

## EVOLUTION OF ORNAMENTATION AND COURTSHIP BEHAVIOR IN *SCHIZOCOSA*: INSIGHTS FROM A PHYLOGENY BASED ON MORPHOLOGY (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** A phylogenetic analysis for the North American *Schizocosa* species was undertaken by scoring 49 morphological characters for 31 taxa representing all of the Nearctic species of *Schizocosa* plus individuals that are hybrids between *S. ocreata* and *S. rovneri*. *Rabidosa rabida*, *Allocosa georgicola* and *Gladicosa pulchra* were used as outgroups. Three clades are recognized: a large clade from eastern North America (Clade A) within which is nested the *S. ocreata* clade; Clade B, which includes the widespread *S. avida* and the western *S. mccooki*, and a smaller, third clade, Clade C. Sexual ornamentation occurs on the first legs of mature males of several species within the *Schizocosa* and takes the form of pigmentation and or bristles primarily on the tibia of leg I; there is at least one species with bristles in each of the three main clades. Mapping the occurrence of male ornamentation on the preferred phylogeny suggests that ornamentation evolved 5 or 6 separate times and was subsequently lost 2 or 3 times. The ornamentation is concentrated in the *S. ocreata* clade, a clade defined by a finger like projection on the paleal process of the male pedipalp. Courtship behavior is known for 20 of the 31 taxa. All species studied utilize chemical communication and seismic signals for communication; some species also have distinct visual signals. Seismic signals are produced by palpal drumming (as is seen in several species within Clade B), or by stridulation (seen in Clade A). Visual signals consisting of movements of the first pair of legs are common in species that are distinctly ornamented. This study provides the first phylogenetic study of a North American genus of wolf spider and provides morphometric comparisons of the North American species in *Schizocosa*.

**Keywords:** Cladistics, sexual selection, secondary sexual characteristics, evolution of behavior, spiders, multimodal signal, seismic signal

In spiders, sexual ornamentation is most evident in groups that have exceptional eyesight (e.g., Salticidae and Lycosidae) with ornaments being found on mature males in places that are visible to females or other males. In contrast to the colorful salticids (e.g. the North American genus *Habronattus* F.O.P Cambridge 1901, Peckham & Peckham 1889, 1890; Griswold 1987; Maddison & Hedin 2003), the ornamentation on lycosids tends to be in black or white, and is generally limited to the first pair of legs or to the pedipalps of mature males. Examples of such ornaments in wolf spiders are wide spread and include dark pigmentation on some part of the first pair of legs as seen in *Alopecosa aculeata* (Clerck 1757) and *A. barbipes* (Sundevall 1833) (Kronstedt 1990) or on the pedipalps as seen in *Pardosa wagleri* (Hahn 1822) and *P. saturator* Simon 1937 (Barthel & Helversen 1990) or *P. saxatilis* (Hentz 1844) (Dondale & Red-

ner 1984). In addition, many members of the North American *Geolycosa* Montgomery 1904 have contrasting pigmented hairs on their first legs (Wallace 1942a). And, as reported in Dondale & Redner (1978) and in this study, males of several members of the genus *Schizocosa* Chamberlin 1904 have darkly pigmented legs and or tibial bristles.

Revised by Dondale & Redner (1978), the Nearctic species of the *Schizocosa* include the 20 species recognized by Dondale & Redner plus *S. rovneri* Uetz & Dondale 1979, *S. stridulans* Stratton 1984 and *S. uetzi* Stratton 1997 and at least one undescribed species. Males of several members of the genus have conspicuous ornamentation in the form of pigmentation and/or bristles on the first legs of mature males. The ornamentation varies considerably from a complete lack of dark pigmentation [e.g., *S. saltatrix* (Hentz 1844), or *S. rovneri*], to slight pigment on the tibia of males

(e.g., *S. uetzi*), to concentrated tufts of bristles at one end of the tibia (e.g., *S. salsa* Barnes 1953), to bristles that extend the length of the tibia and to the metatarsus [as in *S. ocreata* (Hentz 1844) from Florida]. Indeed, it is this variability in ornamentation that makes this genus particularly interesting for behavioral and evolutionary studies. For some species, the ornamentation has proven useful in species descriptions (Uetz & Dondale 1979; Stratton 1991, 1997a) as well as in mate choice studies (McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000). In some cases, tibial bristles are seen in species that have similar genital morphology, e.g., *S. ocreata* and *S. crassipes*, both commonly called “the brush-legged spider”, suggesting a common origin of the trait, but it is also seen in species with different genitalia [e.g. compare *S. ocreata* with *S. bilineata* (Emerton 1885)], suggesting the possibility of independent origins. Closely related species may be very divergent with respect to ornamentation, as is seen in *S. ocreata* and *S. rovneri*, two species long considered to be sibling to each other.

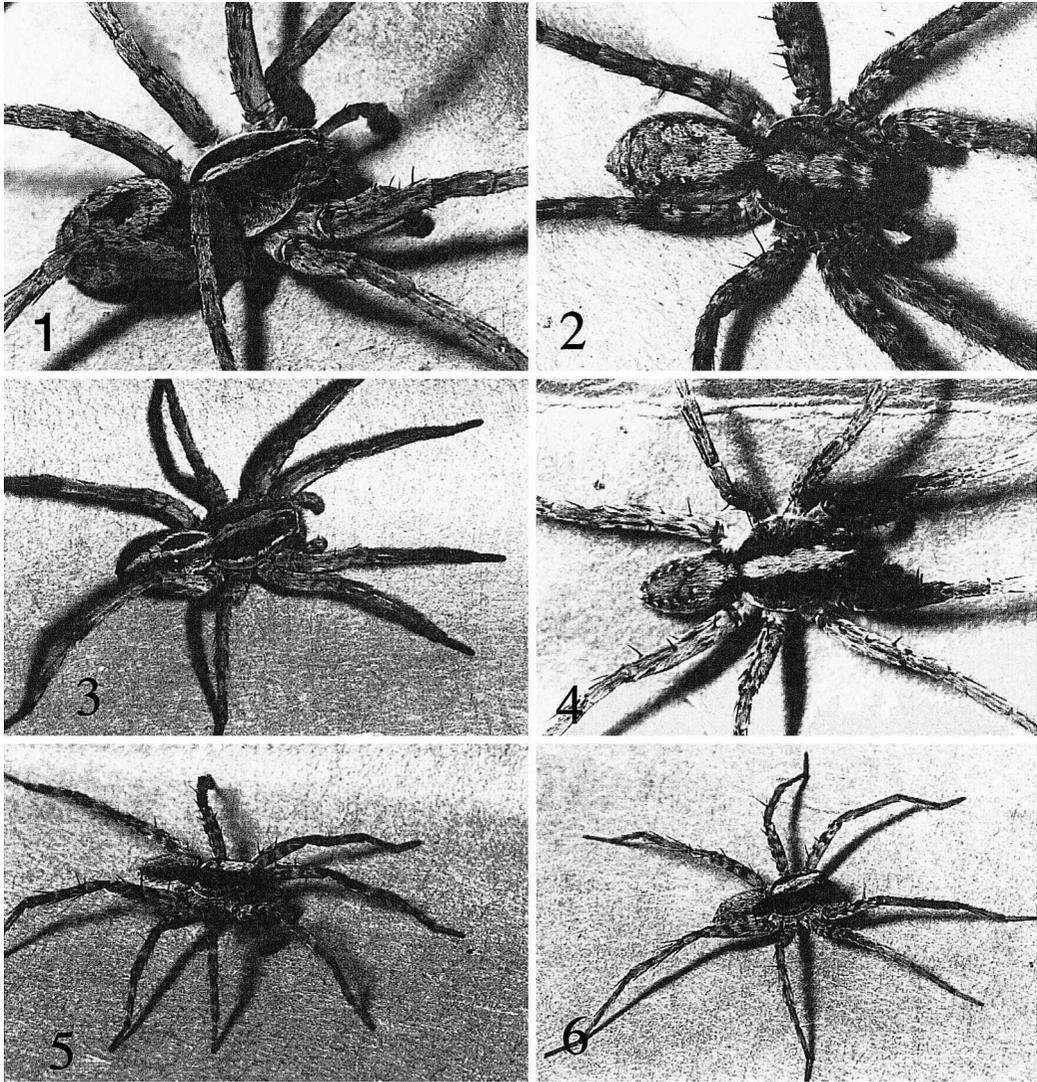
Ornamentation and courtship behavior in *Schizocosa* wolf spiders have been the focus of studies addressing sexual selection and signal evolution, fluctuating asymmetry and reproductive isolation (Hebets & Uetz 1999, 2000; Uetz et al. 1996, Uetz & Smith 1999; McClintock & Uetz 1996; Scheffer et al. 1996; Hebets 2003, 2005). Perhaps most surprisingly, the ornamentation on at least one species (*S. uetzi*) appears to be important in a social learning context (Hebets 2003).

Members of the genus *Schizocosa* use a variety of modes of communication during courtship, including chemical, seismic and visual signals. In two comparative studies, Hebets & Uetz (1999, 2000) found that among six species of *Schizocosa*, females of three species exhibited a vibratory bias during courtship and three showed a visual bias. Hebets & Uetz (2000) found that in species with active visual displays but without ornamentation, an artificial increase in male ornamentation resulted in increased female receptivity. In an attempt to test the hypothesis that ornamentation evolved secondarily in this family to enhance pre-existing visual movement displays, they presented a summary of North American lycosid species which complied in-

formation on the presence/absence of ornamentation and leg waving displays. However, a phylogenetic study including more lycosid species, as in the present study, will provide a more thorough test of such a hypothesis. The mixture of ornamented species and non-ornamented species plus the complexity of courtship interactions makes the *Schizocosa* genus particularly well suited for testing ideas concerning multimodal signaling (Uetz & Roberts 2002; Hebets 2005) and the evolution of complex behaviors. The relative importance of phylogeny compared with sexual selection can be assessed with a robust phylogeny.

McClintock & Uetz (1996) presented evidence that females of *S. rovneri*, a species without leg ornamentation, showed a higher level of response to video images of conspecific males that had been visually manipulated to have tufts on their tibia and to courting heterospecific males than to controls (un-manipulated conspecific males). The preliminary phylogeny presented in their 1996 study (including 16 characters for 7 species) suggested that the female preference for ornamentations may have preceded the evolution of the ornaments themselves and thus be an example of the sensory bias hypothesis (Ryan & Rand 1993). A more complete phylogenetic study of the genus involving more species and more characters will provide a more robust test of the sensory bias hypothesis.

Here, I present the results of a comparison of the sexual ornamentation found in members of *Schizocosa* and the results of a phylogenetic study addressing the Nearctic members of this wolf spider genus. Using the results from my phylogenetic analysis, I address the following four hypotheses: 1. Ornamentation in the form of tibial bristles arose once within this genus; 2. Monophyletic groups show similarities in courtship behavior; 3. *Schizocosa ocreata* and *S. rovneri* are sibling species as was suggested by Uetz & Dondale (1979) and supported by the successful interbreeding reported in Stratton & Uetz (1986); and 4. Finally, this study presents a test of the sensory bias hypothesis presented by McClintock & Uetz (1996) that female preference seen in *S. rovneri* females for males with ornamentation preceded the evolution of ornamentation in closely related species.

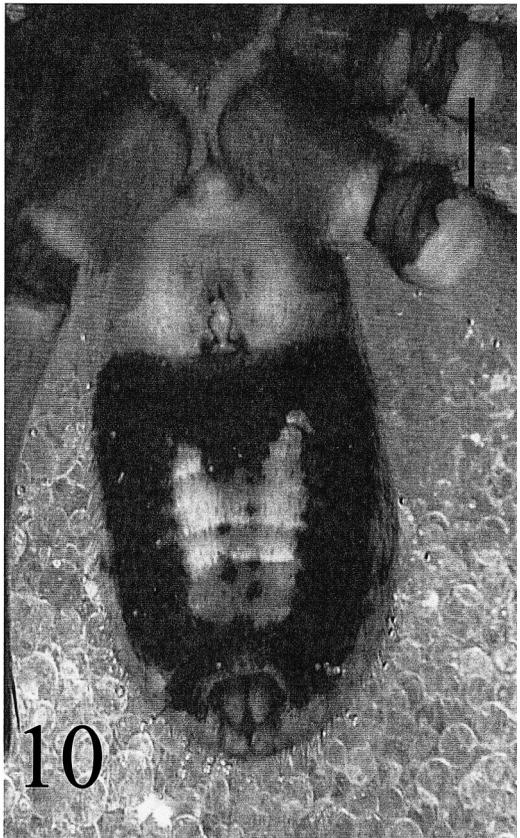
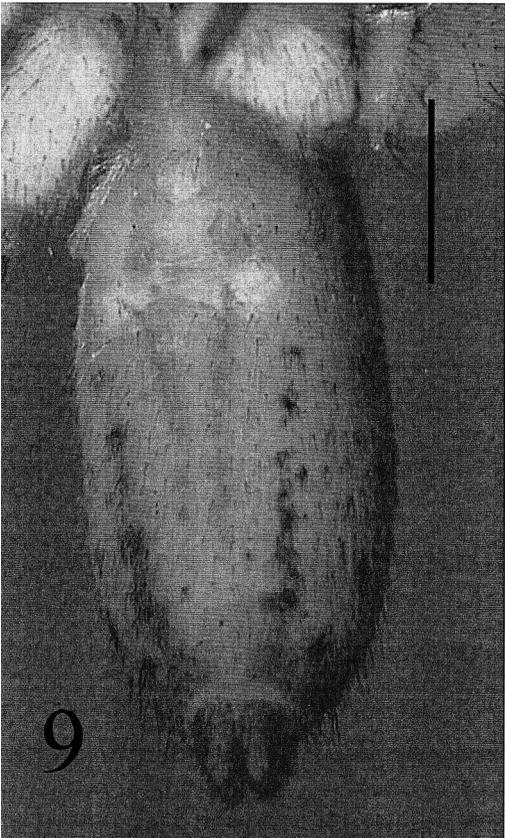
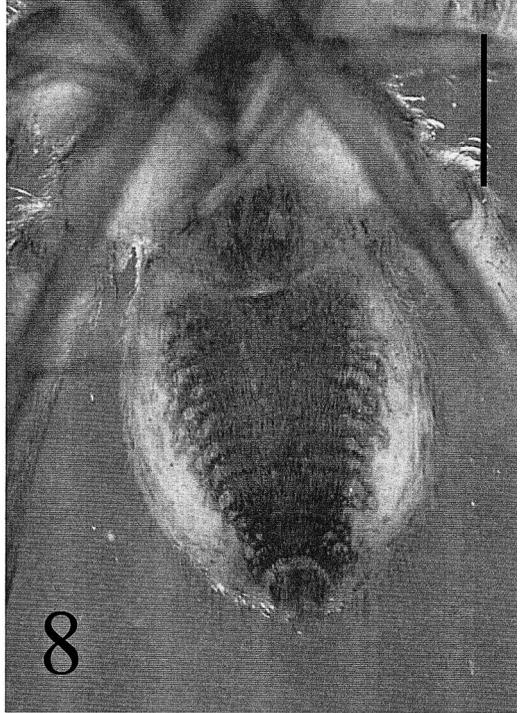
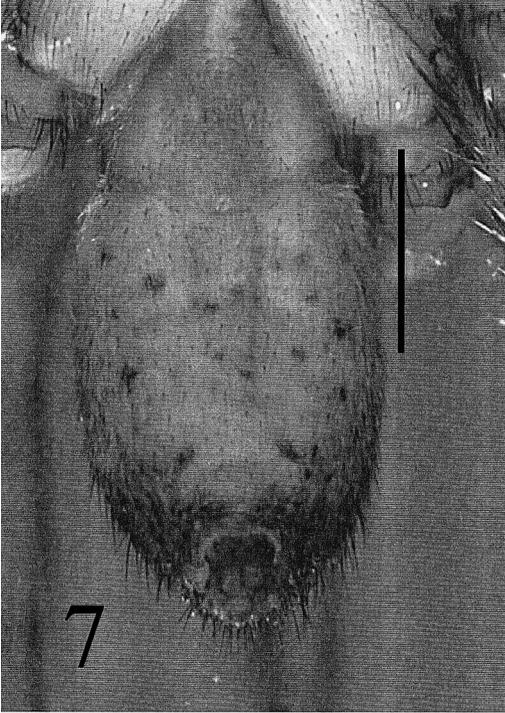


