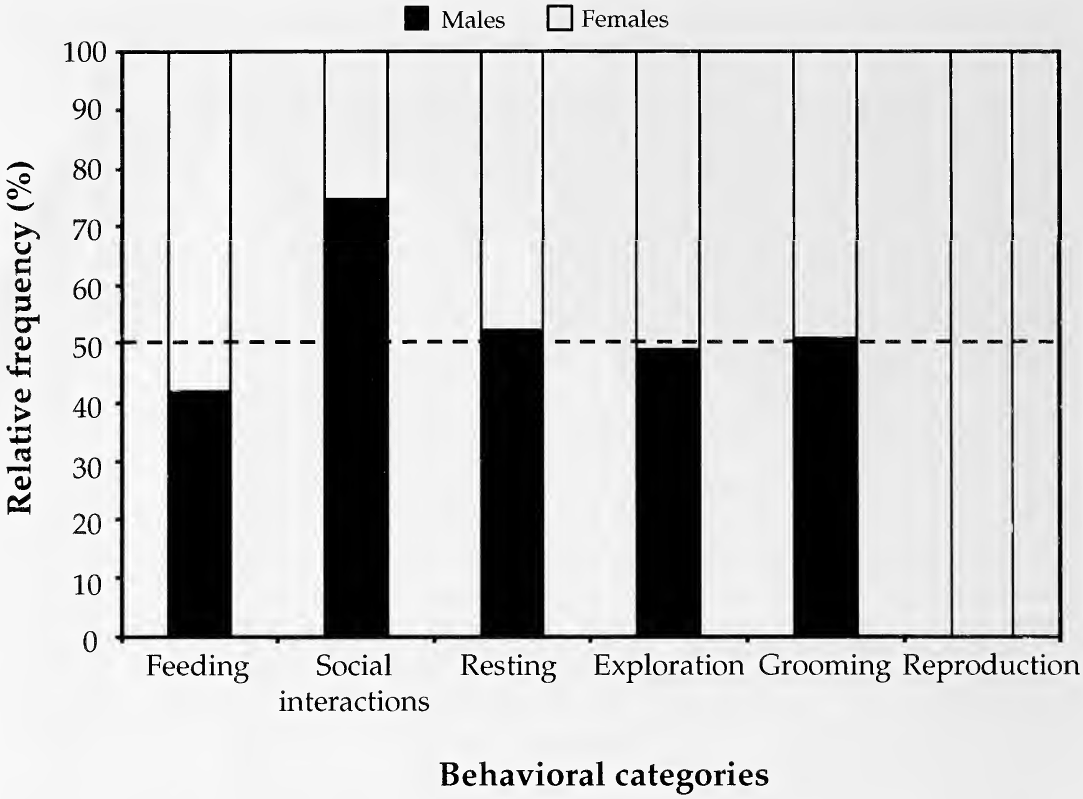

Figure 2.—Comparison of the relative frequency of the behavioral categories observed for males and females of the harvestmen *Ilhaia cuspidata* in captivity.

were found under fallen tree trunks (Fig. 3). The mean number of individuals was 21.6 ± 20.5 for *I. cuspidata*, 5.0 ± 2.2 for *D. oliverioi*, and 2.8 ± 1.8 for *Discocyrtus* sp. Females were always most frequent within the aggregations, and accounted for 55.6%–76.9% of the aggregated individuals of *I. cuspidata.*

Comparisons with *Discocyrtus oliverioi*.—There were both qualitative and quantitative differences between the behavioral repertories of *I. cuspidata* and *D. oliverioi* (Fig. 4). These two harvestmen species showed the same behavioral acts in the categories feeding, social interactions, resting, exploration, and self-grooming (Table 1; Elpino-Campos et al. 2001). In the category reproduction, however, *D. oliverioi* showed a more diversified repertory, including seven acts, whereas *I. cuspitada* showed only one (Table 1; Elpino-Campos et al. 2001). In contrast to *D. oliverioi*, whose females laid a batch of eggs and remained over the eggs, protecting them for about 22 days (Elpino Campos et al. 2001), females of *I. cuspidata* scattered their eggs in time and space and did not actively protect their offspring. The relative frequency of the major behavioral categories differed statistically between the two species ($G = 86.29$; d.f. $= 6$; $P < 0.001$). Individuals of *I. cuspidata* rested and interacted with other individuals more frequently than *D. oliverioi* (Fig. 4). In turn, the frequency of reproductive and cleaning activities were higher in *D. oliverioi* than in *I. cuspidata* (Fig. 4).

DISCUSSION

Although the subfamily Gonyleptinae is one of the largest among the Gonyleptidae (Pinto-da-Rocha 1999), there are few studies describing the ecology and behavior of its representatives (but see Machado & Pizo 2000; Machado & Vidal 2001). Some behavioral patterns of *Ilhaia cuspidata* are very similar to other gonyleptids, especially those of the subfamily Pachylinae (see Acosta et al. 1993, 1995; Capocasale & Bruno-Trezza 1964; Elpino-Campos et al. 2001). Individuals of *I. cuspidata* are mainly nocturnal, generalist

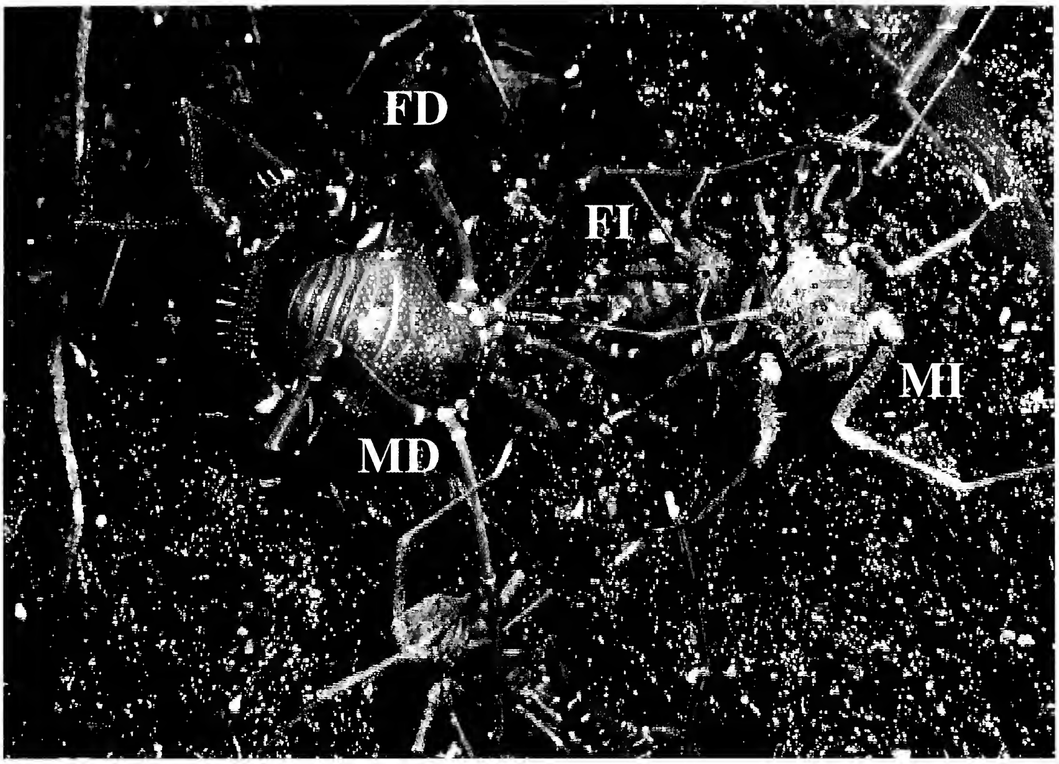

Figure 3.—Multi-species aggregation of harvestmen under a fallen trunk in the Experimental Garden of the Universidade Federal de Uberlândia, in the state of Minas Gerais, southeastern Brazil. MD = male of *Discocyrtus oliverioi*; FD = female of *D. oliverioi*; MI = male of *Ilhaia cuspidata*; FI = female of *I. cuspidata*.

predators that carry their food to shelter before feeding, and may be found in small aggregations during the day, like many gonyleptids (see Capocasale & Bruno-Trezza 1964; Acosta et al. 1993, 1995; Gnaspini 1996; Hoenen & Gnaspini 1999; Machado et al. 2000; Elpino-Campos et al. 2001; Santos & Gnaspini 2002). The defensive behavior, however, is more similar to that of cosmetids (Eisner et al. 1978), manaosbiids (Cokendolpher 1987), and trogulids (Hillyard & Sankey 1989), which also feign death and rarely emit gland secretions.

The most frequent behavioral act for the captive individuals of *I. cuspidata* was to touch the substrate with the second pair of legs. In harvestmen these legs possess numerous sense organs and are used to touch the substrate, food, and other organisms (Edgar 1963). During such activities, offensive organisms and debris come into contact with the sense organs. Thus, the main functions of leg threading probably are to remove pathogenic fungi or other free-loading organisms before they have time to penetrate the cuticle, and to restore sensory receptors to their full sensing status (Edgar 1971).

Males and females of *I. cuspidata* differed in the relative frequency of the behavioral categories, with females feeding more frequently than males. It is known that the respiratory rate of female harvestmen increases when they are producing and maturing eggs (Phillipson 1962, 1963). This physiological change during egg development probably accounts for the higher requirement for food (Phillipson 1962, 1963; Gnaspini 1996). Indeed, in the cavernicolous harvestman *Goniosoma spelaeum* (Mello-Leitão 1923), females bearing eggs leave the cave to forage more frequently than other adult individuals in the population (Gnaspini 1996). The month in which the quantitative observations were conducted in our study (January) coincided with the period when females of *I. cuspidata* were laying eggs in the laboratory. Thus, the higher frequency

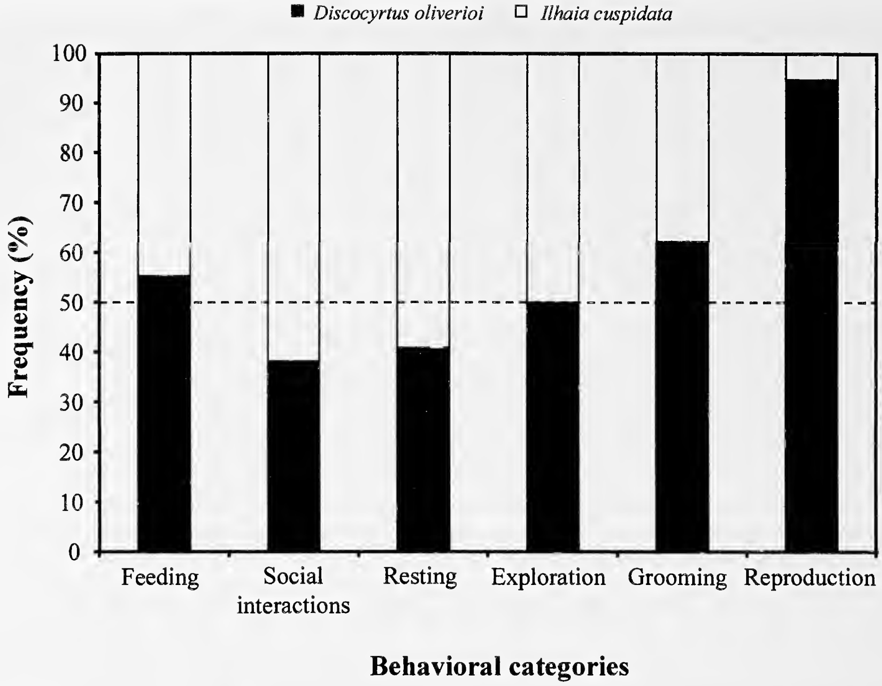

Figure 4.—Comparison of the relative frequency of the behavioral categories observed for the harvestmen *Ilhaia cuspidata* and *Discocyrtus oliverioi* in captivity.

of feeding activities in females compared to males may be related to the accumulation of energy for egg production and maturation.

Males of *I. cuspidata* interacted aggressively with conspecifics at a higher frequency than females. Possible explanations for this behavioral pattern include intolerance among males, competition for females, and territorial fights (see Macías-Ordóñez 1997). More details of the natural history of this species in the field are needed to assess the causes of aggressive behavior in males. The aggressiveness among males, however, may explain why females account for most of the aggregated individuals.

Under natural conditions, *I. cuspidata* and *D. oliverioi* live in the same habitat, use the same microhabitats to forage, take shelter and reproduce, and show a considerable overlap in their periods of activity (see also Elpino Campos et al. 2001). Our results, however, showed that, at least in captivity, these species differ in their allocation of time and energy to the behavioral categories studied. Individuals of *I. cuspidata* rest more and seem to be more aggressive than *D. oliverioi*, which may explain why individuals of the former species tended to rest alone more frequently than in groups in the laboratory.

The main qualitative difference between these two harvestmen species was related to the forms of parental care: females of *D. oliverioi* guarded their eggs and first instar juveniles, whereas females of *I. cuspidata* scattered their eggs in the substrate and did not show any additional interaction with the offspring. Since eggs of *I. cuspidata* and *D. oliverioi* are laid in the same environment and supposedly face similar selective pressures (such as abiotic factors and predators), how can we explain the differences in the forms of parental care?

The evolution of the different forms of parental care is a complex function of many interacting factors including morphology, defensive behavior, and phylogenetic constraints (see Tallamy & Wood, 1986). Harvestmen with a short ovipositor, like all Laniatores, are unable to hide their eggs in deep cavities where they are inaccessible to most predators. In these cases, the physiology of egg production, life span, and defensive strategies may offer a partial explanation on when subsocial behavior may evolve (review in Machado & Raimundo 2001). Maternal care is a viable strategy only when females lay eggs aggregated in the time and space, live long enough to benefit one or more batches, and have defensive strategies that enable them to protect the offspring against predators. Species in which females do not fit these features (or are constrained by phylogenetic inertia) present alternative forms of parental care including egg hiding and/or egg covering. This is probably the case of *I. cuspidata* that, despite living more than one year as adult, may be physiologically constrained to iteroparity and relies mainly on evasive strategies of defense.

Egg hiding by females is probably the most common form of parental investment among harvestmen of the suborder Laniatores (Machado & Raimundo 2001). Generally, nonsubsocial harvestmen hide their eggs inside small natural crevices or cover them with debris and leave the offspring without additional care (Canals 1936; Cokendolpher & Jones 1991; Juberthie 1965, 1972; Willemart 2001). Laying eggs in several batches or scattering single or few eggs over a very wide area may be advantageous and confer protection to the offspring because detection by natural enemies would be reduced (Edmunds 1974; Willemart 2001).

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LITERATURE CITED

Acosta, L.E., F.E. Pereyra & R.A. Pizzi. 1995. Field observations on *Pachyloidellus goliath* (Opiliones, Gonyleptidae) in Pampa de Achala, province of Córdoba, Argentina. Bulletin of the British Arachnological Society 10:23–28.

Acosta, L.E., T.I. Poretti & P.E. Mascarelli. 1993. The defensive secretions of *Pachyloidellus goliath* (Opiliones: Laniatores: Gonyleptidae). Bonner Zoologischer Beitrage 44:19–31.

Adis, J. & M.S. Harvey. 2000. How many Arachnida and Myriapoda are there world-wide and in Amazonia? Studies on Neotropical Fauna and Environment 35:139–141.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, 49:227–265.

Bhatkar, A. & W.H. Whitcomb. 1970. Artificial diet for rearing various species of ants. Florida Entomologist 53:229–232.

Brown, J.L. 1975. The Evolution of Behavior. W.W. Norton, New York.

Canals, J. 1936. Observaciones biológicas en arácnidos del orden Opiliones. Revista Chilena de Historia Natural 40:61–63.

Capocasale, R. & L.B. Bruno-Trezza. 1964. Biología de *Acanthopachylus aculeatus* (Kirby, 1819), (Opiliones: Pachylinae). Revista de la Sociedad Uruguaya de Entomología 6:19–32.

Cokendolpher, J.C. 1987. Observations on the defensive behaviors of a neotropical Gonyleptidae (Arachnida: Opiliones). Revue Arachnologique 7:59–63.

Cokendolpher, J.C. & S.R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones: Cosmetidae). Proceedings of the Entomological Society of Washington 93:86–91.

Edgar, A.L. 1963. Proprioception in the legs of phalangids. Biological Bulletin, Woods Hole 124:262–267.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Miscellaneous Publications, Museum of Zoology, University of Michigan 144:1–64.

Edmunds, M. 1974. Defence in Animals: A Survey of Antipredator Defences. Longman, New York.

Eisner, T., D. Alsop & J. Meinwald. 1978. Secretions of opilionids, whip scorpions and pseudoscorpions. Pp. 87–99. *In* Handbook of Experimental Pharmacology. Vol. 48 (S. Bettini, ed). Springer-Verlag, Berlin.

Elpino-Campos, A., W. Pereira; K. Del-Claro & G. Machado. 2001. Behavioral repertory and notes on natural history of the neotropical harvestman *Discocyrtus oliverioi* (Opiliones: Gonyleptidae). Bulletin of the British Arachnological Society 12:44–150.

Gnaspini, P. 1996. Population ecology of *Goniosoma spelaeum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). Journal of Zoology 239:417–435.

Hillyard, P.D. & J.H.P. Sankey. 1989. Harvestman: Synopses of the British Fauna. London: Linnean Society of London.

Hoenen, S. & P. Gnaspini. 1999. Activity rhythms and behavioral characterization of two epigean and one cavernicolous harvestmen (Arachnida, Opiliones, Gonyleptidae). The Journal of Arachnology 27:159–164.

Juberthie, C. 1965. Données sur l'écologie, le developpement et la reproduction des Opilions. Revue d'Écologie et de Biologie du Sol 2:377–396.

Juberthie, C. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks), de Cuba. Annales de Spéléologie 27: 773–785.

Lehner, P.N. 1940. Handbook of Ethological Methods. New York, Garland STPM Press.

Machado, G., V. Bonato & P.S. Oliveira. 2002. Alarm communication: a new function for the scent gland secretion in harvestmen (Arachnida: Opiliones). Naturwissenschaften 89:357–360.

Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the neotropical harvestman *Goniosoma longipes* (Arachnida: Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. Journal of Zoology 246:359–367.

Machado, G. & M.A. Pizo. 2000. The use of fruits by the Neotropical harvestman *Neosadocus variabilis* (Opiliones, Laniatores, Gonyleptidae). The Journal of Arachnology 28:357–360.

Machado, G. & R.L.G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). Ethology, Ecology and Evolution 13:133–150.

Machado, G., R.L.G. Raimundo & P.S. Oliveira. 2000. Daily activity schedule, gregariousness, and defensive behaviour in the neotropical harvestman *Goniosoma longipes* (Arachnida: Opiliones: Gonyleptidae). Journal of Natural History 34:587–596.

Machado, G. & D.M. Vidal. 2001. On the occurrence of epizoic cyanobacteria and liverworts on a neotropical harvestman (Arachnida: Opiliones). Biotropica, 33:535–538.

Macías-Ordóñez, R. 1997. The mating system of *Leiobunum vittatum* Say 1821 (Arachnida: Opiliones: Palpatores): resource defense polygyny in the striped harvestman. Unpublished PhD Thesis, Lehigh University, USA. 167 pp.

Mora, G. 1990. Parental care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida: Gonyleptidae). Animal Behaviour 39:582–593.

Phillipson, J. 1962. Respirometry and the study of energy turnover in natural systems with particular reference to harvestspiders (Phalangida). Oikos 13:311–322.

Phillipson, J. 1963. The use of respiratory data in estimating annual respiratory metabolism, with particular reference to *Leiobunum rotundum* (Latr.) (Phalangida). Oikos 14:212–223.

Pinto-da-Rocha, R. 1999. Opiliones. Pp. 35—44. *In* Biodiversidade do Estado de São Paulo, Brasil: Invertebrados Terrestres. Vol. 5 (C.R.F. Brandão & E.M. Cancello, eds). FAPESP, São Paulo.

Santos, F.H. & P. Gnaspini. 2002. Notes on the feeding behavior of the Brazilian cave harvestman *Goniosoma spelaeum* (Opiliones, Gonyleptidae). The Journal of Arachnology 30:177–180.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry, 3rd edition. W.H. Freeman, San Francisco.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Tallamy, D.W. & T.K. Wood. 1986. Convergence patterns in subsocial insects. Annual Review of Entomology 31:369–390.

Willemart, R.H. 2001. Egg covering in the harvestman *Promitobates ornatus* (Opiliones, Gonyleptidae). The Journal of Arachnology 29:249–252.

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PREDATORY BEHAVIOR OF TWO EUROPEAN ANT-EATING SPIDERS (ARANEAE, ZODARIIDAE)

Stano Pekár[1]: Department of Zoology and Ecology, Faculty of Science, Masaryk University, Kotlárská 2, 611 37, Brno, Czech Republic

ABSTRACT. Prey specialization and the predatory behavior of two European ant-eating zodariid spiders, *Zodarion germanicum* and *Zodarion rubidum*, were studied in detail. The spiders were offered 12 ant species and seven other insects (termites, beetles, aphids, silverfish, flies, crickets and grasshoppers). Study spiders turned out to be ant specialists as they were able to subdue many ant species but ignored all other insects, except termites, which they attacked but rarely subdued. The best capture success was obtained with medium-sized ants (e.g. *Lasius* and *Formica*). The predatory behavior of the zodariid spiders involves an attacking and a handling phase separated by a period of waiting at a safe distance. The attacking phase consisted of a very rapid lunge from the rear, followed by a bite on the most extended ant leg. After an attack, the spider retreated to a safe distance, perhaps an indication that natural selection has favored such caution in the presence of an aggressive prey. The spider waited until the ant ceased moving. Such predatory behavior, which limits contact with the predator and prey, is clearly an effective means of handling a dangerous prey.

Keywords: Ant predation, myrmecophagy, prey specialization, predatory specialization

Although there is limited information on the diet of many spider species, it is believed that most of the 37,000 species known in the world (Platnick 2002) are generalists, able to subdue and consume a rather wide variety of prey types (Nentwig 1987). A few spiders are specialists such as the araneophagous mimetids (Jackson & Whitehouse 1986) and some genera of salticid spiders (Jackson & Hallas 1986), both of which feed predominantly on web-building spiders. Other spiders, such as the araneid spiders of the genus *Mastophora*, feed exclusively on noctuid moths and psychodid flies (Yeargan & Quate 1997). Yet other spiders are termitophagous, like ammoxenids (Dippenaar-Schoeman et al. 1996) or some theridiids (Eberhard 1991). But most of the specialized spiders are ant-eaters; perhaps a consequence of ants being numerous in the habitats of many spiders. Some of the better known ant-eating spiders are in the families Salticidae (Jackson & Pollard 1996), Theridiidae (Porter & Eastmond 1982), Dinopidae (Austin & Blest 1979), Gnaphosidae (Heller 1974) and Zodariidae (Simon 1864).

Albeit ants provide a rich source of nourishment, they are dangerous prey. Ants recognize each other and become aggressive towards an intruder. They can bite, sting and mount a communal attack and they are so numerous that it is difficult to avoid encountering them (Hölldobler & Wilson 1990). Any ant-eating predator must adopt a foraging tactic which will overcome the ant's defensive system. Some spiders, e.g. a theridiid *Theridion*, capture ants using silk threads. This spider builds a web above ground with several sticky threads hanging down. The ant sticks to the threads and only after it becomes entangled in the web does the spider approach and bite it (Nørgaard 1956). Similarly, *Dinopis* uses a small snare to throw over foraging ants (Austin & Blest 1979) while hanging on a thread above the colony of ants. A gnaphosid spider, *Callilepis*, approaches solitary ants rapidly and bites them on the antennae. In a short time the ant is immobilized and taken away by the spider (Heller 1974). Some salticid spiders, for example *Chrysilla*, *Natta* and *Siler*, stalk solitary ants from behind (Jackson & Van Olphen 1992) dropping down from the foliage on a thread when another ant approaches. Species of the genus *Zodarion* catch ants on the ground (Fig. 1) using a very rapid attack. After the attack, *Zodarion* retreats and waits at a distance until the ant is

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[1] Address for correspondence: Research Institute of Crop Production, Drnovská 507, 161 06 Praha 6—Ruzyne, Czech Republic, E-mail: pekar@vurv.cz

Figure 1.—Male *Zodarion germanicum* carrying a captured ant in the vicinity of *Formica cinerea* nest.

paralyzed (Harkness 1976, 1977). Such a rapid attack raised the question about how zodariid spiders subdue ants. Jocqué & Billen (1987) hypothesized that ants are paralyzed by means of an insecticidal compound released from the femoral organ of these spiders. However, recent investigations of Couvreur (1990) and Cushing & Santangelo (2002) on the foraging of *Zodarion rubidum* Simon 1914 supported an earlier observation of Harkness (1977) that the ants are killed instead by venom injected via the spiders' fangs. This conclusion is also supported by the peculiar morphology of zodariid chelicerae, which are medially fused. Such fusion, according to Wunderlich (1980), enables the short and stout fang to penetrate the strong ant cuticle.

Except for the unpublished study of Couvreur (1989), we have no information on prey preference in *Zodarion*. My first objective in this study was to investigate the degree of prey specialization in two species of Zodariidae that occur in Slovakia: *Zodarion germanicum* (C.L. Koch 1837) and *Z. rubidum*. The second objective was to study the predatory behavior in detail. All previous observations on this behavior come from field studies (Simon 1864; Wiehle 1928; Harkness 1976). As the spiders are quite small and the attack is very quick, the field observations gave a rather superficial description of the predatory behavior. I have therefore used laboratory studies to examine the details of the predatory behavior.

METHODS

Prey preference experiments.—In order to investigate the degree of specialization in the two spider species, I combined field observations with laboratory investigations. The field sites were a mining dump in Nováky (Slovakia) for *Z. rubidum* and a steep outcrop in Opatovce nad Nitrou (Slovakia) for *Z. germanicum*. Field observations were made between 1600 h and 1800 h when the spiders are most active (Pekár & Král 2001). The study sites were visited for three days each month between May and August 1997. During each visit, the frequency of spiders running among or catching various ant species nesting in the ground was recorded. There were 5 and 8 ant species found in the study sites (see Table 1). In total, there were 17 and 21 nests in Nováky and Opatovce nad Nitrou, respectively, visited each time. Each nest was checked for presence of spiders at every visit but it was included in the analysis only once in order to avoid repeated measures. An observation at one nest took about 15 min.

To study the degree of specialization more completely, I performed laboratory experiments. For both spider species, 10 each of first instar, adult male and adult female specimens were used. Each specimen was kept singly in a glass tube (17 mm x 60 mm, with soil substrate) at room temperature (20 ± 2°C) under natural photoperiod (L:D ~ 14:10). The substrate was moistened with a drop of water at 3-day intervals. The spiders were not fed for the five days before the experiment. During this time the majority of spiders constructed an igloo-shaped retreat. Shortly before the experiment, the spiders were pushed out of their retreats using a fine brush. Each spider was offered one individual of each of the following ant species: *Camponotus ligniperda* (Latreille), *Formica cinerea* Mayr, *Formica cunicularia* Latreille, *Formica truncorum* Fabricius, *Lasius flavus* (Fabricius), *Lasius platythorax* Seifert, *Monomorium faraonis* (Linnaeus), *Myrmica sabuleti* Meinert, *Plagiolepis vindobonensis* Lomnicki, *Solenopsis fugax* (Latreille), *Tapinoma erraticum* (Latreille) and *Tetramorium caespitum* (Linnaeus). Most of these species occur at the study sites. Some other species were added in order to represent a wide range of the ant body lengths. Ants were offered to spiders intermixed in a

Table 1.—Relative frequency of successful capture (n = 10) of various ant species observed for juveniles (the first instar), males and females of *Zodarion germanicum* and *Zodarion rubidum*. Ant subfamily (ASF): F = Formicinae, D = Dolichoderinae, M = Myrmicinae. [a]identifies species occurring in Nováky, [b]identifies species occurring in Opatovce nad Nitrou. Spider body sizes are means calculated from 5 individuals. Prey body size is the range of sizes measured on 10 individuals.

		Body	*Z. germanicum*			*Z. rubidum*		
	Species	length	Juv.	♂	♀	Juv.	♂	♀
ASF	Spider body length (mm) →	(mm)	2.6	3.8	5.2	1.9	3.1	4.2
Tiny ant species								
		↓						
M	*Solenopsis fugax*[b]	1.8–2.1	1.0	0	0	1.0	0	0
F	*Plagiolepis vindobonensis*[b]	2.1–2.3	1.0	0	0	1.0	0	0
M	*Monomorium faraonis*	2.2–2.3	0.8	0.4	0.6	0.7	0.9	0.9
Medium sized ant species								
M	*Tetramorium caespitum*[a,b]	2.8–3.3	0.7	1.0	1.0	0.6	0.9	1.0
D	*Tapinoma erraticum*[b]	3.0–3.3		0.9	1.0		1.0	0.9
F	*Lasius flavus*[a]	3.2–3.6	0.8	0.9	1.0	0.6	0.8	0.9
F	*Lasius platythorax*[b]	3.3–3.9		1.0	0.9		0.8	0.9
M	*Myrmica sabuleti*[a]	4.7–4.9		0.2	0.4		0.1	0.3
Large ant species								
F	*Formica cinerea*[b]	5.9–6.3		0.6	0.8		0.8	0.9
F	*Formica cunicularia*[a]	6.2–6.8		0.8	0.9		0.3	0.5
F	*Formica truncorum* [small form][b]	4.9–5.2		1.0	1.0		0.7	0.8
F	*Formica truncorum* [large form][b]	7.7–8.0		0.1	0.2		0	0.1
F	*Camponotus ligniperda*[b]	7.3–8.0		0.3	0.4		0.1	0.1

random order once every 5 days. An ant was released into a tube occupied by a spider and the spider's attack and capture success were recorded. The tests lasted at most 60 min. If the spider did not capture the ant or the ant bit the spider, the ant was immediately taken out of the tube. Ants killed a few spiders. Each killed spider was replaced by other specimen. Juvenile spiders were offered only small ant species.

In another experiment, each specimen of *Z. germanicum* used in the previous experiment was offered one specimen of each of the alternative prey: an aphid (*Aphis fabae*), a beetle (*Tribolium confusum*), a cricket (*Acheta domestica*), a fly (*Drosophila melanogaster*), a grasshopper (*Locusta migratoria*), a silverfish (*Atelura formicaria*) and a termite (*Reticulitermes flavipes*). The prey was offered to spiders in a random order once every 2 days. The experiment was carried out using similar procedures and under similar conditions as the one with ants. The total body size of the spiders and the prey (Table 1 & 2) was estimated

Table 2.—Relative frequency of successful capture (n = 10) of various alternative invertebrates observed for juveniles (the first instar), males and females of *Zodarion germanicum*. Insect orders: A = Caelifera, C = Coleoptera, D = Diptera, E = Ensifera, I = Isoptera, S = Sternorrhyncha, T = Thysanura.

Order	Species	Size [mm]	Juv.	♂	♀
E	*Acheta domestica*	3.7	0	0	0
D	*Drosophila melanogaster*	2.9	0	0	0
A	*Locusta migratoria*	6.9	0	0	0
I	*Reticulitermes flavipes*	3.8	0.1	0.1	0.2
S	*Aphis fabae*	3.4	0	0	0
C	*Tribolium confusum*	3.2	0	0	0
T	*Atelura formicaria*	4.1	0	0	0

under a stereoscopic microscope as a mean number from 5 dead individuals.

The differences in capture success of the tested ant species were compared between the sexes and between *Zodarion* species using log-linear analysis of binary data within generalized linear models as the data followed a binomial distribution. In order to identify the most optimal ant species for the two *Zodarion* species, a regression model was fit to the obtained data. Because the relationship between the spider success and the ant body length turned out to have an unimodal character, polynomial (parabola: $y = a + bx + cx^2$) regression was used. Parameters obtained from the parabola were used to calculate the optima (the ant size that gives maximum capture success) and their standard deviations (see Jongman et al. 1995 for more details). The differences between the optima of the two *Zodarion* species were compared using a t-test.

Predatory behavior experiments.—In order to investigate the details of the predatory behavior, I conducted laboratory observations. Ten third-instar juvenile spiders of *Z. rubidum*, kept singly in a Petri dish (40 mm, with filter paper attached to the bottom moistened at 3-day intervals) were used. Experiments were performed at room temperature (20 ± 2°C) and under natural photoperiod (L:D ~ 14:10). To each spider, one ant worker of each *M. faraonis*, *T. caespitum* and *L. flavus* was offered once every 3 days. Latency to the first attack, frequency of attacks on ant appendages, paralysis time (time from the first attack until ant became motionless), and the timing of attacks were recorded. Pearson correlation was used to study the relationship between frequency of bites of each ant appendage and the length of the appendage. The length of appendages was estimated from an image taken by a digital camera rather than by direct measurement because ants stretch out their appendages differently when moving.

Foraging behavior was recorded on a videorecorder (Sony SLV-E 1000 with 25 fps) using a CCD color camera (SONY DXC-LS1P) attached to a stereoscopic microscope (Nikon SMZ-U). Some sequences were then digitized using a frame-grabber and slowly replayed so that events of prey capture could be recorded. Events were analyzed as first order Markov chains using the UNCERT program (Hailman & Hailman 1993) in order to show that the transitions between events are dependent on one another at some level of probability greater than chance (Lehner 1996). A homogeneity (chi-square) test was used to compare observed frequencies of transitions with the expected ones. Standard errors (SE) are used to show variance of means throughout the paper.

Voucher specimens of spiders and ants are deposited at the Research Institute of Crop Production, Department of Entomology, Prague, Czech Republic.

RESULTS

Prey preference.—In the field, subadult and adult specimens of *Z. germanicum* were often seen feeding on or running among *F. cinerea*, followed by *T. caespitum*, *C. ligniperda*, *F. truncorum*, and *L. platythorax* (Fig. 2). Subadult and adult specimens of *Z. rubidum* were seen feeding most frequently on *T. caespitum* and *L. platythorax* (Fig. 2). Early instars of this species fed on small workers of *T. caespitum*. None of the spider species were seen to catch prey other than ants. In the laboratory experiments, the first instar of both species readily attacked and subdued tiny ant species and some of the medium-sized ants (Table 1). Adult spiders did not attack tiny ants but easily seized all medium sized ants except for workers of *M. sabuleti*, which the spiders attacked but seldom subdued. Some of the large ants (*F. cinerea*, *F. cunicularia* and the small form of *F. truncorum*) were successfully subdued while others (*C. ligniperda* and the large form of *F. truncorum*) were seldom captured by either *Zodarion* species. The two largest ant species often bit legs of the spiders (in 56% of trials, *n* = 80) and in 3 trials (4%) even killed them.

Males of both species attacked and subdued on average (pooled for all ant species) slightly fewer ants than females but this difference was not significant (log-linear analysis: $\chi^2_2 = 1.2$, NS). Neither was there a difference between the capture success of the two zodariid species (males and females combined) (log-linear analysis: $\chi^2_1 = 0.9$, NS). The relationship between the size of ants and the capture success for both *Zodarion* species (pooled for both sexes), disregarding data on *M. sabuleti* (due to low capture success) was modeled using a parabola (Fig. 3). It is apparent from the response curves that the optimal size of ants for *Z. germanicum* is very similar (optimum

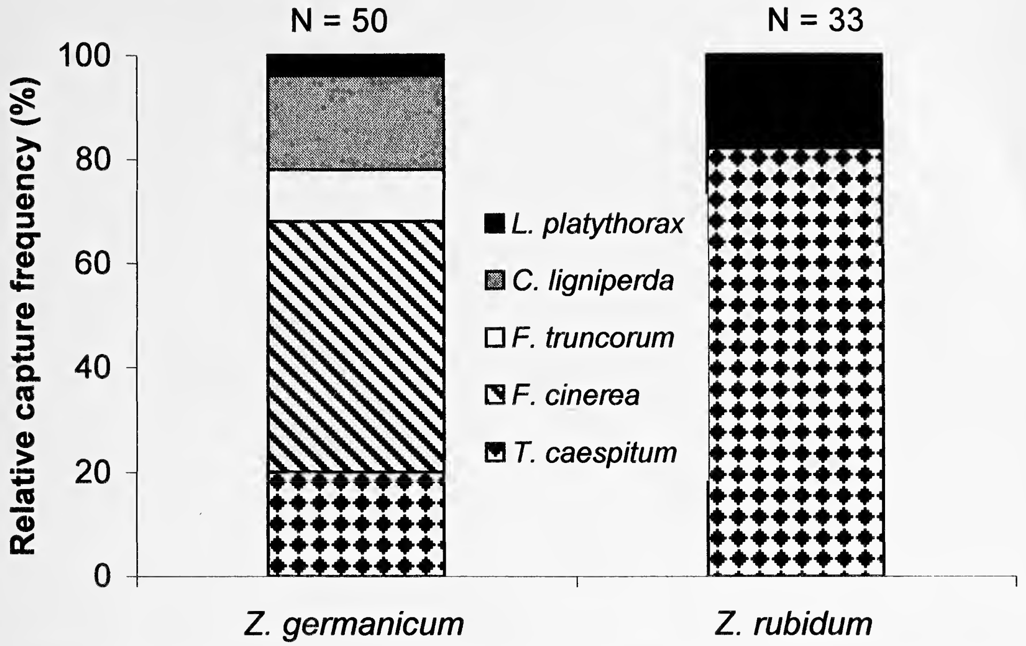


Figure 2.—Relative frequency of ant species captured by subadult and adult specimens of *Zodarion germanicum* and *Zodarion rubidum* observed in the study sites.

= 4.9, SD = 2.1) to that for *Z. rubidum* (optimum = 4.6, SD = 2.3) (t-test: t = 0.29, NS). These values correspond to the size of the small form of *F. truncorum*. The optimal prey is thus equal or smaller in size than adult individuals of *Z. germanicum*, but it is larger than adult individuals of *Z. rubidum*. Of the other insects offered to the spiders, only termites were attacked but rarely subdued by *Zodarion* spiders. No other invertebrate was attacked or subdued (Table 2).

Predatory behavior.—During the attacking phase (Fig. 4), spiders moved slowly while waving the first pair of legs. I recognized five events (I—V) that took place during the attack. After orientation toward an ant, the spider quickly approached (I) it with half-raised forelegs (Fig. 5). As the spider got closer, it first lightly touched (II) the ant's body with the tarsi of the forelegs (Fig. 6); occasionally the spider touched (III) the ant using the tips of the palpal tarsi. Afterwards the spider grabbed hold of a leg by its palps, bit (IV) the leg (Fig. 7), and retreated (V). The sequence of recognized events (Fig. 8) did not occur by chance (Chi-square test: $\chi^2_{29} = 536$, $P < 0.001$). The entire attack sequence, from approaching to retreating, lasted only 0.17 ± 0.01 seconds.

Detailed analysis of the behavior showed that after the first encounter with an ant, the spider often stopped and positioned itself with legs fully outstretched. The spider oriented toward an ant which passed at a distance less than 1.6 mm ($n = 30$) from the tip of its tarsi. When an ant passed by, the spider stalked it and approached it (Fig. 4). Latency to the first attack was similar for all three ant species (*M. faraonis*, *T. caespitum* and *L. flavus*) being on average 70 s. Spiders attacked rapidly by biting any of the ant's appendages. There were many more attacks (pooled for all three ant species) from a side or rear (77%, $n = 102$) than on the head of ants (23 %). Bites were most often applied to the longest appendages, with bite frequency and appendage length being positively correlated (Pearson correlation: r = 0.81, $P = 0.04$). Thus the most frequently bitten leg was the longest, one of the hind legs (Fig. 9). Ants were repeatedly bitten until immobile. There were on average 3.4 attacks made on the study ant species. Most of the attacks (62 %, $n = 102$) occurred within the first 3 min and only 4 % occurred after 10 min. The frequency of attacks tended to decrease steadily with time as the ant slowed down.

Immediately after being bitten the ant be-

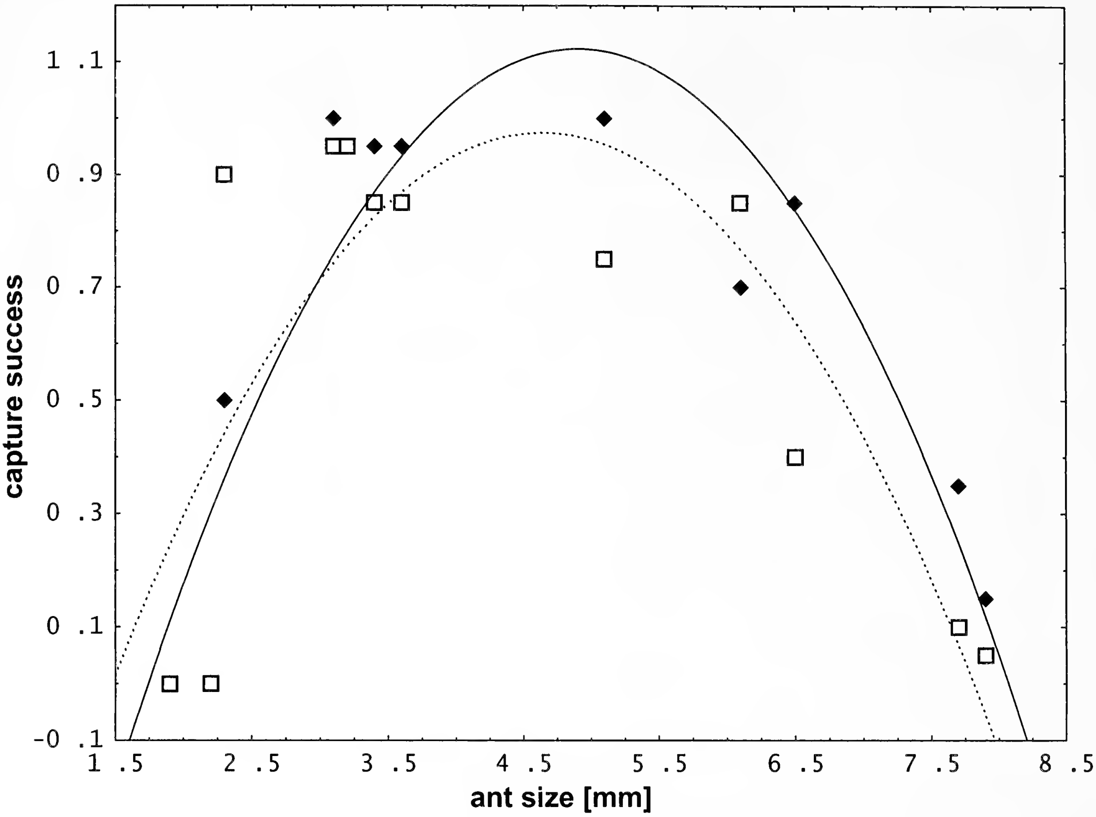


Figure 3.—Parabolic model describing relationship between the capture success of adult spiders of *Zodarion germanicum* (◆) and *Zodarion rubidum* (□) and the size of ants (ordered by size): *M. faraonis*, *T. caespitum*, *T. erraticum*, *L. flavus*, *L. platythorax*, *F. cinerea*, *F. cunicularia*, *F. truncorum*, and *C. ligniperda*. The coefficient of determination (R^2) is 0.91 and 0.81 for *Zodarion germanicum* and *Zodarion rubidum*, respectively.

came excited (open mandibles), moved around and made attacks to the surrounding area. The stabbed leg was visually cramped and the velocity of the ant gradually decreased: it began to stumble, its gaster twisted and finally the whole body was overcome by paralysis. Ants (*T. caespitum*) that had been stabbed only once were immobile 3:35 ± 0.4 min after the stab.

The handling phase was separated from the attacking phase by a period of waiting. After the last attack the spider waited 2–29 min crouched in a corner of the dish. Then it began to search for the immobilized prey. The spider moved slowly with raised forelegs and palps lightly tapping the substrate, then stopped at a distance of 3.2 ± 0.1 mm from the ant, and probed with forelegs waving dorso-ventrally (Fig. 10). It then stretched one foreleg forward and gently touched the prey (Fig. 11). If the prey was quiescent the spider would carefully palpate it (Fig. 12), grab hold of the ant's thorax and carry it away to feed up on. If the prey was still moving, the spider would run away. Sometimes (46%, $n = 30$) the spider grabbed a still wriggling ant. During feeding, the spiders moved the ant corpse around and gradually sucked up various body parts, starting with the thorax, legs, head and abdomen. Feeding took on average 2.5 hours ($n = 30$) but varied considerably (1–7 hours). The remains of the ant were discarded as an empty shell.

DISCUSSION

Unlike ant-eating salticids which are also able to capture other insects (Jackson & Van Olphen 1991), zodariid spiders turned out to be more specialized in their diet. The two species of *Zodarion* were found to feed on ant

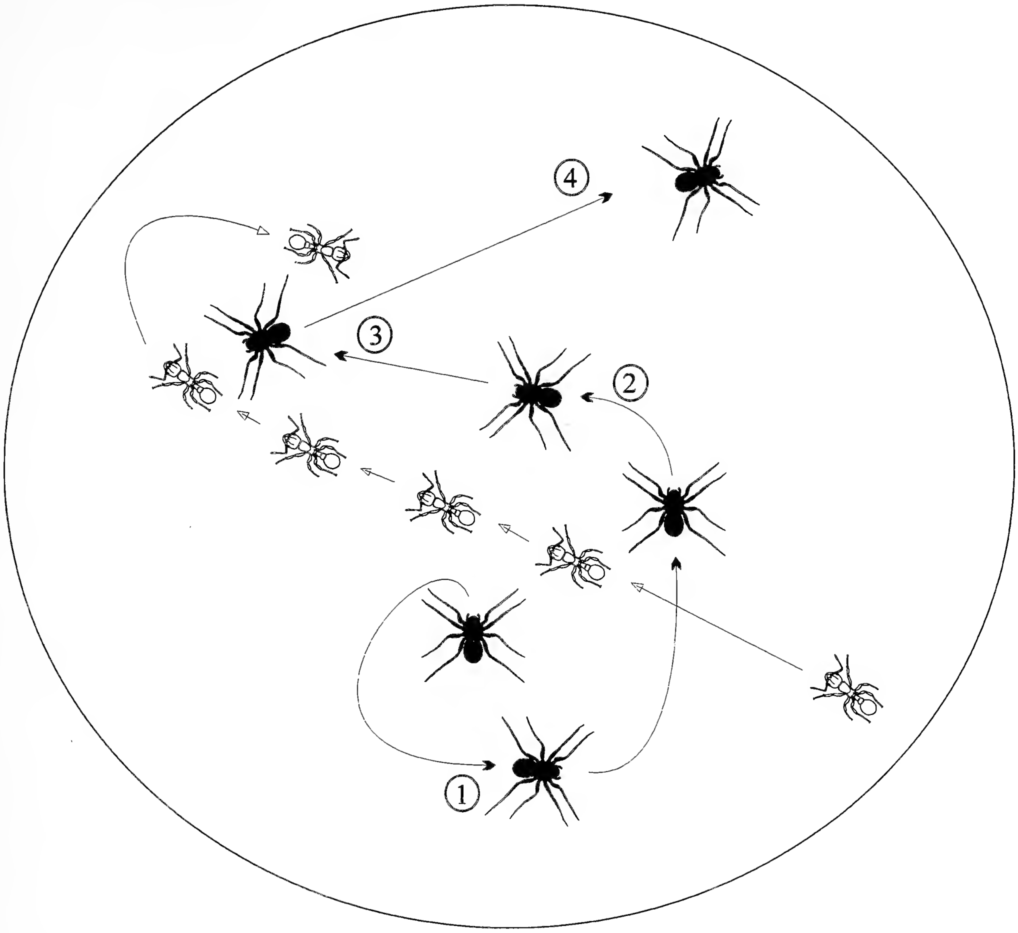
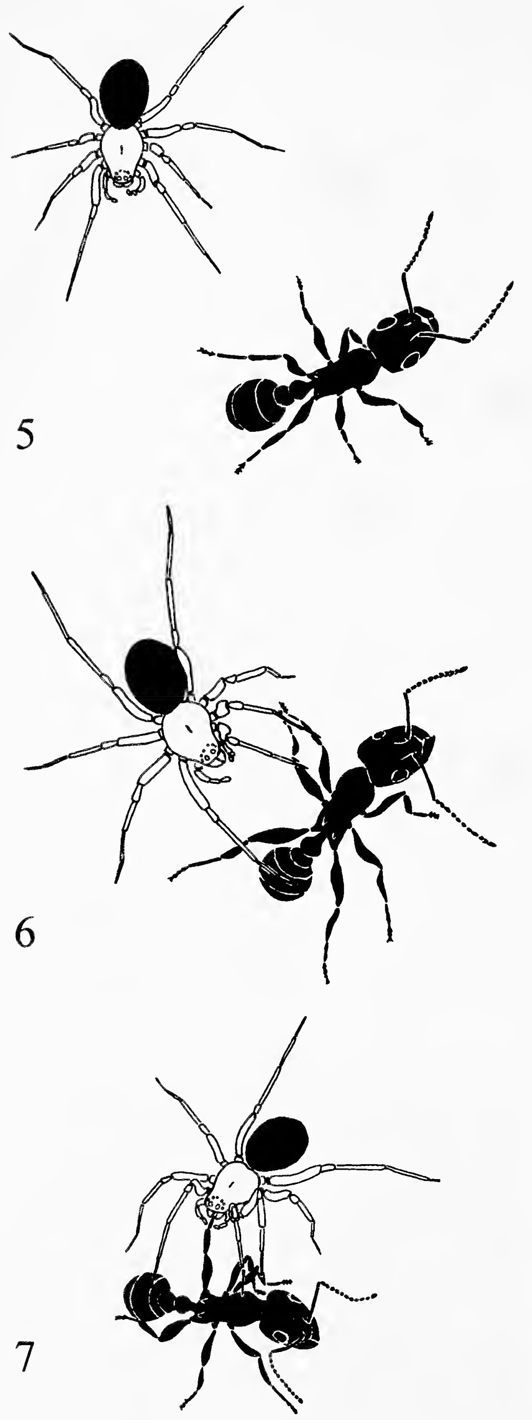


Figure 4.—Sample attack path of *Zodarion rubidum* (black) pursuing the ant (white). 1 = spider orients toward the ant; 2 = spider stalks the ant; 3 = spider attacks the ant from the rear; 4 = spider retreats.

species of different sizes and belonging to different subfamilies. With the exception of termites, they ignored other insects offered. Although the spiders attacked termites, they seldom killed them. Similar results on the prey preference of *Z. rubidum* were obtained by Couvreur (1989). These results suggest that the two study species of *Zodarion* are strict ant specialists.

Couvreur (1990) observed that only females of *Z. rubidum* capture ants. In my experiments, males captured ants as well, although less frequently than females. The ability to subdue ants for both zodariid species in both sexes was found to be dependent to some extent on the size of prey. The best success of adults was obtained with medium sized ants which are about the same size as the tested spiders. The two species showed similar abilities in the capture of the ant species. The tiny ant species were usually not attacked by adult spiders. It appears to me that these ants did not produce a signal, either visual (being too tiny), vibratory (being too light) or olfactory (producing an alarm pheromone that is not detected by spiders), that would elicit attack by *Zodarion*. However, the lack of response can also be explained applying the optimal foraging hypothesis (Riechert & Luczak 1982). Tiny ant species might be considered unprofitable for study *Zodarion* species: greater energy would be spent attacking and subduing them than gained by their consumption.

The red ants (*M. sabuleti*) were seldom subdued by either species of spiders. Unlike in tiny ant species, *M. sabuleti* was attacked by spiders but the attack did not lead to immo-



Figures 5–7.—The attacking phase. Illustrative example of *Zodarion rubidum* capturing the ant (*T. caespitum*). Taken from a video analysis (time frame in parentheses). 6. Spider approaches ant from the rear with raised forelegs (0.00 s); 7. Spider taps the ant's gaster (0.13 s); 8. Spider bites ant's tibia of the third leg (0.19 s).

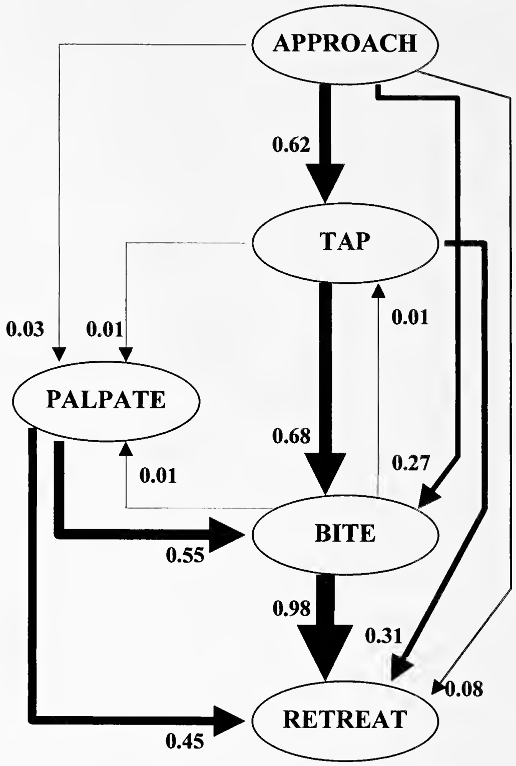


Figure 8.—Flow diagram of the events (pooled for the three ant species) of the attacking phase with probability frequencies (n = 102). After retreating spiders either continued attacking (starting with approach) or waited and continued handling phase.

bilization. I assume that the spiders were not able to penetrate the heavy, sclerotized cuticle of this ant species. Alternatively, the venom of the two spider species might not be effective in immobilizing this ant. The ability to subdue large ants, like *F. truncorum*, was very low in tube trials because the ants often bit the spiders' legs. In the field, the ability is greater because the spider has more room to hide from the excited ant (pers. observ.). Lower capture success might be also due to more agile behavior of larger ant species. Formicinae ants are generally moving fast so the chances of *Zodarion* to attack it might decrease.

The capture of ants is risky. At the study sites I found 47% (n = 30) of *Zodarion* spiders missing at least a part of one leg presumably as a result of an ant's attack. That ants are very dangerous prey for *Zodarion* as can be seen from the analysis of the spider's predatory behavior. First, the behavior is com-

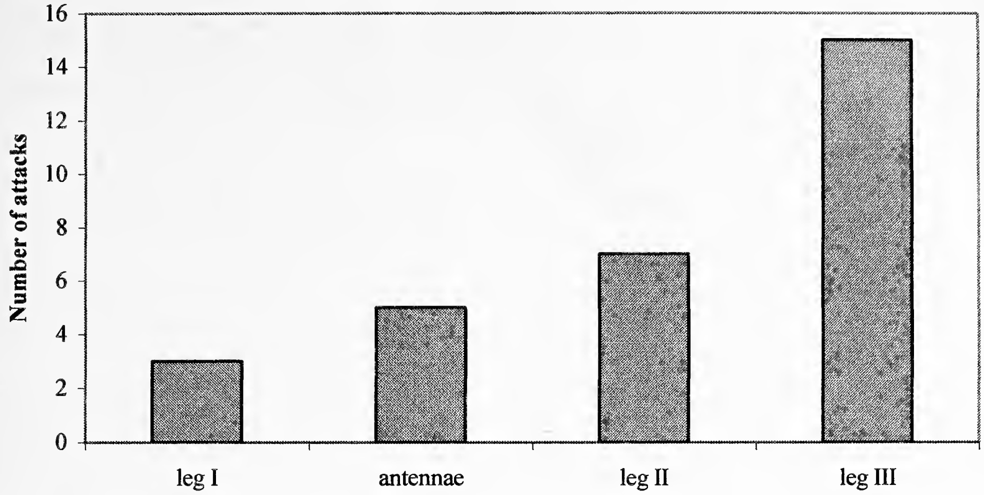


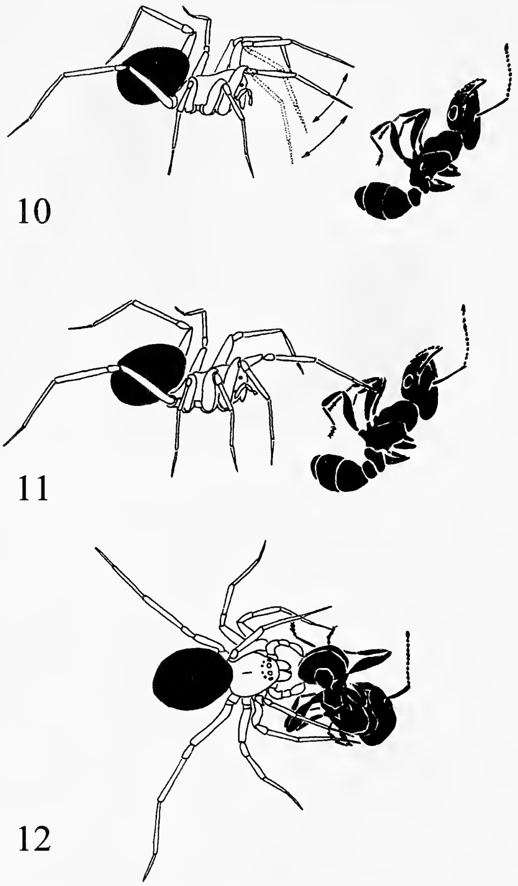
Figure 9.—Relationship between the frequency of the attacks and the length of each ant appendage (pooled for the three ant species). Appendages are ordered by visual size: leg I, antennae, leg II, leg III.

posed of two phases, separated by a period of waiting at a safe distance. As the bitten ant becomes aggressive, spiders are at risk. Indeed, attacked ants often tried to attack the spider which generally fled. Second, the spider generally attacked very quickly by a surprise attack from the rear. Third, the spider bit the most extended appendage. All these acts compose a predatory strategy that enables the spider to stay away from the ant. Finally, the spider handled the ant only when it was immobilized. Such predatory behavior is likely to be an adaptation to the capture of a dangerous prey.

This predatory tactic corresponds well to that adopted by other ant-eating zodariid spiders, namely *Z. elegans* (Simon 1873) and *Z. frenatum* Simon 1884 (Harkness 1976, 1977; Wiehle 1928). A similar tactic, i.e. the attack from the rear followed by a retreat, has also been reported for some ant-eating salticids (Jackson & Van Olphen 1992; Jackson et al. 1998). Such a tactic is obviously a very effective means of overcoming the ant's defenses. Other ant-eating salticid spiders, however, attack ants head-on (Jackson & Van Olphen 1991). So does *Callilepis nocturna* Linnaeus 1758 (Heller 1974), which bites the ant's antennae. This may accelerate the paralysis (since the antennae are close to the ant's brain) and may enable this spider to grab hold of an ant's body within about a minute after the seizure, whereas *Zodarion* has to wait much longer.

There might be a trade-off between the two foraging tactics, attacking head-on and from the rear. The former tactic is obviously more risky as the spider exposes its body close to an ant's mandibles, but enables the spider to take hold of the prey shortly after the attack. The latter tactic is safer (the spider runs away from the excited ant), but the ant can be collected by another predator (or ant nestmates) in the meantime. I suggest that robust and non ant-mimicking spiders, such as *Callilepis*, use the head-on tactic. Slender ant-mimicking spiders, such as the zodariids that are protected from visually hunting predators by mimicry (Pekár & Král 2002) use the rear tactic.

The diet specialization appears to be apomorphic for zodariid spiders. Although very little information is available for the more than 50 genera of zodariid spiders described so far (Jocqué 1991) some common traits are apparent. Primitive representatives of Zodariidae appear to be polyphagous. *Lutica*, from the subfamily Lachesaninae, feeds on various invertebrates and captures prey in a similar fashion to that of *Atypus* (Ramirez 1995). More derived representatives show some specialization. For example, the Namibian zodariid spider *Psammoduon deserticola* (Simon 1910), a member of the subfamily Cydrelinae, feeds mainly on tenebrionid beetles, which are located while diving through the sand but will also prey on syrphid larvae and Thysanoptera (Rössl & Henschel 1999). Finally the most derived representatives seem to be strictly spe-



Figures 10–12.—The handling phase. Illustrative example of *Zodarion rubidum* handling the ants. Taken from a video analysis. 11. Spider approaches and begins to probe (forelegs waved); 12. Spider taps the ant's leg; 13. Spider palpates ant's head.

cialized. South African species of the genus *Diores* feeds on termites which are ambushed on their mounds during the night (Jocqué & Dippenaar-Schoeman 1992). *Acanthinozodium* in North Africa (Pierre 1959) and *Zodarion* in Europe were observed to feed on ants. However, more investigation into the diet of other representatives of zodariid spiders should be carried out in order to support this hypothesis.

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LITERATURE CITED

Austin, A.D. & A.D. Blest. 1979. The biology of two Australian species of dinopid spider. Journal of Zoology 189:145–156.

Couvreur, J.M. 1989. Quelques aspects de la biologie d'une araignée myrmécophage: *Zodarion rubidum*, (Simon, 1914). MSc Thesis, Université libre de Bruxelles, Bruxelles.

Couvreur, J.M. 1990. Quelques aspects de la biologie de *Zodarion rubidum* Simon, 1918. Nieuwsbrief van de Belgische Arachnologische Vereniging 5(2):7–15.

Cushing, P.E., & R.G. Santangelo. 2002. Notes on the natural history and hunting behavior of an ant eating zodariid spider (Arachnida, Araneae) in Colorado. Journal of Arachnology 30(3):618–621.

Dippenaar-Schoeman, A.S., M. De Jager & A. Van den Berg. 1996. *Ammoxenus* species (Araneae: Ammoxenidae)–specialist predators of harvester termites in South Africa. African Plant Protection 2:103–109.

Eberhard, W.G. 1991. *Chrosiothes tonala* (Araneae, Theridiidae): a web-building spider specializing on termites. Psyche 98(1):7–19.

Hailman, E.D. & J.P. Hailman. 1993. UNCERT: Analyses of sequential events by Markov chains (version alpha). A DOS-compatible software. Available at http://gila.cisab.indiana.edu/pub/

Harkness, R.D. 1976. The relation between an ant, *Cataglyphis bicolor* (F.) (Hymenoptera: Formicidae) and a spider, *Zodarion frenatum* (Simon) (Araneae: Zodariidae). Entomologist's Monthly Magazine 111:141–146.

Harkness, R.D. 1977. Further observations on the relation between an ant, *Cataglyphis bicolor* (F.) (Hymenoptera: Formicidae) and a spider, *Zodarion frenatum* (Simon) (Araneae: Zodariidae). Entomologist's Monthly Magazine 112:111–123.

Heller, G. 1974. Zur Biologie der ameisenfressenden Spinne *Callilepis nocturna* Linnaeus 1758 (Araneae, Drassodidae). Dissertation, Johannes Gutenberg-Universität, Mainz.

Hölldobler, B. & E.O. Wilson. 1990. The Ants. Springer-Verlag, Berlin-Heidelberg.

Jackson, R.R. & S.A. Hallas. 1986. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina*, and *Phaeacius* sp. indet. New Zealand Journal of Zoology 13:491–520.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41:287–308.

Jackson, R.R. & A. Van Olphen. 1991. Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae: Salticidae). Journal of Zoology 223:577–591.

Jackson, R.R. & A. Van Olphen. 1992. Prey-capture techniques and prey preferences of *Chrysilla*, *Natta* and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. Journal of Zoology 227:163–170.

Jackson, R.R. & M.E.A. Whitehouse. 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy and prey specialization. Journal of Zoology 210:279–303.

Jackson, R.R., D. Li, A.T. Barrion & G.B. Edwards. 1998. Prey-capture techniques and prey preferences of nine species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines. New Zealand Journal of Zoology 25:249–272.

Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201:1–160.

Jocqué, R. & J. Billen. 1987. The femoral organ of the Zodariinae (Araneae, Zodariidae). Revue de zoologie Africaine 101:165–170.

Jocqué, R. & A.S. Dippenaar-Schoeman. 1992. Two new termite-eating species (Araneae, Zodariidae) and some observations on unique prey immobilization. Journal of Natural History 26:1405–1412.

Jongman, R.H.G., C.J.F. Ter Braak & O.F.R. Van Tongeren. 1995. Data analysis in community and landscape ecology. 2nd ed. Cambridge University Press, Cambridge.

Lehner, P.N. 1996. Handbook of ethological methods. 2nd edition. Cambridge University Press, Cambridge.

Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Nørgaard, E. 1956. Environment and behaviour of *Theridion saxatile*. Oikos 7:159–192.

Pekár S. & J. Král. 2001. A comparative study of the biology and karyotypes of two central European zodariid spiders (Araneae, Zodariidae). Journal of Arachnology 29(3):345–353.

Pekár, S. & J. Král. 2002. Mimicry complex in two central European zodariid spiders (Araneae, Zodariidae): how *Zodarion* deceives ants. Biological Journal of the Linnean Society 75:517–532.

Pierre, F. 1959. Le mimétisme chez les araignées myrmécomorphes. Année biologique 35:191–201.

Platnick, N.I. 2002. The world spider catalog, version 3.0. American Museum of Natural History. Available at http://research.amnh.org/entomology/spiders/catalog 81–87/

Porter, S.D. & D.A. Eastmond. 1982. *Euryopis coki* (Theridiidae), a spider that preys on *Pogonomyrmex* ants. Journal of Arachnology 10:275–277.

Ramirez M.G. 1995. Natural history of the spider genus *Lutica* (Araneae, Zodariidae). Journal of Arachnology 23(1):111–117.

Riechert S.E. & J. Luczak. 1982. Spider foraging: behavioral responses to prey. Pp. 354–385. *In* Spider communication: Mechanisms and ecological significance. (P.N. Witt & J.S. Rovner, eds). Princeton Univ. Press, New Jersey.

Rössl, R. & J.R. Henschel. 1999. Ecology and diet of *Psammoduon deserticola* (Simon) (Araneae: Zodariidae). Bulletin of the British Arachnological Society 11(4):155–157.

Simon, E. 1864. Histoire naturelle des Araignées (Aranéides). Paris.

Wiehle, H. 1928. Beiträge zur Biologie der Araneen insbesondere zur Kenntnis des Radnetbaues. Zeitschrift für Morphologie und Ökologie der Tiere 11:115–151.

Wunderlich, J. 1980. Drei Arten der Gattung *Zodarion* Walckenaer 1847 aus Nordjugoslawien (Arachnida: Araneae: Zodariidae). Senckenbergiana biologica 61:113–117.

Yeargan, K.V. & L.W. Quate. 1997. Adult male bolas spider retain juvenile hunting tactics. Oecologia 112:572–576.

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2004. The Journal of Arachnology 32:42–54

WEB BUILDING BEHAVIOR AND THE PHYLOGENY OF AUSTROCHILINE SPIDERS

Lara Lopardo[1], **Martín J. Ramírez, Cristian Grismado** and **Luis A. Compagnucci**: Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, Buenos Aires C1405DJR, Argentina. E-mail: laralo@gwu.edu

ABSTRACT. We report on the natural history and web building behavior of the South American austrochilids *Thaida peculiaris* and *Austrochilus forsteri*, relatively basal lineages within Araneomorphae. Species of these two cribellate genera construct large, two-dimensional sheet webs with a funnel retreat. When combing cribellate silk, austrochilids use both fourth legs, like entelegyne spiders, and unlike Hypochilidae and Filistatidae. Furthermore, the alternancy of combing legs IV is determined by the leg III involved in the attachment of a cribellate segment; the leg IV ipsilateral to the leg III that made the attachment will comb the next segment, except for the first segment. This similarity to Entelegynae in combing with both fourth legs contradicts current hypotheses of basal araneomorph relationships and suggests that the Austrochilidae may be the sister group of entelegyne spiders.

Keywords: Austrochilinae, combing behavior, systematics, phylogeny

Behaviors associated with web building and web architecture itself are increasingly used as indicators of relationships among higher groups of spiders (e.g., Eberhard 1982, 1988, 1990; Coddington 1986a, 1990; Hormiga et al. 1995; Griswold et al. 1998, 1999; Scharff & Coddington 1997). The nature and disposition of sticky threads seems to be especially informative (Eberhard 1988; Eberhard & Pereira 1993). Most spiders that rely on a web for prey capture have special, adhesive threads to help retain prey until they are subdued. These sticky threads are consistently laid on a non-sticky structural scaffolding (Eberhard 1992). Two basic types of sticky threads exist, each used by different groups of spiders (e.g., Opell 1997). Dry, cribellar capture threads (Fig. 7) have fibrils produced by hundreds of minute cribellar spigots, while araneoid viscid capture threads have droplets of sticky glue produced by two pairs of aggregate gland spigots. Pholcid spiders also produce viscid silk like that of araneoids (Briceño 1985), but both anatomy and phylogeny (Platnick et al. 1991) suggest independent origins of sticky silk in pholcids and araneoids. It is well established that primitive araneomorph spiders were cribellate (Forster et al. 1987; Platnick et al. 1991).

Eberhard (1988) observed and compiled information on combing behavior for many cribellate families. He described two basic patterns of combing behavior. In type I, observed in *Hypochilus* and Filistatidae, the combing leg IV rests on the contralateral leg III, but only leg IV moves. In type II, observed in cribellate entelegynes, the combing leg IV holds on the contralateral leg IV, and both legs move together as an almost rigid unit. Eberhard logically concluded that type II combing behavior is a synapomorphy of Entelegynae (see Fig. 18).

The subfamily Austrochilinae includes two genera endemic to temperate forests in Southern Chile and Argentina (Forster et al. 1987). They comprise, along with the austrochilid Hickmaniinae and Gradungulidae, the superfamily Austrochiloidea, the sister group of Araneoclada (all araneomorph spiders except Hypochilidae, Platnick et al. 1991). Little is known of austrochiline behavior (as is the case in most other Austrochiloidea), other than the general appearance of their webs and their nocturnal habits (Forster et al. 1987 and references therein; Ramírez & Platnick 1999). Because of their basal position, austrochiloids are especially interesting for testing the evo-

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[1] Current address: Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, D.C. 20052 USA.

lution of combing behavior, and may provide an insight into the origin of the sheet webs of araneomorph spiders. We present here the first data on combing behavior in Austrochilinae, and some observations on the web architecture and sequence of construction.

METHODS

Observations were made in three localities in southern Chile and Argentina, in December and January. 1) Aguas Calientes, Parque Nacional Puyehue, elev. 400–500 m, 40°44′S, 72°18′W, Osorno Province, Región X, Chile (13–17 December 1998, M. Ramírez, L. Compagnucci, C. Grismado and L. Lopardo collectors). 2) Monumento Natural Contulmo, elev. 340m, 38°01′S, 73°11′W, Malleco Province, Región IX, Chile (19–21 December 1998, same collectors as above). 3) Puerto Blest, elev. 800m, 41°02′S, 71°49′W, Parque Nacional Nahuel Huapi, Neuquén Province, Argentina (7–19 January 2000, L. Lopardo and A. Quaglino collectors). These are intensively collected localities of Valdivian temperate forest.

The spiders were observed in the field, mostly using the methods described by Eberhard (1992). We selected several large and easily accessible webs, and marked their location with brightly colored ribbons to locate them at night. During the day, we made a large hole in the central part of the sheet, leaving only the retreat and sometimes also the main lateral lines, and returned at dusk to observe repair or reconstruction. Prey capture behavior was observed on insects that came naturally to the webs, as well as others that we tossed onto intact webs when the spider was active. For photography and to facilitate detailed observations we increased contrast by dusting the webs with cornstarch (Carico 1977). Dusting also allowed observation of progress in web building by distinguishing the recent, unpowdered threads from the older ones. Observations of active spiders were made at night with a two D cell flashlight covered with two layers of red cellophane. Even with this red light, the spiders were sensitive to direct illumination. For prolonged observations we illuminated the background just enough to see the spider's outline. Although we tried to minimize disturbances, these spiders were very sensitive and timid and often fled to the retreat after 1–5 minutes of continuous observation. We therefore observed either several individuals for repeated short periods within the same night, or one spider all night long, so it accommodated to the observer from the beginning of its activity period. After observations were complete, we collected the spiders for identification, although some escaped. All adult specimens from Puyehue and Puerto Blest are *Thaida peculiaris* Karsch 1880, and those from Contulmo are *Austrochilus forsteri* Grismado, Lopardo & Platnick in press). We also collected the minute kleptoparasite spiders *Sofanapis antillanca* Platnick & Forster 1989 (Anapidae) from austrochilid webs. The webs and behavior of *Thaida* and *Austrochilus* species appeared indistinguishable. Therefore, we present a general account that applies equally to both genera and, where possible, we identify the specimens from which observations were made. We observed more than 60 spiders in all.

Vouchers of all observations, photographic slides and web samples are labelled with acronyms of collector, date and a sequential number or code, followed by film frame number (e.g., MJR 15.XII.98/Au4, frame 9). Specimens with these labels are deposited in Museo Argentino de Ciencias Naturales (MACN-Ar, Cristina Scioscia, Buenos Aires) and Museo Nacional de Historia Natural de Chile (MHNS, Ariel Camousseight, Santiago de Chile). Web samples and photographs are deposited in MACN-Ar.

Specimens.—*Thaida peculiaris:* Aguas Calientes, Puyehue: 1 ♂, 1 ♀ penultimate, 2 immatures (MACN-Ar 9989); 1 ♀ penultimate (no web, just the retreat) (MACN-Ar 10002); 1♀ (MJR 13.XII.98–1, with eggsac) (MACN-Ar 9991); 1 ♂ (CG 15.XII.98–10) (MACN-Ar 10000); 1 ♀ penultimate (Au4) (MHNS); 1 immature (Au6) (MACN-Ar 9992); 4 immatures (AuX6) (MACN-Ar 10003); 1 indefinite specimen (Au10) (MACN-Ar 9986); 1 ♂ penultimate (Au11) (MHNS); 1 immature (Au12) (MACN-Ar 9999); 1 ♀ (MJR 15.XII.98/Au13, frame C1) (MACN-Ar 9993); 1 indefinite specimen (Au17) (MACN-Ar 9997); 1 immature (MJR 14.XII.98/Au21, frame A7) (MACN-Ar 9994); 1 ♀ penultimate (Au24) (MHNS); 1 indefinite specimen (Au27) (MACN-Ar 10005); 1 ♀ (MJR 16–17.XII.98/Au28A, frames C5, D20) (MACN-Ar 9990); 1 ♀

(Au28B) (MACN-Ar 9998); 1 immature (Au29) (MACN-Ar 10004); 1 ♂ penultimate (Au30) (MHNS); 1 ♀ penultimate (Au31) (MACN-Ar 9985); 1 immature (Au32) (MHNS); 2 indefinite specimens (Au33) (MACN-Ar 9995); 1 indefinite specimen (Au38) (MACN-Ar 9988); 1 immature (Au40) (MACN-Ar 9996); 1 indefinite specimen (Au41) (MACN-Ar 10006); 1 ♀ (Au42B) (MACN-Ar 9987). Puerto Blest: 4 ♀: Au1 (MACN-Ar 9976), Au6 (MACN-Ar 9979), Au9 (MACN-Ar 9977), Au10 (MACN-Ar 9978); 1 ♀ penultimate: Au3 (MACN-Ar 9984); 1 immature: Au7 (MACN-Ar 9980); 3 ♂ penultimate: Au4 (MACN-Ar 9983), Au8 (MACN-Ar 9981), Au11 (MACN-Ar 9982).

Austrochilus forsteri: Monumento Natural Contulmo: 1 male holotype (MHNS); 1 female paratype (MJR 19.XII.98/10; MHNS); 1 ♀, 2 immatures (MHNS); 1 ♀ 4 immatures (MACN-Ar 9845); 1 immature (MACN-Ar 9846); 2 immatures (MHNS); 1 immature (MJR 19.XII.98–7; MACN-Ar 9844); 1 immature (MJR 19.XII.98–9; MACN-Ar 9847); 1 ♀ (MJR 19.XII.98–11, frame E30; MACN-Ar 9839); 1 ♀ (AuX1; MACN-Ar 9838); 1 ♂ (AuX2; MACN-Ar 9837); 1 immature (AuX3; MACN-Ar 9841); 1 immature (AuX4; MACN-Ar 9842); 1 ♂ penultimate (AuX5; MACN-Ar 9840); 1 immature (AuX7; MACN-Ar 9843); 1 ♀ penultimate (AuX8; MHNS).

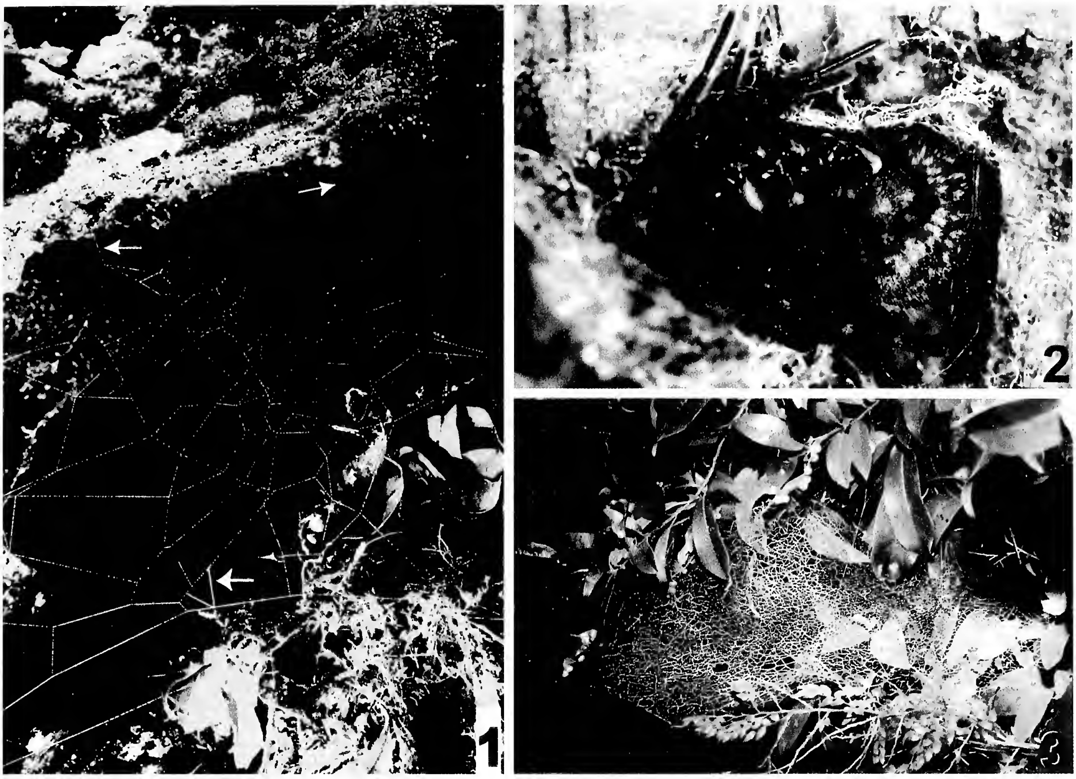
Sofanapis antillanca Platnick and Forster: Aguas Calientes, Puyehue: On web of Austrochilinae: 2 ♂, 3 ♀, 3 immatures (MHNS), 2 ♂, 3 ♀, 3 immatures (MHNS), 2 ♂, 2 immatures (MJR 15.XII.98/2; MACN-Ar), 1 immature (MACN-Ar); 1 ♀ (LL&MJR 15.XII.98/1 on web of Austrochilinae Au4, web sampled; MACN-Ar); 1 immature (on web of Austrochilinae Au11; MACN-Ar); 1 ♂, 1 ♀, 4 immatures (on web of Austrochilinae Au12; MHNS); 3 ♀, 2 immatures (on web of Austrochilinae Au13, two *Sofanapis* escaped; MHNS); 2 immatures (on web of Austrochilinae Au17; MACN-Ar); 3 ♀, 2 immatures (on web of Austrochilinae Au27; MHNS); 1 ♂, 4 ♀, 2 immatures (on web of Austrochilinae Au31; MACN-Ar); 4 immatures (on web of Austrochilinae Au40; MACN-Ar). Monumento Natural Contulmo: 1 ♀ (MHNS); 1 ♀ (MACN-Ar). On web of Austrochilinae: 27 ♀, 6 ♂ (MACN-Ar); 5 ♂, 2 ♀, 2 immatures (MHNS); 1 ♂, 6 ♀, 2 immatures (MHNS); 2 ♀ (MJR 19.XII.98/7, on web of Austrochilinae same reference; MACN-Ar); 2 ♂, 6 ♀, 1 immature (on web of Austrochilinae MJR 19.XII.98/10; MACN-Ar); 2, 7 ♀ (web sampled, on web of Austrochilinae Au100; MACN-Ar). 1 ♂, 2 ♀ (MJR 21.XII.98/9 on *Porteria* sp. web, same reference; MACN-Ar); 1 ♀ (MJR 21.XII.98/10 on *Porteria* sp. web, same reference; MACN-Ar).

RESULTS

Thaida and *Austrochilus* species build large, horizontal or slightly sloping, permanent sheet webs with retreats (Figs. 1, 3, 4). Web size varies greatly (about 50–120 cm), but seems to correlate with specimen size. Austrochilines enlarge the web by adding to its edge on successive nights, at least during the first days of construction. Web shape varies according to available space and attachment points. The distance from the ground to the sheet and refuge ranges from very short (when the external border of the web is attached to the soil) to more than two meters high. A normal web consists of three components: an exposed horizontal sheet, several vertical supporting lines near the retreat (Figs. 1 & 13; thin and thick arrows respectively), and a hidden tube-like retreat (Fig. 4) connected to the sheet by a funnel. Two kinds of thread comprise the sheet: non-sticky supporting lines, and sticky cribellate lines. The mesh cells of the sheet are rather uniform, but the sticky and non-sticky lines do not form any obvious regular pattern or orientation.

The spiders spend the day inside their retreats, which are often inaccessible, deep within tree trunks or rock crevices. If the retreat is opened, or after serious disturbance, they assume a cryptic posture with all legs tightly flexed (Fig. 2), as is typical of most web building araneomorphs, including *Hypochilus* and gradungulids (Shear 1969; Forster et al. 1987). Near sunset, they move to the opening of the retreat, with the abdomen facing outward (Fig. 4). Activity begins right after sunset (about 21:00, summer), when the spiders turn facing outwards. At about 22:00 they gradually emerge onto the sheet and begin activities such as cleaning the web, rebuilding damaged areas, catching prey and feeding, expanding the sheet, or adding sticky silk.

Non-sticky scaffolding.—To elicit web-building behavior, we destroyed the entire



Figures 1–3.—*Austrochilus forsteri* and web of *Thaida peculiaris*. 1. *Thaida peculiaris*, non-sticky scaffolding dusted with cornstarch, upper view. Thin arrows to the vertical supporting lines, thick arrow to first cribellate thread (MJR 14.XII.98/Au21 frame A7, Puyehue). 2. *Austrochilus forsteri*, cryptic posture after disturbance (MJR II.92 frame 807, Contulmo). 3. *Thaida peculiaris*. Webs general appearance (GH 31.XII.2000/ frame Ph9/R5, dusted, Puyehue). Photo by Gustavo Hormiga.

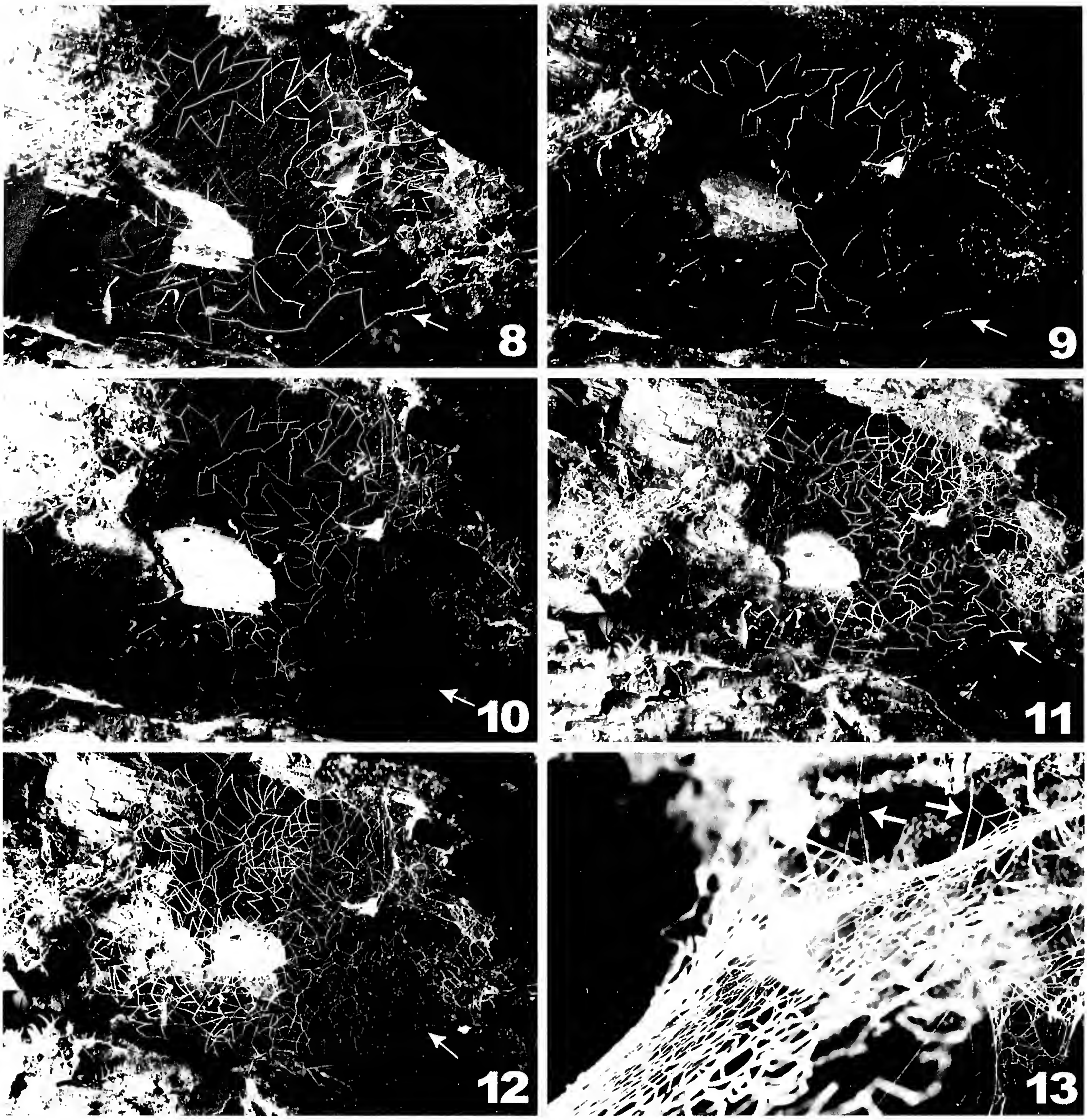
sheet of several *T. peculiaris* from Puyehue, leaving only a few marginal lines attached to the retreat (in one penultimate female (Au31), two penultimate males (Au30, Au39), two immatures (Au40, Au29), and two indeterminate specimens (Au32, Au38). We observed only two individuals (Au31 and Au38) making the first lines of the non-sticky scaffolding, thus these data are preliminary. In general, the pattern observed seems to be similar to the horizontal "extension of the skeleton web" as described by Eberhard for the pholcid *Modisimus guatuso* Huber (Eberhard 1992; Huber 1998). The spiders began by laying two horizontal lines, one on each side from the retreat, thus forming an open "V". Then they attached a new non-sticky line distally to the right line, walked along this line, passed in front of the retreat, and walked a short distance along the left line before attaching the new thread (e.g. L1), thus delimiting an irregular triangle. They then walked further out on the same line, made another attachment, and returned to L1 and attached the thread to it, thus making another triangle. As the spiders repeated this process, the non-sticky scaffolding gradually expanded outward from the retreat. At this point, both spiders detected our presence and stopped building or returned to the retreat, so that subsequent observations are fragmentary. At some point after the initial extension of the sheet the spiders must begin to subdivide the original triangles with non-sticky threads, gradually making a homogeneous, uniform, open scaffolding. Building behavior frequently alternated with pauses or slow movements without attachment. The spiders built most of the non-sticky scaffolding on the first night and adding cribellate sticky threads on following nights. Other undisturbed specimens laid both the support and some cribellate lines in the first night. We do not know how the vertical supporting lines near the retreat are laid.

