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Stingless bee interception is not affected by variations in spider silk decoration

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Abstract. The functional significance of web decorations in orb-web spiders has been an area of intense study for well over a hundred years. Two main hypotheses, (prey attraction and predator avoidance) have had intermittent support and criticism. By varying the decoration pattern, spiders minimize the potential predation costs of constructing a highly visible signal and deter potential prey such as bees from associating decorations with danger. The prey attraction hypothesis implies that as the signal changes, so should the response of the intercepting insects. In this study, I tested the response of bees to varying decoration patterns. I show that stingless bees (*Trigona carbonaria*) respond to the silk decorations of *Argiope keyserlingi* Karsch 1878 in similar ways irrespective of the pattern of decorations. I also demonstrate that the likelihood of prey hitting the capture area is greater than that of hitting the hub area in decorated webs. Since stingless bees respond similarly to different levels of signal strength, I conclude that variation in decorations does not affect prey interception.

Keywords: *Argiope keyserlingi*, *Trigona carbonaria*, decorations, stabilimenta, predator-prey interactions

Orb-web spiders of up to 78 species from 22 genera adorn their webs with extra silk structures called stabilimenta or silk decorations (Herberstein et al. 2000). The functional significance of these structures has been an area of prolonged interest, and there are two main explanations for the evolution and continued presence of silk decorations. The prey attraction hypothesis suggests that since silk decorations reflect light in the ultraviolet part of the light spectrum, in a manner similar to floral nectar guides, flying insects are attracted to the web (Craig & Bernard 1990). The predator avoidance hypothesis suggests that silk decorations are visible to potential predators such as birds and wasps and therefore deter predators either by camouflage or by web protection (Blackledge & Wenzel 2001; Eberhard 2008). Despite a number of studies investigating the function of silk decorations, there is still substantial controversy over their function (Bruce 2006).

While decorations are seen in many species, spiders of the genus *Argiope* occur all over the world and many species in this genus have been studied extensively (Herberstein et al. 2000). These spiders build decorations in the form of bands radiating from the center of the web toward the periphery. These bands vary in length and pattern within individuals as well as across individuals. For example, in the Australian species *Argiope keyserlingi* Karsch 1878, a maximum of four bands is seen, though five or six bands are known to occur rarely (Rao et al. 2007; pers. observ.). Adult *A. keyserlingi* shows the following patterns of decorations: no bands, 1, 2, 3, and 4 bands, while juvenile *Argiope* generally build discoid decorations (Rao et al. 2007). Most studies have focused on variation in decoration between individuals by comparing decorating and non-decorating spiders within the same population; e.g., the Australasian species *Argiope appensa* Walckenaer 1842 (Hauber 1998; Herberstein 2000). While frequency of decoration patterns has been recorded under field conditions (Hauber 1998; Craig et al. 2001; Rao et al. 2007), laboratory tests generally involve a binary choice test (the Neotropical species *Argiope argentata* (Fabricius 1775) [Craig & Bernard 1990], the Southeast Asian *Argiope versicolor* (Doleschall 1859) [Seah & Li 2002], *A. keyserlingi* [Bruce & Herberstein 2005]). Studies that take into account variation in decorations generally quantify decoration presence, area or length (the Neotropical species *Argiope aurantia* Lucas 1833, *Argiope trifasciata* (Forsskål 1775) [Blackledge 1998], *A. argentata* [Craig et al. 2001], *A. versicolor* [Seah & Li 2002; but see Seah & Li 2001]) and ignore the information inherent in the pattern of the decoration. Furthermore, the majority of studies on the function of silk decorations have been from a visual perspective, with the underlying assumption that the decorations are a signal to visually orienting insects and birds as the primary receivers (Craig & Bernard 1990; Bruce et al. 2005; but see Walter et al. 2008).

Silk decorations are highly visible to insects such as bees. Not only do they reflect light in the UV part of the spectrum (Craig & Bernard 1990), they also form a strong contrast against the mostly dull background (Bruce et al. 2005; Rao et al. 2009), which enhances their visibility. Insects such as bees possess a trichromatic photoreceptor system that allows them to see color. Bees have light receptors sensitive in the UV (300–400 nm), blue (400–500 nm) and green (500–600 nm) spectra of light. Furthermore, the sensitivity of this UV-receptor is significantly higher than the green or blue receptor (Briscoe & Chittka 2001). Bees also have innate preferences for certain colors and patterns, and these preferences have coevolved with flower color and patterns (Biesmeijer et al. 2005). Stingless bees prefer dark centers, radiating stripes and spots (Biesmeijer et al. 2005) and honeybees show an innate preference for the kind of radiating patterns normally seen in flowers (Lehrer et al. 1995). Therefore a spider that displays patterns similar to those found among flowers would benefit by exploiting the sensory biases of its insect prey. Tso et al. (2002) showed that a brightly colored form of the giant wood spider *Nephila maculata* (Fabricus 1793) received more prey that of a melanic form (Tso et al. 2002). Since the spiders and decorated webs are visible and contain flower-like characteristics, it is possible that insects such as bees intercept the web in error.

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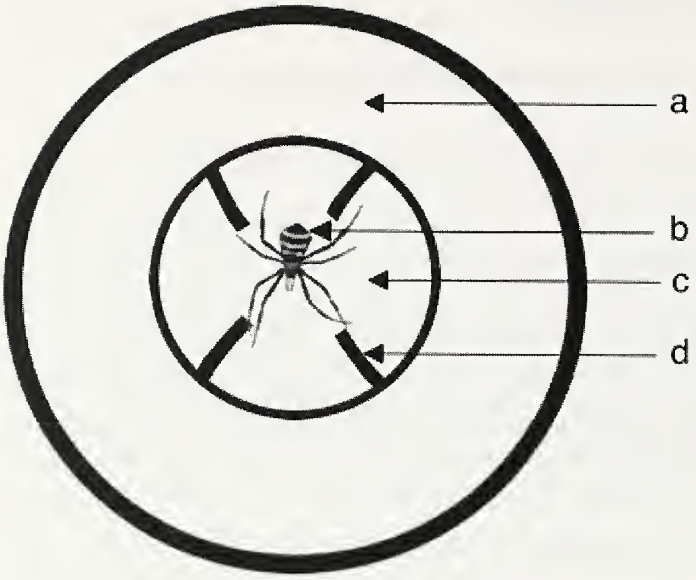

Figure 1.—Schematic representation of the web of *Argiope keyserlingi*. a: Capture area, b: Hub area, c: Position of spider, d: Decorations.

Furthermore, bees that forage 'impulsively' (i.e., make inaccurate decisions quickly) have been shown to benefit in the long run (Burns 2005), and trade-off foraging speed for accuracy (Chittka et al. 2003).

Variation in decoration pattern within a species may be a result of the trade-off between prey attraction and protection from predators (*A. trifasciata*: Blackledge & Wenzel 2001; *A. keyserlingi*: Bruce et al. 2001). There are two main advantages to varying the pattern of decorations: 1) fast learning potential prey, such as bees, are more likely to avoid consistently decorated webs (Craig 1994) and 2) potential predators, such as araneophagic jumping spiders and preying mantids, are prevented from associating decorations with spider prey (*A. keyserlingi*: Bruce et al. 2001; *A. versicolor*: Seah and Li 2001). However, variation in decoration patterns could also be due to a scarcity in silk reserves (*Argiope aetheroides* Yin et al. 1989 [Tso 2004]; *Argiope bruennechi* (Scopoli 1772); *Argiope sector* (Forsskål 1776); *A. keyserlingi* [Walter et al. 2008]) or that decorating behavior has a heritable component (*A. argentata* [Craig et al. 2001]). Most *Argiope* spiders show variation in decoration building, both in frequency of decorations as well as in the patterns of decorations, with the exception of *Argiope picta* L. Koch 1871, which decorates its webs obligately (Bruce & Herberstein 2005). The prey attraction hypothesis predicts an increase in insect interception rates due to the presence of decorations. If the decorations function as a deceptive signal to flower-seeking insects, then the presence of a stronger signal should elicit a greater response. This prediction is supported by the finding that bees trained to certain reward-bearing signals show a receiver bias for exaggerated signals (Naug & Arathi 2007). Furthermore, if the decorations attract insects, then there should be more interception in the hub area than the capture area, since decorations in *Argiope* rarely extend beyond the hub (Eberhard 1990).

In this study I tested the response of potential prey to variation in decoration patterns. Specifically, I asked if stingless bees respond differentially to this visual signal, which varied in intensity and pattern. I tested if the location of insect interception within the web (i.e., between hub and capture area) differs when insects are presented with a low signal versus a high signal.

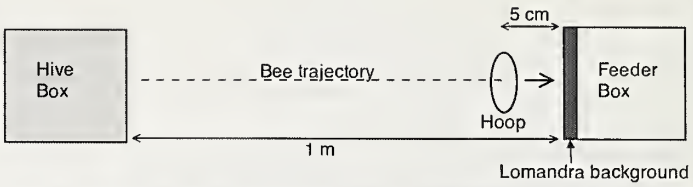

Figure 2.—Schematic representation of the experimental setup.

METHODS

Study species.—*Argiope keyserlingi*, also known as the St. Andrew's Cross spider, is an orb-web weaver distributed along the eastern coast of Australia (Levi 1983; Platnick 2009) in a wide variety of habitats, ranging from rainforest margins to urban gardens. It is locally abundant and typically found on long-leaved bushes such as *Lomandra longifolia* and *Pandanus* sp. (Rao et al. 2007). Mature spiders build silk decorations in the form of zigzag deposits of silk (hereafter referred to as 'bands') stretching outward from the center of the web (Fig. 1), while circular silk decorations are typically found only in juveniles' webs. A maximum of four diagonal bands is seen in this species (Rao et al. 2007).

Trigona carbonaria Smith 1863 (Hymenoptera: Apidae) are stingless bees found all along the eastern coast of Australia and occur in the same habitat as *A. keyserlingi*. Typically, these insects nest in hollow logs (Michener 1961). The bees are quite small (body length of worker bees: 3.9–4.3 mm), and average colonies contain a single queen and hundreds of workers (Dollin et al. 1997). Stingless bees of the genus *Trigona* are known to be common prey of *A. argentata* (Craig et al. 2001).

Experiment set up.—A commercially available hive box of *T. carbonaria* (Russell and Janine Zabel Pty. Ltd.) was set up on a table in a semi-enclosed greenhouse located on the campus of Macquarie University in Sydney, Australia. The greenhouse had mesh walls and a transparent plastic roof (VP Structures Pty. Ltd., Australia). Bees were trained to approach a feeder with sugar water (sugar:water = 1:3) that was placed 1 m away from the hive (Fig. 2).

Subsequently, I trained the bees to fly through an empty hoop (28 cm diam.) en route to the feeder. The empty hoop was considered to be the control and a measure of bee activity or hive activity, since the number of bees that forage daily is known to depend on environmental conditions (Heard & Hendrikz 1993). For the experiments, I then swapped the empty hoop with hoops containing female *A. keyserlingi* webs. Spider webs were affixed to hoops by pressing one side of the hoop (with layer of glue) onto a web, and cutting away the extraneous parts. Approaching bees always encountered the web against a background of *Lomandra* photographs, which have similar color properties to those of actual plants (Hoese et al. 2006). Using *Lomandra* photographs rather than real plants as background offers the advantage of having the background as a constant for all experiments, thereby eliminating any effect of plant variation on bee behavior.

There were four treatments based on the signal strength: 1) webs with no decorations (0-band; the weakest signal), 2) webs

Table 1.—Mean (± SD, n = 15 trails) number of bee interceptions in each of four decoration treatments.

Number of decoration bands	Bee intereeptions (mean ± SD)
0	6.8 ± 2.01
1	7.2 ± 3.49
2	8.7 ± 2.96
4	7.5 ± 2.50

with one band (1-band), 3) webs with two bands (2-band) and 4) webs with four bands (4-band; the strongest signal). These treatments were chosen to reflect the most common decoration patterns found in the field (Rao et al. 2007). All treatments included spiders of similar body lengths on their webs. Approaching bees were monitored during fifteen 1-min trials for each treatment, and all bees intercepting the web were counted. Bees that did not intercept the web were not counted. The order of the treatments and control was randomized, and there was a delay of at least 10 min between two consecutive treatments. In all treatments, I ensured that the stingless bees flew in a northerly direction and were on their foraging flight, since previous experiments had revealed that bees were most responsive in this context (Rao et al. 2008).

Since the data were normally distributed, I conducted an analysis of variance on the number of bees that hit the web (termed as interceptions and weighted by bee activity), using the signal strength treatments (i.e., the number of decoration bands) as independent variables. I tested for homogeniety of variance using Bartlett's test and normality with the Kolmogorov-Smirnov test. For two of the treatments (webs with 2-bands - low signal and with 4-bands - high signal), I noted the location of interception within the web by recording whether the bees intercepted the hub or the capture area. These two treatments were chosen because the 2-band decoration is one of the most common patterns seen in field conditions, and the 4-band pattern is the maximum number of bands usually seen in this species (Rao et al. 2007). I compared the interception rates between the hub and the capture area using a Mann-Whitney U test.

RESULTS

Signal strength.—The number of decoration bands (0, 1, 2 or 4) did not significantly affect the number of bees intercepted (one way ANOVA, $F_{3,59} = 1.07$, $P = 0.37$; Table 1, Fig. 3).

Interception location.—Bees intercepted the capture area at significantly higher rates than the hub (4-bands; Mann-Whitney U test, $U = 12.5$, $n = 15$, $P < 0.0001$; 2-bands, Mann-Whitney U test, $U = 45$, $n = 15$, $P < 0.01$; Table 2, Fig. 4). In the hub area, more bees intercepted the web in the 2-band treatment than in the 4-band treatment (Mann-Whitney U test, $U = 60.5$, $n = 15$, $P = 0.03$; Fig. 4). However, in the capture area there was no difference in the number of bees intercepting the web across the 4-band or 2-band treatments (Mann-Whitney U test, $U = 108.5$, $n = 15$, $P = 0.88$).

DISCUSSION

Bee interception on spider webs did not change with varying signal strengths, ranging from the 4-band to the 0-band decoration pattern. More bees intercepted the capture area than the hub area in both low signal and high signal treatments.

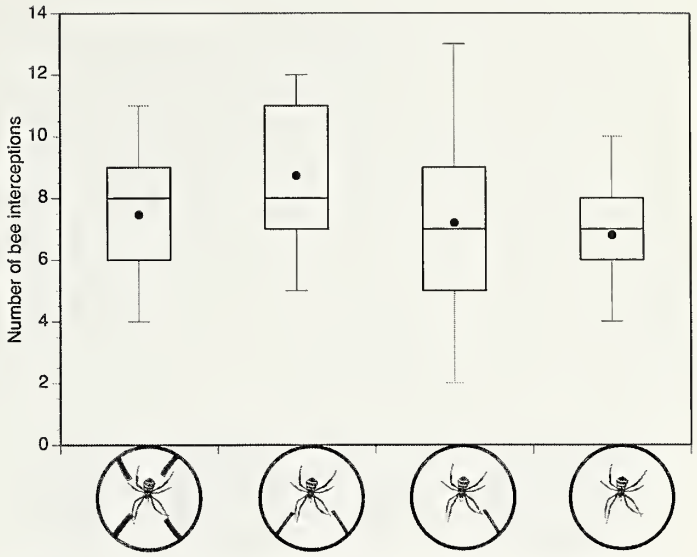

Figure 3.—There was no significant difference in the number of bees intercepting webs with 0, 1, 2, or 4 bands of silk decoration. The figure shows box plots with median (center of box), 25 and 75 percentile (edges of box) and ranges (whiskers); dots in the center represent the means.

The prey attraction hypothesis predicts an increase in the rate of insect interceptions with the presence of decorations, and I therefore expected a proportional increase in interception with an increase in the strength of the signal. In this study, I showed that stingless bees do not discriminate between the different decoration patterns and intercept the webs at similar rates. These results are not in congruence with other studies that have demonstrated a prey-attraction function to silk decorations (*A. argentata*: Craig & Bernard 1990; *A. versicolor*: Li 2005; *Argiope aenula* (Walckenaer 1841): Cheng & Tso 2007). This study adds further support to an earlier study using the same system demonstrating that stingless bees respond more strongly to spiders than to silk decorations (Rao et al. 2008). This implies that *A. keyserlingi* varies its decoration in order to decrease the possibility of learning in bees (*sensu* Craig [1994]). With respect to location of interceptions, more bees intercepted the capture area than the hub with both low and high signal treatments, suggesting that decorations do not attract bees to the hub. However, insect attraction by decorations could be a function of the distance from which the insect sees the web, and the decorations may draw bees in as they go about foraging. Once they get close enough, bees may respond by changing their trajectory towards the periphery. There is some support for this hypothesis by the result that more bees intercepted the hub in the low signal treatment than the high signal treatment

Table 2.—Differences in the mean number of stingless bee interception between different locations (hub or capture area) in 4-band and 2-band treatments (Mann-Whitney U test, n = 15).

Decoration bands	Hub Area (mean ± SD)	Capture Area (mean ± SD)	U	P
4-bands	1.8 ± 1.5	5.6 ± 2.1	12.5	< 0.05
2-bands	3.2 ± 1.5	5.5 ± 2.3	45.0	< 0.05

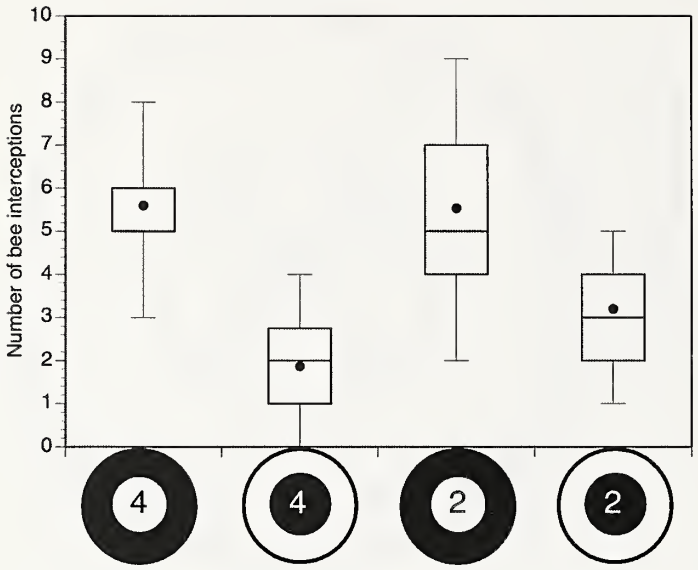

Figure 4.—Bees were more likely to intercept the hub than the capture area when corrected for area. Y-axis shows the number of bees that intercepted the web per hub area. Figure shows box plots with median (center of box), 25 and 75 percentile (edges of box) and ranges (whiskers); dots in the center represent the means. For X-axis, inner circle is darkened to depict the hub, outer circle is darkened to depict capture area, and number in center of the circles refers to number of decoration bands.

(Fig. 3), but there was no difference in the number of bees that intercepted the capture area in both treatments. Further experiments should reveal the precise effect of decorations on the trajectories of bee flight.

Most studies that address the effect of decorations on prey generally compare webs with and without decorations by reporting the area or length of decorations, providing little information about the pattern of the decoration. However, the pattern of decorations influences signal strength in two ways. First, there can be an increase in amount of silk used in building decorations without changing the pattern (e.g., by making the bands longer rather than increasing the number of bands). Second, there can be an increase in signal strength by changing the pattern of decoration when more bands are added. In this study, the four treatments represented both a change in the amount of silk incorporated into the decorations as well as a change in the pattern.

Since stingless bees do not respond to variation in decoration pattern and overall signal strength, there may be other explanations for why spiders vary the size and number of decorating bands (Bruce 2006). For example, the decorating frequency displayed by an individual spider is inherited from both parents (Craig et al. 2001). It has been shown to depend on ambient light conditions, with spiders in dim light more likely to build decorations (*A. versicolor*: Seah & Li 2002; *A. keyserlingi*: Herberstein & Fleisch 2003), and silk reserves, with a threshold of silk in the aciniform glands beyond which the spider is less likely to build decorations (Tso 2004).

There are limits to drawing general conclusions from this study. I used a single species of spider and a single species of prey. The patterns of interception seen here may be species-specific, and decorating spiders may be targeting other prey species entirely. Stingless bees have previously been used in tests of decoration function with mixed results (Craig et al. 2001, Bruce & Herberstein 2005). *Trigona carbonaria* in particular did not respond selectively to different decorations in Y-maze experiments (Bruce & Herberstein 2005), and in another study, *T. carbonaria* responded more explicitly to the presence of the spider than to decorations (Rao et al. 2008). This suggests that *T. carbonaria* may not be susceptible to the visual signal created by web decorations. Further experiments with other model prey species may yield a better understanding of the influence of decoration variation on potential receivers.

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Aterigena, a new genus of funnel-web spider, shedding some light on the *Tegenaria-Malthonica* problem (Araneae: Agelenidae)

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Abstract. *Aterigena* n. gen. is erected for four Palearctic species of funnel-web spiders previously placed in *Tegenaria* Latreille 1804 or *Malthonica* Simon 1898 (Agelenidae: Tegenariini) and *A. aspromontensis* n. sp., an Italian species described here. The following new combinations are proposed: *Aterigena aculeata* (Wang 1992), *A. ligurica* (Simon 1916), n. comb. (from *Tegenaria*), as well as *A. aliquoi* (Brignoli 1971) and *A. soriculata* (Simon 1873), n. comb. (from *Malthonica*). The latter two species were originally described in *Tegenaria*. The new genus is diagnosed by the unique combination of several morphological character states (e.g., notched trochanters III and IV, lateral spines on patellae, shape of vulvae). The monophyly of the new genus is also supported by a molecular analysis based on CO1 sequences of several taxa. Keys are provided for the identification of the recognized genera of Tegenariini and the species of *Aterigena* n. gen. Several species of *Pseudotegenaria* Caporiacco 1934, originally described in *Tegenaria*, are morphologieally close to *Tegenaria tridentina* L. Koch 1872, a species that is grouped in the cladistic analysis using CO1 in the monophyletic taxon "*Tegenaria* clade 1". The species are therefore transferred back to *Tegenaria* as *Tegenaria animata* Kratochvíl & Miller 1940 stat. rev., *T. bayeri* Kratochvíl 1934 stat. rev., *T. bosnica* Kratochvíl & Miller 1940 stat. rev. and *T. decolorata* Kratochvíl & Miller 1940 stat. rev. *Aterigena* n. gen. has an interesting geographical distribution: it is widely disjunct in the Palearctic. Four species occur in the Mediterranean and one in China, respectively. *A. ligurica* is relatively widely distributed in mainland Italy and adjacent Southern France with a single specimen known each from Spain and Egypt (Alexandria), respectively. The latter may be the result of an accidental introduction. The other three European species are endemic to Sicily, Corsica (perhaps also Sardinia) and Calabria, respectively.

Keywords: Taxonomy, new taxa, biogeography, Palearctic, disjunct distribution, endemism

Some representatives of the araneomorph funnel-web spiders (Agelenidae) are well known even to the general public: i.e., the very large and long-legged European house spiders (*Tegenaria atrica* C.L. Koch 1843, *T. duellica* Simon 1875 and *T. domestica* (Clerck 1757)) or the notorious hobo spider (*T. agrestis* (Walckenaer 1802)). The last has been introduced into North America where it is blamed for biting humans and causing necrotic wounds (Akre & Myhre 1991; Baird & Stoltz 2002; Binford 2001; Vest 1987; Vetter et al. 2003; Vetter & Swanson 2004). Despite this publicity, the taxonomic and phylogenetic relationships within the Agelenidae are still poorly understood (e.g., Zhang et al. 2006).

Currently the Agelenidae consists of 42 genera and 514 described species (Platnick 2010). There is an ongoing discussion about the definition of the Agelenidae and, in particular, whether the subfamily Coelotinae belongs to the Agelenidae or the Amaurobiidae (Lehtinen 1967; Wunderlich 1986; Griswold et al. 1999; Bi et al. 2005; Spagna & Gillespie 2008) and whether the Australian genera currently affiliated with Agelenidae are phylogenetically closely related to it (Spagna & Gillespie 2008; see Endnote). Within the subfamily Ageleninae, Lehtinen (1967) recognized four tribes: Agelenopsini (Nearctic and Neotropical), Agelenini (Holarctic and Afrotropical), Textricini and Tegenariini (mainly Palearctic). The European tribes Agelenini, Textricini and Tegenariini, of relevance here, can be recognized with the table published by Lehtinen (1967:344, table 23; but also see Table 2).

According to Lehtinen (1967) the Tegenariini comprises the following nominal genera: *Hadites* Keyserling 1862, *Histopona* Thorell 1869, *Malthonica* Simon 1898, *Pseudotegenaria* Caporiacco 1934 and *Tegenaria* Laterille 1804. Most species have been associated with *Tegenaria* and *Malthonica*. The original definitions of the two genera are vague. In its present composition, *Tegenaria* is probably not monophyletic (e.g., Levy 1996). The transfer of many *Tegenaria* species to *Malthonica* by Guseinov et al. (2005) did not render the genera more natural, but rather added more taxonomic confusion: apparently closely related species based on morphological and molecular characters now belong to two different genera (e.g., *Tegenaria parietina* (Fourcroy 1785) and *Malthonica ferruginea* (Panzer 1804), or *Tegenaria henroti* Dresco 1956 and *Malthonica eleonorae* (Brignoli 1974; Bolzern et al. 2008). Guseinov et al. (2005) erected a new genus, *Azerithonica*, which seems to be closely related to *Tegenaria* and *Malthonica*, also belonging to the tribe Tegenariini. Barrientos & Cardoso (2007) redefined *Malthonica*, but this was not followed by Deltshev (2008) and Seyyar et al. (2008).

Dankittipakul & Zhang (2008) erected the genus *Acutipetala*, which they compared to *Agelena* and *Tegenaria*, but did not assign to a particular tribe. The strongly procurved eye-rows (in frontal and dorsal view) and the spination of the patellae in combination with the devided colulus, mentioned in their description, suggest that it is a member of the Agelenini.

The aim of the present work is to improve the taxonomy of *Tegenaria*, *Malthonica* and relatives.

METHODS

The specimens examined in this work are preserved in 75% ethanol at the Naturhistorisches Museum Basel (NMB), the Muséum d'Histoire Naturelle Genève (MHNG), the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt a. M.

(SMF), the Naturhistorisches Museum Wien (NHMW), the Muséum National d'Histoire Naturelle Paris (MNHN), the Museo Civico di Storia Naturale Verona, (MCSN), the Brignoli Collection housed in the Museo Civico di Storia Naturale Verona (PMBC), the Museo Civico di Scienze Naturli "E. Caffi" Bergamo (MSNB) and the private collections of Z. Zhang, China (ZZ) and K. van Keer, Belgium (KK).

For the morphological examination and the preparation of drawings a Leica stereomicroscope MZ12 (up to 110 × magnification) and MZ Apo with drawing tube were used. Most measurements were taken from digital pictures made with a Leica DFC320 camera and calculated with the program ImageJ 1.38 × (http://rsb.info.nih.gov/ij/). Photographs were stacked using the program CombineZM (http://hadleyweb.pwp.blueyonder.co.uk/CZM/News.htm) and processed with Adobe Photoshop and Illustrator. For clearing the vulva, the removed epigynum was placed into clove oil for several minutes. The descriptions of the bulb are given from a ventral view. The spines on the male palp are not illustrated, as they are considered of minor taxonomic significance. Leg measurements were taken from the dorsal side. All measurements are given in millimeters. The color description is based on ethanol-preserved specimens. The nomenclature of morphological structures follows Jocqué & Dippenaar-Schoeman (2006) and Bolzern et al. (2008). The following abbreviations are used: AER = anterior eye row; ALE = anterior lateral eyes; AME = anterior median eyes; ALS = anterior lateral spinnerets; PMS = posterior median spinnerets; PER = posterior eye row; PLA = posterior lateral eyes; PME = posterior median eyes; PLS = posterior lateral spinnerets; RTA = retrolateral tibial apophysis (used here as the sum of all structures in retrolateral position of the tibia of the male pedipalp).

For the DNA extraction, one leg was removed from freshly sampled specimens and stored in pure ethanol. The legs were then placed into a vacuum centrifuge for 30 min at 40° C to remove the ethanol. Then the legs were processed according to the protocol for the purification of total DNA from animal tissues (Spin-Column Protocol) of the DNeasy Blood & Tissue Kit (Qiagen). The DNA concentration of the resulting solution was measured with NanoDrop equipment. A 471-bp sequence of the cytochrome oxidase 1 gene (CO1) was amplified using primers C1-J-1718 and C1-N-2191 (Simon et al. 1994). For the PCR illustra PuReTaq Ready-To-Go PCR Beads (GE Healthcare) were used. The following thermocycling conditions were applied: initial denaturation step of 93° C for 3 min, followed by 35 cycles of 95° C for 30 s, an annealing temperature of 55° C for 30 s and an extension temperature of 72° C for 45 s. This was then followed by an additional extension of 72° C for 7 min. To eliminate incorporated dNTP and primers, the PCR products were treated with ExoSAP-IT® (GE-Healthcare). Then the fragments were sequenced in both directions using ABI PRISM® BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems). Sequences were then analysed using an ABI Prism 3100 Genetic Analyzer and edited with the software Sequence Navigator (Applied Biosystems).

The complementary sequences (5′ and 3′ directions) of each specimen were aligned using ClustalW2 (Larkin et al. 2007) and checked manually. All processed sequences and additional sequences from GenBank (Table 5) were aligned using ClustalW2. The aligned sequences were then translated into amino acids to check for any inappropriately placed stop codons and the triplet positions.

Bayesian analysis was applied using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The software jModelTest 0.1.1 (Psoda 2008; Guindon & Gascuel 2003) was used for the selection of best-fit models of nucleotide substitution for the present alignment. Since the underlying sequences are coding for a protein, the analyses were performed with respect to the codon position, allowing MrBayes to use different substitution models with independent rates for each partition (one partition for each codon position). The models statistically chosen under the Akaike information criterion, with correction for small samples (AICc), were K80+G (1^{st}), JC+I (2^{nd}) and HKY+G (3^{rd}). Two parallel and independent analyses, each with four chains (three heated, one cold MCMC chains) were run for 5 million generations, sampling trees every 1000 generations. At the end of the analysis, the first quarter of the collected trees was discarded as "burnin". Of the remaining trees, a consensus tree was calculated (50% majority rule).

Maximum parsimony analysis was performed using PAUP* (Swofford 2003). Transversions were weighted twice transitions. Additionally, the 1^{st}, 2^{nd} and 3^{rd} positions of the codons were weighted 3:6:1, an approximation of the inverse observed relative frequency of substitution. Full heuristic search was performed with random addition of sequences (1000 replications). The branch-swapping algorithm tree-bisection-reconnection (TBR) on best trees was applied to escape local optima. Bootstrap support values were calculated in PAUP* based on 1000 replicate searches, each with 1000 replications of random taxon addition. The analyses were carried out on the freely available Bioportal (www.bioportal.uio.no). Trees were drawn using FigTree v1.2.2 (Freeware from Andrew Rambaut, Institute of Evolutionary Biology, University of Edinburgh; available at: http://tree.bio.ed.ac.uk/software/figtree/) and edited in Adobe Illustrator.

RESULTS

Phylogeny.—The Bayesian analysis reached convergence before 3,000,000 generations, after which the deviation of split frequencies remained below 0.01. The tree presented in Fig. 57 was calculated using the last 7,502 trees (5,001 were sampled from each run and the first 25% discarded as "burnin"). The tree was rooted with the *Amaurobius* spp. clade. The topology and the posterior probability values suggest that *Aterigena* n. gen. is the sister clade of *Malthonica+Histopona*. In this tree 1) the only possibility for a monophyletic Agelenidae is to include the subfamily Coelotinae; 2) the relationships between most genera and the tribes *Tegenariini*, *Agelenini*, *Agelenopsini* are not completely resolved; and 3) the genera *Agelena* and *Textrix* are not monophyletic.

The Maximum Parsimony Analysis resulted in the two shortest trees. In the strict consensus tree, most clades at genus rank were identical to those from the Bayesian analysis (indicated in Fig. 57 with a +). However, the relationship between the genera and/or the subgenera are unresolved (Fig. 57). The bootstrap values are generally very low.

Relative to the support of the other genera, that for *Aterigena* n. gen. is relatively high (83%).

TAXONOMY

Family Agelenidae C.L. Koch 1837
Tribe Tegenariini Lehtinen 1967

The tribe Tegenariini comprises the genera *Azerithonica* Guseinov et al. 2005, *Hadites*, *Histopona* and the taxonomically problematic *Malthonica-Tegenaria* complex, including *Pseudotegenaria*. Guseinov et al. (2005) transferred several species from *Tegenaria* to *Malthonica* using characters of doubtful phylogenetic significance (Jäger 2006, see also Bolzern et al. 2008; Bolzern et al. 2009). These transfers are not followed here: instead we adopt the narrow definition of *Malthonica* by Barrientos & Cardoso (2007), which includes only the type species, *Malthonica lusitanica* Simon 1898, along with *M. oceanica* Barrientos & Cardoso 2007.

Pseudotegenaria was established by Caporiacco (1934). His description is not diagnostic. *Pseudotegenaria* allegedly differs from *Tegenaria* in the anterior eye row, which is strongly recurved, and the posterior row, which is weakly recurved (Caporiacco 1934:140). This character is variable in *Tegenaria* sensu lato. In the original description, the drawing of the vulva of the type species, *Pseudotegenaria parva* Caporiacco 1934 (only female known), is uninformative. Therefore, we follow Brignoli (1971a:60, 61), rather than Lehtinen (1967), who added four species to *Pseudotegenaria*. Apart from *P. parva*, for which no material was available for examination and whose original description is not diagnostic, all species currently included in *Pseudotegenaria* show a striking morphological similarity to *Tegenaria annulata* Kulczyński 1913 and *T. tridentina* L. Koch 1872 (Brignoli 1971a; Kratochvíl & Miller 1940). Here we transfer these species from *Pseudotegenaria* back to *Tegenaria*: *T. animata* Kratochvíl & Miller 1940, stat. rev., *T. bayeri* Kratochvíl 1934, stat. rev., *T. bosnica* Kratochvíl & Miller 1940, stat. rev. and *T. decolorata* Kratochvíl & Miller 1940, stat. rev.

Based on the examination of extensive material a monophyletic group of species, described here as a new genus, is recognized within *Tegenaria* s.l., which is supported by morphological and molecular characters (Fig. 57, Table 4; also see following key). The remainder of *Tegenaria* species studied (mostly European species) form two monophyletic clades (*Tegenaria* Clade 1 and *Tegenaria* Clade 2: Fig. 57). Apart from *Azerithonica*, for which no specimens were available for examination, the genera of Tegenariini, can be recognized by following key:

KEY TO THE GENERA OF TEGENARIINI

1 Trochanters III and IV notched 2
All trochanters straight or only slightly curved 5
2 Dorsal and lateral spines present on patellae III and IV, 1–2 ventral spines present on tarsus IV . . . . . *Aterigena* n. gen.
Only dorsal spines present on all patellae, tarsus IV ventrally lacking spine 3
3 Colulus reduced, only hairs present, patellar apophysis on male palps absent, median apophysis present 4
Colulus developed as two separated plates, patellar apophysis on male palps sometimes present, median apophysis absent . . . *Histopona*
4 Eyes fully developed, tarsi with less than 7 dorsal trichobothria . . . . . *Malthonica*
Eyes very small or lacking, tarsi with 7 or more dorsal trichobothria . . . . . *Hadites*
5 Conductor lamelliform, terminal end often bifid, distal apex of conductor longer than its width, median apophysis strongly protruding, RTA mostly with three branches, vulva forming only convoluted duct or with more or less evenly sclerotized, globular receptacula . . . . . *Tegenaria*-Clade 1
Conductor massive, terminal end of conductor simple or ending in several points, distal apex of conductor smaller than its width (exceptions possible), RTA mostly with two branches, vulva irregularly sclerotized enclosing convoluted ducts, and/or with diverticulae attached to the copulatory duct . . . . . *Tegenaria*-Clade 2

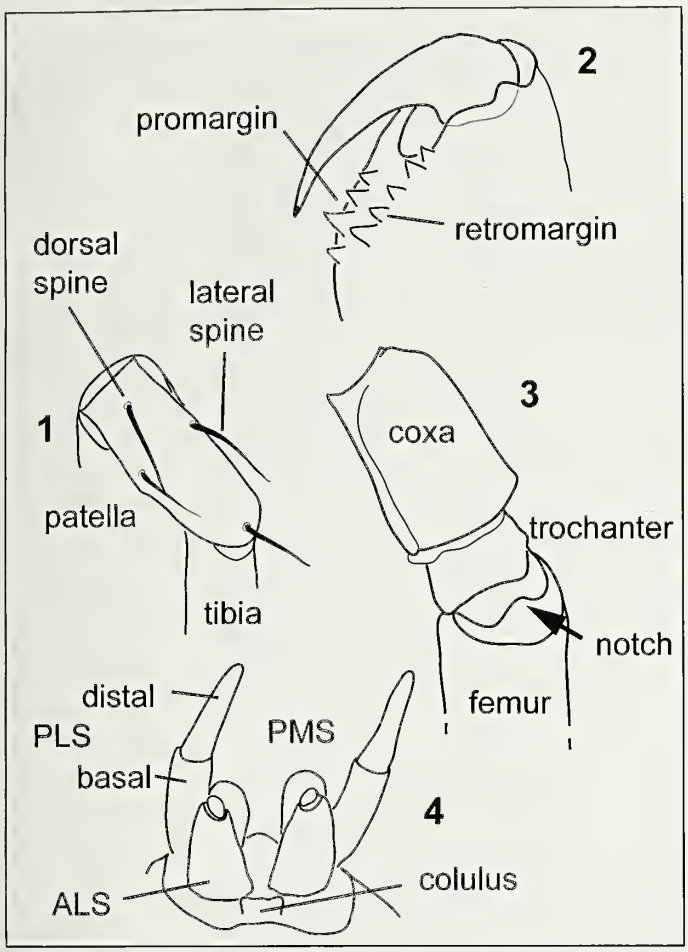
Genus *Aterigena* new genus

Type species.—*Tegenaria ligurica* Simon 1916, by present designation.

Diagnosis.—Agelenid spiders bearing the combination of following characters: presence of notched trochanter on legs III and IV (present also in *Hadites*, *Histopona* and *Malthonica* but absent in other European agelenids) (Fig. 3); presence of lateral spines on patellae I–IV (absent in other Tegenariini but present in Agelenini and Textricini) (Fig. 1); presence of ventral spines on tarsus IV (absent in other Tegenariini but present in several genera of other tribes); both eye rows straight in dorsal view (anterior row can be slightly recurved) and straight or slightly procurved in frontal view (Figs. 5, 7, 9, 11, 48); most proximal teeth at the retromargin of chelicerae biggest (Fig. 2); colulus distinctly trapezoidal or rectangular (present also in *Tegenaria* s.l., other genera with reduced or divided colulus) (Fig. 4); male palp with lamelliform and laterally folded conductor, terminal end simply pointed (Figs. 13–20); median apophysis with membranous base and distally with thin and curved plate-like sclerite; vulva consisting of a straight and short copulatory duct, smoothly sclerotized globular receptacula and convoluted fertilization ducts (Figs. 30, 32, 34, 36, 38, 39).

Etymology.—Anagram of *Tegenaria*, gender feminine.

Description.—Body size medium to large (carapace length between 3 and 7 mm). Margin of carapace narrowly and continuously darkened; two symmetric longitudinal dark bands dorsally on carapace present (sometimes intensified by white and black plumose hairs). Sternum longer than wide with an indistinct pattern of bright median band; plumose hairs present on carapace, legs and opisthosoma. Four promarginal teeth, second from proximal is largest; 4–6 retromarginal teeth, most proximal tooth largest. Trochanter III and IV notched. Colulus developed as rectangular plate, distal margin more or less straight. PLS longer than all others, with distal segment as long as or slightly longer than basal segment. In dorsal view both eye rows straight or slightly recurved; in frontal view PER procurved and AER straight or slightly procurved. Smallest eyes are AME or PME. Male palp without femoral and patellar



Figures 1–4.—Diagnostic characters of *Aterigena* n. gen. (schematic). 1. Patella IV with dorsal and lateral spines; 2. Left chelicera with dentition of pro- and retromargin; 3. Trochanter of leg IV, ventral view; 4. Colulus and spinnerets in ventral view.

apophyses; RTA with large dorsal branch, distally more or less obtuse and strongly sclerotized; lateral branch expressed as sclerotized, elongate process; ventrally with weakly developed rounded ridge. Embolus filiform, getting thinner to apex. Conductor elongate distally (parallel to cymbium) and folded along the whole length laterally, terminal end (proximal) forming sclerotized peak; median apophysis consisting of membranous base and thin and broad sclerotized distal plate, base as broad as or slightly smaller than length of median apophysis. Other tegular apophyses absent. Epigynal plate strongly sclerotised with distinct atrium; receptacula visible through plate; copulatory duct short and straight; one pair of smooth, sclerotized receptacula, medium to large in size, oval to globular; fertilization ducts long and mostly strongly convoluted. Constructing horizontal funnel web in which they live (characteristic for family).

Distribution.—Disjunct in the Palearctic, with four species in the Mediterranean Basin and one species in China.

Phylogenetic relationships.—The eye arrangement, the pattern of cheliceral teeth, the notched trochanter on legs III–IV and the distinct trapezoidal colulus place *Aterigena* n. gen. in the tribe Tegenariini. However, *Aterigena* n. gen. bears lateral spines on patellae III and IV and ventral tarsal spines, which are absent in other Tegenariini but usually present in the other tribes (Table 2). This shows that the last two characters are not diagnostic for the agelenid tribes. In removing *Aterigena* n. gen. from *Tegenaria* s.l. the latter becomes morphologically more homogeneous. In addition to the morphological characters the monophyly of *Aterigena* n. gen. is also supported by molecular characters (Fig. 57). Three apomorphic amino acid substitutions are present in a very short sequence section of the mitochondrial CO1 gene (Table 4).

Comments.—*Aterigena* n. gen. comprises five species (Table 1), four transferred from *Tegenaria* and one described here as new.

KEY TO THE SPECIES OF *ATERIGENA*

1 Carapace longer than 5.2, cymbium longer than 2.0, dorsal branch of RTA more or less conical (in retrolateral view), embolus longer than twice cymbium width, epigynal plate wider than 0.8; atrium of epigynum rectangular or trapezoidal; if transversally divided, posterior part much shorter than anterior part 2
Carapace smaller than 5.2, cymbium shorter than 2.0 mm, tip of dorsal branch of RTA skewed ventrad (in retrolateral view), embolus shorter than twice cymbium width, epigynal plate smaller than 0.8; atrium of the epigynum oval; tranversely subdivided into subequal parts 4

2 Lateral branch of RTA relatively long, distal apex of conductor only weakly bent, ratio bulb length to cymbium length smaller than 0.7, atrium of the epigynum transversally divided, forming membranous oval part anteriorly, and sclerotized semicircular bar posteriorly . . . . . *aliquoi*
Combination of characters different 3

3 Ratio of palpal tibia length to cymbium length smaller than 0.43, dorsal branch of RTA originating approximately in middle of tibia, copulatory openings well visible, lateral margins of epigynal atrium converging posteriad, each vertex forming strongly elongated process . . . . . *ligurica*
Ratio of palpal tibia length to cymbium length larger than 0.43, dorsal branch of RTA originating in distal half of tibia, lateral margin of epigynal atrium diverging posteriad, each vertex froming at most blunt tubercle . . . . . *aculeata*

4 Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length smaller than 0.7; ratio tibia length to cymbium length smaller than 0.6; distal apex of conductor longer than wide; transverse separation of epigynal atrium more or less straight; receptacula globular, round; fertilization ducts strongly convoluted . . . . . *soriculata*
Ratio bulb length to cymbium length larger than 0.7; ratio tibia length to cymbium length larger 0.6; distal apex of conductor as long as or shorter than wide; transverse separation of epigynal atrium in the middle slightly curved posteriad; receptacula oval; fertilization ducts weakly convolute . . . . . *aspromontensis* n. sp.

Table 1.—Checklist of *Aterigena* n. gen. species with known geographic distributions.

Taxon name	Original genus	Distribution
Aterigena aculeata (Wang 1992)	*Tegenaria*	southern China
Aterigena aliquoi (Brignoli 1971)	*Tegenaria*	Sicily
Aterigena aspromontensis n. sp.	-----	Calabria (Italy)
Aterigena ligurica (Simon 1916)	*Tegenaria*	Italy, southern France, Spain, Egypt (possibly introduced)
Aterigena soriculata (Simon 1873)	*Tegenaria*	Corsica, Sardinia?

Aterigena ligurica (Simon 1916) new combination
Figs. 5, 6, 13, 14, 23, 24, 29, 30, 40, 41

Tegenaria ligurica Simon 1916:210, male and female; Platnick 2009.

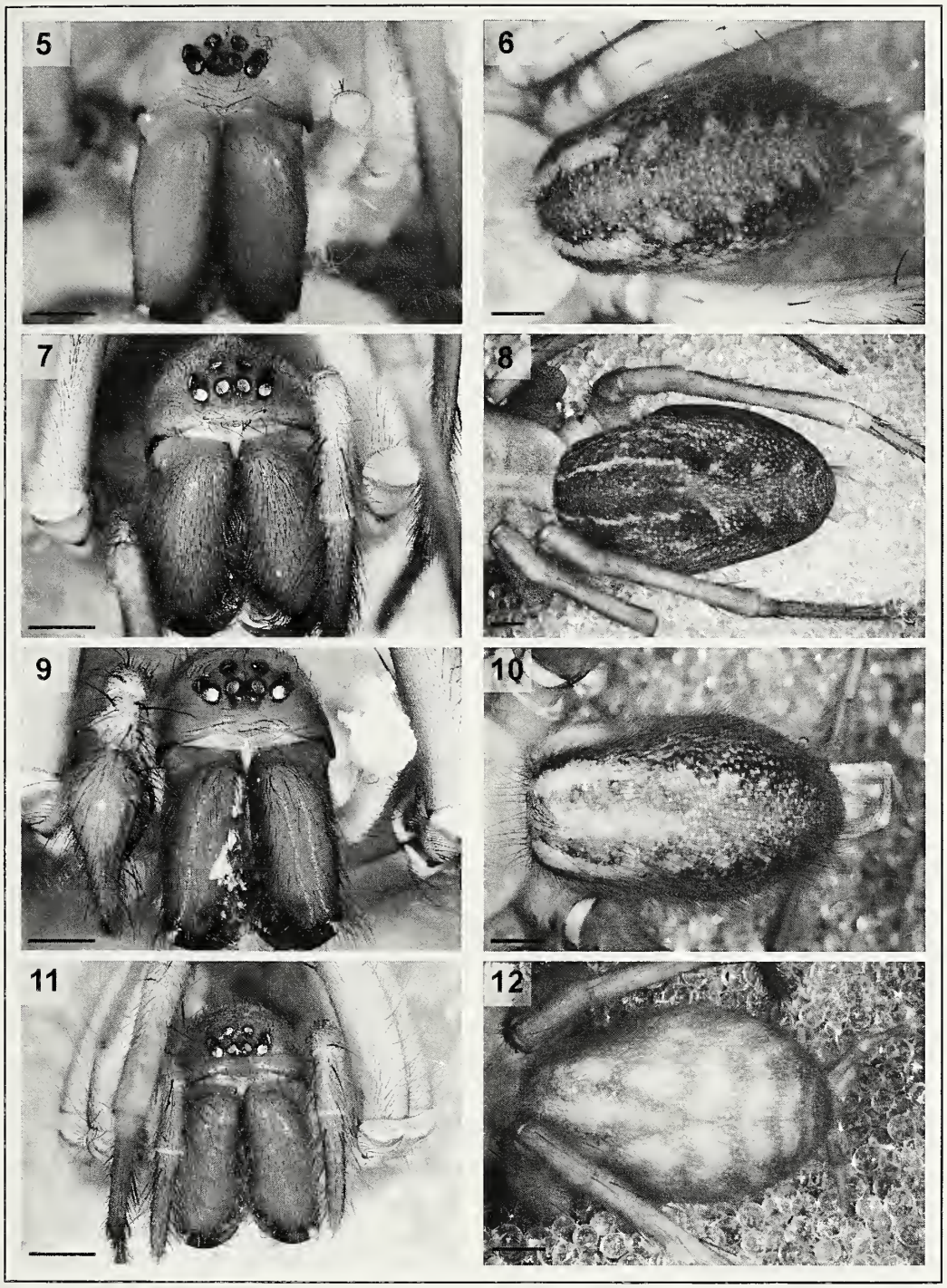
Type material.—FRANCE: *Alpes-Maritimes*: Menton, le Moulinet: lectotype female, paralectotype male, 1915, Dalmas (MNHN), present designation.

Other material.—FRANCE: *Alpes-Maritimes*: 1 male, 4 females, April 1905, E. Simon (MNHN, Nr. 614); Lantosque, NE exp. slope close to village (43.97416°N, 7.31104°E, 484 m): 1 male, 3 September 2008, Schönhofer (NMB); dry valley between Villars-sur-Var and tunnel of Mescla (43.93119°N, 7.13273°E, 231 m): 3 females, 1 juvenile, 2 September 2008, Schönhofer (NMB); Vallon de Cervagne at Roquebillière (44.01562°N, 7.29831°E, 685 m): 1 male, 2 September 2008, Schönhofer (NMB); Mercantour National Park, Paganin Gorge (44.02833°N, 7.57712°E, 500 m): 1 male, 4 September 2008, Schönhofer (NMB); Les Mèces, Mercantour National Park: 2 males, 2 females, 16 July 1986, Maurer & Thaler (NMB, 1 male measured, MHNG). ITALY: *Liguria*: Savona, Bormida, km 17 on provincial road 15: 1 male, 11 October 2001, Pantini (MSNB); Savona, Calizzano, Colla Melogno (920 m): 1 female, 1 juv., 17 July 2001, Mus. Bergamo (MSNB); *Piemonte*: Cuneo, Val Pesio, Pian delle Gorre: 1 male, 15 August 1983, Giachino (MSNB); Cuneo, Garessio: 1 male, 2 females, 3 October 2004, Isaia & Beikes (MSNB); Cuneo, National Park Alpi Marittime, Bousset-Valley, Ponte di Porcera (44.20097°N, 7.44126°E, 1117 m): 1 female, 11 September 2008, Schönhofer (NMB); Cuneo, Nava (44.1°N, 7.87°E, 890 m): 1 male, 8 September 2008, Schönhofer (NMB); *Marche*: Ascoli Piceno, Montemonaco, Isola S. Biagio (990 m): 1 male, 1 September 2004, Rismondo & Fabbri (MSNB); *Abruzzo*: Teramo, Isola del Gran Sasso d'Italia, Gran Sasso, toward Lake Pagliara (900 m): 5 males, 2 females, 3 October 2002, 1 male, 28 August 2003, 3 males, 7 October 2003, Marotta & Carissimi (MSNB); Teramo, Monti della Laga, Valle Castellana, 1 km next to Ceraso (750 m): 1 male, 7 August 2003, Marotta (MSNB); Teramo, Monti della Laga, toward Valley Castellana, 2 km next to Ceraso (655 m): 1 male, 1 female, 28 October 2001, Marotta (MSNB); Teramo, Tossicia, Tozzanella, towards Colle Petato, Gran Sasso (1050 m): 1 female, 18 November 2001, 1 male, 27 August 2002, 5 males, 2 females, 3 October 2002, 1 female, 26 October 2002, Marotta, Matin, Di Marco & Carissimi (MSNB); *Basilicata*: Potenza, Viggianello, Torno (650 m): 2 females, June 1989, Valle (MSNB); Potenza, San Severino Lucano, close to Santuario (1500 m): 1 male, June-August 1989, Valle (MSNB); Potenza, San Severino Lucano, below Santuario Madonna del Pollino: 1 female, 27 August 2008, Valle (MSNB); *Campania*: Avellino, Pietrastornina, M. Parteni, Acqua Vene (1200 m): 3 males, 12 August 1981, Boffa, Giachino & Verna (MSNB); *Calabria*: Cosenza, SE of Paola (39.33306°N, 16.06083°E, 564 m): 1 male, 29 May 2007, Bolzern & Mühlethaler (NMB, was juvenile till end of August). SPAIN: 1 female, no further information (MNHN, Nr. 12602). EGYPT: *Alexandria*: 1 female, E. Simon (sub *T. domestica*) (MNHN, Nr. 1976, 5960).

Table 2.—Character table based on Lehtinen (1967) supplemented with additional characters. <: smaller than; >: bigger than; =: equal. Characters supporting the tribe are shaded.

	Agelenini	Tegenariini	Textricini
Eye-rows (frontal)	stongly procurved	straight or procurved	straight of recurved
Eye-rows (dorsal)	procurved	straight	strongly recurved
Biggest eyes	not PME	not PME	PME
Cheliceral teeth (pro-/retromargin)	3–4/2–4	3–5/3–12	3/2–4
Sternal pattern	central bright area or none	distinct or none	central bright area or none
Special feathery hairs at legs and carapace	present	present	absent or different
Patellar apophysis	present	present or none	present or none
Embolus shape	broad, membranous or filiform	filiform, somtimes truncated	broad, membranous or filiform
Conductor shape	strong or spiral helical	lamelliform or massive	lamelliform or massive
Median apophysis	present	present or absent	present or absent
Trochanter IV notched	absent	present or absent	absent
Colulus	2 separated plates	absent or trapezoidal	2 separated plates
PLS, distal to basal segment length	(=) >	< = >	>
Special dark and strong hairs at analtubus	present	absent	absent
Lateral patellar spines	present	absent (present*)	present
Ventral tarsal spines (IV)	present / absent	absent (present*)	present
MA with sclerit	absent	present	present

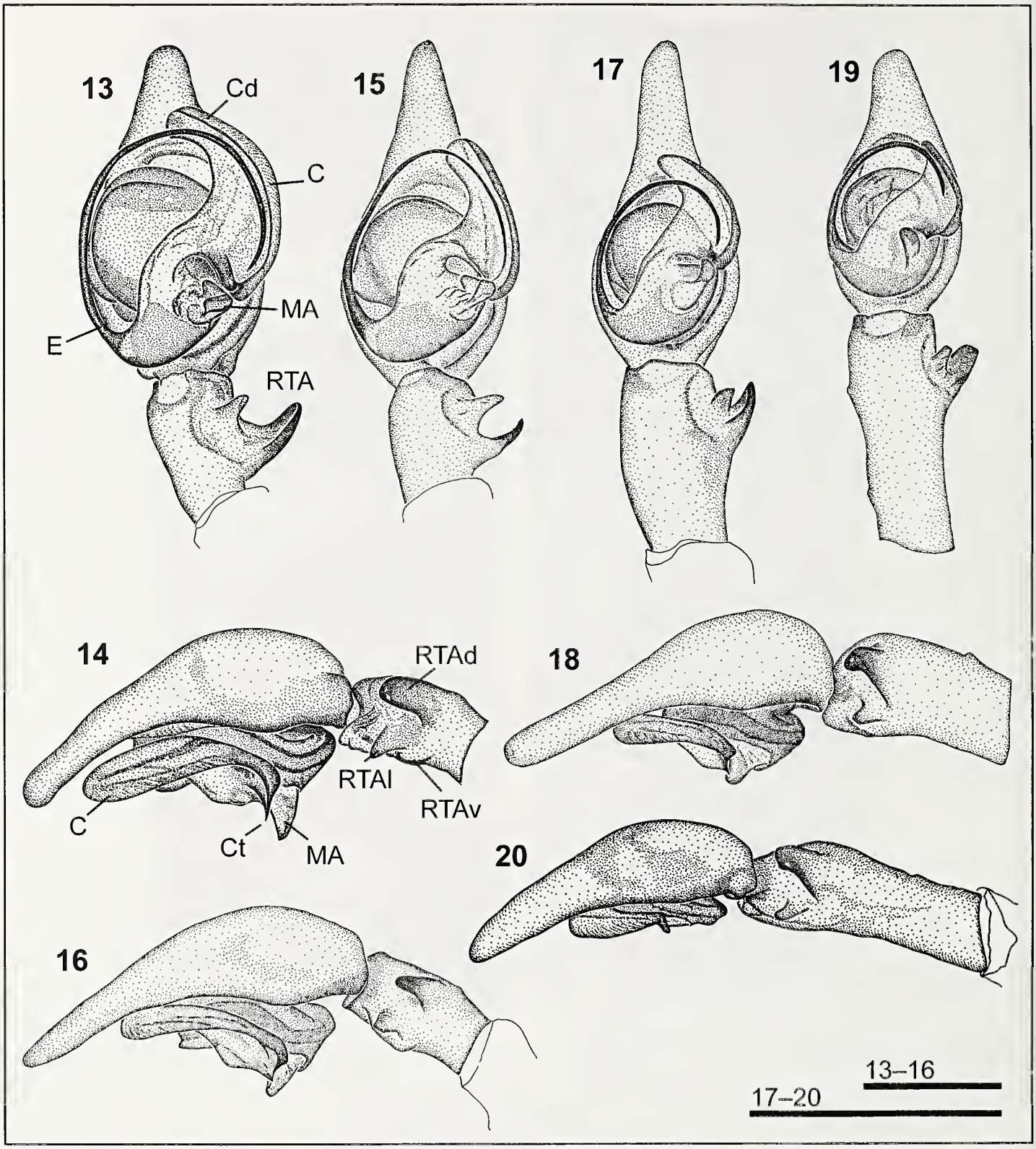
* Present only in *Aterigena* n. gen.



Figures 5–12.—Face and opisthosoma. 5, 6. *Aterigena ligurica*, male; 7, 8. *A. aculeata*, female; 9, 10. *A. aliquoi*, male; 11, 12. *A. soriculata*, female. Scale = 1.0 mm.

Description.—*Male* (*n* = *1*): Carapace 6.82 long, 4.52 wide. Head region 2.65 wide; PER 1.4 wide. Chelicerae 2.94 long, 1.31 wide. Labium as long as wide. Gnathocoxa ratio width to length: 0.6. Sternum 3.11 long, 2.53 wide. Opisthosoma 6.37 long, 3.8 wide. Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length: 0.72. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	2.31	0.94	1.07	-	2.67	6.99
I	5.71	2.28	4.67	5.77	3.78	22.21
II	5.63	2.29	4.38	5.72	3.41	21.43
III	5.28	2.24	4.20	6.01	3.34	21.07
IV	6.62	2.27	5.45	8.44	4.02	26.80



Figures 13–20.—Left male palp in ventral and retrolateral view. 13, 14. *Aterigena ligurica*; 15, 16. *A. aliquoi*; 17, 18. *A. soriculata*; 19, 20. *A. aspromontensis* n. sp. C: conductor; Cd: distal apex of C; Ct: terminal end of C; E: embolus; MA: median apophysis; RTA: retrolateral tibial apophyses; RTAd: dorsal branch of RTA; RTAl: lateral branch of RTA; RTAv: ventral branch of RTA. Scale = 1.0 mm.

Females (*n* = 3): Carapace 5.63–6.58 long, 3.77–4.49 wide. Head region 2.43–2.9 wide; PER 1.25–1.44 wide. Chelicerae 2.28–3.04 long, 1.17–1.54 wide. Labium as long as wide. Gnathocoxa ratio width to length: 0.6–0.7. Sternum 2.65–3.40 long, 2.20–2.79 wide. Opisthosoma 6.47–9.43 long, 4.10–6.62 wide. Epigynal plate 1.12 long, 1.3 wide; atrium 0.27–0.29 long, 0.37–0.41 wide. Receptacula 0.50–0.62 wide. Leg measurements:

	fe	pa	ti	mt	ta	total
Palp	1.79–2.17	0.87–1.09	1.09–1.35	-	2.03–2.46	5.78–7.07
I	4.16–4.93	1.98–2.27	3.19–3.89	3.64–4.52	2.26–2.96	15.23–18.57
II	4.00–4.90	1.98–2.25	2.93–3.59	3.52–4.35	2.26–2.90	14.69–17.99
III	3.11–4.95	1.47–2.14	2.46–3.56	3.25–4.77	1.88–2.45	12.17–17.87
IV	4.88–5.71	1.84–2.32	4.04–4.61	5.74–6.36	2.67–3.14	19.17–22.14

Eyes: In dorsal view both eyerows straight or slightly recurved; in frontal view PER procurved and AER straight or slightly procurved (Fig. 5). Diameters: PME: 0.21–0.23; PLE: 0.20–0.24; AME: 0.18–0.21; ALE: 0.21–0.24. Distances: PME–PME less or equal diameter of PME; PME–AME less than diameter of PME; PME–PLE about diameter of PME; PME–ALE about diameter of PME or slightly more; AME–AME 0.5–1.0 times diameter of AME; AME–ALE about half diameter of AME. Clypeus height (measured under AME) less than or equal to 3 times diameter of AME; (measured under ALE) about twice diameter of ALE or slightly more.

Coloration: Carapace with narrow, continuous dark margin; two longitudinal symmetrical darkened bands present on carapace, interrupted and sometimes reduced to triangular dots. Sternum with brighter median band, sometimes very weak. Opisthosoma with red-brown median band, anterolaterally with two bright bands, continuing posteriorly as dots (Fig. 6). Legs weakly annulated best expressed ventrally on femora.

Additional somatic characters: Distal margin of labium weakly concave. Plumose hairs present on carapace, legs and opisthosoma. Four promarginal teeth, the second one from proximal largest; 4–5 retromarginal teeth, most proximal tooth largest. Trochanter III and IV notched. Tarsi I and II with 7–8 dorsal trichobothria and 8–9 on tarsi III and IV. Colulus forming rectangular plate, distal margin straight, only partly colored. PLS longer than all others with distal segment as long as or slightly longer than basal segment, both darkened. PMS as long as ALS. ALS slightly darkened. The formulae of leg spination are listed in Table 3.

Male palp (*Figs. 13, 14, 23, 24*): RTA with a large dorsal branch, distally pointed and strongly sclerotized; lateral branch forming sclerotized finger-shaped appendix; ventrally bearing a weakly developed rounded ridge. Embolus originating (free apex) at 7 o'clock position; length (only the free apex) slightly more than twice cymbium width; distal tip between 3 and 4 o'clock position. Conductor lamella-like, distally elongated (parallel to cymbium), arcuated and laterally folded along the whole length; as long as alveolus, distally reaching beyond alveolus margin; terminal end forming sclerotized peak, pointing ventrally (in lateral view). Connection of conductor and tegulum membranous. Median apophysis consisting of membranous base and thin and broad sclerotized distal plate, pocket-like; originating at 5 o'clock position; protruding ventrally; basis as wide as median apophysis length. Tegular apophysis absent.

Epigynum and vulva (*Figs. 29, 30, 40, 41*): Epigynal plate strongly sclerotized, trapezoidal, with distinct atrium; atrium posteriorly reaching epigastral furrow. Ground plate of atrium strongly sclerotized, anterior distinctly connected with epigynal plate, undivided reversed trapezoidal shaped. Lateral margins of atrium converging posteriad, strongly elongated vertices present. Receptacula visible through plate. Copulatory openings well-visible as holes, located at anterior border of atrium. Copulatory duct short and straight. Receptacula large, oval to globular, almost touching each other; fertilization ducts long and strongly convoluted.

Comparison to other species.—The description of the male of *A. aculeata* provided by Wang (1992:287, figs. 1–3) suggests that it is closely related to *A. ligurica*. No male material of *A. aculeata* was available for study, and our conclusions are based on the literature only. Based on the original description (Wang 1992) the female holotype and the male allotype of *A. aculeata* are similar in size to *A. ligurica*. In contrast, the relative height of the clypeus is larger in *A. ligurica* than in *A. aculeata* (Figs. 5, 7). The male of *A. ligurica* apparently has a relatively smaller ratio of palpal tibia length to cymbium length than *A. aculeata* (Figs. 13, 14, 21, 22). Furthermore, the RTA originates approximately in the middle on the tibia in *A. ligurica*, but more distally in *A. aculeata*. The male of *A. ligurica* can be separated from the other *Aterigena* n. gen. species by the conical shape of the dorsal RTA branch (distally skewed ventrad in *A. soriculata* and *A. aspromontensis* n. sp.), the relatively short lateral branch of the RTA (in relation to the dorsal branch, this lateral branch is longer in *A. aliquoi*) and the size of the cymbium (much larger than in *A. soriculata* and *A. aspromontensis* n. sp.) (Figs. 13, 14, 23–25). The female of *A. ligurica* can be separated from all other species of the genus by the presence of the well-visible copulatory openings anteriorly on the epigynal atrium (absent in *A. aliquoi*, *A. soriculata* and *A. aspromontensis* n. sp.), the undivided and anteriorly connected ground plate of the atrium with diverging lateral margins (converging in *A. aculeata*) and the strongly developed and elongated vertices (tubercular in *A. aculeata*, Figs. 29, 40, 41). Additionally, the vulva is distinct in shape and larger than in all other species of the genus (Fig. 30).

Natural history.—Specimens of *Aterigena ligurica* were found in different types of Mediterranean forests with rocky or stony ground layers. There the spiders live in funnel webs, characteristic for the whole family Agelenidae. The spiders, collected by A. Bolzern, were caught on and under stones and on the bark of pine trees. Maurer & Thaler (1988) caught many specimens in pitfall traps. The available data are insufficient for drawing any conclusions on the phenology of *A. ligurica*. The specimens listed here were caught from April to October.

Distribution.—*Aterigena ligurica* was previously known only from the Maritime Alps and questionably from southern Italy (Brignoli 1971b; Dresco & Célérier 1976; Maurer & Thaler 1988; Pesarini 1994). The revision of the MSNB collection yielded many additional stations from Italy (Fig. 56). Two

Table 3.—Spination of legs of *Aterigena ligurica* (Simon 1916), *A. aculeata* (Wang 1992), *A. aliquoi* (Brignoli 1971), *A. soriculata* (Simon 1873) and *A. aspromontensis* n. sp. The formula gives the number of spines as follows: dorsal - prolateral - retrolateral - ventral. A "p" indicates that at this position the spine is paired (1p = 2 spines at almost the same longitudinal position). A "(s)" indicates very short but strong spines. A superscript "−" or "+" indicates fewer or more spines than indicated have been observed at this position.

Leg	Species	Femur	Patella	Tibia	Metatarsus	Tarsus
Palp	*A. ligurica*	3-0-0	2-1-0	1^{+}-2p-0	-	-
	A. aculeata	3-0-0	2-1-0	2-2p-0	-	-
	A. aliquoi	3^{+}-0-0	2-1-0	1^{+}-2p-0	-	-
	A. soriculata	3-0-0	$2\text{-}0^{+}$-0	1^{+}-2p-0	-	-
	A. aspromontensis	3-0-0	$2\text{-}0^{+}$-0	1^{+}-2p-0	-	-
I	*A. ligurica*	$3\text{-}3^{-}\text{-}3^{-/+}$-0	$2\text{-}1\text{-}0^{+}$	$2\text{-}2^{+}\text{-}0^{++}$-3p	0-2-2-1+2p+1 0-2-2-1p+1+1p+1 0-2-2-3p+1 0-2-2-3p+1+1(s)	0
	A. aculeata	$3^{+}\text{-}4^{--/++}\text{-}3^{--}$-0	2-1-0	2-2-0-3+1p 2-3-0-3p	$0\text{-}2\text{-}0^{+}$-3p+1	0
	A. aliquoi	$3\text{-}2^{+}$-2-0	2-1-0	$2\text{-}3^{-}\text{-}0^{++}$-3p 2-3-2-2p+1	$0\text{-}2^{+}\text{-}2^{+}$-3p+1	0
	A. soriculata	$3\text{-}2\text{-}1^{+}$-0	2-1-0	$2^{--}\text{-}2^{+}$-0-3p	0-2-2-3p+1	0
	A. aspromontensis	$3\text{-}1\text{-}1^{+}$-0	2-1-0	$2\text{-}2^{+}$-0-3p	$0\text{-}2\text{-}1^{+}$-3p+1	0
II	*A. ligurica*	$3\text{-}3^{++}\text{-}3^{+}$-0	$2\text{-}1\text{-}0^{+}$	2-2-0-1+2p $2\text{-}2\text{-}0^{++}$-3p	0-3-2-3p+1p(s)+1 1-3-3-1+2p+1p(s)+1	0
	A. aculeata	$3\text{-}2^{++}\text{-}2^{+}$-0	2-1-0	2-2-0-1+2p 2-2-0-2+1p	$0\text{-}2^{+}\text{-}1^{+}$-3p+1	0
	A. aliquoi	$3\text{-}2^{+}$-2-0	$2\text{-}1\text{-}0^{+}$	2-2-0-3p	$0^{+}\text{-}3\text{-}2^{+}$-3p+1p(s)+1	0
	A. soriculata	3-2-2-0	2-1-0	2-2-0-1+2p 2-2-0-3p	$0^{+}\text{-}3\text{-}2\text{-}3$p+1p(s)+1	0
	A. aspromontensis	3-2-2-0	2-1-0	2-2-0-1+2p	0-3-2-3p+1+1(s) 0-3-2-3p+1p(s)+1	0
III	*A. ligurica*	$3\text{-}3^{+}\text{-}2^{++}$-0	2-1-1	$2\text{-}2^{+}$-2-3p	1+1p-3-4-3p+1p(s)+1 1+1p-4-3-1p+1+2p+1p(s)+1 1p-4-3-1p+1+2p+1p(s)+1 3-4-4-1p+1+2p+1p(s)+1	$0\text{-}2^{+}\text{-}1\text{-}1^{+}$
	A. aculeata	3-2-2-0	2-1-1	2-2-2-1p+1+2p 2-2-2-2+1p	1-3-3-3p+1+1(s) 1p-3-3-3p+1	$0\text{-}2^{-/+}\text{-}1\text{-}1^{+}$
	A. aliquoi	$3\text{-}2^{++}$-2-0	2-1-1	2-2-2-1+2p 2-2-2-2p+	1-3-3-3p+1p(s)+1 1+1p-3-3-3p+1p(s)+1 $2\text{-}3^{+}$-3-3p+1p(s)+1	$0\text{-}2^{+}$-1-0
	A. soriculata	3-2-2-0	2-1-1	$2\text{-}2\text{-}2\text{-}1^{+}$+2p- 2-2-2-3p	1-3-3-3p+1p(s)+1 1p-3-3-3p+1p(s)+1	$0\text{-}2^{-}\text{-}1\text{-}1^{-}$
	A. aspromontensis	3-2-2-0	2-1-1	$2\text{-}2\text{-}2\text{-}1^{+}$+2p-	1-3-3-3p+1p(s)+1 1p-3-3-3p+1p(s)+1 2-3-3-3p+1+1(s)	0-2-1-1
IV	*A. ligurica*	$3\text{-}4^{+}\text{-}1^{+}$+-0	2-1-1	2-2-2-1+2p 2-2-2-3p 2-2-3-1p+2+1p	1+1p-4-3-2p+3+1p+1(s)+1 1+2p-4-3-1p+1+2p+1(s)+1 1+1p+1-4-3-4+2p+1	$0\text{-}2^{+}\text{-}2^{+}$-2
	A. aculeata	$3^{-}\text{-}2^{-/+}\text{-}1^{+}$-0	2-1-1	$2\text{-}2\text{-}2\text{-}2^{-/+}$+1p^{+}	1-4-3-1+3p+1 1-4-3-1p+1+2p+1+1(s) 2-4-3-1p+1+2p+1	0-2-2-2
	A. aliquoi	$3\text{-}2^{++}$-1+-0	2-1-1	2-2-2-3p	2-3-3-1p+1+2p+1+1(s) 2-3-3-3+2p+1+1(s)	$0\text{-}2\text{-}2\text{-}1^{+}$
	A. soriculata	$3\text{-}2\text{-}1^{+}$-0	2-1-1	$2\text{-}2\text{-}2\text{-}1$p+$2^{+}$+1p	2-3-3-1+3p+1+1(s) 2-3-3-1p+1+2p+1+1(s)	0-2-2-2
	A. aspromontensis	3-2-1-0	2-1-1	2-2-2-1+2p	2-3-3-1p+1+2p+1+1(s)	0-2-2-2

samples from the MNHN containing a single female each are from outside this range: they are labeled "Hispania" and "Alexandria", respectively. The latter specimens may have been accidentally introduced; the data for the former are too vague for any interpretation. Additional field work is required to solve this puzzle.

Comment.—In accordance with article 74.1 of the Code (ICZN 1999) the female syntype is designated here as lectotype for stabilizing the nomenclature. As the morphology of the epigynum is a good distinctive character for separating the species from its closest relatives, the female has been chosen as lectotype. The male syntype becomes paralectotype.

Table 4.—Apomorphic amino acid substitutions of *Aterigena* n. gen. detected within a small sequence of the mitochondrial CO1 gene. Numbers refer to the *Drosophila yakuba* gene presented by Clary & Wolsenholme (1985).

Triplet #	622			623			624			625			626			627			628			629			630			631		
Nucleotide position	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Amaurobius fenestralis (Ström 1768)	G	C	T	T	C	T	A	T	A	A	T	A	G	G	G	C	A	T	T	C	A	G	G	A	A	G	A	G	C	T
Textrix denticulata (Olivier 1789)	.	.	.	.	.	C	.	C	T	.	.	.	.	.	C	.	.	.	A	G	T	.	.	.	.	.	.	T	.	.
Tegenaria domestica (Clerek 1757)	.	.	.	.	.	.	T	C	T	.	.	G	.	.	A	.	.	.	A	T	.	.	.	G	.	.	.	.	.	.
Tegenaria atrica C.L. Koch 1843	.	.	.	.	.	.	T	C	T	.	.	T	.	.	T	.	.	.	.	T	T	.	.	T	.	A	.	T	.	.
Histopona torpida (C.L. Koch 1837)	.	.	.	.	.	.	T	C	T	.	.	T	.	.	A	.	.	.	A	T	.	.	.	T	.	.	.	T	.	.
Malthonica oceanica Barrientos & Cardoso 2007	.	.	.	.	.	.	T	C	T	G	.	T	.	.	A	.	.	.	G	.	G	.	.	T	.	.	.	T	.	.
Aterigena ligurica (Simon 1916)	T	.	.	.	.	.	T	.	T	.	.	T	.	.	C	.	.	.	G	.	T	.	A	T	.	.	.	A	G	A
Aterigena aliquoi (Brignoli 1971)	T	.	.	.	.	.	T	.	T	.	.	.	.	.	T	.	.	.	G	.	T	.	A	T	.	.	.	A	G	C
Aterigena aculeata (Wang 1992)	T	.	.	.	.	.	T	.	T	.	.	T	.	.	A	.	.	.	G	.	T	A	A	T	.	.	.	A	G	A
synapomorphic amino acid subst.	A →S			-			M,I,S →F			-			-			-			-			G,S →D,N			-			-		

Aterigena aculeata (Wang 1992) new combination
Figs. 7, 8, 21, 22, 31, 32, 42, 43

Tegenaria aculeata Wang 1992:286, figs. 1–5, male and female; Platnick, 2009.

Material examined.—CHINA: *Guizhou*: Daozhen, Natural Reserve Dashahe (27.8333°N, 106.8333°E): 6 females, Zhang, 24–25 August 2004 (3 females ZZ, 3 females NMB).

Description.—As *A. ligurica* but differing in the following characters:

Females (n = 3)*:* Carapace 5.50–6.10 long, 3.70–4.25 wide. Head region 2.0 wide; PER 1.15 wide. Chelicerae 2.40–2.75 long, 1.00–1.30 wide. Gnathocoxa ratio width to length: 0.6. Sternum 2.60–3.10 long, 2.15–2.35 wide. Opisthosoma length: 7.25–7.75 long, 4.00–4.90 wide. Epigynal plate 0.7–0.9 long, 0.9–1.0 wide; atrium 0.22 long, 0.33 wide. Receptacula 0.38 wide. Leg measurements:

	fe	pa	ti	mt	ta	total
Palp	1.95	0.88	1.22		1.95	6.00
I	4.90–5.55	2.00–2.25	4.65–5.25	4.55–5.50	2.85–3.15	18.95–21.70
II	4.50–5.50	2.00–2.15	3.90–4.50	4.25–4.75	2.25–2.75	16.90–19.65
III	4.35–5.05	1.65–1.95	3.60–4.50	4.25–5.00	2.25–2.50	16.10–19.00
IV	5.50–6.25	1.50–2.20	4.75–5.50	6.00–7.00	2.80–3.10	20.55–24.05

Eyes: In dorsal view both eye rows straight (frontal view: Fig. 7). Diameters: PME: 0.26; PLE: 0.28; AME: 0.25; ALE: 0.29. Distances: PME–PME equal diameter of PME; PME–AME less than or equal diameter of PME; PME–PLE about diameter of PME or slightly more. Clypeus height (measured under AME) less than or equal to twice diameter of AME; (measured under ALE) about 1.5 times diameter of ALE or less.

Coloration: Two longitudinal symmetrical darkened bands present on carapace, interrupted and sometimes reduced to only triangular dots, intensified by white and black plumose hairs. Anterolateral bright bands on opithosoma smaller than in *A. ligurica* (Fig. 8).

Additional somatic characters: Chelicerae with five to six retromarginal teeth, all equal or most proximal tooth biggest. Tarsi I–III with 7–8 dorsal trichobothria, tarsus IV with 8. Formulae of leg spination listed in Table 3.

Male palp (*Figs. 21, 22*)*:* No males were available for examination; for description see Wang (1992:286–290, figs. 1–3).

Epigynum and vulva (*Figs. 31, 32, 42, 43*)*:* Ground plate of atrium strongly sclerotized, undivided and trapezoidal. Lateral margin of atrium without elongate vertices. Copulatory openings indistinctly visible as gaps, located at anterior border of atrium. Receptacula large, globular.

Comparison to other species.—Based on the original description, *A. aculeata* is probably most closely related to *A. ligurica*, but males are required to confirm this. The characters separating males of *A. aculeata* and *A. ligurica* are detailed under the latter. Female *A. aculeata* can be separated from *A. ligurica* by the much smaller and less visible copulatory opening (very distinct in *A. ligurica*), the trapezoidal shape of the atrium (rectangular in *A. ligurica*), the outline of the lateral margin of the atrium (vertices not elongated in *A. aculeata* but in *A. ligurica*) (Fig. 31), the dimensions of the vulva and the shape of the fertilization ducts (Fig. 32).

Natural history.—No information is available on the habitat of *A. aculeata*. All known specimens were collected in summer (August).

Distribution.—Known from southern China (Hunan, Guangxi and Guizhou provinces) (Wang 1992).

Comment.—The type material of *A. aculeata* is probably lost (Xiang Xu, Hunan Normal University, China pers. comm.), and no males were available for this study.

Aterigena aliquoi (Brignoli 1971) new combination
Figs. 9, 10, 15, 16, 25, 26, 33, 34, 44, 45

Tegenaria aliquoi Brignoli 1971a:86–88, figs. 31–34, male; Brignoli 1977:47, fig. 23, female.

Malthonica aliquoi (Brignoli); Guseinov et al. 2005:164; Platnick 2009.

Type material.—ITALY: *Sicily*: Palermo, Parco Regionale delle Madonie, Piano della Battaglia: holotype male, 28 July 1968, Aliquo (MCSN).

Other material.—ITALY: *Sicily*: Portella di Femminamorta, Monte dei Nebrodi: 1 female, 26 March 1967 (MCSN, PMBC); Palermo, Parco Regionale delle Madonie, Piano della Battaglia (37.875°N, 14.023°E, 1574 m): 1 male, 1 female, 24 May 2007,

Table 5.—Genbank accession numbers of all included CO1 sequences. Sequences that have already been published have been aligned with the new ones to a length of 471 nucleotides.

Taxon name	Accession #	Specimen origin	Voucher specimen	Comments / Reference
Agelena canariensis Lucas 1838	FN554798	ES: Gran Canaria	Departament de Biologia Animal, Universitat de Barcelona: NTxTeg1	
Agelena labyrinthica (Clerck 1757)	FN554797	IT: Sardinia	NMB: AB 424	
Ageleuopsis aperta (Gertsch 1934)	DQ628604	-	-	Spagna & Gillespie (2008)
Allageleua gracileus (C.L. Koch 1841)	DQ628606	-	-	Spagna & Gillespie (2008)
Amaurobius fenestralis (Ström 1768)	FN554820	CH: Solothurn	NMB: AB 1006	
Amaurobius ferox (Walchenaer 1830)	FN554819	CH: Basel-Land	NMB: AB 959	
Amaurobius similis (Blackwall 1861)	DQ628608	-	-	Spagna & Gillespie (2008)
Aterigena aculeata (Wang 1992)	FN554790	CN: Guizhou	NMB: AB 591	
Aterigena aliquoi (Brignoli 1971)	FN554791	IT: Sicily	NMB: AB 720	
Aterigena ligurica (Simon 1916)	FN554789	IT: Calabria	NMB: AB 812	
Barronopsis barrowsi (Gertsch 1934)	DQ628609	-	-	Spagna & Gillespie (2008)
Calymmaria sp. 1	DQ628611	-	-	Spagna & Gillespie (2008)
Coelotes terrestris (Wider 1834)	DQ628627	-	-	Spagna & Gillespie (2008)
Cybaeus sp.	FN554818	US: Oregon	NMB: AB 615	
Eurocoelotes inermis (L. Koch 1855)	DQ628628	-	-	Spagna & Gillespie (2008)
Histopoua torpida (C.L. Koch 1837)	FN554793	CH: Basel-Land	NMB: AB 212	
Hololena sp. 1	FN554799	US: California	NMB: AB 613	
Hololena sp. 2	FN554800	US: Washington	NMB: AB 883	
Lycosoides coarctata (Dufour 1831)	FN554815	PT: Algarve	NMB: AB 766	identical haplotype as a specimen from IT
Maiuuua cretica (Kulczyn'ski 1903)	FN554795	GR: Crete	NMB: AB 855	
Malthouica campestris (C.L. Koch 1834)	FN554770	DE: Hessen	NMB: AB 290	
Malthonica dahuatica (Kulczyński 1906)	FN554781	LB: Mount Lebanon	NMB: AB 577	
Malthonica dahuatica (Kulczyński 1906)	FN554806	IT: Campania	NMB: AB 434	
Malthonica dahuatica (Kulczyński 1906)	FN554811	IT: Sicily	NMB: AB 840	
Malthonica eleonorae (Brignoli 1974)	FN554772	IT: Sardinia	NMB: AB 428	
Malthonica ferruginea (Panzer 1804)	FN554777	GR: Crete	NMB: AB 894	
Malthonica ferruginea (Panzer 1804)	FN554802	FR: Alsace	NMB: AB 293	identical haplotype as a specimen from CH
Malthonica ueuorosa (Simon 1906)	FN554780	BG: Sofia	NMB: AB 242	
Malthouica oceauica Barrientos & Cardoso 2007	FN554792	PT: Lisbon	NMB: AB 933	
Malthonica picta (Simon 1870)	FN554785	ES: Pais	NMB: AB 669	
Malthouica ramblae (Barrientos 1978)	FN554774	PT: Lisbon	NMB: AB 589	
Malthouica sardoa Brignoli 1977	FN554786	IT: Sardinia	NMB: AB 580	
Malthouica sicana Brignoli 1976	FN554787	IT: Sardinia	NMB: AB 841	
Malthonica vouneroi (Brignoli 1977)	FN554814	IT: Campania	NMB: AB 734	
Novalena iutermedia (Chamberlin & Gertsch 1930)	DQ628618	-	-	Spagna & Gillespie (2008)
Tegeuaria ariadnae Brignoli 1984	FN554769	GR: Crete	NMB: AB 845	
Tegeuaria ariaduae Brignoli 1984	FN554821	GR: Crete	NMB: AB 974	
Tegenaria agrestis (Walckenaer 1802)	FN554804	DE: Baden-Württemberg	NMB: AB 252	identical haplotype as a specimen from CZ
Tegeuaria agrestis (Walckenaer 1802)	FN554816	US: Washington	NMB: AB 880	identical haplotype as a specimen from DE
Tegeuaria atrica C.L. Koch 1843	FN554801	ES: Catalonia	NMB: AB 570	
Tegenaria atrica C.L. Koch 1843	FN554805	SE: Uppsala	NMB: AB 610	identical haplotype as specimens from CH and DE
Tegenaria domestica (Clerck 1757)	FN554817	US: Washington	NMB: AB 885	
Tegeuaria domestica (Clerck 1757)	FN554808	CH: Basel	NMB: AB 217	identical haplotype as specimens from CN, PT and US
Tegeuaria feuiuea Simon 1870	FN554783	PT: Algarve	NMB: AB 587	
Tegenaria henroti Dresco 1956	FN554771	IT: Sardinia	NMB: AB 584	
Tegeuaria herculea Fage 1931	FN554788	ES: Andalusia	NMB: AB 576	
Tegenaria iucognita Bolzern, Crespo & Cardoso 2009	FN554784	PT: Lisbon	NMB: NMB-2805c	
Tegenaria nirifica Thaler 1987	FN554775	CH: Grisons	NMB: AB 367	
Tegeuaria parietina (Fourcroy 1785)	FN554778	GR: Crete	NMB: AB 864	

Table 5.—Continued.

Taxon name	Accession #	Specimen origin	Voucher specimen	Comments / Reference
Tegenaria parietina (Fourcroy 1785)	FN554807	IT: Sicily	NMB: AB 816	identical haplotype as a specimen from DE
Tegenaria parmenidis Brignoli 1971	FN554773	IT: Calabria	NMB: AB 820	
Tegenaria parmenidis Brignoli 1971	FN554809	IT: Campania	NMB: AB 811	
Tegenaria parmenidis Brignoli 1971	FN554810	IT: Calabria	NMB: AB 732	
Tegenaria parmenidis Brignoli 1971	FN554812	IT: Campania	NMB: AB 834	
Tegenaria saeva Blackwall 1844	FN554782	FR: Morbihan	NMB: AB 289	
Tegenaria saeva Blackwall 1844	FN554813	ES: Pais	NMB: AB 668	
Tegenaria sp.	FN554779	GR: Rhodes	Coll.van Keer: 2617	
Tegenaria tridentina L. Koch 1872	FN554776	CH: Grisons	NMB: AB 375	
Textrix caudate L. Koch 1872	FN554803	IT: Lazio	NMB: AB 749	
Textrix cf. caudata	FN554796	IT: Lazio	NMB: AB 467	
Textrix denticulata (Olivier 1789)	FN554794	CH: Basel-Land	NMB: AB 216	
Wadotes dixiensis Chamberlin 1925	DQ628623	-	-	Spagna & Gillespie (2008)

Bolzern & Mühlethaler (NMB, measured); Palermo, Parco Regionale delle Madonie, Monastery close to Piano Zucchi (37.987°N, 14.021°E, 792 m): 1 male, 24 May 2007, Bolzern & Mühlethaler (NMB); Siracusa, Noto (360 m): 1 female, 27 July 1995, Pantini & Valle (MSNB). The males collected in May 2007 were juvenile and reached maturity in July 2007 and July 2008.

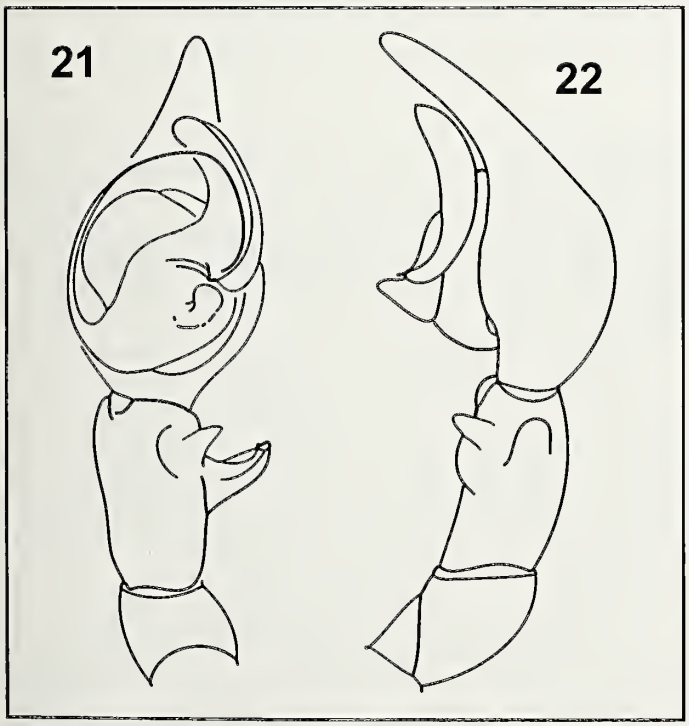
Description.—As *A. ligurica*, but differing in the following characters:

Male: Carapace 6.78 long, 5.0 wide. Head region 2.62 wide; PER 1.58 wide. Chelicerae 2.82 long, 1.27 wide. Labium as long as wide or slightly longer than wide. Sternum 3.27 long, 2.61 wide. Opisthosoma 5.82 long, 3.54 wide. Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length: 0.66. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	2.33	0.92	1.06	-	2.71	7.02
I	6.12	2.40	5.46	6.75	3.85	24.58
II	6.18	2.52	5.60	7.30	3.75	25.35
III	6.12	2.46	4.95	7.20	3.60	24.33
IV	7.90	2.36	6.53	10.10	4.10	30.99

Female: Carapace 5.3 long, 3.65 wide. Head region 2.25 wide; PER 1.30 wide. Chelicerae 2.24 long, 1.10 wide. Labium as long as wide or somewhat longer than wide. Gnathocoxa ratio width to length: 0.6. Sternum 2.61 long, 2.12 wide. Opisthosoma 6.0 long, 3.6 wide. Epigynal plate 0.84 long, 1.05 wide; atrium 0.26 long, 0.22 wide. Receptacula 0.33 wide. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	1.71	0.81	1.06	-	1.85	5.43
I	4.27	1.81	3.38	3.85	2.23	15.54
II	4.15	1.79	3.09	3.81	2.21	15.05
III	4.00	1.70	2.97	3.96	2.00	14.63
IV	5.00	1.90	4.20	5.75	2.50	19.35



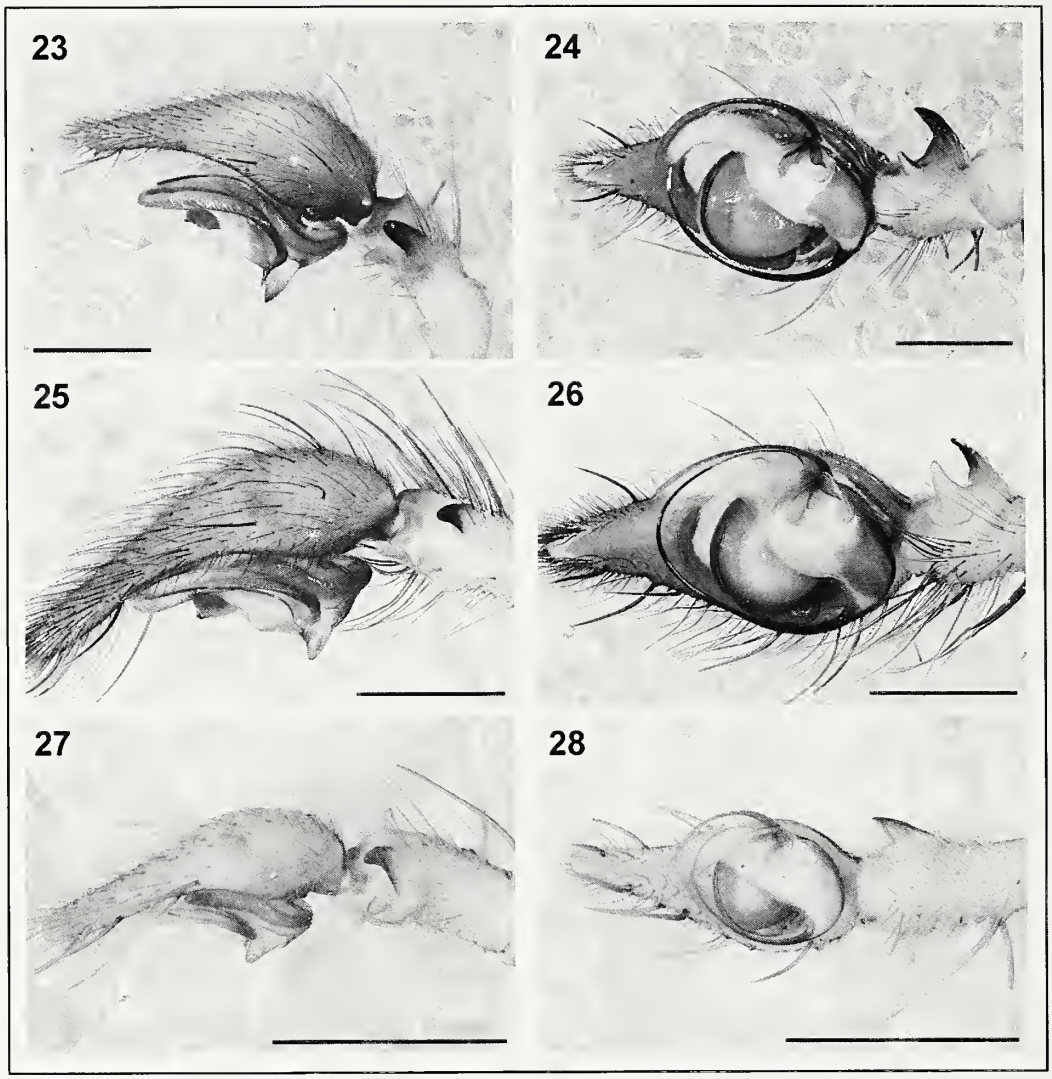
Figures 21, 22.—Left male palp of *Aterigena aculeata*, modified from Wang, 1992:287, figs. 2–3.

Eyes: In frontal view PER procurved and AER slightly procurved (Fig. 9). Diameters: PME: 0.19–0.23; PLE: 0.21–0.31; AME: 0.19–0.29; ALE: 0.29. Distances: PME–PME equal to diameter of PME; PME–PLE more than diameter of PME; PME–ALE about 1.5 diameter of PME. Clypeus height (measured under AME) less than 2.5 times diameter of AME; (measured under ALE) about 1.5 times diameter of ALE.

Coloration: two longitudinal symmetric darkened bands on carapace, interrupted and sometimes reduced to triangular dots, intensified by white and black plumose hairs. Opisthosoma with red-brown median band, slightly paler than in *A. ligurica* (Fig. 10).

Additional somatic characters: Distal segment of PLS slightly longer than basal segment, both very weakly darkened. Formulae of leg spination listed in Table 3.

Male palp (Figs. 15, 16, 25, 26): Embolus originating (free apex) between 7 and 8 o'clock position. Conductor as long as the alveolus. Median apophysis originating between 4 and 5 o'clock position.



Figures 23–28.—Male palp in retrolateral and ventral view. 23, 24. *Aterigena ligurica*; 25, 26. *A. aliquoi*; 27, 28. *A. soriculata*. Scale = 1.0 mm.

Epigynum and vulva (*Figs. 33, 34, 44, 45*): Epigynal plate sclerotized with a distinct atrium, reversed trapezoid in shape; anterior margin of atrium continuous change from sclerotized epigynal plate to membranous white skin. Ground plate of the atrium transversally divided: anterior part membranous and oval; posterior part forming strongly sclerotized semicircular bar. Receptacula visible through plate. Copulatory openings barely visible as gaps, located medial of atrium. Receptacula large, globular, touching each other; fertilization ducts very long and strongly convoluted.

Comparison to other species.—The male of *A. aliquoi* can be separated from *A. ligurica* by the relation of bulb length to cymbium length (cymbium tip from alveolus to distal end is relatively shorter in *A. ligurica*), the relatively straight distal apex of conductor (distinctly bent in *A. ligurica*), the more slender dorsal branch of the RTA (broader in *A. ligurica*) and the slightly longer lateral branch of RTA (Figs. 15, 16, 25, 26). The female can easily be separated from all other species by the divided ground plate of the atrium in a pale larger oval anterior part and a semicircular posterior bar (not divided in *A. ligurica* and *A. aculeata*; anterior part semicircular in *A. soriculata* and *A. aspromontensis* n. sp.) and the shape of the fertilization ducts (Figs. 33, 34, 44, 45).

Natural history.—The specimens collected by A. Bolzern were caught out of their typical funnel webs attached to stones in a beech forest and a mixed deciduous forest. Adult specimens were collected during summertime (end of May until August).

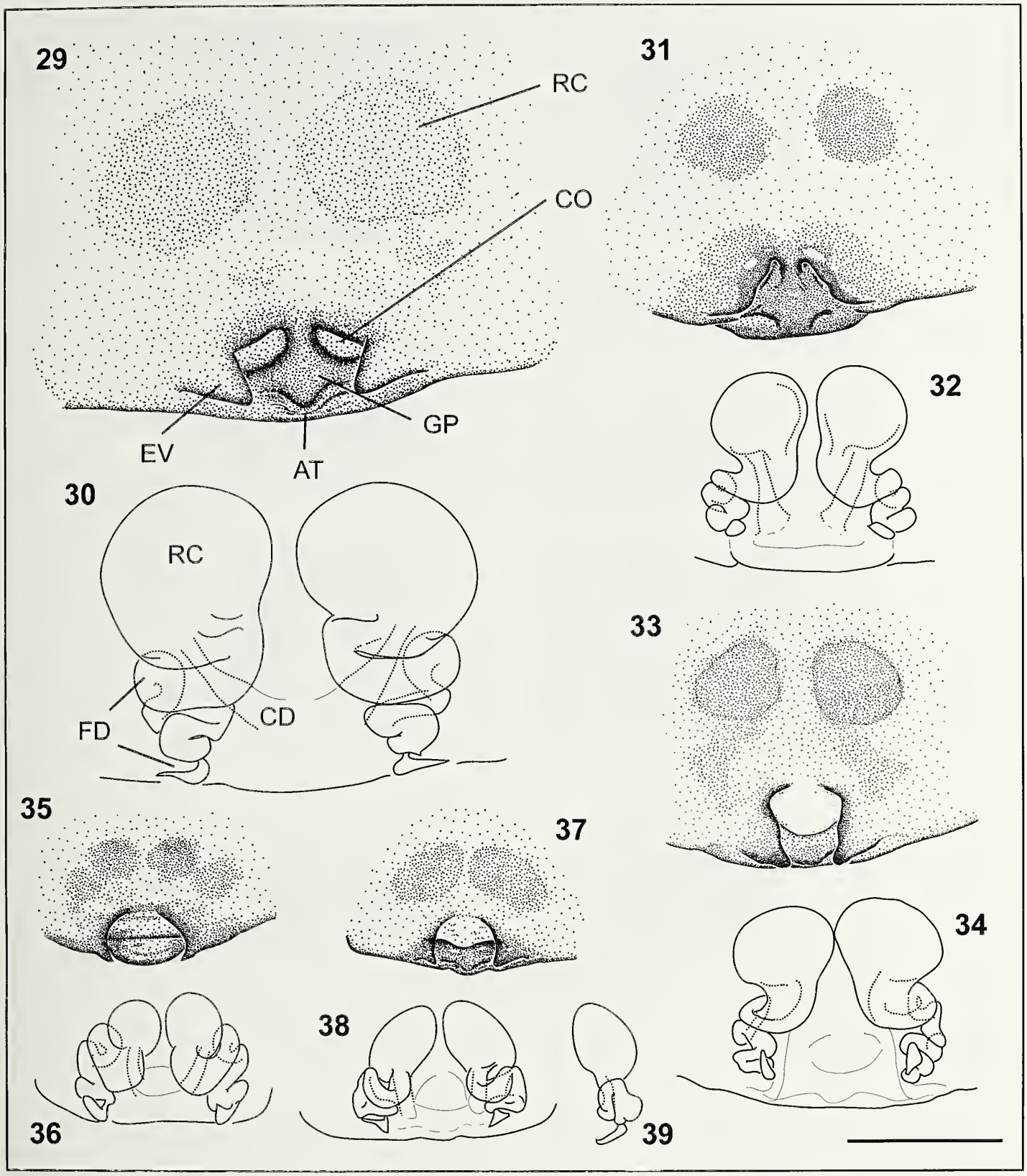
Distribution.—Only known from Sicily, Italy (Fig. 56).

Remarks.—In the original description, Brignoli (1971a) placed this species close to *Tegenaria atrica* C.L. Koch 1843 and *Tegenaria nervosa* Simon 1870. Later, Brignoli (1977) mentioned that this species, or at least the epigynum, shows morphological similarities to *Aterigena soriculata* (Simon 1937) (sub *Tegenaria soriculata*). The holotype is much smaller than the measured male caught in 2007.

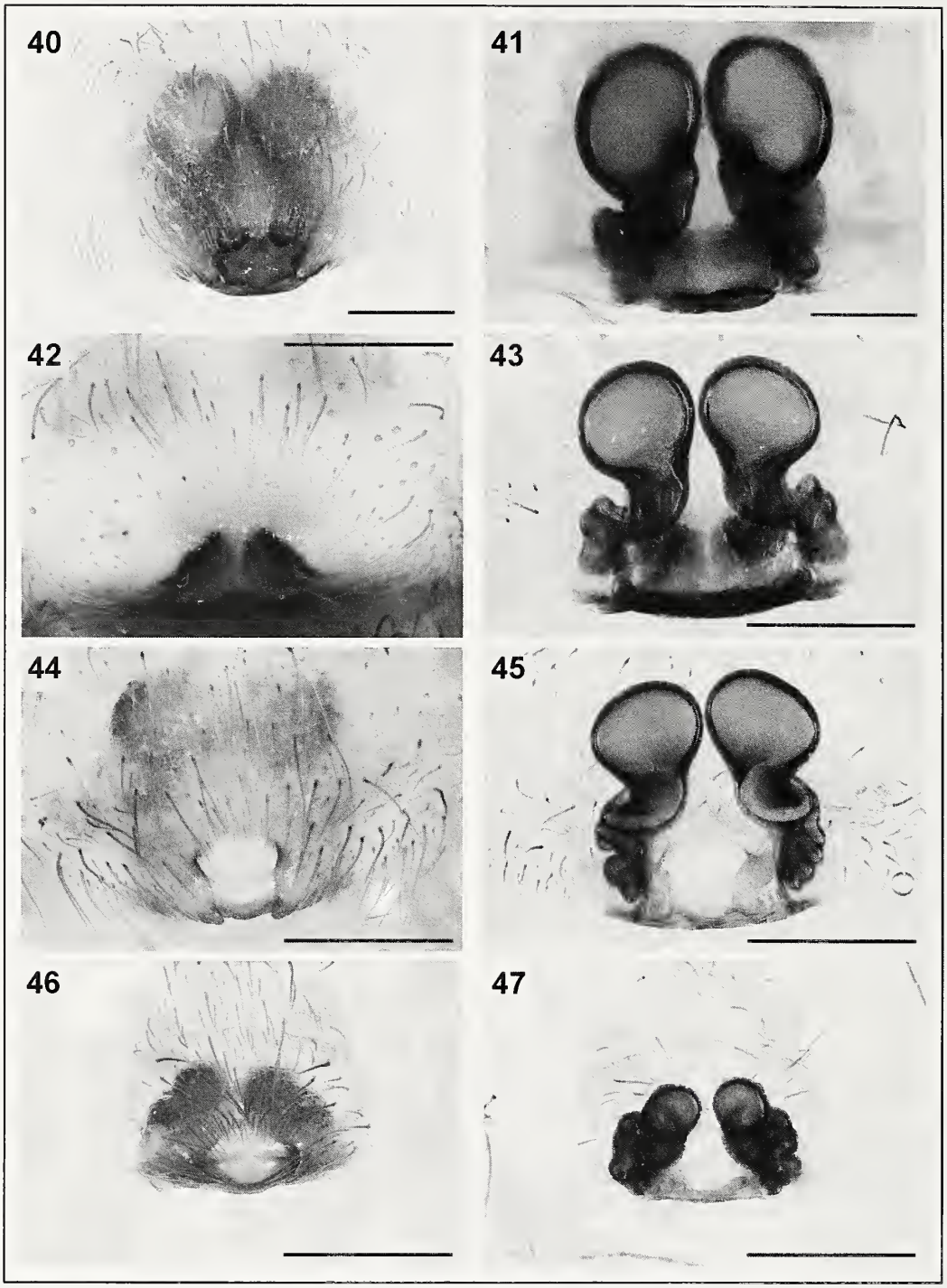
Aterigena soriculata (Simon 1873) new combination
Figs. 11, 12, 17, 18, 27, 28, 35, 36, 46, 47

Tegenaria soriculata Simon 1873:144–146, pl. 1, fig. 20, male and female.

Tegenaria cyrnea Brignoli 1974:392–393, male and female, synonymized by Dresco & Célérier 1979:230.



Figures 29–39.—Female epigynum in ventral and vulva in dorsal view. 29, 30. *Aterigena ligurica*; 31, 32. *A. aculeata*; 33, 34. *A. aliquoi*; 35, 36. *A. soriculata*; 37, 39. *A. aspromontensis* n. sp.; 39, vulva in lateral view. AT: atrium; CD: copulatory duct; CO: copulatory opening; FD: fertilization duct; GP: ground plate of the atrium; EV: epigynal vertices projection of lateral margin of the atrium; RC: receptacula. Scale = 0.5 mm.



Figures 40–47.—Female epigynum and vulva in ventral and dorsal view. 40, 41. *Aterigena ligurica*; 42, 43. *A. aculeata*; 44, 45. *A. aliquoi*; 46, 47. *A. soriculata*. Scale = 0.5 mm.

Malthonica soriculata (Simon): Guseinov et al. 2005:164; Platnick 2009.

Type material.—Several specimens in the collection of the MNHN were found in the jar labeled "1967" and containing several unlabeled vials. According to Dresco & Célérier (1979) these represent Simon's syntypes. The samples contain one male and several females with dissected and removed epigynes that were not traceable. Sub *Tegenaria cyrnea* Brignoli: FRANCE: *Corsica*: Poggiolo: Holotype male, summer 1922 (MHNG); 1 male, 2 females, paratypes, same locality and collecting data as holotype (MHNG, 1 male and 1 female measured).

Other material.—FRANCE: *Corsica*: Forêt de Valdo Niello: 5 females, 7 juv., 22 May 1974 (NHMW); Haute-Corse, Corte, Gorge de la Restonica (42.3N, 9.1333E): 1 female, 1 June 1999, van Keer (KK, Nr. 1917, measured); Col de Vizzavona: 1 female, 2 September 1953, Kahman (SMF, Nr. 8937/1-135); Mt. S. Pietro at Morosaglia: 1 female, 22

September 1953, Kahman (SMF, Nr. 8938/1-135); Mt. d'Oro: 2 females, 3 September 1953, Kahman (SMF, Nr. 8936/2-135); Vizzavona: 1 male, 1 female, 29 April 1928, Wiehle (SMF, Nr. 20668/2-135).

Description.—As *A. ligurica*, but differing in the following characters:

Measurements of male: Carapace 4.47 long, 3.23 wide. Head region 1.91 wide; PER 1.0 wide. Chelicerae 2.06 long, 0.91 wide. Labium wider than long. Sternum 2.24 long, 1.86 wide. Opisthosoma 3.42 long, 1.88 wide. Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length: 0.64. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	1.64	0.66	0.74	-	1.37	4.41
I	3.63	1.68	3.11	3.46	2.09	13.97
II	3.49	1.53	2.72	3.12	2.10	12.96
III	3.49	1.50	2.60	3.64	1.99	13.22
IV	3.92	1.63	3.52	4.79	2.31	16.17

Measurements of females ($n = 2$)*:* Carapace 4.14–5.07 long, 2.93–3.48 wide. Head region 1.56–2.16 wide; PER 0.93–1.0 wide. Chelicerae 2.02–2.22 long, 0.97–1.05 wide. Gnathocoxa ratio width to length: 0.6. Sternum 2.29–2.57 long, 1.81–2.02 wide. Opisthosoma 5.99 long, 3.71 wide. Epigynal plate 0.36–0.39 long, 0.56–0.59 wide; atrium 0.16–0.18 long, 0.23–0.27 wide. Receptacula 0.17 wide. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	1.48–1.73	0.71–0.86	0.88–1.00		1.53–1.75	4.60–5.34
I	2.87–3.39	1.38–1.67	2.44–2.78	2.57–2.98	1.82–1.98	11.08–12.8
II	3.03–3.28	1.42–1.57	2.21–2.4	2.45–2.95	1.56–1.85	10.67–12.05
III	3.07–3.31	1.39–1.62	2.1–2.33	2.46–3.37	1.64–1.73	10.66–12.36
IV	3.63–3.93	1.64	3.00–3.17	3.91–4.57	1.89–2.26	14.07–13.93

Eyes (*Fig. 11*)*:* Diameter: PME: 0.17–0.18; PLE: 0.18–0.21; AME: 0.13–0.18; ALE: 0.19–0.21. Distances: PME–PME less than diameter of PME; PME–AME less than or equal to diameter of PME; PME–PLE less than or equal to diameter of PME; PME–ALE less than 1.5 diameter of PME; AME–AME about 0.5 diameter of AME. Clypeus height (measured under AME) less than 2.5 times diameter of AME; (measured under ALE) about 1.5 times diameter of ALE.

Coloration: Two longitudinal symmetrical dark bands present on carapace, interrupted, sometimes reduced to triangular dots, intensified by white and black plumose hairs. Opisthosoma dark green-brownish, at the cardiac mark yellowish with dots on the sides, continuing in broad chevrons (~ 5) posteriorly (Fig. 12). Legs not annulated.

Additional somatic characters: Tarsus I with 7–8 dorsal trichobothria, tarsi II–IV with 7. Colulus dark, sometimes only partially. Both segments of PLS very weakly darkened. PMS slightly smaller than ALS. The formulae of leg spination are listed in Table 3.

Male palp (*Figs. 17, 18, 27, 28*)*:* RTA with large dorsal branch, distally truncated and strongly sclerotized; lateral branch developed as a weakly sclerotized point. Embolus originating (free apex) between 7 and 8 o'clock position; length (only free apex) less than 1.75 times cymbium width; distal tip between 2 and 3 o'clock position. Median apophysis originating between 4 and 5 o'clock position.

Epigynum and vulva (*Figs. 35, 36, 46, 47*)*:* Epigynal plate sclerotized with distinct atrium, transversely oval in shape; anterior margin of atrium sclerotized at epigynal plate, gradually becoming membranous. Ground plate of atrium transversally subdivided by straight groove: anterior part membranous or weakly sclerotized, semicircular in shape; posterior part sclerotized, forming semicircular bar. Copulatory openings barely visible, located medially of atrium. Receptacula small, globular.

Comparison to other species.—*A. soriculata* differs from the other congeners in the smaller dimensions of carapace and cymbium; in the ventral margin of dorsal branch of RTA, which is slightly bent ventrally (straight in *A. ligurica*, *A. aculeata* and *A. aliquoi*); in the distal plate of median apophysis (simpler and relatively narrower than in *A. ligurica* and *A. aliquoi*); in the embolus, which is shorter than twice cymbium width (more than twice cymbium width in *A. ligurica*, *A. aculeata* and *A. aliquoi*); in the relatively short male palpal tibia (much longer in *A. aspromontensis* n. sp.) (Figs. 17, 18, 27, 28); in the transversally divided atrium (by straight groove, but curved in *A. aspromontensis* n. sp.) with semicircular anterior part and relatively small and globular receptacula (relatively large in *A. ligurica*, *A. aculeata* and *A. aliquoi*, also small but oval in *A. aspromontensis* n. sp.) (Figs. 35, 36, 46, 47).

Natural history.—Adult specimens collected from May to October. Little information available on habitat requirements. One specimen collected under stones in a pine forest.

Distribution (Fig. 56).—Corsica (France) (Dresco & Célérier 1979; Simon 1873). The species was also reported from Sardinia (Italy) (Garneri 1902; Kraus 1955). The record by Garneri (1902:72) was unavailable for study. Material by Kraus (1955:379, SMF-Nr. 9110) concerns *T. parietina* (cf. Bolzern et al. 2008).

Aterigena aspromontensis new species
Figs. 19, 20, 37–39, 48–55

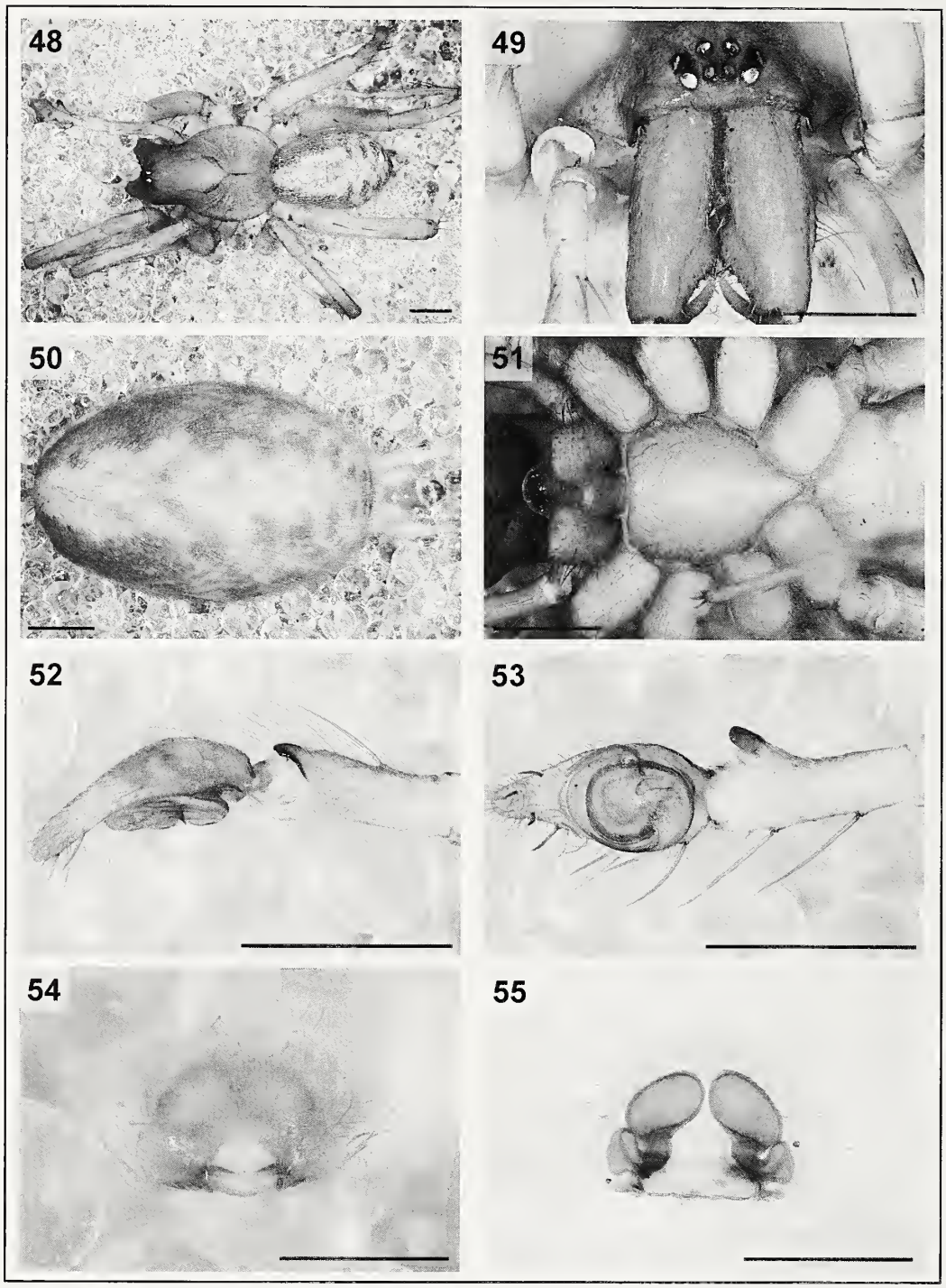
Type material.—ITALY: *Calabria*: Reggio Calabria, Santo Stefano d'Aspromonte, above Gambarie (1600 m): holotype male, 5 female paratypes, 18 August 1978, Bianchi (MSNB).

Other material.—ITALY: *Calabria*: Reggio Calabria, Santo Stefano d'Aspromonte, between Gambarie and Montalto (1500 m): 3 females, June 1990–1991, Buttarelli, Ghilardi, Pantini & Valle (MSNB).

Etymology.—The new species is named after the mountain massif Aspromonte in the province of Reggio Calabria where the known specimens have been found.

Description.—*Male holotype:* carapace 3.27 long, 2.27 wide. Head region 1.45 wide; PER 0.75 wide. Chelicerae 1.69 long, 0.71 wide. Labium as wide as long. Gnathocoxa ratio width to length: 0.6. Sternum 1.65 long, 1.44 wide. Opisthosoma 3.03 long, 1.91 wide. Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length: 0.73. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	1.63	0.67	0.92	-	1.06	4.28
I	2.52	1.15	2.12	2.48	1.64	9.91
II	2.48	1.09	1.91	2.42	1.51	9.41
III	2.52	1.03	1.94	2.73	1.49	9.71
IV	3.03	1.09	2.64	3.64	1.82	12.22



Figures 48–55.—*Aterigena aspromontensis* n. sp. 48. Habitus, male holotype; 49. Face, male holotype; 50. Opisthosoma, female paratype; 51. Sternum, male holotype; 52. Left male palp, retrolateral view; 53. Left male palp, ventral view; 54. Epigynum, ventral view; 55. Vulva, dorsal view. Scales: 48–53 = 1.0 mm, 54, 55 = 0.5 mm.

Female paratypes (*n* = 5): carapace 3.13–4.26 long, 2.10–2.76 wide. Head region 1.50–1.95 wide; PER 0.75–0.95 wide. Chelicerae 1.6–2.0 long, 0.7–1.0 wide. Labium as long as wide. Gnathocoxa ratio width to length: 0.6–0.7. Sternum 1.75–2.20 long, 1.55–1.95 wide. Opisthosoma 4.75–5.00 long, 3.1–3.4 wide. Epigynal plate 0.49–0.57 long, 0.61–0.73 wide; atrium 0.16–0.17 long, 0.18–0.19 wide. Receptacula 0.24 wide. Leg measurements:

	fe	pa	ti	mt	ta	total
palp	1.27–1.51	0.60–0.70	0.77–1.00	-	1.33–1.52	3.97–4.73
I	2.50–2.94	1.13–1.40	1.88–2.33	2.00–2.58	1.42–1.76	6.93–8.43
II	2.27–2.85	1.06–1.24	1.61–2.06	1.82–2.49	1.45–1.58	6.39–7.73
III	2.21–2.76	1.00–1.27	1.58–1.91	2.24–2.72	1.30–1.55	6.09–7.49
IV	2.79–3.48	1.12–1.39	2.33–2.91	3.12–3.88	1.64–1.91	7.88–9.69

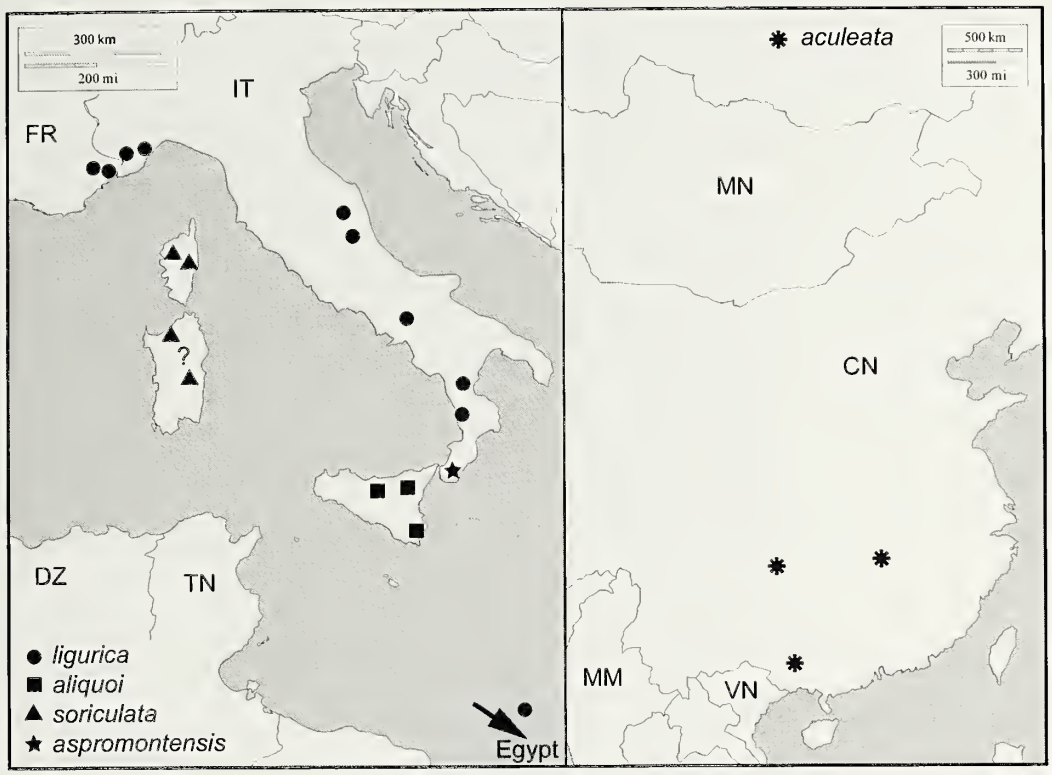


Figure 56.—Known sites of *Aterigena* n. gen.. *A. ligurica* also mentioned from "Hispania". Digital map provided by http://histgeo.ac-aix-marseille.fr.

Eyes: In dorsal view both eye rows straight or slightly recurved; in frontal view PER procurved and AER straight or slightly procurved (Fig. 48). Diameters: PME: 0.124–0.143; PLE: 0.143–0.162; AME: 0.095–0.133; ALE: 0.143–0.162. Distances: PME–PME less than diameter of PME; PME–AME less than diameter of PME; PME–PLE equal to diameter of PME; PME–ALE less than 1.5 diameter of PME; AME–AME about 0.5 times diameter of AME or slightly more; AME–ALE about 0.5 times diameter of AME. Clypeus height (measured under AME) less than 2.5 times diameter of AME; (measured under ALE) less than 1.5 times diameter of ALE.

Coloration: Margin of carapace narrowly and continuously dark; two longitudinal symmetrical dark bands on carapace, interrupted and sometimes reduced to triangular dots. Sternum with indistinct light median band (Fig. 50). Opisthosoma dark green-grayish, anteriorly with two light and partially fused bands, continuing in fused chevrons posteriorly (Fig. 49). Legs weakly annulated, hardly visible on femora ventrally.

Additional somatic characters: distal margin of labium weakly concave. Plumose hairs present on carapace, legs and opisthosoma. Promargin with 4 teeth, second one from proximal largest; retromargin with 4–5, most proximal tooth biggest. Trochanter III and IV notched. Tarsus I with 5–8 dorsal trichobothria, tarsi II–IV with 6–8. Colulus forming rectangular plate, pale, distal margin straight. PLS longer than all others with distal segment shorter than or as long as basal segment, both darkened. PMS as long as ALS. ALS not darkened. The formulae of leg spination are listed in Table 3.

Male palp (Figs. 19, 20, 51, 52): RTA with big dorsal branch, distally truncated and strongly sclerotized; lateral branch developed as weakly sclerotized digitiform appendix; ventral branch forming weakly developed rounded ridge. Embolus originating (free apex) between 8 and 9 o'clock position; length (only free apex) less than 1.75 times width of cymbium; distal tip at 2 o'clock position. Conductor lamella-like, distally only weakly elongate (parallel to cymbium), very weakly arched and laterally folded along entire length; shorter than alveolus; distally not reaching beyond distal margin of alveolus; terminal end forming sclerotized peak, pointing ventrally (in retrolateral view). Connection of conductor and tegulum membranous. Median apophysis consisting of membranous base and thin, broad sclerotized distal plate, spoon-like, originating between 4 and 5 o'clock position; protruding ventrodistally (MA on left palp of holotype slightly retracted, probably due to desiccation; see Figs. 19, 20); basi slightly smaller than median apophysis long.

Epigynum and vulva (Figs. 37, 39, 53, 54): Epigynal plate sclerotized with distinct atrium, transversely oval in shape; anterior margin of atrium gradually changing from sclerotized epigynal plate to membranous structure; atrium reaching posteriorly epigastral furrow. Ground plate of atrium transversally subdivided (slightly concave medially): anterior part membranous or weakly sclerotized, semicircular in shape; posterior part stronger sclerotized forming semicircular band. Lateral margin of atrium with elongated vertices. Receptacula visible through plate. Copulatory openings indistinct, located medially of atrium. Copulatory duct short, straight; receptacula small, oval or globular; fertilization ducts short, weakly convoluted.

Comparison to other species.—*A. aspromontensis* differs from other *A.* spp. as indicated in the key (also see discussion of *A. soriculata*). Male *A. aspromontensis* n. sp. can be

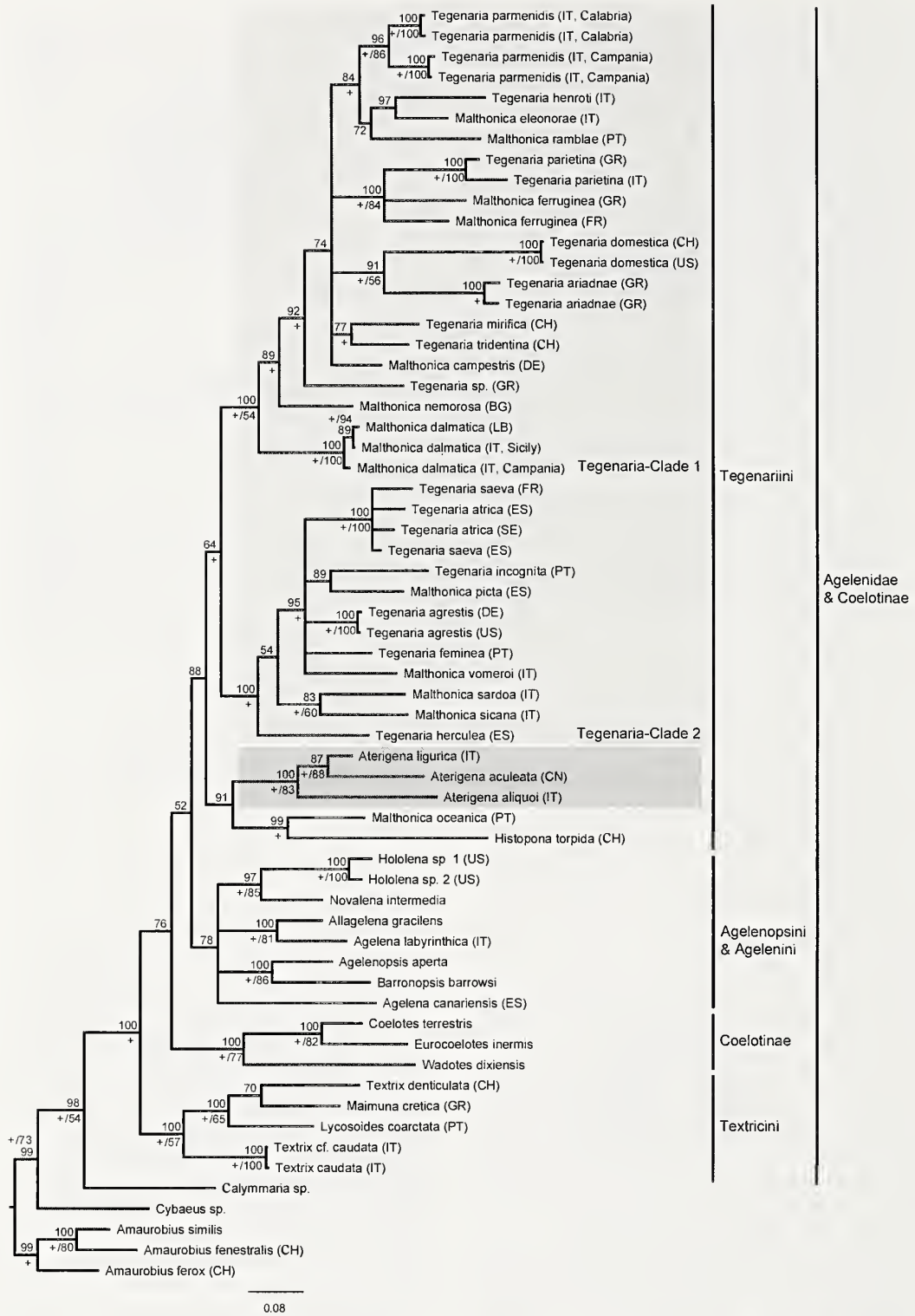


Figure 57.—Cladogram of Tegenariini from Bayesian analysis of CO1 sequences. Only clades supported by a posterior probability larger than 50% are shown (values given at each node). Clades present in maximum parsimony analysis are indicated by "+". Values after slash indicate Bootstrap values higher than 50%. The nomenclature strictly follows Platnick (2010).

separated from those of *A. soriculata* by shorter and smaller distal apex of conductor and relatively long palpal tibia (much shorter in *A. soriculata*) (Figs. 19, 20, 51, 52). Females can be separated from *A. soriculata* by transverse dividing groove of atrium being slightly concave (straight in *A. soriculata*), oval-shaped receptacula and only weakly convoluted and short fertilization ducts (stronger convoluted and longer in *A. soriculata*) (Figs. 37–39, 53, 54).

Natural history.—No information available.

Distribution.—Calabria (Italy) (Fig. 56).

DISCUSSION

The tribe Tegenariini currently comprises six nominal genera in addition to *Aterigena* n. gen., which is described here. *Aterigena* n. gen. resembles *Hadites*, *Histopona* and *Malthonica* in the notched trochanters III and IV. It differs from them in the presence of dorsal and lateral spines on patellae III and IV as well as 1–2 ventral spines on tarsus IV. In erecting *Aterigena* n. gen. and hereby removing some species from *Tegenaria* s.l., the latter becomes morphologically more homogeneous. In addition, the narrow definition of *Malthonica* by Barrientos & Cardoso (2007) and the concept of *Pseudotegenaria* by Brignoli (1971a), rather than that of Lehtinen (1967), are adopted here. With these actions the genera become morphologically compact and, above all, diagnosable. Morphological and molecular data support the monophyly of these taxa (also see key to genera and Fig. 57).

The phylogenetic relationships between the genera of Tegenariini, in contrast, remain unclear. For resolving the intrageneric relationships, additional morphological characters and genes will be analyzed (Bolzern et al. in prep.).

Aterigena n. gen. includes five species, which have a widely disjunct distribution in the Palearctic region (4 spp. in the Mediterranean Basin and 1 sp. in China). *A. ligurica* is relatively widely distributed in continental Italy and adjacent areas of Southern France, possibly also in Spain; *A. aliquoi* is endemic to Sicily; *A. soriculata* to Corsica (maybe also Sardinia) and *A. aspromontensis* n. sp. to Calabria (Fig. 56). Two female specimens of *A. ligurica* are reported from outside Italy and France. One specimen is recorded from Spain without further information. Additional collecting is necessary to confirm its occurrence in Spain. The second specimen is reported from Alexandria (Egypt), which may be the result of inadvertent human introduction.

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Endnote.—Recently, J.A. Miller, A. Carmichael, M.J. Ramírez, J.C. Spagna, C.R. Haddad, M. Rezác, J. Johannesen, J. Král, X.P. Wang & C.E. Griswold transferred Coelotinae to Agelenidae and placed the Australian genera outside Agelenidae. [2010. Phylogeny of entelegyne spiders: affinities of the family Penestormidae (NEW RANK), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). Molecular Phylogenetics and Evolution 55, 786–804]

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Webs in vitro and in vivo: spiders alter their orb-web spinning behavior in the laboratory

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Abstract. Many studies of the elegant architectures of orb webs are conducted in controlled laboratory environments that remove environmental variability. The degree to which spider behavior in these circumstances resembles that of spiders in the wild is largely unknown. We compared web arehitecture and silk investment of furrowed orb weavers *Larinioides cornutus* (Clerck 1757) building webs in laboratory cages and spinning webs on fences in the field and found significant differences. The volume of major ampullate silk in radii was 53% lower in cage webs, primarily because the silk was 50% thinner, but also because spiders tended to spin 14% fewer radii than in fence webs. Cage spiders also invested about 40% less flagelliform silk and aggregate glue in the capture spiral, although the difference was not statistically significant, a trend primarily driven by a decrease in the length of the glue-coated capture spiral. These patterns were consistent with spiders reducing silk investment when building at new web sites while they assessed insect abundance. Differences in the type of substrate for web attachment, amount of available space, and condition may also have influenced web architecture. Cage webs were more symmetrical than fence webs, which displayed an unusual horizontal asymmetry that may have maximized their capture areas within the constraints of the available fence-railing attachment sites. Our findings suggest using caution when generalizing the properties of laboratory-spun webs to more natural conditions. More importantly, they demonstrate that orb spiders actively modify their behaviors when spinning webs under different conditions.