Figures 1–6.—Dorsal view of males of several of the species used in the phylogenetic study: 1. *Allocosa georgicola*; 2. *Gladicosa pulchra*; 3. *Schizocosa avida*; 4. *Schizocosa retrorsa*; 5. *Schizocosa rovneri*; 6. *Schizocosa uetzi*.

## METHODS

**Ornamentation and courtship behavior.**—As comparative data on male ornamentation and courtship behavior were not available for all species of *Schizocosa*, I initially measured the form and extent of male tibial bristles for all members of the genus and recorded the courtship behavior for selected (available) species. To document the ornamentation of each species, a lateral view of the first pair of legs for males of all species included in the study was photographed using a

dissecting microscope (Olympus SZX12) and dedicated digital camera (Olympus 750). Courtship behavior (for available species not reported in the literature) was documented by collecting subadult males and females, maintaining them in the laboratory until mature (see Stratton et al. 1996, Miller et al. 1998) and then videotaping courtship behavior. The standard protocol for recording behavior was as follows. Twenty-four hours before testing, females were fed an appropriately-sized cricket and were placed in a recording chamber



with filter paper as substrate. Males were introduced to the chamber and all interactions were recorded with either a Panasonic WD-5000 camera with Kiron 105 mm f2.8 macro-lens on standard VHS tapes or by using a Sony TRV-22 taping to a mini-DV tape. Seismic recordings were made by using a sound transducer attached to an EG&G PARC Model 113 pre-amp connecting to the video recorder. Video and seismic recordings were made for the following species, whose behavior is not yet described in the literature (summarized in Table 5): *S. avida*, *S. crassipal-pata*, *S. floridana*, *S. saltatrix*, *S. nr saltatrix*, *Gladicosa pulchra* and *Allocosa georgicola*. As courtship behavior remains unknown for several species, the behavior was not used in the parsimony analysis.

**Phylogenetic study: choice of taxa and material examined.**—There are 63 species currently listed in the genus *Schizocosa* (Platnick 2005) from all over the world. However, in this study, I chose to focus solely on the Nearctic species; explicit in the exclusion the species from the Philippines, South Africa and other localities outside of North America is the assumption that the Nearctic species are monophyletic, an hypothesis not tested in this study. However, the names of several large genera of wolf spiders (e.g., *Lycosa*, *Schizocosa* and others) were often categories of convenience rather than hypotheses of relationship for some earlier workers. For example, recent taxonomic work of New Zealand wolf spiders suggests that previous placement of species into Holarctic genera is erroneous (Vink 2002) and *Schizocosa berenice* L. Koch 1877 from Australia actually belongs in the genus *Artoria* (Framenau pers. comm.).

Additionally, I excluded species that were excluded from the genus by Dondale & Redner (1978). Many of these, e.g., *S. incerta* (Bryant 1934), *S. perplexa* Bryant 1936, *S. puebla* Chamberlin 1925, *S. tamae* (Gertsch & Davis 1940), *S. tristani* (Banks 1909) and *Avicosa ceratiola* (Gertsch & Wallace 1935) have yet to be placed in another genus but

were judged to be outside the scope of this project.

This study is thus based on direct examination of preserved specimens of the 20 *Schizocosa* species recognized by Dondale & Redner (1978), plus *S. rovneri*, *S. stridulans*, *S. uetzi* and one undescribed species. In addition, I scored 3 populations of *Schizocosa ocreata*: one from Cincinnati, OH that has been used extensively in behavioral research (see references by Uetz, Hebets, McClintock and Stratton), a second from Central Mississippi (see Miller et al. 1998) and a third from Gainesville, Florida; and two populations of *Schizocosa crassipes*: (separate populations from Florida and Mississippi). Finally, I also scored individuals that are hybrids between *S. ocreata* (OH) and *S. rovneri* (available from a previous study [Stratton & Uetz 1986]). Appendix 2 summarizes the specimens of the 31 taxa used and their deposition. Voucher specimens from my own collection will be deposited at the AMNH.

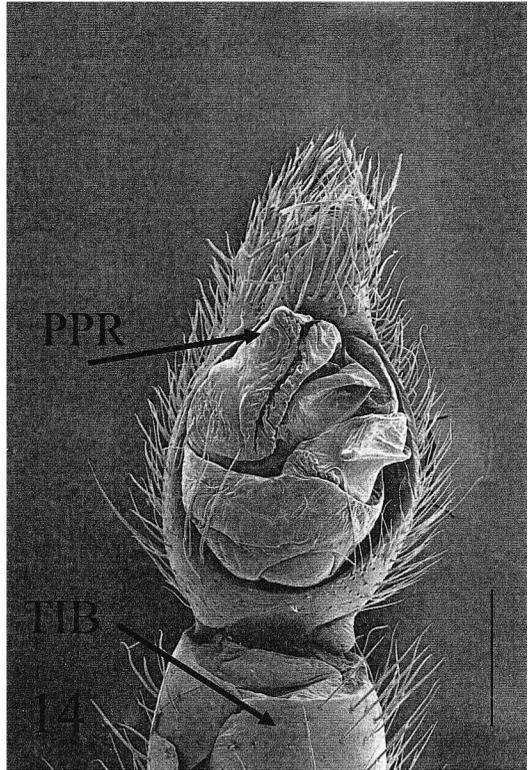
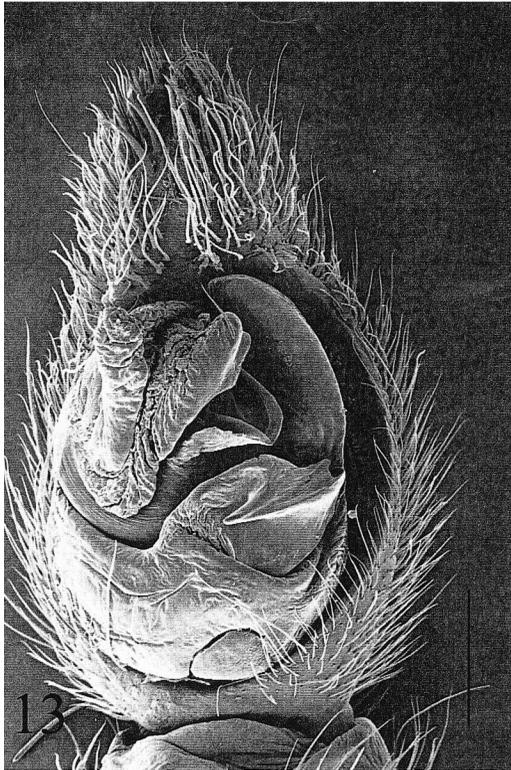
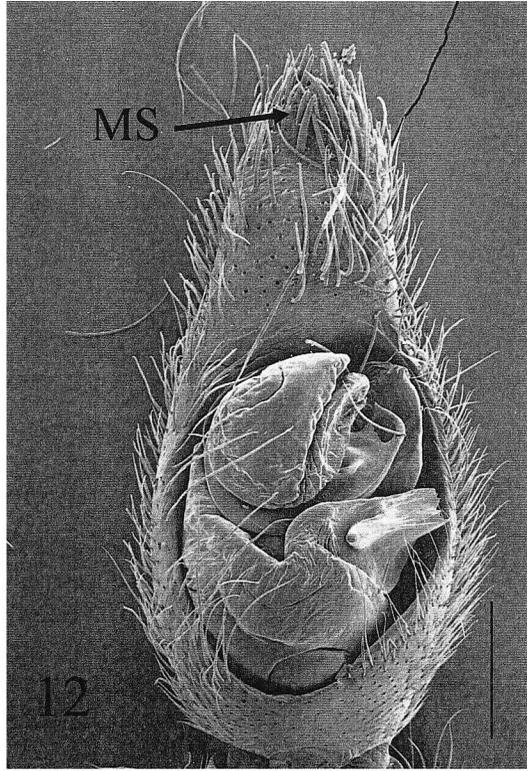
**Outgroups.**—The choice of outgroups for this study was difficult due to the incomplete knowledge of lycosid generic relationships. As the sister-group for the *Schizocosa* is not known, representatives from several different North American lycosid genera were scored and included in this analysis. *Gladicosa pulchra* (Keyserling 1877), *Allocosa georgicola* (Walckenaer 1837) and *Rabidosa rabida* (Walckenaer 1837) were chosen as outgroups for the final analysis as they all share some characters with *Schizocosa* but also have clearly distinguishing features (locality, deposition and citations for figures are given in Appendix 2). *Allocosa georgicola* has affinities to the *H. helluo* species group (Brady pers. comm.).

**Choice of characters.**—Forty nine morphological characters were found to be informative and were scored by direct examination of specimens (data matrix in Appendix 1; details of the characters are provided below). During the course of the study numerous additional characters were identified and scored

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Figures 7–10.—Venter of selected species: 7. Male of *Schizocosa crassipes*; 8. Male of *Schizocosa retrorsa*; 9. Female of *Schizocosa bilineata* (epigynum has been dissected); 10. Female of *Schizocosa avida*.



but discarded as too variable or uninformative. Characters were chosen by comparing the different subfamilies of Lycosidae (Dondale 1986), by screening revisions, descriptions and illustrations of other wolf spiders and by direct examination of the specimens. Figures from the following references were found to be useful: *Schizocosa* (Dondale & Redner 1978), *Trochosa* (Brady 1979); *Gladicosa* (Brady 1986); *Rabidosia* (Brady & McKinley 1994); *Geolycosa* (Wallace 1942a); *Hogna georgicola* (Chamberlin & Ivie 1944) and *Isohogna lenta* (Wallace 1942b).

As characters were treated as unordered, hypotheses of polarity are an emergent property of the analysis. Forty characters are binary; nine are multistate characters. Six of the characters are morphometric (characters 1, 17, 20, 33, 37, 39) with three being expressed as ratios (characters 17, 33, 37). To assign states for the morphometric data, I examined the data for gaps. In several cases, I opted for independent coding of variables for a given structure as opposed to coding as a multistate character with linked states to minimize assumptions of congruence (e.g., characters 21–25). However, a potential problem with this is the duplication of absences (Maddison 1993).

For the final analysis, the 49 characters were grouped in the following manner: 19 somatic characters, 14 male palpal characters, 10 female epigynal characters and six male secondary sexual characters. Several additional characters (e.g., behavioral and ecological characters) were used a posteriori and mapped onto the resulting cladograms. As data for these latter characters were not available for all species, they were not used in the parsimony analysis (Platnick et al. 1991; Maddison 1993).

**Data analysis.**—Maximum parsimony analyses were conducted using PAUP\* (Version 4.0b10) (Swofford 2002) with 1000 random starting point heuristic searches using Stepwise-addition option and 1000 random taxon addition sequences and tree-bisection-reconnection (TBR) branch swapping. The re-

sults from other swapping algorithms were compared to TBR branch swapping. All characters were unordered and several weighting schemes were examined. The trees were rooted by setting the three non-congeners as outgroups. Characters were mapped using MacClade Version 3.0 (Maddison & Maddison 1992). The degree of internal support for the resulting clades was estimated using bootstrap analysis (using 100 random addition sequence replicates and 100 bootstrap replicates).

**Weighting options.**—The data set was first analyzed with all characters weighted equally. However, preliminary analyses suggested there was little phylogenetic signal in the somatic characters. Subsequent analysis investigated several different weighting options including reweighting with the rescaled consistency index as well as weighting the genitalic characters more heavily. As most modern students of wolf spiders use genitalic characters extensively in revisions and descriptions (Dondale & Render 1978, 1990; Brady 1962, 1979, 1986; Brady & McKinley 1994) and because wolf spiders appear to be very conservative in their somatic morphology, I favor the trees produced by weighting the genitalic characters more heavily. In the final analysis, I used the following weighting scheme: somatic characters weighted as “2”; genitalic characters weighted as “3” and secondary sexual characters weighted as “1.” Finally, as I was interested in the evolution of secondary sexual characters, I compared trees produced by excluding secondary sexual characters with trees including those characters.