Figures 4–5.—*Thaida peculiaris* from Puyehue, feeding on a wrapped prey. Many *Sofanapis antillanca* are around the prey (MJR 16.XII.98/Au37). 4. Holding prey in the retreat opening. The abdomen is orientated outward (frame C26). 5. Same. Many *Sofanapis antillanca* are descending from the sheet to land on the prey (frame C18).

Figures 6–7.—*Austrochilus forsteri* female combing a cribellate thread (MJR 19.XII.98/11 frame E30, Contulmo). 6. The right leg III is holding the last attachment position, the left leg III is testing threads where the next attachment will be made. 7. Same, detail of the cribellate thread.

Sticky lines and combing.—Combing behavior is performed at intervals, usually starting at 22:30, and continuing to at least 05:00. The spider combs with one leg IV and attaches the sticky thread to a non-sticky line held with either leg III. The tarsus-metatarsus joint of the contralateral leg IV supports the combing leg IV, and they move simultaneously as an almost rigid unit (Fig. 6, type II combing of Eberhard 1988). As the spider combs, it moves slowly forward, gently exploring with legs III, apparently probing for a non-sticky line to which the cribellate thread will be attached. Once the sticky segment is spun, the spider stops, one leg III grasps the non-sticky line near the future point of attachment, the abdomen rises towards that point, and the cribellate thread is attached with the spinnerets. Legs IV do not touch the web at that moment and are not involved in attachment. The first attachment before combing begins is made on the line held by either leg III, and then the spider starts to comb the cribellate silk with one leg IV (usually ipsilateral to the leg III that guided the attachment), then attaches the sticky segment adjacent to either leg III, and then always combs the next segment with the ipsilateral leg IV. Completed sticky lines are always attached to a line held by a leg III, and so on. Commonly, left and right legs III alternate consecutive attachments, forming a zig-zag pattern, but this often varies (Figs. 9, 14). However, the leg III involved in attachment consistently determines that the ipsilateral leg IV will comb the next segment (except for the first segment in a bout of sticky silk construction). Thus, if two consecutive segments are attached using the same leg III, they are combed with the same ipsilateral leg IV.

Occasionally the spider switches the combing leg IV during the spinning of one segment, suggesting a preference to comb with a particular leg. One *T. peculiaris* female (Puerto Blest, Au9) clearly tended to comb with the left leg IV. Once it started to comb with the disfavored (i.e. right) leg (as implied by the prior attachment with right leg III), the spider soon switched to the "preferred" left combing leg and continued combing the same segment. In 34 observed sticky silk segments, 17 segments were made with left legs III and IV, five with right legs III and IV, 11 segments were begun with the right leg IV but soon switched to left leg IV, and just one segment started



Figures 8–13.—*Thaida peculiaris* from Puyehue, successive stages of the same web; arrows of the same type indicate same threads (MJR 15–17.XII.98/Au20). 8. Non-sticky scaffolding and first cribellate threads, with cornstarch, first night. (frame B16). 9. Second night, without further cornstarch (new cribellate threads are not visible). Note the alterations on previous cribellate threads (frame C14). 10. Same as 9, with cornstarch making visible the cribellate threads of first and second night (frame C15). 11. Third night, without further cornstarch (frame D13). 12. Same as 11, with cornstarch. Note the extension of the left and the bottom-right edges (frame D14). 13. Third night, lateral view near the retreat's mouth roof, showing slope and vertical supporting lines (thick arrows) (frame D16).

with left leg IV and near the end switched to right leg IV.

Cribellate lines in webs usually zigzag (Figs. 8–12, 14), angling sharply at the attachment points. This pattern probably occurs because the animals tend to alternate left and right third legs when attaching. Occasionally, two consecutive sticky silk attachments are made on the same non-sticky line, so that sticky and non-sticky lines run as one (Fig. 14, arrow). This behavior is similar to that described by Eberhard (1988) for *Psechrus* (Psechridae). We perceived no definite overall trajectory during cribellate silk-spinning bouts;

the zigzags may rotate or be interrupted without any apparent regularity (Figs. 8, 14). However, the spiders commonly place the first cribellate lines near the outer edge (e.g., thick arrow in Fig. 1). The mesh of the sheet becomes denser from night to night, as more cribellate threads are laid.

Adding new lines at the edges of the web.—One or two-night old sheets are typically smaller than older webs. We marked the edges of several recently made sheets with cornstarch, and returned the following day (or night) to see the new lines. The spider extended the sheet from the borders (compare Figs. 8–12, arrows). The spider continues to expand the sheet in subsequent nights, first adding new non-sticky supporting structure to the outer edge, and afterwards the cribellate silk.

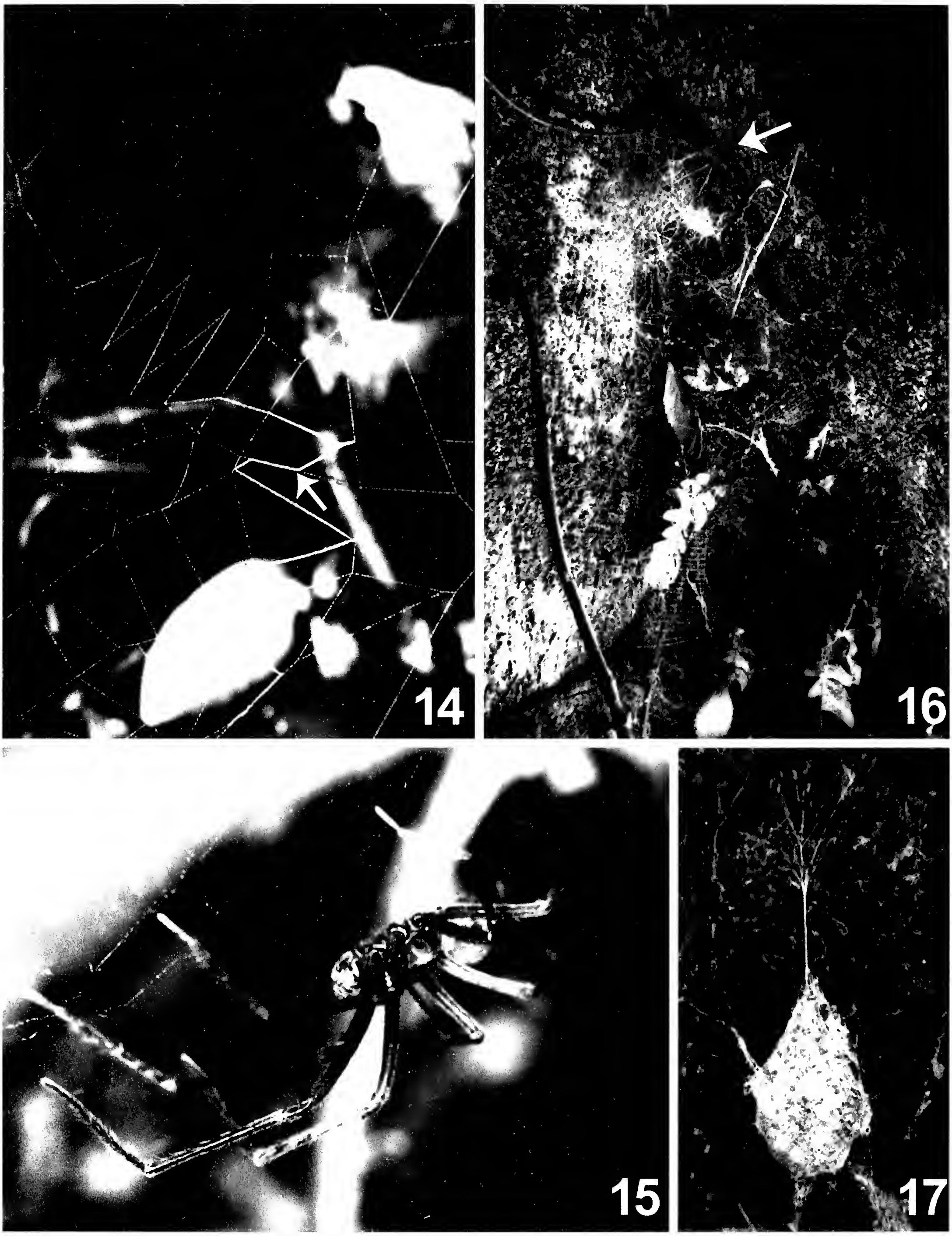
Cleaning the sheet.—Webs are usually quite clean, in spite of considerable accumulation of detritus during the day. We observed cleaning behavior in many individuals. Having touched an entangled object, the spider pulls it down with the palps and legs I and II, and cuts entangling threads one by one, apparently with the chelicerae. The object is drawn through the resulting hole in the sheet, handled with palps and forelegs, and dropped. The spider then repairs the hole.

Rebuilding the damaged patches of the web.—As has been observed in other cribellate spiders (due to "fabricational (constructional) constraints", Seilacher 1973; Coddington 1986b), austrochilines first build the non-sticky scaffolding, and then the cribellate threads, both during web construction and during web repair. Holes in the sheet due to cleaning, prey, or made artificially by us, were all repaired the same way. The spider spins a non-sticky supporting mesh similar to the normal one, and then adds cribellate silk.

Territoriality and aggression.—Webs are individual, occur quite close to each other, but do not share threads. On three occasions, we observed two *T. peculiaris* (in Puyehue, Au41) on the same web. In each case, the larger owners were near their retreats, and the smaller visitor walked slowly at the periphery of the sheet. The owner made no response, and the foreign spider shortly went away. We saw several males (Fig. 15) walking near the retreats of females. In one case a male approached a female guarding an eggsac (in Puyehue, Au42B), and they started touching each other with legs I and II, the male vibrated his body at intervals. The male went away and soon returned near to the female. The female seemed neither receptive nor aggressive. Many individuals were collected by hand and never tried to bite. It seems that austrochilids are neither very territorial nor aggressive.

Attack and feeding.—Several individuals fed on beetles, flies and moths subequal to the spider's body size or smaller. Much smaller insects, such as mosquitoes, were ignored. The spider usually runs towards an entangled prey and bites it repeatedly, then leaves it for a while. After a delay, the spider approaches the immobile prey and transfers it to the lower web surface in order to handle and carry it to the retreat for feeding (Fig. 4). Sometimes animals remain on the sheet for feeding. Prey may or may not be wrapped before eating (the prey in Fig. 5 was wrapped). An immature *T. peculiaris* (Puerto Blest, Au7) bit a moth, passed it through the sheet, and then wrapped it with alternating legs IV. The moth (still partially entangled) was held with legs III, palps, and sometimes with a leg II, thus the spider hung from the web only by legs I. After that, the spider held the moth with legs I and II while feeding on it, hanging from the sheet only by legs IV and sometimes III. It alternated wrapping and feeding for six consecutive hours; and then, near sunrise, dropped the prey and went to the retreat.

Eggsacs.—Oviposition seems fairly synchronous because all eggs collected from the same locality were at a similar developmental stage (observed as in Holm 1940) (in another field trip in Argentina, Neuquén Province, Quetrihué, 24 February 1996, MJR found all eggsacs of *T. peculiaris* empty). Eggsacs are laid in protected places not associated with webs, or near the retreat, but never inside it. They are ovoid (ca. 4 cm long and 2.5 cm wide) and hang from a pedicel (Fig. 17). They have an internal lining of white, finely meshed silk, and are externally covered by cribellate silk, non-sticky silk, and detritus. We saw one female *T. peculiaris* (in Puyehue, Au28B) combing and attaching cribellate silk to the eggsac, as has been seen in many other entelegyne spiders (e.g., Peters & Kovoor 1989; Kraus 1988). Females remain near their own eggsacs and may or may not maintain a sheet web while guarding eggs. The guarding fe-



Figures 14–17.—*Thaida peculiaris* from Puyehue. 14. Detail of sticky thread. Note the sticky thread laid along a non-sticky line (arrow) (MJR 15.XII.98/Au14 frame B9). 15. Male on web of female Au13 (MJR 15.XII.98/Au13 frame C1). 16. Closed retreat of female guarding an eggsac, without sheet web (arrow to retreat; an orb-web of the tetragnathid *Metabus* sp. covers the entire area) (MJR 16.XII.98/Au28A frame C5). 17. Eggsac, same as before, after removing the protection web (MJR 17.XII.98/Au28A frame D20).

males of *T. peculiaris* in Puerto Blest maintain normal sheets, but those in Puyehue, and the guarding females of *A. forsteri* in Contulmo, lacked sheets. Those lacking a sheet had a vertical barrier covering the entrance of the retreat (Fig. 16). Some females may have moved from their original retreats to lay the eggsac, because some *T. peculiaris* (in Puyehue) were found in atypical, more exposed places, such as isolated trees without any nearby point to which to attach a sheet. It is not clear how the spiderlings manage to leave the eggsac.

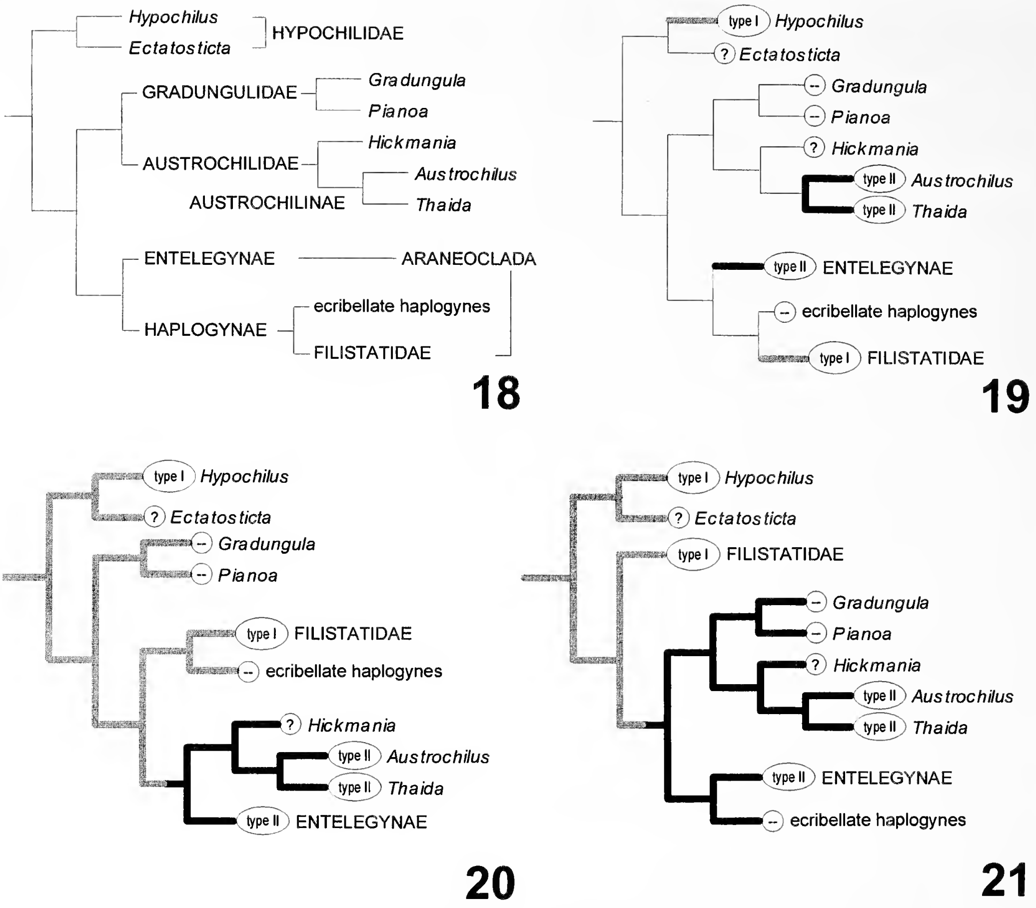
Kleptoparasites.—The anapid kleptoparasitic spider *Sofanapis antillanca*, infested all but one of the observed Chilean *T. peculiaris* and *A. forsteri* webs, with a number of individuals that varied from 1–33 individuals per host web. *Sofanapis antillanca* is known from very humid localities in Chile, but it was never found on any *T. peculiaris* web in Puerto Blest, the most humid forest locality in Argentina (Ramírez & Platnick 1999). They usually occur near the mouth of the retreat, but were seen feeding on the host's prey only at night (Figs. 4, 5). Once we saw a female *T. peculiaris* (Puyehue, Au37) trying to remove the anapids from the prey with its legs. A few *S. antillanca* were collected on the sheet webs of a *Porteria* species (Desidae) in Contulmo, but never in high densities.

Cladistic analysis.—We scored the data matrix of haplogyne spiders by Platnick et al. (1991) as modified by Ramírez (2000) for a binary character expressing the two types of combing behavior (0: type I; 1: type II). *Hypochilus* and the filistatid genera *Kukulcania* and *Filistata* (MJR, pers. obs.) have state 0; the state for *Progradungula* and *Macrogradungula* (Gradungulidae), and *Pikelinia* (Filistatidae), *Ectatosticta*, *Hickmania*, ecribellates and the root vector is unknown or inapplicable (missing entries); all other cribellates (entelegynes) and the austrochilids *Austrochilus* and *Thaida* have state 1. The analysis of this data matrix (using the same analytical procedures as in Ramírez 2000) yields the same cladogram unaltered (Figs. 18, 19). The Bremer support for Araneoclada, however, decreases from 4.8 to 3.3 units of fit (under constant of concavity K = 3; length = 245 steps; Fit = 920.4; CI = 0.51; RI = 0.79).

DISCUSSION

Our observations on Austrochilinae agree with previous knowledge about the general sequence of construction of a non-sticky scaffolding followed by the addition of sticky silk (Eberhard 1992). Austrochilinae webs resemble those of *Psechrus* (Robinson & Lubin 1979), and the basic structure resembles many cribellate entelegynes, such as amphinectids and titanoecids (*Metaltella* Mello-Leitão, *Goeldia* Keyserling, MJR & LL pers. obs.). Stereotyped type II combing behavior in austrochilines is, however, quite surprising, because the phylogenetic position of austrochiloids implies that they should have type I combing behavior. Combing behavior optimizes as type II at the entelegyne node and at the ancestor of *Austrochilus* + *Thaida* of the Platnick et al. (1991) phylogenetic tree (Fig. 19). Type I occurs in *Hypochilus* and Filistatidae, but the combing behavior is ambiguous for all other internal nodes (Fig. 19). This ambiguity has two equally parsimonious reconstructions: either type II combing behavior originated independently in Entelegynae and Austrochilinae, or type I originated independently in filistatids and *Hypochilus* (Fig. 19). However, current reexamination of some internal anatomical features (such as the presence of small posterior booklungs in early stages of the filistatid *Kukulcania hibernalis*; MJR pers. obs.), and current investigations on the outgroups of the Entelegynae (Griswold et al. in prep.) suggests two other possible hypotheses (Figs. 20, 21), each implying different predictions for the combing behaviors for cribellate gradungulids. In one resolution, Austrochilidae is closer to entelegynes than to Gradungulidae (Fig. 20), thus predicting type I combing behavior for cribellate gradungulids. In the other (Fig. 21), Filistatidae is sister to all other Araneomorphae except Hypochilidae, predicting the derived type II combing behavior in cribellate gradungulids.

Data on the combing behavior of other cribellate Austrochiloidea (*Progradungula* Forster & Gray, *Macrogradungula* Gray, and *Hickmania* Gertsch), as well as the ultrastructure of their cribellate silk (Eberhard & Pereira 1993) may help to resolve the phylogeny of basal Araneomorphae and the evolution of web architecture in spiders. Thus far reconstructing the primitive spiders webs is difficult



Figures 18–21.—Different hypotheses and predictions related to combing behavior. 18. Cladogram of major groups of Araneomorphae and basal cribellates, according to Platnick et al. (1991) and Ramírez (2000). 19. Types of combing behavior optimized on the cladogram of Fig. 18. 20. One possible resolution: Austrochilids are most closely related to entelegynes than to Gradungulids. 21. Another alternative topology: Filistatids are the sister group of all other Araneomorphae except Hypochilidae.

because most key taxa build such different webs that comparisons are not straightforward. *Hypochilus* construct "lamp-shade" webs (Shear 1969), quite different from those of any other spiders (except the obviously derived webs of some stiphidiids, Gray 1992). The other hypochiloid genus, *Ectatosticta*, builds a large two-dimensional sheet web (Peter Jäger, pers. comm.). Ecribellate gradungulids do not spin webs, but cribellate species make highly modified snares, reminiscent of the ogre-faced deinopid spiders (Coddington 1986c; Gray 1983; Forster et al. 1987). Filistatines construct funnel webs (Eberhard 1988). Fortunately enough, *Hickmania troglodytes* constructs a sheet web quite similar to that of austrochilines (Hickman 1967; Forster et al. 1987; Doran et al. 2001).

The acquisition of ampullate gland spigots by the Araneomorphae may have played an important role in spider phylogeny. Spiders use these glands to produce thin, strong cables to support their weight, manipulate prey, and construct structures that support specialized, adhesive fibers. Aerial webs are seemingly an acquisition of araneomorph spiders (the derivative webs of some mygalomorphs excepted), but the details of their evolution remain so far elusive.

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LITERATURE CITED

Briceño, R.D. 1985. Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). Journal of Arachnology 13:267–269.

Carico, J.E. 1977. A simple dusting device for coating orb webs for field photography. Bulletin of the British Arachnological Society 4:100.

Coddington, J.A. 1986a. The genera of the spider family Theridiosomatidae. Smithsonian Contributions to Zoology 422:1–96.

Coddington, J.A. 1986b. The monophyletic origin of the orb web. Pp. 319–363. *In* Spider Webs, Behavior and Evolution. (W. A. Shear, ed.). Stanford University Press.

Coddington, J.A. 1986c. Orb webs in "non-orb weaving" ogre-faced spiders (Araneae: Deinopidae): a question of genealogy. Cladistics 2:53–67.

Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496:1–52.

Doran, N.E., A.M.M. Richardson & R. Swain. 2001. The reproductive behaviour of the Tasmanian cave spider *Hickmania troglodytes*, (Araneae, Austrochilidae). Journal of Zoology, London 253:405–418.

Eberhard, W.G. 1982. Behavioural characters for the higher classification of orb-weaving spiders. Evolution 36:1067–1095.

Eberhard, W.G. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic complications. Bulletin of the British Arachnological Society 7:247–251.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Annual Review of Ecology and Systematics 21:341–372.

Eberhard, W.G. 1992. Web construction by *Modisimus* sp. (Araneae, Pholcidae). Journal of Arachnology 20:25–34.

Eberhard, W.G. & F. Pereira. 1993. Ultrastructure of cribellate silk of nine species in eight families and possible taxonomic implications. (Araneae: Amaurobiidae, Deinopidae, Desidae, Dictynidae, Filistatidae, Hypochilidae, Stiphidiidae, Tengellidae). Journal of Arachnology 21:161–174.

Forster, R.R., N.I. Platnick & M.R. Gray. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). Bulletin of the American Museum of Natural History 185:1–116.

Gray, M.R. 1983. The male of *Progradungula carraiensis* Forster and Gray (Araneae, Gradungulidae) with observations on the web and prey capture. Proceedings of the Linnean Society of New South Wales 107:51–58.

Gray, M.R. 1992. The troglobitic spider genus *Tartarus* Gray with a cladistic analysis of *Tartarus* and *Baiami* Lehtinen (Araneae, Stiphidiidae). Proceedings of the Linnean Society of New South Wales 113:165–173.

Grismado, C.J., L. Lopardo & N.I. Platnick. 2003. A new species of *Austrochilus* from Chile (Araneae, Austrochilidae, Austrochilinae). Journal of Arachnology 31:148–150.

Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Griswold, C.E., J.A. Coddington, N.I. Platnick & R.R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). Journal of Arachnology 27:53–63.

Hickman, V.V. 1967. Some common spiders of Tasmania. Tasmanian Museum and Art Gallery 112 pp.

Holm, Å. 1940. Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. Zoologiska Bidrag från Uppsala 19:1–214.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). Australian Journal of Zoology 43:313–364.

Huber, B. 1998. Notes on the Neotropical spider genus *Modisimus* (Pholcidae, Araneae), with descriptions of thirteen new species from Costa Rica and neighboring countries. Journal of Arachnology 26:19–60.

Kraus, M. 1988. Cocoon-spinning behavior in the social spider *Stegodyphus dumicola* (Arachnida, Araneae): Cooperating females as "helpers". Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 30:305–309.

Opell, B.D. 1997. The material cost and stickiness of capture threads and the evolution of orbweaving spiders. Biological Journal of the Linnean Society 62:443–458.

Peters, H.M. & Kovoor, J. 1989. Die Herstellung der Eierkokons bei der Spinne *Polenecia producta* (Simon, 1873) in Beziehung zu den Leistungen des Spinnapparates. Zoologische Jahrbucher—Abteilung fur Allgemeine Zoologie und Physiologie der Tiere 93:125–144.

Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016:1–73.

Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Journal of Arachnology 28:149–157.

Ramírez, M.J. and N.I. Platnick. 1999. On *Sofanapis antillanca* (Araneae, Anapidae) as a kleptoparasite of austrochiline spiders (Araneae, Austrochilidae). Journal of Arachnology 27:547–549.

Robinson M.H. & Y.D. Lubin. 1979. Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea, 2. *Psechrus argentatus* and *Fecenia* sp. (Araneae: Psechridae). Pacific Insects 21:133–164.

Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120:355–434.

Seilacher, A. 1973. Fabricational noise in adaptive morphology. Systematic Zoology 22:451–465.

Shear, W.A. 1969. Observations on the predatory behavior of the spider *Hypochilus gertschi* Hoffman (Hypochilidae). Psyche 76:407–417.

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2004. The Journal of Arachnology 32:55–108

A REVIEW OF THE SPIDER GENERA *PARDOSA* AND *ACANTHOLYCOSA* (ARANEAE, LYCOSIDAE) OF THE 48 CONTIGUOUS UNITED STATES

Beatrice R. Vogel: Research Associate, Denver Museum of Nature and Science, 46 South Howie, Helena, Montana 59601 USA. E-mail: beavogel@earthlink.net

ABSTRACT. In the 48 contiguous United States, the wolf spider subfamily Pardosinae is represented by 65 species of *Pardosa* and 1 species of *Acantholycosa*. This study provides a comprehensive account of all species of Pardosinae in the USA including keys, some of which are new, for their identification. Based on genital morphology, the species of *Pardosa* in the USA can be divided into 14 species groups containing from one to 17 species. The male of *P. ourayensis* Gertsch 1933 is illustrated for the first time. Difficulties arise in the identification of some sister species which are both morphologically and geographically close; and also many of the species in the sternalis group which can be identified only by their distribution.

Keywords: Pardosinae, wolf spiders, keys, genitalia, taxonomy, species groups, range

The lycosid genus *Pardosa* C.L. Koch 1847 is among the five largest spider genera in the world, trailing *Araneus* Clerck 1757 and *Theridion* Walckenaer 1805 in number of species. The World Spider Catalog (Platnick 2003) lists over 530 species world-wide, occurring on all continents. Seventy-five currently recognized *Pardosa* species occur in North America, 65 of these south of Canada. The 45 species in Canada and Alaska, including 35 shared with the United States, have received excellent treatment (Dondale & Redner 1990), but it requires at least 13 papers (Barnes 1959; Dondale 1999; Dondale & Redner 1984, 1986, 1987, 1990; Jimenez 1986; Kronestedt 1975, 1981, 1988, 1993; Lowrie & Dondale 1981; Vogel 1964, 1970a) to identify *Pardosa* species in the contiguous United States.

In addition to scattered published information, some of the difficulty in identifying spiders arises from a lack of knowledge of the morphological variation in a species, and the lack of knowledge of the geographical range of a species. For example, such difficulty exists between *P. lapidicina* and *P. mercurialis*. *Pardosa lapidicina* Emerton 1885 was described from Salem, Massachusetts and Meriden, Connecticut and it ranges to the Midwest. *Pardosa mercurialis* Montgomery 1904 was described from Austin, Texas. There are no published records of these species occurring in Colorado but these spiders are collected there. Barnes (1959:7) was unable to distinguish the females of these two species, but the males may be separated by the shape of the terminal apophysis of the palp (Barnes' median accessory process). In *P. lapidicina* it is a blunt lobe and in *P. mercurialis* a pointed tooth. However it is reasonable that a blunt lobe may grade into a pointed tooth across a geographical range. In any case, one must bear in mind that within given species there is variation in genital morphology, especially the epigynum, and that that variation may exceed the variation between sister species. A study of intra-population variation would be particularly useful in these species.

Until recently, *Pardosa* was the only genus in the subfamily Pardosinae Simon 1898 in North America. However, for some years, arachnologists have recognized that *Pardosa solituda* Levi & Levi 1951 may belong in *Acantholycosa* Dahl 1908 (Lowrie 1973: 12). Kronestedt & Marusik (2002) have now formally placed that species in *Acantholycosa*, which adds *Acantholycosa* to the list of genera, and to Pardosinae in North America.

Subfamily Pardosinae Simon 1898

Remarks.—The Pardosinae is characterized by the cephalic region of the cephalothorax which is relatively higher than in other lycosid genera and the sides of the face are nearly vertical. In most species the legs are slender. The median apophysis is thick and well sclerotized; the embolus is a long curved spine; and the epigynum usually has a median inverted T-shaped structure (Zyuzin 1993: 696). The terminal apophysis is tooth-like, situated retrolaterally on the palea (Dondale 1986:331).

KEY TO THE GENERA OF PARDOSINAE

1. Tibia I with 3 pairs of spines ventrally, of which the apical pair may be short ...... *Pardosa*
   Tibia I with 5–7 pairs of spines ventrally .... *Acantholycosa*

Genus *Pardosa* C.L. Koch 1847

Remarks.—Members of the *Pardosa* are one of the smaller wolf spiders in North America. They range in size, measured as total body length, from about 3.0 mm in *P. parvula* Banks 1904 males, to greater than 12 mm in *P. groenlandica* (Thorell 1872) females. Most of the species are clothed with fine hair, brown or gray in color, with mottled black markings. The dorsum of the cephalothorax bears a more or less distinct lighter median band. The thoracic region may have additional pale lateral bands making five bands altogether on the prosoma. The dorsum of the abdomen usually has an anterior diamond shape (also referred to as "heart mark" (Dondale & Redner 1990)) followed by paired eyespots (Fig. 1). A few species have unique color patterns. Genital morphology is usually used to identify species but is not definitive in all cases. In a few species a single male or female cannot be identified unless it is collected together with a specimen of the other sex. Some of the smaller species, when the specimen is fresh, can be easily identified by color pattern, but red and yellow colors fade in alcohol.

There are 14 *Pardosa* species groups represented in this region: four containing only one species and ten containing from two to 17 species. The key to species groups is new as is the key to the lapidicina group. Barnes (1959) did not publish a key in his revision of the group. The distincta group key published in Vogel (1964) is revised. The modica group key includes several recently described species not included in the key in Dondale & Redner (1990) as well as species not occurring in Canada. The milvina group key is tailored from Dondale & Redner (1984) for species only in the 48 United States. Finally, most of the key to the nigra group is from Lowrie and Dondale (1981). Note that there may be other species in these species groups that are Holarctic, or from Canada or Mexico and the Caribbean, but they are not considered here. Refer to the literature cited for such species. For the most part, except for recent synonymies, literature citations for individual species are not included. These can be found in the World Spider Catalog (Platnick 2003). Many of the older original descriptions do not include enough information to be useful in identifying specimens. Abbreviated synonymies for some species are included, especially for names that have been used recently. The range maps show only state records, not collection localities.

METHODS

To simplify identifying a specimen, the keys are constructed in two steps. Step one keys to a species group, and step two keys to species within the group. "Species group" is an informal group similar to subgenus, used by authors for convenience and consists of species with similar genital morphology; however, species group is not a taxon recognized by the International Commission on Zoological Nomenclature. A species group may be based on either the epigynum, or on the male palp. The genital morphology of the respective other sex may show greater variation. Within a species group some of the species are morphologically very similar, separated by subtle characters or only by range.

The sexes are keyed separately, but in neither species groups nor species (except for four small groups) do both sexes key in the same order. For this reason the species groups and the brief species descriptions are presented in alphabetical order. If one uses this paper repeatedly, species group recognition will occur, and the first step in the keys may be bypassed.

All genital drawings, except for Figs. 2 & 3, are made to the same scale so comparisons

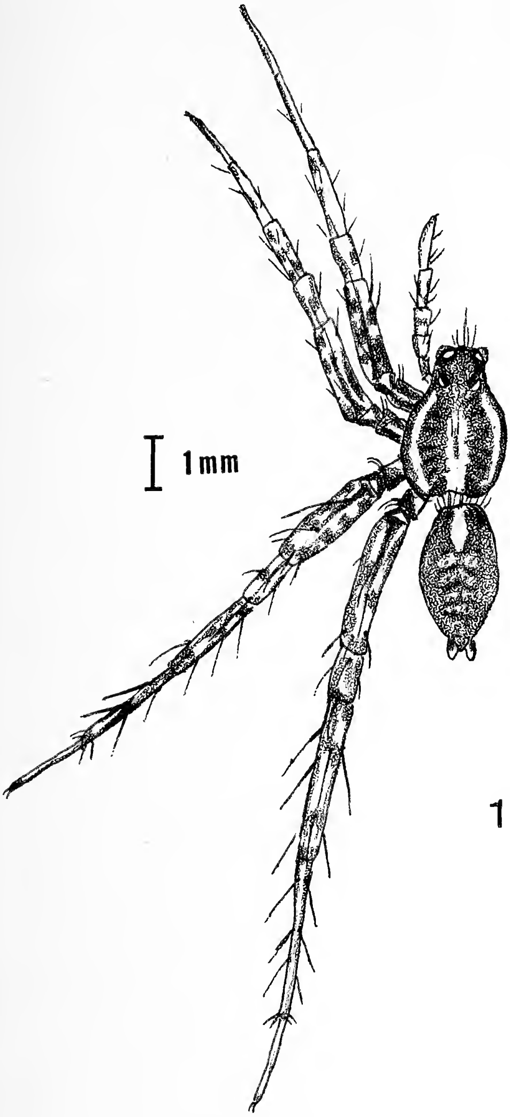

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Figure 1.—Habitus of *Pardosa sternalis*.

may be made between related species. The drawings were made at a magnification of 60 X using an ocular grid in a Unitron binocular microscope and transferred to a 1 cm grid on paper. The drawings are reproduced here at 80%. The epigyna were drawn on the intact abdomen but some of the protective hairs were scraped off one side. Internal (dorsal) views are not used. Minor dissection may be required in some of the species in the nigra group to examine the structures in posterior view. For males, the spider's left palp is used in all illustrations. Drawings of the palp are made with the bulb intact. Setae and spines on the cymbium and the tibia of the pedipalp are not included except when they are diagnostic. There is no specifically accepted standard for genital terminology in Lycosidae. Terms used here (Figs. 2 & 3) follow various authors' usages (Dondale & Redner 1984:108; Dondale & Redner 1990:125, 131; Kronestedt 1975: 218; Lowrie & Dondale 1981:128; Vogel 1970a, 77, 78), however some clarification may be helpful.

The epigynal hood is a pocket-like structure at the apical end of the septum on the rim of the epigynum. It may be formed by the thickened rim of the cavity or a separate cap-like structure or both. The lateral swellings are slightly mounded portions of the epigynal plate, curving around the cavities and may be enlarged basally. They may extend apically along the septum. Lateral wings (Fig. 7, not shown in Fig. 2) are lightly sclerotized, triangular or lobed projections of the epigynal plate.

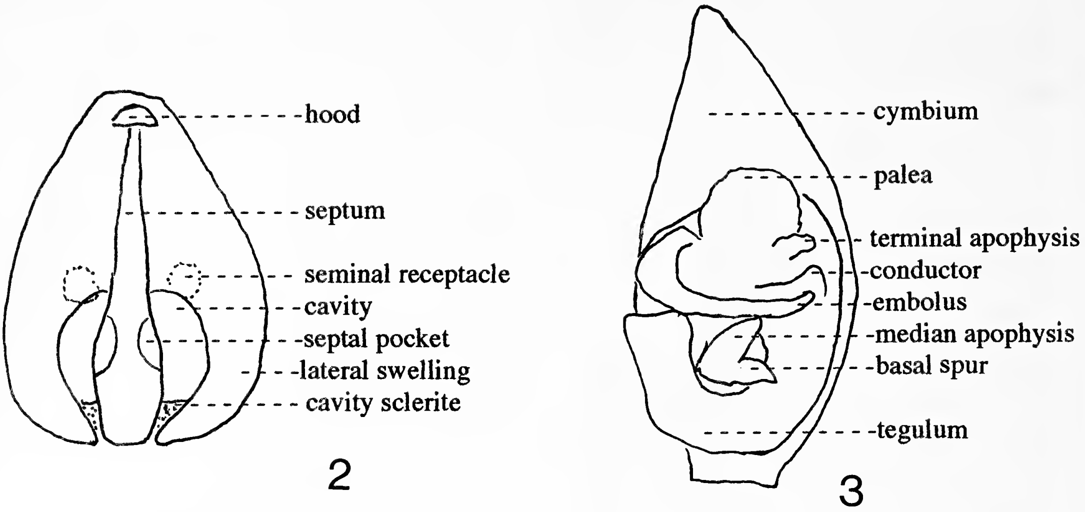
The term tegular lobe (Figs. 27, 118–119) refers to an apical bulge on the rim of the tegulum. Terminal apophysis may not be homologous among the species groups when there is more than one paleal process (Zyuzin 1993:699). This is the case in the nigra group, but the authors' usage (Lowrie & Dondale 1981: fig. 10) is followed here.

KEYS TO *PARDOSA* SPECIES GROUPS IN THE USA

Females

1. Epigynum without hood; apical end of epigynum smoothly domed (Figs. 6–8, 138) 2
Epigynum with hood, may be pointed, narrow or nearly the width of epigynum or paired (Figs. 4, 75, 116) 3

2. Cavities very narrow, reduced or indistinct: 3 species (Figs. 6–8) .... coloradensis group
Cavities large, oval, diverging apically, covering more than 1/2 of epigynum: 1 species (*P. xerampelina*) (Fig. 138) .... xerampelina group



Figures 2–3.—Diagrams of genitalia with terminology used in this paper. 2, epigynum. 3, palP.

3. Single hood formed by apical extension of joined cavities, surrounding septum; apical end of septum may not extend to margin of epigynum (Figs. 29, 30–35, 94) 4
   Hood single or paired; septum longer than cavity or cavity extension 6
4. Basal portion of cavities concealed by expanded base of septum; apical end of cavity extension expanded laterally forming a wide hood: 1 species (*P. moesta*) (Fig. 94) .... moesta group
   Apical cavity extension approximately the same width throughout 5
5. Cavity widest basally; lateral swellings skimpy; septum with wide, short, transverse base and narrow ridge apical to base; lateral wings lacking: 6 species (Figs. 30–35) .... lapidicina group
   Cavity widest apical to bulbous base of lateral swellings; septum of moderate width for 2/3 of length, apical 1/3 slim; small lateral wings: 1 species (*P. concinna*) (Fig. 29) .... lapponica group
6. Paired hoods, flanking apical end of septum (Figs. 60–67, 134–145) 7
   Single hood at apical end of septum; or if apparently paired, hoods widely separated 8
7. Cavities reduced or nearly covered by septal expansions, cavities without apical extensions; epigynum longer than wide: 2 species (Figs. 134–135) .... tesquorum group
   Cavities conspicuous, oval or semicircular, with apical extensions (arms) to hoods, flanking septum (except *wyuta*, which has shallow depressions flanking septum); epigynum as wide or wider than long: 17 species (Figs. 60–76) .... modica group
8. Cavities very large, circular; hood a point directed basally: 1 species (*P. fuscula*) (Fig. 4) .... atrata group
   Cavities reduced, concealed or indistinct 9
9. Epigynum as wide as long; septum broad, covering most of epigynum; hood as broad as apical end of epigynum, may appear as paired hoods; cavities without lateral rim: 2 species (Figs. 116–117) .... saltuaria group
   Epigynum various shapes; septum, if broad basally, is narrow apically; hood not as broad as apical end of epigynum unless apical end is very narrow 10
10. Cavities not apparent; base of septum somewhat rectangular with transverse wrinkles; septum apical to base a trough extending to hood: 8 species (Figs. 96–106) ...... nigra group
    Cavities small to indistinct; base of septum variable but without transverse wrinkles; septum apical to base raised 11
11. Cavities oval or semi-circular with distinct rim; lateral swellings encircling cavities ... 12
    Cavities without distinct rim and may be mostly covered by septal expansions 13

12. Cavities without sclerites; septum without pockets: 6 species (Figs. 120–125) . . . . sternalis group
Cavities with sclerites arising from septum, filling half of cavity; septum with longitudinal pockets: 2 species (Figs. 24, 25) . . . . falcifera group
13. Epigynum longer than wide; margin of epigynum usually distinct; apical rim of epigynum and hood thickened, hood a curved pocket: 9 species (Figs. 42–50) . . . . milvina group
Epigynum as wide as long or wider; margin of epigynum often indistinct; apical rim not thickened, hood various shapes: 6 species (Figs. 12–17) . . . . distincta group

Males

1. Median apophysis extending to edge of cymbium and beyond (Figs. 18–23, 26–28, 51–53, 128–133) 2
Median apophysis may extend partway across bulb, but not to edge of cymbium; median apophysis lump-like, knob-like, flattish or hooked 6
2. Embolus traverses bulb arching apically in a large semicircle (Figs. 26–27, 128–133) . . . 3
Embolus traverses bulb without semicircular arch (Figs. 18–23, 25, 51–53) 4
3. Median apophysis with conspicuous bulge mid-length: 2 species (Figs. 26–27) . . . . falcifera group
Median apophysis without a conspicuous mid-length bulge: 6 species (Figs. 128–133) . . . . sternalis group
4. Median apophysis extending beyond edge of cymbium, tip visible in dorsal view; basal spur small, thin, and pointed: 6 species (Figs. 18–23) . . . . distincta group
Median apophysis not extending beyond edge of cymbium, basal spur short and stubby . . 5
5. Median apophysis broad and very slightly curved, basal spur with truncate tip: 1 species (*P. concinna*) (Fig. 28) . . . . lapponica group
Median apophysis strongly curved in distal half; basal spur with blunt point: 9 species (Figs. 51–53) . . . . milvina group (in part)
6. Tegulum widely projecting from palp in lateral view (Fig. 107): median apophysis strap-like, basal spur curved, tapered, nearly half as long as median apophysis: 8 species (Figs. 107–115) . . . . nigra group
Tegulum more vertical and bowl-like; median apophysis and basal spur variable 7
7. Median apophysis stout, curved, tip pointed, various lengths (Figs. 9–11, 53–59, 136–137) . . 8
Median apophysis short, lumpish, pyramidal, or rounded distally (Figs. 36–41, 77–93, 95, 118–119, 139) 11
8. Bulb very wide; lobe on apical rim of tegulum low; embolus whip-like; median apophysis stout, with single or double curve, tip pointed; basal spur about half the size of median apophysis: 3 species (Figs. 9–11) . . . . coloradensis group
Palp without this combination of characters 9
9. Body length 6.5–7.5 mm; median apophysis stout, bent nearly at a right angle; stout process traversing bulb behind median apophysis: 1 species (*P. fuscula*) (Fig. 5) . . . . . . atrata group
Body length less than 5.5 mm; or if greater than 6 mm, without stout sclerotized process near base of embolus 10
10. Basal spur short, slender, directed laterally; occurs in the northern Great Plains and Rocky Mountains: 2 species (Figs. 136–137) . . . . tesquorum group
Basal spur short, stout, curved, tip pointing basally; if basal spur slender, occurs in southern California: 6 species (Figs. 54–59) . . . . milvina group (in part)
11. Median apophysis lumpish, barely extending beyond tegulum, tip with blunt lateral protuberance, basal spur absent: 6 species (Figs. 36–41) . . . . lapidicina group
Median apophysis short with basal spur directed basally or laterally; spur may arise apically . . 12
12. Median apophysis pyramidal, truncate or roundish apically; basal spur long, directed laterally; tip may be bent basally: 17 species (Figs. 77–93) . . . . modica group
Median apophysis rounded apically, basal spur directed basally 13
13 Palea with apical triangular process pointing basally; tibia of the pedipalp swollen: 1 species (*P. moesta*) (Fig. 95) . . . . moesta group

Palea without sclerotized triangular process; tibia of the pedipalp not swollen 14
14. Median apophysis with large spur arising apically, but directed basally; terminal apophysis small and squarish: 1 species (*P. xerampelina*) (Fig. 139) .... xerampelina group
Median apophysis with small basal spur, arising medially and directed basally; terminal apophysis not small and squarish: 2 species (Figs. 118–119) .... saltuaria group

Atrata Group

Remarks.—The atrata group consists of one species in North America, and two Palearctic species. The epigynum has large roundish cavities that nearly cover the entire epigynal plate and are without arms extending apically. The median septum has a pair of lateral lobes basally, and the hood has a pointed lobe directed basally. The male palp is large, with a stout, curved median apophysis extending halfway across the bulb. The basal spur is a stout pointed triangle. The palea bears a large sclerotized structure curving behind the median apophysis.

Pardosa fuscula (Thorell 1877)

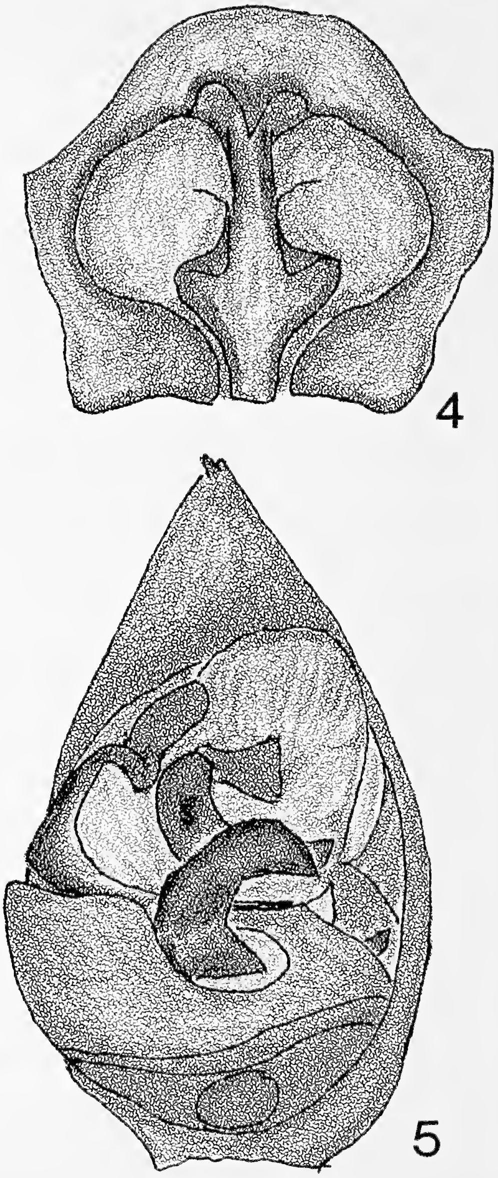
Figs. 4, 5; Map 1

Diagnosis.—Females and males are nearly the same size. Body length of females ranges from 6.7–7.8 mm; that of males 6.6–7.7 mm. The spiders are a reddish brown with a narrow yellow median stripe on the carapace and unbroken yellow lateral bands. The abdominal markings are of low contrast, displaying a diamond mark apically and paired lighter patches behind. The diamond mark covers nearly half the length of the abdomen. The legs are reddish, slightly marked with longitudinal dark lines. The genital characters described above distinguish this species.

Distribution.—Rocky Mountain states to Great Lakes and New England; Canada, Alaska (Dondale & Redner 1987: map 1).

Coloradensis Group

Remarks.—The coloradensis group consists of three Nearctic species. The color pattern is typical of the genus. The cephalothorax usually has five longitudinal bands except in dark spiders. The abdomen may have five pairs of light spots basal to the diamond mark. The epigynum is slightly wider than long, broadly rounded apically, without a hood. The septum and cavities are no more than 1/2 the length of the epigynum. The cavities are very narrow and mostly concealed by either the septum or lateral swellings. The bulb of the male pale is round and wide. The median apophysis is short, stout, with one or two curves, ending in a sharp point. The triangular basal spur is also pointed. The tip of the embolus is slender. The terminal apophysis is a thin finger directed basally.



Figures 4–5.—Genitalia of *Pardosa*, atrata group, *P. fuscula*. 4. Epigynum. 5. Palp. s, sclerite.

KEYS TO SPECIES OF THE COLORADENSIS GROUP

Females

1. Cavities very narrow, about 1/2 length of epigynum; septum broad basally, tapering to apical end of cavities (Fig. 6) . . . . *Pardosa metlakatla*
   Cavities greatly reduced, less than 1/4 the length of epigynum; base of septum with a short basal ridge or spine, which may be tucked into genital furrow 2
2. Septum with truncated base and basal spine; cavities curving apically around corners of septum base (Fig. 7) . . . . *Pardosa coloradensis*
   Base of septum with a double arch, divided by the spine; cavities lying within the double arch (Fig. 8) . . . . *Pardosa ontariensis*

Males

1. Median apophysis with a single curve, tip pointing laterally; embolus slender, arching across bulb apical to the median apophysis, entirely exposed (Fig. 9) . . . . *Pardosa metlakatla*
   Median apophysis with a double curve, tip directed apically; embolus partly concealed crossing bulb 2
2. Bulb, in ventral view, wider than long; terminal apophysis a long slender hook with tip bent basally (Fig. 10) . . . . *Pardosa coloradensis*
   Bulb, in ventral view, not wider than long; terminal apophysis directed basally, bent mid-length (Fig. 11) . . . . *Pardosa ontariensis*

Pardosa coloradensis Banks 1894
Figs. 7, 10; Map 1

Diagnosis.—Females can be recognized by the short narrow cavities curving around the base of the septum. The wide bulb of the palp and stout median apophysis with a double curve characterize the male.

Remarks.—Fittingly, *P. coloradensis* is one of the most commonly collected *Pardosa* on the east side of the Rocky Mountains in Colorado.

Distribution.—Washington, Oregon, Montana, Wyoming, Utah, Colorado, Arizona, New Mexico; Canada, Alaska (Dondale & Redner 1986: map 2; pers. obs.).

Pardosa metlakatla Emerton 1904
Figs. 6, 9; Map 1

Diagnosis.—The narrow finger-like cavities 1/2 the length are uniquely identify *P. metlakatla* females. Unlike the other two species in this group, the median apophysis of the male palp has only a single curve.

Distribution.—Washington, Oregon; coastal British Columbia (Dondale & Redner 1986; map 3).

Pardosa ontariensis Gertsch 1934
Figs. 8, 11; Map 1

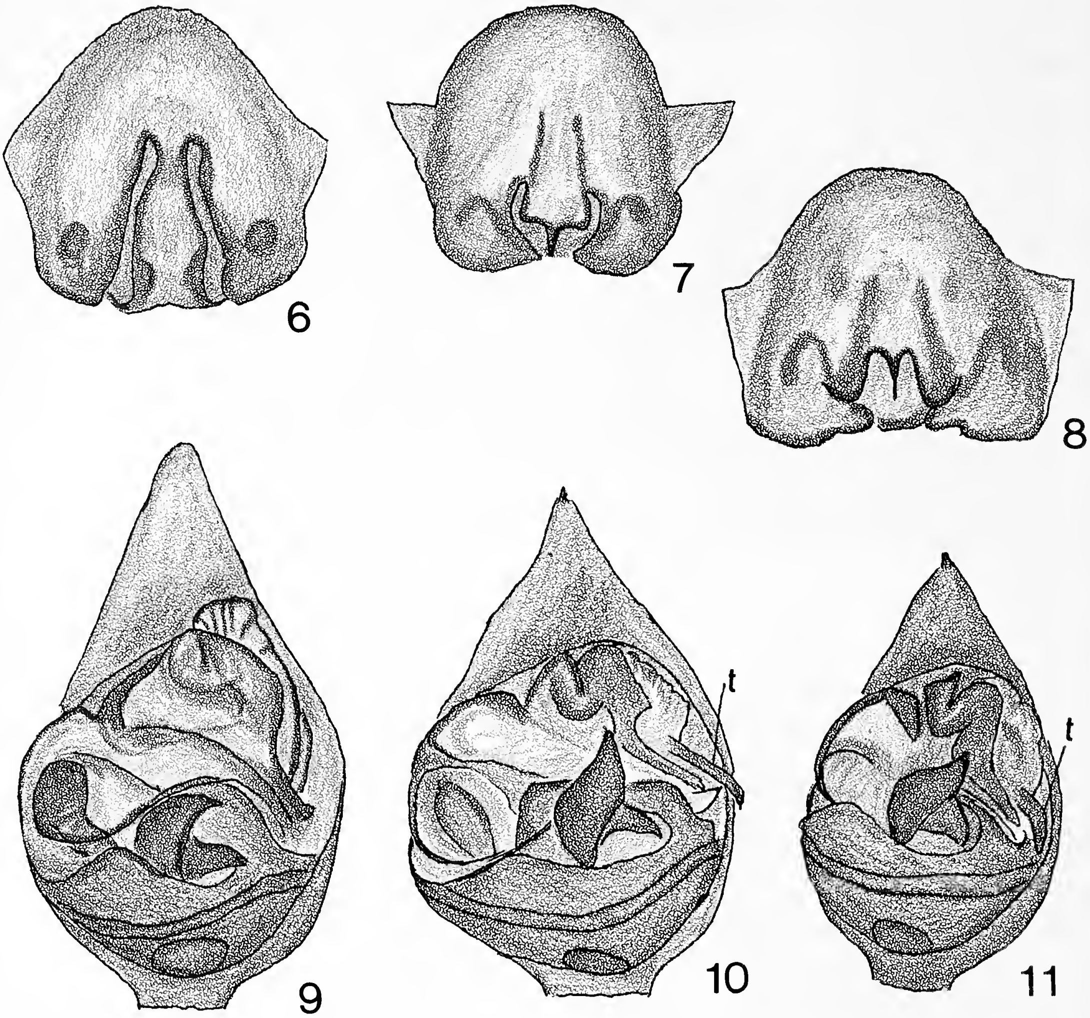
Diagnosis.—The genitalia of both sexes are very similar to *P. coloradensis*. Females can be distinguished by the small double arch at the basal margin of the septum. Males are distinguished by the bend mid-length in the terminal apophysis.

Remarks.—Range of *P. ontariensis* is about the same as that of *P. coloradensis*, but *P. ontariensis* is not common.

Distribution.—Oregon, Montana, Wyoming, Colorado; Canada (Dondale & Redner 1986, map 3).

Distincta Group

Remarks.—The distincta group consists of six species, which occur in Rocky Mountain states and three species known only from Mexico. These are among the smaller of *Pardosa* species, from 4–7 mm in length, and live spiders have noticeable and characteristic color patterns. The cephalothorax is marked with five longitudinal bands. The median and outer lateral bands are a light color ranging from yellow to light brown. The inner lateral bands are darker, light brown to dark brown. The abdomen also bears a median light band, often mottled pale yellow like curdled milk, which contrasts highly with the lateral dark areas. The apical end of the median band is the diamond heart mark, with dark outline, sometimes more than 1/2 the length of the abdomen. Males are darker than females, sometimes dark enough that the light bands



Figures 6–11.—Genitalia of *Pardosa*, coloradensis group. Figs. 6–8. Epigyna. 6. *P. metlakatla*. 7. *P. coloradensis*. 8. *P. ontariensis*. Figs. 9–11. Palpi. 9. *P. metlakatla*. 10. *P. coloradensis*. 11. *P. ontariensis*. s, sclerite. t, terminal apophysis.

are indistinct. The epigynum is small, septum more or less flask-shaped, with expanded base. A small hood is situated at the apical end of the septum. The cavities are either lacking or small and entirely covered by the septum. The palp of males is characterized by a long, slightly curved median apophysis reaching the edge of cymbium and slightly beyond. The embolus is not conspicuous and does not form a semicircular arch as in the falcifera and sternalis groups. These genital characteristics and conspicuous abdominal markings distinguish species in this group from all other *Pardosa*.

Members of the distincta group are often found syntopically. *Pardosa distincta* is an extremely common and wide-spread species and is often found alone, but it also occurs with *P. yavapa*, which is also quite common, or with *P. utahensis*, and sometimes both. *Pardosa orophila* occurs with *P. yavapa* on the foothills of the Rocky Mountains west of Denver, Colorado, more often than by itself.

Map 1.—State records for *P. fuscula* (✸), *P. coloradensis* (★), *P. metlakatla* (☆), *P. ontariensis* (❖).

KEYS TO USA SPECIES OF THE DISTINCTA GROUP

Females

1. Carapace with a thin "mustache" of white hair below eye rows; septum with small bilobed base and expanded apically to a heart shape; hood with a long basally pointing finger (Fig. 12) . . . . *Pardosa orophila*
   Median septum without small bilobed base, not heart-shaped apically 2
2. Spider 5–7 mm in length, pale color; epigynal plate minimal, epigynum reduced to septum and hood; base of septum apple-shaped, 1/2 the length of septum; apical end about 1/3 width of base, hood small (Fig. 13) . . . . *Pardosa distincta*
   Size and color of spider variable; epigynal plate apparent; apical end of septum slender . . 3
3. Spider 5–7 mm in length; expanded base of septum pear-shaped, nearly the length of septum, apical end of septum very thin; hood somewhat rectangular (Fig. 14) . . . . . *Pardosa utahensis*
   Expanded base of septum flask-shaped, not more than half length of septum 4
4. Median band on carapace tapers nearly to a point at pedicel; spider quite dark; septum hourglass shaped, with expanded base and an arched structure trailing basally at apical end just before a small hood (Fig. 15) . . . . *Pardosa yavapa*
   Median band not tapering to pedicel, or not tapering to a point; median septum apically slender without an arched structure 5
5. Epigynal plate with long wings directed laterally (Fig. 16) . . . . *Pardosa montgomeryi*
   Epigynal plate with indistinct border, without long laterally directed wings (Fig. 17) . . . . *Pardosa xerophila*

Males

1. Slender brush of longer dark hair on median side of palp; tibia of pedipalp with distal dark band and brush of hair (Fig. 18) . . . . *Pardosa xerophila*
   Palp may be clothed with black hair but without a conspicuous brush 2
2. Median apophysis somewhat thick, bending apically, with longitudinal wrinkles, extending

noticeably beyond edge of cymbium; spider may be yellow ochre or nearly black (Fig. 19) . . . . *Pardosa distincta*

Median apophysis without longitudinal wrinkles, extending to edge of cymbium but scarcely beyond 3

3. Median apophysis with a strong bend apically in mid-length, giving it a "sway-back" look (Fig. 20) . . . . *Pardosa montgomeryi*

Median apophysis without a strong bend apically 4

4. Median apophysis very slightly curved at tip, but with a bulge on the basal edge, like a pot belly (Fig. 21) . . . . *Pardosa orophila*

Median apophysis gently curved, edges either relatively smooth or bulged on both edges . . 5

5. Small spider (4–5 mm), carapace glabrous, very dark brown; median band on carapace tapering to a point at waist; median apophysis nearly same width throughout length (Fig. 22) . . . . *Pardosa yavapa*

Larger spider (5–7 mm), medium brown color, carapace not glabrous; median band on carapace not tapered; median apophysis with a constriction near base and slight bulge midway to tip (Fig. 23) . . . . *Pardosa utahensis*

Pardosa distincta (Blackwall 1846)
Figs. 13, 19; Map 2

Diagnosis.—Length 5–7 mm. Females of *P. distincta* are light colored, sometimes seeming to have five longitudinal bands on the entire body, not just the prosoma. The legs are pale without distinct markings. The epigynum, reduced to the septum and hood, is uniquely recognizable. Males east of the Rocky Mountains are colored like the females, only slightly darker. Males in the Rocky Mountain region are more likely to be nearly black, both dorsally and ventrally, with an iridescent blue sheen of the anterior side of femora. This character is shared by males of *P. sternalis*, but the two species can readily be distinguished by the palp. The median apophysis of *P. distincta* has longitudinal wrinkles and extends beyond the edge of the cymbium with the tip showing in dorsal view.

Remarks.—*Pardosa distincta* is among the two or three most common spiders in the lower elevations of the central Rockies. *Pardosa distincta* prefers mesic habitats and is often found with *Pardosa* species in other species groups. While *P. distincta* is also collected by itself, it may be collected with *P. utahensis* or *P. yavapa* or both.

Distribution.—Rocky Mountains from Alberta to Arizona, across northern United States to New England. (Dondale & Redner 1990: map 32; Vogel 1964:13; pers. obs.).

Pardosa montgomeryi Gertsch 1934
Figs. 16, 20; Map 2

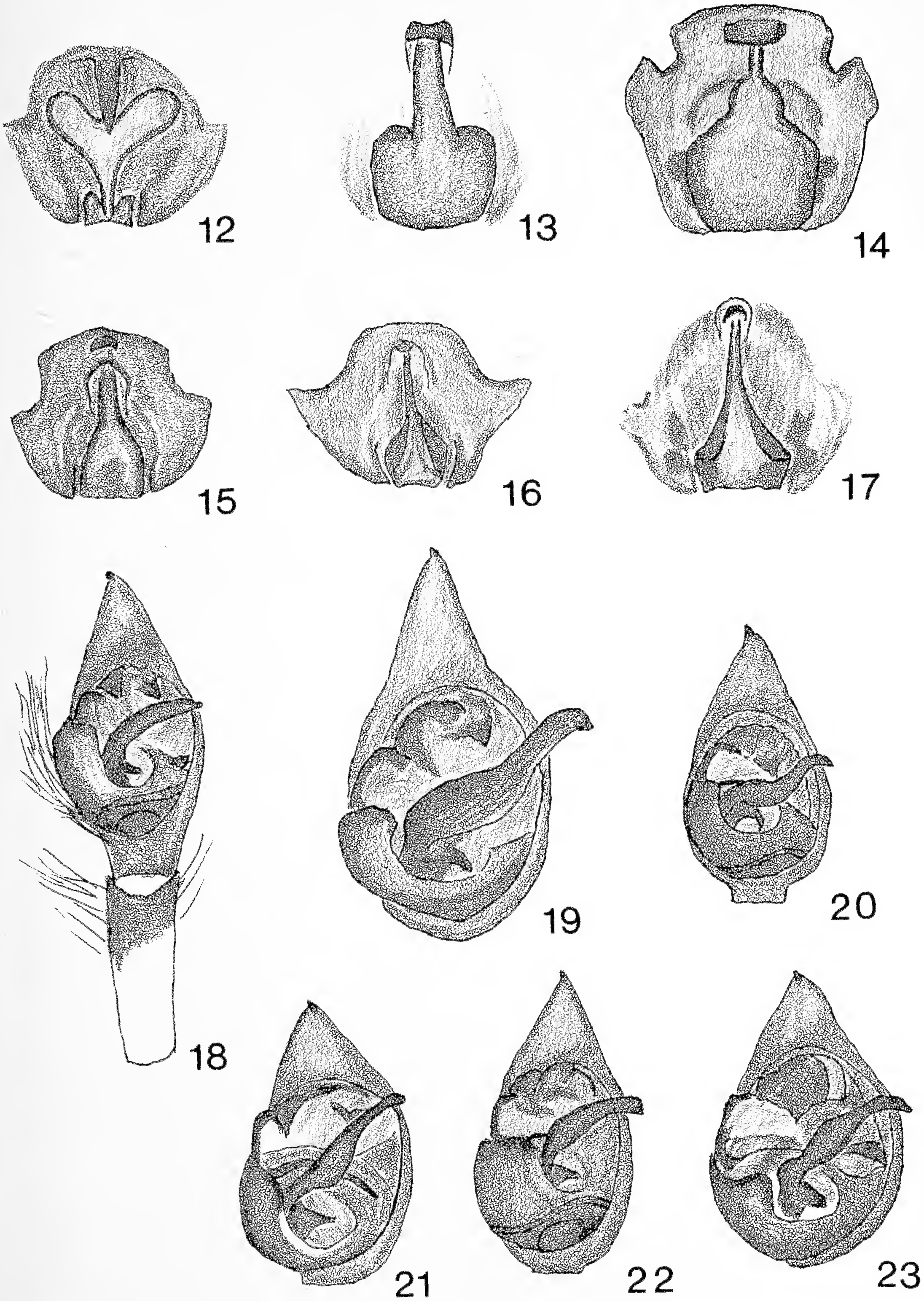
Diagnosis.—Females are 4–5 mm in length. The color pattern is typical for the group with five longitudinal bands on the cephalothorax, and the abdomen bears a light median band. The legs are yellow ochre mottled with gray or brown. The epigynal plate with its long wings pointing laterally, characterize these females. Males of *P. montgomeryi* are among the smallest *Pardosa*, 3–4 mm in length. The carapace is glabrous and dark brown. The lighter bands may not be distinct except near the pedicel. These males are distinguished by the bend in the median apophysis of the palp, giving a "sway-back" look.

Distribution.—Arizona, Colorado, New Mexico; Mexico (Vogel 1964:15).

Pardosa orophila Gertsch 1933
Figs. 12, 21; Map 2

Diagnosis.—Fresh specimens have a cherry red spot basal to the eyes. Females and some males and juveniles have a "mustache" of white hair below the basal eye rows. This is difficult to see in preserved males. The median band on the abdomen of females consists of paired yellow patches instead of a continuous band of color. The carapace of males is glabrous and dark reddish brown. The median band is brown, and the outer lateral bands very narrow. The median band of the abdomen is composed of paired lighter patches like the female. The apical lobes of the epigynal septum characterize females of *P. orophila*. The "pot-bellied" look of the median apophysis in the male palp sets *P. orophila* off from other species in this group.

Remarks.—On the foothills of the Rocky



Figures 12–23.—Genitalia of *Pardosa*, distincta group. Figs. 12–17. Epigyna. 12. *P. orophila*. 13. *P. distincta*. 14. *P. utahensis*. 15. P. *yavapa*. 16. *P. montgomeryi*. 17. *P. xerophila*. Figs. 18–23. Palpi. 18. *P. xerophila*. 19. *P. distincta*. 20. *P. montgomeryi*. 21. *P. orophila*. 22. *P. yavapa*. 23. *P. utahensis*.

Map 2.—State records for *P. distincta* (✹), *P. montgomeryi* (★), *P. orophila* (☆), *P. utahensis* (❖), *P. xerophila* (❂), *P. yavapa* (✣).

Mountains west of Denver, Colorado, *P. orophila* occurs syntopically with *P. yavapa* more frequently than by itself.

Distribution.—Colorado, Arizona, New Mexico; central Mexico (Vogel 1964:18).

Pardosa utahensis Chamberlin 1919

Figs. 14, 23; Map 2

Diagnosis.—Length 5–7 mm. Males and females both have the color pattern typical of the group. The median band on the cephalothorax is yellow to yellow ochre. The median band on the abdomen is pale yellow contrasting sharply with the dark abdomen. The legs are yellow ochre with darker mottled markings. Females of *P. utahensis* can be recognized by the pear-shaped basal expanded portion of the epigynal septum. Males can be recognized by their size and color and by the slight constriction at the base of the median apophysis.

Remarks.—Of all the species in this group, *P. utahensis* is found in the driest habitats, even plowed fields. They have also been collected sympatrically with *P. yavapa* and *P. distincta*.

Distribution.—Montana, Wyoming, Colorado, Utah (Vogel 1964:21, fig. 3; pers. obs.).

Pardosa xerophila Vogel 1964

Figs. 17, 18; Map 2

Pardosa xerophila Vogel 1964:21, figs. 13–14 (female holotype); Jiménez 1986: 27, figs. 5–6 (male).

Diagnosis.—Length 5–7 mm. Females are yellow and brown, and similar in size to *P. distincta*. The legs have brown longitudinal markings dorsally, especially on the patellae. The expanded base of the septum tapers apically with concave margins and septal pockets are present. Males are colored similarly to females, except for the legs. The legs are yellow, entirely without markings except for a dark ring on the distal ends of tarsus and metatarsus I, and the dark ring on the distal end of the tibia of the pedipalp. The palp is uniquely adorned with a brush of long black setae on the medio-lateral side of the cymbium.

Remarks.—The male described as *P. xerophila* (Vogel 1964) was collected with the female holotype. Later collections produced different males, described by Jemenez (1986), who speculated that the original male was a variant of *P. montgomeryi*.

Distribution.—New Mexico, Arizona; Mexico (Vogel, 1964: fig. 4).

Pardosa yavapa Chamberlin 1925

Figs. 15, 22; Map 2

Diagnosis.—Both male and female of *P. yavapa* are small, female body length is 4.8–5.2 mm, male body length 4.0–4.5 mm. The median band on the cephalothorax is dark and tapers to a point at the pedicel. The outer lateral bands are reduced to a few paler spots on the female and obscured on the male. The carapace of the male is glabrous and mahogany colored. On the female, the median band of the abdomen, hardly a band, is patterned with paired brown patches, scarcely lighter than the rest of the abdomen. This is usually obscured on the male. In addition to size and color, the hourglass appearance of the epigynal septum identifies the female. The slender median apophysis of the male palp, lacking sways or bulges and the absence of a brush of dark setae separate *P. yavapa* from the rest of the species group.

Remarks.—*Pardosa yavapa* is fairly common and is found with other species in the distincta group.

Distribution.—Utah, Colorado, Arizona, New Mexico (Vogel 1964: fig. 4).

Falcifera Group

Remarks.—The falcifera group consists of two species throughout the Southwest to Central America. Their body length is 5–8 mm. The color pattern is typical of the genus. The cephalothorax usually has five longitudinal bands, except in dark spiders. The abdomen may have five pairs of light spots basal to the diamond mark. This group is very closely related to the sternalis group. The epigynum is small with small lateral wings. Paired semicircular cavities are about 1/2 the length of the plate. The lateral swellings surrounding the cavities extend apically to the hood. The cavities are nearly filled with cavity sclerites extending laterally from the septum. The male palp separates the falcifera group from all other *Pardosa*. The embolus curves in a low semicircular arch behind the median apophysis. The median apophysis is long, with a mid-section bulge and reaches to the edge of the cymbium. The basal spur is short, wide, and curved basally. The median apophysis is stouter than that of sternalis group males and the arch of the embolus is lower. The males of falcifera group are distinguished from all other *Pardosa* by the feathery brush of hair on tarsus and metatarsus I. In alcohol these hairs may appear colorless but in life they are black and erectile when displayed in courtship (Vogel 1970b).

KEYS TO SPECIES OF THE FALCIFERA GROUP

Females

1. Median septum wider at base; apical end of cavity forming acute angle with septum; cavity sclerites a D-shaped lobe without basal or apical extensions parallel to septum (Fig. 24) . . . . *Pardosa falcifera*
   Median septum rectangular through cavities; apical end of cavity forming nearly a right angle with septum; cavity sclerites smallish lobes with basal and apical extensions along the septum (Fig. 25) . . . . *Pardosa zionis*

Males

1. Median apophysis tapers distal to bulge, ending in a point; tip of terminal apophysis bilobed (Fig. 26) . . . . *Pardosa falcifera*
   Median apophysis not tapering distal to bulge, tip somewhat truncate; terminal apophysis not bilobed (Fig. 27) . . . . *Pardosa zionis*

Pardosa falcifera F. Pickard-Cambridge 1902

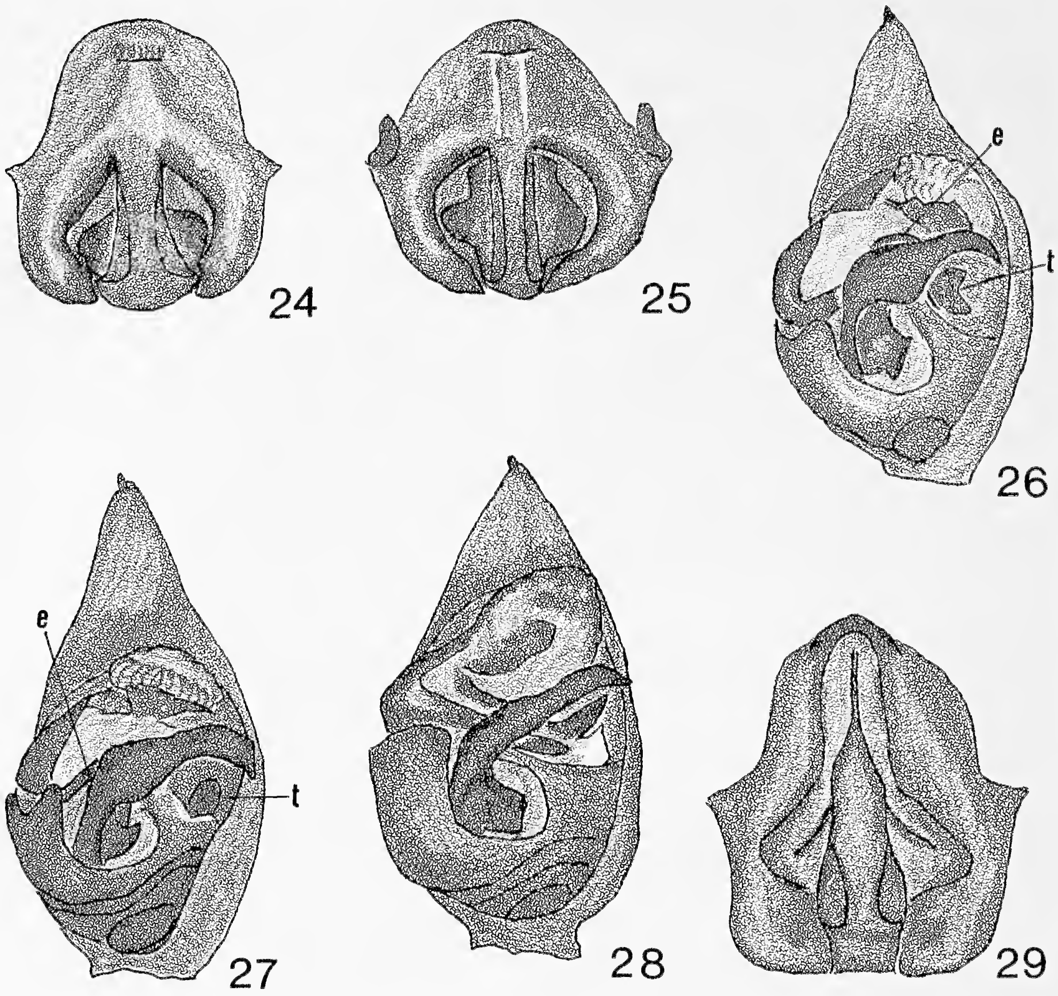
Figs. 24, 26; Map 3

Pardosa falcifera F. Pickard-Cambridge 1902:318, plate 30, figs. 23, 24.

Pardosa hopi Chamberlin & Ivie 1942:34, fig. 66; Vogel 1970a:15 (= *Pardosa falcifera*)

Diagnosis.—The distinguishing feature of *P. falcifera* females is the D-shaped cavity sclerite within a semicircular cavity. The feathery brushes of hair on tarsus and metatarsus I and the bilobed terminal apophysis are the distinguishing features of *P. falcifera* males.

Remarks.—Both *P. falcifera* and *P. zionis*



Figures 24–29.—Genitalia of *Pardosa* species groups. Figs. 24–27. Falcifera group. Figs. 24–25.Epigyna. 24. *P. falcifera*. 25. *P. zionis*. Figs. 26–27. Palpi. 26. *P. falcifera*. 27. *P. zionis*. Figs. 28–29 Lapponica group, *P. concinna*. 28. Palp. 29. Epigynum. e, embolus. t, terminal apophysis,

are found in wet meadows, streamsides, and lawns, but never together.

Distribution.—California, Utah, Colorado, Kansas, Arizona, New Mexico, Texas; south to Costa Rica (Vogel 1970a:20–21; pers. obs.).

Pardosa zionis Chamberlin & Ivie 1942
Figs. 25, 27; Map 3

Diagnosis.—*Pardosa zionis* is closely related to *P. falcifera*. The cavity sclerites in females differ by having basal and apical extensions along the septum. Males of *P. zionis* are differentiated by the terminal apophysis which is not bilobed.

Remarks.—This species is not common in the United States.

Distribution.—Utah, Arizona, New Mexico, Texas; Mexico (Vogel 1970a:22; pers. obs.).

Lapidicina Group

Remarks.—The lapidicina group consists of six species in the United States and two in Mexico. The color pattern is typical of *Pardosa* but the legs bear annular markings. Body length of females ranges 6.2–10.4 mm and the males are slightly smaller. The cavity is conspicuous, featuring a wide basal expansion and a single broad extension apically to the

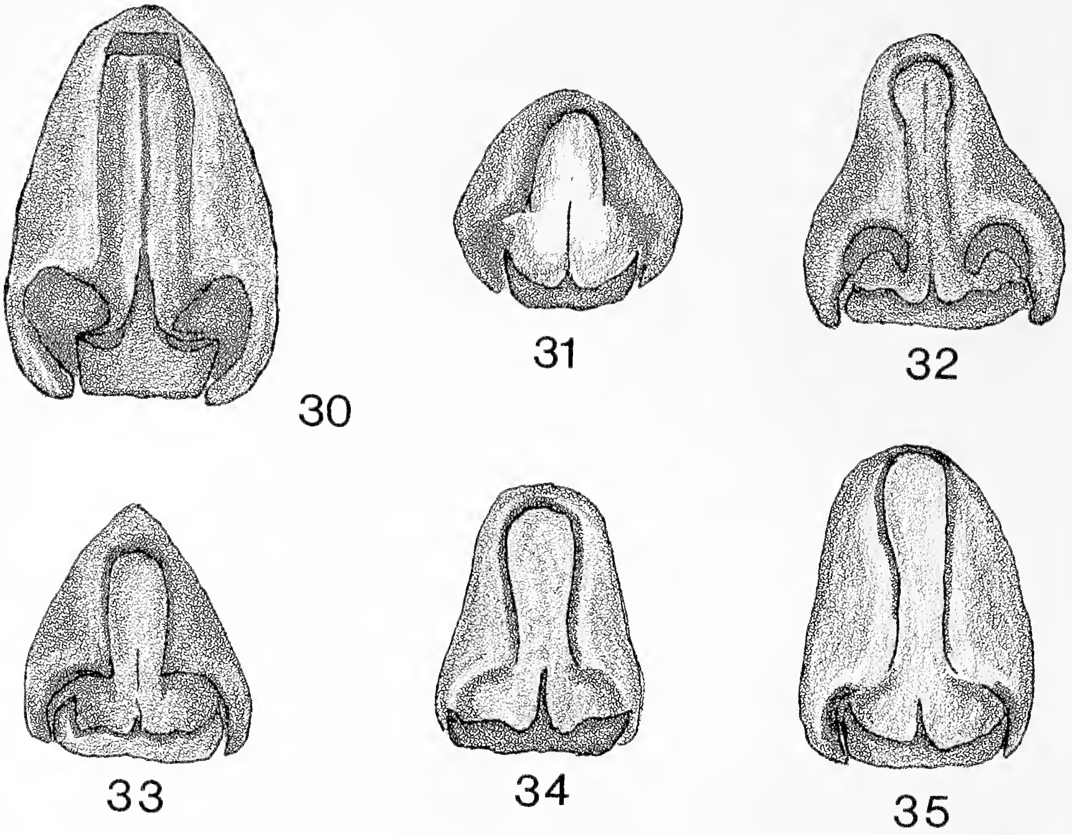
Map 3.—State records for *P. concinna* (✸), *P. falcifera* (★), *P. zionis* (☆), *P. moesta* (❖).

end of the epigynum. The apical cavity rim forms the hood. The transverse base of the septum is short, but nearly as wide as the epigynum. The septum apical to the base is reduced to a thin ridge which may be quite short or extend nearly to the hood. The median apophysis of the palp is short, lumpish, barely extending beyond the encircling tegulum. The median apophysis lacks a basal spur, but the apical end has a blunt lateral protuberance. The embolus is slender and traverses the bulb apically to the median apophysis.

KEYS TO USA SPECIES OF THE LAPIDICINA GROUP

Females

1. Transverse base of septum rectangular; septal ridge four times longer than base, extending to hood (Fig. 30) . . . . *Pardosa valens*
   Transverse base of septum somewhat canoe-shaped; septal ridge usually not extending to hood 2
2. Basal expansion of cavity 1/2 the total length of cavity; spider pale, tan or yellow (Fig. 31) . . . . *Pardosa vadosa*
   Basal expansion of cavity less than 1/2 the total length of cavity 3
3. Basal expansion of cavity deeply excavated with sclerotized crescents apically (Fig. 32) . . . . *Pardosa sierra*
   Basal expansion of cavity without sclerotized crescents apically 4
4. Apical rim of basal expansion of cavity distinct, forming a sharp point medially with longitudinal rim of apical portion of cavity (Fig. 33) . . . . *Pardosa steva*
   Apical rim of basal expansion of cavity indistinct, forming a rounded corner medially with longitudinal rim of apical portion of cavity 5
5. Apical rim of transverse base of septum with shallow notches flanking septal ridge (Fig. 34) . . . . *Pardosa lapidicina*
   Apical rim of transverse base of septum without shallow notches flanking septal ridge; ends of base turned slightly apically (Fig. 35) . . . . *Pardosa mercurialis*



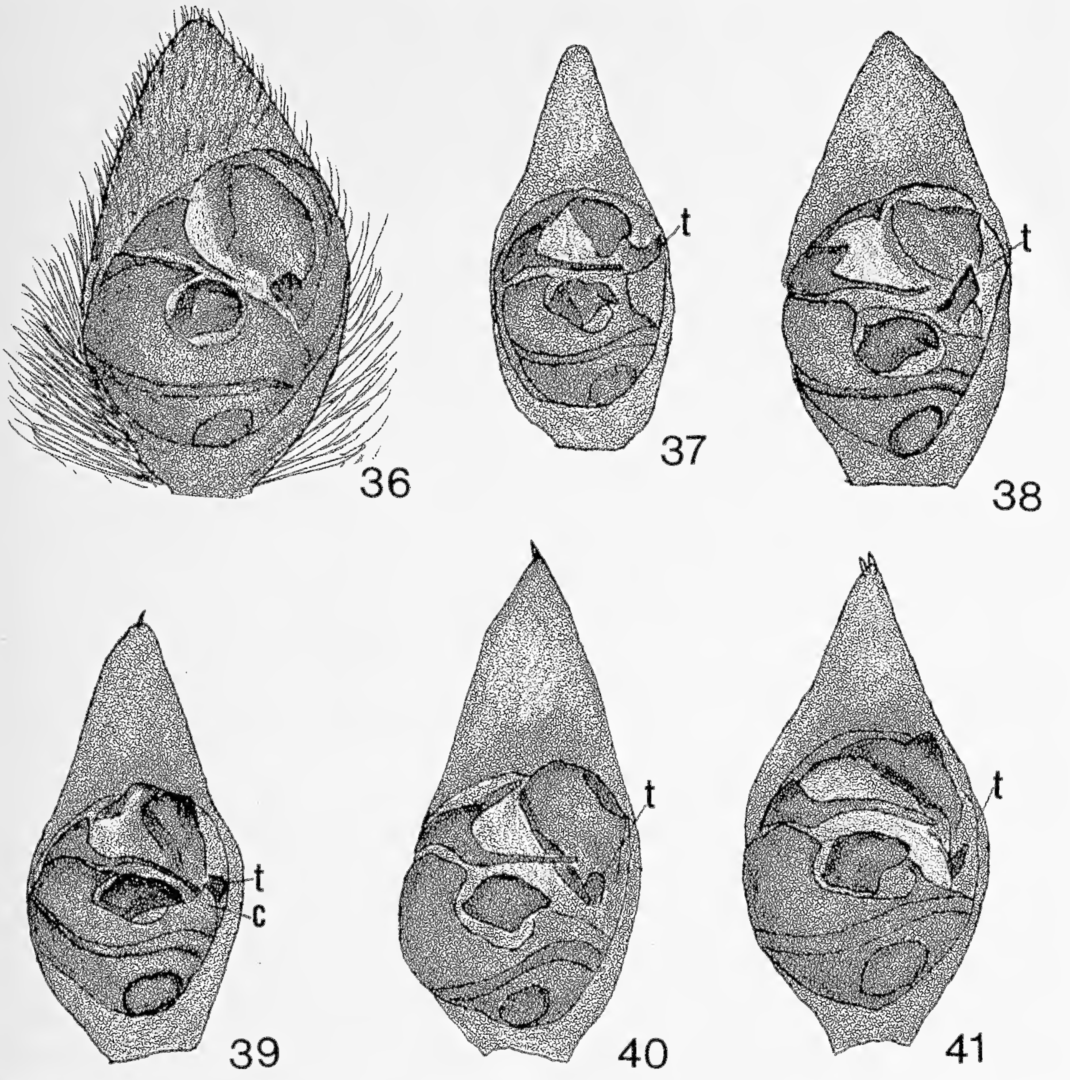
Figures 30–35.—Epigyna of *Pardosa*, lapidicna group. 30. *P. valens*. 31. *P. vadosa*. 32. *P. sierra*. 33. *P. steva*. 34. *P. lapidicina*. 35. *P. mercurialis*.