Keywords: Foraging, silk investment, behavioral plasticity, silk thread size, web architecture

The silk that orb spiders invest in webs is critical for determining energetic gain through captured insect prey (Sherman 1994; Blackledge & Eliason 2007). Therefore, the rich variation in sizes and shapes of orb webs among different species of spiders may potentially be explained by the relative costs and benefits of silk investment and web architecture for particular environments (Shear 1986; Eberhard 1990; Higgins 1995). For instance, spiders should invest more silk in environments that are least likely to damage the web or that are most likely to yield prey (Higgins & Buskirk 1992; Blackledge & Wenzel 2001; Segoli et al. 2004). Spiders modify web-spinning behavior in response to environmental factors that include wind (Eberhard 1971; Henschel & Lubin 1992), prey abundance (Pasquet et al. 1994; Higgins 1995; Blackledge 1998; Herberstein et al. 2000; Blackledge & Zevenbergen 2007), prey taxon (Sandoval 1994; Tso et al. 2007), competition with other individuals (Leborgne & Pasquet 1987; Ward & Lubin 1992), frequency of damage by non-prey animals (Chmiel et al. 2000), and size of the vegetation scaffold on which the web is constructed (Lubin et al. 1991). Typically, such studies document changes in specific web properties including size of the capture area as well as the total length or spacing of threads, and then attempt to relate these changes to foraging investment under different environmental conditions.

However, accurately assessing foraging investment is difficult, as it may be possible to divert available silk resources in multiple ways to achieve equivalent foraging success. For example, a web with closely spaced threads is very good at stopping and retaining large insects, but a larger web increases the number of interceptions (Eberhard 1986; ap Rhisiart & Vollrath 1994; Nakata & Ushimaru 2004; Blackledge & Eliason 2007). For a given volume of silk, thick, high energy absorbing threads necessarily trade off with large capture area or a fine mesh width. The important role of tradeoffs between web architecture and silk structure has largely been ignored by studies that focus solely on changes in web architecture, which represent almost all previous work in this area (e.g. Sherman 1994; Herberstein et al. 1997; Nakata & Ushimaru 1999; Heiling & Herberstein 2000; Nakata 2007).

Orb webs are spun largely using two very different types of fibrous silk. The potential for a web to stop the flight of different insects depends on the amount and placement of each silk within the web. Spiders first produce an outer framework and supporting radial threads using dry dragline silk from the major ampullate (MA) silk glands (Foelix 1996). They then spin a spiral of elastic, adhesive silk onto the radial threads using a combination of fibrous flagelliform (Flag) silk and gluey aggregate (Ag) silk (Foelix 1996). Together these different silks compose a planar orb (Fig. 1) that functions in first intercepting insects, then absorbing the kinetic energy of their flight, and finally adhering to the insects long enough for the spider to capture them (Blackledge & Hayashi 2006).

Many studies of orb webs are based on laboratory-confined spiders due to experimental convenience and control over the environment (Zschokke & Herberstein 2005). However, such spiders spin webs in an environment that is fundamentally different from their natural habitat. This could potentially influence many features of webs (Brown 1981; Gillespie & Caraco 1987; Higgins et al. 2001). Here, we compare the difference in web investment between spiders spinning in an outdoor setting along fence railings that impose size constraints on webs but is otherwise natural and a laboratory environment that imposes not just size constraints but also changes in prey cues, web supports and weather, using the furrowed orb spider *Larionioides cornutus* (Clerck 1757) (Araneae: Araneidae). We test the prediction that the

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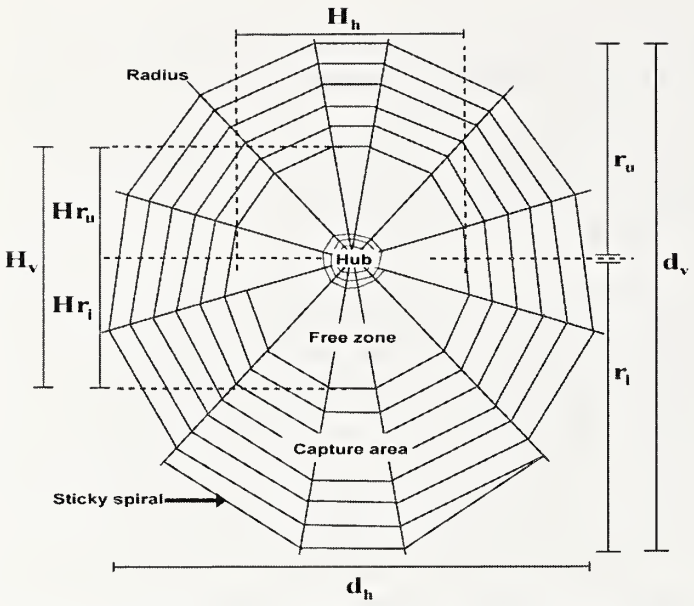

Figure 1.—Web architecture parameters measured: Vertical diameter (d_v) of the capture area, horizontal diameter of the capture area (d_h), upper radial length (r_u), lower radial length (r_l), upper free zone length (Hr_u), lower free zone length (Hr_l), free zone vertical diameter (H_v), and free zone horizontal diameter (H_h). Capture area is delimited by the outermost sticky spirals.

laboratory environment will affect silk investment and web architecture and find that some measures of investment are reduced in the laboratory environment.

METHODS

Study species.—We compared silk investment and architecture of webs spun by a single population of *L. cornutus* in the field versus laboratory. *L. cornutus* is a common nocturnal orb-weaving spider, a cosmopolitan species known for building webs above or near water, particularly on human-made structures such as bridges (Burgess & Uetz 1982; see also Heiling 1999; Heiling & Herberstein 1999). These spiders often spin webs at unusually high population densities for orb-weaving spiders. All of the spiders in this study came from a 100-m long bridge over the Cuyahoga River in Akron, Summit County, Ohio, USA. Multiple generations of spiders coexisted, and webs were in close proximity but not interconnected. These spiders usually initiate web construction at dusk and then hunt at the hub during the night while remaining in a retreat located above or to the side of the web during daylight.

Fence spiders.—We sampled the webs of 11 sexually mature females [132 ± 64 mg, (mean ± SD) and 4.3 ± 0.6 mm carapace length] on the fence railings of the bridge in August and September 2008. This population was also the source of the specimens used for the cage treatment. Fence webs were spun between the vertical confines of wooden railings, 18–25 cm apart; or metal railings, 23–24 cm apart (Fig. 2). Spiders were collected from the webs and web measurements made between 21:00 and 23:00 h, shortly after webs were spun. We recognized freshly spun webs by their intact spirals and radial spokes as well as the lack of insects or detritus.

Caged spiders.—Thirteen sexually mature female *L. cornutus* (131 mg ± 63 mg and 4.7 mm ± 0.6 mm carapace length) were captured in August 2007, placed in cages measuring 40 × 40 × 10 cm in the laboratory, and allowed to spin webs (Agnarsson & Blackledge 2009). The cages were composed of metal frames, with clear plexiglass on the 40 × 40 cm faces, and insect screen on the remaining four 10-cm-wide edges. Spiders experienced minimal temperature variation (22 ± 3 °C), airflow and insect cues, as well as a constant 15:9 h L:D cycle in the laboratory. The cages also provided stiff vertical supports for the sides of webs, which were generally lacking for one or both sides of fence webs. Spiders typically constructed webs within 1–5 days of captivity and were not fed prior to web spinning.

Fence (n = 11) and caged spiders (n = 13) were equivalent in body mass and carapace width but differed in body

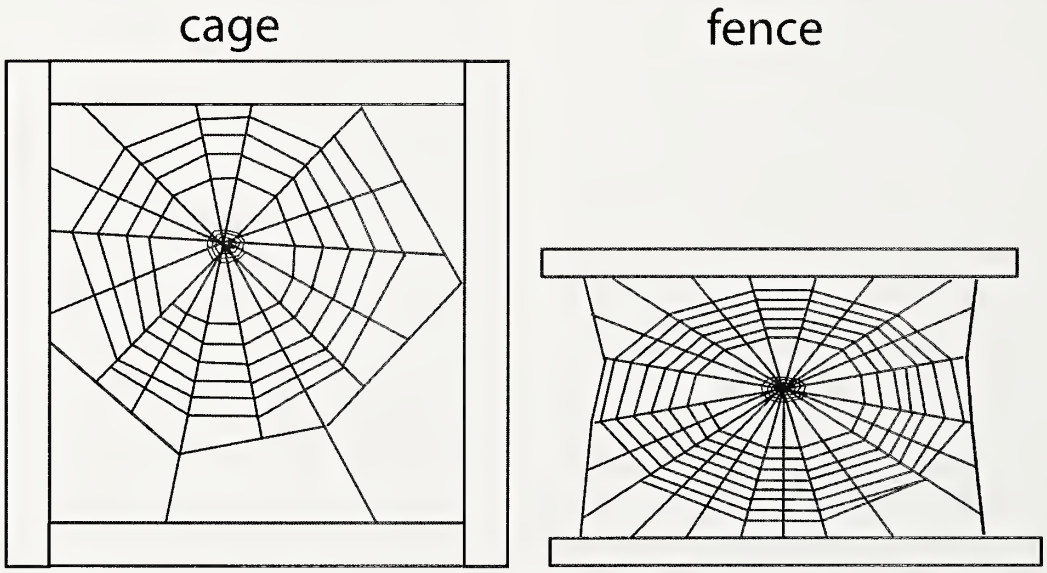

Figure 2.—Sketch summarizing the important differences between cage and fence webs. The relative sizes of the substrates reflect the different shapes of space available to spiders in the laboratory and field. Cages measured 40 × 40 × 10 cm, while fence railings were separated by 18–25 cm but allowed semi-unconstrained widths of webs. Only 1/3 of the typical spiral threads are shown, but radii count is similar to real webs.

Table 1.—Body parameters (median, minimum, maximum) of spiders used in the cage ($n = 13$) and fence ($n = 11$) web comparisons. Weight and carapace width did not differ in median between cage and fence spiders (Mann-Whitney U test by ranks, $P = 1.00$ and $P = 0.28$, respectively). Body condition was significantly lower in cage spiders (Mann-Whitney U test by ranks, $P = 0.01$).

	Cage spiders (median, min, max)	Fence spiders (median, min, max)
Weight (mg)	102, 64, 265	117, 42, 213
Carapace width (mm)	3.7, 3.2, 5	3.6, 2.6, 4.1
Body condition	−0.12, −0.33, 0.27	0.07, −0.07, 0.16

condition, with fence spiders having higher body condition (Table 1). For each spider, we measured aspects of silk structure and orb-web architecture that played potentially critical roles in prey capture and allowed quantification of total silk investment by spiders.

Web architecture measurements.—For caged spiders, web architecture was measured from digital photographs taken from webs placed in front of a shadow box and illuminated from the sides by fluorescent lighting (Langer & Eberhard 1969; Zschokke & Herberstein 2005). For fenced spiders, it was difficult to obtain clear photographs of entire webs so that architecture was instead measured directly in the field using techniques described by Blackledge et al. (2003). For both types of webs, we measured the vertical diameter of the capture area (d_v), horizontal diameter of the capture area (d_h), upper radial length (r_u), lower radial length (r_l), upper free zone length (Hr_u), lower free zone length (Hr_l), free zone vertical diameter (H_v), and free zone horizontal diameter (H_h) (Fig. 1).

Capture area is delimited by the outermost sticky spirals and determines the number of insects that a web potentially intercepts. Capture area was measured directly from photographs of laboratory webs using Image J (Rasband 1997–2009) and was calculated for field webs using the Adjusted Radii-Hub formula (Blackledge & Gillespie 2002):

$$\text{Capture area} = \left[\tfrac{1}{2}\pi\, r_{au}^2 - \tfrac{1}{2}\pi(Hr_u)^2\right] + \left[\tfrac{1}{2}\pi r_{al}^2 - \tfrac{1}{2}\pi\,(Hr_l)^2\right],$$

$$\text{where } r_{au} = (r_u + d_h/2)/2 \text{ and } r_{al} = (r_l + -d_h/2)/2.$$

The density of threads within webs influences the sizes of insects likely to be intercepted, but more importantly affects both the ability of webs to absorb the kinetic energy of flying insects and whether webs retain insects long enough to be captured by spiders (Blackledge & Zevenbergen 2006). Therefore we counted the number of radii and the number of spiral threads along four axes (top, bottom, left, and right). Mesh width, the distance between adjacent capture spirals, was calculated along each axis and then averaged (Herberstein & Tso 2000).

Spiders usually place the web hub above the center of the orb, resulting in a web with a larger lower capture region (Krink & Vollrath 1997, 2000). This hub asymmetry typically increases with spider size (Kuntner et al. 2008) and is hypothesized to decrease the time necessary for a heavy spider to reach an insect caught in the lower catch region (Masters & Moffet 1983; Nentwig 1985; Herberstein & Heiling 1999; Heiling 2004). Alternately, the larger lower capture area may reduce the high metabolic cost of raising the abdomen above the body when spiders spin the capture spiral in the upper region of the web (Herberstein & Heiling 1999). Hub asymmetry is defined in Blackledge & Gillespie (2002) as:

$$\text{Hub asymmetry} = 1 - r_u/r_l.$$

Most orb webs are not round, but rather elliptical. The exaggerated vertical axis of webs may facilitate prey capture by taking advantage of the tendency of prey to tumble downward as they struggle. Web asymmetry describes the relationship between height and width of the orb and is defined in Blackledge & Gillespie (2002) as:

$$\text{Web asymmetry} = 1 - d_h/d_v.$$

Perfectly round webs have a web asymmetry value of 0. A web asymmetry < 0 indicates a web that is wider than it is tall, and web asymmetry > 0 indicates a web that is taller than wide.

Silk structure.—Finally, investment of silk in a web can be quantified by measuring the structural sizes of threads and glue droplets. For each web, four radial threads, one from each cardinal axis, were collected onto cardboard holders described in Agnarsson & Blackledge (2009). Cyanoacrylate adhesive (Superglue™) was applied to two sides of a 16 mm hole in the center of the card, which was then pressed against a radius. After drying for several seconds, the radial thread was cut on either end of the card using a portable soldering iron, releasing the thread from the web.

To measure spiral thread diameter, the silk was collected directly onto a glass microscope slide by placing the slide behind the four outermost strands and then gently pressing the slide against the web. The spiral threads were then cut along the edges of the slide with a portable soldering iron. The glass slide caused the glue droplets to adhere and flatten, thereby securing the threads to the slide and making the core axial thread visible. We used the same procedure as Agnarsson & Blackledge (2009) and Blackledge et al. (2005) to measure radial and spiral thread diameters using polarized light microscopy at 1000× magnification.

Total volume of flagelliform silk in the capture spiral was calculated by first determining the total length of the capture spiral, typically designated as capture thread length (CTL) (Sherman 1994):

$$\text{CTL} = \pi\,(\text{average \# spirals along the 4 web axes})\,[(r_u + d_h + r_l)/4 - (Hr_u + H_h + Hr_l)/4].$$

The factor in the brackets represents the average width of the capture area and is estimated by subtracting the average free zone radius along the four cardinal axes from the average capture area radius along the four cardinal axes.

Volume was then computed as:

$$\text{total spiral thread volume} = (\text{CTL})\,\pi\,(\text{hypothetical spiral diameter}/2)^2.$$

The diameter of a hypothetical thread that would be equivalent in cross-sectional area to the two strands of

spiral fibers that typically compose capture spirals was calculated as:

$$\text{hypothetical spiral thread diameter} = 2\left[2\pi r_{ss}^{2}\right]^{0.5}/\pi,$$

where r_{ss} was the measured radius of a single strand, assuming equal radius of each strand. Hypothetical radial thread diameter was calculated in an identical manner, also assuming that the radial thread was composed of two equally sized strands. In the rare instances in which we observed four-stranded radial or capture threads, all four strands were assumed to be of equal diameter, and a factor of $\sqrt{2}$ was included in the hypothetical thread diameter formula shown above. The average hypothetical thread diameter for a specific web and specific silk type was then calculated as the average of the four collected thread samples.

Total radial thread volume was calculated as:

$$\begin{aligned}&\text{Total radial thread volume}\\ &= (\text{average single radial length})\\ &\quad (\#\text{ radial threads})(\text{average cross-section area})\\ &= (r_u + d_h + r_u)/4\ (\text{radii count})\\ &\quad \pi\,(\text{hypothetical radial thread diameter}/2)^2.\end{aligned}$$

To measure glue droplet volume on the capture spiral silk, we suspended threads between 3 mm diameter wooden supports secured to a microscope slide. The four outermost capture spiral rows, adjacent to those already captured by direct adhesion to glass, were collected simultaneously by pressing this slide against the web so that the threads bridged the gap between the parallel supports (Agnarsson & Blackledge 2009). Glue droplets were photographed at 10 or 100× magnification, and the length and width of the first and third droplet from the left edge of the photo were measured. This avoided experimenter bias toward measuring large or small droplets. We did not measure the much smaller secondary droplets that often occur between primary droplets because secondary droplets contribute minimally to total glue volume (Opell & Hendricks 2007). The volume of a single droplet of glue (SDV) was calculated as:

$$\text{SDV} = (\text{droplet width})^2(\text{droplet length})/15.$$

This formula accounts for the anisotropy of the droplet shape, which tends to be longer than wide as it adheres to the spiral thread (Opell et al. 2008). The average distance between glue droplets was measured across 10 adjacent droplets. Total volume of glue within the web was then calculated as:

$$\begin{aligned}&\text{Total glue volume} =\\ &(\text{SDV})(\text{CTL})/\text{average distance between droplets.}\end{aligned}$$

Droplet size can increase with the relative humidity of the air due to the hygroscopicity of glue silk (Mark et al. 1991; Opell & Schwend 2008). Laboratory relative humidity was between 40–60% R.H. during measurement of all threads and thus was lower than the occasional high humidity (90%) that occurred in the field. For all spiders, droplets were measured within approximately 2 h of collection, and hence 2–4 h after web production, to minimize any effect of drying or swelling on droplet volume.

STATISTICAL METHODS

Comparing spider body condition.—Because spiders were collected from the same bridge on consecutive years in autumn, we first determined whether the spiders from fence webs and cage webs differed in body size or condition. Body condition was calculated as the residuals of the regression of log weight onto log carapace width (Table 1) (Jakob et al. 1996). Mann-Whitney U tests were used to test for differences between weight, carapace width, and spider body condition, because these variables were not normally distributed. These tests found that spiders collected from fence and cage webs did not differ in weight ($P = 1.00$) or carapace width ($P = 0.28$), but did differ in body condition ($P = 0.02$), with fence spiders having higher body condition (Table 1). The most likely reason for this difference is that the cohort associated with each year experienced slightly different foraging histories. Thus, location is confounded with body condition, so that some differences between fence and cage webs could be due to difference in body condition.

Comparing webs.—The effect of captivity on web architecture was then tested using Multivariate Analysis of Variance (MANOVA) implemented in Statistica 6.1. We included 13 variables in the model (Table 2). Cross-sectional area of radial (MA) and spiral (Flag) threads, volume of capture silk, volume of glue, and glue droplet spacing were log transformed to meet assumptions of the normal distribution (Shapiro-Wilks W test, $P > 0.05$) and homogeneous variance (Levene's Test for Homogeneity of Variances, $P > 0.05$). Radial volume was transformed by a power exponent of 0.25 to achieve normality. Radii number and web asymmetry were normally distributed but could not be successfully transformed to achieve homogenous variance between cage and fence webs. There is no readily available non-parametric equivalent to MANOVA, hence the MANOVA was also performed without these two variables to confirm that their inclusion did not affect the results. Post-hoc unequal n honest significant difference (HSD) mean comparison tests were used to detect which variable means differed between webs on fences and in cages. Because radial count and web asymmetry did not satisfy all assumptions of parametric tests, and radial volume did so only marginally even after transformation, we also performed univariate Mann-Whitney U tests by ranks for these three variables as raw variables.

RESULTS

There was a significant difference in web properties between cage and fence spiders (MANOVA, Wilks $\Gamma = 0.052$, $F_{13,\,6} = 8.37$, $P = 0.008$). Unequal n HSD tests indicated that laboratory webs had shorter CTL ($P = 0.008$) (Fig. 3D), smaller radial cross-sectional area ($P = 0.03$), and lower asymmetry ($P = 0.006$) than field webs (Table 2). The significant effect of web location in the overall model and the significant post-hoc mean differences of CTL and radial cross-sectional area were not changed by excluding the non-parametric variables, web asymmetry and radial count, from the MANOVA model.

The univariate Mann-Whitney U tests identified lower median web asymmetry in fence webs (fence median −0.27, range −0.8 to 0.5, cage median 0.11, range −0.18 to 0.4, Mann-Whitney $U = 19$, $P = 0.003$, Fig. 3G). The Mann-

Table 2.—Web architecture (mean ± SD, *n*) compared between cage and fence spiders. For the variables that met the normal distribution and homogeneous variance assumptions of MANOVA, significant post-hoc unequal *n* HSD mean differences between cage and field are indicated with a * ($P < 0.05$). Significant median differences identified by the Mann-Whitney *U* tests are indicated with a † ($P < 0.05$). Sample size for the glue measurements was smaller than for the other samples due to accidental destruction prior to measurement. Capture thread length is abbreviated as CTL.

	Cage webs	Fence webs	% difference
Web architecture			
Capture area (cm^2)	462 ± 213 (13)	593 ± 247 (11)	22
Number of radii	17.8 ± 2.0 (13)	21 ± 3.2 (11)	14†
CTL (cm)	555 ± 217 (13)	963 ± 277 (11)	42*†
Mesh width (mm)	4.6 ± 0.8 (13)	4.2 ± 0.8 (11)	−10
Web asymmetry	0.1 ± 0.1 (13)	−0.3 ± 0.3 (11)	136†
Hub asymmetry	0.3 ± 0.2 (13)	0.2 ± 0.2 (11)	−50
Silk structure			
Radial (MA) cross-section area(μm^2)	5.6 ± 3.6 (13)	11.3 ± 5.8 (11)	50*†
Capture spiral (Flag) cross-section area (μm^2)	6.7 ± 1.9 (13)	4.5 ± 1.0 (11)	−33
Glue single drop vol.(μm^3)	7087 ± 5062 (12)	7800 ± 5592 (8)	10
# glue droplets/mm	17 ± 6 (12)	16 ± 6 (9)	−8
Silk investment			
Radial volume (mm^3)	0.016 ± 0.008 (13)	0.034 ± 0.019 (11)	53†
Spiral volume (mm^3)	0.026 ± 0.020 (13)	0.045 ± 0.029 (11)	41
Glue volume (mm^3)	0.6 ± 0.5 (12)	1.0 ± 0.7 (8)	38

Whitney *U* tests also identified a greater median number of radii in fence webs (fence median 22, range 15–25, cage median 18, range 15–22, Mann-Whitney $U = 35$, $P = 0.037$, Fig. 3B) and greater median radial volume in fence webs (fence median 0.033 mm^3, range 0.006 to 0.07, cage median 0.013 mm^3, range 0.004–0.03, Mann-Whitney $U = 28$, $P = 0.01$, Fig. 3C, Table 2, Fig. 4A). Because of the non-homogeneous and marginally homogeneous variance of these two variables (Levene's Test for Homogeneity of Variances, $P = 0.03$, $P = 0.08$), respectively, the Mann-Whitney *U* tests may have offered greater power to reject the null hypothesis than the MANOVA.

DISCUSSION

Most research on energetic investment associated with construction of orb webs focuses on total thread length (e.g. Turnbull 1964; Nakata & Ushimaru 2004; Kawamoto & Japyassu 2008). However, this ignores the important contribution of thread diameter to web function and total silk investment. Our study quantifies this potentially important parameter and directly compares web architecture and silk investment between fence and cage webs to gain a more accurate estimate of the material investment of spiders in webs. On average, cage webs were smaller and rounder than fence webs, contained shorter lengths of capture spirals, and were supported by fewer, as well as thinner, radii. Thus, spiders invested significantly less radial (MA) silk in the cage webs. There was also a consistent, albeit non-significant, trend toward lower volumes of flagelliform capture spiral silk (Flag) and aggregate glue (Ag). These differences suggest that spiders may initially reduce silk investment in webs when moved into cages. However, several other factors, particularly spider condition, cohort, and available web frame size may also contribute to the observed differences in investment. These factors were confounded with the transition from fence to cage. Our study primarily addresses the concerted changes of silk and web architecture. Secondarily, we speculate on the adaptive significance of those changes.

Decreased investment in silk likely has implications for web performance. In other web systems, recent investigations of the tradeoffs inherent in modifying web architectures revealed that the effective capture of larger prey depends more upon the increased energy absorption and stickinesss supplied by a concentrated capture spiral than on increased capture area (Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007). High capture area remains, however, as an effective strategy of increasing interception rate of all prey sizes and successful capture of small prey. Larger mesh width, in conjunction with greater capture area, has been reported as a typical response to larger prey (Herberstein & Heiling 1998; Schneider & Vollrath 1998). However, all of these studies largely assume that size and mechanical properties of silk threads are invariant in different spinning scenarios. We show here that, at least in this species, the common simplification of invariant thread size is not valid for radial threads, but the data are consistent with bigger webs as "better" webs. For *L. cornutus* caged webs, the reduced capture area, increased mesh width, and decreased silk volume all predict that these webs should function poorly at intercepting, stopping and retaining prey compared to field webs. The reduction of radial thread cross-sectional area in *L. cornutus* caged webs thus accompanies the reduction in many other parameters associated with high prey energy absorption, suggesting a concerted decline in web investment rather than a compensatory effect.

Spiders in laboratory cages built architecturally different webs from those on fences. Such shape variation may result in part from the reduced silk investment in cage webs, but also likely relates to the characteristics of the available supports for webs in cages versus fences. In both environments, web spinning was constrained by the rigid dimensions of the

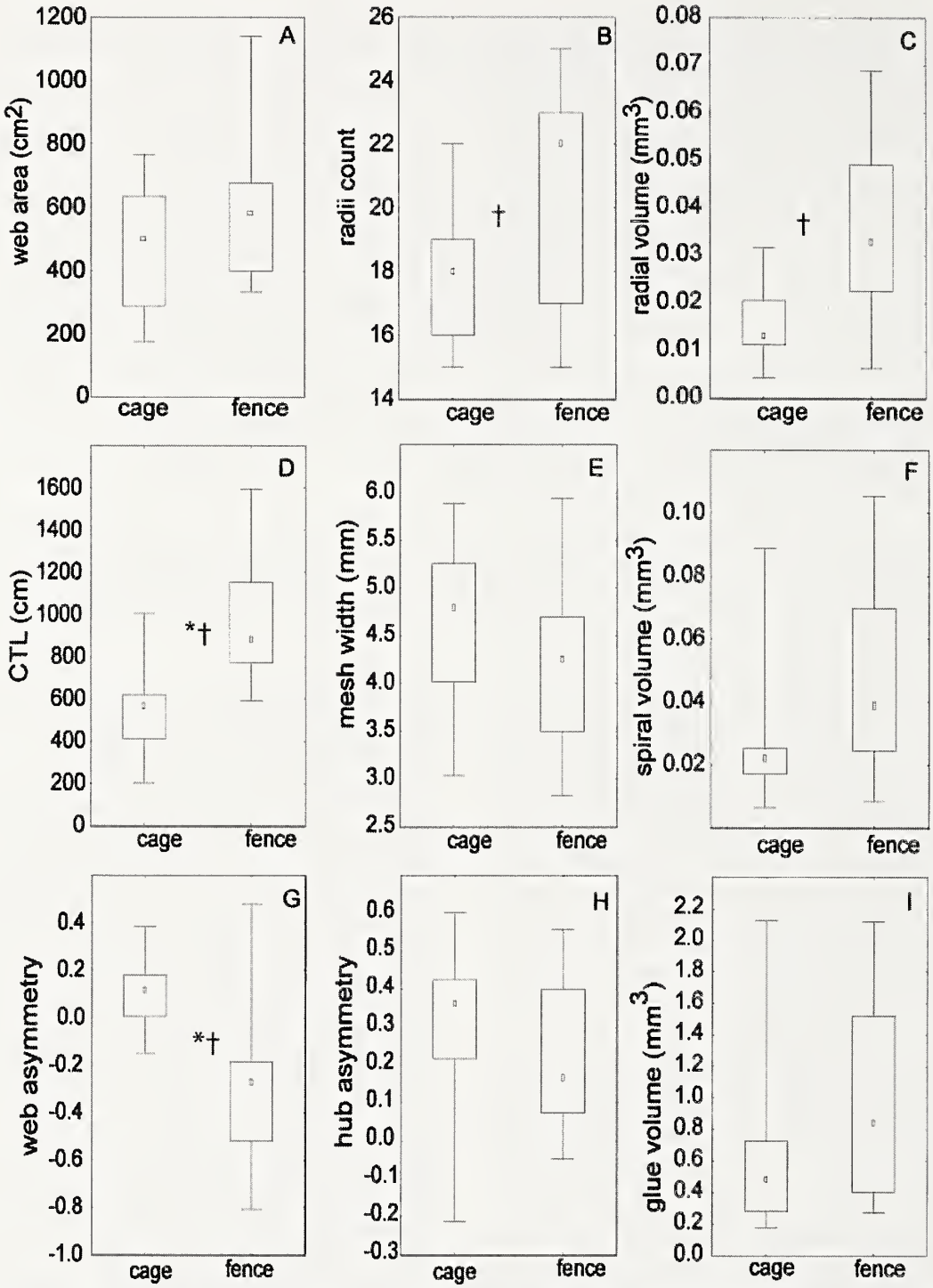

Figure 3.—Web architecture and silk investment in laboratory cage and fence webs (median indicated by small box, 25–75 percentiles indicated by large box, and range indicated by capped bars). Non-parametric values of median, minimum, and maximum are shown because the parametric parameters of mean and standard deviation are presented in Table 2. Statistically significant differences in MANOVA post-hoc unequal n HSD tests are indicated by * ($P < 0.05$). Significant median differences identified by the Mann-Whitney U tests are indicated with a † ($P < 0.05$). A. Capture area (MANOVA post-hoc unequal n HSD test, $P = 0.52$); B. Number of radii (Mann-Whitney $U = 35$, $P = 0.037$); C. Radial volume (Mann-Whitney $U = 35$, $P = 0.037$); D. Capture thread length, CTL (MANOVA post-hoc unequal n HSD test, $P = 0.008$); E. Mesh width (MANOVA post-hoc unequal n HSD test, $P = 0.21$); F. Total spiral volume (MANOVA post-hoc unequal n HSD test, $P = 0.31$); G. Web asymmetry (Mann-Whitney $U = 19$, $P = 0.003$); H. Hub asymmetry (MANOVA post-hoc unequal n HSD test, $P = 0.13$); I. Total glue volume (MANOVA post-hoc unequal n HSD test, $P = 0.18$).

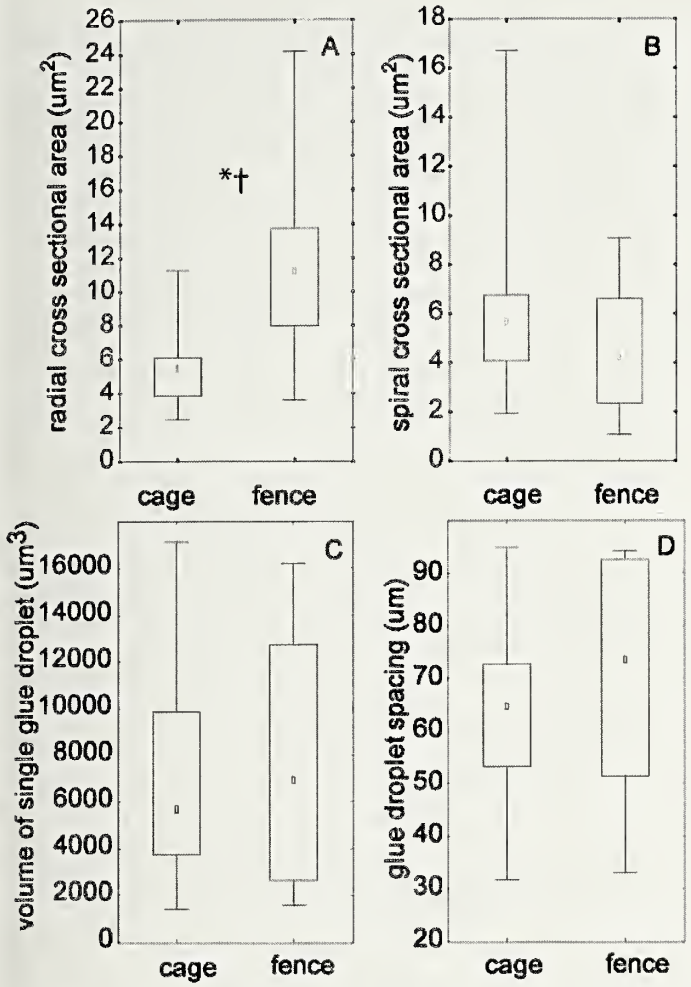

Figure 4.—Thread properties of cage and fence webs (median indicated by small box, 25–75 percentiles indicated by large box, and range indicated by capped bars). Statistically significant differences in MANOVA post-hoc unequal n HSD test indicated by *($P < 0.05$). Significant median differences identified by the Mann-Whitney U tests are indicated with a † ($P < 0.05$). A. Radial cross sectional area of the double-stranded radial (MA) fiber ($P = 0.03$); B. Spiral cross-sectional area of the double-stranded capture (Flag) fiber ($P = 0.74$); C. Single glue droplet volume ($P = 0.79$); D. Glue droplet spacing ($P = 0.77$).

surroundings. Cage spiders could, and did, attach frame threads above, below, and to either side of the web, resulting in webs supported along both vertical and horizontal axes. In contrast, the frame threads of webs on fences were usually attached only to upper and lower fence railings with no lateral support, resulting in webs with tension derived solely from the top and bottom (Fig. 2). While speculative, supporting webs along two axes rather than one may improve function in mechanical systems such as orb webs that must distribute the energy from impacts of flying prey and wind (Vollrath 1992; Lin et al. 1995). In other words, spiders may have reacted to the better support available to webs in laboratory cages by reducing the total number of radii in webs, while still maintaining the same effective degree of overall stiffness and function. Cage webs were elongated vertically (web asymmetry = 0.1) while fence webs were wider than tall (web asymmetry = −0.3). This shape is unusual for orb webs, but fence spiders expended relatively large volumes of silk into webs that had to fit between the available fence rails. Therefore, they expanded laterally and ultimately produced capture areas similar to cage webs. This is similar to a study on *A. diadematus* where orb-web shape changed to optimally fill the space available in small, irregularly shaped cages, but only after overall web size was drastically reduced (Krink & Vollrath 1997, 2000). This suggests that spiders do have the capacity to assess the microhabitat available for webs and subsequently adjust the shapes of webs to maintain or maximize overall sizes.

Most research on orb-web function primarily focuses on changes in the shapes of webs and lengths of threads. However, there is growing evidence that spiders actively vary the diameters of silk threads within and between webs (Blackledge et al. 2005; Blackledge & Zevenbergen 2007; Boutry & Blackledge 2008). In general spiders increase silk diameter with body size, particularly given the role of draglines in suspending falling and hanging spiders (Brandwood 1985; Osaki 1996; Ortlepp & Gosline 2008). Some spiders even control silk diameter in response to different types of prey (Boutry & Blackledge 2008). The cross-sectional areas of silk threads directly influence important mechanical properties such as the total loading and energy-absorbing capabilities of webs. In our study the greater volume of radial (MA) silk was driven primarily by the 50% greater cross-sectional areas of radii in fence webs, which would greatly increase the kinetic energy these webs could absorb from wind and prey impacts. In contrast, the cross-sectional areas of capture spirals were relatively similar between laboratory and fence webs, although the total length of the capture spiral was 42% shorter in cage webs.

In summary, we found that caged spiders in the laboratory invested less material in their webs than did fence spiders in the field. Several factors may explain the lower investment in webs by cage spiders: 1) spiders may first test foraging sites before building more substantial webs in new locations (Riechert & Gillespie 1986; Nakata & Ushimaru 1999); 2) caged spiders were exposed to fewer insect cues, such as wing vibrations and odor, and may have altered web spinning in response to perceptions of a poor foraging environment (Pasquet et al. 1994 Nakata & Ushimaru 2004); 3) the stiff supports of the laboratory cages provided structures on which mechanically effective webs could be built using less material (Wirth & Barth 1992) and reduced investment may reflect loss of silk resources when a spider is removed from its old web in the field without being allowed to recycle the silk (Zschokke 1997). Our study was not intended to distinguish among these factors, but only to determine the general effects of captivity on spider webs. Controlling for such factors in future studies of orb spinning could reveal the relative importance of each for spider behavior. Regardless, our study is consistent with the growing body of evidence that spiders modulate web-spinning behaviors in response to changing environments.

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Additive partitioning of spider diversity in a fragmented tropical dry forest (Valle del Cauca, Colombia)

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Abstract. Understanding the variation of diversity patterns requires analysis at multiple spatial scales. In this study we estimated the diversity components (alpha, beta and gamma) of the spider community at El Vínculo Natural Regional Park, using the additive partitioning of diversity (species richness, Shannon's diversity index and Simpson's index) for the first time on this taxon in Colombia. We collected the specimens following a nested sampling design that consisted of two spatial scales. At the local scale, we quantified additive diversity components in 238 sampling units, and at the regional scale in five vegetation types. Total observed regional diversity (γ) was partitioned into its additive components: within sampling units (α_1), among sampling units (β_1) and among vegetation types (β_2). We used the same approach to compare common and infrequent spider species and to compare sampling methods. A total of 1565 adult spiders and 72 identifiable juveniles, including 193 morphospecies from 36 families, was sampled during the study. In all cases (entire community, infrequent species, common species and four different sampling methods) we found that a significant percentage, relative to that of randomization tests, of the diversity measurements used was attributed to beta diversity among vegetation types. The relative contributions of alpha and beta diversity to total observed regional diversity depended on the diversity measurement used. The contribution of beta diversity with respect to alpha diversity was low using Simpson's index (less than 20%), whereas with species richness and Shannon's index the contribution was high (up to 90% and up to 66%, respectively). Our results suggest that beta diversity is the main component of diversity in the natural park. We concluded that the maintenance of a large variety of vegetation types can be an important tool for the conservation of spider richness at the natural park.

Keywords: Diversity components, spatial scale, sampling methods, El Vínculo Natural Regional Park

Traditional measurements of diversity have focused on the search for parameters to characterize it as an emergent property of biotic communities (Moreno 2001). However, since communities are not isolated in a neutral environment, the separation of alpha, beta and gamma components of diversity has been useful for measuring and monitoring the effects of human activities on biotic communities and understanding the changes of diversity related to landscape structure (Moreno 2001; Veech et al. 2002; Gering et al. 2003; Halffter & Moreno 2005).

Tropical dry forest (Bs-T) is one of the most endangered ecosystems in the Neotropics (Janzen 1988). Due to the fertility of its soils it has been the focus for the development of human populations, and it has suffered an intense transformation for the benefit of agriculture and livestock (Álvarez et al. 1998). In Colombia, the tropical dry forest is considered among the three ecosystems most degraded, fragmented and least known, with only 1.5% of its original area remaining. In the case of Valle del Cauca province, Arcila (2007) suggests that the fragmentation of the dry forest has been dramatic, because nearly the entire forest has been replaced with crops and pastures, leaving remnant fragments surrounded by a highly intervened matrix and therefore causing major changes in its physical environment and associated biota. The El Vínculo Natural Regional Park (NRP), is part of the few remaining remnants of Bs-T located in the valley of Cauca river and is the largest fragment in Valle del Cauca province, with an area of about 70 ha (Parra & Adarve 2001; Arcila 2007).

In areas with a high level of habitat loss, such as the Colombian tropical dry forest, conservation strategies focusing on the effective protection of the remaining habitats must take into account how biological diversity is organized across different spatial scales (Gering et al. 2003; Ribeiro et al. 2008). The additive partitioning of diversity is a promising approach that can address this problem. The additive model analytically demonstrated by Lande (1996) considered alpha diversity as the average of within-sample diversities, regardless of whether the diversities are measured by species richness, Simpson's index or Shannon's index. Likewise, beta diversity is an average of diversities among samples within a habitat (Veech et al. 2002). This implies that beta diversity can be measured and defined relative to alpha diversity, allowing direct comparison of its contributions to gamma diversity (Veech et al. 2002; Gering et al. 2003; Crist & Veech 2006). The additivity allows analysis of the proportion of total diversity found in a hierarchy of different scales (Ribeiro et al. 2008). Thus, gamma diversity in a given scale is equal to the alpha diversity at the next scale; for this reason total diversity can be conveniently expressed as $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3 + \ldots\ldots + \beta n$, where n is the number of scales in the study (Veech et al. 2002).

Despite their fundamental roles in natural ecosystems and their potential use in identifying conservation priority areas, arthropods have been largely ignored in conservation studies (Kremen et al. 1993; Cardoso et al. 2008). Some authors (Coddington et al. 1991; Kremen et al. 1993; Toti et al. 2000; Cardoso et al. 2008), argue that it is necessary to understand the diversity patterns in communities of terrestrial arthropods, because they can provide complementary information to that obtained with the traditional groups (vertebrates and vascular plants), due to their high species richness and abundance.

Spiders, which include about 41,000 described species (Platnick 2009), comprise a significant portion of the terrestrial arthropod diversity (Toti et al. 2000), being the

top predators of invertebrate food webs in these environments (Foelix 1996). Spiders are abundant and ubiquitous, employ a remarkable diversity of predation strategies, occupy a wide array of spatial and temporal niches, exhibit taxon- and guild-specific responses to environmental changes and have close relationships with the structure of vegetation (Marc et al. 1999; Toti et al. 2000).

The features listed above, make the spiders a very important group for conservation studies. However, like any megadiverse taxon, the disadvantages associated with the sampling of spiders, such as the number of sampling methods, collectors and sampling units, the spatiotemporal scale associated with the sampling, taxonomic identification and details associated with data analysis, make the design of the sampling protocol a very important subject (Coddington et al. 1991; Cardoso et al. 2008). The objective of the present study is to estimate the components of spider diversity (alpha, beta and gamma) in a fragmented tropical dry forest using the additive partitioning of diversity. We collected spider species following a nested sampling design that consisted of two hierarchical scales (sampling units and vegetation types). We evaluated the relative contributions of diversity components to total observed regional diversity. In addition, we used the additive partitioning approach in a comparison of common and infrequent spider species and in a contrast between different sampling methods.

METHODS

Study area and sampling design.—The study was carried out in El Vínculo Natural Regional Park (3°50′23″N, 76°18′07″W), Buga municipality, Valle del Cauca province, southwest Colombia (Fig. 1). The park covers an area of about 70 ha in process of regeneration at different stages. The area belongs to the Instituto para la Investigación y la Preservación del Patrimonio Cultural y Natural del Valle del Cauca, INCIVA. The altitude is between 950–1150 m above sea level, the average annual temperature is 25° C and the average annual precipitation is 1400 mm. According to Holdridge's life zone classification system, the natural park belongs to the tropical dry forest (Bs-T) life zone.

We used a hierarchical sampling design that consisted of two nested spatial scales. The highest level (broadest spatial scale), was represented by five vegetation types based on the plant communities classification by Parra & Adarve (2001). In each vegetation type we collected spiders by means of five sampling methods, grouped into 238 sampling units (finest spatial scale). The vegetation types are as follows:

a) Secondary forest (SF): This forest type covers about 20 ha in the natural park and was probably dedicated to coffee cultivation about 40 yr ago. It is located on hills with moderate slopes. The most common tree species are *Eugenia biflora*, *Myrtus* sp., *Zanthoxylum verrucosa*, *Guazuma ulmifolia* and *Cytharexylum kunthianum*; the understory has an average height of 6 m. The shrub layer has tree saplings of the same species listed above and other species such as *Croton gossypiifolius*, *Euphorbia* sp., *Sapindus saponaria*, and *Amiris pinnata*.
b) Riparian forest (RF): This forest type covers an area of about 15 ha. Formerly it was used for coffee and cacao cultivation, as well as for provision of wood. The most common tree species are *Trichillia pallida*, *Licaria* sp., *Guapira* sp., *Myrtus* sp., *Croton gossypiifolius*, *Acalipha macrostachya*, *Pithecellobium lanceolatum* and *Senna spectabilis*, with average heights of 15 m. The shrub layer contains tree saplings of the same species as listed above.
c) Shrubs (S): This vegetation type covers an area of about 15 ha and exhibits a strong exposure to sunlight and a high water deficit. The vegetation is dominated by *Panicum* sp., which can reach heights of 2 m. In addition, it has other plants between 1.2 and 2 m tall, such as *Acacia farnesiana* and *Bidens pilosa*. This area is periodically cut down by the staff of INCIVA.
d) Grasslands (G): This vegetation type corresponds to the area bordering the southern edge of the park that belongs to the farm "La Campiña", an area mainly devoted to livestock breeding, The area has some individuals of *Acacia farnesiana* that are pruned regularly. Floristically, these grasslands are composed of both native and introduced grass species and a few scattered shrubs.
e) Highly disturbed area (HA): This vegetation type consists of about one hectare in the southwestern extremity of the natural park. INCIVA constantly intervenes in this area, which is also open to the public. The most common tree species are *Guazuma ulmifolia*, *Senna spectabilis*, *Achatocarpus nigricans* and *Bambusa guadua*. This area is the closest to Panamericana highway, which borders the park on the west (Fig. 1).

Sampling methods.—Spiders were collected between August and December 2008 in three field trips carried out by a single collector (first author). Both day (07:00–17:00 h) and night (20:00–02:00 h) samples were collected. Specimens were collected with pitfall traps, Berlese funnel litter extraction and semi-quantitative methods. Sampling followed a balanced design as closely as possible, with the same effort applied to sampling schedule, sampling methods and vegetation types (Table 1). However, Berlese funnel litter extraction was not used in the shrubs and grasslands, where there was no defined litter layer, and beating was not used in shrubs due to the absence of a defined understory layer.

An hour of effective fieldwork was used as a sampling unit; this time included the logistics of handling samples in the collection sites and excluded interruptions. The main objective of this sampling design was to obtain a representative sample of each vegetation type to allow an objective comparison of spider assemblage composition and a better understanding of spider diversity organization aeross different spatial scales.

Pitfall traps (PT): Traps consisted of plastic cups of 8 cm diameter and 10 cm depth filled with preservative (70% water, 29% ethanol and 1% detergent) and covered with a circular plastic plate placed about 10 cm above the ground. Thirty-two pitfall traps were laid along random transects in each vegetation type. Traps were left in the field for five days. A

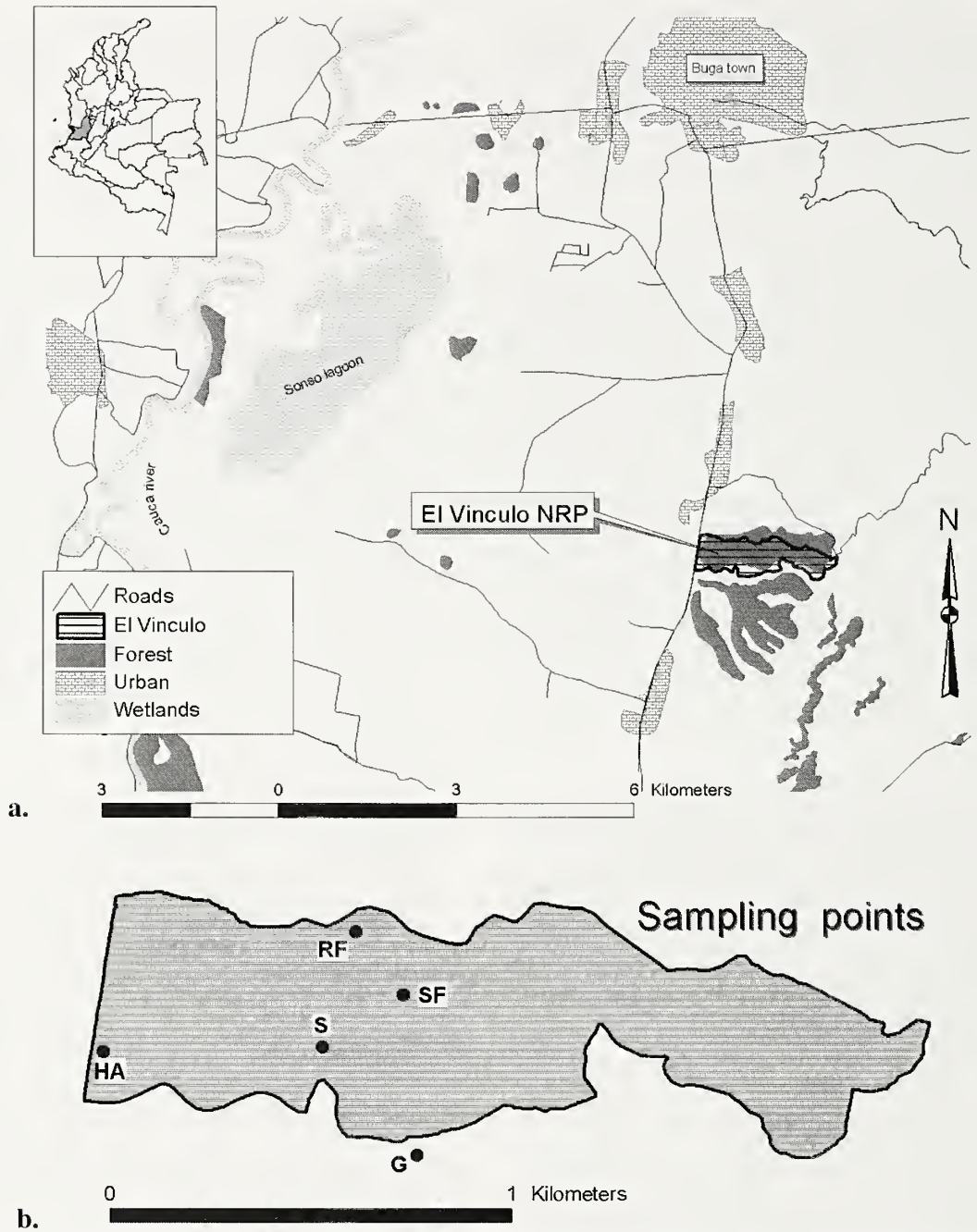

Figure 1.—Map of El Vínculo NRP, Colombia, showing the isolation of this forest fragment in a surrounding matrix composed mainly of sugar cane and cattle grasslands. a. Detailed map showing the location and relative distances of vegetation types. b. HA = Highly disturbed area; S = Shrubs; SF = Secondary forest; G = Grasslands; RF = Riparian forest.

group of four pooled traps (arranged in a square with an area of 1 m^2) separated by 5 m constituted one sampling unit.

Berlese funnel litter extraction (BF)*:* Samples of litter (5000 cm^3 each) were randomly collected in the vegetation types RF, SF, and HA for subsequent processing in Berlese funnels at the laboratory of Entomology at Universidad del Valle. Thirty samples were collected, each used as a sampling unit for the data analysis.

Semi-quantitative sampling: Three methods were included: a) Aerial hand collection, "looking up" according to Coddington et al. (1996), involved searching leaves, branches, tree trunks, and spaces in between, from knee height (50 cm) up to maximum overhead arm's reach (2 m). b) Ground hand collection, "looking down" according to Coddington et al. (1996), involved searching on hands and knees, exploring the leaf litter, logs, rocks, and plants that are below knee level (50 cm). The hand collection was performed with a dusting device for detecting inconspicuous webs. c) A beating event consisted of hitting a randomly chosen vegetation unit (shrub, tree or tree branch etc.) with a 1-m-long stick and catching the falling spiders on a tray (0.5 m^2) held horizontally below the vegetation until no more spiders fell down. In this study, 25 events constituted one sampling unit (Coddington et al. 1991).

Table 1.—Number of sampling units for the vegetation type, the sampling method and the time of day. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs; B = Beating; AHC= Aerial hand collection; GHC = Ground hand collection; BF = Berlese funnel litter extraction; PT = Pitfall traps.

	Vegetation types										
	RF		SF		HA		G		S		
Method	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Total
B	6	6	6	6	6	6	6	6	0	0	48
AHC	6	6	6	6	6	6	6	6	6	6	60
GHC	6	6	6	6	6	6	6	6	6	6	60
BF	10		10		10		0		0		30
PT	8		8		8		8		8		40
Total	54		54		54		44		32		238

Processing samples.—We sorted spider specimens and identified them to family and then separated them into adults and juveniles. Each adult specimen was photographed and identified to species using existing identification keys wherever possible. Juvenile specimens were discarded from the data analysis because their identification to species level is difficult and ambiguous in many cases. However, because of careful observations in the field, juveniles of the following species were considered to be reliably identifiable and were included in the analyses: *Mimetus* sp. 1 (Mimetidae), *Thaumasia argenteonotata* Simon 1898 (Pisauridae), *Episinus* sp. 1 (Theridiidae), *Ypypuera* sp. 1 (Hersiliidae), *Micrathena horrida* Taczanowski 1873 (Araneidae), *Tibellus* sp. (Philodromidae), *Senoculus canaliculatus* F.O. Pickard-Cambridge 1902 (Senoculidae), *Dolichognatha* sp. (Tetragnathidae) and *Cybaeus* sp. (Cybaeidae).

The unidentified species were recorded as morphospecies, after a detailed analysis of male and female genitalia using the techniques of expansion of the male palpi and the clarification of the female epigynium placed in a 10% KOH solution. The vouchers are deposited in the arachnological collection of Museo de Entomología de la Universidad del Valle (MEUV), Cali, Colombia, and in the arachnological collection of Museo de Ciencias Naturales Federico Carlos Lehmann Valencia, Cali, Colombia (IMCN). In this study we use the term morphospecies for consistency with the previous investigations; however, as Krell (2004) says, the use of this term in the context of the analysis of diversity is inadequate.

Data analysis.—*General community patterns:* We estimated species richness for each vegetation type and sampling method as well as for the regional data set using the nonparametric estimators Chao 1, ACE, Chao 2, Jackknife 1, Jackknife 2 and ICE. We visualized differences of alpha diversity through the inspection of the 95% confidence intervals of both sample and individual-based rarefaction curves (Gotelli & Colwell 2001). Sample-based rarefaction curves were calculated using EstimateS© 8.0 (Colwell 2008), while individual-based curves were calculated using EcoSim© 7.0 (Gotelli & Entsminger 2008). The x-axis of both curves is scaled to represent the number of individuals (not the number of samples), as this process is necessary to evaluate patterns of richness at comparable levels of sampling effort when data sets are likely to differ systematically in the mean number of individuals per sample (Gotelli & Colwell 2001). In addition to assessing the performance of the sampling protocol, we calculate the completeness of the inventory for each data partition (by sampling method and vegetation type) and the natural park as a whole using the Chao 1 estimator, completeness being the ratio between observed and estimated richness (Sørensen et al. 2002; Scharff et al. 2003).

To examine the similarity of spider assemblages between vegetation types, we used hierarchical cluster analysis with the Jaccard index of similarity. Due to the differences in the sampling effort between vegetation types this index of similarity can be biased; however, this bias can be reduced if almost complete inventories are reached in each vegetation type (Chao et al. 2005). Moreover, we tested spatial autocorrelation in species composition data using the Mantel test to relate a matrix of similarity between vegetation types based on the Jaccard index of similarity to a matrix of geographic distance. This spatial analysis was carried out using XLStat© 9.0 (Addinsoft 2008).

Additive partitioning of diversity: Lande (1996) demonstrated that any metric can be partitioned into its components provided that it exhibits strict concavity, which means that the overall value of that metric for a pool set of communities equals or exceeds the average diversity within communities. Species richness, Simpson's index and Shannon's index are all strictly concave. The richness takes into account only the number of species, while the indices consider both the number of species and abundance. In this study, we evaluated the additive partitioning of the whole community and for each method using these three measures of diversity. The program PARTITION© 2.0 was used (Veech & Crist 2007) to additively decompose the total observed regional diversity (γ) into its average components within (α_2) and among (β_2) vegetation types. To investigate diversity patterns at the local scale of the hierarchical sampling design, we decomposed the average within-vegetation type (α_2) into the within- (α_1) and among-sampling unit (β_1) components, $\alpha_2 = \alpha_1 + \beta_1$. Therefore, the overall spider diversity in our study can be described by the following formula: $\gamma = \alpha_1 + \beta_1 + \beta_2$. The observed partitioning patterns were compared with a null distribution generated from a program of 10,000 individual-based randomizations (Crist et al. 2003). In addition, we applied separate analyses to compare common (abundance greater than 0.3% of the total identifiable specimens) and infrequent (abundance less than 0.12% of the total identifiable specimens) spider species and to analyze the effect of spatial scale on the diversity of these species. These cutoffs were defined considering the level of

Table 2.—Composition of the spider fauna sampled in five vegetation types at NRP El Vínculo. UJ = Unidentifiable juveniles; IJ = Identifiable juveniles.

Family	Total specimens	UJ	IJ	Adults	Morpho-species
Theridiidae	1474	1110	5	359	46
Araneidae	1125	939	1	185	28
Linyphiidae	362	141	0	221	14
Salticidae	349	234	0	115	22
Lycosidae	307	151	0	156	8
Tetragnathidae	235	197	10	28	4
Thomisidae	178	131	0	47	11
Uloboridae	160	101	0	59	5
Anyphaenidae	142	104	0	38	4
Ctenidae	129	114	0	15	6
Oxyopidae	102	76	0	26	5
Mimetidae	78	25	17	36	1
Sparassidae	68	41	0	27	2
Hersiliidae	62	0	15	47	1
Pholcidae	61	49	0	12	2
Ochyroceratidae	42	0	4	38	1
Miturgidae	36	14	0	22	2
Oonopidae	33	13	0	20	4
Theridiosomatidae	28	21	0	7	3
Dipluridae	25	9	0	16	1
Scytodidae	25	20	0	5	1
Hahniidae	24	0	0	24	1
Dictynidae	17	3	0	14	4
Corinnidae	14	1	0	13	4
Pisauridae	13	0	5	8	1
Senoculidae	13	0	10	3	1
Cybaeidae	10	0	4	6	1
Clubionidae	7	4	0	3	1
Mysmenidae	5	1	0	4	2
Deinopidae	3	0	0	3	1
Nephilidae	3	0	0	3	1
Theraphosidae	3	2	0	1	1
Gnaphosidae	2	0	0	2	1
Zodariidae	2	1	0	1	1
Philodromidae	1	0	1	0	1
Titanoecidae	1	0	0	1	1
Total	5139	3502	72	1565	193

rarity that quantifies the non-parametric, abundance-based estimators: number of species represented by only one or two individuals in the entire data set (Colwell & Coddignton 1994; Toti et al. 2000). Due to the different nature of the sampling methods used, we also analyzed the effect of spatial scale on spider diversity according to each sampling method.

RESULTS

General community patterns.—We captured 5139 spiders, of which 3502 (68.1%) were unidentified juveniles, 1565 (30.5%) were adults and 72 (1.4%) were identifiable juveniles (Table 2, Appendix 1). The most abundant and diverse families were Theridiidae and Araneidae, which contributed 50.57% of all captures and 74 of the 193 morphospecies collected (Table 2). Theridiidae was also the family with the largest number of identifiable specimens (364) and morphospecies (46). The second dominant group of families comprised the Linyphiidae, Salticidae, Lycosidae, Tetragnathidae, Thomisidae, Uloboridae, Anyphaenidae and Ctenidae, which collectively contributed 35.82% of all captures. This group includes 73 of the 193 morphospecies collected in the area (Table 2). All families were found in the five vegetation types. All other families contributed less than 2% of all captures each and contributed 46 morphospecies. Four families were represented only by singletons or doubletons (Table 2).

The dominant species (in terms of abundance) were *Ypypuera* sp. 1 (Hersiliidae), *Novafrontina uncata* F.O. Pickard-Cambridge 1902 (Linyphiidae), *Trochosa* sp. 1 (Lycosidae), *Mimetus* sp. 1 (Mimetidae), *Ochyrocera* sp. 1 (Ochyroceratidae), Salticidae sp. 5 (Salticidae), *Faiditus caudatus* Taczanowski 1874, *Episinus* sp. 1 (Theridiidae) and *Tidarren haemorrhoidale* Bertkau 1880 (Theridiidae), which accounted for 29.1% of all identifiable specimens collected in the natural park.

The non-parametric estimators used (Table 3) indicate variation in the estimated number of morphospecies between 41.68 (95% lower confidence limit of the Chao1 estimator at Shrubs) and 110.49 (95% upper confidence limit of the Chao1 estimator at secondary forest). More than 49% of the morphospecies were singletons or doubletons in each vegetation type (Table 3). The species accumulation curve does not reach the asymptote by the end of the sampling process (Fig. 2). However, curves representing the mean values of the non-parametric estimators approached the asymptote very closely. Based on estimated species richness our inventory was almost complete at the regional scale and in each vegetation type (Table 3). Both curves, based on samples and individuals (Fig. 3), indicate that there is no difference in the species richness of the five vegetation types.

Aerial hand collecting captured most species (Table 4). In general, all sampling methods presented high inventory completeness (more than 78% in all cases), despite the differences in sampling effort, and each method sampled unique species not found by the other methods (Table 4).

The cluster analysis used shows strong differences in community composition among vegetation types (Fig. 4). In general, there was a higher degree of similarity between areas without a defined canopy layer (grasslands and shrubs) than areas with a defined one. Due to the great number of rare species in each vegetation type and its possible influence in the similarity values (Table 3), we explored the effect of these species in the index value, removing all singleton species. In general the index values still indicate a large (although reduced) difference in species composition (Table 5). Furthermore, Mantel statistics supported the null hypothesis that no significant spatial autocorrelation was present between spider communities and the distance matrix for vegetation types ($r = -0.643$, $P = 0.092$).

Additive partitioning of diversity.—The additive partitioning showed in all cases that the highest beta component (β_2) in models was always greater than expected by chance (Table 6), whereas the β_1 component was always lower than expected, except for the Simpson's index of ground hand-collecting (Table 6). The contribution of the beta component to the regional diversity (γ) was in all cases more than 90% for the partitioning of species richness and more than 66% for that of the Shannon's index (Fig. 5). On the other hand, the contribution of the alpha component to the partitioning of Simpson's index was higher than 78% in all cases (Fig. 5). We

Table 3.—Summary data for the overall captures of this study. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

	RF	SF	HA	G	S	Total
Morphospecies	69	71	79	51	42	193
Total specimens	1570	958	1417	785	409	5139
Identifiable specimens	382	402	510	207	136	1637
Sampling units	54	54	54	44	32	238
Identifiable specimens / sampling unit	7.07	7.44	9.44	4.70	4.25	6.88
Morphospecies / sampling unit	1.27	1.31	1.46	1.16	1.31	0.81
Singletons	9	26	21	17	6	40
Doubletons	26	13	20	8	23	36
Uniques	20	28	26	19	11	56
Duplicates	21	16	28	10	22	38
Estimates						
ACE	74.37	100.13	95.09	66.3	44.65	221.07
ICE	85.88	104.46	107.44	66.16	51.26	240.32
Chao 1 ± SD	70.56 ± 1.65	97 ± 13.49	90.03 ± 6.34	69.06 ± 11.65	42.78 ± 1.1	215.22 ± 9.24
Chao 2 ± SD	78.52 ± 5.6	95.5 ± 12.16	91.07 ± 6.3	69.05 ± 10.92	44.75 ± 2.42	234.26 ± 14.41
Jackknife 1 ± SD	88.55 ± 5.32	98.48 ± 5.9	104.41 ± 5.65	69.57 ± 4.72	52.66 ± 2.99	248.74 ± 8.32
Jackknife 2	88.06	110.33	103.12	78.38	43.01	266.75
Inventory completeness (%)	97.78	73.20	87.75	73.85	98.18	89.67

do not employ the additive partitioning for Berlese funnel litter extraction due to its low capture rate (Table 4).

DISCUSSION

The additive partitioning of species richness and Shannon's index suggest that beta diversity was the principal component of regional diversity in all cases (total community, infrequent and common species). Likewise, our results suggest that this pattern remains constant in the samples obtained with different sampling methods.

Our finding that the broad-scale beta component of diversity was greater than expected supports the idea that vegetation types structure the composition of spiders in the El Vínculo NRP. This is supported by the cluster analysis, which identified strong differences in community composition between vegetation types. The contribution of each vegetation type to the regional diversity in terms of unique species highlights the importance of evaluating different elements in the natural park for the analysis of diversity patterns. In the case of spider fauna, if the sampling had been focused on the secondary forest, we might have reached an asymptote of accumulation curves (due to the reduction of the area covered by the sampling), but at the same time, we had extremely undervalued species richness for the whole park.

The richness of both common and infrequent species was enhanced (i.e., greater than expected) only at the highest level (β_2). These results contrast with those obtained by Gering et al. (2003) for beetle communities, who reported this trend only

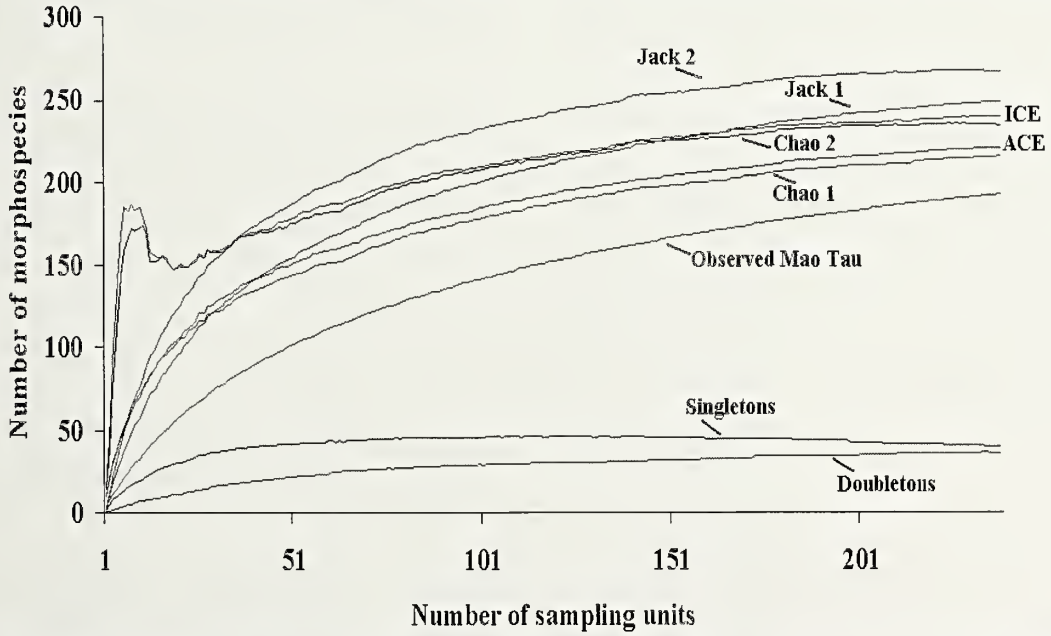

Figure 2.—Randomized accumulation curves for observed species richness, singletons, doubletons, uniques, duplicates and richness estimators for all data. Curves were generated from 100 randomizations.

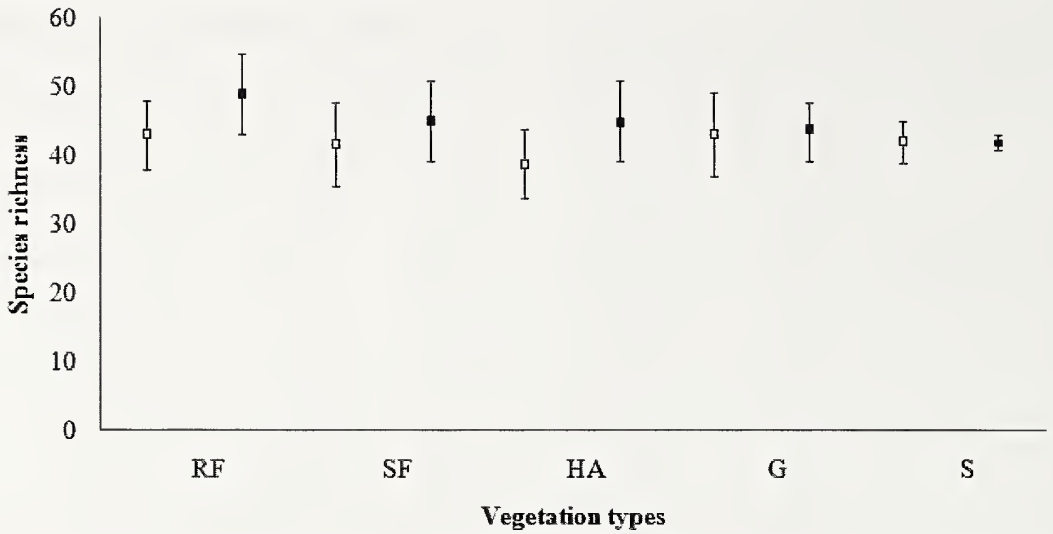

Figure 3.—Comparison of species richness values (± 95% confidence intervals) at the lowest number of individuals (136), derived from sample-based rarefaction curves (open squares) and individual-based rarefaction curves (filled squares). RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

for the infrequent species. Our results show that the partitioning pattern for the entire community mirrors those of infrequent and common species. This suggests that no group (infrequent or common species) is driving the patterns of the entire community in the El Vínculo NRP.

Beta diversity at each scale can be seen as the result of environmental heterogeneity in space and time, in combination with niche differences among species (Loreau 2000). Movements between spatial units, such as dispersal or migration, can lead to an increase in alpha diversity and therefore a decrease of beta diversity, due to a homogenizing effect (Loreau 2000). However, the spatial analysis conducted in this study demonstrated that spider communities in the natural park were not spatially autocorrelated, indicating that spatial heterogeneity in diversity among vegetation types (β_2) was not lowered due to a homogenizing effect. This is consistent with the results obtained by Klimek et al. (2008) with plant communities.

The partitioning of Simpson's index showed a contrasting pattern to that obtained with Shannon's index and species richness, since the alpha component was the largest contributor to gamma diversity (Fig. 5). These results are consistent with the results obtained by Wagner et al. (2000) and Chandy et al. (2006) for plants, Gering et al. (2003) for beetles, Stendera & Johnson (2005) for aquatic invertebrates and Summerville et al. (2006) for Lepidoptera. Thus, the partitioning suggests that the smaller scale of analysis (sampling units) is dominated by common species, which is directly related to the sensitivity of the Simpson's index to the abundance of these species. This demonstrates the importance of using different indices of diversity that consider diverse properties of the communities to understand in a more

Table 4.—Species richness and abundance per method. AHC= Aerial hand collection; B = Beating; GHC = Ground hand collection; BF = Berlese funnel litter extraction; PT = Pitfall traps.

	AHC	GHC	B	BF	PT
Morphospecies	102	101	77	1	29
Unique morphospecies	33	31	20	1	15
Total specimens	2125	1788	801	18	407
Identifiable specimens	571	576	241	10	239
Sampling units	60	60	48	30	40
Identifiable specimens / sampling unit	9.52	9.60	5.02	0.33	5.98
Morphospecies / sampling unit	1.70	1.68	1.60	0.03	0.73
Singletons	27	33	30	0	8
Doubletons	21	21	21	0	9
Estimates					
ACE	123.97	135.25	110.66	1	35.27
ICE	139.72	141.21	126	1	35.91
Chao 1 ± SD	119.36 ± 8.74	126.93 ± 11.81	98.43 ± 10.22	1 ± 0.01	32.56 ± 3.36
Chao 2 ± SD	142.11 ± 17.29	135.78 ± 14.43	115.03 ± 16.57	1 ± 0.13	32.56 ± 3.36
Jackknife 1 ± SD	139.37 ± 6.87	140.33 ± 8.02	113.23 ± 7.03	1 ± 0.01	36.8 ± 2.86
Jackknife 2	158.99	157.14	131.8	1	36.07
Inventory completeness (%)	85.46	79.57	78.23	100	89.07

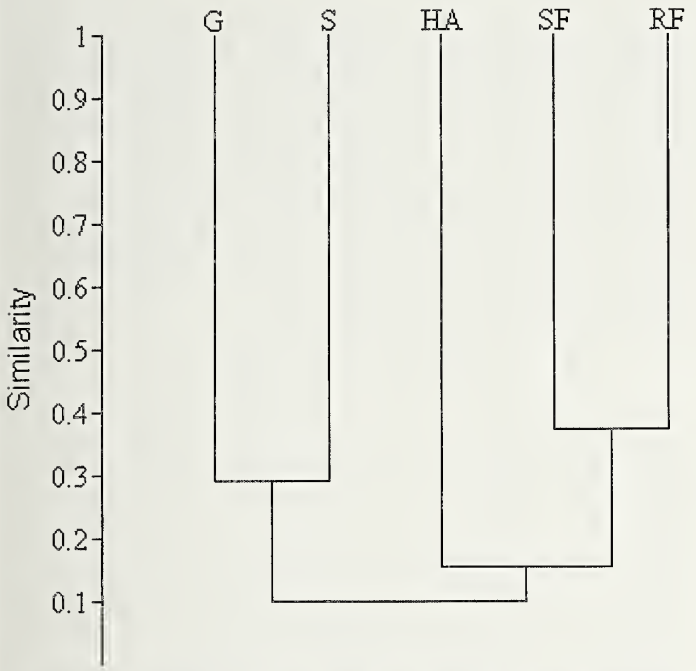

Figure 4.—Dendrogram showing clustering of five vegetation types at EL Vínculo NRP, based on Jaccard index of similarity. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

objective way the contributions of the alpha and beta components to regional diversity (Gering et al. 2003).

Veech (2005) suggests that intraspecific aggregation is a common feature in different communities of arthropods. He states that this property should limit the mean alpha diversity of the communities to a level less than what it would be if individuals were randomly distributed among the communities, as a result enhancing beta diversity. This could be one of the explanations for the pattern observed in this investigation. However, we require a more detailed knowledge of the natural history of various species to test this hypothesis, as well as biotic and abiotic factors influencing the aggregation of conspecifics (Veech 2005).

It is important to recognize that differences in the area of the vegetation types did not involve changes in the richness of communities (Fig. 3). This is consistent with the findings of Whitmore (2000), who suggests that many other factors can influence the patterns of diversity in communities of spiders. Additionally, it is important to note that despite the high degree of isolation of the forests evaluated with respect to other fragments of Bs-T at Valle del Cauca province (Arcila

Table 5.—Values of the Jaccard index of similarity for the five vegetation types. Index values in parentheses were generated after removing all singletons. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

Vegetation type	SF	HA	G	S
RF	0.372 (0.452)	0.165 (0.194)	0.043 (0.049)	0.057 (0.061)
SF		0.145 (0.183)	0.079 (0.097)	0.118 (0.138)
HA			0.16 (0.198)	0.141 (0.165)
G				0.291 (0.328)

Table 6.—Significance values for tests of actual diversity estimates from additive partitioning against null estimates from the PARTITION© 2.0 program. All values determined at the 0.05 level. + = significantly larger; − = significantly smaller; AHC = Aerial hand collection; B = Beating; GHC = Ground hand collection; PT = Pitfall traps; ns = not significant.

Group	Level	Richness	Simpson	Shannon
Entire community	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
Infrequent species	β_2	+	+	+
	β_1	−	−	−
	α_1	+	+	+
Common species	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
AHC	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
B	β_2	+	+	+
	β_1	−	−	−
	α_1	−	ns	−
GHC	β_2	+	+	+
	β_1	−	+	−
	α_1	−	−	−
PT	β_2	+	+	+
	β_1	−	−	−
	α_1	−	ns	−

2007), and its small area compared to the highly intervened matrix, the composition of spider assemblages in these vegetation types is very different (Fig. 4), a pattern that seems to have no relation to rare species (Table 5), demonstrating the importance of protecting these areas for the conservation of the spider richness in the natural park.

As expected, and in accordance with all previous studies (Coddington et al. 1991, 1996; Sørensen et al. 2002; Scharff et al. 2003; Cardoso et al. 2008, 2009), sampling methods directly influence the results. Here all methods, including the least productive, sampled unique species, which justifies the use of the broadest possible spectrum of collecting methods in spider inventories that aim to be complete (Scharff et al. 2003). We attribute the low productivity of the Berlese funnel litter extraction (Table 4) to the small amount of litter processed in each sampling unit. We believe that a larger quantity of litter would give better results. It is interesting to note that despite the different nature of the sampling methods used, the additive partitioning pattern for each one was very similar (Table 6), which supports the idea that beta diversity among vegetation types is the main component of spider diversity in the natural park, regardless of any data partitioning, at least at the level of sampling methods.

Many factors have been shown to influence the structure and composition of spider communities at multiple spatial scales, including intra- and interspecific competition, predation, spatial heterogeneity, environmental stability, availability of prey and productivity (Turnbull 1973; Uetz 1979; Greenstone 1984; Riechert & Gilliespie 1986; Marc et al. 1999; Shochat et al. 2004; Pinkus-Rendón et al. 2006). However, understanding the impact of these factors on diversity patterns in spider communities of the El Vínculo NRP requires much

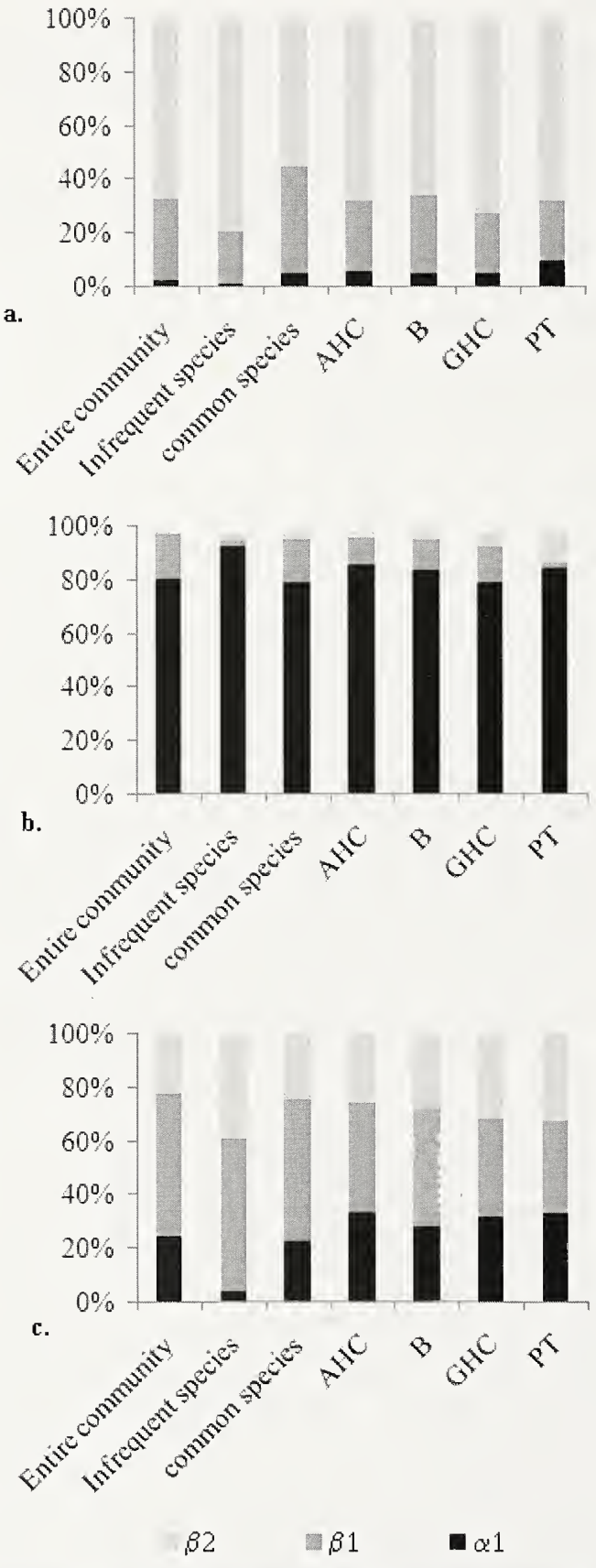

Figure 5.—Additive partitioning of (a) species richness, (b) Simpson's index, and (c) Shannon's index at NRP El Vínculo, following a hierarchical sampling design of two spatial scales: sampling units and vegetation types. AHC = Aerial hand collection; B = Beating; GHC = Ground hand collection; PT = Pitfall traps.

more detailed analysis in future research. The additive partitioning performed in this study suggests that faetors related to a higher scale of analysis (vegetation types) such as topography, dominant tree species, land-use patterns and habitat heterogeneity could involve strong differences in the composition of spider assemblages but not in species richness. Additionally, our results indicate that the maintenance of a large variety of vegetation types, along with heterogeneous abiotic environmental conditions, can be an important tool for the conservation of spider richness due to the enhancement of beta diversity among vegetation types.

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Appendix 1.—Species, morphospecies and number of identifiable spiders collected in Natural Regional Park El Vínculo, Colombia. RF = Riparian forest; SF = Secondary forest; G = Grasslands; S = Shrubs; HA = Highly disturbed area.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Anyphaenidae						
Wulfila sp. 1	3	12	0	0	2	17
Anyphaenidae sp. 1	0	0	2	0	14	16
Anyphaenidae sp. 2	0	0	1	0	0	1
Anyphaenidae sp. 3	0	0	0	2	2	4
Araneidae						
Acacesia hamata Hentz 1847	0	0	11	0	3	14
Acacesia tenella L. Koch 1871	1	1	1	0	0	3
Alpaida leucogramma White 1841	0	0	19	0	0	19
Alpaida truncata Keyserling 1865	1	0	0	0	0	1
Argiope argentata Fabricius 1775	0	1	6	4	3	14
Cyclosa sp. 1	0	1	0	0	7	8
Cyclosa sp. 2	0	0	1	0	0	1
Cyrtophora citricola Forsskål 1775	0	0	3	0	0	3
Edricus spiniger O. Pickard-Cambridge 1890	2	3	0	0	0	5
Eriophora ravilla C.L. Koch 1844	2	0	2	0	4	8
Eriophora sp. 1	0	0	0	2	0	2
Eustala fuscovittata Keyserling 1864	0	0	4	0	4	8
Eustala sp. 1	0	0	0	0	1	1
Eustala sp. 2	0	0	0	2	0	2
Eustala sp. 3	0	0	3	0	0	3
Gasteracantha cancriformis Linnaeus 1758	0	0	4	3	15	22
Gea heptagon Hentz 1850	0	0	8	2	0	10
Mangora melanocephala Taczanowski 1874	11	0	0	0	19	30
Mastophora dizzydeani Eberhard 1981	0	0	0	0	1	1
Metazygia octama Levi 1995	1	0	0	0	0	1
Metazygia sp. 1	0	0	0	0	2	2
Metepeira sp. 1	0	0	5	0	0	5
Micrathena horrida Taczanowski 1873	3	1	0	0	3	7
Pronous pance Levi 1995	0	1	0	0	0	1
Scoloderus cordatus Taczanowski 1879	0	1	0	0	0	1
Verrucosa sp. 1	0	0	4	0	6	10
Wagneriana undecimtuberculata Keyserling 1865	0	0	0	0	1	1
Witica crassicaudus Keyserling 1865	3	0	0	0	0	3
Clubionidae						
Clubionidae sp. 1	0	3	0	0	0	3
Corinnidae						
Castianeira sp. 1	0	0	0	1	0	1
Mazax sp. 1	0	0	6	2	0	8
Mazax sp. 2	0	0	1	0	2	3
Trachelas sp. 1	0	0	0	0	1	1
Ctenidae						
Ctenus sp. 1	0	1	0	0	0	1
Ctenus sp. 2	0	1	0	0	0	1
Ctenidae sp. 1	2	1	0	0	0	3
Ctenidae sp. 2	0	4	0	1	0	5
Ctenidae sp. 3	3	1	0	0	0	4
Ctenidae sp. 4	0	1	0	0	0	1
Cybaeidae						
Cybaeus sp. 1	0	10	0	0	0	10
Deinopidae						
Deinopis sp. 1	0	0	1	1	1	3
Dictynidae						
Lathys sp.1	2	2	0	0	2	6
Lathys sp.2	0	1	0	1	0	2
Dictynidae sp. 1	0	2	1	0	0	3
Dictynidae sp. 2	1	2	0	0	0	3

Appendix 1.—Continued.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Dipluridae						
Ischnothele caudata Ausserer 1875	0	0	0	0	16	16
Gnaphosidae						
Gnaphosidae sp. 1	0	0	1	1	0	2
Hahniidae						
Hahniinae sp. 1	0	0	15	6	3	24
Hersiliidae						
Ypypuera sp. 1	34	28	0	0	0	62
Linyphiidae						
Dubiaranea margaritata Millidge 1991	0	0	0	0	23	23
Erigoninae sp. 1	20	5	4	6	20	55
Erigoninae sp. 2	1	4	0	0	0	5
Erigoninae sp. 3	0	0	0	0	23	23
Erigoninae sp. 4	2	0	0	0	0	2
Erigoninae sp. 5	2	0	0	0	2	4
Erigoninae sp. 6	0	1	0	0	0	1
Novafrontina uncata F.O. Pickard-Cambridge 1902	38	0	0	0	46	84
Linyphiinae sp. 1	2	9	0	0	0	11
Linyphiinae sp. 2	4	0	0	0	0	4
Linyphiinae sp. 3	0	0	0	3	0	3
Linyphiinae sp. 4	0	0	0	2	0	2
Linyphiinae sp. 5	0	0	0	2	0	2
Linyphiidae sp. 1	2	0	0	0	0	2
Lycosidae						
Aglaoctenus sp. 1	5	16	0	0	0	21
Allocosa sp. 1	15	0	0	0	2	17
Hogna sp. 1	0	0	9	2	0	11
Hogna sp. 2	0	0	2	0	0	2
Hogna sp. 3	0	0	13	2	0	15
Hogna sp. 4	0	0	1	2	0	3
Hogna sp. 5	0	0	4	2	0	6
Trochosa sp. 1	0	1	0	4	76	81
Mimetidae						
Mimetus sp. 1	5	48	0	0	0	53
Miturgidae						
Cheiracanthium inclusum Hentz 1847	0	0	4	3	0	7
Teminius hirsutus Petrunkevitch 1925	0	0	7	8	0	15
Mysmenidae						
Calodipoena sp.	0	0	0	0	1	1
Microdipoena guttata Banks 1895	0	1	1	1	0	3
Nephilidae						
Nephila clavipes Linnaeus 1767	0	0	0	0	3	3
Ochyroceratidae						
Ochyrocera sp. 1	23	19	0	0	0	42
Oonopidae						
Ischnothyreus sp. 1	0	0	10	0	1	11
Heteroonops sp. 1	0	0	3	2	0	5
Oonops sp. 1	0	1	0	0	0	1
Orchestina sp. 1	0	0	2	0	1	3
Oxyopidae						
Hamatilawa sp. 1	2	5	0	0	0	7
Oxyopes salticus Hentz 1845	0	0	4	0	2	6
Oxyopes sp. 1	0	6	0	0	0	6
Oxyopes sp. 2	0	1	0	0	0	1
Peucetia rubrolineata Keyserling 1877	0	0	0	3	3	6
Philodromidae						
Tibellus sp. 1	0	0	0	0	1	1

Appendix 1.—Continued.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Pholcidae						
Metagonia sp. 1	6	2	0	0	0	8
Wanana sp. 1	4	0	0	0	0	4
Pisauridae						
Thaumasia argenteonotata Simon 1898	0	0	0	3	10	13
Salticidae						
Beata sp. 1	0	0	0	0	2	2
Lyssomanes bitaeniatus Peckham & Wheeler 1889	7	12	0	0	0	19
Lyssomanes jeminens Peckham & Wheeler 1889	0	0	0	0	3	3
Lyssomanes sp. 1	0	0	0	0	1	1
Lyssomanes sp. 2	0	0	0	0	1	1
Mexigonus sp. 1	0	2	0	0	0	2
Thiodina sp. 1	3	4	0	0	8	15
Zygoballus sp. 1	0	0	1	0	0	1
Salticidae sp. 1	0	0	2	0	0	2
Salticidae sp. 2	0	0	0	2	0	2
Salticidae sp. 3	0	0	0	0	1	1
Salticidae sp. 4	0	3	0	0	0	3
Salticidae sp. 5	4	12	0	12	11	39
Salticidae sp. 6	4	2	0	0	0	6
Salticidae sp. 7	2	0	0	0	0	2
Salticidae sp. 8	1	0	0	0	0	1
Salticidae sp. 9	0	0	0	0	2	2
Salticidae sp. 10	2	0	0	0	0	2
Salticidae sp. 11	1	0	0	0	0	1
Salticidae sp. 12	2	0	0	0	0	2
Salticidae sp. 13	6	0	0	0	0	6
Salticidae sp. 14	0	0	0	0	2	2
Scytodidae						
Scytodes sp. 1	0	0	0	0	5	5
Senoculidae						
Secoculus canaliculatus F.O. Pickard-Cambridge 1900	8	2	0	0	3	13
Sparassidae						
Sparassidae sp. 1	0	0	0	24	2	26
Sparassidae sp. 2	0	0	1	0	0	1
Tetragnathidae						
Chrysometa sp. 1	10	6	0	0	3	19
Dolichognatha sp. 1	8	4	0	0	0	12
Leucauge sp. 1	0	0	0	0	4	4
Plesiometa sp. 1	0	0	3	0	0	3
Theraphosidae						
Pamphobeteus sp. 1	0	1	0	0	0	1
Theridiidae						
Anelosimus sp. 1	0	5	4	2	0	11
Anelosimus sp. 2	8	1	0	0	0	9
Anelosimus sp. 3	2	0	0	0	0	2
Anelosimus sp. 4	0	0	5	2	0	7
Anelosimus sp. 5	2	0	0	0	0	2
Anelosimus sp. 6	0	1	0	0	2	3
Anelosimus sp. 7	2	0	0	0	0	2
Anelosimus sp. 8	0	0	10	0	0	10
Argyrodes elevatus Taczanowski 1873	0	0	0	2	2	4
Argyrodes weyrauchi Exline & Levi 1962	0	0	0	0	1	1
Coleosoma acutiventer Keyserling 1884	2	0	0	0	0	2
Dipoena sp. 1	0	1	0	0	0	1
Dipoena sp. 2	0	2	0	0	0	2
Dipoena sp. 3	16	27	2	2	0	47
Dipoena sp. 4	0	0	0	5	0	5
Dipoena sp. 5	0	2	1	0	1	4
Dipoena sp. 6	0	0	0	2	0	2

Appendix 1.—Continued.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Episinus sp. 1	10	12	0	2	21	45
Episinus sp. 2	3	3	0	0	0	6
Euryopis sp. 1	0	0	1	2	1	4
Euryopis sp. 2	0	0	0	0	3	3
Euryopis sp. 3	0	0	0	0	1	1
Faiditus caudatus Taczanowski 1874	4	0	0	0	29	33
Faiditus cochleaformus Exline 1945	0	0	0	0	1	1
Meotipa sp. 1	0	0	0	0	2	2
Paratheridula perniciosa Keyserling 1886	0	0	2	0	0	2
Phycosoma altum Keyserling 1886	0	32	0	0	0	32
Theridion sp. 1	2	2	0	0	3	7
Theridion sp. 2	19	0	0	0	0	19
Theridion sp. 3	2	0	0	0	0	2
Theridion sp. 4	8	0	0	0	0	8
Tidarren haemorrhoidale Bertkau 1880	5	1	0	0	32	38
Tidarren sp. 1	0	0	0	0	1	1
Tidarren sp. 2	0	0	0	0	1	1
Theridiidae sp. 1	0	0	2	0	0	2
Theridiidae sp. 2	2	0	0	0	0	2
Theridiidae sp. 3	2	2	0	0	0	4
Theridiidae sp. 4	2	1	0	0	0	3
Theridiidae sp. 5	0	1	0	0	0	1
Theridiidae sp. 6	2	2	0	0	0	4
Theridiidae sp. 7	0	0	0	2	0	2
Theridiidae sp. 8	0	1	0	0	0	1
Theridiidae sp. 9	14	2	0	0	1	17
Theridiidae sp. 10	0	0	0	0	2	2
Theridiidae sp. 11	0	0	0	0	6	6
Theridiidae sp. 12	0	0	1	0	0	1
Theridiosomatidae						
Theridiosoma sp. 1	0	4	0	0	0	4
Theridiosoma sp. 2	2	0	0	0	0	2
Theridiosoma sp. 3	1	0	0	0	0	1
Thomisidae						
Misumena sp. 1	0	0	0	0	3	3
Misumena sp. 2	3	3	6	2	1	15
Misumena sp. 3	0	0	0	0	3	3
Misumenops sp. 1	2	0	0	0	2	4
Tmarus sp. 1	0	0	0	0	2	2
Tmarus sp. 2	0	0	0	0	2	2
Tmarus sp. 3	0	0	0	0	3	3
Tmarus sp. 4	0	0	0	0	3	3
Tmarus sp. 5	2	5	0	0	2	9
Tmarus sp. 6	2	0	0	0	0	2
Thomisidae sp. 1	0	0	1	0	0	1
Titanoecidae						
Titanoeca sp. 1	0	0	1	0	0	1
Uloboridae						
Miagrammopes sp. 1	1	23	0	0	0	24
Philoponella sp. 1	4	11	0	2	0	17
Philoponella sp. 2	0	5	0	0	0	5
Philoponella sp. 3	0	7	0	0	0	7
Uloborus sp. 1	0	0	1	0	5	6
Zodariidae						
Zodariidae sp. 1	0	1	0	0	0	1
Total	382	402	207	136	510	1637

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Genetic diversity within scorpions of the genus *Buthus* from the Iberian Peninsula: mitochondrial DNA sequence data indicate additional distinct cryptic lineages

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Abstract. Historically *Buthus occitanus* (Amoreux 1789) was recognized as the sole species of the genus present in the Iberian Peninsula, but recent morphological studies have identified and named two additional species. In addition, molecular data on the Moroccan fauna has shed light on the diversity within the genus. More species have since been described from North Africa, where diversity within the genus is highest. In this study we assessed the genetic diversity within specimens of *Buthus* Leach 1815 from across the Iberian Peninsula using cytochrome oxidase 1 (CO1) mitochondrial DNA sequences. The known range of *B. ibericus* Lourenço & Vachon 2004 was greatly expanded, with the species widespread in most of the western part of the Iberian Peninsula. Five distinct mtDNA lineages were found within *Buthus* from the Iberian Peninsula, two of which were reported for the first time in this study. However, both *B. ibericus* and *B. occitanus* included highly divergent lineages and thus further studies are needed to fully comprehend the taxonomy of *Buthus* from this region.

Keywords: CO1, phylogeny, Scorpiones

Historically only one species of the scorpion genus *Buthus* Leach 1815, *Buthus occitanus* (Amoreux 1789) was recognized from the Iberian Peninsula (Fet & Lowe 2000). Recently two new endemic species were described, *Buthus ibericus* Lourenço & Vachon 2004 and *Buthus montanus* Lourenço & Vachon 2004, from the southern Spanish provinces of Cadiz, and Granada and Almeria, respectively. These authors also suggest that *B. ibericus* may be present in the Algarve, southern Portugal, but these specimens were not included in their morphological analyses due to the poor state of the museum specimens examined. All other European specimens, from France and Spain, were attributed to *B. occitanus*. Later Teruel & Pérez-Bote (2005) examined a population of scorpions from Caceres Province in Extremadura (Central Spain) and concluded the specimens were also *B. ibericus*.

Phylogenetic and taxonomic assessments of *Buthus* in Iberia and North Africa have generally been in a state of rapid progression in recent years. As well as *B. ibericus* and *B. montanus*, several new species have been described from Morocco (e.g., Lourenço & Geniez 2005). Regarding their phylogenetic relationships, various studies have been performed using mitochondrial DNA (mtDNA) and nuclear DNA sequences (e.g., Gantenbein & Largiadèr 2003) and allozymes (Gantenbein 2004), and all have recognized that extensive cryptic genetic variation occurs. Gantenbein & Largiadèr (2003) found that European samples were highly distinct from North African populations, and could be divided into three distinct subclades. However, sampling in Europe was limited to 12 individuals from eight populations – four from the northeastern limit of the range in Catalonia (northeastern Spain) and France, and four from southern Spain and Portugal. Three of these southern populations, from Picacho and Benaocaz in Spain and Mértola in Portugal, could correspond to *B. ibericus*, which was described from this geographic region after this work, since they were genetically very distinct from the northern specimens of *B. occitanus*.

Despite this recent work, various basic aspects of species distribution, phylogeography and taxonomy of *Buthus* from the Iberian Peninsula remain unknown. Further, extensive sampling of this biodiverse region is needed to recover the complete phylogeographic pattern – genetically distinct lineages that appear to represent cryptic incipient species are still regularly being discovered in vertebrates (e.g., Pinho et al. 2006; Paulo et al. 2008). The aim of this study was therefore to assess genetic diversity within specimens from across the Iberian Peninsula using cytochrome oxidase 1 (CO1) mtDNA sequences, the gene typically included in barcoding studies (e.g., Hebert et al. 2003), and already employed by Gantenbein & Largiadèr (2003). These results are then compared to the specific status of the specimens to better assess diversity and distributions of the described forms.

METHODS

Information and geographic location of the specimens are given in Table 1 and Fig. 1. Adult and late instar specimens were examined morphologically, and identified to species level following Lourenço & Vachon (2004) and Teruel & Pérez-Bote (2005).

For the genetic analyses, whole genomic DNA was extracted from preserved (ethanol 96%) muscle tissue (leg fragment) using a standard high-salt protocol (Sambrook et al. 1989). A fragment of the cytochrome oxidase 1 (CO1) was amplified by polymerase chain reaction (PCR) using the primers from Folmer et al. (1994), LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′).

The PCR conditions (25 ml reactions) were as follows: each reaction contained 2.5 ml 10× Promega Buffer B, 0.5 ml 10 mM of each primer, 1.5 ml 25 mM MgCl2, 0.5 ml 10 mM dNTP's, 0.1 ml Promega Taq DNA polymerase and approxi-

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Table 1.—Localities of samples used, their position in Figure 1, and their respective MtDNA lineages in Figure 2; juvenile specimens could not be confidently identified to species levels and thus are represented as *Buthus* sp.; a - individuals identified before Lourenço & Vachon (2004) study; α, β and γ share haplotypes, only one of each is represented in Figure 2.

MtDNA lineage	*Buthus* Id	Taxonomy	Sex	Lat.	Long.	Country	GenBank Code
1	Sc084	*Buthus ibericus*	f	38.130	−7.019	Portugal	GQ168519
1	Sc089	*Buthus ibericus*	f	38.052	−7.028	Portugal	GQ168520
1	Sc095[α]	*Buthus* sp.	m	41.549	−6.231	Portugal	GQ168521
1	Sc100	*Buthus ibericus*	m	38.074	−7.046	Portugal	GQ168525
1	Sc104[α]	*Buthus* sp.	m	41.439	−6.324	Portugal	GQ168526
1	Sc105	*Buthus ibericus*	f	40.055	−7.193	Portugal	GQ168527
1	Sc106	*Buthus ibericus*	f	40.055	−7.193	Portugal	GQ168528
1	Sc107	*Buthus ibericus*	f	39.954	−7.119	Portugal	GQ168529
1	Sc108	*Buthus ibericus*	f	39.954	−7.119	Portugal	GQ168530
1	Sc109	*Buthus ibericus*	m	39.954	−7.119	Portugal	GQ168531
1	Sc112	*Buthus ibericus*	f	38.528	−8.004	Portugal	GQ168532
1	Sc113	*Buthus ibericus*	m	37.055	−8.924	Portugal	GQ168533
1	Sc114	*Buthus* sp.	m	37.022	−8.924	Portugal	GQ168534
1	Sc115	*Buthus ibericus*	f	38.163	−8.579	Portugal	GQ168535
1	Sc116	*Buthus ibericus*	m	38.685	−8.346	Portugal	GQ168536
1	Sc120	*Buthus ibericus*	m	38.528	−8.004	Portugal	GQ168537
1	Sc121	*Buthus ibericus*	f	37.186	−7.914	Portugal	GQ168538
1	Sc157	*Buthus ibericus*	f	39.433	−7.578	Portugal	GQ168539
1	Sc158	*Buthus ibericus*	f	39.512	−7.065	Spain	GQ168540
1	Sc161	*Buthus* sp.	f	39.360	−4.358	Spain	GQ168541
1	Sc190	*Buthus ibericus*	f	36.797	−6.378	Spain	GQ168542
1	Boo IB5a	*Buthus occitanus*[a]		37.717	−7.600	Portugal	AJ506911
1	Boo IB5b	*Buthus occitanus*[a]		37.717	−7.600	Portugal	AJ506912
2	Boo IB7a[β]	*Buthus occitanus*[a]		36.534	−5.650	Spain	AJ517182
2	Boo IB7b[β]	*Buthus occitanus*[a]		36.534	−5.650	Spain	AJ517183
2	Boo IB8	*Buthus occitanus*[a]		36.700	−5.417	Spain	AJ517184
3	Sc098	*Buthus* sp.	m	36.639	−5.248	Spain	GQ168523
3	Sc099	*Buthus occitanus*	m	36.639	−5.248	Spain	GQ168524
4	Sc096	*Buthus* sp.	f	37.740	−2.569	Spain	GQ168522
5	Boo IB1a[γ]	*Buthus occitanus*[a]		43.488	3.558	France	AJ506905
5	Boo IB1b	*Buthus occitanus*[a]		43.488	3.558	France	AJ506906
5	Boo IB2	*Buthus occitanus*[a]		43.183	3.000	France	AJ506907
5	Boo IB3a[γ]	*Buthus occitanus*[a]		42.433	3.117	France	AJ506908
5	Boo IB3b[γ]	*Buthus occitanus*[a]		42.433	3.117	France	AJ506909
5	Boo IB4	*Buthus occitanus*[a]		42.050	2.582	Spain	AJ506910
5	Boo IB6[γ]	*Buthus occitanus*[a]		36.831	−2.467	Spain	AJ517296
5	EU523755[γ]	*Buthus occitanus*				Unknown	EU523755
	Bop MA1	*Buthus paris*		31.566	−7.686	Morocco	AJ506913
	Bop MA2	*Buthus paris*		31.738	−7.029	Morocco	AJ506914
	Bom HA3a	*Buthus mardochei*		30.918	−6.924	Morocco	AJ506896
	Bom HA3b	*Buthus mardochei*		30.918	−6.924	Morocco	AJ506897
	Bom HA6a	*Buthus mardochei*		30.943	−7.123	Morocco	AJ506901
	Bom HA6b	*Buthus mardochei*		30.943	−7.123	Morocco	AJ506902
	Bot TA1	*Buthus tunetanus*		32.523	8.054	Tunisia	AJ506916

mately 100 ng per ml DNA template. The cycle parameters were: initial denaturation at 94° C (3 min), denaturation at 94° C (30 s), annealing at 53° C (45 s) and extension at 72° C (45 s) repeated for 35 cycles. Amplified DNA templates were enzymatically purified and sequenced using the ABI PRISM BigDye Terminator protocols. The sequencing primers were the same as those used in the PCR reactions. Sequences were visualized on an ABI-310.

DNA sequences were aligned by eye, but this posed no problems as no indels were found. All new sequences were submitted to GenBank (Table 1). All available CO1 sequences from Iberian *Buthus* on GenBank were aligned to the new data, as were four samples of *B. mardochei* Simon 1878 from the High Atlas in Morocco that appear most closely related to Iberian specimens (Gantenbein & Largiadèr 2003). Three more distantly related samples of *B. tunetanus* (Herbst 1800) and *B. paris* (C.L. Koch 1839) (from Gantenbein & Largiadèr 2003) were included as outgroups following the estimated relationships presented by Gantenbein & Largiadèr (2003).

Sequences were imported into PAUP* 4.0b10 (Swofford 2003). For the phylogenetic analysis Maximum Likelihood (ML) and Maximum Parsimony (MP) approaches were used, with random sequence addition (100 replicate heuristic search with TBR branch swapping; in MP search all characters were equally weighted). Support for nodes was estimated with the bootstrap technique (Felsenstein 1985) using 1000 replicates for both ML and MP analyses. The AIC criteria carried out in Modeltest 3.06 (Posada & Crandall 1998) was used to choose

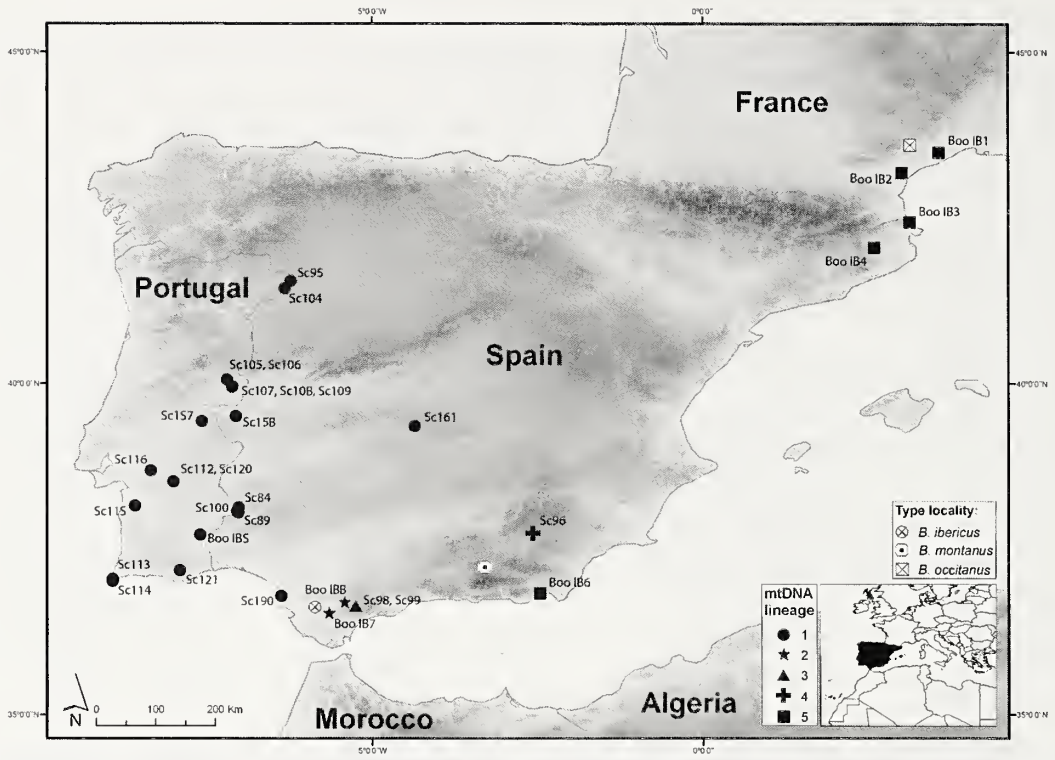

Figure 1.—Map showing the sampling locations of *Buthus* from the Iberian Peninsula and southern France included in this study. Samples are grouped in mtDNA lineages. Specimen codes follow Table 1. Type localities of the three *Buthus* species present in the Iberian Peninsula are also represented.

the model of evolution and the parameters for the ML analysis. Bayesian analysis was implemented using MrBayes v.3.1 (Huelsenbeck & Ronquist 2001), using a GTR + I + γ model with parameters estimated as part of the analysis and four incrementally heated Markov chains with the default heating values. The analysis was run for 10^6 generations, saving one tree in each 100 generations. The log-likelihood values of the sample point were plotted against the generation time, and all the trees prior to reaching stationary were discarded. The remaining trees were combined in a 50% majority consensus tree, in which the frequency of any particular clade represents the posterior probability (Huelsenbeck & Ronquist 2001).

All specimens are deposited in the collection of CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Vila do Conde, Portugal.

RESULTS

In total, 24 new specimens were sequenced, from 19 locations in the Iberian Peninsula, for a total of 596 base pairs. Twenty-two new haplotypes were resolved, and combined with 15 from GenBank, from eight localities from Iberia and southwestern France, although these were slightly shorter fragments than the new sequences. Ninety polymorphic sites were found, 64 of which are parsimony informative. High levels of genetic variability were found in the analyzed sequences (*Hd* = 0.994, π = 0.05589, with similar levels within *Buthus occitanus* lineages: *Hd* = 1.000, π = 0.04723; and *B. ibericus* lineages: *Hd* = 0,990, π = 0.04098). Low proportion of G's (especially in 3rd position sites), lack of stop codons in the translated sequences, no insertions or deletions and similarity with published sequences all indicate these are mtDNA coding COI sequences, and not nuclear copies. Tajima's neutrality test was non significant (Tajima's $D = -0{,}47912$; $P > 0.10$).

The most appropriate model of evolution for this dataset was the general time reversible model, with an estimate of invariable sites (0.55) and of the gamma shape parameter (1.04). The ML analysis recovered a single tree (−ln 2588, Fig. 2). 1121 MP trees were recovered (337 steps), the strict consensus of which differed from the ML tree only at nodes with <50% support in either analysis (Fig. 2). The Bayesian analysis recovered a similar tree to the ML analysis, again differing only at weakly supported nodes.

DISCUSSION

As noted in *Buthus* (Gantenbein & Largiadèr 2003) and in the genus *Scorpio* Linnaeus 1758 (Froufe et al., 2008) mtDNA variation is very high in many phylogeographic studies of scorpions (15% and 10% nucleotide divergence respectively, compared to average between species of considerably less than this in vertebrates, Johns & Avise 1998). Here variation is again notable, with 23 of 25 new specimens sequenced having unique haplotypes. At least five highly differentiated lineages occur in the Iberian Peninsula. One clearly corresponds to *B. occitanus* and is found in the northeast part of the range (Boo IB1 and Boo IB2 from close to the type locality) and in a sample from Almeria (Boo IB6), in southern Spain. Variation within this clade is low (0.6%, K2P distance, Table 2), possibly indicating a rapid expansion, presumably from the south along the east coast of Spain towards the north. A separate clade includes all the samples from the western part of the

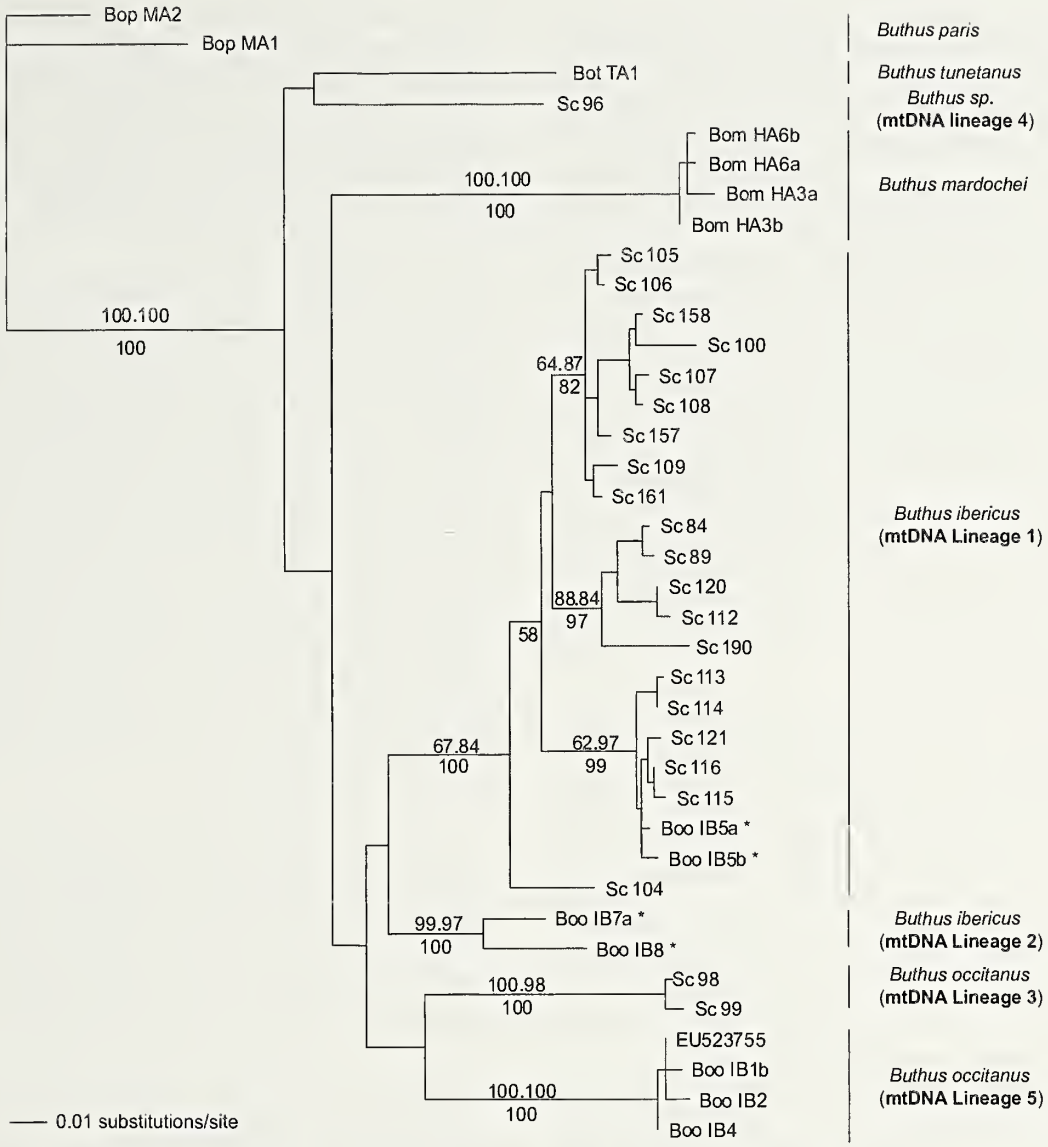

Figure 2.—Phylogram showing phylogenetic relationships estimated using maximum likelihood as described in the text. ML and MP bootstrap support is indicated above nodes, Bayesian posterior probabilities below nodes. The tree was rooted using three specimens of *B. tunetanus* and *B. paris*. Codes refer to Table 1. * indicate specimens identified as *B. occitanus* in Gantenbein & Largiadèr (2003), but assumed to correspond to the later-described *B. ibericus* based on their geographic origin and their position in the phylogenetic analysis.

Iberian Peninsula, including two samples from Mértola (Portugal) reported by Gantenbein & Largiadèr (2003). Substructuring within this clade seems to be present, with four subregions, although with relatively low support levels. Although the four subregions identified are generally geographically separate, in one area of Alentejo (southern Portugal) two sublineages occur in the same region (specimens Sc 84 and Sc 100). Three subregions occur in Central and Southern regions, but one (specimens Sc 95 and Sc 104) is currently only known from northern Portugal. However, extensive sampling would be needed to fully assess phylogeographic variation within this lineage.

Morphologically, all specimens that could be fully assessed from this clade appear to be *B. ibericus* following Teruel &

Table 2.—Net pairwise sequence divergence (Kimura 2-parameter) between the five lineages found in the Iberian Peninsula. In the last column values for within lineage divergence are present.

	lineage1	lineage2	lineage3	lineage4	within lineage estimates
lineage1	-				0.030
lineage2	0.043	-			0.043
lineage3	0.073	0.063	-		0.005
lineage4	0.085	0.062	0.074	-	-
lineage5	0.075	0.064	0.086	0.095	0.006

Pérez-Bote (2005). However, to complicate matters the samples reported from southern Spain by Gantenbein & Largiadèr (2003) are also from the area where *B. ibericus* was described (Figure 2, lineage 2), but form a highly distinct lineage (4.3%, K2P distance, Table 2). Adult *B. ibericus* are easily distinguished from *B. occitanus* by the presence of a node on the base of the movable finger of the chela (Lourenço & Vachon 2004). Unfortunately this is not clear in juveniles, making separation of the two species in early instars very difficult (Teruel & Pérez-Bote 2005). The previously reported presence of *B. occitanus* in western Iberia may be due to misidentification of specimens, or *B. ibericus* and *B. occitanus* may occur here in sympatry.

In this study two new and highly distinct lineages are also reported for the first time. One sample, Sc 96 (Figure 2, lineage 4), comes from the Sierra Nevada region and may correspond to *B. montanus*, but unfortunately the specimen is an early instar so could not be assigned with confidence to this species based on morphological characters. The other new lineage (samples Sc 98 and Sc 99; Figure 2, lineage 3), from southern Spain, morphologically resembles *B. occitanus*, but differs from the other specimens of this species by 8.6% (K2P distance from lineage 5, Table 2).

Although all five lineages are highly distinct (Table 2), relationships between them are poorly supported (Fig. 2). In MP no relationship between lineages has >50% bootstrap support. In the ML analyses the Iberian forms are not monophyletic, with one specimen (Sc 96) being the sister taxon to a specimen from Tunisia, although again support levels between lineages are low. In the Bayesian analysis the Iberian forms are monophyletic (posterior probability 23), with the specimen Sc 96 sister taxon to the *B. occitanus* mtDNA lineage 3 (posterior probability 41; Fig. 2). These differences have very low support levels and highlight only that relationships between lineages remain essentially unresolved.

The Iberian Peninsula, along with other southern European regions such as Italy and the Balkans, has long been viewed as an important refugia for biodiversity that was greatly reduced in northern Europe during Pleistocene glaciations (Hewitt 2000). Recent phylogeographic studies have extended this line of reasoning stressing the cryptic diversity found in the Iberian Peninsula, particularly in the southeast as evidence for "refugia within refugia" (reviewed in Gómez & Lunt 2007). This seems likely to be due to the complex geology of the region, especially during the Miocene when, prior to the Messinian salinity crisis, much of this region was an archipelago, allowing allopatric differentiation and also linking North African and European forms (reviewed in Paulo et al. 2008). *Buthus* is another example of this cryptic diversity, with multiple distinct lineages in the region, some of which appear to be more similar to North African lineages than to other Iberian lineages.

Although genetic diversity within *Buthus* from the Iberian Peninsula is very high, it is widely accepted as essentially impossible to consistently delimit species based solely on pairwise distances (Meier et al. 2006). In their study of 449 species of Diptera, Meier et al. (2006) showed that 33% of currently accepted species harbored lineages with greater than 3% CO1 sequence divergence, and thus would be considered species complexes if this was used as a threshold value. On the other hand, various recent barcoding studies have identified cryptic species based on CO1 divergences less than this (e.g. Ståhls et al. 2009). The divergence between lineages reported in this study also vary considerably from 4.3 to 9.5%, further highlighting the difficulties in defining thresholds based on single markers. Therefore the finding of these lineages within *Buthus* does not on its own indicate that undescribed species exist in the Iberian Peninsula, but the highly divergent lineages do warrant further investigation.

In conclusion, at least five distinct mtDNA lineages occur within *Buthus* from the Iberian Peninsula, two of which are reported for the first time in this study. Relationships between lineages are not well supported, but Iberian forms do not appear to be monophyletic. Specimens morphologically attributable to the recently described *B. ibericus* are widespread in the western part of the Iberian Peninsula, greatly expanding the range of this species. Additional fieldwork and analysis of museum specimens is necessary to clarify ranges of the newly described Iberian species. Of particular importance is the collection of specimens from the type locality of *B. ibericus*, in order to clarify the identity of one of the mtDNA lineages (lineage 2) found in this study. However, both *B. ibericus* and *B. occitanus* include highly divergent lineages, and thus more detailed morphological analyses, together with the analysis of nuclear genes, are needed to redefine the taxonomy of *Buthus* from this region.

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Taxonomic review of the Neotropical spider genus *Paradossenus* (Araneae: Lycosoidea: Trechaleidae: Trechaleinae) with a new erection of the subfamily Trechaleinae and a key to included genera

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Abstract. The Neotropical spider genus *Paradossenus* is revised and currently comprises a total of 14 species. *P. andinus* (Simon 1898), *P. protentus* (Karsch 1879) and *P. venezuelanus* (Simon 1898) are new junior synonyms of *P. longipes* (Taczanowski 1874), the type species of the genus. Five known species, *P. longipes*, *P. caricoi* Sierwald 1993, *P. pulcher* Sierwald 1993, *P. corumba* Brescovit & Raizer 2000, and *P. mininus* (Mello-Leitão 1940), are redescribed and illustrated. New species: *P. isthmus*, *P. benicito*, *P. amazonensis*, *P. acanthocymbium*, *P. tocantins* and *P. pozo* are described from both male and female. The new species *P. sabana* is described only from the male while *P. junin* is described only from the female. The subfamily Trechaleinae is erected, diagnosed, and an illustrated key to all the included genera is presented.

Keywords: New species, taxonomy, Neotropical region

The genus *Paradossenus* was described by F.O. Pickard-Cambridge (1903) originally as a genus in the family Pisauridae. Following the reintroduction (Carico 1981) of Simon's (1890) family, Trechaleidae, the genus was subsequently transferred to the latter family (Carico 1993; Sierwald 1993). Sierwald (1993) in the first taxonomic revision of the genus *Paradossenus*, found synonymies and described two new species, *P. pulcher* and *P. caricoi*. In addition, she included an opinion on the taxonomic position of the subfamily Rhoicininae in the Trechaleidae, pointed out the synonymy of *Xingusiella* (Mello-Leitão 1940) with *Paradossenus*, and discussed synapomorphies of the female genitalia in the family Trechaleidae. Brescovit et al. (2000) redescribed the recently rediscovered *P. mininus* (Mello-Leitão 1940), and included notes on the distribution and morphology of *P. longipes* (Taczanowski 1874). In this same paper, the latter authors also described *P. corumba* and included notes on the web-building behavior and ecology of this species.

The current paper reviews the taxonomy of the genus *Paradossenus*, a project made possible as a result of numerous new collections available through the cooperation of several museums, particularly those in South America. In addition, we describe the new subfamily, Trechaleinae, to include that group of non-Rhoicininae genera that has been identified as the core group of genera of the family from the beginning, as well as some new ones. Because we believe that the maturity level of the taxonomy of this subfamily sufficiently warrants it following recent generic revisions of all polytypic genera, we offer a diagnostic key to the genera of the same subfamily. However, because of the lack of females in three monotypic genera, it is obvious that this key will be substantially improved as these sexes are discovered as well as by any new genera and species which may be found subsequently.

METHODS

The material examined belongs to the following institutions: American Museum of Natural History, New York (AMNH); British Museum of Natural History, London (BMNH); California Academy of Science, San Francisco (CAS); Instituto Butantan, São Paulo (IBSP); Field Museum of Natural History, Chicago (FMNH); Polish Academy of Science, Museum of the Institute of Zoology Warsaw (PAN); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Division Entomologia, Buenos Aires (MACN); Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul – PUCRS, Porto Alegre (MCTP); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Museu Equitoriano Ciências Naturales, Quito, Ecuador (MECN); Muséum National d'Histoire Naturelle, Paris (MNHN); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Laboratório de Aracnologia da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (LAMG); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM); Museo Zoologico "La Specola", Firenze (MZUF); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP); Zoologisches Museum der Humboldt Universität, Museum fur Naturkunde der Humboldt Universität, Berlin (ZMHU).

All measurements are in mm. As an index to the size of the body, only the length of the relatively rigid carapace is given because of variability in the condition of the softer abdomen. Following critical point drying, the scanning electron micrographs (SEM) were made with a Philips XL 30 scanning electron microscope in the Centro de Microscopia e Microanálises (CEMM) of Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS).

The nomenclature and anatomy of the male palpus and female epigynal structures follows Carico (1993), Silva et al. (2008) and Sierwald (1993). Abbreviations are used throughout the manuscript: AE, anterior eyes, or length of anterior eye row; AF, anterior field of epigynum; ALE, anterior lateral eyes; AME, anterior median eyes; AS, accessory spermathecae; CO, copulatory ducts; D, duct; DD, dorsal division of median apophysis; E, embolus; ECD, ectal division of retrolateral tibial apophysis (RTA); END, ental division of

[1] Deceased 24 March 2009

RTA; G, guide, terminal portion of median apophysis; HS, head of spermathecae; LL, lateral lobes of epigynum; MA, median apophysis; MF, middle field of epigynum; OQA, anterior part of ocular quadrangle, or length of line composed of anterior median eyes; OQH, ocular quadrangle height, or length of a line composed of anterior median eye and posterior median eye; OQP, posterior part of ocular quadrangle, or length of line composed of posterior median eyes; PE, posterior eyes, or length of posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes; RTA retrolateral tibial apophysis of male palpal tibia; S, spermathecae; ST, subtegulum; T, tegulum; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

TAXONOMY

Family Trechaleidae Simon 1890

Diagnosis.—The spider family Trechaleidae is defined as follows: eyes arranged in two rows, tibial apophysis and a ventro-distal refolded rim on male palpal tibia; male palpus with a large median apophysis with a dorsal embolic groove extending into the guide; female epigynum generally heavily sclerotized, dark and opaque; epigynal plate conspicuous, anterior field wide and usually distinct from the lateral lobes. Female builds discoid and flattened egg sac, fixed and carried on the spinnerets (Carico 1993; Silva et al. 2008).

Subfamily Trechaleinae Simon 1890

Type genus.—*Trechalea* Thorell 1869

Note.—Since in the original description of the family Trechaleidae there is no mention of a name for a subfamily, because when the subfamily Rhoicininae was included in Trechaleidae (Griswold 1993; Sierwald 1993) it presented a group of genera included in Rhoicininae and the remaining genera were not included in any named subfamily, we felt the need to erect a name of a subfamily to include these remaining genera.

Diagnosis.—The subfamily Trechaleinae can be securely distinguished from the subfamily Rhoicininae by characters of the eye pattern and male palpus. The tibia of the male pedipalp in the Trechaleinae has a well-developed retrolateral apophysis composed of either a single part or a pair of subdivisions; a retrolateral apophysis is lacking in the Rhoicininae. The width of the anterior eye row is equal to or only slightly larger than the length of the posterior median row of eyes, and the anterior lateral eyes are always smaller than the anterior median eyes. In the Rhoicininae the anterior eye row is distinctly wider than the posterior median eye row, and if it is narrower, then the anterior lateral eyes are smaller than the anterior median eyes.

Description.—Eye pattern in two rows, PE row recurved, wider than AE row, width of anterior eye row equal to or only slightly greater than length of posterior ocular quadrangle, ALE often situated adjacent to and beneath PLE, PE equal in size and larger than AE, ALE smaller than AME, AME/ALE interdistance separated by less than the diameter of ALE and less than AME/AME interdistance. Palpal bulb in ventral view in three distinct and consistent subdivisions; subtegulum smaller than tegulum and situated slightly prolaterally; tegulum extending diagonally over full width of bulb face and median apophysis apical, variable but divided into ventral and dorsal divisions with the guide tip located on the dorsal division and usually visible as a short, acute point. The RTA is located on the distal rim of the tibia; a broad, membranous concavity is present on the ventro-distal end of the tibia.

PLACEMENT OF GENERA INTO SUBFAMILIES

Genera included in the subfamily Rhoicininae.—Since the introduction of this subfamily by Simon (1898a) as a group within the Lycosidae, it has been moved to other families including the Agelenidae (Petrunkevitch 1928), the Pisauridae (Exline 1950, 1960), and currently the Trechaleidae (Griswold 1993; Sierwald 1993; Brescovit & Höfer 1994). Genera currently (Platnick 2009) in the Rhoicininae are *Barrisca* Chamberlin & Ivie 1936 (generic revision, see Platnick 1979), *Heidrunea* Brescovit & Höfer 1994, *Rhoicinus* Simon 1898a (generic revision, see Exline 1950), *Shinobius* Yaginuma 1991, none of which possess the combination of characters that define the Trechaleinae (see diagnosis in this paper).

Genera included in the subfamily Trechaleinae.—We place the following genera into the subfamily Trechaleinae: *Amapalea* Silva & Lise 2006, *Caricelea* Silva & Lise 2007, *Dossenus* Simon 1898b (generic revision, see Silva et al. 2007), *Dyrines* Simon 1903 (generic revision, see Carico & Silva 2008), *Enna* O. Pickard-Cambridge 1897 (generic revision, see Silva, et al. 2008), *Hesydrus* Simon 1898a (generic revision, see Carico 2005a), *Magnichela* Silva & Lise 2006, *Paradossenus* F.O. Pickard-Cambridge 1903 (generic revisions, see Sierwald 1993; current paper), *Paratrechalea* Carico 2005b, *Syntrechalea* F.O. Pickard-Cambridge 1902 (generic revision, see Carico 2008b), *Trechalea* Thorell 1869 (generic revision, see Carico 1993) and *Trechaleoides* Carico 2005b. For a diagnostic key to the identification of the genera in the subfamily Trechaleinae, see Appendix I.

Genus excluded from the Trechaleinae.—*Neoctenus* Simon 1897, which has been a matter of considerable dispute (see review in Platnick 2009) regarding its family placement, is excluded here from the subfamily Trechaleinae and the diagnostic key below because it does not comply with the character set used to define Trechaleinae. Further, it is not our objective in this study to confirm or dispute the taxonomic position of *Neoctenus* in any family or subfamily.

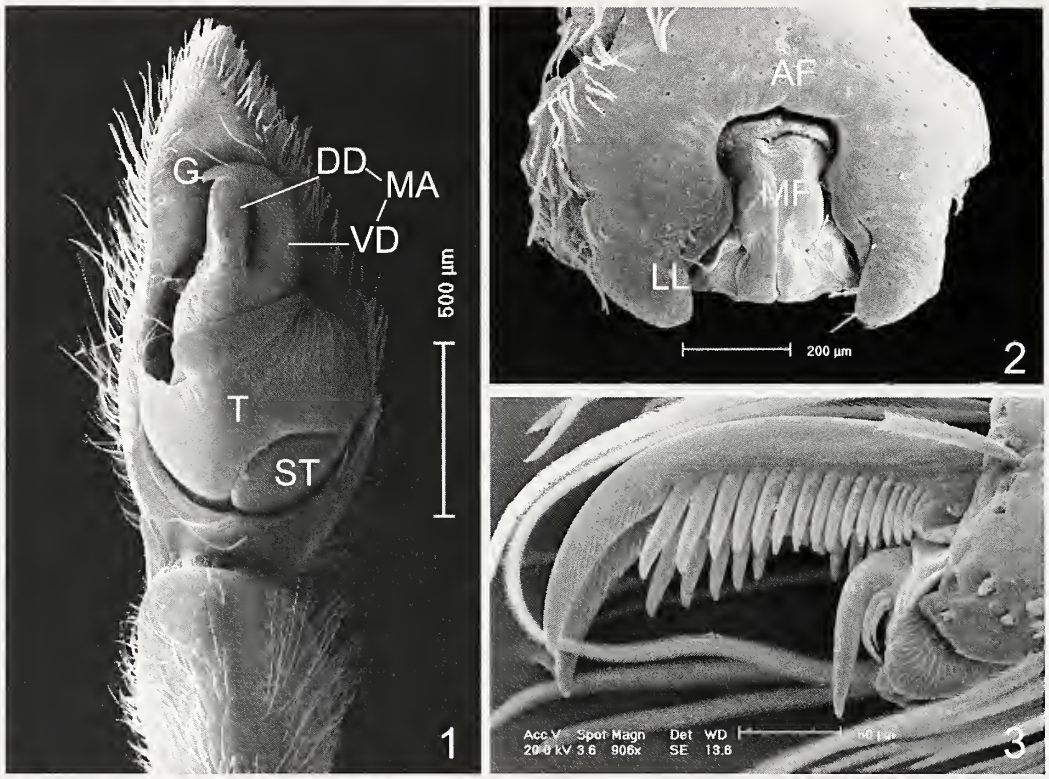
Genus *Paradossenus* F.O. Pickard-Cambridge 1903

Paradossenus F.O. Pickard-Cambridge 1903:155; Roewer 1954:139; Bonnet 1958:3325; Carico 1993:226; Sierwald 1993:53–74; Brescovit, et al. 2000:7–15; Platnick 2009.

Xingusiella Mello-Leitão 1940:23, fig. 1 (junior synonym of *Paradossenus*); Sierwald 1993:55; Platnick 2009.

Type species.—*Paradossenus longipes* (Taczanowski 1874).

Diagnosis.—This genus resembles *Dossenus* Simon 1898 by the absence of the ental division (END) of the retrolateral tibial apophysis (RTA) (Figs. 6, 12, 22, 26, 31, 44, 48), but can be distinguished by the combination of the following characters: metatarsi and tarsi of the legs are straight and neither bent nor flexible as in some other relatively typical trechaleid genera; i.e., *Trechalea* Thorell 1869 and *Hesydrus* Simon 1898. Males are distinguished by the presence of a conspicuous ectal division of the RTA (ECD), not divided, except in *P. amazonensis* and *P. acanthocymbium* (Figs. 35,



Figures 1–3.—*Paradossenus longipes*. 1. Left male pedipalpus (reversed), ventral view; 2. Female epigynum, ventral view; 3. Tarsal claw, left leg; IV, lateral view. Abbreviations: AF, anterior field of epigynum; DD, dorsal division of median apophysis; G, guide, terminal portion of median apophysis; MA, median apophysis; MF, middle field of epigynum; ST, subtegulum; T, tegulum; VD, ventral division of median apophysis.