**Description of characters.**—*Somatic characters*: 1. Body size: 0 = medium; 1 = large; 2 = small. Measurements of the carapace were made as the best representation of body size, as unlike the spider's abdomen, it does not vary with a recent meal. Carapace length and width were measured dorsally using an ocular micrometer. The ratio of the carapace length to width was similar across all species used in this study (Table 1). Carapace length

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Figures 11–14.—Left pedipalps of males from selected species of *Schizocosa*. Localities are indicated in Appendix 2: 11. *S. avida*; 12. *S. retrorsa*; 13. *S. saltatrix*; 14. *S. duplex*. ELL = ear-like lobe, IPE = intromittent portion of embolis, MA = median apophysis, TA = terminal apophysis. Scale lines = 500  $\mu$ m.

Table 1.—Body size (carapace length, carapace width and ratio of length/width) of male and female *Schizocosa* and outgroups used in this study. All measures are in mm. Measures of female *S. aulonia*, and *S. maxima* are from Dondale & Redner (1978), measures from *S. salsa* are from Barnes (1952).

Species	Male			Female		
	Length	Width	L/W	Length	Width	L/W
<i>S. aulonia</i>	4.0	2.8	1.4	5.5	4.0	1.4
<i>S. avida</i>	4.8	3.6	1.3	6.8	5.0	1.4
<i>S. bilineata</i>	2.9	2.1	1.4	3.5	2.5	1.4
<i>S. cespitum</i>	3.6	2.6	1.4	4.2	3.0	1.4
<i>S. chiricahua</i>	4.2	3.0	1.4	3.8	2.5	1.5
<i>S. communis</i>	4.6	3.4	1.4	4.0	3.0	1.3
<i>S. crassipalpata</i>	3.1	2.3	1.3	3.1	2.2	1.4
<i>S. crassipes</i> (FL)	3.2	2.6	1.2	3.8	2.7	1.4
<i>S. crassipes</i> (MS)	3.2	2.4	1.3	3.4	2.6	1.3
<i>S. duplex</i>	3.2	2.5	1.3	3.2	2.4	1.3
<i>S. floridana</i>	2.6	2.0	1.3	3.1	2.5	1.2
<i>S. humilis</i>	3.1	2.3	1.3	3.6	2.6	1.4
<i>S. maxima</i>	9.0	7.7	1.2	12.1	9.0	1.3
<i>S. mccooki</i>	3.7	2.8	1.3	4.2	3.2	1.3
<i>S. mimula</i>	4.0	2.9	1.4	4.2	2.8	1.5
<i>S. minnesotensis</i>	4.6	3.2	1.4	4.9	3.6	1.4
<i>S. ocreata</i> (OH)	3.8	2.8	1.4	4.1	3.2	1.3
<i>S. ocreata</i> (MS)	3.7	2.7	1.4	4.5	3.4	1.3
<i>S. ocreata</i> (FL)	4.0	3.0	1.3	4.2	3.3	1.3
<i>S. retrorsa</i>	3.7	2.7	1.4	3.4	2.7	1.3
<i>S. rovneri</i>	3.4	2.6	1.3	3.7	3.0	1.2
<i>S. salsa</i>	4.1	3.0	1.4	4.1	2.9	1.4
<i>S. saltatrix</i>	3.7	3.0	1.2	3.6	3.0	1.2
<i>S. S. sp. nr. saltatrix</i>	4.0	3.2	1.3	3.6	2.8	1.3
<i>S. segregata</i>	3.0	2.2	1.4	3.2	2.2	1.5
<i>S. stridulans</i>	3.2	2.4	1.3	3.0	2.3	1.3
<i>S. uetzi</i>	3.6	2.8	1.3	3.7	3.0	1.2
<i>S. ocr</i> × <i>rov</i> hybrids	3.8	3.1	1.2	4.3	3.5	1.2
<i>A. georgicola</i>	8.0	6.9	1.2	10.0	7.5	1.3
<i>G. pulchra</i>	6.0	4.5	1.3	6.4	5.0	1.3
<i>R. rabida</i>	7.8	5.9	1.3	9.8	7.4	1.3

as states: carapace length  $\geq 4.5$  mm for “large”, carapace length between 3.5 and 4.5 mm for “medium” and carapace length  $\leq 3.5$  mm for “small”.

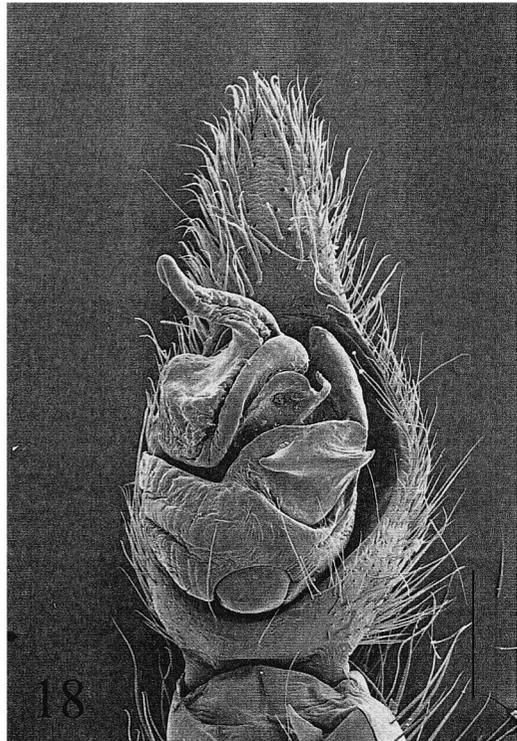
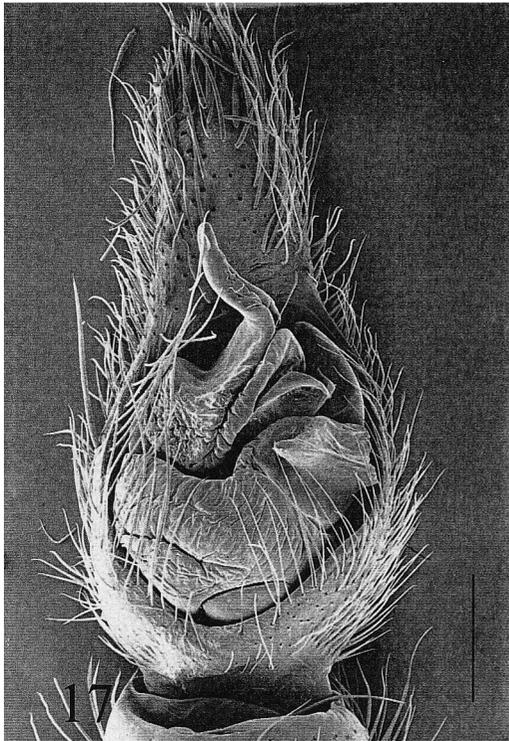
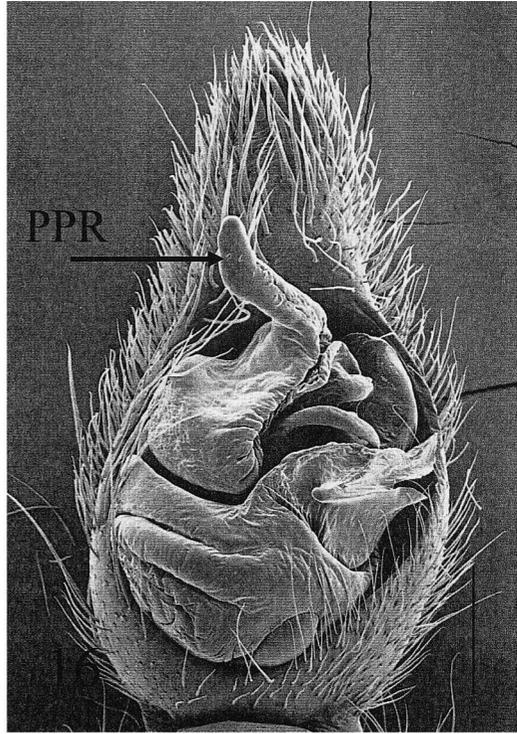
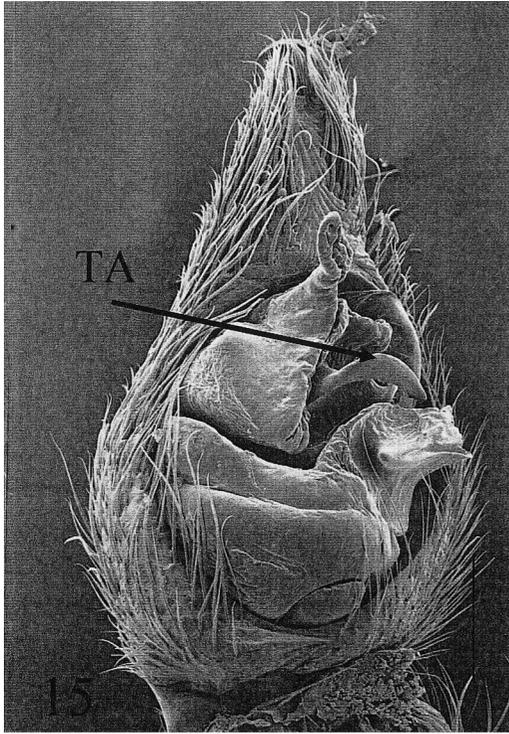
2. Median band (MB) width: 0 = narrow; 1 = medium; 2 = broad. The median band is a light band on the dorsal surface of the carapace. It may be a thin line (as in *A. georgicola*, Fig. 1, which is distinctly thinner than the posterior median eyes) or it may be “broad,” or as broad as the posterior median eyes (as in *G. pulchra*, Fig. 2, and members of *Schizocosa*, Figs. 3–6). A medium-sized median band is present in *Rabidosa* spp. (Brady and McKinley 1994, p. 140, figs. 1–5).

3. Median band edges: 0 = straight; 1 = not straight. The edges of the median band can

be straight as in Fig. 1, 3, 5, 6), or can have some constriction as is seen in *G. pulchra* or *S. retrorsa* Banks 1911 (Figs. 2, 4).

4. Submarginal band (SMB), edges: 0 = absent; 1 = smooth; 2 = wavy or spots. The submarginal band is a light band near the edges of the carapace. It can be present as either a relatively smooth band (as in *S. avida* and *S. rovneri*, Figs. 3, 5) or diffuse or lacking as in *A. georgicola* (Fig. 1). In *S. retrorsa* (Fig. 4) the SMB consists of spots at the edges of the carapace.

5. Submarginal band, size: 0 = absent; 1 = narrow; 2 = broad. In most species of *Schizocosa*, the SMB is narrow or absent. In *Rabidosa* spp. (Brady & McKinley 1994, figs. 1–5, p. 140) and in *S. salsa*, the SMB is wider



Figures 15–18.—Pedipalps of males from selected populations of *Schizocosa ocreata* and *S. crassipes*. Localities as indicated in Appendix 2: 15. *S. ocreata* (FL); 16. *S. ocreata* (MS); 17. *S. crassipes* (FL); 18. *S. crassipes* (MS). Scale lines = 500  $\mu$ m.

than the median band and scored as broad (Barnes 1953, fig. 16).

6. Heart mark (HM): 0 = absent or faint; 1 = strong. In some Lycosinae, the heart mark is a darkened region on the dorsum of the abdomen where the heart is located (e.g. *A. georgicola* & *S. avida*, Figs. 1, 3).

7. Light bands on abdomen: 0 = absent; 1 = present. In some cases, the HM is apparently accentuated by the presence of white lines on either side of the HM (as in *S. avida*, Fig. 3).

8. Sternum color: 0 = yellow or light brown; 1 = orange, dark brown or black.

9. Bands on sternum: 0 = absent; 1 = present. Sternum bands, as used for this study, are longitudinal bands that extend from the anterior to the posterior end of the sternum.

10. Shield on venter: 0 = absent; 1 = present. When present, this is a light patch on black background on the venter of the animal as in *S. avida* (Fig. 10). The shape of the light patch varies between individuals from the same geographic area (Stratton, unpublished data).

11. Ventral color of abdomen: 0 = light or mostly light; 1 = black or mostly black; 2 = light shield on black. Light or mostly light is as in *S. crassipes* or *S. bilineata* (Emerton 1885) (Figs. 7, 9); black or mostly black, as in *S. retrorsa* (Fig. 8); and light shield on black as in *S. avida* (Fig. 10).

12. "V" on venter: 0 = absent; 1 = present. The "V" is formed by dark pigmented spots near the lateral edges of the venter (*S. bilineata*, Fig. 12). The inner "V" on *S. bilineata* is not pigmented and originates in points of muscle attachment.

13. Spots on venter: 0 = absent; 1 = present. Similar to character 12 but in some cases and in *S. crassipes*, the spots on the venter are scattered.

14. Color of coxae: 0 = light to light brown; 2 = dark brown.

15. Color of coxae relative to the femur: 0 = same as femora; 1 = lighter than femur; 2 = darker than femur.

16. Dark lines on chelicerae: 0 = absent; 1 = present. When present, these are vertical lines running the length of the chelicerae when viewed from the front.