Males

1. Cymbium and tibia of the pedipalp heavily clothed with thick black hair (Fig. 36). . . . . *Pardosa valens*
   Cymbium and tibia of the pedipalp clothed but without thick black hair 2
2. Cymbium very slender; terminal apophysis a stout curved hook arising apical to tip of embolus (Fig. 37) . . . . *Pardosa vadosa*
   Cymbium not especially slender; terminal apophysis not a stout curved hook 3
3. Terminal apophysis straight and thumb-like, nearly equal in length to median apophysis; tip of embolus curves apically (Fig. 38) . . . . *Pardosa sierra*
   Terminal apophysis short, a small knob or thorn; tip of embolus pointing laterally or basally 4
4. Embolus extending all the way across bulb, tip bent basally and ending behind hyaline conductor; terminal apophysis a small knob next to conductor (Fig. 39) . . . . . . *Pardosa steva*
   Embolus extending only slightly beyond median apophysis; tip of embolus plainly visible . . 5
5. Terminal apophysis a rounded knob (Fig. 40) . . . . *Pardosa lapidicina*
   Terminal apophysis a pointed thorn (Fig. 41) . . . . *Pardosa mercurialis*

Pardosa lapidicina Emerson 1885
Figs. 34, 40; Map 4

Diagnosis.—*Pardosa lapidicina* may be a dark chocolate brown without markings or lighter brown with typical markings. The lateral bands on the carapace are represented by three or four pale blotches. The abdomen is also marked with blotches, not bands. The femora bear dark annulations. The epigynum of *P. lapidicina* features a broad apical exten-



Figures 36–41.—Palpi of *Pardosa*, lapidicina group. 36. *P. valens*. 37. *P. vadosa*. 38. *P. sierra*. 39. *P. steva*. 40. *P. lapidicina*. 41. *P. mercurialis*. c, conductor. t, terminal apophysis.

sion of the cavity. The transverse base of the septum is a short broad canoe shape with a short ridge directed apically and shallow notches flanking the ridge. The palp of males of *P. lapidicina* differs from other males in the lapidicina group by the terminal apophysis, which is a rounded knob, and by the embolus, which is directed laterally.

Remarks.—Females of *P. lapidicina* are very difficult to separate from *P. mercurialis* by genital morphology. Currently location is more reliable because there is no known overlap in range.

Distribution.—Montana, Wyoming, Colorado, Nebraska, Arkansas, Minnesota, Wisconsin, Pennsylvania, New York, Maine, Massachusetts, Rhode Island, Connecticut, New Jersey, West Virginia, Virginia, North Carolina; Ontario to Nova Scotia (Barnes 1959: fig. 1; Dondale & Redner 1990: map 55; pers. obs.).

Pardosa mercurialis Montgomery 1904
Figs. 35, 41; Map 4

Diagnosis.—The lateral band on the carapace of females of *P. mercurialis* consists of four wide yellow blotches. The median band is orangish. The abdomen is marked with yellow blotches, and the basal half is a single wide yellow blotch. The legs are annulate.

Males are dark brown with lighter brown markings. The transverse base of the septum in *P. mercurialis* is short, broad and without shallow notches flanking the short septal ridge. The ends of the transverse base turn slightly apically. The basal expanded portion of the cavity is about 1/4 the total length of the cavity. Males of *P. mercurialis* are characterized by the terminal apophysis in the form of a sharp tooth pointing apically, and the tip of the embolus which is turned basally.

Distribution.—Oklahoma, Texas (Barnes 1959: fig. 1).

Pardosa sierra Banks 1898

Figs. 32, 38; Map 4

Diagnosis.—Females of *P. sierra* have a body length of 9.0–9.5 mm. The carapace is a reddish brown with the median band orangish. The abdomen is pale with the yellow areas larger than the dark areas. The carapace and legs of males are brown and orange brown, and the abdomen is yellow and brown. The epigynum of *P. sierra* is unique in the lapidicina group. Crescent-shaped sclerites lie at the apical edge of the lateral expansions of the cavity. The thin septal ridge extends apically to the hood. The palp of the male features an embolus which extends only part way across the bulb with the tip curving apically. The terminal apophysis is nearly as long as the median apophysis. It is thumb-like and straight.

Distribution.—Oregon, California, Idaho, Wyoming west of the Continental Divide, Colorado, Arizona, New Mexico, Texas; Mexico (Barnes 1959: fig. 5; pers. obs.).

Pardosa steva Lowrie & Gertsch 1955

Figs. 33, 39; Map 4

Diagnosis.—Females of *P. steva* are dark, pattern with low contrast. The legs are annulate with dark gray and chestnut brown; the diamond on the abdomen is outlined in black, lateral blotches are chestnut. Males similarly marked. The epigynum is differentiated from other females in this group by the apical rim of basal expansions of the cavity. The rim is crisply defined, not softly rounded, and meets the rim of the apical extension in a sharp point. Males of *P. steva* can be identified by the embolus, which extends all the way across the bulb. The tip of the embolus is bent basally and ends behind a hyaline conductor. The terminal apophysis is a small knob.

Distribution.—California, Oregon, Idaho, Montana, Wyoming, Utah, Colorado, Arizona, New Mexico; Canada, Mexico (Barnes 1959: fig. 4; Dondale & Redner 1990: map 55).

Pardosa vadosa Barnes 1960

Figs. 31, 37; Map 4

Diagnosis.—Spiders are of a very light color, yellow to yellow ochre, and marked with light brown. The legs bear light brown annulations. The abdomen is marked with chalky yellow blotches. The distinguishing character of *P. vadosa* is the cavity of the epigynum. The basal expansion of the cavity is about 1/2 the length of the epigynum, longer than any other species in the lapidicina group. The cymbium of the male palp *P. vadosa* is very slender. The terminal apophysis is a stout hook arising apical to the tip of embolus. The tip of the terminal apophysis is turned apically.

Distribution.—California, Utah, Colorado, Arizona, Texas; Mexico (Barnes 1959: fig. 2; pers. obs.).

Pardosa valens Barnes 1960

Figs. 30, 36; Map 4

Diagnosis.—*Pardosa valens* is a dark-colored spider. Its carapace is mahogany. The body length of females is 7.0–9.3 mm. Males range in size from 6.8–8.0 mm. The transverse base of the septum differs from the other females in this group. It is rectangular and about 2/3 as long as wide. Additionally, the hood is a rectangular pocket. The septal ridge extends to the hood. Males can be recognized by the heavy black hair on the palp and the tibia of the pedipalp. The tegulum nearly surrounds the lumpish median apophysis.

Distribution.—Colorado, Arizona, New Mexico; Mexico (Barnes 1959: fig. 3; pers. obs.).

Lapponica Group

Remarks.—The lapponica group consists of one species in North America, one Holarctic species and several Palearctic species. The epigynum of this group, along with the lapidicina and moesta group, has a cavity that is wide basally and has a single apical extension surrounding the septum. The apical end of the cavity extension reaches the end of the epi-

Map 4.—State records for *P. lapidicina* (✷), *P. mercurialis* (❂), *P. sierra* (★), *P. steva* (☆), *P. vadosa* (❖), *P. valens* (✛).

gynum and forms a sclerotized hood. The tegulum of the male palp is a robust, rounded bowl. The median apophysis is thick, long, and reaches the edge of the cymbium without curves. The basal spur is short and truncated. The embolus is moderately wide in the distal portion and nearly straight. The terminal apophysis is situated basally to the tip of the median apophysis.

Pardosa concinna (Thorell 1877)
Figs. 28, 29; Map 3

Diagnosis.—The spiders are brown with a yellow median and unbroken lateral bands on the carapace. The abdomen is mottled brown with a diamond mark apically and paired lighter patches basally. The abdominal markings are of low contrast. The legs are brown and the sternum is nearly black. The cavity of *P. concinna* is as described above. The septum is moderately wide for 2/3 to 3/4 of its length, narrowing to a spine apically. Drop-shaped septal pockets lie near the base of the septum. The palp of *P. concinna* conforms to the diagnosis of the lapponica group, above.

Distribution.—Washington, Oregon, Montana, Wyoming, Utah, Colorado, New Mexico, New York, Vermont, New Hampshire, Maine; Alaska, Canada (Dondale & Redner 1986: map 7).

Milvina Group

Remarks.—The milvina group consists of nine species in the United States and at least eight more in Mexico, and Central and South America. The cephalothorax usually has five longitudinal bands except in dark spiders. The median band bulges posteriorly of the eye area, is constricted, then bulges again and ends as a slender band at the pedicel. The median band of the abdomen is usually ragged or poorly defined aside from the diamond mark. Males are darker than females and usually with a glabrous carapace. The spiders range in size from 3.5–7.5 mm, but the majority are small. The genitalia of the milvina group is more variable than any other group considered here, except perhaps, for the modica group. The epigynum is longer than wide; in some species, twice as long as wide. The apical rim of the epigynum is broad, rounded and thickened. The thickened rim also forms the hood and may bear an additional structure. The expanded base of the septum is generally triangular, but appears anchor shaped because of the septal pockets. The septum apical to the expanded base may be a furrow flanked by ridges, although five species have raised septa extending to the hood. The cavities have no distinct rim and are mostly concealed by the expanded base of the septum, except for *P. milvina*. Females of the milvina group strongly resemble those of the distincta group, but the thickened apical rim of the epigynum will distinguish milvina group from distincta group females. There is considerable variation in the male palp, especially in the median apophysis. In three species the median apophysis is long, curved, slender, and extends to the edge of the cymbium, with a small basal spur. In the other species the median apophysis is a short, stout, curved hook with a short, stout, strongly curved basal spur.

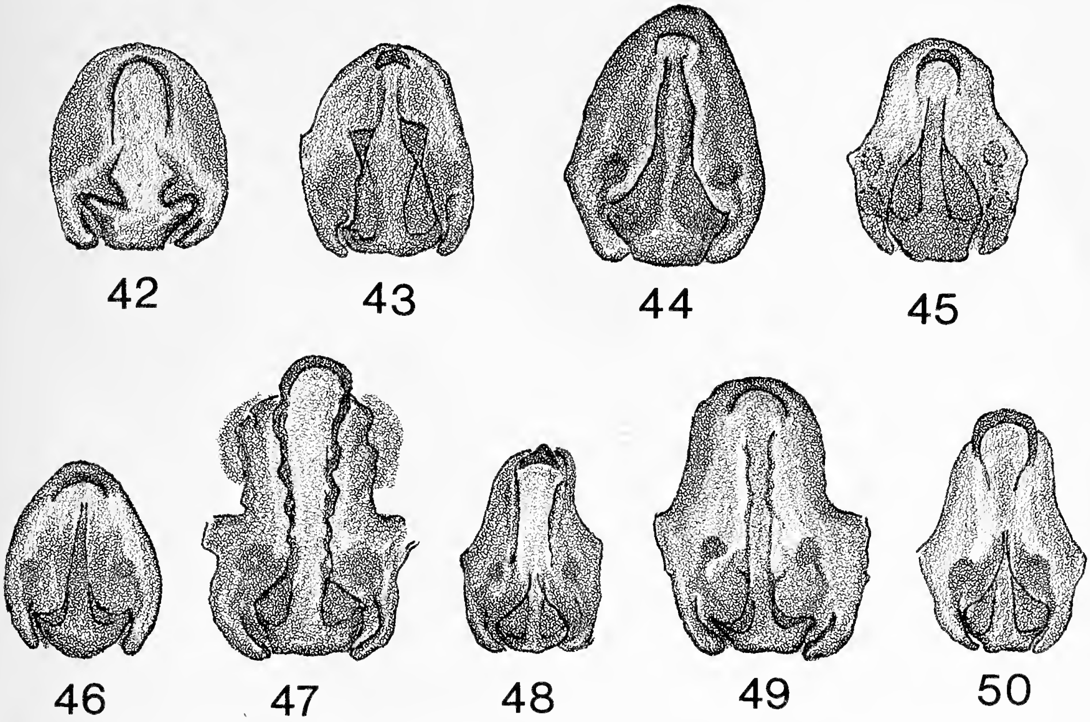
KEYS TO USA SPECIES OF THE MILVINA GROUP

Females

1. Expanded base of septum nearly 1/2 the length of epigynum or longer (Figs. 42–45) 2
   Expanded base of septum 1/3 the length of epigynum or less (Figs. 46–50) 5
2. Expanded base of septum with a pair of deep lateral notches (Fig. 42) .... *Pardosa saltonia*
   Expanded base of septum without notches 3
3. Expanded base of septum rectangular, with triangular sclerotized structures apical to cavities (Fig. 43) .... *Pardosa bellona*
   Expanded base of septum triangular, without sclerotized structures 4
4. Sides of expanded base of septum concave, apical portion of septum tapering slightly (Fig. 44) .... *Pardosa littoralis*
   Sides of expanded base of septum convex, apical portion of septum not tapering (Fig. 45) .... *Pardosa delicatula*
5. Septum apical to base is a raised structure extending to hood (Fig. 46) .... *Pardosa pauxilla*
   Septum apical to base a furrow 6
6. Hood with ridges trailing basally along septal furrow to, or nearly to, expanded base of septum 7
   Hood without ridges trailing nearly to expanded base of septum 8
7. Spider nearly 6 mm; trailing ridges of hood thick and very wrinkled (Fig. 47) .... *Pardosa saxatilis*
   Spider not more than 4 mm; trailing ridges of hood narrow and straight (Fig. 48) .... *Pardosa parvula*
8. Spider 6.0–6.5 mm; hood narrow; septal pockets shallow with concave rim (Fig. 49) .... *Pardosa milvina*
   Spider 4.0–4.5 mm; hood broad; septal pockets deep with convex rim (Fig. 50) .... *Pardosa atlantica*

Males

1. Median apophysis slender, extending nearly to edge of cymbium, base wide; basal spur short and truncate (Fig. 51–53) 2
   Median apophysis more stout, short, not reaching cymbium; basal spur a curved hook 4
2. Dorsum of cymbium, tibia, and patella of pedipalp completely clothed with stiff shiny white hair; palp as in Fig. 51 .... *Pardosa parvula*
   Not all three segments so clothed 3
3. Dorsum of patella, and tibia of the pedipalp, and only narrow basal portion of cymbium clothed with stiff shiny white hair; palp as in Fig. 52 .... *Pardosa atlantica*
   Only patella of the pedipalp clothed with stiff shiny white hair; cymbium dark basally, with tip paler; palp as in Fig. 53 .... *Pardosa saxatilis*
4. Cymbium very narrow and long, tegulum flattish; bulb embedded deeply in cymbium (Fig. 54) .... *Pardosa saltonia*
   Cymbium not unusually narrow and long; tegulum protruding from cymbium 5
5. Median apophysis medium long, base wide; basal spur short and pointed and slightly curved (Figs. 55, 56) 6



Figures 42–50.—Epigyna of *Pardosa*, milvina group. 42. *P. saltonia*. 43. *P. bellona*. 44. *P. littoralis*. 45. *P. delicatula*. 46. *P. pauxilla*. 47. *P. saxatilis*. 48. *P. parvula*. 49. *P. milvina*. 50. *P. atlantica*.

Median apophysis short and thick, basal spur a stout curved hook 7

6. Palea with a long, slender, tapered process extending behind median apophysis (Fig. 55) .... *Pardosa littoralis*

Palea without such a process (Fig. 56) .... *Pardosa milvina*

7. Median apophysis very short, basal spur strongly curved and much larger than median apophysis (Fig. 57) .... *Pardosa bellona*

Basal spur not larger than median apophysis 8

8. Tip of median apophysis a curved pointed hook, basal spur a small hook; palea membranous (Fig. 58) .... *Pardosa pauxilla*

Tip of median apophysis curved and blunt, basal spur a wide hook; palea sclerotized (Fig. 59) .... *Pardosa delicatula*

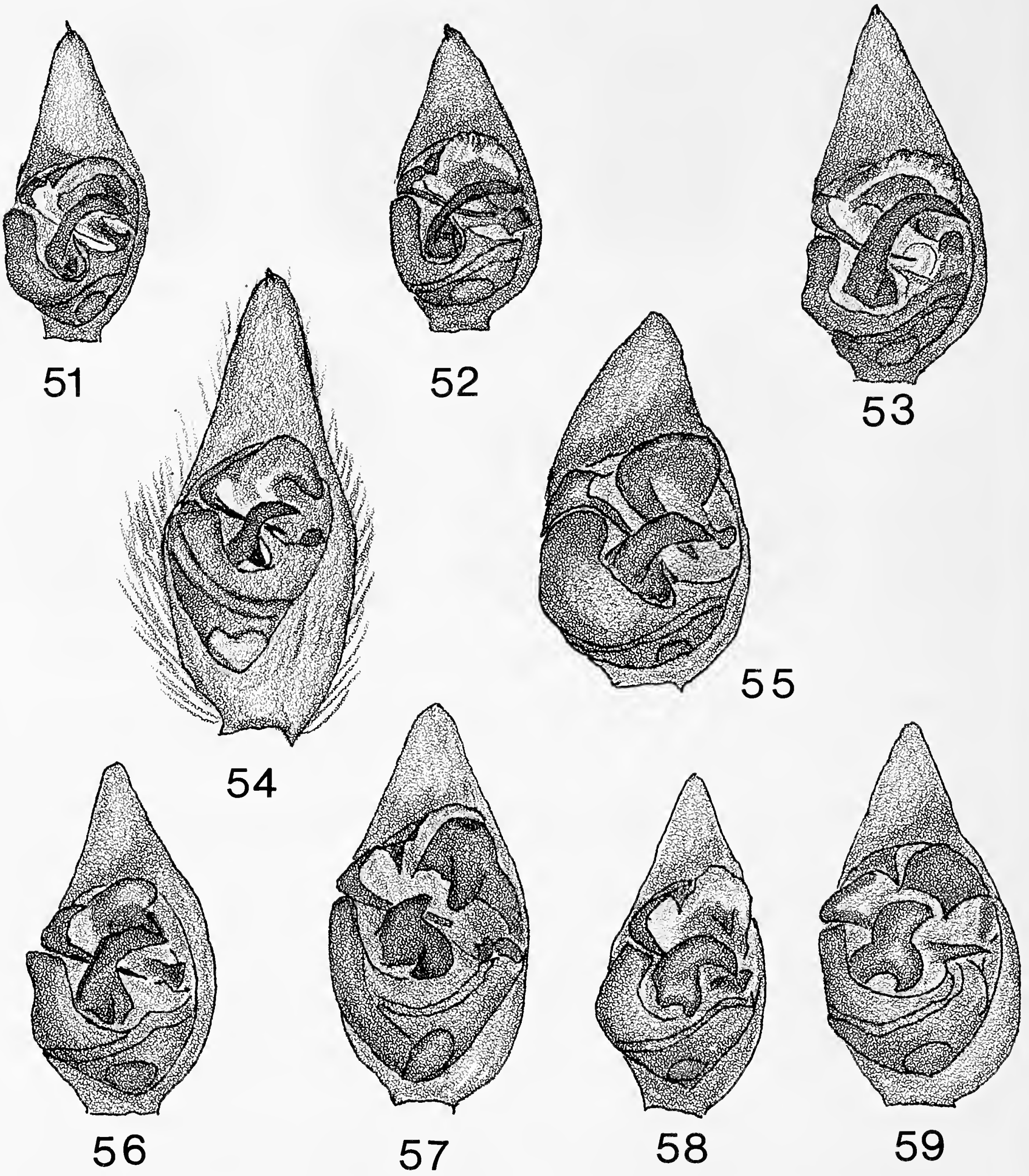
Pardosa atlantica Emerton 1913
Figs. 50, 52; Map 5

Diagnosis.—The abdomen of the female is characterized by four pairs of eye spots basal to diamond mark. The septal pockets of the epigynum are deep with convex apical margins. Males of *P. atlantica* have a long slender median apophysis that nearly reaches the cymbium, and a small truncated basal spur. Males of *P. atlantica* cannot be separated by palpal morphology from *P. parvula* and *P. saxatilis*. The distribution of white, shiny hair on the pedipalp distinguish these three species. In *P. atlantica* they occur only on the tibia and patella of the pedipalp and a very narrow band on the base of the cymbium.

Distribution.—Nebraska, Oklahoma, Texas, Arkansas, Mississippi, Kentucky, New Jersey, Maryland, West Virginia, Virginia, Georgia (Dondale & Redner 1984: map 3).

Pardosa bellona Banks 1898
Figs. 43, 57; Map 5

Diagnosis.—Females of *P. bellona* can be identified by the expanded base of the septum, which is more than half the length of the epigynum, and bears triangular sclerotized struc-



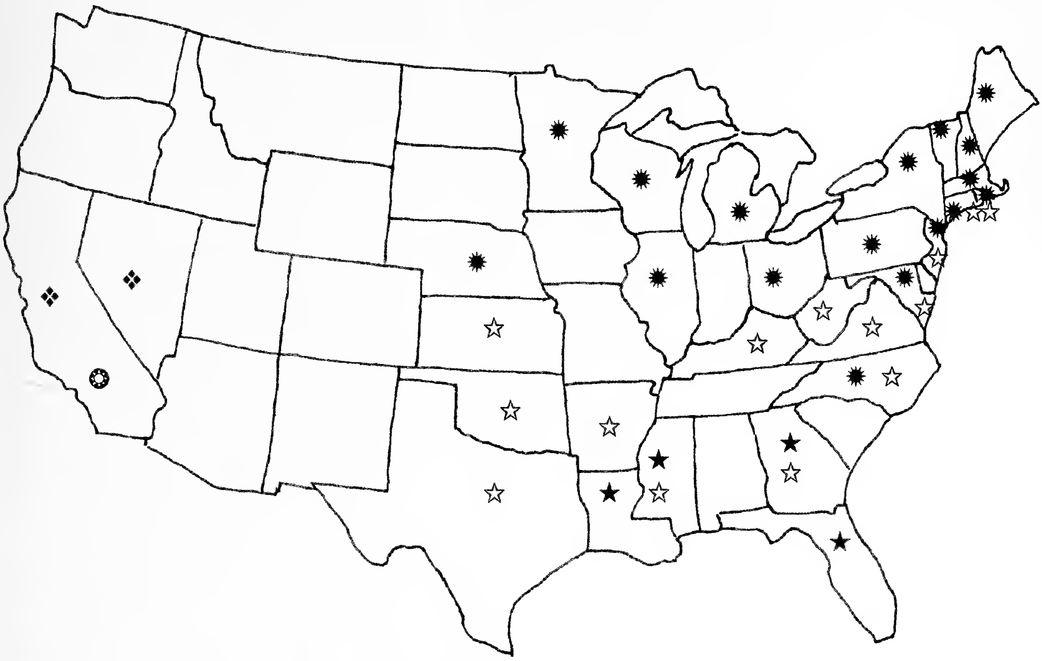
Figures 51–59.—Palpi of *Pardosa*, milvina group. 51. *P. parvula*. 52. *P. atlantica*. 53. *P. saxatilis*. 54. *P. saltonia*. 55. *P. littoralis*. 56. *P. milvina*. 57. *P. bellona*. 58. *P. pauxilla*. 59. *P. delicatula*.

tures apical to the cavities. Males of *P. bellona* can be identified by the short stout median apophysis with a blunt tip, a strongly curved, pointed basal spur, which is much larger than the median apophysis, and a tongue-shaped structure on the palea extending toward the median apophysis.

Distribution.—California, Nevada; Mexico (Dondale & Redner 1984:77, map 1).

Pardosa delicatula Gertsch & Wallace 1935
Figs. 45, 59; Map 6

Diagnosis.—The carapace of the females is pale, yellow marked with brown. The median band of the abdomen is a pale yellow, and the diamond is tan. Males are darker and the median band of the abdomen is about the same color as the diamond mark. The expanded



Map 5.—State records for *P. atlantica* (☆), *P. parvula* (★), *P. saxatilis* (✹), *P. bellona* (❖), *P. saltonia* (◎).

base of the septum is more than half as long as the epigynum, with convex sides. The apical portion extends to the hood as a ridge, not a furrow. The palp of the male has a short stout median apophysis with a blunt curved tip. The basal spur is a stout curved hook. The palp of *P. delicatula* is similar to the palp of *P. pauxilla*, but the palea of *P. delicatula* is sclerotized and the palea of *P. pauxilla* is membranous.

Distribution.—Nebraska, Oklahoma, Texas, Mississippi, Louisiana; Mexico (Dondale & Redner 1984: map 1).

Pardosa littoralis Banks 1896
Figs. 44, 55; Map 6

Pardosa littoralis Banks, 1896:192.
Pardosa longispinata Tullgren 1901:23; Dondale & Redner 1984:91 (= *Pardosa littoralis*)
Pardosa floridana Banks 1904:136; Dondale & Redner 1984:91 (=*Pardosa littoralis*)
Pardosa banksi Chamberlin 1904:175; Dondale & Redner 1984:91 (=*Pardosa littoralis*)
Pardosa ocala Bryant 1935:81; Dondale & Redner 1984:91 (=*Pardosa littoralis*)

Diagnosis.—The epigynal septum characterizes females of *P. littoralis*. The expanded base is about half the length of the epigynum with concave sides. The apical portion of septum is a ridge, not a furrow. The median apophysis of the male palp is medium long with a wide base and a short broad basal spur. The palea bears a long tapered process that crosses the bulb behind the median apophysis.

Distribution.—Texas, Louisiana, Mississippi, Alabama, New York, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida; Canada (Dondale & Redner 1984: map 1).

Pardosa milvina (Hentz 1844)
Figs. 49, 56; Map 6

Diagnosis.—The epigynum of *P. milvina* is longer than wide. The expanded base of the septum is very short, about 1/5 the length of the septum, and does not conceal the cavities. The septum apical to the base is a furrow. The male palp features a somewhat stout median apophysis, with a broad base and a small, hooked basal spur. The palea bears a sclerotized structure, but it is not long, tapered, and crossing behind the median apophysis.

Distribution.—Nebraska, Kansas, Oklahoma, Texas, Iowa, Missouri, Arkansas, Louisiana, all states east of the Mississippi River; Canada (Dondale & Redner 1984: map 5).

Pardosa parvula Banks 1904
Figs. 48, 51; Map 5

Diagnosis.—*Pardosa parvula* is the smallest *Pardosa* in the United States. The female body length is 3.4–4.2 mm and the male's is 3.1–3.5 mm. The cephalothorax is very high and the median pale band is wide. Males have pale legs, but femur I is brown. The expanded base of the septum is less than a third of the length of the epigynum. The apical half of the septum is a furrow flanked by straight ridges trailing basally from a triangular hood. *Pardosa parvula* males cannot be distinguished from *P. atlantica* and *P. saxatilis* palpal morphology, but is unique in the distribution of shiny white hair on the dorsum of the pedipalp. All three segments, of the pedipalp, patella, tibia and cymbium, are clothed by these hairs.

Distribution.—Louisiana, Mississippi, Georgia, Florida (Dondale & Redner 1984: map 3).

Pardosa pauxilla Montgomery 1904
Figs. 46, 58; Map 6

Pardosa georgiae Chamberlin and Ivie; 1944 Dondale & Render 1984:94 (= *pauxilla*)

Diagnosis.—These spiders are small, only slightly larger than *P. parvula*. The females are 4.5–5.5 mm in length, males are 4.0–4.4 mm. The abdomen of females is marked with a pale yellow median band, tan diamond and gray sides. The expanded base of the epigynal septum is less than a third the length of the epigynum. The apical portion of the septum is a ridge extending to the hood. The epigynum lacks lateral wings. The male palp of *P. pauxilla* bears a short, stout median apophysis with a curved pointed tip. The basal spur is a wide curved hook. The palea is membranous.

Distribution.—New Mexico, Kansas, Oklahoma, Texas, Louisiana, Mississippi, New Jersey, Maryland, Virginia, Georgia, Florida (Dondale & Redner 1984: map 5).

Pardosa saltonia Dondale & Redner 1984
Figs. 42, 54; Map 5

Diagnosis.—This species is the largest of the group. Female body size ranges from 6.5–8.5 mm and male body size ranges from 6.0–6.8 mm. The females are pale, mostly yellow ochre marked with tan. The median band on the abdomen is a chalky pale yellow, and the diamond is tan. The median on the abdomen of the male is yellow ochre and the diamond is brown. The expanded base of the epigynal septum is about half the length of the epigynum with a pair of deep notches on its sides. The septum apical to the base is a wide furrow and flanked by trailing ridges of the wide hood. The epigynum lacks lateral wings. The male of *P. saltonia* has a long narrow cymbium heavily clothed with long hair. The tegulum is flat and the bulb seems to be embedded in the cymbium.

Distribution.—Salton Sea, California; Mexico (Dondale & Redner 1984: map 5).

Pardosa saxatilis (Hentz 1844)
Figs. 47, 53; Map 5

Pardosa platta Chamberlin and Ivie 1942:31; Dondale & Redner 1984:87 (= *saxatilis*)

Diagnosis.—Females of *P. saxatilis* are characterized by an epigynum about twice as long as wide. The expanded base of septum is less than a third the length of epigynum. The septum apical to base is a furrow flanked by thick wrinkled ridges trailing from the hood. Males of *P. saxatilis* are distinguished from all other *Pardosa* by the slender curved median apophysis that nearly reaches the cymbium, and small truncate basal spur. *Pardosa saxatilis* is distinguished from *P. atlantica* and *P. parvula*, not by palpal morphology, but rather by the distribution of white shiny hair on the pedipalp, that occurs only on the dorsum of the patella.

Distribution.—Nebraska, Minnesota, Wisconsin, Illinois, Michigan, Ohio, Maine, New Hampshire, Vermont, New York, Massachusetts, Rhode Island, Connecticut, New Jersey, Pennsylvania, Maryland, Virginia; Canada (Dondale & Redner 1984: map 3).

Modica Group

Remarks.—The modica group is represented by 23 recognized species in North America; 17 in the lower United States, 17 in Canada, with 11 in common between these two regions. Alaska has eight species, three of which occur in the lower 48 states. The modica group is by far the richest group and it is suspected that there are still more to be named. A few species have sister species, which are not only close morphologically but

Map 6.—State records for *P. milvina* (❂), *P. delicatula* (☆), *P. littoralis* (★), *P. pauxilla* (❖).

geographically as well. Many of the species are large, up to 13 mm long. Even the smallest species exceed 6 mm in total body length The spiders are dark. The median pale band on the carapace has sinuous margins and the lateral pale bands may be entire, broken into three or four large pieces, three or four small spots, or obscure. The femora of females are mottled, and in most males are marked with longitudinal dark bands.

The epigynum is characterized by large oval cavities, covering about half the epigynal area in the majority of species. The septum extends the entire length as a sclerotized structure or raised ridge to paired hoods at the apical rim of the epigynum. The septum may be narrow and fairly straight, or have lateral expansions, chiefly in the cavity portion.

The male palp is large, with a short lumpish median apophysis scarcely extending apical to the tegulum. The basal spur is as large or larger than the apophysis. The palea is large and usually has a sclerotized area. The embolus in some species has a wide basal portion and the tip may be whip-like or somewhat broad.

KEYS TO USA SPECIES OF THE MODICA GROUP

Females

1. Oval cavities not more than 1/2 the length of epigynal plate; cavity without arms extending apically; septum apical to cavities a slightly raised ridge flanked by shallow furrows (Fig. 60) . . . . *Pardosa wyuta*
   Septum extending length of epigynum from base to hoods, cavities with arms extending to hoods (Figs. 61–76) 2
2. Cavities not more than 1/3 the length of epyginal plate, with large triangular sclerites basally; septum flaring from base to apical rim of cavity concealing basal part of cavity arms; arms diverging apically (Fig. 61) . . . . *Pardosa labradorensis*
   Widest part of septum not concealing basal part of cavity arms 3
3. Septum slender at both ends, expanded at apical end of cavities to a diamond shape with lateral ridges trailing basally on cavity floor; cavity sclerites a large V-shape situated basally 4

Septum various shapes, without a diamond shape at apical end of cavities; cavity sclerites not V-shaped, or absent 5

4. The septal branch of the V extending nearly to the diamond expansion of septum (Fig. 62) .... *Pardosa ourayensis*

The septal branch of the V not extending to diamond expansion (Fig. 63) ..... *Pardosa modica*

5. Septum except for base, quite slender throughout length (Figs 64–68) 6

Septum with basal part somewhat or greatly wider than apical part (Fig. 69–76) 10

6. Base of septum thin and wide like an inverted T, septal pockets on base; cavities wide and elongated without distinct apical rim; hoods wide, reaching to sides of epigynal plate (Fig. 64) .... *Pardosa wasatchensis*

Base of septum scarcely wider than septum or triangular in shape; cavity arms narrow and distinct 7

7. Floor of cavity with conspicuous serial ridges extending from septum to side of cavity . . 8

Floor of cavity may have small wrinkles lacking apparent pattern 9

8. Cavity ridges with apical arch near septum, then curving posterio-laterally (Fig. 65) .... *Pardosa tristis*

Cavity ridges without apical arch near septum, extending posterio-laterally more or less straight (Fig. 66) .... *Pardosa lowriei*

9. Base of septum scarcely wider than septum, septum evenly narrow from base to hood; cavity sclerites triangular (Fig. 67) .... *Pardosa bucklei*

Base of septum a narrow triangle with septal pockets along the sides; septum narrowing to a line between cavity arms, widening toward hoods; cavity sclerites oval (Fig. 68) .... *Pardosa albomaculata*

10. Basal expanded portion of septum a long rectangle, sides parallel or slightly concave, with long narrow septal pockets 11

Basal expanded portion of septum not a rectangle with rectangular septal pockets 14

11. Expanded portion of septum more than half the length of septum; hoods straight, perpendicular to septum (Fig. 69–70) 12

Expanded portion of septum less than half the length of septum; hoods curved (Figs. 72–73) 13

12. Rim of cavity and lateral rim of cavity arm crisply defined; cavity sclerites absent or at most a small knob (Fig. 69) .... *Pardosa confusa*

Rim of cavity and lateral rim of cavity arm gently rounded; cavity sclerites triangular at base of cavity (Fig. 70) .... *Pardosa tetonensis*

13. Cavity sclerites may not touch septum; total length of female 9–10 mm; higher elevations; montane, alpine (Fig. 71) .... *Pardosa groenlandica*

Cavity sclerites spanning base of cavity and abutting septum; total length of female < 9 mm; foothills and plains (Fig. 72) .... *Pardosa dromaea*

14. Base of septum 1/3 the width of epigynum, tapering from base to hood without an abrupt decrease; septal pockets bilobed (Fig. 73) .... *Pardosa sinistra*

Septum narrowing abruptly between cavity arms, septal pockets not bilobed (Figs. 74–76) . . 15

15. Cavities small, semicircular, placed somewhat apically, with heavily sclerotized rim; basal part of septum with parallel sides; hoods very narrow (Fig. 74) .... *Pardosa crassistyla*

Septum amphora shaped, bulging widely in cavity, with a narrow rounded base 16

16. Basal half of septum nearly covering cavities, large semicircular septal pockets; hoods reduced (Fig. 75) .... *Pardosa anomala*

Basal half of septum more evenly wide from base; entire septum with transverse wrinkles; hoods heavily sclerotized and contiguous (Fig. 76) .... *Pardosa vogelae*

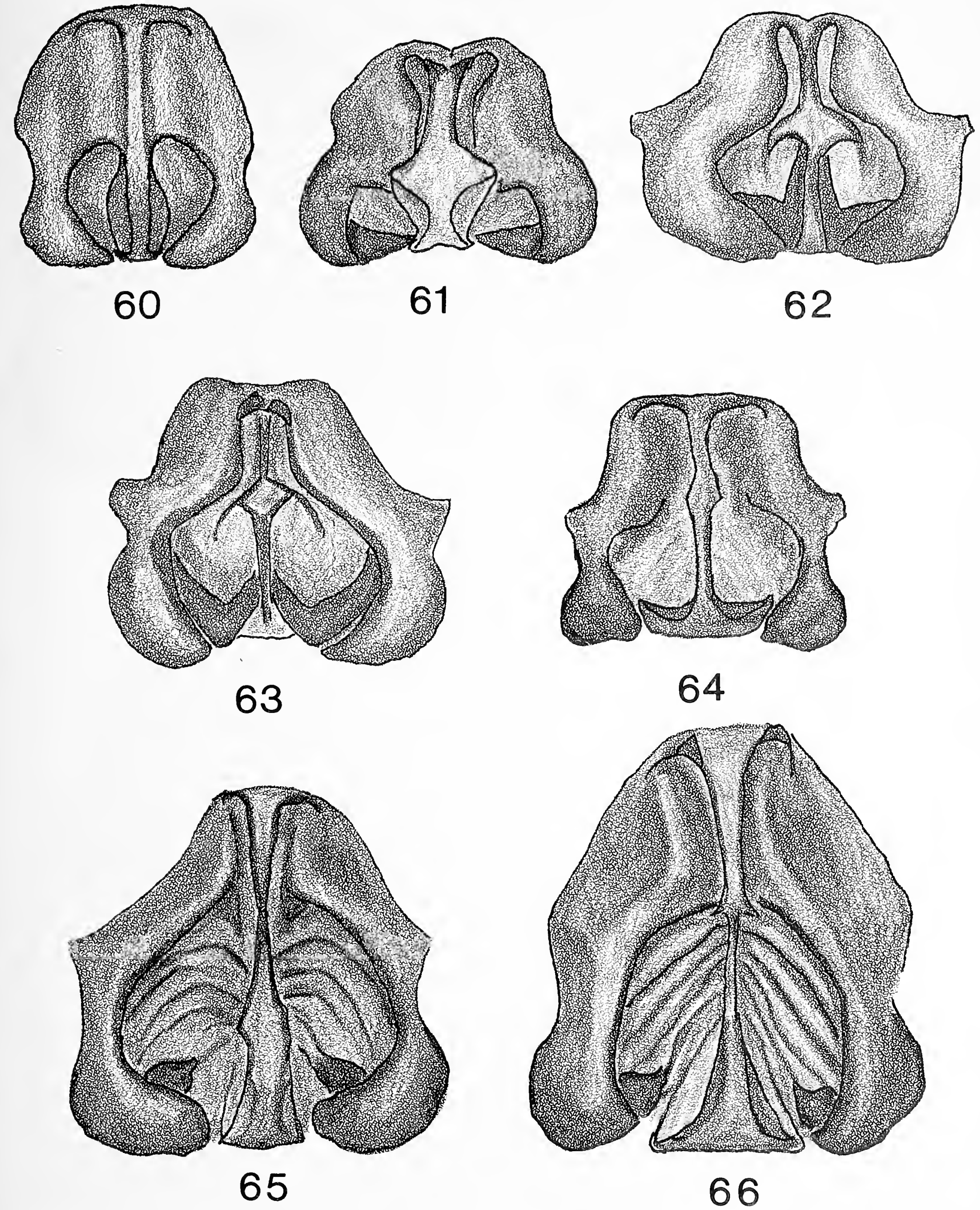
Males

1. Pale lateral bands on carapace unbroken or unmarked with darker spots 2

Lateral bands broken with darker marks or indistinct 8

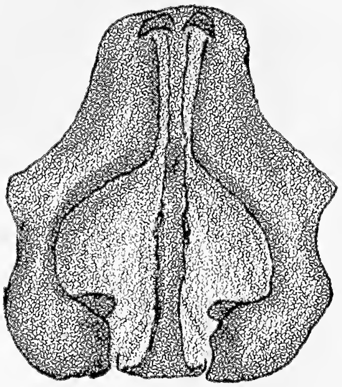
2. Embolus with broad, heavily sclerotized base, tip broad or slender (Figs. 77–79) 3

Embolus slender, hair-like at tip 5



Figures 60–66.—Epigyna of *Pardosa*, modica group. 60. *P. wyuta*. 61. *P. labradorensis*. 62. *P. ourayensis*. 63. *P. modica*. 64. *P. wasatchensis*. 65. *P. tristis*. 66. *P. lowriei*.

3. Median apophysis short, not extending apical to basal spur; large bulbous structure (B in Fig. 77) situated between median apophysis and base of median apophysis; terminal apophysis a large hook (Fig. 77) .... *Pardosa crassistyla*
   Median apophysis extending apical to basal spur, no bulbous structure between median apophysis and base of embolus 4
4. Base of embolus wide, apical portion thin and hair-like (Fig. 78) ...... *Pardosa tetonensis*



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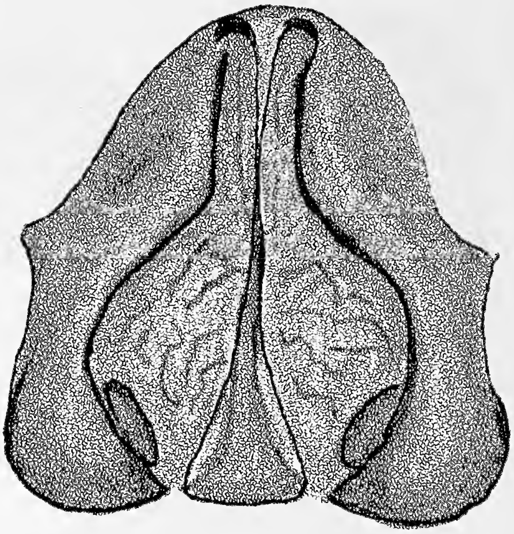

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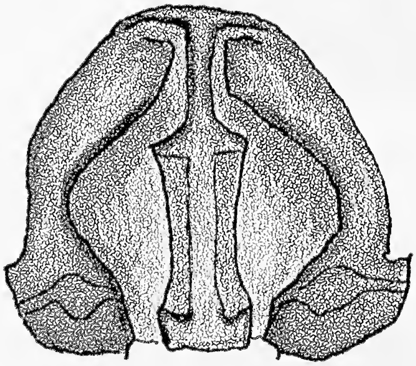

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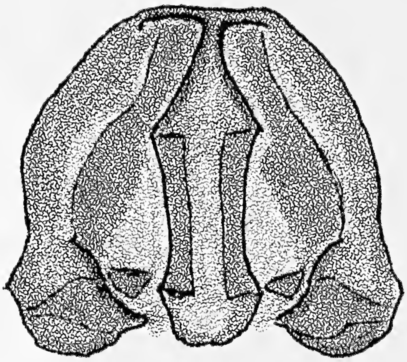

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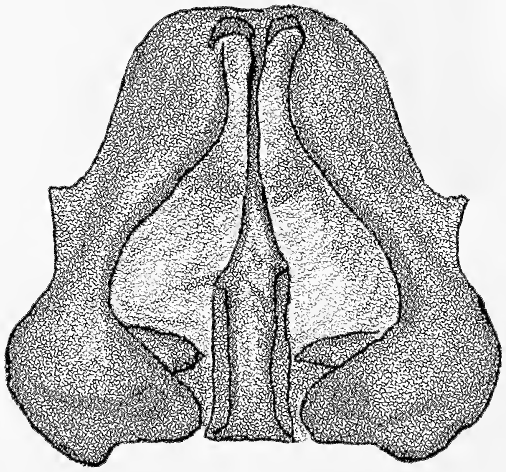

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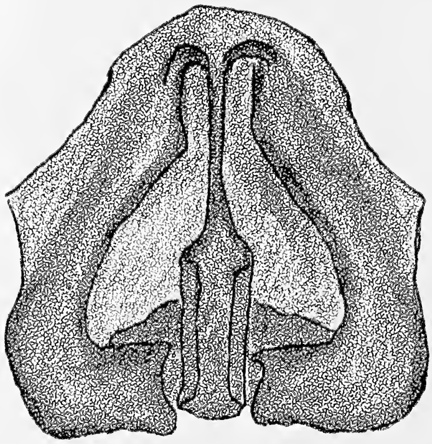

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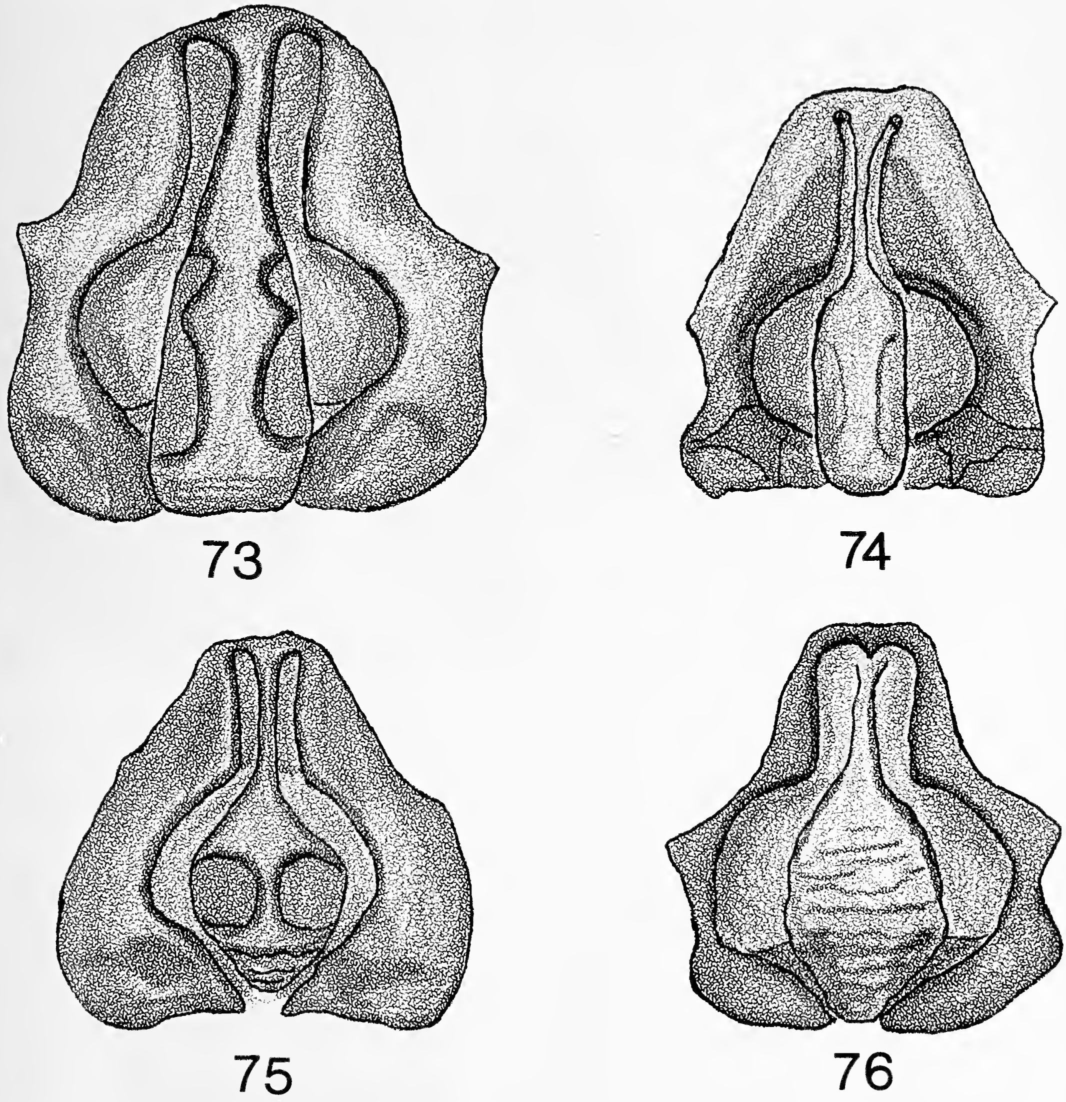
Figures 67–72.—Epigyna of *Pardosa*, modica group. 67. *P. bucklei*. 68. *P. albomaculata*. 69. *P. confusa*. 70. *P. tetonensis*. 71. *P. groenlandica*. 72. *P. dromaea*.



Figures 73–76.—Epigyna of *Pardosa*, modica group. 73. *P. sinistra*. 74. *P. crassistyla*. 75. *P. anomala*. 76. *P. vogelae*.

Base of embolus wide, apical portion broad and curved apically, tip broad and bifid (Fig. 79) . . . . *Pardosa confusa*

5. Palea with a large, strongly wrinkled pillow-like structure on most of its apical margin, and a somewhat L-shaped, sclerotized structure medially (Fig. 80) . . . . . . *Pardosa anomala*

Pillow-like structure on margin of palea smaller and not strongly wrinkled, sclerotized structure on palea slender basally, expanding to a large oval apically (Figs. 81–83) 6

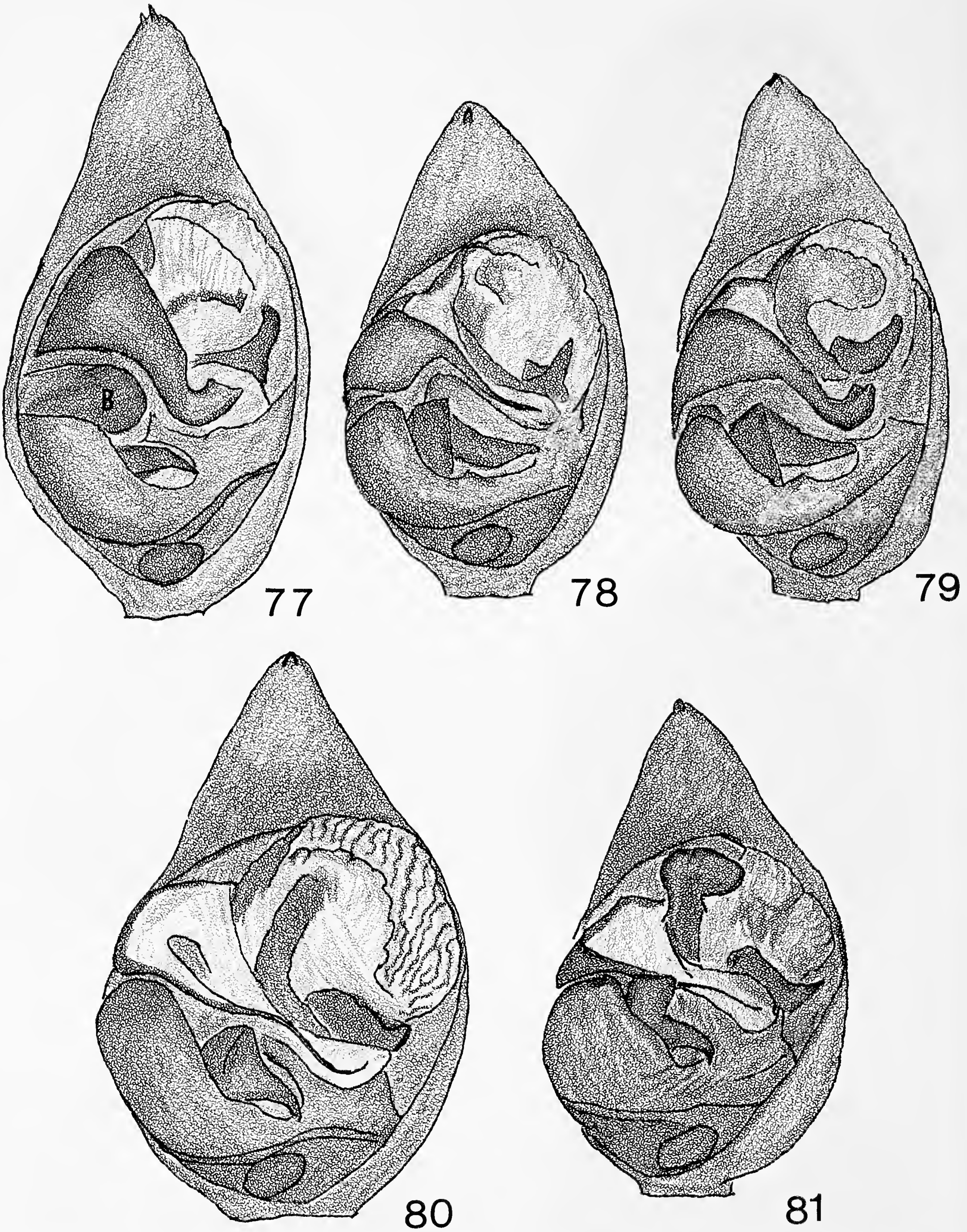
6. Median apophysis block-like, stocky, and truncate (Fig. 81) . . . . *Pardosa labradorensis*

Median apophysis triangular or pyramidal 7

7. Terminal apophysis somewhat horizontal with basal hump and apical edge of lateral extension straight and ending in slight point (Fig. 82) . . . . *Pardosa modica*

Terminal apophysis somewhat horizontal with basal hump and apical edge of lateral extension with 2 or 3 small bumps (Fig. 83) . . . . *Pardosa ourayensis*

8. Lateral bands of carapace indistinct or a series of small spots 9



Figures 77–81.—Palpi of *Pardosa*, modica group. 77. *P. crassistyla*. 78. *P. tetonensis*. 79. *P. confusa*. 80. *P. anomala*. 81. *P. labradorensis*. B, bulbous structure.

Lateral bands of carapace as 3 or 4 tan or yellowish segments 13
9. Median apophysis rounded, basal spur curved apically, looks like a bird's head (Fig. 84) .... *Pardosa vogelae*
Median apophysis does not look like a bird's head 10
10. Base of embolus not heavily sclerotized; distal portion slender, hair-like (Figs. 85–86) .. 11

Base of embolus broadly sclerotized, distal portion slender but not hair-like (Figs. 87–88) . . 12

11. Total length < 7 mm; tip of basal spur of median apophysis blunt, squarish (Fig. 85) . . . . *Pardosa wyuta*

Total length > 8 mm; tip of basal spur a sharp curved point (Fig. 86) . . . . *Pardosa sinistra*

12. Median apophysis rounded apically; occurs in Maine and New Hampshire (Fig. 87) . . . . *Pardosa albomaculata*

Median apophysis triangular, tip pointing apically; occurs in Washington and Oregon (Fig. 88) . . . . *Pardosa lowriei*

13. Basal spur of median apophysis larger than median apophysis, arises from apical edge of apophysis, with a broad triangular tip; terminal apophysis a sharply pointed horn (Fig. 89) . . . . *Pardosa wasatchensis*

Basal spur of median apophysis a longish slender hook arising below apical edge of apophysis (Figs. 90–93) 14

14. Distal part of embolus somewhat broad and truncate, tip slightly transparent; sclerotized oval structure on palea mostly concealing pillow-like structure (Fig. 90) . . . *Pardosa bucklei*

Distal part of embolus slender; exposed, wrinkled pillow-like structure bordering edge of sclerotized oval structure on palea 15

15. Large sclerotized process on palea (P in Fig. 92) curving retrolaterally between embolus and terminal apophysis (t in Fig. 92) with an angular ridge throughout its length 16

Large sclerotized process on palea curving retrolaterally between embolus and terminal apophysis with a smoothly rounded ridge (Fig. 91) . . . . *Pardosa tristis*

16. Spider 9 mm long or larger; higher elevations, alpine; palp as in Fig. 92 . . . . *Pardosa groenlandica*

Spider around 8 mm long; lower elevations, great plains, cobbley river sides; palp as in Fig. 93 . . . . *Pardosa dromaea*

Pardosa albomaculata Emerton 1885
Figs. 68, 87; Map 7

Pardosa tristoides Chamberlin & Ivie 1947:22; Kronestedt 1975:218 (= *Pardosa albomaculata*)

Diagnosis.—The spiders are a reddish brown with a narrow yellow median stripe on the carapace. The epigynum of *P. albomaculata* is characterized by a slender septum with a triangular base. Small random wrinkles cover the floor of cavity. Oval cavity sclerites lie on the basal side of cavity. The lateral bands on the carapace of male *P. albomaculalta* are reduced to three yellow spots. The base of embolus is heavily sclerotized and distal portion is slender but not hair-like. The median apophysis is pyramidal but rounded apically.

Remarks.—This spider is found in Maine and New Hampshire at higher elevations. The palpal morphology is very similar to *P. lowriei*, which occurs in the Pacific Northwest.

Distribution.—New Hampshire, Maine; Canada, Alaska (Dondale & Redner 1984: map 50; Kronestedt 1975: fig. 9).

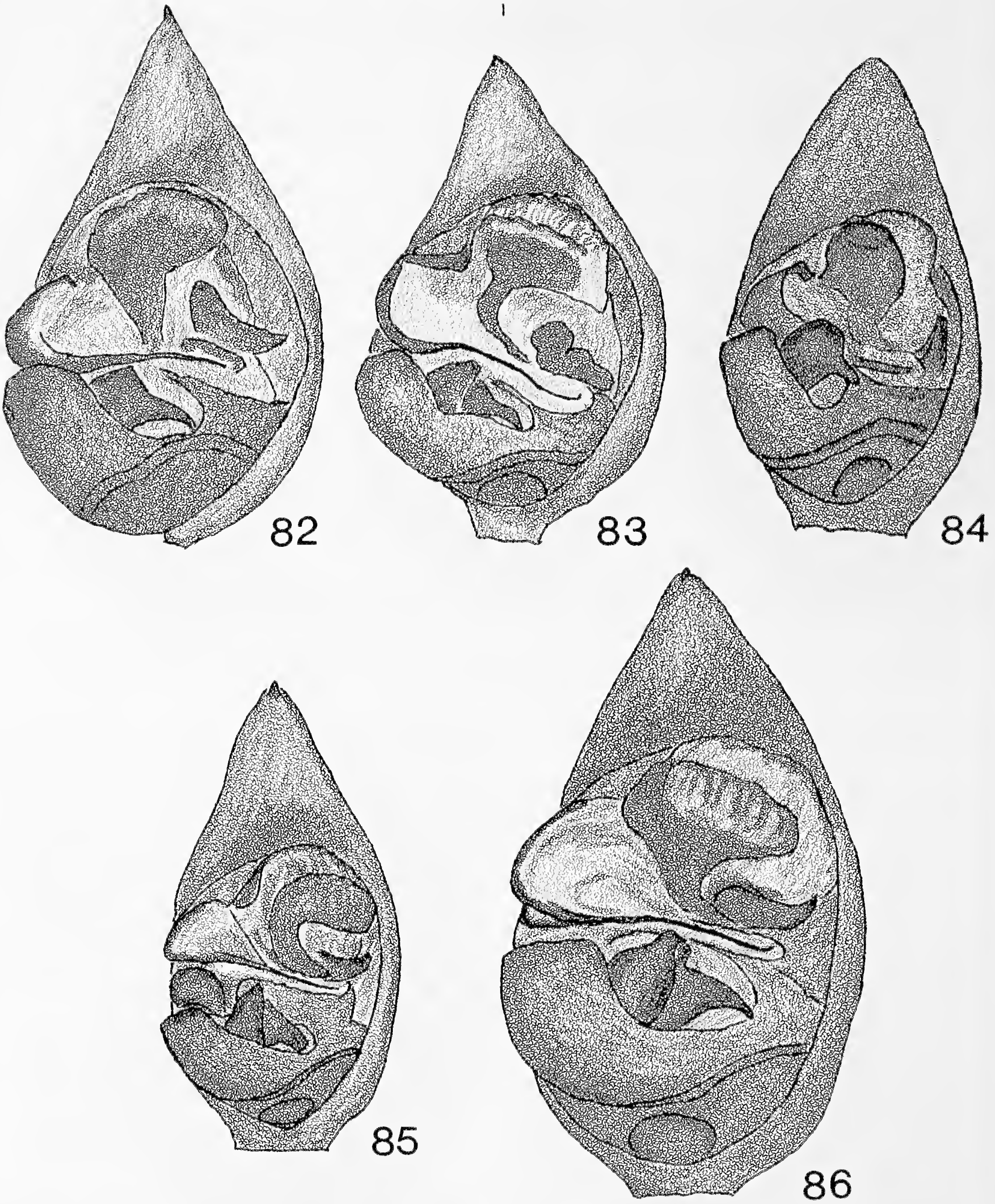
Pardosa anomala Gertsch 1933
Figs. 75, 80; Map 7

Diagnosis.—The pale lateral bands on the carapace are unbroken by darker color. The basal half of the epigynal septum is a broad oval covering most of the cavities. Large semicircular septal pockets are inserted into the sides of the oval. The palea of the male palp is unique with a large, strongly wrinkled pillow-like structure in its apical margin. Males of *P. anomala* can be distinguished from all other *Pardosa* by lateral bands of the carapace unbroken, slender embolus with hair-like tip, palea with large strongly wrinkled pillow-like structure in apical margin.

Distribution.—Montana, Wyoming, Utah, Colorado; Canada (Dondale & Redner 1990: map 41; pers. obs.).

Pardosa bucklei Kronestedt 1975
Figs. 67, 90; Map 7

Diagnosis.—*Pardosa bucklei* is one of the smaller species in the modica group. The body length of females is 7–9 mm, that of males is 6–7.5 mm. Lateral bands of the carapace are represented by three or four tan patches The septum of the epigynum is slender except for triangular base. The floor of cavity has faint random wrinkles and small cavity sclerites situated laterally and pointing toward the septum. The base of the embolus is broad and sclerotized. The distal portion of embolus somewhat



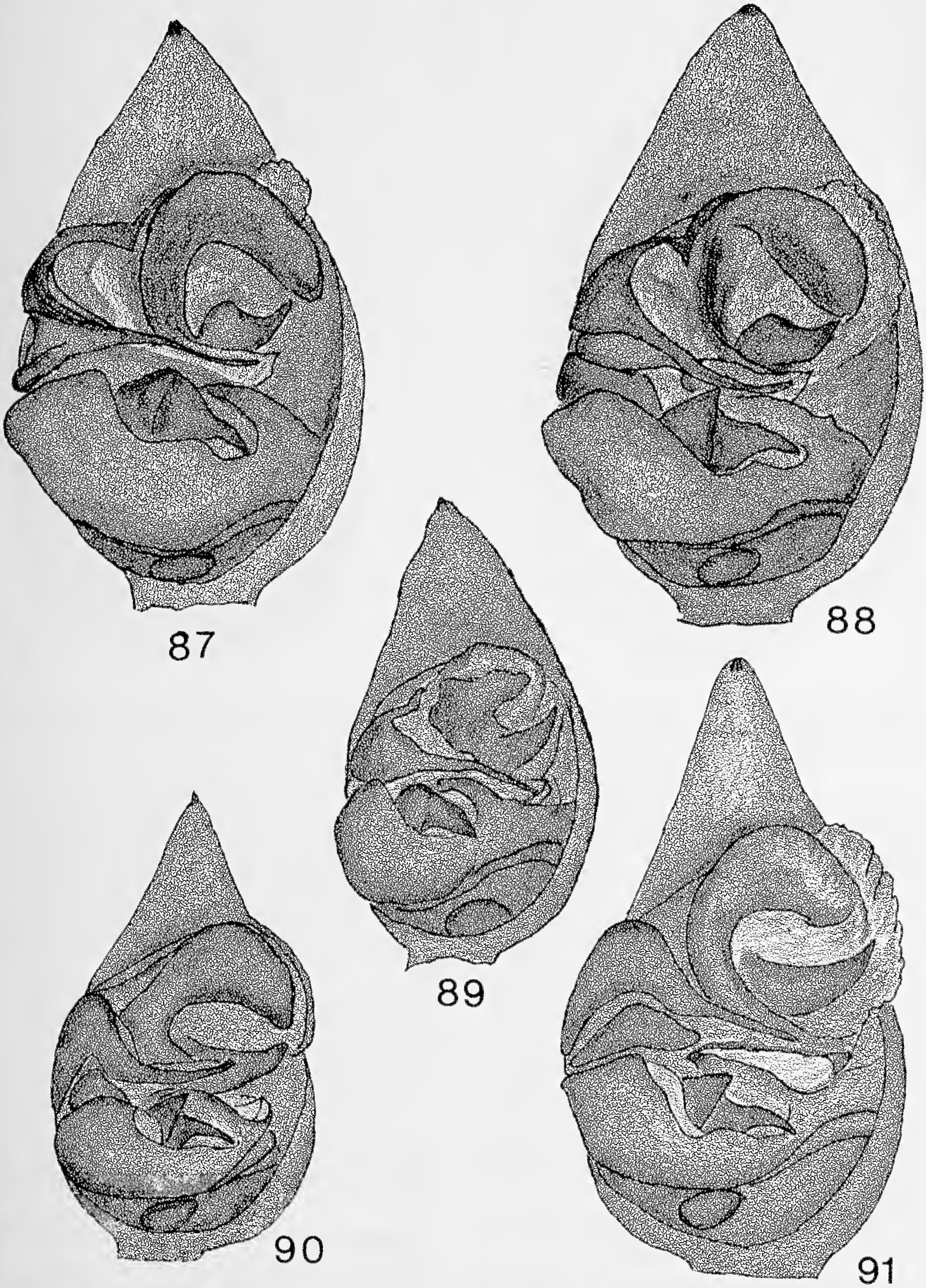
Figures 82–86.—Palpi of *Pardosa*, modica group. 82. *P. modica*. 83. *P. ourayensis*. 84. *P. vogelae*. 85. *P. wyuta*. 86. *P. sinistra*.

broad and truncate. The tip slightly transparent. The pillow-like structure of the palea is mostly concealed by a sclerotized structure.

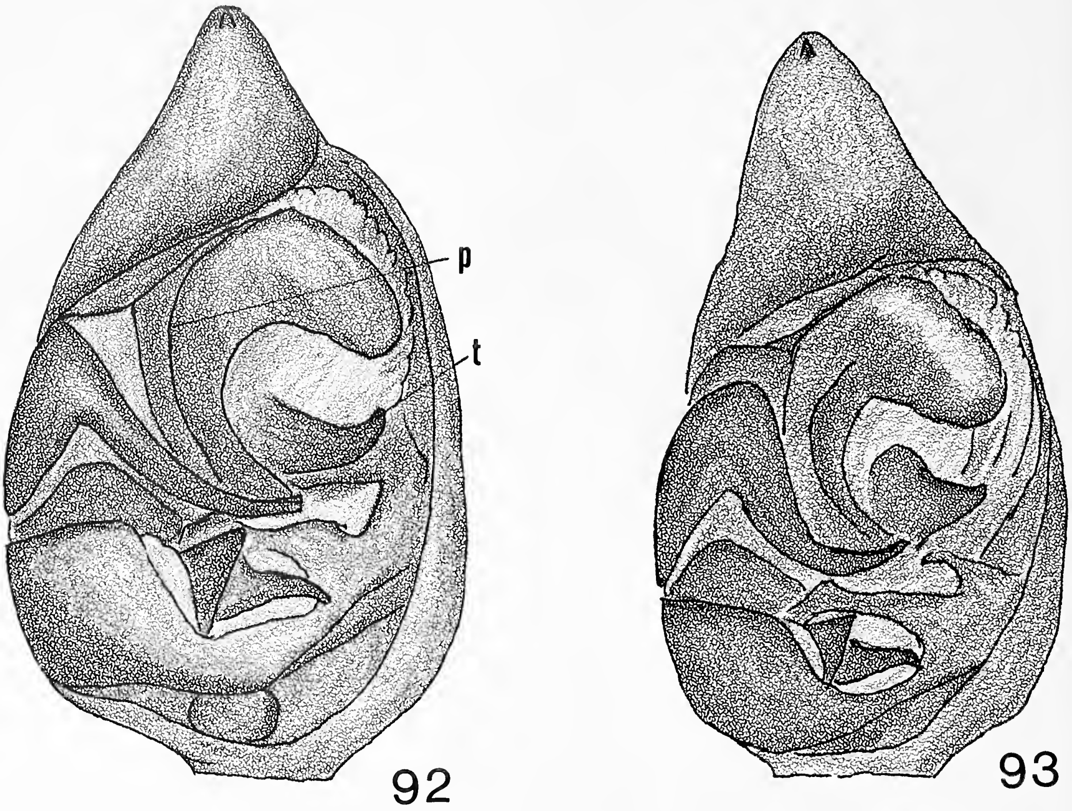
Distribution.—Oregon, California, Idaho, Montana, Wyoming, Utah, Colorado, Arizona, New Mexico, Nebraska; Canada (Dondale 1999: fig. 17).

Pardosa confusa Kronestedt 1988
Figs. 69, 79; Map 7

Diagnosis.—The average body length of females is 6.5 mm, the average length of males is 6.2 mm. The pale lateral bands of carapace are unbroken by darker color. The



Figures 87–91.—Palpi of *Pardosa*, modica group. 87. *P. albomaculata*. 88. *P. lowriei*. 89. *P. wasatchensis*. 90. *P. bucklei*. 91. *P. tristis*.



Figures 92–93.—Palpi of *Pardosa*, modica group. 92. *P. groenlandica*. 93. *P. dromaea*. p, paleal process. t, terminal apophysis.

basal expanded portion of the epigynum is 2/3 the length of the of septum. It is a narrow rectangle with rectangular septal pockets. Cavity sclerites are very small or absent. *Pardosa confusa* and *P. tetonensis* are sister species. The cavity rim is crisply defined in *P. confusa* and softly rounded in *P. tetonensis*. The base of the embolus of the palp of *P. confusa* is broad and sclerotized. The distal portion is broad, and the tip is bifid and curved apically. In *P. tetonensis* the distal portion of the embolus of is very slender and the tip is not turned apically.

Distribution.—Oregon, Utah, Colorado (Kronestedt 1988: 419–420).

Pardosa crassistyla Kronestedt 1988
Figs. 74, 77; Map 8

Diagnosis.—Pale lateral bands of carapace unbroken by darker color. The epigynal cavities of *P. crassistyla* large and semicircular with heavily sclerotized rims. The base of the septum is rounded. The cavity arms and paired hoods are very narrow. The most conspicuous feature of the male palp is a bulbous structure between base of embolus and the median apophysis. The base of the embolus is broad and sclerotized. The short median apophysis does not extend apical to the basal spur.

Distribution.—Oregon, California, Idaho, Montana, Wyoming, Utah, Colorado (Kronestedt 1988: fig. 10; pers. obs.).

Pardosa dromaea (Thorell 1878)
Figs. 72, 93; Map 8

Pardosa nebraska Chamberlin & Ivie 1942:30; Dondale & Redner 1990:209 (=*Pardosa dromaea*)

Diagnosis.—Lateral band of carapace consists of a series of pale blotches. *Pardosa dromaea* is a sister species of *Pardosa groenlandica*. The basal half of the epigynal septum is a long rectangle with rectangular septal pockets. *Pardosa dromaea* may differ from *P. groenlandica* by the position cavity sclerites,

Map 7.—State records for *P. albomaculata* (✹), *P. anomala* (★), *P. bucklei* (☆), *P. confusa* (❂), *P. tetonensis* (❖).

which abut the septum, but may not in *P. groenlandica*. Males of *P. dromaea* can be distinguished by the pyramidal median apophysis and the basal spur shaped like a long slender hook. The large sclerotized structure of the palea has an angular ridge.

Remarks.—Genital morphology is not useful in separating *P. dromaea* from *P. groenlandica*. *Pardosa dromaea* is smaller than *P. groenlandica*. The body length of females of *P. dromaea* is 7.6–9.7 mm; length of males 7.2–8.8 mm. The body length of *P. groenlandica* females is 8.2–10.6 mm and the length of males is 8.1–9.4 mm. *Pardosa dromaea* lives at lower elevations, foothills and plains. The species is regarded as a member of the Great Plains fauna (Dondale 1999:444).

Distribution.—Montana, Wyoming, Colorado, New Mexico, North Dakota, Nebraska, Iowa, Minnesota, Wisconsin; Canada (Dondale 1999: fig. 16).

Pardosa groenlandica (Thorell 1872)

Figs. 71, 92; Map 8

Lycosa iracunda Thorell 1877:514; Dondale 1999: 439 (= *Pardosa groenlandica*)

Diagnosis.—*Pardosa groenlandica* is a sister species of *Pardosa dromaea*. See "Diagnosis" and "Remarks" above in *P. dromaea*.

Remarks.—*Pardosa groenlandica* lives at higher elevations, forest to tundra.

Distribution.—Idaho, Montana, Wyoming, Utah, Colorado, Minnesota, Wisconsin, Michigan, Maine; Canada, Alaska (Dondale & Redner 1990: fig. 16).

Pardosa labradorensis (Thorell 1875)

Figs. 61, 81; Map 8

Pardosa lenghi Gertsch 1933:23, figs. 24, 34; Kronestedt 1981:119 (= *Pardosa labradorensis*)

Diagnosis.—Spider is lightly colored with wide yellow lateral bands on the carapace unbroken by darker color. The epigynum is wider than long. The cavities have large, triangular cavity sclerites that lie on the basal ends of the cavities. A transverse diamond-shaped expansion of the septum at the apical end of the cavities conceals the basal end of the cavity arms. This feature is unique in the modica group. The median apophysis of the male palp is block-like, stocky, and truncated. The basal spur is long and stout with the tip bent basally. The palea bears large sclerotized oval.

Distribution.—New Hampshire; Canada

Map 8.—State records for *P. crassistyla* (❖), *P. dromaea* (☆), *P. groenlandica* (✸), *P. labradorensis* (◎), *P. lowriei* (✢), *P. tristis* (★).

(Dondale & Redner 1990: map 44; Kronestedt 1981: map 1).

Pardosa lowriei Kronestedt 1975
Figs. 66, 88; Map 8

Diagnosis.—Spiders are dark brown, lateral bands on carapace represented by three or four paler spots. The floor of the epigynal cavity features serial ridges or wrinkles. These ridges extend posterio-laterally from the septum without an apical arch. The base of the septum is a long thin triangle with septal pockets. The epigynum is very similar to *P. tristis*, but in *P. tristis* the wrinkles have an apical arch. The median apophysis of the male palp is pyramidal with an acute tip. The basal spur is long and slender with the tip turned basally.

Remarks.—Palpal morphology is very like that of *P. albomaculata*, which occurs in Maine and New Hampshire. *Pardosa lowriei* occurs in the Pacific Northwest.

Distribution.—Oregon, Washington; Canada, Alaska (Dondale & Redner 1990: map 52; Kronestedt 1975: fig. 9; pers. obs.).

Pardosa modica (Blackwall 1846)
Figs. 63, 82; Map 9

Diagnosis.—The lateral band on the carapace is entire, unmarked by darker lines. *Pardosa modica* and *P. ourayensis* are sister species. The epigynum is wider than long. The septum is slender with a transverse diamond-shaped expansion at the apical end of the cavities with lateral ridges that trail basally across the cavity floor. V-shaped cavity sclerites lie on the basal end of the cavity. In *P. modica*, one branch of the V does not extend to the diamond-shaped expansion along the septum as it does in *P. ourayensis*. Males of *P. modica* have an embolus which is slender and hair-like. The palea has a pillow-like structure apically which is not strongly wrinkled, but with a large sclerotized oval basally. The median apophysis is pyramidal. The terminal apophysis points laterally. In *P. modica* it has a basal hump and a straight margin on the distal part. In *P. ourayensis* it has a basal hump and a bumpy margin on the distal part.

Distribution.—Idaho, Montana, Wyoming, Colorado, Michigan, New York, Connecticut; Canada (Dondale 1999: map 44; Kronestedt 1981:119; pers. obs.).

Pardosa ourayensis Gertsch 1933
Figs. 62, 83; Map 9

Diagnosis.—*Pardosa ourayensis* and *P. modica* are sister species Refer to "Diagnosis" in *P. modica*.

Distribution.—Colorado, Montana (pers. obs.)

Pardosa sinistra (Thorell 1877)
Figs. 73, 86; Map 9

Pardosa cascadae Schenkel 1951:25; Kronestedt 1981:121 (= *Pardosa sinistra*)

Diagnosis.—The shape of the septum distinguishes females of *P. sinistra*. The base is about 1/3 the width of the basal end of the epigynum It tapers apically to the hoods smoothly ending in a short neck. The septal pocket is bilobed, with the basal lobe about three times as long as the apical lobe. The lateral bands of the carapace of *P. sinistra* males are indistinct or absent. The base of embolus is sclerotized but the tip is slender and hair-like. The median apophysis is pyramidal with a basal spur wide basally and tip pointed. The body length is greater than 8 mm. The palp of *P. sinistra* is very like that of *P. wyuta*, but the tip of the basal spur is pointed not truncate.

Distribution.—Washington, Montana, Colorado; western Canada (Kronestedt 1981: 123).

Pardosa tetonensis Gertsch 1933
Figs. 70, 78; Map 7

Diagnosis.—The pale lateral bands of the carapace are entire. Females average 7.2 mm, males 6.3 mm. *Pardosa tetonensis* and *P. confusa* are sister species. The basal expanded portion of the epigynum is 2/3 the length of the septum. It is a narrow rectangle with rectangular septal pockets. The cavity rim is softly rounded in *P. tetonensis* and crisply defined in *P. confusa*. Small cavity sclerites lie near the basal end of the cavity. The base of the embolus of the palp of *P. tetonensis* is broad and sclerotized. The distal portion is very slender and the tip is not turned apically. The distal portion of the embolus of *P. confusa* is broad, and the tip is bifid and curved apically.

Distribution.—Montana, Wyoming, Colorado (Kronestedt 1988: 412–413; pers. obs.).

Pardosa tristis (Thorell 1877)
Figs. 65, 91; Map 8

Diagnosis.—Lateral bands on the carapace are represented by three paler segments. The body length of females is 8.2–10.6 mm, that of males is 8.0–9.3 mm. The epigynum of *P. tristis* is very similar to the epigynum of *P. lowriei*. The septum is slender with a long triangular base. The septal pockets are also long and slender. The floor of the cavity features serial ridges or wrinkles, which extend laterally with a conspicuous apical arch near the septum. The ridges in the epigynum of *P. lowriei* are straight. The male palp of *P. tristis* is morphologically close to the palps of *P. dromaea* and *P. groenlandica*. The median apophysis is pyramidal with a long basal spur. The tip of the spur is pointed basally. The terminal is a curved horn with the tip pointing apically. *Pardosa tristis* differs from *P. dromaea* and *P. groenlandica* by the large sclerotized structure on the palea that curves laterally between the embolus and the terminal apophysis. It is smoothly rounded in *P. tristis*, but angular in *P. dromaea* and *P. groenlandica*.

Distribution.—Washington, Oregon, California, Idaho, Nevada, Montana, Wyoming, Utah, Colorado, Arizona, New Mexico; Canada (Dondale 1999: fig. 17).

Pardosa vogelae Kronestedt 1993
Figs. 76, 84; Map 9

Diagnosis.—Pale lateral band on the carapace is entire. The genitalia of this species are very distinctive. The basal expanded portion of the epigynal septum is an oval as long as the cavities, with a narrow rounded base, sides strongly convex, narrowing between the cavity arms. The oval is covered with transverse wrinkles. The short, rounded median apophysis of the male palp looks like a bird's head.

Distribution.—Utah (Kronestedt 1993: fig. 22).

Pardosa wasatchensis Gertsch 1933
Figs. 64, 89; Map 9

Diagnosis.—The pale lateral band of the carapace is crossed by two dark streaks. The epigynal septum is slender for most of its length with a slight expansion at the apical end of the cavities. The base is short and wide, like an inverted T, with transverse septal pockets. The hoods are wide and flat, not arched. The short median apophysis of the male palp is shorter than the wide basal spur, which arises from the apical edge of the median apophysis. The tip is a broad triangle pointing basally. The terminal apophysis a sharply pointed horn directed apically.

Distribution.—Washington, Oregon, Ida-

Map 9.—State records for *P. modica* (❂), *P. ourayensis* (✸), *P. sinistra* (❖), *P. vogelae* (✛), *P. wasatchensis* (★), *P. wyuta* (☆).

ho, Montana, Wyoming, Utah, Colorado (Kronestedt 1993: fig. 22).

Pardosa wyuta Gertsch 1933
Figs. 60, 85; Map 9

Diagnosis.—The pale lateral band of the carapace is represented by several blotches. The epigynum of *P. wyuta* is atypical for the modica group in lacking distinct cavity arms. The septum apical to paired oval cavities is represented by a ridge flanked by a pair of furrows, instead of the characteristic troughs, which extend to the paired hoods. The hoods are flat and wide, not arched. The median apophysis is pyramidal with the basal spur somewhat stout and its tip is truncated. The base of the embolus not heavily sclerotized and tip hair-like. The palp of *P. wyuta* is very like that of *P. sinistra* but the tip of the basal spur in *P. wyuta* is truncate not pointed.

Distribution.—Washington, Idaho, Montana, Wyoming, Utah, Colorado; western Canada (Dondale & Redner 1990: map 49; pers. obs.).

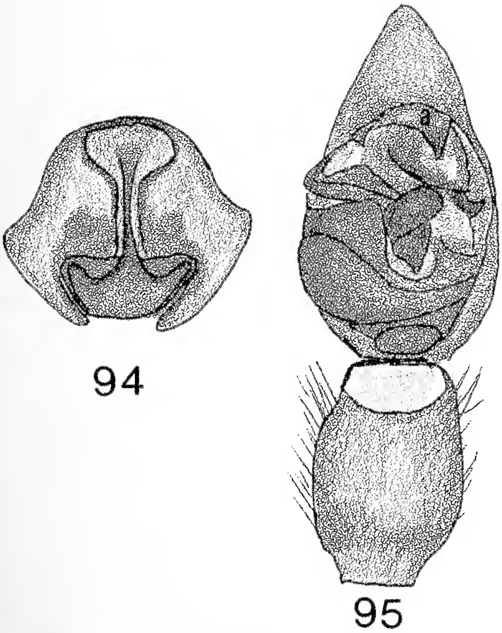
Moesta Group

Remarks.—The moesta group consists of one species in North America. The group is characterized by the genitalia. The epigynum (Fig. 94) features an apical extension of the cavity to the edge of the epigynum where it widens to a transverse oval. The cavity surrounds the narrowed apical portion of the septum. The base of the septum is a trapezoidal shape with transverse cavity sclerites on the apical edge. The basal portion of the cavity has an indistinct rim and is mostly covered by the expanded base of the septum. The male palp (Fig. 95) is small and compact. The median apophysis is blunt and rounded apically. The basal spur, a fairly large triangular shape, arises medially and is directed basally. The palea has a prominent sclerotized hook directed basally.

Pardosa moesta Banks 1892
Figs. 94, 95; Map 3

Diagnosis.—The spiders are small, the body length 4–6 mm. The female carapace is brown with lighter median area that is not a well-defined band. The abdomen is marked with a diamond apically and lighter paired marks posteriorly. The epigynum and palp are as described above. The male carapace is glabrous and shiny chestnut brown color which makes this spider instantly recognizable. The

Map 10.—State records for *P. dorsalis* (★), *P. dorsuncata* (☆), *P. uncata* (❖), *P. gothicana* (◎).



Figures 94–95.—Genitalia of *Pardosa*, moesta group, *P. moesta*. 94. Epigynum. 95. Palp. a, apical process.

tibia of the male pedipalp is barrel-shaped and nearly as wide as the palp.

Remarks.—*Pardosa moesta* is widely distributed and relatively common at lower elevations.

Distribution.—Washington to New England, West Virginia, Tennessee; Canada, Alaska (Dondale & Redner 1987: map 4).

Nigra Group

Remarks.—The nigra group consists of eight species in the contiguous United States, five of these also occur in Canada, and six Palearctic species. The group is characterized by the genitalia. Cavities are not apparent on the epigynum. The base of the septum is expanded, rectangular or somewhat triangular, with transverse wrinkles. The apical portion of the septum is a narrow trough flanked by ridges, extending to the end of the epigynum, where it forms the hood. Conspicuous lateral swellings flank the expanded base of the septum.

The male palp is immediately recognizable by the jutting tegulum that extends from the cymbium almost horizontally. The bulb is very open, and the median apophysis somewhat strap-like and also leaning away from bulb. The basal spur is curved basally and generally about half the length of the median apophysis. The terminal apophysis is a twig-like process arising from the medial end of the palea and traversing to the edge of the cymbium (Fig. 108).

The general color pattern is low contrast between dark and lighter colors. The median band of the carapace, when present, has undulating edges; lateral pale bands usually not apparent. The abdomen has a broad median pale area.