39), which is slender, acute and sometimes somewhat curved (Figs. 6, 12, 22, 26, 31, 44, 48). The female epigynum has a distinct middle field that is situated between a pair of distinct lateral elevations; internally there is wide variation, with the presence of conspicuous spermathecae and the presence of an accessory spermathecae (except in *P. pozo*, Fig. 50) attached to a sclerotized arch with membranous wings (W) (except in *P. corumba*, *P. pulcher* and *P. benicito*) (Figs. 8, 14, 16, 18, 20, 24, 28, 33, 37, 42, 46).

Description.—Carapace moderately high to low, height of cephalic area higher or not, length 1.7–4.4, AE row slightly procurved. Sternum about as long as wide, almost always unmarked. Paturon generally swollen anteriorly, with a diagonal groove above fang origin (Fig. 22); chelicerae with promargin typically with three teeth with middle largest (none in *P. acanthocymbium*); retromarginal teeth variable from three to 4. Median apophysis of male palpus conspicuous, (Fig. 1) with short, curved guide arising from dorsal division; ventral division variable, typically rounded on retrolateral edge (except *P. corumba*); tibia shorter than cymbium and with a single, narrow, tapered retrolateral apophysis (except *P. amazonensis* and *P. acanthocymbium*, which have an additional, small, proximal projection). Female epigynum, in ventral view, with a distinct but variable middle field and lobular lateral elevations (Figs. 7, 13, 15, 17, 19, 23, 27, 32, 36, 41, 45, 49); internal components very variable but usually with small spermathecae and large accessory spermathecae (Figs. 8, 14, 16, 18, 20, 24, 28, 33, 37, 42, 46, 50).

Distribution.—The genus *Paradossenus* extends from southeastern Nicaragua southward to northern Uruguay, and locality labels with specimens commonly include names of streams suggesting that aquatic habitats are essential for their occurrence (Fig. 4).

Paradossenus longipes (Taczanowski 1874)
Figs. 1–9

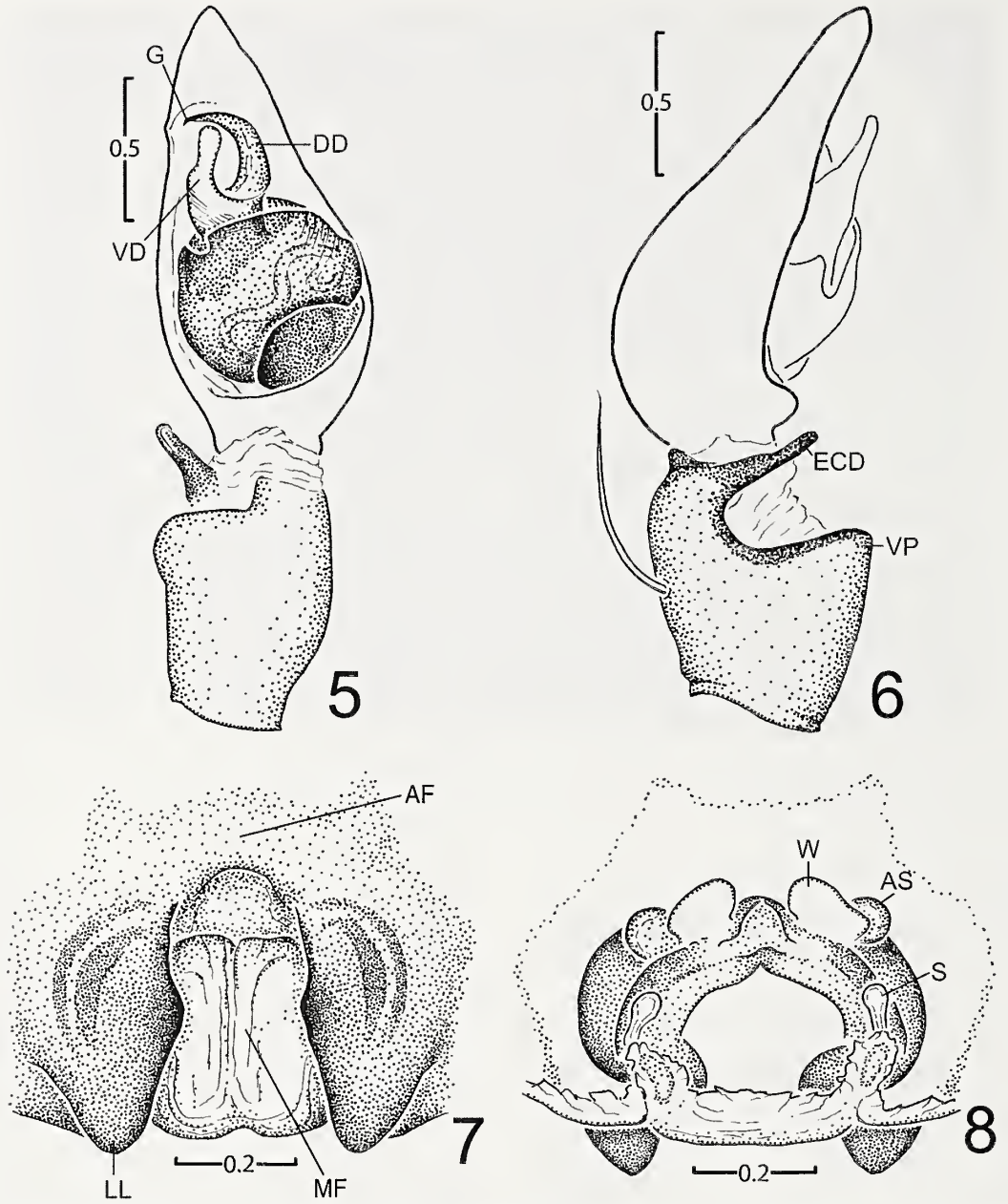
Dolomedes longipes Taczanowski 1874:88.
Hygropoda andina Simon 1898a:316, 1898b:22; Roewer 1954:138; Bonnet 1957:2243.
Paradossenus andinus Carico 1993:231; Platnick 2009. New synonymy.
Paradossenus nigricans F.O. Pickard-Cambridge 1903 (= *P. longipes*, Sierwald 1993:57); Roewer 1954:139; Bonnet 1958:3325.
Paradossenus taczanowskii Caporiacco 1948:631 (= *P. longipes*, Sierwald 1990:35).
Trechalea protenta Karsch 1879:540.
Paradossenus protentus Carico 1993:231; Platnick 2009. New synonymy.
Hygropoda venezuelana Simon 1898b:22; Roewer 1954:138; Bonnet 1957:2244.
Paradossenus venezuelanus Carico 1993:231; Platnick 2009. New synonymy.

Type material.—Female lectotype, male paralectotype: FRENCH GUIANA: Cayenne, K. Jelski (PAN), examined.

Other material examined:—ARGENTINA: *Chaco*, 2 females, Selva del Rio de Oro, 27°04′S, 58°34′W, 27 January 1965, Galiano (MLP); *Parque*, "Islas Malvinas" (Mnes.), 1 female, 2 February 1988, Goloboff & Szumik (MACN); *Salta*,

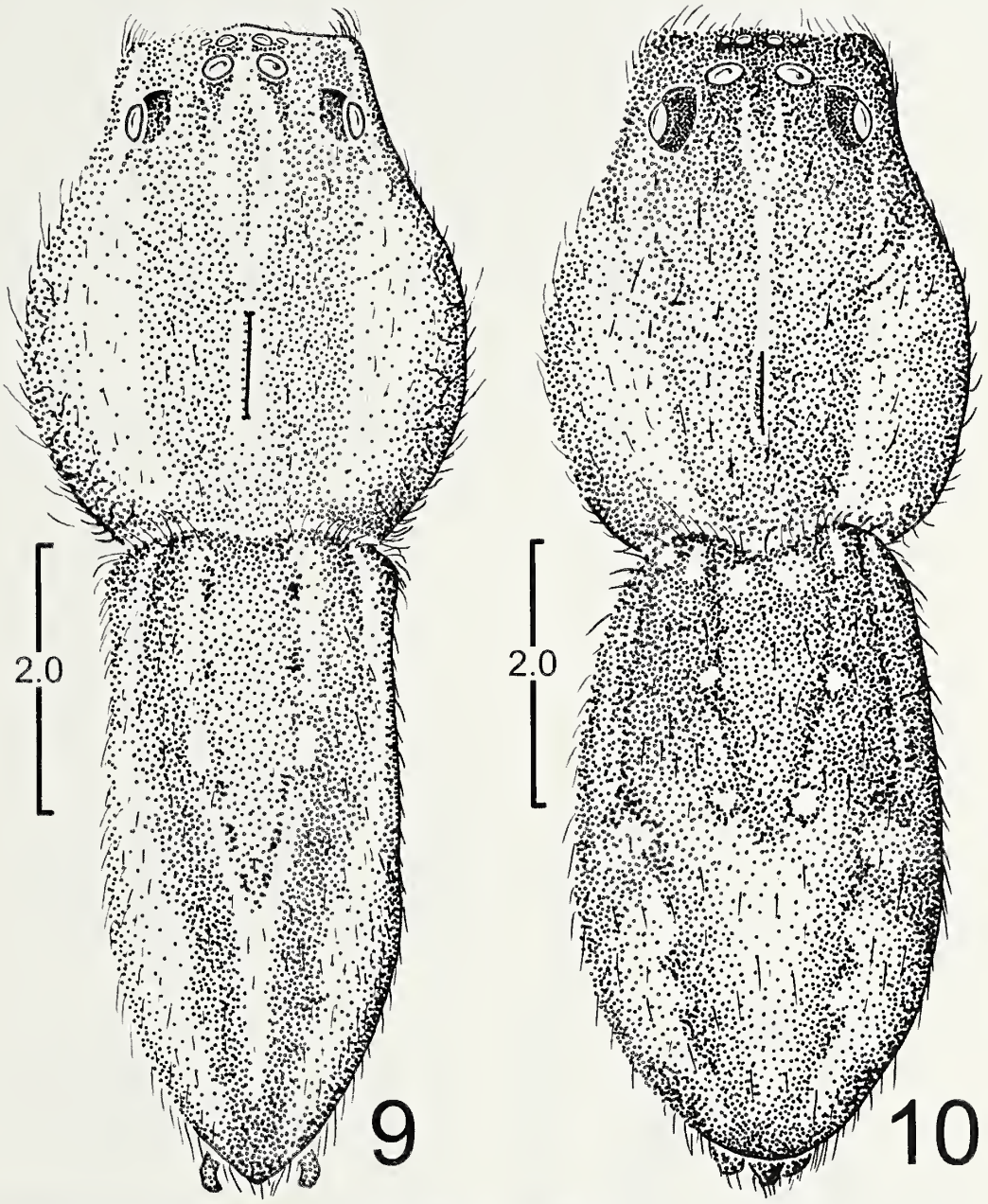
Figure 4.—Distribution of species of *Paradossenus*.

Rinadavia, Santa Victoria, 22°11′S, 64°45′W, 1 female, June 1961, Bachman (MACN); *Misiones*, 1 female, 3–12 December 1989, Garabi (MCTP 1289); Ste Maria, 22°11′S, 64°45′W, 1 female, no date, Sciap. Delan. etc. (MACN); *Buenos Aires*, Carapachay, km. 10 Delta, Bs. Is., 34°25′S, 58°35′W, 1 male, 2 females, December 1986, Goloboff (MACN). BRAZIL: *Amazonas*, Manaus, Reserva Florestal Adolpho Ducke, 3°06′S, 60°01′W, 1 female, 8 April 1992, S. Darwich (MCTP 2846); 1 female, 8 April 1992, U. Barbosa (MCTP 2719); 1 female, 8 April 1992, S. Darwich (MCTP 2718); Rio Purus, NW of Sena Madureira, Boca do Matapa, 1°54′S, 53°29′W, 1 male, 22 September 1973, B. Patterson (MCZ); *Acré*, Rio Purus, NW of Sena Madureira, Seringal Santo Antonio (above Manuel Urbana), 8°13′S, 72°59′W, 1 female, 15–18 September 1973, B. Patterson (MCZ); *Pará*, Canindé, Rio Gurupi, 0°31′S, 51°14′W, 1 male, 27–31 October 1964, B. Malkin (AMNH); 2 females, 3–11 June 1963, B. Malkin (AMNH); Rio Gurupi, 1°13′S, 46°06′W, 1 female, 7–15 April 1963, B. Malkin (AMNH); *Mato Grosso*, Barra do Taparape, 1 female, 17 December 1963–2 February 1964, B. Malkin (AMNH); Usina Hidrelétrica Guaporé, 15°58′S, 59°53′W, 1 female, 4–14 October 2002, Operação Coatá (MCTP 17586); *Minas Gerais*: Santana do Riacho, Parque Nacional da Serra do Cipó, Rio do Peixe, 1 male, 2 females, 10–14 February 2001, E.S.S. Álvarez (LAMG 568); *São Paulo*: Pirassununga, Rio dos Cocais, 21°59′S, 47°25′W, 1 female, 1 March 1940,



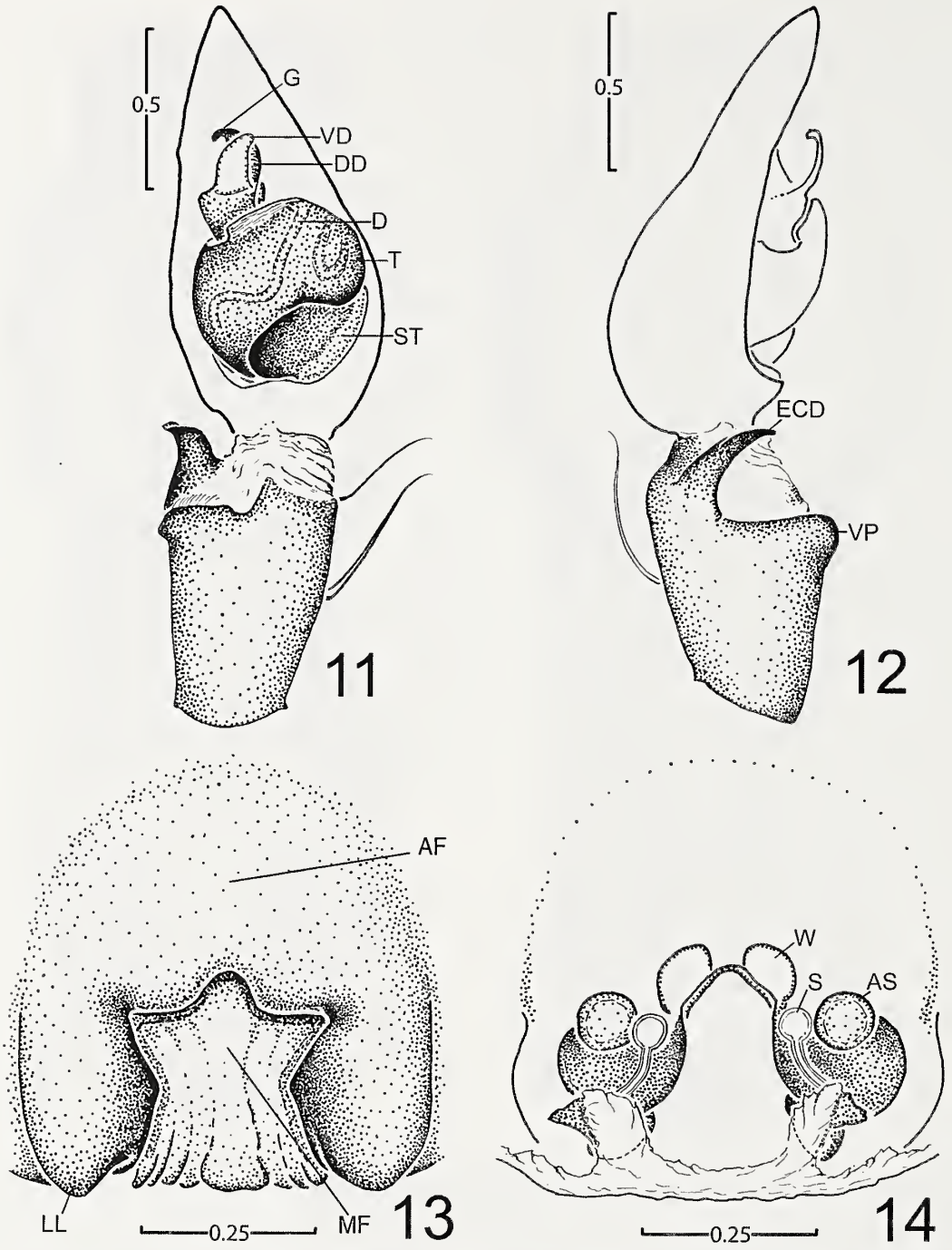
Figures 5–8.—Genitalia of *Paradossenus longipes*. 5, 6. Right pedipalpus; 5. Ventral view; 6. Retrolateral view; 7, 8. Epigynum; 7. Ventral view; 8. Dorsal view. Abbreviations: AF, anterior field of epigynum; AS, accessory spermathecae; DD, dorsal division of median apophysis; ECD, ectal division of retrolateral tibial apophysis (RTA); G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; MF, middle field of epigynum; S, spermathecae; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

Schulbart (MZSP 7073); Mogi Guaçu, Rio Mogiguaçú, 22°22′S, 46°56′W, 1 female, 18 October 1940, Schulbart (MZSP 7146); *Rio Grande do Sul*: Sapiranga, Arroio Feitoria, 29°35′S, 51°15′W, 1 female, 23 February 2004, E.L.C. Silva (MCTP 16571); 2 females, 23 February 2006, E.L.C. Silva (MCTP 21718); 1 female, 20 February 2008, E.L.C. Silva (MCTP 21719); 1 male, 1 female, 31 January 2004, E.L.C. Silva (MCTP 21720); 1 male, 2 females, February 2008, E.L.C. Silva (MCN 37300); Mampituba, Rio Mampituba, 29°10′S, 49°43′W, 1 male, 1 female, 26 March 2006, E.L.C. Silva (MCTP 0870); Rio Uruguai, BR-153, 34°12′S, 58°18′W, 1 male, February 1989, Itá-Machadinho (MCTP 1296); Estrela Velha, Barragem Itaúba, 29°10′S, 53°09′W, 1 female, 8 March 2001, R. Ott (MCN 33722); 2 females, 6 March 2001, R. Ott (MCN 33684); Porto Alegre, Ilha do Laje, 29°57′S, 51°16′W, 1 female, 22 March 1983, J.E. Lang (MCN 11486); Ilha das Flores, 29°59′S, 51°15′W, 2 females, 17 June 1992, C.S. Bastos (MCN 10487); São Leopoldo, 30°05′S, 51°36′W, 1 female, 6 August 1982, C.J. Becker (MCN 10663); 2 females, 25 March 1983, C.J. Becker (MCN 11518); 1 female, 17 March 1965, C. Valle (MZSP 4796); Eldorado do Sul, Parque Estadual Delta do Jacuí, 30°05′S, 51°36′W, 1 female, 5 January 2000, A. Barcelos (MCN 32095); Triunfo, 29°56′S, 51°43′W, 1 female, 12 January 1989, H.A. Gastal (MCN 18086); Pinhal Grande, Rio Jacuí, 29°16′S, 53°20′W, 1 female, 7 May 1998, M.A.L. Marques (MCN 29390); Terra de Areia, Rio dos Pintos,



Figures 9–10.—*Paradossenus* species, dorsal views. 9. *P. longipes*; 10. *P. isthmus*.

29°35′S, 50°04′W, 1 male, 27 December 2002, E.L.C. Silva (MCN 37301); Júlio de Castilhos, Barragem Itaúba, 29°16′S, 53°20′W, 1 female, 22 October 1998, L. Moura (MCN 30604). ECUADOR: *Napo*, R.F. Cuyabeno, Rio Cuyabeno, 0°16′S, 75°53′W, 1 female, 25 July 1985, L. Avilés (MECN); *Pastaza*, Cusuimi, on Rio Cusuimi, 150 km SE Puyo, 2°48′S, 77°38′W, 1 male, 15–31 June 1971 (also 15–22 May 1971), W.B. Malkin (FMNH); *Sucumbios*, Lago Agrio nr. Entrance to Cuyabeno, 0°06′N, 76°54′W, 2 females, 20–30 September, V. Roth (CAS). GUYANA: *Upper Takkutu-Upper Essequebo*, Kkuyuwimi River. From K Landing to Essequebo River, 7°02′N, 58°27′W, 1 male, 2 females, 1 juvenile, 1–8 December 1937, W.G. Hassler (AMNH); Shudicar River, Upper Essequibo River, 1 female, 1 January 1938, W.B. Hassler (AMNH); *Cuyuni-Mazaruni*, Bartica District, Kartabo, 6°24′N, 58°37′W, 1 female, unknown date, W. Beebe #22467 (AMNH); 1921, Beebe (AMNH); 1 female, 1924, unknown collector, (AMNH); (*unknown province*), Onoro Region, 1°37′N, 58°38′W, 1 female, 13–18 December 1937, W.G. Hassler (AMNH). PARAGUAY: *Amambay*, near Pedro Juan Caballero, 22°34′S, 55°37′W, 1 female, 25–27, November 1956, C.J.D. Brown (MCZ); *Paraguari*, ca. Ybtymi, 25°46′S, 56°47′W, 1 female, 1957, J.P. Rivaldi (AMNH). PERU: *Madre de Dios*, Rewervada de Manu, Puesto de Vigil. Pakitza, quebrada Il Bano, 11°58′S, 71°18′W, 1 female, 5 October 1987, D. Silva & J. Coddington; *Loreto*, Alto Amazonas, Pastaza, 4°55′S, 76°24′W, 1 female, October 1973, J.C. Olin (MCZ); Caballococha, 1 male , no date and collector (MUSM #00500058); *Huanuco*, Monson Valley, Tingo Maria, 9°17′ 76°00′ W, 1 female, 19 November 1954, E.I. Schlinger & E.S.

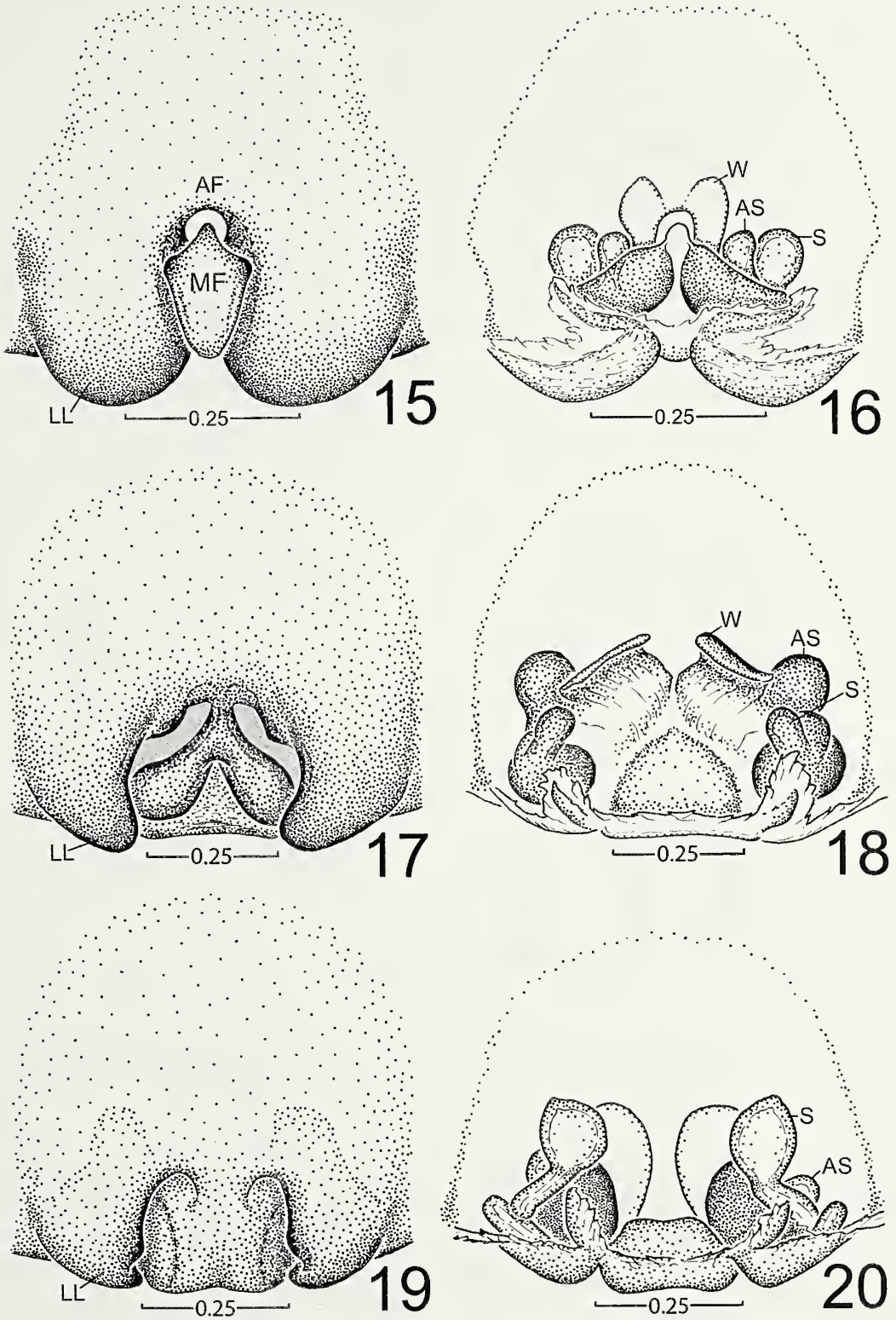


Figures 11–14.—*Paradossenus isthmus*. 11, 12. Right pedipalpus; 11. Ventral view; 12. Retrolateral view; 13, 14. Epigynum; 13. Ventral view; 14. Dorsal view. Abbreviations: AF, anterior field of epigynum; AS, accessory spermathecae; DD, dorsal division of median apophysis; D, duct; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; MF, middle field of epigynum; S, spermathecae; ST, subtegulum; T, tegulum; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

Ross (CAS); 1 male, 1 female, 26 October 1954, E.I. Schlinger & E.S. Ross (CAS); *Ucayali*, La Frontera, Upper Utoquinia, 8°13′S, 74°31′W, 1 male, 1928, H. Bassler (AMNH). URUGUAY: *Salto*, Rio Arape (Tangarupa), 31°01′S, 57°30′W, 1 male, 1 female, 20 December 1954, collector unknown (MACN). VENEZUELA: *Territorio Federal*, Delta Amaccuro, Rio Orinoco Delta, 8°30′N, 60°50′W, 1 female, January–February, 1935, N. Weber (MCZ); *Amazonas*, Rio Yaciba, 0°50 N, 66°10′W, 1 male, 3 December 1953, unknown collector (AMNH).

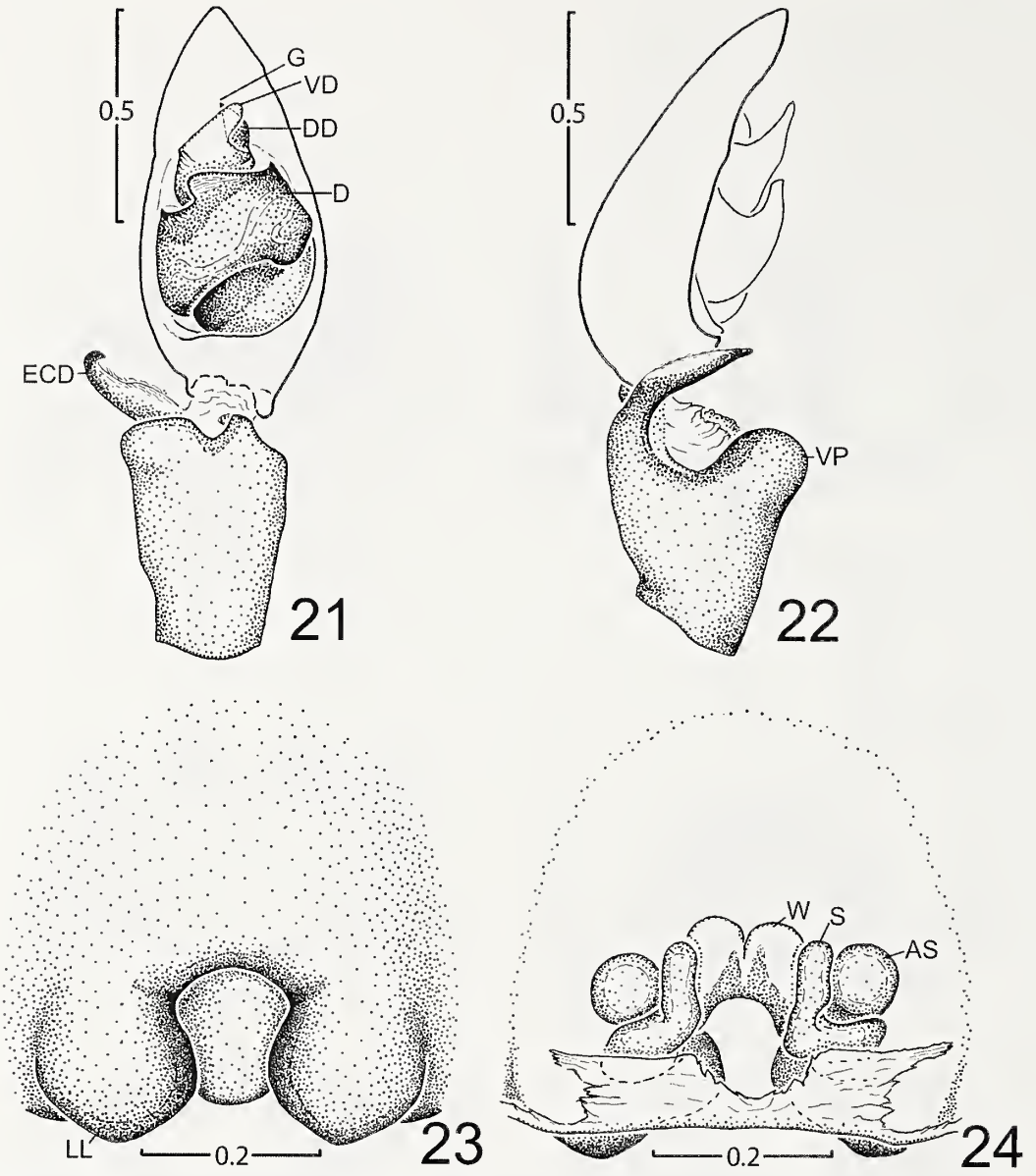
Diagnosis.—The females of *P. longipes* resemble those of *P. anazonensis* (Fig. 36) by the general shape of their epigynum, but can be distinguished by the wider middle field (MF), straight-edged laterally, whitish and with shallow grooves (Figs. 2, 7). The males are similar to those of *P. isthmus* (Fig. 11) by the general shape of the median apophysis, but can be distinguished by the more developed dorsal division (DD) of median apophysis (MA) that presents a "hook-like" shape (Figs. 1, 5).

Description.—*Female* (*lectotype*): Carapace length 3.5, width 3.1. Sternum length 1.72, width 1.60, light and



Figures 15–20.—Epigyna of *Paradossenus* species. 15, 16. *P. caricoi*; 15. Ventral view; 16. Dorsal view; 17, 18. *P. pulcher*; 17. Ventral view; 18. Dorsal view; 19, 20. *P. junin*; 19. Ventral view; 20. Dorsal view. Abbreviations: AF, anterior field of epigynum; AS, accessory spermathecae; LL, lateral lobes of epigynum; MF, middle field of epigynum; S, spermathecae; W, wings.

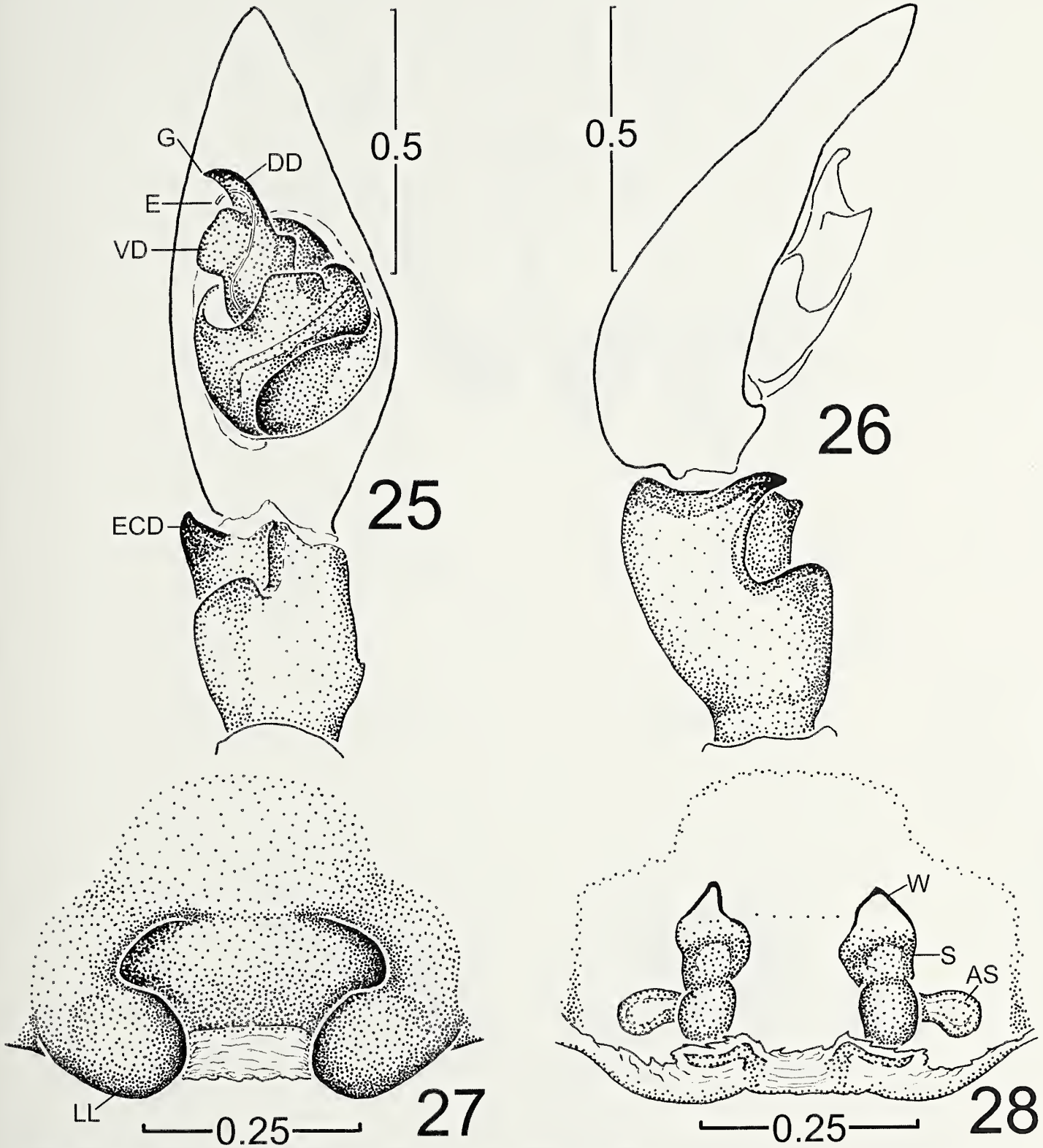
unmarked; labium length 0.68, width 0.64, dark but lighter anteriorly. Clypeus height 0.22, width 1.50. Carapace with longitudinal wide median dark band divided medially with narrow light band; dark reticulations laterally in lateral light areas. Anterior eye row slightly recurved, eye measurements in Table 1. Cheliceral teeth: promarginal 3, proximal one shortest, remainder subequal; retromarginal 4, second from proximal shortest, remainder subequal. Color of legs light with small maculae around base of setae. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 5.8, 7.4, 5.6,



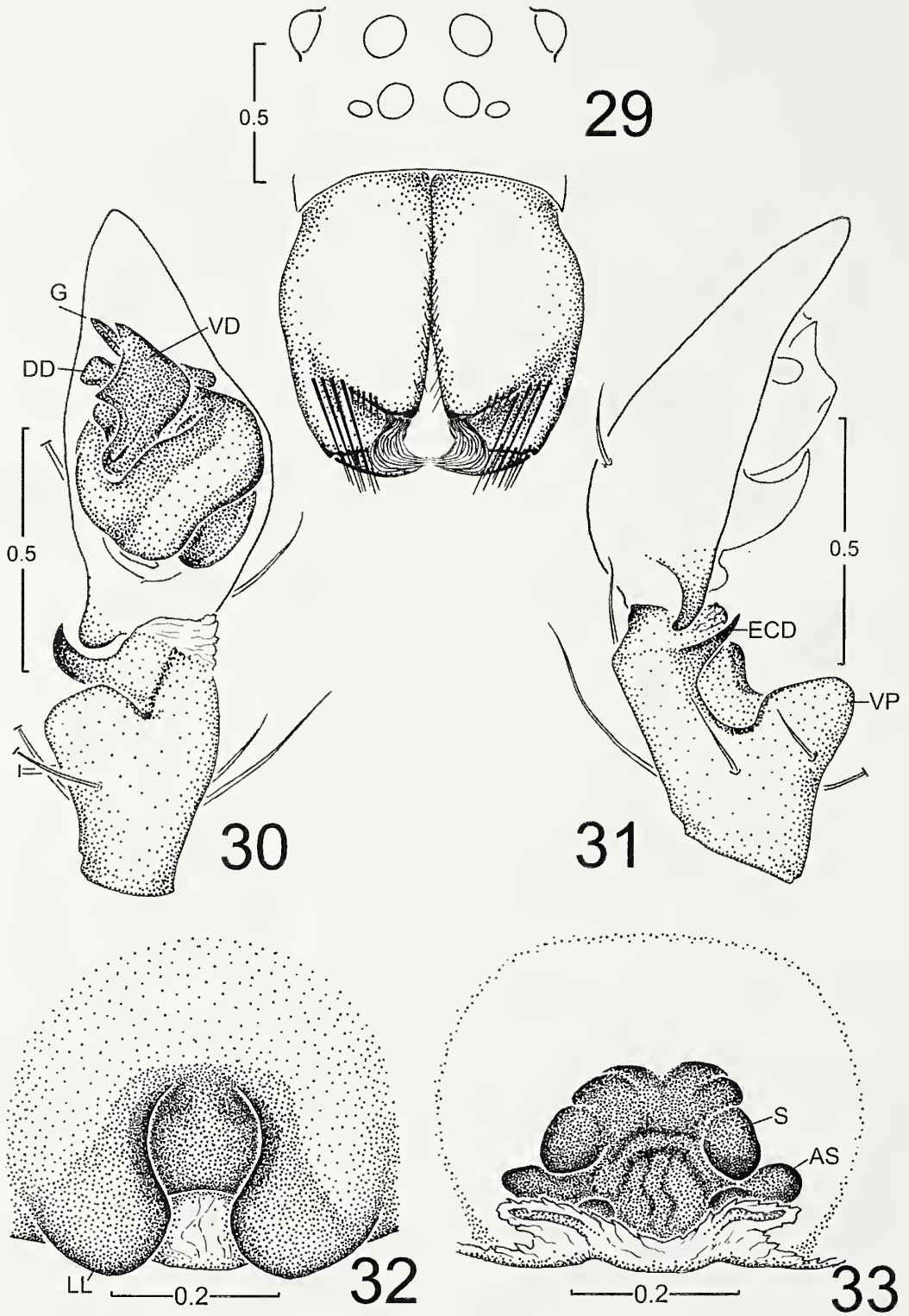
Figures 21–24.—Genitalia of *Paradossenus benicito*. 21, 22. Right pedipalpus; 21. Ventral view; 22. Retrolateral view; 23, 24. Epigynum; 23. Ventral view; 24. Dorsal view. Abbreviations: AS, accessory spermathecae; DD, dorsal division of median apophysis; D, duct; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

2.4, 21.2; II – 4.8, 5.7, 4.1, 1.8, 16.4; III – 2.8, 3.0, 2.3, 1.2, 9-3; IV – 4.7, 5.0, 4.5, 1.7, 15.9; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 5.0; anterior margin notched, median band above cardiac area tapered posteriorly with incomplete narrow light bands laterally; ventrally light and without distinct pattern. Middle field (MF) of female epigynum white, rectangular with longitudinal grooves, deep cavity anteriorly; lateral lobes (LL) triangular at posterior margin (Figs. 2, 7); spermathecae attached to a sclerotized arch, with small, stalked, accessory spermathecae conspicuous dorsally (Fig. 8).

Male (*paralectotype*): Carapace length 3.9, width 3.2. Sternum length 1.68, width 1.52; labium length 0.68, width 0.60. Clypeus height 0.28, width 1.80. Carapace (Fig. 9) with longitudinal median wide dark band divided medially with narrow light band; dark reticulations laterally in lateral light areas also covered with light hairs extending to corner of clypeus. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark reddish brown with diagonal depression distally; 4–5 curved macrosetae emerging from a tubercle distally near fang; cheliceral teeth, promarginal 3, middle largest, remainder subequal; retromarginal 4, second from proximal shortest, remainder subequal. Color of legs light, lacking distinct pattern. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 10.5, 14.2, 10.7, 4.2, 39.6; II – 6.6, 8.5, 6.5, 2.5, 24.1; III – 3.7, 4.0, 3.2, 1.4, 12.3; IV – 6.5, 6.9, 6.8, 2.4, 22.6; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3; each paired tarsal claw with 15 teeth, unpaired claw with two small teeth (Fig. 3). Abdomen length 5.2; anterior margin notched;

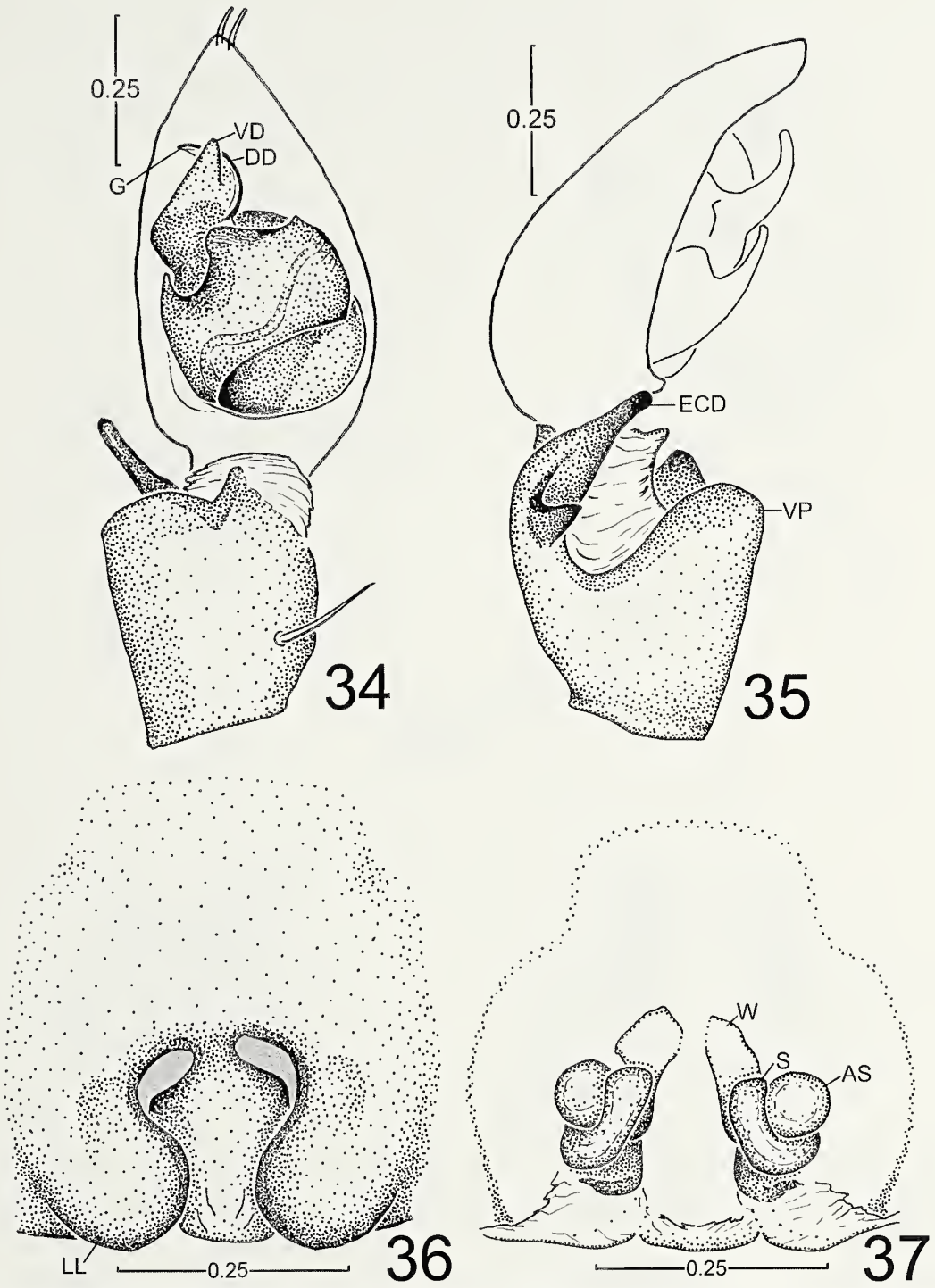


Figures 25–28.—Genitalia of *Paradossenus tocantins*. 25, 26. Right palpus; 25. Ventral view; 26. Dorsal view; 27, 28. Epigynum; 27. Ventral view; 28. Dorsal view. Abbreviations: AS, accessory spermathecae; DD, dorsal division of median apophysis; E, embolus; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; VD, ventral division of median apophysis; W, wings.



Figures 29–33.—*Paradossenus corumba*. 29. Eyes and chelicerae, frontal view; 30, 31. Right pedipalpus; 30. Ventral view; 31. Retrolateral view; 32, 33. Epigynum; 32. Ventral view; 33. Dorsal view. Abbreviations: AS, accessory spermathecae; DD, dorsal division of median apophysis; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia.

median dark band above cardiac area tapered posteriorly, surrounded laterally by narrow light bands joining posteriorly which, in turn, are bordered laterally with outer dark bands that join posteriorly (Fig. 9); venter light and unmarked. Dorsal division (DD) of the median apophysis (MA) of male palpus composed of conspicuous curved, sickle-shaped guide (G) and ventral division (VD) single, flattened, spatula-shaped rounded apically; dorsal division narrow, "hook-like" (Figs. 1, 5). Retrolateral tibial apophysis (RTA) single, tapered, directed ventrally (Fig. 6).

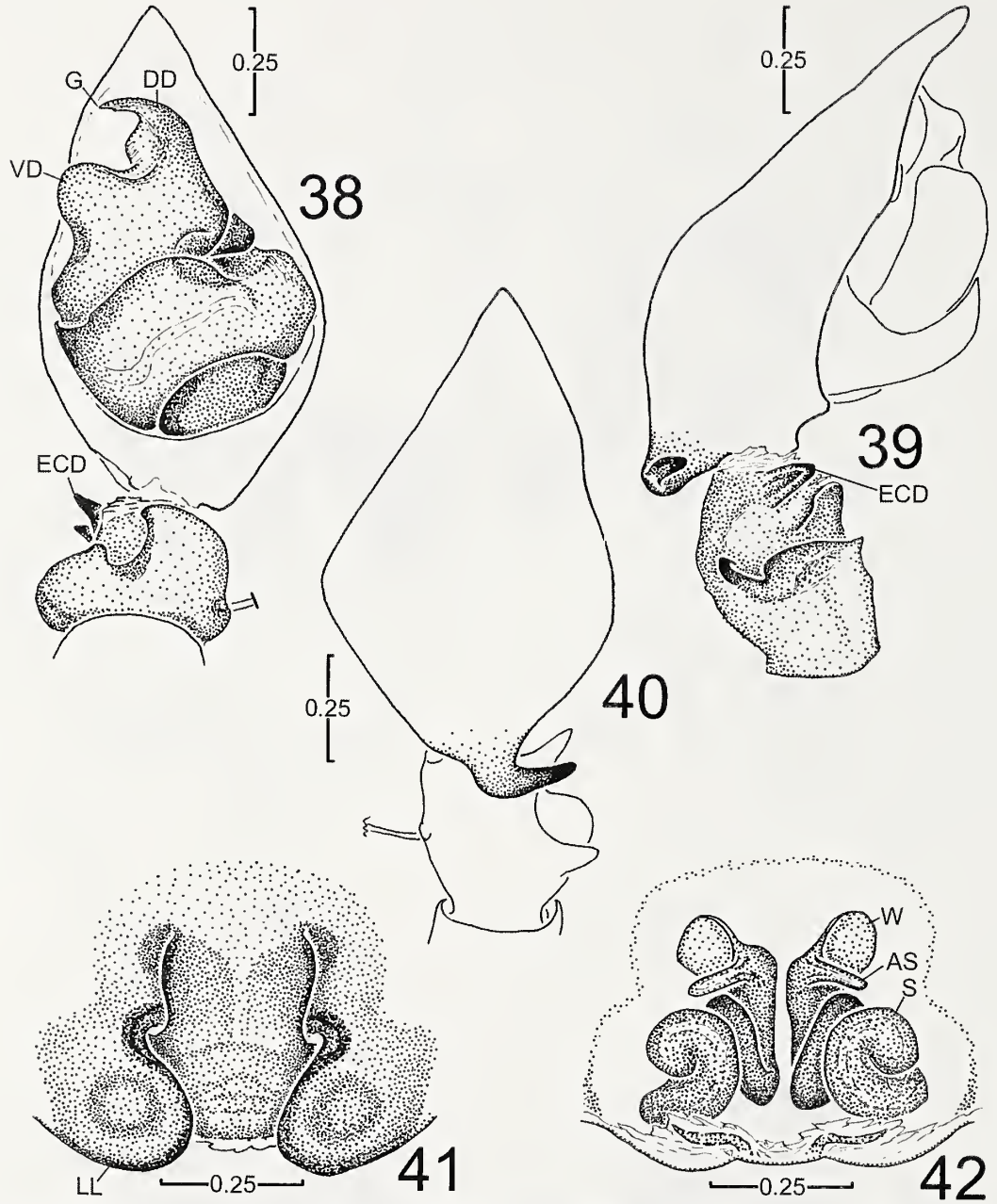


Figures 34–37.—Genitalia of *Paradossenus amazonensis*. 34, 35. Right pedipalpus; 34. Ventral view; 35. Retrolateral view; 36, 37. Epigynum; 36. Ventral view; 37. Dorsal view. Abbreviations: AS, accessory spermathecae; DD, dorsal division of median apophysis; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

Variation.—The average carapace length of eleven males is 3.82 (range 3.4–4.6) and the average carapace length of fifteen females is 3.68 (range 3.2–4.6).

Natural history.—Representatives of this species were found exclusively on the vegetation near rocky streams. Adult males and females are found from December to April (field observations in Rio Grande do Sul, southern Brazil, made by ELCS).

Distribution.—The range extends from Guyana and coastal Venezuela southward through the Amazon River basin to Uruguay and Argentina (Fig. 4). For additional notes on the distribution of this species, see Sierwald (1993) and Brescovit et al. (2000).



Figures 38–42.—Genitalia of *Paradossenus acanthocymbium*. 38–40. Right pedipalpus; 38. Ventral view; 39. Retrolateral view; 40. Dorsal view; 41, 42. Epigynum; 41. Ventral view; 42. Dorsal view. Abbreviations: AS, accessory spermathecae; DD, dorsal division of median apophysis; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; VD, ventral division of median apophysis; W, wings.

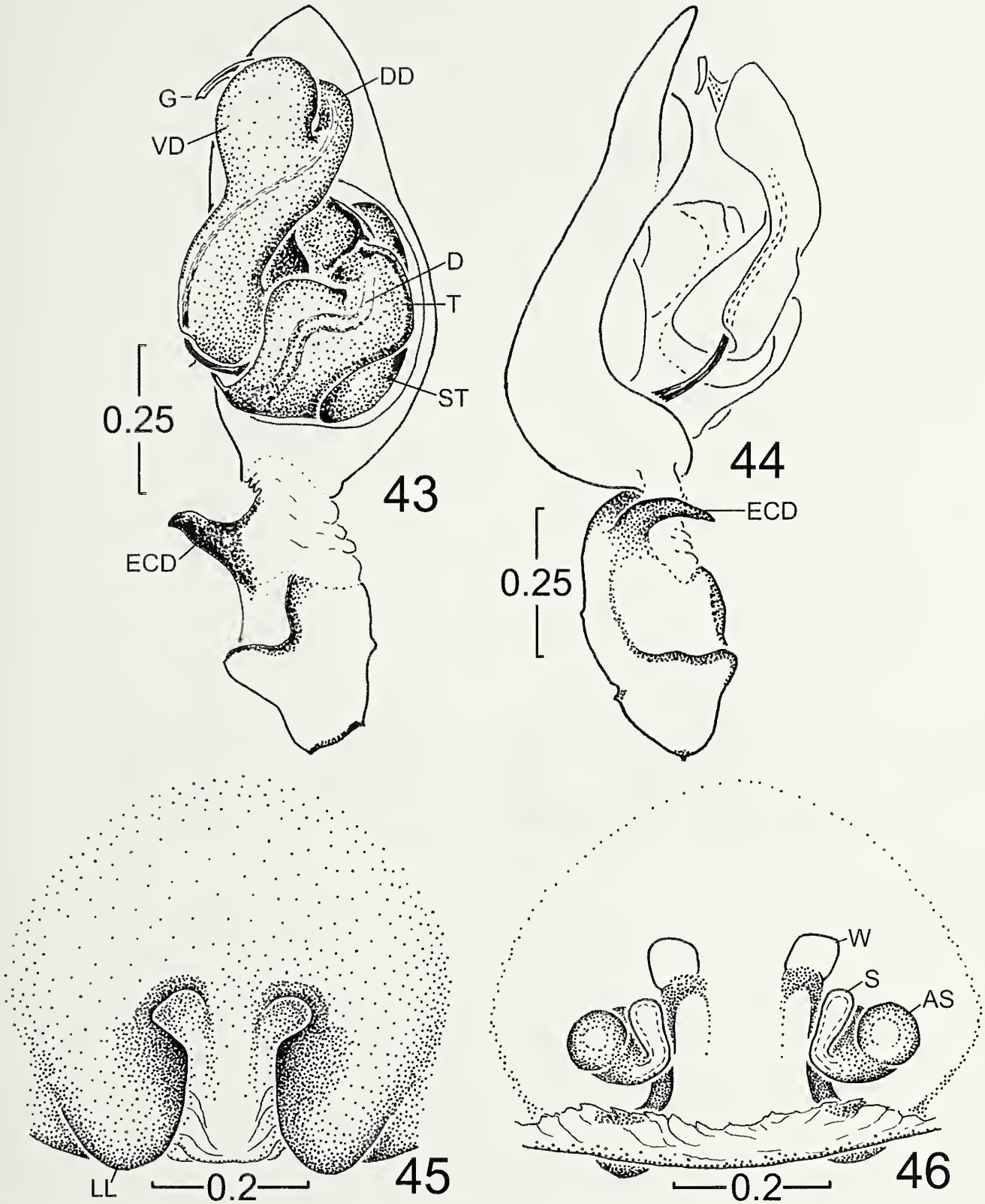
Paradossenus isthmus new species
Figs. 4, 10–14

Type material.—Holotype male, 1 paratype male, 5 paratype females: PANAMA: *Canal Zone*: Barro Colorado Island, edge of Lake Gatun, 9 09′N, 79°50′W, 4 August 1983, J.E. Carico (AMNH).

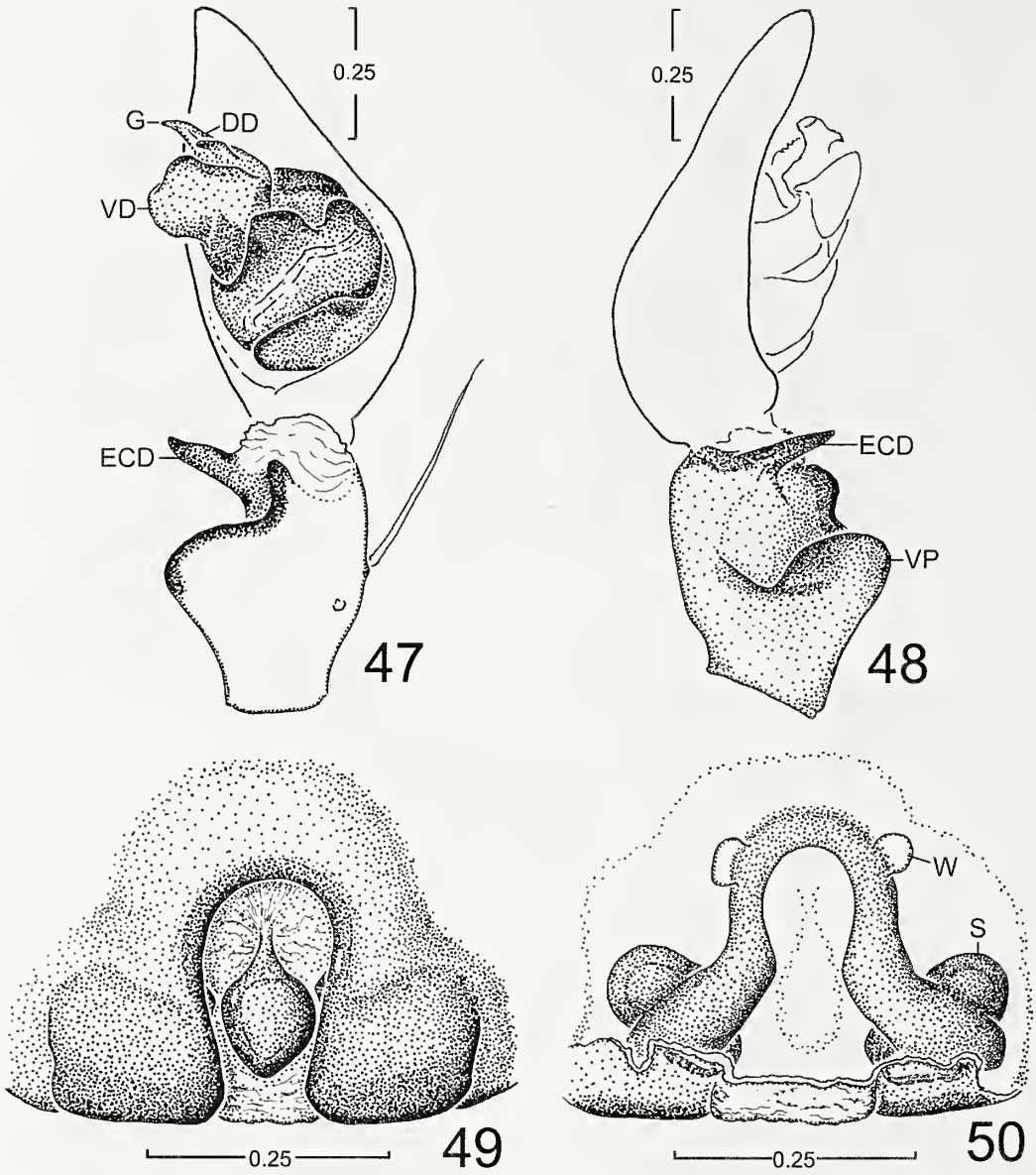
Other material examined:—PANAMA: *Canal Zone*: Barro Colorado Island, 9°09′N, 79°50′W, 57 males, 86 females, 16 June 1934–5 March 1958), A.M. Chickering (MCZ); 1 female, 30 July–1 September 1928, Chamberlin (MCZ); Colón: 2 males, 22 females, Frijoles, 9°10′N, 79°47′W, 25 January 1958, A.M. Chickering (MCZ). NICARAGUA: *Atlàntico Norte*: Masawas, Rio Waspuk, 14°38′N, 84°26′W, 10–31 October 1955, 1 female, W. B. Malkin (AMNH). COLOMBIA: *Chocó*: Quebrada Taparral, 15 km N of Palestina, Rio San Juan, 4°09′N, 77°04′W, 28–31 May 1969, 2 females, B. Malkin (AMNH).

Etymology.—The name is a noun in apposition suggested by the term describing the physiographical feature of the area of distribution ("*isthmus*" = narrow portion of land that connects two continents).

Diagnosis.—The males of *P. isthmus* resemble those of *P. benicito* (Figs. 21, 22) by the general shape of the median



Figures 43–46.—Epigyna of *Paradossenus* species. 43, 44. *P. sabana*, right palpus; 43. Ventral view; 44. Dorsal view; 45, 46. *P. minimus*, epigynum; 45. Ventral view; 46. Dorsal view. Abbreviations: AS, accessory spermathecae; D, duct; DD, dorsal division of median apophysis; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; LL, lateral lobes of epigynum; S, spermathecae; ST, subtegulum; T. tegulum; VD, ventral division of median apophysis; W, wings.



Figures 47–50.—Genitalia of *Paradossenus pozo*. 47, 48. Right pedipalpus; 47. Ventral view; 48. Retrolateral view; 49, 50. Epigynum; 49. Ventral view; 50. Dorsal view. Abbreviations: DD, dorsal division of median apophysis; ECD, ectal division of RTA; G, guide, terminal portion of median apophysis; S, spermathecae; VD, ventral division of median apophysis; VP, ventral protuberance of male palpal tibia; W, wings.

apophysis and retrolateral tibial apophysis, but can be distinguished by narrow and acute terminal portion of the ectal division of RTA (Fig. 12). The female epigynum is similar to those of *P. longipes* (Figs. 2, 7) by the general shape of the middle field (MF), but can be distinguished by the conspicuous grooves on the anterior margin of epigynum (Fig. 13).

Description.—*Male* (*holotype*): Carapace length 3.7, width 3.1. Sternum length 1.88, width 1.64; labium length 0.80, width 0.68. Clypeus height 0.20, width 1.80. Carapace with longitudinal wide median dark band divided medially with narrow light band; light setae in lateral light areas extending to lateral corners of clypeus. Anterior eye row recurved, eye measurements in Table 1. Chelicerae dark reddish brown with diagonal depression distally; 4–5 curved macrosetae emerging from a tubercle distally near fang; cheliceral teeth, promarginal 3, middle largest, remainder subequal; retromarginal 4, second from proximal shortest, remainder subequal. Color of legs light, lacking distinct pattern. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 9.5, 12.2, 10.2, 3.7, 35.6; II – 6.0, 7.9, 6.0, 2.4, 22.3; III – 3.5, 3.9, 3.2, 1.4, 12.0; IV – 6.0, 6.4, 6.6, 2.2, 21.2; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 4.6; anterior margin notched; median dark band over cardiac area tapered posteriorly, surrounded laterally by lines of light spots joining posteriorly which, in turn, are bordered laterally with outer dark bands that join posteriorly and extend to anal tubercle; venter light and unmarked. Male palpus with dorsal division (DD) of median apophysis (MA) composed of conspicuous curved, sickle-shaped guide (G) and ventral division (VD) single, flattened, tapered distally, curved and rounded apically (Fig. 11). Retrolateral tibial apophysis (RTA) single, acute and curved ventrally (Fig. 12).

Table 1.—Eye measurements for species of *Paradossenus*. Measurements are dimensions with outer limits of entities included. AE row = width of anterior eye row, PE row = width of posterior eye row, OQA = width of ocular quadrangle anteriorly or width of anterior median eyes, OQP = width of ocular quadrangle posteriorly or width of posterior median eyes, OQH = height of ocular quadrangle or height of anterior median eye at posterior median eye, PLE = diameter of posterior lateral eye, PME = diameter of posterior median eye, ALE = diameter of anterior lateral eye, AME = diameter of anterior median eye, PLE–PME = inter-distance between posterior lateral eye and posterior median eye, PME–PME = inter-distance between posterior median eyes, ALE–AME = inter-distance between anterior lateral eye and anterior median eye, AME–AME = inter-distance between anterior median eyes.

	P. longipes, ♂	*P. longipes*, ♀	*P. isthmus*, ♂	*P. isthmus*, ♀	*P. caricoi*, ♀	*P. pulcher*, ♀	*P. jamin*, ♀	*P. benicito*, ♂	*P. benicito*, ♀	*P. tocantins*, ♂	*P. tocantins*, ♀	*P. corumba*, ♂	*P. corumba*, ♀	*P. amazonensis*, ♂	*P. amazonensis*, ♀	*P. acanthocymbium*, ♂	*P. acanthocymbium*, ♀	*P. sabana*, ♂	*P. minimus*, ♀	*P. pozo*, ♂	*P. pozo*, ♀
AE row	0.86	0.76	0.80	0.87	0.59	1.19	0.78	0.62	0.64	0.50	0.50	0.55	0.60	0.58	0.73	0.55	0.50	0.50	0.66	0.48	0.50
PE row	1.88	1.76	1.78	1.92	1.44	1.94	1.46	1.50	1.56	1.00	1.10	0.96	1.09	1.35	1.62	1.05	1.01	0.86	1.58	0.90	0.93
OQA	0.52	0.44	0.48	0.50	0.36	0.62	0.43	0.40	0.40	0.28	0.28	0.33	0.35	0.36	0.45	0.31	0.30	0.25	0.40	0.30	0.30
OQP	0.74	0.70	0.70	0.77	0.60	1.04	0.79	0.66	0.66	0.50	0.50	0.48	0.51	0.60	0.75	0.50	0.50	0.43	0.68	0.45	0.43
OQH	0.69	0.62	0.64	0.67	0.48	0.63	0.53	0.56	0.54	0.42	0.45	0.45	0.45	0.48	0.56	0.46	0.42	0.36	0.53	0.41	0.40
PLE	0.32	0.28	0.26	0.28	0.26	0.28	0.26	0.24	0.24	0.20	0.22	0.20	0.18	0.25	0.30	0.20	0.20	0.14	0.25	0.18	0.19
PME	0.32	0.24	0.26	0.25	0.23	0.27	0.25	0.24	0.24	0.19	0.20	0.18	0.18	0.24	0.28	0.20	0.18	0.14	0.25	0.17	0.19
ALE	0.16	0.12	0.13	0.15	0.10	0.18	0.13	0.10	0.12	0.10	0.08	0.11	0.10	0.10	0.11	0.10	0.10	0.07	0.12	0.08	0.09
AME	0.22	0.20	0.20	0.20	0.14	0.26	0.17	0.18	0.16	0.13	0.12	0.15	0.15	0.15	0.18	0.12	0.12	0.11	0.18	0.14	0.13
PLE–PME	0.40	0.41	0.41	0.48	0.35	0.39	0.27	0.32	0.38	0.20	0.22	0.20	0.27	0.32	0.40	0.19	0.20	0.23	0.35	0.17	0.20
PME–PME	0.22	0.18	0.23	0.25	0.19	0.59	0.38	0.25	0.26	0.15	0.16	0.15	0.17	0.15	0.28	0.14	0.16	0.14	0.23	0.16	0.14
ALE–AME	0.04	0.06	0.04	0.03	0.02	0.15	0.06	0.02	0.02	0.03	0.02	0.02	0.05	0.02	0.06	0.03	0.02	0.09	0.03	0.02	0.03
AME–AME	0.08	0.10	0.10	0.13	0.10	0.11	0.10	0.06	0.08	0.05	0.06	0.05	0.07	0.08	0.10	0.09	0.08	0.07	0.10	0.05	0.05

Female (*paratype*): Carapace length 4.1, width 3.6. Sternum length 2.00, width 1.88, light and unmarked; labium length 0.84, width 0.72, dark but lighter anteriorly. Clypeus height 0.65, width 1.80. Carapace with longitudinal wide median dark band divided medially with narrow light band; light setae in lateral light areas extending to lateral corners of clypeus. Anterior eye row recurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, proximal one shortest, remainder subequal; retromarginal 5, varying sizes, plus an additional one in the right fang groove. Color of legs light with small maculae around base of some setae. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 7.8, 10.3, 7.7, 3.4, 29.2; II – 5.8, 7.4, 5.3, 2.5, 21.0; III – 3.5, 3.9, 3.0, 1.4, 13.2; IV – 5.9, 6.3, 6.0, 2.8, 21.0; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 4.9; anterior margin notched, median dark band over cardiac area tapered posteriorly, surrounded laterally by lines of light spots joining posteriorly which, in turn, are bordered laterally with outer dark bands that join posteriorly and extend to anal tubercle; venter light and unmarked. Middle field (MF) of female epigynum broad at distal portion, with longitudinal grooves, no cavity at anterior margin; lateral lobes (LL) rounded at posterior margin (Fig. 13); spermathecae small, stalked, attached to a sclerotized arch with two conspicuous wings and accessory spermathecae (Fig. 14).

Variation.—The average carapace length of sixteen males is 4.07 (range 3.7–4.6) and the average carapace length of thirteen females is 3.97 (range 3.3–4.3). The average diameter of nine egg sacs is 6.91 (range 6.3–7.8).

Natural history.—In Barro Colorado Island, Canal Zone, Panama, this species is found on vegetation at the margins of streams.

Distribution.—Range of distribution extends from southeastern Nicaragua to the northern Pacific coast of Colombia (Fig. 4).

Paradossenus caricoi Sierwald
Figs. 4, 15, 16

Paradossenus caricoi, Sierwald 1993; Platnick 2009.

Type material.—Female holotype: GUYANA: *Demerara*: Tibicuri-CuyahB [Tibikuri?], 6°07′W, 58°21′N, October 1931, Beccari & Romiti, (MZUF #537), examined.

Other material examined:—COLOMBIA: *Meta*: Pto. Lleras, Lomalinda, 3°18′N, 73°22′W, 1 female, March 1988, B.T. Carroll, V.D. Roth (CAS). GUYANA: *Essequibo*: Kuyuwini River, from K. Landing to Essequibo River, 2°16′N, 58°16′W, 1 female, 1–8 December 1937, W.G. Hassler (AMNH). VENEZUELA: *Bolivar*: Cono Corozo, 7°19′N, 61°31′W, 1 female, 11 January 1956, Wurdack & Monachino (AMNH).

Diagnosis.—The females of *P. caricoi* are similar to those of *P. benicito* (Fig. 23) by the general shape of the middle field of the epigynum, but can be distinguished by being narrowed posteriorly and have the uniquely anterior end constricted and imbedded in a circular concavity, while the lateral elevations are large and prominent (Fig. 15).

Description.—*Female* (*holotype*): Carapace length 2.4, width 2.1. Sternum length 1.28, width 1.16, medium grey, lighter in anterior one-third, covered with fine, light, prostrate setae; labium length 0.48, width 0.48, medium brown, lighter distally. Clypeus height 0.14, width 1.12. Carapace medium height, medium brown, becoming darker laterally and in eye region; narrow median lighter band in posterior one-half. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, proximal one shortest, equidistant; retromarginal 4, second to proximal one largest, remaining three equal in size, all equidistant. Color of legs light, with scattered dark maculae above. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 3.9, 5.1, 3–7, 1.8, 14.5; II – 3.4, 4.2, 3.0, 1.5, 12.1; III – 2.0, 2.2, 1.6, 0.9, 6.7; IV – 3.2, 3.3, 3.1, 1.3, 10.9; total leg length sequence: I-II–IV-III; ventral macrosetae pairs on tibiae: I-5, II-5, III-3, IV-3. Abdomen length 2.9; anterior margin notched, medium band composed of several, narrow, transverse dark lines; pair of small light spots one-third from anterior margin; larger light spots laterally in posterior half; sides covered by alternating light and dark lines; venter light and unmarked. Middle field (MF) of female epigynum wider anteriorly and narrowing posteriorly; lateral lobes (LL) rounded in posterior margin (Fig. 15); spermethecae attached to a sclerotized arch, with a dorsally conspicuous spermathecae; wings located anteriorlly (Fig. 16).

Natural history.—The label in the collection from Colombia states: "grasslands; patches of jungle, woods, marsh".

Distribution.—Based on the three known collection localities, this species is distributed in northern South American from Colombia to Guyana (Fig. 4).

Paradossenus pulcher Sierwald 1993
Figs. 4, 17, 18

Paradossenus pulcher Sierwald 1993:58; Platnick 2009.

Type material.—Female holotype: VENEZUELA: *Amazonas*: Upper RPo BarPa, ca. 100 m elevation, 1°28′N, 66°31′W, 20 July 1984, Linda S. Ford & Charles W. Myers (AMNH), examined.

Other material examined:—ECUADOR: *Sucumbios*: 1 female, Cabanas Cuybeno, 0°16′S, 75°53′W, 24–29 September 1994, V. Roth (CAS). BRAZIL: *Mato Grosso*: Usina Hidrelétrica de Guaporé, 13°59′S, 60°33′W, 1 female, 4–14 October 2002, Operação Coatá (MCTP 13572).

Diagnosis.—The females of *P. pulcher* can be distinguished from other females of *Paradossenus* by the unique shape of the middle field, which is connected anteriorlly to the anterior field of the epigynum by a narrow bridge, and by a deep cleft posteriorly at the midline forming a pair of lobes (Fig. 17).

Description.—*Female* (*holotype*): Carapace length 4.4, width 3.6. Sternum length 2.05, width 1.95; labium length 0.90, width 0.80, light brown, lighter distally. Clypeus height 0.30, width 1.85. Carapace light brown without distinct pattern. Anterior eye row recurved, eye measurements in Table 1. Chelicerae medium brown becoming gradually darker distally; cheliceral teeth, promarginal 3, middle largest, remainder subequal; retromarginal 5, irregular sizes both left and right. Color of legs light, lacking distinct pattern. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 7.9, 10.4, 6.6, 2.9, 27.8; II – 5.7, 6.8, 4.5, 2.0, 19.0; III – 3.5, 4.5, 4.2, 1.3, 13.5; IV – 6.3, 7.4, 5.7, 1.9, 21.3; total leg length sequence: I-IV-II-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 5.2; anterior margin slightly notched; median dark band over cardiac area tapered posteriorly, surrounded

laterally by short, narrow, light bands anteriorlly; pair of undulating, narrow, light lines laterally on dorsum; sides light with indistinct, scattered darker spots, venter light and unmarked. Middle field of epigynum (MF) shaped as an inverted "V" with the apex anteriorlly attached to anterior field, thus without a cavity at anterior margin, separated from lateral lobes by deep grooves; lateral lobes (LL) rounded in posterior margin (Fig. 17); spermathecae heavily sclerotized, attached to a bulbous elevation, with a small conspicuous accessory spermathecae, unstalked, heavily sclerotized (Fig. 18).

Natural history.—A note with the type collection states: "fallen into dugout canoe from overhanging vegetation".

Distribution.—Ecuador, Venezuela and Brazil (Fig. 4).

Paradossenus junin new species
Figs. 4, 19, 20

Type material.—Female holotype: PERU: *Junin*: Huacapistana, 11°14′S, 75°29′W, 27–30 July 1965, P. & B. Wygodzinsky (AMNH).

Etymology.—The name is a noun in apposition suggested by the name of the province of the type locality.

Diagnosis.—The females of *P. junin* are similar to those of *P. amazonensis* (Fig. 36) by the general shape of the middle field of the epigynum, but can be distinguished by the anterior field that presents a wide bridge and bears a pair of longitudinal creases (Fig. 19).

Description.—*Female* (*holotype*): Carapace length 3.1, width 2.7. Sternum length 1.48, width 1.56, light with indistinct dark areas laterally; labium length 0.55, width 0.55, light brown, lighter distally. Clypeus height 0.27, width 1.43. Carapace light brown with irregular and interrupted lateral light bands. Anterior eye row recurved, eye measurements in Table 1. Chelicerae medium brown, becoming gradually lighter distally; cheliceral teeth, promarginal 3, middle largest, remainder subequal; retromarginal 3, subequal, equidistant. Color of legs light with indistinct, faint pattern on dorsal side of femora and tibiae. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 3.9, 4.6, 3.1, 1.4, 13.0; II – 3.5, 4.4, 3.0, 1.3, 12.2; III – 3.1, 3.4, 2.6, 1.1, 10.2; IV – 3.1, 3.6, 2.7, 1.2, 10.6; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 5.5; cuticle separated from body with possible distortion of shape and size, no apparent distinct pattern. Middle field (MF) of epigynum broad, covered antero-laterally by lateral lobes (Fig. 19); spermathecae large, stalked, dorsal, conspicuous, and obscuring the accessory spermathecae from dorsal view (Fig. 20).

Natural history.—Nothing is known.

Distribution.—Known only from the type locality (Fig. 4).

Paradossenus benicito new species
Figs. 4, 21–24

Type material.—Male holotype and female paratype: BOLIVIA: *Beni*: Rio Benicito, Chacobo Indian Village, open river, swept from river vegetation, 11°23′S, 65°47′W, 13–26 July 1960, B. Malkin (AMNH).

Other material examined.—BRAZIL: *Rondônia*: Porto Velho, 9°12′S, 64°18′ W, 1 male, 25–29 January 1922, J.H. Williamson (MCZ).

Etymology.—The name is a noun in apposition suggested by the name of the river of the type locality.

Diagnosis.—The male of *P. benicito* resembles those of *P. amazonensis* (Fig. 34) by the general shape of the medina apophysis, but can be distinguished by the narrowed and curved tip of the ectal division of RTA and the absence of a lateral projection (Figs. 21, 22). The middle field of the female epigynum is wider anteriorly and concave in outline; the spermathecae are not stalked, but parallel in their orientation to each other (Figs. 23, 24).

Description.—*Male* (*holotype*): Carapace length 2.9, width 2.3. Sternum length 1.10, width 1.12; labium length 0.58, width 0.48, darker posteriorly. Clypeus height 0.14, width 1.06. Carapace low, rubbed, dark brown, graduating to lighter medially and with triangular light area posteriorly; scattered light setae in eye region. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae dark reddish brown with diagonal depression distally and lateral carinae; 4–5 curved macrosetae emerging from the medial and distal margin of paturon near fang; cheliceral teeth, promarginal 2, subequal; retromarginal 4, second from proximal shortest, remainder subequal. Color of legs light, lacking distinct pattern. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I & II missing; III – 2.4, 2.6, 2.2, 0.9, 8.1; IV – 4.5, 4.7, 4.2, 1.4, 14.8; ventral macrosetae pairs on tibiae: III-3, IV-3. Abdomen length 3.1; anterior margin damaged; narrow median dark band over cardiac area tapered posteriorly, laterally with reticulating dark color; venter light and unmarked. Dorsal division (DD) of median apophysis (MA) composed of inconspicuous triangular-shaped guide (G) and ventral division (VD) single, flattened, narrowed distally, directed medially and rounded apically (Fig. 21). Retrolateral tibial apophysis (RTA) single, tapered, hooked ventrally (Fig. 22).

Female (*paratype*): Carapace length 2.6, width 2.3. Sternum length 2.80, width 2.40, light and unmarked, dense hair at outer edge; labium length 0.54, width 0.46, medium brown but lighter anteriorly. Clypeus height 0.16, width 1.10. Carapace low, medium brown; scattered light setae in eye region. Anterior eye row slightly recurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, middle one shortest, remainder subequal; retromarginal 4, second from proximal smallest, remainder subequal. Color of legs light, unmarked. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 4.5, 5.3, 3.8, 1.7, 15.3; II – 3.7, 3.5, 3.0, 1.4, 11.6; III – 2.0, 2.3, 1.6, 0.8, 6.7; IV – 3.7, 3.7, 3.5, 1.3, 12.2; total leg length sequence: I-IV-II-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 4.0; anterior margin notched, narrow median dark band over cardiac area tapered posteriorly, surrounded laterally by series of indistinct light spots; venter light and unmarked. Middle field (MF) of epigynum without longitudinal grooves, no cavity at anterior margin; lateral lobes (LL) rounded in posterior margin (Fig. 23); spermathecae attached to a sclerotized arch, with small, un-stalked, accessory spermathecae conspicuous dorsally (Fig. 24).

Natural history.—Nothing is known.

Distribution.—Northern Bolivia and Brazil (state of Rondônia) (Fig. 4).

Paradossenus tocantins new species
Figs. 4, 25–28

Type material.—Male holotype: BRAZIL: *Tocantins*: Miracema, Usina Hidrelátrica Luís Eduardo Magalhães, 9°34′S,

48°23′W, 11–21 October 2001, R. Bertani & I. Toledo (IBSP 31553). Male and female paratypes, same location, date and collectors as in holotype (MCTP 22512).

Other material examined:—BRAZIL: *Tocantins*: Miracema, Usina Hidrelátrica Eduardo Magalhães, 9°34′S, 48°23′W, 1 male, 11–21 October 2001, R. Bertani & I. Toledo (IBSP 31542); 1 male, 3 females (IBSP 126736); 1 female, 1–11 October 2001, E.K. Kashimata & C.K. Fukami (IBSP 31591); 3 males, 4 females (IBSP 31523); 2 males, 6 females (IBSP 31554); *Mato Grosso do Sul*: Corumb, Passo do Lontra, Miranda e Abobral, 19°00′S, 57°39′W, 1 female, July 1998–November 1999, J. Raizer (MCTP).

Etymology.—The specific name is a noun in apposition taken from the name of the province of the type locality.

Diagnosis.—The males of *P. tocantins* are similar to those of *P. pozo* (Fig. 47) by the general shape of the median apophysis, but can be distinguished by the thickened and slightly curved dorsal division of the median apophysis, and the ventral division is small and straight on the retrolateral margin (Fig. 25). The middle field of the female epigynum, as in *P. corumba* (Fig. 32), is divided into an anterior heavily sclerotized part and a white, membranous posterior part, but differs from the latter by having the whole middle field distinctly wider than long (Fig. 27).

Description.—*Male* (*holotype*): Carapace length 2.1, width 1.7. Sternum length 1.10, width 0.95, unmarked; labium length 0.33, width 0.36, darker posteriorly. Clypeus height 0.12, width 0.92. Carapace low, medium brown reticulations except with light submarginal and median bands. Anterior eye row straight, eye measurements in Table 1. Chelicerae light brown, with diagonal depression distally, no lateral carinae; 4–5 curved macrosetae emerging from the medial and distal protuberance of paturon near fang; cheliceral teeth, promarginal 4, equidistant, second to proximal largest; retromarginal 4, equidistant, subequal. Color of leg IV light, bearing scattered small maculae except black on retrolateral sides of femur, patella-tibia. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I, II, III missing; IV – 2.8, 2.9, 2.9, 1.0, 9.6; ventral macrosetae pairs on tibiae: IV-3. Abdomen length 2.5; anterior margin indented; dorsally light brown with lighter chevrons in posterior half, laterally with dark lines, venter light and unmarked.

Palpus with dorsal division (DD) of median apophysis is composed of curved, triangular guide (G) and ventral division (VD) flattened, rounded (Fig. 25). Retrolateral tibial apophysis (RTA) single, triangular (Fig. 26).

Female (*paratype*): Carapace length 2.0, width 1.8. Sternum length 1.12, width 1.00, light and unmarked; labium length 0.30, width 0.34, light. Clypeus height 0.12, width 0.81. Carapace medium height, color light marked by light brown medially lighter submarginal bands, black marginal bands posteriorly. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, equal distance, middle largest; retromarginal 3, tending larger distally, equidistant. Color of legs light, marked by scattered dark spots concentrating in a narrow band on retrolateral surfaces. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I & II missing; III – 1.8, 1.9, 1.6, 0.7, 6.0; IV – 2.5, 2.5, 2.7, 1.0, 8.7; ventral macrosetae pairs on tibiae: I & II missing, III-3, IV- 3. Abdomen rounded and widest posteriorly, color light and darker posteriorly, light gray area over cardiac area, dark band laterally; light and unmarked ventrally. Epigynum wider than long, middle field (MF) twice as wide as long (Fig. 27); lateral lobes (LL) rounded, very widely separated in posterior margin; spermathecae and accessory spermathecae small; wings pointed anteriorlly (Fig. 28).

Natural history.—Nothing is known.

Distribution.—Brazil (states of Tocantins and Mato Grosso do Sul) (Fig. 4).

Paradossenus corumba Brescovit & Raizer 2000
Figs. 4, 29–33

Paradossenus corumba Brescovit et al. 2000:8–12, figs. I–5, II–17, 23; Platnick 2009.

Type material.—Male holotype (IBSP #6901) and paratype female (IBSP #6903), BRAZIL: *Mato Grosso do Sul*: Corumbà, 19°00′S, 57°39′W, 1994, R. Raizer, examined.

Other material examined:—PARAGUAY: *Concepcion*: Puerto Vallemi, confluence of R. Apa & R. Paraguay, 22°08′S, 57°58′W, 1 male, 8–21 May 1952, A. Bachman. See Brescovit et al. (2000) for additional distributional notes.

Diagnosis.—The male cymbium bears a unique apophysis retrolaterally at the base; the median apophysis differs from all other species by the angular outline of the ventral division and the additional projections from the dorsal division (Figs. 30, 31). The epigynum is similar to *P. tocantins* (Fig. 27) in having the middle field continuous with the anterior field, and being composed of a dark, heavily sclerotized anterior portion and a posterior clear, membranous portion but differs from the latter by the middle field being longer than wide (Fig. 32).

Description.—*Male* (*holotype*): Carapace length 2.2, width 1.8. Sternum length 0.60, width 0.55, light and unmarked; labium length 0.37, width 0.45, light. Clypeus height 0.15, width 0.98. Carapace medium height, highest posteriorly, color medium brown marked by distinct light submarginal bands and narrow dark marginal bands; medial, narrow light line extending from fovea to edge of clypeus. Anterior eye row slightly procurved, eye measurements in Table 1. Paturon with antero-proximal knobs bearing series of strong setae clusters of sinuous bristles covering each fang (Fig. 29). Cheliceral teeth, promarginal 3, equal distance, middle largest (all smaller than typical); retromarginal 3, equal size, equidistant. Color of legs light, marked by indistinct light maculae and longitudinal lines on lateral margins of femora and tibiae. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 3.9, 4.9, 3.8, 1.8, 14.4; II – 3.3, 3.9, 3.0, 1.0, 11.6; III – 2.0, 2.2, 1.6, 0.7, 6.5; IV – 3.3, 3.5, 3.3, 1.2, 11.3; ventral macrosetae pairs on tibiae: I-3, II-3, III-3, IV-3 (terminal pair present only on III & IV). Abdomen dorsal color pattern on anterior two-thirds with dark grey folium flanked by 2 pairs of white spots; posterior third with 4 transverse medium grey bands; sides with reticulated dark lines; venter with semi-circular white area anteriorly. Cymbium of male palpus with a flattened projection located proximally and retrolaterally(Figs. 30, 31); dorsal division (DD) of median apophysis (MA) composed by a small spatulate projection and a distal, straight guide (G) (Fig. 30); ventral division (VD) with 2 retrolateral acute projections (Fig. 30). Retrolateral tibial apophysis (RTA) single, tapered, pointed distally (Fig. 31).

Female (*paratype*): Carapace length 2.3, width 2.1. Sternum length 1.10, width 1.1, light and unmarked; labium length 0.30, width 0.34, light. Clypeus height 0.17, width 0.90. Carapace medium height, highest posteriorly, color medium brown marked by distinct light submarginal bands and narrow dark marginal bands; medial, narrow light line extending from fovea to edge of clypeus. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, equal distance, middle largest; retromarginal 3, size increases distally, equidistant. Color of legs light, marked by scattered light grey, incomplete bands on femora and tibiae. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 3.1, 3.8, 2.6, 1.2, 10.7; II – 2.8, 3.2, 2.4, 1.1, 9.5; III – 1.8, 2.0, 1.5, 0.8, 6.1; IV – 3.1, 2.9, 2.9, 1.1, 10.0; ventral macrosetae pairs on tibiae: I–3, II-3, III-2, IV-3 (terminal pair present only on IV). Abdomen color pattern obscured because of poor condition. Middle field of female epigynum subdivided with posterior half with irregular grooves (Fig. 32); lateral lobes (LL) rounded, widely separated in posterior margin (Fig. 32); spermathecae dark and heavily sclerotized (Fig. 33).

Natural history.—Brescovit et al. (2000) have described the web-building and prey capture behavior of this species. See this reference also for details of the anatomy.

Distribution.—Found in the Pantanal, states of Mato Grosso do Sul, Brazil and Concepcion, Paraguay (Fig. 4).

Paradossenus amazonensis new species
Figs. 4, 34–37

Type material.—Holotype male, paratype female, juvenile male; BRAZIL: *Amazonas*: Novo Airão, Arquipálago de Anavilhanas, 2°37′S, 60°56′W, July 2004, S.C. Dias (MCTP #22514).

Other material examined:—BRAZIL: *Pará*: Oriximiná, Lago Iripixi, 1°46′S, 55°50′W, 17 January 2009, 1 male, 1 female, E.L.C. Silva (MCTP # 8834); Prainha, Curuana, Restinga do Moreru, 2°38′S, 50°32′W, 1 female, 24 Oct. 2003, F. Rego (IBSP 91605). *Mato Grosso*: Nossa Senhora do Livramento, Pantanal de Poconé, Pirizal, Fazenda Retiro Novo, 16°15′S, 57°56′W, 23 March 2005, L. P. Battirola (IBSP 91481).

Etymology.—The name means "from Amazon" taken from the name of the province of the type locality.

Diagnosis.—The male of *P. amazonensis* is similar to those of *P. corumba* Brescovit & Raizer, 2000 (Figs. 30, 31) by the general shape of the RTA, but can be distinguished by the divided ectal division (ECD) of RTA and the lack of the projection, present only in *P. corumba* and *P. acanthocymbium* (Figs. 31, 39, 40). The middle field of the female epigynum presents some unique characters: it is joined by a narrow bridge to the anterior field and is overlapped significantly by the lateral elevations (Fig. 36).

Description.—*Male* (*holotype*): Carapace length 2.5, width 2.5. Sternum length 1.20, width 1.08, medium brown, lighter in the center; labium length 0.32, width 0.40, lighter distally. Clypeus height 0.10, width 0.95. Carapace low, medium brown with darker reticulations. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae medium brown with small maculae in proximal half, with diagonal depressions distally, lateral carinae on distal third; slight distal protuberance of paturon near fang; cheliceral teeth, promarginal 3, middle one largest; retromarginal 4, proximal 2 much smaller than other two. Color of legs light, scattered indistinct maculae except darker ones on leg III. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I missing; II – 3.5, 4.4, 3.2, 1.4, 12.5; III – 1.9, 2.1, 1.7, 0.8, 6.5; IV – 3.5, 3.6, 3.4, 1.3, 11.8; ventral macrosetae pairs on tibiae: II–4, III–3, IV-3. Abdomen length 2.6; anterior margin indented; dorsally medium brown with pair of light spots in posterior half, laterally medium brown, venter light and unmarked. Cymbium of male palpus longer than tibia, dorsal division (DD) of median apophysis (ma) composed of curved, subtriangular guide (G) and ventral division (VD) triangular with distal portion light and covering guide (Fig. 34). Retrolateral tibial apophysis composed of two parts, distal division one longer, directed ventrally, narrow and rounded distally, proximal division shorter, triangular and acute (Fig. 34).

Female (*paratype*): Carapace length 3.0, width 2.8. Sternum length 1.60, width 1.32, light and unmarked; labium length 0.52, width 0.48, light grey. Clypeus height 0.19, width 1.31. Carapace low, medium brown; darker in eye region. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, proximal one shortest, proximal two closest; retromarginal 4, variable but proximal two largest, equidistant. Color of legs light, with scattered faint markings above, more distinct on leg III. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 4.9, 6.4, 4.4, 2.1, 17.8; II – 4.1, 5.0, 3.5, 2.0, 14.6; III – 2.1, 2.4, 2.0, 1.0, 7.5; IV – 4.0, 4.0, 3.9, 1.6, 13.5; total leg length sequence: I-II-IV-III; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 3.8; anterior margin notched, narrow median dark band over cardiac area tapered posteriorly, surrounded laterally by indistinct, alternating light and dark bands; venter light and unmarked. Middle field of epigynum wider anteriorly and partially overlapped posteriorly by lateral lobes (LL) (Fig. 36); lateral lobes rounded in posterior margin (Fig. 36); spermathecae attached to a sclerotized arch, with accessory spermathecae conspicuous dorsally; wings located anteriorly (Fig. 37).

Natural history.—One female were observed in Pará (northern Brazil) foraging in the lower vegetation on inundated areas near the large rivers (field observation made by ELCS).

Distribution.—Brazil (Amazonas, Pará and Mato Grosso) (Fig. 4).

Paradossenus acanthocymbium new species
Figs. 4, 38–42

Type material.—Male holotype: BRAZIL: *Mato Grosso do Sul*: Corumb, Passo do Lontra, Miranda e Abobral, 19°00′S, 57°39′W, July 1998–November 1999, J. Raizer (IBSP 91560). Paratypes: six males and four females, same data as holotype (IBSP 126737; MCTP 22513).

Other material examined:—BRAZIL: *Rio Grande do Sul*: Uruguaiana, 29°42′S, 57°07′W, 2 males, 2 females, 22 January 2009, R. Alves (MCTP).

Etymology.—The specific name refers to the prominent acute projection (*acantho* = spine) on the dorsal surface of the male cymbium.

Diagnosis.—The male of *P. acanthocymbium* resembles those of *P. corumba* (Fig. 30) by the general shape of the median apophysis of the male palpus (Fig. 38), but can be

distinguished by the curved acute projection on the dorsal side at the base of the cymbium (Figs. 39, 40). The retrolateral side of the palpal tibia has an additional apophysis to the usual RTA (Fig. 39), a character shared only with *P. amazonensis* (Fig. 35), but differs from the latter in shape and position (Fig. 39). Middle field of female epigynum broad, extending three-fourths length of epigynal field; lateral lobes (LL) rounded, widely separated in posterior margin (Fig. 41).

Description.—*Male* (*holotype*): Carapace length 2.3, width 2.1. Sternum length 1.20, width 1.10, light, unmarked; labium length 0.30, width 0.34, light, lighter distally. Clypeus height 0.16, width 0.92. Carapace medium height, higher in cephalic region, color marked by reddish-brown reticulations darkening laterally to black marginal bands, with lighter areas medially, posteriorly and with isolated light areas submarginally. Anterior eye row slightly procurved, eye measurements in Table 1. Chelicerae brownish laterally, gradually becoming darker medially and with narrow light bands medially, with shallow diagonal depressions distally, lateral carinae absent; cheliceral teeth, promarginal 0; retromarginal 3, equidistant, equal size. Color of legs light, marked by dark maculae concentrating in pro- and retrolateral surfaces. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I missing; II – 2.7, 3.5, 2.7, 1.1, 10.0; III – 2.1, 2.3, 2.0, 0.8, 7.2; IV – 2.6, 2.9, 2.8, 1.1, 9.4; ventral macrosetae pairs on tibiae: I – missing, II–4, III–3, IV-3. Abdomen widest posteriorly, color pattern with indistinct pattern, lighter medially, becoming darker laterally; medium gray in cardiac area. Male palpus with a distinct, proximal, dorsal curved, projection on the cymbium longer than tibia (Figs. 39, 40); dorsal division (DD) of median apophysis composed of curved, flattened guide (G) and ventral division (VD) rounded in outline and not greatly distinct from dorsal division (Fig. 38). Retrolateral tibial apophysis composed of a short, apically flattened distal division and a widely separated small, pointed, medial division (Fig. 39).

Female (*paratype*): Carapace length 2.1, width 1.9. Sternum length 1.10, width 1.05, light and unmarked; labium length 0.28, width 0.38, light. Clypeus height 0.16, width 0.88. Carapace medium height, higher in cephalic region, color marked by reddish-brown reticulations darkening laterally to black marginal bands, with lighter areas medially, posteriorly and with irregular light submarginal bands. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, equal distance, middle largest; retromarginal 3, tending larger distally, equidistant. Color of legs light, marked by dark maculae concentrating in pro- and retrolateral surfaces. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 2.7, 3.4, 2.5, 1.0, 9.6; II – 2.6, 3.1, 2.1, 0.9, 8.7; III – 2.0, 2.2, 1.9, 0.8, 6.9; IV – 2.6, remainder of segments missing; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV- missing. Abdomen widest posteriorly, color dark grey with pair of large white spots anteriorly; three medial, transverse, bands posteriorly. Middle field of female epigynum broad, extending three-fourths length of epigynal field; lateral lobes (LL) rounded, widely separated in posterior margin (Fig. 41); spermathecae broadly looped, with head of spermathecae located transversely in dorsal half (Fig. 42).

Natural history.—Nothing is known.

Distribution.—Only known from the type locality (Fig. 4).

Paradossenus sabana new species
Figs. 4, 43, 44

Type material.—Male holotype: VENEZUELA: *Bolivar*: Parupa, Gran Sabana, 1500 m, 5°30′N, 61°30′W, 27 June–10 July 1987, S. & J. Peck (AMNH).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Diagnosis.—The male of *P. sabana* can be distinguished by all the other known males of *Paradossenus* by the median apophysis that is uniquely longer than the palpal tibia, the embolus is conspicuous and the ventral division broadly rounded (Fig. 43).

Description.—*Male* (*holotype*): Carapace length 2.3, width 1.8. Sternum length 1.04, width 0.96, light, unmarked; labium length 0.33, width 0.36, light. Clypeus height 0.13, width 0.88. Carapace medium height, distinct, wide, medium brown, median band, light submarginal bands with dark narrow margins. Anterior eye row slightly procurved, eye measurements in Table 1. Chelicerae light brown, with diagonal depressions distally, lateral carinae absent; cheliceral teeth, promarginal 3, middle one largest; retromarginal 3 equal size. Color of legs light, dark lines on prolateral and retrolateral sides of femora of legs I, II, IV; scattered small maculae on dorsal surface of femora, tibia and all of leg IV. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 3.5, 4.9, 3.4, 1.3, 13.7; II – 3.1, 4.0, 2.9, 1.2, 11.2; III – 1.7, 2.0, 1.6, 0.7, 6.0; IV – 3.5, 3.6, 3.4, 1.2, 11.6; ventral macrosetae pairs on tibiae (terminal pair missing on all tibiae): I–5, II–5, III–2, IV-2. Abdomen damaged. Palpus with median apophysis longer than tibia, dorsal division (DD) composed of curved, triangular guide (G) and ventral division (VD) rounded in outline (Fig. 43). Retrolateral tibial apophysis composed of single, tapered, acute and directed ventrally (Fig. 44).

Distribution.—Known only from the type locality (Fig. 4).

Paradossenus mininus (Mello-Leitão 1940)
Figs. 4, 45, 46

Xingusiella minima Mello- Leitão 1940:23; Roewer 1954:144.
Paradossenus mininus, Sierwald 1993:57; Brescovit et al. 2000:13,14; Platnick 2009.

Type material.—Female holotype of *Xingusiella minima*: BRAZIL: *Pará*: Rio Xingu, 3°24′S, 51°50′W, H. Leonardos (MNRJ 585), examined.

Other material examined:—BRAZIL: *Mato Grosso*: 2 female, Posto Indígena Capitão Vasconcelos, Parque Indígena do Xingu, Rio Tuatuari, 11°59′S, 54°00′W, 1 female, 29 July–4 August 1957, B. Malkin & S. Bunell, Jr. (AMNH).

Diagnosis.—The female epigynum middle field resembles those of *P. longipes* (Figs. 2, 7) by its transparent, grooved surface, but differs from the latter by the comparatively very small internal structures (Fig. 46).

Description.—*Female* (*holotype*): Carapace length 2.6, width 2.4. Sternum length 1.48, width 1.12, light anteriorly becoming darker laterally and posteriorly; labium length 0.50, width 0.45, medium brown, lighter distally. Clypeus height 0.16, width 1.10. Carapace medium brown becoming darker laterally and anteriorly, light area from cephalic groove to posterior edge. Anterior eye row straight, eye measurements in Table 1. Chelicerae medium brown becoming gradually lighter distally; cheliceral teeth, promarginal 3, subequal; retro-

marginal 4, distal two equal size and largest, proximal next largest, remaining one very small. Color of legs light with gray annuli. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – missing; II – 3.6, 4.4, 3.0, 1.3, 12.3; III – 2.0, 2.1, 1.7, 0.9, 6.7; IV – 3.7, 3.7, 3.2, 1.3, 11.9; ventral macrosetae pairs on tibiae: II-4, III-2 (apical pair missing), IV-3. Abdomen length 3.6; dorsum with light gray over cardiac area and a pair of parallel, irregular, wavy bands posteriorly; sides with irregular parallel, narrow lines; venter light, unmarked.

Middle field of epigynum light colored, widened anteriorly, covered posteriorly by darker lateral lobes (Fig. 45); spermathecae small, narrow, stalked, dorsal; accessory spermathecae spherical, heavily sclerotized (Fig. 46).

Distribution.—Along tributaries of Rio Xingu in the states of Para and Mato Grosso, Brazil (Fig. 4).

Paradossenus pozo new species
Figs. 4, 47–50

Type material.—Male holotype: COLOMBIA: *Magdalena*: Pozo Colorado, 11 km W Santa Maria, 11°10′N, 74°14′W, 25–30 April 1986, B. Malkin (AMNH). Paratypes: 9 males and 5 females, same location, date and collector as holotype (AMNH).

Other material examined:—COLOMBIA: *Magdalena*: 82 km W of Santa Marta, Island Salamanca Parque National, 11°03′N, 74°48′W, 1 female, 22 February 1968, B. Malkin (AMNH). VENEZUELA: *Guarico*: Hato Masaquari, 60 m, 8°34′N, 67°35′W, 3 males, 3–29 May 1985, J. Carpenter & A. Menke (MCZ).

Etymology.—The name is a noun in apposition suggested by the name of the type locality.

Diagnosis.—The males of *P. pozo* resemble those of *P. tocantins* (Fig. 25) by the swollen shape of the ventral division of the median apophysis, but can be distinguished by the presence of a unique spur at the base of the dorsal division and guide (Fig. 47). The female epigynum also has a unique middle field, whieh is recessed within an archway and has a small, prominent elevation; internally, the spermathecae and small wings are mounted on a thick and very prominent sclerotized arch (Figs. 49, 50).

Description.—*Male* (*holotype*): Carapace length 1.7, width 1.9. Sternum length 1.00, width 1.15, light, unmarked; labium length 0.26, width 0.33, medium brown, lighter distally. Clypeus height 0.14, width 0.92. Carapace medium height but higher posteriorly, indistinct, wide, light brown, median band with lighter median triangle posterior to eyes; indistinct light submarginal bands with dark narrow margins. Anterior eye row slightly procurved, eye measurements in Table 1. Chelicerae medium brown, with diagonal depressions distally, lateral carinae absent; cheliceral teeth, promarginal 3, equal size, equidistant; retromarginal 3, equidistant, middle largest. Color of legs light, unmarked. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I missing; I – 2.8, 3.7, 2.8, 1.3, 10.6; II – 2.5, 3.1, 2.3, 1.0, 8.9; III – 1.6, 1.8, 1.4, 0.7, 5.5; IV – 2.5, 2.6, 2.6, 1.0, 8.7; ventral macrosetae pairs on tibiae: I–3, II–3, III–2, IV-3. Abdomen damaged.

Dorsal division (DD) of median apophysis composed of curved, triangular guide (G), and ventral division (VD) rounded in outline (Fig. 47). Retrolateral tibial apophysis composed of single, tapered, pointed part (Fig. 48).

Female (*paratype*): Carapace length 1.9, width 1.6. Sternum length 0.90, width 1.00, light and unmarked; labium length 0.28, width 0.34, light grey. Clypeus height 0.15, width 0.85. Carapace medium height but higher posteriorly, indistinct, wide, light brown, median band with lighter median triangle posterior to eyes; indistinct light submarginal bands with dark narrow margins. Anterior eye row slightly procurved, eye measurements in Table 1. Cheliceral teeth, promarginal 3, equal distance, middle largest; retromarginal 3, equal size, equidistant. Color of legs light, unmarked. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 2.2, 2.8, 2.1, 1.1, 8.2; II – 2.1, 2.6, 2.1, 1.0, 7.8; III – 1.5, 1.7, 1.3, 0.7, 5.2; IV – missing; ventral macrosetae pairs on tibiae: I-3, II-3, III-2, IV- missing. Abdomen damaged. Middle field (MF) of female epigynum, wider anteriorly and partially overlapped posteriorly by lateral lobes (LL) (Fig. 49); lateral lobes rounded in posterior margin (Fig. 49); spermathecae attached to a sclerotized arch; wings located anteriorly (Fig. 50).

Variation.—Average carapace length for ten males = 2.0 (range 1.7–2.5); average carapace length for five females = 1.8 (range 1.7–1.9.

Natural history.—The female from Island Salamanca was taken from vegetation at the shore of a strongly brackish pond.

Distribution.—Known only from the northern coast of Colombia and central Venezuela (Fig. 4).

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APPENDIX I

Note on the key to the Trechaleinae.—This review of the taxonomy of *Paradossenus* represents the final one in a series of generic revisions in the subfamily; therefore we can now offer this key to the Trechaleinae as an aid for those engaged in work in the taxonomy and biology of the family Trechaleidae. Because of the lack of females for three trechaleine genera, it must be assumed that the key will be substantially improved in the future following the discovery of these females. We recommend that the key be used in conjunction with the published resources upon which it is based.

PROVISIONAL DIAGNOSTIC KEY TO GENERA OF THE SUBFAMILY TRECHALEINAE

1a Width of anterior eye row distinctly larger than length of AME of posterior ocular quadrangle, anterior lateral eyes often placed under posterior lateral eyes (Fig. A1) ..... Subfamily Rhoicininae

1b Width of anterior eye row equal to or only slightly greater than length of AME of posterior ocular quadrangle (Fig. A2) ..... Subfamily Trechaleinae 2

2a Tarsi flexible and usually bent 3

2b Tarsi not flexible and straight 7

3a Metatarsi flexible and usually bent 4

3b Metatarsi not flexible and always straight 5

4a 6 or more ventral macrosetae pairs on tibia I ..... *Syntrechalea*

4b 4 or less ventral macrosetae pairs on tibia I ..... *Hesydrus*

5a Ventral division of median apophysis angular in outline (Fig. A3), middle field of epigynum not divided posteriorly and usually wider anteriorly (Fig. A4) ..... *Trechalea*

5b Ventral division of median apophysis rounded in outline (Fig. A5), middle field divided into two lateral parts (Fig. A6), or wider posteriorly if not divided 6

6a Ventral division of median apophysis small (Fig. A5), middle field of epigynum divided into two lateral parts (Fig. A6) ..... *Trechaleoides*

6b Ventral division of median apophysis large (Fig. A7), middle field of epigynum not divided into two lateral parts, wider at posterior margin (Fig. A8) ..... *Paratrechalea*

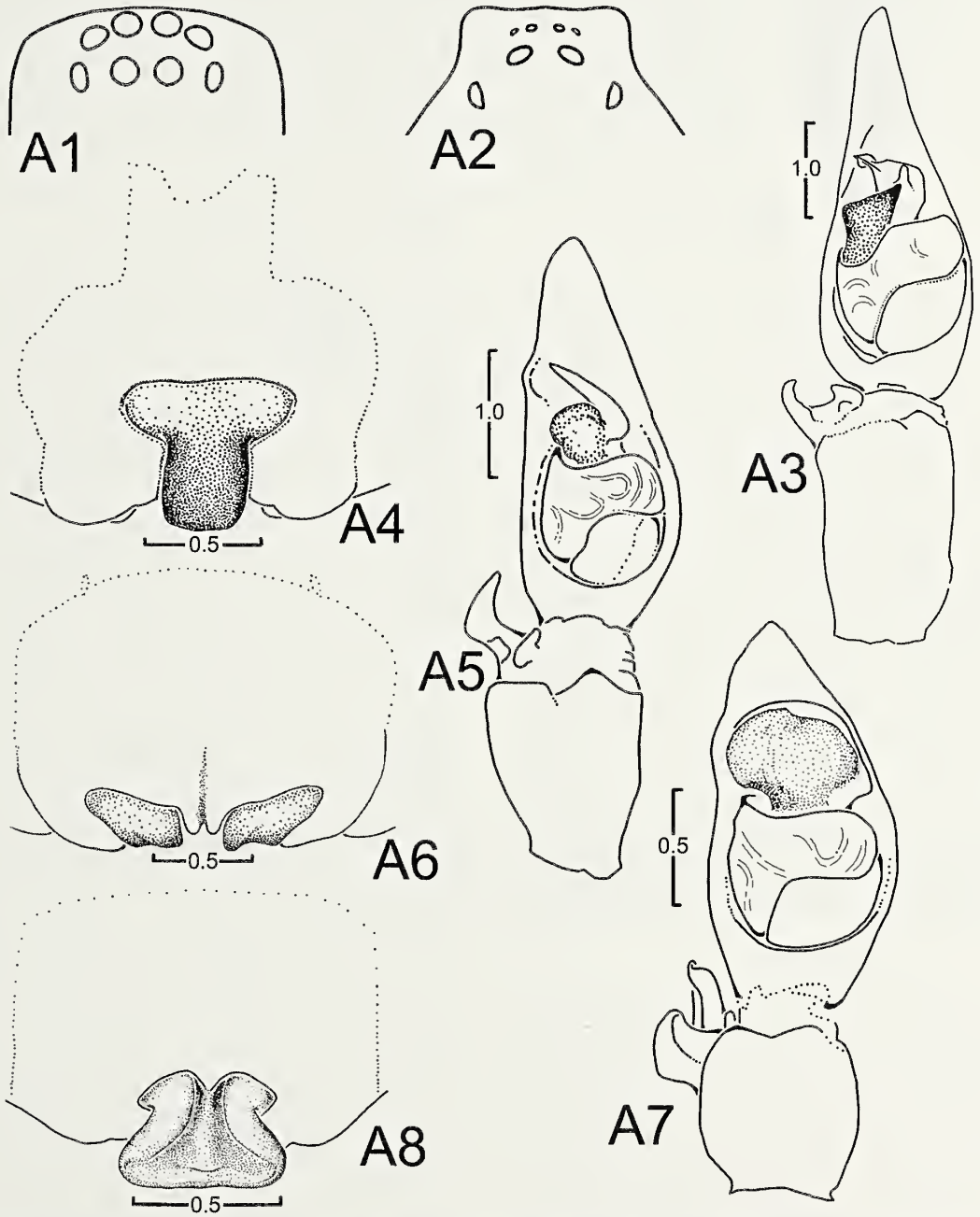
7a Both sexes with a broad, bold, dark band extending length of body and limited laterally by narrow white lines (Fig. A9) *Dossenus*

7b Median band absent, or, if present, with uneven edge and not bold 8

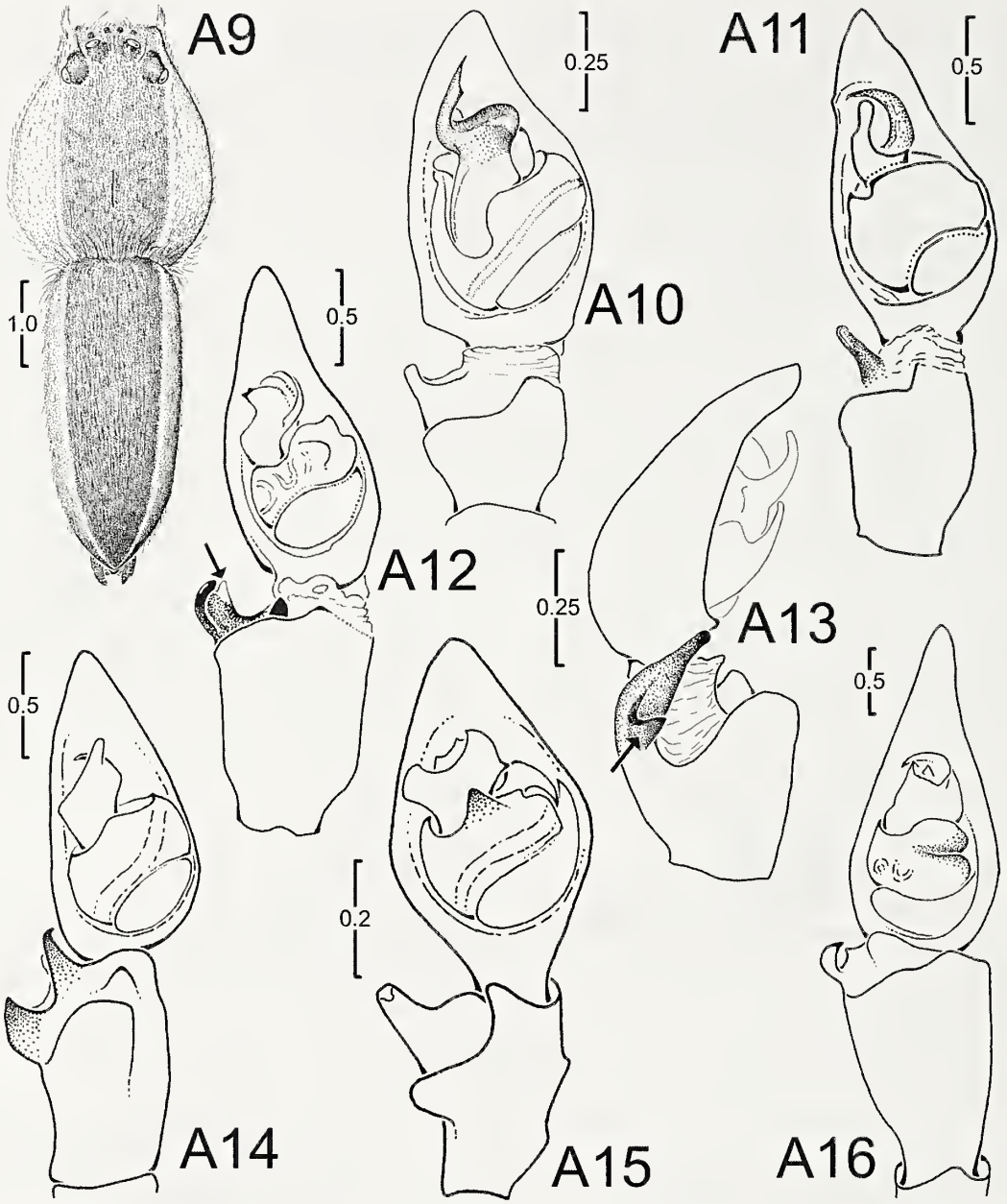
8a Legs with several distinct, parallel, longitudinal dark lines; guide tip of male palpus directed distally (Fig. A10) ..... *Dyrines*

8b Leg pattern not as above, guide tip of male palpus directed retrolaterally (Fig. A11) 9

9a RTA composed of two divisions located at or near the distal rim of tibia (Fig. A12) 10
9b RTA composed of one division (Fig. A11), or if two, the ectal division located proximally along rim distant from ental division (Fig. A13) 11
10a RTA with ental division distinctly smaller than ectal division, ental division with small, translucent protuberance along distal edge (Fig. A12); epigynum middle field hood-like and concave beneath ..... *Enna*
10b RTA with ental division as large as or larger than ectal division, ectal division without translucent protuberance (Fig. A14); female unknown ..... *Magnichela*
11a Tegulum with projection directed distally (Fig. A15); female unknown ..... *Amapalea*
11b Tegulum without projection (Fig. A11) 12
12a Tegulum with transverse groove; female unknown (Fig. A16) ..... *Caricelea*
12b Tegulum without transverse groove (Fig. A11) ..... *Paradossenus*



Figures A1–A8.—Key characters of Trechaleinae and Rhoicininae. A1. Eye pattern of *Rhoicinus*; A2. Eye pattern of *Trechalea*, dorsal view; A3. *Trechalea longipes*, right palpus, ventral view; A4. *Trechalea longipes*, epigynum, ventral view; A5. *Trechaleoides keyserlingi*, right palpus, ventral view; A6. *Trechaleoides keyserlingi*, epigynum, ventral view; A7. *Paratrechalea ornata*, right palpus, ventral view; A8. *Paratrechalea ornata*, epigynum, ventral view.



Figures A9–A16.—Key characters of the subfamily Trechaleinae. A9. *Dossenus marginatus*, habitus, dorsal view; A10. *Dyrines striatipes*, right palpus, ventral view; A11. *Paradossenus longipes*, right palpus, ventral view; A12. *Enna velox*, right palpus, ventral view; A13. *Paradossenus amazonensis*, right palpus, retrolateral view; A14. *Magnichela santaremensis*, left palpus (reversed), ventral view; A15. *Amapalea brasiliana*, left palpus (reversed), ventral view; A16. *Caricelea wayrapata*, left palpus (reversed), ventral view.

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Molecular detection and the phylogenetics of *Wolbachia* in Chinese spiders (Araneae)

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Abstract. Maternally inherited endosymbiotic bacteria *Wolbachia pipientis* have been shown to have wide-ranging effects on the reproduction of their hosts. This study presents the first survey and characterization of *Wolbachia pipientis* that have infected spiders collected from Wuhan, Hubei Province, China. First, we used universal primers of the *wsp* gene (*Wolbachia* Surface Protein, WSP) to examine the infection of *Wolbachia* in spiders. We found that, out of 31 spider species, 7 species were infected with *Wolbachia*. Then we used the specific primers of the A and B *Wolbachia* supergroups for the *wsp* gene to determine if there are super-infections in these infected spiders. Specimens of *Nephila clavata* were infected with strains of both A and B *Wolbachia*, while the others were infected with either strain A or B. Lastly, we aligned the sequences obtained with published ones to establish the phylogenetic relationships among *Wolbachia* found in spiders. The *Wolbachia* in *Larinia argiopiformis* Bösenberg & Strand 1906, *Eriovixia cavaleriei* (Schenkel 1963), *Araneus ventricosus* (L. Koch 1978), and *Pholcus crypticolens* Bösenberg & Strand 1906 belong to the A supergroup and the other three species, *Nephila clavata* (L. Koch 1878), *Oxyopes sertatus* L. Koch 1877 and *Coleosoma octonaculatum* Bösenberg & Strand 1906 belong to the B supergroup.

Keywords: Phylogenetic analysis, *wsp* gene, super-infection

Wolbachia is a common and widespread group of symbiotic bacteria found in the reproductive tissues of arthropods. These bacteria are transmitted through the cytoplasm of eggs and have evolved various mechanisms for manipulating the reproduction of their hosts, including induction of cytoplasmic incompatibility (CI), parthenogenesis, feminization, male-killing, and modification of fecundity or fertility (Werren et al. 2008). *Wolbachia* is thought to be a major factor in the evolution of sex determination, eusociality, and speciation.

At present eight different supergroups (A–H) of *Wolbachia pipientis* have been recognized based on phylogenetic analysis with the *wsp*, *ftsZ*, and 16S rRNA loci (Lo et al. 2002; Rowley et al. 2004; Bordenstein & Rosengaus 2005). The *wsp* gene encodes a surface protein and is the most rapidly evolving of the three. It is therefore more often phylogenetically informative and the most commonly used *wsp* gene for strain differentiation (Zhou et al. 1998; Rowley et al. 2004). *Wolbachia* strains of supergroups A and B are present in arthropods, whereas C and D are so far found only in filarial nematodes. Strain E is known only from springtails (Lo et al. 2002; Czarnetzki & Tebbe 2004); F exists both in arthropods and nematodes, including termites (*Microcerotermes* sp. and *Kalotermes flavicollis*), filarial nematodes (*Mansonella* spp.), a weevil (*Rhinocyllus conicus*) and two cimicids (Lo et al. 2002; Rasgon & Scott 2004; Casiraghi et al. 2005). Subsequently a lineage of *Wolbachia* outside of A–F supergroups was discovered in Australian spiders (Rowley et al. 2004) and was placed in new supergroup G, while another lineage in termites of the genus *Zootermopsis* has been placed in supergroup H (Bordenstein & Rosengaus 2005).

In some species of arthropods, individuals are infected with more than one strain of *Wolbachia*, which is called *Wolbachia* super-infection (Werren 1997; Zhou et al. 1998; Narita et al. 2007). Since most infected species belong to supergroups A and B, Zhou et al. (1998) designed specific primers of the *wsp* gene for these two groups to quickly identify super-infections. Double infections with supergroup A- and B-*Wolbachia* have been found in over 15 species (Zhou et al. 1998). By using a beta-binomial model, Hilgenboecker et al. (2008) estimated that 66% of insects are infected with *Wolbachia*. Most *Wolbachia* research has focused on insect hosts and non-spider arachnids such as ticks and mites (Vala et al. 2004; Ros & Breeuwer 2009). Although spiders (Araneae) are one of the largest taxonomic groups of arthropods, there are only a few reports of *Wolbachia* infections in spiders (Oh et al. 2000; Cordaux et al. 2001; Rowley et al. 2004; Goodacre & Martin 2006; Baldo et al. 2008). Recent work has also identified the presence of three other reproductive parasites in spiders, *Spiroplasma*, *Rickettsia* (Goodacre & Martin 2006) and *Cardinium* (Duron et al. 2008; Martin & Goodacre 2009). These symbionts have effects on the reproduction of their arthropod hosts very similar to those of *Wolbachia*. Furthermore, Goodacre et al. (2009) reported that *Rickettsia* could modify the long-distance dispersal capacity in a spider host, *Erigone atra* Blackwall 1833 .

Here we tested a range of Chinese spiders for the presence of *Wolbachia* based on the *wsp* gene to determine 1) the occurrence of multiple infections and 2) the phylogenetic relationships of the *Wolbachia* present in Chinese spiders.

METHODS

Spider collection and DNA extraction.—A total of 930 spiders of 31 species and 11 families was collected from the suburbs in Wuhan, Hubei Province, China from March 2006 to April 2008 (see Table 1). Thirty individuals were sampled from each of these 31 spider species for DNA extraction.

Depending on the size of the spider, we harvested 1–4 legs from each individual for DNA extraction. We used leg tissue samples to avoid potentially contaminating gut contents, but also extracted DNA from tissue taken from the abdomens of a subset of specimens. Legs were rinsed with 70% ethanol and then homogenized in Holmes-Bonner buffer. We extracted DNA from the homogenate following standard procedures (Sambrook et al. 1989). DNA extractions of *Wolbachia*-

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Table 1.—Results of PCR-screening for *Wolbachia* using specific *wsp* primers in spiders sampled from Wuhan, Hubei Province, China. All spiders were adults, and 30 individuals for each species of spiders were tested for the rate of *Wolbachia* infection. N.A. indicates no infection found.

Family	Spider species	Rate of *Wolbachia* infection	*Wolbachia* strain
Araneidae	*Larinioides cornuta* Grasshoff 1983	-	N.A.
	Larinia argiopiformis Bösenberg & Strand 1906	40%	*w*Lararg
	Argiope amoena (L. Koch 1878)	-	N.A.
	Eriovixia cavaleriei (Schenkel 1963)	26.7%	*w*Ericav
	Araneus ventricosus (L. Koch 1878)	20%	*w*Araven
	Araneus nitificus (Simon 1886)	-	N.A.
Clubionidae	*Clubiona japonicola* Bösenberg & Strand 1906	-	N.A.
Nephilidae	*Nephila clavata* (L. Koch 1878)	63.3%	*w*Nepcla
Lycosidae	*Pardosa laura* Karsch 1879	-	N.A.
	Pardosa astrigera L. Koch 1878	-	N.A.
	Pardosa pseudoannulata Bösenberg & Strand 1906	-	N.A.
	Pirata piraticus (Clerck 1757)	-	N.A.
	Pirata piratoides (Bosenberg & Strand 1906)	-	N.A.
	Pirata subpiraticus (Bosenberg & Strand 1906)	-	N.A.
	Pirata tenuisetaceus Liu 1987	-	N.A.
Linyphiidae	*Hylyphantes graminicola* (Sundevall 1830)	-	N.A.
	Neriene radiata (Walckenaer 1842)	-	N.A.
	Erigone prominens Bösenberg & Strand 1906	-	N.A.
	Neriene japonica (Oi 1960)	-	N.A.
	Neriene limbatinella (Bösenberg & Strand 1906)	-	N.A.
	Ummeliata insecticeps (Bösenberg & Strand 1906)	-	N.A.
Oxyopidae	*Oxyopes sertatus* L. Koch 1877	73.3%	*w*Oxyser
Pholcidae	*Pholcus crypticolens* Bösenberg & Strand 1906	56.6%	*w*Phocry
Salticidae	*Marpissa magister* (Karsch 1879)	-	N.A.
	Plexippus paykulli (Audouin 1826)	-	N.A.
Thomisidae	*Misumenops tricuspidatus* (Fabricius 1775)	-	N.A.
	Thomisus labefactus Karsch 1881	-	N.A.
Tetragnathidae	*Tetragnatha squamata* Karsch 1879	-	N.A.
	Tetragnatha praedonia L. Koch 1878	-	N.A.
Theridiidae	*Coleosoma octomaculatum* Bösenberg & Strand 1906	13.3%	*w*Coloct
	Achaearanea tepidariorum (C.L. Koch 1841)	-	N.A.

infected *Drosophila melanogaster* served as a template for positive controls in PCR reactions.

PCR detection of *Wolbachia*.—Since the primers hedin-O and hedin-C work well in a range of Araneae, we used these to amplify the D2–D3 region of the spider 28S nuclear ribosomal RNA gene to control for the quality of DNA extracted from each specimen (Goodacre & Martin, 2006). To detect the presence of *Wolbachia*, we performed PCR for the *wsp* gene using the primers 81F and 691R (Braig et al. 1998). The primers for detecting super-infection in spiders are 136F/ 691R (primers for supergroup A *Wolbachia*) and 81F/552R (primers for supergroup B *Wolbachia*) (Zhou et al. 1998). We cloned any positive amplifications for both loci into the vector pGEM-T Easy according to the manufacturer's protocol (Promega). Three independent clones were sequenced for each *Wolbachia* strain to ensure that there were no polymerase errors. If more than one sequence variant was present in the sample, we sequenced a further 7 clones for a total of 10. Every clone was sequenced in both directions by an ABI automated sequencer. All sequences have been deposited in GenBank under accession numbers listed in the phylogenetic trees (Figure 1).

Multiple alignments and phylogenetic analysis.—*Wolbachia* DNA sequences from seven infected spider species were aligned together with other representative *wsp* sequences from the various supergroups, using ClustalX v. 1.8 (Thompson et al. 1997) followed by manual modifications based on the amino acid translation of different genes. We constructed phylogenetic trees using maximum likelihood (ML) and Bayesian inference (BI). ML trees were constructed with PAUP4.0 b1 (Swofford 2003) after determining the model HKY _ G with Modeltest 3.06 (Posada & Crandall 1998); BI trees were constructed using MrBayes (Huelsenbeck & Ronquist 2001) with the following parameters: brlenspr = clock:uniform, 1,000,000 generations, burnin = 1,000. Tree topologies were congruent across both phylogenetic construction methods and, therefore, only ML trees with posterior probabilities are reported.

RESULTS

We screened 930 spiders from 11 families and 31 species for *Wolbachia* infection by PCR assays with *Wolbachia*-specific *wsp* gene primers. The infection status of each tested spider species and the infection rate are listed in Table 1. We found seven spider species to be infected with *Wolbachia*. The percentage of *Wolbachia* infection among tested species was 22.6%, which is very low compared to previous surveys in insects (Jeyaprakash & Hoy 2000). There was a wide range in infection rates for the infected spider species sampled. The highest infection rate was found in *Oxyopes sertatus* L. Koch

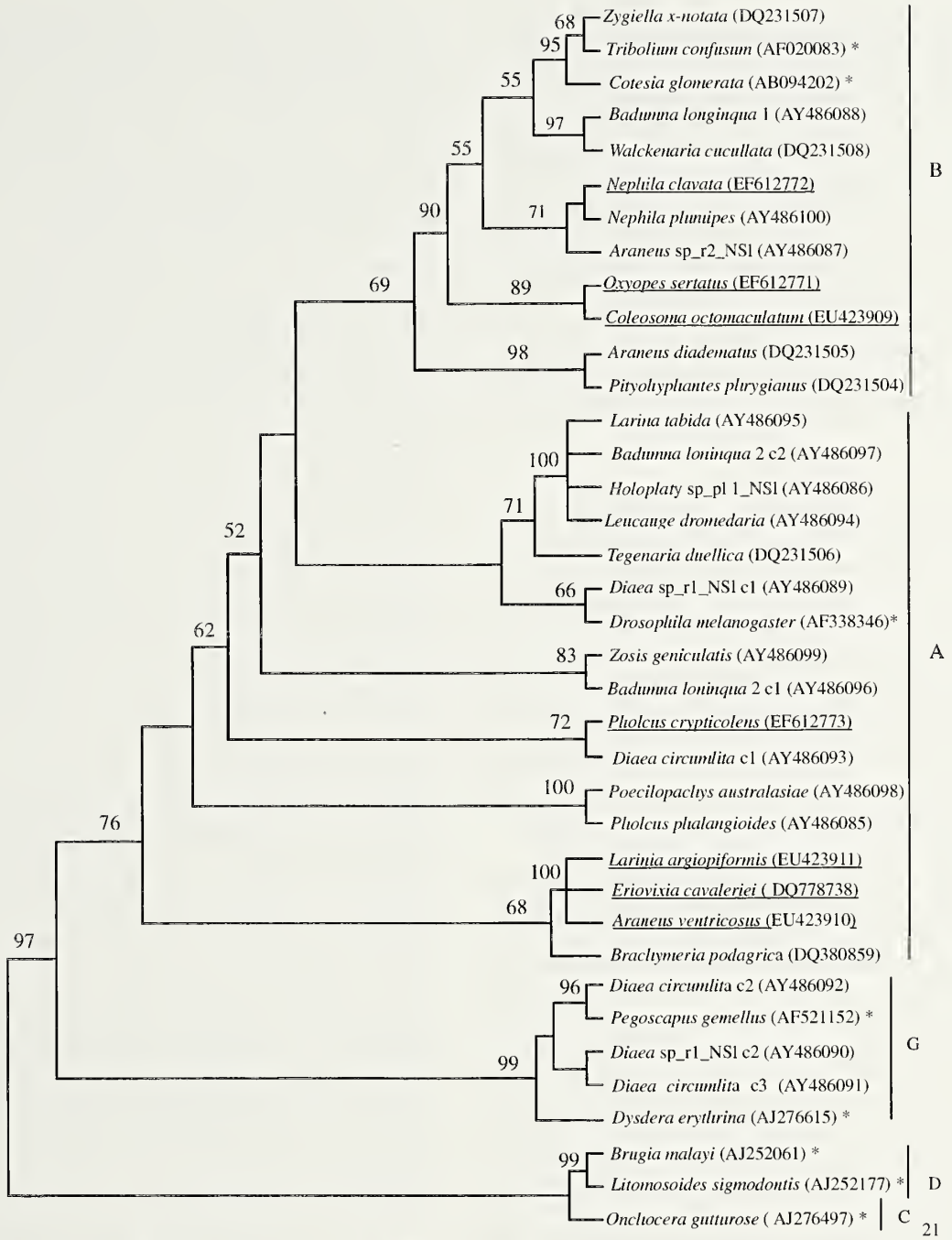

Figure 1.—Phylogeny of spider *Wolbachia* based on *wsp* gene sequence. Taxonomic names refer to host species (Table 1). Underlined designations are strains sequenced in this study. GenBank accession numbers are listed in parentheses. Asterisks after taxa indicate these strains are not from spider families. Bootstrap values of 1,000 replicates are presented above the branch (bootstrap scores less than 50 are not shown). Major supergroup lineages are indicated (A–D and G).

1877 (73.3%), and the lowest infection rate occurred in *Coleosoma octomaculatum* Bösenberg & Strand 1906 (13.3%). From the data presented here, it appears that *Wolbachia* is not widespread in the spider species that we tested.

We used the specific primers of the A and B *Wolbachia* supergroups for the *wsp* gene to identify a super-infection in the infected spiders. *Nephila clavata* (L. Koch 1878) specimens were infected with strains of both A and B *Wolbachia*; the others were infected with either strain A or B. The lengths of *wNepA* and *wNepB* (the strain A and B *wsp* genes found in *Nephila clavata*) were 522bp and 455bp, respectively. These two genes are largely different. Based on the alignment of these two genes by BLASTn in GenBank, they were only 50% similar.

Wolbachia sequences were obtained from infected individuals in each of the seven infected spider species in this study (sequences have been deposited in GenBank; accession numbers DQ778738, EF612771–612773, EU423909–EU423911). We also included a range of sequences from

closely related bacteria found in other insects, mites, and spiders (from GenBank) in our phylogenetic analyses. Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI). Tree topologies were congruent across both phylogenetic construction methods and therefore only ML trees with posterior probabilities are reported in Fig. 1. The *Wolbachia* phylogeny can be compared broadly with the analysis by Rowley et al. (2004), who found that *Wolbachia* strains carried by spider hosts can be from a variety of clades. The *Wolbachia* found in *Larinia argiopiformis* Bösenberg & Strand 1906, *Eriovixia cavaleriei* (Schenkel 1963), *Araneus ventricosus* (L. Koch 1878) and *Pholcus crypticolens* Bösenberg & Strand 1906 belong to the A supergroup and the other three species, *Nephila clavata*, *Oxyopes sertatus* and *Coleosoma octomaculatum* belong to the B supergroup.