17. Relative tibial length of males: 0 = short to medium; 1 = long. Examination of the specimens suggested that some of the spe-

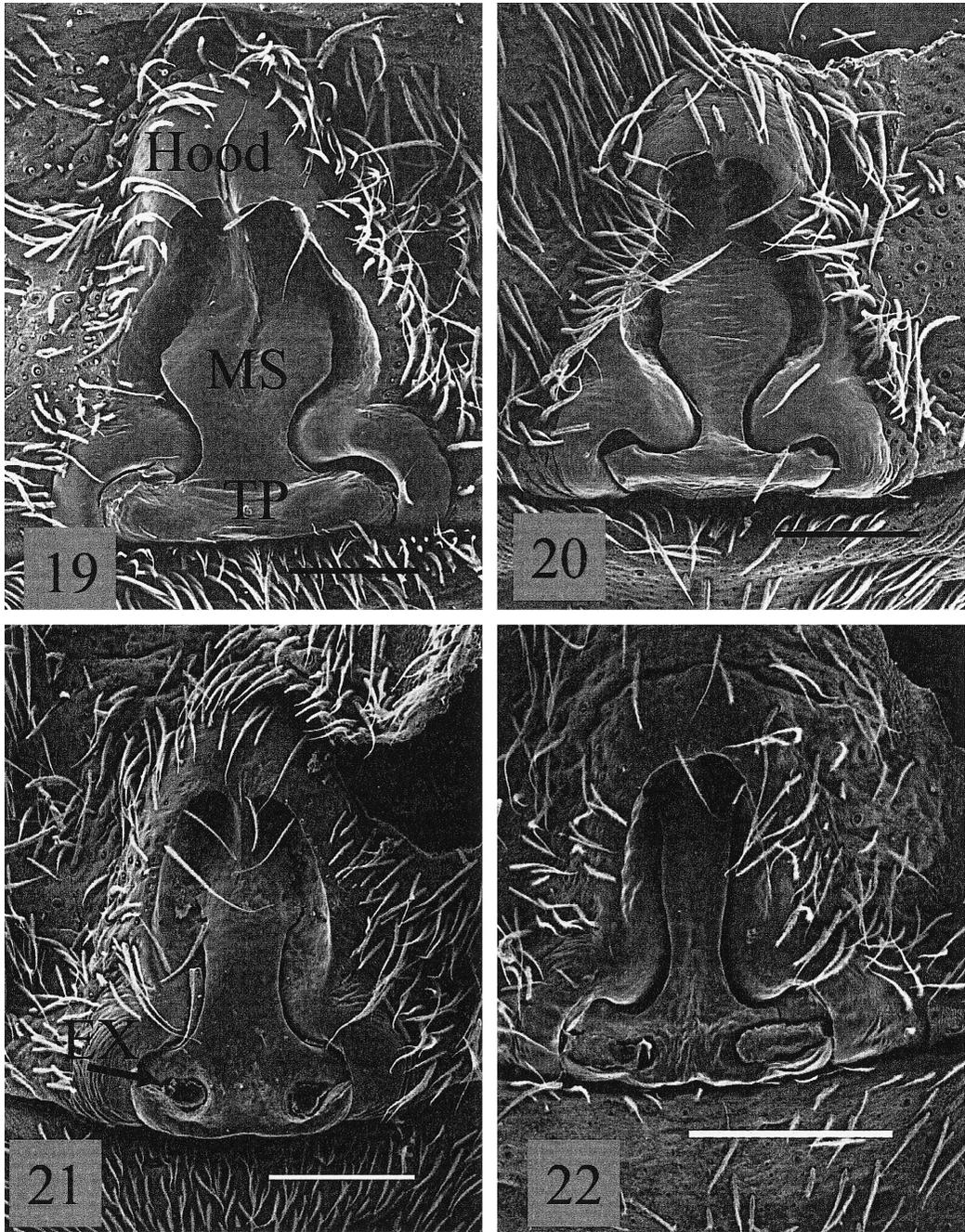
cies had particularly stout legs, others were relatively long-legged, while many fell between these extremes (also noted by Kronestedt 1990). Since there was a wide range of body sizes in the examined species, I took a relative measure for leg length. Tibia 1 (measured with an ocular micrometer along the dorsal edge) divided by the carapace length was taken as the relative measure of leg length that could be potentially informative. Values for this ratio ranged from 0.5 for *S. cespitum* Dondale & Redner 1978 to 0.92 for *S. salsa* (Table 2). Gaps were identified by examination of the distribution of values. These data were first collapsed into a binary coding (0 = short to medium,  $tl/cl \leq 0.71$  and 1 = long  $tl/cl > 0.71$ ). The data were also scored as a multistate character with any gap  $> 0.03$  used to define states. With this coding there were seven character states. During character exploration, analyses were run both ways; this character was judged to have a large amount of homoplasy and in the final analysis, I used the binary coding.

18. Femur I annulations (male): 0 = absent; 1 = present.

19. Femur II-IV annulations (male): 0 = absent; 1 = present.

*Male palpal characters:* Palpal structures have been successfully employed in spider taxonomy and have been central in wolf spider revisions. Eberhard (1994) suggested that the complexity of genitalic characters has been shaped by sexual selection. The complexity of the pedipalps has made determination of homologies of structures between families difficult. Even within a single family, such as the Lycosidae, terms have been used in a variety of ways. I here follow the terminology suggested by Dondale & Redner (1978) with comparisons to Brady (1986) and have focused primarily on structures that aid in the determination of species.

The cymbium of the tarsus (terminal segment) forms the body of the tarsus of the pedipalp and holds the sclerites (genital bulb) involved in copulation. At the tip of the cymbium there may be macrosetae (MS, Fig. 12), which function to hold the pedipalp in place while the spider stridulates [e.g., *S. saltatrix* and *R. rabida* (Walckenaer 1837), Rovner 1975]. The genital bulb is an interconnected assemblage of sclerites and distensible sacs (the hematodocha). During copulation,



Figures 19–22.—Epigyna of selected species. Localities as indicated in Appendix 2: 19. *S. avida*, 20. *S. retrorsa*, 21. *S. crassipes* (MS); 22. *S. duplex*. MS = median septum, TP = transverse piece. Scale lines = 250  $\mu$ m.

the hematodocha becomes visible as an expanding sac of haemolymph. The cymbium is attached to the palpal tibia (Tib, Fig. 14).

Located on the genital bulb is the terminal

apophysis (TA, Fig. 11) which in *Schizocosa* is a small, free sclerite near the base of the intromittent portion of the embolus (IPE) (Figs. 11–18; see also Dondale & Redner

Table 2.—Tibial length and relative tibial length (tibial L/carapace L) of males of *Schizocosa* and outgroups. All measures are in mm.

Species	Male		
	Cara length	Tibia length	Tibial L/ Cara L
<i>S. aulonia</i>	4.0	2.5	0.61
<i>S. avida</i>	4.8	3.6	0.75
<i>S. bilineata</i>	2.9	2.0	0.67
<i>S. cespitum</i>	3.6	2.0	0.50
<i>S. chiricahua</i>	4.2	2.5	0.60
<i>S. communis</i>	4.6	2.5	0.68
<i>S. crassipalpata</i>	3.1	1.8	0.57
<i>S. crassipes</i> (FL)	3.2	2.8	0.85
<i>S. crassipes</i> (MS)	3.2	2.5	0.84
<i>S. duplex</i>	3.4	2	0.66
<i>S. floridana</i>	2.6	1.5	0.58
<i>S. humilis</i>	3.1	1.8	0.58
<i>S. maxima</i>	9.0	6.4	0.71
<i>S. mccooki</i>	3.7	2.7	0.74
<i>S. mimula</i>	4.0	2.7	0.68
<i>S. minnesotensis</i>	4.6	2.4	0.51
<i>S. ocreata</i> (OH)	3.8	3	0.78
<i>S. ocreata</i> (MS)	3.7	2.6	0.71
<i>S. ocreata</i> (FL)	4.0	2.6	0.65
<i>S. retrorsa</i>	3.7	2.6	0.71
<i>S. rovneri</i>	3.4	2.6	0.76
<i>S. salsa</i>	4.1	3.8	0.92
<i>S. saltatrix</i>	3.7	2.5	0.67
<i>S. S. sp. nr. saltatrix</i>	4.0	2.5	0.62
<i>S. segregata</i>	3.0	1.8	0.59
<i>S. stridulans</i>	3.2	2.4	0.75
<i>S. uetzi</i>	3.6	3.0	0.83
<i>S. ocr</i> × <i>rov</i> hybrids	3.8	2.6	0.68
<i>A. georgicola</i>	8.0	5.5	0.68
<i>G. pulchra</i>	6.0	4.8	0.83
<i>R. rabida</i>	7.8	7.0	0.89

1978). In *Gladicosa* and *Hogna*, the TA is an elongate structure that parallels the embolus and may assist in the proper placement of the IPE in the female epigynum (see Brady 1986, p. 314, fig. 41). Also clearly visible is the median apophysis (MA, Figs. 11–18) which is directed retrolaterally and has a sinuous channel on the dorsal surface, which are defining characters of the subfamily Lycosinae. A spur of the median apophysis engages the hood of the female epigynum during copulation. The palea is a partly sclerotized pad at the distal end of the genital bulb that sometimes bears processes or extensions (PPR) (Figs. 14–18). An ear-like lobe (ELL, Fig. 11) is also present in *Schizocosa* and *Gladicosa* (called the con-

ductor by Dondale & Redner 1978). The base of the cymbium holds the scraper portion of the stridulatory structure, not visible in the ventral view shown. The tip of the tibia has the file of the stridulatory organ, found only in mature males.

20. Palpal tibia: 0 = length > width; 1 = length ≤ width. Measured ventrally using an ocular micrometer. For some species (i.e., *A. georgicola*), the tibia of the pedipalp is long and thin (nearly twice as long as wide) (Table 3). For others, as in *S. ocreata* (FL), it is very stout and is wider than long (Table 3). A short, stout tibial palp is probably related to muscle mass needed for stridulation during courtship (Rovner 1975). Although all members of the *Schizocosa* and outgroups included here possess a stridulatory organ, for some, palpal drumming is an important component of the courtship behavior (Table 5; see discussion below).

21. Terminal apophysis (TA): 0 = present; 1 = small or absent.

22. Terminal apophysis, size: 0 = elongate; 1 = small or absent. The TA in *Schizocosa* is generally present but relatively small compared to that in the outgroups, *A. georgicola* and *G. pulchra* (Figs. 11–18; compare to, Brady 1986, p. 314, fig. 41), where the TA is an elongate structure.

23. Terminal apophysis with slight arch: 0 = absent; 1 = present. The TA may form a slight arch, as seen in Figs. 15 and 16.

24. Terminal apophysis, with tear-drop shape: 0 = absent; 1 = present. See fig. 13 in Dondale & Redner (1978).

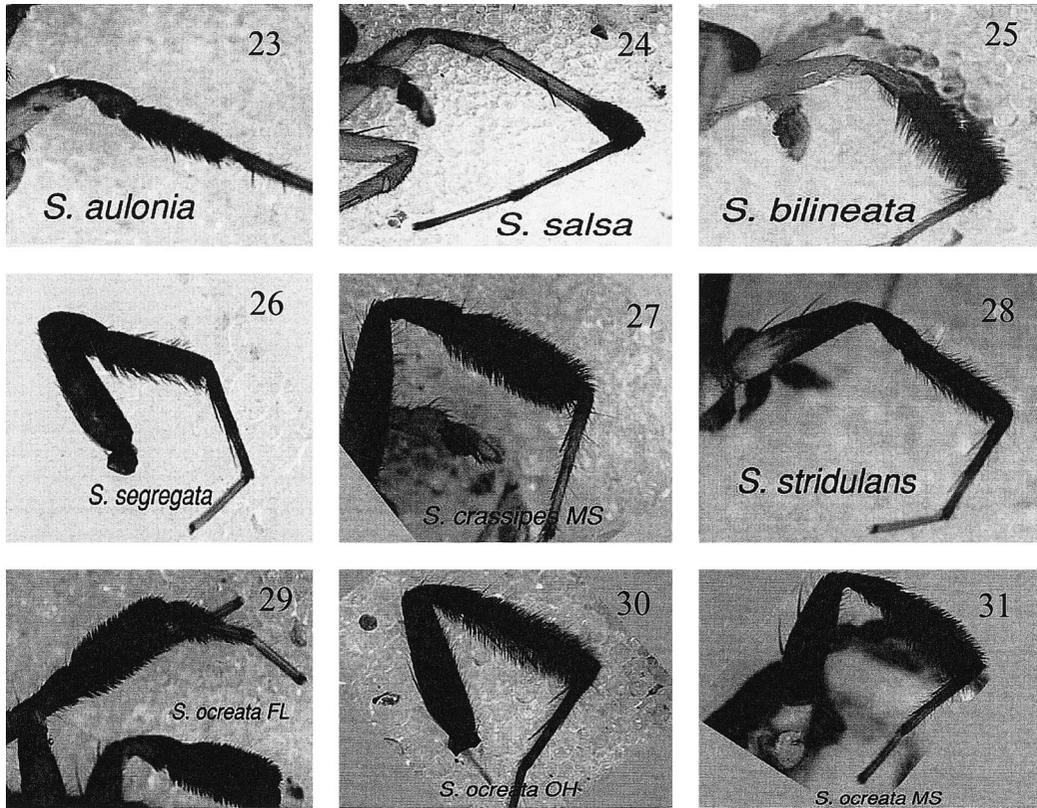
25. Terminal apophysis as inverted triangle: 0 = absent; 1 = present.

26. Embolus, basic shape: 0 = hair-like; 1 = sword-like. All pedipalps in Figs. 11–18 show a hair-like embolus. The sword-like embolus is found in *Gladicosa*, whose name refers to a sword (Brady 1986, p. 314, fig. 41).

27. Width of intromittent portion of embolus (IPE, Fig. 11): 0 = thin; 1 = stout.

28. Palea of pedipalp with triangular process: 0 = absent; 1 = present. In a few species, notably *S. duplex*, *S. saltatrix* and an undescribed species, the pedipalp has a triangular shaped process (Fig. 13, 14).

29. Palea of pedipalp with finger-like process: 0 = absent; 1 = present. A finger-like process (PPR) is shown in Fig. 15–18. During copulation this process pushes against the cu-



Figures 23–31.—Shape and size of tibial bristles in all taxa with the tibial bristles in the Nearctic *Schizocosa*: 23. *S. aulonia*; 24. *S. salsa*; 25. *S. bilineata*; 26. *S. segregata*; 27. *S. crassipes* (MS); 28. *S. stridulans*; 29. *S. ocreata* (FL); 30. *S. ocreata* (OH); 31. *S. ocreata* (MS).

ticle to the side of the female epigynum (Stratton, unpublished data).

30. Number of macrosetae: 0 = few (4–9); 1 = many (10 or more). The macrosetae can be found on the tip of the cymbium. Often there is a dense cluster, but sometimes they are much fewer and easily counted.