KEYS TO USA SPECIES OF THE NIGRA GROUP

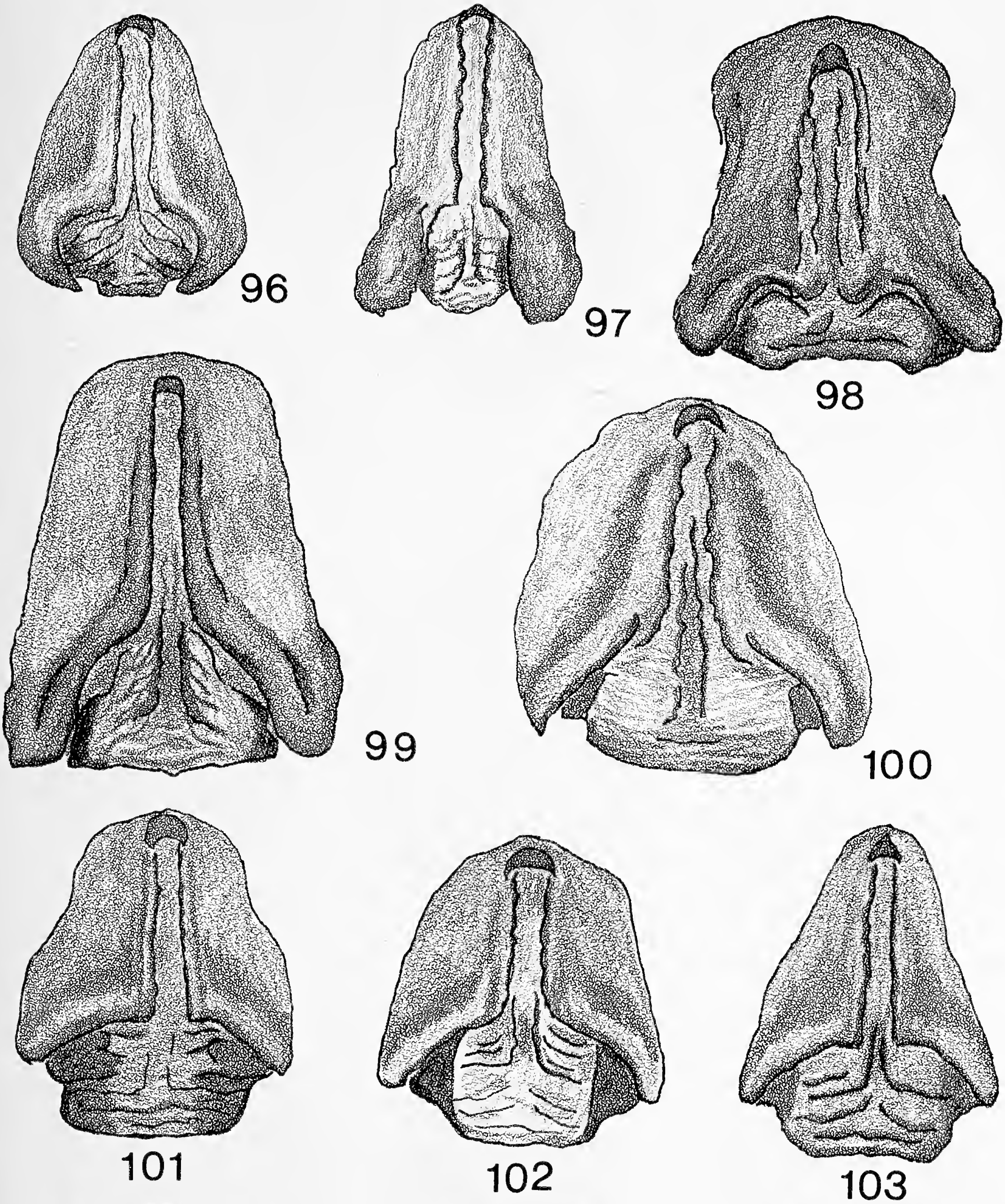
Females

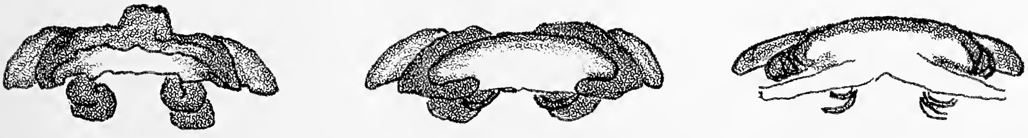
1. Lateral swellings of the epigynum converging basally (Fig. 96) . . . . *Pardosa uintana*
   Lateral swellings parallel or diverging basally 2
2. Lateral swellings parallel, extending slightly basal to expanded base of septum (Fig. 97) . . . . *Pardosa gothicana*
   Lateral swellings diverging basally (Figs. 98–103) 3
3. Lateral swellings extending basally nearly as far as base of septum (Figs. 98–100) 4
   Expanded base of septum extending basally much further than lateral swellings (Figs. 101–103) 6
4. Expanded base of septum with lateral lobes (Fig. 98) . . . . *Pardosa hetchi*
   Expanded base of septum without lateral lobes 5
5. Epigynum much longer than wide (Fig. 99) . . . . *Pardosa rainieriana*
   Epigynum nearly as wide as long (Fig. 100) . . . . *Pardosa mackenziana*
6. Copulatory tubes broad, not looped (in posterior view) (Figs. 101, 104) . . . . *Pardosa dorsuncata*
   Copulatory tubes coiled (in posterior view) (Figs. 102, 103, 105, 106) . . . . *Pardosa dorsalis* and *Pardosa uncata*

Note.—Females of *P. dorsalis* and *P. uncata* cannot be identified unless collected with males. In fact, it is difficult to separate females of *P. dorsalis*, *P. dorsuncata*. and *P. uncata* because the copulatory tubes are difficult to see without dissection. Furthermore, the range of *P. dorsuncata* and *P. dorsalis* are almost completely congruent, and both share much of the range of *P. uncata*. Individual variation in epigynal structure within a species probably exceeds variation between these species.

Males

1. Carapace dark without discrete median pale area 2
   Carapace with tan median band or at least a defined pale area 3
2. Body length < 5 mm; spider collected in Colorado; palp as in Fig. 108 . . . . *Pardosa gothicana*
   Body length > 6 mm; spider collected in the Pacific Northwest; palp is in Fig. 109 . . . . *Pardosa rainieriana*
3. Median apophysis spatulate, tip rounded, wider than base; spider collected in interior California (Fig. 110) . . . . *Pardosa hetchi*
   Tip of median apophysis truncate, with blunt point, not wider than base 4
4. Distal half of embolus thin, hair-like (Figs. 111–113) 5
   Distal half of embolus flattened, tapering but not hair-like (Figs. 114–15) 7
5. Tip of median apophysis truncate, erose (Fig. 111) . . . . *Pardosa mackenziana*
   Tip of median apophysis pointed or blunt with off-center point 6
6. Median apophysis 3 to 4 times as long as basal spur (Fig. 112) . . . . *Pardosa dorsalis*
   Median apophysis not more than twice as long as basal spur (Fig. 113) . . . . . *Pardosa uncata*
7. Tip of embolus flat and curved 360 degrees like a corkscrew (Fig. 114) . . . . *Pardosa uintana*
   Tip of embolus flat and only slightly curved (Fig. 115) . . . . *Pardosa dorsuncata*





Figures 96–106.—Epigyna of *Pardosa*, nigra group. 96. *P. uintana*. 97. *P. gothicana*. 98. *P. hetchi*. 99. *P. rainieriana*. 100. *P. mackenziana*. 101. *P. dorsuncata*. 102. *P. dorsalis*. 103. *P. uncata*.

Figures 104–106.—Epigyna, posterior view. 104. *P. dorsuncata*. 105. *P. dorsalis*. 106. *P. uncata*.

Pardosa dorsalis Banks 1894
Figs. 102, 105, 112; Map 10

Diagnosis.—The lateral swellings of the epigynal plate do not extend basal of the expanded base of the septum. The expanded base is somewhat rectangular and covered with transverse wrinkles. In posterior view, the copulatory tubes are coiled but *P. dorsalis* cannot be distinguished from *P. uncata*. The embolus of the male palp is whip-like in distal half. The median apophysis is three to four times longer than basal spur. The long slender terminal apophysis is untoothed.

Distribution.—Washington, Oregon, Idaho, Montana, Wyoming, Utah, Colorado, Arizona; Canada (Lowrie & Dondale 1981: map 5).

Pardosa dorsuncata Lowrie & Dondale 1981
Figs. 101, 104, 115; Map 10

Diagnosis.—Spiders are light reddish-brown, and the median area on the abdomen is yellow ochre. The lateral swellings of the epigynal plate do not extend basal of the expanded base of the septum. The expanded base is somewhat rectangular and covered with transverse wrinkle. In posterior view the copulatory tubes are broad and not looped. The embolus of the male palp is flattened and its tip is curved only slightly. The median apophysis is blunt and the tip slightly widened. The terminal apophysis is very slender and minutely toothed.

Distribution.—Arizona, California, Colorado, Montana, Oregon, Utah, Washington, Wyoming; Canada, Alaska (Lowrie & Dondale 1981: map 2; pers. obs.).

Pardosa gothicana Lowrie & Dondale 1981
Figs. 97, 108; Map 10

Diagnosis.—The body length of females is 4.5–5.5 mm, and the body length of males 3.5–4.5 mm. The body is dark brown. The carapace and abdomen are without pale median areas. The epigynum is narrow. The lateral swellings are approximately parallel and bulbous. They extends basally slightly more than the expanded base of the septum. The embolus of the male palp is flattened and not whip-like. The tip of the median apophysis is somewhat blunt and erose. The palpal morphology is very similar to that of *P. rainieriana*.

Remarks.—*Pardosa gothicana* is smaller than *P. rainieriana*, and the two species are geographically separated. *Pardosa gothicana* has been collected only in Colorado and *P. rainieriana* is found in the Pacific Northwest.

Distribution.—Colorado (Lowrie & Dondale 1981: map 3).

Pardosa hetchi Chamberlin and Ivie 1942
Figs. 98, 110; Map 11

Diagnosis.—The spider is brown to reddish brown. The median band on the carapace is somewhat hourglass shaped, and the lateral pale bands are broken. The abdomen is brown marked with black. Males are darker than females. The transverse base of the epigynal septum is not strongly wrinkled and is lobed laterally. The diverging lateral swellings droop around these lobes. The median apophysis of the male palp is spatulate, wider at the tip than at the base. The embolus is flattened, but narrowed at the tip. The terminal apophysis is also widened at the tip and toothed.

Distribution.—California (Lowrie & Dondale 1981: map 3).

Pardosa mackenziana (Keyserling 1877)
Figs. 100, 111; Map 11

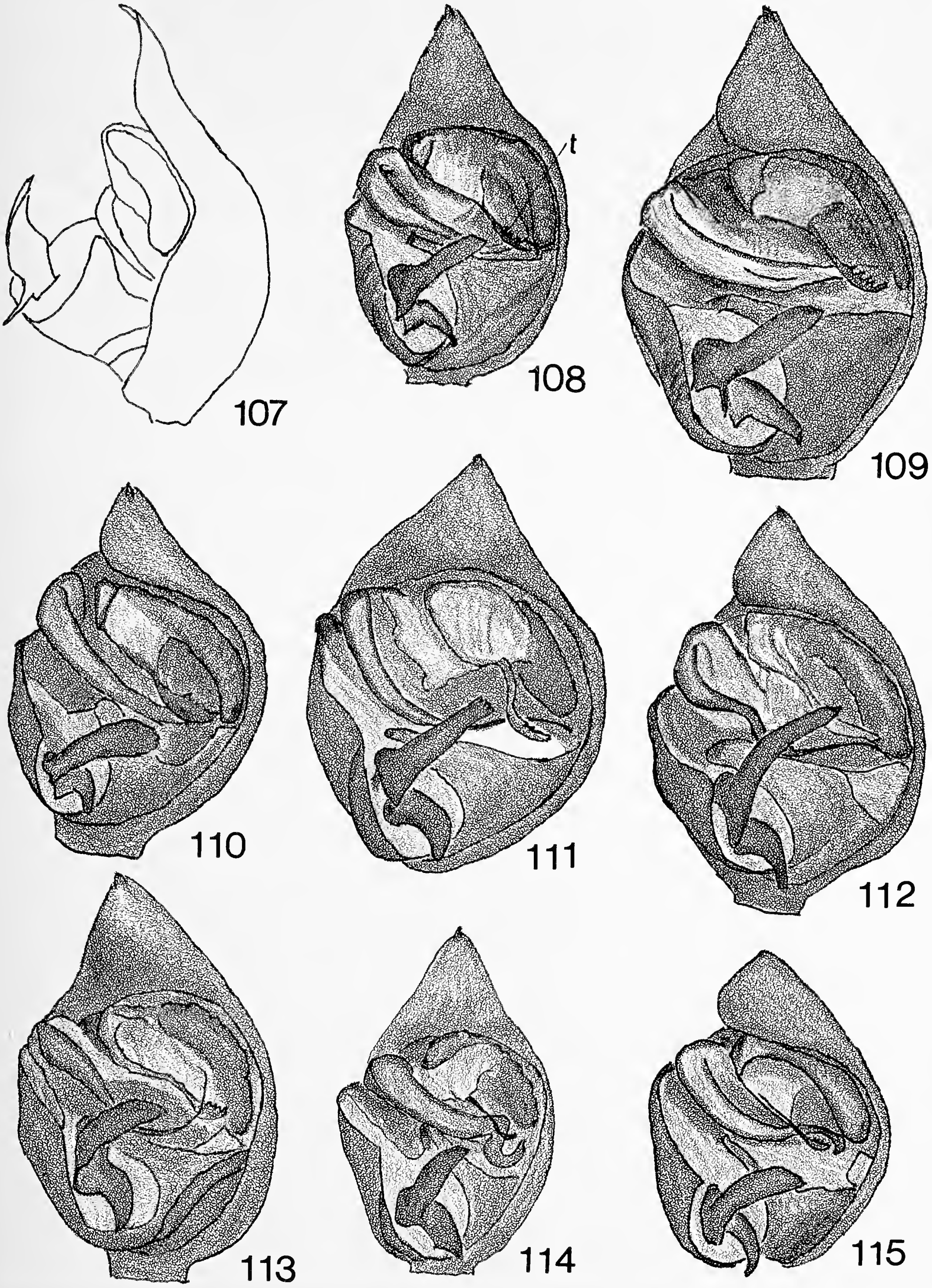
Diagnosis.—These spiders are large, the female body length is 7.4–8.6 mm, the male's is 6.0–7.1 mm. The epigynum is as wide as long. The lateral swellings diverge basally and extend to the basal edge of the septum. Additionally, the lateral swellings extend apically along the septum. The expanded base is more or less rectangular. The median apophysis of the male palp tapers slightly to the tip, which is blunt, and erose with irregular teeth. The distal half of the embolus is whip-like. The terminal apophysis has minute teeth.

Remarks.—This species is common in dryish forests and is widely distributed.

Distribution.—Washington, Oregon, California, Idaho, Montana, Wyoming, Colorado, south Dakota, Minnesota, Wisconsin, Michigan, Connecticut, Rhode Island, Massachusetts, Maine; Canada, Alaska (Lowrie & Dondale 1981: map 4).

Pardosa rainieriana Lowrie & Dondale 1981 Figs. 99, 109; Map 11

Diagnosis.—The color of *P. rainieriana* ranges from dark brown to light brown. Fe-



Figures 107–115.—Palpi of *Pardosa*, nigra group. 107. *P. uncata*, lateral view. Figs. 108–115. Distroventral view. 108. *P. gothicana*. 109. *P. rainieriana*. 110. *P. hetchi*. 111. *P. mackenziana*. 112. *P. dorsalis*. 113. *P. uncata*. 114. *P. uintana*. 115. *P. dorsuncata*. t, terminal apophysis.

Map 11.—State records for *P. hetchi* (✪), *P. mackenziana* (✸), *P. rainieriana* (❖), *P. uintana* (★).

male body length is 8–9 mm, male body length is 7–8 mm. The epigynum is longer than wide. The lateral swellings diverge basally. They extend to the edge of the expanded base of the septum, and at the lateral margin of the epigynum turn abruptly and extend apically for a short distance. The median apophysis of the male palp is broad with a somewhat blunt tip. The basal spur is broad and only slightly curved. The embolus is broad and flat. The terminal apophysis is slender with a toothed tip.

Remarks.—This species is the largest in the nigra group. The palpal morphology of *P. rainieriana* is very similar to *P. gothicana* but size and geography separate them.

Distribution.—Oregon, Washington; Canada (Lowrie & Dondale 1981: map 3).

Pardosa uintana Gertsch 1933
Figs. 96, 114; Map 11

Diagnosis.—Some of the darker brown spiders have conspicuous annulations on the femora. Females of *P. uintana* are the only species in the group in which the lateral swellings of the epigynum converge basally. The male palp is also unique in the group. The tip of the embolus has a 360 degree curve like a corkscrew.

Distribution.—Washington, Oregon, Wyoming, Utah, Colorado, Vermont, New Hampshire, Maine; Canada, Alaska (Lowrie & Dondale 1981: map 1).

Pardosa uncata (Thorell 1877)
Figs. 103, 106, 107, 113; Map 10

Diagnosis.—This species is a brown spider with a median pale area on carapace and the lateral bands are represented by yellow ochre blotches. The lateral swellings of the epigynum of *P. uncata* diverge basally but do not extend as far as the basal edge of the expanded base of the septum. The expanded base is rectangular and strongly wrinkled. In posterior view the copulatory tubes are slender and coiled, as in *P. dorsalis*. The median apophysis of the male palp is short, not more than two times the length of the stout basal spur. The distal half of the embolus is whip-like. The tip of the terminal apophysis is toothed.

Remarks.—Females of *P. uncata* and *P. dorsalis* are not distinguishable. They are also very similar to *P. dorsuncata*, but differ in the copulatory tubes, which are not looped in the latter species.

Distribution.—Montana, Utah, Colorado, Arizona, New Mexico (Lowrie & Dondale 1981: map 6; pers. obs.).

Saltuaria Group

Remarks.—The saltuaria group consists two species in the United States, one of which is Holarctic, and four Palearctic species. The septum and hood are nearly as wide as the epigynum. The cavities open laterally. The median apophysis of the male palp is short, lumpish, and rounded apically. The short straight basal spur arises ventrally and is directed basally. The palea is mostly sclerotized.

KEYS TO USA SPECIES OF THE SALTUARIA GROUP

Females

1. Hood broadly rounded, with center apical to ends, rim continuous; median rim of cavities C-shaped; basal corners of septum curve apically into cavities; cavity sclerites lacking (Fig. 116) . . . . *Pardosa californica*
   Apical rim faint in mid portion giving appearance of paired hoods; basal corners of septum not curving into cavities; small triangular cavity sclerites situated on lateral edges of septum (Fig. 117) . . . . *Pardosa hyperborea*

Males

1. Median apophysis wider than long, short basal spur directed basally; tegular lobe is situated laterally (Fig. 118) . . . . *Pardosa californica*
   Median apophysis is longer than wide, short basal spur directed basally; tegular lobe is situated medially (Fig. 119) . . . . *Pardosa hyperborea*

Pardosa californica Keyserling 1887
Figs. 116, 118; Map 12

Diagnosis.—The colors are strongly contrasting, brown and yellow. The median band on the carapace is somewhat hourglass shaped and the lateral bands are conspicuous. The femora are reddish brown and yellow. The cavities of the epigynum open laterally with no thickened lateral rim, but with a C-shaped median rim. The lateral corners of the expanded base of septum curve into cavities. The median apophysis of the male palp is wider than long and the tegular lobe is situated laterally.

Distribution.—Oregon, California, Idaho, Nevada, Utah; Mexico (Dondale & Redner 1987: map 7).

Pardosa hyperborea (Thorell 1872)
Figs. 117, 119; Map 12

Diagnosis.—Female *P. hyperborea* is a yellowish spider with tan darker markings. The median band on the carapace is very narrow. The abdomen is tan and the legs are yellow without distinct markings. Males are somewhat darker, tan with brown markings. The basal corners of the expanded base of the epigynal septum are rounded. Small triangular cavity sclerites project from the sides of the septum. The median apophysis of the male palp is longer than wide and the tegular lobe is situated medially.

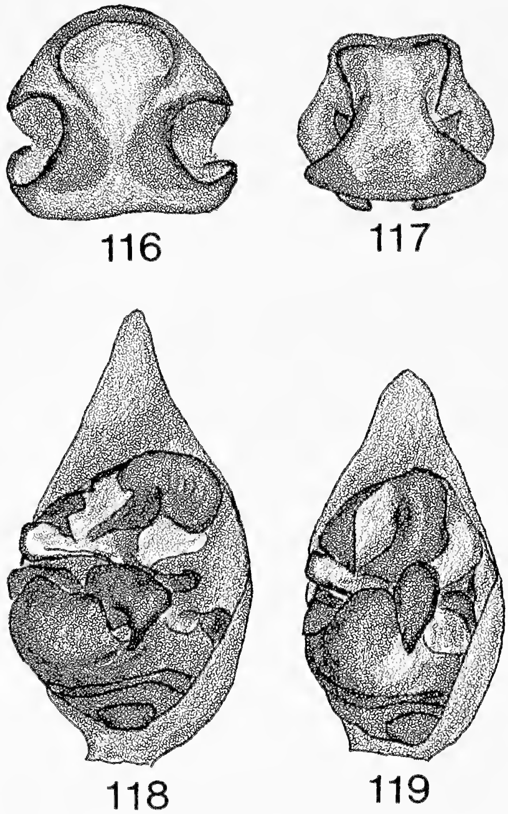
Distribution.—Wyoming, Michigan, New York, Vermont, New Hampshire, Maine; Canada, Palearctic (Dondale & Redner 1987: map 6).

Sternalis Group

Remarks.—The sternalis group consists of six species west of the Mississippi River, and one species south of the Tropic of Cancer. These are among the smaller of *Pardosa* species, with body length of 5–8 mm. The cephalothorax usually has five longitudinal bands unless the spider is dark. The abdomen may have five pairs of light spots posterior to the diamond mark.

The apical part of the septum is a raised ridge ending in a small hood at the margin of the epigynum. Paired oval cavities no greater than 1/3 the length of the plate occur in four of the six species. In these, the septum has an anchor-shaped base and is not wider than a cavity. In *P. orthodox* the cavity is longer and in *P. tuoba* the septum is wider. All six lack cavity sclerites.

The embolus of the male palp curves apically in a slender semicircular arch behind the median apophysis and ends in a thin tip. The median apophysis is long, and somewhat slen-



Figures 116–119.—Genitalia of *Pardosa*, saltauria group. Figs. 116–117. Epigyna. 116. *P. californica.* 117. *P. hyperborea.* Figs. 118–119. Palpi. 118. *P. californica.* 119. *P. hyperborea.*

der. It gently curves to the edge of the cymbium or beyond. The basal spur is short, curved ventrally, the tip pointed or truncate. The terminal apophysis is a slender pointed finger or a knob near the end of the embolus. The palp is similar to the falcifera group palp. Males of the falcifera group bear feathery brushes of fine hair on tarsus and metatarsus I, which sternalis group males lack.

The similarity of epigynal and palpal morphology among the six species in the sternalis group makes difficulties in identifying individuals using genital characters. For the most part, the species occupy different ranges, but there are overlap zones. It is in these zones that species may not be identified with certainly.

Pardosa altamontis ranges from the Pacific Northwest to the Rocky Mountain states. *Pardosa sternalis* is widespread and common in the Rocky Mountain states south into Mexico. *Pardosa vancouveri* occurs in the coastal Pacific Northwest. *Pardosa altamontis* overlaps with *P. sternalis* and may overlap with *P. vancouveri*. Tarsus I, which is swollen in *P. vancouveri* males, separates them from all the other males. The entire dorsum of the cymbium is dark or black in *P. altamontis*, but the tip is always light in *P. sternalis*. Females of these species in overlap zones cannot be identified unless they are collected with males.

Pardosa orthodox occurs in Arizona but is not common. It may overlap with *P. sternalis* and *P. ramulosa*, but *P. orthodox* has distinctive genitalia. The epigynal septum nearly covers the cavities and the tip of the median apophysis is wide not pointed.

Pardosa tuoba is found in California at lower elevations and is almost entirely sympatric with P. *ramulosa*. The width of the epigynal septum distinguishes *P. tuoba*. The palpal structures do not separate the males, but the cymbium of *P. ramulosa* is narrow with a slender tip, while the cymbium of *P. tuoba* is quite wide.

Pardosa ramulosa occurs in California and Nevada and may overlap with *P. sternalis* in the Southwest. Neither palpal morphology nor external epigynal morphology can be used to separate these species, but internal epigynal morphology supports the validity of separate species. The seminal receptacle of females in southern California is bilobed, but in Colorado females the seminal receptor has a single lobe. Dissection is required to view this.

KEYS TO USA SPECIES OF THE STERNALIS GROUP

Females

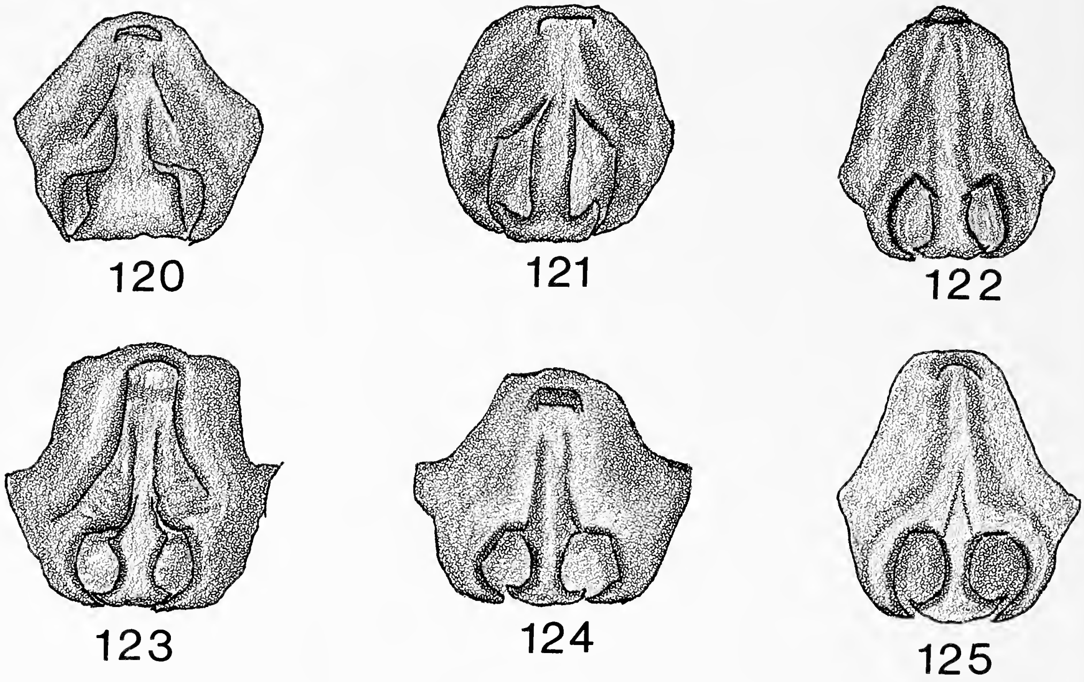
1. Median septum with anchor-shaped base and not wider than a cavity (Figs. 121–125) 2
   Median septum rectangular and nearly covering cavities (Fig. 120) . . . . *Pardosa tuoba*
2. Cavities at least 1/2 the length of epigynal plate; apical end of cavity steeply slanting medially (Fig. 121) . . . . *Pardosa orthodox*
   Cavities roundish, less than 1/3 the length of epigynal plate (Figs. 122–125) 3

Map 12.—State records for *P. californica* (❂). *P. hyperborea* (❖), *P. mulaiki* (☆), *P. tesquorum* (★), *P. xerampelina* (✸).

3. Spider collected in California, Nevada or Baja California; epigynum as in Fig. 122 .... *Pardosa ramulosa*
   Spider collected in other states (Figs 123–125) 4
4. Spider collected in coastal Oregon or Washington or with males of *P. vancouveri*; epigynum as in Fig. 123 .... *Pardosa vancouveri*
   Spider collected in the Cascade Mountains or anywhere east of the Cascades 5
5. Spiders collected in central Oregon or Washington, or west of the Continental Divide in Colorado, Idaho, Montana, Utah, or Wyoming; epigynum as in Fig. 124 .... *Pardosa altamontis*
   Note.—Females cannot be identified with certainty unless collected with males. Spiders collected in Arizona, Colorado, New Mexico, Utah, or east of the Continental Divide in Montana or Wyoming; epigynum as in Fig. 125 .... *Pardosa sternalis*

Males

1. Tarsus I slender, no different than other tarsi (Fig. 126) 2
   Tarsus I swollen, thicker than tarsi of other legs (Fig. 127); palp as in Fig. 128 .... *Pardosa vancouveri*
2. Tip of median apophysis somewhat flared and truncate (Fig. 129) .... *Pardosa orthodox*
   Tip of median apophysis pointed (Figs. 130–133) 3
3. Tip of cymbium dorsally paler than base; palp as in Fig. 130 .... *Pardosa sternalis*
   Tip of cymbium dark throughout, may have brush of dark hair 4
4. Spider collected in Idaho, Utah or west of the Continental Divide in Colorado, Montana or Wyoming; palp as in Fig. 131 .... *Pardosa altamontis*
   Spider collected elsewhere 5
5. Tip of cymbium quite narrow; tibia of pedipalp unmarked or with 1 or 2 dark patches (Fig. 132) .... *Pardosa ramulosa*
   Tip of cymbium wide; tibia of pedipalp dark, clothed with dark hair (Fig. 133) .. *Pardosa tuoba*



Figures 120–125.—Epigyna of *Pardosa*, sternalis group. 120. *P. tuoba*. 121. *P. orthodox*. 122. *P. ramulosa*. 123. *P. vancouveri*. 124. *P. altamontis*. 125. *P. sternalis*.

Pardosa altamontis Chamberlin & Ivie 1946

Figs. 124, 131; Map 13

Diagnosis.—Genitalia are not useful in identification. The cymbium is entirely dark dorsally.

Distribution.—Washington, Oregon, Idaho, Montana, Wyoming, Utah; Canada (Dondale & Redner 1990: map 42; Vogel 1970a: 18, fig. 89).

Pardosa orthodox Chamberlin 1924

Figs. 121, 129; Map 13

Diagnosis.—The epigynal cavities more than 1/2 the length of epigynum with the apical edge slanting basally from the septum. The median apophysis of the male palp is wide at the tip.

Remarks.—This species is not common.

Distribution.—Utah, Arizona; Mexico (Vogel 1970a:18, fig. 89).

Pardosa ramulosa (McCook 1884)

Figs. 122, 131; Map 13

Lycosa ramulosa McCook 1884: pl.30, figs. 5, 6 (no verbal description); Gertsch 1934:23 (= *Pardosa sternalis*)

Pardosa peninsulana Banks 1898:274; Gertsch 1934:23 (=*Pardosa sternalis*); Vogel 1970a:12 (=*Pardosa ramulosa*).

Pardosa ramulosa (McCook 1884): Vogel 1970a: 12.

Diagnosis.—Location is more useful for identification than genital morphology.

Distribution.—California, Nevada, Utah; Mexico (Vogel 1970a:12, fig. 89).

Pardosa sternalis (Thorell 1877)

Figs. 125, 127, 130; Map 13

Diagnosis.—Location is more useful for identification than genital morphology.

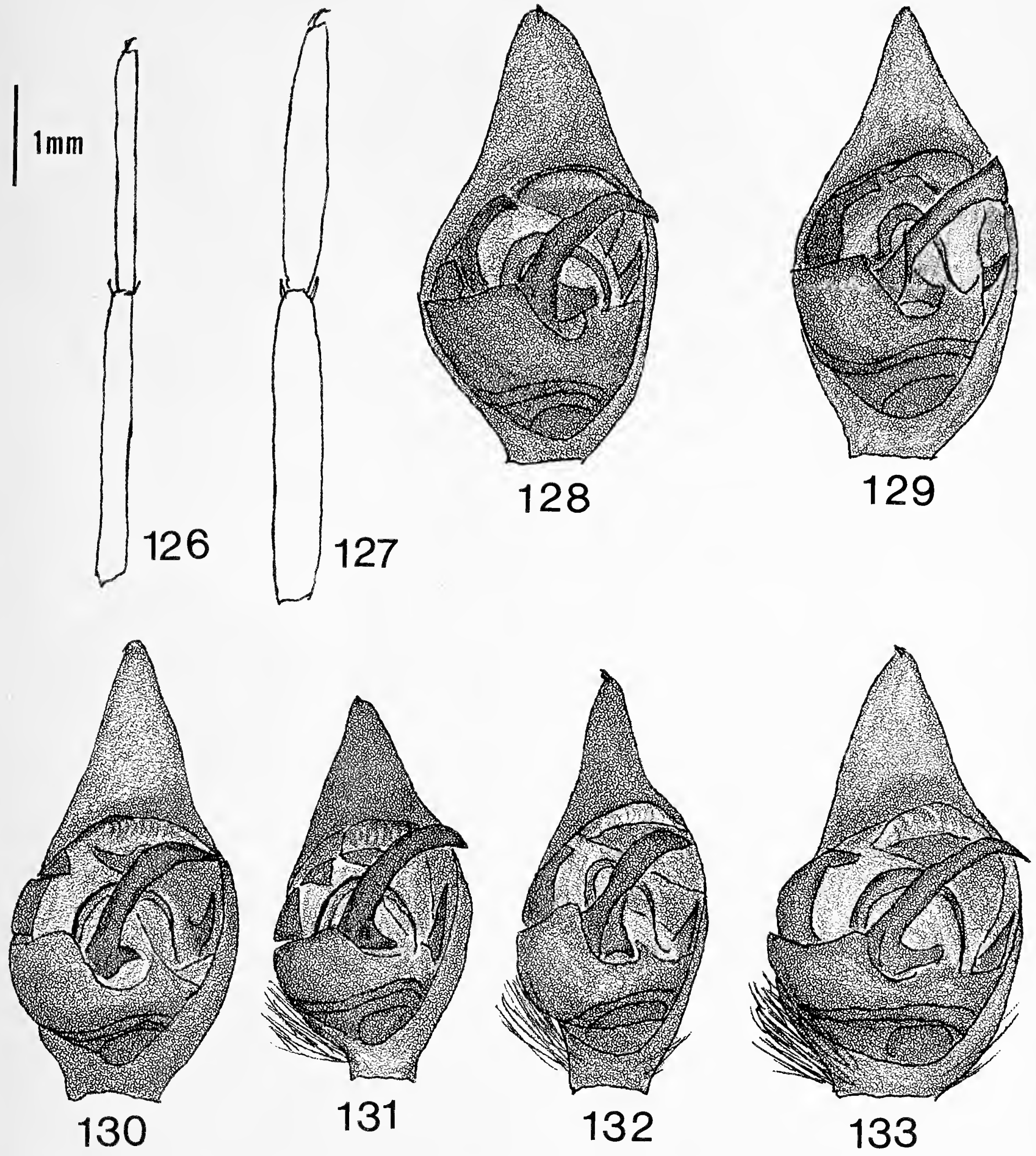
Remarks.—This species is extremely common and abundant on wet meadows, stream sides, and lawns.

Distribution.—California, Idaho, Montana, Wyoming, Utah, Colorado, Arizona, New Mexico, Nebraska, Kansas, Texas; Alberta to Central Mexico (Dondale & Redner 1990: map 24; Vogel 1970a: 16, fig 89).

Pardosa tuoba Chamberlin 1919

Figs. 120, 133; Map 13

Diagnosis.—Females can be identified by the basal portion of the septum which is wide enough to nearly cover the cavities. The cym-



Figures 126–133.—Males of *Pardosa*, sternalis group. 126. *P. sternalis*, tarsus and metarsus I. 127. *P. vancouveri*, tarsus and metarsus I. Figs. 128–133. Palpi. 128. *P. vancouveri*. 129. *P. orthodox*. 130. *P. sternalis*. 131. *P. altamontis*. 132. *P. ramulosa*. 133. *P. tuoba*.

bium of the male palp is very wide and the tip is stout.

Remarks.—*Pardosa tuoba* occurs at low elevations, perhaps under 500’. They are almost entirely sympatric with *P. ramulosa*.

Distribution.—California (Vogel 1970a: 20, fig. 83).

Pardosa vancouveri Emerton 1917

Figs. 123, 127, 128; Map 13

Diagnosis.—The epigynum does not separate females from other species. Males of *P. vancouveri* can be distinguished by the thickened “club foot” of tarsus I.

Map 13.—State records for *P. altamontis* (★), P. *orthodox* (❖), *P. ramulosa* (☆), *P. sternalis* (✹), *P. tuoba* (❂), *P. vancouveri* (✢).

Remarks.—This species is found in marshes, grasslands, and meadows at low elevations.

Distribution.—Oregon, Washington; British Columbia (Dondale & Redner 1990: map 24; Vogel 1970a:20, fig. 89).

Tesquorum Group

Remarks.—The tesquorum group consists of two species in the USA (one Nearctic and one Holarctic), and possibly two Palearctic species. The cephalothorax usually has five longitudinal bands except in dark spiders. The abdomen may have five pairs of light spots posterior to the diamond mark. The epigynum is longer than wide. The cavities partially covered by lateral expansions of the septum. The apical part of the septum is slender and straight. A small pair of hoods flank the septum. The male palp is compact. The median apophysis is stout, curved and extends only halfway to the cymbium. The basal spur is short, narrow, and pointed. The tip of the embolus is slender. All segments of the pedipalp are dark except the patella which is a pale color.

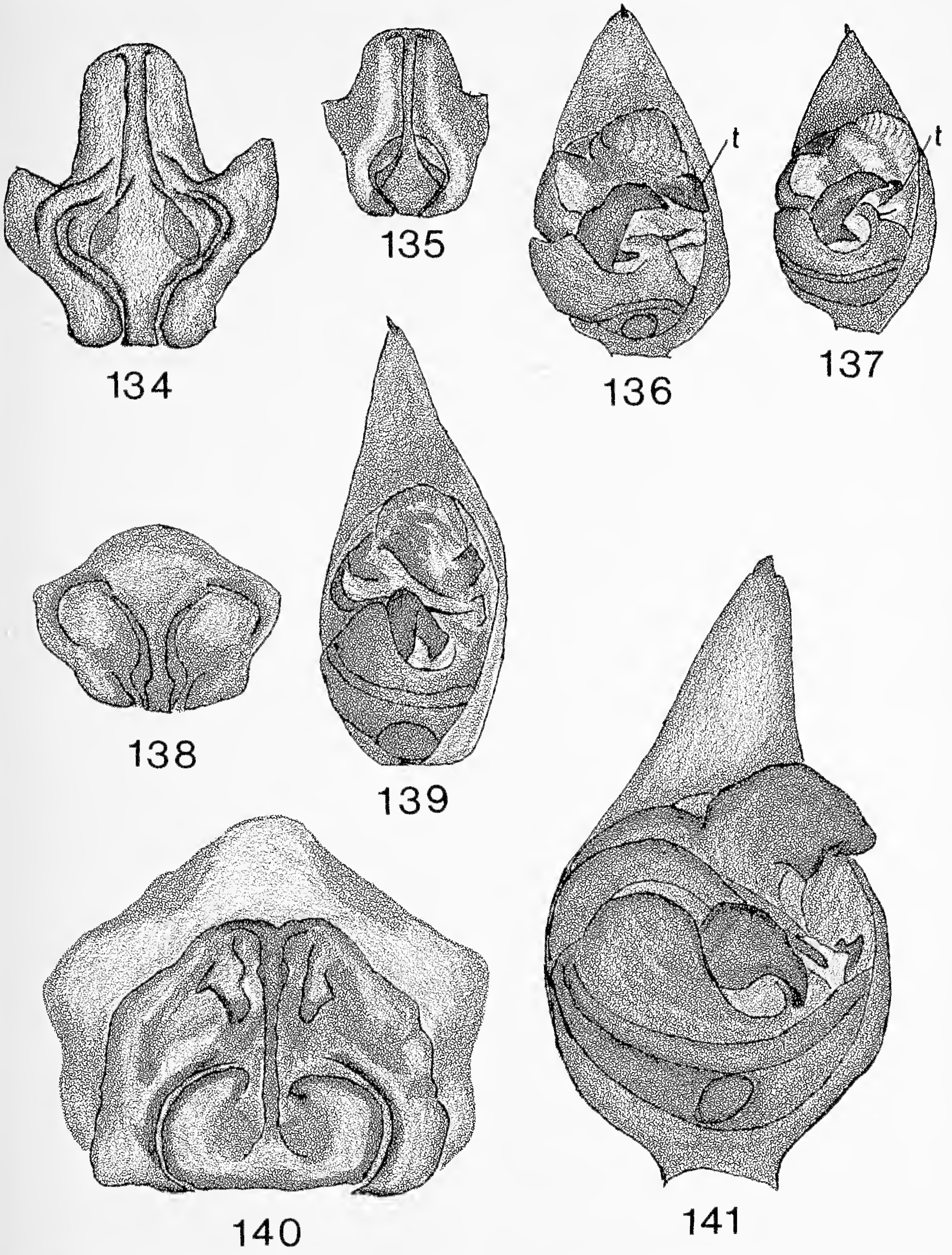
KEYS TO USA SPECIES OF THE TESQUORUM GROUP

Females

1. Epigynum with wide lateral wings; septum with a basal pedicel and lateral expansions nearly covering the cavities; septal pockets oval (Fig. 134) .... *Pardosa tesquorum*
Epigynum with small lateral wings; septum lacks pedicel basal to expansions; septal pockets triangular (Fig. 135) .... *Pardosa mulaiki*

Males

1. Median apophysis stout with a right angle bend, ending in a point; terminal apophysis broad and flat (Fig. 136) .... *Pardosa tesquorum*
Median apophysis stout and curved, but not a right angle bend; terminal apophysis small with a rounded tip (Fig. 137) .... *Pardosa mulaiki*



Figures 134–141.—Genitalia of *Pardosa*. Figs. 134–137. *Pardosa*, tesquorum group. 134. Epigynum of *P. tesquorum*. 135. Epigynum of *P. mulaiki*. 136. Palp of *P. tesquorum*. 137. Palp of *P. mulaiki*. t, terminal apophysis.

Figures 138–139.—*Pardosa*, xerampelina group, *P. xerampelina*. 138. Epigynum. 139. Palp.

Figures 140–141.—*Acantholycosa solituda*. 140. Epigynum. 141. Palp.

Pardosa mulaiki Gertsch 1934

Figs. 135, 137; Map 12

Diagnosis.—Lateral bands of the carapace on the female are wide, but mostly obscured on the male. The median band on the male is limited to the posterior half of the carapace. Females of *P. mulaiki* lack a pedicel on the septum basal to the expanded portion. Males of *P. mulaiki* differ from *P. tesquorum* by the short rounded terminal apophysis.

Distribution.—Montana, Wyoming, Colorado, New Mexico, North Dakota; Canada (Dondale & Redner 1986: map 9; pers. obs.).

Pardosa tesquorum (Odenwall 1901)

Figs. 134, 136; Map 12

Diagnosis.—*Pardosa tesquorum* is brown and light brown, with pale legs. The epigynum *P. tesquorum* are differs from *P. mulaiki* by the basal pedicel of the septum. Males of *P. tesquorum* are distinguished by the broad flat terminal apophysis.

Distribution.—Montana, Wyoming, Utah, Colorado, New Mexico, South Dakota, North Dakota; Canada, Alaska, eastern Siberia (Dondale and Redner 1986: 827, map 8).

Xerampelina Group

Remarks.—The xerampelina group consists of one species in North America, two more in Canada and Alaska, and one Palearctic species. The apical end of the epigynum is smoothly domed, without a hood. The cavities are oval, diverging apically. The septum is somewhat narrow basally and widens apically to edge of epigynum. The male palp is long and slender with the apical portion of the cymbium more than 1/2 the length of the bulb. Median apophysis is short, stout and blunt. The spur arises apically rather than basally.

Pardosa xerampelina (Keyserling 1887)

Figs. 138, 139; Map 12

Diagnosis.—The genitalia are as described above.

Distribution.—Across the northern tier from the Pacific coast to New England; Canada, Alaska: (Dondale & Redner 1986: map 5).

Genus *Acantholycosa* Dahl 1908

Remarks.—The genus *Acantholycosa* consists of 13 species in Europe and Asia and one in North America. The spiders in this genus closely resemble *Pardosa* in appearance, especially the shape of the cephalothorax and slenderness of the legs. The distinguishing feature is the number of spines, 5–7, on the ventral side of tibia I.

Solituda Group

Remarks.—The solituda group consists of one species in North America and a closely related Palearctic species. The central part of the epigynum is strongly sculptured. The base of the septum is about 1/4 the length of the septum. The apical 3/4 of the septum is slender, and flanked by a pair of hoods at the rim. The base of the septum is more than 1/2 the width of the epigynum with large bulbous lobes laterally, filling in the cavities. The lateral swellings are strongly sclerotized and closely apposed to the basal lobes of the septum. There is an apical pair of ridges flanking the septum. The strongly sculptured central part of the epigynum is surrounded laterally and apically by a lightly sclerotized plate. The part of the cymbium surrounding the bulb is nearly circular with the tip much narrower. The median apophysis is short, stout, and rounded apically. The spur arises apically and is directed basally. The palea bears a large sclerotized process, larger than the median apophysis. It protrudes from the cymbium and curves basally with a shallow notch in the wide end. The embolus is wide at the base tapering distally.

Acantholycosa solituda (Levi & Levi 1951)

Pardosa solituda Levi & Levi 1951: 225–226, figs. 11, 16.

Acantholycosa solituda (Levi & Levi): Kronestedt & Marusik 2002:63

Figs. 140, 141.

Diagnosis.—The carapace is brown, lateral bands are faint. The abdomen is dark gray with a brown diamond mark apically. The epigynum and palp are as described for the group.

Remarks.—Occurs at high elevations, above timberline, in talus.

Distribution.—Montana, Wyoming, Utah, Colorado; Canada [Kronestedt & Marusik 2002:65, 66); pers. obs.].

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LITERATURE CITED

Banks, N. 1896. Additions to the list of Long Island spiders. Journal of the New York Entomological Society 4:190–192.

Banks, N. 1904. New genera and species of Nearctic spiders. Journal of the New York Entomological Society 12:109–119.

Barnes, R.D. 1959. The *lapidicina* group of the wolf spider genus *Pardosa* (Araneae, Lycosidae). American Museum Novitates 1960:1–20.

Bryant, E.B. 1935. A few southern spiders. Psyche 42:73–83.

Chamberlin, R.V. 1904. Notes on generic characters in the Lycosidae. Canadian Entomologist 36: 145– 148,173–178.

Chamberlin, R.V. and W. Ivie. 1942. A hundred new species of American spiders. Bulletin of the University of Utah (Biological Series) 32(13):1–117.

Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae, Lycosidae). Actas del X Congreso Arachnologico, Jaca, Espana 1:327–332.

Dondale, C.D. 1999. Revision of the *groenlandica* subgroup of the genus *Pardosa* (Araneae, Lycosidae). Journal of Arachnology 27:435–448.

Dondale, C.D. & J.H. Redner. 1984. Revision of the *milvina* group of the wolf spider genus *Pardosa* (Araneae, Lycosidae). Psyche 91:67–117.

Dondale, C.D. & J.H. Redner. 1986. The *coloradensis*, *xerampelina*, *lapponica* and *tesquorum* groups of the genus *Pardosa* (Araneae: Lycosidae) in North America. Canadian Entomologist 118:815–835.

Dondale, C.D. & J.H. Redner. 1987. The *atrata*, *cubana*, *ferruginea*, *moesta*, *monticola*, *saltuaria* and *solituda* groups of the genus *Pardosa* (Araneae: Lycosidae) in North America. Canadian Entomologist 119(1):1–19.

Dondale, C.D. & J.H. Redner. 1990. The insects and arachnids of Canada Part 17. The wolf spiders, nurseryweb spiders and lynx spiders of Canada and Alaska (Araneae: Lycoside, Pisauridae, and Oxyopidae). Research Branch Agriculture Canada Publication 1856:1–383.

Gertsch, W.J. 1933. New genera and species of North American spiders. Amereican Museum Novitates 636:1–28.

Jiménez, M.L. 1986. Descripciones de aranas del genero *Pardosa* grupo "*distincta*" (Araneae, Lycosidae). Folia Entomologica Mexicana No 70: 123–129.

Kronestedt, T. 1975. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). I. Redescription of *Pardosa albomaculata* Emerton, and description of two new species from North America, with comments on some taxonomic characters. Zoologica Scripta 4:217–228.

Kronestedt, T. 1981. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). II. Redescription of *Pardosa modica* (Blackwall), *Pardosa labradorensis* (Thorell) and *Pardosa sinistra* (Thorell). Bulletin of the American Museum of Natural History 170:111–124.

Kronestedt, T. 1988. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). IV. Redescription of *Pardosa tetonensis* Gertsch and description of two new species from the western United States. Entomologica Scandinavica 18: 175–183.

Kronestedt, T. 1993. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). V. Redescription of *Pardosa wasatchensis* Gertsch and description of a new species from Utah. Journal of Arachnology 27:435–448.

Kronestedt, T. & Y.M. Marusik. 2002. On *Acantholycosa solituda* (Levi & Levi) and *A. sterneri* (Marusik) (Araneae: Lycosidae), a pair of geographically distant allied species. Acta Arachnologica 51(1):63–71.

Levi, H.R. & L.R. Levi. 1951. Report on a collection of spiders and harvestmen from Wyoming and neighboring states. Zoologica 36(4):214–219.

Lowrie, D.C. 1973. The microhabitats of western wolf spiders of the genus *Pardosa*. Entomological News 84:103–116.

Lowrie, D. C. & C.D. Dondale. 1981. A revision of the *nigra* group of the genus *Pardos*a in North America (Araneae, Lycosidae). Bulletin of the

American Museum of Natural History 1960:1–20.

Pickard-Cambridge, F.O. 1902. Arachnida, Araneida and Opiliones. Pp. 313—424. *In* Biologia Centrali-Americana, vol. 2. Taylor and Francis, London.

Platnick, N.I. 2003. The world spider catalog version 3.5. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81–87/index.html.

Schenkel, E. 1951. Spinnentiere aus den westlichen Nordamerika, gesammelt von Dr. Hans Schenkel-Rudin. Verhandlungen der Naturforschenden Gesellschaft in Basel 62:24–62.

Thorell, T. 1877. Descriptions of the Araneae collected in Colorado in 1885 by A.S. Packard Jr, M.D. Bulletin of the United States Geological Survey 3:477–529.

Tullgren, A. 1901. On the spiders collected in Florida by Dr. Einar Lonnberg 1892–93. Kungliga Svenska Vetenskaps-akademiens Handlingar 27: 1–29.

Vogel, B.R. 1964. A taxonomic revision of the *distincta* group of the wolf spider genus *Pardosa* in America north of Mexico (Araneida, Lycosidae). Postilla 82:1–30.

Vogel, B.R. 1970a. Taxonomy and morphology of the *sternalis* and *falcifera* species groups of *Pardosa* (Araneida, Lycosidae). Armadillo Papers 3: 1–31.

Vogel, B.R. 1970b. Courtship of some wolf-spiders. Armadillo Papers 4:1–7.

Zyuzin, A.A. 1993. Studies on the wolf spiders (Araneae: Lycosidae). I. A new genus and species from Kazakhstan, with comments on the Lycosinae. Memoirs of the Queensland Museum 33: 693–700.

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THE SYSTEMATICS OF SOUTHERN AFRICAN *PARABUTHUS* POCOCK (SCORPIONES, BUTHIDAE): REVISIONS TO THE TAXONOMY AND KEY TO THE SPECIES

Lorenzo Prendini: Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA. E-mail: lorenzo@amnh.org

ABSTRACT. The southern African species of *Parabuthus* Pocock 1890 are reviewed. Twenty valid species are recognized and an illustrated key is provided for their identification. The diagnosis of each species is revised, its known distributional range summarized, and notes on its ecology and conservation provided. Three species are redescribed and their distributions mapped: *P. calvus* Purcell 1898; *P. capensis* (Ehrenberg 1831); *P. planicauda* (Pocock 1896). Six new synonyms are proposed: *Buthus brevimanus* var. β *segnis* Thorell 1876 = *P. granulatus* (Ehrenberg 1831); *Buthus villosus* var. β *dilutus* Thorell 1876 = *P. raudus* (Simon 1888); *P. granulatus strenuus* Hewitt 1918 = *P. granulatus* (Ehrenberg 1831); *P. capensis frenchi* Purcell 1901 = *P. planicauda* (Pocock 1889); *Scorpio teter* Müller 1828 = *P. transvaalicus* Purcell 1899; *P. brachystylus* Lawrence 1928 = *P. villosus* (Peters 1862). Two species, synonymized by previous authors, but subsequently resurrected, are returned to synonymy: *P. neglectus* Purcell 1899 = *P. capensis* (Ehrenberg 1831), first synonymized by Kraepelin (1908); *P. flavidus* Pocock 1899 = *P. mossambicensis* (Peters 1861), first synonymized by Kraepelin (1914).

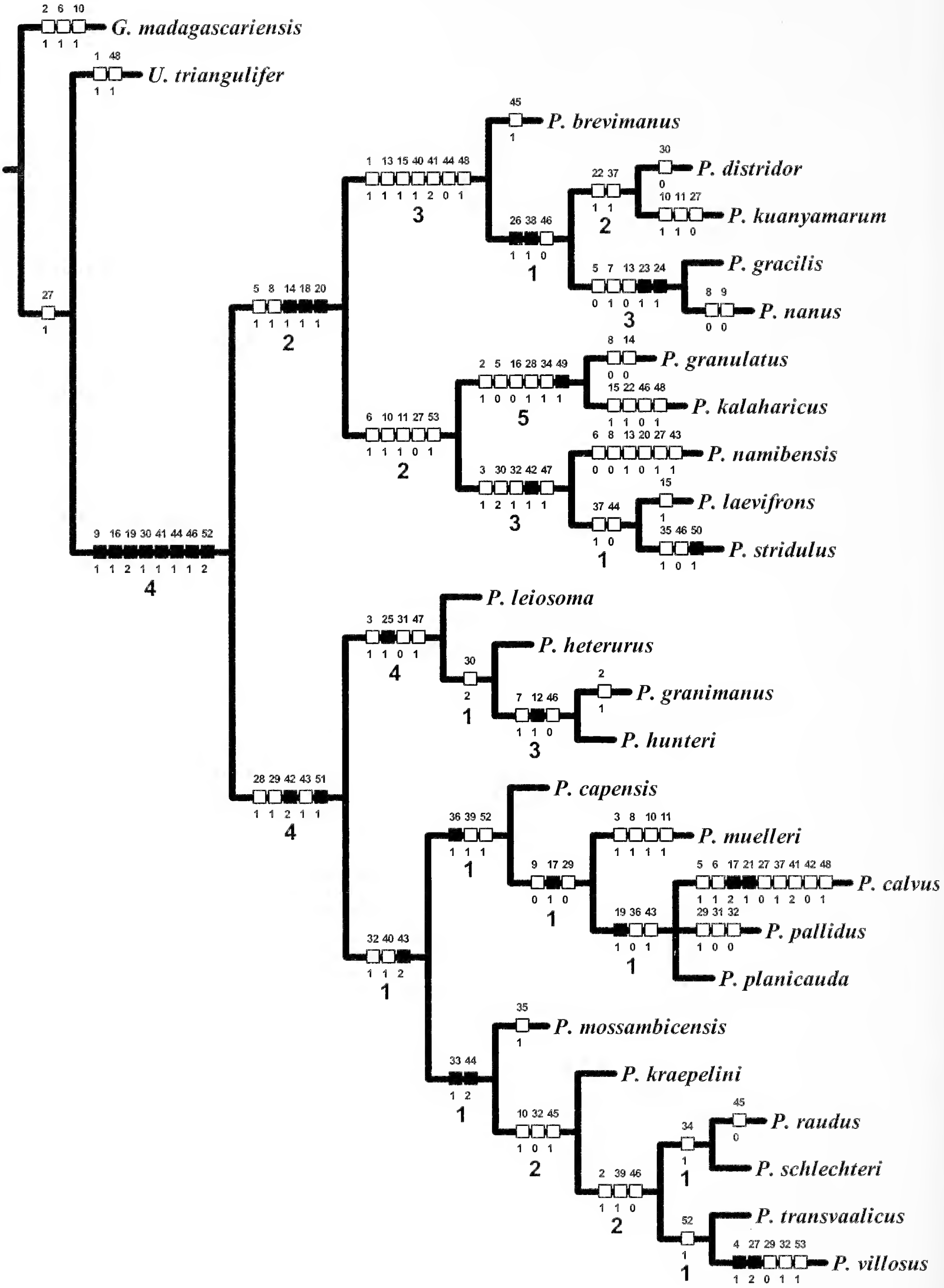
Keywords: Scorpiones, Buthidae, *Parabuthus*, taxonomy, identification, distribution, ecology

Parabuthus Pocock 1890 is an exclusively Old World genus of scorpions, one of 82 genera in the diverse, cosmopolitan family Buthidae (Fet & Lowe 2000; Kovařík 2001, 2002, 2003a). The genus includes the world's largest buthid scorpions, e.g., *P. granulatus* (Ehrenberg 1831), *P. schlechteri* Purcell 1899, *P. transvaalicus* Purcell 1899 and *P. villosus* (Peters 1862), which reach lengths of up to 140 mm and masses of up to 14 g (Newlands 1974a, 1978a). It also includes the world's only diurnal buthid, *P. villosus* (Newlands 1974a; Harington 1982).

Parabuthus displays a classic "arid corridor" pattern of distribution (Balinsky 1962), occurring in two disjunct geographical regions: (1) arid southwestern Africa; (2) arid northeastern Africa and the Arabian Peninsula. During past periods of increased aridity, such as the Pliocene and the Upper Pleistocene (Tankard & Rogers 1978; Lancaster 1981, 1984; Ward et al. 1983), these two areas were contiguous, allowing dispersal or range expansion of arid-adapted taxa between them. As evidence for their arid requirements, the southern African species of *Parabuthus* are today restricted to areas receiving less than 600 mm of annual rainfall (Newlands 1978a, b).

The dependence of *Parabuthus* species on aridity has some fortunate implications for the geographical distribution of scorpionism in southern Africa, as *Parabuthus* includes some of the world's most dangerously venomous scorpions. Envenomation by these scorpions is a significant cause of morbidity and, in some instances, mortality, in the sparsely populated arid to semi-arid western regions of southern Africa (Müller 1993; Bergman 1997a, b). However, the more densely populated mesic eastern regions are devoid of *Parabuthus* (Prendini 1995) and the incidence of scorpion envenomation in southern Africa is therefore lower than might be expected, given the abundance of medically important scorpion species in the region.

The medical importance of *Parabuthus*, especially *P. granulatus* and *P. transvaalicus*, has received increasing attention during the past 25 years (Newlands 1974a, 1978a; Newlands & Martindale 1980; Petersen 1987; Hill 1990; Saunders & Morar 1990; Lee 1991; Müller 1993; Bergman 1995, 1997a, 1997b; Swerts et al. 1997; DeBont et al. 1998; Tytgat


2 6 10
1 1 1
G. madagascariensis
1 48
1 1
U. triangulifer
45
1
P. brevimanus
1 13 15 40 41 44 48
1 1 1 1 2 0 1
3
30
0
P. distridor
22 37
1 1
2
10 11 27
1 1 0
P. kuanyamarum
26 38 46
1 1 0
1
P. gracilis
5 7 13 23 24
0 1 0 1 1
3
8 9
0 0
P. nanus
27
1
5 8 14 18 20
1 1 1 1 1
2
8 14
0 0
P. granulatus
2 5 16 28 34 49
1 0 0 1 1 1
5
15 22 46 48
1 1 0 1
P. kalaharicus
6 10 11 27 53
1 1 1 0 1
2
6 8 13 20 27 43
0 0 1 0 1 1
P. namibensis
3 30 32 42 47
1 2 1 1 1
3
15
1
P. laevifrons
37 44
1 0
1
35 46 50
1 0 1
P. stridulus
9 16 19 30 41 44 46 52
1 1 2 1 1 1 1 2
4
P. leiosoma
3 25 31 47
1 1 0 1
4
P. heterurus
30
2
1
2
1
P. granimanus
7 12 46
1 1 0
3
P. hunteri
28 29 42 43 51
1 1 2 1 1
4
P. capensis
36 39 52
1 1 1
1
3 8 10 11
1 1 1 1
P. muelleri
9 17 29
0 1 0
1
5 6 17 21 27 37 41 42 48
1 1 2 1 0 1 2 0 1
P. calvus
19 36 43
1 0 1
1
29 31 32
1 0 0
P. pallidus
P. planicauda
32 40 43
1 1 2
1
35
1
P. mossambicensis
33 44
1 2
1
P. kraepelini
10 32 45
1 0 1
2
45
0
P. raudus
34
1
1
P. schlechteri
2 39 46
1 1 0
2
P. transvaalicus
52
1
1
4 27 29 32 53
1 2 0 1 1
P. villosus

et al. 1998; Dyason et al. 2002; Huys et al. 2002). In comparison, attention to the systematics of these scorpions has lagged behind. The most significant recent contribution to the taxonomy of *Parabuthus* was produced by Lamoral (1979), who revised eleven species occurring in Namibia, described three new species, and proposed eight synonyms. Probst (1973) reviewed the two species occurring in Kenya and Tanzania, and Vachon (1979) and Sissom (1994) reviewed the type species, *P. leiosoma* (Ehrenberg 1828), in the Arabian Peninsula. Newlands & Martindale (1980) and FitzPatrick (1994) reviewed the *Parabuthus* species occurring in Zimbabwe. Kovařík (2003b) reviewed the *Parabuthus* species of Djibouti, Eritrea, Ethiopia and Somalia, described a new species and proposed seven new synonyms. Additional contributions to *Parabuthus* systematics in southern Africa were produced by Newlands (1970), Eastwood (1977), Lamoral (1977, 1980), Harington (1984) and Prendini (2000, 2001a, 2003).

Parabuthus currently includes 27 species and eight subspecies, four of which are nominotypic (Lamoral & Reynders 1975; Fet & Lowe 2000; Kovařík 2003b). Twenty of these species and all eight subspecies are endemic to the southern African region. The recent discovery of a new species in Namibia (Prendini 2000), and the synonymy of *P. neglectus* Purcell 1899 with *P. capensis* (Ehrenberg 1831), proposed here, retains the total number of southern African species at 20.

This contribution focuses on the southern African species of *Parabuthus* for the following reasons. (1) *Parabuthus* is more diverse in southern Africa than in northeastern Africa and Arabia. (2) The most venomous species occur in southern Africa. (3) A limited quantity of colonial-era material from the countries of greatest *Parabuthus* diversity in northeastern Africa (particularly Somalia), coupled with political instability, hampers an adequate revision of the *Parabuthus* fauna of that region.

No existing publication has synthesized the taxonomic status of all described southern African *Parabuthus* species and subspecies, or provided information on the whereabouts of type specimens. Two species, viz. *P. calvus* Purcell 1898 and *P. planicauda* (Pocock 1896), have not been revised since their original description. Confusion surrounds the status of *P. brachystylus* Lawrence 1928, *P. flavidus* Pocock 1899 and *P. neglectus*, the first two of which are currently regarded as subspecies of *P. villosus* and *P. mossambicensis* (Peters 1861), respectively. The status of the remaining subspecies is also uncertain.

This contribution addresses these gaps in the knowledge of southern African *Parabuthus* by updating the taxonomy and providing a key to the valid species of the region. The diagnosis of each species is revised, its known distributional range summarized, and notes on its ecology and conservation provided. *Parabuthus calvus*, *P. capensis* and *P. planicauda* are redescribed and their distributions mapped. A cladistic analysis of the southern African species, including five of the eight northeastern African and Arabian species, based on morphological data, has been published elsewhere (Prendini 2001a, 2003; Fig. 1). A larger study, involving a simultaneous analysis of morphological and molecular (DNA sequence) data, is underway (Prendini, Esposito & Wheeler in prep.).

METHODS

In the present contribution, nomenclatural emendations are based primarily upon the examination of type material. However, taxonomic decisions presented here are not derived solely from examination of the types. Additional specimens were examined in all

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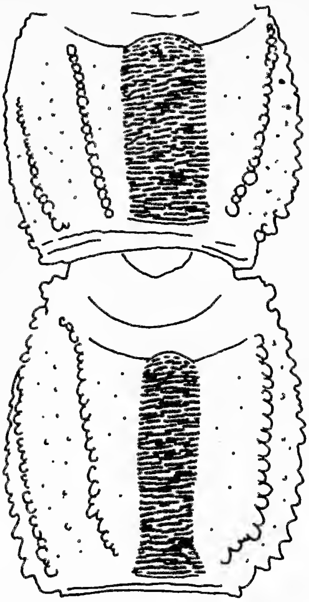
Figure 1.—The optimal tree obtained by an analysis (Prendini 2003) of 53 morphological characters scored for 25 species of *Parabuthus* Pocock 1890 (and two outgroup taxa). This topology was retrieved under weighting regimes that maximized fit and minimized length (length: 132 steps; fit: 59 %; CI: 44; RI 74). Zero-length branches are collapsed. Solid bars indicate uniquely derived apomorphic character states, whereas empty bars indicate parallel derivations of apomorphic states under ACCTRAN optimization. The number above each bar gives the character number, whereas the number below gives the character state. Branch support values of nodes are provided below branches. Refer to Appendix 1 for character descriptions.



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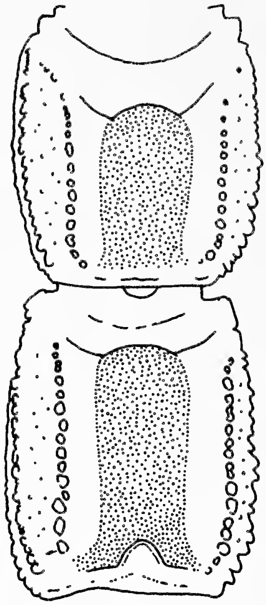

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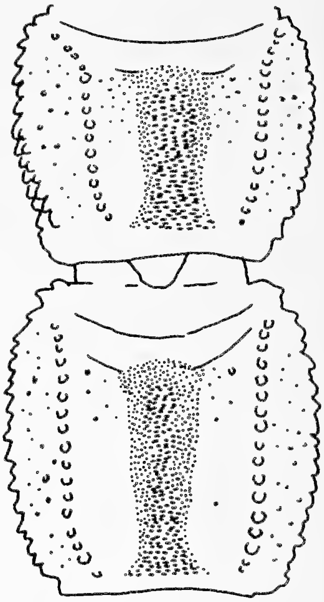

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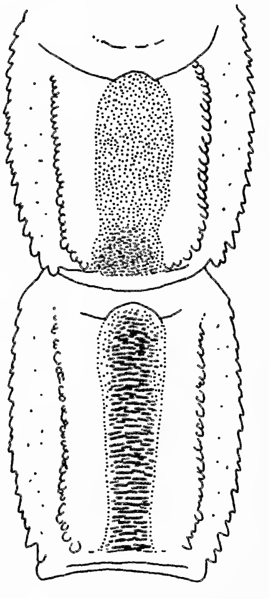

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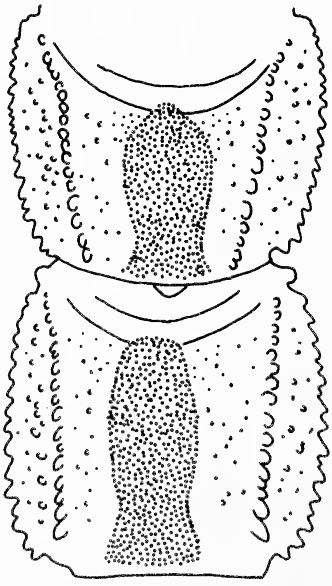

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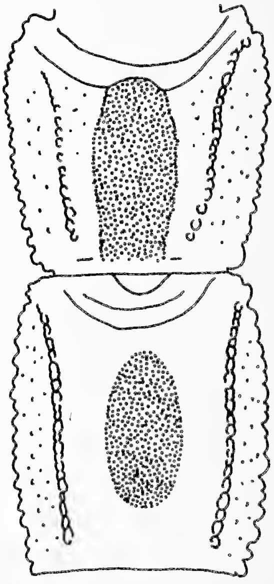

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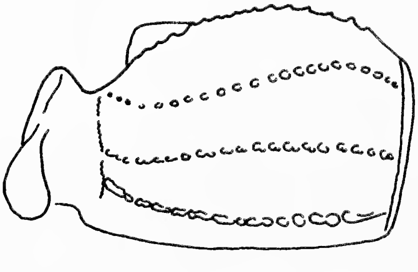

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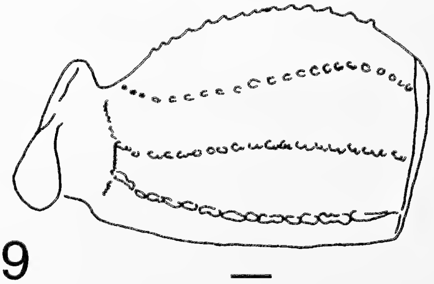

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cases, in order to assess the extent of geographical variation and identify characters that are consistent across the distributional range.

Species are delimited here in accordance with the phylogenetic species concept, where a species is defined as a minimum diagnosable unit (Nelson & Platnick 1981; Cracraft 1983, 1989; Wheeler & Nixon 1990; Nixon & Wheeler 1990; Davis & Nixon 1992; De Pinna 1999). As such, all subspecies are considered junior synonyms of their respective species unless they can be consistently separated based on somatic characters. In that case, they represent valid species in the diagnostic sense and are elevated accordingly. Note that this view differs from traditional usage of the subspecies category in scorpion systematics, in which the biological species concept, according to which species are defined based on reproductive isolation (Dobzhansky 1937; Mayr 1963), still prevails. Unlike most insects and spiders, scorpion genitalia seldom provide sufficient characters at the species level (although there are notable exceptions, e.g., Bothriuridae). For example, Lamoral (1979) and FitzPatrick (1994) found no discrete diagnostic differences in the hemispermatophores of ten species of *Parabuthus*, all of which are diagnosable based on consistent somatic differences. Presumably, differences in the specific-mate recognition system (Paterson 1985), i.e., pre-mating isolation mechanisms (Mayr 1963), of scorpions occur at the behavioral or chemical level (e.g., see Gaffin & Brownell 1992) rather than at the genitalic level. Because of this common paucity of genitalic variation, taxonomists have often resorted to subspecies for delimiting somatic variation in complexes of closely related scorpion species. For example, Harington (1984:404–405) regarded *P. brachystylus* as a subspecies of *P. villosus* on the grounds that morphology "has a strictly secondary role as a criterion of species rank", while acknowledging that this "is a partly arbitrary decision". In reality, many (probably most) scorpion subspecies are diagnosable based on somatic characters, and thus represent valid species in the diagnostic sense. A classic example is *Scorpio maurus* Linnaeus 1758 (family Scorpionidae Latreille 1802), with 19 currently accepted subspecies, each allopatric or parapatric, without intermediates. Neither Vachon (1952) nor Levy & Amitai (1980) were able to perceive diagnostic characters for species delimitation in *S. maurus*. Nonetheless, these authors were able to differentiate subspecies and describe them in the absence of more "reliable" characters. Vachon (1952) even provided a key to the subspecies, by means of which they may be consistently diagnosed. Levy & Amitai (1980) provided conclusive evidence that *Scorpio maurus fuscus* (Ehrenberg 1829) and *S. maurus palmatus* (Ehrenberg 1828) are ecological species (sensu Van Valen 1976), each adapted to slightly different substrata. No evidence has thus far been presented to suggest that the morphological variation in *S. maurus* is clinal, a basic tenet of the hypothesis that this is a widespread polymorphic species. The distribution of the subspecies of *S. maurus* conforms to the typical distributional pattern of localized endemics exhibited by other speciose African scorpionid genera such as *Pandinus* Thorell 1876 and *Opistophthalmus* C.L. Koch 1837.

Personally collected specimens were found by turning stones during the day, or by ultraviolet (UV) light detection at night (Honetschlager 1965; Stahnke 1972a; Sissom et al. 1990). A portable UV lamp, comprising two mercury-vapor tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 Amp/hr, 12 V battery, was used for fieldwork. A portable Garmin™ GPS II Plus device was used for recording the geographical coordinates of collection localities in the field.

Depositories for specimens are abbreviated as follows: AMGS = Albany Museum (Grahamstown, South Africa); AMNH = American Museum of Natural History (New York,

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Figures 2–9.—Diagnostic characters of *Parabuthus* species. 2–7. Metasomal segments I and II, dorsal aspect, illustrating stridulatory surface. 2. *Parabuthus mossambicensis* (Peters 1861). 3. *Parabuthus capensis* (Ehrenberg 1831). 4. *Parabuthus kraepelini* Werner 1902. 5. *Parabuthus stridulus* Hewitt 1913. 6. *Parabuthus transvaalicus* Purcell 1899. 7. *Parabuthus villosus* (Peters 1862). 8–9. Metasomal segment I, lateral aspect. 8. *Parabuthus villosus*. 9. *Parabuthus transvaalicus*. Scale bars = 1 mm.

NY); BMNH = The Natural History Museum (London, UK); CASC = California Academy of Sciences (San Francisco, CA); GNME = Göteborgs Naturhistoriska Museet (Göteborg, Sweden); MCZ = Museum of Comparative Zoology, Harvard University (Cambridge, MA); MHNC = Musée d'Histoire Naturelle (La-Chaux-de-Fond, Switzerland); MMKZ = McGregor Museum (Kimberley, South Africa); MNHN = Museum National d'Histoire Naturelle (Paris, France); NHMB = Naturhistorisches Museum Basel (Basel, Switzerland); NHMW = Naturhistorisches Museum Wien (Vienna, Austria); NHRS = Naturhistoriska Riksmuseet (Stockholm, Sweden); NMNW = National Museum of Namibia (Windhoek, Namibia); NMSA = Natal Museum (Pietermaritzburg, South Africa); SAMC = South African Museum (Cape Town, South Africa); TMSA = Transvaal Museum (Pretoria, South Africa); ZMHB = Zoologisches Museum, Universität Humboldt (Berlin, Germany).

Illustrations were produced using a Leica MZ16 stereomicroscope and camera lucida. Photographs were taken using a digital photomicrography system (Microptics™ ML-1000). Measurements were made with Mitutoyo® digital calipers (model NTD12-6″C). Color designation follows Smithe (1974, 1975, 1981), trichobothrial notation follows Vachon (1974), sternum terminology follows Soleglad & Fet (2003) and measurements follow Stahnke (1970), Eastwood (1977) and Lamoral (1979). Morphological terminology follows Couzijn (1976) for the segmentation of legs, Hjelle (1990) and Sissom (1990) for the segmentation of pedipalps, Prendini (2000, 2001a, 2003) for metasomal carinae, and Stahnke (1970), Lamoral (1979), Sissom (1990) and Prendini (2001a) for remaining characters.

Distribution maps for *P. calvus*, *P. capensis* and *P. planicauda* were produced using ArcView GIS Version 3.2 (Environmental Systems Research Institute [ESRI], Redlands, CA), by superimposing point locality records on coverages depicting the topography (500 m contour interval), major sand systems and political boundaries of southern Africa. A topographic contour coverage was created from the GTOPO30 raster grid coverage, obtained from the website of the U.S. Government Public Information Exchange Resource: http://edcdaac.usgs.gov/gtopo30/gtopo30.html. A coverage of sand systems was created by clipping and merging relevant polygons extracted from a coverage of the geology of Africa provided by the Department of Marine Geoscience, University of Cape Town, with polygons extracted from a coverage of Namibian landforms from the Namibian National Biodiversity Task Force (Barnard 1998), downloaded from their website: http://www.dea.met.gov.na/programmes/biodiversity/countrystudy.htm.

In order to create a point locality geographical dataset for mapping distributional ranges, all records of sufficient accuracy were isolated from the material examined. Only a small proportion of the records were accompanied by geographical coordinates or quarter-degree squares (QDS), usually entered by the collector or subsequently added by the curator or collections manager. These were checked for accuracy and an attempt was made to trace coordinates for as many of the remaining records as possible, by reference to gazetteers, the official 1:250 000 and 1:500 000 topo-cadastral maps of South Africa and neighboring countries published by the Government Printer, and the GEOnet Names Server: http://164.214.2.59/gns/html/cntry_files.html. Names of Namibian regions and magisterial districts and South African provinces and magisterial districts listed in the material examined follow the most recent system (post-1994).

Genus *Parabuthus* Pocock 1890

Buthus (*Parabuthus*) Pocock 1890: 124, 125; type species by original designation *Androctonus leiosoma* Ehrenberg 1828 [= *Parabuthus leiosoma* (Ehrenberg 1828)].

Heterobuthus Kraepelin 1891: 63–68; type species by subsequent designation (Kraepelin 1895: 78), *Androctonus leiosoma* Ehrenberg 1828 [= *Parabuthus leiosoma* (Ehrenberg 1828)] (synonymized by Thorell 1893: 366).

Parabuthus: Kraepelin 1895: 82; Pocock 1895: 309; Laurie 1896: 131; Lönnberg 1897; 194; Kraepelin 1899: 28; Birula 1917a: 164; Birula 1917b: 55; Pavlovsky 1924: 77; Werner 1934: 269; Kästner 1941: 232; Bücherl 1964: 57; Stahnke 1972b: 130; Lamoral 1979: 560, 561; Francke 1985: 11, 16; Sissom 1990: 102; Nenilin & Fet 1992; Kovařík 1998: 116; 117; Fet & Lowe 2000: 200; Prendini 2001a: 13–35; Dyason et al. 2002: 768–773; Prendini 2003: 5, 19–22.

Diagnosis.—The genus *Parabuthus* is most closely related to the Afrotropical buthid genera *Grosphus* Simon 1888 and *Uroplectes* Peters 1861 (Prendini 2001a, 2004). All species of *Parabuthus*, with one exception (viz. *P. distridor* Lamoral 1980), are readily distinguished from *Grosphus*, *Uroplectes* and other buthid genera by the presence of a distinct stridulatory surface, composed of fine to coarse granules, sometimes forming transverse ridges, on the dorsal surfaces of tergite VII, and metasomal segments I, II and, to a lesser extent, III (Newlands 1974a, 1978a; Lamoral 1977, 1979, 1980; Figs. 2–7). This stridulatory surface is used to make an audible sound (stridulation) when the scorpion is alarmed by repeatedly scraping the aculeus across the granules or ridges (Dumortier 1964; Newlands, 1974a, 1978a; McCormick & Polis 1990). Additionally, all species of *Parabuthus* (including *P. distridor*) are characterized by the following unique combination of characters: carapace without granular carinae; mesosomal tergites with only a single, weakly developed median carina; proximal median lamella of pectines, enlarged and lobate (dilate) in female (Fig. 11; *P. granulatus* and *P. kalaharicus* Lamoral 1977 are exceptions in this regard); basitarsi of legs I and II with macrosetal combs (Fig. 12); metasomal segment IV, ventrosubmedian carinae becoming obsolete distally (Figs. 14, 15); metasomal segment V, ventrolateral carinae comprising distinct spinose or lobate processes subdistally (Figs. 22, 29, 31).

Remarks.—Prior to the present contribution, all but two of the southern African species had been revised to some extent. In contrast, only one of the northeastern African and Arabian species, *P. leiosoma* has been partially revised (Sissom 1994). The limited quantity of material available for most northeastern African species (except *P. leiosoma*) remains an obstacle for revising the species in that region, given the extent of geographical variation in *Parabuthus* species.

Distribution.—Angola, Botswana, Djibouti, Egypt, Ethiopia, Kenya, Mozambique, Namibia, Saudi Arabia, Somalia, South Africa, Sudan, Tanzania, Yemen, Zambia, Zimbabwe. Twenty-eight species are currently recognized, 20 of which are endemic to the southern African region, whereas eight are endemic to northeastern Africa and the Arabian Peninsula.

Ecology.—All species of *Parabuthus* are adapted for a burrowing existence (Newlands 1974b, 1978a, b). The thickened metasoma, especially the processes on the ventrolateral carinae of metasomal segment V, is used to loosen the soil, whereas the anterior two pairs of legs are used to scrape and rake the loosened soil out of the burrow (Eastwood 1977, 1978b; Lamoral 1979; Prendini 2001b). Burrows are constructed in open ground, at the base of shrubs or under stones (Newlands 1974b, 1978a, b; Eastwood 1977, 1978b; Lamoral 1979; Newlands & Martindale 1980; Harington 1984; Prendini 2000, 2001a, 2001b).

Many *Parabuthus* species are morphologically specialized for life on particular substrata. Some (e.g., *P. distridor*, *P. kalaharicus* and *P. kuanyamarum* Monard 1937) are restricted to the sand dune systems of the Namib and Kalahari deserts, and exhibit ecomorphological adaptations to facilitate locomotion and burrowing in the soft sand (Lamoral 1977, 1979, 1980; Prendini 2001b). Others (e.g., *P. planicauda* and *P. villosus*) appear to be morphologically specialized for inhabiting rocky areas (Prendini 2001b).

Adaptive radiation in *Parabuthus* may be related to the evolution of burrowing behavior in the genus. According to the "Effect Hypothesis of macroevolution" (Vrba 1980), repeated allopatric speciation in *Parabuthus* is the predicted outcome of vicariance, promoted by stenotopic habitat requirements, in this case "substratum specialization" (Prendini 2001b).

ILLUSTRATED KEY TO IDENTIFICATION OF THE SOUTHERN AFRICAN SPECIES OF *PARABUTHUS* POCOCK 1890

1. Metasomal segment IV, ventrosubmedian and ventrolateral carinae absent (Fig. 13) 2
   Metasomal segment IV, ventrosubmedian and ventrolateral carinae present, but ventrosubmedian carinae becoming obsolete distally (Figs. 14, 15) 7
2. Pedipalp chela asetose; trichobothrium *dt* in line with or distal to *et* (Figs. 55, 56) .... *P. calvus*
   Pedipalp chela covered in setae; trichobothrium *dt* proximal to *et* (Figs. 42–45) 3

3. Metasomal segments I and II, dorsal stridulatory surface absent, ventrosubmedian and ventrolateral carinae absent (Fig. 28) .... *P. distridor*
   Metasomal segments I and II, dorsal stridulatory surface present (Figs. 2–7), ventrosubmedian and ventrolateral carinae present (Figs. 25–27) 4
4. Metasomal segments II and III, distal section of ventrolateral carinae composed of strongly elevated, crescent-shaped tubercles, forming a broad U-shaped pattern (Fig. 27); metasomal segment V, ventrolateral carinae with lobate processes (broad and presenting a flat surface apically) subdistally (Fig. 29) .... *P. brevimanus*
   Metasomal segments II and III, distal section of ventrolateral carinae costate or composed of isolated, round granules, not forming a U-shaped pattern (Figs. 25, 26); metasomal segment V, ventrolateral carinae with spinose processes (narrow, conical or flattened, and tapering apically) subdistally (Fig. 30) 5
5. Pedipalp chela smooth and shiny (Fig. 46); carapace (female) with smooth areas .... *P. kuanyamarum*
   Pedipalp chela granular (Figs. 43–45); carapace (female) entirely granular 6
6. Pedipalp chela movable finger, short, compared with manus (measured along ventroexternal carina), length finger/length carina: ± 1.50 (Fig. 43); chela manus (adult male) incrassate (bulbous or swollen) (Fig. 43) .... *P. gracilis*
   Pedipalp chela movable finger, long, compared with manus (measured along ventroexternal carina), length finger/length carina: 1.70–2.00 (Figs. 44, 45); chela manus (adult male) slender (Fig. 44) .... *P. nanus*
7. Metasomal segment IV, median lateral carina absent or more weakly developed than dorsolateral and ventrolateral carinae (Figs. 16, 17) 8
   Metasomal segment IV, median lateral carina as strongly developed as dorsolateral and ventrolateral carinae (Fig. 18) 12
8. Metasomal segment II, dorsal stridulatory surface reaching posterior margin (Figs. 2–6); width of telson vesicle equal to distal width of metasoma V (Figs. 29, 30, 32) 9
   Metasomal segment II, dorsal stridulatory surface not reaching posterior margin (Fig. 7); telson vesicle narrower than distal width of metasoma V (Fig. 31) 11
9. Pedipalp chela manus covered in setae; metasomal segment V, dorsosubmedian carinae present but weakly developed (Figs. 20, 23) .... *P. namibensis*
   Pedipalp chela manus asetose; metasomal segment V, dorsosubmedian carinae absent (Figs. 19, 22) 10
10. Metasomal segment II, dorsal stridulatory surface composed of granules (Figs. 3, 4, 6, 7); telson vesicle dorsoproximal surface very shallowly excavated along longitudinal half (Fig. 34) .... *P. laevifrons*
    Metasomal segment II, dorsal stridulatory surface composed of granular ridges (Fig. 5); telson vesicle dorsoproximal surface deeply excavated along longitudinal half (Fig. 33) .... *P. stridulus*
11. Pedipalp chela, trichobothrium *dt* in line with or distal to *et* (Figs. 39, 40); metasomal segment IV, ventrosubmedian carinae becoming obsolete in distal third of segment (Fig. 15) .... *P. granulatus*
    Pedipalp chela, trichobothrium *dt* proximal to *et* (Figs. 37, 38); metasomal segment IV, ventrosubmedian carinae becoming obsolete in proximal third of segment (Fig. 14) .... *P. kalaharicus*
12. Metasomal segment II, posterodorsal edge extended forwards in V-shape (Fig. 3) 13
    Metasomal segment II, posterodorsal edge straight (Figs. 2, 4–7) 14
13. Pedipalp chela fingers fit together with distinct proximal gap, when closed (Fig. 41); telson aculeus short, sharply curved (Fig. 36); chela manus (adult male) slender (Figs. 44, 55, 83) .... *P. muelleri*
    Pedipalp chela fingers fit together without gap, when closed (Figs. 69, 70); telson aculeus long, gently curved (Fig. 35); chela manus (adult male) incrassate (Fig. 69) .... *P. capensis*
14. Metasomal segment V, ventrolateral carinae with lobate processes (Figs. 22, 29, 31) 15
    Metasomal segment V, ventrolateral carinae with spinose processes (Figs. 24, 30, 32) 17

15. Metasomal segment II, dorsal stridulatory surface composed of ridges (Fig. 2) .... *P. mossambicensis*
    Metasomal segment II, dorsal stridulatory surface composed of granules (Figs. 3, 4, 6, 7) 16
16. Metasomal segments I and II, dorsal stridulatory surface extended anteriorly (Fig. 8); chela manus (adult male) slender (Fig. 83) .... *P. planicauda*
    Metasomal segments I and II, dorsal stridulatory surface truncated anteriorly (Fig. 9); chela manus (adult male) incrassate (Figs. 37, 39, 43, 46, 69) .... *P. kraepelini*
    Metasomal segment V, ventrolateral carinae converging distally (Fig. 30); coloration pale, although metasomal segments IV and V and telson may be infuscated .... *P. raudus*
    Metasomal segment V, ventrolateral carinae subparallel to diverging distally (Figs. 29, 31, 32); coloration dark (pedipalps and legs may be pale) 18
17. Metasomal segments I and II, dorsal stridulatory surface extended anteriorly (Fig. 8); metasoma densely setose; metasoma I wider than IV .... *P. villosus*
    Metasomal segments I and II, dorsal stridulatory surface truncated anteriorly (Fig. 9); metasoma moderately setose; metasoma I narrower than IV 19
18. Metasomal segment II, dorsal stridulatory surface reaching posterior margin (Fig. 6); coloration of pedipalps and legs dark, not contrasting markedly with dark pro-, meso- and metasoma .... *P. transvaalicus*
    Metasomal segment II, dorsal stridulatory surface not reaching posterior margin of segment (Fig. 7); coloration of pedipalps and legs pale, contrasting markedly with dark pro-, meso- and metasoma .... *P. schlechteri*

Parabuthus brevimanus (Thorell 1876)
Figs. 27, 29

Buthus brevimanus Thorell 1876b: 110–113.

Heterobuthus brevimanus: Kraepelin 1891: 69.

Parabuthus brevimanus: Pocock 1895: 309; Kraepelin 1899: 32; Purcell 1901: 149–151; Kraepelin 1908: 250; Hewitt 1913: 146; Kraepelin 1914: 111, 112; Hewitt 1918: 104, 176; Fage 1925: 189; Lawrence 1927: 72; Lawrence 1928: 269; Werner 1936: 177; Monard 1937: 256, 257; Lawrence 1955: 225; Lawrence 1959: 383; Lawrence 1962: 220; Lamoral & Reynders 1975: 514, 515; Lamoral 1979: 561–566, figs. 87–94, 97–99; Kovařík 1998: 116; Fet & Lowe 2000: 201; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 20.