DISCUSSION

We detected *Wolbachia* in 22.6% of the spider species sampled, based on the PCR assays with *Wolbachia*-specific *wsp* gene primers. That is lower than the frequency reported by Goodacre & Martin (2006), who screened 121 spider species from 9 families in southeastern Britain. They found that 37 spider species (30.6%) were infected with *Wolbachia*. Among their species, nine Araneidae were infected, but none of their twenty lycosids were infected. Similar to their results, we found that more araneids (three out of six) were infected with *Wolbachia*, whereas none of our seven lycosids were infected. The uneven distribution of *Wolbachia* among spider populations may be associated with different host (spider) conditions, host behaviors, and the efficiency of spread of *Wolbachia*.

Based on phylogenetic analysis, multiple lines of evidence indicate that at least some of the associations between spiders and *Wolbachia* are of recent origin, likely to have arisen through horizontal transmission. First, the *Wolbachia* strains found in *Larinia argiopiformis*, *Eriovixia cavaleriei*, and *Araneus ventricosus* have almost identical gene sequences and are in the same subgroup with bootstrap support of 100% for the maximum likelihood analysis. We interpreted small sequence differences among these three species to be PCR artifacts: compared to *Araneus ventricosus*, our *Larinia argiopiformis* sequence had a T instead of a C at position 118, and an A instead of a C at position 280; our *Eriovixia cavaleriei* sequence had a G instead of a T at position 518 and a T instead of an A at position 584. This finding of three distantly related Araneidae species infected with the same strain of *Wolbachia* suggests a very recent horizontal transmission. Second, closely related spider hosts do not necessarily share closely related *Wolbachia* strains. Different members of a single spider family may harbor infections from distinct supergroups (Fig. 1).

Third, using the specific primers of the A and B *Wolbachia* supergroups for the *wsp* gene, we identified one superinfection. Specimens of *Nephila clavata* were infected with distinct strains of both A and B *Wolbachia*. Spider species are generalist predators, and they prey mostly on terrestrial arthropods (insects, myriapods, and arachnids). Feeding on common prey infected with *Wolbachia* could provide the link for horizontal transfer of the same strain across related species. However, the possible role of horizontal transmission via parasitoids in spiders cannot be excluded. Spiders are known to suffer parasitoid attack from several taxa (La Salle 1990; Vavre et al. 1999). Routes and vectors of *Wolbachia* horizontal transfer remain one of the main unsolved questions. It is, for example, unclear whether horizontal transfer of *Wolbachia* is more likely to occur within the same host taxonomic group (at different levels, such as genus or species) than among different groups.

Rowley et al. (2004) reported that several *Wolbachia* infections present in the genus *Diaea* appear to be phylogenetically distinct from the A–F clades. The stability of the cluster is strengthened by the inclusion of *Wolbachia* strains infecting the spider *Dysdera erythrina* (Walckenaer 1802) and the fig wasp *Pegoscapus gemellus*. They had tentatively called this lineage supergroup G., but we did not find the G supergroup in any of the Chinese spiders tested. Thus the independence of this new supergroup should be re-examined more closely when related *wsp* sequences are published.

It has been argued that endosymbiotic bacteria that are widespread among hosts are very important in the evolution of hosts, including effects on reproduction, gene flow, and individual or population fitness, with possible impacts on reproductive isolation or extinction (Werren 1997; Werren et al. 2008). Shoemaker et al. (1999) found that behavioral isolation and *Wolbachia*-induced CI acted as complementary asymmetrical isolating mechanisms between *Drosophila recens* and *D. subquinaria*. Some unique characteristics of spider reproductive biology facilitate studies of sexual selection (Eberhard 2004), and there have already been studies examining the relationship between sexual selection in spiders and speciation (Gage et al. 2002). We suggest that, combined, comparative studies and manipulations of endosymbiont infections in spiders will help allow us to predict the relationships between bacterial infections and the evolution of host traits under sexual selection.

This study was conducted as a first step to screen the prevalence of *Wolbachia pipientis* in Chinese spiders, to determine the occurrence of super-infections in the infected spiders and the relationship of these strains to the existing *Wolbachia* supergroups. Based on these results, the effects of the bacteria upon the host, the full extent of infection throughout the order Araneae, and the practical implications of such infections all require further investigation.

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Genitalic variation and taxonomic discrimination in the semi-aquatic spider genus *Paratrechalea* (Araneae: Trechaleidae)

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Abstract. For spiders, morphological differentiation within genitalic traits is the main diagnostic criterion of a species. Beside some well-described exceptions of genitalic polymorphism and crypticity, spider genitalic variation is seldom quantitatively analyzed. Using geometric morphometrics landmark analysis, we report clear evidence of quantitative interspecific divergence and intraspecific variation in the genital shape of three species of the genus *Paratrechalea* (*P. azul*, *P. ornata* and *P. galianoae*). The genitalic species recognition was very consistent with our quantitative data for both sexes. Interspecific variation suggested a character displacement pattern between two syntopic populations of *P. azul and P ornata*, and also a possible case of species crypticity in *P. ornata* that will involve splitting the Uruguayan populations from the Brazilian ones.

Keywords: Morphological evolution, geometric morphometrics, character displacement

The line between what distinguishes a true species from a simple case of intraspecific variation is not only subtle, but also dependent on the species definition assumed (Bond et al. 2001; Huber 2004; Mutanen 2005). Within this fuzzy zone lie a large number of separate biological entities that remain undetected because of their morphological similarities (Adams & Funk 1997). Therefore, morphological species delimitation may pose a problem for some specific groups with a high degree of resemblance.

Systematic practice is based strongly upon the correlation of morphology and the recognition of the limits of true species, and there is no exception for spiders (Huber 2003, 2004; Huber et al. 2005). Spiders are one of the most diverse metazoan groups, with 40,998 described species (Platnick 2009). The structures with the most diagnostic traits for spider species are the genitalia, which in general have a high degree of specificity associated with a faster evolutionary pace that may be guided mainly by mechanisms of sexual selection (Eberhard 1985; Arnqvist 1997; Hosken & Stockley 2004; Mutanen 2005; but see also Costa & Capocasale 1984; Pérez-Miles 1989; Jocqué 2002; Huber 2003; Huber et al. 2005).

Leaving processes aside, two opposing cases of genitalic phenotypic expression may pose a problem for the usual taxonomic species recognition: cryptic species and polymorphism. Both cases have been described for spiders (crypticity: Ramirez & Chi 2004; Johannesen et al. 2005; Huber et al. 2005; polymorphism: Pérez-Miles 1989; Huber & González 2001; Jocqué 2002), suggesting that neither may be an exception. Cryptic species complexes can be found in several organisms (Bond & Sierwald 2002; Muster et al. 2004) and they are often revealed by integration of molecular and/or behavioral tools, and not by the definition of morphological apomorphies (Adams & Funk 1997). On the other hand, genitalic polymorphism can be discovered by several methods, the best evidence being the hatching of different morphs from a single egg-sac (Jocqué 2002).

During recent decades the establishment of geometric morphometrics as a new morphometric paradigm has made a significant contribution to the study of shape variation (Rohlf & Marcus 1993). For example, using geometric morphometrics, cryptic species complexes can be not only quantitatively described by their morphological properties, but also can allow the testing of differences in shape consensus for the observed groups. This approach has already been applied in some spider studies (Bond & Beamer 2006; Costa-Schmidt 2008; Crews 2009), and despite the limitations of using morphometric data as phylogenetic characters (Zelditch et al. 2004; Bond & Beamer 2006), geometric morphometric tools can improve the capacity of taxonomic discrimination.

Here we present quantitative analyses of genitalic variation within three species of the semi-aquatic spider genus *Paratrechalea* Carico 2005 (Araneae: Trechaleidae): *P. azul* Carico 2005, *P. ornata* (Mello-Leitão 1943) and *P. galianoae* Carico 2005. The taxonomic status of the first two species can be questioned, since they share strong morphological and ecological crypticity and considerable intraspecific genitalic variation (Carico 2005; Silva et al. 2006). This last feature means that the formal descriptions are difficult to apply to some populations of those species, and for this reason we include in our analysis two samples from Uruguay representing the intraspecific variation within *P. ornata*.

The general aim of this work is to improve our knowledge of the morphometric properties of shape and size for genital traits of these species based on quantitative analyses. The specific aim is to quantify the visual genitalic variation observed within each species, identifying the main differences among them, and to infer the degree of intraspecific variation observed among three *P. ornata* samples.

METHODS

Study species and sampling design.—Three *Paratrechalea* species were analyzed in this work: *P. azul* Carico 2005, *P. ornata* (Mello-Leitão, 1943), and *P. galianoae* Carico 2005.

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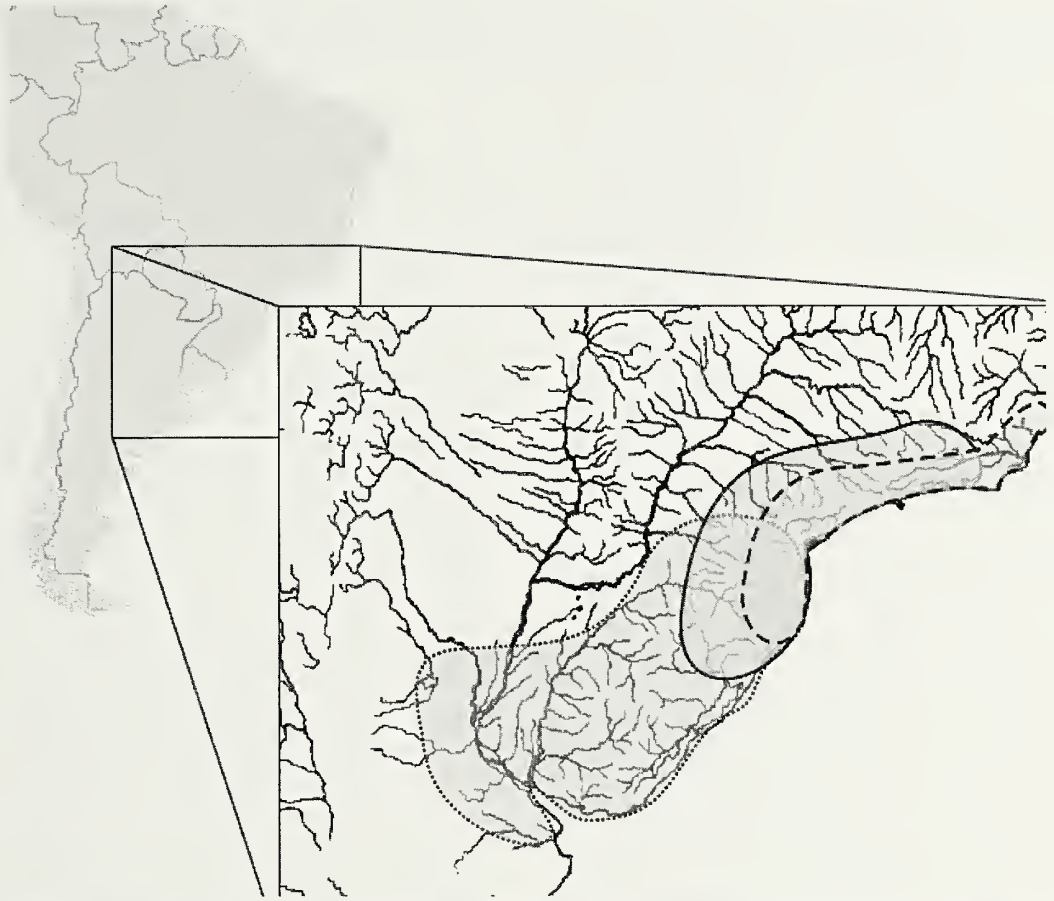

Figure 1.—Estimated geographic distribution of the study species based on the sampling data from Carico (2005) and Silva *et al.* (2006). Continuous line: *Paratrechalea azul*, dotted line: *P. ornate*, dashed line: *P. galianoae*.

Beside the cryptic aspect of somatic characters among these species, *P. azul* and *P. ornata* have a marked genital resemblance in both males and females. *P. galianoae* is easily recognized based on genital morphology, thus the insertion of this species within the data set will serve as a control group for the levels of divergence found between the two other species.

The three species have nocturnal semi-aquatic habits, and are easily found living next to streams and rivers. *P. azul* and *P. ornata* have a syntopic distribution in the northeastern region of Rio Grande do Sul (Brazil) (Fig. 1). The entire zone of overlap is not yet established. Sampling efforts did not find any isolated populations of *P. azul* in the Rio Grande do Sul State, even though there are large sampling gaps. We assume that they are sibling species, based on ecological requirements (Costa-Schmidt & Araújo, pers. observ.), on genitalic resemblance (Carico 2005; Silva et al. 2006) and by quantitative morphological analyses of non-genitalic characters (Costa-Schmidt 2008).

Within their known distributions (Fig. 1), *P. azul* and *P. ornata* can be found in second to higher order streams at altitudes ranging from sea level to 200 meters. *P. galianoae* seems to be strongly associated with dense riparian vegetation, typically being found along first and second order streams in an altitudinal level starting at ca 300 m. There is a clear checkerboard distribution between *P. ornata* and *P. galianoae* (Costa-Schmidt, unpub. data), and we assume that this distribution is a direct response of the habitat structure and altitudinal restrictions.

Comparisons were made of field-collected adult males and females from four different locations (Table 1, Fig. 1). We considered each sampled population as a single level of a classification factor. All specimens were preserved in 80% alcohol. Voucher specimens are deposited in the Museu de Ciências Naturais – Fundação Zoobotânica do Rio Grande do Sul (MCN-FZB/RS), and in the Facultad de Ciências (Montevideo – Uruguay).

Geometric morphometrics procedures.—Digital images were made by attaching a camera (Nikon Coolpix 5400) to the ocular of a stereomicroscope (Nikon SMZ600), using the same magnification for each structure. An ocular scale was subsequently used to make pixel/millimeter conversions. All images were arranged in a single folder, and tpsUtil v. 1.33 (Rohlf 2004) was used to create a file containing the sequence of pictures to be further analyzed.

We have chosen to analyze the genital structures used in species diagnoses. The generic diagnosis was presented by Carico (2005), emphasizing the ventral division of the median apophysis of the male pedipalpus and the external posterior-median scape of the female epigynum. Additionally, the same author and Silva et al. (2006) used the ectal division of the retrolateral tibial apophysis (Fig. 2A, RTA) as a component of the male diagnosis. Thus, based on this and also on Huber

Table 1.—Sampling location, city, country, geographic coordinates, and sample size of each studied population.

Sampling location	City, country	Coordinates	Sample size					
			P. azul		*P. ornata*		*P. galianoaez*	
			F	M	F	M	F	M
Pedra de Amolar River, Barra do Ouro	Maquiné, Brazil	29°32'20.52"S, 50°14'46.83"W	38	35	35	37	–	–
Santa Lucia River, Paso del Molino	Minas, Uruguay	34°16'40.10"S, 55°14"00.80"W	–	–	21	14	–	–
Yerbal Chico River, Quebrada de los Cuervos	Treintay y Tres, Uruguay	32°55"30.50"S, 54°27"33.10"W	–	–	20	19	–	–
Pedras Brancas River, Pedra Branca Fall	Itati, Brazil	29°23"45.59"S, 50°02'42.44"W	–	–	–	–	34	17

(1995), we assumed that the analyses of the ectal division of the RTA and the epigynal scape (Fig. 2B) present the most diagnostic information needed to delimit the species. Since males have two symmetrical palps (assumption made visually), we chose to analyze only the RTA of the left palp.

Only Type II landmarks (Slice et al. 1996); i.e., those defined by local properties such as maximum curvatures, were plotted in each image. The already created tpsUtil file was loaded with the tpsDig 2.04 software (Rohlf 2005) for plotting of landmarks, consisting the rough data. Landmarks descriptions for each genital structure are presented in Table 2.

Using a simple morphological formula, "form = shape + size", we first isolated these two morphological components (also addressed here as morphological properties). To isolate all landmark configurations, we applied a General Procrustes Superimposition analysis (GPS). Each landmark configuration was translated, rotated and scaled to the unit centroid size, using a least squares procedure. After this treatment, each configuration was described by a single point within a multidimensional space, called the pre-form space. Because of its multidimensionality and non-Euclidian properties, the pre-form residuals were projected into a plane that is tangent to the mean pre-form shape, where Euclidian properties are fulfilled and conventional statistical analyses were applied. After this projection, a Principal Component Analysis was made over the scores of this projection, composing the shape variables. More information about these methods can be found elsewhere (Rohlf & Slice 1990; Zelditch et al. 2004; Crews in press). These morphometric procedures and the further analyses and graphic outcomes were made using the RMorph library (Baylac 2007) developed for R environment (R Development Core Team 2007).

Size component was estimated by centroid size, which is defined as the square root of summed squared distances of landmarks from their centroid (Swiderski 2003). The advantage of this method is that it takes an overall size measurement of the form, while linear estimates of size underestimate other two-dimensional variables of the same structure.

Shape analysis.—Differences in genital structures were tested by a one-way MANOVA using species and populations as a descriptor factor composed by the following levels: *P. azul*, *P. galianoae*, *P. ornata* (MaqB) (*Maquine* population), *P. ornata* (PasU) (Paso del Molino population), and *P. ornata* (QueU) (Quebrada de los Cuervos population), where "B" means Brazil and "U" means Uruguay. Pairwise comparisons were performed between all possible combination levels using the same model in the case of significant analysis. The probability results of these pairwise tests were corrected with a Bonferroni correction for multiple comparisons. Discriminant analysis based on shape variables was applied in order to verify the percent of correct classifications achieved by the tested factor, which is a way to confirm whether the informed classification within the factor levels does represent variation among groups.

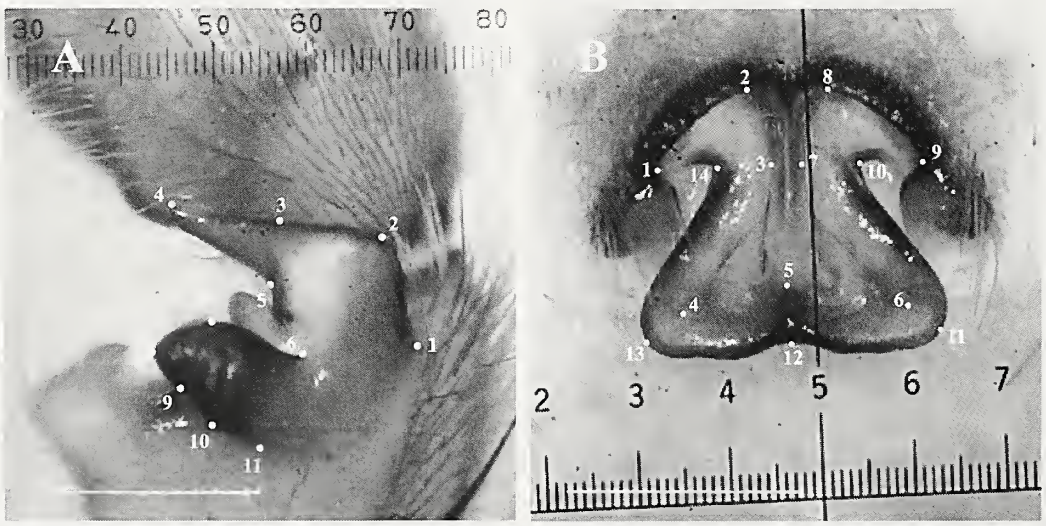

Figure 2.—Landmark positions within each analyzed structure. A. Ectal division of the retrolateral tibial apophysis (11 landmarks); B. Epigynum scape (14 landmarks). Photos from *Paratrechalea ornata* specimens. Scale = 1 mm.

Table 2.—Morphological landmarks used in this study for each genital structure analyzed.

RTA landmark	Description
1	Insertion point of the distal lobe into the palpal tibia
2	Maximum curvature of the distal lobe anterior margin
3	Mid-point of the distal lobe anterior margin
4	Tip of the distal lobe
5	Mid-point of the distal lobe posterior margin
6	Maximum curvature between the distal and basal lobes
7	Point of maximum inflection of the basal lobe anterior margin
8	Tip of the basal lobe
9–10	Equidistant inflexion points along the basal lobe posterior margin
11	Insertion point of the basal lobe into the palpal tibia

Epigynum landmark	Description
1–2–8–9	Connection points of the scape with the posterior margin of the anterior field
3–4–6–7	Maximum inflexion points on the margin of the inner fold
10–11–13–14	Points of maximum inflexion on the rim of the scape
12	Midline point on the posterior rim of the scape
5	Midline point on the margin of the inner fold

Because we could describe an average shape for each considered level using shape variables only, we were able to estimate the Mahalanobis distance as a dissimilarity measure among the average shapes under analysis. This estimate is directly related to morphological divergence; i.e., the higher this estimated value, the bigger the morphological divergence. Permutation tests among individuals of each pairwise group comparison were done in order to verify whether the estimated distances between those groups could not be achieved by random sampling.

RESULTS

The analyses suggest that shape is the most informative morphological property in assigning groups. Size showed different patterns within each genital structure, demanding different interpretations of their size variation. The overall findings are summarized below. First, analyses of both structures resulted in similar groupings of species and populations. Second, *P. galianoae* was the most divergent in all analyses, thus corroborating the assumption of its use as an outgroup for analysis of the *P. azul* and *P. ornata* relationship. Third, there is an expected shape difference among species for both genital structures, with *P. azul* and *P. ornata* populations being closer within the shape space. Fourth, all shape analyses indicate that two populations, initially presumed to be *P. ornata*, can be interpreted as being a new species.

Shape analysis.—Genital structures showed strong differentiation among groups for all analyses. Principal Component Analysis (PCA) indicated the presence of at least three groups based on the first two components (PC1 and PC2, Figs. 3, 4), corresponding to the three studied species. The addition of the third PC allows us to distinguish another group, composed of the Uruguayan populations of *P. ornata* (Fig. 5).

Discriminant analysis confirms that the assumed classification explains the observed shape variation for both RTA and epigynum shape variables (Table 3); i.e., genital structures are good predictors of species classification. This analysis also suggests that the group formed by the Uruguayan populations is consistent with a few misclassifications, including a single female specimen from Paso del Molino that was initially placed as being from Maquine.

MANOVA models were highly significant for both genital structures (Table 4). All pairwise comparisons showed the same highly significant levels; i.e., the samples have different shapes of RTA and epigynum (Table 4). Again, we observed a splitting behavior between Uruguayan *P. ornata* populations from the Brazilian population. The comparison between the Paso del Molino and Quebrada de los Cuervos samples was also significant for both structures, but with contrasting lower significant levels in relation to other comparisons (Table 4, last row).

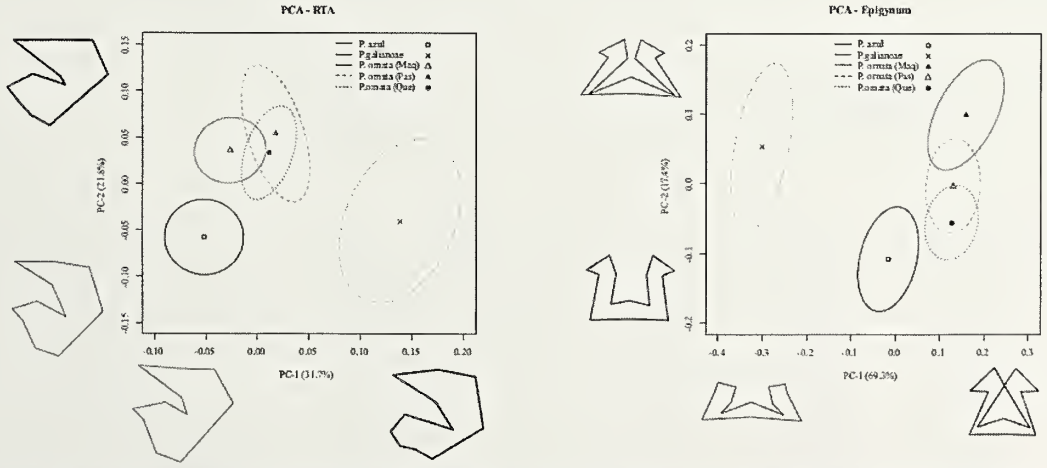

Figure 3.—Projections of the first and second scores of the Principal Component Analysis for RTA (left) and epigynum scape (right). Symbols represent the consensus shape of each species/population, with delimiting 95% confidence ellipses. Illustrations within the axes represent the shape variation along each axis.

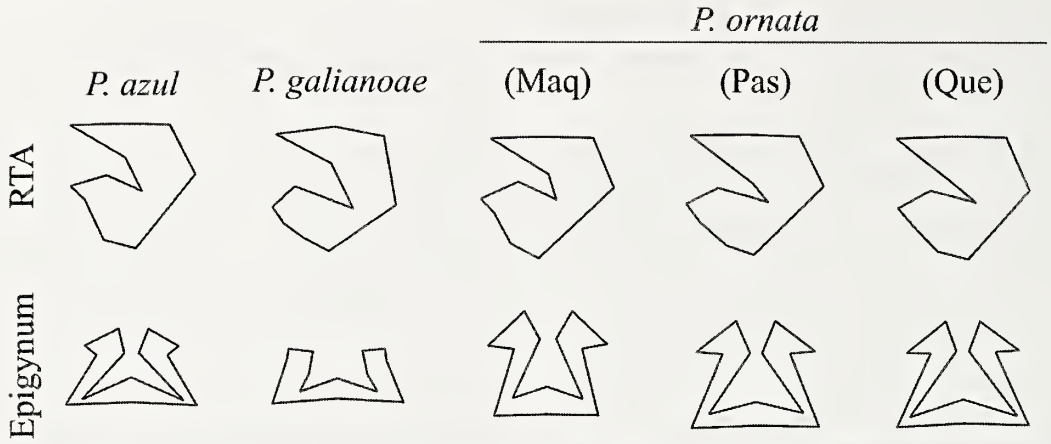

Figure 4.—Shape consensus observed for each species/population within the first component of a Principal Component Analysis.

The Mahalanobis distance between the samples' mean shapes also confirms the same diverging pattern of *P. ornata* between the Brazilian and the Uruguayan populations (Table 5). It is important to emphasize that the observed Mahalanobis distance for RTA between the Maquine and Uruguayan populations was even higher than that between *P. ornata* and *P. azul*. This was not observed for the epigynum, however, which showed lower Mahalanobis distances when comparing the Maquine population with the Uruguayan ones (Table 5). Permutation tests indicate that the estimated distances were significant for all comparisons and for both structures ($P \leq 0.0003$ for *P. ornata* (PasU) and *P. ornata* (QueU) comparisons; $P \approx 0$ for all other comparisons).

DISCUSSION

Here we report the application of a robust morphometric method to discriminate among a small group of samples representing three putatively related spider species. The outcome of such analyses ranged from the determination of species using their genital shape to the recognition of a splitting within what was once considered a single species. This latter conclusion has important and deep roots in the standard methodology used in spider systematics. Much of spider systematics has been based upon the assumption that genital specificity (Huber 2003, 2004) is directly linked to the widespread pattern of a faster rate of genital evolution (Eberhard 1985; Hosken & Stockley 2004). So, for genital traits, we are facing the challenging task of distinguishing between interspecific shape divergence and intraspecific shape variation.

The application of geometric morphometrics proved to be highly important for the discrimination of cryptic spider species within two different taxonomic situations. The first one deals with two already-described taxonomic entities that have a strong niche overlap (*P. azul* and *P. ornata*), but with known behavioral reproductive isolation and non-genital morphometric differences (Costa-Schmidt 2008; Costa-Schmidt et al. 2008). The second case deals with our findings that within *P. ornata*, two cryptic entities exhibit clear spatial niche segregation (geographical allopatry).

Evolutionary explanations for the observed pattern are suggested below, based on available information about the species and populations, which opens the subject for further studies and/or interpretations. On the other hand, the observed split of *P. ornata* demands a taxonomic description based on consistent characters identified in each group.

Genital variation between *P. azul* and *P. ornata*.—This work fulfills an important aspect related to the morphological

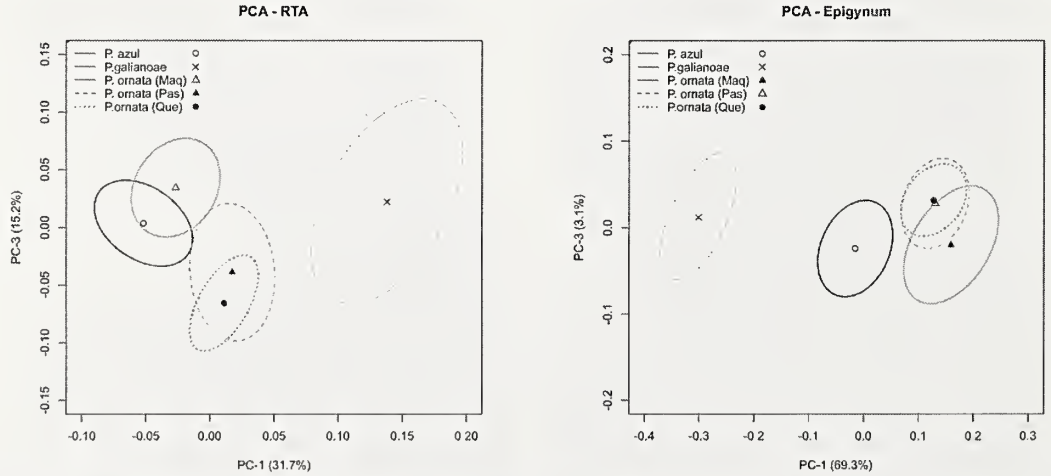

Figure 5.—Projections of the first and third scores of the Principal Component Analysis for RTA and epigynum scape. Symbols represent the consensus shape of each species/population, with delimiting 95% confidence ellipses.

Table 3.—Correct classification percentages achieved by discriminant analyses.

Species	RTA	Epigynum
P. azul	100%	100%
P. galianoae	100%	100%
P. ornata (Maq)	100%	100%
P. ornata (Pas)	85.7%	71.4%
P. ornata (Que)	100%	100%

Table 5.—Estimated Mahalanobis distances between the average shapes of the compared groups. Above diagonal: species/population comparisons for epigynum scape. Below diagonal: species/population comparisons for RTA.

	azul	*gal*	*orn* (Maq)	*orn* (Pas)	*orn* (Que)
azul	–	273.80	65.98	37.32	30.05
gal	207.19	–	374.06	357.83	367.72
orn (Maq)	56.37	160.14	–	16.34	23.92
orn (Pas)	147.95	124.33	68.58	–	5.16
orn (Que)	140.98	140.28	69.92	10.01	–

variation of genital structures and the recognition of distinct species within the genus *Paratrechalea*. Since the beginning of our efforts in studying *P. azul* and *P. ornata*, we have been able to gather fundamental information supporting their taxonomic status as two different species (non-genital morphometry: Costa-Schmidt 2008; reproductive behavior: Costa-Schmidt et al. 2008), and this was also corroborated here by information gained from genitalic analysis.

The previously described genital variation within these two species shows quantitatively that the variation does not overlap along their shape space, mainly for the syntopic interspecific samples from Maquine. We believe that such divergence may be due to a reinforcement mechanism, such as character displacement (Brown & Wilson 1956), avoiding possible hybrid formation between the syntopic populations. The hypothesis of character displacement was also raised in the analysis of non-genital structures, especially for those populations sampled along the region of syntopy (Costa-Schmidt 2008).

Genital morphology species-specificity.—Another important aspect is the almost impossible discovery of genital polytypism within a species (Huber 2003), mainly if those morphs are dispersed along a geographical continuum where they can be easily misinterpreted as different species. In other words, genitalic differences found along the spatial distribution of a single species may lead to taxonomic inflation because of systematic methodological bias. Moreover, we cannot deny the huge influence that Mayr's non-dimensional definition has on taxonomic practice (Mayr 1963; Huber 2003), which is the basis of species-specific genitalic morphology.

As we found sharp limits for the shape component of male and female genitalia, we must try to translate those differences into something that can be used by a taxonomist when analyzing a particular sample; i.e., we must apply some effort in order to describe which shape trait is shared in each group (Zelditch et al. 2004). Such information was necessarily proposed elsewhere (Carico 2005; Silva et al. 2006), consisting of formal descriptions of diagnostic characters of each species, even though our data demonstrate that the diagnosis of *P. ornata* is not capable of distinguishing the new split species. This effort will be presented elsewhere, when additional diagnostic characters that better describe the species studied will be followed with the description of a new species.

CONCLUSIONS

In a broader sense, the observed interspecific divergence patterns were expected in relation to empirical and theoretical data of genital traits used in taxonomy. The number of shape differences among species was lower between *P. azul* and *P. ornata*, which may induce us to believe that they are sister species, even though this assumption will only be resolved after a robust cladistic analysis. Intraspecific analysis showed an interesting divergent pattern, suggesting that we have two separate taxonomic entities within the *P. ornata* dataset.

Table 4.—MANOVA of shape principal components for species/population (the first 18 and 24 PCS were selected for RTA and epigynum scape respectively), and pairwise comparisons for all levels combinations.

	RTA[a]			Epigynum[b]		
	Wilks	*F*	*P*	Wilks	*F*	*P*
Samples ($df = 4$) Residuals ($df = 117$)	0.0003	38.804	$< 2.2\ e^{-16}$	0.0007	26.501	$< 2.2\ e^{-16}$
Pairwise comparisons						
P. azul vs. *P. galianoae*	0.0484	109.1597	$2.3\ e^{-57}$	0.0463	103.0024	$1.3\ e^{-68}$
P. azul vs. *P. ornata* (MaqB)	0.0828	61.5561	$7.7\ e^{-46}$	0.1267	34.4585	$8.7\ e^{-43}$
P. azul vs. *P. ornata* (PasU)	0.0598	87.3079	$8.2\ e^{-53}$	0.2015	19.8172	$4.0\ e^{-31}$
P. azul vs. *P. ornata* (QueU)	0.0564	92.9630	$4.4\ e^{-54}$	0.2411	15.7367	$1.1\ e^{-26}$
P. galianoae vs. *P. ornata* (MaqB)	0.0590	88.5747	$4.2\ e^{-53}$	0.0217	225.5691	$3.0\ e^{-88}$
P. galianoae vs. *P. ornata* (PasU)	0.1092	45.3268	$6.2\ e^{-40}$	0.0299	162.4213	$5.9\ e^{-80}$
P. galianoae vs. *P. ornata* (QueU)	0.0851	59.7632	$2.9\ e^{-45}$	0.0300	161.9082	$7.2\ e^{-80}$
P. ornata (MaqB) vs. *P. ornata* (PasU)	0.1438	33.0732	$4.4\ e^{-34}$	0.4001	7.4973	$1.4\ e^{-14}$
P. ornata (MaqB) vs. *P. ornata* (QueU)	0.1176	41.6779	$2.4\ e^{-38}$	0.3196	10.6436	$7.7\ e^{-20}$
P. ornata (PasU) vs. *P. ornata* (QueU)	0.5919	3.8304	$7.7\ e^{-6}$	0.7302	1.8473	0.01648529

[a] Samples: num $df = 72$, den $df = 395.6$; Pairwise comparisons: $df1 = 18$, $df2 = 100$
[b] Samples: num $df = 96$, den $df = 477.9$; Pairwise comparisons: $df1 = 24$, $df2 = 120$

It is still early to state an evolutionary explanation in this system, since fundamental reproductive aspects (like the presence of polyandry) remain to be answered. Subsequent approaches must be applied in order to evaluate better the hypothesis raised. For example, careful sampling design associated with the analytical procedures presented here would allow us to understand whether character displacement did influence the evolutionary history of these spider species.

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Revision of *Iviella* Lehtinen (Araneae: Dictynidae), with description of a new species from Newfoundland

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Abstract. The genus *Iviella* Lehtinen 1967 (Dictynidae) comprises three North American species, *I. ohioensis* (Chamberlin & Ivie 1935), *I. reclusa* (Gertsch & Ivie 1936) and a new species from the Northern Peninsula of Newfoundland. We provide a new diagnosis of the genus, describe the new species and describe the previously unknown male of *I. reclusa*. We also describe or re-describe the intricate copulatory ducts and spermathecae of the three species.

Keywords: *Iviella newfoundlandensis*, Canadian spiders, limited distribution

The genus *Iviella* Lehtinen has been poorly diagnosed (Bennett 2005) until now. It was created for two unusual species of the Dictynidae (Lehtinen 1967), based on both sexes of *I. ohioensis* (Chamberlin & Ivie 1935) but only females of *I. reclusa* (Gertsch & Ivie 1936). Chamberlin & Gertsch (1958) had placed both species in *Tricholathys* Chamberlin & Ivie 1935 because of the long, slender loop of the embolus of *I. ohioensis* and the supposedly diagnostic characteristics of the external female genitalia. However, Lehtinen (1967) recognized that the peculiar embolus in *I. ohioensis* is accompanied by a similarly elongated tegular apophysis, a characteristic he regarded as indicative of generic distinctness. Discovery of male *I. reclusa* in Saskatchewan and examination of the details of the convoluted copulatory ducts and spermathecae of females has helped to more clearly delineate *Iviella* and allowed us to recognize a third species.

In this paper we describe (or re-describe) the complex female genital anatomy and the male palp of *I. ohioensis*, *I. reclusa* and *I. newfoundlandensis* new species. The species are diagnosed, a key is given for their identification and a map of collection localities is provided.

METHODS

Definitions of measurements used.—Carapace width: measured at the widest point, in dorsal view; Cymbium length: measured in dorsal view; Overall length of spider: measured from anterior edge of carapace (excluding legs and palps) to posterior end of abdomen (excluding spinnerets if visible dorsally) viewed dorsally with body in one plane (i.e., with long axes of both cephalothorax and abdomen in the same plane); for other technical terms we have followed the glossary in Ubick et al. (2005).

Abbreviations used in text.—AMNH: American Museum of Natural History, New York, New York; DB: D. Buckle collection, Saskatoon, Saskatchewan, Canada; RMNL: The Rooms Provincial Museum, St. John's, Newfoundland and Labrador, Canada (in previous publications this collection was referred to as the J.R. Pickavance collection); CNC: Canadian National Collection of Insects and Arachnids, Ottawa, Ontario.

TAXONOMY

Family Dictynidae O. Pickard-Cambridge 1871
Genus *Iviella* Lehtinen 1967

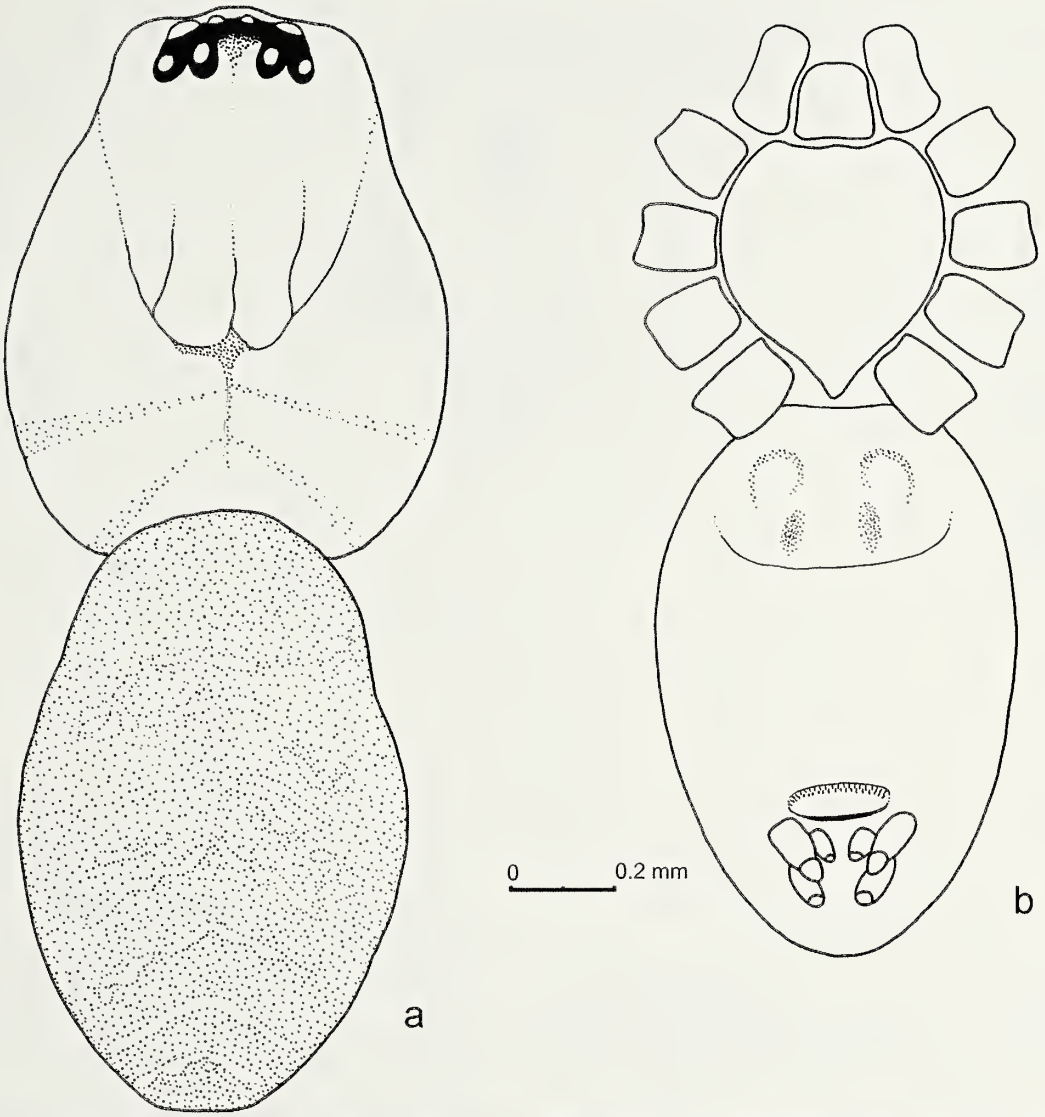
Type species.—*Argenna ohioensis* Chamberlin & Ivie 1935. Designated by Lehtinen 1967.

Iviella: Lehtinen 1967:241.
Iviella: Bennett 2005:99.

Description of the genus.—General characters as for the family (Bennett 2005). Small (overall length 1.68–3.72 mm; carapace width 0.531–1.14 mm), cribellate dictynids. Shape uniform and without unusual features (Figs. 1a, 1b). Carapace and sternum pale to dark amber, glabrous except for occasional setae around the fovea and anterior to the eyes, with a dorsal, branched trident-mark (Fig. 1a) varying from nearly invisible to dark and pronounced. Abdomen dorsally and ventrally finely setose, pale to dark brown, with ill-defined, paler lines and spots which may approximate to chevrons dorso-posteriorly (Fig. 1a), but are elsewhere asymmetrical. Cribellum entire and evident in both sexes; calamistrum obvious in females, but ill defined in males.

Adult male palpal tarsus with tegular apophysis and embolus forming a conspicuous, elongated loop extending at least slightly and at most obviously beyond the distal end of the cymbium (Figs. 2a–c). Epigynal atria widely spaced, inconspicuous, with lightly sclerotized rims (Figs. 1b, 4a–d). Copulatory openings within or at the margin of the atria; usually indistinct and difficult to see. Copulatory ducts invisible or at best partially visible externally in undissected specimens, fully visible only by dissection and clearing. Copulatory ducts long and coiled, each about 5.5–13 times as long as a spermatheca according to species (Figs. 4a–d). Spermathecae in undissected specimens visible externally as blurred outlines with orientation varying between parallel and 90° to the long axis of the body (Fig. 1b).

Diagnosis.—*Iviella* is distinguished from other genera in the family by the following combination of characters: Eight eyes. Cribellate, with cribellum entire. Tarsi with trichobothria, which may be indistinct on tarsi III and IV. Anterior one-third

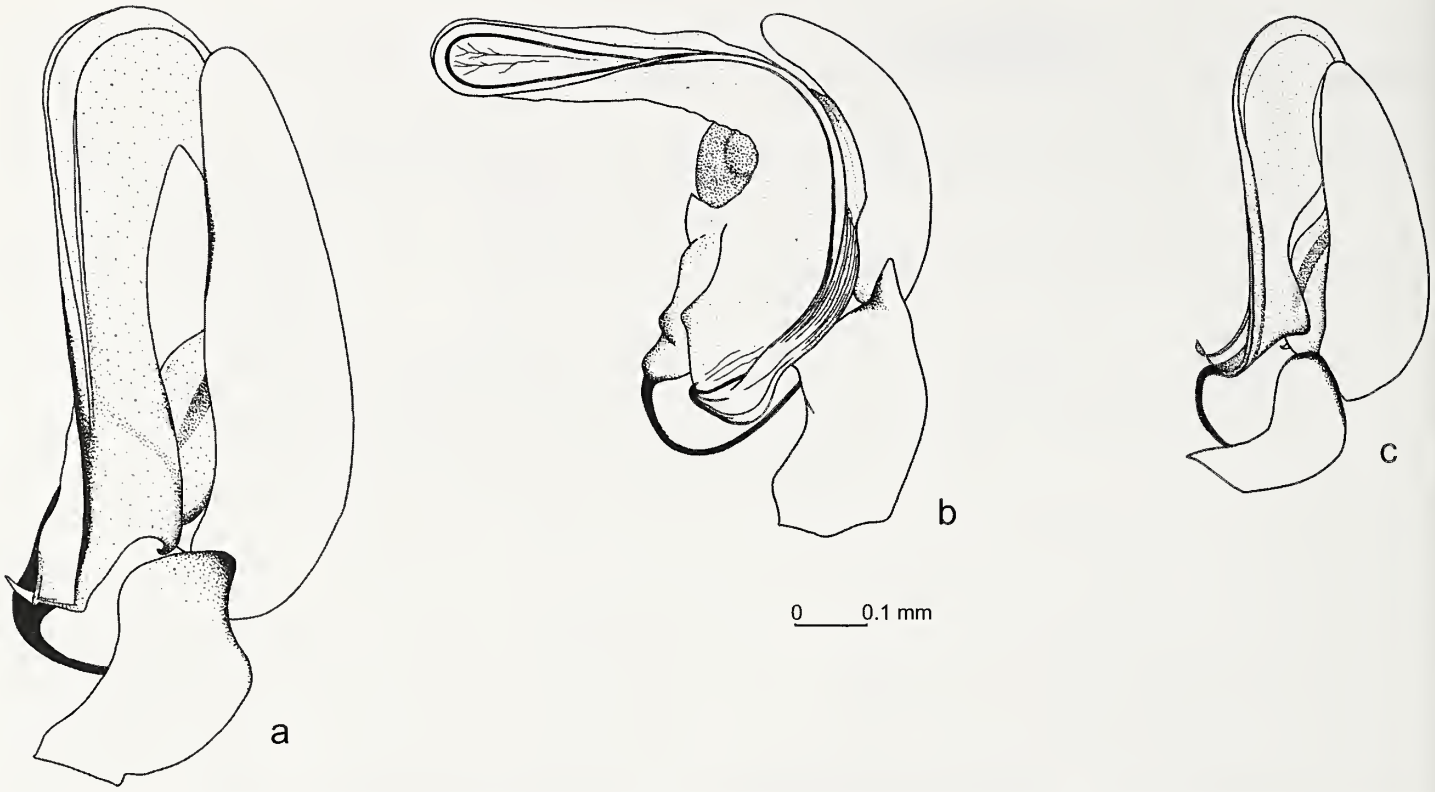


Figures 1a, b.—General external morphology of *Iviella* illustrated by two species. a. *I. ohioensis* ♀ dorsal view; b. *I. reclusa* ♀ ventral view (Saskatchewan specimen). Scale = 0.2 mm.

of carapace not elevated more than the middle one-third. Clypeus low, equal to or less than diameter of the anterior lateral eyes. Retro-margin of cheliceral fang furrow with 3 or 4 teeth. Tegular apophysis of male palpal tarsus extending beyond the distal margin of the cymbium by 20–100% of the length of the cymbium, and with proximal end not an obvious loose coil. Copulatory ducts of female long and coiled, each at least five times the length of a spermatheca.

KEY TO SPECIES OF *IVIELLA*

1. Female 2
   Male 4
2. Spermathecae lying approximately 90° to long axis of body (Fig. 4b) ..... *I. ohioensis*
   Spermathecae approximately parallel (Fig. 4c) or at 45° to long axis of body (Fig. 4a) 3
3. Spermathecae approximately parallel to the long axis of body (Fig. 4c); smaller species, overall length about 1.7–2.1 mm .... *I. reclusa*
   Spermathecae oriented between about 45° and sub-parallel to long axis of body (Fig. 4a); larger species, overall length about 2.8–3.8 mm ..... *I. newfoundlandensis*
4. Tegular apophysis about twice as long as cymbium and bent through about 90° between proximal and distal ends (Fig. 2b) ... *I. ohioensis*
   Tegular apophysis not twice as long as cymbium and not bent through 90° between proximal and distal ends (Figs. 2a, 2c) 5
5. Retrolateral tibial apophysis smoothly rounded (Fig. 3c); smaller species, overall length about 1.8–2.4 mm ..... *I. reclusa*
   Retrolateral tibial apophysis bluntly pointed (Fig. 3a); larger species, overall length about 2.8–3.4 mm .... *I. newfoundlandensis*



Figures 2a–c.—Male *Iviella* palpal tarsi, retrolateral views. a. *I. newfoundlandensis* ♂; b. *I. ohioensis* ♂; c. *I. rechusa* ♂ (Saskatchewan specimen). Scale = 0.1 mm.

Iviella ohioensis (Chamberlin & Ivie 1935)
Figs. 1a, 2b, 3b, 4b.

Argenna ohioensis Chamberlin and Ivie 1935:26, pl.12, figs. 93, 94♂ (but not fig. 92 as stated on p. 26); Bonnet 1955:665.

?*Tricholathys ohioensis* Chamberlin 1948:17 (Note: in this paper Chamberlin refers to *ohioensis* while describing the new species *Tricholathys saltona*: "... conductor and embolus well developed but less so than in *ohioensis*...". Whether he intended *ohioensis* to be included under *Tricholathys* is not clear. However, Platnick (2009) includes this reference as *Tricholathys ohioensis*); Roewer 1954: 1335; Chamberlin and Gertsch 1958:24, pl. 2, figs. 6, 8 ♂, fig. 7♀; Kaston 1976:58, figs. 69♂, 70♀ (illustrations after Chamberlin and Gertsch 1958).

Iviella ohioensis Lehtinen 1967:241; Bennett 2005:99, figs. 25.41♂, 25.42♀.

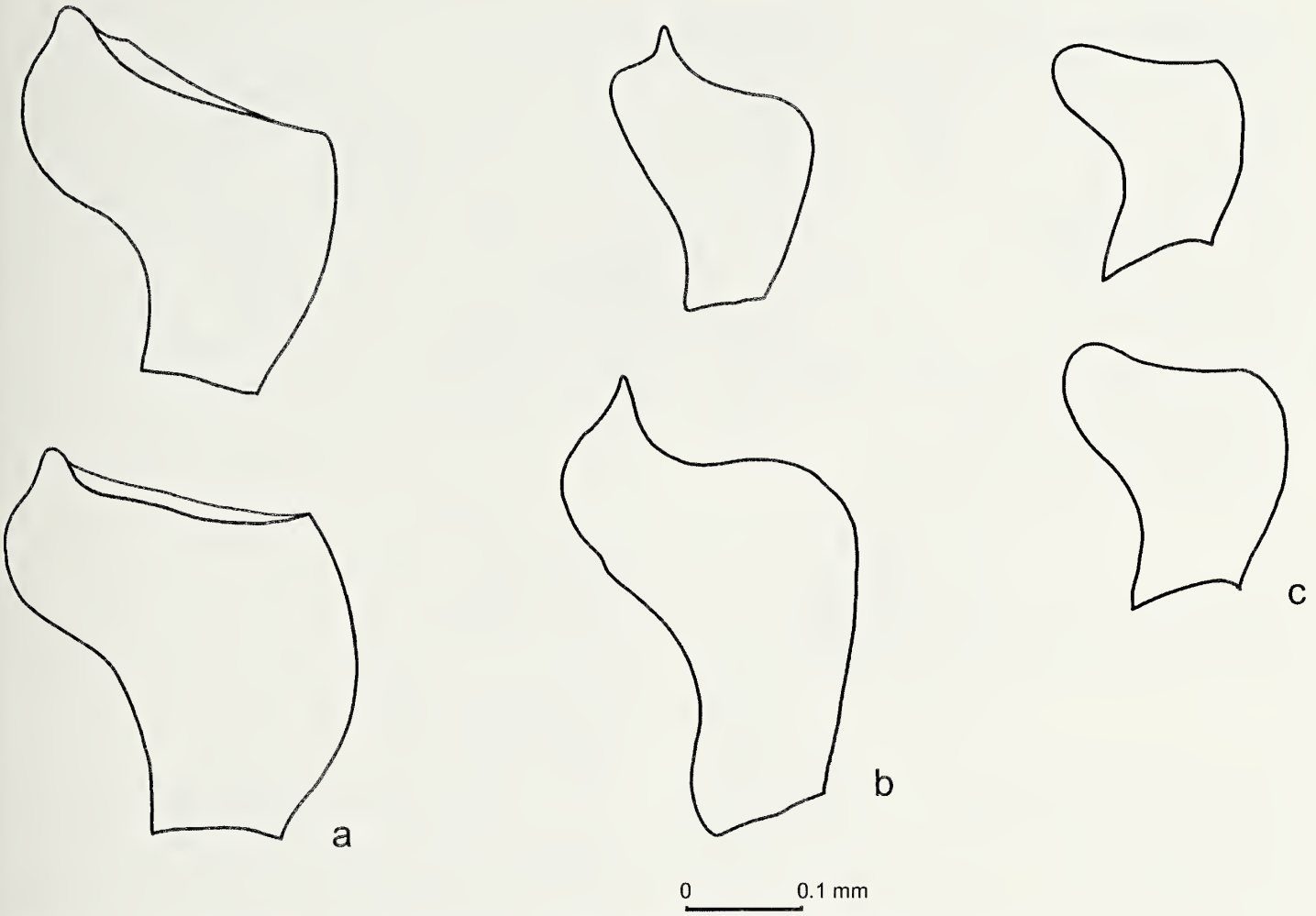
Description.—General characters as for the genus. Male (n = 6): overall length 1.72–2.25 mm; carapace width 0.622–0.824 mm; cymbium length 0.385–0.476 mm. Tegular apophysis extending beyond distal end of cymbium by approximately the length of the cymbium. Tegular apophysis bent through about 90° between proximal and distal ends (Fig. 2b). Palpal tibia with characteristic shape in dorsal view with a sharply pointed retrolateral tibial apophysis (Fig. 3b). Female (n = 4): overall length 1.96–2.14 mm; carapace width 0.622–0.659 mm. Spermathecae 0.052–0.065 mm wide by 0.081–0.112 mm long. Spermathecae with long axes approximately 90° to long axis of body (Fig. 4b). Copulatory duct about 12–13 times as long as the length of a spermatheca. Copulatory openings and ducts as in Fig. 4b.

Distribution.—USA: Ohio, Nebraska, West Virginia, New Jersey and Kansas (Fig. 5).

Habitat.—The habitat appears to vary: prairie, mixed oak-hardwood and parkland. The nature and placement of the web is unknown.

Material examined.—In this section and similar sections elsewhere the lack of uniformity of style in the presentation of data from different vials and collections is because we have in all cases quoted the original vial labels verbatim. The only exception to this policy is where we have added the location of the collection (see abbreviations above) where specimens are housed. USA: Holotype: 39N, 83W, *Ohio*, Columbus, 1 May 1933, (W. M. Barrows) 1♂ AMNH. Paratype: 39N, 83W, (label in microvial: 39Bd28) 1♂ AMNH. *Kansas*, Sallyards, 37.47N, 96.30W, 26 April 1962, 1♀(W. Ivie) AMNH. *Nebraska*, Lincoln, prairie pitfall, 6 May 1939, 1♂ (E. Fichter) AMNH. Nebraska, 9 mi NW Lincoln, pitfalls on prairie, 40N, 96W, 3 June 1939, 2♀ (E. Fichter) AMNH. *New Jersey*, Ramsey, July1939, 1♀ (W.J. Gertsch) AMNH. *Ohio*, Franklin Co., Sharon Woods Metropolitan Park 0.8 km south of Park Road Entrance sta 18, 8–15 May 1973 1♂ (A.J. Penniman) AMNH. Ohio, Franklin Co., Sharon Woods Metropolitan Park 0.8 km S of Park Road Entrance sta 19, 8–15 May 1973 1♂ (A.J. Penniman) AMNH. *West Virginia*, Preston Co., WV University Forest Chestnut Ridge, Mixed oak-hardwood, Stand 7 plot 20, pitfall trap, 1–8 May 1990, 1♂ (D.T. Jennings) AMNH.

Diagnosis.—Males of *I. ohioensis* are distinguished from those of both *I. rechusa* and *I. newfoundlandensis* by the 90° bend of the tegular apophysis (Fig. 2b) and the more sharply pointed retrolateral tibial apophysis (Fig. 3b). Female *I.*



Figures 3a–c.—Male *Iviella* palpal tibia showing retrolateral tibial apophysis (larger and smaller examples shown for each species to illustrate variation). a. *I. newfoundlandensis* ♂; b. *I. ohioensis* ♂; c. *I. reclusa* ♂ (Saskatchewan specimen). Scale = 0.1 mm.

ohioensis are distinguished from both *I. reclusa* and *I. newfoundlandensis* by the spermathecae lying with their long axes approximately 90° to the long axis of body (Fig. 4b).

Iviella reclusa (Gertsch and Ivie 1936)
Figs. 1b, 2c, 3c, 4c, 4d.

Argennina reclusa Gertsch & Ivie 1936:3, figs. 19, 20♀; Chamberlin 1948:6; Roewer 1954:1335; Bonnet 1955:667.

Tricholathys reclusa Chamberlin & Gertsch 1958:24, pl. 2, fig. 9♀.

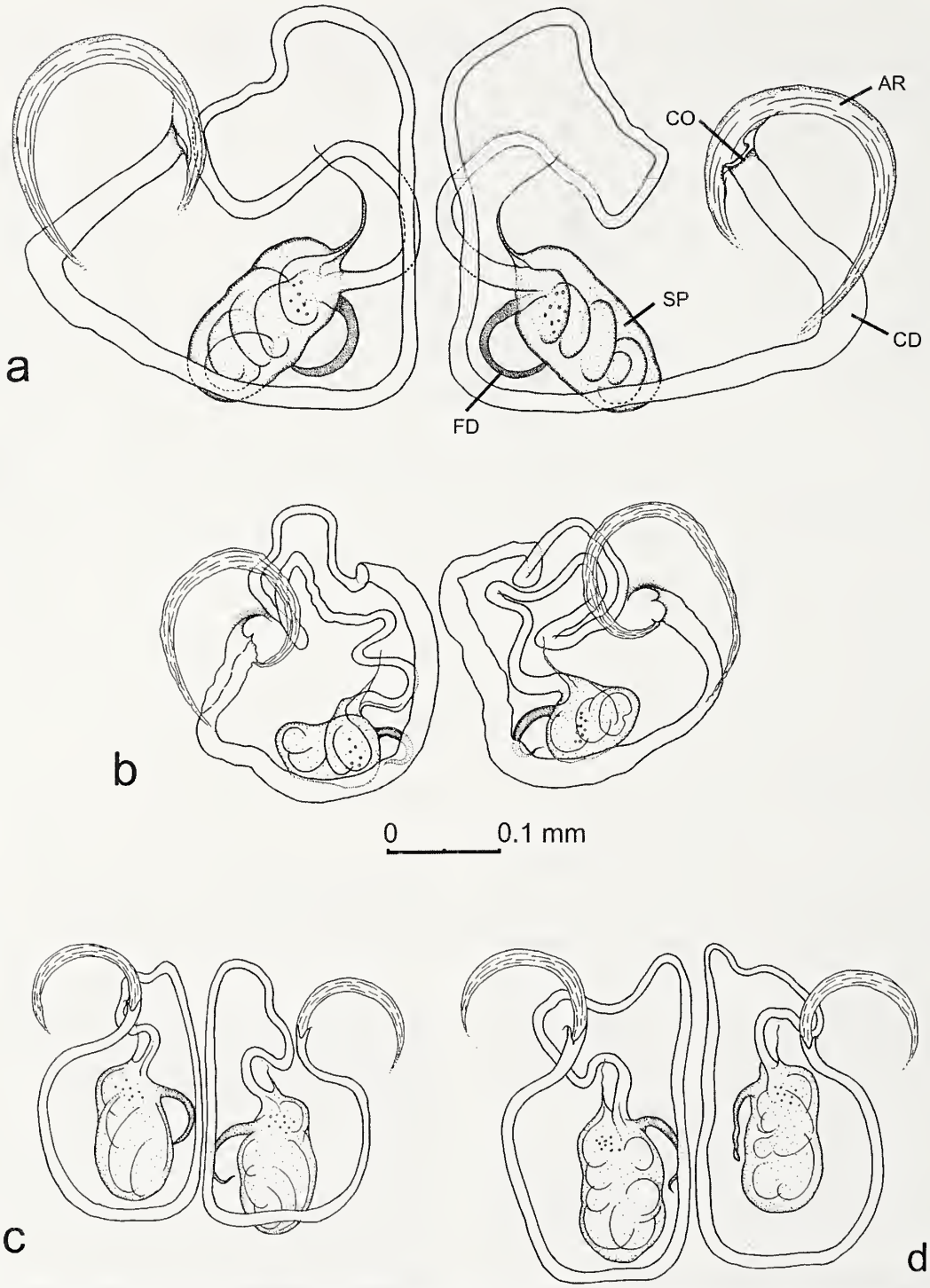
Iviella reclusa Lehtinen 1967:241; Bennett 2005:99.

Description.—General characters as for the genus. Male (n = 17; all Saskatchewan specimens): overall length 1.81–2.62 mm; carapace width 0.622–0.952 mm; cymbium length 0.439–0.540 mm. Tegular apophysis extending beyond distal end of cymbium by approximately 15–20% of length of cymbium, and not bent between proximal and distal ends (Fig. 2c). Palpal tibia with characteristic shape in dorsal view with a smoothly rounded retrolateral tibial apophysis (Fig. 3c). Female (n = 20; 3 USA specimens, 17 Saskatchewan specimens): overall length 1.68–2.51 mm; carapace width 0.531–0.732 mm. Spermathecae 0.065–0.075 mm wide by 0.112–0.130 mm long, with long axes approximately parallel to long axis of body (Figs. 4c, 4d). Copulatory duct about 5.5–7 times as long as the length of a spermatheca. Copulatory openings and ducts as in Figs. 4c, 4d.

Distribution.—USA: Utah, Arizona; Canada: Saskatchewan (Fig. 5).

Habitat.—Other than the geographical location, we have no information about the habitat of the USA specimens. The Saskatchewan specimens are from various types of grassland: prairie and grazed prairie, crested wheatgrass, and a flooded grassy area. The nature and placement of the web is unknown.

Material examined.—USA: Holotype: 38N, 112W, *Uta*h, 10 mi N Cove Fort, 15 April 1933 1♀ (W. Ivie) AMNH. *Arizon*a, 20 mi S Flagstaff, Oak Creek Canyon, 12 April 1935, 2♀ (W. Ivie) AMNH. Note: Chamberlin & Gertsch (1958) reported an immature male: Arizona, 4 mi SE Ruby, 5 Sep 1950 (W.J. Gertsch) AMNH. They called it a penultimate stage male, probably *I. reclusa*. We examined this specimen and do not think it is in the penultimate stage because no internal details of the swollen palps are visible externally as is the case with late-stage males of other species of *Iviella*. Therefore, although this specimen might be an immature *I. reclusa*, it will not be referred to further because it is impossible to be certain of its specific identity. CANADA:



Figures 4a–d.—Female *Iviella* epigyna, spermathecae and associated ducts (drawn from dissected, cleared and mounted parts of specimens with consequent risk of distortion). a. *I. newfoundlandensis* ♀; b. *I. ohioensis* ♀; c. *I. reclusa*♀ (holotype, USA); d. *I. reclusa*♀ (Saskatchewan specimen). Scale = 0.1mm. AR = atrial rim, lightly sclerotized; CO = copulatory opening; CD = copulatory duct; FD = fertilization duct; SP = spermatheca.

Saskatchewan, 10 km S Cadillac, Auvergne prairie, pittraps, 21–27 June1995, 1♂ (J. Pepper) DB. Saskatchewan, Grasslands National Park, 49°10.7′N, 107°24.4′W, crested wheatgrass, pittraps, 1–27 July 1996, 8♀ 11♂ (A. T. Finnamore) (label says 9♀, but only 8♀ in vial) 3♀ RMNL, remainder DB. Saskatchewan, Grasslands National Park, 49°8.4′N, 107°35.8′W, crested wheatgrass, pittraps, 5–13 July 1996, 2♀ (A.T. Finnamore) DB. Saskatchewan, Grasslands National Park, 49°7.9′N, 107°36.0′W, crested wheatgrass, pittraps, 5–19 July1996, 6♀4♂ (A. T. Finnamore) 1♂1♀ CNC, 1♂ RMNL, 1♂1♀ AMNH, remainder DB. Saskatchewan, Grasslands National Park, 49°11.4′N, 107°22.6′W, grazed prairie, pittraps, 11–14 July

Figure 5.—Collection localities of *Iviella* species. (Map courtesy of P. Paquin.)

1996, 1♂ (A.T. Finnamore) DB. Saskatchewan, Val Marie, flooded grassy area, 30 May1985, 1♀ (K. Roney) DB.

Diagnosis.—Males of *I. reclusa* are distinguished from those of *I. ohioensis* by the straight tegular apophysis (i.e., not bent through 90°) (Fig. 2c) and the smoothly rounded retrolateral tibial apophysis (Fig. 3c). They are distinguished from males of *I. newfoundlandensis* by the smoothly rounded retrolateral tibial apophysis (Fig. 3c) and smaller size: shorter overall, with narrower carapace and shorter cymbium (Table 1). Female *I. reclusa* are distinguished from both *I. ohioensis* and *I. newfoundlandensis* by the spermathecae lying with their long axes approximately parallel to the long axis of body (Figs. 4c, d).

Iviella newfoundlandensis new species
Figs. 2a, 3a, 4a.

Iviella sp.: Bennett 2005:99, fig. 25.43♀; Pickavance & Dondale 2005:258.

Types.—All types: CANADA: *Newfoundland*, Point Riche, NE of lighthouse, upper terrace (50°42.2′N, 57°24.1′W), rocky *Empetrum* barrens, hand caught, collector J.R. Pickavance. Holotype and female paratype: 19 August 2000, deposited CNC. Male and female paratype: 19 August 2000, deposited AMNH. Male and female paratype: ♂ 19 August 2000, ♀ 20 August 2002, deposited RMNL.

Etymology.—Named for the island where it was discovered and for the respect and affection the authors feel for the people of that island.

Description.—General characters as for the genus. Male (n = 25): overall length 2.89–3.41 mm; carapace width 1.01–1.21 mm; cymbium length 0.677–0.824 mm. Tegular apophysis extending beyond the distal end of the cymbium by about 10–15% of the length of the cymbium; not bent between proximal and distal ends (Fig. 2a). Palpal tibia with characteristic shape in dorsal view with a bluntly pointed retrolateral tibial

Table 1.—Comparative measurements of *Iviella* species (USA and Saskatchewan , Canada specimens of *I. reclusa* kept separate for future reference). All measurements in mm. OVL = overall length; CW = carapace width; SPW = spermatheca width; SPL = spermatheca length; CBL = cymbium length.

Females	OVL	CW	SPW	SPL
I. newfoundlandensis	2.86–3.72	0.952–1.14	0.089–0.109	0.169–0.195
I. ohioensis	1.96–2.14	0.622–0.659	0.052–0.065	0.081–0.112
I. reclusa (USA)	1.76–2.08	0.531–0.640	0.074–0.075	0.120–0.124
I. reclusa (Sask.)	1.68–2.51	0.531–0.732	0.065–0.075	0.112–0.130

Males	OVL	CW	CBL
I. newfoundlandensis	2.89–3.41	1.01–1.21	0.677–0.824
I. ohioensis	1.72–2.25	0.622–0.824	0.385–0.476
I. reclusa (Sask.)	1.81–2.62	0.622–0.952	0.439–0.540

apophysis (Fig. 3a). Female (n = 25): overall length 2.86–3.72 mm; carapace width 0.952–1.14 mm. Spermathecae 0.089–0.109 mm wide by 0.169–0.195 mm long with long axes between about 45° to sub-parallel to long axis of body (Fig. 4a). Copulatory duct about 8.5–9.5 times as long as the length of a spermatheca. Copulatory openings and ducts as in Fig. 4a.

Distribution.—Canada: Newfoundland, Northern Peninsula (Fig. 5).

Habitat.—*Empetrum* barrens with stones and rocks of various sizes, particularly but not exclusively near the coast. In areas where the species occurs it is easily found by turning over stones. Smaller stones (e.g., 10–20 cm) will typically harbor only one spider, while larger stones (e. g., 30–50 cm) may have two or more. The presence of a specimen is indicated by a small, gauzy web, and close inspection often reveals an inconspicuous spider at one side. The web may be either on the undersurface of the turned-over stone or (more often) slung between smaller stones beneath.

Material examined.—CANADA: *Newfoundland* (all collections except where noted caught by hand by Pickavance): Point Riche, NE of lighthouse, upper terrace (50°42.2′N, 57°24.1′W), rocky *Empetrum* barrens: 24 Jul 1998, 5♀; 17 Aug 1998, 1♂; 28 Jun 1999, 1♀; 2 Aug 1999, 15♀; 25 Jun 2000, 3♀; 15 Jul 2000, 3♀; 24 Jul 2000, 4♀; 29 Jul 2000, 16♀; 12 Aug 2000, 17♀1♂; 18 Aug 2002, 17♀5♂ RMNL. 19 Aug 2000, 44♀18♂: 1♂CNC; 1♂AMNH; 1♂DB; 2♀CNC; 2♀AMNH; 1♀DB, remainder RMNL. 20 Aug 2002, 14♀3♂: 1♀DB, remainder RMNL. Point Riche, SE of lighthouse, lower coastal terrace (50°41.8′N, 57°23.3′W), rocky *Empetrum* barrens: 2 Aug 1999, 1♀; 4 Aug 2000, 1♀; 8 Jul 2004, 61♀ RMNL. Point Riche, Phillips Garden (50°42.9′N, 57°23.1′W), rocky *Empetrum* at back of beach, 5 Jul 2004, 4♀1♂ RMNL. Table Point (50°22.5′N, 57°31.6′W), coastal rocky *Empetrum* barrens: 30 Sep 1998, 1♂; 16 Aug 1999, 1♀ RMNL. Eddies Cove East, 17 km inland (east) from the community (51°22.7′N, 56°13.1′W), rocky *Empetrum* barrens, 21 Jun 2000, 1♀ RMNL. Burnt Cape (51°22.7′N, 56°13.1′W), rocky *Empetrum* barrens, pitfall traps, Aug 2003, 1♀5♂ (A.-M. Hynes) RMNL.

Diagnosis.—Males of *I. newfoundlandensis* are distinguished from those of *I. ohioensis* by the straight tegular apophysis (i.e., not bent through 90°) (Fig. 2a) and the bluntly pointed retrolateral tibial apophysis (Fig. 3a). They are distinguished from males of *I. reclusa* by the bluntly pointed retrolateral tibial apophysis (Fig. 3a) and larger size: longer overall, with wider carapace and longer cymbium (Table 1). Female *I. newfoundlandensis* are distinguished from both *I. ohioensis* and *I.reclusa* by the spermathecae lying with long axes between about 45° to sub-parallel to long axis of body (Fig. 4a).

DISCUSSION

This paper hinges on our assignation of Saskatchewan *Iviella* males to *I. reclusa* because of their close association with female *Iviella*, which in turn are considered conspecific with female *I. reclusa* from the USA. The females are considered conspecific because of the similarity in shape, size and orientation of the spermathecae and copulatory ducts (Figs. 4c, 4d; Table 1). However, there are rare cases in the Araneae where males of closely related species are distinguishable but the females are not. For example, males of *Pirata insularis* Emerton 1885 and *P. cantralli* Wallace & Exline 1978 (Lycosidae) are morphologically distinguishable but the females are not and can only be assigned to species by association with the male (Dondale & Redner 1990). There is therefore the possibility that in future *Iviella* males will be found in close association with females from one of the known USA localities (Arizona and Utah), which will be different from the Saskatchewan males. In this case the Saskatchewan specimens will need to be described as a separate, new species (hence distinguishing between USA and Saskatchewan specimens in the figures and keeping the data separate in Table 1).

Although the new species *I. newfoundlandensis* is known only from Newfoundland, we do not consider this a case of endemic speciation because of the recent (geologically speaking) glaciation of the Island of Newfoundland (Dyke et al. 2002). Rather, we think this is simply a case of a boreal or subarctic species that possibly has a wider distribution, but has been overlooked elsewhere. Part of why this species has not been found previously may be because of its reluctance to fall into pitfall traps. The senior author has regularly caught this species by hand in close proximity to pitfalls in which not a single specimen was taken over a period of 10 weeks. The six Newfoundland specimens found in a pitfall are very much the inexplicable exception to a general rule.

This study was made difficult by the lack of specimens for dissection and comparison. Before this study, no male and only three female *I. reclusa* were known, and recent intensive searches of one of the two recorded USA localities of this species (Oak Creek Canyon, Arizona), undertaken specifically for this study, failed to reveal further specimens. There are only 10 known specimens of *I. ohioensis*. The new species from Newfoundland described here is known from only a small number of localities, although it can usually be found if a specific habitat is searched.

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Ground-living spider assemblages from Mediterranean habitats under different management conditions

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Abstract. Ground-living spiders of different habitats in the Cabañeros National Park, central Spain, each under different management conditions, were studied to characterize their community richness and composition. Five different habitats were selected: Mediterranean forest, abandoned pine plantations and three kinds of *dehesas* or meadows (differing in their understory management). In three sampling periods, during two springs and one in fall (2001–2002), a total of 1,152 pitfall traps were deployed in five different habitats. A total of 3,801 adult spiders, representing 105 species from 24 families were collected, among which 13 are considered endemic for the Iberian Peninsula. Correspondence analysis and indicator species analysis showed that spider richness and assemblages differed considerably among the different habitats. The scrub *dehesa* had the highest ground-living spider richness. Twenty-three indicator species were identified for the different habitats, of which four are considered endemic for the Iberian Peninsula. Gnaphosidae have a high potential as indicators of habitat quality.

Keywords: Araneae, *dehesa*, endemic, Iberian Peninsula, indicator species

Ground-living spider (Araneae) assemblages are influenced by environmental heterogeneity and land use (Grill et al. 2005). Spiders are ubiquitous predators in terrestrial ecosystems and generalist feeders that primarily attack insects; therefore, these arthropods play a main role in terrestrial population control (Wise 1993).

The Mediterranean region exhibits high biological richness, apparently due to its diverse evolutionary pathways and in situ speciation processes (Blondel & Aronson 1999). This region has had to bear the brunt of intensive human activity: woodcutting, land clearing for cultivation and settlement, grazing, fire, and in recent years, pollution, pesticides and other biocide applications. These activities have all left their footprints on the ever-changing Mediterranean landscape (Perevolotsky & Seligman 1998). They have led to a characteristic landscape with a strong cultural component, resulting in a "successful" integrated, semi-natural system that has been maintained through time (Pineda 2001). The ensuing heterogeneous landscape has elements of diverse ecological maturity, ranging from forests to crops (Médail & Quézel 1999; Ramírez-Sanz et al. 2000; Schmitz et al. 2003). Long-term effects of land use by human communities and the impact of their livestock on the vegetation and fauna have been emphasized by Blondel and Aronson (1999). The Iberian Peninsula contains 1,500,000–3,400,000 ha of wooded *dehesa*, mainly in the southwest. Among exploitation systems, the *dehesa*, derived from the original Mediterranean forest landscape use (Díaz et al. 2003a), has been exploited throughout history as a diverse resource, providing not only pasture for livestock but also building material, fuel, food, spices, and medicines (Perevolotsky & Seligman 1998). In central and southwestern Spain, the *dehesa* is an ancient wood-pasture with oak *Quercus* spp. trees, a mixture of cereal cultivation, open grasslands and Mediterranean scrub beneath the tree canopy (Díaz & Pulido 1995). Agricultural and pastoral uses affect the structure and diversity of the *dehesa* (Pineda & Peco 1987; Joffre et al. 1988; Díaz et al. 2003a).

Mediterranean forests, together with the *dehesas*, have high biodiversity levels and were consequently included as protected habitats on the EU Habitat Directive (92/43/CEE). This is true for several taxa across the range of environmental conditions and geographical scales (Díaz & Pulido 1995; Jiménez-Valverde et al. 2004).

World conservation priorities are based on biodiversity studies focused on relatively well known groups of organisms, such as vascular plants and vertebrates: mammals, birds, reptiles and amphibians (Myers et al. 2000). However, fewer systematic and biogeographical data are available for hyperdiverse" groups such as spiders (Colwell & Coddington 1994), but which nevertheless need to be included in conservation policies (Kremen et al. 1993). Taking into consideration the lack of proper systematie surveys from many regions, Coddington & Levi (1991) estimate that 25–75% of the spider species are yet to be discovered. Within this range Melic (2001) estimates that ca 25% of spiders in the Iberian Peninsula are not yet described.

Spiders react mainly to habitat heterogeneity and land-use type, their richness is mainly determined by humidity and vegetation structure, reflecting the differing hunting strategies of ground-living and web-building spiders (Grill et al. 2005). Significant declines in spider and other arthropod diversity and abundance occur with increasing logging and decreasing herb cover (Willett 2001). A well-known local scale relationship between spider diversity and habitat structure suggests that spiders are a suitable group to test how communities change under different management practices and disturbance regimes (Uetz 1990).

The present study was undertaken within the pan-European project BIOASSESS Biodiversity Assessment Tools" (http://www.nbu.ac.uk/bioassess/), whieh is aimed to develop a set of ecological indicators according to a land-use disturbance

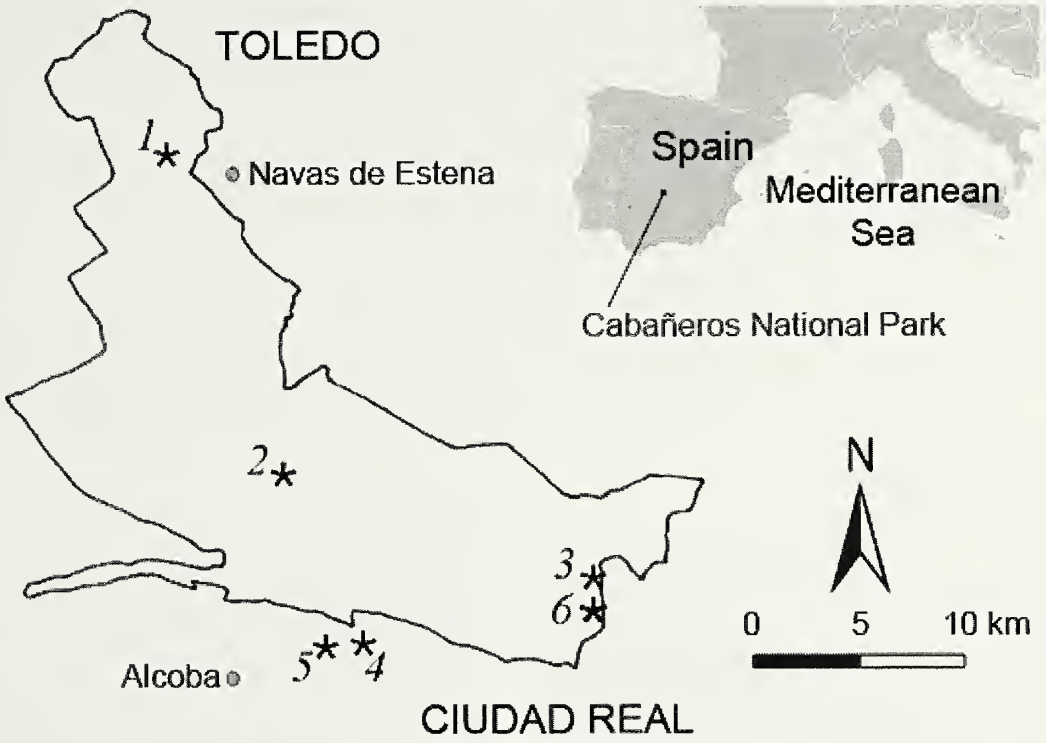

Figure 1.—Map of land units from BioAssess Project in the National Park Cabañeros, Spain.

gradient, with a significant increase of open landscapes (e.g., pastures and arable crops) in comparison to an old-growth woodland, including groups such as vascular plants (Fédoroff et al. 2005), lichens (Bergamini et al 2005), carabid beetles (Silva et al. 2008) and colembollans (Sousa et al. 2004, 2006; Ponge et al. 2003, 2006). This work aims to describe and compare the richness and species composition of ground-living spiders in several habitats of the Cabañeros National Park under different management conditions. Indicator species for each habitat are identified as well.

METHODS

Study area.—The study area was located in Cabañeros National Park, between northwestern Ciudad Real and southeastern Toledo provinces (39°23′47″N, 04°29′14″W of Spain and in surrounding private properties. The Park, situated in the "Montes de Toledo", is an area with typical Mediterranean forest in the center of the Iberian Peninsula, bordered by the Estena and Bullaque rivers (Fig. 1). Altitudes range from 620 to 1448 m above sea level, giving it a Mesomediterranean bioclimatic stage, with a dry to subhumid tendency (mixed oak forests of *Quercus pyrenaica*, *Q. suber*, and *Q. ilex* ssp. *ballota*), characterized by dry and hot summers. The Park contains *dehesas*, savannah-like landscapes of grassland and scattered trees, mainly *Quercus* ssp. Average annual temperature and precipitation are 14.9°C and 607 mm, respectively. The area (41,000 ha) is highly representative of the vegetation, fauna and land uses in the southern high plain of the Iberian Peninsula.

In each European country participating in the pan-European project BIOASSESS, six Land Units, one square kilometer each, were intuitively selected on the basis of regional knowledge and aerial photographs, taking into account the distribution of forested areas, meadows and agricultural crops (for further information see Sousa et al. 2006). In this study five habitats were clearly identified and selected according to their different management practices along a gradient: from forest habitat units to agriculture-dominated ones (Table 1). Forest habitats differed in the heterogeneity of strata and in the composition of dominant trees and understory vegetation, whereas *dehesas* differed in grass layers and scrub density. The following habitat types were surveyed:

1. *Mediterranean forest (MF)*: A shaded slope located inside the Park extending 5 km^2 along the Estena River. Soil shows poorly developed horizons with superficial litter. This habitat is characterized by a mosaic of evergreen oaks, holly oaks (*Q. ilex* ssp. *ballota*), corks (*Q. suber*); deciduous oaks (*Q. faginea* ssp. *broteroi* and *Q. pyrenaica*) and strawberry trees (*Arbutus unedo*). Its understory is heterogeneous, composed mainly of sclerophyllous shrubs such as *Cistus ladanifer*, *Erica arborea*, *E. scoparia*, and *Phyllirea angustifolia*. This forest was probably used in the past for timber and charcoal production. Currently, the area is used for the extraction of wood by pollarding and coppicing (around 0.6 m^3/ha/yr). Cork extraction is limited to the largest individuals every 10 yr. Scrub removal is sometimes done for fire prevention. Goat grazing is allowed 100 days/yr, with an animal density lower than one goat per hectare.
2. *Old-pine plantation (OP)*: a 40-yr-old *Pinus pinaster* forest practically undisturbed (no commercial exploitation) for the last 15 yr that extends over 48 km^2 inside the Park. Its understory is composed of common shrub species of the Mediterranean woodland: *E. arborea*, *C. laurifolius*, *C. ladanifer*, and *Lavandula stoechas*. Com-

Table 1.—Characteristics of the five habitats and number of sampling plots used for ground-living spiders sampling.

		Land units[a]						Habitat characteristics				
	Sampled area (ha)	1	2	3	4	5	6	Vegetational layers[b]	Trees	Scrub	Grass	Management
Mediterranean forest	100	36						3	Abundant	Medium	Medium	Protected area
Old-pine plantation	100		42					3	Abundant	Few	Few	Protected area, without exploitation
Scrub *dehesa*	144			21	10	14	7	3	Medium	Abundant	Few	Protected area, lightly grazed
Grazed *dehesa*	144			8	9	16	14	2	Few-scattered	Absent	Abundant	Extensive grazing
Cultivated *dehesa*	112			8	17	11	12	1[c] or 2	Few-scattered	Absent	Absent or crop	Agricultural traditional land

[a] Land Units from Bioassess Project
[b] number of strata (trees, scrub or grass) presented in each habitat
[c] absence of cultivation or ploughing.

mon forest management practices consist of low-shrub removal and firebreak areas.

3. *Scrub dehesa (SD)*: These are lightly grazed habitats of typical Mediterranean scrublands and correspond to 24% of the total area under study (Jiménez-Valverde et al. 2004). They are Open forests consist of sparse holly oak and *Q. faginea* trees of medium height with a dense and diverse understory composed mainly of *C. ladanifer*, *A. unedo*, *Erica* spp., and *P. angustifolia*. they have abundant litter and soils, with a well-developed A-horizon.
4. *Grazed dehesa (GD)*: These are pastures or grassland habitats with low holly oak density, whose open habitats are grazed by domestic (from farms) and wild herbivores (in the Park); they make up 24% of the total area under study (Jiménez-Valverde et al. 2004). The coverage is characterized by a large area of short grass at ground level and a low area of shrubs. The area is also used for cereal cultivation and cork removal.
5. *Cultivated dehesa (CD)*: These are located in privately owned farms in the neighborhood of the Park. These homogeneous habitats, characterized by large areas of bare ground, have very scattered trees and are used intensely for arable crops. Cereal shifting cultivation is a common agricultural management practise, and it corresponds to 18% of the total area under study (Jiménez-Valverde et al. 2004). Ploughing is carried out yearly in late autumn and early spring, but sowing is performed every two years.

Sampling method.—Ground-living spiders were sampled in each Land Unit in which a grid of 16 sampling plots was established, all sampling points 200 m apart. Ground-living spiders were sampled from each sampling point using four unbaited pitfall traps (8 cm diameter × 10.5 cm depth) placed in a 2 × 2 quadrant, each pitfall 4 m apart (Silva et al. 2008). Traps were partly filled with propylene glycol (20%), and large stones were placed above them to minimize both flooding and damage from wild animals.

There were three sampling periods: May–June and October–December 2001, with 67 sampling plots each, and April–June 2002, with 91 sampling plots. During these periods 288 sampling plots were placed, of which 225 were recovered. Sampling periods were established based on the reported times of maximum abundance of adult spiders in Spain (Barrientos 1985), For short-term sampling programs, a period from the end of May to early June is recommended for the Iberian Peninsula (Cardoso et al. 2007) and other Mediterranean ecosystems (Chatzaki et al. 1998). The spiders collected were identified using a family level key (Barrientos & Ferrández 1985) and several papers for identification at the genus and species level (see Barriga et al. 2006) and deposited in the collection of the Museo Nacional de Ciencias Naturales de Madrid (MNCN). Most of the specimens (87%) were identified to the species level, 10.5% were identified to genera level and 2% were identified only to family level. Species richness is considered as one of the paramount parameters, useful and easy to interpret, to assess the biological diversity of a particular locality (Magurran 1989).

To know if our effort sufficed to provide a thorough representation of the spider community we used EstimateS Version 8.0 (Colwell 2001) to calculate accumulation curves of observed species richness using several different estimators (Chao 1, Chao 2 and second order Jackknife). Inventory sampling completeness, defined as the percentage of species estimated to exist in the sampling plots that are actually observed, was calculated using Chao 1 estimator (Cardoso et al. 2009). Accumulation curves have been performed in STATISTICA 6 (StatSoft, Inc. 1997), using the Clench equation.

Statistical analysis.—A correspondence analysis (CA) was performed with the initial data matrix of species (variables) and sampling plots (occurrences) (Benzecri 1973) to study the relationship between the new synthetic variables (ordination analysis axis coordinates with the higher variance absorption) and the factor habitat (five levels). Species with an occurrence below 10% of the total collection (Norris 1995) were neglected and not used for the analysis, meaning that only species present in more than 22 sampling plots were used. In order to detect the species of the outmost extremes of the gradients with a good representation of quality in the first and second axes, we selected those that had highest values of absolute contributions and relative contributions (Bordons et al. 2004).

Table 2.—Estimates of total ground-living spiders and those endemic to the Iberian Peninsula for each habitat.

	MF	OP	SD	GD	CD
Richness of species	46	28	69	55	45
Abundance average	307	714	423	513	380
Endemics	12 (4)	3	14 (2)	10 (1)	5
Singletons	18 (39%)	8 (11%)	29 (42%)	20 (36%)	17 (38%)
Doubletons	6 (13%)	1 (3%)	8 (12%)	9 (16%)	7 (15%)
Chao1	67.86	42.00	113.11	75.00	63.00
Chao2	67.25	41.67	112.24	74.60	62.65
Jackknife2	75.00	42.50	116.79	86.29	72.37
Completeness[a]	68%	66%	61%	73%	71%

( ) = exclusive to each habitat.
[a] = percentage of species estimated to exist in the sampling plots that are actually observed.

We performed two separate one-way ANOVAs using the scores obtained for each sampling plot in the first two axes as dependent variables and habitat as the independent factor.

To analyse the effect of factor habitat on the richness found in each sampling plot, a one-way ANOVA was performed. We used a post-hoc LSD test to detect differences between groups and subsequently applied a multiple test significance correction based on Benjamini & Hochberg's (1995) False Discovery Rate (FDR) method. The FDR method was chosen because it is less restrictive and has stronger inference properties than conventional methods (García 2004). A graphic representation of total richness found in each habitat (total and by sampling season) was also generated.

Indicator Species Analysis (INDVAL analysis: Dufrêne & Legendre 1997) was used to detect the characteristic species of each habitat. A Monte Carlo permutation test with 9999 permutations was carried out to test the significance for each indicator value (I.V.). Statistical analyses and calculations were performed on PC-ORD 4.0 (McCune & Mefford 1999) and STATISTICA 6 (StatSoft, Inc. 1997) software.

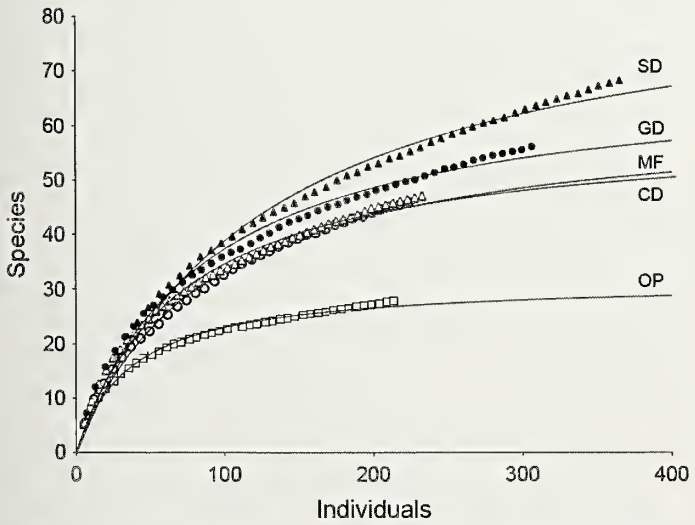

Figure 2.—Randomized accumulation curve for the five habitats; ○ Mediterranean forest (MF), □ Old-pine plantation (OP), ▲ Shrubby *dehesa* (SD), ● Grazed *dehesa* (GD), △ Cultivated *dehesa* (CD). Lines correspond to Clench equation.

RESULTS

Specimens were found in each of the 225 sampling plots. A total of 3,801 adult ground-living spiders were collected, representing 105 species and 24 families (see Appendix 1). The Gnaphosidae had the largest species representation (25 species), followed by Salticidae (13 species) and Linyphiidae (11 species). Thirteen species are cited in the Iberian Peninsula Endemic spider list (Melic 2001). The species richness and results of species richness estimators for each habitat are shown in Table 2. Species accumulation curves for each habitat indicate that species richness has not yet reached its maximum for any of the habitats (Fig. 2). The highest completeness value (73%) was found for GD and the lowest for SD (61%).

The non-parametric estimators indicate that species richness varies from 66% to 67.2% in the OP, from 68% to 68.4% in the MF, from 61% to 61.5% in the SD, from 73% to 73.7% in the GD, and from 71% to 71.8% in the CD (Table 2). Thus, the exhaustiveness of sampling in each of the five habitats is similar, so that abundances and species richness are comparable among habitats.

The highest richness and number of endemic species were found for SD (69 species, 14 endemic) with an estimate of 116.79 species (second-order Jackknife, Table 2). The lowest richness was found for OP (28 species, 3 endemic) with an estimate of 42.5 species (second-order Jackknife). Species richness dropped in the autumn. The forest habitats, MF and OP, showed minor differences in species richness between seasons, while the *dehesa*-type habitats (SD, GD and CD) showed the largest seasonal differences in species richness (Fig. 3). During spring, species presence was consistently above 80% of the total species sampled, even increasing to values over 90% in the *dehesas*. Few species were collected exclusively during autumn. *Xysticus robustus* was only collected in an open habitat (GD), and *Tegenaria atrica*, *Harpactocrates globifer*, *Drassodes fugax* and *Microlinyphia impigra* were collected in habitats with soils protected by several litter and vegetation layers (MF and OP).

In the CA performed on a data set comprising only the 20 most common species (those present in at least 10% of the sampling plots), the total inertia was 42%, with 14.9% and 11.7% for the first and second axes (Fig. 4). Using the sampling plot scores of the first axis, habitats differed significantly (one-way ANOVA, $F_{4,\ 215} = 88.3$, $P < 0.001$). No significant difference was found among habitats using

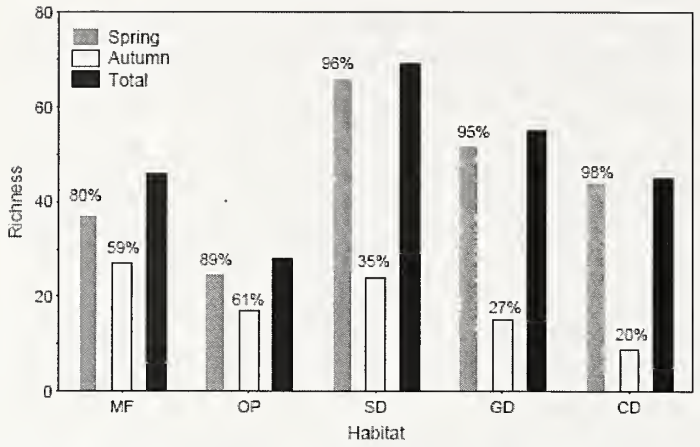

Figure 3.—Species richness of ground-living spiders during the course of the season in the different habitats. MF = Mediterranean forest, OP = Old-pine plantation, SD = Shrubby *dehesa*, GD = Grazed *dehesa*, CD = Cultivated *dehesa*. The relative proportions refer to each season with respect to the total richnness in each habitat.

scores of the second axis (ANOVA, $P > 0.05$). Post hoc tests showed significant differences among all habitats except for GD and CD. This ordination analysis showed a clear relationship between the first gradient and the habitat factor. Sampling plots corresponding to the OP habitat are clearly placed on the negative side of axis 1, while sampling plots from the CD habitat all fall furthest to the right. *Phrurolithus festivus* represents the negative extreme of the first CA axis, and *Nomisia exornata* and *Alopecosa albofasciata* account for the positive extreme. The second axis, without marked polarity ordination results, is influenced by the presence of *Zelotes aeneus* on the positive side. *Z. aeneus* and *Tegenaria feminea* were the only species found in all habitat types.

Habitat also had a significant effect on the richness of sampling plots ($F_{4,\ 91} = 5.3$, $P < 0.001$; Fig. 5). Post hoc analysis showed that GD habitat has significantly higher richness (13.1 species) than OP and CD (9.4 and 8.6 species, respectively), but is similar to SD and MF (11.7 and 11.6 species, respectively).

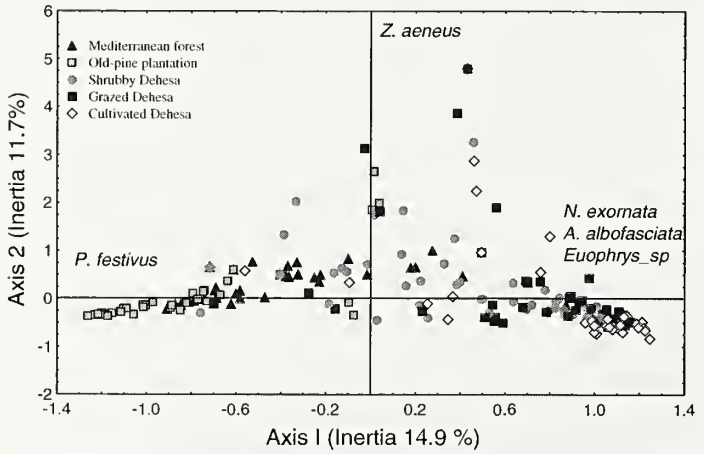

Figure 4.—Sampling plot distribution along the first two axes of the correspondence analysis. Symbols represent each of the five habitats studied. The main contributing species are listed on each end of axis.

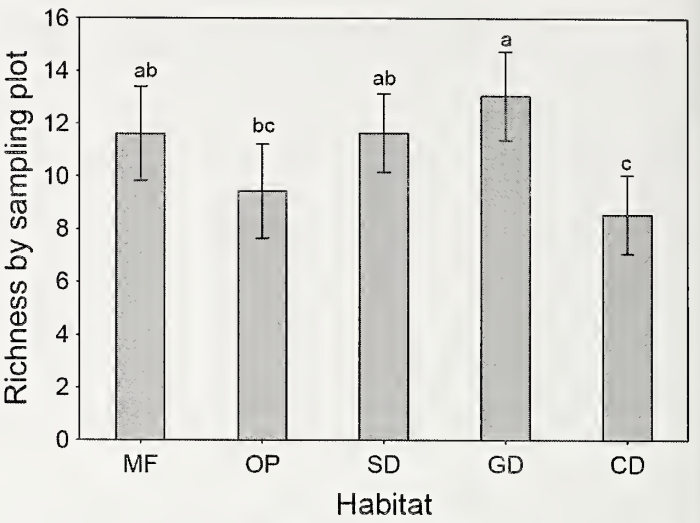

Figure 5.—Comparison of mean species richness in each habitat. Different lower case letters indicate significant difference. Whiskers denote 95% confidence intervals. Note: ANOVA was performed on logarithmically transformed species richness values.

INDVAL analysis revealed significant differences in spider assemblages among the five habitats (Table 3). All habitats included significant indicator species. OP, GD and MF had the highest numbers of indicator species (7, 5 and 5 species, respectively). The highest indicator value (I.V. = 55) corresponded to *Harpactea* sp. n. in MF. *Parachtes loboi* (I.V. = 51) was the most representative species for OP and *Nomisia exornata* for GD (I.V. = 50). The lowest number of indicator species was found for CD and SD (3 and 2 species, respectively) with I.V. < 50. Some of the indicator species are Iberian endemics, such as *Tegenaria feminea* in MF, *Zodarion alacre* in SD, and *Oecobius machadoi* in GD.

DISCUSSION

Our results show how different ground-living spider assemblages vary according to habitat type in the Cabañeros National Park. Wise (1993) indicates that habitat complexity (e.g., vegetation layers) can be the most important factor determining spider distribution. This relation is often evident in web-building spiders (Enders 1974; Greenstone 1984; Ysnel & Canard 2000); however, it has also been demonstrated for ground-living spiders (Hsieh et al. 2003; Pearce et al. 2004).

Along the first CA axis the different plots have been ordered according to their habitats (Fig. 4). The OP plots (with three vegetation layers and without exploitation) are placed at the negative extreme of this axis. This axis is characterised by a great abundance of *P. festivus* (see Appendix 1). This species, which has a Palearctic distribution, has been found in all habitats. *P. festivus* might have reached OP habitat during an initial stage, when the trees were planted, and found itself benefited by the current status of the National Park. In OP plots, *P. festivus* dominance, low species richness, absence of exclusive spiders (taking into account all samples), low number of endemic species and large number of species shared with other habitats, characterize exotic conifer plantations. Unlike Atauri et al. (2005), who claims that "where forest plantations are an alternative for conserving regional biodiversity, a landscape perspective is needed", we do not think

Table 3.—IndVal results for the five habitats. Number of localities for Iberian Peninsula, according to Morano (2005) for Spain and Cardoso (2009) for Portugal. Distribution is according to Platnick (2009). Species with most significant presence in each habitat ($P < 0.05$) and their indicator value (I.V.) are presented.

Habitat	Family	Species	I.V.	Spain	Portugal	Distribution
MF	Dysderidae	*Harpactea* sp. n.	55			
MF	Agelenidae	*Tegenaria feminea*	42	51	54 (13)	Iberian endemic. Portugal, Spain
MF	Gnaphosidae	*Micaria coarctata*	42	19	8	Mediterranean to Central Asia
MF	Liocranidae	*Mesiotelus tenuissimus*	41	9	7 (1)	Europe, North Africa, Ukraine, Turkmenistan
MF	Agelenidae	*Tegenaria picta*	33	57	27 (6)	Europe, Russia, North Africa
OP	Dysderidae	*Parachtes loboi*	51	1	0	Spain
OP	Zoropsidae	*Zoropsis media*	44	5	5 (2)	Western Mediterranean
OP	Corinnidae	*Phrurolithus festivus*	35	5	9	Palearctic
OP	Lycosidae	*Trabea cazorla*	35	4	0	Spain, Morocco, Algeria
OP	Agelenidae	*Tegenaria atrica*	31	130	24	Europe
OP	Gnaphosidae	*Zelotes thorelli*	31	17	42 (5)	Southern Europe
OP	Liocranidae	*Scotina celans*	31	13	23 (4)	Europe, Algeria, Russia
SD	Zodariidae	*Zodarion alacre*	37	15	53	Iberian endemic. Portugal, Spain
SD	Salticidae	*Aelurillus aeruginosus*	35	4	0	Mediterranean
SD	Gnaphosidae	*Drassodes rubidus*	22	4	1	Spain to Italy
GD	Gnaphosidae	*Nomisia exornata*	50	29	19 (2)	Europe to Central Asia
GD	Lycosidae	*Alopecosa albofasciata*	35	37	44 (1)	Mediterranean to Central Asia
GD	Gnaphosidae	*Drassodes lapidosus*	29	52	29 (2)	Palearctic
GD	Lycosidae	*Hogna radiata*	28	52	48 (2)	Central Europe to Central Asia, Central Africa
GD	Oecobiidae	*Oecobius machadoi*	24	3	24	Iberian endemic. Portugal, Spain
CD	Gnaphosidae	*Setaphis carmeli*	39	18	10	Mediterranean
CD	Linyphiidae	*Prinerigone vagans*	26	6	18 (1)	Old World

( ) = Number of times that has been collected in the same habitat.

this habitat needs to be protected from an arachnological standpoint. However, these ecosystems hold a certain interest because of the presence of *Parachtes loboi* (Iberian endemic), and as ideal locations for the establishment of species with wide distribution ranges, such as *Zoropsis media*, *Trabaea cazorla*, *Scotina celans* or *Tegenaria atrica*.

Mediterranean forests are highly diverse in growth forms, structure and phenology (Blondel & Aronson 1999). This particular site is located on a stony hillside, with several free boulders and pebbles that offer shelter for spiders, insects, and other animals. The lack of substrate, the thick litter layer and the steep slope that prevents effective soil retention on the rocky surfaces account for the presence of small trees with dense cover. These variables may explain the low diversity of ground-living spiders relative to meadow habitats. Cardoso et al. (2008) found 57 spider species in a similar habitat in Portugal, using the same sampling method, presenting an estimate of richness (Chao1, 67.86) very similar to that found in this study (68). It is worth noting the high number of endemic species, four of which were restricted to this particular habitat (Table 2), likely due to a low degree of human disturbance.

Although the methodology of this study does not allow us to draw strong conclusions on the effect of seasonality, we observed a noticeable seasonal drop in species richness in habitats of *dehesa*, greater than in habitats with higher forest cover, MF and OP. Microclimate conditions below the canopy, such as lower wind exposure and more humidity, and litter regulation of ground temperature are paramount in habitat choice (Wise 1993; Cole et al. 2005) and behavior (Chatzaki et al. 1998; Samu et al. 1999) overall and particularly for ground-living spiders. Hsieh et al. (2003) have reported a strong seasonal influence on spider abundance and habitat preferences. Seasonality seems to determine not only the duration of growth, development stages, age and size at sexual maturity (Higgins 2000), but also vertical movement and dispersion patterns (Duffey 1969).

SD is the richest habitat (69 species), a value similar to that found by Cardoso et al. (2009) in similar habitats in Portugal (65 species). It is also the habitat with the largest number of endemic species (14). Two species, *Drassodes rubidus* and *Typhochrestus hispaniensis*, were found exclusively in this habitat. A similar richness pattern was found for other animal groups (such as mammals and reptiles) strongly associated with scrub *dehesa* (Martín & López 2003; Díaz et al. 2003a). According to Díaz et al. (2003b), the rich environment that results from the intimate mixing of diverse habitat types (such as forests, scrub, grasslands, and crops) explains their high species richness. This mosaic in the physical environment structure allows the coexistence of species with different habitat preferences, as seen in 29 and 23 species shared with GD and CD, respectively.

GD has a form of disturbance, in this case conditioned by the same grazing activity (regulated, unregulated or normalized) during the last hundred years. The high richness (relative to other habitats in the study) is consistent with the assertion of Perevolotsky & Seligman (1998) that in sub-humid areas with a long grazing history, species diversity increases as a result of expanded grazing intensity and reaches much higher levels of diversity than in regions with a short history. Among the different *dehesa*-type habitats, grazing *dehesa* has the highest passerine bird, earthworm and ground-beetle diversity values (Marañon 1991; Díaz et al. 2003a; Silva et al. 2008).

High values of species richness were found in all *dehesa*-like habitats, including cultivated *dehesa* (CD), despite it having slightly lower values than those of the other two *dehesas*. This

difference probably results from the large number of shared species (23 species with SD and 21 species with GD) and similar colonizing strategy of these species. Sunderland and Samu (2000) investigated the influx of spiders into cultivated fields from surrounding areas. Other studies on ground-living spiders in cultivated areas show that high species richness depends partly on the landscape conformation of surrounding areas. This influence has been addressed at local and regional scales (Samu et al. 1999; Clough et al. 2005; Tscharntke et al. 2005), as well as with different crop types (Schmidt et al. 2005). The high abundance of spider species on cultivated fields must be regarded as potentially useful for the control of harmful insects (Samu et al. 1999; Sunderland & Samu 2000). Spider community structure in agro-ecosystems and grasslands changes with the latitude (Dennis et al. 2001). The northern-temperate zone of Europe is strongly dominated by small linyphiid spiders that capture tiny insects, including large numbers of aphids, in their sheet webs. A similar situation was reported by Bolduc et al. (2005) in Canada. Samples collected on CD habitats show a strong similarity in ground-living spider community composition to that reported for the northern USA (humid continental climate) where the hunter families, Oxyopidae, Salticidae, Clubionidae, Thomisidae, and Lycosidae, predominated (Nyffeler & Sunderland 2003). Additionally, specific Mediterranean families like Gnaphosidae (*Setaphis carmeli* as indicator species) or Titanoecidae were common in the study area. Linyphiid spiders (*Prinerigone vagans* as indicator species) are very common in central and northern Europe, and were also present here (CD with 3 unique species) but at a lower abundance.

Studies by Cardoso et al. (2004) in Portugal suggest the Gnaphosidae and Theridiidae as families with high potential as indicators of habitat that should be conserved in the Iberian Peninsula. These results are consistent with those obtained in this study, because among the indicator species found for each habitat in this study, there is at least one species of gnaphosid.

Mediterranean ecosystems exhibit high ground-living spider richness, especially in protected habitats and in those where human intervention is low. We have shown the existence of a strong relationship between ground-living spider communities and different management conditions. Our work suggests that some ground-living spiders (indicator species) are strongly related to specific habitats and could serve to guide future studies. Since the estimation of ground-living spiders using semi-quantitative sampling is partial, and species that may be adult at another time of the year are not accessible to the methods applied, real total species richness of the investigated area is expected to be somewhat higher (Cardoso et al. 2008).

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Appendix 1:—List of spider species collected by pitfall traps showing relative abundance in the five habits and of each season. MF = Mediterranean Forest, OP = Old-pine Plantation, SD = Scrub Dehesa, GD = Grazed Dehesa, CD = Cultivated Dehesa, s = spring, a = autumn, * = endemic Iberian species.

FAMILY / *Species*	MF-s	MF-a	OP-s	OP-a	SD-s	SD-a	GD-s	GD-a	CD-s	CD-a
AGELENIDAE										
Tegenaria atrica C.L. Koch 1843	0.33	1.5		6						
Tegenaria feminea Simon 1870*	10.83	13.5	18.33	3	2.5	9	1.33	2	1.5	2
Tegenaria picta Simon 1870	11.83	0.5	12.33		3		4			
CORINNIDAE										
Castianeira badia (Simon 1877)*		1			1			0.5		1
Phrurolinillus lisboensis Wunderlich 1995*	0.33					0.5				
Phrurolithus festivus (C.L. Koch 1835)	33.67	8.5	363	103	12.33	0.5	5		4	
Phrurolithus szilyi Herman 1879					0.5				1	
DYSDERIDAE										
Harpactocrates globifer Ferrández 1986*		3.5								
Parachtes loboi Jiménez, Barriga & Moreno 2006*		0.5	17	1						
Dysdera sp. n.		0.5			0.5		0.5			
Harpactea sp. n.	6.83	0.5			10					
GNAPHOSIDAE										
Drassodes fugax (Simon 1878)		1								
Drassodes lapidosus (Walckenaer 1802)	1.33		2		9.17		26.67		23.17	
Drassodes rubidus (Simon 1878)*					4.5	0.5				
Gnaphosa alacris Simon 1878					2		5.33		5	
Haplodrassus invalidus (O. Pickard-Cambridge 1872)	0.33	3			3	1	6.5	1	12.67	
Leptodrassus albidus Simon 1914					1				0.5	
Leptodrassus femineus (Simon 1873)							1		1.5	
Micaria coarctata (Lucas 1846)	55.67	13	23.17	8	5.83	0.5	30.5	1	1	
Nomisia celerrima Simon 1914	0.5				0.5					
Nomisia exornata (C.L. Koch 1839)					28		80		26	
Setaphis carmeli (O. Pickard-Cambridge 1872)					4.67		15.33		28.83	1
Synophosus sauvage Ovtsharenko, Levy & Platnick 1994					0.5					
Trachyzelotes holosericeus (Simon 1878)	2.17	0.5	1		14		25.67		9.5	
Trachyzelotes sp.					0.5		0.5			
Zelominor algarvensis Snazell & Murphy 1997*					2				2	
Zelotes aeneus (Simon 1878)	1.5	1	0.5	3.5	4.5	9	2.5	34.5	1.83	3
Zelotes dentatidens Simon 1914		0.5					1			
Zelotes fulvopilosus (Simon 1878)	0.67		3		4.5	1	0.5			
Zelotes manius (Simon 1878)						1	1	1	1	1
Zelotes tenuis (L. Koch 1866)					6				12.5	
Zelotes thorelli Simon 1914	23.83	6	50.17	13	26	9.5	8	7	3	4
Zelotes sp. 1.							0.33		1	
Zelotes sp. 2.	1.5									
Zelotes sp. 3.		1								
Zelotes sp. 4.					4.5		3			
HERSILIIDAE										
Hersiliola macullulata (Dufour 1831)			2				4.67	1		
LINYPHIIDAE										
Erigoninae undet. genus									1	
Erigonoplus castelkanus (O. Pickard-Cambridge 1875)*							0.5			
Frontinellina frutetorum (C.L. Koch 1834)			1.5	0.5	1				1	
Linyphiidae sp.	0.5									
Meioneta sp. 1.									1.5	
Meioneta sp. 2.							0.5			
Microlinyphia impigra (O. Pickard-Cambridge 1871)		1								
Neriene montana (Clerck 1757)							0.5			
Palludiphantes stygius (Simon 1884)	0.5									
Prinerigone vagans (Audouin 1826)									4	1
Typhochrestus hispaniensis Wunderlich 1995*						1				

Appendix 1—Continued.

FAMILY / *Species*	MF-s	MF-a	OP-s	OP-a	SD-s	SD-a	GD-s	GD-a	CD-s	CD-a
LIOCRANIDAE										
Agroeca inopina O. Pickard-Cambridge 1886				1						
Agroeca sp.	0.33									
Mesiotelus mauritanicus Simon 1909	8		4.5		6					
Mesiotelus tennissimus (L. Koch 1866)	7.33	7	5		0.5	1				
Scotina celans (Blackwall 1841)	0.83	1	6	2.5						
LYCOSIDAE										
Alopecosa albofasciata (Brullé 1832)	1.5		10.5		52.5	1	53.67		71.5	
Arctosa perita (Latreille 1799)							0.5			
Arctosa personata (L. Koch 1872)			0.5	2.5	1	2				
Hogna radiata Latreille 1817					12.83		15.33		7.33	1
Pardosa proxima (C.L. Koch 1847)			8.5	3.5	1.5		10		7.33	
Trabaea cazorla Snazell 1983			15	1.5	0.83	1	4	1		
NEMESIIDAE										
Nemesia dubia O. Pickard-Cambridge 1874		3.5	1		2.5	3.5		2		
OECOBIIDAE										
Oecobius machadoi Wunderlich 1995*					0.5	1	15.33			
Uroctea durandi (Latreille 1809)	0.33	1		0.5	0.5	2	1.5	0.5	3	
OONOPIDAE										
Oonops procerus Simon 1882*	0.33				1					
OXYOPIDAE										
Oxyopes heterophthalmus Latreille 1804					0.33					
Oxyopes nigripalpis Kulczynski 1891					0.33					
PALPIMANIDAE										
Palpimanus gibbulus Dufour 1820	0.83	1.5			1	1.5	0.5			
PHILODROMIDAE										
Philodromus dispar Walckenaer 1826	1.5		0.5		1					
Philodromus rufus Walckenaer 1826							0.5			
Thanatus atratus Simon 1875					10.33		13.33		26.83	
Thanatus sp.					1.5		1			
PISAURIDAE										
Pisaura mirabilis (Clerck 1758)					0.5					
SALTICIDAE										
Aelurillus aeruginosus (Simon 1871)					14.67	0.5				
Ballus chalybeius (Walckenaer 1802)							1.5			
Chalcoscirtus infimus (Simon 1868)					1.5				0.5	
Cyrba algerina (Lucas 1846)	0.5				1					
Euophrys sp.	1.33				14.5		27.83	1	40	
Heliophanus sp.					0.5					
Icius hamatus (C.L. Koch 1846)							0.5		1	
Neathea membrosa (Simon 1868)					1				0.5	
Pellenes arciger (Walckenaer 1837)					0.5					
Pellenes geniculatus (Simon 1868)					0.5					
Phlegra sp. 1.	3.5									
Phlegra sp. 2.							1.5	1	2	
Thyene imperialis (Rossi 1846)					0.5					
SCYTODIDAE										
Scytodes velutina Heineken & Lowe 1836	3.33	6.5			14.83	1.5	0.5			
SICARIIDAE										
Loxosceles rufescens (Dufour 1820)					0.5		0.5			
SPARASSIDAE										
Eusparassus dufouri Simon 1932					0.5					
Micrommata ligurina (C.L. Koch 1845)									0.33	

Appendix 1—Continued.

FAMILY / *Species*	MF-s	MF-a	OP-s	OP-a	SD-s	SD-a	GD-s	GD-a	CD-s	CD-a
THERIDIIDAE										
Achaearanea tepidariorum (C.L. Koch 1841)					0.5		0.33			
Enoplognatha sp.	1.17		0.5						2.5	
Robertus sp.					1				2	
Steatoda paykulliana (Walckenaer 1805)	0.33									
Steatoda phralerata (Panzer 1801)					4.17		15.83		14	
Theridiidae sp.					1.83		1.5		4.5	
THOMISIDAE										
Ozyptila pauxilla (Simon 1870)					6.5		3.83		8	
Xysticus bliteus (Simon 1875)							0.5		1	
Xysticus nubilus Simon 1875					0.5		1		1	
Xysticus robustus (Hahn 1832)								2		
TITANOECIDAE										
Titanoeca hispanica Wunderlich 1995							1		1	
Titanoeca praefica Simon 1870					0.5		1		14.5	
ZODARIIDAE										
Selamia reticulata (Simon 1870)	5.17	2	5	3	10.33	0.5	8.5		2.5	
Zodarion alacre (Simon 1870)*	1.67	2			31	0.5	2.5			
Zodarion segurense Bosman 1994*	1.5									
Zodarion styliferum (Simon 1870)	29.83	3.5	1.5	3.5	16.67	4	37.33	12	6.5	5
ZOROPSIDAE										
Zoropsis media Simon 1878	0.33		4.83	1						

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Bromeliads as biodiversity amplifiers and habitat segregation of spider communities in a Neotropical rainforest

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Abstract. Although bromeliads can be important in the organization of invertebrate communities in Neotropical forests, few studies support this assumption. Bromeliads possess a three-dimensional architecture and rosette grouped leaves that provide associated animals with a good place for foraging, reproduction and egg laying, as well as shelter against desiccation and natural enemies. We collected spiders from an area of the Atlantic Rainforest, southeastern Brazil, through manual inspection in bromeliads, beating trays in herbaceous+shrubby vegetation and pitfall traps in the soil, to test if: 1) species subsets that make up the Neotropical forest spider community are compartmentalized into different habitat types (i.e., bromeliads, vegetation and ground), and 2) bromeliads are important elements that structure spider communities because they generate different patterns of abundance distributions and species composition, and thus amplify spider beta diversity. Subsets of spider species were compartmentalized into three habitat types. The presence of bromeliads represented 41% of the increase in total spider richness, and contributed most to explaining the high beta diversity values among habitats. Patterns of abundance distribution of the spider community differed among habitats. These results indicate that bromeliads are key elements in structuring the spider community and highlight the importance of Bromeliaceae as biodiversity amplifiers in Neotropical ecosystems.

Keywords: Alpha and beta diversity, Atlantic rainforest, bromeliad-dwelling spiders, community structure, habitat type

Habitat structural complexity (i.e., physiognomic diversity) plays an important role in population dynamics and in the distribution and organization of animal communities in natural systems (Lawton 1983; Langellotto & Denno 2004; Srivastava 2006). Structurally more complex habitats can increase food availability, provide more shelter against predators and climatic harshness and supply alternative resources (Langellotto & Denno 2004).

Several studies have shown that habitat complexity (architecture) is a key factor determining spider species richness and composition (Robinson 1981; Greenstone 1984; Wise 1993; Halaj et al. 2000; Langellotto & Denno 2004; Beals 2006). For example, using an artificial structure made of wood and wire, Robinson (1981) showed that spiders with different foraging strategies use habitats according to their architectural characteristics, which end up segregating the spiders into species subsets. If this experiment foretells the real spider distribution in natural communities, structurally different habitats will be represented by non-random species subsets with lower percentages of shared species as habitat dissimilarity increases. Indeed, habitat structure is an important predictor of the spider communities in several natural ecosystems (e.g., Halaj et al. 2000).

Considering that most of the animals associated with the plant family Bromeliaceae are habitat specialists (Greeney 2001; Romero 2006; Balke et al. 2008; Omena & Romero 2008), different habitat architectures could generate differentiated subsets of spider communities. Bromeliads occur almost exclusively in Neotropical regions (with the exception of an African species: Benzing 2000) and represent an excellent study system to investigate compartmentalization phenomena. Bromeliads are a good example of complex structures because they have leaves organized in a rosette, which usually form a tank that accumulates rainwater and nutrient-rich debris (Benzing 2000). Such characteristics result in a great variety of microhabitats for terrestrial (Romero & Vasconcellos-Neto 2005a, b; Romero 2006; Omena & Romero 2008) and aquatic animals (Greeney 2001; Srivastava 2006; Balke et al. 2008), which generally use bromeliads for foraging, reproduction, egg laying, nursery, and shelter against desiccation and natural enemies (Romero & Vasconcellos-Neto 2005a). For these reasons, bromeliads were considered to be biodiversity amplifiers (sensu Rocha et al. 2000). However, although various studies have suggested several advantages of bromeliads for the fauna of Neotropical forests (Benzing 2000; Greeney 2001; Romero 2006), to our knowledge there is no study showing that these plants are important in structuring spider communities and as amplifiers of total richness and beta diversity (i.e., species turnover among habitats: Tuomisto & Ruokolainen 2006; Novotny et al. 2007).

Our hypothesis is that bromeliads are key elements of spider community structure and that they contribute to amplifying the diversity of these arthropods in Neotropical ecosystems. To evaluate this hypothesis, we compared species abundance distribution patterns (dominance curves) and species composition (beta diversity) of spiders in bromeliads, herbaceous+shrubby vegetation and ground habitats to test whether 1) species subsets that make up the spider Neotropical forest community are compartmentalized in different habitat types (i.e., bromeliads, vegetation and ground) and 2) whether bromeliads are important elements that structure spider communities because they generate different patterns of abundance distributions and species composition, and thus amplify spider beta diversity. In this study, we consider total richness as the total number of spider species from the three habitat types (bromeliads, herbaceous and shrubby vegetation

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and ground), and beta diversity as the difference in the spider speeies composition between habitats.

METHODS

Study site.—This work was done at the Santa Lúcia Biological Station (SLBS) (19°57′S, 40°31′W, 600–900 m asl), an area of 440 ha in Santa Teresa County, Espírito Santo State, southeast Brazil. The vegetation of SLBS is characterized as primary Atlantic Rainforest. The region has an average rainfall of 1868 mm with November being the wettest month, with an average rainfall of 268.8 mm and June the driest of the year with 58.9 mm (for more details see Mendes & Padovan 2000).

At SLBS, the Bromeliaceae family is of great importance in the physiognomy of the vegetation, dominating various stretches of forest understory, generally making up large agglomerates of multispecific patches that occur naturally between forests and rocky outerops on shallow and structurally poor ground (hereafter named "bromeliad patches": Wendt et al. 2008). Small patches vary from 0.005 to 0.14 ha and large ones from 0.43 to 0.93 ha (see Wendt et al. 2008). The forest vegetation, with a not-well-defined canopy stratification, is predominated by members of the family Myrtaceae (e.g., genus *Eugenia*), followed by species of *Ocotea* (Lauraceae), *Pouteria* (Sapotaceae) and some Rubiaceae, Melastomataceae, Fabaceae and Arecaceae (see Thomaz & Monteiro 1997).

Data surveying.—We sampled spiders from bromeliads, herbaceous and shrubby vegetation (hereafter called vegetation) and ground in nine bromeliad patches 125 to 1031 m apart. Surveying was done in 24 permanent plots during ten sampling periods between February 2006 and September 2007, in one-month intervals. Numbers of plots per patch and plot size were weighed according to the area of each patch. Plot size was 7 × 3 m (n = 6) for small patches and 20 × 3 m (n = 18) for large patches of bromeliad and ground samples. In bromeliad patches with at least two plots (n = 5 patches), each plot was 21 m from the nearest. We sampled terrestrial and epiphytic bromeliads (up to 1.5 m high) in all plot areas and manually collected spiders on all the plant foliage surfaces (dead and live leaves), in the interior of the rosette and between the leaf axils of 1110 bromeliads of 32 species. Bromeliaceae sampling was done using non-destructive methods. We kept collected spiders in 75% ethanol for later identification.

In contrast to the bromeliads, the vegetation is usually less dense; thus we had to increase sampling effort (plot size). We used plots of 20 × 20 m (n = 18) in large patehes, and of 20 × 7 m (n = 6) in small patches. Each plot was 1 m apart; although this distance might not distinguish between two vegetation communities, plots at a distance of more than 1 m could include fauna outside the bromeliad patch. The number of plots per bromeliad patch varied from one to five depending on the size of the patch. For example, in the smallest bromeliad patch (0.005 ha) we made a single 7 × 3 m plot, while for a larger one (0.93 ha) we made five 20 × 3 m plots. To avoid temporal discrepancies in comparative analysis, the three habitat types were coneomitantly sampled in each sampling period. We used beating trays to sample twenty herbaceous-shrubby plants from each plot of the large patches (n = 18) and ten plants from each plot of the small patches (n = 6), for a total of 420 sampled plants. Chosen plants were not higher than 3 m, and the distance between them varied from 1 to 3 m. Beating trays were made up of a 1 × 1 m square wooden beam frame holding a $1m^2$ cotton cloth; these trays were placed under the shrub to be sampled and, with the help of a stick, we beat the shrub 20 times so that the spiders would fall onto the cloth. After this procedure, we preserved the spiders in 75% ethanol.

We collected ground spiders in 195 pitfall traps distributed in 24 plots; the pitfall traps were set up inside each bromeliad plot. Each trap was 2 m (large plots) to 1.5 m (small plots) apart. The number of traps in each bromeliad patch varied aecording to the size of the patch; ten and five ground traps were set up in large and small patches, respectively. Those plots in rocky outcrops (n = 3) did not receive pitfalls. The traps were made of plastic (500 ml) and contained approximately 400 ml water, 10 ml detergent and 10 g thick salt. Each trap had a slab of polystyrene as a roof to avoid capturing leaves and rainwater. Traps remained active in the field for seven days only during the sampling period, after which the material was collected, sorted in a laboratory and the spiders stored in 75% ethanol. Voucher specimens were deposited in the Instituto Butantan (IBSP, Brazil).

We used different sampling methods for each habitat type to maximize spider collection. Each method used here is the most appropriate for the purpose of this study (Santos 1999; Romero & Vasconcellos-Neto 2005a, b).

Statistical analyses.—We ran an individual-based rarefaction to control for variation in sampling effort among habitats using the software EstimateS 8.0 (Cowell 2006); we used confidence intervals of 95% for the three habitats. This method allowed comparisons among unbalanced samples or with samples having different patterns of species distribution (Gotelli & Colwell 2001). To test whether spider communities were organized in subsets of compartmentalized species in each habitat type, and whether bromeliads amplify the beta diversity of spider communities, we used Bray-Curtis, Chao-Jaccard and Chao-Sorensen quantitative similarity indexes. The Bray-Curtis index is positively biased toward unbalanced samples, while Chao-Jaccard and Chao-Sorensen indexes are generally resistant to undersampling (Chao et al. 2005, 2006). The indices proposed by Chao et al. (2005, 2006) are particularly important for our work, since our samples are not balanced and include many rare species. We calculated the three index values and the variances with bootstrap methods (n = 200 iterations) using SPADE (Chao & Shen 2003). We also calculated the estimated relative abundance values of the shared species ($\hat{U}$ and $\hat{V}$) between two separate communities, in which $\hat{U}$ is the estimated relative abundance of the shared species of community 1, while $\hat{V}$ is that of community 2 (Chao et al. 2005, 2006). With $\hat{U}$ and $\hat{V}$ values we could infer whether dominant spiders were bromeliad specialists (i.e., lower values of relative abundance). The three index values varied from 0 (maximally dissimilar communities, with no shared species) to 1 (identical communities; Chao et al. 2006) and represent, respectively, high rate of change in species composition (high beta diversity) and low rate of change in species composition (low beta diversity: Novotny et al. 2007).

We repeated the similarity index calculations with the ten most dominant spider species in each type of habitat, because rare speeies could be responsible for a high dissimilarity

between these habitats (Brown 1984). Additionally we estimated the similarity of the two most common spider families, Salticidae and Theridiidae, among habitats. If these spider families represent very different guilds (Romero & Vasconcellos-Neto 2007), they could respond differentially to habitat structure. We also applied a Non-metric Multidimensional Scaling (NMDS) analysis to Bray-Curtis dissimilarity matrices using Primer 6.0 software (Clarke & Gorley 2006) to represent species composition graphically. Values of stress < 0.05 are considered indicative of an excellent representation of the data, while stress < 0.1 indicates a good scaling with a low tendency to error, and stress > 0.3 is typical of points that are arbitrarily disposed in a two-dimensional classification (Clarke & Gorley 2006).

To test whether bromeliads increased spider beta diversity, we partitioned the total diversity (measured as species richness) into average alpha diversity (within habitat types) and beta diversity (among habitat types) following Crist et al. (2003). Since the sampling unit was habitat type, we considered plots nested inside habitats and habitats nested inside patches to perform the partitioning procedure. We ran the analysis and tested the significance of the alpha and beta values with 10,000 randomizations (individual-based procedure) using the program PARTITION (Veech & Crist 2007). This randomization generates a null distribution of each alpha and beta diversity estimated, which was compared with the observed alpha and beta values (Summerville et al. 2006). In addition, to test how much each habitat contributed to the total beta diversity, we performed four different partitioning analyses: 1) total, including all habitat types, 2) excluding bromeliad data, 3) excluding vegetation data, and 4) excluding ground data. The explanation percentage for beta diversity obtained in the first analysis was used as a standard to calculate whether exclusion of data of one habitat diminished the percentage of explanation of beta diversity.

Species abundance distribution (diversity dominance curves) is one of the most used approaches to describe community structure, because it is possible to compare communities with few or no species in common (McGill et al. 2007). This characteristic is especially important in the case of the community we are studying, since the three habitat types have few species in common (see results). To be able to compare the communities of the three habitats and to verify whether bromeliads have distinct patterns of spider abundance, we drew dominance curves for each habitat with a ranking-abundance diagram (RAD), in which the y axis represents species abundance and the x axis the species rank (organized from the most to the least abundant species on a logarithmic scale) (Magurran 2004; Fattorini 2005). A number of theoretical distributions have been proposed to model observed RAD, the most commonly used being the broken stick model (BS), the lognormal model (LN), the log series (LS), and the geometric series (GS). To assess which model best fit the data, we calculated the expected frequencies under each model and compared these expected frequencies with the observed frequencies, using χ^2 tests calculated by the program PAST (Hammer et al. 2001). When observed data did not differ significantly (i.e., $P > 0.05$) from the expected frequencies calculated under a given model, the model was considered to fit the data well (Magurran 2004).

When more than one model adjusted an observed distribution, we made a linear regression to choose the model that better fit the data (Fattorini 2005). This was the case for the BS distribution and GS model, because some data did not show distributions statistically different from these models. In such circumstances, the goodness-of-fit of regression was evaluated considering a fit index (FI: an alternative R^2 which can be used to compare models based on different transformation), standard error of estimate in actual units (S_e) and the coefficient of variation (CV), and Akaike's Information Criterion (AIC) (see Fattorini 2005 for details). Values of S_e calculated for the GS models can be compared with $S_{y.x}$ values of BS models (Fattorini 2005). We did not analyze data with linear regression using the LS model because this model is mathematically similar to the geometric series (May 1975) and because the LS model has a statistical origin and little use with ecological data (May 1975, Fattorini 2005).

RESULTS

Species richness of spider communities.—We collected 617 adult spiders belonging to 155 morphospecies and 33 families in the three habitats (Appendix 1). On the bromeliads, we found 348 adult spiders belonging to 75 morphospecies and 22 families. In the vegetation we collected 220 individuals belonging to 95 morphospecies and 16 families. Finally, on the ground we collected 49 individuals belonging to 25 morphospecies and 16 families. Whereas in the vegetation the most speciose groups were Theridiidae ($n = 25$ species) and Salticidae ($n = 19$), on the ground the most speciose families were Salticidae ($n = 5$) and Linyphiidae ($n = 4$) (Appendix 1). The most speciose families on the bromeliads were Salticidae and Theridiidae, with 16 and 11 species, respectively. Based on a smaller sample ($n = 45$ individuals), a rarefaction procedure detected that the vegetation habitat had the highest richness, followed by ground and bromeliad habitats (Fig. 1). However, the presence of Bromeliaceae was responsible for a 41% increase in the total spiders' species richness, because this habitat possessed an exclusive spider fauna (see below). Without taking the bromeliad samples into account the number of spider species in SLBS was 110, but including the bromeliad fauna the number of spider species increased to 155. Likewise, the vegetation sampling was responsible for a 74% increase in spider richness.

Beta diversity.—Similarity values of spider community composition in the three habitats were low (Table 1). None of the three indices gave similarity values larger than 0.5 for any habitat comparison. Similarity values were even lower when we used only the ten most abundant species of each habitat in the analysis (Table 1). The similarity of the species composition of the two most common families (i.e., Salticidae and Theridiidae) among the three types of habitat was also low (Fig. 2, Table 1). The low stress values in Figs. 2A–C indicate good scaling with little possibility of data being inadequately interpreted. Although the Bray-Curtis index appears biased positively due to unbalanced samples, we consider our results conservative to bias, indicating that the spider communities were compartmentalized.