31. Long hair-like setae between macrosetae and genital bulb: 0 = absent; 1 = present.

32. Relative size of macrosetae: 0 = thin; 1 = stout or very stout.

33. Cymbium (tarsus) of pedipalp, length to width: 0 = short to regular; 1 = long and thin. Measured ventrally with an ocular micrometer (Table 3). As with other quantitative characters, the data were examined for gaps. During character analysis, this character was first scored as a multistate character but for the final analysis, it was treated as a binary character. The species that showed palpal drumming during courtship had relatively long, thin

pedipalps (e.g. *S. avida*, *S. retrorsa*, *S. mccooki*, and *S. communis*; Tables 3 & 5).

*Female epigynal characters:* The prominent features of the female epigynum include the well sclerotized median septum (MS, Figs. 19–22), the posterior transverse piece (TP, Fig. 19). The edges of the median septum can be flared at the posterior end, parallel, or can be widest at the center. The anterior end of the median septum has a funnel-like hood (Hood, Fig. 19) that generally is double but is single in *S. bilineata* and *S. crassipalpa* Roewer 1951. The median apophysis of the male “catches” on the hood of the female epigynum during the first stages of copulation; this serves to brace the pedipalp and immediately following the engagement of the MA with the hood, one can see the expansion of the hematodocha of the male pedipalp (Dondale & Redner 1978; Stratton, unpublished data) The depth of the hood varies between species and

Table 3.—Length, width and length/width of tibia and tarsus of pedipalp for *Schizocosa* and outgroups. All measures in mm.

Species	Tibia of palp			Tarsus of palp		
	Length	Width	L/W	Length	Width	L/W
<i>S. aulonia</i>	0.2	0.2	1.2	1.1	0.5	2.0
<i>S. avida</i>	0.7	0.5	1.5	0.9	0.4	2.4
<i>S. bilineata</i>	0.4	0.4	1.0	0.9	0.5	1.8
<i>S. cespitum</i>	0.5	0.4	1.3	1.2	0.6	2.1
<i>S. chiricahua</i>	0.5	0.4	1.4	1.2	0.6	2.1
<i>S. communis</i>	0.6	0.4	1.4	1.3	0.6	2.1
<i>S. crassipalpata</i>	0.4	0.3	1.1	0.9	0.5	1.7
<i>S. crassipes</i> (FL)	0.3	0.3	1.0	0.7	0.4	1.9
<i>S. crassipes</i> (MS)	0.6	0.5	1.1	1.1	0.6	1.9
<i>S. duplex</i>	0.4	0.5	0.9	1.0	0.5	1.9
<i>S. floridana</i>	0.5	0.4	1.3	0.9	0.5	1.9
<i>S. humilis</i>	0.5	0.5	1.1	1.0	0.6	1.7
<i>S. maxima</i>	0.4	0.3	1.3	1.0	0.6	1.6
<i>S. mccoeki</i>	0.6	0.4	1.4	1.2	0.6	2.1
<i>S. mimula</i>	0.3	0.2	1.5	1.1	0.6	2.1
<i>S. minnesotensis</i>	0.7	0.5	1.4	1.5	0.7	2.2
<i>S. ocreata</i> (OH)	0.6	0.6	1.0	1.4	0.8	1.9
<i>S. ocreata</i> (FL)	0.5	0.6	0.8	1.3	0.8	1.7
<i>S. ocreata</i> (MS)	0.6	0.6	1.0	1.3	0.7	1.8
<i>S. retrorsa</i>	0.6	0.4	1.3	1.3	0.6	2.1
<i>S. rovneri</i>	0.6	0.6	0.9	1.3	0.7	1.8
<i>S. salsa</i>	0.7	0.5	1.3	1.3	0.6	2.3
<i>S. saltatrix</i>	0.7	0.6	1.1	1.1	0.6	1.8
<i>S. sp. nr saltatrix</i>	0.7	0.6	1.1	1.2	0.7	1.8
<i>S. segregata</i>	0.4	0.4	1.1	0.9	0.5	1.9
<i>S. stridulans</i>	0.5	0.5	1.0	1.1	0.6	1.8
<i>S. uetzi</i>	0.6	0.6	1.1	1.3	0.7	1.9
<i>S. ocr. × rov hybrids</i>	0.6	0.6	1.0	1.1	0.6	1.8
<i>A. georgicola</i>	1.6	0.8	1.9	2.7	1.1	2.4
<i>G. pulchra</i>	1.0	0.6	1.6	2.1	1.1	1.9
<i>R. rabida</i>	1.7	0.8	2.1	2.9	1.1	2.6

is much deeper in *G. pulchra* and *A. georgicola* than most of the *Schizocosa* species (Table 4; compare Figs. 19–22).

The transverse piece (TP) in *Schizocosa* is either truncate as in *S. avida* and *S. retrorsa* (Figs. 19 & 20) or has excavations (Figs. 21 & 22). The excavations can be located at the lateral edges of the transverse piece as seen in *S. duplex* (Fig. 22) and *S. saltatrix*, or the excavations can be almost touching near the center of the transverse piece as seen in *S. uetzi* (see Stratton 1997a). More often, the location of the excavations are somewhat between these extremes.

In lycosids, the copulatory opening is near lateral edges of the transverse piece and the genital opening (where the eggs leave the genital tract) is in the epigastric furrow. When the

female genitalia are dissected and the dorsal side is examined, the spermathecae are the dominant structures (see Stratton 1997, fig. 5).

34. Edges of median septum (MS): 0 = MS widest at center; 1 = edges of MS parallel; 2 = MS widest at base. For MS widest at center, see Figs. 19 and 20 (*S. avida* and *S. retrorsa*). *Schizocosa duplex* provides an example of the parallel edges (Fig. 22) while *S. crassipes* shows a MS widest at its base (Fig. 21).

35. Excavations on transverse piece of epigynum: 0 = absent; 1 = present; see Figs 19–22.

36. Separations of excavations: 0 = absent; 1 = widely separated with excavations near lateral edge; 2 = intermediate in placement; 3 = narrowly separated. The excavations were considered widely separated if a hypothetical

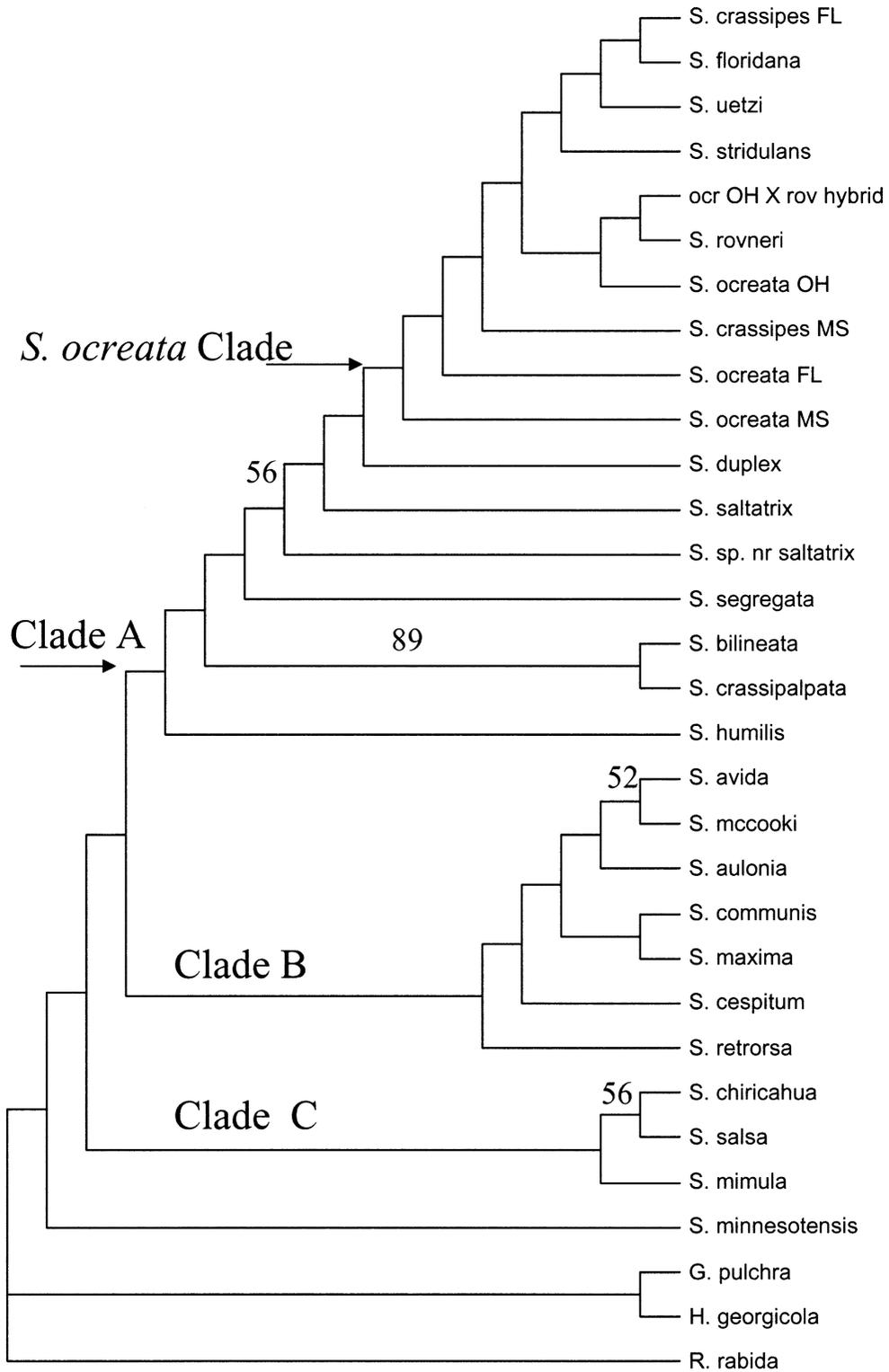


Figure 32.—Single most parsimonious tree from heuristic searches including all taxa, excluding secondary sexual characters and applying preferred weighting (somatic characters = “2,” genitalic characters = “3.”) The tree shows clades A, B, & C as well as the *S. ocreata* clade. Bootstrap values above 50% are shown.

additional excavation could fit between the excavations.

37. Ratio of median septum to transverse piece: 0 =  $MS/TP \leq 0.72$ ; 1 =  $MS/TP < 1.179$ ; 2 =  $MS/TP < 1.357$ ; 3 =  $MS/TP \leq 1.52$ ; 4 =  $MS/TP = 1.583$ . As with other quantitative characters, the ratio of MS to TP was sorted, graphed and examined for gaps. The ratio of the overall length to width was also examined but for this latter ratio, there were no clear gaps.

38. Epigynal hood, single or double: 0 = double; 1 = single. Figs 19–22 show a double hood; a single hood seen in *S. bilineata* and *S. crassipalata* (Dondale & Redner 1978; figs. 47 & 49).

39. Depth of epigynal hood: 0 = deep; 1 = shallow. See Table 4.

40. Spermathecae, shape: 0 = rounded; 1 = elongate; 2 = pointed.

41. Spermathecae texture: 0 = smooth; 1 = bumpy. The “bumpy” texture was visible with light microscopy; the function of these bumps is unknown.

42. Copulatory tube: 0 = simple; 1 = complex. The copulatory ducts for *Schizocosa* (Dondale & Redner 1978; e.g. figs. 28, 32 & 37) have a single elbow and were scored as simple. The copulatory duct in *R. rabida* (Brady & McKinley 1994; fig. 13) is convoluted and was scored as complex.

43. Pigment around the epigynum: 0 = absent; 1 = present. In some species, there is a distinct “box” of dark pigment surrounding the epigynum.

Male secondary sexual characters (ornamentation): Male secondary sexual characters include both pigmentation on the first legs and bristles or brushes, primarily on the tibia of legs I. Work by Stratton & Uetz (1986) showed that through hybridization of *S. ocreata* and *S. rovnneri* these characters are inherited independently.

44. Femur I with dark stripe: 0 = absent; 1 = present.

45. Femur I with dark pigment: 0 = absent; 1 = present.

46. Femur II-IV with longitudinal stripe: 0 = absent; 1 = present.

47. Presence of bristles on tibia: 0 = absent; 1 = present (see Figs. 23–31 for examples of species with bristles).

48. Dark pigment covering tibia I: 0 = absent; 1 = present.

49. Metatarsus I bristles: 0 = absent; 1 = present (e.g., *S. ocreata*, FL, Fig. 29).

## RESULTS

**Sexual ornamentation.**—Sexual ornamentation in the Nearctic genus *Schizocosa* consists of pigmentation on all or part of the legs I of mature males and/or bristles which are generally limited to all or part of the tibia of legs I. Dark pigmentation can be limited to the femur of leg I (as in *S. retrorsa*, Fig. 4), or to part of the femur and extending to the tibia (as in *S. stridulans*) (Fig. 28), or may be limited to the tibia (as in *S. uetzi*, Fig. 35), or extend from the patella to the metatarsus (as in *S. floridana* Bryant 1934, Fig. 35). In some cases, such as *S. humilis* and *S. retrorsa*, the dark pigmentation of the femur contrasts sharply with light hairs found on the tibia. Dark pigmentation can occur without bristles, as is seen in *S. retrorsa*, *S. uetzi* and in the outgroup, *Rabidosa rabida*.

When present, the bristles are always associated with the tibia of legs I of mature males but may be found only on the distal end of the tibia (as in *S. salsa*, Fig. 24), may extend to much of the metatarsus, as is seen in *S. ocreata* from Florida (Fig. 29), or may be limited to the tibia as is seen in *S. bilineata* (Fig. 25). In *S. aulonia* Dondale 1969 and *S. segregata*, the bristles are longest along the ventral side of the tibia (Figs. 23, 26), while in *S. crassipes* and *S. ocreata* (Figs. 27, 29, 30, 31), the bristles extend both dorsally and ventrally, providing a large rectangular appearance when viewed from the side. In general, the bristles are largest when viewed from the side, at eye-level with the spider. A discussion of the phylogenetic distribution of the bristles follows the presentation of the preferred phylogeny.