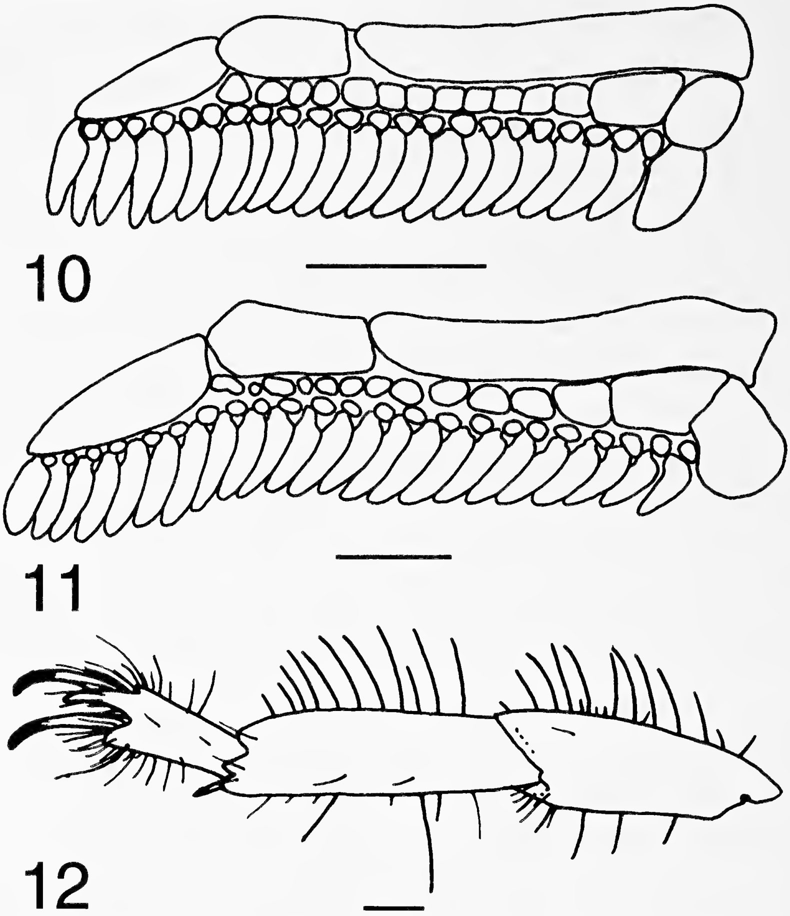
Parabuthus cristatus Pocock 1901: 284, 285 (synonymized by Kraepelin 1908: 250; Lamoral 1979: 561); Pocock 1902: 367, 368.

Type material.—*Buthus brevimanus:* Lectotype ♀ (GNME) [designated by Lamoral (1979)], "S. Afrika", 28.xi.1864 [not 23.xi.1864], C.J. Andersson. Paralectotype ♂ (NHRS) [designated by Lamoral (1979)], "Caffraria", 1840–1845, J. Wahlberg.

Parabuthus cristatus: Holotype ♀ (BMNH), "Congo" [probably Angola].

Diagnosis.—*Parabuthus brevimanus* is basal to the clade comprising the *P. distridor*–*P. kuanyamarum* and *P. gracilis*–*P. nanus* sister groups (Fig. 1). The five species may be separated from all other species of *Parabuthus* by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; pedipalp chela with trichobothrium *dt* situated proximal to *et*; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segment IV with median lateral, ventrolateral and ventrosubmedian carinae absent; metasomal segment V with dorsosubmedian, dorsolateral and ventromedian carinae absent.

Parabuthus brevimanus is most easily confused with *P. gracilis*, with which it is sympatric in the northwestern part of its distributional range (Erongo and Kunene regions, Namibia). However, *P. brevimanus* may be separated from *P. gracilis*, as well as *P. distridor*, *P. kuanyamarum* and *P. nanus*, on the basis of the following combination of characters: surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; pedipalp chela manus smooth; metasomal segments I–IV with dorsosubmedian carinae present, but obsolete; metasomal segments II and III, distal section of ventrolateral carinae, and posteroventral margin composed of strongly elevated, crescent-shaped tubercles, forming a broad U-shaped pattern; metasomal segment IV, anteroventral margin demarcated by a transverse



Figures 10–12.—Diagnostic characters of *Parabuthus* species [modified from Lamoral (1979)]. 10, 11. Dextral pecten of ♀, ventral aspect. 10. *Uroplectes carinatus* (Pocock 1890). 11. *Parabuthus gracilis* Lamoral 1979. 12. *Parabuthus stridulus* Hewitt 1913, distal segments of dextral leg I, dorsal aspect, illustrating macrosetal combs along retrolateral edge. Scale bars = 1 mm.

row of 5–6 strongly elevated crescent-shaped tubercles; metasomal segment V with distally diverging ventrolateral carinae, each comprising several prominent lobate processes subdistally.

Remarks.—Purcell (1901) listed *P. cristatus* as a junior synonym of *P. brevimanus*, but placed a question mark next to the synonymy, as he had not examined the type specimens. Kraepelin (1908) confirmed the synonymy by comparing the type specimens. Most subsequent authors adopted the synonymy (Kraepelin 1914; Hewitt 1918; Lawrence 1955), but Lamoral & Reynders (1975) continued to regard *P. cristatus* as a distinct species. Lamoral (1979) later revised *P. brevimanus*, re-examined the type specimens of *P. brevimanus* and *P. cristatus*, and erroneously claimed that *P. cristatus* was a new synonym.

Distribution.—Recorded from Angola, Namibia, and South Africa. The distribution of this species extends across the Orange River.

Ecology.—*Parabuthus brevimanus* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty substrata, where it excavates burrows in open ground and at the base of shrubs and grass tufts. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype. Metasomal segments IV and V are mostly lacking carinae.

Parabuthus brevimanus is syntopic with *P.*

granulatus throughout its distributional range. *Parabuthus brevimanus* is less often syntopic with *P. laevifrons*, *P. schlechteri*, *P. villosus* and the closely related *P. gracilis*. *Parabuthus brevimanus* occupies a distinctly harder range of substrata than the sand dunes inhabited by *P. kuanyamarum* and *P. nanus* and, although Lamoral (1979) reports that these species are often sympatric, no records document their occurrence as such.

Material examined.—NAMIBIA: *Erongo Region*: Karibib District: Farm Kranzberg 59 [21°58′S 15°39′E], 23.iii.1976, B. Lamoral & L. Ferguson, 20 ♂, 5 ♀, 2 subad. ♂, 2 juv. ♂, 8 juv. ♀ (NMSA 10819); Farm Sandamap 64, 21°56′S 15°16′E, 13.ii.1969, B.H. Lamoral, 1 ♀ (NMSA 10010) [homotype designated by Lamoral (1979)]. SOUTH AFRICA: *Northern Cape Province*: Namaqualand District: Richtersveld, Springbokvlakte [28°23′S 17°04′E], 20–21.ii.1973, B. Lamoral, 3 ♂, 1 ♀, 1 juv. ♀ (NMSA 10442).

Parabuthus calvus Purcell 1898
Figs. 47–60, Table 1

Parabuthus calvus Purcell 1898: 28–30, pl. IV, fig. 7; Purcell 1901: 148, 149; Kraepelin 1908: 250; Hewitt 1918: 104; Lawrence 1955: 226; Lamoral & Reynders 1975: 515; Kovařík 1998: 116; Fet & Lowe 2000: 201; Prendini 2001a: 17; Prendini 2001b: 137; Prendini 2003: 20.

Type material.—Holotype ♂ (SAMC 1201), SOUTH AFRICA: Onder Bokkeveld, Bokkeveld Mountains [31°20′S 19°04′E], Calvinia [*Northern Cape Province*: Calvinia District], M. Schlechter, 1897. At the time of publication of my first contribution on the phylogeny of *Parabuthus* (Prendini 2001a), a thorough search for the holotype of *P. calvus* had failed to locate it in the SAMC or any other South African museum. The holotype was subsequently discovered by Dr. G.J. Müller at the Department of Pharmacology, University of Stellenbosch, among material loaned from the SAMC many years earlier.

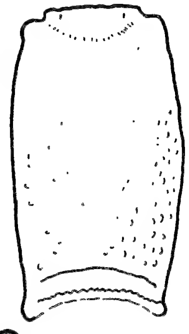
Diagnosis.—*Parabuthus calvus* is similar to *P. planicauda*, with which it shares the following combination of characters: pedipalp chela manus of adult male, slender as in adult female; proximal median lamella of pectines in male, lobate; metasomal segments broad (length IV/width IV: 1.2–1.5); basitarsi of legs I and II, macrosetal combs weakly developed; metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous; metasomal segment V, dorsosubmedian carinae poorly developed with blunt, rounded granules, dorsolateral carinae distally obsolete.

Parabuthus calvus may be separated from *P. planicauda*, and all other species of *Parabuthus*, on the basis of the following combination of characters: surface of median ocular tubercle (male, female), surrounding surfaces of carapace (female), and lateral intercarinal surfaces of metasomal segments IV and V, smooth and shiny; pedipalp chela manus, metasomal segments I–V and telson virtually asetose; proximal median lamella of pectines in male, strongly lobate; basitarsi of legs III and IV, prolateral surfaces with dense tufts of macrosetae; metasomal segment IV, median lateral, ventrosubmedian and ventrolateral carinae absent; metasomal segment V, ventromedian carina absent.

Redescription.—The following description supplements Purcell's (1898) original description of the male and subsequent description of the female (Purcell 1901), and is based on the holotype male (SAMC 1201), and three female specimens (AMNH; SAMC 2228, C4615).

Color (based on a recently collected female specimen in the AMNH): Carapace, tergites and sternites: Clay Color No. 123B. Metasoma and telson: Yellow Ocher No. 123C. Chelicerae, pedipalps and legs: Buff-Yellow No. 53. Pectines: Pale Horn Color No. 92. Pedipalps, legs, chelicerae, metasoma and telson are slightly lighter than carapace and tergites (Figs. 51, 52). Metasomal segments and telson are uniformly shaded.

Carapace: Carapace sparsely covered by uniform, coarse granulation on interocular and posterolateral surfaces (male) or entirely smooth (female). Anterior and posterior margins of carapace straight or slightly procurved (Figs. 47, 49, 51). Five pairs of lateral ocelli. Median ocelli considerably larger than lateral ocelli, situated anteromedially. Ocular tubercle with pair of smooth superciliary carinae, protruding slightly above median ocelli. An-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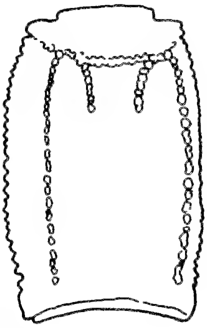
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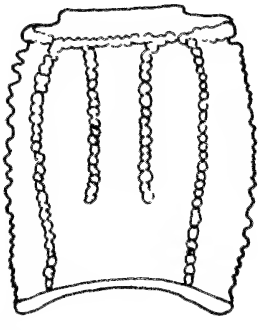
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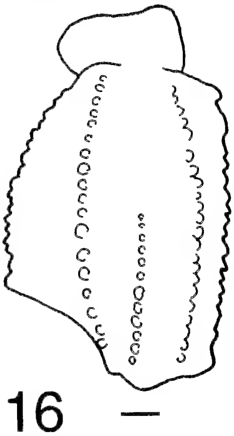
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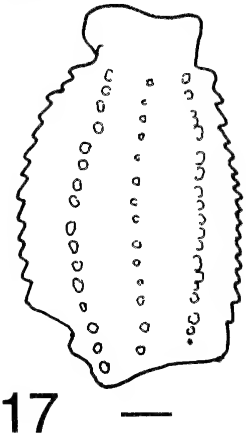
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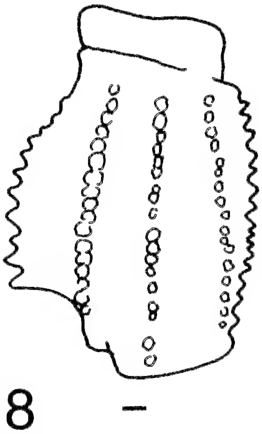
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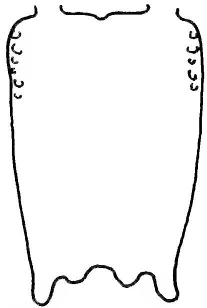
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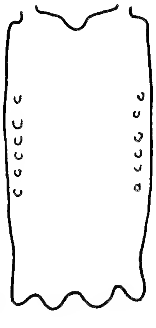
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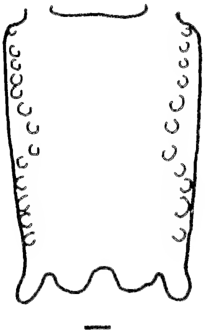
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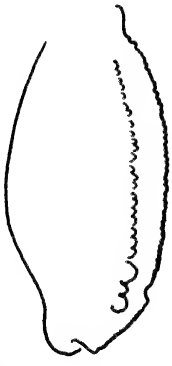
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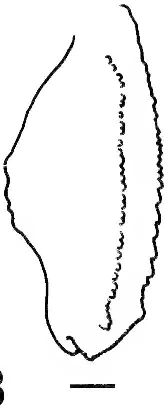
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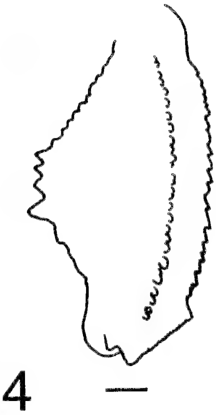
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teromedian furrow shallow; posteromedian furrow shallow anteriorly, becoming deeper posteriorly; posterolateral furrows shallow, wide and curved; posteromarginal furrow narrow, deep.

Chelicerae: Movable finger with distal external and distal internal teeth equal, opposable. Ventral aspect of fingers and manus with long, dense macrosetae. Fixed finger with a pair of denticles on ventral surface.

Sternum: Type I, subtriangular (Figs. 48, 50, 52). Median longitudinal furrow Y-shaped, shallow anteriorly, deep, narrow posteriorly.

Pedipalps: Pedipalps virtually asetose (Figs. 47–52). Femur dorsal surface finely and uniformly granular (male) or smooth (female), all other surfaces smooth (Fig. 59); pentacarinate, all carinae distinct, granular, except for internomedian carina, comprising spiniform granules, and costate externomedian carina. Patella smooth (Figs. 57, 58); carinae absent or obsolete; dorsointernal and ventrointernal carinae each comprising few granules proximally; internomedian carina comprising large spiniform granule, proximally (male, female), and few smaller granules, distally (male only). Chela smooth (Figs. 55, 56); carinae absent. Chela long, slender (male, female), length along ventroexternal carina 38% (male) or 24–31% (female) greater than chela width and 37% (male) or 24–28% (female) greater than chela height (Table 1); length of movable finger 66% (male) to 69–70% (female) greater than length along ventroexternal carina. Chela fixed and movable fingers straight, such that proximal dentate margin linear when fingers closed (Figs. 55, 56). Dentate margins of chela fingers with 11–12 oblique granular rows, each comprising 4–6 small granules and large proximal granule, flanked by inner and outer accessory granules; chela fingers each with terminal denticle.

Trichobothria: Orthobothriotaxic, type A, α configuration (Figs. 55–59), with following segment totals: femur, 11 (5 dorsal, 4 internal, 2 external), patella, 13 (5 dorsal, 1 internal, 7 external) and chela, 15 (8 manus, 7 fixed finger). Total number of trichobothria per pedipalp, 39. Chela with *eb* situated proximal to basal dentate margin of fixed finger, and *esb* situated distal to it; *dt* distinctly distal to *et*; *db* closer to *est* than to *esb*. Patella with esb_2 level with esb_1. Femur with d_2 on proximointernal side of dorsointernal carina; d_3 distal to d_2; d_4 closer to d_3 than to d_5.

Mesosoma: Pre-tergites smooth, shiny (male, female), granular along posterior margins (male only). Post-tergites entirely covered with very fine, even granulation, imparting matt appearance (male) or smooth, shiny (female); I–VII each with weakly developed, costate median carina (male) or without median carina (female); VII additionally with distinct pairs of costate granular dorsosubmedian and dorsolateral carinae, and well-developed stridulatory surface between dorsosubmedian carinae, consisting of round to slightly crescent-shaped granules reaching posterior margin. Sternites entirely smooth; lateral and distal margins each with few macrosetae; sternite VII with pairs of costate ventrosubmedian and ventrolateral carinae obsolete to absent (Figs. 48, 50, 52).

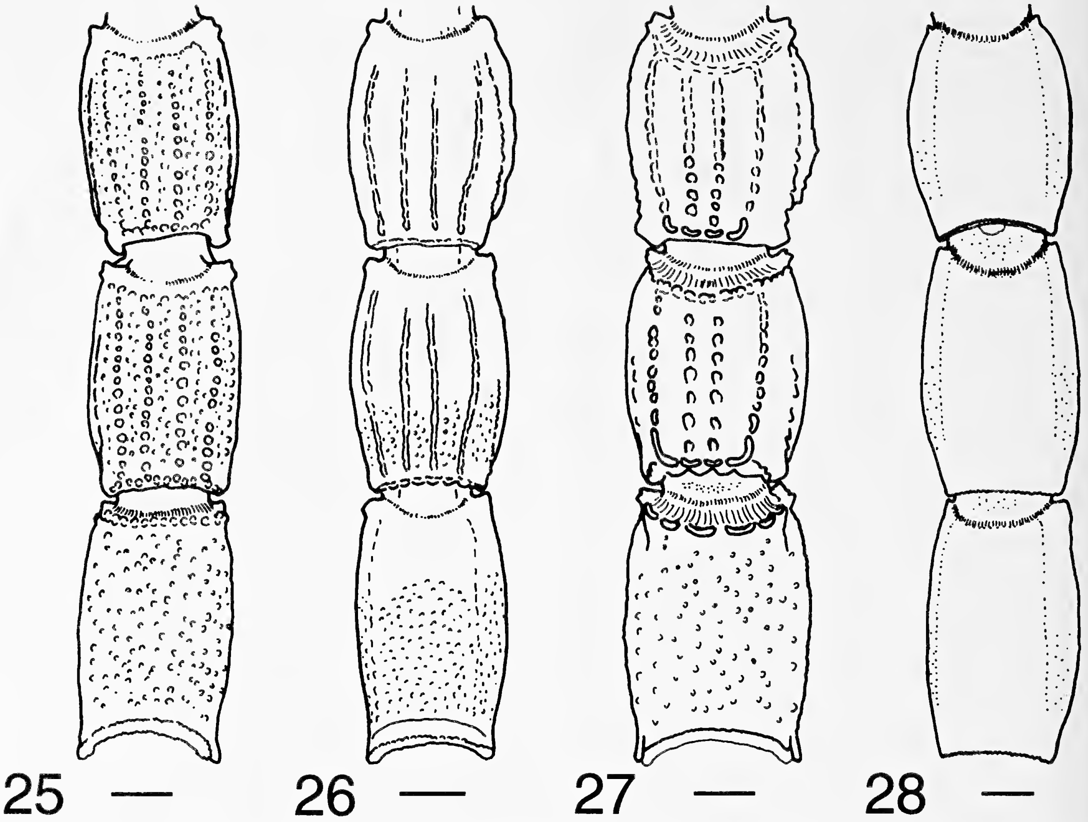
Pectines: First proximal median lamella of each pecten suboval, mesally enlarged, lobate in female and, to lesser extent, in male (Figs. 48, 50, 52). Pectinal teeth: 25/26 (male), 23–24/23–24 (female).

Genital operculum: Completely divided longitudinally. Genital papillae present (male), absent (female).

Legs: Tibiae III and IV with spurs; retrolateral margins with scattered macrosetae. Basitarsi I and II not dorsoventrally com-

←

Figures 13–24.—Diagnostic characters of *Parabuthus* species. 13–15. Metasomal segment IV, ventral aspect, illustrating carinal development. 13. *Parabuthus nanus* Lamoral 1979. 14. *Parabuthus kalaharicus* Lamoral 1977. 15. *Parabuthus villosus* (Peters 1862). 16–18. Metasomal segment IV, lateral aspect, illustrating carinal development. 16. *Parabuthus granulatus* (Ehrenberg 1831). 17. *Parabuthus laevifrons* (Simon 1888). 18. *Parabuthus villosus*. 19–21. Metasomal segment V, dorsal aspect, illustrating carinal development. 19. *Parabuthus stridulus* Hewitt 1913. 20. *Parabuthus namibensis* Lamoral 1979. 21. *Parabuthus transvaalicus* Purcell 1899. 22–24. Metasomal segment V, lateral aspect, illustrating carinal development. 22. *Parabuthus laevifrons*. 23. *Parabuthus namibensis*. 24. *Parabuthus schlechteri* Purcell 1899. Scale bars = 1 mm.



Figures 25–28.—Diagnostic characters of *Parabuthus* species [25–27 modified from Lamoral (1979)]. Metasomal segments II–IV, ventral aspect, illustrating carinal development. 25. *Parabuthus kuanyamarum* Monard 1937. 26. *Parabuthus gracilis* Lamoral 1979. 27. *Parabuthus brevimanus* (Thorell 1876). 28. *Parabuthus distridor* Lamoral 1980. Scale bars = 1 mm.

pressed, retrolateral margins each with sparse row of long, fine macrosetae; III and IV, prolateral surfaces with dense tufts of macrosetae. Telotarsi each with paired ventrosubmedian rows of fine macrosetae. Telotarsal laterodistal lobes truncated; median dorsal lobes extending to ungues. Telotarsal ungues short, distinctly curved, equal in length.

Metasoma and telson: Metasomal segments I–V width/length ratio progressively decreasing (Table 1), width percentage of length 114% (male) or 93–101% (female) for I, 107% (male) or 89–94% (female) for II, 107% (male) or 85–94% (female) for III, 88% (male) or 72–78% (female) for IV, and 73% (male) or 60–67% (female) for V. Telson oval, globose, height 65% (male) or 57–70% (female) of length, with flattened dorsal surface, rounded ventral surface; vesicle not distinctly narrower than metasomal segment V, width 81% (male) or 77–80% (female) of metasomal segment V. Metasoma entirely smooth, except for stridulatory surfaces on dorsal surfaces of segments I and II, each consisting of fine round to slightly crescent-shaped granules extending to posterior margin (Fig. 51); segment III with stridulatory surface absent (female) or obsolete (male), comprising few granules in proximal third of segment; segments II and III with posterodorsal edge straight (Fig. 51). Metasoma almost asetose, with few short macrosetae on ventral surface of telson (Figs. 47–52). Metasomal segments I–III each with ten distinct carinae; segments IV and V each with four obsolete carinae, IV with paired dorsosubmedian and dorsolateral carinae, all other carinae absent, V with paired dorsosubmedian carinae, comprising few rounded granules medially, and paired ventrolateral carinae, reduced to few granules and lobate processes subdistally, all other carinae absent. Metasomal segments I–V with dorsosubmedian carinae converging distally in segment I, subparallel in segments II–V; ventrolateral carinae converging distally in segments I–III, diverging in segment V. Dorsosubmedian and dorsolateral carinae weakly granular, ventrosubmedian and ventrolateral carinae of segment I costate, of segments II and III costate granular, of segment V granular. Metasomal segments I–IV with distal granules of dorsosubmedian carinae very slightly enlarged; segments II and III with distal granules of ventrosubmedian carinae and, to lesser extent, ventrolateral carinae, distinctly enlarged, obtuse, elevated; segment V with subdistal granules of ventrolateral carinae enlarged into laterally compressed, lobate processes. Aculeus short, sharply curved, 51% (43–59%) of vesicle length.

Hemispermatophore: Flagelliform.

Geographic variation: The female from Betjesfontein (SAMC 2228, Figs. 49, 50) is more granular than those from Vanrhynsdorp (SAMC C4615), Paulshoek (AMNH, Figs. 51, 52), Komaggas (ZMHB 11365) further to the north. In SAMC 2228, the interocular and posterolateral surfaces of the carapace are sparsely, but coarsely granular, the median surfaces of the tergites are finely granular, the posterior margins of the tergites are coarsely granular (these surfaces are smooth in the other specimens), and the metasomal carinae are more strongly developed. The metasoma and telson of SAMC 2228 are also more setose than the other specimens.

Ontogenetic variation: All known specimens are adult.

Sexual dimorphism: Unlike most species of *Parabuthus* (except *P. muelleri*, *P. nanus*, *P. pallidus* Pocock 1895 and *P. planicauda*), *P. calvus* is not sexually dimorphic with respect to the shape of the chela manus. The manus of the adult male is slender and similar in shape to that of the adult female (Pocock 1890, 1902; Purcell 1898, 1901; Kraepelin 1908; Hewitt 1918; Prendini 2001a; Figs. 55, 56). However, the adult male is proportionally more slender than the adult female, and differs in the other characters mentioned above (Figs. 47, 48).

Remarks.—*Parabuthus calvus* has not been revised since the original description of the male (Purcell 1898), and subsequent description of the female (Purcell 1901). However, it can be readily distinguished from all other species of the genus on the basis of the diagnostic characters provided above.

This species is extremely rare in collections. It is presently known from only five specimens (1 ♂ and 4 ♀, all examined for this study), each from a different locality.

Distribution.—All known localities fall within the Namaqualand region of the Northern and Western Cape provinces of South Africa, to which this species is endemic (Fig. 60). No records are known from north of the Orange River.

Ecology.—The only specimen for which collection data are available (AMNH) was collected at night by means of UV light detection. This specimen was found resting on the surface of coarse, granitic loam soil, in a rocky habitat. As with the related species, *P. planicauda*, elongation of the pedipalps and legs are indicative of a semi-lithophilous ecomorphotype, whereas reduction in the macrosetal combs of basitarsi I and II in *P. calvus* may be associated with its occurrence in regions of hard, compacted soil (Eastwood 1977; Prendini 2001a). Metasomal segments IV and V are mostly lacking carinae.

Although the distribution of *P. calvus* overlaps entirely with that of *P. capensis*, it is not known whether these species occur in sympatry.

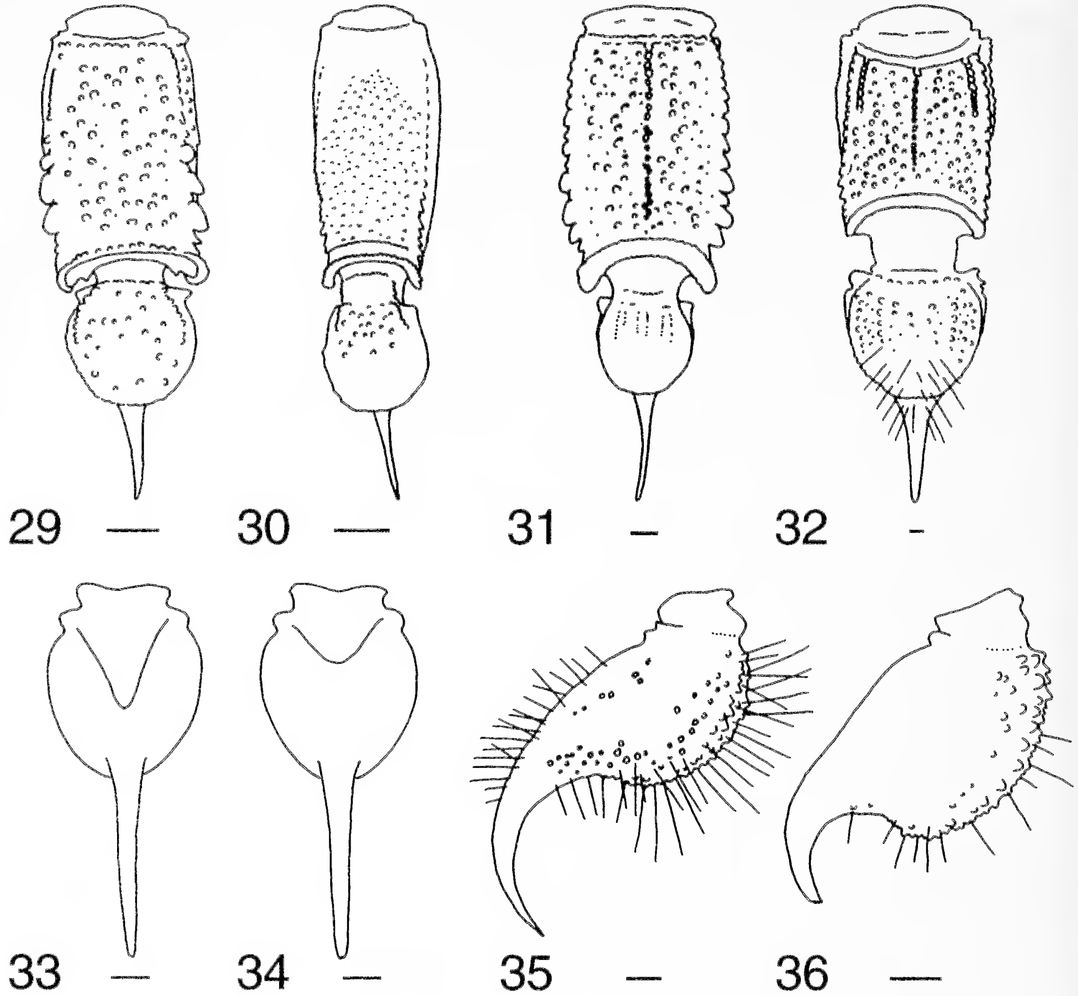
Material examined.—SOUTH AFRICA: *Northern Cape Province*: Namaqualand District: Kamaggas [Komaggas, 32°07′S 19°07′E], v. 1904, L. Schultze, 1 ♀ (ZMHB 11365); Paulshoek, E of Garies, 30°22′S 18°16′E, i.1997, S. Todd, 1 ♀ (AMNH). *Western Cape Province*: Clanwilliam District: Betjesfontein [Biesjesfontein, ca. 32°07′S 19°07′E], 1898, M. Bergh, 1 ♀ (SAMC 2228). Vanrhynsdorp District: Knersvlakte, N of Vanrhynsdorp, 31°37′S 18°44′E, 1999, M. de Jager, 1 ♀ (SAMC C4615).

Parabuthus capensis (Ehrenberg 1831)
Figs. 3, 35, 61–74, Table 1

Androctonus (*Prionurus*) *capensis* Ehrenberg in Hemprich & Ehrenberg 1831 [pages unnumbered]; Moritz & Fischer 1980: 311.

Androctonus iros C.L. Koch 1839: 93, 94, pl. CLXIX, fig. 401 (synonymized by Kraepelin 1899: 31; Kraepelin 1908: 254); C.L. Koch 1850: 89.

Scorpio (*Androctonus*) *kochii* Gervais 1844: 45



Figures 29–36.—Diagnostic characters of *Parabuthus* species [29, 30 modified from Lamoral (1979), 35 modified from Eastwood (1977), 36 modified from Prendini (2000)]. 29–32. Metasomal segment V and telson, ventral aspect. 29. *Parabuthus brevimanus* (Thorell 1876). 30. *Parabuthus kuanyamarum* Monard 1937. 31. *Parabuthus granulatus* (Ehrenberg 1831). 32. *Parabuthus villosus* (Peters 1862). 33, 34. Telson, dorsal aspect. 33. *Parabuthus stridulus* Hewitt 1913. 34. *Parabuthus laevifrons* (Simon 1888). 35, 36. Telson, lateral aspect. 35. *Parabuthus capensis* (Ehrenberg 1831). 36. *Parabuthus muelleri* Prendini 2000. Scale bars = 1 mm.

(synonymized by Kraepelin 1899: 31; Kraepelin 1908: 254).

Parabuthus planicauda: Pocock 1889: 344–346 (misidentification: males only).

Parabuthus capensis: Kraepelin 1895: 83; Pocock 1895: 309; Kraepelin 1899: 31; Penther 1900: 154; Kraepelin 1901: 267; Purcell 1901: 143–147; Werner 1902: 598; Kraepelin 1908: 254; Hewitt 1912: 302; Kraepelin 1914: 110, 111; Lampe 1917: 193; Hewitt 1918: 107, 178, pl. XXI, fig. 29; Werner 1936: 178; Roewer 1943: 207; Lawrence 1946: 399; Lawrence 1955: 226; Belfield 1956: 45; Lamoral & Reynders 1975: 515; Eastwood 1977: 200–203, figs. 1, 3a, 4, 6a, 7; Eastwood 1978a: 244; Kovařík 1992: 184; Braunwalder & Fet 1998: 29–35; Kovařík 1998: 116; Fet & Lowe 2000: 201, 202; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 20.

Parabuthus neglectus Purcell 1899b: 433–434 (synonymized by Kraepelin 1908: 254); Purcell 1901: 155–158; Pocock 1902: 366; Eastwood 1977: 203–207, figs. 2, 3b, 5, 6b, 7; Kovařík 1998: 117; Fet & Lowe 2000: 208.

Type material.—*Androctonus* (*Prionurus*) *capensis:* Holotype ♀ (ZMHB 133), SOUTH AFRICA: Cape of Good Hope [*Western Cape*

Province: Simon's Town District: 34°00′S 18°25′E], Lichtenstein.

Androctonus iros: Holotype, "southern Africa" [lost].

Parabuthus neglectus: Lectotype: 1 subad. ♂ (SAMC 1197/1) [designated by Eastwood (1977)], SOUTH AFRICA: between Pakhuisberg [32°10′S 19°00′E] and Oorlogskloof [31°30′S 19°27′E], Clanwilliam and Calvinia Divs. [*Western Cape Province*: Clanwilliam District/*Northern Cape Province*: Calvinia District], 1897, M. Schlechter. Paralectotypes: 2 ♂, 9 ♀, 1 subad. ♂, 1 subad. ♀, 1 juv. ♀ (SAMC 1197/2), same data as lectotype.

Diagnosis.—*Parabuthus capensis* forms part of a group of species that also includes *P. calvus*, *P. capensis*, *P. pallidus* and *P. planicauda* (Fig. 1). It is morphologically most similar to *P. muelleri*, with which it shares the following combination of characters: metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform or subspiniform granules, dorsolateral carinae distally obsolete.

Parabuthus capensis and *P. muelleri* may be separated from all other *Parabuthus* on the basis of the following character: metasomal segment II, and to a lesser extent III, with posterodorsal edge elevated and slightly curved forward medially, forming a subtriangular V-shape. *Parabuthus capensis* may be separated from *P. muelleri* by the following characters: pedipalp chela, fixed and movable fingers straight, such that proximal dentate margin linear when fingers are closed (i.e., no proximal "gap" is evident); metasomal segment I narrower than segment IV; telson without distal "bulge"; aculeus long, gently curved; pedipalp chela manus of adult male, incrassate (bulbous or swollen), compared with adult female, in which it is slender; proximal median lamella of pectines in male, not lobate.

Redescription.—The following redescription supplements Eastwood's (1977) redescriptions of *P. capensis* and *P. neglectus*. It is based on several typical specimens of *P. capensis* (SAMC C98, C4567), several specimens of the "dark form" of *P. capensis* (SAMC C36, C74, C4564), the syntypes of *P. neglectus* (SAMC 1197), and several additional specimens that would key to the latter (SAMC C3830, C4513, C4565).

Color (based on SAMC C3830): Carapace, pedipalps and metasomal segments I–III: Yellow Ocher No. 123C. Tergites and sternites: Cinnamon No. 39. Metasomal segments IV and V: Clay Color No. 123B. Telson: Tawny No. 38. Chelicerae and legs: Buff-Yellow No. 53. Pectines: Cream Color No. 54. Metasomal segments IV, V and telson are slightly to considerably darker than segments I–III (Figs. 53–64), except in the dark form (Figs. 65–68).

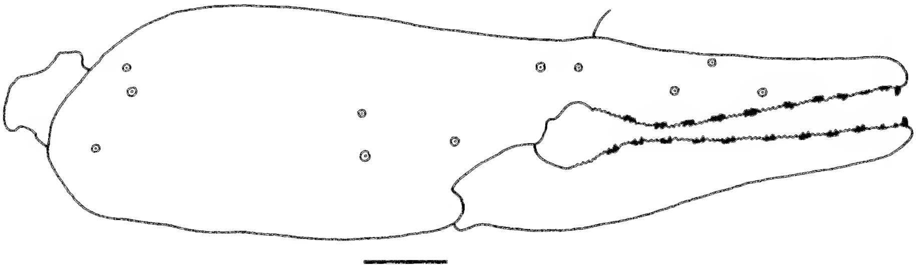
Carapace: As for *P. calvus*, except as follows. Carapace covered entirely by uniform, coarse granulation, becoming coarser on interocular and posterolateral surfaces. Anterior margin of carapace procurved; posterior margin straight (Figs. 53, 61, 63).

Chelicerae: As for *P. calvus*.

Sternum: As for *P. calvus* (Figs. 54, 62, 64).

Pedipalps: As for *P. calvus*, except as follows. Pedipalps covered in short macrosetae (Figs. 53, 54, 61–68). Femur finely and uniformly granular (Fig. 73); pentacarinate, all carinae distinct, granular, except for internomedian carina, comprising spiniform granules. Patella finely and uniformly granular (Figs. 71, 72); carinae absent or obsolete; dorsointernal and ventrointernal carinae each comprising row of granules proximally; internomedian carina comprising large spiniform granule, proximally, and few smaller granules, distally. Chela smooth (Figs. 69, 70); carinae absent. Chela long, slender (female) or incrassate (male), length along ventroexternal carina 29–31% (male) or 26–37% (female) greater than chela width and 35–40% (male) or 34–41% (female) greater than chela height (Table 1); length of movable finger 30–33% (male) to 41–49% (female) greater than length along ventroexternal carina. Chela fixed finger straight or slightly curved dorsally and movable finger straight, such that proximal dentate margin linear when fingers closed (Figs. 69, 70).

Trichobothria: As for *P. calvus*, except as follows (Figs. 69–73). Chela with *dt* situated almost level with or slightly distal to *et*; *db*



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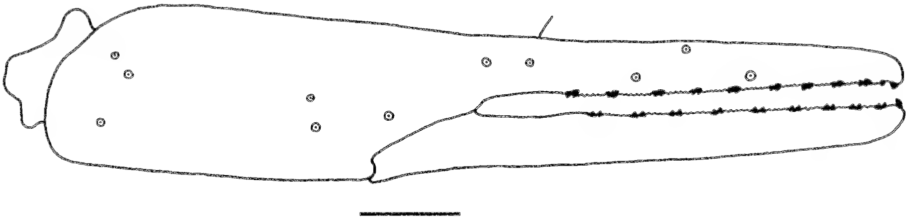

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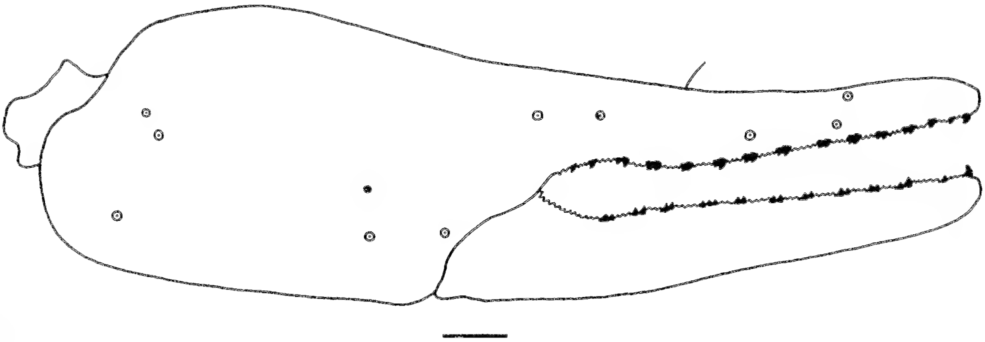

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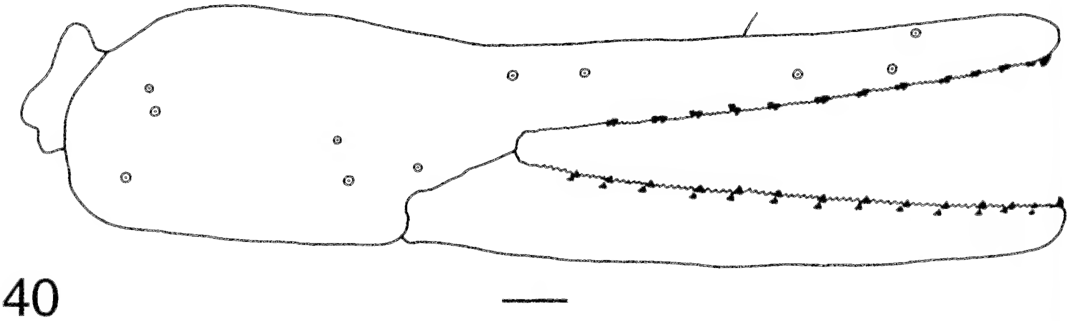

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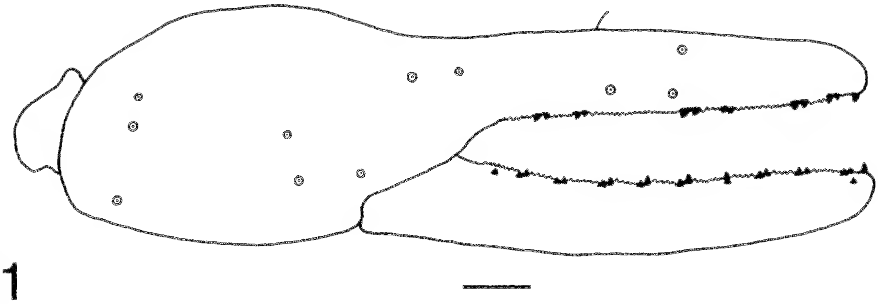

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equidistant between *est* and *esb*. Patella with esb_2 level with or slightly distal to esb_1.

Mesosoma: As for *P. calvus*, except as follows. Pre-tergites smooth, shiny, granular along posterior margins. Post-tergites entirely coarsely granular, granulation becoming coarser distally; I–VII each with weakly developed, granular median carina. Sternites entirely smooth, except for posterolateral surfaces of sternite VII, which are sparsely granular; lateral and distal margins each with sparse row of macrosetae; sternite VII with weakly developed pairs of costate ventrosubmedian and ventrolateral carinae (Figs. 54, 62, 64).

Pectines: First proximal median lamella of each pecten suboval, mesally enlarged, lobate in female but not male (Figs. 54, 62, 64). Pectinal teeth: 37–41/35–41 (male), 32–37/32–38 (female).

Genital operculum: As for *P. calvus*.

Legs: As for *P. calvus*, except as follows. Basitarsi I and II dorsoventrally compressed, retrolateral margins each with dense row of long, fine macrosetae; III and IV, prolateral surfaces without dense tufts of macrosetae. Telotarsal ungues long, distinctly curved, equal in length.

Metasoma and telson: Metasomal segments width/length ratio decreasing from I–II, increasing from II–III and decreasing from III–V (Table 1), width percentage of length 77–83% (male) to 82–95% (female) for I, 78–81% (male) to 81–88% (female) for II, 79–105% (male) to 86–89% (female) for III, 67–79% (male) to 74–77% (female) for IV, and 53–63% (male) to 59–60% (female) for V. Telson oval, globose, height 61–64% (male) or 59–72% (female) of length, with flattened dorsal surface, rounded ventral surface; vesicle not distinctly narrower than metasomal segment V, width 75–80% (male) to 83–86% (female) of metasomal segment V. Metasoma entirely granular, except for ventromedian surfaces of segments I or I and II, and dorsomedian surfaces of IV, V and telson, or V and telson. Metasomal segments I–III each with well-developed dorsal stridulatory surface, consisting of fine round to slightly crescent-shaped granules extending to posterior margin (Figs. 53, 67); stridulatory surface of segment III narrower and less developed than on preceding segments; segment II, and to lesser extent III, posterodorsal edge elevated and slightly curved forward medially, forming subtriangular V-shape (Fig. 3). Metasoma sparsely to densely covered with long macrosetae, especially on ventral surface of telson (Figs. 53, 54, 61–68). Metasomal segments I–IV each with ten carinae; segment IV with ventrosubmedian and median lateral carinae becoming obsolete distally; segment V with seven carinae, including single, obsolete granular ventromedian carina, pair of distinct ventrolateral carinae, pair of dorsolateral carinae, distinct only in proximal half of segment, and pair of dorsosubmedian carinae reduced to few prominent rounded or spiniform granules medially. Metasomal segments I–V with dorsosubmedian carinae converging distally in segment I, subparallel in segments II–V; ventrolateral carinae converging distally in segments I–III, subparallel in segment IV, subparallel to diverging in segment V. All metasomal carinae costate granular to granular, except for ventrosubmedian and ventrolateral carinae of segment I, which are costate to costate granular. Metasomal segments I–IV with distal granules of dorsosubmedian carinae slightly to considerably enlarged, spiniform; segments II and III with distal granules of ventrosubmedian carinae and, to lesser extent, ventrolateral carinae, distinctly enlarged, obtuse, elevated; segment V with subdistal granules of ventrolateral carinae enlarged into laterally compressed, lobate processes. Aculeus long, shallowly curved, 65% (57–73%) of vesicle length.

Hemispermatophore: Flagelliform, with *pars recta* parallel to axis of distal lamina.

Geographic variation: Parabuthus capensis exhibits considerable geographic variation in size, color, granulation, setation, and pectinal tooth count across its distributional range (Figs. 53, 54, 61–68; Table 1). Typical spec-

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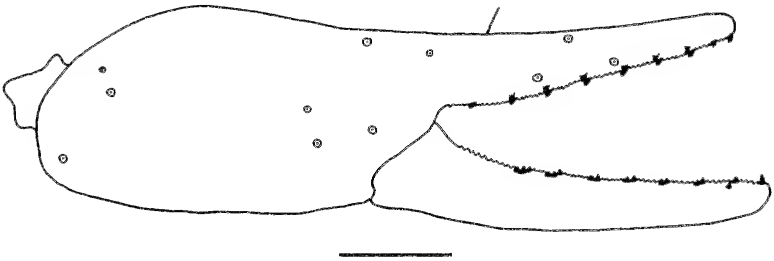
Figures 37–41.—Diagnostic characters of *Parabuthus* species [37–40 modified from Lamoral (1979), 41 modified from Prendini (2000)]. Dextral pedipalp chela. 37. *Parabuthus kalaharicus* Lamoral 1977, ♂. 38. *Parabuthus kalaharicus*, ♀. 39. *Parabuthus granulatus* (Ehrenberg 1831), ♂. 40. *Parabuthus granulatus*, ♀. 41. *Parabuthus muelleri* Prendini 2000, ♀. Scale bars = 1 mm.



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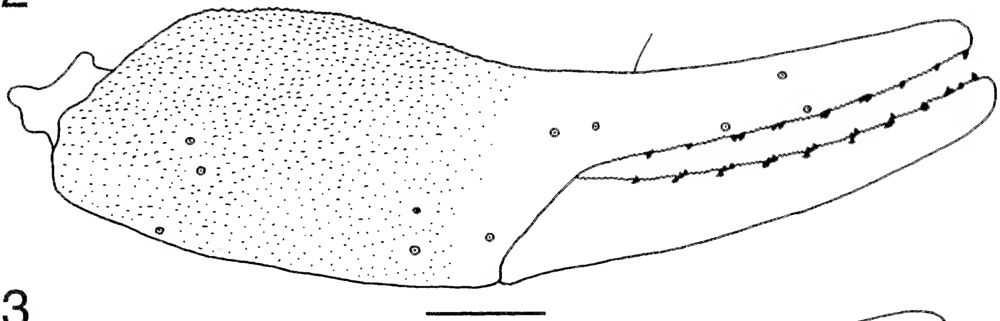

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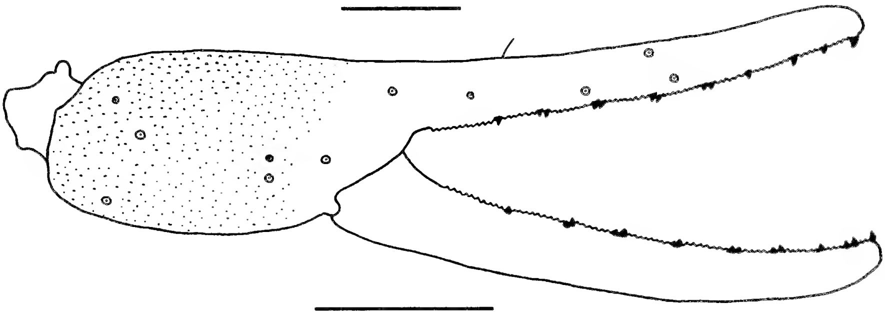

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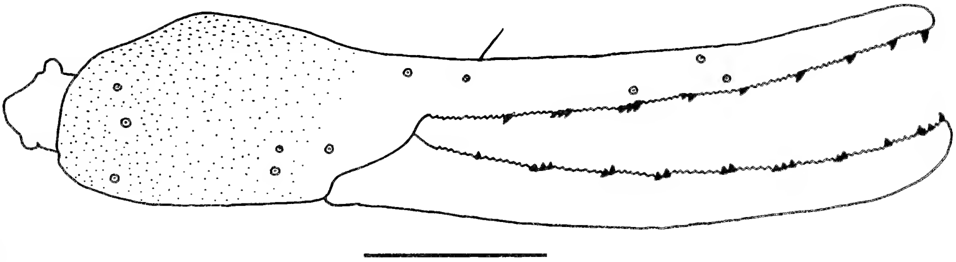

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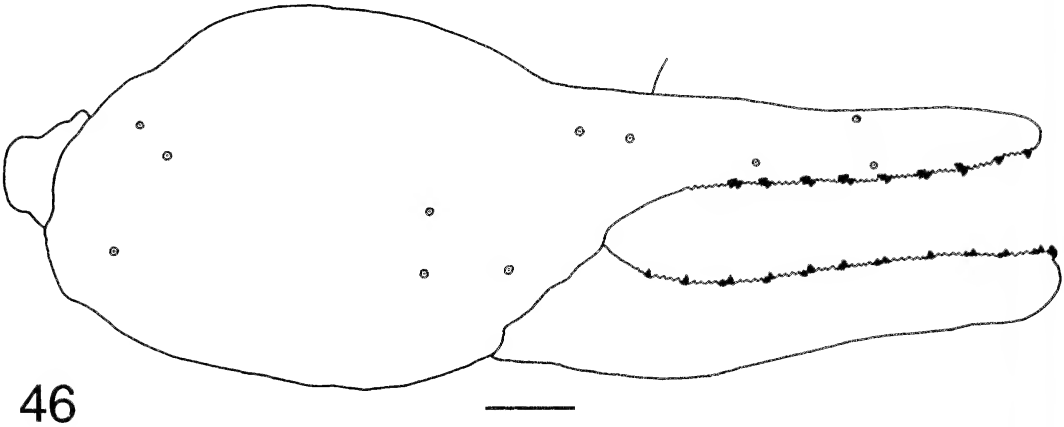

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imens from mesic fynbos and renosterveld habitats in the southwestern part of the distribution are smaller, uniformly pale in color, more sparsely setose (especially on the metasoma and telson), less coarsely granular, with weaker development of the metasomal carinae, with the posterodorsal edge of metasomal segments II and III less strongly curved anteriorly, and with a lower pectinal tooth count (Figs. 63–64). A dark brown to black form, differing from typical *P. capensis* only in color (Figs. 65–68), occurs in the coastal part of this region (Eastwood 1977).

Specimens from xeric karroid habitats further north and east in the range are larger, often display a characteristic darkening of metasomal segments IV, V and telson, are more densely setose (especially on the metasoma and telson), more coarsely granular, with stronger development of the metasomal carinae, with the posterodorsal edge of metasomal segments II and III more strongly curved anteriorly, and with a higher pectinal tooth count (Figs. 53, 54, 61, 62). Eastwood (1977) regarded these differences as sufficient justification for resurrecting *P. neglectus* as a species, distinct from *P. capensis*. As argued below, these differences merely reflect intraspecific variation, perhaps associated with differences in habitat and possibly with a clinal basis. In contrast, distinct differences in venom composition between pale specimens of *P. capensis* (referable to *P. neglectus* or to the typical form) and specimens of the dark form (Dyason et al. 2002), suggest that the dark form may represent a sibling species (Paterson 1985), a question that is currently under investigation with DNA sequence data.

Ontogenetic variation: As in other species of *Parabuthus*, male resembles female very closely until the final instar. Juveniles and subadults may be readily sexed by examination of the pectines and genital aperture.

Sexual dimorphism: Besides the abovementioned characters, *P. capensis* is sexually dimorphic with respect to the shape of the chela manus, as in most species of *Parabuthus*. The manus of the adult male is noticeably incrassate, compared with that of the adult female, which is more slender (Pocock 1889, 1890, 1902; Kraepelin 1899, 1908; Purcell 1898, 1899b, 1901; Werner 1916; Hewitt 1913, 1915, 1918; Eastwood 1977; Lamoral 1977, 1979, 1980; Newlands & Martindale 1980; Figs. 69, 70). In addition, adult males are proportionally more slender than adult females (Figs. 61, 62, 65, 66).

Remarks.—*Androctonus capensis* was described by Ehrenberg (in Hemprich & Ehrenberg 1831), not by Hemprich & Ehrenberg (1831), as recorded in most literature (e.g., Eastwood 1977). Since this description, seven taxa have been listed in synonymy by various authors: *Scorpio teter*, *Androctonus iros*, *Scorpio kochii*, *Prionurus mossambicensis*, *Buthus brevimanus* var. β *segnis*, *Buthus planicauda*, and *Parabuthus neglectus*. Kraepelin (1891) erroneously listed the first six taxa, and *P. capensis*, in synonymy with *P. leiosoma* (as *Heterobuthus liosoma*) but subsequently (Kraepelin 1899) retracted this synonymy, perhaps on the advice of Pocock (1895), who suggested that he had confused several valid species, including *P. planicauda*, under *P. leiosoma*. Pocock (1895) further suggested that *Androctonus iros* (as *P. iros*), *Buthus brevimanus* var. β *segnis* (as *P. segnis*) and *P. planicauda* might be synonymous with *P. capensis*.

Kraepelin (1899) listed *Androctonus iros*, *Scorpio teter* (as *Androctonus teter*), *Scorpio kochii* (as *Androctonus kochii*), *Prionurus mossambicensis* (as *Buthus mosambicensis*), *Buthus brevimanus* var. β *segnis* (as *Buthus segnis*), and *Buthus planicauda* in synonymy with *P. capensis*. *Androctonus iros* and *S. kochii* were also listed as synonyms of *P. capensis* by subsequent authors (Purcell 1899b, 1901; Lamoral & Reynders 1975; Fet & Lowe 2000). *Scorpio kochii* was a replacement name, created by Gervais (1844) when he transferred *A. capensis* to the genus *Scorpio*, in order to avoid homonymy with *Scorpio capensis* Herbst 1800, now *Opistophthalmus ca-*

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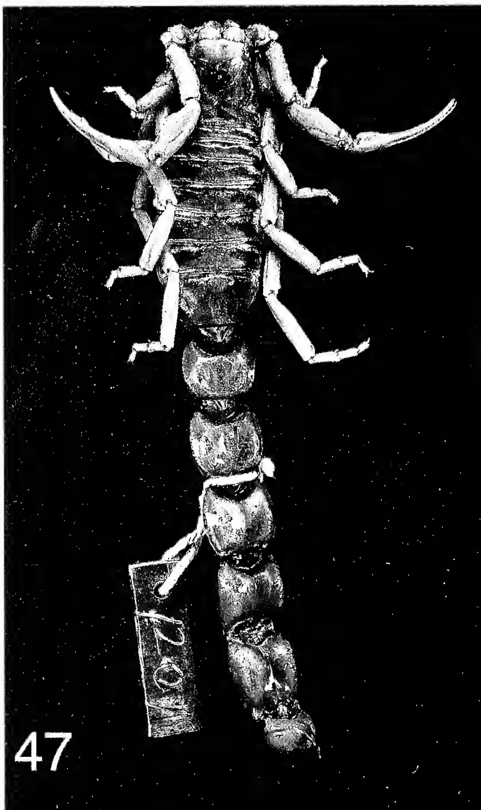
Figures 42–46.—Diagnostic characters of *Parabuthus* species [42 modified from Lamoral (1980), 43–46 modified from Lamoral (1979)]. Dextral pedipalp chela. 42. *Parabuthus distridor* Lamoral 1980, ♂. 43. *Parabuthus gracilis* Lamoral 1979, ♂. 44. *Parabuthus nanus* Lamoral 1979, ♂. 45. *Parabuthus nanus*, ♀. 46. *Parabuthus laevifrons* (Simon 1888), ♂. Scale bars = 1 mm.



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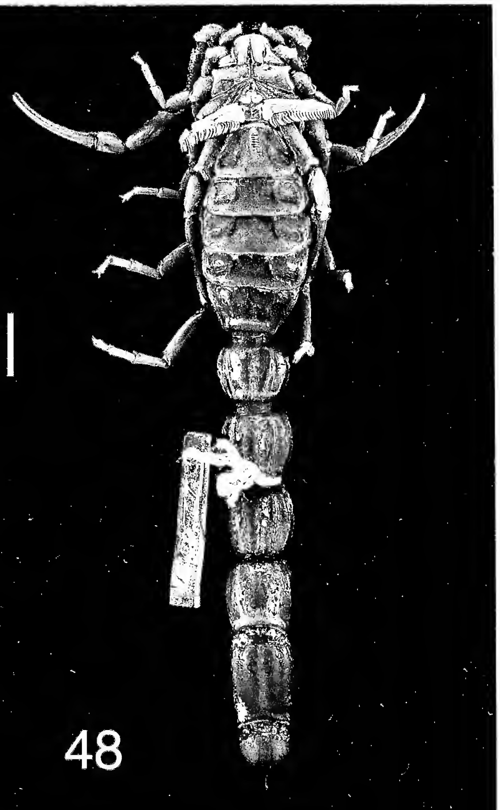

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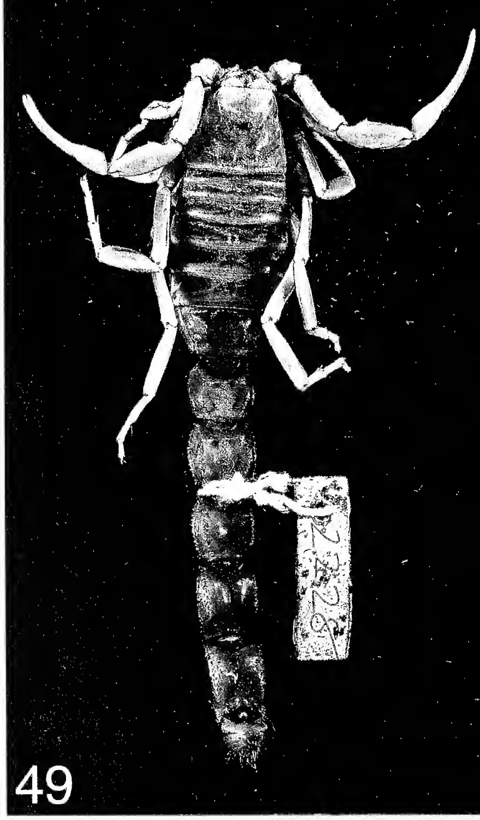

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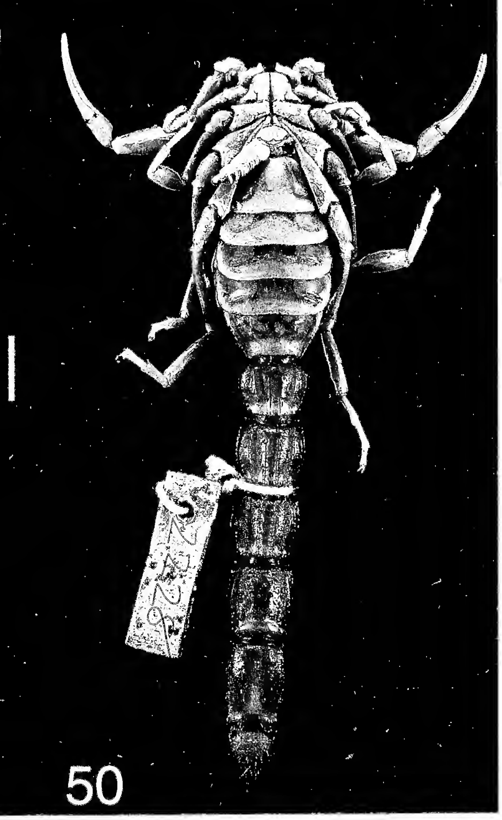

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pensis (Herbst 1800), family Scorpionidae (Fet & Lowe 2000). *Scorpio teter*, ignored since Kraepelin (1899), was recently discussed by Fet & Lowe (2000), who listed it as a synonym of *P. capensis*. In the present study, it is instead synonymized with *P. transvaalicus* (discussed below). Similarly, *B. brevimanus* var. β *segnis*, listed as a synonym of *P. capensis* by some authors (e.g., Lamoral & Reynders 1975; Fet & Lowe 2000), is synonymized with *P. granulatus* (discussed below). *Parabuthus mossambicensis* has not been regarded as a synonym of *P. capensis* since Kraepelin (1899).

The superficial morphological similarity between *P. planicauda* and *P. capensis*, which are sympatric in the southwestern part of their distributional ranges (Eastern, Northern and Western Cape provinces of South Africa), has caused widespread confusion in the literature about the status of these species, and resulted in the description of *P. neglectus*.

According to Pocock's (1889) original description of *P. planicauda*, the pedipalp chela manus of the adult male is round and considerably thicker than the patella. Pocock (1895) was the first to suggest that *P. planicauda* might be synonymous with *P. capensis*. In response to Pocock's suggestion, Kraepelin (1899) listed *P. planicauda* as a synonym in his redescription of *P. capensis*. Meanwhile, Purcell (1899b) also listed *P. planicauda* as a synonym of *P. capensis* and described a new species, *P. neglectus*. According to Purcell (1899b) the metasoma of *P. neglectus* is similar that of *P. capensis*, but the posterodorsal edge of segment II is strongly elevated and curved forwards in the middle, forming a characteristic tongue-like elevation that is also present, but less strongly developed, in segment III. In addition, the pedipalp chela manus and patella of females and juveniles is unusually wide, the chela manus being almost as wide as that of the adult male.

Purcell (1901) redescribed *P. capensis*, again listing *P. planicauda* in synonymy, and stated that its principal feature is the narrow chela manus of the adult male. According to Purcell (1901), the manus of the adult male is incrassate in almost all other species of *Parabuthus*, including *P. neglectus*, and statements by previous authors that this is also the case in *P. capensis* represented the confusion of several species. Purcell (1901) referred not only to Pocock (1889) but also to Kraepelin (1899), who had stated that the chela manus of the male *P. capensis* is much thicker than that of the female. In his key to the *Parabuthus* species, Purcell (1901) reiterated the difference between *P. neglectus*, in which the posterodorsal edge of metasomal segment II is strongly elevated and curved forwards in the middle, and the remaining species of *Parabuthus*, in which it is straight. Purcell (1901) further commented on the large stridulatory surface of metasomal segments II and III, and the stout pedipalp patella in *P. neglectus*.

Pocock (1902) realized that the two male specimens in his original description of *P. planicauda* were conspecific with *P. neglectus*, whereas the female specimens were conspecific with the form that Purcell (1899b, 1901) had referred to as *P. capensis*. Contradicting his earlier opinion (Pocock 1895), Pocock (1902) presented three lines of evidence to support his view that *P. capensis* and *P. planicauda* were distinct species and that Purcell (1899b) had redescribed *P. capensis* as *P. neglectus*. (1) The types of *P. capensis* in the Berlin Museum probably came from German rather than from British territory in South Africa. *Parabuthus neglectus* inhabits German South-West Africa [now Namibia], but *P. planicauda* does not. [This was only recently confirmed (Prendini 2000)]. (2) When Ehrenberg described *P. capensis*, he also described *P. granulatus*, which is known to occur in German South-West Africa, where it coexists with *P. neglectus*. It is possible that the types of both species were collected together. [This is incorrect because the type locality for both *P. capensis* and *P. granulatus* is the Cape of Good Hope, formerly British territory]. (3) Several specimens from Keyserling's collection in the British Museum, identified as "*Prionurus capensis*", are labelled "Cap b. espér.". According to Pocock, these specimens were identified by F. Karsch, who had

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Figures 47–50.—*Parabuthus calvus* Purcell 1896, habitus (dorsal and ventral aspects). 47, 48. Holotype ♂ (SAMC 1201). 49, 50. ♀ (SAMC 2228). Scale bars = 5 mm.

Table 1.—Meristic data for *Parabuthus calvus* Purcell 1898, *P. capensis* (Ehrenberg 1831) and *P. planicauda* (Pocock 1896), including syntypes of *P. neglectus* Purcell 1899 (SAMC 1197) and *P. capensis frenchi* Purcell 1901 (SAMC 5207), and specimens of the "dark form" of *P. capensis* (SAMC C4564). Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2000). [1]Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; [2]sum of tergites I–VII; [3]sum of metasomal segments I–V and telson; [4]measured from base of condyle to tip of fixed finger; [5]sinistral pecten missing, dextral damaged.

		Parabuthus calvus Purcell				*Parabuthus capensis* (Ehrenberg)	
Specimen	sex	♀	♀	♀	♂	♀	♀
	collection	SAMC	SAMC	AMNH	SAMC	SAMC	SAMC
	number	2228	C4615		1201	C98	C4513
	type				holotype		
Total length[1]		62.05	70.63	66.40	62.95	92.77	90.08
Carapace	length	6.78	7.69	6.89	6.98	9.95	9.72
	anterior width	4.16	4.38	4.05	3.60	5.82	5.68
	posterior width	7.73	8.63	7.52	7.66	10.74	10.19
Mesosoma	total length[2]	16.86	21.51	19.28	19.16	26.37	25.01
Sternite VII	length	4.85	5.09	4.80	4.70	6.70	5.87
	width	7.25	8.11	7.24	7.67	9.85	9.81
Metasoma	total length[3]	38.41	41.43	40.23	36.81	56.45	55.35
Metasoma I	length	5.55	5.98	5.80	5.04	8.29	7.81
	width	5.16	6.03	5.40	5.74	6.79	6.95
Metasoma II	length	5.89	6.40	6.04	5.47	8.47	8.26
	width	5.38	6.04	5.35	5.88	6.88	7.25
Metasoma III	length	6.01	6.47	6.17	5.54	8.22	8.20
	width	5.40	6.05	5.27	5.94	7.13	7.28
Metasoma IV	length	6.40	7.39	6.94	6.40	9.10	9.24
	width	5.02	5.70	4.99	5.66	7.03	7.11
Metasoma V	length	7.58	8.04	7.91	6.96	10.85	10.36
	width	4.53	5.35	4.83	5.07	6.36	6.08
Telson	total length	6.98	7.15	7.37	7.40	11.52	11.48
	aculeus length	2.10	2.49	2.74	2.69	4.19	4.50
	vesicle length	4.88	4.66	4.63	4.71	7.33	6.98
	vesicle width	3.60	4.14	3.85	4.09	5.44	5.25
	vesicle height	2.78	3.25	3.05	3.07	4.32	4.38
Pedipalp	total length	23.03	24.60	23.47	24.22	30.14	31.24
Femur	length	4.94	5.41	5.10	5.30	6.64	7.22
	width	1.61	1.82	1.68	1.79	2.59	2.45
Patella	length	5.68	6.50	6.05	5.90	6.89	7.42
	width	2.16	2.56	2.39	2.32	3.57	3.64
Chela	length[4]	9.69	10.18	9.85	10.34	12.73	13.58
	width	1.50	1.70	1.71	1.59	2.94	3.24
	height	1.56	1.73	1.71	1.60	3.03	3.05
	length of ventroext. carina	2.17	2.34	2.26	2.55	4.57	5.18
	length movable finger	7.12	7.73	7.31	7.43	8.28	8.83
Pectines	total length	5.20	6.03	5.54	5.58	8.95	10.60
	length dentate margin	4.11	4.86	5.01	5.49	8.50	9.14
	tooth count (left/right)	–/13[5]	24/23	23/24	25/26	32/32	37/38

access to Ehrenberg's types for comparison, and are conspecific with *P. neglectus*, not *P. planicauda*. (4) Kraepelin described the male of *P. capensis* as having a wide pedipalp chela manus. This is true of *P. neglectus*, not *P. planicauda*. Kraepelin also had access to Ehrenberg's type.

Pocock's (1902) suspicions were correct. Purcell (1899b, 1901) had not examined the holotype of *P. capensis* [Eastwood (1977) lat-

Table 1.—Extended.

Parabuthus capensis (Ehrenberg)				*Parabuthus planicauda* (Pocock)			
♀ SAMC C4564	♂ SAMC 1197 syntype	♂ SAMC C4565	♂ SAMC C4564	♀ BMNH 1870.26 lectotype	♀ SAMC 5207 syntype	♂ SAMC 5207 syntype	♂ SAMC C4580
99.12	79.07	75.28	56.46	85.30	75.80	67.93	63.27
10.68	7.73	8.66	6.53	8.82	7.77	6.86	6.17
6.16	4.21	5.20	3.42	5.37	4.55	4.26	3.61
11.90	7.73	8.90	6.56	10.14	7.87	7.27	6.17
27.00	23.09	19.95	12.72	24.13	20.65	18.69	17.66
6.30	5.70	5.73	3.47	5.57	4.92	4.63	4.51
11.69	7.82	8.32	5.61	9.45	8.88	7.13	6.19
61.44	48.25	46.67	37.21	52.35	47.38	42.38	39.44
8.14	6.86	7.62	5.71	7.37	6.44	6.15	5.83
7.72	5.67	6.18	4.37	6.44	5.46	4.70	4.39
9.66	7.18	8.12	5.73	7.75	6.89	6.36	5.85
7.78	5.78	6.46	4.45	6.46	5.33	4.76	4.54
9.28	7.25	7.75	5.73	7.95	7.24	6.49	5.94
8.01	5.88	8.16	4.51	6.52	5.34	4.94	4.35
10.48	8.11	9.02	5.74	8.89	7.95	7.37	6.68
7.72	5.63	6.04	4.51	6.44	5.15	4.76	4.25
11.78	9.58	10.40	6.42	10.36	9.25	7.89	7.65
6.97	5.15	5.51	4.03	5.78	4.71	4.28	3.93
12.10	9.27	11.22	7.88	10.03	9.61	8.12	7.49
5.03	3.64	4.71	3.32	3.83	3.97	2.81	2.84
7.07	5.63	6.51	4.56	6.20	5.64	5.31	4.65
5.76	4.14	4.42	3.04	4.63	4.04	3.38	3.08
5.08	3.58	3.97	2.83	3.88	3.66	3.17	2.53
33.89	27.36	31.60	22.63	30.36	28.27	27.43	23.11
7.55	5.88	6.75	5.04	6.78	6.23	6.36	5.36
2.77	2.00	2.41	1.65	2.14	2.21	1.75	1.66
7.87	6.27	7.77	5.54	7.58	6.95	6.59	5.64
4.15	2.55	3.67	2.39	3.16	2.75	2.12	2.12
14.68	12.08	13.38	9.69	12.25	11.69	10.91	9.28
3.59	3.53	3.86	2.73	2.50	2.23	1.77	1.71
3.19	3.12	3.52	2.39	2.39	2.16	1.69	1.66
4.82	5.00	5.41	3.98	4.04	3.66	3.33	2.96
9.40	7.12	7.97	5.93	8.54	8.23	7.35	6.06
10.54	9.33	10.36	8.14	9.32	8.85	8.68	7.61
9.44	9.14	9.98	8.01	8.13	8.11	9.17	8.13
34/34	37/35	41/41	38/38	31/31	34/35	40/40	34/34

er examined it and noted that the posterodorsal edge of segment II is elevated and slightly curved forward medially, forming a subtriangular "lip"]. Purcell (1899b, 1901), probably misled by Pocock's (1889) erroneous statement that the male of *P. planicauda* had round and thick hands, and Pocock's (1895) suggestion that *P. planicauda* was synonymous with

P. capensis, had redescribed *P. planicauda* as *P. capensis* and *P. capensis* as *P. neglectus*.

Kraepelin (1908) subsequently synonymized *P. neglectus* with *P. capensis*, and recognized the diagnostic differences (notably the shape of the posterodorsal edge of metasomal segment II) between *P. capensis* and *P. planicauda*, proposed originally by Purcell (1899b, 1901) for *P. neglectus* and *P. capensis*, respectively. Kraepelin (1914) again commented on the previous confusion between *P. capensis* and *P. planicauda* and on Purcell's (1899b) redescription of *P. capensis* as *P. neglectus*. The status of *P. capensis* and *P. planicauda* as distinct species has not been contested since, and, until Eastwood (1977), all authors similarly accepted the synonymy of *P. neglectus* with *P. capensis* (Hewitt 1912, 1918; Lawrence 1946; Lawrence 1955; Lamoral & Reynders 1975).

Eastwood (1977) redescribed *P. capensis* (including a distinctive dark color form), erroneously credited Hewitt (1918) with the synonymy of *P. neglectus*, and removed *P. neglectus* from synonymy. According to Eastwood (1977), *P. capensis* and *P. neglectus* are separable on the granulation of the dorsosubmedian carinae of metasomal segment V, the granulation of the ventrosubmedian and ventrolateral carinae, the posterodorsal "lip" of metasomal segments II and III, the density and length of meso- and metasomal setae, and the pectinal tooth count. The granules of the dorsosubmedian carinae on metasomal segment V are low and rounded in *P. capensis*, but elongated and sharply pointed in *P. capensis*. The ventrosubmedian and ventrolateral carinae of metasomal segments II and III consist of low, almost contiguous granules in *P. capensis* whereas, in *P. neglectus*, these carinae are separate and prominent. The posterodorsal edge of metasomal segments II and III is less strongly curved anteriorly in *P. capensis* than in *P. neglectus*. The meso- and metasomal setae are sparse and short in *P. capensis*, but long and dense in *P. neglectus*. The pectinal tooth count is lower in *P. capensis* (33–35 for males, 31–35 for females) than in *P. neglectus* (36–38 for males, 35–36 for females).

The first three diagnostic differences proposed by Eastwood (1977) are merely a function of increased granulation in *P. neglectus*, compared with *P. capensis*. As intraspecific variation in granulation has been shown to occur in many other species of *Parabuthus* (Lamoral 1979; Harington 1984; FitzPatrick 1994), these differences cannot be used for species delimitation. Similarly, the increased setation cannot be considered diagnostic, for this is also known to vary in other species of *Parabuthus*. For example, a considerable increase in the extent of setation on the meso- and metasoma occurs from north to south in the distributional range of *P. villosus* (Harington 1984). The increased granulation and setation of specimens referred to as *P. neglectus* may be correlated with occurrence on sandy substrata. Eastwood (1977) noted that *P. capensis* was always collected in areas of hard-packed soil whereas *P. neglectus* was always collected in sandy habitats. It thus appears that the increased granulation and setation, considered diagnostic for *P. neglectus*, is merely intraspecific variation in a widespread species, perhaps associated with differences in habitat. The moderate differences in pectinal tooth counts presented by Eastwood cannot be regarded as diagnostic either. Purcell (1899a) has stated that pectinal tooth counts should not be considered of specific importance as they are one of the first characters to change in local varieties. In view of this evidence, I hereby return *P. neglectus* to synonymy with *P. capensis*.

Distribution.—Endemic to the Lüderitz District (Karas Region) of Namibia and to the Eastern, Northern and Western Cape provinces of South Africa (Fig. 74). Lamoral (1979) omitted *P. capensis* from his revision of the scorpions of Namibia and the occurrence of this species north of the Orange River was only recently confirmed (Prendini 2000).

Ecology.—*Parabuthus capensis* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty sub-

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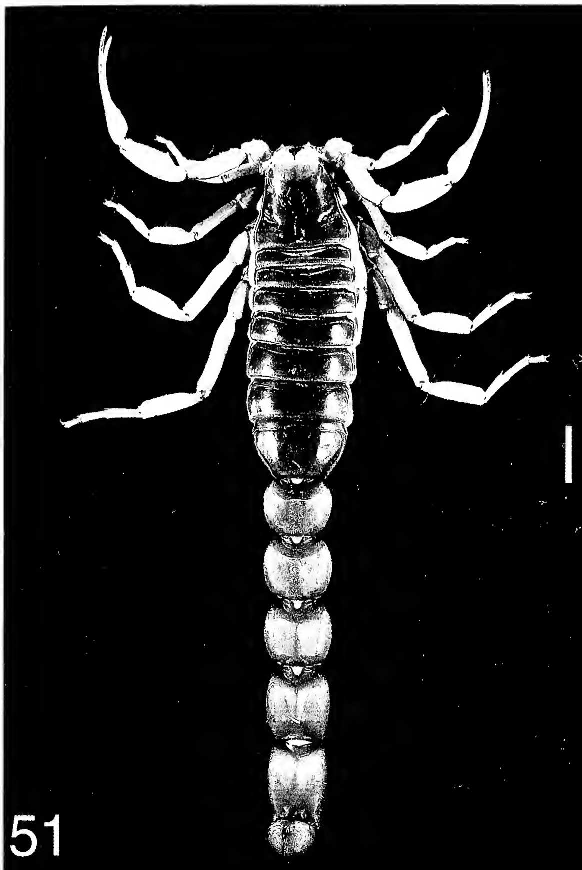
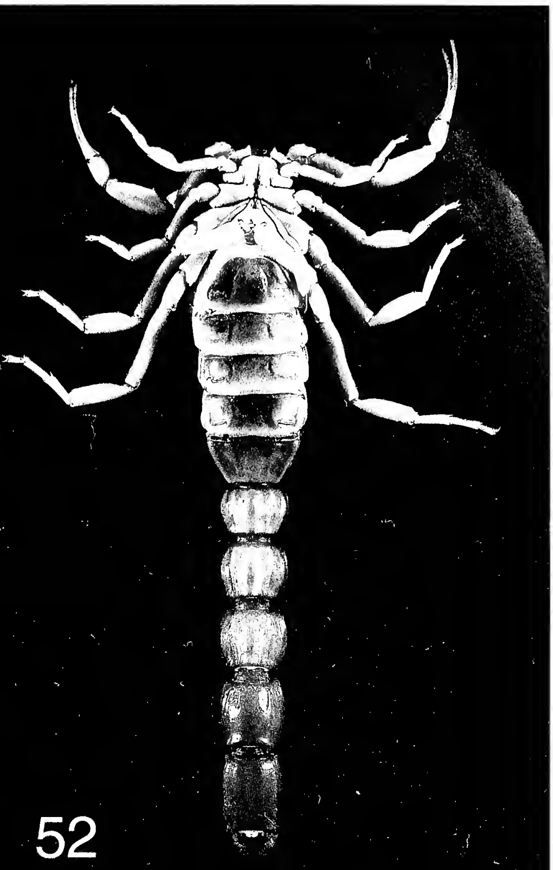
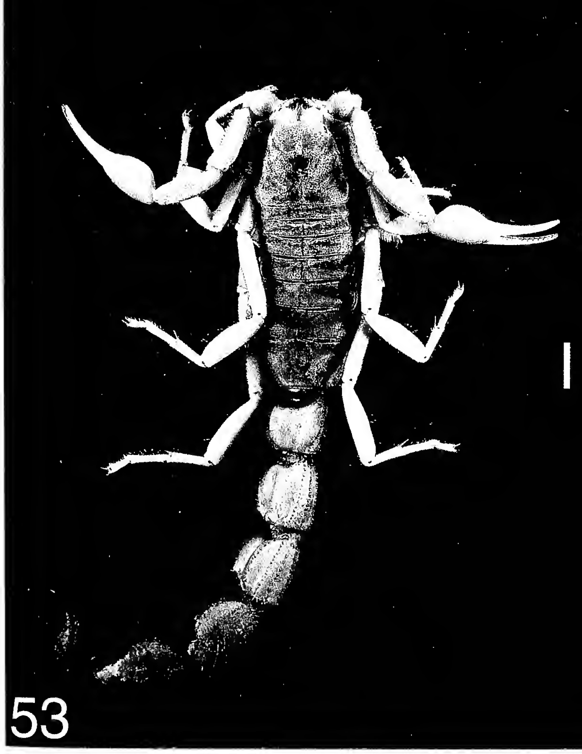
Figures 51–54.—Habitus (dorsal and ventral aspects). 51, 52. *Parabuthus calvus* Purcell 1896, ♀ (AMNH). 53, 54. *P. capensis* (Ehrenberg 1831), ♂ (SAMC C3830). Scale bars = 5 mm.



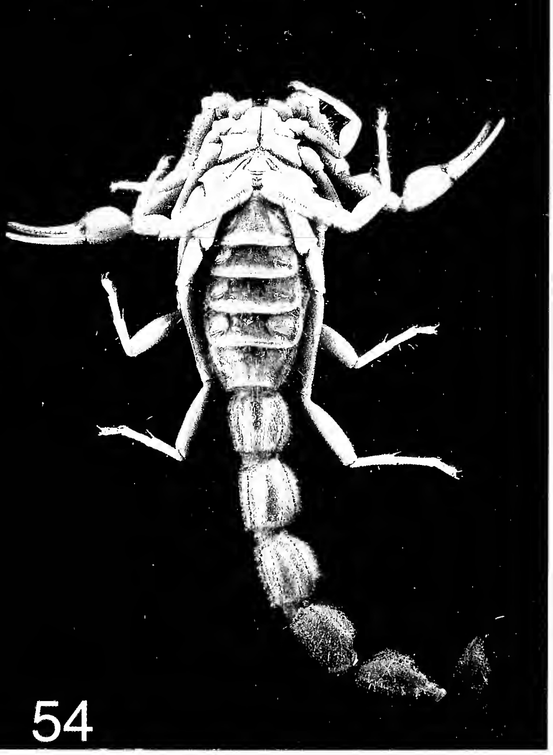
51



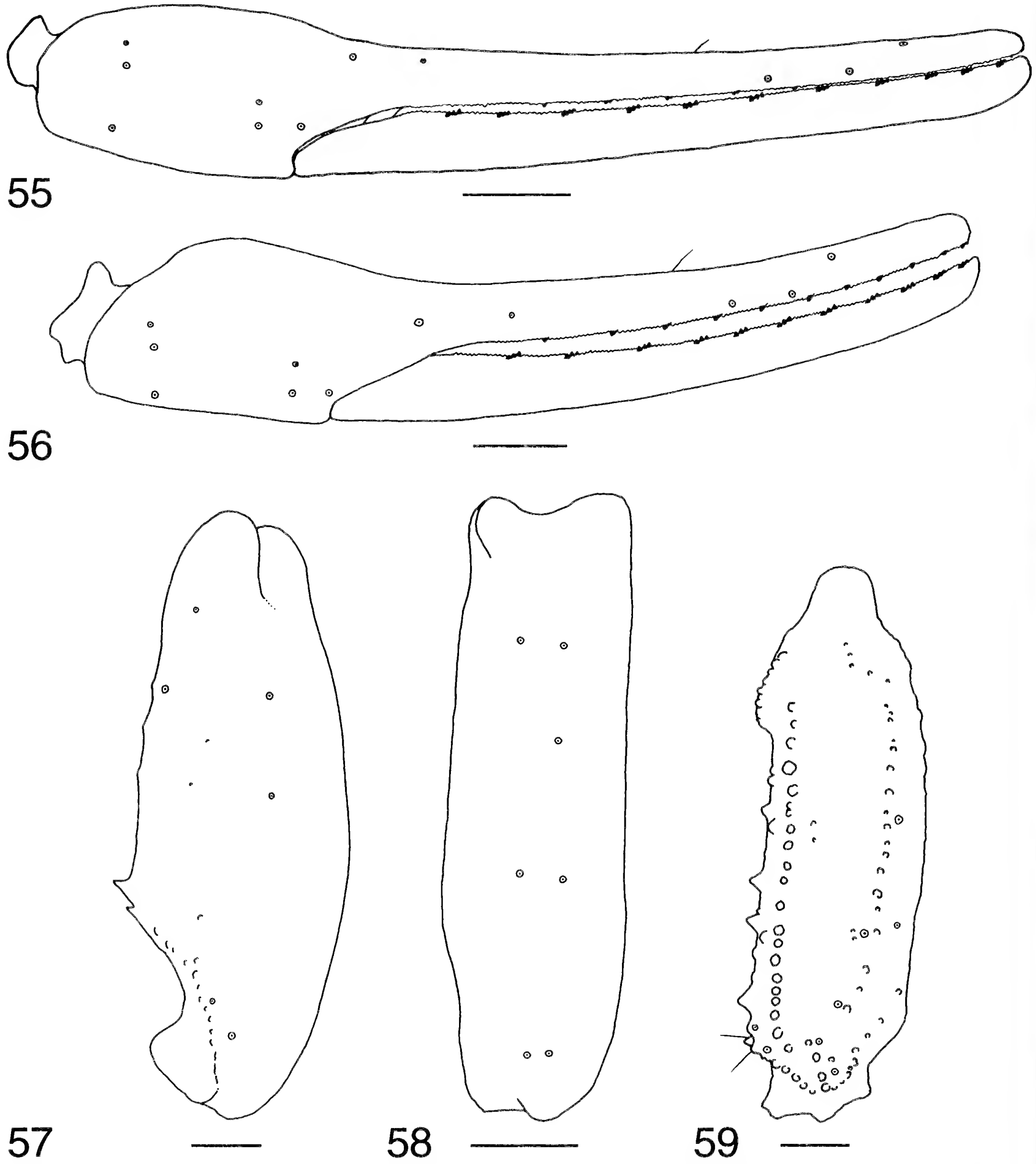
52



53



54



Figures 55–59.—*Parabuthus calvus* Purcell 1896, dextral pedipalp segments, illustrating shape, granulation and trichobothrial distribution. 55. Holotype ♂ (SAMC 1201). 56–59. ♀ (SAMC 2228). 55, 56. Chela, dorsal aspect. 57. Patella, dorsal aspect. 58. Patella, external aspect. 59. Femur, dorsal aspect. Scale bars = 1 mm.

strata, where it excavates burrows in open ground and at the base of shrubs and grass tufts. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semipsammophilous ecomorphotype.

Parabuthus capensis is syntopic with *P. brevimanus*, *P. distridor* and *P. granulatus* in parts of its range. The ranges of *P. capensis* and *P. planicauda* overlap extensively, and these species are occasionally found in syntopy. However, *P. capensis* is more commonly encountered in open sandy habitats, whereas *P. planicauda* frequents rocky habitats.