Some spider families were restricted to a specific habitat type: nine were exclusive to bromeliads, seven to the ground and four to the vegetation (Appendix 1). Families found only

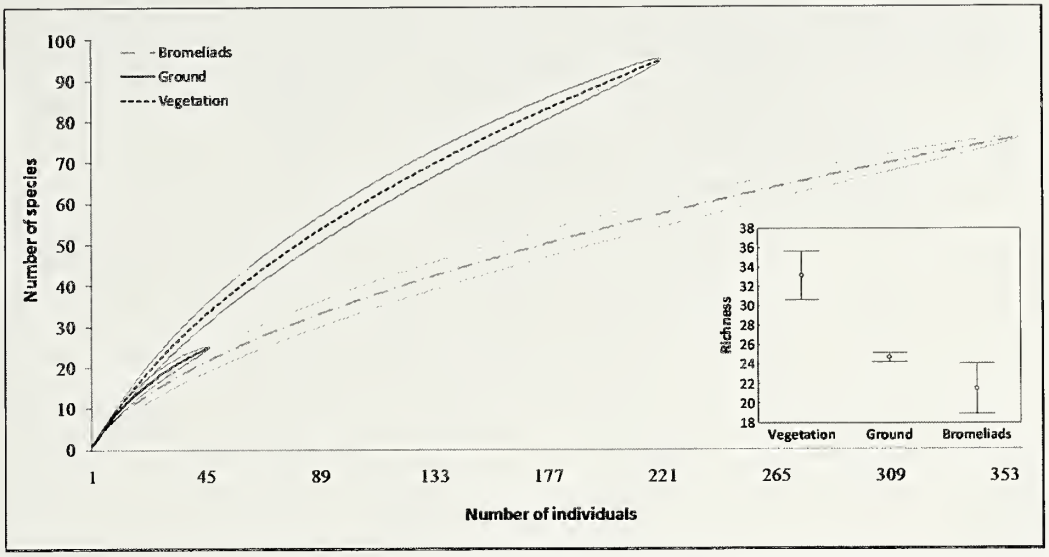

Figure 1.—Individual-based rarefaction and 95% elipsoid confidence intervals (CI 95%) for the three habitat types. In detail (inferior right) we show the comparison of the three habitats rarefied to the smaller sample (ground habitat, $n = 45$ individuals). The bars in the detailed graph also represent the CI 95%.

in the bromeliad habitat were Ctenidae, Hahniidae [although one occasional individual (i.e., 0.86% of all individual from this family) was found in vegetation], Miturgidae, Mysmenidae, Ochyroceratidae, Pisauridae, Scytodidae, Segestriidae, Sparassidae and Trechaleidae (Appendix 1). Sixty percent of the bromeliad spider species occurred only on bromeliads ($n = 45$ species), 69.5% of the vegetation species were exclusive to this habitat ($n = 66$ species) and 40% of ground spiders were exclusively associated with the ground ($n = 10$ species). When bromeliads were excluded from the partition analysis, the percentage explained by observed beta diversity (comparing with total diversity) decreased by 11%. In contrast, when vegetation and ground data were removed, the percentage explained by observed beta diversity decreased only by 2.4% and 1%, respectively. In all calculations of partitioned diversity, the value of beta diversity was higher than expected by chance ($P < 0.0001$: Table 2). Thus, bromeliad habitat contributed to the increase in beta diversity by intensifying the species turnover among habitats.

Most of the species shared between bromeliads and other habitats were rare species, as shown by the low relative abundance of the species in common between bromeliads and vegetation ($\hat{U} = 0.287$) and between bromeliads and ground ($\hat{U} = 0.112$: Table 1). The five most abundant spider species on bromeliads were exclusively associated with these plants and represented 59% of all individuals found in this habitat.

Table 1.—Bray-Curtis, Chao-Jaccard and Chao-Sorensen (± SE) similarity index values comparing all spider species (total), the ten most abundant species and the two most common families (Salticidae and Theridiidae). $\hat{U}$ (± SE) represents the estimated relative abundance of shared species in community 1 and $\hat{V}$ (± SE) the estimated relative abundance of shared species in community 2. Compared habitats were bromeliad (Br), vegetation (Veg) and ground (Gr).

	Bray-Curtis index	Chao-Jaccard index	Chao-Sorensen index	$\hat{U}$	$\hat{V}$
Total					
$Br^1 \times Veg^2$	0.130±0.02	0.225±0.04	0.367±0.06	0.287±0.09	0.509±0.14
$Br^1 \times Gr^2$	0.071±0.01	0.104±0.02	0.188±0.04	0.112±0.03	0.591±0.18
$Veg^1 \times Gr^2$	0.089±0.02	0.268±0.04	0.422±0.07	0.267±0.07	1.000±0.15
Ten most abundant species					
$Br^1 \times Veg^2$	0	0	0	0	0
$Br^1 \times Gr^2$	0	0	0	0	0
$Veg^1 \times Gr^2$	0.035±0.02	0.038±0.02	0.074±0.03	0.066±0.04	0.083±0.05
Salticidae					
$Br^1 \times Veg^2$	0.104±0.04	0.131±0.04	0.232±0.07	0.145±0.05	0.570±0.24
$Br^1 \times Gr^2$	0.076±0.05	0.101±0.04	0.184±0.08	0.113±0.05	0.498±0.29
$Veg^1 \times Gr^2$	0.113±0.04	0.138±0.05	0.242±0.09	0.138±0.06	1.000±0.326
Theridiidae					
$Br^1 \times Veg^2$	0.193±0.05	0.245±0.07	0.393±0.10	0.724±0.21	0.270±0.09
$Br^1 \times Gr^2$	0	0	0	0	0
$Veg^1 \times Gr^2$	0.05±0.03	0.027±0.02	0.053±0.04	0.027±0.02	1.000±0.39

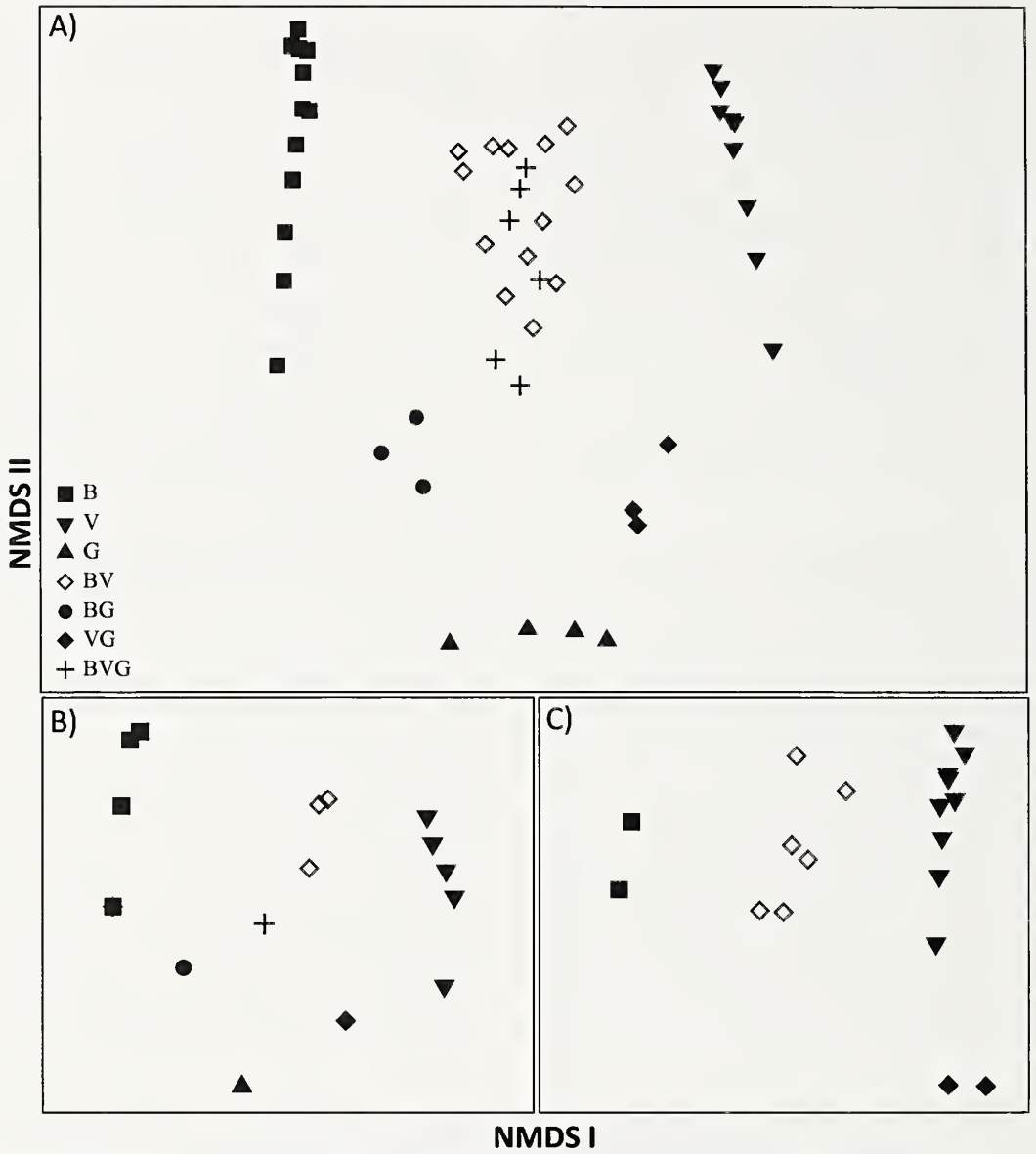

Figure 2.—Result of non-metric multidimensional scaling (NMDS) analysis showing segregation of whole spider communities among the three habitat types (A: 2D stress = 0.07), as well as for community of Salticidae (B: 2D stress = 0.04) and Theridiidae (C: 2D stress = 0.05). The symbols represent spider species that were exclusively associated with one habitat type; i.e., bromeliad (B), vegetation (V), ground (G), and species that occur in two [bromeliad and vegetation (BV), bromeliad and ground (BG), and vegetation and ground (VG)] or three habitats (BVG).

Species abundance distributions.—The abundance distribution pattern of bromeliad-living spiders did not deviate from a LN distribution (Fig. 3, Table 3), with few dominant species and many intermediate and rare ones (42 singletons and 13 doubletons). Abundance distribution of spiders in the vegetation habitat was better modeled by BS ($y = 11.288 - 5.752x$, $S_e = 0.788$, CV [%] = 33.450, FI = 0.899) than by the GS model ($y = 0.696 - 0.001x$, $S_e = 1.487$, CV [%] = 68.502, FI = 0.634). Abundance distributions of ground spiders were better modeled by BS ($y = 4.825 - 3.018x$, $S_e = 0.431$, CV [%] = 23.489, FI = 0.870) than GS ($y = 0.577 - 0.031x$, $S_e = 0.465$, CV [%] = 25.686, FI = 0.848). According to the values of the AIC, the abundance distribution of spiders in these two habitats is actually better explained by the BS model (vegetation: $\Delta AIC = 122.981$, ground: $\Delta AIC = 3.689$; Fig. 3, Table 3), which suggests an equitable abundance distribution among species.

DISCUSSION

Our results show that spider communities are compartmentalized according to the habitat type. Formation of compartments in the interactions between animals and plants is commonly observed between phytophagous insects and their host plants (e.g., Prado & Lewinsohn 2004) because of chemical and/or physical restrictions determined by the plants (Schoonhoven et al. 2005). Compartmentalizing was also found in mutualistic networks of ants and myrmecophytic plants (Guimarães et al. 2007), probably due to limited space in the colonies and olfactory restrictions that make it impossible for the queen to find other non-hosting plant

Table 2.—Partitioning of species diversity in three habitat types into alpha and beta components. We performed the partitioning in alpha and beta diversity considering all habitat types, excluding vegetation, ground and bromeliad from the analysis. The expected value (mean, maximum, minimum) was assessed with 10,000 randomizations. In all comparisons the P-value was < 0.0001.

	Species richness			
		Expected		
Habitat type	Observed	Mean	Maximum	Minimum
Within habitat (alpha diversity)				
Total (three habitat types)	12.1	16.9	18.2	15.4
Without vegetation	9.3	11.6	12.7	10.6
Without ground	12.5	17	18.5	15.6
Without bromeliad	18.6	25.1	28.5	22
Between habitat (beta diversity)				
Total (three habitat types)	134.9	130.1	131.6	128.8
Without vegetation	79.7	77.4	78.4	76.3
Without ground	125.5	121	119.5	122.4
Without bromeliad	82.4	75.9	79	72.5

species. In contrast to this, spiders do not usually feed on plants, and few species have a mutualistic association with their host plants (see Romero & Vasconcellos-Neto 2007; Romero et al. 2008).

So, what process is responsible for spiders forming compartmentalized communities? According to Uetz (1991), spiders use tactile and vibratory clues to select a habitat, and choose substrates that are the best conductors of these stimuli. Spiders specialized to live on bromeliads can benefit from the three-dimensional structure of these plants, being favored not only by conductors of tactile and vibratory stimuli but also by visual stimuli, which are fundamental for foraging and mating (e.g., Barth et al. 1988). Moreover, the characteristic structure of bromeliads makes it easier to construct webs for various spider guilds and provide protection against natural enemies and climatic conditions (Romero & Vasconcellos-Neto 2005a; Romero 2006). Therefore, the specialization of individuals for specific plant or substrate structural characteristics could be responsible for spiders and other organisms compartmentalizing communities. However, this specialization may prevent species from using other habitats (Rosenzweig 1987; Morris 1987, 2003). Community compartmentation could also be seen for Salticidae and Theridiidae, two families belonging to distinct functional groups (Romero & Vasconcellos-Neto

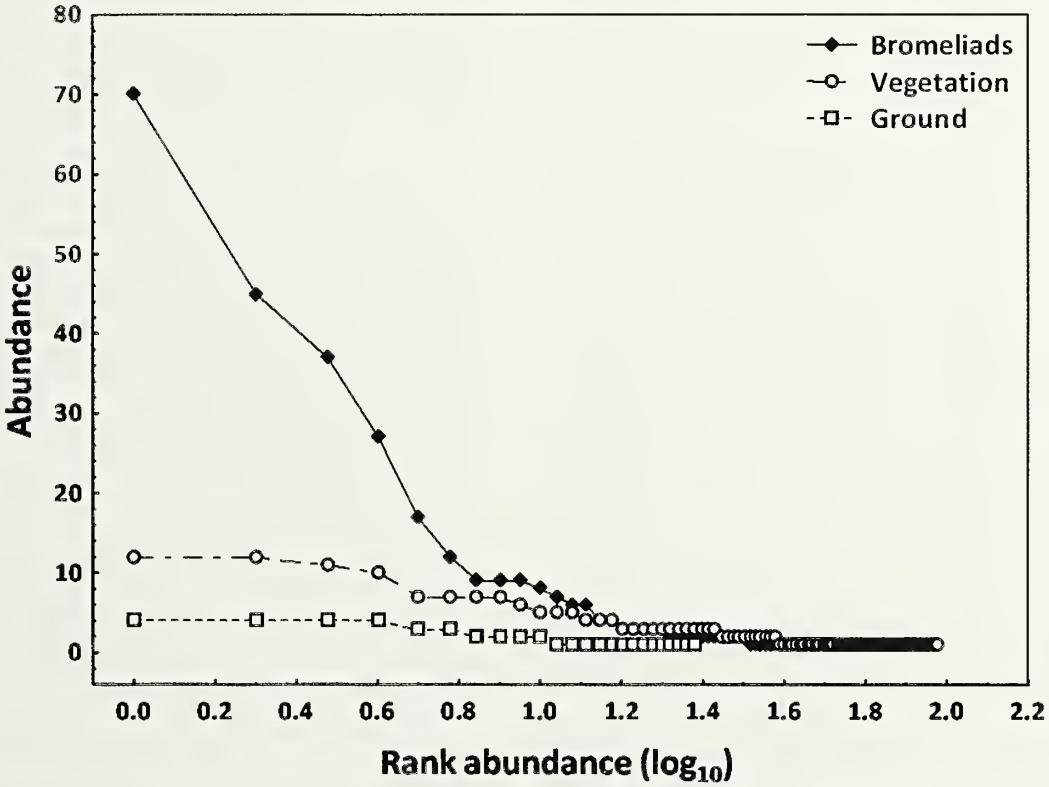

Figure 3.—Abundance ranking diagram (dominance curve) showing a lognormal distribution of bromeliad spiders, and broken stick distribution of non-bromeliad vegetation and ground. We found 75 species in the bromeliads, 95 species in the vegetation and 24 on the ground.

Table 3.—Comparisons between observed and expected values of species abundance in spiders that occur in bromeliads, vegetation and on the ground. The asterisk indicates that the data do not fit/deviate from to the model ($P < 0.05$).

	Habitat type					
	Bromeliad		Vegetation		Ground	
Model	χ^2	P	χ^2	P	χ^2	P
Broken stick (BS)	237.5	<0.0001*	6.5	1	1.6	0.977
Lognormal	4.8	0.183	7.2	0.028*	0	0
Logseries	126.3	<0.0001*	3.4	1	1.1	0.955
Geometric Series (GS)	812.7	<0.0001*	47.8	0.132	1.2	0.976

2007). This pattern reinforces the role of habitat structure on the organization of different organisms in a community.

Although bromeliads have the smaller rarefied richness, plants of the Bromeliaceae family create a habitat that amplifies total richness and beta diversity of spider communities, possibly because of their specific fauna. The variety of spatial niches available in bromeliads (e.g., foliar axils, foliar blades, space between leaves, dry and green leaves, central and peripheral tanks) could be responsible not only for the specialization of various arthropod groups in bromeliads [e.g., aquatic beetle (Balke et al. 2008), some jumping spiders (Romero 2006; Romero & Vasconcellos-Neto 2007)], but also for the increase in total spider species richness. A larger number of niches makes specialization easier and reduces competition through spatial segregation (Cramer & Willig 2005), which usually increases biological diversity (habitat heterogeneity hypothesis: MacArthur & MacArthur 1961). Despite not having sampled forest areas without bromeliads, we believe that our results are robust enough to infer that the Bromeliaceae amplify spider diversity, because the spiders that specialize on bromeliads (i.e., the subset of bromeliad spider species) do not occur in association with other types of substrates (e.g., Romero 2006; Omena & Romero 2008).

The species abundance distribution patterns in the three habitat types also support the hypothesis that bromeliads are important elements in structuring spider communities. Even though species abundance related to vegetation and ground was equitable (broken-stick model), the bromeliads were dominated by a few common species and many intermediate and rare spiders (lognormal model). It is possible that the high dominance of certain spider species in bromeliads is related to interspecific interactions in which competitively superior spiders win or even feed on smaller spiders (Wise 1993). A monopolization of better sites or resources by competitively superior animals was reported for other animals (e.g., birds: Fretwell & Lucas 1970; salmon: Hendry et al. 2001), and in the case of spiders such disputes could be related to the benefits that bromeliads provide to resident animals. Indeed, the body size (measured as prosoma length) of bromeliad spiders was 16% greater than in the vegetation spiders (t-test = 2.26, P = 0.024). This may suggest that large-sized spiders are superior competitors, which, because of their larger dimensions, are able to drive off or catch smaller species. It is also possible that bromeliads support larger numbers of prey, relative to other habitats, thus allowing the persistence of larger spiders, which in other habitats cannot find adequate prey for their higher energetic needs. These two mechanisms are not mutually exclusive, and possibly they combined to produce a concentration of spiders on the bromeliads.

In conclusion, we have shown that spiders form subsets of communities compartmentalized according to the habitat type and that bromeliads represent an important habitat that influences the structure of these communities. As far as we know, this is the first work to show the formation of between-habitat compartments in spider-plant interactions. Our data reinforce the importance of habitat structure in determining community structure and diversity patterns in spiders (e.g., Robinson 1981; Greenstone 1984). Plants of the Bromeliaceae family seem to provide essential habitats for some taxonomic groups of spiders (this study, also see Romero 2006) and for other animals in Neotropical regions (e.g., Greeney 2001; Balke et al. 2008) because they are able to support a larger number of individuals and species and, consequently, amplify the total richness and beta diversity of the animals they host. These plants possibly represent a fundamental structural component for the arrangement of biological communities and can be used as model organisms in studies concerning animal-plant interactions. However, experimental studies manipulating vegetation structures are necessary to understand the causal factors related to the influence of architecture/complexity of the habitat on the spider communities.

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Appendix 1.—List of families and spider morphospecies and their abundances in each habitat type.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Amaurobiidae			**2**
Amaurobiidae gen.n.1			2
Anyphaenidae	2	9	
Aysha gr. *helvola*		1	
Bromelina oliola Brescovit, 1993	1		
Iguarima censoria (Keyserling, 1891)		1	
Katissa sp.1		1	
Macrophyes jundiai Brescovit, 1993		2	
Osoriella rubella (Keyserling, 1891)		1	
Osoriella sp.1	1	1	
Tendis sp.1		1	
Wulfilopsis leopoldina Brescovit, 1997		1	
Araneidae	4	16	
Alpaida atomaria Simon, 1895		1	
Alpaida sp.1		1	
Araneus stabilis (Keyserling, 1892)		1	
Araneus sp.1		1	
Cyclosa fililineata Hingston, 1932		3	
Eustala sp.1		1	
Hypognatha sp.1		1	
Mangora aripeba		2	
Mangora sp.1	1	1	
Metazygia sp.1	2		
Micrathena acuta (Walckenaer, 1842)	1		
Micrathena clypeata (Walckenaer, 1805)			1
Micrathena sp.1		1	
Ocrepeira guono Mello-Leitão, 1943		1	
Testudinaria sp.1		2	
Barychelidae			**4**
Neodiplothele sp.1			4
Corinnidae	8	**3**	**3**
Castianeira sp.1	3	3	2
Corinna gr. *rubripes* C.L. Koch, 1841	1		
Corinna sp.1			1
Corinna sp.2	1		
Corinna sp.3	1		
Corinna sp.4	1		
Corinna sp.5	1		

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Ctenidae	4		
Ctenus aff. *oruatus*	1		
Enoplocteuus cyclothorax (Bertkau, 1880)	1		
Isocteuus sp.1	2		
Dictynidae		**1**	
Dictyna sp.1		1	
Hahniidae	116	1	
Hahniidae sp.1	70		
Hahniidae sp.2	37		
Hahniidae sp.3	9	1	
Linyphiidae	52	29	5
Anodoration claviferum (Millidge, 1991)		4	
Dubiaranea sp.1	4	1	
Dubiaranea sp.2	1		
Eurymorion insigne Millidge, 1991	2		
Fissiscapus pusillus Millidge, 1991	27		
Linyphiidae sp.1	3	12	1
Linyphiidae sp.2		2	
Linyphiidae sp.3	9	1	
Linyphiidae sp.4	1	1	
Meioneta sp.1	1	1	1
Sphecozone sp.1	3	7	2
Sphecozone sp.2	1		1
Lycosidae			4
Allocosa sp.1			4
Mimetidae	2		1
Ero sp.1	2		1
Miturgidae	1		1
Radulphius laticeps Keyserling, 1891	1		1
Mysmenidae	1		
Mysmenidae sp.1	1		
Nemesiidae			2
Stenoterommata sp.1			2
Ochyroceratidae	1		
Ochyrocera sp.1	1		
Oonopidae	8		
Oonops sp.1	8	2	
Palpimanidae			3
Otiothops sp.1			3
Philodromidae			1

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Berlandiella sp.1			1
Pholcidae	50	6	2
Carapoia ubatuba Huber, 2005	1		2
Mesabolivar sp.1		3	
Metagonia sp.1		1	
Metagonia sp.2		1	
Psilochorus sp.1	45		
Tupigea nadleri Huber, 2000		1	
Tupigea sp.1	4		
Pisauridae	2		
Architis sp.1	2		
Salticidae	49	36	5
Alcmena sp.1		1	
Arnoliseus sp.1	1	2	
Beata sp.1		4	
Chira micans (Simon, 1902)		1	
Chirothecia sp.1		1	
Consingis sp.1	1	1	
Coryphasia sp.1	12		
Cotinusa sp.1		5	
Cotinusa sp.2		2	
Cylistella sp.1		3	
Erica sp.1		1	
Euophryinae sp.1		1	1
Euophryinae sp.2	2	1	1
Euophryinae sp.3	2	7	
Euophryinae sp.4			1
Euophryinae sp.5	1		1
Euophryinae sp.6		1	
Euophryinae sp.7		1	
Euophryinae sp.8	1		
Salticidae			
Euophryinae sp.9	1		
Fluda sp.1	6		
Lyssomanes sp.1		1	
Lyssomanes sp.2		1	
Martella sp.1	3		
Myrmarachne sp.1	1		
Noegus sp.1	1		
Psecas sp.1	6		
Sarinda sp.1	1		
Vinnius sp.1	9		
Zuniga sp.1		1	
Salticidae sp.1		1	1
Salticidae sp.2	1		
Scytodidae			
Scytodes sp.1	1	3	
Segestriidae			
Ariadna sp.1	2		
Sparassidae			
Olios sp.1	3		
Symphytognathidae		1	
Symphytognatha sp.1		1	
Synotaxidae		2	
Synotaxus sp.1		2	
Tetragnathidae	4	8	
Chrysometa sp.1	1	1	

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Chrysometa sp.2		3	
Homalometa sp.1	2		
Leucauge sp.1		1	
Leucauge sp.2	1		
Tetragnatha sp.1		3	
Theridiidae	18	74	7
Achaearanea sp.1		1	
Argyrodes sp.1		1	
Audifia sp.1	1		
Chrysso sp.1		10	
Chrysso sp.2		2	
Theridiidae			
Dipoena woytkowskii Levi, 1963		1	3
Dipoena sp.1		7	
Dipoena sp.2		1	4
Dipoena sp.3		5	
Dipoena sp.4		1	
Echinotheridion sp.1		1	
Episinus sp.1		1	
Episinus sp.2		1	
Euryopis sp.1	1	1	
Faiditus sp.1		1	
Platnickina mneon Bösenberg & Strand, 1906		4	
Phycosoma altum (Keyserling, 1886)		6	
Rhomphae sp.1	2		
Spintharus gracilis Keyserling, 1886		3	
Tekellina sp.1	7	1	
Theridion sp.1		3	
Theridion sp.2		12	
Theridion sp.3		1	
Theridion sp.4	1	5	
Theridion sp.5	1		
Theridion sp.6	1		
Thwaitesia affinis O. Pickard-Cambridge, 1882		1	
Thwaitesia sp.1	1	2	
Thymoites sp.1	1	2	
Thymoites sp.2	1		
Thymoites sp.3	1		
Theridiosomatidae	2	8	
Chthonos sp.1		7	
Oguhnius sp.1		1	
Naatlo sp.1	2		
Thomisidae	4	7	1
Acentroscelus sp.1		1	
Epicadus sp.1	1	3	1
Strophius sp.1	1		
Tmarus sp.1	2	3	
Trechaleidae	17		
Barrisca sp.1	17		
Uloboridae		3	
Miagrammopes sp.1		3	
Zodariidae			4
Tenedos sp.1			4
Families total	22	16	16
Species total	75	95	25
Specimens total	348	220	49

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Simulated climate change in dry habitats: do spiders respond to experimental small-scale drought?

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Abstract. Ground invertebrates such as spiders react to changing conditions in their terrestrial environments. Due to climate change, changes of species diversity, community composition and ecological traits (e.g., habitat speeialization) can be assumed. Since it is often impossible or impracticable to carry out large-scale investigations concerning the impact of microclimate change on soil arthropods, studies on responses of arthropod communities to simulated climate change at a smaller scale may be a useful alternative. I conducted a field experiment to detect potential changes in species richness, community structure and ecological traits of spiders caused by prolonged drought. In a semi-dry grassland/*Juniperus communis* heath complex, five 16-m^2 plots were subjected to either a drought (excluding all rain) or non-drought treatment. Activity densities of spiders were measured using pitfall traps from July to September, 2008. Although differences in microclimate between treatments were significant, no significant treatment effect on either species richness or activity densities was found. Ordination analyses (NMDS) and multivariate analysis of variance (MANOVA) revealed no significant difference in assemblage composition between the treatments, nor were any changes in ecological traits detected. Spiders were not a suitable model group for detecting any changes in the present study, but comparable experiments yielded changes for at least some spider families and especially for microarthropods. For future small-scale studies I recommend a multi-species group approach with micro- and macroarthropods, using a broad spectrum of sampling techniques.

Keywords: Araneae, dry grassland, global change, heathland, suboceanic climate

Due to global climatic change, microclimate and soil conditions in some places are dramatically changing (Spekat et al. 2006; IPCC 2007). Since most soil invertebrates, such as spiders, react to changing conditions in their terrestrial environments (Frampton et al. 2000; Lindberg et al. 2002; Whitehouse et al. 2002; Lensing et al. 2005), changes in invertebrate diversity, community structure and ecological traits can be expected.

Merkens (2002) stated that the present Atlantic climate of Northwest Germany reduces the extreme character of dry habitats, making them more suitable for habitat generalists. Thus, habitat generalists are very abundant in dry grasslands and heathlands of this area (Merkens 2002; Buchholz 2008; Buchholz & Hartmann 2008). But, as climate changes, species composition should change toward a dominance of drought-resistant habitat specialists that can cope with more extreme microclimatic conditions. Simultaneously, drought-sensitive habitat generalists should decline. Apart from shifts in habitat preferences, further changes in ecological traits due to warming might be detected. For example, since dry and warm habitat conditions favor large-bodied spiders, the proportion of small-bodied species should decrease (Remmert 1981; Entling et al. 2009).

Hence, it seems worthwhile to study responses of soil invertebrates to changes in microclimate. It has already been proven that spiders are a suitable model group to detect such changes. Changes in moisture have direct effects (Dondale & Binns 1977; Rushton et al. 1987; Frampton et al. 2000; Wagner et al. 2003), or in the case of changes in habitat structure, an indirect impact on spider populations (Ward & Lubin 1993; Foelix 1996). Because it is often impossible or at least impracticable to carry out investigations of responses to changing microclimate at a larger scale, studies of small-scale responses of arthropod communities to simulated climate change may provide a useful alternative (Greenslade 1981; Whitford 1992; Hodkinson et al. 1998; Lensing et al. 2005; Lensing & Wise 2006). Thus, the aim of the present study is to investigate spider responses to microclimatic ehanges by focusing on the following hypotheses:

1) Increased drought will reduce species richness and activity density of particular species.
2) The spider community structure will change due to increased drought.
3) The average niche position of the spider community for moisture will shift to more dry and warm conditions (decreasing moisture preference), and the niche width will be reduced (increasing habitat specialization; e.g., number of xerothermophilic species).
4) Species will on average be larger in the drought plots.

METHODS

Study site.—The study was performed in a semi-dry grassland/*Juniperus communis* heath complex with the following vegetation structure (mean ± SD): coverage of herbal layer (20 ± 9%), moss (40 ± 30%), litter (10 ± 5%), bare ground (40 ± 30%), height of herbal layer (10 ± 1.5 cm). The site was located near Münster (51°57′46.6″N, 7°37′43.3″E) in North Rhine-Westphalia, Germany. The climate in this region is suboceanic, with an average annual temperature of 7.9° C and an average annual precipitation of 758 mm (Murl NRW 1989). During the investigation period (July–September 2008) the mean daily temperature was 16.5° C (mean minimum = 12.7° C, mean maximum = 20.7° C). Total rainfall was 42 mm (meteorological station of the Institute of Landscape Ecology, University of Münster).

Study design and sampling.—Five 16-m^2 unfenced plots were each subjected to a drought treatment (drought plots excluding all rain) or a non-drought treatment (control plots), respectively. Thus two treatments were compared with five replicates each. The five treatment pairs (drought/control plot,

side by side) were located randomly in the study site, keeping a minimum distance of 10 m between each other and from *Juniperus* stands. Rainout shelters were placed over the five drought plots on 28 June 2008. The roofs (wooden frame, transparent plastic cover – polyethylene, 0.2 mm thick) were positioned with a slope above each drought plot so that the height on the outside was 60 cm and 80 cm in the middle. The slope ensured that water would immediately flow off the roof. On 11 July 2008 a circle of four pitfall traps (diameter 9 cm, 10 cm apart, filled with a 4% formalin-detergent solution) were installed around the center of each plot. Afterward they were emptied every two weeks until 5 October 2008. The catches were transferred to 75% ethanol, and adult spiders were identified to species level using Roberts (1987, 1998) and Nentwig et al. (2003). The nomenclature follows Platnick (2008).

To compare microclimatic conditions in drought and control plots, air temperature and air humidity were measured once per hour 10 cm above the soil surface in the center of each plot with a data logger (Fourier Systems: MicroLog EC 650 including external temperature sensor). Precipitation data were taken from the Münster meteorological station (Institute of Landscape Ecology, ca. 12 km from the study area).

Statistical analyses.—Species richness was calculated as the number of species per treatment unit (McCune & Grace 2002). Three ecological traits were chosen to investigate responses to treatment: moisture niche position, niche width (Entling et al. 2007) and body size. Niche position values range from 0 to 1, where low values indicate a preference for moist habitats (niche position is 0 for species that prefer the moistest habitats). Low values for niche width include a narrow niche and high habitat specialization. Roberts (1987, 1998) was consulted for the average body sizes of spiders. For all subsequent analyses mean values of females were used.

All statistical analyses were done using the free software environment R 2.9.0 (R Development Core Team 2009) including packages VEGAN (Oksanen et al. 2008) and MASS (Ripley 2008) for multivariate statistics. Prior to the analyses of differences in microclimate and ecological traits between treatments, variables were tested for normal distribution using the Shapiro-Wilk test. If normal distribution of data was not met (even with transformed data) Wilcoxon rank tests were applied. In case of normal distribution, *t*-tests were applied. To detect possible responses of species richness and species activity to increased drought, generalised linear models (GLM) were used. To compensate for overdispersion, standard errors were corrected using a quasi-Poisson model (Crawley 2008; Zuur et al. 2009). Treatments (drought, control) were chosen as predictors for species richness (number of species), total counts of individuals, adults and juveniles.

To analyse differences in species distribution between drought and control plots non-metric multidimensional scaling (NMDS) was used. For ordination, the abundances of each species were square-root transformed and standardized (individual sums/number of sampling days/number of pitfall traps).

Vagrant species that occurred with only one individual per plot were omitted from the analyses to minimize their influence. Altogether, counts of 25 species were subjected to the ordination. For further statistical background about NMDS see Clarke (1993) and McCune & Grace (2002). A maximum of 20 random starts was used in search of a stable two-dimensional ordination model. A multivariate analysis of variance (MANOVA, 10000 permutations) was then performed to establish significant differences between species abundances between treatments and to test whether microclimate (predictor variables: mean temperature, mean maximum temperature, mean minimum temperature, mean air humidity, mean rainfall) had a significant influence on species distribution.

Vagrant species excluded from the analysis: *Alopecosa cuneata* (Clerck 1757), *Enoplognatha thoracica* (Hahn 1833), *Euophrys frontalis* (Walckenaer 1802), *Evarcha falcata* (Clerck 1757), *Heliophanus flavipes* (Hahn 1832), *Malthonica silvestris* (L. Koch 1872), *Meta segmentata* (Clerck 1757), *Micaria fulgens* (Walckenaer 1802), *M. pulicaria* (Sundevall 1831), *Microlinyphia pusilla* (Sundevall 1830), *Philodromus albidus* Kulczyn'ski 1911, *Phrurolithus minimus* C.L. Koch 1839, *Pisaura mirabilis* (Clerck 1757), *Steatoda phalerata* (Panzer 1801), *Tiso vagans* (Blackwall 1834), *Walckenaeria furcillata* (Menge 1869), *Xysticus kochi* Thorell 1872, *Zelotes subterraneus* (C.L. Koch 1833).

RESULTS

A total of 707 adult individuals belonging to 43 species and 357 juvenile spiders was captured. The most abundant species was *Zelotes petrensis* (C.L. Koch 1839) ($n = 218$), representing 32% of all caught specimens. Other frequent species were *Erigone dentipalpis* (Wider 1834) ($n = 80$), *Xerolycosa nemoralis* (Westring 1861) ($n = 79$), *Tegenaria agrestis* (Walckenaer 1802) ($n = 50$) and *Erigone atra* (Blackwall 1833) ($n = 48$).

Different treatments had significantly different microclimates. Mean temperature in drought plots was about 2.5° C and temperature maxima about 7° C higher than in control plots (Table 1). In contrast to this, mean temperature minima showed only a small difference between treatments. The mean air humidity was 10% lower in the drought plots that were totally protected from rain. Although these differences in microclimate between both treatments were significant, GLM indicated no significant effect either on number of species or on total counts of individuals (total, adult, juvenile) (Table 1). After ordination using non-metric multidimensional scaling (stress = 10.3) it was not possible to find any general groupings in species distribution between either treatment (Fig. 1). MANOVA showed no significant difference in assemblage composition of drought and control plots per se ($P = 0.96$). In accordance with this, a further MANOVA indicated no significant impact of any microclimate variable on species abundances (mean temperature: $P = 0.32$, mean temperature maxima: $P = 0.66$, mean temperature minima: $P = 0.58$, mean air humidity: $P = 0.64$, mean rainfall: $P = 0.20$).

No changes in ecological traits were detected (Table 2). Moisture niche position was slightly higher in the drought plots (indicating lower preference for moisture) but differences were not significant. There was no increase in habitat specialization in the drought treatment, since moisture niche width did not differ significantly. Furthermore, the present

Table 1.—Main characteristics of drought and control plots: mean and standard deviation or median and 25% / 75%-quartiles (*) of captured spider species, individuals, adults, juveniles and microclimate (temp. = temperature, ampl. = amplitude). The differences were tested using GLM (F), t-test (t) or Wilcoxon rank test (W).

	Drought plot (n = 5)	Control plot (n = 5)	Test result			
Spiders			F	P		
No. species	17 (4)	15 (5)	0.14	0.71	.	.
No. individuals	111 (32)	101 (33)	0.19	0.67	.	.
No. adults	77 (26)	64 (21)	0.62	0.45	.	.
No. juveniles	34 (8)	37 (15)	0.13	0.73	.	.
Microclimate			t	P	W	P
Temp. [° C]	18.1 (0.1)	15.6 (0.1)	45.60	< 0.001	.	.
Temp. max [° C]	30.9 (30.9/30.9)*	23.9 (23.9/23.9)*	.	.	25	< 0.001
Temp. min [° C]	10.0 (9.9/10.4)*	9.1 (9.1/9.7)*	.	.	25	< 0.05
Day/night ampl. [° C]	20.8 (0.3)	14.6 (0.1)	34.23	< 0.001	.	.
Air humidity [%]	70 (0)	80 (0)	.	< 0.001	.	.
Rain [mm]	0 (0)	42 (0)	.	< 0.001	.	.

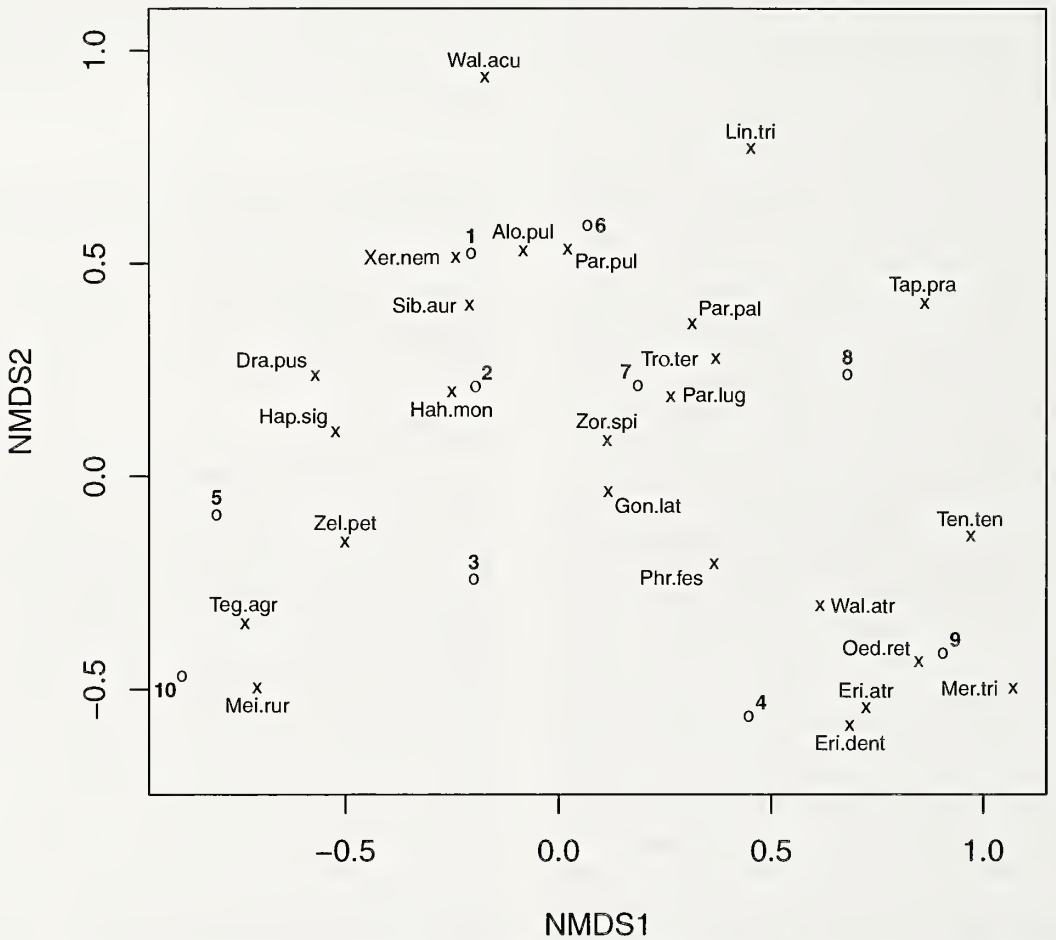

Figure 1.—Non-metric multidimensional scaling (NMDS) ordination (stress = 10.3) based on the Bray-Curtis dissimilarity matrix of spider species in drought (1–5) and control plots (6–10). Abbreviated species names: Alo-pul = *Alopecosa pulverulenta* (Clerck 1757), Dra-pus = *Drassyllus pusillus* (C.L. Koch 1833), Eri-atr = *Erigone atra* (Blackwall 1833), Eri-dent = *E. dentipalpis* (Wider 1834), Gon-lat = *Gongylidiellum latebricola* (O. Pickard-Cambridge 1871), Hah-mon = *Hahnia montana* (Blackwall 1841), Hap-sig = *Haplodrassus signifer* (C.L. Koch 1839), Lin-tri = *Linyphia triangularis* (Clerck 1757), Mei-rur = *Meioneta rurestris* (C.L. Koch 1836), Mer-tri = *Mermessus trilobatus* (Emerton 1882), Oed-ret = *Oedothorax retusus* (Westring 1851), Par-lug = *Pardosa lugubris* (Walckenaer 1802), Par-pal = *P. palustris* (Linnaeus 1758), Par-pul = *P. pullata* (Clerck 1757), Phr-fes = *Phrurolithus festivus* (C.L. Koch 1835), Sib-aur = *Sibianor aurocinctus* (Ohlert 1865), Tap-pra = *Tapinocyba praecox* (O. Pickard-Cambridge 1873), Teg-agr = *Tegenaria agrestis* (Walckenaer 1802), Ten-ten = *Tenuiphantes tenuis* (Blackwall 1852), Tro-ter = *Trochosa terricola* Thorell 1856, Wal-acu = *Walckenaeria acuminata* Blackwall 1833, Wal-atr = *Walckenaeria atrotibialis* O. P.-Cambridge 1878, Xer-nem = *Xerolycosa nemoralis* (Westring 1861), Zel-pet = *Zelotes petrensis* (C.L. Koch 1839), Zor-spi = *Zora spinimana* (Sundevall 1833).

Table 2.—Means (± SD) of ecological traits of spiders in the drought and control plots. The lower the values of moisture niche position the stronger the preference for moist habitats. Low values of niche width indicate a narrow niche (cf. Entling et al. 2007). Body size referred to the average body size of females. The differences were tested using *t*-tests.

Ecological trait	Drought plot	Control plot	*t*	*P*
Moisture niche position	0.456 ± 0.04	0.438 ± 0.04	0.697	0.51
Moisture niche width	0.177 ± 0.01	0.174 ± 0.01	0.495	0.63
Body size [mm]	4.81 ± 0.55	4.96 ± 0.62	0.396	0.70

results indicated that species were not on average larger in the drought plots.

DISCUSSION

The present experiment revealed no responses of spider fauna to altered drought at a small scale. Although microclimatic conditions in drought and control plots differed signifieantly, it was not possible to detect any differences in spider fauna. Neither the total speeies richness nor the activity densities of spider species and species composition differed between treatments. Furthermore, no significant changes in ecological traits (e.g., increasing habitat specialization) could be found.

There are several explanations for missing responses to changes in microclimate. First, the size of the plots could have been too small. Especially highly mobile spiders may be able to cope with unsuitable habitat conditions in a small area of 16 m^2. On the other hand, Muff et al. (2009) showed that spider assemblages can change considerably within a few meters. Second, this study was planned to simulate a dry spell during the summer months, July to September, since changes in rainfall are expected to have the most significant effects. However, this study period could have been too short. Although the microclimate was significantly different in the drought plot, it may require more than three months until the soil is totally parched, especially because of the effect of dew formation at night. Nevertheless, one can conclude that a single drought period extending over three months had no significant impact on the spider fauna of dry grasslands and heathlands in the suboceanic climate region. As opposed to this, annual dry spells due to long-term climate change may indeed have an increasing impact on spider fauna. Lastly, the microclimatic conditions may not have been extreme enough to have an impact on spiders. Many species may have a wider ecological amplitude than assumed and thus be able to cope with higher temperatures and increasing drought than studied here.

Considering possible biases of the present experimental setup, further studies should last longer; for example, starting in May. Drought is expected to have a stronger impact during spring and early summer when precipitation is usually higher than in midsummer. On the other hand, spiders may be more influenced by drought during their breeding season; i.e., from April to June (cf. Tretzel 1954; Merrett 1967, 1968; Foelix 1996). Furthermore, larger shelters may be more suitable for detecting changes in speeies richness, abundance, composition or ecological traits in response to increasing drought. Lastly, it is strongly recommended to use a range of sampling techniques for further studies, including litter extraction (cf. Wagner et al. 2003), since responses of spider densities to changing microclimate seem to be more complex than what may be revealed by pitfall trapping alone. During this study, at least the small-bodied spiders were expected to respond to drought. Most of them are web-building species, such as Dictynidae, Linyphiidae or Theridiidae that have a small habitat size and thus might be influenced by changing microclimate. A general problem of this experiment may have been the use of only one sampling method. Several species may have responded to altered drought, but these responses were not detected by means of pitfall trapping. Pitfall trapping favors ground-dwelling spiders, but might be inappropriate for capturing species normally occurring in higher strata (Merrett & Snazell 1983; Harwood et al. 2001, 2003; Wagner et al. 2003).

Further investigations are necessary in order to understand the mechanisms underlying the responses of spiders in terms of species richness, community composition and ecological traits to microclimatic changes. Spiders were not a suitable model group to detect any changes during the present study. In contrast to this study, Frampton et al. (2000) and Lensing et al. (2005) observed effects of drought and altered precipitation on some spider families (e.g., Gnaphosidae). But, when comparing these results one have to keep in mind that all studies were conducted in habitat types providing totally different initial conditions (Frampton et al. 2000 - farmland, Lensing et al. 2005 - oak-maple forest, present study - dry grassland) that might determine the effect of changing microclimate (e.g., changes due to increased drought may be more drastic in humid than in dry habitats). However, comparable experiments yielded significant changes for microarthropods such as Collembola, Mesostigmata and Oribatida (Lindberg et al. 2002; Lensing et al. 2005). Within this context, Lindberg et al. (2002) outlined the suitability of oribatid mites as bioindicators, since oribatids have a low dispersal ability and low reproductive rates (MacLean et al. 1977; Hopkin 1997). In conclusion, for future small-scale studies I would recommend a multi-species group approach comprising micro- and macroarthropods using a broad spectrum of sampling techniques.

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Vaejovis montanus (Scorpiones: Vaejovidae), a new species from the Sierra Madre Occidental of Mexico

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Abstract. A new species of montane scorpion is described from the Sierra Madre Occidental of Mexico. The species is morphologically similar to scorpions distributed throughout the "sky island" region of the southwestern United States and northwestern Mexico and is a member of the "vorhiesi" subgroup of the *Vaejovis* "mexicanus" group. The morphology of the new species is compared to that of "vorhiesi" subgroup taxa, and biogeographic hypotheses about the diversification of this group are provided.

Keywords: Scorpion, "mexicanus" group, "vorhiesi" subgroup, taxonomy

The *Vaejovis* "mexicanus" group is a heterogeneous mix of scorpions comprised mostly of small, mountain-dwelling species that prefer similar habitat (Sissom 2000; Graham 2007). The group is relatively widespread in North America, occurring from as far south as the Mexican state of Chiapas, north to southern Utah, and east to North Carolina in the United States. Several of these scorpions are morphologically similar (and presumably closely related) and occur in geographic proximity, together comprising the "vorhiesi" subgroup (Soleglad & Fet 2008). Species in this subgroup (*V. cashi*, *V. deboerae*, *V. feti*, *V. paysonensis*, and *V. vorhiesi*) are disjunctly distributed throughout the mountain isolates of southern Arizona and New Mexico and northwestern Mexico in a region referred to as the "sky islands."

Strikingly rich in biodiversity (Warshall 1995), the sky island region forms an archipelago of mesic mountain habitat flanked by vast expanses of desert and grassland plains. The sky islands provide a link between the northern Sierra Madre Occidental and the southern Rocky Mountains, effectively acting as a stepping stone of montane ecosystems (Holycross & Douglas 2007). Interestingly, however, the "mexicanus" group has never been documented in the well-studied Rocky Mountains, suggesting that these generally abundant and accessible scorpions likely do not occur there at all. Given that the "mexicanus" group is widespread in Mexico and conspicuously lacking from the Rocky Mountains, it is plausible that the ancestral stock of the "vorhiesi" subgroup came from the Sierra Madre Occidental. This has led to the suggestion that explorations of the Sierra Madre Occidental mountain ecosystems would reveal undescribed "mexicanus" group species (Sissom 2000).

As predicted, while searching under rocks, logs, and pine-oak forest litter during herpetofaunal surveys in the Sierra Madre Occidental, we discovered a new species of scorpion belonging to the "vorhiesi" subgroup of the "mexicanus" group. Presented herein is a description of the new species, with comments on the biogeographic implications of this discovery.

METHODS

Measurements are as described by Stahnke (1970), trichobothrial patterns are as in Vachon (1974) and Soleglad & Fet (2003), pedipalp finger dentition follows Soleglad & Sissom (2001), and hemispermatophore terminology is from Soleglad & Fet (2008). Ventral submedian setal counts on metasomal segments I to IV are presented as the number of pairs of setae on each metasomal segment between the anterior and posterior margins, beginning with segment I, with counts for each segment separated by a semicolon. For measurements, the words "length", "width", and "depth" are abbreviated as L, W, and D. Total lengths were measured from the anterior margin of the carapace to the aculeus tip with the telson fully extended.

Acronyms of depositories.—CAS, California Academy of Sciences, San Francisco, California, USA; UANL, Universidad Autónoma de Nuevo León, Mexico; MRG, personal collection of Matthew R. Graham, Las Vegas, Nevada, USA.

Material examined (other than types).—*Pseudouroctonus apacheanus* (Gertsch & Soleglad 1972): MEXICO: *Sonora*: 14.2 km E of Yécora on Hwy 16, 5.3 km S on dirt road E of kilometer marker 294, 28.3384°N,108.8331°W, 1772 m, 25 August 2007, M.R. Graham & R.W. Bryson, Jr., 2 ♀ (CAS); El Horquetudo, ca 16 km S Yécora, 28.2663°N,108.8907°W, 1920 m, 10 July 2008, R.W. Bryson, Jr., 1 ♀ (MRG).

Vaejovis cashi Graham 2007: USA: *Arizona*: Herb Martyr Canyon, Chiricahua Mountains, Cochise County, 31.8901°N,109.1686°W, 1530 m, 15 March 2008, R.W. Bryson, Jr., 8 ♀ (MRG).

Vaejovis feti Graham 2007: USA: *New Mexico*: Meadow Creek, Grant County, 6 July 1978, M. Muma, 1 ♂, 1 ♀ (MRG).

Vaejovis franckei Sissom 1989: MEXICO: *Oaxaca*: Cerro Corral del Piedra, 17.1696°N, 96.6571°W, 3270 m, 18 June 2007, R.W. Bryson, Jr. & F. Mendoza-Quijano, 1 ♂, 6 ♀ (CAS).

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Vaejovis paysonensis Soleglad 1973: USA: *Arizona*: Payson, Gila County, 2001, D. Vernier, 1 ♀ (MRG).

Vaejovis vaquero Gertsch & Soleglad 1972: MEXICO: *Chihuahua*: Sierra del Nido, 29.506111°N,106.748556°W, 2731 m, 27 July 2007, R.W. Bryson, Jr., 2 ♀ (CAS).

Vaejovis vorhiesi Stahnke 1940: USA: *Arizona*: Cave Creek Canyon, Santa Rita Mountains, Santa Cruz County, 31.7130°N,110.8241°W, 1890 m, 20 March 2008, R.W. Bryson, Jr., 1 ♂, 3 ♀ (MRG).

Figures 1–2.—*Vaejovis montanus* new species, male holotype (CAS). 1. Dorsal aspect. 2. Ventral aspect. Scale bar represents 5 mm.

TAXONOMY

Family Vaejovidae Thorell 1876
Subfamily Vaejovinae Thorell 1876
Genus *Vaejovis* Koch 1836

Vaejovis Koch 1836:51.

Type species.—*Vaejovis mexicanus* Koch 1836, by monotypy.

Vaejovis montanus new species
(Figs. 1–6, 8–24)

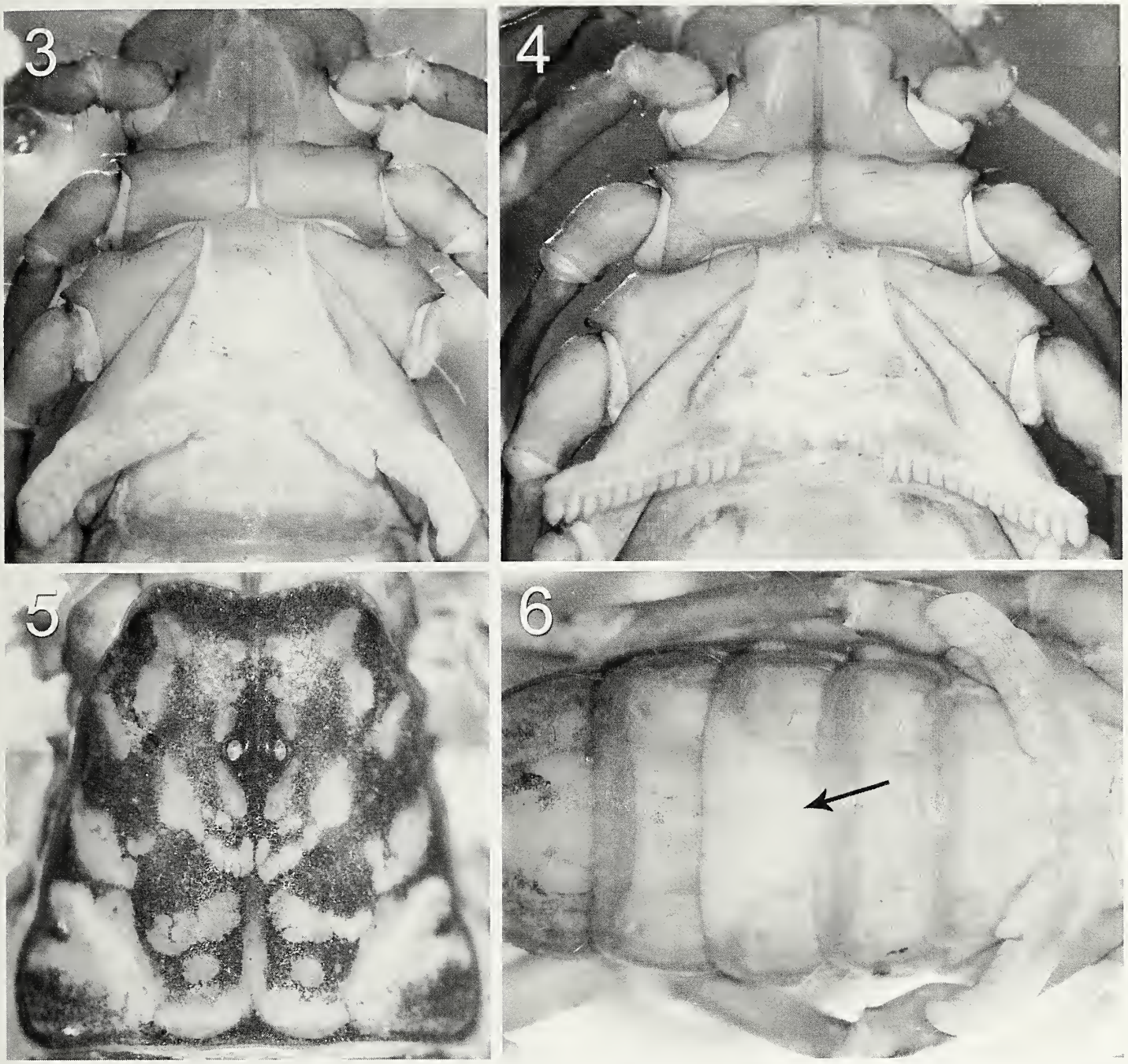
Type material.—MEXICO: *Chihuahua*: male holotype, Sierra Madre Occidental southeast of Zorillo, a small ejido ca 5 km SW Guadalupe y Calvo, 26.0398°N,106.9396°W, 2625 m, 14 July 2008, R.W. Bryson, Jr., M. Torocco, & F. Mendoza-Quijano (CAS Type No. 18488). Paratypes: 5 females, collected with holotype (CAS); 1 male, 5 females, collected with holotype (UANL).

Other material examined.—MEXICO: *Sonora*: 2 females, El Horquetudo, ca 16 km S Yécora, 28.2663°N,108.8907°W, 1920 m, 10 July 2008, R.W. Bryson, Jr. (CAS).

Etymology.—The specific epithet is the Latinized form of "montane," referring to high-elevation habitats in the Sierra Madre Occidental where the species was discovered.

Diagnosis.—Small, with females slightly larger than males (up to approximately 34.2 mm for females). Brown base color with darker mottling on the carapace, legs, tergites, and metasoma (Figs. 1, 2, 5). Males with an area of reduced pigmentation on sternite V, herein referred to as the 'white patch' (Fig. 6). Hemispermatophores lamelliform with well developed distal lamina and distinct distal crest about 1/3 length of lamina (Figs. 16, 17). Possesses following criteria of the "mexicanus" group (Soleglad 1973): genital operculum of females divided on posterior 1/5; fixed finger equal or longer than palm width; inner ventral carina of chelal palm variable, from obsolete to well developed; chelal trichobothria *ib* and *it* are located proximally on the fixed finger, not on palm; anterior margin of carapace concave but not deeply bilobed. Further distinguishable from all other vaejovids in the following combination of characters: pectine count 11–13 (Figs. 3, 4); 7 ID denticles on the pedipalp movable finger (Fig. 15) and 6 on the fixed finger. This species is a member of the "vorhiesi" subgroup, all of which are small (total L of 33 mm or less), inhabit montane forests, have single pair of distal spinules on ventral surface of leg tarsus, and have trichobothrum *Db* ventral to *D1* carinae on chelal palm (Graham 2007; Ayrey 2009; Soleglad & Fet 2008).

It appears that *V. montanus* is also closely related to *V. vaquero* (Fig. 7), a montane species endemic to the Sierra del Nido Mountains in north-central Chihuahua (Sissom & Hendrixson 2005) that should also be considered a member of the "vorhiesi" subgroup. In fact, *V. montanus* is morphologically most similar to *V. vaquero*, since both share ID denticle counts, have similar femur and patella L/W ratios, and overlap in pectine tooth counts. However, *V. montanus* can be distinguished from *V. vaquero* and all other known sky island *Vaejovis* species by the following combination of characters: large adult size (26.7–34.2),



Figures 3–6.—*Vaejovis montanus* new species. 3. Pectines and sternum, male holotype. 4. Pectines and sternum, female paratype. 5. Carapace, male holotype. 6. White patch (arrow), an area of reduced pigmentation, on sternite V, male holotype.

more robust femur (L/W ratio 2.58–2.92) and pedipalp (L/W ratio 2.25–2.83), 7 ID denticles on the pedipalp movable finger and 6 on the fixed finger, pectine count 11–13, 6–7 middle lamellae, and darker coloration with strong mottling. A comparison of taxonomically important characters is provided in Table 1.

Vaejovis montanus can be further distinguished from other sky island *Vaejovis* species by possessing a more horizontally aligned external median (*em*) trichbothria series on the pedipalp patella (Figs. 8–13), and by differences in the white patch on sternite V in adult males. In *V. montanus*, the white patch is large and V-shaped, comprising about 50% of the surface area of the sternite, whereas in both *V. deboerae* and *V. feti* the white patch is restricted to the posterior 1/3 of the sternite and not nearly as pronounced. Unfortunately, adult male specimens of the other sky island *Vaejovis* species are lacking, so the presence or absence of the white patch in those species remains unknown.

Superficially, *V. paysonensis* from central Arizona could also be confused with *V. montanus*. However, this species has more elongated chelae, less robust pedipalp patellae, faded mottling, and a lighter coloration. Another species, *V. pequeno* (currently *incertae sedis*) is similar in general morphology and has been found at mid-elevations in central and southeast

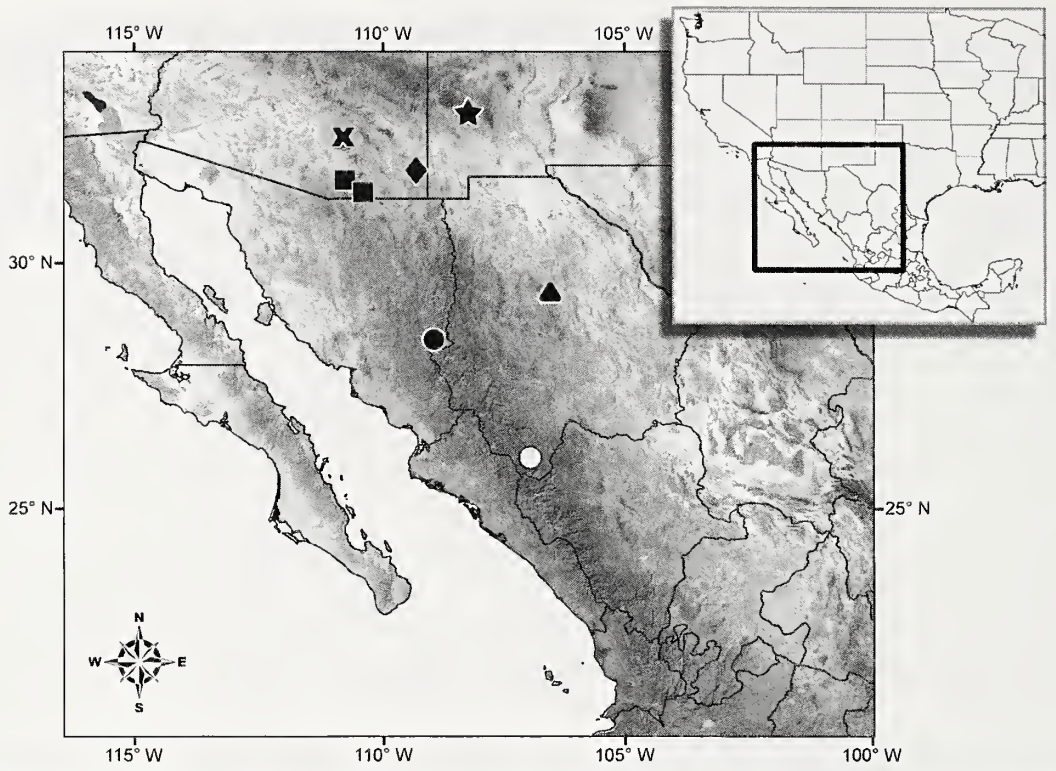
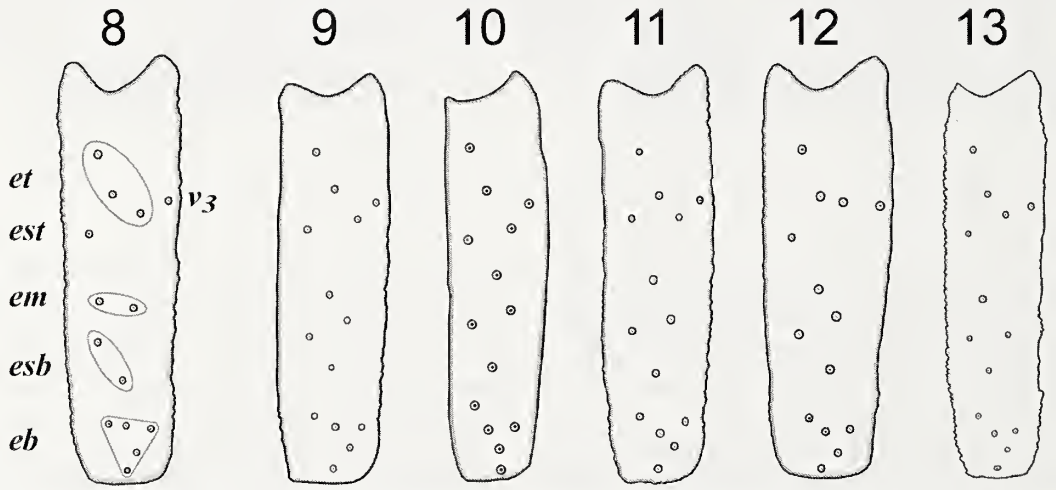


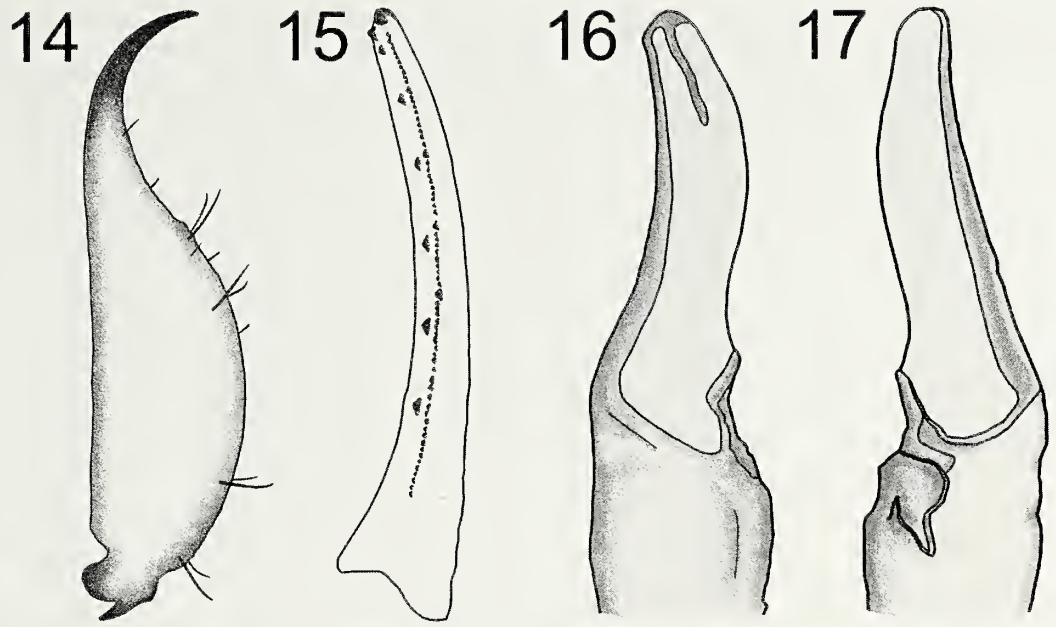
Figure 7.—Distribution of *Vaejovis montanus* new species (circles) and four closely related "mexicanus" group species: *V. cashi* Graham (diamond), *V. deboerae* Ayrey (X), *V. feti* Graham (star), *V. vaquero* Gertsch & Soleglad (triangle), and *V. vorhiesi* Stahnke (squares). The white circle depicts the type locality of *V. montanus*.

Sonora (Hendrixson 2001). This species, however, can readily be distinguished from *V. montanus* by its smaller adult size (adults up to 19.85 mm in *V. pequeno*) and position of trichobothria *ib* and *it* just basal to sixth inner accessory denticles (positioned at the base of the fixed finger in *V. montanus*). Furthermore, *V. montanus* is located in high elevation pine-oak forests in the Sierra Madre Occidental and is not known to be sympatric with any other "mexicanus" group species.

Description of holotype.—*Color:* Carapace, tergites, femur, patella, legs, and metasoma with a yellow-brown base color and mottled with dark brown to black markings dorsally. Pedipalp chela also mottled but with a reddish-brown base color. Chelicerae yellow-brown with mottling on distal 1/2. Telson reddish-brown with two light colored stripes ventrally. Pectines and genital operculum light yellow to light orange, and there is a white patch (area of reduced pigmentation) on sternite V in males.

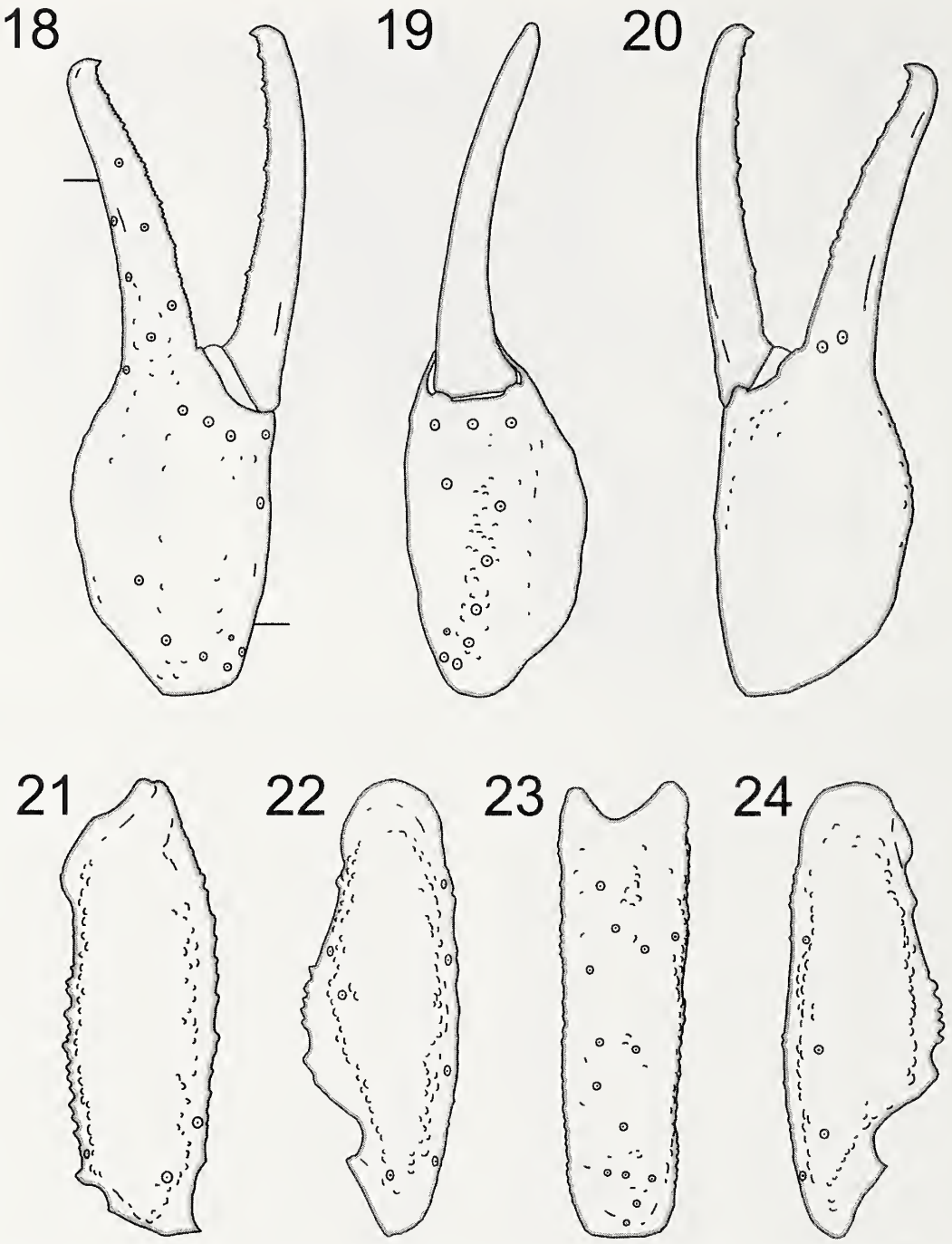


Figures 8–13.—Trichobothrial patterns of pedipalp patellae (external view) of "sky island" *Vaejovis* species. 8. *V. montanus* new species, holotype male. 9. *V. cashi*, holotype female. 10. *V. deboerae*, holotype female, adapted from Ayrey (2009). 11. *V. feti*, holotype male. 12. *V. vaquero*, female. 13. *V. vorhiesi*, holotype female. Trichbothrial abbreviations: eb = external basal; esb = external suprabasal; em = external median; est = external subterminal; et = external terminal; v3 = ventral trichobothrium number 3.



Figures 14–17.—*Vaejovis montanus* new species, male holotype. 14. Telson, lateral view. 15. Movable finger of right pedipalp. 16. Right hemispermatophore, dorsointernal view. 17. Right hemispermatophore, ventral view.

Morphology: Carapace: anterior margin slightly emarginate, with three lateral eyes on each side; moderately convex dorsolaterally; finely granular with scattered small granules; median furrow slight and traversing length of carapace, excluding the median eyes; ratio of median eyes location (distance from anterior edge)/carapace L = 0.35; carapace L/W at median eyes = 1.37. Tergites: coarsely granular with weak median carinae from distal 1/2 of tergite I to proximal half of VII; strong granular dorsolateral and lateral supramedian carina on posterior 4/5s of VII; pretergites very finely granular. Sternites: III–VI smooth to very finely granular and without carinae; VII with granular ventral lateral carinae on posterior 1/5 to posterior 3/5s. Spiracles: ovoid with median side rotated 35° away from posterior sternite margin. Genital Operculum: sclerites separated on posterior 1/5 with genital papillae protruding well beyond posterior of operculum plates. Pectines: tooth count 11/12; middle lamellae 7/7; sensorial areas present on all pectine teeth (sensorial areas present on all teeth in females, but slightly reduced on the most basal tooth). Metasoma: ratio of segment I L/W 0.80; segment II L/W 0.88; segment III L/W 1.06; segment IV L/W 1.46; segment V L/W 2.22. Segments I–IV: dorsolateral carinae strong and serrate with distal denticle of II–IV enlarged and spinoid; of segment I only slightly enlarged and spinoid with serration of carina less pronounced; lateral supramedian carinae I–III with serrated granules and enlarged spinoid distal denticle; carinae of segment IV less pronounced, crenulate to serrate, and flared on distal terminus; space between dorsolateral and supramedian carinae of segments I–III with several scattered granules; lateral inframedian carinae serrulate to finely crenulate on length of segment I, posterior 1/4 of II, 1/5 of III, and absent on IV; ventrolateral carinae I weak and crenulate to serrulate; on II–III serrulate to serrate; on IV serrate; ventral submedian carinae granular to serrulate on I and serrate to crenate on II–IV; dorsal and lateral intercarinal spaces very finely granular; ventral submedian setae pairs 3:3:3:3. Segment V: dorsolateral carinae moderate, distally crenulate, basally granular to serrate; lateromedian carinae moderate and granular on basal 2/3, obsolete on distal 1/3; ventrolateral and ventromedian carinae moderate and serrate; ventromedian carinae continuous and straight for full length of segment, not posteriorly bifurcated; intercarinal spaces finely granular; ventrolateral setae pairs 5. Telson: smooth to slightly granular with very small bump in place of a subaculear tubercule; LAS denticles (Fet et al. 2006) lacking. Chelicerae: dorsal edge of movable cheliceral finger with two subdistal (sd) denticles; ventral edge smooth with well developed serrula comprised of approximately 20 tines on distal half. Pedipalps: trichobothrial pattern type C (Figs. 18–24); ratio of chela L/W = 3.85; femur L/W = 2.84; patella L/W = 2.83; fixed finger L/carapace L = 0.73. Chela: carinae weak and smooth except for a few weak to moderate granules on D4 and D5; median (MD) denticles of fixed finger aligned and divided into six sub rows by five outer (OD) denticles; flanked by six inner (ID) denticles; movable finger with six sub rows, five OD denticles and seven ID denticles; movable finger shorter than both the carapace and metasomal segment V. Femur: dorsoexternal, dorsointernal, and ventrointernal carinae crenulate, ventroexternal with several strong serrations; internal surface with scattered granules on the proximal 3/4s. Patella: internal carinae oblique and granulose; all other carinae strong and crenulate. Legs: ventral surface of tarsus with single median row of spinules terminating distally with one spinule pair. Hemispermatophore (Figs. 16, 17): Lamelliform type with well developed distal lamina with a distinct distal crest about 1/3 the length of the lamina; truncal flexure present but not conspicuous. Slight basal constriction located just proximal of lamina midpoint where it terminates in well-developed intact (not bifurcated or grooved) lamellar hook. Lamellar hook is moderately elongated and about1/4 the lamina length. A sclerotized mating (= sperm) plug was not found in either hemispermatophore.



Figures 18–24.—Trichbothrial patterns of *Vaejovis montanus* new species, based on male holotype. 18. Right pedipalp chela, external. 19. Right pedipalp chela, ventral. 20. Right pedipalp chela, internal. 21. Right pedipalp femur, dorsal. 22. Right pedipalp patella, dorsal. 23. Right pedipalp patella, external. 24. Right pedipalp patella, ventral.

Mensuration (mm): Male holotype: total L = 28.16; carapace L = 3.39; mesosoma L = 7.35; metasoma L = 10.22 (excluding telson); Metasoma: segment I L/W = 1.41/1.77; segment II L/W = 1.55/1.77; segment III L/W = 1.77/1.67; segment IV L/W = 2.33/1.60; segment V L/W = 3.39/1.53. Telson: L = 3.60; vesicle L/W/D = 2.31/1.29/1.06; aculeus L = 1.29. Pedipalps: total L = 10.87; femur L/W = 2.73/0.96; patella L/W = 3.06/1.08; chela L = 5.08; palm L/W/D = 2.47/1.32/1.62; movable finger L = 3.06; fixed finger L = 2.47. Female allotype: total L = 31.73; carapace L = 3.93; mesosoma L = 11.55; metasoma L = 12.05 (excluding telson); Metasoma: segment I L/W/D = 1.57/2.26/1.81; segment II L/W/D = 1.86/2.14/1.79; segment III L/W/D = 1.90/2.10/1.81; segment IV L/W/D = 2.62/2.05/1.79; segment V L/W/D = 4.10/1.86/1.57. Telson: L = 4.21; vesicle L/W/D = 2.67/1.57/1.21; aculeus L = 1.55. Pedipalps: total L = 12.38; femur L/W = 3.19/1.19; patella L/W = 3.38/1.36; chela L = 5.81; palm L/W/D = 2.62/1.52/1.83; movable finger L = 3.60; fixed finger L = 2.81. Female (El Horquetudo locality): total L = 26.74; carapace L = 3.26; mesosoma L = 10.24; metasoma L = 10.05 (without telson); Metasoma: segment I L/W/D = 1.31/1.88/1.57; segment II L/W/D = 1.52/1.79/1.52; segment III L/W/D

Table 1.—Distribution of selected characters in *Vaejovis montanus* new species, and related "mexicanus" group species. Average values are presented with minimum and maximum values in brackets. One-way ANOVA used to compare means of all female total lengths and morphometric ratios, and Student's t-test was used to compare the female character means of each species to that of *V. montanus*. Data on *V. deboerae* are from Ayrey (2009). Significantly different means indicated by asterisks (* $P < 0.05$; ** $P < 0.001$).

	Females						Males			
	montanus	*cashi*	*deboerae*	*feti*	*vaquero*	*vorhiesi*	*montanus*	*deboerae*	*feti*	*vorhiesi*
n =	12	7	2	3	3	4	2	1	3	1
Total length ($F = 24.2$, $P < 0.001$)	30.6 [26.74–34.2]	21.77** [20–24.6]	32.65* [32.2–33.1]	22.19** [21.8–22.4]	25.67* [23.8–28]	26.15* [24.28–28.5]	27.15 [26.7–27.6]	25.47	17.4 [16.8–18]	19.5
Pedipalp femur L/W ($F = 9.6$, $P < 0.001$)	2.75 [2.58–2.92]	2.89* [2.74–3.03]	2.82 [2.74–2.89]	2.92* [2.89–2.97]	2.74 [2.72–2.77]	3.06** [3–3.13]	2.89 [2.84–2.93]	2.89	3.03 [2.92–3.15]	3.17
Pedipalp patella L/W ($F = 12.45$, $P < 0.001$)	2.64 [2.55–2.71]	2.84* [2.67–3]	3.00 [2.91–3.09]	2.77* [2.74–2.82]	2.53 [2.48–2.58]	2.9* [2.82–2.98]	2.81 [2.80–2.83]	2.95	2.98 [2.93–3.04]	3
Pedipalp palm L/W ($F = 24.64$, $P < 0.001$)	1.67 [1.6–1.73]	1.89** [1.79–2]	1.97 [1.91–2.03]	1.72 [1.68–1.78]	1.53* [1.49–1.57]	1.82* [1.69–1.9]	1.75 [1.62–1.87]	1.87	1.66 [1.62–1.71]	2.07
Carapace L/Palm L ($F = 5.98$, $P < 0.01$)	1.51 [1.45–1.68]	1.68** [1.61–1.73]	1.50 [1.36–1.63]	1.67 [1.56–1.84]	1.54 [1.52–1.55]	1.64** [1.62–1.68]	1.38 [1.37–1.38]	1.41	1.66 [1.64–1.67]	1.74
Carapace L/Palm W ($F = 17.18$, $P < 0.001$)	2.52 [2.35–2.82]	3.18** [3.05–3.4]	2.88 [2.77–3.11]	2.88 [2.76–3.09]	2.51 [2.26–2.85]	2.99** [2.85–3.15]	2.41 [2.24–2.57]	2.63	2.76 [2.7–2.86]	3.6
Carapace L/Patella L ($F = 5.68$, $P = 0.01$)	1.14 [1.11–1.19]	1.13 [1.11–1.15]	1.05 [1.03–1.06]	1.22 [1.15–1.35]	1.13 [1.12–1.14]	1.11 [1.06–1.16]	1.10 [1.08–1.11]	0.99	1.65 [1.62–1.69]	1.8
Pectine teeth	12.0 [11–13]	11.0 [10–12]	11.75 [11–13]	10 [10]	13.33 [11–15]	13 [12–14]	12.25 [11–13]	14	11.67 [11–12]	14.5 [14–15]
Middle lamellae	6.86 [6–7]	6.5 [6–7]	7	6 [6]	8	7.29 [7–8]	7	7	6	8
Movable finger ID Denticles	7	6	6	6	7	6	7	6	6	6
Fixed finger ID denticles	6	5	5	5.33 [5–6]	6	5.5 [5–6]	6	5	5.33 [5–6]	5

= 1.67/1.74/1.55; segment IV L/W/D = 2.21/1.67/1.5; segment V L/W/D = 3.33/1.67/1.43. Telson: L = 3.19; vesicle L/W/D = 2.00/1.19/0.93; aculeus L = 1.19. Pedipalps: total L = 10.19; femur L/W = 2.62/1.05; patella L/W = 2.86/1.10; chela L = 4.71; palm L/W/D = 2.02/1.12/1.33; movable finger L = 2.76; fixed finger L = 2.17.

Variability.—There appears to be little variation between the two known populations of *V. montanus*, with only differences in size of pedipalp chelae noted. Female specimens from Zorillo have slightly larger pedipalp chelae (palm L/carapace L = 0.66−0.69) than that of the two females from El Horquetudo in the north (palm L/carapace L = 0.59−0.63). The shape of the chelae (L/W ratio), however, does not differ between the two populations.

Sexual dimorphism in *V. montanus*, as in most vaejovids, is strong. Males appear to be much smaller in total length and possess smaller and more elongated pedipalps (Table 1). Pectine tooth counts between the sexes are the same, but pectine teeth of adult males are larger. As characteristic of the subfamily Vaejovinae, the sclerites of the genital operculum of females operate as a single unit and are separated on the posterior 1/3 (Soleglad & Fet 2008).

Distribution.—Known only from the type locality in southern Chihuahua and from El Horquetudo near Yécora, Sonora, Mexico (Fig. 7). This species probably occurs throughout much of the intervening Sierra Madre Occidental as well.

Ecology.—This species was found primarily under rocks and logs in small exposed clearings on or adjacent to hillsides within high-elevation mesic pine-oak forests (Fig. 25). We observed *V. montanus* syntopically with two other scorpion species: an unidentified *Centruroides* sp. and *Pseudouroctonus apacheanus*. The latter was only observed at the El Horquetudo locality, representing the first record of this species in Mexico and extending the known range more than 300 km south of other records from mountains in southern Arizona, New Mexico, and Texas (Gertsch & Soleglad 1972).

Biogeography.—The topographic complexity of the Sierra Madre Occidental has profoundly influenced the evolutionary history of highland taxa. The main bulk of the range extends from northern Chihuahua and Sonora south across Durango. To the north and to a lesser degree the south, the sierra is broken up into 'sky island' isolates. Extensive post-Pleistocene development of grasslands and desert has increasingly separated these forested peaks from each other and the main

Figure 25.—High-elevation pine-oak forest habitat at the type locality of *Vaejovis montanus* new species, near Zorillo, Chihuahua. Several specimens of *V. montanus* were found under the rocks in the foreground.

sierra, and mountaintop isolation has likely driven evolutionary diversification of "vorhiesi" subgroup species.

Vaejovis montanus probably occurs throughout the Madrean pine-oak woodlands within the main Sierra Madre Occidental south to at least the type locality near Guadalupe y Calvo in southern Chihuahua. In this region, a series of deep east-west canyons ('barrancas') dissect the mountains and seemingly form a filter barrier for montane taxa (Smith et al. 1997). Several highland-adapted amphibians and reptiles, for example, are taxonomically subdivided north and south of this putative break (Barker 1992; Smith et al. 1997; Duellman 2001). Additional collecting in Durango would verify if the range of *V. montanus* is continuous across this break, or if an undescribed "mexicanus" group scorpion inhabits the mountains of this state.

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A review of the pseudoscorpion genus *Oreolpium* (Pseudoscorpiones: Garypinidae), with remarks on the composition of the Garypinidae and on pseudoscorpions with bipolar distributions

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Abstract. A review of the pseudoscorpion genus *Oreolpium* Benedict & Malcolm reveals two species, the type species *O. nymphum* Benedict & Malcolm 1978 from northwestern USA and *O. semotum*, new species, from southern Tasmania. *Oreolpium* is most similar to *Neominniza* Beier, *Thaumatolpium* Beier and *Teratolpium* Beier from South America, and to *Protogarypinus* Beier from southern Australia. These genera are confirmed as members of Garypinidae, and both species of *Oreolpium* are found to lack glandular setae on sternites VI–VIII, which is an unusual feature for Garypinidae. *Oreolpium* demonstrates a remarkable bipolar distribution, similar to that of the pseudoscorpion groups Pseudotyrannochthoniidae, Pseudogarypidae and Syarininae, and to several water mite taxa.

Keywords: Biogeography, Pangaea, new species, taxonomy

The discovery of the pseudoscorpion *Dracochela deprehendor* Schawaller, Shear & Bonamo 1991 and other arachnids from the Devonian represented a quantum shift in evolutionary studies with the Arachnida, extending the fossil record of most major arachnid lineages to the Paleozoic (Hirst 1923; Hirst & Maulik 1926; Shear et al. 1987; Norton et al. 1988; Kethley et al. 1989; Shear et al. 1989a; Shear et al. 1989b; Shear & Kukalová-Peck 1990; Schawaller et al. 1991; Selden et al. 1991). Whilst *D. deprehendor* could not be assigned to a living family, many of the Mesozoic pseudoscorpions recorded from Cretaceous deposits can be readily assigned to modern families, including Garypinidae (Judson 1997), Cheiridiidae (Judson 2000) and Chernetidae (Schawaller 1991), highlighting that many pseudoscorpion families can trace their origins to at least the Cretaceous. Current hypotheses on the positions of continental blocks during the Mesozoic indicate that after the Jurassic, when the continents were largely coalesced into a single supercontinent Pangaea, the continents fragmented and dispersed (Smith et al. 1994). The continental fragments took with them life forms, many of which have survived to the present. With the majority of the pseudoscorpion families presumably extant by the end of the Mesozoic, it is likely that traces of their past distributions can be discerned if vicariance, rather than dispersal, has occurred (Nelson & Platnick 1981).

Harvey (1998b) documented two distinct pseudoscorpion clades with bipolar distributions – taxa found in the temperate regions of the Holarctic and Gondwanan realms but without any records from intervening regions. The family Pseudogarypidae is currently known from seven Recent species in North America and Tasmania (e.g., Benedict & Malcolm 1978a; Muchmore 1981a; Harvey 2009) and four Tertiary fossil species from European Baltic amber (Beier 1937, 1947; Henderickx et al. 2006). The subfamily Syarininae (a member of the neobisioid family Syarinidae) contains six Recent species of *Syarinus* Chamberlin 1930 in North America and Europe (e.g., Mahnert 1976a; Schawaller 1987; Schmarda 1997; Ducháč 1998; Harvey 2009) and two species of *Anysrius* Harvey 1998 in Tasmania (Harvey 1998b, 2009). The chthoniid subfamily Pseudotyrannochthoniidae also seems to have a bipolar distribution with some found in extreme southern latitudes (*Pseudotyrannochthonius* Beier 1930 in Australia and Chile, and *Afrochthonius* Beier 1930 and *Selachochthonius* Chamberlin 1929 in southern Africa) and others found in northern latitudes (*Pseudotyrannochthonius* in East Asia and western North America, *Allochthonius* Chamberlin 1930 in East Asia, and *Centrochthonius* Beier 1931 in Central and East Asia) (see Harvey 2009). The anomalous presence of two species of *Afrochthonius* in Sri Lanka (Beier 1973) may be the result of vicariance when the Indian subcontinent broke away from Gondwanaland during the late Cretaceous (e.g. Besse & Courtillot 1988; Smith et al. 1994; Scotese 2001).

Recently another pseudoscorpion taxon displaying evidence of bipolar distributions has emerged with the discovery of a small, peculiar pseudoscorpion from southern Tasmania. Initial study of this species suggested a similarity with the genus *Oreolpium* Benedict & Malcolm 1978, only known from the species *O. nymphum* Benedict & Malcolm 1978 from corticolous habitats in northwestern USA (e.g. Benedict & Malcolm 1978b), originally referred to the olpiid subfamily Olpiinae. A reappraisal of the North American species confirmed that the Tasmanian species is indeed congeneric with *O. nymphum*, which shares a number of morphological features with four genera from South America (*Neominniza* Beier 1930, *Teratolpium* Beier 1959 and *Thaumatolpium* Beier 1931) and Australia (*Protogarypinus* Beier 1954). We here present a review of *Oreolpium* and the two known species, and assess their relationships.

METHODS

The material examined in the present study is lodged in the American Museum of Natural History, New York (AMNH); California Academy of Science, San Francisco (CAS); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Natural History Museum, Vienna (NHMW); Tasmanian Museum and Art Gallery, Hobart (TMAG); and Western

Australian Museum, Perth (WAM). Details of the specimens examined are provided in Appendix 1. Terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey 1992) and chelicera (Judson 2007).

Specimens studied by MSH were examined with an Olympus BH-2 compound microscope and those studied by FS were examined with a Leica MZ125 stereomicroscope and a Leitz Diaplan microscope. The illustrations were prepared with the aid of a drawing tube fitted to the Olympus microscope. Measurements were taken at the highest possible magnification using an ocular graticule and are presented in mm. The Tasmanian specimens were examined by preparing temporary slide mounts by immersing the specimens in 75% lactic acid at room temperature for several days and mounting them on microscope slides with 10 or 12 mm coverslips supported by small sections of 0.25 mm or 0.50 mm diameter nylon fishing line. After study the specimens were returned to 75% ethanol with the dissected portions placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.). Some of the type specimens of *Oreolpium nymphum* were originally mounted on microscope slides in Hoyer's medium by E. Benedict or D. Malcolm. Unfortunately the mountant has dried and contracted, probably due to the lack of a suitable ringing compound around the edge of the coverslip, compressing the specimen and the dissected parts such that detailed examination was impossible. Some of these slides were soaked in warm distilled water until the mountant became pliable. The pieces of the specimen were removed from the mountant with fine forceps, rinsed in clean distilled water and transferred to concentrated detergent (Extran 100®). After 10–20 min in detergent the pieces were returned to water where the crushed segments returned to their approximate original shape.

SYSTEMATICS

Family Garypinidae Daday 1888

Garypininae Daday 1888:123, Chamberlin 1930:590–591, Chamberlin 1931:225, Beier 1932: 203, Roewer 1937:263, Hoff 1956:27, Morikawa 1960:129, Hoff 1964:35, Benedict & Malcolm 1978:124, 125, Muchmore 1980:165, Tooren, 2002:470.

Garypinidae Daday: Judson 2005:128.

Remarks.—Since its inception as a family (Chamberlin 1930), the Olpiidae has included two subfamilies, Olpiinae and Garypininae, differing by the morphology of the arolia (not divided in olpiines and divided in garypinines), the tergites (not divided in olpiines and at least some divided in garypinines) and the rallum (two or three blades in olpiines, four blades in garypinines). The Garypininae were treated by Daday (1888) as a subfamily of the Cheliferidae, along with the Cheliferinae and Garypinae, and although he noted the strongly divided arolium in the only included species *Garypinus dimidiatus* (L. Koch 1873), he focused on characters such as the presence of a cheliceral galea, the absence of an epistome on the carapace, the presence of a single furrow on the carapace, the number of eyes and the leg segmentation to segregate the garypinines from the other subfamilies. Apart from the divided arolium, these features are no longer used to define the group. Recently, the garypinines were treated as a separate family from Olpiidae (Judson 1992a, 1993, 2005). In addition to features traditionally used to support the garypinines, Judson (2005) added two character states to support the assignment of the Tertiary fossil *Garypinus electri* Beier 1937 to the Garypinidae: paraxially offset chelal pedicel, and the basal concentration of the trichobothria of the internal series. Looking outside of the Garypinidae, it is apparent that these features are not totally restricted to members of the family, with members of the ideoroncid genus *Albiorix* Chamberlin 1930 also bearing divided arolia, all sternophorids bearing an offset pedicel, and many different pseudoscorpion taxa with basally concentrated internal trichobothria. Indeed, the last two features are not found in all garypinids, as the pedicel is not paraxially offset in *Garypinus afghanicus* Beier 1959 (Beier 1959b, figs. 11, 12), *Garypinidius mollis* Beier 1955 (Beier 1955, fig. 10) or *Serianus galapagoensis* Beier 1978 (Beier 1978, fig. 3) and the internal trichobothria are not always grouped basally, as all described species of *Amblyolpium* Simon 1898 and *Neoamblyolpium* Hoff 1956 clearly have three of these trichobothria situated medially on the internal margin of the chelal finger (e.g., Beier 1932; Hoff 1956; Beier 1959c; Morikawa 1960; Beier 1966b, 1967b, 1970b, 1970a; Heurtault 1970; Lazzeroni 1970; Beier 1971; Mahnert 1976b; Muchmore 1980; Harvey 1988; Tooren 2002).

In addition to the genera traditionally assigned to the Garypininae, several genera originally attributed to the Olpiidae have basally located internal trichobothria with all four trichobothria situated on the internal face of the chela: *Neominniza* from Chile; *Oreolpium* from Oregon, USA; *Protogarypinus* from Australia; *Teratolpium* from Peru; and *Thaumatolpium* from Chile (e.g. Beier 1954, 1959c, 1964, 1975; Benedict & Malcolm 1978b). Of these genera, all except *Neominniza* and *Thaumatolpium* bear the offset pedicel and all of these genera possess divided or at least partially divided tergites (regrettably, the published descriptions of several species fail to specifically mention this feature). Whilst many species of these genera have been reported to have four blades in the rallum, *Teratolpium andinum* Beier 1959 (the sole member of the genus), was reported as possessing only three blades (Beier 1959c), but we were unable to confirm this feature during our examination of specimens of *T. andinum*. Members of these genera lack the divided arolium, which has traditionally served to define the group (e.g. Chamberlin 1930; Beier 1932). As noted below, we believe that these genera are best included in Garypinidae, rather than Olpiidae, as they share several major character states with garypinids.

In addition to the features listed above that serve to define the Garypinidae, most garypinids bear at least one pair of conspicuous glandular setae on the medial portion of the medial sternites slightly forward of the regular setal row, and they may exhibit sexual dimorphism in their shape and size, being slightly smaller in females. A single pair of glandular setae on the medial region of sternites VI, VII and VIII occur in species currently assigned to the following genera: *Aldabrinus* Chamberlin 1930 (Muchmore 1974), *Galapagodinus* Beier 1978 (Beier 1978), *Garypinidius* Beier 1955, *Garypinus* Daday 1888 (Hadži 1933; Mahnert 1988), *Haplogarypinus* Beier 1959 (Beier 1959a), *Hemisolinus* Beier 1977 (Beier 1977), *Indogarypinus* Murthy and Ananthakrishnan

1977 (Murthy & Ananthakrishnan 1977), *Nelsoninus* Beier 1967 (Beier 1967a), *Neominniza* (Beier 1964), *Paraldabrinus* Beier 1966 (Beier 1966b), *Protogarypinus dissimilis* Beier 1975, some species of *Serianus* Chamberlin 1930 (Chamberlin 1930; Beier 1964, 1966a; Mahnert 1988), *Solinellus* Muchmore 1979 (Muchmore 1979), *Solinus* Chamberlin 1930 (Dashdamirov 1996) and *Thaumatolpium* (Beier 1964). Variant morphologies occur in some species of *Serianus* where sternites VI–VII possess multiple glandular setae arranged in two groups and sternite VIII bears paired setae (e.g., Chamberlin 1930; Hoff 1956; Beier 1959c; Hoff 1964; Muchmore 1968; Mahnert 1988), or where sternites VI–VIII each bear a median group of four setae (Muchmore 1981b). Similarly, males, females and nymphs of *Protogarypinus gigantens* Beier 1954 bear multiple glandular setae arranged in two groups on sternites VI, VII and VIII (Harvey personal observation). Species of *Amblyolpium* bear a single pair of glandular setae only on sternites VI and VII, with such setae absent from sternite VIII (e.g., Chamberlin 1930; Beier 1966b, 1970b, 1970a; Heurtault 1970; Beier 1971; Mahnert 1976b; Harvey 1988). Sternal glandular setae are definitely absent in *Pseudogarypinus costaricensis* Beier 1931, *P. frontalis* (Banks 1909) and *P. cooperi* Muchmore 1980 (Harvey & Šťáhlavský, personal observations), and these observations accord with the lack of any mention of these distinctive setae in modern descriptions of species of *Pseudogarypinus* (e.g. Hoff 1961; Benedict & Malcolm 1978b; Muchmore 1980). They are also absent in males and females of *Neoamblyolpium alienum* Hoff 1956 from western USA (Harvey personal observation) and in *Teratolpium andinum* Beier 1959 (Šťáhlavský personal observation). Of the remaining genera attributed to the Garypinidae, the recent description of *Caecogarypinus* Dashdmirov 2007 failed to mention the presence or absence of glandular setae (Dashdamirov 2007). Conspicuous glandular setae are found in a variety of different pseudoscorpions (Judson 1992b), including some members of the Neobisiidae, Syarinidae, Geogarypidae, Garypinidae and Withiidae.

A further feature found in many garypinids but absent from olpiids is the paired and enlarged dorsal anterior glands of the male genital system. These have been found in species of *Aldabrinus* (Muchmore 1974), *Amblyolpium* (Harvey 1988), *Pseudogarypinus* (Muchmore 1980), *Serianus* (Chamberlin 1923; Hoff 1956; Muchmore 1980; Mahnert 1991), *Solinellus* (Muchmore 1979) and *Solinus* (Chamberlin 1923; Dashdamirov 1996) and observed in males of *Galapagodinus* sp., *Neoamblyolpium alienum*, *Neominniza* sp., *Pseudogarypinus frontalis*, *Protogarypinus gigantens*, *Serianus argentinae* Muchmore 1981, *S. dolosus* Hoff 1956, *S. gratus* Hoff 1964, *S. minutus* (Banks 1908), *Solinus* sp. and *Thaumatolpium* sp. (Harvey personal observations). They are clearly absent in *O. nymphum* and *O. semotum* (Figs. 9, 20). We were unable to confirm the presence of these glands in *Teratolpium*, the other putative relative of *Oreolpium*. Similar enlarged glands are present in a few other garypoid genera such as the two genera of Larcidae, *Larca* Chamberlin 1930 and *Archeolarca* Hoff & Clawson 1952 (Harvey personal observation), but appear to be absent from all other garypoids including all members of the Garypidae, Olpiidae and Menthidae (e.g., Vachon 1938; Muchmore 1979; Harvey 1987b; Harvey & Muchmore 1990) (Harvey personal observation).

Therefore, we propose that the Garypinidae and Olpiidae be defined as follows:

Garypinidae: Trichobothrium *isb* (when present) on internal margin of chelal fingers, tergites and sternites usually divided or partly divided, cheliceral rallum of four blades (but apparently only three blades in *Teratolpium*), median sternites usually with conspicuous glandular setae (absent in *Neoamblyolpium*, *Oreolpium*, *Pseudogarypinus* and *Teratolpium*), arolium usually divided (but not divided in *Neominniza*, *Oreolpium*, *Protogarypinus*, *Teratolpium* and *Thaumatolpium*), chela with paraxially offset pedicel (except in *Neominniza* and *Thaumatolpium*), male genitalia with paired and enlarged dorsal anterior gland (except in *Oreolpium*). See Table 1 for a list of genera included within the Garypinidae.

Olpiidae: Trichobothrium *isb* on external margin of chelal fingers; tergites and sternites not divided; cheliceral rallum of three blades, occasionally reduced to two blades (*Neopachyolpium*, *Aphelolpium* and *Planctolpium*); median sternites without conspicuous glandular setae; arolium not divided; chela without paraxially offset pedicel; male genitalia without paired and enlarged dorsal anterior gland. The majority of features used to diagnose the Olpiidae do not, however, appear to be synapomorphic, as all of the character states listed above are generally plesiomorphic within the Garypoidea. A list of genera included in Olpiidae is provided by Harvey and Leng (2008).

There is some evidence that garypinids might not be the sister-group to the Olpiidae, despite their long association with each other within the same family. The movement of trichobothrium *isb* onto the internal margin of the fixed chelal finger is also found in all species of the garypoid families Larcidae and Geogarypidae (Harvey 1990, 1992), and the presence of glandular setae on the median sternites is also found in at least some Geogarypidae (Judson 1992b). A recent molecular phylogeny of the Pseudoscorpiones using two nuclear ribosomal genes and one mitochondrial protein-encoding gene found the two garypinids used in the analysis (*Protogarypinus giganteus* and *Pseudogarypinus cooperi*) to nest with *Larca lata* (Hansen 1894) (Larcidae), the neobisioid *Syarinus* sp. (Syarinidae) and the cheliferoid *Neochelanops* sp. (Chernetidae), a very bizarre arrangement given that *Syarinus* and *Neochelanops* have never previously been considered garypoids. These incongruent data suggest that different markers and a greater array of taxa are required to fully assess the relationships of the garypinids.

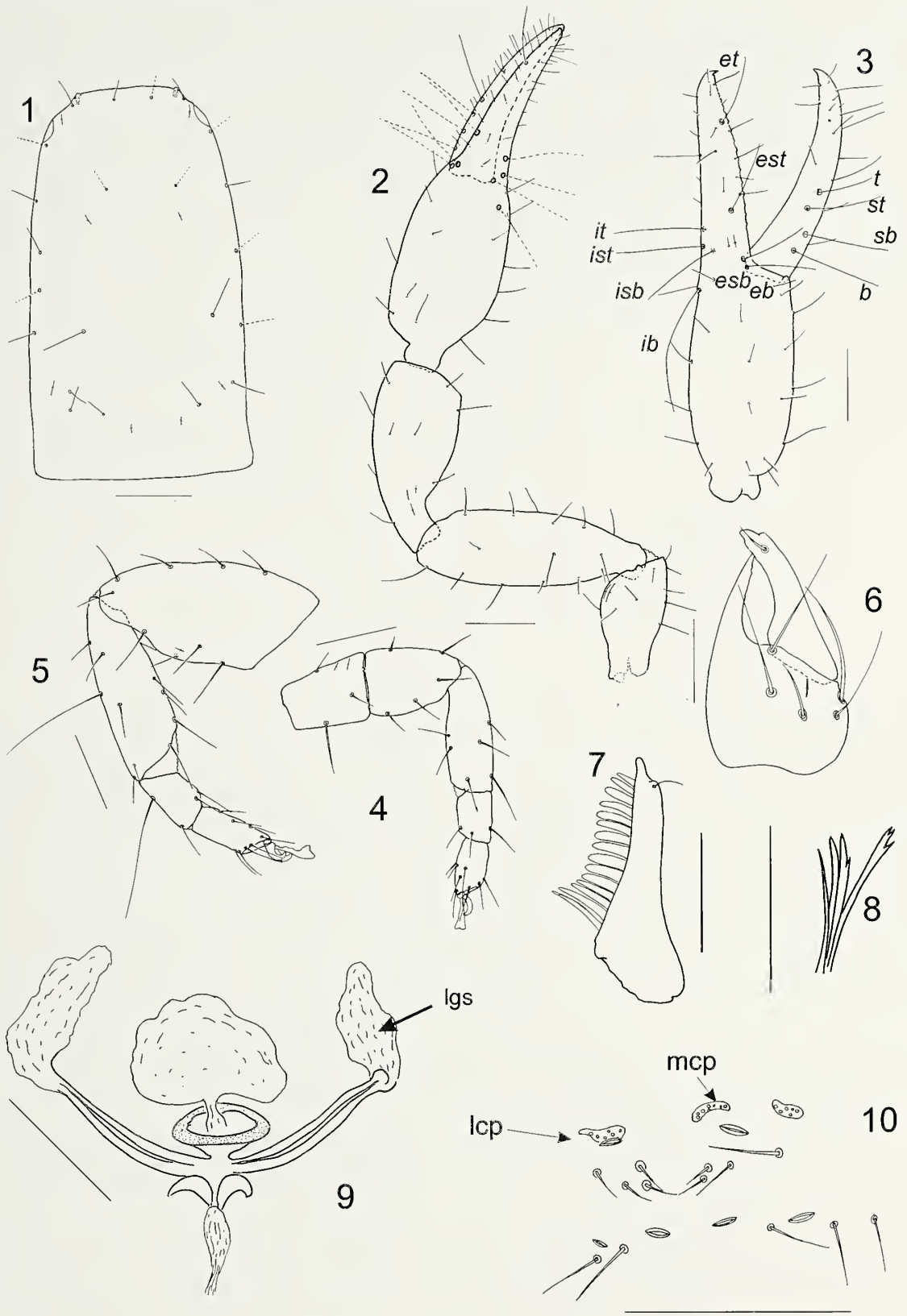
Oreolpium Benedict & Malcolm 1978

Oreolpium Benedict & Malcolm 1978:120, Harvey 1991:294, Harvey 2009:[unpaginated].

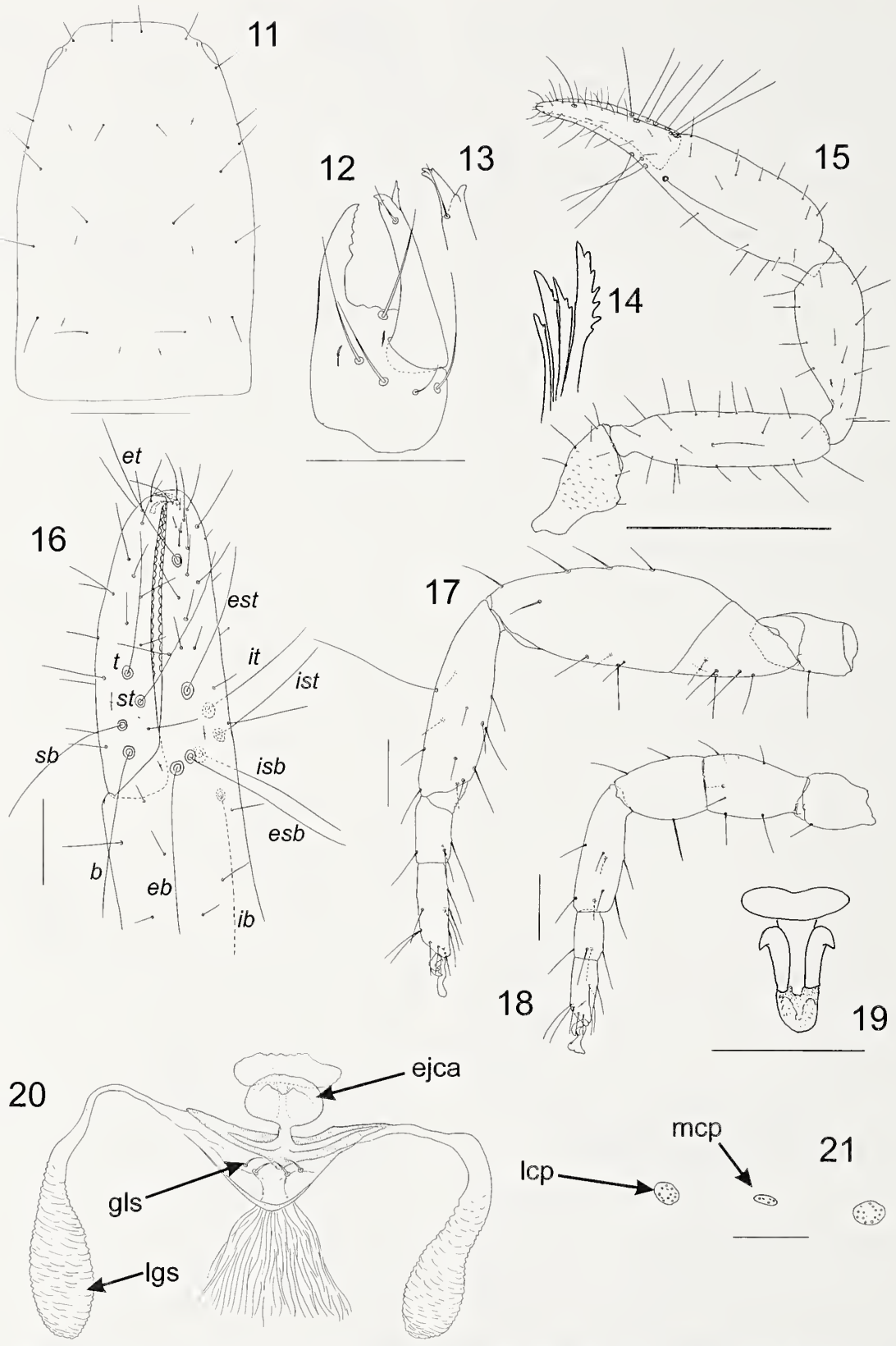
Type species.—*Oreolpium nymphum* Benedict & Malcolm 1978, by original designation.

Diagnosis.—A genus of Garypinidae with the following combination of characters: sternal glandular setae absent; male genitalia without paired dorsal anterior glands; carapace with 1 small pair of eyes and 20–22 setae; cheliceral hand with 5 setae; rallum of 4 blades, all denticulate; pedipalpal femur with 1 or 2 tactile setae; chela with paraxially offset pedicel; arolium much longer than claws, not divided.

Description.—*Chelicera:* With 5 setae on hand, all setae acuminate; movable finger with 1 subdistal seta; subterminal



Figures 1–10.—*Oreolpium nymphum* Benedict & Malcolm 1978: 1. Carapace, dorsal aspect, female paratype (CAS, EB-1634.01002); 2. Left pedipalp, dorsal aspect, female paratype (CAS, EB-1503.01004); 3. Right chela, lateral aspect, female paratype (CAS, EB-1503.01004); 4. Leg I, lateral aspect, female paratype (CAS, EB-1634.01002); 5. Leg IV, lateral aspect, female paratype (CAS, EB-1634.01002); 6. Right chelicera, dorsal aspect, male paratype (CAS, EB-1503.01003); 7. Movable cheliceral finger, lateral aspect, female paratype (CAS, EB-1506.01001); 8. Right rallum, lateral aspect, female paratype (CAS, EB-1558.02003); 9. Male genitalia, ventral aspect, male paratype (CAS, EB-1503.01003); 10. Female genitalia and sternites, ventral aspect, female paratype (CAS, EB-864.01001). Abbreviations: lcp, lateral cribriform plate; lgs, lateral genital sac; mcp, median cribriform plate. Scale lines = 0.1 mm (Figs. 1–5, 10), 0.04 mm (Fig. 6); 0.05 mm (Figs. 7, 9).



Figures 11–21.—*Oreolpium semotum* new species, male holotype unless stated otherwise: 11. Carapace, dorsal aspect; 12. Right chelicera, dorsal aspect; 13. Tip of movable chelicceral finger and galea, dorsal aspect, female paratype; 14. Right rallum, lateral aspect; 15. Right pedipalp, dorsal aspect; 16. Left chela, lateral aspect; 17. Left leg IV, lateral aspect; 18. Left leg I, lateral aspect; 19. Claws and arolium, ventral aspect, female paratype; 20. Male genitalia, ventral aspect; 21. Female genitalia, ventral aspect, female paratype. Abbreviations: ejca, ejaculatory canal atrium; gls, glandular setae; lcp, lateral cribriform plate; lgs, lateral genital sac; mcp, median cribriform plate. Scale lines = 0.05 mm (Figs. 19, 21), 0.1 mm (Figs. 12, 16–18), 0.2 mm (Fig. 11), 0.5 mm (Fig. 15).

Table 1.—List of genera of Garypinidae, with numbers of named Recent species and distributions.

Genus	No. of named species	Distribution
Aldabrinus Chamberlin 1930	2	Seychelles (Aldabra Islands); southeastern USA
Amblyolpium Simon 1898	14	Asia; northern Africa; Caribbean region; South America; New Caledonia; Papua New Guinea; Solomon Islands; Mediterranean region
Caecogarypinus Dashdamirov 2006	1	Vietnam
Galapagodinus Beier 1978	1	Ecuador (Galapagos Islands)
Garypinidius Beier 1955	2	South Africa
Garypinus Daday 1888	6	South Africa; western and southeastern Asia; Hawaii; Mediterranean region
Haplogarypinus Beier 1959	1	Democratic Republic of Congo (Zaire)
Henisolinus Beier 1977	1	Saint Helena
Indogarypinus Murthy and Ananthakrishnan 1977	1	India
Nelsoninus Beier 1967	1	New Zealand
Neoamblyolpium Hoff 1956	2	Southwestern USA
Neominniza Beier 1930	2	Chile
Oreolpium Benedict and Malcolm 1978	2	Western USA; Australia (Tasmania)
Paraldabrinus Beier 1966	1	New Caledonia
Protogarypinus Beier 1954	2	Australia
Pseudogarypinus Beier 1931	4	Western USA; Costa Rica
Serianus Chamberlin 1930	18	Northern Africa; North and South America; Arabian Peninsula; central Asia; Solomon Islands
Solinellus Muchmore 1979	1	Southeastern USA
Solinus Chamberlin 1930	9	Eastern Africa; Central America; central Asia; Australia; Papua New Guinea; Mediterranean region
Teratolpium Beier 1959	1	Peru
Thaumatolpium Beier 1931	5	Chile

tooth of movable finger not bifurcate and not enlarged; rallum of 4 denticulate blades; lamina exterior very thin in *O. semotum* and apparently absent in *O. nymphum*.

Pedipalp: Femur with 1 or 2 tactile setae, situated in basal half. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria; *eb* and *esb* situated basally; *est* clearly in basal half of fixed finger, situated closer to *eb* and *esb* than to *et*; trichobothria *ib*, *isb*, *ist* and *it* grouped subbasally, with *ib* slightly separated from others; trichobothria of movable finger situated in basal half of finger; *st* situated closer to chelal finger margin than *b*, *sb* and *t*. Venom apparatus present in both chelal fingers, venom ducts very short, terminating in nodus ramosus almost immediately.

Cephalothorax: Carapace sub-rectangular; with 1 pair of flat, corneate eyes situated near anterior margin of carapace; with 20–22 setae, including 4 near anterior margin and 4 near posterior margin.

Abdomen: Pleural membrane longitudinally striate. Tergites and sternites with faint medial suture, or with suture apparently absent; glandular setae absent. Spiracular helix present.

Genitalia: Male: dorsal anterior glands absent; lateral genital sacs large; with 2 pairs of internal glandular setae. Female: with paired lateral cribriform plates and single median cribriform plate.

Legs: Junction between femora and patellae I and II broad and apparently sub-mobile; femur I barely longer than patella I; tibiae III and IV with long sub-medial tactile seta; metatarsi III and IV with long subbasal tactile seta; metatarsus and tarsus stocky; arolium much longer than claws, not divided.

Remarks.—*Oreolpium nymphum* and *O. semotum* share a number of similarities: both possess an undivided arolium; a single sub-medial tactile seta on the pedipalpal femur; 1 pair of eyes; rallum with 4 blades; low numbers of carapaceal seta with 4 on the anterior margin and 4 on the posterior margin (22 setae in *O. semotum* and usually 20–22 setae in *O. nymphum*); the position of trichobothrium *st*, which is situated slightly closer to the dental margin than the other trichobothria on the movable chelal finger; and the lack of abdominal glandular setae. The only obvious discrepancy is the relative lengths of femur and patella of legs I and II. In *O. nymphum* the patella is marginally longer than the femur, whereas in *O. semotum* the femur is slightly longer than the patella, but these differences are extremely trivial and do not necessarily preclude a close relationship between *O. semotum* and *O. nymphum*.

As discussed previously, *Oreolpium* resembles four other garypinid genera (*Neominniza*, *Protogarypinus*, *Teratolpium* and *Thaumatolpium*), in which the arolium is not divided. It is similar to *Thaumatolpium* and *Teratolpium* by the presence of only one pair of eyes; two pairs of eyes are present in *Neominniza* and *Protogarypinus* (Beier 1954, 1964, 1975). It differs from *Neominniza* in that all of the trichobothria of the internal series are basally grouped; in species of *Neominniza* trichobothria *isb*, *ist* and *it* are more medially placed and separated from *ib* (Beier 1964). *Oreolpium* differs from *Thaumatolpium* by possessing fewer setae on the carapace: *Oreolpium* has 20–22 setae, including 4 near the anterior margin and 4 near the posterior margin, while *Thaumatolpium* has 28–32 setae with 6 near the anterior margin and 6 near the posterior margin (Beier 1964). In addition, species of *Thaumatolpium* bear a pair of glandular setae on sternites VI–VIII (Beier 1964), but *O. nymphum* and *O. semotum* lack such glandular setae. It differs from species of *Neominniza* and

Thaumatolpium by the presence of a chela with paraxially offset pedicel (not offset in *Neominniza* and *Thaumatolpium*). *Oreolpium* differs from *Protogarypinus* by the lack of glandular setae on the abdominal sternites. *Oreolpium* differs from *Teratolpium* by the lack of a heart-shaped median depression on the carapace (Beier 1959c, fig. 8), and the presence of four rallar blades (three in *Teratolpium*).

Oreolpium nymphum Benedict & Malcolm 1978
Figs. 1–10, 21

Oreolpium nymphum Benedict and Malcolm 1978:120–124, figs. 9–14; Zeh 1987:1086; Muchmore 1990:515; Harvey 1991:294; Harvey 2009: [unpaginated].

Material examined.—Paratypes, USA: *Oregon*: 1 female, Douglas County, 8 miles S, 4 mi E of Tiller, ca 42°56′N, 122°57′W, 13 September 1973, E.M. Benedict (CAS, EB-1558.02003); 1 female, Jackson County, 6 mi S, 12 mi W of Ashland, ca 42°12′N, 122°42′W, 17 September 1972, E.M. Benedict (CAS, EB-864.01001); 1 female, Lane County, 4 mi N, 13 mi E of Lowell, ca 43°55′N, 122°47′W, 30 August 1973, E.M. Benedict (CAS, EB-1506.01001); 1 male, same data (CAS, EB-1503.01003); 1 female, same data (CAS, EB-1503.01004); 1 female, same data (CAS, EB-1503.01005); 1 female, Marion County, 5 mi due N of Mill City, ca 44°45′N, 122°29′W, 17 September 1973, E.M. Benedict (CAS, EB-1634.01002).

Diagnosis.—*Oreolpium nymphum* is substantially smaller than *O. semotum*, e.g., pedipalpal femur length 0.33–0.35 (♂), 0.33–0.39 (♀) mm in *O. nymphum* compared with 0.547 (♂), 0.563 (♀) mm in *O. semotum*, and chela (with pedicel) length 0.56–0.59 (♂), 0.62–0.63 (♀) mm in *O. nymphum* compared with 0.802 (♂), 0.845 (♀) mm in *O. semotum*.

Description.—*Adult:* Body strongly flattened. Color with sclerotized portions generally very pale, pedipalps and anterior portion of carapace slightly darker.

Chelicera: With 5 setae on hand, all setae acuminate (Fig. 6); movable finger with 1 subdistal seta (Fig. 7); subterminal tooth of movable finger not bifurcate and not enlarged; with 3 lyrifissures, 2 on dorsal face and 1 on ventral face; galea of ♂ not discernible in only specimen available, of ♀ long with 3 terminal rami; rallum of 4 blades, distal and subdistal blade each with 1 large serration on leading edge (Fig. 8); serrula exterior with 14 blades; lamina exterior apparently absent.

Pedipalp: Trochanter, femur, patella, and chela completely smooth (Fig. 2); setae very long and acicular; trochanter elongate, without any discernible tubercles; trochanter 2.1–2.3 × (♂), 2.3 × (♀), femur 3.6–4.0 × (♂), 3.4–3.9× (♀), patella 2.6–2.7 × (♂), 2.6–3.0 × (♀), chela (with pedicel) 4.4 × (♂), 4.0–4.1 × (♀) longer than broad, hand long and cylindrical, 1.6 × (♂), 2.1 × (♀) longer than deep, movable finger 1.2 × (♂), 1.1 × (♀) longer than hand. Femur with 2 long tactile setae situated in basal half (Fig. 2). Patella with three long lyrifissures situated dorsally near pedicel (Fig. 2). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 3): *eb* and *esb* situated basally; *est* clearly in basal half of fixed finger, situated closer to *eb* and *esb* than to *et*; trichobothria *ib*, *isb*, *ist* and *it* grouped sub-basally, with *ib* separated from others; ca 4–5 microsetae (chemosensory setae) present on fixed finger distal to *et*; trichobothria of movable finger situated in basal half of finger; *st* situated closer to chelal finger margin than *b*, *sb* and *t*; microsetae (chemosensory setae) not present on movable finger. Venom apparatus present in both chelal fingers, venom ducts very short, terminating in nodus ramosus almost immediately. Chelal teeth retrorse with obvious pointed tips; fixed finger with 18 (♂, ♀) teeth; movable finger with 18 (♂, ♀) teeth; accessory teeth absent.

Cephalothorax: Carapace sub-rectangular (Fig. 1); with 1 pair of flat, corneate eyes situated near anterior margin of carapace, posterior pair missing; generally with 20 setae, including 4 near anterior margin and 4 near posterior margin; without furrows; with 4 pairs of lyrifissures. Manducatory process with 1 long distal, 1 long sub-distal and very small internal, sub-oral seta; remainder of maxilla with 8–9 setae. Chaetotaxy of coxae I–IV: 6: 6: 4: 3–4.

Abdomen: Pleural membrane longitudinally striate. Tergites and sternites apparently without medial suture. Tergal chaetotaxy: ♂, ♀, 6: 4–6: 4–6: 5–6: 6: 6: 6: 6: 6: 10: 10: 2; uniseriate; all setae acicular. Sternal chaetotaxy: ♂, 7–8: (0) 7–8 [2+2] (0): (2) 5–6 (2): 6: 6: 6: 6: 6: 10: 6: 2; ♀, 7–8: (0) 7–8 [2+2](0): (2) 5–6 (2): 6: 6: 6: 6: 6: 10: 6: 2; setae uniseriate and acuminate; glandular setae absent; anus not surrounded by sternite XI.

Genitalia: Male: with large lateral genital sacs; without dorsal anterior glands; cup-shaped ejaculatory canal atrium (Fig. 9). Female: with paired lateral cribriform plates and single median cribriform plate (Fig. 10).

Legs: Junction between femora and patellae I and II broad and apparently sub-mobile (Fig. 4); femur I approximately equal in size to patella I; femur + patella of leg IV 3.4–3.5 × (♂), 3.2–3.4 × (♀) longer than broad; femora I and II with 2 perpendicular lyrifissures situated sub-distally; tibiae III and IV with long sub-medial tactile seta (Fig. 5); metatarsi III and IV with long subbasal tactile seta (Fig. 5); metatarsus and tarsus stocky; subterminal tarsal setae arcuate and acute; arolium much longer than elaws, not divided (Figs. 4, 5).

Dimensions (mm): See Benedict & Malcolm (1978b).

Remarks.—*Oreolpium nymphum* was found by Benedict & Maleolm (1978b:124) to occur in "old mature bark taken from western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and sugar pine (*Pinus lambertiana*) trees located in forests at elevations of 1,000 to 6,000 ft in western Oregon." The species has not been subsequently reported in the primary literature and remains one of the least known of all North American pseudoscorpion species.

The written description of *O. nymphum* by Benedict & Malcolm (1978b) specifically mentions five setae on the cheliceral hand, but the accompanying illustration (Benedict & Malcolm 1978b:fig. 11) shows only four setae. We can confirm that five setae are indeed present in all specimens that were examined for this study.

Oreolpium semotum new species
Figs. 11–22

Material examined.—AUSTRALIA: *Tasmania*: Holotype male, The Needles Picnic Ground, Southwest National Park, 42°45′17″S, 146°24′36″E, 12–13 March 1997, under bark, F. Šťáhlavský (TMAG). Paratype: 1 female, collected with holotype (TMAG).

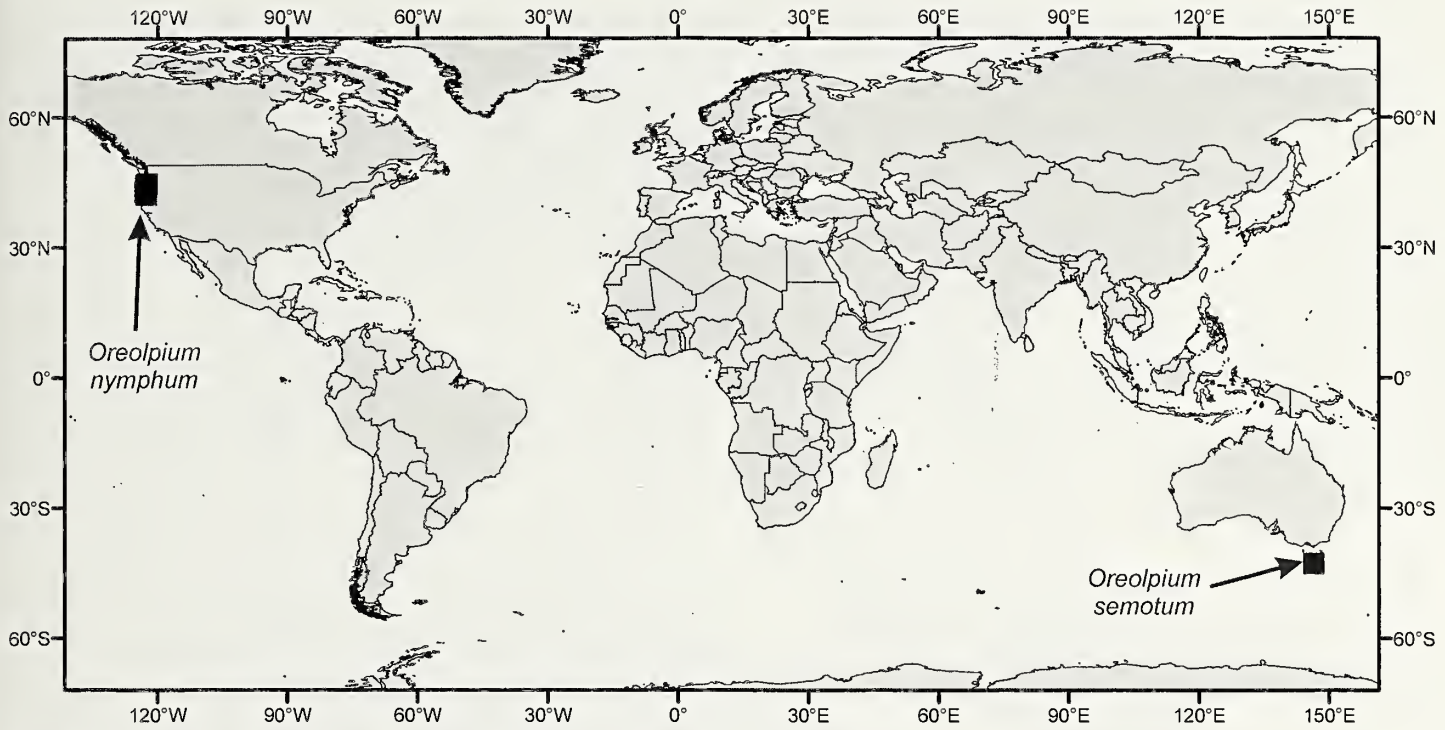


Figure 22.—Map depicting known distribution of species of *Oreolpium* (Garypinidae).

Etymology.—The specific epithet, which is Latin for "distant, far-off", refers to the highly disjunct distribution of the two known species of *Oreolpium* (Fig. 22).

Diagnosis.—*Oreolpium semotum* is larger than *O. nymphum*, e.g., pedipalpal femur length 0.547 (♂), 0.563 (♀) mm in *O. semotum* compared with 0.33–0.35 (♂), 0.33–0.39 (♀) mm in *O. nymphum*, and chela (with pedicel) length 0.802 (♂), 0.845 (♀) mm in *O. semotum* compared with 0.56–0.59 (♂), 0.62–0.63 (♀) mm in *O. nymphum*.

Description.—*Adults:* body strongly flattened. Color of sclerotized portions generally very pale, pedipalps and anterior portion of carapace slightly darker.