**Comparison of courtship behavior.**—Courtship behavior for 20 of the 31 taxa represented in this study has been documented (summarized in Table 5), including all members of the *S. ocreata* clade, as well as the hybrids between *S. ocreata* (OH) and *S. rovnneri*. All species studied to date show chemosignaling by males in the presence of females or female silk (indicating the presence of chemical signals) and males of all species produce seismic signals either by stridulation by the male palp (first described by Rovner 1975), palp drumming (Stratton & Lowrie

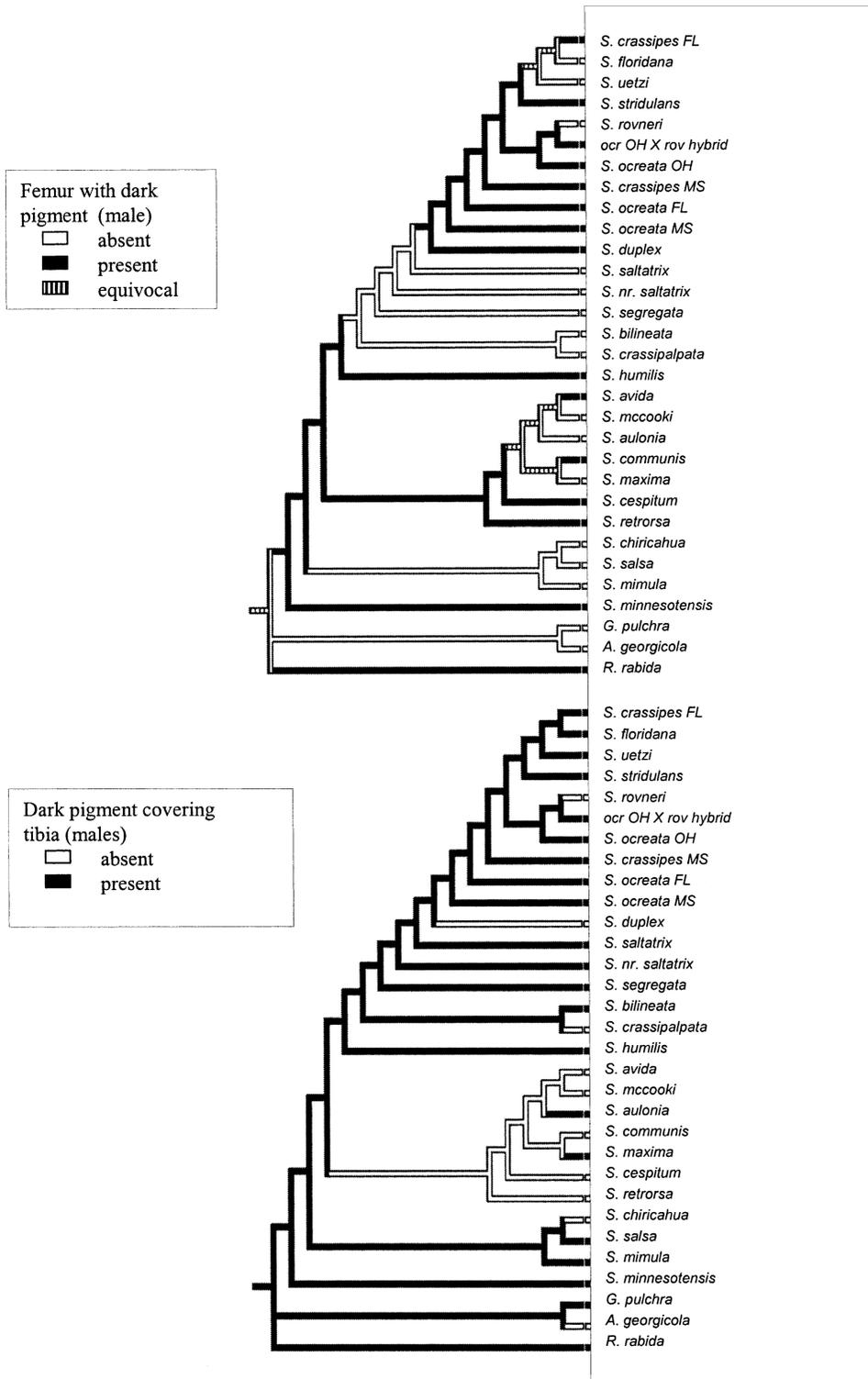


Figure 33.—Mapping of the ornamentation characters “pigment on femur” and “pigment on tibia,” seen in mature males on the preferred phylogeny.

1984; Hebets et al. 1996), body vibration or some combination of these (Table 5). Many species (but not all) also have some movement that appears to be a visual signal produced by males during courtship. Several species incorporate an arch of legs 1 (scored as a "+" in Fig. 36). For example, this is seen in *S. avida*, and *S. saltatrix* as well as *S. ocreata* (OH) (Table 5). Other species have movements that appear to be more intense visual signals. For example, *S. retrorsa* males have a vigorous leg 1 wave that is associated with courtship (Hebets et al. 1996), and *S. ocreata* (FL) has a bilateral double arch of the first pair of legs. These more overt visual signals are scored as "++" in Fig. 36. One species that apparently lacks visual signals is *S. duplex*. All populations of *S. ocreata* and *S. crassipes* have leg arching plus either leg waving or tapping. When the different populations of *S. crassipes* were compared, each population showed similar elements of courtship but differed in the proportion of time spent doing each behavior and in the sequences of behavior (e.g., Miller et al. 1998; Germano et al., unpublished data). Kaston (1936) included *S. bilineata* in his comparative courtship study but he did not see any behaviors preceding copulation in this species. Finally, the behavior of several species remains unknown and it is hoped that this study may stimulate interest in the behavior and ecology of these species.

**Results of phylogenetic analysis.**—Parsimony analysis with all characters weighted equally and trees not rooted resulted in very little resolution of clades. The agreement subtree for these trees did not include the three outgroups, suggesting their position in the tree was not stable. When the preferred weighting option was applied and the trees rooted with the three outgroups, there was more resolution. A single most parsimonious was tree resulted from the analysis with the secondary sexual characters excluded and is the preferred tree presented here (Fig. 32; bootstrap values above 50% shown on figures; 570 steps, Consistency Index = 0.271, Retention Index = 0.567, Homoplasy Index = 0.729). When secondary sexual characters were included, a consensus of seven trees had 578 steps (Consistency Index = 0.265, Homoplasy Index = 0.735 and Retention Index = 0.549) and when compared to the preferred tree, differed only

Table 4.—Epigynal measures including total length of epigynum, and width of epigynum, the ratio of epigynal length/width, and depth of the epigynal hood. All measures in mm. Values for three species (*S. salsa*, *S. segregata*, *S. aulonia*) were not available and for these species, ratio of length to width was calculated from published figures in Dondale & Redner (1978).

Species	Length	Width	L/W	Hood
<i>S. aulonia</i>			1.4	
<i>S. avida</i>	0.9	0.7	1.3	0.3
<i>S. bilineata</i>	0.5	0.6	0.9	0.1
<i>S. cespitum</i>	0.7	0.7	1.0	0.1
<i>S. chiricahua</i>	0.7	0.6	1.2	0.1
<i>S. communis</i>	0.8	0.7	1.1	0.1
<i>S. crassipalata</i>	0.5	0.5	0.9	0.1
<i>S. crassipes</i> (FL)	0.7	0.6	1.2	0.1
<i>S. crassipes</i> (MS)	0.7	0.6	1.3	0.1
<i>S. duplex</i>	0.6	0.6	1.0	0.1
<i>S. floridana</i>	0.6	0.5	1.2	0.1
<i>S. humilis</i>	0.8	0.6	1.3	0.1
<i>S. maxima</i>	0.8	0.7	1.2	0.1
<i>S. mccooki</i>	0.7	0.7	1.0	0.1
<i>S. mimula</i>	0.8	0.6	1.3	0.1
<i>S. minnesotensis</i>	0.9	0.6	1.7	0.1
<i>S. ocreata</i> (OH)	0.8	0.7	1.1	0.1
<i>S. ocreata</i> (FL)	0.9	0.7	1.3	0.1
<i>S. ocreata</i> (MS)	0.8	0.6	1.3	0.1
<i>S. retrorsa</i>	0.8	0.6	1.3	0.1
<i>S. roverni</i>	0.8	0.7	1.1	0.1
<i>S. salsa</i>			1.1	
<i>S. saltatrix</i>	0.7	0.7	1.1	0.1
<i>S. sp. nr. saltatrix</i>	0.6	0.7	1.0	0.1
<i>S. segregata</i>			1.2	
<i>S. stridulans</i>	0.6	0.6	1.1	0.1
<i>S. uetzi</i>	0.8	0.7	1.2	0.1
<i>S. ocr</i> × <i>rov</i> hybrids	0.7	0.6	1.2	0.1
<i>A. georgicola</i>	1.4	1.0	1.4	0.2
<i>G. pulchra</i>	0.9	0.8	1.1	0.2
<i>R. rabida</i>	1.3	1.0	1.3	1.8

in the positions of *S. aulonia* and *S. maxima* Dondale & Redner 1978.

The analysis resulted in three main clades, with *S. minnesotensis* basal to these clades. The largest clade (Fig. 32, Clade A) is comprised of species found in the eastern half of North America; the range of some of the species is limited to the Northeast, some to the Southeast and some ranges extend to the Midwest (see range maps, Dondale & Redner 1978; Stratton 1991, 1997a). Clade A includes 9 of the 11 taxa with tibial bristles (Fig. 34). Nested within Clade A is a clade that includes *S. duplex*, *S. saltatrix* and *S. nr. saltatrix* plus

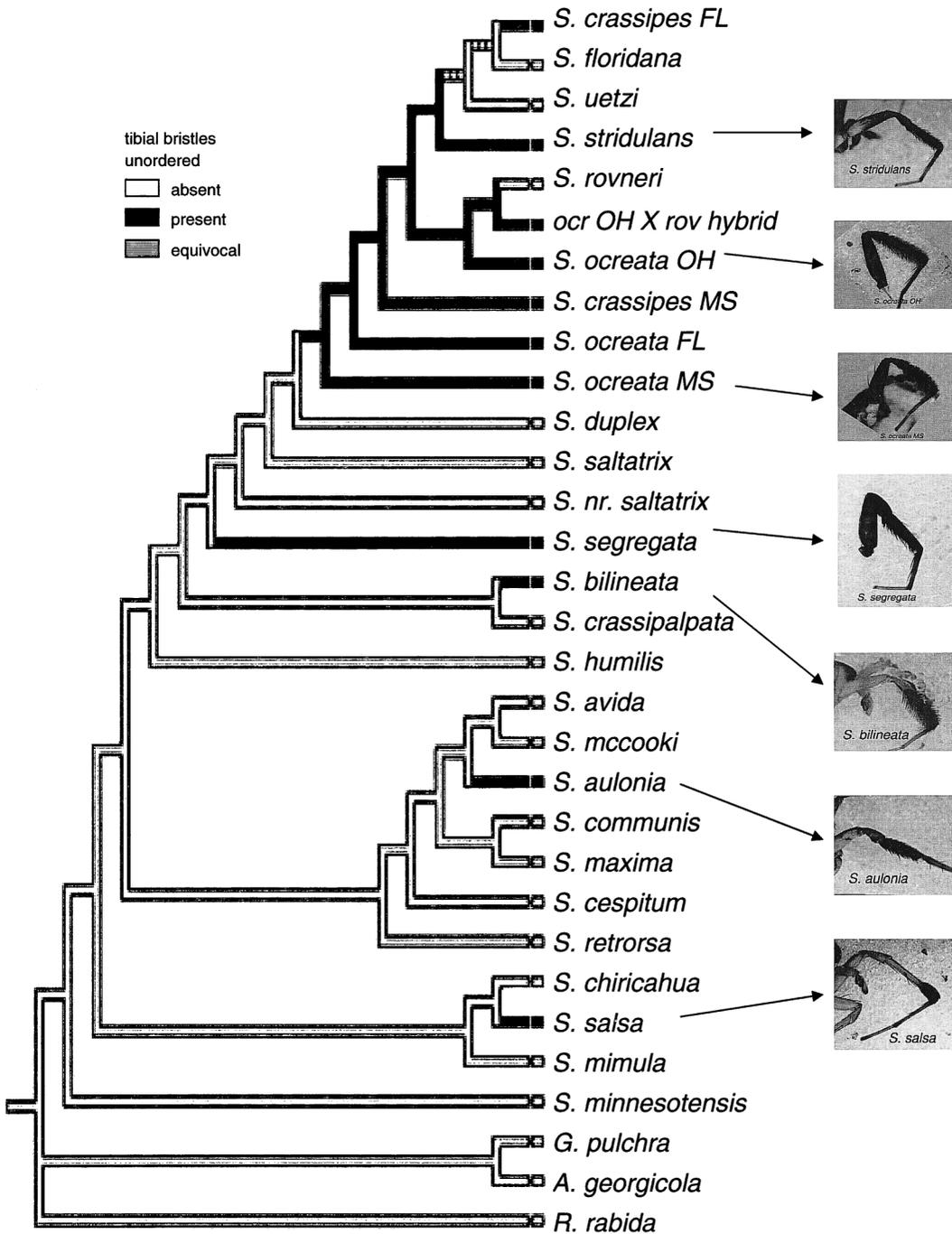


Figure 34.—Mapping of representative tibial bristles, seen in mature males, on the preferred phylogeny.

the *S. ocreata* clade, all defined by a process on the palea of the pedipalp of the male (either a triangular process, Fig. 14, or a finger-like process, Fig. 15) and all found in deciduous woods, or a mix of deciduous and pine forests.

Also within Clade A is a clade that includes *S. bilineata* + *S. crassipalpata*, one of the few clades with significant support from the bootstrap analysis and defined by six characters shared in common.