Material examined.—1 ♂ (SAMC C4533). NAMIBIA: vii.1988, ex M. Filmer, 1 ♀

(SAMC C4568). *Karas Region*: Lüderitz District, Farm Namuskluft 88 [27°53′S 16°50′E], 12–15.ix.1973, E. Mokgoabone, under stones, 1 ♂ (NMNW 480), 21–22.ix.1973, C.G. Coetzee, J. Batista & E. Mokgoabone, in sand, 1 ♀ (NMNW 487); Lüderitz [dubious] [26°40′S 15°10′E], iii.1988, J. Visser, 1 juv. ♂ (SAMC C3882). Fish River Canyon National Park: Boomrivier [28°01′S 17°04′E], 13.i–26.xi.1992, E. Marais, preservative pitfall trap, 1 ♂ (NMNW 1509). Lüderitz District, Diamond Area I: Aurus mountains (Sperrgebiet), Northern end [27°39′S 16°19′E], 19.ix.1978, R.A. Butler, 1 juv. ♀ (AMNH [AH 657]). SOUTH AFRICA: 2 ♂, 4 ♀, 3 subad. ♂, 1 juv. ♂, 6 juv. ♀ (SAMC), 1 ♂ (SAMC C3879), 1 ♀ (SAMC B627), 1 subad. ♂ (SAMC B628), 1895, W.F. Purcell, 1 juv. ♀ (SAMC 507). *Eastern Cape Province*: Graaff-Reinet District, Graaff Reinet [32°15′S 24°33′E] and Kruidfontein, 8 mi from Graaff Reinet [32°22′S 24°36′E], ix.1902, J. Paynter, 5 ♂, 2 ♀, 2 juv. ♀ (SAMC 12010). *Northern Cape Province*: Britstown District, Renostervlei, between Strydenburg and Britstown [30°11′20″S 23°47′51″E], 5.ii.1995, P. Horn, 1088 m, 1 ♀ (AMNH [AH 2506]), 1 subad. ♂ (AMNH [AH 2505]). Calvinia District: Bokkeveld, between Pakhuis Berg and Oorlogskloof [31°40′S 19°02′E], 1897, M. Schlechter, (SAMC 1197); Calvinia [31°25′S 19°45′E], i.1903, G. French, 2 ♀, 1 juv. ♂, 5 juv. ♀ (SAMC 12710), [31°28′S 19°47′E], 11.vi.1997, A. Harington, 2 ♀ (AMNH [AH 4670, 4770]); Farm Botterkloof 973 [31°48′S 19°18′E], 12.vi.1997, A. Harington, 2 subad. ♂ (AMNH [AH 5050, 5051]); Farm Klippe Rivier 630, 1.5 km from Nieuwoudtville on R27 to Vanrhynsdorp, 31°22.226′S 19°05.521′E, 18.ii.2003, L. Prendini & E. Scott, 2469 ft, sandstone outcrops, arid fynbos next to seep, under stone, 1 ♀ (AMNH); Nieuwoudtville, Bokkeveld Mts. [31°23′S 19°06′E], ix.1898, F. Treleaven, 2 ♂, 1 subad. ♂, 1 subad. ♀, 1 juv. ♀ (SAMC 4035); Onder Bokkeveld, Oorlogskloof [31°26′S 19°09′E], 1897, M. Schlechter, 2 ♀ (SAMC 1200); Van Rhyns Pass, Nieuwoudtville [31°23′S 19°01′E], 5.iv.1933, V. Fitzsimons, 1 ♂ (TMSA 6550). Gordonia District: Kakamas, 28°45′S 20°38′E, xii.1996, I. Engelbrecht, 1 ♂ (AMNH); Upington [28°27′S 21°15′E], Boonstra & Thorne, Kalahari Expedition, 1 ♂, 3 ♀, 5 subad. ♂ (SAMC B8943). Hanover District: Hanover [31°04′S 24°27′E], ix.1901, O. Schreiner, 2 ♀ (SAMC 9989). Namaqualand District: T. Wellington, 1 ♀, 1 subad. ♂ (SAMC B9450), viii.1972, 1 ♀, 1 subad. ♀, 1 juv. ♂ (SAMC C1376), 1885, L. Péringuey, 1 ♂, 1 ♀ (SAMC 472), 1897, L. Mally, 1 ♀, 1 juv. ♂ (SAMC C1743); 4 km E Beauvallon, NE of Alexander Bay [28°31′S 16°37′E], 28.i.1995, A. Harington, 1 ♂ (AMNH [AH 2545]); Aggeneys [29°12′S 18°51′E], 2.iii.1880, M. Schlechter, 1 ♂ (SAMC 2948); Base of Anenous Pass, 29°15.180′S 17°35.549′E, 25–27.ii.2003, L. Prendini & E. Scott, 550 m, UV detection on coarse sandy-loam flats at base of pass, succulent karoo, 4 ♂ (AMNH); Anenous Pass, 10 km E [29°14′S 17°42′E], 10.x.1983, J. Visser, 1 ♀ (SAMC C3824); Concordia [29°32′S 17°57′E], 1897, M. Schlechter, 1 ♀ (SAMC 1702); Concordia, 2 km N [29°31′S 17°56′E], 13.i.1995, A. Harington, 1 ♂ (AMNH [AH 2377]), 1 ♀ (AMNH [AH 2376]); Doringpoort, Richtersveld [28°34′S 16°56′E], 7.ix.1976, S. Endrödy-Younga, 1 juv. ♂ (TMSA 12222), 1 juv. ♀ (TMSA 12221); Eksteenfontein, 1–2 km NE [28°49′S 17°14′E], 2.vi.1997, A. Harington, 2 ♀ (AMNH [AH 4964, 4965]), 1 subad. ♂ (AMNH [AH 4966]); Eksteenfontein, 6 km NE [28°47′S 17°16′E], 20.i.1995, A. Harington, 3 ♂ (AMNH [AH 2636–2638]); Farm Gemsbokvlakte [30°23′S 17°23′E], 1.ix.1977, S. Endrödy-Younga, 1 juv. ♀ (TMSA 11660); Farm Perdekraal [30°46′S 17°53′E], 24.viii.1979, S. Endrödy-Younga, 1 ♀ (TMSA 12285), 1 subad. ♂ (TMSA 12286); Farm Quaggafontein [30°08′S 17°38′E], 29.viii.1977, S. Endrödy-Younga, 1 subad. ♂ (TMSA 11654), 1 juv. ♂ (TMSA 11655); Farm Rondabel [30°47′S 17°50′E], 24.viii.1979, S. Endrödy-Younga, 2 subad. ♂ (TMSA 12287, 12289); Farm Rooidam [31°04′S 17°48′E], 26.viii.1979, S. Endrödy-Younga, 1 ♀ (TMSA 12294); Farm Schaaprivier 208, W of Springbok [29°40′S 17°36′E], 27.v.1997, A. Harington, 1 ♂ (AMNH [AH 4812]); Farm Waterval [31°03′S 17°46′E], 25.viii.1979, S. Endrödy-Younga, 2 subad. ♀ (TMSA 12290, 12292), 2 juv. ♀ (TMSA 12291, 12293); Farm Wolfkraal 367 [30°00′S 18°32′E], 9.vi.1997, A. Harington, 1 ♂ (AMNH [AH 5013]); Garies [30°33′S 17°59′E], 1897, M. Schlechter, 1 ♀, 2 subad. ♂ (SAMC 1703), v.1928, B. Peers, 4 ♀, 1 juv. ♀ (SAMC B7295), 18.xi.1975, E.B. Eastwood, 1 juv. ♂ (SAMC C43), 21.v.1997, A.

Harington, 1 ♀ (AMNH [AH 4726]); Groenriviermond [30°51′S 17°35′E], 30.xi.1976, V.B. Whitehead, under stone, 1 juv. ♂ (SAMC C1337); Hartbeesfontein, near Steinkopf [29°14′S 17°48′E], 1897, M. Schlechter, 1 juv. ♂ (SAMC 1713); Helskloof Pass, Richtersveld [28°18′S 16°58′E], 1 subad. ♂ (TMSA 17646); Hoekbaai, 2 km ENE [31°11′S 17°47′E], 27.viii.1979, S. Endrödy-Younga, 1 ♀ (TMSA 12303); Hoits Mine, 10 km E of Springbok [29°54′S 17°57′E], 18.iv.1986, J. Visser, 1 subad. ♂ (SAMC C3867); Holgat, Port Nolloth [29°17′S 16°51′E], 9.iii.1985, J. Visser, 1 ♀ (SAMC C3856); Jakkalsputs, Richtersveld [28°40′S 16°57′E], 21.xi.1975, V.B. Whitehead, on red sand dunes at night, 1 ♀ (SAMC C49); Kamies [30°17′S 18°04′E], vii.1929, B. Peers, 1 ♂, 1 ♀ (SAMC B7314); Kamieskroon [30°12′S 17°56′E], ix.1930, S.A. Museum expedition, 1 ♀, 2 subad. ♂, 1 subad. ♀ (SAMC B7338); Kamieskroon, 20 km E [30°12′S 18°03′E], 19.xi.1975, E.B. Eastwood, under stone, 1 ♀ (SAMC C37); Khubus, Richtersveld [28°27′S 16°59′E], 1.vi.1997, A. Harington, 3 ♀ (AMNH [AH 4896–4898]); Kuboos [Khubus], Richtersveld [28°27′S 17°00′E], R. Smithers, 1 ♂, 2 ♀, 1 subad. ♂ (SAMC B8944), i.1911, C.L.L. Biden, 1 ♂ (SAMC B571); Khubus, ca. 10 km SE (on Farm The Richtersveld 11), 28°25.450′S 17°00.189′E, 1.iii.2003, L. Prendini & E. Scott, 300 m, UV detection in rocky canyon at start of 4x4 trail, succulent karoo, 3 ♂, 1 ♀, 1 juv. ♂, 3 juv. ♀ (AMNH); Kinderlê, 8 km N of Steinkopf [29°11′S 17°48′E], 16.x.1987, J. Visser, 1 ♀ (SAMC C3877); Richtersveld, 8 km N of Kinderlê [29°05′S 17°47′E], v.1987, J. Visser, 1 ♀ (SAMC C3871); Klein Kogelfontein [31°10′S 17°50′E], 27.viii.1979, S. Endrödy-Younga, 1 subad. ♂ (TMSA 12297); Kleinsee [29°40′S 17°05′E], ix.1987, J. Visser, 1 ♂ (SAMC C3878), 1 ♀ (SAMC C3881); Klipdam, SE of Nababeep [29°38′S 17°50′E], 26.v.1997, A. Harington, 1 ♂ (AMNH [AH 4795]); Klipfontein [29°14′S 17°39′E], 1899, R.H. Howard, 1 juv. ♂ (SAMC 5152); Klipfontein mountain, W Steinkopf [29°14′S 17°39′E], 17.i.1995, A. Harington, 1 ♀ (AMNH [AH 2413]); Komaggas [29°48′S 17°30′E], 14.i.1995, A. Harington, 4 ♂ (AMNH [AH 2622–2625]); Kotzesrus [30°57′S 17°50′E], 23.viii.1979, S. Endrödy-Younga, 4 ♀ (TMSA 12273, 12278, 12283, 12284), 4 subad. ♂ (TMSA 12274, 12275, 12277, 12279), 1 juv. ♂ (TMSA 12281); Lekkersing [29°00′S 17°06′E], 30.xi.1962, 1 ♀ (TMSA 14089); Lekkersing, 7 km NW (turnoff 0.85 km from last house on road to Richtersveld National Park), 29°00.723′S 17°02.086′E, 28.ii.2003, L. Prendini & E. Scott, 265 m, UV detection on red sand dune and sandy/alluvial flats in dry riverbed, succulent karoo, syntopic with *P. distridor*, 1 subad. ♂, 1. subad. ♀, 1 juv. ♂, 1. juv. ♀ (AMNH); Lekkersing, 6 km S [29°03′S 17°07′E], 20.i.1995, A. Harington, 3 ♂ (AMNH [AH 2633–2635]), 1 ♀ (AMNH [AH 2632]); Lekkersing, 12 km S [29°06′S 17°07′E], 20.i.1995, A. Harington, 3 ♂ (AMNH [AH 2592, 2594, 2595]), 1 ♀ (AMNH [AH 2593]); Leliefontein [30°19′S 18°05′E], 20.ix.1985, A. V. Evans, 1 ♂ (AMNH [AH 4269]), 1 ♀ (AMNH [AH 4268]); Little Rock, near Springbok [29°38′S 17°52′E], iv–v.1978, S. Salter, 1 ♂ (AMNH [AH 672]), 1 ♀ (AMNH [AH 671]), 1 subad. ♂ (AMNH [AH 673]), xii.1978, S. Salter, 1 ♀ (AMNH [AH 801]); McDougall Bay (near Port Nolloth), 1 km E [29°17′S 16°53′E], 19.i.1995, A. Harington, 1 ♂ (AMNH [AH 2613]), 1 ♀ (AMNH [AH 2614]), 1 subad. ♂ (AMNH [AH 2615]); Middelpos, 1 km N [29°33′S 18°01′E], 13.xii.1984, C.R. Owen, 1 ♂ (AMNH [AH 3600]); Okiep [29°36′S 17°53′E], 1897, M. Schlechter, 1 ♀, 1 subad. ♂ (SAMC 1701); O'okiep [29°36′S 17°53′E], 8.iv.1984, C.R. Owen, 1 ♀ (AMNH [AH 3786]); Port Nolloth [29°15′S 16°52′E], 17.xii.1983, J. Visser, 1 ♂ (SAMC C3825), 9.iii.1985, J. Visser, 1 ♂ (SAMC C3855), v.1986, A.J. Prins, 1 subad. ♀, 1 juv. ♂ (SAMC C4525), ii.1997, L. Prendini & G.J Müller, collected at night with UV light, 2 ♀ (SAMC C4558, C4562); Port Nolloth, 20 km E at turnoff to Lekkersing, 29°15.180′S 17°03.933′E, iii.1997, L. Prendini & E. Scott, 185 m, red sand flats, succulent karoo, collected at night with UV light, 1 subad. ♂ (SAMC C4557), 25.ii.2003, L. Prendini & E. Scott, 1 juv. ♂, 1. juv. ♀ (AMNH); Farm Kannikwa 156, 20 km E Port Nolloth, at turnoff to Lekkersing [29°17′S 17°05′E], 16.i.1999, G.J. Müller, J.J. van der Walt & J. du Plessis, collected at night with UV light, 3 ♂ (AMNH), 1 juv. ♀ (SAMC C4554); Port Nolloth, 36 mi up rail [29°11′S 17°23′E], i.1911, C.L.L. Biden, 1 ♀ (SAMC B568); Rietfontein [28°48′S 16°35′E], 2.ix.1976, S. Endrödy-

Younga, 1 subad. ♀ (TMSA 12218); Rooipoort (E Springbok), 5 km E (near 1090) [29°30'S 18°03'E], 25.v.1997, A. Harington, 1 ♀ (AMNH [AH 4793]); Spektakel Mine, on Farm Spektakel 202, W Springbok [29°39'S 17°34'E], 15.ii.1995, A. Harington, 1 ♂ (AMNH [AH 2692]), 1 juv. ♀ (AMNH [AH 2693]); Springbok [29°40'S 17°53'E], xii.1997, L. Prendini & E. Scott, collected at night with UV light, 1 ♂ (SAMC C4561); S of Springbok [29°54'S 17°52'E], 10.ix.1983, J. Visser, 1 ♀ (SAMC C3822); Springbok, 30 km S [29°55'S 17°53'E], 10.x.1983, J. Visser, 1 ♂ (SAMC C3823); Springbok, 3 km W [29°40'S 17°52'E], 25.xi.1983, J. Visser, 1 ♂ (SAMC C3830); Springbok, 23 km W [29°42'S 17°44'E], 11.xii.1984, C.R. Owen, 1 juv. ♂ (AMNH [AH 3860]); Springbok, 57 km W (Farm Wolfberg 187) [29°34'S 17°28'E], 11.xii.1984, C.R. Owen, 1 ♂ (AMNH [AH 4409]), 1 juv. ♀ (AMNH [AH 2474]), G. Newlands, 1 ♂ (AMNH [AH 3268]); Springbok to Aggeneys [29°30'S 18°10'E], iii.1985, G. Behr, 1 ♂ (SAMC C3852), 1 ♀ (SAMC C3851); Springklipberg, Richtersveld, red sand dunes 2 km E [28°37'S 16°52'E], ii.1997, L. Prendini & G.J. Müller, collected at night with UV light, 1 ♀ (SAMC C4556); Springklipberg, 2 km E S tip [28°38'S 16°54'E], 21.i.1995, A. Harington, 1 ♂ (AMNH [AH 2660]), 1 ♀ (AMNH [AH 2659]); Steinkopf [29°16'S 17°44'E], 1897, M. Schlechter, 1 ♂ (SAMC 1704), W.H. Turle, 1 ♂, 2 ♀ (SAMC 567); Farm Steinkopf 22, 11 km S of Steinkopf, 29°20.367'S 17°47.282'E, 26.ii.2003, L. Prendini & E. Scott, 900 m, UV lighting at night on red sandy flats and loose sand around granite koppies, 1 ♂, 3 ♀, 2 juv. ♂ (AMNH); between Springbokfontein and Steinkopf [29°22'S 17°52'E], 1897, M. Schlechter, 2 ♀ (SAMC 1711); Wildepaardehoek [29°53'S 17°38'E], 28.viii.1977, S. Endrödy-Younga, 1 subad. ♂ (TMSA 11652). Richtersveld National Park: 28°12'S 17°07'E, 14.i.1999, G.J. Müller, J.J. van der Walt, J. Tytgat, J. du Plessis, et al., collected at night with UV light, 1 ♂ (AMNH), 2 juv. ♀ (SAMC C4555); 28°14'S 17°02'E, i.1999, G.J. Müller, J.J. van der Walt, J. Tytgat, J. du Plessis, et al., collected at night with UV light, 1 ♂ (AMNH); 28°18'S 17°05'E, i.1999, G.J. Müller, J.J. van der Walt, J. Tytgat, J. du Plessis, et al., collected at night with UV light, 1 ♂ (AMNH); 28°15'S 17°05'E, x–xii.1994, H. Braack, 2 ♂, 2 ♀ (SAMC C4553); Gannakouriep River bed [28°23'S 17°10'E], ii.1997, L. Prendini, G.J. Müller, et al., collected at night with UV light, 1 ♀ (SAMC C4563); Kokerboomkloof, 28°18.5'S 17°16.0'E, i.1999, G.J. Müller, J.J. van der Walt, J. Tytgat, J. du Plessis, et al., collected at night with UV light, 2 ♂ (AMNH); Potjiespram [28°06'S 16°57'E], 23.i.1995, A. Harington, 1 ♂ (AMNH [AH 2734]), 1 ♀ (AMNH [AH 2733]), [28°10'S 16°53'E], 7.ii.1997, L. Prendini, G.J. Müller, et al., collected at night with UV light, 1 ♂ (SAMC C4560); S of Peilkop [28°11'S 17°02'E], ix.1996, P. Lloyd, collected at night with UV light, 1 ♀ (SAMC C4513); Tatasberg [28°19'S 17°15'E], ii.1997, L. Prendini, G.J. Müller, et al., collected at night with UV light, 1 ♀ (SAMC C4559). Prieska District: Farm Boegoeberg Settlement/Buchuwater Reserve, 5 km S of Water Affairs office, 29°05.368'S 22°11.738'E, 8.iii.2003, L. Prendini & E. Scott, 890 m, UV detection on sandy flats near riverbed, 1 ♀, 1 juv. ♂, 1 juv. ♀ (AMNH), 6 km S of Water Affairs office, 29°05.535'S 22°11.897'E, 914 m, UV detection on rocky flats, 1 subad. ♂, 1 subad. ♀, 1 juv. ♂ (AMNH); Farm Middelwater 18, 3.5 km S of De Duinen homestead towards fountain, 29°25.936'S 22°27.120'E, 9–10.iii.2003, L. Prendini & E. Scott, 935 m, Asbesberge foothills, ironstone, basalt and metamorphic mixture on loamy soil, arid savanna, UV detection, 1 ♀, 5 juv. ♂, 3 juv. ♀ (AMNH), 4.4 km S of De Duinen homestead at fountain, 29°26.282'S 22°27.464'E, 1021 m, 1 ♂, 1 juv. ♂, 1 juv. ♀ (AMNH). Sutherland District: Verlatenkloof, S of Sutherland [32°32'S 20°36'E], J. Visser, 1 ♀ (SAMC C3866). Victoria West District: Victoria West [31°24'S 23°07'E], 7.ix.1983, J. Visser, 1 ♂ (SAMC C3820). Williston District: Zak River [31°37'S 21°37'E], xi.1916, F.M. Wilson, 1 ♀ (SAMC B1753). *Northern Cape and Western Cape Provinces*: Calvinia, Vanrhynsdorp, Clanwilliam and Namaqualand Districts, 1897, L. Mally, 2 ♂, 1 ♀, 2 juv. ♂, 1 juv. ♀ (SAMC 1721). *Western Cape Province*: 'Great Karoo', M. Stiller, 1 ♀ (SAMC C1518). Beaufort West District: Beaufort West [32°21'S 22°35'E], 24–30.x.1905, W.F. Purcell, 1 juv. ♂ (SAMC 14361), ii.1958, S.A. Museum expedition, 1 ♂ (SAMC C195), 2.iv.1985, C.R. Owen, 1 juv. ♀ (AMNH [AH

4297]). Karoo National Park [32°23′S 22°38′E], 13.vii.1988, A.J. Prins, 1 ♂ (SAMC C4524), 1.iv.1994, J. Leeming, mid plateau, sympatric with *P. planicauda*, 1 ♂ (SAMC C4545). Bellville District: Belhar [33°57′S 18°38′E], 1998, ex G.J. Müller, brought into Tygerberg hospital, 1 ♀ (SAMC C4547); Japonica Steet, Belhar [33°57′S 18°38′E], 28.iii.1998, ex G.J. Müller, brought into Tygerberg hospital, 1 ♀ (SAMC C4546). Cape District: Devil's Mt., above Woodstock, Park Road [33°55′S 18°26′E], viii.1903, Dreyer, 1 ♀, 2 subad. ♂, 3 subad. ♀, 3 juv. ♂, 1 juv. ♀ (SAMC 12813); Silverstrand, 45 km N of Cape Town [33°34′S 18°22′E], 7.iii.1993, J. Visser, 1 ♂ (SAMC C3885); Table View, Cape Town [33°49′S 18°29′E], 29.iv.1986, Louw, 1 ♀, 1 juv. ♂ (SAMC C1618). Ceres District: Hanglip, ca. 2 km from Farm Bizansgat towards Ceres on R356 from Sutherland (800 m off road)/44 km NE of Karoopoort junction between R355 and R356, 32°53.254′S 19°58.129′E, 12.iii.2003, L. Prendini & E. Scott, 616 m, Tankwa karoo valley floor, Nama karoo-succulent karoo transition on shaley-loam soil, UV detection, 1 ♂ (AMNH). Clanwilliam District: 5 km from Citrusdal on road to Citrusdal Baths [32°36′S 19°01′E], 13.iii.1998, L. Prendini & E. Scott, collected at night with UV light, 2 ♂, 1 ♀ (SAMC C4548); Biedouws Pass [32°02′S 19°24′E], 25.ix.1973, L. Schulze, 1 ♀ (TMSA 12639); Biedouwvallei [32°09′S 19°15′E], ix.1996, J.J. van der Walt, collected at night with UV light, 1 ♂ (AMNH); Blikhuis, 15–20 mi S of Clanwilliam to Modderfontein [32°26′S 18°57′E], viii.1898, R.M. Lightfoot, 1 ♀ (SAMC 3760); Boontjies River, near Pakhuisberg [32°34′S 19°01′E], 1897, M. Schlechter, 1 ♀, 3 juv. ♂ (SAMC 1199); Boshof, western Cedarberg [32°21′S 18°59′E], 14.v.1997, A. Harington, 1 ♀ (AMNH [AH 4699]); Cedar Mountains near Pakhuis [32°07′S 18°52′E], xi.1899, R.M. Lightfoot, 1 ♂ (SAMC 5206); Clanwilliam [32°08′S 18°51′E], 6.ix.1997, J.J. van der Walt, collected at night with UV light, 1 ♀ (SAMC C4550), xii.1997, L. Prendini & E. Scott, collected at night with UV light, 1 ♂ (SAMC C4549); Clanwilliam, 25 km N [32°08′S 18°51′E], 18.xi.1975, E.B. Eastwood, in burrow under stone, 1 ♀ [dark form] (SAMC C36); Keurboschkraal River, Cedar Mts., Clanwilliam [32°40′S 18°45′E], viii.1898, R.M. Lightfoot, 1 ♀ (SAMC 3754); Lambert's Bay [32°06′S 18°19′E], J. Visser, 1 subad. ♂ [dark form] (SAMC C3887), 29.v.1978, sand and bushes, 1 subad. ♂ [dark form] (SAMC C1382), v.1982, J. Visser, 1 subad. ♂ [dark form] (SAMC C3796), 4.vi.1982, J. Visser, 1 ♀ [dark form] (SAMC C3797); Matjiesfontein [32°23′S 19°23′E], 13.vi.1982, J. Visser, 1 subad. ♂ (SAMC C3795), 17.viii.1982, J. Visser, 1 ♂ (SAMC C3800); Olyvenboschkraal, near Bergvlei, north of Piketberg Mts. [32°19′S 18°50′E], 1898, C.L. Leipoldt, 4 ♂ (SAMC 4048); Onderbergvlei Farm, in Zuid Zandvelt Wyk [32°36′S 18°45′E], 24.viii.1898, C.L. Leipoldt, 1 ♂ (SAMC 3755); Rondegat, 5 mi SSE Clanwilliam [32°14′S 18°54′E], 1897, M. Schlechter, 1 juv. ♂ (SAMC 1198). Goodwood District: Goodwood, near Bellville [33°54′S 18°33′E], 3.iii.1996, F. Piser, 1 ♀ (AMNH [AH 2924]). Hermanus District: Hermanuspetrusfontein [dubious] [Hermanus, 34°25′S 19°15′E], on flats near village, ii–iii.1902, R.M. Lightfoot & H. Herman, 2 ♀ (SAMC 11511), near village, 17.ii.1902, R.M. Lightfoot, 2 ♀, 1 subad. ♀, 3 juv. ♂ (SAMC 11506). Hopefield District: Donkergat [33°04′S 18°00′E], ix.1976, G. McLachlin, 2 subad. ♀ (SAMC C80); Hopefield [33°04′S 18°21′E], 16.iii.[?], A.J. Prins, 1 ♂ [dark form] (SAMC C2246), v.1987, H. Schelten, 1 ♀ [dark form] (SAMC C1624); Langebaan [33°06′S 18°02′E], 21.x.1983, J. Visser, 3 subad. ♂ (SAMC C3826–C3828); Saldanha Bay [33°00′S 18°03′E], 1980, A.J. Prins, 1 juv. ♂ (SAMC C4526), viii.1991, N. Larsen, under stone, 1 ♂ (SAMC C2285). Kuils River District: Kuilsrivier [34°02′S 18°42′E], 1997, ex G.J. Müller, brought into Tygerberg Hospital, 1 ♀ (SAMC C4551). Laingsburg District: Matjiesfontein [33°14′S 20°35′E], viii.1903, W.F. Purcell, 1 subad. ♀ (SAMC 12809), 1–3.xi.1905, W.F. Purcell, 1 juv. ♀ (SAMC 14363). Malmesbury District: Klipheuwel, N Durbanville [33°42′S 18°42′E], 5.viii.1982, J. Visser, 2 ♀ (SAMC C3798, C3799), 2 juv. ♂ (SAMC C3778, C3779), ix.1982, J. Visser, 1 subad. ♀ (SAMC C3801); Melkbosstrand [33°44′S 18°26′E], v.1997, M.D. Picker, 1 juv. ♀ (SAMC C4552). Montagu District: Montagu [33°47′S 20°07′E], xi.1919, R.W.E. Tucker, 1 ♀ (SAMC B3979). Piketberg District: Eendekuil [32°41′S 18°53′E], Muller, 2 ♀ (SAMC B8934); Laaiplek [32°46′S

18°10′E], ix.1976, G. McLachlin, in sand dune, 1 ♂, 2 ♀, 1 subad. ♂ [dark form] (SAMC C74); Laaiplek near Veldrift [32°46′S 18°09′E], 10.i.1979, A. Harington, under carton boxes and drums on white coastal dunes, 4 ♂ [dark form] (AMNH [AH 1503–1505, 1176]); Laaiplek, near Velddrif [32°46′S 18°10′E], xii.1998, Zoology Department, University of the Western Cape, under stones, ♂ attempted to mate with ♀ of typical *P. capensis*, 1 ♂, 1 ♀ [dark form] (SAMC C4564); Piekenierskloof Pass [32°37′S 18°57′E], 30.xi.1976, E.B. Eastwood, under stones, 1 ♀, 1 subad. ♀, 3 juv. ♀ (SAMC C98). Prince Albert District: Farm Zwartskraal [33°10′S 22°32′E], 5.ix.1979, S. Endrödy-Younga, 1 ♀ (TMSA 12310), 25.x.1979, S. Endrödy-Younga, 1 juv. ♂ (TMSA 12340), 5.xii.1979, S. Endrödy-Younga, 1 juv. ♀ (TMSA 12349), 15.xii.1979, S. Endrödy-Younga, 1 juv. ♀ (TMSA 12352), 1.ii.1980, S. Endrödy-Younga, 1 subad. ♂ (TMSA 12256), 1 subad. ♀ (TMSA 12369), 18.iii.1980, S. Endrödy-Younga, 1 subad. ♀ (TMSA 12261), 1 juv. ♂ (TMSA 12266); Swartberg [33°25′S 22°40′E], 17.xii.1978, S. Endrödy-Younga, 1 subad. ♂ (TMSA 12235). Saldanha Bay District: Langebaanweg [32°58′S 18°09′E], vii.1973, B. Kensley, 1 subad. ♂ (SAMC C6). Simon's Town District: Cape Peninsula [34°07′S 18°22′E], 26.v.1907, C.J. French, 1 ♀ (SAMC B545). Tulbagh District: Piquetberg Road Station, Gouda [33°22′S 19°07′E], viii.1898, R.M. Lightfoot, 1 ♀, 1 juv. ♂ (SAMC 3758); Tulbagh Road Station [33°19′S 19°06′E], 1895, J.P. Cregoe, 1 ♀ (SAMC 504). Vanrhynsdorp District: Farm Rietpoort [30°59′S 18°06′E], 22.viii.1979, S. Endrödy-Younga, 1 subad. ♂ (TMSA 12271); Klawer [31°47′S 18°37′E], v.1996, L. Prendini, collected at night with UV light, 1 subad. ♂ (SAMC C4566); Kliprand [30°36′S 18°42′E], 21.xi.1975, A.J. Prins, under stone, 1 juv. ♂ (SAMC C41); Vanrhynsdorp [31°37′S 18°44′E], 5.vi.1968, G.R. McLachlan, 1 juv. ♂ (TMSA 17645), [31°36′S 18°44′E], 12.xii.1984, C.R. Owen, 2 ♂ (AMNH [AH 3489, 4325]), 1 ♀ (AMNH [AH 4324]), G. Newlands, 3 ♂ (AMNH [AH 3179, 3181, 3182]), 1 ♀ (AMNH [AH 3180]); Vanrhynsdorp, 12 km N near Varschrivier [31°33′S 18°32′E], xii.1997, L. Prendini & E. Scott, collected at night with UV light, 1 ♂ (SAMC C4565); Vanrhynsdorp, 60 km N [31°10′S 18°25′E], v.1987, J. Visser, 1 ♂ (SAMC C3874). Vredenburg District: Jacobsbaai, N of Saldanha Bay [32°58′S 17°54′E], 21.viii.1975, V. Branco, under stones, 1 subad. ♂, 1 juv. ♀ (SAMC C27), 14.viii.1977, E.B. Eastwood, 1 juv. ♀ (SAMC C170), xii.1985, A.J. Prins, 1 ♀, 1 juv. ♂ (SAMC C4523); Steenberg's Cove, St Helena Bay [32°46′S 18°02′E], v.1902, J.E.C. Goold, 1 subad. ♀, 1 juv. ♂, 4 juv. ♀ (SAMC 11501); Stompneus, St Helena Bay [32°44′S 17°58′E], ii–iii.1902, J.E.C. Goold, 3 ♀ (SAMC 10007), v.1902, J.E.C. Goold, 2 juv. ♂ (SAMC 10009), vi.1902, J.E.C. Goold, 1 ♀ (SAMC 11500), vii.1903, J.E.C. Goold, 1 ♀, 3 juv. ♂, 2 juv. ♀ (SAMC 12807). Vredendal District: Koekenaap [31°32′S 18°14′E], 30.viii.1979, S. Endrödy-Younga, 3 ♀ (TMSA 12304, 12308, 12309), 2 subad. ♂ (TMSA 12305, 12306). Wellington District: Bartholomeus Klip, Bo-Hermon [33°26′S 18°58′E], iii.1997, L. Prendini & E. Scott, under stones on ridge, sympatric with *P. planicauda*, 2 ♀, 1 subad. ♂, 1 subad. ♀ (SAMC C4567). Worcester District: De Doorns [33°29′S 19°41′E], xii.1906, J. Paynter, 6 ♂, 12 ♀, 1 juv. ♂, 5 juv. ♀ (SAMC B609); Touws River station [33°20′S 20°03′E], xii.1904, J. Paynter, 1 ♀ (SAMC 14263); Touws River [33°20′S 20°03′E], 5.xi.1905, W.F. Purcell, 1 ♀ (SAMC 14365), xii.1905, J. Paynter, 1 ♀ (SAMC 14378).

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Parabuthus distridor Lamoral 1980: 206–210, figs. 12–22; Kovařík 1998: 116; Fet & Lowe 2000: 202; Prendini 2001a: 17; Prendini 2001b: 136; Prendini 2003: 20.

Type material.—Holotype ♀ (NMSA 11435), SOUTH AFRICA: Cape Province, sandy ridge, 8 km south of Springklipberg, Richtersveld [*Northern Cape Province*: Namaqualand District], 28°40′S 16°53′E, 21.ii.1979, B.H. Lamoral. Paratypes: 1 ♂ (AMNH), 1 ♂ (BMNH), 1 ♂ (CASC), 1 ♂ (MNHN), 1 ♂ (NMSA 11436), 11 ♂, ♀, 2 subad. ♂, 2 juv. ♀ (NMSA 11305), same data as holotype.

Diagnosis.—*Parabuthus distridor* is most closely related to *P. kuanyamarum*, the two species forming a sister group to the *P. gracilis–P. nanus* group (Fig. 1). Both species may be separated from all other species of *Parabuthus* by means of the following combination

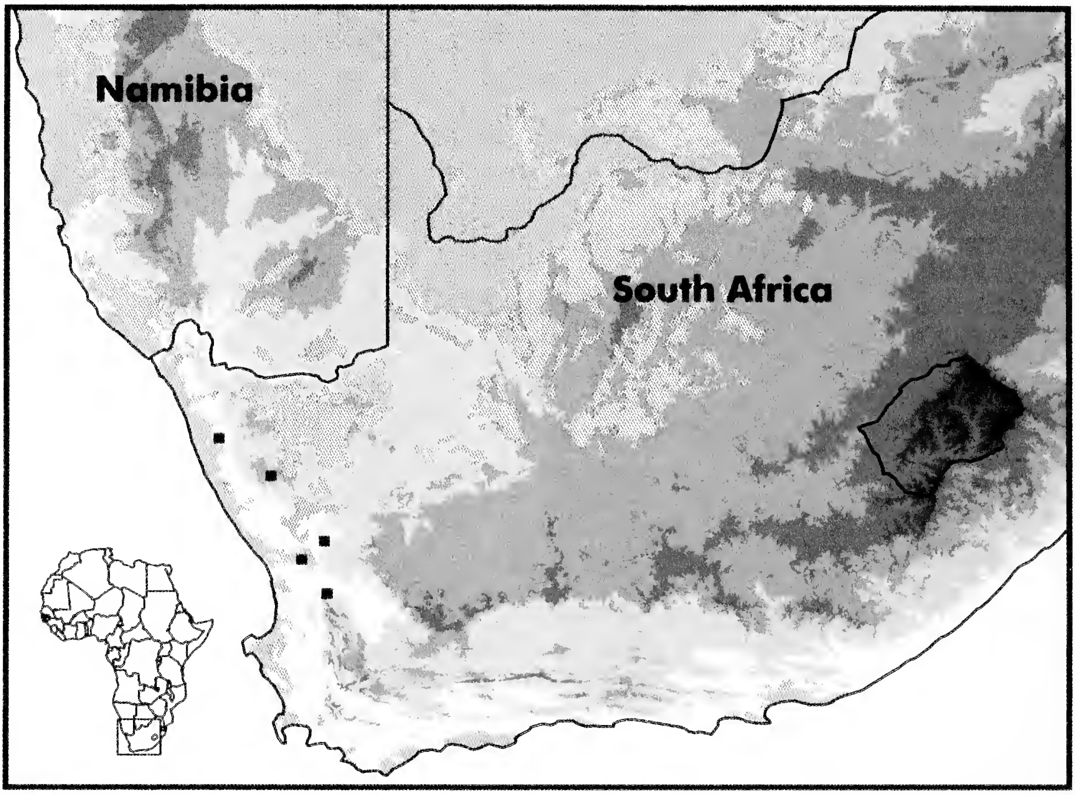


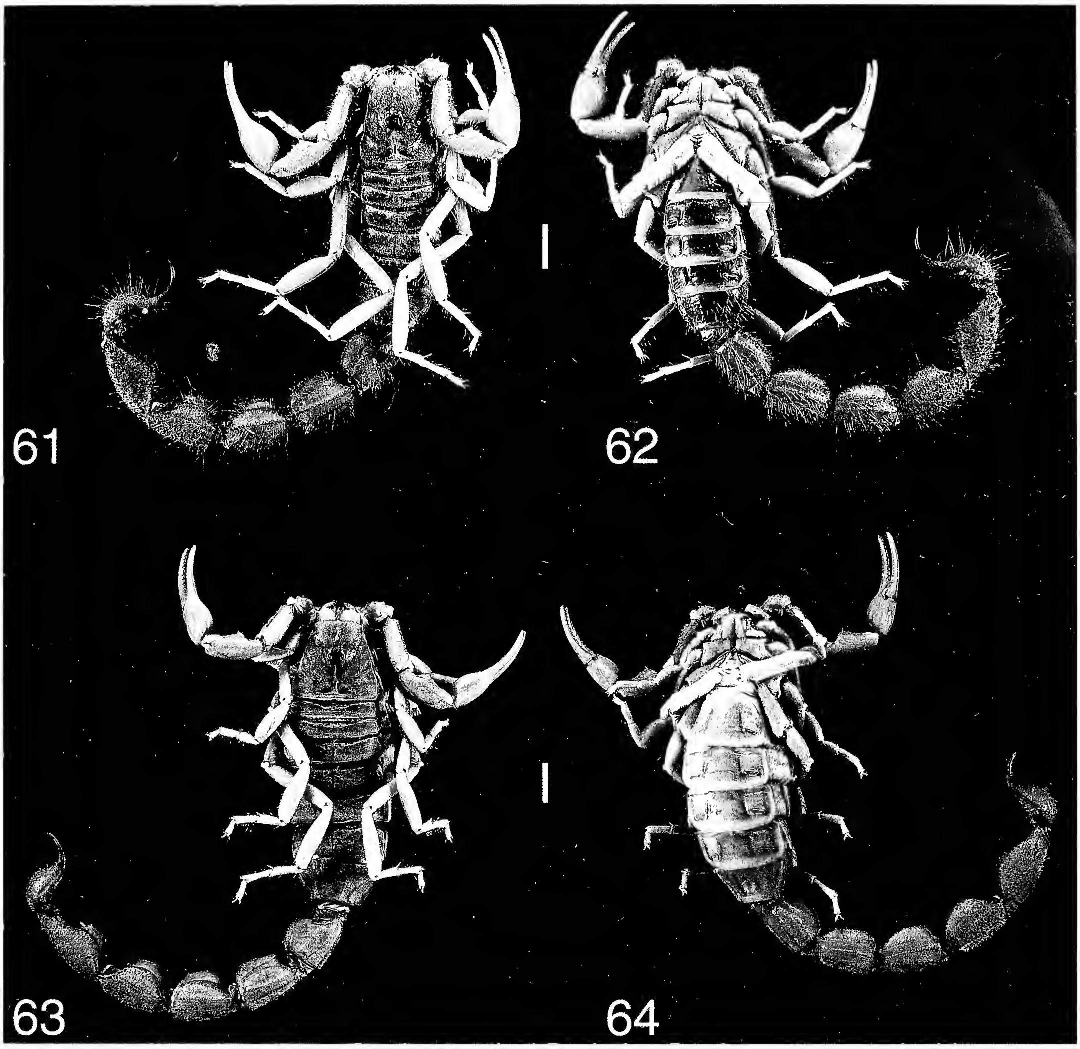
Figure 60.—The known distribution of *Parabuthus calvus* Purcell 1896 (■), which is endemic to South Africa. Contour interval = 500 m. Major sand systems stippled.

of characters: small adult size, carapace length 2.5–5.0 mm; surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; pedipalp chela manus smooth; pedipalp chela with trichobothrium *dt* situated proximal to *et*; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae absent; metasomal segments II and III, posteroventral margins not demarcated by a transverse row of granules or tubercles; metasomal segment IV with median lateral, ventrolateral and ventrosubmedian carinae absent; metasomal segments IV and V, lateral intercarinal surfaces smooth; metasomal segment V with dorsosubmedian, dorsolateral and ventromedian carinae absent, but with ventrolateral carinae present, converging distally, and comprising spinose processes subdistally.

Parabuthus distridor may be separated from *P. kuanyamarum*, and all other species of *Parabuthus*, by means of the following characters: metasomal segments I–III, median lateral, ventrolateral, and ventrosubmedian carinae absent; metasomal segments I and II, dorsal stridulatory surface absent. Additional characters separating *P. distridor* from *P. kuanyamarum* are as follows: chela (adult male), fixed and movable fingers straight, such that proximal dentate margin linear when fingers are closed (i.e., no proximal "gap" is evident); metasomal segments I–V and telson, moderately setose.

Distribution.—Endemic to sandy areas in the Richtersveld located in the northwestern corner of the Northern Cape Province (Namaqualand District), South Africa. This species has not been recorded north of the Orange River.

Ecology.—*Parabuthus distridor* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated, unequal telotarsal ungues; dorsoventral compression of the basitarsi of legs I and II, with comb-like rows of long



Figures 61–64.—*Parabuthus capensis* (Ehrenberg 1831), habitus (dorsal and ventral aspects). 61, 62. ♂ (SAMC C4565). 63, 64. ♀ (SAMC C98). Scale bars = 5 mm.

macrosetae ("sand combs") on the retrolateral margins; metasoma and telson lacking carinae on segments I–V. All specimens thus far collected were located at night with the aid of UV light detection, resting on the surface of unconsolidated red sand dunes. *Parabuthus distridor* is syntopic with *P. capensis* throughout its distributional range. The species is allopatric with its sister species, *P. kuanyamarum*.

Material examined.—SOUTH AFRICA: *Northern Cape Province*: Namaqualand District, 25 km E of Port Nolloth at turn-off to Wolfberg, iii.1997, L. Prendini & E. Scott, 2 ♂, 1 ♀ (SAMC C4604).

Parabuthus gracilis Lamoral 1979

Figs. 11, 26, 43

Parabuthus gracilis Lamoral 1979: 566–571, figs. 96, 103, 104, 107–116; Kovařík 1998: 116; Fet & Lowe 2000: 202; Prendini 2001a: 17; Prendini 2001b: 136; Prendini 2003: 20.

Type material.—Holotype ♀ (NMSA 10925), NAMIBIA: Messum Crater [*Erongo Region*: Omaruru District], 21°16′S 14°13′E, 26.iii.1976, B.H. Lamoral. Paratypes: NAMIBIA: 8 ♂, 1 ♀, 4 juv. (NMSA 10848), 1 ♂ (NMSA 10926), same data as holotype; 2 ♂ (NMSA 10854), Cape Cross [*Erongo Region*: Swakopmund District], 21°43′S

13°58′E, 25.iii.1976, B.H. Lamoral; 1 subad. ♀, 1 juv. ♀ (NMSA 10857), Möwebaai [*Kunene Region*: Opuwo District: Skeleton Coast National Park], 16°20′S 12°43′E, 28.iii.1976, B.H. Lamoral; 3 ♂, 1 ♀, 4 juv. (NMSA 10859), same data, except 29.iii.1976; 1 ♂, 1 juv. ♂ (NMSA 10860), Torra Bay [*Kunene Region*: Khorixas District: Skeleton Coast National Park], 20°12′S 13°11′E, 30.iii.1976, B.H. Lamoral.

Diagnosis.—*Parabuthus gracilis* is most closely related to *P. nanus*, the two species forming a sister group to the *P. distridor–P. kuanyamarum* group (Fig. 1). *Parabuthus gracilis* is most easily confused with *P. brevimanus*, but may be separated from that species, and from all other species of *Parabuthus*, except *P. nanus*, by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; carapace, including median ocular tubercle (male, female), entirely granular; pedipalp chela manus granular; pedipalp chela with trichobothrium *dt* situated proximal to *et*; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae absent; metasomal segments II and III, posteroventral margins demarcated by a transverse row of isolated, round granules; metasomal segment IV with median lateral, ventrolateral and ventrosubmedian carinae absent; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V with dorsosubmedian, dorsolateral and ventromedian carinae absent, but with ventrolateral carinae present, converging distally, and comprising spinose processes subdistally.

Parabuthus gracilis may be separated from *P. nanus* by both of the following characters: pedipalp chela movable finger of female, short, compared with manus (measured along ventroexternal carina), length finger/length carina: ± 1.50; manus of adult male, noticeably incrassate, compared with that of adult female, which is slender.

Distribution.—Endemic to sandy areas in the central and northern Namib (Khorixas, Omaruru, and Swakopmund districts of northwestern Namibia), north of the Kuiseb River.

Ecology.—*Parabuthus gracilis* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins; metasoma and telson lacking carinae on segments III−V. Specimens of *P. gracilis* have been found at night with UV light detection, resting on the surface of unconsolidated white sand dunes, and have been excavated from burrows in shrub-coppice dunes.

Parabuthus gracilis is syntopic with *P. stridulus* in the coastal part of its distributional range, and with *P. brevimanus* and *P. granulatus* inland, e.g., at the Brandberg (pers. obs.) and the Messum Crater (Lamoral 1979). *Parabuthus gracilis* generally inhabits softer substrata than *P. brevimanus*. The species is allopatric with its sister species, *P. nanus*.

Material examined.—NAMIBIA: *Erongo Region*: Omaruru District: Messum Crater area, 21°25′S 14°13′E, 21.i.1981, A. Harington, 1 ♂ (AMNH [AH 2164]). *Erongo Region*: Swakopmund District: Cape Cross, 5 km N [21°43′S 13°56′E], 13.i.1981, A. Harington, 1 ♀ (AMNH [AH 3608]).

Parabuthus granulatus (Ehrenberg 1831)
Figs. 16, 31, 39, 40

Androctonus (*Prionurus*) *granulatus* Ehrenberg in Hemprich & Ehrenberg 1831 [pages unnumbered]; Moritz & Fischer 1980: 315.

Scorpio (*Androctonus*) *granulatus*: Gervais 1844: 45.

Buthus brevimanus var. β *segnis* Thorell 1876b: 110, 112 (NEW SYNONYMY)

Buthus fulvipes Simon 1888: 378, 379 (synonymized by Purcell 1899b: 434; Lamoral 1979: 571).

Parabuthus fulvipes: Pocock 1895: 309; Kraepelin 1899: 30.

Parabuthus granulatus: Kraepelin 1899: 30; Purcell 1901: 168–173; Pocock 1902: 367; Kraepelin 1908: 251, 252; Hewitt 1912: 302; Hewitt 1913: 146; Kraepelin 1914: 110; Lampe 1917: 192; Hewitt 1918: 108; Lawrence 1928: 270; Monard 1937: 257; Roewer 1943: 207; Lawrence 1946: 399; Lawrence 1955: 226; Lawrence 1959: 383; Lawrence 1961: 153; Lawrence 1962: 220; Probst 1973: 330; Lamoral & Reynders 1975: 516, 517; Lamoral 1977: 105; Lamoral 1979: 571–576, figs. 117–124; FitzPatrick 1994: 7, 8; Braunwalder & Fet 1998: 33, 34; Jäger 1998: 87, 88; Kovařík 1998: 116; Fet & Lowe 2000: 203; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 20.

Parabuthus granulatus fuscus Pocock 1901: 285 (synonymized by Kraepelin 1908: 251, 252; Lamoral 1979: 571); Pocock 1902: 367; Hewitt

1918: 108; Hewitt 1935: 467, 468; Lamoral & Reynders 1975: 517.

Parabuthus granulatus bergeri Werner 1916: 83, 84 (synonymized by Lamoral 1979: 571); Lampe 1917: 192; Lawrence 1955: 226; Lamoral & Reynders 1975: 517.

Parabuthus granulatus fulvipes: Lampe 1917: 192; Hewitt 1918: 108; Werner 1936: 177, 178; Lamoral & Reynders 1975: 517.

Parabuthus granulatus strenuus Hewitt 1918: 176 (NEW SYNONYMY); Lawrence 1955: 226; Lamoral & Reynders 1975: 517; Kovařík 1998: 116; Fet & Lowe 2000: 203.

Parabuthus bergeri: Werner 1936: 178.

Parabuthus granulatus granulatus: Fet & Lowe 2000: 203.

Type material.—*Androctonus* (*Prionurus*) *granulatus:* Holotype 1 subad. ♂ (ZMHB 132), SOUTH AFRICA: Promont bonae spei [Cape of Good Hope, *Western Cape Province:* Simon's Town District: 34°00′S 18°25′E], Lichtenstein.

Buthus brevimanus var. β *segnis:* Holotype ♂ [not ♀] (GNME), "S. Afrika", 28.xi.1864 [not 23.xi.1864], C.J. Andersson.

Buthus fulvipes: Holotype ♀ (MNHN RS 0311), NAMIBIA: "sud-ouest Afrique", 1884–1886, Dr H. Schinz.

Parabuthus granulatus fuscus: Holotype ♀ (BMNH 1894.5.3.4), "Kalahari Desert", R.J. Cunningham.

Parabuthus granulatus bergeri: Syntypes: NAMIBIA: 3 ♂, 4 ♀ (NHMW 1046), Berseba, Deutsch-Südwest-Afrika [*Karas Region*: Keetmanshoop District: 25°59′S 17°47′E]; 1 ♂, 3 juv. (NHMW 1047), Haruchas, near Gochas, Deutsch-Südwest-Afrika [*Hardap Region*: Mariental District: 24°50′S 18°55′E].

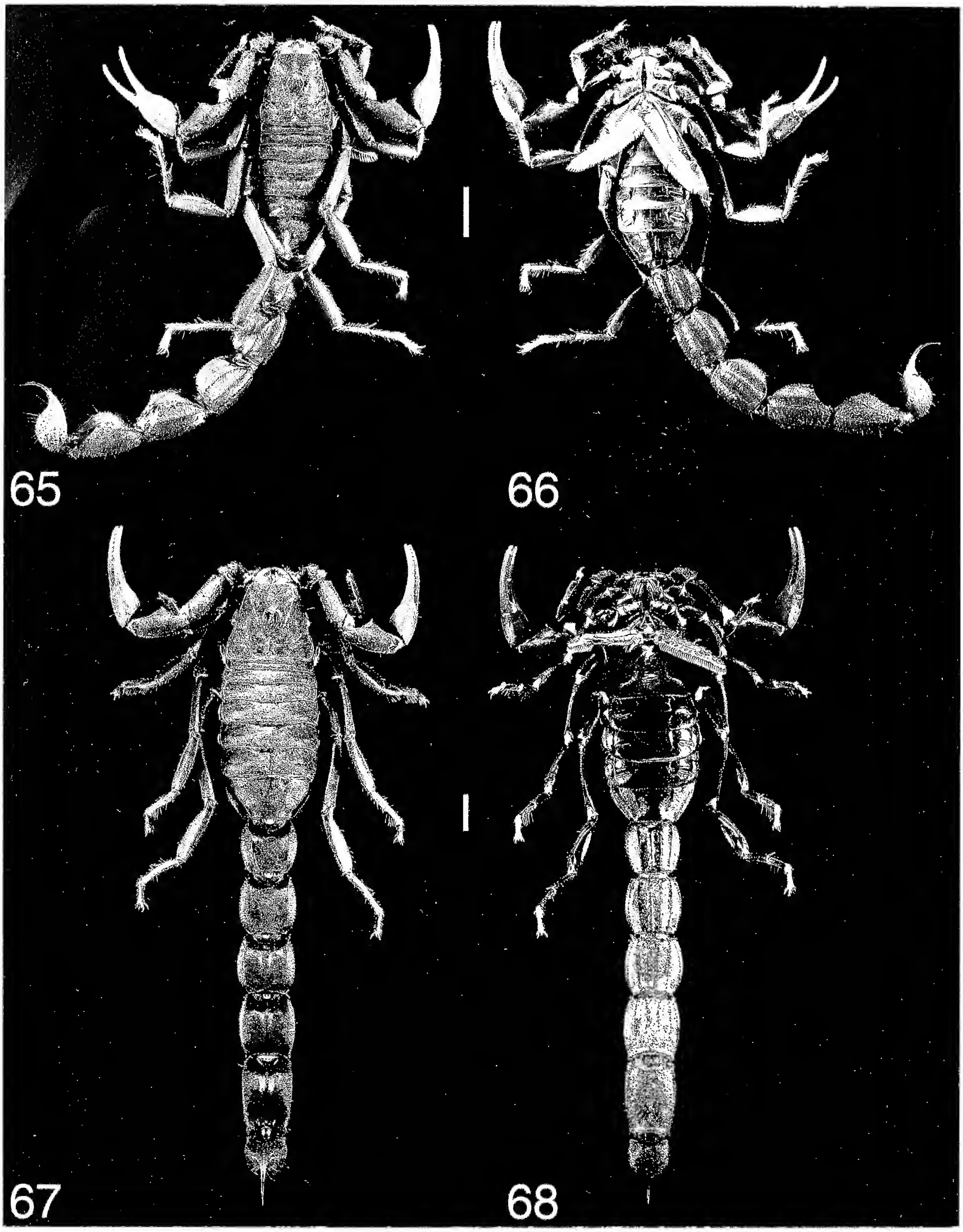
Parabuthus granulatus strenuus: Holotype ♂ (MMKZ), SOUTH AFRICA: Worcester, Cape Province [*Western Cape Province*: Worcester District: 33°39′S 19°25′E], G.B. Townsend.

Diagnosis.—*Parabuthus granulatus* is most closely related to *P. kalaharicus* (Fig. 1). The two species may be separated from all other species of *Parabuthus* by means of the following combination of characters: pedipalp chela, asetose; chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); chela manus, smooth and shiny; first proximal median lamella of pectines (female) suboval, with mesal margin arcuate (i.e., not enlarged and lobate) and free of teeth; metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segments I–V and telson, virtually asetose; metasomal segment II, stridulatory surface not reaching posterodorsal margin of segment; metasomal segment IV, median lateral carinae proximally obsolete; metasomal segment V, dorsosubmedian carinae absent, dorsolateral carinae distally obsolete; telson vesicle, width considerably narrower (65–72%) than width of metasomal segment V.

Parabuthus granulatus may be separated from *P. kalaharicus* by means of the following characters: pedipalp chela fixed finger, trichobothrium *dt* situated in line with or distal to *et*; chela movable finger of female, long, compared with manus (measured along ventroexternal carina), length finger/length carina: 1.70–2.00; metasomal segment IV, ventrosubmedian carinae becoming obsolete in distal third of segment; metasomal segment V, ventromedian carina present, ventrolateral carinae comprising enlarged, lobate processes subdistally.

Remarks.—Pocock (1895) suspected that *Buthus brevimanus* var. β *segnis* (as *P. segnis*) was a junior synonym of *P. capensis*. Kraepelin (1899) subsequently listed *Buthus segnis* in synonymy with *P. capensis*, but placed a questionmark next to the synonymy. Purcell (1901) noted that *P. segnis* was doubtfully described as a variety of *P. brevimanus* and doubtfully referred to *P. capensis* by later authors. Purcell further suggested that *P. segnis* and *P. capensis* are unlikely to conspecific, because the type of *P. segnis* was collected by C.J. Andersson, who travelled in Damaraland and Ovamboland (northern Namibia). Kraepelin (1908) again suggested that *P. segnis* does not belong to *P. brevimanus*, but probably to *P. capensis* or *P. granulatus*. Lamoral & Reynders (1975) listed *Buthus segnis* as a synonym of *P. capensis*.

During the present investigation, the holotype of *B. brevimanus* var. β *segnis*, which had not been examined since its description by Thorell, was obtained from the Göteborg Museum for study. The adult male holotype was found to be conspecific with *P. granulatus*, not with *P. capensis*, thus supporting the suspicions of Purcell (1901) and Kraepelin (1908). *Buthus brevimanus* var. β *segnis* is therefore synonymized with *P. granulatus*.



Figures 65–68.—*Parabuthus capensis* (Ehrenberg 1831), habitus (dorsal and ventral aspects). 65, 66. ♂ (AMNH [AH 1176]). 67, 68. ♀ (SAMC C4564). Scale bars = 5 mm.

Purcell (1899b, 1901) first listed *Buthus fulvipes* in synonymy with *P. granulatus* and noted (1901) that the holotype, from German South-West Africa (Namibia), agrees closely in coloration with specimens of *P. granulatus* from Bushmanland (Northern Cape Province, South Africa), as does *P. granulatus fuscus*. Kraepelin (1908) subsequently listed *P. granulatus fuscus* in synonymy with *P. granulatus*.

Subsequent authors appear to have overlooked these synonyms. Werner (1916) described *P. granulatus bergeri*, without citing Purcell (1901) or Kraepelin (1908), and subsequently (Werner 1936) raised *P. bergeri* to species level, while recognizing *P. granulatus fulvipes*. Hewitt (1918) regarded *P. fulvipes* and *P. granulatus fuscus* as local races of *P. granulatus* and described a new variety, *P. granulatus strenuus*. Lawrence (1955) may have been aware of these synonyms, for he listed *P. granulatus bergeri* and *P. granulatus strenuus* in his checklist, but omitted *P. granulatus fulvipes* and *P. granulatus fuscus*. However, Lawrence (1955) did not list these taxa as synonyms of *P. granulatus*.

Lamoral & Reynders (1975) again ignored these synonyms when they listed the following subspecies: *P. granulatus bergeri*, *P. granulatus fulvipes*, *P. granulatus fuscus*, and *P. granulatus strenuus*. Lamoral (1979) later revised *P. granulatus*, synonymizing *P. granulatus bergeri* and erroneously claiming that *Buthus fulvipes* and *P. granulatus fuscus* were new synonyms. Lamoral (1979) neglected to address the status of *P. granulatus strenuus*, presumably because it was extralimital. FitzPatrick (1994) recently provided additional diagnostic differences between *P. granulatus* and other members of the genus, but again omitted to address *P. granulatus strenuus*, perhaps for the same reason.

Hewitt (1918) distinguished *P. granulatus strenuus* solely on the extent of the stridulatory surface on metasomal segments I and II. According to Hewitt (1918), these segments are less deeply grooved dorsomedially in *P. granulatus strenuus* than in the typical form, and the stridulatory surface of segment II occupies a fairly deep independent excavation rather than a portion of one continuous groove. In both segments of *P. granulatus strenuus*, the anterior edge of the stridulatory surface descends obliquely, but more abruptly than in the typical form. In segment I, the stridulatory surface is very wide anteriorly, and laterally includes several enlarged granules that also occur in the typical form, but in which they are closer to the dorsosubmedian carinae than to the stridulatory surface. The stridulatory surface of *P. granulatus strenuus* extends posteriorly almost to the hind margin of the segment and broadens out near to the margin. The stridulatory surface of segment II is about twice as long as wide.

Lamoral (1979) provided evidence of extensive morphological variation in *P. granulatus*, which is the most widely distributed scorpion species in southern Africa (Prendini 1995). Harington (1984) has shown that the extent of the stridulatory surface is highly variable and cannot be used to separate *P. brachystylus* from *P. villosus* (discussed below). Newlands & Martindale (1980) also noted that this character is prone to considerable individual variation among species of *Parabuthus*. Even Hewitt (1918) admitted that the stridulatory surface is variable within *P. granulatus*. *Parabuthus granulatus strenuus* clearly represents nothing more than intraspecific polymorphism within a widespread species and is hereby synonymized with the typical form.

Distribution.—Recorded from Angola, Botswana, Namibia, South Africa, and Zimbabwe. Newlands & Martindale (1980) omitted this species in their review of the Zimbabwean scorpion fauna, but FitzPatrick (1994) and Bergman (1995, 1997b) provided records from Zimbabwe. *Parabuthus granulatus* is the most widespread species of *Parabuthus* in southern Africa. Its distribution crosses all major drainage systems in the region (e.g., Kunene, Orange, Limpopo), extending from the Western Cape Province of South Africa, throughout Namibia, to Angola, and across Botswana to Zimbabwe and the Limpopo Province of South Africa (Prendini 1995). The species probably also occurs in southern Zambia. It has not been recorded from Mozambique.

Ecology.—*Parabuthus granulatus* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty substrata, where it excavates burrows in open ground, at the base of shrubs and grass tufts and, less commonly, under logs and stones. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

The widespread distribution of *P. granulatus* may be related to its ecology. Available data suggest that *P. granulatus* is more abundant in disturbed areas, such as dry riverbeds, where other large, potentially competitive species of *Parabuthus* (e.g., *P. raudus*, *P. schlechteri* and *P. transvaalicus*) are uncommon, suggesting that *P. granulatus* may be competitively superior in disturbed areas. As disturbed areas are often associated with human habitation, *P. granulatus* comes into contact more regularly with humans than most other species of *Parabuthus*, with consequent implications for envenomation by this species. The widespread distribution of *P. granulatus*, not to mention the prevalence of envenomation by this species, which is more often implicated in serious envenomations than other species in the genus (Müller 1993), may thus be directly related to the spread of human-induced environmental disturbance in southern Africa.

The widespread distribution of *P. granulatus* may also be related to the fact that this is one of the only large *Parabuthus* species (other than *P. kalaharicus* and *P. villosus*) that consistently adopts an "errant" mode of foraging (Polis 1990). Unlike many other large species of the genus (e.g., *P. raudus* and *P. schlechteri*), *P. granulatus* usually hunts actively, rather than lying in wait for prey (the "sit-and-wait" strategy). The errant foraging strategy may allow *P. granulatus* to disperse further on average than other species in ecological time, resulting in a broader distribution in evolutionary time. The errant strategy may also contribute to the prevalence of envenomation by this species, compared with species characterized by the sit-and-wait strategy, because *P. granulatus* may come into more frequent contact with humans as a consequence of its greater surface activity (e.g., by wandering indoors at night).

Due to its widespread distribution and generalist habitat requirements, *P. granulatus* has been recorded in sympatry with most other southern African species of *Parabuthus*: *P. brevimanus*, *P. capensis*, *P. gracilis*, *P. kalaharicus*, *P. kraepelini*, *P. kuanyamarum*, *P. laevifrons*, *P. mossambicensis*, *P. muelleri*, *P. nanus*, *P. planicauda*, *P. raudus*, *P. schlechteri*, *P. transvaalicus*, *P. villosus*.

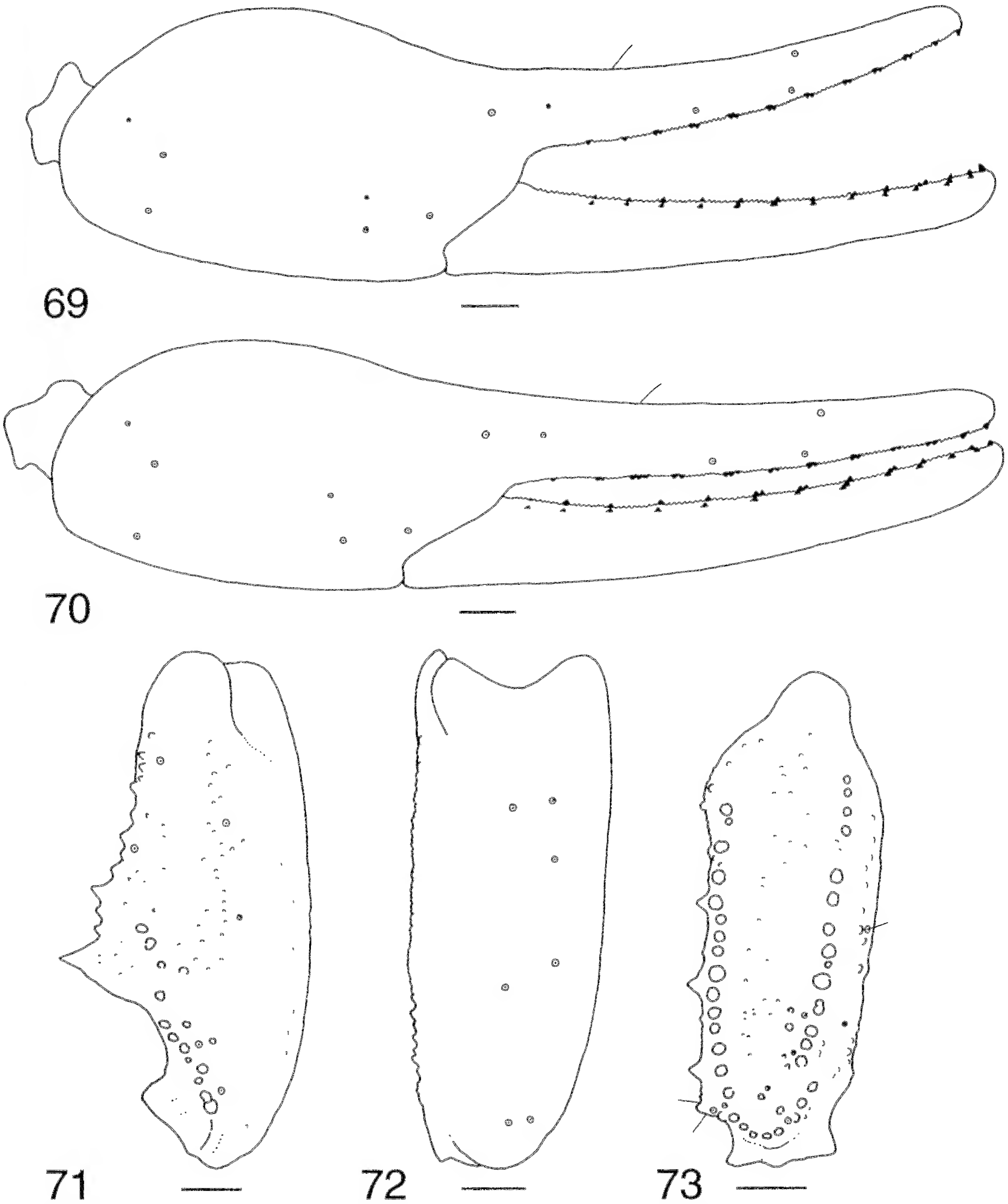
Material examined.—NAMIBIA: *Karas Region*: Keetmanshoop District: Berseba, 10 km S, 26°07′S 17°46′E, 27.ii.1976, B. Lamoral 9 ♂, 2 ♀, 1 juv. ♂, 1 juv. ♀ (NMSA 10731). *Khomas Region*: Windhoek District: Farm Frischgewaagd 289, 22°32′S 17°50′E, 20.iii.1976, B.H. Lamoral, 1 ♂ (NMSA 10900) [homotype designated by Lamoral (1979)]. *Kunene Region*: Khorixas District: Farm Vrede 719, 20°23′S 14°14′E, 31.iii.1976, B. Lamoral & L. Ferguson, 4 ♂, 2 ♀, 3 subad. ♀, 9 juv. (NMSA 10836).

Parabuthus kalaharicus Lamoral 1977
Figs. 14, 37, 38

Parabuthus kalaharicus Lamoral 1977: 101–107, figs. 1–5; Lamoral 1979: 576–579, figs. 125–132; Kovařík 1998: 116; Fet & Lowe 2000: 204; Prendini 2001a: 17; Prendini 2001b: 136; Dyason et al. 2002: 769; Prendini 2003: 20, 21.

Type material.—Holotype ♂ (NMSA 10945), SOUTH AFRICA: Twee Rivieren, Kalahari Gemsbok National Park [*Northern Cape Province*: Gordonia District], 26°30′S 20°35′E, iii.1970, B.H. Lamoral, caught at night. Paratypes: SOUTH AFRICA: 80 ♂ (NMSA 10439; AMNH; BMNH; CASC; MCZ; MNHN; TMSA 17984–17985), 4 ♂ (NMSA 10452), 2 ♀ (NMSA 10946), same data as holotype; 70 ♂ (NMSA 10455; BMNH; CASC; MCZ; MNHN; SAMC C213; TMSA 12453–12455), Twee Rivieren, 1960–1970, le Riche family and staff; 29 ♂ (NMSA 10948), Mata Mata [*Northern Cape Province*: Gordonia District: Kalahari Gemsbok National Park], 25°53′S 20°01′E, 24.iv.1970, B.H. Lamoral; juv. ♂ (NMSA 10453), same data except 27.iv.1970; NAMIBIA: 9 ♂ (NMSA 10947), Farm Sterkstroom 320 [*Karas Region*: Keetmanshoop District], 25°43′S 19°19′E, 19.iii.1969, B.H. Lamoral.

Diagnosis.—*Parabuthus kalaharicus* is most closely related to *P. granulatus* (Fig. 1). The two species may be separated from all other species of *Parabuthus* by means of the following combination of characters: pedipalp chela, asetose; chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); chela manus, smooth and shiny; first proximal median lamella of pectines (female) suboval, with mesal margin arcuate (i.e., not enlarged and lobate) and free of teeth; metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segments I–V and telson, virtually asetose; metasomal segment II, stridulatory surface not reaching posterodorsal margin of segment; metasomal segment IV, median lateral carinae proximally obsolete; metasomal segment V, dorsosubmedian carinae absent, dorsolateral carinae distally obsolete; telson vesicle, width consider-



Figures 69–73.—*Parabuthus capensis* (Ehrenberg 1831), dextral pedipalp segments, illustrating shape, granulation and trichobothrial distribution. 69. ♂ (SAMC C4565). 70–73. ♀ (SAMC C4513), 69, 70. Chela, dorsal aspect. 71. Patella, dorsal aspect. 72. Patella, external aspect. 73. Femur, dorsal aspect. Scale bars = 1 mm.

ably narrower (65–72%) than width of metasomal segment V.

Parabuthus kalaharicus may be separated from *P. granulatus* by means of the following characters: pedipalp chela fixed finger, trichobothrium *dt* situated proximal to *et*; chela movable finger of female, short, compared with manus (measured along ventroexternal carina), length finger/length carina: ± 1.50; metasomal segment IV, ventrosubmedian carinae reduced to the proximal third of segment (posterior three quarters obsolete); metasomal segment V, ventromedian carina absent, ventrolateral carinae comprising spinose processes subdistally.

Remarks.—Lamoral (1979) added further comparative morphological data to his original description of *P. kalaharicus* (Lamoral 1977).

Distribution.—Endemic to the southwestern part of the Kalahari sand system, with records from Namibia (Keetmanshoop District, Karas Region) and South Africa (Gordonia District, Northern Cape Province). No specimens of *P. kalaharicus* have yet been recorded from Botswana. However, the association of this species with the Kalahari sand system in Namibia and South Africa suggests that it must also occur in the Kgalagadi District of southwestern Botswana, adjacent to the Kalahari Gemsbok National Park of South Africa, where most of the specimens have been collected. This species has not been recorded south of the Orange River.

Ecology.—*Parabuthus kalaharicus* is a psammophilous species, which displays several ecomorphological adaptations to its sand dune habitat: elongated, unequal telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins; metasoma lacking some carinae on segments IV and V. Specimens of *P. kalaharicus* have been found at night with UV light detection, walking on the surface of unconsolidated red sand dunes, and have also been excavated from burrows at the base of shrubs growing on the sand dunes. As with *P. granulatus*, *P. kalaharicus* is an errant forager, which moves about actively in search of prey, rather than adopting a sit-and-wait strategy.

Parabuthus kalaharicus is syntopic with *P. granulatus*, *P. kuanyamarum* and *P. raudus* throughout its distributional range, and has been recorded in syntopy with *P. laevifrons* at Twee Rivieren (pers. obs.). *Parabuthus kalaharicus* and *P. kuanyamarum* inhabit softer sand on the dune crests, whereas *P. granulatus*, *P. laevifrons*, and *P. raudus* are more common in the interdune valleys, where the sand is more compacted.

Material examined.—SOUTH AFRICA: *Northern Cape Province*: Gordonia District: Askham [26°59′S 20°47′E], i.2000, G.J. Müller et al., collected at night with UV light, 1 ♂ (AMNH); Farm Alpha, 40 km S of Twee Rivieren on road to Andriesvale [26°47′S 20°10′E], iii.2000, J. du Plessis et al., collected at night with UV light, 4 ♂ (AMNH).

Parabuthus kraepelini Werner 1902
Fig. 4

Parabuthus kraepelini Werner 1902: 599; Kraepelin 1914: 111; Werner 1916: 82, 83; Lampe 1917: 193; Hewitt 1918: 108–111; Lawrence 1928: 270; Roewer 1943: 207; Lawrence 1955: 227; Lamoral & Reynders 1975: 518; Lamoral 1979: 579–583, figs. 133–139; Kovařík 1998: 116; Fet & Lowe 2000: 205; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Parabuthus flavidus: Kraepelin 1908: 254, 255.

Type material.—Holotype: 1 juv. ♀ (NHMW 2080), NAMIBIA: Windhoek, South West Africa [*Khomas Region*: Windhoek District, 22°34′S 17°06′E].

Diagnosis.—*Parabuthus kraepelini* is basal to the clade comprising *P. raudus*, *P. schlechteri*, *P. transvaalicus* and *P. villosus* (Fig. 1). The five species may be separated from all other species of *Parabuthus* by means of the following combination of characters: pedipalp chela (adult male), fixed finger strongly curved dorsally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus kraepelini may be separated from the other four species in this clade by means of the following combination of characters: metasomal segment IV, dorsosubmedian carinae continuous; metasomal segment V, ventrolateral carinae comprising lobate processes subdistally.

Remarks.—Kraepelin (1908) erroneously listed *P. kraepelini* as a junior synonym of *P. flavidus*, which he, in turn, suggested might be a junior synonym of *P. mossambicensis*, and later (Kraepelin 1914) listed as such (discussed below). Kraepelin (1914), apparently prompted by Hewitt's (1912) remarks, retracted his synonymy of *P. kraepelini* with *P. mossambicensis*, and instead considered them distinct species. The status of *P. kraepelini* remained uncontested by subsequent authors (e.g., Hewitt 1918; Lawrence 1928, 1955; Roewer 1943; Lamoral & Reynders 1975) and the species was revised by Lamoral (1979).

Distribution.—Endemic to consolidated sandy areas in central and northern Namibia, north of 23°S latitude, east of the Namib sand system, and west of the Kalahari sand system. This species has not been recorded north of the Kunene River (Prendini 1995). However, its occurrence throughout the northern half of Namibia suggests that it may also occur in regions of similar soil and vegetation in southern Angola. Furthermore, in the northern part of its range, *P. kraepelini* is sympatric with a scorpionid, *Opistophthalmus gibbericauda* Lamoral 1979, which has similar substratal requirements, and has been recorded from southern Angola (Lamoral 1979).

Ecology.—*Parabuthus kraepelini* is a semi-psammophilous species, inhabiting consolidated sandy and gritty substrata, where it excavates burrows in open ground and at the base of shrubs and grass tufts. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

Parabuthus kraepelini is syntopic with *P. brevimanus*, *P. granulatus* and *P. villosus* in part of its range. Where they occur in sympatry (e.g., at Hobatere in the Kunene Region of Namibia), *P. kraepelini* is generally found in open sandy habitats, whereas *P. villosus* frequents rocky habitats.

Material examined.—NAMIBIA: *Hardap Region*: Rehoboth District: Farm Kangas 371, 23°36′S 17°03′E, 14.iii.1976, B. Lamoral, 1 subad. ♂ (NMSA 10850). *Kunene Region*: Outjo District: Etosha National Park: Aus [19°15′S 16°15′E], 2–6.iii.1969, B. Lamoral & R. Day, 1 ♀ (NMSA 10022); Gemsbokvlakte, 4.iii.1969, B. Lamoral & R. Day, 2 ♀ (NMSA 10019). *Otjozondjupa Region*: Okahandja District: Okahandja [21°59′S 16°55′E], 24.ix.1994, I. Engelbrecht, 2 ♂, 2 ♀ (SAMC C4605).

Parabuthus kuanyamarum Monard 1937
Figs. 25, 30

Parabuthus kuanyamarum Monard 1937: 258, 259; Forcart 1961: 48; Lamoral & Reynders 1975: 518; Lamoral 1979: 583–586, figs. 95, 140–147; FitzPatrick 1994: 8; Kovařík 1998: 116; Fet & Lowe 2000: 205; Prendini 2001a: 17; Prendini 2001b: 136; Dyason et al. 2002: 769; Prendini 2003: 21.

Type material.—Lectotype ♀ (MNHN) [designated by Lamoral (1979)], ANGOLA: Mupanda [*Cunene Province*: Omupanda, 17°08′S 15°46′E], vii.1933, A. Monard. Paralectotypes: (NHMB 96a), same data as lectotype. Monard's (1937) original description was based on 4 male and 3 female syntypes. Lamoral (1979) discovered one of these in the MNHN collection, which he designated as the lectotype, but noted that the remaining syntypes, formerly in the MHNC, were lost. Lamoral was apparently unaware of the existence of two syntypes in the NHMB (Forcart 1961).

Diagnosis.—*Parabuthus kuanyamarum* is the sister species of *P. distridor*, the two species forming a sister group to the *P. gracilis–P. nanus* group (Fig. 1). Both species may be separated from all other species of *Parabuthus* by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; pedipalp chela manus smooth; pedipalp chela with trichobothrium *dt* situated proximal to *et*; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae absent; metasomal segments II and III, posteroventral margins not demarcated by a transverse row of granules or tubercles; metasomal segment IV with median lateral, ventrolateral and ventrosubmedian carinae absent; metasomal segments IV and V, lateral intercarinal surfaces smooth; metasomal segment V with dorsosubmedian, dorsolateral and ventromedian carinae absent, but with ventrolateral carinae present, converging distally, and comprising spinose processes subdistally.

Parabuthus kuanyamarum may be separated from *P. distridor* by means of the following characters: pedipalp chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly

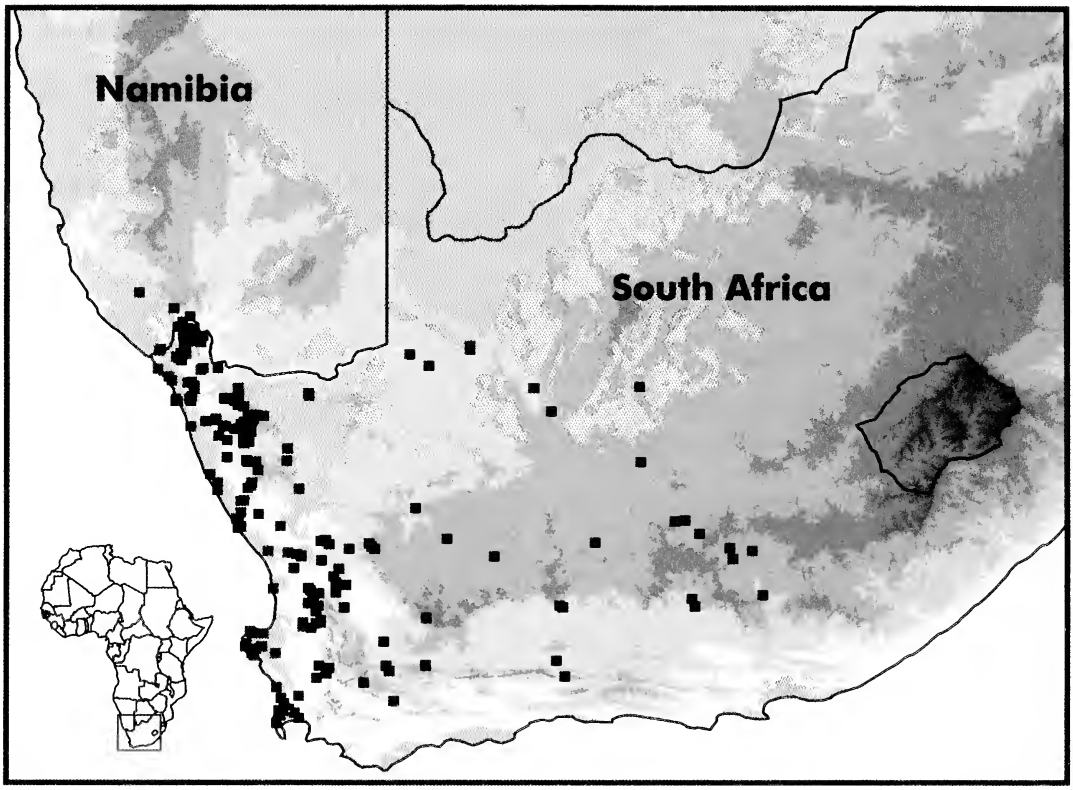


Figure 74.—The known distribution of *Parabuthus capensis* (Ehrenberg 1831) (■), which is endemic to Namibia and South Africa. Contour interval = 500 m. Major sand systems stippled.

emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments I–V and telson, virtually asetose; metasomal segments I–III, median lateral, ventrolateral, and ventrosubmedian carinae present; metasomal segments I and II, dorsal stridulatory surface present.

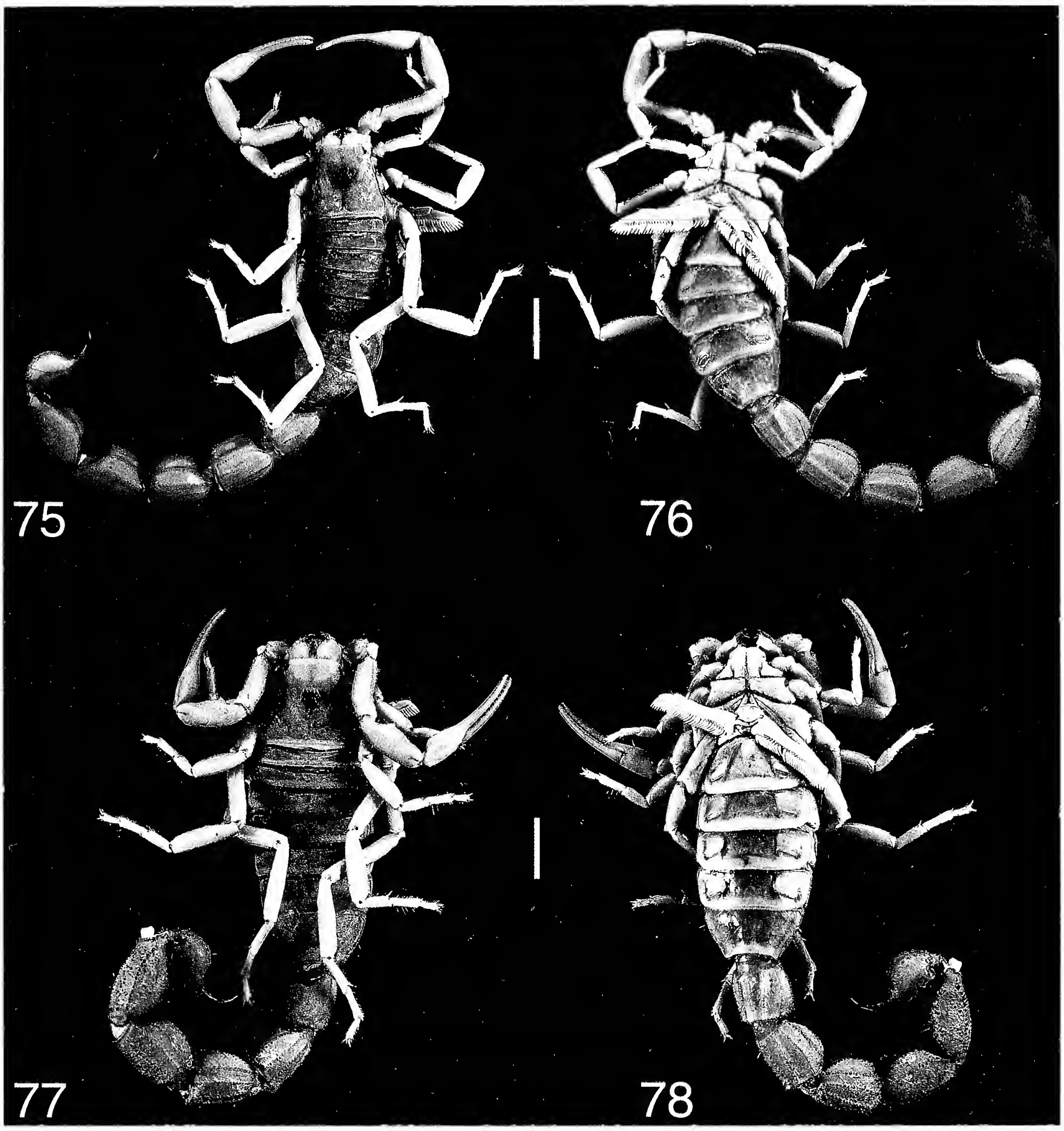
Remarks.—*Parabuthus kuanyamarum* was revised by Lamoral (1979). FitzPatrick (1994) provided additional diagnostic differences between this species and other members of the genus.

Distribution.—Endemic to the Kalahari sand system, with records from Angola, Botswana, Namibia, South Africa, Zambia, and Zimbabwe. Lawrence (1955) omitted *P. kuanyamarum* from his checklist to the scorpions of South Africa and Newlands & Martindale (1980) omitted it from their review of the Zimbabwean buthid fauna. This species has not been recorded south of the Orange River.