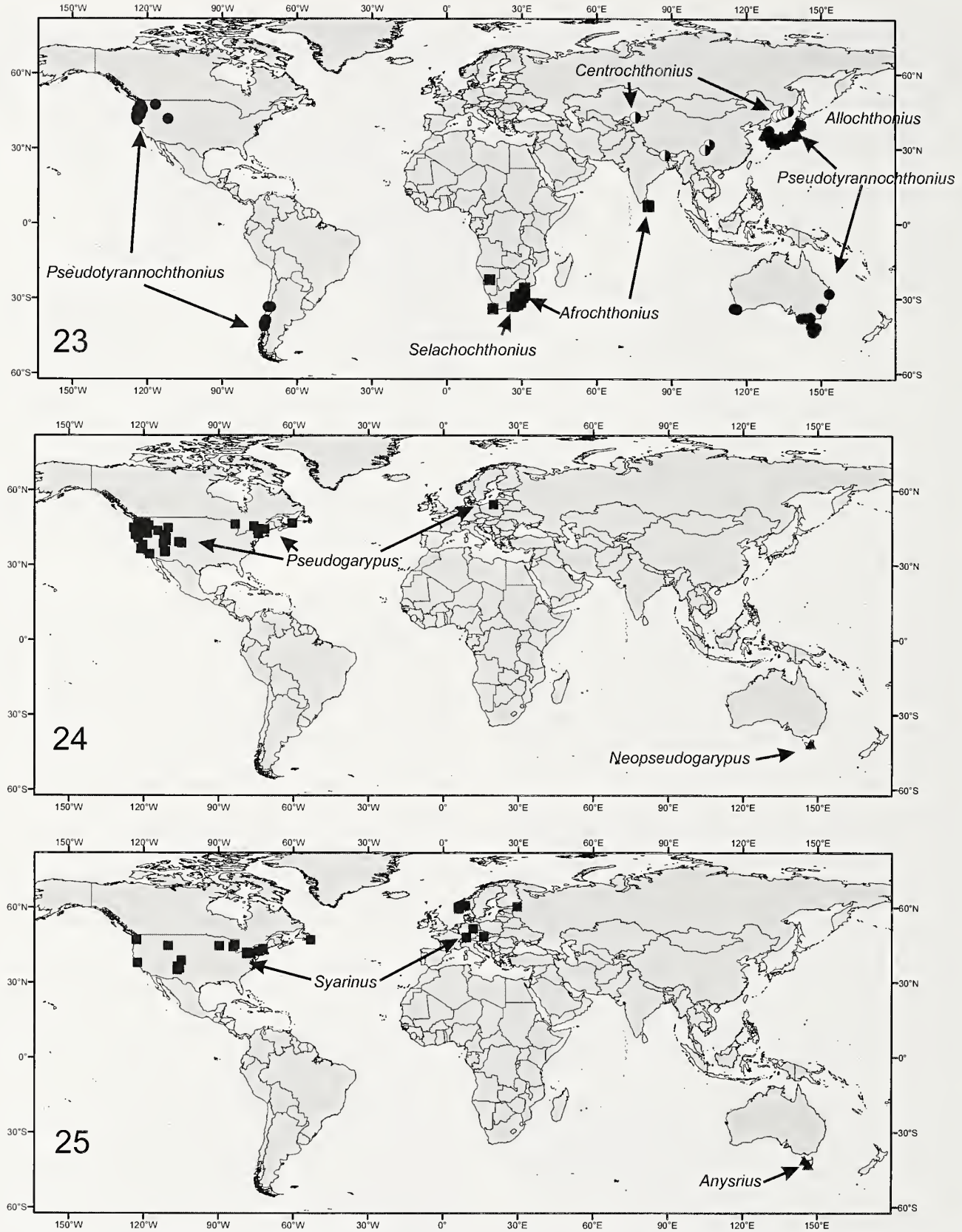
Chelicera: With 5 setae on hand, all setae acuminate (Fig. 12); movable finger with 1 subdistal seta (Fig. 13); subterminal tooth of movable finger not bifurcate and not enlarged; with 3 lyrifissures, 2 on dorsal face, and 1 on ventral face; galea of ♂ with pointed tip and 1 small sub-medial ramus, of ♀ long with 3 terminal rami; rallum of 4 blades, the most distal blade with 6 large serrations on leading edge, middle blades with 2 serrations, basal blade with 1 serration (Fig. 14); serrula exterior with 17 blades; lamina exterior present, very thin.

Pedipalp: Trochanter sparsely granulate on dorsal surface, femur, patella, and chela completely smooth (Fig. 15); setae very long and acicular; trochanter elongate, with faint tubercles, with roughened posterior tubercle; trochanter 2.11 × (♂), 1.96 × (♀), femur 4.05 × (♂), 3.88 × (♀), patella 2.72 × (♂), 2.73 × (♀), chela (with pedicel) 4.05 × (♂), 4.04 × (♀), chela (without pedicel) 3.78 × (♂), 3.78 × (♀) longer than broad, hand long and cylindrical, 2.08 × (♂), 2.02 × (♀) longer than broad, movable finger 0.84 × (♂), 0.91 × (♀) longer than hand. Femur with 1 long tactile seta situated in near middle of segment (Fig. 15). Patella with three lyrifissures situated dorsally near pedicel. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 16): *eb* and *esb* situated basally; *est* clearly in basal half of fixed finger, situated closer to *eb* and *esb* than to *et*; trichobothria *ib*, *isb*, *ist* and *it* grouped sub-basally, with *ib* slightly separated from others; ca. 6 microsetae (chemosensory setae) present on fixed finger distal to *et*; trichobothria of movable finger situated in basal half of finger; *st* situated closer to chelal finger margin than *b*, *sb* and *t*; microsetae (chemosensory setae) not present on movable finger. Venom apparatus present in both chelal fingers, venom ducts very short, terminating in nodus ramosus almost immediately. Chelal teeth rounded, basal teeth slightly flattened; fixed finger with 21 (♂), 22 (♀) teeth; movable finger with 21 (♂), 23 (♀) teeth; accessory teeth absent.

Cephalothorax: Carapace (Fig. 11) 1.45 × (♂), 1.62 × (♀) longer than broad; sub-rectangular but slightly narrowed anteriorly; with 1 pair of flat, corneate eyes situated near anterior margin of carapace, posterior pair missing; with 22 setae, including 4 near anterior margin and 4 near posterior margin; without furrows; with 5 pairs of lyrifissures. Manducatory process with 1 long distal, 1 long sub-distal and very small internal, sub-oral seta; remainder of maxilla with 5 setae. Chaetotaxy of coxae I–IV: 6: 5: 4: 3 (♂, ♀).

Abdomen: Pleural membrane longitudinally striate. Tergites and sternites with very faint medial suture. Tergal chaetotaxy: ♂, 4: 4: 4: 4: 4: 6: 6: 6: 6: T1T2T1T: T1T2T1T: 2; ♀, 4: 4: 4: 6: 4: 6: 6: 6: 6: T1T2T1T: T1T2T1T: 2; uniseriate; all setae acicular. Sternal chaetotaxy: ♂, 11: (0) 6 [2+2] (0): (2) 6 (2): 5: 5: 6: 6: 6: T1T2T1T: T1T2T1T: 2; ♀, 9: (0) 6 (0): (3) 8 (3): 6: 6: 6: 6: 6: T1T2T1T: T1T2T1T: 2; setae uniseriate and acuminate; glandular setae absent; anus not surrounded by sternite XI.

Genitalia: Male: With large lateral genital sacs, without dorsal anterior glands;, cup-shaped ejaculatory canal atrium (Fig. 20). Female: with paired lateral cribriform plates and single median cribriform plate (Fig. 21).



Figures 23–25.—Maps depicting known distribution of pseudoscorpion taxa with bipolar distributions based upon published records: 23. Pseudotyrannochthoniidae; 24. Pseudogarypidae; 25. Syarininae (Syarinidae).

Legs: Junction between femora and patellae I and II broad and apparently sub-mobile (Fig. 18); femur I barely longer than patella I (Fig. 18); femur + patella of leg IV 3.08 × (♂), 3.14 × (♀) longer than broad; femora I and II with 2 perpendicular lyrifissures situated sub-distally; tibiae III and IV with long sub-medial tactile seta (Fig. 17); metatarsi III and IV with long subbasal tactile seta (Fig. 17); metatarsus and tarsus stocky (Fig. 17); subterminal tarsal setae arcuate and acute; arolium much longer than claws, not divided (Fig. 19).

Dimensions (mm).—*Male holotype:* Body length 2.48. Pedipalps: trochanter 0.325/0.154, femur 0.547/0.135, patella 0.454/0.167, chela (with pedicel) 0.802/0.198, chela (without pedicel) 0.750, hand length 0.411, movable finger length 0.346. Chelicera 0.170/0.090, movable finger length 0.131. Carapace 0.637/0.438; eye diameter 0.080. Leg I: femur 0.166/0.090, patella 0.141/0.093, tibia 0.203/0.046, metatarsus 0.077/0.045, tarsus 0.101/0.040. Leg IV: femur + patella 0.474/0.154, tibia 0.314/0.087, metatarsus 0.104/0.057, tarsus 0.146/0.046.

Female paratype: Body length 3.23. Pedipalps: trochanter 0.314/0.160, femur 0.563/0.145, patella 0.466/0.171, chela (with pedicel) 0.845/0.209, chela (without pedicel) 0.790, hand length 0.422, movable finger length 0.384. Chelicera 0.173/0.099, movable finger length 0.128. Carapace 0.704/0.435; eye diameter 0.051. Leg I: femur 0.166/0.098, patella 0.141/0.101, tibia 0.218/0.069, metatarsus 0.083/0.046, tarsus 0.109/0.043. Leg IV: femur + patella 0.503/0.160, tibia 0.288/0.090, metatarsus 0.104/0.058, tarsus 0.147/0.506.

Remarks.—*Oreolpium semotum* is currently known from only a single location in south-western Tasmania where it was taken from under the bark of a tree. Due to the highly localised distribution of this species, it is likely to represent a short-range endemic species (Harvey 2002).

DISCUSSION

Enormous disjunctions in the distribution of organisms that are apparently incapable of long-range dispersal are generally thought to represent vicariance events (Nelson & Platnick 1981). The presence of species of *Oreolpium* in Oregon and southern Tasmania (Fig. 22) is one such disjunction that can be explained by only one of two scenarios. The first postulates that one or both sites of occupancy are the result of recent inter-continental dispersal. The other hypothesis suggests that the common ancestor of both species was found on land masses that were once contiguous and that have since rafted away from each other due to sea-floor spreading and continental drift, taking their biological cargo with them. Harvey (1998b) nominated two pseudoscorpion groups that appeared to fit the criteria of the second theory, Pseudogarypidae and Syarininae, each with representatives in the northern hemisphere and in Tasmania (Figs. 24, 25). The two known pseudogarypid genera occur in totally different regions of the world, with the sole species of *Neopseudogarypus* Morris 1948, *N. scutellatus* Morris 1948, found in northern Tasmania, and Recent species of *Pseudogarypus* Ellingsen 1909 found in North America (Harvey 2009; Fig. 24). Several species of *Pseudogarypus* have also been described from Tertiary amber deposits collected in the Baltic region of northern Europe (see Harvey 2009), but no Recent pseudogarypids are known from the region, suggesting that they have become locally extinct since the Eocene.

A third group, the chthoniid subfamily Pseudotyrannochthoniidae, also has a very similar distribution pattern with representatives found in austral regions (southern Australia, southern Africa and Chile) and boreal regions (western North America, and Central and East Asia) (Fig. 23). There are five recognised pseudotyrannochthoniid genera, with *Centrochthonius* and *Allochthonius* in Asia; *Pseudotyrannochthonius* in Australia, Chile, western USA and East Asia, and *Afrochthonius* and *Selachochthonius* in southern Africa (Harvey 2009). The sole exception to the bipolar pattern is the presence of two species of *Afrochthonius* in Sri Lanka (Beier 1973), located in a tropical biome slightly north of the equator. This anomalous pattern is presumably best explained by the rafting of the Indian subcontinent from Gondwanaland during the late Cretaceous (e.g. Besse & Courtillot 1988; Smith et al. 1994; Scotese 2001).

We here propose a fourth pseudoscorpion group, the garypinid genus *Oreolpium*, which has a very similar distribution pattern to Syarininae and Pseudogarypidae, with *O. nymphum* found in northwestern USA and *O. semotum* found in southern Tasmania (Fig. 22). Whilst putative relatives of *Oreolpium* occur in Australia and South America, the monophyly of the genus seems assured as they share a number of reductive features (lack of dorsal glands in the male genitalia and lack of glandular setae on the medial sternites) that are present in all other garypinids without divided arolia, although the morphology of the male genitalia are presently unrecorded for *Teratolpium*.

Some water mite taxa seem to have the same pattern (Harvey 1998a). The hydryphantid genus *Tartarothyas* Viets 1934 occurs in Europe, North America and southern Australia (Cook 1974; Harvey 1987a, 1998a:fig. 5b; Smith & Cook 1999). Similarly, members of the *Panisellus* group (Hydryphantidae: Thyadinae) are found in Europe, North America, South Africa and Australia (Cook 1974; Harvey 1996; 1998a:fig. 5a). The subfamily Piersigiinae comprises two genera of which *Piersigia* Protz 1896 is found throughout the Holarctic region (Cook 1974) and *Austrapiersigia* Smit 1998 occurs in southeastern Australia (Harvey 1998a; Smit 1998). Finally, the pionid subfamily Huitefeldtiinae is found in Europe and North America (*Huitfeldtia* Thor 1898) and southwestern Australia (*Larri* Harvey 1996) (Cook 1974; Harvey 1998a:fig. 5d). These patterns are largely congruent and likely to have their origins in the same processes, which we here postulate to be the vicariant break-up of Pangaea which began during the Cretaceous.

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APPENDIX 1
Specimens of Garypinidae examined for this study.

Aldabrinus sp.: AUSTRALIA: *Western Australia*: Waychinicup Nature Reserve, S of Mt. Manypeaks, Surprise Gully, 34°54′11″S, 118°23′57″E, 13 March 2007, on reeds/grasses, M.L. Moir et al., 1 ♀ (WAM T79640); Mt Hallowell, 35°00′34″S, 117°18′04″E, 6 November 2006, on plants, M.L. Moir, D. Jolly, 1 nymph (WAM T78899); Bremer Bay, Native Dog Beach, 34°27′17″S, 119°21′43″E, 21 November 2006, on plants, M.L. Moir, 2 nymphs (WAM T78821); Woodman Point Nature Reserve, Woodman Point, 32°07′50″S, 115°45′28″E, 1 September–4 November 1994, pitfall traps, J.M. Waldock, A.F. Longbottom, 1 ♀, 1 tritonymph (WAM T63240, T63242); Woodman Point Nature Reserve, Woodman Point, 32°07′50″S, 115°45′28″E, 4 November 1994-19 January 1995, pitfall traps, J.M. Waldock, M.S. Harvey, 1 ♀ (WAM T63241).

Amblyolpium anatolicum Beier 1967: TURKEY: *Isparta*: Egridir, 37°52′N, 30°51′E, 19 May 1965, F. Ressl, 1 ♀ (holotype) (NHMW).

Amblyolpium franzi Beier 1970: PORTUGAL: *Madeira*: Porto Santo, 33°03′N, 16°20′W, 13 April 1968, H. Franz, 1 ♂ (holotype) (NHMW).

Anublyolpium novaeguineae Beier 1971: PAPUA NEW GUINEA: *Morobe*: Heads Hump, Bulolo, 7°12′S, 146°39′E, 2 May 1970, B. Gray, 1 ♂, 1 ♀ (types) (NHMW); *Morobe*: Bulolo, 7°12′S, 146°39′E, 18 August 1970, B. Gray, 6 ♂, 2 ♀ (paratypes) (NHMW).

Anublyolpium ruficeps Beier 1966: NEW CALEDONIA: Niaouli forest near Col Boa, 21°16′S, 165°14′E, 11 August 1965, A. Kaltenbach, 1 ♂ (holotype) (NHMW).

Amblyolpium sp.: AUSTRALIA: *Western Australia*: Ravensthorpe Range Middle, 33°34′04.09″S, 120°02′51.05″E, 210 m, 28 May 2007, leaf litter, M.C. Leng, M.L. Moir, 1 ♀, 1 protonymph (WAM T86787); Ravensthorpe Range, Ravensthorpe Townsite (Site WAM 48), 33°34′04.09″S, 120°02′51.05″E, 8 September 2007, leaf litter, M.C. Leng, M. Lyons, 2 ♀ (WAM T81308); Mcdermid Rock, 32°01′S, 120°44′E, 27 September–3 October 1978, under litter, T.F. Houston et al., 1 ♀ (WAM 81/183).

Galapagodinus franzi Beier 1978: ECUADOR: *Galápagos*: Galapagos Islands: Isla San Salvador (as Isla Santiago), 1°16′S, 90°42′E, 16 June 1975, H. Franz, 1 ♂ (paratype) (NHMW); Isla San Salvador (as Isla Santiago), 1°16′S, 90°42′E, 16 June 1975, H. Franz, 1 ♀ (paratype) (NHMW); Isla San Salvador (as Isla Santiago), 1°16′S, 90°42′E, 16 June 1975, H. Franz, 1 ♂ (holotype), 1 ♀ (allotype) (NHMW).

Galapagodinus sp.: ECUADOR: *Galápagos*: Galapagos Islands: Rabida Island, 0°24′S, 90°42′W, 15 May 1983, Y. Lubin 1983, 1 ♂, 1 tritonymph (MCZ, Muchmore slide no. WM6317.01001-2).

Garypinidius capensis (Ellingsen 1912): SOUTH AFRICA: *Western Cape Province*: de Hoop Nature Reserve, Lakkerwater Rd., 32°24′12″S, 20°33′09″E, 26 September 2007, C. Haddad, 1 ♂ (WAM T86745).

Garypinus asper Beier 1955: LEBANON: *Mont-Liban*: Ouadi el Fouar (as Anteljas-Fluss), 33°59′N, 35°35′E, 11 September 1952, K. Christiansen, 1 specimen (paratype (NHMW).

Garypinus dimidiatus (L. Koch 1873): GREECE: *Crete*: Ákra Síderos (as Sideros), 35°19′N, 26°19′E, 5 May 1965, E. Kritscher, O. Paget and Bilek, 1 specimen (NHMW); Paximadia Island, 35°00′N, 24°35′E, 30 April 1965, E. Kritscher, O. Paget and Bilek, 13 specimens (NHMW); Aghios Nikolaos, 34°52′N, 32°45′E, 8 May 1965, E. Kritscher, O. Paget and Bilek, 2 specimens (NHMW). TURKEY: *Antalya*: Antalya, 36°55′N, 30°41′E, 15 May 1965, F. Ressl, 2 specimens (NHMW); *İçel*: Anamur, 36°05′N, 32°50′E, 21 April 1963, F. Ressl, 35 specimens (NHMW); *Muğla*: Marmaris, 36°51′N, 28°16′E, 12 April 1966, Franz, 5 specimens (NHMW).

Garypinus afghanicus minor Beier 1959: AFGHANISTAN: *Kandahar*: Dalah near Arghandab, 31°39′N, 65°39′E, 6 May 1958, K. Lindberg, 1 ♀ (paratype) (NHMW).

Hemisolinus helenae Beier 1977: ST. HELENA: east Prosperous Bay Plain, 15°57′S, 05°39′W, 4 January 1966, Terunrenlop, 1 ♂ (paratype) (NHMW); east Prosperous Bay Plain, 15°57′S, 05°39′W, 5 February 1967, 1 ♂, 1 ♀ (paratypes) (NHMW).

Neoamblyolpium alienum Hoff 1956: USA: *New Mexico*: Valencia County: Mt. Taylor, near Grants, 35°14′N, 107°36′W, 7,500 ft, 20 October 1951, pinyon litter, C.C. Hoff, 1 ♂ (holotype) (AMNH, Hoff slide no. S-1801.1); Torrance County: 1 mi W of Mountainair, 34°31′N, 106°15′W, 6,800 ft, 15 September 1954, in dead yucca, C.C. Hoff, 1 ♀ (allotype, Hoff slide no. S-2165.6), 1 ♂ (paratype) (Hoff slide no. S-2165.7), 1 ♀ (paratype) (Hoff slide no. S-2165.10) (AMNH); San Miguel County: 2 mi S of Villanueva, 35°14′N, 105°22′W, 6,600 ft, 3 September 1954, juniper litter, C.C. Hoff, 1 ♀ (paratype) (AMNH, Hoff slide no. S-2147.1); Santa Fe County: near Edgewood, 35°03′N, 106°11′W, 6,700 ft, 27 September 1954, pinyon litter, C.C. Hoff, 1 deutonymph (paratype) (AMNH, Hoff slide no. S-1916); *Colorado*: Garfield County: 4 mi E of Glenwood Springs, 39°31′N, 107°19′W, 6,000 ft, 1 September 1958, C.C. Hoff, 1 ♂ (AMNH, Hoff slide no. S-3731.2); Chaffee County: 6 mi NW of Salida, 38°35′N, 106°05′W, 4–5 September 1958, C.C. Hoff, 1 ♀ (AMNH, Hoff slide no. S-748.1); Larimer County: 30 mi W of Fort Collins, 40°34′N, 105°38′W, 6400 ft, 12 August 1958, trunk debris, yellow pine, C.C. Hoff, 1 ♂ (MCZ, Hoff slide no. S-3684.3).

Neominniza divisa Beier 1930: CHILE: *Región Metropolitana*: Farellones, 33°18′S, 70°15′W, 10 November 1959, 1 ♂ (NHMW); Farellones, 33°18′S, 70°15′W, 27 September 1959, 1 specimen (NHMW); *Bío-Bío*: Rinconada, 36°49′S, 72°33′W, 20 March 1959, Noodt, 1 ♂ (NHMW); Rinconada, 36°49′S, 72°33′W, 28 July 1959, Noodt, 1 ♂ (NHMW).

Neominniza halophila Beier 1964: CHILE: *Coquimbo*: Punta Taetinos, 29°49′S, 71°17′W, 12 km N of La Serena, 31 October 1954, Kuschel, 1 ♀ (NHMW).

Neominniza sp.: CHILE: *Valparaíso*: Petorca: Los Molles, Route 5, km 188, 32°14′S, 71°30′W, 10 m, 10 January 1995, Platnick, Catley, Silva, 1 ♂ (AMNH).

Oreolpium uyuphum Benedict and Malcolm 1978: see text.

Oreolpium senotum new species: see text.

Paraldabrinus novaecaledoniae Beier 1966: NEW CALEDONIA: Gorge de Ndokoa, 21°19′S, 165°16′E, between Pic Adio and Dent de Poya, 11 August 1965, A. Kaltenbach, 1 ♂, 2 ♀ (types) (NHMW).

Protogarypinus dissimilis Beier 1975: AUSTRALIA: *South Australia*: Flinders Ranges, Mt. Remarkable National Park, Alligator

Gorge, 32°50′S, 138°02′E, 24 March 1967, T.G. Wood, R.W. George, 2 ♂, 1 ♀, 5 nymphs (paratypes) (NHMW); Mt. Remarkable National Park, Mambray Creek camping ground, 32°50′19″S, 138°02′13″E, 22 November 2002, under rocks, M.S. Harvey, M.E. Blosfelds, 1 ♂ (WAM T88509).

Protogarypinus giganteus Beier 1954: AUSTRALIA: *Western Australia*: Walpole-Nornalup National Park, The Tingle Tree, 34°58′58″S, 116°47′09″E, 12 February 2002, under bark of *Eucalyptus diversicolor*, M.S. Harvey, M.E. Blosfelds, F. Harvey, E. Harvey, 5 ♂, 3 ♀ (with brood-sacs), 1 tritonymph, 2 deutonymphs, 7 protonymphs (WAM T65459).

Pseudogarypinus cooperi Muchmore 1980: USA: *California*: Riverside County: James Reserve, Lake Fulmor, 33°48′33″N, 116°46′30″W, 1690 m, 29 June 2002, under rocks, M.S. Harvey, 3 ♂, 3 ♀, 1 tritonymph (WAM T63230, T63231); Los Angeles County: Santa Monica Mts,, Piuma Road, 34°04′33″N, 118°41′25″W, 23 June 2002, under stones, M.S. Harvey, 1 ♂ (WAM T63232); Los Angeles County: Devils Punch Bowl, 34°25′N, 117°51′W, 22 May 2002, underside of rocks, G. Lowe, 2 ♂ (WAM T63243); Los Angeles County: 1 mi NE of Camp Valcrest, Angelas Crest Highway, 34°21′N, 117°59′W, 27 January 1982, under logs embedded in moist soil, G. Lowe, 1 ♂ (WAM T63244); San Bernadino County: Mt. Baldy Road, Manker Flats, 34°16′N, 117°38′W, 15 April 1987, under rocks, G. Lowe, 1 ♀ (WAM T63245).

Pseudogarypinus costaricensis Beier 1931: COSTA RICA: *Cartago*: Irazú, 9°59′N, 83°51′W, 25 May 1930, 2 specimens ("Typen") (NHMW); Irazú, 9°59′N, 83°51′W, 20 May 1930, 1 ♂ (paratype) (NHMW); Irazú, 9°59′N, 83°51′W, 26 May 1930, 2 ♂, 4 ♀ (paratypes) (NHMW).

Pseudogarypinus frontalis (Banks 1909): USA: *California*: Los Angeles County: Toyon Canyon, Santa Catalina Island, 33°22′N, 118°21′W, 1 September 1984, G. Lowe, 1 ♂ (WAM T75555); *Colorado*: Larimer County: Rist Canyon, Fort Collins, 40°38′N, 105°12′W, 6,000 ft, 20 July 1956, C.C. Hoff, 1 ♂ (AMNH, Hoff slide no. S-1057.1); Mesa Verde National Park, 37°14′N, 108°29′W, 7,000 ft, 1953, P. Van Cleave, 1 ♀ (AMNH, Hoff slide no. S-2183.3).

Serianus arboricola (Chamberlin 1923): MEXICO: *Baja California Sur*: Isla San Esteban, 28°42′N, 112°36′W, 19 April 1921, under mesquite bark, J.C. Chamberlin, 1 ♂ (holotype), 2 ♂, 1 ♀ (paratypes) (CAS, holotype, Type No. 1284; paratypes JC-172.01001–3); Isla Cerralvo [as Ceralbo Island], 24°14′N, 109°51′W, Rufo's ranch house, 7 June 1921, under bark, J.C. Chamberlin, 1 ♂, 1 ♀ (paratypes) (CAS, JC-171.01001, 2); north end of Isla San Jose (as San Josef Island), near lagoon, ca. 25°02′N, 110°43′W, 28 May 1921, under bark, J.C. Chamberlin, 3 ♂, 1 ♀ (paratypes) (CAS, JC-174.01004); *Sonora*: San Pedro Nolasco, 27°58′N, 111°23′W, 17 April 1921, under *Acacia* bark, J.C. Chamberlin, 1 ♂ (paratype) (CAS, JC-173.01001).

Serianus argentinae Muchmore 1981: ARGENTINA: *Buenos Aires*: Punta Piedras, 35°24′S, 57°06′W, 1 May 1942, J.A. Rosas Costa, 1 ♂, 2 ♀ (paratypes of *S. minutus* Hoff 1950) (AMNH, Hoff slide no. 6278-S-1054.5–7).

Serianus biimpressus (Simon 1890): MOROCCO: *Nador*: Kebdana, Granja del Muluye, 35°07′N, 02°20′W, July 1952, 3 ♂, 3 ♀ (NHMW).

Serianus bolivianus (Beier 1939): BOLIVIA: *Oruro*: Pazña, 18°36′S, 66°55′W, 14 August 1937, P. Sladen, 2 specimens (paratypes) (NHMW); Pazña, 18°36′S, 66°55′W, 14 August 1937, P. Sladen, 1 ♂ (paratype) (NHMW).

Serianus carolinensis Muchmore 1968: USA: *North Carolina*: Carteret County: near Beaufort, 34°43′N, 76°40′W, March–July 1966, P. Weygoldt, 1 ♂ (holotype), 5 ♂, 6 ♀ (paratypes) (AMNH, Muchmore slide no. WM-917.01010, holotype; WM 917.01005, 06, 08, 11, 16, ♂♂; WM 917.01001–04, 07, 09, ♀♀).

Serianus dolosus Hoff 1956: USA: *New Mexico*: Santa Fe County: 8 miles N of Golden, Ortiz Mountains, 35°23′N, 106°13′W, 7,000 ft, no date, C.C. Hoff, 1 ♂ (holotype) (AMNH, Hoff slide no. S-1883.7); Santa Fe County: 8 mi N of Golden, Ortiz Mountains, 35°23′N, 106°13′W, 7,000 ft, 11 August 1952, C.C. Hoff, 1 ♂ (paratype (AMNH, Hoff slide no. S-1883.1); Bernalillo County: Cedro Canyon, Manzano Mountains, east of Albuquerque, 35°04′N, 106°23′W, 6,600 ft, no date, C.C. Hoff, 1 ♀ (allotype), 3 deutonymphs (paratypes) (AMNH, Hoff slide no. S-1503.1, 4–6); Bernalillo County: west side of Sandia Mountains, ca. 35°14′N, 106°30′W, 6,400 ft, May 1952, C.C. Hoff, 1 ♂ (paratype) (AMNH, Hoff slide no. S-1727).

Serianus galapagoensis Beier 1978: ECUADOR: *Galápagos*: Galapagos Islands: Isla Santa Fe, 0°49′S, 90°04′W, 15 May 1975, H. Franz, 1 ♂ (holotype), 1 ♀ (allotype) (NHMW); Galapagos Islands: Island Santa Fe, 0°49′S, 90°04′W, 15 May 1975, H. Franz, 6 specimens (paratypes) (NHMW); Galapagos Islands: Isla Pinzón, 0°36′S, 90°40′W, 22 June 1975, H. Franz, 1 ♂ (paratype) (NHMW); Galapagos Islands: Island Pinzón, 0°36′S, 90°40′W, 22 June 1975, H. Franz, 1 ♀ (paratype) (NHMW).

Serianus gratus Hoff 1964: JAMAICA: *St Thomas Parish*: 2 miles W of Morant Bay, 17°53′N, 76°27′W, 25 May 1956, C.C. Hoff, 1 ♂ (paratype) (AMNH, Hoff slide no. S-3096.1); Morant Point, 17°55′N, 76°10′W, 6 May 1956, C.C. Hoff, 1 ♀ (paratype) (AMNH, Hoff slide no. S-2966); *St Catherine Parish*: Port Henderson, 17°57′N, 76°53′W, 4 May 1956, C.C. Hoff, 1 ♀ (paratype) (AMNH, Hoff slide no. S-2952.6); Port Henderson, 17°57′N, 76°53′W, 4 May 1956, C.C. Hoff, 1 tritonymph (paratype) (AMNH, Hoff slide no. S-2953.5.1).

Serianus litoralis (Chamberlin 1923): MEXICO: *Baja California Sur*: Golfo de California, Isla Monserrat (as Monserrate Island), 25°41′N, 111°03′W, 25 May 1921, on beach under stone, J.C. Chamberlin, 1 ♂ (holotype) (CAS, Type No. 1283, JC-161.03001).

Serianus minutus (Banks 1908): USA: *Texas*: Travis County: Austin, 30°16′N, 97°45′W, no date, nest of *Eciton caecum* (now *Labidus coecum*), C.T. Brues, 1 ♂, 1 ♀, 1 nymph (syntypes) (MCZ).

Serianus patagonicus (Ellingsen 1904): CHILE: *Los Lagos*: Lago Toro, 40°45′S, 72°18′W, 18 February 1957, Kuschel, 1 ♀ (NHMW); *Magallanes y Antártica Chile*: Puerto Williams, 54°56′S, 67°37′W, 9 February 1959, Kuschel, 1 ♂, 1 ♀ (NHMW); *Coquimbo*: 22 mi S of La Serena, ca 30°14′S, 71°14′W, 9 December 1950, Ross and Michelbacher, 1 ♀ (NHMW); ARGENTINA: *Rio Negro*: El Bolsón, 41°58′S, 71°31′W, 27 July 1961, Topál, 9 specimens (NHMW); El Bolsón, Cerro Piltriquitrón, 41°58′S, 71°29′W, 22 August 1961, Topál, 16 specimens (NHMW); Laguna El Trebol (as Lago Trebol), San Carlos de Bariloche (as Bariloche), 41°04′S, 71°30′W, 23 November 1950, P. Wygodzinsky, 1 ♂ (NHMW).

Serianus salomonensis Beier 1966: SOLOMON ISLANDS: Guadalcanal, Kukum, 9°26′S, 159°59′E, 9 December 1965–13 January 1966, P. Greenslade, 1 ♂ (holotype) (NHMW).

Serianus serianus (Chamberlin 1923): MEXICO: *Sonora*: Golfo de California, Isla Pelícano (as Pelican Island), Bahía de Kino, 28°49′N, 111°58′W, 5 July 1921, under stone, J.C. Chamberlin, 1 ♂ (holotype) (CAS (Type No. 1279); Golfo de California, Isla Pelícano (as Pelican Island), Bahía de Kino, 28°49′N, 111°58′W, 5 July 1921, J.C. Chamberlin, 2 ♂, 2 ♀ (paratypes) (CAS, JC-164.01001–4); *Baja California Sur*: Golfo de California, Isla Angel de la Guarda, opposite Isla Estanque (as Pond Island), 29°03′N, 113°06′W, 30 June 1921, J.C. Chamberlin, 1 ♂ (CAS, JC-165.01001–4).

Serianus solus (Chamberlin 1923): MEXICO: *Baja California Sur*: Golfo de California, South Islas Santa Inés, 27°03′N, 111°54′W, 13 May 1921, under stone, J.C. Chamberlin, 1 ♂ (holotype) (CAS, Type no. 1281); Golfo de California, South Islas Santa Inés, 27°03′N, 111°54′W, 13 May 1921, under stone, J.C. Chamberlin, 2 ♂, 1 ♀ (paratypes) (CAS, JC-169.01001–03); Golfo de California, Isla Ballena, near Espiritu Santo, 24°29′N, 110°24′W, 9 June 1921, under stone, J.C. Chamberlin, 1 ♀ (paratype) (CAS, JC-168.01001); *Baja California Norte*: Golfo de California, Isla Angel de la Guarda, Palm Canyon, ca 29°15′N, 113°20′W, 3 May 1921, J.C. Chamberlin, 1 specimen (paratype) (CAS, JC-167.01001).

Serianus validus (Beier 1971): IRAN: *Hormozgan*: 30 km NW of Bandar Abbas, ca. 27°22′N, 56°03′E, 4 April 1970, Rcssl and Bilek, 4 ♀ (syntypes) (NHMW).

Serianus sp.: USA: *California*: Los Angeles County: Santa Monica Mts, Piuma Road, 34°04′33″N, 118°41′25″W, 23 June 2002, under stones, M.S. Harvey, 1 ♂ (WAM T63229).

Solinus corticola (Chamberlin 1923): MEXICO: *Baja California Sur*: La Paz, 24°08′N, 110°17′W, 12 April 1921, under palo verde bark, J.C. Chamberlin, 1 ♂ (holotype) (CAS, Type No. 1277); La Paz, 24°08′N, 110°17′W, 12 April 1921, under palo verde bark, J.C. Chamberlin, 1 ♂, 1 ♀ (paratypes) (CAS, JC-175.01001, 2); Mulegé, 26°53′N, 111°59′W, 14 May 1921, J.C. Chamberlin, 3 ♂, 3 ♀ (paratypes) (CAS, JC-179.01001–4, 6, 7); Bahía Agua Verde, 25°31′N, 111°04′W, 26 May 1921, J.C. Chamberlin, 1 ♂ (paratype) (CAS, JC-182.01001); *Baja California Norte*: Bahía San Luis Gonzales, 29°46′N, 114°21′W, 27 April 1921, J.C. Chamberlin, 3 ♀ (paratypes) (CAS, JC-180.01001–3); *Sonora*: Bahía San Pedro, 28°03′N, 111°14′W, 7 July 1921, under bark, J.C. Chamberlin, 4 ♀ (paratypes) (CAS, JC-177.01001–4); Guaymas, 27°56′N, 110°54′W, 14 April 1921, under mesquite bark, J.C. Chamberlin, 1 ♂ (paratype) (CAS, JC-178.01001); SE. corner of Isla Tiburón (as Tiburon Island), near Punta Monumento (as Monument Point), 28°45′N, 112°19′W, 4 July 1921, J.C. Chamberlin, 1 ♀ (paratype) (CAS, JC-183.01001).

Solinus rhodius Beier 1966: GREECE: *Dodekanisos*: Rhodos Island: between Rhodos and Kritica [location not traced], 11 April 1966, H. Franz, 1 ♀ (holotype) (NHMW).

Solinus sp. 1: USA: *New Mexico*: Dona Ana County: Mt Summerford, Jornada del Muerto, 25 mi NNE. of Las Cruces, 32°31′N, 106°49′W, 11 October 1982, G. Ettershank, 3 ♂, 2 ♀, 3 nymphs (WAM T54076).

Solinus sp. 2: AUSTRALIA: *Western Australia*: Rottnest Island, ca 32°00′S, 115°36′E, 24 August, 2003, F. Šťáhlavský, 1 ♂, 1 ♀, 1 nymph (WAM T54068, T81113); 67 km S of Pannawonica, 22°15′47″S, 116°15′31″E, 21 June 2007, under bark, P. Runham, J. Adcroft, 1 ♂, 1 ♀ (WAM T81353).

Teratolpium andinum Beier 1959: PERU: *Ancash*: Laguna Jahuacocha (as Jahua-Kocha), 10°14′S, 76°58′W, 2 July 1954, H. Höffler, 2 ♂ (syntypes) (NHMW).

Thaumatolpium kuscheli Beier 1964: CHILE: *Coquimbo*: Los Choros, 29°19′S, 71°21′W, 3 October 1952, Kuschel, 1 ♂, 2 ♀, 1 tritonymph (paratypes) (NHMW); *Atacama*: Carrizal Bajo, 28°05′S, 71°09′W, 19 September 1952, Kuschel, 2 ♀ (paratypes) (NHMW).

Thaumatolpium robustius Beier 1964: CHILE: *Atacama*: Huasco, 28°28′S, 71°11′W, 11 October 1957, Kuschel, 1 ♂ (paratype) (NHMW).

Thaumatolpium sp.: CHILE: *Coquimbo*: Elqui, 20 km N. of La Serena, Route 5, km 491, 29°46′S, 71°20′W, 120 m, 8 February 1994, N. Platnick, K. Catley, P. Calderón, R.T. Allen, 1 ♂, 1 ♀ (AMNH).

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Effect of prey size on growth of newly emerged crab spiderlings *Misumena vatia*

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Abstract. Capturing unusually profitable prey early in life potentially enhances one's future fecundity and survival. Newly emerged crab spiderlings *Misumena vatia* (Araneae: Thomisidae) occasionally capture prey that greatly exceed them in size. I attempted to evaluate what if any long-term advantage these kills provided by presenting naïve, just-emerged spiderlings with syrphid flies *Toxomerus marginatus* that exceeded the initial mass of the spiderlings six-fold, a prey that the spiderlings occasionally captured in the field. A second group of spiderlings received a single syrphid initially and subsequently a single fruit fly *Drosophila melanogaster* every other day, and a control group received a fruit fly every other day. The few spiderlings that regularly captured the syrphids gained significantly more mass than the other groups. Individuals taking an initial syrphid and then fruit flies did not gain more mass than controls fed on solely on fruit flies. Neither did a group of spiderlings followed in the field nor a small group of individuals fed multiple fruit flies every other day in the laboratory differ in growth rates from the syrphid + fruit fly or single fruit fly groups. Thus, capture of a single bonanza prey does not provide the spiderlings with a significant advantage over those that did not obtain this reward, and in the field they probably do not manage to duplicate the capture success of the surviving members of the syrphid-only group.

Keywords: Dance fly, foraging, large prey, starvation, Thomisidae, *Toxomerus*

An individual's first foraging efforts often are inefficient, and without rapid improvement may result in a high probability of death. This problem may exist for a wide range of animals, from those provisioned by their parents as newborns and early juveniles (e.g., altricial birds: Lack 1966) to those that must forage for themselves from birth (e.g., many invertebrate species: Heinrich 1979; Morse 2000). If individuals must forage for themselves from the very start, innate traits will probably play a dominant role in governing initial responses. Still, since many animals, especially predators, potentially feed upon a wide variety of food items, an entirely innate response may not serve them well. Although naïve young may have little prior basis for discrimination (Persson & Brönmark 2009), it has become increasingly clear that the young of some species can rapidly modify their behavioral traits in a way that improves their performance in tasks such as foraging and hunting (Abramson 1994; Morse 2000).

Crab spiderlings *Misumena vatia* (Araneae: Thomisidae) (Clerck 1757) newly emerged from their natal nest sacs will attack a wide variety of prey, usually insects, on the flowers they occupy as hunting sites (Morse 1986). In response to the initial capture of a fruit fly *Drosophila melanogaster*, spiderlings may change their frequency of orientation and success of capture in subsequent attacks (Morse 2000). Spiderlings encounter a wide variety of insects on late-summer and early-autumn flowers in their natural habitat, ranging from ones far too large to capture (e.g., social bees) to easily captured ones (e.g., thrips, dance flies). Though at ca. 0.6 mg they obviously cannot capture the largest items with which they come in contact, they occasionally do take impressively large prey ranging up to several times their own body mass (Erickson and Morse 1997). It is thus of considerable interest to ask whether these endeavors are profitable in the long term (Christensen 1996; Sih & Christensen 2001) and if not, whether they are subsequently excluded from the foraging repertoire.

One such common visitor to these flowers that the spiderlings occasionally capture is the syrphid fly *Toxomerus marginatus*, which averages 4.0 mg (Erickson and Morse 1997; Morse 1998), over six times the mass of a newly-emerged spiderling. In fieldwork with these spiderlings I have observed such captures often enough (three in the past five summers of intensive fieldwork) to establish that they represent highly unusual, but by no means unique, events among spiderlings hunting on flowering goldenrod *Solidago* spp. (Asteraceae) inflorescences in late summer. The question thus arises, given the uncertain nature of prey capture at flower sites, how much advantage does such an apparent bonanza bestow on a just-emerged spiderling? In addition to lowering the danger of starvation (see Vogelei and Greissl 1989; Morse 1993a), a large capture might shorten the overall development time to adulthood and allow an individual to reach a greater size (Beck and Connor 1992) with potential enhanced fecundity (Morse and Fritz 1982). In contrast, poor early hunting success may lower any or all of these variables. Although some species can compensate for poor early success (Arendt 1997; Jespersen & Toft 2003), it may impose long-term fitness costs, such as decreased survival or reproduction (Metcalfe & Monaghan 2001).

I thus tested the question: does the initial capture or regular capture of extremely large prey items, here *T. marginatus*, provide newly emerged *M. vatia* spiderlings with significantly greater early gains in mass than those provided entirely by small prey? The results presented here took place during the first month following the spiderlings' emergence from their nest sacs. Although they represent only the first part of a juvenile's life, early success should enhance future fitness (Morse 2000).

METHODS

I carried out this work at the Darling Marine Center, South Bristol, Lincoln County, Maine (43.57°N, 69.33°W), in a 3.5 ha field containing several forbs that provide hunting sites for the spiderlings. During the period of study in August (2003–2008), large numbers of flowers, primarily goldenrods *Solidago* spp., bloom in this field, which I have described in detail elsewhere (Morse 2007). Voucher specimens from this population of *M. vatia* have been deposited in the American Museum of Natural History, New York.

To test whether they would gain additional mass under the most favorable of possible circumstances, I provided naïve, newly-emerged *M. vatia* spiderlings with one of three feeding regimes: regular access to the syrphid *T. marginatus*, a single *T. marginatus* followed by regular access to fruit flies, and regular access to fruit flies only. Juvenile *M. vatia* will readily progress through several instars with fruit flies fed on standard media (Carolina Biological Supply, Burlington, North Carolina) (D.H. Morse 2000, unpublished data), although most females experience difficulties maturing on this diet (see Uetz et al. 1992; Mayntz and Toft 2001).

Spiderlings were housed in 7-dram vials (5 cm high × 3 cm diam.) at ambient temperature and day-length and offered a prey item every other day. Earlier efforts (Morse 2000) demonstrated that the spiderlings would not regularly accept prey more frequently than every second or third day. Clearly the capture of a syrphid by a newly emerged individual is a prodigious feat, even within the artificial confines of a small vial. Relatively few of these individuals captured syrphids within a two-day period. I only retained the spiderlings that initially captured a syrphid and released the unsuccessful individuals into the field. Spiderlings that captured syrphids were randomly assigned to either a pure syrphid diet or a fruit fly diet. I compared the success of spiderlings assigned to a pure syrphid diet with the success of all spiderlings presented with syrphids for the first time. Control spiderlings, drawn from the same pool of individuals as those exposed to the syrphids, also received one fruit fly every other day. I repeated these efforts until I had obtained *n*'s of approximately 20 for each of the three groups. Additionally, I ran a small sample of 10 spiderlings that had initially captured a syrphid with several fruit flies every other day.

I maintained the spiderlings in these feeding trials for one month, recording molts and mortality and subsequently comparing the final masses of individuals from the three main conditions with a one-way ANOVA, followed by Tukey-Kramer tests. I subsequently compared the syrphid + fruit fly and syrphid + several fruit flies samples with a two-tailed *t*-test for the difference between two means.

Although artificial, these conditions provide insight into the most advantageous conditions that the spiderlings could experience in the field. To provide a realistic comparison, I followed a set of 10 spiderlings for one month on goldenrod (*Solidago canadensis*), regularly weighing these individuals. Goldenrods are abundant herbaceous perennials that form large inflorescences of tiny flowers, those of *S. canadensis* being plume-like in character. Observations and measurements of these spiderlings ended when the goldenrod floral substrate had almost completely senesced, resulting in dispersal of the spiderlings.

To provide a natural comparison with the laboratory feeding regime, I censused insect visitors to several goldenrod inflorescences during mid-day (11:30–13:30 h) at several times over the flowering season. In addition to the syrphids, large numbers of a small dance fly (Empididae) frequented the site (Morse 1993b). The spiderlings readily captured these 0.8–0.9 mg flies and fed exclusively or nearly exclusively on them at this time; thus, their diet bore considerable similarity to the laboratory spiderlings' fruit fly (ca. 1 mg) diet.

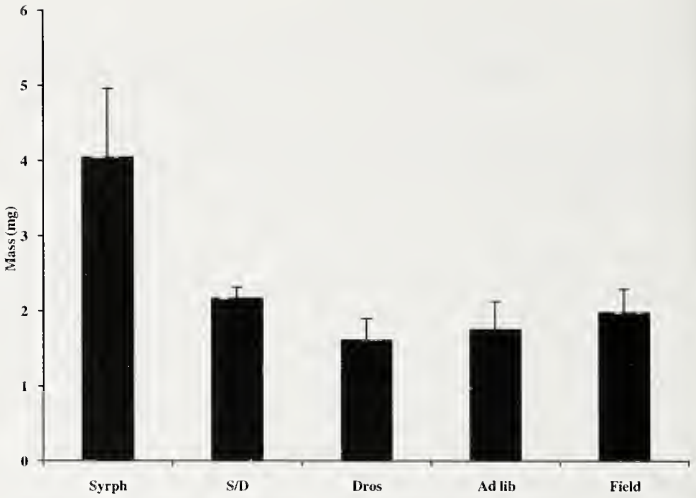

Figure 1.—Gains in mass (mg) of newly emerged spiderlings *Misumena vatia* that survived one month + 1 SE. Syrph = fed only one syrphid fly *Toxomerus marginatus* every other day, S/D = fed initial syrphid and then one *Drosophila melanogaster* every other day, Dros = fed one *Drosophila* every other day, Ad lib = five or more *Drosophila* every other day, Field = free-ranging in field on goldenrod *Solidago canadensis* inflorescences.

RESULTS

Gains in mass differed significantly among the three basic laboratory feeding regimes (Fig. 1: $F_{2,61} = 18.42$; $P < 0.0001$ in a one-way ANOVA). Individuals that fed only on syrphids weighed significantly more than those taking an initial syrphid and then fruit flies or from those presented only fruit flies (Tukey-Kramer tests, $P < 0.05$). The mass of the latter two groups did not differ significantly from each other ($P > 0.05$, same test). However, the syrphid-only group also experienced much higher mortality rates than the other groups (Fig. 2: $G_2 = 18.41$, $P < 0.001$ in a *G*-test of independenee), due to the failure of several individuals to capture these large prey on a regular basis, as opposed to the fruit fly only or syrphid + fruit fly groups. Thus, the mortality rate obtained for the syrphid-only group is likely to be conservative, since individuals that did not capture syrphids in the first place would seem unlikely to capture as many of these prey as those spiderlings that made an initial capture. In fact, spiderlings that had already caught a syrphid were more than twice as successful as those attempting to capture a syrphid for the first time [45% (18 of 40) vs. 17% (57 of 330): $G_1 = 14.28$, $P < 0.001$ in a *G*-test of independence]. The syrphid + fruit fly group did not differ in mass from the small group that I provided with several fruit flies after they captured a syrphid ($t_{29} = 0.64$, $P > 0.5$ in a two-tailed *t*-test).

Gains in mass of the syrphid-only spiderlings significantly exceeded those from the field test, those fed on fruit flies only, and those fed with an initial syrphid followed by fruit flies (Fig. I: $F_{3,20} = 13.66$, $P < 0.001$ in a one-way ANOVA). None of the other groups differed significantly among themselves ($P > 0.05$ in Tukey-Kramer tests). Thus, the laboratory studies using fruit flies presented a realistie estimate of growth in the field.

The spiderlings in the field fed nearly exclusively on dance flies, whose densities varied between 8.0 ± 1.26 and 0.0 flies per goldenrod inflorescence (n = 83–486 inflorescences on

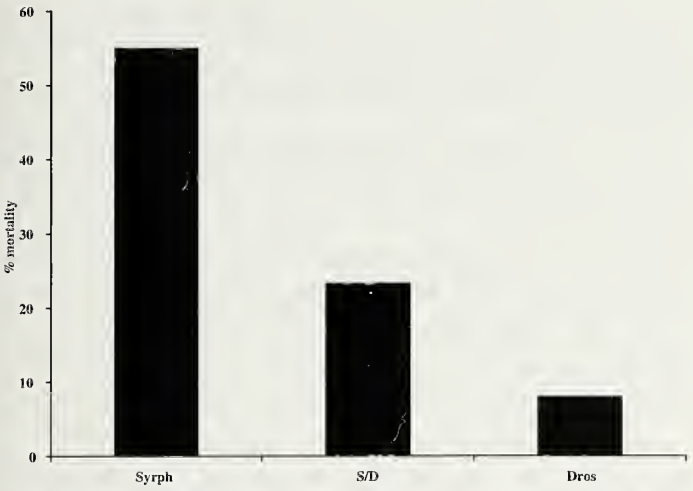

Figure 2.—Percentage of spiderlings that died over one month in growth experiment shown in Figure 1. Spiderling groups as in Figure 1.

different census days from 8–30 clones on evenly-spaced census days over the flowering period), the 0.0 recording a probable consequence of the increasing senescence of these flowers at the end of the season. *Toxomerus marginatus* ranged from 1.1 ± 0.02 to 0.0 per inflorescence in the same censuses. I made no observations of these spiderlings feeding on *T. marginatus* during regular monitoring in the field. Since spiderlings typically feed upon a *T. marginatus* for several hours, my failure to obtain any observations of such a kill during censusing of the spiderlings is consistent with their failure to capture any of them at this time. Given the above-noted infrequent observations of kills made in earlier years, I did not anticipate such an observation during the time devoted to the censuses.

Molt patterns closely followed those of the gains in mass over the study period ($F_{2,61} = 54.02$, $P < 0.001$ in a one-tailed ANOVA). All but one surviving individual fed only on syrphids molted twice during the test period; members of the other groups molted only once, at most. The syrphid-only group averaged 1.9 ± 0.09 molts; the syrphid + fruit fly group, 0.9 ± 0.08 molts; and the fruit fly-only group, 0.8 ± 0.08 molts. The syrphid-only group molted significantly more often than the other two groups ($P < 0.05$ in Tukey-Kramer test); the latter two groups did not differ among themselves ($P > 0.05$: same test).

DISCUSSION

Attacking exceptionally large prey.—Clearly, extreme success in prey capture, such as that attained by some of the syrphid-only spiderlings, can result in large, rapidly developing spiderlings. However, the experiments did not suggest a high probability of such success under field conditions. Individuals capturing a single large prey item appear unlikely to gain significantly more mass or produce more molts over the long term than otherwise similar individuals that fail to make such a capture and otherwise have similar access to prey. Those that captured syrphids in this study did so under considerably more favorable conditions than they would experience in the field and probably approached the maximum rate that a spiderling can hypothetically gain during its early instars. I observed no apparent mortality from this exuberant intake, a source of high mortality among fourth-instar *Nephila clavipes* (Linneaus 1767) reared by Higgins and Rankin (2001). With exception of the few individuals that managed to specialize on *T. marginatus*, the similarity in performance of the spiderlings from the different tests appeared as if constrained by intrinsic factors (Jackson & Rundle 2008). Although capture of a first syrphid enhanced the probability of capturing subsequent ones, a majority of these spiderlings failed to capture a second syrphid, further emphasizing the difficulty of achieving enhanced success in this way. The similarity of gains in mass by the spiderlings fed a single syrphid + fruit flies ad libitum, those fed single fruit flies, and those free-ranging in the field suggests that the group fed single fruit flies served as an adequate control set.

The failure to capture a second syrphid accounted for the high level of mortality through apparent starvation in that group, a result consistent with these individuals subsequently narrowing their range of acceptable prey after an initial experience. These individuals thus serve as a subsequent starvation group. In addition to any effort expended, attacks on extremely large prey often are dangerous (Norris & Johnstone 1998; Roger et al. 2000; Smallegange et al. 2008). Successfully attacked syrphids initially struggled violently for several seconds after spiderlings contacted them and in some instances managed to dislodge the spiderlings by wiping them against the substrate, an action likely to damage the spiderlings' mouthparts and limbs. However, I did not observe these unsuccessful spiderlings continually and thus could not unequivocally establish whether their failure to capture subsequent syrphids resulted solely from refraining to attack them or from the simple failure to make a kill.

Success in the field.—Although sizes of juvenile *M. vatia* in the field vary widely at any given time, this study suggests that the capture of relatively huge prey by second-instar spiderlings does not make an important contribution to this variance. The rather wide range of spiderling emergence dates (Morse 2007) probably plays an important role in the size-spread observed, and differences in initial offspring size (Morse 2000) will further modify the sizes of individuals at a site at any given time. However, low prey availability probably accounts for a strikingly large variation in size and growth rates in the field. Numbers of prey visiting the flowers fluctuate widely, with occasional pulse years and many years in which few are present at the times critical for spiderling growth (Morse 2007). The spiderlings share the ability to engorge themselves with a number of species that depend on highly unpredictable food sources (Schneider & Lubin 1997), though only the pure syrphid diet, unlikely to be achieved in the field, yielded a significantly greater growth rate than that of other ad lib regimes tested.

Since the overwintering mortality of particularly small young may considerably exceed that of individuals completing one or more molts after emergence from their egg sac (Jespersen & Toft 2003; Morse 2007), and size at the end of the season is likely enhanced by high prey numbers, selection should strongly favor the ability to capture profitable prey efficiently. However, the low success rate of concentrating on prey as large as *T. marginatus* seems unlikely to enhance selection for specializing on prey of this size range. Neverthe-

less, no size groups of *M. vatia* appear to exhibit strong size selection in their attacks on prey (Morse 1979; Erickson & Morse 1997), even though success rates declined with increasing prey size, a common pattern with active prey (Werner & Gilliam 1984; Christensen 1996).

Relation to the life cycle.—As individuals grow, their available resource bases change (Werner and Gilliam 1984). Subsequent juvenile instars enjoy considerably higher success rates in capturing *T. marginatus* than do the second-instar spiderlings. In fact, this abundant prey species is the most important food for many middle-instar *M. vatia* in the study area (Erickson & Morse 1997).

As boom-or-bust hunters adult female *M. vatia* depend on an ability to capture substantial numbers of relatively large prey, but few reach maximum possible size, and most adult females reaching a minimal size for egg-laying (ca 115 mg) will lay their eggs if they do not capture a prey item within a few days (Morse & Fritz 1982; Fritz & Morse 1985). Penultimate female *M. vatia* appear to require unusually large prey items to molt into adults (Morse 1999), a problem seen in other species often lacking sufficient numbers of appropriate-sized prey (Werner & Gilliam 1984; Olson 1996; Persson & Brönmark 2009). These critical demands for large prey by later stages make it plausible that *M. vatia* exhibit a general predisposition to attack prey that are large relative to their own size, even though with experience they might subsequently refrain from such attacks. Such a trait might serve them well at several life stages.

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Is movement behavior of riparian wolf spiders guided by external or internal information?

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Abstract. Orientation is an essential process preceding movement behavior. Information necessary for orientation toward suitable habitat can be gathered by acute and internal information. The former comprises directly detectable, external stimuli, whereas internal information includes earlier experienced environmental cues and inherited information related to an individual's origin. In habitats that can suddenly be disturbed (such as river banks), an accurate orientation is of prime importance for successful movement toward safe habitat. In a common-garden field experiment, we studied between-population variation in movement responses toward safe winter habitat (dike vegetation) of two sympatric riparian wolf spiders, the stenotopic riparian species *Pardosa agricola* (Thorell 1856) and the generalist *P. amentata* (Clerck 1757). Both responses to direct visual cues and orientation toward home habitat were investigated on an unfamiliar river bank upstream from the original populations. Movement toward safe habitat was mainly controlled by previously collected information on the riverbank location in the stenotopic species and additionally influenced by visual cues and the prevailing weather conditions. Movements in *P. amentata* were flexible and not systematically guided by either internal information or direct visual cues. Experience on the location of safe habitat consequently guided orientation in the stenotopic species. Internal information is therefore hypothesised to favor the stenotopic wolf spider by restricting unnecessary movements when sudden threatening situations emerge. Generalist species have less experience with the specific disturbance and do not show pronounced orientation capabilities toward safe habitat.

Keywords: Between-population variation, Lycosidae, orientation behavior, *Pardosa agricola*, *Pardosa amentata*

Effieient movement toward safe habitat is essential when sudden perturbations occur in the currently occupied habitat (Zollner & Lima 1999, 2005; Fahrig 2007). Optimal movements should therefore be preceded by precise orientation behavior. This orientation should be based on information either collected instantaneously from the local environment or based on internal information eollected during an individual's life or on information shaped by natural selection (Dall et al. 2005).

Homeward orientation mechanisms, for instance, unidirectional zonal recovery in intertidal zones [e.g., sandhoppers (Borgioli et al. 1999a; Ugolini 2001), wolf spiders (Morse 2002)], are considered to be beneficial risk-avoiding strategies. Homeward orientation may lead to profitable outeomes in familiar environments, guiding such cursorial organisms as wolf spiders directly toward suitable conditions (Morse 1997, 2002). Visually detectable cues, either local landmarks such as vegetation structure (e.g., Bonte et al. 2004) or celestial cues (e.g., Papi 1955), also eontribute to accurate orientation. By gathering information from the environment, organisms reduce the ecological uncertainty of that environment (Wehner 1997; Dall et al. 2005), eventually leading to movement or dispersal (Lima & Zollner 1996; Pulido 2007). Perception, however, mainly depends on an organism's sensory abilities (Wehner 1997). For cursorial spiders in particular, there is no doubt that detectable factors are integrated into orientation and movement decisions (Land 1971; Persons & Uetz 1996; Ortega-Escobar & Muñoz-Cuevaz 1999; Norgaard et al. 2007; Rypstra et al. 2007).

Organisms may also rely on information collected during their life or on inherited movement rules (Pullido 2007; Clobert et al. 2009). In this ease, organisms do not need to spend time and energy to collect information on the most advantageous movement direction and rely on internally shaped movement rules (Papi & Tongiorgi 1963; Borgioli et al. 1999a; Morse 2002). However, since inherited information and experience might deceive an organism in unfamiliar or quickly changing conditions (Schlaepfer et al. 2002), their importance is relative to detectable sources of external information (Wehner 2003; Bowler & Benton 2005; Danchin et al. 2008). Moreover, orientation can be refined by learning (Papi & Tongiorgi 1963; Scapini et al. 1988; Collet et al. 2001). Learning results from the spatial relationships among objects in the organism's perceptible range and from previous experienced proximate cues (Persons & Uetz 1996; Giraldeau 1997). Since consistent movements shaped by internal movement rules can be disadvantageous (Bowler & Benton 2005), especially for organisms occurring in unpredictably disturbed environments (Lytle & Poff 2004), orientation behavior has to be flexible to some extent. Whenever different modalities that guide orientation decisions are opposed (e.g., accustomed cues on the location of natal or safe habitat vs. celestial information), inaccurate orientation and movement direction might emerge (Papi & Tongiorgi 1963; Borgioli et al. 1999b). Hence, plasticity in orientation or movement behavior will benefit organisms occurring in disturbed environments (Scapini et al. 1988, 2002; Bonte et al. 2007).

It is suggested that experience with long-term characteristics of the environment may be inherited (Danchin et al. 2008). Hence, species that differ in their ecological life history or originate from populations exposed to different environmental conditions possibly respond differently under stressful circumstances by integrating internal and external information in a different way (Dall et al. 2005; Danchin et al. 2008). Since flood events imply severe fitness costs for shore-inhabiting organisms (drowning or washing away), mobile species are expected to show a directed response away from the rising water level (moving ashore) and even withstand flooding during transient inundation events (Rothenbücher & Schaefer 2006; Lambeets et al. 2008). Since flooding is a constant

component of the riparian environment, organisms that are familiar with this detectable yet unpredictable factor (riparian stenotopic species) are more likely to transmit knowledge about the directional component 'flooding' across generations than are their generalist congeners (Lytle & Poff 2004). Therefore, populations at opposite sides of the river might be expected to differ in their response to visual cues associated with the riparian environment. As proven by Morse (2002) for the intertidal *Pardosa lapidicina* Emerton 1885, external information, such as substrate structure, guides movements of the wolf spider away from the rising tide. Moreover, movements toward adjacent upland overwintering sites before the onset of long-lasting winter floods have been recorded for mobile, predatory arthropods from river bank habitats (Lang & Pütz 1999; K. Lambeets unpubl. data).

Here, we aimed to determine whether between-population variation in movement responses of riparian wolf spiders before the onset of the long-lasting winter flood remains consistent when they are subjected to different visual stimuli. These wolf spiders are short-lived (two-year life cycle with overwintering subadults), but able to build up experience with flooding during spring and autumn when riverbanks are subject to unpredictable flood events. This hypothesis was tested with two congeneric and sympatric wolf spiders (Lycosidae) with different ecological life histories. We considered the outcome of this orientation behavior as a good proxy for ashore movement toward suitable wintering habitats. *Pardosa agricola* (Thorell 1856) is a stenotopic riparian species (Harvey et al. 2002) that inhabits flood-disturbed riverbanks throughout the year (Lambeets et al. 2007). In contrast, *P. amentata* (Clerck 1757) occurs commonly in a wide range of rather humid habitats and rough growth (Alderweireldt & Maelfait 1988). Thus, the latter is considered to encounter the typical conditions met on riverbanks (e.g., flooding) more sporadically, since the surrounding grasslands are its main habitat. Both species are diurnal and actively hunt across the bare gravel or among the scarce, short riverbank vegetation (K. Lambeets, pers. obs.). Since *P. agricola* spends its life entirely in patchy distributed river banks, it is expected to be familiar with their dynamic character and the spatial arrangement of river bank structures. We therefore expected *P. agricola* to rely predominantly on inherited or experienced sources of information (population of origin) to restrict unnecessary movements. In contrast, cues from the vegetation are expected to act as an orientation landmark for the generalist wolf spider, *P. amentata*, leading to movements toward safe habitat.

METHODS

Experimental field set-up.—During August 2005 and 2006, before the onset of the long-lasting winter flood (Van Looy & De Blust 1995), individuals of *P. agricola* and *P. amentata* were collected from four highly isolated river banks in the downstream section of the Common Meuse. Voucher specimens are deposited at the Royal Museum of Natural History (KBIN) in Brussels. Two isolated populations of both species (mean interpopulation geographical distance = 2504 m ± 532 SE, mean F_{st} = 0.0248 ± 0.0046 SE; Lambeets et al. 2009) were sampled on both sides of the river. Only individuals occurring on the bare gravel were collected. The riverbanks were similar in flooding susceptibility (flooded at 179 m^3/s ± 13 SE), size (area: 10202 m^2 ± 1940 SE) and vegetation structure (Lambeets et al. 2007). Behavioral differences arising from dissimilar stand conditions may consequently be ruled out (Papi & Syrjämäki 1963). All individuals were collected in separate plastic vials with a humid plaster bottom and fed ad libitum with *Drosophila melanogaster* prior to testing (climatic chamber under ambient light conditions and constant temperature, 15° C). Earlier experiments had already shown that a short time under controlled conditions did not change behavior to tactile stimuli (Lambeets & Bonte 2009). Within a week, orientation behavior (ashore movement toward safe habitat, dike vegetation) was tested in a large arena constructed of transparent plexiglass sides (160 × 60 × 25 cm) with the bottom covered by a sand-gravel mixture. The arena was placed on an unfamiliar river bank upstream that was structurally the same as the natal river bank habitat (soft slope, bare gravel for > 20 m from the waterline onwards). Alternately, the arena was positioned directly along the waterline and the dike where vegetation was perceptible. These test locations were approximately 40m apart. For each test, weather conditions (sunny, overcast) were recorded. All spiders were tested in groups of ten individuals per population and per species. The sun was between the southeast and southwest quarter during the tests (Fig. 1). Since the river banks of origin were all oriented in an east-west direction (i.e., for river banks along the right side of the river the dike vegetation was present in the east and the waterline in the west, for banks at the left river side the other way around), diurnal variation in orientation was confined to a minimum. Each group of wolf spiders was successively released in the middle of the arena. We scored whether or not individuals within each group were inclined to move ashore. Ashore movement was considered a proxy for unidirectional orientation; i.e., away from the waterline or toward the dike vegetation. In this way, a simple proportional measure of orientation was recorded as the proportion of individuals moving ashore. For all groups, tests were repeated three times for the test locations (waterline, dike vegetation), but in random order to avoid newly gained experience (cf. Papi & Tongiorgi 1963; Persons & Uetz 1996). If ambient conditions exceeded 30° C the field experiment was stopped to prevent severe dehydration. In total, 28 groups of *P. agricola* and 21 groups of *P. amentata* were tested.

Statistical analysis.—We analysed whether orientation behavior differed according to population of origin (two populations from each river side), weather conditions (sunny, overcast), test locations (visual cues: waterline, dike vegetation) and their interactions. The binomially scored responses were analysed by Generalised Linear Mixed Models with logit-link (GLMM, SAS 9.1.3). Repeated tests and test groups were treated as random factors. Insignificant terms were sequentially removed. Corrected degrees of freedom were calculated by Satterthwait's procedure (Verbeke & Molenberghs 2000). Post-hoc Tukey tests were applied to reveal significant proportional differences in ashore movement.

RESULTS

Wolf spiders clearly differed in their orientation behavior according to their geographical origin, weather conditions and

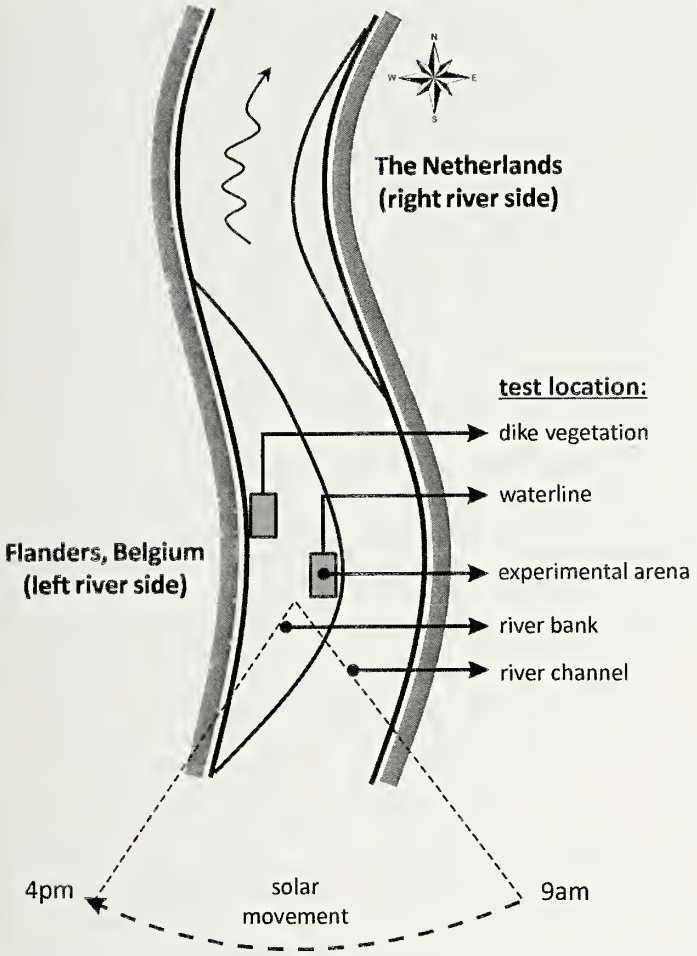

Figure 1.—Experimental field setup to test for orientation behavior preceding movement of riparian wolf spiders along the Common Meuse.

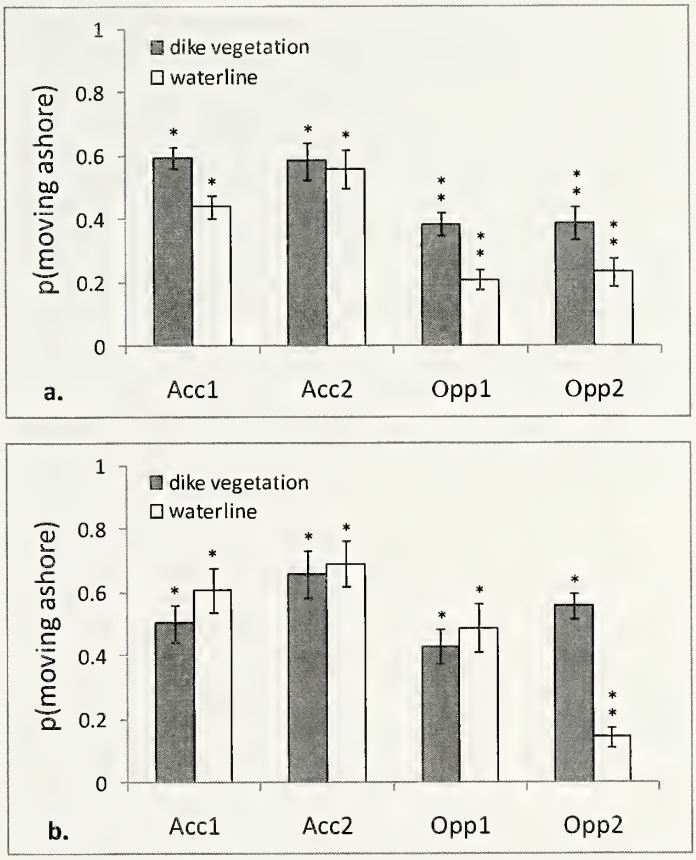

Figure 2.—Estimated mean proportions for orientation behavior per population of a) the stenotopic riparian wolf spider *Pardosa agricola* and b) the generalist *P. amentata*. Four populations, two from each side of the river, were tested during a field experiment, alternately at two locations (waterline, dike vegetation). Acc1, Acc2 indicate individuals collected on the same side of the river (accustomed) as where they were tested; Opp1, Opp2 point to individuals ascending from the opposite side. Columns represent the mean response per population during overcast conditions (see text for differences according to weather and test location). Error bars = standard error of the mean. A different number of asterisks indicate that populations proportionally differed in ashore movement (all $P < 0.001$).

location of testing (location*origin*weather*species: $F_{2,263} = 0.01$, $P > 0.9$; location*origin*species: $F_{3,263} = 4.94$, $P < 0.01$; location*weather*species: $F_{1,263} = 7.29$, $P < 0.01$). Therefore, further analyses were applied for each species separately (Fig. 2a–b).

The effect of origin in orientation behavior was clear for *P. agricola*. Individuals appeared to move ashore more when originating from the same river shore as where tested (accustomed populations) than when they originated from the opposite shore (Fig. 2a, origin: $F_{3,156} = 22.52$, $P < 0.0001$). Moreover, ashore movement increased proportionally when vegetation was perceptible (tests close to the dike vegetation) (+15.3% for location: $F_{1,156} = 28.44$, $P < 0.0001$) and increased marginally under sunny conditions (+6.1% for weather: $F_{1,155} = 3.29$, $P = 0.07$). Other factors were not explanatory (all $F < 1.52$, $P > 0.2$). Behavioral responses of *P. amentata* were more variable. There were no significant differences in orientation outcomes between the accustomed populations (Fig. 2b), nor between populations from different river shores (Fig. 2b: Opp1 vs. Acc1,2). Differences only appeared for those *P. amentata* groups originating from the opposite shore (Fig. 2b: Opp2, location*origin: $F_{3,116} = 7.22$, $P < 0.001$). Sunny weather conditions led to a significantly decreased tendency to move ashore only when tested at the waterline (−41.3% for location*weather: $F_{1,116} = 12.81$, $P < 0.001$), but not when tested adjacent to the dike. Marginally more individuals from accustomed populations of *P. amentata* moved ashore during overcast conditions (origin*weather: $F_{1,115} = 3.87$, $P > 0.05$). All other terms were insignificant (all $F < 2.1$, $P > 0.2$).

DISCUSSION

The stenotopic riparian wolf spider used both directly received information on the vegetation structure and internal information to perform optimal ashore movements toward safe habitat in response to future flooding. In contrast, a more generalist species not strictly bound to the river bank habitat used these sources of information in a less efficient and more variable manner. Our data suggest that inherited factors or experience (population of origin) and detectable external information (dike vegetation, waterline) guide orientation outcomes and movement behavior of wolf spiders on river banks.

Factors underlying variability in orientation of arthropods in unstable environments have been studied mainly in predictably disturbed intertidal zones (e.g., Scapini et al. 1988; Borgioli et al. 1999a,b; Morse 2002). Behavioral responses at infrequently disturbed habitats such as river banks were subject to earlier studies (Papi & Tongiorgi 1963; Papi & Syrjämäki 1963; Bates et al. 2006). These studies, however, merely considered typical riparian species, and did not compare behavioral traits between sympatric congeners (but see Lambeets & Bonte 2009). A comparative approach might elucidate the adaptive value of such behavior. Since a risk-avoiding strategy, thus evading the flood, has an obvious survival value along flood-disturbed shorelines, adjusting movement in response to predictable or sudden detectable environmental variation is essentially advantageous (Jander 1975; Scapini et al. 1999). From this, it is evident that a riparian species, which is assumed to be familiar with flood events (Lytle & Poff 2004), would benefit from weighing costs and benefits of movement by integrating various information sources. This is demonstrated here by the orientation behavior related both to population of origin (inherited information/experience) and externally collected (visual) cues. The two wolf spider species differ in their ecological history (riparian specialist vs. grassland generalist) and colonise the river banks quickly after the floodwater recedes in spring; however, they clearly show different orientation outcomes. Movement behavior can also be expected to change over the season or with the life stage (Papi & Tongiorgi 1963; Scapini et al. 1999), with orientation being mainly directed toward overwintering habitats before the onset of annually reoccurring floods (Lang & Pütz 1999). Correspondingly, Morse (1997) argued that the movement of intertidal wolf spiders increased when they occurred near the waterline (visual cue), and even more when being splashed by surf (tactile cue). On the other hand, Kraus & Morse (2005) clearly associated seasonal habitat shifts of an intertidal wolf spider with environmental variation.

Movements away from safe habitat when tested on the opposite side of the river were detected in the stenotopic riparian wolf spider. Papi & Syrjämäki (1963) proved that *P. agricola* relied on an internal solar compass as well, even adjusting its orientation according to the time of day (time-compensatory mechanisms; Jander 1975). Despite the apparent necessity of sunny conditions for orientation, *P. agricola* behaved more consistently than *P. amentata* under different weather conditions (Fig. 2a, b). Early-life experience with the river bank surroundings, whether visual or tactile, might explain this behavior, which has been suggested for other wolf spiders in disturbed environments as well (Papi & Tongiorgi 1963; Persons & Uetz 1996; Morse 2002). Differences in orientation, however, might be less pronounced after long-term captivity (Papi & Syrjämäki 1963; K. Lambeets, unpubl. data). Ortega-Escobar (2002) and Norgaard et al. (2007) also showed the necessity of external visual input during homing behavior of two wandering spiders. Since *P. amentata* prefers rough growth and grassy habitats, it is expected to lack sufficient information and/or experience for accurate orientation on the river banks and, consequently, to show increased variation in its responses to unfamiliar detectable visual cues in the direct vicinity (Fig. 2b). Therefore, it is expected to orientate primarily on external visual stimuli and much less on inherited information related to its population of origin. Morse (2002) noted similar behavior for *P. lapidicina*, since individuals that were familiar with tidal floods and typical cobble beach structures (scarce vegetation, bare ground) were more reluctant to orientate and move in the appropriate direction than individuals that lacked experience and lived in higher zones with denser vegetation. This might be the most beneficial (or least adverse) strategy for *P. amentata*, because gathering more information might be more costly than responding in a stereotyped way (DeWitt et al. 1998), since the latter will lead individuals directly to suitable habitats in a variety of situations. The presence of the waterline did not lead to an increased ashore movement for *P. amentata*, whieh indicates it is unfamiliar with the visual perception of flooding (Fig. 2b).

Our results indicate that internal factors related to the population of origin affect orientation outcomes less under benign circumstances than in stressful situations such as being washed offshore (Morse 1997; Lambeets & Bonte 2009). However, Papi & Tongiorgi (1963) and Riechert & Hall (2000) showed the ability of spiders to change their behavior quickly to their own benefit. Experience, for instance with geotactic landmarks such as bank inclination or a humidity gradient (Papi & Tongiorgi 1963), might be necessary to develop a precise orientation strategy (Scapini et al. 1999; Morse 2002). Moreover, other factors such as temperature, dietary conditions or population density can affect specific behavioral responses as well (Nylin & Gotthard 1998; for wolf spiders: Wagner & Wise 1997; Walker et al. 1999). Since factors related to both the population of origin and vegetation landmarks guide the movement behavior of a stenotopic riparian wolf spider, it leads to a more efficient movement strategy to carry it to its safe winter habitat in autumn. A generalist wolf spider, on the other hand, might be negatively affected by flooding, since its orientation behavior seems guided mainly by acute external information. Generally, decision-making that precedes movement is guided both by factors related to inherited information and external stimuli such as detectable visual cues (Clobert et al. 2009). Individuals from different populations, however, may convert inherited or experienced information into different behavior (Scapini et al. 2002; Bonte et al. 2006).

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Orb web features as taxonomic characters in *Zygiella* s.l. (Araneae: Araneidae)

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Abstract. The species classically grouped in the genus *Zygiella* F.O. Pickard-Cambridge 1902 are thought to all possess a characteristic orb web feature – a spiral-free sector in the upper part of the orb. *Zygiella* s.l. has recently been split into four genera, *Zygiella* s.s., *Leviellus* Wunderlich 2004, *Parazygiella* Wunderlich 2004 and *Stroemiellus* Wunderlich 2004, and proposed to belong to family Zygiellidae, rather than the classical Araneidae. To find orb web features that could potentially diagnose these species and/or genera, we investigated female web architectures of *L. thorelli*, *P. montana*, *S. stroemi*, *Z. keyserlingi* and *Z. x-notata*. We investigated a total of 278 female webs and compared 16 characters emphasizing web size, web and hub asymmetry, as well as radial and spiral counts. The free sector may be present in all species but its prevalence in female webs varied from 41% in *Z. keyserlingi* to 94% in *P. montana*. Various combinations of web architecture characters may diagnose those species that in our sample represented all four genera: *Zygiella* s.s. may be diagnosed by the median number of non-circulating sticky spirals below hub, *Stroemiellus* by the small web size with small mesh width and the non-circulating spirals above hub, *Parazygiella* by few primary radii and sticky spirals, and *Leviellus* by a pronounced vertical hub displacement. This suite of diagnostic features may provide preliminary support for the current taxonomy of *Zygiella* s.l., although the ultimate test, i.e., a phylogeny, is needed to test the validity of the genera. Seven out of 16 web characters are potentially phylogenetically informative because they show a statistically significant shared variation among species. Our study, which pioneers the quantification of web data to distinguish species, implies that the interspecific variation in webs may turn out to reflect phylogenetic relationships among *Zygiella* s.l.

Keywords: Zygiellidae, web architecture, taxonomy, diagnosis, behavior

Many studies show that behavioral characters are taxonomically and phylogenetically useful (Eberhard 1982; Prum 1990; Wenzel 1992; Miller & Wenzel 1995; Scharff & Coddington 1997; Griswold et al. 1998; Price & Lanyon 2002; Freudenstein 2005; Kuntner et al. 2008a). This is also true of spider webs, which are static manifestations of certain behaviors and as such represent an extension of the spider's phenotype (Agnarsson 2004; Benjamin & Zschokke 2004; Lopardo et. al 2004). Orb webs and building behaviors are complex, apparently stereotyped features that are taxonomically informative (Eberhard 1982; Kuntner 2005, 2006, 2007). Some details in web architecture and building behavior are conservative enough to characterize families, genera and even intrageneric groupings (Eberhard 1990; Benjamin & Zschokke 2004; Kuntner & Agnarsson 2009). For example, all nephilid genera can be diagnosed by orb web features, which also serve as synapomorphies for individual groups (Kuntner 2005, 2006, 2007; Kuntner et al. 2008a). On the other hand, contradicting evidence suggests that spider web architectures evolve rapidly as a response to different selection pressures (Eberhard 1990), and as such may be of lesser use in phylogenetic and taxonomic diagnoses. For example, Eberhard et al. (2008) showed that theridiid webs (themselves derivatives of the orb, see Coddington 1986; Griswold et al. 1998) are highly evolutionarily labile and plastic, and in many cases cannot diagnose genera. Although on a macroevolutionary scale the evolution of the orb web and its modifications is now reasonably well understood (Opell 1999; Blackledge et al. 2009), the microevolutionary patterns within smaller groups are poorly known, and the generalization of the orb web utility in taxonomic diagnoses is far from resolved.

Here we focus on comparative orb web biology of a poorly known, small group of araneoid spiders, whose taxonomic status is controversial. The species classically grouped in the Holarctic genus *Zygiella* F.O. Pickard-Cambridge 1902 (hereafter *Zygiella* s.l.) all possess a characteristic, and presumably diagnostic, orb web feature – a sector in the upper part of the orb that is spiral-free (Fig. 1A; Levi 1974). *Zygiella* s.l. is traditionally placed in Araneidae (Levi 1974; Platnick 2009). Although Levi (1980) considered *Zygiella* closer to Tetragnathidae, the cladistic analysis of Scharff & Coddington (1997) placed it back in Araneidae. *Zygiella* s.l. was recently split into four genera (*Zygiella* s.s., *Leviellus* Wunderlich 2004, *Parazygiella* Wunderlich 2004 and the monotypic *Stroemiellus* Wunderlich 2004), and Wunderlich (2004) proposed these genera to belong to a new family Zygiellidae, along with the tetragnathid *Chrysometa* Simon 1894. Although the new genera have been catalogued (Platnick 2009), the family Zygiellidae is not generally accepted. However, the most recent phylogeny, combining molecular and morphological data, casts new doubt on the araneid affinity of *Zygiella* (Blackledge et al. 2009) and thus suggests that perhaps Zygiellidae may be a valid taxonomic concept after all.

According to Wunderlich (2004), *Zygiella* s.s. is diagnosed by the absence of the terminal apophysis and the epigynal scape, and by the small palpal bulb; *Leviellus* by the hooked male endite, the terminal apophysis being close to the embolus, and the short epigynal scape; *Parazygiella* by the terminal apophysis being distinctly apart from the embolus; and *Stroemiellus* by the very long epigynal scape and the apically strongly widened and flattened embolus. All these

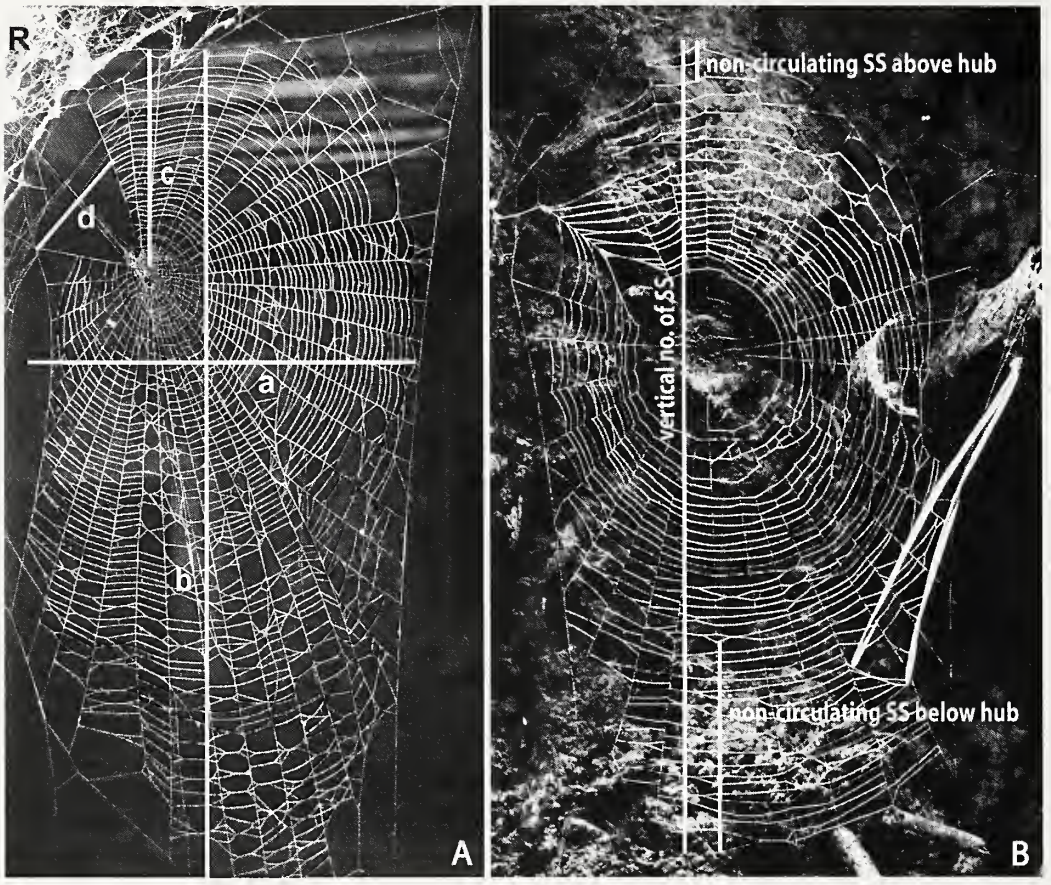

Figure 1.—Webs of *Leviellus thorelli* (A) and *Stroemiellus stroemi* (B). Note absence of the free sector, with investigated parameters: web-width (a), web-height (b), top to hub distance (c), free sector (d), retreat (R), vertical number of sticky spirals (SS), and non-circulating SS above and below hub.

generic diagnostics concerned morphology only. However, Wunderlich (2004) treated the free sector as a web character uniting these genera.

The aim of this paper is to establish whether "zygiellid" orb webs are evolutionarily constrained and thus useful for taxonomic diagnoses at the species level, or evolutionarily plastic and prone to change in response to ecological factors. We examine the statistical prevalence of the free sector in *Zygiella* s.l., investigate if and to what extent orb web features may be used to diagnose the species and/or genera within the group, and identify potentially phylogenetically informative traits. We investigated 278 adult female web architectures of *Leviellus thorelli* (Ausserer 1871), *Parazygiella montana* (C.L. Koch 1834), *Stroemiellus stroemi* (Thorell 1870), *Zygiella keyserlingi* (Ausserer 1871) and *Zygiella x-notata* (Clerck 1757), and perused 16 characters emphasizing web size, web and hub asymmetry, and radial and spiral counts. We predicted that if Wunderlich's taxonomy holds, a combination of these characters will unequivocally diagnose each species that, in our sample, represents a genus (*Leviellus*, *Parazygiella*, *Stroemiellus*, *Zygiella*). We further predicted that some of the characters will be shared by several taxa, thus revealing potential phylogenetic information.

METHODS

At 25 localities in Slovenia and one in Croatia (2006–2008) we investigated 88 webs of *L. thorelli*, 71 webs of *P. montana*, 36 webs of *S. stroemi*, 39 webs of *Z. keyserlingi* and 44 webs of *Z. x-notata*. We selected only adult and in some cases subadult female webs, dusted them with cornstarch to increase visual contrast for measurement and photography, and measured them with a tape measure. We previously identified 38 behavioral characters from araneoid web literature (Eberhard 1982; Zschokke 1993; Griswold et al. 1998; Blackledge & Gillespie 2002; Kuntner 2005, 2006, 2007; Kuntner et al. 2008a), which we further modified to fit the taxonomic context, and in addition tested new ones. Out of this pool of characters 16 turned out informative, and we included only those in the analysis.

Field measured characters.—We measured the following parameters in the field:

1. *Web width* (Fig. 1A: a) as the horizontal distance between outermost spirals.
2. *Web height* (Fig. 1A: b) as the vertical distance between outermost spirals.
3. *Distance from top frame to hub* (Fig. 1A: c).
4. *Presence of the free sector* (Fig. 1A: d); defined as absent (0), rudimentary (1) or present (2). A rudimentary free sector is lacking some, but not all sticky spirals (Fig. 5C).
5. *Web shape*: Either downward convergent (0), parallel (1) or downward-divergent side frames (2). Similar to side frame curvature (round, subparallel, parallel) sensu Kuntner et al. (2010), this character describes

the shape of the orb web, delimited with its side frames.

6. *Number of primary radii* as those radii that run from the hub to the frame (Kuntner et al. 2008a).
7. *Vertical number of sticky spirals (SS)* (Fig. 1B).
8. *Horizontal number of sticky spirals (SS).*
9. *Number of non-circulating SS below hub* (Fig. 1B): Non-circulating SS are defined as sticky threads, running through less than a third of web-height.
10. *Presence of non-circulating SS above hub* (Fig. 1B).

We attempted to collect all voucher specimens to measure the length of their patella and tibia on leg I. A representative sample of all species studied is deposited in the collections of the National Museum of Natural History, Smithsonian Institution.

Derived characters.—We calculated the following indices:

11. *Mesh width*, defined as the number of SS per centimeter of web-height.
12. *Web area*, used as in Blackledge & Gillespie (2002) and defined with the formula (a/2)*(b/2)*π.
13. *Relative SS number*, defined as the number of sticky spirals corrected for spider size.
14. *Radii-SS ratio*: defined as the ratio of primary radii to vertical number of SS.
15. *Web asymmetry (WA)*; used as in Blackledge & Gillespie (2002), similar to web shape *sensu* Zschokke (1993) and ladder index *sensu* Kuntner et al. (2008b). It is defined as the departure of the outermost SS of an orb web from a circular shape and calculated with the formula WA = 1 − a/b.
16. *Hub displacement (HD)*; used as in Kuntner et al. (2008b), similar to hub asymmetry *sensu* Blackledge & Gillespie (2002) and defined with the formula HD = 1 − c/b.

A perfectly circular web with the hub in the geometric center thus has a WA value of 0 and a HD value of 0.5. These values increase as the web becomes more vertically asymmetric and the hub displaced towards the top frame.

Statistical analysis.—We used SPSS (version 13.0, SPSS Inc.) for all statistics. Parameters were tested for normality using the Shapiro-Wilk test. Interspecific differences in web measures were tested using the Kruskall-Wallis test and Mann-Whitney *U*-test. The significance level was set to 0.005 or lower (Bonferroni correction). Correlation and regression analyses were done using Spearman's rho and linear regression, respectively.

Diagnostic versus phylogenetic characters.—Features used for the sole purpose of species diagnosis are phenetic characters, which unite taxa based on their overall similarity, regardless of their phylogenetic relationship (Schuh 2000). Phylogenetic characters, on the other hand, can infer the evolutionary relationships among groups (Pleijel 1995; Schuh 2000; Freudenstein 2005) and will therefore unite several taxa. In the context of a given taxon sample, potentially phylogenetically useful characters are those that show statistically significant shared variation among species. They are, therefore, a subset of diagnostic characters (Fig. 2). Although the best test of the utility of a taxonomic character would be to optimize it on a phylogeny, the scope of this paper is not a phylogenetic hypothesis for *Zygiella* s.l., much less of Zygiellidae. Rather, our study aims to establish diagnostically useful characteristics, and those that may potentially be used in future phylogenetic studies.

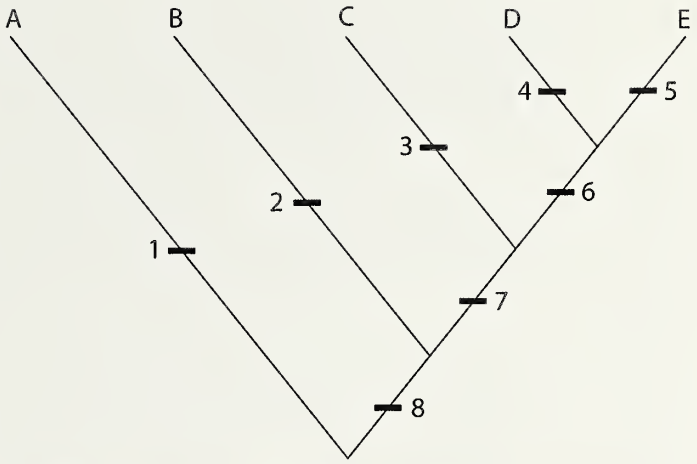

Figure 2.—A hypothetical phylogeny with species as terminals (A–E) and optimized characters (1–8; for clarity, all characters are homoplasy-free). Characters 1–5 are autapomorphies, which may diagnose species A–E. Characters 6–8 may diagnose more inclusive groups/clades. Phylogenetically informative characters (6, 7, 8) are thus a subset of diagnostic characters (all).

RESULTS

The five species investigated are similar in certain behavioral and web features. Except for the arboricolous *S. stroemi* they are at least partially synanthropic and build vertical orb webs on houses, fences, etc. (Fig. 5). The retreat is always built off-web, touching the substrate, and is connected to the hub via a signal line (Fig. 5). The web is never decorated with debris as in *Cyclosa*, *Dolicognatha* (Levi 1977) or *Clitaetra* (Kuntner & Agnarsson 2009), or by stabilimenta as in many araneid, uloborid and nephilid genera (Robinson & Robinson 1973; Scharf & Coddington 1997; Kuntner et al. 2008a). They attack prey by biting first and then wrapping (Eberhard 1982). Individuals of all investigated species hide in the retreat during the day. They do not shake their body on the web when threatened, as in *Argiope*, *Azilia*, *Nephilengys*, *Nephila* and *Clitaetra* (Kuntner 2006; Kuntner et al. 2008a), but rather run to the retreat or jump off the web.

Table 1 lists medians and interquartile ranges (IQR) for the quantitative parameters. Figs. 3 and 4 show the web properties in *L. thorelli*, *P. montana*, *S. stroemi*, *Z. keyserlingi* and *Z. x-notata*, with the letters above the columns showing the differences between pairs of species (Mann-Whitney *U* test).

Stroemiellus stroemi differed significantly from all other species by the presence of non-circulating sticky spirals (SS) above the hub ($P < 0.002$), by the frequent parallel side frames (Fig. 3D, $P < 0.004$), by building the most asymmetric web (Fig. 4D, $P < 0.001$), and by the small web size (Figs. 3A, B; 4B; $P < 0.002$). More than half (56.52%) of the *S. stroemi* females possessed the non-circulating SS above the hub, whereas these were almost absent in the other species (prevalence of 0–5.55%). The webs of *Parazygiella montana* were small (Fig. 4B, $P < 0.01$), had the highest prevalence of

Table 1.—The medians, sample sizes, and interquartile ranges (IQR) for the examined quantitative parameters of orb webs. (Medians are in bold if diagnostic).

		Character										
Species		Web width [cm]	Web height [cm]	No. of primary radii	No. of non-circulating SS below hub	No. of non-circulating SS above hub	Vertical no. of SS	Horizontal no. of SS	Mesh width	Web area [cm^2]	Hub displacement (HD)	Web asymmetry (WA)	Spider size (patella+tibia [mm])
L. thorelli	Median	15.60	**24.15**	33.00	19.50	0.00	66.00	40.00	2.63	295.21	**0.69**	**0.35**	**5.53**
	n	88	88	88	88	88	88	88	88	88	88	88	22
	IQR	3.95	9.50	11.50	14.50	0.00	22.00	16.75	0.64	150.02	0.09	0.14	1.69
P. montana	Median	**13.00**	17.00	**21.00**	**5.00**	0.00	**31.00**	**21.00**	**1.79**	180.25	0.64	0.23	3.60
	n	71	71	71	71	71	71	71	71	71	71	71	31
	IQR	5.50	6.50	9.00	3.00	0.00	14.00	13.00	0.47	119.38	0.11	0.14	0.79
S. stroemi	Median	**6.00**	**11.00**	35.00	22.00	**0.00**	86.00	37.00	**5.83**	**49.68**	0.57	**0.49**	**2.30**
	n	36	36	36	36	36	36	35	36	36	36	36	18
	IQR	3.25	5.95	12.00	15.00	2.50	35.00	16.75	3.03	68.25	0.14	0.23	0.43
Z. keyserlingi	Median	15.00	19.00	**41.00**	8.00	0.00	61.00	**49.00**	3.06	208.92	0.63	0.24	3.28
	n	39	39	31	38	38	38	38	38	39	39	39	25
	IQR	8.25	7.25	9.00	6.50	0.00	22.00	28.50	2.15	226.39	0.12	0.20	0.67
Z. x-notata	Median	14.25	19.00	36.00	11.00	0.00	60.50	47.00	3.41	223.65	0.63	0.29	3.69
	n	44	44	43	44	44	44	44	44	44	44	44	19
	IQR	3.88	4.00	8.25	10.75	0.00	21.50	17.50	0.74	76.57	0.08	0.17	0.68

the free sector at 94% (Fig. 3C, $P < 0.001$), the fewest non-circulating SS below hub (Fig. 3H; $P < 0.001$), the fewest total SS (Fig. 3F, G, $P < 0.001$), the smallest relative number of SS (Fig. 4C, $P < 0.001$) and the highest radii-SS ratio (Fig. 4F, $P < 0.001$). In *Leviellus thorelli* the hub was displaced toward the top frame significantly more than in the other species (Fig. 4E, $P < 0.001$). *Zygiella* s.s. was diagnosed by the intermediate numbers of non-circulating SS below hub (Fig. 3H, $P < 0.001$). The web of *Z. keyserlingi* had significantly more primary radii than the other species (Fig. 3E, $P < 0.001$), whereas *Z. x-notata* did not differ from the other species in any character. The largest spider species was *L. thorelli* and the smallest was *S. stroemi*, while the other three did not differ significantly in size (Table 1, $P < 0.001$). We deem seven out of 16 web characters as potentially phylogenetically informative because they showed statistically significant shared variation among investigated species. Web height (Fig. 3B) and web asymmetry (Fig. 4D) consistently group two or three species to the exclusion of *Leviellus thorelli* and *Stroemiellus stroemi*. Web-width (Fig. 3A) and mesh width (Fig. 4A) group two or three species to the exclusion of *Parazygiella montana* and *Stroemiellus stroemi*. The number of primary radii (Fig. 3E) and the horizontal number of SS (Fig. 3G) group two or three species to the exclusion of *Parazygiella montana* and *Zygiella keyserlingi*. Finally, the variation in the number of non-circulating SS below the hub (Fig. 3H) and radii-SS ratio (Fig. 4F) group the species in three potential groups: *P. montana*, both *Zygiella* species, and *L. thorelli* with *S. stroemi*, and therefore also contain potential grouping information.

DISCUSSION

Our study did not reexamine Wunderlich's morphological diagnoses for Zygiellidae, *Zygiella* s.s., *Leviellus*, *Parazygiella* and *Stroemiellus*, but rather explored web characteristics as taxonomic features for the species within these taxa. We closely examined 16 web architecture characters representative of Zygiellidae *sensu* Wunderlich (2004) and confirmed the presence of the free sector as potentially diagnostic for the group that we refer to as *Zygiella* s.l. However, the prevalence of the free sector strongly varies, from 41% in *Z. keyserlingi*, 60% in *L. thorelli*, and 61% in *S. stroemi* and *Z. x-notata* to 94% in *P. montana*. Although not emphasized by Wunderlich, all these taxa further possess a tubular silk retreat (Fig. 1A) that touches the substrate and is connected to the hub via a signal line that runs through the free sector (if present). The retreat is always positioned off-web, be it above the orb, at its upper side, or directly behind it; i.e., between the orb and the substrate (notably *S. stroemi*). The presence of the off-web retreat is probably homologous in these genera and perhaps even more broadly in "araneids" where various combinations of the presence of the signal line, free sector and off-web hiding spots, including retreats, occur. The *Zygiella* retreat also resembles that in the nephilid *Nephilengys* (Kuntner 2007), but in *Nephilengys* the retreat is in contact with the modified hub, whereas in "zygiellids" it connects to the hub via a distinct signal line.

Our results indicate that various combinations of the 16 web characters may indeed diagnose those species that in our sample represented all four genera (Table 1), which suggests that zygiellid webs are reasonably evolutionarily constrained.

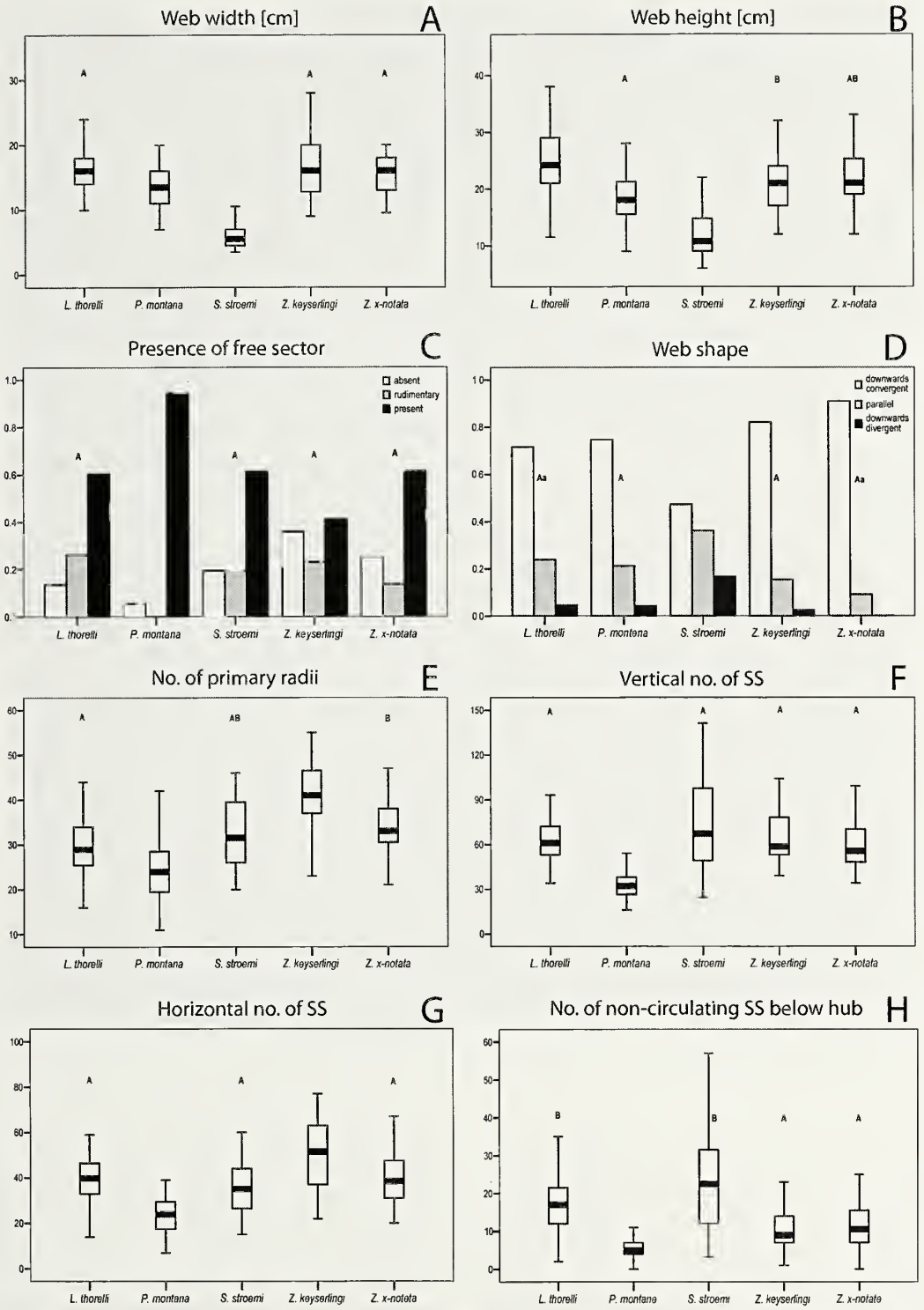

Figure 3.—Field-measured web characters: A. Web width. B. Web height. C. Presence of the free sector. D. Web shape. E. Number of primary radii. F. Vertical number of sticky spirals (SS). G. Horizontal number of SS. H. Number of non-circulating SS below hub. There are no significant differences between two species if they share at least one capital letter ($P > 0.01$). A shared small letter means a trend is present, but the difference is not significant ($0.005 < P < 0.01$). No shared letter means the difference between two species is significant ($P < 0.005$).

Overall, *S. stroemi* (and thus the monotypic *Stroemiellus*) has the smallest, most asymmetric webs with the smallest mesh width, which frequently contain non-circulating SS above the hub (Fig. 1B). *Leviellus thorelli* builds asymmetric webs with the most pronounced hub displacement (Fig. 4E). The web of *P. montana* is small (Fig. 4B), usually contains an intact free sector (Fig. 3C) and has significantly fewer primary radii and sticky spirals than the others (Figs. 3E–H, 4C). The genus *Zygiella* s.s. could be diagnosed by medium numbers of non-circulating SS below the hub (Fig. 3H). *Zygiella x-notata*

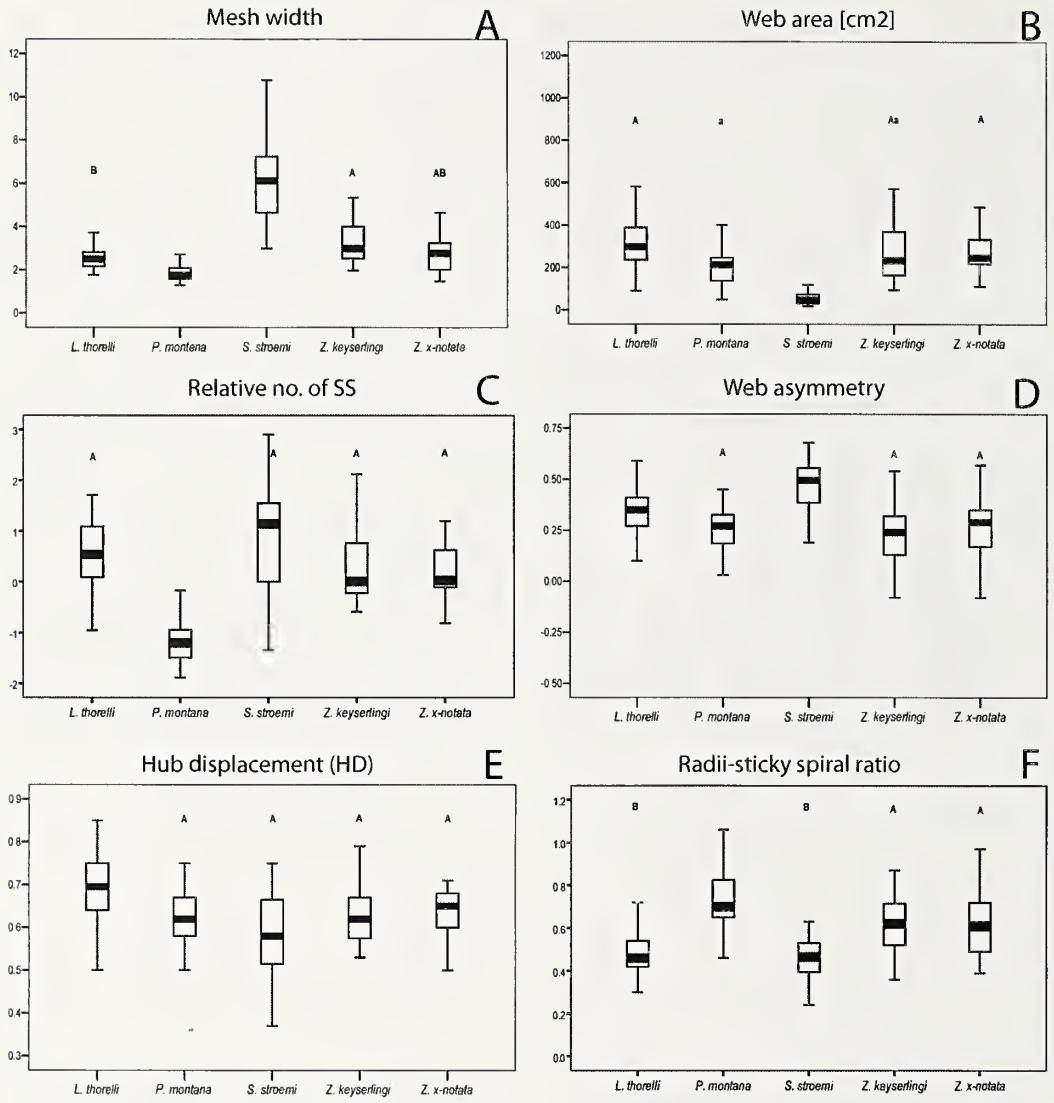

Figure 4.—Derived web characters: A. Mesh width. B. Web area. C. Relative number of stick spirals. D. Web asymmetry. E. Hub displacement. F. Radii-sticky spiral ratio. There are no significant differences between two species if they share at least one capital letter ($P > 0.01$). A shared small letter means a trend is present, but the difference is not significant ($0.005 < P < 0.01$). No shared letter means the difference between two species is significant ($P < 0.005$).

could not be diagnosed by any character, while the webs of *Z. keyserlingi* had significantly more primary radii than the other species (Fig. 3E).

The above diagnostics hold for the species investigated and for the genus *Stroemiellus*, since it is monotypic. Because all genera but *Stroemiellus* contain more species, future studies should test to what extent the above diagnoses for *P. montana* and *L. thorelli* also hold for the genera *Parazygiella* and *Leviellus*, respectively. The diagnosis for *Zygiella* s.s. should also be considered preliminary, since we only included two species.

Web features as diagnostic characters.—Using quantitative parameters to diagnose closely related species is problematic due to overlapping data, even if interspecific differences in means are statistically significant. The reliability of taxonomic diagnoses will obviously increase with the use of several parameters, and with data coming from several populations to account for intraspecific variation. Such diagnoses are further complicated by the rarity of decisive qualitative parameters. For example, the presence versus absence of the free sector cannot diagnose the taxa studied if only a limited number of observations is available. We did not intend to provide decisive species diagnoses using continuous web data, but rather use this dataset to test the limits of behavior in taxonomic diagnosing. Of course, for more decisive diagnostic hypotheses, future studies should expand our pool of characters to include morphology and molecules.

Web biology.—We showed that the free sector may be present in all *Zygiella* s.l. species (Fig. 3C), but that its prevalence in adult female webs is significantly higher in *P. montana* than in all other species. We cannot support the hypothesis that the presence of the free sector is habitat-dependent (Roberts 1995; Foelix 1996), because all species except *S. stroemi* appeared in similar habitats: *Parazygiella montana* had significantly lower and *Z. keyserlingi* had significantly higher numbers of primary radii than other species (Fig. 3E). Spider size (and thus weight) does not explain this pattern because primary radii numbers of the

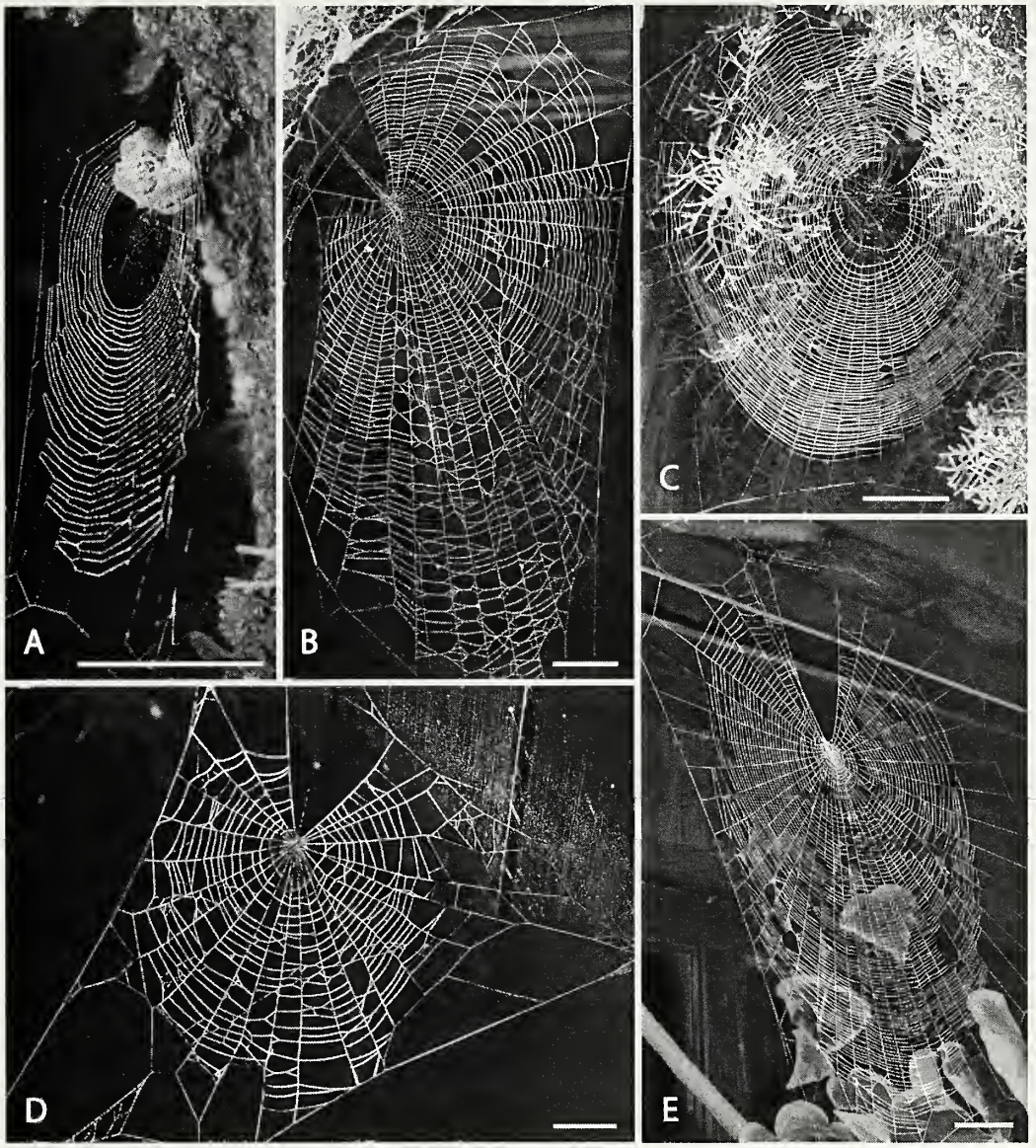

Figure 5.—Photographs of *Zygiella* s.l. webs: A. *Stroemiellus stroemi* usually builds its webs against tree bark. B. Web of *Leviellus thorelli* on a building. C. Web of *Zygiella keyserlingi* with a rudimentary free sector. D. Sparser web of *Parazygiella montana* on a wooden house. E. Web of *Zygiella x-notata* on a building. Scale bar = 3 cm.

smallest species (*S. stroemi*) and the largest (*L. thorelli*) were similar, and both outliers regarding radii numbers are not exceptional in size. Alternatively, microhabitat and/or prey size and weight might influence the radial and spiral numbers (Shear 1986). The least dense webs (few primary radii, absolutely and relatively few spirals) were found in *P. montana* (Figs. 3E–H; 4A, C) and the densest in *S. stroemi* (Fig. 4A). However, these two species had the smallest webs, and thus web size cannot explain web density. Rather, prey size and specialization is known to correlate with web architecture and thus may explain web density patterns *Zygiella* s.l.: dense webs increase prey retention and represent adaptations to small prey and/or prey with high impact energy, while the less dense webs are energetically less costly, decrease visibility and may be adaptations to prey with a low impact energy (Rypstra 1982; Eberhard 1986, 1990; Blackledge et. al 2003; Blackledge & Zevenbergen 2006).

The largest species *L. thorelli* has the most displaced hubs (Fig. 4). Due to gravity effects, hubs are often displaced towards the top web frame in araneoid spiders with vertical orb webs, notably in araneids and nephilids (Masters and Moffat 1983; Kuntner et al. 2008a, b). In heavier orb weavers, predation success improves in webs with hubs displaced above the geometric center, because the time to reach prey upwards and downwards is much altered by the spider's mass (Masters and Moffat 1983; ap Rhisiart & Vollrath 1994). However, gravity alone might be an insufficient explanation because all species investigated here, which differed greatly in size, had hubs displaced to some extent. Other explanations could include the spider's orientation in the hub (Zschokke & Nakata 2010) and web building costs (Coslovsky & Zschokke 2009). In our case, the presence of the retreat in all species might also favor hub displacement, as such architecture will decrease the time needed to shift from retreat to the hub

(Zschokke 2002), where the signals in the web concentrate. Most retreats are in the vertical axis relative to the orb plain. However, in the cases of horizontal retreat placement, the hub was accordingly shifted horizontally in all species, (but did not significantly differ between them; $P = 0.077$), a pattern resembling vertical versus horizontal web asymmetry in *Nephilengys* (Kuntner 2007).

The statistically significant web shape (Fig. 3D) and high web asymmetry (Fig. 4D) of *S. stroemi* could be explained by its arboricolous life history. Highly asymmetric webs with (sub)parallel side frames, the so called ladder webs, evolved convergently in araneids and nephilids, probably to exploit new habitats or food sources (Eberhard 1975; Kuntner 2005, 2006; Kuntner et al. 2008a, b, 2010; Harmer & Framenau 2008). Although *S. stroemi* webs are not on average twice the height over width, which defines ladders (Kuntner et al. 2010), they come closest to this among *Zygiella* s.l. The limiting spatial factor on a tree is its circumference – the horizontal website availability (Kuntner 2005, 2008a, b). The specific habitat of *S. stroemi* thus might favor ladder-like webs with parallel side frames and non-circulating sticky spirals (Figs. 3A, B, D; 4B).

Web features as homologies.—The suites of diagnostic characters for each of the species investigated (Table 1) also provide characters that potentially diagnose the genera *Zygiella* s.s., *Leviellus*, *Parazygiella* and *Stroemiellus* (Wunderlich 2004; Platnick 2009). However, our results should not be interpreted as a test of Wunderlich's (2004) taxonomy, but rather as the exploration of orb webs as taxonomically diagnostic features. This study merely provides a pool of statistically tested behavioral characters related to web architecture that show potential phylogenetic promise. Seven of 16 studied characters indicate potential homologies (Table 1) and should be used in upcoming phylogenetic studies. Of course, it is possible that, depending on the taxon sample, some of the web features might need to be further filtered due to interdependence.

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The genus *Ummidia* Thorell 1875 in the western Mediterranean, a review (Araneae: Mygalomorphae: Ctenizidae)

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Abstract. The presence and origin of the mygalomorph spider genus *Ummidia* Thorell 1875 in the western Mediterranean region is reconsidered. The traditional idea, expressed in the works of Walckenaer and Simon, that *Ummidia* is a recent American import in the Mediterranean region, is opposed by the observation that at least four distinct *Ummidia* species inhabit different geographical areas within the western Mediterranean. The taxonomical revision of the Mediterranean *Ummidia* fauna presented here results in the description of one new species (*Ummidia algarve* n. sp.), the removal of *U. picea* Thorell 1875 and *U. algeriana* (Lucas 1846) from synonymy with *U. aedificatoria* (Westwood 1840) and the placing of *U. occidentalis* (Simon 1909) in synonymy with *U. aedificatoria* (Westwood 1840).

Keywords: Taxonomy, synonomy, new species, spider

The trapdoor spider genus *Ummidia* Thorell 1875 is taxonomically grouped with the genus *Conothele* Thorell 1878 in the Ctenizidae subfamily Pachylomerinae (Raven 1985), recently renamed Ummidiinae (Ortiz 2007), which name is here used. The genus *Hebestatis* Simon 1903, traditionally also included in the Ummidiinae (Simon 1903; Raven 1985), is here excluded on grounds discussed below (see discussion). The Ummidiinae, as understood here, are distinguished from other ctenizids on the basis of a pronounced and unique combination of macromorphological characters (see Fig. 1) that include a proximal dorsal glabrous depression or saddle on tibia III, a sharp apophysis on the dorsal-prolateral trochanter III, clavate trichobothria on the proximal dorsal tarsi, curvy short spines on the lateral faces of the distal segments of the palps and anterior legs and a compact eye-group placed on and around a distinct ocular tubercle (A.E. Decae personal observation). Furthermore, spiders of the Ummidiinae show a remarkable sexual dimorphism in the texture of the carapace. In females, the carapace is smooth and shiny as if polished; in males, the carapace surface is dull and typically rugose or granulated (Figs. 2, 3). Finally, females of the Ummidiinae differ from other ctenizid genera by the possession of three-partite spermathecae with a distinctly sclerotized central section connecting the proximal and distal membranous sections (Figs. 16–19). Geographically, the ranges of the genera *Ummidia* and *Conothele* are separated (Fig. 4), although the presence of *U. gandjinoi* Andreeva 1968 in Tajikistan (see also Zonstein 2007) appears to be a bridgehead of *Ummidia* in *Conothele* territory. The genus *Ummidia*, with around 20 described and many undescribed species (Bond & Hendrixson 2005), has a predominantly American distribution and *Conothele*, with 18 recorded species (Platnick 2009) is widely distributed in the Orient and Australasian region. Both genera, contrary to most trapdoor spiders, are not only found in continental regions, but also occur on oceanic and volcanic islands which suggests a relatively strong capacity for dispersal, either natural or man - aided. *Conothele* has been reported from several Pacific Islands (Pocock 1898; Berland 1938; Roewer 1963) and from the Seychelles (Saaristo 2002). *Ummidia* is reported from several Caribbean islands, including volcanic St. Vincent (Simon 1891), and from Bermuda (Whitehead unpublished). If this last record is correct *Ummidia* inhabits an Atlantic island over a thousand kilometers off the American east coast. The ability for aerial dispersal in *Ummidia*, originally reported by Bearg (1928) and recently confirmed by Coyle (1985) and Eberhard (2005), might have played a key role in reaching such far out locations. The presence of a geographically isolated *Ummidia* population in the western Mediterranean (extreme NW Africa and southern parts of the Iberian Peninsula) is of special interest in this respect. Is it a product of eastward cross-Atlantic dispersal as Simon believed, is it a relict of a former pan-Eurasian *Ummidia*/*Conothele* distribution, or does it have an endemic identity of its own? To solve these questions more suitable material for study, more advanced research techniques and more coordinated research efforts will be necessary (e.g., to establish the phylogenetic relations within and between geographically isolated species), but a taxonomical review of the currently available data on the western Mediterranean *Ummidia* fauna, as presented here, is a useful first step.

METHODS

Material.—The material studied consisted of a sample of 36 *Ummidia* specimens (23 female + 13 male). Fourteen females and 11 males were recently collected from southern parts of the Iberian Peninsula, both in Spain and in Portugal. Nine females from North Africa and one male from Spain (Cartagena) were found in Simon's collection at the Museum National d' Histoire Naturelle (MNHN) in Paris and a single male from Spain was found in the collection of the British Museum Natural of History (BMNH), London. Although not explicitly stated on the tube labels, type specimens of *Actinopus (Ummidia) algerianus* (Lucas 1846) and *Pachylomerus (Ummidia) occidentalis* (Simon 1909) were probably among the material studied in Paris. Further relevant information was obtained through the kind cooperation of the Oxford University Museum (OUM), which provided photographs of the dried type specimens of *Actinopus*

Figure 1.—Right lateral view of a *Ummidia* (female), highlighting diagnostic characters for the subfamily; Sd = saddle depression on dorsal tibia III; Ap = apophysis on dorsal trochanter III; CT = clavate trichobothria; CS = curly spines in dense spine fields; OT = ocular tubercle.

(Ummidia) aedificatoria (Westwood 1840). Specimens described here as *U. algarve* n. sp. and *U. picea* Thorell 1875 are placed in the collection of the Natural History Museum Rotterdam (NHMR).

Morphological studies were carried out with the aid of several different stereomicroscopes (as available in the above-mentioned institutions), all equipped with camera lucida drawing devices and ocular micrometers. Photographs were taken with an Olympus E-500 reflex camera equipped with a 50mm macro-lens and a ring-flash. Methods of measurement and abbreviations are as given in Figs. 5–9. All linear measures are given in mm.

Abbreviations: BL = total body length, CL = carapace length, CW = carapace width, Cap = caput length, EL = length eye-group, EW = width eye-group, SL = sternum length, SW = sternum width, LL = labium length, LW = labium width, ML = maxillum length, MW = maxillum width, Tar = tarsus, Met = metatarsus, Tib = tibia, Pat = patella, Fem = femur, l = length, w = width.

Length/width ratios of sclerotized body parts (carapace, sternum, labium, maxillae) are given in all descriptions. The length/width ratio of the ocular quadrangle (Fig. 6) is of important diagnostic value. The location of the fovea is indicated by its position relative to the anterior edge of the carapace expressed as Cap/CL (Fig. 5).

TAXONOMY

Genus *Ummidia* Thorell 1875
Ummidia Thorell 1875:102.

Type species.—*Ummidia picea* Thorell 1875:102 by original designation.

Synonymy.—All characters, morphological or behavioral, that have been proposed to distinguish *Ummidia* from *Conothele* (Simon 1892; Roth 1982; Raven 1985; Haupt 2005) have proved to be insubstantial (A.E. Decae personal observation). Therefore Main's (1982, 1998) postulate that *Ummidia* and *Conothele* are synonyms is followed here. The name *Ummidia* is retained on grounds of priority to indicate a nearly cosmopolitan genus with representative species on all inhabitable continents and several oceanic islands.

Species list, Western Mediterranean.—The following four *Ummidia* species are regarded taxonomically valid and indigenous to the Western Mediterranean region: *U. algarve* n.sp.; *U. picea* Thorell 1875; *U. algeriana* (Lucas 1846); *U. aedificatoria* (Westwood 1840). All these species are diagnosed and described below.

Ummidia algarve new species
Figs. 2, 3, 10, 11, 17, 21, 23.

Pachylomerus aedificatorius: O. Pickard-Cambridge 1907:818–819, pl. L, figs. 1–6. MISIDENTIFICATION.

P. piceus: Frade & Bacelar 1931:510, figs. 3, 4; Bacelar 1937:1568–1571, figs. 1, 2. MISIDENTIFICATION.

Type specimens.—Southern PORTUGAL: 1 ♂ holotype, 22 March 2007 by S. Huber at Quelfes Algarve 37.217°N, 7.839°W, slope along a field road. 1 ♀ paratype, 22 October 2006, S. Huber, east of Alte, Algarve at Pena da Rocha 37.250°N, 8.098°W, southern slope along walking trail.

Other material studied.—1 ♂, 13 August 1996 coll. P. Selden, Praia da Marinha Algarve 37.14°N, 8.45°W; 4 ♂♂, October 2003 coll. P. Cardoso, Ribeira de Limas Mertola Beja Alentejo 37.82°N, 7.62°W; 4 ♂♂, October–November 2003 coll. P. Cardoso, Corredura Beja Alentejo 37.75°N, 07.64°W; 3 ♀♀,

Figures 2, 3.—*Ummidia algarve* n. sp. 2. male, note the dull granulated carapace. 3. female, note the shiny polished carapace.

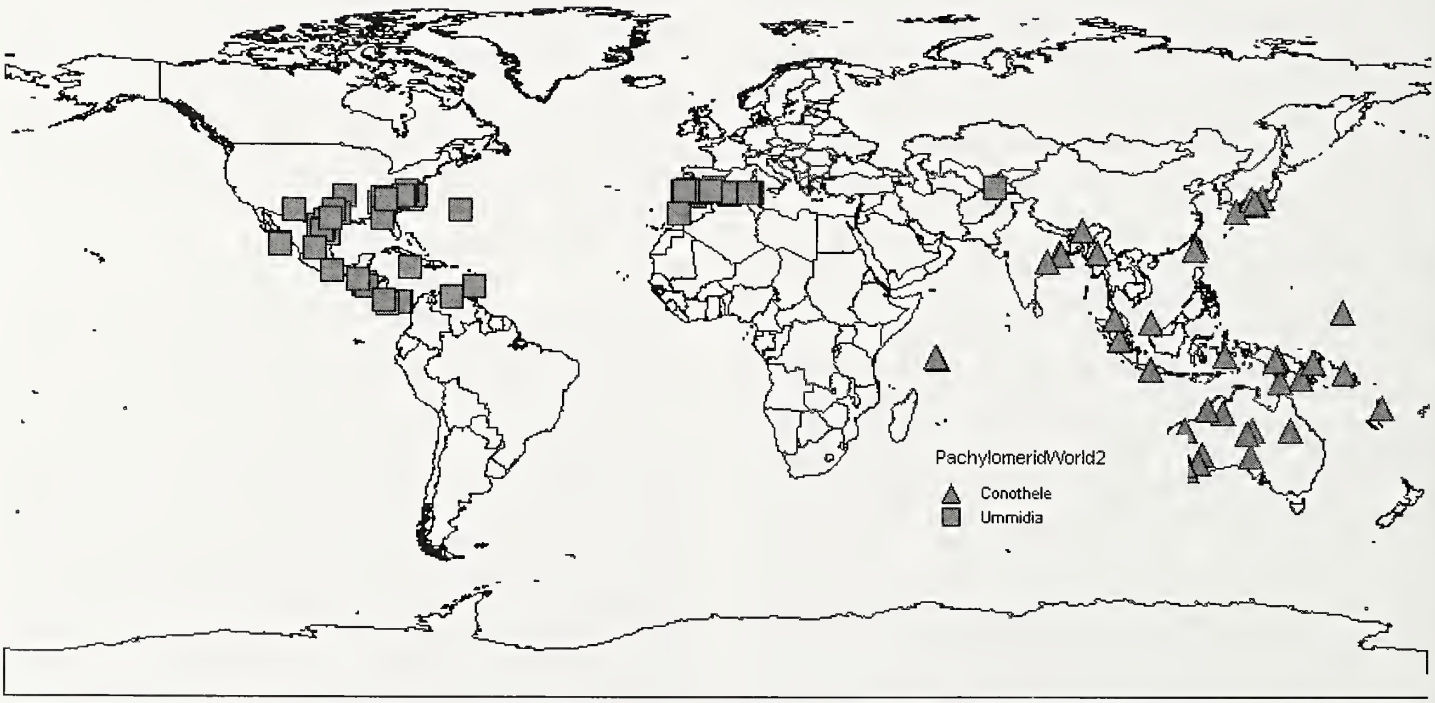
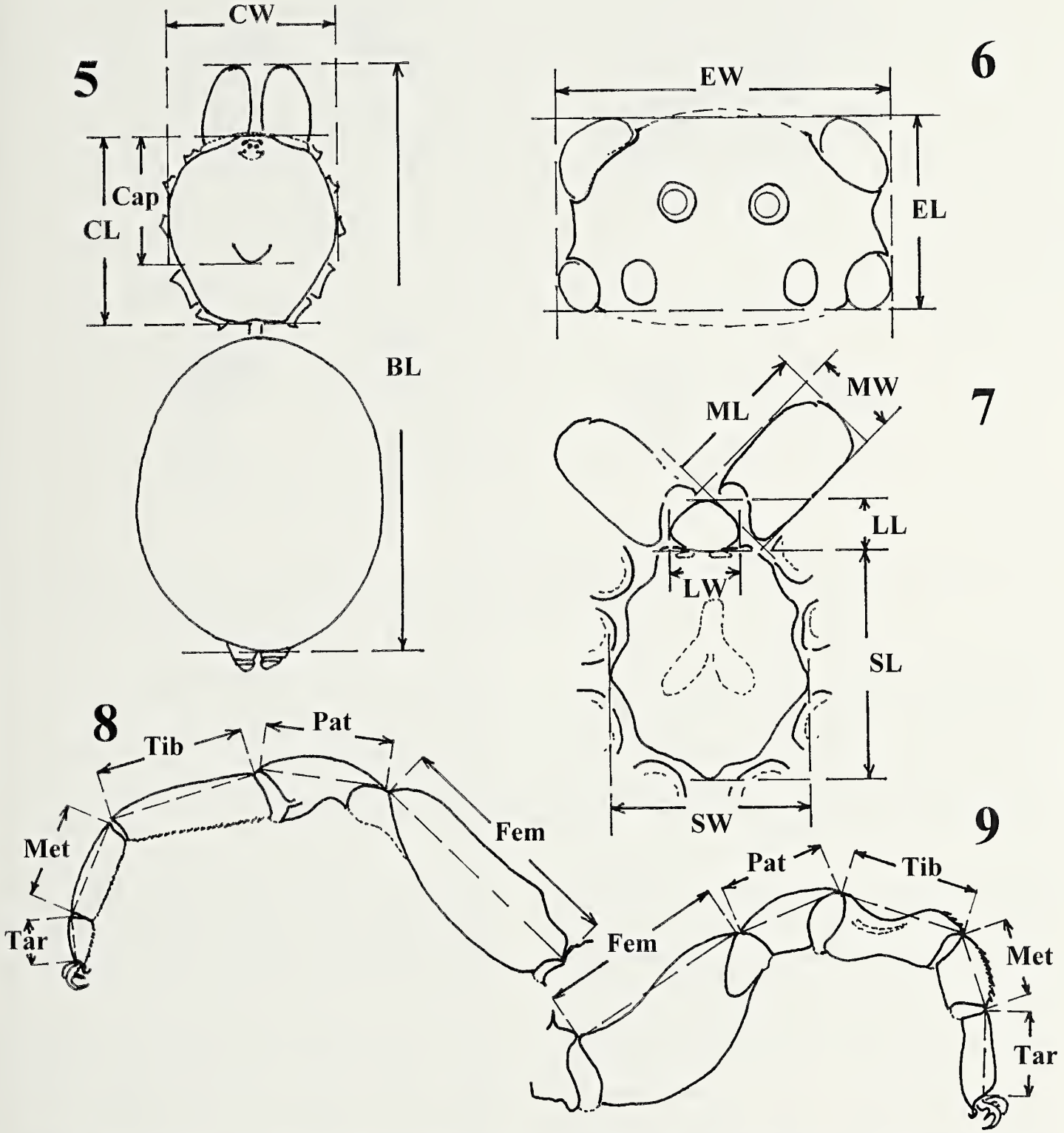
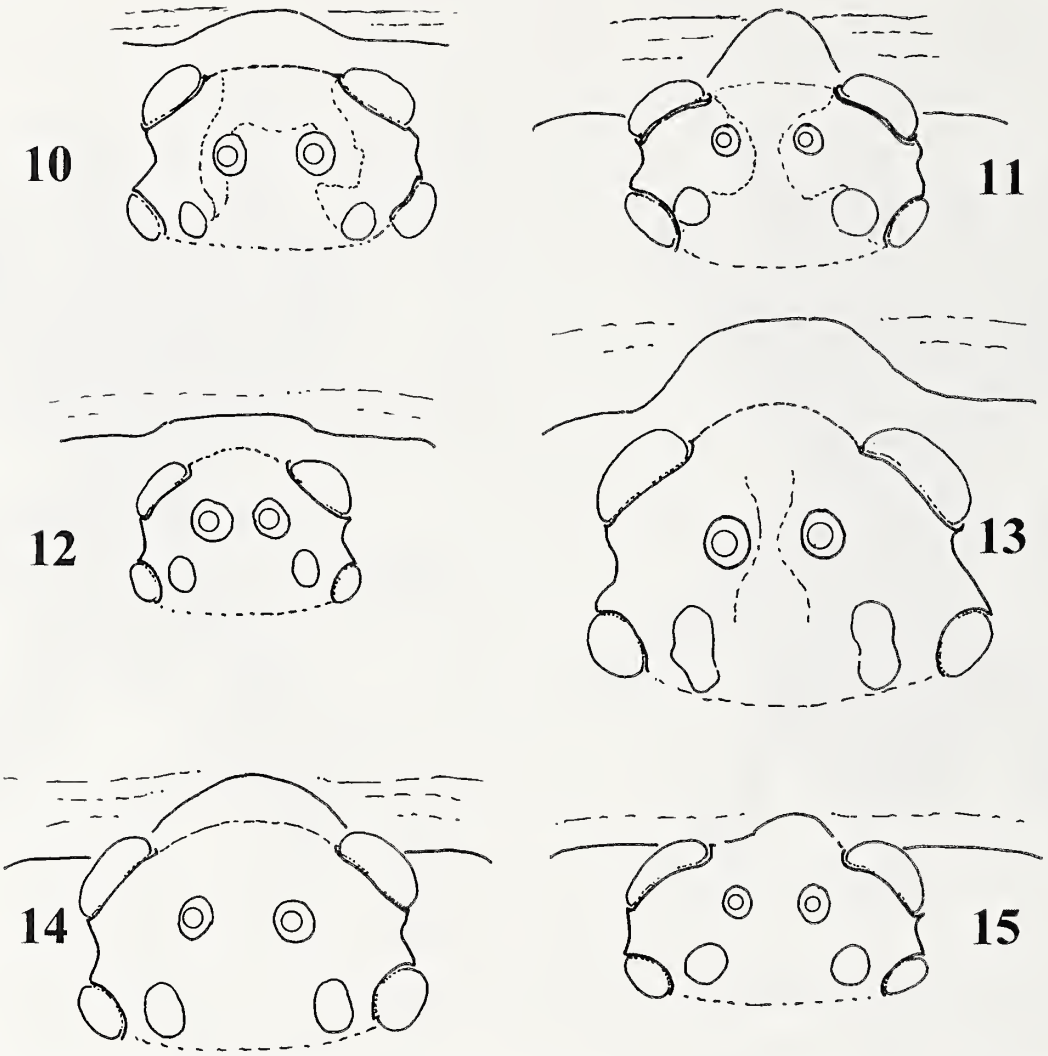


Figure 4.—World distribution of Ummidiinae based on currently available data. Squares = *Ummidia* spp., triangles = *Conothele* spp.