Also nested within Clade A is the *S. ocreata* clade, which consists of *S. ocreata* (multiple populations), *S. crassipes* (multiple populations), *S. rovnneri*, *S. stridulans*, *S. uetzi* and *S. floridana*. The clade is unified by the very distinctive finger-like process on the palea of the male pedipalp (Character 29), sternum color (Character 8), long setae on the ventral surface of the pedipalp (Character 31), and the relative size of the macrosetae (Character 32). Of these characters, only Character 29 is not lost or reversed. Members of this clade have been the most intensively studied with respect to courtship and mating behavior. Two of the taxa in this clade are paraphyletic (*S. ocreata* and *S. crassipes*), suggesting that there are possibly multiple (yet unrecognized) cryptic species.

Clade B includes the widespread eastern *S. avida*, the western *S. mccoooki*, as well as *S. maxima*, *S. aulonia*, *S. cespitum*, *S. communis* and *S. retrorsa*.

The third clade, Clade C include *S. chira-cahua*, *S. mimula* and *S. salsa*. The former two are western, while *S. salsa* is found on the Gulf Coast and Atlantic coast.

**Mapping ornamentation and behavior on preferred phylogenies.**—An examination of the distribution of pigmentation on the first legs of males and bristles on the first pair of legs in males across all taxa in this study suggests that pigmentation may have evolved independently of the bristles, and that both traits can be gained and lost (Figs. 33, 34). For example, pigmentation without bristles is seen in *S. retrorsa*, *S. uetzi* and *R. rabida*, while bristles without pigmentation is seen in *S. bilineata*. When the tibial bristles are mapped onto the preferred phylogeny (Fig. 34) it appears that it evolved independently five or six times with two or three losses in the *S. ocreata* clade. A more detailed comparison of ornamentation on legs of males in the *S. ocreata* clade is presented in Fig. 35. It is clear that in this clade, the full range of pigmentation and bristles occur.

Mapping the major patterns of seismic communication (i.e., drumming vs. stridulation) onto the preferred cladogram shows that the palpal drumming is concentrated in Clade B, while stridulation is prevalent in Clade A (Fig. 36). The *S. ocreata* clade is of particular interest with respect to courtship behavior as within the clade there is the full range of sec-

ondary sexual characters (full tibial bristles, pigment on tibia and or femur, or complete lack of pigmentation or bristles). Within the *S. ocreata* clade, there is a correlation between overt visual signals and the presence of ornamentation. Several species within the clade have reduced or absent pigmentation (*S. rovnneri* and *S. uetzi*); these also have reduced visual signals. This study suggests that *S. rovnneri*, *S. uetzi* and *S. stridulans* evolved from ancestors that had overt visual signals and these species have subsequently lost visual signals in their courtship. However, as courtship behavior is still unknown for several species with tibial bristles outside of the *S. ocreata* clade (e.g. *S. bilineata*, *S. salsa*, *S. segregata* and *S. aulonia*) strong conclusions concerning the correlation of ornamentation and behaviors throughout the genus is not yet possible.

**Comparison of genital morphology.**—Examination of the pedipalps of these species in light of the hypothesized phylogeny sheds some light on potential homologies of genitalic structures. The most distinctive feature in the male pedipalp of some members of *Schizocosa* is the finger like paleal process (Fig. 16), which is solely found in the *S. ocreata* group. However, the presence of a triangular structure in the same location in the species immediately basal to the *S. ocreata* clade, e.g., *S. saltatrix* (Fig. 13) and *S. duplex* (Fig. 14), suggests that both forms of the paleal process are homologous.

## DISCUSSION

This phylogenetic study confirms that members of Lycosidae are conservative in morphology with large amounts of homoplasy in many characters and low bootstrap support for several branches. The preferred phylogeny presented here (Fig. 32) is a hypothesis of relationships within *Schizocosa* based on a weighting scheme that weights genitalia more heavily than somatic characters and excludes secondary sexual characters. The main clades that are proposed in this study are grouped either by geography (i.e. Clade A) or by a suite of morphological characters (i.e. *S. ocreata* clade, Clade B and Clade C).

This genus is of particular interest for evolutionary biologists because of the relatively large number of species with ornamentation (Figs. 33 & 34). Mapping the tibial bristles on

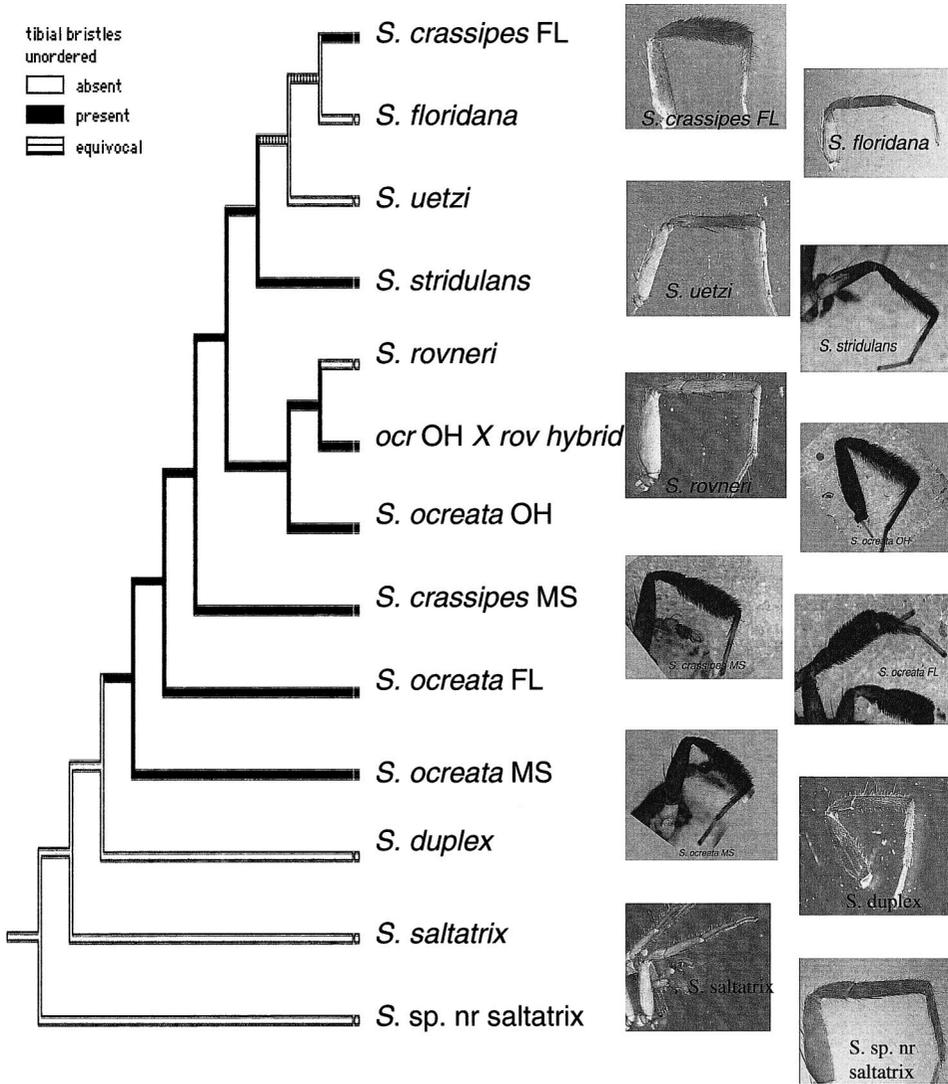


Figure 35.—Cladogram of *S. ocreata* clade + basal species showing presence and extent of bristles on leg I.

the preferred phylogeny shows the distribution (and variation) of the ornamentation. For the tibial bristles, there appears to be five or six independent gains of this character across all of the species in this study, with losses occurring in *S. rovneri*, *S. uetzi* and *S. floridana*. In Clade A, the character possibly evolved two or three separate times.

While it is challenging to trace the evolution of specific courtship elements, there is clearly a grouping of taxa that show palpal drumming in courtship and a grouping of those that show stridulation in courtship. If the

phylogeny presented in this study is correct, it appears that the species immediately basal to the *S. ocreata* clade (e.g., *S. duplex* and *S. saltatrix*) rely primarily on seismic signals in their courtship. The brush-legged taxa within the *S. ocreata* clade (e.g. populations of both *S. ocreata* and *S. crassipes*) have courtship that involves both seismic signals and visual signals. And, several species within the *S. ocreata* clade have apparently subsequently lost some of the more visual aspects of courtship (e.g., *S. uetzi*, *S. stridulans* and *S. rovneri*).

Table 5.—Comparison of elements of courtship behavior (both seismic and visual) in species of *Schizocosa*, *Gladicosa* and *Allocosa*.

Species	This study	Previous studies	Not known
<i>S. aulonia</i>			Behavior not known
<i>S. avida</i>		rapid papal drumming, leg 1 arch (Grey & Stratton 1998)	
<i>S. bilineata</i>			Behavior not known
<i>S. cespitum</i>			Behavior not known
<i>S. chiricahua</i>			Behavior not known
<i>S. communis</i>		Palpal drumming (Dondale & Redner 1978)	
<i>S. crassipalpata</i>	Stridulation		
<i>S. crassipes</i> (FL)		Stridulation, cheliceral strike, leg 1 extend and wave (Miller et al. 1998)	
<i>S. crassipes</i> (MS)		Stridulation, cheliceral strike, leg 1 extend and wave (Miller et al. 1998)	
<i>S. duplex</i>	Stridulation	Stridulation (Hebets & Uetz 2000)	
<i>S. floridana</i>	Stridulation, leg 1 tap		Behavior not known
<i>S. humilis</i>			Behavior not known
<i>S. maxima</i>			
<i>S. mccooki</i>		Papal drumming (Stratton & Lowrie 1984)	
<i>S. mimula</i>			Behavior not known
<i>S. minnesotensis</i>			Behavior not known
<i>S. ocreata</i> (OH)		“Jerky walk” “double tap” (Stratton & Uetz 1983, 1986)	
<i>S. ocreata</i> (FL)	Cheliceral strike double (bilateral arch with legs 1) Stratton, Miller & Miller unpublished data)		
<i>S. ocreata</i> (MS)	Cheliceral strike walk and tap legs 1 (Stratton, Miller & Miller unpublished data)		
<i>S. retrorsa</i>		Palpal drumming, leg 1 wave (Hebets et al. 1996)	
<i>S. rovneri</i>		Series of body bounces (Uetz & Denterlein 1979; Stratton & Uetz 1983, 1986)	
<i>S. salsa</i>			Behavior not known
<i>S. saltatrix</i>	Stridulation, leg 1 arch		
<i>S. sp. nr. saltatrix</i>	Stridulation or body vibration		
<i>S. segregata</i>			Behavior not known
<i>S. stridulans</i>		Stridulation, quick tap of leg 1 (Stratton 1991, 1997a 1997b)	

Table 5.—Continued.

Species	This study	Previous studies	Not known
<i>S. uetzi</i>		Stridulation, leg 1 arch (Stratton 1997b; Hebets 2003)	
<i>S. ocr</i> × <i>rov</i> hybrids		Stridulation, body bounce, double tap, jerky walk (Stratton & Uetz 1986)	
<i>A. georgicola</i>	Stridulation, leg 1 extend and vibrate		
<i>G. pulchra</i>	Stridulation		
<i>R. rabida</i>	Stridulation	Papal scraping, stridulation leg wave (Rovner 1968)	

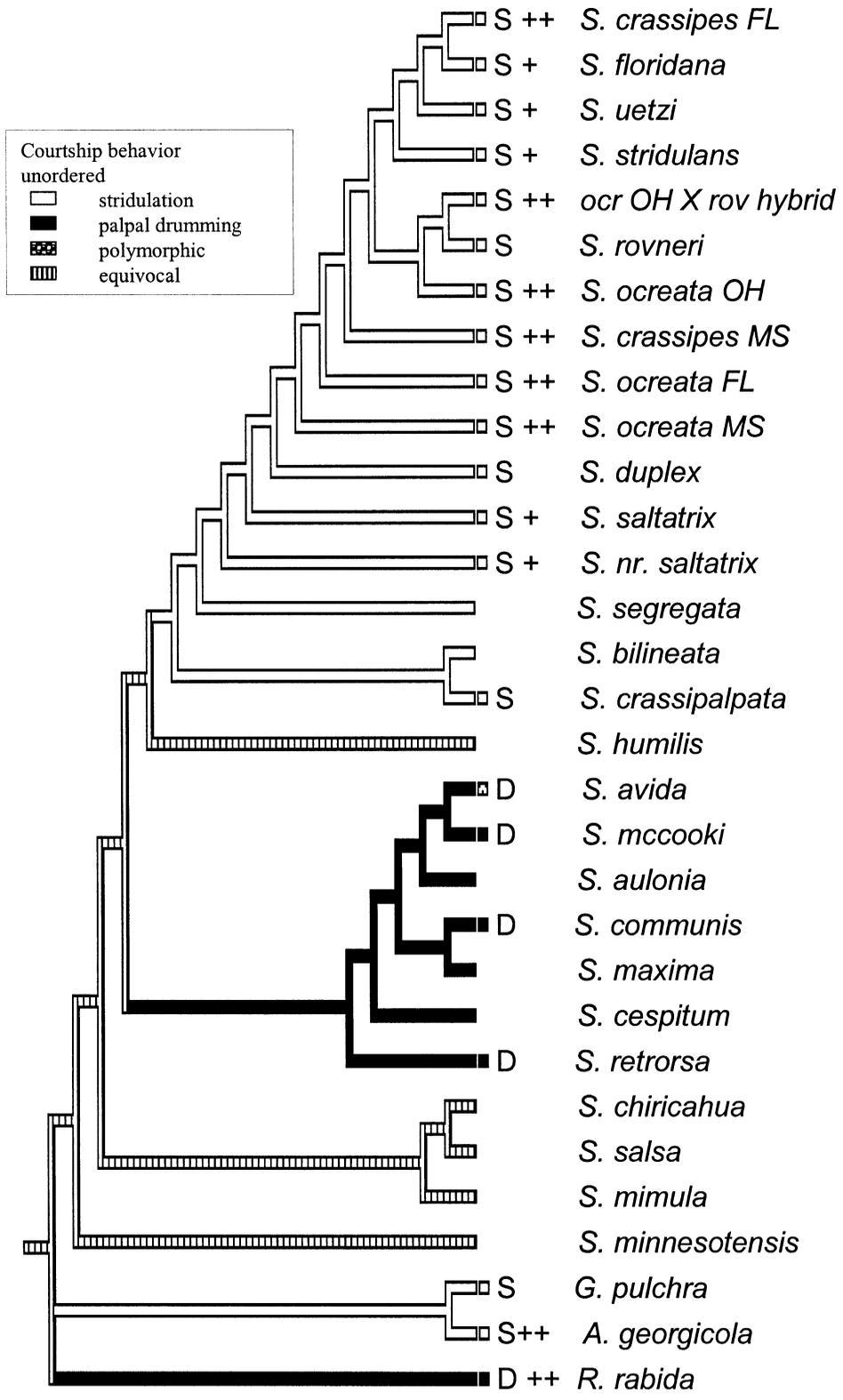
Early work on *S. ocreata* from Ohio and *S. rovneri* suggested that these two species were sibling species (Uetz & Denterlein 1979; Stratton & Uetz 1983, 1986). The subsequent discovery of additional species in the clade (*S. stridulans* and *S. uetzi*) raised questions about the relationship between *S. ocreata* and *S. rovneri*. However, this phylogenetic analysis confirms that these two taxa are each other's closest relatives.