Ecology.—*Parabuthus kuanyamarum* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated, unequal telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins; metasoma and telson lacking carinae on segments III–V. Specimens of *P. kuanyamarum* have been found at night with UV light detection, resting on the surface of unconsolidated red sand dunes, and have also been excavated from burrows in the side of sand dunes.

Parabuthus kuanyamarum is syntopic with *P. granulatus* and *P. raudus* throughout its distributional range, and with *P. kalaharicus* and *P. laevifrons* in the southwestern part of its range. Like *P. kalaharicus*, *P. kuanyamarum* inhabits softer sand on the dune crests, whereas *P. granulatus*, *P. laevifrons*, and *P. raudus* are more common in the interdune valleys, where the sand is more compacted.

Parabuthus kuanyamarum is sympatric with *P. brevimanus* on the western periphery of its range (Lamoral 1979), and with *P. mossambicensis* and *P. transvaalicus* on the east-



Figures 75–78.—*Parabuthus planicauda* (Pocock 1889), habitus (dorsal and ventral aspects). 75, 76. ♂ (SAMC C4580). 77, 78. ♀ (SAMC C128). Scale bars = 5 mm.

ern periphery (pers. obs.). However, *P. kuanyamarum* inhabits softer substrata than these species and is rarely syntopic. The species is allopatric with its sister species, *P. distridor*.

Material examined.—BOTSWANA: Ngamiland District: N Khwaai and Lechwee camps, 18°40′S–19°00′S 23°00′E–23°45′E, 16–20.xi.1979, B. Lamoral, 3 ♀ (NMSA 13972). NAMIBIA: *Hardap Region*: Rehoboth District: Farm Ghobab 381, 23°26′S 17°21′E, 12.iii.1976, B. Lamoral, 13 ♂, 1 ♀, 7 juv. (NMSA 10813). SOUTH AFRICA: *Northern Cape Province*: Gordonia District: Kalahari Gemsbok National Park: Mata Mata, 25°53′S 20°01′E, 24.iv.1970, B.H. Lamoral, 1 ♀ (NMSA 10430) [homotype designated by Lamoral (1979)].

Parabuthus laevifrons (Simon 1888)
Figs. 17, 22, 34, 46

Buthus laevifrons Simon 1888: 379, 380.

Parabuthus laevifrons: Kraepelin 1899: 30, 31; Purcell 1901: 151–155; Kraepelin 1908: 251; Hewitt 1912: 301; Kraepelin 1914: 109; Hewitt 1918: 104, 105; Werner 1936: 177; Roewer 1943: 207; Lamoral & Reynders 1975: 518; Lamoral 1979: 586–591, figs. 148–154; Kovařík 1998: 117; Fet

& Lowe 2000: 205; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Parabuthus ibelli Werner 1916: 84–86 (synonymized by Lamoral 1979: 586); Lampe 1917: 193.

Parabuthus laevifrons australis Hewitt 1918: 105, 177 (synonymized by Lamoral 1979: 586); Lawrence 1955: 227; Lamoral & Reynders 1975: 518.

Parabuthus laevifrons ibelli: Lawrence 1955: 227; Lamoral & Reynders 1975: 519.

Type material.—*Buthus laevifrons:* Holotype ♀ (not ♂) (formerly in the MNHN, now lost). NAMIBIA: "sud-ouest Afrique", 1884–1886, Dr H. Schinz. Neotype ♀ (NMSA 10436) [designated by Lamoral (1979)]. NAMIBIA: Hardap Dam, Mariental [*Hardap Region*: Mariental District: 24°30′S 17°52′E], x.1968, R.F. Lawrence.

Parabuthus ibelli: Syntypes: 1 ♂, 1 ♀ (NHMW 1056–1057). NAMIBIA: Berseba, South West Africa [*Karas Region*: Keetmanshoop District: 25°59′S 17°47′E].

Parabuthus laevifrons australis: Syntypes: SOUTH AFRICA: 1 ♂, 1 ♀ (MMKZ), south of the Orange River [*Northern Cape Province*]; 1 ♂ (MMKZ), Upington [*Northern Cape Province*: Gordonia District: 28°26′S 21°14′E], Miss H. Lennox.

Diagnosis.—*Parabuthus laevifrons* is most closely related to *P. stridulus* (Fig. 1). The two species may be separated from all other species of *Parabuthus* by means of the following combination of characters: surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; pedipalp chela, asetose; chela manus, smooth and shiny; chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); chela movable finger of female, short, compared with manus (measured along ventroexternal carina), length finger/length carina: ± 1.50; metasomal segments slender (length IV/width IV: 1.7–2.11), virtually asetose; metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments IV and V, lateral intercarinal surfaces smooth; metasomal segment IV, median lateral carinae poorly developed; metasomal segment V, dorsosubmedian carinae and dorsolateral carinae absent, but ventrolateral carinae distinct.

Parabuthus laevifrons may be separated from *P. stridulus* by means of the following characters: pedipalp chela fixed finger with trichobothrium *dt* situated proximal to *et*; metasomal segment II dorsal stridulatory surface composed of fine granules; metasomal segments III–V and telson strongly infuscated, contrasting markedly with segments I and II, which are pale in coloration; metasomal segment V, ventrolateral carinae comprising lobate processes subdistally; telson vesicle shallowly excavated along longitudinal half of dorsoproximal surface.

Remarks.—Lawrence (1955) suggested that *P. laevifrons militum* is a junior synonym of *P. ibelli.* Lamoral (1979) revised *P. laevifrons*, and demonstrated that *P. ibelli* and *P. laevifrons australis* are junior synonyms, whereas *P. laevifrons militum* is synonymous with *P. stridulus.*

Distribution.—Endemic to consolidated sandy areas in the Hardap and Karas regions of southern Namibia and the Northern Cape Province (Gordonia, Kenhardt and Namaqualand districts) of South Africa. The distribution of this species extends across the Orange River.

Although no specimens of *P. laevifrons* have yet been recorded from Botswana, the occurrence of a few records from the Kalahari Gemsbok National Park of South Africa (Gordonia District, Northern Cape Province) suggests that this species may also occur in the Kgalagadi District of southwestern Botswana, adjacent to the park. *Parabuthus laevifrons* is largely absent from the Kalahari sand system, only appearing in association with major dry watercourses, e.g., the Auob and Nossob riverbeds.

Ecology.—*Parabuthus laevifrons* is a psammophilous species, which excavates burrows in open ground, at the base of shrubs, grass tufts and shrub coppice dunes. The species displays several ecomorphological adaptations to its sandy habitat: unequal telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins.

Parabuthus laevifrons is syntopic with *P. granulatus*, *P. nanus* and *P. schlechteri* throughout its distributional range and with *P.*

brevimanus, *P. kalaharicus*, *P. kuanyamarum* and *P. raudus* in part of its range. The species is sympatric (but not syntopic) with *P. villosus* in some areas. It is allopatric with its sister species, *P. stridulus*.

Material examined.—NAMIBIA: *Karas Region*: Karasburg District: Farm Ortmansbaum 120, 28°19′S 18°43′E, 26–28.i.1973, B. Lamoral & L. Ferguson, 2 ♂, 1 ♀, 1 juv. ♀ (NMSA 10509). Keetmanshoop District: Tses, dune strip SE, 25°53′S 18°10′E, 23–24.ii.1973, B. Lamoral & K. Porter, 1 ♂, 4 ♀, 2 subad. ♀, 3 juv. ♂, 3 juv. ♀ (NMSA 10521).

Parabuthus mossambicensis (Peters 1861)
Fig. 2

Prionurus mossambicensis Peters 1861: 516.

Parabuthus capensis: Kraepelin 1899: 31.

Parabuthus flavidus Pocock 1899: 419, 420 (synonymized by Kraepelin 1914: 111; Newlands & Martindale 1980: 54, 55); Pocock 1902: 367; Kraepelin 1908: 254, 255, fig. 1b; Hewitt 1912: 300, 301; Hewitt 1918: 108, 178. pl. XXVII, fig. 69; Hewitt 1935: 467; Lawrence 1942: 235; Lawrence 1955: 226; Lamoral & Reynders 1975: 516.

Parabuthus mosambicensis: Kraepelin 1908: 255, 256, fig. 1a; Newlands & Martindale 1980: 54, 55; Kovařík 1998: 117.

Parabuthus truculentus Hirst 1911: 2 (synonymized by FitzPatrick 1994: 8); Loveridge 1925: 306; Bacelar 1950: 5; Lamoral & Reynders 1975: 523; Newlands & Martindale 1980: 58–60, fig. 17.

Parabuthus triradulatus Hewitt 1914: 1, fig. 1 (synonymized by FitzPatrick 1994: 8); Lawrence 1942: 235; Lawrence 1955: 228; Lawrence 1964: 34; Lawrence 1967: 85; Lamoral & Reynders 1975: 523; Aguiar 1978: 108, fig. 1.

Parabuthus mossambicensis: Werner 1916: 83; Lamoral & Reynders 1975: 520; Moritz & Fischer 1980: 319; FitzPatrick 1994: 8–10, fig. 2; Fet & Lowe 2000: 207, 208; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Parabuthus mossambicus: Bacelar 1950: 5.

Parabuthus scobinifer: Newlands & Martindale 1980: 54, 55.

Parabuthus mossambicensis flavidus: FitzPatrick 1994: 10, 11; Fet & Lowe 2000: 208.

Parabuthus mosambicensis flavidus: Kovařík 1998: 117.

Parabuthus mossambicensis mossambicensis: FitzPatrick 1994: 8–10; Fet & Lowe 2000: 208.

Type material.—*Prionurus mossambicensis:* Holotype 1 subad, ♂ (ZMHB 2305), MOZAMBIQUE: Tette [*Tete Province*: Tete, 16°10′S 33°35′E], W. Peters.

Parabuthus flavidus: Holotype ♀ (BMNH 1897.12.4.2). SOUTH AFRICA: Taungs [Taung, 27°32′S 24°48′E], Bechuanaland [*Northern Cape Province*: Taung District], H.A. Spencer.

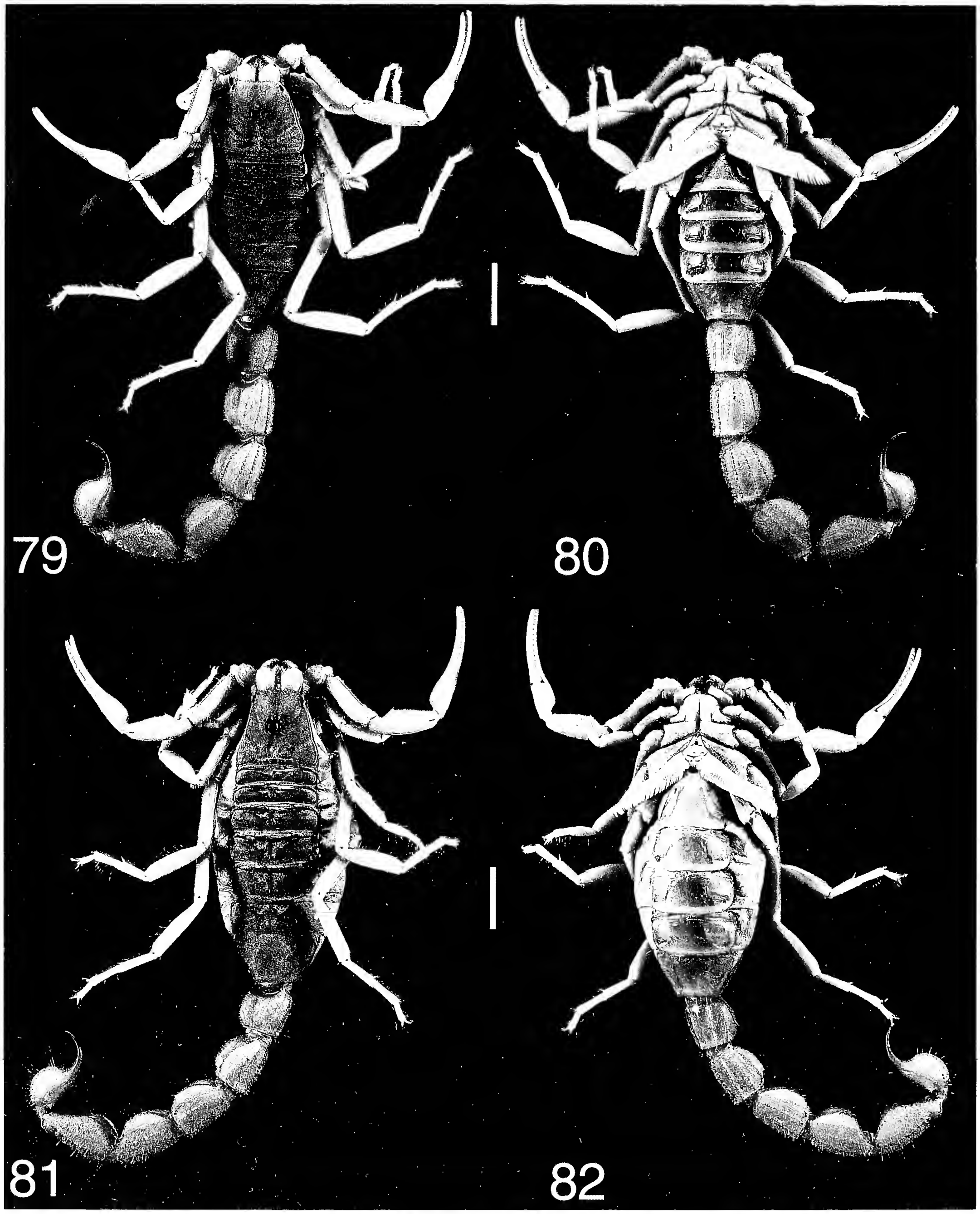
Parabuthus truculentus: Holotype ♀ (BMNH 1911.8.2.1). MOZAMBIQUE: East bank of Loangwa, Portuguese East Africa, 15.vii–1.x.1904.

Parabuthus triradulatus: Syntypes: 1 subad. ♂ [not ♀] (TMSA 1867), 1 ♀ (AMGS), SOUTH AFRICA: Transvaal, N of Soutpansberg, between Sand and Nwanedzi Rivers [*Limpopo Province*: Soutpansberg District], 28.ix.1913, Messrs. Noomé and Roberts. As noted by FitzPatrick (1994), the syntypes of *P. triradulatus* in the TMSA collection have dried out and been rehydrated. They are therefore very brittle.

Diagnosis.—*Parabuthus mossambicensis* is basal to the clade comprising *P. kraepelini*, *P. raudus*, *P. schlechteri*, *P. transvaalicus* and *P. villosus* (Fig. 1). The six species differ from all other species of *Parabuthus* by means of the following combination of characters: metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus mossambicensis may be separated from all species of *Parabuthus* by means of the following combination of characters: pedipalp chela (adult male), fixed and movable fingers straight, such that proximal dentate margin linear when fingers are closed (i.e., no proximal "gap" is evident); metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect, and composed of transverse ridges, some of which extend right across the surface.

Remarks.—Confusion has surrounded the identity of *P. mossambicensis* since its description more than a century ago. Kraepelin



Figures 79–82.—*Parabuthus planicauda* (Pocock 1889), habitus (dorsal and ventral aspects). 79, 80. ♂ (SAMC C4575). 81, 82. ♀ (SAMC C4575). Scale bars = 5 mm.

(1891) first listed the species in synonymy with *P. leiosoma* (as *Heterobuthus liosoma*) but subsequently (Kraepelin 1899) listed it (as *Buthus mosambicensis*) in synonymy with *P. capensis*. Kraepelin (1908) later regarded *P. mossambicensis* as a distinctive species, and mentioned an apparent similarity to *P. planicauda*. However, Purcell (1901), who regarded *P. planicauda* as a junior synonym of *P. capensis* (discussed above), doubted that *P. mossambicensis*, collected at Tete (Mozambique), could be synonymous with *P. capen-*

sis, an opinion later supported by Lamoral & Reynders (1975).

Pocock (1899) described *P. flavidus*, from Taung (Northern Cape Province, South Africa), which he believed to be allied to *P. capensis*. However, Purcell (1901) considered *P. flavidus* more closely related to *P. raudus* and *P. schlechteri*. One year later, Werner (1902) described *P. kraepelini*, from Windhoek (Namibia). Kraepelin (1908) then erroneously listed *P. kraepelini* in synonymy with *P. flavidus* (discussed above), an error compounded by his fig. 1, demonstrating the dorsal stridulatory surfaces of metasomal segments I and II in *P. mossambicensis* and *P. flavidus*, which he treated as distinct species. Kraepelin's (1908) fig. 1 was a source of great confusion in the literature because, whereas his diagram of *P. mossambicensis* (fig. 1a) was based on Peters' holotype, his diagram of *P. flavidus* (fig. 1b) was based on a nontype specimen of *P. kraepelini*. Hewitt (1912) commented on the discrepancy, noting that Kraepelin had recorded *P. flavidus* from Windhoek, but that his figure appeared to refer to another species (viz. *P. kraepelini*), whereas his figure of *P. mossambicensis* was barely distinguishable from the true *P. flavidus* suggesting, as also suggested by Hirst (1911), that *P. flavidus* and *P. mossambicensis* are synonymous. Hewitt (1918) provided a diagram (Text-Fig. 1) of the stridulatory surfaces on metasomal segments I and II in a specimen of *P. kraepelini* from Heichamchab (Namibia), demonstrating the similarity to Kraepelin's (1908) fig. 1b.

Kraepelin (1908) had evidently suspected that *P. flavidus* was a junior synonym of *P. mossambicensis* as he commented on the close similarity between them and, to a lesser extent, *P. planicauda*. However, although Newlands & Martindale (1980) credited Kraepelin (1908) for the synonymy of *P. flavidus* with *P. mossambicensis*, it was not until later that Kraepelin (1914) officially listed *P. flavidus* in synonymy. It does not appear that Kraepelin ever actually examined the type specimen of *P. flavidus* from the BMNH.

Kraepelin's (1908, 1914) synonymy of *P. flavidus* with *P. mossambicensis* was accepted by some authors (e.g., Hirst 1911; Werner 1916), but not others (e.g., Hewitt 1913, 1914, 1915, 1918, 1935; Lawrence 1942). For example, Kraepelin's (1908) erroneous synonymy of *P. kraepelini* discouraged Hewitt (1918) from accepting the synonymy of *P. flavidus* until more material from Tete was available.

During this period, two more species, *P. truculentus* and *P. triradulatus*, distinguished from each other, and from *P. mossambicensis* and *P. flavidus*, only by the stridulatory surface (Hirst 1911; Hewitt 1914), were described from the region between the type localities of the latter species. According to Hewitt (1914), *P. triradulatus* belongs to the group including *P. flavidus*, *P. truculentus* and perhaps *P. mossambicensis*, but differs from these based on the ridged stridulatory surface of the last mesosomal tergite. Hewitt (1918) maintained that *P. triradulatus* is closely related to, or conspecific with, *P. truculentus*, and further suggested that both might be synonymous with *P. mossambicensis*. Hewitt (1918) examined the type of *P. truculentus* and noted that the median portion of the last tergite is coarsely granular, and that the medial granules in the posterior third of the tergite are transversely elongated into short stout ridges, although none stretch across even half the breadth of the surface, as in *P. triradulatus*. Hewitt (1918) also noted that the four carinae of the last sternite are more strongly developed than in *P. triradulatus*, but suggested that this may be because the type of *P. triradulatus* is subadult.

Thirty years later, when Lawrence's (1955) key and checklist to the South African scorpions was published, *P. flavidus* and *P. triradulatus* were included, whereas *P. mossambicensis* and *P. truculentus* were omitted, perhaps because they were extralimital. Furthermore, Lawrence (1955) made no mention of the discussion raised by Kraepelin (1908, 1914), Hirst (1911), or Hewitt (1914, 1918). More recently, Lamoral & Reynders (1975) listed all four species as valid, noting the arguments of Kraepelin (1908) and Hewitt (1918), but omitting to mention Kraepelin's (1914) synonymy of *P. flavidus* with *P. mossambicensis*.

Newlands & Martindale (1980) subsequently revised the Zimbabwean buthid scorpions, returning *P. flavidus* to synonymy with *P. mossambicensis*, and listing yet another species, *P. scobinifer*, as a new synonym of the latter. Newlands & Martindale (1980) did not examine the type of *P. mossambicensis*, but accepted Kraepelin's opinion based on an examination of nontype material from Mozambique. The types of *P. scobinifer* and *P. flavidus* were compared in the BMNH and deemed conspecific by Newlands & Martindale (1980). Apparently, the only difference between them was the relative area covered by the stridulatory surface of metasomal segment II, which did not quite reach the posterior margin in *P. scobinifer* but did so in *P. flavidus*. The type of *P. flavidus* came from Taung (Northern Cape Province, South Africa) whereas the type of *P. scobinifer* was collected in "N.W. Rhodesia" [N.W. Zimbabwe, not Zambia as stated by Newlands & Martindale (1980)]. According to Newlands & Martindale (1980), the stridulatory surface of several *Parabuthus* species varies with geographical location and this single character cannot be considered sufficient grounds for specific status.

Newlands & Martindale (1980) also synonymized *P. triradulatus* with *P. truculentus*, after a comparison of the types revealed no meaningful morphological differences which could justify the validity of *P. triradulatus*. However, the failure of Newlands & Martindale (1980) to synonymize *P. truculentus* and *P. triradulatus* with *P. mossambicensis* contradicts their justification for synonymizing *P. flavidus* and *P. scobinifer* with the latter. According to these authors, the only consistent character distinguishing *P. truculentus* is the stridulatory surface of metasomal segment I, which is composed of distinct transverse ridges compared with the broadened granules seen in *P. mossambicensis*. However, FitzPatrick (1994) recently examined some of the specimens examined by Newlands & Martindale (1980) and found none with broadened granules but only ridges.

FitzPatrick (1994) set out to clarify the status of *P. flavidus*, *P. mossambicensis*, *P. scobinifer*, *P. triradulatus* and *P. truculentus* anew by means of a comparison of the types and a large number of additional specimens, the localities of which were mapped to determine whether there was any geographic pattern to the variation. FitzPatrick (1994) demonstrated that *P. scobinifer* is actually a junior synonym of *P. raudus* (discussed below), and that *P. truculentus* and *P. triradulatus* are junior synonyms of *P. mossambicensis*. FitzPatrick (1994) observed an increase in metasomal length and granulation from northeast to southwest in the distributional range she mapped from the locality records, but noted that intraspecific variation in scorpion tail length and granulation are known to occur (Lamoral 1979; Harington 1984). According to FitzPatrick (1994), the holotypes of *P. mossambicensis*, *P. truculentus*, and *P. triradulatus*, all of which originate from northeast in the distributional range, are identical morphologically, demonstrating short ridges on tergite VII, and metasomal segments IV and V that are slightly longer and less granular than in specimens from southwest in the distributional range. FitzPatrick (1994) concluded that they are conspecific and should therefore be synonymized.

Rather than following Newlands & Martindale (1980) in retaining *P. flavidus* as a junior synonym of *P. mossambicensis*, FitzPatrick (1994) provided subspecific status for *P. flavidus*. FitzPatrick (1994) offered no substantial reasons for this decision, which was supported by the following arguments: (1) The holotype of *P. flavidus* is juvenile, (2) The type locality of *P. flavidus* is located southwest in the distributional range, (3) Trichobothrial patterns are the same in all four holotypes (*P. flavidus*, *P. mossambicensis*, *P. triradulatus* and *P. truculentus*) and in nontype specimens from both regions, (4) Haemolymph electrophoresis could be used to confirm the specific status of specimens from the southwestern region, (5) *Parabuthus flavidus* should be regarded as a subspecies of *P. mossambicensis* until this is performed.

It is unclear as to why, in the absence of consistent morphological differences, FitzPatrick (1994) rejected Kraepelin's (1914) synonymy of *P. flavidus*, later adopted by Newlands & Martindale (1980). FitzPatrick (1994) erroneously stated that this was the first time the type of *P. mossambicensis* had been re-examined since Peters (1861) described it. According to FitzPatrick (1994), Kraepelin (1908) claimed to have examined the type but erroneously stated that the dorsal carina of metasomal segment V is present throughout its length, published diagrams to show this, and synonymized *P. flavidus* with *P. mossambicensis* on this basis. But it is evident, from the above discussion, that Kraepelin (1908) did indeed examine the type of *P. mossambicensis*, and thus came to the correct conclusion, although his formal synonymy of *P. flavidus* with *P. mossambicensis* only appeared later (Kraepelin 1914). Contrary to FitzPatrick's (1994) assertion, Kraepelin's (1908) fig. 1 shows metasomal segments I and II, not V.

Given the evidence presented here, it is clear that no morphological character or combination thereof can be used to separate *P. flavidus*, *P. mossambicensis*, *P. triradulatus* and *P. truculentus*. Neither an appeal for unavailable electrophoretic evidence, nor the arbitrary partitioning of continuous variation across the distributional range of a widespread, polymorphic species, can justify retaining FitzPatrick's (1994) putative subspecies distinction between *P. mossambicensis mossambicensis* and *P. mossambicensis flavidus*. Moreover, providing subspecific status for *P. flavidus*, while placing *P. truculentus* and *P. triradulatus* in synonymy, is logically inconsistent. Accordingly, *P. flavidus* is returned to synonymy with *P. mossambicensis*.

Distribution.—Recorded from east of the Kalahari sand system in Botswana, Mozambique, South Africa, Zambia, and Zimbabwe. This species has not been recorded south of the Orange River.

Ecology.—*Parabuthus mossambicensis* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty substrata, where it excavates burrows in open ground and at the base of shrubs. Comblike rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

Parabuthus mossambicensis is syntopic with *P. transvaalicus* throughout its range and with *P. granulatus* and *P. kuanyamarum* in part of its range. Where they occur in sympatry (e.g., at Rochdale in the Limpopo Province of South Africa), *P. mossambicensis* is generally found in open sandy habitats, whereas *P. transvaalicus* frequents rocky habitats.

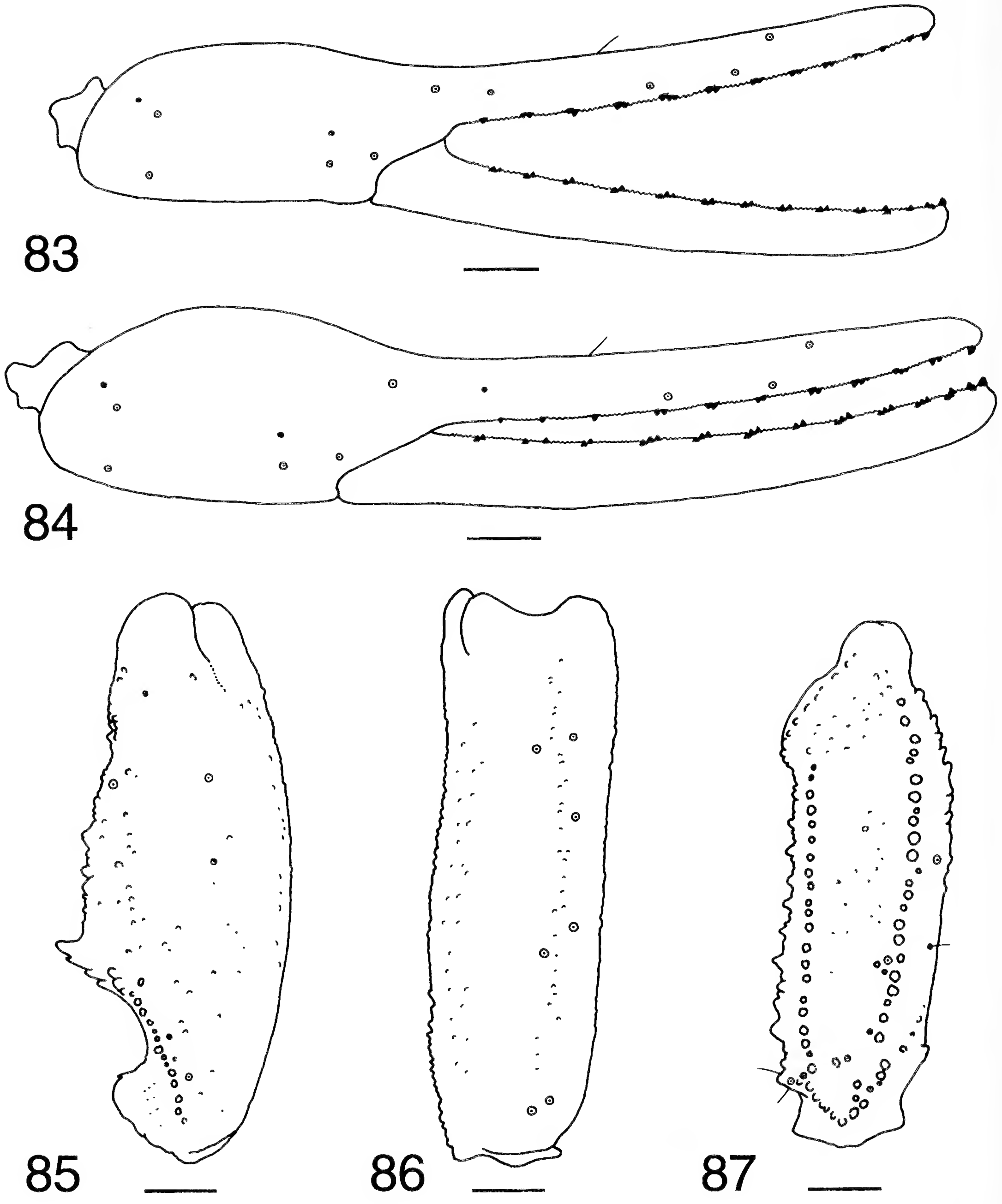
Conservation.—The international trade in exotic pets poses a small, but ever-increasing threat to the future survival of *Parabuthus* species, which have recently become extremely popular among amateur enthusiasts. Two southern African species, *P. mossambicensis* (the "Mozambique fat-tailed" scorpion) and *P. transvaalicus* (the "S.A. giant fat-tailed" scorpion), allegedly imported from Mozambique, are commonly available in Europe, the U.S.A. and Japan. The increasing appearance of such species in international collections is a matter of concern, given the frequency with which invertebrates are being smuggled illegally, along with insects and reptiles, out of southern African countries (A.L. de Villers, K. de Wet, M. Forsyth, P. Geldenhuys, A. Leroy, R. Stals, pers. comm.). The presence in the international pet trade of scorpions that originated from South Africa has always been difficult to verify given the fact that the distributional ranges of most species traded extend beyond South African borders, and dealers usually cite neighboring states with relaxed collecting and export regulations (e.g., Mozambique) as the source of specimens. As with most other scorpions imported into the pet trade, species of *Parabuthus* are not CITES-listed and there is little or no regulation on their harvesting from the wild, a situation that is clearly inadequate for safe-guarding their future survival.

Material examined.—"Kalahari Desert", R.J. Cunningham, 1 ♂ [not type as stated on label] (BMNH 1894.5.3.3). MOZAMBIQUE: *Sofala Province*: Gorongoza [18°41′S 34°19′E], 22.ii.1971, G. Vasse, 1 ♂ (NMSA 10088). SOUTH AFRICA: *Limpopo Province*: Messina District: Messina Nature Reserve [22°22′S 30°03′E], xii.1993, L. Prendini & K.M.A. Prendini, 1 ♂ (SAMC C4606). Soutpansberg District: Farm Rochdale 700 [22°54′S 29°42′E], i.1996, L. Prendini & J. Laing, 3 ♂ (SAMC C4607); Waterpoort [22°54′S 29°37′E], i.1996, L. Prendini & J. Laing, 3 ♀ (SAMC C4608).

Parabuthus muelleri Prendini 2000
Figs. 36, 41

Parabuthus muelleri Prendini 2000: 32–38, figs. 1–9, table 2; Prendini 2001a: 17; Prendini 2001b: 137; Prendini 2003: 5, 7, 9–16, 21, figs. 2–14, table 4.

Type material.—Holotype ♀ (NMNW 1854), NAMIBIA: *Hardap Region*: Maltahöhe District, Farm Onis 8, 82 km from Sesriem to Naukluft, 24°22.46′S 16°13.17′E, 1260 m, 7.i.1998, L. Prendini & E. Scott. Paratype ♀ (SAMC C4514), NAMIBIA: Karas Region: *Lüderitz District*: Farm Plateau 38, near Aus, 26°40.62′S 16°31.85′E, 1550 m, 30.xii.1997, L. Prendini & E. Scott.



Figures 83–87.—*Parabuthus planicauda* (Pocock 1889), dextral pedipalp segments, illustrating shape, granulation and trichobothrial distribution. 83. ♂ (SAMC C4573). 84–87. ♀ (SAMC C4573), 83, 84. Chela, dorsal aspect. 85. Patella, dorsal aspect. 86. Patella, external aspect. 87. Femur, dorsal aspect. Scale bars = 1 mm.

Diagnosis.—*Parabuthus muelleri* is part of a group of species that also includes *P. calvus*, *P. capensis*, *P. pallidus* and *P. planicauda* (Fig. 1), but is morphologically most similar to *P. capensis*, with which it shares the following combination of characters: metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform or subspiniform granules, dorsolateral carinae distally obsolete.

Parabuthus muelleri and *P. capensis* may be separated from all other *Parabuthus* on the basis of the following character: metasomal segment II, and to a lesser extent III, with posterodorsal edge elevated and slightly curved forward medially, forming a subtriangular V-shape. *Parabuthus muelleri* may be separated from *P. capensis* by the following characters: pedipalp chela, movable finger curved ventrally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segment I wider than segment IV; telson with distal "bulge" and a very short, sharply curved aculeus; pedipalp chela manus of adult male, slender as in adult female; proximal median lamella of pectines in male, lobate.

Distribution.—Endemic to Namibia (Lüderitz and Maltahöhe districts). This species has not been recorded south of the Orange River. It is known from only three specimens.

Ecology.—The only specimens of *P. muelleri* for which ecological data are available were collected in a region of compacted, chalky soil, calcrete nodes and dolomite rocks. The holotype was excavated from the burrow of a scorpionid, *Opistophthalmus opinatus* (Simon 1888), under a stone, whereas the paratype was found sitting on a stone at night. The paratype was syntopic with *P. granulatus* and *P. villosus* at Plateau.

Material examined.—NAMIBIA: *Karas Region*: Lüderitz District: Locality uncertain, probably Aus [26°41′S 16°15′E], A. Harington, 1 ♂ (AMNH [AH 3991]).

Parabuthus namibensis Lamoral 1979
Figs. 20, 23

Parabuthus namibensis Lamoral 1979: 591–594, figs. 155–163; Kovařík 1998: 117; Fet & Lowe 2000: 208; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Type material.—Holotype ♀ (NMSA 10822), NAMIBIA: 5 km N of Cape Cross, Skeleton Coast [*Erongo Region*: Swakopmund District], 21°43′S 13°56′E, 25.iii.1976, B.H. Lamoral. Paratypes: NAMIBIA: 1 ♂ (NMSA 10822), same data as holotype; 1 ♂ (TMSA 9787), Gobabeb [*Erongo Region*: Swakopmund District: Namib-Naukluft Park], 23°34′S 15°03′E; 1 subad. ♂ (TMSA 11086), 32 km from Gobabeb on way to Mirabib [*Erongo Region*: Swakopmund District: Namib-Naukluft Park], 23°02′S 15°02′E, S. Endrödy-Younga.

Diagnosis.—*Parabuthus namibensis* is most closely related to the *P. laevifrons–P. stridulus* group (Fig. 1). The three species may be separated from all other species of *Parabuthus* by means of the following combination of characters: surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segment IV, median lateral carinae poorly developed; metasomal segment V, dorsolateral carinae absent to distally obsolete, ventrolateral carinae distinct.

Parabuthus namibensis may be separated from *P. laevifrons* and *P. stridulus* by means of the following characters: pedipalp chela covered in setae; pedipalp chela fixed finger with trichobothrium *dt* situated distal to *et*; chela movable finger of female, long, compared with manus (measured along ventroexternal carina), length finger/length carina: 1.70–2.00; metasomal segments I–V and telson moderately setose; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V, dorsosubmedian carinae poorly developed and comprising blunt, rounded granules.

The following additional characters separate *P. namibensis* from *P. stridulus*, the distributional ranges of which overlap in the central and northern Namib: metasomal segment II, stridulatory surface composed of fine granules; metasomal segments III–V and telson strongly infuscated, contrasting markedly with segments I and II, which are pale in coloration; ventrolateral carinae comprising lobate processes subdistally; telson vesicle very shallowly excavated along longitudinal half of dorsoproximal surface.

Distribution.—Endemic to gravel plains in the central and northern Namib, north of the Kuiseb River (Swakopmund and Walvis Bay districts of northwestern Namibia).

Ecology.—*Parabuthus namibensis* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty substrata (gravel plains of the central Namib), where it presumably excavates burrows in open ground and at the base of shrubs. All specimens collected to date were either captured in pitfall traps or at night by means of UV light detection. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

Parabuthus namibensis is syntopic with *P. gracilis* and *P. stridulus* in part of its range. It is also sympatric (and possibly syntopic) with *P. brevimanus* in part of its range.

Material examined.—NAMIBIA: *Erongo Region*: Swakopmund District: Rössing, Lower Ostrich Gorge, 22°30′S 14°58′E, 8.v–5.vi.1984, E. Griffin, 1 ♀, 1 juv. ♂ (NMNW 845), 2–3.xi.1985, J. Irish & H. Rust, 1 ♂ (NMNW 896).

Parabuthus nanus Lamoral 1979
Figs. 13, 44, 45

Parabuthus nanus Lamoral 1979: 594–597, figs. 100–102, 105, 106, 164–172; Kovařík 1998: 117; Fet & Lowe 2000: 208; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Type material.—Holotype ♀ (NMSA 10926), NAMIBIA: Farm Noachabeb 97 [*Karas Region*: Keetmanshoop District], 27°24′S 18°30′E, 6.ii.1973, B.H. Lamoral. Paratypes: NAMIBIA: 1 ♂ (NMSA 10926), 2 ♂ (NMSA 10927), same data as holotype; 1 ♂, 1 subad. ♀, 1 juv. ♂ (NMSA 10698), same data as holotype, except 8.ii.1973; 1 ♂ (NMSA 10701), Farm Belda 361 [*Karas Region*: Karasburg District], 28°27′S 18°01′E, 1.ii.1973, B.H. Lamoral; 1 ♂, 1 ♀, 2 subad. ♂ (NMSA 10702), same data except 28.i.1973; 1 ♀ (NMSA 10699), Farm Louwshoop 330 [*Karas Region*: Karasburg District], 28°07′S 18°07′E, 3.ii.1973, B.H. Lamoral; 1 ♂, 1 ♀ (NMSA 10772), Farm Tsirub 13 [*Karas Region*: Lüderitz District: Diamond Area I], 26°52′S 16°02′E, 3.iii.1976, B.H. Lamoral. SOUTH AFRICA: 1 ♂ (NMSA 10703), Goodhouse (*Northern Cape Province*: Namaqualand District), 29°00′S 18°13′E, 29–31.i.1973, B.H. Lamoral; 1 ♀ (NMSA 10700), same data except 30.i.1973.

Diagnosis.—*Parabuthus nanus* is most closely related to *P. gracilis*, the two species forming a sister group to the *P. distridor–P. kuanyamarum* group (Fig. 1). *Parabuthus nanus* may be separated from all other species of *Parabuthus*, except *P. gracilis*, by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; carapace, including median ocular tubercle (male, female), entirely granular; pedipalp chela manus granular; pedipalp chela with trichobothrium *dt* situated proximal to *et*; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae absent; metasomal segments II and III, posteroventral margins demarcated by a transverse row of isolated, round granules; metasomal segment IV with median lateral, ventrolateral and ventrosubmedian carinae absent; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V with dorsosubmedian, dorsolateral and ventromedian carinae absent, but with ventrolateral carinae present, converging distally, and comprising spinose processes subdistally.

Parabuthus nanus is the smallest species of *Parabuthus*. In addition to its smaller size, *P. nanus* may be separated from *P. gracilis* by both of the following characters: chela movable finger of female, long, compared with manus (measured along ventroexternal carina), length finger/length carina: 1.70–2.00; manus of adult male, slender as in adult female.

Distribution.—Endemic to sandy areas in the Karas Region of southern Namibia and the Northern Cape Province (Namaqualand District) of South Africa. The distribution of this species extends across the Orange River.

Ecology.—*Parabuthus nanus* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins; metasoma and telson lacking carinae on segments III–V. Specimens of *P. nanus* have been found at night with UV light detection, resting on the surface of unconsolidated sand dunes, and have been excavated from burrows at the base of shrubs.

Parabuthus nanus is syntopic with *P. granulatus*, *P. laevifrons*, and *P. schlechteri* throughout its distributional range. *Parabuthus nanus* is sympatric with *P. brevimanus* in part of its range, e.g., at Aggeneys in the Northern Cape Province of South Africa (pers. obs.) and Noachabeb in the Karas Region of Namibia (Lamoral 1979), but these species are not syntopic: *P. nanus* inhabits softer substrata than *P. brevimanus*. The species is allopatric with its sister species, *P. gracilis*.

Material examined.—NAMIBIA: *Karas Region*: Lüderitz District, Diamond Area II: Awasib [25°23′S 15°39′E, 26.ii.1981, G. Newlands, 1 ♂ (AMNH [AH 4345]).

Parabuthus planicauda (Pocock 1889)
Figs. 75–88, Table 1

Buthus planicauda Pocock 1889: 344–346, pl. XV, fig. 5.

Parabuthus planicauda: Pocock 1895: 309; Pocock 1902: 365, 366; Hewitt 1912: 302; Hewitt 1918: 104, 178, pl. XXI, fig. 31; Pavlovsky 1924: 77; Pavlovsky 1925: 140; Lawrence 1946: 399; Lawrence 1955: 227; Lamoral & Reynders 1975: 521; Eastwood 1978b: 251, 252; Kovařík 1998: 117; Fet & Lowe 2000: 209; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Parabuthus capensis: Purcell 1901: 143–147.

Parabuthus capensis frenchi Purcell 1901: 148 (NEW SYNONYMY); Pocock 1902: 366.

Parabuthus planicauda frenchi: Hewitt 1918: 104, 178, pl. XXI, fig. 32; Lawrence 1955: 227; Lamoral & Reynders 1975: 521; Kovařík 1998: 117; Fet & Lowe 2000: 209.

Parabuthus planicauda planicauda: Fet & Lowe 2000: 209.

Type material.—*Buthus planicauda:* Lectotype ♀ (BMNH 1870.26), SOUTH AFRICA: Dr Quain. In the original description, Pocock (1889) listed five specimens, but did not state whether these were syntypes, or one was a holotype: 2 ♂ (BMNH), "West Africa" [erroneous]; 2 ♀ (BMNH), South Africa, Dr Quain & Dr Smith; 1 ♀ (BMNH), locality unknown, presented by Capt. Belcher, R.N. Subsequently, Pocock (1902) realized that two of these specimens, i.e., the two males labelled "W. Africa" that he originally referred to as *P. planicauda*, were conspecific with *P. neglectus* (itself a junior synonym of *P. capensis*). Pocock (1901) then specified a holotype for *P. planicauda*, i.e., the female specimen measured and described in the original description. According to the description, measurements were based on the largest specimen (Pocock 1889), but it is not known whether that specimen was one of the pair collected by Dr Quain & Dr Smith, or the single specimen presented by Capt. Belcher. Of these syntypes, only a single female (BMNH 1870.26), labelled "South Africa, Dr Quain", remains (J. Margerison, pers. comm.). This specimen is hereby designated as the lectotype of *P. planicauda*.

Parabuthus capensis frenchi: Syntypes: 1 ♂, 4 ♀ (SAMC 5207). SOUTH AFRICA: Graaff-Reinet, Cape Province (*Eastern Cape Province*: Graaff-Reinet District: 32°16′S 24°33′E), G. French; 1 juv. (SAMC) (lost, M. Cochrane, pers. comm.), Graaff-Reinet, C.L. Leipoldt.

Diagnosis.—*Parabuthus planicauda* is closely related to *P. calvus* (Fig. 1), with which it shares the following combination of characters: pedipalp chela manus of adult male, slender as in adult female; proximal median lamella of pectines in male, lobate; metasomal segments broad (length IV/width IV: 1.2–1.5); basitarsi of legs I and II, macrosetal combs weakly developed; metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous; metasomal segment V, dorsosubmedian carinae poorly developed and comprising blunt, rounded granules, dorsolateral carinae distally obsolete.

Parabuthus planicauda may be separated from *P. calvus* on the basis of the following combination of characters: surface of median ocular tubercle (male, female), surrounding surfaces of carapace (female) and lateral intercarinal surfaces of metasomal segments IV and V, granular; pedipalp chela manus, metasomal segments I–V and telson setose; proximal median lamella of pectines in male, weakly lobate; basitarsi of legs III and IV, prolateral surfaces without dense tufts of macrosetae; metasomal segment IV, median lateral, ventrosubmedian and ventrolateral carinae present; metasomal segment V, ventromedian carina present.

Parabuthus planicauda is commonly misidentified as *P. capensis*, a species of similar size and coloration, the distributional range of which overlaps in the Eastern, Northern and Western Cape provinces of South Africa. Both species share the following combination of characters: metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous, median lateral carinae continuous and distinct; metasomal segment V, dorsolateral carinae distally obsolete. *Parabuthus planicauda* can be readily separated from *P. capensis* on the basis of the following character: metasomal segments II and III, posterodorsal edge straight, not elevated and curved forward medially into a subtriangular V-shape.

Redescription.—The following description is based on the lectotype female (BMNH 1870.26), several specimens of the typical form (SAMC C118, C4580), the syntypes of *P. planicauda frenchi* (SAMC 5207), and several other specimens that could be assigned to the latter subspecies (SAMC C128, C4573, C4575).

Color: (based on SAMC C4575 and C4580): Carapace, metasoma and telson: Buff-Yellow No. 53 to Yellow Ocher No. 123C. Chelicerae, pedipalps, legs and sternites: Cream Color No. 54 to Chamois No. 123D. Tergites: Clay Color No. 123B to Cinnamon No. 39. Pectines: Pale Horn Color No. 92. Pedipalps, legs, chelicerae, metasoma and telson are slightly paler than carapace and tergites, but metasomal segments and telson are uniformly shaded (Figs. 75–82).

Carapace: As for *P. calvus*, except as follows. Carapace covered entirely by uniform, coarse granulation, becoming coarser on interocular and posterolateral surfaces. Anterior margin of carapace straight or slightly procurved; posterior margin straight (Figs. 75, 77, 79, 81).

Chelicerae: As for *P. calvus*.

Sternum: As for *P. calvus* (Figs. 76, 78, 80, 82).

Pedipalps: As for *P. calvus*, except as follows. Pedipalps covered in short macrosetae (Figs. 75–82). Femur dorsal, internal and dorsoexternal surfaces finely and uniformly granular, ventroexternal surface finely granular (male) to smooth (female) (Fig. 87); pentacarinate, all carinae distinct, granular, except for internomedian carina, comprising spiniform granules. Patella finely and uniformly granular; carinae absent or obsolete (Figs. 85, 86); dorsointernal and ventrointernal carinae each comprising row of granules proximally; internomedian carina comprising large spiniform granule, proximally, and few smaller granules, distally. Chela smooth (Figs. 83, 84); carinae absent. Chela long, slender (male, female), length along ventroexternal carina 42–47% (male) or 38–39% (female) greater than chela width and 44–49% (male) or 41–42% (female) greater than chela height (Table 1); length of movable finger 51–55% (male) to 53–56% (female) greater than length along ventroexternal carina. Chela fixed and movable fingers straight, such that proximal dentate margin linear when fingers closed (Figs. 83, 84).

Trichobothria: As for *P. calvus*, except as follows (Figs. 83–87). Patella with esb_2 distal to esb_1.

Mesosoma: As for *P. calvus*, except as follows. Pre-tergites smooth and shiny, granular along posterior margins. Post-tergites entirely coarsely granular, granulation becoming coarser distally; I–VII each with weakly developed, granular median carina. Sternites entirely smooth, except for posterolateral surfaces of sternite VII, which are sparsely granular; lateral and distal margins each with sparse row of macrosetae; sternite VII with weakly developed pairs of costate ventrosubmedian and ventrolateral carinae (Figs. 76, 78, 80, 82).

Pectines: First proximal median lamella of each pecten suboval, mesally enlarged, lobate in female and, very slightly, in male (Figs. 76, 78, 80, 82). Pectinal teeth: 34–40/34–40 (male), 31–34/31–35 (female).

Genital operculum: As for *P. calvus*.

Legs: As for *P. calvus*, except as follows.

Basitarsi III and IV, prolateral surfaces without dense tufts of macrosetae.

Metasoma and telson: Metasomal segments I–V width/length ratio progressively decreasing (Table 1), width percentage of length 75–76% (male) to 85–87% (female) for I, 75–78% (male) to 77–83% (female) for II, 73–76% (male) to 74–82% (female) for III, 64–65% (male) to 65–72% (female) for IV, and 51–54% (male) to 51–56% (female) for V. Telson oval, globose, height 54–60% (male) to 63–65% (female) of length, with flattened dorsal surface, rounded ventral surface; vesicle not distinctly narrower than metasomal segment V, width 78–79% (male) to 80–86% (female) of metasomal segment V. Metasoma entirely granular, except for dorsomedian surfaces of IV, V and telson, or V and telson. Metasomal segments I–III each with well-developed dorsal stridulatory surface, consisting of fine round to slightly crescent-shaped granules, which may or may not extend to posterior margin of segment II (Figs. 75, 79); stridulatory surface of segment III narrower and less developed than on preceding segments; segments II and III with posterodorsal edge straight (Figs. 75, 79). Metasoma sparsely covered with short macrosetae, especially on ventral surface of telson (Figs. 75–82). Metasomal segments I–IV each with ten carinae; segment IV with ventrosubmedian and median lateral carinae becoming obsolete distally; segment V with seven carinae, including single, obsolete granular ventromedian carina, pair of distinct ventrolateral carinae, pair of dorsolateral carinae, distinct only in proximal half of segment, and pair of dorsosubmedian carinae reduced to few prominent rounded granules medially. Metasomal segments I–V with dorsosubmedian carinae converging distally in segment I, subparallel in segments II–V; ventrolateral carinae converging distally in segments I–IV, subparallel in segment V. All metasomal carinae costate granular to granular, except for ventrosubmedian and ventrolateral carinae of segment I, which are costate to costate granular. Metasomal segments I–IV with distal granules of dorsosubmedian carinae slightly enlarged; segments II and III with distal granules of ventrosubmedian carinae and, to lesser extent, ventrolateral carinae, distinctly enlarged, obtuse, elevated; segment V with subdistal granules of ventrolateral carinae enlarged into laterally compressed, lobate processes. Aculeus long, shallowly curved, 61.5% (53–70%) of vesicle length.

Hemispermatophore: Flagelliform, with *pars recta* parallel to axis of distal lamina.

Geographic variation: In specimens from mesic fynbos and renosterveld habitats south and west of the Cape Fold Mountains (typical form; Figs. 75–78), the stridulatory surface on the dorsal surface of metasomal segment II reaches the posterior margin of the segment, whereas in specimens from xeric karroid habitats north and east of the Cape Fold Mountains (previously referred to as *P. planicauda frenchi*), the stridulatory surface does not reach the posterior margin of metasomal segment II. Specimens from the north and east of the Cape Fold Mountains are also slightly darker, with longer legs and pedipalps, and higher pectinal tooth counts, than those from the south and west (Figs. 79–82).

Ontogenetic variation: As in other species of *Parabuthus*, male resembles female very closely until the final instar. However, juveniles and subadults may be readily sexed by examination of the pectines and genital aperture.

Sexual dimorphism: Unlike most species of *Parabuthus* (except *P. calvus*, *P. muelleri*, *P. nanus* and *P. pallidus*), *P. planicauda* is not sexually dimorphic with respect to the shape of the chela manus. The manus of the adult male is slender and similar in shape to that of the adult female (Pocock 1890, 1902; Purcell 1898, 1901; Kraepelin 1908; Hewitt 1918; Prendini 2001a; Figs. 83, 84). However, the adult male is proportionally more slender than the adult female, and differs in the other characters mentioned above (Figs. 75, 76, 79, 80).

Remarks.—Much confusion has surrounded the status of *P. planicauda*, which was viewed as a junior synonym of *P. capensis* by various authors (discussed above). *Parabuthus planicauda* has not been revised since Purcell (1901) redescribed it as *P. capensis*. In addition, the status of the subspecies, *P. planicauda frenchi*, originally described as *P. capensis frenchi*, has not been addressed since its description. Comparison of the type specimens of *P. capensis frenchi* confirmed that this subspecies differs from *P. planicauda* only in the extent of the stridulatory surface of metasomal segment II, which reaches the posterior margin of the segment in *P. planicauda*, but does not in *P. planicauda frenchi* (Purcell

1901). Harington (1984) has shown that the extent of the stridulatory surface is highly variable and cannot be used to separate *P. brachystylus* from *P. villosus* (discussed below). Newlands & Martindale (1980) have also noted that this character is prone to considerable individual variation amongst species of *Parabuthus*. Purcell (1901) even mentioned that a small stridulatory surface occurs at the posterior edge of metasomal segment II in some specimens of *P. planicauda frenchi* and that, in one specimen, it is almost connected medially to the anterior surface by a few isolated granules. This variety clearly represents nothing more than intraspecific polymorphism within a widespread species. I therefore synonymize *P. capensis frenchi* with *P. planicauda*.

Distribution.—Endemic to South Africa (Fig. 88). Recorded from the Eastern Cape Province, Northern Cape Province, Western Cape Province and the Free State. No records are known from north of the Orange River.

Ecology.—*Parabuthus planicauda* is a semi-lithophilous species, inhabiting consolidated sandy, gritty and clayey substrata in rocky habitats. This species excavates burrows under rocks or stones and never in open ground. Elongation of the pedipalps and legs, as well as slight dorsoventral compression are indicative of a semi-lithophilous ecomorphotype, whereas a reduction in the macrosetal combs on the basitarsi of legs I and II in this species may be associated with its occurrence in regions of hard, compacted soil (Eastwood 1977; Prendini 2001a, b).

Parabuthus planicauda is sympatric with *P. granulatus* in parts of its range, but it is not known whether these species are syntopic. The range of *P. planicauda* overlaps extensively with that of *P. capensis*, and these species are occasionally found in syntopy. However, *P. capensis* is more commonly encountered in open sandy habitats.

Material examined.—SOUTH AFRICA: 3 ♂ (NMSA 9056, 9065, 9066), 2 ♂ (SAMC B630, B631), 1 ♀ (SAMC B629), 37 1st instars (SAMC 6315), J. Visser, 1 ♂ (SAMC C3862), 1914, 2 ♀ (SAMC B617, B618), 1 juv. ♀ (SAMC B619), 1895, W.F. Purcell, 1 ♀ (SAMC 506). *Eastern Cape Province*: Adelaide District: Adelaide, 2 km SE [32°43′S 26°19′E], 6.vii.1997, A. Harington, 2 ♀ (AMNH [AH 5090, 5091]). Albany District: Alicedale [33°19′S 26°05′E], 1915, 2 ♀ (NMSA 658), 18.vi.1913, P.A. Methuen, 1 subad. ♂ (TMSA 1825); Alicedale, 1 km behind town [33°19′S 26°05′E], 25.i.1979, A. Harington, 1 ♂ (AMNH [AH 928]), 1 ♀ (AMNH [AH 929]); Brakkloof, Grahamstown [33°14′S 26°23′E], 1897, J. White, 4 ♂, 6 ♀, 2 subad. ♂, 1 juv. ♀ (SAMC 1734); Grahamstown [33°19′S 26°31′E], 8.x.1905, W.F. Purcell, 2 ♀ (SAMC 14357), vii.1910, R.H. Ivy, 2 ♂ (TMSA 1821, 1823), 2 ♀ (TMSA 1820, 1822); Groot Brak Valley [33°19′S 26°31′E], 10–21.iii.1986, MacPherson & Roux, Water Affairs Survey, N face, fynbos and aloe, 1 juv. ♂ (SAMC C4527); Resolution Halt, near Grahamstown [33°10′S 26°37′E], v.1928, A. Walton, 1 ♂, 1 ♀, 2 subad. ♂, 1 juv. ♂ (SAMC B7297), xi.1928, A. Walton, 1 ♂, 1 ♀, 2 juv. ♂, 3 juv. ♀ (SAMC B7303), xii.1929, A. Walton, 1 ♀ (SAMC B7330); Farm Resolution [33°08′S 26°37′E], i.1910, A. Walton, 1 ♀ (TMSA 4862), i.1928, A. Walton, 2 ♂ (TMSA 4873, 4876), 3 ♀ (TMSA 4863, 4874, 4875), 4 juv. ♂ (TMSA 4872), 1 juv. ♂ (TMSA 4867), vi.1928, A. Walton, 2 ♂, 2 subad. ♂ (TMSA 4963), 1 ♂ (TMSA 4958), 5 ♀ (TMSA 4956, 4957, 4959, 4961, 4962), 1 subad. ♂ (TMSA 4960). Albert District: Burgersdorp [30°59′S 26°19′E], 1900, Schönland, 1 ♂, 1 ♀ (SAMC 6400), ix.1909, Kannemeyer, 1 ♂ (SAMC B554), 2 ♀ (SAMC B551, B552), 1 subad. ♂ (SAMC B553), 1 subad. ♀ (SAMC B559). Aliwal North District: Aliwal North [30°42′S 26°42′E], 18.ii.1971, R.H. Jones, 1 subad. ♂ (TMSA 10043); St Stephany, Aliwal North [30°42′S 26°42′E], xii.1916, Albany Museum, 1 ♀ (TMSA 1177). Bathurst District: Port Alfred [33°36′S 26°54′E], 19.i.1911, R.H. Ivy, 1 ♀ (TMSA 1824). Cradock District: Cradock [32°11′S 25°37′E], x.1918, G.P.F. van Dam, 2 ♂ (TMSA 2005, 2006), 2 juv. ♂ (TMSA 2007, 2008), 24.v.1987, A.J. Prins & A. Roux, 1 juv. ♀ (SAMC C4528), 29.iv.1997, M. de Jager, 1 ♂ (SAMC C4572). Mountain Zebra National Park: [32°07′S 25°32′E], iii.1998, M. de Jager, 1 ♂, 2 ♀ (SAMC C4571); Berylfberge [32°16′S 25°28′E], 15.xi.1976, 1 ♂ (AMNH [AH 440]), 1 ♀ (AMNH [AH 441]); Boesmanskloof [32°14′S 25°27′E], 11.xi.1976, J. Clarke, 1 ♂ (AMNH [AH 675]); Langkloof [32°15′S 25°29′E], 8.xi.1976, 1 ♀ (AMNH [AH 454]); Rooiplaats [32°11′S 25°27′E], 1 subad. ♂ (AMNH [AH 462]); Wilgerboomrivier bo Berghof [32°15′S 25°28′E], 7.vi.1976, 1 ♀ (AMNH [AH 436]). Glen Grey District: Bankies, 20 km S Dordrecht [31°32′S 26°57′E], 17.i.1996, A. Harington, 1 ♀ (AMNH [AH 3054]). Graaff-Reinet District: Farm Opreisfontein, 27 km SW Graaff-Reinet [32°15′S 24°44′E], 3.viii.1976, A. Harington, 2 ♂ (AMNH [AH 686, 687]); Graaff-Reinet [32°15′S 24°33′E], ii.1906, Meyer, 3 ♂ (SAMC B592–B594), 3 ♀ (SAMC B589–B591), 12.xii.1976, A. Harington, 1 juv. ♂ (AMNH [AH 517]); Graaff-Reinet and Kruidfontein, 8 mi from Graaff-Reinet [32°22′S 24°36′E], ix.1902, J. Paynter, 15 ♂, 28 ♀ (SAMC 12008); Karoo Nature Reserve, Graaff-Reinet [32°12′S 24°28′E], 8–9.ix.1987, S. van Noort, 1 ♂ (SAMC C3751), 2 ♀ (SAMC C3748, C3749), 1 juv. ♀ (SAMC C3750); near Valley of Desolation, Graaff-Reinet, 1600 ft [32°17′S 24°28′E], 1.vi.1900, M. Robinson & M. Way, 1 juv. ♀ (SAMC 5790). Jansenville District: Waterford [33°05′S 25°01′E], 17.xi.1969, H.C. Snyman, 1 ♀ (TMSA 9452). King William's Town District: King William's Town [32°53′S 27°24′E], 14.v.1941, H.W. Bell-Marley, 1 ♀ (TMSA 8298). Kirkwood District: Addo Elephant National Park [33°30′S 25°45′E], 21.v.1987, A.J. Prins & A. Roux, under elephant dung, 1 ♀ (SAMC C2321), 2 juv. ♂, 1 juv. ♀ (SAMC C4529), 1 juv. ♀ (SAMC C2320); Dunbrody, near Blue Cliff [33°28′S 25°33′E], 1899, 1901, J.A. O'Neil, 4 ♂, 2 ♀, 2 subad. ♀ (SAMC 5184, 5770, 6483). Lady Grey District: Kafferskop [30°30′S 27°04′E] on Paardeverlies, near Lady Grey, viii.1995, A. Thornley, 1 ♂ (AMNH [AH 3249]), 1 ♀ (AMNH [AH 3248]), 2 ♀, 1 subad. ♀ (AMNH [AH 3250]). Middelburg District: Farm Meent Kamp West, 5 km W [31°03′S 25°00′E], 1997, M. de Jager, under stones, 2 ♂, 2 ♀ (SAMC C4573); Klerksdale, Middelburg (31°03′S 25°00′E), 1915, 1 subad. ♀ (NMSA 649); Ludlow [31°16′S 24°40′E], 1917, Albany Museum, 1 ♂ (TMSA 1175), 1 ♀ (TMSA 1176); Middelburg (31°29′S 25°01′E), 1968, C.H. Steenkamp, 2 ♂ (TMSA 18065, 18066), 1 ♀ (TMSA 18064), v.1968, C.H. Steenkamp, 1 ♂ (TMSA 18163), vi.1968, C.H. Steenkamp, 2 ♂ (TMSA 18059, 18060), 9.vi.1968, C.H. Steenkamp, 2 subad. ♂ (TMSA 18062, 18063), 1 subad. ♀ (TMSA 18061), (31°30′S 25°00′E), ii.1997, M. de Jager, 1 ♀ (SAMC C4574), iii.1998, M. de Jager, under stones, 2 ♂ (SAMC C4576, C4577), 1 ♀, 1 subad. ♂, 1 subad. ♀ (AMNH). Oorlogspoort, 10 km NE (31°03′S 25°00′E), 15.viii.1996, M. de Jager, under dolerite stones, 1 ♂, 1 ♀ (SAMC C4575); Sneeuwkuil, Sneeuwbergen, about 40 mi from Richmond (31°38′S 24°32′E), xii.1901–ii.1902, S.C. Schreiner, 1 ♂ (SAMC 11517). Pearston District: Pearston (32°35′S 25°08′E), 1 ♀ (NMSA 8347); Zwagershoek, near Pearston, Somerset East (32°30′S 25°25′E), 1902, R. Broom, 1 ♀ (SAMC 12026). Port Elizabeth District: Coega (33°46′S 25°40′E), xi.1899, J.L. Drège, 1 ♀ (SAMC 5203), vi.1998, Zoology Department, University of the Western Cape, 1 ♂ (SAMC C4578); Port Elizabeth (33°58′S 25°36′E), 1897, xi.1898, J.L. Drège, 3 ♂, 4 ♀, 3 subad. ♀ (SAMC 1740, 4053, 5270); Redhouse, Port Elizabeth (33°50′S 25°34′E), 1891, H.A. Spencer, 1 ♂, 1 ♀ (SAMC 521), 1914, Mrs Paterson, 1 ♀ (SAMC B651), Stephenson, 1 ♂ (SAMC B653), 1 ♀ (SAMC B652), iii.1915, Mrs Paterson, [see SAMC B610] (SAMC B688). Somerset East District: Cookhouse (32°45′S 25°49′E), iii.1998, M. de Jager, 1 ♂ (SAMC C4579). Steynsburg District: Steynsburg (31°18′S 25°49′E), 1910, F. Eleuberger, 1 ♂ (NMSA 10087), (31°18′S 25°50′E), 1903, R. Broom, 1 ♂ (SAMC 12732), [31°22′S 25°52′E], 1904, S.S. Ponder, 2 juv. ♂, 2 juv. ♀ (SAMC 14267). Tarka District: Tarkastad [32°01′S 26°16′E], 1903, R. Broom, 1 ♀ (SAMC 12727); Towerkop (Toorkop), Tarkastad (31°51′S 26°19′E), ix.1976, V.B. Whitehead, under stone, 1 ♂ (SAMC C75). Willomore District: Kougakop, Langkloof (33°57′S 24°00′E), i.1975, Louw, 1 juv. ♂ (SAMC C1756); Willomore (33°18′S 23°29′E), 1901, H. Brauns, 2 ♂, 1 ♀, 3 subad. ♂, 3 juv. ♂, 2 juv. ♀ (SAMC 8871), 1901–1902, H. Brauns, 1 ♂, 1 ♀, 1 juv. ♂ (SAMC 8872). *Free State Province*: Smithfield District: Smithfield (30°13′S 26°32′E), 1912, Kannemeyer, 1 subad. ♂ (SAMC B549), 1914, Kannemeyer, 1 ♀ (SAMC B576), 4 juv. ♀ (SAMC B578); Tussen-die-Rivieren Game Reserve (30°28′S 26°12′E), 24.iii.2000, C. Haddad, under stones, 1 ♀, 1 subad. ♂ (AMNH). *Northern Cape Province*: Sutherland District: Sutherland (32°24′S 20°40′E), 4.i.1983, J. Visser, 3 ♂ (SAMC C3810, C3811, C3816), under rock, 1 ♀ (SAMC C3809), 23.v.1983, J. Visser, 3 ♀ (SAMC C3817, C3818, C3819), 16.ix.1983, J. Visser, 1 ♀ (SAMC C3821), 31.xii.1985, J. Visser, 1 ♀ (SAMC C3860), 30.x.1994, C.R. Owen, 1 juv. ♂ (TMSA 18745); Sutherland, 9 km S (32°28′S 20°39′E), J. Visser, 1 ♀ (SAMC C3865); Sutherland, 9 km S and 34 km E (32°22′S 20°52′E), J. Visser, 1 ♀ (SAMC C3863), 1 juv. ♂ (SAMC C3793); Sutherland, 10 km S (32°28′S 20°39′E), 11.i.1986, J. Visser, 1 ♀ (SAMC C3861). *Western Cape Province*: 'South Western Cape', M. Stiller, 2 ♂ (SAMC C1508), 1 ♂, 1 ♀ (SAMC C1509), 1 ♂ (SAMC C1507), 1 ♂ (SAMC C1511), 1 ♂ (SAMC C1512), 1 ♂ (SAMC C1516), 2 ♀ (SAMC C1517), 1 ♀ (SAMC C1505), 1 ♀ (SAMC C1510), 1 subad. ♂ (SAMC C1513). Beaufort West District: Beaufort West (31°48′S 19°18′E), 12.vi.1997, A. Harington, 1 subad. ♂ (AMNH [AH 5086]); Karoo National Park: [32°13′S 22°33′E], 7.iv.1994, J. Leeming, mid plateau, sympatric with *P. capensis*, 1 ♂ (SAMC C4569); Lammertjiesleegte [32°23′S 22°19′E], 6.iv.1994, A. Leroy, 1 ♀ (SAMC C4570). Bredasdorp District: Brandfontein Reserve [34°46′S 19°52′E], 16–18.x.1992, H.G. Robertson, under rock (Table Mountain sandstone), this species was also found in limestone region, 1 ♂ (SAMC C4531); Bredasdorp [34°32′S 20°02′E], H. Robertson, 1 ♀ (AMNH [AH 3909]), 19.v.1976, E.B. Eastwood, under stones, 2 ♂, 2 ♀, 1 subad. ♀ (SAMC C66), 8.vi.1977, E.B. Eastwood, under stone, 1 ♂ (SAMC C119), 15.i.1979, A. Harington, 2 ♀ (AMNH [AH 1120, 1121]); Cape Agulhas [34°50′S 20°00′E], 27.x.1940, V. Fitzsimons, 1 ♀ (TMSA 8402); De Hoop Nature Reserve, near Bredasdorp (34°28′S 20°30′E), i.1992, N. Larsen, 1 ♀ (SAMC C2424), 17–20.iv.1992, N. Larsen, under stone, 1 ♀ (SAMC C2522); De Hoop Nature Reserve, Koppie Alleen (34°28′S 20°30′E), 3–7.x.1994, S. van Noort, Strandveld, pitfall trap, 1 ♀ (SAMC C3501), 1 subad. ♂ (SAMC C3503); Elim (Mission Station) (34°35′S 19°45′E), 8.vi.1977, E.B. Eastwood, under stones, 7 ♂, 2 juv. ♂ (SAMC C118); Potberg, near Bredasdorp (34°22′S 20°33′E), i.1982, A. Robertson, 1 subad. ♂ (AMNH [AH 3178]); Soetendal's Vallei (Zoetendalsvlei, 34°43′S 19°59′E), 19–26.x.1940, V. Fitzsimons, 8 ♂ (TMSA 8404, 8417, 8423, 8425, 8426, 8428, 8430, 8432), 16 ♀ (TMSA 8403, 8405–8413, 8415, 8419, 8421–8422, 8424, 8431), 1 juv. ♂ (TMSA 8427), 22.x.1940, V. Fitzsimons, 2 juv. ♂ (TMSA 8568); Struisbaai (34°48′S 20°03′E), 8.vi.1977, E.B. Eastwood, under stones, 1 ♀ (SAMC C121), 5.iv.1994, Keuck, 1 ♀ (SAMC C3441). Caledon District: Caledon (34°13′S 19°25′E), v.1900, C.L. Leipoldt, 1 ♂, 2 ♀ (SAMC 5787); Greyton, Kanoberg Mts (34°01′S 19°36′E), vi.1988, C. & T. Stuart, on rocky plateau, 1000 m, 1 ♀ (NMSA 3668); Honingklip, near Botrivier (34°14′S 19°12′E), 14.vi.1970, J. Visser, 3 ♂, 1 subad. ♂, 2 juv. ♂ (NMSA 10005); Houw Hoek (34°13′S 19°10′E), v.1897, W.L. Sclater, 1 ♂ (SAMC 3006), 16.viii.1900, W.F. & Mrs W.F. Purcell, under stone near hotel, 1 ♂, 3 ♀ (SAMC 6412); River Zonde Ende, Caledon (34°09′S 19°54′E), 20.viii.1900, W.F. Purcell, under stone, 1 ♂ (SAMC 6409); Swartberg (Caledon), NW slope, near telephone tower, 34°13.510′S 19°25.868′E, 25.xii.2000, L. Prendini & E. Scott, mountain fynbos on sandstone, in shallow scrape under stone, 1 ♂ (AMNH); Viljoenspass, near Grabouw (34°06′S 19°03′E), 12.i.1979, A. Harington, 2 ♀ (AMNH [AH 1136, 1222]); Villiersdorp (33°59′S 19°17′E), 17.i.1963, C. Gow, 2 ♀ (SAMC C21); Villiersdorp Wildflower Reserve, entrance (33°58′S 19°15′E), 26.xii.2000, L. Prendini & E. Scott, mountain fynbos on sandstone, in shallow scrape under stone, 1 ♀ (AMNH). Calitzdorp District: Gamkaberg Nature Reserve (Inspection quarters) (33°40′S 21°53′E), 21.i.2000, Park staff, 1 ♀ (SAMC C4616). Ceres District: Hex River Mtn foothills, 40 km E Ceres (33°14′S 19°41′E), 23.xi.1981, C.A. Car, 1 ♂ (SAMC C2244); Spekrivierskloof (Hexrivierberge), N end (33°21′S 19°38′E), 5.i.2001, L. Prendini, C. Toffoli & H.M.B. Toffoli, mountain fynbos on sandstone, in shallow scrape under stone, 1 ♂ (AMNH). Hermanus District: Hermanus [34°25′S 19°14′E], 13.i.1979, A. Harington, 3 ♀ (AMNH [AH 1237–1239]); Onrus, Hermanus (34°24′S 19°11′E), 12.x.1975, V.B. Whitehead, 1 ♂, 4 ♀, 1 subad. ♂, 1 subad. ♀, 1 juv. ♀ (SAMC C1762). Ladismith District: Ladismith (33°29′S 21°16′E), 10.vi.1977, E.B. Eastwood, 2 ♀, 1 juv. ♂, 4 juv. ♀ (SAMC C126); Seven Weeks Poort (33°22′S 21°25′E), 17–18.xi.1940, V. Fitzsimons, 1 ♂ (TMSA 8462), 2 subad. ♂ (TMSA 8463, 8464); Seven Weeks Poort (33°24′S 21°24′E), 17–18.xi.1940, V. Fitzsimons, 2 ♂ (TMSA 8458, 8459), 1 ♀ (TMSA 8461); Vanwyksdorp (33°37′S 21°23′E), 10.vi.1977, E.B. Eastwood, under stones, 1 ♂, 1 ♀ (SAMC C120). Laingsburg District: Laingsburg (33°12′S 20°51′E), 17.viii.1903, W.F. Purcell, 1 juv. ♀ (SAMC 12949); Prinsrivierdam (33°31′S 20°45′E), 29.iii.1985, C.R. Owen, 1 ♂ (AMNH [AH 4100]). Montagu District: Ashton (33°49′S 20°03′E), i.1914, W.F. Purcell, 6 ♀ (SAMC B1748); Ashton, Zandvliet Farm (33°50′S 20°02′E), 1900, E. de Wet, 2 ♀ (SAMC 6423); Kogmanskloof, Ashton side (33°49′S 20°05′E), 27.viii.1900, W.F. Purcell, 2 juv. ♂ (SAMC 6421); Montagu (33°47′S 20°07′E), x.1919, R.W.E. Tucker, 3 ♀, 1 subad. ♂ (SAMC B3975); Montagu Baths (33°47′S 20°07′E), xi.1902, W.F. Purcell, 1 ♂ (SAMC 12034); Montagu Triangle (33°47′S 20°07′E), R.F. Lawrence, 2 ♀ (SAMC B5405), 12.x.1922, R.F. Lawrence, 1 ♀ (SAMC B5404). Mosselbaai District: Cloete's Pass, Herbertsdale (33°57′S 21°47′E), 9.vi.1977, E.B. Eastwood, under stones, 1 ♀, 1 subad. ♂, 1 subad. ♀ (SAMC C125); Herbertsdale (34°01′S 21°46′E), iv.1976, E.B. Eastwood, 4 juv. ♂, 4 juv. ♀ (SAMC C82), 9.vi.1977, E.B. Eastwood, under stones, 1 ♂, 2 juv. ♂ (SAMC C132); Mossel Bay (34°11′S 22°08′E), 1896, W.F. Purcell, 3 ♂, 4 ♀, 3 subad. ♀ (SAMC 425), iv.1899, J.L. Drège, 3 ♀ (SAMC 5080), 28.v.19[?], E.B. Eastwood, under stone, 1 ♀ (SAMC C63); Mosselbaai (34°07′S 21°52′E), 20.i.1979, A. Harington, 2 ♀ (AMNH [AH 1240, 1241]), 18.i.1996, A. Harington, 1 ♂ (AMNH [AH 2954]), 3 ♀ (AMNH [AH 2951–2953]); Mossel Bay, Herbertsdale Road (34°07′S 21°52′E), 2.iii.1973, A.J. Prins, under stone, 1 ♂, 2 ♀, 1 subad. ♂ (SAMC C22); Ottershoek near Herbertsdale (34°01′S 21°46′E), 19.i.1979, A. Harington, 2 ♀ (AMNH [AH 920, 921]). Murraysburg District: turnoff to Richmond, between Murraysburg and Graaff-Reinet (31°58′S 24°04′E), 5.vii.1997, A. Harington, 1 ♂ (AMNH [AH 5139]). Oudtshoorn District: Cango Caves (33°24′S 22°13′E), 1.iv.1985, 1 subad. ♂ (AMNH [AH 3218]). Prince Albert District: Farm Zwartskraal (33°10′S 23°32′E), 1.ii.1979, S. Endrödy-Younga, 1 juv. ♀ (TMSA 11865); Prince Albert Poort (33°14′S 22°03′E), 1895, W.F. Purcell, 1 ♀, 3 juv. ♂ (SAMC 509). Riversdale District: Garcia Forest Station (34°00′S 21°15′E), 14–15.xi.1940, V. Fitzsimons, 1 ♂ (TMSA 8498), 1 ♀ (TMSA 8500); Garcia's Pass road, Langeberg (33°52′S 21°07′E), 21.v.1976, A.J. Prins, under stone, 1 ♂ (SAMC C68); Gouritzmond (River mouth) [34°21′S 21°53′E], 8.vi.1977, E.B. Eastwood, under stones, 7 ♀ (SAMC C128); Gous River (34°05′S 21°15′E), 1910, H. Hermann, 1 ♂ (SAMC B1728); Jonkersberg, Attaquasberg (33°52′S 21°57′E), 22–28.xi.1940, V. Fitzsimons, 1 ♀ (TMSA 8460); Riversdale Mts, 2000–4500 ft. (33°52′S 21°07′E), x.1926, K.H. Barnard (see SAMC B610) (SAMC B6997); Stilbaai (34°22′S 21°24′E), 8–12.xi.1940, V. Fitzsimons, 7 ♂ (TMSA 8522–8525, 8527, 8529, 8531), 1 ♂, 1 ♀ (TMSA 8530), 1 ♂, 6 subad. ♂, 2 juv. ♂ (TMSA 8532), 3 ♀ (TMSA 8521, 8526, 8528); Stilbaai (34°22′S 21°25′E), 8–12.xi.1940, V. Fitzsimons, 5 ♂ (TMSA 8512, 8513, 8515, 8517, 8518), 1 ♂, 1 ♀ (TMSA 8520), 3 ♀ (TMSA 8514, 8516, 8519). Robertson District: Farm Viljoen (33°53′S 19°38′E), 30.x.1978, S. Endrödy-Younga, 5 ♂ (TMSA 11733, 11736–11739), 4 ♀ (TMSA 11727, 11731, 11743, 11744), 2 subad. ♂ (TMSA 11730, 11740), 3 subad. ♀ (TMSA 11734, 11742, 11748), 2 juv. ♂ (TMSA 11724, 11746), 3 juv. ♀ (TMSA 11728, 11729, 11747), 5.xii.1978, S. Endrödy-Younga, 13 ♂ (TMSA 11812, 11815, 11818–11821, 11824, 11825, 11827, 11832, 11833, 11835, 11836), 5 ♀ (TMSA 11810, 11813, 11823, 11826, 11834), 1 subad. ♂ (TMSA 11822), 1 subad. ♀ (TMSA 11811), 1 juv. ♂ (TMSA 11831), 2 juv. ♂, 3 juv. ♀ (TMSA 11817), 2 juv. ♂, 4 juv. ♀ (TMSA 11838), 3 juv. ♀ (TMSA 11829, 11830, 11837); Robertson (33°48′S 19°53′E), xi.1897, W.F. Purcell, 1 ♂, 2 subad. ♂, 2 subad. ♀, 2 juv. ♀ (SAMC 1752), 1901, R.J.M. Melle, 1 subad. ♂ (SAMC 6477), 1912, R.J.M. Melle, (see SAMC B610) (SAMC B642); Robertson, 10 km S (33°53′S 19°57′E), 29.x.1978, S. Endrödy-Younga, 2 ♂ (TMSA 11699), 1 ♂ (TMSA 11684), 2 ♀ (TMSA 11680, 11690), 5 subad. ♂ (TMSA 11683, 11689, 11692, 11695, 11702), 1 subad. ♀ (TMSA 11694), 8 juv. ♂ (TMSA 11685, 11697, 11703, 11704, 11706–11709), 1 juv. ♀ (TMSA 11687, 11688, 11691, 11696, 11710, 11711), 5.xii.1978, S. Endrödy-Younga, 11 ♂ (TMSA 11782, 11788, 11790, 11799–11806), 2 ♀ (TMSA 11776, 11807), 1 subad. ♂ (TMSA 11785), 7 juv. ♂ (TMSA 11781, 11783, 11784, 11789, 11795, 11798, 11808), 5 juv. ♂, 10 juv. ♀ (TMSA 11809), 2 juv. ♀ (TMSA 11786, 11793); Robertson, 15 km W (33°53′S 19°54′E), 29.x.1978, S. Endrödy-Younga, 2 ♂ (TMSA 11712, 11717), 1 subad. ♂ (TMSA 11721), 5.xii.1978, S. Endrödy-Younga, 1 ♂ (TMSA 11774), 1 subad. ♂ (TMSA 11762), 1 subad. ♀ (TMSA 11764), 1 juv. ♂ (TMSA 11765), 2 juv. ♀ (TMSA 11769, 11772); Vrolijkheid Nature Reserve, near Robertson (33°56′S 19°55′E), ix.1999, L. Prendini & E. Scott, under stones on clay flats near road, 3 juv. ♀ (AMNH). Sutherland District: 6.9 km from Farm Driefontein towards Sutherland on road from Oubergspas, near Farm Hottentotsfontein (32°27.650′S 20°30.875′E), 12.iii.2003, L. Prendini & E. Scott, 1564 m, central mountain renosterveld, shale and sandstone outcrop on roadside, under stones, 2 juv. ♂, 2 juv. ♀ (AMNH). Swellendam District: Bonnievale Farm, at Bushmansdrift on Breede River near Ashton (33°56′S 20°06′E), 1901, C. Groom, 2 ♀ (SAMC 6478); Bontebok National Park (34°04′S 20°27′E), 1.vi.1987, A.J. Prins & A. Roux, 2 juv. ♂ (SAMC C4530), 1 juv. ♂, 1 juv. ♀ (SAMC C1585), after 1 inch rain, 1 ♂, 1 ♀ (SAMC C1584); Infanta (34°25′S 20°51′E), 26.v.1975, E.B. Eastwood, under stone, 1 ♂, 1 ♀ (SAMC C16), 19.v.1976, E.B. Eastwood, under stones, 1 ♂, 4 ♀, 1 subad. ♂, 2 subad. ♀ (SAMC C67), 5 juv. ♂, 5 juv. ♀ (SAMC C69); Pass at Avontuur, River Zonder End Range, Swellendam (34°04′S 20°06′E), 21.viii.1900, Mrs W.F. Purcell, 1 ♀ (SAMC 6414); Swellendam (34°02′S 20°26′E), ix.1976, J.C. Allegrucci, under stone, 1 ♂ (SAMC C89), 4.i.1983, J. Visser, 1 juv. ♀ (SAMC C3780), 24.iii.1983, J. Visser, 1 ♂ (SAMC C3833), 1 ♀ (SAMC C3832), iv.1983, J. Visser, 1 ♀ (SAMC C3781), 3 juv. ♂ (SAMC C3782), 24.xi.1983, J. Visser, 1 ♀ (SAMC C3829), 30.xii.1983, J. Visser, 1 ♀ (SAMC C3831), 9.vi.1984, J. Visser, 3 ♂ (SAMC C3837, C3838, C3844), 8 ♀ (SAMC C3839–C3843, C3845–C3847), 4 juv. ♂ (SAMC C3784, C3789–C3791), 5 juv. ♀ (SAMC C3785–C3788, C3792), 23.vi.1984, J. Visser, 2 ♀ (SAMC C3849–C3850); Swellendam, 40 km S (34°22′S 20°22′E), 1.vii.1976, N. Smith, under stone, 1 ♀ (SAMC C88). Bontebok National Park (34°04′S 20°27′E), x–xii.1977, H. Braack, 2 ♀ (AMNH [AH 4090, 4091]), xi–xii.1977, J. Braack, 3 ♀ (AMNH), 5 ♀ (AMNH [AH 857–861]), 16.i.1979, A. Harington, 1 ♀ (AMNH [AH 870]). Tulbagh District: Piquetberg Road Station, Gouda (33°22′S 19°07′E), viii.1898, R.M. Lightfoot, 1 juv. ♂, 1 juv. ♀ (SAMC 3759); Tulbagh Road Station (33°19′S 19°06′E), 1895, F. Treleaven, 1 ♀ (SAMC 505), R.M. Lightfoot, 1 ♀ (SAMC 508). Wellington District: Bartholomeus Klip, Bo-Hermon (33°26′S 18°58′E), iii.1997, L. Prendini & E. Scott, under stones on ridge, sympatric with *P. capensis*, 1 ♂ (SAMC C4580). Worcester District: Brandvlei (33°44′S 19°24′E), 29.viii.1900, W.F. Purcell & I. Meiring, under stone on hillside, 5 ♀ (SAMC 6424); Breede River, at Darling Bridge (33°32′S 19°13′E), x.1902, H. Hermann, 1 ♂ (SAMC 12033); De Doorns (33°29′S 19°41′E), xii.1906, J. Paynter, 1 ♂, 1 ♀, 3 subad. ♂, 1 subad. ♀, 3 juv. ♂, 4 juv. ♀ (SAMC B610), 1 ♀ (SAMC B608); De Doorns, Touws River road (33°28′S 19°42′E), xi.1977, E.B. Eastwood, under stone in burrow, 1 subad. ♂ (SAMC C206); De Wet (33°36′S 19°40′E), 29.ix.1940, V. Fitzsimons, 4 ♂ (TMSA 8349, 8355, 8356, 8358), 9 ♀ (TMSA 8346–8348, 8350–8354, 8357); Hex River Valley (33°41′S 19°27′E), x.1898, F. Treleaven, 1 ♂, 3 ♀, 1 subad. ♀ (SAMC 4037); Karoo Botanical Garden, Worcester (33°37′S 19°25′E), 16.xi.1972, J. van Reenen, 1 juv. ♂ (TMSA 10681); Matroosberg Mts, Ceres, 4000 ft (33°23′S 19°40′E), xii.1917, R.W.E. Tucker, 1 ♂ (SAMC B3164); Matroosberg Mts. (33°22′S 19°37′E), xii.1916, R.W.E. Tucker, 1 ♀ (SAMC B3150), i.1917, R.W.E. Tucker, 1 ♀ (SAMC B3103), 18.i.1917, R.W.E. Tucker, 1 ♀, 35 juv. ♀ (SAMC B3108), 1 ♀ (SAMC B3106), (see SAMC B610) (SAMC B3107), 30.xi.1917, R.W.E. Tucker, 1 ♂ (SAMC B3157), 2 ♀ (SAMC B3154, B3155); Matroosberg Mts., 3500–3700 ft (33°22′S 19°37′E), 10.i.1917, R.W.E. Tucker, (see SAMC B610) (SAMC B3116); Matroosberg Mts., 4000 ft (33°23′S 19°40′E), 30.xi.1917, R.W.E. Tucker, 1 ♂, 1 ♀ (SAMC B3156); Matroosberg, Ceres (33°22′S 19°19′E), xii.1917, R.W.E. Tucker, (see SAMC B610) (SAMC B3165); Pienaarskloof (Hoek), Touws River (33°11′S 20°04′E), iv.1939, R. Smithers, 1 juv. ♂ (SAMC C3739); Rawsonville (33°41′S 19°19′E), ix.1976, G. McLachlin, under stones, 3 ♀, 1 subad. ♀ (SAMC C79); Touws River, on hill behind station (33°20′S 20°03′E), viii.1903, W.F. Purcell, 1 juv. ♂ (SAMC 12738); Touws River (33°20′S 20°03′E), xii.1904, J. Paynter,

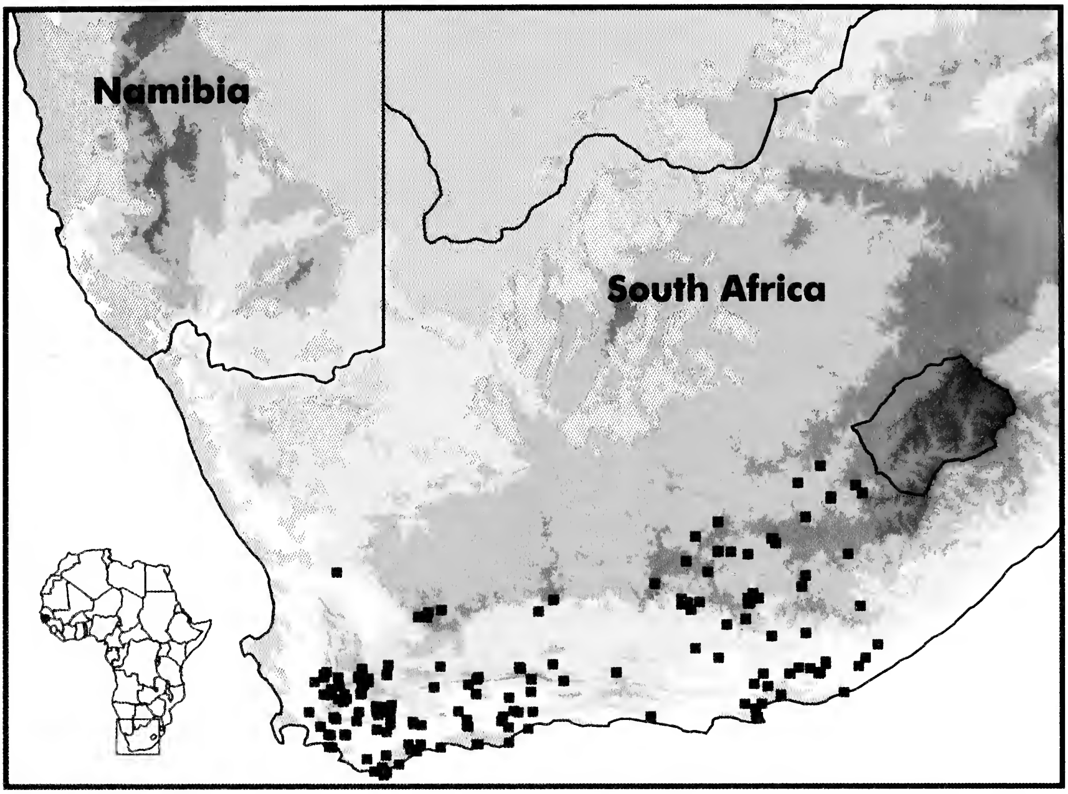


Figure 88.—The known distribution of *Parabuthus planicauda* (Pocock 1889) (■), which is endemic to South Africa. Contour interval = 500 m. Major sand systems stippled.