Figures 5–9.—Methods of measurement and abbreviations used. 5. Dorsal body parts: BL = total length of body, CL = carapace length, CW = carapace width, Cap = caput length; 6. Ocular quadrangle: EL = eye group length, EW = eye group width; 7. Ventral body parts: SL = sternum length, SW - sternum width, LL = labium length, LW = labium width, ML = maxillum length, MW = maxillum width; 8. Anterior legs and palps, length only measured along retrolateral face: Tar = tarsus, Met = metatarsus, Tib = tibia, Pat = patella, Fem = femur; 9. Posterior leg length measured along prolateral face abbreviations as in 8.



Figures 10–15.—Eye-formations in dorsal view of western Mediterranean *Ummidia* species. 10. *U. algarve* male holotype; 11. *U. algarve* female paratype; 12. *U. picea male*; 13. *U. picea female*; 14. *U. algeriana* female; 15. *U. aedificatoria* female.

October 2003, coll. P. Cardoso, Ribeira de Limas Mertola, Beja Alentejo 37.82°N, 07.62°W; 2 ♀♀, 22 August 1996, coll. P. Selden, Praia da Oura Algarve 37.08°N, 08.24°W; 1 ♀, 16 August 1996, coll. P. Selden, Belem-Monchique Algarve 37.31°N, 08.59°W; 1 ♀, 15 August 1986, coll. P. Selden, Senhora de Rocha Algarve 37.10°N, 08.37°W.

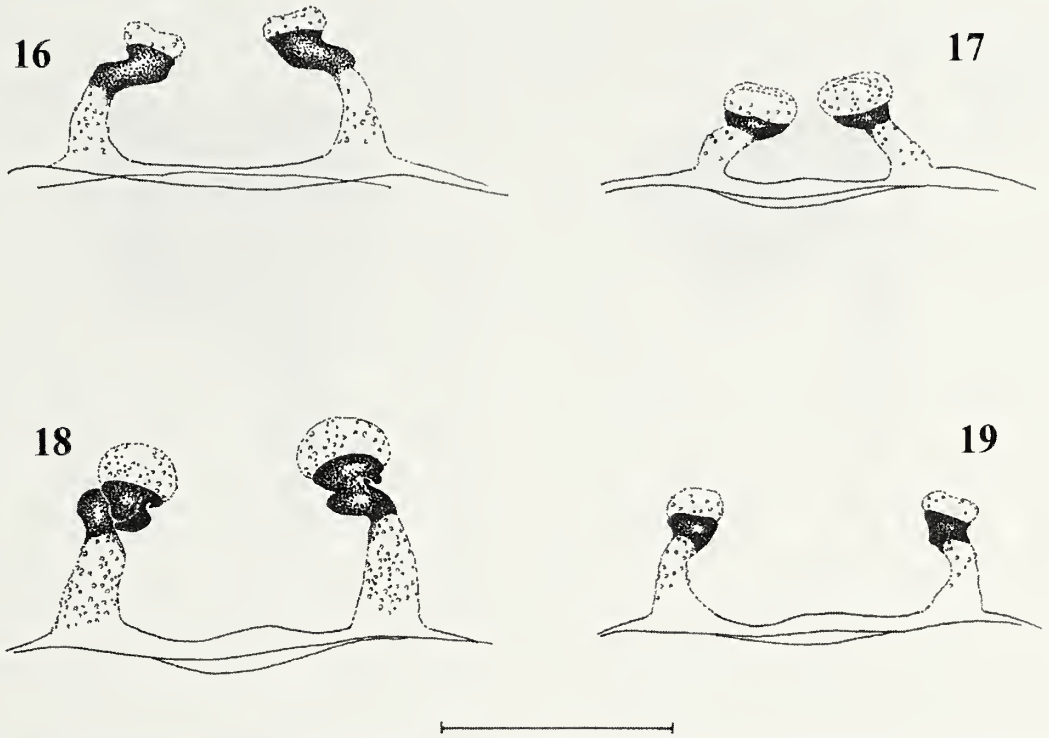
Etymology.—The species is named after the region and former Moorish kingdom Algarve in South Portugal where it was first discovered (O. Pickard-Cambridge 1907). The geographically inspired name was chosen because it is regarded appropriate for a trapdoor spider species, since these species tend to be local endemics. An earlier suggestion by Amelia Bacelar (1937:1369) to name the Portuguese *Ummidia* species after O. Pickard-Cambridge, who first reported it in scientific literature, is not followed because of potential confusion with *Conothele cambridgei* Thorell 1890 upon future revision of the Ummidiinae.

Diagnosis.—Differs from all other western Mediterranean *Ummidia* species by the small straight mushroom shaped spermathecae (Fig. 17) and the warty texture of the abdominal cuticle. Differs from *U. piceus* by the relatively short, strong and smoothly curved embolus with sub-apical fishhook tooth (Fig. 23) and low ocular quadrangle ratio (l/w = 0.58).

Measurements.—*Male holotype:* BL = 14.5; CL = 6.8; CW = 6.7; Cap = 4.8; EL = 3.0; EW = 4.2; SL = 4.2. SW = 3.7; LL = 0.8; LW = 1.3; ML = 2.7; MW= 1.6.

	Tar	Met	Tib	Pat	Fem	Total
Palp	1.4	–	3.3	2.1	4.4	11.2
Leg 1	1.2	2.5	3.3	2.8	5.3	17.6
Leg 2	1.2	2.2	3.2	2.8	4.9	16.4
Leg 3	1.6	2.1	2.6	2.1	4.1	14.6
Leg 4	1.8	3.5	2.3	2.8	5.5	18.6

Description.—*Male holotype* (Fig. 2): Carapace: (l/w = 1.0) black with shades of dark red, cephalic area slightly darker than thorax part, few bristles on clypeus and on cephalic area crest, cuticle strongly granulated with thicker rim around edges. Clypeus: narrow. Cephalic area: moderately elevated.



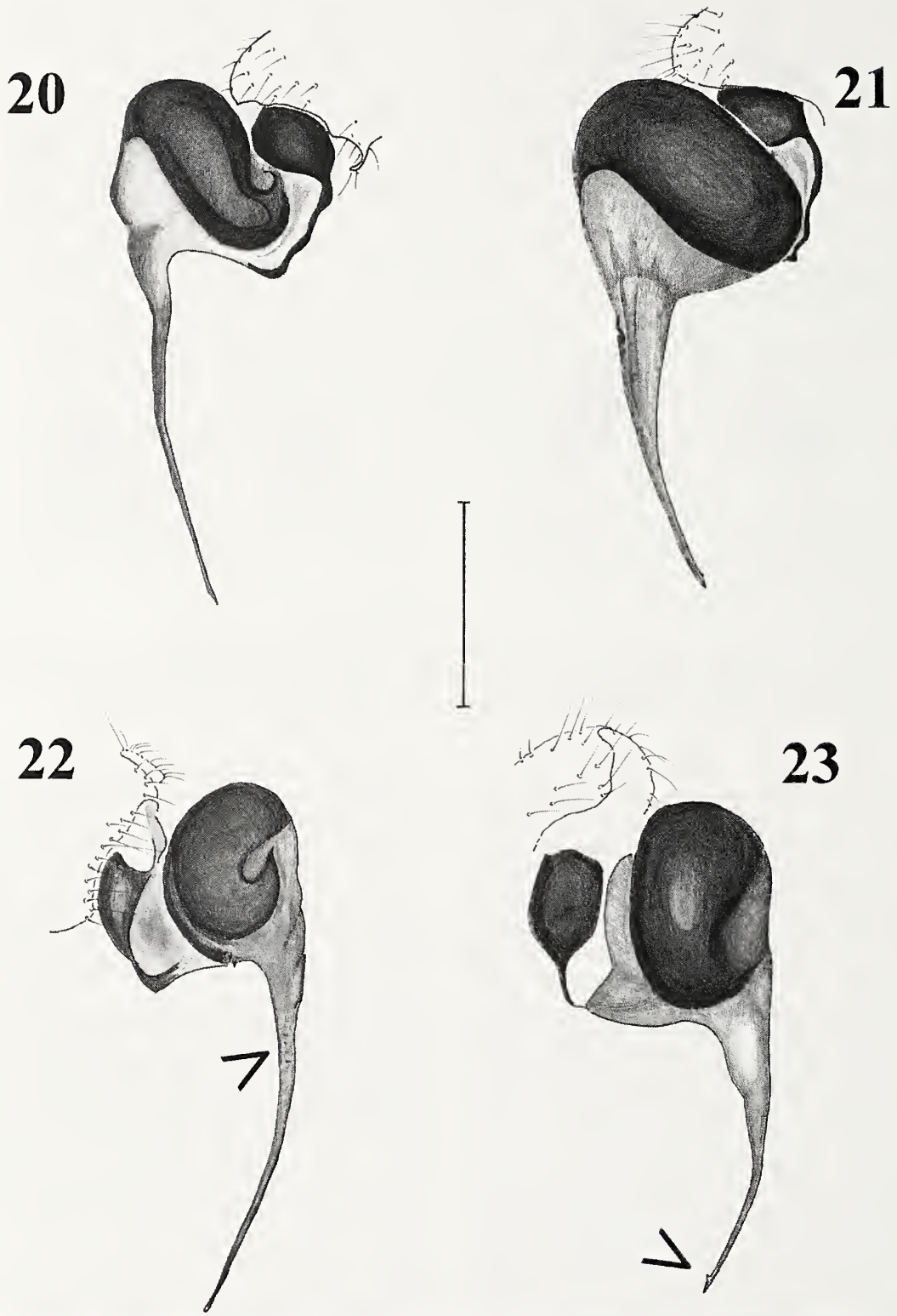
Figures 16–19.—Studies of the spermathecae of western Mediterranean *Ummidia* species in ventral view. Note sclerotized central sections of the spermathecae: 16. *U. picea* (note double-bent central sections); 17. *U. algarve* (note mushroom type and cup-shaped central sections); 18. *U. algeriana* (note twisted central sections); 19. *U. aedificatoria* (note short bent central sections). Scale-line = 1 mm.

Eye-group: (l/w = 0.6) eight eyes compactly grouped in two rows on and around low ocular process, anterior row strongly procurved, posterior row straight (Fig. 10). Fovea: position Cap/CL = 0.7, deep, smoothly procurved. Chelicerae: strong, dorsally black, cuticle granulated, few setae mainly in apical zone; ventrally warm orange brown, cheliceral furrow lined with rows of teeth on either side, 5 prolateral, 6 retrolateral. Rastellum: tight group of strong teeth on well developed apical process. Fangs: with distinct serrated ventral ridges. Maxillae: (l/w = 1.7) trapezoid, orange brown, cuspules groups strongly reduced both in sizes of cuspules and in numbers. Palp trochanters: without ventral cuspules. Labium: (l/w = 0.6) triangular shape, dark grey-brown, cuspules reduced. Sternum: (l/w = 1.1) brown, grading to lighter shades posterior, setae concentrated in lateral zones around glabrous central zone. Anterior legs & palps: dark brown, tarsi and metatarsi legs I & II light yellow brown, cuticle proximal segments ribbed and granulate, spines absent from palps and arranged in ventral lateral groups on tibiae, metatarsi and tarsi legs I & II, strong distal spines on ventral patellae I & II, trichobothria present on all metatarsi and tibiae, most strongly developed on all dorsal tarsi in dense disordered groups of both filiform- and clavate-bothria; dense scopula of short hairs on ventral tarsi and metatarsi I & II, paired claws with variable number of strong lateral teeth (sometimes fused into an irregular comb), 3rd claw very small.: trochanter apophysis reduced armed with a strong spine, femur bent and ventrally enlarged (Fig. 9: Fem), with spines distributed on dorsal and prolateral faces, patella short with group of sharp spines along dorsal prolateral side, tibia with shallow saddle and spines along distal edge and, retrolaterally, metatarsus narrowing distally with strong spines along distal edge, tarsus cylindrical with numerous spines ventrally and distally, paired claws with one large and one small tooth. Leg IV: lighter in color than other legs, femur finely ribbed with few short spines dorsally, patella with elliptical glabrous patch dorsally lined with fine denticles proximally, distally segments unmodified. Abdomen: with strongly developed wart-like sockets for individual bristles as in female. Spinnerets: PMS digitiform, proximally light brown, distally creamy white with numerous small spigots and one apical macro-spigot, PLS three equally short segments all proximally light brown and distally creamy white fields with numerous fine spigots and few macro-spigots. Bulb: (Figs. 21–23) as described in diagnosis.

Measurements.—*Female paratype* (Fig. 3): BL = 14.5; CL = 6.9; CW = 6.2; Cap = 4.8; EL = 2.8; EW = 5.5; SL = 4.5; SW = 3.9; LL = 1.0; LW =1.6; ML = 2.9; MW = 1.6.

	Tar	Met	Tib	Pat	Fem	Total
Palp	1.9	–	2.0	2.1	3.7	9.7
Leg 1	1.0	1.7	2.4	2.6	4.1	11.7
Leg 2	1.0	1.4	2.0	2.4	3.7	10.6
Leg 3	1.2	1.4	1.7	2.1	3.6	9.9
Leg 4	1.4	2.2	2.5	2.6	4.7	13.5

Description.—*Female paratype:* Carapace: (l/w = 1.1) smooth, shining, with bristles only around eye-group, short crest-row with two lateral bristle rows reduced to only one pair of bristles. Clypeus: protracted onto membranous connection between carapace and chelicerae. Cephalic area: smoothly elevated. Eye-group: (l/w = 0.6) eight eyes placed in two rows



Figures 20–23.—Studies of the right bulb in Iberian *Ummidia* species. 20. *U. picea* prolateral; 21. *U. algarve* prolateral; 22. *U. picea* retrolateral (arrow indicates denticles); 23. *U. algarve* retrolateral (arrow indicates fish-hook). Scale-line = 1 mm.

near anterior edge of carapace and compactly set around small ocular process, anterior row strongly procurved, posterior row slightly recurved. Fovea: (Cap/CL = 0.7) deep, strongly procurved with distinct light colored anterior tips. Chelicerae: massive, black contrasting with color of carapace, bristles concentrated along dorsal crests, ventrally orange, cheliceral furrow with 5 prolateral and 7 retrolateral denticles, rastellum of compactly set short teeth on strongly developed process. Fangs: strong, blunt with serrated inner ridge. Maxillae (l/w = 1.8) sub-rectangular, anterior light orange brown with greyish

scopula, cuspules strongly developed, organized in two groups; one with 25 larger cuspules more proximal and anterior and one with 21 smaller cuspules distal and posterior, anterior apical maxillary process indistinct. Palp trochanter: with distinct group of cuspules. Labium: (l/w = 0.6) semi-dome shaped, posterior sloping steeply to labial furrow; distinctly bicolored with anterior light crescent carrying an oval-shaped group of 11 strong cuspules. Sternum (l/w = 1.2) smooth, with large glabrous central area (fused sigilla) and evenly set setae along lateral zones. Anterior legs & palps: dense lateral fields of short curvy and curved spines on tarsus, metatarsus and tibia (absent from retrolateral tarsus, metatarsus and tibia of leg II), anterior patellae and femora without spines with the exception of one distal prolateral spine on palp patella. Leg III: blunt pointed apophysis on prolateral dorsal trochanter, femur curved and ventrally enlarged (Fig. 9: Fem), patella short strong with prolateral field of short straight spines, tibia with dorsal proximal dark colored, glabrous, saddle flanked on either side by narrow membranous slits, distal field of short curved spines on distal upward curved part of tibia (Fig. 9: Tib), metatarsus short with dorsal field of strong short spines along full length of segment, tarsus short with dense prolateral spine field along full length of segment and retrolateral spine field distally restricted. Leg IV: trochanter and femur unmodified, patella dorsal glabrous patch with prolateral dense fields of fine cuspules, tibia unmodified without prolateral spines, metatarsus unmodified with dorsal and ventral prolateral rows of 2 spines, tarsus unmodified with apical prolateral group of strong short spines. Trichobothria: large groups of filiform trichobothria and small groups of clavate trichobothria dorsal on all tarsi, few filiform trichobothria in disordered row on dorsal metatarsi; two small rows of filiform trichobothria in proximal half of dorsal tibiae. Abdomen: egg-shaped with evenly distributed bristles set in strongly developed wart-like sockets. Spinnerets: as described for male. Spermathecae: (Fig. 17) short, distally converging mushroom-shaped, proximal part tubular, lightly glandular, medial part sclerotized, distal part donut-shaped lightly glandular.

Variation.—Morphological variation in this species is small, the bulb structure and the structure of the spermathecae were found to be constant in all specimens studied. Total body sizes vary between 12.6 mm and 18.2 mm in males (n = 10) and between 12.4 mm and 19.6 mm in females (n = 8). Carapace shape as judged by the CL/CW ratios quite constant in females (CL/CW 1.2–1.3: n = 8) and somewhat more variable in males (CL/CW 1.0–1.2; n = 10).

Natural History.—*U. algarve* is reported to be very common and occurring in quite dense populations, often in close association with nemesiid trapdoor spiders (S. Huber pers. comm.). The burrow structure, with a trapdoor at the entrance of the burrow and a second up-side down trapdoor in the bottom of the burrow has attracted much attention in the literature (O. Pickard- Cambridge 1907; Bacelar 1937; Buchli 1962). This type of burrow distinguishes *U. algarve* from all other Mediterranean *Ummidia* species that construct simple trapdoor burrows with no other internal structures than a dense silken lining of the burrow walls. Buchli (1962) reported that the inverted trapdoor at the bottom of the burrow might only be built by female spiders. Although this curious type of burrow is presently not known from any other *Ummidia* species, a similar type of burrow has recently been reported from *Conothele varvarti* in eastern India (Siliwal et. al. 2009).

Ummidia picea Thorell 1875
Figs. 12, 13, 16, 20, 22

Ummidia picea Thorell 1875a:102.
U. picea: Thorell 1875b:121.
U. piceus: Frade & Bacelar 1931:511, fig. 4bis.
Pachylomerus aedificatorius: Simon 1909:42. Misidentification.

Diagnosis.—Differs from all other western Mediterranean *Ummidia* species by double bent central sclerotized section of the spermathecae (Fig. 16). Differs from *U. algarve* by the long slender curved embolus, proximal sclerite with distal denticles (Fig. 22).

Material studied.—1 ♂ (described) collected as juvenile 6 April 2007, adult 11 September 2008, coll. A.E. Decae, Barranco de Rio Higueron, Frigliana, Andalusia 36.802°N, 03.875°W. 1 ♀ (described) 4–6 April 1989, coll. A.E. Decae, Nerja, Andalusia 36.764°N, 03.865°W. 1 ♂ MNHN Coll Simon (undated) Cartagena, 37.61°N, 01.00°W. 1 ♂ MNHN 18 September 1919 BMNH Cartagena, 37.61°N, 01.00°W. 3 ♀♀ 4–6 April 2007, coll. A.E. Decae, Barranco de Rio Higueron, Frigliana, Andalusia 37.80°N, 03.83°W. 2 ♀♀ 4–6 April 1989, coll. A.E. Decae, Nerja, Andalusia 36.764°N, 03.865°W.

Measurements.—*Male:* BL = 13.3; CL = 5.6; CW = 5.2; Cap = 3.9; EL = 2.7; EW = 4.1; SL = 3.2; SW = 2.7. LL = 1.0; LW = 1.2; ML = 2.1; MW = 1.2.

	Tar	Met	Tib	Pat	Fem	Total
Palp	1.2	–	2.8	1.7	3.9	9.6
Leg 1	1.2	2.3	2.9	2.3	4.7	13.5
Leg 2	1.2	2.2	2.5	2.2	4.2	12.4
Leg 3	1.4	2.2	2.1	1.9	3.5	11.0
Leg 4	1.7	3.0	2.7	2.0	4.5	13.8

Description.—*Male:* Carapace: (l/w = 1.1) glabrous, surface finely striated and granulated. Clypeus: width as longest diameter of ALE, with two brownish lines running from the base of ALE to clypeus edge, setae fully absent. Cephalic area: elevated, laterally not delineated from thorax part of carapace. Fovea: (Cap/CL = 0.7) regularly procurved. Eye-group: (l/w = 0.6) on dome-shaped process, anterior row strongly procurved, posterior row straight, ALEs largest, PMEs teardrop shaped. Chelicerae: basal segment striated and granulated as earapace, black dorsally grading into warm brown ventrally, distal sharp bristles evenly spaced around very short strong teeth of the rastellum. Rastellar process ventrally pronounced, fangs brown, long, sharp and slightly translucent, with ventral retrolateral serrated ridge. Cheliceral furrow warm brown, bordered with rows of teeth 5 prolateral, 6 retrolateral. Maxillae: (l/w = 1.8) sub-rectangular, dark brown, proximally lighter, with distinct light colored anterior edges and silvery white scopulae, cuspules reduced and irregularly spread along ventral surface, proximally more concentrated, distally absent. Labium: (l/w = 0.8) relatively

long striated, with contrasting color zones, proximal dark brown, distal light brown, small group of distal cuspules. Sternum: (l/w = 1.2) greyish brown, lateral zones lighter than central zone, centrally fused sigilla, widely spaced sharp bristles predominantly in finely striated lateral zones. Palps: long and slender; femur is longest segment; tegument structure, color and setae as described for legs; spines absent from all segments. Legs: dorsally black striated, ventrally greyish, tarsi and metatarsi I & II ventrally light colored and scopulate. Leg III: trochanter with small dorsal apophysis, femur slightly thickened with group of 4 short strong apical spines dorsally, patella with short curved spines along dorsal prolateral face, tibia with transverse striated saddle and few sharp spines irregularly placed, metatarsus with numerous irregularly placed sharp spines, tarsus with numerous ventral spines. Leg IV: trochanter unmodified, femur with few apical dorsal short spines, patella with longitudinal dorsal glabrous zone flanked on either side by short spiny bristles, tibia with ventral longitudinal row of sharp spines, metatarsus and tarsus with numerous sharp ventral spines, dorsal patella IV with central brown zone. Filiform trichobothria on all dorsal tibiae, metatarsi and tarsi. Clavate trichobothria in small groups on proximal dorsal surfaces of all tarsi. Abdomen: evenly covered with fine, spiky bristles, dorsally purplish brown with irregular creamy blotches, ventrally yellowish brown, integument not warty. Spinnerets: PMS short, light colored with few apical spigots, PLS three-segmented with groups of spigots on ventral distal parts of proximal and medial segment and dense apical spigot field on domed distal segment. Bulb (Figs. 20, 22).

Measurements.—*Female:* BL = 26.0; CL = 9.5; CW = 8.5; Cap = 6.8; EL = 4.8; EW = 7.0; SL = 6.5; SW = 5.4; LL = 1.2; LW = 1.9; ML = 3.5; MW = 2.1.

	Tar	Met	Tib	Pat	Fem	Total
Palp	2.9	–	3.7	3.3	5.0	14.9
Leg 1	1.2	2.4	3.5	3.8	5.6	16.5
Leg 2	0.7	2.4	3.3	3.4	5.5	15.3
Leg 3	1.7	1.7	2.7	2.6	4.5	13.1
Leg 4	2.1	3.4	3.1	3.2	6.1	17.8

Description.—*Female:* Carapace: (l/w = 1.1) smooth, shining and shaded brown, darkest zones around fovea and above coxa III; crest-line narrow, dark contrasting with lighter crest-zone; crest-bristles strongly developed in straight line and only in anterior half of crest-zone, few finer bristles lateral of crest-zone; no setae along carapace edge. Clypeus: mottled brown, with small group of setae on protracted semi-circular process anterior of eye-formation. Cephalic area: smoothly elevated. Eye-group: (l/w = 0.6) on distinct ocular process, anterior row strongly procurved, posterior row straight; ALE largest, AME slightly wider than their diameter apart, PME pearly and caudally protracted projecting caudally beyond PLE. PLE distinctly smaller than AME; groups of strong setae both anterior and posterior of AME on ocular process. Fovea: (Cap/CL = 0.7) deep, strongly and smoothly procurved. Chelicerae: basal segment strong, dark brown distally grading to black and contrasting in color with carapace, dorsally slightly lighter in color than laterally, ventrally bright orange brown in and along the cheliceral furrow, glabrous between three distinct longitudinal zones with bristles. Cuticle dorsally smooth, distally (in rastellar zone) striated; furrow lined with two irregular rows of 7 or 8 strong stubby teeth, no denticles on furrow bottom, rastellum dense group short strong teeth on distinct process. Fangs: strong, short, and blunt. Fang ridge: smooth. Maxillae: (l/w = 1.7) cuspules spiky spread in two size classes over ventral surface, about 35 larger cuspules anterior, about 33 small more posterior. Palp trochanters: with short cusp-like setae. Labium: (l/w = 0.6) somewhat diamond shaped, 10 strong distal cuspules in distal half. Labial furrow: glabrous, shallow, with two distinct elliptical sigilla. Sternum: (l/w = 1.2) light brown with dark edge, setae mainly in peripheral zone, sigilla fused in central glabrous field. Legs: dorsally dark brown, ventrally lighter, ventral femora III & IV light yellowish brown, anterior coxae darker than posterior coxae; (spine patterns) dense fields short curvy and curved spines on lateral tibiae metatarsi and tarsi I & II, short straight spines on all patellae and on tibiae, 0metatarsi and tarsi III & IV, no spines on femora; patella III with transverse row of short strong spines along the distal edge, tibia III, with dense transverse group of short strong spines along full dorsal width distal of black saddle depression, metatarsus III with group of short strong spines along full dorsal length of segment (apical spines strongest), tarsus III with few prolateral spines and dense spine groups ventrally around apical claw implant; leg IV with dense 'rasp-like' field of very small short spines on dorsal patella and only few fine spines in distal halves of tibia, metatarsus and tarsus; trochanter III with anterior dorsal apophysis. Tarsi with proximal groups of clavate trichobothria (reduced or absent in posterior legs), surrounded by irregularly placed filiform trichobothria; metatarsi with central dorsal longitudinal row of very fine filiform trichobothria (absent from leg I), tibiae with two distally converging rows of very fine filiform trichobothria in proximal quarter; leg scopulae absent; paired claws with one long proximal tooth & one much smaller more distal tooth, 3rd claw vestigial. Abdomen: evenly covered with fine setae, mottled purplish grey with irregular light colored blotches, ventrally overall lighter color. Spinnerets: PMS: digitiform, with distinct lighter colored apical spinneret field with few micro-spigots and one macro-spigot, PLS all three segments short and distally light colored, proximal and medial segment with transverse distal rows of macro-spigots, distal segment with apical spigot field with exclusively micro-spigots. Spermathecae: see diagnosis.

Variation.—The emboli of the 2 male spiders found, one in the BMNH, London, and one in MNHN, Paris, were not as elongated as the embolus in the specimen here described and figured. This could well be the result of handling damage over a long period of time. The material available, however, was insufficient to test this hypothesis, and the possibility that the Spanish *Ummidia* population is more diverse at the species level than presently conceived cannot be ruled out.

Remarks.—Thorell's original description of the male of *U. picea* is very short and inadequate (Thorell 1875:102); the female described as *U. picea* by Frade & Bacelar 1931 actually was a specimen of *U. algarve*. Therefore, both sexes are fully described here.

Natural History.—*U. picea* was found to inhabit steep banks along trails, creeks and canyons in Andalusia, particularly in shady locations. Different from *U. algarve* (see above), *U. picea* does not form aggregations of nests. Single burrows were found throughout the area. Specimens were collected from a number of burrows for further study of morphology (taxonomy) and behavior in the laboratory. The trapdoors were typically, as reported for several *Ummidia* species, placed sideways or even upside down with respect to the slope. A remarkable difference in behavior between *U. picea* and *U. algarve* is the immediate strong holding down of the trapdoor in the first species upon disturbance, and the absence of this behavior in the second species. *U. picea* burrows may be found close to burrows of both nemesiid *Nemesia* and *Cyrtauchenius* trapdoor spiders.

Ummidia algeriana (Lucas 1846) comb. nov.
Figs. 14, 18

Actinopus algerianus Lucas 1846:96–97, pl. 1, fig. 5.
Cteniza algeriana: Ausserer 1871:155.
Pachylomerus aedificatorius: Simon 1892, fig. 86; 1903:887, fig. 1048; 1909:42–43.
P. aedificatorius: Frade & Bacelar 1931:509 figs. 1, 2. MISIDENTIFICATIONS.

Remarks.—Lucas' (1846:96–97) description and figures are very accurate and complete, here only further observations on the morphology of the spermathecae and measurements are given. The measurements are taken from a specimen in Lucas' type series, the spermathecae are drawn after one of the larger specimens in Simon's collection.

Material studied.—9 ♀♀ including a probable type specimen collected by Lucas and found in Simon's collection at the MNHN, Paris.

Diagnosis.—Differs from all other Mediterranean *Ummidia* species in the possession of a twisted central sclerotized section in the spermathecae (Fig. 18). Differs from *U. aedificatoria* in the higher l/w-ratio of the ocular quadrangle (Figs. 14–15), the strong development of the rastellar process, the deep labial furrow with distinct elliptical sigilla and the texture of the abdominal cuticle.

Measurements.—*Female:* BL = 24.4; CL = 8.6; CW = 7.9; Cap = 5.0; EL = 3.7; EW = 6.1; SL = 5.5; SW = 5.0; LL = 1.0; LW = 1.7; ML = 2.7; MW = 1.4.

	Tar	Met	Tib	Pat	Fem	Total
Palp	2.4	–	2.9	2.8	4.8	12.9
Leg 1	1.1	2.3	2.9	3.5	5.2	15.0
Leg 2	1.3	2.2	2.4	3.2	4.6	13.7
Leg 3	1.4	1.9	2.6	2.4	4.3	12.7
Leg 4	1.7	3.0	3.1	3.2	5.7	16.8

Variation.—Total sizes (BL) in the sample of 9 ♀♀ varied between 29.1mm and 17.0mm. Variation in the shape of the carapace (CL/CW = 1.1–1.2; n =9), the position of the fovea (CL/Cap = 1.4–1.5; n = 9) appeared to be very low. Differences found in the length/width ratio of the ocular quadrangle (l/w = 0.6–0.8; n=9) suggest some local geographical variability or cryptic diversity.

Natural History.—Simon (1888) reported this species to be widespread in the Tell region of Algeria and western Tunisia, where its burrows were all dug in steep to vertical surfaces along roads and rivers. The burrows were reported to be shallow (6–10 cm), internally lined with dense white silk and closed at the entrance by a stiff thin trapdoor.

Ummidia aedificatoria (Westwood 1840)
Figs. 15,19

Actinopus aedificatorius Westwood 1840:175, pl. 10.
Spliodros aedificatorius: Walckenaer 1842:438.
Cteniza aedificatoria: Ausserer 1871:155.
Pachylomerus occidentalis Simon 1909:8 New synonym.
Pachylomerus occidentalis: Frade & Bacelar 1931:512, figs. 5, 6.

Remark.—The type of *U. aedificatoria* is a dried specimen in the Oxford University Museum collection, of which photographs by Ray Gabriel were seen, but diagnostic details of the sexual organs could not be studied. Westwood's original description fortunately is very detailed and extensive and is furthermore accompanied by a good set of illustrations (Westwood 1840: Plate 10). Two characters of supposedly diagnostic value – the relatively short ocular quadrangle and the reduced rastellar process– are sufficiently clear in the dried specimen and the illustrations to synonymize Westwood's type of *U. aedificatoria* with Simon's type of *U. occidentalis* that originated from roughly the same type location (Tangiers province in northwestern Morocco; Fig. 24). Because Simon's spider at the MNHN Paris is the only specimen available for closer study, the limited additional diagnostic and descriptive information given here is based on that specimen.

Material studied.—2 ♀♀ on photographs in the Westwood collection, preserved in dry condition in the Oxford University Museum. 1 ♀ found in Simon's collection at the MNHN, Paris, probable type specimen of *U. occidentalis* that is here synonymized with *U. aedificatoria*.

Diagnosis.—Differs from all other Mediterranean *Ummidia* species by the short bent central section of the spermathecae (Fig. 19), the low length/width ratio of the ocular quadrangle (Fig. 15) and the reduced rastellar process.

Measurements.—*Female:* BL = 18.1; CL = 8.2; CW = 6.7; Cap = 5.8; EL = 0.4; EW = 0.8.

Variation.—Only three female specimens are currently known, two of which have been preserved in dried condition for almost 170 years. Nevertheless, it is clear that *U. aedificatoria* falls in the same size range as the other western Mediterranean *Ummidia* species. Total body lengths of adult females in the small sample range from 18.1 to 29.0mm.

Natural History.—Neither Westwood (1840) nor Simon (1909) provides any information about the natural conditions in which *U. aedificatoria* is found. Westwood, however, received the spiders he described alive in their natural burrows. From Westwood's descriptions and figures, and also from photographs of the preserved burrow material in the Oxford University Museum, it might be concluded that *U. aedificatoria* builds the typical shallow silk-lined trapdoor burrow that is very similar to the burrows of *U. algeriana* and *U. picea*.

DISCUSSION

Simon (1903:887–888) included three genera (*Ummidia*, *Conothele* and *Hebestatis*) in his Pachylomereae based on the

Figure 24.—Currently known distribution of the genus *Ummidia* in the western Mediterranean Region based on specimens seen in this study: black circle = *U. aedificatoria*, grey square = *U. algarve*, grey triangle = *U. algeriana*, grey circle = *U. picea*.

shared absence of lateral sternal sigilla. Raven (1985) followed this classification but used the eye tubercle and saddle tibia. However, the probable type specimen in Simon's collection (AR12317 MNHN examined) labelled *Hebestatis theveneti* actually possesses lateral sternal sigilla and furthermore shows suffieient morphological differences from both *Ummidia* and *Conothele* (dorsal saddle on tibia III not pronounced and not glabrous, absence of curvy spines, absence of tarsal clavate trichobothria, absence of centrally sclerotized spermathecae) to exclude the genus *Hebestatis* from the Ummidiinae.

The taxonomy of the genus *Ummidia* in the western Mediterranean has been disputed from the start. Shortly after Westwood (1840) had presented the discovery and description of his *Actinopus aedificatorius* (now *Ummidia aedificatoria*) from Morocco to the Entomological Society of London, Walckenaer (1842) explicitly expressed his doubts about these findings. Walckenaer suspected that Westwood was mistaken in either the origin or the identity of the species described (see also Westwood 1840:181). Westwood had obtained the specimens he presented and described from Mr. Drummond Hay, H.M.'s agent and Consul-general at Tangiers in the far northwest of Morocco. Furthermore, he classified this newly discovered species as belonging "to the same genus as Mr. Sell's Jamaica species, to which it is so closely allied as scarcely to present any specific distinction beyond that of size" (Westwood 1840:174–175). Mr. Sell's Jamaican species is now known as *Ummidia nidulans* (Fabricius 1787) and the fact that Westwood regarded his Moroccan species so closely allied with a Caribbean species caused much skepticism among the leading arachnologists at that time. The discovery of several other *Ummidia* species in the Americas in the 19th century (e.g., Ausserer 1871:146–147) reinforced the idea that *Ummidia* was naturally restricted in its distribution to the New World and that the incidental finding of *Ummidia* east of the Atlantic must be the result of human-mediated introduetion. This idea was most vividly expressed in the work of Simon: "le genre Pachylomerus, qui est assez nombreux, est américain, il a cependant un représentant au Japon (d'après Dönitz)" et un autre dans la région méditerranéenne occidentale (Algérie et Espagne), mais ce dernier paraît y avoir été introduit en même temps que les Opuntia et les Agave d'origine américaine" (Simon 1892:86).

In short, Simon regarded *Pachylomerus* (*Ummidia*) in the western Mediterranean as an American species that was probably introduced with imports of ornamental plants. Central in Simon's opinion was his conviction that only one *Ummidia* species (*U. aedificatoria* Westwood 1840), inhabits the western Mediterranean. In forming his opinion about *Ummidia* in the western Mediterranean, Simon had apparently overlooked the work of Lucas who had described a second *Ummidia* species in North Africa, this time from eastern Algeria. Lucas (1846:96–97) had collected this new species near the town of Bône (now Annabah) over 1200 km east of the locality from where Westwood had obtained *U. aedificatoria*. Lucas furthermore was well aware of the diagnostic differences between his new species, which he described as *Actinopus algerianus* (now *Ummidia algeriana*) and Westwood's *U. aedificatoria*. He distinguished the two species on

the grounds of differences in the morphology of the rastellum, the curved anterior edge of the sternum, the different texture of the abdominal cuticle and the leg-formula (Lucas 1846). Lucas does not mention any differences in the configuration of the eyes (the most commonly used diagnostic feature in classical species-level *Ummidia* taxonomy), but in the excellent figures that both Lucas (1846:pl. 1–5) and Westwood (1840:pl. 10) produced of their type specimens, a difference in the configuration of the eyes between *U. aedificatoria* Westwood and *U. algeriana* Lucas is obvious.

It is therefore unclear why Simon, who collected *Ummidia* in Algeria, never mentioned the differences that Lucas had found between *U. algeriana* and *U. aedificatoria*. Probably as the result of a preconceived conviction that *Ummidia* must be a recent American import in the western Mediterranean Simon, until 1909, regarded all Old World reports of *Ummidia* as reports of *U. aedificatoria* (Westwood 1840). It was Simon (1889) who declared Thorell's *U. picea* from Spain to be the male of *U. aedificatoria* and who convinced O. Pickard-Cambridge (although not wholeheartedly, see Cambridge 1907:818 and Frade & Bacelar 1931:507) that his newly found *Ummidia* species from Portugal also was *U. aedificatoria*. When Simon (1909) worked on the spiders collected by Martínez de la Escalera in Morocco he encountered a species of *Ummidia* that clearly differed from the Algerian *Ummidia* species that he knew so well. That this new species was collected near Tangiers, roughly the type location of *U. aedificatoria*, did not spark his realization that, for the first time, he might actually see Westwood's species under the microscope, so he proceeded to describe a new species *Pachylomerus (Ummidia) occidentalis* (Simon 1909). Simon's description of *U. occidentalis* is brief and without illustrations and he states that the new species is "sub similar –cui subsimilis est" – to *U. aedificatoria*, from which it only differs in the shape of the eye-formation, the spine pattern on the tibia of the palp and the number of spines on the prolateral face of tibia IV. Simon concludes his description of *U. occidentalis* with the somewhat casual and vague remark: "remplace probablement le *P. aedificatorius* au Maroc" (Simon 1909:8). The discovery of a second *Ummidia* species in North Africa apparently did not change Simon's opinion about the origin of the Mediterranean *Ummidia* species, and a year after his description of *U. occidentalis* Simon notes: "le genre *Pachylomerus*" (read *Ummidia*) "dont tous les autres représentants sont américains." (Simon 1910:266).

Frade & Bacelar (1931) in their revision of the Mediterranean *Ummidia* species found that the spine patterns Simon used were strongly variable in *Ummidia* at the species level and even in individual specimens, rendering them unfit for use in species level taxonomy. Furthermore, Frade and Bacelar (1931) found that at least three different *Ummidia* species inhabit the Mediterranean, indicating that Simon had underestimated the species diversity in the region. Nevertheless, Simon's arachnological influence has proved to be far reaching and today, a hundred years after his slip of not recognizing *U. aedificatoria* in the Moroccan spider material he examined, Simon's classification of western Mediterranean *Ummidia* species is still reflected in the World Spider Catalog (Platnick 2009).

The species descriptions given above, however, show that at least four different *Ummidia* species inhabit the western Mediterranean. Moreover, these species each appear to inhabit distinct geographical regions. *U. algarve* is common in southern Portugal and probably extends into southwestern Spain where the great delta (las marismas) and the alluvial plains of the Guadalquivir may separate it from *U. picea*. *U. picea* is widespread in southern Spain between Valencia and Malaga and probably beyond, towards Gibraltar. *U. aedificatoria* has until now only been reported from Tangiers in the far northwest of Morocco. *U. algeriana* is widespread in the Algerian Tell region, as Simon (1888) reported, from Bougie (Bejaia) in the west to Kroumirie (Ain Drahan) in the east and probably even further east into Tunisia. There are some indications (variation in configuration of the eyes, spermathecae morphology and some other morphological traits) that further geographically-related cryptic diversity is present in the Mediterranean *Ummidia* populations, but the still very limited availability of well documented and usefully preserved material for study currently prevents further conclusions. The idea that *Ummidia* is a recent and probably human-aided introduction in the western Mediterranean appears to be unlikely on grounds of the here-presented observations. The question of whether the Mediterranean *Ummidia* species complex is more closely related to the American *Ummidia* fauna or to the *Ummidia* (*Conothele*) fauna of Australasia remains to be investigated.

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Balancing predator avoidance with hunting opportunities: substrate choice by *Misumena vatia* spiderlings

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Abstract. When crab spiderlings *Misumena vatia* (Clerck 1757) emerge from their natal nests their small resource reserve makes them vulnerable to starvation, while their small size makes them vulnerable to many predators. Choosing substrates that allow hunting opportunities as well as protection from predators may thus be life or death decisions. Here we investigate the substrate choice of crab spiderlings on goldenrod *Solidago canadensis* and *Solidago juncea* inflorescences in relation to a frequently encountered predator, the jumping spider *Pelegrina insignis* (Banks 1892). Flower heads of *S. canadensis* are smaller and more densely packed on branches of the inflorescences than the heads of *S. juncea*, but the two species attract similar numbers of small flies, the major prey of the spiderlings and jumping spiders. Crab spiderlings significantly preferred *S. canadensis*, both in initial choice and length of time occupied, as did their jumping spider predator. However, capture times of spiderlings by small jumping spiders (< 5 mg) did not significantly differ on the two goldenrods, although the preferred goldenrod, *S. canadensis*, provided superior protection from larger jumping spiders (>5 mg). Thus, although occupancy on the preferred goldenrod does not make spiderlings safer from all jumping spiders, it provides superior protection from large ones and may be the basis for the substrate preference of the spiderlings.

Keywords: Crab spider, foraging, jumping spider, *Pelegrina insignis*, Salticidae, Thomisidae

When selecting an appropriate foraging site, an individual should, if possible, choose an area that provides abundant resources (maximizing benefit) and a low risk of predation (minimizing cost) (Lima & Dill 1990; Dukas 1998). Unfortunately for the forager, abundant resources may attract that forager's predators as well, either directly to the resource or to the foragers frequenting it. Animals may make distinct choices between substrates with relatively similar but subtly different characteristics, and these decisions may have important consequences for their survival and growth (Morse 2007).

In this study we evaluate the substrate choices (flowers) made by newly-emerged second-instar crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae), henceforth spiderlings, in relation to availability of prey and the danger resulting from their most common predator, the jumping spider *Pelegrina insignis* (Banks 1892) (Salticidae) (Morse 1992, 2007) on these sites. As soon as the spiderlings emerge from their natal nests during late summer, they become part of the jumping spiders' prey, although the jumping spiders also capture many of the same small insects that constitute the spiderlings' diet.

Spiderlings leave their nests in their second instar and begin hunting immediately. Since they have only recently ventured outside their natal nest, experience plays little or no role in site selection at this time. Spiderlings prefer goldenrod (*Solidago* spp.) as a foraging substrate to other flowers (Morse 2000a, 2005), but the interspecific variation in inflorescence structure and flower head sizes (Semple & Cook 2006) provide a range of both hunting and hiding sites available for small prey (primarily small Diptera) and small predators. To test such variation, we compared the availability of prey and vulnerability of newly emerged spiderlings on two common goldenrod species: *S. canadensis* and *S. juncea*, species whose size and packing of flower heads on an inflorescence differ quantitatively.

Jumping spiders possess a highly developed sense of sight (Jackson & Pollard 1996), which makes concealment especially important to the spiderlings. Jumping spiders of different sizes even within a species exhibit different levels of maneuverability in these inflorescences as a consequence of the size and spacing of the flower heads (see below) and, likely, their ability to find spiderlings. We treat spiderling size variation as negligible since they are of similar age and relatively small in relation to their substrate and in relation to their jumping spider predators.

Here we investigate whether the goldenrod species favored by the spiderlings will 1) provide the safest inflorescence structure and/or 2) the most favorable hunting site. We predicted that small jumping spiders (2–3 times the mass of spiderlings) would be more dangerous to the spiderlings than larger ones by virtue of their superior maneuverability within the small inflorescence structures. Thus we asked the following questions: Do spiderlings prefer one goldenrod over another (flower choice)? Do spiderlings remain on one goldenrod species longer than another (higher site fidelity)? Do jumping spiders follow the same pattern of use? Does one goldenrod species provide more safety than the other in the presence of predators? Does one goldenrod species provide more food than the other? If one goldenrod species is safer, is that consistent with spiderling preference? How does jumping spider size affect the vulnerability of spiderlings?

METHODS

Study area and vegetation.—We carried out this study in a 3.5 ha field during July–August 2007 and 2008 at the Darling Marine Center of the University of Maine, South Bristol, Lincoln Co., Maine USA (43.57°N, 69.33°W). The field, mown in October but otherwise unmanaged, contains several grasses (Gramineae) and interspersed forbs. During late summer the principal blooming flowers consist of goldenrods (*Solidago spp.*) and asters (*Aster umbellatus*) (Morse 2005). Goldenrods are dominant plants in many old-field communities. In the study area different species of goldenrod produce flowering stems ranging from 0.5 to 1.5 m in height, culminating in large pyramidal inflorescences, with flower heads clustered along several relatively horizontal branches.

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Solidago canadensis is the most common goldenrod in the study area. Its flower heads average 4.1 ± 0.10 mm (mean ± SE) in height and 2.3 ± 0.05 mm in diameter, with a density of 19.4 ± 2.33 flower heads cm^{-1} (n = 10). The next most common goldenrod species in bloom at this time, *S. juncea*, has larger flower heads, 5.6 ± 0.12 mm in height and 3.1 ± 0.09 mm in diameter, and a lower density of 14.2 ± 1.6 flower heads cm^{-1} (n = 10). The space between the *S. juncea* flower heads is thus 1.4 ± 0.16 times greater than that of *S. canadensis*, making flower-head density a potentially important factor for both the spiderlings and their variably-sized jumping spider predators (Morse 2006, pers. observ.).

Spiders.—Newly emerged spiderlings weigh from 0.4 to 0.7 mg, most of them from 0.5 to 0.6 mg (Morse 1993). As the spiderlings emerge from their nests, they immediately begin to seek a suitable hunting substrate (Morse 2005). Small jumping spiders, the commonest predators of the spiderlings at this time (Morse 1992), weigh between 0.9 and 10 mg, depending on their instar. Of the small jumping spiders in the study area, *P. insignis* is the most common, making up 88% of the small jumping spiders on goldenrods during this period (Morse 2006). We used *P. insignis* in all of the experiments.

Acquisition of spiders.—Spiderling broods were obtained from nests collected from the field a few days before emergence and used within two days of emergence to minimize possible effects of variability resulting from age, hunger, or experience. Jumping spiders were collected from goldenrod inflorescences throughout the field and from neighboring goldenrod patches.

Time on the two goldenrods.—To determine how long spiderlings and jumping spiders would remain on the two goldenrod inflorescences in the field, we ran four retention tests: *M. vatia* on *S. canadensis*, *M. vatia* on *S. juncea*, *P. insignis* on *S. canadensis*, and *P. insignis* on *S. juncea*. We first lightly dusted the subjects with red powdered micronite dye to distinguish them from others in the field (Morse 2000a). Previous studies have shown that this treatment does not affect the behavior of these spiderlings and small jumping spiders or increase their risk of predation (Morse 2000a, 2006).

We placed the spiderlings and jumping spiders on goldenrod inflorescences, subsequently censusing the inflorescences, one at a time, by visual inspection. If we did not find the individuals by visual inspection, we lightly tapped the entire inflorescence against a white clipboard to dislodge any hiding individuals, subsequently returning them back to the inflorescence. This procedure does not significantly affect the probability of finding the spiderling on a subsequent visit (Morse 2000a). Each census began at approximately 11:00 and ran until 18:00 of that day. We censused the spiderlings each hour, and jumping spiders each half-hour, for the first two hours, to accommodate for the jumping spiders' occasional rapid departure. We then censused all individuals hourly. Individuals that left the substrate immediately were removed from the data set.

Selection of flower heads.—To test further which goldenrod the crab spiders preferred, we made equal-sized blooming branches of the two goldenrods into small bouquets. Using a fine-tipped brush in the laboratory, we placed the spiderlings with their left legs on one goldenrod species and the right ones on the other (Morse 2005). After 30 min we recorded which flower species the spiderling had selected. Following each run we provided fresh branches and switched the position of the two goldenrod species to control for any variation in the light source. Morse (2005) describes this setup in greater detail. Additionally, to test whether tactile stimulation of the stem explained the spiderlings' choice we repeated the same flower selection procedure but removed the inflorescences, leaving only the stems. This test allowed us to establish the role of the stem, the initial point of contact for many spiderlings, in determining their choice of inflorescences.

Prey visitation to goldenrod inflorescences.—In order to compare the availability of potential prey visiting the two goldenrod species, we counted the number of small dipterans, the major prey of the spiderlings (Morse 2005, 2006) at inflorescences of the two goldenrods during mid-day on 11 days spaced through the study period (maximum of 10 *S. juncea* and 5 *S. canadensis* inflorescences). We also measured the size of the inflorescences of the two species, estimated as the volume of a cone. All counts were made on adjacent pairs of inflorescences in order to provide as direct a comparison as possible.

Predation on flower heads.—We used paired sets of Petri dishes (9 cm diam) as arenas to test the safety of spiderlings on flower heads of the two goldenrod species. Each Petri dish contained part of an inflorescence branch of *S. canadensis* or *S. juncea*. We placed a spiderling on the inflorescence in each Petri dish and allowed it 2 min to settle among the flower heads before placing a jumping spider of known mass (range = 1.0–11.9 mg) in the Petri dish. The jumping spiders had been starved for two days to ensure that they would be adequately hungry to hunt. We ran each trial for 8 h, checking the Petri dishes every 30–60 min to record predation times.

Voucher specimens were placed in the American Museum of Natural History, New York, and the Florida State Collection of Arthropods, Gainesville, Florida.

RESULTS

Time on the two goldenrods.—Spiderlings introduced to inflorescences of the two goldenrod species remained significantly longer on *S. canadensis* than on *S. juncea* (Fig. 1: t_{123} = 7.32, $P < 0.0001$ in two-tailed t-test). Jumping spiders introduced to the goldenrod inflorescences also remained significantly longer on *S. canadensis* than on *S. juncea* (Fig. 1: t_{38} = 3.00, $P < 0.005$).

Selection of flower heads.—When given a choice between *S. canadensis* and *S. juncea* in the laboratory tests, 80% of the spiderlings (32 of 40) chose *S. canadensis* and 20% (8 of 40) chose *S. juncea*, a highly significant difference (X^2_1 = 14.40, $P < 0.001$ in a X^2 one-sample test). In a further effort to test choice, we ran a second trial, simultaneously exposing individuals to the stems of *S. canadensis* and *S. juncea* (n = 10). All individuals tested continually moved freely between the two stems, clearly demonstrating that they did not distinguish between the two goldenrods on the basis of their stems, but on the inflorescences themselves.

Prey visits to the goldenrod inflorescences.—Inflorescences of *S. juncea* averaged 46.4% larger than those of *S. canadensis* (1986 ± 291.0 SE cm^3 vs 1064 ± 202.4 cm^3). When corrected for inflorescence size, visitation of prey to the two goldenrods did not differ significantly (*S. juncea* = 0.6 ± 0.13 SE, *S.*

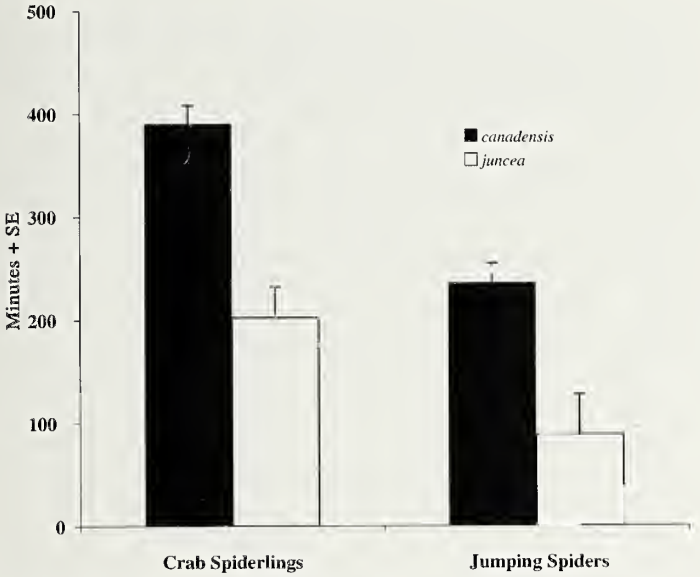

Figure 1.—Length of time (mean ± SE) spiders remained on goldenrod. White bars = *S. juncea*, n = 60, 15; Black bars = *S. canadensis*, n = 65, 25.

canadensis = 0.7 ± 0.13 SE prey per inflorescence; $t_{21} = 0.638$, $P > 0.5$ in a two-tailed t-test for the difference between two means). However, evaluating prey in terms of number per inflorescence rather than per inflorescence area would favor *S. juncea* over *S. canadensis* as the more productive substrate ($t_{21} = 2.297$, $P = 0.03$, same test.

Predation on flower heads.—Jumping spiders preyed on spiderlings in 26 (38%) of 69 eight-hour trials on *S. canadensis* and in 18 (27%) of 66 eight-hour trials on *S juncea*. These frequencies did not differ significantly ($X^2_1 = 1.67$, $P > 0.1$ in a X^2 test). Predation occurred on average 177 ± 34.4 min. after release on *S. canadensis* and 173 ± 48.2 min after release on *S. juncea*. These predation times did not differ significantly, either ($t_{42} = 0.06$, $P > 0.9$).

Size vs predation risk.—No significant correlation took place between jumping spider size and predation times on *S. canadensis* (Fig. 2: $R^2_{1,24} = 0.019$, $P > 0.5$), but a significant inverse correlation took place on *S. juncea* (Fig. 3: $R^2_{1,19} = -0.271$, $P < 0.02$). On *S. juncea* large jumping spiders captured spiderlings more rapidly than did smaller ones. Thus, predation patterns differed with the substrate in jumping spiders of different size.

DISCUSSION

Time on the two goldenrods.—Spiderlings remained significantly longer on *S. canadensis* than *S. juncea*. Jumping spiders exhibited the same pattern, although staying for shorter times than the spiderlings on both substrates, probably a consequence of their different hunting strategies. Spiderlings are sit-and-wait predators (Morse 2007) that routinely remain for extended periods on satisfactory hunting sites, while jumping spiders are cursorial predators that roam continually (Jackson & Pollard 1996; Foelix 1996). The relatively long retention times exhibited by both species on *S. canadensis* strongly suggest a preference for *S. canadensis*.

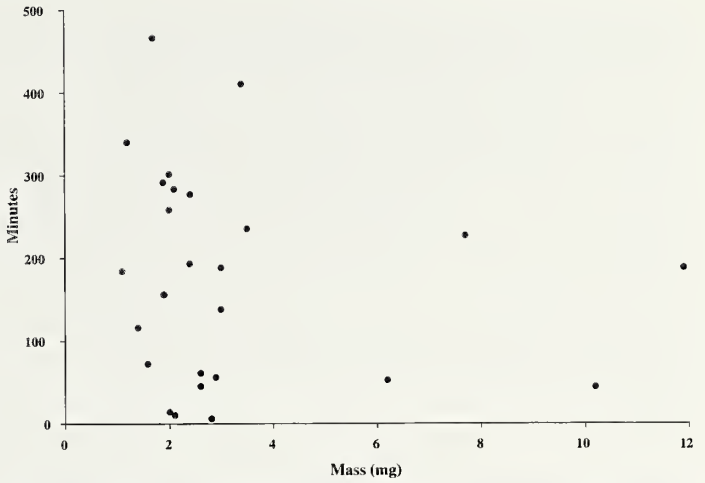

Figure 2.—Time for predation to occur vs. mass (mg) of jumping spider on the goldenrod *S. canadensis*.

These results suggest that predator avoidance plays a role in the substrate choice of the spiderlings, likely a response to the relatively rapid capture times by the large jumping spiders on *S. juncea*. They are also consistent with earlier studies showing that *M. vatia* on normal-density *S. canadensis* inflorescences initially spent much more of their time in hiding positions than did sibs on inflorescences thinned to about two-thirds normal density (Morse 2006), a density similar to that of *S. juncea*. The short capture times by the large jumping spiders on *S. juncea* suggest that they would frequently discover spiderlings on these sites in the field before quitting an inflorescence. These capture times of the large jumping spiders are also consistent with their capture patterns on the thinned *S. canadensis* inflorescences (Morse 2006), on which they maneuvered more easily than on the unthinned inflorescences.

Selection of flower heads.—The spiderlings leave their natal nests without maternal assistance (Morse 1992) and choose a substrate on their own. The significant choice of *S. canadensis* over *S. juncea* in the simultaneous choice experiment further supports the preference of *S. canadensis* by the spiderlings. The failure of the usually sedentary spiderlings to settle on the

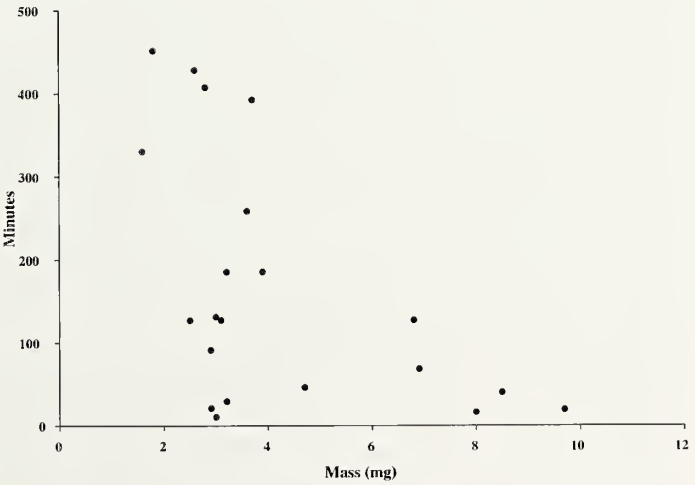

Figure 3.—Time for predation to occur vs. mass (mg) of jumping spider on the goldenrod *S. juncea*.

stems in the stem preference test suggests that their choice of *S. canadensis* does not result from tactile stimulation from the stem, although the stem is sometimes the first part of a goldenrod they encounter.

Previous studies have found no sign of *M. vatia* using chemical signals (LeGrand & Morse 2000; Anderson & Morse 2001; Leonard & Morse 2006), which renders an olfactory response to the vegetation unlikely, although not disproved. Information to date suggests tactile and/or visual cues as the best candidates, though the spiderlings do not discriminate among floral displays at distances of 10 cm (Morse 2005).

Predation on flower heads.—Predation times of the jumping spiders did not differ significantly on the two goldenrods, but they did demonstrate that large individuals were more effective on *S. juncea* than smaller ones. Although these predation setups do not closely match conditions in the field, they suggest that fine-level inflorescence structure may affect the vulnerability of the spiderlings to jumping spiders of different size.

It is important to consider variables controlled in the laboratory experiments that may affect safety on goldenrod in the field. The crab spiderlings' hiding positions in the field probably serve best in concealing them from passing predators as opposed to when confined for a considerable period in a small enclosure in the laboratory experiments. Jumping spiders have highly developed sight, making them formidable visual hunters (Jackson and Pollard 1996). The jumping spiders in this experiment had considerably more time to inspect the goldenrod branch containing the hiding spiderling than they would have in the field. However, if the preferred *S. canadensis* provided the safer hiding place, one would predict longer capture times on this substrate than on *S. juncea*.

This experiment compared jumping spider hunting performances on equal-sized branches of an inflorescence, not the entire inflorescences. Comparing same-sized branches of the two goldenrods may remove any potential safety advantage resulting from unequal sized branches routinely encountered in the field. Jumping spiders moved much faster than spiderlings, and when a jumping spider attacked a spiderling it captured the spiderling easily, even if the spiderling had hidden between the flower heads (Y. Garcia-Bengochea, pers. observ.). Thus, maneuverability within an inflorescence does not play an important role in predator avoidance by the spiderlings.

Prey visitation rates clearly did not play the central role in substrate choice by the spiderlings, since *S. canadensis* did not attract significantly more small insects than *S. juncea*. Although visitation rates of the spiderlings' major prey did not differ significantly, if these prey selected feeding sites on the basis of entire inflorescences, rather than on their density, the spiderlings might favor *S. juncea*, rather than *S. canadensis*, in that it attracted the most prey per inflorescence. At that rate, the spiderlings chose *S. canadensis* in spite of its slightly inferior prey-attracting ability.

Size vs. predation risk.—The significant inverse relationship between size of jumping spider and capture time on *S. juncea* suggests that *S. canadensis* is the safer substrate for spiderlings in the presence of large jumping spiders, and *S. juncea* is relatively safer for spiderlings in the presence of small jumping spiders. This result provides another test of the hypothesis that the spiderling's preferred substrate is the safer one.

Although we predicted that the small jumping spiders would have an advantage in finding and capturing spiderlings hidden in the dense goldenrod inflorescences, we found the opposite relationship on *S. juncea*. Infloreseences of *S. juncea* are less dense than *S. canadensis*, which may increase the predator's range of sight and/or maneuverability, giving the larger jumping spiders a better hunting opportunity and explaining the observed pattern. Earlier studies have revealed that when jumping spiders hunt large prey (relative to their own size), they will try to ambush the prey from behind (Jackson & Pollard 1996). The small jumping spiders may have been close enough in size to the crab spiderling to exploit this ambush technique under field conditions. However, the experimental setup did not allow the smaller jumping spiders (< 5 mg) to ambush their spiderling prey in this way, which may have prevented them from capturing the spiderlings more rapidly.

Implications at the community level.—How important are these interactions at the community level? They could easily drive the relative importance of jumping and crab spiders in the community level. As members of different hunting guilds (sit-and-wait vs. active hunter), these spiders may affect their principal herbivore prey in different ways. In an old field in Connecticut, Schmitz (2008) found that the relative abundance of sit-and-wait predators and hunters affected the impact of the commonest herbivore (a grasshopper), with the result that different grasses and herbs predominated in response to the different spider-mediated responses of the herbivores, and plant diversity and nitrogen mineralization ultimately varied as a result.

Our results thus support the hypothesis that subtle differences in inflorescence structure may play a major role in establishing the relationships among these important community members, and potentially the role of both species on herbivores and pollinators in old-field ecosystems. Millimeters matter! Not only do modest differences in size make a difference, but the sizes of the spiders change rapidly. This picture takes on added interest in that late-instar female *M. vatia* literally turn the tables and prey on *P. insignis* and other small jumping spiders (Morse 1992, 2006). These shifts are probably not unusual among old-field inhabitants (e.g., Persons et al. 2001). The spiderlings will also gain experience (Morse 2000b), a variable that we did not explore in this study because we used young, naive individuals. Lastly, the jumping spiders themselves have highly developed learning abilities (Harland & Jackson 2004) that may counter those of the spiderlings.

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Web gigantism in Darwin's bark spider, a new species from Madagascar (Araneidae: *Caerostris*)

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Abstract. The remarkable bark spiders (genus *Caerostris*: Araneidae) are poorly known Old World tropical orb-weavers, whose diversity, currently at 11 species, is grossly underestimated. Most species build large webs at forest edges, clearings, and gardens, but in Madagascar, probably the hot spot of *Caerostris* diversity, at least one speeies occupies a unique ecological niche: casting its web across streams, rivers and lakes, so that the orb is suspended above water and attached to substrate on each riverbank via bridgelines up to 25 m. Here, we summarize current knowledge on *Caerostris* natural history, and specifically focus on the remarkable web architecture and biology of the newly described *Caerostris darwini* n. sp. Darwin's bark spider builds its web, a regular orb suspended above water, and maintains it with daily reinforcing of bridgelines and renewal of orb for many days. Web size ranged from 900–28,000 cm^2, with the largest measured web of about 2.8 m^2 being the largest orb ever measured, to our knowledge. With anchor lines capable of bridging over 25 m, it also builds the longest webs among all spiders—a unique form of web gigantism. We report on mass capture of ephemeropteran prey items in *C. darwini* n. sp. webs during a single day. Webs contained up to 32 mayflies that were subsequently wrapped *en masse* before the spider fed on them. We also provide the first evidence of kleptoparasitism in these webs both by other spiders (Argyrodinae) and by newly documented, undescribed symbiotic flies. *Caerostris* display extreme sexual size dimorphism with large females and small males, which is manifested in enigmatic sexual behaviors such as mate guarding, male-male aggressiveness, genital mutilation, mate plugging, and self castration. *Caerostris* is thus a promising candidate for evolutionary studies, and its diversity, biology, and phylogenetic relationships all deserve a closer scrutiny.

Keywords: Diversity, DNA barcode, genital mutilation, morphology, orb web architecture, sexual behavior, sexual size dimorphism

Spiders of the genus *Caerostris* (Araneidae), known in Africa under the vernacular 'bark spiders', are eye-catching orbweavers that are widespread throughout the Old World tropics. *Caerostris* spiders all make sizable orb webs, with some of the webs reported here, to the best of our knowledge, qualifying as the largest spider webs ever documented. *Caerostris* are also remarkable for their extreme sexual size dimorphism, with huge females and small males (Grasshoff 1984; Kuntner et al. 2008a). The large females are highly conspicuous when sitting in the center of their webs; however, their name stems from the habits of at least some species to mimic dead bark, twigs or thorns (Fig. 1), making them quite cryptic but also resulting in exceptional morphological diversity. Surprisingly, given the size of the spiders and their webs, virtually nothing is known about *Caerostris* natural history, and the genus is also poorly known taxonomically and phylogenetically.

Caerostris, first described by Thorell (1868), is a seemingly species-poor genus, with only 11 species recognized throughout the Old World tropics (Platnick 2010). Most descriptions have been based on female material alone (Grasshoff 1984), since the small males are cryptic and very rarely observed or collected. In the only taxonomic revision of the entire genus, Grasshoff (1984) only examined a total of 16 *Caerostris* males, and these only belonged to three widespread Afrotropical species, the type *C. mitralis* (Vinson 1863), *C. sexcuspidata* (Fabricius 1793) and *C. vicina* (Blackwall 1866). According to Grasshoff, an additional six species are known (females only) from the Afrotropics: *C. corticosa* Pocock 1902 from South Africa, *C. cowani* Butler 1882, *C. ecclesiigera* Butler 1882, *C. extrusa* Butler 1882 and *C. hirsuta* (Simon 1895), all from Madagascar, and *C. mayottensis* Grasshoff 1984 from Mayotte. Grasshoff also recognized two Asian species based on female material, *C. indica* Strand 1915 from Myanmar and the widespread *C. sumatrana* Strand 1915 (for the description of the male, see Jaeger 2007). The revision is devoid of biology, as it only mentions that female *Caerostris* construct orb webs (Grasshoff 1984:765).

Of the 11 currently recognized *Caerostris* species, six occur in Madagascar (Platnick 2010). However, this diversity is hugely underestimated; for example, we observed and collected female vouchers of perhaps seven speeies in sympatry in the Andasibe-Mantadia National Park alone (Fig. 2A, D–I), some diurnal and some nocturnal. We found that males of the diurnal species usually hide in vegetation away from female webs (Fig. 2B), and were thus able to collect more males during our three field expeditions than exist in all museum collections of all species worldwide (own data). Hence, a new global taxonomic revision is necessary to 1) match sexes of species previously known from females only, 2) understand *Caerostris* diversity better and describe new species, and 3) obtain *Caerostris* DNA data for taxonomic and phylogenetic investigations; this work is already underway in the authors' laboratories. The goal of this paper is to introduce some of the most striking aspects of *Caerostris* biology, based mostly on original observations of a new species from Madagascar, which we named *C. darwini* n. sp. precisely 150 yr after the date of the publication of Charles R. Darwin's *Origin of Species* (see Etymology).

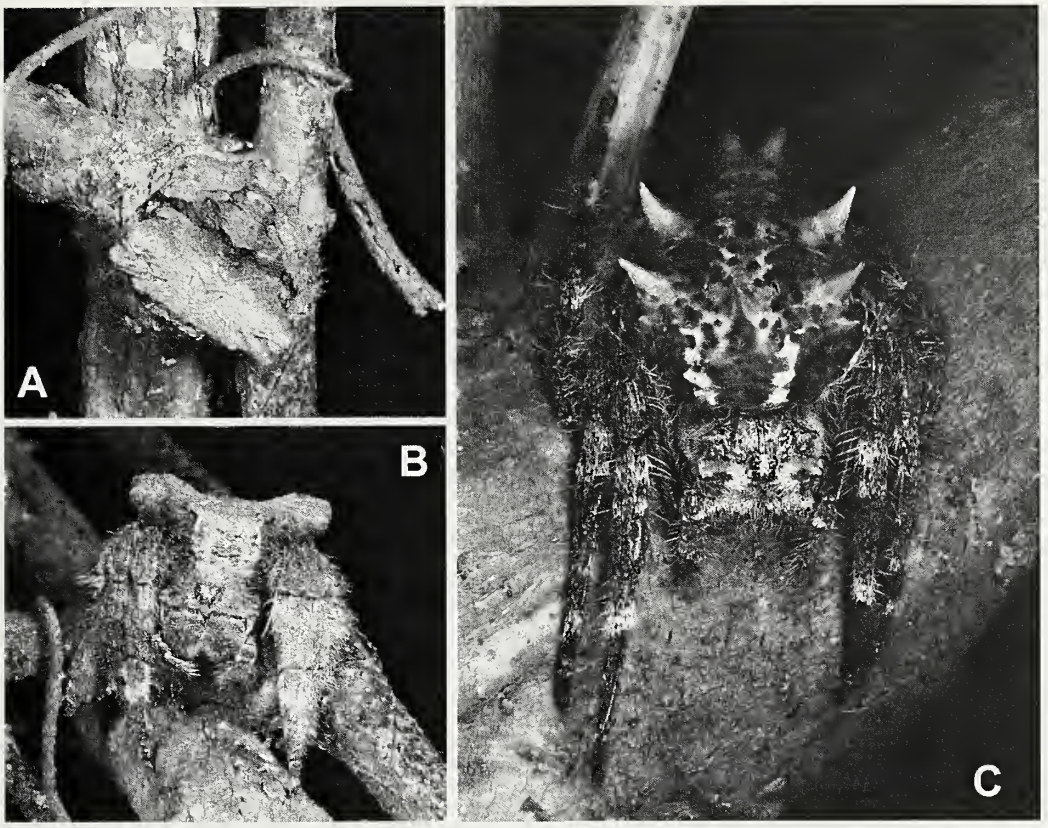

Figure 1.—Extreme crypsis of bark spiders, *Caerostris* spp: A. Bark, lichen, or what...?; B. Same female *Caerostris* spider from a different angle, South Africa; C. Female *Caerostris* from Madagascar.

We provide a preliminary assessment of *Caerostris* diversity on Madagascar and present the first natural history observations made on the newly described diurnal species, provide information on female and male sexual biology including genital damage, describe egg sac structure, and provide preliminary information on prey and prey capture. Additionally, we present the data on kleptoparasitism in *Caerostris* webs by other spiders (Argyrodinae) and by newly discovered undescribed dipterans (Fig. 4). Our main focus is on the biology and web architecture of the new riverine *Caerostris* species due to it combining extraordinary web architecture with exceptional silk mechanical properties (Agnarsson et al. 2010). In addition, we contrast this newly understood biology of the new species with certain aspects of the biology of other diurnal and nocturnal *Caerostris* species, based on preliminary and opportunistic observations from Madagascar (2001, 2008, 2010) and South Africa (2001).

Based on our observations on *C. vicina*, African *Caerostris* do not maintain webs diurnally, but cryptically hide during the day and construct large webs (up to 1.5 m across), often in the forest edge or clearings, at night. However, in Madagascar *C. darwini* n. sp. occupies a unique ecological niche: females cast their giant webs across streams, rivers and lakes, suspending the orb directly above the water on anchor threads that can span up to 25 m (M. Gregorič pers. comm.), attached to vegetation on each side of the river (Fig. 3). Although some other spiders build webs above water (Eberhard 1990), no others can, to our best knowledge, routinely utilize as habitat the air column immediately above sizeable rivers and up to several meters above water. We thus provide baseline information that we hope will inspire further work on this poorly known, but remarkable group of spiders. We believe *Caerostris* spiders have the potential to become exemplar organisms in the study of web biology (e.g., Blackledge & Hayashi 2006; Swanson et al. 2006; Agnarsson et al. 2009, 2010) and sexual behavior studies related to antagonistic interactions between the highly dimorphic sexes (e.g., Miller 2007;Kuntner et al. 2009b, c).

METHODS

Literature review.—We reviewed the literature on *Caerostris* biology, and summarize it along with our own observations (behavioral descriptions follow Eberhard 1982; Scharff & Coddington 1997; Griswold et al. 1998; Kuntner et al. 2008a). The only published accounts on *Caerostris* natural history appear in popular science works on common African species (Yates 1968; Filmer 1991; Dippenaar-Schoeman & Jocque 1997; Leroy & Leroy 2000). Nothing has been published on the biology of *Caerostris* species from Madagascar or Asia (Grasshoff 1984; but, see Jaeger 2007).

Field methods.—Fieldwork took place 21–25 April 2001 around Namorona River in Ranomafana NP (elev. 1000 m, see locality data below) and Fianarantsoa Province, eastern Madagascar; and 29 March–24 April 2008 in and around the two patches of forest protected by the Andasibe-Mantadia National Park (Périnet special reserve and Mantadia forest), in Toamasina Province, eastern Madagascar (elev. 900–1000 m, see locality data below). Additional data on *C. darwini* n. sp. comes from February–March 2010 fieldwork from both the above reserves and from Tzimbazaza Zoo in

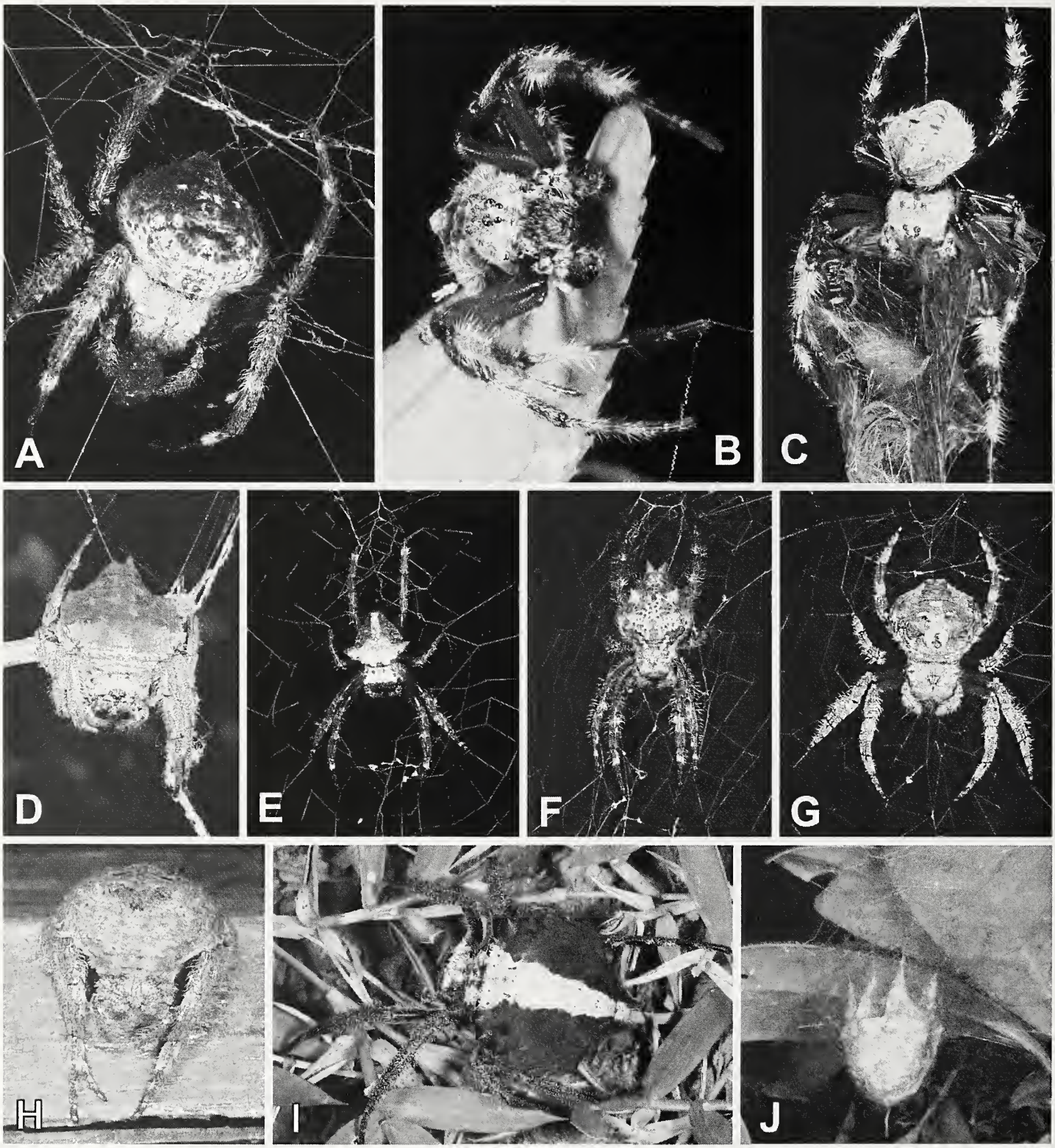

Figure 2.—A glimpse into Madagascar *Caerostris* diversity, all from a single reserve, Andasibe-Mantadia NP. A–C. The commonly encountered riverine species, *C. darwini* n. sp.: A. Female feeding at hub; B. Male hiding in vegetation near female web; C. Male feeding on prey caught and wrapped by female. D–I. Females of six other morphospecies in sympatry. J. Egg sac of undescribed *Caerostris* species from Madagascar.

Antananarivo, Madagascar. Additional, more sporadic data on *Caerostris* natural history are from Phinda Reserve and Tembe Elephant Park, South Africa during March–April 2001. Vouchers of all morphospecies are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In Andasibe-Mantadia NP we encountered webs of about six different morphospecies (possibly new species, but

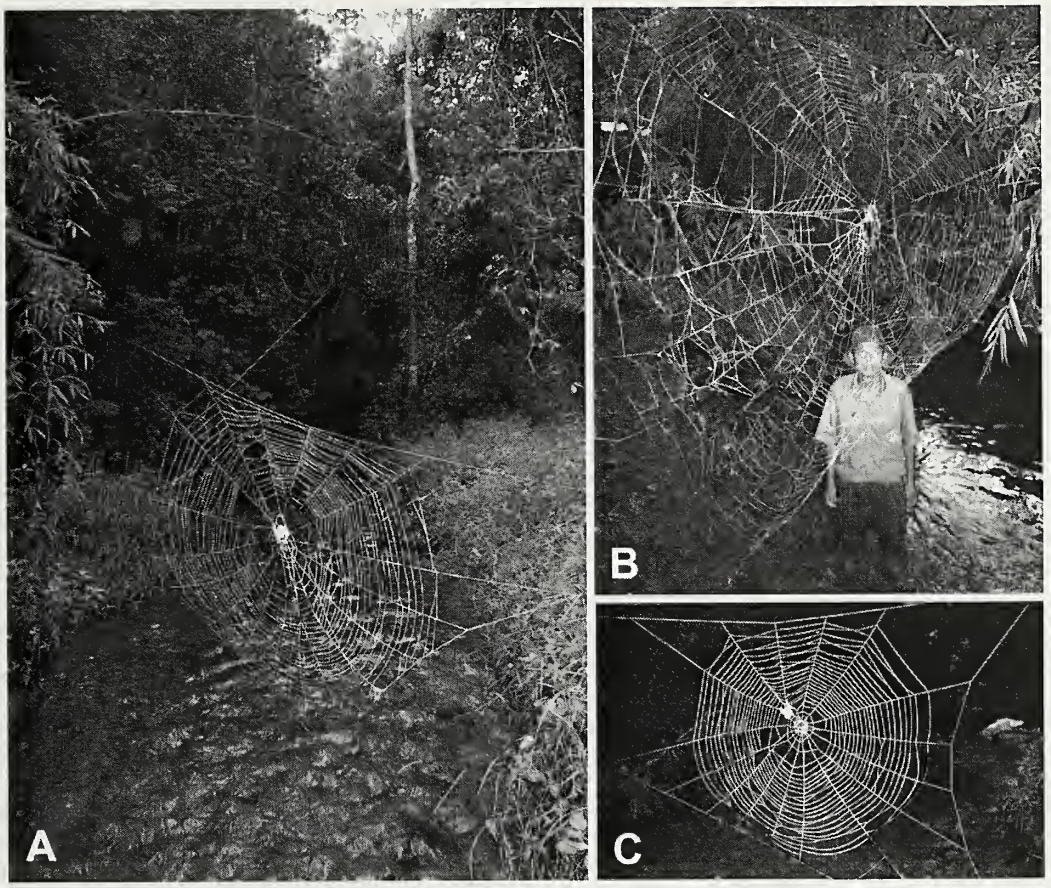

Figure 3.—*Caerostris darwini* n. sp. webs cast over streams and rivers in Andasibe-Mantadia NP, Madagascar.

represented by females only) along the road, at forest edges and in clearings, and of the focal species *C. darwini* n. sp., across streams and rivers (Figs. 2, 3). We also observed numerous *C. darwini* n. sp. along and across rivers in Ranomafana. We measured webs in the field, and when possible, we photographed each web for subsequent measuring. The parameters measured, all described elsewhere (Kuntner & Agnarsson 2009; Kuntner et al. 2008b), were 1) web width; 2) web total height; 3) distance from top web frame to hub; 4) maximal mesh width; 5) total bridge line length; 6) number of radii; 7) hub height above water/ground; and 8) maximal distance between sticky spirals. All web measurements are in cm, presented as the range and average ± SD.

Webs were also examined for prey items as well as kleptoparasitic organisms, and vouchers were collected. The web, and the vegetation to which the web was attached, was surveyed for egg sacs and for adult males. Prey items were photographed and collected for identification. Observations were made on web building and architecture, prey wrapping and feeding, including interactions between the spider host and kleptoparasites sharing her food, and on sexual biology.

Coddington's sound test involved a human emitted noise (humming) made close to the spider sitting at the web hub.

Taxonomic methods.—We used Grasshoff's (1984) revision of *Caerostris* to differentially diagnose *C. darwini* n. sp. from all other known species. Previously, Kuntner et al. (2008:fig. 16) used this species as an outgroup exemplar in a phylogenetic study focusing on nephilid spiders, and illustrated its genital anatomy. Here, we illustrate, diagnose and describe this new species (taxonomic methods follow Kuntner 2007), and provide the barcode COI sequence for reference (standard COI primers used; T. Blackledge pers. comm.).

Abbreviations.—The following anatomical abbreviations are used in the text and figures: ALE = anterior lateral eyes, AME = anterior median eyes, BH = basal hematodocha, C = conductor, CB = cymbium, CD = copulatory duct, E = embolus, EB = embolic base, Etm = embolus-tegulum membrane, FD = fertilization duct, PLE = posterior lateral eyes, PME = posterior median eyes, PP = pars pendula, S = spermatheca, SD = sperm duct, ST = subtegulum, T = tegulum.

RESULTS AND DISCUSSION

Our study revealed a high diversity of *Caerostris* in Madagascar (Figs. 1, 2), with several new species restricted to small remaining pockets of montane rainforest. The lack of available males still precludes a clear assessment of the numbers of new species, and we here only describe the one new species for which sufficient material of both sexes became available. Clear understanding of this diversity is critical to conserving these giant orbweavers and their habitat in the rapidly diminishing forests of Madagascar. *Caerostris* are strongly sexually dimorphic. Males are small, cryptic, and thus rarely discovered. These males are critical for identifying species and for phylogenetics. In addition to its conservation aspects, understanding Malagasy *Caerostris* diversity is also crucial to determine the evolutionary origin of web gigantism.

Our preliminary data suggest that *Caerostris* species exhibit two quite distinct biologies. The typical African and possibly

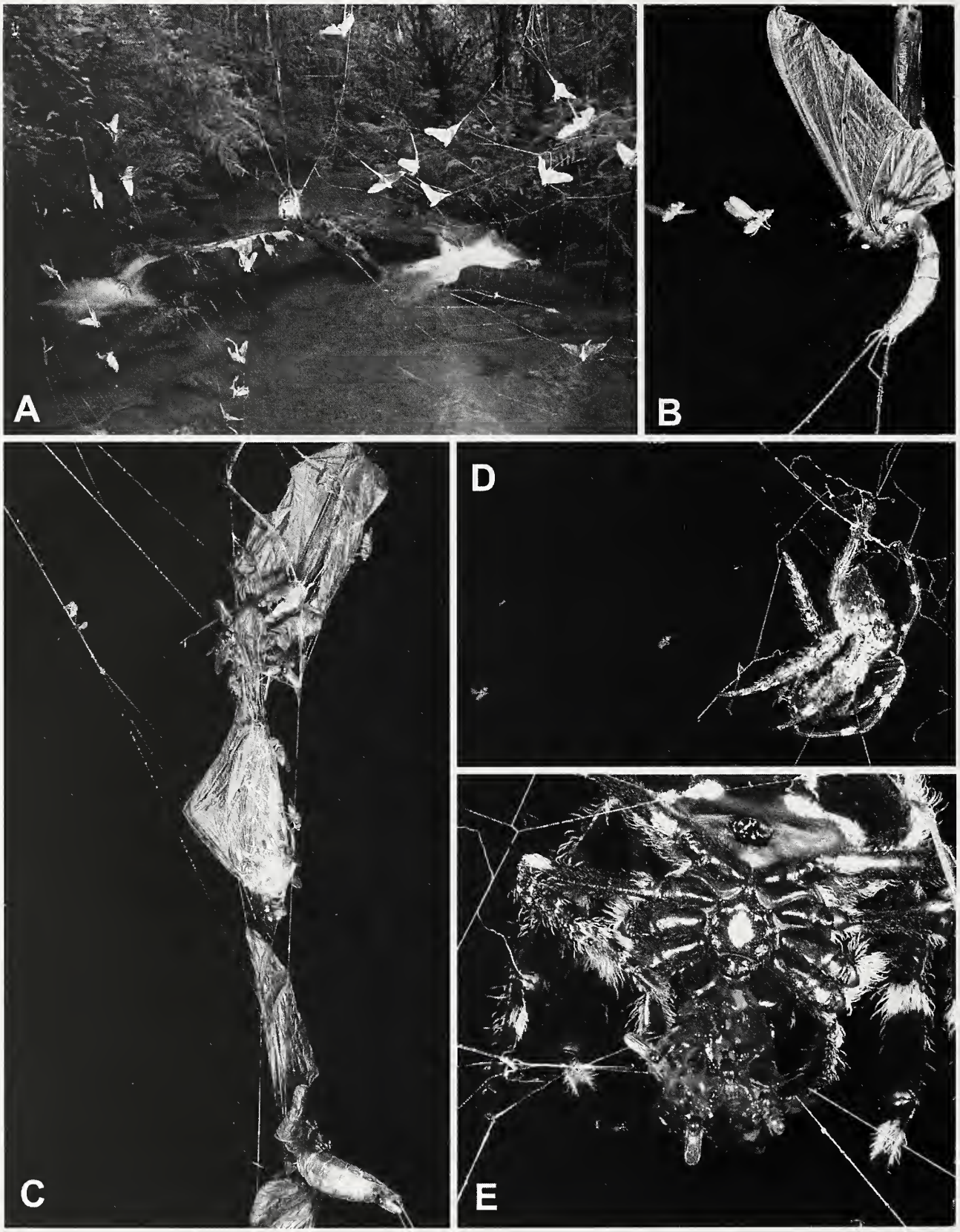

Figure 4.—*Caerostris darwini* n. sp. prey and their symbionts. A. Web with 22 newly caught mayflies. B–E. Kleptoparasitic flies interacting with spider and her prey: B. Landing on spider prey; C. At least 16 flies on and around three wrapped packages of spider prey; D. Flying in to feed with the spider female, who showed occasional aggressiveness; E. Close-up of feeding spider, involuntarily sharing food with four flies.

Asian species live away from webs cryptically on twigs during the day, resembling dead bark or twigs (Fig. 1A, B; see also Filmer 1991; Leroy & Leroy 2000). These species blend into the environment by their coloration and general morphology (flattened legs, hairy bodies with thorny projections (Fig. 1) and probably only build and occupy their webs at night (own data). The second lifestyle, typical of certain species from Madagascar and exemplified by *C. darwini* n. sp., is to live permanently in the web, which is typically spun over flowing bodies of water (Fig. 3). Smaller species in Madagascar utilize small streams and the large ones, like *C. darwini* n. sp., cast their impressive webs with anchor threads spanning on average 3.5 m, but up to 14 m wide over medium sized rivers that may be about 10 m wide (e.g., Namorona River at Ranomafana, 2001), and even 25 m wide over lakes (M. Gregorič pers. comm.).

Web architecture and gigantism.—We documented webs of several *Caerostris* species in Andasibe-Mantadia NP. *Caerostris darwini* n. sp. was the most common species and well represented by both sexes. According to our observations, webs of *Caerostris* species are rather uniform and fairly typical araneid orbwebs (Fig. 3). All species make large orbs with a an open hub (rarely closed), gradual hub-loop to sticky-spiral transition, temporary spiral removed in finished web, relatively few radii, few or no secondary radii, and lacking a retreat or other auxiliary silk structures such as barrier web, and very rarely containing a stabilimentum (Kuntner et al. 2008a). We did not observe web construction in full, but new comprehensive data on *C. darwini* web construction will soon be made available (M. Gregorič pers. com.). One female *C. vicina* was observed partially building sticky spiral in Tembe Elephant Park, S. Africa. In a typical araneid fashion, she used the oL1 tap and removed the temporary non-sticky spiral; oL1 tap was also observed in another undescribed species in Périnet (2001), and in *C. darwini* n. sp. in Andasibe-Mantadia NP (2008). We encountered *Caerostris* webs mostly at forest edges or clearings, along rivers, and in the case of *C. darwini* n. sp., across rivers. The females typically rested in their webs head down (but often head up), during night. During day females of most species rested cryptically on bark away from the web (Fig. 1), *C. darwini* n. sp., on the other hand, was active day and night, sitting in the center of its web (Fig. 3A).

The *C. darwini* n. sp. webs were usually vertical, but sometimes inclined at 80, 70, or even 50 degrees ($n = 18$). They typically had open hubs (Fig. 3B, but see Fig. 3C), and the hubs were slightly displaced toward the top frame (Fig. 3A). The sticky spiral was circular and covered an area limited to the length of the shortest radii in the web. Many webs showed conspicuous sign of damage and repair, others had large open holes, suggesting that the spider does not immediately replace a damaged web, but continues to use it through periodic renewal. The *C. darwini* n. sp. female web data from Andasibe-Mantadia NP (2008) are summarized here as the range, average ± SD (all measurements in cm, $n = 18$ females): web width 31.5–105.0 (63.6 ± 21.7), web total height 30.0–130.0 (71.2 ± 30.3), distance from top web to hub 10.0–56.0 (28.5 ± 13.8), maximal mesh width 11.0–30.5 (17.6 ± 5.4), total bridge line length 180.0–700.0 (354.2 ± 152.7), number of radii 17–25 (21.8 ± 4.0), hub height above water 86.0–240.0 (152.3 ± 48.3), maximal distance between sticky spirals 0.8–3.5 (2.0 ± 0.8).

In comparison to *C. darwini* n. sp., the three other *Caerostris* species measured in Andasibe-Mantadia made denser webs with 34–36 radii and some secondary radii, with an average of 0.7 cm spacing between spirals. *Caerostris darwini* n. sp. webs had large capture areas (1900–28,000 cm^2 in size, area of capture spiral only), with the largest observed web exceeding even the giant *Nephila* orb webs (Kuntner & Coddington 2009). Additionally, the anchor threads may form the longest recorded bridgelines of any orb web, as they extend up to 25 m over rivers and lakes. How the spiders establish lines across the river, allowing the building of the web, is currently being researched (M. Gregorič pers. comm.).

Based upon the large size of the orbs as well as the spiders building them, and the webs' suspension on such extremely long anchor lines above water where the web is exposed to the elements, we might expect that the dragline silk of *C. darwini* would exhibit particularly high mechanical performance properties. In particular, high ability to absorb energy before breaking (high toughness) would help prevent bridgeline failure leading to webs collapsing into the water. Indeed, as we report elsewhere, *C. darwini* n. sp. silk is exceptionally tough, even compared to the already exceptional silk of other orbweavers (Agnarsson et al. 2010).

Prey capture and kleptoparasitism.—Although we observed numerous *Caerostris* webs over a long period of time, prey items were rarely observed in *C. darwini* n. sp. webs. Prey items include relatively small insects such as bees, small dragonflies and damselflies (M. Gregorič pers. comm.). However, on a single day we observed abundant mayflies (Ephemeroptera) emerging from the stream that were caught in large numbers in several webs (Fig. 4A). Up to 32 unwrapped prey items were counted in a single web. Prey were then subsequently wrapped *en masse*, the spider wrapping together several prey items before feeding on them. Most wrapped prey packages were heavily kleptoparasitized by flies (Fig. 4B, C), apparently undescribed and of several species and at least two families (P. O'Grady pers. comm.). Up to 10 flies were observed on a single package being consumed by the host spider, and numerous flies were constantly hovering around the spider and its prey. Flies were also found on prey items that had not been wrapped by the spider. The female spiders reacted aggressively toward the flies as they approached to feed directly on the prey in her mouth (Fig. 4D, E), and repeatedly shook their legs and web to chase off the flies. One male *C. darwini* n. sp. was observed eating prey wrapped by the female in her web; the male occasionally paused to chase off the flies (Fig. 2C).

Although flies have not been observed before in *Caerostris* webs, they are known kleptoparasites in certain other orbweaving spiders (Sivinski & Stowe 1980). Eisner et al. (1991) studied the flies belonging to three genera of Milichiidae and their kleptoparasitism in webs of the giant golden orbweaver *Nephila clavipes* (Linnaeus 1767) in Florida. These flies were chemically attracted to the spiders' heteropteran prey (stink- and squash bugs), but the spider host was not severely affected by such kleptoparasitism. *Nephila pilipes* (Fabricius 1793) from SE Asia also hosts flies in the web and on the body (Kuntner pers. obs.). Other families of flies have also been lured to spider webs (Chloropidae, Phoridae). Sivinski et al. (1999) reviewed kleptoparasitism in Diptera.

Spiders, dung-feeding scarab beetles as well as social and prey storing insects are common hosts because of the delay between prey acquisition and its consumption (e.g., spiders masticate and pre-orally digest their prey). These authors noted that flies associated with predators were mostly female, while scarab kleptoparasites were of both sexes.

Caerostris kleptoparasites often include other spiders. Argyrodine kleptoparasites, belonging to two potentially new, sympatric species, were found in about 30% of the *Caerostris* webs encountered in 2008, with 0–3 individuals per web (0.5 ± 0.9). In 2001, 11 argyrodines were observed in a single large (100 × 110 cm) *Caerostris* web (a third, undescribed species). Although these small spiders are known to steal food from their hosts in other orbweaving genera (e.g., *Nephila*, see Agnarsson 2003), our preliminary data lack notes on their behavior in *Caerostris* webs.

Males and sexual biology.—Most male *C. darwini* were found on the female web's bridge lines, and on leaves in vegetation to which they are attached. At most two males were found associated with a single (sub)adult female web (0.5 ± 0.6). In Andasibe-Mantadia (2008), adult females had at most one male associated with their web, but subadult females had sometimes more than one male effectively waiting for their maturation, a common pattern of pre-copulatory mate guarding in orbweaving spiders (see below). In Ranamofana (22 April 2001) we observed the here-designated type specimens (holotype male, paratype male and female) engaging in sexual behavior (Fig. 5). First, a male was found copulating with a large female, while she was at the hub of the web in a copulation position head facing upwards, with no mating thread present. This male (M1) had the right palpal hematodochae expanded and copulated only with that palp (Fig. 5 shows that he lacked the left palp). During copulation, a second male (M2) approached the hub from the web periphery. M1 aggressively chased the intruder off the female web to the anchor line. M2 retreated and waited, while M1 returned to the hub. The female had at first not moved from the copulating posture, but later switched to the usual head down position at hub before M1 could return to resume mating. On M1 return, she aggressively shook the web towards him, and he retreated a short distance. Then M2 approached the female on another thread, and she reacted aggressively, and he also retreated. M1 then tried to re-approach. Approaching involved no signaling; the male simply walked directly to the female. He stopped when she responded aggressively and groomed his expanded right palp. M2 attempted to re-approach, but the female again responded aggressively and the male retreated. No further attempts occurred, and all the animals were collected (see Types).

Caerostris darwini n. sp. exhibits mating behaviors reminiscent of sexually dimorphic nephilid and certain araneid spiders (see e.g., Kuntner et al. 2009a–c): males plug female copulatory openings with embolic parts, and they sometimes lack one or both palpal distal parts (eunuchs, Fig. 5). However, in *Caerostris* such males retain the cymbium whereas in nephilid eunuchs the palpal breaking point is between the tibia and tarsus (Kuntner 2005, 2007). Adult males were observed in the webs of subadult females, presumably a form of pre-copulatory mate guarding. In one case a mated male with no palps (full eunuch) was collected in the web of a subadult female, apparently mate-guarding her, which is a paradox also known from nephilids. However, despite the extreme sexual size dimorphism and apparent male-male antagonism in *Caerostris*, males do not appear to accumulate in female webs in large numbers, as is the case in some comparable orbweavers such as nephilids (Miller 2007; Kuntner et al. 2009b, c).

Other observations.—*Caerostris vicina* repeatedly reacted to Coddington's sound test by rapidly flexing their legs (South Africa). When a grasshopper was thrown in her web she bit it immediately, then held the prey in her chelicerae for a long time. Later she wrapped it slightly.

The egg sac architecture of *Caerostris* is unlike any other araneids, a dumbbell-shaped sac with ridged edges and one side of the sac attached to a leaf (Fig. 2J). The egg sac is placed away from the web, but close to the attachment of anchor threads to the substrate.

Conclusions.—Future work should aim to gain a clearer understanding of *Caerostris* diversity and biology for several reasons. First, it is critical to conserve these giant orbweavers and their habitat in the rapidly diminishing forests of Madagascar. Second, *Caerostris* appears to have evolved extraordinary silk, which allowed the spiders to conquer a unique ecological niche (Agnarsson et al. 2010). Third, an array of ecological interactions takes place in these fascinating spiders, including the newly discovered kleptoparasitic flies. Fourth, the genus may provide an interesting model for sexual selection studies, as *Caerostris* species seem to display a number of sexual behaviors very similar and potentially homologous to those in araneids and nephilids, such as mate guarding, male accumulation, male-male aggressiveness, male genital mutilation and mate plugging, and self castration (Kuntner et al. 2008a, 2009a–c). All these behaviors and sexual dimorphism observed in this enigmatic group makes them excellent models for future evolutionary studies, especially if such can be based on comprehensive biodiversity data, encompassing all known species in the group in a robust phylogenetic framework.

TAXONOMY

Family Araneidae

Genus *Caerostris* Thorell 1868 (Bark spiders)

Caerostris Thorell 1868; Simon 1895; Grasshoff 1984; Jaeger 2007; Platnick 2010; *Trichocaris* Simon 1895.

Type species.—*Epeira mitralis* Vinson 1863, designated by Thorell 1868:4.

Diagnosis.—Species of *Caerostris* of both sexes differ from other araneid spiders by the combination of the following morphologies: prosoma and opisthosoma wider than long, prosomal head region much elevated from the thoracic region, with one or two pairs of carapaceal projections, and with the median and lateral eyes grouped into separate elevations (Fig. 1C), the presence of a frontal rostrum (FigS. 1B, 2B), the presence of unpaired and/or paired projections on flattened opisthosoma (Figs. 1, 2), the flattened tibiae I, II, IV, and hairy legs with spatulate setae on femur IV (Grasshoff 1984:figs. 43–48). Female *Caerostris* epigynum is well sclerotized (Fig. 4E) and has conspicuous copulatory chambers and a pair of hooks (Fig. 6F). Male palpal subtegulum is of exaggerated proportions, the palp lacks paracymbium, and

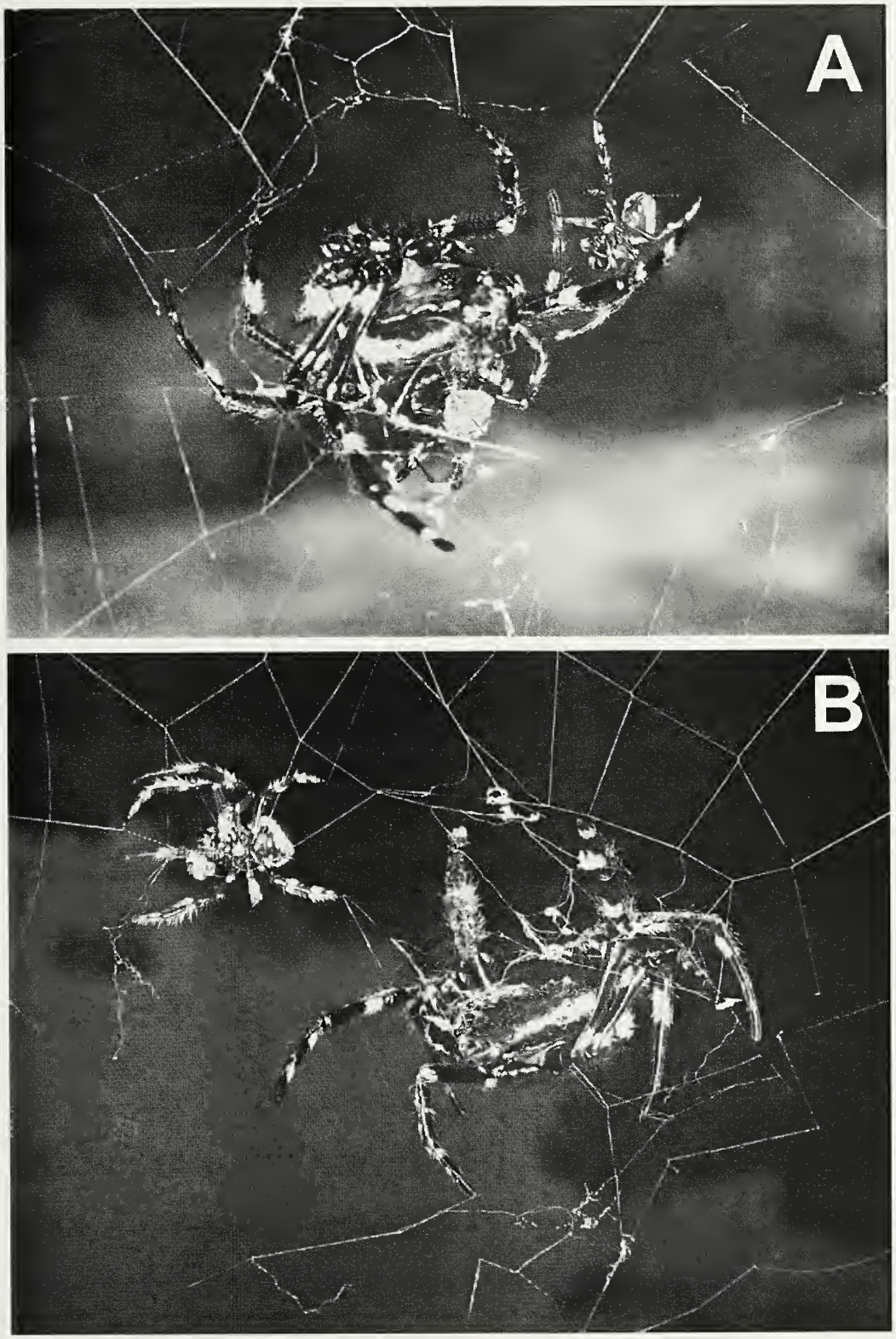

Figure 5.—Observations of *Caerostris darwini* n. sp. sexual behaviors, from Ranomafana: A. Single-palped male ("eunuch", below the female) and an intact intruder (to the right of the female) compete for a female at the hub of her web; B. The "eunuch" prevails, but fails to mate for the second time. See text for details.

has a fully enclosed embolus in a terminal sclerite (Fig. 6A–C) termed here the conductor (see Kuntner et al. 2008a).

Taxonomic history.—Thorell (1868) described the genus *Caerostris*. Simon (1895:831) erected the group Caerostreae within Argiopinae of the family Argiopidae, to include *Caerostris* and *Trichocaris* Simon 1895. Grasshoff (1984) considered *Trichocaris* a junior synonym of *Caerostris*, which he placed in the araneid subfamily Araneinae. However,

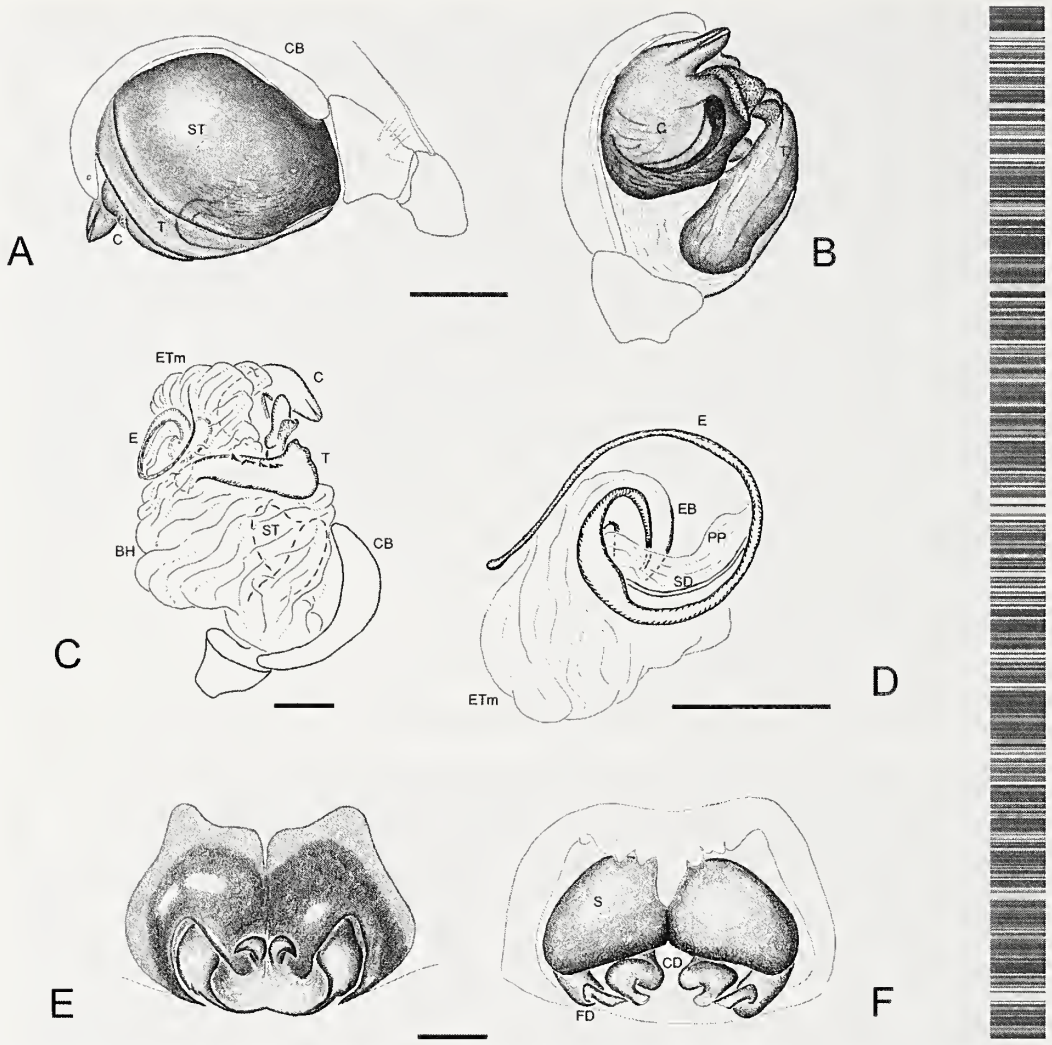

Figure 6.—*Caerostris darwini* n. sp.: A. Male left palp, retrolateral view; B. Same, ventral view; C. Male right palp, expanded; D. Detail of embolus showing pars pendula (PP); E. Female epigynum, ventral; F. Same, dorsal. Scale bars = 0.5 mm. CO1 barcode (female from Andasibe-Mantadia NP) provided on the side.

phylogenetic analyses based on morphological and behavioral characters place *Caerostris* into the 'argiopoid clade' (Scharff & Coddington 1997; Kuntner et al. 2008a). Aecording to Scharff & Coddington (1997), *Caerostris* and *Aspidolasius* Simon 1887 form a doublet within 'gasteracanthoids'. In order to establish a *Caerostris* ground plan, Scharff & Coddington (1997) examined *C. sexcuspidata* and *C. vicina* [=*C. vinsoni*], and Kuntner et al. (2008:fig. 16) examined *C. darwini* n. sp. Jaeger (2007) described the male of the SE Asian species, *C. sumatrana* Strand 1915, from Laos.

Caerostris darwini new species (Darwin's bark spider)
Figs. 2A–C, 3, 4A, D, E, 5, 6

Types.—Male holotype, male paratype, female paratype in National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), labeled: MADAGASCAR: Fianarantsoa Province, Ranomafana NP. Research station at Namorona River and surrounding forest, elev. 1000 m, 21°15′S, 47°25′E, 21–25.iv.2001. Agnarsson & Kuntner.

Etymology.—The species description was prepared on 24 November 2009, precisely the 150th anniversary of the publication of the first edition of Darwin's book *On the Origin of Species*. The species is thus named in honor of Charles R. Darwin, 200 years after his birth.

Diagnosis.—*Caerostris darwini* n. sp. somatic morphology resembles that of *C. vicina*, *C. sexcuspidata* and *C. extrusa*. However, female *C. darwini* n. sp. differ from all other Afrotropical *Caerostris* species by the well defined separate epigynal chambers and the pair of hooks positioned in the posterior part of the epigynal plate rather than anteriorly to medially (Fig. 6E, compare with Grasshoff 1984:figs. 16, 17, 19, 20, 23, 24, 26, 27, 29, 30, 31, 34, 37, 39). Male *C. darwini* n. sp. differ from all other Afrotropical *Caerostris* species by the massive conductor with a straight tip, by the relatively shorter pars pendula and relatively longer and spatulate embolus ending (Fig. 6A–D, compare with Grasshoff 1984:figs. 13, 14, 15, 22).

DNA barcode.—*Female from Andasibe-Mantadia NP:* TATATTTTATTTTCGGAATTTGAGCAGGAATAGTTGGCTCATCTTTAAGAATAATTATTCGAACAGAATTAGGAATACCAGGCTCTTTAATCGGAAATGATCAAATTTTTAATGTAATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGGGGATTCGGAAACTGACTTGTACCCCTTATACTGGGGGCCCCAG-

ATATAGCATTCCCTCGAATAAATAACATAAGATTTT-GACTACTCCCACCATCCCTTTCCCTACTTACTATAAG-AAGAATTGTAGAAAATGGAGCAGGCACTGGTTGAA-CTGTTTATCCCCCCCTATCCTCAAATATCGGACACGC-TGGTAGATCAGTAGACTTAACTATTTTCTCCCTTCAT-CTTGCAGGAATTTCTTCAATTTTAGGGGCTATCAATT-TTATCACAACAGTAATCAATATACGTTCAAAGGGAA-TATCACTAGACCAAATACCTTTATTTGTATGATCAGT-TGTAATTACAGCTTTACTTCTTTTACTTTCTCTACCT-GTTTTAGCAGGTGCTATCACAATACTACTAACTGAC-CGAAATCTAAATACCTCTTTTTTTGACCCAGCAGGA-GGGGGCGACCCCATTTTATACCAACATTTA

Description.—*Female (paratype):* Base color black (live) to red-brown (in ethanol), but prosoma, opisthosoma and appendages in live spider partly white due to setae color (Fig. 2A). Total length 17.9. Prosoma 6.2 long, 8.6 wide. Sternum 3.7 long, 3.9 wide, widest between second leg coxae, with paired tubercles between all leg coxae, black with a white center (Fig. 4E; but, this not visible in ethanol). AME diameter 0.28, PME 0.28, AME separation 0.42, PME separation 0.91, PME–PLE separation 2.47, ALE–PLE separation 0.54. Leg I length 34.9 (femur 9.8, patella 5.2, tibia 7.9, metatarsus 9.1, tarsus 2.9). Opisthosoma 12.8 long, 14.5 wide. Dorsum with paired lateral and caudal humps (Fig. 2A). Epigynum as diagnosed (Fig. 6E, F), spermathecae juxtaposed, spermathecae and ducts heavily sclerotized, frontal inner wall denticulated (Fig. 6F).

Male (paratype): Base color red and light brown (live and in ethanol), but prosoma, opisthosoma and distal parts of appendages in live spider whitish due to setae color, and femora strikingly red and glabrous (Fig. 2B, C). Total length 5.7. Prosoma 3.0 long, 3.1 wide. Sternum 1.3 long, 1.4 wide; unicolor red, without conspicuous humps. AME diameter 0.22, PME 0.17, AME separation 0.18, PME separation 0.59, PME–PLE separation 0.86, ALE–PLE separation 0.07. Leg I length 15.0 (femur 4.1, patella 2.0, tibia 3.6, metatarsus 4.1, tarsus 1.2). Opisthosoma 3.3 long, 4.3 wide. Dorsal paired humps inconspicuous, but unpaired frontal hump present. Pedipalp as diagnosed, with extensive membranes between the sclerites, a denticulated tegulum and long embolus with spatulate ending (Fig. 6A–D).

Variation.—*Female:* Prosoma length 6.2–6.7; total length 17.9–22.0. *Male:* Prosoma length 2.7–3.0; total length 5.7–6.1.

Additional material examined.—Numerous males and females to be deposited in USNM from the type locality and the following, all collected by I. Agnarsson and M. Kuntner: MADAGASCAR: *Toamasina Prov.*, Andasibe-Mantadia NP, Tsakoka. Montane rain forest, at or above river, elev. 952 m, S18°47′54″, E48°25′34″, 30 March and 24 April 2008; Andasibe-Mantadia NP, Mantadia. Montane rain forest edge, at or above stream, elev. 952 m, S18°51′18″, E48°25′42″, 30 March and 24 April 2008; Andasibe-Mantadia NP, Périnet Spec. Res., Montane rain forest streams and rivers, elev. 900–1000 m, S18°56′10″, E48°25′11″, 29 March–23 April 2008.

Natural history.—The species inhabits montane rainforests and their edges in eastern Madagascar, where they construct their webs over water (small streams to medium sized rivers, even lakes). See Results for details.

Distribution.—Eastern Madagascar, currently known from Ranomafana NP and Andasibe-Mantadia NP.

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SHORT COMMUNICATION

On the taxonomy of Trechaleidae (Araneae: Lycosoidea) from South America

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Abstract. A new species of *Trechalea* Thorell 1869, *T. rothi* from Colombia, South America, is described, illustrated and compared with the only other two species of the genus also known from Colombia, *T. longitaris* (C.L. Koch 1848) and *T. lonalinda* Carico 1993. Additionally, it is compared with the similar speeies, *T. trinidadensis* Carico 1993. A single female from Pará, Brazil, is also described and illustrated as a new species, *Enna xingu*, based on features of the genitalia.

Keywords: Taxonomy, morphology, new species, Neotropical region

The genus *Trechalea* Thorell 1869 was revised by Carico (1993), who redescribed seven species and described three new species. This genus occurs from the southern USA to southern Brazil (Platnick 2009). Representatives of *Trechalea* can be distinguished from *Syntrechalea* F.O. Pickard-Cambridge 1902 and *Hesydrus* Simon 1898 by having only the tarsi flexible; the latter two genera present both flexible tarsi and metatarsi. *Trechalea* can also be separated from the other two genera by the male palpal bulb; median apophysis with acute, conspicuous guide; ventral division variable but thickened, tibial retrolateral apophysis divided with ental division distinct, often lobed and partly surrounded by ventral-cymbium tibial membrane, ectal division conspicuous and in various forms. Female epigynal plate with middle field about as wide as long or only slightly longer than wide, usually widest anteriorlly.

The single female specimen that is the subject of this paper was found in a collection of unidentified material borrowed from the California Academy of Sciences, San Francisco, California. In a recent revision of the genus (Carico 1993), the total number of species in this mostly Neotropical genus was determined to be eleven, and that number remains to date (Platnick 2009). With the new species described herein, the total number rises to twelve.

The genus *Enna* was recently revised by Silva et al. (2008), and this genus is now considered the most diverse in the family Trechaleidae, with 24 known species occurring from Mexico to southern Brazil (Platnick 2009). Most of the species occur in Central America.

The representatives of *Enna* resemble *Dossenus* Simon 1898 by the shape of the dorsal division of the median apophysis (Silva et al. 2007, fig. 5), which is concave and ends in an acute guide, and by the tarsi and metatarsi, which are short and straight when compared to the long and flexible tarsi of *Trechalea* Thorell 1869 and *Trechaleoides* Carico 2005. The middle field of the female epigynum is conspicuous, hood-like, concave beneath, and comprises part of the dorsal rim of the epigastric furrow (Silva et al. 2008).

A female spider of the genus *Enna* was found in a shipment of unidentified pisaurids and trechaleids from the National Museum of Natural History, Washington, D.C., and is here described as a new species. This new species further illustrates the unique biogeographic pattern of the genus that is presented in the generic revision of this Neotropical genus (Silva et al. 2008). Specifically, the numerous members of the genus tend to be found with limited distributions in very scattered localities ranging from southern Mexico to Bolivia.

[1] Deceased 24 March 2009

The objective of this work is to describe and illustrate a new species of *Trechalea* from Colombia and a new species of *Enna* from northern Brazil.

METHODS

The material examined is deposited in California Academy of Sciences, San Francisco (CAS: C. Griswold) and National Museum of Natural History, Washington, D.C. (USNM: J.A. Coddington). The nomenclature of the female epigynal structures follow Carico (1993) and Silva et al. (2008). To study the excised epigyna, the soft tissue was removed by a combination of dissection with a small surgical blade and immersion in the enzyme trypsin for 48 h at 25° C to remove the soft tissue. All the measurements are in mm. The abbreviations relate to eye measurements, including diameter, interdistances and median ocular quadrangle, following Carico (1993) and Silva et al. (2008).

Family Trechaleidae Simon 1890
Subfamily Trechaleinae Simon 1890
Genus *Trechalea* Thorell 1869

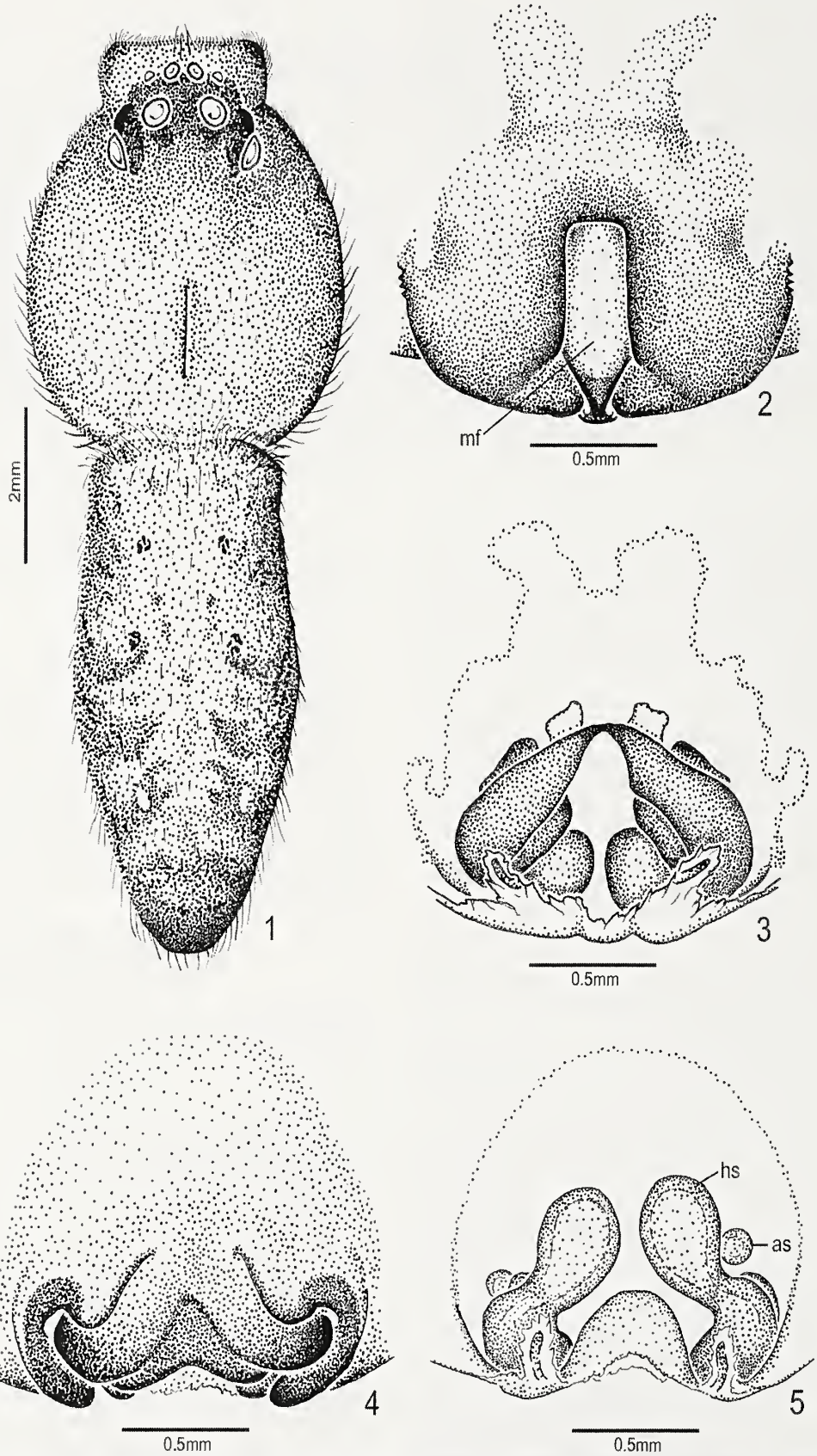
Type species.—*Triclaria longitarsis* C.L. Koch 1848, original designation.

Trechalea rothi new species
Figs. 1–3

Type specimen.—Holotype female, COLOMBIA: *Meta*: Puerto Lleras (72°22′W, 03°18′N), March 1994, B.T. Carroll, V. & B. Roth leg. (CAS).

Etymology.—The species name is in honor of a collector of the specimen, Vincent D. Roth, for his many contributions to Arachnology.

Diagnosis.—This species differs from other Colombian species by the following characters: *Trechalea longitarsis* (C.L. Koch 1848) has a higher number of tibial ventral macrosetae pairs (I-4, II-4, III-3, IV-3), light submarginal carapace bands, unmarked legs, and an epigynum whose middle field is wider anteriorly. *Trechalea lonalinda* Carico 1993 has the middle field of the epigynum triangular and internally the accessory spermathecae is more slender and not dark in color. *T. rothi* resembles most closely the female of *T. trinidadensis* Carico 1993, but the latter has 5, 5, 3, 3 tibial ventral macrosetae pairs versus 4, 4, 3, 3 for *T. rothi*, a different abdominal dorsal pattern, and an epigynum with a significantly wider middle field. *T. trinidadensis* is currently known only from Trinidad (Carico 1993) and Rio Solimões, Amazonas, Brazil (Carico 2008).



Figures 1–5.—Two new trechalid spiders. 1–3. *Trechalea rothi* new species: 1. Dorsal pattern of female; 2. Epigynum, ventral view; 3. Epigynum, dorsal view. 4, 5. Epigynum of *Enna xingu* new species: 4. Ventral view; 5. Dorsal view. Abbreviations: as = accessory spermathecae; hs = head of spermathecae; mf = middle field.

Description.—*Female (holotype):* Carapace (Fig. 1) low, cephalic area not elevated, length 5.3, width 5.2, light brown with indistinct pattern, narrow dark marginal band, dark in eye region. Sternum light, unmarked, length 2.8, width 2.6; labium dark brown, lighter at anterior margin, length 1.16, width 1.00. Clypeus height 1.20, width 2.56. Anterior eye row straight, a cluster of strong setae posterior to each PLE, measurements: AE 2.60, PE 5.20, OQA 1.60, OQP 2.72, OQH 2.24, PLE 1.16, PME 1.16, ALE 0.36, AME 0.64, PLE–PME 0.92, PME–PME 0.68, ALE–AME 0.12, AME–AME 0.32. Chelicerae face dark brown, darker distally, clothed in long light hairs, three prolateral teeth, equidistant, middle largest; three prolateral teeth, equal size, distal two closer. Leg segment lengths: femur, patella-tibia, metatarsus, tarsus, total: I – 7.9, 10.3, 6.2, 3.8, 28.2; II – 8.3, 10.1, 6.9, 4.2, 29.5; III – 7.1, 8.0, 6.3, 4.1, 25.5; IV – 9.4, 10.6, 9.6, 5.5, 35.1; tibial ventral maerosetae pairs: I- 4, II- 4, III-3, IV-3. Color of legs light, darker above with irregular maculae. Abdomen (Fig. 1) length 6.8, dorsally with three pairs of distinct dark spots amid other irregular markings, long setae at anterior edge and laterally at the outer edge, light ventrally. Epigynum middle field about twice as long as wide, straight sides, white but black at posterior tip (Fig. 2); internal structures heavily sclerotized and dark, accessory spermathecae large, conspicuous, positioned diagonally, with head of spermathecae (*hs*) small, lying upon anterior surface of the later (Fig. 3).

Male.—Unknown.

Natural history.—Unknown.

Distribution.—Known only from the type locality.

Note.—This specimen was collected with a female of *Trechalea lomalinda* Carico 1993.

Genus *Enna* O. Pickard-Cambridge 1897

Type species.—*Enna velox* O. Pickard-Cambridge 1897, by original designation.

Enna xingu new species
Figs. 4, 5

Material examined.—Holotype female: BRAZIL: *Pará*: ca 60 km S. Altamira, Rio Xingu Camp, (52°22′W, 03°39′S), 1–7 Oct. 1986, P. Spangler & O. Flint leg. (USNM 2048172).

Etymology.—The name is a noun in apposition derived from the name of the type locality.

Diagnosis.—This species is distinguished by details of the genitalia, specifically by the width and indented margin of the posterior part of the middle field of the epigynum and the rim of the posterior concavity beneath the hood-like middle field is almost circular in posterior view (Figs. 4, 5).

Description.—*Female (holotype):* Carapace (crushed, dimensions estimated) length 4.3±, width 3.0±. Sternum length 1.64, width 1.80, light, unmarked; labium length 0.76, width 0.72, dark brown, lighter distally. Clypeus height 0.32, width 1.92. Carapace light, dark in ocular area. Anterior eye row straight. Eye measurements: AE 0.96, PE 1.84, OQA 0.58, OQP 1.00, OQH 0.65, PLE 0.33, PME 0.30, ALE 0.18, AME 0.22, PLE–PME 0.32, PME–PME 0.48, ALE–AME 0.05, AME–AME 0.17. Chelicerae medium brown, becoming gradually lighter distally; cheliceral teeth: promarginal 3, middle largest, remainder subequal; retromarginal 3, subequal, equidistant. Color of legs light with indistinct, faint pattern on dorsal side of femora and tibiae. Leg segment lengths: I – femur 4.4, patella-tibia 5.9, metatarsus 4.1, tarsus 1.9, total 16.3; II – 4.3, 5.5, 3.8, 1.7, 15.3; III – 3.5, 4.1, 3.0, 1.3, 11.9; IV – 4.3, 5.1, 4.9, 1.9, 16.2; total leg length sequence: I- III- II- IV; ventral macrosetae pairs on tibiae: I-4, II-4, III-3, IV-3. Abdomen length 4.5; light background color; dorsum mostly with small, scattered, dark maculae, but with a pair of large maculae centrally; sides with parallel dark lines; venter dusky. Middle field (*inf*) of epigynum much wider than long, incurved and very dark at posterior margin (Fig. 4); head of spermathecae (*hs*) large, dorsal, conspicuous, and mostly obscuring the small accessory spermathecae (*as*) from dorsal view (Fig. 4).

Male.—Unknown.

Natural history.—Unknown.

Distribution.—Known only from the type locality.