Some currently recognized species within this genus may not reflect phylogenetic lineages as several of the taxa used in this study are paraphyletic (e.g., *S. ocreata*, *S. crassipes* and *S. saltatrix*). The separation of *S. ocreata* (OH) from *S. ocreata* (FL and MS) suggests that these populations are diverging and could be considered separate taxa if a phylogenetic species concept is applied. Miller et al. (1998) showed reduced breeding between crosses composed of *S. ocreata* (OH) and *S. ocreata* (MS, population from Washington Count, Leroy Percy State Park, indicated LP in that study). Likewise, the clear separation of *S. crassipes* (MS) from *S. crassipes* (FL) also suggests divergence. An unpublished study showed reduced interbreeding but a similarity of courtship behavior between both populations of *S. crassipes* (Germano et al. unpublished data). It is intriguing that the *S. ocreata* from Mississippi is basal in the *S. ocreata* clade. The Mississippi River valley has been suggested to be a refuge of deciduous woods during the last ice ages (Delcourt et al. 1980; Delcourt & Delcourt 1987); it is tempting to speculate that perhaps the *S. ocreata* clade diverged from populations along the Mississippi

River valley in the time since the last glaciers. By this scenario, as glaciers retreated in the north, and deciduous woods expanded in the southeast, *S. ocreata* spread first across the southeast and, as populations became isolated they speciated to *S. ocreata* (FL), then *S. crassipes* and the other species within the clade eventually spreading north. The *S. ocreata* clade is now found throughout the eastern U.S.A. with most species found in the southeast. Molecular data could provide an independent test of this hypothesis.

McClintock & Uetz (1996) showed that females of *S. rovneri* preferred *S. rovneri* males that were artificially given tibial bristles. Their preliminary phylogenetic study suggested that *S. rovneri* was basal to *S. ocreata*, thus potentially providing an example of the sensory bias hypothesis or an example where the female preference for a trait (in this case, ornamentation in the form of tibial bristles) preceded the evolution of the trait and provided selection for the trait in subsequent species (in this case *S. ocreata*). However, based on the analyses presented here, *S. rovneri* is derived relative to *S. ocreata* and thus the *S. rovneri* female preference for males with bristles (reported by McClintock & Uetz 1996) is a retained characteristic.

The finger-like process on the palea of the pedipalp seen in the *S. ocreata* clade is unique in wolf spiders. The somewhat similar process seen in *Sosippus* does not appear to be homologous to this structure (Sierwald 2000, fig. 7). High magnification video from the ventral view during copulation confirms that the median apophysis of the male engages the epi-



gynal hood of the female, and the paleal process of the male pinches against the side of the epigynum of the female (Stratton, Miller & Miller, unpub. data). Eberhard (1994) suggested that any time there is physical contact between structures during copulation, the potential exists for that trait to be influenced through female choice during copulation. Thus, this character may give females an additional means to evaluate mates and potentially exercise female choice of gametes. After the examination of thousands of male specimens I have never seen the paleal process broken. It is curious that the clade with a concentration of species with conspicuous secondary sexual characters also has the unique trait of the paleal process that could also be shaped by female choice. It is suggested here that the morphology of primary and secondary genitalic characters in males in this clade may be largely shaped by sexual selection by female choice.

As may be expected due to a lack of informative characters in Lycosinae, the preferred phylogeny did not have strong bootstrap support and a combined morphological and molecular analysis may show better supported results in regard to the phylogenetic relationships of *Schizocosa*.

Indeed, further clarification of this genus and its relatives will provide the phylogenetic context to best interpret behavioral, ecological and evolutionary questions.

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Figure 36.—Distribution of major courtship elements on the preferred phylogeny. The symbol “D” refers to species in which the males are known to show palpal drumming during courtship, “S” refers to species in which males are known to show palpal stridulation. The “+” symbol shows there is arching of leg 1, “++” shows species which have extensive visual signals.

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Riegert, 1 ♂, 3 ♀ paratypes (AMNH). Published figures: Dondale & Redner (1978, figs. 20, 69, 70).

***Schizocosa chiricahua Dondale & Redner 1978.***—U.S.A.: *Arizona*: Chochise County, Chiricahua Mts, Southwest Research Station [31°53'N, 109°12'W], 5400', in swimming pool, 15 July 1967 & June 7 1968, V. Roth, 2 ♂ paratypes (AMNH); *Arizona*: Graham County, near Safford [32°50'N, 109°42'W], 14 July 1956, W. Gertsch & V. Roth, 2 ♂ paratypes, 1 ♀ paratype (AMNH). Published figures: Dondale & Redner (1978, figs. 18, 19, 66–68).

***Schizocosa communis (Emerton 1885).***—CANADA: *Ontario*: 9 miles NW. of Bloomfield, 44°04'N, 77°18'W, 17 July 1965, Jean & Wilton Ivie, 1 ♂ (AMNH); U.S.A.: *Pennsylvania*: Berks County, Lenhartsville [40°34'N, 75°53'W], July 1964, Vaurie, 1 ♀ (AMNH). Published figures: Dondale & Redner (1978, figs. 14, 55–58).

***Schizocosa crassipalata Roewer 1951.***—CANADA: *Ontario*: Rednersville [44°07'N, 77°27'W], field pitfall, 3–19 June 1964, C.D. Dondale, 2 ♂, 2 ♀ (FSCA). Published figures: Dondale & Redner (1978, figs. 9, 49, 50).

***Schizocosa crassipes (Walckenaer 1837).***—U.S.A.: *Florida*: Alachua County, 0.25 miles E. of River Styx on Highway 346 [29°31'17"N, 82°15'47"W], 10 May 1994, G.B. Edwards & P. Cushing, 3 ♂, 4 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 2, 27–30); Stratton (1991, fig. 4).

***Schizocosa crassipes (Walckenaer 1837).***—U.S.A.: *Mississippi*: Grenada County, T21N R2E sect. 12, 13N & R3E Sec 7S, 18N [33°44'N, 90°00'W], deciduous woods on hillside, 16 May 1993, G. Stratton, P. Miller, W. Miller, B. Grantham, 1 ♂, 1 ♀ (GES).

***Schizocosa duplex Chamberlin 1925.***—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, in pine litter, 18 May 1993, G. Stratton, E. Hebets, 1 ♂, 2 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 6, 42–44).

***Schizocosa floridana Bryant 1934.***—U.S.A.: *Florida*: Marion County, Hopkins Prairie, Ocala National Forest [29°10'N, 81°47'W], 25 March 1983, G. Stratton, litter, 4 ♂, 2 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 3, 31–34, 35).

***Schizocosa humilis (Banks 1892).***—U.S.A.: *Pennsylvania*: Bucks County, east of Jamieson, Horseshoe Bend, Neshaminy Creek, May 1954, W. Ivie (GES). Published figures: Dondale & Redner (1978, figs. 7, 45, 46).

***Schizocosa maxima Dondale & Redner 1978.***—U.S.A.: *California*: Solano County, Fairfield [38°15'N, 122°02'W], April–August 1955, K.W. Haller, 1 ♂ paratype (AMNH); *California*: Tuolumne County, S. of Highway 108, 5 miles E of

Sonora, elev. 2000', drowned in swimming pool, 14 October 1973, W. Icenogle, 1 ♀ paratype (AMNH). Published figures: Dondale & Redner (1978, figs. 16, 17, 63–65).

***Schizocosa mccooki (Montgomery 1904).***—U.S.A.: *New Mexico*: Santa Fe County, Santa Fe [35°31'N, 105°56'W], in pinyon scrub, 17 June 1979, D. Lowrie, 3 ♂, 1 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 13, 15, 59–62).

***Schizocosa mimula (Gertsch 1934).***—U.S.A.: *Colorado*: Otero County, Highway 109, 5 June 1967, 1 ♂ (AMNH).

***Schizocosa minnesotensis (Gertsch 1934).***—U.S.A.: *Wyoming*: Lincoln County, Kemmerer [41°48'N, 110°32'W], 24 August 1983, R. Parmenter, 2 ♂, 2 ♀ (AMNH).

***Schizocosa ocreata (Hentz 1844).***—U.S.A.: *Ohio*: Clermont County, Cincinnati Nature Center [39°07'N, 84°15'W], 6 May 1980, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 3, 9).

***Schizocosa ocreata (Hentz 1844).***—U.S.A.: *Mississippi*: Washington County, Leroy Percy State Park, N. of Highway 12 near entrance of park, T15N R7W, 90°50'W, 33°10'N, 9 April 1993, on knoll by flooded bottomlands, G. Stratton, P. Miller, 1 ♂, 1 ♀ (GES).

***Schizocosa ocreata (Hentz 1844).***—U.S.A.: *Florida*: Alachua County, 0.25 miles E. of River Styx on Highway 346 [29°31'17"N, 82°15'47"W], 1 March 1993, G.B. Edwards, P. Cushing, 9 ♂, 3 ♀ (GES).

***Schizocosa retrorsa (Banks 1911).***—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, pitfall in pine woods, 28 June–5 July 1993, 1 ♂, 1 ♀, G. Stratton (GES). Published figures: Dondale & Redner (1978, figs. 21, 75–78).

***Schizocosa rovneri Uetz & Dondale 1979.***—U.S.A.: *Kentucky*: Boone County, 5 miles W. of Taylorsport, floodplain of Ohio River, "Sandy Run" [39°05'N, 84°41'W], 3 May 1996, K. Delaney, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 2, 7).

***Schizocosa salsa Barnes 1953.***—U.S.A.: *Mississippi*: Hancock County, mouth of Jordan River [30°16'N, 89°37'W], on *Juncus* marsh island, 25 June 1993, 1 ♂ (PRM). Published figures: Dondale & Redner (1978, figs. 24, 79, 80).

***Schizocosa saltatrix (Hentz 1844).***—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," pine deciduous woods, 16 March 1996, G. Stratton & P. Miller, 1 ♂, 1 ♀ (GES). Published figures: Dondale & Redner (1978, figs. 4, 39–41).

***Schizocosa sp. nr saltatrix.***—U.S.A.: *Mississippi*: Wilkinson County, 5 miles E of Doloroso on Smith Rd, S. of Homochito River, 31°20'N,

92°45'W, uplands deciduous forest, 10 April 1993, G. E. Stratton, P.R. Miller, 1 ♂, 1 ♀ (GES).

***Schizocosa segregata* Gertsch & Wallace 1937.**—U.S.A.: *Florida*: Levy County, 28 April 1934, # 298, H.K. Wallace, 1 ♂, 1 ♀, paratypes (poor condition); *Texas*: Edinburg [26°18'N, 98°10'W], 1934, S. Mulaik, 1 ♂ (poor condition) (AMNH). Published figures: Dondale & Redner (1978, figs. 23, 81, 82).

***Schizocosa stridulans* Stratton 1984.**—U.S.A.: *Illinois*: Mason County, Sand Ridge State Forest [40°24'N, 89°52'W], 7 June 1985, G. Stratton, L. Hartz, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1991, figs. 1, 5, 6, 13).

***Schizocosa uetzi* Stratton 1997.**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," mixed pine and hardwoods, 4 July 1992, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Stratton (1997, figs. 1–5).

***Schizocosa ocreata* × *Schizocosa rovneri* hybrids.**—Cross between *S. ocreata* ♀ from Ohio and *S. rovneri* ♂ from Kentucky, 1980–1982, 1 ♂ (GES). Cross between *S. rovneri* ♂ from Kentucky

and *S. ocreata* ♀ from Ohio, 1980–1982, 1 ♀ (GES).

***Allocosa georgicola* (Walckenaer 1837).**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, "Lonesome 80," pitfall in mixed pine and hardwoods, 16–24 September 1992, G. Stratton, P. Miller, 1 ♂, 1 ♀ (GES). Published figures: Chamberlin & Ivie (1944, fig. 57). Pedipalps and epigyna of the closely related *H. helluo* (Walckenaer 1837) are figured in Kaston (1948, figs. 1065, 1066, 1090, 1105) and Dondale & Redner (1990, figs. 43–47).

***Gladicosa pulchra* (Keyserling 1877).**—U.S.A.: *Tennessee*: Hardeman County, Chickasaw State Park [35°22'N, 88°50'W], pine deciduous woods, 1 November 1992, G. Stratton, 1 ♂, 1 ♀ (GES). Published figures: Brady (1986, figs. 3, 10–14, 39–42).

***Rabidosa rabida* (Walckenaer 1837).**—U.S.A.: *Mississippi*: Lafayette County, 8 miles SE. of Oxford, T10S R3W Sec 35, 34°36'N, 89°29'W, pine deciduous mixed, 5 August 1991, G. Stratton, P. Miller, G. Miller, 1 ♂, 1 ♀ (GES). Published figures: Brady & McKinley (1994, figs. 1, 6, 11–14) and Kaston (1948, figs. 1077, 1079, 2006).