1 ♀ (SAMC 14264), xii.1905, J. Paynter, 1 ♂, 1 ♀ (SAMC 14379), 1974, M.A. Cluver, under stones, 1 ♂, 2 ♀ (SAMC C71), 23.i.1981, C.A. Car, under stone, 1 juv. ♂ (SAMC C210); Triangle (33°26′S 19°46′E), 30.v.1898, R.M. Lightfoot, 1 ♀ (SAMC 2989); upper Hex River (33°22′S 19°37′E), ix.1903, J. Paynter, 1 ♂, 20 ♀ (SAMC 12821); upper Hex River Valley, Matroosberg (33°23′S 19°46′E), x.1899, F. Treleaven, 1 subad. ♂ (SAMC 5201); Waaihoek Kloof, Goudini (33°30′S 19°20′E), 25.v.1928, K.H. Barnard, 1 ♀ (SAMC B7289); Worcester, near village (33°39′S 19°25′E), 30.v.1898, R.M. Lightfoot, 3 ♀ (SAMC 2986); Worcester (33°39′S 19°25′E), 1896, W.F. Purcell, 1 ♂ (SAMC 513), 1900, I. Meiring, 1 ♀ (SAMC 6471).

Parabuthus raudus (Simon 1888)

Buthus villosus var. β *dilutus* Thorell 1876b: 103–107 (NEW SYNONYMY)

Buthus raudus Simon 1888: 377.

Parabuthus raudus: Kraepelin 1899: 32; Kraepelin 1908: 252–254; Kraepelin 1914: 110; Hewitt 1918: 108, 178; Monard 1930: 40, 41; Schenkel 1932: 386; Hewitt 1935: 468, 469; Monard 1937: 257, 258; Lawrence 1955: 228; Lawrence 1961: 153; Lamoral & Reynders 1975: 521, 522; Lamoral 1979: 598–602, figs. 173–180; Newlands & Martindale 1980: 55–57, fig. 15; FitzPatrick 1994: 11, 12; Kovařík 1998: 117; Fet & Lowe 2000: 209; Prendini 2001a: 17; Prendini 2001b: 136; Dyason et al. 2002: 769; Prendini 2003: 21.

Parabuthus scobinifer Hewitt 1915: 102–104 (synonymized by FitzPatrick 1994: 11); Lamoral & Reynders 1975: 522.

Type material: Buthus villosus var. β *dilutus*: Holotype ♀ (NHRS), "Patria ignota".

Buthus raudus: Lectotype ♀ (MNHN), NAMIBIA: "sud-ouest Afrique", 1884–1886, Dr H. Schinz. Simon's (1888) male and female syntypes were presumed lost according to Hewitt (1918) until the female was rediscovered in the MNHN collection (Lamoral 1979) and designated as lectotype. Both Hewitt (1918) and Lawrence (1955) maintained that the syntypes of *P. raudus* were collected in the Kalahari. Lawrence (1955) stated further that the type locality may be between Damaraland (northwestern Namibia) and Lake Ngami (northern Botswana).

Parabuthus scobinifer: Holotype: 1 juv. ♂ (BMNH 1915.5.28.1), ZIMBABWE: N.W. Rhodesia, presented by Dr L. Colyer.

Diagnosis.—*Parabuthus raudus* is most closely related to *P. schlechteri* (Fig. 1). Both species share the following combination of characters: pedipalp chela (adult male), fixed finger strongly curved dorsally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segment II, stridulatory surface (dorsal aspect) not reaching posterodorsal margin; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus raudus may be separated from *P. schlechteri* by means of the following combination of characters: carapace, mesosoma, metasoma and legs with uniform pale yellow to light brown coloration (segments III–V and telson may be infuscated, i.e., darker than segments I and II); metasomal segment V, ventrolateral carinae comprising fine spinose processes subdistally; metasomal segment V, ventrolateral carinae converging distally.

Remarks.—*Parabuthus raudus* was revised by Lamoral (1979) as part of his revision of the scorpions of Namibia but Lamoral (1979) did not address possible synonyms described from beyond Namibian borders. Newlands & Martindale (1980) subsequently reviewed the buthid species of Zimbabwe, provided additional diagnostic differences between *P. raudus* and other members of *Parabuthus*, and synonymized *P. scobinifer* with *P. mossambicensis* (discussed above). However, FitzPatrick (1994) recently demonstrated that *P. scobinifer* is actually a junior synonym of *P. raudus*.

Kraepelin (1899) synonymized *Buthus villosus* var. β *dilutus* with *P. villosus*. When the holotype of *B. villosus* var. β *dilutus*, was obtained for study during the present investigation, it was found to be conspecific with *P. raudus*, not with *P. villosus*. *Buthus villosus* var. β *dilutus* is therefore a senior synonym of *P. raudus*. However, this name has not been used since its description, whereas *P. raudus* has won general acceptance. Therefore, it seems prudent to retain use of the name *P. raudus*.

Distribution.—Associated with the Kalahari sand system and sandy deposits along the banks of the Orange River (distribution extends across the latter). Recorded from Angola, Botswana, Namibia, South Africa, Zambia, and Zimbabwe.

Ecology.—*Parabuthus raudus* is a semi-psammophilous species, inhabiting unconsolidated to semi-consolidated sand dunes, where it excavates burrows in open ground and at the base of shrubs and grass tufts. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

Parabuthus raudus is syntopic with *P. granulatus* and *P. kuanyamarum* throughout its distributional range and with *P. kalaharicus* and *P. laevifrons* in the southwestern part of its range. It is the most commonly found species in the Kalahari sand system, where it is more common in the interdune valleys than on the dune crests.

This species is allopatric with its sister species, *P. schlechteri*, but sympatric with *P. villosus* along the banks of the Orange River. However, *P. villosus* is a semi-lithophilous species, restricted to rocky slopes in the Orange River valley, whereas *P. raudus* inhabits the alluvial sand dunes along its banks, hence these species are not syntopic.

Material examined.—NAMIBIA: *Khomas Region*: Windhoek District: Farm Frischgewaagd 289 (22°32′S 17°50′E), 20.iii.1976, B. Lamoral, 8 ♂, 5 ♀, 1 subad. ♀, 3 juv. ♂, 1 juv. ♀ (NMSA 10817). SOUTH AFRICA: *Northern Cape Province*: Gordonia District: Kalahari Gemsbok National Park: Mata Mata (25°53′S 20°01′E), iv.1970, B.H. Lamoral, 1 ♀ (NMSA 10444) [homotype designated by Lamoral (1979)]; Mata Mata, 3 miles N (25°43′S 20°00′E), 24.iv.1970, B. Lamoral, 1 ♀, 2 subad. ♂ (NMSA 10931). Namaqualand District: Richtersveld, Swaartpoort near Ochta

Diamond Mine, 28°07′S 16°56′E, ii.1974, R. Faber, 3 ♂, 2 ♀ (NMSA 10924).

Parabuthus schlechteri Purcell 1899
Fig. 24

Parabuthus schlechteri Purcell 1899b: 434; Purcell 1901: 164–168; Pocock 1902: 367; Hewitt 1912: 301, 302; Hewitt 1913: 146; Lampe 1917: 193; Hewitt 1918: 107, 108, 178, pl. XIX, fig. 2; Lawrence 1955: 228; Lawrence 1962: 220; Lamoral & Reynders 1975: 522; Lamoral 1979: 602–606, figs. 181–187; Kovařík 1998: 117; Fet & Lowe 2000: 209, 210; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21.

Type material.—Holotype ♀ (damaged) (SAMC 2177), SOUTH AFRICA: between Henkries (28°54′S 18°08′E) and Wolftoon (29°03′S 18°13′E), Little Bushmanland (*Northern Cape Province*: Namaqualand District), 1.xii.1897, M. Schlechter. Lamoral (1979) erroneously referred to syntypes. Purcell (1899b, 1901) clearly specified an adult female (SAMC 2177) as the holotype. The holotype is completely dismembered, as is the male specimen from the same locality, the dismembered pieces of both specimens residing in the same jar, with the same accession number. As the holotype is not destroyed, a neotype cannot be designated. Lamoral (1979) therefore designated a homotype.

Diagnosis.—*Parabuthus schlechteri* is most closely related to *P. raudus* (Fig. 1). Both species share the following combination of characters: pedipalp chela (adult male), fixed finger strongly curved dorsally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segment II, stridulatory surface (dorsal aspect) not reaching posterodorsal margin; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus schlechteri may be separated from *P. raudus* by means of the following combination of characters: carapace, mesosoma and metasoma, dark brown to black in color, contrasting with pale pedipalps and legs; metasomal segment V, ventrolateral carinae comprising coarse spinose processes subdistally; metasomal segment V, ventrolateral carinae diverging distally.

Parabuthus schlechteri is easily confused with *P. transvaalicus* and *P. villosus*, but may be separated from these species by means of the following character: metasomal segment II, stridulatory surface (dorsal aspect) not reaching posterodorsal margin. It may also be separated from *P. transvaalicus* and some populations of *P. villosus* by means of coloration: pale pedipalps and legs pale contrasting with dark brown to black carapace, mesosoma, and metasoma.

Remarks.—Newlands (1974a) suggested that *P. schlechteri* is a junior synonym of the closely related *P. raudus*,. a subject that he indicated would be further examined in a future taxonomic paper. The latter contribution never appeared, and *P. schlechteri* and *P. raudus* were subsequently revised by Lamoral (1979), who provided diagnostic differences for both species. However, the two species are very similar morphologically and it remains to be seen whether they will be upheld as more data (including DNA sequences) accrue.

Distribution.—Endemic to sandy areas in southern Namibia (Hardap and Karas regions) and the Northern Cape Province of South Africa. The distribution of this species extends across the Orange River.

Ecology.—*Parabuthus schlechteri* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy and gritty substrata, where it excavates burrows in open ground and at the base of shrubs and grass tufts. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype. There appears to be little evidence to support Lamoral's (1979) statement that *P. schlechteri* excavates shallow scrapes under rocks—specimens are seldom, if ever, collected in rocky habitats.

Parabuthus schlechteri is syntopic with *P. brevimanus*, *P. granulatus*, and *P. laevifrons* throughout its range and with *P. nanus* and *P.*

stridulus in part of its range. The species is allopatric with its sister species, *P. raudus*.

Material examined.—NAMIBIA: *Karas Region*: Keetmanshoop District: Keetmanshoop, Farm Noachabeb (27°26'S 18°31'E), 7–12.i.1972, 1 ♂, 1 ♀ (NMSA 11406). Lüderitz District, Diamond Area I: Farm Tsirub 13, 26°52'S 16°02'E, 3.iii.1976, B. Lamoral, 1 ♀, 1 subad. ♂, 1 subad. ♀ (NMSA 10730). SOUTH AFRICA: *Northern Cape Province*: Namaqualand District: Aggeneys (29°15'S 18°50'E), 6–8.xii.1997, L. Prendini, G.J. Müller, K. Rostoll, & J. du Plessis, 1 ♂, 1 ♀ (SAMC C4609); S of Goodhouse (29°00'S 18°13'E), 30.i.1973, B.H. Lamoral, 1 ♂ (NMSA 10935) [homotype designated by Lamoral (1979)]. *Western Cape Province*: Prince Albert District: Gamkaskloof Nature Reserve (33°31'S 21°37'E), 21.ii.1997, M. de Jager, 1 ♂ (SAMC C4610).

Parabuthus stridulus Hewitt 1913
Figs. 5, 12, 19, 33

Parabuthus stridulus Hewitt 1913: 146, 147; Lamoral 1979: 606–610, figs. 188–197; Kovařík 1998: 117; Fet & Lowe 2000: 209; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 21, 22.

Parabuthus laevifrons: Kraepelin 1914: 109 (specimens from Lüderitzbucht, see Hewitt 1918: 105).

Parabuthus laevifrons militum Hewitt 1918: 105, 176, pl. XIX, fig. 5 (synonymized by Lamoral 1979: 606); Lawrence 1955: 227, pl. XIX, fig. 5; Lamoral & Reynders 1975: 519.

Parabuthus laevifrons concolor Hewitt 1918: 176, 177 (synonymized by Lamoral 1979: 606); Lawrence 1955: 227; Lamoral & Reynders 1975: 519.

Type material.—*Parabuthus stridulus:* Holotype ♂ (TMSA 1868, formerly TMSA 1030), NAMIBIA: Lüderitzbucht, South West Africa [*Karas Region*: Lüderitz District: 26°35'S 15°10'E), 26.xi.1912.

Parabuthus laevifrons militum: Holotype ♂ (AMGS), NAMIBIA: Aus, South West Africa [*Karas Region*: Lüderitz District: 26°40'S 16°16'E].

Parabuthus laevifrons concolor: Syntypes: 2 ♀ (AMGS, MMKZ) [♂ syntypes, also listed in the original description, are presumed lost], NAMIBIA: Keetmanshoop [dubious locality], South West Africa, [*Karas Region*: Keetmanshoop District: 26°35'S 18°08'E], E. Murray.

Diagnosis.—*Parabuthus stridulus* is most closely related to *P. laevifrons* (Fig. 1). The two species may be separated from all other species of *Parabuthus* by means of the following combination of characters: surface of median ocular tubercle (male, female) and surrounding surfaces of carapace (female), smooth and shiny; pedipalp chela, asetose; chela manus, smooth and shiny; chela (adult male), fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); chela movable finger of female, short, compared with manus (measured along ventroexternal carina), length finger/length carina: ± 1.50; metasomal segments slender (length IV/width IV: 1.7–2.11), virtually asetose; metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect; metasomal segments IV and V, lateral intercarinal surfaces smooth; metasomal segment IV, median lateral carinae poorly developed; metasomal segment V, dorsosubmedian carinae and dorsolateral carinae absent, but ventrolateral carinae distinct.

Parabuthus stridulus may be separated from *P. laevifrons* by means of the following characters: pedipalp chela fixed finger with trichobothrium *dt* situated in line with or distal to *et*; metasomal segment II dorsal stridulatory surface composed of transverse ridges, some of which extend across the surface; metasomal segments III–V and telson weakly infuscated, contrasting in color only slightly with segments I and II; metasomal segment V, ventrolateral carinae comprising spinose processes subdistally; telson vesicle very distinctly and deeply excavated along longitudinal half of dorsoproximal surface.

Remarks.—Kraepelin (1914) evidently misidentified specimens of *P. stridulus* as *P. laevifrons* (Hewitt 1918). *Parabuthus laevifrons* was revised by Lamoral (1979), who synonymized Hewitt's (1918) subspecies, *P. laevifrons militum* and *P. laevifrons concolor*, with *P. stridulus*.

Distribution.—Endemic to Namibia (Lüderitz, Maltahöhe and Swakopmund districts). Although *P. stridulus* has been recorded at Oranjemund, on the northern bank of the Orange River, no records are known from south of the river. The species is absent from the Central Namib Sand Sea and from the sand systems of the northern Namib.

Ecology.—*Parabuthus stridulus* is a psammophilous species, which excavates burrows in open ground, at the base of shrubs, grass tufts and shrub coppice dunes. The species displays several ecomorphological adaptations to its sandy habitat: unequal telotarsal ungues; basitarsi of legs I and II dorsoventrally compressed, with comb-like rows of long macrosetae ("sand combs") on the retrolateral margins.

Parabuthus stridulus is syntopic with *P. gracilis*, *P. granulatus*, *P. namibensis* and *P. schlechteri* in part of its range, but allopatric with its sister species, *P. laevifrons*.

Material examined.—NAMIBIA: *Erongo Region*: Swakopmund District: Cape Cross, 5 km N, 21°43′S 13°56′E, 25.iii.1976, B. Lamoral & L. Ferguson, 1 ♂ (NMSA 10904), 1 ♀ (NMSA 10907). *Karas Region*: Lüderitz District: Agate Beach [26°36′S 15°10′E], Lüderitz, ii.1973, B. Lamoral, 1 ♂, 2 ♀ (NMSA 10573); Farm Plateau 38, near Aus (26°38.63′S 16°30.77′E), 30.xii.1997, L. Prendini & E. Scott, 1 ♂, 1 ♀ (SAMC C4611); Kolmanskop, 12 km E Lüderitz (26°43′S 15°17′E), iii.1973, C.J. Coetzee, 1 ♂, 1 subad. ♂ (NMSA 10501).

Parabuthus transvaalicus Purcell 1899
Figs. 6, 9, 21

Scorpio teter Müller 1828: 64 (NEW SYNONYMY); Hemprich & Ehrenberg 1829: 349; Peters 1861: 507.

Androctonus teter: Kraepelin 1891: 68 (in synonymy with *Heterobuthus liosoma*); Kraepelin 1899: 31.

Parabuthus transvaalicus Purcell 1899b: 434, 435; Purcell 1901: 162–164; Hewitt 1912: 302; Hewitt 1918: 107, 179, pl. XXI, fig. 30; Werner 1933: 323; Hewitt 1935: 466, 467; Lawrence 1938: 289; Lawrence 1955: 228; Lawrence 1961: 153; Lawrence 1964: 37; Lawrence 1967: 85; Lamoral & Reynders 1975: 522, 523; Newlands & Martindale 1980: 57, 58, fig. 16; FitzPatrick 1994: 12–14; Kovařík 1998: 117; Fet & Lowe 2000: 210; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 22.

Parabuthus obscurus Penther 1900: 154, 155 (synonymized by Kraepelin 1914: 112; Newlands 1970: 203); Lawrence 1955: 228; Newlands 1970: 203.

Parabuthus pachysoba Penther 1900: 155, 156 (synonymized by Kraepelin 1914: 112; Newlands 1970: 203, 204); Lawrence 1955: 228; Newlands 1970: 203, 204.

Type material.—*Scorpio teter:* Holotype (ZMHB?), locality unknown.

Parabuthus transvaalicus: Lectotype ♀ (SAMC 3003), SOUTH AFRICA: "Transvaal." Paralectotypes: 1 ♀ (SAMC 3003), 3 ♀ (TMSA), same data as lectotype. Purcell (1899b) did not specify type specimens, but based his description on "a couple of" females (SAMC 3003) from the Transvaal. The larger of the two female syntypes in SAMC 3003 is hereby designated as the lectotype of *P. transvaalicus*, the remaining specimens in the SAMC and TMSA collections, as paralectotypes.

Parabuthus obscurus: Syntypes: 1 juv. ♂, 2 juv. ♀ (NHMW 2090), BOTSWANA: Britisch-Betschuanaland, vii.1893, A. Penther.

Parabuthus pachysoba: Holotype ♂ (NHMW 2089), BOTSWANA: Britisch-Bechuanaland, vii.1893, A. Penther.

Diagnosis.—*Parabuthus transvaalicus* is most closely related to *P. villosus* (Fig. 1). Both species share the following combination of characters: pedipalp chela (adult male), fixed finger strongly curved dorsally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segment II, stridulatory surface (dorsal aspect) reaching posterodorsal margin; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus transvaalicus may be separated from *P. villosus* by means of the following combination of characters: carapace not dorsoventrally compressed; metasomal segments I–V and telson sparsely to moderately setose; metasomal segments I–IV, becoming wider distally, metasomal segment I narrower than segment IV; metasomal segments I and II, stridulatory surface (lateral aspect) truncated at anterodorsal edge of segment.

Parabuthus transvaalicus is easily confused with *P. schlechteri*, but may be separated from the latter by means of the following characters: metasomal segment II, stridulatory surface (dorsal aspect) reaching posterodorsal margin; carapace, mesosoma, metasoma, pedipalps and legs uniform dark brown to black in color.

Remarks.—Purcell (1901) suggested that *P. obscurus* and *P. pachysoba* are synonymous with *P. transvaalicus*, differing only in having a relatively shorter and stouter metasoma, but did not examine the type specimens. Kraepelin (1908) examined the types, and concurred with Purcell's view, but did not list them in formal synonymy until later (Kraepelin 1914). Although both synonyms were accepted by Hewitt (1918) and Lawrence (1955), the types were not actually examined by a South African worker until Newlands (1970), who also accepted the synonyms and is often mistakenly credited for them (e.g., by Lamoral & Reynders 1975). Newlands & Martindale (1980) later revised *P. transvaalicus*, and FitzPatrick (1994) provided additional diagnostic differences between this species and other members of the genus.

The name *Scorpio teter* was first mentioned by Müller (1828) with reference to the Berlin Museum (ZMHB). Kraepelin (1891: 68) incorrectly referred to it as "*Androctonus teter* Nordm., 1839" and placed it (under question) as a synonym of *P. leiosoma* (as *Heterobuthus liosoma*). Kraepelin (1899) later suggested that this name was a *nomen nudum* [Moritz & Fischer (1980) also omitted this name from their list of type specimens in the ZMHB], but proceeded to describe the type specimen, which he regarded as a dark color variety of *P. capensis*. However, the characters of this specimen, and another described by Kraepelin (1899) from the Hamburg Museum (ZMUH), viz. the dark reddish-brown coloration and the well developed spiniform granules of the dorsosubmedian carinae on metasomal segment V, are diagnostic for *P. transvaalicus*. The collection locality that Kraepelin mentions for the ZMUH specimen (Delagoa Bay, Mozambique) also occurs within the distributional range of *P. transvaalicus*. It is clear from this description that *Scorpio teter* is a senior synonym of *P. transvaalicus*, not of *P. leiosoma* or *P. capensis*. However, as noted by Fet & Lowe (2000), Müller's name has never been used since its description. In contrast, *P. transvaalicus* has won general acceptance. Therefore, it seems prudent to retain use of the name *P. transvaalicus*.

Distribution.—Recorded from east of the Kalahari sand system in Botswana, Mozambique, South Africa, and Zimbabwe.

Ecology.—*Parabuthus transvaalicus* is a semi-psammophilous species, inhabiting semi-consolidated to consolidated sandy, gritty and loamy substrata, where it excavates burrows under stones or fallen trees. Comb-like rows of long macrosetae ("sand combs") on the retrolateral margins of the basitarsi of legs I and II indicate a semi-psammophilous ecomorphotype.

Parabuthus transvaalicus is sympatric with *P. mossambicensis* throughout its range and with *P. granulatus* and *P. kuanyamarum* in part of its range. Where they occur in sympatry (e.g., Langjan Nature Reserve in the Limpopo Province of South Africa), *P. granulatus*, *P. kuanyamarum* and *P. mossambicensis* are generally found in open sandy habitats, whereas *P. transvaalicus* frequents rocky habitats. The species is allopatric with its sister species, *P. villosus*.

Conservation.—Refer to the discussion under *P. mossambicensis*.

Material examined.—SOUTH AFRICA: *Limpopo Province*: Pietersburg District: Dendron [23°23′S 29°20′E], Soutpansberg, 18.iii.1970, 1 ♀ (NMSA 11449). Sekgosese District: Mphakane, S, granite koppies 1 km from turnoff to Munnik (23°32.20′S 29°42.42′E), 29.xii.1999, L. Prendini & E. Scott, 1 ♂, 1 ♀ (SAMC 4612). Soutpansberg District: Kruger National Park, Pafuri (22°27′S 31°17′E), 18.x.1980, L. Braack, 1 ♀ (NMSA 13899); Langjan Nature Reserve (22°51′S 29°13′E), i.2000, L. Prendini & E. Scott, 1 ♂ (SAMC C4613).

Parabuthus villosus (Peters 1862)
Figs. 7, 8, 15, 18, 32

Scorpio australis (*nec* Linnaeus 1758; misidentification): Herbst 1800: 48–52, pl. IV, fig. 1.

Prionurus (*Androctonus*) *villosus* Peters 1862: 26, 27.

Buthus craturus: Thorell 1876a: 7, *nomen nudum* (no description published) (see Thorell 1876b: 103).

Buthus villosus: Thorell 1876b: 103; Pocock 1889: 343, 344; Simon 1890: 130.

Heterobuthus liosoma villosa: Lenz 1894: 97.

Parabuthus villosus: Pocock 1895: 309, pl. IX, figs. 6a, b; Kraepelin 1899: 31, 32; Kraepelin 1901:

267; Purcell 1901: 158–162; Werner 1902: 598; Simon 1904: 444; Kraepelin 1908: 252; Hewitt 1913: 146; Kraepelin 1914: 112; Werner 1916: 82; Lampe 1917: 193; Hewitt 1918: 107, 178, pl. XIX, fig. 1; Werner 1934: 269; Werner 1936: 178; Roewer 1943: 208; Lawrence 1955: 228; Lawrence 1962: 220; Lawrence 1965: 4; Lamoral & Reynders 1975: 523, 524; Lamoral 1979: 610–616, figs. 198–204, 206, 207; Harington 1984: 393–406; Kovařík 1998: 117; Fet & Lowe 2000: 210, 211; Prendini 2001a: 17; Prendini 2001b: 137; Dyason et al. 2002: 769; Prendini 2003: 22.

Parabuthus brachystylus Lawrence 1928: 270 (NEW SYNONYMY); Lawrence 1955: 225; Lawrence 1961: 153; Lamoral & Reynders 1975: 514; Lamoral 1979: 616–618, figs. 205, 207; Kovařík 1998: 116.

Parabuthus villosus dilutus: Roewer 1943: 208.

Parabuthus villosus brachystylus: Harington 1984: 405; Fet & Lowe 2000: 211.

Parabuthus villosus villosus: Fet & Lowe 2000: 211.

Type material.—*Prionurus* (*Androctonus*) *villosus*: Lectotype ♂ (ZMHB 2303) [designated by Lamoral (1979)], NAMIBIA: Neu Barmen, Otjimbingue [*Erongo Region*: Karibib District: 22°21′S 16°08′E], Hahn. Paralectotype ♀ (ZMHB 2304), same data as lectotypes. The syntypes of *P. villosus* were presumed lost until rediscovered in the collection of the ZMHB (Lamoral 1979). Lamoral selected one as a lectotype, but Moritz & Fisher (1980) omitted *P. villosus* from their list of type specimens in the ZMHB collection.

Parabuthus brachystylus: Lectotype ♀ (SAMC B6087) [designated by Lamoral (1979)], NAMIBIA: Kamanjab, South West Africa (*Kunene Region*: Outjo District: 19°34′S 14°48′E), 1926, R.F. Lawrence. Paralectotypes: 1 juv. ♀ (SAMC B6072), 1 ♀, 3 subad. ♂, 3 juv. ♂, 2 juv. ♀ (SAMC B6794), 2 juv. ♂ (SAMC B6989), 2 juv. ♂, 1 juv. ♀ (SAMC B6072/B6087/B6794/B6989), NAMIBIA: Kaoko Otavi, South West Africa *Kunene Region*: Opuwo District (18°18′S 13°42′E), 1926, R.F. Lawrence.

Diagnosis.—*Parabuthus villosus* is most closely related to *P. transvaalicus* (Fig. 1). Both species share the following combination of characters: pedipalp chela (adult male), fixed finger strongly curved dorsally, such that proximal dentate margin distinctly emarginate when fingers are closed (i.e., a proximal "gap" is evident); metasomal segments broad (length IV/width IV: 1.2–1.5); metasomal segment I, stridulatory surface (dorsal aspect) extended forwards in V-shape onto anterior surface; metasomal segment II, stridulatory surface (dorsal aspect) reaching posterodorsal margin; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules noticeably more pronounced than preceding granules; metasomal segment IV, median lateral carinae continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct, comprising sharp spiniform granules, dorsolateral carinae continuous to distal edge of segment.

Parabuthus villosus is easily confused with *P. schlechteri* and *P. transvaalicus* but may be separated from these, and all other species of *Parabuthus*, by means of the following combination of characters: carapace dorsoventrally compressed; metasomal segments I–V and telson very densely setose (mesosomal tergites often also densely setose); metasomal segments I–IV becoming narrower distally, metasomal segment I wider than segment IV; metasomal segments I and II, stridulatory surface extended anteriorly beyond anterodorsal edge of segment, giving a step-like appearance in lateral aspect. Most populations of *P. villosus* may also be separated from *P. transvaalicus* on the basis of coloration: pale pedipalps and legs pale contrasting with dark brown to black carapace, mesosoma, and metasoma.

Remarks.—Kraepelin (1899) synonymized Thorell's *Buthus villosus* var. β *dilutus* with typical *P. villosus*. However, when the holotype of *B. villosus* var. β *dilutus* was examined for the present investigation, it was instead found to be conspecific with *P. raudus* and synonymized accordingly (see above).

Lamoral (1979) revised *P. brachystylus* and *P. villosus* and regarded them as sibling species (Paterson 1985). Lamoral (1979) maintained that *P. brachystylus* can be separated from *P. villosus* on the following combination of morphological characters, originally proposed by Lawrence (1928): dorsal stridulatory surface of metasomal segment II reaching the posterior margin; metasomal segment I 106% (103–109%) wider than long. Lamoral (1979) noted that, in *P. villosus*, the dorsal stridulatory surface of metasomal segment II does not reach the posterior margin and metasomal segments I–III are 95% (92–98%) longer than wide. The two species were further distinguished by differences in the number of haemolymph protein bands in electrophoregrams.

Harington (1984) conducted a detailed reinvestigation of morphological, morphometric and electrophoretic variation across the distributional ranges of *P. brachystylus* and *P. villosus*. According to Harington (1984), electrophoresis of venom and haemolymph on Sodium Dodecyl Sulphate polyacrylamide gels failed to reveal significant differences between *P. brachystylus* and *P. villosus*. Nondenaturing disc electrophoresis of haemolymph did not show any differences either. On re-examination, Lamoral's (1979) "diagnostic" morphological characters proved to be subject to extensive variation, particularly in an area juxtaposed between the main distributions of the two species. Two ratios, width/length of metasomal segment I and length of stridulatory surface/length of metasomal segment II, were calculated to track the change in morphology. These parameters were then plotted against latitude. In addition, the discriminant scores of three classes, namely *P. villosus*, intermediates and *P. brachstylus*, were plotted against latitude because the discriminant score gives a more inclusive assessment of morphological differences than simple ratios. The three most important characters used in the calculation of the discriminant scores were length of metasomal segment III, length of stridulatory surface and length of metasomal segment I. Neither the qualitative morphological characters nor any of the 15 meristic characters tested by Harington (1984) could be considered truly diagnostic. Harington (1984) therefore concluded that the various color morphs of *P. villosus* and *P. brachystylus* are conspecific.

Despite his evidence of intermediates, Harington (1984) did not synonymize *P. brachystylus* with *P. villosus*, although credited as such by Fet & Lowe (2000: 211), but instead retained it as a subspecies of the latter. As these taxa cannot be viewed as phylogenetic species in the diagnostic sense, I hereby synonymize *P. brachystylus* with *P. villosus*. The possibility that *P. villosus* is a complex of sibling species nevertheless remains. For example, I. Engelbrecht (pers. comm.) recently discovered two color forms of *P. villosus* (also differing in setation and several morphometric parameters) in syntopy at Klein Pella (Northern Cape Province, South Africa). A thorough investigation of species limits within *P. villosus* is now underway using DNA sequence data.

Distribution.—Endemic to Namibia and South Africa. The distribution of *P. villosus* extends across the Orange River. This species has not been recorded from north of the Kunene River (Prendini 1995), but its association with rocky mountain desert in the Kaokoveld of northwestern Namibia (Kunene Region) suggests that this may be due to undersampling, and that it may yet be discovered in the Namibé Province of southwestern Angola.

Ecology.—*Parabuthus villosus* is a semi-lithophilous species, inhabiting consolidated sandy, gritty and clayey substrata in extremely rocky habitats. This species excavates burrows under rocks or stones and never in open ground. Dorsoventral compression (especially of the carapace), reduction in the macrosetal combs of basitarsi I and II, and increased curvature of the telotarsal ungues indicate a semi-lithophilous ecomorphotype (Eastwood 1977; Prendini 2001a, b).

Parabuthus villosus is unusual among species of the genus, and indeed among scorpions generally, in that it is commonly active during the day (Newlands 1974a; Harington 1982). This species is an errant forager that may be observed actively hunting for prey from midday through the afternoon and on into the night.

Parabuthus villosus is sympatric with *P. brevimanus*, *P. granulatus* and *P. raudus* in parts of its distributional range. However, due to its occurrence in extremely rocky habitats, *P. villosus* is rarely found in syntopy with other species of *Parabuthus*. The species is allopatric with its sister species, *P. transvaalicus*.

Material examined.—NAMIBIA: *Karas Region*: Lüderitz District: Farm Plateau 38, 26°40′S 16°30′E, 29.ii.1976, B. Lamoral, 1 ♂, 3 ♀ (NMSA 10805). *Kunene Region*: Khorixas District: Farm Grootberg 191, 19°46′S 14°15′E, 2.iv.1976, B. Lamoral & L. Ferguson, 1 subad. ♂ (NMSA 10913). Opuwo District: Sesfontein, 3 km N clinic, 19°07′S 13°36′E, 3.iv.1976, B. Lamoral, 1 ♀ (NMSA 10738). Outjo District: Kamanjab, 3 km W, 19°37′S 14°48′E, 5.iv.1976, B. Lamoral & L. Ferguson, 1 ♀ (NMSA 10833). SOUTH AFRICA: *Northern Cape Province*: Namaqualand District: Pella pumpstation [28°59′S

19°10′E], iii.1997, L. Prendini & G.J. Müller, 2 ♂ (SAMC C4614); Vioolsdrift, 28°46′S 17°37′E, ii.1973, B.H. Lamoral, 1 ♂ (NMSA 10531) [homotype designated by Lamoral (1979)].

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LITERATURE CITED

Aguiar, O.B. 1978. Alguns escorpiões de Moçambique. Garcia de Orta: Série de zoologia. Junta de Investigacãos Cientificas do Ultramar 7:107–114.

Bacelar, A. 1950. Notas acerca dos aracnideos do ultramar português. Junta de Investigacãos Colonais, Lisboa, 17:1–24.

Balinsky, B.I. 1962. Patterns of animal distribution on the African continent. Annals of the Cape Provincial Museums 2:299–309.

Barnard, P. (Ed.) 1998. Biological diversity in Namibia: A country study. Namibian National Biodiversity Task Force, Windhoek.

Belfield, W. 1956. A preliminary check list of the West African scorpions and key for their identification. Journal of the West African Science Association 2:41–47.

Bergman, N.J. 1995. Scorpionism in Zimbabwe. An epidemiological and clinical investigation into scorpionism in the Gwanda District of Zimbabwe, with particular reference to *Parabuthus transvaalicus* (Purcell). M.D. thesis, University of Zimbabwe, Harare.

Bergman, N.J. 1997a. Scorpion sting in Zimbabwe. South African Medical Journal 87:163–167.

Bergman, N.J. 1997b. Clinical description of *Par-*

abuthus transvaalicus scorpionism in Zimbabwe. Toxicon 35:759–771.

[Birula, A.A.] Byalynitskii-Birulya, A.A. 1917a. Arachnoidea Arthrogastra Caucasica. Pars I. Scorpiones. Zapiski Kavkazskogo Muzeya (Mémoires du Musée du Caucase), Tiflis, Imprimerie de la Chancellerie du Comité pour la Transcaucasie. Ser A, 5:1–253. [in Russian; English translation: Byalynitskii-Birulya, A.A. 1964. Arthrogastric Arachnids of Caucasia. 1. Scorpions. Israel Program for Scientific Translations, Jerusalem.]

[Birula, A.A.] Byalynitskii-Birulya, A.A. 1917b. Faune de la Russie et des pays limitrophes fondee principalement sur les collections du Musée zoologique de l'Académie des sciences de Russie. Arachnides (Arachnoidea). 1:1–227. [in Russian; English translation: Byalynitskii-Birulya, A. A. 1965. Fauna of Russia and adjacent countries. Arachnoidea. Vol. I. Scorpions. Israel Program for Scientific Translations, Jerusalem.]

Braunwalder, M.E. & V. Fet. 1998. On publications about scorpions (Arachnida, Scorpiones) by Hemprich and Ehrenberg (1828–1831). Bulletin of the British Arachnological Society 11:29–35.

Bücherl, W. 1964. Distribução geográfica dos aracnóides peçonhentos temíveis (class Arachnomorpha, sub-class Arachnoidea, ordens Scorpiones e Araneida). Mémorias do Instituto de Butantán 31:55–66.

Couzijn, H.W.C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. Netherlands Journal of Zoology 26:453–501.

Cracraft, J. 1983. Species concepts and speciation analysis. Current Ornithology 1:159–187.

Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59. *In* Speciation and its Consequences. (D. Otte & J.A. Endler, eds.). Sinauer Associates, Sunderland, MA.

Davis, J.I. & K.C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Systematic Biology 41:421–435.

DeBont, T., A. Swerts, J.J. van der Walt, G.J. Müller, F. Verdonck, P. Daenens & J. Tytgat. 1998. Comparison and characterization of the venoms of three *Parabuthus* scorpion species occuring in southern Africa. Toxicon 36:341–352.

De Pinna, M.C.C. 1999. Species concepts and phylogenetics. Reviews in Fish Biology and Fisheries 9:353–373.

Dobzhansky, T. 1937. Genetics and the Origin of Species. Columbia University Press, New York.

Dumortier, B. 1964. Morphology of sound emission apparatus in Arthropoda. Pp. 277–345. *In* Acoustic behaviour of animals. (R.-G. Busnel, ed.). Elsevier, Amsterdam.

Dyason, K., W. Brandt, L. Prendini, F. Verdonck, J. Tytgat, J. du Plessis, G. Müller. & J. van der Walt. 2002. Determination of species-specific components in the venom of *Parabuthus* scorpions from southern Africa using matrix-assisted laser desorption time-of-flight mass spectrometry. Rapid Communications in Mass Spectrometry 16:768–773.

Eastwood, E.B. 1977. Notes on the scorpion fauna of the Cape. Part 2. The *Parabuthus capensis* (Ehrenberg) species-group; remarks on taxonomy and bionomics (Arachnida, Scorpionida, Buthidae). Annals of the South African Museum 73:199–214.

Eastwood, E.B. 1978a. Notes on the scorpion fauna of the Cape. Part 3. Some observations on the distribution and biology of scorpions on Table Mountain. Annals of South African Museum 74: 229–248.

Eastwood, E.B. 1978b. Notes on the scorpion fauna of the Cape. Part 4. The burrowing activities of some scorpionids and buthids (Arachnida, Scorpionida). Annals of South African Museum 74: 249–255.

Fage, L. 1925. Arachnides. *In* Mission Rohan Chabot, Paris 4:189–198.

Fet, V. & G. Lowe. 2000. Family Buthidae C.L Koch, 1837. Pp. 54–286. *In* Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder). New York Entomological Society, New York.

FitzPatrick, M.J. 1994. A checklist of the *Parabuthus* Pocock species of Zimbabwe with a re-description of *P. mossambicensis* (Peters, 1861) (Arachnida: Scorpionida). Transactions of the Zimbabwe Scientific Association 68:7–14.

Forcart, L. 1961. Katalog der Typusexemplare in der Arachnida-Sammlung des Naturhistorischen Museums zu Basel: Scorpionidea, Pseudoscorpionidea, Solifuga, Opilionidea und Araneida. Verhandlungen der Naturforschenden Gesellchaft in Basel 72:47–87.

Francke, O.F. 1985. Conspectus genericus scorpionorum 1758–1982 (Arachnida: Scorpiones). Occasional Papers of the Museum, Texas Tech University 98:1–32.

Gaffin, D.D. & P.H. Brownell. 1992. Evidence of chemical signaling in the sand scorpion *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). Ethology 91:59–69.

Gervais, P.M. 1844. Scorpions. *In* Histoire naturelle des Insectes. Aptères. (C.A. Walckenaer, ed.). Librarie encyclopédique de Roret, Paris 3:14–74.

Harington, A. 1982. Diurnalism in *Parabuthus villosus* (Peters) (Scorpiones, Buthidae). Journal of Arachnology 10:85–86.

Harington, A. 1984. Character variation in the scorpion *Parabuthus villosus* (Peters) (Scorpiones, Buthidae): a case of intermediate zones. Journal of Arachnology 11:393–406.

Hemprich, F.W. & C.G. Ehrenberg. 1828. Zoologica II. Arachnoidea. Plate I: *Buthus*; plate II: *Androctonus*. *In* Symbolae Physicae seu Icones et Descriptiones Animalium evertebratorum sepositis Insectis quae ex itinere per Africam borealem et Asiam occidentalem. Friderici Guilelmi Hemprich et Christiani Godofredi Ehrenberg, medicinae et chirurgiae doctorum, studio novae aut illustratae redierunt. Percensuit et regis iussu et impensis edidit Dr. C. G. Ehrenberg. Decas prima. Berolini ex officina Academica, Venditur a Mittlero.

Hemprich [F.W.] & [C.G.] Ehrenberg. 1829. Vorläufige Uebersicht der in Nord-Afrika und West-Asien einheimischen Skorpione und deren geographischen Verbreitung. Verhandungen der Gesellschaft der naturforschender Freunde in Berlin 1:348–362.

Hemprich, F.W. & C.G. Ehrenberg. 1831. Animalia articulata, Arachnoidea. Scorpiones Africani et Asiatici. *In* Symbolae Physicae. Animalia evertebrata exclusis insectis percensuit Dr. C. G. Ehrenberg. Series prima cum tabularum decade prima. Continet Animalia Africana et Asiatica 162. Berolini ex officina Academica, Venditur a Mittlero, 12 pp. [unnumbered, a separate text which was intended to be a part of the 1828 issue of "Symbolae Physicae"].

Herbst, J.F.W. 1800. Naturgeschichte der Skorpionen. *In* Natursystem der Ungeflügelten Insekten. Gotlieb August Lange, Berlin 4:1–86.

Hewitt, J. 1912. Records and descriptions of some little known South African scorpions. Records of the Albany Museum 2:300–311.

Hewitt, J. 1913. The Percy Sladen Memorial Expedition to Great Namaqualand, 1912–1913. Records and descriptions of the Arachnida of the collection. Annals of the Transvaal Museum 4: 146–159.

Hewitt, J. 1914. Descriptions of new Arachnida from South Africa. Records of the Albany Museum 3:1–37.

Hewitt, J. 1915. Descriptions of new South African Arachnida. Records of the Albany Museum 3: 70–106.

Hewitt, J. 1918. A survey of the scorpion fauna of South Africa. Transactions of the Royal Society of South Africa 6:89–192.

Hewitt, J. 1935. Scientific results of the Vernay-Lang Kalahari expedition, March to September, 1930. The trap-door spiders, scorpions and solifuges. Annals of the Transvaal Museum 16:459–479.

Hill, G. 1990. A tale with a sting. Journal of the Medical Defence Union 6:69.

Hirst, S. 1911. On a collection of Arachnida and Chilopoda made by Mr. S. A. Neave in Rhodesia, north of the Zambezi. Memoirs of the Linnean Philosophical Society 56:1–11.

Hjelle, J.T. 1990. Anatomy and morphology. Pp. 9–63. *In* The Biology of Scorpions (G.A. Polis, ed.). Stanford University Press, Stanford, CA.

Honetschlager, L.D. 1965. A new method for hunting scorpions. Turtox News 43:69–70.

Huys, I., K. Dyason, E. Waelkens, F. Verdonck, J. van Zyl, J. du Plessis, G.J. Müller, J. van der Walt, E. Clynen, L. Schoofs & J. Tytgat. 2002. Purification, characterization and biosynthesis of parabutoxin 3, a component of *Parabuthus transvaalicus* venom. European Journal of Biochemistry 269:1854–1865.

Jäger, P. 1998. Das Typenmaterial der Spinnentiere (Arachnida: Acari, Amblypygi, Araneae, Opiliones, Pseudoscorpiones, Scorpiones, Uropygi) aus dem Museum Wiesbaden. Jahrbücher des Nassauischen Verein für Naturkunde 119:81–91.

Kästner, A. 1941. 1. Ordnung der Arachnida: Scorpiones. *In* Handbuch der Zoologie (T. Krumbach, ed.). Walter de Gruyter Verlag, Berlin 3:117–240.

Koch, C.L. 1839. Die Arachniden. C.H. Zeh Buchhandlung, Nürnberg 6:1–156.

Koch, C.L. 1850. Scorpionen. *In* Übersicht des Arachnidensystems. C. H. Zeh Buchhandlung, Nürnberg 5:86–92.

Kovařík, F. 1992. A checklist of scorpions (Arachnida: Scorpiones) in the collections of the zoological department, National Museum in Prague. Acta Societatis Zoologicae Bohemoslovenicae 56:181–186.

Kovařík, F. 1998. Štíři (Scorpions). Madagaskar, Jihlava. [in Czech.]

Kovařík, F. 2001. Catalog of the Scorpions of the World (1758–1998) by V. Fet, W.D. Sissom, G. Lowe, and M. Braunwalder (New York Entomological Society, 2000:690 pp.) Discussion and supplement for 1999 and part of 2000. Serket 7: 78–93.

Kovařík, F. 2002. Co nového u štírů v roce 2000. Akvárium Terárium 45:55–61. [in Czech.]

Kovařík, F. 2003a. Co nového u štírů v roce 2001 Akvárium Terárium 45:55–61. [in Czech.]

Kovařík, F. 2003b. Scorpions of Djibouti, Eritrea, Ethiopia, and Somalia (Arachnida: Scorpiones), with a key and descriptions of three new species. Acta Societatis Zoologicae Bohemoslovenicae 67:133–139.

Kraepelin, K. 1891. Revision der Skorpione. I. Die Familie der Androctonidae. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten 8:1–144.

Kraepelin, K. 1895. Nachtrag zu Theil I der Revision der Scorpione. Beiheft zum Jahrbuch der Hamburgischen wissenschaftlichen Anstalten 12: 73–96.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. *In*

Das Tierreich. (F. Dahl, ed.). R. Friedlander, Berlin. 8:1–265.

Kraepelin, K. 1901. Catalogue des scorpions des collections du Museum d'Historie Naturelle de Paris. Bulletin du Muséum National d'Histoire Naturelle, Paris 7:265–274.

Kraepelin, K. 1908. Skorpione und Solifugen. *In* Forschungsreise im Westlichen und Zentralen Südafrika, Ausgeführt in den Jahren 1903–1905. (L.G. Schultze, ed.). Fischer, Jena 1:247–282.

Kraepelin, K. 1914. Skorpione und Solifugae. *In* Beiträge zur Kenntnis der Land- und Süßwasserfauna Deutsch-Südwestafrikas. (W. Michaelsen, ed.). Ergebnisse der Hamburger deutsch-südwestafrikanischen Studienreise 1911 1:107–136.

Lamoral, B.H. 1977. *Parabuthus kalaharicus*, a new species of scorpion from the Kalahari Gemsbok National Park in the Republic of South Africa (Buthidae, Scorpionida). Koedoe 20:101–107.

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:498–783.

Lamoral, B.H. 1980. Two new psammophile species and new records of scorpions from the northern Cape Province of South Africa (Arachnida: Scorpionida). Annals of the Natal Museum 24:201–210.

Lamoral, B.H. & S.C. Reynders. 1975. A catalogue of the scorpions described from the Ethiopian faunal region up to December 1973. Annals of the Natal Museum 22:489–576.

Lampe, E. 1917. Katalog der Skorpione, Pedipalpen und Solifugen des Naturhistorischen Museums der Residenzstadt Wiesbaden. Jahrbücher des Nassauischen Vereine für Naturkunde 70:185–203.

Lancaster, N. 1981. Paleoenvironmental implications of fixed dune systems in southern Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 33:327–346.

Lancaster, N. 1984. Aridity in southern Africa: Age, origins and expression in landforms and sediments. Pp. 433–444. *In* Late Cainozoic Palaeoclimates of the Southern Hemisphere. Proceedings of an International Symposium held by the South African Society for Quaternary Research, Swaziland, 29 August–2 September 1983. (J.C. Vogel, ed.). A.A. Balkema, Rotterdam.

Laurie, M. 1896. Further notes on the anatomy and development of scorpions, and their bearing on the classification of the order. Annals and Magazine of Natural History (6) 18:121–133.

Lawrence, R.F. 1927. Contributions to a knowledge of the fauna of South-West Africa. V. Arachnida. Annals of the South African Museum 25:1–75.

Lawrence, R.F. 1928. Contributions to a knowledge of the fauna of South-West Africa. VII. Arachnida (Part 2). Annals of the South African Museum 25:217–312.

Lawrence, R.F. 1938. The Arachnida of the Transvaal Museum expedition to South Rhodesia, November–December, 1937. Scorpions and Solifugae. Annals of the Transvaal Museum 19:289–296.

Lawrence, R.F. 1942. The scorpions of Natal and Zululand. Annals of the Natal Museum 10:221–235.

Lawrence, R.F. 1946. A collection of scorpions and solifuges in the Transvaal Museum, with notes on two Natal solifuges. Annals of the Transvaal Museum 20:399–408.

Lawrence, R.F. 1955. Solifugae, scorpions and Pedipalpi, with checklists and keys to South African families, genera and species. Results of the Lund University Expedition in 1950–1951. *In* South African Animal Life. (B. Hanström, P. Brinck & G. Rudebeck, eds.). Almqvist & Wiksells, Uppsala 1:152–262.

Lawrence, R.F. 1959. A collection of Arachnida and Myriapoda from the Transvaal Museum. Annals of the Transvaal Museum 23:363–386.

Lawrence, R.F. 1961. New scorpions and solifuges from South West Africa and Angola. Kungliga Fysiografiska sällskapets i Lund förhandlingar 31:147–160.

Lawrence, R.F. 1962. Solifuges, scorpions and Chilopoda of the Namib Desert. Annals of the Transvaal Museum 24:213–222.

Lawrence, R.F. 1964. The Solifugae, scorpions and Pedipalpi of the Kruger National Park. Koedoe 7:30–39.

Lawrence, R.F. 1965. New and little known Arachnida from the Namib Desert, S.W. Africa. Scientific Papers of the Namib Desert Research Station 27:1–12.

Lawrence, R.F. 1967. Supplementary list of the Solifugae, scorpions and Pedipalpi of the Kruger National Park. Koedoe 10:82–86.

Lee, N.C. 1991. Scorpion stings. South African Medical Journal 79:120.

Lenz, H. 1894. Fische, Myriapoden, Arachnoideen und Crustaceen. *In* Reiseausbeute aus Südwest-Africa. (E. Fleck, ed.). Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main 1894:96–98.

Levy, G. & P. Amitai. 1980. Scorpiones. (Fauna Palaestina. Arachnida I). The Israel Academy of Sciences and Humanities, Jerusalem.

Linnaeus, C. [C. von Linné]. 1758. Systema Naturae per regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Ed. 10. Laurentii Salvii, Holmiae (Stockholm). Vol. 1. [Scorpions: pp. 624–625].

Lönnberg, E. 1897. Om skorpionernas och pedipalpernas geografiska utbredning. Entomologisk tidskrift 18:193–211.

Loveridge, A. 1925. Notes on East African scorpions and Solifugae, collected 1916–23. Proceedings of the Zoological Society of London 1925: 303–309.

Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, MA.

McCormick, S.J. & G.A. Polis. 1990. Prey, predators, parasites. Pp. 294–320. *In* The Biology of Scorpions (G.A. Polis, ed.). Stanford University Press, Stanford, CA.

Monard, A. 1929 [1930]. Matériaux de la mission scientifique suisse en Angola. Scorpiones. Bulletin de la Société neuchateloise des sciences naturelles 54:37–43.

Monard, A. 1937. Scorpions, solifuges et opilions d'Angola. Revue Suisse de Zoologie 44:251–270.

Moritz, M. & S.C. Fischer. 1980. Die Typen der Arachniden-Sammlung des Zoologisches Museums Berlin. III. Scorpiones. Mitteilungen aus dem Zoologischen Museums Berlin 56:309–326.

Müller, G.J. 1993. Scorpionism in South Africa. A report of 42 serious scorpion envenomations. South African Medical Journal 83:405–411.

Müller, J. 1828. Beiträge zur Anatomie des Scorpions. Archiv für Anatomie und Physiologie (Leipzig), 1828:29–71.

Nelson, G. & N.I. Platnick. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia University Press, New York.

Nenilin, A.B. & V. Fet. 1992. Zoogeographical analysis of the world scorpion fauna (Arachnida: Scorpiones). Arthropoda Selecta 1:3–31 [in Russian].

Newlands, G. 1970. A re-examination of some southern African scorpion species (Arachnida, Scorpionidea). Annals of the Transvaal Museum 26:199–210.

Newlands, G. 1974a. The venom-squirting ability of *Parabuthus* scorpions (Arachnida: Buthidae). South African Journal of Medical Science 39: 175–178.

Newlands, G. 1974b. Transvaal scorpions. Fauna and Flora 25:3–7.

Newlands, G. 1978a. Review of southern African scorpions and scorpionism. South African Medical Journal 54:613–615.

Newlands, G. 1978b. Arachnida (except Acari). Pp. 687–702. *In* Biogeography and ecology of Southern Africa. Vol. 2. (M.J.A. Werger, ed.). W. Junk, The Hague.

Newlands, G. & C.B. Martindale. 1980. The buthid scorpion fauna of Zimbabwe-Rhodesia with checklists and keys to the genera and species, distribution and medical importance (Arachnida: Scorpiones). Zeitschrift für angewandte Zoologie 67:51–77.

Nixon, K.C. & Q.D. Wheeler. 1990. An amplification of the phylogenetic species concept. Cladistics 6:211–223.

Paterson, H.E.H. 1985. The recognition concept of species. Pp. 21–29. *In* Species and Speciation (E.S. Vrba, ed.). Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria.

Pavlovsky, E.N. 1924. On the morphology of the male genital apparatus in scorpions. Trudy Leningradskogo Obshchestva Yestestvoispytatelei (Transactions of the Leningrad Society of Naturalists) 53:17–86.

Pavlovsky, E.N. [Pavlovskij, E.]. 1925. Zur Morphologie des weiblichen Genitalapparatus und zur Embryologie der Skorpione. Annuaire du Musée Zoologique de l'Académie des Sciences d'URSS 26:137–205.

Penther, A. 1900. Zur Kenntnis der Arachnidenfauna Südafrikas (Scorpiones). Annalen des Kaiserlich-Königliches Naturhistorischen Hofmuseums in Wien 15:153–163.

Peters, W. 1861. (Über eine neue Eintheilung der Skorpione und über die von ihm in Mossambique gesammelten Arten von Skorpionen). Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1861:507–516.

Peters, W. 1862. (Eine neue Skorpionenart. . .). Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1862: 26–27.

Petersen, J. 1987. Death due to a scorpion sting. South African Medical Journal 71:406.

Pocock, R.I. 1889. Notes on some Buthidae, new and old. Annals and Magazine of Natural History (6) 3:334351.

Pocock, R.I. 1890. A revision of the genera of scorpions of the family Buthidae, with descriptions of some South-African species. Proceedings of the Zoological Society 1890:114–141.

Pocock, R.I. 1895. On the Arachnida and Myriopoda obtained by Dr. Anderson's collector during Mr T. Brent's expedition to the Hadramaut, South Arabia, with a supplement upon the scorpions obtained by Dr. Anderson in Egypt and the Eastern Soudan. Journal of the Linnean Society 25: 292–316.

Pocock, R.I. 1899. Descriptions of some new species of scorpions. Annals and Magazine of Natural History (7) 3:411–420.

Pocock, R.I. 1901. Descriptions of some new African Arachnida. Annals and Magazine of Natural History, (7) 7:284–287.

Pocock, R.I. 1902. A contribution to the systematics of scorpions. I. Some corrections in nomenclature. II. Notes on some species of *Parabuthus* contained in the British Museum. III. Descriptions of some new and old species. Annals and Magazine of Natural History (7) 10:364–380.

Polis, G.A. 1990. Ecology. Pp. 247–293. *In* The

Biology of Scorpions (G.A. Polis, ed.). Stanford University Press, Stanford, CA.

Prendini, L. 1995. Patterns of scorpion distribution in southern Africa: A GIS approach. B.Sc. Hons thesis, University of Cape Town.

Prendini, L. 2000. A new species of *Parabuthus* Pocock (Scorpiones: Buthidae), and new records of *Parabuthus capensis* (Ehrenberg), from Namibia and South Africa. Cimbebasia 16:31–45.

Prendini, L. 2001a. Phylogeny of *Parabuthus* (Scorpiones, Buthidae). Zoologica Scripta 30: 13–35.

Prendini, L. 2001b. Substratum specialization and speciation in southern African scorpions: The Effect Hypothesis revisited. Pp. 113–138. *In* Scorpions 2001. *In Memoriam* Gary A. Polis (V. Fet & P.A. Selden eds.). British Arachnological Society, Burnham Beeches, Buckinghamshire, UK.

Prendini, L. 2003. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). American Museum Novitates 3408:1–24.

Prendini, L. 2004. Systematics of the genus *Pseudolychas* Kraepelin (Scorpiones: Buthidae). Annals of the Entomological Society of America 97:37–63.

Probst, P.J. 1973. A review of the scorpions of East Africa with special regard to Kenya and Tanzania. Acta Tropica 30:312–335.

Purcell, W.F. 1898. Descriptions of new South African scorpions in the collection of the South African Museum. Annals of the South African Museum 1:1–32.

Purcell, W.F. 1899a. On the species of *Opistophthalmus* in the collection of the South African Museum, with descriptions of some new forms. Annals of the South African Museum 1:131–180.

Purcell, W.F. 1899b. New South African scorpions in the collection of the South African Museum. Annals of the South African Museum 1:433–438.

Purcell, W.F. 1901. On some South African Arachnida belonging to the orders Scorpiones, Pedipalpi, and Solifugae. Annals of the South African Museum 2:137–225.

Roewer, C.F. 1943. Über eine neuerworbene Sammlung von Skorpionen des Natur-Museums Senckenberg. Senckenbergiana, 26:205–244.

Saunders, C.R. & A.B. Morar. 1990. Beware the scorpion *Parabuthus*. Central African Journal of Medicine 36:114–115.

Schenkel, E. 1932. Notizen über einige Scorpione und Solifugen. Revue suisse de zoologie 39:375–396.

Simon, E. 1887 [1888]. Études arachnologiques. 20^{e} Memoire. XXVIII. Arachnides recueillis dans le sud de l'Afrique par M. le docteur Hans Schinz. Annales de la Société Entomologique de France (6) 7:369–384.

Simon, E. 1890. Études arachnologiques. 22e Mémoire. XXXV. Étude sur les arachnides recueillis par M. L. von Höhnel officier de la marine autrichienne, pendant l'expédition de M. le comte Teleki dans l'Afrique orientale équatoriale, en 1887–1888. Annales de la Société Entomologique de France (6) 10:125–130.

Simon, E. 1904. Étude sur les arachnides recueillis au cours de la mission du Bourg-de-Bozas en Afrique. Bulletin du Muséum National d'Histoire Naturelle, Paris 7:442–448.

Sissom, W.D. 1990. Systematics, biogeography and paleontology. Pp. 64–160. *In* The Biology of Scorpions (G.A. Polis, ed.). Stanford University Press, Stanford, CA.

Sissom, W.D., G.A. Polis & D.D. Watt. 1990. Field and laboratory methods. Pp. 445–461. *In* The Biology of Scorpions (G.A. Polis, ed.). Stanford University Press, Stanford, CA.

Sissom, W.D. 1994. Descriptions of new and poorly known scorpions of Yemen (Scorpiones: Buthidae, Diplocentridae, Scorpionidae). Fauna of Saudi Arabia 14:3–39.

Smithe, F.B. 1974. Naturalist's Color Guide Supplement. The American Museum of Natural History, New York.

Smithe, F.B. 1975. Naturalist's Color Guide. The American Museum of Natural History, New York.

Smithe, F.B. 1981. Naturalist's Color Guide. Part III. The American Museum of Natural History, New York.

Soleglad, M.E. & V. Fet. 2003. The scorpion sternum: Structure and phylogeny (Scorpiones: Orthosterni). Euscorpius 5:1–34.

Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. Entomological News 81:297–316.

Stahnke, H.L. 1972a. UV light, a useful field tool. BioScience 22:604–607.

Stahnke, H.L. 1972b. A key to the genera of Buthidae (Scorpionida). Entomological News 83: 121–133.

Swerts, A., T. Debont, F. Verdonck, J.J. van der Walt, P. Daenens & J. Tytgat. 1997. Development and optimization of a purification strategy for the venom of the scorpion *Parabuthus transvaalicus*. Journal de Pharmacie de Belgique 52:194–195.

Tankard, A.J. & J. Rogers. 1978. Late Cenozoic palaeoenvironments on the west coast of southern Africa. Journal of Biogeography 5:319–337.

Thorell, T. 1876a. On the classification of scorpions. Annals and Magazine of Natural History (4) 17:1–15.

Thorell, T. 1876b. Études scorpiologiques. Atti della Società Italiana di Scienze Naturali 19:75–272.

Thorell, T. 1893. Scorpiones exotici R. Musei Historiae Naturalis Florentini. Bollettino della Società Entomologica Italiana 25:356–387.

Tytgat, J., T. DeBont, K. Rostoll, G.J. Müller, F. Verdonck, P. Daenens, J.J. van der Walt & L.D. Possani. 1998. Purification and partial characterization of a 'short' insectotoxin-like peptide from the venom of the scorpion *Parabuthus schlecteri*. FEBS Letters 441:387–391.

Vachon, M. 1952. Études sur les scorpions. Archives de l'Institut Pasteur d'Algerie, Algiers.

Vachon, M. 1973 [1974]. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris (3) 140:857–958.

Vachon, M. 1979. Arachnids of Saudi Arabia. Scorpiones. Fauna of Saudi Arabia 1:30–66.

Van Valen, L.M. 1976. Ecological species, multispecies, and oaks. Taxon 25:233–239.

Vrba, E.S. 1980. Evolution, species and fossils: How does life evolve? South African Journal of Science 76:61–84.

Ward, J.D., M.K. Seely & N. Lancaster. 1983. On the antiquity of the Namib. South African Journal of Science 79:175–183.

Werner, F. 1902. Die Scorpione, Pedipalpen und Solifugen in der zoologisch-vergleichend-anatomischen Sammlung der Universität Wien. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 52:595–608.

Werner, F. 1916. Über einige Skorpione und Gliederspinnen des Naturhistorischen Museums in Wiesbaden. Jahrbücher des Nassauischen Vereins für Naturkunde 69:79–97.

Werner, F. 1933. Die von Dr. Fritz Haas auf der Schomburg-Afrik-Expedition 1931–32 gesammelten Skorpione. Senckenbergiana 15:323–324.

Werner, F. 1934. Scorpiones, Pedipalpi. *In* Klassen und Ordnungen des Tierreichs (H.G. Bronn, ed.). Akademische Verlaggesellschaft, Leipzig. 5, IV, 8, Lief. 1–2 [Scorpiones, 1–316].

Werner, F. 1936. Neu-Eingänge von Skorpionen im Zoologischen Museum in Hamburg. Festschrift zum 60. Geburstage von Professor Dr. Embrik Strand 2:171–193.

Wheeler, Q.D. & K.C. Nixon. 1990. Another way of *looking at* the species problem: A reply to de Queiroz and Donoghue. Cladistics 6:77–81.

Appendix 1

Characters and character states used for cladistic analysis of the genus *Parabuthus* Pocock 1890 (Prendini 2003). Character states were scored 0–2, ? (unknown), – (inapplicable) or * (polymorphic). Multistate characters were treated as unordered (nonadditive). Three autapomorphies, indicated by †, were excluded from the analysis.

General

1. Adult general size: large, carapace length 6.5–17.0 mm (0); small, carapace length 2.5–5.0 mm (1).
2. Color of carapace, mesosoma and metasoma: pale yellow to light brown (0); dark brown to black (pedipalps and legs may be dark or pale) (1); polymorphic (*).
3. Color pattern of metasoma: metasomal segments I–V and telson uniformly colored (0); metasomal segments III–V and telson infuscated (i.e., darker than segments I and II) (1); polymorphic (*).

Carapace

4. †Carapace dorsoventrally compressed: absent (0); present (1).
5. Granulation of median ocular tubercle (♂, ♀) and surrounding surfaces (♀): entire (0); smooth areas (1).

Pedipalps

6. Pedipalps, setation: setose (0); smooth (1).
7. Chela manus, surface: smooth (0); granular (1).
8. Chela movable finger, length compared with length of manus (measured along ventroexternal carina), in ♀: long (length finger/length carina: 1.70–2.00) (0); short (length finger/length carina: ± 1.50) (1).
9. Chela manus, shape in adult ♂, compared with adult ♀: similar (0); sexually dimorphic (1).
10. Chela fixed finger, shape in adult ♂: straight or slightly curved dorsally, such that proximal dentate margin linear when fingers are closed (0); strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers are closed (1).
11. Chela movable finger, shape in adult ♂: straight, proximal dentate margin linear when fingers are closed (0); curved ventrally, proximal dentate margin distinctly emarginate when fingers are closed (1).
12. Chela fixed and movable fingers with basal lobe in adult ♂: absent (0); present (1).

Trichobothria

13. Pedipalp femur, position of e_1: level with or distal to d_5 (0); almost halfway between d_4 and d_5 (1).
14. Pedipalp patella, position of esb_2: distinctly distal to esb_1 (0); level with or slightly distal to esb_1 (1).
15. Chela fixed finger, position of *dt*: in line with or distal to *et* (0); proximal to *et* (1).

Pectines

16. Proximal median lamella of pectines, in ♀: arcuate (0); enlarged and lobate (dilate) (1).

17. Proximal median lamella of pectines, in ♂: subrectangular (0); weakly lobate (dilate) (1); strongly lobate (dilate) (2).

Legs

18. Legs IV, length: moderately long, not reaching to posterior edge of metasomal segment III (0); very long, reaching past posterior edge of metasomal segment III (1).
19. Basitarsi of legs I and II, macrosetal combs: absent (0); weakly developed (1); strongly developed (2).
20. Basitarsi of legs I and II, dorsoventrally compressed: absent (0); present (1).
21. †Basitarsi of legs III and IV, prolateral surfaces with dense tufts of macrosetae: absent (0); present (1).
22. Telotarsal ungues, relative length: equal (0); subequal (1).

Hemispermatophore

23. Hemispermatophore, *pars recta*: parallel to axis (0); S-shaped (1).

Mesosoma

24. Sternites, surface: smooth (0); punctate (1).
25. Sternite III, "pit" organ at proximal apex: absent (0); present (1).
26. Sternite VII, carinae: present (0); absent (1).

Metasoma

27. Metasomal segments I–V and telson, setation: virtually asetose (0); sparsely to moderately setose (1); very densely setose (2).
28. Metasomal segments, width relative to length: much narrower (length IV/width IV: 1.7–2.11) (0); slightly narrower (length IV/width IV: 1.2–1.5) (1).
29. Metasomal segments, width from I–IV: becoming narrower distally, metasomal segment I wider than segment IV (0); becoming wider distally, metasomal segment I narrower than segment IV (1).
30. Metasomal segments I–III, dorsal stridulatory surface: absent from I–III (0); strongly developed on I–III (1); strongly developed on I and II, weakly developed to absent on III (2).
31. Metasomal segment I, shape of stridulatory surface (if present) in dorsal aspect: narrow, parallel-sided (0); broad, rounded anteriorly, with posterior constriction (1); inapplicable (–).
32. Metasomal segments I, and to a lesser extent II, shape of stridulatory surface (if present) in lateral aspect: truncated at anterodorsal edge of segment (0); rounded, extended beyond anterodorsal edge of segment (1); inapplicable (–).
33. Metasomal segment I, extent of stridulatory surface (if present) in dorsal aspect: terminating at anterodorsal edge of segment (0); extended forwards in V-shape onto anterior surface (1); inapplicable (–).
34. Metasomal segment II, extent of stridulatory surface (if present) in dorsal aspect: reaching posterodorsal margin (0); not reaching posterodorsal margin (1); inapplicable (–); polymorphic (*).
35. Metasomal segment II, nature of stridulatory surface (if present): fine to coarse granules (0); horizontal ridges (1); inapplicable (–).
36. Metasomal segments II and III, posterodorsal edge: straight (0); anteromedially curved in a V-shape (1).
37. Metasomal segments IV and V, lateral intercarinal surfaces: granular (0); smooth (1).
38. Metasomal segments I–IV, dorsosubmedian carinae: present (0); absent (1).
39. Metasomal segment IV, dorsosubmedian carinae (if present): continuous (0); discontinuous (1); inapplicable (–).
40. Metasomal segments II–IV, distal spiniform granules of dorsosubmedian carinae (if present), size relative to preceding granules: equally developed (0); noticeably more pronounced (1); inapplicable (–).
41. Metasomal segment IV, ventrosubmedian and ventrolateral carinae: present and continuous to edge of segment (0); present but ventrosubmedian carinae becoming obsolete distally (1); absent (2).
42. Metasomal segment IV, median lateral carina: absent to proximally obsolete (0); continuous but poorly developed (1); continuous and distinct (2).
43. Metasomal segment V, dorsosubmedian carinae: absent (0); present, poorly developed with blunt, rounded granules (1); present, distinct with sharp, spiniform granules (2).
44. Metasomal segment V, dorsolateral carinae: absent, except for a few proximal granules (0); distally obsolete (1); continuous to distal edge of segment (2).
45. Metasomal segment V, ventrolateral carinae: converging distally (0); subparallel to diverging distally (1).
46. Metasomal segment V, distal half of ventrolateral carinae: with spinose processes (0); with lobate processes (1).
47. Metasomal segment V, ventrosubmedian carinae: absent or indistinct from surrounding granules (0); distinct (1).
48. Metasomal segment V, ventromedian carina: present (may be indistinct) (0); absent (1).

Telson

49. Telson vesicle, width relative to width of metasomal segment V: approximately equal (0); considerably narrower (1).
50. †Telson vesicle, dorsoproximal surface: very shallowly excavated along longitudinal half (0); deeply excavated (1).
51. Telson aculeus, shape: gently curved (0); abruptly bent (1).

Behavior

52. Diurnal retreat: hides under rocks (0); burrows under rocks (1); burrows in open ground (2); unknown (?); polymorphic (*).
53. Foraging strategy: sit-and-wait (0); errant (1); unknown (?).

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SHORT COMMUNICATION

A NEW BROMELIAD-DWELLING JUMPING SPIDER (ARANEAE, SALTICIDAE) FROM BRAZIL

Adalberto J. Santos: Pós-graduação em Zoologia, Universidade de São Paulo, Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brazil 1500, CEP 05503-900, São Paulo, SP, Brazil. E-mail: oxyopes@yahoo.com

Gustavo Q. Romero: Pós-graduação em Ecologia, Departamento de Zoologia, Universidade Estadual de Campinas (UNICAMP), CP. 6109, CEP 13083-970, Campinas, SP, Brazil

ABSTRACT. *Eustiromastix nativo* new species is described and illustrated based on specimens collected from bromeliads in northeastern and southeastern Brazil.

Keywords: Salticidae, *Eustiromastix*, Bromeliaceae, new species

The spider genus *Eustiromastix* Simon 1902 has 10 species distributed all over South America and the southern West Indies (Bauab & Soares 1978; Galiano 1979, 1981). Although relatively well known taxonomically, and widely distributed, nothing is known about the natural history of this group. Recently, during a study on bromeliad-inhabiting spiders in northeastern and southeastern Brazil, the second author collected several specimens of a new species. The males of this species present a characteristic apically curved cymbium, like several species of the genus *Eustiromastix*. The females resemble other species of *Eustiromastix* by the wide, flattened and folded copulatory ducts, which are as wide as the spermathecae.

All specimens examined in this study were collected only on bromeliads with which they apparently maintain a specific relationship (Romero & Vasconcellos-Neto pers. obs.). This observation is reinforced by the fact that at the type locality, this species was not collected outside bromeliads during an extensive spider diversity inventory (Santos 1999). In this paper, this new species is described and illustrated.

The female genitalia were removed and examined immersed in clove oil. All measurements are in mm. All the specimens are deposited in the collection of the Instituto Butantan, São Paulo, Brazil (IBSP).

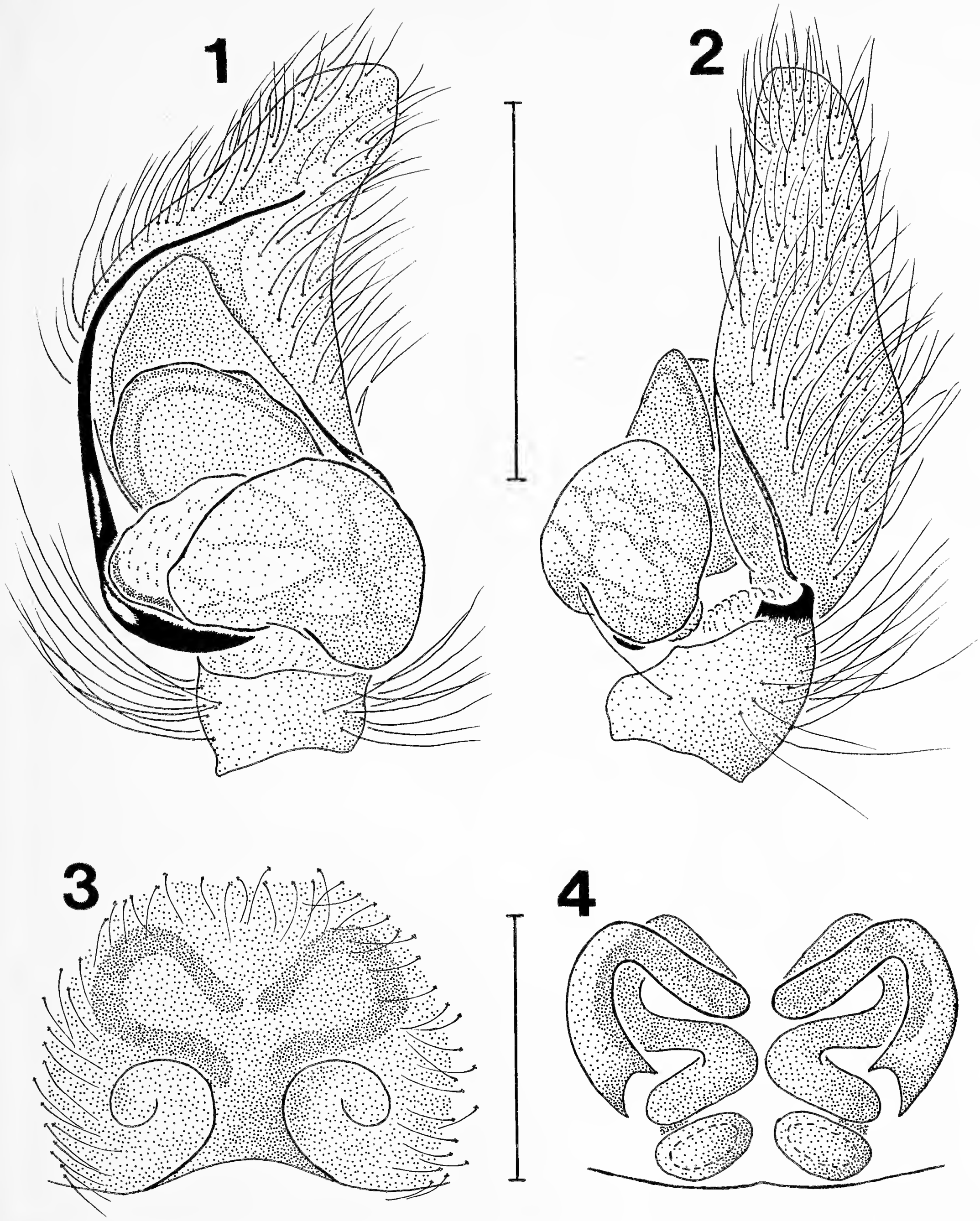
Eustiromastix nativo new species
Figs. 1–4

Type specimens.—Male holotype and female paratype from Brazil, *Espírito Santo,* São Mateus, Reserva Florestal da Companhia Vale do Rio Doce (19°06′S, 39°45′W), G. Q. Romero & J. Vasconcellos-Neto, 25–30 August 2002 (deposited in IBSP 34769 and IBSP 34770 respectively).

Etymology.—The specific epithet is a noun in apposition taken from the vegetation formation where the type specimens were collected (campos nativos).

Diagnosis.—*Eustiromastix nativo* males shares with *E. obscurus* (Peckham & Peckham 1893) and *E. macropalpus* Galiano 1979 an expanded, soft area in the tegulum, close to the embolus base. It can be distinguished from that species by that shape of the soft tegular area, which is large and spherical; and by a large hyaline retrolateral tegular process (Figs. 1–2). Female resembles those of *E. vincenti* (Peckham & Peckham 1893) by the lateral, spiral shaped copulatory openings (Galiano 1979, fig. 14), and differ by the copulatory openings closer to the epigastric sulcus (Fig. 3) and by the differently folded trajectory of the copulatory ducts (Fig. 4).

Description.—Male (holotype): Carapace black with a median triangular patch of white cuticular scales, close to posterior lateral eyes; another median spot of white scales close to anterior median eyes, and a lateral band of white scales from the posterior border to the area between posterior median and anterior lateral eyes. Clypeus black, chelicerae black and iridescent. Labium, endites and sternum dark brown, covered with white hairs. Endites with a small antero-lateral pointed cusp. Palps dark brown, with an apical cream spot on the venter of the femur. Venter of palpal patella cream. Coxae and trochanter I faint brown, yellow on other legs.



Figures 1–4.—*Eustiromastix nativo* new species. 1. Male palp, ventral view. 2. Lateral. 3. Female epigynum, ventral. 4. Dorsal. Scale bars: Figs. 1–2 = 1.0 mm, 3–4 = 0.5 mm.

Femur brown, patella and tibia cream with irregular brown spots. Metatarsus I red brown, orange on other legs. Tarsi yellow. Dorsum of abdomen with two anterior orange spots covered with white scales and with a median cream band separated from anterior spots and laterally delimited by dark spots. Sides and venter gray, with dark irregular spots. Venter with a red brown spot on posterior third. Spinnerets dark brown. Total length 6.4, carapace 3.4 long, 2.5 wide. Tibia I length 2.5, II 1.4, III 1.5, IV 1.7. Abdomen 3.1 long, 1.6 wide.

Female (paratype): Carapace dark brown, ocular area black and iridescent. Cephalic region with scattered white scales. Clypeus and chelicerae dark brown. Labium, endites and sternum red brown, labium darker and sternum with a large central brown spot. Palpus cream, with orange tarsus. Legs cream. Dorsum of abdomen cream, with a lateral dark band covering the posterior 80% of abdominal length. Sides and venter gray. Spinnerets gray, dark brown laterally. Total length 7.9, carapace 3.4 long, 2.6 wide. Tibia I length 1.6, II 1.6, III 1.6, IV 1.7. Abdomen 4.1 long, 2.4 wide.

Variation.—*Males (n = 3):* total length 6.1–8.6, carapace length 3.0–4.0, carapace width 2.5–3.1. *Females (n = 5):* total length 6.5–9.1, carapace length 3.4–3.7, carapace width 2.5–2.7.

Natural history.—All specimens examined were collected from two species of bromeliads (*Vriesea neoglutinosa* Mez. in São Mateus and *Aechmea blanchetiana* (Baker) L.B. Sm., in Trancoso) in two vegetation formations, respectively campos nativos and restingas. Both formations are similar, presenting a low, scattered vegetation over a sandy soil (Jesus 1988; Lacerda et al. 1984).

Distribution.—Northeastern and southeastern Brazil.

Additional material examined.—BRAZIL: *Bahia*: Trancoso, 7–12 October 2001, G.Q. Romero, 1 ♂, 1 ♀ (IBSP 34772); *Espírito Santo*: same data as types, 1 ♂, 3 ♀ (IBSP 34771).

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LITERATURE CITED

Bauab V., M.J. & B.A.M. Soares. 1978. Contribuição ao estudo dos Salticidae do Brasil. III. (Araneae). Revista Brasileira de Biologia 38:359–361.

Galiano, M.E. 1979. Revision del genero *Eustiromastix* Simon, 1902 (Araneae, Salticidae). Journal of Arachnology 7:169–186.

Galiano, M.E. 1981. Three new species of Salticidae (Araneae). Bulletin of the American Museum of Natural History 170:216–218.

Jesus, R.M. 1988. A reserva florestal da CVRD. Pp. 59–112. *In* Anais do VI Congresso Florestal Estadual, vol. 1.

Lacerda, L.D., D.S.D. Araujo, R. Cerqueira & B. Turcq. 1984. Restingas: origem, estrutura e processos. Centro Editorial da Universidade Federal Fluminense, Niterói.

Santos, A.J. 1999. Diversidade e composição em espécies de aranhas da Reserva Florestal da Companhia Vale do Rio Doce (Linhares, ES). Masters Thesis, Universidade Estadual de Campinas, Campinas.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Illustrations.—Original illustrations should not be sent until the article is accepted for publication. Address all questions concerning illustrations to the Editor of the *Journal of Arachnology*: **Dan Mott, *Editor-In-Chief*; Lincoln Land Community College, 5250 Shepherd Road, PO Box 19256, Springfield, IL 62794-9256 USA** [*Telephone* (217) 786-2384; *FAX:* (217) 786-2251; *E-mail:* dan.mott@llcc.cc.il.us] All art work must be camera-ready – i.e., mounted and labeled – for reproduction. Figures should be arranged so that they fit (vertically and horizontally) the printed journal page, either one column or two columns, with a minimum of wasted space. When reductions are to be made by the printer, pay particular attention to width of lines and size of lettering in line drawings. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. Indicate whether the illustration should be one column or two columns in width. The overall dimensions should be no more than 11 inches (28 cm) x 14 inches (36 cm). Larger drawings present greater difficulty in shipping and greater risks of damage for which the *Journal of Arachnology* assumes no responsibility. In manuscripts for review, photocopies should be included, and should be reduced to the exact measurements that the author wants to appear in the final publication. Make notations in the text margins to indicate the preferred position of illustrations in the printed text. Color plates can be printed, but the author must assume the full cost, currently about $600 per color plate.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1-4.— *A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence; title page, abstract, text, footnotes, tables with legends, figure legends, figures.

Page charges, proofs and reprints.—There are no page charges, but the author will be charged for changes made in the proof pages. Reprints are available only from the Allen Press and should be ordered when the author receives the proof pages. Allen Press will not accept reprint orders after the paper is published. The *Journal of Arachnology* also is published by BioOne. Therefore, if your institution is a member of BioOne, copies of each article can be downloaded as PDF files.

SHORT COMMUNICATIONS

Short Communications are usually limited in length to three journal pages, including tables and figures. They will be printed in a smaller (10 point) typeface. The format for these is less constrained than for feature articles: the text must still have a logical flow, but formal headings are omitted and other deviations from standard article format can be permitted when warranted by the material being covered.

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