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SHORT COMMUNICATION

Sexual behavior of *Bothriurus buecherli* (Scorpiones: Bothriuridae) and comparison with the *B. prospicuus* group

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Abstract. This paper describes the sexual behavior of *Bothriurus buecherli* San Martín 1963 and compares it with the rest of the *B. prospicuus* group. The mating behavior was very similar to other species of the group, but *B. buecherli* presented some differences in the initial stages, one being a long period of inactivity after the male grasps the female pedipalps. Information presented includes reference to the sexual sting, post-partum copulation, and an analysis of a case of cannibalism by the female.

Keywords: Scorpions, sexual sting, *prospicuus* group, Uruguay

Scorpions exhibit a complex and ritualized sexual behavior during which sperm transfer occurs indirectly through a sclerotized spermatophore (Polis & Sissom 1990). However, our knowledge of sexual behavior is very limited. In-depth studies have only been published for thirty species of seven families (Polis & Sissom 1990; Tallarovic et al. 2000). Within the Bothriuridae, published documentation exists for five genera of 176 know so far (Fet et al 2000): *Bothriurus* Peters 1861; *Brachistosternus* Pocock 1893; *Timogenes* Simon 1880 (Peretti 1995a, 1995b, 1996); *Urophonius* Pocock 1893 (Maury 1968) and *Thestylus* Simon 1880 (Machado & Vasconcellos-Neto 2000). In the current note, I describe the sexual behavior of *Bothriurus buecherli* San Martín 1963, a small bothriurid in the *B. prospicuus* group endemic to Uruguay.

Bothriurus buecherli is distributed along the highland areas of Southeast Uruguay in the Departments of Montevideo, Canelones, Maldonado, Rocha, and Lavalleja (San Martín 1963; Toscano-Gadea 2002). The *B. prospicuus* group includes four other species endemic to the Republic of Argentina: *B. cordubensis* Acosta 1995, *B. paupa* Ojanguren-Affilastro 2002, *B. noa* Maury 1984, and *B. prospicuus* Mello-Leitão 1932 (Ojanguren-Affilastro 2002).

I collected adult *B. buecherli* under stones at Piedras de Afilar (31°24′42.7″S, 55°33′10.6″W) in the Department of Canelones, Uruguay from December to April in 2006, 2007, and 2008. Voucher specimens were placed in the Entomology collection of the Facultad de Ciencias, Montevideo, Uruguay. In the laboratory, I kept them individually in petri dishes (9 cm diameter × 1.5 cm high), with soil as substrate and cotton absorbed in water. I fed them larvae of *Tenebrio molitor* (Coleoptera: Tenebrionidae) ad libitum. I made observations from January to May in 2006 (n = 3), 2007 (n = 1), and 2008 (n = 3) at an average temperature of 19.5° C (range = 14.5–26° C). The females were used only once. I used glass containers of 19 cm diameter and 10 cm height as arenas for these observations, with soil and sand as substrate and some stones for shelter. I carried out the observations at night (after 19:00 h) under red light (40 watts) located 30 cm from the container, which does not alter the behavior of the animals (Peretti 1993).

I placed the females in the arena 24–48 h before the observations and the males immediately before initiating the observations, introducing them extremely carefully and far from the female. For the identification of the behavioral units, I followed the methods and terminology of Polis & Sissom (1990), Benton (1992, 2001), Peretti et al. (2000) and Peretti & Carrera (2005). I recorded the trials with a SONY DCR-SR40 digital video camera, equipped with night shot, registering the beginning and end of each behavioral unit. Also, I estimated the time required by males to regenerate the hemispermatophores and by females to accept mating after leaving their offspring. Likewise, I analyzed two naturally interrupted courtships during the Promenade phase, as well as one case of cannibalism by a female.

Sexual behavior.—In total, I analyzed seven mating sequences (five with sperm transfer) and recognized 26 behavioral units (Fig. 1). A description and the duration (mean ± SD) of the most relevant units are shown in Table 1.

The Introductory phase began when the male grasped the female by any part of the body, depending on how he found her at the beginning. Afterward, the male holding different part of the female's body (*reorientation* unit), tried to reach the pedipalps (*pedipalp grip* unit). During the entire process, the female maintained the *submissive female* unit with the pedipalps next to the body, the metasoma supported completely on the mesosoma, and the legs withdrawn towards the body. The duration of this phase averaged 1.52 ± 0.88 min (range = 1–3.5).

The mating dance or "*promenade a deux*" is carried out during the Promenade phase. The total duration of this phase averaged 129.5 ± 98.8 min (range = 85–371). The couple passed through the *pause* unit, remaining motionless (while still in *pedipalp grip*) from 4 to 28 min, representing from 4% to 12% of the total mating time. During this phase, the male performed *sexual sting*, the unit where he introduced the sting almost completely into the female's body. Although this behavior can be very intense, emission of hemolymph was not observed at the site either when the *sting* occurred during the experience or afterward when analyzed with a stereoscopic magnifying glass. In three cases, the male introduced the aculeus almost completely into the pleura of the prosoma (between the coxae of the legs II and III) of the female and in the remaining four cases, the male pierced the female between the pedipalps and legs I, near the lateral eyes (Fig. 2). In all the cases, the female stayed next to the male with no evident resistance.

During the spermatophore deposition phase, the couple stopped their movements, and the male carried out the *spermatophore deposition* unit. The average duration of this phase was 14.3 ± 6.6 min (range = 9.3–260). In two cases, the transference did not occur: in one of them the couple carried out the *telson rubbing* unit until they separated, while in the other case, the male tried to repeat the *sexual sting* unit close to the lateral eyes but without achieving it. In this case, the female tried to sting the male near the chelicerae (*female sting*). No females were observed eating the spermatophore upon finalizing this phase.

Cannibalism.—During one experience carried out 22 January 2008, a male and a female captured individually 72 h before, faced one

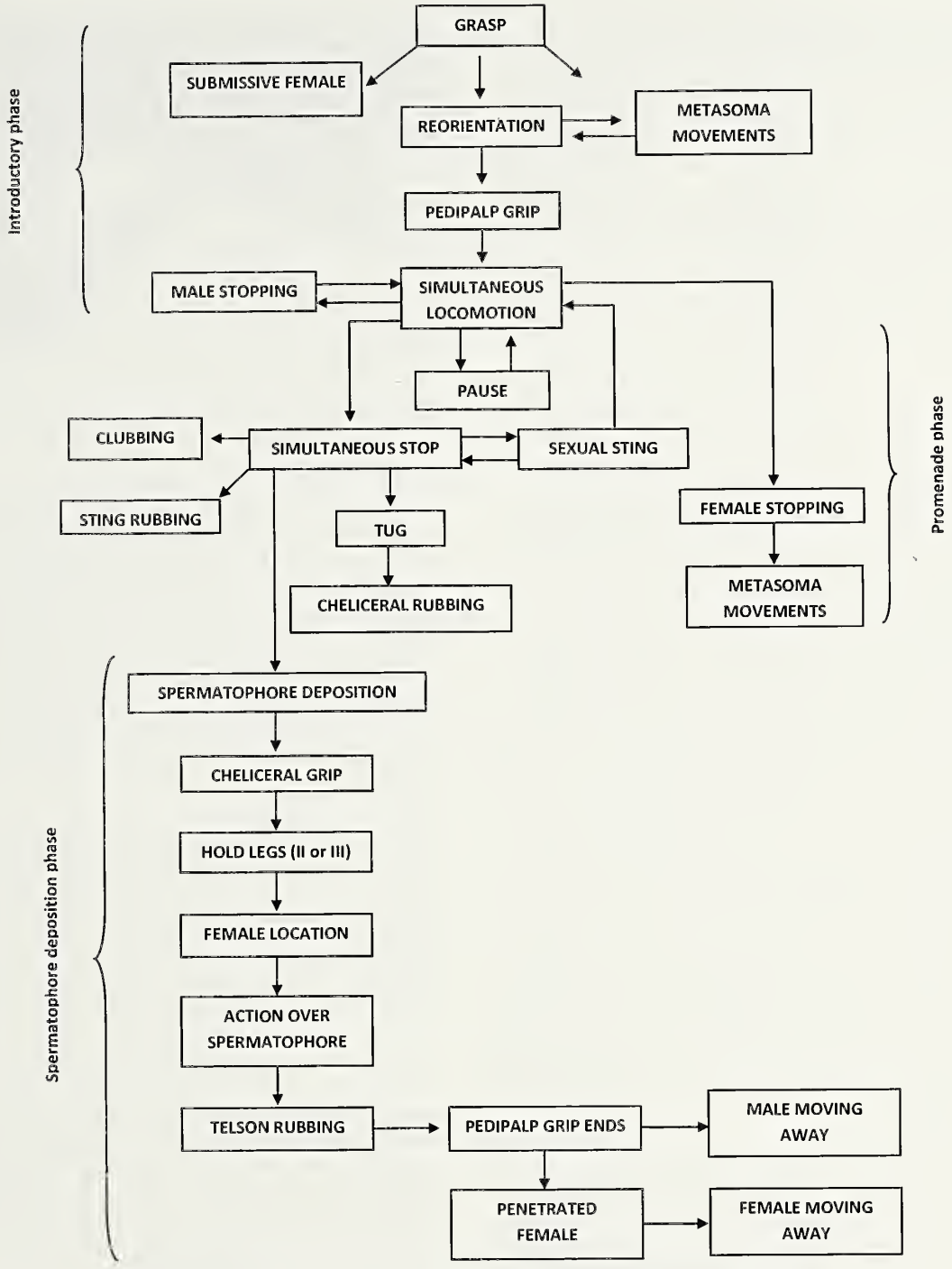

Figure 1.—Schematic diagram of the sexual behavior of *Bothriurus buecherli*.

another. After touching the female two times, the male held the female's right pedipalp. The female held the male's left pedipalp, elevated its mesosoma, and stung the male on its right side, near leg IV. The male tried to sting the female, without success. The female withdrew its stinger 20 min after, grasped the male with its chelicerae, and dragged it under a stone, beginning to eat him, beginning with the right pedipalp. The female exhibited no confrontation or aggressive behavior before or during the interaction. I removed the remainder of the male to evaluate the presence of hemispermatophores. Twenty-four h later, the female was fixed and examined, and a transparent gelatinous substance was found in the genital atrium.

Birth period-new matings.—Since the females live beyond one reproductive period, at least in laboratory conditions (Toscano-Gadea, pers. obs.), I was able to use two females captured in the field in 2007, which had descendants in the laboratory, in January 2008. In one case, the female copulated 54 days after having offspring and in the remaining case, after 48 days.

The mating behavior of *B. buecherli* exhibited similarities to the rest of the species of the *prospicuus* group. Almost all of the behavior units detailed by Peretti et al. (2000) were found, although I observed some differences. The total duration of mating time for *B. buecherli* was greater than that published for other species of this group. This

Table 1.—Average (± SD) duration of the most relevant behavioral units present during mating in *B. buecherli*.

Behavioral unit	Phase	Duration
Reorientation	Introductory	68.8 ± 24.6 s
Pause	Promenade	11.6 ± 8.14 min
Graze with chelicerae	Promenade	1.27 ± 0.11 min
Sexual sting	Promenade	35.2 ± 68.2 min
Spermatophore deposition	Spermatophore deposition	1.4 ± 0.10 min
Action over spermatophore	Spermatophore deposition	44.2 ± 6.02 s
Penetrated female	Spermatophore deposition	28.4 ± 3.6 s
Telson rubbing	Spermatophore deposition	22.9 ± 12.3 s

difference was primarily due to the time taken up by the units *simultaneous locomotion*, *pause*, and *sexual sting*. The unit *sinultaneous locomotion* (together with *simultaneous stop*) is hypothesized to reflect the degree of sexual excitation (Peretti et al. 2000). In *B. buecherli*, the duration of this unit varied between 1.51 and 3.33 min, whereas in the other species of the group, it did not surpass 1 min (Peretti et al. 2000).

The extended *pause* unit observed in the *B. buecherli* couples has not been described for any of the species of the *prospicuus* group. This unit could be related to *pedipalp grip* and the mutual recognition of the couple. Peretti (1995b) indicates that males of *Bothriurus bonariensis* and *Timogenes elegans* (Bothriuridae) are able to stay motionless and carry out the unit *pedipalp grip* for several minutes even though the female is dead. According to this author, *B. buecherli* could possibly perform this unit by means of sexual recognition through a chemical channel or by means of recognizing the shape of the female's pedipalp. Although I tried not to interfere with the behavior of the scorpions in these experiments, it is possible that the duration of this behavior was altered by the laboratory conditions.

The occurrence of "*sexual sting*" during the Promenade phase correlates with observations in *B. cordubensis* and *B. noa*; the site where the *sexual sting* unit occurs is similar to the one observed in *B. noa*. The duration of this unit in *B. buecherli* (35.2 min) is noticeably greater than that observed in the rest of the *prospicuus* species (range = 77–142 s according to Peretti et al. 2000). Unlike the injuries noted by Francke (1979), hemolymph was never observed after the termination of this unit.

I observed no malformations of the spermatophores from the two experiments in which sperm transfer was not achieved; these spermatophores were similar to the ones described by San Martin & Gambardella (1967). Alexander (1957); Peretti (1996) and Tallarovic et al. (2000) indicate that unsuccessful mating sequences are frequent in scorpions either due to the male's inability to locate the spermatophore correctly or due to the female's resistance. In both cases, no female resistance was detected.

If the period of latency between the birth and new mating sequences of *B. buecherli* females (48–54 days) observed in the laboratory is comparable to that in natural conditions, the number of matings during the same reproductive period could be between three and four, similar to what Castelvetri & Peretti (1999) observed in *B. bonariensis*. This number of matings suggests the existence of strong sperm competition between the males. It would be necessary to carry out new experiments at different time intervals to determine the precise moment at which the female becomes receptive.

Castelvetri & Peretti (1999) and Peretti (2001) indicate that at the beginning of every reproductive season, adult females can present different degrees of sexual receptivity: positive, intermediate, and negative. The female *B. buecherli* that attacked and killed the male did not present the unit *submissive female*, suggesting negative receptivity (common after several inseminations or when the female is gestating). Analysis of the female genitalia revealed a slimy and transparent substance that could be a membranous genital plug similar to that of *B. flavidus* (Mattoni & Peretti 2004). Nevertheless, Castelvetri & Peretti (1999) and Contreras-Garduño et al. (2005) indicate that the presence of a genital plug does not prevent the females from accepting a new mate. Considering that this attack happened before the male started the courtship, this could be a case of an antagonistic sting, when the female is not receptive and tries to kill the male to obtain food. Also, considering the reduced size of the containers used, we cannot dismiss the possibility that this behavior results from laboratory conditions.

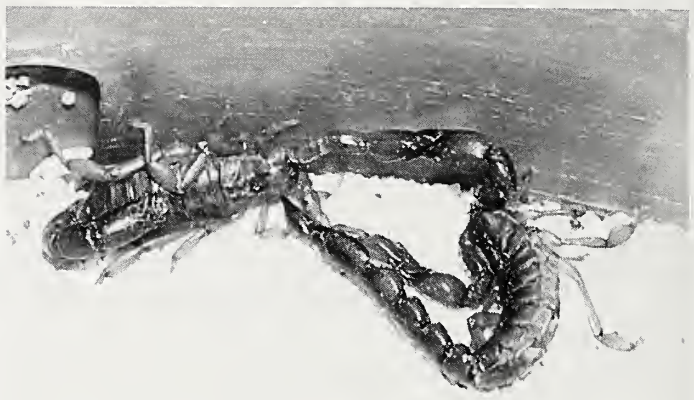

Figure 2.—Detail of the sexual sting unit in *B. buecherli*. (Photo C.A. Toscano-Gadea).

The sexual behavior observed in *B. buecherli* is similar to that described in other species of the *prospicuus* group. Considering both allopatry and the morphological and behavioral similarities of *B. buecherli* to the other species of the group, it would be interesting to attempt interspecies matings between them, following previous analyses by Peretti et al. (2000). Furthermore, new experiments testing possible causes for the long sexual sting under male coercion or female choice hypotheses would further enlighten researchers about the sexual tactics used by these fascinating scorpions.

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SHORT COMMUNICATION

Loxosceles chapadensis (Araneae: Sicariidae): a new recluse spider species of the *gaucho* group from Brazil

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Abstract. A new species of the medically important recluse spider genus *Loxosceles* Heinecken & Lowe 1832 is described from the State of Bahia, Brazil. The species occurs between rocks and crevices, as well as in and around man-made structures. The new species belongs to the *gaucho* group, as evidenced by the spermathecal shape and color pattern. The presence of a long male palpal tibia is unusual in the *gaucho* group; thus, the inclusion of the new species in this group is discussed.

Keywords: Chapada Diamantina, Bahia, spider of medical importance, taxonomy

The recluse spiders of the genus *Loxosceles* Heineken & Lowe 1832 comprise a large group, with more than one hundred known species so far recorded in temperate and tropical areas of various continents (Platnick 2009), the majority in North and South Ameriea (Gertsch 1958, 1967; Gertsch & Ennik 1983). These spiders live in different natural habitats and near or inside houses and buildings. In natural conditions they may live under rocks, tree trunks, in tree holes and other natural openings (Gertsch 1967).

Despite being a taxon of medical importance, with thousands of spider bites recorded yearly, especially in Southern Brazil (Ribeiro et al. 1993; Marques-da-Silva et al. 2005), the genus has received little taxonomic attention in the last decades. Since Gertsch & Ennik's (1983) revision, taxonomic publications have been limited to a few redescriptions and four species descriptions-two from China (Wang 1994), one from Brazil (Martins et al. 2002) and another from Tunisia (Ribera & Planas 2009).

To date, 10 species of *Loxosceles* occurring in Brazil can be divided in four groups according to Gertsch's revision (1967): *Loxosceles adelaida* Gertsch 1967, *Loxosceles gaucho* Gertsch 1967 and *Loxosceles similis* Moenkhaus 1898 (in *gaucho* group); *Loxosceles amazonica* Gertsch 1967 (in *amazonica* group); *Loxosceles anomala* (Mello-Leitão 1917), *Loxosceles hirsuta* Mello-Leitão 1931, *Loxosceles intermedia* Mello-Leitão 1934 (in *spadicea* group); and *Loxosceles laeta* (Nicolet 1849) and *Loxoesceles puortoi* Martins et al. 2002 (in *laeta* group). *Loxosceles immodesta* (Mello-Leitão 1917) was poorly described and the type could not be located. Therefore, it cannot be placed in any group. Here we describe a new species of *Loxosceles* belonging to the *gaucho* group, from Northeastern Brazil.

METHODS

Abbreviations.—ALE = anterior lateral eyes; PLE = posterior lateral eyes, PME = posterior mcdian eyes; MNRJ = Museu Nacional do Rio de Janeiro, Rio de Janciro.

The illustrations were done using a Nikon SMZ1500 dissecting microscope with a camera lucida attachment. Measurements are in mm. The species description format follows Martins et al. (2002); terminology of genitalia mostly follows Gertsch (1967). All the examined specimens are deposited in MNRJ.

TAXONOMY

Loxosceles Heinecken & Lowe 1832

Loxosceles chapadensis sp. nov.

Figs. 1–12

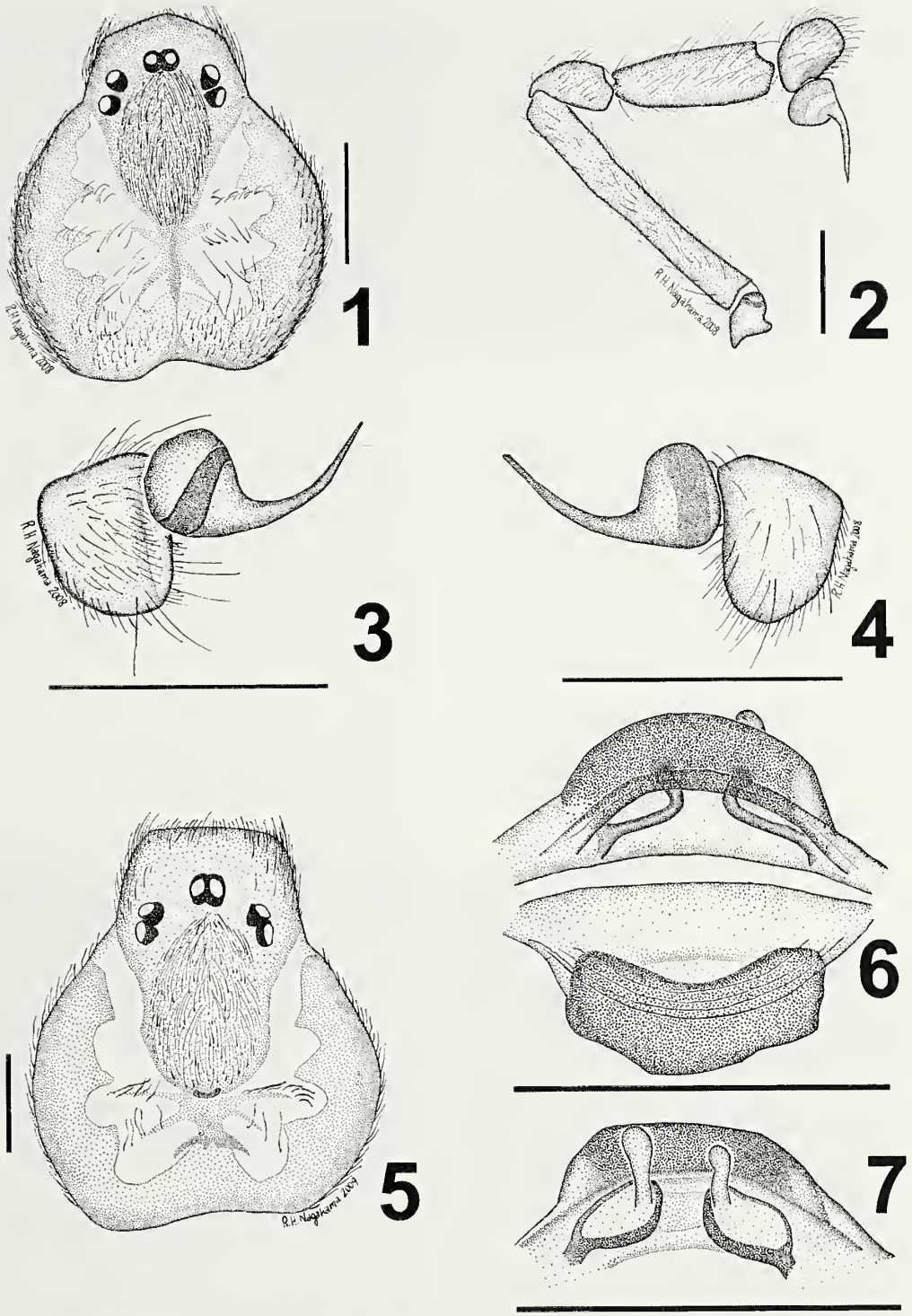
Etymology.—The specific name refers to the type locality of the species, the Parque Nacional da Chapada Diamantina, State of Bahia, Brazil.

Diagnosis.—The male can be readily distinguished from other species by a palpal tibia 2.2 times longer than the cymbium and a thickened embolus (Fig. 2). The female can be recognized by its broad transversal plate, straight, apically enlarged seminal receptacles and dorsal part of the bursa copulatrix strongly sclerotized for half of its length (Fig. 6).

Type material.—*Holotype:* BRAZIL: *Bahia*, male, Palmeiras, Parque Nacional da Chapada Diamantina (11°28′S, 41°25′W), 15 February 2008, R. Bertani, C.S. Fukushima & R.H. Nagahama, (MNRJ 6047).

Paratypes: BRAZIL: *Bahia*, 1 female, same locality and collectors of holotype (MNRJ 6048); Lençóis, 3 females, 1 male, Parque Nacional da Chapada Diamantina (12°33′S, 41°23′W), 19 February 2008, same collectors, (MNRJ 6049); Iraquara, 1 female, Fazenda Pratinha (12°21′1.13″S, 41°32′4.82″W), 16 February 2008, same collectors, (MNRJ 6050).

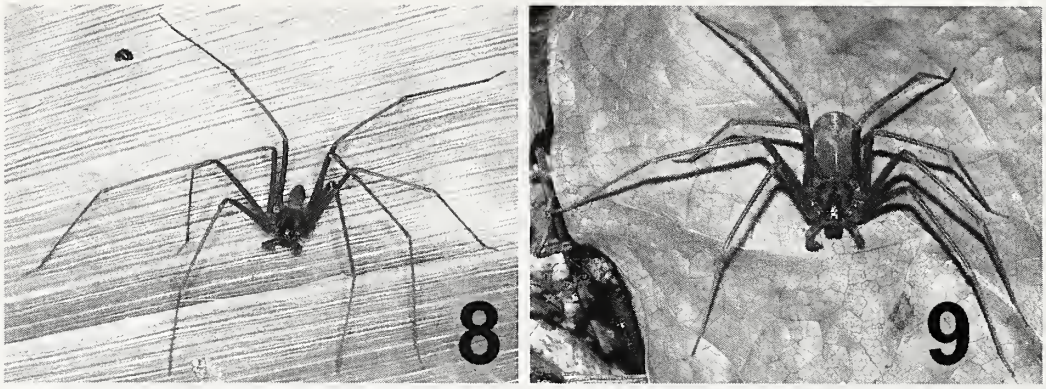
Description.—*Male (Holotype, MNRJ 6047):* Total length 5.60. Carapace 3.49 long, 2.97 wide. Eye sizes and interdistances: ALE 0.17, PME 0.12, PLE 0.15, PME–PLE 0.41, PME–ALE 0.21; clypeus 0.31. Leg formula II, IV, I, III. Leg lengths: leg I: femur 6.61/ patella 1.07/ tibia 8.04/ metatarsus 7.94/ tarsus 1.61/ total 25.27, II: 8.27/ 1.28/ 9.63/ 10.78/ 1.88/ 31.84, III: 6.47/ 1.09/ 6.52/ 7.56/ 1.64/ 23.28, IV: 7.63/ 1.15/ 7.70/ 8.92/ 1.83/ 27.23. Palp: femur 2.41 long, 0.37 wide; patella 0.75 long, 0.46 wide; tibia 1.45 long, 0.48 wide; cymbium 0.66 long, 0.49 wide. Labium 0.79 long, 0.47 wide. Sternum 1.67 long, 1.35



Figures 1–7.—*Loxosceles chapadensis* sp. nov. 1–4. Holotype male: 1. Carapace; 2. left palp; 3. Bulb, prolateral view; 4. Bulb, retrolateral view. 5–7. Paratype female: 5. Carapace; 6. Spermathecae, dorsal view; 7. Spermathecae, ventral view. Scale bars = 1 mm.

wide. Femur I 1.9 times longer than carapace. Palpal femur 6.5 times longer than wide, tibia 3 times longer than wide, cymbium slightly elongated (Fig. 2). Bulb suboval and shorter than cymbium. Embolous slightly curved, approximately two times longer than bulb width, without carina (Figs. 3, 4). Cephalic region of carapace covered by many long setae (Fig. 1). Presence of dentate, dark side bands on the dorsal carapace (Figs. 1, 8). Pars thoracica pale yellow. Legs and palps light brown, covered by short grayish setae on the femora and patellae, becoming gradually brownish from the tibiae to the tarsi (Fig. 8). Endites, coxae and sternum light brown. Labium dark brown.

Female (Paratype, MNRJ 6048): As in male, except Total length 8.76. Carapace 4.02 long, 3.81 wide. Eye sizes and interdistances: ALE 0.16, PME 0.13, PLE 0.15, PME–PLE 0.46, PME–ALE 0.26; clypeus 0.45. Leg formula II, I, IV, III. Leg lengths: leg I: femur 7.27/ patella 1.46/ tibia 8.47/ metatarsus 7.73/ tarsus 2.07/ total 27.00, II: 8.58/ 1.47/ 10.03/ 9.34/ 1.91/ 31.33, III: 7.11/ 1.35/ 6.68/ 7.58/ 1.70/ 24.42, IV: 7.76/ 1.60/ 7.61/ 7.92/ 1.61/ 26.50. Palp: femur 2.14 long,

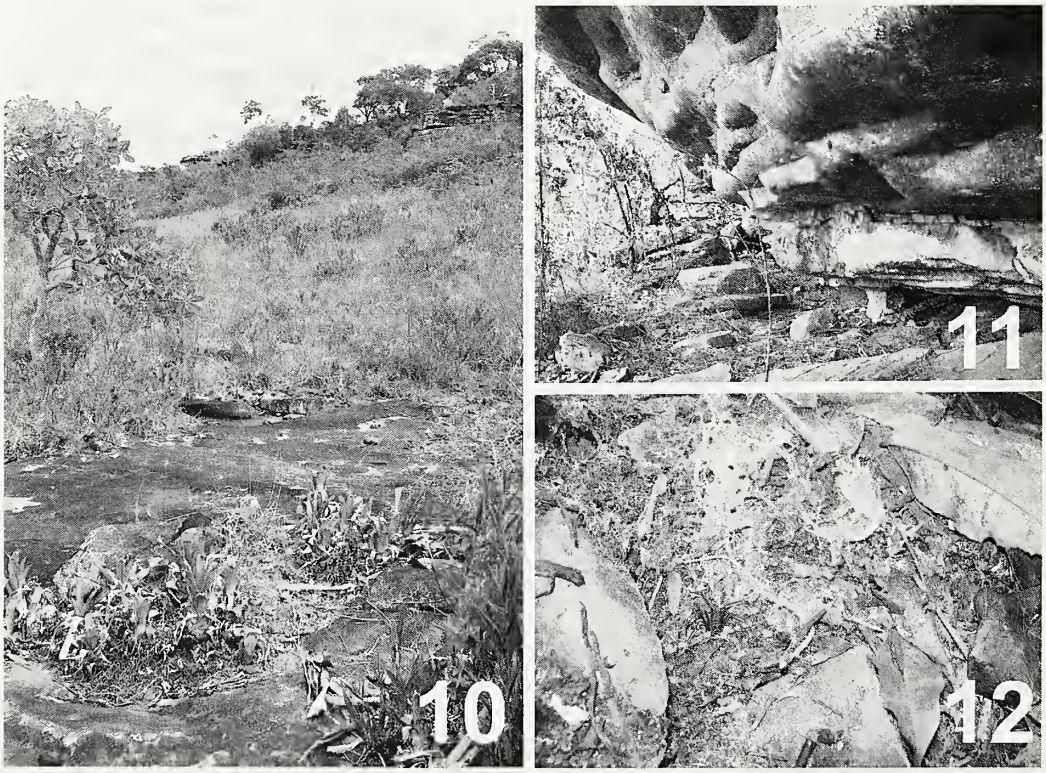


Figures 8–9.—*Loxosceles chapadensis* sp. nov. 8. Male; 9. Female. Photos: R. Bertani.

0.37 wide; patella 0.63 long, 0.43 wide; tibia 1.13 long, 0.46 wide; tarsus 1.88 long, 0.45 wide. Labium 0.92 long, 0.83 wide. Sternum 2.27 long, 1.84 wide. Femur I 1.8 times longer than carapace. Palpal femur 5.8 times longer than wide, tibia 2.5 longer than wide, tarsus not incrassate. Spermathecae with long, straight, apically enlarged seminal receptacles; transversal plate broad, strongly sclerotized; atriobursal orifices hidden under transversal plate, ovals, positioned on the internal edge of the central windows; dorsal part of bursa copulatrix strongly scletorized for half of its length (Figs. 6, 7). Palps brown, except by pale patellae and distal femora. Endites dark brown.

Natural History.—Individuals of *Loxosceles chapadensis* sp. nov. were collected in rock crevices and under rocks in natural environments at Palmeiras and Lençóis in Bahia State (Figs. 10–12). Other specimens were found under rocks, bricks and roof tiles near human dwellings at Iraquara, also in Bahia. These localities are in the vicinity of the Parque Nacional da Chapada Diamantina, which contains ecotonal areas of diverse types of vegetation such as the savannah-like formation called "cerrado"; gallery forests; "campo rupestre" areas–which are characterized by their height above sea level (above 900m), in association with a high degree of outcropping and consequent reduction of soil depth (Giulietti & Pirani 1988); Brazilian Atlantic rainforest and "caatinga", a semi-arid vegetation. All specimens constructed a loose web in their retreat (Fig. 12). A female maintained in captivity constructed two egg sacs. Twenty-seven spiderlings hatched from the first egg sac between 1 and 6 July 2008. The second egg sac, constructed on 3 November 2008, produced 23 spiderlings on 22 December 2008.

Distribution.—Brazil, State of Bahia, northern portion of Parque Nacional da Chapada Diamantina.



Figures 10–12.—Habitat of *Loxosceles chapadensis* sp. nov. in Parque Nacional da Chapada Diamantina, Palmeiras, State of Bahia, Brazil. 10. General view of the area showing Campo Rupestre and Chapada formation; 11. Chapada formation showing crevices and rocks over the ground; 12. Same area showing a removed rock having a specimen of *Loxosceles chapadensis* sp. nov. on its retreat. Photos: C.S. Fukushima.

DISCUSSION

Gertsch (1967) separated the South-American *Loxosceles* into four groups based on the proportions of palpal lengths and specific features of the bulb and embolus in males and spermathecal characteristics of females. The *spadicea* group was characterized by males with short bulbs and thin emboli, and with a carina, and by females bearing small, tubular, widely separated spermathecae. Males of the *laeta* group have palpal tibia two or more times as long as the cymbium, and females have closely positioned seminal receptacles, lacking a transversal plate and apical globular lobes. Males of the *gaucho* and *amazonica* groups have incrassated palpal tibia less then 1.5 times the cymbium length. Females of the *gaucho* group bear spermathecae with a transversal plate, whereas those of *amazonica* group have apical globular lobes.

On the basis of the characteristics mentioned above, *Loxosceles chapadensis* sp. nov. males have some characteristics of the *laeta* group, since the male palpal tibia is two times as long as the cymbium. On the other hand, the female has spermathecae with a broad transversal plate, a characteristic of the *gaucho* group. We prefer to include the new species in the *gaucho* group due to the female's highly modified spermathecae and the presence of a transversal plate. The relatively longer palpal tibia of the male could be a result of homoplasy with species of the *laeta* and *spadicea* groups or even a plesiomorphy, indicating a more basal position of the species in the *gaucho* group relative to these other species. Further, both males and females of the new species have lateral dentate dark bands on the dorsal side of the carapace, which is typical of the *gaucho* group (Figs. 1, 5, 8, 9).

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SHORT COMMUNICATION

First description of the female of *Sarotesius melanognathus* Pocock 1898 (Araneae: Sparassidae: Palystinae)

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Abstract. The female of *Sarotesius melanognathus* Pocock 1898 is described for the first time. According to characters of the copulatory organs of both male and female as well as to cheliceral dentition the monotypic genus is placed in the Palystinae Simon 1897.

Keywords: Description, taxonomy, huntsman spider, Malawi

Pocock (1898) described the genus *Sarotesius* with its type species *Sarotesius melanognathus* from East Africa. It took over one hundred years for the genus to appear again in the scientific literature with illustrations based on the type material published by Jäger & Kunz (2005). During a visit to the Museum of Comparative Zoology in Cambridge, Massachusetts, the second author located a series of reasonably recent material, including one male and three females that were recognised as being conspecific to *Sarotesius melanognathus* Pocock 1898. Thus, here we present a redescription of the male, with new details of the palp structures, and the first description of the female and its copulatory organ. In addition, we comment on the relationships between this genus and the remaining Sparassidae genera.

The examined spiders were preserved in 70% denatured ethanol. Examination and drawings were carried out with a Leica MZ 16 stereomicroscope with drawing mirror. Female copulatory organs were dissected and the sclerotised internal duct system was cleared in 96% DL-lactic acid ($C_3H_6O_3$). All measurements are in mm. Leg formula, leg spination pattern and size classes follow Jäger (2001). Palp and leg lengths are listed as: total (femur, patella, tibia, metatarsus, tarsus). Arising points of tegular appendages in males are described as clock-positions of the left pedipalpus. The part of the internal duct system with glandular pores is called "turning point", as at this point the duct system changes its direction. In schematic courses it is marked with "T", the copulatory orifice with a circle, and the end of the fertilization duct in direction of the *uterus externus* with an arrow. As in Jäger (2005:88), slit sense organs close to the epigyne are illustrated as descriptive character.

Abbreviations: ALE = Anterior lateral eye, AME = Anterior median eye, PJ = Numbers represent subsequent numbers of Sparassidae examined by the authors, PLE = Posterior lateral eye, PME = Posterior median eye, RTA = Retrolateral tibial apophysis, I–IV = Referring to leg numbers.

Museum collections (with curators): MCZ = Muscum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (Gonzalo Giribet, Laura Leibensperger), NHM = Natural History Museum, London (Janet Beccaloni).

Sparassidae Bertkau 1872
Palystinae Simon 1897
Sarotesius melanognathus Pocock 1898
Figs. 1–4

Sarotesius melanognathus Pocock 1898:443, pl. 13, fig. 6 (Description of male, male holotype from East Africa, Ishiromo, H.H. Johnston leg. 1894/10, NHM 1894.1.15.20, examined); Jäger & Kunz 2005:167, figs. 142–148 (Illustration of male); Platnick 2009.

Note.—Pocock (1898) did not state clearly in which country the type locality Ishiromo is situated. However, in Pocock (1896) he mentions Ishiromo as belonging to Nyasaland (= Malawi) and naming H.H. Johnston as collector. Although the exact position of Ishiromo cannot be cleared, Malawi, as only country where *Sarotesius* occurs according to our current knowledge, can be fixed.

Additional material examined.—1 male, 3 females, Nyasaland [= Malawi], A. Loveridge, III.1948, Cholo ??? (unreadable word) [= Thyolo], Rheims det. 2006, MCZ 69105.

Diagnosis.—Large Palystinae (body length: males 19.3–23.0, females 19.6–21.8) with 3 anterior and 3 similar sized posterior teeth and a flat prosoma. Males can be distinguished mainly by the shape of the embolus (Fig. 1; see also Jäger & Kunz 2005:figs. 142–145): 1) wide at its base, 2) with distal loop, tapering continuously, 3) between basal and distal part with distinct round apophysis, 4) first, prolateral part of distal loop with indistinct membranous lobe. Females (Figs. 2–4) may be recognised by 1) median septum rounded rectangular with concave posterior margin and separated from epigastric furrow, 2) internal duct system with first winding membranous, covering large parts except for anterior median and posterior part, 3) Internal duct system medially with two tapering glandular appendages and two globular appendages.

Redescription of male (PJ 3212).—Prosoma length 11.2, prosoma width 11.3, anterior width of prosoma 6.8, opisthosoma length 11.8, opisthosoma width 9.7. Eyes: AME 0.53, ALE 0.50, PME 0.55, PLE 0.45, AME–AME 0.52, AME–ALE 0.96, PME–PME 0.94, PME–PLE 1.65, AME–PME 0.45, ALE–PLE 0.60, clypeus height at AME 0.43, clypeus height at ALE 0.33. Spination: Palp: 131, 001, 2111; legs: femur I–III 313, IV 310; patella I–III 001, IV 000; tibia 2026; metatarsus I–III 2024, IV 3025. Ventral metatarsus III and IV with 1 distal median spine and dense scopula. Leg formula: 2143. Measurements of palp and legs: Palp 14.3 (4.7, 2.2, 2.7, -, 4.7), leg I 53.2 (14.6, 6.4, 13.9, 15.0, 3.3), leg II 56.4 (16.3, 6.6, 16.2, 13.9, 3.4), leg III 39.0 (11.6, 5.1, 10.2, 9.1, 3.0), leg IV 42.4 (12.5, 4.8, 11.1, 10.9, 3.1). Cheliceral furrow without denticles. Promargin of chelicerae with 3 teeth, retromargin with 3 similar sized teeth, one side with a small denticle between the median and proximal tooth.

Male palp: As in diagnosis. RTA arising distally on tibia; simple, stout, slightly bent in retrolateral view. Cymbium longer than tibia, without retrolateral bulge. Embolus arising in a 6-o'clock-position on tegulum, tip of embolus prolatero-distad. Basal part of embolus with

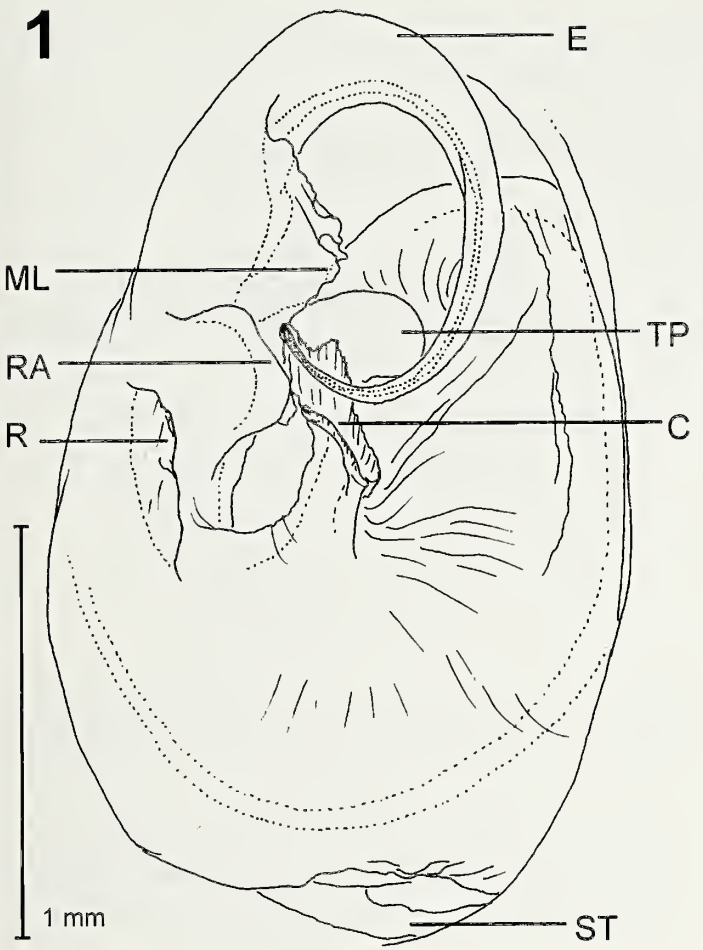

Figure 1.—*Sarotesius melanognathus* Pocock 1898, male from Malawi. Tegulum, retrolatero-ventral view. C = conductor, E = embolus, ML = membranous lobe, R = ridge, RA = round apophysis, ST = subtegulum, TP = tegular process.

ridge. Membranous conductor reduced, situated in the center of tegulum. Behind conductor with dorsal tegular process, which latter arises from the prolateral side between tegulum and subtegulum (Fig. 1). This process is so far unique for the entire family (but compare *Heteropoda lomstu* Jäger 2008 in Jäger 2008:fig. 266 for a similar but most likely analogous structure).

Coloration: Generally reddish to yellowish brown without distinct pattern. Dorsal shield of prosoma with striae and a longitudinal line medially and one on each side between head part and thorax part; eye region a bit darker. Sternum dark brown with bright radial lines with anterior margin as center. Labium, gnathocoxae and chelicerae dark red-brown. Ventral coxae and appendages yellowish brown with distal segments darker, turning into reddish brown. Opisthosoma grayish brown with dorsal bright patch above heart and four ventral longitudinal parallel lines, the lateral two broader.

Description of female (PJ 3213).—Prosoma length 9.1, prosoma width 9.4, anterior width of prosoma 6.0, opisthosoma length 10.7, opisthosoma width 8.5. Eyes: AME 0.57, ALE 0.50, PME 0.40, PLE 0.49, AME–AME 0.35, AME–ALE 0.83, PME–PME 0.80, PME–PLE 1.41, AME–PME 0.35, ALE–PLE 0.55, clypeus height at AME 0.30, clypeus height at ALE 0.29. Spination: Palp: 131, 001, 2111, 1013; legs: femur I 3(2)13, II–III 313, IV 310; patella I–III 001, IV 000; tibia I 2026, II 1014(2028), III–IV 2026; metatarsus I 2021(4), II 1023(2015), III 3024, IV 3035(2033). Ventral metatarsus III and IV with one distal median spine and dense scopula. Leg formula: 2143. Measurements of palp and legs: Palp 10.7 (3.5, 1.9, 2.2, -, 3.1), leg I 35.7 (9.7, 5.0, 8.8, 9.4, 2.8), leg II 39.4 (11.1, 5.2, 10.1, 10.2, 2.8), leg III 26.9 (8.3, 3.9, 6.6, 6.0, 2.1), leg IV 28.6 (9.0, 3.6, 7.1, 6.8, 2.1). Cheliceral furrow without denticles. Promargin of chelicerae with 3 teeth, retromargin with 3 similar sized teeth. Palpal claw like leg claw, with 10 teeth.

Copulatory organ: As in diagnosis. Epigynal field rounded, longer than wide, with two slit sense sensilla close to the field. Lateral lobes almost touching each other between median septum and epigastric furrow. Median septum less sclerotised than lateral lobes, bright. Subseptal pocket present, bordered dorsally by membranous part. Copulatory opening situated at anterior margin of median septum. Posterior part of internal duct system running laterally posteriorad.

Coloration: As in male. Dorsal shield of prosoma and opisthosoma covered by soft hairs. Sternal pattern with bright patches, rather than with lines. Dorsal opisthosoma with distinct transversal bar at anterior margin, six muscle sigilla distinctly marked with black, middle largest.

Variation.—*Males* (n = 1, holotype): Prosoma length 8.4, opisthosoma length 10.8. Spination: Palpal femur 131; Femur IV 311; Tibia I 202(3)6; Metatarsus III 3124, IV 302(3)6.

Females (n = 2): Prosoma length: 9.6, opisthosoma length 10.0–12.2. Spination: palpal patella: 130, Femur I 113/314/313, II 312/313, III 311/312, IV 310; Patella II 002/001, III 000/001; Tibia I–II 2026, III 2016/2026, IV 2006/2026; Metatarsus I–II 2024, III 1024/3024, IV 3025.

Distribution.—The species is known from the type locality (East Africa, Malawi, Ishiromo) and from S-Malawi: Thyolo (= Cholo).

Relationships.—*Sarotesius melanognathus* is identified as member of the subfamily Palystinae by the cheliceral dentition (3 anterior and 3 siminar sized posterior teeth) and the overall similarity of its copulatory organs with those of the genus *Palystes* L. Koch 1875 and other representatives (see also Rheims 2007). Especially, the congruence with copulatory organs of the *Palystes superciliosus* species group (Croeser 1996; Jäger & Kunz 2005) is striking: males have a similarly simple RTA, a distal embolus with a loop, a centrally arising conductor; females exhibit the same general course of the internal duct system with the first, membranous winding running anteriorly then medially, where glandular appendages are observed in almost all species and roundish appendages in some species. The posterior part of the internal duct system runs laterally from the epigastric furrow to the fertilization ducts. Both sexes have a distinctive sternal pattern. Differences in *Sarotesius* are the distance between the median septum and the epigastric furrow (without distance in *Palystes*) and the flat prosoma, the subequal size of the eyes and the large distance between anterior median and anterior lateral eyes (raised prosoma, larger anterior lateral eyes, the latter close to the anterior median eyes in *Palystes*). Several taxa that show similar and intermediate combinations of the character states listed above inelude "*Olios*" *fasciiventris* Simon 1880 from Zanzibar, "*Olios*" *spinipalpis* (Pocock 1901), from South Africa and *Remmius vultuosus* Simon 1897 from Congo, type species of the genus *Remmius* Simon 1897. Without a revision of Palystinae no certain statement can be made on the systematic position of *Sarotesius*.

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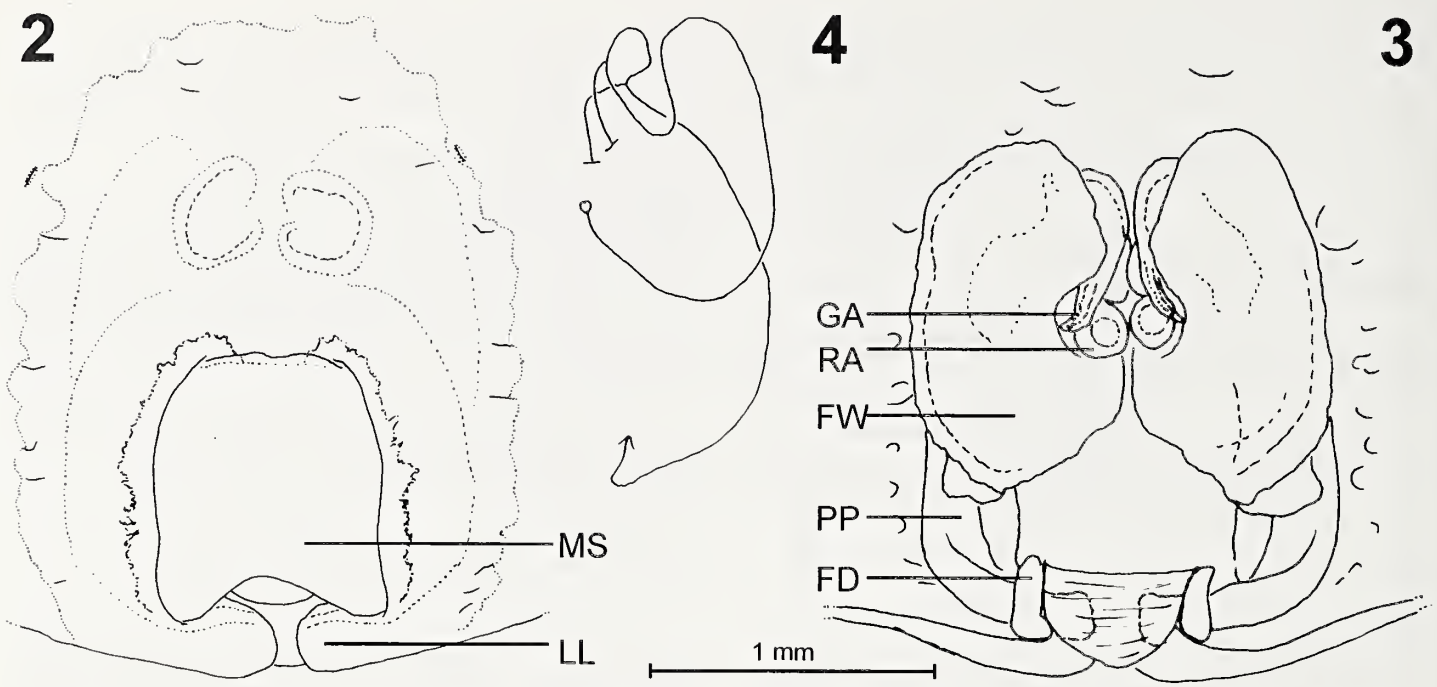

Figures 2–4.—*Sarotesius melanognathus* Pocock 1898, female from Malawi. 2. Epigyne, ventral view. 3. Vulva, dorsal view. 4. Schematic course of internal duct system, dorsal view. FD = fertilization duct, FW = first winding of internal duct system, GA = glandular appendage, LL = lateral lobe, MS = median septum, PP = posterior part of internal duct system, RA = round appendage.

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SHORT COMMUNICATION

Egg sac construction by folding dead leaves in *Pozonia nigroventris* and *Micrathena* sp. (Araneae: Araneidae)

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Abstract. Published descriptions of egg sac construction behavior in araneids are scarce. We describe egg sac construction and oviposition in one individual of the poorly known araneid *Pozonia nigroventris* (Bryant 1936) and two individuals of *Micrathena* sp. These spiders folded dead leaves to protect their eggs. All individuals pulled up and hung a dead leaf above the forest floor, oviposited on the leaf, and then folded the leaf around the egg sac. They then deposited the enclosed egg sac in the leaf litter below. The use of dead leaves in this way probably evolved convergently, since these genera are only distantly related.

Keywords: Canopy spider, convergent behavior, oviposition, predator defense

Spider egg sacs protect eggs from damage by both biotic and abiotic factors (Austin 1985). Protection is not absolute, and spider eggs frequently suffer high mortality from organisms such as ants, wasps, flies and birds (Austin 1985; Hieber 1992). Egg sac construction varies widely among different spider taxa (Kullmann 1961; Robinson & Robinson 1973, 1976; Eberhard 1980; Manuel 1984; Austin 1985; Levi 1985; Barnes et al. 1992; Bukowski & Christenson 1997; Guarisco 2001; Gheysens et al. 2005). However, detailed descriptions of egg sae construction are lacking for many groups.

Here we describe for the first time the egg sac construction behavior of the araneid *Pozonia nigroventris* (Bryant 1936) and include additional information on the egg sac construction of an unidentified species of *Micrathena* Sundevall 1833. *Pozonia* is thought to inhabit the canopy of tropical forests (Levi 1993). *Micrathena*, in contrast, builds diurnal webs in the understory and has been more extensively studied (e.g., Uetz & Hartsock 1987; Bukowski & Christenson 1997).

We observed spiders opportunistically, including one *P. nigroventris* that was observed continuously between 21:38 and 03:20 h on 30–31 May 2009 in mature rainforest at La Tirimbina Biological Reserve (Heredia Province, Costa Rica: 10°26′N,83°59′W, 150 m elevation), and two individuals of *Micrathena* sp. on 13 June 2009 at 01:00 and 23:30 h in mature rainforest at the Alberto Manuel Brenes Biological Reserve (Alajuela Province, Costa Rica: 10°13′N,84°32′W, 800 m elevation). We identified the spiders using publications by Levi (1985, 1993). Voucher specimens of both species were deposited in the Museo de Zoología of the Universidad de Costa Rica. The *Micrathena* species did not match the descriptions of any of the species in Levi (1985).

Pozonia nigroventris.—We first noted the female *P. nigroventris* as she pulled up a nearly flat leaf (20 cm long and 6 cm wide) from the forest floor (Fig. 1). The line was attached above to a thick horizontal vine approximately 1.75 m above the ground. An additional, nearly vertical silk line extended upward out of sight from the vine toward the canopy. The horizontal line had several masses of white fluff, perhaps representing lines that had been reeled up by the spider in previous ascents.

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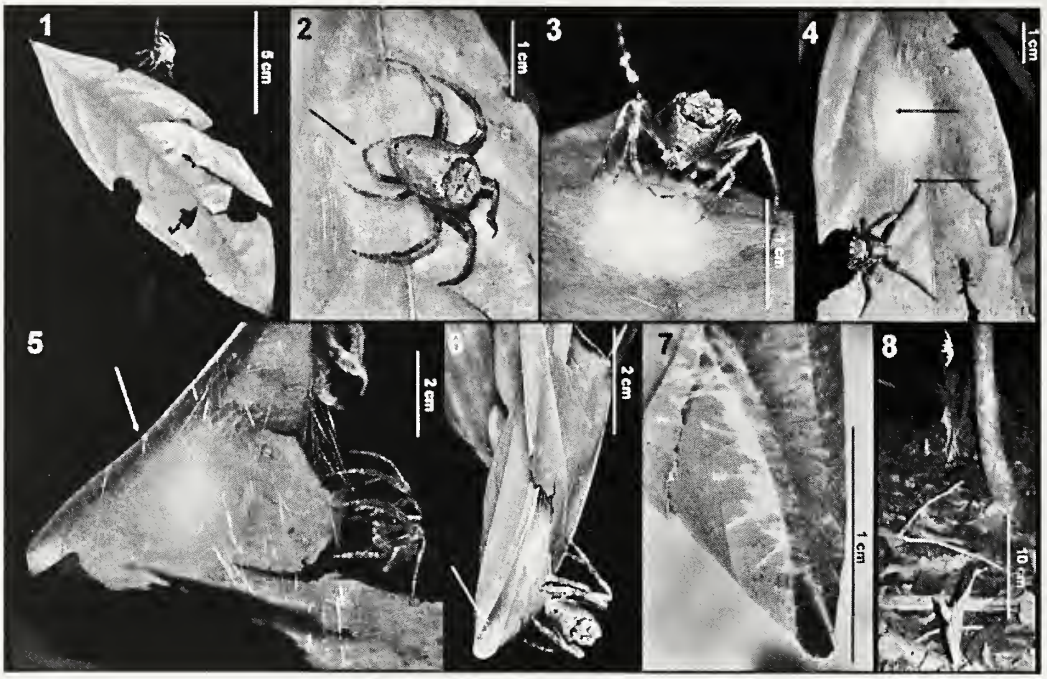
The spider reattached the vertical line to several points on and near the petiole of the leaf, and then began to lay fluffy white silk in a circular area 2–3 cm in diameter on the leaf. She laid lines by repeatedly touching the leaf and other silk lines with her widely-spread spinnerets as her abdomen bobbed dorsal-ventrally; occasionally she also pushed ventrally near her spinnerets with one tarsus IV (Fig. 2) or (less frequently) with both tarsi IV while continually touching the mass of silk with her palps. The circular silk mat eventually became a mound of fluffy silk several mm thick, with its peak slightly indented in the center (Fig. 3). Then, after a short pause, a mass of yellowish eggs gradually emerged on the female's ventral surface during approximately 3 min. The egg mass was pressed into the accumulation of fluffy silk while the spider's legs II and III held the sides of the silk mat. As soon as all the eggs had emerged, the spider began to add further fluffy white silk. She repeatedly dabbed her spread spinnerets to the sac wall and immediately raised her abdomen away from the sac as she pushed ventrally against the sac with both hind legs. Sometimes the spider made two or three dabs and pushes with her legs IV before she touched the sac again with her spinnerets. Up to three pairs of lines were seen being pulled simultaneously from her spinnerets (Fig. 3).

As soon as construction of the egg sac proper ended, the spider began to attach tight lines to the leaf using her spinnerets (her legs did not touch them). Most lines were oriented more or less vertically, running back and forth between the edge of the leaf above the sac and the leaf surface below it. Some early lines pressed against the sac, producing indentions in the fluffy silk mass (Fig. 4). The leaf gradually began to fold near the lower edge of the sac (Fig. 5), and the spider attached new threads farther down on the leaf. When the leaf was folded about 60°, she sealed the package with several short lines across the sharply folded portion of the leaf, which she attached to the leaf surface opposite the egg sac (Fig. 6). Then she walked over the leaf's surface, covering holes and cracks with silk (Fig. 7). Finally the spider lowered the leaf package to the forest floor. First she climbed up the line, cut it above the package, and began to descend by paying out silk (Fig. 8). When the folded leaf reached the leaf litter below, the spider gave three bursts of strong vertical shakes on the line. She then moved down, broke the line near where it was attached to the leaf package, and ascended her drag line.

Micrathena sp.—Egg sac construction behavior by *Micrathena* sp. was similar to that of *P. nigroventris* in several respects: an approximately circular accumulation of cotton-like silk was produced

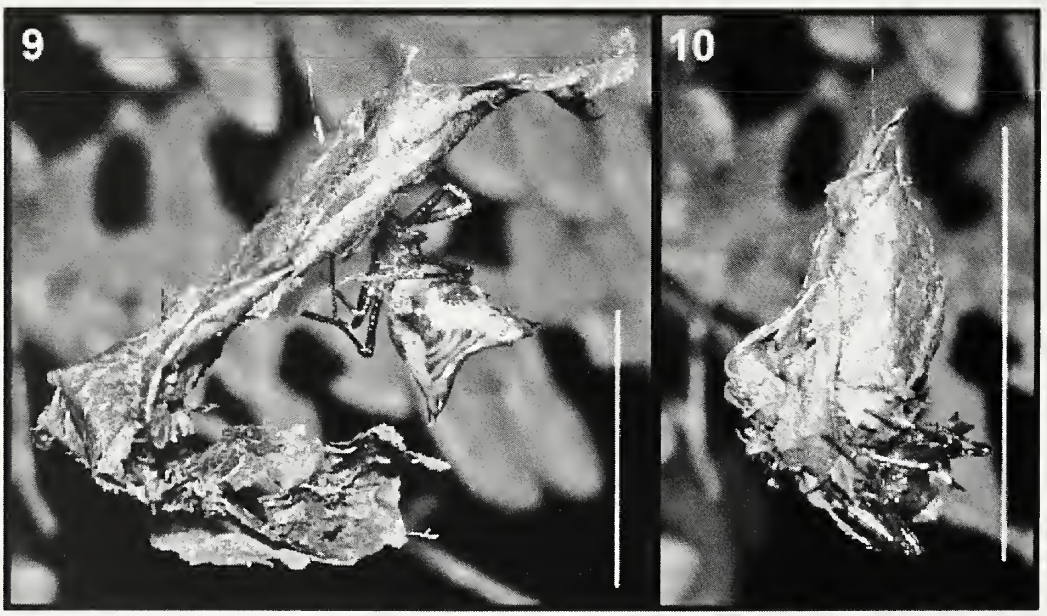


Figures 1–8.—Egg sac construction of *Pozonia nigroventris*. 1. Pulling up the leaf from the forest floor; 2. While constructing the basal pad of egg sac, spider pulls lines from her spinnerets by pressing one leg IV against the sac (arrow); 3. Spider uses both legs IV to pull multiple lines of silk from her spread spinnerets; 4–6. Spider gradually folds leaf. 4. Some early tense lines attached to leaf (arrows) caused indentations in the sac; 5, 6. Several lines attached to the edges of the leaf (arrows in 5 and 6); 7. Close-up shows how spider's lines sealed the sharp fold in the leaf; 8. Spider (top) lowers folded leaf with egg sac to forest floor. Photographs by J. Moya.

on a suspended dead leaf by dabbing the spinnerets repeatedly on the pile of fluffy silk; an egg mass was then laid, and further fluffy silk was added to the sac; finally the leaf was folded to seal the egg sac into a tight package, the package was lowered by paying out trail line, and the package was shaken with several bursts of vertical jerks.

In other aspects *Micrathena* sp. behavior differed from that of *P. nigriventris*. The leaves where *Micrathena* built the egg sac were only irregular pieces (Fig. 9). The spider pulled multiple silk threads from her spinnerets with alternate movements of her fourth legs and only seldom attached the lines by dabbing her spinnerets to the leaf or the pile of fluffy silk, and the leaf was rolled instead of folded (Fig. 10). When one sac was about 30 cm above the forest floor it encountered a fern leaf below, and the spider shook it with several vertical movements. She then lifted the package by reeling in the line, and cut the line near the leaf and let it fall to the leaf litter below.

Folding the leaf, sealing it tightly, and then placing it in the leaf litter may reduce damage to the eggs from aerial predators or parasites (Robinson & Robinson 1976; Hieber 1992; Bukowski &



Figures 9–10.—Egg sac construction of *Micrathena sp.* 9. Female makes mat of fluffy silk on partially curled leaf prior to oviposition; 10. Leaf folded around egg sac; scale = 1 cm. Photographs by J. Moya.

Christenson 1997). The egg mass wrapped in a dead leaf was extremely cryptic in the leaf litter, and this may protect it from large animals like birds foraging on plants, though it must expose them to another set of potential predators such as ants on the forest floor (Hieber 1992). The size and shape of a dead leaf would seem crucial, and we suspect spiders actively select appropriate leaves.

The similarity between egg sac construction behavior in *Pozonia nigriventris* and *Micrathena* sp. is impressive, especially the ratchet-like mechanism that sums up small increments in tension in order to fold relatively stiff dead leaves, and the agitation of the finished sac as it was lowered into the litter, which was apparently an attempt to insert it more securely. This behavior differs sharply from that of *Gasteracantha cancriformis*, a close relative of *Micrathena* (Scharff & Coddington 1997), which deposits its egg sac on the underside of a flat, unfolded leaf (Muma 1971), and also from that of other spiders (Blanke 1973; Jackson et al. 1997; Morse 1985; Li et al. 2002) The striking similarities between the distantly related genera *Pozonia* and *Micrathena* (Scharff & Coddington 1997) suggests that wrapping the eggs in a leaf evolved convergently in the two genera. However, further information, particularly on the use of leaves, in other araneid species is necessary to fill in the evolutionary history of egg sac construction behavior.

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SHORT COMMUNICATION

Harvestmen as predators of bird nestlings

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Abstract. We report the first confirmed cases of harvestmen (Opiliones) feeding upon live vertebrates. In June and July of 2007, in two independent studies of the ecology of Swainson's warblers (*Limnothlypis swainsonii* Audubon) in Arkansas and North Carolina, we recorded predation of nestlings at two separate nests by harvestmen. Both events were nocturnal, involved relatively young and dependent nestlings, and contributed to or resulted in the death of one or more nestlings. One event involved a group of at least four harvestmen with one to four individuals feeding upon a brown-headed cowbird (*Molothrus ater*) nestling at one time, and the other involved up to two harvestmen present at the nest, but only one individual fed upon the two Swainson's warbler nestlings.

Keywords: Diet, Opiliones, opportunism, predation, vertebrate prey

Harvestmen (Opiliones) are noted opportunists, with individuals documented feeding upon live and dead invertebrates, fungi, fruit, and other plant matter (Halaj and Cady 2000; Machado and Pizo 2000; Acosta and Machado 2007). Additionally, harvestmen have been observed to feed upon dead vertebrates, including birds, mammals, and frogs (Sankey 1949; Castanho and Pinto da Rocha 2005; Acosta and Machado 2007). Although some harvestmen are ambush predators that feed on relatively small food items, other species hunt actively in groups and consume relatively large prey (Acosta and Machado 2007). Harvestmen may subdue large prey over a relatively long period of time while feeding, often while the prey item is still alive, and feeding consists of consuming small pieces of the food item (Acosta and Machado 2007). Here, we report two independent cases of harvestmen attacking and feeding upon live vertebrates (bird nestlings). We observed these events as part of two independent studies on the breeding biology and nest predators of Swainson's warblers (*Limnothlypis swainsonii* Audubon) in Arkansas and North Carolina in June and July 2007, respectively.

The first event occurred on 3 and 4 June 2007 at White River National Wildlife Refuge (WRNWR) in eastern Arkansas. Located in Arkansas, Desha, Phillips, and Monroe counties, WRNWR, at >62,000 ha, is among the largest continuous tracts of bottomland hardwood forest remaining in the Mississippi Alluvial Valley (see Benson et al. 2009). On 15 May 2007, we found a Swainson's warbler nest 1.6 m above the ground in a cane (*Arundinaria gigantea*) plant with four warbler eggs. Later the same day, we installed a time-lapse video system at the nest that included a weatherproof camera with infrared diodes to allow recording at night (Benson et al. 2010). Over the next 7 days, three of the Swainson's warbler eggs were removed by brown-headed cowbirds (*Molothrus ater*), an obligate brood parasite that lays its eggs in the nests of other species, and one cowbird egg was laid. On 2 June at 11:24 h, the cowbird egg hatched. For the next 1.5 days, the female Swainson's warbler continued to incubate the remaining Swainson's warbler egg and brood the newly hatched brown-headed cowbird nestling and began to make periodic trips from the nest to gather food for the nestling. The male Swainson's warbler also periodically delivered food for the nestling. The female was last on the nest from 18:57 to 20:20 h on 3 June after which she left and did not return until the next morning at 05:44 h.

At 23:56 h on 3 June, a harvestman arrived at the nest and began biting the cowbird nestling on the back of the neck at 23:59 h and stopped after about 2 min. The harvestman appeared to bite the nestling several more times before moving to the nest rim 3 min later where it appeared to move one of its forelegs over the nestling for about 6 min. The harvestman continued to alternate between biting the nestling and moving around on the nest cup for several minutes at a time before leaving the nest for 23 min; at this time the nestling was still able to rotate its body within the nest cup. A harvestman returned to the nest and resumed biting the nestling from 00:56 to 02:25 h; it appeared to bite the head or neck of the nestling as the bird began to move less vigorously but continued to make small movements. At 02:25 h, two additional harvestmen appeared at the nest and immediately climbed onto the nestling while the original harvestman continued to take bites. One of the new harvestmen continued to move around, while the other appeared to participate in the biting and presumably feeding upon the nestling; the nestling continued to make occasional slight twitching movements. This feeding continued with one to four harvestmen until 05:11 h. The nestling stopped twitching around 0400 h and appeared to be dead. During the 5.2 h-long event, at least one harvestman was present at the nest ≥94% of the time. At 05:44 h, the female Swainson's warbler returned to the nest and began incubating/brooding. At 06:08 h, the male Swainson's warbler arrived at the nest with food and the female began to poke the dead nestling; at 06:10 h one of the Swainson's warblers removed the dead nestling from the nest, a typical behavior when nestlings die.

The second event occurred on 12 and 13 July 2007 at the Roanoke River National Wildlife Refuge (RRNWR), a temporarily to semi-permanently flooded forested wetland in eastern North Carolina. RRNWR is located on the lower Roanoke River in Bertie County, NC, covers 8,490 ha, and is among the largest intact and relatively undisturbed bottomland forests remaining in the South Atlantic Coastal Plain (Lynch 1981). The primary natural communities at RRNWR are Coastal Plain levee forest and cypress (*Taxodium distichum*) - tupelo (*Nyssa aquatica*) swamp forest (Schafale and Weakley 1990).

On 27 June 2007, we found a Swainson's warbler nest with three warbler eggs. The nest was 1.7 m above the ground in a giant cane plant. Later that day, we installed a time-lapse, infrared video system

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at the nest similar to that described for the Arkansas study site above. This was the fourth nest attempt by this female that was monitored with time-lapse video. The first nest was abandoned on 24 May after the death of a brown-headed cowbird nestling, the second, also parasitized by a cowbird, was abandoned on 3 June after a rain storm, and the third was depredated by a rat snake (*Elaphe obsoleta*) on 20 June. Her fourth nest contained three Swainson's warbler eggs; the first hatched on 10 July at 16:19 h, the second egg hatched on 11 July between 09:30 and 10:32 h, and the last egg did not hatch. For the next 1.5 days, the female continued to brood the two nestlings and incubate the unhatched egg, and began to periodically leave the nest to gather food for the nestlings. During this period, the male also periodically delivered food to the nestlings. The female was last on the nest from 19:56 to 23:26 h on 12 July.

At 23:37 h on 12 July, ants (likely *Aphaenogaster* sp.) arrived at the nest and soon began biting the nestlings. At 00:34 h on 13 July, the first harvestman arrived at the nest, touched the nestlings with its forelegs, and moved out of camera view. Seven min later, with four or five ants present and biting the nestlings, a harvestman arrived, bit a nestling on the head causing it to violently squirm, and moved out of camera view. From 00:50 to 00:58 h, the harvestman alternated between biting the nestling, standing on the nest rim, and standing over the nestling while touching it with its forelegs before leaving the camera view for 10 min. At 01:14 h, as the first harvestman continued to move around the nest touching the nestlings with its forelegs, a second harvestman arrived then moved out of camera view 1 min later without interacting with the nestlings. As four or more ants continued moving over and biting the nestlings, the harvestman continued to move around the nest rim, touching the nestlings with its forelegs, and occasionally biting the nestlings until again leaving at 01:58 h. At this point, the nestlings continued to make small, but less vigorous movements. At 02:24 h, as three or more ants continued to bite the nestlings occasionally, a harvestman moved over a nestling and bit it on the neck, lifting the nestling slightly, and then moved to the nest rim. For the next 30 min, the harvestman alternated between biting the head, neck, and back of the nestlings and standing on the nest rim; ants appeared to briefly drive the harvestman out of camera view twice during this period. The nestlings were now only occasionally making slight twitching movements. While being harassed by ants, the harvestman continued to move across, touch, or bite the nestlings periodically from 03:09 to 04:37 h and appeared to be driven away from the nest three times by ants. By 03:26 h, neither of the nestlings was moving, and both were presumed to have died. During the ~4 h-long event, a harvestman was at or near the nest approximately 70% of the time. The Swainson's warbler female visited the nest at least twice during the night, but did not sit on the nest, touch the egg or nestlings, or attempt to remove ants or harvestmen. She returned to the nest at 05:46 h, sat on the nest for 12 min, and then carried away a dead nestling. She returned at 06:02 h, sat on the nest for 20 min, and then removed the remaining dead nestling. After incubating the remaining egg for a short time, the Swainson's warbler female abandoned the nest later that morning.

Both events were similar in that they largely occurred between midnight and 05:00 h, involved 1- to 2-day-old nestlings, which are featherless and <5 g, in situations where the female was absent but normally would have been brooding, and resulted in or contributed to the death of the nestlings. In both cases, the harvestmen made repeated trips away from the nest and alternated between biting nestlings and standing on the nest rim. Although the events at these two widely separated locations were similar, there were notable differences. The WRNWR event involved multiple harvestmen simultaneously attacking the nestling, which conclusively resulted in the mortality of the cowbird. However, whether mortality resulted directly from harvestman bites or was facilitated by a stress response of the nestling is unknown. The RRNWR event involved only one harvestman attacking the nestlings, although two individuals were observed at the nest on at least one occasion. Additionally, the RRNWR event involved the nestlings simultaneously being attacked by ants. Because up to 10 ants were present and apparently biting the nestlings during most of the observed 4 h event and biting by the harvestman was more sporadic, the mortality of the nestlings in this case may have been primarily caused by the ants. Nonetheless, despite being driven away by the ants on several occasions, the harvestman spent considerable time biting the nestlings. Unfortunately, the placement and resolution of the cameras did not allow us to determine the extent of injuries to the nestlings.

To our knowledge, this is the first confirmed case of harvestmen feeding on live vertebrates. Harvestmen are known to feed upon dead vertebrates (Sankey 1949). Likewise, Castanho and Pinto da Rocha (2005) found harvestmen feeding on frogs, although it was unknown whether the prey items were captured alive. Our observations are consistent with the known opportunism of harvestmen, and the observation that they forage above the ground (Todd 1949; Adams 1984). Likewise, as we observed, harvestmen primarily forage at night and may devote considerable time to searching for prey during this period (Pereira et al. 2004; Acosta and Machado 2007). Unfortunately, the quality of the video footage did not allow us to identify the harvestmen or ants with greater taxonomic resolution.

When they hatch, songbird nestlings are featherless, have closed eyes, and have limited mobility. For several days, these nestlings are largely helpless and, because of their limited perception and mobility, they might appear functionally similar to carrion for harvestmen. This similarity to carrion likely accounts for the long time period that harvestmen were at or near the nest at both sites. Like other passerines, female Swainson's warblers normally brood nestlings at night until they are fully feathered and are presumably less vulnerable to attack by invertebrate predators. The reason that each warbler female was absent from the nest in these two cases is unknown, but may be related to the presence of biting ants in the second case. Indeed, the nestling period is a vulnerable time for predation by other arthropods, and ants have been observed to cause nest failures for other songbird species (Stake and Cimprich 2003; Reidy et al. 2008) or, as in the RRNWR event, contribute to Swainson's warbler nest failure. Although young songbird nestlings generally are not vulnerable to nocturnal predation by opportunistic groups such as harvestmen because females usually brood during this period, individual harvestmen may exploit these opportunities when present. However, these appear to be rare events. At WRNWR and RRNWR, with >40,000 h of nest monitoring with infrared video cameras, these were the only two recorded events where harvestmen actually fed on nestlings, although they are often present around nests but presumably deterred by the presence of adult birds or older nestlings. Nonetheless, these events indicate that harvestmen display these opportunistic behaviors at widely separated geographic locations, and this may apply beyond bird nestlings to other relatively immobile vertebrates.

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SHORT COMMUNICATION

The utility of ITS2 in spider phylogenetics: notes on prior work and an example from *Anelosimus*

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Abstract. The ribosomal internal transcribed spacer ITS2 is probably the most popular nuclear DNA marker used to examine relationships among and within species in animals and plants. ITS2 sequences have also begun to be used as DNA barcodes. ITS2, however, has rarely been used in studies of spiders. Here, I examine the potential utility of this marker for spider phylogenetics based on preliminary data for *Anelosimus* spiders and a brief summary of prior work. The secondary structure of ITS2 facilitated alignment of highly divergent sequences and indicated that secondary structure morphology might be phylogenetically informative in itself. Phylogenetic analysis of *Anelosimus* species was congruent with a prior study based on a combination of six mitochondrial and nuclear loci plus morphology regarding the deeper clades within the genus. However, ITS2 had insufficient variation to resolve relationships within species and among closely related species. Previous studies have also discovered relatively little within-species variation in ITS2. In sum, ITS2 is an easily amplified and sequenced marker that is underutilized in spider phylogenetics; however, it has limited uses at the lowest taxonomic levels and is not likely to be a universally useful DNA barcode marker.

Keywords: Phylogeny, DNA barcode, ITS2 secondary structure, sociality, Theridiidae

ITS2, which is flanked by the 5.8S and large ribosomal subunit (28S) nuclear genes, is perhaps the most popular marker used to resolve relationships among and within species in animals and plants (Alverez & Wendel 2003; Bailey et al. 2003; Young & Coleman 2004; Schultz et al. 2005; Coleman 2009; Schultz & Wolf 2009). ITS2 sequences have also been proposed as effective DNA barcodes (e.g., Ben-David et al. 2007; Park et al. 2007). The popularity of this marker stems from a generally high level of variation, yet relatively conserved secondary structure, and ease of amplification and sequencing. However, comparatively few studies on spider phylogenetics have utilized this marker despite these benefits and a general paucity of good primers for nuclear markers. Among the few ITS2 studies in spiders, most focus on low taxonomic levels, reconstructing relationships among, and in some cases, within, species (Hedin 1997; Hormiga et al. 2003; Arnedo & Gillespie 2006; Chang et al. 2007; Bond & Stockman 2008). In spiders, ITS2 has generally been found to be a useful marker offering resolution at the species level, especially so in more genetically structured systems such as in trapdoor spiders (Bond & Stockman 2008), cave dwelling nesticids (Hedin 1997), and island radiations (Hormiga et al. 2003; Arnedo & Gillespie 2006). Other studies have used ITS2 as a tool to help separate closely related species. Variation allowing separation of closely related species/populations was found in *Poltys* (Smith 2006), *Pardosa* (Chang et al. 2007) and *Latrodectus* (Vink et al. 2008). However, variation was insufficient to separate closely related North American *Latrodectus* species (Zhang et al. 2004) or populations of *L. katipo* Powell 1870 (Vink et al. 2008).

This note reports on the utility of ITS2 data to resolve phylogenetic relationships among and within *Anelosimus* spider species, well known for their multiple origin of social behavior (Avilés 1997; Agnarsson 2006; Agnarsson et al. 2006). I use exemplar species from across the phylogeny of the genus and specimens representing most of the known 16S mitochondrial haplotype diversity within one species, *A. eximius* (Keyserling 1884). As the goal of this paper is practical application, I do not see a reason to prune the analyzed matrix to the exact ITS2 sequences, but I refer rather loosely to the entire region amplified by the FITS and RITS primers (see below) as ITS2.

I collected specimens in the field and placed them in 95% ethanol. Genitalia were abscised and stored as vouchers at the Zoological Museum of the University of Puerto Rico, while DNA was isolated from each individual using the prosoma, the abdomen, or both, with the QIAGEN DNAeasy Tissue Kit (Qiagen, Inc., Valencia, CA). I used the ITS-5.8S (FITS) and ITS-28S (RITS) primers (White et al. 1990) (FITS GGGACGATGAAGAACGGAGC, RITS TCCTCCGCTTATTGATATGC), using standard protocols with an annealing temperature of 47° C for 30 cycles. The PCR products were sequenced by the MACROGEN service, and sequences were submitted to GenBank (Accession numbers: HM584843–HM584883). Data for outgroups (*Latrodectus*, *Enoplognatha*), were obtained from GenBank. Preliminary alignments were done using ClustalW (Thompson et al. 1994) with gap opening and extension costs set at 24/6 and 8/2. Most of the sequences aligned readily; however, these preliminary alignments revealed an area of a particularly difficult alignment. Analyses of Clustal aligned matrices gave results largely incongruent with prior phylogenetic hypotheses, which were based on more data, mostly due to the placement of the root of the *Anelosimus* tree. Therefore, preliminary alignments were followed by manual and automated alignments taking into consideration the implied secondary structure of ITS2 (Fig. 1). I used the ITS2 database (online at http://its2.bioapps.biozentrum.uni-wuerzburg.de/cgi-bin/index.pl?about) to annotate the sequences and find the 5.8 and 28S flanking regions. *Anelosimus* ITS2 sequences were generally short, ranging from 223–305 bp. Non-ITS2 sequences were then removed and ITS2 secondary structure implied using the 4Sale software (Seibel et al. 2006, 2008). A standard model of ITS2 secondary structure was developed by Sehultz et al. (2005). This model has one long arm, or 'helix' (helix III), and three shorter helices (helices I, II, and IV), all four radiating from an area of a large loop. Secondary structure analyses reveal that the region that aligns poorly using Clustal corresponds to helix IV of the consensus ITS2 secondary structure model (Schultz et al. 2005) which is present in *Latrodectus*, *A. rupununi* Levi 1956, and a short version of it in *Enoplognatha*, *A. nigrescens* (Keyserling 1884) and *A. ethicus* (Keyserling 1884), but lost in the '*eximius* lineage' (Fig. 1).

Once this helix is identified, manual alignment of this region is facilitated, essentially aligning apparently homologous regions of helix IV in those taxa that have it, and inserting a gap for the entire arm region in those taxa that lack it. Automated alignment was also

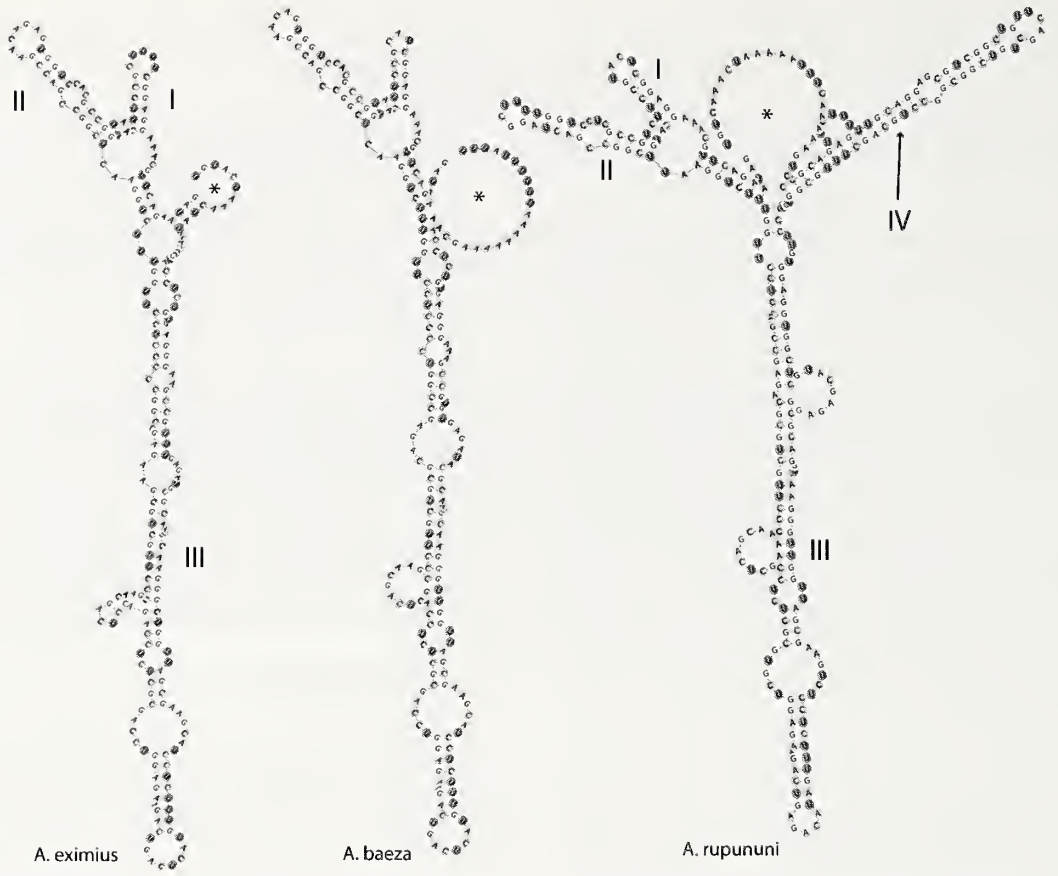

Figure 1.—Secondary structure (Bruccoleri layout) of ITS2 as implied by 4SALE for two species of the *eximius* lineage (*A. eximius* and *A. baeza*) and *A. rupununi*. The overall similar secondary structure reflects sequence similarity across most of the ITS2 sequence in these taxa that is readily alignable. However, *A. rupununi* has a helix (arrow), corresponding to helix IV of the ITS2 consensus structure of Schultz et al. (2005) that has been lost in the *eximius* lineage. A second region of difficult alignment is a loop region preceding this helix IV (stars).

conducted with the 4Sale software, using the remote 4Sale option. The automated alignment was not modified other than by fixing the first eight aligned characters, representing a five base pair sequence identical in all taxa, which had been rather randomly spread out. The remainder of the automated alignment did not contain conspicuous areas of misalignment. Aligned matrices and results are available from the author upon request.

The appropriate substitution model was selected with Modeltest (Posada and Crandall 1998), using the AIC criterion (Posada and Buckley 2004) with a parsimony tree chosen as the basis for Modeltest. The best model was GTR + Γ + I (Yang 1994). Bayesian analysis was performed using MrBayes V3.1.2 (Huelsenbeck and Ronquist 2001). The Markov chain Monte Carlo was run with four chains for 10,000,000 generations (repeated twice), sampling the Markov chain every 1000 generations, and the sample points of the first 5,000,000 generations were discarded as "burnin". Maximum likelihood analyses were conducted in the program Garli (Zwickl 2006), using the GTR + Γ + I model and 200 search replications. Parsimony analysis was done using TNT default settings under traditional search, with 1000 search replications. To calculate divergences among and within species in previous studies (Table 1), I downloaded sequences from GenBank via Mesquite (Maddison and Maddison 2009) and calculated uncorrected genetic distances in Mesquite.

The phylogenies are largely congruent using the Bayesian, likelihood, or parsimony criteria, and whether based on the manual or automated alignment (Fig. 2); hence, only the Bayesian results are discussed. To the extent that the current results are comparable to prior studies that included more taxa, they recapitulate the deeper-level phylogeny of Agnarsson et al. (2007, 2010) based on six molecular loci combined with morphology (Fig. 2). However, the analysis does not resolve relationships among closely related species of the *studiosus/jucundus* groups and does not reflect strong mitochondrial population structure within *A. eximius*.

Within *Anelosimus*, therefore, the utility of ITS2 seems very limited at the lowest taxonomic level (within species, between closely related species), but higher at intermediate taxonomic levels. Other studies of closely related theridiid species have also found little to no informative variation among closely related species (Zhang et al 2004, Vink et al. 2008). However, in cases where population structuring is particularly strong, such as in trapdoor spiders (Bond & Stockman 2008) and cave-dwelling nesticids (Hedin 1997), ITS2 was found to be useful at the interspecific, and even intraspecific level. Based on this and prior studies, ITS2 is a useful and readily obtainable marker for phylogenetic studies that look at relationships within genera and families of spiders. In general, intraspecific variation is low in spiders (about 1% on average, Table 1), as is the variation between sister species, but the variation differs across groups and is notably high in some trapdoor and cave dwelling spiders (Table 1). Closely related *Anelosimus* and *Latrodectus* species have very low interspecific variation (typically < 1%, about 0.7% in *A. eximius*, which shows high mitochondrial variation), insufficient to resolve relationships among closely related species, or to diagnose species. The utility of ITS2 at lower taxonomic levels thus will vary depending on the group. At higher taxonomic levels the main difficulty will be extreme sequence divergence (e.g., 27% between *A. rupununi* and *A. eximius*), thus complicating alignment. However, ITS2 secondary structure can facilitate alignment of divergent

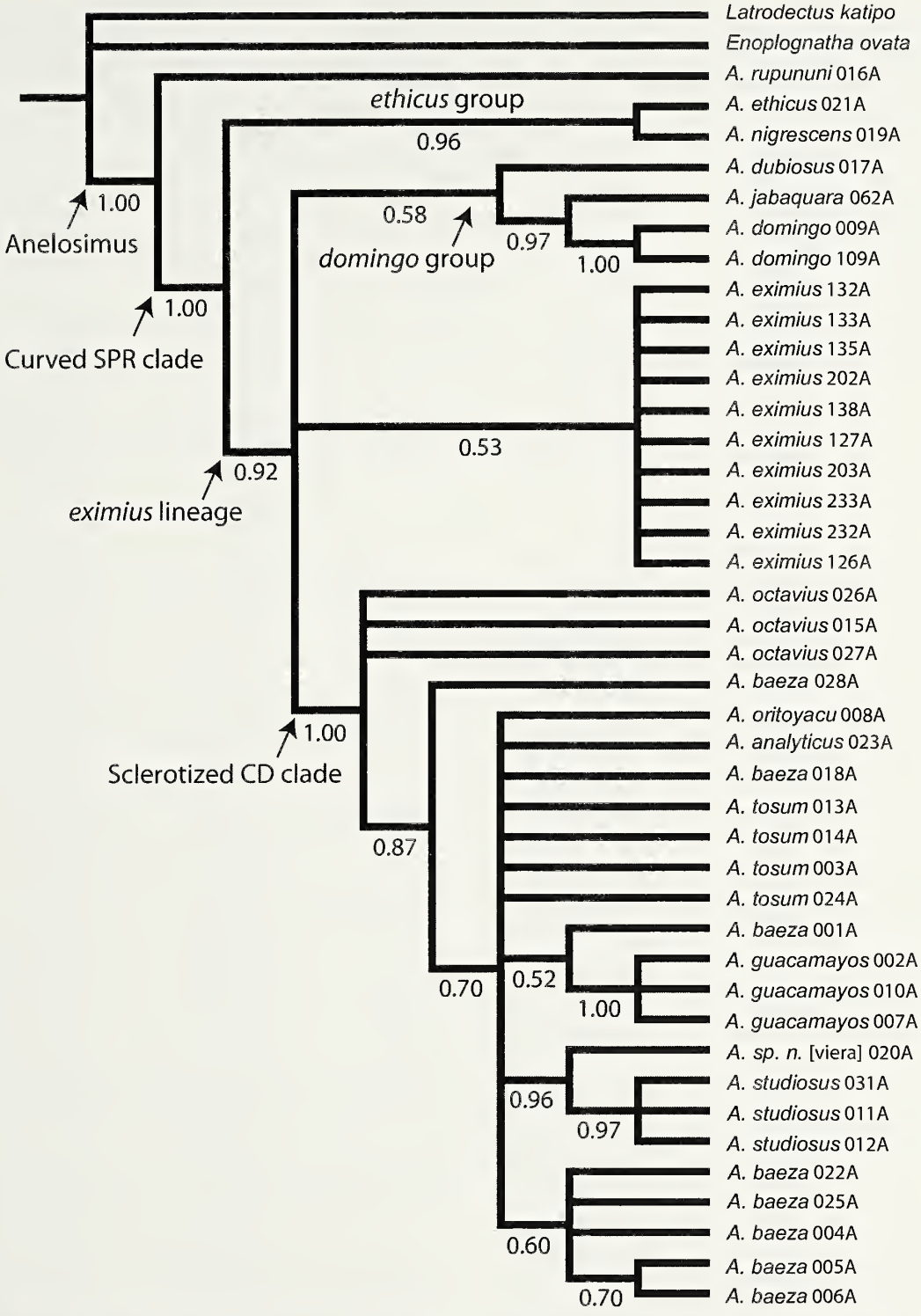

Figure 2.—50% Majority consensus from the Bayesian analysis of secondary-structure-informed manual alignment with numbers showing posterior probability support values. Major deeper level clades and species groups well supported by prior work are recovered: see clade labels. All labeled clades were recovered in all analyses, except the '*domingo* group'. However, at lower taxonomic levels very little variation was observed, resulting in low resolution. Within the 'sclerotized CD clade' (*A. analyticus* plus the *jucundus/studiosus* complex) only *A. guacamayos* Agnarsson 2006 and *A. studiosus* (Hentz 1850) were recovered as monophyletic, the relationships among species were largely unresolved and inconsistent with prior work (Agnarsson 2006, 2010; Agnarsson et al. 2007). Within *A. eximius*, a species showing population division and strong mitochondrial structuring, no phylogenetic structure was recovered.

Table 1.—ITS2 maximum intraspecific sequence divergences, and estimation of maximium and minimum divergences between sister species, in previously published studies of spiders. Estimated intraspecific sequence divergence is likely conservative overall, as some species were sampled only by 2–3 individuals. However, even for species sampled by 10 or more individuals and from geographically distant localities (e.g., *Latrodectus katipo*, *Anelosimus eximius*) the divergences were low.

Family	Genus	Species or putative species	Maximum intraspecific sequence divergence	Reference
Araneidae	*Poltys*	*illepidus*	0	Smith 2006
Araneidae	*Poltys*	*stygius*	0	Smith 2006
Araneidae	*Poltys*	*laciniosus*	0	Smith 2006
Cyrtaucheniidae	*Aptostichus*	clade 5	0.039	Bond and Stockman 2008[4]
Cyrtaucheniidae	*Aptostichus*	Clade 2	0	Bond and Stockman 2008
Cyrtaucheniidae	*Aptostichus*	Clade 3	0.025	Bond and Stockman 2008
Cyrtaucheniidae	*Aptostichus*	Clade 1	0.004	Bond and Stockman 2008
Linyphiidae	*Orsonwelles*	*graphica*	0.005	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*macbeth*	0.01	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*falstaffius*	0	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*polites*	0	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*otliello*	0.005	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*aubersonorum*	0	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*malus*	0.002	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*arcanus*	0.02	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*calx*	0.002	Hormiga et al. 2003
Linyphiidae	*Orsonwelles*	*ventus*	0.02	Hormiga et al. 2003
Lycosidae	*Pardosa*	*astigera*	0.03	Chang et al. 2007
Lycosidae	*Pardosa*	*astigera* (phenotype A)	0.003	Chang et al. 2007
Lycosidae	*Pardosa*	*astigera* (phenotype B)	0.005	Chang et al. 2007
Nesticidae	*Nesticus*	*barri*	0.0025	Hedin 1997[1]
Nesticidae	*Nesticus*	*barrowsi*	0.0102	Hedin 1997
Nesticidae	*Nesticus*	*bishopi*	0.0051	Hedin 1997
Nesticidae	*Nesticus*	*cooperi*	0.0059	Hedin 1997
Nesticidae	*Nesticus*	"*dellingeri*"	0.0076	Hedin 1997
Nesticidae	*Nesticus*	*gertschi*	0.0152	Hedin 1997
Nesticidae	*Nesticus*	*minus*	0.0119	Hedin 1997
Nesticidae	*Nesticus*	*nasicus*	0.0077	Hedin 1997
Nesticidae	*Nesticus*	*silvanus*	0.0034	Hedin 1997
Nesticidae	*Nesticus*	*stupkai*	0.0102	Hedin 1997
Nesticidae	*Nesticus*	*carteri*[2]	0.0321	Hedin 1997
Nesticidae	*Nesticus*	nov. sp	0.0051	Hedin 1997
Nesticidae	*Nesticus*	*paynei*	0.0076	Hedin 1997
Nesticidae	*Nesticus*	*tennesseensis*	0.0085	Hedin 1997
Salticidae	*Havaika*	OK9, OK24, OW28, OW29	0.0176	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	OK8, OK23, OW111, OW158	0.03	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	H83, H109, H137	0.005	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	EM128, WM88, WM159	0.018	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	K85, K86, K87	0.03	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	EM81, MK82, WM89	0.0025	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	H10, H110, EM90	0.015	Arnedo and Gillespie 2006[3]
Salticidae	*Havaika*	WM88, WM159, EM128	0.018	Arnedo and Gillespie 2006[3]
Theridiidae	*Latrodectus*	*katipo*[5]	0.002	Vink et al. 2008
Theridiidae	*Latrodectus*	*hasselti*	0	Vink et al. 2008
Theridiidae	*Latrodectus*	*hasselti*	0.0027	Zhang et al. 2004
Theridiidae	*Latrodectus*	*mactans*[6]	0.014	Zhang et al. 2004
Theridiidae	*Anelosimus*	*eximius*	0.007	This study
Theridiidae	*Anelosimus*	*domingo*	0	This study
Theridiidae	*Anelosimus*	*tosum*	0.008	This study
Theridiidae	*Anelosimus*	*studiosus*	0.01	This study
Theridiidae	*Anelosimus*	*guacamayos*	0.002	This study
Theridiidae	*Anelosimus*	*octavius*	0.007	This study
Theridiidae	*Anelosimus*	*baeza*	0.02	This study
Average			**0.01**	

Table 1.—Continued.

	Interspecific sequence divergence (sister species)		
	Min	Max	Reference
Nesticus	0.40%	~9%	Hedin 1997
Latrodectus	0%	0.50%	Vink et al. 2008
Latrodectus	0%	0.83%	Zhang et al. 2004
Havaika	2%	4%	Arnedo and Gillespie 2006[3]
Pardosa	2.50%	6.70%	Chang et al. 2007
Orsonwelles	0.70%	5.90%	Hormiga et al. 2007
Anelosimus	0.60%	2.80%	This study
Poltys	0.70%	~10%	Smith 2006
Aptostichus	2.20%	5.30%	Bond and Stockman 2008

[1] Note that multiple individuals within populations always had zero sequence divergence, interspecific sequence divergences reflect those among isolated populations
[2] Represented two species, each with intraspecific divergence less than 1.5%
[3] Informal species, reflecting putative species from Fig. 5 in Arnedo and Gillespie (2006), codes in 'species' column refer to specimens
[4] Sequences from 'clade 4' were not found on Genbank
[5] One variable site
[6] More divergence found within than between individuals

sequences (Young & Coleman 2004) (Fig. 1). Based on my findings and those of Vink et al. (2008) and Zhang et al. (2004), ITS2 does not emerge as a suitable choice of universal DNA barcode.

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SHORT COMMUNICATION

Redescription of *Geogarypus irrugatus* from Sumatra (Pseudoscorpiones: Geogarypidae)

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Abstract. The geogarypid pseudoscorpion *Geogarypus irrugatus* (Simon 1899) is redescribed based upon the syntype series from Sumatra. All subsequent records of this species from Asia are shown to be misidentifications.

Keywords: Taxonomy, morphology, Asia

The pseudoscorpion *Garypus irrugatus* Simon 1899 was described from an unspecified number of specimens collected from the Indonesian island of Sumatra by J.-L. Weyers. Simon's (1899) description was relatively brief and without figures (which was quite standard for the era). It was transferred to *Geogarypus* Chamberlin 1930 when the genus was formed by Chamberlin (1930). Subsequent literature records of *G. irrugatus* all appear to be based upon misidentifications, which began with the attribution by With (1906) of specimens collected from Thailand to *Garypus irrugatus*. Later, Chamberlin (1930) reported specimens from the Philippines, China and Indonesia under this name, following the concept of the species portrayed by With (1906). Many of the specimens examined by With (1906) and Chamberlin (1930) were reexamined by Harvey (2000) who found that all represent *G. longidigitatus* (Rainbow 1897), a distinct species with long chelal fingers and a distinct colored carapace. In addition, Harvey (2000) found a further seven species or subspecies to be synonyms of *G. longidigitatus*: *Garypus personatus* Simon 1900 from Hawaii (Simon 1900), *G. javanus* Tullgren 1905 from Java (Tullgren 1905), *Geogarypus formosanus* Beier 1931 from Taiwan (Beier 1931), *G. (G.) marquesianus* Chamberlin 1939 from Îles Marquises (Chamberlin 1939), *G. audyi* Beier 1952 from Malaysia (Beier 1952), *G. (G.) micronesiensis* Morikawa 1952 from Japan (Morikawa 1952), and *G. (G.) javanus takensis* Beier 1967 from Thailand (Beier 1967).

In addition, several other literature records of *G. irrugatus* were based upon other species. Beier (1976) reported three adults and four nymphs from Bhutan, which are lodged in Naturhistorisches Museum, Basel and have been examined during this study. Although similar to *G. irrugatus*, they are certainly not referrable to this species but their identity is currently uncertain. Mahnert (1977) listed several specimens from Kirghizia (Tien-Shan: Terskey-Ala-Too), but Schawaller (1985) noted that these specimens were referrable to *G. continentalis*, a correction that was overlooked by Harvey (1991). Schawaller (1994, 1995), using the traditional redescriptions of *G. irrugatus* (e.g., With 1906; Chamberlin 1930), tentatively suggested that *G. irrugatus* may be a synonym of *G. javanus* (Tullgren 1905), which is now a junior synonym of *G. longidigitatus* (Harvey 2000).

Thus, it appears that all subsequent specimens that have been referred to *G. irrugatus* represent other species and that only the type specimens can be unequivocally referred to *G. irrugatus*. To clarify the status of this species, a redescription of *G. irrugatus* is presented, based upon the type series.

METHODS

The material examined for this study is lodged in the Muséum National d'Histoire Naturelle, Paris (MNHN) and Naturhistorisches Museum, Basel (NMB). The terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey 1992) and chelicera (Judson 2007). Simon's (1899) description was translated from Latin with the assistance of the online translation service Translation Guide (http://www.translation-guide.com/free_online_translators.php) and Brown (1956).

The specimens were examined with an Olympus BH-2 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule and are presented in mm. The specimens were examined using temporary slide mounts by immersing the specimens in a mixture of 90% glycerol and 10% lactic acid, and mounting them on microscope slides with 10 mm coverslips supported by small sections of 0.25 mm diameter nylon fishing line.

SYSTEMATICS

Family Geogarypidae Chamberlin 1930
Genus *Geogarypus* Chamberlin 1930

Type species.—*Geogarypus minor* L. Koch 1873, by original designation.

Remarks.—The genus *Geogarypus* was segregated by Harvey (1986) from *Afrogarypus* Beier 1931 and *Indogarypus* Beier 1957 by the lack of obvious sulci on the dorsal (*Afrogarypus*) or internal (*Indogarypus*) margins of the chelal hand. The clade *Geogarypus* + *Indogarypus* was defined by the presence of accessory chelal teeth on the fixed chelal finger (Harvey 1986), but this leaves *Geogarypus* without any discernible synapomorphies. Because *Geogarypus irrugatus* lacks a dorsal sulcus and has accessory chelal teeth, it is retained in *Geogarypus*.

Geogarypus irrugatus (Simon 1899)
Figs. 1–5

Garypus irrugatus Simon 1899:122.

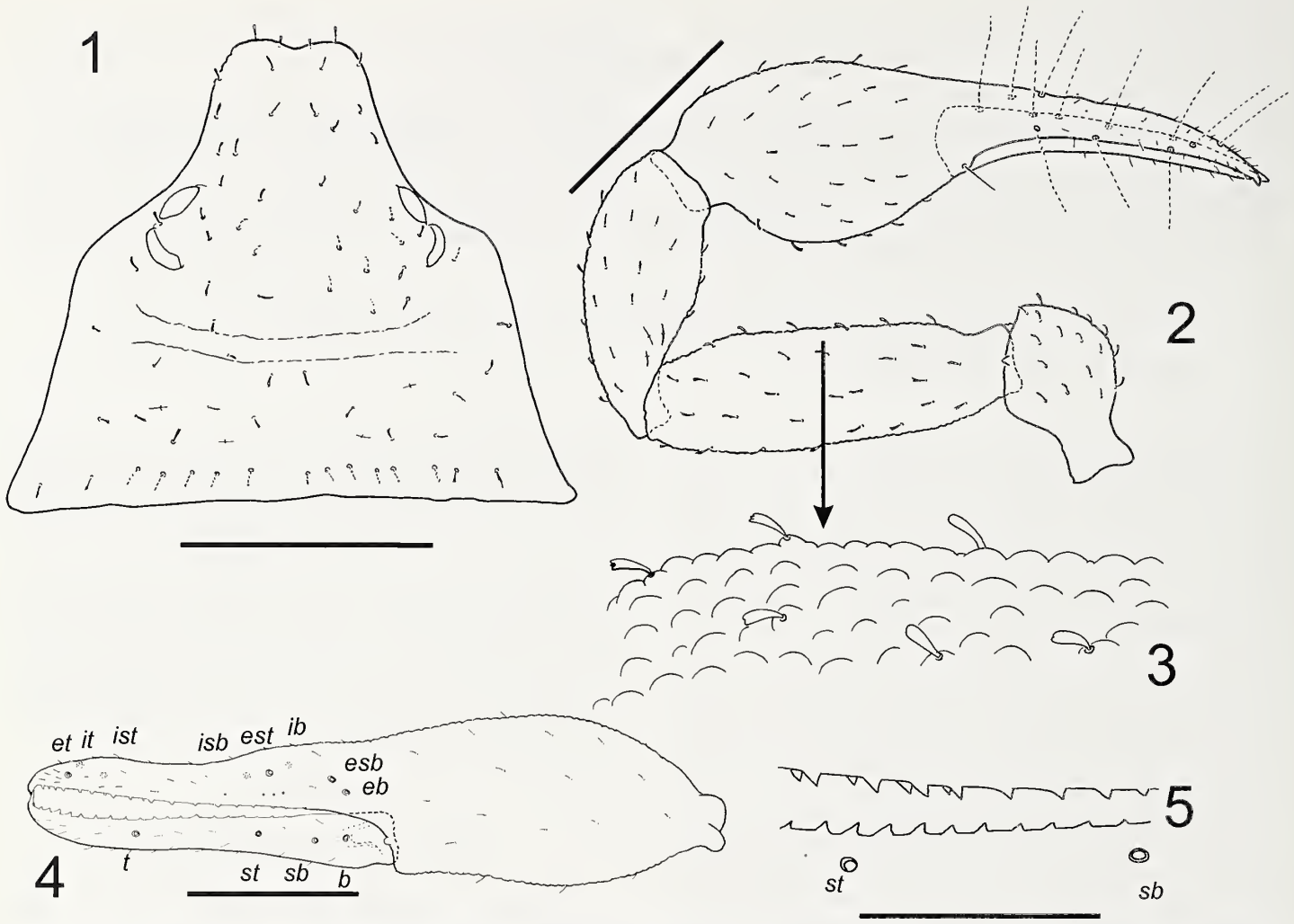
Geogarypus (Geogarypus) irrugatus (Simon): Beier 1932:233 (in part); Roewer 1937:270, fig. 221 (in part).

Geogarypus irrugatus (Simon): Roewer 1936:figs. 40a, b, 42c, d (in part); Harvey 1986:760 (in part); Harvey 1991:255 (in part); Beron 2002:34 (in part); Harvey 2009 (in part).

Not *Garypus irrugatus* Simon: With 1906:28–29, 104–107, figs. 8a, b, plate 1 figs. 6a–d, plate 2 figs. 1a–d [misidentification; *G. longidigitatus* (Rainbow 1897)]

Not *Geogarypus irrugatus* (Simon): Chamberlin 1930:611 [misidentification; *G. longidigitatus*]; Chamberlin 1931:114, figs. 9m, 15o, 16g, 17z, 32k, l, 37w [misidentification; *G. longidigitatus*]; Beier 1976:99–100 [misidentification; true identity uncertain]; Mahnert 1977:94 [misidentification; *G. continentalis* (Redikorzev 1934)].

Material examined.—*Lectotype (present designation):* 1 female, INDONESIA: Sumatra, J.-L. Weyers (MNHN 21313). *Paralecto-*



Figures 1–5.—*Geogarypus irrugatus* (Simon), female lectotype from Sumatra: 1. Carapace, dorsal aspect; 2. Left pedipalp, dorsal aspect; 3. Detail of pedipalpal femur, dorsal aspect; 4. Left chela, lateral aspect; 5. Detail of chelal teeth, lateral aspect. Scale lines = 0.3 mm (Figs. 1, 2), 0.2 mm (Fig. 4), 0.1 mm (Fig. 5).

types: 6 males, 2 females, 1 tritonymph, collected with lectotype (MNHN 21313).

Diagnosis.—*Geogarypus irrugatus* is a small species [e.g., pedipalpal femur 0.442 (♂), 0.518 (♀) mm], with strongly clavate vestitural setae, and without an internal constriction on the chelal hand.

Description.—*Adults:* Color impossible to discern (all specimens very strongly bleached), but according to Simon (1899, translated from the original Latin description), "Abdomen dorsally dark tawny, cephalothorax, especially anteriorly, very dark, abdomen darkly spotted, regularly quadriseriate, marked anteriorly. Pedipalps dark, femora internally within and hand intensely dark and olive. Legs pale yellow." Most setae clavate and with rounded tips. Surface of most cuticular regions strongly and evenly granulate.

Chelicera: with 5 setae on hand, all setae acuminate; movable finger with 1 subdistal seta; subterminal tooth of movable finger not bifurcate and not enlarged; galea of ♂ and ♀ apparently simple, without rami; rallum of 1 small blade, without serrations; serrula exterior with 14 blades (♂); lamina exterior present.

Pedipalp: All pedipalpal segments strongly granulate (Figs. 2, 3); trochanter 1.66 × (♂), 1.56 × (♀), femur 3.37 × (♂), 3.20 × (♀), patella 2.31 × (♂), 2.32 × (♀), chela (with pedicel) 3.39 × (♂), 3.39 × (♀), chela (without pedicel) 3.25 × (♂), 3.26 × (♀) longer than broad, hand rounded, bulging medially, 1.39 × (♂), 1.45 × (♀) longer than broad, movable finger 1.35 × (♂), 1.25 × (♀) longer than hand. Femur without tactile setae (Fig. 2). Patella with three lyrifissures situated dorsally near pedicel. Hand with long straight spine on internal face, near base of fixed finger. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 2): *eb*, *esb* and *est* situated on external margin of fixed finger, sub-basally; *isb* on internal margin, closer to *ib* than to *ist*; *it*, *ist* and *et* grouped distally on fixed finger; trichobothria of movable finger arranged with *b* and *sb* situated basally, and *sb* midway between *b* and *st*. Venom apparatus present in both chelal fingers, venom duets and nodus ramosus not discernible. Chelal teeth acute, retrorse and widely spaced (Fig. 5); fixed finger with ca. 17 (♂, ♀) teeth plus ca. 8 accessory teeth; movable finger with ca. 16 (♂) or 15 (♀) teeth. Fixed chelal fingers undulate in lateral view with noticeable dorsal constriction near middle of finger (Fig. 4); fixed finger with a row of 4 pit-like sensillae on external margin (Fig. 4).

Cephalothorax: carapace (Fig. 1) strongly sub-triangular, 0.83 × (♂), 0.78 × (♀) longer than broad; with 2 pairs of corneate eyes situated away from the anterior margin of carapace; with numerous setae, including 4 (♂, ♀) near anterior margin and 17 (♂) or 18 (♀) near posterior margin; with single medial furrow. Pedipalpal coxa with distinct coxal shoulder; medial maxillary lyrifissure situated distally.

Abdomen: pleural membrane wrinkled-plicate, with investing setae. Tergal chaetotaxy: ♂, 10: 12: 13: 11: 13: 12: 14: 11: 8: 8: 7: 2; ♀, 8: 12: 12: 11: 14: 13: 12: 11: 9: 8: 7: 6: 2; setae uniseriate and clavate. Sternal

chaetotaxy: ♂, 10: (0) 9 (0): (0) 8 (0): 8: 9: 10: 9: 10: 7: 7: 0; ♀, 7: (0) 8 (0): (0) 8 (0): 8: 11: 12: 10: 9: 7: 6: 0; setae uniseriate and acuminate; glandular setae absent; anus not surrounded by sternite XI.

Genitalia: not discernible.

Legs: femora of legs I and II much longer than patellae 1 and II, respectively; femur + patella of leg IV 3.06 × (♂) longer than broad; metatarsi and tarsi not fused; legs without tactile setae; subterminal tarsal setae arcuate and acute; arolium much longer than claws, not divided.

Tritonymph: Generally as for adults except:

Chelicera: galea with 4–5 distal rami.

Pedipalp: trochanter 1.59 ×, femur 3.16 ×, patella 2.59 ×, chela (with pedicel) 3.73 ×, chela (without pedicel) 3.60 ×, hand 1.54 × longer than broad, movable finger 1.32 × longer than hand. Fixed chelal finger with 7 trichobothria, movable chelal finger with 3 trichobothria, *isb* and *sb* absent. Fixed finger with ca. 16 plus 6 accessory teeth; movable finger with ca. 18 teeth.

Cephalothorax: carapace 0.81 × longer than broad.

Legs: metatarsi and tarsi not fused.

Dimensions (mm).—*Male paralectotype:* Body length 1.18. Pedipalps: trochanter 0.234/0.141, femur 0.442/0.131, patella 0.314/0.136, chela (with pedicel) 0.672/0.198, chela (without pedicel) 0.644, hand length 0.275, movable finger length 0.371. Carapace 0.464/0.562; anterior eye diameter 0.48, posterior eye diameter 0.41. Leg IV: femur + patella 0.352/0.115, tibia 0.255/0.080, metatarsus 0.128/0.052, tarsus 0.141/0.040.

Female lectotype: Body length 1.41. Pedipalps: trochanter 0.262/0.168, femur 0.518/0.162, patella 0.571/0.160, chela (with pedicel) 0.837/0.247, chela (without pedicel) 0.805, hand length 0.358, movable finger length 0.448. Carapace 0.538/0.691; anterior eye diameter 0.058, posterior eye diameter 0.060.

Tritonymph paralectotype: Body length 0.992. Pedipalps: trochanter 0.173/0.109, femur 0.325/0.103, patella 0.262/0.101, chela (with pedicel) 0.575/0.154, chela (without pedicel) 0.554, hand length 0.237, movable finger length 0.314. Carapace 0.324/0.400.

Remarks.—The small size of *Geogarypus irrugatus* [e.g., pedipalpal femur 0.442 (♂), 0.518 (♀) mm] renders it most similar to several other Asian species such as *G. asiaticus* Murthy and Ananthakrishnan 1977 from India [e.g., pedipalpal femur 0.52 (♀) mm (Murthy & Ananthakrishnan 1977)], *G. ceylonicus* Beier 1973 from Sri Lanka [e.g., pedipalpal femur 0.40 (♂), 0.49 (♀) mm (Beier 1973)], *G. globulus* Sivaraman 1980 from India [e.g., pedipalpal femur 0.456 (♂) mm (Sivaraman 1980)], *G. granulatus* Murthy and Ananthakrishnan 1977 from India [e.g., pedipalpal femur 0.46 (♀) mm (Murthy & Ananthakrishnan 1977)], *G. palauanus* Beier 1957 from Palau [e.g., pedipalpal femur 0.59 (♂), 0.51 (♀) mm (Beier 1957)], *G. pisinnus* Harvey 1986 from Australia [e.g., pedipalpal femur 0.45–0.50 (♂), 0.54–0.585 (♀) mm (Harvey 1986)], and *G. sagittatus* Beier 1965 from Papua New Guinea and West Papua [e.g., pedipalpal femur 0.52–0.67 (♀) mm (Beier 1965)]. Many of these small species have been included in the subgenus *Indogarypus* Beier 1957 (Beier 1957, 1965; Murthy & Ananthakrishnan 1977; Sivaraman 1980), which was based on the posterior transverse carapaceal furrow situated basally with the sides directed anteriorly and flattened laterally; the pedipalpal vestitural setae short but distinct, the medial setae slightly clavate; the pedipalps with some seta-bearing granules; the presence of a internal constriction of the chelal hand at the base of the fingers; stouter legs with the metatarsal and tarsal suture less distinct (Beier 1957). *Geogarypus irrugatus* mostly fits this diagnosis, but appears to lack the internal constriction on the chelal hand, and does not bear any enlarged seta-bearing granules on the pedipalps. The description of *G. pisinnus* by Harvey (1986) partly conforms to this diagnosis, but it too does not possess any larger seta-bearing granules. Harvey (1986) restricted *Indogarypus*, which was recognised as a distinct genus of Geogarypidae, to just the type species *G. indicus* (Beier 1930), but it is clear that the status and composition of *Indogarypus* requires further research after a more comprehensive review of these small Australasian geogarypids.

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SHORT COMMUNICATION

Proximate cues governing egg sac discrimination and recognition in the wolf spider *Pardosa milvina* (Araneae: Lycosidae)

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Abstract. Female lycosids carry their egg sacs on their spinnerets until spiderlings emerge but spiders are occasionally found carrying shells, dirt, or other objects on their spinnerets, suggesting recognition errors can occur. We investigated some proximate cues that may influence egg sac recognition and discrimination in the wolf spider *Pardosa milvina* (Hentz 1844). We tested the ability of female *P. milvina* to discriminate among egg sacs based on size, texture, and contrast. We also tested the ability of *P. milvina* to discriminate between its own or a conspecific's egg sac, and the ability to discriminate between an egg sac that had just been removed and an egg sac that was removed seven days earlier. When given a choice, females significantly chose their own egg sac over plastic beads of equal mass, preferred large plastic beads equal in mass to an egg sac over small plastic beads, round over faceted beads, and showed a non-significant tendency to attach black rather than white beads of equal mass. When given a choice between two conspecific egg sacs, spiders more often rejected those that had been removed from the mother seven days earlier than those that had been freshly removed. Spiders were unable to recognize their own egg sacs versus a conspecific's. Although spiders recognize egg sacs from non-egg sacs based on mass, texture, and presumably odor when given the choice, acceptance of non-egg sacs was common when no real egg sac was available. Also, females would not reattach their own egg sac once an artificial one had been attached. Attachment of any object on the spinnerets apparently ceases searching or attachment behavior.

Keywords: Chemical recognition, dropping, artificial egg sac, lycosid

Adult female wolf spiders attach their egg sacs to their spinnerets and transport them as they move through the environment. The wolf spider, *Pardosa milvina* (Hentz 1844), is especially active (Walker et al. 1999; Samu et al. 2003), and females carry egg sacs that average 72% of the female's post-reproductive weight (Colancecco et al. 2007). Because of the large relative size of the egg sac and high activity level of these spiders, female *P. milvina* may be especially prone to dropping or losing the egg sac. Misidentification and subsequent adoption of another spider's egg sac is known to occur in some wolf spider species (Fujii 1980; Wagner 1995). There are also many anecdotal observations of adult female wolf spiders carrying other objects on their spinnerets such as pebbles, snail shells, pieces of cork, bits of soil, small seeds, rabbit droppings, thread pellets, bread pieces, and wads of paper or cotton (O'Connor 1896; Fabre 1912; Locket & Marsh 1957; Bristowe 1958; Fuji 1980). Such observations suggest that misidentification of egg sacs may be common despite the large potential fitness consequences of such errors. We investigated some of the proximate cues that may be used by female *P. milvina* to recognize its egg sac and also measured the frequency of errors in choosing various spherical objects that are not egg sacs. We measured the influence of five factors that may govern egg sac recognition ineluding size, texture, brightness contrast, diserimination of their own vs. a conspecific egg sac, and time elapsed since egg sac removal.

METHODS

Adult female *P. milvina* with egg sacs were collected in August and September from corn and soybean fields in Selinsgrove, Snyder County, Pennsylvania. Spiders were individually housed in 150-ml (= 5-oz) plastic containers with moistened peat moss and were fed a mixed diet of house cricket nymphs (*Acheta domesticus*) and fruit flies (*Drosophila melanogaster*) twice weekly. All test spiders received approximately equal quantities of both food types while being housed. We conducted a series of independent choice experiments with a sample size of 50 spiders for each of six experiments and 40 spiders for a seventh experiment. Each spider was used only once (i.e., a total of 340 females with egg sacs was used as test subjects for the experiments. We obtained extra egg sacs from an additional 40 females. These egg sacs were used as one of the egg sac choices, but these females were not used as test subjects.

Prior to a choice test, we placed each spider in a glass vial on ice for one minute to slow the spider and used entomological forceps to then remove the egg sac. After egg sac removal, the spider was immediately placed in a 166-ml (= 45-dram) plastic vial (10 cm high × 5 cm diameter), with a choice between two objects. Seven separate experiments were performed, six of which involved simultaneous presentation of two objects. The paired choices were as follows: 1) its own egg sac vs. a randomly selected conspecific egg sac removed from another female at the same time, 2) its own egg sac vs. a white plastic bead of approximate equal mass (11 mg) and diameter to that of a natural egg sac (3 mm), 3) a black plastic bead vs. a white plastic bead of equal mass (each 11 mg, 3mm diameter), 4) a small black plastic bead (2 mg, 1.8mm diameter) vs. a large black plastic bead approximately equal in mass and diameter to a female egg sac (11 mg, 3 mm diameter), and 5) a multi-faceted black plastic bead vs. a round black plastic bead of approximately equal mass and diameter (10.9 mg and 11 mg respectively, both 3 mm diameter). In a sixth experiment, we used a sequential presentation. A female was given its own egg sac immediately after it had attached a white plastic bead (11 mg, 3mm diameter) to its spinneret to determine if it would exchange the attached bead. Except for the choice test of small and large plastic beads, the artificial egg sacs consisted of plastic beads approximately equal in mass and diameter to that of a female's egg sac (female *P. milvina* egg sac = 13.1 mg, SE ± 01.6 mg, $n = 15$). To minimize possible effects of time, spider age, or egg sac developmental stage, we ran all six of the experiments concurrently. For a seventh experiment, we used an additional 80 spiders with egg sacs not used in any previous experiment. Forty females were used as sources for egg sacs, and the remaining 40 were used as test subjects. We randomly selected and removed 40 egg sacs from females and placed the egg sac individually for seven days within separate sealed plastic vials. Each

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Table 1.—Preference for one of two objects by adult female *P. milvina* that had recently had its egg sac removed. The first binomial test (Choice/No choice) *P*-values are based on significant differences from a 50% probability distribution for accepting one of the objects offered (attaching an object) versus ignoring both objects within the allowed time. The *P*-values for the second binomial test (among egg sacs chosen) compare only the frequency of choosing between the two objects of those females that made any choice at all. The seventh test recorded the number of females that would accept their own egg sac after attaching a plastic bead to their spinnerets.

Experiment	Choice	Choice	No. choice made	Binomial Test Choice/No. choice	Binomial test among egg sacs chosen
1. Own vs. Conspecific	Own: 20	Conspecific: 15	15	0.0020	0.0945
2. Own vs. Bead	Bead: 1	Own: 36	13	0.0003	< 0.0001
3. Black vs. White	Black: 21	White: 13	16	0.0044	0.0540
4. Small vs. Large	Small: 5	Large: 12	33	0.0087	0.0472
5. Round vs. Faceted	Round: 13	Faceted: 5	32	0.0160	0.0327
6. Fresh vs. Seven-day old	Fresh: 32	7-day old: 4	4	0.0008	< 0.0001
7. Attached vs. Own	Didn't switch: 49	Switched: 1	*	*	< 0.0001

166-ml vial was previously rinsed with alcohol and allowed to dry prior to placing the egg sac in the container. After 7 days, we then removed another 40 egg sacs from an additional 40 females. Each female from the second set of 40 spiders was then offered a choice between either the freshly removed egg sac of another female or the egg sac that had been removed from a conspecific seven days earlier.

For all experiments, test objects (egg sacs or plastic beads) were placed immediately adjacent to each other along the edge of the vial where the spider traveled. The position of each pair was alternated for every trial to minimize any potential bias due to placement. Spiders were observed for 15 min, after which we counted the number of individuals that attached each object. A positive choice was scored if the egg sac or bead was attached to the spinnerets with silk and the abdomen rose to a normal upright position within the 15-min period. Failure to attach the egg sac during the 15-min trial was scored as a no choice. The results were analyzed using two sets of binomial tests. Among all choice experiments, we used a binomial test comparing individuals that made a choice of either test object offered or made no choice at all. For this analysis, we tested whether the spiders showed a significant preference for attaching objects or ignoring them. We also used a binomial test to test for a significant preference among those individuals that attached one of the two objects offered. In this test, individuals that made no choice were dropped from the analysis.

RESULTS AND DISCUSSION

Pardosa milvina females showed significant differences in their tendency to ignore or attach various objects depending on the pair of test objects presented. Spiders attached objects to their spinnerets significantly more than 50% of the time when they were given choices between their own egg sacs and those of conspecifics. They also preferred to attach an object when the choice was its own egg sac or a white bead, black bead or a white bead, or the choice between a freshly removed egg sac or one that had been removed seven days earlier (Table 1). However, when spiders were given a choice between a small and large artificial egg sac, or a round versus faceted artificial egg sac, they were significantly more likely to ignore both objects (Table 1).

Females showed no significant preference for their own versus a conspecific's egg sac when given a choice (Table 1); however, a power test with a beta error level of 50% suggests a possible sample size too small to reliably accept the null hypothesis. A sample size of 188 rather than 35 would be needed to demonstrate a non-significant effect. Spiders also showed no significant preference between a black and white artificial egg sac of equal size, but there was a non-significant tendency to prefer black over white plastic beads (Table 1). However, here too, a power test suggests an insufficient sample size to accept the null hypothesis. Based on a 50% beta error level, a sample size of 69 would be required to reliably accept the null hypothesis. Females showed a small but significant preference for a large artificial egg sac equal in size to a natural egg sac compared to a smaller artificial egg sac. They also preferred a round plastic bead to a faceted one of equal mass (Table 1). Females attached their own egg sac significantly more often than a plastic white bead of approximately equal mass (Table 1); however, out of 50 females that had already attached a white plastic bead, only one female dropped it and reattached her own egg sac when given a choice. Females that were given a choice between another female's egg sac that was freshly removed or one that was removed seven days earlier, showed a highly significant preference for the freshly removed egg sac (Table 1).

Regardless of the choices available, some females failed to reattach any object even when offered their own egg sac, but the rejection rates tended to be lower when at least one of the choices was a real egg sac. The rejection rate of all offered objects varied considerably, from a low of 10% for individuals offered fresh or older conspecific egg sacs to a high of 66% for individuals offered large or small plastic beads. It is unknown if rejecting egg sacs after removal is a generally maladaptive response. It is possible that various egg sac parasites may cause the female to drop her egg sac during parasitism. Females that then reject these parasitized egg sacs may benefit by depositing and brooding a second egg sac rather than carrying one that was parasitized.

Females were unable to discriminate between their own and another female's egg sac. This is surprising, since kin recognition of offspring is known to exist in *P. milvina* (Anthony 2003). Anthony (2003) found that *P. milvina* females with egg sacs or with recently dispersed spiderlings preferentially avoided preying on their own offspring. This study, combined with our data, suggests that a cuticular compound or other substance intrinsic to the spider itself may be important in kin recognition and that the egg sac surface, egg surface, or both may interfere or inhibit such chemical recognition. Other studies have documented that the sicariid, *Loxoceles gaucho* (Gertsch 1967) and salticid *Portia labiata* (Thorell 1887) can discriminate between their own egg sac and that of a conspecific (Clark & Jackson 1994; Japyassú et al. 2003). However, in both of these studies, the web itself seemed to be an important factor in discrimination, rather than the egg sac per se and in *L. gaucho*, egg sac adoption was common as measured by time near the egg sac.

Although *P. milvina* exhibit some ability to discriminate between egg sacs and non-egg sacs, errors were frequent. *Pardosa milvina* appear to have a weak preference based on size, relative shape, and perhaps brightness contrast when attaching an object after egg sac loss. Spiders do have a strong preference for their own egg sacs over round plastic objects of equal mass and contrast, suggesting that mass and contrast alone were not the primary means of discrimination, but that texture, size, and relative shape provided composite information for recognition. Despite a strong preference for attaching real egg sacs

rather than artificial ones, when females lack a real egg sac as a ehoice, attachment of artificial ones was quite common. Acceptance of artificial egg sacs varied considerably from a low of 34% for small versus large plastic beads to a high of 68% when the choice was black versus white plastic beads.

It remains unclear if the fitness costs of lost egg sacs are high, but certainly carrying a misidentified object would incur significant energetic and fitness costs. Lycosid egg sacs usually require that the mother open them to release the spiderlings; thus, the loss of an egg sac would result in the complete failure to produce offspring from that clutch. Further, a female is unlikely to produce another egg sac when an object is already attached to her spinnerets (Wagner 1995). During our study, many females quickly produced a second egg sac within as little as two days after the first was removed. However, we found that females that attached other objects failed to produce another egg sac. In a short breeding season, this delay may have significant consequences for reproduction.

Poor egg sac recognition implies that seleetion pressure on discrimination is weak. Either the cost of such recognition errors is far lower than we believe or the accidental loss of an egg sac is a very rare event and of little evolutionary consequence. Despite observing high rates of artificial egg sac attachment under laboratory conditions, few field-caught wolf spiders are found with foreign objects on their spinnerets. Out of 382 wolf spiders initially collected for this study, only two spiders (0.5%) had objects other than an egg sac attached to their spinnerets (these were not used in this study). In one case, it was a small, unidentified seed and in the other case, it was a small bit of soil attached to the spinnerets. Since errors appear to be common under laboratory conditions, this suggests that females either rarely have their egg sacs become detached or that few objects sufficiently resemble an egg sac for a mistake to be made during the critical period in which females search for them. Alternatively, artificial objects may be attached somewhat frequently, but may not remain on long enough to be observed under field conditions.

We suggest caution in interpreting the apparently low frequency of egg sac loss and attachment of artificial egg sacs found in our field census. Our field data are based on a static frequency of 0.5% (i.e., that 0.5% of all egg sac carrying females are carrying non-egg sacs at any given time). This is quite different than assuming that 0.5% of all females lose their egg sacs or that 0.5% of all females attach other objects to their spinnerets. As our study indicates, many females made no choice once their egg sacs were removed. These females would be indistinguishable from gravid females that have not produced egg sacs, post-reproductive females that had spiderlings already dispersed, or virgin females. Thus, egg sac loss may be considerably more frequent than ean be reliably measured in the field. Further, if females that carry artificial egg sacs are more likely to drop them later, as is the case with *P. milvina* (Colancecco et al. 2007), this will further underestimate the true frequency of artificial egg sac carrying. We must also be very cautious in equating the frequency of field observations with the evolutionary significance of the behavior. Copulation, parasitism, and feeding (including cannibalism) are also infrequently observed among field populations of cursorial spiders. Although observed infrequently, these behaviors are under strong selection and likely occur at much higher frequencies than can be easily observed. Our field observations could be erroneously interpreted to mean that only 0.5% of wolf spiders lose their egg sacs and reattach foreign objects. More likely, it means that, like copulation, feeding, and parasitism, it is of short duration and females with egg sacs may seek refuge. Our field data may also be biased toward encumbered females that engage in risky behaviors.

Colancecco et al. (2007) found that female *P. milvina* readily drop artificial egg sacs but rarely drop real ones while subduing large prey or escaping larger predatory wolf spiders. They also found that once artificial egg sacs were dropped, females failed to search for them or reattach them during a 2-h period. This study suggests that females may preferentially drop artificial egg sacs over real egg sacs and may use a post-attachment tactile cue to evaluate artificial egg sacs. However, Colancecco et al. (2007) also suggested that while grappling with prey or predators, spiders may become displaced from their egg sacs, making lost egg sacs more difficult to locate. Our result showed that females will rarely drop artificial egg sacs when offered their own back, which suggests that reattachment itself inhibits searching and additional reattachment behavior.

During our study, the spiders usually contacted both offered objects before making a choice and only rarely immediately chose the first object they contacted. Even when choosing between their own egg sacs and conspecifics' egg sacs, the spiders would often contact both egg sacs before choosing one. Females responded qualitatively differently to artificial egg sacs. Spiders tended to contact artificial beads with outstretched legs more often than with real egg sacs. With real egg sacs, females would tend to touch the objects less with outstretched legs but instead grasp, hold, or pick up the egg sacs with their chelicerae and pedipalps more often before attachment. Many times the spider would pick up different objects, manipulate them and drop them, or just hold them for the duration of the fifteen minutes suggesting that acceptance of egg sacs may require a longer time interval. Colancecco et al. (2007) allowed female *P. milvina* 12 h to accept or reject a single round black plastic bead very similar to those used for this study. Acceptance rates were between 52–69% for this study, suggesting that a longer period of time may have modestly increased overall acceptance rates of artificial egg sacs.

Females did show a remarkable ability to distinguish between egg sacs that were recently removed from those that had been removed a week earlier. We were uncertain of the precise mechanism by which females made these evaluations. Fungi or bacteria may have attacked the week-old egg sacs and provided an odor cue. However, we saw no indication of fungus or decomposition on the outside surface of these egg sacs. This is also unlikely given that the container was sterilized prior to placing the egg sac in a sealed vial. It is also possible that the eggs within the sac require periodic turning to remain viable as is necessary with some tarantula species (Marshall 1996; Saul-Gershenz 1996). In this case, females may have been able to evaluate viability by assessing if the eggs moved within the sac and remained non-agglutinated. Females periodically added loose silk to their egg sac. This fresh silk or a pheromone embedded in it could also potentially provide a means to distinguish freshly removed egg sacs from older ones.

Female lycosids clearly use composite information rather than a single cue to recognize egg sacs. Size, texture, shape, and odor are almost certainly involved. However, the strong preference for fresh compared to older egg sacs suggests that odor cues may be a particularly strong means of recognition. Additional studies that examine chemical recognition of egg sacs or state-dependent value of searching and attachment (i.e., female body condition or age) may prove fruitful.

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Figures 1a–e. *A-us x-us*, male from Timbuktu. a. Left leg; b. Right chelicerae; c. Dorsal aspect of genitalia; d. Ventral aspect of abdomen. Scale = 1.0 mm.

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